

Research Article

Revision of *Amana yunjuensis* (Liliaceae) based on morphological and molecular evidence: synonym of *Amana anhuiensis*Meizhen Wang^{1,2}, Shenlu Zhang³, Liang Guo², Qing Ma², Pan Li^{4,5}¹ Keqiao Science and Technology Innovation Center, Zhejiang Shuren University, Hangzhou, Shaoxing 312028, China² College of Biology and Environmental Engineering, Zhejiang Shuren University, Hangzhou 310015, China³ Agricultural and Rural Bureau of Lin'an District, Hangzhou 311300, China⁴ Key Laboratory of Biodiversity and Environment on the Qinghai-Tibetan Plateau, Ministry of Education, School of Ecology and Environment, Xizang University, Lhasa 850000, China⁵ Motuo Biodiversity Observation and Research Station of Xizang Autonomous Region, Motuo 860700, China

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Abstract

Based on the integrated morphological and molecular evidence, *Amana yunjuensis*, originally described from Mt. Yunju in Jiangxi province, is demonstrated not essentially different from *A. anhuiensis*. Indistinguishable diagnostic characters, nested phylogenomic relationships, and no genetic distinctiveness of population genomic structure all indicate that *A. yunjuensis* does not represent an independent evolutionary lineage. Accordingly, *A. yunjuensis* should be treated as a taxonomic synonymy of *A. anhuiensis*.

Key words: *Amana anhuiensis*, *Amana yunjuensis*, synonym, taxonomic revision

Introduction

Amana Honda (1935: 20) is endemic to East Asia (the eastern and central part of China, Japan and the Korean Peninsula) and composed of 12 species: *A. edulis* (Miq.) Honda (1935: 20), *A. erythronioides* (Baker) D.Y.Tan & D.Y.Hong (2007: 441), *A. anhuiensis* (X.S. Shen) D.Y.Tan & D.Y.Hong (2008: 394), *A. kuocangshanica* D.Y.Tan & D.Y.Hong (2007: 437), *A. wanzhensis* L.Q.Huang, B.X.Han & K.Zhang (2014: 120), *A. baohuaensis* B.X.Han, Long Wang ter & G.Y.Lu (2019: 45), *A. latifolia* (Makino) Honda (1935: 21), *A. nanyueensis* P.Li & L.X.Liu (2023: 65), *A. tianmuensis* P.Li & M.Zhen Wang (2023: 66), *A. hejiaqingii* M.Zhen Wang & P.Li (2022: 287), *A. yunmengensis* P.Li, M.Zhen Wang & Zi Yi Wang (2023: 18) and *A. polymorpha* M.Zhen Wang & P.Li (2024: 151) (Ohwi and Kitagawa 1992; Chen and Mordak 2000; Shen 2001; Tan et al. 2007, 2008; Han et al. 2014; Wang et al. 2019; Wang et al. 2022; Wang et al. 2023a; Wang et al. 2023b; Wang et al. 2024). Nearly half of these species were newly discovered and published in recent years. The morphology of *Amana* is relatively simple, and interspecific difference is mainly reflected in characters such as the density of hair inside the bulb tunic, leaf shape and vein, bract type and number, and the colour of flowers and anthers (Wang et al. 2024). Besides, during our comprehensive and systematic field surveys, some individuals with atypical traits were occa-



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sionally found, for example, *Amana edulis*, with three bracts and one white vein. Therefore, species identification in *Amana* cannot rely solely on morphological traits, which correspond only to the morphological species concept (Wilkins 2009). Instead, multiple lines of evidence are required to corroborate taxonomic boundaries with confidence, namely integrative taxonomy (de Queiroz 2007; Liu 2016; Hong 2020).

In 2024, we noted the publication of a new species *Amana yunjuensis* B.X.Han & X.W.Song (2024: 232) (Song et al. 2024). However, based on comprehensive field investigations and molecular data analyses (Wang et al. 2024; Liang et al. 2024), we conclude that this *Amana* population distributed in Mt. Yunju should, in fact, be referred to as *Amana anhuiensis*. We therefore propose the following taxonomic revision.

Material and methods

Sampling and sequencing

In addition to the data previously reported by Wang et al. (2024), sampled populations from Mt. Tianzhu in Anhui Province, Mt. Yunju and Mt. Lushan in Jiangxi Province, and Tuanfeng County in Hubei Province were studied through morphology and molecular analyses (Table 1). Fresh leaf tissues were immediately frozen in liquid nitrogen and subsequently stored at −80 °C. RNA libraries were prepared using the NEBNext Ultra RNA Library Prep Kit for Illumina (NEB, USA) according to the manufacturer’s protocol, and sequencing was performed on an Illumina NovaSeq 6000 platform, generating 150-bp paired-end reads (Novogene, Tianjin, China).

