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AN INFRASPECIFIC TAXONOMIC REVISION OF *BEGONIA MICRANTHERA* (BEGONIACEAE)

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Two new infraspecific taxa of *Begonia micranthera* Griseb. are described. *Begonia micranthera* subsp. *albonervia* Tebbitt is described and illustrated as a new subspecies native to the Andes of southern Bolivia (Chuquisaca, Cochabamba and Santa Cruz Departments). *Begonia micranthera* subsp. *micranthera* var. *flava* Andrada & Bulacio is newly described from Argentina's Jujuy Province. *Begonia micranthera* var. *rhacophylla* Irmsch. is raised to subspecies and newly recorded from Bolivia. *Begonia micranthera* var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub. is recognised as *B. micranthera* subsp. *rhacophylla* var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub. The type collection of *Begonia micranthera* var. *foliosa* L.B.Sm. & B.G.Schub. is newly recognised as a hybrid between *B. micranthera* Griseb. subsp. *micranthera* and *B. micranthera* subsp. *rhacophylla* (Irmsch.) Tebbitt. *Begonia micranthera* var. *fimbriata* L.B.Sm. & B.G.Schub. is newly synonymised with *B. cinnabarina* Hook. *Begonia cinnabarina* is newly recognised from Argentina and is lectotypified. *Begonia micranthera* subsp. *micranthera* var. *nana* L.B.Sm. & B.G.Schub. is also lectotypified. A key, diagnoses and illustrations are provided for all the recognised infraspecific taxa of *Begonia micranthera*.

Keywords. Argentina, *Begonia* sect. *Eupetalum*, Bolivia.

Introduction

Begonia, with more than 1800 species (Hughes *et al.*, 2015), is one of the largest genera of angiosperms. The bulk of the species in this genus are narrow endemics, typically restricted to humid locations in tropical or subtropical regions (Tebbitt, 2005). *Begonia micranthera* Griseb., of *Begonia* sect. *Eupetalum*, is an atypical species, because it has a large distribution, is highly variable in its morphology, and occurs in both seasonally dry and perpetually humid locations. *Begonia micranthera* has been confused with *B. cinnabarina* Hook. in the past, sharing with that species a combination of an aerial stem arising from a tuber and asymmetric leaf blades, but differing most notably in flower colour. The tepals of *Begonia cinnabarina* are orange, whereas those of

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B. micranthera are never this colour but may be white to pink, or occasionally pale yellow. *Begonia micranthera* is widespread in the Andean regions of southern Bolivia (Smith & Schubert, 1945) and northern Argentina (Smith & Schubert, 1941; Instituto de Botánica Darwinion, no date), where it occurs from approximately 17°4′S (e.g. *Hawkes* et al. 6577) to 27°35′S (e.g. *Schickendantz* 168). Reflecting the highly variable nature of the species, Smith and Schubert (1941) recognise six varieties of *Begonia micranthera* in their account of the *Begonia* of Argentina, three of which they also list from neighbouring Tarija Province, Bolivia (Smith & Schubert, 1945). In a later publication, Smith and Wasshausen (1984) add one more variety from Argentina. The online *Begonia* account for the *Flora of Argentina* (Instituto de Botánica Darwinion, no date) similarly recognises these same seven varieties of *B. micranthera*.

Fieldwork conducted throughout the species' range found that the pattern of infraspecific variation is more complex than the existing infraspecific taxonomy indicates. For example, several more local variants of the species occur than have been formally described. Multiple correlated characters distinguish some of the named and unnamed variants of *Begonia micranthera*. Sometimes these variants occur as geographically isolated populations. At other times they co-occur in the same area, where they occupy distinct altitude ranges or microhabitats that may be physically separated by just a few metres. In at least these latter cases, reproductive isolating mechanisms appear to be present between the distinct variants. In almost all cases, however, the taxonomic boundaries of these variants are blurred in part of their ranges by the occurrence of plants with intermediate morphologies. Smith and Schubert (1941) previously acknowledged that there are no distinct boundaries between any of the morphological extremes represented by the six varieties that they recognise. Our studies indicate that the intermediate plants appear to represent in some cases hybrids and in others incomplete divergence of populations.

We have refrained from formally naming the majority of the undescribed variants because they have small distributions, differ from one another only in minor ways and are often very difficult to distinguish in the herbarium. Furthermore, the addition of large numbers of new infraspecific taxa would produce an unwieldy infraspecific taxonomy. Instead, we describe just two new infraspecific taxa, of which one is both particularly distinct and widespread, while the other has a unique chromosome count and is of considerable interest to horticulturalists because, uniquely for *Begonia micranthera*, its tepals are yellow, a colour that is rare in New World *Begonia* as a whole. Previous treatments (Smith & Schubert, 1941, 1945; Smith & Wasshausen, 1984; Instituto de Botánica Darwinion, no date) recognise the infraspecific variation within *Begonia micranthera* by designating varieties. In contrast, we recognise a combination of subspecies and varieties to more precisely reflect the assumed relationships and the degree of morphological differences between these taxa. Three subspecies are recognised herein. Of these, *Begonia micranthera* subsp. *albonervia* is newly described, while *B. micranthera* subsp. *rhacophylla* represents a new combination. *Begonia micranthera* var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub. is treated as a variety of *B. micranthera* subsp. *rhacophylla*. We recognise *Begonia micranthera* subsp.

micranthera as containing four named varieties: var. *micranthera*, var. *nana*, var. *venturii* and var. *flava*, the last of which is newly described. Two of the previously recognised varieties of *Begonia micranthera*, namely var. *fimbriata* and var. *foliosa*, are no longer recognised as such, as further discussed below.

Examination of the type of *Begonia micranthera* var. *fimbriata* (*West* 8413 [GH, MO, UC]) along with an additional collection (*Schreiter* 10886 [GH (2), LIL]) cited by Smith and Schubert (1941) in their original description showed that these specimens have the distinctive combination of velutinous hairs on their stems, leaves and peduncles, ovate leaf blades with crenately toothed margins, and orange perianth characteristic of *B. cinnabarina*. Accordingly, *Begonia micranthera* var. *fimbriata* is newly synonymised here with *B. cinnabarina*. *Begonia cinnabarina* is thus recognised as occurring in Argentina, as well as in Bolivia.

Smith and Schubert (1941) in their original description of *Begonia micranthera* var. *foliosa* state that this variety is distinguished by its branched stems, numerous leaves, firm leaf blades that are 5–7(–11) cm long, and 3- or 4-locular ovaries. They also state that the plants are typically dioecious and more variable as to locule number than other varieties. Examination of the herbarium material cited by Smith and Schubert (1941) and field observations at the locations where many of these specimens were collected indicates that the original description of *Begonia micranthera* var. *foliosa* includes two entities. One is composed of plants that are dioecious, with upright stems, and which have outer perianth segments that are more sepal-like than those of the inner whorl and have distinct acute apices and fimbriate margins. In the flower buds, the two outer perianth segments resemble forward-projecting horns. These plants also have 3 or 4 styles and 3 or 4 ovary locules and 4–6 female tepals (Fig. 1C–E). It was from this population, located near Yala in Argentina's Jujuy Province, that Smith and Schubert (1941) selected the type (*West* 6216) of *Begonia micranthera* var. *foliosa*. The other entity (i.e. Jujuy, Dep. Dr Manuel Belgrano, Lagunas de Yala, *C.A. O'Donell* 4662 [LIL]; Tucumán, Dep. Trancas, Camino a Lara, 26°22′16.8S, 65°40′16.3″W, 3245 m, 20 iv 2014, *N.B. Muruaga & A. Slanis* 1069 [LIL (2)]; Dep. Tafi, Cerro San José, [27°16′S, 65°58′W], 3200 m, 11 iii 1925, *S. Venturi* 3629 [B, LIL, US]), is morphologically similar but can be distinguished by its monoecious breeding system, less upright habit with more spreading branches, outer tepals that are more petaloid, and its female flowers that consistently have 5 tepals, 3 styles and 3-locular ovaries. We propose that the element that does not contain the type represents an unnamed variant of *Begonia micranthera* subsp. *micranthera*, while the type population of Smith and Schubert's *B. micranthera* var. *foliosa* represents a hybrid between this taxon and *B. micranthera* subsp. *rhacophylla*. Evidence of the hybrid nature of this taxon comes from multiple data sources. There is an unusually large amount of morphological variation in this population, and these plants combine characteristics usually restricted to one or other of the two subspecies (e.g. the female perianth segments vary from 4 to 6, while the locule and style numbers vary from 3 to 4). Furthermore, these putative hybrid plants exhibit irregularities during meiosis, as well as very low seed viability (only 5% of seed germinated under controlled conditions; Andrada, Páez & Tebbitt,

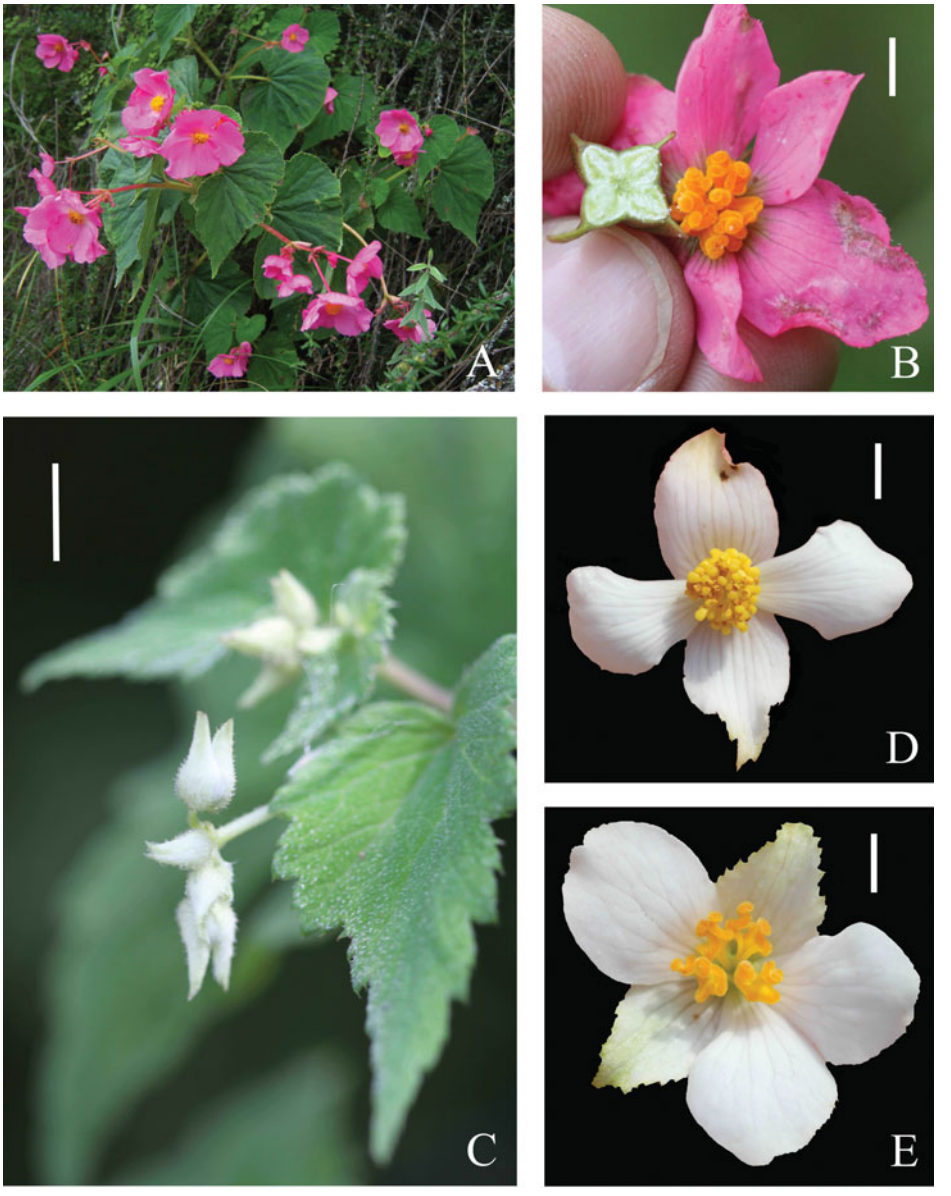

FIG. 1. *Begonia micranthera* subsp. *rhacophylla* var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub.: A, male plant; B, female flower and sectioned ovary with 4 locules; *Begonia micranthera* Griseb. subsp. *micranthera* × *Begonia micranthera* subsp. *rhacophylla* (Irmsch.) Tebbitt: C, male buds; D, male flower; E, female flower. Scale bars: B and C, 1 cm; D and E, 5 mm. (A, *A.R. Andrada s.n.* [LIL 611455]; B, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0010; C–E, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0014.)

unpublished). Photographs on the online *Flora of Argentina* (Instituto de Botánica Darwinion, no date) identified as *Begonia micranthera* var. *hieronymi* depict the undescribed variant of *B. micranthera* subsp. *micranthera*, while the photographs on that database identified as *B. micranthera* var. *fimbriata* represent the putative hybrid. Photographs on the online *Flora of Argentina* (Instituto de Botánica Darwinion, no date) identified as *Begonia micranthera* var. *foliosa* are *B. micranthera* subsp. *rhacophylla*.

