

Rediscovery of *Lysimachia peduncularis* in China: amended description, complete plastid genome, and phylogenomic placement in subgenus *Idiophyton* (Primulaceae)

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Abstract

Background and aims – *Lysimachia peduncularis* has not been recorded in China for nearly half a century. Its recent rediscovery in southern Yunnan provides a critical opportunity to update its taxonomic description, clarify its nomenclatural history, and re-evaluate its systematic placement using comprehensive genomic data.

Material and methods – We conducted detailed comparative morphological analysis based on newly collected specimens. Molecular phylogenetic relationships were reconstructed using nrITS, three plastid DNA regions (*atpF-atpH*, *trnL-trnF*, and *rpl32-trnL*), and the first reported complete plastome for this species.

Key results – Phylogenomic evidence strongly supports *L. peduncularis* as sister to a clade comprising *L. laxa* and *L. lancifolia*, nested firmly within *L.* subg. *Idiophyton*. This robust placement revises its traditional classification, which was based solely on morphology. Notably, *L. peduncularis* exhibits an atypical ratio of filament-to-anther length, departing from the general pattern observed in *Lysimachia*. While this trait remains a key diagnostic character for the subgenus, its variation in this species underscores the need for caution when using single morphological traits for infrageneric classification.

Conclusion – This rediscovery not only confirms the current status of *L. peduncularis* in China and expands its known distribution but also resolves its phylogenetic position. These findings contribute to a more nuanced understanding of the evolutionary history and character evolution within *Lysimachia*.

Keywords

lectotypification, seed micromorphology, molecular phylogeny, transboundary conservation

INTRODUCTION

Lysimachia L. (Linnaeus 1753: 146) is a morphologically diverse genus, representing the second-largest group within the subfamily Myrsinoideae of Primulaceae (Angiosperm Phylogeny Group 2016). It comprises approximately 250 species globally, primarily distributed across temperate and subtropical regions of the Northern Hemisphere (Hu and Kelso 1996), with particularly high diversity observed in the tropical Karst landform areas of

Asia (Yan et al. 2018, 2025). The monophyly of *Lysimachia* s.s. has been challenged by both morphological and molecular data. Subsequent phylogenetic analyses confirmed this by demonstrating that several satellite genera (namely *Anagallis* L., *Asterolinon* Hoffmanns. & Link, *Glaux* L., *Pelletiera* A.St.-Hil., and *Trientalis* L.) are deeply embedded within *Lysimachia*, thereby establishing a more robust phylogenetic framework for the genus (Anderberg and Ståhl 1995; Hao et al. 2004; Anderberg et al. 2007; Liu et al. 2023; Dong et al. 2025).

China represents a major centre of *Lysimachia* diversity, encompassing 138 to 150 species (Chen et al. 1989; Hu and Kelso 1996), with the highest concentrations found in its southern and southwestern regions. Due to this complexity and high endemism, recent systematic efforts continue to result in the discovery and formal description of numerous new species (e.g. Huang et al. 2020; Mou et al. 2020; Ke et al. 2021; Lu et al. 2021; Zhang et al. 2024; Quan et al. 2025; Xiong et al. 2025; Xu et al. 2025).

The *Lysimachia* flora of southwestern China exhibits strong biogeographical affinities with that of Southeast Asia, including Myanmar, Thailand, Laos, Vietnam, and the Malay Peninsula. During recent botanical expeditions in southern Yunnan (2021–2022), we rediscovered *L. peduncularis* Wall. ex Kurz, representing its first record in China in nearly half a century. This prolonged hiatus has not only hindered conservation assessments but also obscured the species' taxonomic identity and phylogenetic position. Furthermore, existing descriptions in Flora Reipublicae Popularis Sinicae and Flora of China remain rudimentary, providing insufficient morphological detail for robust species delimitation or systematic comparison. Consequently, a comprehensive re-evaluation of this elusive species is urgently required.

