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The phylogenomic position and barcoding resources of *Ficus conglobata* with additional notes to its distribution ranges

SHUAI LIAO[1,3,6,†], BAI-GE MIAO[2,7,†], JIN-XIA GAO[2,8], JIE GAO[2,9], DA-RONG YANG[2,10], YONG-MEI XIONG[3,11], SREYOSHEE SENSARMA[4,12], YAN-QIONG PENG[2,13,*] & ZHEN ZHANG[5,14,*]

[1]*State Key Laboratory of Plant Diversity and Specialty Crops, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*
[2]*State Key Laboratory of Plant Diversity and Specialty Crops, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China*
[3]*Guangzhou International Ficus Research Center, Guangzhou Institute of Forestry and Landscape Architecture, Guangzhou 510405, China*
[4]*Assam down town University, Guwahati, 781026, India*
[5]*Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, Shanghai 201602, China*
[6] *shuai.liao.cn@gmail.com; https://orcid.org/0000-0002-3876-8002*
[7] *miaobaige@xtbg.org.cn; https://orcid.org/0000-0003-0947-1602*
[8] *gaojinxia@xtbg.ac.cn; https://orcid.org/0009-0007-0452-7984*
[9] *gaojie@xtbg.org.cn; https://orcid.org/0000-0002-2640-5116*
[10] *yangdr@xtbg.ac.cn; https://orcid.org/0000-0003-2531-4471*
[11] *ymxiong1004@126.com; https://orcid.org/0009-0002-5903-9260*
[12] *sreyosheesen400@gmail.com; https://orcid.org/0009-0008-7806-7383*
[13] *pengyq@xtbg.ac.cn; https://orcid.org/0000-0002-7453-9119*
[14] *zhangzhen@csnbgsh.cn; https://orcid.org/0000-0003-0271-0973*
†*These authors contributed equally to this work.*
**Authors for correspondence: pengyq@xtbg.ac.cn, zhangzhen@csnbgsh.cn*

Abstract

Ficus conglobata, a fig tree previously reported in the east Himalaya region, including northeast India, Bhutan, and Bangladesh, is additionally recorded here in Motuo County, Xizang Autonomous Region in China and Putao District, Kachin State in Myanmar. This less known species is distinguishable from its morphologically related taxa, such as *F. heterostyla*, *F. hispida*, and *F. squamosa*, by its fascicular and ramous breeding shoots bearing numerous figs. Phylogenomic investigation based on a large nuclear dataset and chloroplast genomes were implemented to verify its phylogenetic position. Furthermore, we annotated and provided its barcodes for future research, including a super-barcode (the complete chloroplast genome) and a nuclear barcode (internal transcribed spacer, ITS).

Key words: fig tree, distribution region, Motuo County, east Himalaya, phylogenomics

Introduction

Ficus Linnaeus (1753: 1059) is a huge woody genus with approximately 800 species ranging from pantropical to subtropical regions (Berg & Corner 2005; Pederneiras *et al.* 2018; Zhang *et al.* 2020b). In which, east Himalaya region has the best well-developed and unbroken evergreen broad-leaved subtropical to monsoon forests compared to other regions at the same latitude, making it the northern limit of the distribution of *Ficus* together with Sino-Japanese region (Chen *et al.* 2012). Recently, some fig trees were newly described from east Himalaya region, such as *F. cornelisiana* Chantarasuwan & Peng in Chantarasuwan *et al.* (2014: 6), *F. motuoensis* Zhang & Li in Zhang *et al.* (2022: 122), and *F. muricata* Zhang & Li in Zhang *et al.* (2023: 22), indicating an impressive potential for biodiversity. However, for the comprehensive impacts of the diverse ecological and altitudinal gradients, insufficient Flora and field surveys, and huge population size, the biodiversity of east Himalaya, is confronted with serious threats to climate change and human activities before fully explored (Chettri *et al.* 2010).

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During several recent field investigations in east Himalaya region (including southwest China and north Myanmar), we discovered an arboreal fig tree with round, large leaves and prolific acervate figs. These traits set it apart from other sympatric fig trees. Through comprehensive morphological evaluations and specimen examinations, it is considered *Ficus conglobata* King (1888: 99), which was reported as a species distributed in India, Bhutan, and Bangladesh (Zhou & Gilbert 2003; Chaudhary *et al.* 2012; Sudhakar *et al.* 2022). Meanwhile, considering the lack of genetic data for this species, we also confirmed its phylogenetic position and provided barcoding resources via high-throughput resequencing.

