

SHORT COMMUNICATION

Characterisation and Phylogenetic Analysis of the Complete Plastid Genome of *Physalis minima* L. from Malaysia

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HIGHLIGHTS -

- The complete plastid genome of a *Physalis minima* sample from Malaysia was sequenced, assembled and annotated.
- The P. minima plastid genome was circular and 156,973 bp in size, and had a GC content of 37.5% and 129 annotated genes.
- Phylogeny showed genetic differentiation between accessions from Malaysia and China, and both clustered away from P. angulata.



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Characterisation and Phylogenetic Analysis of the Complete Plastid Genome of *Physalis minima* L. from Malaysia

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Abstract: Physalis minima L. is an herbaceous plant with ethnobotanic importance across many Asian cultures. In this study, we sequenced and assembled the plastid genome (plastome) of a P. minima sample from Malaysia, and conducted intraspecific pairwise and phylogenetic analyses with available data of its relatives. Our sample had a plastome of 156,973 bp in size with a GC content of 37.5%. The genome was circular, consisting of a large single-copy of 87,196 bp, a small single-copy of 18,447 bp and a pair of inverted repeats of 25,665 bp each. A total of 129 genes were annotated, including 84 CDSs, 37 tRNAs and eight rRNAs. Between the China and Malaysia accession, 458 variable sites were identified, and the pairwise distance was 0.003. Phylogenetic analysis was conducted using the complete plastome sequence based on the maximum likelihood and Bayesian inference methods. The findings revealed that our sample was significantly differentiated from the accession from China, and that both P. minima accessions clustered away from P. angulata, the synonym suggested by certain taxonomic authorities. This study facilitates precise taxonomic identification of P. minima within ethnomedicinal frameworks, enabling its distinction from closely related or putatively synonymous species that may exhibit divergent phytochemical compositions. These results provide important insights into the genetic diversity and taxonomic status of P. minima, and support its informed use in future research, conservation, and medicinal applications.

Keywords: Genetic Resources, Next-Generation Sequencing, Physaleae, Chloroplast Genome, Solanaceae

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Abstrak: Physalis minima L. ialah tumbuhan herba yang mempunyai kepentingan etnobotani dalam banyak budaya Asia. Dalam kajian ini, kami menjujuk dan menyusun genom plastid (plastom) bagi satu sampel P. minima dari Malaysia, serta menjalankan analisis pasangan dan filogenetik intraspesifik menggunakan data yang tersedia daripada spesies yang berkaitan dengannya. Sampel kami mempunyai plastom bersaiz 156,973 bp dengan kandungan GC sebanyak 37.5%. Genom ini berbentuk bulat, terdiri daripada satu salinan besar tunggal (87,196 bp), satu salinan kecil tunggal (18,447 bp) dan sepasang ulangan terbalik (25,665 bp setiap satu). Sebanyak 129 gen berjaya dianotasi, termasuk 84 CDS, 37 tRNA, dan lapan rRNA. Antara aksesi China dan Malaysia, 458 tapak berubah dikenal pasti, dengan jarak pasangan sebanyak 0.003. Analisis filogenetik dijalankan menggunakan jujukan lengkap plastom berdasarkan kaedah kemungkinan maksimum dan inferens Bayesian. Dapatan kajian menunjukkan bahawa sampel kami berbeza dengan ketara daripada aksesi China, dan kedua-dua aksesi P. minima mengelompok jauh daripada P. angulata, sinonim yang dicadangkan oleh pihak berkuasa taksonomi tertentu. Kajian ini memudahkan pengenalpastian taksonomi yang tepat bagi P. minima dalam kerangka etnomedik, membolehkan pembezaannya daripada spesies yang berkait rapat atau dianggap sinonim yang mungkin mempunyai komposisi fitokimia berbeza. Hasil kajian ini memberikan pandangan penting mengenai kepelbagaian genetik dan status taksonomi P. minima, serta menyokong penggunaannya secara berinformasi dalam penyelidikan, pemuliharaan, dan aplikasi perubatan pada masa akan datang.

