

RESEARCH

Open Access



# Sequencing and analysis of the complete mitochondrial genomes of *Toona sinensis* and *Toona ciliata* reveal evolutionary features of *Toona*

Youli Li<sup>1</sup>, Min Gu<sup>1</sup>, Xuanzhe Liu<sup>1</sup>, Jianna Lin<sup>1</sup>, Huier Jiang<sup>1</sup>, Huiyun Song<sup>1</sup>, Xingcui Xiao<sup>2\*</sup> and Wei Zhou<sup>1\*</sup>

## Abstract

**Background** *Toona* is a critical genus in the Meliaceae, and the plants of this group are an asset for both restorative and restorative purposes, the most flexible of which are *Toona sinensis* and *Toona ciliata*. To concentrate on the advancement of mitochondrial(Mt) genome variety in *T.sinensis* and *T.ciliata*, the Mt genomes of the two species were sequenced in high throughput independently, after de novo assembly and annotation to construct a Mt genome map for comparison in genome structure. Find their repetitive sequences and analyze them in comparison with the chloroplast genome, along with Maximum-likelihood(ML) phylogenetic analysis with 16 other relatives.

**Results** (1) *T. sinensis* and *T.ciliata* are both circular structures with lengths of 683482 bp and 68300 bp, respectively. They share a high degree of similarity in encoding genes and have AT preferences. All of them have the largest Phe concentration and are the most frequently used codons. (2) Both of their Mt genome are highly preserved in terms of structural and functional genes, while the main variability is reflected in the length of tRNA, the number of genes, and the value of RSCU. (3) *T. sinensis* and *T. ciliata* were detected to have 94 and 87 SSRs, respectively, of which mononucleotides accounted for the absolute proportion. Besides, the vast majority of their SSRs were found to be poly-A or poly-T. (4) 10 and 11 migrating fragments were identified in the comparison with the chloroplast genome, respectively. (5) In the ML evolutionary tree, *T.sinensis* and *T.ciliata* clustered individually into a small branch with 100% support, reflecting two species of *Toona* are very similarly related to each other.

**Conclusions** This research provides a basis for the exploitation of *T.sinensis* and *T.ciliata* in terms of medicinal, edible, and timber resources to avoid confusion; at the same time, it can explore the evolutionary relationship between the *Toona* and related species, which does not only have an important practical value, but also provides a theoretical basis for future hybrid breeding of forest trees, molecular markers, and evolutionary aspects of plants, which has great scientific significance.

**Keywords** *Toona sinensis*, *Toona ciliate*, High-throughput sequencing, Mitochondria genome, Phylogenetic relationship

\*Correspondence:

Xingcui Xiao  
xiaoxingcui@126.com  
Wei Zhou  
wzhou@scau.edu.cn

<sup>1</sup> College of Forestry and Landscape Architecture, South China Agricultural University, Guangzhou 51000, Guangdong, China

<sup>2</sup> Sichuan Academy of Forestry Sciences, Chengdu 61008, Sichuan, China



© The Author(s) 2023. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

## Introduction

*Toona* plants have magnificent material, straight surface, and radiance, turning into the predominant furnishings and inside adornment wood, known as "Chinese mahogany", which is greatly esteemed by individuals [1–5]. *T.sinensis* and *T.ciliata* have the most noteworthy application in the *Toona*. *Toona sinensis* (A. Juss) Roem is a unique species of vegetable in China, its young shoots and leaves are crisp and juicy, fragrant and unique in flavor, it is a traditional and valuable woody vegetable that our people like to eat, and is also a local product for foreign trade export [6, 7]. *T.sinensis* is not only an excellent vegetable but also a natural green nutritious food of medicinal and food origin. It has somewhat high happiness of flavone and other pharmacologically dynamic mixtures [8, 9]. *T.ciliata* is a Grade II safeguarded plant, an important timber tree, and a therapeutic plant that has acquired broad consideration as of late [10–13]. The roots, stems, and leaves of *T.ciliata* can be utilized as medication and have successful restorative properties [14–16]. The monetary worth of this variety is quite high, and it is generally utilized and has extraordinary potential for advancement and utilization [17–20].

Mitochondria are organelles in higher plant cells with a semi-autonomous genetic system that provides the majority of the energy required for cellular and other life activities [21–24]. Mitochondria are particularly important in the study of the origin and evolution of living things. Mitochondrial DNA (mtDNA) is a genetic material found outside the nucleus that is normally a double-stranded circular molecule with a covalent closure [25–27]. Advanced plants have the largest mitochondria of any known higher organism species, ranging from 200 to 2400 kb [28–30].

Plant Mt genomes have been increasingly studied and more and more Mt genomes have been sequenced in recent years, which is very important for studying the diversity of biological phenotypes, functional diversity, as well as species evolution. This is critical for understanding biological phenological diversity, functional diversity, and the emergence of new functions during species evolution [31, 32].

Even though *Toona* plants have a long history of cultivation in China, most studies have been limited to chemical pathology, physiology, biochemistry, introduction, and breeding, with little research done on its origin, taxonomy, cytogenetics, and so on. There are still some issues with *Toona* classification, such as interspecific hybridization, that need to be addressed [33, 34]. Furthermore, *Toona* plants have a geographically dispersed distribution in China, resulting in a scarcity of natural forests and susceptibility to natural and anthropogenic

breakage, *T.ciliata* has now been classified as an endangered species, listed as a Class II key protected wild plant in China, and included in the Reference List of Major Cultivated Precious Tree Species in China and [35–38].

Subsequently, this review, given Mt near genomic examination through trend-setting innovations, for example, sub-atomic sequencing of Mt DNA, makes it conceivable to concentrate on *Toona* further top to bottom according to a minuscule viewpoint notwithstanding plainly visible morphological characterization and makes the preservation of excellent hereditary assets of the imperiled species *T.ciliata*, determination and reproducing of good species, and advancement and usage with significant hypothetical and functional importance.

## Materials and methods

### Plant material, DNA extraction, and library construction

While *T.sinensis* was acquired from Pingxiang, Guangxi, *T.ciliata* was obtained from Baoshan, Yunnan (Longitude: 106.75 E, Latitude: 22.12 N.) Before this investigation, both species completed seedling trials and were found to be suitable for cultivation in Guangzhou, Guangdong. (Note: Professor Xiaoyang Chen and Teacher WeiZhou conducted a detailed identification of the plant material. The seed trial forest is situated near the South China Agricultural University's teaching and research facility in Guangzhou, China, at N23°16' and E113°37'.)

High-quality total DNA is the primary prerequisite for obtaining the whole Mt genome sequence. Fresh leaves of *T.sinensis* and *T.ciliata* were taken and whole genome DNA was extracted by the CTAB [39] method. high-quality genome DNA was extracted and quality checked for purity, concentration, and integrity using Nanodrop [40], 1% (w/v) agarose gel electrophoresis. DNA samples that passed the electrophoresis test were randomly broken into fragments of approximately 350 bp in length using a Covaris ultrasonic fragmentation machine [41]. After processing, the DNA fragments were subjected to end repair, A-tail addition, sequencing junction addition, purification, PCR amplification, and other steps to complete the entire library preparation. After the library was constructed, the initial quantification was performed using Qubit 3.0, and the library was diluted to 2 ng/ul. The insert size (insert size) of the library was then detected using Agilent 2100 [42, 43]. After the inserts met the expectation, the effective concentration of the library was accurately quantified by Q-PCR [44] to ensure the quality of the library. After the libraries passed the test, they were sent to Guangzhou Ruike Gene Technology Co.

### Sequencing, assembly, and annotation

Qualified DNA libraries were sequenced using the Illumina HiSeq 4000 High-throughput Sequencing Platform. Once the sequencing was completed, the sequenced data were spliced into the Mt genome. The reads with low sequencing quality (<40 bp in length) were filtered by Trimmomatic [45], the overlapping reads were filtered out by Blast to obtain Clean Data, and the sequencing data were analyzed by 15-mer using K-mer software to obtain high-quality reads. Assembly was performed using SOAP denovo [46] assembly software. The preliminary assembly results were optimized and holes were filled using krskgf and gapclose [47] software to obtain the specific assembly results.

