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Organelar genome evolution in *Camellia tianeensis* (Theaceae): comparative insights into RNA editing, codon usage, and DNA transfer between chloroplast and mitochondrion

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Abstract

Camellia tianeensis, a rare member of sect. *Chrysanth* Chang of the family Theaceae, is widely known for its ornamental and medicinal importance and is often referred to “Queen of the Tea Family”. Despite its biological and economic value, little is known about the structure and evolution of its organellar genomes. In this study, we assembled and compared the complete chloroplast and mitochondrial genomes of *C. tianeensis* using combined short- and long-read sequencing. The chloroplast genome was 156,865 bp in length and encoded 131 genes, whereas the mitochondrial genome measured 1,098,121 bp and contained 51 genes. Four protein-coding genes—*rps12*, *rps14*, *rps16*, and *rps7*—were shared by both organelles. The mitochondrial genome exhibited 404 RNA-editing sites, about 6.2 times more than the chloroplast genome (65 sites), primarily resulting in conversions from hydrophilic to hydrophobic amino acids. The mitochondrial genome contained more simple sequence repeats (SSRs) and dispersed repeats than the chloroplast genome, with complementary repeats absent in both. Codon-usage analysis revealed a strong bias toward A/U-ending codons in both genomes, with ten optimal codons shared, suggesting the action of translational selection. Phylogenetic analysis confirmed that *C. tianeensis* belongs to sect. *Chrysanth* and showed close affinity to *C. nitidissima*. Moreover, nine chloroplast-derived fragments totaling 42.9 kb were identified within the mitochondrial genome, indicating active inter-organelle DNA transfer. These results provide the first comprehensive organellar genomic resources for sect. *Chrysanth* and offer valuable insights into organelle evolution, RNA-editing diversity, and horizontal DNA exchange in higher plants.

Keywords *Camellia tianeensis*, Chloroplast genome, Mitochondrial genome, Homologous gene, Comparative analysis

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Introduction

Plants, as the foundation of terrestrial ecosystems, possess three interdependent genomes: the nuclear, chloroplast, and mitochondrial genomes. Among these, chloroplasts and mitochondria are semi-autonomous organelles that play crucial roles in photosynthesis and energy metabolism, respectively. Each organelle contains its own genome, with distinct mechanisms for replication, transcription, and translation, which function in coordination with the nuclear genome to ensure normal plant growth and development [1]. Comparative studies of plant organellar genomes have revealed notable differences in genome structure, gene content, and evolutionary rate between chloroplasts and mitochondria. These differences not only provide important clues for understanding genome evolution but also offer practical applications in molecular breeding and conservation genetics [2, 3]. Recent advances in high-throughput sequencing and bioinformatics have further enabled the discovery of widespread DNA fragment exchanges between chloroplasts and mitochondria across multiple plant lineages [4–6]. Such inter-organellar DNA transfers, also known as intracellular horizontal gene transfer (HGT), have profound evolutionary implications, contributing to genome expansion, sequence rearrangement, and functional innovation [7, 8]. Moreover, transferred genes and sequences often influence key biological processes such as photosynthesis, respiration, and stress response, thereby contributing to the adaptation and diversification of plants across different ecological conditions [9, 10].

The genus *Camellia* (Theaceae) comprises more than 200 species distributed mainly in East and South-east Asia. Within this genus, sect. *Chrysanth* Chang is morphologically unique, being the only lineage bearing golden-yellow petals. Members of this section are of high ornamental and pharmacological value due to their bioactive compounds with antihypertensive, hypolipidemic, and antioxidant effects [11–14]. Approximately 40 species and five varieties of sect. *Chrysanth* are native to southern China and northern Vietnam, with the greatest diversity found in Guangxi Province [11, 12, 15, 16]. The section has attracted growing attention in horticulture and medicinal research, and several molecular studies have investigated its chloroplast genomes, secondary metabolite pathways, and phylogenetic relationships [17–20]. However, mitochondrial genome information for this group remains largely unexplored.

Camellia tianeensis S. Yun Liang & Y. T. Luo is an endemic member of sect. *Chrysanth* characterized by elliptic leaves, solitary yellow flowers, and brown seeds. Since its description in 1995 [21], studies have mainly focused on its morphology, conservation, and population structure [22–27]. Despite its significance, no comprehensive molecular data have been reported for this

species. Therefore, in the present study, we sequenced and assembled the complete chloroplast and mitochondrial genomes of *C. tianeensis* for the first time. We conducted comparative analyses of genome structure, repeat sequences, RNA editing, codon usage bias, and inter-organellar DNA transfer. Our findings aim to: (1) enrich genomic resources for sect. *Chrysanth*; (2) clarify the evolutionary relationship of *C. tianeensis* within *Camellia*; and (3) provide a molecular basis for future studies on its evolution, conservation, and applied utilization.

Results

Genome assembly and general features

The complete chloroplast genome of *C. tianeensis* was assembled into a typical quadripartite circular structure with a total length of 156,865 bp, consisting of a large single-copy (LSC) region of 86,579 bp, a small single-copy (SSC) region of 18,236 bp, and two inverted repeat (IR) regions of 52,050 bp each (Fig. 1A). The overall GC content was 37.32%, with the IR region showing the highest GC content (42.99%) and the SSC region the lowest (30.59%). The chloroplast genome encoded 131 unique genes, including 90 protein-coding genes (PCGs), 37 tRNA genes, and four rRNA genes (Table 1). Among these, 14 genes were duplicated in the IRs, one gene was triplicated, and 13 genes contained introns (Table S1).

The mitochondrial genome was also circular, totaling 1,098,121 bp (Fig. 1B), and encoded 51 genes: 31 PCGs, 18 tRNAs, and two rRNAs. The GC content was higher (45.71%) than that of the chloroplast genome. The total CDS length accounted for 2.5% (27,387 bp) of the mitochondrial genome (Table 1). Functional annotation grouped the PCGs into three main categories: (1) electron transport and ATP synthesis; (2) transcription and translation; and (3) miscellaneous functions (Table S2). Four ribosomal protein genes—*rps12*, *rps14*, *rps16*, and *rps7*—were shared between the chloroplast and mitochondrial genomes.

Repeat sequence analysis

A total of 69 simple sequence repeat (SSR) loci were identified in the chloroplast genome of *C. tianeensis*. Mononucleotide SSRs were the most abundant type, accounting for 75% of all SSR loci, a proportion substantially higher than that of the other repeat types (Fig. 2A). In terms of genomic regions, 48 SSR loci were located in the LSC region, 11 in the SSC region, and 10 in the IR region (Fig. 2B). We also detected 38 dispersed repeats belonging to three types, 15 forward (F), one reverse (R), and 22 palindromic (P), whereas no complement (C)-type repeats were found (Fig. 2C). With respect to motif composition, these 69 SSRs comprised 52 mononucleotides (mono-) (A-21, T-31), four dinucleotides (di-) (AT-3, TA-1), one trinucleotide (tri-) (TTC-1), and

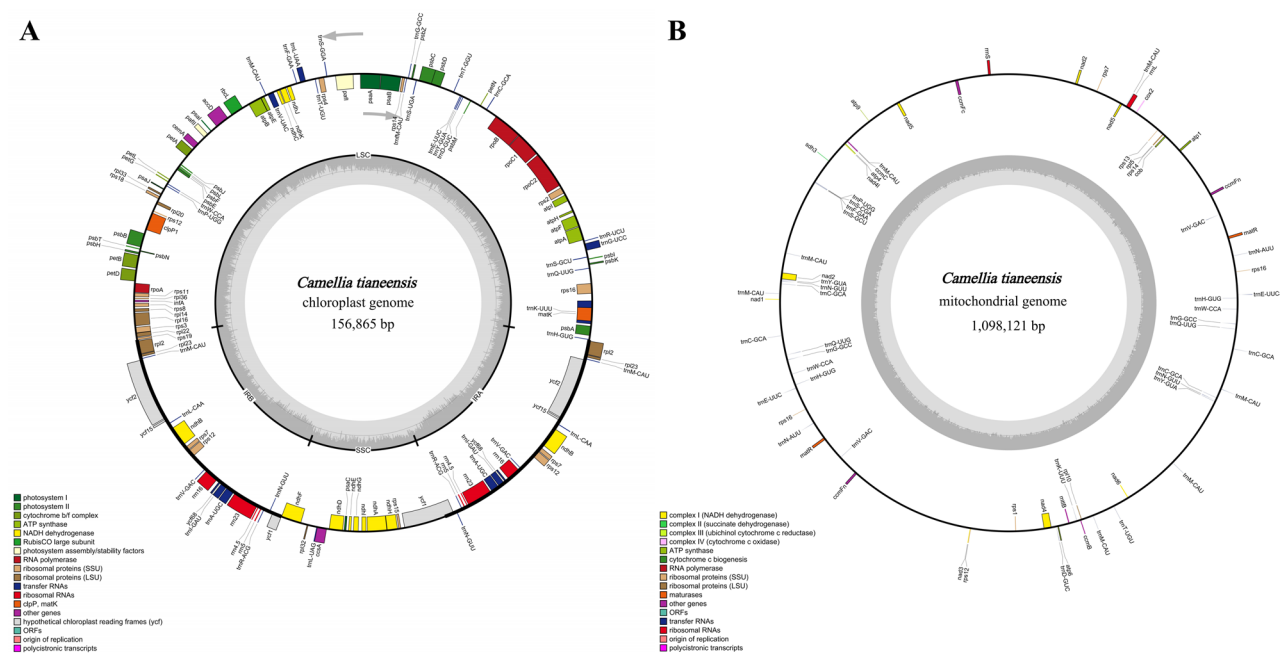


Fig. 1 Gene map of the chloroplast (A) and mitochondrial (B) genomes of *C. tianeensis* (Genes on the outside and inside of the outer circle are transcribed in clockwise and counter-clockwise directions, respectively. The inner grey circle shows the GC-content distribution along each genome)

Table 1 Features of the complete chloroplast and mitochondrial genomes of *C. tianeensis*

	cpDNA	mtDNA
Genome size (bp)	156,865	1,098,121
GC (%)	37.32	45.71
LSC size (bp)	86,579	-
SSC size (bp)	18,236	-
IR size (bp)	52,050	-
GC in LSC (%)	35.33	-
GC in SSC (%)	30.59	-
GC in IR (%)	42.99	-
GC in CDS (%)	37.58	44.08
1st position GC (%)	45.19	48.68
2nd position GC (%)	37.91	43.86
3rd position GC (%)	29.62	39.71
Length of CDS (bp)	81,273	27,387
Number of genes	131	51
Number of PCG	90	31
Number of tRNA	37	18
Number of rRNA	4	2

12 tetranucleotides (tetra-) (AGAT-1, AAAT-1, AATA-1, ATAG-1, GTCT-1, GAAA-1, GAGG-1, CCCT-1, TCTT-1, TTTC-1, TCTA-1) (Fig. 2D). However, pentanucleotides (penta-) and hexanucleotides (hexa-) were not detected. The long dispersed repeats ranged from 30 to 70 bp in length, with most falling between 30 and 34 bp (Fig. 2E). Mononucleotide SSRs were particularly enriched in the LSC region, where 40 sites were recorded, accounting for 77% of all SSRs in the LSC (Fig. 2F).

