

A NEW SPECIES OF TUBEROUS *BEGONIA* (*BEGONIACEAE*) FROM ANDEAN PERU

P. W. MOONLIGHT¹, R. HOLLANDS¹, A. CANO² & D. A. PURVIS¹

A striking new species of *Begonia*, *B. joshii*, is described from Amazonas Region, Peru. The new species is unusual among the South American members of the genus both in its combination of tuberous habit with peltate leaves and in living in a seasonally dry tropical forest environment. A phylogeny of this and closely related species is presented, and its sectional affiliation and IUCN conservation status are discussed. A key to the peltate Peruvian species of *Begonia* is provided.

Keywords. *Begonia* sect. *Eupetalum*, large genera, new species, Peru.

INTRODUCTION

The genus *Begonia* L. is the fastest-growing angiosperm genus; in the decade to 2015, more species were described in *Begonia* than in any other genus (Moonlight *et al.*, 2018). The genus includes 1930 currently accepted species (Hughes *et al.*, 2015–). The Peruvian species of *Begonia* were included in a floristic treatment by Smith & Schubert (1941), which covered 33 species. However, 76 species have now been recorded from Peru (Hughes *et al.*, 2015–), including many that were either recently described (Moonlight & Tebbitt, 2016; Tebbitt, 2016; Moonlight *et al.*, 2017; Moonlight & Reynel, 2018) or recorded (Esquerre-Ibañez & Tebbitt, 2018). A particular focus for these new records is the northern Peruvian Andes, and recent fieldwork has highlighted a further new tuberous species from this area.

The majority of tuberous Andean species of *Begonia* belong to *Begonia* sect. *Australes* L.B.Sm. & B.G.Schub. or *Begonia* sect. *Eupetalum* (Lindl.) A.DC. (Moonlight *et al.*, 2018). These two sections were treated by Doorenbos *et al.* (1998) as a single section but separated by Moonlight *et al.* (2018) based on phylogenetic information. *Begonia* sect. *Australes* consists of tuberous, caulescent species with four tepals on the staminate flower and bifid styles, whereas *Begonia* sect. *Eupetalum* includes principally geophytic, rhizomatous species with more than five tepals on the staminate flower and multifid styles. Three further species are placed in *Begonia* sect. *Eupetalum* based on phylogenetic information (Moonlight *et al.*, 2018) but differ from this general description in minor characters. These are *Begonia tumbezensis* Irmsch. and *B. weberbaueri* Irmsch., which both have four tepals on the staminate flower, and *B. geraniifolia* Hook. (the type of *Begonia* sect. *Eupetalum*), which is tuberous and caulescent.

¹ Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, UK.
E-mail: pmoonlight@rbge.org.uk

² Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Casilla 14-0434, Lima 14, Peru.

The new species described herein as *Begonia joshii* is most similar to *B. geraniifolia*, particularly populations of this species with peltate leaves (e.g. *P.W. Moonlight & A. Daza* 109 [E, MOL] and 116 [E, MOL]) and crenate leaf margins (e.g. *L. García Llatas* 9594 [USM]). Shared characters include its tuberous habit, multifid styles, and the number of tepals in both the staminate and the pistillate flowers. However, the new species is easily distinguished as a larger plant that lacks an aerial stem and has succulent leaves with crenate margins. To aid in the identification of the new species, we provide a key to the peltate species of *Begonia* known from Peru. Considering its unusual combination of characters, we aimed to confirm the phylogenetic placement of *Begonia joshii* before assigning the species to section.

MATERIALS AND METHODS

The data set comprised sequence data from three non-coding plastid DNA regions (*ndhA* intron, *ndhF-rpl32* spacer and *rpl32-trnL* spacer) and 123 accessions of *Begonia* (see [Appendix table](#)). Accessions were chosen to be representative of all major clades of *Begonia* and all species with available sequence data within Neotropical clade 2-ii (NC2-ii) as defined by Moonlight *et al.* (2015, 2018). African *Begonia* was chosen as an outgroup.

A total of 309 sequences were downloaded from GenBank, and 20 sequences were newly generated for this study following the methods detailed in Moonlight *et al.* (2015, 2018). Sequences were manually aligned in BioEdit version 7.2.5 (Hall, 1999). Bayesian phylogenetic analyses were carried out in MrBayes version 3.2.1 (Huelsenbeck & Ronquist, 2001). Two searches, each comprising two Markov chain Monte Carlo chains, were run for 2,500,000 generations and sampled every 1000 generations. The burn-in was determined as 250,000 generations, following analysis of time series plots in Tracer version 1.7.1 (Rambaut *et al.*, 2018) to ensure adequate sample size.

Taxonomic descriptions were produced based on herbarium specimens at E and USM, plants observed in the field, and living plants grown at the Royal Botanic Garden Edinburgh. A photographic plate was produced from living plants at the Royal Botanic Garden Edinburgh.

RESULTS

The relationships among the major clades in the 50% majority rule consensus tree are shown in Fig. 1. We resolve the three accessions of *Begonia joshii* as monophyletic (posterior probability = 1.0) and within clade NC2-ii as defined by Moonlight *et al.* (2015, 2018). The species is further placed within a clade containing all sampled species in *Begonia* sect. *Eupetalum*, although this clade has only moderate support (posterior probability = 0.74) and is placed as sister to an accession of *Begonia geraniifolia* (*M.C. Tebbitt & A. Daza* 840).

