

## CHARACTERIZATION AND PHYLOGENETIC ANALYSIS OF THE PLASTID GENOME OF *IPOMOEA DUMOSA* (CONVOLVULACEAE)

LUIS FERNANDO CUÉLLAR-GARRIDO<sup>1</sup>, MILTON H. DÍAZ-TORIBIO<sup>2</sup>, ANDREW P. VOVIDES<sup>1</sup>, VICTORIA SOSA<sup>1\*</sup>

<sup>1</sup> Biología Evolutiva, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.

<sup>2</sup> Jardín Botánico Francisco Javier Clavijero, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.

\*Corresponding author: [victoria.sosa@inecol.mx](mailto:victoria.sosa@inecol.mx)

### Abstract

**Background:** *Ipomoea*, with a controversial classification, is one of the largest genera of the angiosperms. Relative to the enormous number of members of this genus, only a few plastid genomes of *Ipomoea* species have been sequenced.

**Questions and Hypotheses:** We focus on sequencing and characterizing the plastid of an underutilized edible Mesoamerican species, *I. dumosa*, known as “Xonequi” to conduct phylogenetic analyses. We hypothesize that *I. dumosa* will prove to be related to species previously identified in the “Quamoclit clade”.

**Studied species:** Twenty-seven plastid genomes of *Ipomoea* species have been fully sequenced and were included in phylogenetic analyses, and the outgroup was *Merremia hederacea*.

**Methods:** Sequencing was conducted using the PacBio HiFi technology and the assembly with Organelle\_PBA. Model Test was implemented on the non-partitioned alignment to find the evolutionary model. Maximum Likelihood tree reconstruction was conducted, with 1,000 bootstrap replicates.

**Results:** The plastid genome of *Ipomoea dumosa* shows similar size and characteristics to previously analyzed chloroplast genomes of the genus. The phylogenetic reconstruction depicts *I. dumosa* as closely related to *I. quamoclit*.

**Conclusions:** Our results suggest that *I. dumosa* belongs to the Quamoclit clade, with which it shares several vegetative and floral traits.

**Keywords:** edible Ipomoeas, Quamoclit clade, xonequi.

### Resumen:

**Antecedentes:** El género *Ipomoea*, con una clasificación controversial, es uno de los géneros más diversos en las angiospermas. A pesar de su gran número de especies solo unos cuantos genomas de cloroplasto han sido secuenciados.

**Preguntas y/o hipótesis:** Nos enfocamos en secuenciar y caracterizar el genoma de cloroplasto de una especie cuyas hojas son utilizadas como saborizante, conocida como “Xonequi”, *Ipomoea dumosa*. Nuestra hipótesis es que los análisis filogenéticos la identificarán en el clado “Quamoclit”.

**Especies estudiadas:** Las 27 especies cuyos genomas de cloroplasto se han secuenciado fueron consideradas en los análisis y como el grupo externo se incluyó a *Merremia hederacea*.

**Métodos:** La secuenciación se llevó a cabo usando la tecnología Sequencing PacBio HiFi y el ensamblaje con el software Organelle\_PBA. El “Model Test” fue implementado en el alineamiento sin particiones para encontrar el modelo evolutivo. El árbol filogenético fue construido por Máxima Verosimilitud con 1,000 réplicas de bootstrap.

**Resultados:** El genoma de cloroplasto de *Ipomoea dumosa* mostró un tamaño similar y características a los genomas previamente analizados del género. La reconstrucción filogenética identificó a *I. dumosa* cercanamente relacionada con *I. quamoclit*.

**Conclusiones:** Los resultados sugieren que *I. dumosa* pertenece al clado Quamoclit, con el que comparte varios caracteres vegetativos y florales.

**Keywords:** *Ipomoea* comestible, clado Quamoclit, xonequi.

*Ipomoea* L. is the largest genus of Convolvulaceae and is one of the largest genera of angiosperms, with approximately 800 species (Wood *et al.* 2020). The distribution of the genus is pantropical, and even reaches temperate regions, with 425 species native to the New World (Wood *et al.* 2020, Muñoz-Rodríguez *et al.* 2023). Diverse life forms such as herbs, shrubs, vines, lianas, and trees have been documented in the genus (Muñoz-Rodríguez *et al.* 2023). Although most of its species have cordate or pandurate leaves, sagittate, reniform, retuse, pinnate, oblong, and palmate leaf forms have also been recorded (Inamdar & Shenoy 1982, Simões & Staples 2017, Aye & Lwin 2018, Wood *et al.* 2020, Paramesh & Reddy 2021). The flowers are trumpet- or funnel-shaped with variable colors. They can be lavender, purple, or whitish, frequently darker inside the floral tube, stamens unequal, ovary 3-loculate, with trilobed stigma (Inamdar & Shenoy 1982, Simões & Staples 2017, Aye & Lwin 2018, Wood *et al.* 2020, Paramesh & Reddy 2021).