In the mitochondrial genome, 306 SSRs were detected, including six repeat types, of which tetranucleotides were the most abundant (124, 40.5%). A total of 2,010 dispersed repeats were found, predominantly forward repeats (1,024), while no complementary repeats were present. Long repeat sequences were most frequent within the range of 30–1,036 bp. After normalization, the mitochondrial genome still exhibited significantly higher repeat content, with 0.279 SSRs per kilobase (kb) compared to 0.440 SSRs per kb in the chloroplast genome, a 63% reduction in SSR content. The mitochondrial genome had 1.83 dispersed repeats per kb, compared to 0.242 per kb in the chloroplast genome, resulting in a 7.57-fold higher content of dispersed repeats.

RNA-editing site prediction

RNA editing sites in 90 chloroplast and 31 mitochondrial protein-coding genes of *C. tianeensis* were predicted using Prep-Cp and Prep-Mt, respectively. In the chloroplast genome, 32 genes were predicted to contain RNA editing sites, with a total of 65 C to U edits (Fig. 3A). In the mitochondrial genome, 404 RNA-editing sites were identified across 23 genes (Fig. 3B). At the codon level (Fig. 3C), chloroplast editing events were confined to the first and second positions: 15 sites occurred at the first codon position and 50 at the second, with no edits at the third position. In contrast, mitochondrial editing sites were more broadly distributed but showed a strong bias toward the second codon position, which accounted for 66% of all mitochondrial edits.



Fig. 2 Comparative analysis of repetitive sequences of *C. tianeensis* chloroplast and mitochondrial genomes. **A** The numbers of the six SSR types; **B** The number of SSRs in different regions of the chloroplast genome; **C** The number of six types of SSRs in different regions of the chloroplast genome; **D** The numbers of different SSR repeat unit types; **E** The numbers of the four dispersed repeat sequence types. **F** The length of the four dispersed repeat sequence types

All 65 chloroplast editing sites resulted in amino acid changes, which could be grouped into 11 types: A(Ala)→V(Val), H(His)→Y(Tyr), L(Leu)→F(Phe), P(Pro)→L(Leu), P(Pro)→S(Ser), R(Arg)→C(Cys), R(Arg)→W(Trp), S(Ser)→F(Phe), S(Ser)→L(Leu),

T(Thr)→I(Ile), and T(Thr)→M(Met) (Fig. 3D). The most frequent changes was S(Ser)→L(Leu), which appeared 23 times and accounting for 35% of all chloroplast edits. Two amino acid changes, R(Arg)→C(Cys) and R(Arg)→W(Trp), were observed only once each,

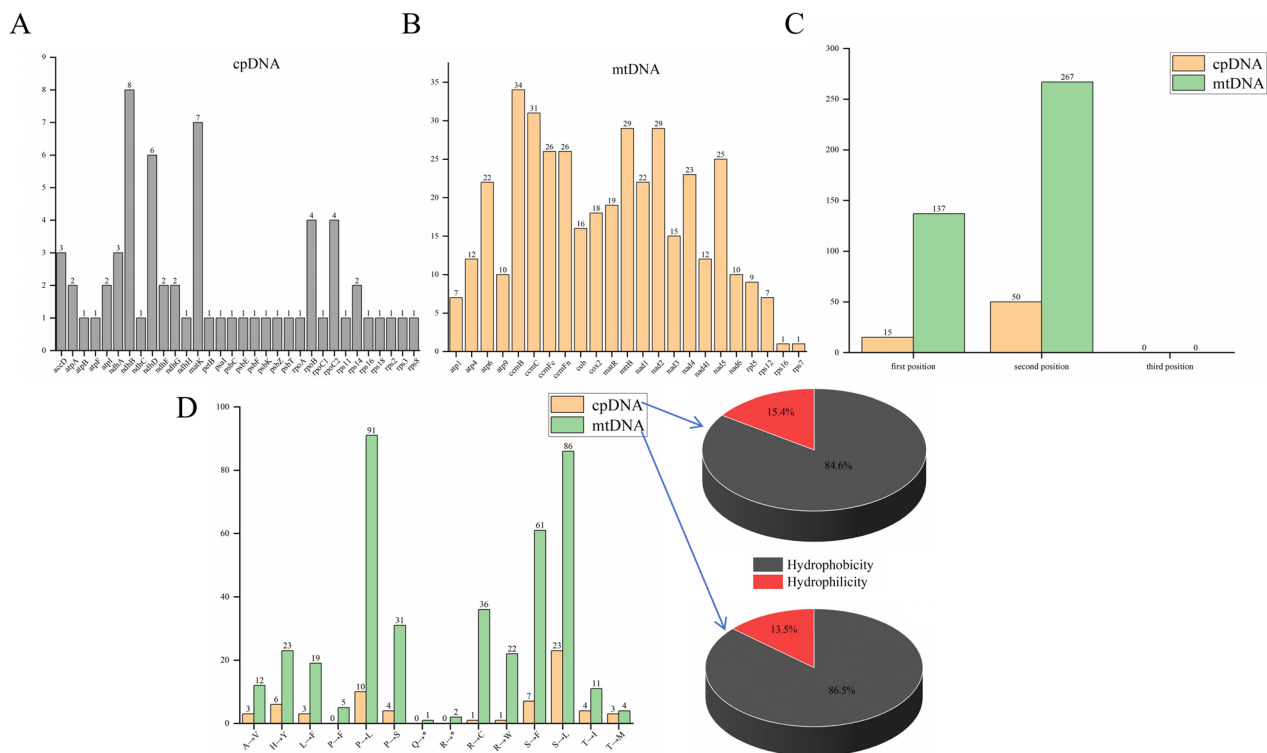


Fig. 3 *C. tianeensis* chloroplast and mitochondrial genomes RNA editing sites. **A** Number of RNA-editing sites in cpDNA; **B** Number of RNA-editing sites in mtDNA; **C** Codon changes at different positions; **D** Characterization of RNA editing sites

whereas the remaining eight types occurred between 3 and 10 times. Overall, 84.6% of the edited chloroplast sites involved hydrophobic amino acids, compared with 15.4% involving hydrophilic ones.

In the mitochondrial genome, three editing sites were predicted to generate premature stop codons (Q→stop, R→stop), while the remaining 401 sites were predicted to cause amino acid substitutions (Fig. 3D). Among these, Pro→Leu was the most frequent change, occurring 91 times. Hydrophobic amino acid changes accounted for 86.5% of all mitochondrial editing events. Taken together, these results indicate that RNA editing in both organelles preferentially increases protein hydrophobicity and frequently results in substitutions toward leucine residues.

Codon-usage bias

The CDSs of the *C. tianeensis* chloroplast and mitochondrial genomes were filtered to remove sequences shorter than 300 bp and then analyzed. The mean total GC contents (GCall) of the chloroplast and mitochondrial CDSs were 38.25% and 42.44%, respectively (Tables S3). In the chloroplast genome, the mean GC₁, GC₂ and GC₃ values were 47.07%, 39.71% and 27.99%, respectively, whereas in the mitochondrial genome they were 47.77%, 42.61% and 36.95%. In both organelles, GC content at each codon position was below 50% and followed the pattern GC₁>GC₂>GC₃, indicating a general preference for

A/U-ending codons, with the third position showing the strongest bias. The ENC values of chloroplast and mitochondrial CDSs ranged from 34.68 to 56.27 and from 37.79 to 61, with mean values of 44.99 and 51.65, respectively, consistent with overall weak codon usage bias.

Correlation analysis of the GC_{all}, GC₁, GC₂, GC₃, GC₁₂, and ENC revealed distinct patterns in the two organelles (Fig. 4A). In the chloroplast genome, GC₁ and GC₂ were significantly positively correlated with each other ($P<0.01$), but both were negatively correlated with GC₃ (although not significantly), suggesting that codon composition varies more at the third position than at the first and second positions. ENC was highly positively correlated with GC₃, indicating that variation at the third codon position has a strong influence on chloroplast codon usage bias. In the mitochondrial genome, GC_{all} showed highly significant correlations with GC₁, GC₂, GC₃, GC₁₂ and ENC. By contrast, GC₃ was not correlated with GC₁ or GC₂, suggesting that the third position differs from the first and second positions, whereas GC₃ was highly significantly correlated with both GC_{all} and ENC, implying that mitochondrial codon usage is mainly shaped by changes in GC₃ content.

