







# The complete chloroplast genome sequence of *Psittacanthus schiedeanus* (Cham. & Schltdl.) G.Don. (Santalales: Loranthaceae), the first plastome of a mistletoe species in the Psittacanthae tribe

Saddan Morales-Saldaña<sup>a</sup> , Emanuel Villafán<sup>b</sup> , Antonio Acini Vásquez-Aguilar<sup>a</sup> , Santiago Ramírez-Barahona<sup>c</sup> , Enrique Ibarra-Laclette<sup>b</sup>  and Juan Francisco Ornelas<sup>a</sup> 

<sup>a</sup>Red de Biología Evolutiva, Instituto de Ecología, A.C. (INECOL), Xalapa, Veracruz, Mexico; <sup>b</sup>Red de Estudios Moleculares Avanzados, Instituto de Ecología, A.C. (INECOL), Xalapa, Veracruz, Mexico; <sup>c</sup>Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, Mexico

## ABSTRACT

*Psittacanthus schiedeanus* (Cham. & Schltdl.) G.Don., 1834, is a mistletoe species in the Loranthaceae, characteristic of the canopy in cloud forest edges and widely distributed in northern Mesoamerica. Here, we report the complete chloroplast genome sequence of *P. schiedeanus*, the first for a species in the Psittacanthae tribe. The circularized quadripartite structure of the *P. schiedeanus* chloroplast genome was 122,586 bp in length and included a large single-copy region of 72,507 bp and two inverted repeats of 21,283 bp separated by a small single-copy region of 7,513 bp. The genome contained 112 genes, of which 96 are unique, including 65 protein-coding genes, 27 transfer RNA, and four ribosomal RNA. The overall GC content in the plastome of *P. schiedeanus* is 36.9%. Based on 43 published complete chloroplast genome sequences for species in the families Loranthaceae and Santalaceae (Santalales), the maximum-likelihood phylogenetic tree with high-support bootstrap values indicated that *P. schiedeanus* in the Psittacanthae tribe is sister to the tribe Loranthaeae. The chloroplast genome provided in this study represents a valuable resource for genetic, phylogenetic and conservation studies of *Psittacanthus* species, and an important advance for unraveling the evolutionary history of these hemiparasitic plants.

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*Psittacanthus*; chloroplast genome (cpDNA); hemiparasitic plants; mistletoes; Loranthaceae


## Introduction

The Loranthaceae Juss., 1808, is the most prominent family in the Santalales, with 76 genera and over 1000 species distributed worldwide classified into five tribes: Nuytsiae, Gaiadendreae, Elytrantheae, Loranthaeae, and Psittacanthae (Nickrent et al. 2010; Liu et al. 2018). Since the early chloroplast genomes of two Loranthaceae species (Li et al. 2017), around 68 plastome sequences have been reported representing three of the five tribes of Loranthaceae (Nuytsiae 1, Elytrantheae 6 and Loranthaeae 61; Shin and Lee 2018; Yu et al. 2018; Yuan et al. 2018; Guo and Ruan 2019; Liu et al. 2019; Cho et al. 2020; Li et al. 2021; Su et al. 2021; Nickrent et al. 2021; Darshetkar et al. 2023). Comparisons of Loranthaceae plastomes have revealed among-species variation in pseudogenization or loss of genes. The idea of a host-parasite arms race in Loranthaceae is supported by several photosynthetic genes undergoing relaxed selection. These genes are associated with lower photosynthetic rates in parasitic plants, whereas several respiratory genes exhibit intensified selection (Shin and Lee 2018; Darshetkar et al.

