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PLASTOME REPORT

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The plastid genome and phylogenetic status of *Sinosenecio eriopodus* C. Jeffrey & Y. L. Chen 1984 (Asteraceae)

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ABSTRACT

The genus *Sinosenecio* B. Nordenstam (1978) is a challenging taxonomic group with complex infrageneric relationships. Here, we newly report the plastid genome of S. *eriopodus* (Cumm.) C. Jeffrey & Y. L. Chen (1984). Whole genome exhibited a typical quadratic structure with a total size of 151,212 bp and 132 genes. We revealed for the first time that the matK and rpoA were positively selected genes within *Sinosenecio*. Phylogenetic reconstruction based on whole plastid genome sequences indicated that *S. eriopodus* was not clustered into a monophyletic clade with members belonging to the S. *oldhamianus* group of *Sinosenecio* but rather was closely related to some genera in the subtribe Tussilaginae s.s. of Asteraceae.

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Asteraceae; *Sinosenecio eriopodus*; plastid genome; adaptive evolution; phylogeny

Introduction

The genus *Sinosenecio* B. Nordenstam (1978), a group of perennial or sometimes annual or biennial herbs within the family Asteraceae, is home to approximately 47 species predominantly found in the central and southwestern regions of China (Liu 2010; Liu and Yang 2011a, 2011b; 2012; Liu et al. 2019; Zou et al. 2020; Chen et al. 2022; Peng et al. 2022; Su et al. 2023a,b). Prior cytology, floral micromorphology and molecular DNA studies have indicated that *Sinosenecio* was polyphyletic, with rather complex relationships to the genera *Ligularia* Cass., *Parasenecio* W. W. Sm. & J. Small, *Petasites* Mill., *Nemosenecio* (Kitam.) B. Nord. and *Tephroseris* (Rchb.) Rchb. (Wang et al. 2009; Liu and Yang 2011a, 2011b). Currently, the genus is recognized as divisible into two species assemblages: the *Sinosenecio s.s.* group and the *S. oldhamianus* group, with different chromosome count ($x = 30$ vs. 24 or 13), patterns of endothecial cell wall thickenings (strictly polarized vs. polarized and radial), and phylogenetic affliation (subtribe Tussilagininae *s.s.* vs. subtribe Thephroseridinae) (Liu 2010; Liu and Yang 2011a, 2011b; 2012; Liu et al. 2019; Zou et al. 2020; Peng et al. 2022).

As an ideal molecular resource, the plastid genome has fully penetrated the research fields of phylogenetics and evolutionary biology. The plastid genomes of diverse plant taxa exhibit fine collinearity for comparative analysis, while genomic variation is also important for unraveling large-scale evolution (Zhang and Li 2011; Wang et al. 2023). In recent years, as more and more plastid genomes from species of the *S. oldhamianus* group were published (Xu et al. 2019; Zhou et al. 2021; Peng et al. 2022; Xie et al. 2022; Wang et al. 2024), a foundation has been laid for the study of the genetic structure and genetic diversity of plastomes in the genus. In this context, we newly report the plastid genome of *S. eriopodus* C. Jeffrey & Y. L. Chen (1984), a member from the *Sinosenecio s.s.* group, which marks another significant stride in enriching the genetic repository for *Sinosenecio*. Our aims were (1) to explore the adaptive evolution of *Sinosenecio* combined with available plastome data and (2) to clarify the *S. eriopodus* phylogenetic status. The present work through genomic insights is expected to enhance our understanding and grasp the evolutionary process of this genus.

Materials and methods

Plant sampling, DNA extraction and sequencing

The living plant *S. eriopodus* (Figure 1) in this study was collected from Wufeng county, Hubei, China (30°1′17.12″ N, 110°45′59.60″ E). Voucher specimen (JIUzhou01) and its DNA materials were deposited at the herbarium of Jishou University (Hunan, China) (Qiang Zhou, zhouqiang@jsu.edu.cn). Plant material used for sequencing was silica gel-dried leaf. Total genomic DNA extraction, library preparation, and sequencing were performed by Novogene (Beijing, China), and the library was sequenced on the Illumina Hiseq 4000 platform.

