Phytotaxa 371 (1): 001–016
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.371.1.1

Apios chendezhaoana (Fabaceae), an overlooked species and a new combination from China: evidence from morphological and molecular analyses

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Abstract

Apios chendezhaoana, a new combination derived from *Sinolegumenea chendezhaoana*, is recognized by both morphological and molecular evidence. It is a new member within *Apios*, and it is also an endemic and endangered species from East and South China. Phylogenetic analyses indicate that it could be sister to *A. fortunei*, but morphologically it differs from all its allies by its broad triangular leaflets with caudate apices, white corolla, pink markings on the lower part of the keel, and dilated style with tufted hairs beneath the stigma. We provide a detailed description, photographs, illustrations, and distribution map. We also estimate its conservation status according to IUCN criteria. A key to *Apios* is also provided, together with a brief revision.

Key words: endangered species, legume, new synonym, taxonomy

Introduction

Apios Fabricius (1759: 176) (Fabaceae) is a small genus of herbaceous climbers with pinnate leaves, which occurs in both Asia and North America (Sa & Gilbert 2010). Two species, *A. americana* Medikus (1787: 355) and *A. priceana* B.L. Robinson (1898: 451–452), are recorded from North America, while no consensus has been reached on the number of species in Asia. A lot of research has been done on the North American species (Seabrook & Dionne 1976; Blackmon 1986; Walter *et al.* 1986; Woods 1988, 2005; Bruneau & Anderson 1988, 1994; Kajita *et al.* 2001), but few studies on the Asian species. Sa & Gilbert (2010) accepted six Asian species, four of which are China endemics, while Woods (1988, 2005) considered that there are only three species in Asia. J. Li *et al.* (2014) included five species in their phylogenetic and biogeographic analyses, in which the Asian species *A. carnea* (Wall.) Bentham *ex* Baker (1876: 188) is sister to the remaining *Apios* species. They suggested that the ancestral population of the North American species may have migrated from Asia via the Bering land bridge and that later parapatric speciation led to the present unequal distribution. Tubers of both *A. americana* and *A. fortunei* Maximowicz (1873: 396–397) are collected as food or medicine, so *Apios* species are considered to have economic potential (Woods 2005; Hu *et al.* 2017).

Yang *et al.* (2004) introduced a new genus *Sinolegumenea* Yong-Kang Yang, Lin-Han Liu & Jia-Kun Wu (2004: 63), with a single species, *S. chendezhaoana* Yong-Kang Yang, Lin-Han Liu & Jia-Kun Wu (2004: 64). The authors provided Latin descriptions, placed it in tribe Phaseoleae, and emphasized the unusual occurrence of single leaves, trifoliolate leaves, and 5-pinnate leaves on one plant, the persistent stipules and stipels, and the 4-lobed calyx. Unfortunately, the new taxon was published in an obscure journal and was overlooked by most botanists. We rediscovered it during a field survey, searched relevant herbaria and libraries, and also did careful morphological

Accepted by Jinshuang Ma: 27 Jul. 2018; published: 25 Sept. 2018

observations and molecular phylogenetic analyses. We confirmed that it is undoubtedly a new *Apios* species and here we propose a new combination, *Apios chendezhaoana.*

Materials and methods

Taxon sampling: We sampled 21 species from 16 genera of the phaseoloid legumes. This sampling scheme covered almost all subtribes of Phaseoleae (Lewis *et al.* 2005) and the genera related to *Apios* (Stefanovic *et al.* 2009; Hong-Lei Li *et al.* 2013; LPWG 2017). In the *Apios*, three species (*A. carnea*, *A. delavayi* Franchet (1890: 180–181), and *A. fortunei*), close to *A. chendezhaoana* in distribution and morphology, were included, as well as *A. americana* and *A. priceana*. Our outgroup included four species (*Platycyamus regnellii* Bentham (1862: 323), *Millettia peguensis* Ali (1968: 489–490), *Clitoria ternatea* Linnaeus (1753a: 753), and *Centrosema pubescens* Bentham (1837: 55)), following the results of Stefanovic *et al.* (2009) and Hong-Lei Li *et al.* (2013).

Molecular analysis: For the phylogenetic analyses, we used one nuclear DNA fragment (ITS) and one chloroplast gene (matK) from 21 taxa (Table 1). Most sequences were acquired from GenBank, except for those of *Apios chendezhaoana*, *Shuteria vestita* Wight & Arnott (1834: 207), and *Cajanus crassus* (Prain *ex* King) Maesen (1986: 110) (Appendix 1). For these three species, total genomic DNA was extracted from silica-dried leaflets with the improved CTAB protocol (Doyle 1987) and sent to Novogene, Tianjin, China, for next generation sequencing using a Hiseq 4000 platform. The reads were assembled into contigs, connected into a complete plastome, and annotated according to Wariss *et al*. (2017). We then extracted matK and ITS sequences from the assembled plastomes and contigs for phylogenetic analyses. Sequences were deposited in GenBank under the accessions MG674200 to MG674204.

TABLE 1. Accession numbers of ITS and matK sequences of sampled species obtained from GenBank.

Species	Accession Number	
	matK	ITS
Apios americana	KF279516	KF272978
Apios carnea	KF279517	KF272981
Apios delavayi	KF272955	KF272993
Apios fortunei	KF272966	KF272994
Apios priceana	KF279519	KF273005
Apios chendezhaoana	MG674203	MG674200
Butea monosperma (Lam.) Taubert (1984: 366)	KY628018	KJ436382
Cajanus crassus	MG674204	MG674201
Centrosema pubescens	KX652115	AF467036
Clitoria ternatea	KX652128	AF467038
Desmodium floridanum Chapman (1860: 102)	EF549994	EF517898
Flemingia macrophylla (Willd.) Kuntze *ex* Merrill (1910: 130)	KF621101	KX277642
Glycine max (L.) Merrill (1917: 274)	EF550007	FJ609734
Lablab purpureus (L.) Sweet (1826: 481)	EU717408	FJ599758
Millettia peguensis	KY241805	KC960439
Mucuna macrocarpa Wallich (1830: 41)	AB627858	AB775133
Pachyrhizus erosus (L.) Urban (1905: 311)	EU717401	AY293846
Platycyamus regnellii	AF142709	AF467491
Pueraria candollei var. *mirifica* (Shaw & Suvat.) Niyomdham (1992: 345)	EU106110	KY860925
Shuteria vestita	EU717423	MG674202
Vigna unguiculata (L.) Walpers (1843: 779)	AY589510	JF430412

Phylogenetic position detection: Sequences were aligned with MAFFT (Katoh *et al.* 2013) using default parameters (Auto algorithm) in Geneious v.9.1.4 (Kearse *et al.* 2012). Alignments were subsequently analyzed visually and adjusted manually. Phylogenetic analyses were performed using the Bayesian inference (BI) and maximum-likelihood (ML) methods. The BI analysis was performed using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003) with four Markov Chain Monte Carlo (MCMC) runs using a random starting tree, TVM+I+G model and 10 million generations, with a sampling frequency of one every 1000 generations and 25% of the trees were discarded as burn-in. The ML analysis was performed using RAxML v7.2.8 (Stamatakis 2006) in Linux OS, including tree robustness assessment using 1000 replicates of rapid bootstrap with the GTRCAT substitution model to assess branch support (Stamatakis 2006).

Results

Morphological observations: Yang *et al.* (2004) made morphological comparisons of this species and *Dunbaria* Wight & Arnott (1834: 258), and listed their differences: 1–5-foliolate (vs. 3-foliolate); stipules and stipels persistent (vs. caducous or absent); calyx lobes triangular and wide (vs. lanceolate and narrow); corolla white (vs. purple or yellow); root tuberous (vs. not tuberous). However, this comparison is not comprehensive and made its placement in the legume family confusing. Pocket-shaped standard, reflexed wings, coiled style, pinnate leaves, starchy tubers, and white latex are key characters of *Apios* species. All characters we observed in *Sinolegumenea chendezhaoana* indicate that it should be placed in *Apios*, rather than a new genus. This newly recognized species, *Apios chendezhaoana*, most resembles *A. fortunei*, but differs by its white corolla, wide wings and keel, broad triangular terminal leaflets, caudate apices, keel curved but not twisted, pink markings on the lower part of keel, and dilated style with several tufted hairs beneath its capitate stigma.

