

Comparative analysis of organelle genomes in three *Terminalia* species reveals structure evolution and phylogenetic position

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Abstract

Background

Plant organelle genomes are critical for evolutionary biology research, yet their characteristics in the *Terminalia* genus (Combretaceae, ~ 200 tropical species of which some possess medicinal and edible value) remain unstudied. This study systematically analyzes the mitochondrial genomes (mitogenomes) and chloroplast genomes (plastomes) of three *Terminalia* species (*T. chebula*, *T. franchetii*, *T. intricata*).

Results

Using high-throughput sequencing, we successfully obtained sequences of plastomes and mitogenomes for three plants, enabling comparative and evolutionary genomic analysis. Plastomes of the three species shared a typical quadripartite structure, with similar sizes (159,700–159,971 bp) and gene compositions (103–107 genes), but differed in specific regions. In contrast, mitogenomes showed significant structural size variation (350,904–365,711 bp), with *T. chebula* and *T. intricata* having three circular and one linear molecule, and *T. franchetii* has two linear molecules, reflecting extensive recombination. Ka/Ks analysis indicated positive selection on mitogenome genes (e.g., *rps1*, *nad4*) linked to adaptation. RNA editing (all C-to-U) enhanced protein hydrophobicity. Phylogenetic trees clarified *Terminalia*'s position.

Conclusions

This study provides crucial genomic data for phylogenetic research and molecular ecology within the *Terminalia*, holding significant value for future research.

Background

Terminalia belongs to the Combretaceae family, comprising approximately 200 species widely distributed across tropical and subtropical regions, particularly in Asia, Africa, and Australia. Most *Terminalia* species are deciduous or evergreen trees or shrubs, commonly found in forests, riverbanks, and wetlands [1]. Numerous *Terminalia* plants have extensive applications in traditional ethnopharmacology, serving as herbal remedies or formulations for treating various ailments such as headaches, fever, pneumonia, influenza, geriatric diseases, and cancer [2–4]. Additionally, they are employed to alleviate symptoms including memory loss, abdominal pain, back pain, cough, colds, conjunctivitis, diarrhea, heart disease, leprosy, sexually transmitted diseases, and urinary tract infections [5–7]. Research indicates these plants exhibit diverse biological activities, encompassing antibacterial, antifungal, anti-inflammatory, antiviral, antiretroviral, and antioxidant properties [8–10]. Current research on *Terminalia* primarily focuses on pharmacological effects [11], active constituents [12, 13], processing methods, and molecular identification. However, no studies have reported on its mitochondrial genome

(mitogenome) or chloroplast genome (plastome). Unraveling its mitogenomes and plastomes is crucial for the phylogenetic studies of *Terminalia*, providing vital clues for species origins, evolutionary relationships, and taxonomy.

With the advancement of high-throughput sequencing, the genomes of organelles from an increasing number of plants have been sequenced, offering significant data for studying plant physiological functions, evolutionary relationships, and germplasm resource conservation. Both mitochondria and chloroplasts are believed to have evolved from ancient free-living bacteria through endosymbiosis [14]. Mitochondria, serving as the “powerhouse” of the cell, generate ATP through oxidative phosphorylation and function as the central hub of plant energy metabolism [15]. Compared to animal mitogenomes, plant mitogenomes contain not only genes related to mitochondrial function but also repetitive sequences. While plastomes typically maintain a relatively uniform circular structure [16, 17], mitogenomes are characterized by a high incidence of repetitive sequences and exhibit significant structural heterogeneity, including polycyclic [18], linear [19], and branched forms [20]. Studying plant mitogenomes can reveal mechanisms of plant energy metabolism [21], providing new theoretical foundations for agricultural production, such as enhancing plant stress resistance and advancing breeding efforts [22].

In this study, we successfully assembled the plastomes and mitogenomes of three previously unreported *Terminalia* species: *Terminalia chebula*, *Terminalia franchetii*, and *Terminalia intricata*. We analyzed the organelle genomes of these *Terminalia* species by comparing the newly obtained sequences with existing organelle genome data. Analyses included GC content, codon usage bias, repetitive sequences, Ka/Ks ratios, prediction of RNA editing events, and nucleotide polymorphism analysis. Homologous sequences found in both chloroplast and mitogenomes were also analyzed. Furthermore, maximum likelihood phylogenetic trees were constructed using PCGs from 17 mitogenomes and 18 plastomes, respectively. We reconstructed phylogenetic relationships within the *Terminalia*, exploring connections and taxonomic boundaries between different species groups, and identified key regions of genetic variation. These findings will provide important references and valuable insights for molecular marker development and phylogenetic studies in the *Terminalia*.

Results

Genome organization of three *Terminalia* organelles

The plastomes sizes of *T. chebula*, *T. franchetii*, and *T. intricata* were 159,915 bp, 159,700 bp, and 159,971 bp, respectively (Figure 1). All three genomes exhibited a typical quadripartite structure, consisting of a pair of inverted repeats (IRs) with lengths of 26,339 bp in *T. chebula*, 26,278 bp in *T. franchetii*, and 26,345 bp in *T. intricata*. The small single-copy region (18,888 bp in *T. chebula*, 18,734 bp in *T. franchetii*, and 18,908bp in *T. intricata*) and a large single-copy region (71,568 bp in *T. chebula*, 71,290 bp in *T. franchetii*, and 71,600 bp in *T. intricata*). In the plastomes of *T. chebula*, *T. franchetii*, and *T. intricata*, 76, 76, and 73

PCGs were annotated, respectively, along with 27, 26, and 26 tRNA genes. All three species contained 4 rRNA genes.

Interestingly, the mitogenome structures of the three *Terminalia* species showed significant differences and were highly complex. The mitogenomes structure of *T. chebula* and *T. intricata* consisted of three circular molecules and one linear molecule, while *T. franchetii* had two linear molecules. (Figure 1). The sizes of the mitogenomes for *T. chebula*, *T. franchetii*, and *T. intricata* were 354,989 bp, 365,711 bp, and 350,904 bp, respectively. In these genomes, 35, 34, and 38 PCGs were annotated for *T. chebula*, *T. franchetii*, and *T. intricata*, respectively. Additionally, *T. chebula* contained 17 tRNA genes, *T. franchetii* had 18, and *T. intricata* had 17. The rRNA gene counts were 3 for *T. chebula*, 4 for *T. franchetii*, and 3 for *T. intricata*. The GC contents of the mitogenomes for *T. chebula*, *T. franchetii*, and *T. intricata* were 45.5%, 44.3%, and 44.7%, respectively.

The plastomes of the three *Terminalia* species exhibited a circular structure, with sizes ranging from 159,700bp to 159,971 bp, showing a maximum size difference of 271 bp. The number of genes in the plastomes varied between 106 and 108 across species. In contrast, the mitogenomes displayed significant structural variations, with sizes ranging from 350,904 bp to 365,711 bp, resulting in a maximum size difference of 14,807 bp. The number of genes in the mitogenomes varied between 55 and 58 across species (Table 1). These results indicate that the mitogenomes exhibit substantial fluctuations in structure, genome size, and GC content, whereas the plastomes appear to be more conserved throughout evolution (Additional file 1).