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Plastid genome assembly and annotation

A total of 1.8 GB of clean data (paired-end sequencing) were assembled into the plastome sequence using GetOrganelle (Jin et al. 2020). To ensure the accuracy of the assembly, the coverage depth was measured by mapping reads onto the plastid genome sequence using bowtie2 (Langmead and Salzberg 2012). The resulting genome sequence was annotated *via* the website Geseq (https://chlorobox.mpimp-golm.mpg.de/geseq.html) (Tillich et al. 2017), and the annotations were reviewed and refined for checking and correcting start and stop codons using Geneious v.9.0.2 with the plastid genomes of other *Sinosenecio* species as references. Finally, the fully annotated plastome of *S. eriopodus* was subsequently archived in the NCBI GenBank database (https://www.ncbi.nlm.nih.gov) under the accession number PQ164523. Additionally, to visually represent the plastid genome and splicing genes, the Chloroplot (Zheng et al. 2020) and the Chloroplast Genome Viewer (CPGView) (Liu et al. 2023) tools were employed to create a detailed genome map.

Phylogeny reconstruction

Our phylogenetic matrix included 15 species plastid sequences (14 sequences obtained from NCBI). These sequences were aligned using MAFFT (Katoh and Standley 2013), of which 13 species belong to the tribe Senecioneae and two to the tribe Anthemideae (*Chrysanthemum indicum* L. (1753) and *Soliva sessilis* Ruiz & Pav. (1794)). The maximum likelihood (ML) analysis was executed through RAxML v.8.2.10 under the GTRGAMMA model with 1,000 bootstrap replicates on Cipres Portal (https://www.phylo.org/portal2) (Stamatakis 2014), and *C. indicum* and *S. sessilis* were selected to serve as outgroups in this phylogenetic reconstruction. Besides, plastid genome sequences obtained from NCBI were used for downstream analysis.

Adaptive evolution analysis

Considering the non-monophyletic nature of *Sinosenecio* and in order to reduce evolutionary bias, we selected 11 species used in phylogenetic reconstruction for adaptive evolution analysis on the Genepioneer platform (http://cloud.genepioneer.com:9929). We chose six *Sinosenecio* species (*S. oldhamianus* (Maxim.) B.Nord. (1978), *S. jishouensis* D.G.Zhang, Ying Liu & Q.E.Yang (2008), *S. baojingensis* Ying Liu & Q.E.Yang (2009), *S. albonervius* Ying Liu & Q.E.Yang (2011), *S. globigerus* (C.C.Chang) B.Nord. (1978) and *S. eriopodus*) in turn as a reference to *Ligularia intermedia* Nakai (1917), *L. jaluensis* Kom. (1901), *L.*

