Phytotaxa 184 (2): 061–099
www.mapress.com/phytotaxa/

Article

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

http://dx.doi.org/10.11646/phytotaxa.184.2.1

Systematics of *Berberis* sect. *Wallichianae* (Berberidaceae) of Taiwan and Luzon with description of three new species, *B. schaaliae, B. ravenii*, and *B. pengii*

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Abstract

Berberis sect. *Wallichianae* are species of evergreen shrubs that in Taiwan are found in subalpine and montane-temperate areas and which have a notoriously controversial taxonomic history. Based on multivariate statistical analyses of morphometric data and an explicitly stated species criterion, the taxonomy of the group in Taiwan and its close relative in Luzon (*B. barandana*) is revised and their endemicity is evaluated by molecular data. In addition to the six species recognized in the Flora of Taiwan, 2nd ed. (i.e., *B. aristatoserrulata*, *B. brevisepala*, *B. chingshuiensis*, *B. kawakamii*, *B. mingetsensis*, and *B. tarokoensis*), *B. hayatana* (synonymized under *B. mingetsensis*) and *B. nantoensis* (synonymized under *B. brevisepala*) are reinstated, and three new species (*B. pengii*, *B. ravenii*, and *B. schaaliae*) are described and illustrated. Phylogenetic analyses using three chloroplast DNA sequence regions (*rbcL*, *ycf6-psbM*, and *psbA-trnH*) place all Taiwanese species and *B. barandana* in a strongly supported clade derived from within the continental Asian species of sect. *Wallichianae*, indicating their independent evolutionary history and supporting their endemic status.

Key words: chloroplast phylogeny, General Lineage Concept of species (GLCS), herbarium taxonomy, multivariate statistical analyses

Introduction

Plants of the traditionally defined barberry genus, *Berberis* Linnaeus (1753: 330; *Berberis s.s.*), are simple-leaved shrubs or rarely small tree-like bushes known for their characteristic 1–5-armed spines or spiniform structures at the stem nodes (Ahrendt 1961, Landrum 1999, Adhikari *et al.* 2012, Pabón-Mora & González 2012). With an estimated number of species ranging from 400 to 500, *Berberis s.s.* occurs widely across temperate, alpine, or semi-arid habitats of the Northern Hemisphere, with a secondary center of species diversity in the South American Andes (Ahrendt 1961, Landrum 1999, Adhikari *et al.* 2012, Harber 2012). Some recent treatments of *Berberis* (e.g., Laferrière 1997, Marroquín & Laferrière 1997, Whittemore 1997, Stevens 2001 onwards), however, favor the inclusion of the ca. 100–200 species (Ahrendt 1961) of the compound-leaved *Mahonia* Nuttall (1818: 211) within *Berberis* (i.e., *Berberis s.l.*), as supported by molecular phylogenetic studies (Kim & Jansen 1998, Kim *et al.* 2004, Adhikari 2010). Together with ca. 500–600 species, *Berberis s.l.* is the largest woody plant genus of the basal eudicots (Frodin 2004).

Taxonomic history of *Berberis* sect. *Wallichianae* of Taiwan

Within *Berberis s.s.*, species characterized by evergreen and coriaceous leaves, fascicled or solitary flowers, and blue-black to black fruits have long been assigned to section *Wallichianae* Schneider (1905: 400; Schneider 1939, 1942, Ahrendt 1941, 1961, Chamberlain & Hu 1985, Harber 2012), a prominent group comprising more than 75 taxa distributed in highlands and mountains of India, Nepal, Bhutan, Myanmar, Vietnam, China, Taiwan, Java, Sumatra, and Luzon (Chamberlain & Hu 1985, Harber 2012). Across the distributional range of sect. *Wallichianae*, the species in Taiwan have attracted much attention for their extensive morphological variation (Mizushima 1954, Ahrendt 1961, Chamberlain & Hu 1985). The extent of morphological diversity of the group in Taiwan was first recogized by Ahrendt (1941) and Schneider (1942) and later summarized in Ahrendt's (1961) monograph where the seven recognized Taiwanese species were placed in six subsections. In contrast to Ahrendt's (1961) treatment, however, Chamberlain & Hu (1985) recognized only four species in Taiwan, all placed in the series *Barandanae* (Schneider) Chamberlain & Hu (1985: 538) of the subsection *Wallichianae*. The various classifications of the Taiwanese *Berberis* sect. *Wallichianae* are summarized in Table 1.

Accepted by Libing Zhang: 20 Aug. 2014; published: 31 Oct. 2014

TABLE 1. Classifications of Taiwanese *Berberis* of sect. *Wallichianae* by different authors.

Author	Ahrendt (1941)	Schneider (1942)	Ahrendt (1961)	Chamberlain & Hu (1985)
	subsection	subsection	subsection	series
B. barandana (1886)	*Barandanae*[1]	*Barandanae*[1]	*Barandanae*[1]	*Barandanae*[10]
B. alpicola (1939)	*Barandanae*[1]	*Barandanae*[1]	*Barandanae*[1]	*Barandanae*[10]
B. aristatoserrulata (1913)	*Subleves*[2]	*Acuminatae*[3]	*Acuminatae*[3]	*Barandanae*[10]
B. brevisepala (1913)	*Euwallichianae*[4]	*Subleves*[2]	*Leves*[5]	*Syn*
B. hayatana (1954)	—	—	*Subleves*[2]	*Barandanae*[10]
B. kawakamii (1911a)	*Soulieanae*[6]	*Barandanae*[1]	*Barandanae*[1]	*Barandanae*[10]
B. mingetsensis (1915)	*Manipuranae*[7]	*Insignes*[8]	*Manipuranae*[7]	*Syn*
B. nantoensis (1939)	*Soulieanae*[6]	*Barandanae*[1]	*Replicatae*[9]	*Syn*

[1]Schneider (1905: 401), [2]Ahrendt (1941: 31), [3]Ahrendt (1941: 32), [4]Schneider (1905: 402), [5]Ahrendt (1941: 18), [6]Ahrendt (1941: 23), [7]Ahrendt (1941: 36), [8]Schneider (1905: 401), [9]Schneider (1961: 41), [10]Chamberlain & Hu (1985: 538, as "Baranadanae").

The radically different classifications of Ahrendt (1961) and Chamberlain & Hu (1985) further examplify the long-standing controversies regarding species delimitation of Taiwanese *Berberis*. In addition to the endemic deciduous *B. morrisonensis* Hayata (1911a: 25) of the sect. *Angulosae* Schneider (1905: 396), six species of sect. *Wallichianae* were recognized in the Flora of Taiwan, 2nd ed. (Lu & Yang 1996), while only four in the first edition (Liu 1976), but eight in a recent work (Lu *et al.* 2010). These discrepancies, in addition to the successively described new species, were results of highly disconcordant species circumscriptions among various treatments. For instance, while *B. brevisepala* Hayata (1913: 14) and *B. chingshuiensis* Shimizu (1963: 29) were both accepted in Lu & Yang (1996), these two species were synonymized under *B. kawakamii* Hayata (1911a: 24) in Liu (1976). Another major disagreement is associated with the circumscription of *B. mingetsensis* Hayata (1915: 4). Since its description, *B. mingetsensis* had been variously synonymized under *B. bicolor* Léveillé (1911: 454; Mizushima 1954, Liu 1960, 1976, Liu & Liao 1980, Liu *et al.* 1988, 1994) or *B. aristatoserrulata* Hayata (1913: 13; Chamberlain & Hu 1985, Ying 2001, 2011), or treated as conspecific with *B. hayatana* Mizushima (1954: 31; Lu & Yang 1996, Yang *et al.* 1997). Table 2 summarizes the complicated taxonomic history of *Berberis* sect. *Wallichianae* of Taiwan.

Despites these controversies and drawbacks of previous taxonomic treatments, species of *Berberis s.s.* of Taiwan have almost unanimously all been regarded as endemics (Kanehira 1936, Ahrendt 1961, Chamberlain & Hu 1985, Lu & Yang 1996, Ying 2001, 2011, Lu *et al.* 2010), except for earlier treatments such as Merrill (1923) where *B. kawakamii* was considered as conspecific with the Luzonese species *B. barandana* Vidal (1886: 45), and by Mizushima (1954) where *B. mingetsensis* was mistakenly synonomized under the Chinese species *B. bicolor*. Mizushima's treatment was followed by several subsequent authors (Liu 1960, Liu 1976, Liu & Liao 1980, Liu *et al.* 1988, 1994). Given the high endemicity and great extent of morphological variation, *Berberis* sect. *Wallichianae* of Taiwan thus is an ideal study group for an enquiry into mechanisms that had generated the high species diversity in the island (Hsieh 2002, Chung *et al.* 2009).

Methodology of herbarium taxonomy

One essential issue undermined previous taxonomic studies of Taiwanese *Berberis* of sect. *Wallichianae* is that only very limited materials, for some species only the type collection, were examined or reported on. Additionally, most authors had not seen many of or in some cases any of the types. Moreover, although Schneieder (1939, 1941) and Ahrendt (1961) had elaborated the importance of floral characters, the distinctness of style of mature fruits, the number of ovules, and leaf morphology such as leaf shape and venation (e.g., Chamberlain & Hu 1985, Landrum 1999, Adhikari *et al.* 2012), none of the recent studies of *Berberis* sect. *Wallichianae* in Taiwan seemed to be aware of and followed these important literatures. Furthermore, like most taxonomic studies, the major drawback of previous taxonomic treatments of the group is that none had attempted to adopt a rigorous scientific procedure for species delimitation (e.g., Henderson 2005, 2012, Valcárcel & Vargas 2010), resulting in widely different numbers of species recognized in Taiwan.

In herbarium taxonomy, Henderson (2005) argues that a sound scientific procedure can be formulated in monographic and revisionary work based on morphology alone through a stated species concept that is composed of theoretical foundation and operational criteria. Under his proposition, de Queiroz's (1998, 2005, 2007) General Lineage Concept of species (GLCS), which has gained popularity in recent taxonomic works (e.g., Valcárcel & Vargas 2010, Caddah *et. al.* 2013, Luebert 2013, Orgaz *et al.* 2013, Hong-Wa & Besnard 2014), is applied in this study as the theoretical background of species delimitation. de Queiroz's GLCS identifies the general conceptual agreement among

TABLE 2. Taxonomic history of *Berberis* sect. *Wallichianae* of Taiwan. Species in bold denote the author(s) and year of publication.

Present study	Kawakami (1910, 1911)	Hayata (1911a, b, 1913, 1915)	Schenider (1918)	Byhouwer (1928)	Kanehira (1936)	Schneider (1939, 1942)
B. aristatoserrulata		***B. aristatoserrulata*** (1913)	*B. aristatoserrulata*	*B. aristatoserrulata*	*B. aristatoserrulata*	*B. aristatoserrulata* (1942)
B. brevisepala		***B. brevisepala*** (1913)	*B. brevisepala*	*B. brevisepala* *B. kawakamii**	*B. brevisepala*	*B. brevisepala* (1942) ***B. alpicola*** (1939, 1942)
B. kawakamii	*B. barandana*	***B. kawakamii*** (1911a, 1911b)	*B. kawakamii*	*B. kawakamii*	*B. kawakamii*	*B. kawakamii* (1942)
B. mingetsensis		***B. mingetsensis*** (1915)	*B. mingetsensis*	*B. mingetsensis*	*B. mingetsensis*	*B. mingetsensis* (1942)
B. nantoensis				***B. densifolia*** (non Rusby)	*B. densifolia*	***B. nantoensis*** (1939, 1942)
Present study	Kimura (1940)	Ahrendt (1941)	Li (1952)	Mizushima (1954)	Liu (1960)	Ahrendt (1961)
B. aristatoserrulata		*B. aristatoserrulata*				*B. aristatoserrulata*
B. brevisepala	*B. morrisonesis*	*B. brevisepala* *B. alpicola*	*B. brevisepala* *B. alpicola*		*B. brevisepala*	*B. brevisepala* *B. alpicola*
B. hayatana			***B. formosana*** (non Ahrendt)	***B. hayatana***		*B. hayatana*
B. kawakamii		*B. kawakamii* ***B. formosana***			*B. kawakamii*	*B. kawakamii* ***B. kawakamii* var. *formosana***
B. mingetsensis		*B. mingetsensis*		?*B. bicolor*	*B. bicolor*	*B. mingetsensis*
B. nantoensis		*B. nantoensis*	*B. brevisepala*		*B. brevisepala*	*B. nantoensis*
Present study	Shimuzu (1963, 1964)	Li (1963)	Liu (1976)	Liu & Liao (1980)	Chamberlain & Hu (1985)	Liu *et al.* (1988)
B. aristatoserrulata		*B. aristatoserrulata*	*B. bicolor*	*B. bicolor*	*B. aristatoserrulata*	*B. aristatoserrulata*
B. brevisepala		*B. brevisepala* *B. alpicola*	*B. kawakamii* *B. alpicola* *B. kawakamii*	*B. kawakamii* *B. alpicola*	*B. kawakamii* *B. alpicola*	*B. brevisepala* *B. alpicola*
B. chingshuiensis	***B. chingshuiensis***					
B. hayatana		*B. hayatana*	*B. hayatana*	*B. hayatana*	*'B. hayata'*	*B. hayatana*
B. kawakamii		*B. kawakamii*	*B. kawakamii*	*B. kawakamii*	*B. kawakamii*	*B. kawakamii*
B. mingetsensis		*'B. mingetsuensis'*	*B. bicolor*	*B. bicolor*	*B. aristatoserrulata*	*B. bicolor*
B. nantoensis		*B. brevisepala*	*B. kawakamii*		*B. kawakamii*	*B. brevisepala*
Present study	Liu *et al.* (1994)	Lu & Yang (1996)	Yang *et al.* (1997)	Ying (2001, 2011)	Yu & Chung (2009)	Lu *et al.* (2010)
B. aristatoserrulata	*B. bicolor*	*B. aristatoserrulata*	*B. aristatoserrulata*	*B. aristatoserrulata*	*B. aristatoserrulata*	*B. aristatoserrulata*
B. brevisepala	*B. kawakamii* *B. alpicola*	*B. brevisepala*	*B. brevisepala*	*B. kawakamii* *B. alpicola*	*B. brevisepala*	*B. brevisepala* *B. alpicola*
B. chingshuiensis		*B. chingshuiensis*	*B. chingshuiensis*	*B. kawakamii*	*B. chingshuiensis*	*B. chingshuiensis*
B. hayatana	*B. hayatana*	*'B. mingetsuensis'*	*'B. mingetsuensis'*	*B. hayatana*	*B. hayatana*	*B. hayatana*
B. kawakamii	*B. kawakamii*	*B. kawakamii* *B. brevisepala*	*B. kawakamii*	*B. kawakamii*	*B. kawakamii*	*B. kawakamii*
B. mingetsensis	*B. bicolor*	*'B. mingetsuensis'*	*'B. mingetsuensis'*	*B. aristatoserrulata*	*'B. mingetsuensis'*	*'B. mingetsuensis'*
B. nantoensis		*B. brevisepala*	*B. brevisepala*	*B. kawakamii*	*B. tarokoensis*	*B. tarokoensis*
B. pengii sp. nov.		*B. aristatoserrulata*			*B. aristatoserrulata*	
B. schaaliae sp. nov.		*B. chingshuiensis*	*B. chingshuiensis*		*B. chingshuiensis*	*B. chingshuiensis*
B. ravenii sp. nov.					***Berberis sp.***	
B. tarokoensis		***B. tarokoensis***	*B. tarokoensis*		*B. tarokoensis*	*B. tarokoensis*

**E. H. Wilson 10952*, the type of *B. alpicola*, was treated as *B. kawakamii* in Byhouwer (1928).

different species concepts, defining species as "*segments of separately evolving meta-population lineages*" while respective contingent properties (e.g., intrinsic reproductive isolation, reciprocal monophyly, ecologically specific niche, fixed character state differences, etc.) are those acquired independently during the process of species divergence at different times along the evolutionary branch in various geographic contexts (de Queiroz 1998, 2005, 2007). GLCS highlights that the taxonomic disparity of contingent biological properties acquired during speciation can be used as evidence for assessing species divergence (de Queiroz 1998, 2005, 2007). In this study therefore the morphological divergences are adopted as the main line of evidence for multivariate analyses to delimit species boundaries (e.g., Valcárcel & Vargas 2010, Caddah *et. al.* 2013, Luebert 2013, Orgaz *et al.* 2013, Hong-Wa & Besnard 2014).

This article reports the taxonomic revision of *Berberis* sect. *Wallichianae* of Taiwan based on the concept and operational procedure of herbarium taxonomy advocated by Henderson (2005), with practical modifications for currently available materials (e.g., Valcárcel & Vargas 2010). Because *B. barandana* had long been allied with the Taiwanese species of *Berberis* sect. *Wallichianae* (Merrill 1923, Ahrendt 1961, Chamberlain & Hu 1985), this Luzonese species is also investigated in this study. DNA sequences of chloroplast genome were gathered to test questions pertaining to their taxonomic placements, evolutionary origins, and endemic status.

Material and Methods

Multivariate statistical analyses

In total, 189 herbarium specimens of A, CAHUP, HAST, KYO, NTUF, PH, PNH, TAI, TAIF, TCF, TI, TNS, and TNM were examined for multivariate statistical analyses. All type specimens of published names of *Berberis* sect. *Wallichianae* of Taiwan and Luzon Island of the Philippines were examined. Additionally, 260 specimens collected by the authors in 2008–2014 were also added for multivariate analyses. Each herbarium collection irrespective of the names they bore initially was reassigned to one of the previous species hypotheses. Twenty-three morphological attributes, including five qualitative attributes and 18 continuous, meristic quantitative attributes (Appendix 1) that were used in previous taxonomic treatments were measured for multivariate analyses. Qualitative attributes were subjected to cluster analysis (CA) to test whether the groups identified cover any previous species hypothesis. Because our main goal was to identify the most species diversity in *Berberis* sect. *Wallichianae* of Taiwan, when a qualitative character group encompasses more than one species hypothesis, quantitative attributes were analyzed to test whether more subgroupings could be detected within the group initially identified by CA.

Principle component analysis (PCA) or two-tailed t-test were performed either for better visualizing the morphological differences along selected continuous quantitative attributes or for detecting the significant difference between specific continuous quantitative attributes of species. Box-and-whisker plots were drawn to display the range of variation of selected continuous quantitative attributes measured among species. The CAs and PCAs were carried out in the software PASW statistics v.18 (SPSS, Chicago, USA), while the statistical t-test and descriptive statistics were carried out by R (R Development Core Team 2011). Prior to PCA, continuous and meristic variations were standardized (Zuur *et al*. 2010). The performance of PCA was based on a correlation matrix and the principal components (PCs) were kept by eigenvalue-greater-than-one rule.

Phylogenetic analyses

To address questions pertaining to the taxonomic placements and evolutionary origin of the Taiwanese and Luzonese species of *Berberis* sect. *Wallichianae*, 12 recognized species in this study and 24 species of the section distributed in China, India, Nepal, and Vietnam were sampled for phylogenetic analyses, with a deciduous species of sect. *Angulosae,* B. angulosa Wall. ex Hooker & Thomson (1855: 227), and *M. oiwakensis* Hayata (1916: 1–2) chosen as outgroup taxa (Table 3) based on phylogenetic structures revealed in Kim *et al.* (2004). Three chloroplast DNA sequence regions, *rbcL*, *ycf6-psbM*, and *psbA-trnH*, were concatenated for phylogenetic analyses after preliminary tests for phylogenetic resolution of the internal transcribed spacers of nuclear ribosomal DNA (nrITS) and five cpDNA sequence regions (*rbcL*, *trnL-trnF*, *accD-psaI, ycf6-psbM*, and *psbA-trnH*). Although adopted in previous studies (Kim *et al.* 2004, Adhikari 2010, Roy *et al.* 2010), sequence variation in ITS is too limited to distinguish Taiwanese species from other barberry species of sect. *Wallichianae* in our preliminary study and therefore discarded in current study. Total genomic DNA was extracted from silica-gel dried leaves using the Viogene Plant Mini Kit (Viogene, Taiwan) following the manufacture's protocol. The primers *rbc*L-1F (forward) and *rbc*L-1494R (revered) of Chen *et al*. (1998) were used for

TABLE 3. Materials, voucher information and GenBank accession numbers. Asterisks (*) denote Julian Harber's living collection.

