



Research article

Begonia elachista Moonlight & Tebbitt sp. nov., an enigmatic new species and a new section of *Begonia* (Begoniaceae) from Peru

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Abstract. The world's smallest *Begonia*, *Begonia elachista* Moonlight & Tebbitt sp. nov., is described and illustrated from a limestone outcrop in the Amazonian lowlands of Pasco Region, Peru. It is placed within the newly described, monotypic *Begonia* sect. *Microtuberosa* Moonlight & Tebbitt sect. nov. and the phylogenetic affinities of the section are examined. *Begonia elachista* sp. nov. is considered Critically Endangered under the International Union for the Conservation of Nature (IUCN) criteria.

Keywords. *Begonia*, sectional classification, limestone endemics, Peru, Amazonia.

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Introduction

Begonia L. is a megadiverse, pantropically distributed genus with 1821 currently accepted species (Hughes *et al.* 2015). The majority of species are understory herbs and shrubs with many prized in the horticulture industry. L'Héritier de Brutelle described the first *Begonia* species from Peru, *B. octopetala* L'Hér., in 1788 (L'Héritier de Brutelle 1788). Since this date, the number of *Begonia* species known from the country has increased rapidly. Smith & Schubert (1941) covered 34 species in their treatment of the Begoniaceae of Peru, although it did not cover all species known from the country at the time (e.g. *B. albomaculata* C.DC., described from Peru in 1906 (de Candolle 1906)). Recent field and herbarium work continues to yield new species (e.g. Tebbitt 2011, 2015, 2016) and new records for Peru (e.g. Tebbitt *et al.* 2015). Hughes *et al.* (2015) now list more than 75 species classified in 15 sections from Peru and at least ten species remain undescribed (unpubl. data). The *Begonia* flora of Peru is now the third largest in the Americas after Brazil (242 species) and Colombia (101 species). This study describes a highly unusual new species (*B. elachista* Moonlight & Tebbitt sp. nov.) from a limestone outcrop in lowland Pasco, Peru.

The phylogenetic relationships within Neotropical *Begonia* were first investigated in depth by Moonlight *et al.* (2015), who used three cpDNA markers and identified two clades of American *Begonia* within paraphyletic African *Begonia*: Neotropical Clade 1 (NC1) and Neotropical Clade 2 (NC2). This study presents a phylogeny of NC2 with increased sampling. We demonstrate that *B. elachista* sp. nov. is distantly related to all other tuberous western South American species and sections of *Begonia*; is resolved outside all closely related sections; and, given the species' unusual morphology, we describe a new section to encompass it (*B. sect. Microtuberosa* Moonlight & Tebbitt sect. nov.).

Materials and methods

Phylogenetics

The dataset consisted of data from three non-coding plastid DNA regions (*ndhA* intron, *nhdF-rpl32* spacer and *rpl32-trnL* spacer) and 68 species of *Begonia* (see Appendix). Species were chosen to be representative of all major groups within NC2 with *B. sect. Augustia* (Klotzsch) A.DC. chosen as an outgroup. A particular emphasis was placed upon the inclusion of other tuberous, western South American species and sections of *Begonia*. Ninety two sequences were newly generated for this analysis following the methods described in Moonlight *et al.* (2015).

Sequences were aligned manually in BioEdit v.7.2.5 (Hall 1999). Bayesian phylogenetic reconstruction was carried out in MrBayes v.3.2.1. (Huelsenbeck & Ronquist 2001). Models of molecular evolution were determined with jModelTest 2.1.7 (Darriba *et al.* 2012) on a maximum-likelihood topology with the Bayesian information criterion, resulting in the selection of the GTR+I+ Γ model. Two searches each comprising two Markov chain Monte Carlo chains were run for 2.5×10^7 generations and sampled every 2500 generations with the burn-in determined as 6.25×10^6 generations following analysis of time series plots in Tracer v.1.6 (Rambaut & Drummond 2013) to ensure adequate sample size.

Taxonomic descriptions

The descriptions of *B. sect. Microtuberosa* sect. nov. and *B. elachista* sp. nov. presented herein are derived from herbarium material, material grown at the Royal Botanic Garden Edinburgh, and field observations made by the authors during an expedition to Peru in 2016. Stable links to specimens held at E are included as hyperlinks and images of all cited specimens are available from Hughes *et al.* (2015). Comparisons to other sections of *Begonia* were made by reference to Doorenbos *et al.* (1998) and through reference to living material grown at the Royal Botanic Garden Edinburgh and Glasgow Botanic Gardens.