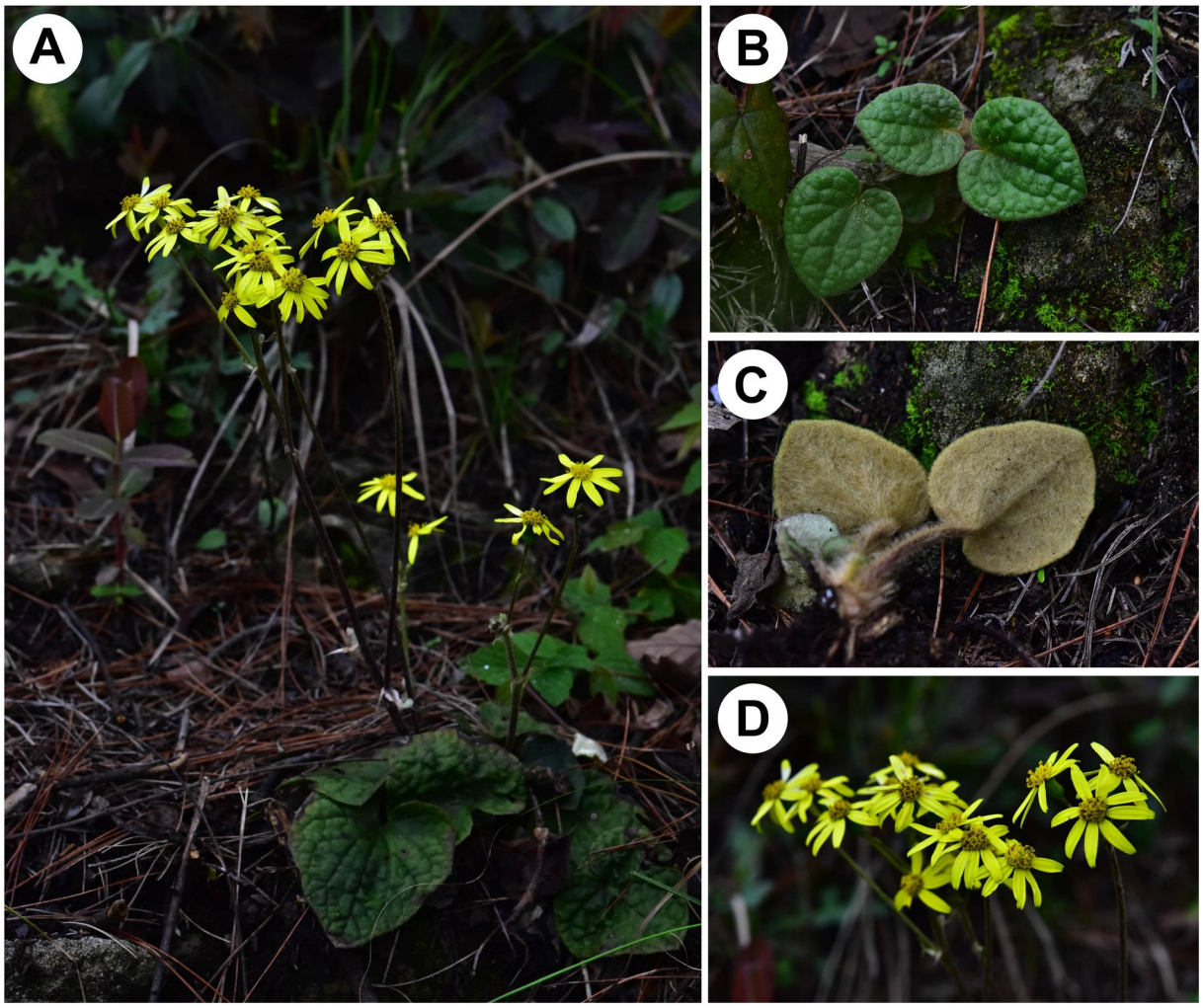

Figure 1. Photographs of (A) individual plant, (B,C) leaves, and (D) inflorescence of *Sinosenecio eriopodus* taken by Cheng Zhang in Wufeng county, Hubei, China. Leaves radical and few, abaxially densely lanate with fulvous hairs or sericeous, adaxially sparsely sericeous-villous and densely adpressed puberulent, capitula 8–13, involucres without outer bracts, flowers with pappus are characteristics of the species.

fischeri (Ledeb.) Turcz. (1847), *Parasenecio latipes* (Franch.) Y.L.Chen (1999) and *P. palmatisectus* (Jeffrey) Y.L.Chen (1999) for the alignment of 79 shared protein-coding gene sequences (CDS) with the following settings in calculating the Ka/Ks values (Ka/Ks: the ratio of non-synonymous to synonymous nucleotide substitution rates): genetic code table 11 (bacterial and plant plastid code); method: YN (Ivanova et al. 2017).

Results

We obtained an average sequencing depth of 671.66× for the *S. eriopodus* plastid genome (Figure S1), which exhibited a typical quadratic structure with a total size of 151,212 bp, along with a pair of inverted repeat regions (IRs) of 24,835 bp, a large single-copy region (LSC) of 83,339 bp, and a small single-copy region (SSC) of 18,203 bp (Figure 2). The genome contained 132 annotated genes, including 88 genes that encode for proteins (CDS), 36 genes for transfer RNA (tRNA), and 8 genes for ribosomal RNA (rRNA). Among them, 11 cis-splicing genes—*rps*16, *atp*F, *rpo*C1, *ycf*3, *clp*P, *pet*B, *pet*D, *rpl*16, *rpl*2, *ndh*A and *ndh*B, and one single trans-splicing gene—*rps*12, have been identified (Figure S2). Moreover, the overall GC content of the plastid genome was 37.4%, with the IR, LSC, and SSC regions showing GC percentages of 43.0%, 35.6%, and 30.7%, respectively.

To test the *S. eriopodus* phylogenetic position, we constructed a matrix of plastid genomic dataset containing 158,922 bp, generating a ML phylogenetic tree with excellent resolution (Figure 3). In our phylogenetic result, *Sinosenecio* species were not all clustered together but were resolved into two clades. The first clade consisted of members from the *S. oldhamianus* group (BS = 100), and was sister to the