The complete Mt genome sequence was annotated utilizing CPGAVAS [48] software together with DOGMA [49] software. Comparison analysis of blast on the proximal edge, followed by manual correction (Specific results of *T.sinensis* and *T.ciliata* annotations can be detailed in Additional file 7 and 8: Appendices G and H, respectively). Transfer RNA (transfer RNA, tRNA) genes were identified along with manual correction employing tRNAscan-SE [50] software. The BLAST [51] search method was performed to align [52–54] and validate [55] the information sites such as gene boundaries, intron, exon, and coding regions.

The annotated genome sequences were submitted to NCBI according to the requirements, resulting in the definitive accession numbers *T.sinensis* (GenBank: OM574631.1) and *T.ciliata* (GenBank: OM574630.1).

### Superior Mt genome analysis

#### Structure and composition

Mitochondria were mapped by OGDRAW v1.2 (Organelle Genome DRAW) [56] online website (<https://chlorobox.mpimp-golm.mpg.de/OGDraw.html>). The circular structure of the genome sequence was mapped. The base content of the Mt genome was calculated using Editseq [57] software to obtain the ratio of A, T, C, G, and GC content respectively.

#### Frequency of codon usage

Considering the formula mentioned in Sharp PM literature [58], the utilization of relative equivalent codon use (RSCU) was examined utilizing CodonW [59] software.

#### Simple sequence repeats

Simple Sequence Repeats (SSRs) of the Mt genome of *T. sinensis* and *T. ciliata* were analyzed using MISA [60] software, with the tandem repeat unit length and a minimum number of repeats set to >10 for single nucleotide repeats, >6 for dinucleotide repeats, and >5

for trinucleotide, tetranucleotide, pentanucleotide, and hexanucleotide repeats. The minimum distance between SSRs was set to 100 bp.

### Chloroplast and Mt genomes

The chloroplast genome sequences of *T.sinensis* (GenBank: OK572965) and *T. ciliata* (GenBank: OK572964.1) on NCBI were uploaded by our group before completion. Match them with the mitochondrial genome for Blastn (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to find out the migrating gene sequences. Regions with similarity greater than 90% and comparison lengths greater than 50 bp were screened as migration sequences.

### Phylogenetic tree analysis

Species (The specific Mt information etc. of the tree species can be detailed in a file called taxonomy in Additional file 4: Appendices D) with complete Mt genome arrangements and explanations in direct relation to the objective species were downloaded from NCBI for phylogenetic tree development. For more details on structural trees, the ML construction tree method is described in the folder titled "Description of the structure tree" in Additional file 4: Appendices D, while the Bayesian construction tree method is detailed in Additional file 5: Appendices E.

## Results

### Genome features

The total Mt genome length of *T.ciliata* was 683,000 bp, the composition of bases was A (27.31%), T (27.29%), C (22.56%), and G (22.85%), and the C+G content was 45.40%. The size of the *T. sinensis* Mt genome was 638,482 bp, and its base makeup was A (27.35%), T (27.09%), C (22.79%), and G (22.76%), with a C+G content of 45.56%. All of them have a circumferential Mt genome construction, where their longest gene is the *rrn26* gene in the transfer RNA, measuring 3116 bp (Table 1, Fig. 1).

### Functional gene

#### Gene encoding protein

*T.ciliata* encodes 71 genes while *T.sinensis* encodes 72 genes. Protein-coding genes of both *Toona* plants are consistent in frequency, types, and measurements (Additional file 1: Appendices A), whereas the predominant divergence is in tRNAs, with *T.ciliata* encoding 33 tRNAs and *T. sinensis* encoding 34 (Additional file 2: Appendices B).

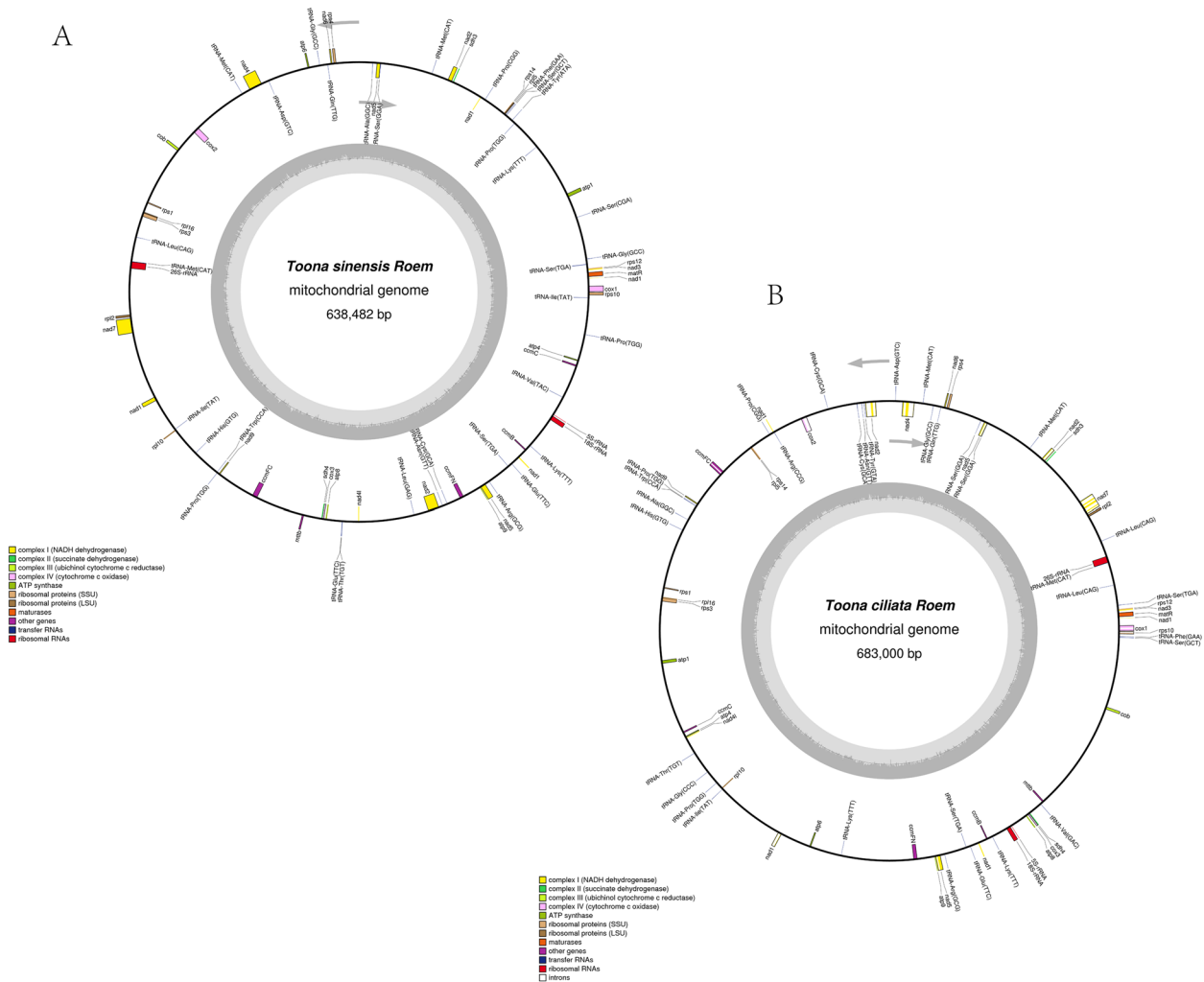
Employing NCBI-BLAST analysis, 38 genes encoding proteins were obtained on the Mt genomes of both *T.ciliata* and *T. sinensis*. We categorized the protein-encoding genes into the following eight categories

**Table 1** Results of mt DNA genome sequence analysis of two plants

Type	<i>Toona ciliata</i>		<i>Toona sinensis</i>	
	Size	Proportion	Size	Proportion
A content	186,538	27.31%	174,629	27.35%
T content	186,361	27.29%	172,983	27.09%
G content	156,039	22.85%	145,343	22.76%
C content	154,062	22.56%	145,527	22.79%
Total content	683,000		638,482	
G+C content	310,101	45.40%	290,870	45.56%
longest gene	3,116	50.77%	3,116	50.77%

Both mitochondria of the longest gene are 26S-rRNA, 50. The GC content of the gene is 50.77%

according to their gene functions (Table 2): including Complex I genes (*nad1*, *nad2*, *nad3*, *nad4*, *nad4L*, *nad5*, *nad6*, *nad7*, and *nad9*) involved in the synthesis of NADH deaminase subunits; Complex II genes (*sdh3* and *sdh4*) participated in the synthesis of cytochrome b precursor subunits; Complex III gene (*cob*) implicated in the synthesis of the cytochrome C oxidase subunit; Complex IV genes (*cox1*, *cox2*, and *cox3*); Complex V genes (*atp1*, *atp4*, *atp6*, *atp8*, and *atp9*), associated with the synthesis of ATP synthase subunits; Cytochrome c biosynthetic genes (*ccmB*, *ccmC*, *ccmFC* and *ccmFN*) engaged in the synthesis of cytochrome C synthase subunits; Ribosome protein genes synthesized by ribosome protein synthesis genes (*rps1*, *rps3*, *rps4*, *rps10*, *rps12*, *rpl2*, *rpl5*, *rpl10* and *rpl16*); The ribosomal RNA genes (*rrn5*, *rrn18* and *rrn26*) as well as the *matR* gene (encoding a maturation-like enzyme) and the *mttB* gene (encoding a transporter).



