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Taxonomic revision of the genus *Spiranthes* (Orchidaceae) in Taiwan

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Abstract

The taxonomy of *Spiranthes* is highly challenging due to its phenotypic plasticity, morphological convergence, and hybridization. This paper presents a re-evaluation of the genus *Spiranthes* (Orchidaceae) in Taiwan, with special reference to the taxonomic identity of *S. suishaensis* that has often been considered the earlier name of *S. nivea* or *S. hongkongensis.* Nonetheless, the floral dissection of the type specimen revealed that *S. suishaensis* has a well-developed rostellum that separates the stigma and pollinarium of each flower, in contrast to autogamous taxa such as *S. nivea* and *S. hongkongensis*. Given the morphological evidence and that only *S. sinensis* was collected in the *S. suishaensis* type locality, we concluded that *S. suishaensis* is neither an earlier name for *S. nivea* nor *S. hongkongensis* but a synonym of *S. sinensis.* During morphological comparisons of *S. suishaensis* with other taxa of *S. sinensis* complex, we also found that the taxon illegitimately described as "*S. minutiflora*" could be treated as a variant of *S. nivea.* Given that it is distinguishable from *S. nivea* var. *nivea* by its more densely pubescent rachis and ovaries (vs. sparsely pubescent rachis and ovaries), narrower sepals with white tinged with pink or purple at apex (vs. wider and entirely white sepals), and papillose labellum disc (vs. almost glabrous labellum disc), we described it as a new variety of *S. nivea*, which we propose to name *S. nivea* var. *papillata* T.C. Hsu & Suetsugu. Consequently, we concluded that three species (*S. sinensis*, *S. hongkongensis,* and *S. nivea* [including var. *nivea* and var. *papillata*]) and one hybrid, *S. australis* × *S. sinensis*, occur in Taiwan.

Keywords: Orchidaceae, *Spiranthes sinensis* species complex, taxonomy

Introduction

The genus *Spiranthes* (Richard 1817) includes about 50 species and is widely distributed in tropical and temperate regions of the Americas, Eurasia, and Australia (Dueck *et al.* 2014; Pace *et al.* 2019; Surveswaran *et al.* 2017, 2018). Nevertheless, delimitation of closely related *Spiranthes* species based solely on morphology is hampered by phenotypic plasticity, morphological convergence, and hybridization (Dueck *et al.* 2014; Pace *et al.* 2019; Pace & Cameron 2017; Surveswaran *et al.* 2017, 2018; Tao *et al.* 2018). In particular, the taxonomy of Old World *S. sinensis* (Persoon 1807: 511) Ames (1908: 53) species complex is highly challenging, due to its wide distribution and morphological variation (Hsu & Chung 2014; Hu & Barretto 1976; Lin & Lin 2011). Nevertheless, the phylogeny of the *S. sinensis* species complex has been resolved with molecular approaches (Pace *et al.* 2019; Surveswaran *et al.* 2017, 2018). The molecular evidence, combined with phenological and morphological data facilitated the recognition of seven distinct taxa within the complex (Surveswaran *et al.*, 2018; Pace *et al.*, 2019). However, although the recognition of seven distinct taxa within the complex has generally been accepted, there is some debate as to which scientific names are the earliest name for the seven taxa because of their morphological complexity (Pace & Cameron 2020; Surveswaran *et al.* 2020).

Three species, *S. sinensis*, *Spiranthes suishaensis* (Hayata 1916: 86) Schlechter (1919: 161), *S. hongkongensis* (Hu & Barretto 1976), and one natural hybrid *Spiranthes australis* (R. Brown 1810: 219) Lindley (1824: 823) × *S. sinensis* have been generally accepted as Taiwanese *Spiranthes* (Lin *et al.* 2016; Pace *et al.* 2019; Suetsugu *et al.* 2020). In addition, *S. minutiflora* Hsu (2016: 187) in Hsu & Chung (2016) was described as a new species that is morphologically most similar to *S. nivea* T.P. Lin & W.M. Lin (2011: 320). However, this name is illegitimate since the specific epithet has been occupied by *S. minutiflora* Richard & Galeotti (1845: 32). Therefore, if this taxon is distinct from other species, it should be given a different epithet. Moreover, the taxonomic identity of *S. suishaensis* remains somewhat problematic.