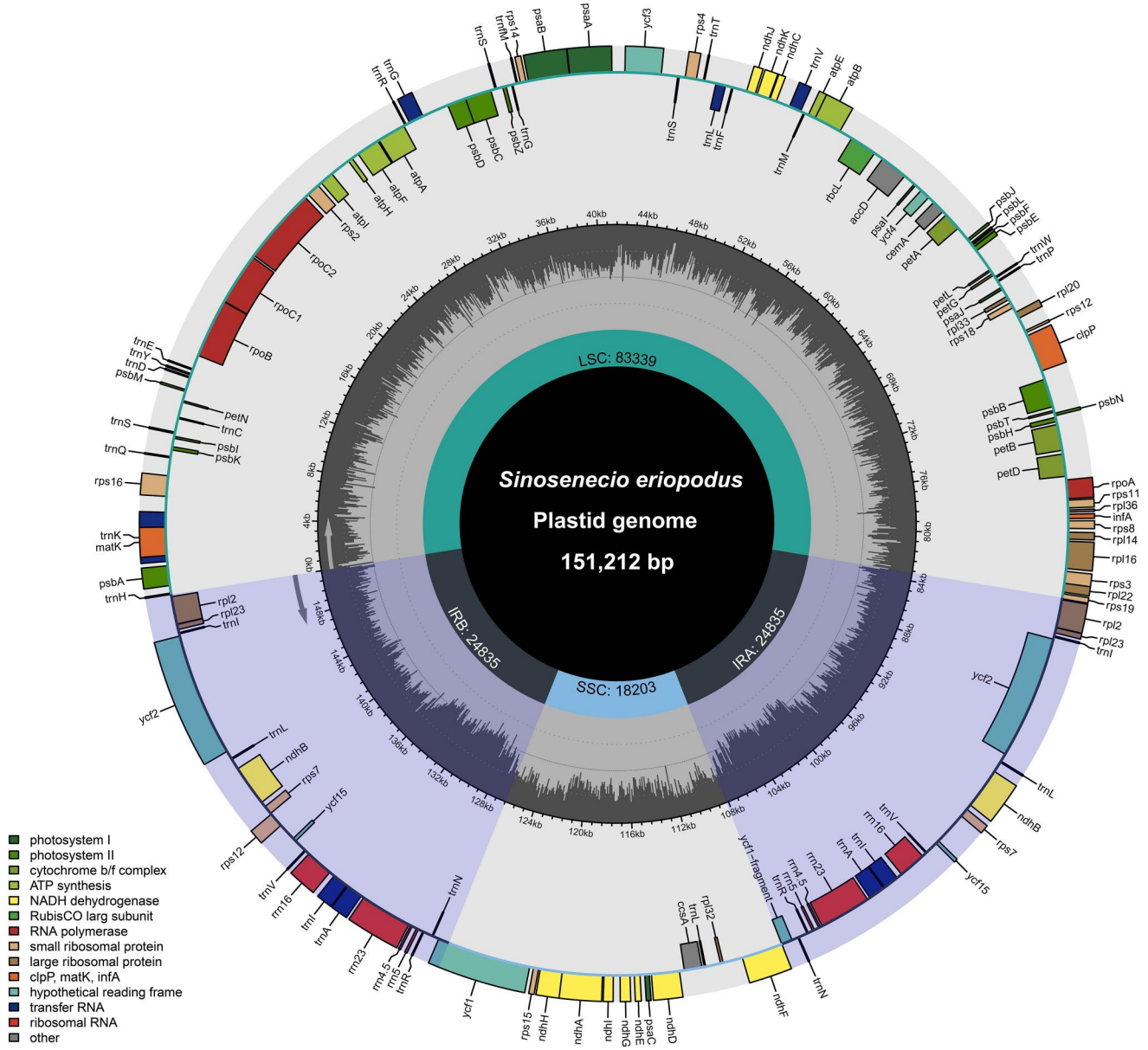

Figure 2. The plastid genome map of *Sinosenecio eriopodus* was drawn using the Chloroplot to show the genes present in each region (LSC, SSC and IRs). The transcription directions for the inner and outer genes are clockwise and anticlockwise, respectively, and each functional group of genes is distinctively color-marked. In the inner circle, the darker gray shades represent the GC content, and the lighter gray shades signify the AT content.

clade formed by *Ligularia* and *Parasenecio* (BS = 100), while the second clade was represented only by *S. eriopodus* belonging to the *Sinosenecio s.s.* group.