Materials and methods

Morphological observations:—The populations of *Ficus conglobata* were surveyed and collected in east Himalaya region, between 2014 and 2023. The morphological characteristics were measured and photographed. The voucher specimens were stored in the herbaria of Xishuangbanna Tropical Botanical Garden (HITBC) and East China Normal University (HSNU). A detailed morphological comparison between *F. conglobata* and its allies was accomplished to confirm its status.

Phylogenomics:—Five samples representing *Ficus conglobata* were chosen for further phylogenetic studies. To explore its phylogenetic position, we extendedly included some morphologically related taxa. In total, sixteen samples were used in the study, in which six were obtained from other studies (Zhang *et al.* 2020a; Fungjanthuek *et al.* 2022; Huang *et al.* 2022). *Ficus auriculata* Loureiro (1790: 666) was set as the outgroup. Detailed information on the materials is shown in Table 1.

Total DNA was extracted from silica-dried leaves using the DNAsecure Plant Kit, DP320 (TIANGEN, Beijing, China). After quality control (NanoDrop and Qubit 2.0), eligible purified DNA was randomly ultrasonicated into approximately 350 bp segments in size and then used to construct a paired-end (PE) library. Whole genome sequencing (WGS) was implemented by the MGI DNBSEQ-T7 (Annoroad, Beijing, China) using the PE150 sequencing strategy. After filter and cleaning used by Trimmomatic (Bolger *et al.* 2014), 10–22 G cleaned data (about 30–60 X) were obtained from every individual.

Ficus1316 is a set of coding nuclear loci screened for the evolutionary study of *Ficus* specifically (Bruun-Lund 2019; Gardner *et al.* 2023), and has been confirmed to have a satisfactory phylogenetic resolution in *Ficus* (Gardner *et al.* 2023). HybPiper 1.2 (Johnson *et al.* 2016) was used to assemble the nuclear *Ficus1316* dataset with default parameters. The sequences of each coding locus were aligned solely using MAFFT v7.490 (Katoh & Standley 2013) and then concatenated. The phylogenetic relationship was reconstructed using the maximum likelihood method and Bayesian inference (BI). IQ-TREE 2.0 (Nguyen *et al.* 2015) was used to finish maximum likelihood tree reconstruction with 10000 ultrafast bootstrap and other default parameters. The optimal nucleotide substitution model for BI was selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) (parameters: -m TESTONLY -mset mrbayes). The Bayesian phylogenetic tree was reconstructed via MrBayes 3.2.6 with 3000000 generations, sampling every 1000 generations to check the convergence (i.e., the average deviation of split frequencies was less than 0.01 and the effective sample sizes were over 200). The first 1/4 of sampling trees were omitted as burin-in, and the remaining trees were used to generate the consensus tree and posterior probabilities.

The universal barcode internal transcribed spacer (ITS) was assembled with HybPiper 1.2 with specified parameter (--cov-cutoff 10000) to avoid possible paralogs. The chloroplast genome was assembled with GetOrganelle v1.6.4 (Jin *et al.* 2020), under the "embplant_pt" model. When the results were not circular, the assembled parameters (R, number of runs, and W, word size) were modified until a circular plastome was obtained. PGA was used to annotate the chloroplast genome utilizing the default parameter (Qu *et al.* 2019). The chloroplast genome was visualized by the online OGDRAW tool (https://chlorobox.mpimp-golm.mpg.de/OGDraw.html) (Greiner *et al.* 2019). The phylogenetic tree reconstruction of the chloroplast genomes followed the methods of the nuclear phylogeny, with one of two repeated regions removed.

Results

Morphology of *Ficus conglobata*

Ficus conglobata King (1888: 99, t. 123); Hooker (1888: 522); Prain (1903: 982); Corner (1965: 89); Bennet

TABLE 1. Collecting information and data repository for sequencing data of the samples in the study. Taxa with bold font are newly obtained in the study.