Kata kunci: Sumber Genetik, Penjujukan Generasi Akan Datang, Physaleae, Genom Kloroplas, Solanaceae

INTRODUCTION

The Physalis (Solanaceae) plant genus, which includes around 120 species, is primarily found in the Americas, Europe and Asia (Liang et al. 2024). In Malaysia, P. minima L. 1753 is the only native Physalis species recorded in the country (MyBIS 2024). The plant is traditionally consumed for treating illnesses such as fever, constipation, sore throat, stomachache, gastric and diabetes. (Lem et al. 2022). Research has shown that it is a phytochemically rich medicinal plant containing flavonoids, alkaloids and antioxidants. It exhibits notable antidiabetic, anti-inflammatory, analgesic, antimicrobial and diuretic activities (Novita et al. 2020). Due to its bioactive profile and edible, nutrient-dense fruit, the plant presents significant potential for application in pharmaceutical development, functional food products and the broader nutraceutical industry. However, the plastid genome (plastome) sequences of only 13 Physalis species are publicly available. For P. minima, a record for the complete plastome sequence of an accession from Shandong, China, was published (GenBank accession no. MH045577; Feng et al. 2020). Plastomes are essential for elucidating plant evolutionary relationships and taxonomy, given their conserved structure and phylogenetically informative mutation rates. They enable the resolution of complex lineages, identification of hypervariable regions for species delimitation, and detection of cryptic diversity. Such insights are vital for refining classifications and informing conservation strategies, particularly in taxa with threatened or morphologically similar species

(Xu et al. 2022). As an important herb in Malaysia, the genomic information of *P. minima* is currently lacking. In this study, we sequenced and assembled the plastome sequence of *P. minima* from Malaysia using next-generation sequencing (NGS) technology and bioinformatics tools. As Shandong, China, has a profoundly different climate compared to Malaysia, we assessed the intraspecific pairwise analysis and genomic variation of *P. minima* between the two accessions and performed phylogenetic analysis to determine the molecular placement of *P. minima* from Malaysia among other *Physalis* taxa.

MATERIAL AND METHODS

Fresh leaves of a *P. minima* individual (Fig. 1) were collected from a natural population in Ipoh, Perak, Malaysia (4.617991° N, 101.044373° E) and transported to the Biotechnology Laboratory of the Faculty of Health and Life Sciences, INTI International University, in a zip-lock bag containing silica gel. A voucher specimen with the collection number XMUM-PL-2023-YYS001 has been deposited at the Xiamen University Malaysia Specimen Collection (contact: Dr. Wei Lun Ng, weilun.ng@xmu. edu.my). Total genomic DNA extraction was performed using the DNeasy Plant Mini Kit (Qiagen, USA) following the manufacturer's protocol. The DNA extract was quantified using a Qubit 4 fluorometer (Thermo Fisher Scientific, USA) for its purity and concentration prior to being sent to Guangzhou Jierui Biotechnology Company, Ltd. (Guangzhou, China) for next-generation sequencing (NGS).



FIGURE 1: Physalis minima (A) whole plant in its habitat, (B) fruits (Photos by Y.S. Yong and C. Gnanaraj).

A 350-bp paired-end genomic library was prepared using the TrueSeq DNA Sample Prep Kit (Illumina, USA), and 150-bp paired-end reads were produced on a NovaSeq 6000 platform (Illumina, USA). Approximately 3 Gb of raw NGS data was generated and fed into the NOVOwrap v1.20 (Wu et al. 2021) pipeline, based on the seed-and-extend algorithm, for the plastome sequence assembly process. The partial rbcL gene sequence of *Physalis minima* (GenBank accession no. MH767730) was selected as the seed sequence. By obtaining a single contig at the end of the plastome assembly step, gene annotation and identification of the IR regions were carried out using GeSeq v2.03 (Tillich et al. 2017), based on the BLAT-based homology search and the Chloë module. The annotated plastome sequence was manually checked for errors and the physical map was visualised using OGDraw v1.3.1 (Greiner et al. 2019).