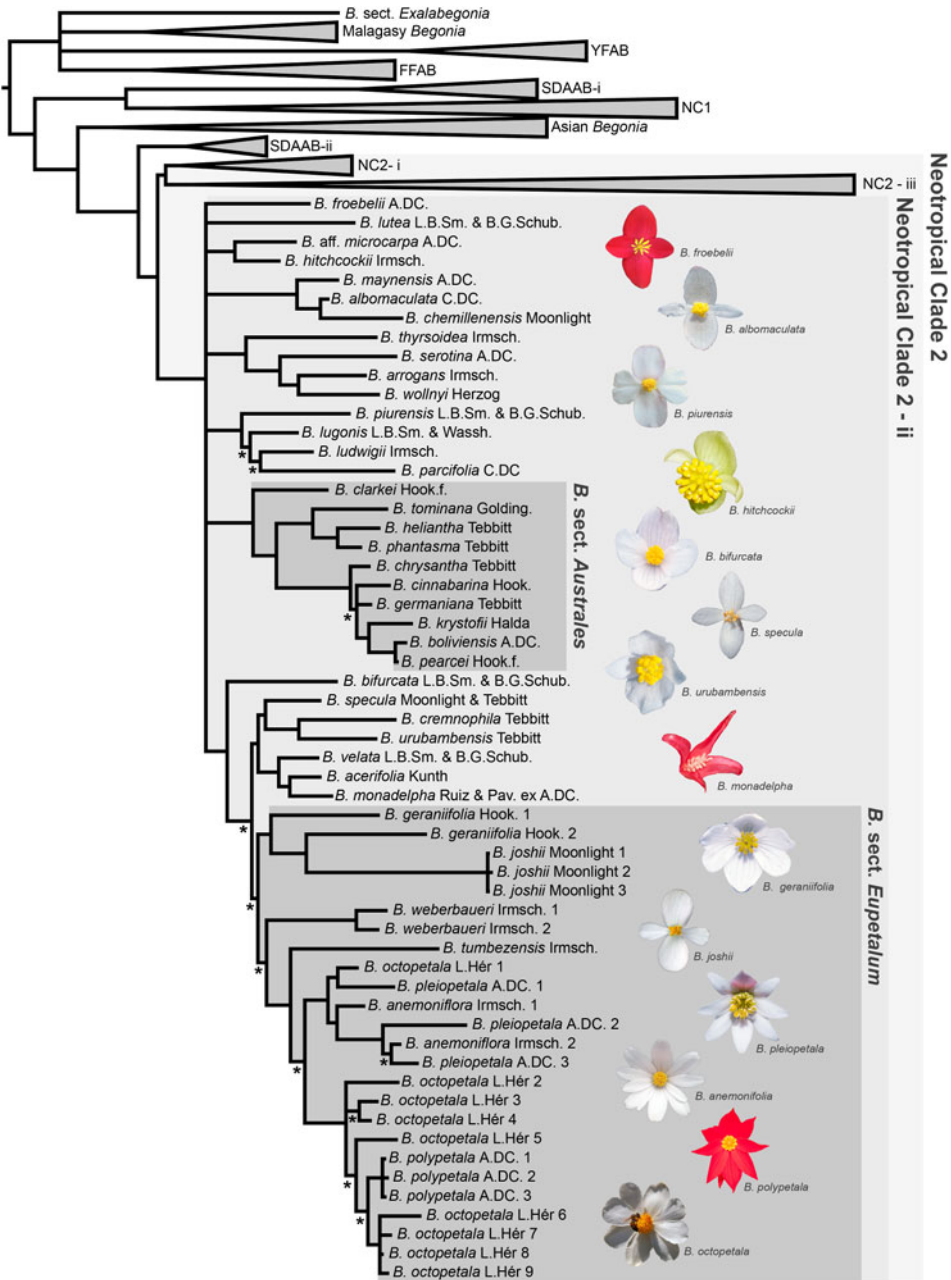


FIG. 1. The 50% majority rule consensus tree from MrBayes analysis of *Begonia*. Selected clades are highlighted and a selection of staminate flowers of *Begonia* species shown. Asterisks indicate posterior clade probabilities of < 0.85. All clade names are as defined in Moonlight *et al.* (2015, 2018). Abbreviated clade names: FFAB, fleshy-fruited African *Begonia*; NC1, Neotropical clade 1; NC2, Neotropical clade 2; SDAAB, seasonally dry adapted African *Begonia*; YFAB, yellow-flowered African *Begonia*.

DISCUSSION

The relationships among the major clades in the 50% majority rule consensus tree in the present study are consistent with those described by Moonlight *et al.* (2015, 2018). Our phylogenetic analyses confirm that *Begonia joshii* should be placed within *Begonia* sect. *Eupetalum* as circumscribed by Moonlight *et al.* (2018), which we resolve here as monophyletic. Within this section, the new species is resolved as most closely related to *Begonia geraniifolia*, which is paraphyletic in our results. *Begonia geraniifolia* has a wide distribution encompassing both Andean montane forests and coastal lomas habitats in Ecuador and Peru (Hughes *et al.*, 2015–) and is highly morphologically diverse. A revision of *Begonia* sect. *Eupetalum* is currently ongoing (Tebbitt, in preparation) and we suggest that particular attention is given to the circumscription of this species.

KEY TO THE PELTATE SPECIES OF PERUVIAN *BEGONIA*

- 1a. Plants tuberous or rhizomatous, terrestrial herbs; internodes short or lacking _____ 2
 1b. Plants lacking a tuber or rhizome, climbing herbs; internodes elongate
 7 [*Begonia* sect. *Gobenia* A.DC.]
- 2a. Plants rhizomatous _____ 3 [*Begonia* sect. *Knesebeckia* (Klotzsch) A.DC.]
 2b. Plants tuberous _____ 6 [*Begonia* sect. *Eupetalum* (Lindl.) A.DC.]
- 3a. Leaf laminae moderately to densely pubescent _____ 4
 3b. Leaf laminae glabrous _____ 5
- 4a. Leaf laminae with 1 or more large triangular lobes, margins entire; tepals deciduous in fruit _____ *B. acerifolia* Kunth
 4b. Leaf laminae lobate, margins serrulate; tepals persistent in fruit
 B. gorgonea Tebbitt
- 5a. Plant lacking an aerial stem; tepals deciduous in fruit ____ *B. urubambensis* Tebbitt
 5b. Plant with an aerial stem; tepals persistent in fruit _____ *B. serotina* A.DC.
- 6a. Plant with an aerial stem; leaf margin serrate to dentate, rarely crenate; ovary and fruit wing apices acute _____ *B. geraniifolia* Hook.
 6b. Plant lacking an aerial stem; leaf margin crenate; ovary and fruit wing apices rounded to truncate _____ ***B. joshii*** Moonlight
- 7a. Petiole insertion < 1/4 of the way up the lamina; tepals red
 B. aeranthos L.B.Sm. & B.G.Schub.
 7b. Petiole insertion > 1/4 of the way up the lamina; tepals white to yellow or green _____ *B. hitchcockii* Irmsch.

