Research paper

Two new species of *Yushania* (Poaceae: Bambusoideae) from South China, with a taxonomic revision of related species

Xia-Ying Ye a, b, Yu-Xiao Zhang c, De-Zhu Li a, *

a Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, China

b Agronomy and Life Science Department, Zhaotong University, Zhaotong, Yunnan 657000, China

c Yunnan Academy of Biodiversity, Southwest Forestry University, Kunming, Yunnan 650224, China

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**A B S T R A C T**

Two new species of *Yushania* (Poaceae, Bambusoideae, Arundinarieae) are described and illustrated from Hunan, China. *Yushania longshanensis* D.Z. Li & X.Y. Ye is distinguished from related species (*Y. confusa*, *Y. angustifolia* and *Y. pachyclada*) by having a thinner culm (0.2–0.3 cm in diameter), glabrous sheath scar, no oral setae, a large glabrous leaf blade (10–20 × 0.9–1.3 cm) and 3–4 pairs of secondary veins. *Yushania stoloniforma* D.Z. Li & X.Y. Ye has a distinctive scrambling habit, which differs from its putative close allies. Both of these two new species have a solitary branch at the basal nodes and can be assigned to *Yushania* sect. *Yushania* based on morphological features. Additionally, we treated *Yushania gigantea* T.P. Yi & L. Yang as a new synonym of *Y. elevata* T.P. Yi and renamed *Y. microphylla* T.P. Yi & L. Yang as *Y. weiningensis* D.Z. Li & X.Y. Ye.

**1. Introduction**

*Yushania* P.C. Keng (1957) belongs to the subtribe Arundinarieae and is one of the most species-rich genera in the temperate woody bamboos (Poaceae, Bambusoideae) (Li et al., 2006; Vorontsova et al., 2017; Yi et al., 2008; Zhang et al., 2020). Species of *Yushania*, which are mainly distributed in China but also in the Himalayas, Indo-China and the Philippines, are morphologically diverse, shrubby or arborescent bamboos, with culm height ranging from 0.35 m to 7 m (Li et al., 2006). *Yushania* have long necked pachymorph rhizomes (up to 100 cm), branches at each node range from solitary to many, and some of which are as thick as the culm or have no secondary branches. The inflorescence is semelaucant, open and paniculate, with three stamens. *Yushania* was previously divided into two sections based on culm height and branch number: *Yushania* sect. *Brevipaniculatae* T.P. Yi and Y. sect. *Yushania* (Yi, 1986, 1995). Section *Brevipaniculatae* is characterized by taller culms, many and subequal branches at each node, which are usually thinner than the culm, and terminal racemes or panicles. In contrast, species of section *Yushania* are shorter and have only one branch at each node or one branch at lower nodes but more than three branches at upper nodes; the diameter of branches are usually as thick as culms when only one at the node, and terminal panicles.

*Yushania* is distributed in the mid-elevation and subalpine mountain areas, from low hills at 500 m to high elevation mountains (up to 3800 m), and its center of diversity is in Southwest China (Keng and Wang, 1996; Li et al., 2006; Ohrnberger, 1999; Vorontsova et al., 2017; Yi, 2000; Yi et al., 2008). The species of *Yushania* are ecologically important because they play a role in water and soil conservation and provide food and habitat for many endangered animals, including the giant panda (*Yi and Jiang, 2010*).

Because of infrequent flowering (Janzen, 1976), the inflorescence of only 11 species of *Yushania* have been hitherto described; thus, most of the taxa are described based on the vegetative morphology (Li et al., 2006; Yang and Yi, 2013, 2014; Yi et al., 2008; Yi and Yang, 2016; Zhang et al., 2019). In 2015, several species in *Yushania* without flowers were collected by the authors during field investigations in Hunan Province, south-central China. The morphological character of several taxa could not be matched to any described species, and molecular analyses demonstrated that their positions on phylogenetic trees were unique (Ye et al., 2019). Here, we described two new species (referred to as *Y. sp.3* and *Y. sp.4*, respectively, in Ye et al., 2019) based on the morphological and phylogenetic evidence, with comments on morphologically
and phylogenetically related species. In addition, we revised the taxonomy of two *Yushania* species based on morphological comparisons in the field and herbaria, and our phylogenetic results.

