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Begonia balangcodiae sp. nov. from northern Luzon, the Philippines and its natural hybrid with *B. crispipila*, *B.* × *kapangan nothosp. nov.*

SHIH-HUI LIU[1], YU-HSIN TSENG[1], DIAITI ZURE[1,2,3], ROSARIO RIVERA RUBITE[4], TEODORA D. BALANGCOD[5], CHING-I PENG[1,†] & KUO-FANG CHUNG[1,*]

[1]*Research Museum and Herbarium (HAST), Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan.*
[2] *Biodiversity Program, Taiwan International Graduate Program, Academia Sinica and National Taiwan Normal University, Taipei 11529, Taiwan.*
[3]*Department of Life Science, National Taiwan Normal University, Taipei 11677, Taiwan.*
[4]*Department of Biology, College of Arts and Sciences, University of the Philippines Manila, Padre Faura, Manila, Philippines.*
[5]*Department of Biology, University of the Philippines Baguio, Baguio City, Benguet, Philippines.*
[†]*Deceased*
**Author for correspondence; e-mail: bochung@gate.sinica.edu.tw*

Abstract

The pantropically distributed *Begonia* (Begoniaceae) is one of the most species-rich genera. Philippines is one of the diversity centers of Southeast Asian *Begonia*. In our 2012 field survey, three species of *Begonia* section *Petermannia* were collected in Barangay Sagubo, Municipality of Kapangan, Province of Benguet in the northern Luzon Island, Philippines. Our study on literatures and herbarium specimens suggests that these collections consist of *B. crispipila*, an unknown new species hereby we named *B. balangcodiae*, and the natural hybrid between them. Molecular analyses confirm that the former contributed the maternal genome while the latter provided the paternal genome. We name the natural hybrid *B.* × *kapangan*, which is the first natural hybrid reported in sect. *Petermannia*.

Key Words: Begoniaceae, *Begonia* sect. *Petermannia*, ITS, *trn*L-*trn*F

Introduction

Begonia Linnaeus (1753: 1056) is one of the most diverse genera in angiosperm and currently comprises more than 1,800 species (Frodin 2004, Hughes *et al.* 2015, Christenhusz & Byng 2016). It is worldwide distributed in tropical, subtropical areas with two diversity hotspots, South America and South East Asia (Tebbitt 2005, Kiew 2006, Dewitte *et al.* 2011). Within the genus *Begonia*, the Asian section *Petermannia* (Klotzsch 1854: 124) de Candolle (1859: 128) contains over 400 species and is known as one of the largest sections in the genus (Doorenbos *et al.* 1998, Hughes & Coyle 2009). The monophyly of this sect. remains unclear. While Thomas *et al.* (2011)'s molecular phylogenetic analyses based on three chloroplast regions suggested that sect. *Petermannia* is paraphyletic, this section appears as a monophyletic group in Chung *et al.* (2014) based on chloroplast *rpl16* and nuclear ITS regions.

Philippines is one of the *Begonia* diversity centers in Southeast Asia (Hughes *et al*. 2015, 2018). Up to date, ca. 120 *Begonia* species have been reported in the Philippines (Hoover *et al.* 2004, Hughes *et al.* 2018, Nakamura *et al.* 2013, Rubite 2013, Rubite *et al.* 2014, 2015, 2018, Peng *et al.* 2017a, 2017b, Tandang *et al.* 2016). More than half of Philippian *Begonia* species (53%; 64 out of 121 species) are classified in sect. *Petermannia* (Rubite 2013, Peng *et al.* 2017a).

Natural hybridization has driven the evolution and diversity of many plant taxa (Arnold 1997, Soltis & Soltis 2009). Earlier experimental studies on both wild species and horticultural varieties have indicated that *Begonia* plants have weak reproductive barriers and low genetic incompatibility (Tebbitt 2005, Dewitte *et al.* 2011). An increasing number of natural hybrids in *Begonia* has also been reported, *e.g.*, *B. buimontana* Yamamoto (1933: 353), a natural hybrid (Peng & Chen 1991) between *B. palmata* Don (1825: 223) of the sect. *Platycentrum* (Klotzsch 1855: 243) de Candolle (1859: 134) and *B. taiwaniana* Hayata (1911: 125) of the sect. *Diploclinium* (Lindley 1846: 319) de Candolle (1859: 129), and *B.* × *breviscapa* C.I Peng, Yan Liu & S.M.Ku (Peng *et al.* 2010: 108), a hybrid between *B. variifolia*

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Shui & Chen (2005: 372) of the sect. *Coelocentrum* Irmscher (1935: 553) and *B. leprosa* Hance (1883: 202) of the sect. *Leprosae* (Ku 1999: 401) Y.M.Shui (Shui *et al.* 2002: 321). In a recent molecular phylogenetic study, Hughes *et al.* (2015) also shows that natural hybridization has been common among the Philippine species of sect. *Baryandra* de Candolle (1859:122).

During our 2012 field surveys Barangay Sagubo, Municipality of Kapangan, Province of Benguet in the northern Luzon Island, Philippines, an unknown *Begonia* species allying to taxa in sect. *Petermannia* was discovered. A putative natural hybrid between the unknown species and a sympatric species *B. crispipila* Elmer (1910: 737) in sect. *Petermannia* was also recorded. To identify these unknown species, we investigated their morphology, the literatures and herbarium vouchers of the potentially allied *Begonia* species. Moreover, using molecular phylogenetic analyses, we intended to confirm the sectional assignment of these three *Begonia* taxa and to unveil the origin of the putative natural hybrid. Based on these information, a new Philippine *Begonia* species in sect. *Petermannia* and the first natural hybrid assigned to sect. *Petermannia* are described.

Material and methods

Plant materials

Plant vouchers of *B. crispipila*, unknown *Begonia*, and their putative hybrid for morphological study and molecular work were collected during the field surveys in Luzon Island of Philippines (N 16°36'43", E 120°33'48"). Studied plants were also cultivated in the experimental greenhouse at the Academia Sinica, Taipei, Taiwan for the morphological investigation. The artificially self-pollination experiments were conducted to understand the reproductive abilities of the studied plants. The foliar samples of each voucher were also dried and stored in silica gel before the genomic DNA extraction. The vouchers were deposited at herbaria (HAST and PNH) for further studies. The detail collection information of the studied plants is provided in Appendix 1.

Morphological investigation

Type collections from B, BM, BO, E, FI, HAST, K, L, MO, NY, P, PNH, US, and UVM herbaria and relevant taxonomic literatures of potentially allied *Begonia* species in sect. *Petermannia* from Luzon Island were examined (Appendix 2). Morphological traits of the studied plants were observed visually in the field as well as in the greenhouse.

Genomic DNA extraction, amplification, cloning, and sequencing

To verify that *B. crispipila*, unknown *Begonia*, and the putative hybrid are members in the sect. *Petermannia* as well as to understand the origin of the putative hybrid, total genomic DNA of the studied samples was extracted using the DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany). The nuclear ribosomal internal transcribed spacer (ITS) and chloroplast *trnL-trnF* intergenic spacer—which have been successfully used in earlier molecular phylogenetic studies on *Begonia* and many other plant groups (Forrest *et al.* 2005, Chung *et al*. 2014, Leong *et al.* 2015, Gong *et al*. 2017, Leng 2017, Liu *et al.* 2017, Nakamura *et al.* 2015)—were amplified. The PCR amplifications were conducted using primers developed by earlier studies (Eckenrode *et al.* 1985, Taberlet *et al.* 1991, Clement *et al.* 2004, Leong, 2017) with the mixture of 2 μL genomic DNA, 1 μL 10 mM forward primer, 1 μL 10 mM reverse primer, 12.5 μL 2X Taq DNA Polymerase Mastermix-RED (Bioman, Taipei, Taiwan), and 8.5 μL deionized water. The primer sequences and optimal thermal cycling conditions are shown in Tables 1 and 2, respectively. The PCR products were then purified with the PCR Advanced™ Clean Up (Viogene BioTek Corp., New Taipei City, Taiwan) and commercially sequenced in an ABI 3730 XL DNA Analyzers with the Genomics BioSci & Tech, Taiwan. The newly generated sequences were deposited in Genbank, and the accession numbers are provided in Appendix 1.

