

On the occurrence of asymmetrical underleaves associated with left-right symmetry in *Spruceanthus mamillilobulus* (Herzog) Verd. (Lejeuneaceae), a little-known species from China and Vietnam

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Spruceanthus mamillilobulus (Herzog) Verd., a rare species previously known only from China, is reported here for the first time from Vietnam. Sexual organs and asymmetric base of the underleaf, auriculate on one side and cuneate on the opposite side are described for the first time. Detailed description, illustration, and a distribution map of *S. mamillilobulus* are provided.

Keywords: China, Distribution, Ptychanthoideae, *Spruceanthus mamillilobulus*, Vietnam

Introduction

Spruceanthus mamillilobulus (Lejeuneaceae) was first described by Herzog as *Ptychanthus mamillilobulus* Herzog (Nicholson *et al.*, 1930) based on sterile material from Guizhou province, southwest China. Verdoorn (1936) subsequently transferred the species to the genus *Spruceanthus*, as *S. mamillilobulus* (Herzog) Verd. The species has long remained known only from the type material from Guizhou province (Piippo, 1990; He, 1997; Zhang & Chen, 2006) and its taxonomic affinities remained unclear due to the lack of information on reproductive structures, oil bodies, etc. Recently, additional collections of *S. mamillilobulus* were made in the provinces of Guangdong and Guangxi, China (Wang, 2010; Jia & He, 2013), and, in October 2013, in northern Vietnam (Cao Bằng and Hà Giang provinces). The plants from Guangdong and Guangxi were sterile or with immature gynoecia, but those from northern Vietnam were copiously fertile, containing androecia and mature perianths. Based on the new collections, a first detailed description of *S. mamillilobulus*, including characters of oil bodies and gametoecia, is provided.

Taxonomic Description

Spruceanthus mamillilobulus (Herzog) Verd., Hep. Select. Crit. 9, n. 447. 1936. (Figures 1–2) ≡ *Ptychanthus mamillilobulus* Herzog, in Handel-Mazzetti, Symb. Sin. 5: 44. 1930. Type: Guizhou, 'Auf Walderde (Konglomerat) in der str. St. beim Tempel Yanggumiao nächst Gudschou', 300 m, 20 July 1917, *Handel-Mazzetti 10867* (holotype: JE n.v.; isotype: JE (2 Packets n.v.), W!).

Plants dull green when fresh, becoming pale yellowish when dry, shoots to *ca* 4 cm long and 3.7 mm wide, pinnately branched, branching of the *Lejeunea*-type, curved microphyllous branches present at bases of stems and branches. *Stems* 160–255 µm in diameter, in transverse section with 26–29 epidermal cells and 66–87 medullary cells, epidermal cells slightly larger and thinner-walled than medullary cells; ventral merophyte *ca* 9 cells wide. *Rhizoids* at base of underleaves, tufted, brown, primary rhizoid disc usually present. *Leaves* imbricate, widely spreading when moist, diverging from stem at an angle of *ca* 90°, sometimes becoming falcate; leaf lobes oblong-ovate, 0.8–2.1 mm long, 0.44–1.40 mm wide, ventral margin usually upcurved, entire, dorsal margin slightly arched and auriculate at base, entire, apex usually acute-apiculate, sometimes rounded, irregularly dentate to nearly entire; leaf lobules small, oblong-ovate, $\frac{1}{7}$ – $\frac{1}{9}$ as long

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Figure 1 *Spruceanthus mamillilobulus* (Herzog) Verd. (A) Habit. (B) Median leaf cells, showing homogeneous, *Massula*-type oil bodies. A taken from R.-L. Zhu et al. 20131029-222; B from Y.-M. Wei & T. Peng 20100917-28.

