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PLASTOME REPORT

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The complete chloroplast genome sequencing and phylogenetic analysis of *Ludwigia peruviana* (L.) H.Hara 1953 (Onagraceae)

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ABSTRACT

Ludwigia peruviana (L.) H.Hara 1953, a member of the Onagraceae, exhibits diverse potential applications, yet genomic resources – particularly chloroplast (cp) genome data – remain limited. Here, we sequenced and characterized the complete cp genome of *L. peruviana,* which was 158,938 bp in length and encoded 113 unique genes, including 79 protein-coding genes, 30 transfer RNA genes, and four ribosomal RNA genes. Phylogenetic analyses indicate a close relationship between *L. peruviana* and *Ludwigia hyssopifolia*. These results provide a useful genetic resource for further phylogenetic and taxonomic investigations of *Ludwigia* and Onagraceae, contributing to a more comprehensive understanding of their relationships.

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Peruvian primrose-willow; plastome; phylogenomics; Vietnam

Introduction

Ludwigia peruviana (L.) H.Hara 1953 (Onagraceae), the Peruvian primrose-willow, is native to the Americas but now widely invasive across Asia and the southern United States (Jacobs et al. 1994). The medicinal potential of the *Ludwigia* species is underpinned by a rich phytochemical profile, including flavonoids, triterpenoids, phenolic acids, saponins, and tannins (Chang and Kuo 2007; Mabou et al. 2016; Baky et al. 2022). Specific analyses of *L. peruviana* have identified bioactive compounds, including 2-methoxy-4-vinylphenol, 1-deoxy-D-mannitol, and 4-hydroxy-cyclohexanone (Midhuna et al. 2025), supporting significant biological activities of *L. peruviana*, including anti-malarial effects, anti-inflammation, and benefits for gastrointestinal disorders (Dike et al. 2012; Midhuna et al. 2025).

Within Onagraceae, *Ludwigia* represents an early-diverging lineage. However, its evolutionary history is notoriously complex, with taxa exhibiting diploid to decaploid levels, indicative of rampant hybridization and allopolyploidization events (Dike et al. 2012; Liu et al. 2017; Barloy et al. 2024; Midhuna et al. 2025). This complexity can obscure phylogenetic reconstruction using conventional markers, necessitating the use of more comprehensive genomic approaches.

Chloroplast (cp) genomes provide an ideal dataset for addressing these challenges and serve as a powerful 'super-barcode' for the definitive species authentication in medicinal plants (Ruhfel et al. 2014; Daniell et al. 2016). Despite this utility, cp genomic resources for *Ludwigia* remain scarce, with only five characterized to date (Liu et al. 2016; Shen et al. 2023; Nguyen et al. 2024). Here, we report the complete cp genome of *L. peruviana* to provide a reference genome, clarify its phylogenetic position, and establish a genomic foundation for conservation, authentication, and pharmacophylogenetic-guided drug discovery.

Materials and methods

Fresh leaves of *L. peruviana* were collected in Dak Lak Province, Vietnam (12°32′29.5″N 107°53′19.4″E) (Figure 1). Leaves were dried in silica gel at room temperature and deposited at the NTT Hi-Tech Institute under a voucher (registered number FRGC_2022_10_01) (contact: Dr. Hoang Dang Khoa Do, dhdkhoa@ntt.edu.vn). Total genomic DNA was extracted using a modified CTAB method (Porebski et al. 1997). The extracted DNA had a concentration of 75.2 ng/μL, with A260/280 and A260/230 ratios of 1.88 and 2.15, respectively, and its integrity was confirmed on a 1% agarose gel. The DNA sample was sent for the paired-end (150 bp × 2) sequencing on an Illumina MiSeq system at KTest Science Co. Ltd. (Ho Chi Minh City, Vietnam). Raw reads were trimmed and quality-filtered with fastp v0.24.0 (Chen et al. 2018), yielding 29,715,291 reads of clean data.