In addition to the named infraspecific taxa that we recognise here, we would also like to draw attention to a distinct population of *Begonia micranthera* subsp. *micranthera* from the mountains above San Pedro de Colalao, in Argentina's Tucumán Province (Fig. 2). This population is of considerable interest because it has a unique breeding system within *Begonia*. The population consists of three kinds of individual, with plants being male, female or monoecious. Furthermore, the female plants often have inflorescences bearing two kinds of flower: those with 5 tepals, 3 styles and 3 locular ovaries, and those with 4 tepals (resembling the perianth of male flowers), 2 styles and 2 locular ovaries. Although we are not proposing to formally name this variant, we suggest that this population deserves further study because it may offer insights into the genetic basis for the different breeding systems found in *Begonia* as a whole. Provisional cytological data suggest that this population is not of hybrid origin because no significant meiotic irregularities were found during our cytological studies (Andrada, Páez & Tebbitt, unpublished).

Taxonomic Treatment

Key to the infraspecific taxa of Begonia micranthera

1a. Perianth obviously separated into 2 sepal-like and 3 or 4 petal-like segments; flower buds with the outer two sepal-like perianth segments resembling forward-projecting horns
11. B. micranthera subsp. micranthera × B. micranthera subsp. rhacophylla

1b. Perianth not obviously separated into sepal-like and petal-like segments, all perianth segments petaloid; flower buds with perianth segments not resembling horns ____ 2

2a. Plant dioecious; leaf blade coriaceous or succulent; ovary locules and styles usually 4, very rarely 3; tepals usually bright pink, occasionally white; female tepals usually 6, rarely 5 ____ 3

2b. Plant usually monoecious, very rarely dioecious; leaf blade usually slightly fleshy, occasionally subcoriaceous; ovary locules and styles 3; tepals usually white or pale pink, occasionally bright pink or pale yellow; female tepals 5 ____ 4

3a. Leaf blades coriaceous; margin typically lobed, rarely unlobed, lobes 1.5–3.5 cm deep; upper surface obviously pubescent
8. B. micranthera subsp. rhacophylla var. rhacophylla

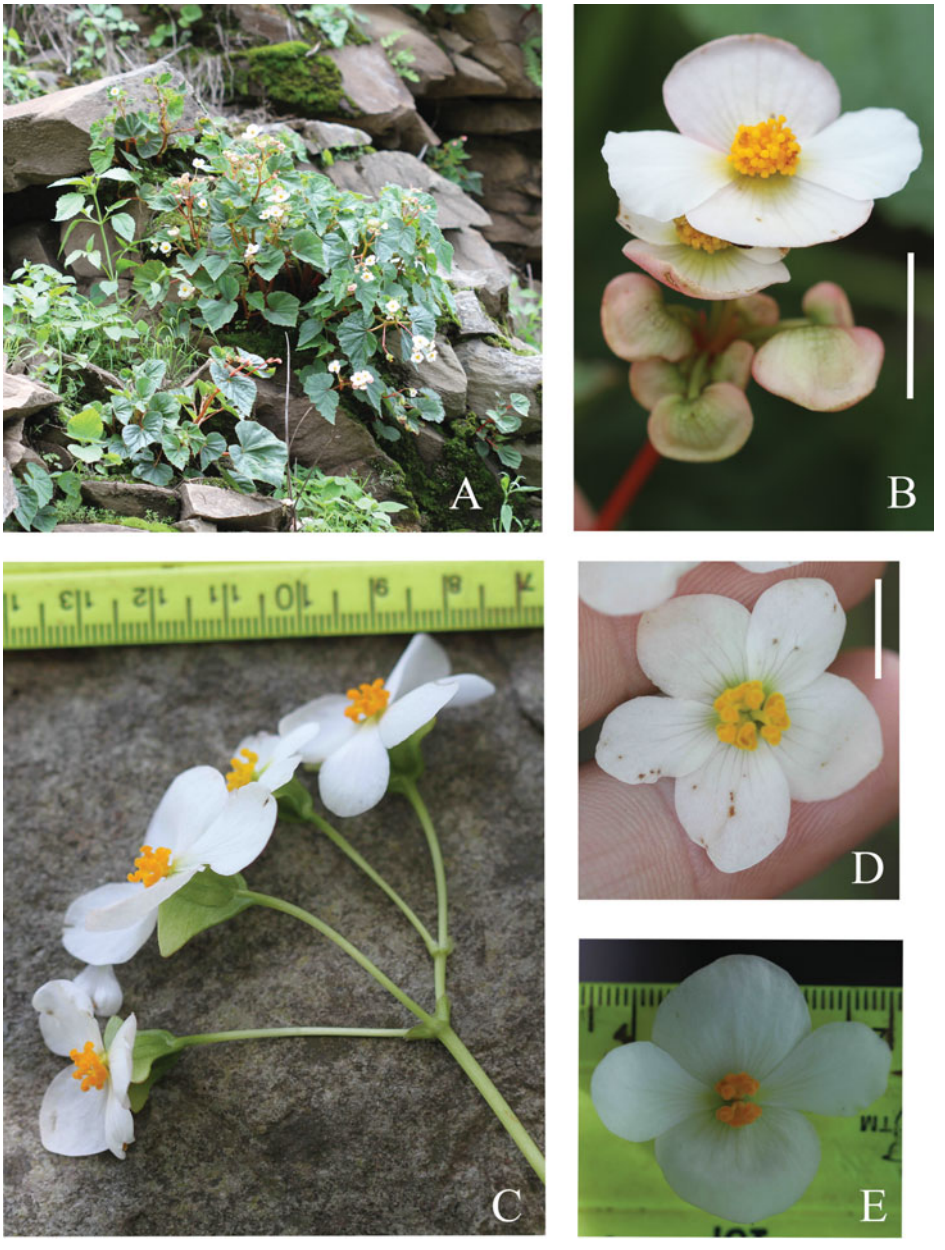

FIG. 2. Unnamed variant of *Begonia micranthera* Griseb. subsp. *micranthera*. A, Monoecious plant; B, inflorescence of male plant; C, inflorescence of female plant; D, close-up of female flower with 5 tepals, and 3 styles and ovary locules from female plant; E, close-up of female flower with 4 tepals, and 2 styles and ovary locules from female plant. All scale bars: 1 cm. (A–E, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0015.)

3b. Leaf blades succulent; margin unlobed to lobed, lobes when present to 1 cm deep; upper surface glabrous or with microscopic hairs that are not visible with the naked eye ____ **9. B. micranthera subsp. rhacophylla var. hieronymi**

4a. Leaf blade narrowly reniform to reniform-orbicular, upper surface usually matt green above with greyish white veins but occasionally concolorous matt green throughout; inflorescences 1 or 2, in upper leaf axils; flowers held high above top of foliage on conspicuous, erect peduncles, 10–45 cm long **10. B. micranthera subsp. albonervia**

4b. Leaf blade narrowly to broadly ovate, upper surface concolorous matt green throughout; inflorescences usually 3 to many, in upper leaf axils or along length of stem; flowers held to side or slightly above foliage on inconspicuous peduncles, 1.2–25 cm long ____ 5

5a. Tepals pale yellow ____ **4. B. micranthera subsp. micranthera var. flava**

5b. Tepals white or pink ____ 6

6a. Bracts usually entire rarely ciliate; leaf blades typically 2–4(-8) cm long; leaf blade under-surfaces usually purple, rarely green; margin crenate; tepals usually deep pink ____ **5. B. micranthera subsp. micranthera var. nana**

6b. Bracts usually ciliate to ciliate-dentate, occasionally entire; leaf blades typically 5–22 cm long; leaf blade under-surfaces usually green, rarely purple; margin usually denticulate, dentate or serrate, rarely crenate; tepals white to pale pink ____ 7

7a. Leaf blades narrowly ovate, upper surface of blade with patches of black hairs ____ **6. B. micranthera subsp. micranthera var. venturii**

7b. Leaf blades broadly ovate, upper surface of blade with an even cover of sparse white hairs ____ **3. B micranthera subsp. micranthera var. micranthera**

1. Begonia micranthera Griseb., Abh. Konigl. Ges. Wiss. Gottingen 19: 148 (1874). – Type: Argentina, Siambón, iii 1872, *P.G. Lorentz* 281 (lecto GOET!, designated Martín *et al.*, 2017); B drawings of specimen from GOET [2]!).

Perennial dioecious or monoecious tuberous herb, 2–100 cm tall. *Tuber* ± ellipsoid, 1.5–5 cm in diameter. *Stem* erect or suberect, glabrous to densely pubescent. *Stipules* ovate, triangular-ovate or lanceolate, 2–12 × 1–6 mm, margin entire to denticulate-fimbriate. *Leaves* few to many, alternate, basifixed; petiole 1–21.5 cm long, glabrous or with hairs as in stem; blade moderately succulent to coriaceous, asymmetric, ovate, narrowly reniform, reniform or reniform-orbicular, 2–22 × 2–20 cm, apex acuminate, abruptly acuminate or obtuse, base very shallowly obliquely cordate to obliquely cordate, margin crenate, denticulate, dentate or serrate, sometimes angular lobed or with regular or irregular ± triangular lobes, lobes to 3.5 cm deep, surfaces glabrous to pubescent, veins palmate, 7 or 8. *Inflorescences* 1 to many, axillary, erect

or ascending, a symmetric cyme, with up to 2 branches, bearing 1–15 flowers, bisexual or unisexual; peduncle 1.2–45 cm long, pubescence same as stem; pedicels of male flowers 0.9–3 cm long, glabrous; pedicels of female flowers 0.5–2.4 cm long, glabrous to densely pubescent; bracts elliptic, transversely elliptic, transversely obovate, ovate or broadly ovate, 0.6–1.4 × 0.5–1.55 cm, apex usually obtuse, occasionally acute, margin usually denticulate-fimbriate or ciliate-toothed, but occasionally entire. *Male flowers*: tepals 4, usually white to pink, occasionally pale yellow, outer two ovate to orbicular, ovate-elliptic to broadly elliptic, or obovate, 0.9–2.7 × 0.7–2.7 cm, apex obtuse to almost truncate, margin entire or fimbriate-denticulate, inner two suborbicular, elliptic or obovate, 0.9–2.7 × 0.6–1.8 cm, apex usually ± truncate and shallowly notched, occasionally obtuse, margin entire; stamens 40–140, attached along the length of a 1–1.5 mm tall torus, filaments 1–5 mm long, anthers obovoid to broadly obovoid, 0.75–1 mm long, dehiscing via unilateral slits, connectives not extended. *Female flowers*: bracteoles absent; tepals 4–6(–7), same colour as males, outer whorl suborbicular, broadly elliptic, elliptic to obovate, or occasionally ovate, inner whorl usually obovate to spatulate, occasionally broadly spatulate or elliptic, subequal, 0.8–2.8 × 0.4–2.5 cm, apex acute to obtuse, sometimes shallowly notched, margin of outer tepals entire or fimbriate-denticulate, margin of inner tepals entire; ovary body ellipsoid to broadly ellipsoid, 3–10 × 3–7 mm, glabrous to pubescent, subequally 3- or 4-winged, or rarely unequally 3- or 4-winged or wingless, wings when present triangular to deltoid, to 1.4 × 1 cm, (2-)3- or 4-locular; placentas axile, bifid; styles (2–)3 or 4, shortly fused at base, 2–5 mm long, bifid from about half their height, stigmatic papillae in a spiral band. *Fruiting pedicels* to 45 cm long. *Capsules* usually erect but frequently subnutant, body ellipsoid to almost spherical, to 1.5 × 1.2 cm, glabrous to sparsely pubescent, subequally to unequally 3- or 4-winged, rarely wingless, wings when present usually triangular, occasionally ligulate, to 2.7 cm long and 1.7 cm wide.