MATERIAL AND METHODS

Specimen collection and morphological analysis

Living individuals of *L. peduncularis* were collected from southern Yunnan, China, and subsequently maintained under ex situ cultivation at the Shanghai Chenshan Botanical Garden for phenological observation and morphological study. Voucher specimens were deposited in the Herbarium of Shanghai Chenshan Botanical Garden (CSH). Critical morphological identifications and the amended description were based on an integrative examination of five living individuals and three herbarium collections (*Wu Zhi-jin* WZJ00369, CSH, six specimens; 孟连调查队 10213, HITBC 042682; *Larsen et al.* 44904, AAU). These materials were compared with historical literature and type specimens accessed via digital databases, including China Virtual Herbarium, AAU, E, and K, (herbarium acronyms follow Thiers 2025).

Geographic coordinates of the newly collected Chinese specimens were recorded in the field using the mobile GPS application 2bulu (Shenzhen 2bulu Information Technology Co., Ltd., China). For the remaining known localities, coordinates were georeferenced from collection locality descriptions in the literature (Hu 1985). All coordinates were imported into Google Earth Pro (Google LLC, Mountain View, CA, USA), verified for accuracy, and exported to generate the distribution map.

Detailed macromorphological analyses were conducted using an Olympus SZ60 stereo dissecting microscope. Quantitative traits, including the relative lengths of filaments and anthers, were measured using a precision

steel ruler and digital callipers. Qualitative features, such as the distribution of glandular dots and trichomes, were observed and documented. Seed micromorphology was examined following the protocols of Oh et al. (2008), with shapes and surface ornamentation patterns documented for 20 mature seeds. Specimen photography was performed using a Nikon Z7 II digital camera equipped with a 50 mm macro lens; all herbarium sheets included a standard X-Rite Color Checker and a metric scale to ensure colour fidelity and dimensional accuracy.

DNA extraction, sequencing, and assembly

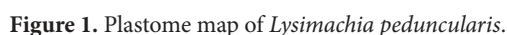
Leaf tissues were collected from the field and sent to Biowefind in Wuhan, China, for genomic DNA extraction, library construction, and genome skimming. Genomic DNA was extracted using a modified CTAB protocol (Doyle and Doyle 1987). The prepared library was quality-assessed and subsequently sequenced on an Illumina NovaSeq 6000 platform using a 150 bp paired-end strategy, yielding approximately 3 GB of high-quality data. Quality control was performed using SOAPnuke (Chen et al. 2018). The complete plastid genome (plastome) and nuclear ribosomal DNA (nrDNA) of *L. peduncularis* were assembled de novo using GetOrganelle v.1.7 (Jin et al. 2020) with default parameters. The ITS1-5.8S-ITS2 region (nrITS) was extracted with ITSx v.1.1.3 (Bengtsson-Palme et al. 2013). The assembled plastome was manually checked and adjusted in Geneious Prime 2021.2.2 (<https://www.geneious.com>). Plastome annotation and the graphical circular map were generated using CPGAVAS2 (Shi et al. 2019), with the published plastid genome of *L. laxa* Baudo (GenBank accession number: [LC758780](https://www.ncbi.nlm.nih.gov/nuclot/LC758780)) serving as the reference sequence. Assembled sequences of nrITS and plastid loci were uploaded to GenBank. All the accession numbers of sequences used in this study are listed in Suppl. materials 1 and 2.

Phylogenetic analyses

Phylogenetic analyses were conducted using three separate datasets: (1) nrITS, (2) combined three plastid loci (*atpF-atpH*, *trnL-trnF*, and *rpl32-trnL*), and (3) the complete plastid genome dataset. Species sampling, including outgroup sampling followed several previous studies (Mou et al. 2020; Lu et al. 2021; Liu et al. 2023). Sequences were aligned in Geneious Prime using MAFFT (Katoh and Standley 2013) with default settings. Best-fit models for maximum likelihood (ML) and Bayesian inference (BI) were selected using PartitionFinder 2 (Lanfear et al. 2017) and implemented in PhyloSuite (Zhang et al. 2020). Bayesian phylogenies were inferred using MrBayes v.3.2.7a (Ronquist et al. 2012) with two parallel runs of 20 million generations, discarding the initial 25% of sampled data as burn-in. Maximum likelihood phylogenies were inferred using IQ-TREE v.2.2.0 under the edge-linked partition model, with 10,000 ultrafast bootstraps (Minh et al. 2020). Tree files were visualized in iTOL