TAXONOMIC TREATMENT

Begonia joshii Moonlight, **sp. nov.** Sect. *Eupetalum*

Begonia joshii is similar to *B. geraniifolia* Hook. but differs in lacking an aerial stem, its succulent leaves, and its crenate leaf margins, although the last of these characters is rarely found in *B. geraniifolia*. – Type: Cultivated collection, 29 xi 2018, *P.W. Moonlight* 1277 (holo USM, iso E). Cultivated in the Royal Botanic Garden Edinburgh from seed collected in the wild (accession no. 20180923: Amazonas Region, Prov. Chachapoyas, trail over Puente La Florida from km 278 of Pedro Ruiz Gallo–Bagua Grande road, c.4 km from trail head, 5°54'13''S, 78°4'33''W, 2064 m, 3 vii 2018, *P.W. Moonlight* 1253). **Fig. 2.**

Acaulescent, tuberous herb. *Tuber* subglobose, 1.5–4 × 1.5–5 cm, with a single growing point. *Stipules* tardily deciduous, lanceolate, c.8 × 5 mm, translucent, white to pink, glabrous, apex acute to mucronate, margin entire, aciliate. *Leaves* 5–15, alternate, peltate but the first 1–3 leaves often basifixed; petiole lengthening through the life of the leaf, to 18 cm long, glabrous, pink to vivid red; blade subsymmetrical, ovate, to 10.5 × 8.5 cm, succulent, apex rounded, base rounded to notched, basal lobes overlapping or not overlapping, sinus to 15 mm deep, margin irregularly crenate, revolute, aciliate, upper surface glabrous, mid green, lower surface glabrous, very pale green, veins peltate-palmate, c.8 veined from the base, secondary veins indistinct. *Inflorescences* 1–3, axillary, erect, an asymmetrical cyme, with 1 branch, bearing up to 4 staminate flowers and 2 pistillate flowers, protandrous; peduncle to 28 cm long, glabrous, bracts tardily deciduous, lanceolate, c.6 × 3.5 mm, glabrous, apex obtuse, margin entire, aciliate, pale green. *Male flowers*: pedicels to 28 mm long, glabrous; tepals 4, spreading, white, outer two narrowly ovate, 11–12 × 9–11 mm, apex rounded, base rounded, margin entire, glabrous, inner oblanceolate, 10–11 × 6 mm, apex truncate, sometimes notched, base cuneate, margin entire, glabrous; stamens 11–16, projecting, yellow, filaments c.1 mm long, free, anthers linear, c.2 × 1 mm long, dehiscent by lateral slits, connectives not extending, symmetrically basifixed. *Female flowers*: pedicels to 30 mm long, bracteoles 2, positioned directly below the ovary, elliptic to narrowly lanceolate, 1–1.5 × 0.5 mm, apex rounded, glabrous, margin entire, aciliate, translucent, white; pedicels of female flowers 20–35 mm long, glabrous; tepals 5, persisting in fruit, spreading, white, flushed light green, oblanceolate to obovate, subequal, the largest 11 × 9 mm, the smallest 9 × 5 mm, apex truncate to rounded, margin entire, glabrous; ovary body ovoid, 8–9 × 5–7 mm, glabrous, light green, unequally 3-winged, wings triangular, largest 10–13 × 9–14 mm, smallest 5–6 × 9–11 mm; 3-locular, placentae entire, bearing ovules on both surfaces; styles 3, light green, free to base, c.2–3 mm long, 4-lobed, stigmatic papillae in a band around the lobes. *Fruiting pedicel* to 25 mm long. *Fruit* a capsule, body globose, to 6 × 6 mm, glabrous, drying brown, wings same shape as in ovary, expanding to 2.5 mm tall. *Seeds* not examined.

Phenology. The species has been collected in flower in February.

Distribution and ecology. The species is known from a single small population in the Chachapoyas Province of Amazonas Region, Peru (Fig. 3). It was found growing on steep