*Ipomoea* species are frequently known as “Morning Glory” because the flowers of many cultivated species such as *I. indica* (Burm.) Merr. open at dawn and close by midday (Wood *et al.* 2020). In addition to sweet potato (*Ipomoea batatas* (L.) Poir.), several species of the genus are edible. The leaves of some *Ipomoeas* are eaten, e.g., the water spinach *I. aquatica* Forssk, native to Southeast Asia. Here, we focus on *I. dumosa* (Benth.) L.O. Williams, which is another edible species and is commonly known as “Xonequi”. The leaves of this species are added as a flavoring to dishes in several regions of Mexico (Piedra-Malagón *et al.* 2022). It is a perennial herbaceous vine with petiolate cordate leaves, fibrous roots, and pink or purplish funnel-shaped flowers with exerted stamens and styles (Austin & Huáman 1996, Wood *et al.* 2020). It has a widespread distribution occurring in both the Sierra Madre Occidental and the Sierra Oriental in Mexico, reaching Central America and the north of South America (Wood *et al.* 2020). Leaves of *I. dumosa* have been utilized by different ethnic communities in Mexico as a condiment and for their antioxidant and medicinal properties for humans and animals during pregnancy, birth, and puerperium ailments (Heindorf *et al.* 2020, De Jesús *et al.* 2024, Espinoza-Pérez *et al.* 2024).

Several molecular phylogenies have been implemented in *Ipomoea*, the majority based on the nuclear marker ITS with distinct sampling (Miller *et al.* 1999, Manos *et al.* 2001, Miller *et al.* 2004, Zhao *et al.* 2019, Muñoz-Rodríguez *et al.* 2024). In the ITS phylogeny of New World *Ipomoea*, *I. dumosa* was retrieved in the “Quamoclit clade”, in a small group with *I. seducta* House and *I. uhdeana* D.F. Austin, and with a sister clade comprising *I. aristolochiifolia* G. Don, *I. variabilis* (Schltdl. & Cham) Choisy, *I. meyeri* (Spreng.) G. Don, and *I. expansa* J.A. McDonald (Wood *et al.* 2020). However, these phylogenies were poorly resolved and, considering the status of *Ipomoea* as one of the largest genera of the angiosperms, it has been indicated that diagnostic characters along with the use of novel molecular data would help clarify the recognition of monophyletic groups within the genus (Muñoz-Rodríguez *et al.* 2023).

The objectives of this study are to perform phylogenetic analyses based on the accessible plastid genomes of *Ipomoea* to determine the position of *I. dumosa* and to assemble and annotate its plastome as the first step to further elucidate genetic differences related to the management of this species by different ethnic groups. Genomic approaches are a valuable resource for understanding the domestication and management of underutilized edible plants (Li *et al.* 2021, Teshome *et al.* 2024, Chai & Sun 2025). Notwithstanding the enormous number of members of this genus, only 27 plastid genomes of *Ipomoea* species have been fully sequenced (e.g., *Ipomoea alba* L., *I. batatas* (L.) Lam., *I. nil* (L.) Roth, *I. purpurea* (L.) Roth, *I. quamoclit* L., *I. trifida* (Kunth) G. Don, *I. triloba* L., etc.) and utilized to determine phylogenetic relationships (Park *et al.* 2018, Sun *et al.* 2019, Xiao *et al.* 2021, Yang *et al.* 2022, Wang *et al.* 2021, 2023, Laux *et al.* 2022, Li *et al.* 2024, Sudmoon *et al.* 2024). We hypothesize that *I. dumosa* will prove to be related to species previously identified in the “Quamoclit clade” by Wood *et al.* (2020).

## Materials and methods

**Plant material.** Young leaves of *Ipomoea dumosa* were collected from the living collections of the Francisco Javier Clavijero Botanic Garden, placed in liquid nitrogen, and processed. The source plants were originally wild-collected in Veracruz and the voucher was deposited at XAL (Piedra-Malagón, López & Sosa 767). For DNA extraction, the DNeasy Plant Maxi Kit of QIAGEN®, Aarhus, Denmark, was utilized with a sample of 0.85-0.90 gr of leaves, yielding a DNA concentration between 10.00 to 11.34 µg.

*Genome sequencing, assembly, and annotation.* Sequencing was performed by MacroGen ([www.macrogen.com](http://www.macrogen.com)) using the PacBio HiFi technology. Assembly was performed with Organelle\_PBA following default parameters in the Instituto de Ecología, AC. bioinformatic cluster (Soorni *et al.* 2017). The published *Ipomoea nil* plastome (Park *et al.* 2018) was used in Organelle\_PBA to search for reads of organelle origin and then perform a *de novo* assembly. Annotation and image construction of the plastome genome were performed with CPGAVAS2, using the GeneBank annotation of *Ipomoea nil* as a reference (Shi *et al.* 2019). The resulting plastome genome of *Ipomoea dumosa* can be reviewed through GenBank accession PV762244.

*Phylogenetic analysis.* Based on previous *Ipomoea* plastome genome research (*e.g.*, Park *et al.* 2018, Wang *et al.* 2023, Sudmoon *et al.* 2024), twenty-seven *Ipomoea* plastomes, plus *Merremia hederacea*, the closest outgroup genome to *Ipomoea* (Sudmoon *et al.* 2024), were downloaded from NCBI ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)) (Supplementary material, [Table S1](#)) and aligned with *ClustalW* (Thompson *et al.* 2003) alongside the newly-sequenced *I. dumosa* plastome genome. The alignment obtained with *ClustalW* was used to reconstruct the plastome phylogeny of *Ipomoea* species. The alignment was manually edited using the UGENE v. 42.0 software (Okonechnikov *et al.* 2012). The alignment flanks that contained more than 50 % gaps were manually removed. The program Trimal v. 1.4.1 (Capella-Gutiérrez *et al.* 2009) was then applied to the alignment to eliminate any poorly aligned regions. ModelTest-NG v. 0.1.7 (Darriba *et al.* 2020) was implemented on the non-partitioned alignment (both inversions and inverted repeats were kept) to find the best-fitting evolutionary model.