The systematic position of *L. peduncularis* was evaluated using three datasets: nrITS, combined plastid loci, and the complete plastome. All three datasets consistently resolved *L. peduncularis* as firmly nested within *L. subg. Idiophyton* (Fig. 2). Specifically, the species consistently formed a strongly supported clade as the sister species to the lineage comprising *L. laxa* and *L. lancifolia* Craib (Suppl. material 3). The statistical support for this sister relationship remained high across all datasets. The nrITS phylogeny provided strong support (BS = 99; PP = 1.00); the combined three plastid loci phylogeny also showed high support (BS = 89; PP = 0.99); and the complete plastome phylogeny yielded the highest support (BS = 100) (Fig. 2). The phylogenetic analyses thus confirm the systematic position of the species and provide a robust molecular framework for the subsequent re-evaluation of its morphology.

The nuclear ribosomal DNA (nrITS) sequence of *L. peduncularis* was determined to be 627 bp in length (GenBank accession number: [PQ451564](#)). The assembled complete plastid genome (plastome) of *L. peduncularis* (GenBank accession number: [PV299159](#)) spanned 155,376 bp in length and exhibited a typical quadripartite (QP) structure (Fig. 1). This structure consists of a large single-copy (LSC) region of 70,374 bp, a small single-copy (SSC) region of 17,648 bp, and two inverted repeats (IRs) of 26,361 bp each.



Based on the confirmed systematic position through molecular data, and the critical comparison with type specimens, the rediscovery of *L. peduncularis* in China is formally confirmed and a detailed supplementary description is provided.

TAXONOMIC TREATMENT

Lysimachia peduncularis Wall. ex Kurz (Kurz 1877: 219)

Figs 3–7

Type. MYANMAR • Ava, Taong Dong; 1826; *Wallich Cat.* 1489; lectotype (**designated here**): K [K000750700] image!; isolectotype: K [K001113215] image! • Prome;

1826; *Wallich Cat.* 1489; syntypes: K [K001113216] image!, E [E00062010] image!.

Description. Herbs annual, 4–30 cm tall. Stems erect or decumbent, angular and narrowly winged, slightly striate, branched near the base. Leaves spirally arranged or crowded toward the apex of the stem, petiole 0.5–1 cm long, leaf blade lanceolate, 1.5–4.5 × 0.5–1 mm, strigillose adaxially and along midvein abaxially, base cuneate-attenuate, decurrent to petioles, apex acute to short acuminate, veins 5–7 pairs, veinlets prominent and glandular dotted abaxially. Pedicel slender, 2.5–5 cm long, sparsely strigose, usually longer than leaves. Flowers solitary, axillary. Calyx lobes oblong-lanceolate, 3–5 mm long, apex short acuminate to acute, conspicuously