It is known that the ambiguous sites detected in a direct sequencing of the multi-copy ITS region infer some critical phylogenetic information, and a cloning has been suggested to clarify the phylogenetic information (Baldwin *et al.* 1995, Soltis & Soltis 1998, Alvarez & Wendel 2003). While no polymorphism was found in the direct-sequencing ITS regions of *B. crispipila* and unknown *Begonia*, the ITS sequence of the putative hybrid has multiple ambiguous sites. A cloning was applied using the pGEM®-T Vector Systems (Promega, Madison, Wisconsin, USA) and ECOS™ 101 Competent Cells [DH5a] (Yeastern Biotech, Taipei, Taiwan) for the putative hybrid. The T7 and SP6 primers and a PCR reaction with the optimal thermal cycling conditions for the ITS region (Table 2) were used to screen the positive colonies. In total, seven positive clones were selected to sequencing.

TABLE 1. Primers used in this study and their origins.

DNA regions	Primers	Primer Sequences (5' -->3')	References
ITS	5P	GGAAGGAGAAGTCGTAACAAGG	(Eckenrode *et al.* 1985)
	26S1Rev	CGCCTGACCTGGGGTCG	(Clement *et al.* 2004)
trnL-trnF	*trnL*(c)	CGAAATCGGTAGACGCTACG	(Taberlet *et al.* 1991)
	trnF(f)	ATTTGAACTGGTGACACGAG	(Taberlet *et al.* 1991)
	trnL-s	AAATCGTGAGGGTTCAAGTC	(Leong 2017)

TABLE 2. The optimal thermal cycling conditions of studied regions for *Begonia*.

	PCR thermal cycling conditions						
DNA regions	Initial denaturation	Denaturation	Annealing temperature	Elongation temperature	Final extension	Number of cycles	References
Nuclear region							
ITS	94°C, 5 min	94°C, 30 sec	60°C, 30 sec	72°C, 1 min	72°C, 5 min	30	(Chung *et al.*, 2014)
Chloroplast region							
trnL-trnF	94°C, 5 min	94°C, 30 sec	53–60°C, 30 sec	72°C, 60–90 sec	72°C, 5 min	30	(Leong, 2017)

Moreover, additional twenty-five *Begonia* species from sect. *Petermannia*, one species (*B. symsanguinea* L.L. Forrest & P.M. Hollingsworth) from sect. *Symbegonia* (Warb.) L.L. Forrest & P.M. Hollingsworth, and five species from other closely related sections (two species from sect. *Coelocentrum*, one from sect. *Platycentrum*, one from sect. *Diploclinium*, and one from sect. *Sphenanthera*) were selected for the phylogenetic analyses. The additional species sampled are listed in Appendix 1. Note that earlier molecular phylogenetic studies have supported that *B. symsanguinea* is nested in members of sect. *Petermannia* (Thomas *et al.* 2011, Chung *et al.* 2014, Leong 2017). The DNA sequences of these additional species were obtained from earlier phylogenetic work on *Begonia* (Chung *et al.* 2014, Leong, 2017) and NCBI GenBank. The GenBank accession numbers of the additional *Begonia* species are also provided (Appendix 1).

Phylogenetic analyses

Sequences were aligned using MAFFT 7 (Katoh 2002, Katoh & Standley 2013) on the CIPRES Science Gateway (Miller *et al.* 2010). Additional adjustments for the alignments were applied in Mesquite 3.11 (Maddison & Maddison 2016) if needed.

Phylogenetic trees were reconstructed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) algorithms for each region. For the MP analyses, 1,000 searches were performed using PAUPRat (Sikes & Lewis 2001). A strict consensus tree was then generated from the 1,000 most parsimonious trees. The consistency index (CI) and retention index (RI) were calculated using Mesquite 3.11 (Maddison & Maddison 2016), and the rescaled consistency (RC) and homoplasy index (HI) were also estimated to understand the degree of homoplasy of each region. The best-fit nucleotide substitution models for each region were estimated with jModeltest 2.1.8 (Darriba *et al.* 2012) using the Akaike information criterion (AIC) and then applied for the ML and BI trees reconstructions. Ten runs in RAxML 8.2.10 (Stamatakis 2014) with 1,000 rapid bootstrap procedure (bs) were conducted to generate the ML trees on the CIPRES Science Gateway (Miller *et al.*, 2010). Two independent Markov chain Monte Carlo (MCMC) runs in MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist *et al.* 2012) with 5×10^6 generations in each run were also performed to generate the BI trees on the CIPRES Science Gateway (Miller *et al*. 2010). One BI tree was sampled every 1,000th generation. The initial 25% of the BI trees were ignored as burn-in, while the remaining trees were selected to produce a 50% majority rule consensus BI tree and to calculate the posterior probabilities (pp) on each branch of the consensus BI trees. All trees were visualized using FigTree 1.4.3 (Rambaut 2014).

Results and Discussion

Morphological investigation

Based on the relevant literatures, type collections, and living studied plants in the field and in the greenhouse, we affirm that the unknown *Begonia* is a new species, which is described here as *B. balangcodiae* Rubite, S.H.Liu & K.F.Chung. Mature fruit sets of *B. balangcodiae* were successfully obtained in the artificially self-pollination experiments. Moreover, the morphological comparison shows that the putative natural hybrid is an intermediate between *B. crispipila* (Fig. 1) and *B. balangcodiae* (Fig. 2) in indumentum, leaf color, inflorescence, tepal size, and tepal color (Table 3; Figs. 3–4). The putative natural hybrid shows some abnormal morphology, *e.g.*, ovary lacking in pistillate flower occasionally and pistillate segment number various (3–5). No mature fruit of the putative natural hybrid was observed in our artificially self-pollination experiments. Here, we describe the putative natural hybrid as *B.* × *kapangan* Rubite, S.H.Liu & K.F.Chung.

TABLE 3. Comparison among *Begonia crispipila*, *B.* × *kapangan*, and *B. balangcodiae*.