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Spiranthes suishaensis was first described from Suisha Lake (currently Sun Moon Lake), Nantou County, Taiwan. Although it had long been considered a synonym of the allogamous taxon *S. sinensis* (Lin 1975; Liu & Su 1978; Lang 1999; Chen *et al.* 2009), *S. suishaensis* was recently reinstated and accepted as the earliest name of the autogamous *S. nivea* possibly owing to the similarities such as their white flowers and nearly 100% fruit set of the type specimen (Lin *et al.* 2016; Pace *et al.* 2019). When studying the type materials of *S. suishaensis*, however, we noticed that some of its morphological characteristics, including the bracts that are not or only slightly exceeding ovaries, and the lips which are much protruding from lateral sepals and more strongly recurved, do not fall into the typical variation range of *S. nivea* (Hsu & Chung 2016; Lin & Lin 2011). Instead, these characteristics agree well with *S. sinensis* or *S. hongkongensis* S.Y. Hu & Baretto (1976: 2), another autogamous species with white flowers within the *S. sinensis* species complex.

Although *S. nivea* has previously been found on slopes or cliffs in mountainous regions of ca. 1500-2000 m elev. (Hsu & Chung 2016; Lin *et al.* 2016), the type locality of *S. suishaensis* (Suisha Lake) is located at 750 m elevation. Therefore, ecological information provides indirect evidence for our notion that *S. suishaensis* is not the earlier name of *S. nivea.* In fact, no *S. nivea* has been collected around the type locality since then, and so far, we could only find *S. sinensis* around it. It is also noteworthy that only very recently, Lin (2019) considered *S. hongkongensis* as a junior synonym of *S. suishaensis*, resurrecting *S. nivea* as the earliest name for the identity, mainly because the plant height, leaf length, and bract length of *S. suishaensis* type specimen are closer to those of *S. hongkongensis* than those of *S. nivea.* Nonetheless, the plant height, leaf length, and bract length of *S. suishaensis* type specimen also fall into the typical variation range of *S. sinensis* (Surveswaran *et al.* 2017; Pace *et al.* 2019). Subsequently, given that precise identification of *Spiranthes* species requires the observation of floral characteristics that are hidden in the perianth tube (Surveswaran *et al.* 2017; Pace *et al.* 2019), we decided to remove some flowers of the *S. suishaensis* type specimen from the herbarium sheet and rehydrated them by boiling in water. After that, the flowers were carefully dissected to investigate their inner floral morphology. The structure of the specimen was observed using a stereomicroscope (M165C; Leica Microsystems, Cambridge, UK). In addition, herbarium specimens of the *S. sinensis* species complex were reviewed from several herbaria (KYO, KPM, TAIF, TI, and TNS), as well as from online digitized plant collections, such as JSTOR Global Plants (http://plants.jstor.org/).

Consequently, we found that, in contrast to the ovate labellum of *S. nivea* with epichile much narrower than hypochile, the labellum of the *S. suishaensis* type specimen is somewhat oblong or oblong-ovate with epichile as wide as or slightly larger than hypochile. Moreover, *S. suishaensis* has glabrous rachis and ovaries, in contrast to *S. nivea* (sparsely pubescent) and *S. hongkongensis* (densely pubescent). More importantly, *S. suishaensis* has a well-developed rostellum that separates the stigma and pollinarium of each flower, pollinia with a viscidium, and suborbicular stigma, whereas *S. nivea* and *S. hongkongensis* have a degenerated rostellum, pollinia without a viscidium, and a distinctly 3-lobed stigma that are associated with its autogamous breeding system (Surveswaran *et al.* 2017; Pace *et al.* 2019; Suetsugu & Hayakawa 2019). All the characteristics described above are consistent with *S. sinensis.* Taken together with the fact that only *S. sinensis* has been collected around the *S. suishaensis* type locality, we concluded that *S. suishaensis* is not an earlier name for either *S. nivea* or *S. hongkongensis*, but a synonym of *S. sinensis.* During morphological comparisons of *S. suishaensis* with other taxa of *S. sinensis* complex, we also found that *S. minutiflora* illegitimately described by Hsu (2016: 187) in Hsu & Chung (2016) should be a variant of *S. nivea.* Considering that it can still be distinguishable from *S. nivea* by its more densely pubescent rachis and ovaries, narrower sepals with white tinged with pink or purple at the apex, and papillose labellum disc, we described it as a new variety of *S. nivea*, which we propose to name *S. nivea* var. *papillata* T.C. Hsu & Suetsugu.

During the preparation of this paper, a new species *Spiranthes pitouchaoensis* S.S. Ying (2022: 19) was described based on a single specimen collected from the coastal region of northeastern Taiwan. Although the author proclaimed that the holotype was deposited in NTUF, this specimen is not located there (J.-M. Hu, pers. comm. in December 2022) and is thus improbable for a direct examination. Nonetheless, judging from the description and images available in the protologue, we consider that none of the diagnostic characters announced by Ying (2022) exceeds the known morphological and ecological ranges of *S. sinensis*, and hence we synonymized it under *S. sinensis*. Based on our observations mentioned above, we concluded that three species (*S. sinensis*, *S. hongkongensis,* and *S. nivea* [including var. *nivea* and var. *papillata*]), and one natural hybrid, *S. australis* × *S. sinensis*, occur in Taiwan.