Species	Distribution	Collector	GenBank Accession No.		
			rbcL	*ycf6-psbM*	*psbA-trnH*
Mahonia oiwakensis Hayata	Taiwan, Chiayi, Arisan	*C.-C. Yu 908* (TAI)	KJ741012	KJ741006	KJ741009
Berberis angulosa Wall. ex Hook. f. & Thoms.	Nepal	*D. Ketley s.n.**	KC788463	KF829904	KF855335
B. aristatoserrulata Hayata	Taiwan, Hualien, Rontaiwenshan	*C.-C. Yu 880* (TAI)	KJ741010	KJ741004	KJ741007
B. asiatica Roxb. ex DC.	India	*C. Chadwell s.n.**	KC788465	KF829906	KF855337
B. atrocarpa C.K.Schneid.	UK Maidwell Hall	*E. H. Wilson s.n.**	KC788466	KF829907	KF855338
B. barandana S.Vidal	Philippines, Luzon, Mt. Data	*K.-F. Chung 1958-2* (HAST)	KC788467	KF829908	KF855339
B. bergmanniae C.K.Schneid.	China, Sichuan, Wenchuan	*E. H. Wilson 4149**	KC788468	KF829909	KF855340
B. brevisepala Hayata	Taiwan, Hualien, Rontaiwenshan	*C.-C. Yu 902* (TAI)	KJ741011	KJ741005	KJ741008
B. cavaleriei H. Lév.	China, Guizhou, Hauxi	*GUIZ 286**	KC788469	KF829910	KF855341
B. chingii Cheng	China, Guangdong,	*K.-F. Chung 1764* (HAST)	KC788470	KF829911	KF855342
B. chingshuiensis T.Shimizu	Taiwan, Huanlien, Chuilushan	*C.-C. Yu 483* (TAI)	KC788471	KF829912	KF855343
B. deinacantha C.K.Schneid.	China, Yunnan, Zhaotong	*A. Clark 1010**	KC788472	KF829913	KF855344
B. dumicola C.K.Schneid.	China, Yunnan, Gongshan	*G. Forrest 13295**	KC788473	KF829914	KF855345
B. ferdinandi-coburgii C.K.Schneid.	Vietnam, Lao Cai, Phan Xi Păng	*HWJ 730**	KC788474	KF829915	KF855346
B. grodtmanniana C.K.Schneid.	China, Sichuan, Huili	*B. &. S. Wynne-Jones 7889**	KC788475	KF829916	KF855347
B. hayatana Mizush.	Taiwan, Yilan, Tsueifeng Lake	*C.-C. Yu 351* (TAI)	KC788476	KF829917	KF855348
B. impedita C.K.Schneid.	China, Guangdong, Mt. Nanling	*K.-F. Chung 1756* (HAST)	KC788477	KF829918	KF855349
B. insolita C.K.Schneid.	China, Sichuan, Zhaojui	*SICH 1200**	KC788478	KF829919	KF855350
B. julianae C.K.Schneid.	Maidwell Hall, Northamptonshire	*E. H. Wilson s.n.**	KC788479	KF829920	KF855351
B. kawakamii Hayata	Taiwan, Chiayi, Yushan	*C.-C. Yu 472* (TAI)	KC788480	KF829921	KF855352
B. levis Franch.	China, Yunnan, Mt. Yulong	*DJHC 140**	KC788481	KF829922	KF855353
B. mingetsensis Hayata	Taiwan, Chiayi, Alishan	*C.-C. Yu 246* (TAI)	KF881016	KF829923	KF855354
B. nantoensis C.K.Schneid.	Taiwan, Nantou, Yantoushan	*C.-C. Yu 611* (TAI)	KC788482	KF829924	KF855355
B. pengii C.C.Yu & K.F.Chung	Taiwan, Pingtung, Bayu Lake	*C.-C. Yu 563* (TAI)	KC788464	KF829905	KF855336
B. ravenii C.C.Yu & K.F.Chung	Taiwan, Kaohsiung, Upunuhu Lake	*C.-C. Yu 295* (TAI)	KC788483	KF829925	KF855356
B. sanguinea Franch.	China, Sichuan, Baoxing	*B & S. Wynne-Jones 8172**	KC788484	KF829926	KF855357
B. sargentiana C.K.Schneid.	China, Hubei, Xingshan	*E. H. Wilson 564**	KC788485	KF829927	KF855358
B. schaaliae C.C.Yu & K.F.Chung	Taiwan, Hualien, Chuilushan	*C.-C. Yu 595* (TAI)	KC788486	KF829928	KF855359
B. simulans C.K.Schneid.	China, Sichuan, Mt. Emei	*D. J. Hinkley 811**	KC788487	KF829929	KF855360
B. subacuminata C.K.Schneid.	Vietnam, Hoang Lien range	*KWJ 12280*	KC788488	KF829930	KF855361
B. tarokoensis S.Y.Lu & YuenP.Yang	Taiwan, Hualien	*C.-C. Yu 402* (TAI)	KC788489	KF829931	KF855362
B. phanera C.K.Schneid.	China, Sichuan, Daocheng	*SICH 1379**	KC788490	KF829932	KF855363
B. photiniifolia C.M.Hu	China, Guangdong	*K.-F. Chung 1732* (HAST)	KC788491	KF829933	KF855364
B. praecipua C.K.Schneid.	Bhutan, Thimphu, Chu	*R. Liddington s.n.**	KC788492	KF829934	KF855365
B. pruinosa Franch.	China, Yunnan, Eryuan	*A. Clark 1401**	KC788493	KF829935	KF855366
B. wallichiana DC.	Nepal, Malaku	*EMAK 1066**	KC788494	KF829936	KF855367
B. xanthoclada C.K.Schneid.	China, Guangxi, Kali Xian	*A. Clark 4280**	KC788495	KF829937	KF855368

the polymerase chain reaction (PCR) of *rbcL*. For *ycf6-psbM*, the universal primers ycf6F (forward) and psbMR (reversed) outlined in Shaw *et al*. (2005) were used. For *psbA-trnH*, the primers psbA (forward) and trnH (reversed) in Kress *et al*. (2005) were adopted.

All three chloroplast regions were PCR amplified in a 20 μL reaction. The PCR program for *rbcL* started with 5 min at 96°C, followed by 35 cycles containing 60 s at 94°C, 60 s at 55°C, and 70 s at 72°C, and a final step of 5 min at 72°C. For both *ycf*6-*psbM* and *psb*A-*trnH*, the program started with 5 min at 96°C, followed by 35 cycles containing 40 s at 94°C, 40 s at 55°C, and 40 s at 72°C, and a final step of 5 min at 72°C. Multiple sequence alignment was conducted by MUSCLE launched in MEGA5.05 (Tamura *et al*. 2011) under the default parameters, with subsequently manual adjustments. Indels and regions of ambiguous sites were excluded in all phylogenetic analyses. Statistics for molecular markers used in this study are given in Table 4.

Phylogenetic relationships were reconstructed based on maximum likelihood (ML) and Bayesian MCMC inference with sequence data partitioned. The best nucleotide substitution models for both analyses were determined by jMODELTEST (Guindon & Gascuel 2003, Posada 2008). The model GTR+I+G was selected for *rbc*L, HKY+G for *ycf6-psbM*, and HKY for *psbA-trnH*. The program RAxML-HPC2 v7.2.7-3 (Stamatakis *et al*. 2008) was used to reconstruct the ML topology with 1000 boostrapping via the CIPRES Portals (http://www.phylo.org/index.php/portal/). For Bayesian MCMC inference, the consensus topology with posterior clade probability of each node was obtained by Mr.Bayes 3.2 (Ronquist & Huelsenbeck 2003) based on parameters setting as follows: random starting tree, 8,000,000 generation runs with sampling occurring every 1000 generations, and the first 5% of runs was discarded as burn-in.

TABLE 4. Statistics for molecular markers used for 38 accessions, and for maximum likelihood analysis and Bayesian inference. PICs=parsimony-informative characters.

Character set	Aligned Length (bp)	Total no. of variable sites	Total no. of PICs
*rbc*L	1230	28	15
*ycf*6-*psb*M	660	24	14
*psb*A-*trn*H	421	25	16
Combined	2311	-	-

Results and Discussion

Multivariate statistical analyses

Cluster analysis (CA) was first performed based on the matrix containing 99 specimens scored for four qualitative attributes (Appendix 1), including two vegetative attributes (VC and USL) and two fruit attributes (FS and FSH). Fig. 1 illustrates diagnostic qualitative attributes. CA uncovered six major groups separated at 0.69 similarity level. Each of these groups can be described using a unique combination of attribute states. **Group 1**, with the type specimens of *B. hayatana* and *B. formosana* Li (1952: 41) included, was represented by specimens characterized by simple-vein type (Fig. 1A), dull adaxial leaf surface (Fig. 1C & 1E), and ellipsoid (Fig. 1N) and estylose (Fig. 1O) berries. **Group 2** was represented by three specimens assignable to *B. aristatoserrulata* that were featured by complex-vein type (Fig. 1B), dull adaxial leaf surface, and ellipsoid and estylose berries. **Group 3** was represented by specimens possessing leaves of complex-vein type, shinning adaxial leaf surface (e.g., Fig. 1D & 1F), and globose estylose berries (Fig. 1O). Group 3 included no species hypothesis and was treated as a new species (i.e., *B. pengii*). **Group 4**, with types of *B. tarokoensis* Lu & Yang (1996: 581) and *B. formosana* Ahrendt (1961: 65), and specimens assignable to *B. barandana* and *B. kawakamii* included, was featured by leaves of simple-vein type, and ellipsoid stylose berries. **Group 5**, with the type specimens of *B. alpicola* Schneider (1939: 253*), B. nantoen*sis Schneider (1939: 252) and specimens assignable to *B. brevisepala* included, was characterized by leaves of simple-vein type, shining adaxial leaf surface, and estylose, ellipsoid berries. **Group 6**, with specimens assignable to *B. chingshuiensis* and *B. mingetsensis* included, was characterized by leaves of complex-vein type, shining adaxial leaf surface, and ellipsoid estylose berries.

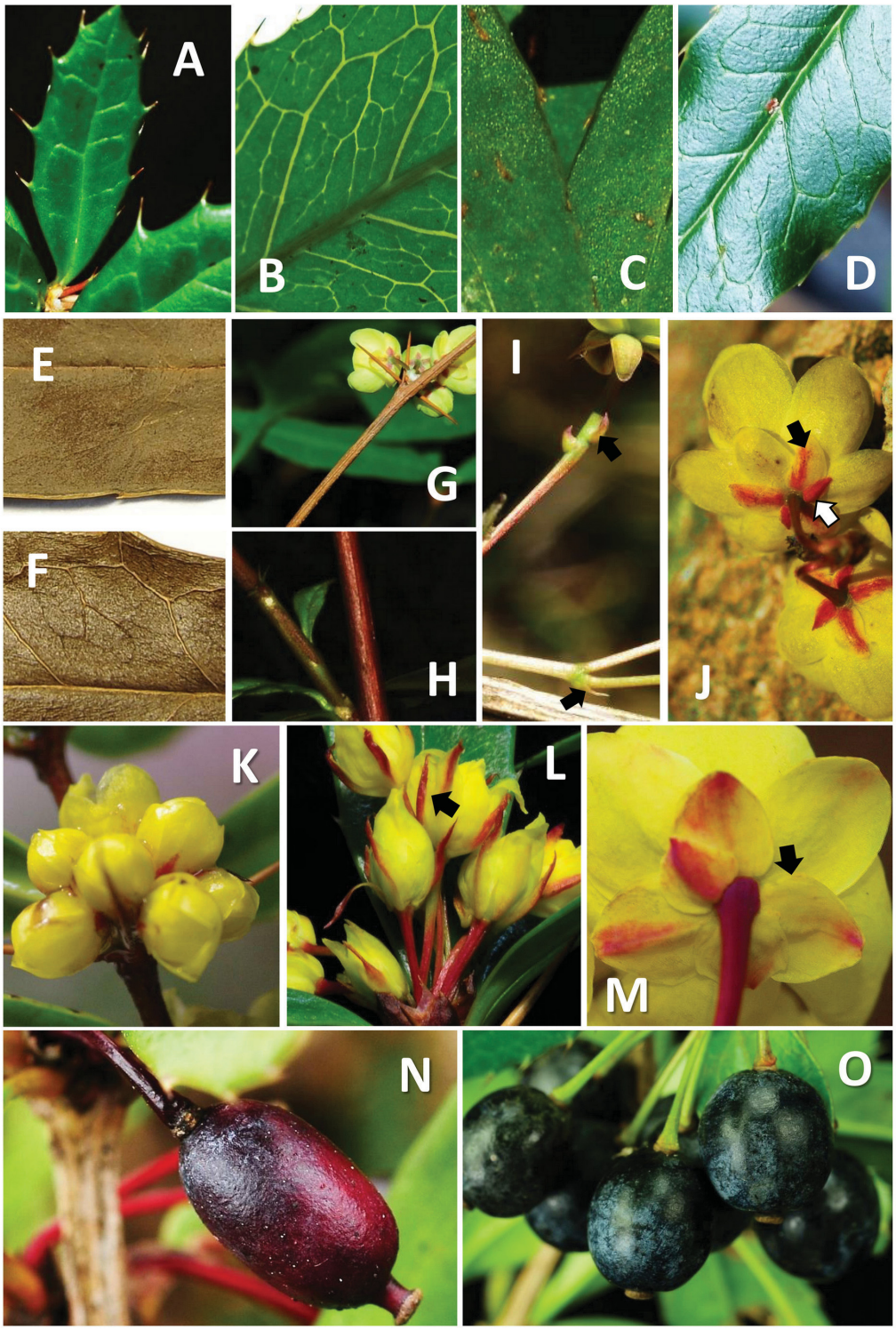

FIGURE 1. Diagnostic morphological attributes. **A.** Simple-veined leaf, with prominent midvein and pinnate, jointly looped secondary veins (*B. brevisepala*). **B**. Complex-veined leaf, secondary veins are pinnate, jointly looped and multi-festooned, and the tertiary veins are weakly reticulated (*B. pengii*). **C.** Simple-veined leaf with dull and silky-luster adaxial surface (*B. hayatana*). **D.** Complex-veined leaf with waxy-shinning adaxial surface (*B. mingetsensis*). **E**. Leaf specimen of *B. hayatana*, showing the dull adaxial surface when desiccated. **F**. Leaf specimen of *B. brevisepala*, showing the simple-vein type and waxy-shinning adaxial surface when desiccated. **G**. Brownish mature stem (*B. hayatana*). **H.** Purplish-red mature stem (*B. ravenii*). **I.** Bracts (*B. mingetsensis*). **J**. Bracteoles (white arrow) and outermost sepals (black arrow) in *B. brevisepala*. **K.** A dense, congested fascicle inflorescence with invisible pedicels (*B. nantoensis*). **L**. A congested fascicle inflorescence with long pedicels in *B. kawakamii*, showing the narrowly triangular-oblong outermost sepals (black arrow). **M**. The round (ovate or obovate) outermost or first whorl of sepals (*B. tarokoensis*). **N**. Ellipsoid, stylose berry (*B. tarokoensis*). **O**. Globose or nearly globose, estylose berries (*B. pengii*). A, C, D, N, and O: courtesy of Chi-Kai Yang.

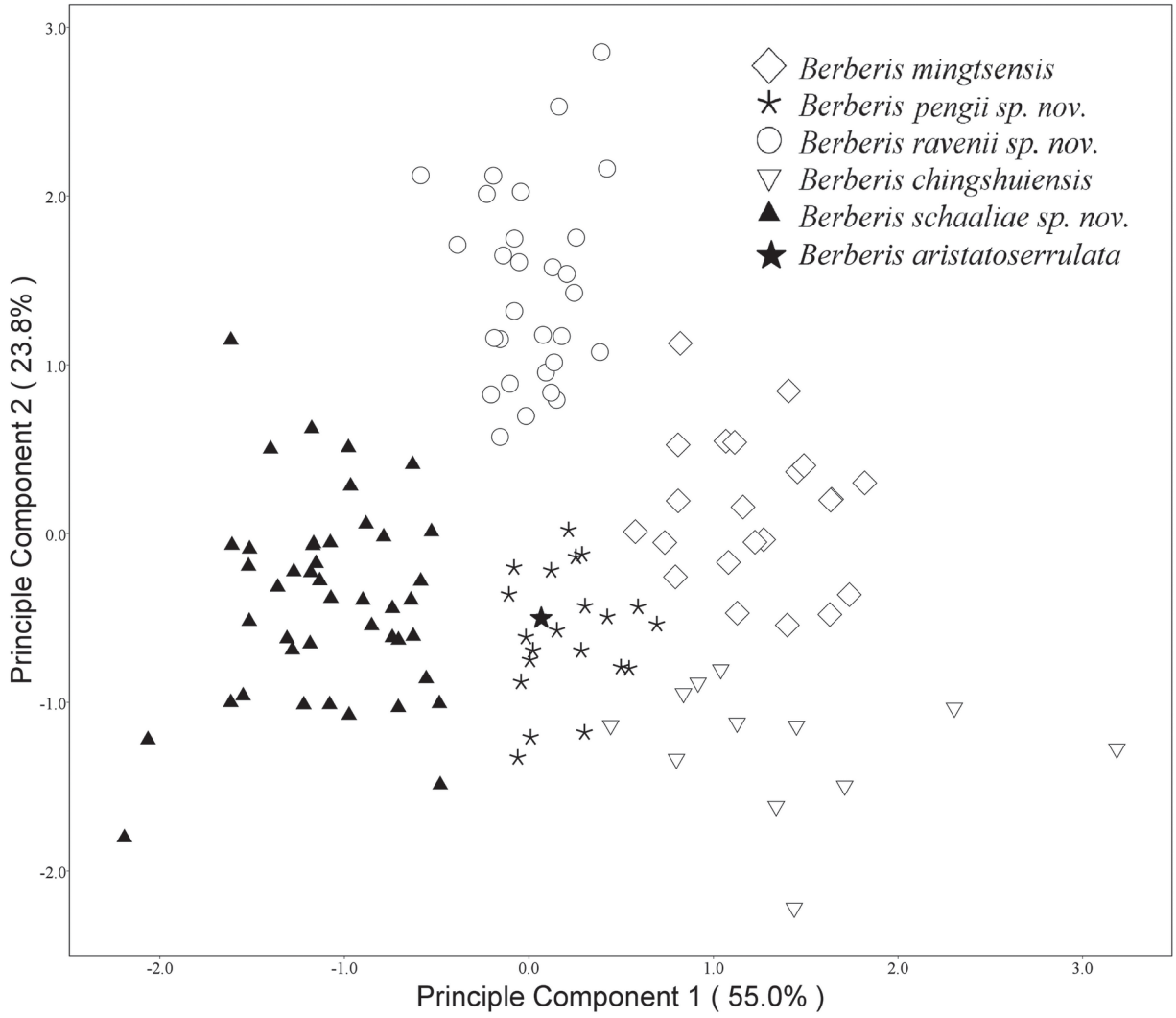

FIGURE 2. Scatterplot of the first two principal components extracted in the PCA performed based on vegetative meristic quantitative matrix of complex-vein group of *Berberis* sect. *Wallichianae* of Taiwan. Percentage of total variance explained by each component is specified in parenthesis.

Groups including only one species hypothesis (i.e., Group 2 and 3) were treated as confirmed species while second run of CA based on floral attributes was performed for groups encompassing more than one species hypothesis. As a result, additional group structures were only detected in Group 4 (27 specimens) based on shape of first-whorled sepal (FWS) at 0.85 similarity level. **Subgroup 4a**, characterized by triangular-oblong outermost sepals (Fig. 1L), contained the specimens of *B. kawakamii* and type of *B. formosana* Ahrendt. **Subgroup 4b** included both types and specimens of *B. tarokoensis* and *B. barandana* that are featured by round (ovate to obovate) outmost sepals (e.g., Fig. 1M).

As multiple species hypotheses remained in Group 1, 5 and 6, and Subgroup 4a and 4b, PCAs or two-tailed t-test were applied to those groupings based on numerical matrix of continuous quantitative attributes. Consequently because no significant differences along quantitative attributes were detected (data not shown) in Group 1, *B. formosana* H.L.Li was synonymized under *B. hayatana* and *B. formosana* Ahrendt was lumped into *B. kawakamii* in Subgroup 4a. Within Subgroup 4b, however, two additional groupings, corresponding to *B. tarokoensis* and *B. barandana*, were validated by two-tailed t-test (p<0.001) by the number of spinules per centimeter (NSP) based on 47 specimens. Within Group 5 based on 23 specimens, a significant difference (p<0.001) in the average length of pedicel (PL) was detected by two-tailed t-test between **Subgroup 5a** (represented by *B. alpicola* and *B. brevisepala*) and **Subgroup 5b** (represented by *B. nantoensis*). In Subgroup 5a, no more grouping structure could be validated by statistical tests using quantitative attributes based on 52 specimens, therefore *B. alpicola* was synonymized under *B. brevisepala*.

Although Group 2 (i.e., *B. aristatoserrulata*) and 3 (i.e., *B. pengii*) were statistically supported in CA, sterile specimens of group 2 and 3 are hard to be separated from Group 5. Thus, a matrix of 130 specimens including

specimens possessing the complex-vein type (Group 2, 3, 5 and 6) was assembled and analyzed based on a numeric matrix of seven continuous quantitative vegetative attributes (NSP, %ADBS, NSMWLBP, %DBMWB, %DBBSLB, %DBTSLB, and %LBMW; see Appendix 1) to test whether quantitative attributes could work well in uncovering further subordinate grouping structure. The outcome revealed five subordinate groups (Fig. 2), corresponding to *B. pengii* (including the type specimen of *B. aristatoserrulata*), *B. chingshuiensis*, *B. mingetsensis*, and two that did not include any previous species hypotheses (labeled with white circles and black triangles in Fig. 2). These latter two subgroups were recognized as new species and named *B. ravenii* and *B. schaaliae*, respectively. The inclusion of the type of *B. aristatoserrulata* within Group 3 (Fig. 2) in the PCA indicates a high foliar similarity between the *B. aristatoserrulata* and *B. pengii*. Indeed, the treatment of *B. aristatoserrulata* in the Flora of Taiwan, 2nd ed. (Lu & Yang, 1996) cited four specimens (*Liu 513*, *Lu 13014* & *13594*, and *Wang et al. 9153*) that are assignable to Group 2. Nevertheless, these two species are clearly distinguishable by their texture of upper leaf surface (dull in *B. aristatoserrulata* vs. shinning in *B. pengii*), the shape of first-whorled sepal (ovate in *B. aristatoserrulata* vs. triangular-oblong in *B. pengii*) and number of ovules (2–4 in *B. aristatoserrulata* vs. 6 or 8 in *B. pengii*).

Morphology

To aid species identification for *Berberis* sect. *Wallichianae* of Taiwan and Luzon, morphological attributes and their diagnostic values are discussed as follows:

Stem—The color of mature stems of new shoots can be yellow, yellowish grey, or brownish for most species in Taiwan (Fig. G) except for *B. ravenii* which has purplish-red mature stems (Fig. H).

Spines—The characteristic 3-armed spines at the stem nodes are always present, moderately developed for most species, except for *B. hayatana* and *B. schaaliae*. The spines of these latter two species are weakly developed, often being short and slender, or even sometimes absent. Particularly in *B. schaaliae*, small, palmate-like spines are often found. It is interesting to report that, as noticed by Ahrendt (1961), the spineless or weak-spined species are generally found in moist environments. *Berberis hayatana* and *B. schaaliae* both thrive in the moist, wet forests of northeastern Taiwan.

Leaves—Leaves are elliptic, lanceolate, or obovate, with mean length ranging widely (Fig. 3) from 3.7 cm (*B. brevisepala*) to 13 cm (*B. schaaliae*). Although leaf shape alone usually does not provide sufficient diagnostic value (Landrum 1999, Adhikari *et al.* 2012), it remains essential as an initial tool for identifying certain species. For instance, the lanceolate to narrowly lanceolate leaves are mostly found in *B. ravenii*.