Clean reads were *de novo* assembled using NOVOPlasty v4.3.3 (Dierckxsens et al. 2017) with the *Ludwigia adscendens* (L.) H.Hara 1953 cp genome (NC_081012) as the seed. The resulting circular cp genome was imported into Geneious

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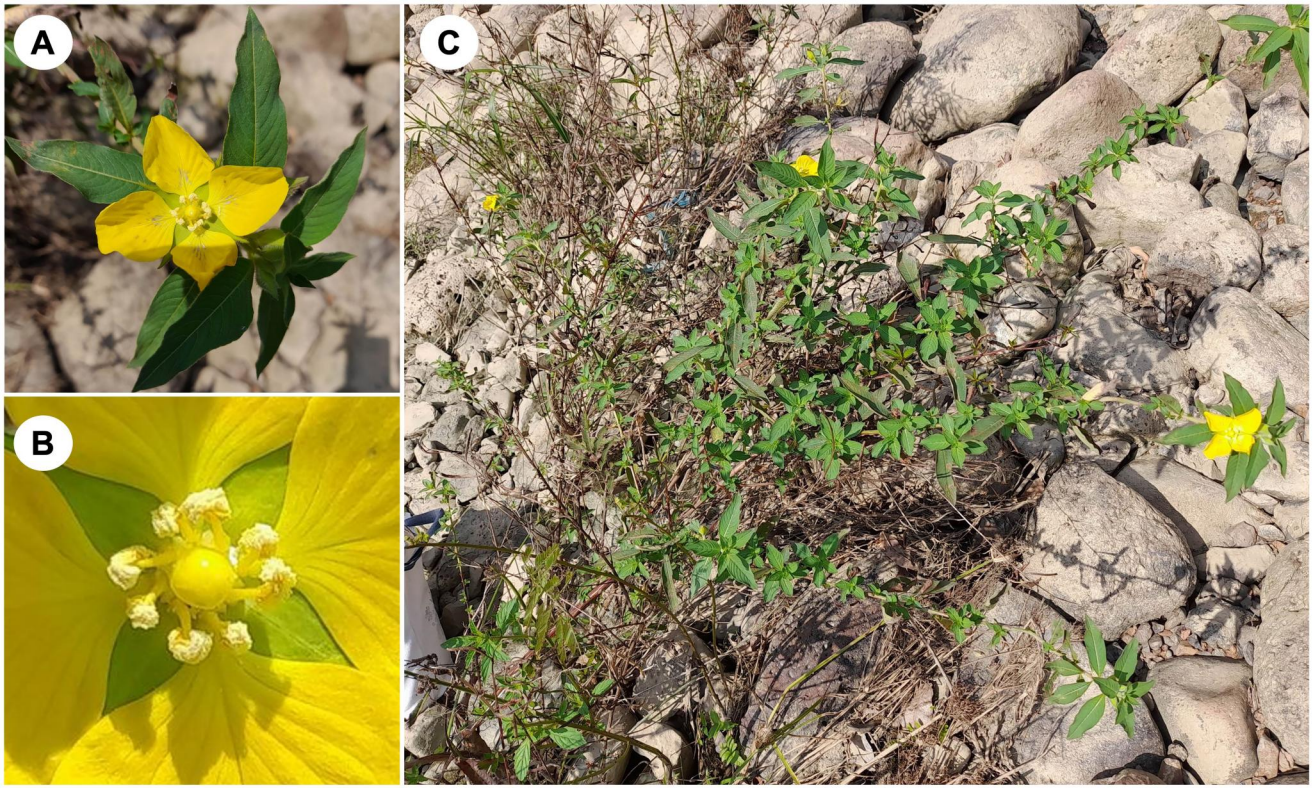

Figure 1. Photograph of *Ludwigia peruviana*. (A) Leaves and flowers. The leaves are lanceolate or obovate-lanceolate, with flowers on the upper leaf axil. Petals are suborbicular, short-clawed, and yellow with brownish nerves. (B) Stamens and stigma (8 or 10 subequal yellow stamens). (C) Whole plant. The photo was taken by the author Hoang Dang Khoa Do.

Prime v2025.0.2, cleaned Illumina short reads were mapped back to the assembly (Map to Reference), and coverage depth and read support for variants were manually inspected across the genome – with particular attention to the LSC/IRb/SSC/IRa junctions. No additional polishing was required. Annotation was performed using GeSeq (Tillich et al. 2017), followed by manual curation in Geneious Prime v2025.0.2 with reference to three cp genomes (*L. adscendens*, *Ludwigia octovalvis* (Jacq.) P.H.Raven 1962, and *Ludwigia prostrata* Roxb. 1982). Intron–exon structures were illustrated using CPGView (Liu et al. 2023) and the circular genome map was generated using OGDRAW v1.3.1 (Greiner et al. 2019).