Taxonomic treatment

Spiranthes sinensis (Persoon 1807: 511) Ames (1908: 53)—Fig. 1.

Type:—CHINA: prope Cantonem Sinarum, 1790, *J. de Loureiro 5221* (holotype: P00150857, image!).

= ***Spiranthes suishaensis*** (Hayata 1916: 86) Schlechter (1919: 161) ≡ *Spiranthes australis* (R. Brown 1810: 319) Lindley (1824: 823) var. *suishaensis* Hayata (1916: 86). Type:—TAIWAN. Nantou: Lake Suisha, 28 April 1916, *B. Hayata s.n.* (holotype: TI00010424!).—Fig. 2.

= ***Spiranthes pitouchaoensis*** S.S. Ying (2022: 19), *syn. nov.* Type:—TAIWAN. New Taipei: Ruifang District, Pitouchao, 28 June 2020, *S.S.Ying s.n.* (holotype: NTUF, not located; image available in Ying (2022: 23)).

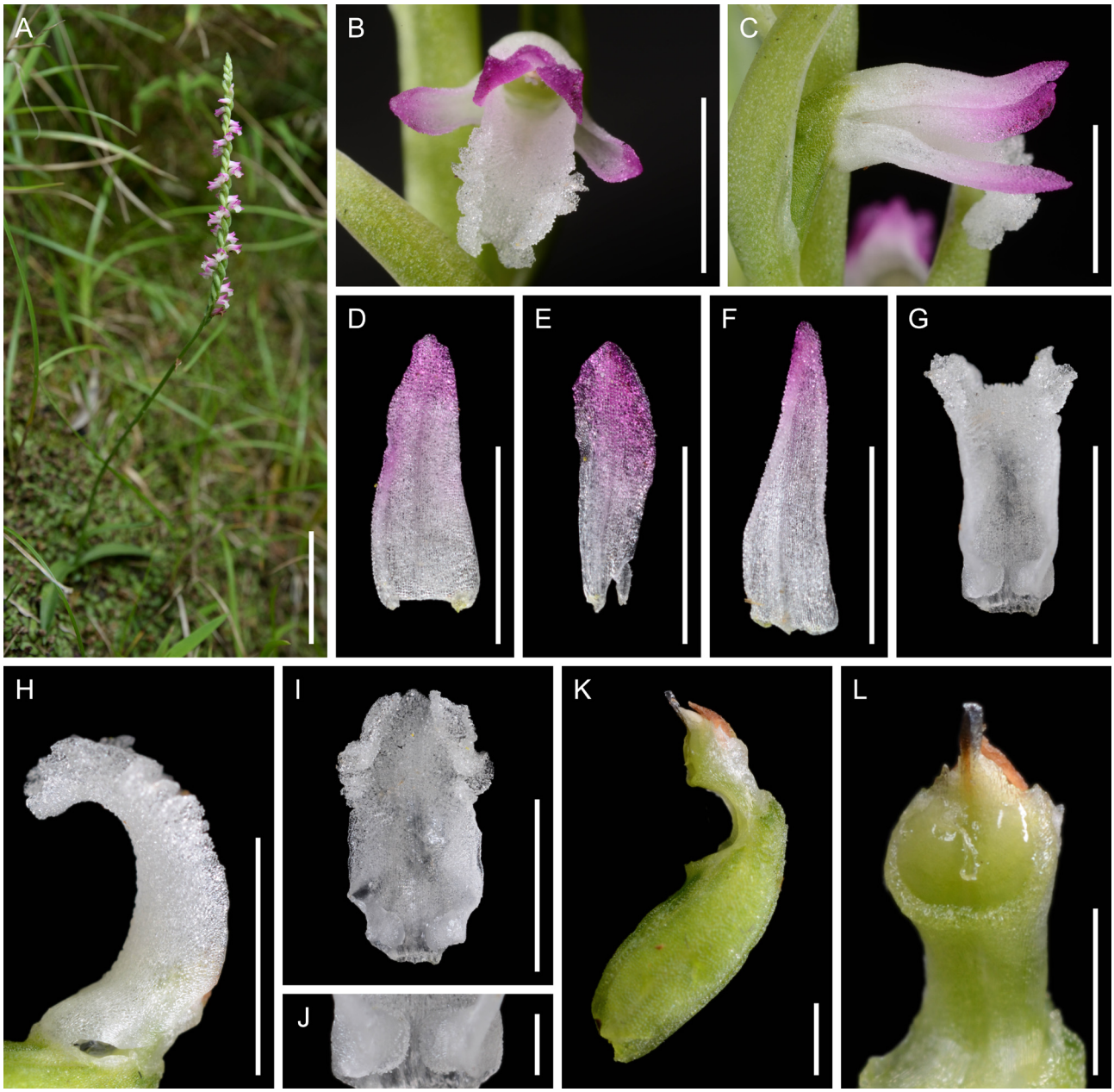

FIGURE 1. *Spiranthes sinensis* (*Tian-Chuan Hsu 10400* [A] & *Tian-Chuan Hsu 6393* [B–L], TAIF). (A) Habit. (B) Flower, front view. (C) Flower, lateral view. (D) Dorsal sepal. (E) Petal. (F) Lateral sepal. (G) Labellum. (H) Labellum and column, lateral view. (I) Flattened labellum. (J) Close-up of basal callosities of labellum. (K) Ovary and column. (L) Column. Scale bars: 30 mm (A), 3 mm (B–I), 0.5 mm (J) and 1 mm (K–L).

Morphological descriptions and illustrations:—See Lin (1975: 244–245; 2019: 267; f. 118; pl. 13), Liu & Su (1978: 1103; pl. 1642), Surveswaran *et al.* (2017: 125; f. 4) and Hsu & Chung (2016: 188).

Distribution and Ecology:—*Spiranthes sinensis* occurs from the southern part of the Hengduan Mountains, eastward across northern Laos, northern Vietnam, southern and eastern China, northward across Taiwan and the Ryukyu Islands, southward across the northern Malay Archipelago, New Guinea, and New Caledonia. In Taiwan, this species is widespread throughout the main island and recorded from neighboring islets, including Pengchiayu, Lyudao (Green Island) and Lanyu (Orchid Island). It usually occurs at sunny