Morphological analysis

The morphological characteristics of bulbs, bracts, leaves, flowers and fruits were measured and recorded. Principal coordinates analysis was conducted based on 15 traits with R package vegan v.2.8.0 (Oksanen et al. 2025) and ggplot2 v.3.3.6 (Wickham 2016), including inner side of bulb tunic texture (thinly papery: 0; papery:1), bulb tunic inside (glabrous: 0; sparsely villous: 1; densely villous-woolly: 2), length and width of lower leaf, lower leaf length/width, length and width of upper leaf, upper leaf length/width, length from the apex to the

Table 1. Information of collected samples of *Amana anhuiensis* and *A. yunjuensis*.

Species	Collect number	GPS coordinates	Altitude/m	Location
<i>Amana anhuiensis</i>	LJK61	30.7235°N, 116.4537°E	1711	Mt. Tianzhu, Qianshan County, Anhui Province
	LJK62	30.7235°N, 116.4537°E	1711	Mt. Tianzhu, Qianshan County, Anhui Province
	CMQ2015075	30.7410°N, 116.4526°E	1207	Mt. Tianzhu, Qianshan County, Anhui Province
	WMZ1480	30.7235°N, 116.4537°E	1711	Mt. Tianzhu, Qianshan County, Anhui Province
	WMZ1750	30.8623°N, 115.0971°E	789	Tuanfeng County, Hubei Province
	WMZ1755	29.5553°N, 115.9719°E	616	Mt. Lu, Lushan City, Jiangxi Province
<i>Amana yunjuensis</i>	LJK63	29.0967°N, 115.5767°E	703	Mt. Yunju, Yongxiu County, Jiangxi Province
	LP173014	29.0968°N, 115.5767°E	703	Mt. Yunju, Yongxiu County, Jiangxi Province
	WMZ1499	29.0968°N, 115.5768°E	711	Mt. Yunju, Yongxiu County, Jiangxi Province

widest part of the lower and upper leaf, number of bract, bract length and width, number of flower and colour of anther (yellow: 0; purple: 1). A total of 21 individuals (13 of *A. anhuiensis* from two populations and eight of *A. yunjuensis* from two populations) were used for analysis (Suppl. material 1).

To assess morphological differences in bulb traits between *Amana anhuiensis* and *A. yunjuensis*, the bulb diameter and bulb height of each individual were measured using a vernier caliper to the nearest 0.01 mm (Suppl. material 2). For each specimen, a bulb size index was calculated as the product of bulb diameter and height (diameter × height) to approximate overall bulb volume. Statistical comparisons of the three variables (diameter, height and size index) between species were performed using the non-parametric Wilcoxon rank-sum test (Wilcoxon 1945), as the data did not conform to normal distribution. Boxplots were generated in R (v4.5.0) using the ggplot2 and patchwork packages (Pedersen 2024) to visualize the distributions, and p-values were displayed above each comparison.

Phylogenetic analyses

Transcripts were assembled using Trinity v2.14.0 (Grabherr et al. 2011) with default parameters, and putative protein-coding sequences were predicted using TransDecoder v5.5.0 (Haas et al. 2013). Redundant transcripts were removed with CD-HIT v4.8.1 (Li and Godzik 2006) using the parameters '-c 0.95 -n 8'. Orthologous groups were identified across all samples (12 species and 101 individuals) using OrthoFinder (Emms and Kelly 2019), and gene clusters present in all individuals with a maximum copy number of fewer than three were retained, resulting in 2,567 protein sequences. Orthologs were inferred following the tree-based orthology strategy proposed by Yang and Smith (2014). Gene trees were reconstructed using RAxML v8.2.12 (Stamatakis 2014), and long terminal branches (more than 0.5 or 10 times longer than their sister lineages) as well as deep paralogs were pruned. The Monophyletic Outgroups (MO) approach (Yang and Smith 2014) was applied to infer orthologs, with the minimum taxon occupancy set to 60, resulting in 1,652 monophyletic trees. Maximum likelihood (ML) analyses were conducted in IQ-TREE 2 (Minh et al. 2020) using 1,000 bootstrap replicates, and the best-fitting models for each gene partition were selected with ModelFinder (Kalyaanamoorthy et al. 2017). The final phylogenetic trees were visualized and exported using FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Admixture analysis

Orthologous genes shared by at least 75% of individuals across the 12 *Amana* species were merged and used as a reference dataset. In total, 13,023 genes were obtained, and the longest transcript of each gene was retained to represent its sequence. Clean reads were aligned to the reference using BWA-MEM v0.7.17 (Li 2013) and sorted with SAMtools v1.14 (Danecek et al. 2021) to remove unmapped and mate-unmapped reads. PCR duplicates were identified and marked using MarkDuplicates in the PICARD package (<https://broadinstitute.github.io/picard/>). Genotype calling for each individual was performed using GATK HaplotypeCaller (<https://github.com/broadinstitute/gatk/>), and individual variant files were merged with CombineGVCFs. Variants were jointly