Taxon	Voucher no.	Data repository	Accession no.	Collected Date	Collector	Longitude	Latitude	Altitude	Reference
***F. conglobata* 1**	MT101	GSA	CRR1246385	20230512	D.-R. Yang *et al.*	95.44	29.47	889	
***F. conglobata* 2**	2014546	GSA	CRR1246384	20140828	H.-Q. Li *et al.*	95.29	29.3	750	
***F. conglobata* 3**	MT130	GSA	CRR1246387	20230512	D.-R. Yang *et al.*	95.3	29.32	845	
***F. conglobata* 4**	MT238	GSA	CRR1246388	20230515	D.-R. Yang *et al.*	94.98	29.17	572	
***F. conglobata* 5**	MT114	GSA	CRR1246386	20230512	D.-R. Yang *et al.*	95.4	29.41	804	
F. squamosa	LWY04	GSA	CRR1246392	20220424	Z.-R. Zhang	101.39	21.73	782	
F. squamosa	RT17F	GSA	CRR1246391	20210323	Z.-R. Zhang	101.38	21.73	755	
F. squamosa	SQU10F	NCBI	SRR15882953	-	-	Living plant in XTBG			Fungjanthuek *et al.*, 2022
F. hispida	FhF3_1	NCBI	SRR13279575	-	G. Wang	Living plant in XTBG			Zhang *et al.*, 2020
F. hispida	FhF3	GSA	CRR034458	-	G. Wang	Living plant in XTBG			Zhang *et al.*, 2020
F. hispida	LWY102	GSA	CRR1246393	20221019	Z.-R. Zhang	101.28	21.92	568	
F. hispida	DYR	GSA	CNS0285143	-	-	Living plant in GZUCM			Huang *et al.*, 2022
F. auriculata	BNFA6	NCBI	SRR15882846	-	-	101.34	21.93	-	
F. heterostyla	ZZRhet6	NCBI	SRR15883057	-	-	101.25	21.93	-	Fungjanthuek *et al.*, 2022
F. heterostyla	ZZRhet4	GSA	CRR1246389	20220524	Z.-R. Zhang	101.26	21.93	565	
F. heterostyla	ZZRhet5	GSA	CRR1246390	20220524	Z.-R. Zhang	101.26	21.93	565	

NOTE. GSA, Genome Sequence Archive in National Genomics Data Center (https://ngdc.cncb.ac.cn/gsa). NCBI, National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/). D.-R. Yang *et al.*, Da-Rong Yang, Yan-Qiong Peng, Bai-Ge Miao, and Jin-Xia Gao. H.-Q. Li *et al.*, Hong-Qing Li, Wei Zhang, and Zhen Zhang. Z.-R. Zhang, Zheng-Ren Zhang. G. Wang, Gang Wang. -, Information not obtained. XTBG, Xishuangbanna Tropical Botanical Garden. GZUCM, Guangzhou University of Chinese Medicine.

(1985: 319); Buragohain *et al.* (2012: 416); Chaudhary *et al.* (2012: 205); Sudhakar *et al.* (2022: 339). **Lectotype (designated here):**—INDIA. Sikkim, east Himalaya, 1877, *G. King 8732* (CAL0000014309[image!], Fig. 1; isolectotypes CAL0000014304[image!], CAL0000014305[image!], CAL0000014308[image!], K000880231[image!], L0931312[image!], MH, P00389793[image!]). Syntypes:—BHUTAN. 1837–1839, *W. Griffith 4639* (CAL0000014302[image!], K000880232[image!], K000880233[image!], P00389794[image!]);—BANGLADESH. Chittagong, 1876, *J. L. Lister s.n.* (CAL0000014372[image!], CAL0000014373[image!], CAL0000014374[image!]). (Fig. 2 A–E)