Phylogenetic position detection: This species could be sister to *A. fortunei* (Figure 1) with the Posterior Probability $(PP)_{BI} = 0.84$, Bootstrap $(BP)_{ML} = 0.57$.

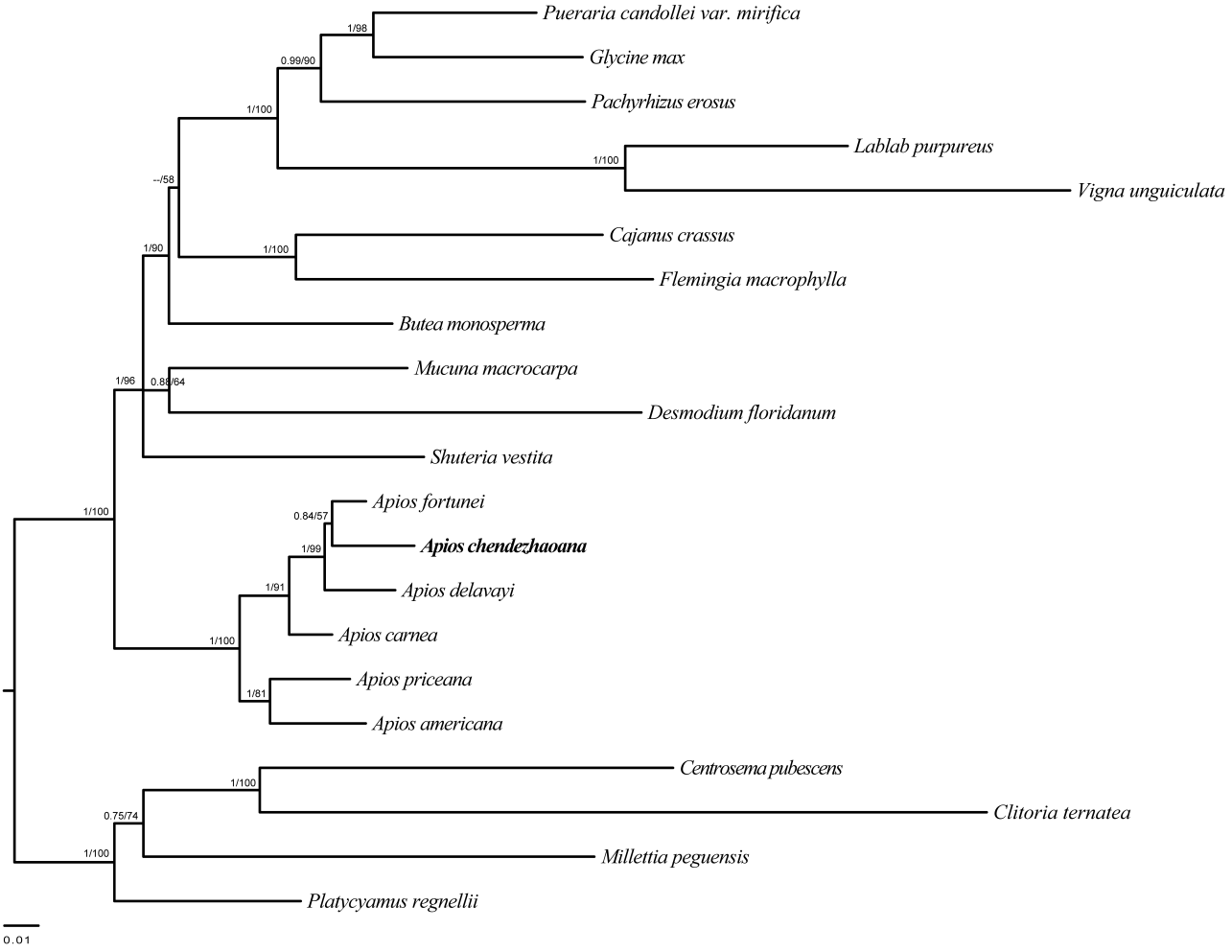

FIGURE 1. The 50% majority rule consensus tree resulting from Bayesian analysis of the combination of ITS and matK. Numbers near the nodes are posterior probabilities and bootstrap percentage (PP, BP) from Bayesian analysis and Maximum likelihood, respectively. A dash (--) indicates a node is inconsistent between the topology of the BI and ML trees. The new combination (species) in this study is shown in bold type.

Taxonomy

Apios chendezhaoana (Y.K. Yang, L.H. Liu & J.K. Wu) Bo Pan (潘勃), Xun-Lin Yu, & Fan Zhang, ***comb. nov.*** (Figure 2 & 3) (南岭土栾儿)

Basionym:—*Sinolegumenea chendezhaoana* Yong-Kang Yang, Lin-Han Liu & Jia-Kun Wu, (2004: 62–76). ***syn. nov.***

Type:—CHINA. Hunan: Yanling, Pikeng Forestry Station, hillside, 600 m, sandy soil, among roadside grasses, rare, ca. 1.5 m long, 30 July 1973, Barcode 18447, labelled '*Dunbaria hunanica sp. nov. ined.*', *Lin-Han Liu 11227* (holotype HNNU!).

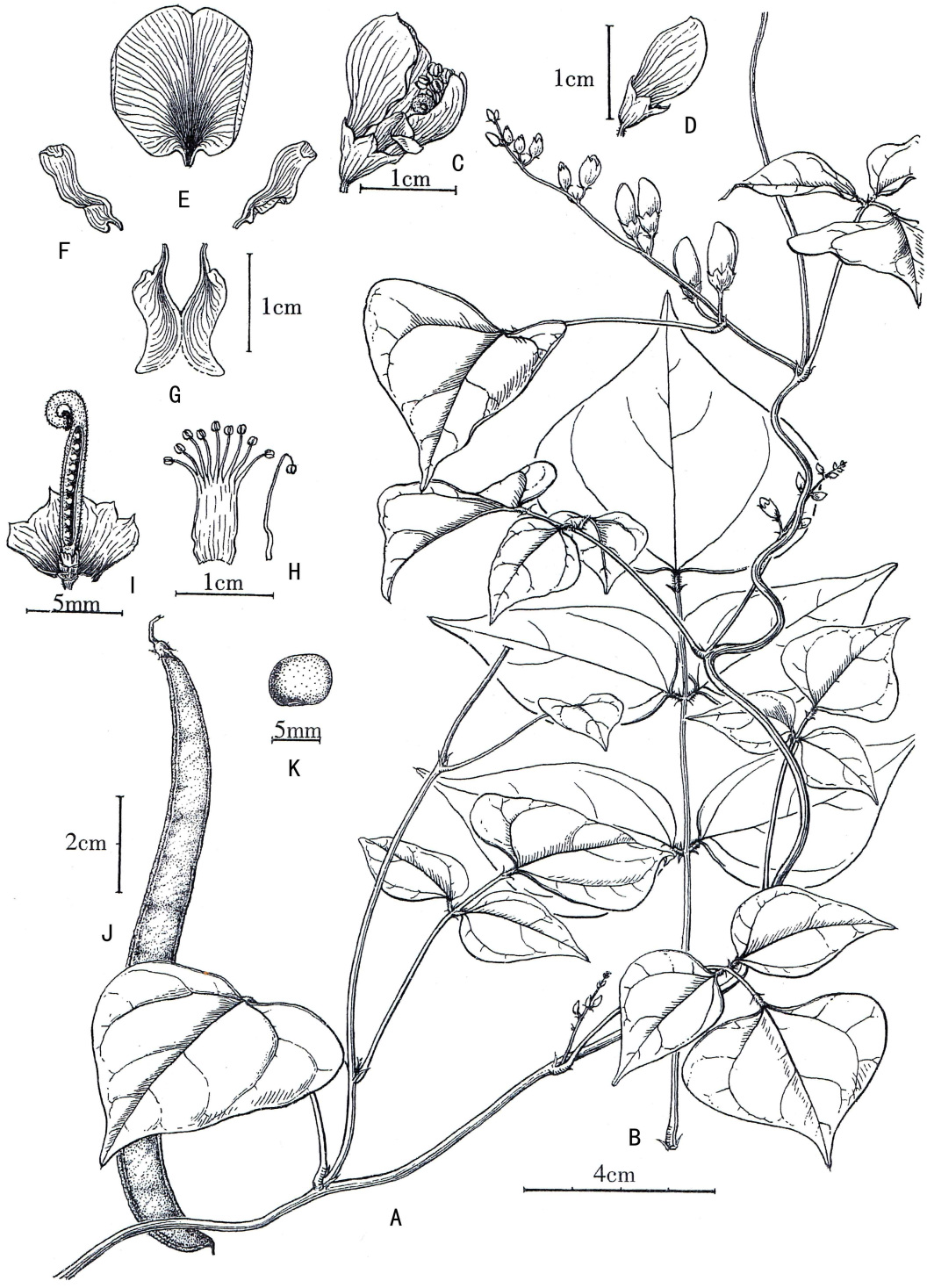

FIGURE 2. *Apios chendezhaoana* (Y.K. Yang, L.H. Liu & J.K. Wu) Bo Pan (潘勃), Xun-Lin Yu & Fan Zhang, *comb. nov.* (A) Flowering branch; (B) Leaves with 5-leaflets; (C) Flower; (D) Unopened flower; (E) Standard; (F) Wings; (G) Keel; (H) Stamens; (I) Calyx & pistil; (J) Pod; (K) Seed. Illustrated by Lin-Han Liu, from the type—CHINA. Hunan: Yanling, Pikeng forestry station, 30 July 1973, Barcode 18447, labelled '*Dunbaria hunanica sp. nov. ined.*', *Lin-Han Liu 11227* (HNNU).