Neutrality plot analysis further supported the role of selection in shaping codon usage (Fig. 4B). The GC₁₂ values of chloroplast and mitochondrial genes ranged from 32.54% to 55.035% and from 36.915% to 51.59%,

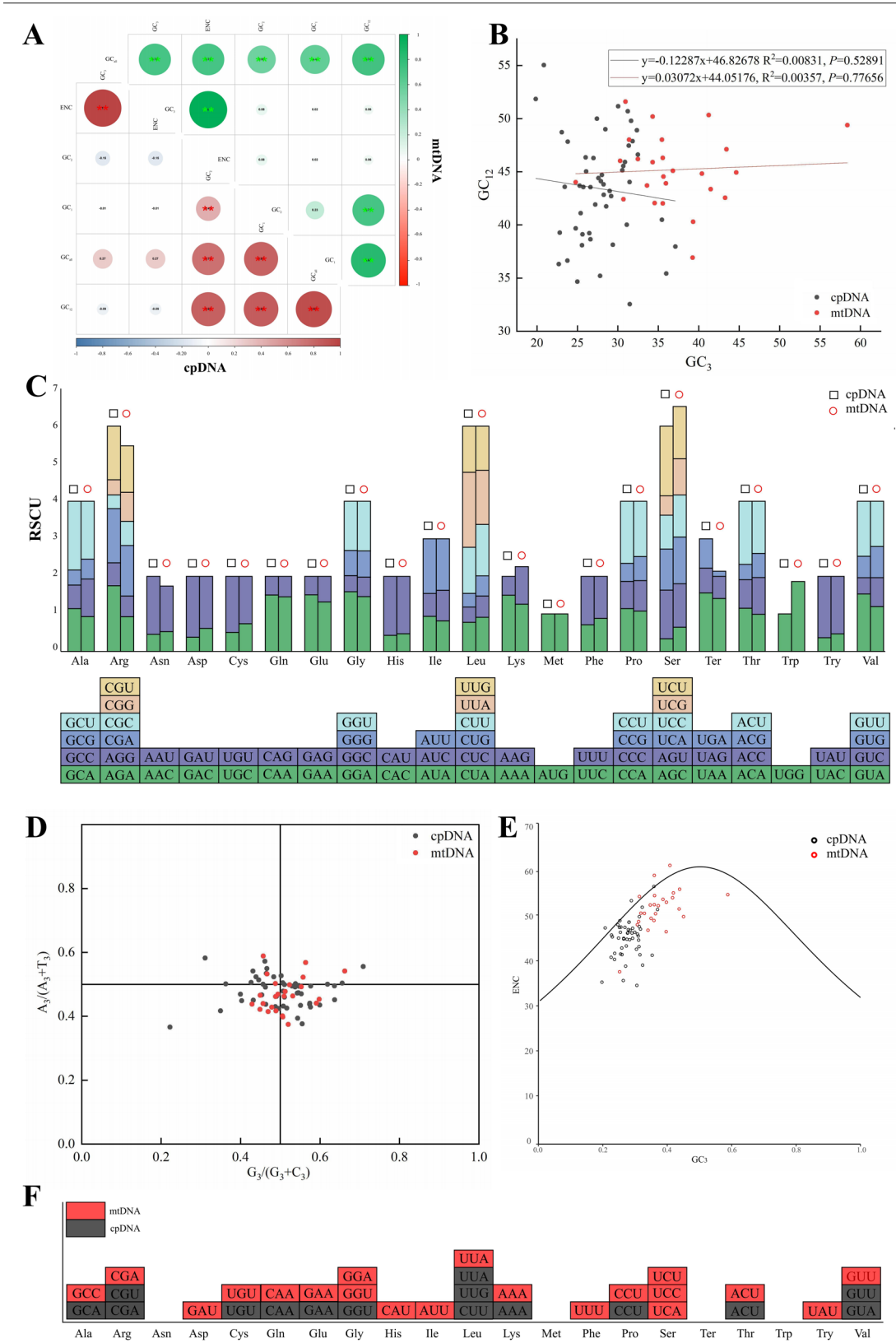


Fig. 4 Codon preferences in the *C. tianeensis* chloroplast and mitochondrial genomes. **A** Correlation analysis of codon parameters; **B** Analysis of neutrality plot; **C** Relative synonymous codon usage; **D** Analysis of PR2 plot; **E** Analysis of ENC plot; **F** Optimal codon

respectively. Most genes in both genomes were located far from the expected standard curve, indicating that codon usage is strongly influenced by natural selection. The regression slopes were -0.12287 for chloroplast genes and 0.03072 for mitochondrial genes, showing a negative correlation between GC_{12} and GC_3 in the chloroplast genome and a weak positive correlation in the mitochondrial genome, consistent with the correlation analysis above.

Relative synonymous codon usage (RSCU) values for all 64 codons were calculated for both organelles (Fig. 4C, Table S4). RSCU values ranged from 0.3368 to 1.9959 in the chloroplast genome and from 0.1368 to 1.8632 in the mitochondrial genome. Excluding the three stop codons (UAG, UAA and UGA), the codons with the highest RSCU values were Leu (UUA) in the chloroplast genome and Trp (UGG) in the mitochondrial genome, whereas the lowest values were observed for Ser (AGC) and Tyr (UAC), respectively. Among the 61 sense codons, 30 chloroplast codons and 29 mitochondrial codons had $RSCU > 1$, indicating that they are strongly preferred and represent high-frequency codons. Of these, 13 and 10 codons ended with A, 1 and 2 with G, 16 and 16 with U, and 0 and 1 with C in the chloroplast and mitochondrial genomes, respectively. Thus, 96.6% and 89.6% of high-frequency codons ended in A or U, confirming that both organellar genomes preferentially use A/U-ending codons.

The PR2-plot analysis (Fig. 4D) showed that both chloroplast and mitochondrial genes were unevenly distributed across the four quadrants and most points were located away from the centre, indicating that codon usage in *C. tianeensis* organellar genomes is influenced by both natural selection and mutational bias rather than by a perfect $A = T$ and $G = C$ equilibrium. ENC-plot analysis provided further support for the predominant role of selection (Fig. 4E). Only a few genes were located on or near the expected standard curve, whereas most genes fell below and at some distance from the curve, suggesting that codon usage patterns in both chloroplast and mitochondrial genomes are less constrained by mutational pressure and more strongly shaped by natural selection. This result is consistent with the neutrality plot.

A codon was defined as optimal when it simultaneously satisfied $RSCU > 1$ and $\Delta RSCU \geq 0.08$. According to this criterion, the *C. tianeensis* chloroplast genome contained 15 optimal codons and the mitochondrial genome contained 20 (Fig. 4F, Table S5). Most optimal codons in both genomes ended in A or U, with codons ending in U being more frequent. Ten optimal codons were shared between the two organelles: CGA, UGU, CAA, GAA, GGU, UUA, AAA, CCU, ACU and CUU, indicating a partially

common set of preferred codons in the chloroplast and mitochondrial genomes.

Phylogenetic relationships

The chloroplast genomes of 23 plants were downloaded from the NCBI (6 of the plants were close relatives of *C. tianeensis*) to determine the phylogenetic position of *C. tianeensis*. The results showed that the phylogenetic trees constructed using the maximum likelihood and Bayesian methods based on the protein-coding genes of 24 plants had the same topological structure (Fig. 5A). There was high support for all of the nodes in the generative tree. *C. tianeensis* and its six close relatives clustered on Branch Cade I (BS = 89%; PP = 0.77).

Due to the paucity of reports on plant mitochondrial genome data, we found only one report of a mitochondrial genome from a closely related species. It was therefore not possible to select species with identical chloroplast genomes for comparative analyses. However, we selected protein-coding genes from the mitochondrial genomes of 19 species for phylogenetic position exploration. As shown in Fig. 5B, the phylogenetic trees constructed by the two methods had the same topology, and both methods yielded highly supported branch nodes. *C. tianeensis* and *Camellia nitidissima* were clustered in branch Cade III (BS = 61%; PP = 0.69), and all the other Theaceae species were in branch Cade II (BS = 100%; PP = 1.00).

DNA fragment transfer between organelles

Nine chloroplast-derived DNA fragments were identified in the mitochondrial genome of *C. tianeensis*, ranging from 127 to 9,572 bp in length and totaling 42,875 bp (3.9% of the mitochondrial genome and 27.3% of the chloroplast genome) (Fig. 6; Table 2). These fragments originated mainly from chloroplast CDSs (*psbC*, *atpB*, *rpl16*, *rpl23*, and *rpl2*), rRNAs, and tRNAs. The largest fragment (9,572 bp) comprised rRNA, tRNA, exon, and intron regions, and likely represents a hotspot of inter-organelle DNA transfer. Most transferred sequences showed > 95% identity to their chloroplast counterparts, suggesting relatively recent transfer events with limited subsequent divergence. These results indicate extensive plastid-to-mitochondrion DNA transfer in *C. tianeensis* and point to intracellular gene transfer as an important contributor to the structural evolution of its mitochondrial genome.

Discussion

Overall organellar genome features

Chloroplasts and mitochondria are the two major energy-producing organelles in plant cells, and comparative analyses of their genomes provide complementary perspectives on genome evolution and species

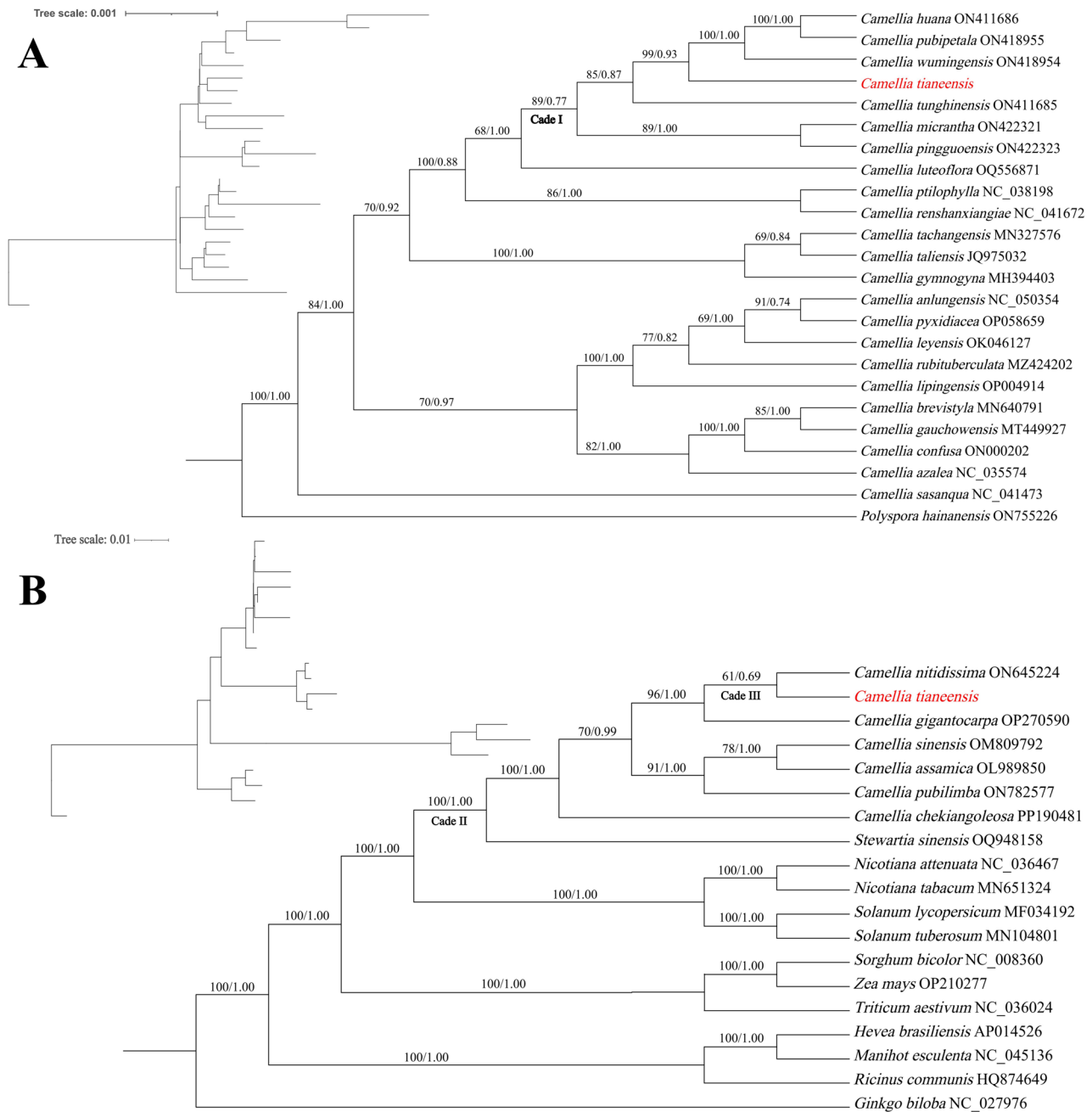


Fig. 5 Construction of a phylogenetic tree based on protein-coding genes (**A**) chloroplast and genome; (**B**) mitochondrial genome

