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ARTICLE

Taxonomic Clarification and Revision of *Lycoris haywardii* Traub

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ABSTRACT: Based on an integrative analysis of morphological traits, phenological characteristics, karyotype, and chloroplast genome data, we revised the taxonomic status of *Lycoris haywardii* Traub, reclassifying it as a cultivar of *Lycoris rosea* Traub ex Moldenke, designated as *Lycoris rosea* 'Lin'. *Lycoris haywardii* Traub was originally published by Traub in 1957 as a spring-leafing taxon with orchid purple flowers and stamens slightly shorter than the perianth, with a flowering period from July to mid-August and a purported distribution in Japan. However, populations cultivated in Hangzhou Botanical Garden, previously referred to as *L. haywardii*, exhibited autumnal leaf emergence, deep purple-pink flowers, and stamens longer than the perianth. Previous artificial hybridization experiments and our current chloroplast genome analyses, along with detailed morphological and phenological observations, confirmed that it is not conspecific with the original *L. haywardii.* In addition, they are natural hybrids derived from *L. radiata* var. *pumila* Grey and *L. insularis* S. Y. Zhang & J. W. Shao, the same as the origin of *L. rosea.* Therefore, we formally revised the taxonomy and provided a detailed morphological description of this cultivar.

KEYWORDS: *Lycoris haywardii* Traub; *L. insularis* S. Y. Zhang & J. W. Shao; *L. rosea* Traub ex Moldenke; taxonomic revision; chloroplast genome

1 Introduction

The genus *Lycoris* Herb., belonging to the family Amaryllidaceae, is primarily distributed across East Asia, including China, Japan, and the Korean Peninsula. Scattered populations also occur in parts of Southeast Asia (Laos, Myanmar, Thailand, and Vietnam) and South Asia (India and Pakistan) [1]. To date, a total of 31 species and 5 varieties of *Lycoris* have been validly published worldwide. The highest species diversity is in eastern China, which is regarded as the center of diversity for the genus [2,3]. Most *Lycoris* species were described prior to the 1950s by Western botanists based on cultivated or imported specimens, without comprehensive or systematic investigation of wild populations. Many species lacked the designation of type specimens at the time of publication (before 1958); and where types were designated, most are now untraceable.

Lycoris haywardii Traub was published by Traub in 1957. It was characterized by spring-emerging leaves, floral coloration darker than that of *L. sprengeri* Comes ex Baker but lighter than that of *L. aurea*, and stamens slightly shorter than the perianth. Flowering occurs from July to mid-August, approximately two weeks earlier than *L. sprengeri.* Its original distribution was reported as Japan [4]. The designated specimens include No. 554 (holotype, TRA), collected by Sam Caldwell in Nashville, Tennessee, and No. 291 (paratype, TRA), collected by Wyndham Hayward in Winter Park, Florida.

Hsu et al. [5] revised the taxonomic identity of a cultivated population maintained at the Hangzhou Botanical Garden, reporting an autumnal leaf emergence rather than spring. The material studied was of cultivated origin only. In addition, Hsu et al. [5] observed that the stamens were clearly exserted beyond the perianth, traits not consistent with Traub's original description. According to Adams [6], the distribution of *L. haywardii* was reported in both China and Japan. However, the species is not included in either *Flora Reipublicae Popularis Sinicae* [7] or *Flora of China* [1]. Within the taxonomy of *Lycoris*, leaf emergence phenology and floral morphology are considered key diagnostic characters. The traits described by Hsu et al. [5] in the Hangzhou cultivated population differ significantly from those originally documented by Traub [4].

In this study, we conducted morphological observations, karyotype analysis, and chloroplast genome sequencing to clarify the taxonomic identity of the population described by Hsu et al. [5] cultivated in Hangzhou Botanical Garden, providing a scientific basis for the rational conservation and utilization of this genetic resource. Based on our findings, we propose that this population represents a cultivar of *L. rosea* and designate it as *L. rosea* 'Lin'.

