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A new species of *Solanum* (Solanaceae) from South Africa related to the cultivated eggplant

M.S. Vorontsova[1], S. Knapp[2]

1 *Herbarium, Library and Archives, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 1AD, United Kingdom* **2** *Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom*

Corresponding author: *M.S. Vorontsova* (m.vorontsova@kew.org)

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Abstract

A new andromonoecious species related to the eggplant and belonging to *Solanum* subgenus *Leptostemonum* from southern Africa is described. *Solanum umtuma* Voronts. & S.Knapp, **sp. nov.** is found in the eastern part of South Africa, and is sympatric with its close relative *S. linnaeanum* Hepper & P.M-L.Jaeger. It is morphologically very similar to *S. cerasiferum* Dunal of northern tropical Africa. A comparison table with similar and closely related species is provided, as are a distribution map and illustration of S. *umtuma*.

Keywords

Africa, andromonoecy, eggplant, endemic, South Africa, "spiny solanum"

Introduction

The Solanaceae is an economically important, cosmopolitan family with approximately 3000 species in some 90 genera. The Solanaceae include globally important food crops such as the cultivated potato (*Solanum tuberosum* L.), tomato (*S. lycopersicum* L.), aubergine (*S. melongena* L.), and chilli pepper (*Capsicum* spp.) as well as a number of widely used drug plants such as tobacco (*Nicotiana tabacum* L.), *Datura*, and *Atropa belladonna* L., the source of atropine. The giant genus *Solanum* L. with ca. 1500 species has become a model system for collaborative online taxonomy in challenging tropical plant groups (see Knapp et al. 2004 and http://www.solanaceaesource.org). Many new species of *Solanum* have been described as part of the PBI (Planetary Biodi-

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versity Inventory) *Solanum* project (e.g. Knapp 2010; Vorontsova et al. 2010a, 2010b; Vorontsova and Mbago 2011) that aims to produce a complete species-level on-line monograph of the genus. In the course of work on the prickly solanums in Africa and Madagascar we discovered the new species described here.

The "spiny" (or more accurately prickly) solanums (*Solanum* subgenus *Leptostemonum* Dunal) are the largest clade in the genus, with some 750 species (Whalen 1984; Bohs 2005). Most species in subgenus *Leptostemonum* are found in the New World, but approximately 150 species occur in the Old World, including taxa from Africa, Asia, and Australia. These Old World species form a monophyletic clade (see Levin et al. 2006; Weese and Bohs 2010). In the Old World clade of prickly solanums, the wild relatives of the cultivated eggplant (or aubergine) *S. melongena* are one of the most variable and confusing groups. They have been classified as *Solanum* section *Melongena* (Mill.) Dunal (Bitter 1923) or the *Solanum incanum* species group (Whalen 1984), and many taxa, both at the specific and infraspecific rank, have been described for these variable plants.

Although the eggplant is generally considered to be a vegetable of Asian origin and distribution (see Wang et al. 2008), it is a member of a predominantly African clade within the prickly solanums (Weese and Bohs 2010). In addition to *S. melongena* (including *S. ovigerum* Dunal) the "wild eggplants" currently include seven species of prickly subshrubs native to Africa and Asia: *Solanum aureitomentosum* Bitter, *S. campylacanthum* Hochst. ex A.Rich. (including *S. panduriforme* Dunal and *S. delagoense* Dunal), *S. cerasiferum* Dunal, *S. incanum* L., *S. insanum* L. (including *S. cumingii* Dunal), *S. lichtensteinii* Willd., and *S. linnaeanum* Hepper & P.-M.L.Jaeger (for complete synonymy of these taxa see the Solanaceae Source website, http://www.solanaceaesource.org; complete synonymy will also be included in the upcoming monograph). These species are all bushy erect subshrubs 0.5–2 m tall with lobed leaves, an andromonoecious breeding system with 1(-3) larger hermaphrodite flowers at the base of every inflorescence and smaller functionally male flowers at the distal parts of inflorescences, 1(-3) large yellow fruits, and variable pubescence composed of stellate trichomes. They occupy similar ecological niches throughout their respective ranges (see Table 1 for a comparison of the accepted species in this group) and usually are found growing in open disturbed areas between sea level and approximately 2000 m elevation. Complex species boundaries and high levels of morphological variability have led to much confusion between these species of eggplant relatives, and all of them have been placed in *Solanum incanum* sensu lato at one time or another (e.g., in floristic works such as D'Arcy and Rakotozafy 1994; Gonçalves 2005), with the exception of the morphologically quite distinct *S. linnaeanum* with rounded leaf lobes that has historically been called "*S. sodomeum* L." (Hepper and Jaeger 1986). *Solanum linnaeanum* is probably native to southern Africa although it is a common weed in North Africa and southern Europe.

Work on species limits in the eggplant group was carried out by the late Richard Lester's students (Jaeger 1985; Hasan 1989; Lester and Hasan 1991; Samuels 1994, 1996) using morphological and biosystematic methods. Molecular phylogenetic re-

Table 1. Morphological differences between *Solanum umtuma* and other eggplant relatives in Africa. Calyx characters refer to the long-styled flowers at the base of the inflorescence and not to the smaller, functionally male, short-styled flowers in the distal parts of the inflorescence. This comparison focuses on the characters relevant to the identification of *S. umtuma* and does not include all the characters useful for separating the other members of this group (these will be presented in an up-coming monographic treatment of the prickly solanums of Africa and Madagascar, Vorontsova and Knapp, in prep.).

	Leaf shape	**Leaf base**	**Apices of primary leaf lobes**	**Secondary leaf lobes**	**Total calyx length**	**Calyx lobe length**	**Calyx lobe shape**	**Calyx lobe apex**	**Prickle # on calyx at anthesis**	**Distribution**
Solanum aureitomentosum	ovate	obtuse to cordate	rounded to obtuse	absent	12–19 mm	7–10 mm	ovate to oblong and foliaceous	obtuse	30–60	Southern Africa, from southern DR Congo to Angola, southern Tanzania, Zambia, and Zimbabwe
Solanum campylacanthum	ovate to elliptic or lanceolate	rounded to cordate	rounded, sometimes acute	absent	7–15 mm	5–10 mm	deltate to narrow-deltate	acute to obtuse or acuminate	0–20	Ubiquitous weed of low altitudes in Southern and Eastern Africa
Solanum cerasiferum	ovate to elliptic	attenuate	rounded to acute	sometimes present	7–12 mm	4–7 mm	deltate to narrow-deltate	acuminate	0–20	From Senegal to Cameroon, Sudan and Ethiopia
Solanum incanum	ovate	rounded to cordate	rounded	absent	6–10 mm	2.5–5 mm	deltate to narrow-deltate	acute to obtuse	15–60	Predominantly in Ethiopia, Somalia, Arabia, and India, with some populations in N Kenya, Sudan, and extending to Mali
Solanum insanum	ovate	truncate, sometimes obtuse	rounded	absent	5–10 mm	4–6 mm	deltate	acute	0–15	Madagascar, India to SE Asia
Solanum umtuma	**elliptic**	**cuneate to truncate**	**obtuse to acute**	**often present**	**11–22 mm**	**7–10 mm**	**ovate and foliaceous**	**bluntly acute**	**30–80**	**South Africa**
Solanum lichtensteinii	ovate	cordate, sometimes cuneate	rounded	absent	7–15 mm	3.5–6 mm	deltate to narrow-deltate	acute to obtuse	20–50	Angola to South Africa, DR Congo, and Tanzania
Solanum linnaeanum	elliptic, sometimes ovate or obovate	cuneate or obtuse	rounded	always present and often well-developed	10–14 mm	5–6 mm	deltate to ovate	acute to rounded	30–100	Native to South Africa and naturalised in disturbed, often coastal, habitats worldwide
Solanum melongena	ovate	cordate to obtuse	rounded	absent	10–40 mm	5–17 mm	deltate to narrow-deltate	acute to long-acuminate	0(-30)	Cultivated worldwide (commonly cultivated in West Africa, sometimes in southern Africa, rarely cultivated in tropical Africa)

construction by Weese and Bohs (2010) confirmed Lester's hypothesis (e.g., Mace et al. 1999) that the cultivated eggplant has its closest relatives in Africa, although few Asian members of the Old World clade were examined. As part of of a larger monographic project on the African prickly solanums, examination of collections from South Africa identified a group of specimens distinct from the sympatric *S. campylacanthum*, *S. lichtensteinii*, and *S. linnaeanum* but with morphological similarity to the allopatric northern tropical African *S. cerasiferum* (Table 1). Preliminary molecular phylogenetic reconstruction using the nuclear ITS and *waxy* regions and the plastid *trnT-F* region confirms that this morphologically identified entity is distinct from *S. cerasiferum* and places it as sister to *S. linnaeanum* (S. Stern and L. Bohs, unpublished data). This new species is described here and the type selected from specimens in South African herbaria, following the recommendations of Smith and Figueiredo (2011).

Taxonomic treatment

Solanum umtuma **Voronts. & S.Knapp, sp. nov.**
urn:lsid:ipni.org:names:77116656-1
http://species-id.net/wiki/Solanum_umtuma
Figs 1–3

Diagnosis. Differs from *Solanum cerasiferum* Dunal by its cuneate to truncate leaf bases (versus short-attenuate leaf bases in *S. cerasiferum*), ovate foliaceous calyx lobes 7–10 mm long with between 30–80 prickles at anthesis on long-styled flowers (versus deltate to long-deltate membranous calyx lobes 4–7 mm long with only 0–20 prickles on long-styled flowers of *S. cerasiferum*); also differs from *S. linnaeanum* Hepper & P.-M.L.Jaeger by its shallow, obtuse to acute leaf lobes (versus deep, rounded leaf lobes in *S. linnaeanum*).

Type. South Africa. Eastern Cape: Elliotdale District, The Haven [32°14'S, 28°54'E], forest margin, flower white, 17 Nov 1966, *J.L. Gordon-Gray 1017* (holotype: NU [NU-40255]).

Description. Shrub, 0.5–1.5 m. Young stems erect, slender, moderately stellate-pubescent to glabrescent, with porrect sessile or variously stalked trichomes, the stalks to 0.2 mm long, the rays 6–8, ca. 0.2 mm long, the midpoints approximately the same length as the rays, armed with straight prickles 3–4 mm long, 1–2 mm wide at base, deltate, flattened, pale yellow-orange, glabrous, spaced 5–20 mm apart; bark of older stems glabrescent, green-brown to dark brown. Sympodial units plurifoliate. Leaves lobed; blades 8–20 cm long, 5–15 cm wide, 1.5–2 times longer than wide, elliptic, chartaceous, drying concolorous to weakly discolorous, green-brown, moderately stellate-pubescent on both surfaces, with porrect, sessile or stalked trichomes, the stalks to 0.2 mm long, the rays 6–8, 0.2–0.5(-0.8) mm long, the midpoints approximately the same length as the rays, with 5–20 prickles on both surfaces; the primary veins 4–6 pairs, the tertiary venation clearly visible abaxially and not visible adaxially; base