**Fig. 1** A map of the Mt genome of the Toona. **A** *T. sinensis*, **B** *Toona ciliata*. Reverse transcription is indicated by genes outside of the circles, and clockwise transcription is indicated by genes inside the circles. The two IR regions are represented by the thick black line on the outside circle. The GC content is represented by the inner nucleus' dark gray graph

**Table 2** Number and proportion of each type of SSR in *T.sinensis* and *T.ciliata*

Type	<i>Toona_ciliata</i>		<i>Toona_sinensis</i>	
	Number	Ration	Number	Ration
mono-nucleotides	75	78.13%	70	78.65%
di-nucleotides	14	14.58%	13	14.61%
tri-nucleotides	6	6.25%	6	6.74%
tetra-nucleotides	0	0.00%	1	1.12%
penta-nucleotides	0	0.00%	0	0.00%
hexa-nucleotides	1	1.04%	0	0.00%

**Gene encoding tRNA**

Utilizing tRNAscan-SE, 33 and 34 genes encoding transfer RNAs were identified separately on the Mt genomes of *T.ciliata* and *T. sinensis*.

In the *T.ciliata*, a total of 33 tRNAs encode 20 amino acids ranging from 66 bp-88 bp in length. five of these tRNAsers, Leucine(LeU), Glycine(Gly), Gly, Cysteine(Cys), Arginine(Arg), and Lysine(Lys) each have two tRNAs encoding, Met and Pro are distributed with three tRNAs encoding, and the remaining amino acids all have one tRNA Editor. In contrast to *T.ciliata*, *T. sinensis* has 34 tRNAs encoding 20 amino acids, ranging from 63–167 bp in length. compared to *T.ciliata*, *T. sinensis* has 2 fewer tRNAs encoding Cys and Arg, but 3 more tRNAs encoding Proline(Pro), Isoleucine(ILe), and Glutamic acid(Glu) (Additional file 2: Appendices B).

**Codon Usage bias**

RSCU (Relative Synonymous Codon Usage) is a relative synonymous codon usage measure, indicating the proportion of a given synonymous codon usage among all synonymous codons. The Mt genomes of *T.ciliata* and *T. sinensis* have a codon usage bias for all amino acids except for the Tryptophane (Trp) of only one codon, TGG.

The codon TTT was the most frequently accessed codon in the Mt protein-coding genes of *T.ciliata* and *T. sinensis*, with the second commonest codon being ATT and the third being TTC. The termination codon TAG was the least frequently addressed codon, being exclusively indexed on six and five occasions respectively (Additional file 3: Appendices C).

**SSRs**

A total of 94 simple sequence repeats were detected in the mitochondrial genome of *T.sinensis* while 87 were detected in *T. ciliata* (Annex E). The distribution of each type of SSRs can be observed from the statistical results (Table 2), where *T. sinensis* mono-, di-, tri-, and

hexa-nucleotides had 75, 14, 6, and 1, respectively. No tetra-nucleotides were detected and penta-nucleotides. *T.ciliata*, on the other hand, had 70, 13, 6, and 1, respectively. However, *T.ciliata* also detected 1 tetra-nucleotides (CGA).

The major repeat types of SSRs are single nucleotide repeats, with the number of A/T in the relevant single nucleotide repeats being much larger than the number of G/C (Table 3). The proportion of A/T on polynucleotide repeats is also greater than the proportion of G/C, judging from the data in Additional file 6: Appendices F. It is consistent with the results of their codon preferences.

**Genome alignment and migration sequence**

Even though *T. sinensis* and *T.ciliata* mitochondrial genomes are up to four times longer than those of chloroplasts, they only have half as many protein-coding genes, making up less than one-fifth of the total length, whereas the proportion of protein-coding in chloroplasts is around 50% of the total length (Table 4). There were no introns found in the chloroplast genome of *T. sinensis* or *T. ciliata*, 21 introns were released in the mitochondrial genome, and the rRNA numbers of the two tree species were very congruent in both genomes. *T. sinensis* was larger than *T.ciliata* in the mitochondrial genome but had one more tRNA, which may be related to the exchange of genetic material in nuclear genes or cytoplasm. Both *T. sinensis* and *T. ciliata* had 37 numbers in the chloroplast genome.

We discovered that *T. ciliata* had 11 migratory sequences and *T. sinensis* had 10 when we compared the chloroplast and mitochondrial genome sequences under the screening criteria of areas with similarity greater than 90% and comparison length greater than 50 bp(Table 5). The largest of these migratory sequence segments measured 4124 bp. Comparatively, we discovered that *T.sinensis* While only one sequence fragment of *T.ciliata* was consistent, with a variation of 1–8 bp, we discovered that only three sequence fragments of *T. sinensis* and mitochondria were consistent in size, with the others varying by 1–3 bp. The mitochondrial genome’s recombination and gene rearrangement were linked to variations in sequence, which may indicate

**Table 3** Distribution of the number of single nucleotide repeats

p1Type	<i>Toona_ciliata</i>		<i>Toona_sinensis</i>	
	Number	Ration	Number	Ration
A	353	43.53%	301	40.35%
T	347	42.79%	374	50.13%
G	79	9.74%	71	9.52%
C	32	3.95%	0	0.00%



**Table 4** Comparison of chloroplast and mitochondrial genomes of *T. sinensis* and *T. ciliata*

	<i>T.ciliata</i>		<i>T.sinensis</i>	
	Chloroplast	Mitochondrion	Chloroplast	Mitochondrion
Genome size(bp)	159618	683000	159139	638,482
GC(%)	37.89	45.4	37.9	45.56
Depth(X)	1,175	233	1,917	391
Genes no	132	71	132	72
Protein-coding sequence(%)	49.63	4.65	49.78	4.97
Intron no	not detected	21	not detected	21
tRNA no	37	33	37	34
tRNA Sequence(%)	1.76	0.37	1.77	0.41
rRNA no	8	3	8	3
rRNA Sequence(%)	5.67	0.76	5.69	0.81

**Table 5** Gene sequences of *T. sinensis* and *T. ciliata* mitochondrial genomes derived from the chloroplast genome

Species	Identity	Map length	Chloroplast start position	Chloroplast end position	Mitochondrial start position	Mitochondrial end position
<i>Toona sinensis</i> (CP ID:OK572965.1 Mt ID:NC_065061.1)	97.468	79	1	79	398,284	398,362
	95.077	2458	43876	46292	156,746	154,329
	96.392	1774	46606	48355	154,342	152,577
	93.671	79	54778	54856	213,727	213,805
	98.719	4137	87332	91456	237,563	233,440
	99.558	906	106599	107502	144,514	145,419
	98.516	1415	108259	109668	382,302	383,708
	93.939	66	110916	110981	131,432	131,497
	97.468	79	112237	112314	516,703	516,781
	98.516	1415	136179	137588	635,165	633,759
	97.5	80	3	82	292,191	292,112
<i>Toona ciliata</i> (CP ID:OK572964.1 Mt ID:NC_065060.1)	99.642	279	41,482	41,759	333,893	333,615
	98.14	484	42,343	42,826	333,143	333,625
	95.556	2453	44,221	46,632	129,322	126,895
	97.463	1774	46,946	48,713	126,908	125,143
	93.671	79	55,119	55,197	154,865	154,787
	98.598	4136	87,716	91,840	210,015	205,899
	93.939	66	111,301	111,366	104,004	104,069
	97.468	79	112,623	112,700	183,954	184,032
	99.011	1415	136,667	138,076	424,683	426,096
	98.896	906	138,833	139,736	117,993	117,088

that after migratory integration, these fragments may have undergone separate replication and recombination within the mitochondrial genome recombination.