2 Materials and Methods

2.1 Plant Materials

Bulbs of *L. rosea* 'Lin' were collected in Hangzhou Botanical Garden which is cultivated abundantly nowadays. Hangzhou Botanical Garden is located at 30°15′34″ N, 120°07′15″ E, a typical subtropical monsoon climate, and an average altitude is 20 m. Other materials used for karyotype analysis or molecular phylogenetic studies were collected from a wild population located in Chunxiao Town, Ningbo City, Zhejiang Province (29°47′33″ N, 121°57′07″ E), and introduced for cultivation in Hangzhou Botanical Garden.

2.2 Methods

2.2.1 Morphology and Chromosome Observations

Morphological traits examined in this study included: bulb size, presence of a pale central band on the leaf blade, leaf emergence phenology, leaf color, leaf length, leaf width (the widest site), leaf apex shape, flower morphology, flower color, flowering period, scape height, spathe length, number of individual flowers per umbel, perianth length, perianth width, perianth tube length, stamen length, pistil length, flower diameter, and fruit set. For each trait, measurements were taken from ten individual plants per taxon.

2.2.2 Acquisition, Annotation, Comparison and Phylogenetic Analysis of Chloroplast Genome

Genome DNA was extracted from fresh leaves of two individuals of *L. rosea* 'Lin' (Voucher No. HZ077536, HHBG) and one individual of wild *L. rosea* using the modified CTAB (mCTAB) method [8,9]. After Polymerase Chain Reaction (PCR), we used a NanoDrop 1000 Spectrophotometer and agarose gel electrophoresis to check the DNA quality. DNA library building, Genome Skimming and FastQC were outsourced to Wuhan Frasergen Genetic Information Co., Ltd. (Wuhan, China), which employed Illumina HiSeq 6000 for analysis. In this study, the 3 Gb raw data generated by genome skimming were assembled and analyzed. With *Lycoris insularis* (OP034614) as the reference, the complete chloroplast genome sequences were assembled using GetOrganelle v.1.7.1, followed by genome annotation performed with PGA [10–12]. Finally, the annotated sequences were submitted to the National Center for Biotechnology Information

(NCBI) with the accession numbers PV839568–PV839570 (Fig. 1). This study was performed on the eleven complete chloroplast genomes in *Lycoris* Herb., of which ten were downloaded from NCBI. *Narcissus poeticus* (MH706763) was selected as the outgroup. All sequences were aligned by MACSE v.2 [13]. Maximum Likelihood (ML) and Bayesian Inference (BI) methods were used to determine the phylogenetic relationships, which the best-fit model of DNA substitution being estimated by ModelFinder [14,15]. ML analysis was conducted using the GTR+G+I model with 1000 bootstrap replicates by IQtree v.1.6.8 [16]. Bayesian analysis was constructed with eight independent chains for 1,000,000 generations and sampling every 1000 generations by MrBayes v.3.2.6 [17,18]. All phylogenetic analyses were performed in Phylosuite [18].