We separately calculated ka/ks values for 79 CDS in *S. oldhamianus*, *S. jishouensis*, *S. baojingensis*, *S. albonervius*, *S. globigerus* and *S. eriopodus*, respectively, and then averaged the Ka/Ks values for the same CDS as their respective final Ka/Ks to assess the adaptive evolution of *Sinosenecio*. The Ka/Ks > 1 and <1 indicated that the gene was under positive selection and purifying selection, respectively. Our analysis (Figure S3) found that almost all of the genes were undergoing strong purifying selection in the *Sinosenecio* plastome, but with the exception of *mat*K and *rpo*A, both were subjected to positive selection (*mat*K$^{Ka/Ks=1.64}$, *rpo*A$^{Ka/Ks=1.42}$). Additionally, 25 genes (*atp*F, *cem*A, *ndh*B, *ndh*C, *pet*N, *psb*E, *psb*F, *psb*H, *psb*I, *psb*J, *psb*L, *psb*M, *psb*N, *psb*Z, *rpl*2, *rpl*23, *rpl*36, *rps*12, *rps*14, *rps*15, *rps*16, *rps*18, *rps*7, *ycf*15 and *ycf*3) yielded the indeterminate Ka/Ks value (Ka/Ks = NA).

Discussion and conclusions

The *S. eriopodus* plastome was structurally similar to that of other *Sinosenecio* species and was more consistent in terms of gene counts (Xu et al. 2019; Zhou et al. 2021; Peng et al. 2022; Xie et al. 2022; Wang et al. 2024), suggesting that the plastid genomes of species in this genus were highly conserved. We reconstructed the phylogeny of *Sinosenecio* based on the whole plastid genome sequence and determined the *S. eriopodus* phylogenetic position. Compared with prior phylogenomics that sampled exclusively within the *S. oldhamianus* group (Xu et al. 2019; Zhou et al. 2021; Peng et al. 2022; Xie et al. 2022; Wang et al. 2024), the present study reaffirmed the polyphyly of *Sinosenecio*. The relationships among the five species of the *S. oldhamianus* group have been supported in previous studies (Zou et al. 2020; Wang et al. 2024), and this group was closely related to some genera of the subtribe Tephroseridinae (such as *Nemosenecio* and *Tephroseris*) (Liu 2010; Zou et al. 2020). As a member of the *Sinosenecio s.s.* group, *S. eriopodus* was phylogenetically close to the subtribe Tussilaginae *s.s.*, and these plants also showed a remarkable correspondence in chromosome number ($x = 30$) and patterns of endothecial cell wall thickenings (strictly polarized) (Liu 2010; Zou et al. 2020). Besides, we further explored the adaptive evolution of *Sinosenecio*. Adaptive evolution of plastomes was a common phenomenon, as the environment can exert a strong selective force on the evolution of plant organisms (Ai et al. 2015), while the ratio of non-synonymous to synonymous nucleotide substitution rates (Ka/Ks) was an important measure of gene selective pressure (Hurst 2002). However, we detected positive selection only for *mat*K and *rpo*A genes in *Sinosenecio* plastomes. The *rpo*A encoded the alpha subunit of RNA polymerase, while the *mat*K was one of the fastest evolutionary genes, playing a significant role in light-regulated activities and plant development (Huang et al. 2021; Wen et al. 2024). These two genes being positively selected may represent a response of *Sinosenecio* species to adapt to the environment. Our result also indicated most genes were under strong