Species	*Begonia crispipila*	*Begonia* × *kapangan*	*Begonia balangcodiae*
Character			
Stem	Densely pubescent	Pubescent	Glabrous
stem color	Usually green, sometimes reddish	Usually green, sometimes reddish	Usually greenish, sometimes reddish
Petiole length (cm)	1–3 cm	1–4 cm	1–4 cm
Leaf			
Shape	Obovately oblong	Obovately oblong	Lanceolate
Apex	Acute	Acute	Acute
Base	Oblique and cordate	Oblique and cordate	Oblique and cordate
Adaxial color	Green	Green; dark green or reddish on veins; sometimes with sparse, small, white spots between veins	Green; reddish along veins; with sparse, large, white spots between veins
Abaxial color	Green; sometimes reddish on margin and veins	Green; reddish on margin and veins	Reddish
Blade indumentum	Densely pubescent; hairs between veins on abaxial with red basal cells	Pubescent	Glabrous
Stipule	Greenish; turn brown when dry; abaxial densely pubescent, adaxial sparsely pubescent; ovate-triangular, mucronate at apex.	Greenish; turn brown when dry; sparsely pubescent on both sides; ovate-triangular, mucronate at apex.	Greenish; turn brown when dry; glabrous; ovate-triangular, mucronate at apex.
Inflorescence	2–7 flowers; cyme; short, < 3 cm long; bisexual	2–7 flowers; compound cymose; bisexual	2–7 flowers; compound cymose; unisexual
Bract	Lightly green; lower bracts pubescent, upper bracts nearly glabrate; 7–9 mm long × 7–9 mm wide.	Lightly green; glabrous; 8–10 mm long × 8–10 mm wide.	Lightly green; glabrous; 4–6 mm long × 2–4 mm wide.
Staminate flower			
Perianth segment	2	2	2
Tepal shape	Widely ovate	Widely ovate	Ovate
Tepal size (mm) (long × wide)	6–9 × 6–9	6–9 × 8–10	12–18 × 10–12
Tepal indumentum	Abaxial pubescent, hairs with red basal cells; adaxial glabrous	Abaxial sparsely pubescent, hairs with red basal cells; adaxial glabrous	Glabrous
Tepal color	Pinkish	White	White, sometimes greenish at apex
Pistillate flower			
Pistillate segment	4–5	2–3–4–5	5
Style	(2–)3	3	3
Tepal shape	Obovate to oblanceolate	Obovate	Obovate
Tepal size (mm) (long × wide)	10–14 × 5–8	12–14 × 8–10	12–18 × 14–18
Tepal indumentum	Abaxial pubescent, hairs with red basal cells; adaxial glabrous	Abaxial sparsely pubescent, hairs with red basal cells; adaxial glabrous	Glabrous
Tepal color	Pinkish	White	White, sometimes greenish at apex
Ovary			
Shape	Elliptic with (2-)3 equal wings	Elliptic with 3 equal wings	Elliptic with 3 equal wings
Color	Pinkish ovary with reddish wings	Green ovary with red or reddish wings	Green ovary with reddish wings
Indumentum	Densely pubescent, hairs with red basal cells	Nearly glabrous, a few hairs with read basal cells	Glabrous

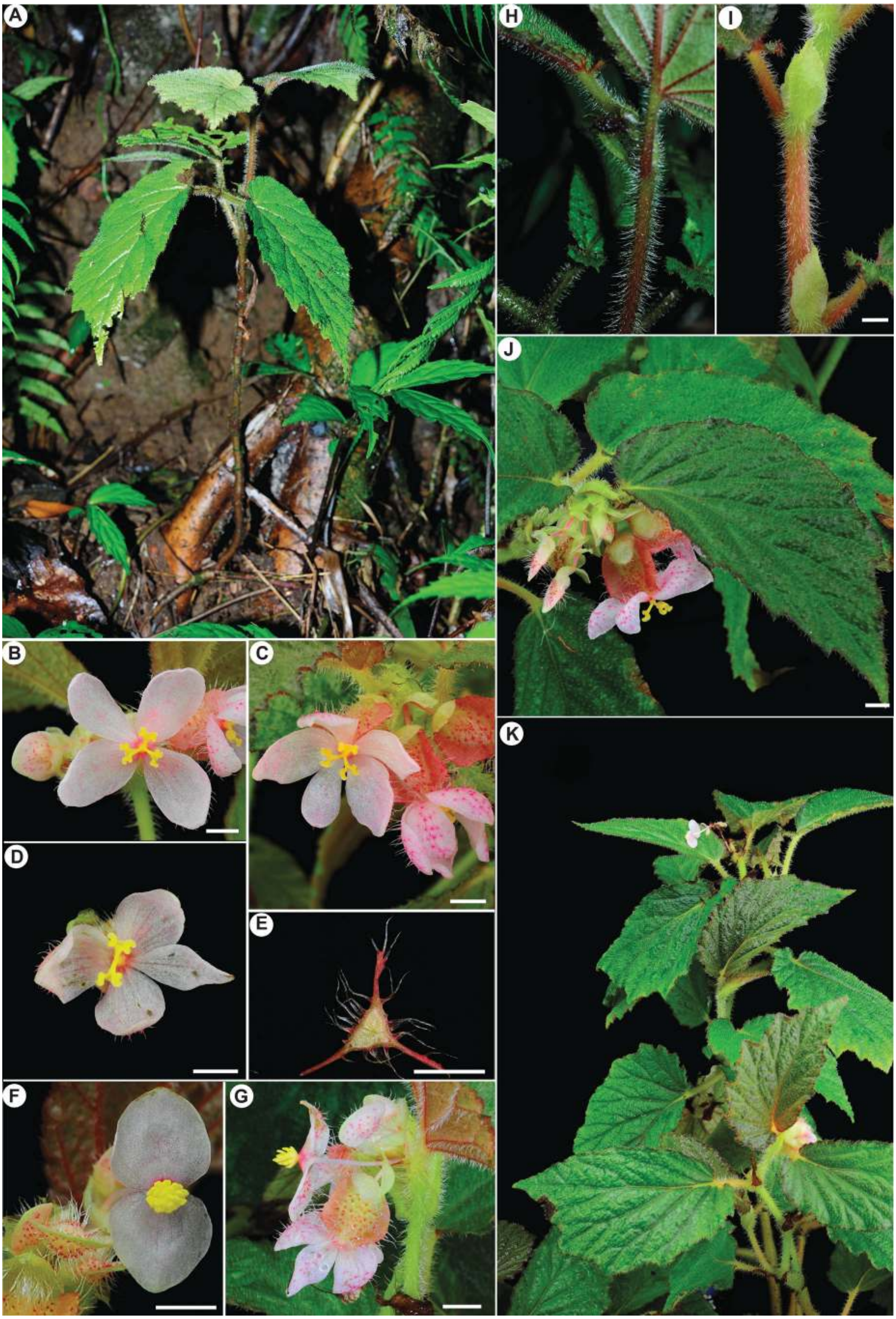

FIGURE 1. *Begonia crispipila* Elmer. A, habitat and habit; B, pistillate flowers; C, inflorescence, bracts, and pistillate flowers; D, abnormal pistillate flower; E, cross section of ovary; F, staminate flower and staminate flower buds; G, inflorescence, bracts, staminate flowers, and pistillate flower; H, stem and petiole; I, stem and stipules; J, leaves and inflorescence; K, habit. Scale bar = 5 mm.