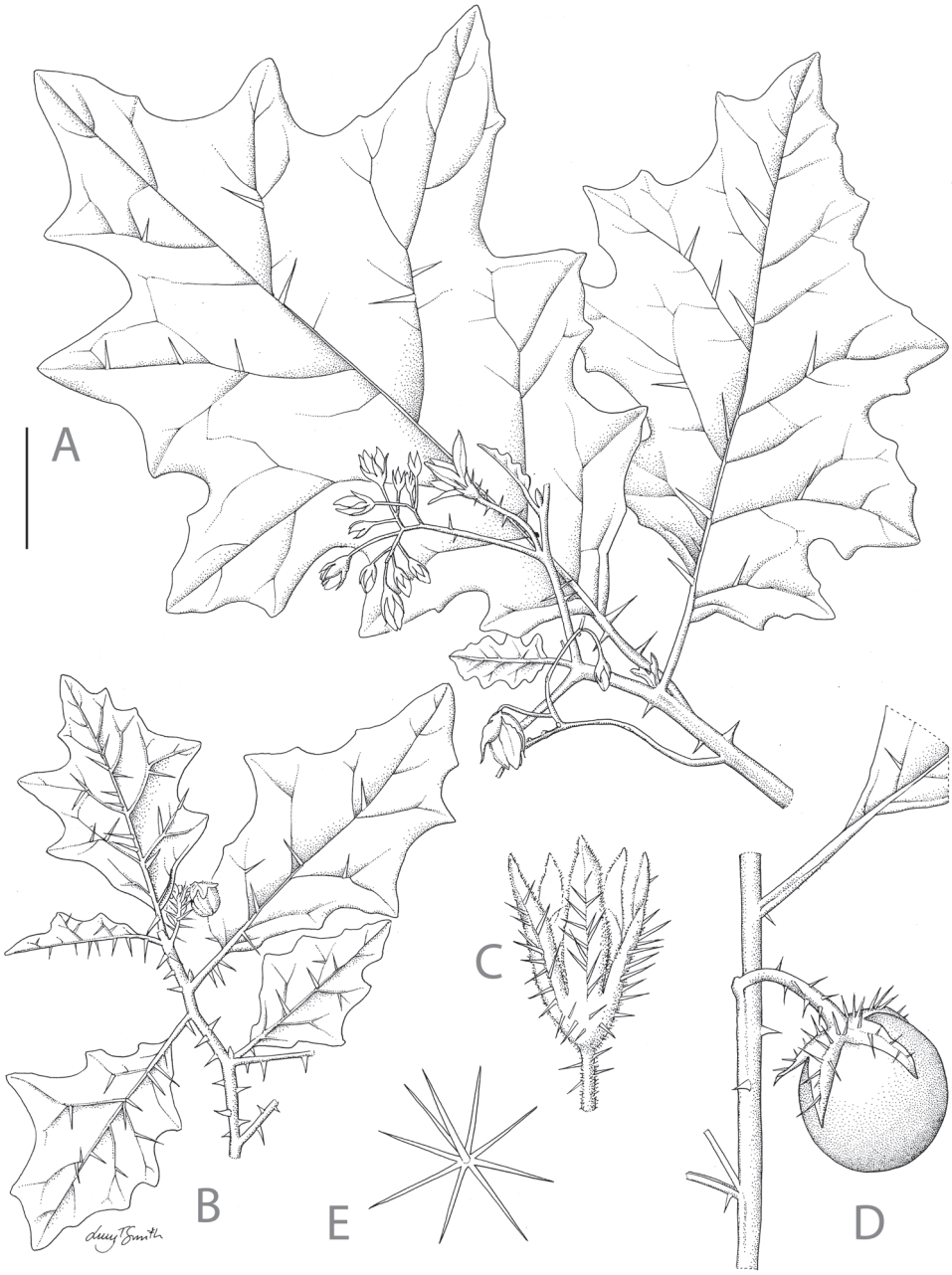

Figure 1. *Solanum umtuma*. **A** Habit with pronounced secondary leaf lobes and sparse prickles **B** Habit with few secondary leaf lobes and dense prickles **C** Calyx of a long-styled flower at anthesis **D** Fruiting branch **E** Porrect stellate trichome from the adaxial surface of a leaf. Scale bar: A, B, C = 3 cm; C = 1.5 cm; E = 0.5 mm. A, E from *Gerrard 295*; B-D from *Arnold 35934*. Drawn by Lucy T. Smith.

Figure 2. Photograph of the holotype of *Solanum umtuma* (*J.L. Gordon-Gray 1017*, NU-40255).

cuneate to truncate; margins lobed, the lobes 3–4 on each side, 1–3 cm long, deltate, apically obtuse to acute, extending approximately 1/3 of the distance to the midvein, often with secondary lobing; apex obtuse to acute; petiole 1–3 cm long, approximately 1/6 of the leaf blade length, moderately stellate-pubescent, with 0–5 prickles. Inflorescences apparently lateral, 3.5–9 cm long, rarely branched, with 6–15(-20) flowers, 1–4 flowers open at any one time, weakly stellate-pubescent, with 0(-5) prickles; peduncle 1–3 mm long; pedicels 1–2.3 cm long in long-styled flowers, 0.8–1.2 cm long in short-styled flowers, erect to pendent, articulated at the base, moderately stellate-pubescent to glabrescent, with 0–20 prickles on long-styled flowers, unarmed on short-styled flowers; pedicel scars spaced 2–8 mm apart. Flowers 5-merous, heterostylous and the plants andromonoecious, with the lowermost 1–3 flowers long-styled and hermaphroditic, the distal flowers short-styled and functionally male. Calyx 11–22 mm long in long-styled flowers, 5–9 mm long in short-styled flowers, the lobes 7–10 mm long in long-styled flowers, 3–4 mm long in short-styled flowers, ovate and foliaceous in long-styled flowers, deltate in short-styled flowers, apically bluntly acute in long-styled flowers and acute to obtuse in short-styled flowers, moderately stellate-pubescent, with 30–80 prickles in long-styled flowers and 0–30 prickles in short-styled flowers. Corolla 2.5–3.3 cm in diameter in long-styled flowers, 1.5–2.5 cm in diameter in short-styled flowers, usually white or white with purple midveins, sometimes mauve, stellate, lobed

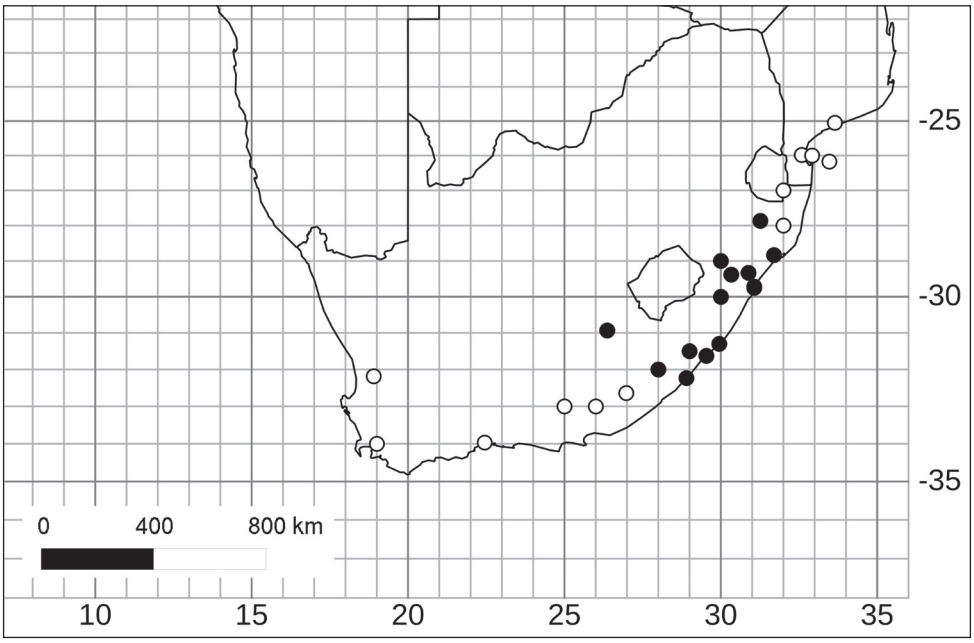

Figure 3. Distribution of *Solanum umtuma* (black circles) and its putative sister species *S. linnaeanum* (white circles) in southern Africa (specimen details for *S. linnaeanum* can be found on the Solanaceae Source website, http://www.solanaceaesource.org).

for 1/4–1/2 of its length, the lobes ca. 7 mm long, ca. 10 mm wide in long-styled flowers, 6–10 mm long and 5–8 mm wide in short-styled flowers, broad-deltate, spreading, sparsely stellate-pubescent abaxially, the trichomes porrect, sessile or stalked, the stalks to 0.2 mm, the rays 5–8, 0.2–0.4 mm long, the midpoints approximately the same length as the rays. Stamens equal, with the filament tube 1–3 mm long, the free portion of the filaments ca. 0.5 mm long; anthers 5–6 mm long in long-styled flowers, 4.5–5.8 mm long in short-styled flowers, connivent, tapering, poricidal at the tips. Ovary glabrous, with a few stellate trichomes towards the apex; style 1.1–1.2 cm long in long-styled flowers, stout, straight or gently curved, moderately stellate-pubescent for most of its length. Fruit a spherical berry, 1(-2) per infructescence, 2.7–3.5 cm in diameter, the pericarp smooth, dark green with pale green and cream markings when young, yellow at maturity; fruiting pedicels 2–3 cm long, 1.2–2.2 mm in diameter at base, woody, pendulous, with 0–20 prickles; fruiting calyx not accrescent, covering 1/4–1/3 of the mature fruit, reflexed, with 10–80 prickles. Seeds ca. 100–200 per berry, 2.7–3.5 mm long, 2–2.5 mm wide, flattened-reniform, orange-brown.

Distribution (Fig. 3). Endemic to South Africa in KwaZulu-Natal and Eastern Cape provinces (most specimens from KwaZulu-Natal); 50–1300 m elevation. *Solanum umtuma* is limited to the Maputaland-Pondoland Floristic Region (van Wyk and Smith 2001) and spans the Maputaland and Pondoland Centres of endemism.

Ecology. Occasional on grassland, scrub, and forest edges, usually growing on sandy soil.

Etymology. "Umthuma" is an isiXhosa vernacular name for many species of prickly *Solanum*; in the Xhosa language the "th" is pronounced as "t", so we have here written the epithet phonetically as "*umtuma*". The epithet is used here as a noun is apposition and thus not latinized to agree in gender.

Preliminary conservation status. *Solanum umtuma* is a species of open and somewhat disturbed habitats (as are many prickly solanum species) and occupies an area of approximately 8000 km^2 and appears to be relatively evenly distributed within that area (Fig. 3). Although not normally common where it occurs, it is not a species of immediate conservation concern.

Selected specimens examined. South Africa. Eastern Cape: Transkei, outside Umtata [31 °30'S, 29 °00'E], 17 May 1975, *M.N.M. Arnold s.n.* (K [K000441994]); Port St Johns, 1 May 1899, *E.E. Galpin 2869* (K [K000545863]); Port St. Johns, 21 Dec 1932, *A.O.D. Mogg 1300* (K [K000545864]). —KwaZulu Natal: 50 km from Nongoma, 13 May 1975, *M.N.M. Arnold 35934* (K [K000795077]); Berea, 1862, *T. Cooper 1272* (BM [BM000887022], K [K000441992, K000441993]); Berea, 1862, *T. Cooper 1273* (K [K000441998, K000441999]); Noodsberg, Feb 2002, *T. Edwards 2973* (NU); location unknown, "Zululand", received Jul 1865, *W.T. Gerrard 295* (BM [BM000887021], K [K000795076]); Umhlanga Rocks, 2 Sep 1966, *R.K. Grosvenor 168* (K [K000441995]); Weza forestry Area - beyond Lorna Doone [31°18'S, 29°57'E], 2 Jul 1986, *P.E. Hulley 134* (NU); Mkambati, Mkambati Envi-

romental Education Centre, 6 Apr 1988, *P.E. Hulley 230* (NU); Umgeni Park near Howick; Endulu Camp road, 18 Dec 1988, *P.E. Hulley & T. Olckers 279* (NU); 11 km N of Butterworth, 27 Apr 1990, *P.E. Hulley & T. Olckers* 333 (NU); Vernon Crookes Nature Reserve, 27 Apr 1990, *P.E. Hulley & T. Olckers 336* (NU); Umvoti, Umvoti valley S.W. of Mapumulo river bank, 9 Feb 1965, *E.J. Moll 1538* (K [K000442000]); Swart Umfolozi, Mpembeni, 1257 m, 27 Jan 2005, *L.S. Nevhutalu, LA. Nkuna, & E. van Wyk 921* (K [K000441997]); La Lucia, 14 Aug 1966, *R.G. Strey 6750* (K [K000441991]); Umhlanga Rocks, on gentle slopes above Umhlanga Rocks Hotel, 30 Dec 1959, *R.H. Watmough 461* (K [K000441996]); Ixopo, 22 Aug 1986, *J.O. Wirminghaus s.n.*(NU); Ngoye Forest, Zululand [28°50'S, 31°42'E], 17 Sep 1987, *J.O. Wirminghaus 628* (NU).

Discussion. *Solanum umtuma* is a medium-sized subshrub with straight prickles, acute to obtuse leaf lobes, and large yellow fruits. It is almost certainly a close relative of the sympatric *S. linnaeanum*; the two species share long, leafy, prickly calyx lobes on long-styled flowers and fruits and differ primarily in the shape of their leaf lobes. *Solanum linnaeanum* is immediately recognisable by its quite deeply incised leaves with rounded lobes; a few intermediate specimens of *S. umtuma* have somewhat rounded lobes, e.g. *R.G. Strey 6750* (K000441991). Label data indicate that *S. umtuma* has white or only occasionally violet to mauve flowers, while *S. linnaeanum* always has purple flowers.

Solanum umtuma is morphologically very similar to *S. cerasiferum* and more superficially similar to other species with straight prickles and acute to obtuse leaf lobes, including the African highland *S. dasyphyllum* Schumach. & Thonn. (Solanaceae Source 2011) and *S. robustum* H.Wendl. of the New World (see Nee 1999). It is not sympatric with any of those species, so confusion is only possible in the herbarium. *Solanum umtuma* can be distinguished from *S. cerasiferum* by its cuneate to truncate leaf bases (versus short-attenuate leaf bases in *S. cerasiferum*), ovate foliaceous calyx lobes 7–10 mm long on long-styled flowers (versus deltate to long-deltate membranous calyx lobes 4–7 mm long on long-styled flowers in *S. cerasiferum*), and the densely spiny calyx of long-styled flowers with ca. 30–80 prickles at anthesis (versus flower calyces with only 0–20 prickles at anthesis in *S. cerasiferum*). *Solanum dasyphyllum* and *S. robustum* both have leaf blades that are markedly attenuate on the petiole and decurrent onto the stem, the stems are usually somewhat winged from these decurrent leaf bases. *Solanum umtuma* is sympatric with *S. lichtensteinii* and differs from it by its obtuse to acute leaf lobes (versus rounded leaf lobes in *S. lichtensteinii*).