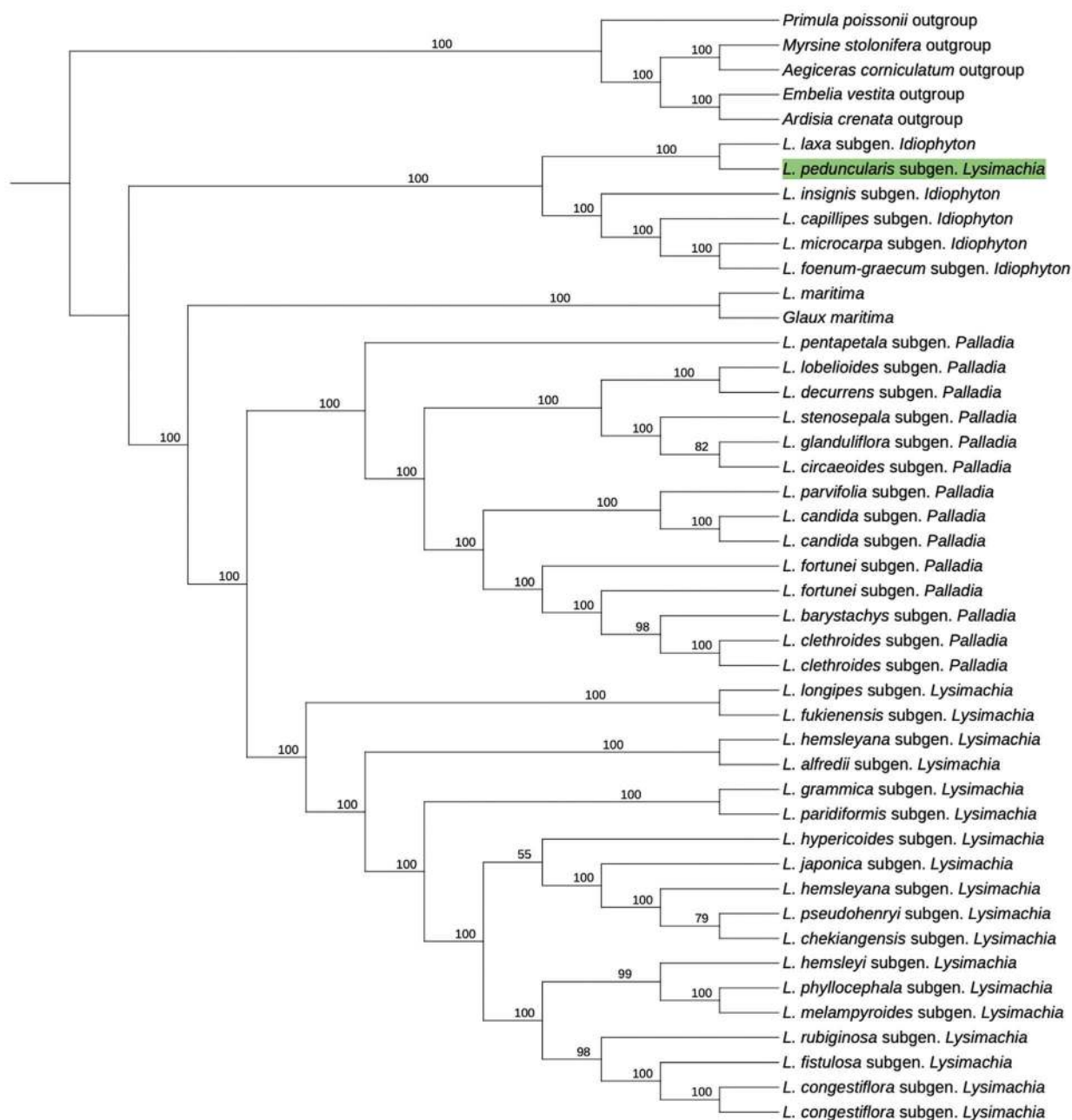
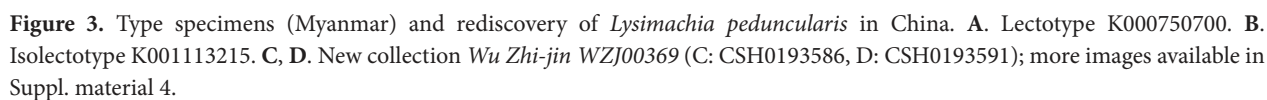


Figure 2. Phylogenetic tree of *Lysimachia* generated by ML analysis based on complete plastid genomes.