To reconstruct the phylogeny of *L. peruviana*, we retrieved cp genomes of 32 other Onagraceae species and an outgroup *Lagerstroemia villosa* Wall. ex Kurz 1873 (NC_042894) (Lythraceae) from GenBank database. Seventy-nine protein-coding genes (PCGs) from cp genomes were extracted and aligned with MAFFT in Geneious Prime. Phylogenetic trees were constructed using maximum-likelihood (ML) in IQ-TREE v2.4.0 (Minh et al. 2020) and Bayesian inference (BI) methods in MrBayes v3.2.7a (Huelsenbeck and Ronquist 2001). Both methods employed the best-fit model GTR + I + G, predicted by jModelTest v2.1.10 (Posada 2008). IQ-TREE 2 was run with ultrafast bootstrap (BS) approximation and 1000 replicates. MrBayes was run for 1,000,000 MCMC generations with a 25% burn-in. Nodes with BS support value $\geq$70% and posterior probability (PP) $\geq$0.95 were considered robustly supported. Trees were visualized with FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

The complete cp genome of *L. peruviana* (GenBank: PV207539) is a 158,938 bp circular molecule with an average coverage depth of 1922× (Figure S1). It exhibits a canonical quadripartite, comprising a large single-copy region (89,836 bp), a small single-copy region (19,550 bp), and two inverted repeat (IR) regions (24,776 bp each) with an overall GC content of 37.3% (Figure 2).

The genome comprises 129 genes, including 84 PCGs, 37 transfer RNA genes, and eight ribosomal RNA genes (Table 1). Seventeen genes were duplicated in the IRs (including *rpl*2, *rpl*23, *rps*7, *rps*12, *ndh*B, *ycf*2, *rrn*4.5, *rrn*5, *rrn*16, *rrn*23, *trn*A-UGC, *trn*I-GAU, *trn*I-CAU, *trn*L-CAA, *trn*N-GUU, *trn*R-ACG, and *trn*V-GAC). Nine PCGs (*atp*F, *ndh*A, *ndh*B, *rpl*2, *rpl*16, *pet*D, *rps*16, *rpo*C1, and *pet*B) harbor a single intron, while *clp*P and *paf*I contain two introns (Figure S2). The *rps*12 gene exhibits trans-splicing, with exons 2 and 3 located in the IRs (Figure S3).

The phylogenetic trees from ML and BI analyses produced identical, strongly supported topologies (Figure 3). Onagraceae were recovered as two major subfamilies: Onagroideae and Ludwigioideae, with most clades receiving maximum support (BS = 100, PP = 1.0). The genus *Ludwigia* formed a monophyletic clade in the tribe Jussiaeeae of Ludwigioideae subfamily. Within *Ludwigia*, *L. peruviana* is most closely related to *L. hyssopifolia* with maximum support (BS = 100, PP = 1.0).