Table 1 Genomic characteristics of three *Terminalia* species

Species	Genome Type	Genome Size (bp)	Protein Genes	tRNA Genes	rRNA Genes	Total Genes
<i>T. chebula</i>	plastome	159,915	76	27	4	107
<i>T. franchetii</i>	plastome	159,700	76	26	4	106
<i>T. intricata</i>	plastome	159,971	73	26	4	103
<i>T. chebula</i>	mitogenome	354,989	35	17	3	55
<i>T. franchetii</i>	mitogenome	365,711	34	18	4	56
<i>T. intricata</i>	mitogenome	350,904	38	17	3	58

Repeat sequence analysis of three *Terminalia* organelles

In the plastomes of *T. chebula*, *T. franchetii*, and *T. intricata*, 73, 70, and 70 simple sequence repeats (SSRs) were identified, respectively (Figure 2A). All SSRs in *T. chebula* were haploid, *T. franchetii* only contained one diploid SSR, while *T. intricata* had one diploid SSR and one triploid SSR, with no higher

ploidy detected. The plastomes of all three *Terminalia* species contained complementary, palindromic, forward, reverse, and tandem repeats, with tandem and palindromic repeats being the predominant types. Among these species, *T. chebula* exhibited the highest number of tandem repeats, with 41 in total.

In the mitogenomes of *T. chebula*, *T. franchetii*, and *T. intricata*, 57, 56, and 57 SSRs were identified, respectively. Among these, haploid repeats predominated, followed by diploid and triploid repeats, with no higher ploidy detected. The mitogenomes of three *Terminalia* species contained complementary, palindromic, forward, reverse, and tandem repeats. In *T. chebula*, forward (42.1%, 86 repeats) and palindromic (28.9%, 59 repeats) repeats were the most common. In *T. franchetii*, forward (41%, 41 repeats) and palindromic (38%, 38 repeats) repeats were also dominant. Notably, *T. franchetii* exhibited the highest number of tandem repeats among the three species, with 42 repeats. In *T. intricata*, forward (42.7%, 85 repeats) and palindromic (31.1%, 62 repeats) repeats were similarly predominant (Figure 2B).

In the plastomes and mitogenomes of the three *Terminalia* species, several types of repeat sequences were present, including complementary repeats, palindromic repeats, forward repeats, reverse repeats, and tandem repeats. The distribution of simple sequence repeats (SSRs) across the two types of genomes showed similarities, with haploid repeats predominating. Although diploid and triploid repeats were also found in the mitogenomes, haploid repeats formed the highest proportion (Additional file 2).

Codon usage analysis of three *Terminalia* organelles

This study compared the codon usage preferences in the mitochondrial and plastomes of *T. chebula*, *T. franchetii*, and *T. intricata*, and analyzed their relative synonymous codon usage frequencies (Figure 3A). Arginine and Leucine were the most frequently used amino acids in the organellar genomes of the three *Terminalia* species, accounting for 9.8% of mitogenomes and 9.6% of plastomes, respectively. In comparative studies of plastomes across species, the TTA codon exhibited a strong preference (2.12) in *T. chebula*, while AGA showed the highest codon usage preference in *T. franchetii* and *T. intricata*, with values of 1.9269 and 1.9988, respectively. Conversely, codons such as CTG and GCG exhibited significantly lower RSCU values across all three species, indicating their infrequent usage.

In the mitogenomes of the three *Terminalia* species, the ATG and TGG codons did not have synonymous codons, and their RSCU values were both 1 (Figure 3B). There were differences in codon usage preferences among the species. In *T. chebula*, the most preferred codon was GCT (1.57), followed by TTA (1.55), while the least preferred codon was GCG, with an RSCU value of 0.47. In contrast, *T. franchetii* and *T. intricata* showed highly consistent codon usage preferences, with the most commonly used codon being AGA, with RSCU values of 1.77 and 1.73, respectively. The lowest RSCU value for both species was CGT, with values of 0.59 and 0.56, respectively (Additional file 3).

RNA editing site analysis of mitogenomes

RNA editing involves the addition, deletion, or alteration of bases in the coding region of the transcribed RNA [23], and it occurs in all eukaryotes, including plants [24]. The results showed that 311, 364, and 349

RNA editing sites were predicted in mitogenomes of *T. chebula*, *T. franchetii*, and *T. intricata*, respectively, with all editing events involving a C-to-U base conversion (Additional file 4). This editing pattern is consistent with that observed in other plants. In all three species of the *Terminalia*, genes such as *mttB*, *rps4*, and *cob* have a higher number of editing sites, while genes like *atp8*, *atp9*, and *sdh3* have fewer editing sites. In the effective amino acid editing events of the three species, hydrophobic amino acids dominated, accounting for approximately 71.3% to 71.5%, while hydrophilic amino acids accounted for around 28.5%. The high-frequency codons were biased toward hydrophobic amino acid coding, with the codons for leucine (L) and phenylalanine (F) being more frequent. Specifically, UUA and UUC appeared frequently across the three species (Figure 4A).

Substitution rates of mitochondrial PCGs

Different species face varying ecological pressures during evolution, leading to genomic changes. The Ka/Ks ratio measures selection pressure on PCGs, helping infer species adaptation and evolutionary trajectories. When the Ka/Ks ratio is > 1 , genes are undergoing positive selection, conversely, $Ka/Ks < 1$ denotes negative selection, and $Ka/Ks = 1$ represents neutral selection. To calculate the selective pressure on mitogenomes PCGs in three species of *Terminalia*, we computed the Ka/Ks values for the PCGs of 37 mitogenomes (Additional file 5). The Ka/Ks values of most PCGs were found to be below 1, while genes like *nad4*, *rps1*, *rps4*, and *rps7* had Ka/Ks values exceeding 1 (Figure 4B).

Homology analysis of genome sequences

We searched for homologous sequences between the plastomes and mitogenomes in three *Terminalia* species to identify potential gene transfer events. We identified 17-26 homologous sequences between the plastomes and mitogenomes in the three species, with lengths ranging from 28bp to 7035bp (Figure 4C). Interestingly, we identified some complete plastid genome-derived PCGs in the mitogenomes, including *petB*, *petG*, *psaA*, *psbJ*, *petB*, *psbM*, *ycf2*, and *psb*, among others. Notably, *psbJ*, *psaA*, *petB*, and *petG* were shared by all three species.

Collinearity analysis of the mitogenomes

Mauve was used to analyze the synteny and rearrangements of the mitogenomes across the three species. The three genomes exhibited a large number of locally collinear blocks (LCBs) with consistent coloring, indicating that they share a substantial number of conserved gene segments, which reflects the close evolutionary relationship within the genus. These homologous regions (LCBs) had different relative positions, suggesting the presence of extensive rearrangements within the mitogenomes (Figure 5A).