genotyped with GATK GenotypeGVCFs to estimate parameters such as QUAL, allele count, and allele frequency. INDELs were excluded from subsequent analyses, resulting in 5,594,839 SNPs. Hard filtering was conducted based on the distribution of multiple statistics following GATK recommendations (QUAL < 40.0 || QD < 2.0 || MQ < 50.0 || FS > 30.0 || SOR > 8.0 || MQRankSum < -0.5 || ReadPosRankSum < -4.0), and loci unique to individual samples (max-missing 0.01) were removed, yielding 4,683,563 high-quality SNPs for all samples. Population structure analysis was conducted with ADMIXTURE v1.3.0 (Alexander et al. 2009), applying maximum-likelihood estimation of individual ancestries with K values ranging from 2 to 6 for all individuals of *A. baohuaensis*, *A. wanzhensis*, *A. hejiaqingii*, *A. yunmengensis*, *A. anhuiensis* and *A. yunjuensis* with 4,665,822 SNPs. For the admixture analysis, K was selected based on the resolution of species-level genetic clusters, with cross-validation (CV) values used as a reference rather than a strict criterion.

Results

Morphological comparison

The results of principal coordinates analysis showed that *Amana yunjuensis* and *A. anhuiensis* were not morphologically distinguishable (Fig. 1). There was a clearly overlapping area between these two groups. The first principal component (PCoA1) and second principal component (PCoA2) accounted for 49.6% and 29.1% of total variance, respectively. Moreover, no significant morphological differences were detected in bulb traits between *Amana anhuiensis* and *A. yunjuensis* (Fig. 2). The two species exhibited largely overlapping variation ranges in bulb diameter ($p = 0.222$), bulb height ($p = 0.791$), and overall bulb size index (diameter $\times$ height; $p = 0.634$). Although *A. yunjuensis* tended to have slightly larger bulb diameter, this difference was not statistically significant ($p \geq 0.05$). These results suggest that the bulbs of *A. anhuiensis* and *A. yunjuensis* are morphologically comparable, showing similar size and proportion despite minor individual variation.

Phylogenetic analyses

The phylogenetic tree based on nuclear genes revealed that *Amana yunjuensis* (LJK63, WMZ1499) was nested within the *A. anhuiensis* clade (WMZ1755, LJK61, LJK62, WMZ1750-1, WMZ1750-2), and the two species together formed a strongly supported monophyletic group (bootstrap = 100, Fig. 3). Besides, the phylogenetic relationship between *A. yunjuensis* and *A. anhuiensis*_WMZ1755 distributed in Mt. Lu in Jiangxi Province is the closest. Consistent with previous studies (Wang et al. 2024), *Amana* can be divided into three major clades: clade I ((*Amana edulis*, *A. tianmuensis*), *A. nanyueensis*), clade II ((*A. baohuaensis*, *A. wanzhensis*), ((*A. hejiaqingii*, *A. yunmengensis*), *A. anhuiensis*)) and clade III (*A. polymorpha*, (*A. erythronioides*, (*A. kuocangshanica*, *A. latifolia*))).

Admixture analysis

The ADMIXTURE analysis ($K = 2\sim6$) clearly distinguished the species within clade II (*Amana baohuaensis*, *A. wanzhensis*, *A. hejiaqingii*, *A. yunmengensis*,