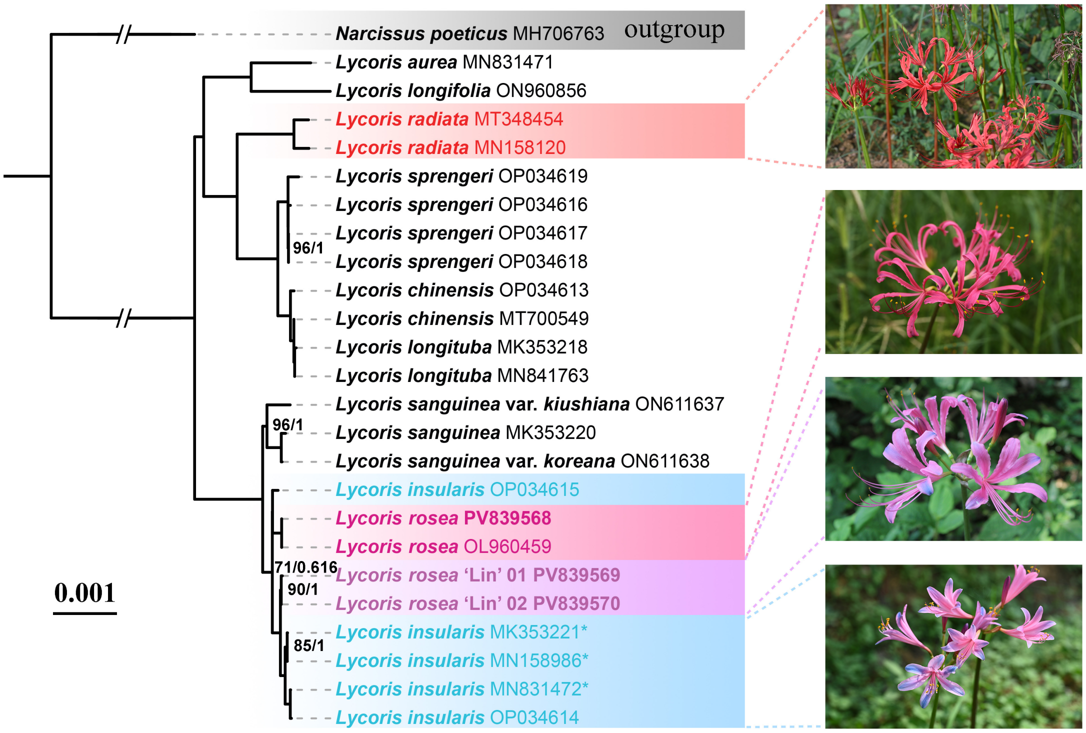

Figure 1: Phylogeny of 11 taxa in *Lycoris* Herb., based on the complete chloroplast genome. Numbers above branches are Maximum Likelihood bootstrap values (BS)/Bayesian posterior probability (BPP), unlabeled branches indicate support values of 100/1. The species name with accession numbers were download from NCBI. *showing those sequences which were misidentified as *L. insularis* in NCBI [10].

3 Results

3.1 The Origin of the *Lycoris haywardii* Bulbs

In the protologue of *Lycoris haywardii* [4] listed Japan as the place of origin. However, at the beginning of the same publication, Traub noted that Hayward had imported *Lycoris* bulbs from China between the early 1940s and 1948. After 1945, Hayward and others also imported numerous bulbs from Japan. Although *L. haywardii* was included among these imported materials, its precise geographic origin was not explicitly stated.

Caldwell [19,20] documented that in October 1948, he received three bulbs labeled "*L. incarnata*" from Hayward. These bulbs were part of a lot of approximately 100 bulbs purchased from Shanghai, China. After five years of cultivation, the plants flowered. Based on his observations, Caldwell considered this taxon closely related to *L. sprengeri*, with distinguishing features including less overlap at the base of the perianth segments, reduced recurving at the apex, lighter flower color, and a non-overlapping flowering period. It was from this population that Traub, honoring Hayward, formally described *L. haywardii*.

Hsu et al. [5] revised the taxonomic identity of *L. haywardii* based on specimens cultivated in Hangzhou Botanical Garden (voucher specimens: J. Z. Lin 002, 003; Z. Z. Yu 026). In agreement with Traub's assertion, they recognized the taxon as of cultivated origin and revised its distribution to "cultivated only." However, the voucher specimens cited in Hsu et al.'s revision are currently untraceable, and the evidence supporting the amended distribution remains unverified.

Lin et al. [21] reported results from an artificial hybridization experiment conducted in 1984 between *L. radiata* var. *pumila* and *L. sprengeri*. The F1 generation exhibited phenotypic traits highly similar to *L. rosea*. Morphological, phenological, vegetative (leaf shape, leaf color, bulb morphology), and karyotypic characteristics of *L. rosea* 'Lin' were consistent with those of *L. rosea* [22]. This supports the hypothesis that both taxa likely originated from a natural hybridization event between *L. radiata* var. *pumila* and *L. sprengeri*. This may have been a key reason why Hsu et al. [5] revised the distribution of *L. haywardii* Traub to cultivated status only.