To detect intraspecific genomic variation at the plastome level between the *P. minima* accessions from China and Malaysia, the two complete plastome sequences were aligned using MAFFT v7 (Katoh & Standley 2013). The number of variable sites was estimated using DnaSP v5 (Librado & Rozas 2009), and the intraspecific pairwise distance between the two accessions was calculated using MEGA7 (Kumar *et al.* 2016) based on the Kimura two-parameter (K2P) model under uniform rates and 1,000 bootstrap replicates. Gaps and missing data were treated as pairwise deletions. The model was selected for its capacity to differentiate substitution types, enhancing accuracy in closely related plastome comparisons.

To elucidate the phylogenetic relationship between P. minima from Malaysia and other related taxa, the complete plastome sequences of 18 other Physaleae accessions were included in a phylogenetic analysis: Alkekengi officiniarum var. franchetii (GenBank accession number: MH045575; Feng et al. 2020), Iochoroma salpoanum (GenBank accession number: KU315119; unpublished), I. stenanthum (GenBank accession number: KP262399; unpublished), Physalis angulata (GenBank accession number: MH045574; Feng et al. 2020), P. angulata var. villosa (GenBank accession number: OM257167; Zhan et al. 2022), P. chenopodiifolia (GenBank accession number: MN508249; Zamora-Tavares et al. 2020), P. cordata (GenBank accession number: MH045575; Sandoval-Padilla et al. 2020a), P. ixocarpa (GenBank accession number: OP748223; Zhang et al. 2022), P. longifolia var. subglabrata (GenBank accession number: OP748222; Zhang et al. 2022), P. minima (GenBank accession number: MH045577; Feng et al. 2020), P. peruviana (GenBank accession number: KP295964 and OP028208; unpublished), P. philadelphica (GenBank accession number: MN192191, MT254545, and MZ539568; Sandoval-Padilla et al. 2019; 2022b), P. pubescens (GenBank accession number: MH045576; Feng et al. 2020), Whithania adpressa (GenBank accession number: BK010847;

Mehmood et al. 2020), W. riebeckii (GenBank accession number: BK010849; Mehmood et al. 2020). Two closely related species, Capsicum annuum (GenBank accession no. KR078313; Raveendar et al. 2015) and C. baccatum (GenBank accession no. KR078314; Kim et al. 2016) were also included as outgroups. The analysis was conducted using maximum likelihood (ML) and Bayesian inference (BI) methods through RAXML-HPC2 v8.2.12 (Stamatakis 2014) and MrBayes v3.2.7a (Ronquist et al. 2012), respectively, accessible via the CIPRES Science Gateway (Miller et al. 2011). For the ML tree, the general time reversible nucleotide substitution model (GTR) with gamma rate (+G) (=GTR+G) was selected, with branch support calculated under 1,000 bootstrap replicates. For the BI tree, a mixed number of substitution types and a 4-by-4 nucleotide substitution model were applied. Each Markov chain Monte Carlo was run for 2,000,000 generations, sampling at every 100 generations, with the first 25% of the trees discarded as burn-in. The final tree was visualised using FigTree version 1.4.4 (Rambaut 2018).

RESULTS

The minimum and average read mapping depths were 265× and 1038.5×, respectively (Fig. 2). The complete plastome sequence of *P. minima* (GenBank accession no. PP471919) was 156,973 bp in size. The genome has a typical quadripartite structure, consisting of a large single-copy (LSC), a small single-copy (SSC), and a pair of inverted repeats (IR_A and IR_B) (Fig. 3), which were 87,196 bp, 18,447 bp and 25,665 bp in length, respectively. The total GC content was 37.5%. A total of 129 genes were annotated, including 84 CDSs, 37 tRNAs and eight rRNAs (Table 1). The annotation of the trans-splicing gene, rpl12, was identified, and for the cis-splicing genes, 16 contained one intron, i.e., *atp*F, *ndh*A, *ndh*B, *pet*B, *pet*D, *rpl*16, *rpo*C1, *rps*16, *rrn*23, *trnA*-UGC, *trnG*-UCC, *trnI*-GAU, *trnK*-UUU, *trnL*-UAA and *trnV*-UAC; while two contained two introns, i.e., *paf*I, and *rps*12 (Fig. 4).