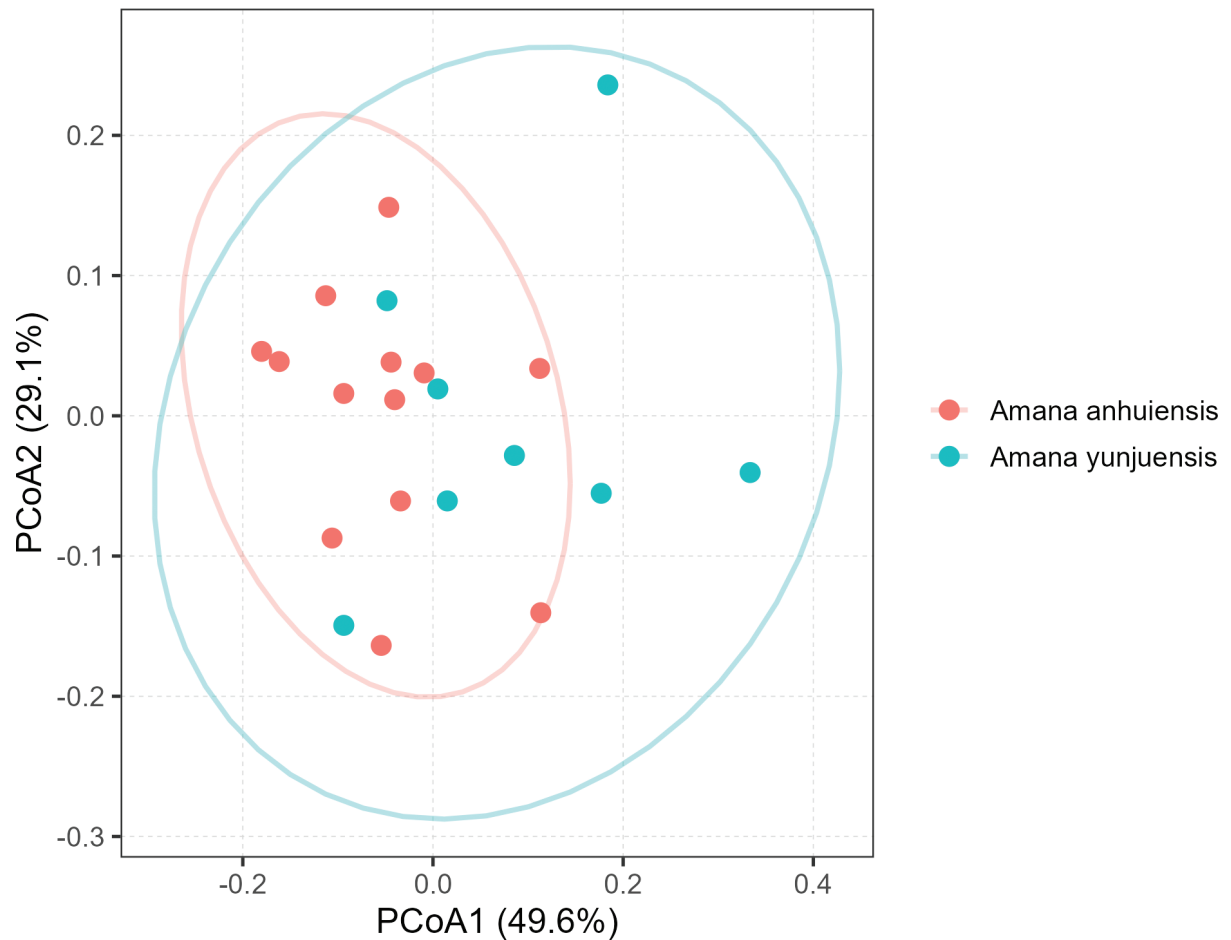


Figure 1. Principal coordinates analysis of *Amana anhuiensis* and *A. yunjuensis*. Ellipses represent the 95% confidence interval.

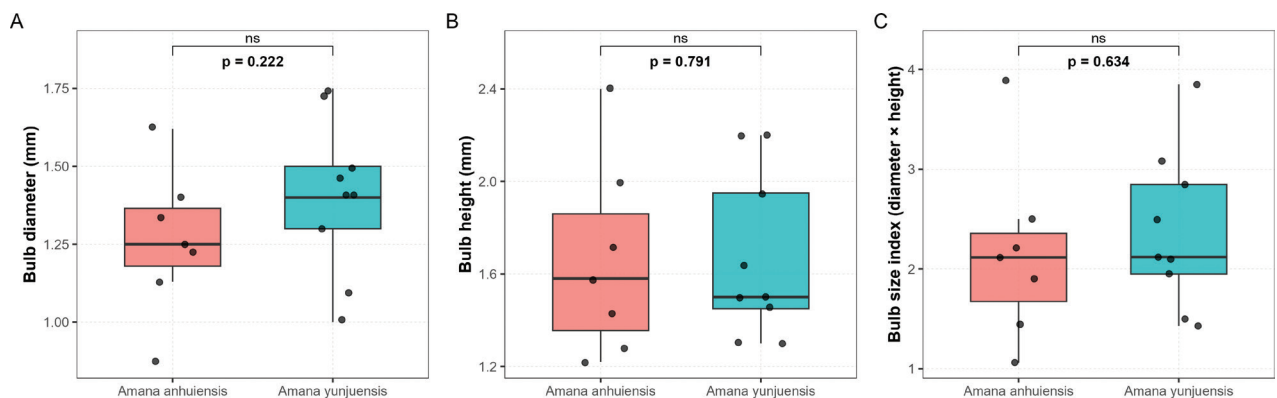


Figure 2. Comparison of bulb morphology between *Amana anhuiensis* and *A. yunjuensis*. Boxplots showing the variation in (A) bulb diameter, (B) bulb height, and (C) bulb size index (diameter × height) between *A. anhuiensis* and *A. yunjuensis*. Boxes indicate the interquartile range (IQR) and horizontal lines represent medians. The p-values above the plots were obtained from Wilcoxon rank-sum tests. No significant differences were detected for any of the three traits ($p \geq 0.05$).

A. anhuiensis). But the result showed that the two individuals of *A. yunjuensis* (LJK63 and WMZ1499) shared an identical ancestry composition with *A. anhuiensis* populations, without any unique genetic component across all K values (Fig. 4). This pattern, together with the phylogenetic nesting of *A. yunjuensis* within *A. anhuiensis*, indicates that these taxa are genetically indistinguishable