Specimens of *Solanum umtuma* have sometimes been annotated as "*Solanum fuscatum* L." or "*Solanum ferrugineum* Jacq." These names are both widely misapplied. No original material of *S. fuscatum* L. has been located and the application of this name has been in doubt (Knapp and Jarvis 1990) and it has been proposed for rejection (Knapp 2011). *Solanum ferrugineum* Jacq. is the accepted name for a member of section *Torva* from the New World; this species occurs from Mexico to Costa Rica (Nee 1999; L. Bohs pers. comm.).

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Frullania knightbridgei, a new liverwort (Frullaniaceae, Marchantiophyta) species from the deep south of Aotearoa-New Zealand based on an integrated evidence-based approach

Matt von Konrat[1], Peter de Lange[2], Matt Greif[1,3], Lynika Strozier[1], Jörn Hentschel[4], Jochen Heinrichs[5]

1 *Department of Botany, The Field Museum, 1400 South Lake Shore Drive, Chicago IL 60605-2496, USA* **2** *Ecosystems and Species Unit, Department of Conservation, New Zealand* **3** *Biology Department, Wilbur Wright College, 4300 N. Narragansett, Chicago, IL, USA* **4** *Department of Systematic Botany with Herbarium Haussknecht and Botanical Garden, Friedrich Schiller University, Fürstengraben 1, 07743 Jena, Germany* **5** *Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, Georg August University, Untere Karspüle 2, 37073 Göttingen, Germany*

Corresponding author: *Matt von Konrat* (mvonkonrat@fieldmuseum.org)

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Abstract

Frullania is a large and taxonomically complex genus. A new liverwort species, *Frullania knightbridgei* **sp. nov.** from southern New Zealand, is described and illustrated. The new species, and its placement in *Frullania* subg. *Microfrullania*, is based on an integrated evidence-based approach derived from morphology, ecology, experimental growth studies of plasticity, as well as sequence data. Diagnostic characters associated with the leaf and lobule cell-wall anatomy, oil bodies, and spore ultra-structure distinguish it from all other New Zealand species of *Frullania.* A critical comparison is also made between *Frullania knightbridgei* and morphologically allied species of botanical regions outside the New Zealand region and an artificial key is provided. The new species is similar to some forms of the widespread Australasian species, *F. rostrata*, but has unique characters associated with the lobule and oil bodies. *Frullania knightbridgei* is remarkably interesting in comparison with the majority of *Frullania* species, and indeed liverworts in general, in that it is at least partially halotolerant. Maximum parsimony and maximum likelihood analyses of nuclear ribosomal ITS2 and plastidic *trn*L-*trn*F sequences from purported related species confirms its independent taxonomic status and corroborates its placement within *Frullania* subg. *Microfrullania*.

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Keywords
Frullaniaceae, *Frullania*, subg. *Microfrullania*, *Frullania knightbridgei* sp. nov., morphology, DNA sequence data, New Zealand Flora, halotolerant liverwort

Introduction

Frullania Raddi (Frullaniaceae) is a large and complex liverwort (Marchantiophyta) genus with a worldwide distribution (Yuzawa 1991, von Konrat and Braggins 2001a). The number of published *Frullania* names has been reported to be over 2000 (von Konrat et al. 2010). Published estimates of the number of accepted species for the genus that have become widely recognized range from 300–375 accepted species (e.g., Schuster 1992, Gradstein et al. 2001). However, there is no evidence whatsoever to support these suppositions as no worldwide monographic treatment of *Frullania* has ever been attempted (von Konrat et al. 2006a, 2010). On the contrary, growing data and evidence may suggest the number of 300–375 species is a minimum estimate at best (von Konrat et al. 2010); in some cases the underestimation of the *Frullania* species diversity has been attributed to conservative morphology within species complexes (Heinrichs et al. 2010). In New Zealand, the current number of accepted taxa is 33, including 31 species and two varieties of which 10 are apparently endemic (Hattori 1979a, b; 1983; Glenny 1998; von Konrat and Braggins 2005; von Konrat et al. 2006b; von Konrat et al. 2010, 2011, this issue). Here we present a study of a newly discovered species that is morphologically close to *Frullania rostrata* (Hook. f. et Taylor) Hook. f. et Taylor, which is considered a widespread, polymorphic and common Australasian species (von Konrat et al. 2006b). The new species would be lumped under *F. rostrata* based on overall gross morphology.

Our paper is part of a broader, on-going, regional study of *Frullania* species by us that includes the botanical regions of New Zealand, Australia, the Pacific, South East Asia, and South America. Our new species occurs on Stewart Island/Rakiura and the Auckland Islands group of the New Zealand botanical region (as defined by de Lange and Rolfe 2010). Both areas are regarded as extremely biologically and biogeographically significant (Given and Hnatiuk 1995; McGlone and Wilson 1996; Wilson 1987; Wagstaff et al. 2011). Stewart Island/Rakiura, is the southernmost and third largest island of the New Zealand archipelago, with about 85% of the island comprising Rakiura National Park (Heenan et al. 2009). Although the fauna and flora has been partially modified as a consequence of historical Maori and European settlement, the island's vegetation patterns are little altered from their pre-human state (Wilson 1987). On the other hand, the Auckland Island group is one of five New Zealand sub-Antarctic island groups (including Snares, Bounty, Antipodes, Auckland, and Campbell islands) and are all World Heritage Areas (Chown et al. 2008). The distinctive flora of the subantarctic islands includes some of the last remnants of a once-diverse Antarctic flora, with examples of many plants possibly still retaining distinctive features of their ancestors (Wagstaff et al. 2011).

The new species of *Frullania* described below is assigned to *Frullania* subg. *Microfrullania* (R.M.Schust.) R.M.Schust., which is confirmed by molecular evidence. Detailed microscopic and SEM micrographs as well as a brief comparison with morphologically similar species are provided. This new species is remarkable in comparison with the majority of *Frullania* species in New Zealand for its least partial tolerance and exposure to salt spray. For consistency and clarity through this article, the results and discussion that follows refers to the newly recognised species as *Frullania knightbridgei*.

Methods

Living material

In order to monitor the stability of character-states and assess whether some characters varied independently of the genotype, material was grown under uniform environmental conditions described by von Konrat and Braggins (2001a). The same individual colonies were grown under three different light and water regimes and characters subsequently monitored for stability or variation. Voucher specimens of cultivated material are deposited at AK and F.

Herbarium material

Dried herbarium material was examined from AK, AKU, CANB, BM, CRI, F, G, GOET, MEL, MELU, MPN, NICH, NY, P, S, WELT, and WTU. Herbarium acronyms follow Holmgren and Holmgren (2003).

Morphological study

Where necessary, plant material was cleared to remove pigmentation using the method outlined by von Konrat and Braggins (2001a) and the cell layers of the capsule wall were separated as described by von Konrat et al. (1999). Microscopy techniques, measurements, the use of descriptors to indicate abundance and frequency, terminology of spore ornamentation, preparation of material (including spores for the SEM studies) are outlined in detail by von Konrat and Braggins (2001b) and von Konrat et al. (2006a, b).

DNA extraction, PCR amplification and sequencing

Dried tissue was disrupted with the aid of a sterile steel bead in a Qiagen tissuelyser (Qiagen Inc. Hilden, Germany) set at 30 Hz for 45 s. Genomic DNA was extracted and

purified using an Invisorb Spin Plant Mini Kit (Invitek, Berlin, Germany) according to the manufacturer's specifications. Two molecular markers, the internal transcribed spacer 2 of nuclear ribosomal DNA, and the plastidic *trn*L-F region were sequenced using the primer sets presented by Hartmann et al. (2006) and Gradstein et al. (2006). Approximately 525 base pairs (bp) of the 5.8S-nrITS2 region were sequenced, along with 500 bp of the *trn*L-*trn*F region per isolate. PCR for each sample was performed in a total of 25 µl and contained 2.5 µl dntp mix, 2.5 µl $MgCl_2$, 5 µl of Bovine Serum Albumin (New England Biolabs, Ipswich, Massachusetts, USA) 1 µl of the forward primer, 1 µl of the reverse primer, 0.5 µl Taq (Roche diagnostics, Indianapolis, Indiana, USA), 10.5 µl of dH_20, and 2 ul of sample DNA. PCRs were run for 37 cycles in a Dyad DNA engine (Bio-Rad Laboratories, Inc., Hercules, California, USA) set to the following parameters: initial denaturation at 94°C for 2 min, denaturation at 94°C for 1 min, annealing at 55°C for 1 min, extension at 72°C for 1 min, then final extension at 74°C for 7 min followed by a cool down stage at 4°C. The amplicon was purified using a Nucleofast 96 well PCR plate (Macherey-Nagel, Evanton, Pennsylvania, USA). Cycle sequencing was performed using the same primer sets as for the PCRs. Sequencing reactions were done using the BigDye terminator cycle sequencing kit (Applied Biosystems, Foster City, California, USA) and amplicons were run on an ABI 3730 (Amersham Pharmacia Biotech Inc., Piscataway, New Jersey, USA). A consensus sequence was constructed and edited using Sequencher version 4.10 (Gene Codes Corp., Ann Arbor, Michigan, USA).

Taxon sampling and outgroup selection

Initially, the new sequences were compared with GenBank sequences using the BLASTN program (Altschul et al. 1990). The BLAST searches confirmed the position within *Frullania* subg. *Microfrullania*. Ingroup taxa representing representatives of this subgenus were selected to test taxonomic hypotheses based on morphology. Several accessions of *F. rostrata* were included because *F. knightbridgei* shares several morphological characters with this morphologically rather variable taxon. Based on the analyses of Hentschel et al. (2009), three representatives of *F.* subg. *Thyopsiella* [*F. asagrayana* Mont., *F. microphylla* (Gottsche) Pearson, *F. tamarisci* (L.) Dumort.] were designated as outgroup taxa for phylogenetic reconstruction. Taxa studied, including GenBank accession numbers and voucher details, are listed in Table 1.

Phylogenetic analyses

All sequences were aligned manually in Bioedit version 7.0.5.2 (Hall 1999). Ambiguous positions were excluded from the alignment and lacking parts of sequences were coded as missing. Maximum parsimony (MP) and maximum likelihood (ML) analyses were carried out with PAUP* version 4.0b10 (Swofford 2000).

Table 1. *Frullania* taxa used in the present study, including information about the origin of the studied material, voucher information, and the herbarium where the voucher is deposited, as well as GenBank accession numbers. Sequences in bold were obtained from GenBank.

Taxon	Origin	Voucher	GenBank accession number	
			ITS2	*Trn*L-*trn*F
F. asagrayana	U.S.A.	Davison 6912	**FJ380498**	**FJ380344**
F. knightbridgei von Konrat & de Lange	Stewart Island, New Zealand	von Konrat 99/12-09 (AK)	JQ283996	JQ284003
F. lobulata (Hook.) Hook. & Nees	Chile	Buck 39518 (GOET)	**FJ380305**	**FJ380465**
F. magellanica F. Weber & Nees	Chile	Engel 25265 (GOET)	**FJ380464**	**FJ380304**
F. microcaulis Gola	Chile	Engel 25351 (GOET)	**FJ380466**	**FJ380306**
F. microphylla (Gottsche) Pearson	Tenerife	Eckstein 2287 (GOET)	**FJ380512**	**FJ380358**
F. parhamii R.M. Schust.	Fiji	von Konrat 6/14-27 (GOET)	**FJ380463**	**FJ380303**
F. rostrata (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche et al.	South Island (I), New Zealand	Engel & von Konrat 27369 (GOET)	**FJ380461**	**FJ380301**
F. rostrata	South Island (II), New Zealand	Schäfer-Verwimp & Verwimp 13897 (GOET)	**FJ380462**	**FJ380302**
F. rostrata	Motukowhai Island, New Zealand	Cameron 12503 (AK)	JQ283999	JQ284006
F. rostrata	Raoul Island (I), Kermadec Islands	Stanley s.n. (AK)	JQ284000	JQ284007
F. rostrata	Raoul Island (II), Kermadec Islands	de Lange & Havell K376 (AK)	JQ284001	JQ284008
F. rostrata	North Cape (I), New Zealand	de Lange 8034 (AK)	JQ283997	JQ284004
F. rostrata	North Cape (II), New Zealand	de Lange 8037 (AK)	JQ283998	JQ284005
F. sp.	North Cape, New Zealand	de Lange 8038 (AK)	JQ284002	JQ284009
F. tamarisci	Germany	Hentschel Bryo0733	**FJ380502**	**FJ380348**

MP heuristic searches were conducted with the following options: heuristic search mode, 1.000 random-addition-sequence replicates, tree bisection-reconnection (TBR) branch swapping, MULTrees option on, and collapse zero-length branches off. All characters were treated as equally weighted and unordered. Non-parametric bootstrapping values (Felsenstein 1985) were generated as heuristic searches with 1.000 replicates, each with ten random-addition replicates. The number of rearrangements was restricted to ten million per replicate. Bootstrap percentage values (BP) above 70 were regarded as good support (Hillis and Bull, 1993). Where more than one most parsimonious tree was found, trees were summarised in a strict consensus tree.