#### Phylogeny analysis

Aiming to ascertain the evolutionary status of *T. ciliata* and *T. sinensis* in the plant system, we downloaded the mtDNA sequences of the same ORDER relatives that have published their mtDNA sequences on NCBI. The

two approaches of amino acid construction tree and DNA sequence construction tree are described in Additional file 3: Appendices C. Six Anacardiaceae species, five Sapindaceae species, three Rutaceae species, two Nitrariaceae species, and two Meliaceae species, *T. ciliata* (OM574630) and *T. sinensis* (OM574631), for a total of 18 tree species. The outgroup for the Mt genome was *Morus notabilis* (NC 041177.1), and an evolutionary tree was constructed using the maximum likelihood method using

the software MEGA 11. Bayesian tree (BI) and maximum likelihood method (ML) to create phylogenetic tree topology are similar, only the support at a few branches varies (Only the values between the large branches clustered into Anacardiaceae and Nitrariaceae had large divergences, where the ML tree had a support of 69, while the BI tree was 99). In this research, the tree with the maximum likelihood tree is selected, detailed in Fig. 2, while the result regarding the BI development tree is detailed in Fig. 3. In the likelihood ML phylogenetic tree (Fig. 2), a total of 15 nodes were formed, nine of which had 100 percent support, except for the large branch of Anacardiaceae and Nitrariaceae, which had 69 percent support, and *Xanthoceras sorbifolium* (MK333231.1) and *Sapindus mukorossi* (MT806100.1), which formed a minor branch with only 56 percent support, but all the other nodes had no less than 93% support.

**Discussion**

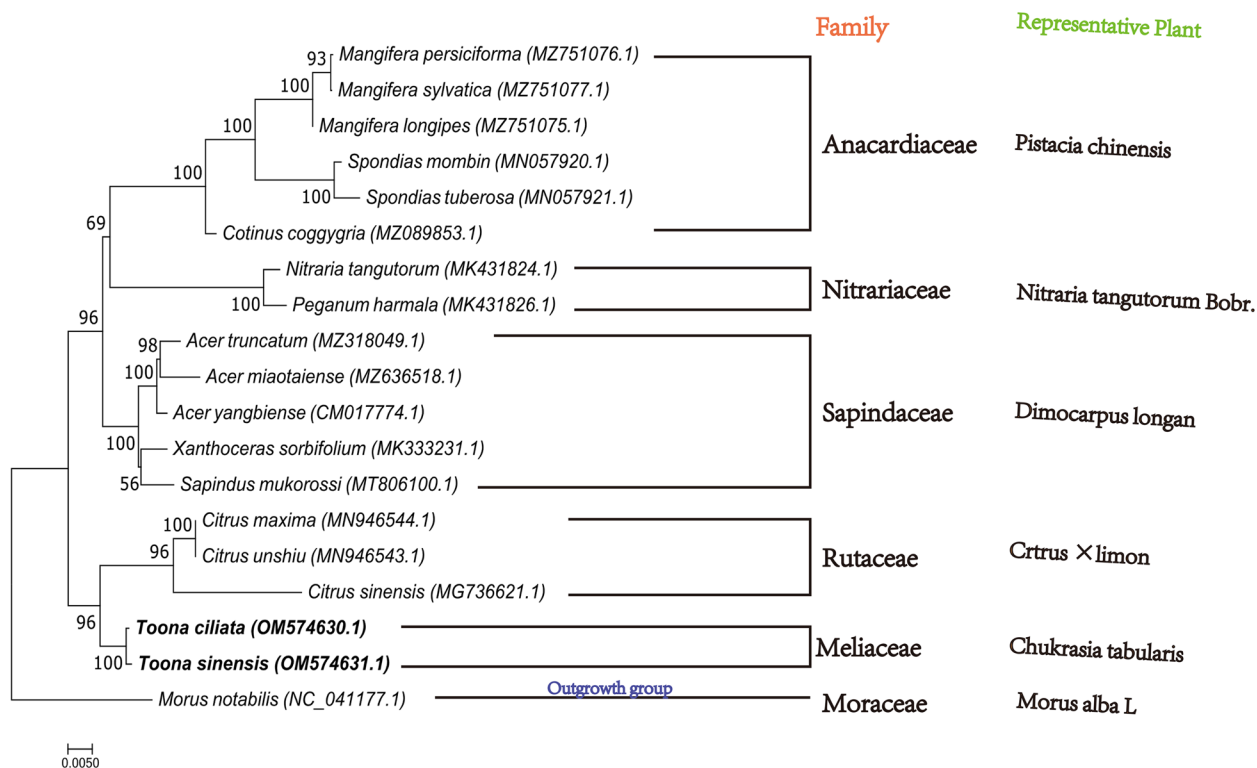
**Mitochondrial Structure and Genetic Information**

In terms of GC content, gene content, and genetic codon usage preference, functional gene and the numerical Mt genomes of *T.ciliata* and *T. sinensis* were well conserved. Moreover, they are similar in the results of codon preference and RSCU values. These encoded genes are mainly concerned with the synthesis of ATP synthase subunits,

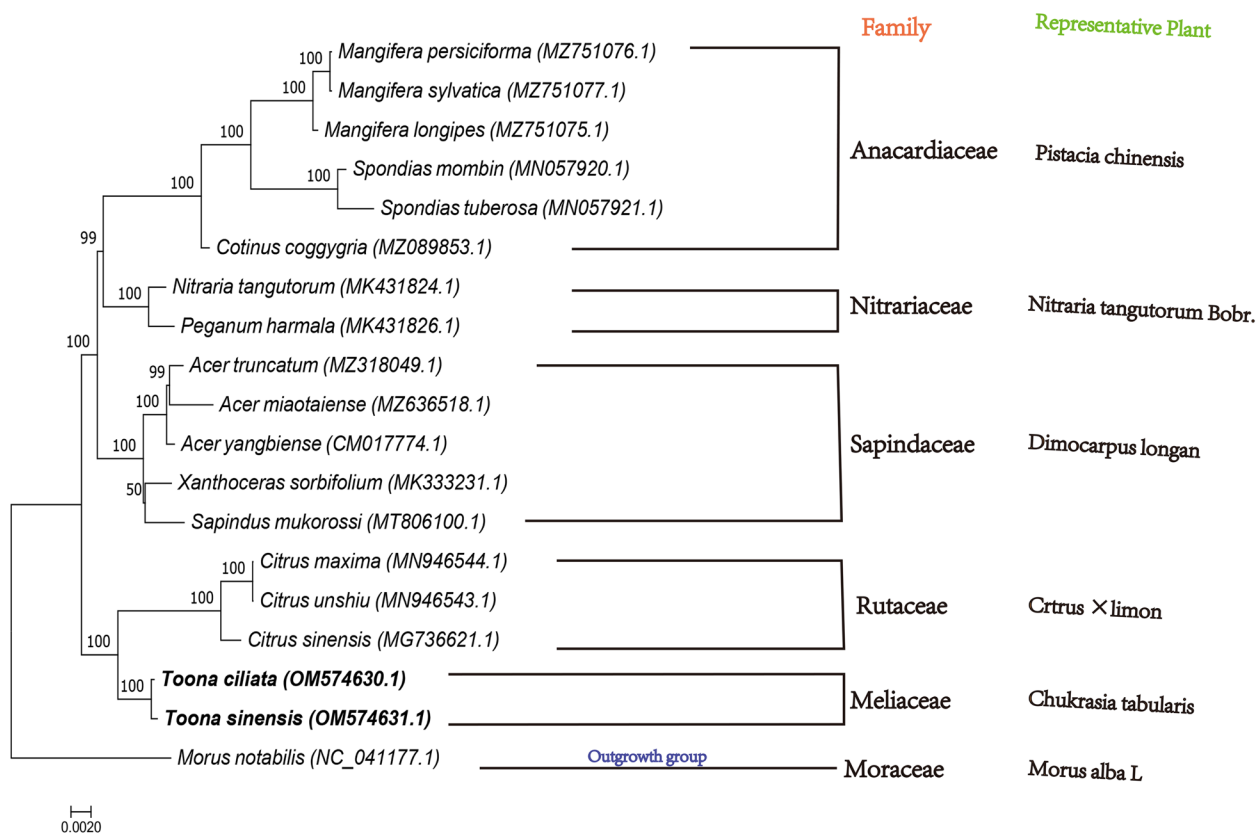
cytochrome C synthesis, and ribosomal protein synthesis. This provides the theoretical conditions for the exploration of the mechanisms and pathways of metabolite synthesis reactions including respiration and other related metabolites between the two species.