Results

Phylogenetics

The topology of the 50% majority rule consensus tree (Fig. 1) is entirely consistent with that of Moonlight *et al.* (2015). We resolve *B. elachista* sp. nov. within a clade of exclusively eastern South American species. The monophyly of *B. elachista* sp. nov. is well-supported ($p = 1.00$) and it is resolved as sister to three species of *B. sect. Gaertdia* (Klotzsch) A.DC., which will form the reinstated *B. sect. Pereira* Brade (Moonlight *et al.* in prep.), and *B. sect. Trachelocarpus* (Müll.Berol.) A.DC. as reciprocally monophyletic groups. This placement is moderately well-supported ($p = 0.88$). We resolve all other tuberous western South American species within a distantly-related clade containing all sampled members of *B. sect. Eupetalum* (Lindl.) A.DC.; *B. sect. Barya* (Klotzsch) A.DC.; all western South American members of *B. sect. Knesebeckia* (Klotzsch) A.DC.; and *B. thyrsoides* Irmsch., the only Andean member of *B. sect. Quadriperigonina* Ziesenh.

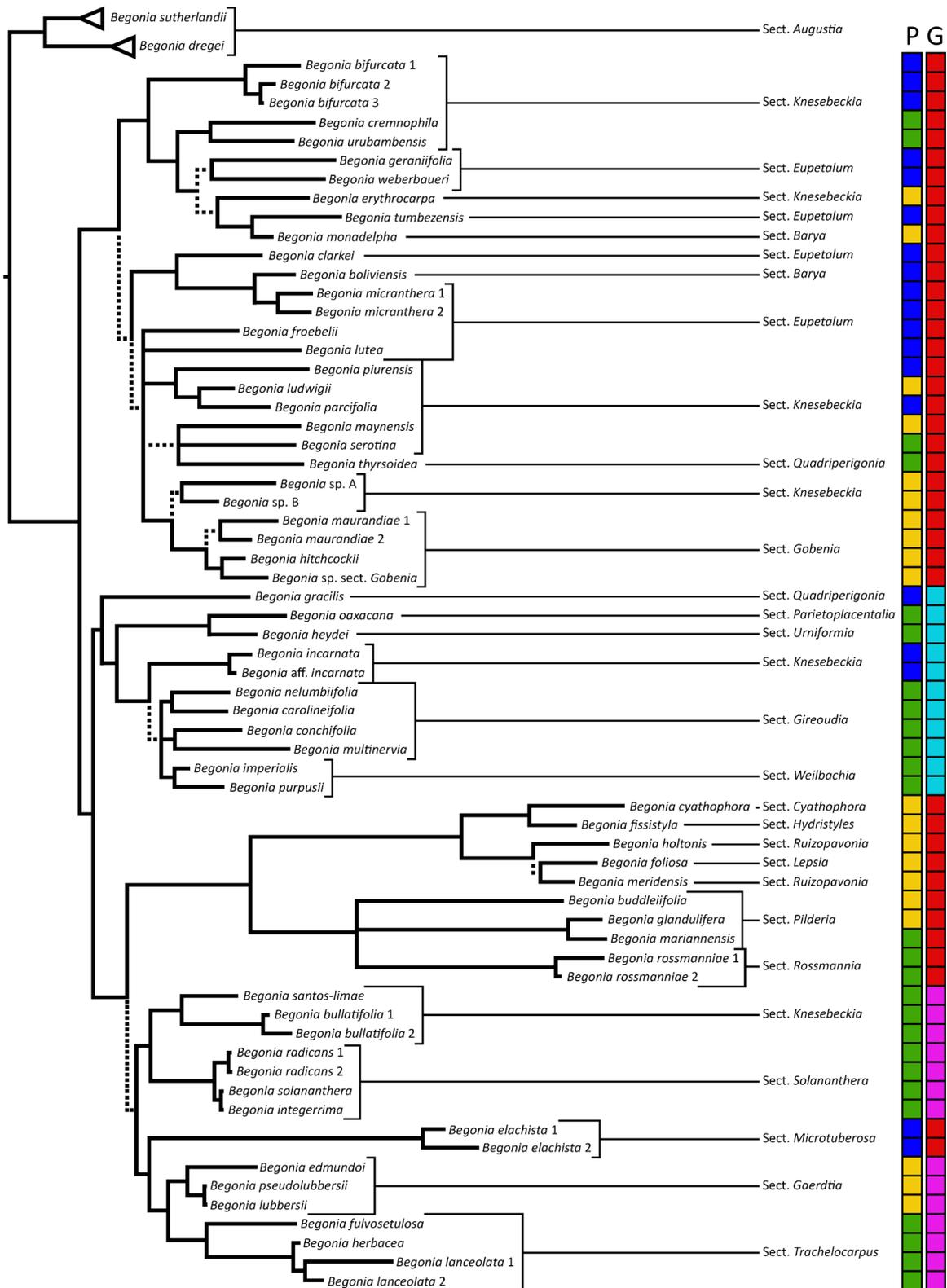


Fig 1. 50% majority rule consensus tree of MrBayes analysis of Neotropical Clade 2 (NC2) of *Begonia*. Dotted lines indicate posterior clade probabilities < 0.85. P, perenniation of species in NC2: blue, tuberous; green, rhizomatous; yellow, upright stems. G, geographic range of species in NC2: red, western South American; pink, eastern South America; light blue, Central America and Mexico.