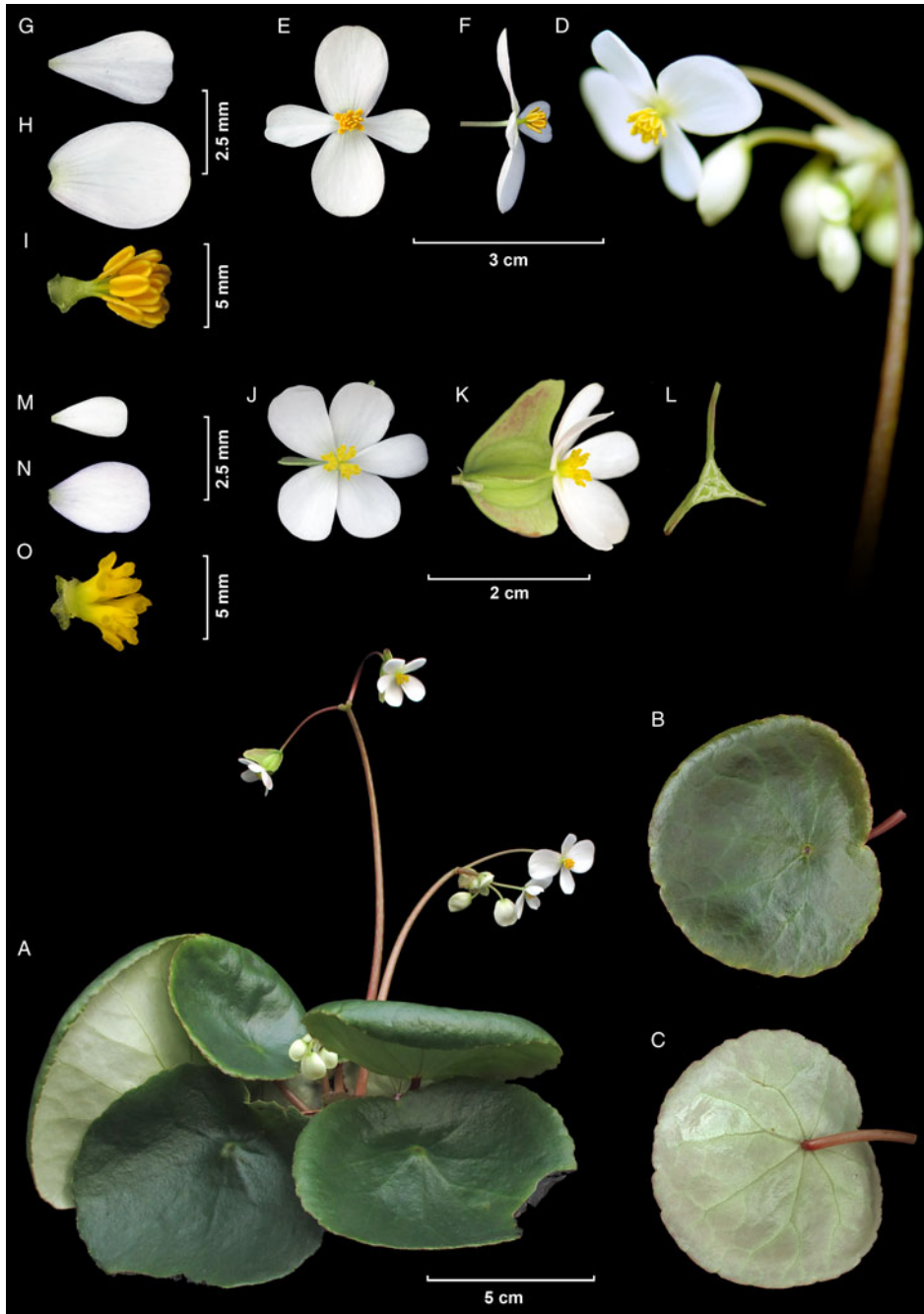


FIG. 2. *Begonia joshii* Moonlight, sp. nov. A, Habit; B, leaf (adaxial surface); C, leaf (abaxial surface); D, inflorescence; E, staminate flower (front view); F, staminate flower (side view); G, inner tepal of staminate flower; H, outer tepal of staminate flower; I, androecium (side view); J, pistillate flower (front view); K, pistillate flower ovary, and bracteole (side view); L, transverse section of ovary; M, inner tepal of pistillate flower; N, outer tepal of pistillate flower; O, gynoecium (side view). All photographs taken by D. A. Purvis of the type collection in the living collections of the Royal Botanic Garden Edinburgh (accession no. 20180923).

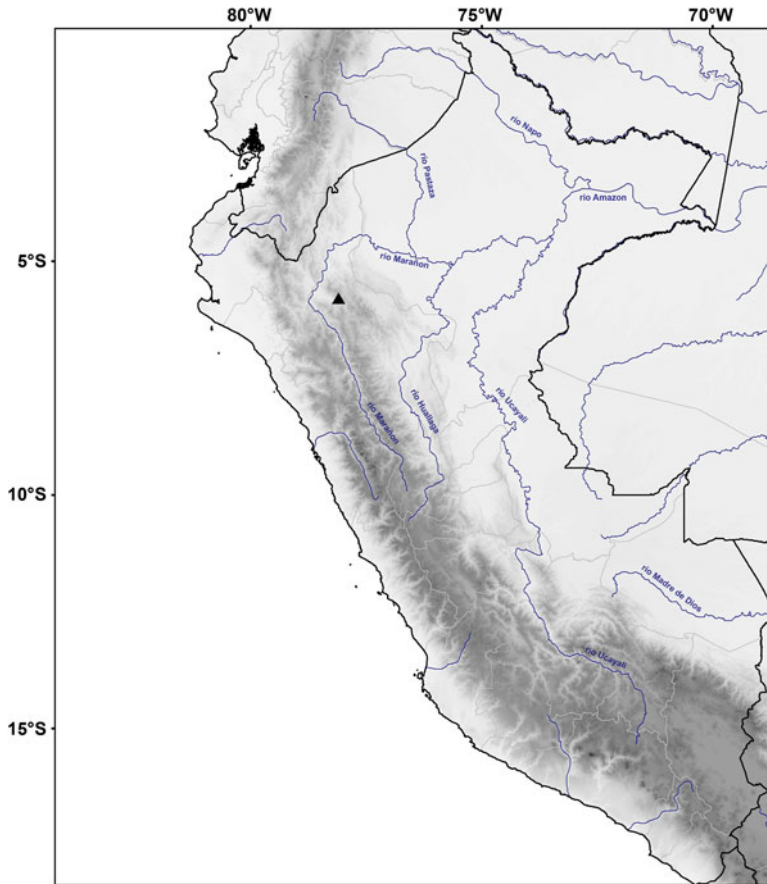


FIG. 3. Known distribution of *Begonia joshii* Moonlight. Major rivers and political divisions are shown. Shading indicates elevation.

rock and soil banks on the boundary between seasonally dry tropical forest and humid gallery forest.

Proposed IUCN conservation assessment. The species is known from three collections along 300 m of a single trail. From this locality, it was evident that that similar but inaccessible habitat was abundant nearby, but it is unclear if the species was present. Accordingly, we assess the species as Data Deficient under IUCN (2012) criteria.

Etymology. The species is named for Josh Allen, who photographed the species in the wild in 2017, alerted the authors to the species and visited the locality in 2018 with the first author.

Additional specimens examined. PERU. **Amazonas Region:** Prov. Chachapoyas, trail over Puente La Florida from km 278 of Pedro Ruiz Gallo–Bagua Grande road, c.4 km from trail head, 1441 m, 5°54'17''S, 78°4'42''W, 3 vii 2018, *P.W. Moonlight* 1251 (E, USM); *ibid.*, 1469 m, 5°54'14''S, 78°4'40''W, 3 vii 2018, *P.W. Moonlight* 1252 (E, USM); *ibid.*, 1520 m, 5°54'13''S, 78°4'33''W, 3 vii 2018, *P.W. Moonlight* 1253 (E, USM).