**Genome comparison and genetic sequence migration**

The tRNA from the chloroplast or nucleus will be involved in the transport of amino acids to reach the number of amino acids required for life. They encode the same 20 amino acids, but *T. sinensis* has one more tRNA than *T.ciliata*. Gene transfer in cells occurs between different organelles, including chloroplasts, mitochondria, and the nucleus [61, 62]. The vast majority of sequences in the mitochondrial genome that migrate from the chloroplast genome are currently considered "dead on arrival", except tRNAs [63]. Expression of chloroplast-derived tRNA genes in the mitochondrial genome has been shown to exist [64, 65]. For the extra tRNA in the *T.sinensis* mitochondria, there is no relationship with the transfer of tRNAs from the chloroplast to the *T. sinensis* mitochondria, which should be associated with the nuclear genome. However, regarding specific gene exchange, it is required to develop in-depth research on gene communication between the nuclear genome and organelles.



**Fig. 2** Phylogenetic trees constructed based on the ML method for 19 related plants



**Fig. 3** Phylogenetic trees constructed based on the BI method for 19 related plants

**Repeat sequence**

Simple sequence repeats (SSRs), also known as microsatellites, are widely distributed on the mitochondrial genome [66]. Due to their high polymorphism and co-dominance, microsatellites are often used as molecular markers to assist in breeding [67] construction of genetic linkage maps and gene mapping, etc. [68].

In contrast, there are some significant variations in SSRs between *T.sinensis* and *T.ciliata*, for example, *T.ciliata* has one more tetra-nucleotides (CGA), whether this has an evolutionary link to the two plants. It will provide a point for the subsequent screening of genetic molecular markers. In addition, further research on homologous recombination mediated by repeated sequences, *Toona* kinship, and genetic distance will be conducted.

**Systematic evolution**

*T.ciliata* and *T.sinensis* have similar morphological characteristics and cultivate in similar environments, so the traditional morphological taxonomy considers the two plants to be cloplantssely related [69, 70]. In the

phylogenetic tree, the target tree species *T.ciliata* and *T.sinensis*, belonging to the Meliaceae, clustered into a narrow branch with 100% support. This unifies with the results of traditional morphological taxonomy.

Since plants in the Sapindaceae are more susceptible to geographical location and their genetic variation, the evolutionary distance and genetic variation of plants within the Sapindaceae vary widely [71, 72]. Flora of China records that Meliaceae, Rutaceae, Anacardiaceae, Sapindaceae, and Nitrariaceae are natural taxon.

Taxonomists such as Rendle, Hutchinson, and others, who have organ morphological classification, have concluded that Meliaceae and Rutaceae are closely related, but for the classification of the degree of affinity between them, most of them are distinguished from plant physiology and morphology, less from the molecular level of genes [73, 74]. The establishment of the ML evolutionary tree provides a preliminary evolutionary relationship between Meliaceae and Rutaceae at the Mt genome level, but there are limitations because the published Mt genome sequences of plants are still quantitatively insufficient to represent the family level.



## Conclusion

The completion of the Mt genome sequencing of *T.ciliata* and *T. sinensis* has enriched the Mt genome library of *Toona*. and is important for investigating interspecific species relationships and researching the genetics and evolution of *Toona*.

The Mt genomes are predominantly maternally inherited and do not originate in the recombinant genome, therefore, they may have dissimilar evolutionary mechanisms and might reflect different evolutionary information. Further research on gene recombination, locus analysis, etc. can theoretically be supported by the identified moving sequence fragments. Phylogenetic tree building also further illustrates that the simulation of Mt genomic evolutionary tree outcomes is moderately compatible with the traditional classification. The Mt genome can be acclaimed as a molecular marker for the investigative assessment of phylogenetic relationships among species and the genetic structure of populations.

Regarding *T.ciliata* and *T. sinensis*, it is of great value for the data on their energy metabolism, growth and development, and hybrid breeding.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12864-023-09150-6>.

Additional file 1.  
Additional file 2.  
Additional file 3.  
Additional file 4.  
Additional file 5.  
Additional file 6.  
Additional file 7.  
Additional file 8.  
Additional file 9.  
Additional file 10.

## Acknowledgements

We thank the Guangdong Key Laboratory of Innovative Development and Utilization of Forest Plant Germplasm Resources for providing the experimental platform and Guangdong Forestry Science and Technology Innovation Special Project for providing the fund support. Appreciate the cooperation from Guangzhou Ruike Gene Technology Co.

## Authors' contributions

Conceptualization: Youli Li and Min Gu; Data curation: Youli Li, Xuanzhe Liu and Jiana Lin; Formal analysis: Min Gu, Huier Jiang and Jiana Lin; Funding acquisition: Xingcui Xiao and Wei Zhou; Project administration: Xingcui Xiao; Supervision: Huiyun Song, Xingcui Xiao and Wei Zhou; Validation: Jiana Lin; Writing – original draft: Youli Li and Min Gu. Xiao and Zhou are co-corresponding authors. All authors will be informed about each step of manuscript processing including submission, revision, revision reminder, etc. The author(s) read and approved the final manuscript.

## Funding

The project bonus was obtained from Guangdong Forestry Science and Technology Innovation Special Project (2011KJCX002,2012KJCX002,2013KJCX002).

## Availability of data and materials

The datasets generated during the current study are available in the [NCBI] repository, [*Toona sinensis* (GenBank: OM574631.1) and *Toona ciliata* (GenBank: OM574630.1)].

## Declarations

### Ethics approval and consent to participate

*Toona sinensis* and *Toona ciliata* was grown and collected at South China Agricultural University (Guangzhou, Guangdong Province) and identified by Professor Xiaoyang Chen and teacher Wei Zhou. The identified samples were preserved in South China Agricultural University Herbarium(CANT), where the voucher for *T.sinensis* was 33208 and the voucher for *T.ciliata* was 33209. All samples were adopted for the total experiment. No specific permits are required for sample collection in this study. We comply with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora. Each member of the team declared that has read the relevant institutional, national, and international guidelines and legislation before the commencement of the experiment and had complied with each of the legislative requirements during the experiment.

### Consent for publication

All authors consistently consent to publish the article.

### Competing interests

The authors declare no conflict of interest.

Received: 25 July 2022 Accepted: 24 January 2023

Published online: 01 February 2023

## References

- Shilpi JA, Saha S, Chong SL, Nahar L, Sarker SD, Awang K. Advances in chemistry and bioactivity of the genus *Chisocheton* Blume. *Chem Biodivers*. 2016;13(5):483–503. <https://doi.org/10.1002/cbdv.201400373>. PMID: 26970405.
- Liu J, Jiang JM, Chen YT. Genetic diversity of central and peripheral populations of *Toona ciliata* var. *pubescens*, an endangered tree species endemic to China. *Genet Mol Res*. 2014;13(2):4579–90. <https://doi.org/10.4238/2014.June.17.10>. PMID: 25036507.
- Pan J, Wang Q, Guo X, Jiang X, Cheng Q, Fu L, Liu W, Zhang L. Fungal diversity and community structure in a natural *Toona ciliata* var. *pubescens* forest in South Central China. *PeerJ*. 2021;9:e11331. <https://doi.org/10.7717/peerj.11331>. PMID: 33987014; PMCID: PMC8101450.
- Yang HL, Chang WH, Chia YC, Huang CJ, Lu FJ, Hsu HK, Hseu YC. *Toona sinensis* extracts induces apoptosis via reactive oxygen species in human premyelocytic leukemia cells. *Food Chem Toxicol*. 2006;44(12):1978–88. <https://doi.org/10.1016/j.fct.2006.06.027>. Epub 2006 Jul 18 PMID: 16945458.
- Yang H, Gu Q, Gao T, Wang X, Chue P, Wu Q, Jia X. Flavonols and derivatives of gallic acid from young leaves of *Toona sinensis* (A. Juss.) Roemer and evaluation of their anti-oxidant capacity by chemical methods. *Pharmacogn Mag*. 2014;10(38):185–90. <https://doi.org/10.4103/0973-1296.131034>. PMID:24914286. PMCID: PMC4048567.
- Li WZ, Han WN, Liu B, Ding SH, Zhang XK, Wang RS. Extraction of proteins and preliminary characterization of physicochemical properties in *Toona sinensis* fruit. *Genet Mol Res*. 2017;16(1). <https://doi.org/10.4238/gmr16019177>. PMID: 28198502.
- Yang Z, Li L, Chen CH, Zhang YY, Yang Y, Zhang P, Bao GH. Chemical composition and antibacterial activity of 12 medicinal plant ethyl acetate extracts using LC-MS feature-based molecular networking. *Phytochem Anal*. 2022;33(3):473–89. <https://doi.org/10.1002/pca.3103>. Epub 2022 Jan 18 PMID: 35042282.