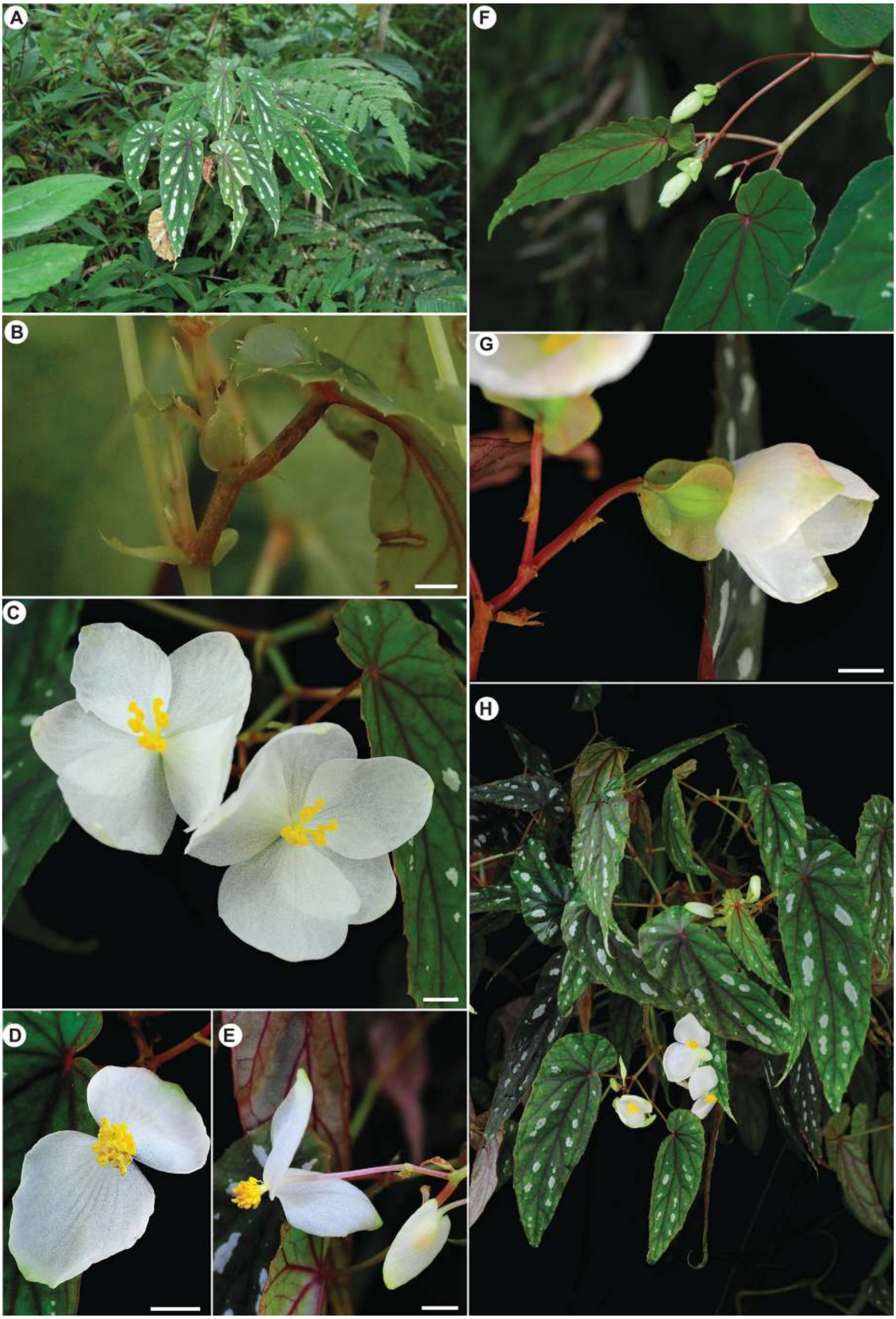

FIGURE 2. *Begonia balangcodiae* Rubite, S.H.Liu & K.F.Chung. A, habitat and habit; B, stem and petiole; C, pistillate flowers; D, staminate flower; E, staminate flower and staminate flower bud; F, inflorescence, and pistillate flower buds; G, ovary and bracts; H, habit. Scale bar = 5 mm.

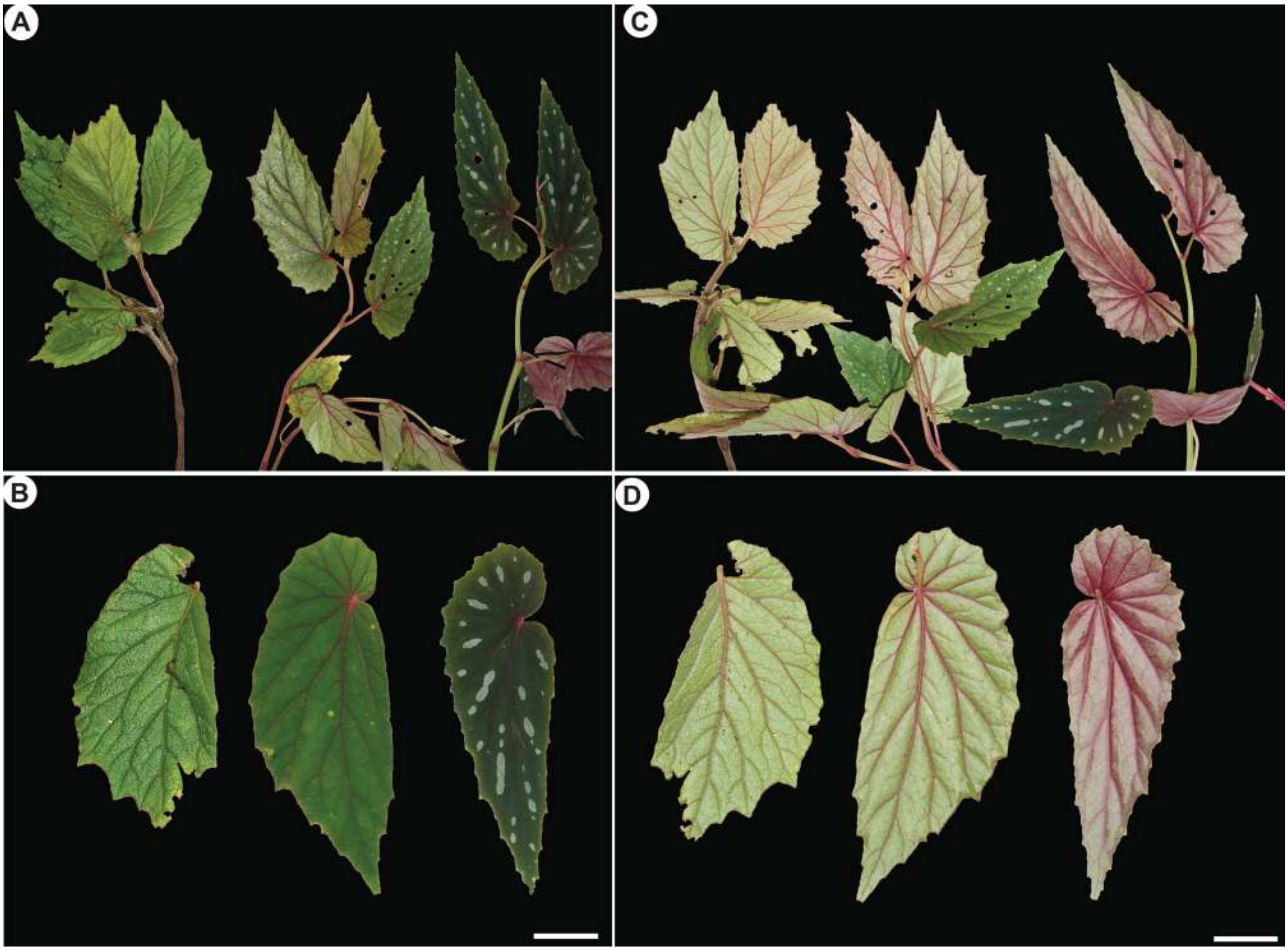

FIGURE 3. Comparisons among *Begonia crispipila* (left), *B.* × *kapangan* (middle), and *B. balangcodiae* (right). A, adaxial surface of the plants B, adaxial surface of the leaves; C, abaxial surface of the plants; D, abaxial surface of the leaves. Scale bar = 10 mm.

