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lancangensis (Saxifragaceae)

Taxonomic resurrection of Saxifraga

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# Abstract

Background Accurate species delimitation is fundamental for testing evolutionary theory and provides essential implications for conservation management. The arctic-alpine genus Saxifraga L. (Saxifragaceae) is taxonomically complex and many species have not been critically assessed. The taxonomic and phylogenetic status of Saxifraga lancangensis Y.Y.Qian, considered as a synonym of Saxifraga mengtzeana Engl. & Irmsch. in previous studies, is re-evaluated in light of new evidence presented here.

Results Evidence from morphological comparison and sequencing of plastid genome indicate that S. lancangensis belongs to Saxifraga sect. Irregulares Haw., and is closely related to Saxifraga geifolia Balf.f., and S. mengtzeana. However, S. lancangensis can be diagnosed by its petals with red and clawless base, leaf blade orbicular and leaf margin shallowly dentate.

**Conclusions** The morphological and molecular evidence support the resurrection of *S. lancangensis* as a distinct species. An updated morphological description based on protologue and fresh material, diagnostic characters, and original photographs of the resurrected species are presented.

Keywords Saxifragaceae, Taxonomy, Yunnan, China, Phylogeny

# Background

The species-rich genus Saxifraga L. comprises more than 400 species that are mainly distributed in arctic and mountainous regions of the Northern Hemisphere (Ebersbach et al. 2017; Pan et al. 2001; Tkach et al. 2015). Saxifraga is taxonomically difficult for their remarkable morphological variation, hybridization and

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<sup>2</sup>University of Chinese Academy of Sciences, 100049 Beijing, China <sup>3</sup>School of Life Sciences, Yunnan University, 650500 Kunming, China polyploidization (Ebersbach et al. 2020; Zhang et al. 2022). Recent taxonomic revision recognized 13 sections and nine subsections within this genus (Tkach et al. 2015). Saxifraga sect. Irregulares Haw., currently encompasses ca. 22 species concentrated in eastern Asia, is one of the earliest lineages of Saxifraga to diverge (Tkach et al. 2015; Zhang et al. 2020b, 2021). It is well characterized by asymmetric flowers with three short and two unequally elongated petals (Magota et al. 2021; Soltis et al. 2001; Zhang et al. 2017).

In China, fifteen species of S. sect. Irregulares were recorded, including eight recently reported new species (Chen et al. 2022; Zhang et al. 2017, 2018, 2019, 2021, 2022, 2023b; Zhao et al. 2019), and a resurrected species (Zhang et al. 2023a). Most members of this section are confined to small areas (Magota et al. 2021; Pan et



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al. 2001), and many of them are known only from type specimens or a handful of herbarium collections. More investigations are needed to clarify the patterns of variation and the delimitation of these species.

In 2021, during an examination of Saxifraga specimens in the herbarium of the Kunming Institute of Botany (KUN), the first author found a specimen of Saxifraga identified as Saxifraga mengtzeana Engl. & Irmsch. (KUN 1,238,150). However, the locality of this specimen was Lancang County (Yunnan Province, China), which is out of the distribution range of S. mengtzeana, but coincides with the type locality of Saxifraga lancangensis Y.Y.Qian (Qian 1995; Zhang et al. 2023a). In 2022, Dr. Guo Yongjie shared a plant photograph of Saxifraga from the above locality with us. Recently, we conducted a fieldwork and collected living material of this plant from the above locality. After a comprehensive morphological comparison of the type specimens and herbarium materials and review of the relevant taxonomic literature, we confirmed that this plant represented S. lancangensis, which is considered as a synonym of S. mengtzeana in the Flora of China (Govaerts et al. 2021; Pan et al. 2001). The purpose of this study was to re-evaluate the taxonomic status of S. lancangensis. Based on the protologue and type specimens, S. lancangensis differs from S. mengtzeana by its petals with red base and orbicular leaf blade (Qian 1995). Geographically, the type locality of S. lancangensis is some 500 km distant from the type locality of S. mengtzeana. The flowering time of S. lancangensis is