Notably, according to Lin et al. [23] and Lin [24], both *L. rosea* 'Lin' and *L. rosea* were originally collected from Hangzhou, Zhejiang Province, China.

3.2 Morphological Comparison

Table 1 summarizes the comparative morphological characteristics described by Traub [4], Caldwell [19], Hsu et al. [5], and those observed in *L. rosea* 'Lin'. Fig. 2 shows photographs taken by Caldwell in 1957 of *L. sprengeri* and *L. haywardii* cultivated in Nashville, Tennessee.

Hsu et al. [5] conducted a taxonomic revision of *L. haywardii* based on a cultivated population at the Hangzhou Botanical Garden. They revised the leaf emergence period from spring (as originally described by Traub) to autumn. Additionally, Hsu et al. noted that the stamens of voucher specimens were prominently exserted beyond the perianth, indicating bilateral floral symmetry. According to Traub [4], *L. haywardii* exhibits spring-emerging leaves and actinomorphic (radially symmetrical) flowers, while Hsu et al. [5] reported autumn-emerging leaves and zygomorphic (bilaterally symmetrical) flowers in the revised concept of *L. haywardii*. These differences are taxonomically significant.

Currently, the cultivated *L. rosea* 'Lin' at Hangzhou Botanical Garden (referenced in Table 1) displays a smaller flowering bulb diameter (~2 cm), shorter but broader leaves (30–40 cm in length, 1.2–1.4 cm in width), and a typical bilaterally symmetrical floral morphology. The flower color is darker (deep purple-pink), the scape is taller (60–70 cm), the spathe is longer (4–4.5 cm), and the number of flowers per umbel is greater (6–8). The perianth segments are also longer, measuring approximately 5.5–6 cm.

Table 1: Comparative Morphological Characteristics of *L. haywardii* and *L. rosea* 'Lin'.

Character	***L. haywardii* Traub [4,19]**	***L. haywardii* Traub [5]**	***L. rosea* 'Lin'**
Bulb size	3/4—1 1/8 inch (1.89–2.86 cm)	—	2 cm
Pale midrib on leaf blade	Absent	—	Absent
Leaf emergence period	Late January to early February	Autumn	November
Leaf color	Deep green, slightly glaucescent	Deep green, slightly glaucescent	Greyish olive green
Leaf length	46–48 cm	48 cm	30–40 cm
Leaf width	8–9 mm (middle part)	7–11 mm	12–14 mm

Table 1: *Cont.*

Character	*L. haywardii* Traub [4,19]	*L. haywardii* Traub [5]	*L. rosea* 'Lin'
Leaf apex shape	Rounded obtuse	—	Rounded obtuse
Flower symmetry	Actinomorphic (radially symmetrical)	Actinomorphic	Zygomorphic
Flower color	Orchid purple	Reddish violet	Deep purple pink
Flowering period	July to mid-August	July–August	July–August
Scape height	46–48 cm	—	60–70 cm
Spathe length	3.7 cm	—	4–4.5 cm
Number of flowers per umbel	4–5	—	6–8
Perianth length	4.2–5.5 cm	4.4–5.5 cm	5.5–6 cm
Perianth width	1–1.1 cm	1–1.1 cm	1.1–1.2 cm
Corona tube length	1.1 cm	1.1–1.3 cm	1–1.2 cm
Stamen length	Slightly shorter than perianth segments	Slightly shorter than perianth segments	Ca. 1/6 longer than perianth
Pistil length	Slightly longer than perianth segments	Slightly longer than perianth segments	Longer than perianth
Flower diameter	2 3/4 inch (7 cm)	—	6–7 cm
Fertility	Fertile	—	Fertile

Figure 2: *L. sprengeri* (**left**) and *L. haywardii* (**right**) cultivated by Caldwell in Nashville, Tennessee (photographed in 1957).