diversification [28–31]. In this study, we assembled and analyzed the complete chloroplast and mitochondrial genomes of *C. tianeensis*, allowing a joint assessment of genome architecture, repeat dynamics, RNA editing, codon-usage patterns and inter-organelle DNA transfer in this rare yellow-flowered species of sect. *Chrysanthia*. Both organellar genomes exhibited circular structures typical of most higher plants [32–34]. Several genes contain one or more introns, which may play important roles in the regulation of gene expression [35]. The chloroplast genome of *C. tianeensis* (156,865 bp) is similar in size and

structure to those reported from other *Camellia* species (150–160 kb), whereas its mitochondrial genome (1.10 Mb) is considerably larger, consistent with the wide size variation observed among plant mitochondrial genomes (66 kb–11.3 Mb) [36]. The low proportion of coding DNA, in the mitogenome reinforces the view that plant mitochondrial genomes expand mainly through accumulation of noncoding sequence, repeats and foreign (including plastid-derived) DNA rather than through an increase in core gene content [37–39].

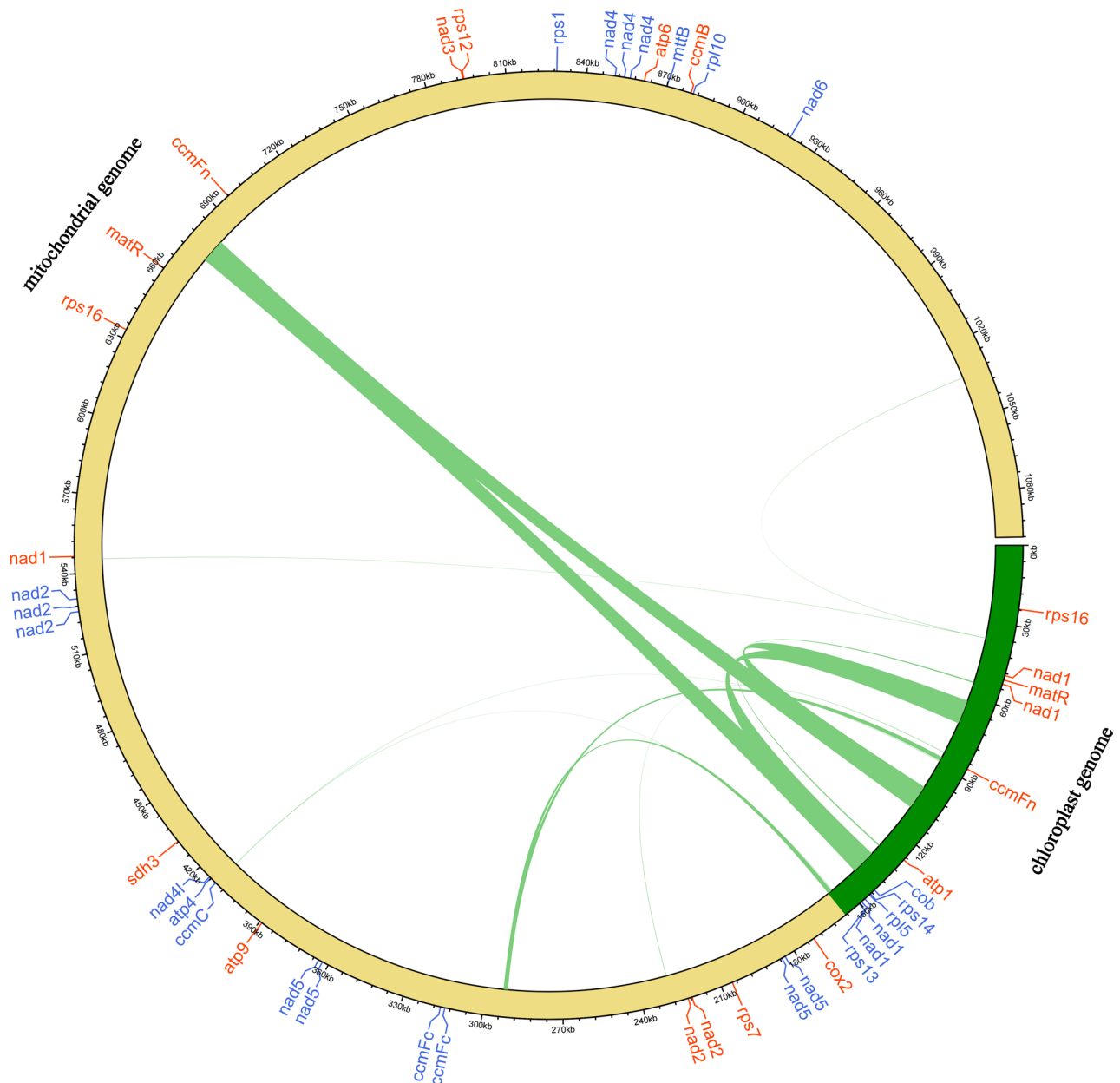


Fig. 6 Covariance analysis of homologous fragments of *C. tianeensis* chloroplast and mitochondrial genomes

Repetitive elements and genome structure

Repetitive sequences are major contributors to plant organelle genome size variation and structural rearrangement [40]. The chloroplast genome of *C. tianeensis* contained 69 SSRs and 38 dispersed repeats, whereas its mitochondrial genome harbored 306 SSRs and more than 2,000 dispersed repeats. Such repeat inflation is characteristic of many mitochondrial genomes and is often associated with intramolecular recombination, which can give rise to multipartite structures and alternative chromosomal isoforms [41, 42]. In *C. tianeensis*, forward and palindromic repeats dominate the mitochondrial repeat landscape, and complement-type repeats were not

detected. Although we did not directly assess recombination activity, the abundance and distribution of these repeats suggests that the mitochondrial genome may be structurally dynamic, with repeated elements likely contributing to subtle rearrangements and the generation of subgenomic molecules. These processes may in turn influence gene copy number and expression among tissues or developmental stages [43, 44]. In the chloroplast genome, SSRs and long repeats are concentrated in the LSC region and are largely composed of A/T-rich motifs, a pattern consistent with many land-plant plastomes [45]. Such repeats can serve as useful sources of polymorphic markers for population genetic and conservation studies

Table 2 Transfer of the *C. tianeensis* Chloroplast genome to mitochondrial genome gene fragments

No	Length	Identity	Mt-start	Mt-end	Cp-start	Cp-end	Type
1	147	0.95	1,033,685	1,033,831	36,657	36,803	<i>PsbC</i> CDS
	147	0.95	545,189	545,335	36,657	36,803	
2	487	1	129,549	129,063	54,493	54,979	<i>atpB</i> CDS
3	174	0.98	228,546	228,719	84,563	84,736	<i>rpl16</i> CDS
4	1689	1	291,351	293,039	86,640	88,328	<i>rpl23</i> CDS
5	127	1	411,170	411,296	88,593	88,719	<i>trnM</i> -CAU exon
6	9572	0.99	681,494	672,005	100,280	109,851	23 S rRNA
	9572	0.99	71,870	62,381	100,280	109,851	
7	9572	0.99	62,381	71,870	133,594	143,165	<i>trnV</i> -GAC intron
	9572	0.99	672,005	681,494	133,594	143,165	
8	127	1	411,296	411,170	154,726	154,852	<i>trnM</i> -CAU exon
9	1689	1	293,039	291,351	155,117	156,805	<i>rpl2</i> CDS

in this highly endangered species and its close relatives, particularly in the karst habitats where effective population sizes are often small and fragmented.

RNA editing in chloroplasts and mitochondria

RNA editing is a widespread post-transcriptional process in plant organelles that alters mRNA sequences and can increase proteomic diversity [46]. A growing body of work suggests that mitochondrial RNA editing is associated with important agronomic traits and stress responses in plants [47, 48]. In *C. tianeensis*, the mitochondrial genome harbors 404 predicted RNA-editing sites, approximately six times more than in the 65 sites inferred for the chloroplast genome. This editing load is comparable to that reported for other angiosperms, such as *Arabidopsis thaliana* (441 sites) and *Oryza sativa* (491 sites) [49, 50], and is concentrated in protein-coding genes involved in electron transport and ATP synthesis. Most mitochondrial edits are predicted to convert hydrophilic residues to hydrophobic ones, particularly leucine, a pattern that has been interpreted in other species as potentially enhancing protein stability and facilitating assembly of membrane-bound respiratory complexes [51, 52]. A small number of mitochondrial editing events in *C. tianeensis* affect codons that encode or are adjacent to stop codons, and are predicted to generate premature termination codons. The functional consequences of these events are currently unclear and cannot be resolved from in silico predictions alone. Experimental validation of editing status and protein products, especially in key respiratory genes such as *nad*, *cox* and *atp*, will be an important next step to link editing patterns more directly to mitochondrial function and stress responses.