 
 Table 1
 Voucher information and genbank accessions for phylogenetic analysis

Taxon	Voucher	GenBank
		accession
		number
Saxifraga lancangensis	YNS0740 (KUN)	PP359606
Saxifraga geifolia 1	deng10896 (KUN)	OQ428204
Saxifraga geifolia 2	deng11665 (KUN)	OQ428205
Saxifraga geifolia 3	deng12605 (KUN)	OQ428206
Saxifraga geifolia 4	zwy-972 (SYS)	OQ428202
Saxifraga mengtzeana 1	zhangxj104 (KUN)	OQ406248
Saxifraga mengtzeana 2	zhangxj110 (KUN)	OQ406247
Saxifraga mengtzeana 3	zhangxj106 (KUN)	OQ406246
Saxifraga mengtzeana 4	Zhangxj177 (KUN)	OQ406249
Saxifraga viridiflora 1	deng12030 (KUN)	OQ428208
Saxifraga viridiflora 2	zhangxj98 (KUN)	NC_073566
Saxifraga damingshanensis	zwy-1208 (SYS)	NC_073565
Saxifraga daqiaoensis	deng12102 (KUN)	NC_073560
Saxifraga shennongii	LXP- 09- 09089 (SYS)	OQ434240
Saxifraga kegangii	BJ4668 (JIU)	NC_073562
Saxifraga kwangsiensis	deng12168 (KUN)	NC_073561
Saxifraga luoxiaoensis	LXP-13-16785(SYS)	NC_073563
Saxifraga rufescens	deng13173 (KUN)	OQ129932
Saxifraga sinomontana	/	MN104589
Saxifraga stolonifera	/	MN496079

December to January of the next year, while the flowering time of *S. mengtzeana* is September to November (Zhang et al. 2023a). These differences suggest that the taxonomic status of *S. lancangensis* should be re-examined.

# Methods

# Morphological comparison

Morphological data were recorded based on both fresh and dried plant samples from field collections and herbarium specimens. Voucher specimens of our collections were deposited in the herbarium of the Kunming Institute of Botany (KUN), Kunming, China. Herbarium specimens of Saxifraga sect. Irregulares from the herbaria CDBI, CSFI, GXMG, HITBC, IBSC, KUN, PE, SYS, and WUK (Thiers, (updated continuously)) were examined either through direct examination of the specimens or by viewing their digital images provided by the National Plant Specimen Resource Center (https://www.cvh. ac.cn/index.php) and the JSTOR Global Plants web portal (https://plants.jstor.org/). Voucher specimens for the morphological observations of S. lancangensis are cited under Additional specimens examined in the Taxonomic treatment.

## **Phylogenetic reconstruction**

We collected 20 samples representing S. lancangensis, S. mengtzeana and related taxa (Table 1), which included 12 species of S. sect. Irregulares. Saxifraga sinomontana J.T.Pan & Gornall from Saxifraga sect. Ciliatae Haw. was selected as the outgroup based on previous molecular studies (Li et al. 2019; Tkach et al. 2015; Zhang et al. 2020b, 2023a). Leaf materials were collected from both field (silica-gel-dried leaves) and dry herbarium specimens. Molecular analyses were conducted using genome skimming data. The procedures for DNA extraction, library preparation, and sequencing were carried out at Novogene (Beijing, China). Sequencing libraries were generated using the NEB Next<sup>®</sup> Ultra DNA Library Prep Kit for Illumina® (NEB, USA). The prepared libraries were sequenced on an Illumina Hiseq 4000 platform with 150 bp paired-end reads. The GetOrganelle pipeline was used to assemble plastid genome data (Jin et al. 2020). Complete plastid genome was annotated in batches using the web application GeSeq (https://chlorobox.mpimpgolm.mpg.de/geseq.html) (Tillich et al. 2017). A concatenation-based approach was conducted for shared protein coding genes (PCGs) regions of the plastid genome, and sequences were aligned in MACSE v2 and trimmed by Gblocks 0.91b implemented in Phylosuite v1.2.3 (Ranwez et al. 2018; Talavera and Castresana 2007; Zhang et al. 2020a). Phylogenetic reconstruction was performed using both maximum likelihood (ML) and Bayesian inference (BI) methods. The GTR+I+G model of sequence evolution was selected as identified by jModeltest ver.

2.1.7 (Posada 2008). Maximum likelihood analysis was conducted in IQ-Tree with 1000 bootstrap (BS) replicates to estimate clade support (Bui Quang et al. 2013; Nguyen et al. 2015). Bayesian analysis was conducted in MrBayes v3.2 (Ronquist et al. 2012). Four parallel Markov Chains Monte Carlo (MCMC) simulations were run and sampled every 1000 generations for 20 million generations in total, with the first 25% trees discarded as burn-in. Runs were considered to have converged when the average standard deviation of split frequencies was less than 0.01 (Ronquist et al. 2012).