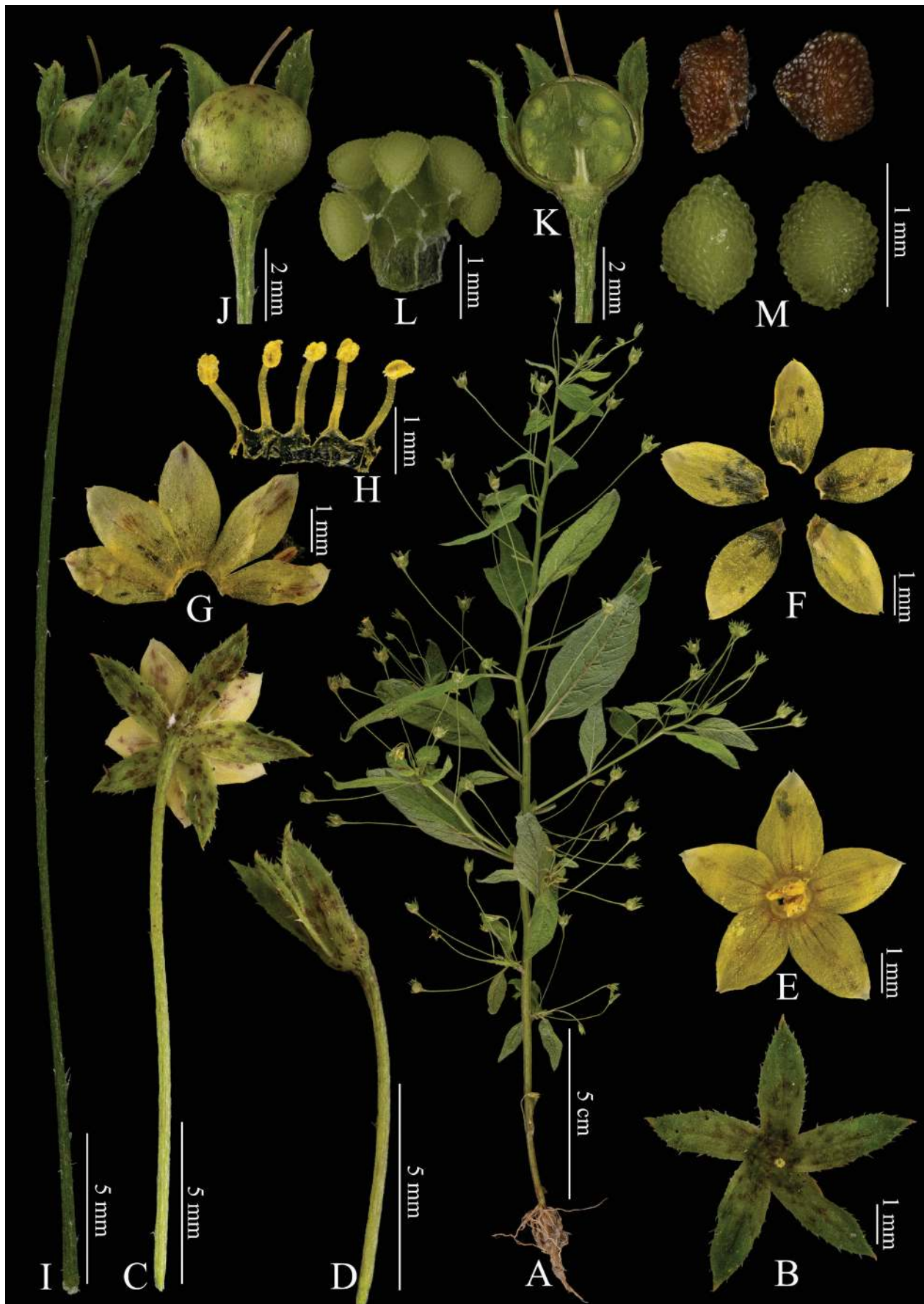


Figure 4. Detailed morphology of *Lysimachia peduncularis* based on fresh material (southern Yunnan, China). **A.** Habit. **B.** Calyx. **C,** **D.** Pedicel. **E.** Flower. **F, G.** Petals. **H.** Stamens. **I.** Pedicel. **J, K, L.** Capsule. **M.** Seeds.

glandular dotted, midrib prominent, margin strigose. Corolla yellow, 5-lobed, opposite to sepals, 3–4 mm long, parted to near base, lobes elliptic, apex acute. Stamens connate basally into a ca 0.5 mm high ring, free parts including anthers 1.5–2.5 mm long; anthers indistinctly dorsifixed to nearly basifixed, opening by lateral slits, erect, ca 0.5 mm long. Capsule globose, shorter than calyx. Seeds small, ca 0.7 mm in diameter, obliquely sectoroid or polyhedral, tuberculate, dark brown when mature.

Distribution. Myanmar: Taong Dong, Mindat, Maymyo, Gokteih; China, southern Yunnan: Menglian and Simao (Puer City, Simao district, Liushun town, 22°37'54.978"N, 100°43'18.276"E, 1364 m); India: Bihar; Thailand, Vietnam, Cambodia, and Malaysia (Malay Peninsula). A distribution map based on specimens cited in Hu (1985) and on new specimens collected is presented in Fig. 5.