Chloroplast editing in *C. tianeensis* is less frequent but shows similarly non-random patterns: all sites are of the canonical C-to-U type, confined to the first and second codon positions, and nearly all result in nonsynonymous substitutions that increase amino acid hydrophobicity. This falls within the range of 30–80 plastid editing sites

typically reported for angiosperms [53, 54], and underscores that even modest levels of plastid editing can influence the composition and stability of photosynthetic complexes. Taken together, our results support the view that mitochondrial RNA editing generally exerts a stronger post-transcriptional influence than chloroplast editing, while both organelles appear to use editing to adjust the properties of core bioenergetic proteins. However, functional interpretations remain tentative until transcript- and protein-level data become available.

Codon usage patterns in organellar genes

Both organellar genomes of *C. tianeensis* display a strong preference for A/U-ending codons, particularly at the third codon position, but overall codon-usage bias is relatively weak according to ENC values. This pattern is broadly consistent with codon-usage profiles reported for plastid and mitochondrial genomes in many seed plants, including other *Camellia* species [55, 56]. Our correlation analyses, together with neutrality and PR2 plots, indicate that mutational bias alone cannot fully account for the observed codon-usage patterns and that natural selection is likely to make a non-negligible contribution [57]. In the chloroplast genome, GC₃ content is tightly linked to ENC and is largely decoupled from GC₁ and GC₂, suggesting that codon composition varies mainly at the third position and that selection on synonymous sites may act to optimize translational efficiency and accuracy, particularly for highly expressed photosynthetic genes [58, 59]. In the mitochondrial genome, GC_{all} and GC₃ show strong correlations with ENC, whereas GC₃ is not strongly associated with GC₁ or GC₂. This suggests that mitochondrial codon bias is also influenced by changes in third-position GC content, but operates against a background of more complex mutational processes, possibly reflecting the interplay of DNA repair, recombination and the integration of foreign sequences [38].

The identification of partially overlapping sets of optimal codons in chloroplasts and mitochondria, with a

strong enrichment of A/U-ending codons, further suggests that organellar translation systems in *C. tianeensis* may be co-adapted to a broadly similar codon landscape. From an applied perspective, these patterns provide a useful reference for codon optimization in transgene design and for tailoring plastid- or mitochondrion-targeted constructs in *Camellia* breeding programs. At the same time, more direct measures of gene expression and tRNA abundance would be valuable to quantify the extent to which translational selection shapes codon usage in this species.

Phylogenetic position of *C. tianeensis*

Phylogenetic analyses based on both chloroplast and mitochondrial genomes confirmed the placement of *C. tianeensis* within sect. *Chrysanth*. The phylogenetic trees constructed from chloroplast genomes and mitochondrial genomes consistently showed that *C. tianeensis* clustered with its close relatives in distinct clades. Specifically, in the chloroplast tree, *C. tianeensis* and its six close relatives clustered in branch cade I, while in the mitochondrial tree, *C. tianeensis* and *C. nitidissima* were positioned together in branch cade III. Despite the difference in species sampled between the two trees, the similar topological structure and clustering patterns observed in both trees suggest a consistent phylogenetic position of *C. tianeensis* within sect. *Chrysanth*. These findings align with previous phylogenetic studies, which have also placed *C. tianeensis* within sect. *Chrysanth*, reinforcing the stable phylogenetic grouping based on both chloroplast and mitochondrial data [60–62]. However, it is important to note that mitochondrial genomes generally evolve more rapidly than chloroplast genomes and are subject to frequent recombination and DNA transfer events [63, 64]. These evolutionary dynamics can occasionally introduce complexities that result in topological discrepancies. In the present study, although the mitochondrial tree corroborates the findings from the chloroplast tree, the different support values observed in the two trees (BS = 89%, PP = 0.77 for the chloroplast tree; BS = 61%, PP = 0.69 for the mitochondrial tree) reflect the differences in evolutionary rates and biological processes between the two genomes.

To further refine the understanding of the phylogenetic relationships within sect. *Chrysanth*, expanding the taxon sampling and integrating nuclear genomic data will be essential. Such approaches could provide more resolution, especially in light of the complex evolutionary mechanisms such as horizontal gene transfer, recombination, and mutation rates in mitochondrial genomes, which may obscure deeper evolutionary signals. Including nuclear data will be crucial for providing a more comprehensive understanding of the evolutionary processes shaping this lineage.

Plastid-to-mitochondrion DNA transfer

DNA fragment transfer between chloroplasts and mitochondria is a major force shaping organellar genome evolution. In *C. tianeensis*, nine chloroplast-derived fragments totaling 42.9 kb were identified in the mitochondrial genome. Most of the transferred segments originate from coding regions (*psbC*, *atpB*, *rpl16*, *rpl23*, *rpl2*), rRNAs and tRNAs, and retain > 95% sequence identity to their plastid counterparts, suggesting relatively recent transfer events and limited subsequent divergence [65, 66]. The proportion of the mitochondrial genome occupied by chloroplast origin sequences (3–5%) is comparable to that reported for other angiosperms [67, 68].

Similar chloroplast-to-mitochondrion transfers have been reported in other *Camellia* species [61] and in a wide range of angiosperms, where they are thought to occur via non-homologous end joining and recombination during double-strand break repair [69]. The functional consequences of these transfers can vary: some fragments degrade into pseudogenes or contribute to structural rearrangements, while others, particularly intact tRNA genes, may be co-opted into the mitochondrial translation machinery. The conservation of complete *trnM-CAU* copies in the *C. tianeensis* mitogenome suggests a plausible functional role of at least some transferred genes, and raises the possibility that plastid derived tRNAs help to expand or stabilize the mitochondrial tRNA repertoire.

The overall picture emerging from *C. tianeensis* is that extensive, recent plastid-to-mitochondrion DNA transfer has contributed substantially to mitochondrial genome expansion and structural complexity. Mapping these transferred regions across additional sect. *Chrysanth* species will be informative for reconstructing the timing of transfer events and for disentangling lineage-specific from shared mtpt insertions. Such comparative work could also help identify potential associations between mtpt dynamics, mitochondrial genome architecture and ecological specialization on karst substrates. Moreover, further investigations into the functional consequences of these transfers in relation to ecological adaptation are warranted. The high rate of plastid-to-mitochondrion DNA transfer observed in *C. tianeensis* may be linked to the species' adaptation to its unique karst habitat. However, Although this study primarily focuses on plastid-to-mitochondrion DNA transfer (MTPT), we have not excluded the possibility of mitochondrial-to-plastid DNA transfer (PTMT), which, although rare, should not be dismissed. DNA transfer between mitochondria and plastids is facilitated by repair and recombination mechanisms, and these processes may not be limited to one direction. While research has primarily focused on MTPTs, PTMTs, though less studied, could also influence genome dynamics and adaptive evolution in certain species or

environments [70, 71]. Given the rarity of PTMT, future genomic and transcriptomic studies should investigate its occurrence and role in plant evolution. Expanding sample sizes, conducting comparative studies, and integrating functional validation will help assess the ecological and evolutionary significance of PTMT. Moreover, combining genomic data with experimental analysis and exploring the relationship between inter-organelle DNA transfer dynamics, mitochondrial complexity, and environmental adaptation could provide deeper insights into plant speciation and ecological specialization.

This study identified nine chloroplast-derived fragments in the mitochondrial genome of *C. tianeensis*, indicating ongoing plastid-to-mitochondrion DNA transfer. The mitochondrial genome is larger and repeat-rich compared to the conserved plastome. Phylogenetic analyses place *C. tianeensis* within sect. *Chrysanth* and show a close relationship with *C. nitidissima*. Additionally, the mitochondrial genome contains chloroplast-derived sequences, which likely contribute to its structural complexity. These findings provide valuable genomic resources for sect. *Chrysanth* and offer insights into the role of DNA transfer in organellar genome evolution. Future research combining nuclear genomic data, population-level sampling, and functional validation of RNA-editing sites and transferred genes will be crucial for linking these organellar features to ecological adaptation and conservation priorities in this species.

Conclusions

This study presents the first integrated analysis of the chloroplast and mitochondrial genomes of *C. tianeensis*, a rare yellow-flowered species of sect. *Chrysanth*. The plastome exhibits the typical quadripartite structure and conserved gene content characteristic of *Camellia*, whereas the mitogenome is strongly expanded and highly enriched in dispersed repeats and plastid-derived DNA, illustrating the contrasting evolutionary trajectories of the two organelles. Across both genomes, codon-usage analyses reveal a shared preference for A/U-ending codons and indicate that codon bias is shaped by a combination of mutational bias and translational selection, with several lines of evidence pointing to an important role of selection at synonymous sites. Mitochondrial RNA editing is far more frequent than chloroplast editing and predominantly increases protein hydrophobicity. Phylogenetic reconstructions based on complete sets of organellar protein-coding genes consistently place *C. tianeensis* within sect. *Chrysanth* and recover a close evolutionary relationship with *C. nitidissima*, in broad agreement with previous plastid and mitochondrial studies, although mitochondrial support values remain moderate. This congruence across genomic compartments strengthens confidence in the inferred relationships and

provides a framework for future taxonomic and biogeographic work on golden camellias. Finally, the identification of nine large chloroplast-derived fragments in the mitochondrial genome demonstrates ongoing intracellular DNA transfer and underscores its contribution to mitochondrial genome expansion and structural complexity in *C. tianeensis*. Together, these results deepen our understanding of organellar genome evolution in sect. *Chrysanth* and furnish valuable genomic resources for subsequent studies on systematics, conservation genetics and molecular breeding of sect. *Chrysanth* species, including the development of molecular markers and codon-optimized genes tailored to the organellar genetic background of this group.

Materials and methods

Material collection, DNA extraction, and sequencing

The *C. tianeensis* plant samples in this study were collected as transplants from Tianba village (N 25.583482, E 106.964236), Luodian County, Guizhou Province (Fig. 7). The specimens were preserved in the Tree Specimen Laboratory, School of Forestry, Guizhou University (GZAC, LZ-20221101-1). Fresh, young leaves were sampled and ground to break the cells and release the organelles. Then, chloroplasts and mitochondria were isolated from the ruptured cells using density gradient centrifugation. Finally, chloroplast and mitochondrial DNA were extracted using an optimized cetyl-trimethylammonium bromide (CTAB) method [72]. The integrity of the DNA was determined by 1% glucose agar gel electrophoresis, and the purity and content of the DNA were assessed by nucleic acid proteomics. Sequencing libraries were then constructed by fragmenting, end-repairing, and ligating the DNA at the junctions. Libraries were sequenced using an Illumina NovaSeq 6000 platform with 150 bp paired-end read lengths. The short raw reads were assessed using FastQC and trimmed using Trimmomatic v0.39, with the following parameters: Remove adapters (ILLUMINA-CLIP: TruSeq3-PE.fa:2:30:10), Remove leading low quality or N bases (below quality 3) (LEADING:3), Remove trailing low quality or N bases (below quality 3) (TRAILING:3), Scan the read with a 4-base wide sliding window, cutting when the average quality per base drops below 15 (SLIDINGWINDOW:4:15), and Drop reads below the 36 bases long (MINLEN:36). The long raw reads were base-called using Albacore v2.1.7 (mean q-score > 7) on a Oxford Nanopore platform with barcode demultiplexing and converted to fasta format using SAMtools Fasta.