Taxonomic Treatment

Class Equisetopsida C.Agardh (Agardh *et al.* 1825)
Subclass Magnoliidae Novák ex Takht. (Takhtajan 1967)
Superorder Rosanae Takht. (Takhtajan 1967)
Order Cucurbitales Juss. ex Bercht. & J.Presl (von Berchtold & Presl 1820)
Family Begoniaceae C.Agardh (Agardh 1824)

Genus *Begonia* L. (Linnaeus 1753)

Begonia sect. *Microtuberosa* Moonlight & Tebbitt sect. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77160200-1>

Diagnosis

Begonia sect. *Microtuberosa* sect. nov. is most closely related to *B.* sect. *Trachelocarpus* and three species of *B.* sect. *Gaerdtia*. Both of these sections are endemic to eastern Brazil and differ markedly from sect. *Microtuberosa* sect. nov. in both their habit and floral characteristics (see Table 1). However, all three sections share their filaments fused at least at the base and *B.* sect. *Microtuberosa* sect. nov. further shares its androecium morphology with *B.* sect. *Pereira* and its lack of bracteoles with *B.* sect. *Trachelocarpus*. The majority of both floral and vegetative characters are, however, markedly different among the three sections.

Begonia sect. *Microtuberosa* sect. nov. is readily identified as the only Neotropical section of *Begonia* with male flowers with four or fewer stamens, and the combination of ovaries with two or three locules and entire placentas, and a tuberous habit.

Etymology

The name ‘*Microtuberosa*’ emphasises the diminutive and tuberous habit of the type species.

Type species

Begonia elachista Moonlight & Tebbitt sp. nov.

Description

Cauliscent, tuberous herbs, perennial. Stems erect. Stipules persistent, entire. Leaves alternate, 2–4(–6), basifixed, blade symmetrical or subsymmetrical, veins palmate. Inflorescence axillary, an asymmetric dichasial cyme, protandrous, bracts persistent. Male flowers: with 2–4 free perianth segments; stamens 2 or 4, filaments united into a column for more than half their length, anthers elliptic, dehiscing via lateral slits, connective not projecting. Female flowers: bracteoles absent, with 2–3 free perianth segments; ovary and fruit with 2–3 wings, wings equal, 2–3-locular, placentas entire, bearing ovules on both surfaces; styles 2–3, free to base, bifid from about $\frac{2}{3}$ their height, stigmatic papillae in a once spirally twisted band. Fruit a capsule. Seeds not examined.

Distribution

On a limestone outcrop in lowland Amazonian Peru to the east of the Chemillén Cordillera at an altitude of 430 m.

Table 1. Comparison between *Begonia* sect. *Microtuberosa* Moonlight & Tebbitt sect. nov. and closely related sections.

Character	<i>B. sect. Microtuberosa</i>	<i>B. sect. Pereira</i>	<i>B. sect. Trachelocarpus</i>
Habit	Tuberous, stems erect	Lacking tubers or rhizomes, stems erect	Rhizomatous (creeping up the side of a tree), lacking an erect stem
Leaves	Alternate	Alternate	Whorled at the apex of rhizome
Venation	Palmate	Pinnate, palmate-pinnate	Pinnate
Inflorescence	Bisexual	Bisexual	Separate male and female
Bracteoles	Absent	Absent or 2 spaced from the base of the ovary	Absent
Androecium	Filaments fused for more than half their length; 2 or 4 stamens; anthers elliptic, dehiscent through lateral slits	Filaments fused for less than half their length; stamens many; anthers obovate, dehiscent through lateral slits	Filaments entirely fused into a column; stamens many; anthers obovate, dehiscent through lateral pores
Male perianth	2–4 tepals	4 tepals	2 tepals
Ovaries	2–3 locular with 2–3 styles; 1 placental branch per locule	3 locular with 3 styles; 2 placental branch per locule	3 locular with 3 styles; 1 placental branch per locule
Female perianth	2–3 tepals	5 tepals	3 tepals

Begonia elachista Moonlight & Tebbitt sp. nov. sect. *Microtuberosa*

<http://www.ipni.org/urn:lsid:ipni.org:names:77160201-1>

Figs 2, 3

Diagnosis

Begonia elachista sp. nov. is a highly distinct species with an unusual combination of features that is easily recognized as the only Peruvian species of *Begonia* that reaches maturity at fewer than 5 cm in height. It is also unique within Peru in having ovate leaves smaller than 3 × 3 cm and a combination of entire placentae and a tuberous habit.

Etymology

The epithet ‘*elachista*’ comes from the Greek for ‘least’ and emphasizes the diminutive size of this species, which is the smallest known species of *Begonia*.