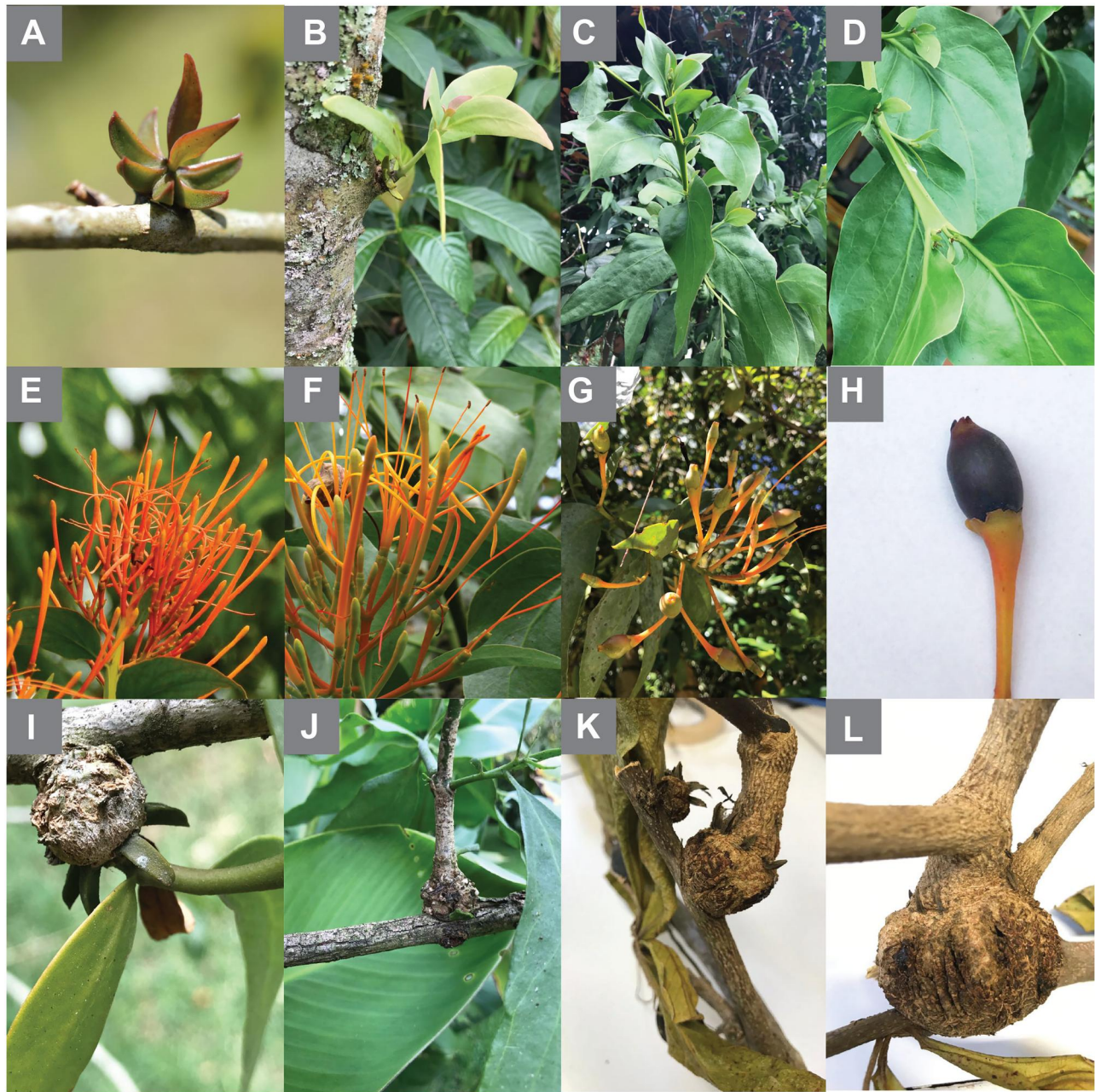
2023). However, despite the increasing number of plastomes reported for Loranthaceae, there is still no chloroplast genomes available for species in the tribe Psittacanthae Horan., which is almost restricted to the Americas, except *Tupeia* from New Zealand (Nickrent et al. 2010; Liu et al. 2018).