The two genomic regions were first analysed separately to check for incongruence. The strict consensus trees of the non-parametric bootstrap analyses were compared by eye to identify conflicting nodes supported by at least 70% (Mason-Gamer and Kellog 1996). The trees gave no evidence of incongruence. Hence the datasets were combined. jModeltest 0.1 (Posada 2008) was used to select the TIM2 + G model of evolution for the ML analysis of the combined dataset. The analysis was performed as heuristic search using ten random-sequence addition replicates, MULTrees option on, collapse zero length branches off, and TBR branch swapping. The confidence of branching was assessed with PAUP* using 200 non-parametric bootstrap resamplings generated as heuristic searches.

Species concept

Although the determination of species is regarded as one of the most important activities of the taxonomist, the majority of systematists undertaking monographs and revisions of vascular plants do not discuss the concepts or the criteria to delimit species (McDade 1995). A similar statement can undoubtedly be applied to liverwort systematics (von Konrat et al. 2006a, 2010). Here, we adopt a hierarchical model as promoted by Mayden (1997). This model considers the Evolutionary Species Concept as a theoretically robust primary species concept, as well as a bridging, secondary or operational species concept. This is discussed in the context of *Frullania* by von Konrat et al. (2006a).

Data resources

The occurrence data underpinning the analysis has been uploaded as a Darwin Core Archive (DwC-A), to the Global Biodiversity Information Facility (GBIF) via the Pensoft Data Hosting Center at the GBIF's Integrated Publishing Toolkit (IPT) (http://ipt.pensoft.net/ipt/manage/resource.do?r=deep_south_frullania_species). The genomic sequences are deposited at GenBank and their hyperlinked accession numbers are listed in Table 1.

In addition to the current paper semantically tagged and enhanced using the Pensoft Mark Up Tool (PMT), repository data and images, including images with zoom capability can also be accessed at www.discoverlife.org and www.symbiota.org for selected species that are closely allied to the newly described species. The Consortium of North American Bryophyte Herbaria (CNABH) was created to serve as a gateway to distribute data resources of interest to the taxonomic and environmental research community, offering a common web interface, including tools to locate, access and work with a variety of data (see http://symbiota.org/bryophytes/index.php).

Frullania rostrata can be accessed at the following urls:
http://www.discoverlife.org/mp/20q?search=Frullania+rostrata

http://symbiota.org/bryophytes/taxa/index.php?taxon=Frullania%20rostrata
http://symbiota.org/bryophytes/taxa/index.php?taxon=166175
http://emuweb.fieldmuseum.org/botany/botanytaxDisplay.php?irn=93741

Frullania magellanica can be accessed at the following url's:
http://www.discoverlife.org/mp/20q?search=Frullania+magellanica
http://symbiota.org/bryophytes/taxa/index.php?taxon=166024

Frullania truncatistyla can be accessed at the following url:
http://symbiota.org/bryophytes/taxa/index.php?taxon=232649

Results and discussion

In the present study, hypotheses of species differences are based on support from multiple lines of evidence, including morphology, experimental growth studies, and nucleotide sequences. This is discussed below.

Phylogeny

Of a total of 964 molecular characters, 127 were parsimony informative, 62 autapomorphic, and 775 constant (Table 2). The MP analysis resulted in two trees of 304 steps with a consistency index of 0.78 and a retention index of 0.80 (not depicted). A single most likely tree was found in the ML analysis (Fig. 1, ln = -2984.6458). MP and ML topologies differ only slightly. In the MP topology, *F. parhamii* R.M.Schust. is placed in a polytomy with the *F. rostrata* (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees representatives whereas in the ML trees, *F. parhamii* is placed sister to *Frullania rostrata* in an unsupported relationship. *Frullania knightbridgei* is well separated from *Frullania rostrata*, and placed in a paraphyletic grade with other members of *F.* subg. *Microfrullania*. The morphologically similar *F. truncatistyla* von Konrat, Hentschel, Heinrichs & Braggins has not yet been included in molecular studies.

Table 2. Distribution of constant and phylogenetically informative sites for aligned positions of the two genomic regions.

	L-F*trn*	**ITS1-5.8S-ITS2**	**Total**
Number of sites in matrix	516	448	964
constant	465	310	775
autapomorphic	28	34	62
parsimony informative	23	104	127

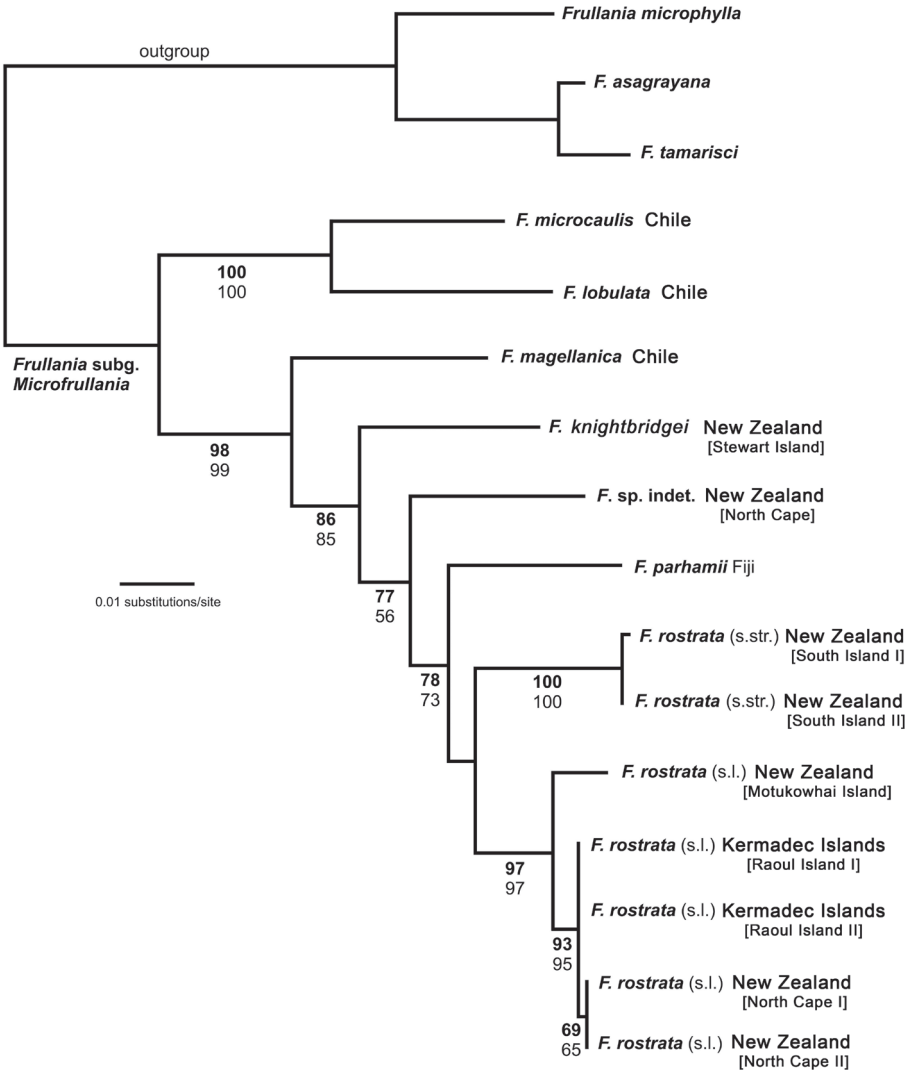

Figure 1. Maximum likelihood phylogeny (ln = -2984.6458) derived from an nrITS2 – *trn*L-F sequence alignment including 14 new sequences and 18 sequences from Hentschel et al. (2009). ML bootstrap percentage values (> 50) in bold face, MP bootstrap percentage values (>50) not bold.

Frullania rostrata is split in two robust subclades. Hence, the ML phylogeny indicates that *F. rostrata* - despite exclusion of *F. knightbridgei* - is part of a species complex, possibly with some geographical structure. This may be supported by the significant number of synonyms and herbarium specimens summarised under *F. rostrata* (von Konrat et al. 2006a). *Frullania rostrata* might well be regarded as a Southern Hemisphere equivalent of the Holarctic *Frullania tamarisci*. Heinrichs et al. (2010) investigated *F. tamarisci*, which is typically regarded as a single polymorphic species. Using sequences from the nrITS

region and plastid *trn*L-*trn*F and *atp*B-*rbc*L, their analyses resolved eight partly sympatric monophyletic groups representing distinct species rather than subspecies or varieties.

The number of molecular studies at the population level in liverworts is still limited. This hampers our efforts to quantify the contribution of cryptic species to the global biodiversity of liverworts (von Konrat et al. 2010). Existing studies suggest a significant part of bryophyte biodiversity is undetected with traditional morphological concepts alone (Heinrichs et al. 2009). It is clear, we urgently need more species-level phylogenies with extensive population sampling to approximate the actual diversity of *Frullania*, and to elucidate speciation processes and distribution range formation (Bombosch et al. 2010, Heinrichs et al. 2010, Ramaiya et al. 2010).

Growth studies

In *Frullania*, as well as liverworts generally, there remains a large gap between characters used for delimitation and our understanding and knowledge of their plasticity in nature (von Konrat et al. 2006b). *Frullania rostrata* and the new species, *F. knightbridgei*, responded well to growing in controlled environmental conditions in a glasshouse unit. Oil bodies in particular were monitored. The stability of oil body characters indicates that the differences have some underlying genetic basis; thus it is likely that the salient characters of this species are genetically dependent rather than influenced by the environment.

Morphology

Many critical morphological features have often been neglected in liverwort systematics (Schuster 1992; von Konrat et al. 1999, 2001a, 2006b), and scores of studies have been restricted to herbarium material where ephemeral structures; e.g., sporophytes and oil bodies, have not been available (von Konrat et al. 2006a,b; Heinrichs et al. 2009). The new species is morphologically aligned to a group of species representing *F.* subg. *Microfrullania*, which has been resolved as a monophyletic group (Hentschel et al. 2009). Inclusion of *F. knightbridgei* in *F.* subg. *Microfrullania* is also supported by molecular evidence as discussed above. *Frullania* subg. *Microfrullania* represents a clade with the most historical confusion out of all *Frullania* subgenera with taxa occurring in southern South America, Australasia and islands of the South Pacific, New Guinea, and Indonesia (von Konrat et al. 2006a, 2010).

The new species appears almost to lie intermediate between *F. rostrata*, of New Zealand and Australia, and *F. pseudomeyeniana* S. Hatt. of New Caledonia. The latter is only known from the type material (New Caledonia, Mont Mou, N of Paita, 1100 m., *Kitagawa 21422*, NICH), which was examined by the senior author. *Frullania knightbridgei* also has some similarity with *F. magellanica* (Spreng.) F. Weber et Nees of Chile. *Frullania knightbridgei* superficially strongly resembles some forms of *F. rostrata* in plant