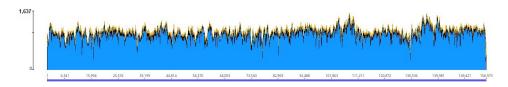


FIGURE 2: Read mapping depth (blue region) of the plastome sequence generated in this study. Y-axis shows the read mapping depth, while X-axis indicates the nucleotide position of the plastome.

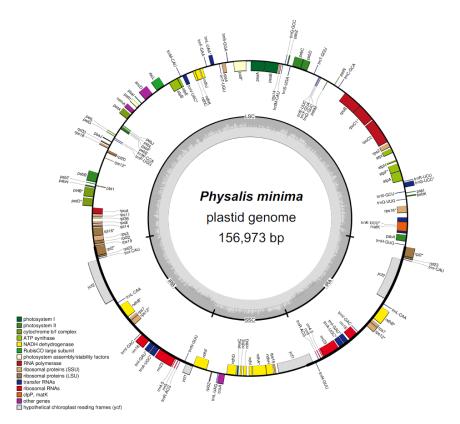


FIGURE 3: Plastid genome map of *Physalis minima*. Genes annotated in the circle are transcribed counterclockwise, while the genes annotated outside the circle are transcribed clockwise.

TABLE 1. List of annotated genes in the plastid genome of *Physalis minima*, along with their group and function. Genes that are duplicated in the inverted repeat region are indicated with an asterisk (*).

Function	Gene group	Name of gene
Photosynthesis pathway	Photosystem I	psaA, psaB, psaC, psaI, psaJ
	Photosystem II	psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbM, psbT, psbZ
	ATP synthase	atpA, atpB, atpE, atpF, atpH, atpl
	NADH complex	ndhA, ndhB*, ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK
	Cytochrome b6/f complex	petA, petB, petD, petG, petL, petN
	Large subunit of Rubisco	rbcL
	Photosystem biogenesis	pbf1

(Continued on next page)

Table 1 (Continued)

Function	Gene group	Name of gene
Structural RNAs	Transfer RNAs	trnA-UGC*, trnC-GCA, trnD-GUC, trnE-UUC, trnF-GAA, trnfM-CAU, trnG-GCC, trnG-UCC, trnH-GUG, trnI-CAU*, trnI-GAU*, trnK-UUU, trnL-CAA*, trnL-UAA, trnL-UAG, trnM-CAU, trnN-GUU*, trnP-UGG, trnQ-UUG, trnS-GGA, trnS-UGA, trnT-GGU, trnT-UGU, trnY-GAC*, trnV-UAC, trnW-CCA, trnY-GUA
Genetic	Large subunit of	rpl2*, rpl14, rpl16, rpl20, rpl22,
apparatus	ribosomal protein	rpl23*, rpl32, rpl33, rpl36
	Small subunit of ribosomal protein	rps2, rps3, rps4, rps7*, rps8, rps11, rps12*, rps14, rps15, rps16, rps18, rps19
	Subunits of RNA polymerase	pafl, pafll, rpoA, rpoB, rpoC1, rpoC2
Others	Maturase	matK
	Inner envelope membrane	cemA
	Cytochrome biogenesis protein	ccsA
	Fatty Acid synthesis	accD
Unknown	Open-reading frame	ycf1*, ycf2*

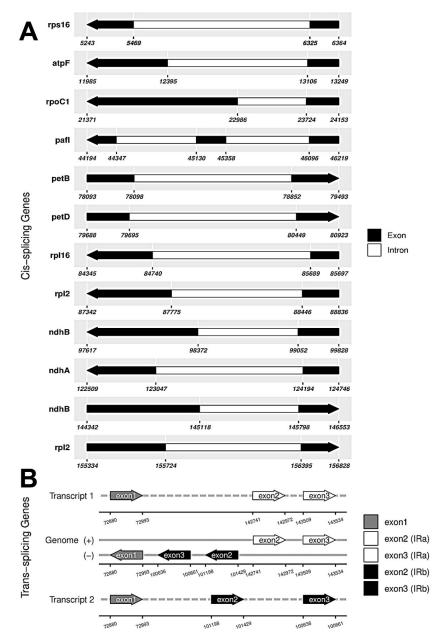


FIGURE 4: Structure of the genes that are difficult to annotate, including (A) cissplicing genes, and (B) trans-splicing genes.