### 2. Materials and methods

Molecular phylogeny of *Yushania* was reconstructed based on ddRAD-seq data (Ye et al., 2019). Measurements and morphological character assessments of the putative new species were carried out on living plants in the field and herbarium specimens. Related species were chosen from morphological comparisons and phylogenetic results, with the morphological features of these species culled from specimens and descriptions in previous studies (Keng and Wang, 1996; Li et al., 2006; Yi et al., 2008).

### 3. Results

In the ddRAD phylogeny of alpine bamboos with a broad sampling, *Yushania* is represented by 74 samples of 70 species covering 87.5% of the global species. A simplified phylogeny of *Yushania* is presented in Fig. 1, showing the phylogenetic position of the putative new species and *Y. tongpeii* D.Z. Li, Y.X. Zhang & E.D. Liu, a species described recently based on the vegetative morphology (Zhang et al., 2019).

#### 3.1. Taxonomic treatment

**Yushania longshanensis** D.Z. Li & X.Y. Ye, sp. nov.

Figs. 2—4.

**Diagnosis.** Similar to *Yushania confusa* (McClure) Z.P. Wang & G.H. Ye, *Y. angustifolia* T.P. Yi & J.Y. Shi and *Y. pachyclada* T.P. Yi, but differs by having a thinner culm with only 0.2—0.3 cm in diameter, glabrous sheath scar, oral setae absent, longer leaf blade (up to 20 cm) and fewer secondary veins.

**Type.** CHINA, Hunan, Longshan County, Da’an Township, Wanbaoshan Forest Farm Department, 29°34′10″N, 109°40′15″E, 1256 m, 19 July 2015, X.Y. Ye & J.X. Liu YXY222 (holotype & isotype: KUN!).

**Description.** Rhizomes pachymorph, culm neck 18—30 cm long, 0.3—0.4 cm in diameter, solid. Shrubby bamboo, 1—1.5 m tall, 0.2—0.3 cm in diameter; internodes terete, 12—23 cm long, initially sparsely purple spotted, with a white powdery ring below nodes, glabrous, nearly solid; nodes with weakly prominent supra-nodal ridge; sheath scar prominent, with persistent remains of sheath base. Branches 1 at lower nodes, up to 80 cm long, 3 at upper nodes, bearing secondary branches or sometimes none. Culm sheaths persistent, yellow-brown, 1/4—1/3 as long as internode, cartilaginous, sparsely yellow-brown setose, readily deciduous, margins brown setose; auricles and oral setae absent; ligules truncate, ca. 1 mm; blades reflexed, linear-lanceolate, deciduous. Foliage leaves 2—4 per ultimate branch; sheaths 3—5 cm long, glabrous, margins glabrous; auricles and oral setae absent or 2—3, deciduous; ligules truncate, ca. 1 mm; petioles 2—6 mm long, glabrous; blades lanceolate, 10—20 × 0.9—1.3 cm, wavy when dry, glabrous, secondary veins 3—4 pairs, transverse veins conspicuous, apex tapering, base cuneate, margins serrate. Fertilization unknown.

**Phenology.** New shoots June to July.

**Etymology.** The specific epithet refers to the type locality, Longshan county.

**Vernacular name.** 龙山玉山竹 (Chinese Pin-Yin transliteration); 龍山玉山竹 (Chinese name).

**Distribution and habitat.** To date, this species is only found in Longshan County, northwest Hunan, China. This species grows with miscellaneous shrubs (Fig. 2A) from 1200 m to 1300 m in the Wanbaoshan Forest Farm.

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**Fig. 1.** The simplified phylogeny of *Yushania* based on ddRAD-seq data (adapted from Ye et al., 2019), highlighting the position of the two putative new species and *Y. tongpeii*, a species described recently.
Yushania weiningensis D.Z. Li & X.Y. Ye, nom. nov.

Yushania microphylla T.P. Yi & L. Yang, J. Bamboo Res., 32: 5. 2013. nom. illeg.

Type: CHINA. Guizhou, Weining County, Xiaohai Town, Xiaozhangguan Village, 26°56′29″N, 104°4′17″E, 2300 m, 15 November 2005, Yi Tongpei 05111 (holotype, SIFS). Non Y. microphylla (Munro) R.B. Majumdar in S. Karthikeyan & al., Fl. Ind. Enum. – Monocot.: 283 (1989); non Y. microphylla (Munro) Ohnhr., Bamboos of the World Intro. 2 10 (1996). Isonym: Arundinaria microphylla Munro, Trans. Linn. Soc. London 26(1): 32 (1868).