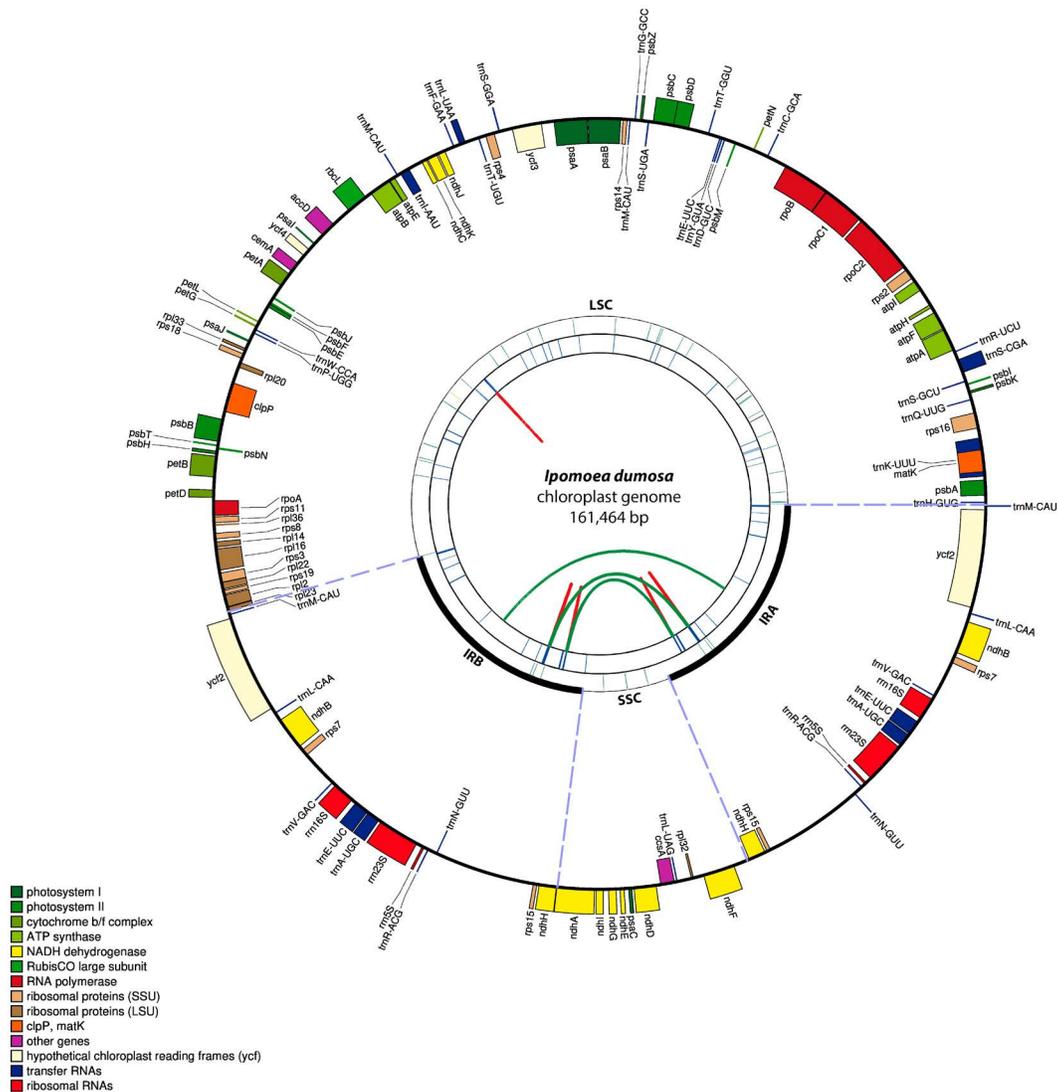
The Maximum Likelihood tree reconstruction was conducted using the program RAxMLHPC-PTHREADS-SSE3 v. 8.2.12 (Stamatakis 2006) under the best-fit evolutionary model produced by the ModelTest-NG test (GTR+I+G4), with 1,000 bootstrap replicates. The resulting bootstrap output was used as the maximum likelihood tree. Visual representation of the maximum likelihood tree was edited with customized templates on the online platform iTOL v. 6 (Letunic & Bork 2019).

## Results

*Ipomoea dumosa* plastid. The plastome of *Ipomoea dumosa* has a typical quadripartite structure containing a large single-copy (LSC) region, a small single-copy (SSC) region, and a pair of inverted repeats (IR) regions ([Figure 1](#)). The plastome size of *I. dumosa* was 161,464 bp, containing 88,457 bp in the LSC, 29,771 bp in the IR, and 13,465 in the SSC (Supplementary material, [Table S2](#)). The plastome of *I. dumosa* is composed of 128 genes, including 83 protein-coding sequences (CDS), 37 tRNA, and eight rRNA genes (Supplementary material, [Table S3](#)). Total GC content was 37.56 %, while a GC content of 36 % was found in the LSC, 39.34 % in the IR, and 32.35 % in the SSC.