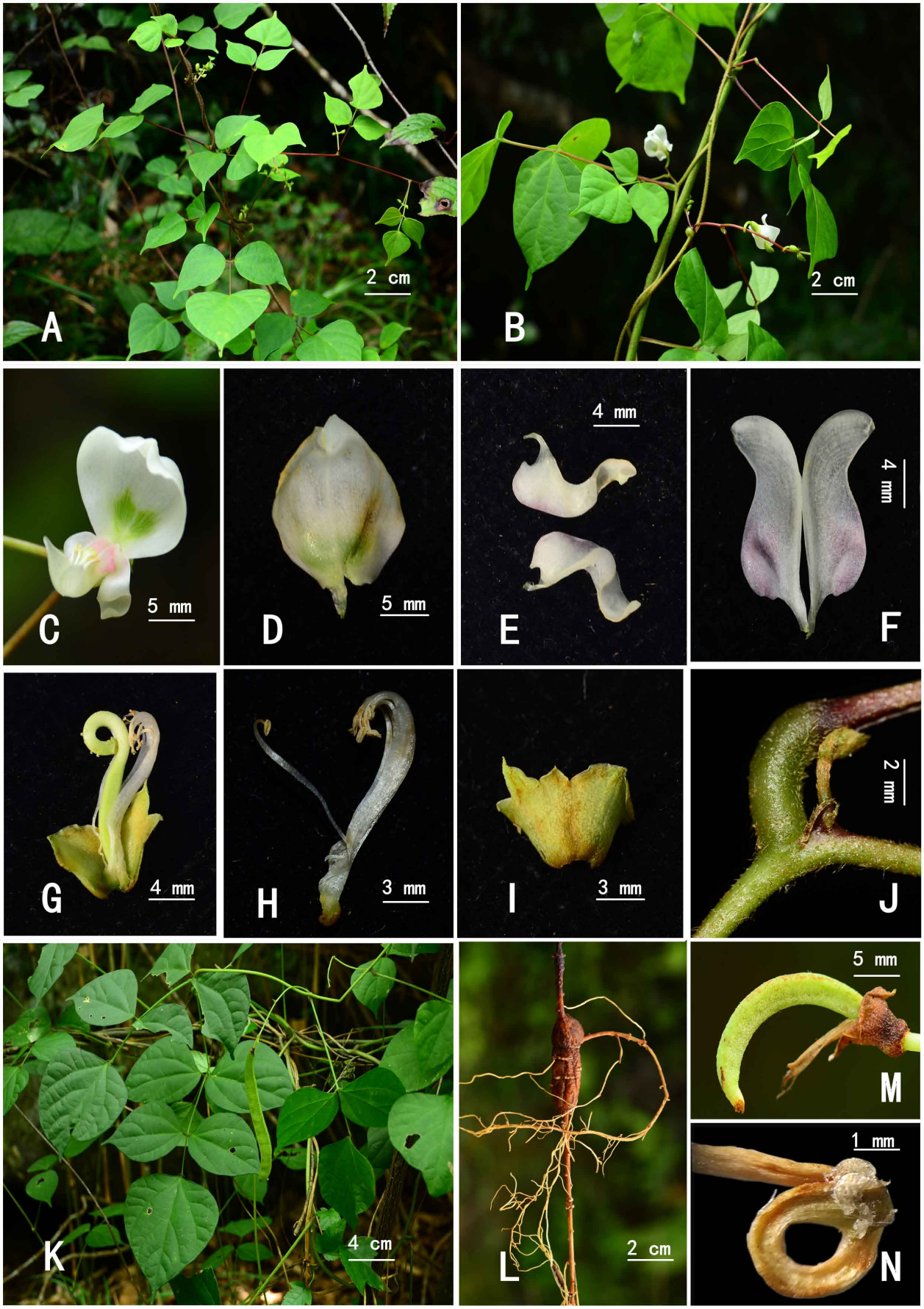

FIGURE 3. *Apios chendezhaoana*. (A) Habit; (B) Flowering branch; (C) Flower; (D) Standard; (E) Wings; (F) Keel; (G) Flower with petals removed; (H) Stamens; (I) Calyx; (J) Stipule; (K) Fruiting branch; (L) Tuber; (M) Young fruit; (N) Stigma. Photographed by Fan Zhang.

Perennial, herbaceous, twining climber, 1.5–3 m long, above-ground part deciduous in winter. Broken parts produce white latex. **Root** usually with 2–4 tubers, 3–7 cm long, connected by long stalks. Tubers fusiform, 3–7 cm long, 5–10 mm in diameter, sometimes segmented. Rootstalk 4–12 cm long, erect, connected to the top of tubers. Adventitious roots usually clustered at the end of lower tubers, ca. 30 cm long, horizontally stretched in the top soil on the surface of granite rocks. Soil layer on the rock is about 20 cm deep, soft, dark brown in color and humid. **Stem** slender, dark reddish brown, tomentose. **Leaves** 3–5 pinnately foliolate, sometimes only one foliolate. Stipules filiform, ca. 4 mm, hirsute, caduceus. Petiole green or dark reddish brown, ca. 3–9 cm, tomentose. Petiolules small, densely hirsute. Stipels small, 1–2 mm, awn-shaped. Leaflets membranous, all 10 mm caudate, tips mucronate, glabrous on both sides, or with sparse horizontal hairs along main veins. Upper side green, lower side glaucous. Terminal leaflet broad triangular or triangular-ovate, membranous, 3.5–10 × 3.5–10 cm; apex acute, base truncate and wide. Lateral leaflets smaller, rhomboid ovate, oblique, 2.5–9 × 1.5–6 cm. **Inflorescence** 6–22 flowered, a nodose pseudoraceme, solitary and axillary, sometimes 2–3 clustered from one axil, 2–8 (–13) cm, usually 2 flowers per node; peduncle 1–2 cm; rachis somewhat zigzag; nodes swollen; sometimes the lowest node subtended with 1-foliolate leaf; bracts linear, 1–3 mm, minute; bracteoles subtending the calyx, 1.5 mm; pedicels ca. 7 mm. **Calyx** campanulate, 5–7 mm, 4 toothed, the upper lobe the widest, and the lower tooth the longest, appressed hairy on the outer surface; inner surface of calyx sparsely hairy on the teeth and the upper area along the calyx tube, while glabrous on the lower part. **Corolla** white, exerted, longer than the calyx, ca. 15–17 mm. Flowers usually incompletely open, with standard apex and keel apex very close to each other. Standard the largest, covering up all the other petals, ca. 12–17 × 11–16 mm, like a pocket in shape, not revolute, with a green patch at the lower part, shortly auriculate at both sides, shortly clawed 2.5 mm; wings much smaller, 8 × 3 mm, oblong, refolded into a S shape, auriculate on one side, ca. 2 mm clawed; keel ca. 14 × 5 mm, falcate and very curved, the lower 2/3 connate, and the upper 1/3 separate; keel claw 3 mm; lower part of blades with pink markings. Stamens diadelphous, 9+1, 10–13 mm; anthers ovoid, equal in size. Pistil filiform, 10–12 ovuled, ca. 13 mm, shortly hairy; style coiled and dilated; stigma capitate, with several short tufts of hairs beneath. Floral disc at the base of the pistil, yellowish green, 1.5 mm. Pods linear to falcate, glabrous, 9–13 cm long, 7–11 mm wide, attenuate towards base, ca. 10 seeded; valves leathery, twisted when dry; seeds orbicular, laterally compressed, 7–10 mm, black and nitid; aril short, 0.5–1 mm; hilum linear, 0.5–0.7 mm, slightly sunken, white in color,

Phenology:—Flowering June to August, fruiting August to October.