Distribution. To date, this species is only found in Weining, Guizhou, China.

Notes. Yang and Yi described a new Yushania species from Guizhou, China, in 2013, named as Y. microphylla T.P. Yi & L. Yang (Yang and Yi, 2013). However, we found that this name (Y. microphylla (Munro) R.B. Majumdar) has been used to describe a small and shrubby bamboo distributed in northeast India, Sikkim, Khasi Hills in Meghalaya and Bhutan (Munro, 1868; Noltie, 2000; Seethalakshmi and Muktesh Kumar, 1998; Stapleton, 1994; Vorontsova et al., 2017). According to the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), Y. microphylla T.P. Yi & L. Yang is a later homonym and is illegitimate. This species was sister to Yushania maculata T.P. Yi in phylogenetic trees (Ye et al., 2019). We confirmed that Y. microphylla T.P. Yi & L. Yang is an independent species after morphological comparisons of closely related species (Table 3). Therefore, we propose Y. weiningensis D.Z. Li & X.Y. Ye as a new name for Y. microphylla T.P. Yi & L. Yang. The specific epithet of the new name refers to the type locality, Weining County.

Specimens examined. CHINA, Guizhou, Weining County, Xiaohai Town, Xiaozhangguan Village, 26°56′46″N, 104°4′58″E, 2363 m, 13 May 2015, X.Y. Ye & M.Y. Zhou YXY180 (KUN!).

Yushania elevata T.P. Yi

Yushania elevata T.P. Yi, J. Bamboo Res., 5 (1): 17. 1986. Type: CHINA. Yunnan, Tengchong County, 20 August 1983, Yi Tongpei 83142 (holotype, SIFS!).

Yushania gigantea T.P. Yi & L. Yang, Bull. Bot. Res., 31 (1): 1. 2014. Syn. nov. Type: CHINA. Yunnan, Lushui County, 25°58′47″N, 98°39′41″E, 2300 m, 26 October 2005, Yi Tongpei 05080 (holotype, SIFS).
Description. Culm neck to 70 cm; internodes solid. Culms 4–7 m, 1.4–6 cm in diameter; internodes terete, 15–60 cm, glabrous or initially brown setulose below nodes; wall 3–8 mm thick; nodes with weakly prominent to prominent supra-nodal ridge; sheath scar prominent, initially brown setose. Branches 8–20, solid or nearly so. Culm sheaths persistent or gradually deciduous, narrowly triangular, ca. 1/2–2/3 as long as internodes, leathery to cartilaginous, densely yellow-brown woolly setose, margins densely brown setose, longitudinal ribs prominent; auri- cles absent; oral setae absent or gradually deciduous; ligules convex or rarely truncate, 1–2 mm tall, glabrous; blades linear-lanceolate, 2–7 × 0.3–0.6 cm, revolute, glabrous. Foliage leaves
Fig. 4. *Yushania longshanensis* D.Z. Li & X.Y. Ye. **A.** Individual **B.** Branches at the upper nodes **C.** Culm sheaths with sparsely yellow-brown setose **D.** Foliage leaves **E.** Leaf sheaths.
4–7 per ultimate branch; sheaths 2–5.5 cm long, longitudinal ribs prominent, glabrous; auricles absent; oral setae absent or several, erect or curved, brown, 0.5–6 mm; ligules convex, 0.5–1 mm tall, glabrous; petioles 1–2.5 mm long, glabrous; blades narrowly lanceolate, 3.5–20 × 0.4–1.8 cm, glabrous, secondary veins 2–4 pairs, transverse veins distinct, base cuneate, one margin serrulate, another margin smooth, apex acuminate.

**Phenology.** New shoots July.

**Distribution and habitat.** *Yushania elevata* occurs under the broadleaved forest or *Pinus yunnanensis* Franch. forest in western Yunnan, at the elevations of 2000–2300 m.