*Phylogenetic analysis.* Based on complete plastomes, the phylogenetic tree of *Ipomoea* species, including *I. dumosa*, depicted the outgroup *Merremia hederacea* (Burm f.) Hallier as closest to *Ipomoea biflora* (L.) Pers., *I. dumosa* as sister to *I. quamoclit* L. (bootstrap bst 100), followed by two clades, the first comprising *I. maurandioides* Meisn. and *I. asarifolia* Roem. & Schult (bts 100), and the second comprising *I. goyazensis* Gardner and *I. cavalcantei* D.F.Austin (bts 94) ([Figure 2](#)). Two major clades were retrieved ([Figure 2](#)). Clade 1 had *I. pes-caprae* (L.) Roth as a sister lineage and comprised the following species: *I. alba* L., *I. purpurea* (L.) Roth, *I. indica* (Burm) Merr., *I. nil*, *I. imperati* (Vahl) Griseb., *I. aquatica*, *I. cairica* (L.) Sweet, *I. tiliifolia* (Desr.) Roem. & Schult., and *I. obscura* (L.) Kew Gawl (bts 89). Between these two major clades, there is a small clade comprised of *I. carnea* Jacq. and *I. marabensis* D.F.Austin & Secco (bts 100) ([Figure 2](#)). Clade 2 included *I. splendor-sylvae* House as a sister lineage and comprised *I. trifida* (Kunth) G.Don, *I. tabascana* J.A.McDonald & D.F.Austin, *I. batatas*, *I. lacunosa* L., *I. cordatotriloba* Dennst., *I. ramosissima* (Poir.) Choisy, *I. triloba* L., and *I. cynanchifolia* Meisn. (bts 100) ([Figure 2](#)). In addition, Clade 1 was further divided into two subclades: Clade 1A, comprising *I. alba* L., *I. purpurea* (L.) Roth, *I. indica* (Burm) Merr., and *I. nil* (bts 100) and Clade 1B, comprising *I. imperati* (Vahl) Griseb., *I. aquatica*, *I. cairica*, *I. tiliifolia* (Desr.) Roem. & Schult., and *I. obscura* (bts 97) ([Figure 2](#)). High bootstrap values (Hillis & Bull 1993) supported the clades in the phylogenetic tree ([Figure 2](#)).

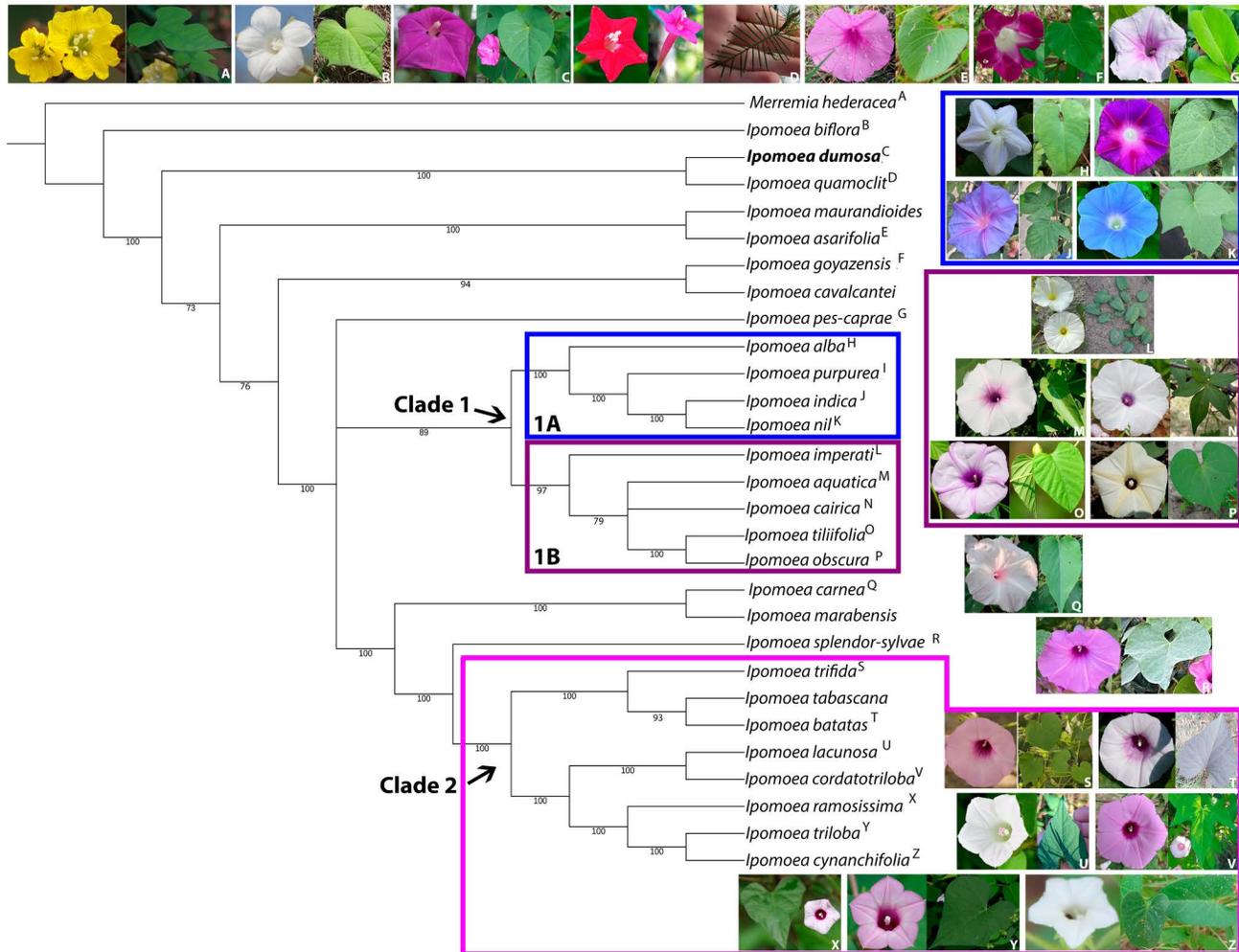
## Plastid genome of *Ipomoea dumosa*



**Figure 1.** *Ipomoea dumosa* chloroplast genome structure. Genes placed at the outside and inside of the circle are transcribed counterclockwise and clockwise, respectively. Genes are color-coded based on their functional classification. Functional gene names are shown at the bottom-left part of the figure. GenBank accession PV762244.