as the lobes, usually strongly inflated in the basal half and forming a rounded sac, occasionally reduced, apex obliquely truncate, free margin with 1–3 one-celled teeth, hyaline papilla at the proximal side of the first tooth, oblong, $28\text{--}40 \times 10\text{--}14 \mu\text{m}$; keel almost straight and forming an almost straight or slightly curved line with the ventral margin of the leaf lobe (angle with ventral leaf margin *ca* 170°). Cells of leaf lobe distinctly longer than wide, trigones small to medium, simple-triangular or radiate, intermediate thickenings frequent, 2 on each long cell wall, marginal cells subquadrate to rectangular, $14\text{--}30 \times 8\text{--}18 \mu\text{m}$, median cells hexagonal, $24\text{--}60 \times 20\text{--}30 \mu\text{m}$, basal cells $34\text{--}68 \times 24\text{--}40 \mu\text{m}$. Oil bodies 25–65 per cell, homogeneous, *Massula*-type, ellipsoid or fusiform, $3.5\text{--}7.3 \times 1.2\text{--}3.0 \mu\text{m}$. Ocelli absent. Underleaves imbricate, appressed to the stem, broadly ovate to oblong, $0.60\text{--}0.98 \text{ mm}$ long, $0.34\text{--}0.84 \text{ mm}$ wide, 3–5 times as wide as the stem, apex broadly rounded to truncate, or retuse to very shallowly bilobed, dentate or entire, lateral margin narrowly recurved, bases asymmetrical, shortly auriculate on one side and cuneate on the opposite side in a left–right symmetric pattern, bases free from the leaf base, insertion line shallowly curved.

Autoicous. Androecia on long branches, usually intercalary, bracts in 4–7 pairs, loosely imbricate, hypostatic, obliquely spreading, shallowly bilobed, bract lobe $0.4\text{--}0.5 \text{ mm}$ long, $0.26\text{--}0.34 \text{ mm}$ wide, bract lobule $\frac{2}{3}\text{--}\frac{4}{5}$ as long as the bract lobe, keel arched, bracteoles 4–7, similar to underleaves in shape and size, borne throughout the androecia. Gynoecia on short or long branches, with 1–2 athecal innovations, innovation leaf sequence lejeuneoid; bract lobe oblong, $1.30\text{--}1.75 \text{ mm}$ long, $0.56\text{--}0.72$

mm wide, acute to apiculate at apex, apical margin dentate, bract lobule broad lanceolate, *ca* $\frac{1}{2}$ as long as the bract lobe, $0.56\text{--}0.85 \text{ mm}$ long, $0.28\text{--}0.45 \text{ mm}$ wide, apex acute, margin coarsely dentate, keel nearly straight, *ca* $\frac{1}{2}$ as long as the bract lobule, without wing; bracteole oblong, *ca* 1.25 mm long and 0.85 mm wide, apex retuse to shallowly bilobed, dentate, lateral margin recurved. Perianth cylindrical-obpyriform, inflated, *ca* 1.10 mm long, 0.54 mm wide, and slightly flattened and anisopluriplicate, with 6–8 smooth, unequal keels (2 large lateral ones, 3–4 smaller ventral and 1–2 dorsal ones), apex broadly rounded, not sulcate, beak 9 cells long. Sporophyte and asexual reproductive organs not seen.

Habitat and distribution: *Spruceanthus mamillilobulus* usually occurs at rather low elevations, below 1000 m (*ca* $150\text{--}850 \text{ m}$). This species grows on soil, rock, rock covered with a thin layer of soil, bark and rotten logs, sometimes in association with *Frullania parvistipula* Steph. It is thus far known from China (Guangdong, Guangxi, Guizhou) and northern Vietnam (Cao Bằng, Hà Giang) (Figure 3).