Type

PERU: Region Pasco, Prov. Oxapampa, Dist. Palcazu, Parque Nacional Yanachaga-Chemillén, sector Paujil, 150 m from entrance to Las Cavernas on trail from Paujil, 10°20'40" S, 75°15'1" W, 432 m, 25 Feb. 2016, *Moonlight & Daza 318* (holo-: MOL; iso-: E, MO, USM).

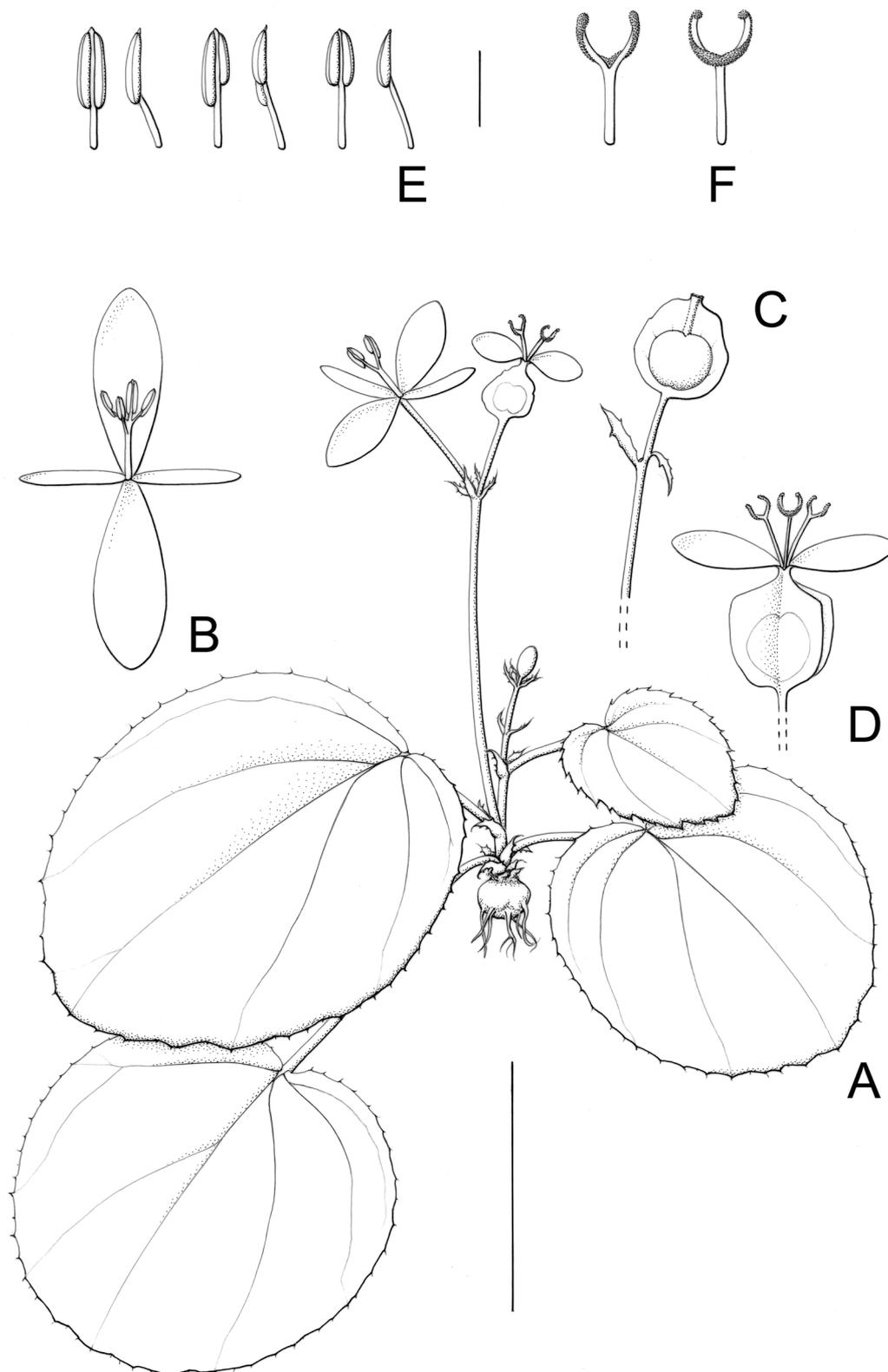


Fig 2. *Begonia elachista* Moonlight & Tebbitt sp. nov. **A.** Habit. **B.** Male flower, front view. **C.** Branch of infructescence. **D.** Female flower, side view. **E.** Stamens, front and side view. **F.** Style, front and back view. Scale bars: A–D = 1 cm; E–F = 1 mm. Drawn by Claire Banks. From *P. Moonlight & A. Daza 318* (E).

Additional material

PERU: Region Pasco, Prov. Oxapampa, Dist. Palcazu, Parque Nacional Yanachaga-Chemillén, sector Paujil, Quebrada Tunel, 10°20' S, 75°15' W, 429 m, 17 Mar. 2008, *Vásquez, Monteagudo, Huamantupa & A. Peña 34030* (E, HOXA, HUT, MO, USM).