Assembly and annotation of chloroplast and mitochondrial genomes

To improve the reliability of the assembled genomes, we used two strategies to assemble both the chloroplast and mitochondrial genomes of *C. tianeensis*. For the



Fig. 7 Morphology of *C. tianeensis* (A) Tree; (B) Bud; (C) Flower; (D) Fruit

first strategy, short clean reads were de novo assembled with GetOrganelle v1.6.4 [73], and potential chloroplast and mitochondrial contigs were extracted via alignment against chloroplast and mitochondrial protein-coding genes from plant chloroplast and mitochondrial databases via BLAST v2.8.1. Then, the putative long chloroplast and mitochondrial reads were baited by mapping the PacBio long reads to the potential chloroplast and mitochondrial contigs using BLASR v5.1. Finally, the putative long chloroplast and mitochondrial reads were assembled by Canu v2.1.1 [74]. In the second strategy, all PacBio long reads were assembled de novo by using Canu directly. Subsequently, we used Burrows–Wheeler Aligner (BWA) to map the short clean reads to the draft contigs and improved the draft contigs with Pilon v1.22. Then, MUMmer v3.23 was used to check whether these contigs were circular. Finally, the corrected contigs

obtained from the above two assembly strategies were aligned with each other using MUMmer. The results showed that these two contigs were identical. Based on the above assembly steps, we generated a master circle for the *C. tianeensis* chloroplast and mitochondrial genomes.

The chloroplast and mitochondrial genes were annotated using the online GeSeq tool [75] with default parameters to predict protein-coding, transfer RNA (tRNA), and ribosome RNA (rRNA) genes. The position of each coding gene was determined using BLAST searches against the reference chloroplast and mitochondrial genes [76]. Manual corrections of genes for start/stop codons and for intron/exon boundaries were performed in SnapGene Viewer by referencing the reference chloroplast genome and mitochondrial genome. The circular *C. tianeensis* chloroplast genome

and mitochondrial genome map were drawn using the OGDRAW tool [77].

Repeat sequence analysis and RNA editing analysis

MISA v2.1 [78] software was used to search for simple sequence repeats (SSRs) in the chloroplast and mitochondrial genome sequences of *C. tianeensis*. The minimum number of repeat units and the number of repeats were set as follows: 10 for a single nucleotide unit, 5 for a dinucleotide unit, 4 for a trinucleotide unit, 3 for a tetranucleotide unit, 3 for a pentanucleotide unit, and 3 for a hexanucleotide unit [79]. Dispersed repeat sequence analyses were performed using the software REPuter [80] (<http://bibiserv.techfak.uni-bielefeld.de/reputer/>) with parameters set to a minimum repeat size of 30 bp, a Hamming distance of 3, and a maximum number of computed repeats of 5000. The four types were forward (F), reverse (R), complement (C), and palindromic (P). Editing site prediction for *C. tianeensis* mitochondrial and chloroplast-encoded protein genes was performed using the online tools Prep-Cp and Prep-Mt (<http://prep.unl.edu/>), with the parameter threshold set at 0.8 [81].

Codon preferences and phylogenetic tree construction

The coding DNA sequence (CDS) of the chloroplast and mitochondrial genomes were analyzed using CodonW v1.4.2 [82] and EMBOS (<https://www.bioinformatics.nl/embossexplorer/>) online software, respectively, and the sequences were counted in Excel software for GC_{all}, GC₁, GC₂, GC₃ (GC₁, GC₂, GC₃, representing the content of guanine and cytosine in positions 1, 2, and 3, respectively); GC₁₂, A₃, T₃, G₃, C₃ (representing the content of A, T, G, and C of the third position of the codon, respectively); the effective number of codons (ENC); and relative synonymous codon usage (RSCU). In Excel software, an ENC plot was constructed with GC values as the X-axis and ENC values as the Y-coordinate; GC₃ values were used as the horizontal coordinates and GC₁₂ values as the vertical coordinates to plot scatter plots; and a PR2 plot was generated with G₃/(G₃ + C₃) and A₃/(A₃ + T₃) values as the horizontal and vertical coordinates, respectively, and the standard deviation of the midpoint extension of the diagonal line. The RSCU values for codons, GC content, and phase relationship analysis plot for each codon were generated in RStudio [83]. The ENC values and CodonW v1.4.2 software were used to construct high- and low-expression gene libraries, and the RSCU values and Δ RSCU values were calculated (Δ RSCU = highly expressed gene RSCU minus weakly expressed gene RSCU). The determination of the optimal codon was then required to satisfy the conditions of both the high-expression codon and the high-frequency codon.

To elucidate the *C. tianeensis* phylogenetic relationships, the chloroplast and mitochondrial genomic

sequences of 23 and 18 plant species, respectively, were downloaded from the NCBI (<https://www.ncbi.nlm.nih.gov/>), and conserved protein-coding genes were extracted using Tbtool software. After a comparison using MAFFT7 [84], the phylogenetic tree was modeled using MEGAX [85] with manual correction, and the best maximum likelihood (ML) method was selected. The phylogenetic tree was subsequently constructed in IQ-TREE v2.2.0, and the self-expansion support was set to 1000 [86]. The optimal model was identified using MrModeltest v2.3, and a Bayesian inference (BI) phylogenetic tree was subsequently reconstructed using MrBayes v3.2.7 [87]. The phylogenetic tree topology was analyzed. Finally, the phylogenetic tree was landscaped using the online tool iTOL v4 (<https://itol.embl.de/>) [88].

Mitochondrial genome and chloroplast genome fragment exchange

The protein-coding and tRNA genes transferred from chloroplasts to mitochondria were identified and tested for homology using BLASTN and LASTZ software [89]. Finally, mitochondrial and chloroplast colocalization were mapped in RStudio.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12864-026-12522-3>.

Supplementary Material 1.
Supplementary Material 2.
Supplementary Material 3.
Supplementary Material 4.
Supplementary Material 5.

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Authors' contributions

ZR and ZL designed the study; XX, JX and MA assembled, annotated and analyzed the organelle genomes; ZG and WG collected the sample; ZR, XX and ZL helped analyzed the data; ZR drafted the manuscript; ZL revised the manuscript. All authors read and approved the final manuscript.

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Data availability

The genome data that supported the findings of this study are openly available in GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide/PP187689,PP727208>).

Declarations

Ethics approval and consent to participate

All materials used in this study comply with international and national legal standards. The collected species material does not pose a threat to other

species, and the collection of the species is recognized by the relevant authorities.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