Additional representative specimens examined: CHINA. Guangdong province: Fengkai County, Qixing Forest Farm, on rock, 6 June 1974, *Fengkai Team 23* (IBSC); Lianping County, from Shangping Community to Gukeng, on rock with a thin layer of soil, 21 September 1973, *Pang-Juan Lin 1536* (IBSC); Shixing County, Zhangdongshui Forest Farm, on tree bark, 750 m , 28 June 1988, *Pei-Zhong Zheng 1195* (IBSC). Guangxi province: Chongzuo City, from Aidian Town to Pingxiang City, Youyiguan Scenic Spot, along the road, $21^\circ 59' 155''\text{N}$, $106^\circ 52' 376''\text{E}$, 151 m , on rock, 10 August 2013, *Jian Wang et al. 20130810-38* (HSNU);

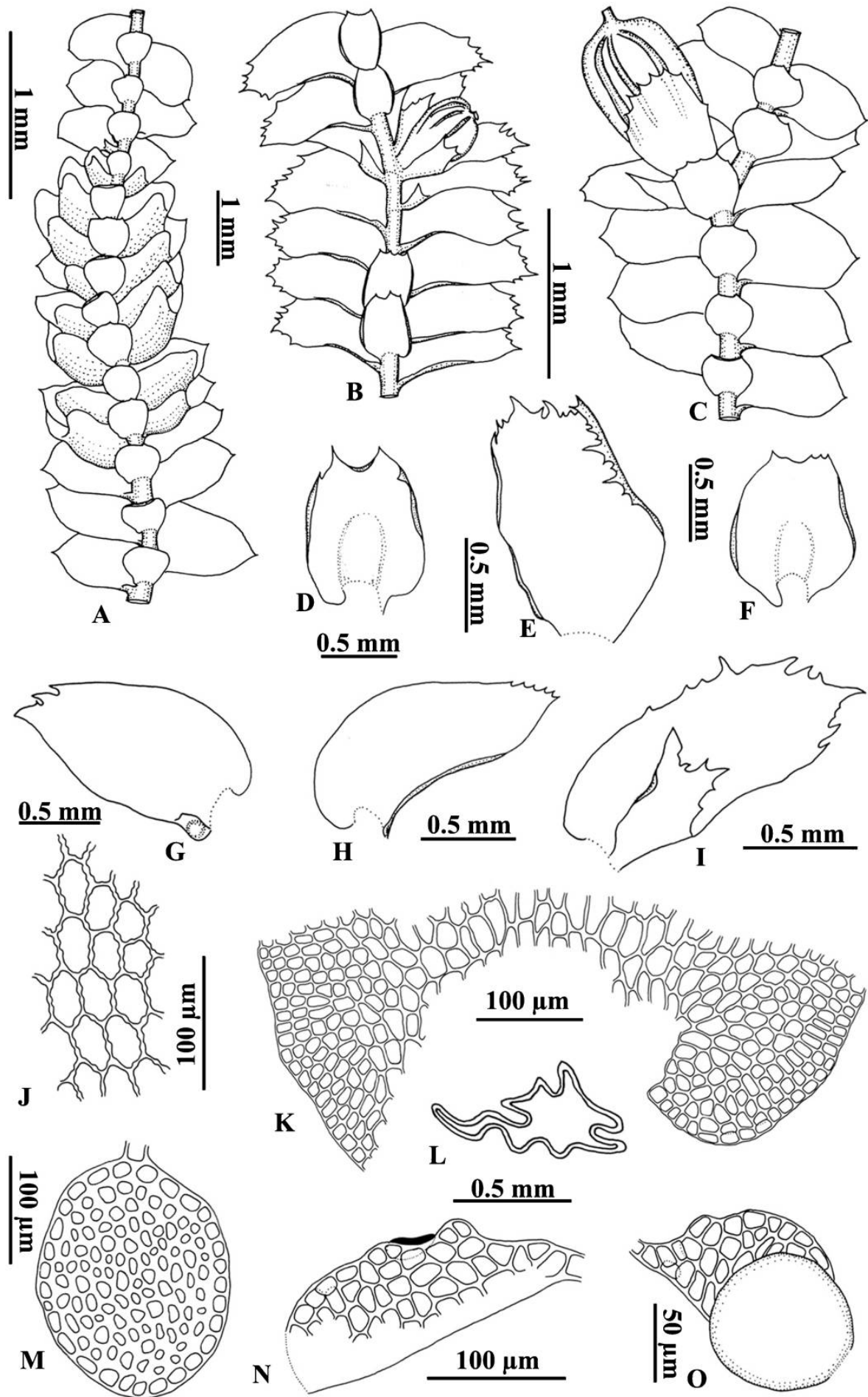


Figure 2 *Spruceanthus mamillilobulus* (Herzog) Verd. (A) Portion of shoot with androecia, ventral view. (B, C) Portion of shoot with perianths, ventral view. (D, F) Underleaves, ventral view. (E) Female bracteole, ventral view. (G, H) Leaves, ventral view. (I) Female bract, ventral view. (J) Median cells of leaf lobe. (K) Base of underleaf, showing asymmetric auriculate and cuneate bases. (L) Transverse section of perianth. (M) Transverse section of stem. (N, O) Leaf lobules, showing pouched base. A and C drawn from R.-L. Zhu et al. 20121101-129; G, O from Fengkai Team 23; J from Y.-M. Wei & T. Peng 20100915-7; N from Y.-M. Wei & T. Peng 20100914-2; the others from R.-L. Zhu et al. 20131105-111.