Description

Caulесcent, tuberous herb. Tuber subglobose, 1–2 mm in diam. Stems 1–3 per tuber, erect, ca 0.2 mm in diam., 5–30 mm long, unbranched, internodes 1.5–7.5 mm long, glabrous, light green. Stipules persistent, narrowly lanceolate, 0.5–1.5 × 0.2–0.5 mm, apex acuminate, aristate, terminal hair ca 0.4 mm long, margin entire, with 1–2 ciliate hairs to 0.2 mm on each side. Leaves 1–4, alternate, basifixed; petiole orientated in same direction as the main vein of blade, 8–25 mm long, glabrous, blade symmetrical to subsymmetric, ovate to suborbicular, 8–30 × 7–25 mm, membranous, apex obtuse, base cordate, basal lobes not overlapping, sinus 0.5–2 mm deep, margin irregularly crenate, ciliate, the hairs to 0.3 mm, upper surface glabrous, light grey-green, lower glabrous, light grey-green, veins palmate, 5–7, secondary veins indistinct. Inflorescences 1–2, axillary, arising from axis of each leaf, erect, an asymmetric dichasial cyme, with 1–2 branches, bearing up to 2 male flowers and up to 2 female flowers, usually protandrous but basal-most female flower often opening concurrently with the apical male flower; peduncle 5–40 mm long, glabrous; pedicels of male flowers 2–6 mm long, glabrous; pedicels of female flowers 1–5 mm long, glabrous; bracts persistent, elliptic, 1.5–2.5 × 0.1–0.3 mm, apex acuminate, margin entire, glabrous or with up to 2 ciliate hairs to 0.2 mm on each side, dark brown.



Fig 3. *Begonia elachista* Moonlight & Tebbitt sp. nov. **A.** Whole plant. **B.** Male and female flower, front view. **C.** Female flower, side view. **D.** Habit and associated vegetation. **E–F.** Habitat and wild population. Scale bars: A = 1 cm; B = 5 mm; C = 2 mm; D = 2 cm; E–F = 10 cm. Photographed by Peter Moonlight. All from *P. Moonlight & A. Daza 318* (E).

Male flowers: tepals 2–4, spreading, white, outer two lanceolate to oblanceolate, $3\text{--}7.5 \times 1\text{--}2.5$ mm, apex obtuse to rounded, margin entire, glabrous, inner 1–2 elliptic if present, $3\text{--}4 \times 0.75\text{--}1.25$ mm, apex obtuse to rounded, margin entire, glabrous; stamens 2 or 4, yellow, filaments 0.25–0.75 mm long, united on a 0.75–1 mm column, anthers elliptic, 0.75–1.5 mm long, often with long and short thecae on the same anther, dehiscing via lateral slits, connectives not projecting, symmetrically basifixed. Female flowers: bracteoles absent; tepals not persisting in fruit, 2 or rarely 3, spreading, white, narrowly elliptic to oblanceolate, equal, $3\text{--}4.5 \times 0.75\text{--}2.5$ mm, apex obtuse to rounded, margin entire, glabrous; ovary body ovoid, $1.5\text{--}2.5 \times 1\text{--}2.5$ mm, glabrous, white, subequally 2–3-winged, wings rounded-oblong, apical edge of wing truncate to convex, basal edge rounded, apex acute to obtuse, 2–2.5 mm long, 1–1.75 mm wide; 2–3-locular, placentas entire, bearing ovules on both surfaces; styles 2–3, yellow, free to base, 2–3 mm long, bifid from about $\frac{2}{3}$ their height, stigmatic papillae in a once spirally twisted band. Fruiting pedicel to 5 mm long. Fruit body globose, to $1.5\text{--}2.5 \times 2\text{--}2.5$ mm, glabrous, drying brown, wings same shape and size as in ovary. Seeds not examined.

Distribution and habitat

Begonia elachista sp. nov. is known only from the type locality in the Peruvian region of Pasco (Oxapampa Province) and has been collected on calcareous rocks by the entrance to a cave within primary lowland Amazonian forest, at an altitude of 430 m. It was observed growing on rocks free from other vascular plants in association with various bryophyte species in the almost continual shade of the surrounding forest.

Conservation status

The known range of *B. elachista* sp. nov. consists of the area immediately around a single cave mouth and nearby limestone outcrops in sector Paujil of Parque Nacional Yanachaga-Chemillén (AOO < 1 km²). There are no other known limestone outcrops in sector Paujil of Parque Nacional Yanachaga-Chemillén or the surrounding areas thus its range is likely limited to this site. Around 5,000 plants are found at this locality and the population appeared stable during fieldwork in February 2016. Although the area is currently protected and tourists are prohibited from visiting the site, the national park authorities are considering building a tourist trail to the cave. The resulting increased footfall would put considerable pressure on the species' habitat and inevitably decrease the population size. Accordingly, we classify *B. elachista* sp. nov. as Critically Endangered: CR B2 ab(iii) (IUCN 2001).