Phenology. Usually flowering December to March but also occasionally in November or April.

Distribution. Eastern Andes of Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca and Tarija) and Argentina (Jujuy, Salta, Tucumán and Catamarca) (see Fig. 3).

2. Begonia micranthera Griseb. subsp. **micranthera**. **Fig. 3.**

Usually monoecious herb, very rarely a population containing both unisexual and bisexual plants. *Stem* 2–50(–100) cm tall, unbranched to few branched, glabrous to pubescent. *Leaves* few to many, membranous to moderately succulent, asymmetric, ovate, margin lacking lobes, crenate, denticulate, dentate or serrate, upper surface green, glabrous to sparsely pubescent, lower surface paler green or purple, glabrous to pubescent, hairs usually denser along the main veins. *Inflorescences* solitary to many; peduncle 1.2–25 cm long. *Bract margins* entire, ciliate, ciliate-dentate or fimbriate. *Male flowers*: tepals usually white to pink, occasionally pale yellow, outer pair suborbicular, transversely ovate or obovate, 0.9–2.7 × 0.7–2.7 cm, inner pair suborbicular, elliptic or

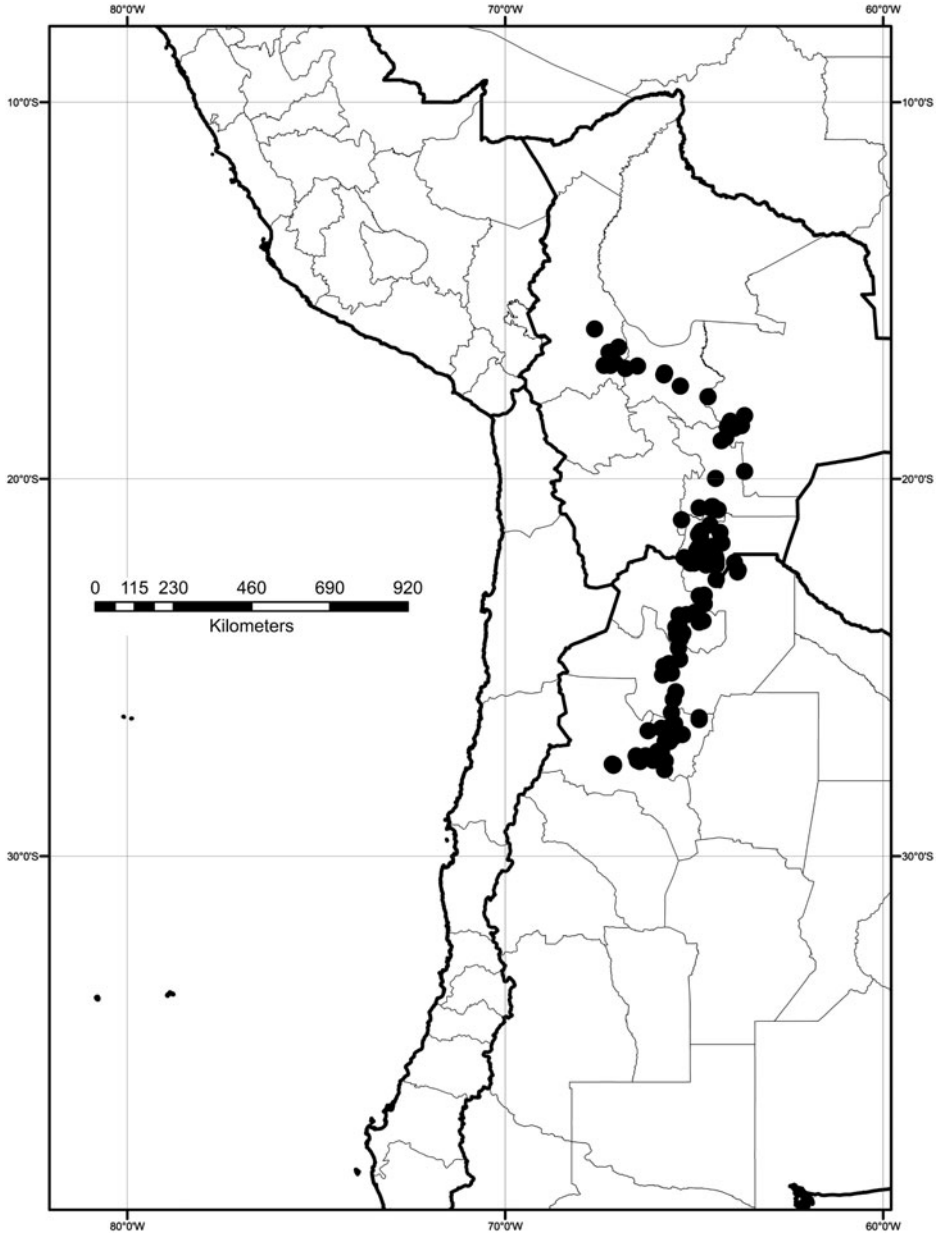

FIG. 3. Distribution of *Begonia micranthera* subsp. *micranthera* (circles).

obovate, 0.9–2.7 × 0.6–1.8 cm. *Female flowers*: tepals (4 or) 5, same colour as in males, outer two or three suborbicular, broadly elliptic, elliptic, obovate, or occasionally ovate, inner (two or) three usually obovate to spatulate, occasionally broadly spatulate, subequal, 0.8–1.8 × 0.4–1.8 cm; margins of outer tepals entire or ciliate, those of inner tepals entire; ovary subequally 3-winged, or rarely unequally 3-winged; 3-locular; styles 3.

Phenology. Flowering November to April, with peak bloom from January to March.

Distribution and habitat. Eastern Andes of Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca and Tarija) and Argentina (Jujuy, Salta, Tucumán and Catamarca) (see Fig. 3). Typically found in semideciduous tropical forest or Tucumano–Boliviano forest and neighbouring montane grassland, often on rocky slopes or ravines near streams, in semi- to deep shade. Usually growing at altitudes of 1000–3400 m but down to 440 m in some Argentinian populations (e.g. *Bailetti* 475).

3. Begonia micranthera Griseb. subsp. **micranthera** var. **micranthera**. **Fig. 4A–C.**

Usually monoecious, rarely dioecious. *Leaf blade* membranous or slightly to moderately succulent, ovate, 2.5–22 × 2–20 cm, glabrous to sparsely pubescent. *Bract margins* entire or ciliate to ciliate-dentate. *Female tepals* (4 or) 5, white to pink, margins of outer tepals usually entire, occasionally ciliate, those of inner tepals entire. *Chromosome number* n = 14 and 2n = 28.

Phenology. Flowering November to April, with peak bloom from January to March.

Distribution and habitat. Eastern Andes of Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca and Tarija) and Argentina (Jujuy, Salta, Tucumán and Catamarca). Typically found in semideciduous tropical forest or Tucumano–Boliviano forest and neighbouring montane grassland, often on rocky slopes or ravines near streams, in semi- to deep shade. Usually growing at altitudes of 1000–3400 m but down to 440 m in some Argentinian populations (e.g. *Bailetti* 475).

Representative specimens examined. Bolivia. **Cochabamba**: Prov. Ayopaya, near Independencia, [17°4′S, 66°49′W], *J.G. Hawkes* et al. 6577 (C); Prov. Carrasco, Carrasco, 17°32′S, 65°22′W, 2900 m, 11 ii 1987, *J.C. Solomon & M.H. Nee* 16053 (LPB, MO); Prov. Chapare, zona del Sillar km 92 a 1 km al Este de la carretera, 17°11′44″S, 65°47′24″W, *J. Terán, D. Soux, E. Rodríguez* 3230 (BOLV, MO). **La Paz**: Prov. Inquisivi, following the slopes E of Comunidad Micayani to the río Khokhoni ± to the junction with a fork flowing down from Comunidad Yamora, and following the río Khokhoni upstream 1 km from this point, c.4 km SE from Inquisivi, 16°55′S, 67°06′W, 14 i 1989, *M. Lewis* 35095 (G, MO, NY); Prov. Nor Yungas, carretera fundam. 3, c.35 km S of Caranavi toward Coroico, road parallel to río Coroico, [16°1′S, 67°38′W], 10 xi 1976, *C. Davidson* 4897 (MO); Prov. Sud Yungas, Puente Villa, [16°23′S, 87°38′W], 1400 m, ii 1946, *M. Cárdenas* 3594 (GH). **Santa Cruz**: Prov. Caballero, 17°49′S, 64°38′W, 2914 m, 16 i 2011, *M.C. Tebbitt* 735 (USZ); Prov. Florida, 18°31′S, 63°55′W, 2475 m, 16 i 2011, *M.C. Tebbitt* 733 (MO, USZ); Prov. Vallegrande, El Khacllu, 5 km E of Vallegrande, farallones encima de la Cañada de Arteaga, 18°28′S, 64°2.5′W, 2100 m, 28–29 xii 1993, *I.G. Vargas & M. Toledo* 3081 (NY, USZ). **Chuquisaca**: Prov. Azurduy, camino de Azurduy cerca a Cañadas, 19°59′S, 64°26′W, 2740 m, 13 i 2004, *H. Huaylla & I. Guachalla* 953 (MO); Prov. Belisario Boeto, 1 km

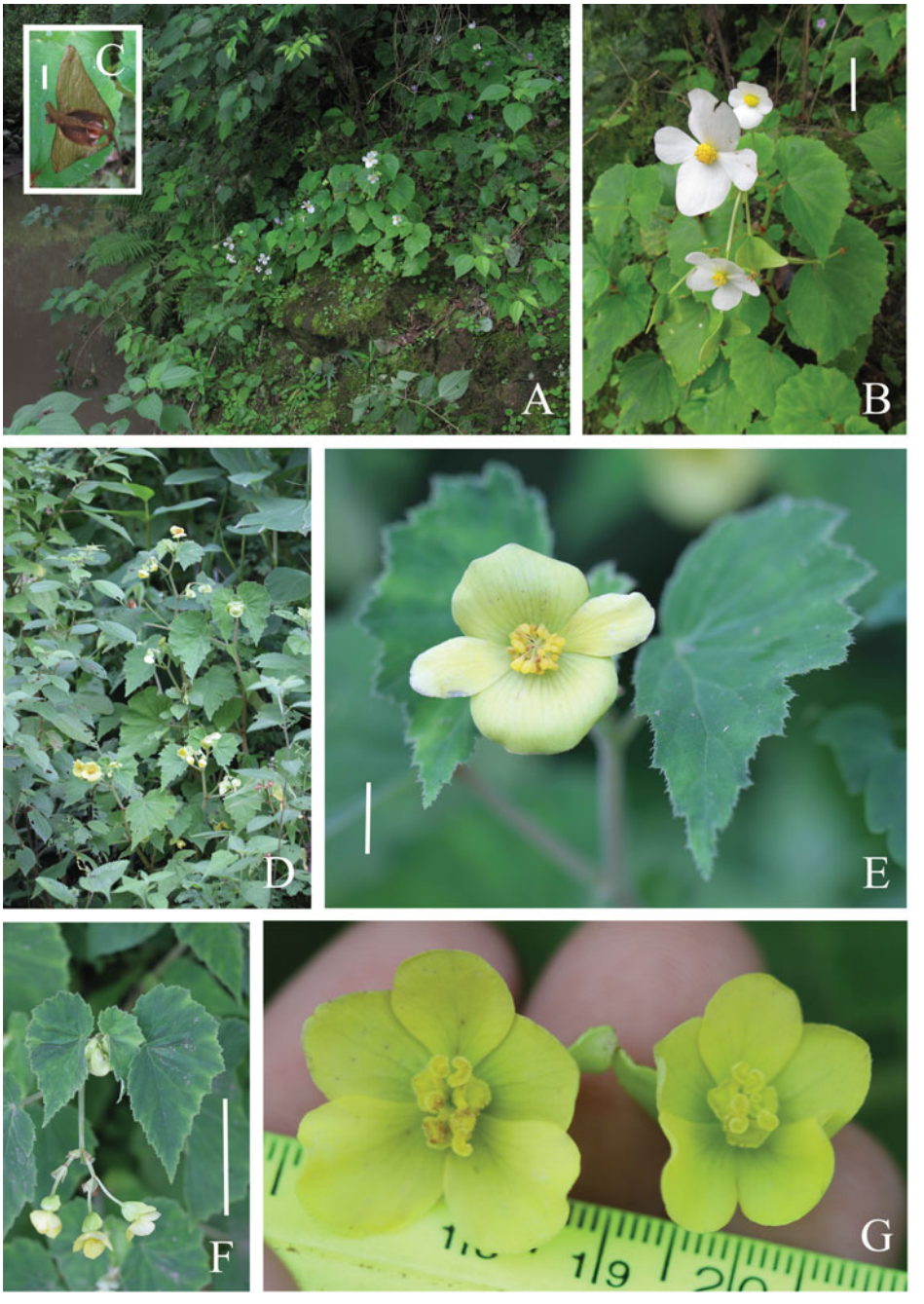

FIG. 4. *Begonia micranthera* Griseb. subsp. *micranthera* var. *micranthera*: A, plant in habitat; B, close-up of plant, showing inflorescence with male and female flowers; C, capsule. *Begonia micranthera* subsp. *micranthera* var. *flava* Andrada & Bulacio: D, habit; E, male flower; F, inflorescence bearing female flowers; G, female flowers. Scale bars: B and E, 1 cm; C and F, 5 mm. (A–C, *R. Andrada* 101; D–G, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0003.)