Nucleotide polymorphism (Pi) analysis of organelle genomes

The Pi analysis was conducted on 77 plastome PCGs from five species of Combretaceae (*Terminalia chebula*, *Terminalia franchetii*, *Terminalia intricata*, *Terminalia phillyreifolia*, *Terminalia guyanensis*). The results revealed that among the 77 PCGs, gene *rp122* exhibited the highest Pi value (0.11406), followed by *rps19* (0.104353). In contrast, the lowest Pi values were observed for *ndhB* (0.009983). We also

performed the Pi analysis on 37 mitochondrial PCGs from three species of *Terminalia*, and the results revealed that the highest Pi value was observed for *rps10* (0.117162), followed by *nad9* (0.1079), while the lowest Pi values, both 0, were found for *rpl16* and *rpl19* (Figure S1. Additional file 6).

Expansion and contraction of the IR region

A comparative analysis of the IR/SSC boundary regions in the plastomes of 6 Combretaceae species revealed subtle differences at the IR/SSC junction. In this study, the *rps19* gene in *Lumnitzera racemosa*, *Lumnitzera littorea* spanned 106 bp of the LSC/IRb region, while in *Terminalia franchetii* and *Terminalia intricata* and *Terminalia chebula* it spanned 16-24 bp of the LSC/IRb region. In contrast, the *rps19* gene in *Laguncularia racemosa* was entirely located within the LSC region. Significant differences were observed at the IRb/SSC junction (JSB). It is noteworthy that the position of the *rpl2* gene in *Terminalia intricata* and *Terminalia chebula* differed significantly from that in other species. This difference may arise from the dynamic evolution of the plastome IR region boundaries. At this junction, only *Lumnitzera racemosa*, *Lumnitzera littorea*, and *Laguncularia racemosa* contained the *ycf1* gene, while the other 3 species lacked it. Additionally, the *ndhF* gene was located at the IRb/SSC junction. In *Lumnitzera racemosa*, *Lumnitzera littorea*, *Laguncularia racemosa*, and *Terminalia chebula*, 15-18 bp of the *ndhF* gene are located in the IRb region, while in *Terminalia franchetii* and *Terminalia intricata*, 70-75 bp were located in the IRb region. Notably, the *ycf1* gene spanned the SSC/IRa junction in all 6 species. The *psbA* and *trnH* genes were completely located in the LSC region (Figure 5B).

Phylogenetic analysis of the organelle genome

A phylogenetic tree of 17 angiosperm species from five orders was constructed by extracting mitogenome PCGs sequences, with *Vitis vinifera* as the outgroup (Figure 6A). *T. chebula* was confirmed as a species of the genus *Terminalia*, *T. intricata* clustering with *T. franchetii*. The phylogenetic tree shows that the bootstrap support values for most nodes were above 95%. The overall topology of the tree is consistent with the classification results of the Angiosperm Phylogeny Group IV (APG IV) system.

To clarify the phylogenetic position and evolutionary relationships of the Combretaceae family within the Myrtales order, a phylogenetic analysis was conducted using plastome sequences from eight species of Combretaceae and ten other plant species, with *R. solosa* from the Malpighiales as the outgroup. The results indicated that species within the *Terminalia* of Combretaceae exhibited a high degree of phylogenetic clustering, with strong branch support, revealing close genetic relationships among the species in this genus. *T. franchetii* and *T. intricata* were closely clustered in one group with a bootstrap support of 100%. The Onagraceae family, represented by *O. biennis* and *O. parviflora*, formed a separate clade, while the Lythraceae family, represented by *P. granatum*, appeared as an independent branch. The Myrtaceae family, which includes *A. costata*, *C. henryi*, *C. gummifera*, *E. aromaphloia*, *E. deglupta*, and *P. trunciflora*, formed a stable cluster. *R. stylosa* from the Rhizophoraceae family clustered separately within the order of the Combretaceae, displaying significant evolutionary divergence from Myrtales species. Furthermore, within the Myrtales, the Onagraceae family exhibited a closer phylogenetic relationship with the Lythraceae family (Figure 6B).

Discussion

With the advent of advanced sequencing technologies, and the successful assembly of an increasing number of genomes, the complexity of mitogenomes has become more evident [25]. The genome structure of mitochondria also exhibits diversity, including linear, circular, highly branched, and networked forms, with such diversity even observed within a single individual, possibly due to frequent recombination [26–28]. The earliest mitogenome sequencing from animals was performed on humans and *Drosophila*, where the genomes were found to be small, circular molecules with highly conserved sequences [29, 30]. As a result, it was once assumed that all mitogenomes were single, circular molecules. However, recent studies have shown that mitogenomes are not always single circular structures. For example, *Quercus acutissima* (Fagaceae) consists of one linear and two circular molecules [31]. *Colocasia esculenta* (Araceae) consists of five circular molecules [32], while *Echinacanthus longipes* (Acanthaceae) consists of two circular and three linear molecules [33]. The mitogenomes of three species in the *Terminalia* exhibit significant structural differences. The mitogenomes of *T. chebula* and *T. intricata* consist of three circular molecules and one linear molecule, while *T. franchetii* has two linear molecules. Mitogenomes in plants can show considerable variation between species. The size of plant mitogenomes also varies widely, typically ranging from 66 kb to 11,000 kb. The mitogenome sizes of the three *Terminalia* species fall between 350,904 and 354,989 bp. Studies have shown that plant mitogenomes can exhibit significant differences between species [34]. The structural and size variations of the mitogenomes in *Terminalia* species are considerable, which may be related to species evolution and phylogenetic affinity.

Furthermore, the plastomes of three *Terminalia* species possess a unique quadripartite structure, consisting of two IR regions, one LSC region, and one SSC region, which is similar to the plastomes structure of other angiosperms [35]. Meanwhile, GC content significantly affects amino acid composition and the structural integrity of genomes during evolutionary processes [36]. Our analysis of the GC content in the plastomes and mitogenomes of the three *Terminalia* species indicates that plastomes exhibit more stable GC content (36.8%-37.0%), while the mitogenomes show greater variability in GC content (44.3%-45.5%). This result supports the conclusion that GC content is highly conserved in higher plants. Interestingly, among the three *Terminalia* species, the plastome lengths of the three *Terminalia* showed a maximum size difference of 271 bp, which suggests that variability in cp genome size is closely related to phylogenetic relationships and evolutionary history [37].

RNA editing is a post-transcriptional process in which nucleotides within mRNA molecules are inserted, deleted, or substituted, resulting in changes to the genetic code [38]. Previous studies have shown that the number of editing sites and the gene with the highest number of editing sites differ across species. For example, there are 455 RNA editing sites in 37 genes in *Primulina hunanensis* [39], 460 RNA editing sites in 34 genes in *Glycyrrhiza glabra* [40], and 441 RNA editing sites in 36 genes in *Arabidopsis thaliana* [41]. In this study, we predicted the RNA editing sites of PCGs in the mitogenomes of three *Terminalia* species and identified 311–369 editing sites, all of which involve the conversion of (C) to (U). Further analysis indicates that these C-U editing events exhibited a significant preference for specific codon

positions, primarily concentrated at the first and second codon positions [42]. This process enhances the interspecies homogeneity of the mitochondrial proteome and promotes adaptive development in plants. Most RNA editing events in the three *Terminalia* species involve the conversion of amino acids to hydrophobic ones, which helps alter their physicochemical properties and enhance protein folding [43]. Therefore, widespread RNA editing leads to an increase in the number of hydrophobic amino acids, which may contribute to the translation of mRNA into polypeptides with the correct folded structure. This finding forms the structural basis for the specific functions of proteins [44].