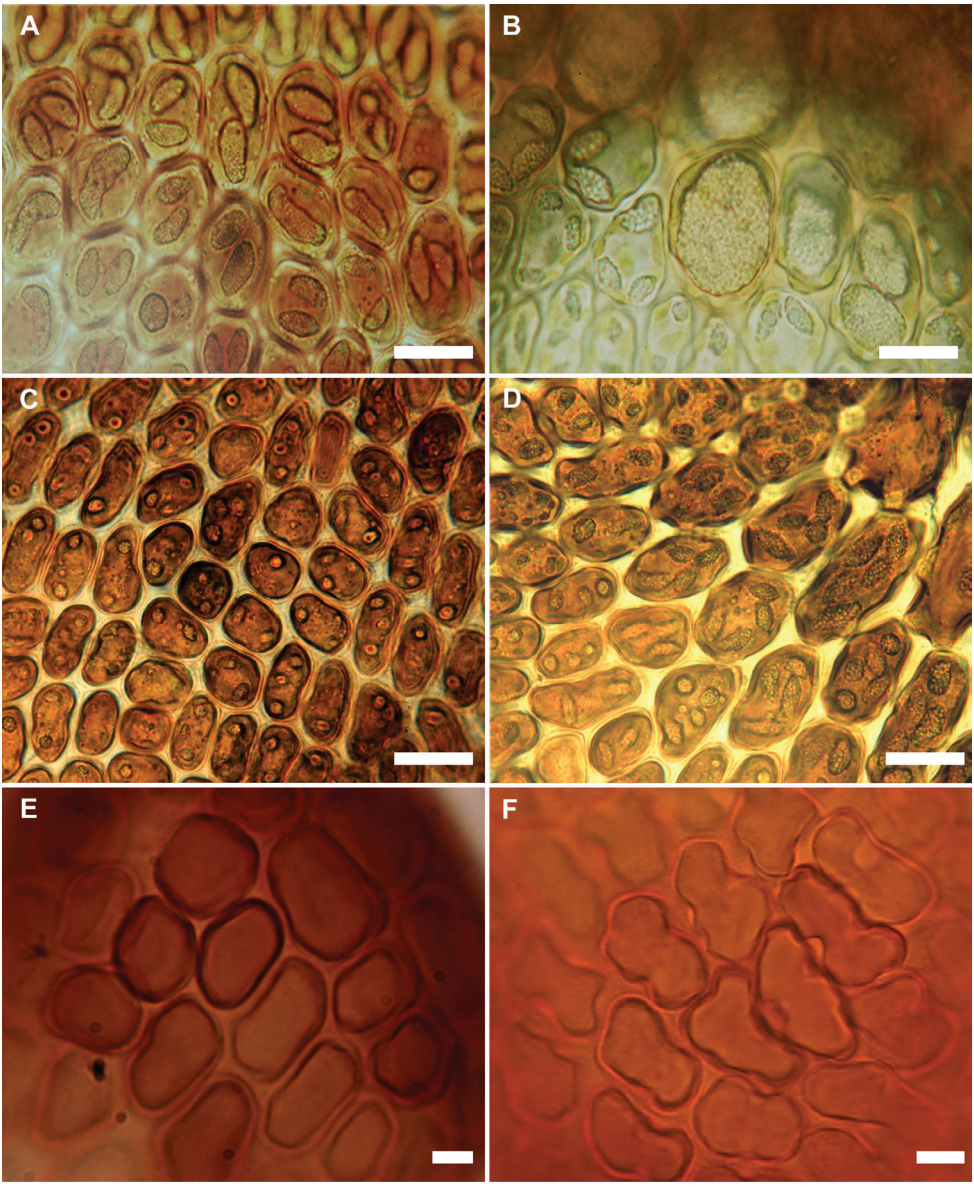

Figure 2. Variation in characters associated with the leaf-lobe oil bodies and leaf-lobule anatomy (**A, B, E** *Frullania knightbridgei*; **C, D, F** *Frullania rostrata*) **A** Oil bodies of the median region of the leaf-lobe, very large, (1)2–(3) per cell, collectively occupying over 75% of the cell lumen **B** Oil bodies of basal cells, a characteristic group of basal ocelli, each ocellus almost occupying the entire cell lumen **C** Oil bodies of median cells, 2–3 per cell, collectively occupying very small area of cell lumen, lacking any significant ornamentation and appearing as almost homogeneous oil droplets **D** Oil bodies of basal cells, 3–5 per cell **E** Semi straight cell walls toward apex leaf-lobule **F** Flexuose cell walls towards apex of leaf lobule. Scale bars A, B = 15 µm; C–F = 10 µm.

size, the large styli and lobules, and the entire underleaves. However, with fresh material, *F. knightbridgei* is immediately discernable from *F. rostrata* by the presence of large oil bodies (usually only 2 per cell, occasionally 1 or 3) that almost occupy the entire cell lumen of basal and median cells of the leaf lobe (Fig. 2a–b). In the absence of oil body data, careful consideration has to be given to the anatomy of the leaf-lobe and -lobule to help differentiate between these species. In *F. knightbridgei*, cells towards the lobule apex progressively develop a more regular shape (quadrate to rectangular) and the cell walls become semi-straight (Fig. 2e). Conversely, the cell walls of both *F. rostrata* and *F. pseudomeyeniana* are flexuose with indistinct trigones, and with small, nodulose intermediate thickenings throughout the lobule, from the base to the apex (Fig. 2f).

The unique cell anatomy of the leaf lobe in *F. knightbridgei* further places it into an isolated position within subg. *Microfrullania*; this species is seemingly unique in having a group of conspicuously enlarged cells, originating from the base of the lobe and extending 10–14 cells out toward the apex, forming a partial band or pseudo vitta up to 4–6 cells wide (Fig. 3). The cells are enlarged to accommodate the typically 2 large oil bodies. The features of the oil bodies are unique within *F.* subg. *Microfrullania*. In those species examined thus far, the oil bodies of the leaf lobe median cells number from 2–4(5) per cell, are of small size and lack any significant ornamentation, almost appearing as homogeneous oil droplets (von Konrat et al. 2006a, 2010) (Fig. 2c–d).

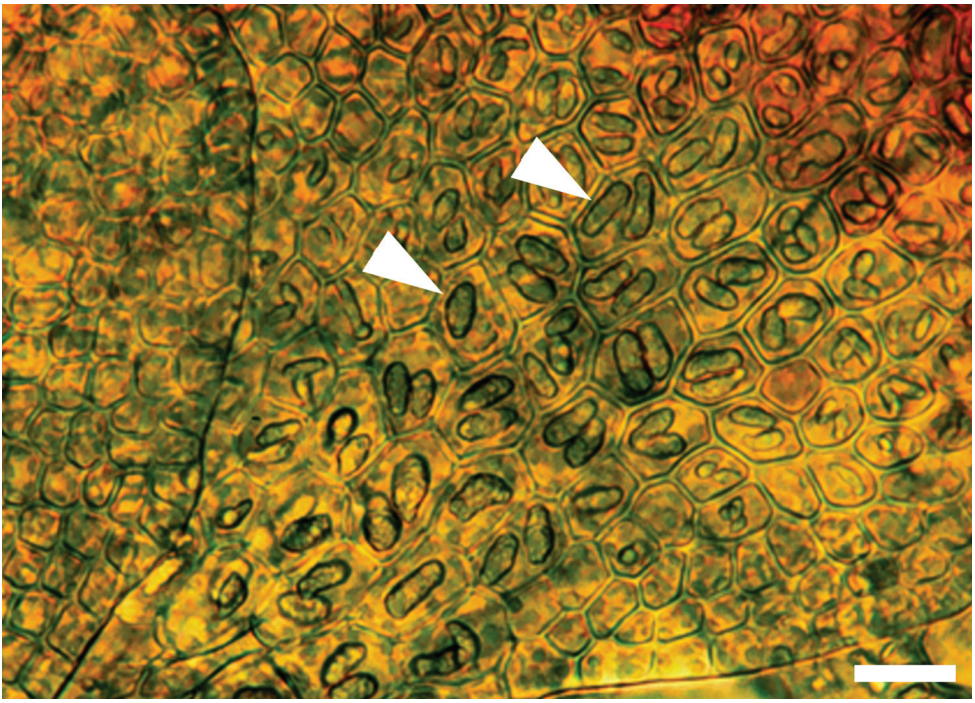

Figure 3. Oil bodies in a leaf shoot of *Frullania knightbridgei* illustrating, in region of arrow, the 1–2 large oil bodies per cell. Scale bar = 20 μm.

The position of the lobules in relation to the stem as well as styli shape and form are often used to help distinguish between taxonomic units of varying levels in *Frullania* taxonomy. Lobule position varies in *F. knightbridgei*, ranging from parallel to subparallel with the stem or with the lobule spreading at a strong angle, so that the lobuli are tilted inwards. *Frullania pseudomeyeniana* and some phenotypes of *F. rostrata* also have lobuli that lie almost parallel or subparallel to the stem for both species. *Frullania magellanica* also has at least some phases with lobules more or less parallel to the stem (Engel 1978). Interestingly, the parallel lobule position is typically a feature associated with species of subg. *Thyopsiella*. Thus lobule position must be used secondary to and in collaboration with more salient characters in circumscribing *F.* subg. *Microfrullania*.

Historically, characters associated with the capsule wall and spore surface ultrastructure have rarely been utilized in *Frullania* systematics (von Konrat et al. 2006b). Yet, it is clear that characters associated with these structures have great utility at various taxonomic levels (e.g., von Konrat et al. 1999, 2006b, 2010). The spores of *F. knightbridgei* have a "rosette" with conspicuous protuberances lacking secondary branches and deposits – a feature used to help characterize *F.* subg. *Microfrullania* (Hentschel et al. 2009). The spores can also be used to distinguish *Frullania knightbridgei* and *F. rostrata* (Table 3, Fig. 5). Differences are also reflected in the epidermal wall of the capsule. In *F. knightbridgei*, the walls are nodular, where the lobes extend irregularly for a

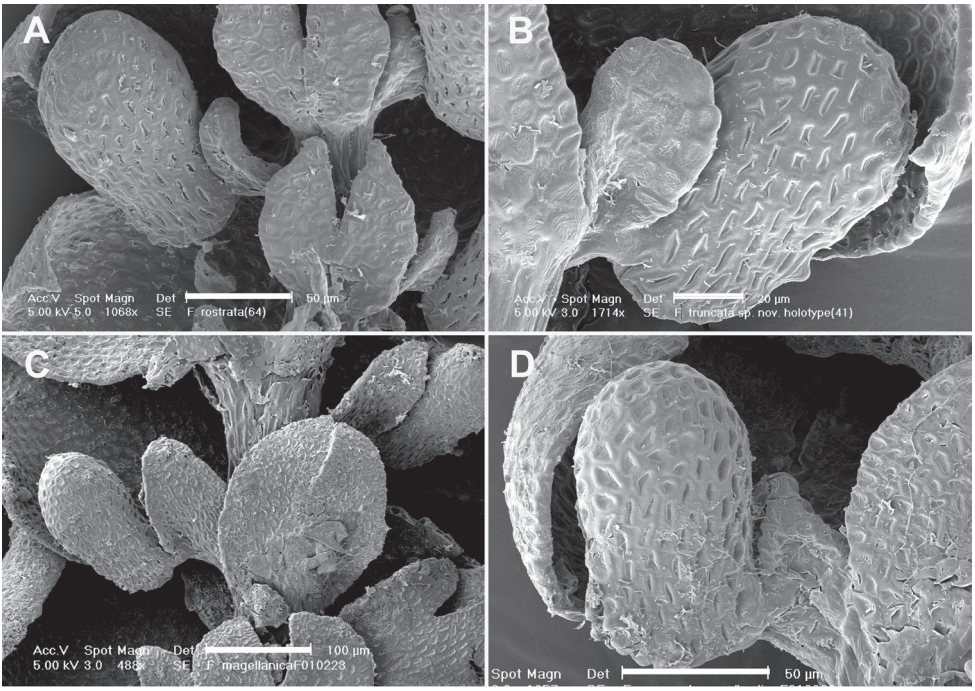

Figure 4. Lobule position and styli. **A** *Frullania rostrata* **B** *Frullania truncatistyla* **C** *Frullania magellanica* **D** *Frullania knightbridgei* Scale bars A, D = 50 µm; B = 20 µm; C = 100 µm.

short distance over the tangential face toward the centre of the cell and have intermediate thickenings near the middle of the longer walls (Fig. 5a). In *F. rostrata*, the lobes extend toward the centre of the tangential face for a short distance, as short rounded or obtuse lobes and the juxtaposed corner thickenings form 3–4 lobed figures; intermediate thickenings are also lacking (Fig. 5b).

Tables 3–5 summarizes the characters differentiating *F. knightbridgei* from two morphologically similar species that it might be confused within the New Zealand bo-