grassy places in lowland regions from sea level to ca. 1000 m elev. and occasionally grows on roadside slopes in mountainous regions between 1000–2000 m elev. Flowers were mainly observed from March to May in lowland populations and from May to September in mountainous populations.

FIGURE 2. *Spiranthes suishaensis* (holotype). (A) Habit. (B) Close-up view of inflorescence. (C) Flower, lateral view. (D) Dorsal sepal. (E) Petal. (F) Lateral sepal. (G) Labellum and column. Rostellum is indicated by the arrow. (H) Close-up of papillate labellum disc. (I) Column, upper view. (J) Column, bottom view. (K) Pollinarium. Scale bars: 100 mm (A), 3 mm (B–G) and 1 mm (H–K).

Additional specimens examined:—TAIWAN. "Formosa": 1862, *R. Swinhoe s.n.* (K!); April 1874, *W. Campbell s.n.* (BM!); 11 March 1912, *W.R. Price 190A* (K!). Keelung City: Pengchiayu, 7 June 2005, *S.-W. Chung 7742* (TAIF!). New Taipei City: Tamsuy, 1864, *R. Oldham 183* (BM!, K!); Urai, April 1914, *U. Faurie 926* (BM!); Shihding Service Area, 18 March 2013, *T.-C. Hsu 6393* (TAIF!). Taichung City: Gaomei, 27 April 2017, *T.-C. Hsu 9045* (TAIF!); Nantou Co.: Suisha, *s.a.*, *B. Hayata s.n.* (TAIF!); Sun Moon Lake, 28 April 2008, *T.-C. Hsu 1347* (TAIF!). Hualien Co.: Hoping Logging Trail, 25 September 2007, *T.-T. Ho 215* (TAIF!); Changhong Bridge, 5 April 2018, *T.-C. Hsu 10400* (TAIF!). Taitung Co.: Lichia Logging Trail, 4 April 2018, *T.-C. Hsu 10399* (TAIF!); Lyudao Island, Chaojih

Hot Spring, 17 April 2018, *T.-C. Hsu 10475* (TAIF!); Lanyu Island, Yehyin, 27 March 2018, *T.-C. Hsu 10318* (TAIF!). JAPAN. Kyushu Dist., Kagoshima Pref.: Amami Island, 8 May 2016, *M. Takashi HH111* (SPMN!). Okinawa Pref.: Okinawa Island, 17 April 2017, *A. Naiki 9922* (RYU!); Iriomote Island, 18 April 2017, *A. Naiki 9925* (RYU!); Ishigaki Island, 27 March 2017, *A. Soejima HH672* (SPMN!).