8. Pramono AA, Palupi ER, Siregar IZ, Kusmana C. Characteristics of Surian Flower, Fruit and Seed Productions (*Toona sinensis* (A. Juss.) M. Roem.) in Sumedang, West Java. *Trop Life Sci Res*. 2016;27(1):77–91 PMID: 27019683; PMCID: PMC4807964.
9. Liu W, Li Y, Tomasetto F, Yan W, Tan Z, Liu J, Jiang J. Non-destructive Measurements of *Toona sinensis* Chlorophyll and Nitrogen Content Under Drought Stress Using Near Infrared Spectroscopy. *Front Plant Sci*. 2022;12:809828. <https://doi.org/10.3389/fpls.2021.809828>. PMID: 35126433; PMCID: PMC8814108.
10. Duan D, Chen L, Yang X, Tu Y, Jiao S. Antidepressant-like effect of essential oil isolated from *Toona ciliata* Roem. Var. *yunnanensis*. *J Nat Med*. 2015;69(2):191–7. <https://doi.org/10.1007/s11418-014-0878-0>. Epub 2014 Dec 3. PMID: 25465853.
11. Pan J, Wang Q, Guo X, Jiang X, Cheng Q, Fu L, Liu W, Zhang L. Local patterns of arbuscular mycorrhizal fungal diversity and community structure in a natural *Toona ciliata* var. *pubescens* forest in South Central China. *PeerJ*. 2021;9:e11331. <https://doi.org/10.7717/peerj.11331>. PMID: 33987014; PMCID: PMC8101450.
12. Li P, Shang Y, Zhou W, Hu X, Mao W, Li J, Li J, Chen X. Development of an efficient regeneration system for the precious and fast-growing timber tree *Toona ciliata*. *Plant Biotechnol* (Tokyo). 2018;35(1):51–8. <https://doi.org/10.5511/plantbiotechnology.18.0130a>. Epub 2018 Mar 25. PMID: 31275037; PMCID: PMC6543735.
13. Li P, Zhan X, Que Q, Qu W, Liu M, Ouyang K, Li J, Deng X, Zhang J, Liao B, Pian R, Chen X. Genetic Diversity and Population Structure of *Toona Ciliata* Roem. Based on Sequence-Related Amplified Polymorphism (SRAP) Markers. *Forests*. 2015;6:1094–106. <https://doi.org/10.3390/f6041094>.
14. Lu Z, Dong X, Fan Y, Liu W, Dai J, Han X, Liu J. Complete chloroplast genome of *Toona ciliata* Roem. Var. *pubescens* (Franch.) Hand.-Mazz (Meliaceae), "Chinese mahogany." *Mitochondrial DNA B Resour*. 2022;7(3):495–7. <https://doi.org/10.1080/23802359.2022.2049987>. PMID: 35311208; PMCID: PMC8933019.
15. Xiang L, Zhang L, Hu J. The complete chloroplast genome of *Toona sinensis*, an important economic and medicinal plant endemic in China. *Mitochondrial DNA B Resour*. 2021;6(3):1025–7. <https://doi.org/10.1080/23802359.2021.1895691>. PMID:33796726;PMCID:PMC7995836.
16. Xin GL, Liu JQ, Liu J. Complete chloroplast genome of an endangered tree species, *Toona ciliata* (Sapindales: Meliaceae). *Mitochondrial DNA B Resour*. 2018;3(2):663–4. <https://doi.org/10.1080/23802359.2018.1476074>. PMID:33474276;PMCID:PMC7799959.
17. Ning J, He HP, Li SF, Geng ZL, Fang X, Di YT, Li SL, Hao XJ. Triterpenoids from the leaves of *Toona ciliata*. *J Asian Nat Prod Res*. 2010;12(6):448–52. <https://doi.org/10.1080/10286020.2010.493329>. PMID: 20552482.
18. Zhou W, Zhang XX, Ren Y, Li P, Chen XY, Hu XS. Mating system and population structure in an endemic plant, *Scutellaria tsinyunensis*, revealed in South China. *Sci Rep*. 2020;10(1):16998. <https://doi.org/10.1038/s41598-020-74123-8>. PMID:33046785;PMCID:PMC7550595.
19. Islam M, Rahman M, Gebrekirstos A, Bräuning A. Tree-ring  $\delta^{18}O$  climate signals vary among tree functional types in South Asian tropical moist forests. *Sci Total Environ*. 2021;756:143939. <https://doi.org/10.1016/j.scitotenv.2020.143939>. Epub 2020 Nov 28 PMID: 33310218.
20. Dos Santos EA, Filho USDS, Barroso GM, Rocha BPJS, Possato EL. Tolerance and remedial potential of trees submitted to atrazine and sulfentrazone in the rhizosphere. *Int J Phytoremediation*. 2020;22(1):78–86. <https://doi.org/10.1080/15226514.2019.1644290>. Epub 2019 Jul 31 PMID: 31364395.
21. Li J, Xu Y, Shan Y, Pei X, Yong S, Liu C, Yu J. Assembly of the complete mitochondrial genome of an endemic plant, *Scutellaria tsinyunensis*, revealed the existence of two conformations generated by a repeat-mediated recombination. *Planta*. 2021;254(2):36. <https://doi.org/10.1007/s00425-021-03684-3>. PMID: 34302538.
22. Jackman SD, Coombe L, Warren RL, Kirk H, Trinh E, MacLeod T, Pleasance S, Pandoh P, Zhao Y, Coope RJ, Bousquet J, Bohlmann J, Jones SJM, Birol I. Complete Mitochondrial Genome of a Gymnosperm, Sitka Spruce (*Picea sitchensis*), Indicates a Complex Physical Structure. *Genome Biol Evol*. 2020;12(7):1174–9. <https://doi.org/10.1093/gbe/evaa108>. PMID:32449750;PMCID:PMC7486957.
23. Aleix-Mata G, Ruiz-Ruano FJ, Pérez JM, Sarasa M, Sánchez A. Complete mitochondrial genome of the Western Capercaillie Tetrao urogallus (Phasianidae, Tetraoninae). *Zootaxa*. 2019;4550(4):585–93. <https://doi.org/10.11646/zootaxa.4550.4.9>. PMID: 30790836.