The alignment of the two P. minima complete plastome sequences was 157,330 bp in length. In the alignment, 458 polymorphic sites were identified, of which 259 were in the LSC region, 117 were in the SSC region and 82 were in the IR region. The intraspecific pairwise distance between the two P. minima accessions was 0.003. As both the ML and BI showed the same topology, only the ML tree was presented (Fig. 5). The phylogenetic relationship within Physalis was well-resolved, with bootstrap support (BS) values $\geq 75\%$ and posterior probability (PP) values ≥ 0.95 . However, a weak BS value was observed at the branch node that indicates the divergence between the Iochroma and Whithania clades (BS = 42%). Based on the current sampling size, both P. minima accessions did not cluster together under one clade; the P. minima from Malaysia was the first to diverge in the P. minima from China.

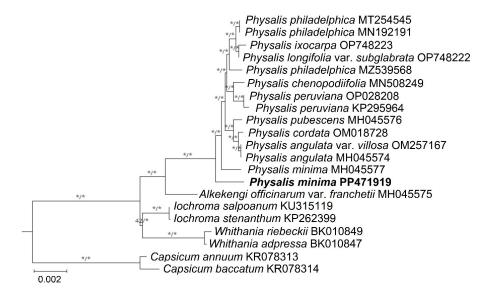


FIGURE 4: Phylogenetic analysis based on the complete plastid genome sequences of 19 Physaleae accessions using the maximum likelihood and Bayesian inference methods. Two closely related species, *Capsicum annuum* (GenBank accession no. KR078313), and *C. baccatum* (GenBank accession no. KR078314) were included as outgroups. Branch support values are indicated above each branch, in which a bootstrap support (left) value ≥ 75% and posterior probability (right) value ≥ 0.95, are considered strongly supported.

DISCUSSION

The complete plastome of P. minima shares key features with its congeneric species, i.e., P. macrophysa and P. ixocarpa (Zhang et al. 2022), reflecting a conserved plastome structure within Physalis. Pairwise comparisons with the accession from China revealed a close intraspecific relationship, with most variable sites in the LSC region and fewest in the IR region, similar to findings on Ipomoea obscura (Sudmoon et al. 2024). The low intraspecific pairwise distance observed between the two P. minima plastomes falls within the typical range of intraspecific plastome variation in angiosperms, which is reported to be generally less than 1.0% (Liu et al. 2024). This low divergence supports their conspecific status and reflects expected plastome-level variation within a species. Within the phylogenetic framework, it is expected that the limited sampling in this study may have reduced resolution at deeper nodes, while variations in analytical frameworks, including substitution models and bootstrap strategies, could significantly impact tree topology and support metrics. This can be explained through the discrepancies in branch support and the phylogenetic placement of Iochroma and Withania, as reported by Sandoval-Padilla et al. (2025). Physalis minima has recently been synonymised with P. angulata (POWO 2024); however, our phylogenetic analysis of complete plastome sequence suggests that they are two natural groups. In the ML tree, P. angulata is placed more closely with the American species, P. cordata and P. pubescens; while the two P. minima accessions form a separate lineage. The divergence between the Malaysian and Chinese accessions of P. minima may reflect geographic structuring and historical isolation, suggesting the presence of distinct evolutionary lineages. This observation has important implications for taxonomic reassessment, as well as conservation, since preserving regionally distinct lineages contributes to the maintenance of genetic diversity and species resilience. Additionally, such genomic divergence may correlate with differences in phytochemical profiles, reinforcing the importance of precise identification in ethnomedicinal contexts (Hao & Xiao 2015). From an ecological perspective, plastome variation may reflect local adaptation to environmental conditions, thereby offering insights for habitat-specific conservation planning (e.g. Hu et al. 2015). Given the unresolved taxonomy of Physalis, where combined plastid and nuclear markers have failed to fully resolve species boundaries (Pere et al. 2023; Whitson & Manos 2005), our results indicate that complete plastome sequences may better resolve these complex relationships. Notably, this study offers a foundation for future ecological and pharmaceutical research on Physalis by resolving taxonomic ambiguities and intraspecific variation, thereby enabling focuses investigations into medicinal properties, phytochemical diversity, and environmental adaptation to support sustainable utilisation