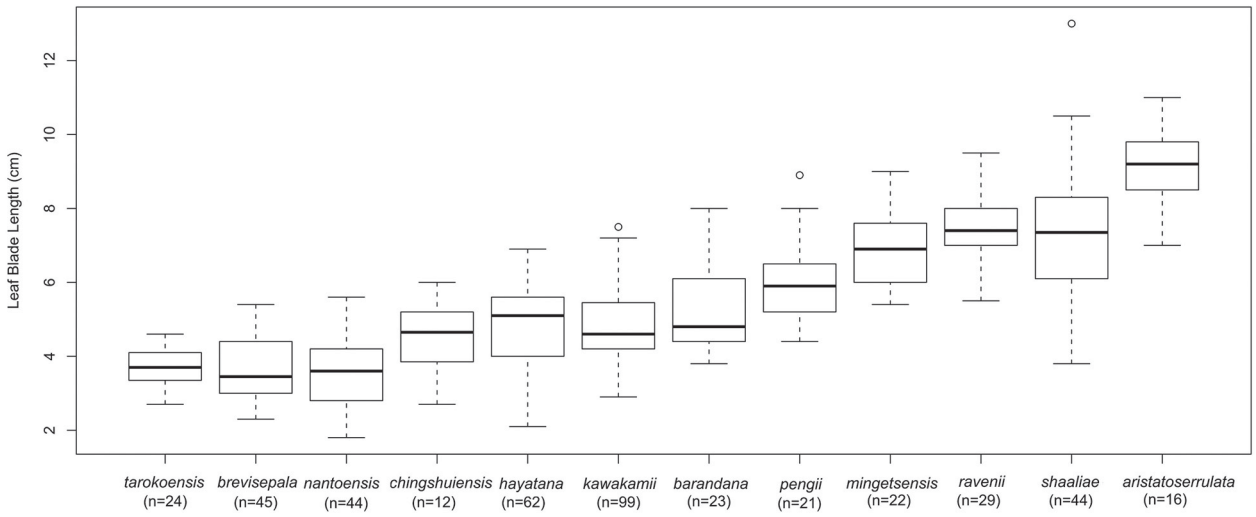

FIGURE 3. Box-and-whisker plots of leaf blade length. Numbers below species name refers to the sample size. Boxes incorporate 50% of values. Horizontal lines in box indicate median value. Open circles indicate extreme values.

Leaf margins, especially the number of spinules, have long been used for species delimitation in *Berberis*, and its range of variation is shown in Fig. 4. Ahrendt (1961) classified leaf margins into three types: entire or nearly so, sparsely or remotely toothed, and densely toothed, providing a useful way for a quick and rough identification of *Berberis* species. Under Ahrendt's classification (1961), eight species (*B. nantoensis* to *B. mingetsensis* in Fig. 4) fall into the category of sparsely or remotely toothed type and four (*B. aristatoserrulata*, *B. pengii*, *B. schaaliae*, and *B. ravenii*) are densely toothed type. Of the species in the former category, some specimens of *B. brevisepala* and *B. mingetsensis* are noted for bearing extremely long spinules exceeding 3 mm. In contrast, spinules in some specimens of *B. hayatana* are so reduced that they are almost invisible. Despite the existence of these extreme, a great extent of variation in the development of spinules was observed in the field, making spinule length a less reliable diagnostic character for species delimitation. Leaf apices in most species are acute to acuminate but mucronate leaf apices are found in some specimens of *B. brevisepala*, *B. nantoensis*, and B. *ravenii*. For a majority of species, petioles are lacking except for *B. aristatoserrula* and occasionally in *B. pengii* where the decurrent petiole can be up to 5 mm long.

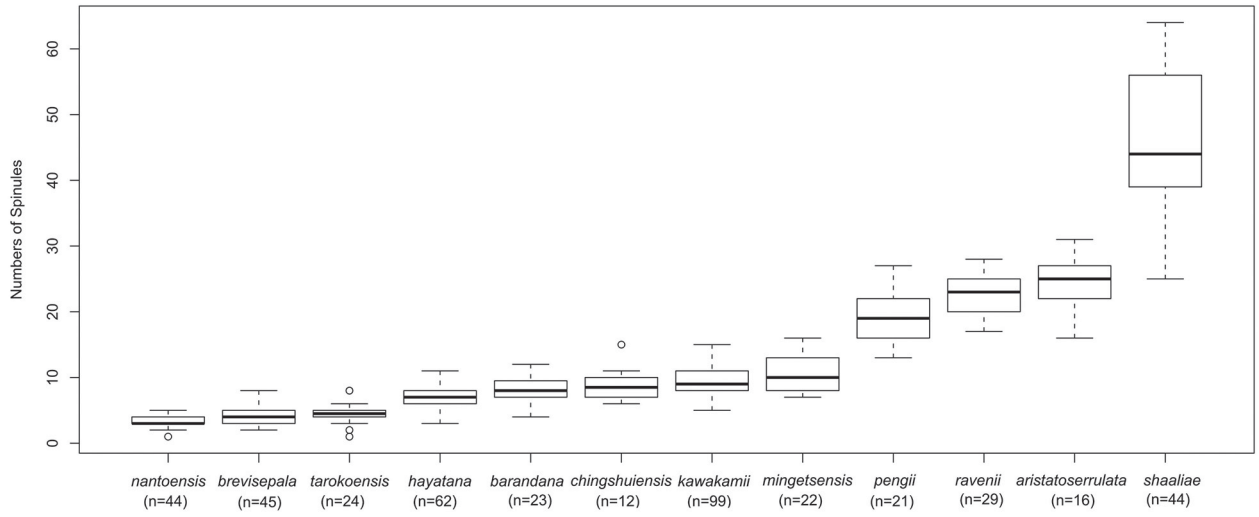

FIGURE 4. Box-and-whisker plots of the number of spinules. Numbers next to species name refer to the sample size. Boxes incorporate 50% of values. Horizontal lines in box indicate median value. Open circles indicate extreme values.

The adaxial surface of leaves is always glabrous. Nine species (i.e., *B. brevisepala*, *B. chingshuiensis*, *B. kawakamii*, *B. mingetsensis*, *B. nantoensis*, *B. pengii*, *B. ravenii*, *B. schaaliae*, and *B. tarokoensis*) have mostly shiny adaxial surface (Fig. 1D), although this feature could be less apparent in specimens (Fig. 1F) and not so distinctively waxy-shining in fresh materials of *B. tarokoensis*. In *Berberis aristatoserrulata* and *B. hayatana*, the adaxial surface of leaves is dull in both fresh materials (Fig. 1C) and herbarium specimens (Fig. 1E). When exposed to sunlight, however, a silky luster is reflected from the dull surface (e.g., Fig. 7B) of these two species, providing a useful tool for species identification in the field.

Patterns of leaf venation can be classified into simple-vein and complex-vein types (cf. Leaf Architecture Working Group 1999). Leaves of the former vein type, as in *B. brevisepala*, *B. hayatana*, *B. kawakamii*, *B. nantoensis*, and *B. tarokoensis*, are characterized by prominent midvein with/without secondary veins (Fig. 1A). The complex-vein type, featured in *B. aristatoserrulata*, *B. chingshuiensis*, *B. mingetsensis*, *B. pengii*, *B. ravenii*, and *B. schaaliae*, is characterized by reticulate venation with secondary veins extending to the leaf margin or pinnate festooned and with/without tertiary veins forming networks (Fig. 1B). In most species, venation is more prominent abaxially with the exception of *B. hayatana* and *B. tarokoensis* (obscure in both sides) and *B. schaaliae* (prominent in both sides).

Inflorescences and flowers—Flowers are solitary or fascicled; however, rarely in *B. mingetsensis* and *B. barandana* highly reduced umbels are observed (Fig. 10F). When such floral structure occurs, a pair of bracts was consistently observed (Fig. 1I). At the tip of the pedicel subtending the flower, 1 or 2 (rarely 3) bracteoles (Fig. 1J), termed 'prophyll' in Ahrendt (1961) and 'bractlet' in Ying (2011) and Harber (2012), were observed in all species except for *B.kawakamii*, *B. nantoensis* and *B. pengii*).

Flowers are bright or pale yellow and their size range from 0.5 cm (*B. nantoensis*) to 1.2 cm (*B. pengii*) in diameter. Each flower has two to five whorls of sepals, with each whorl composed of three sepals. The order of whorls

is counted outwardly and the term 'outermost' sepals (Adhakari *et al.* 2011) is used only when four or five whorls of sepals are present. Sepals are generally ovate or obovate (Fig. 1M) and are consistent for the innermost two whorls within a flower except for two species *B. kawakamii* and *B. pengii* that are characterized by triangularly-oblong, or rarely linear first-whorled sepals (Fig. 1L, as indicated by black arrow). Sepals are usually longer or equal to petals except for the outmost sepals which are always shorter than the other sepals and petals.

As with all species of *Berberis s.s.* the petals are usually obovate but tend to be more elliptic in *B. pengii* and *B. aristatoserrulata*. The apex of petals can range from incised to narrowly incised, obtusely emarginated with acute lobes or acutely emarginated with obtuse lobes. Most species have distinct connectives beyond the anthers while the apices of them are generally truncate or truncate and shortly apiculate. Pistils are usually reddish tinged in *B. kawakamii* and *B. pengii*. The number of ovules varies from one to eight.

Fruit—Fruits are black or black purplish and globose or ellipsoid in shape. Hereby we define stylose as mature fruits with style on the ovary and its length is more than 0.5 mm, while estylose fruits are mature fruits without style or with indistinct style which is less than 0.5 mm. Most species have estylose berries (Fig. 1O) except for *B. kawakamii*, *B. tarokoensis*, and *B. barandana* whose berries possess distinct short style (stylose; Fig. 1N). Fruits are sometimes pruinose in certain species, though not constant.

Phylogenetic Analyses

In the only two genus-wide phylogenetic studies of *Berberis s.l.*, *B. kawakamii* is the only species of sect. *Wallichianae* of Taiwan sampled (Kim *et al.* 2004, Adhikari 2010). In both studies, *B. kawakamii* was grouped in a strongly supported and yet internally unresolved clade composed of seven species of sect. *Wallichianae* based on ITS sequence data. Indeed the ITS sequence is identical in *B. kawakamii* and five other species (i.e., *B. bergmanniae*, *B. julianae*, *B. pruinosa*, *B. sargentiana*, and *B. wallichiana*) of this clade (Kim *et al.* 2004).

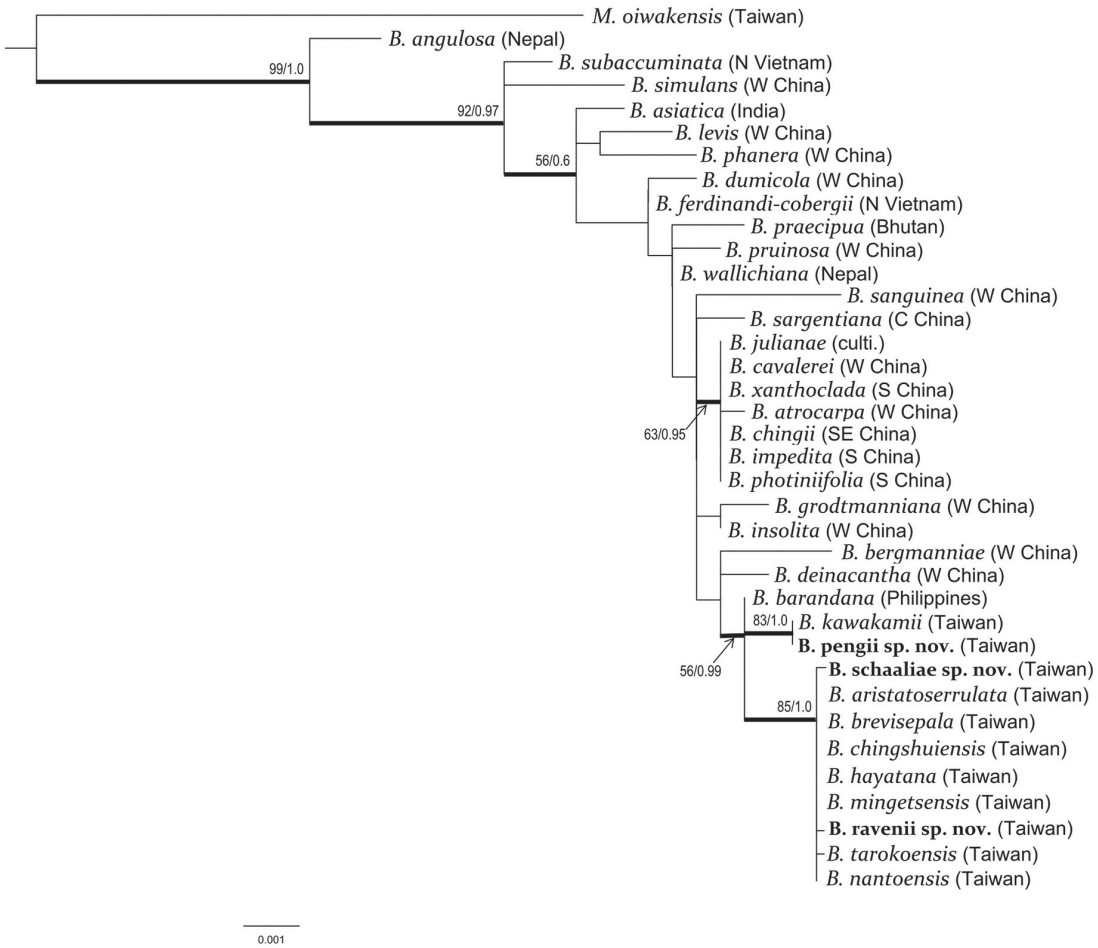

FIGURE 5. The best ML tree from the analysis of three concatnated chloroplast markers. Numbers adjacent to the nodes are ML bootstrap supports (BS) and BI posterior clade probabilities (PP). The well supported clades are denoted by thick line (BS > 50 and PP > 0.6).

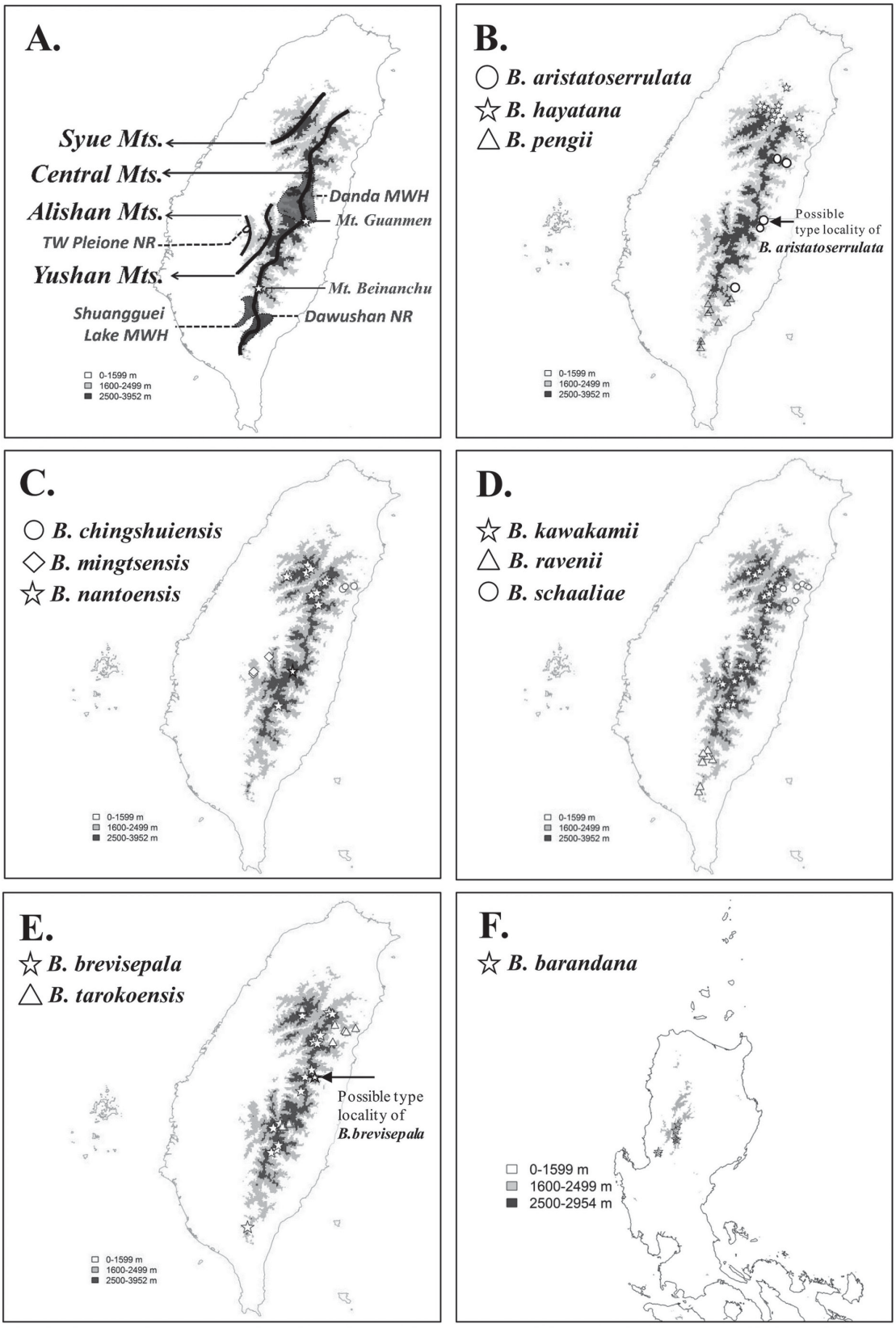

FIGURE 6. Distributions of *Berberis* sect. *Wallichianae* of Taiwan and Luzon. **A.** Major mountain ranges in Taiwan, with possible type localities of *B. aristatoserrulata* and *B. brevisepala*. NR: Nature Preserve. MWH: Major Wildlife Habitat. Mts: Mountain Range. **B.** Distributions of *B. aristatoserrulata*, *B. hayatana*, and *B. pengii*. **C.** Distributions of *B. chingshuiensis*, *B. mingetsensis*, and *B. nantoensis*. **D.** Distributions of *B. kawakamii*, *B. ravenii*, and *B. schaaliae*. **E.** Distributions of *B. brevisepala* and *B. tarokoensis*. **F.** Distribution of *B. barandana* in Luzon Island of the Philippines.

Based on three chloroplast DNA sequence regions, both maximum likelihood (log likelihood score = –3986.85) and Bayesian analyses revealed similar topology with slightly differences in support values. The best-scored maximum likelihood tree with support values of both ML and BI analyses are depicted in Fig. 5. Rooted by *Mahonia oiwakensis*, all sampled species of *Berberis s.s.* forms a well-supported clade in which the only deciduous species, *B. angulosa*, is found to be the sister group to the strongly supported clade (BS: 92; PP: 0.97) that was composed of species of sect. *Wallichianae*. Within the clade of sect. *Wallichianae*, relationships were largely unresolved. The western Chinese *B. simulans* Schneider (1939: 258) and the Vietname*se B. subacumin*ata Schneider (1913: 363) were placed basal to the successive grade composed of the remaining species (Fig. 5). All Taiwanese and Luzonese species were grouped in a clade with weak (BS: 56) or strong (PP: 0.99) support. Within this clade, although sequence divergences among species were low, all Taiwanese species differed from the Luzonese species. Additionally, although relationships among the Taiwanese species were largely unresolved, the eleven species were grouped into two clades, the first including the nine species characterized by the round first-whorled sepals (BS: 95; PP: 1.0) and the second comprising two species featured by the sharp-triangular first-whorled sepals (BS: 83; PP: 1.0).

The phylogenetic relationships revealed in current study clear suggest a single evolutionary origin for the species sect. *Wallichianae* distributed in the West Pacific islands of Taiwan and Luzon. The endemic status of these insular species from their continental relatives was also supported by the molecular data. Although relationships among these species remain resolved, the lack of phylogenetic resolution attest the artificial nature of Schneider's (1942, 1942) and Ahrendt's (1961) infrageneric taxonomy and instead favor the classification scheme of Chamberlain and Hu (1985). The unresolved relationships and short terminal branches leading to most Taiwanese species of sect. *Wallichianae* further suggest a process of rapid species radiation for accounting their great morphological diversity. Unfortunately the unresolved relationship between the Luzonese and Taiwanese species restrain us from further inferring their biogeographic history.

Taxonomic treatment

Berberis L. (1753: 330). Type:—*B. vulgaris* Linnaeus (1753: 330), lectotype (designated by Britton & Brown 1913: 127).

Shrubs or sometimes small tree-like bushes, evergreen or deciduous, wood usually yellow. *Stems* and branches terete, angled, or sulcate, pale yellow, yellowish-brown or dark-reddish brown, dark red, or dark purple, turning into ash grey when older, usually verruculose on the shoots and mature stems. *Spine* 3–5-fid, palmate, or leafy, rarely absent. *Leaves* simple, alternate, in fascicles or in whorls, usually petiolate, margins entire, serrate, to spinose-toothed, venation pinnate, prominent or obscure. *Flowers* solitary, fascicled, or in racemes, umbels, or panicles. *Bracts* usually 1 or 2, smaller in size than sepals and petals. *Bracteoles* usually 1 or 2, smaller in size than sepals and petals. *Flowers* greenish yellow, yellow, or orange. *Sepals* in 3 or 4-merous, concolor with petals, outmost or outer sepals shorter than inner whorls of sepals and petals, middle sepals shorter than innermost sepals and petals, inner sepals usually slightly longer than petals. *Petals* 6 in two whorls, with a pair of nectariferous glands at the base of the adaxial surface. *Stamens* opposite to petals, anthers dehisced by valves. *Ovary* club-shaped and subbasal with ovules numbering in 1–12, rarely to 15 or more. *Styles* distinct or indistinct. *Fruit* a berry, red, purple, dark red, or black.

Key to the species of *Berberis* sect. *Wallichianae* of Taiwan and Luzon

1. Leaf veins simple (simple-veined leaf), primary vein prominent with or without observable secondary veins 2
– Leaf veins complex (complex-veined leaf), secondary veins observable with reticulated tertiary veins 7
2. Adaxial surface of leaves dull ..... 4. *B. hayatana*
– Adaxial surface of leaves shiny with/without waxy luster 3
3. Fruits estylose (style absent or indistinct less than 0.5 mm) 4
– Fruits stylose (style present) 5
4. Flowers in a long-pediceled fascicle, pedicel 0.5–1.3 cm, sepals 4 or 5 whorls .....2. *B. brevisepala*
– Flowers in a dense, congested fascicle, pedicel 0.2–0.3 cm, sepals 3 whorls ..... 7. *B. nantoensis*
5. Flowers in a congested fascicle, pedicels 0.3–1.2 cm, the outer sepals narrowly-triangular, or rarely linear .....5. *B. kawakamii*
– Flowers in a long-pediceled fascicle, pedicels 1.2–1.3 cm, the outer sepals or (for flowers with 5-whorled sepals) the 4-whorled sepals ovate, obovate 6

6. Leaves greyish-green abaxially, spinules 1–8 along leaf margins, 4–10 mm apart, ovules 6 or 8 ..... 11. *B. tarokoensis*
– Leaves green to pale green abaxially, spinules 4–12 along leaf margins, 2–6 mm apart, ovules 4 ..... 12. *B. barandana*
7. Leaves adaxially dull ..... 1. *B. aristatoserrulata*
– Leaves adaxially shiny with/without waxy luster 8
8. The outer sepals narrowly-triangular or triangularly-oblong, fruits globose ..... 8. *B. pengii*
– The outer sepals or (for flowers with 5-whorled sepals) the 4-whorled sepals ovate or oblong-ovate, fruits ellipsoid 9
9. Leaf margins densely spinose, with 31–64 spinules, 0.5–2 mm apart ..... 10. *B. schaaliae*
– Leaf margins sparsely or remotely spinose, with 6–28 spinules, 2–7 mm apart 10
10. Mature stems purplish-red or dark purplish, leaf margins sparsely spinose, with 17–28 spinules, 2–3 mm apart ..... 9. *B. ravenii*
– Mature stems brown, greyish, pale yellow, leaf margins remotely spinose, with 6–17 spinules, 3–9 mm apart 11
11. Leaf blades 2.4–5.7 cm long, ovules 3 ..... 3. *B. chingshuiensis*
– Leaf blades 5.8–9 cm long, ovules 6 ..... 6. *B. mingetsensis*

1. ***Berberis aristatoserrulata*** Hayata (1913: 13, as "*aristato-serrulata*"). Type:—TAIWAN. Central Mountains ("Montibus Centralibus"), April 1910, *sine coll.* (holotype TI-02616!, isotype TAIF-9893!) (Fig. 7A–D).