Taxonomic remarks:—*Spiranthes sinensis* displays allogamous features, including a well-developed rostellum that separates the stigma and pollinarium of each flower, pollinia with a viscidium, and suborbicular stigma, whereas *S. hongkongensis* and *S. nivea* has a degenerated rostellum, pollinia without a viscidium, and a distinctly 3-lobed stigma. Because species in the *S. sinensis* species complex often have pink flowers, the members with entirely white flowers were traditionally recognized as a distinct species only due to their white flowers (Pace *et al.* 2019). However, as demonstrated by Pace *et al.* (2019), it is not appropriate to delimitate *Spiranthes* species based solely on flower color. Because we could not recognize any distinct morphological differences between *S. sinensis* and *S. suishaensis* other than floral coloration (Figs. 1–2), we concluded *S. suishaensis* is a synonym of *S. sinensis.* For a list of synonyms of *S. sinensis* other than *S. suishaensis* and *S. pitouchaoensis*, see Pace *et al*. (2019).

Spiranthes hongkongensis S.Y. Hu & Baretto (1976: 2)—Fig. 3.

Type:—HONG KONG: Tai Po, the garden of Gloria Barretto, 4 April 1975, *S. Y. Hu 13658* (holotype: K000942682!; isotypes: A00104456, image!, CUHK).

Synonym:—*Spiranthes suishaensis* auct. non (Hayata 1916: 86) Schlechter (1919: 161): Lin (2019: 284).

Morphological descriptions and illustrations:—See Hu & Baretto (1976: 2; f. 2), Hsu & Chung (2014: 406; f.1; 2016: 186), Surveswaran *et al.* (2017: 125; f. 4), and Lin (2019: 265; f. 116; pl. 13), as *Spiranthes suishaensis*.

Distribution and ecology:—*Spiranthes hongkongensis* is currently known in Hong Kong, Taiwan, China (Guangdong and Hainan Provinces), Japan, and Borneo. In Taiwan, this species is occasionally found on lowland hills around the Taipei Basin where it grows on very humid sunny grassland accompanied with some wetland plants such as *Eriocaulon* spp. and *Utricularia* spp. It was also found growing as a weed in some greenhouses in southern Taiwan, and these populations are presumed as unintentionally introduced along with horticultural plants. Flowers were observed from April to May.

Additional specimens examined:—TAIWAN. New Taipei City: Chepingliao, 27 May 2009, *T.-C. Hsu 2214* (TAIF!); same loc., 20 April 2014, *T.-C. Hsu 7079* (TAIF!); same loc., 8 May 2015, *T.-C. Hsu 7674* (TAIF!); same loc., 22 April 2017, *J.-Z. Lin 1* (TAIF!). Pingtung Co.: Kaoshu, 26 April 2018, *T.-C. Hsu 10536* (TAIF!). CHINA. Hainan Prov.: Mt. Diaoluo National Forest Park, 26 February 2012, *T.-C. Hsu 5440* (TAIF!). HONG KONG: 20 April 1975, *S. Y. Hu 13673* (KYO!). JAPAN. Okinawa Pref.: Ishigaki Island, Ishigaki City, in campis humidis litoris ad Nagura, 4 April 1937, *Takamine s.n.* (KPM-NA0304131!).

Taxonomic remarks:—*Spiranthes hongkongensis* can be distinguished from the allogamous taxa such as *S. australis* and *S. sinensis* by its modified rostellum and stigma morphology associated with its autogamous breeding system. *Spiranthes hongkongensis* is most similar to *S. nivea*, another autogamous species with white flowers. However, it differs from *S. nivea*, in having papillate (vs. nearly glabrous) labellum disc, larger papillate (vs. smaller glabrous) basal labellum callosities, and densely glandular pubescent (vs. sparsely pubescent) rachis, ovaries, and sepals.

Spiranthes nivea T.P. Lin & W.M. Lin (2011: 320) **var. *nivea***—Fig. 4.

Type:—TAIWAN. Pingtung: Tahanshan, 20 May 2009, *Y.F. Wang s.n.* (holotype: TAI 270634!).

Synonym:—*Spiranthes suishaensis* auct. non (Hayata 1916: 86) Schlechter (1919: 161): Lin (2016: 117).

Morphological descriptions and illustrations:—See Lin & Lin (2011: 320; f. 5), Surveswaran *et al.* (2017: 125; f. 4), Hsu & Chung (2016: 188), as *Spiranthes suishaensis*, and Lin (2019: 266; f. 117; pl. 13).

Distribution and ecology:—The typical variety species is only recorded from the type locality, Tahanshan (Mt. Tahan) in southern Taiwan. It grows on semi-open roadside slopes around 1400–1600 m elev. and flowers from March to April.