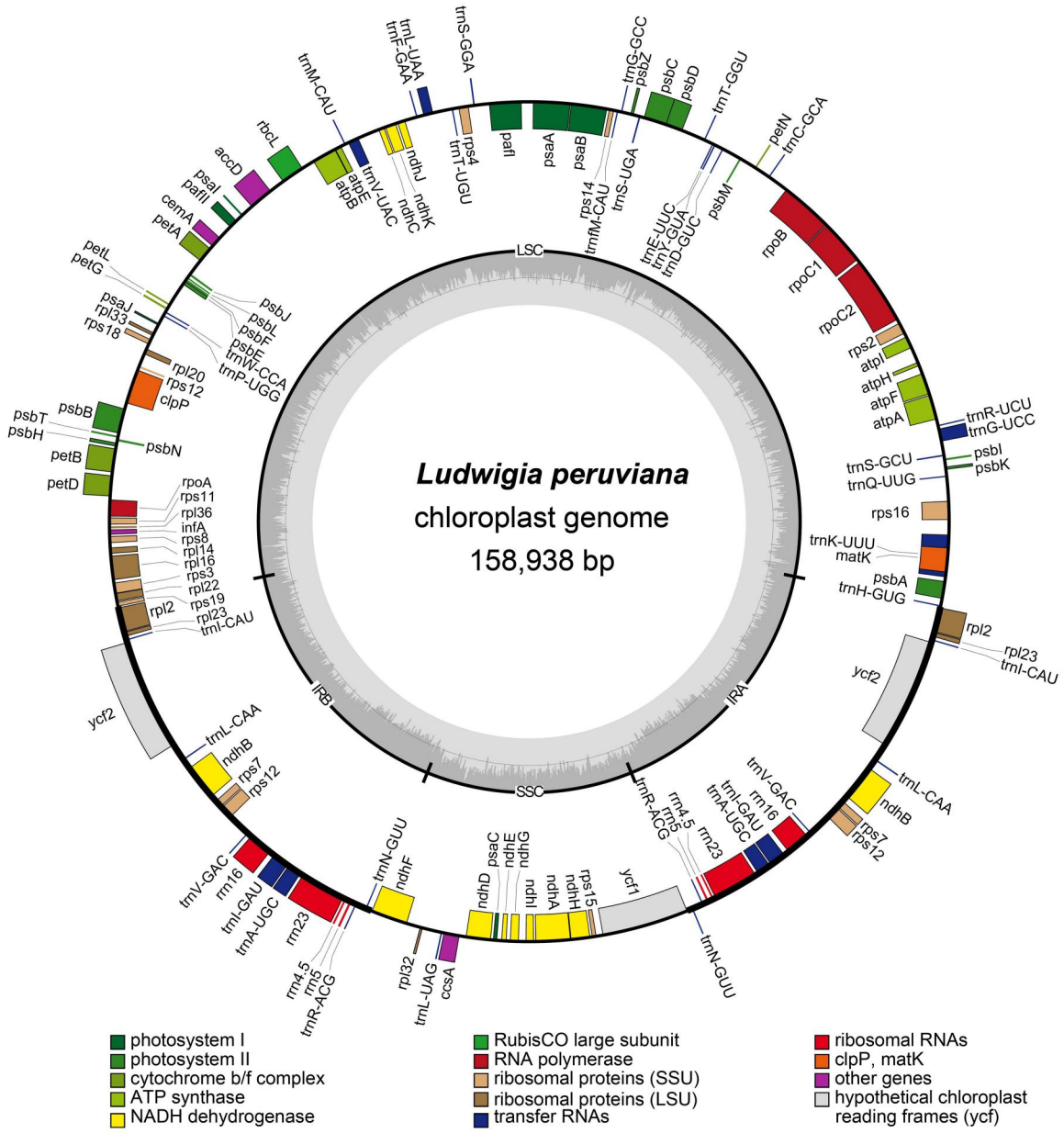

Figure 2. The chloroplast genome map of *Ludwigia peruviana*. The largest circle represents gene location and orientation. Genes located outside the circle are transcribed clockwise, whereas genes inside the circle are transcribed counterclockwise. The smaller inner circle indicates the GC and AT contents, represented by darker gray and lighter gray, respectively. SSC: small single-copy; LSC: large single-copy; IRa, IRb: inverted repeat regions.

Discussion and conclusions

The *L. peruviana* cp genome shows structure and gene content consistent with other members of the genus (Table S1), with *L. adscendens* having the largest cp genome (159,592 bp) and *L. hyssopifolia* the smallest (158,534 bp). *Ludwigia* species have smaller IR regions (~24.8 kb, containing 17 genes) than several other Onagraceae genera (e.g. *Epilobium*, *Circaea*, and *Oenothera*), where IR regions expand from 25,052 bp (*Circaea glabrescens* (Pamp.) Hand.-Mazz. 1933) to 30,844 bp (*Oenothera villaricae* W.Dietr. 1978), incorporating additional genes such as *ndh*F, *rpl*32, *trn*L-CAA, and *ccs*A (Palmer 1985; Luo et al. 2021). These data illustrate that shifts in IR-SC boundaries are a primary source of cp genome size variation in Onagraceae.