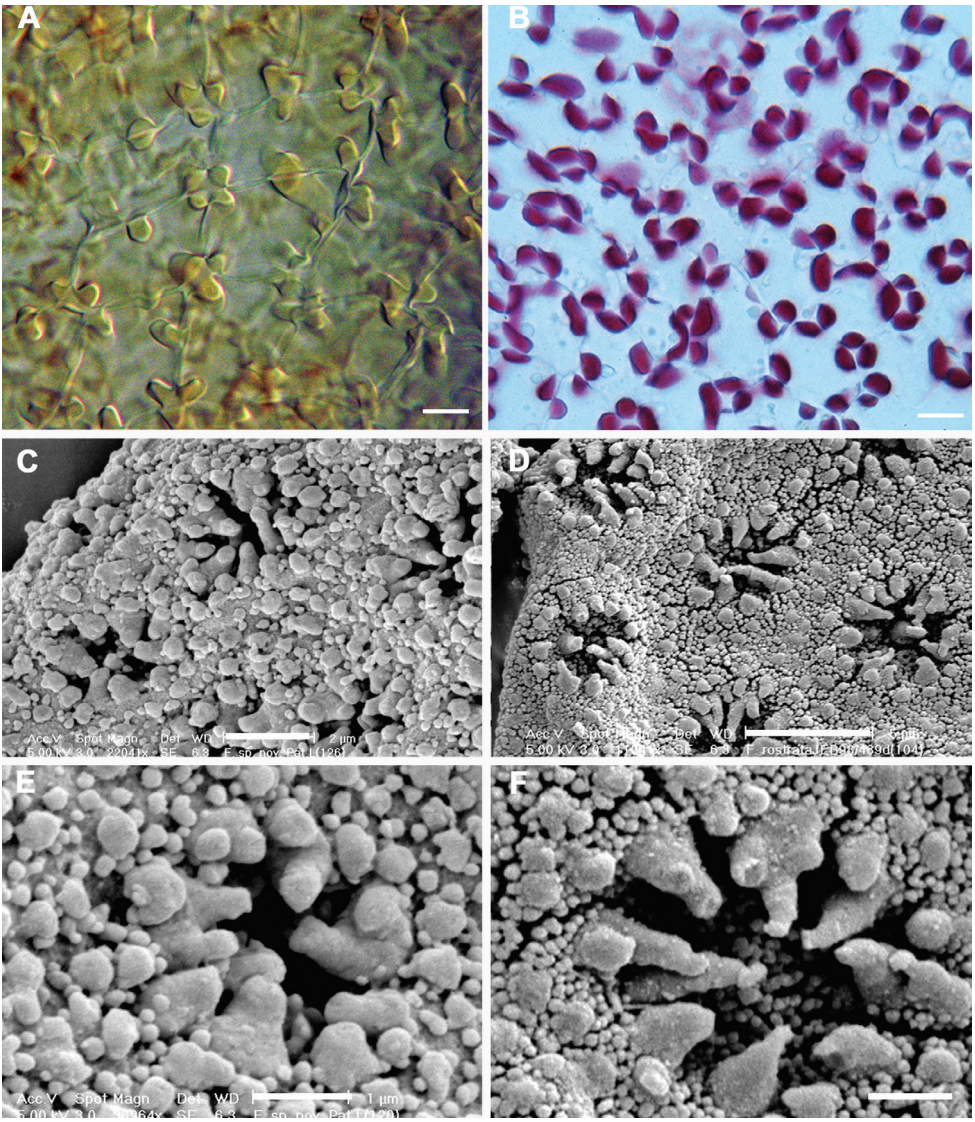

Figure 5. Epidermal layer of the capsule wall and spore surface ultrastructure. **A** Epidermal layer of *Frullania knightbridgei* **B** Epidermal layer of *Frullania rostrata* **C, E** Spore surface of *Frullania knightbridgei* **D, F** Spore surface of *Frullania rostrata*. Scale bars A, B = 10 µm; C = 2 µm; D = 5 µm; E,F = 1 µm.

Table 3. Initial branching appendages.

Branching	***F. knightbridgei***	***F. truncatistyla***	***F. rostrata***
Branching type	*Frullania*-type	Usually *Frullania*-type, occasionally *Lejeunea*-type	Usually *Frullania*-type, occasionally *Lejeunea*-type
First branch underleaf (BUL1)	1 ventral, explanate, bilobed segment + 1 dorsal saccate segment	1 ventral, explanate, bilobed segment + 1 dorsal saccate segment	1 ventral, explanate, bilobed segment + 1 dorsal saccate segment
First branch leaf (BL1) initial appendages	± characteristic of normal stem leaves	Variable, either elobulate, and explanate to sulcate, or ± characteristic of normal stem leaves	Variable, either elobulate, and explanate to sulcate, or ± characteristic of normal stem leaves

Table 4. A comparison of morphological characters between three New Zealand species, *F. knightbridgei*, *F. truncatistyla* and *F. rostrata*.

Character	***F. knightbridgei***	***F. truncatistyla***	***F. rostrata***
Shoot width	To µm 1000 µm	To 550 µm	To 1100 µm
Stem			
Cortical cells	10–34	7–12	10–25
Medullary cells	12–28	8–14	12–30
Leaf-lobe			
Apex	Rounded	Acute	Rounded to sharply acute
Median cell size	Dimorphic; central band of cells similar to basal cells	Markedly uniform and smaller than basal cells	Markedly uniform and smaller than basal cells
Leaf-lobule			
Position in relation to stem	Often almost parallel with the stem, or at most lobules at angles of up to ca. 25°	Angles of 30–50 (60) u with the stem so that lobules tilted outwards	20) 30–50 (60)° with the stem so that lobules tilted outwards
Length:width ratio	1.75–2:1	1.0–2.0:1	1.5–2.25:1
No. of cells in circumference	To 25	To 20	To 28
Colour	Bicoloured	Uniform colour similar to other organs	Uniform colour similar to other organs
Cell walls toward lobule apex	Semi straight	Flexuose	Flexuose
Stem-underleaf			
Margin	Entire	Entire	Entire; occ. angulated or toothed.
No. of cells wide (lobe)			
Width in comparison to stem	(2) 2.5–3.5 (4)	1.0–1.25	(1) 2–3.5 (5)
Stylus			
Shape	± triangular	Subrectangular, apex ± truncate to subtruncate	Variable, subtriangular to foliaceous to sickle-shaped

Character	*F. knightbridgei*	*F. truncatistyla*	*F. rostrata*
Sexuality	Dioecious	Dioecious	Dioecious
Archegonia No.	1	1	1–2
Perianth	Plicate, to 6-keeled	3-keeled	3-5 keeled
Spores			
Form of projections comprising rosette	Taper gradually to a rounded or truncate apex	Not seen	Taper gradually to a rounded or subacute, often hooked apex

Table 5. Characters associated with oil bodies of the leaf-lobe.

Character	*F. knightbridgei*		*F. truncatistyla*	*F. rostrata*
General	**Dimorphic**		**Monomorphic**	**Monomorphic**
	Type 1	Type 2		
Median cells				
Size	(2) 3–7 (9) µm in diam. to (5) 6–11 (13) × (4) 5–10 (12) µm	(1) 2–4 (5) µm in diam. to (2) 3–5 (6) µm × (1) 2–3 (4) µm	(1) 2–3 (4) µm to (2) 2–3 (5) 3 (1) 1–2 (3) µm	(1) 2–3 (4) µm in diam. to (2) 3–5 (6) µm × (1) 2–3 (4) µm
Shape	Rarely subspherical usually ovoid or ellipsoidal	Spherical to ovoid or ellipsoidal	Spherical to ovoid or ellipsoidal	Spherical to ovoid or ellipsoidal
Number	1-2	2–3 (4)	2–3 (4)	2–3 (5)
Density (collectively)	Occupying almost entire cell lumen	Occupying <25% of cell lumen	Occupying <25% of cell lumen	Occupying <25% of cell lumen
Surface	Appearing granular	Appearing ± homogeneous	Appearing ± homogeneous	Appearing ± homogeneous
Basal cells				
Number	1–2		3–5	(2) 3–5 (6)

tanical region - *Frullania truncatistyla* and *F. rostrata*. This includes critical characters associated with initial branching appendages (Table 3), oil bodies and cell anatomy (Table 5, Fig. 2,3), stem anatomy, leaf lobe, underleaf, leaf lobule and stylus (Table 4, Fig. 4), perianth, and sporophyte, including spores (Table 4, Fig. 5).

Taxonomic treatment

Artificial key distinguishing *Frullania knightbridgei* from morphologically allied species of subg. *Microfrullania*, including those distributed in New Zealand.
Fertile and sterile features combined

1 Leaf-lobes with denticulate to coarsely dentate margins ..... **Sect. *Microfrullania*: *Frullania chevalieri*, *F. microscopica*, *F. parhamii* [incl. New Zealand, New Caledonia, and Fiji]**

– Leaf-lobes with entire margins, lacking any form of marginal dentition **2**

2 Stylus a distinct, obovate to subrectangular in shape with a truncate apex; a distinctive angular projection on the lobule immediately above the slit; plants small (c. 250–500 µm) ..... ***F. truncatistyla*** **[North Island, South Island, Stewart Island]**

– Styli sickle-shaped, subtriangular to triangular; distinctive angular projection absent (not to be confused with the ± discoloured, gibbous, cell above mouth); plants small to medium **3**

3 Dioecious, gynoecia terminal on leading stems with subfloral systems (i.e., subfloral innovations or subfloral branches); stylus small to medium, 0.25–0.5× the length of the lobule), typically stylus with up to 10–35 cells **4**

– Monoecious, gynoecia on short lateral branches lacking subfloral systems; stylus typically large, 0.75–1.0× the length of the lobule, stylus with up to 100 cells total ..... ***F. magellanica*** **[Chile]**

4 Lobules typically at an angle in relation to the stem, leaf-lobe median cells smaller than basal cells and with 3–4 oil bodies per cell, occupying <50% of the area of the cell lumen; perianth typically 3-keeled ..... ***F. rostrata*** **s. l. [Australasia]**

– Lobuli varied, typically subparallel to the stem; a band (pseudovitta) of median cells (of leaf-lobe) as large as basal cells and with 1–2 oil bodies per cell, occupying almost entire cell lumen (where known); perianth plicate 5–6 keeled **5**

5 Leaf lobes often squarrose; main stem underleaves small, ± as wide as stem; leaf lobule clavate, cell walls distinctly flexuose toward the lobule apex ..... ***F. pseudomeyeniana*** **[New Caledonia]**

– Leaf lobes flat, not squarrose; main stem underleaves medium to large, wider than stem; leaf lobule cylindrically helmet-shaped, cell walls becoming distinctly semi-straight toward lobule apex ..... ***F. knightbridgei*** **[Stewart Island, Auckland Island]**

Frullania knightbridgei **von Konrat & de Lange, sp. nov.**
http://species-id.net/wiki/Frullania_knightbridgei
Figs 2–7

Diagnosis. *Frullania knightbridgei* is similar to *F. rostrata* (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche et al., but differing by the presence of large oil bodies that occupy almost the entire lumen of the basal and median cells of the leaf lobe, and the often bicoloured lobules, which usually lie almost parallel to the stem. The leaf lobule cell walls of *F. knightbridgei* are distinctly semi-straight toward the lobule apex whereas in *F. rostrata* the cell walls are distinctly flexuose toward the lobule apex.

Type. New Zealand: Stewart Island: Rakiura/Stewart Island National Park, 500 m. from North Arm Hut, on bark of *Dracophyllum longifolium* overhanging water on margin of Patterson Inlet, canopy of stunted *Dacrydium cupressinum* and *Metrosideros*

Figure 6. *Frullania knightbridgei* on twig, Auckland Island. (Coll. *Common C893B*).

umbellata. Near sea level, 46°52'55"S, 168°01'04"E, 12 Dec 1999, *M. von Konrat 99/12-09* (holotype AK; isotypes CHR, F).

Description. Plants small to medium (main shoots to 600 µm wide), forming olive-green, copper-brown, to black patches, closely to loosely adhering to substrate. Leading stem 15–25 mm long and to 90µm in diameter, 6–9 cells wide, little differentiation between cortical cells (18–24 in no.) and medullary cells (14–28 in no.), the former often slightly smaller than the latter, both with firm walls, lumen irregularly shaped. Branching often regularly pinnate, occasionally bipinnate to rarely tripinnate, branches with progressively smaller leaves; *Frullania*-type branching. First branch un-

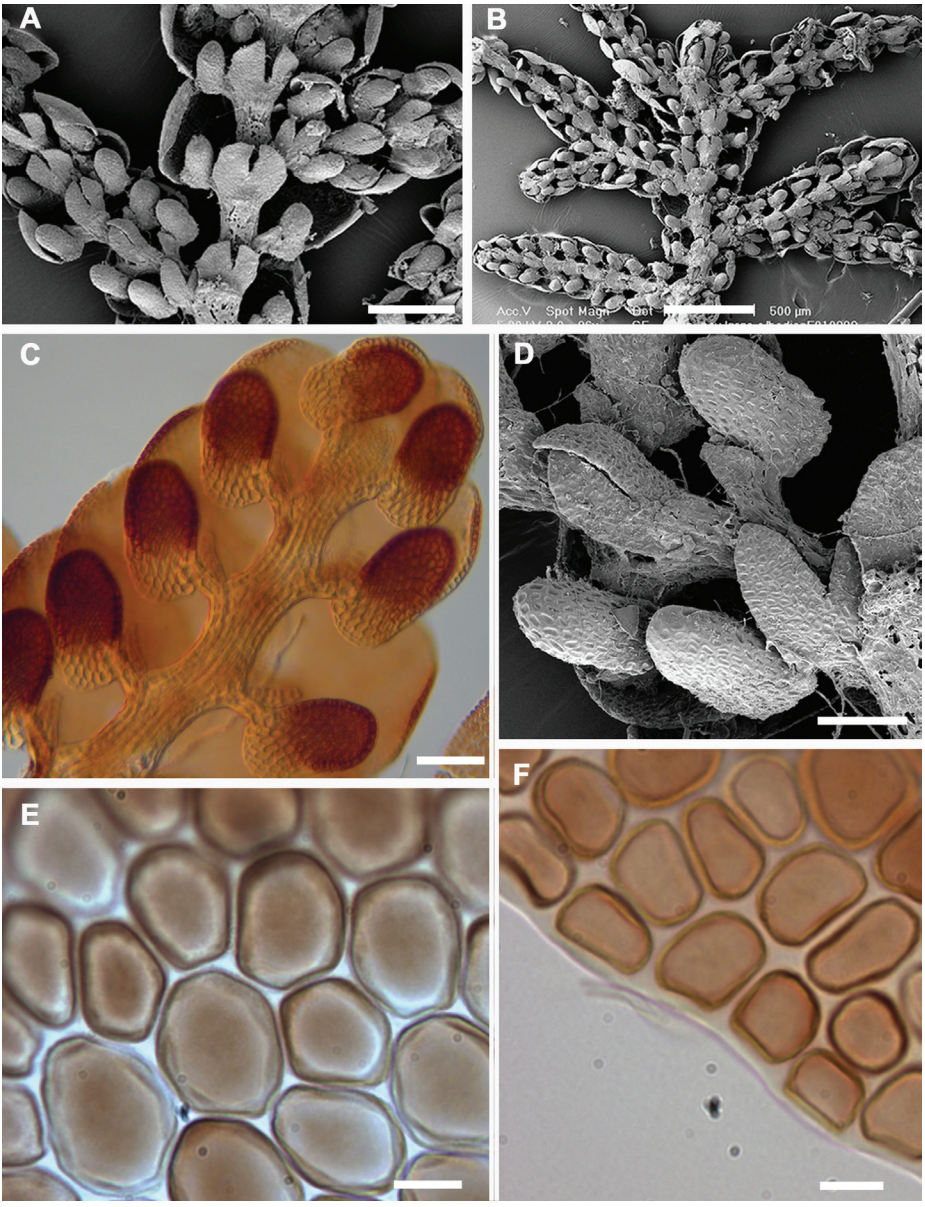

Figure 7. *Frullania knightbridgei* **A, B** Main stem, ventral view. **A** Main stem and lateral branches, lobules subparallel in relation to the stem and occupying ca. 25% of the exposed surface of the dorsal lobe **B** Illustrating terminal position of the gynoecium with 2 subfloral branches immediately below **C** Bicoloured leaf-lobules **D** Initial branching appendages **E** Median cells of the leaf-lobe with subequally thickened cell walls **F** Basal cells of the leaf-lobe. Scale bars A = 200 µm; B = 500 µm; C,D = 50 µm; E, F = 10 µm.