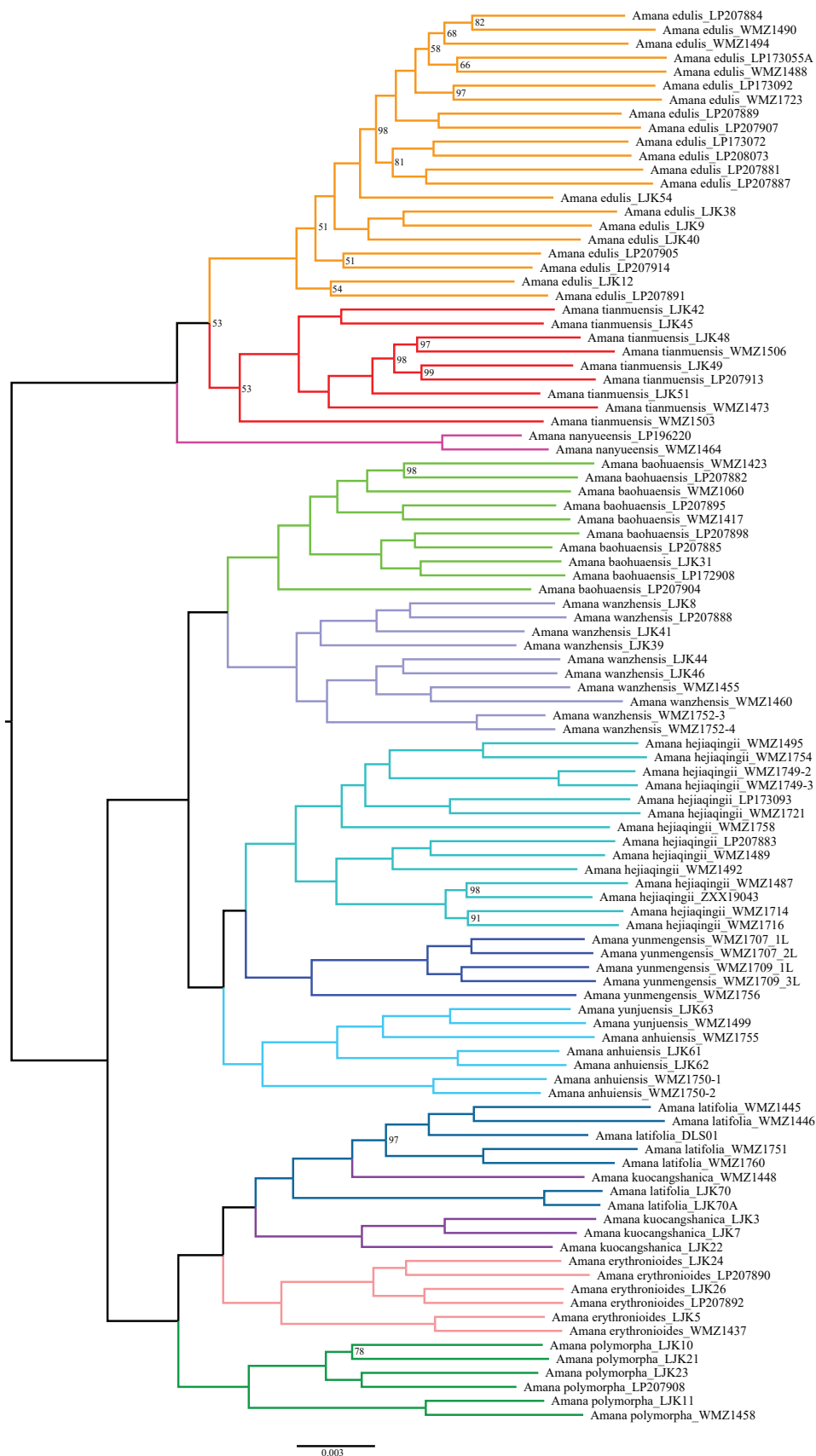


Figure 3. Phylogenetic tree of *Amana* based on nuclear genes. For visualization, the outgroup (*Erythronium japonicum*) was pruned from the displayed tree to avoid distortion caused by its deep divergence from the ingroup. All unlabelled nodes have 100% bootstrap support.