*Psittacanthus* Mart., 1830, the most species-rich genus in the Psittacanthae tribe (110 species), is distributed from Baja California, Sonora, and Tamaulipas in Mexico to northern Argentina (Kuijt 2009; Dettke and Cairns 2021). *Psittacanthus schiedeanus* (Cham. & Schltdl.) G.Don., 1834, is a stem hemiparasite (Figure 1) characteristic of the canopy edges of the cloud forests from northeastern Mexico to Guatemala (Ornelas et al. 2016; Ramírez-Barahona et al. 2017; Baena-Díaz et al. 2018), where it parasitizes more than 20 host tree species, both native and non-native to cloud forests (López de Buen and Ornelas 1999, 2002; López de Buen et al. 2002). It produces orange-to-yellow (Figure 1) and self-compatible bisexual flowers pollinated mainly by hummingbirds (Ramírez and Ornelas 2010), and ripe purplish-black (Figure 1), lipid-rich, one-seed fruits dispersed by a variety of bird species

**CONTACT** Saddan Morales-Saldaña  [saddanms@gmail.com](mailto:saddanms@gmail.com)  Red de Biología Evolutiva, Instituto de Ecología, A.C. (INECOL), Xalapa, Veracruz, Mexico

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**Figure 1.** Morphology of *Psittacanthus schiedeanus*. (A) Germinated seedling with eight cotyledons (polycotylous) and eophyll, 3-mo old; (B) Seedling with true leaves, 6-mo old; (C) Seedling with paired glabrous bluish-green leaves, 1-y old; (D) Stem; (E) Terminal triadic inflorescence with several pairs of triads; (F) Terminal inflorescence with open flowers, each with cupular bract and long, orange-to-red floral petals, stamens and filament; (G) Infructescence with developing, unripe fruits; (H) Ripe black fruit with prominent bright orange cupular pedicel; (I) Young haustorial connection with remaining prismatic cotyledons, plant 6-mo old; (J) Haustorium with remaining cotyledons, plant 1-y old; (K) Haustorium with remaining cotyledons, adult plant; (L) Haustorium, detail. Photos by Eliezer Cocoltzi (A) and Juan Francisco Ornelas (B–L) at La Pitaya, a cloud forest remnant with secondary riparian growth bordering the Río Pixquiac (19°30'25"N, 96°57'39"W; at 1,348 m above sea level) 6 km W of the city of Xalapa, Veracruz, Mexico, in 2022 and 2023, without any copyright issues.

(López de Buen and Ornelas 1999, 2001; Ramírez and Ornelas 2012; Ornelas and Vásquez-Aguilar 2023). Differential gene expression in these mistletoes during processes of attachment and haustorial formation is linked to synthesis, signaling, homeostasis, and response to auxin and jasmonic acid, in which glycoside hydrolases form the cell wall-degrading enzymatic arsenal that these mistletoes likely use to penetrate and break through the tissues of the host (Ibarra-Laclette et al. 2022). For these reasons, *P. schiedeanus* is an interesting model to fill the gap in chloroplast genome availability and to enhance research genomics of American

mistletoes. Here, we report the complete chloroplast genome of *Psittacanthus schiedeanus*, and the phylogenetic tree in the Loranthaceae family.