Our phylogenetic analysis confidently places *L. peruviana* as sister to *L. hyssopifolia* (Figure 3), addressing ambiguities in prior studies using fewer taxa (Nguyen et al. 2024) or single markers like *mat*K (Barloy-Hubler et al. 2024). Accurate species identification is crucial for the safe and effective use of medicinal plants like *L. peruviana*, as adulteration is a major concern. While standard DNA barcodes (*mat*K and *rbc*L) can lack resolution for closely related species, the complete cp genome acts as a 'super-barcode' for developing highly specific identification tools. The cp genome reported here enables the design of species-specific assays to authenticate raw plant materials and safeguard herbal products. The phylogenetic framework also informs drug discovery through pharmacophylogeny – the principle that related species often share similar bioactive compounds. Our phylogeny acts as a predictive map for bioprospecting in *Ludwigia*. Since *L. peruviana* has documented anti-malarial and potential anti-cancer activities, its sister species, *L. hyssopifolia*, and other

Table 1. Gene composition of the *Ludwigia peruviana* chloroplast genome.

Gene categories	Groups of genes	Gene names
Self-replication	Ribosomal RNAs	*rrn*4.5 (2x), *rrn*5 (2x), *rrn*16 (2x), *rrn*23 (2x)
	Transfer RNAs	*trn*A-UGC[a] (2x), *trn*C-GCA, *trn*D-GUC, *trn*E-UUC, *trn*F-GAA, *trn*G-UCC[a], *trn*G-GCC, *trn*H-GUG, *trn*I-CAU, *trn*I-GAU[a] (2x), *trn*K-UUU[a], *trn*L-UAA[a], *trn*L-UAG, *trn*L-CAA (2x), *trnf*M-CAU, *trn*M-CAU (2x), *trn*N-GUU, *trn*P-UGG, *trn*Q-UUG, *trn*R-UCU, *trn*R-ACG (2x), *trn*S-GCU, *trn*S-UGA, *trn*S-GGA, *trn*T-GGU, *trn*T-UGU, *trn*V-UAC[a], *trn*V-GAC (2x), *trn*W-CCA, *trn*Y-GUA
	Large subunit ribosome	*rpl*2[a] (2x), *rpl*14, *rpl*16[a], *rpl*20, *rpl*22, *rpl*23 (2x), *rpl*32, *rpl*33, *rpl*36
	Small subunit ribosome	*rps*2, *rps*3, *rps*4, *rps*7 (2x), *rps*8, *rps*11, *rps*12[a] (2x), *rps*14, *rps*15, *rps*16[a], *rps*18, *rps*19
	RNA polymerase	*rpo*A, *rpo*B, *rpo*C1[a], *rpo*C2
Photosynthesis	ATP synthase subunit	*atp*A, *atp*B, *atp*E, *atp*F[a], *atp*H, *atp*I
	Photosystem I subunit	*psa*A, *psa*B, *psa*C, *psa*I, *psa*J, *paf*I[b], *paf*II
	Photosystem II subunit	*psb*A, *psb*B, *psb*C, *psb*D, *psb*E, *psb*F, *psb*H, *psb*I, *psb*J, *psb*K, *psb*L, *psb*M, *pbf*1, *psb*T, *psb*Z
	Cytochrome b/f complex subunit	*pet*A, *pet*B[a], *pet*D[a], *pet*G, *pet*L, *pet*N
	NADH dehydrogenase	*ndh*A[a], *ndh*B[a] (2x), *ndh*C, *ndh*D, *ndh*E, *ndh*F, *ndh*G, *ndh*H, *ndh*I, *ndh*J, *ndh*K
	Rubisco subunit	*rbc*L
Other genes	ATP-dependent protease subunit P	*clp*P[b]
	Envelope membrane protein	*cem*A
	Acetyl-CoA-carboxylase subunit	*acc*D
	Maturase	*mat*K
	C-type cytochrome synthesis gene	*ccs*A
	Translational initiation factor	*inf*A
Unknown function	Conserved open reading frame	*ycf*1 (2x), *ycf*2 (2x)

(2x) – duplicated gene in IR region.
[a]Gene containing one intron.
[b]Gene containing two introns.

close relatives are now high-priority candidates for screening for similar bioactivities. This provides an actionable roadmap for the targeted discovery of new plant-derived medicines. Future studies incorporating more cp genomes across *Ludwigia* will refine infrageneric relationships and enhance conservation-focused bioprospecting in this ecologically and medicinally significant genus.