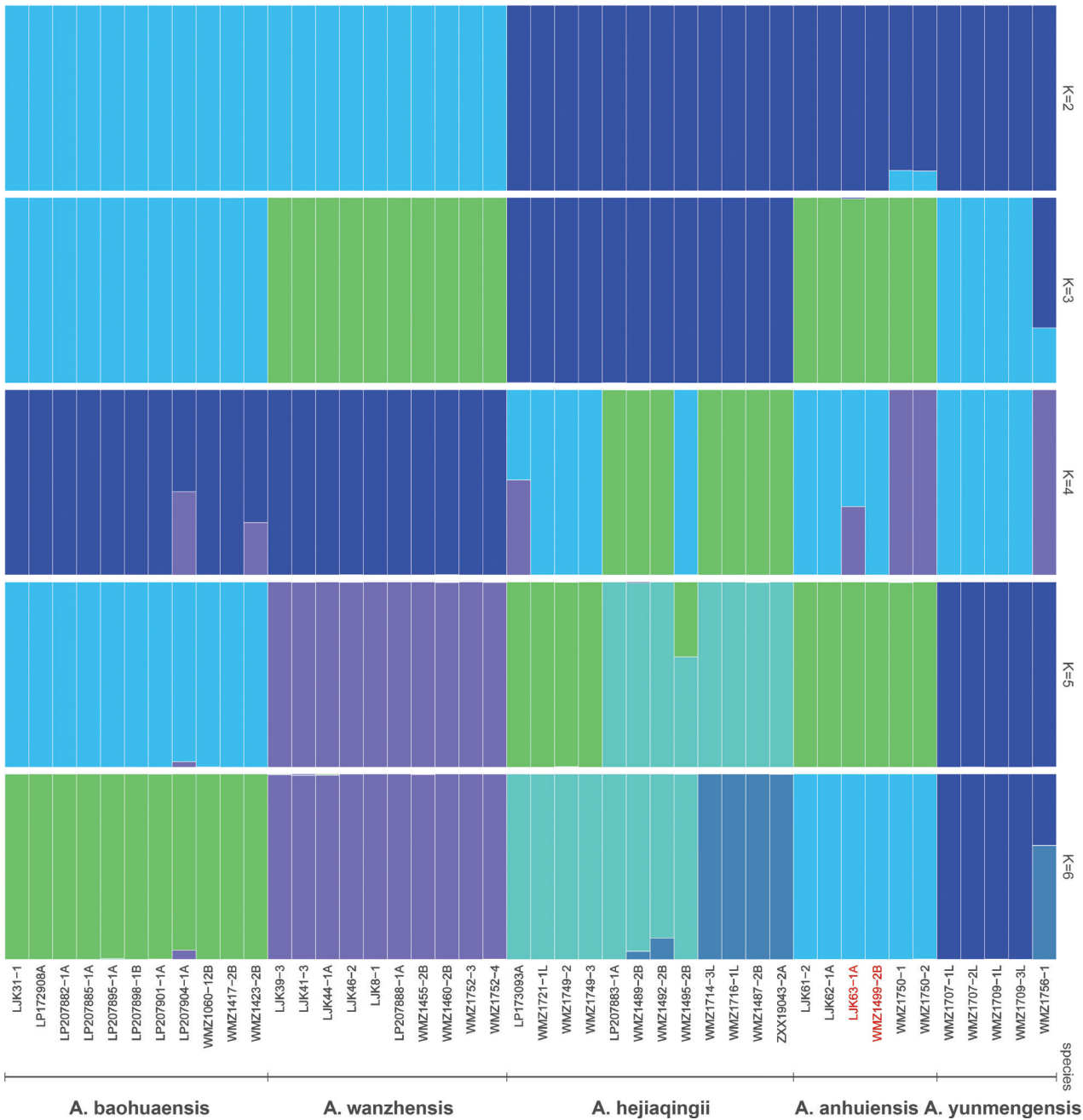


Figure 4. Admixture analysis result of clade II. The individual labelled in red is *Amana yunjuensis*.

and may represent recently diverged populations of the same species or con-specific lineages with ongoing or historical gene flow.

Discussion

Species is the basic units of taxonomy, so reasonable species classification is necessary for the study of evolution and biology (Hong 2020). The integration of molecular evidence with classical morphological taxonomy is crucial for reliable species delimitation (Liu 2016). In this study, we combined morphological comparison, nuclear phylogenomics, and population genomic structure analysis to reassess the taxonomic status of *Amana yunjuensis*. The PCoA

analysis based on morphological traits revealed substantial overlap between the two taxa, with no clear separation along the first two principal coordinate axes, which together explained 78.7% of the total variation. Likewise, the comparison of bulb traits, the diagnostic characters between these two species when published (Song et al. 2024), showed no statistically significant differences. Although *A. yunjuensis* exhibited slightly larger average bulb diameter, the variation ranges of the two taxa exhibited no significant difference, indicating that these differences likely reflect intraspecific variation rather than species level divergence.

Genomic evidence provided further support for their conspecific relationship. In the nuclear phylogeny, the two sampled individuals of *A. yunjuensis* were fully embedded within the *A. anhuiensis* clade, forming a strongly supported monophyletic lineage. Moreover, the individuals of *A. yunjuensis* showed the closest genetic relationship to *A. anhuiensis* populations collected from Mt. Lu in Jiangxi Province, near the type locality region of *A. yunjuensis*, suggesting geographic continuity rather than independent evolutionary history. Although, previous studies of *Amana* have shown that plastid-based phylogenetic trees do not recover individuals of *A. anhuiensis* and *A. yunjuensis* as a monophyletic clade. This pattern is likely attributable to extensive hybridization and introgression within the genus, potentially involving multiple maternal lineages, and represents a common feature of plastid phylogenetic analyses across *Amana* (Wang et al. 2024). Moreover, population structure analysis yielded fully concordant results: across all *K* values (*K* = 2~6), the two *A. yunjuensis* individuals displayed identical ancestry component to *A. anhuiensis* populations, without any detectable private genetic component. The absence of genetic differentiation, coupled with nuclear phylogenetic nesting and shared ancestry, strongly argues against the recognition of *A. yunjuensis* as an independent species.

Taken together, the lack of varying diagnostic morphological characters, complete phylogenomic embedding, and indistinguishable genomic composition collectively demonstrate that *Amana yunjuensis* does not represent a distinct evolutionary lineage but rather falls within the natural variation range of *A. anhuiensis*. Therefore, we conclude that *A. yunjuensis* should be treated as a taxonomic synonym of *A. anhuiensis*.