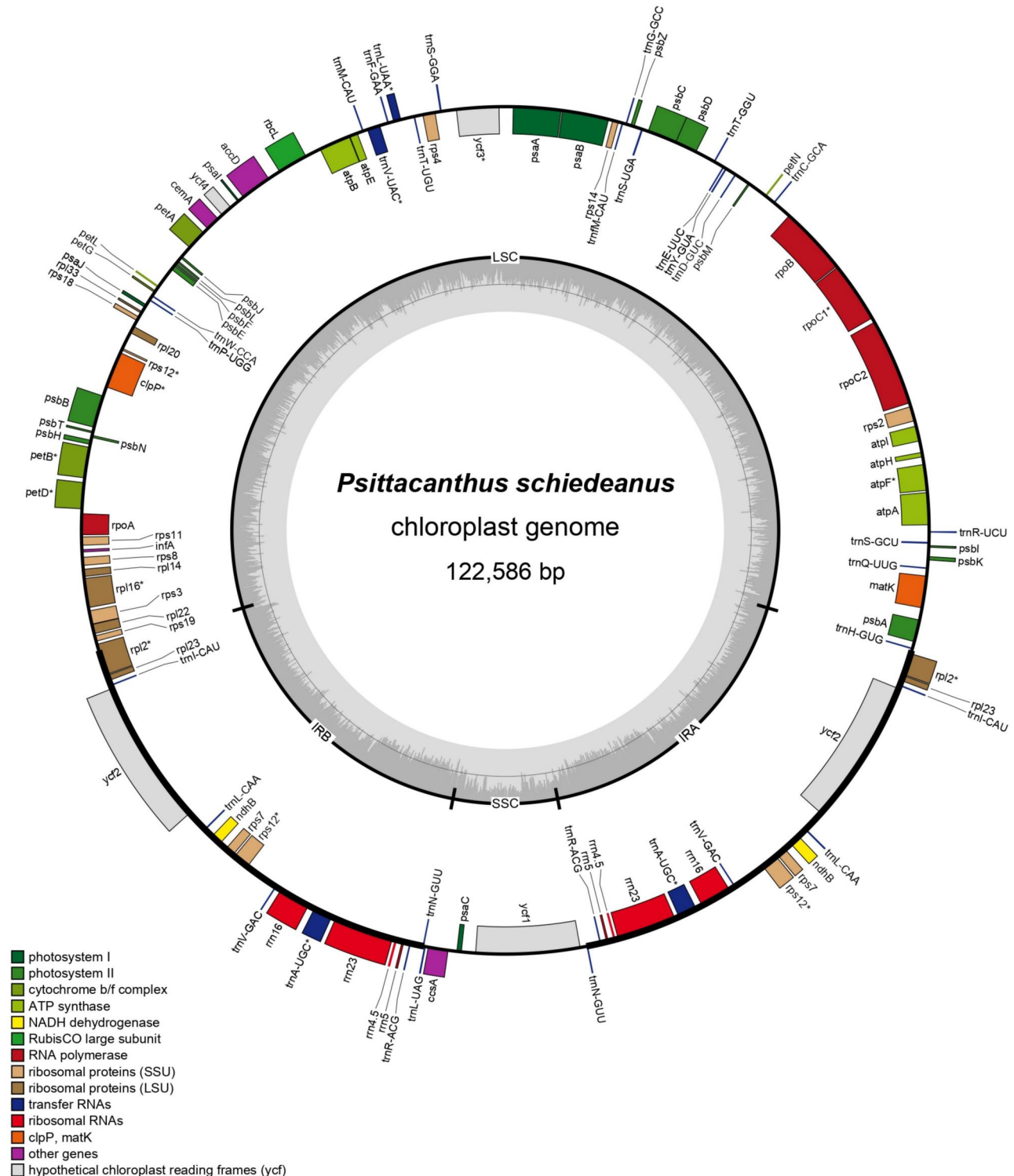
### Materials and methods

We collected specimen and leaf tissues of *P. schiedeanus* from individual plants at Metates, Santiago Comaltepec, Oaxaca, Mexico (17°41'23"N, 96°20'13"W; at 848 m above sea level). The voucher specimen (A. Ortiz-Rodríguez 754)



deposited at the Instituto de Ecología A.C. herbarium (XAL) can be accessed through the contact person Enrique César Crivelli ([enrique.cesar@inecol.mx](mailto:enrique.cesar@inecol.mx)). For DNA extractions, we used leaf tissue samples preserved in silica gel desiccant and the total genomic DNA was extracted using a DNeasy Plant Mini kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Library preparation and Paired-End (PE) sequencing was performed using an Illumina Hi-Seq PE100

platform (San Diego, CA). We used Trimmomatic version 0.38 (Bolger et al. 2014) to remove adapter sequences and low-quality reads with parameters LEADING:5 TRAILING:0 SLIDINGWINDOW:4:20 MINLEN:75. After the filtering process, roughly 80,000,000 clean reads were utilized to assemble the *P. schiedeanus* chloroplast genome using Get Organelle (Jin et al. 2020) obtaining an average and minimum coverage of 6701x and 47x (Figure S1). We employed the Draw\_



**Figure 2.** Chloroplast genome map of *Psittacanthus schiedeanus*. The circular chloroplast genome map displays 112 protein-coding genes (PCGs), of which 96 are unique, including 65 protein-coding genes, 27 transfer RNA (tRNA), and four ribosomal RNA (rRNA). Different categories of genes labeled with distinct colors.