Description:—Tree, up to 15 m tall, extensively branched, dioecious; branchlets pubescent when young, hispid to hirtellous, brownish strigose at maturity, hollow; latex yellowish. **Leaves** opposite or subopposite, sometimes alternate, elliptic, oblong or subobovate, 23–34 × 13–20 cm, base cuneate to subcordate, margin serrate to dentate, apex acuminate with acumen up to 1.5 cm long, chartaceous, hispid; basal veins 3–5; lateral veins 4–6 pairs; waxy glands at axils of basal lateral veins; petioles 4–8 cm long, densely pubescent. Stipules 2–4 axillary, ovate-acute or ovate-lanceolate, strigose or hirtellous above, glabrous beneath, caducous. **Figs** numerous, in fascicles from short much-divided branches, densely crowded with reddish or dark brown appearance with white patches, ramiflorous to cauliflorous; peduncles 3–6 cm long, spotted; basal bracts 3, free, 2–3.5 mm long, glabrous, persistent; receptacle (fig body) pyriform or subglobose, 1–1.3 cm in diam., red to dark brown, black-spotted at maturity, subglabrous or brownish strigose; external lateral bracts few; ostiole concave, opened; internal hairs absent. **Staminate flowers** separate near the ostiole, sessile, 1.5–2 mm long; tepals 3 or 5, free, linear-lanceolate or spathulate; stamens 2–3, occasionally 1; anther broadly ovate; filaments very short to sessile. **Gall flowers** shortly pedicellate, 1–1.5 mm long; tepals united, white; ovary obovoid, white, smooth; style lateral, very short, glabrous; stigma slightly dilated or infundibuliform. **Pistillate flowers** separate in receptacles, funnel-shaped, sessile or shortly pedicellate, 1–1.5 mm long; tepals united, white; ovary obovoid or ovoid, 0.8–1 mm in diam., white, smooth; style lateral, white; stigma simple, infundibuliform. **Achenes** obovoid, 1.5–2 mm in diam., surface rough with rhomboidal structures or smooth.

Additional notes to distribution records in the study:—CHINA. Xizang Autonomous Region, Motuo County. MYANMAR: Kachin State, Putao District.

Distribution worldwide:—INDIA: northeast. BHUTAN. BANGLADESH.

Note:—*Ficus conglobata* morphologically resembles *F. hispida* Linnaeus f. (1781: 442), especially in terms of the shape, texture, margin, and indumentum of leaves, which misled the mistaken identification of its specimens as the latter. However, *F. conglobata* is distinguishable from *F. hispida* by short, fascicular, and numerous figs (Fig. 2 D–E). *F. heterostyla* Merrill (1942: 158) bears rather long stoloniflory (Fig. 2 J) and is easily distinguishable among it, *F. conglobata*, and *F. hispida* (Fig. 2 F and H). A detailed quantitative comparison between *F. conglobata* and its morphological allies is shown in Table 2.

Considering the mass type materials of *F. conglobata* are under diverse preservation conditions, we chose the typical and whole one from the initially stored herbarium (CAL) as the lectotype (Fig. 1).

Additional specimens examined:—CHINA. Xizang Autonomous Region, Linzhi City, Motuo County: Nigulong, 900 m, 30 January 1983, *B. S. Li et S. Z. Cheng 03545* (PE00776836, PE 00776837, PE 00776838, PE 00776839); Beibeng, 29°10'19.294"N, 94°58'59.88"E, 572 m, 15 May 2023, *D. R. Yang et al. MT238* (HITBC); Dexing, 29°18'6.15"N, 95°17'2.00"E, 772 m, 28 August 2014, *H. Q. Li et al. 2014546* (HSNU), 29°19'07.205"N, 95°18'15.59"E, 845 m, 12 May 2023, *D. R. Yang et al. MT130* (HITBC); Kabu, 29°28'28.203"N, 95°26'36.66"E, 889 m, 12 May 2023, *D. R. Yang et al. MT101* (HITBC); Miri, 29°24'48.759"N, 95°23'55.34"E, 804 m, 12 May 2023, *D. R. Yang et al. MT114* (HITBC). MYANMAR: Kachin State, Putao District, Naung Mung, Gathtu to Tongwang Cave, 27°29'55.2444"N, 97°58'29.0778"E, 640 m, 4 June 2018, *Myanmar Expedition, Y. H. Tan et al. M4027* (HITBC).

Phylogenomics of *Ficus conglobata*

Based on the nuclear *Ficus1316* reference dataset, we obtained a concatenate aligned supermatrix including sixteen samples with a length of 1931139 bp and a high-resolution phylogenomic tree (Fig. 3 A). In Fig. 3 A, five samples of *Ficus conglobata* comprise a well-supported monophyly (ultrafast bootstrap = 100 and posterior probability = 1), sister to a lineage including three samples of *F. heterostyla*. *Ficus hispida*, morphologically similar to *F. conglobata*, is unexpectedly sister to a rheophytic species, *F. squamosa* Roxburgh (1832: 531), with a high support value (ultrafast bootstrap = 100 and posterior probability = 1).