Phylogenetic analyses

Our phylogenetic analyses based on the maternal inherited chloroplast *trnL*-trn*F* region suggest that members in sect. *Petermannia* and three studied species are clustered in a clade with a strong support (bs = 100, pp = 1.00). Though the resolutions of the basal branches within sect. *Petermannia* are generally low, our *trnL-trnF* tree strongly supports that *B.* × *kapangan* is sister to *B. crispipila* (Fig. 3) (bs = 98, pp = 0.99). Only the ML trees are showed here (Fig. 3).

Our ITS trees indicate that three studied species are clustered with all additional *Petermannia* species (including *B. symsanguinea*) (bs = 97, pp = 1.00). Although the topological conflict is present between the MP and ML/BI trees, all three trees strongly support that six ITS clones of *B.* × *kapangan* is sister to *B. crispipila* (bs = 99, pp = 1.00) and one ITS clone of *B.* × *kapangan* is grouped with *B. balangcodiae* (bs = 99, pp = 1.00) (Fig. 4). Only the ML trees are showed here (Fig. 4).

All alignments and tree files are available in FigShare (DOI: 10.6084/m9.figshare.5877916). The homoplasy and comparative statistics of MP analyses and the best-fit models are shown in Table 4.

In sum, our phylogenetic analyses confirm that *B. crispipila*, *B. balangcodiae*, and *B.* × *kapangan* are members in sect. *Petermannia*. Moreover, our results suggest that both *B. crispipila* and *B. balangcodiae* have contributed to the origin of the natural hybrid *B.* × *kapangan*. Moreover, *B. crispipila* is likely the maternal donator to *B.* × *kapangan*.

TABLE 4. Characteristics of the alignments used for phylogenetic analyses in this study.

DNA regions	Number of taxa/ ingroups/ outgroups	Length (bp)	Best-fit nucleotide substitution model	Number of parsimony-informative sites (%)	CI/RI/RC/HI*
Nuclear region ITS	34/29/5	713	SYM+G	20.76	0.648/0.701/0.454/0.352
Chloroplast region *trnL-trnF*	16/13/3	835	GTR	1.68	0.936/0.906/0.848/0.094

* CI: Consistency index; RI: Retention index; RC: Rescaled consistency index; HI: Homoplasy index.

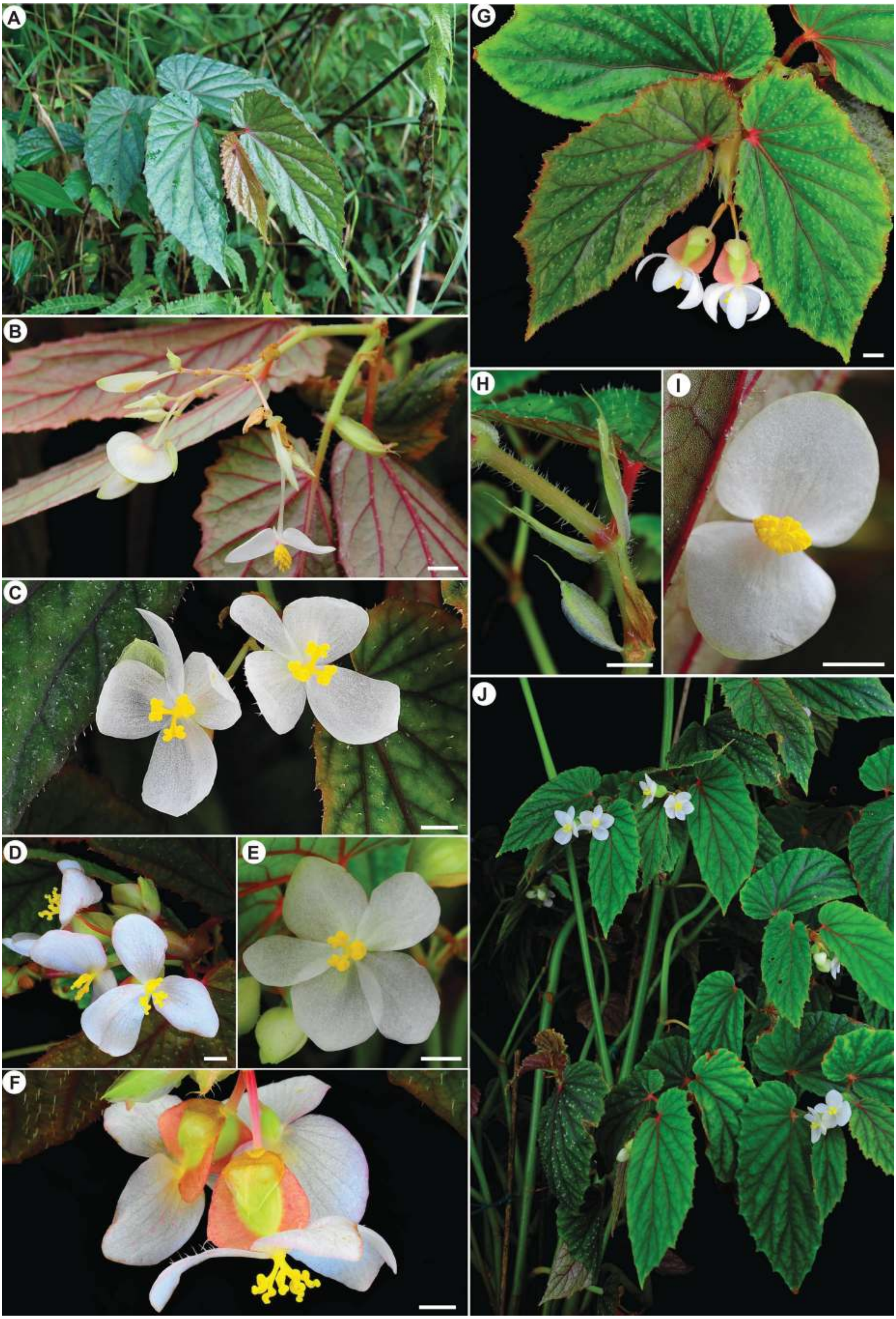

FIGURE 4. *Begonia* × *kapangan* Rubite, S.H.Liu & K.F.Chung. A, habitat and habit; B, inflorescence, bracts, staminate flower buds, and staminate flower; C, D & E, pistillate flowers; F, pistillate flowers, bracts, and ovaries; G, leaves, inflorescence, bracts, and pistillate flowers; H, stem and stipules; I, staminate flower; J, habit. Scale bar = 5 mm.

Taxonomic treatment

1. *Begonia balangcodiae* Rubite, S.H.Liu & K.F.Chung, *sp. nov.*

sect. *Petermannia*

Type:—PHILIPPINES. Luzon, Benguet Province: Municipality of Kapangan, Barangay Sagubo, elveation *ca.* 1,200 m, 16°36'43" N, 120°33'48" E. 2 February 2012. *Kuo-Fang Chung 2012*, with Rosario Rivera Rubite, Severino M. Balangcod, Teodora D. Balangcod, and Han-Yao Huang (holotype PNH; isotype HAST). **Fig. 2–3.**