## Discussion

This is the first phylogeny constructed on plastid genomes including *Ipomoea dumosa*. In our phylogenetic tree, this species is closely related to *I. quamoclit*. Furthermore, Wood *et al.* (2020), presented a summarized phylogeny based on the nuclear ITS, the plastid markers *matK* and *trnH-psbA*, and 605 nuclear genes, in which different analyses with every set of markers included variable sampling. The summarized tree displays two clades in *Ipomoea*: The Old World Clade and the New World Clade (Wood *et al.* 2020). One of the main sub-clades in the New World is a large group, mainly Mexican, including the subgenera proposed by Austin (1979) and *Quamoclit* as well as some other species. *Ipomoea quamoclit* forms part of this clade characterized by twining herbs, variable leaves, sub-crateriform corolla, and exerted stamens (Wood *et al.* 2020) (see [Table 1](#), which includes selected characters for the studied species). Wood *et al.* (2020) suggested that *I. dumosa* shares characters with species in the Calonyction clade, such as subcylindrical corolla and exerted stamens, with varying leaf shape, blunt spines, and gemmiform pollen ([Table 1](#);



**Figure 2.** RAxML *Ipomoea*'s chloroplast genome species phylogenetic consensus tree. A-Z letters: species name referenced to its flower and leaf inset picture. Blue frame: clade 1A. Purple frame: clade 1B. Pink frame: Clade 2. Tree rooted to outgroup species. *Ipomoea dumosa* name in bold. Bootstrap values shown under tree branches. All images are under the CC0 copyright license.

Wood *et al.* 2020). Contrary to this hypothesis regarding the affinities of *I. dumosa*, Austin & Huáman (1996) and McDonald *et al.* (2011) included this species in the subgenus *Quamoclit*, which presents characters such as a large corolla and homomorphic stamens. In our phylogenetic tree, *I. dumosa* was determined closely related to *I. quamoclit* corroborating this hypothesis.

As stated above, *Ipomoea* is one of the largest genera of angiosperms and presents challenges in terms of performing phylogenetic analyses with comprehensive sampling, and informative molecular markers, or even genomic data (Muñoz-Rodríguez *et al.* 2023). Therefore, further analyses using novel molecular data and morphological characters will clarify the relationships and phylogenetic position of *I. dumosa*, which has been considered in the Calonyction clade or the Quamoclit clade. These analyses will also define whether the genus *Merremia* should be considered within *Ipomoea*, as suggested by several authors (Wood *et al.* 2020). However, we have kept the name *Merremia hederacea* as indicated in GenBank and utilized it as the outgroup. Moreover, *Ipomoea* species such as *I. alba*, *I. nil*, and *I. purpurea* from Clade I are among the most important ornamental species in the genus. Species in Clade II such as *I. cynanchifolia* and *I. trifolia* share morphological characters including small-sized flowers, with a corolla of less than 3 cm. in length. It is also worth mentioning that *I. tabascana* has been synonymized under *I. batatas* in the past (Wood *et al.* 2020), which agrees with our phylogenetic tree.

Plastid genome of *Ipomoea dumosa*

**Table 1.** General morphological characters of leaves' shape and flowers stamen/style length of *Ipomoea* and outgroup species considered in phylogenetic analyses based on Wood et al. (2020)