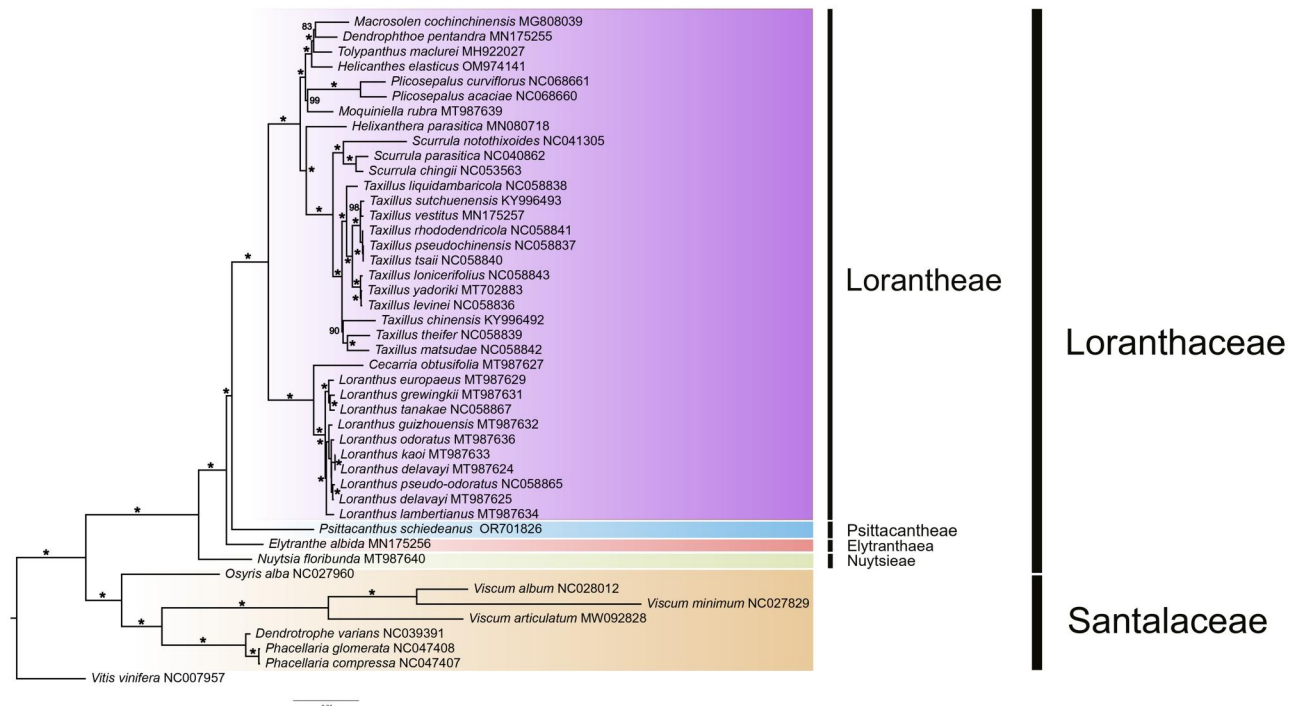
SequencingDepth.py script provided by Ni et al. (2023) to calculate the depth of coverage for the produce chloroplast genome. The parameters applied to the plastome assembly were `-w 95 -R 20 -k 21,35,45,55,65,75 -F embplant_pt`. The chloroplast genome was annotated using GeSeq (Tillich et al. 2017; Chan and Lowe 2019) and manually reviewed and corrected using the Geneious Prime 2023.2.1 program (Kearse et al. 2012). The circular genome map was drawn using the OGDRAW program (<https://chlorobox.mpimp-golm.mpg.de/OGDraw.html>; Greiner et al. 2019). The map of cis-splicing genes and the trans-splicing gene of *P. schiedeanus* were drawn by CPGview (<http://www.1kmpg.cn/cpgview/>; Liu et al. 2023). The complete chloroplast genome sequence of *P. schiedeanus* was submitted to the GenBank database of the National Center for Biotechnology Information (NCBI) under accession number OR701826.