Daxin County, Shulong Town, Xialei Water-source Forest Reserves, 22°52'445"N, 106°43'607"E, 553 m, on tree bark, 13 August 2013, *Jian Wang et al. 20130813-27* (HSNU); Jingxi County, Yuewei Town, Pentun, 22°56'450"N, 106°31'515"E, 555 m, on soil, 14 September 2010, *Yu-Mei Wei & Tao Peng 20100914-2* (HSNU), Ande Town, on the hill behind Sanhejie Middle School, on rock, 15 September 2010, *Yu-Mei Wei & Tao Peng 20100915-7* (HSNU); Napo County, Baisheng town, Mianliang village, Nongmiaotun, 23°11'894"N, 105°32'994"E, 682 m, on rock covered with a thin layer of soil, 17 August 2013, *Jian Wang et al. 20130817-123* (HSNU); Ningming County, Nonggang National Nature Reserve, along the way from Longrui Reserve Office to central point, 23°14'324"N, 107°03'478"E, 193 m, on rock, 11 August 2013, *Jian*

Wang et al. 20130811-26 (HSNU); Nonggang County, Nonggang National Nature Reserve, Nonggang Reserve Office, 22°27'964"N, 106°56'615"E, 226 m, on tree bark, 12 August 2013, *Jian Wang et al. 20130812-141* (HSNU). VIETNAM. Hà Giang Province: Bát Đại Sơn Nature Reserve, Quản Bạ District, Thanh Vân Commune, Thanh Long village, 23°05'035"N, 104°58'216"E, 847 m, on tree bark, 1 November 2013, *Rui-Liang Zhu et al. 20131101-129* (HSNU); Phong Quang Nature Reserve, Vị Xuyên District, Minh Sơn Commune, Tân Sơn village, 23°00'395"N, 104°54'497"E, 463 m, on rotten logs, 5 November 2013, *Rui-Liang Zhu et al. 20131105-111* (HSNU); Phong Quang Nature Reserve, Vị Xuyên District, Thuận Hóa Commune, Lũng Bông village, 22°54'157"N, 104°56'273"E, 289 m, on rock covered with a thin layer of soil, 6 November 2013, *Rui-Liang*