Distribution and habitat: (Figure 4)—*A. chendezhaoana*, endemic to China, occurs only in moist and shady gullies of the Luoxiao, Nanling, and Wuyi Mountains along the borders of Fujian, Guangdong, Hunan, and Jiangxi provinces, at elevations between 400–1300 m. It climbs in bushes of the evergreen broadleaved forest undergrowth. The soil is usually wet, shallow and soft, dark brown in color.

Etymology:—The Latin epithet is in honor of a female botanist, Mrs. Te-Chao CHEN (陈德昭, Chen Dezhao in Chinese pinyin), from the South China Botanical Garden, who contributed to the treatments of many legumes in the *Flora of China*. The Chinese name '南岭' refers to one of its main areas of distribution in China—the Nanling Mountain Range.

Conservation status:—*Apios priceana* was listed as an endangered species in the USA because there are only 47 known populations from 22 counties in four states (Woods 2005). The situation of *A. chendezhaoana* is very similar to this. We have so far found only 23 specimens and 15 recorded populations from four provinces. Each population has only 1–10 known individuals, and each location is very remote from the next. The total number of individuals is estimated to be less than 250, allowing for undiscovered populations. Most specimens were collected decades ago and recent records are rare. Like all its allies, but unlike most legumes, this species prefers shady and undisturbed habitats, shallow and fertile soils, along creeks and streams, so it is very susceptible to human disturbance. In view of the very small number of individuals and scattered distribution, we evaluate this species as **Endangered** (**EN D**) in accordance with the IUCN Red List Categories and Criteria version 3.1 (2001) (http://www.iucnredlist.org/static/categories_criteria_3_1).

Additional specimens examined:—CHINA. Fujian: Taining, Datian, Yangkeng, among grasses in forest, 10 July 1979, labelled '*Apios fortunei*', *Ming-Sheng Li 971* (IBSC). **Guangdong:** Longtou Shan, Lingnan, in small ravine, along hillside. Vine 1.8 m. Flower white. 15 July 1924, labelled '*Apios fortunei*', *To & Tsang 12895* (NAS, P). Beijiang, Yaoshan, Huangdong, 686 m, 19 June 1930, labelled '*Apios fortunei*', *Shu-Chi Xin 10027* (IBSC). Qujiang, Xiaokeng Forestry Station, sparse forest, streamside, rare, 6 August 1985, *Nanling Team 850* (IBSC). Lechang, Liangjiang, Shizishan, 700 m, in valley, sparse forest, 28 October 1987, *Lechang Team 4100* (IBSC). Shixing, Duheng, Taoyuan, 580 m, 17 July 1982, *Gui-Cai Zhang & Hua-Gu Ye 447* (IBSC). Heping, Liyuan, Qutan, 500 m, 5 August 1983, *Gui-Cai Zhang & Hua-Gu Ye 365* (IBSC). **Hunan:** Yanling, Pikeng Forestry Station, 38KM, hillside, 450 m, humid soil, in valley, along roadside within a 25 m distance, sparse forest, canopy cover 15%, scattered, 30 August

1985, *Lin-Han Liu 11439* (HNNU). Yanling, Taoyuandong, Niujiaolong, Qiguxian, Shunfengqiao, 1270 m, in valley, fertile loam, streamside, under dense broadleaved forest, canopy cover 70%, rare and scattered, 14 September 2008, *Lin-Han Liu & Ying-Di Liu 30105* (HNNU). Jianghua, Daxi, Jilong village, hillside, 500 m, in valley, dense forest, roadside, rare, 18 July 1999, *Guang-Wan Hu 219082* (HNNU). Jianghua, Daxi, hillside, 240 m, in valley, sparse forest, rare, 9 September 1999, *Ke-Ming Liu 767215* (HNNU). Yizhang, Qitianling Forestry Station, streamside, under broadleaved forest, 1078 m, 2 August 2017, *Xun-Lin Yu & Fan Zhang 1708020101* (CSFI). **Jiangxi:** Zixi, Matoushan (Wuyi Mountain), in bamboo shade, streamside, 450 m, 15 July 1958, *Min-Xiang Nie & Shu-Shen Lai 3455* (LBG, KUN). Jinggangshan, Ganggangshan, roadside along shady slope, grassland, 1300 m, 9 July 1965, *Shu-Shen Lai, Ru-Jü Yang & Da-Fu Huang 4393* (KUN, LBG). Anfu, Wugongshan, Wenjiadaling, in forest undergrowth, shady slope, along the creek, 800 m, 8 August 1963, *Jun-San Yue 3172* (KUN, NAS). Anfu, Wugongshan, Dabeitou, in streamside bushes, 500 m, 3 August 1963, *Jun-San Yue 2773* (KUN, NAS). No. 007955, Jinggangshan, June 1975, labelled '*Apios fortunei*', *Anonymous 75002* (JXCM). No. 007358, August 1971, *Anonymous s.n.* (JXCM). No. 741143, labelled '*Vigna umbellata*', *Anonymous s.n.* (JXU).

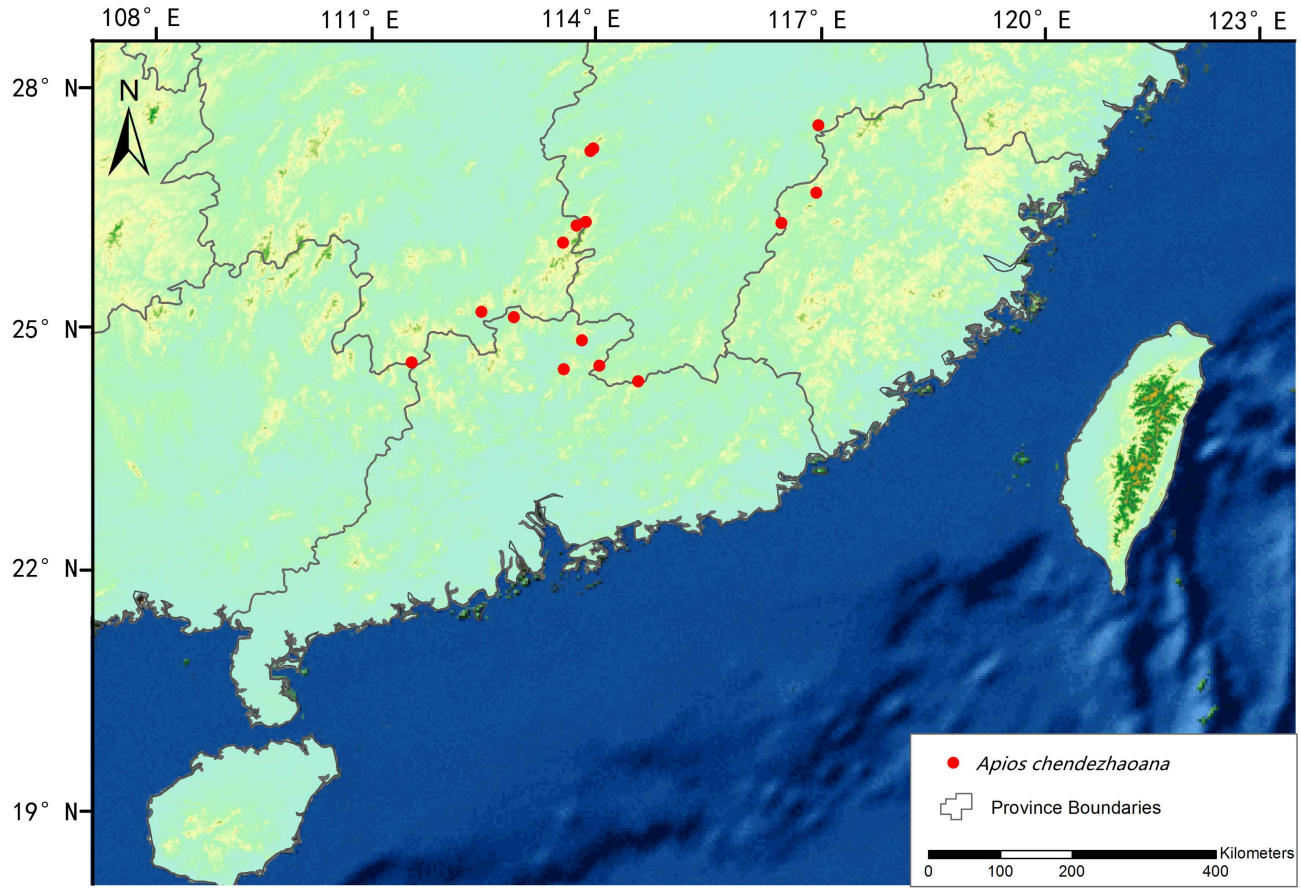

FIGURE 4. Geographical distribution of *Apios chendezhaoana*. Prepared by Dr. Rui-Wu Zhou.