The new species is unlikely to be confused with other peltate Peruvian species of *Begonia* because of its unique combination of a tuberous habit, lack of an aerial stem, and succulent, glabrous leaves.

ACKNOWLEDGEMENTS

We thank the Ministerio del Ambiente del Perú for granting us permission to conduct fieldwork under permit 096-2017-SERFOR/DGGSPFFS and the Royal Botanic Garden Edinburgh for funding the fieldwork. We also thank Josh Allen for alerting the authors to this new species and his help in relocating it. This research was carried out as part of British Council project 418235692, *Increasing knowledge of dry and montane ecosystems across Peru*, at the Royal Botanic Garden Edinburgh, supported by the Scottish Government's Rural and Environment Science and Analytical Services Division.

REFERENCES

- DOORENBOS, J., SOSEF, M. S. M. & DE WILDE, J. J. F. E. (1998). The sections of *Begonia* including descriptions, keys and species lists (Studies in Begoniaceae VI). *Wageningen Agric. Univ. Pap.* 98(2): 1–266.
- ESQUERRE-IBAÑEZ, P. W. & TEBBITT, M. C. (2018). *Begonia ludwigii* y *Begonia parcifolia* (Begoniaceae) dos Registros Nuevos para la Flora Peruana. *Revista Peruana Biol.* 25(4): 437–444.
- HALL, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids Symp. Ser.* 41: 95–98.
- HUELSENBECK, J. P. & RONQUIST, F. (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755.
- HUGHES, M., MOONLIGHT, P. W., JARA-MUÑOZ, A., TEBBITT, M. C., WILSON, H. P. & PULLAN, M. (2015–). *Begonia Resource Centre*. Online database. Available: <http://padme.rbge.org.uk/begonia/> (accessed 10 May 2019).
- IUCN (2012). *IUCN Red List Categories and Criteria*, version 3.1, 2nd edition. IUCN Species Survival Commission. Gland, Switzerland, and Cambridge: International Union for Conservation of Nature.
- MOONLIGHT, P. W. & REYNEL, C. (2018). Two new species of *Begonia* from Andean Peru. *Phytotaxa* 381(1): 116–126.
- MOONLIGHT, P. W. & TEBBITT, M. C. (2018). Two new Peruvian species of *Begonia* (Begoniaceae) and an amended description of *Begonia thyrsoides*. *Edinburgh J. Bot.* 74(2): 111–122.
- MOONLIGHT, P. W., RICHARDSON, J. E., TEBBITT, M. C., THOMAS, D. C., HOLLANDS, R., PENG, C.-I. & HUGHES, M. (2015). Continental-scale diversification patterns in a megadiverse genus: the biogeography of Neotropical *Begonia*. *J. Biogeogr.* 42(6): 1137–1149.
- MOONLIGHT, P. W., REYNEL, C. & TEBBITT, M. (2017). *Begonia elachista* Moonlight & Tebbitt sp. nov., an enigmatic new species and new section of *Begonia* (Begoniaceae) from Peru. *Eur. J. Taxon.* 281: 1–13.

-
- MOONLIGHT, P. W., ARDI, W. H., ARROYO PADILLOA, L., CHUNG, K.-F., FULLER, D., GIRMANSYAH, D., HOLLANDS, R., JARA-MUÑOZ, A., KIEW, R., LEONG, W.-C., LIU, Y., MAHARDIKA, A., MARASINGHE, L. D. K., O'CONNOR, M., PENG, C.-I., PÉREZ, Á. J., PHUTTHAI, T., PULLAN, M., RAJBHANDARY, S., REYNEL, C., RUBITE, R. R., SANG, J., SCHERBERICH, D., SHUI, Y.-M., TEBBITT, M. C., THOMAS, D. C., WILSON, H. P., ZAINI, N. H. & HUGHES, M. (2018). Dividing and conquering the fastest-growing genus: towards a natural sectional classification of the mega-diverse genus *Begonia* (Begoniaceae). *Taxon* 67(2): 267–323.
- RAMBAUT, A., DRUMMOND, A. J., XIE, D., BAELE, G. & SUCHARD, M. A. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer v.1.7. *Syst. Biol.* syy032. doi: [10.1093/sysbio/syy03](https://doi.org/10.1093/sysbio/syy03)
- SMITH, L. B. & SCHUBERT, B. G. (1941). Begoniaceae. In: MACBRIDE, J. F. (ed.) *Flora of Peru*, vol. 13, part 4, pp. 181–202. Chicago: Field Museum of Natural History (Botany).
- TEBBITT, M. C. (2016). Two new species of Andean *Begonia* (Begoniaceae). *Edinburgh J. Bot.* 73(1): 143–152.

Received 10 May 2019; accepted for publication 13 August 2019; first published online 26 September 2019

APPENDIX

The data set used in the phylogenetic analyses included sequence data from 123 accessions of *Begonia*, whose data are summarised in the Appendix table.

APPENDIX TABLE. GenBank accession numbers and voucher information for *Begonia* accessions included in the phylogenetic analyses