3.3 Characteristics of the Complete Chloroplast Genome

The complete chloroplast genome of *L. rosea* 'Lin' was determined to be 158,472–158,478 base pairs in length (Figs. 1 and 3), with an overall GC content of 37.80%. The genome exhibited a typical quadripartite structure consisting of a pair of inverted repeats (IRs), a large single-copy (LSC) region, and a small single-copy (SSC) region, measuring 26,828 bp, 86,278 bp, and 18,541 bp, respectively. A total of 112 unique genes were annotated, including 78 protein-coding genes, 30 tRNA genes, and 4 rRNA genes.

Using *Narcissus poeticus* as the outgroup, a phylogenetic tree was reconstructed based on the complete chloroplast genome sequences of *L. rosea* 'Lin' and 11 other *Lycoris* taxa (Fig. 1). The genus *Lycoris* was divided into two major clades. The first clade comprised *L. aurea*, *L. longifolia*, *L. radiata*, *L. sprengeri*, *L. chinensis* and *L. longituba*, while the second clade included *L. sanguinea*, *L. rosea*, *L. rosea* 'Lin', and *L. insularis*. Notably, the publicly available *L. rosea* plastome (GenBank accession: OL960459) clustered with

L. rosea, *L. rosea* 'Lin', and *L. insularis* in a strongly supported monophyletic group (Bootstrap support = 1.00, Bayesian posterior probability = 100).

Given that chloroplast genomes in *Lycoris* (as in most angiosperms) are maternally inherited [10], the phylogenetic topology suggests that *L. insularis* is the maternal parent of both *L. rosea* and *L. rosea* 'Lin'.