**Notes.** *Yushania gigantea* was described in 2014 by Yang and Yi (2014), and included in our phylogenetic analyses based on dRAD-seq data (Ye et al., 2019). Results show that this species is sister to *Y. elevata* and obtained 100% bootstrap support. Morphological comparison of the two species revealed that they were very similar, differing only in two ambiguous features: *Y. gigantea* has persistent culm sheaths and a longer leaf blade (3.5–20 cm), whereas *Y. elevata* is tardily deciduous and has a shorter leaf blade (4.5–9.5 cm) (Keng and Wang, 1996; Li et al., 2006; Yang and Yi, 2014). Most *Yushania* species are short and shrubby; only few can grow into arboreal plants (about six species). Moreover, the holotype specimen of *Y. gigantea* was collected from Lushui, western Yunnan, China, at an elevation of 2300 m, which is in the distribution range of *Y. elevata* (2000–2300 m in western Yunnan) (Keng and Wang, 1996; Li et al., 2006). It is unlikely that two arboreal species occur in a narrow area. Together with their close relationship and similar morphology, we conclude that *Y. gigantea* and *Y. elevata* are conspecific, and *Y. gigantea* is treated to be a new synonym of *Y. elevata*.

**Specimens examined.** CHINA, Yunnan, Lushui County, Wuzhong Village, 26°07′03″N, 98°35′43″E, 2061 m, 8 May 2011, ZXZ11010 (KUN!); CHINA, Yunnan, Lushui County, Wuzhong Village, 26°03′12″N, 98°36′53″E, 2206 m, 8 May 2011, ZXZ11012 (KUN!); CHINA, Yunnan, Lushui County, along the Pianma Road between 72 and 73 km, 25°59′55″N, 98°39′39″E, 2429 m, 6 August 2014, X.Y. Ye & W.H. Wang XXY134 (KUN!).

### 4. Discussion

*Yushania longshanensis* (i.e., *Y. sp.3* in Fig. 2 in our previous work) (Ye et al., 2019) and *Y. stoloniforma* (i.e., *Y. sp.4* in Fig. 2 in our previous work) (Ye et al., 2019) are here assigned to *Yushania* sect. *Yushania* based on morphological features: solitary branch at the base nodes and three to five branches at the upper nodes, and culms with short or medium height.

*Yushania longshanensis* is most similar to *Y. angustifolia* and *Y. pachyclada* according to morphological characteristics, but can be distinguished by some subtle features: thinner culms (only 0.2–0.3 cm in diameter), sparsely yellow-brown setose, larger leaf blade and type of habitat where distributed. Moreover, molecular phylogenetic analyses indicate that *Y. longshanensis* is distantly related to *Y. angustifolia* (Ye et al., 2019). In addition, phylogenetic analysis shows that *Y. longshanensis* is related to *Y. stoloniforma* and *Y. confusa*. However, *Y. longshanensis* and *Y. stoloniforma* have different growth habit; furthermore, *Yushania longshanensis* and

**Table 1**

Morphological comparison of *Yushania longshanensis* and its related species.

| Character                           | *Yushania longshanensis* | *Y. confusa* | *Y. angustifolia* | *Y. pachyclada* |
|-------------------------------------|--------------------------|--------------|-------------------|-----------------|
| Culm height                         | 1.2–1.5 m                | 1.2–2 m      | 1.5–2 m           | 1.2–2 m         |
| Culm diameter                       | 0.2–0.3 cm               | 0.2–1 cm     | 0.5–0.7 cm        | 0.3–1 cm        |
| Internode                           | 12–23 cm long, a ring of white powder below nodes | 10–33 cm long, initially powdery white | (6) 16–22 cm long, a ring of white powder below nodes | 20–30 cm long, a ring of white powder below nodes |
| Branch complement                   | 1–3                      | 1–5          | 1–3               | 1–5             |
| Sheath scar                         | Prominent, glabrous, with persistent remains of sheath base | Prominent, initially yellow setose | Slightly prominent, glabrous | Prominent |
| Culm sheath                         | Cartilaginous, sparsely yellow-brown setose, margins setose | Leathery, brown setose, margins setose | Densely brown setose, densely ciliate | Leathery, usually glabrous, margins glabrous |
| Culm sheath oral setae              | Absent                   | Several, 1–2 mm long, readily deciduous | 1–2, 1–3 mm long, deciduous early | Absent |
| Culm sheath blade                   | Reflexed, linear-lanceolate, deciduous | Reflexed, linear-lanceolate or linear | Erect or reflected, linear-lanceolate, glabrous | Reflexed, conical or linear-lanceolate, glabrous |
| Leaf number of the ultimate branch  | 2–4                      | 2–5 (7)      | 4–8               | 2–5             |
| Leaf sheath                         | 3–5 cm long, glabrous, margins glabrous | (2) 3–6.5 cm long, glabrous, margins white-gray ciliate | Glabrous | – |
| Leaf oral setae                     | Absent or 2–3, deciduous | Several, 2–3 mm long, gray-yellow | 2–3, 3–8 mm long, erect, purple | Absent |
| Petiole                             | Glabrous                 | Densely pubescent, rarely glabrous | Glabrous | – |
| Leaf blade                          | 10–20 × 0.9–1.3 cm, glabrous, secondary veins 3–4 pairs | (3) 8–13 (21.5) × 0.6–1.5 (21) cm, abaxially basally gray hairy, secondary veins 4–6 pairs | 10–13 × 0.6–1 cm, glabrous, secondary veins 3–4 pairs | 6–14 × 1.1–2 cm, glabrous, secondary veins 4–6 pairs |
| Habitat                             | Growing with miscellaneous shrubs from 1200 m to 1300 m, Longshan, Hunan. | Widely distributed, usually under forest at elevations 1000–2300 m. | Cultivated, 1160 m, Guiyang, Guizhou. | Usually under broadleaved evergreen forest on mountain ridges, 1700–1800 m, southern Sichuan and northeastern Yunnan. |
Fig. 5. *Yushania stolonifera* D.Z. Li & X.Y. Ye. A. Individual, showing 1 branch at lower nodes and scrambling character. B. Branches, showing solitary branch at the basal nodes and three branches at the upper nodes. C. Culm sheath with falcate auricles. D. Leaf sheath, showing developed auricles and oral setae. E. Rhizome. F. Culms, showing branches and culm sheaths. G. Nearly solid internodes. H. Branchlet.
Y. confusa can be distinguished by the presence versus absence of hair on the sheath scar, petiole and leaf blade.