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Author contributions

CRediT: **Thanh Mai Luc**: Formal analysis, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing; **Hoang Danh Nguyen**: Conceptualization, Formal analysis, Methodology, Software, Validation, Writing – review & editing; **Hoang Dang Khoa Do**: Data curation, Methodology, Resources, Software, Supervision, Validation, Writing – review & editing; **Thiet Minh Vu**: Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

Ethics statement

No specific permits or ethical approvals were required for *Ludwigia peruviana* sampling in Vietnam, as this species is an unregulated common weed not listed in the Vietnam Red Data Book, IUCN Red List, or CITES Appendices. The collection occurred outside protected areas and was conducted for noncommercial research under Vietnam's Biodiversity Law (No. 20/2008/QH12) and Decree 59/2017/NĐ-CP. A voucher specimen (registered number FRGC_2022_10_01) was deposited at NTT Hi-Tech Institute's herbarium following standard documentation protocols.

Disclosure statement

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

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Data availability statement

The chloroplast genome of *Ludwigia peruviana* is available in GenBank under accession number PV207539. The associated BioProject, SRA, and BioSample numbers are PRJNA1231038, SRR32555115, and SAMN47199217, respectively.

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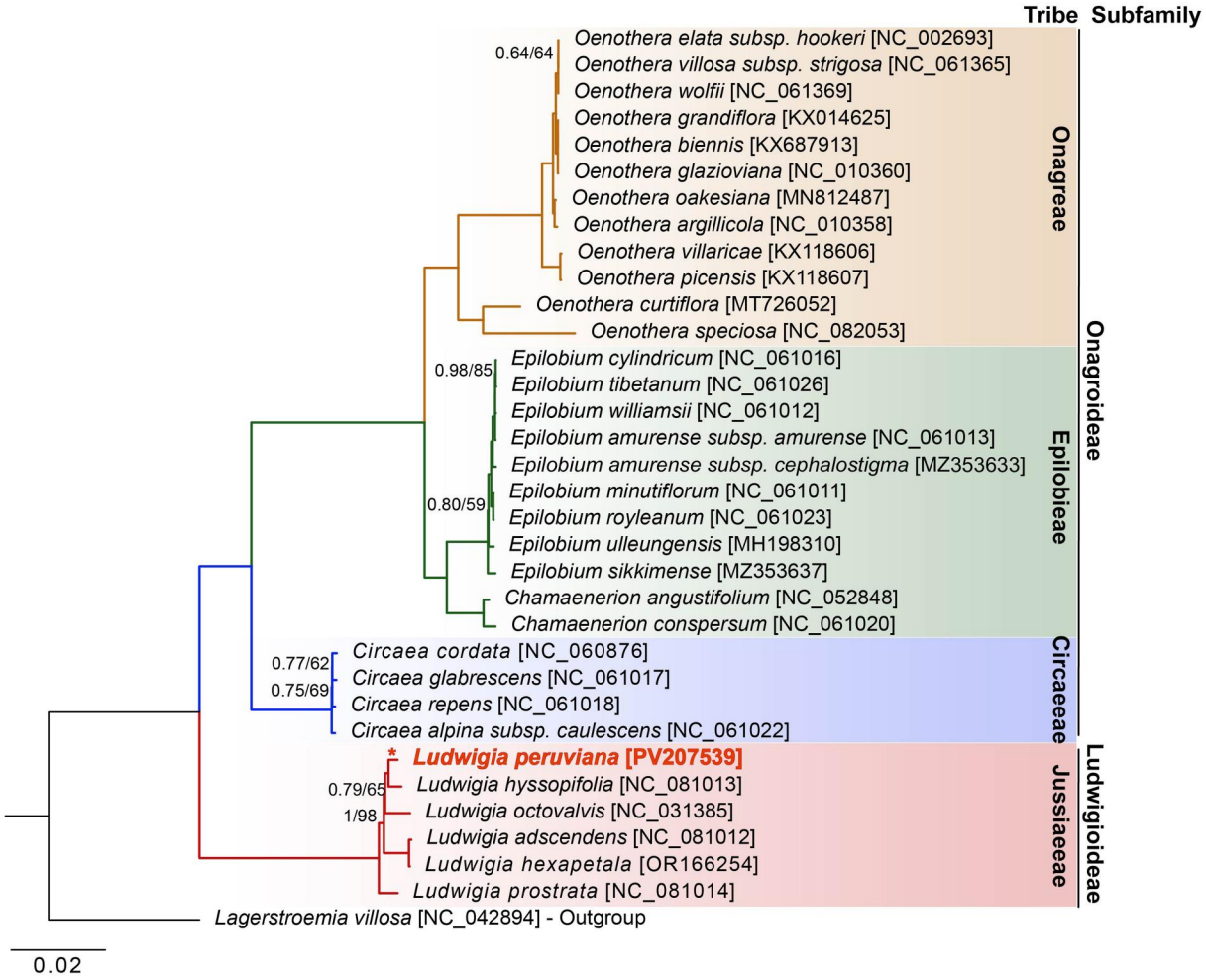