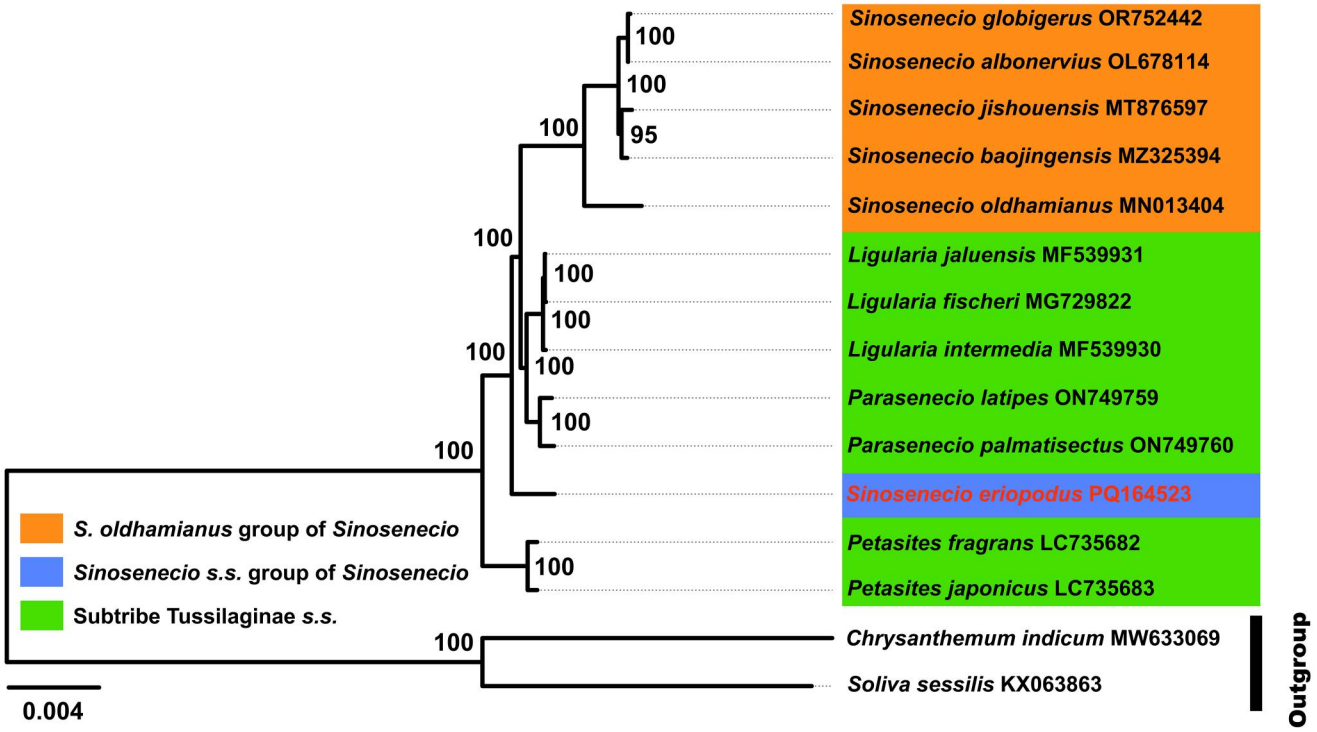

Figure 3. The ML phylogenetic tree with bootstrap (BS) values was constructed based on 15 whole plastid genome sequences, with *Chrysanthemum indicum* and *Soliva sessilis* being used as outgroups, and the scale bar (0.004) was available to specify clade lengths. The phylogenetic position of *S. eriopodus* (genbank accession: PQ164523) is highlighted in red font. Plastome sequences of the species used are as follows: *Ligularia fischeri* MG729822 (Liu et al. 2023), *Ligularia jaluensis* MF539931 (Liu et al. 2023), *Ligularia intermedia* MF539930 (Liu et al. 2023), *Parasenecio latipes* ON749759 (Liu et al. 2023), *Parasenecio palmatisectus* ON749760 (Liu et al. 2023), *Sinosenecio globigerus* OR752442 (Wang et al. 2024), *Sinosenecio albonervius* OL678114 (Peng et al. 2022), *Sinosenecio baojingensis* MZ325394 (Xie et al. 2022), *Sinosenecio jishouensis* MT876597 (Zhou et al. 2021), *Sinosenecio oldhamianus* MN013404 (Xu et al. 2019), *Petasites fragrans* LC735682 (Liu et al. 2023), *Petasites japonicus* LC735683 (Liu et al. 2023), *Chrysanthemum indicum* MW633069 (Liu et al. 2023), *Soliva sessilis* KX063863 (Liu et al. 2023).

purifying selection, a prevalent mechanism in natural selection that continuously eliminated harmful mutations (Wu et al. 2020). Therefore, these genes with purifying selection may be able to retain conserved functions in *Sinosenecio* plants.

In conclusion, this study successfully assembled the *S. eriopodus* plastid genome and identified *mat*K and *rpo*A genes subjected to positive selection within *Sinosenecio* for the first time, which enriches the genomic resources while providing some insights into the plastome evolution and phylogenetic relationships of the genus.

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Ethical approval

The plant material used in the study complied with national and international standards and local laws and regulations. No endangered or protected species were involved in the study, and the collecting of the samples did not require specific permission from authorities.

Authors' contributions

Yao Sun and Qiang Zhou planned and designed the research. Cheng Zhang collected plant materials. Yao Sun, Cheng Zhang and Qiang Zhou performed experiments. Yao Sun and Jingyi Peng analyzed the data. Yao Sun wrote the manuscript. All authors agree to be accountable for all aspects of the work.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Data availability statement

The newly sequenced and assembled plastid genome data in this study has been submitted to the GenBank of NCBI (https://www.ncbi.nlm.nih.gov/) under the GenBank accession PQ164523. The associated BioProject, BioSample, and SRA numbers are PRJNA1147002, SAMN43141378, and SRR30207665, respectively.

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