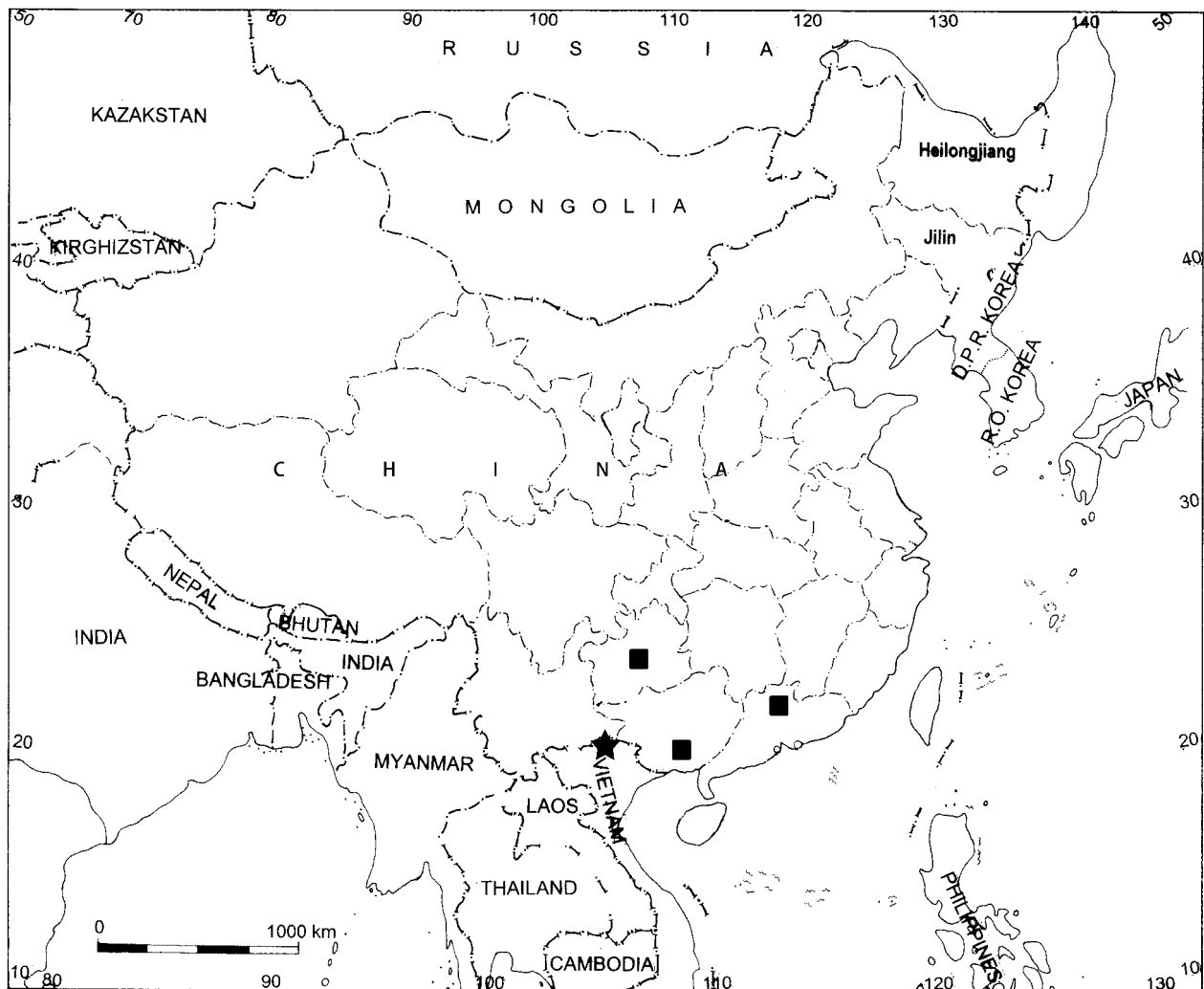


Figure 3 Distribution of *Spruceanthus mamillilobulus* (Herzog) Verd. The new-locality is marked with a star.

Zhu et al. 20131106-61 (HSNU); Bắc Mê Nature Reserve, Bắc Mê District, Thượng Tân Commune, Tà Lượng village, 22°45'184"N, 105°13'468"E, 446 m, on rock, 29 October 2013, Rui-Liang Zhu et al. 20131029-22 (HSNU).