Discussion

The tuberous habit and western South American range of *B. elachista* sp. nov. suggest a close relationship with other tuberous Andean species of *Begonia* but this is not supported by our analysis. The majority of tuberous Andean *Begonia* species are currently classified in *B.* sect. *Eupetalum*, which is distinguished by its geophytic tubers or fleshy rhizomes and relatively large flowers (Doorenbos *et al.* 1998; Tebbitt 2015). All other tuberous Andean species are classified within *B.* sect. *Barya*, *B.* sect. *Knesebeckia* and *B.* sect. *Quadriperigonia*, and all four sections differ from *B. elachista* sp. nov. in a suite of characters including their bifid placentae (except *B. lutea* L.B.Sm. & B.G.Schub.), more numerous stamens and female tepals, and much larger size. We resolve *B.* sect. *Microtuberosa* sect. nov. as distantly related to all tuberous species of Andean *Begonia* and most closely related to rhizomatous and scandent sections from southeast South America. The morphological differences between *B.* sect. *Microtuberosa* sect. nov. and these sections are outlined above (Table 1) and, in combination with the placement of *B. elachista* sp. nov. outside of these sections, strongly support the description of a new section.

The large morphological disparity between *B. elachista* sp. nov. and its nearest relatives is typical of that found in limestone cave endemics (Chung *et al.* 2014). Such species are typically small, often tuberous or rhizomatous, and usually have relatively symmetrical leaves and small, white flowers. Examples of

this syndrome in *Begonia* are found across sections and continents and include *B. antsingyensis* Humb. ex Keraudren & Bosser sect. *Quadrilobaria* A.DC. (Madagascar); *B. cavum* Ziesenh. sect. *Knesebeckia* (Klotzsch) A.DC. (Mexico); *B. hoehneana* Irmsch. sect. Unassigned (Brazil); *B. exigua* Irmsch. sect. *Begonia* (Brazil); *B. minuscula* Aver. sect. *Reichenheimea* (Klotzsch) A.DC. (Vietnam); *B. schulziana* Urb. & Ekman sect. *Begonia* (Haiti); *B. speluncae* Ridl. sect. *Reichenheimea* (Klotzsch) A.DC. (Borneo); and many others. This striking convergence among unrelated *Begonia* species on similar substrates in *Begonia* is worthy of further investigation.

That *B. sect. Microtuberosa* sect. nov. is nested within a group of eastern Brazilian species suggests it represents an independent dispersal across the Amazon basin, in addition to those identified in Moonlight *et al.* (2015). The majority of lowland Amazonia represents unsuitable habitat for most *Begonia* species but the genus appears to have dispersed across the area multiple times. The discovery of a further dispersal event highlights the abundance of ‘rare’ long-distance dispersal events within *Begonia*.

Begonia elachista sp. nov. is one of a number of recently described species of Peruvian *Begonia*. The number of species known from this country has risen from the 34 covered in the Flora of Peru (Smith & Schubert 1941) to more than 75 today (Hughes *et al.* 2015). This continued rapid rate of species discovery suggests many more species may remain undiscovered within the country, particularly in limestone areas.

A number of species are contenders for the world’s smallest *Begonia*, and many have been designated epithets emphasising their diminutive statures. The first of these was *B. minor* Jacq. in 1787, although in this case the name only implied it was slightly smaller than the 20 or so species previously described, and it still grows to more than 1 m. Perhaps the most delicate known *Begonia* species is the Malaysian *B. sibthorpioides* Ridl., whose leaves and flowers are both smaller than those of *B. elachista* sp. nov.; however, the stem of *B. sibthorpioides* trails to 10 cm. Malagasy *Begonia* also include a number of tiny species, including *B. leandrii* Humb., *B. nana* L’Hér. and *B. perpusilla* A.DC., while the smallest mainland African species is *B. wilksii* Sosef, but all exceed the 3 cm total height of *B. elachista* sp. nov. in either their inflorescence height or petiole length. The recently described Vietnamese *B. minuscula* Aver. and Sumatran *B. lilliputana* M.Hughes are both small, but the rhizomes of the former reach 6 cm while the leaf length of the latter equals the entire height of *B. elachista* sp. nov. *Begonia sleumeri* L.B.Sm. & B.G.Schub. is particularly notable in being a small tuberous species from Andean South America. This Argentinian species has smaller leaf blades of a similar size (1–3.1 × 1.4–4.6 cm) to *B. elachista* sp. nov. but has larger tubers (0.5–2 cm in diam.), sometimes has taller stems (up to 4.5 cm tall), often has longer petioles (1.2–5.3 cm long), and almost always has larger flowers. We believe *B. elachista* sp. nov. is the smallest known *Begonia* species in the world.

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Appendix. List of voucher specimens and Genbank accession numbers used in phylogenetic analyses.