# Results

# Morphology

The asymmetric flowers and absence of stolons (Figs. 1 and 2) of *Saxifraga lancangensis* indicate a position in *Saxifraga* sect. *Irregulares* ser. *Rufescentes* J.T. Pan (Pan 1991; Pan et al. 2001). Morphological comparison of *S. lancangensis* and known species of *S.* sect. *Irregulares* 

indicates that S. lancangensis resembles S. mengtzeana and Saxifraga dagiaoensis F.G.Wang & F.W.Xing in having leaf blade with a peltate petiole insertion (Figs. 2 and 3), which distinguish them from other species in S. sect. Irregulares. It is notable that the peltate feature is plastic in S. lancangensis, and there are intermediates with the basifixed phenotypes within the same population, which is consistent with our observations on S. mengtzeana and S. daqiaoensis (Zhang et al. 2023a). Besides, Balfour (1916) described Saxifraga henryi Balf.f. on account of its peltate leaves, but it was now accepted as part of the variation encompassed by *S. mengtzeana* (Pan et al. 2001; Zhang et al. 2023a). S. lancangensis is distinct from the latter two chiefly in its petals with a red and clawless base, and its orbicular leaf blade. The morphological comparisons of these species are presented in Table 2. Geographically, the distribution ranges of these three species are isolated from each other (the type locality of S. lancangensis is about 500 km distant from the type locality of



Fig. 1 (A) Holotype of Saxifraga lancangensis Y.Y.Qian (Qian Yiyong 2409 [HITBC]) and (B) Lectotype of Saxifraga mengtzeana Engl. & Irmsch. (A. Henry 10316B [E])



Fig. 2 Saxifraga lancangensis from type locality. A leaf blade; B petiole base; C pedicel with white glandular pubescent; D inflorescence; E adaxial surface of flower; F abaxial surface of flower; G rhizomes; H&I plant and habitat

*S. mengtzeana*, and some 1300 km distant from the type locality of *S. daqiaoensis*) (Fig. 4).

# **Phylogenetic analyses**

A total of 13 taxa were included in the phylogenetic analysis using 73 shared protein coding genes (PCGs) regions of the plastid genome of 20 samples. The resulting concatenated matrix dataset contained 60,472 bp. The 50% majority-rule consensus tree (Fig. 5) based on maximum likehood bootstraps (ML) and Bayesian posterior probability (PP) of PCGs both revealed a sister relationship between *S. lancangensis* and *Saxifraga geifolia* Balf.f. with strong supports (ML=100, PP=1). The monophyletic clade of *S. lancangensis* and *S. geifolia* grouped together with *Saxifraga viridiflora* X.J.Zhang, T.Deng, J.T.Chen



Fig. 3 Morphological characters of Saxifraga lancangensis (A, F, K, P), Saxifraga mengtzeana (B, G, L, Q), Saxifraga daqiaoensis (C, H, M, R), Saxifraga geifolia (D, I, N, S), Saxifraga viridiflora (E, J, O, T). A-E adaxial surface of flower; F-J inflorescence; K-O adaxial surface of leaf blade; P-T abaxial surface of leaf blade

& H.Sun, and were sister to *S. mengtzeana* (ML=100, PP=1).

# Discussion

Saxifraga lancangensis was listed among the synonyms of S. mengtzeana in the Flora of China, which are widely accepted in reference lists such as POWO (https://powo. science.kew.org/) and Tropicos (https://tropicos.org/ home). In the current study, the taxonomic status of S. lancangensis was re-evaluated by conducting morphological comparison and phylogenetic analysis of this species and related species. Morphological (Table 2) and molecular (Fig. 5) evidence are consistent in distinguishing S. lancangensis from S. mengtzeana. Overall, S. lancangensis is easily distinguished from any other species of Saxifraga sect. Irregulares by its petals with a red, clawless base. Additionally, S. lancangensis differs markedly from others species in S. sect. Irregulares not only by morphological characteristics and geographical distance, but also by flowering time. Most species of S. sect. Irregulares bloom in summer or autumn, while S. lancangensis flowers in winter. The differentiation in flowering time may play an important role in the reproductive isolation of the species in S. sect. Irregulares.

# Taxonomic treatment

# Saxifraga lancangensis

Y.Y.Qian, Acta Bot. Austro Sin. 10: 70–72 (1995) (Figs. 1 and 2).

# Туре

CHINA. Yunnan Province, Lancang County, Zhutang Town, alt. 2000 m, 10 Dec. 1991, *Qian Yiyong, 2409* (Holotype HITBC!, isotype IBSC!).