Discussion

The genus *Spruceanthus* comprises seven extant species, six in Asia and Australia, and one in the Neotropics (Ecuador) (Gradstein, 1991, 1994; Zhu & So, 2001; Wang et al., 2014). In addition, a fossil species of *Spruceanthus* has been described from the Baltic amber of Central Europe (Grolle, 1985). The genus is circumscribed to include species with (1) robust stems with thick-walled cells, and a weakly enlarged epidermis, occasional presence of a brown-coloured sub-epidermis and a broad ventral merophyte (6–12 cells wide); (2) almost exclusively *Lejeunea*-type branching (rarely *Frullania*-type branching in *S. sulcatus*, *S. theobromae* and *S. thozetianus*); (3) presence of curved, microphyllous branches at shoot bases; (4) isodiametric to elongate leaf cells and with simple-triangular to radiate trigones; (5) homogeneous, *Massula*-type oil bodies; (6) lejeuneoid innovations; and (7) pluriplicate perianths with 5–12 equal or unequal, smooth keels (e.g. Gradstein, 1994; Zhu & So, 2001; Wang et al., 2014).

Spruceanthus is sister to *Ptychanthus* (Lehm. & Lindenb.) Nees and *Archilejeunea* (Spruce) Schiffn. subg. *Dibrachiella* (Spruce) Schiffn., and this relationship is supported by recent molecular-phylogenetic studies (Wilson et al., 2007; Wang et al., 2014). Some species, such as *A. planiuscula* (Mitt.) Steph. (= *S. marianus sensu* Mizut.) and the polymorphic *S. polymorphus* (Sande Lac.) Verd. (= *A. polymorpha* [Sande Lac.] B. Thiers & Gradst.), have been associated with either group. *Ptychanthus* is separated from *Spruceanthus* by the dendroid habit plants, the presence of predominantly *Frullania*-type branches, elongate median leaf cells and cordate trigones, segmented oil bodies, and presence of a large wing in the keel of inner female bracts (Sukkharak et al., 2011; Wang et al., 2014). According to Gradstein (1994), Gradstein et al. (2002) and Thiers & Gradstein (1989), *Spruceanthus* and *Archilejeunea* differ mainly by the homogeneous oil bodies in the former and segmented ones in the latter genus. However, observations on fresh material of various species from China indicate that homogeneous oil bodies also occur in *A. amakawana*, *A. kiushiana* and *A. planiuscula* (Zhu & Gradstein, 2005; Wang, 2010). Nevertheless, these species are distinguished from *Spruceanthus* by their smaller size, less robust stems with ventral merophytes only 4–6 cells wide, absence of microphyllous branches, usually simple-triangular trigones (not radiate), and 5-keeled perianths (not pluriplicate).

Spruceanthus mamillilobulus resembles *Bazzania* spp. in the field with its leaves widely spreading when moist. The most outstanding characteristics of the species are the elongated leaf cells, usually with two intermediate thickenings on both long walls and the peculiar, asymmetric base of the underleaf, which is auriculate on one side and cuneate (without auricle) on the opposite side. This kind of underleaf base asymmetry is very rare in liverworts and has thus far only been reported in *Macroclorella sagittistipula* (Spruce) R.M. Schust. (Grolle & Zhu, 2002) and *Mastigolejeunea frauenfeldii* (Reichardt) Verd. (Sukkharak & Gradstein, 2014) in the family Lejeuneaceae. Interestingly, in both of these the underleaf asymmetry alternates in a left–right fashion, in *M. sagittistipula* between adjacent underleaves on a single shoot and in *M. frauenfeldii* among left-hand and right-hand side branches, being uniform on a single shoot (Sukkharak & Gradstein, 2014). The underleaf asymmetry of *S. mamillilobulus* most closely resembles that of *M. frauenfeldii*, being uniform on single shoots and varying among branches in a left–right pattern, but differs by the constant presence of only one auricle, underleaves in *M. frauenfeldii* having two auricles, one large and one small. *S. mamillilobulus* is readily separated from all other species of *Spruceanthus*, except for *S. semirepandus*, by its asymmetrically auriculate underleaves. The elongated leaf cells, usually with two intermediate thickenings on each long wall, distinguishes *S. mamillilobulus* from all other Asiatic species of *Spruceanthus* and is similar only to *S. theobromae* from Ecuador (Gradstein, 1994: Figure 28F). However, *S. theobromae* often has more than two intermediate thickenings on each long cell wall and further differs by having entire leaf and underleaf margins and symmetrical underleaf bases.