Taxonomic notes on allied species

The generic name *Apios* has undergone complicated changes. Cornut (1633) first adopted the generic name '*Apios*' for the groundnut plant, *Apios americana*, before *Species Plantarum* and the modern era of botanical nomenclature. Linnaeus (1753b) established a new genus *Glycine*, and listed *Apios americana* as a synonym of *Glycine apios*. Later, Fabricus (1759) recognized *A. americana*, crediting Cornut as the authority, and listed *Glycine apios* as a synonym. Medikus (1787) reestablished *Apios*, perhaps because he overlooked Fabricus's work. Afterwards, for more than 100 years, both *Apios* and *Glycine* were frequently used until, in the first edition of the Botanical Code in 1905 (Briquet 1906), *Apios* Medikus was chosen as the nomenclatural type against *Glycine* Linnaeus. Lanjouw (1966) confirmed that

Fabricus was the first one who established *Apios*, thus *Apios* Fabricus was accepted against *Apios* Medikus. More than 20 names have been published under *Apios* until now. Hui-Lin Li (1952) accepted eight species, Hutchison (1964), Lackey (1981), S.G. Li (1995) and Chen (1998) thought there were ten *Apios* species, while Woods (1988) confirmed only five species and one variety in his PhD dissertation, two species in North America and the rest in East Asia. Six Chinese *Apios* species were accepted by *Flora Reipublicae Popularis Sinicae*, but *A. bodinieri* H. Léveillé (1914: 225) and *A. delavayi* var. *pteridietorum* Handel-Mazzetti (1933: 580) were not treated because of unavailable materials during that time (S.G. Li 1995). Both names were neither mentioned nor treated in the *Flora of China* (Sa & Gilbert 2010). Since no consensus has been reached on the number and delimitation of species within *Apios*, a brief history of its classification is given here, with new evidence and a new revision:

Apios carnea (Wall.) Bentham *ex* Baker (1876: 188).

Type:—NEPAL. 1 July 1821, *N. Wallich 5527, Barcode E00185070* (lectotype E! here designated).

Apios bodinieri H. Léveillé (1914: 225). ***syn. nov.***

Type:—CHINA. Guizhou: Mei-Tong-Chan, *E.M. Bodinier 499, Barcode E00185067* (lectotype E! here designated).

Twinning climbers 3–4 m long. Sometimes old rootstocks woody. Leaves usually 5-foliolate, 12–25 cm; stipules and stipels persistent; leaflets oblong to ovate-oblong, 3.5–13 × 2–7 cm, papery. Raceme 15–40 cm, 2–3 flowers per node. Calyx campanulate, 4 lobed. Corolla red, reddish purple, or orange, quite open when flowering, twice as long as calyx. Wings shortest, 0.6–1.2 cm; keel curved to semicircular. Style coiled. Legume linear, 8–19 × 0.6–0.7 cm. Seeds 12–21, dark brown.

Distribution and habitat:—*Apios carnea* is distributed in Bhutan, China, India, Laos, Myanmar, Nepal, Thailand, and Vietnam. It grows in forests, or along riversides and roadsides, at elevations between 600–3200 m above sea level.

Phenology:—Flowering from July to September; fruiting from August to November.

Apios bodinieri has lax nodose inflorescences, red and open flowers. It most resembles *Apios carnea* and only differs from the latter by its trifoliolate leaves. Occasionally *A. carnea* has leaves with 3 leaflets, or even 7 leaflets, so we reduce *A. bodinieri* to a synonym of *A. carnea*. Woods (1988) also included *A. bodinieri* within *A. carnea*.

Specimens examined:—CHINA. Chongqing: Chengkou, Baichi Mt. 800m, 10 September 1958, *Tian-Lun Dai 102503* (PE). **Fujian:** Chong'an, Sangang, Nanshan, 6 August 1958, *Pei-Xi Qiu 1653* (PE). **Gansu:** Wenxian, Fanba, 680 m, 21 October 1973, *Zhi-Xin Hu 3496* (IBSC). **Guangdong:** Xinyi, Shuangchangping, Fengdali, 12 August 1931, *Xi-Peng Gao 51790* (PE). **Guangxi:** Damiaoshan, Sanfang, Pingshixiang, Jiuwan Mt., Jiuyang River, 31 August 1958, *Shao-Qing Chen 16576* (IBK). Lingchuan, Dajing, Baotalong, 9 September 1984, *Ru-Rong Yang 84012* (PE). **Guizou:** Bijie, Baohe, 1500 m, 20 August 1957, *Ping-Hua Yu 427* (PE). Xingren, Baling, Chenjiagou, 1300 m, 14 August 1960, *Guizhou Team 7735* (PE). **Hunan:** Xinhuang, Tianleishan, 800 m, 13 July 1988, *Wulingshan Team 836* (PE). Xinning, Ziyun Mt., 1150 m, 16 September 1984, *Ziyun Team 1931* (PE). **Jiangxi:** Jinggangshan, 730 m, 19 October 1963, *Jun-San Yue 4861* (PE). **Sichuan:** Mount Emei, Da'e Temple, 1 September 1939, *Zhong-Wu Wang 4953* (PE). Mianning, Daqiao, Xiaogou, 2100 m, 4 July 1959, *Su-Gong Wu 2192* (PE). Yibin, Gulin, Wulong, Qinglong, 27 August 1976, *Shibao Team s.n.* (SM). **Xizang:** Linzhi, Dongjiu to Tongmai, 3 August 1975, *Qingzang Team 751237* (PE). **Yunnan:** Baoshan, Pupiao, May 1941, *Han-Chen Wang 800* (PE). Gongshan, Dulongjiang, Maku, 5 August 1982, *Qingzang Team 8895* (PE). Songming, Guodong, 25 August 1957, *Bing-Yun Qiu 55047* (PE).

Apios delavayi Franchet (1890: 180–181).

Type:—CHINA. Yunnan, 14 September 1886, *M. Delavay 2323, Barcode P00237786* (holotype P!).

Perennial herbs. Tuber single, fusiform, 2–5 cm in diameter, 5–20 cm long. Leaves pinnately compound, 8–32 cm, (3–) 5–9 (–11) leaflets. Leaflets highly variable, ovate to lanceolate, apex acuminate to acute. Racemes shorter or much longer than leaves. 2–30 flowers, lax. Calyx 2-lipped. Corolla light yellow, yellowish white, greenish yellow, yellowish purple, or dark purple; standard orbicular, pocket shaped, covering the tip of keel; wings shortest, reflexed; keel narrow, curved to semicircular, longer than standard. Legume linear or falcate, attenuate at base, 7–15 cm.

Apios delavayi Franchet (1890), *Apios macrantha* Oliver (1890, October: pl. 1946), *Apios gracillima* Dunn (1903: 488–489), and *Apios delavayi* var. *pteridietorum* Handel-Mazzetti (1933), are all from SW China, and distinguished by flower color, inflorescence length, leaflet width, and flower number of each inflorescence (Sa & Gilbert 2010). However, only the name *A. delavayi* is frequently adopted during identification, and the other three names have seldom been used. Ren *et al.* (2007) considered that *A. gracillima* should be recognized as a distinct species, according to

evidence from the leaf epidermis. However, using only microscopic evidence during taxonomic delimitations and treatments is not recommended. After examination of hundreds of specimens from CDBI, KUN, PE, and SM, we found they all have very similar flower shapes, with various colors from pale yellow, light green, greenish white to yellowish violet, light purple, and even dark purple. Leaflet numbers vary from 3 to 11; leaflet shape from linear to narrow lanceolate, lanceolate, and ovate; inflorescence longer or shorter than leaves, and flowers 6–30 or 2–4 per inflorescence. They all have the following consistent characters: lax inflorescence, broad standard, long curved circular keel, falcate pod, fusiform tuber, and a high elevation distribution between 1300–3800 m. We therefore include all the four taxa into one species, *Apios delavayi*, as synonyms or varieties.