Evergreen shrub, sometimes small tree-like shrub 1–2 m tall. *Mature stems* brown. *Spines* 3-fid, concolorous, sometimes palmate, 0.4–1.2 cm. *Leaves* subsessile, usually with short petioles of ca. 5 mm; leaf blade narrowly-elliptic or lanceolate, abaxially pale green sometimes pruinose, adaxially dull green; 7.0–11.0 × 1.8–3.4 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped and multi-festooned, the tertiary veins weakly reticulated; base attenuate, margins densely spinose with spinules of 16–31 with 2–3 mm apart on each side, apex acute. *Inflorescence* a fascicle, 10–15-flowered. *Bracts* absent. *Pedicel* pale green, 1.6–2.6 cm. *Bracteoles* 2 or 3, red, triangular, 1.5–2 × 1 mm. *Flowers* yellow. *Sepals* in 3 whorls, outer sepals yellow or sometimes reddish tinged obovate 2.5 × 2 mm, middle sepals yellow obovate to narrowly-obovate 5 × 2 mm, inner sepals yellow elliptic or narrowly-obovate 6.5 × 4 mm. *Petals* elliptic, 6 × 4 mm, base clawed with a pair of narrowly-ovoid nectaries very close to each other, apex incised or acutely emarginated. *Stamens* bright yellow ca. 4 mm, anther connective of stamen distinct, apex shortly apiculate. *Pistil* 3.5 mm. *Ovules* 2–4. *Berries* color unknown, ellipsoid 5 × 3 mm, estylose.

Distinguishing features:—*Berberis aristatoserrulata* is similar to *B. pengii* (Fig. 7) in its leaf shape and venation, differing from the latter by its dull upper surface of leaf and the shape of first-whorled sepal which is obovate.

Phenology:—*Flowering* April; *Fruiting* July, August.

Distribution & habitat:—*Berberis aristatoserrulata* is distributed in eastern Taiwan where it is locally common in the understory of coniferous and broad-leaved mixed forests from 1500–2410 m.

Chinese name:—長葉小檗

Proposed IUCN conservation status:—Data Deficient (DD). *Berberis aristatoserrulata* was rediscovered and confirmed in our trip to Guanmen Trail in 2014. It is currently only known from a few localities in eastern Central Mountain Range where it is locally abundant in the cloud forest belt. Because its natural distributional range and population sizes are insufficiently known, we propose a provisional IUCN category of DD for the species (IUCN 2012).

Notes:—*Berberis aristatoserrulata* was described based on a *sine coll.* specimen collected from an uncertain locality in the Central Mountain Range in 1910. Based on the history of early botanical explorations in Taiwan by Japanese collectors, the type specimen was most likely collected by Ushinosuke Mori. After a careful study of Mori's travel log (Mori 2000), we identified that Guanmen Trail, an abandon track constructed in the late Qing Dynasty, was the most likely type locality (Fig. 6B) and we were able to relocate the species there in the spring of 2014.

Additional specimens examined:—TAIWAN. Hualien: 77 Compt. of Mukwashan, 2100–2330 m, 15 August 1956, *Liu et al. 250* (PH); Luanshan to Patolushan, 2000–2100 m, 3 August 1963, *Tamura et al. 21556* (E, HAST, KUN); Yenping Logging Trail, 25 July 1973, *Ou 1941* (TCF); Juisui Forest Road, 6 April 2000, *Yang 5981* (TNM); en route from first river bed of Pingfengshan, 2410 m, 4 September 2009, *Huang 4151* (HAST); near Hoawanshan, 2100 m, 11 April 2014, *Guanmen Expedition-Harber & Yu 7, 8* (TAI); near Rontaiwenshan, 2300 m, 12 April 2014, *Guanmen Expedition-Harber & Yu 2, 3, 4, 5, 6* (TAI); 27 km of Guangfu Logging Trail, 1500m, 13 April 2014, *Guanmen Expedition-Harber & Yu 12* (TAI).

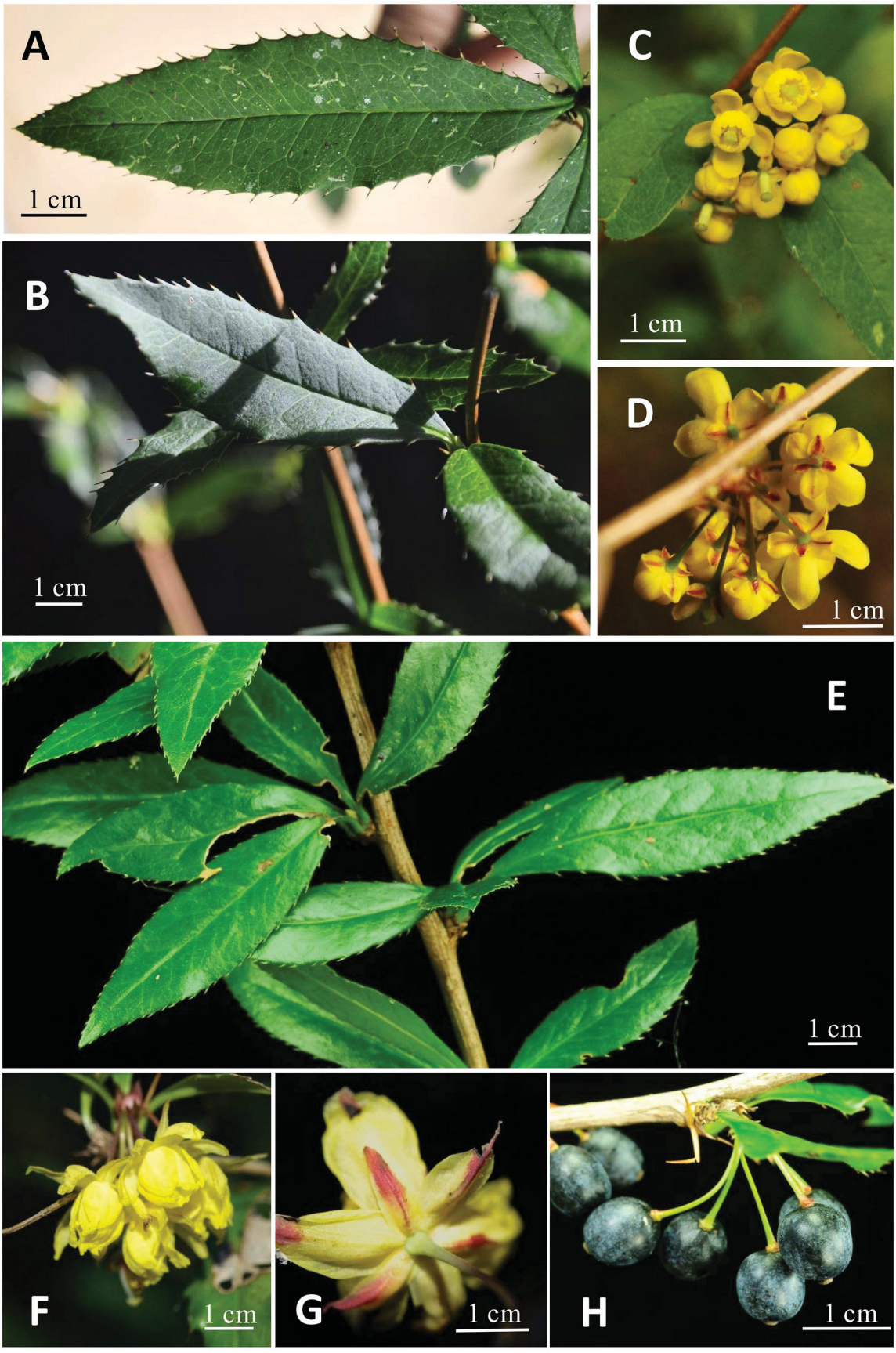

FIGURE 7. *Berberis aristatoserrulata* Hayata (A–D) and *B. pengii* C.C. Yu & K.F. Chung (E–H). **A.** Dull adaxial leaf surface. **B.** Silky-luster adaxial leaf surface when exposed to light. **C.** Flowers, front view. **D.** Flowers, exterior view, showing the sepals. **E.** Leafing braches. **F.** Flowers, front view. **G.** Flowers, exterior view, showing the sepals. **H.** Berries. A–D: Guanmen Historical Trail. E–H: Beitawushan, courtesy of Chi-Kai Yang.

2. ***Berbers brevisepala*** Hayata (1913: 14). Type:—TAIWAN. Mt. Morrison (in protologue), "Central Mountains" (translated from Japanese) on the type, 15 April 1910, *U. Mori s.n.* (holotype TI-02620!) (Fig. 8).

Heterotypic synonym:—Berbers alpicola Schneider (1939: 253). Type:—TAIWAN. Ari-san to Mt. Morrison, bushy side of torrent, 3666 m, 24 October 1918, *Wilson 10952* (holotype A-00038721!, isotype B-100365257, BM-000559458!, K-000644916!, US-00103858)

Evergreen shrub or occasionally small tree-like shrub 0.5–2 m tall. *Mature stems* brown or greyish, subterete, inconspicuous verruculose. *Spines* 3-fid, concolorous, 1.1–2.2 cm. *Leaves* subsessile; leaf blade obovate or elliptic, abaxially pale green sometimes pruinose, adaxially shiny green; 2.3–5.4 × 0.6–1.7 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped if present; base cuniform, margins slightly revolute, sparsely spinose with 2–7 spinules with 3–8 mm apart on each side, apex attenuate or mucronate. *Inflorescence* a fascicle, 3–5-flowered. *Bracts* absent. *Pedicel* pale green, 0.5–1.3 cm. *Bracteoles* usually 2, yellow or sometimes reddish tinged, triangular, 1.5 × 1 mm. *Flowers* bright yellow. *Sepals* in 4 or 5 whorls, outermost sepals of both 4- and 5-whorled flowers yellow with reddish-tinge triangular 1.5–2 × 1–1.5 mm, for flowers with 5-whorled sepals, the 4-whorled sepals yellow sometimes with reddish-tinge ovate 2.5 ×1.5 mm, the third-whorled sepals of both 4- and 5-whorled flowers yellow ovate 3.5 × 2.5 mm, sepals of the innermost two whorls yellow obovate 4–6 × 2.5–4 mm. *Petals* obovate, 4.5 × 3.5 mm, base clawed with a pair of ovoid nectaries, apex incised or acutely emarginated. *Stamens* pale yellow ca. 3.5 mm, anther connective of stamen distinct, apex truncate or slightly apiculate. *Pistil* 4 mm long. *Ovules* 3, 4 or 6. *Berries* black, ellipsoid ca. 5 × 3.5 mm, not pruinose, estylose, or occasionally up to 0.9 mm long.

Distinguishing features:—Given the wide distributional and elevational ranges of the species, it is not surprising that *B. brevisepala* is highly variable both among populations and within an individual plants, as shown by the type specimen (Fig. 8C). At the upper distributional limit (i.e., 3700 m), plants of *B. brevisepla* tend to possess smaller leaves (Fig. 8A) and such individuals were previously identified as *B. alpicola* (see Notes). *Berberis brevisepala* was often misidentified as *B. kawakamii*, or more frequently as *B. nantoensis* when reproductive organs are absent. However, *B, brevisepala* differs from *B. kawakamii* obviously by its outer ovate sepals (v.s. narrow-triangular or rarely linear sepals in *B. kawakamii*) and from *B. nantoensis* by its much longer pedicels and the numbers of whorls of sepals.

Phenology:—*Flowering* May–August; *Fruiting* August–November.

Distribution & habitat:—*Berberis brevisepala* grows in subalpine meadows and the understory of coniferous forests throughout the major high mountain systems of Taiwan from 2100 to 3700 m (Fig. 6E). It is usually a small shrub less than 1 m tall; however, individuals more than 2 m tall can be found in wind-sheltered sites such as wet basins or stream valleys.

Chinese name:—高山小檗

Proposed IUCN conservation status:—Nearly Threatened. *Berberis brevisepala* is common in subalpine and alpine regions along major high mountains in Taiwan, growing into small colonies in its habitats. Although most high mountain areas are under protection in Taiwan, the high mountain ecosystem is currently threatened by global climate change. We therefore propose a provisional IUCN category of NT for the species (IUCN 2012).

Notes:—*Berberis brevisepala* was described based on *Mori s.n.* 1910, a specimen represented by leafy branches and fascicles of flowerless pedicels or early developing fruits. In the protologue of the species, no information regarding its floral ("*Flores non visi*") and fruit morphology was provided (Hayata 1913). The species status of *B. brevisepala* had long been controversial; the species had been synonymized under *B. kawakamii* or expanded to included *B. alpicola* (Table 2). Because of the absence of flowers and fruits, the type specimen of *B. brevisepala* (*Mori s.n.* 1910) could not be included into our multivariate statistical analyses. Our initial attempt to visit the type locality was also hindered by the fact that the information given in the protologue (Mt. Morrison) is not found on the collection label which records only the 'Central Mountains'. By analyzing Mori's travel log (Mori 2000), we identified Danda Major Wildlife Habitat (Danda MWH; Fig. 6A & 6E) as most likely type locality of *B. brevisepala* and this conjecture was confirmed when plants possessing similar leaves to the type specimens were located in this area in April 2014.

With plants collected from Danda MWH (*Guanmen Expedition-Harber & Yu 9, 10, 11*) included, multivariate statistical analyses identified one grouping (Subgroup 5a) composed of specimens assignable to both *B. brevisepala* and *B. alpicola* (type included). Because no attributes could consistently separate *B. brevisepala* from *B. alpicola*, the latter species is synonymized under the former. Under this new circumscription, *B. brevisepala* has a wide distributional and elevational ranges and plants occurring in the upper distributional limits (ca. 3700 m), previously known as *B. alpicola*, tend to have much smaller leaves (Fig. 8A). Additionally, it was also noted in the protolouge of *B. alpicola*

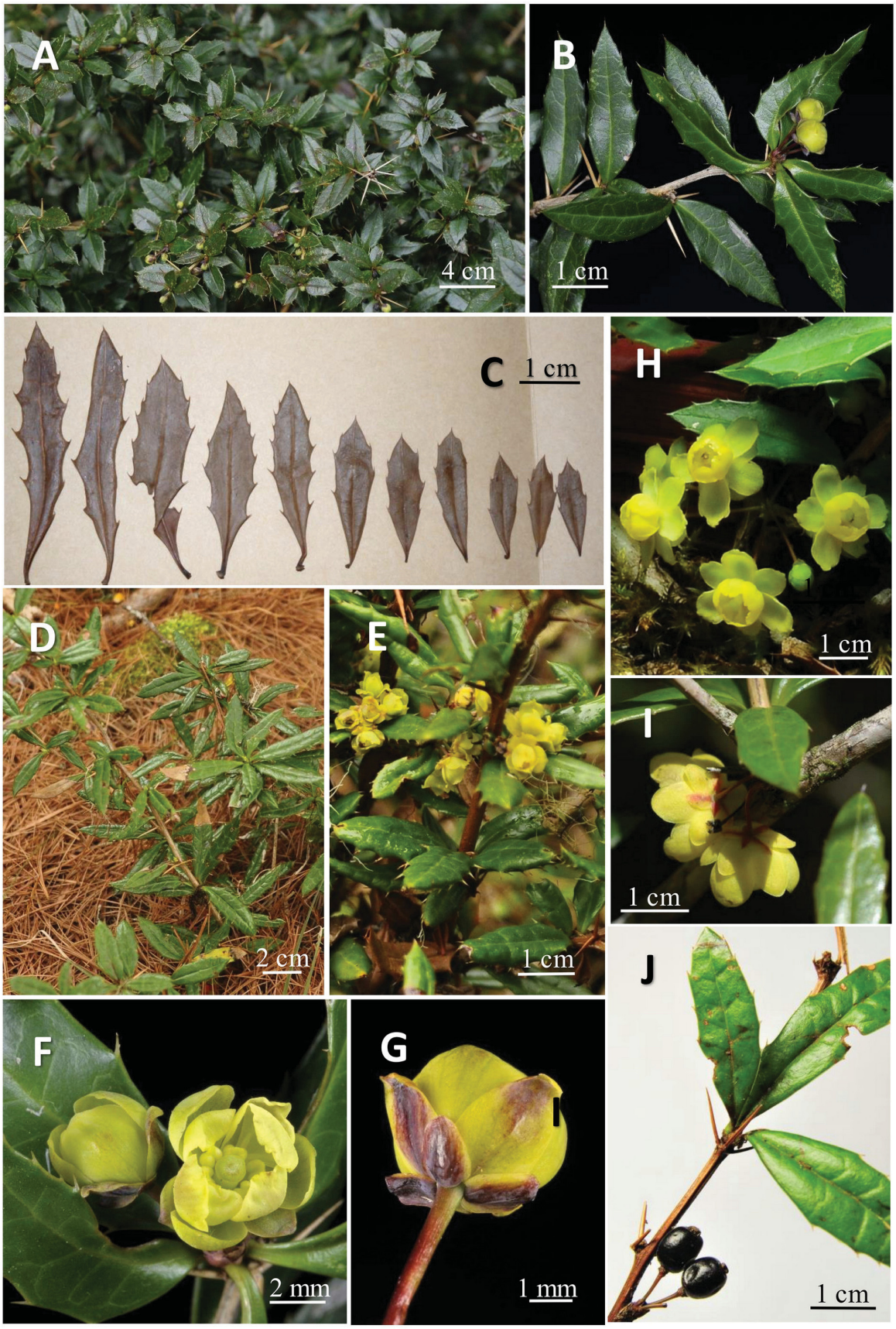

FIGURE 8. *Berberis brevisepala* Hayata. **A.** Branches. **B.** Flowering branch. **C.** Leaves in the envelope of type specimen. **D.** Habitat and habit. **E.** Flowering branches. **F.** Flowers, exterior view. **G.** Flowers, exterior view, showing the sepals. **H.** Flowers. **I.** Flowers, exterior view, showing the sepals. **J.** Berries. A, B, F, G: Peiyun Lodge, type locality of *B. alpicola*, courtesy of Bo-Chang Chen; D, E: Guanmenshan; H: cultivated plant collected from Mt. Syue; I: Beitawushan; J: Shinkangshan.

that 'immature' berries are stylose (Schneider 1939, 1941) and some cultivated plants of '*B. alpicola*' in U.K. also possess stylose berries with short style (Julian Harber, pers. comm.). However, close examination of the specimens from type locality [e.g., *Yang 3618* (TNM)] indicated that all mature berries were estylose.

Additional specimens examined:—TAIWAN. Yilan: Chialohu (Lake Chialo), 2260 m, 11 May 2002, *Huang 839* (HAST); near Fatushan, 2750 m, 10 August 2008, *Yu 112* (TAI); Wulanshan, 2100 m, 16 August 2008, *Yu 107* (TAI); on east-southern range of Nanhutashan, 2600 m, 12 August 2008, *Yu 116* (TAI). Hsinchu: Tapachienshan, 2600–3300 m, 15 May 2003, *Lee 2532* (TAIF); near Kelayehshan, 3000 m, 6 April 2008, *Yu 49* (TAI). Taichung: the east peak of Mt. Syue, 3100 m, 19 July 2009, *Huang 13084* (HAST). Nantou: Shalihsiensi Forest Road, 2550–2680 m, 5 May 1998, *Wang & Tsai 3169* (IBSC, TNM); Wuchieh Logging Trail near Shili River, 2200 m, 8 September 2008, *Yu 140* (TAI); Hohuanshan, 3100 m, 23 December 2008, *Yu 224* (TAI); near Antungchushan, 3000 m, 3 July 2009, *Yu 414* (TAI). Chiayi: Nitakayama (Yushan), 3300 m, 27 October 1918, *Kanehira* and *Sasaki s.n.* (TAIF); Peiyun Lodge to Tatachia Saddle, 3450–2600 m, 11 August 1987, *Yang 3618* (TNM), 3400 m, Peiyun Lodge, 17 May 1991, *Lin s.n*. (TNM), 8 May 1993, *Chiu 1830* (TNM), 5 September 1995, *Chen 1398* (TNM), 12 April 2009, *Yu 434* (TAI). Kaohsiung: Kuanshanlingshan, 24 August 1987, *Kuoh 12484* (TNM), 5 April 1988, *Kuoh 14236* (TNM); trail to Takuanshan, 2940 m, 20 May 1992, *Wang 1077* (HAST); on the way from campsite to the top of Kuanshan, 3026–3150 m, 16 May 1995, *Wang 1096* (HAST); near Kuanshan, 3100–3300 m, 11 October 1996, *Liou 407* (TAIF). Pingtung: the last water resource plot along the trail to Peitawushan, 2700 m, 8 May 2009, *Yu 304* (TAI). Taitung: Siangyang Lodge, 2200 m, 23 November 1987, *Chen 713* (HAST). Hualien: Tonkuran River, 15 April 1910, *Mori s.n.* (TAIF); Yangtoushan, 2800 m, 13 October 2008, *Yu 162* (TAI); Rontaiwen Mts., 2900 m, 12 April 2014, *Guanmen Expedition-Harber & Yu 9, 10, 11* (TAI).

3. ***Berberis chingshuiensis*** Shimizu (1963: 29). Type:—TAIWAN. Pref. Hualien, the summit of Chingshuishan, ca. 2400 m alt., 1 May 1961, T. *Shimizu 12520* (holotype KYO-00022300!, isotype TI-02621!) (Fig. 9A–F).