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
<i>B. acerifolia</i> Kunth	<i>P.W. Moonlight & A. Daza</i> 120 (E)	MH207026	MH207437	MH207854
<i>B. albomaculata</i> A.DC.	<i>P.W. Moonlight & A. Daza</i> 213 (E)	MH207034	MH207445	ND
<i>B. anemoniflora</i> Irmsch. 1	<i>P.W. Moonlight & A. Daza</i> 230 (E)	MH207040	MH207451	MH207867
<i>B. anemoniflora</i> Irmsch. 2	<i>P.W. Moonlight & A. Daza</i> 222 (E)	MH207039	MH207450	MH207866
<i>B. arrogans</i> Irmsch.	<i>P.W. Moonlight & A. Daza</i> 285 (E)	MH207046	MH207456	MH207871
<i>B. bifurcata</i> L.B.Sm. & B.G.Schub.	<i>P.W. Moonlight & A. Daza</i> 105 (E)	KX756296	KX756307	MH207884
<i>B. boliviensis</i> A.DC.	<i>L.L. Forrest</i> 182 (E)	JF756346	JF756430	JF756514
<i>B. chemillensis</i> Moonlight	<i>P.W. Moonlight & A. Daza</i> 292 (E)	MH207097	MH207507	MH207924
<i>B. chrysantha</i> Tebbitt	<i>M.C. Tebbitt</i> 748 (USZ)	MH207102	MH207512	MH207928
<i>B. cinnabarina</i> Hook.	<i>M.C. Tebbitt</i> 705 (USZ)	MH207103	MH207513	MH207929
<i>B. clarkei</i> Hook.f.	<i>M.C. Tebbitt & A. Daza</i> 811 (E)	MH207108	MH207519	MH207933
<i>B. cremophila</i> Tebbitt	<i>M.C. Tebbitt</i> 753 (USZ)	KX756282	KX756309	MH207944
<i>B. froebelii</i> A.DC.	<i>M.C. Tebbitt</i> 786 (QCA)	KX756288	KX756305	MH207977
<i>B. geraniifolia</i> Hook. 1	<i>P.W. Moonlight & A. Daza</i> 116 (E)	KX756283	KX756311	MH207988
<i>B. geraniifolia</i> Hook. 2	<i>M.C. Tebbitt & A. Daza</i> 840 (E)	MH207162	MH207572	MH207987
<i>B. germaniana</i> Tebbitt	<i>M.C. Tebbitt</i> 709 (USZ)	MH207164	MH207574	MH207989
<i>B. heliantha</i> Tebbitt	<i>R.T. Pennington & A.Daza</i> 1113 (E)	ND	MH207587	ND
<i>B. hitchcockii</i> Irmsch.	<i>P.W. Moonlight & A. Daza</i> 151 (E)	MH207187	MH207598	MH208011
<i>B. joshii</i> Moonlight 1	<i>P.W. Moonlight</i> 1251 (E)	MN241961	MN241928	MN241929
<i>B. joshii</i> Moonlight 2	<i>P.W. Moonlight</i> 1252 (E)	MN241961	MN241928	MN241929
<i>B. joshii</i> Moonlight 3	<i>P.W. Moonlight</i> 1253 (E)	MN241960	MN241927	MN241930
<i>B. krystofii</i> Halda	<i>M.C. Tebbitt</i> 701 (USZ)	MH207216	MH207627	MH208041
<i>B. ludwigii</i> Irmsch.	<i>C.-I Peng</i> P23333 (HAST)	MH207231	MH207641	ND
<i>B. lugonis</i> L.B.Sm. & Wassh.	<i>Lyon B.G.</i> 150110 (LBG)	MH207233	MH207644	MH208053
<i>B. lutea</i> L.B.Sm. & B.G.Schub.	<i>Jara-Muñoz</i> AMB 332 (COL)	KX756287	KX756320	ND
<i>B. maynensis</i> A.DC.	<i>C.-I Peng s.n.</i> (HAST)	KP713063	KP713141	ND
<i>B. aff. microcarpa</i> A.DC.	<i>P.W. Moonlight & A. Daza</i> 156 (E)	KX756295	KX756322	MH208194
<i>B. monadelpha</i> Ruiz & Pav. Ex A.DC.	<i>T. Sarkinen</i> 2205 (E)	KP713005	KP713117	MH208071

APPENDIX TABLE. (Continued)

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
<i>B. octopetala</i> L.Hér 1	<i>M.C. Tebbitt & A. Daza</i> 825 (E)	MH207269	MH207680	ND
<i>B. octopetala</i> L.Hér 2	<i>M.C. Tebbitt & A. Daza</i> 787 (E)	MH235388	MH235403	MH235429
<i>B. octopetala</i> L.Hér 3	<i>P.W. Moonlight & A. Daza</i> 67 (E)	MH207266	MH207678	MH208087
<i>B. octopetala</i> L.Hér 4	<i>P.W. Moonlight & A. Daza</i> 208 (E)	MH207272	ND	MH208090
<i>B. octopetala</i> L.Hér 5	<i>M.C. Tebbitt & A. Daza</i> 828 (E)	MH235389	MH235409	ND
<i>B. octopetala</i> L.Hér 6	<i>P.W. Moonlight & A. Daza</i> 70 (E)	MH207267	ND	ND
<i>B. octopetala</i> L.Hér 7	<i>M.C. Tebbitt</i> 790 (QCA)	MH207268	MH207679	MH208088
<i>B. octopetala</i> L.Hér 8	<i>M.C. Tebbitt & A. Daza</i> 842 (E)	MH207270	MH207681	ND
<i>B. octopetala</i> L.Hér 9	<i>M.C. Tebbitt & A. Daza</i> 844 (E)	MH207271	MH207682	MH208089
<i>B. parçifolia</i> C.DC.	<i>M.C. Tebbitt</i> 769 (QCA)	MH207280	MH207691	MH208097
<i>B. pearcei</i> Hook.f.	<i>Lyon B.G.</i> 10128 (LBG)	MH207286	MH207698	MH208103
<i>B. phantasma</i> Tebbitt	<i>M.C. Tebbitt</i> 721 (USZ)	MH207293	MH207707	MH208111
<i>B. piurensis</i> L.B.Sm. & B.G.Schub.	<i>P.W. Moonlight & A. Daza</i> 111 (E)	KX756276	KX756318	ND
<i>B. pleiopetala</i> A.DC.	<i>M.C. Tebbitt & A. Daza</i> 813 (E)	MH207300	MH207714	MH208118
<i>B. pleiopetala</i> A.DC.	<i>P.W. Moonlight & A. Daza</i> 295 (E)	MH207301	MH207715	ND
<i>B. pleiopetala</i> A.DC.	<i>P.W. Moonlight & A. Daza</i> 297 (E)	MH207302	MH207716	MH208119
<i>B. polypetala</i> A.DC. 1	<i>M.C. Tebbitt & A. Daza</i> MT839b (E)	MH207310	MH207724	ND
<i>B. polypetala</i> A.DC. 2	<i>P.W. Moonlight & A. Daza</i> 113 (E)	MH207311	MH207725	MH208127
<i>B. polypetala</i> A.DC. 3	<i>P.W. Moonlight & A. Daza</i> 119 (E)	MH207312	MH207726	MH208128
<i>B. serotina</i> A.DC.	<i>M.C. Tebbitt</i> 773 (QCA)	MH207357	MH207772	MH208169
<i>B. specula</i> Moonlight & Tebbitt	<i>P.W. Moonlight & A. Daza</i> 158 (E)	MH207380	MH207798	MH208191
<i>B. thyrsoidea</i> Irmsch.	<i>M. Tebbitt & A. Daza</i> 809 (E)	ND	MH207820	MH208212
<i>B. tominana</i> Golding	<i>M.C. Tebbitt</i> 719 (USZ)	MH207401	MH207823	MH208214
<i>B. tumbezensis</i> Irmsch.	<i>M.C. Tebbitt</i> 770 (QCA)	ND	MH207828	ND
<i>B. urubambensis</i> Tebbitt	<i>P.W. Moonlight & A. Daza</i> 244 (E)	KX756298	KX756310	ND
<i>B. velata</i> L.B.Sm. & B.G.Schub.	<i>P.W. Moonlight & A. Daza</i> 107 (E)	MH207418	MH207840	MH208227
<i>B. weberbaueri</i> Irmsch. 1	<i>T. Sarkinen</i> 2216 (E)	KP713024	KP713102	KP713340
<i>B. weberbaueri</i> Irmsch. 2	<i>M.C. Tebbitt</i> 829 (USZ)	MH235396	MH235407	MH235428