FIGURE 1. Lectotype of *Ficus conglobata* (*G. King 8732*, CAL0000014309).

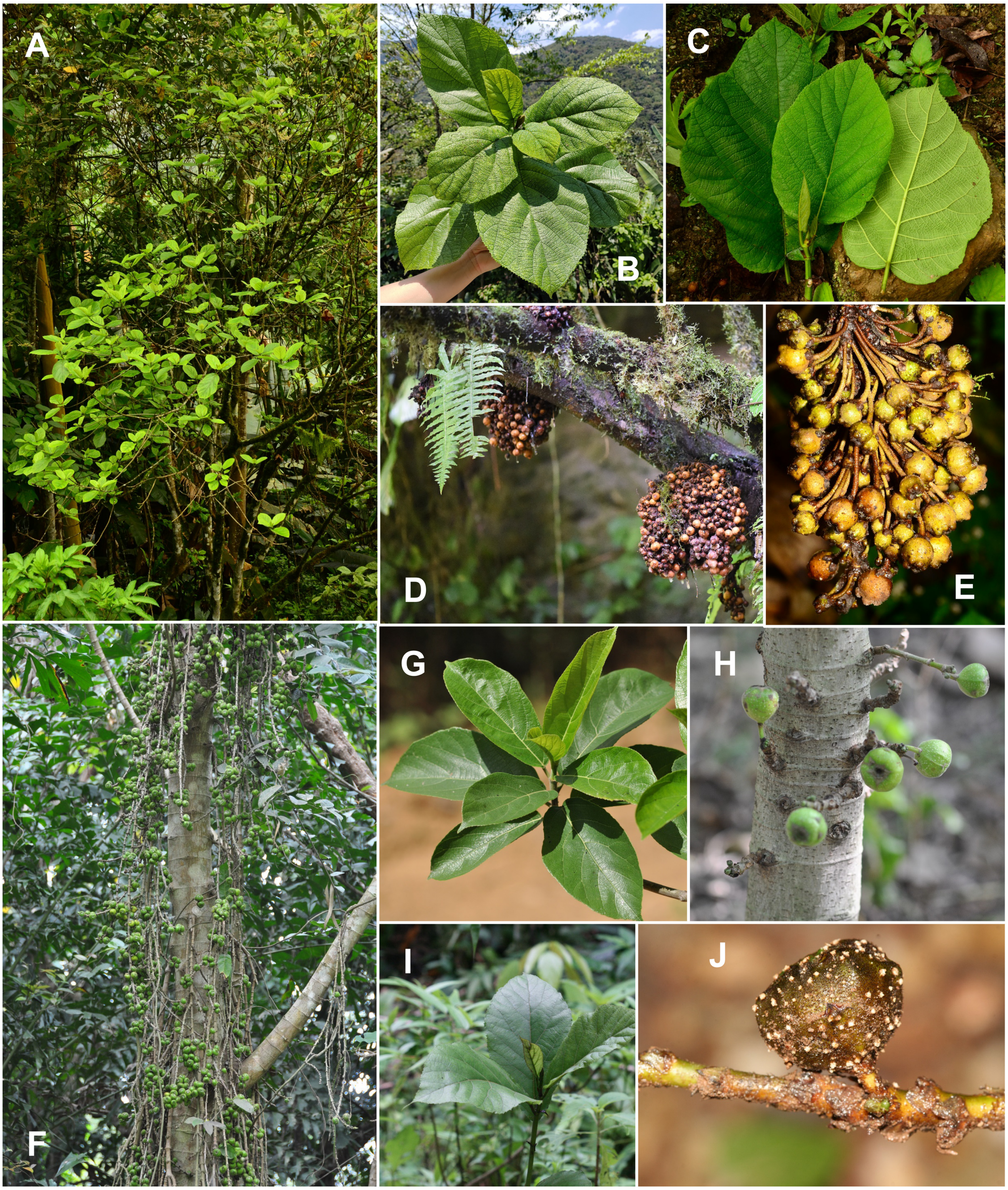

FIGURE 2. Illustrations of *Ficus conglobata* and its allies. A, Crown. B, Leafy branches. C, Leaves. D, Cauliflorous fruits. E, Syconia. F–H, Stoloniflorous figs, leaves, and syconia of *F. hispida*. I–J, Leaves and syconium of *F. heterostyla*.