Small evergreen shrub usually 0.5–1 m tall. *Mature stems* brown or greyish, subterete, inconspicuously verruculose. *Spines* 3-fid, concolorous, 0.5–1.2 cm. *Leaves* subsessile; leaf blade elliptic, abaxially pale green sometimes pruinose, adaxially green; 2.4–5.7 × 1.1–1.7 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped and multi-festooned, the tertiary veins weakly reticulate if present; base cuneate, margins sometimes revolute and remotely spinose with spinules of 6–11 with 3–7 mm apart on each side, apex acute or obtuse. *Inflorescence* a fascicle, 3–6-flowered. *Bracts* absent. *Pedicel* red, 1.3–1.4 cm. *Bracteoles* 2 if present, yellow or sometimes with reddish-tinge, triangular, 1.5 × 1 mm. *Flowers* yellow. *Sepals* in 3 whorls, outer sepals yellow sometimes with reddish-tinged ovate 2.5 × 2 mm, middle sepals yellow elliptic 5.5 × 3.5 mm, inner sepals yellow obovate 7 × 6 mm. *Petals* elliptic, 5.5 × 4 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised and acutely emarginated. *Stamens* pale yellow ca. 4 mm, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long. *Ovules* 3. *Berries* black, ellipsoid ca. 5.5 × 4 mm, not pruinose, estylose.

Distinguishing features: Most herbarium specimens identified as *B. chingshuiensis* in Taiwan are *B. schaaliae* (see below). *Berberis chingshuiensis* can be easily distinguished from *B. schaaliae* by its sparsely to remotely spinose leaves (vs. densely spinose leaf margins in *B. schaaliae*; Fig. 9F vs. 9G) and differs from another similar species, *B. tarokoensis*, by its complex-veined leaves, estylose berries, and relative few number (3) of ovules [vs. simple-veined leaves, stylose berries, and more ovules (6 or 8) in *B. tarokoensis*]. When growing on exposed windy slopes, some individuals of *B.* chingshuiensis develop leaves with more or less revolute margins, rendering them likely misidentified as *B. nantoensis*.

Phenology:—*Flowering* April–May; *Fruiting* May.

Distribution & habitat:—*Berberis chingshuiensis* is a rare species restricted to the exposed limestone outcrops of Taroko Gorge of eastern Central Mountain Range (Fig. 6C) from 1500 to 2400 m where it is co-distributed with *B. tarokoensis* (Fig. 6E).

Chinese name: 清水山小檗

Proposed IUCN conservation status:—Critically Endangered [CR B1ac(iv)]. *Berberis chingshuiensis* is known only from type locality and a few peaks nearby where it is distributed as scattered individuals. The narrow distribution range and low number of mature individuals prompt us to list it at the provisional IUCN category of CR (IUCN 2012), despite the area being protected within the range of Taroko National Park.

Notes: In the protologue, Shimizu (1963) notes the deposition of two isotypes in SHIN and TAI; however, no such materials are found in either SHIN (J. Harber, pers. comm.) or TAI.

Additional specimens examined:—TAIWAN. Hualien: Chingshuishan, 2400 m, 28 April 1989, *Lu s.n*. (HAST, TNM), 2300 m, 11 April 2009, *Chung 9577* (TAIF); Chuilushan, 1500 m, 15 May 2009, *Yu 483* (TAI).

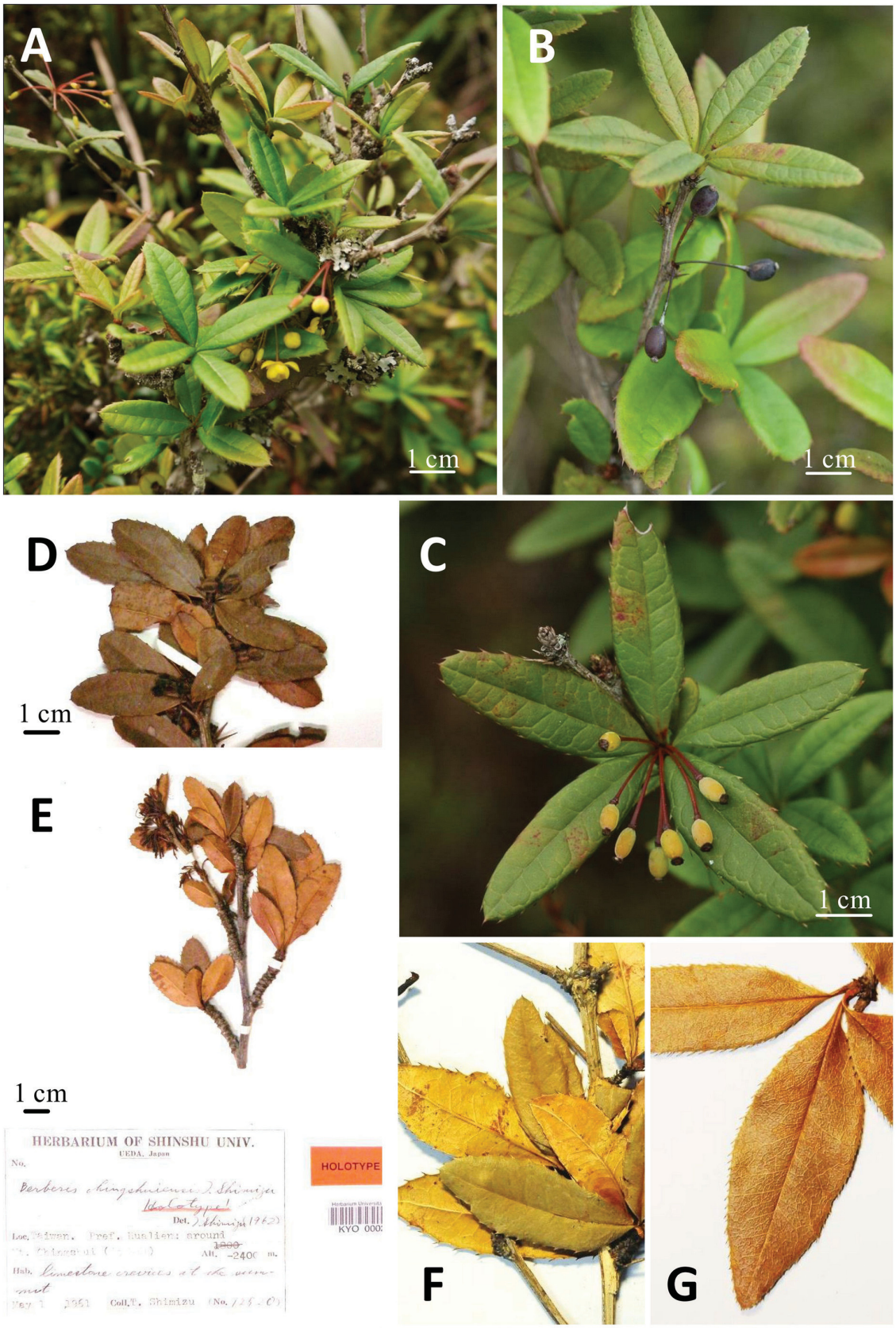

FIGURE 9. *Berberis chingshuiensis* T. Shimizu. **A.** Flowering branches. **B.** Branches with mature fruits. **C.** Fruiting branch, showing the complex-veined leaves and a fascicle of immature fruits. **D.** A portion of holotype, showing branches with adaxial surface of leaves. **E.** A portion of holotype, showing braches with abaxial surface of leaves. **F.** Leaf specimen of *B. chingshuiensis*, showing the sparsely toothed leaves. **G.** Leaf specimen of *B. schaaliae* C.C.Yu & K.F. Chung, showing the densely toothed leaves. A–C: Tatuanyaishan (the Great Cliff).

4. ***Berberis hayatana*** Mizushima (1954: 31). Type:—TAIWAN. Taihoku (Taipei), Taiheizan (Taipingshan), Ratogun (Lo-Tong), 17 May 1917, *Hayata s.n.* (holotype TI!) (Fig. 10A–C).

Heterotypic synonym:—*Berberis formosana* Li (1952: 41), *nom. illeg. non B. formosana* Ahrendt (1941: 24). Type:—TAIWAN. Mountains near Muroroahu, Taihoku-syu, 17 Jul 1932, *Suzuki 7258* (holotype TAI-156164!, isotype PH-66417!).

Evergreen shrub 0.5–1.6 m tall. *Mature stems* brown to reddish-brown, subterete, not verruculose. *Spines* 3-fid, concolorous, 0.6–2.3 cm. *Leaves* subsessile; leaf blade elliptic to narrowly-elliptic, abaxially green sometimes pruinose, adaxially dull dark green; 2.1–6.9 × 0.7–2.1 cm, thin-leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped if present; base cuniform, margins sometimes slightly revolute and remotely spinose with spinules of 3–11 with 2.5–7.0 mm apart on each side, apex acute or acuminate. *Inflorescence* a fascicle, 4–7-flowered. *Bracts* absent. *Pedicel* pale green, 0.6–1.7 cm. *Bracteoles* absent or 2, 3, red, triangular, 1.5 mm × 1 mm. *Flowers* bright yellow. *Sepals* in 2 whorls, outer sepals yellow with reddish-tinged ovate 3.5 × 2 cm, inner sepals yellow obovate 4.5 × 3 mm. *Petals* obovate, 4.5 × 3 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised. *Stamens* pale yellow ca. 3 mm, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long. *Ovules* 2 or 4. *Berries* black, ellipsoid ca. 7 × 4 mm, not pruinose, estylose.

Distinguishing features: *Berberis hayatana* was synonymized under *B. mingetsensis* in Lu & Yang (1996) and Yang *et al.* (1997); however, it can be easily distinguished from the latter by its unique dull adaxial leaf surfaces and generally shorter pedicels (0.6–1.7 vs. 1.3–2.8 cm). In areas of the northern Taiwan where winter northeastern monsoon are strong, *B. hayatana* can be found as low as 700 m. Notably, some individuals of *B. hayatana* from extreme humid environments (e.g., Yaungyang Lake, Lalashan) possess leaves with narrow-elliptic or lanceolate leaves with weakly developed spinose leaf margin.

Phenology:—*Flowering* February–May; *Fruiting* September–to February of the following year.

Distribution & habitat:—*Berberis hayatana* is relatively common in the understories of wet broad-leaved and coniferous and broad-leaved mixed forests from 700 to 2200 m in the northern Syue Mountain Range and northeastern Central Mountain Range (Fig. 6B).

Chinese name: 早田氏小檗

Proposed IUCN conservation status:—Nearly Threatened. *Berberis hayatana* is common in mountain areas of the northeast Taiwan, usually growing into large colonies. Although abundant, populations distributed in lower elevation are potentially threatened by human disturbance. Therefore we propose a provisional IUCN category of NT for the species (IUCN 2012).

Notes: *Berberis hayatana* Mizushima was described by Mizushima (1954) to replace *B. formosana* H.L. Li, a later homonym of *B. formosana* Ahrendt.

Additional specimens examined:—TAIWAN. Taipei: Peichatienshan, 15 December 1972, *Kuo 2609* (TAI); Lupeishan, 1400 m, 1 March 1989, *Hsieh 687* (TAI); Ayushan, 1000–1400 m, 13 September 2001, *Chung 4626* (TAIF); Dapolushan, 1400 m, 15 March 2009, *Yu 263* (TAI); Nanchatienshan, 2200 m, 29 February 2009, *Yu 261* (TAI). Yilan: Chilanshan, 2 April 1984, *Shih 310* (TAIF); Yuanyang Lake, 1600–1700 m, 10 January 1995, *Shen 324* (HAST), 2100 m, 1 December 1 2008, *Yu 190* (TAI); Taipingshan, 2000–2200 m, 27 March 2008, *Yang 1528* (HAST), 2200 m, 3 April 1988, *Kao 10685* (TAI); along Chilan No. 100 Forest Road, 1720 m, 28 October 2008, *Huang 3551* (HAST); Songlohu, 700–1300 m, 28 March 2009, *Lu 18081* (HAST); Tongshan, 2000 m, 9 April 2009, *Yu 311* (TAI); Taipingshan, 2000–2200 m, 27 March 2008, *Yang 1528* (HAST); Siatonshan, 2000 m, 3 April 2009, *Yu 309* (TAI); at Taipingshan, along Taiwn Beech National Trail, 1900 m, 28 June 2011, *Peng et al. 23110* (HAST). Hsinchu: Chenhsibao, 1850–2200 m, July 1999, *Wu 1819* (HAST); Litungshan, 1500–1900 m, 21 July 2002, *Lu 4517* (TAIF); Sichiousihshan, 2000 m, 18 December 2008, *Yu 252* (TAI). Taoyuan: route from Meikueihsimoshan to Papokulushan, 1840 m, 11 April 2002, *Leong 2880* (HAST); Pafu History Road, 1650 m, 27 February 2008, *Huang 3277* (HAST); Lalashan, 18 March 2006, *Lu 11513* (HAST).

5. ***Berberis kawakamii*** Hayata (1911a: 24–25). Type:—TAIWAN. Monte Morrison, ad 9000 ped. alt., Oct 1906, *T. Kawakami 1941* (holotype TI-02622!) (Fig. 11A–C).

Heterotypic synonyms:—Berberis formosana Ahrendt (1941: 24). Type:—TAIWAN. Prov. Kagi, Arisan, 25 October 1918, *Wilson 10910*" (holotype BM-001015554!, isotypes A-00038750!, K-000644915!, US-00956032, *n.v.*, image seen); *B. kawakamii* var. *formosana* (Ahrendt) Ahrendt (1961: 65).

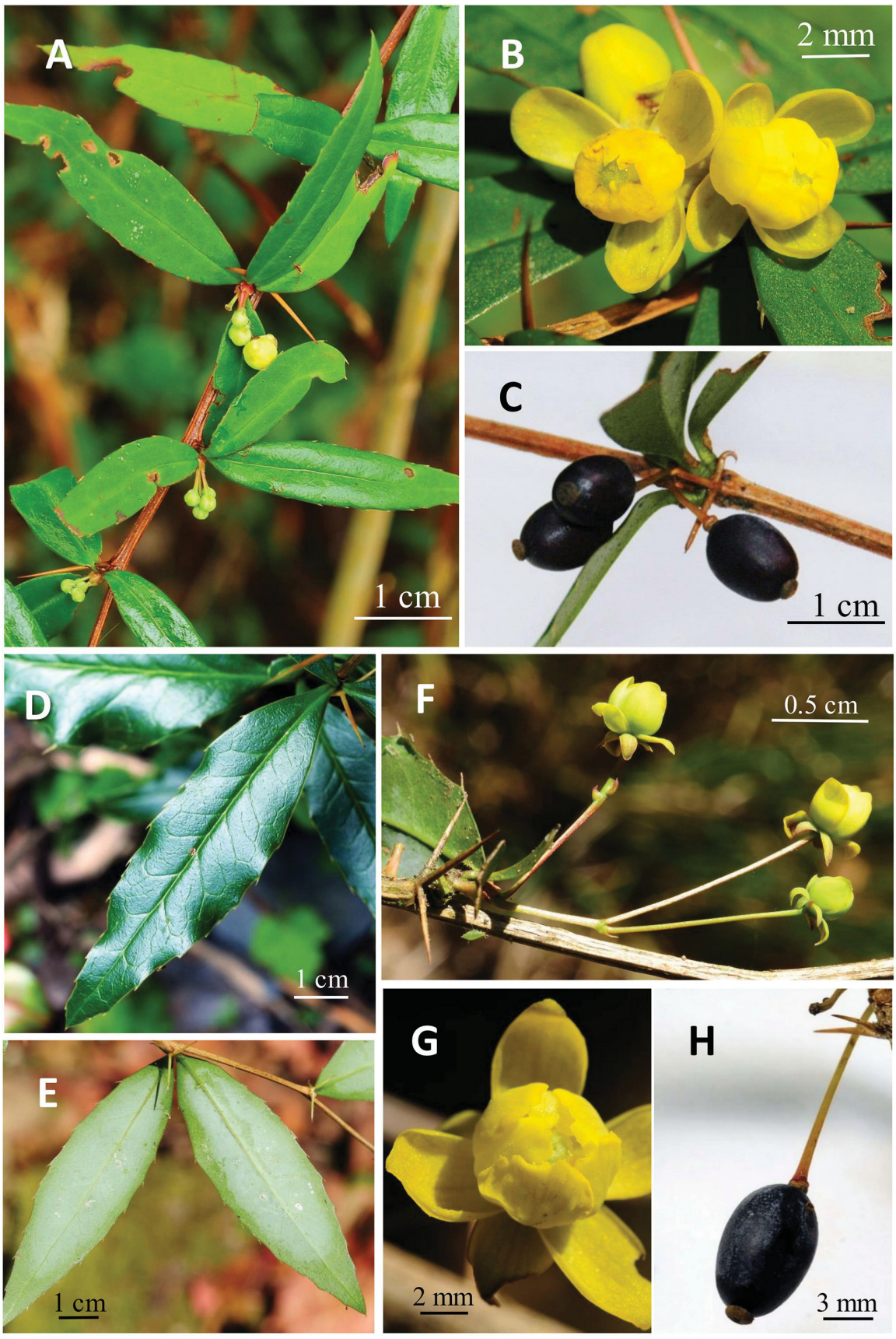

FIGURE 10. *Berberis hayatana* Mizush. (A–C) and *B. mingetsensis* Hayata (D–H). **A.** Flowering branch, showing the dull upper surface of leaves. **B.** Flowers, front view. **C.** Fruits. **D.** Leaves, waxy-shining adaxially. **E.** Leaves, pruinose abaxially. **F.** A solitary flower and a highly reduced umbel with two flowers, showing the long pedicels and bracts. **G.** Flower, front view. **H.** Berry. A, B: Lalashan; C: Tamenshan; D–H: Mienyueh. A, B, D–G: courtesy of Chi-Kai Yang.

Evergreen shrub or small tree-like shrub 0.5–3 m tall. *Mature stems* greyish or brownish-yellow, inconspicuously verruculose. *Spines* 3-fid, concolorous, 0.8–2.7 cm. *Leaves* subsessile; leaf blade elliptic, elliptic-obovate, oblong, oblong-lanceolate, lanceolate, abaxially pale green, adaxially green; 2.9–7.2 ×0.8–2.0 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped; base cuniform or attenuate, margins remotely spinose with spinules of 5–15 with 2.5–6.0 mm apart on each side, apex acuminate. *Inflorescence* a dense, congested fascicle of 6–12 flowers. *Bracts* absent. *Pedicel* red, 0.3–1.2 cm. *Bracteoles* absent. *Flowers* yellow. *Sepals* in 3 whorls, outer sepals yellow with reddish-tinged narrowly-triangular or rarely linear 3–6 × 1 mm, middle sepals yellow triangularly-oblong 5 × 2 mm, inner sepals yellow narrowly obovate 5.5 × 2.5 mm. *Petals* narrowly-oblong 5 × 1.5 mm, base clawed with a pair of ovoid nectaries very close to each other, apex incised with obtuse lobes. *Stamens* pale yellow ca. 3 mm, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long usually with reddish-tinged. *Ovules* 2 or 3. *Berries* black, ellipsoid ca. 5 × 3.5 mm, sometimes slightly pruinose, stylose ca. 0.5–1 mm.

Distinguishing features: The combination of triangular-oblong outer sepals and a densely fascicled inflorescence makes this an easily distinguished species (Fig. 1L & 11B). Early literatures often allied *B. kawakamii* with the Filipino *B. barandana* (Hayata 1908, Kawakami 1910, 1911), such as those by Merrill (1923) who stated that "*I failed to find any reason for distinguishing the Formosan B. kawakamii Hayata*." However, these two species can easily be differentiated by the shape of outer sepals and as noted above molecular analysis places them in different clades (Fig. 5).

Phenology:—*Flowering* March–May, August; *Fruiting* January, April–July, August–December.

Distribution & habitat:—*Berberis kawakamii* is very well represented in herbaria of Taiwan and is undoubtedly the commonest species of sect. *Wallichianae* in Taiwan, occurring throughout all major mountain systems north of Beinanchushan from 1600 to 3100 m (Fig. 6A & D). Across its wide distributional ranges, *B. kawakamii* is found in various habitats, ranging from subalpine and alpine meadows, montane coniferous forests, to coniferous and broad-leaved mixed cloud forests and exhibits substantial local morphological variation in both height and leaf shapes and size.

Chinese name: 臺灣小檗

Proposed IUCN conservation status:—Nearly Threatened. *Berberis kawakamii* is common throughout major high mountains of Taiwan, usually growing into large colonies. However, the high mountain ecosystem of Taiwan is potentially threatened by the effect of global climate change, we therefore propose a provisional IUCN category of NT for the species (IUCN 2012).

Notes: *Berberis kawakamii* var. *formosana* (Ahrendt) Ahrendt was first synonymized under *B. kawakamii* Hayata by Li (1963), a treatment that is confirmed by our multivariate statistical analyses. The name '*Berberis miyabei* Kawakami' *in sched.* was discovered on a specimen of *B. kawakamii* with the label '*T. Kawakami s.n.* (1907) & *U. Mori s.n.* (1907)' in the Herbarium of the University of Tokyo (TI). Accompanied with the specimen, there is also a typed description of *B. miyabei* Kawakami *in sched.* by Takiya Kawakami, to who *B. kawakamii* was attributed to.