de Nuevo Mundo, 18°59′S, 64°17′W, 2231 m, 23 iii 2004, *J.R.I. Wood & H.H. Gutiérrez J.* 20521 (K); Prov. Oropeza, 29 km from Sucre on road to Ravelo, *J.G. Hawkes* et al. 4558 (C [2]); Prov. Sud Cinti, Puca Pampa, c.7.5 km de puesto ganadero, al SW, 20°44′S, 64°32′W, 2410 m, 12 ii 2004, *J. Gutiérrez R., A. Lliully, R. León, I. Guachalla, E. Portal* 580 (MO). **Tarija**: Prov. Arce, Municipio Padcaya, Reserva Nacional de Flora y Fauna Tariquía, bajando del campamento Potreros a la Guardianía de Alisos (SERNAP), 2450 m, 12 xi 2004, *M. Serrano, S. Churchill, J. Villalobos* et al. 5062 (MO); 7.4 km E of Emborozú on road to Bermejo, 22°16′S, 64°30′W, 1100 m, 24 iv 1983, *J.C. Solomon* 10063 (MO); Prov. Avilés, Cruzando el abra entre Pampa Redonda con dirección a Chocloca, [c.21°47′S, 64°30′W], 2250 m, 6 ii 1988, *M. Liberman, F. Pedrotti & R. Venanzoni* 2104 (US); Cuenca del río Camacho, quebrada margen derecho subiendo por el río Alisos, [c.21°54′S, 64°56′W], 2100 m, 19 xii 1987, *M. Liberman & S.G. Beck* 1507 (US); Bajando de Antigal hacia Alisos, 21°49′S, 64°53′W, 2090 m, 24 iv 2000, *S.G. Beck & N. Paniagua* 27263 (US); Prov. O'Connor, 10.8 km W of Narváez (Canaletas), 21°25′S, 64°19′W, 2200 m, 3 v 1983, *J.C. Solomon* 10443 (MO); Prov. Cercado, Rincón de la Victoria, 15 km SW of Tarija, [21°32′S, 64°50′W], 2150 m, 10 ii 1937, *J. West* 8313 (GH, MO, UC); Prov. Méndez, Cuesta de Sama, c.32 km NW of Tarija, on road to Villazón, 2800 m, 12 ii 1937, *J. West* 8330 (GH, MO, UC).

Argentina. **Catamarca**: Dep. Andalgalá, El Candado, [27°20′S, 66°17′W], 12 ii 1915, *P. Jörgensen* 1343 (B [2], GH, LIL, MO, US); Río Potrero, [27°27′S, 66°30′W], 1800 m, 10 ii 1949, *H. & O. Brücher s.n.* (S); Quebrada Muschaca, parte superior, [c.27°29′S, 66°26′W], ii 1876, *F. Schickendantz* 277 (B); Dep. Belén, Quebrada de Río Blanco-El Rincón, arriba de Granadillas, [c.27°34′S, 67°8′W], 2200 m, 26 i 1952, *H. Sleumer* 2469 (LIL, UC, US). **Salta**: Dep. Guachipas, Arroyo Querusillas, [c.25°38′S, 65°29′W], 1600–1800 m, 7 ii 1983, *L. Novara & R. Neumann* 3186 (MO); Estancia Pampa Grande, Cerro Cristal, 25°50′S, 65°33′W, 2300–2400 m, 20 iii 1966, *J.G. Hawkes, J.P. Hjerting & K. Rahn* 3649 (C), 3966 (C, K, MO); Dep. Gral. José de San Martin, 47 km de Piquirenda 7 km de El Chorrito, [c.22°13′S, 63°56′W], 25 xii 2001, *O. Morrone, N.B. Deginini & S.S. Aliscioni* 4095 (MO, SI); Dep. Gral. José de San Martin, Quebrada de la Zanja Honda, [c.22°25′S, 63°50′W], 600 m, 20 ii 1925, *R. Schreiter* 3589 (GH, LIL); Dep. Gral. José de San Martin, Cerro Tartagal, [c.22°28′S, 63°51′W], 17 iii 1948, *S.A. Pierotti* 7173 (LIL); Dep. Orán, Pucara, 2000 m, 3 iv 1945, *S.A. Pierotti* 1144 (NY, S, W); Ruta Prov. 19, 15 km del Puente Internacional Argentina–Bolivia camino a la Finca Yakulica, [c.22°40′S, 64°25′W], 14 xii 1998, *O. Morrone, L.M. Giussani, D. Fernández, & C. Guerrido* 3386 (MO); San Andrés, [c.23°06′S, 64°52′W], 1800 m, 8 ii 1945, *S.A. Pierotti* 308 (GH, NY, LIL); Dep. Rosario de Lerma, Quebrada del Toro, Ruta 51, Km 32.1, [24°53′S, 65°40′W], 1700–1780 m, 16 i 1988, *L.J. Novara* 7485 (G, S). **Tucumán**: Dep. J. B. Alberdi, along the ruta 9 from Juan B. Alberdi to Balcosna, 4 kms below Dique Escaba, [27°42′S, 65°47′W], 720 m, 16 ii 1993, *W. Till* 10251 (LIL, MO); Dep. Burruyacu, Cerro del Campo, 1500 m, 10 iv 1930, *S. Venturi* 10357 (B, MO); Dep. Chicligasta, Saladillo a El Bolsón, [27°14′S, 65°52′W], 2000 m, 5 iii 1949, *T. Meyer* 14846 (LIL); Dep. Lules, Quebrada de Lules, 750 m, 28 xi 1920, *S. Venturi* 1076 (GH); [26°50′S, 65°33′W], 500 m, i 1932, *M. Quiroga s.n.* (GH); 500 m, i 1932, *M. Quiroga* 14403 (GH); Dep. Tafi del Valle, Tafi, 2500 m, 20 ii 1924, *S. Venturi* 2897 (GH, MO); [Dep. Tafi], Siambón, Sierra de Tucumán, 9–18 i 1873, *P.G. Lorentz & L. Hieronymus* 1051 (B [2], F, GOET, NY, US, drawing of specimen in GOET B); Dep. Lules, Quebrada de Lules, 500 m, i 1932, *M. Quiroga s.n.* (LIL 14403); Quebrada de Lules, 550 m, 16 iv 1949, *Hueck s.n.* (LIL 386605); Dep. Tafí Viejo, Reserva Aguas Chiquitas, 26°36′28″S, 65°10′35″W, 612 m, 10 ii 2016, *A.R. Andrada* 101 (LIL); Reserva Aguas Chiquitas, 26°37′26″S, 65°10′29″W, 612 m, *A.R. Andrada s.n.* (LIL 615230); *A.R. Andrada s.n.* (LIL 615247); Tafí, Camino al Indio, 27°02′06″S, 65°39′65″W, 1169 m, *A.R. Andrada s.n.* (LIL 611167).

The nominate variety currently encompasses a great deal of variation and occurs in Bolivia and Argentina as indicated above. The type collection, however, was collected

from a population representing a low-elevation variant restricted to Tucumán Province, Argentina, that is distinguished in particular by its combination of leaf blades that are broadly ovate and distinctly membranous in the dried state.

4. Begonia micranthera subsp. **micranthera** var. **flava** Andrada & Bulacio. – Type: Argentina, Prov. Jujuy, Dep. Ledesma, Parque Nacional Calilegua, Ruta Provincial 83, Difunta, 23°41′10″S, 64°52′59″W, 1500 m, 11 i 2011, *E. Bulacio & H. Ayarde* 2431 (holo LIL!), **var. nov.**
Begonia micranthera subsp. *micranthera* var. *flava* Andrada & Bulacio is distinguished from other infraspecific taxa of *Begonia micranthera* Griseb. by its tepals pale yellow (versus white to pink), its combination of pubescent leaves and stems and 3-locular ovaries, and its unique chromosome number n = 13 and 2n = 26 (versus n = 14 and 2n = 28 in other *B. micranthera* taxa we sampled; Appendix 1). **Fig. 4D–G**.

Monoecious. *Leaf blade* slightly fleshy, ovate, 2.5–14 cm long, upper surface with a covering of short, soft, white hairs. *Bract margin* ciliate-dentate. *Female tepals* 5, pale yellow, margin of outer two tepals shortly ciliate, margin of inner three tepals entire.

Phenology. Flowering January to February.

Distribution and habitat. Endemic to the vicinity of Park Nacional Calilegua, Jujuy Province, Argentina, where it occurs in a narrow altitudinal strip between 1300 and 1500 m. Growing on earth banks among herbaceous vegetation on the Yungas forest edge.

Additional specimens examined. Argentina. **Jujuy**: Dep. Ledesma, Parque Nacional Calilegua, 15 km del Arroyo Aguas Negras, 23°38′S, 64°51′W, 1300 m, 25 ii 1997, *F.O. Zuloaga, O. Morrone, J.F. Pensiero* 6224 (MO); Dep. Ledesma, Camino a Valle Grande desde Ruta Nac. 34, km 27, 16 xii 1996, *F.O. Zuloaga* 2919 (MO); Dep. Ledesma, Camino a río Jordán, a 4 km de Abra de Cañas, 1200 m, 14 ii 1965, *P.R. Legname & A.R. Cuezzo* 5215 C (LIL); Valle Grande, 26 ii 1940, *A. Burkart & N.S. Troncoso* 11483 (SI, UC); Ruta provincial 83, Sevinguillar, 23°41′30″S, 64°52′44″W, 1450 m, 31 i 2010, *E. Bulacio & H. Ayarde* 2055 (LIL); Parque Nacional Calilegua, Ruta provincial 83, 10 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0002 (LIL). Parque Nacional Calilegua, Ruta provincial 83, 23°41′51″S, 64°52′26″W, 1320 m, 14 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0003 (LIL).

5. Begonia micranthera subsp. **micranthera** var. **nana** L.B.Sm. & B.G.Schub., Darwiniana 5: 94, pl. 6 (1941). – Type: Argentina, Prov. Jujuy, Volcán (Loma del Tambo), [c.23°36′S, 65°12′W], 2500 m, 22 ii 1924, *R. Schreiter* 2595 (lecto GH! [barcode 00068254], here designated; isolecto GH!, LIL [2]!). **Fig. 5A–C.**

Monoecious. *Leaf blade* slightly fleshy, ovate, 2–8 cm long, upper surface with a sparse covering of short, black hairs. *Bract margin* entire. *Female tepals* 5, deep pink, margins entire.

Phenology. Flowering January to February.