APPENDIX TABLE. (Continued)

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
<i>B. wollnyi</i> Herzog	<i>M.C. Tebbitt s.n.</i> (USZ)	MH207424	MH207845	MH208232
<i>Begonia</i> sect. <i>Exalabegonia</i>				
<i>B. oxyloba</i> Welw. ex Hook.f.	<i>L.L. Forrest</i> 279 E00205102 (E)	JF756335	JF756419	JF756503
Malagasy <i>Begonia</i>				
<i>B. bogneri</i> Ziesenh.	<i>L.L. Forrest</i> 200 E00171239 (E)	KP712977	KP713185	ND
<i>B. goudotii</i> A.DC.	<i>V. Plana</i> 120 (E)	JF756347	JF756431	JF756515
<i>B. madecassa</i> Keraudren	20132231 (E)	MH207238	MH207648	MH208059
Yellow-flowered African <i>Begonia</i>				
<i>B. ampla</i> Hook.f.	<i>Suksuwan</i> 45 E00198091 (E)	KP712979	ND	ND
<i>B. baccata</i> Hook.f.	<i>M.E. Gardner & C.E. Berthold</i> 5 (E)	MH207049	MH207459	MH207874
<i>B. macrocarpa</i> Warb.	<i>Lyon B.G.</i> 100726 (LBG)	ND	MH207647	MH208058
<i>B. polygonoides</i> Hook.f.	<i>van der Burg</i> 244 (WAG)	JF756336	JF756420	JF756504
<i>B. scutifolia</i> Hook.f.	<i>C.-I Peng</i> 23324 (HAST)	MH207349	MH207764	MH208162
<i>B. squamulosa</i> Hook.f.	<i>C.-I Peng</i> 21280 (HAST)	KP712971	KP713182	ND
<i>B. susaniae</i> Sosef	<i>J. Duruisseau</i> 060661 (LBG)	ND	MH207814	MH208205
Seasonally dry adapted African <i>Begonia</i> -i				
<i>B. annobonensis</i> A.DC.	<i>M.F. Gardner, C.E. Berthold</i> 49 (E)	MH207042	ND	MH207868
<i>B. engleri</i> Gilg.	No voucher	KP712984	KP713133	KP713342
<i>B. johnstonii</i> Oliv. ex Hook.f.	No voucher	KP712996	KP713134	KP713339
Neotropical clade 1				
<i>B. acetosa</i> Vell.	<i>M.C. Tebbitt, S.M. Swensen & J. Yeaton</i> 15 (BKL)	KP712965	KP713154	KP713324
<i>B. aconitifolia</i> A.DC.	<i>Tebbitt s.n.</i>	MH235394	MH235397	MH235432

APPENDIX TABLE. (Continued)