Additional specimens examined:—TAIWAN. Pingtung Co.: Mt. Tahan, 13 March 2013, *T.-C. Hsu 6342* (TAIF!); Tahanshan, 9 April 2013, *S.-S. Lin s.n.* (TAI!).

Taxonomic remarks:—*Spiranthes nivea* is most similar to *S. hongkongensis*, but it differs in having nearly glabrous labellum disc, smaller glabrous basal labellum callosities, and sparsely pubescent glabrous rachis, ovaries, and sepals.

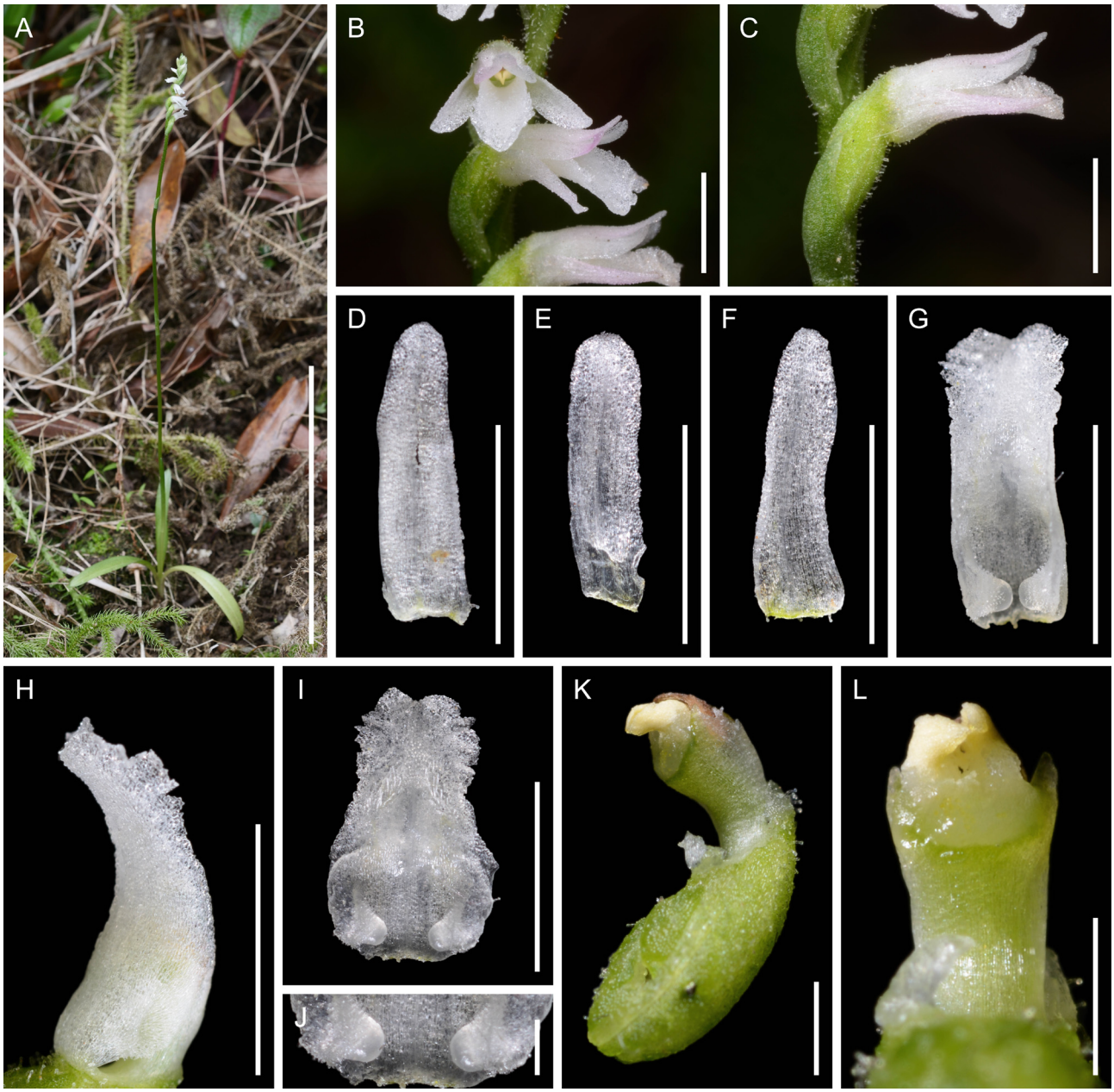

FIGURE 3. *Spiranthes hongkongensis* (*Tian-Chuan Hsu 7079*, TAIF). (A) Habit. (B) Flower, front view. (C) Flower, lateral view. (D) Dorsal sepal. (E) Petal. (F) Lateral sepal. (G) Labellum. (H) Labellum and column, lateral view. (I) Flattened labellum. (J) Close-up of basal callosities of labellum. (K) Ovary and column. (L) Column. Scale bars: 30 mm (A), 3 mm (B–I), 0.5 mm (J) and 1 mm (K–L).