Further noteworthy characters of *Spruceanthus mamillilobulus* include the entire to dentate, acute-apiculate leaves with a very wide angle between keel and ventral lobe margin, the very small lobules ($1/7$ – $1/9$ as long as the lobes) with 1–3 small, one-celled teeth and a pouched base, the shallowly curved insertion line of the underleaves, the autoicous sexuality, and the anisopluriplicate perianth with 6–8 unequal keels and a long beak. The species varies somewhat in size, in the size and shape of leaf lobules and underleaves, and in the dentation of leaves and underleaves, which may be toothed or entire. Entire leaves and underleaves and reduced lobules are most frequently seen in small plants. Such entire-leaved plants somewhat resemble the rare *S. sulcatus* from western Malesia and *S. polymorphus* from Asia and Oceania. *Spruceanthus sulcatus* clearly differs from *S. mamillilobulus* by its symmetrical underleaf bases, female bracts and bracteoles with entire margins, and its isopluriplicate perianth with 10 keels, a sulcate apex

and a very short recessed beak (Gradstein, unpubl. obs.). *Spruceanthus polymorphus* is readily separated from *S. mamillilobulus* by its smaller plant size, the dimorphic differentiation of gynoecial and vegetative shoots, the isodiametric leaf cells, the presence of a border of small cells along leaf margins, the larger leaf lobules ($1/4-2/5$ as long as the lobes), and the symmetrical underleaf bases without auricles.

Key to the species of *Spruceanthus*

1. Leaf apex weakly to strongly toothed.....2
1. Leaf apex entire.....4
2. Plants with dimorphic differentiation of gynoecial and vegetative shoots; symmetrical underleaf bases without auricles; known from Indopacific...
.....*S. polymorphus*
2. Plants without dimorphic differentiation of gynoecial and vegetative shoots; asymmetric base of the underleaf, auriculate on one side and cuneate on the opposite side.....3
3. Median leaf cells distinctly elongate; underleaf usually with a pouched base; known from China and Vietnam.....*S. mamillilobulus*
3. Median leaf cells isodiametric; underleaf without pouched base; known from tropical and subtropical regions of Asia.....*S. semirepandus*
4. Insertion line of underleaves deeply arched.....5
4. Insertion line of underleaves straight or slightly arched.....6
5. Leaves very flat, oblong; lobules with two teeth; known only from western Melanesia...*S. macrostipulus*
5. Leaves convex with often somewhat deflexed apex, ovate; lobules usually with one tooth; known only from New Guinea.....*S. pluriplicatus*
6. Perianth with 10 keels, beak recessed; known from Indonesia and Malaysia.....*S. sulcatus*
6. Perianth with 5–8 keels, beak not recessed.....7
7. Median leaf cells distinctly elongate; autoicous or paroicous; known only from Ecuador.....
.....*S. theobromae*
7. Median leaf cells isodiametric; dioicous; known from Australia, India and New Caledonia.....
.....*S. thozetianus*

Acknowledgements

Thanks are due to the curator of herbarium IBSC for the loan of specimens and to Dr Tao Peng (Guizhou Normal University) and Dr Yu-Mei Wei (Guangxi Institute of Botany, Chinese Academy of Sciences) for making collections available. We are grateful to two anonymous reviewers for constructive comments on the manuscript. Special thanks are due to the managing editor (Elizabeth Kungu) for reading the manuscript and making useful suggestions. The first

author is grateful to the Nonggang National Natural Reserve of Guangxi, China, and Phong Quang Nature Reserve, Bát Đại Sơn Nature Reserve and Bắc Mê Nature Reserve of Hà Giang Province, Vietnam for providing field assistance. This research was supported by the National Natural Science Foundation of China (nos. 31370238, 31300171), the Special Program for the National Basic Work of the Ministry of Science and Technology, China (No. 2012FY 110600), and PhD Program Scholarship Fund of ECNU 2009.

Taxonomic Additions and Changes: Nil.

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