Ecology. In China, *L. peduncularis* was found in broad-leaf forest, on limestone rocks, roadsides, red soil, at an elevation of 1,364 m (Fig. 6). The species occurs in coastal

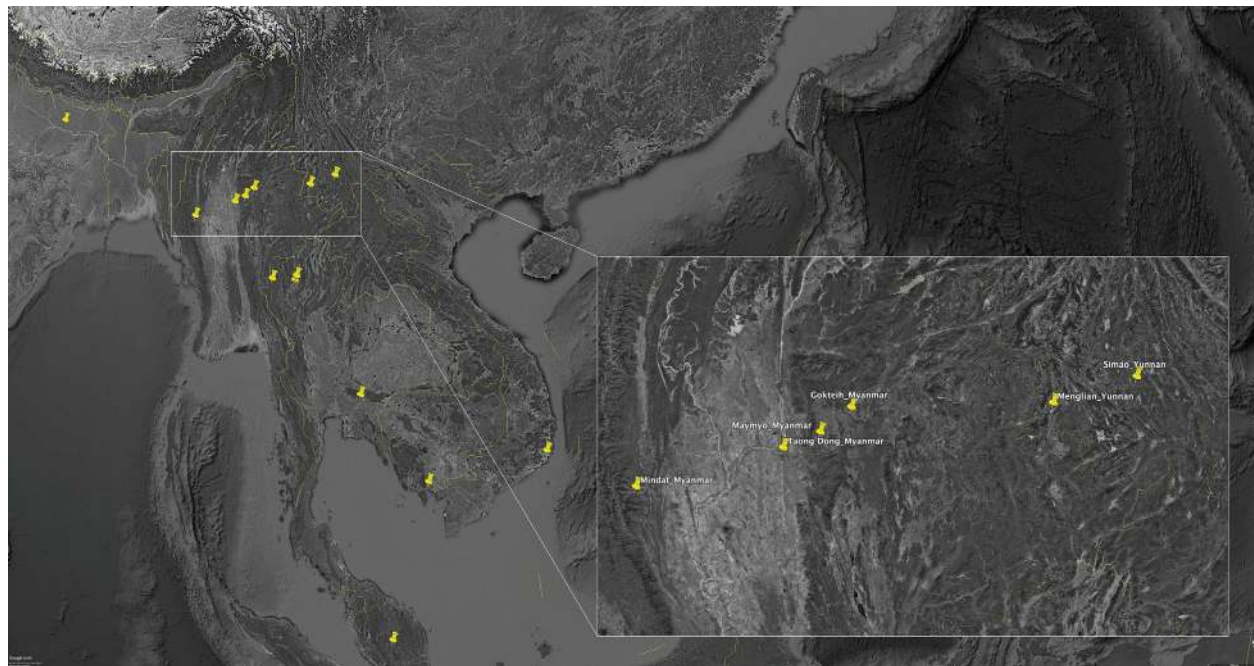


Figure 5. Distribution of *Lysimachia peduncularis* in China and adjacent areas.