Species	Life form	Leaf shape (base/apex)	Corolla	Stamens
<i>I. alba</i> L.	Twining	Cordate	Hypocrateriform	Exserted
<i>I. aquatica</i> Forssk.	Twining	Sagittate/Cordate	Funnel-shaped	Inserted
<i>I. asarifolia</i> Roem. & Schult.	Twining/Prostrate	Reniform	Funnel-shaped	Inserted
<i>I. batatas</i> (L.) Lam.	Twining/Erect/Prostrate	Cordate	Funnel-shaped	Inserted
<i>I. cairica</i> (L.) Sweet	Twining/Prostrate	Leaflets (Palmate like)	Funnel-shaped	Inserted
<i>I. carnea</i> Jacq.	Twining/Erect	Cordate	Campanulate	Inserted
<i>I. cavalcantei</i> D.F. Austin	Erect	Oblong	Hypocrateriform	Exserted
<i>I. cordatotriloba</i> Dennst.	Twining	3-5-lobed (Pandurate like)		Inserted
<i>I. cynanchifolia</i> Meisn.	Twining	Cordate	Funnel-shaped	Inserted
<i>I. goyazensis</i> Gardmer	Twining	Cordate	Campanulate	Inserted
<i>I. imperati</i> (Vahl) Griseb.	Prostrate	Cordate	Campanulate	Inserted
<i>I. indica</i> (Burm.) Merr.	Twining	3-lobed (Pandurate like)	Funnel-shaped	Inserted
<i>I. lacunose</i> L.	Twining	Cordate	Funnel-shaped	Inserted
<i>I. marabensis</i> D.F. Austin & Secco	Twining	Oblong	Campanulate	Inserted
<i>I. maurandioides</i> Meisn.	Twining/Prostrate	Sagittate/Cordate	Campanulate	Inserted
<i>I. nil</i> (L.) Roth	Twining	3-lobed (Pandurate like)	Campanulate	Inserted
<i>I. obscura</i> (L.) Ker Gawl.	Twining/Prostrate	Cordate	Funnel-shaped	Inserted
<i>I. pes-caprae</i> (L.) R.Br.	Twining/Prostrate	Retuse	Campanulate	Inserted
<i>I. purpurea</i> (L.) Roth	Twining	Cordate	Campanulate	Inserted
<i>I. quamoclit</i> L.	Twining	Pinnate	Hypocrateriform	Exserted
<i>I. ramosissima</i> (Poir.) Choisy	Twining	Cordate	Hypocrateriform	Inserted
<i>I. splendor-sylvae</i> House	Twining	Cordate	Funnel-shaped	Inserted
<i>I. tabascanana</i> J.A.McDonald & D.F. Austin	Twining/Prostrate	Sagittate	Funnel-shaped	Inserted
<i>I. dumosa</i> Benth. (L.O. Williams)	Twining	Cordate	Hypocrateriform	Exserted
<i>I. tiliifolia</i> (Desr.) Roem. & Schult.	Twining	Cordate	Funnel-shaped	Inserted
<i>I. trifida</i> (Kunth) G. Don	Twining	Cordate	Funnel-shaped	Inserted
<i>I. triloba</i> L.	Twining/Prostrate	Cordate	Campanulate	Inserted
<i>Ipomoea biflora</i> (L.) Pers.	Twining	Cordate	Campanulate	Inserted
<i>Merremia hederacea</i>	Twining/Prostrate	3-lobed (Pandurate like)	Campanulate	Exserted

In general, recent plastid phylogenetic trees comprising the species of *Ipomoea* described to date (ours included) show some differences in their topology. In our resulting phylogenetic tree, we highlighted major clades such as Clades 1A, 1B, and 2, and a general level of divergence of species since they were retrieved in a very similar manner to that of previous phylogenetic research (*e.g.*, Muñoz-Rodríguez *et al.* 2019, Wood *et al.* 2020, Sudmoon *et al.* 2024). The topological dissimilarities for reconstructing plastid phylogenetic trees of *Ipomoea* species might be attributed to methodological differences in each study case, such as the numbers of *Ipomoea* species and outgroups included and the particular molecular analysis approach employed.

Furthermore, it has been indicated that *I. dumosa* is the best-known of a complex of species that possess very similar floral morphology, including *I. seducta* House and *I. tubulata* Sessé & Mocino. *Ipomoea seducta* is recognized by its funnel-shaped corolla, with a distribution in southern Mexico and Guatemala while the diagnostic characters of *I. tubulata* are a lobed corolla with short, ovate-deltoid lobes and a distribution in western Mexico (Wood *et al.* 2020). However, observations of the distributions of diverse specimens show that these characters are variable (Wood *et al.* 2020). Therefore, to elucidate whether these can be recognized as different species, further sequencing of different populations throughout their entire distribution is required.

In classifying *Ipomoea*, Muñoz-Rodríguez *et al.* (2023) concluded that existing classifications for the genus should be abandoned and that many segregated genera from *Ipomoea* should be incorporated into this genus to reconcile the properties of monophyly, diagnosability, and completeness. The study of plastid genomes in *Ipomoea* can therefore contribute to a better understanding of the systematics and evolution of this genus.

The plastid genome of *Ipomoea dumosa* shows similar size and characteristics to previous plastid genomes of this genus. The phylogenetic reconstruction based on the plastid genomes indicates that *I. dumosa* is closely related to *I. quamoclit*, suggesting that it belongs in the Quamoclit clade. Incorporating *I. seducta* and *I. tubulata*, which have been identified as presenting a very similar morphology to *I. dumosa*, in further phylogenetic analyses will determine whether they are closely related to *I. dumosa*. Studying plastid genomes in *Ipomoea* can further our understanding of the systematics and evolution of this genus.

## Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3685>

## Acknowledgments

We would like to thank Emanuel Villafán de la Torre (INECOL AC.) for helping us install and run the programs used in this study, and Arith Pérez Orozco (INECOL AC.) for her help in the molecular laboratory. Our most sincere thanks to all the wonderful people of the Naturalista website community who uploaded pictures of the species analyzed in this study under the CC0 (public domain copyright), which helps us to practice science without boundaries.

## Literature cited

- Austin DF. 1979. An infrageneric classification for *Ipomoea* (Convolvulaceae). *Taxon* **28**: 359-361. DOI: <https://doi.org/10.2307/1219747>
- Austin DF, Huáman Z. 1996. A synopsis of *Ipomoea* (Convolvulaceae) in the Americas. *Taxon* **45**: 3-38. DOI: <https://doi.org/10.2307/1222581>
- Aye SM, Lwin HW. 2018. Leaf Architectural study on Some Members of Convolvulaceae in Mandalay and Pyin Oo Lwin Area. *Journal of the Myanmar Academy of Arts and Science* **16**: 83-100.
- Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* **25**: 1972-1973. DOI: <https://doi.org/10.1093/bioinformatics/btp348>