Yushania stoloniforma is morphologically similar to Y. pingshanensis and Y. actiaurita. They all have less than five branches at the node, medium culm height, prominent sheath scar, persistent culm sheath, several radiating culm sheath oral setae and reflexed culm sheath blade, but Y. stoloniforma can be easily distinguished from them by its different growth habit, the smaller leaf size and the different arrangement of the leaf blade. Phylogenetic topology indicates that Y. stoloniforma has a sister relationship with Y. confusa (Ye et al., 2019) although the two species have different morphological features, with Y. stoloniforma having scrambling growth habit, glabrous sheath scar, developed culm sheath auricles with radiating oral setae, and glabrous petiole and leaf blade.

Most species of Yushania are distributed in the Hengduan Mountains region and may have begun migrating southward during the late Pliocene (Ye et al., 2019). The migration route of Yushania passes through the Yunnan-Guizhou Plateau, adjacent to Hunan province. Therefore, the discovery of Y. longshanensis and Y. stoloniforma, which are endemic to the Hunan province, provides a means for studying the origin and diversification of Yushania, and may also help to understand the evolutionary history of bamboos distributed in southwestern China. In addition, the discovery of Y. longshanensis and Y. stoloniforma calls attention to these two ecologically important species, which play a role in soil protection and provide food and habitat for animals, including many endangered species.
Table 2

Morphological comparison of Yushania stoloniforma and its related species.