and conservation. Nevertheless, the genomic data presented in this study could offer valuable insights for research on evolutionary patterns and genetic classification within Physalis and Solanaceae.

CONCLUSION

This study reports the complete plastome of *Physalis minima* from Malaysia and provides the first comparative assessment with the previously published accession from China. The plastome structure was highly conserved, but genomic variation and phylogenetic analyses revealed clear genetic differentiation between the two accessions, supporting their recognition as distinct evolutionary lineages. These findings highlight the importance of complete plastome sequences in resolving taxonomic ambiguities within *Physalis* and provide valuable genomic resources for future studies on medicinal properties, phytochemical diversity and conservation of this ethnobotanically important species.

ETHICS STATEMENT

Physalis minima is not a protected plant. Sampling was conducted at an area where no permit is required.

DATA AVAILABILITY STATEMENT

The genome sequence data that support the findings of this study are openly available in GenBank of NCBI at http://www.ncbi.nlm.nih.gov under the accession number PP471919. The associated BioProject, SRA, and BioSample numbers are PRJNA853926, SRR31280283 and SAMN44632072, respectively.

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AUTHOR CONTRIBUTIONS

Wei Lun Ng: Conceptualised the study, wrote the initial manuscript.

Rebecca Jiayiin Ng, Douglas Law and Qiuying Ren: Analysed the data, wrote the initial manuscript.

Charles Gnanaraj: Analysed the data, reviewed the manuscript.

Yoong Soon Yong and Shiou Yih Lee: Conceptualised the study and reviewed the manuscript.

All authors approved the final version of the manuscript.

REFERENCES

- Feng S, Zheng K, Jiao K, Cai Y, Chen C, Mao Y, Wang L, Zhan X, Ying Q and Wang H. (2020). Complete chloroplast genomes of four *Physalis* species (Solanaceae): Lights into genome structure, comparative analysis, and phylogenetic relationships. *BMC Plant Biology* 20: 242. https://doi.org/10.1186/s12870-020-02429-w
- Greiner S, Lehwark P and Bock R. (2019). OrganellarGenomeDRAW (OGDRAW) version 1.3. 1: expanded toolkit for the graphical visualization of organellar genomes. *Nucleic Acids Research* 47(W1): W59–W64. https://doi.org/10.1093/nar/gkz238
- Hao D C and Xiao P G. (2015). Genomics and evolution in traditional medicinal plants: Road to a healthier life. *Evolutionary Bioinformatics* 11: 197–212. https://doi.org/10.4137/EBO.S31326
- Hu S, Sablok G, Wang B, Qu D, Barbaro E, Viola R, Li M and Varotto C. (2015). Plastome organization and evolution of chloroplast genes in *Cardamine* species adapted to contrasting habitats. *BMC Genomics* 16: 306. https://doi.org/10.1186/s12864-015-1498-0
- Katoh K and Standley D M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. https://doi.org/10.1093/molbev/mst010
- Kim T S, Lee J R, Raveendar S, Lee G A, Jeon Y A, Lee H S, Ma K H, Lee S Y and Chung J W. (2016). Complete chloroplast genome sequence of Capsicum baccatum var. baccatum. Molecular Breeding 36: 110. https://doi.org/10.1007/s11032-016-0532-5
- Kumar S, Stecher G and Tamura K. (2016). MEGA7: Molecular evolutionary genetics analysis 7.0 for bigger datasets. *Molecular Biology Evolution* 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054
- Lem F F, Yong Y S, Goh S, Chin S N and Chee F T. (2022). Withanolides, the hidden gem in *Physalis minima*: A mini review on their anti-inflammatory, anti-neuroinflammatory and anti-cancer effects. *Food Chemistry* 377: 132002. https://doi.org/10.1016/j.foodchem.2021.132002
- Liang Y, Liang L, Shi R, Luo R, Yue Y, Yu J, Wang X, Lin J, Zhou T, Yang M, Zhong L, Wang Y and Shu Z. (2024). Genus *Physalis* L.: A review of resources and cultivation, chemical composition, pharmacological effects and applications. *Journal of Ethnopharmacology* 324: 117736. https://doi.org/10.1016/j.jep.2024.117736
- Librado P and Rozas J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25(11): 1451–1452. https://doi.org/10.1093/bioinformatics/btp187
- Liu Z, Lee S Y, Yeh C L, Averyanov L V, Liao W and Suetsugu K. (2024). Plastome analysis elucidates the phylogenetic placement of the mycoheterotrophic genus *Yoania* (Orchidaceae) and its plastomic degeneration during the evolution of mycoheterotrophy. *Botanical Journal of the Linnean Society* 206(4): 313–326. https://doi.org/10.1093/botlinnean/boae028