Monoecious, perennial, glabrous herb. **Stem** erect, to *ca.* 100 cm tall, 1–5 mm in diameter, olive green to crimson, internodes 2–6 cm long, nodes slightly swollen. **Stipules** deciduous, olive green, ovate-triangular, 8–12 × 4–6 mm, slightly keeled, glabrous, margin entire, apex mucronate. **Petioles** terete, 1–4 cm long, *ca.* 0.5 mm in diameter, crimson. **Leaves** lanceolate, asymmetric, base oblique and cordate, apex acute, margin irregularly dentate, 6–12 × 2–5 cm; lamina flat; adaxially dark green, crimson along veins, with sparse, large, white spots between veins; abaxially crimson; venation palmate, primary veins 7 or 8. **Bracts** deciduous, olive green turning brown, narrowly triangular to ovate, 4–6 × 2–4 mm, margin entire. **Inflorescence** axillary, dichasium or cyme, unisexual, peduncle olive green to crimson. **Staminate flower**: pedicel 12–18 mm long; tepals 2, white, sometimes greenish at apex, ovate, 12–18 × 10–12 mm, margin entire, apex rounded; androecium actinomorphic or zygomorphic; stamens 26–38, golden yellow; filaments 2–3 mm, slightly fused at base; anthers obovate, *ca.* 1.5 mm long, apex retuse. **Pistillate flower**: pedicel 12–18 mm long; tepals 5, white, sometimes greenish at apex, obovate, 12–18 × 14–18 mm, margin entire, apex rounded; ovary olive, trigonous-elliptic, 8–10 × 6–8 mm (wings excluded), 3-locular, placentation axile; 3-winged, wings reddish, equal; styles 3, golden yellow, *ca.* 3 mm long, apically 2-cleft; stigmas in a spiral band. **Capsule** trigonous-elliptic, 10–12 mm long, 7–8 mm wide excluding wings or 18–20 mm wide including wings; pedicel *ca.* 18–22 mm long; wings 3, equal, truncate distally, cuneate proximally.

Diagnostic characters:—This species is allied to *B. esculenta* Merrill (1911: 389) from which it is distinguished by its cordate leaf base (vs. not cordate leaf base) and white tepals (vs. vermilion tepals). *Begonia balangcodiae* also resembles *B. leucosticta* Warburg (1904: 55) but differs from the latter by its cordate leaf base (vs. subcordate leaf base) and larger tepals with 12–18 mm (vs. ca. 3–5 mm) long in staminate flowers. In addition, this species is similar to *B. negrosensis* Elmer (1910:736) but has lanceolate, glabrous leaves (vs. obovately oblong and sparsely hairy leaves) and white to greenish tepals (vs. pinkish tepals).

Habitat:—*Begonia balangcodiae* is found on soil slopes in mossy forest at Barangay Sagubo, Benguet Kapangan, Luzon, Philippines, elevation up to 1,200 m.

Etymology:—This species is named in honor of Professor Teodora D. Balangcod and her family for their hospitality during our visit to the University of the Philippines Baguio and her many research contribution for the flora preservation and ecological conservation in the Cordillera Administrative region.

2. *Begonia* × *kapangan* Rubite, S.H.Liu & K.F.Chung, *nothosp. nov.* (*Begonia balangcodiae* Rubite, S.H.Liu & K.F.Chung × *B. crispipila* Elmer)

sect. *Petermannia*

Type:—PHILIPPINES. Luzon, Benguet Province: Municipality of Kapangan, Barangay Sagubo, elveation *ca.* 1,200 m, 16°36'43" N, 120°33'48" E. 2 February 2012. *Kuo-Fang Chung 2013*, with Rosario Rivera Rubite, Severino M. Balangcod, Teodora D. Balangcod, and Han-Yao Huang (holotype PNH; isotype HAST). **Fig. 3–4.**

Monoecious, perennial herb. **Stem** erect, to *ca.* 1.8 m tall, 3–8 mm in diameter, olive green to crimson, pubescent, internodes 2–20 cm long, nodes slightly swollen. **Stipules** deciduous, light green, narrowly triangular-ovate, 12–22 × 4–8 mm, keeled, pubescent on both sides, margin entire, apex mucronate or aristate. **Petioles** terete, 1–4 cm long, *ca.* 0.5 mm in diameter, olive to crimson, pubescent. **Leaves** obovately oblong, asymmetric, base oblique and cordate, apex acute, margin irregularly dentate, 6–17 × 2–7 cm; adaxially olive green, dark green or crimson along veins, sometimes with sparse, small, white spots between veins, pubescent; abaxially olive green, crimson on margin and veins, pubescent; venation palmate, primary veins 7 or 8. **Bracts** deciduous, light green turning brown, triangular to ovate, 8–10 × 8–10 mm, glabrous, margin entire. **Inflorescence** axillary, dichasium or cyme, bisexual, peduncle light green to crimson, glabrous. **Staminate flower**: pedicel 8–16 mm long, glabrous; tepals 2, white, sometimes greenish at apex, widely ovate, 6–9 × 8–10 mm, margin entire, apex rounded, abaxially sparsely pubescent, adaxial glabrous; androecium zygomorphic; stamens 26–30, golden yellow; filaments *ca.* 1 mm, slightly fused at base; anthers obovate,