- Chai Y, Sun Y. 2025. Advances in the biosynthesis, gene mining, and molecular mechanisms of cucurbitacin in Cucurbitaceae crops. *Vegetable Research* **5**: e001. DOI: <https://doi.org/10.48130/vegres-0024-0039>
- Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T. 2020. ModelTest-NG: A New and Scalable Tool for the Selection of DNA and Protein Evolutionary Models. *Molecular Biology and Evolution* **37**: 291-294. DOI: <https://doi.org/10.1093/molbev/msz189>
- De Jesús A, Álvarez Aguirre A, Jeuna Díaz R. 2024. Uso de las plantas ancestrales durante el postparto mediato desde la cosmovisión Nahua. *Medicina Naturista* **18**: 59-64.
- Espinoza-Pérez J, Cortina-Villar S, Perales H, Méndez-Flores OG, Soto-Pinto L. 2024. Edible plants as a complement to the diet of peasant farmers: a case study of the Totonacapan region of Puebla, Mexico. *Frontiers in Sustainable Food Systems* **8**: 1329532. DOI: <https://doi.org/10.3389/fsufs.2024.1329532>
- Heindorf C, van 't Hooft A, Reyes-Agüero JA, Martínez JF. 2020. Folk taxonomy of the inter- and intraspecific edible plant diversity of Huastec Mayan farmers in Mexico. *Journal of Ethnobiology* **40**: 552-568. DOI: <https://doi.org/10.2993/0278-0771-40.4.552>
- Inamdar JA, Shenoy KN. 1982. Leaf architecture of *Merremia* DENNST. ex HALL. f. (Convolvulaceae). *Flora* **172**: 96-104. DOI: [https://doi.org/10.1016/S0367-2530\(17\)31315-4](https://doi.org/10.1016/S0367-2530(17)31315-4)
- Laux M, Oliveira RR, Vasconcelos S, Pires ES, Lima TG, Pastore M, Nunes GL, Alves R, Oliveira G. 2022. New plastomes of eight *Ipomoea* species and four putative hybrids from Eastern Amazon. *Plos One* **17**: e0265449. DOI: <https://doi.org/10.1371/journal.pone.0265449>
- Letunic I, Bork P. 2019. Interactive Tree Of Life (iTOL) v4: recent updates and new developments. *Nucleic Acids Research* **47**: W256-W259. DOI: <https://doi.org/10.1093/nar/gkz239>
- Li G, Zhang H, Lin Z, Li H, Xu G, Xu Y, Ji R, Luo W, Qiu Y, Qiu S, Tang H. 2024. Comparative analysis of chloroplast and mitochondrial genomes of sweet potato provides evidence of gene transfer. *Scientific Reports* **14**: 4547. DOI: <https://doi.org/10.1038/s41598-024-55150-1>
- Li M, Zhang R, Li J, Zheng K, Xiao J, Zheng Y. 2021. Analyses of chloroplast genome of *Eutrema japonicum* provides new insights into the evolution of *Eutrema* species. *Agronomy* **11**: 2546. DOI: <https://doi.org/10.3390/agronomy11122546>
- Manos PS, Miller RE, Wilkin P. 2001. Phylogenetic analysis of *Ipomoea*, *Argyreia*, *Stictocardia*, and *Turbinia* suggest a generalized model of morphological evolution in Morning Glories. *Systematic Botany* **26**: 585-602.
- McDonald JA, Hansen DR, McDill JR, Simpson BB. 2011. A phylogenetic assessment of breeding systems and floral morphology of North American *Ipomoea* (Convolvulaceae). *Journal of the Botanical Research Institute of Texas* **5**: 159-177.
- Miller RE, McDonald JA, Manos PS. 2004. Systematics of *Ipomoea* subgenus *Quamoclit* (Convolvulaceae) based on ITS sequences data and a Bayesian and phylogenetic analysis. *American Journal of Botany* **91**: 1208-1218. DOI: <https://doi.org/10.3732/ajb.91.8.1208>
- Miller RE, Rausher MD, Manos PS. 1999. Phylogenetic systematics of *Ipomoea* (Convolvulaceae) based on ITS and waxy sequences. *Systematic Botany* **24**: 20922. DOI: <https://doi.org/10.2307/2419549>
- Muñoz-Rodríguez P, Carruthers T, Wood JR, Williams BR, Weitemier K, Kronmiller B, Goodwin Z, Sumadijaya A, Anglin NL, Filer D, Harris D, Rausher MD, Kelly S, Liston A, Scotland RW. 2019. A taxonomic monograph of *Ipomoea* integrated across phylogenetic scales. *Nature Plants* **5**: 1136-1144. DOI: <https://doi.org/10.1038/s41477-019-0535-4>
- Muñoz-Rodríguez P, Wood JRI, Wells T, Carruthers T, Sumadijaya A, Scotland RW. 2023. The challenges of classifying big genera such as *Ipomoea*. *Taxon* **72**: 1201-1215. DOI: <https://doi.org/10.1002/tax.12887>
- Okonechnikov K, Golosova O, Fursov M. 2012. Unipro UGENE: a unified bioinformatics toolkit. *Bioinformatics* **28**, 1166-1167. DOI: <https://doi.org/10.1093/bioinformatics/bts091>
- Paramesh L, Reddy AVB. 2021. New Record of *Ipomoea biflora* (L.) Pers. (Convolvulaceae) In Telangana State, India. *Indian Journal of Aerobiology* **34**: 1-3.
- Park I, Yang S, Kim WJ, Noh P, Lee HO, Moon BC. 2018. The complete chloroplast genomes of six *Ipomoea* species and indel marker development for the discrimination of authentic *Pharbitidis* Semen (Seeds of *I. nil* or *I. purpurea*). *Frontiers in Plant Science* **9**: 965. DOI: <https://doi.org/10.3389/fpls.2018.00965>