| Character                  | Yushania stoloniforma | Y. confusa | Y. pinghanensis | Y. auctiaurita |
|----------------------------|-----------------------|------------|-----------------|---------------|
| Clumps                     | Scrambling            | Erect      | Erect           | Erect         |
| Culm height                | 2–2.5 m               | 1–2 m      | 1.2–2 m         | 1–2.5 m       |
| Culm diameter              | 0.2–0.5 cm            | 0.2–1 cm   | 0.5–0.75 cm     | 0.3–0.8 cm    |
| Internode                  | 16–28 cm long, sparsely white powder with a densely ring below node, nearly solid | 10–33 cm long, initially white powder, nearly solid | 13–35 cm long, a ring of white powder below nodes, wall 1.5–2.5 mm thick | 16–22 cm long, white powder below nodes, wall 1–3 mm thick |
| Branch complement          | 1–5                   | 1–5        | 1–3             | 1–3           |
| Sheath scar                | Glabrous, with persistent remains of sheath base | Initially yellow setose | Glabrous | Initially retrorsely brown setose, with persistent remains of sheath base |
| Culm sheath                | Persistent or tardily deciduous, leathery, brown setose, margins setose | Persistent, leathery, brown setose, margins setose | Persistent, densely light yellow verrucose setose abaxially, margins densely ciliate | Persistent, cartilaginous, yellow-brown setose, margins densely ciliate |
| Culm sheath auricle        | Falcate               | Absent     | Small, oblong or falcate | Falcate, large |
| Culm sheath oral setae     | 4–7, 3–4 mm long, radiating | Several, 1–2 mm, readily deciduous | 3–5, 3–6 mm long | Many, 3–6 mm long, radiating, yellow-brown |
| Culm sheath ligule         | Truncate, ca. 1 mm    | Truncate, ca. 1 mm | Truncate or arcuate, ca. 0.6 mm | Arcuate, ca. 0.5 mm |
| Culm sheath blade          | Erect or reflexed, linear-lanceolate | Reflexed, linear-lanceolate or linear | Reflexed, triangular-linear or linear-lanceolate | Erect or decumbent, narrowly triangular or lanceolate, glabrous, margins serratulate 3–8 |
| Leaf number of the ultimate branch | 5–6                   | 2–5 (7)    | 5–9             |              |
| Leaf sheath                | 2–4 cm long, glabrous, margins white ciliolate | (2) 3–6.5 cm long, glabrous, margins white-gray ciliolate | 5.2–6.5 cm long, glabrous, margins glabrous | Glabrous or gray pubescent, apically white powder, margins yellow-brown ciliolate |
| Leaf auricle               | Elliptic              | Absent     | Small, purple   | Falcate, large |
| Leaf oral setae            | Several, 2–5 mm long, yellow, radiating | 2–5 mm long | 4–8, yellow, 3–8 mm long | Many, 2–7 mm long |
| Leaf ligule                | Truncate, ca. 1 mm   | Truncate, glabrous, ca. 1 mm | Truncate, glabrous, ca. 0.3 mm | Arcuate, ca. 1 mm |
| Petiole                    | Glabrous              | Densely pubescent, rarely glabrous | Glabrous | Abaxially occasionally white powder |
| Leaf blade                 | 5–11 × 0.7–1.5 cm, glabrous, secondary veins 3–4 pairs | (3.8–13 (21.5) × 0.6–1.5 (2.1) cm, abaxially basally gray hairy, secondary veins 4–6 pairs | 9–17 × 1.3–2.2 cm, glabrous, secondary veins 6–8 pairs | 8–16 × 1.3–3 cm, glabrous, secondary veins 5–9 pairs |
| Habitat                    | Under the cultivated fir forest, 1100 m, Longshan, Hunan. | Widely distributed, usually under forest at elevations of 1000–2300 m. | Under broadleaved evergreen forest on mountain ridges, 1500–2000 m, Pingshan, Sichuan. | Under broadleaved forest, 1700–1800 m, southeast Guizhou. |

Table 3

Morphological comparison of Yushania weiningensis, Y. microphylla and Y. maculata.

| Character                  | Yushania weiningensis | Y. microphylla | Y. maculata |
|----------------------------|-----------------------|----------------|-------------|
| Culm neck                  | Solid                 | Hollow         | Solid       |
| Culm height                | 3–4 (5) m             | 1.2 m          | 2–3.5 m     |
| Internode                  | (10)28/ (35) cm, glabrous, initially white powdry | ca. 7 cm long, glabrous | 10–30 (40) cm, brown or light yellow setose, initially densely white powder |
| Nodal sheath scar          | Weakly prominent      | Prominent      | Level or weakly prominent |
| Branches                   | 5–8                   | Many           | 7–12        |
| Leaf sheath                | Striate, light-green, glabrous | Striate, dark, scabrous, fimbriate at the top | Glabrous |
| Leaf blade                 | 3.8–8.5 × 0.4–0.7 cm, linear-lanceolate, apex acuminate, secondary veins 2–3 pairs | 3 × 0.3 cm, linear-lanceolate, acute; secondary veins 2 pairs, inconspicuous | 9–15 × 0.9–1.1 cm, linear-lanceolate, apex acuminate, secondary veins 4 pairs |
| Distribution               | Weining, Guizhou, China | Bhutan and India | Southwest Sichuan, northeast Yunnan, China |

Author contributions

XYY conducted the field and phylogenetic work and drafted this paper; YXZ revised the draft; DZL conceived and wrote this paper.

Declaration of competing interest

The authors have no conflicts of interest to declare.

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