Figure 3. Phylogenetic relationship of *Ludwigia peruviana* and related species in Onagraceae based on 79 chloroplast protein-coding genes. The trees were inferred by BI and ML (with 1000 bootstrap replicates) . Node labels show BI posterior probabilities/ML bootstrap percentages (PP/BS). Only non-maximal supports (BS $<$ 100, PP $<$ 1.0) are displayed for readability. The red asterisk marks *L. peruviana* (PV207539) sequenced in this study. The scale bar represents nucleotide substitutions per site. The sequences utilized to reconstruct the phylogenetic tree include: *Ludwigia hyssopifolia* NC_081013 (Nguyen et al. 2024), *Ludwigia octovalvis* NC_031385 (Liu et al. 2016), *Ludwigia adscendens* NC_081012 (Nguyen et al. 2024), *Ludwigia hexapetala* OR166254 (Barloy-Hubler et al. 2024), *Ludwigia prostrata* NC_081014 (Nguyen et al. 2024), *Oenothera elata subsp. hookeri* NC_002693 (Hupfer et al. 2000), *Oenothera villosa subsp. strigosa* NC_061365 (Zupok et al. 2021), *Oenothera wolfii* NC_061369 (Zupok et al. 2021), *Oenothera grandiflora* KX014625 (unpublished), *Oenothera biennis* KX687913 (Sobanski et al. 2019), *Oenothera glazioviana* NC_010360 (Greiner et al. 2008), *Oenothera oakesiana* MN812487 (Zupok et al. 2021), *Oenothera argillicola* NC_010358 (Greiner et al. 2008), *Oenothera villaricae* KX118606 (unpublished), *Oenothera picensis* KX118607 (unpublished), *Oenothera curtiflora* MT726052 (unpublished), *Oenothera speciosa* NC_082053 (unpublished), *Epilobium cylindricum* NC_061016 (Luo et al. 2021), *Epilobium tibetanum* NC_061026 (Luo et al. 2021), *Epilobium williamsii* NC_061012 (Luo et al. 2021), *Epilobium amurense subsp. amurense* NC_061013 (Luo et al. 2021), *Epilobium amurense subsp. cephalostigma* MZ353633 (Luo et al. 2021), *Epilobium minutiflorum* NC_061011 (Luo et al. 2021), *Epilobium royleanum* NC_061023 (Luo et al. 2021), *Epilobium ulleungensis* MH198310 (unpublished), *Epilobium sikkimense* MZ353637 (Luo et al. 2021), *Chamaenerion angustifolium* NC_052848 (unpublished), *Chamaenerion conspersum* NC_061020 (Luo et al. 2021), *Circaea cordata* NC_060876 (Luo et al. 2021), *Circaea glabrescens* NC_061017 (Luo et al. 2021), *Circaea repens* NC_061018 (Luo et al. 2021), *Circaea alpina subsp. caulescens* NC_061022 (Luo et al. 2021), and *Lagerstroemia villosa* NC_042894 (Gu et al. 2019) as an outgroup.

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