Spiranthes nivea* var. *papillata T.C. Hsu & Suetsugu, *var. nov.*—Fig. 5.

≡ *Spiranthes minutiflora* Hsu (2016: 187) in Hsu & Chung (2016), *nom. illeg., non* Richard & Galeotti (1845: 32).

Type:—TAIWAN. Ilan: Tsuifong Lake, 1800–1900 m elev., 3 June 2015, *T.C. Hsu 7743* (holotype: TAIF496968!).

Diagnosis:—*Spiranthes nivea* var. *papillata* is morphologically distinguishable from *S. nivea* var. *nivea* by its more densely pubescent rachis and ovaries (vs. sparsely pubescent rachis and ovaries), narrower sepals that are white tinged with pink or purple at the apex (vs. wider and entirely white sepals), and papillose labellum disc (vs. almost glabrous labellum disc).

Morphological descriptions and illustrations:—See Hsu & Chung (2016: 187), as *Spiranthes minutiflora.*

Distribution and ecology:—This variety is currently recorded around Tsuifong Lake and Taipingshan in northeastern Taiwan. It grows on sunny grasslands, semi-open roadside slopes, and cliffs around 1800–2100 m elev. Flowers were observed from May to July.

FIGURE 4. *Spiranthes nivea* var. *nivea* collected at the type locality (*Tian-Chuan Hsu 6342*, TAIF). (A) Habit. (B) Flower, front view. (C) Flower, lateral view. (D) Dorsal sepal. (E) Petal. (F) Lateral sepal. (G) Labellum. (H) Labellum and column, lateral view. (I) Flattened labellum. (J) Close-up of basal callosities of labellum. (K) Ovary and column. (L) Column. Scale bars: 30 mm (A), 3 mm (B–I), 0.5 mm (J) and 1 mm (K–L).

Etymology:—The specific epithet is named after its papillate lip and papillate-pubescent rachis and ovaries that are diagnostic from the typical variety.

Additional specimens examined:—TAIWAN. Ilan Co.: Taipingshan, 21 May 2012, *T.-C. Hsu 5742* (TAIF!); same loc., 23 June 2017, *T.-C. Hsu 9299* (TAIF!); Tsuifeng Lake, 22 June 2017, *T.-C. Hsu 9287* (TAIF!).

Taxonomic remarks:—*Spiranthes nivea* var. *papillata* shows morphological resemblance to *S. nivea* and *S. hongkongensis*, due to their shared autogamous reproductive biology. Althouth Lin (2019) considered it conspecific with *S. hongkongensis*, this taxon actually differs in having bracts that significantly exceed ovaries, smaller and glabrous basal labellum callosities, ovate labellum, and smaller column. These features imply a closer relationship to *S. nivea*, but it still differs from *S. nivea* var. *nivea* by several morphological characters mentioned in the diagnosis. Given that there are no significant differences in the labellum and column morphology, which are essential characteristics in species delimitation in *S. sinensis* species complex (Pace *et al.* 2019), we concluded that the relatively minor differences are attributed to intraspecific variation, describing it as a new variety of *S. nivea.*