To determine the phylogenetic position of *P. schiedeanus* within the Loranthaceae, we constructed a maximum-likelihood (ML) tree using RAxML version 8.2.10 (Stamatakis 2014) with 1000 rapid bootstraps replicates using the GTR-GAMMA substitution model, based on the alignments of 43 published complete plastomes for the Loranthaceae and Santalaceae families. We used the GTR-GAMMA model because parameter-rich models suffice reliable phylogenetic inferences

(Abadi et al. 2019). We used MAFFT version 7.3.88 (Katoh et al. 2002; Katoh and Standley 2013) to align the plastome of *P. schiedeanus* with a set of other hemiparasitic plants. The concatenated alignment was 264,915 bp long. We used *Vitis vinicola*, a member of superrosids, as an outgroup.

## Results

According to our assembly, the length of the *P. schiedeanus* plastome was 122,586 bp and presented a typical quadripartite structure consisting of a large single-copy region (72,507 bp), a small single-copy region (7,513 bp) and a pair of inverted repeat regions (21,283 bp each) (Figure 2), with an overall GC content of 36.9%. With only one exception (*Dendrophthoe pentandra*), the *P. schiedeanus* chloroplast genome size is comparable to that of other species from the Loranthaceae tribe but slightly less than the Nuytsiae and Elytrantheae tribes, and those which have been reported from the Santalaceae family (Table S1). The chloroplast genome includes 112 genes, of which 96 are unique, comprising 65 protein-coding genes, 27 transfer RNA (tRNA), and four ribosomal RNA (rRNA) (Table S1). Six protein-coding (*atpF*, *petB*, *petD*, *rpl16*, *rpl2*, *rpoC1*) and three tRNA genes harbored one intron (*trnA-UGC*, *trnL-UAA*, *trnV-UAC*), whereas two had



**Figure 3.** Maximum likelihood (ML) phylogenetic tree based on the complete chloroplast genomes of *P. schiedeanus* and 43 plastomes for Loranthaceae and Santalaceae families. The asterisk above branches represents bootstrap values = 100 from 1,000 fast replicates. Labels annotations against each species name represent the accession number on GenBank. The following sequences were used: *Macrosolen cochinchinensis* MG808039 (Shin and Lee 2018), *Dendrophthoe pentandra* MN175255 (Guo and Ruan 2019), *Tolypanthus maclurei* MH922027 (Yu et al. 2018), *Helicanthes elasticus* OM974141 (Darshetkar et al. 2023), *Plicosepalus curviflorus* NC068661, *Plicosepalus acaciae* NC068660 (Al-Juhani et al. 2022), *Moquinella rubra* MT987639 (Nickrent et al. 2021), *Helixanthera parasitica* MN080718 (Liu et al. 2019), *Scurrula notothixoides* NC041305 (Yuan et al. 2018), *Scurrula chingii* NC053563 (Li et al. 2021), *Scurrula parasitica* NC040862 (Shi et al. 2019), *Taxillus yadoriki* MT702883 (Cho et al. 2020), *Taxillus levinei* NC058836, *Taxillus lonicerifolius* NC058843, *Taxillus rhododendricola* NC058841, *Taxillus tsaii* NC058840, *Taxillus pseudochinensis* NC058837, *Taxillus liquidambaricola* NC058838, *Taxillus matsudae* NC058842, *Taxillus theifer* NC058839 (Su et al. 2021), *Taxillus vestitus* MN175257 (Guo et al. 2019), *Taxillus sutchuenensis* KY996493, *Taxillus chinensis* KY996492 (Li et al. 2017), *Cecaria obtusifolia* MT987627, *Loranthus europaeus* MT987629, *Loranthus grewingkii* MT987631, *Loranthus tanakae* NC058867, *Loranthus guizhouensis* MT987632, *Loranthus odoratus* MT987636, *Loranthus kaoi* MT987633, *Loranthus delavayi* MT987624, *Loranthus pseudo-odoratus* NC058865, *Loranthus delavayi* MT987625, *Loranthus lambertianus* MT987634, *Psittacanthus schiedeanus* OR701826 (this study), *Elytranthe albidula* MN175256 (Guo and Ruan 2019), *Nuytsia floribunda* MT987640 (Nickrent et al. 2021), *Dendrotrophe varians* NC039391 (Shin and Lee 2018), *Phacellaria compressa* NC047407, *Phacellaria glomerata* NC047408 (Guo et al. 2021), *Dendrotrophe varians* NC039391 (Shin and Lee 2018), *Viscum album* NC028012, *Viscum minimum* NC027829 (Petersen et al. 2015), *Viscum articulatum* MW092828 (Zhang et al. 2021), and *Vitis vinifera* NC007957 (Jansen et al. 2006).