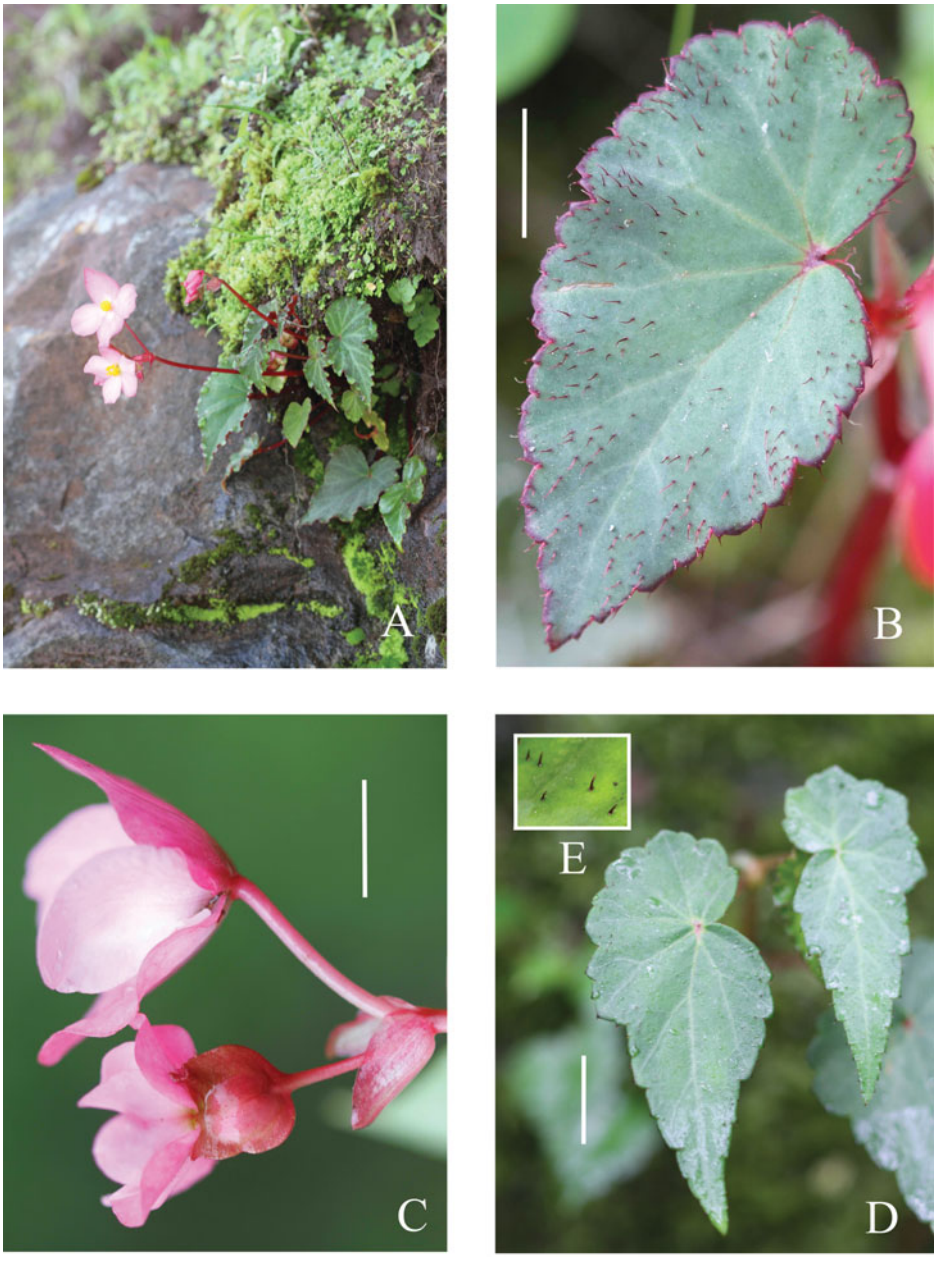

FIG. 5. *Begonia micranthera* Griseb. subsp. *micranthera* var. *nana* L.B.Sm. & B.G.Schub.: A, habit; B, leaf; C, inflorescence and bract. *Begonia micranthera* subsp. *micranthera* var. *venturii* L.B.Sm. & B.G.Schub.: D, leaf; E, close-up of hairs on leaf upper surface. All scale bars: 1 cm. (A–C, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0007; D and E, *A.R. Andrada s.n.* [LIL 610791 A, B].)

Distribution and habitat. Endemic to the mountains of north-western Argentina. This taxon is found in the eastern sector of the Cordillera Oriental, east of the Quebrada de Humahuaca, Jujuy Province, where it occurs from 2500 to 3500 m. Growing on open earth slopes, usually near streams.

Additional specimens examined. Argentina. **Jujuy**: Dep. Tumbaya, Est. Volcán, Mula Muerta, 3000 m, 15 i 1927, *L. Castillón 158* (LIL); Dep. Tilcara, Maimará (Hualchin), [23°37′S, 65°24′W], 28 i 1906, *E. Budin* 53 & 63 (GH, LIL); Río Est. Vieja, cerca de Abra Mayo, 2500 m, 21 iii 1952, *E. Petersen & J.P. Hjerting* 54 (LIL). **Salta**: Dep. Orán, Sierra de Zenta, Yungas, Entre Rios, [c.23°19′S, 64°44′W], 24 iv 1998, *A. Schinini, C. Saravia Toledo & R. Neumann* 34794 (GH); Sierra de Zenta, 3500 m, *E. Budin s.n.* (LIL 14401); Dep. Ledesma, Cerro Hermosos, 2840 m, 11 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0006 (LIL); Dep. Ledesma, Camino a Co. Amarillo 23°35′49″S, 64°54′05″W, 2840 m, 12 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0007 (LIL).

Smith and Schubert (1941) cite numerous collections for this variety, but we consider that those they list from west and south of Jujuy Province's Rio Grande do not belong within this variety but rather represent stunted examples of a mixture of other variants. The specimens that we consider to match the type of *Begonia micranthera* var. *nana* all share with this collection not only their short stature but also leaf margins that are distinctly crenate-toothed and flowers with deep pink tepals. This taxon also only occurs at relatively high elevations, between 2500 and 3500 m.

Smith and Schubert (1941) cite the type of this and other taxa as being located in G, by which they are referring to Harvard University's Gray Herbarium rather than the herbarium of the Conservatoire et Jardin botaniques de la Ville de Genève.

6. Begonia micranthera subsp. **micranthera** var. **venturii** L.B.Sm. & B.G.Schub., Darwiniana 5: 97, pl. 8 (1941). – Type: Argentina, Tucumán, Dep. Tafi, Cerro de Taficillo, barranco en el alisal, 1800 m, 10 iii 1930, *S. Venturi* 10299 (holo GH!). **Fig. 5D,E.**

Monoecious. *Leaf blade* subsucculent, narrowly ovate, 5–8 × 2.5–5 cm, upper surface with a few scattered black hairs. *Bract margins* fimbriate. *Female tepals* 5, white or pink, margins entire. *Chromosome number* n = 14, 2n = 28.

Phenology. Flowering January to March.

Distribution and habitat. A narrow endemic of the Cumbre de Taficillo (Sierra de San Javier), in Argentina's Tucumán Province. Growing on shaded, rocky cliffs at an altitude of 1800–2300 m.

Representative specimens examined. Argentina. **Jujuy**: Dep. Dr. Manuel Belgrano, trail from Rio Yala to laguna near Smythe Hacienda, 16 km W of Yala, 1950 m, 8 iii 1936, *J. West* 6244 (GH, MO [2], UC). **Tucumán**: Dep. Chicligasta, El Bolsón, 2100 m, 9 iii 1949, *T. Meyer* 14834 (LIL); El saladillo a El Bolsón, 5 iii 1949, *T. Meyer* 14929 (LIL); Dep. Tafi Viejo, Cumbre de Taficillo, peñas de una quebrada, 1800 m, 4 iii 1928, *S. Venturi* 5897 (B, CAS, LIL, US); Dep. Tafi del Valle, El Rincón, 26°57′S, 65°46′W, *A. Grau* 03–024 (LIL) El Rincón, 02 iii 2010, *A.R. Andrada s.n.* (LIL 610791 A, B).

7. Begonia micranthera subsp. **rhacophylla** (Irmsch.) Tebbitt, **stat. nov. Fig. 6.**

Begonia hieronymi Lindau var. *rhacophylla* Irmsch., Bot. Jahrb. Syst. 74: 619 (1949). – Type: Argentina, Prov. Jujuy, Dep. Tumbaya, Volcan, Cerro Abra del Paraguay, bajo una peña, 2300 m, 14 ii 1927, *S. Venturi* 4948b (holo US!; iso B!; drawing of holo B!; LIL!).

Begonia micranthera Griseb. var. *rhacophylla* (Irmsch.) L.B.Sm. & D.C.Wassh., Phytologia 54: 467 (1984).

Usually dioecious or very rarely monoecious herb. *Stem* 25–100 cm tall, usually unbranched, rarely unbranched, densely pubescent. *Leaves* usually many, rarely few; blade coriaceous or succulent, asymmetric, lowermost leaf sometimes elliptic, other leaves ovate to broadly ovate, 5–10 × 4–7 cm, margin unlobed or with regular or irregular ± triangular lobes, lobes when present 1.5–3.5 cm deep, dentate or serrate, upper surface green, glabrous or pubescent, lower surfaces slightly paler green, glabrous or pubescent. *Inflorescences* many; peduncle 5.5–6.5 cm long. *Male flowers*: tepals 4–6, usually bright pink, occasionally white, outer two suborbicular, 1.5–1.6 × 1.6–2 cm, inner two obovate, 1.5–1.7 × 1.4–1.6 cm. *Female flowers*: tepals 6, same colour as in males, 0.8–1.8 × 0.4–1.8 cm, outer two or three suborbicular, inner two or three usually obovate, occasionally elliptic; ovary usually subequally 4-winged, or occasionally both subequally 4- and 3-winged on the same individual, or rarely both unequally 4- and 3-winged on the same individual, or occasionally wingless; usually 4-locular, occasionally with both 4- and 3-locular ovaries on the same individual; styles usually 4, occasionally bearing ovaries with both 4 and 3 styles on the same individual.

Phenology. Flowering December to March.

Distribution. Eastern Andes of Bolivia (Santa Cruz, Chuquisaca and Tarija) and Argentina (Jujuy, Salta and Tucumán) (see Fig. 6).

8. Begonia micranthera subsp. **rhacophylla** (Irmsch.) Tebbitt var. **rhacophylla. Figs 6, 7.**

Usually dioecious or very rarely monoecious herb. *Leaf blade* coriaceous, asymmetric, lowermost leaf sometimes elliptic, other leaves ovate, 5–7 × 4–6 cm, margin usually with regular or irregular ± triangular lobes, occasionally unlobed, lobes when present 1.5–3.5 cm deep, serrate, upper surface green, pubescent, lower surface slightly paler green, pubescent. *Male flowers*: tepals 4, usually bright pink, occasionally white. *Female flowers*: tepals 6, usually bright pink, occasionally white. *Capsule* usually subequally 4-winged, or occasionally both subequally 4- and 3-winged on the same individual, or rarely both unequally 4- and 3-winged on the same individual, or occasionally wingless; usually 4-locular, occasionally with both 4- and 3-locular ovaries on the same individual; styles usually 4, occasionally bearing ovaries with both 4 and 3 styles on the same individual. *Chromosome number* n = 14, 2n = 28.

Phenology. Flowering December to March.