derleaf (BUL1) always with three distinct segments, the ventral lamina divided for $^{1}/_{3}$–$^{2}/_{3}$ its length into two unequally or subequally sized lobes + 1 dorsal saccate lobe; First branch leaf (BL1) usually ± characteristic of normal stem leaves (i.e. 1 explanate

dorsal lobe + 1 saccate lobule + 1 stylus). Stem leaves of main branch flat when dry and wet, slightly imbricate to contiguous, suborbicular to broadly ovate, to 375 µm long × 350 µm wide with incurved distal margins, dorsal margins extending beyond the farther edge of the stem, rounded apices, non-auriculate and ± subtruncate at the base, entire margins, smooth dorsal surface. Lobules remote from the stem (lobule attached to stem by 3–4 cells) and usually almost parallel with the stem so that the long axis of the lobule is ± parallel with the main stem (or at most lobules at angles of up to ca. 25° with the stem so that lobules only very slightly tilted outwards); lobules often bicoloured with the basal 2–5 cells towards the mouth (up to 0.25 of the lobule) hyaline to subhyaline, in contrast to the olive-green to brown pigmentation elsewhere; cylindrically helmet-shaped (orbicular in cross-section with up to 25 cells in circumference); lobules ± medium (lobule area obscuring no more than 0.25 × the exposed area of the dorsal lobe), ca. 1.75–2 × long as wide, 110–200 µm long × 60–100 µm wide (up to 12–14 cells high × 6–8 cells wide); ± equally inflated throughout (so that the sides of the lobule are ± parallel), the opening wide, extending only slightly along the abaxial lobule margin; ca. $^{2}/_{3}$ from lobule apex there is usually a ± discoloured, gibbous, cell (the free margin of the cell with a heavily thickened wall); mouth nearest the stylus, truncate at base then cells with septa between adjacent cells ± swollen, the mouth thus then becoming crenulate-sinuate; lobule usually hyaline near mouth, lobule apex obtuse, surface of lobule smooth. Stylus medium in size ($^{1}/_{3}$–$^{2}/_{3}$× the length of the lobule), ± triangular, up to 60 µm long × 50 µm wide, (4) 5–6 (7) cells wide at base, (10) 12–24 (30) cells in total, occasionally with a poorly developed slime papilla at the apex. Underleaves of leading stems bilobed, obovate to rotundate, at most only contiguous with lobules, underleaves contiguous to distant from each other, usually long as wide, occasionally slightly longer than wide, (2) 2.5–3.5 (4)× the stem in width, to 100–175 µm long × 100–150 µm wide, broadest at middle, free lateral margins always entire; apex of underleaf bilobed to $^{1}/_{3}$–½ its length, lobes separated by a V-shaped sinus, the lobes 9–14 cells wide at base and with blunt to subacute or rounded apices. Rhizoid-initial area present near base of underleaf, rhizoids often seen, subhyaline, in bundles, to 400 µm long. Not strictly microphyllous, lobules of secondary stems ± similar size to main stem, but lobes and underleaves of secondary branches slightly smaller than those of leading stems.

Leaf-lobe: to 20 cells long, from base to apex, by 35 cells at widest region; with a band of conspicuously enlarged cells originating from the lobe base and extending out towards the lobe apex 10–12 cells, and up to 6 cells wide at the widest region. Lobe marginal cells ± rectangular to subquadrate, small to 8 µm long × 6 µm wide, hyaline walls subequally thickened, cell cavities brownish red. Cells of the middle region of the lobe are ± dimorphic in size; Type One [see below]: 4–6 rows of median cells, cells to 30 µm long × 22.5 µm wide (usually 2–2.75 × long as wide), thus similar in size to basal cells; Type Two [see below]: cells gradually becoming reduced in size (median cells to 15 µm long × 10 µm wide, usually 1.25–2 × long as wide, between central band of enlarged cells and lobe margin). Both cell types usually pentagonal or hexagonal, hyaline walls subequally thickened, intermediate thickening rare to absent, wall thickness

to 2.75 µm wide, cell cavities of median cells brownish red. Cells becoming gradually larger basally, cavities of the basal cells to 40 µm long × 25 µm wide; walls of basal cells with small indistinct trigones and semi-straight walls without any intermediate thickenings, walls and cavities brownish red. Median cells of underleaves vary in shape and size, cells with heavily equally-thickened walls so that the hyaline trigones and intermediate thickenings become indistinct. Median cells of lobule as long as wide or slightly longer than wide, cell cavities to 14 µm long × 9 µm wide; cells near lobule mouth, irregular in shape with flexuose walls, indistinct trigones and occasional small nodulose intermediate thickenings; towards the lobule apex, cells gradually becoming more regular in shape, quadrate to rectangular and the cell walls becoming semi-straight.

Oil bodies of lobe median cells dimorphic. Type One: (1)2(3) per cell, very large, occasionally spherical (2) 3–7 (9) µm in diam. but usually ovoid or ellipsoidal (5) 6–11 (13) × (4) 5–10 (12) µm, finely granular, occurs from basal cells through to central region of the lobe, occupying 3/4 to almost the entire cell lumen. Type One oil bodies larger than chloroplasts (if chloroplasts present at all). Type Two: 2–3 (4) oil bodies per cell, typically small, spherical (1) 2–4 (5) µm in diam. to ovoid or ellipsoidal (2) 3–5 (6) µm × (1) 2–3 (4) µm, subhyaline, without any significant, visible, internal structure i.e. giving the appearance of being almost homogeneous; these oil bodies often similar in size or slightly smaller than chloroplasts, occasionally slightly larger than chloroplasts. Oil bodies of lobule and underleaf of Type One. Asexual reproduction not recognized.

Plants dioecious, male plants slightly smaller than female plants. Androecia subspherical to spicate, 2–4 (6) pairs of bracts, terminal, usually on very short-stalked branches arising from the main stem, or occasionally from secondary branches (stalk with (1) 2–3 (4) vegetative leaf lobes). Gynoecia terminal on main or leading stem often bearing a subfloral innovation arising 3–4 bract-pair cycles back from the perianth or gynoecia. Innermost bract unequally bilobed; bract-lobe, lobule and innermost bracteole all with entire margins. Bract-lobe ovate to oblong, narrowed toward the rounded or subacute-acute apex, bract-lobule ovate–lanceolate, subacute; innermost bracteole free from bracts, oblong-ovate to oblong-obovate, ca. $^1/_2$ bilobed, lobes convex-sided, subacute at apex, entire margins. Marginal cells of bract and bracteole ± subequally thickened, but towards the median cells, trigones becoming large and bulging. One archegonium per gynoecium. Perianth freely emergent, 900 µm long × 500 µm wide, perianth plicate, 1–2 dorsal keels + 2 lateral keels + 1–2 ventral keels, smooth surface, oblong-ovate, tapering towards the apex into a short beak; perianth beak cylindrical, with a smooth mouth but the inner beak surface densely covered with large single-celled protuberances.

Walls of epidermal layer of capsule wall nodular where the lobes extend irregularly for a short distance over the tangential face toward the centre of the cell and have intermediate thickenings near the middle of the longer walls. Spores globose, 35–45 µm at widest axis, spore wall papillae densely distributed, equatorial face interspersed with 8–10 rosettes, 2.5–3 µm wide in the equatorial diameter, bearing a ring of 7–10 conspicuous primary projections, 0.75–1.5 µm long × 0.5–1.0 µm wide at base (often

with a 1.5–2:1 length to width ratio), tapering gradually to a rounded apex, never papillate or bearing secondary short branches.

Etymology. The species epithet *knightbridgei* is named in honour and memory of an esteemed New Zealand conservation botanist and ecologist, Phil (Philip) Ian Knightbridge (1969–2011) who passed away in April 2011. This southern species of Aotearoa-New Zealand is a small tribute to Phil by the senior authors who knew him as a colleague and friend.

Distribution and ecology. This species is currently known from only four collections; two from the shore margin of Paterson Inlet, Stewart Island and two from the Auckland Islands. *Frullania knightbridgei* probably has a more extensive distribution than is currently known and it is quite likely that it resides unrecognized in New Zealand herbaria filed as a form of *F. rostrata*. Nevertheless, it would appear that *F. knightbridgei* is a species of southern distribution and it would be interesting to see if the distribution extends south to the Campbell Islands of the New Zealand botanical region; further field work is required to establish if the species grows on the other two main islands of the New Zealand archipelago, North and South Islands, it should for example be looked for along the Fiordland and Foveaux Strait coastline of the southern South Island. Note the type of *F. pseudomeyeniana* is a high elevation taxon at 1,100 m whereas the New Zealand taxon is seemingly restricted to or near the shoreline or low elevation.

F. knightbridgei is noteworthy in comparison with the majority of *F.* species in New Zealand for it appears to be a salt tolerant species. This is clearly evident in Stewart Island/Rakiura where *F. knightbridgei* was growing on twigs of *Dracophyllum* immediately adjacent the shoreline, at a height of about 50 cm above the sea. It was evident that for at least some periods of the year, this represented a harsh coastal environment where significant exposure to salt spray from violent wave action would be common. Elsewhere, *F. ericoides* reportedly develops in rock crevices exposed to sea in the Madeiran archipelago (Sim-Sim and Sergio 1992), and Schuster (1992) reported a variety of *F. kunzei* growing in mature mangrove swamp forest where salt spray and even rare submersion was possible. The high rainfall of the region, providing fresh water, is possibly a critical factor as Engel and Schuster (1973) described for tidal zone liverworts in southern Chile. Interestingly however, Engel and Schuster (1973) noted for Stewart Island a notable "lack of any Hepaticae in the intertidal zone where sea spray is a factor". At least in the New Zealand botanical region, it is clear this is a habitat area that has traditionally been underexplored for liverworts. It would also be interesting to perform glasshouse experiments to investigate test the extent of salt tolerance in these organisms.

Paratypes: Stewart Island: Rakiura/Stewart Island National Park, 500 m. from North Arm Hut, on bark of *Dracophyllum longifolium* var. *longifolium* overhanging water on margin of Patterson Inlet, canopy of stunted *Dacrydium cupressinum* and *Metrosideros umbellata*, 12 Dec 1999, *M. von Konrat 99/12-10* (AK, F); Auckland Island: Open *Oreobolus* cushion and *Chionocloa* tussock with scattered groves of *Metrosideros*, above Ranui Cove, 50°32'12"S, 166°16'24"E, 11 Dec 1972, *R. Common C893B* (CHR, F).

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A new species of *Solanum* named for Jeanne Baret, an overlooked contributor to the history of botany

Eric. J. Tepe[1,2], Glynis Ridley[3], Lynn Bohs[1]

1 *Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, Utah 84112, USA* **2** *Department of Biological Sciences, University of Cincinnati, 614 Rieveschl Hall, Cincinnati, Ohio 45221, USA* **3** *Department of English, University of Louisville, 2211 South Brook, Louisville, Kentucky 40292, USA*

Corresponding author: *Eric J. Tepe* (eric.tepe@gmail.com)

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Abstract

We describe *Solanum baretiae* **sp. nov.**, a new species of *Solanum* section *Anarrhichomenum*, named in honor of Jeanne Baret, who sailed as the assistant to botanist Philibert Commerson on Louis Antoine de Bougainville's global circumnavigation (1766–1769). The species is similar to *S. chimborazense*, but differs in having larger flowers, more flowers per inflorescence, and different patterns of pubescence on the filaments (pubescent adaxially and glabrous abaxially) and style (papillose to sparsely pubescent). A description, illustration, photos, and comparisons to similar species are included. Also included is a preliminary conservation assessment, along with a brief account of the important role played by Baret during the expedition. The new species appears to be restricted to the Amotape-Huancabamba zone, an area of southern Ecuador and northern Peru known for its exceptional biodiversity.