- Carraretto L, Teardo E, Checchetto V, Finazzi G, Uozumi N, Szabo I. Ion channels in plant bioenergetic organelles, chloroplasts and mitochondria: from molecular identification to function. *Mol Plant*. 2016;9(3):371–95. <https://doi.org/10.1016/j.molp.2015.12.004>.
- Liere K, Weihe A, Börner T. The transcription machineries of plant mitochondria and chloroplasts: composition, function, and regulation. *J Plant Physiol*. 2011;168(12):1345–60. <https://doi.org/10.1016/j.jplph.2011.01.005>.
- Kersey PJ. Plant genome sequences: past, present, future. *Curr Opin Plant Biol*. 2019;48:1–8. <https://doi.org/10.1016/j.pbi.2018.11.001>.
- Cui HN, Ding Z, Zhu QL, Wu Y, Qiu BY, Gao P. Comparative analysis of nuclear, chloroplast, and mitochondrial genomes of watermelon and melon provides evidence of gene transfer. *Sci Rep*. 2021;11:1595. <https://doi.org/10.1038/s41598-020-80149-9>.
- Raghavendra AS, Padmasree K, Saradadevi K. Interdependence of photosynthesis and respiration in plant cells: interactions between chloroplasts and mitochondria. *Plant Sci*. 1994;97(1):1–14. [https://doi.org/10.1016/0168-9452\(94\)90101-5](https://doi.org/10.1016/0168-9452(94)90101-5).
- Li GL, Zhang H, Lin ZM, Li HW, Xu GC, Xu YQ, Ji RC, Luo WB, Qiu YX, Qiu SX, Tang H. Comparative analysis of chloroplast and mitochondrial genomes of sweet potato provides evidence of gene transfer. *Sci Rep*. 2024;14:4547. <https://doi.org/10.1038/s41598-024-55150-1>.
- Wolf PG, Sessa EB, Marchant DB, Li FW, Rothfels CJ, Sige EM, et al. An exploration into fern genome space. *Genome Biology Evol*. 2015;7(9):2533–44. <https://doi.org/10.1093/gbe/evl163>.
- Hao JJ, Jia XH, Yu JW, Deng SZ. Direct visualization of horizontal gene transfer in cotton plants. *J Heredity*. 2014;105(6):928–30. <https://doi.org/10.1093/jhered/esu052>.
- Budar F, Roux C. The role of organelle genomes in plant adaptation: time to get to work! *Plant Signal Behav*. 2011;6(5):654–9. <https://doi.org/10.4161/psb.6.5.14524>.
- Krupinska K, Sato K, Vothknecht UC. Genome communication in plants mediated by organelle-nucleus-located proteins. *Philosophical Trans Royal Soc B: Biol Sci*. 2020;375(1802):20190397. <https://doi.org/10.1098/rstb.2019.0397>.
- Zhang HD, Ren SX. *Flora of China*. Beijing: Science Press. 1998;49(3):101–112.
- Liang SY. The world list of *Camellia*. *Guangxi Forestry Sci*. 2007;(04):221–223. <https://doi.org/10.19692/j.cnki.gfs.2007.04.013>.
- Huang XC. Overview of the development and utilization of *Camellia nitidissima* and prospect prediction. *Chin J Inf Traditional Chin Med*. 1994;(06):10–11.
- Xia X, Huang JX, Wang ZP, Wang Q, Pan LG. Studies on the hypoglycemic effect and acute toxicity of *Camellia nitidissima* leaves. *Lishizhen Med Materia Med Res*. 2013;24(05):1281–2.
- Huang YL, Chen YY, Wen YX, Li DP, Liang RG, Wei X. Effects of the extracts from *Camellia nitidissima* leaves on blood lipids. *Lishizhen Med Materia Med Res*. 2009;20(04):776–7.
- Wang ZL, Guo YJ, Zhu YY, Chen L, Wu T, Liu DH, Huang BS, Du HZ. Active fractions of *Camellia nitidissima* inhibit non-small cell lung cancer via suppressing epidermal growth factor receptor. *China J Chin Materia Med*. 2021;46(20):5362–71. <https://doi.org/10.19540/j.cnki.cjmm.20210628.701>.
- Gao MZ, Tang JR, Deng J, Cao CW, Zhang YJ, Chai SF, Zhao P, Kan H, Liu Y. Application of polyphenolic compound-based HPLC fingerprint in Chinese golden camellias (*Camellia* sect. *Chrysanthus*). *Food Control*. 2024;161:110414. <https://doi.org/10.1016/j.foodcont.2024.110414>.
- Liu JX, Jiang HD, Huang Y, Zhong LS, Xu Q, Yang QG, Liu SY, Wei X, Liang Y, Chai SF. Combined analysis of metagenome and transcriptome revealed the adaptive mechanism of different golden. *Front Plant Sci*. 2023;14:1180472. <https://doi.org/10.3389/fpls.2023.1180472>.
- Gao YQ, Lin YL, Lai ZX. Cloning and expression of PPO gene during somatic embryogenesis in *Camellia nitidissima* Chi. *J Fujian Agric Forestry Univ (Natural Sci Edition)*. 2014;43(06):602–608.
- Yan F, Qu D, Ji PB, Li XS, Xi LJ. Non-targeted metabolomic characterization of metabolites during the fermentation of 'Golden flower' *Eucommia ulmoides* Leaf Tea. *Food Sci*. 2023;44(10):300–309.
- Liang SY, Luo YT. A new species of *Camellia sinensis* from China. *Guangxi Forestry Sci*. 1995;24(02):83–85. <https://doi.org/10.19692/j.cnki.gfs>.
- Liu HX, Qin L, Chen YL, Xu SY, Zhou XW, Zhu YL, Li B. The complete mitochondrial genome of *Camellia nitidissima* (Theaceae). *Mitochondrial DNA Part B*. 2023;8(5):565–569. <https://doi.org/10.1080/23802359.2023.2209211>.
- Wei SJ, Liufu YQ, Zheng HW, Chen HL, Lai YC, Liu Y, Ye QQ, Tang SQ. Using phylogenomics to untangle the taxonomic incongruence of yellow-flowered *Camellia* species (Theaceae) in China. *J Syst Evol*. 2023;61:748–763. <https://doi.org/10.1111/jse.12915>.
- Xie DZ, Ya ZG, Han JY, Wei Y, Wei L. Study of distribution and protection strategies of *Camellia tianeensis*. *J Green Sci Technol*. 2014;(04):89–91.
- Su FB, Feng LX, Huang HH, Luo QG, Xu RR, Lin H, Li RZ, Li S. Preliminary study of the selection of superior individuals from late blooming *Camellia nitidissima* Chi. In: *tian'e*. J Hechi Univ. 2017;37(05):12–6.
- Luo QG, Shu FB, Feng LX, Huang HH, Su BC, Li S, Mai KL. Study on the effect of fertilization on the growth of a high crown and the total flavonoid content of *Camellia tianeensis*. *J Green Sci Technol*. 2021;23(07):52–4. <https://doi.org/10.16663/j.cnki.lskj.2021.07.020>.
- Xu YT, Su FB, Feng LX, Yang CS, Huang ZX, He HJ, Su BC. High-yield cultivation techniques of *Camellia tianeensis* in forests. *J Smart Agric*. 2022;2(11):49–51. <https://doi.org/10.20028/jzhnydk.2022.11.015>.
- Xu Z, Zhang R, Yang M, Law YS, Sun F, Hon NL, Ngai SM, Lim BL. A balance between the activities of chloroplasts and mitochondria is crucial for optimal plant growth. *Antioxid (Basel)*. 2021;10(6):935. <https://doi.org/10.3390/antiox10060935>.
- Igamberdiev AU, Bykova NV. Mitochondria in photosynthetic cells: coordinating redox control and energy balance. *Plant Physiol*. 2023;191(4):2104–19. <https://doi.org/10.1093/plphys/kiac541>.
- Van Dingenen J, Wuyts N, De Rycke R, Inzé D. Plants grow with a little help from their organelle friends. *J Experimental Bot*. 2016;67:6267–81. <https://doi.org/10.1093/jxb/erw399>.
- Allen JF. Why chloroplasts and mitochondria retain their own genomes and genetic systems: collocation for redox regulation of gene expression. *Proc Natl Acad Sci*. 2015;112:10231–8. <https://doi.org/10.1073/pnas.1500012112>.
- Pring DR, Levings CS, Hu WL, Timothy DH. Unique DNA associated with mitochondria in the "S"-type cytoplasm of male-sterile maize. *Proc Natl Acad Sci United States Am*. 1997;74:2904–8. <https://doi.org/10.1073/pnas.74.7.2904>.
- Lu G, Zhang K, Que Y, Li Y. Assembly and analysis of the first complete mitochondrial genome of *Punica granatum* and the gene transfer from chloroplast genome. *Front Plant Sci*. 2023;14:1132551. <https://doi.org/10.3389/fpls.2023.1132551>.
- Tang P, Ni Y, Li J, Lu Q, Liu C, Guo J. The complete mitochondrial genome of *Paonia lactiflora* Pall. (Saxifragales: Paeoniaceae): evidence of gene transfer from chloroplast to mitochondrial genome. *Genes*. 2024;15:239. <https://doi.org/10.3390/genes15020239>.
- Alzahrani D, Albokhari E, Yaradua S, Abba A. Complete chloroplast genome sequence of *dipterygium glaucum* and *cleome chrysantha* and other cleomeaceae species, comparative analysis and phylogenetic relationships. *Saudi J Biol Sci*. 2021;28(4):106–121. <https://doi.org/10.1016/j.sjbs.2021.01.049>.
- Liao XF, Zhao YH, Kong XJ, Khan A, Zhou B, Liu DM, Kashif MH, Chen P, Wang H, Zhou RY. Complete sequence of Kenaf (*Hibiscus cannabinus*) mitochondrial genome and comparative analysis with the mitochondrial genomes of other plants. *Sci Rep*. 2018;8:12714. <https://doi.org/10.1038/s41598-018-30297-w>.
- Kubo T, Newton KJ. Angiosperm mitochondrial genomes and mutations. *Mitochondrion*. 2008;8:5–14. <https://doi.org/10.1016/j.mito.2007>.
- Gualberto JM, Newton KJ. Plant mitochondrial genomes: dynamics and mechanisms of mutation. *Annual Rev Plant Biology*. 2017;68:225–252. <https://doi.org/10.1146/annurev-arplant-043015-112232>.
- Sloan DB, Wu Z. History of plastid DNA insertions reveals weak deletion and AT mutation biases in angiosperm mitochondrial genomes. *Genome Biology Evol*. 2014;6:3210–21. <https://doi.org/10.1093/gbe/evu253>.
- Guo WH, Zhu AD, Fan WS, Mower JP. Complete mitochondrial genomes from the ferns *Ophioglossum californicum* and *Psilotum nudum* are highly repetitive with the largest organellar introns. *New Phytol*. 2016;213(9):18–31. <https://doi.org/10.1111/nph.14135>.