The Ka/Ks ratio can reveal the evolutionary pathways of genes and their underlying genetic mechanisms [45]. We conducted Ka/Ks analysis on 34 shared mtDNA protein-coding genes (PCGs) across three *Terminalia* species. The results indicate signs of positive selection in *rps1*, *rps4*, *rps7*, and *nad4*. Specifically, *rps1*, *rps4*, and *rps7* may be associated with plant adaptation to environmental changes, while *nad4* is closely linked to mitochondrial energy metabolism. These findings likely reflect adaptive variation in redox reactions and environmental stress responses. As a valuable analytical tool, Ka/Ks analysis not only aids in understanding species adaptability and selective pressures but also offers new perspectives for assessing adaptive potential and studying genetic evolution [46].

A phylogenetic tree of mitochondrial and plastomes was constructed using maximum likelihood (ML) analysis. The results showed that the topology of the ML tree constructed with chloroplast PCGs was largely consistent with that of the ML tree constructed with mitochondrial PCGs. *T. chebula*, *T. franchetii*, and *T. intricata* were all classified within *Terminalia*, with *T. intricata* being a variety of *T. franchetii*, these two species showed a closer relationship. Due to the limited number of published mitogenomes for Myrtales, the mitogenomes tree encompasses a broader range of order-level taxa, reflecting evolutionary signals among distantly related groups. The overall structure of this mitochondrial DNA-based phylogeny is consistent with the latest classification of the Angiosperm Phylogeny Group (APG). In contrast, the plastomes tree focuses on interfamilial relationships within Myrtaceae. The organelle genomes of these three *Terminalia* species will provide valuable and important genetic information for further improving the phylogenetic resolution of angiosperms.

Conclusion

In this study, we successfully assembled the mitogenomes and plastomes of three *Terminalia* species, revealing unique branched conformations in the mitochondrial DNA structure. The results showed that the plastomes of the three *Terminalia* species were similar in GC content and genome size. The ka/ks ratio analysis of the mitogenomes indicated that genes *rps1*, *rps4*, *rps7*, and *nad4* are under positive selection. The presence of gene transfer and conserved syntenic blocks between the three *Terminalia* species reflects gene rearrangements and recombination, providing important genetic insights. RNA editing events revealed that most hydrophilic amino acids were converted to hydrophobic ones, enhancing the stability of protein structures. The construction of the phylogenetic tree deepens our understanding of the evolutionary relationships among *Terminalia* species, particularly highlighting the close relationship between *T. franchetii* and *T. intricata*. Overall, our findings suggest that organellar

genomic data can effectively reveal phylogenetic relationships between plants and can be applied to molecular marker development and genetic evolution studies.

Materials and Methods

Plant materials, DNA extraction and sequencing

Fresh leaves of *T. chebula* were collected from Longling County, Baoshan City, Yunnan Province, China (Sample location: 98°E, 24°N). This specimen was identified by Professor Li Guodong of Yunnan University of Chinese Medicine based on morphological characteristics. *T. franchetii* was collected from Baima Town, Miya County, Panzhihua City, Sichuan Province, China, with coordinates (Sample Location: 102.2°E, 27.0°N). *T. intricata* was collected from Dongwang Township, Shangri-La City, Diqing Tibetan Autonomous Prefecture, Yunnan Province, China (Sample location: 99.5°E, 28.5°N). The specimen was identified by P.R. Luo based on morphological characteristics. The leaves were immediately frozen in liquid nitrogen, and total DNA was extracted using a modified CTAB method. The high-quality DNA samples that passed the test were sent to Novogen Biotechnology Co. for second- and third-generation sequencing, respectively.

Selected high-quality DNA samples that passed the test (main band > 30kb); were randomly fragmented into 15-18kb segments using a G-Tube tube; enriched and purified using magnetic beads; damage repair and end repair was performed on the fragmented DNA; stem-loop sequencing adapters were ligated to both ends of the DNA fragments and exonucleases used to remove failed ligation fragments. The constructed library was then sequenced using the PacBio Revio/Sequel II/IIe platform.

The raw sequencing reads contained a dumbbell-shaped structure with adapters at both ends, referred to as Polymerase reads. The raw data was fragmented at the adapter sites, and the adapter sequences filtered out to obtain subreads. The subreads were filtered according to the standard "Filtering subreads by minimum length = 50". Based on the subreads, high-accuracy HiFi reads were generated using CCS software. All reads had a quality value greater than Q20.

Organelle genome assembly and annotation

The plastomes of *T. franchetii* and *T. intricata* were *de novo* assembled using GetOrganelle v1.7.5.3 [47]. Using PacBio HiFi sequencing data, the mitogenomes of three *Terminalia* species and the plastomes of *T. chebula* was assembled with PMAT v1.5.3 [48]. The assembly parameters were configured as follows: "-st HiFi -tp mt -ml 70 -mi 90". The mitogenomes was visualized using Bandage v0.8.1 [49].

The mitogenomes were annotated using IPMGA (<http://www.1kmpg.cn/ipmga/>), with RNA-seq data used to precisely correct 29 representative angiosperm mitogenomes sequences as the reference genome. Annotation errors for each mitogenome were manually corrected using Geneious Prime [50]. Additionally, the plastomes of *T. chebula*, *T. franchetii* and *T. intricata* were annotated using Geseq[51]. Finally, the organelle genome was visualised using OGDRAW [52].

Analysis of Repeat Elements

MISA (v2.1) (<https://webblast.ipk-gatersleben.de/misa/>), TRF (v4.09) (<https://tandem.bu.edu/trf/trf.unix.help.html>), and REPuter (<https://bibiserv.cebitec.uni-bielefeld.de/reputer/>) were used to identify simple sequence repeats (SSRs), tandem repeats, and dispersed repeats, respectively. The results were visualized using Excel (2021) software and the Circos package (v0.69.9).

Analysis of Codon Usage

The protein-coding sequences of mitogenomes and plastomes were extracted with Phylosuite(v1.1.16) [53]. To analyze the codon bias of the protein-coding genes within the mitogenomes, MEGA v7.0 was used [54], and the Relative Synonymous Codon Usage (RSCU) values were subsequently calculated.

Prediction of RNA editing sites

The RNA editing sites were predicted via PREPACT3 [55]. The analysis employed reference sequences from *Vitisvinifera* and *Millettia pinnata*. The predicted RNA editing sites were subsequently visualized using R (4.4.0) to facilitate interpretation and analysis of the results.

Homologous sequences identification

Homogeneous sequences between the plastomes and mitogenomes of three *Terminalia* were identified using BLAST (v2.16.0) [56], with parameters set to an identity greater than 90% and an e-value of less than $1e - 5$. We then analyzed the homologous sequence regions to determine the length, quantity, and gene type of the mitochondrial plastomes sequences (MTPTs). the results were visualized using the Circos package (v0.69.9) [57].

Substitution rates of PCGs

First, the mitogenomes of three *Terminalia* species were aligned using MAFFT (v7.427) [58]. Subsequently, the Ka/Ks ratio was calculated for each gene pair using the YN method in KaKs_Calculator (v2.0) [59]. The aggregated Ka/Ks ratios were visualized as box plots generated with the ggplot2 package in R.