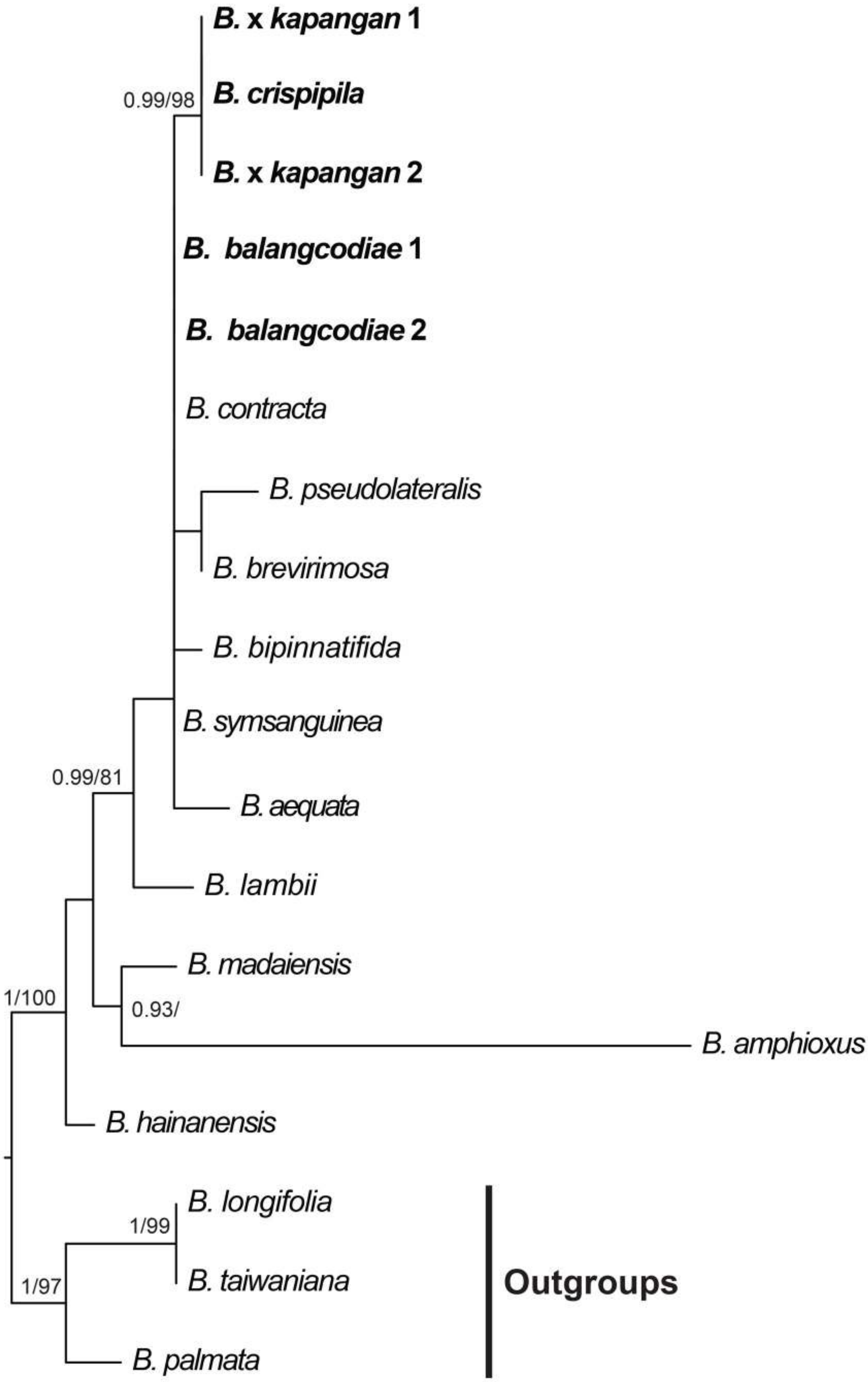

FIGURE 5. Maximum likelihood tree based on chloroplast *trnL-trnF* region of 16 *Begonia* taxa (18 DNA sequences). Numbers on the branches are posterior probability (pp) /maximum likelihood bootstrapping (bs) values. The values are shown only when pp ≥ 0.85 or bs ≥ 70. Taxa in bold are targets in this study.

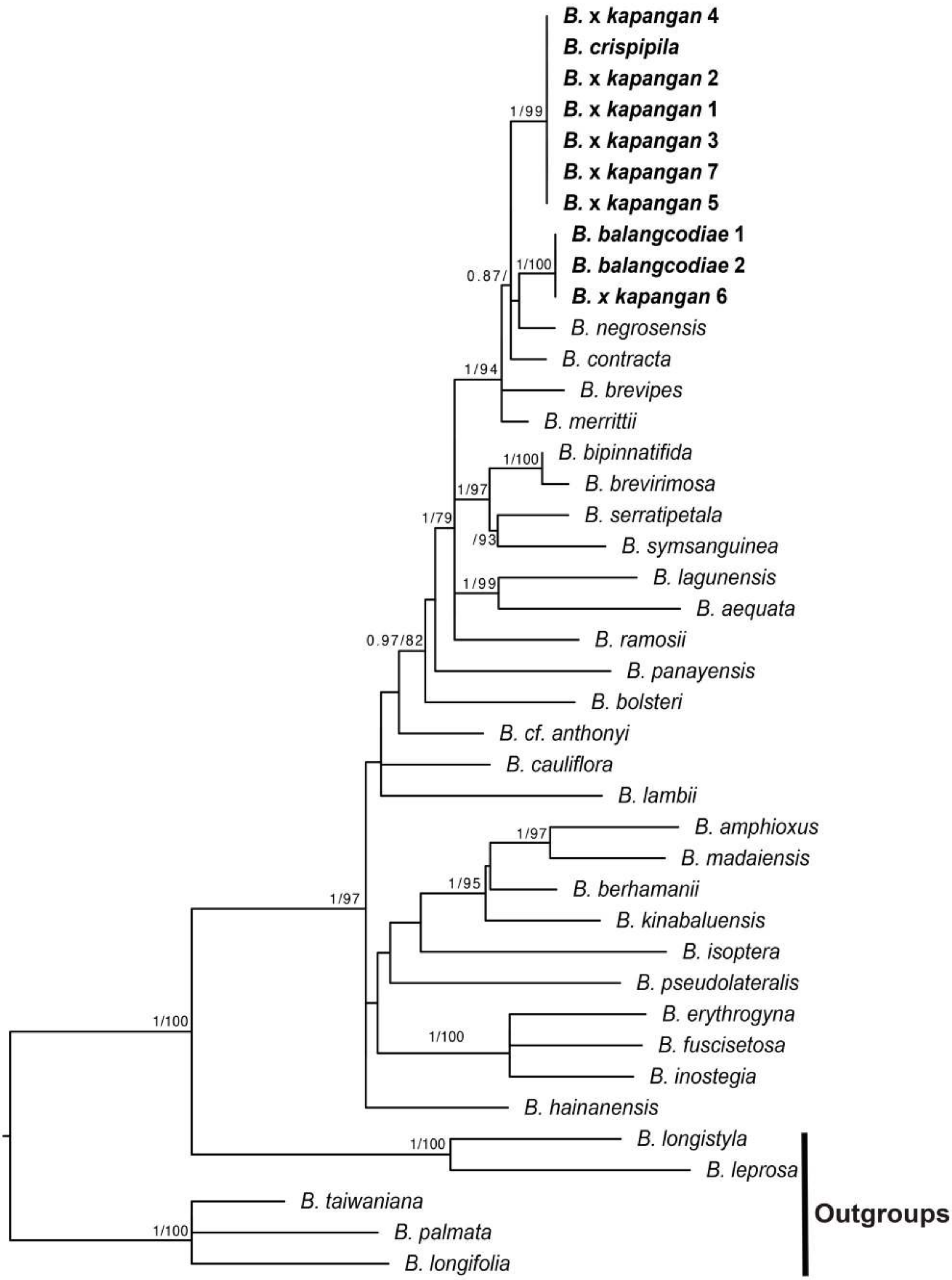

FIGURE 6. Maximum likelihood tree based on ITS region of 33 *Begonia* taxa (40 DNA sequences). Numbers on the branches are posterior probability (pp) /maximum likelihood bootstrapping (bs) values. The values are shown only when pp ≥ 0.85 or bs ≥ 70. Taxa in bold are targets in this study.

ca. 1 mm long, equal or shorter than filaments, apex retuse. **Pistillate flower**: pedicel 12–16 mm long, glabrous; tepals 2–3–4–5, white, obovate, 12–14 × 8–10 mm, margin entire, apex rounded, abaxially sparsely pubescent, adaxial glabrous; ovary present or lacking, green, trigonous-elliptic, 8–10 × 6–8 mm (wings excluded), nearly glabrous, 3-locular, placentation axile; 3-winged, wings reddish, equal; styles 3, golden yellow, *ca.* 3 mm long, apically 2-cleft; stigmas in a spiral band. **Capsule** not observed.

Diagnostic characters:—The natural hybrid *B.* × *kapangan* is an intermediate between *B. crispipila* and *B. balangcodiae* in its morphology (Table 3). *Begonia* × *kapangan* is similar to *B. crispipila* by the form of trichomes, obovately oblong leaves, bract size, and bisexual inflorescences; however, it is distinguished from *B. crispipila* in its sparse pubescence (vs. dense pubescence), white and larger tepals (vs. pink and smaller tepals), larger inflorescences (vs. short inflorescences), and green ovaries (vs. pink ovaries). Moreover, *B.* × *kapangan* is similar to *B. balangcodiae* in having compound cymose inflorescences, white tepals, and green ovaries, but it is different from *B. balangcodiae* in its sparse pubescence (vs. glabrous), obovately oblong leaves (vs. lanceolate leaves), larger bracts (vs. smaller bracts), and bisexual inflorescences (vs. unisexual inflorescences).

Habitat:—*Begonia* × *kapangan* is found on soil slopes in mossy forest at Barangay Sagubo, Benguet Kapangan, Luzon, Philippines, elevation up to 1,200 m.

Etymology:—The epithet refers to the Municipality of Kapangan where the new hybrid was discovered.