- Mehmood F, Abdullah, Ubaid Z, Bao Y, Poczai P and Mirza B. (2020). Comparative plastomics of Ashwagandha (*Withania*, Solanaceae) and identification of mutational hotspots for barcoding medicinal plants. *Plants* 9(6): 752. https://doi.org/10.3390/plants9060752
- Miller M A, Pfeiffer W and Schwartz T. (2011). The CIPRES science gateway:
 A community resource for phylogenetic analyses. In *Proceedings of the*2011 TeraGrid Conference: Extreme digital discovery. New York: Association for Computing Machinery, 1–8. https://doi.org/10.1145/2335755.2335836
- MyBIS (2024). Malaysia biodiversity information system. https://www.mybis.gov. my/ (accessed on 14 May 2024).
- Novita M, Rivai H and Misfadhila S. (2020). Review of phytochemical and pharmacological activities of *Physalis minima*. *International Journal of Pharmaceutical Research and Applications* 5(1): 51–56. https://doi.org/10.35629/7781-05015156
- Pere K, Mburu K, Muge E K, Wagacha J M and Nyaboga E N. (2023). Molecular discrimination and phylogenetic relationships of *Physalis* species based on ITS2 and rbcL DNA barcode sequence. *Crops* 3(4): 302–319. https://doi.org/10.3390/crops3040027
- POWO (2024). Plants of the World Online. https://powo.science.kew.org/ (accessed on 6 November 2024).
- Rambaut A. (2018). FigTree. Tree figure drawing tool. http://tree.bio.ed.ac.uk/software/figtree/ (accessed on 1 October 2024).
- Raveendar S, Jeon Y A, Lee J R, Lee G A, Lee K J, Cho G T, Ma K H, Lee S Y and Chung J W. (2015). The complete chloroplast genome sequence of Korean landrace "Subicho" pepper (*Capsicum annuum* var. *annuum*). *Plant Breeding and Biotechnology* 3: 88–94. https://doi.org/10.9787/PBB.2015.3.2.088
- Ronquist F, Teslenko M, van Der Mark P, Ayres D L, Darling A, Höhna S, Larget B, Liu L, Suchard M A and Huelsenbeck J P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029
- Sandoval-Padilla I, del Pilar Zamora-Tavares M, Ruiz-Sánchez E, Pérez-Alquicira J and Vargas-Ponce O. (2022a). Characterization of the plastome of *Physalis cordata* and comparative analysis of eight species of *Physalis* sensu stricto. *PhytoKeys* 210: 109–134. https://doi.org/10.3897/phytokeys.210.85668
- Sandoval-Padilla I, Pérez-Alquicira J, Rodríguez A, del Pilar Zamora-Tavares M and Vargas-Ponce O. (2022b). The plastome of the husk tomato (*Physalis philadelphica* Lam., Solanaceae): A comparative analysis between wild and cultivated pools. *Genetic Resources and Crop Evolution* 69(3): 1391–1405. https://doi.org/10.1007/s10722-021-01334-x
- Sandoval-Padilla I, Pérez-Alquicira J, Zamora-Tavares MDP, Rodríguez A, Cortés-Cruz M, Alcalá-Gómez G and Vargas-Ponce O. (2019). Complete sequence of wild *Physalis philadelphica* chloroplast genome. *Mitochondrial DNA Part B* 4(2): 3295–3297. https://doi.org/10.1080/23802359.2019.1673231
- Sandoval-Padilla I, Vargas-Ponce O, Orejuela A, Pérez-Alquicira J, Ruiz-Sánchez E, Särkinen T, Dodsworth S and del Pilar Zamora-Tavares M. (2025). Comparative and phylogenomic plastome analysis of the Physalideae tribe (Solanaceae). *Plant Systematics and Evolution* 311(2): 1–17. https://doi.org/10.1007/s00606-025-01939-0
- Stamatakis A. (2014). RAxML version 8: A tool for phylogenetic analysis and postanalysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. https://doi. org/10.1093/bioinformatics/btu033