### Description

Perennial herbs, 10-35 cm tall. Rhizomes short. Stolons absent. Leaves all basal, forming a rosette; petiole 5-15 cm long, fleshy, glandular hairy, base sheathed; leaf blade orbicular, leathery and slightly succulent, 6.5-11.5 cm long  $\times$  5.5–9.5 cm wide, both surfaces sparsely hispid or nearly glabrous, abaxially greenish, with brown spots, base cordate or peltate, margin shallowly dentate, apex obtuse or acute. Inflorescence paniculate, 15-25 cm long. 10–30-flowered; branches 2.0–6.0 cm long, glandular pubescent, 2-5-flowered; pedicels slender, 1.0-2.0 cm long, glandular pubescent. Flowers asymmetric; sepals 5, spreading, oblong-ovate, 4.0–5.0 mm long  $\times$  1.5–2.0 mm wide, adaxially glabrous, abaxially and marginally glandular pubescent. Petals 5, white to greenish, base red, margin entire; shortest 3 petals ovate, 4.0-4.5 mm long  $\times$  1.7–2.0 mm wide, base truncate, apex acute; two long

 Table 2
 Diagnostic characters of Saxifraga lancangensis

 and comparison with other related species of Saxifraga sect.
 Irregulares

Characters	S. lancangensis	S. daq- iaoensis	S. mengtz-	S. geifolia	S. viridi-
Leaf shape	orbicular	reni- form- cordate	trian- gular- cordate	reni- form	reni- form
Leaf margin	shallowly dentate	shal- lowly crenate- ly-lobed to subentire	crenate- dentate	cre- nate- lobed	undu- late to suben- tire
Trichomes on leaf	both sur- faces sparsely hispid or nearly glabrous	adaxially sparsely hispid, abaxially glabrous	both surfaces sparsely hispid or nearly glabrous	both surfaces glan- dular hispid or nearly gla- brous	both sur- faces crisped villous
Spots on abaxial leaf surface	brown spots	brown spots	brown or greenish spots	brown spots	white spots
Trichomes on petiole	glandular hairy	glabrous	brown glandu- lar hairy	brown glandu- lar hairy	crisped villous
Trichomes on inflores- cence	branches glan- dular pubescent	branch- es nearly glabrous	branch- es glan- dular pubes- cent	branch- es glan- dular pubes- cent	branch- es glan- dular pubes- cent
Petal	white to green- ish, base red, base of small petals clawless	white, yellow spotted at base, base of small petals contract- ed into a claw	white, yellow spotted at base, base of small petals con- tracted into a claw	white, yellow spotted at base, base of small petals con- tracted into a claw	green, base unspot- ted, base of small petals con- tracted into a claw
Nectary disc Flowering time	greenish December to January	yellow March to May	yellow Septem- ber to Novem- ber	yellow May to Sep- tember	obscure April to July

petals narrowly ovate to lanceolate,  $10.0-22.0 \text{ mm long} \times 2.0-3.5 \text{ mm wide}$ . Stamens 10, 5.0-7.0 mm long. Ovary ovoid, 1.5-2.0 mm long, with a semiannular greenish nectary disc; styles divergent ca. 2.0-4.0 mm long.

#### Phenology

Flowering was observed from December to January of the next year, and fruiting from January to March.

## Distribution and habitat

Saxifraga lancangensis is native to Zhutang Town, the eastern parts of Lancang County, Yunnan Province. It grows in limestone at altitudes 1780–2000 m under evergreen broad-leaved forest dominated by *Neocinnamomum delavayi* (Lecomte) H.Liu, *Cornus oblonga* Wall, *Piper sarmentosum* Roxb. and *Elatostema salvinioides* W.T.Wang.