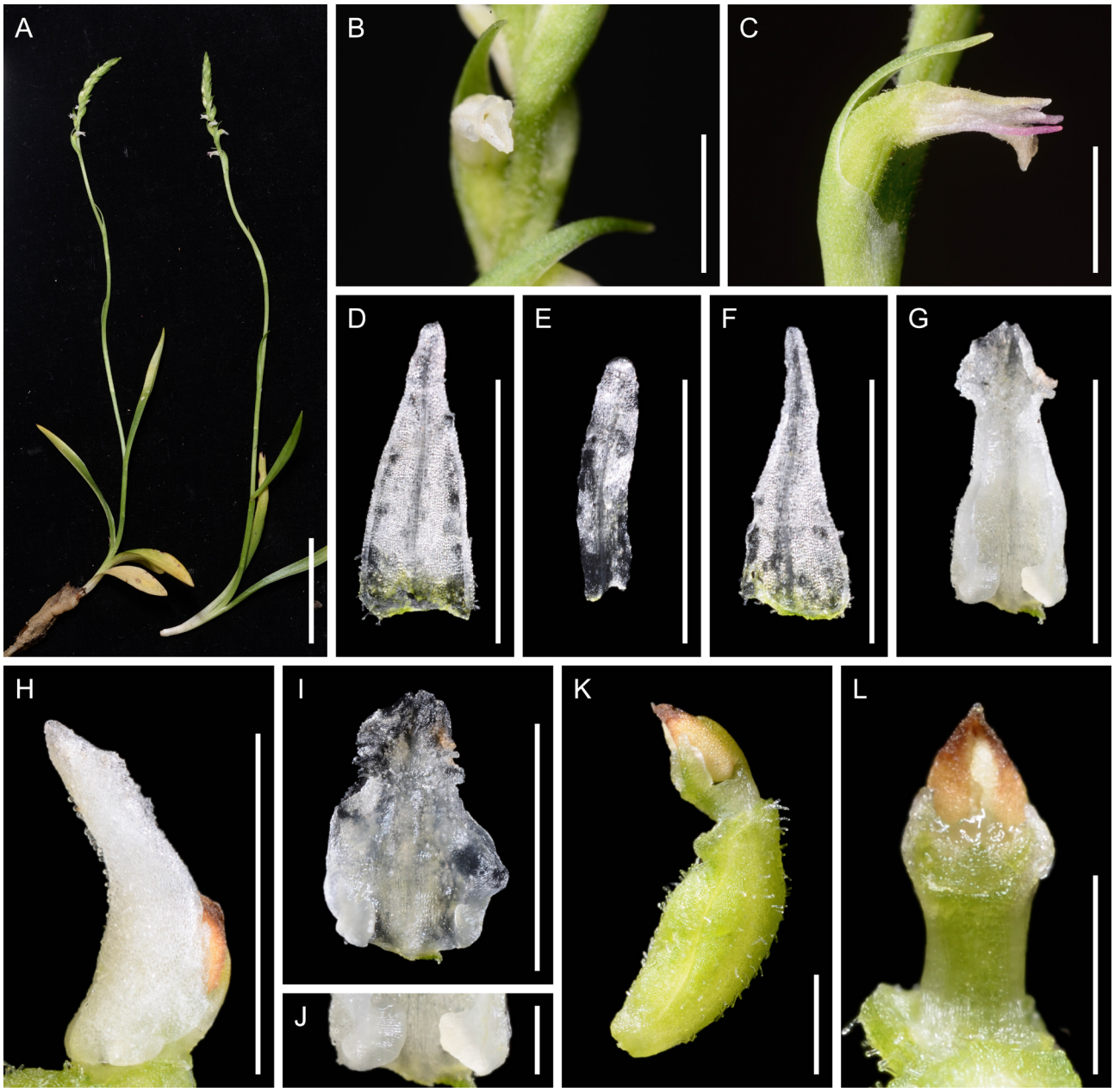

FIGURE 5. *Spiranthes nivea* var. *papillata* (*Tian-Chuan Hsu 7743*, TAIF). (A) Habit. (B) Flower, front view. (C) Flower, lateral view. (D) Dorsal sepal. (E) Petal. (F) Lateral sepal. (G) Labellum. (H) Labellum and column, lateral view. (I) Flattened labellum. (J) Close-up of basal callosities of labellum. (K) Ovary and column. (L) Column. Scale bars: 30 mm (A), 3 mm (B–I), 0.5 mm (J) and 1 mm (K–L).

***Spiranthes australis* (R. Brown 1810: 219) Lindley (1824: 823) × *Spiranthes sinensis* (Persoon 1807: 511) Ames (1908: 53)**

Specimens examined:—TAIWAN. Pingtung: Chunri Township, Tahanshan, 25 April 2017, *J.Z. Lin 3* (TAIF!)

Morphological descriptions and illustrations:—See Suetsugu *et al.* (2020: t2, f2B, f3C & f3G).

Taxonomic remarks:—Two closely related species, *Spiranthes sinensis* and *S. australis*, have been distinguished based on the presence or absence of hairs in their inflorescence and on the stems and ovaries: the stems and ovaries of *S. australis* are generally pubescent, whereas those of *S. sinensis* are glabrous. Intriguingly, although *S. australis* has not been documented to occur in Taiwan, Suetsugu *et al.* (2020) found a population of *Spiranthes* with slightly pubescent stems and ovaries at Tahanshan, southern Taiwan. Because the sequences from the slightly pubescent plants of *Spiranthes* show a combination of sequences between those of *S. australis* and *S. sinensis*, Suetsugu *et al.* (2020) concluded that they were hybrids between *S. sinensis* and *S. australis*.

Acknowledgments

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