Because both *A. delavayi* and *A. macrantha* were published in 1890, while *A. macrantha* is not widely used, here we propose to conserve *A. delavayi* against *A. macrantha*. Interestingly, populations east of the Mekong-Salween Divide always have pale yellow to greenish white flowers, while populations west of the divide have light purple to dark purple flowers. Types of *Apios delavayi* and *A. macrantha* were both collected from the east part, and present greenish white or pale yellow flowers, while the type of *A. delavayi* var. *pteridietorum* was collected from west of the divide, and bears purple flowers. The Mekong-Salween Divide is an important floristic boundary between the eastern Himalaya and Hengduan Mountains (Luo *et al.* 2017), so we adopt both *A. delavayi* var. *delavayi* and *A. delavayi* var. *pteridietorum* as accepted names to represent the distinct distribution of flower colors.

Apios delavayi* var. *delavayi

Apios macrantha Oliver (1890: pl. 1946). ***syn. nov.***

Type:—CHINA. Sichuan, *A. Henry 8984, Barcode K000262502* (lectotype K! here designated).

Flowers pale yellow, or greenish white. This variety represents *A. delavayi* populations east of the Mekong-Salween Divide.

Distribution and habitat:—This variety is distributed in Sichuan and Yunnan provinces of China. It grows in mixed forests, thickets or grasses along rivers at elevations between 1300–3800 m above sea level.

Phenology:—Flowering from June to September; fruiting from September to November.

Specimens examined:—CHINA. Sichuan: Baoxing Shaoqikari Valley, 2350 m, 27 June 1958, *Xiu-Bao Zhang & You-Xi Ren 5656* (PE). Beichuan, Xiaozhaizigou Reserve, 1600 m, 1 August 1984, *Chang-Lin Tang 309* (CDBI). Danba, Gejing, 3100 m, 2 September 1974, *Sichuan Team 7416* (CDBI). Hanyuan, Xianglingshan, 1800 m, 14 September 1938, *T.P. Wang 9692* (WUK). Hongxi, Walijiaomen, 1900 m, 14 July 1959, *Liangshan Team 1209* (KUN). Kangding, Shade, Baimaqiao, 3000 m, 3 August 1982, *Jian Dong 29580* (CDBI). Liangshan, Puge, 14 September 1979, *Puge Team 886* (SM). Litang to Yalung Divide, 9000–10000 ft, *F.K. Ward 4357* (E). Luding, Yangquangou, 1950 m, 20 August 1963, *Ke-Jian Guan et al. 1709* (PE). Maoxian, 1952, *Zhu He & Zi-Lin Zhou 14026* (CDBI). Meigu, Shuwo, 1750 m, 2 July 1976, *Sichuan Team 13533* (CDBI). Muli, Wanglang to Chabulang, 2500 m, 16 September 1983, *Qingzang Team 14134* (PE). Muli or Mill Kingdom, *J.F. Rock 5525&6471* (E). Muli, Wachin, 2800 m, 12 October 1937, *T.T. Yü 14502* (E). Nanping, Wujiao, Laoheba, 2000 m, 1 August 1959, *Nanping Team 4216* (CDBI). Neighbourhood of Tatsien-lu, 1924, *R. Cunningham 506* (E). Pingwu, Wangbachu, 2020 m, 3 July 1984, *Sichuan Team 134* (CDBI). Qianning, Songlinjiang, 3700 m, 22 July 1959, *Shu Jiang & Cun-Li Jin 2181* (PE). Shimian, Jinwo, 2200 m, 1 August 1985, *Guo-Hong Xu 25657* (CDBI). Wenchuan, Hongqiying, 2010 m, 3 June 1975, *Sichuan Team 8124* (CDBI). West Garze, Road from Luding to Kanding, 1875 m, *CEE 322* (E). West of Muli, 10000 ft, July 1922, *G. Forrest 22151* (E). Xiangcheng, Yazha, 3300 m, 2 September 1972, *Sichuan Team 3531* (CDBI). Xiaojin, Pan'an, 2100 m, 1 August 1958, *Sichuan Agricultural College 6707* (CDBI). Yanbian, Waluo, 16 September 1978, *Yanbian Team 446* (SM). **Yunnan:** 1920, *Simeon Ten 135* (E). Binchuan, Xiayang to Waxi, 14 October 1946, *Shen-E Liu 21524* (PE). Chienchuan to Mekong Divide, 9000–10000 ft, August 1922, *G. Forrest 21964* (E). Chungtun Plateau, 12000 ft, July 1914, *G. Forrest 12835* (E). Eryuan, Zhujiaying, Longdingshan, 21 July 1929, *Ren-Chang Qin 23328* (PE). Heqing, Xiangshuihe, 3300 m, 2 September 1929, *Ren-Chang Qin 24285* (PE). Jianchuan, Misha, 2600 m, 13 October 1958, *Wen-Cai Wang 414* (KUN). Lijiang, 2700 m, July 1935, *Qi-Wu Wang 71228* (PE). Luquan, Zhongping, 2400 m, 13 November 1952, *Pin-Yi Mao 1754* (KUN). Mekong Valley, 9000 ft, August 1914, *G. Forrest 13014* (E). North of Jung-Peh, 9000 ft, August 1922, *G. Forrest 22093* (E). Yiliang, Yangzonghai, 1800 m, 6 September 1977, *Bing-Yun Qiu 771272* (KUN). Zhongdian, Baidi, 2700 m, 8 August 1962, *Zhongdian Team 1019* (PE).

Apios delavayi* var. *pteridietorum Handel-Mazzetti (1933: 580).

Type:—CHINA. Yunnan: Salween, *H. Handel-Mazzetti 8990* (holotype WU! Isotype E!).

Flowers yellowish violet, light purple, or dark purple. This variety represents *A. delavayi* populations west of the Mekong-Salween Divide.

Distribution and habitat:—This variety is distributed in China (Xizang and Yunnan) and India (Assam). It grows in pine forests, mixed forests or thickets at elevations between 1700–3500 m above sea level.

Phenology:—Flowering from June to September; fruiting from July to October.

Specimens examined:—CHINA. Xizang: Baiba, 17 June 1952, *Bu-Qiu Zhong 6643* (PE). Bomi, between Bomi and Tongmai, 2600–2800 m, *Su-Gong Wu et al. 105962* (KUN). Chayu, Xialun, 1860 m, 31 July 1980, *Zhi-Cheng Ni et al. 942* (PE). Chayu, Tongmai to Lulang, 2210 m, 27 July 1965, *Yong-Tian Zhang & Kai-Yong Lang 939* (PE). Gorge of the Tsangpo, 8000–10000 ft, 19 July1924, *F.K. Ward 5961* (E). Linzhi, Dongjiu to Chayuan, 2900 m, 17 June 1972, *Xizang Medicinal Plants Team 3466* (PE). Pome, near Showa, Satang, 7500 ft, 19 September 1947, *Ludlow et al. 13192* (E). Salween-Kiuchiang Divide, July 1919, *G. Forrest 19321* (E). Salween valley, 10000 ft, 22 October 1917, *F.K. Ward 5420* (E). **Yunnan:** Deqin, 3000 m, July 1935, *Qi-Wu Wang 64738* (PE). Dulongjiang, Longdang to Longjigeng, 1900–2100 m, 3 September 1982, *Qingzang Team 9873* (KUN). Gongshan, Yu'en, 3300 m, 25 August 1940, *Feng 6898* (PE). Kiukiang Valley, Taron, Chiengen, 1700 m, 26 July 1938, *T.T. Yü 19419* (E, PE). **INDIA. Assam:** Di Chu Gorge, 7000 ft, 6 August 1950, *F.K. Ward 20115* (E).

Apios delavayi* var. *gracillima (Dunn) Bo Pan (潘勃), ***stat. nov.***

Basionym: *Apios gracillima* Dunn (1903: 488–489). ***syn. nov.***

Type:—CHINA. Yunnan: Mengtze, 6000 ft, 14 September, *A. Henry 9828, Barcode K000262506* (lectotype K! here designated).