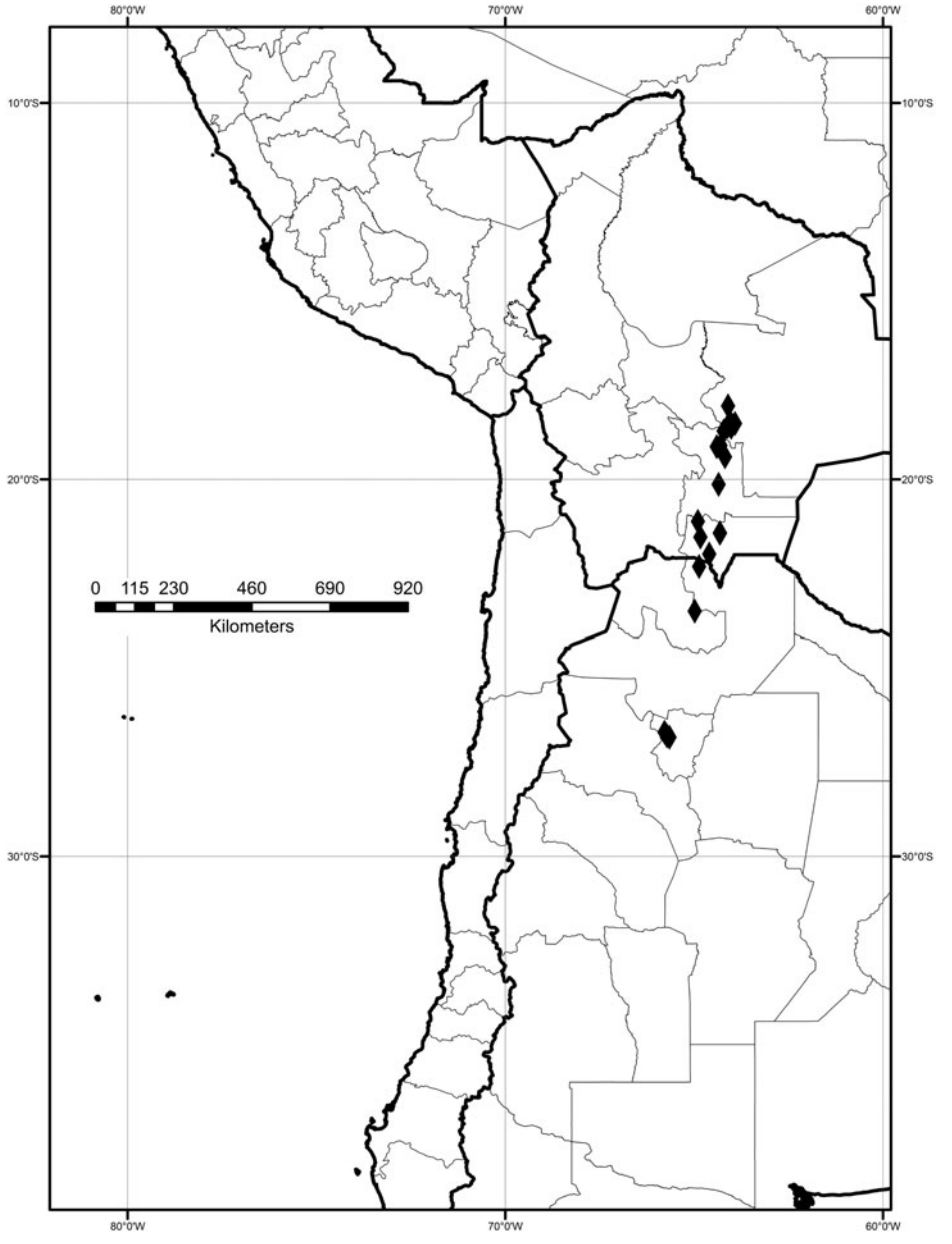

FIG. 6. Distribution of *Begonia micranthera* subsp. *rhacophylla* (diamonds).

FIG. 7. *Begonia micranthera* Griseb. subsp. *rhacophylla* (Irmsch.) Tebbitt var. *rhacophylla*. A, Habit, male plant, Bolivia; B, habit, female plant, Bolivia; C, habit, female plant, Argentina; D, leaf, Argentina; E, male flower, Argentina; F, female flower, Argentina. Scale bars: D and E, 1 cm; F, 5 mm. (A, *M.C. Tebbitt* 733; B, *M.C. Tebbitt* 729; C, D and F, *R. Andrada s.n.* [LIL 611459]; E, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0013.)

Distribution and habitat. Eastern Andes of Bolivia (Santa Cruz, Chuquisaca and Tarija) and Argentina (Jujuy and Salta) (see Fig. 6). *Begonia micranthera* subsp. *rhacophylla* var. *rhacophylla* occurs in and on the margins of Tucumano–Boliviano forest, where it is commonly found on wet seeps on and at the base of cliffs, at an altitude of 1400–2700 m. This taxon often occupies sites that are both wetter and less likely to dry up during the growing season than those of all other infraspecific taxa of *Begonia micranthera*. However, it does occasionally occur in relatively dry situations on open montane pasture, but in these situations the plants are often somewhat stunted. *Begonia micranthera* subsp. *rhacophylla* grows in both shade and full sun but is typically found in open sunny areas, unlike subsp. *micranthera* and subsp. *albonervia*, which usually prefer shaded localities.

Additional specimens examined. Bolivia. **Chuquisaca**: Prov. Azurduy, La Angostura, c.15 km de Azurduy hacia el cañon de la Angostura, 20°8′S, 64°21′W, 2500 m, 11 i 2004, *H. Huaylla & I. Guachalla* 672 (MO); Prov. B. Boeto, Comunidad Ovejeros, 4 km al NE de la localidad de Villa Serrano, 19°6′S, 64°18′W, *M. Serrano* 770 (HSB); Prov. Tomina 19°08′S, 64°24′W, [between Tomina and Villa Serrano], 2692 m, 5 i 2013, *M.C. Tebbitt* 742 (USZ); Prov. Tomina, Padilla 26 km hacia Monteagudo, [c.19°24′S, 64°11′W], 2600 m, 8 iii 1981, *S.G. Beck* 6326 (US). **Santa Cruz**: Prov. Vallegrande, 18°31′S, 63°54′W, [south of Tierras Nuevas], 2446 m, 14 i 2012, *M.C. Tebbitt* 729 (USZ); north west of Piraymiri, 18°32′S, 64°02′W, 2292 m, 10 i 2012, *M.C. Tebbitt* 715 (USZ); Camino entre Vallegrande y Postrervalle. 18°33′S, 64°00′W – 18°31′S, 63°55′W, 2632–2645 m, 3 ii 2009, *L.P. Arroyo, S. Carreño, Y. Inturias, C. Roth & J. Dávalos* 4474 (MO, USZ); north west of Piraymiri, 18°34′S, 64°03′W, 2276 m, 13 i 2012, *M.C. Tebbitt* 726 (USZ); Quebrada honda, c.10–15 km sobre el camino hacia La Higuera, 1 km de la carretera, siguiendo el curso del río, 18°34′S, 64°06′W, 2342 m, 14 iii 2003, *J.M. Mendoza & R.N. Ledezma* 492 (K, USZ); 19 km from Vallegrande on road to Pucará, 18°36′S, 64°07′W, 2650 m, 1 iii 1980, *J.G. Hawkes, J.P. Hjerting & I. Aviles* 6511 (C), 6514 (C [2]); 18°36′S, 64°07′W, 2843 m, 12 iii 2011, *L.P. Arroyo, G.A. Parada, M. Betancur & M. Huanca* 5487 (MO, USZ); north west of Piraymiri, 18°37′S, 64°01′W, 2080 m, 6 i 2012, *M.C. Tebbitt* 703 (USZ); Cala culo c.26 km S of Vallegrande camino a Khasa Monte, 18°38′S, 64°02′W, 2450 m, 27 ii 2002, *L. Arroyo, S. Churchill, D. Arroyo, & C. Torrico* 1873 (MO, USZ); Pucará, 18°43′S, 64°13′W, 2385 m, 3 xii 2011, *G.A. Parada, Y. Inturias & M. Betancur* 3995 (USZ); Tramo entre El Zapallar-Pujio, ubicado a 15 km al S de Pucará (línea recta), 18°54′S, 64°10′W, 2000 m, 29 xii 1990, *I.G. Vargas* 884 (NY, USZ). **Tarija**: Prov. Méndez, 20 km from Iscayachi on road to Tarija, [21°27′S, 64°52′W], 3100 m, 11 iii 1971, *J.G. Hawkes, J.P. Hjerting, P.J. Cribb, & Z. Huamán* 4658 (C [3]); Rincón de la Victoria, [21°32′S, 64°50′W], 14 ii 1960, *T. Meyer & P. Legname* 21259 (LIL, US [2]); Prov. O'Connor, Municipio Entre Ríos, Quebrada Canaletas, 21°26′S, 64°19′W, 2124 m, 16 i 2008, *E. Portal, E. Cervantes & J. Villalobos 413* (MO).

Argentina. **Jujuy**: Dep. Valle Grande, Altos de Calilegua, 23°30′S, 64°59′W, 2600 m, 17 ii 1995, *N.B. Deginani, A.L. Cialdella & E. Bortiri* 934 (MO); Valle Grande, de río Jordán a Duraznillo (Cno. a Alto Calilegua [23°46′S, 64°46′W]), 29 xii 1977, *R. Kiesling, E. Ulibarry & A.G. López* 1630 (NY); Dep. Ledesma, Cerro Hermoso, 26°36′24″S, 64°54′15″W, 2833 m, 11 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0011 (LIL); 0012 (LIL); Dep. Ledesma, Camino a Co. Amarillo, 23°35′48″S, 64°54′09″W, 2833 m, 12 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0013 (LIL). **Salta**: Dep. Rosario de Lerma, río Manzano, 2000 m, 4 ii 1941, *T. Meyer s.n.* (LIL 79834); Dep. Santa Victoria, Santa Victoria, 2385 m, 28 i 1943, *T. Meyer* 4601 (LIL), 27 i 1945, *T. Meyer* 5025 (LIL); Santa Victoria, ente Lizonte y Rodeo Pampa, 3800 m, 04 ii 1943, *T. Meyer* 5027 (LIL); Santa Victoria – Cañani, [22°19′S, 64°52″W], 24 i 1983, *E.M. Zardini, M.L. Pochettino, J.A. Hurrell, C. Ludica & D. Ramadori* 1763 (MO);

Poscaya-Alrededores, 22°27′42″S, 65°05′39″W, 3300 m, 24 i 2010, *A.C. Slanis, A.M. Kortsarz, A. Grau, K. Lázaro & F. Choin* 3081 (LIL [2]); Cañani, [26°44′S, 65°36′W], 25 i 1983, *E.M. Zardini, M.L. Pochettino, J.A. Hurrell, C. Iudica & D. Ramadori* 1806 (MO); camino Nazareno-Poscaya, 2 km de Nazareno, 3300 m, 24 i 2010, *A.C. Slanis, A.M. Kortsarz, A.Grau, K. Lázaro & F. Choin* 3121 (LIL); Rincon de la Victoria, 2200 m, 27 i 1953, *T. Meyer* 17494 (LIL); Rincon de la Victoria, 14 ii 1960, *T. Meyer, R. Cuezzo & R. Legname* 21237 (LIL); Cuesta de Mesón, 2600–2700 m, 12 ii 1953, *H. Sleumer* 3976 (LIL); Los Toldos, entre Nogalar y El Mesón, 1700 m, 19 ii 1960, *T. Meyer, R. Cuezzo & R. Legname* 20536 (LIL).

Begonia micranthera subsp. *rhacophylla* was previously recognised at the rank of variety. Irmscher (1949) originally described the taxon as a variety of *Begonia hieronymi* Lindau, whereas Smith and Wasshausen (1984) treated it as a variety of *B. micranthera*. *Begonia micranthera* subsp. *rhacophylla* is distinguished by its dioecious breeding system, coriaceous leaf blades, usually 4 ovary locules and styles (occasionally 3), tepals that are usually bright pink (occasionally white), and female flowers with 6 (versus 5) tepals. Irmscher (1949) described his *Begonia hieronymi* var. *rhacophylla* as a narrow endemic of the Cerro Abra del Paraguay in Jujuy Province, Argentina. In contrast, we consider *Begonia micranthera* subsp. *rhacophylla* as occurring in Bolivia as well as Argentina. In fact, the taxon is widespread, being found along the eastern Andes for a distance of about 900 km.