24. Liu H, Yu J, Yu X, Zhang D, Chang H, Li W, Song H, Cui Z, Wang P, Luo Y, Wang F, Wang D, Li Z, Huang Z, Fu A, Xu M. Structural variation of mitochondrial genomes sheds light on evolutionary history of soybeans. *Plant J*. 2021;108(5):1456–72. <https://doi.org/10.1111/tpj.15522>. Epub 2021 Oct 13 PMID: 34587339.
25. Hisano H, Tsujimura M, Yoshida H, Terachi T, Sato K. Mitochondrial genome sequences from wild and cultivated barley (*Hordeum vulgare*). *BMC Genomics*. 2016;17(1):824. <https://doi.org/10.1186/s12864-016-3159-3>. PMID:27776481;PMCID:PMC5078923.
26. Huo TB, Peng L, Jiang ZF, Lu J. Complete mitochondrial genome of the *Lampetra reissneri*. *Mitochondrial DNA A DNA Mapp Seq Anal*. 2016;27(2):1795–6. <https://doi.org/10.3109/19401736.2014.947597>. Epub 2014 Aug 8 PMID: 25103436.
27. Park J, Xi H, Kim Y, Nam S, Heo KI. The complete mitochondrial genome of new species candidate of *Rosa rugosa* (Rosaceae). *Mitochondrial DNA B Resour*. 2020;5(3):3435–7. <https://doi.org/10.1080/23802359.2020.1821820>. PMID:33458196;PMCID:PMC7782103.
28. Makarenko MS, Omelchenko DO, Usatov AV, Gavrilova VA. The Insights into Mitochondrial Genomes of Sunflowers. *Plants* (Basel). 2021;10(9):1774. <https://doi.org/10.3390/plants10091774>. PMID:34579307;PMCID:PMC8466785.
29. Small RL, Wendel JF. The mitochondrial genome of allotetraploid cotton (*Gossypium* L.). *J Hered*. 1999;90(1):251–3. <https://doi.org/10.1093/jhered/90.1.251>. PMID: 9987935.
30. Dong S, Chen L, Liu Y, Wang Y, Zhang S, Yang L, Lang X, Zhang S. The draft mitochondrial genome of *Magnolia biondii* and mitochondrial phylogenomics of angiosperms. *PLoS One*. 2020;15(4):e0231020. <https://doi.org/10.1371/journal.pone.0231020>. PMID: 32294100; PMCID: PMC7159230.
31. Zhang W, Li L, Li G. Characterization of the complete chloroplast genome of shrubby sophora (*Sophora flavescens* Ait.). *Mitochondrial DNA B Resour*. 2018;3(2):1282–3. <https://doi.org/10.1080/23802359.2018.1532839>. PMID: 33490578; PMCID: PMC7800985.
32. Jang W, Lee HO, Lee JW, Kwon N, Kim DH, Bang KH, Jo IH. The complete mitochondrial genome of *Panax ginseng* (Apiales, Araliaceae): an important medicinal plant. *Mitochondrial DNA B Resour*. 2021;6(10):3080–1. <https://doi.org/10.1080/23802359.2021.1981167>. PMID:34595343;PMCID:PMC8477949.
33. Wang X, Xiao Y, He ZH, Li LL, Song HY, Zhang JJ, Cheng X, Chen XY, Li P, Hu XS. A Chromosome-Level Genome Assembly of *Toona ciliata* (Meliaceae). *Genome Biol Evol*. 2022;14(8):121. <https://doi.org/10.1093/gbe/evac121>. PMID: 35880739; PMCID: PMC9348625.
34. Nie P, Qu F, Lin L, He Y, Feng X, Yang L, Gao H, Zhao L, Huang L. Trace Identification and Visualization of Multiple Benzimidazole Pesticide Residues on *Toona sinensis* Leaves Using Terahertz Imaging Combined with Deep Learning. *Int J Mol Sci*. 2021;22(7):3425. <https://doi.org/10.3390/ijms22073425>. PMID:33810447;PMCID:PMC8037687.
35. Gautam A, Jhade D, Ahirwar D, Sujane M, Sharma GN. Pharmacognostic evaluation of *toona ciliata* bark. *J Adv Pharm Technol Res*. 2010;1(2):216–20 PMID: 22247848; PMCID: PMC3255442.
36. Liu J, Jiang JM. Sampling strategies for natural *Toona ciliata* populations. *Genet Mol Res*. 2016;15(4). <https://doi.org/10.4238/gmr15047751>. PMID: 27813550.
37. Liu B, Zhang J, Shi Y. Complete chloroplast genome of *Toona sinensis* (Meliaceae), a goliathous "tree vegetables." *Mitochondrial DNA B Resour*. 2019;4(2):3025–6. <https://doi.org/10.1080/23802359.2019.1666664>. PMID: 33365839;PMCID:PMC7706505.
38. Liu J, Sun ZX, Chen YT, Jiang JM. Isolation and characterization of microsatellite loci from an endangered tree species, *Toona ciliata* var. *pubescens*. *Genet Mol Res*. 2012;11(4):4411–7. <https://doi.org/10.4238/2012.September.194>. PMID: 23079981.
39. Abdel-Latif A, Osman G. Comparison of three genomic DNA extraction methods to obtain high DNA quality from maize. *Plant Methods*. 2017;3(13):1. <https://doi.org/10.1186/s13007-016-0152-4>. PMID:28053646; PMCID:PMC5209869.
40. Vennapusa AR, Somayanda IM, Doherty CJ, Jagadish SVK. A universal method for high-quality RNA extraction from plant tissues rich in starch, proteins and fiber. *Sci Rep*. 2020;10(1):16887. <https://doi.org/10.1038/s41598-020-73958-5>. PMID:33037299;PMCID:PMC7547072.
41. Huptas C, Scherer S, Wenning M. Optimized Illumina PCR-free library preparation for bacterial whole genome sequencing and analysis of factors influencing de novo assembly. *BMC Res Notes*. 2016;12(9):269.