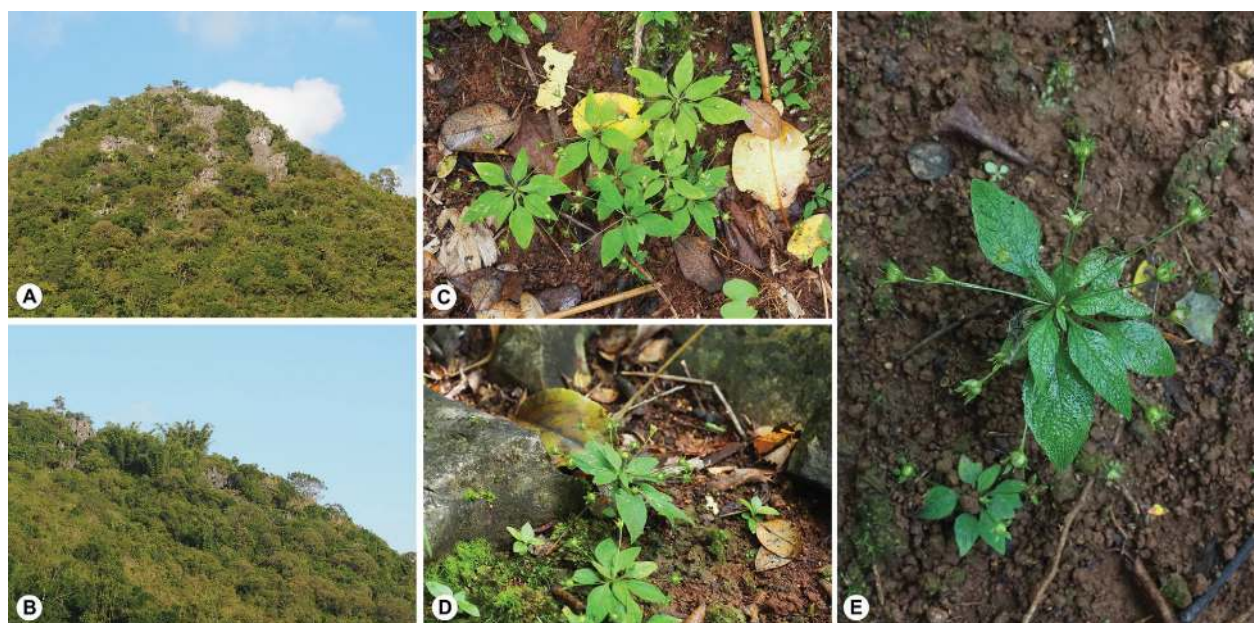


Figure 6. Habitat and population of *Lysimachia peduncularis* in China. A, B. Limestone mountains. C, D, E. Wild population. Photos by Xiao-Chen Li.

limestone vegetation in Malaysia, and in damp places with bamboo vegetation in Bihar (India).

Flower and fruit were observed in October and November in southern Yunnan. Associated species including *Asplenium simaoense* K.W.Xu, Li Bing Zhang & W.B.Liao, *Botrychium lanuginosum* Wall. ex Hook. & Grev., *Catunaregam* sp., *Crassocephalum rubens* (Jacq.) S.Moore, *Colquhounia compta* W.W.Sm., *Dumasia yunnanensis* Y.T.Wei & S.K.Lee, *Eriolaena candollei* Wall., *Grona heterocarpus* (L.) H. Ohashi & K. Ohashi, *Pistacia weinmanniifolia* J. Poiss. ex Franch., *Isodon* sp., *Helicteres* sp., *Paraboea* sp., *Phyllodium longipes* (Craib) Schindl., *Polygala cardiocarpa* Kurz, *Reinwardtia indica* Dumort., *Stemona tuberosa* Lour., *Tithonia diversifolia* (Hemsl.) A. Gray.

Additional material examined. CHINA – Yunnan • Puer City, Simao district, Liushun town; 22°37'54.978"N, 100°43'18.276"E; 1,364 m; collected 14 Oct. 2022; Wu Zhi-jin WZJ00369; cultivated at the Shanghai Chenshan Botanical Garden; CSH [CSH 0193586, CSH 0193587, CSH 0193588, CSH 0193589, CSH 0193590, CSH 0193591] • Menglian; 18 Aug. 1973; 孟连调查队 10213; HITBC [HITBC 042682].

THAILAND • Chiangmai Province, Pong Dueat National Park, c 55 km NNE of Chiangmai, km 40 on the Pai road 1095, 5 km to NE; 600 m; 26 Nov. 1993; K. Larsen, S.S. Larsen, C.T. Nørgaard, K. Pharsen, P. Puudjaj & W. Uerchirakan 44904; secondary evergreen forest rich in bamboo, along stream, waterfall and hot springs; AAU.

DISCUSSION

The collection *Wallich Cat. 1489* comprises material from two localities: Ava, Taong Dong and Prome Hills, both collected in 1826. These specimens represent syntypes of *L. peduncularis*, as Kurz validated the name without designating a holotype. Bennell and Hu (1983) conducted a detailed morphological and palynological comparison and confirmed that the material from both localities unquestionably belongs to the same species. No formal lectotypification has been published to date.

When verifying the identity of newly collected *Lysimachia* material, we were confronted with the question of which duplicate best serves as the nomenclatural type of *L. peduncularis*, even though all syntypes are taxonomically conspecific. Following the implicit reference in Hu (1985) to the Taong Dong



Figure 7. A. New collection of *Lysimachia peduncularis* from China (Wu Zhi-jin WZJ00369, CSH0193590). B. Thai voucher specimen Larsen et al. 44904 (AAU) for which DNA barcodes sequences are available on GenBank.

gathering and in accordance with Art. 9.3, 9.11, and 9.12 of the International Code of Nomenclature for algae, fungi, and plants (Madrid Code) (Turland et al. 2025), we here designate as lectotype the best-preserved and most complete specimen from Taong Dong housed at K (Wallich Cat. 1489, K000750700), which fully matches the protologue and exhibits all diagnostic characters.