Taxonomic treatment

***Amana anhuiensis* (X.S.Shen) D.Y.Tan & D.Y.Hong in Acta Bot. Boreal, 28: 0393-0395, 2008**

Type. CHINA. • Anhui: Qianshan, Mt. Tianzhu. In bamboo forests or in bushes, 850~1,250 m alt., 14 March 2002, D. Y. Tan & Z. Zhang 皖006 (neotype: PE; neoisotype: XJA).

=*Amana yunjuensis* B.X.Han & X.W.Song, syn. nov.

Type. CHINA. • Jiangxi Province: Jiujiang City, Mt. Yunju, 5 Mar 2019, Song SXW190305 (holotype: ACM; isotype: PE).



Figure 5. *Amana anhuiensis*. A. Habitat. B. Population with flowers. C. Population with fruits. D. Whole plant. E Front view of flower. F. Side view of flower. G. Floral dissection. H. Bulb. I. Leaves. J. Fruits. Scale bar = 1 cm. Photographs by Shenglu Zhang and Pan Li.

Description. Perennial herbs; bulbs ovoid, 0.87–3.0 cm in diameter, tunics yellowish-brown, thinly papery, sparsely villous-woolly inside. Stems 1.8–16.8 cm tall, glabrous, simple. Leaves usually 2, opposite, green with white veins, oblanceolate; the lower leaf 7.8–30.6 × 0.9–3.1 cm, the upper leaf 11–28.9 × 0.7–1.9 cm. Scapes 1.5–10.5 cm tall, glabrous, simple. Bracts usually 3, verticillate, narrowly lanceolate, green, 2–5 × 0.3–0.75 cm; pedicels 1.1–6.6 cm. Flowers solitary, funnel-shaped; tepals 6, white or light-pink, with a green or yellowish-green blotch at the very base inside and purple-red or light-pink streaks on the back; outer tepals lanceolate, acute, 2.3–4.5 × 0.6–0.95 cm, inner tepals elliptic-lanceolate, acute, 2.1–4.25 × 0.7–1.15 cm. Stamens 6, two-wheeled, the inner three slightly longer than the outer; filaments yellowish-green, 5–8.5(9) mm long, middle slightly dilated, gradually attenuate towards apex, glabrous; anthers light-purplish, the outer three 5–9.5 mm long, the inner three 6–9.5(10) mm long. Oval ovaries, yellowish-green, constricted below the style, 0.5–1 cm long, styles 0.4–0.7 cm long. Capsule subglobose, triquetrous, 0.5–1.31 cm in diameter, apex long beaked, 0.4–0.91 cm long. Fl. March–April, fr. April–May.

Phenology. Flowering from March to April; fruiting from April to May.