two introns each (*ycf3* and *clpP*) (Figure S2), and one included a trans-splicing gene (*rps12*) (Figure S3). The *P. schiedeanus* plastome exhibited the loss of all *ndh* (except the *ndhB* gene), *rpl32* and *rps16* genes, losses observed in all reported Lorantheaceae plastomes (Darshetkar et al. 2023). Additionally, *rps15*, *ycf15* and *trnI-GAU* genes were missing (Table S2). Finally, and as a novelty, the *trnV-UAC* gene is reported for the first time in the Lorantheaceae family.

The phylogenetic tree we generated based on 43 published complete chloroplast genome sequences for the families Lorantheaceae and Santalaceae (Santalales) indicated that *P. schiedeanus* is sister to members of the tribe Lorantheae (Figure 3). The current data showed high support to most nodes in the plastome ML tree (BS > 90), except the node for the split between *Macrosolen cochinchinensis* and *Dendrophthoe pentandra* (BS = 83).

## Discussion and conclusions

A total of 112 genes were annotated in the *P. schiedeanus* plastome. This number is greater than those in the plastomes for the genera *Dendrophthoe*, *Elytranthe*, *Helixanthera*, *Macrosolen*, *Plicosepalus*, and *Scurrulla*, but smaller for species in *Ceacarria*, *Loranthus*, *Moquinella*, *Nuytsia*, *Taxillus*, and *Tolypanthus*. Phylogenetic analysis demonstrated that *P. schiedeanus* (Psittacanthaceae tribe) is sister to the Lorantheae tribe, which is consistent with the results of the phylogenetic analysis based on five nuclear and chloroplast DNA regions (Liu et al. 2018).

Increasing phylogenetic sampling through diverse lineages of hemiparasitic plants will enhance our understanding of the transition from autotrophs to parasitic plants. The complete chloroplast genome of *P. schiedeanus* reported in this study is the first genomic resource for the Psittacanthaceae tribe, a valuable resource for unraveling the evolutionary history of these hemiparasitic plants. Furthermore, our results provide a valuable resource for conservation, genetics, and phylogenetic studies of *Psittacanthus* species.

## Author contributions

Juan Francisco Ornelas and Enrique Ibarra-Laclette designed the research study and obtained the funding. Antonio Acini Vásquez-Aguilar, Santiago Ramírez-Barahona, Emanuel Villafán, and Enrique Ibarra-Laclette performed laboratory work (sample collection, DNA extraction). Saddam Morales-Saldaña and Enrique Ibarra-Laclette analyzed and interpreted the data for the work. Saddam Morales-Saldaña and Juan Francisco Ornelas wrote and revised the manuscript. All authors read and approved the final manuscript before submission.

## Ethical approval

We conducted this research and collection of plant material were conducted with permission granted by the Mexican government (Instituto Nacional de Ecología, Secretaría del Medio Ambiente y Recursos Naturales, Mexico) under grant number SGPA/DGGFS/712/1299/12.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## ORCID

Saddan Morales-Saldaña  <http://orcid.org/0000-0001-6844-356X>  
 Emanuel Villafán  <http://orcid.org/0000-0001-8542-3923>  
 Antonio Acini Vásquez-Aguilar  <http://orcid.org/0000-0002-4920-7278>  
 Santiago Ramírez-Barahona  <http://orcid.org/0000-0003-3999-6952>  
 Enrique Ibarra-Laclette  <http://orcid.org/0000-0003-1441-1938>  
 Juan Francisco Ornelas  <http://orcid.org/0000-0002-1124-1163>

## Data availability statement

The genome sequence data supporting the findings of this study can be publicly obtained at NCBI GenBank in <https://www.ncbi.nlm.nih.gov> with the accession number OR701826. Associated BioProject, SRA, and BioSample numbers are PRJNA1032607, SRR26557592, and SAMN37997932.

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