Nucleotide diversity

Sequences of protein-coding genes (PCGs) from organelle genomes were aligned using MAFFT (v7.477) [60], while the Pi value for each gene was calculated using DnaSP (v5.0) [61].

Analysis of Plastomes Boundaries

Based on annotations, the plastome boundaries between the IR, LSC, and SSC regions were analyzed, and a schematic diagram was constructed using Irscope [62].

Collinearity Analysis and Phylogenetic Analysis

Mauve was employed to analyze homology and sequence rearrangements within the mitogenomes of three *Terminalia* species [63]. All conserved PCGs from mitogenomes and plastomes were extracted using Phylosuite [64] and aligned with MAFFT (v7.427) [65]. The results were then imported into MACSE for optimization. The optimal model was selected via ModelFinder (v2.2.2) [66]. Bayesian analysis was performed on the PCGs concatenated data matrix using MrBayes (v.3.2) [67]. The final phylogenetic tree was constructed in IQ-tree and visualized with iTOL [68] for aesthetic refinement.

Abbreviations

- NCBI National Center for Biotechnology Information.
- PCGs Protein-coding genes.
- RSCU Relative synonymous codon usage.
- SSRs Simple sequence repeats.
- cpDNA Plastomes.
- mtDNA Mitogenomes.
- MTPTs Mitochondrial plastid DNAs.
- Ka Nonsynonymous substitutions.
- Ks Synonymous substitutions.
- Pi Nucleotide Diversity

Declarations

Authorship contribution statement

Xingyu Liu: Data curation, Visualization, Writing – original draft& editing. Pengrui Luo: Data curation, Writing – review & editing, Resources, Validation. Yingmei Zou: Data curation, Writing – original draft, Validation. M. James C. Crabbe: Data curation, Visualization, Writing – original draft. Guodong Li: Conceptualization, Supervision, Writing – review & editing, Funding acquisition. Ticao Zhang: Conceptualization, Resources, Supervision, Writing – review & editing, Funding acquisition.

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Ethics approval and consent to participate

Not applicable. This study did not use animal or human materials. Our experimental research, including the collection of plant materials, complies with institutional, national, or international guidelines. The voucher specimen of *T. chebula* is deposited in the Herbarium of Yunnan University of Chinese Medicine, voucher numbers 2503. The voucher specimens of *T. franchetii* and *T. intricata* are deposited in the Kunming Institute of Botany Chinese Academy of Sciences. Voucher numbers 1651612 (*T. franchetii*) and 1651613 (*T. intricata*).

Consent for publication

Not applicable

Declaration of Competing Interest

We declare that we have no conflicts of interest.

Data availability

The dataset generated and analyzed by this graduate student has been submitted to the NCBI database. The current provisional accession number is SUB15777329. The final permanent accession number will be provided prior to the publication of the thesis.

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Figures

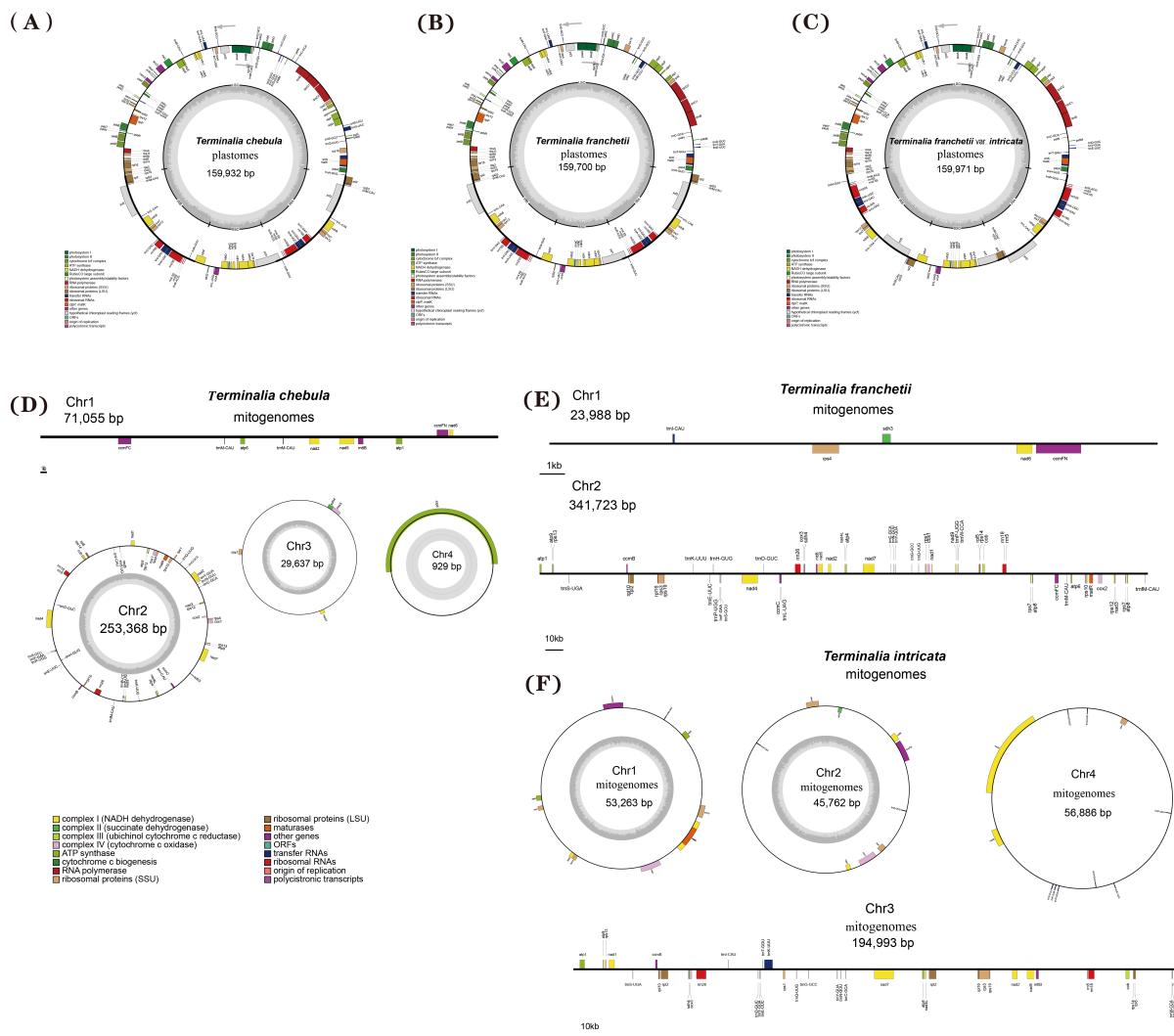


Figure 1

Genome maps of the plastomes of three *Terminalia* Species. (A-C) plastomes, (D-F) mitogenome