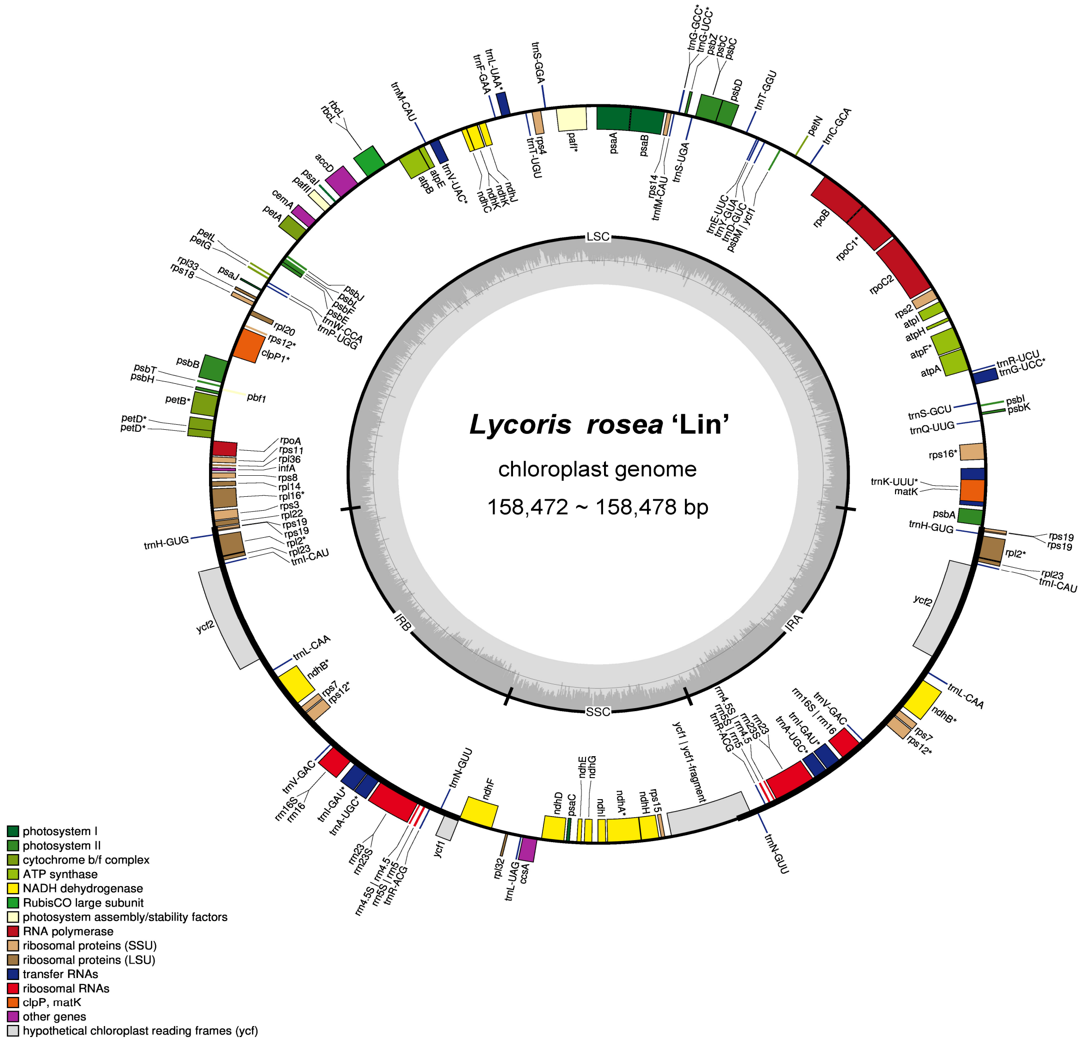

Figure 3: Plastid genome map of *L. rosea* 'Lin'. Genes marked with an asterisk (*) harbor a single intron.

3.4 Taxonomic Revision of Lycoris haywardii

L. rosea was first published in 1949 by Traub and Moldenke [25] in *Amaryllidaceae: Tribe Amarylleae*, and was classified under subgenus *Eulycoris*. The authors established this taxon based on the description of a variant group of *L. radiata* provided by Worsley [26]. The original diagnosis was relatively brief: the leaves are much broader than those of *L. radiata*, the umbel contains five flowers, the flowers are larger and pink in color, and the perianth segments are ascending and spreading. Chromosome number was unknown, and the distribution was reported as East Asia. No type specimen was designated.

Worsley [26] considered the taxon to possess intermediate traits between *L. albiflora* and *L. straminea*, and suggested a probable hybrid origin. Both the *Flora Reipublicae Popularis Sinicae* and *Flora of China* have recognized this species, listing its native range as Jiangsu and Zhejiang provinces, with the type locality reported as Shanghai.

Shi et al. [27] conducted sequence comparisons of the internal transcribed spacer (ITS) region of the nuclear genome and provided molecular evidence supporting the hypothesis that both *L. rosea* and *L. rosea* 'Lin' are hybrid derivatives of *L. radiata* var. *pumila* and *L. sprengeri*.

Comparative analysis of chloroplast genome structures further supports their close relationship. *L. rosea* 'Lin' and *L. rosea* exhibit identical lengths in their inverted repeat (IR) and small single-copy (SSC) regions, measuring 26,828 bp and 18,541 bp, respectively. They also share an identical GC content of 37.8%. However, significant differences exist in the total number of genes, protein-coding genes, and tRNA gene content. *L. rosea* harbors 133 genes, including 87 protein-coding genes, 38 tRNA genes, and 4 rRNA genes, whereas *L. rosea* 'Lin' contains 112 genes, with 78 protein-coding genes, 30 tRNA genes, and 4 rRNA genes [28].

Morphologically, *L. rosea* and *L. rosea* 'Lin' are also remarkably similar, as evidenced by Table 1 and Fig. 4.

Figure 4: *L. rosea* 'Lin' (**left**) and *L. rosea* (**right**).

4 Discussion

When *Lycoris haywardii* was described by Traub in 1957, its habitat was recorded as Japan. However, in the same journal issue, Caldwell provided a detailed morphological and phenological description of the species, stating its origin as Shanghai. Both authors had received their bulbs from the same source, Hayward. Adams [6] later considered *L. haywardii* to be distributed in both Japan and China. All three sources—Traub [4], Caldwell [19], and Adams [6]—consistently documented spring leaf emergence and stamens that were slightly shorter than the perianth segments.