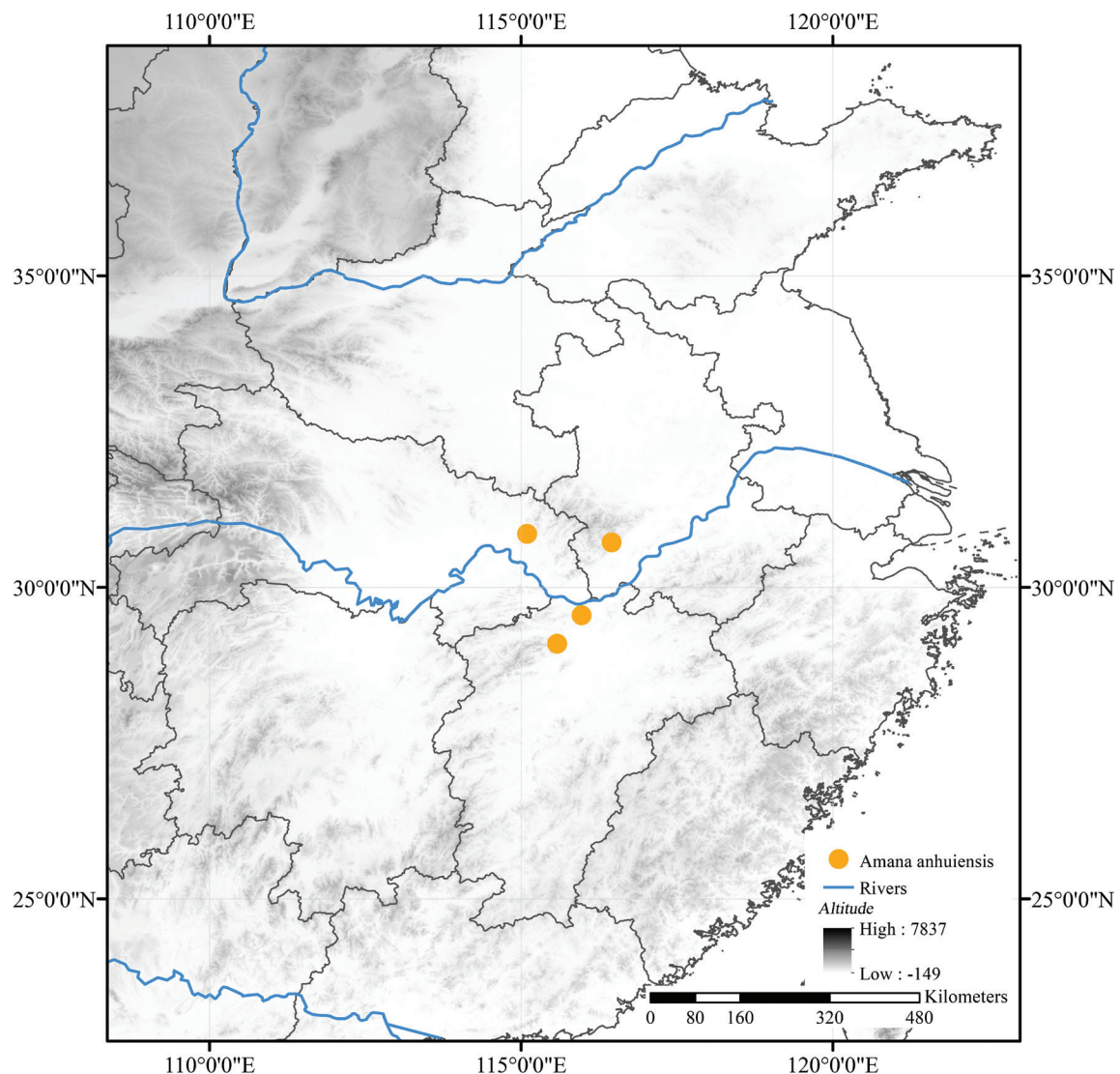


Figure 6. Distribution of *Amana anhuiensis*.

Distribution and habitat. *Amana anhuiensis* is distributed in Mt. Tianzhu in Anhui Province, Mt. Yunju and Mt. Lu in Jiangxi Province and Tuanfeng County in Hubei Province, China (Fig. 6). It mostly grows in moist deciduous broad-leaved forests and bamboo forests, at elevations of 600–1,710 m.

Additional specimens examined. CHINA. • **Anhui** Province: Qianshan County, Mt. Tianzhu, Zongguanzhai (总关寨), 850–1300 m, Fl. & Fr., 14 March 2002, *Dunyan Tan 006* (PE); *ibidem*, 1207 m, Fr., 9 May 2015, *Minqi Cai CMQ2015075* (HZU); *ibidem*, 1183 m, Fl., 4 April 2016, *Minqi Cai CMQ16215* (HZU); *ibidem*, 1183 m, Fl., 24 March 2019, *Pan Li & Junke Li LJK62* (HZU); Qianshan County, Mt. Tianzhu, Foguang Temple (佛光禅寺), 697 m, Fl., 4 April 2016, *Minqi Cai CMQ16216* (HZU); Qianshan County, Mt. Tianzhu (天柱山), 1711 m, Fl., 6 March 2021, *Pan Li et al. WMZ1480* (HZU). • **Jiangxi** Province: Jiujiang City, Yongxiu County, Mt. Yunju, Zhenru Temple (真如寺), 703 m, Fl., 21 March 2019, *Pan Li & Junke Li LJK 63* (HZU); *ibidem*, 711 m, Fl. & Fr., 10 March 2021, *Pan Li et al. WMZ1499* (HZU); Jiujiang City, Mt. Lu, Shimenjian (石门涧), 616 m, Fl., 11 March 2023, *Tongjun Liang LTJ 20230308* (LBG). • **Hubei** Province: Huanggang City, Tuanfeng County, Jiamiao Town, 789 m, Fl., 5 March 2023, *Xinxin Zhu WMZ1750* (HZU).

Conservation status. *Amana anhuiensis* is only known from four places in Mt. Tianzhu, Mt. Lu, Mt. Yunju and Tuanfeng County, but with thousands of individuals at each site, thus we suspect that *Amana anhuiensis* could be categorized as Vulnerable (VU) according to IUCN criteria (IUCN 2022).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

M.Z. W and P. L planned and designed the research. M.Z. W, S.L. Z and P. L collected the materials. S.L. Z and P. L took the photograph of plants. M.Z. W performed the morphological and molecular analyses. L. G and Q. M reviewed the manuscript. M.Z. W wrote the article with contributions from all authors. All the authors approved the final version of the manuscript.

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Data availability

RNA-seq data were deposited at the National Genomics Data Center, China National Center for Bioinformation/Beijing Institute of Genomics under BioProject accession number PRJCA013174.

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Supplementary material 1

Morphological data used in the principal coordinates analysis for *Amana anhuiensis* and *A. yunjuensis*

Authors: Meizhen Wang, Shenlu Zhang, Liang Guo, Qing Ma, Pan Li

Data type: xlsx

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Supplementary material 2

Bulb diameter and height measurements of *Amana anhuiensis* and *A. yunjuensis*

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Data type: xlsx

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