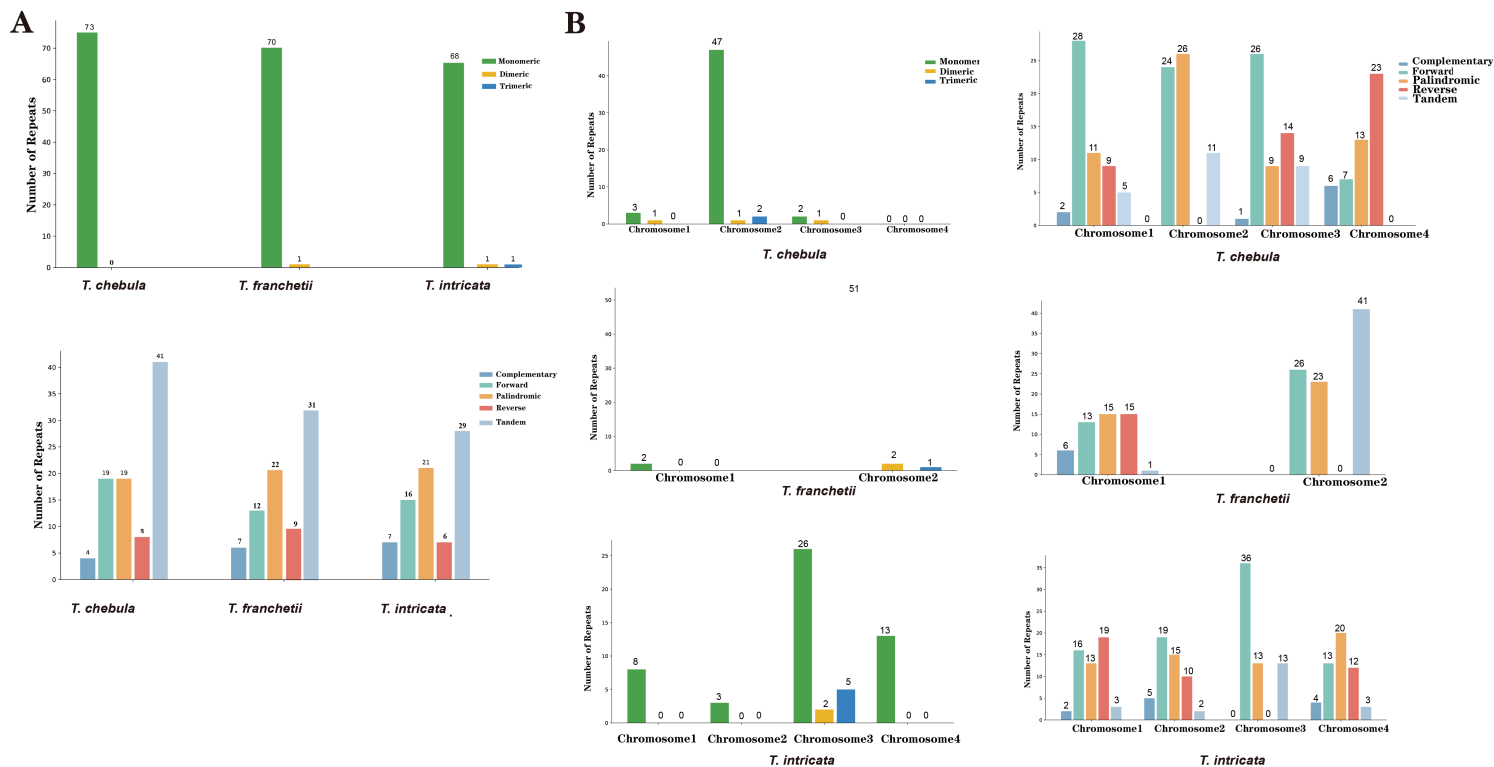


Figure 2

The repeat sequences in the plastomes of the three *Terminalia* species: (A) plastome (B) mitogenome

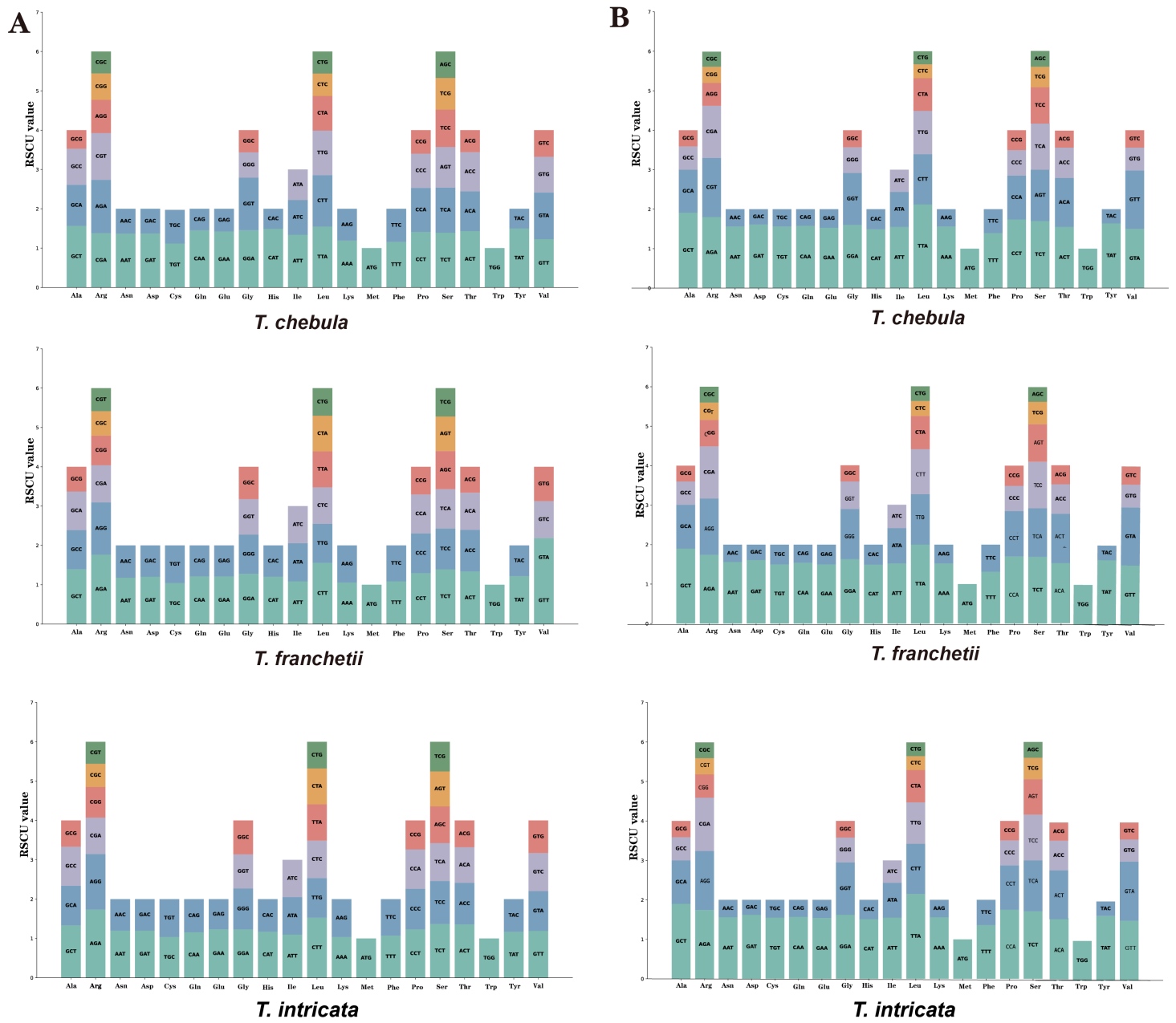


Figure 3

Relative synonymous codon usage (RSCU) of 3 *Terminalia ganelle* genes. (A) mitogenome, (B) plastome.