Additional specimens examined:—TAIWAN. Yilan: Nanhu River, 2800–3000 m, 13 May 1989, *Leu 24993* (TAIF); Szuyuanyakou, 1600 m, 5 April 2008, *Lu 15630* (HAST); Wulanshan, 2400 m, 12 August 2008, *Yu 117* (TAIF). Hsinchu: Chiuchiushanchuang ("99 Lodge"), 2694 m, 6 September 1993, *Huang 45* (HAST); Kelayehshan, 3000 m, 6 April 2008, *Yu 50* (TAI). Miaoli: Leshan-Kuanwu, 2000–2300 m, 24 July 1987, *Wang & Yang 4685* (TAI). Taichung: Anmashan, 2200 m, 22 April 2004, *Wang 7290* (TNM); Chica Lodge to 369 Lodge, 2900 m, 12 November 12 1989, *Her 14* (TNM), Chika Lodge, 2600 m, 18 August 2008, *Yu 99* (TAI); Taoshan, 3300 m, October 1981, *Ou s.n.* (TNM); en route from Wuling Lodge to Taoshan, 2600 m, August 1988, *Peng 12018* (HAST); Tienchih-Nengkaopeifeng, 3100 m, 16 June 1996, *Chiu 3433* (HAST); along trail from Tienluanchih to Hohuanpeifeng, 2950 m, May 2002, *Huang 1089* (HAST). Nantou: Chichia Lake, 2800–2900 m, 3 September 1998, *Chen 321* (TAI); Pass Nengkao, 14 August 1955, *Hsii 19* (TAI); Hohuanshan, 26 April 1985, *Lu 15953* (TAIF); roadside, Pilushan, 2600–2900 m, 25 July 1990, *Lin & Lin s.n.* (TNM); Kuankao-Chunyangchinkuang, 2500–2900 m, 8 July 1993, *Yang 5287* (TAI); Chuntashan, 3175 m, 8 March 1999, *Liou 1147* (TAIF); Chilaishan shelter, 2700–3000 m, 30 April 2004, *Chung 1013* (TAI); Puli, 18 March 2009, *Yang 6203* (TNM); Hsiluantashan, 2850 m, 11 April 2009, *Yu 399* (TAI). Chiayi: Alishan-Chushan, 2300 m, 22 March 1985, *Huang 2584* (TAI); Tatashan, 2400–2663 m, 23 September 2000, *Kuo 98* (HAST); Tatakaanpu-Yushanchienfu, 3100 m, 11 November 1990, *Wu & Lai s.n*. (TNM); Yushan, 3300 m, 13 April 1996, *Yang 4684* (TAIF). Kaohsiung: trail to Takuanshan, 2690 m, 20 May 1992, *Wang 1074* (HAST); on the way from Chinching Bridge to a campsite by the trail to Kuanshan, 2500–2700 m, 17 May 1995, *Wang 1122* (HAST); Kuanshanlingshan, 2900–3175 m, 12 August 2002, *Lee 244* (TAIF); Shunyunshan, 2500 m, 31 March 2003, *Lu 5727* (TAIF); Kuanshan, 3050 m, 2 February 2008, *Yu 9* (TAI). Taitung: South Cross Highway, 2600 m, 30 March 1996, *Lu 25003* (TAIF). Hualien: Yuanfeng adjacent to Prov. Rd. 14, 2700–2800 m, 28 March 1994, *Chen 469* (HAST); near Liwuchushan, 3000 m, 21 November 2004, *Yang 804* (TNM); Yangtoushan, 2900 m, 12 October 2008, *Yu 158* (TAI); Chukushan, 2200 m, 27 January 2012, *Yu 693* (TAI).

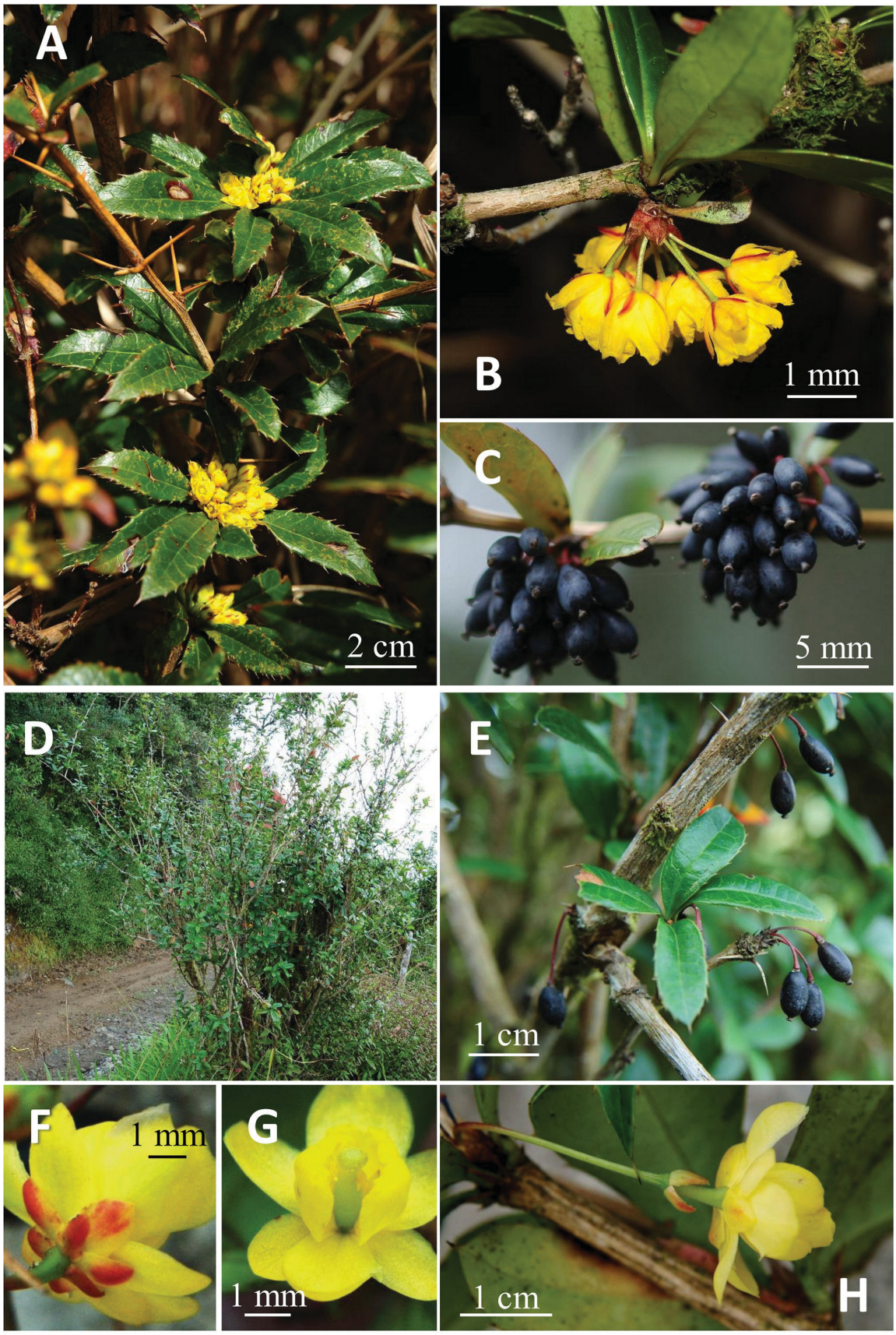

FIGURE 11. *Berberis kawakamii* Hayata (A–C) and *B. barandana* S. Vidal (D–H). **A.** Flowering branches. **B.** Flowers, showing the reddish, narrow-triangular outer sepals. **C.** Stylose, ellipsoid fruits. **D.** Habitat and habit. **E.** Fruiting branches. **F.** Flower, exterior view, showing the bracteoles, and outermost sepals. **G.** Flower, front view, with parts of the petals removed. **H.** Flowering branch, showing the pair of bracts. A, B: Hohuanshan; C: Liwuchushan, courtesy of Chi-Kai Yang; D–H: Mt. Santo Thomas, Luzon, Philippines.

6. ***Berberis mingetsensis*** Hayata (1915: 4). Type:—TAIWAN. Arisan, Mingetsukei, April 1914, *Hayata s.n.* (holotype TI-02625!) (Fig. 10D–H).

Evergreen shrub, semi-prostate, 0.5–1.5 m tall. *Mature stems* brown or pale yellow, subterete, not verruculose. *Spines* 3-fid, concolorous, 0.5–2.2 cm. *Leaves* subsessile; leaf blade narrowly-elliptic to elliptic or sometimes lanceolate, abaxially green and usually strongly pruinose, adaxially dark green; 5.8–9.0 × 1.3–2.9 cm, thinly-leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped and muliti-festooned, the tertiary veins weakly reticulate if present; base cuneate, margins remotely spinose with spinules of 7–16 with 3.0–9.0 mm apart on each side, apex acuminate or mucronate. *Inflorescence* a fascicle or rarely a highly reduced umbel, 4–8-flowered. *Bracts* 1 or 2 if present, pale green or yellow with reddish-tinged narrowly-triangular 2 × 1 mm. *Pedicel* pale green with partly red, 1.3–2.8 cm. *Bracteoles* 2 or 3, red, triangular, 1.5 × 1 mm. *Flowers* bright yellow. *Sepals* in 3 whorls, bright yellow, outer and middle sepals usually outwardly revolute, outer sepals yellow usually with reddish-tinged ovate 3 × 2 mm, middle sepals yellow ovate 5 × 3.5 mm, inner sepals yellow obovate or elliptic 6.5 × 4.5 mm. *Petals* elliptic, 4.5 × 3 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised. *Stamens* pale yellow ca. 4 mm, anther connective of stamen distinct, apex truncate. *Pistil* 5 mm long. *Ovules* 6. *Berries* black or dark blue, ellipsoid ca. 7 × 4.5 mm, more or less pruinose, estylose.

Distinguishing features: *Berberis mingetsensis* is similar to *B. ravenii*, differing from the latter by its remotely spinose margin of leaves.

Phenology:—*Flowering* March–April, December; *Fruiting* May, September.

Distribution & habitat:—*Berberis mingetsensis* is an understory shrub of the coniferous and broad-leaved mixed forest of 2300 to 2800 m. Most individuals are found from Taiwan Pleione Nature Reserve (TW Pleione NR) of Alishan (Fig. 6A & 6C), especially from along the Mienyueh Spur Line of Alishan Forest Rail System, with the exception of a small, disjunct population in Nantou County.

Chinese name: 眠月小檗

Proposed IUCN conservation status:—Critically Endangered [CR B1a+c(ii, iii)]. *Berberis mingetsensis* is known only from two restricted localities in Chiayi and Nantou County where they occur as scattered individuals on the mountain ridges or along the abandoned railway. Habitat disturbance brought about by tourists and development of the railway construction in Alishan areas may have a negative impact on the survival of the species (IUCN 2012).

Notes: This rare species has an early and complicated taxonomic history (Table 2). Mizushima (1954) argued that *Berberis mingetsensis* is very similar to the Chinese species *B. bicolor*, though he refrained from uniting the two. This was clearly a mistaken since *B. bicolor* is unique in being the only species in the whole genus with flowers that are white and red whereas the flowers of *B. mingetsensis* are yellow. Unfortunately, Mizushima's (1954) statement was taken into action by Liu (1960, 1976), whose treatment also followed in Liu & Liao (1980) and Liu *et al.* (1988, 1994). Subsequently *B. mingetsensis* was synonymized under *B. aristatoserrulata* without explanation by Chamberlain & Hu (1984) and this was followed by Ying (2001, 2011). In 1963, Li corrected the species epithet to '*mingetsuensis*', as to make it conform to the spelling of its type locality 'Mingetsukei' (which literally means Mingetsu 'creek') and this was followed by Lu & Yang (1996), Yang *et al.* (1997), and Lu *et al.* (2010). However there is no reason to believe Hayata's use of 'mingetsensis' was not intentional since he also applied it to his *Rubus mingetsensis* Hayata (1915: 40–42) whose type was also collected in Mingetsukei. One possible explanation for his leaving out the letter 'u' from these two names is because there is no difference between the Japanese pronunciation of 'mingetsuensis' and 'mingetsensis.' Given this in accordance with Art. 60.1 of the Melbourne Code (McNeill *et al.* 2012) Hayata's name stands.

Additional Specimens examined:—TAIWAN. Nantou: Siluantashan, 2800m, 11 April 2009, *Yu 398* (TAI). Chiayi: Alishan, 2500 m, June 1914, *Faurie 447* (HAST); Alishan Museum, 1 August 1957, *Lu s.n*. (HAST); Alishan, by railroad between Alishan Station and Mienyiieh Station, 2300 m, 20 March 1983, *Peng 4566* (A, HAST); Shihhou, 11 March 1990, *Ou s.n*. (TNM); Alishan-Fengshan, 2400 m, 14 May 1992, *Wang s.n.* (TNM); Mienyueh Spur Line 7.9k, 2500 m, 10 September 2008, *Yu 145* (TAI); Songshan, 2600 m, 26 January 2012, *Yu 707* (TAI).

7. ***Berberis nantoensis*** Schneider (1939: 252) = *Berberis densifolia* Byhouwer (1928: 133) [*non B. densifolia* Rusby (1920: 16)]. Type:—TAIWAN. Nanto, Mount Kiraishui, 3500-3600 m, 6 March 1918, *Wilson 10074* (holotype A-00038729!, isotype BM-000810310!, PNH-28859!, US-1053600, *n.v.*, image seen) (Fig. 12A–C).

Evergreen shrub, 1–2 m tall. *Mature stems* red-brownish, subterete, inconspicuous verruculose. *Spines* 3-fid, concolorous, 1.0–2.3 cm. *Leaves* subsessile; leaf blade elliptic, abaxially pale green sometimes pruinose, adaxially green; 1.2–3.4 × 0.4–1.7 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised,

the secondary veins pinnate but not jointly together; base cuniform, margins usually strongly revolute, entire or remotely spinose with spinules of 1–4 with 4.0–18.0 mm apart on each side, apex acute, mucronate to obtuse. *Inflorescence* a dense, congested fascicled of 7–9 flowers. *Bracts* absent. *Pedicel* pale green, 0.2–0.3 cm. *Bracteoles* absent. *Flowers* bright yellow. *Sepals* in 3 whorls, outer sepals yellow with partly reddish-tinged ovate 4 × 3 mm, middle sepals yellow obovate 6 × 3 mm, inner sepals yellow obovate 8 × 4 mm. *Petals* elliptic, 6 × 4 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised or emarginated with acute lobes. *Stamens* pale yellow ca. 3 mm, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long. Ovules 2 or 3. *Berries* black or dark blue, sub-globose ca. 6 × 5 mm, sometimes pruinose, estylose.

Distinguishing features: *Berberis nantoensis* is easily recognized by its dense, congested fascicle inflorescence, short-pediceled flowers, and revolute leaf margins, although the last feature is occasionally found in *B. chingshuiensis*, *B. kawakamii*, and *B. schaaliae*.

Phenology:—*Flowering* January, March–June; *Fruiting* January, July–December.

Distribution & habitat:—*Berberis nantoensis* are shrubs or occasionally tree-like shrubs mainly distributed in subalpine meadows, exposed rocky habitats, and the understories of coniferous forests from 2000 to 3300 m in Syue and Central Mountain Ranges (Fig. 6C).

Chinese name: 南投小檗

Proposed IUCN conservation status:—Vulnerable [VU B1b(iii)c(iii)]. *Berberis nantoensis* usually occurs as scattered individuals in subalpine and alpine regions in major high mountains of Taiwan. Although most high mountain areas are under protection in Taiwan, this species is potentially under risk due to its restricted and scattered distributional ranges. We propose a provisional IUCN category of VU for the species (IUCN 2012).

Additional specimens examined:—TAIWAN. Yilan: Taipingshan, 2200 m, 24–29 April 1930, *Sasaki s.n.* (TAI); Gilitin-Denshankou, 1200–2580 m, 20 August 1969, *Hsu 5912* (TAI); Nanhutashan, July 1940, *Nakamura 3040* (TAI), 2800–3100 m, 4 May 1990, *Liou 560* (HAST); Loyehweishan, 2800 m, 8 December 2008, *Yu 192* (TAI). Miaoli: en route from "99 villa" to Tapachienshan, 2700–2800 m, 11 August 1985, *Peng 8482* (HAST); ca. 10 km from entrance of on Hsuehshan No. 230 forest road, 2400 m, 4 May 1999, *Wu 1201* (HAST, KUN). Taichung: Shenmachanshan, 3100 m, 28 May 1974, *Huang 5925* (TAI); Shenmachenshan to Yunling Lodge, 3400 m, 18 July 1996, *Liu 1021* (HAST); Hsiaohsuehshan, 2900 m, 14 January 1997, *Lu 25178* (HAST). Nantou: Nengkoshan, 6 March 1918, *Sasaki s.n.* (TAI); Patunkuan, 2500 m, 20 March 1987, *Yang 82* (TNM); Hohuanshan, 2900 m, 10 November 1989, *Lu 24977* (HAST); Chilaichunanfeng, 3200 m, 4 September 1998, *Yang 11189* (TNM); Tayuling 820 Forest Road, about 1.4 km from entrance, 2530 m, 13 May 2004, *Wu 588* (HAST); Yangtoushan, 2900 m, 13 October 2008, *Yu 159* (TAI). Kaohsiung: Shunyun Lodge, 2500 m, 10 January 2011, *Yu 701* (TAI).

8. ***Berberis pengii*** C.C.Yu & K.F.Chung, *sp. nov.* (Figs. 7E–H, 13).

Type:—TAIWAN. Pingtung: Taiwu, Kuaiku Lodge, 22°36'48"N, 120°44'39"E, 2150 m, 18 April 2011, *Chih-Chieh Yu 683* (holotype TAI -284283!).

Diagnosis: *Berberis pengii* is similar to *B. aristatoserrulata*, *B. chingshuiensis*, and *B. mingetsensis* in its leaf shape, differing from the latters by its narrow-triangular or triangular-oblong outer sepals and from the former by its globose berries.

Evergreen shrub or small tree-like shrub, 1.5–4 m tall. *Mature stems* yellowish-brown, not verruculose. *Spines* 3-fid, concolorous, 0.8–1.8 cm. *Leaves* subsessile or sometimes with short petioles ca. 2–5 mm; leaf blade elliptic or narrowly-elliptic, abaxially pale green sometimes pruinose, adaxially shiny green; 4.4–8.9 × 1.4–2.6 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped and multi-festooned, the tertiary veins weakly reticulated; base cuniform, margins densely spinose with spinules of 13–27 with 1.5–3.5 mm apart on each side, apex acute or attenuate. *Inflorescence* a fascicle, 4–7-flowered. *Bracts* absent. *Pedicel* pale green, 0.4–1.6 cm. *Bracteoles* absent. *Flowers* yellow. *Sepals* in 3 whorls, outer sepals with midveins slightly raised yellow or reddish tinge narrowly-triangular or triangularly-oblong 5 × 1 mm, middle sepals yellow or reddish tinge ovate 7.5 × 2.5 mm, inner sepal yellow obovate 8 × 4 mm. *Petals* elliptic, 7 × 4 mm, base clawed with a pair of narrowly-ovoid nectaries very close to each other, apex acutely emarginated with margins slightly ragged. *Stamens* bright yellow ca. 5 mm, anther connective of stamen distinct, apex truncate. *Pistil* 5.5 mm long, usually red. *Ovules* 6 or 8. *Berries* black, globose or sub-globose ca. 10 × 10 mm, more or less pruinose, estylose.

Phenology:—*Flowering* April–May; *Fruiting* April–June, October, November.

Distribution & habitat:—*Berberis pengii* is large understory shrubs of 1–2 m tall commonly found in the coniferous and broad-leaved mixed forests in the southern Central Mountain Range at 2100 to 2500 m (Fig. 6B).

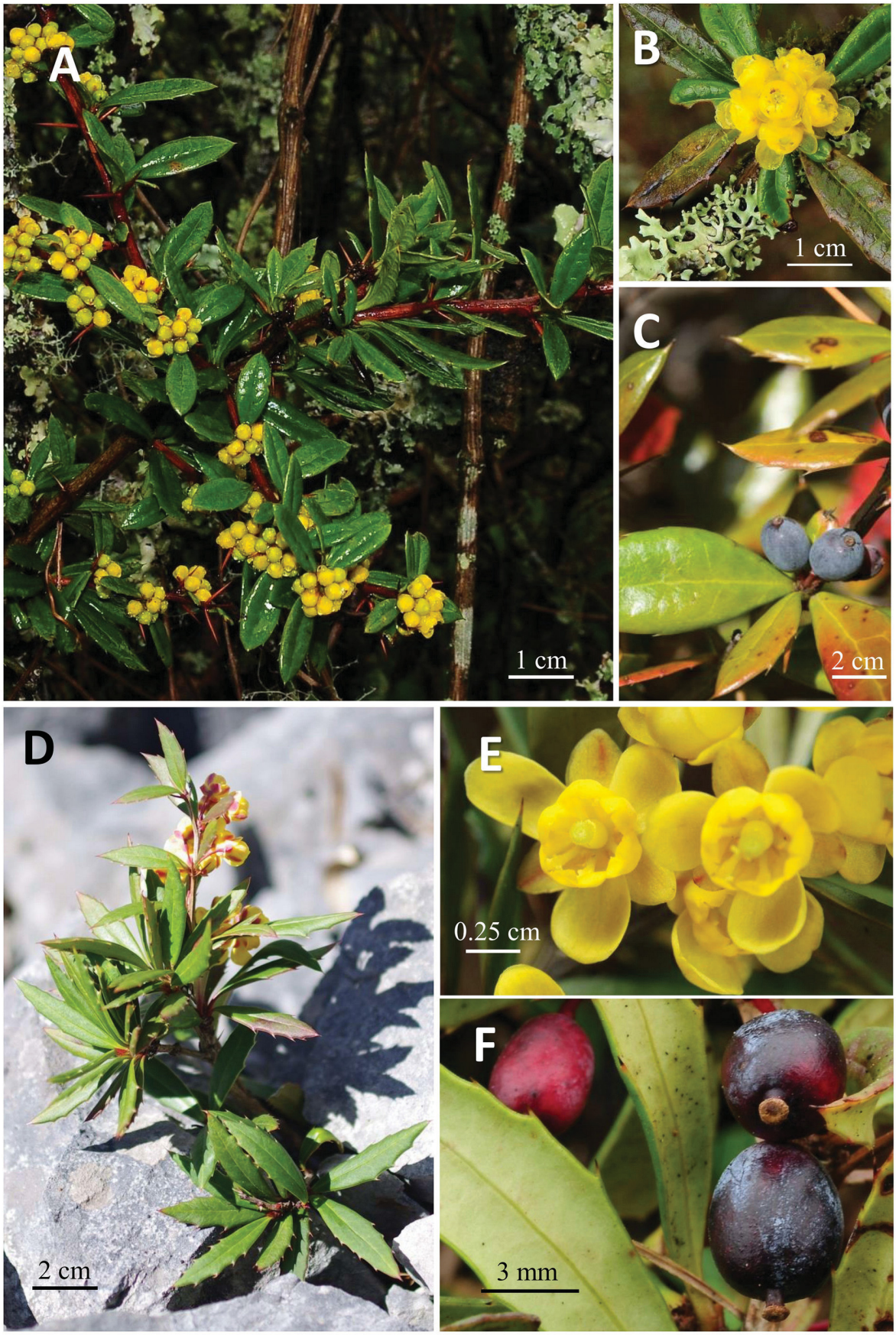

FIGURE 12. *Berberis nantoensis* C.K. Schneid. (A–C) and *B. tarokoensis* S.Y. Lu & Yuen P. Yang (D–F). **A.** Flowering branches. **B.** Flowers, front view. **C.** Fruiting branch. **D.** Habitat and habit. **E.** Flowers, front view. **F.** Stylose fruits. A, B: Hsiaochilai Trail; C. Nanhutashan, courtesy of Cheng-Dao Lin; D, E: Yenhai Logging Road; F: Tatuanyaishan (the Great Cliff), courtesy of Chi-Kai Yang.