### Comparison with close Saxifraga species

Peltate-leaved feature was found in S. lancangensis. There are only two known species with peltate petiole insertions in S. sect. Irregulares—S. daqiaoensis and S. mengtzeana. S. lancangensis differs from latter two species in flower color (petals white to greenish, base red vs. petals white, base with yellow spots), petals shape (base of small petals clawless vs. base of small petals contracted into a claw), nectary disc (greenish vs. yellow). S. lancangensis is also distinct from S. mengtzeana in leaf shape (orbicular vs. triangular-ovate), leaf margin (shallowly dentate vs. crenate-dentate), flowering time (December to January of the next year vs. September to November). S. lancangensis is also distinguished from S. daqiaoensis by leaf shape (orbicular vs. reniform-cordate), trichomes on petiole (glandular hairy vs. glabrous), flowering time (December to January of the next year vs. March to May). Molecular phylogenetic analyses indicated a close relationship within S. lancangensis, S. geifolia and S. viridiflora. However, S. lancangensis can easily be distinguished from latter two species by its petals with red base. Additionally, S. lancangensis is also different from S. geifolia in leaf margin (shallowly dentate vs. crenate-lobed), flowering time (December to January of the next year vs. May to September). S. lancangensis is also distinguished from S. viridiflora by petal color (white to greenish vs. green), sepals (green, glandular pubescent, without verruculose vs. red, glabrous, abaxially white verruculose), trichomes on leaf (nearly glabrous vs. crisped villous), flowering time (December to January of the next year vs. April to July). Geographically, S. viridiflora is an endemic species of Guilin, Guangxi Province, and S. geifolia is restricted to northern Yunnan and Sichuan, both are more than 500 km distant from the type locality of S. lancangensis. It is worth noting that Saxifraga cataphracta X.J.Zhang, T.Deng & H.Sun is also closely related to S. geifolia (Zhang et al. 2023b), however, S. cataphracta morphologically differs from other species of S. sect. Irregulares by its abaxial leaf surface covered with white or virescent streaks. The capsule beaks of S. cataphracta is winged when mature (vs. capsule beaks divergent in S. geifolia



Fig. 4 Distribution of Saxifraga lancangensis (red) and Saxifraga mengtzeana (blue) in southwestern China. Prepared by Xin-Yuan Kuai

and *S. lancangensis*). *S. cataphracta* is known from northeastern Yunnan, Chongqing and southern Sichuan, which is more than 500 km distant from the geographical distribution of *S. lancangensis*.

# Additional specimens examined: CHINA

Yunnan Province, Lancang County, 22 Feb. 1992, *Qian Yiyong, 2493* (Paratype HITBC!, IBSC! ); Yunnan Province, Lancang County, limestone under forest, 24 Oct.

1989, Tao Guoda, Li Xiwen, 39,839 (HITBC); Yunnan Province, Lancang County, Zhutang Town, alt. 2015 m, 28 Jan. 2010, Hu Qihe, Zhao Qiang, Zhou Ying, Zhang Shaoyun, YNS0740 (KUN); Yunnan Province, Puer City, 19 Mar. 2012, Zhang Shaoyun, Ye Jinke, Hu Qihe, YNS1206 (KUN); Yunnan Province, Lancang County, Zhutang Country, alt. 1833 m, 8 Dec. 2023, Deng Tao, Zhang Xinjian, lc-7 (KUN).



Fig. 5 The phylogenetic position of *Saxifraga lancangensis* in *Saxifraga* sect. *Irregulares* derived from the combined 73 shared protein coding genes (PCGs) regions of the plastid genome, with *Saxifraga sinomontana* as outgroup. Numbers above branches indicate ML bootstraps, numbers below branches are Bayesian posterior probability

# Conservation significance

*Saxifraga lancangensis* is an endemic species with narrow geographical distribution only known from Zhutang Town, Lancang County of Yunnan, China. It grows in limestone under forest close by the road, which can be easily disturbed. We estimate that the population size at the type locality comprises less than 300 individuals. Due to its limited range, fragile habitat and low population size, *S. lancangensis* should be considered as a protected plant in China.

#### Abbreviations

- BS Boostrap
- CDBI Chengdu institute of biology, chinese academy of Sciences, Herbarium
- CSFI Central-south forestry university, herbarium
- GXMG Guangxi medicinal botanic garden, herbarium
- HITBC Xishuangbanna tropical botanical garden, academia sinica, herbarium
- IBSC South china botanical garden, chinese academy of sciences, herbarium

- KUN Kunming institute of botany, chinese academy of sciences, herbarium
- MCMC Markov chains monte carlo
- ML Maximum likelihood
- PE Institute of botany, chinese academy of sciences, herbarium
- PCG Protein-coding gene
- PP Posterior probability
- STEP Second tibetan plateau scientific expedition and research program
- SYS Sun Yat-sen University, Herbarium
- WUK Northwestern Institute of Botany,, Chinese Academy of Sciences, Herbarium

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#### Author contributions

XJZ, KZJ, JTC conducted the field work. XJZ analyzed the data. XYK and PRL conducted the visualization. XJZ designed and drafted the manuscript. KZJ and TD reviewed the manuscript. TD and HS supervised the study and

provided the funding. All authors have read and agreed with the submission of this manuscript. All authors read and approved the final manuscript.

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#### Data availability

The sequences of this study have been deposited in The National Center for Biotechnology Information (NCBI) database. GenBank accession numbers of the sequencing data can be found in Table 1.

## Declarations

**Ethics approval and consent to participate** Not applicable.

#### **Consent for publication**

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

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