- Sudmoon R, Kaewdaungdee S, Ho H X, Lee S Y, Tanee T and Chaveerach A. (2024). The chloroplast genome sequences of *Ipomoea alba* and *I. obscura* (Convolvulaceae): genome comparison and phylogenetic analysis. *Scientific Reports* 14(1): 14078. https://doi.org/10.1038/s41598-024-64879-8
- Tillich M, Lehwark P, Pellizzer T, Ulbricht-Jones E S, Fischer A, Bock R and Greiner S. (2017). GeSeq versatile and accurate annotation of organelle genomes. Nucleic Acids Research 45(W1): W6–W11. https://doi.org/10.1093/nar/gkx391
- Whitson M and Manos P S. (2005). Untangling *Physalis* (Solanaceae) from the Physaloids: a two-gene phylogeny of the Physalinae. *Systematic Botany* 30(1): 216–230. https://doi.org/10.1600/0363644053661841
- Wu P, Xu C, Chen H, Yang J, Zhang X and Zhou S. (2021). NOVOWrap: an automated solution for plastid genome assembly and structure standardization. *Molecular Ecology Resources* 21(6): 2177–2186. https://doi.org/10.1111/1755-0998.13410
- Xu K, Lin C, Lee S Y, Mao L and Meng K. (2022). Comparative analysis of complete *Ilex* (Aquifoliaceae) chloroplast genomes: Insights into evolutionary dynamics and phylogenetic relationships. *BMC Genomics* 23(1): 203. https://doi.org/10.1186/s12864-022-08397-9
- Zamora-Tavares M D P, Sandoval-Padilla I, Chávez Zendejas A, Pérez-Alquicira J and Vargas-Ponce O. (2020). Complete chloroplast genome of *Physalis chenopodifolia* Lam. (Solanaceae). *Mitochondrial DNA Part B* 5(1): 162–163. https://doi.org/10.1080/23802359.2019.1698364
- Zhan X, Zhang Z, Zhang Y, Gao Y, Jin Y, Shen C, Wang H and Feng S. (2022). Complete plastome of *Physalis angulata* var. *villosa*, gene organization, comparative genomics and phylogenetic relationships among Solanaceae. *Genes* 13(12): 2291. https://doi.org/10.3390/genes13122291
- Zhang Z, Jin Y, Gao Y, Zhang Y, Ying Q, Shen C, Lu J, Zhan X, Wang H and Feng S. (2022). The complete chloroplast genomes of two *Physalis* species, *Physalis macrophysa* and *P. ixocarpa*: Comparative genomics, evolutionary dynamics and phylogenetic relationships. *Agronomy* 13(1): 135. https://doi.org/10.3390/agronomy13010135