Species	Section	Voucher specimen	Genbank voucher		
			<i>ndhA</i> intron	<i>ndhF-rpl32</i>	<i>Rpl32-trnL</i>
<i>Begonia dregei</i>	<i>Augustia</i>	McLellan 415 (E)	JF756338	JF756422	JF756506
<i>Begonia sutherlandii</i>	<i>Augustia</i>	Thomas 08-140 (E)	JF756337	JF756421	JF756505
<i>Begonia boliviensis</i>	<i>Barya</i>	Forrest 182 (E)	JF756346	JF756430	JF756514
<i>Begonia monadelpha</i>	<i>Barya</i>	Sarkinen 2205 (E)	KP713005	KP713117	KY070215
<i>Begonia cyathophora</i>	<i>Cyathocnemis</i>	no voucher	KP713075	KP713171	KP713255
<i>Begonia clarkei</i>	<i>Eupetalum</i>	Tebbitt 824 (E)	KX756293	KX756304	KY070198
<i>Begonia froebelii</i>	<i>Eupetalum</i>	Tebbitt 789 (COL)	KX756288	KX756305	KY070199
<i>Begonia geraniifolia</i>	<i>Eupetalum</i>	Moonlight 116 (E)	KX756283	KX756311	KY070205
<i>Begonia lutea</i>	<i>Eupetalum</i>	Jara AMB 332 (COL)	KX756287	KX756320	n/a
<i>Begonia micranthera</i> 1	<i>Eupetalum</i>	Sarkinen 2029 (E)	KP713032	KP713204	n/a
<i>Begonia micranthera</i> 2	<i>Eupetalum</i>	Sarkinen 2043 (E)	KP713066	KP713198	n/a
<i>Begonia tumbezensis</i>	<i>Eupetalum</i>	Tebbitt 770 (QCNE)	n/a	KX756312	n/a
<i>Begonia weberbaueri</i>	<i>Eupetalum</i>	Sarkinen 2216 (E)	KP713024	KP713102	KP713340
<i>Begonia edmundoi</i>	<i>Gaertdia</i>	Forrest 196 (E)	KP712994	KP713216	KP713261
<i>Begonia lubbersii</i>	<i>Gaertdia</i>	Forrest 194 (E)	KP712981	KP713100	KP713237
<i>Begonia pseudolubbersii</i>	<i>Gaertdia</i>	GBG 045-023-92 (GBG)	KP713072	KP713203	KP713329
<i>Begonia carolineifolia</i>	<i>Gireoudia</i>	Tebbitt 80 (BKL)	KP713033	KP713103	KP713244
<i>Begonia conchifolia</i>	<i>Gireoudia</i>	Tebbitt 89 (BKL)	KP713021	KP713083	KP713305
<i>Begonia multinervia</i>	<i>Gireoudia</i>	Tebbitt 131 (BKL)	KP713023	KP713163	KP713258
<i>Begonia nelumbiifolia</i>	<i>Gireoudia</i>	Hollands 009 (E)	KP713040	KP713077	KP713230
<i>Begonia maurandiae</i> 1	<i>Gobenia</i>	Jara, A (2758)	KX756291	KX756313	KY070206
<i>Begonia maurandiae</i> 2	<i>Gobenia</i>	Duruisseau s.n. (LBG)	KX756281	KX756314	n/a
<i>Begonia hitchcockii</i>	<i>Gobenia</i>	Moonlight 123 (E)	KX756290	KX756315	KY070207
<i>Begonia</i> sp. sect. <i>Gobenia</i>	<i>Gobenia</i>	EQ-JD-04 (LBG)	KX756292	KX756316	KY070208
<i>Begonia fissistyla</i>	<i>Hydristyles</i>	Forrest 157 (E): E00205201	KP713051	KP713173	KP713250
<i>Begonia</i> aff. <i>incarnata</i>	<i>Knesebeckia</i>	Twyford 587 (E)	KP713065	KP713090	KP713232
<i>Begonia bifurcata</i> 1	<i>Knesebeckia</i>	Tebbitt 782 (QCNE)	n/a	KX756306	KY070200
<i>Begonia bifurcata</i> 2	<i>Knesebeckia</i>	Moonlight 105 (E)	KX756296	KX756307	KY070201
<i>Begonia bifurcata</i> 3	<i>Knesebeckia</i>	Moonlight 117 (E)	KX756278	KX756308	KY070202
<i>Begonia bullatifolia</i> 1	<i>Knesebeckia</i>	Peng 21323 (HAST)	KP713073	KP713128	n/a
<i>Begonia bullatifolia</i> 2	<i>Knesebeckia</i>	Duruisseau s.n. (LBG)	KX756303	n/a	KY070224
<i>Begonia erythrocarpa</i>	<i>Knesebeckia</i>	Sarkinen 2058 (E)	KP713031	KP713140	n/a
<i>Begonia incarnata</i>	<i>Knesebeckia</i>	Peng 20869 (HAST)	KP713069	KP713076	n/a

Appendix (cont.).