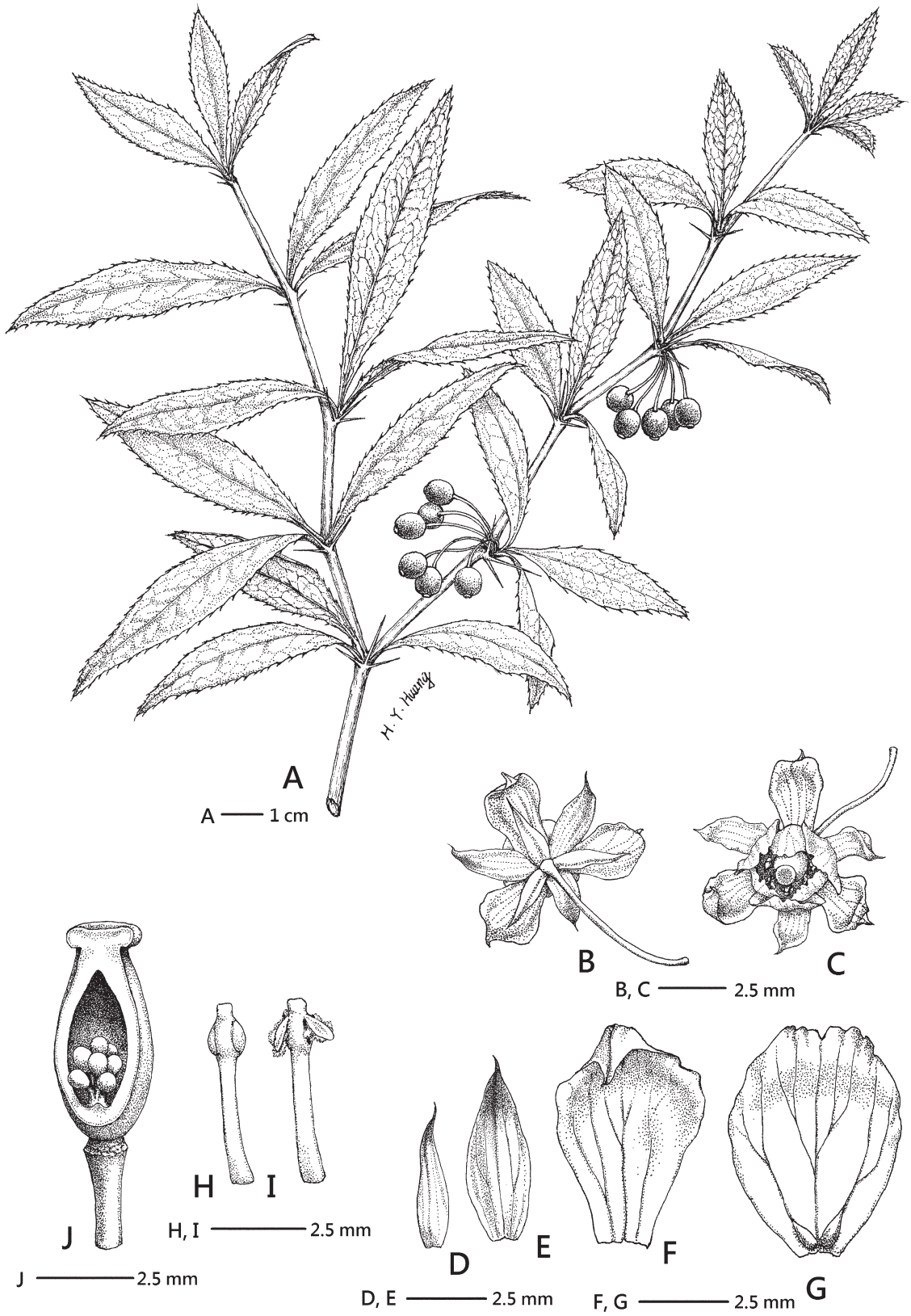

FIGURE 13. *Berberis pengii* C.C. Yu & K.F. Chung. **A.** Fruiting branch. **B.** Flower, exterior view, showing the sepals. **C.** Flower, front view. **D.** Outermost sepal. **E.** Secondary-whorled sepal. **F.** Inner whorl of sepal. **G.** Petal with a pair of ovoid nectaries at base. **H.** Stamen. **I.** Stamen with opened anthers. **J.** Ovary, longitudinal dissected showing ovules. Drawn by Han-Yau Huang.

Etymology:—The specific epithet is named in honor of Dr. Ching-I Peng, mentor and collaborator of the senior author, for his continuous guidance, supports, and friendship, and for his great contribution to the studies of Asian Flora.

Chinese name: 南臺灣小檗

Proposed IUCN conservation status:—Nearly Threatened. *Berberis pengii* is endemic to south Taiwan and its natural range is mostly within the range of national preservation areas. Therefore we propose a provisional IUCN category of NT for the species (IUCN 2012).

Additional specimen examined:—TAIWAN. Kaohsiung: Dagueii Lake, 2150 m, 11 February 2009, *Yu 338* (TAI), near the Blue Ghost Lake, 2400 m, 10 February 2009, *Yu 339* (TAI), Juniper Camping Site, 2250 m, 12 February 2009, *Yu 378* (TAI), the "Big Field" near Dagueii Lake, 2250 m, 10 February 2009, *Yu 379* (TAI); near Camp Yukuting, 2400 m, 12 February 2009, *Yu 355*, *358* (TAI); Dona Logging Trail, 2100 m, 12 February 2009, *Yu 347* (TAI). Pingtung: Peitawushan, 3000 m, 6 June 1988, *Huang 13670* (TAI), 2400–2600 m, 30 November 1997, *Liu 146* (TNM), 2500–2900 m, 24 April 2008, *Wu 165* (TNM); en route from the first Lodge to Chih-pen-chu-shan, 1900 m, 10 March 1990, *Lin 408* (HAST); Pa-yu lake to Lakalakashan, 14 February 1993, *Yang 30239* (HAST, PE); Kuaiku Lodge, 2250–2900 m, 2 April 1994, *Chen 595* (HAST, TNM), 1600–2150 m, 9 October 2006, *Wang 9342* (TNM), 2150 m, 18 April 2011, *Yu 683* (TAI); Tamaru Camping Site, near Damumushan, 2200 m, 21 May 2009, *Yu 325* (TAI); behind Nantawushan, 2500 m, 2 May 2009, *Yu 330* (TAI); Linpalapalashan, 2300 m, 22 May 2009, *Yu 377* (TAI). Taitong: near Shishuitoushan, 2300 m, 11 February 2009, *Yu 341* (TAI).

9. ***Berberis ravenii*** C.C.Yu & K.F.Chung, *sp. nov.* (Figs. 14, 15).

Type:—TAIWAN. Kaohsiung: Maolin, Shuangguie Lake Major Wild Life Habitat, Lake Upunuhu (Wan-shan-shen Lake), 22°54'53"N, 120°49'41"E, 2150 m, 7 February 2009, *Chih-Chieh Yu 267* (holotype TAI-284282!).

Diagnosis: *Berberis ravenii* differs from all Taiwanese species of sect. *Wallichianae* in having purplish or red mature shoots of the first year, and lanceolate to narrowly-lanceolate leaves. It is similar to *B. mingetsensis*, differing from the latter by its sparsely spinose margin of leaves with 17–28 spinules, and between each is 2–3 mm apart (v.s. leaf margins remotely spinose, with 6–16 spinules of 3–9 mm apart).

Small evergreen shrub, more or less decumbent, 0.5–1 m tall. *Mature stems* purplish red, terete, not verruculose. *Spines* 3-fid, concolorous, 0.8–2.3 cm. *Leaves* subsessile; leaf blade elliptic to lanceolate, abaxially green or dark green not pruinose, adaxially green or dark-greenish; 5.5–9.5 × 1.2–2.0 cm, slightly leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped and muliti-festooned, the tertiary veins reticulate; base cuneate, margins sometimes slightly revolute and remotely spinose with spinules of 16–28 with 2–3 mm apart on each side, apex acuminate or mucronate. *Inflorescence* a fascicle, 4–7-flowered. *Bracts* absent. *Pedicel* pale green, 1.3–1.5 cm. *Bracteoles* absent or 2, pale yellow or greenish-yellow triangular 1 × 1 mm. *Flowers* pale yellow, greenish-yellow. *Sepals* in 3 whorls, outer sepals yellow or reddish tinge or pale green ovate 2.5 × 2 mm, middle sepals yellow ovate 4 × 2.5 mm, inner sepals yellow obovate 5 × 4.5 mm. *Petals* obovate, 4.5 × 3 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised. *Stamens* pale yellow ca. 3 mm, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long. *Ovules* 2 or 3. *Berries* black, ellipsoid ca. 7 × 4 mm, not pruinose, estylose.

Phenology:—*Flowering* April; *Fruiting* February.

Distribution & habitat:—*Berberis ravenii* occurs in the coniferous and broadleaved mixed forests of Shuanggui Lake Major Wildlife Habitat of southern Central Mountain Range at 1400 to 2300 m (Fig. 6A & 6D).

Etymology:—The specific epithet commemorates Dr. Peter H. Raven, mentor of the senior author, for his enduring support, guidance, and encouragement, and for his tremendous contribution to botanical research and the conservation of global biodiversity.

Chinese name: 神武小檗

Proposed IUCN conservation status:—Data Deficient (DD). *Berberis ravenii* is currently known only from the mid-elevation cloud forests in Shuanggui Lake Major Wildlife Habitat and its precise distributional range remains to be explored (IUCN 2012).

Additional specimen examined:—TAIWAN. Kaohsiung: Chunyunshan, 700 m, 7 March 1996, Liou 5 *(*TAIF); mountains near Lake Dalubaling, 2150 m, 8 February 2009, *Yu 265, 277, 279* (TAI); Peak 2080 near Lake Upunuhu, 2080 m, 6 February 2009, *Yu 271* (TAI); Shihsueitoushan Front Peak, 2200 m, 7 February 2009, *Yu 282* (TAI); Lake Upunuhu, 2150 m, 7 February 2009, *Yu 287, 293* (TAI); Damumushan, 2400 m, 21 May 2009, *Yu 322, 323* (TAI). Pingtong: Chutunshan Japanese Subpolice Office, 12 August 1937, *Ito 516* (TAI); Kuaiku, 23 January 1988, *Kuoh*

13554 (TNM); en route to Tawushan, 2100-3090 m, 16-17 July 1988, *Huang et al. 13678* (TAI); Linpalapalashan, 2300 m, Apr. 2008, *Yu 127, 130, 132, 134, 327* (TAI); Wantoulanshan, 1900 m, 6 February 2009, *Yu 289* (TAI); Paiwanese historical trail (south line), 1400 m, 27 December 2009, *Yu 269, 270, 272, 276, 362* (TAI); Southern flank Wutoushan, 2000 m, 28 December 2009, *Yu 380* (TAI); trail to North peak of Tawushan, 2305 m, 29 December 2009, *Yu 278, 294, 299* (TAI); near South peak of Tawushan, 2200 m, 2 May 2009, *Yu 329* (TAI).

10. *Berberis schaaliae* C.C.Yu & K.F.Chung, *sp. nov.* (Figs. 9G, 16, 17).

Type:—TAIWAN. Hualien, Sioulin, Tatuanyaishan (The Great Cliff), 24°12'16.46"N, 121°34'47.52"E, 1500 m, 8 August 2008, *Chih-Chieh Yu 147* (holotype TAI-284281!).

Diagnosis: *Berberis schaaliae* is similar to *B. chingshuiensis*, differing from the latter by its densely spinose leaf margin (31–64 vs. 6–11 spinules).

Evergreen shrub, 1–1.5 m tall. *Mature stem* brown, subterete, not verruculose. *Spines* 3-fid, sometimes palmate, concolorous, 0.2–1.2 cm, sometimes absent. *Leaves* subsessile; leaf blade ovate or elliptic, abaxially pale green not pruinose, adaxially green; 5.4–10.5 × 1.4–3.3 cm, thickly-leathery; midvein abaxially raised and adaxially impressed, lateral veins raised, the secondary veins pinnate, jointly looped and multi-festooned, the tertiary veins strongly-reticulated; base acute to attenuate, margins sometimes slightly revolute, closely spinose with spinules of 31–64 with 0.5–2 mm apart on each side, apex acute or mucronate. *Inflorescence* a fascicle, 3–12-flowered. *Bracts* absent. *Pedicel* red, 0.7–2.3 cm. *Bracteoles* 1 or 2, red, triangular, 0.5 × 0.5 mm. *Flowers* yellow. *Sepals* in 3 whorls, outer sepals yellow with partially reddish-tinged triangular 2 × 1.5 mm, middle sepals yellow elliptic to ovate 3 × 2 mm, inner sepals yellow obovate 6.5 × 4 mm. *Petals* elliptic, 4.5 × 3 mm, base clawed with a pair of ovoid nectaries very close to each other, apex usually dentate. *Stamens* pale yellow 3 mm long, anther connective of stamen distinct, apex truncate. *Pistil* 4 mm long. *Ovules* 3 or 4. *Berries* dark purple to black, ellipsoid ca. 7 × 4 mm, not pruinose, estylose.

Phenology:—*Flowering* April–May; *Fruiting* March–June, August, and December.

Distribution & habitat:—*Berberis schaaliae* occurs in the limestone terrains of eastern Central Mountain Range of Hualien County (Fig. 6D). It is locally common in the understories of lower warm temperate montane forests at the elevation at 1100 to 2400 m.

Etymology:—This species is named in honor of Dr. Barbara A. Schaal, mentor of the senior author, for her enduring support, guidance, and encouragement, and for her prodigious contribution to plant evolutionary biology.

Chinese name: 花蓮小檗

Proposed IUCN conservation status:—Nearly Threatened. *Berberis schaaliae* is distributed in eastern Taiwan, especially common in Hualien County. It is abundant in the understory of warm temperate forests, growing into large colonies locally. However, because it appears to only grow in limestone areas, we propose a provisional IUCN category of NT for the species (IUCN 2012).

Notes:—*Berberis schaaliae* is well collected and represented in the main herbaria in Taiwan and is easily recognized by its densely spinose leaf margin (31–64 spinules on each side) and reticulated third level veins; however, this species has long been misidentified as *B. chingshuiensis*, a much rarer species with remotely spinose leaf margin (6–11 spinules on each side). Across East Asia, only two other Chinese species, *B. ferdinandi-coburgii* Schneider (1913: 364) and *B. acuminata* Franchet (1886: 387) possess leaves with densely spinose margin comparable to *B. schaaliae*.

Additional specimen examined:—TAIWAN. Hualien: Chingshuishan, 1400–2200 m, 31 March 1961, *Shimizu 11822* (TAI), 2300 m, 12 April 1984, *Lu 14494* (TAIF), 2000–2400 m, 25 July 1986, *Huang 12838* (TAI), 1500–2000 m, 3 June 1993, *Leu 1806* (HAST), 1800 m, 7 December 2000, *Chen 581* (HAST), 1910 m, 27 June 2005, *Huang 2102* (HAST), 2200 m, 4 April 2011, *Yu 673–679* (TAI)*, 681* (TAI), *Chao 1783* (TCF), 2300 m, 30 April 2011, *Yu 713* (TAI); Chuilushan, 1650 m, 30 March 2007, *He 118* (TAIF); near the summit of Chingshuishan, 2350 m, 5 April 2008, *Yu 56 & 57* (TAI); near the entrance of Chingshuishan, 2300 m, 12 August 2009, *Yu 103* (TAI); Hoping Logging Trail, 1600 m, 24 May 1993, *Huang 5131* (TAIF); Near Jhugushan, 2200 m, January 2011, *Yu 695–697* (TAI); Pilu, 2300 m, 9 August 2000, *Chen 10817* (TAIF); Sanchiaochuishan, 1800 m, 14 January 1990, *Lu 24956* (TAIF); Sheauchingshoei, 900 m, 17 May 1986, *Lu 19302* (HAST); on the way to Tashan, 2450 m, 19 April 2005, *Yang 996* (TNM); Tatuanuaishan (The Great Cliff), 1700 m, 16 March 2008, *Yu 21–22* (TAI) *& 27–28* (TAI), 1600 m, 14 August 2008, *Yu 147, 148* (TAI); 1800 m, 18 November 2009, *Yu 496–502* (TAI) ; Yangtoushan, 2600 m, 21 March 2009, *Yu 613* (TAI); Yanhai Logging Trail, 1450 m, 14 August 2002, *Huang 1180* (HAST).

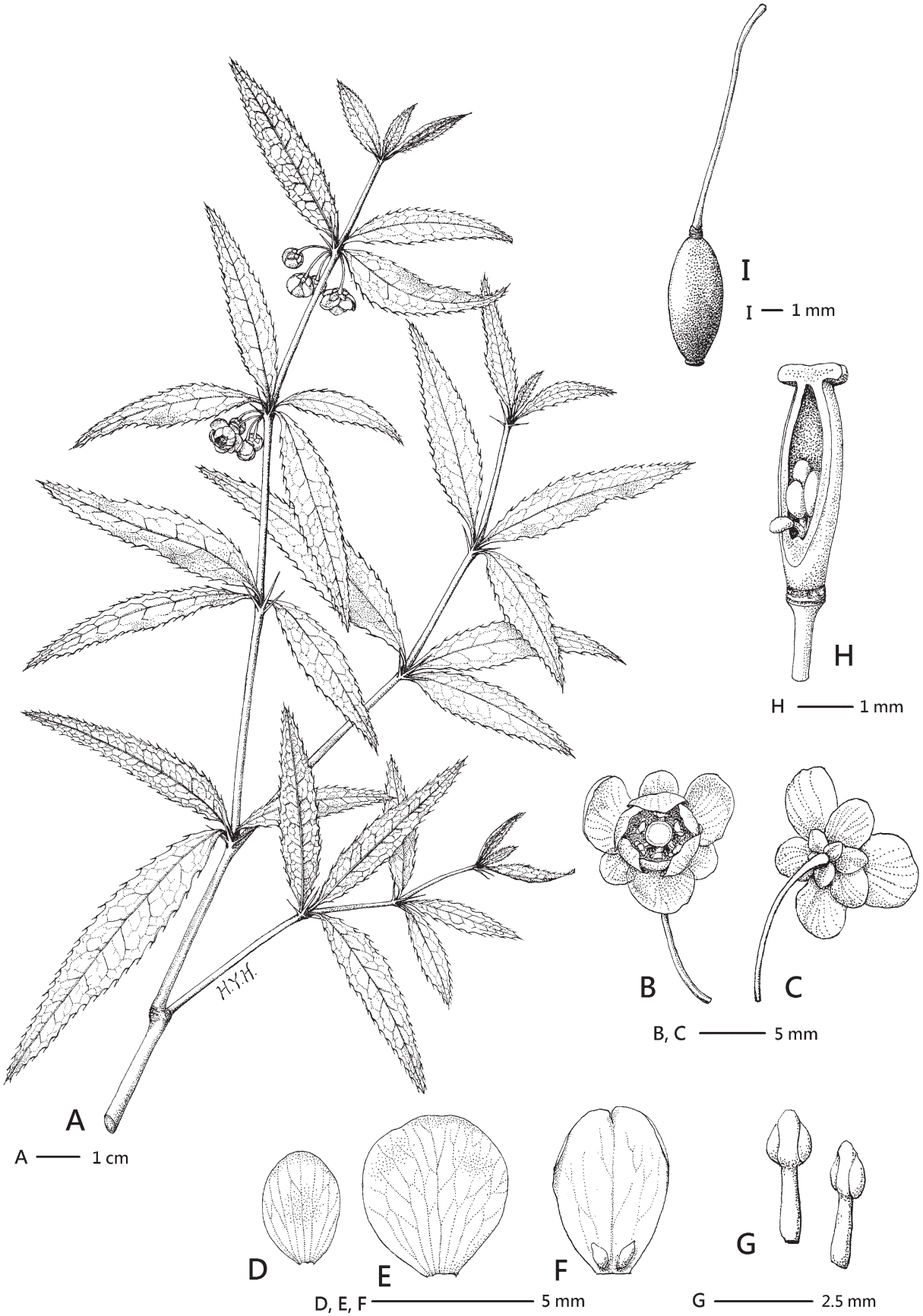

FIGURE 14. *Berberis ravenii* C.C. Yu & K.F. Chung. **A.** Flowering branches. **B.** Flower, front view. **C.** Flower, exterior view, showing the sepals. **D.** Secondary-whorled sepal. **E.** Inner sepal. **F.** Petal with a pair of ovoid nectaries at base. **G.** Stamens. **H.** Dissected pistil showing 4 ovules. **I.** Fruit. Drawn by Han-Yau Huang.