Apios gracillima is unique by its linear to narrow oblong or lanceolate leaflets with rounded apex, and 2–4 purple flowers in each inflorescence. It is very rare and scattered, although the name *A. gracillima* has always been used for specimens of *A. delavayi* var. *pteridietorum*. All the specimens including the type are collected from the Honghe River drainage. Due to its similarity with *A. delavayi*, we reduce *A. gracillima* to a variety of *A. delavayi*.

Distribution and habitat:—This variety is only found from the Honghe River drainage, Yunnan province, at ca. 1800 m above sea level.

Phenology:—Flowering from September to October; fruiting unknown.

Specimen examined:—CHINA. Yunnan: Chuxiong, Baomanjie, Lianwangba, 1800 m, 18 September 1958, *Shu-Qiong Huang 11* (KUN). Menghua, top of Lung Yu Mt., 5 September 1935, *McLaren 111* (E). Yao-chou, summit of a mountain, October, *McLaren F66* (E).

Apios fortunei Maximowicz (1873: 396–397).

Type:—CHINA. 1845. *A. Fortune 44, Barcode K000262505* (lectotype K! here designated).

Apios taiwaniana Hosokawa (1932: 310). ***syn. nov.***

Type:—CHINA. Taiwan, 17 July 1931, *Hosokawa 3026* (holotype TAI!).

Twining herbs. Root with 1–4 spherical tubers. Stem sparsely hirsute. Leaves pinnately 3–7-foliolate, 10–25 cm, leaflets ovate or rhomboid-ovate, 3–7.5 × 1.5–4 cm, apex acute. Pseudoraceme axillary, 6–26 cm. Calyx shallowly 2-lipped. Corolla yellowish green or light green; wings reflexed, almost half as long as standard, usually with a red purple edge; keels much longer than standard, twisted to one side, and curled into a semicircle. Legume linear, ca. 8 cm long.

Apios fortunei and *A. taiwaniana* both have narrow petals and a twisted keel, and present very few differences. However, *A. taiwaniana* is claimed to be a Taiwan endemic (Sa & Gilbert 2010), while *A. fortunei* is widespread in E China and Japan. Their morphological differences are minor: *A. fortunei* has ovate to rhomboid-ovate leaflets and 3–7 flowers per node, while *A. taiwaniana* has ovate-lanceolate to ovate leaflets, and 3–4 flowers per node (Sa & Gilbert 2010). Michael Woods annotated Taiwan specimens as *A. fortunei*, according to labels attached to herbarium specimens. J. Li *et al.* (2014) also considered that *A. taiwaniana* is a synonym of *A. fortunei*. We carefully compared specimens from Taiwan with *A. fortunei* from the China mainland, and found the shape of leaflets variable, from ovate-lanceolate to rhomboid-ovate, and flowers numbers usually 3–4, but sometimes 5 or more. All the distinct characters claimed by Hosokawa (1932) were within the range of variation of *A. fortunei* so there is no need to retain *A. taiwaniana* as a separate species. We therefore treat *A. taiwaniana* as a synonym of *A. fortunei*.

TABLE 2. Morphological comparison of *A. chendezhaoana* and its Asiatic allies.

	A. chendezhaoana	*A. fortunei*	*A. carnea*	*A. delavayi*		
				var. *delavayi*	**var. *pteridietorum***	**var. *gracillima***
Tubers	usually 2–4, fusiform, 3–7 cm long, 5–10 mm in diameter, connected by thin stalks	spherical, single or 2–6 moniliform, 2–6 cm long	undeveloped or slightly swollen	single, fusiform 7–20 cm long	single, fusiform, 7–20 cm long	unknown
Leaflet number	(1–) 3–5	3–7	(3–) 5 (–7)	(3–) 5–9 (–11)	(3–) 5–9 (–11)	5–7(–9)
Terminal leaflet	broad triangular	ovate to rhomboid ovate	oblong to oblong ovate	ovate to lanceolate ovate	ovate to lanceolate ovate	lanceolate to linear
Leaflet apex	caudate	acuminate	acuminate to acute	acuminate to acute	acuminate to acute	obtuse
Inflorescence	lax, 2–13 cm long, 6–22 flowered	lax, 10–25 cm long, 25–40 flowered	lax, 15–40 cm long, 8–25 flowered	lax, 5–25 cm long, 6–30 flowered	lax, 5–25 cm long, 6–30 flowered	lax, 2–6 cm long, 2–4 flowered
Flower color	white	light green or yellowish green	red, reddish purple, or orange	pale yellow, greenish white	yellowish purple to dark purple	purple
Standard	pocket shaped	pocket shaped at the tip	flat	pocket shaped at the tip	pocket shaped at the tip	pocket shaped at the tip
Keel	incurved but not twisted, pink markings on lower side	incurved and strongly twisted to one side	incurved but not twisted	petals narrow, incurved but not twisted	petals narrow, incurved but not twisted	petals narrow, incurved but not twisted
Legume	linear to falcate, base attenuate, 9–13 cm long, 7–11 mm wide	linear, 7–8 cm long, 5–6 mm wide	linear, 8–20 cm long, 6–7 mm wide	linear or falcate, base attenuate, 7–15 cm long, 8–13 mm wide	linear or falcate, base attenuate, 7–15 cm long, 8–13 mm wide	unknown