In contrast, Hsu et al. [5] revised the taxonomic identity of *L. haywardii* based on a cultivated population at Hangzhou Botanical Garden, which is now known as *L. rosea* 'Lin'. They modified the phenology, reporting autumn leaf emergence, restricted the distribution to cultivated material only, and noted prominently exserted stamens extending beyond the perianth, indicating clear morphological divergence. Evidently, the plant materials used by Hsu et al. [5], i.e., *L. rosea* 'Lin', are not conspecific with the taxon described by Traub [4], Caldwell [19], or Adams [6].

The confusion between *L. haywardii* and *L. rosea* 'Lin' may partly stem from their shared chromosome number and fertility. Bose [29] reported the karyotype of *L. haywardii* as 2n = 22 = 16B + 2B+ 4C (=22A), including four satellited chromosomes with proximal centromeres. Similarly, Xu et al. [30] and Liu & Xu [31] documented the karyotype of *L. rosea* 'Lin' as 2n = 22, consistent with Bose's findings. Both taxa are self-fertile. Phylogenetic analyses based on inter-simple sequence repeat (ISSR) molecular markers conducted by Shi et al. [27] also confirmed a close genetic relationship between *L. rosea* and *L. rosea* 'Lin'.

Taken together, morphological, cytological, and molecular evidence all support the conclusion that *L. haywardii* and *L. rosea* 'Lin' are distinct taxa. Both *L. rosea* 'Lin' and *L. rosea* are of hybrid origin, likely derived from hybridization between *L. radiata* var. *pumila* and *L. insularis*. Therefore, it is taxonomically more accurate and scientifically justified to regard the populations currently referred to as *L. haywardii* by Hsu et al. [5] as a cultivar of *L. rosea*, under the name *L. rosea* 'Lin'.

L. rosea 'Lin' P. C. Zhang, S. Y. Zhang & Y. H. Zheng, stat. nov.

Herbs perennial. Bulbs subglobe, Ca. 3–4 cm in diam. Leaves appearing in late Autumn, ligulate, Ca. 30 × 0.7–1.3 cm, apex abtuse. Peduncle solid Ca. 60 cm, umbel 4–8 flowered. Spathe-valves 2, lanceolate, Ca. 3.5 × 1.5 cm. Perianth zygomorphic, red-purple and blue at the tip, tube 1–1.3 cm, lobes oblanceolate, Ca. 4.5–5.5 × 1 cm, margin slightly undulate, apex moderately recurved. Stamens distinctly longer than perianth, Ca. 6 cm, filament red. Style long, filiform, stigma capitate, minute. Flowering late July to mid-August, capsule membranous, loculicidally 3-valved after one and a half months of flowering, seeds few, turgid, testa black, opaque.

Karyotype: 2n = 22 [30,31].

Distribution: Cultivated in Hangzhou Botanical Garden.

Specimens: Holotype: HHBG077679, Isotype: HHBG077680.

Notes: The epithet of cultivar is in honor of Ms. Lin Jinzhen.

5 Conclusions

Combined with morphological traits, phenological characteristics, karyotype, and chloroplast genome data, *L. haywardii* Traub, which is known only from cultivation in Hangzhou Botanical Garden, is revised as *L. rosea* 'Lin'. It has red-purple flowers with blue in the tips. As with *L. rosea*, it is a fall-leaf species with a flowering period from July to mid-August. Artificial hybridization confirmed that it originated from L. radiata var. pumila and L. *insularis*. Its chromosome number is 2n = 22. Chloroplast genome sequencing showed *L. rosea* 'Lin' and *L. rosea* exhibit identical lengths in their inverted repeat (IR) and small single-copy (SSC) regions and share an identical GC content.

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Availability of Data and Materials: The authors confirm that the data supporting the findings of this study are available within the article.

Ethics Approval: Not Applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

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