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
<i>B. bahiensis</i> A.DC. 1	<i>B. Gregorio da Silva</i> 231 (HUEFS)	ND	ND	MN241931
<i>B. bahiensis</i> A.DC. 2	<i>B. Gregorio da Silva</i> 239 (HUEFS)	MN241949	MN241917	MN241945
<i>B. dichroa</i> Sprague	<i>Glasgow B.G.</i> 001-096-95 (E)	KP712931	KP713192	KP713343
<i>B. dietrichiana</i> Irmsch. ^b	<i>Glasgow B.G.</i> 009-007-97 (E)	KP712975	KP713190	KP713270
<i>B. digitata</i> Raddi	<i>B. Gregorio da Silva</i> 199 (HUEFS)	ND	ND	MN241938
<i>B. epibaterium</i> Mart ex A.DC.	<i>B. Gregorio da Silva</i> 234 (HUEFS)	MN241951	MN241922	MN241933
<i>B. glabra</i> Aubl.	<i>Z. Badcock</i> 7 (E)	MH207166	ND	MH207992
<i>B. hispida</i> var. <i>cucullifera</i> Irmsch.	<i>M.C. Tebbitt</i> 122 (BKL)	KP713064	KP713159	KP713281
<i>B. hoehneana</i> Irmsch.	20131494 (E)	MH207188	MH207599	MH208012
<i>B. itaguassuensis</i> Brade	<i>B. Gregorio da Silva</i> 205 (HUEFS)	MN241944	MN241924	MN241957
<i>B. kuhlmannii</i> Brade	<i>Glasgow B.G.</i> 004-029-07 (E)	KP712942	KP713157	KP713272
<i>B. ulmifolia</i> Willd.	<i>L.L. Forrest</i> 169 E00183958 (E)	KP713043	KP713135	KP713273
Asian <i>Begonia</i>				
<i>B. amphioxus</i> Sands	<i>D.C. Thomas</i> 08116 (E)	MH207038	MH207449	MH207865
<i>B. blancii</i> M.Hughes	<i>C.-I Peng</i> P22545 (HAST)	KR186450	KR186537	KR186711
<i>B. bracteata</i> Jack	<i>W.H. Ardi</i> 25 (E)	KP712991	KP713110	KP713323
<i>B. dipetala</i> Graham	<i>D.C. Thomas</i> 100468 (E)	JF756341	JF756425	JF756509
<i>B. erythrogyna</i> Sands	<i>S. Follin</i> 90517 (LBG)	MH207140	MH207550	KP713342
<i>B. grandis</i> Dryand.	<i>D.C. Thomas</i> 08-145 (E)	JF756351	JF756435	JF756519
<i>B. masoniana</i> Irmsch. ex Ziesenh.	<i>L.L. Forrest s.n.</i> (E)	JF756372	JF756456	JF756540
<i>B. pavonina</i> Ridl.	<i>S. Neale</i> 9C (E)	JF756356	JF756440	JF756524
<i>B. pteridifomis</i> Phutthai	<i>Lyon B.G. s.n.</i> (LBG)	MH207319	MH207732	MH208132
<i>B. rajah</i> Ridl.	<i>Lyon B.G.</i> 880168 (LBG)	MH207327	MH207741	MH208139
<i>B. socotrana</i> Hook.f.	<i>T. Miller</i> 19210/10 (E)	JF756340	JF756424	JF756508
<i>B. yapenensis</i> M.Hughes	<i>ABEG</i> 211 (E)	MH207425	MH207846	MH208233
<i>B. yunnanensis</i> H.Lév.	<i>C.-I Peng</i> 20941 (HAST)	MH207426	MH207847	MH208234

APPENDIX TABLE. (Continued)

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
Seasonally dry adapted African				
<i>Begonia</i> -ii				
<i>B. dregei</i> Otto & A.Dietr.	<i>T. McLellan</i> 415 (E)	JF756338	JF756422	JF756506
<i>B. sutherlandii</i> Hook.f.	<i>Jasper</i> 1200-5 (HAST)	KR186518	KR186605	KR186778
Neotropical clade 2-i				
<i>B. gracilis</i> Kunth	<i>Z. Badcock</i> 9 (E)	KP713004	KP713078	KP713260
<i>B. heydei</i> C.DC.	<i>C.-I Peng</i> P22624 (HAST)	MH207180	MH207591	ND
<i>B. incarnata</i> Link & Otto	<i>A. Twyford</i> 587 (E)	KP713065	KP713090	KP713232
<i>B. involucrata</i> Liebm.	<i>Tebbutt, Swensen & Yeadon</i> 23 (BKL)	KP712995	KP713082	KP713332
<i>B. nelumbiifolia</i> Schlttdl. & Cham.	<i>R. Hollands</i> 009 (E)	KP713040	KP713077	KP713230
<i>B. oaxacana</i> A.DC.	No voucher	KX756280	KX756325	ND
<i>B. peltata</i> Otto & A.Dietr.	<i>C.-I Peng</i> P233332 (HAST)	KP712988	KP713104	ND
<i>B. plebeja</i> Liebm.	<i>A. Twyford</i> 606 (E)	MH207299	MH207713	MH208117
<i>B. thiemei</i> C.DC.	<i>A. Twyford</i> 205 E00668802 (E)	KP713003	KP713094	KP713229
Neotropical clade 2-iii				
<i>B. bissei</i> J.Sierra	<i>W.G.C.</i> 655 (E)	MH207059	ND	MH207887
<i>B. bullatifolia</i> L.Kollmann	<i>J. Duruisseau</i> 120348 (LBG)	KX756303	ND	MH207905
<i>B. cyathophora</i> Poepp. & Endl.	No voucher	KP713075	KP713171	KP713255
<i>B. edmundoi</i> Brade	<i>L.L. Forrest</i> 196 (E)	KP712994	KP713216	KP713261
<i>B. elachista</i> Moonlight	<i>P.W. Moonlight</i> 318 (E)	KX756285	KX756324	MH207961
<i>B. fissistyla</i> Irmsch.	<i>L.L. Forrest</i> 157 E00205201 (E)	KP713051	KP713173	KP713250
<i>B. foliosa</i> Kunth	<i>Unknown s.n.</i> E19480286 (E)	KP713060	KP713176	KP713310
<i>B. lanceolata</i> Vell.	<i>Tebbutt</i> MBG02 (E)	KP713068	KP713101	KP713101
<i>B. semiovata</i> Liebm.	<i>P.W. Moonlight & A. Daza</i> 172 (E)	MH207352	MH207767	ND
<i>B. solananthera</i> A.DC.	<i>Glasgow B.G.</i> 021-070-04 (E)	KP712999	KP713098	KP713243

APPENDIX TABLE. (Continued)

Taxon	Voucher	Genbank accession no. ^a		
		<i>ndhA</i>	<i>trnL-trnF</i>	<i>trnF-rpL32</i>
<i>B. subvillosa</i> Klotzsch	<i>C.-I Peng</i> 21291 (HAST)	KP713046	KP713122	KP713262
<i>B. tetrandra</i> Irmsch.	<i>A. Jara-Muñoz</i> 2632 (COL)	MH207395	MH207816	MH208207
<i>B. toledana</i> L.B.Sm. & B.G.Schub.	<i>A. Jara-Muñoz</i> 2750 (COL)	MH207400	MH207822	MH208213
<i>B. viridiflora</i> var. <i>parviflora</i> L.B.Sm. & B.G.Schub.	<i>P.W. Moonlight</i> & <i>A. Daza</i> 216 (E)	MH207421	MH207842	MH208229

ND, no data.

^a Sequences newly generated for the present study are shown in bold.

^b This accession is incorrectly identified on GenBank as *Begonia odetiantha* Brade.