Species	Section	Voucher specimen	Genbank voucher		
			<i>ndhA</i> intron	<i>ndhF-rpl32</i>	<i>Rpl32-trnL</i>
<i>Begonia ludwigii</i>	<i>Knesebeckia</i>	Peng 23333 (HAST)	KP712990	KP713112	n/a
<i>Begonia maynensis</i>	<i>Knesebeckia</i>	Peng s.n. (HAST)	KP713063	KP713141	n/a
<i>Begonia parcifolia</i>	<i>Knesebeckia</i>	Tebbitt 783 (QCNE)	KX756277	KX756317	KY070209
<i>Begonia piurensis</i>	<i>Knesebeckia</i>	Moonlight 111 (E)	KX756276	KX756318	KY070210
<i>Begonia santos-limae</i>	<i>Knesebeckia</i>	Peng 21320 (HAST)	KP713016	KP713126	n/a
<i>Begonia serotina</i>	<i>Knesebeckia</i>	Tebbitt 776 (QCNE)	KX756284	KX756319	KY070211
<i>Begonia</i> sp. A	<i>Knesebeckia</i>	Moonlight 156 (E)	KX756295	KX756322	KY070214
<i>Begonia</i> sp. B	<i>Knesebeckia</i>	Moonlight 159 (E)	KX756301	KX756321	KY070213
<i>Begonia foliosa</i>	<i>Lepsia</i>	Unknown s.n. (E) E19480286	KP713060	KP713176	KP713310
<i>Begonia elachista</i>	<i>Microtuberosa</i>	Moonlight 318 (E)	KX756285	KX756324	KY070216
<i>Begonia elachista</i>	<i>Microtuberosa</i>	Moonlight 318 (E)	KX756297	KX756324	KY070217
<i>Begonia oaxacana</i>	<i>Parietoplacentia</i>	no voucher	KX756280	KX756325	KY070218
<i>Begonia buddleiifolia</i>	<i>Pilderia</i>	Jara 2599 (E)	KX756286	KX756327	KY070220
<i>Begonia glandulifera</i>	<i>Pilderia</i>	Gardner 6608 (E)	KX756294	KX756328	KY070220
<i>Begonia mariannensis</i>	<i>Pilderia</i>	Duruiseau s.n. (LBG)	KX756299	KX756329	KY070221
<i>Begonia gracilis</i>	<i>Quadriperigonia</i>	Badcock 9 (E)	KP713004	KP713078	KP713260
<i>Begonia thyrsoides</i>	<i>Quadriperigonia</i>	Tebbitt 809 (E)	n/a	KX756320	KY070212
<i>Begonia rossmanniae</i> 1	<i>Rossmannia</i>	Scherberich 1095 (LBG)	KX756300	KX756330	KY070223
<i>Begonia rossmanniae</i> 2	<i>Rossmannia</i>	Moonlight 315 (E)	KX756302	n/a	KY070223
<i>Begonia holtonis</i>	<i>Ruizopavonia</i>	Forrest 152 (E): E00205231	KP713062	KP713175	KP713307
<i>Begonia meridensis</i>	<i>Ruizopavonia</i>	Forrest 151 (E): E00205112	KP713057	KP713132	KP713308
<i>Begonia integerrima</i>	<i>Solananthera</i>	Tebbitt 69 (BKL)	KP713000	KP713099	KP713242
<i>Begonia radicans</i>	<i>Solananthera</i>	GBG 009-089-95 (GBG)	JF756345	JF756429	JF756513
<i>Begonia solananthera</i>	<i>Solananthera</i>	GBG 021-070-04 (GBG)	KP712999	KP713098	KP713243
<i>Begonia fulvosetulosa</i>	<i>Trachelocarpus</i>	Sénéchal s.n. (LBG)	KX756279	KX756331	KY070225
<i>Begonia herbacea</i>	<i>Trachelocarpus</i>	Forrest 163 (E): E00205153	KP713015	KP713202	KY070225
<i>Begonia lanceolata</i> 1	<i>Trachelocarpus</i>	no voucher	KP713068	KP713101	KP713253
<i>Begonia lanceolata</i> 2	<i>Trachelocarpus</i>	Sénéchal s.n. (LBG)	KX756289	KX756332	KY07022
<i>Begonia cremnophila</i>	Unassigned	Tebbitt 753 (LPB)	KX756282	KX756309	KY070204
<i>Begonia urubambensis</i>	Unassigned	Moonlight 244 (E)	KX756298	KX756310	KY070204
<i>Begonia heydei</i>	<i>Urniformia</i>	Peng 22624 (HAST)	KP713030	KP713114	n/a
<i>Begonia imperialis</i>	<i>Weilbachia</i>	Forrest 187 (E)	KP713008	KP713088	KP713228
<i>Begonia purpusii</i>	<i>Weilbachia</i>	Tebbitt 70 (BKL)	KP713028	KP713087	KP713251