The phylogenetic tree based on chloroplast genomes (Fig. 3 B) is obviously inconsistent with the tree from the nuclear dataset. Such as *Ficus conglobata*, which is sister to the clade consisting of all remaining species. However, among the three species, only the samples of *F. heterostyla* form a monophyletic group, but *F. squamosa* and *F. hispida* are polytomous.

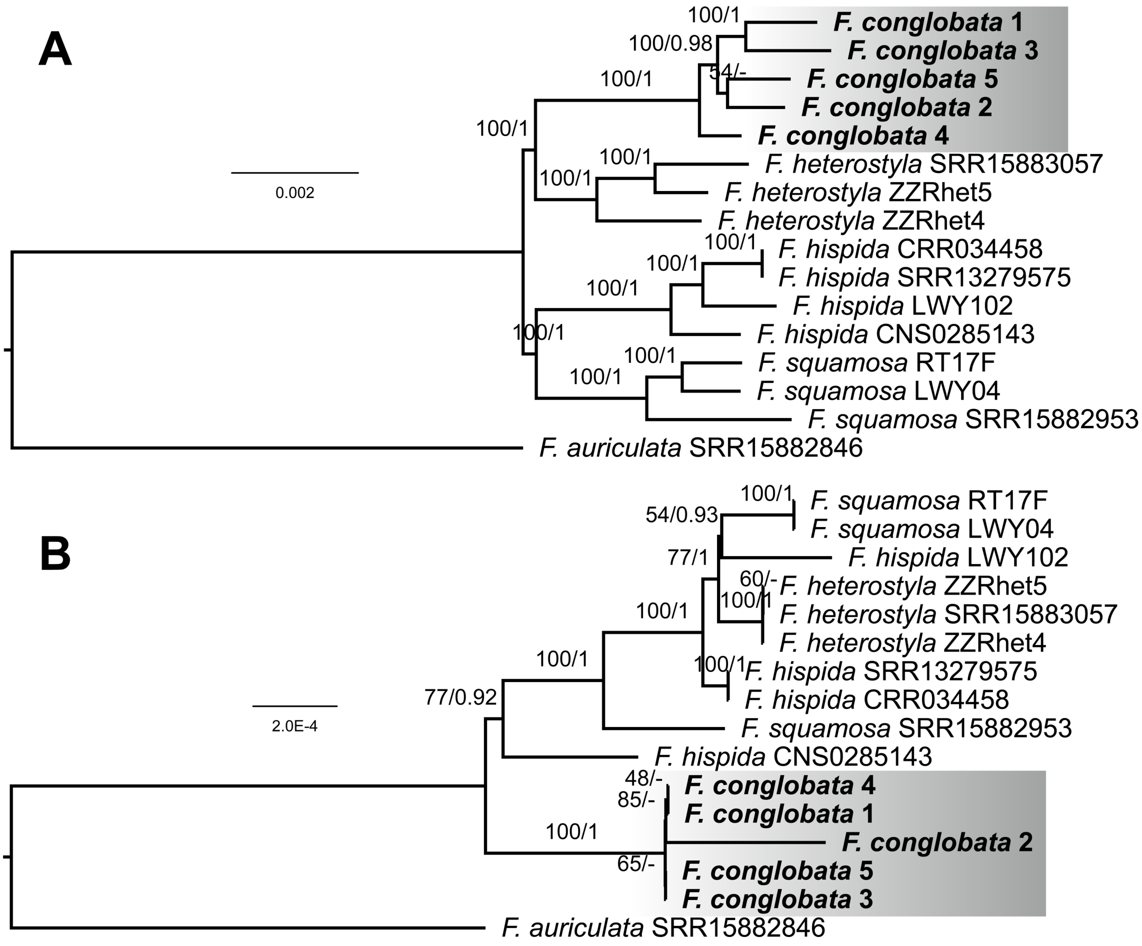

FIGURE 3. Phylogenetic position of *Ficus conglobata* shown by the maximum likelihood tree with ultrafast bootstrap values and posterior probabilities shown on the branches. A, tree based on the nuclear *Ficus1316* dataset. B, tree based on chloroplast genome with one of two repeated regions omitted.

TABLE 2. Morphological comparison between *Ficus conglotata* and its allies.