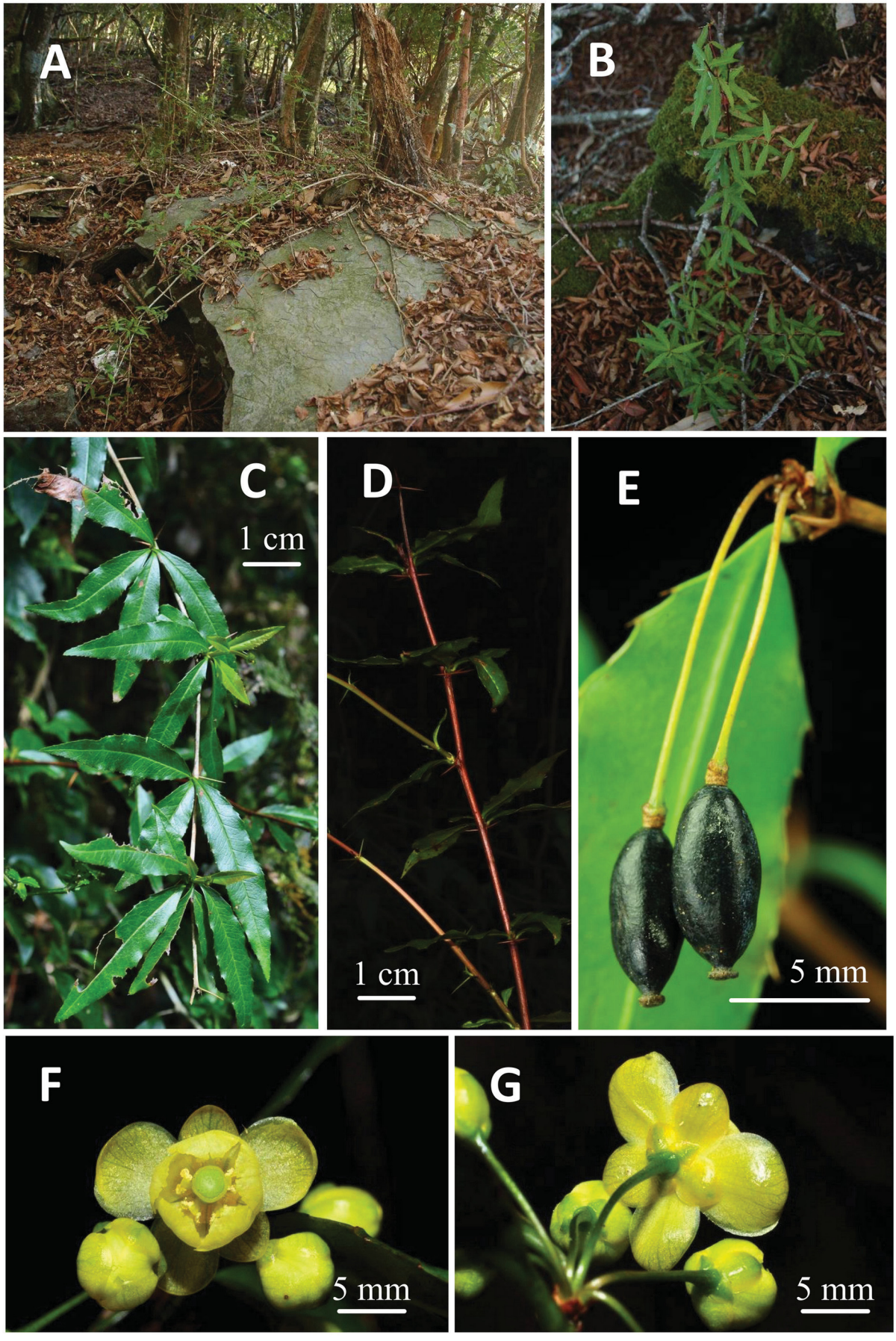

FIGURE 15. *Berberis ravenii* C.C. Yu & K.F. Chung. **A.** Habitat and habit. **B.** Habit. **C.** Leafing branch. **D.** Color of shoot on a new branch. **E.** Fruits. **F.** Flower, front view. **G.** Flowers, exterior view. A, B: Wantoulanshan; C–G: Linpalapalashan; E: courtesy of Chi-Kai Yang.

11. ***Berberis tarokoensis*** Lu & Yang (1996: 581). Type:—TAIWAN. Hualien, Yenhai Logging Trail, *Lu 23713* (holotype TAIF-76154!) (Fig. 12D–F).

Evergreen shrub ca. 0.5 m tall. *Mature stems* reddish-brown, subterete, not verruculose. *Spines* 3-fid, concolorous, 0.3–1.4 cm. *Leaves* subsessile; leaf blade elliptic, abaxially pale green not pruinose, adaxially dark green; 2.7–4.6 cm × 0.8–1.2 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins indistinct, the secondary veins usually obscure but if present, pinnate not jointly looped; base cuniform, margins sometimes slightly revolute, entire or remotely spinose with spinules of 1–8 with 4–10 mm apart on each side, apex acute to acuminate. *Inflorescence* a fascicle, 2–7-flowered. *Bracts* absent. *Pedicel* red to reddish purple, 1.2–1.4 cm. *Bracteoles* 1–3 if present, yellow or sometimes reddish tinge triangularly-ovate 1.5 × 1.5 mm. *Flowers* bright yellow. *Sepals* in 3 whorls, outer sepals yellow usually with reddish-tinged elliptic or ovate 3 × 2.5 mm, middle sepals yellow elliptic 4.5 × 3 mm, inner sepals yellow obovate 5 × 4.5 mm. *Petals* obovate, 4 × 3 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised or acutely emarginated. *Stamens* pale yellow ca. 4 mm, anther connective of stamen distinct, apex slightly apiculate. *Pistil* 5 mm long. *Ovules* from 6 or 8. *Berries* dark purple, ellipsoid ca. 7 × 5.5 mm, more or less pruinose, stylose ca. 1–1.3 mm.

Distinguishing features: *Berberis tarokoensis* is characterized by its obscure leaf venation; though this particular characteristic can also be found in *B. nantoensis* and in the highly variable *B. brevisepala*. Nevertheless, *B. tarokoensis* can also be distinguished by its unusually large number of ovules and its dark purple fruits with a pronounced style (Fig. 12F).

Phenology:—*Flowering* February–April; *Fruiting* April–June, August.

Distribution & habitat:—*Berberis tarokoensis* is a low growing shrub rarely more than 50 cm tall and is sparsely distributed in the Syue and Central Mountain Ranges, with most populations being found on bare limestone terrains exposed to constant rainfall on the side of the Taroko Gorge (Fig. 6E), from 1200 to 2200 m, with one exceptionally low collection from 500 to 800 m (*Lu 22029*) and a disjunct population from northern Taiwan (*Yang 2843*).

Chinese name: 太魯閣小檗

Proposed IUCN conservation status:—Endangered [EN B1ab(iv)]. Most individuals of *Berberis tarokoensis* are found in eastern limestone area of Taiwan, restricted to a few peaks in Taroko Gorge where it occurs as scattered individuals. The narrow distribution and dependence on limestone means that a provisional IUCN category of EN is appropriate, despite the area being protected by the national park (IUCN 2012).

Additional specimens examined:—TAIWAN. Hsinchu: Chenghsipao, 2200 m, 20 April 2003, *Yang 2843* (TNM). Nantou: Shalihsien Stream, 2500–2600 m, 13 August 2011, *Lu 22642* (TAIF). Chiayi: Nansi Forest Logging Trail, 2000 m, 14 March 1986, *Kuoh 13022* (TNM). Hualien: Yenhai Forest Road, 1100 m, April 1991, *Yang 5469* (TNM); the terminus of cable way of the Yenhai Forest Road, 1200 m, March 2009, *Huang 3717* (HAST); Chuilushan, 1800 m, 15 March 2010, *Yu 489* (TAI); Chuilu Historical Trail, 500–800 m, 22 May 2011, *Lu 22029* (HAST).

12. ***Berberis barandana*** Vidal (1886: 45).Type:—PHILIPPINES. Luzon, Mt. Province, Distr. Lepanto, Iloeas N. Luzon, November 1884, *Vidal 1911* (K-000644928!, lectotype (designated by Ahrendt 1961), isolectotypes A-00038831!, MA-728006, *n.v.*, image seen) (Fig. 11D–H).

Evergreen shrub ca. 1.5–2.5 m tall. *Mature stems* brown, subterete, not verruculose. *Spines* 3-fid, concolorous, 0.8–1.7 cm. *Leaves* subsessile; leaf blade elliptic, abaxially pale green not pruinose, adaxially dark-green; 3.8–7.6 × 0.9–2.4 cm, leathery; midvein abaxially raised and adaxially impressed, lateral veins slightly raised, the secondary veins pinnate, jointly looped; base cuneate to cuniform, margins remotely spinose with spinules of 4–12 with 2–6 mm apart on each side, apex acuminate. *Inflorescence* a fascicle, 1–12-flowered. *Bracts* 2 if present, narrowly-ovate, yellow partially red 1.5 × 1 mm. *Pedicel* pale green, 1.2–3 cm. *Bracteoles* absent, 2 or 3, red or yellow with reddish tinge narrowly-ovate 1.5 × 1 mm. *Flowers* bright yellow. *Sepals* in 4 whorls, the outermost sepals yellow with reddish tinge narrowly-ovate to elliptic 2.5 × 1.5 mm, outer sepals yellow usually with reddish tinge ovate to elliptic 3.5 × 2.5 mm, middle sepals yellow obovate 4.5 × 3 mm, inner sepals yellow obovate 5 × 4.5 mm. *Petals* obovate to elliptic, 4.5 × 3.5 mm, base clawed with a pair of ovoid nectaries close to each other, apex incised or acutely emarginated. *Stamens* pale yellow ca. 4 mm, anther connective stamen of distinct produced, apex truncate. *Pistil* 5 mm long. *Ovules* 4. *Berries* black, ellipsoid ca. 7 × 4.5 mm, more or less pruinose, stylose ca. 0.5–1 mm.

Phenology:—*Flowering* January and March; *Fruiting* April–May, October–January.

Distribution & habitat:—*Berberis barandana* is large shrub up to 1.5 m tall distributed in the mountainous areas of the Mountain and Benquet Provinces of Luzon in the Philippines, occurring on margins of cloud forest, sunny slopes and along roadsides, from 1800 to 2900 m.

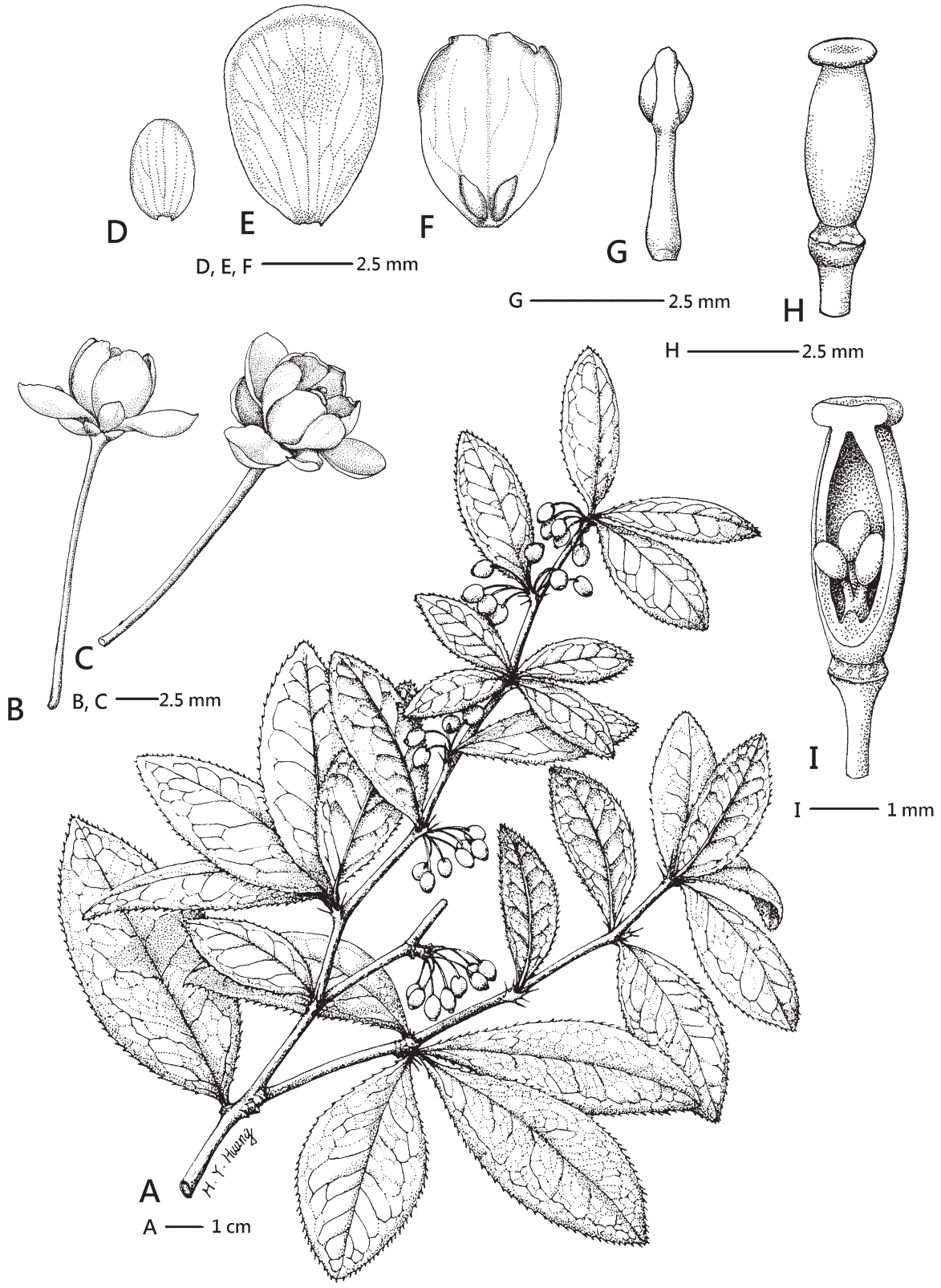

FIGURE 16. *Berberis schaaliae* C.C. Yu & K.F. Chung. **A.** Fruiting branch. **B, C.** Flower. **D.** The secondary-whorled sepal. **E.** Inner sepals. **F.** Petal with a pair of ovoid nectaries at base. **G.** Stamen. **H.** Pistil. **I.** Dissected pistil showing 3 ovules. Drawn by Han-Yau Huang.

Proposed IUCN conservation status:—Vulnerable [VU B1ac (ii, iii)]. *Berberis barandana* is almost always found associated with cloud forest, a highly threatened ecosystem in the Philippines due to rapid deforestation. We hereby propose a provisional IUCN category of VU for the species (IUCN 2012).

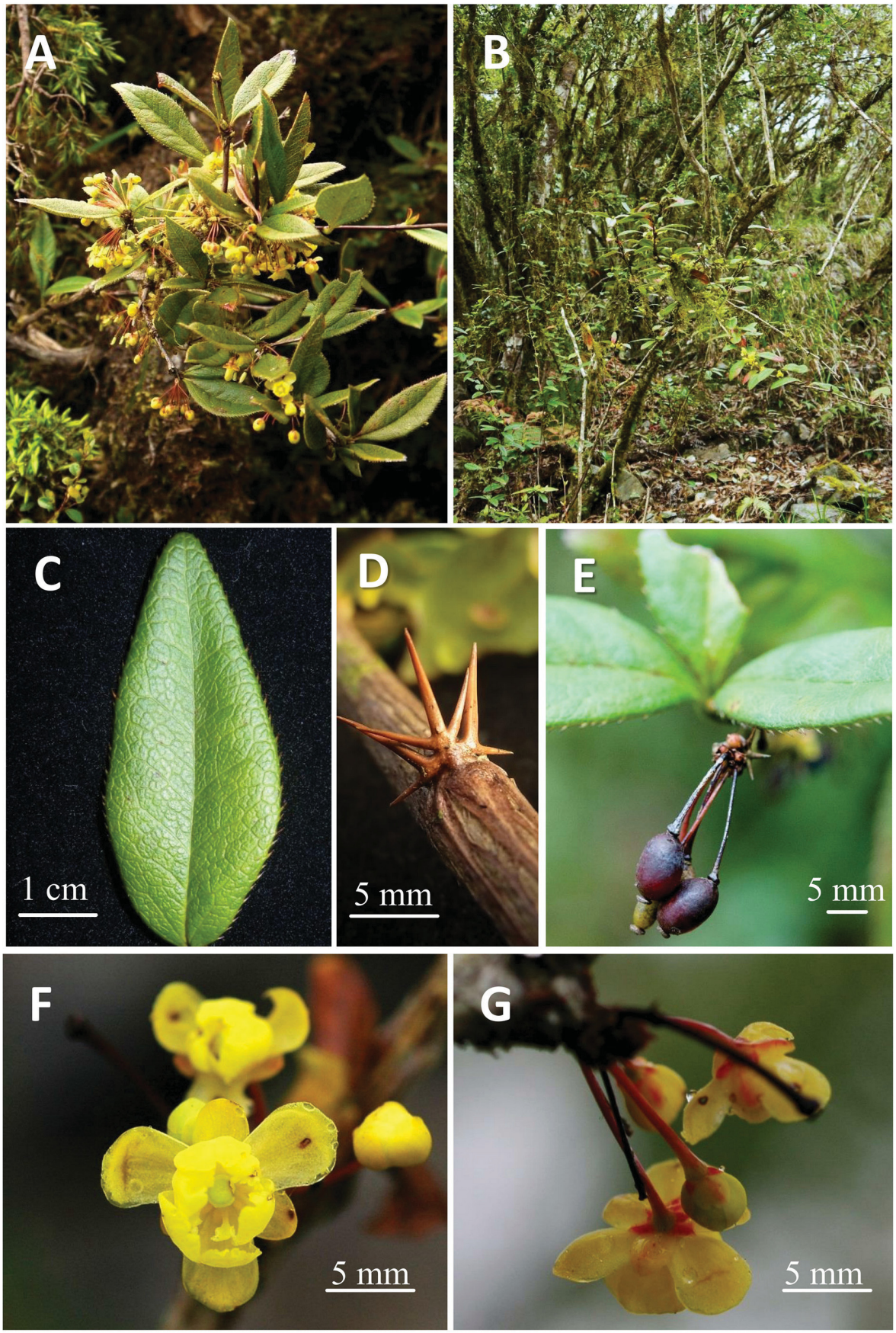

FIGURE 17. *Berberis schaaliae* C.C. Yu & K.F. Chung. **A.** Flowering branch. **B.** Habitat and habit. **C.** Leaf, adaxial view showing the complex vein. **D.** Palm-like spine. **E.** Fruits. **F.** Flower, front view. **G.** Flowers, exterior view, showing the sepals. A–G: Tatuanyaishan (The Great Cliff).

Notes: The original set of Vidal's specimens in Manila, including the holotype of *Berberis barandana* (*Vidal 1911*), was destroyed in a fire in 1897 (Stafleu & Cowan 1986, Calabrese & Velayos 2009). In revising the genus, Ahrendt (1961: 65) designated an isotype at K as the lectotype ("*Type K*"), rendering the isotypes at MA (Calabrese & Velayos 2009) and A as isolectotypes. This Filipino endemic species had been allied with *B. kawakamii* (Merrill 1923); however, *B. barandana* can be easily distinguished from the latter by its ovate outermost sepals. LaFrankie (2010) also documents an unauthenticated report of *B. wallichiana* DC. (as *B.* '*wallichii*') in the Philippines as well as a possible new species from Zambales Mountains, Luzon, neither with any specimen details. However, *B. wallichiana* is endemic to Nepal (Adhikari *et al.* 2010).

Additional specimens examined:—PHILIPPINESS. Luzon Island: Benguet Province, Mt. Sto Tomas, 12 October 1904, *Williams 1347* (US), 2440 m, 3 December 1953, *van Steenis s.n.* (PNH), *Walker 7536* (US), 2200 m, 13 May 2006, *Yang 17998* (TNM), Barangay Lab-ang Resthouse Relay Station, 2200 m, 31 January 2012, *Chung 1958* (HAST). Mountain Province, Distr. Lepanto, Mt. Data, November 1905, *Merrill 4506* (US)*, 4607* (US), 1800 m, 2 April 1946, *Alcasid 7* (PNH), Mt. Data Watershed, 1800 m, 1 February 2012, *Chung 1984* (TAI). Bontoc Province, 26 October 1974, *Apolinarno 251* (UPLB). Mt. Nangaoto, 2300 m, 23 February 1948, *Sulit 2529* (PNH). Mt. Pauai, 5 February 1948, *Sulit 2351* (PNH), 2250 m, 28 April 1960, *Sulit 10733* (UPLB)*, 10734* (UPLB). Mt. Pulog, January 1909, *Curran et al. 80140-2* (US), 2900 m, 11 March 1948, *M. Celesto s.n.* (PNH), 2650 m, 12 June 1965, *Poicho 19829* (UPLB)*, 19808* (UPLB).

Acknowledgements

We thank Julian Harber for his generous assistance, suggestions, and critical review of the early draft and the manuscript, Han-Yau Huang for handsome line drawings of the three new species, and Cheng-Dao Lin, Chih-Kai Yang, and Bo-Chang Chen for permissions for the photographs. We are grateful to the comments and suggestions by the Section Editor Li-Bing Zhang. The following herbaria are greatly appreciated for granting access to the collections: A, BM, E, HAST, K, KYO, NTUF, PE, PH, PNH, TAI, TAIF, TCF, TI, TNM, TNS, and UPLB. We greatly thank members of the Mountaineering Club of National Taiwan University and the Mountaineering Association of National Cheng Kung University for field assistance and collecting materials throughout the high mountains in Taiwan, and Rosario Rubite (PNH) and Teodora Balangcod (NLUH) for assistance of fieldwork in Luzon. This study was supported by National Science Council grants of Taiwan (NSC 97-2321-B-002-035-MY2 and NSC 99-2621-B-001-001-MY3) to Kuo-Fang Chung and the student travel grants of Taiwan Society of Plant Systematics to Chih-Chieh Yu and Han-Yau Huang.

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APPENDIX 1. List of continuous and meristic quantitative characters recorded in the study. Asterisk indicates those used for morphometric analyses.

Abbreviation	Character (Abbreviation)
Qualitative	
1. VC	Vein category (VC): simple vs. complex
2. USL	The upper surface of leaves (USL): shinning vs. dull
3. FWS	First-whorled sepal (FWS): round (obovate or ovate) vs. sharp-triangle
4. FS	Fruit style (FS): stylose (present) vs. stylose (absent or indistinct)
5. FSH	Fruit shape (FSH): ellipsoid vs. globose
Quantitative	
6. LBL	Leaf blade length
7. WM	Width at middle part of leaf blade
8. MW	Maximum width of leaf blade
9. DBMWB	Distance between maximum width of leaf blade and leaf base
10. DBBSLB	Distance between the basal-most serrate to leaf base
11. DBTSLA	Distance between the tip-most serrate to leaf apex
12. LS	Length of spinules
13. NS	Numbers of spinules
14. SpL	Spine length
15. PL*	Pedicel length
16. ADBS	Average distance between spinules
17. NSP*	Numbers of spinules per cm (NSP*= NS/LBL)
18. NSMWLB	Numbers of spinules along the leaf between the maximum width and leaf base
19. %ADBS*	Ratio of the average distance between spinules and leaf blade length: (%ADBS*= ADBS/LBL)
20. NSMWLBP*	Numbers of spinules along the leaf between the maximum width and leaf base per cm: (NSMWLBP*= NSMWLB/DBMWB)
21. %DBMWB*	Ratio of the distance between maximum width of leaf blade and leaf base To leaf blade length: (%DBMWB*= DBMWB/LBL)
22. %DBBSLB*	Ratio of the distance between the basal-most spinules and leaf base To leaf blade: (%DBBSLB*= DBBSLB/LBL)
23. %DBTSLB*	Ratio of the distance between the tip-most spinules and leaf apex To leaf blade length: (%DBTSLB*= DBTSLB/LBL)
24. %LBMW*	Ratio of length of leaf blade To maximum width of leaf blade: (%LBMW*LBL/MW)