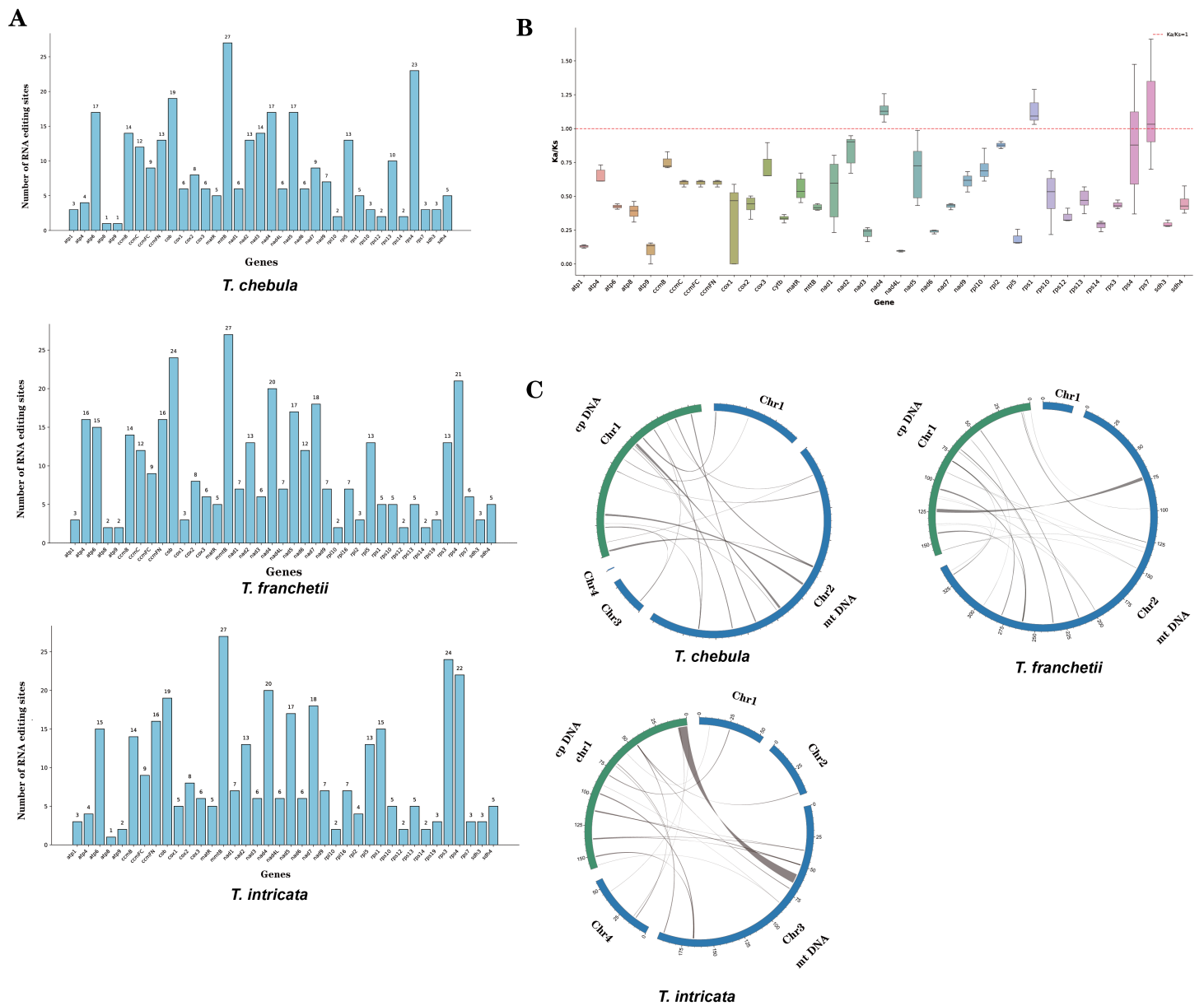
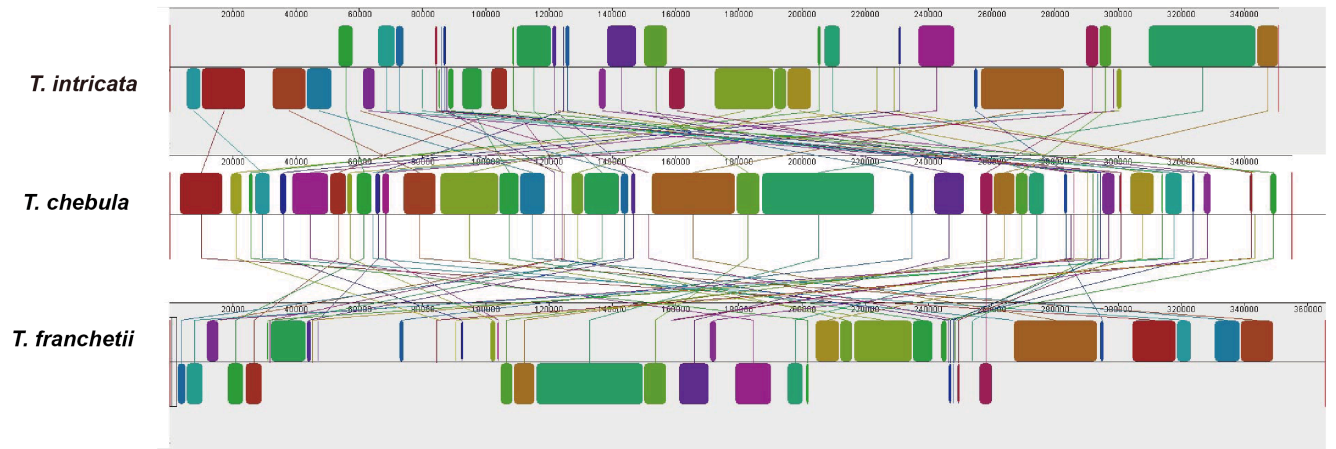


Figure 4

(A). The RNA editing sites of mitogenomes of three *Terminalia* species. (B). Boxplots of the pairwise Ka/Ks values among every shared mitogenomes of the 37 PCGs. The x-axis represents gene names, and the y-axis represents the values of Ka and Ks. The red dashed line represents 1. In the box plot, the vertical lines above and below the box indicate the upper and lower quartiles of the data, while the thick line inside the box represents the median. (C). Homology analysis between mitogenomes and plastomes of three *Terminalia* species. The blue and the green arcs denote the mtDNA and cpDNA, respectively. The grey lines signify the homologous sequence