	F. conglobata	*F. heterostyla*	*F. hispida*	*F. squamosa*
Phyllotaxy	opposite or subopposite, sometimes alternate	opposite	opposite	alternate
Leaf size	23–34 × 13–20	25–30 × 10–14	10–25 × 5–10	4.5–13 × 1.2–3.2
Leaf shape	elliptic, oblong, or subobovate	oblong to obovate	ovate, oblong, or obovate–oblong	oblanceolate to oblong
Petiole length (cm)	4–8	5–6	1–4	0.5–1
Leaf indumentum	upper surface hispid, rough and with short thick hairs, lower surface papillose with coarse grey hairs	upper surface rough, lower surface with castaneous hispid and hirsute	upper surface white pubescent, lower surface brown or white hispid	upper surface scabrous and strigose, lower surface scaberulous or glabrous
Inflorescence pattern	cauliflorous with fascicular short branches (< 0.2m)	stoloniflorous with obviously elongated epigeous branches (3–4m)	axillary and cauliflorous with short and unbranched branches (< 1m)	axillary or on tuberculate branchlets from old stems
Syconium diameter (cm)	1–1.3	ca. 1.5	1.2–3	1.5–2
Syconium shape	pyriform or subglobose	obovoid	top–shaped	globose
Peduncle length (cm)	3–6	0.5–0.7	0.8–3	0.5–1.2
Syconium indumentum	subglabrous or brownish strigose	castaneous to black hispid and hirsute	short scattered hairs	densely covered with thick rust-colored hairs or villous