41. Arrieta-Montiel MP, Mackenzie SA. Plant mitochondrial genomes and recombination. In: Kempken, F (eds) Plant mitochondria. New York: Springer, pp 65–82.
42. Sloan DB. One ring to rule them all? Genome sequencing provides new insights into the 'master circle' model of plant mitochondrial DNA structure. New Phytology. 2013;200:978–85. <https://doi.org/10.1111/nph.12395>.
43. Chevigny N, Schatz-Daas D, Lotfi F, Gualberto JM. DNA repair and the stability of the plant mitochondrial genome. Int J Mol Sci. 2020;21:328. <https://doi.org/10.3390/ijms21010328>.
44. Zardoya R. Recent advances in understanding mitochondrial genome diversity. F1000Research. 2020;9:270. <https://doi.org/10.12688/f1000research.21490.1>.
45. Zhu M, Feng P, Ping J, Li J, Su Y, Wang T. Phylogenetic significance of the characteristics of simple sequence repeats at the genus level based on the complete Chloroplast genome sequences of Cyatheaaceae. Ecol Evol. 2021;11:14327–14340. <https://doi.org/10.1002/ece3.8151>.
46. Bi CW, Paterson AH, Wang XL, Xu YQ, Wu DY, Qu YS, Jiang AN, Ye QL, Ye N. Analysis of the complete mitochondrial genome sequence of the diploid cotton *Gossypium raimondii* by comparative genomics approaches. BioMed Res Int. 2016;2016:1–18. <https://doi.org/10.1155/2019/9691253>.
47. He P, Xiao GH, Liu H, Zhang LH, Zhao L, Tang MJ, Huang S, An YJ, Yu JN. Two pivotal RNA editing sites in the mitochondrial *atp1m*RNA are required for ATP synthase to produce sufficient ATP for cotton fiber cell elongation. New Phytol. 2018;18(3):167–182. <https://doi.org/10.1111/nph.14999>.
48. Yang YF, Zhu GN, Li R, Yan SJ, Zhu BZ, Tian HQ, Luo YB, Zhu HL. The RNA editing factor SIOORM4 is required for normal fruit ripening in tomato. Plant Physiol. 2017;175(4):1690–1702. <https://doi.org/10.1104/pp.17.01265>.
49. Unseld M, Marienfeld JR, Brandt P, Brennicke A. The mitochondrial genome of *Arabidopsis thaliana* contains 57 genes in 366,924 nucleotides. Nat Genet. 1997;15(1):57–61. <https://doi.org/10.1038/ng0197-57>.
50. Notsu Y, Masood S, Nishikawa T, Kubo N, Akiduki G, Nakazono M, Hiral A, Kad-owaki K. The complete sequence of the rice (*Oryza sativa* L.) mitochondrial genome: frequent DNA sequence acquisition and loss during the evolution off lowering plants. Mol Genet Genomics. 2002;268(4):434–445. <https://doi.org/10.1007/s00438-002-0767-1>.
51. He P, Xiao G, Liu H, Zhang L, Zhao L, Tang M, Huang S, An Y, Yu J. Two pivotal RNA editing sites in the mitochondrial *atp1* mRNA are required for ATP synthase to produce sufficient ATP for cotton fiber cell elongation. New Phytology. 2018;218:167–182. <https://doi.org/10.1111/nph.14999>.
52. Giegé P, Brennicke A. RNA editing in Arabidopsis mitochondria effects 441 C to U changes ORFs. PNAS. 1999;96:15324–15329. <https://doi.org/10.1073/pnas.96.26.15324>.
53. Chen Y, He XX, Priyadarshani SN, Wang Y, Ye L, Shi C, Ye KZ, Zhou Q, Luo ZQ, Deng F, Cao L, Zheng P, Aslam M, Qin Y. Assembly and comparative analysis of the complete mitochondrial genome of *Suaeda glauca*. BMC Genomics. 2021;22(1):167. <https://doi.org/10.1186/s12864-021-07490-9>.
54. Li L, Hu Y, He M, Zhang B, Wu W, Cai P, Huo D, Hong YC. Comparative chloroplast genomes: insights into the evolution of the chloroplast genome of *Camellia sinensis* and the phylogeny of *Camellia*. BMC Genomics. 2021;22:138. <https://doi.org/10.1186/s12864-021-07427-2>.
55. Li L, Li X, Liu Y, Li JD, Zhen XY, Huang Y, Ye JH, Li F. Comparative analysis of the complete mitogenomes of *Camellia sinensis* var. *sinensis* and *C. sinensis* var. *assamica* provide insights into evolution and phylogeny relationship. Front Plant Sci. 2024;15:1396389. <https://doi.org/10.3389/fpls.2024.1396389>.
56. Wang B, Yuan J, Liu J, Jin L, Chen JQ. Codon usage bias and determining forces in green plant mitochondrial genomes. J Integr Plant Biology. 2011;53(4):324–334. <https://doi.org/10.1111/j.1744-7909.2011.01033.x>.
57. Zhou M, Long W, Li X. Patterns of synonymous codon usage bias in chloroplast genomes of seed plants. Forestry Stud China. 2008;10:235–242. <https://doi.org/10.1007/s11632-008-0047-1>.
58. Suzuki H, Morton BR. Codon adaptation of plastid genes. PLoS ONE. 2016;11:e0154306. <https://doi.org/10.1371/journal.pone.0154306>.
59. Wang Y, Jiang D, Guo K, Zhao L, Meng FF, Xiao JL, Niu Y, Sun YL. Comparative analysis of codon usage patterns in Chloroplast genomes of ten *Epimedium* species. BMC Genomic Data. 2023;24:3. <https://doi.org/10.1186/s12863-023-01104-x>.
60. Liu Y, Xue N, Xu C, Wang YH, Huang XN, Sun R, Yang XY, Zhang J, Sun JH, Zhou SL. Species concept of golden flower *camellias* in China. BMC Plant Biol. 2025;25:1010. <https://doi.org/10.1186/s12870-025-07067-8>.
61. Li Z, Ran Z, Xiao X, Yan C, Xu J, Tang M, An MT. Comparative analysis of the whole mitochondrial genomes of four species in sect. *Chrysanthra* (*Camellia* L.), endemic taxa in China. BMC Plant Biol. 2024;24:955. <https://doi.org/10.1186/s12870-024-05673-6>.
62. Wei SJ, Liufu YQ, Zheng HW, Chen HL, Lai YC, Liu Y, Ye QQ, Tang SQ. Using phylogenomics to untangle the taxonomic incongruence of yellow-flowered *Camellia* species (Theaceae) in China. J Syst Evol. 2023;61:748–63. <https://doi.org/10.1111/jse.12915>.
63. Chevigny N, Schatz-Daas D, Lotfi F, Gualberto JM. DNA repair and the stability of the plant mitochondrial genome. Int J Mol Sci. 2020;21(1):328. <https://doi.org/10.3390/ijms21010328>.
64. Ni Y, Li JL, Chen HM, Yue JW, Chen PH, Liu C. Comparative analysis of the Chloroplast and mitochondrial genomes of *Saposhnikovia divaricata* revealed the possible transfer of plastome repeat regions into the mitogenome. BMC Genomics. 2022;23:570. <https://doi.org/10.1186/s12864-022-08821-0>.
65. Nam NN, Thi NA, Do HK. New insights into the diversity of mitochondrial plastid DNA. Genome Biology Evol. 2024;16(9):evae184. <https://doi.org/10.1093/gbe/evae184>.
66. Wang D, Rousseau-Gueutin M, Timmis JN. Plastid sequences contribute to some plant mitochondrial genes. Mol Biology Evol. 2012;29(7):1707–1711. <https://doi.org/10.1093/molbev/mss016>.
67. Mower JP, Sloan DB, Alverson AJ. Plant mitochondrial genome diversity: the genomes revolution. 2012;1:123–44. https://doi.org/10.1007/978-3-7091-1130-7_9.
68. Hoffmann M, Kuhn J, Däschner K, Binder S. The RNA world of plant mitochondria. Progress Nucleic Acid Res Mol Biology. 2001;70:119–154. [https://doi.org/10.1016/S0079-6603\(01\)70015-3](https://doi.org/10.1016/S0079-6603(01)70015-3).
69. Park S, Park SJ. Intrageneric structural variation in organelle genomes from the genus *Dystaenia* (Apiaceae): genome rearrangement and mitochondrion-to-plastid DNA transfer. Front Plant Sci. 2023;14:1283292. <https://doi.org/10.3389/fpls.2023.1283292>.
70. Smith DR. Mitochondrion-to-plastid DNA transfer: it happens. New Phytol. 2014;202(3):736–738. <https://doi.org/10.1111/nph.12704>.
71. Straub SCK, Cronn R, Edwards C, Fishbein M, Liston A. Horizontal transfer of DNA from the mitochondrial to the plastid genome and its subsequent evolution in milkweeds (Apocynaceae). Genome Biology Evol. 2013;5(10):1872–1885. <https://doi.org/10.1093/gbe/evt140>.
72. Pahlich E, Gerliz C. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemistry. 1980;19(1):11–3.
73. Jin JJ, Yu WB, Yang JB, Song Y, dePamphilis W, Yi C, Li TS. GetOrganelle: a fast and versatile toolkit for accurate de Novo assembly of organelle genomes. Genome Biol. 2020;21:241. <https://doi.org/10.1186/s13059-020-02154-5>.
74. Koren S, Walenz BP, Berlin K, Miller JR, Bergman NH, Phillippy AM. Canu: scalable and accurate long-read assembly via adaptive k-mer weighting and repeat separation. Genome Res. 2017;27:722–36. <https://doi.org/10.1101/gr215087>.
75. Tillich M, Lehwark P, Pellizzer T, Ulbricht-Jones ES, Fischer A, Bock R, Greiner S. GeSeq – versatile and accurate annotation of organelle genomes. Nucleic Acids Res. 2017;45(1):W6–W11. <https://doi.org/10.1093/nar/gkx391>.
76. Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. Basic local alignment search tool. J Mol Biology. 1990;215(3):403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2).
77. Greiner S, Lehwark P, Bock R. OrganellarGenomeDRAW (OGDRAW) version 1.3.1: expanded toolkit for the graphical visualization of organellar genomes. Nucleic Acids Res. 2019;47:W59–W64. <https://doi.org/10.1093/nar/gkz238>.
78. Beier S, Thiel T, Munch T, Scholz U, Mascher M. MISA-web: a web server for microsatellite prediction. Bioinformatics. 2017;33(16):2583–5. <https://doi.org/10.1093/bioinformatics/btx198>.
79. Ran ZH, Li Z, Xiao X, An MT, Yan C. Complete Chloroplast genomes of 13 species of sect. *Tuberculata* Chang (*Camellia* L.): genomic features, comparative analysis, and phylogenetic relationships. BMC Genomics. 2024;25:108. <https://doi.org/10.1186/s12864-024-09982-w>.
80. Kurtz S, Choudhuri JV, Ohlebusch E, Schleiermacher C, Stoye J, Giegerich R. REPuter: the manifold applications of repeat analysis on a genomic scale. Nucleic Acids Res. 2001;29(22):4633–42. <https://doi.org/10.1093/nar/29.22.4633>.
81. Mower JP. The PREP suite: predictive RNA editors for plant mitochondrial genes, Chloroplast genes and user-defined alignments. Nucleic Acids Res. 2009;37:W253–9. <https://doi.org/10.1093/nar/gkp337>.
82. Shields DC, Sharp PM. Synonymous codon usage in *Bacillus subtilis* reflects both translational selection and mutational biases. Nucleic Acids Res. 1987;15(19):8023–40. <https://doi.org/10.1093/nar/15.19.8023>.
83. Racine JS, RStudio. A Platform-Independent IDE for R and Sweave. J Appl Econom. 2012;27:167–72. <https://doi.org/10.1002/jae.1278>.

84. Katoh K, Standley DM. MAFFT: iterative refinement and additional methods. *Methods Mol Biol.* 2014;1079:131–46. https://doi.org/10.1007/978-1-62703-646-7_8.
85. Kumar S, Stecher G, Li M, Knyaz C, Tamura K. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution.* 2018;35(6):1547–1549. <https://doi.org/10.1093/molbev/msy096>.
86. Trifinopoulos J, Nguyen LT, Von HA, Minh BQ. W-IQTREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Res.* 2016;44(W1):232–5. <https://doi.org/10.1093/nar/gkw256>.
87. Huelsenbeck JP, Ronquist F. MRBAYES: bayesian inference of phylogenetic trees. *Bioinformatics.* 2001;17(8):754–5. <https://doi.org/10.1093/bioinformatics/17.8.754>.
88. Letunic I, Bork P. Interactive tree of life (iTOL) v5: an online tool for phylogenetic tree display and annotation. *Nucleic Acids Res.* 2021;49(W1):293–6. <https://doi.org/10.1093/nar/gkab301>.
89. Chen Y, Ye WC, Zhang YD, Xu YS. High speed BLASTN: an accelerated Mega-BLAST search tool. *Nucleic Acids Res.* 2015;43(16):7762–7768. <https://doi.org/10.1093/nar/gkv784>.

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