- Piedra-Malagón EM, Sosa V, Angulo DF, Díaz-Toribio M. 2022. Edible native plants of the Gulf of Mexico Province. *Biodiversity Data* **10**: e80565. <https://doi.org/10.3897/BDj.10.380565>
- Shi L, Chen H, Jiang M, Wang L, Wu X, Huang L, Liu C. 2019. CPGAVAS2, an integrated plastome sequence annotator and analyzer. *Nucleic acids research* **47**: W65-W73. DOI: <https://doi.org/10.1093/nar/gkz345>
- Simões AR, Staples G. 2017. Dissolution of Convolvulaceae tribe Merremieae and a new classification of the constituent genera. *Botanical Journal of the Linnean Society* **183**: 561-586. DOI: <https://doi.org/10.1093/botlinnean/box007>
- Soorni A, Haak D, Zaitlin D, Bombarely A. 2017. Organelle PBA, a pipeline for assembling chloroplast and mitochondrial genomes from PacBio DNA sequencing data. *BMC genomics* **18**: 1-8. DOI: <https://doi.org/10.1186/s12864-016-3412-9>
- Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688-2690. DOI: <https://doi.org/10.1093/bioinformatics/btl446>
- Sudmoon R, Kaewdaungdee S, Ho HX, Lee SY, Tanee T, Chaveerach A. 2024. The chloroplast genome sequences of *Ipomoea alba* and *I. obscura* (Convolvulaceae): genome comparison and phylogenetic analysis. *Scientific Reports* **14**: 14078. DOI: <https://doi.org/10.1038/s41598-024-64879-8>
- Sun J, Dong X, Cao Q, Xu T, Zhu M, Sun J, Dong T, Ma D, Han Y, Li Z. 2019. A systematic comparison of eight new plastome sequences from *Ipomoea* L. *PeerJ* **7**: e6563. DOI: <https://doi.org/10.7717/peerj.6563>
- Teshome A, Habte E, Cheema J, Mekasha A, Lire H, Muktar MS, Quiroz-Chavez J, Domoney C, Jones CS. 2024. A population genomics approach to unlock the genetic potential of lablab (*Lablab purpureus* (L.) Sweet), an underutilized tropical forage crop. *BMC Genomics* **25**: 1241 DOI: <https://doi.org/10.1186/s12864-024-11104-5>
- Thompson JD, Gibson TJ, Higgins DG. 2003. Multiple sequence alignment using ClustalW and ClustalX. *Current protocols in bioinformatics* **00**: 1-2. DOI: <https://doi.org/10.1002/0471250953.bi0203s00>
- Wang QJ, Wang R, Zhang L, Zhang XJ. 2021. Characterization and phylogenetic analysis of the complete plastome of *Ipomoea aquatica* (Convolvulaceae), an edible vegetable. *Mitochondrial DNA Part B* **6**: 990-992. DOI: <https://doi.org/10.1080/23802359.2021.1891985>
- Wang Y, Xu J, Hu B, Dong C, Sun J, Li Z, Ye K, Deng F, Wang L, Aslam M, LW, Qin Y, Cheng, Y. 2023. Assembly, annotation, and comparative analysis of *Ipomoea* chloroplast genomes provide insights into the parasitic characteristics of *Cuscuta* species. *Frontiers in Plant Science* **13**: 1074697. DOI: <https://doi.org/10.3389/fpls.2022.1074697>
- Wood JRI, Muñoz-Rodríguez P, Williams BRM, Scotland RW. 2020. A foundation monograph of *Ipomoea* (Convolvulaceae) in the New World. *PhytoKeys* **143**: 1-823. DOI: <https://doi.org/10.3897/phytokeys.143.32821>
- Xiao S, Xu P, Deng Y, Dai X, Zhao L, Heider B, Zhang A, Zhou Z, Cao Q. 2021. Comparative analysis of chloroplast genomes of cultivars and wild species of sweet-potato (*Ipomoea batatas* [L.] Lam). *BMC genomics* **22**: 1-12. DOI: <https://doi.org/10.1186/s12864-021-07544-y>
- Yang Z, Ni Y, Lin Z, Yang L, Chen G, Nijiati N, Hu Y, Chen, X. 2022. De novo assembly of the complete mitochondrial genome of sweet potato (*Ipomoea batatas* [L.] Lam) revealed the existence of homologous conformations generated by the repeat-mediated recombination. *BMC Plant Biology* **22**: 285. DOI: <https://doi.org/10.1186/s12870-022-03665-y>
- Zhao H, Tao W, Zhang W. 2019. DNA barcoding and molecular phylogeny indicate that three members of the “Morning glory” (*Ipomoea nil* species complex) are conspecific. *Biology* **74**: 1455-1463. DOI: <https://doi.org/10.2478/s11756-019-00328-6>

**Associate editor:** Eduardo Ruiz-Sanchez

**Author contributions:** VS designed the study; LFC-G performed the analyses; LFC-G and VS directed the writing of the manuscript. APV and MHD-T provided the funds. All authors contributed critically to drafts and gave final approval for publication.

**Supporting agencies:** Consejo Nacional de Humanidades, Ciencia y Tecnología (CONAHCYT, Mexico) (RENAJEB 2023-14).

**Conflict of interest:** The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.