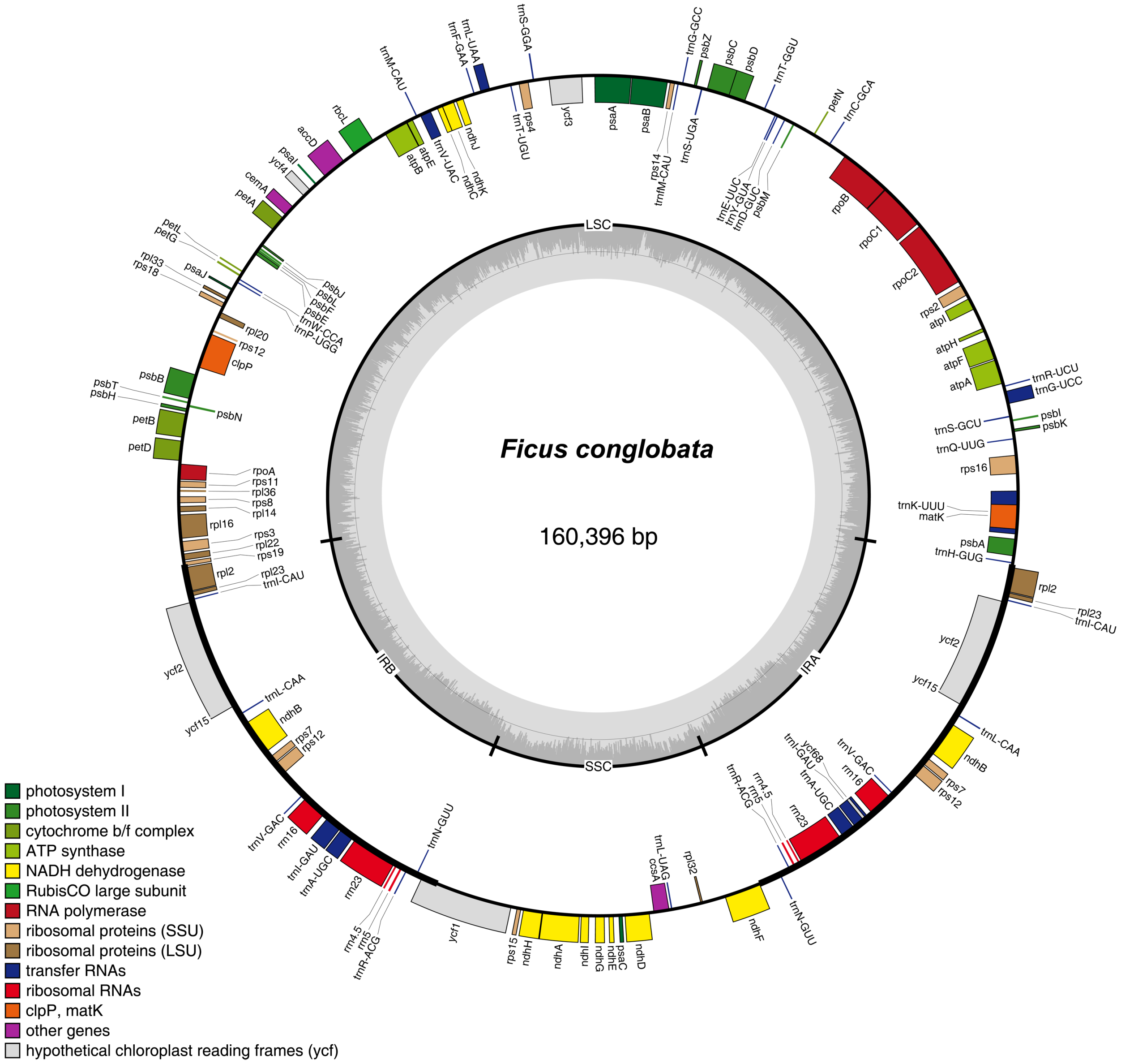

FIGURE 4. Chloroplast gene map of *Ficus conglobata*. Genes drawn inside are transcribed clockwise, and genes drawn outside are counterclockwise. Genes belonging to different functional groups are color-coded. In the inner circle, dark gray and light gray indicate the GC content and AT content, respectively.

Chloroplast genomes and nrDNA sequences of *Ficus conglobata*

Given the absence of genetic data, we annotated and visualized a complete chloroplast genome of *Ficus conglobata* (Fig. 4) as a super-barcoding resource. A typical quadripartite structure was discovered, including one large single copy, one small single copy, and two inverted repeats, similar to other chloroplast genomes in *Ficus* (Fungjanthuek *et al.* 2022; Zhang & Zhang 2022). Besides, we also submitted several universal nuclear barcoding sequences (internal transcribed spacer, ITS) for further biogeographical and conservation biology research.

Discussion

In the study, we reported a terrestrial arboreal fig tree, *Ficus conglobata* from southwest China (Motuo) and north Myanmar (Putao), adjacent to its previously reported distribution region east Himalaya, such as northeast India, Bhutan, and Bangladesh (Chaudhary *et al.* 2012). These new collection points are located in the southern foothills of the Himalayas, have monsoon forests and abundant tropical genera. Besides, in which, Motuo County is the region with the most Chinese taxa newly published in 2022 (Du *et al.* 2023). Thus, it can be believed that there are more species that urgently need to be reported here before habitat degradation.

Given that there are no available genetic data for this abegging species, we also confirmed its reliable phylogenetic sister relationship to *Ficus heterostyla* based on a large nuclear dataset (Fig. 3 A). However, a common nuclear-cyto discordance (Duan *et al.* 2023) exists in the phylogeny of *F. conglobata* and its allies. In the phylogenetic tree of the chloroplast genomes, two related species of *F. conglobata* failed to comprise monophyletic groups. Due to the apparently more genes and biparental inherited features, the phylogenetic tree from the nuclear *Ficus1316* dataset should be more in accordance with the real evolutionary history than the plastid tree (Zeng *et al.* 2014; Xu *et al.* 2024).

Besides, another remarkable thing is that *Ficus heterostyla* is far away from *F. hispida* (Fig. 3 A), although the former is often treated as a synonym of the latter (Corner 1960, 1965; Chang *et al.* 1998). The traits such as brownish black bristles on the branchlets and figs, longer stoloniflory (3–4 m), and smaller syconium (0.8–1.7 cm) set *F. heterostyla* apart from *F. hispida*, leading some researchers to recognize the species status of *F. heterostyla* (Berg *et al.* 2011). In view of the wide distribution and variable morphological traits of *F. hispida*, more materials are necessary to resolve the evolutionary relationship between *F. heterostyla* and *F. hispida*.

Data availability statement

The raw sequencing reads reported in the study can be acquired in the Genome Sequence Archive (GSA) in National Genomics Data Center, China National Center for Bioinformation / Beijing Institute of Genomics, Chinese Academy of Sciences with the accession number: CRA018089 (https://ngdc.cncb.ac.cn/gsa). The new complete chloroplast genome sequence and barcodes of internal transcribed spacer (ITS) of *Ficus conglobata* are deposited in the NCBI with accession numbers PQ126534 and PQ108607-PQ108611.

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