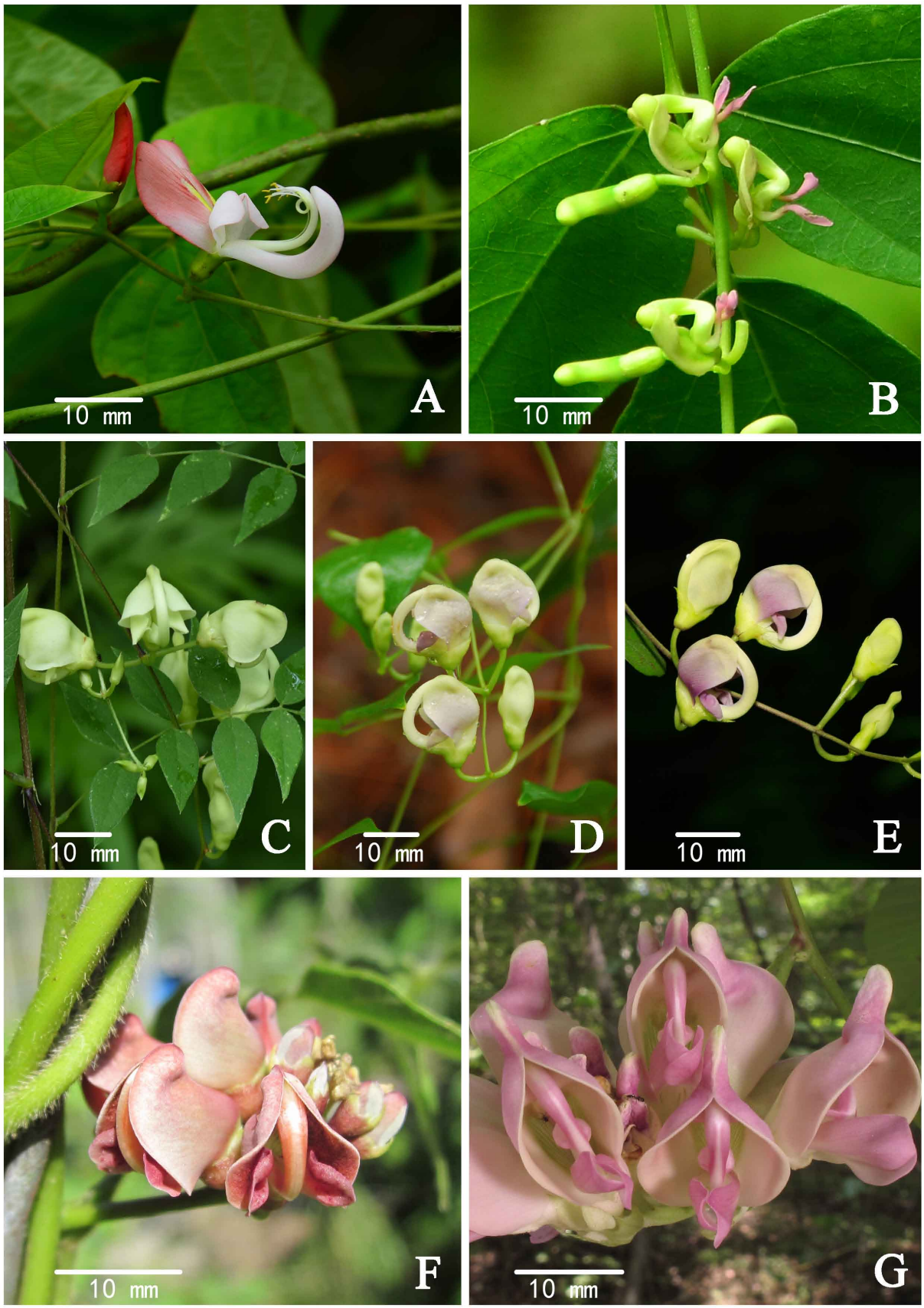

FIGURE 5. Floral comparison of *Apios* species: (A) *A. carnea* from Hunan, China, courtesy of Lei Wu; (B) *A. fortunei* from Hunan, China, photographed by Fan Zhang; (C) *A. delvavayi* var. *delavayi* from Sichuan, China, courtesy of Ang Liu; (D–E) *A. delavayi* var. *pteridietorum*. (D) from Chayu, Xizang, China, courtesy of Chun-Mei He. (E) from Gongshan, Yunnan, China, courtesy of Bin Chen; (F) *A. americana*, from Washington, United States, courtesy of Adam J. Peterson; (G) *A. priceana*, from Maryland, United States, courtesy of Alan Cressler.

Distribution and habitat:—*Apios fortunei* is distributed in China and Japan. It grows on mountain slopes, usually in moist areas at elevations between 50–1900 m above the sea level.

Phenology:—Flowering from June to August, fruiting from September to October.

Specimens examined:—CHINA. Anhui: Guangde, Baidian Gaoshan, 250 m, 26 July 1959, *Anonymous 3194* (PE). **Chongqing:** Wushan, Luoping, Shaping, 1100 m, 13 August 1964, *Hong-Fu Zhou 109761* (PE). **Fujian:** Yanping, Banyan, 13 June 1925, *Xin-Xuan Zhong 3381* (AU). **Guangdong:** Tuantang, 4 August 1930, *Xi-Peng Gao 50730* (PE). **Guizhou:** 8 July 1930, *Jiangying 5693* (PE). Fanjingshan, 1932, *Da-Hua Du 33510* (PE). **Henan:** Qintou Mt., July 1959, *Jie Chen 655* (HENU). **Hubei:** Yingshan, Santan, 500 m, June 1992, *Dong-Sheng Lu 156* (HENU). **Hunan:** Yongshun, Liuxi, Mengdong River, 20 June 1988, *Beijing Team 1737* (PE). **Jiangsu:** Lianyungang, Sucheng, Dazhuyuan, 60 m, 21 August 2011, *Zeng-Lai Xu & Bao-Cheng Wu 943* (NAS). **Jiangxi:** Chongyi, Mixi, Xikengwei, 800 m, 9 June 1965, *Min-Xiang Nie 8783* (IBSC). Jing'an, Shijing, 960 m, 1 July 1997, *Ce-Ming Tan 971087* (PE). **Shanghai:** Pudong, Chuanshajiang, 23 August 1958, *De-Xian Ye 1577* (HHBG). **Sichuan:** Youyang, 350 m, 19 July 1984, *Shi-Xian Tan 153* (PE). **Taiwan:** Jiayi, Shizhuo, Alishan, 12 November 1985, *Y. Tateishi & H. Hoshi 21514* (TAI). Gaoxiong, Tengzhi, 22 October 1982, *H. Ohashi et al. 182089* (TAI). Miaoli, Xiangtianhu, 14 July 1986, *M.T. Kao 10268* (TAI). Nantou, Bihu, 5 May 1984, *S.F. Huang 1845* (TAI). Nantou, Meifeng Farm, Musya-Santinozyo, 30 July 1939, *Masamune, Mori, & Nakamura 2381* (TAI). Nantou, Ren'ai, Wushe, 17 May 1985, *M.C. Tsai 32* (TAI). Nantou, Riyuetan, 21 September 1929, *Kudo & Sasaki 15604* (TAI). Taizhong, Huanshan, 4 September 1993, *K.C. Yang s.n.* (TAI). Taizhong, Wuling Farm, 8 October 1986, *J.C. Wang et al. 3913* (TAI). Taizhong, Wuling Farm, 4 September 1985, *S.F. Huang 3162* (TAI). **Zhejiang:** Dongtianmu, Wuli Temple, 11 July 1957, *Yu-Xian He 24867* (NAS). Longquan, Chengbei, Huanghe, Yangwu, 26 June 1972, *Medicinal Plants Team 1070* (ZM). **JAPAN. Shimotsuke:** Tochigi, Hondo, 6 August 1980, *Miyoshi Furuse 14337* (PE).

Woods (1988) and Ren (2005) both came to similar conclusions as those above in their dissertations, but they did not publish their results. We therefore recognize four *Apios* species in Asia, i.e., *A. carnea*, *A. chendezhaoana*, *A. fortunei*, and *A. delavayi*. Three varieties of *A. delavayi* are recognized as well, i.e., var. *dalavayi*, var. *gracillima*, and var. *pteridietorum*. A morphological comparison between them is provided in Table 2.

Key to *Apios* species: Figure 5

1. Tubers usually undeveloped; corolla red, reddish purple or orange; standard flat, fully open when flowering ..... *A. carnea*
1. Roots starchy and tuberous; corolla white, pale yellow, greenish white, maroon, pink, or purple; standard in a pocket shape, incompletely open when flowering 2
2. Terminal leaflets broad triangular ..... *A. chendezhaoana*
2. Terminal leaflets lanceolate, ovate or rhomboid ovate 3
3. Leaflets ovate to rhomboid ovate; upper half of keel twisted to one side ..... *A. fortunei*
3. Leaflets ovate to lanceolate; keel curved but not twisted 4
4. Inflorescences with lax flowers; corolla pale yellow, greenish white, light purple, or dark purple; plant of SW China 5
4. Inflorescences with densely congested flowers; corolla maroon or pink; plant of N America 7
5. Flowers pale yellow or greenish white, plant of Sichuan and Yunnan, east of the Mekong-Salween Divide ..... *A. delavayi* var. *delavayi*
5. Flowers purple, plant of NE India, Xizang and Yunnan 6
6. Leaflets lanceolate to ovate, apex acute to acuminate; inflorescence 6–30 flowered; plant of Assam (India), SE Xizang and NW Yunnan (China), west of the Mekong-Salween Divide ..... *A. delavayi* var. *pteridietorum*
6. Leaflets linear to narrow lanceolate, apex acute to rounded; inflorescence 2–4 flowered; plant of Central and SE Yunnan ..... *A. delavayi* var. *gracillima*
7. Corolla maroon; standard with a short prolongation (1.5–2 mm) at the tip ..... *A. americana*
7. Corolla pink; standard with a long prolongation (6–8 mm) at the tip ..... *A. priceana*

Acknowledgements

Many people contributed to this research. The authors are grateful to the anonymous reviewers for their valuable comments. We would like to thank Prof. Richard Corlett and Dr. Sven Landrein for improving the English. We also thank Prof. Hua-Gu Ye, Dr. Xin-Xin Zhu, Dr. Yan-Song Peng, Dr. Bo Li, Dr. Ming Tang, Dr. Rui-Wu Zhou, Dr. Xiao-Fang Chu, Dr. Jing Tian, Dr. Zhu-Qiu Song, Dr. Ren-Bin Zhu, Dr. Bo Xu, Mr. Heng-Bin Chen, Mr. Gan Yao, Mr. Tong-Jun Liang, Mr. Kai-Wen Jiang, Mr. Gui-Zhi Zhang and Mr. Ze-Jing Mu for their help with this research. We appreciate the curators of CSFI, HNNU, IBSC, JXCM, JXU, KUN, LBG, and NAS for providing access to their herbaria. Online herbarium catalogues of E, K, P, PE, and TAI also provided photos of important specimens. Dr. Lei Wu, Dr. Bin Chen,

Mrs. Chun-Mei He, Mr. Ang Liu, Mr. Adam J. Peterson, and Mr. Alan Cressler provided beautiful photos. This work was supported by the project of Hunan Forestry Department—'Investigation of Forestry Genetic Resources in Hunan' (101-5555), and by a grant from the 1000 Talents Program (WQ20110491035) of the Chinese Academy of Sciences.

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