A hybrid population between *Begonia micranthera* subsp. *rhacophylla* and *B. micranthera* subsp. *micranthera* was seen along a 20-km stretch of the Cuesta del Obispo (Route Provincial 33) in Salta Province, Argentina (Fig. 8A–C). Plants along this road were highly variable in their morphology but at the same time also showed a rough morphological cline, whereby at lower elevations they were morphologically similar to *Begonia micranthera* subsp. *micranthera* and at higher elevations morphologically similar to *B. micranthera* subsp. *rhacophylla*. At lower elevations, plants had subcoreacous leaf blades, either 3 or 4 styles and ovary locules, white to pale pink flowers, and female flowers with 5 tepals, and the outermost male and female tepals had fimbriate margins. At higher elevations along this road, the population included a large proportion of plants with thicker leaf blades, tepals of a deeper pink colour, up to 7 female tepals (a number not otherwise found in *Begonia micranthera*), and 4-locular ovaries and 4 styles. In the eastern part of the range of *Begonia micranthera* subsp. *rhacophylla* var. *rhacophylla* in Bolivia's Santa Cruz Department, a limited number of intermediate specimens (e.g. *Tebbitt* 715 and *Tebbitt* 732) also occur between it and *B. micranthera* subsp. *micranthera* and may similarly represent hybrids.

The online database for the Flora Argentina (Instituto de Botánica Darwinion, no date) includes several photographs that represent *Begonia micranthera* subsp. *rhacophylla* but which are misidentified as *B. micranthera* var. *foliosa*.

9. Begonia micranthera subsp. **rhacophylla** var. **hieronymi** (Lindau) L.B.Sm. & B.G.Schub. **Fig. 1A,B.**

Begonia hieronymi Lindau, Bot. Jahrb. Syst. 19 (Beibl. 18): 14 (1894).

FIG. 8. *Begonia micranthera* hybrids. *Begonia micranthera* Griseb. subsp. *micranthera* × *B. micranthera* subsp. *rhacophylla* (Irmsch.) Tebbitt, Cuesta de Obispo, Salta, Argentina: A, low-elevation plant; B, mid-elevation plant; C, high-elevation plant. *Begonia micranthera* Griseb. subsp. *albonervia* Tebbitt: D, habit. Scale bars: A–C, 1 cm, D, 10 cm. (A–C, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0016; D, *M.C. Tebbitt* 763.)

Begonia micranthera var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub., Darwiniana 5: 96, pl. 7, (1941). – Type: Argentina, Tucumán, La Ciénaga, 10–17 i 1874, *P.G. Lorentz & G.H.E.W. Hieronymus* 644 (lecto, designated Martín *et al.*, 2017: B 10 0186668!; isolecto B [3]!, CORD!, GOET!).

Begonia coriacea A.DC. sensu Griseb., Abh. Kgl. Ges. Wiss. Goett. XXIV: 136 (1879).

Usually dioecious, rarely monoecious herb. *Leaf blade* succulent, asymmetric, broadly ovate, 6–10 × 4–7 cm, lacking lobes or with triangular lobes to 1 cm deep, margin

serrate, upper surface moderately covered with short white hairs barely visible to the naked eye or glabrous in plants growing in sunny situations. *Male tepals* 4–6, bright pink. *Female tepals* 5 or 6, bright pink. *Capsule* usually 4-locular with 4 styles and 4 short ± subequal wings, occasionally 3-locular with 3 styles and 3 short subequal wings, or rarely with both 4- and 3-locular ovaries on the same individual.

Phenology. Flowering December to February.

Distribution and habitat. A narrow endemic of Tafi del Valle Department, Tucumán Province, Argentina, that grows on rocky humid slopes in montane grassland from 2000 to 3500 m. *Begonia micranthera* subsp. *rhacophylla* var. *hieronymi* occurs approximately 350 km to the south of the known distribution range of subsp. *rhacophylla* var. *rhacophylla*.

Representative specimens examined. ARGENTINA. **Tucumán**: Dep. Tafi del Valle, La Ciénaga, playa del arroyo cerca de la casa grande, 2500 m, 27 i 1950, *H. Sleumer* 269 (LIL); La Ciénaga, 12 xii 1888, *M. Lillo s.n.* (LIL 14315); La Ciénaga, 2500 m, 19 xii 1888, *M. Lillo* 1198 B (LIL); La Ciénaga, 13 iv 1901, *M. Lillo* 2752 (LIL); La Ciénaga, 2500 m, 13 ii 1905, *M. Lillo* 3998 (LIL); La Ciénaga, [26°44′S, 65°36′W], 14 ii 1905, *M. Lillo* 4027 (GH, LIL); La Ciénegas, 10–17 i 1874, *G.H.E.W. Hieronymus & P.G. Lorentz* 724 (B [2], GOET); Arroyo antes de la Bolsa, 2591 m, i 2003, *A. Grau* 03–022/023 (LIL); Camino a Amaicha del Valle, cerca del arroyo, 26°48′31″S, 65°43′30″W, 2542 m, 28 ii 2011, *A.R. Andrada s.n.* (LIL 611455); Camino a Amaycha, 26°42′47″S, 65°47′48″W, 2927 m, 15 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0010 (LIL).

Begonia micranthera var. *hieronymi* (Lindau) L.B.Sm. & B.G.Schub. is newly recognised as *B. micranthera* subsp. *rhacophylla* var. *hieronymi*. In Lindau's original description of *Begonia hieronymi* (1894), this taxon was described as having 3-locular ovaries and 4 branched styles. Examination of the herbarium material cited by Lindau, however, found that they have 4-locular ovaries with 4 styles, and that each style is bifid. Observation of living material from the type location and its vicinity (see Fig. 1A,B), indicates that the majority of these populations are composed of plants with 4-locular ovaries and 4 styles, but that a few populations are composed of plants with 3-locular ovaries and 3-styles. Furthermore, some individuals have female flowers with 5 tepals, whereas others have 6 tepals. These populations of var. *hieronymi* uniquely share with *Begonia micranthera* subsp. *rhacophylla* var. *rhacophylla* a dioecious breeding system, bright pink tepals, 6 female tepals, 4-locular ovaries and 4 styles, and for this reason are recognised here as belonging to subsp. *rhacophylla*.

Smith and Schubert (1941) cite the collection *Burkart & Troncoso* 11483 (SI, UC) as being *Begonia micranthera* var. *hieronymi*, but our studies show it to be the newly recognised *B. micranthera* subsp. *micranthera* var. *flava*.

10. Begonia micranthera subsp. **albonervia** Tebbitt. – Type: Bolivia, Dep. Santa Cruz. Prov. Florida, Bella Vista bosque Chiquitano, sendero ecológico 'El Chorro del El Fraile' sobre la orilla del río, 18°18′S, 63°40′W, 1210 m, 13 xii 2007, *D. Villarroel, N. Vargas, N. Vega, G. Cordova, O. Apaza & A. Yanana* 1687 (holo MO!, iso USZ!), **subsp. nov.**

Begonia micranthera subsp. *albonervia* Tebbitt is distinguished from other infraspecific taxa of *Begonia micranthera* Griseb. by its narrowly reniform to reniform-orbicular leaf blades (versus leaf blades narrowly to broadly ovate, or elliptic), leaf blade upper surface usually with conspicuous greyish white veins (versus concolorous green), and inflorescences held on conspicuous, 10–45 cm long, erect peduncles (versus peduncles less conspicuous, because usually ascending and [1–]6–10[–25] cm long). **Figs 8D, 9, 10**.

Monoecious herb. *Stem* 15–40 cm tall, unbranched, glabrous. *Leaves* typically 3–5; blade slightly succulent, never coriaceous, subsymmetric, narrowly reniform, reniform or reniform-orbicular, 5–11 × 5–11 cm, margin shortly triangular–lobed, dentate, upper surface usually matt green above with greyish white veins but occasionally concolorous matt green throughout, sparsely to moderately pubescent, lower surface concolorous green or with green veins and reddish tinged intervenal lamina, sparsely to moderately pubescent along veins, and intervenal regions glabrous. *Inflorescences* solitary to many; peduncle 10–45 cm long. *Male flowers*: tepals usually pink, rarely white, outer pair usually elliptic to broadly elliptic, occasionally orbicular, ovate-elliptic or obovate, 1.5–2.3 × 1.5–2.5 cm, inner pair obovate to spatulate, 2–2.8 × 1.6–1.9 cm. *Female flowers*: tepals same colour as males, outer two elliptic to elliptic-obovate, inner three obovate to spatulate, subequal, 1.3–1.5 × 0.7–0.9 cm; ovary unequally 3-winged with one wing longer than the other two; 3-locular, styles 3.

Phenology. Collected in flower from January to March.

Distribution and habitat. *Begonia micranthera* subsp. *albonervia* is locally common in Bolivia's Chuquisaca Department, and occasionally in south-western Cochabamba and western Santa Cruz Departments, occurring along the eastern Andes for a distance of about 400 km (see Fig. 10). The subspecies typically occurs in moist locations, often growing on rocky damp cliffs in wet gullies in the shade of *Polylepis* Ruiz & Pav., *Alnus* Mill. or *Eucalyptus* L'Hér., at an altitude of 1210–3362 m. Because this subspecies inhabits moist shady streamside microhabitats, it is remarkable in occurring in this microhabitat in an otherwise semiarid landscape.

Additional specimens examined. BOLIVIA. **Cochabamba**: Prov. Ayopaya, Sailapata, [c.16°52′S, 66°55′W], 2500 m, ii 1935, *D. Cárdenas* 3036 (US). **Santa Cruz**: Prov. Florida, Bella Vista, circuito ecotouristíco el "Chorro del Fraile", 18°19′S, 63°40′W, 1249 m, 28 i 2007, *M. Vargas C.* 312 (MO, USZ); Prov. Vallegrande, camino de Vallegrande a San Blas, 18°27′S, 64°03′W, 2065 m, *G.A. Parada* et al. 2953 (FCQ, MO, USZ). **Chuquisaca**: Prov. Oropeza, 8 km from Poroma, 18°36′S, 65°24′W, 3362 m, 18 i 2013, *M.C. Tebbitt* 765 (USZ); 29 km from Sucre on road to Ravelo, 18°58′S, 65°23′W, 3314 m, 17 i 2013, *M.C. Tebbitt* 762 (USZ); Cajamarca, Cerro Chataquila, 18°58′S, 65°23′W, 3329 m, 17 i 2013, *M.C. Tebbitt* 763 (USZ); base of Cerro Chataquila, 18°58′S, 65°23′W, 3362 m, 18 i 2013, *M.C. Tebbitt* 764 (USZ); Prov. Tomina, Padilla, 21 km hacia Monteagudo, [c.19°22′S, 64°13′W], 2370 m, 8 iii 1981, *S.G. Beck* 6319 (US).