- <https://doi.org/10.1186/s13104-016-2072-9>. PMID:27176120;PMCID: PMC4864918.
42. Panaro NJ, Yuen PK, Sakazume T, Fortina P, Kricka LJ, Wilding P. Evaluation of DNA fragment sizing and quantification by the agilent 2100 bioanalyzer. *Clin Chem*. 2000;46(11):1851–3. PMID: 11067828.
  43. Kirchner TW, Niehaus M, Debener T, Schenk MK, Herde M. Efficient generation of mutations mediated by CRISPR/Cas9 in the hairy root transformation system of *Brassica carinata*. *PLoS One*. 2017;12(9):e0185429. <https://doi.org/10.1371/journal.pone.0185429>. PMID: 28937992; PMCID: PMC5609758.
  44. Al-Nakeeb K, Petersen TN, Sicheritz-Pontén T. Norgal: extraction and de novo assembly of mitochondrial DNA from whole-genome sequencing data. *BMC Bioinformatics*. 2017;18(1):510. <https://doi.org/10.1186/s12859-017-1927-y>. PMID:29162031;PMCID:PMC5699183.
  45. Bolger AM, Lohse M, Usadel B. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*. 2014;30(15):2114–20. <https://doi.org/10.1093/bioinformatics/btu170>. Epub 2014 Apr 1. PMID: 24695404; PMCID: PMC4103590.
  46. Shulze CN, Cole BJ, Ciobanu D, Lin J, Yoshinaga Y, Gouran M, Turco GM, Zhu Y, O'Malley RC, Brady SM, Dickel DE. High-Throughput Single-Cell Transcriptome Profiling of Plant Cell Types. *Cell Rep*. 2019;27(7):2241–2247.e4. <https://doi.org/10.1016/j.celrep.2019.04.054>. PMID:31091459;PMCID:PMC6758921.
  47. Xu M, Guo L, Gu S, Wang O, Zhang R, Peters BA, Fan G, Liu X, Xu X, Deng L, Zhang Y. TGS-GapCloser: A fast and accurate gap closer for large genomes with low coverage of error-prone long reads. *Gigascience*. 2020;9(9):giaa094. <https://doi.org/10.1093/gigascience/giaa094>. PMID: 32893860; PMCID: PMC7476103.
  48. Liu C, Shi L, Zhu Y, Chen H, Zhang J, Lin X, Guan X. CpGAVAS, an integrated web server for the annotation, visualization, analysis, and GenBank submission of completely sequenced chloroplast genome sequences. *BMC Genomics*. 2012;20(13):715. <https://doi.org/10.1186/1471-2164-13-715>. PMID:23256920;PMCID:PMC3543216.
  49. Wyman SK, Jansen RK, Boore JL. Automatic annotation of organellar genomes with DOGMA. *Bioinformatics*. 2004;20(17):3252–5. <https://doi.org/10.1093/bioinformatics/bth352>. Epub 2004 Jun 4. PMID: 15180927.
  50. Chan PP, Lin BY, Mak AJ, Lowe TM. tRNAscan-SE 2.0: improved detection and functional classification of transfer RNA genes. *Nucleic Acids Res*. 2021;49(16):9077–96. <https://doi.org/10.1093/nar/gkab688>. PMID: 34417604; PMCID: PMC8450103.
  51. Liu XF, Zhu GF, Li DM, Wang XJ. Complete chloroplast genome sequence and phylogenetic analysis of *Spathiphyllum* "Parrish." *PLoS One*. 2019;14(10):e0224038. <https://doi.org/10.1371/journal.pone.0224038>. PMID: 31644545; PMCID: PMC6808432.
  52. Abascal F, Zardoya R, Posada D. ProtTest: selection of best-fit models of protein evolution. *Bioinformatics*. 2005;21(9):2104–5. <https://doi.org/10.1093/bioinformatics/bti263>. Epub 2005 Jan 12. PMID: 15647292.
  53. Tamura K, Stecher G, Kumar S. MEGA11: molecular evolutionary genetics analysis version 11. *Mol Biol Evol*. 2021;38(7):3022–7. <https://doi.org/10.1093/molbev/msab120>. PMID:33892491;PMCID:PMC8233496.
  54. Tang M, Chen Z, Grover CE, Wang Y, Li S, Liu G, Ma Z, Wendel JF, Hua J. Rapid evolutionary divergence of *Gossypium barbadense* and *G. hirsutum* mitochondrial genomes. *BMC Genomics*. 2015;16:770. <https://doi.org/10.1186/s12864-015-1988-0>. PMID: 26459858; PMCID: PMC4603758.
  55. Kersten B, Favre Rampant P, Mader M, Le Paslier MC, Bounon R, Berard A, Vettori C, Schroeder H, Leplé JC, Fladung M. Genome Sequences of *Populus tremula* Chloroplast and Mitochondrion: Implications for Holistic Poplar Breeding. *PLoS One*. 2016;11(1):e0147209. <https://doi.org/10.1371/journal.pone.0147209>. PMID: 26800039; PMCID: PMC4723046.
  56. Lohse M, Drechsel O, Bock R. OrganellarGenomeDRAW (OGDRAW): a tool for the easy generation of high-quality custom graphical maps of plastid and mitochondrial genomes. *Curr Genet*. 2007;52(5–6):267–74. <https://doi.org/10.1007/s00294-007-0161-y>. Epub 2007 Oct 24. PMID: 17957369.
  57. Arnold C, Clewley JP. From ABI sequence data to LASERGENE's EDITSEQ. *Methods Mol Biol*. 1997;70:65–74. <https://doi.org/10.1385/0-89603-358-9:65>. PMID: 9089603.
  58. Sharp PM, Li WH. The codon Adaptation Index—a measure of directional synonymous codon usage bias, and its potential applications. *Nucleic Acids Res*. 1987;15(3):1281–95. <https://doi.org/10.1093/nar/15.3.1281>. PMID:3547335;PMCID:PMC340524.
  59. Ma QP, Li C, Wang J, Wang Y, Ding ZT. Analysis of synonymous codon usage in FAD7 genes from different plant species. *Genet Mol Res*. 2015;14(1):1414–22. <https://doi.org/10.4238/2015.February.13.20>. PMID: 25730080.
  60. Beier S, Thiel T, Münch 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>. PMID:28398459;PMCID:PMC5870701.
  61. Hao W, Palmer JD. Fine-scale mergers of chloroplast and mitochondrial genes create functional, transcompartmentally chimeric mitochondrial genes. *Proc Natl Acad Sci U S A*. 2009;106(39):16728–33. <https://doi.org/10.1073/pnas.0908766106>. Epub 2009 Sep 15. PMID: 19805364; PMCID: PMC2757801.
  62. Tsunewaki K. Interorganellar DNA transfer in wheat: dynamics and phylogenetic origin. *Proc Jpn Acad Ser B Phys Biol Sci*. 2011;87(8):529–49. <https://doi.org/10.2183/pjab.87.529>. PMID:21986316;PMCID:PMC3313693.
  63. Richardson AO, Rice DW, Young GJ, Alverson AJ, Palmer JD. The "fossilized" mitochondrial genome of *Liriodendron tulipifera*: ancestral gene content and order, ancestral editing sites, and extraordinarily low mutation rate. *BMC Biol*. 2013;15(11):29. <https://doi.org/10.1186/1741-7007-11-29>. PMID: 23587068;PMCID:PMC3646698.
  64. Joyce PB, Gray MW. Chloroplast-like transfer RNA genes expressed in wheat mitochondria. *Nucleic Acids Res*. 1989;17(14):5461–76. <https://doi.org/10.1093/nar/17.14.5461>. PMID:2762145;PMCID:PMC318170.
  65. Miyata S, Nakazono M, Hirai A. Transcription of plastid-derived tRNA genes in rice mitochondria. *Curr Genet*. 1998;34(3):216–20. <https://doi.org/10.1007/s002940050389>. PMID: 9745025.
  66. Lin HS, Chiang CY, Chang SB, Kuoh CS. Development of Simple Sequence Repeats (SSR) markers in *Setaria italica* (Poaceae) and cross-amplification in related species. *Int J Mol Sci*. 2011;12(11):7835–45. <https://doi.org/10.3390/ijms12117835>. Epub 2011 Nov 11. PMID: 22174636; PMCID: PMC3233442.
  67. Rafalski JA, Tingey SV. Genetic diagnostics in plant breeding: RAPDs, microsatellites and machines. *Trends Genet*. 1993;9(8):275–80. [https://doi.org/10.1016/0168-9525\(93\)90013-8](https://doi.org/10.1016/0168-9525(93)90013-8). PMID: 8104363.
  68. Pugh T, Fouet O, Risterucci AM, Brottier P, Abouladze M, Deletrez C, Courtois B, Clement D, Larmande P, N'Goran JA, Lanaud C. A new cacao linkage map based on codominant markers: development and integration of 201 new microsatellite markers. *Theor Appl Genet*. 2004;108(6):1151–61. <https://doi.org/10.1007/s00122-003-1533-4>. Epub 2004 Feb 4. PMID: 14760486.
  69. Liu J, Gao S, Xu Y, Wang M, Ngiam JJ, Rui Wen NC, Yi JJJ, Weng X, Jia L, Salojärvi J. Genetic Diversity Analysis of *Sapindus* in China and Extraction of a Core Germplasm Collection Using EST-SSR Markers. *Front Plant Sci*. 2022;13:857993. <https://doi.org/10.3389/fpls.2022.857993>. PMID: 35685004; PMCID: PMC9171133.
  70. Boyung Liao, Fang Wang, Lijun Chen, Pei Li, Kunxi Ouyang, Ruiqi Pian, Mingqian Liu, Qingmin Que, Xiangbin Zhou, Wenkai Xi, Xiaoyang Chen. Population Structure and Genetic Relationships of *Melia* Taxa in China Assayed with Sequence-Related Amplified Polymorphism (SRAP) Markers. *Forests*. 2016;7(4). <https://doi.org/10.3390/f7040081>.
  71. Zuo R, Jiang P, Sun C, Chen C, Lou X. [Analysis of the chloroplast genome characteristics of *Rhus chinensis* by de novo sequencing]. *Sheng Wu Gong Cheng Xue Bao*. 2020;36(4):772–781. Chinese. <https://doi.org/10.13345/j.cjb.190354>. PMID: 32347071.
  72. Buerki S, Callmänder MW, Acevedo-Rodríguez P, Lowry PP 2nd, Munzinger J, Bailey P, Maurin O, Brewer GE, Epitawalage N, Baker WJ, Forest F. An updated infra-familial classification of Sapindaceae based on targeted enrichment data. *Am J Bot*. 2021;108(7):1234–51. <https://doi.org/10.1002/ajb2.1693>. Epub 2021 Jul 5. Erratum in: *Am J Bot*. 2022 Aug;109(8):1326–1327. PMID: 34219219; PMCID: PMC8361682.
  73. Hedtke B, Wagner I, Börner T, Hess WR. Inter-organellar crosstalk in higher plants: impaired chloroplast development affects mitochondrial gene and transcript levels. *Plant J*. 1999;19(6):635–43. <https://doi.org/10.1046/j.1365-3113.1999.00554.x>. PMID: 10571849.
  74. Sun C, Lin H. The complete chloroplast genome and phylogenetic analysis of *Citrus clementina* (Rutaceae). *Mitochondrial DNA B Resour*. 2021;6(10):2926–7. <https://doi.org/10.1080/23802359.2021.1972860>. PMID:34532587;PMCID:PMC8439215.

## Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.