A



Inverted Repeats

B

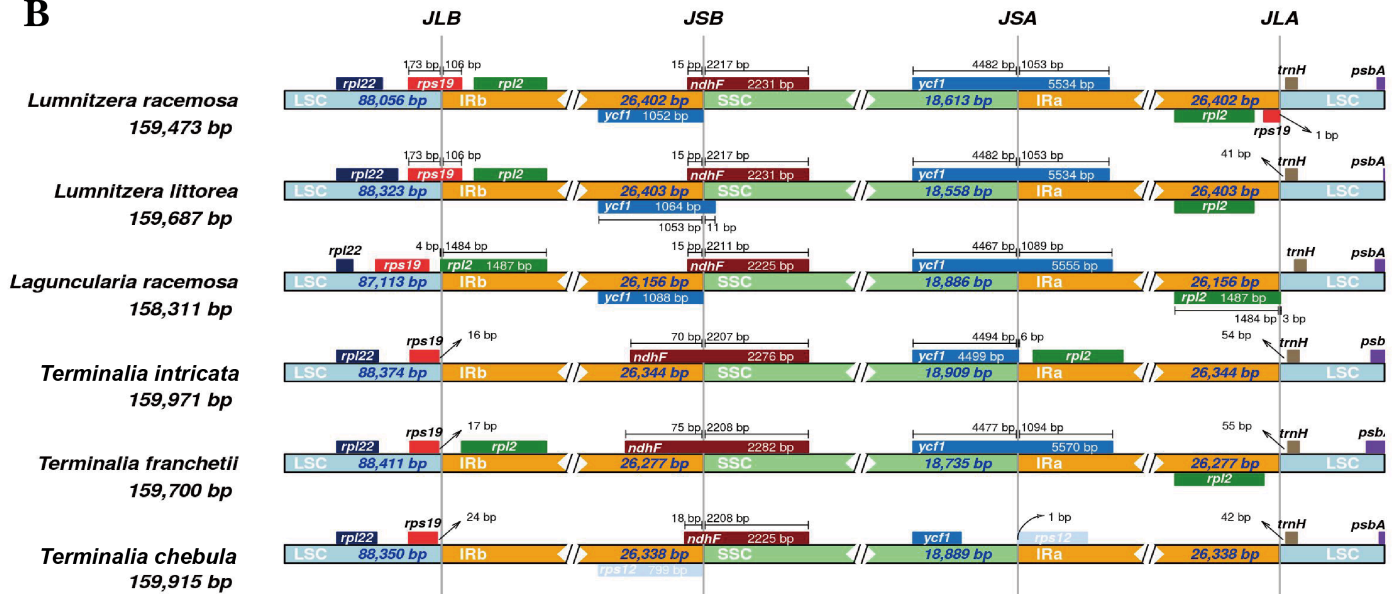


Figure 5

(A). Mauve visualization of synteny analysis among three *Terminalia* species: Colored blocks (LCBs) represent homologous gene segments, with consistent coloring indicating conserved sequences (homologous relationships). Connecting lines show the syntenic associations of LCBs across different genomes (indicating the order and direction of arrangement). (B) Comparison of the borders of the LSC, SSC, and IR regions among the six plastomes of Combretaceae species. (JLB: junction of the LSC and IRB; JSB: junction of the SSC and IRB; JSA: junction of the SSC and IRA; and JLA: junction of the LSC and IRA).

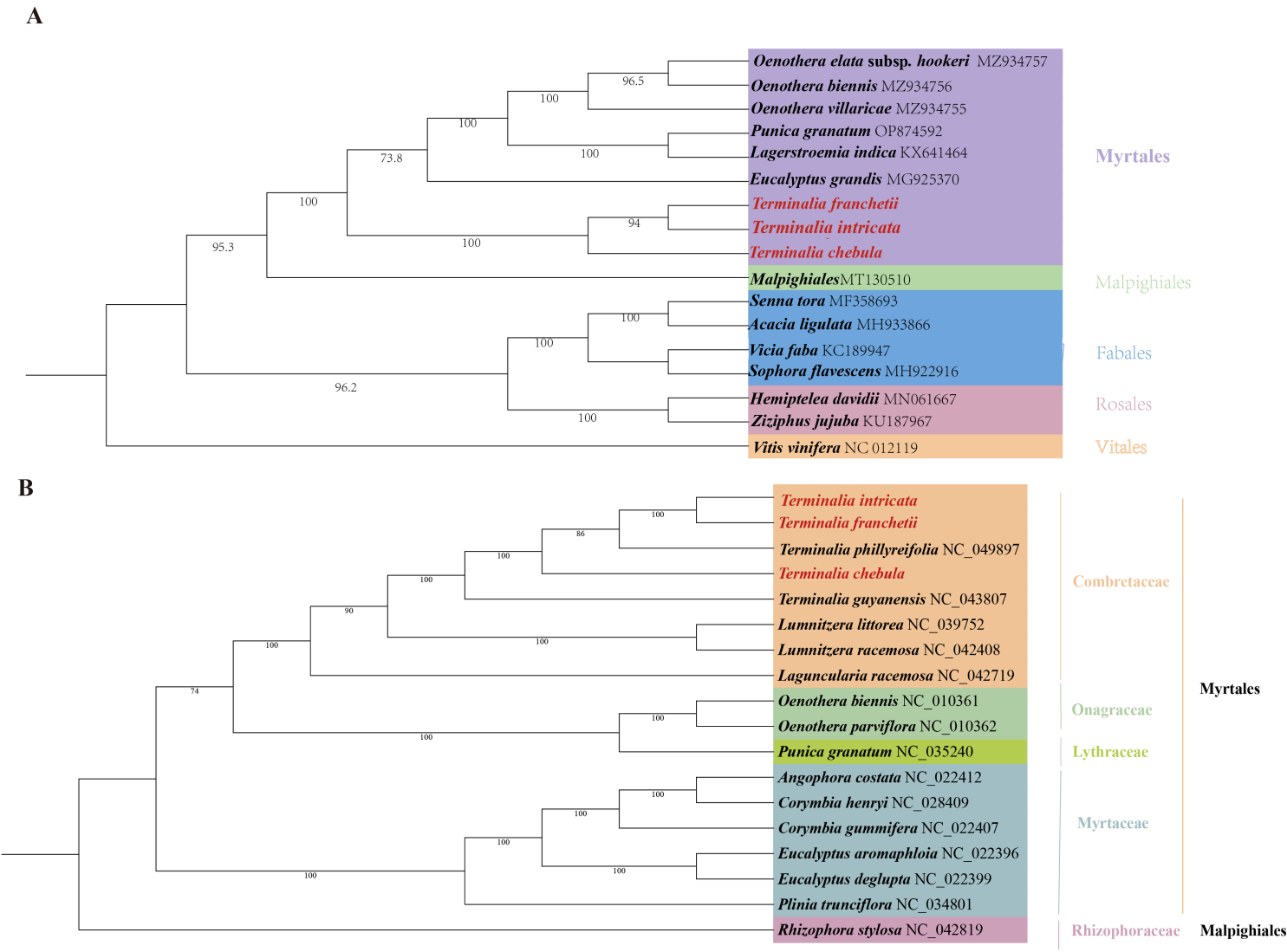


Figure 6

(A) Phylogenetic tree of the mitogenomes constructed using the ML method. (B) Phylogenetic tree of the plastomes constructed using the ML method.