Notes:—*Begonia* × *kapangan* is a nothospecies of the cross between *B. crispipila* and *B. balangcodiae* found at Barangay Sagubo, Benguet Kapangan, Luzon, Philippines. This is confirmed by the results of our morphological investigation (Table 3) and phylogenetic analyses (Figs. 5–6). *Begonia* × *kapangan* has some abnormal morphology—like ovary sometimes lacking, floral segment number various, and fruit aborting—and shows intermediate morphology between *B. crispipila* and *B. balangcodiae* (Table 3). Moreover, the phylogenetic study based on ITS and *trn*L-*trn*F regions support that both *B. crispipila* and *B. balangcodiae* contributed to the origin of *B.* × *kapangan* and the former parental species is the maternal donator (Figs. 5–6).

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APPENDIX 1. Voucher information and NCBI accession number of *Begonia* samples used in this study is listed in following order: ***taxon name***, *section*, voucher specimen (herbarium acronym), locality, GenBank accession numbers of nuclear ribosomal DNA / chloroplast *trnL-trnF* sequences. The GenBank accession numbers with asterisks identify the sequences newly generated for this study. Double dashes indicate that the sequences are not available.

Target *Begonia* species:
Begonia crispipila Elmer, *Petermannia*, K.-F. Chung, 2011 (HAST), Philippines: Cordillera Administrative Region, MG945949* / MG938473*; ***Begonia balangcodiae*** Rubite, S.H.Liu & K.F.Chung, *Petermannia*, K.-F. Chung, 2012 (HAST, PNH), Philippines: Cordillera Administrative Region, MG945945*, MG945946* / MG938474*, MG938475*; ***Begonia* × *kapangan*** Rubite, S.H.Liu & K.F. Chung, *Petermannia*, K.-F. Chung, 2013 (HAST, PNH), Philippines: Cordillera Administrative Region, MG945947*, MG945948*, MG945950*, MG945951*, MG945952*, MG945953*, MG945954* / MG938476*, MG938477*.

Additional *Petermania* species:
Begonia aequata A. Gray, *Petermannia*, AF485147 / MG938482; ***Begonia amphioxus*** Sands, *Petermannia*, AF485150 / MG938486; Begonia anthonyi Kiew, *Petermannia*, KF636431 / --; ***Begonia berhamanii*** Kiew, *Petermannia*, KF636426 / --; ***Begonia bipinnatifida*** J.J. Sm, *Petermannia*, KF636427 / MG938478; ***Begonia bolsteri*** Merr., *Petermannia*, KF636428 / --; ***Begonia brevipes*** Merr., *Petermannia*, KF636429 / --; ***Begonia brevirimosa*** Irmsch., *Petermannia*, AF485145 / MG938481; ***Begonia contracta*** Warb., *Petermannia*, KF636433 / MG938479; ***Begonia erythrogyna*** Sands, *Petermannia*, KF636438 / --; ***Begonia fuscisetosa*** Sands, *Petermannia*, KF636440 / --; ***Begonia hainanensis*** Chun & F. Chun, *Petermannia*, KF636443 / MG938485; ***Begonia inostegia*** Stapf, *Petermannia*, KF636446 / --; ***Begonia isoptera*** Dryand. ex Sm., *Petermannia*, KF636447 / --; ***Begonia kinabaluensis*** Sands, *Petermannia*, KF636450 / --; ***Begonia lagunensis*** Elmer, *Petermannia*, KF636453 / --; ***Begonia lambii*** Kiew, *Petermannia*, KF636454 / MG938483; ***Begonia madaiensis*** Kiew, *Petermannia*, KF636462 / MG938487; ***Begonia merrittii*** Merr., *Petermannia*, KF636464 / --; ***Begonia negrosensis*** Elmer, *Petermannia*, HQ729055 / --; ***Begonia panayensis*** Merr., *Petermannia*, KF636469 / --; ***Begonia paracauliflora*** Rimi, C.I Peng & S.M.Ku, *Petermannia*, KF636470 / --; ***Begonia pseudolateralis*** Warb., *Petermannia*, KF636476 / MG938484; ***Begonia ramosii*** Merr., *Petermannia*, KF636478 / --; ***Begonia serratipetala*** Irmsch., *Petermannia*, KF636484 / --; ***Begonia symsanguinea*** L. Forrest & Hollingsw., *Symbegonia*, AF485151 / MG938480.

Outgroups:
Begonia leprosa Hance, *Coelocentrum*, KF636457 / --; ***Begonia longistyla*** Y.M. Shui & W.H. Chen, *Coelocentrum*, KF636460 / --; ***Begonia taiwaniana*** Hayata, *Diploclinium*, KF636488 / KP763589; ***Begonia palmata*** D. Don, *Platycentrum*, KF636468 / KP763594; ***Begonia longifolia*** Blume, *Sphenanthera*, AF485105 / KP763600.

APPENDIX 2. Herbarium specimens and relevant literatures examined.

Begonia balangcodiae Rubite, S.H.Liu & K.F.Chung, this study. *K.-F. Chung 2012* (Holotype: PNH; Isotype: HAST), PHILIPPINES, Luzon, Benguet Prov.: Kapangan, Barangay Sagubo, February 2 2012.
Begonia crispipila Elmer (1910) *Leaflets of Philippine Botany* 2: 737. Merr. (1911[1912]) *Philippine Journal of Science* 6: 384. *A.D.E. Elmer 8687* (Isotype: E, NY, US), PHILIPPINES, Luzon, Benguet Prov.: Baguio, March 1907. *A.D.E. Elmer 6149* (K), PHILIPPINES, Luzon, Benguet Prov.: Sablan, April 1904. *K.-F. Chung 2011* (HAST), PHILIPPINES, Luzon, Benguet Prov.: Kapangan, Barangay Sagubo, February 2 2012.
Begonia esculenta Merr. (1911[1912]) *Philippine Journal of Science* 6: 389–390. *Robinson, C. B. Bur. Sci. 9449* (Isotype: US), PHILIPPINES, Luzon, Quezon Prov.: Infanta, Mt. Binuang, August 1909. *M. Ramos 33347* (US, P), PHILIPPINES, Luzon, Ilocos Norte Prov.: Mt. Palimlim, August 1918.
Begonia* × *kapangan Rubite, S.H.Liu & K.F.Chung, this study. *K.-F. Chung 2013* (Holotype: PNH; Isotype: HAST, E), PHILIPPINES, Luzon, Benguet Prov.: Kapangan, Barangay Sagubo, February 2 2012.
Begonia leucosticta Warb. (1904) *Fragmenta Florae Philippinae* 1: 55. Merr. (1923) *An Enumeration of Philippine Flowering Plants* 3: 124. *O. Warburg 12004* (Type: B), PHILIPPINES, Luzon, Isabela Prov.: Dizamai. *E.D. Merrill 5274* (B), PHILIPPINES, Luzon, Bucas Island, October 1906.
Begonia macgregorii Merr. (1912) *Philippine Journal of Science* 7:310. *McGregor, R.C. 11334* (Holotype: B, P; Isotype: L, BO, BM), PHILIPPINES, Luzon, Nueva Vizcaya Prov.: Dupax, March 1912.
Begonia negrosensis Elmer (1910) *Leaflets of Philippine Botany* 2: 736. *A.D.E. Elmer 9903* (Isotype: BM, BO, E, FI, K, L, MO, NY, UVM), PHILIPPINES, Negros, Negros Oriental Prov.: Dumaguete, April 1908.
Begonia platyphylla Merr. (1915) *The Philippine Journal of Science. Section C, Botany* 10: 46. *R.C. McGregor 20074* (Holotype: P; Isotype: K, BM), PHILIPPINES, Luzon, Nueva Vizcaya Prov.: Imugan, January 1912.