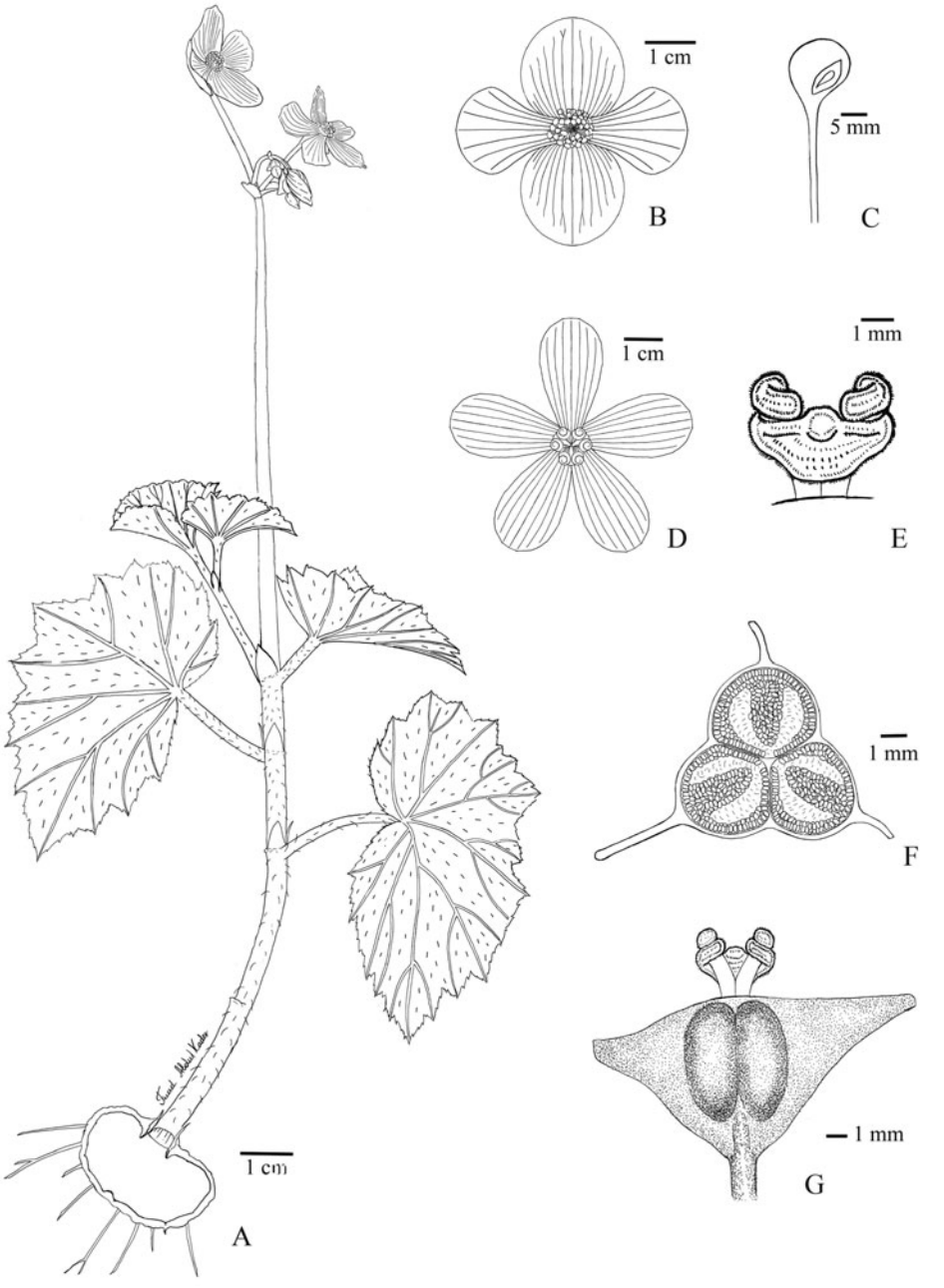

FIG. 9. *Begonia micranthera* subsp. *albonervia* Tebbitt. A, Habit; B, male flower; C, stamen, side view; D, female flower; E, style and stigma, front view; F, ovary, transverse section; G, ovary, side view. (Drawn by Fuad Abdulkader, based on *Tebbitt* 762.)

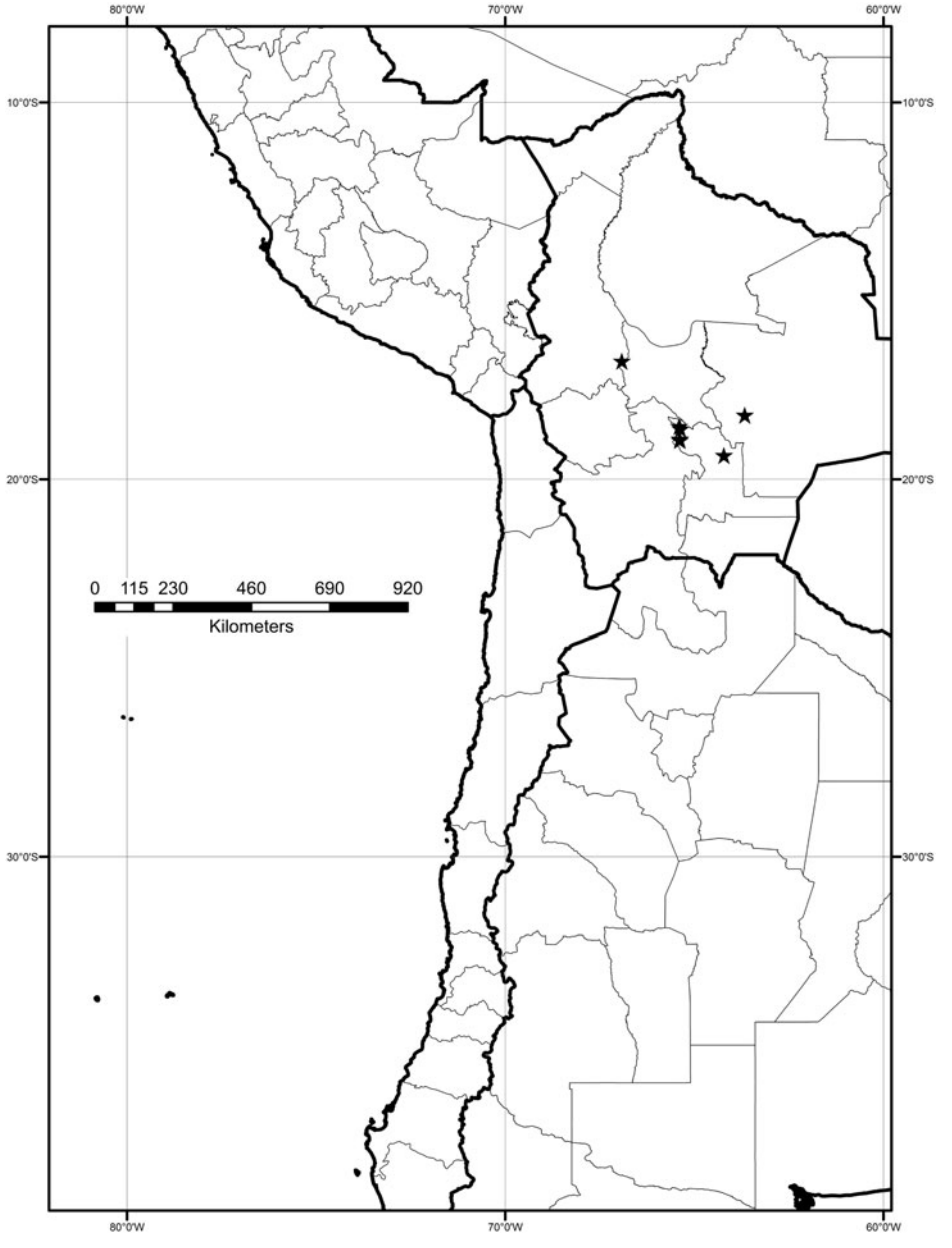

FIG. 10. Distribution of *Begonia micranthera* subsp. *albonervia* (stars).

11. Begonia micranthera Griseb. subsp. **micranthera** × **B. micranthera** subsp. **rhacophylla** (Irmsch.) Tebbitt. **Fig. 1C–E.**

Begonia micranthera Griseb. var. *foliosa* L.B.Sm. & B.G.Schub., Darwiniana 5: 92, pl. 5 (1941). – Type: Argentina, Prov. Jujuy, 15 km west of Yala, [24°8′S, 65°28′W], 1800 m, 8 iii 1936, *J. West* 6216 (holo GH!; iso MO! [2], UC!, US!), **syn. nov.**

Dioecious. *Leaves* broadly ovate, 4.3–11 × 2.7–8.2 cm, slightly fleshy, with a moderate covering of short hairs. *Female flowers* with 2 sepal-like perianth segments and 3 petal-like perianth segments, or 2 sepal-like perianth segments and 4 petal-like perianth segments, sepal-like perianth segments white with a greenish tinge, petal-like perianth segments white, margin of sepal-like perianth segments ciliate-dentate, margin of petal-like perianth segments ciliate to entire; ovary locules 4. *Chromosome number* n = 14, 2n = 28.

Phenology. Flowering January to March.

Distribution and habitat. Restricted to the vicinity of the Lagunas de Yala in Argentina's Jujuy Province. Growing on earth banks on forest edge along the side of the road, at an altitude of 1600–2100 m.

Additional specimens examined. Argentina, **Jujuy**: Without further locality, ii 1907, *L. Castillón s.n.* (LIL); Dep. Dr. Manuel Belgrano, Lagunas de Yala, 24.1170°S, 65.4688°W, 1860 m, 21 i 2007, *J. Paula-Souza* 7551 (HUEFS); Lagunas de Yala, 2100 m, 10 i 1947, *G. Romero s.n.* (LIL); Yala, 2086 m, 22 i 1941, *G. Romero* 58 (LIL); camino de Yala a la Lagunas, 30 i 1947, *C.A. O'Donell s.n.* (LIL); Yala, camino a la laguna de Yala, 24°07′23″S, 65°27′50″W, 1669 m, 7 iv 2011, *A.R. Andrada s.n*. (LIL 611459); Cuesta a Tiraxi, 4–8 km NE del río Grande, [24°5′S, 65°18′W], 1500 m, 17 iii 1982, *A. Schinini & R. Vanni* 22455 (MO, UC, US); Juan Galán – Nogelo, 2000 m, 16 i 1918, *L. Castillón* 540242 (LIL); Juan Galán, Villa Concepción, 1600 m, 10 i 1918, *L. Castillón* 479181 (LIL); Camino a Laguna de Yala, 24°07′14″S, 64°27′42″W, 1713 m, 8 i 2017, *A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde* 0014 (LIL).

12. Begonia cinnabarina Hook., Bot. Mag. 75: tab. 4483, 1849. – Type: based on cultivated material collected as seed by Thomas Bridges in Bolivia and cultivated by Edward Henderson at Pine Apple Place Nursery, London (no material preserved). (lecto, here designated: Plate in W. J. Hooker, Bot. Mag. 75: tab. 4483 [1849]).

Begonia aurantiaca hort. ex Planchon, Fl. Serres Jard. Eur. I., 5: 530, pl. 1849, pro syn. *Begonia cinnabarina* W.J. Hooker (1849).

Begonia micranthera Griseb. var. *fimbriata* L.B.Sm. & B.G.Schub., Darwiniana 5: 98, pl. 9 (1941). – Type: Argentina, Prov. Salta, Hills back of Tartagal, [c.22°30′S, 63°49′W], 400 m, 23 ii 1937, *J. West* 8413 (holo GH!; iso MO!, UC!), **syn. nov.**

William Hooker (1849) originally described *Begonia cinnabarina* based on living material grown at Edward Henderson's Pine Apple Place Nursery in London, and which Thomas Bridges had collected as seed in Bolivia. Unfortunately, Bridges kept few records of where he collected, and subsequent scholars have found it difficult to retrace his collecting routes (Johnston, 1928). Bridges' exact collecting locality remains uncertain but given our limited knowledge of his general route into the Andes and the morphological characteristics of the plants that he collected as seed, it was likely

made in Bolivia's Chuquisaca Department. No preserved material representing this collection could be located in the herbaria where Bridges' specimens are housed (BM, K, G, GH, OXF and P) or in the other herbaria utilised in this study. Likewise, Hooker does not appear to have made a voucher specimen of the cultivated material that he examined. Accordingly, the plate accompanying Hooker's original publication is here designated as the lectotype.

Additional specimens examined. Argentina. **Salta**: Dep. Santa Victoria, Los Toldos-camino a Parque Nacional Baritú, 20 xii 2009, *A.R. Andrada* 075 (LIL). Camino de los Toldos a Lipeo, por una senda a la derecha, por el viejo camino a 5 km del Lipeo, 1300 m, 10 xii 1973, *P.R. Legname & A.R. Cuezzo* 9865c (LIL); Dep. Orán, La Marama, 23 i 1945, *S.A. Pierotti* 57 (LIL).

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APPENDIX 1

Specimens examined in the cytological study

Begonia micranthera Griseb. subsp. *micranthera* var. *micranthera*
A.R. Andrada s.n. (LIL 615247)
Chromosome counts n = 14, 2n = 28

Begonia micranthera Griseb. subsp. *micranthera* var. *flava* Andrada & Bulacio
A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde 0003 (LIL)
Chromosome counts n = 13, 2n = 26

Begonia micranthera Griseb. subsp. *rhacophylla* (Irmsch.) Tebbitt
A.R. Andrada s.n. (LIL 610775)
Chromosome counts n = 14, 2n = 28

Begonia micranthera Griseb. subsp. *micranthera* var. *venturii* L.B.Sm. & B.G.Schub.
A.R. Andrada s.n. (LIL 615243)
Chromosome counts n = 14, 2n = 28

Begonia micranthera Griseb. subsp. *micranthera* × *Begonia micranthera* subsp. *rhacophylla* (Irmsch.) Tebbitt
A.R. Andrada, M.C. Tebbitt, E. Bulacio & H. Ayarde 0014 (LIL)
Chromosome counts n = 15 and 16 bivalents

Begonia cinnabarina Hook.
A.R. Andrada 075 (LIL)
Chromosome counts n = 14, 2n = 28