The most recent confirmed collection of *L. peduncularis* in China dates back to 1973 (孟连调查队 10213, HITBC 042682), marking a nearly half-century hiatus in regional records. This study formally reports the rediscovery of *L. peduncularis* in southern Yunnan, to the north of the former record, a finding crucial for confirming the species' current status and expanding its known distribution. Prior molecular studies on *L. peduncularis* relied solely on an accession from Thailand (Larsen et al. 44904, AAU; Fig. 7) (Anderberg et al. 2007). By including newly collected Chinese specimens, comparing them morphologically and molecularly with Thai material, and, crucially, presenting the first complete plastid genome of the species, our work provides a robust and long-overdue update to its taxonomy and systematics (Fig. 2; Suppl. material 3).

Traditionally, *L. peduncularis* was placed within *L. subg. Lysimachia* sect. *Alternifoliae* because its filaments significantly exceed the anthers in length (Handel-Mazzetti 1928; Chen and Hu 1979; Bennell and Hu 1983). This elongated filament character was recognized as a key evolutionary polarity in the Chinese *Lysimachia* flora (Chen and Hu 1979). Such morphological evidence appeared to justify the species' previous systematic status by aligning macroscopic observations with traditional taxonomic views (Bennell and Hu 1983).

However, our molecular phylogenetic analyses robustly place *L. peduncularis* within *L. subg. Idiophyton*. This result reaffirms earlier studies based on a limited number of markers (Anderberg et al. 2007; Yan et al. 2018) and confirms that its former classification under *L. subg. Lysimachia* was incorrect. The strong support across all phylogenies for *L. peduncularis* as sister to the *L. laxa* and *L. lancifolia* clade reinforces this conclusion. Furthermore, our results confirm the monophyly of *L. subg. Idiophyton* and highlight the paraphyly of *L. subg. Lysimachia*, which is consistent with recent findings (Liu et al. 2023). This phylogenetic framework underscores the necessity of a formal taxonomic revision to transfer *L. peduncularis* to *L. subg. Idiophyton*.

In light of this molecular placement, our documentation of seed morphology provides critical supplementary evidence. According to the character types defined by Oh et al. (2008), the small, obliquely sectoroid to polyhedral seeds of *L. peduncularis*, which measure approximately 0.7 mm in diameter, align with the predominant forms observed in the genus. Crucially, the tuberculate surface ornamentation serves as a significant diagnostic feature that distinguishes this species from many members of *L. subg. Lysimachia*, which typically possess winged or smooth seeds. This micromorphological consistency

supports our phylogenomic results and indicates that despite its misleading floral morphology, the reproductive characters, particularly seed shape and seed coat texture, retain conservative characters congruent with its placement in *L. subg. Idiophyton*.

Beyond these taxonomic implications, the rediscovery of *L. peduncularis* after a nearly half-century absence of botanical records underscores its extreme rarity within China. The biogeographical continuity between southern Yunnan and adjacent Southeast Asian regions suggests that effective conservation should adopt a transboundary perspective to fully comprehend the population dynamics and long-term viability of the species across its entire range. Accordingly, the limited size of the confirmed population necessitates immediate attention through a formal IUCN Red List assessment and the swift implementation of targeted protection measures in China.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

GenBank accession numbers of ITS and the three plastid loci *atpF-atpH*, *trnL-trnF*, and *rpl32-trnL*.

<https://doi.org/10.5091/plecevo.176521.suppl1>

Supplementary material 2

GenBank accession numbers of the plastid genomes.

<https://doi.org/10.5091/plecevo.176521.suppl2>

Supplementary material 3

Phylogenetic trees of *Lysimachia* generated based on ITS and three plastid loci.

<https://doi.org/10.5091/plecevo.176521.suppl3>

Supplementary material 4

Additional scans of *Lysimachia peduncularis* (collection *Wu Zhi-jin* WZJ00369, six specimens).

<https://doi.org/10.5091/plecevo.176521.suppl4>