Resumen

Se describe *Solanum baretiae* **sp. nov.**, una nueva especie de *Solanum* sección *Anarrhichomenum*, en homenaje a Jeanne Baret, quien viajó como asistente del botánico Philibert Commerson en la circunnavegación mundial de Louis Antoine de Bougainville (1766–1769). La especie se asemeja a *S. chimborazense* pero se diferencia de ella por sus flores más grandes, más flores por inflorescencia, y por tener patrones diferentes de pubescencia en los filamentos (pubescentes adaxialmente y glabros abaxialmemte) y el estilo (papiloso a escasamente pubescente). Se presentan una descripción, ilustración, fotos, y comparaciones con especies similares. Se incluye también una estimación preliminar de su conservación, junto con una descripción breve del papel importante que tuvo Baret durante la expedición. La especie nueva parece estar restringida a la zona Amotape-Huancabamba, un área del sur de Ecuador y norte de Perú notable por su excepcional biodiversidad.

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Keywords
Amotape-Huancabamba zone, Andes, Ecuador, Jeanne Baret, new species, Peru, *Solanum* section *Anarrhichomenum*

Introduction

Botanizing in the 15th–19th centuries, when naturalists traveled on board ships that sailed to little known parts of the world, must have been truly extraordinary. The hardships endured on these voyages are unfathomable to field biologists these days and, although many of the plant families seen on voyages across the seas were familiar to European naturalists, many of the genera and nearly all of the species encountered and collected were new to Western science. Discovery on such a grand scale is no longer a reality, but detailed focus on groups of plants reveals that a great deal of diversity remains to be uncovered. Fieldwork associated with the PBI (Planetary Biodiversity Inventory) *Solanum* project has resulted in the collection or description of nearly 50 new species of *Solanum* L. to date (recent examples include Tepe and Bohs 2009, Stern and Bohs 2009, 2010, Farruggia and Bohs 2010, Farruggia et al. 2010, Knapp 2010a, b, Vorontsova and Mbago 2010, Vorontsova et al. 2010), including the new species of *Solanum* sect. *Anarrhichomenum* Bitter from southern Ecuador and northern Peru described here.

Solanum, with an estimated 1500 species, is not only one of the world's largest genera of plants (Frodin 2004), but, considering that it includes the tomato (*S. lycopersicum* L.), potato (*S. tuberosum* L.), and eggplant (*S. melongena* L.), it is also one of the most economically important. The PBI: *Solanum* project is an effort to provide a worldwide revision of *Solanum* and make data freely available online at www.solanaceaesource.org; a taxonomic revision of *Solanum* section *Anarrhichomenum* forms part of this project. The section encompasses a group of 10 to 20 viny species found primarily in mountainous habitats from Mexico to Bolivia (Correll 1962, Nee et al. 2006). It is closely related to the pepino (*S. muricatum* Ait.) and the clade that contains the tomato and potato (Spooner et al. 1993), and is part of the larger Potato clade *sensu* Bohs (2005) and Weese and Bohs (2007). Members of this section can be distinguished by fruits that mature to red or orange, seeds with a prominent wing in most species, and the presence of a single or strongly anisophyllous pair of pseudostipules at each node. Pseudostipules, which are leaf-like, often crescent-shaped appendages located near the point of petiole insertion, are present in several groups within *Solanum* and other genera of Solanaceae. They do not appear to be part of the leaves that they accompany, but are instead interpreted to be the first leaf or leaves of an arrested axillary shoot (for further discussion see Spooner et al. 2004, Peralta et al. 2008). The leaves of many species are also punctate with whitish deposits of crystal sand ("sand punctate" hereafter). Cells containing deposits like these are found in several groups within *Solanum* (Whalen et al. 1986, Bohs 1990, Knapp 1992) and in other groups of angiosperms (Metcalfe and Chalk 1983).

Correll (1962) provided a revision of *Solanum* section *Anarrhichomenum* [as *Solanum* section *Tuberarium* (Dunal) Bitter subsection *Basarthrum* Bitter series *Appendiculata* Rydb.] in his monograph of the potatoes *s.l.* Subsequent studies have clarified the limits of the section as well as many of its component species using a variety of techniques, including morphological examination of the plants, pubescence, pollen, and chromosomes (Anderson 1979a, 1979b, Anderson and Gensel 1976, Anderson and Levine 1982, Seithe and Anderson 1982, Levine and Anderson 1986, Bernardello and Anderson 1990, Anderson et al. 1999), biosystematic studies (Mione and Anderson 1992), analyses of foliar flavonoids (Anderson et al. 1987), and, most recently, molecular techniques (Spooner et al. 1993, Anderson and Jansen 1994). Despite this attention, other species of *Solanum* section *Anarrhichomenum* remain poorly understood and new species exist. The section is currently under revision by the first author, who is attempting to update Correll's (1962) treatment. This study will incorporate results from the studies mentioned above, specimens from extensive collecting in recent decades, and data derived from additional morphological and molecular studies. During this work, the following new species was recognized.

Throughout this paper, herbarium barcodes and accession numbers are listed in brackets; barcode numbers include the herbarium acronym within the brackets, whereas accession numbers are listed as the number only, without the acronym.

Taxonomic treatment

Solanum baretiae **Tepe, sp. nov.**
urn:lsid:ipni.org:names:77116659-1
http://species-id.net/wiki/Solanum_baretiae
Figs 1–2

Diagnosis. Solano chimborazensi *Bitter primo adspectu maxime similis sed floribus maioribus et pilis e filamentis abaxialiter plerumque carentibus differt.*

Type. PERU: Cajamarca: Prov. Contumazá, Bosque de Cachil, 2500 m, 28 Jun 1992 (fl), *A. Sagástegui A. et al. 14710* (holotype: HUT [028009] (photo); isotypes: F [2114228] (photo), GB [0167885], NY [NY00726434]).

Description. Vine, trailing along ground or climbing on other vegetation to 3 m or more, rooting at the nodes. Stems slender, woody, moderately to densely covered with crisped transparent to tawny pubescence of unbranched, eglandular, multicellular trichomes. Sympodial units plurifoliate, not geminate. Leaves simple to 7-pinnate, most commonly 3–5-pinnate, the blades 0.8–12 × 0.5–8 cm, chartaceous, moderately to densely pubescent adaxially and abaxially, sand punctate abaxially, the rachis densely pubescent, the margins entire to irregularly revolute resulting in somewhat undulate margins, the leaflets decreasing markedly in size toward the base of the leaf, the distal leaflet of the lowermost pair typically smaller than its match or completely absent; interjected leaflets absent; lateral leaflets 0.3–3.5 × 0.2–1.5 cm, ovate to elliptic, the bases

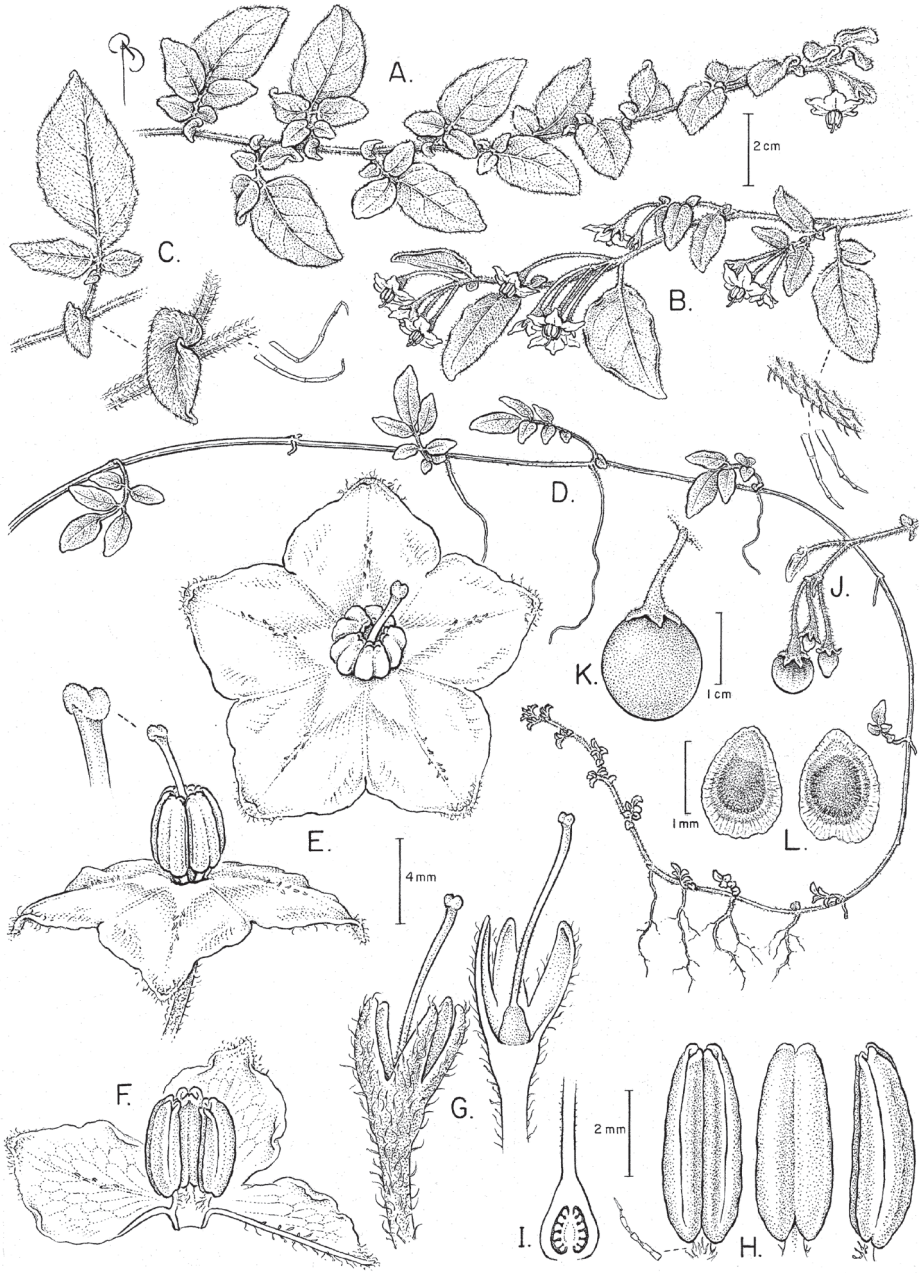

Figure 1. *Solanum baretiae* Tepe. **A** Habit of flowering branch **B** Flowering branch with close-up of pubescence **C** Pseudostipules with close-up of pubescence **D** Habit of vegetative branch **E** Flower and detail of stigma **F** Longitudinal section of flower **G** Calyx (left) and longitudinal section of calyx, showing ovary (right) **H** Stamens in ventral, dorsal, and side view with close-up of pubescence **I** Longitudinal section of ovary **J** Infructescence with immature fruits **K** Fruit, mature **L** Seeds. [**A** and **J** drawn from Tepe et al. 2888; **B–D, F–I** drawn from Tepe et al. 2886; **E** drawn from Tepe et al. 2885; **K–L** drawn from Bohs et al. 3735].

rounded to truncate, oblique, the apices obtuse to acute, the petiolules nearly lacking to 2 mm long, moderately to densely pubescent; apical leaflet 1.2–8(–9.5) × 0.7–3(–4) cm, ovate to elliptic to oblong, the apex obtuse to acute to acuminate, the base obtuse to truncate to cordate, the petiolules nearly lacking to 7 mm long, moderately to densely pubescent; petioles 0.1–2.5(–4.5) cm, moderately to densely pubescent. Pseudostipules present at most nodes, one per node, 0.5–1.5 × 0.4–0.8 cm, obliquely ovate to elliptic, sometimes lunate, the apices obtuse to acute, the bases sometimes strongly lobed, oblique. Inflorescence 1.5–3.5 × 1–3 cm, extra-axillary on main stems or terminal on short, axillary spur shoots, simple to sometimes once branched in the extra-axillary inflorescences, with 1–8 flowers (1–3 on spur shoots [mean = 1.9], 3–8 on main stems [mean = 4.6]), with all flowers apparently perfect, the axes densely pubescent; peduncle 0.5–1 cm long; rachis nearly lacking to 1.5 cm; pedicels 7–15 mm in flower, 10–20 mm in fruit, somewhat expanded distally in flower and fruit, spaced contiguously to 6 mm apart, articulated at the base. Spur shoots 0.5–3.5(–8) cm long, bracteate, with 2–8 bracts per shoot, the bracts similar in shape to the cauline leaves, simple to occasionally 3–5-pinnate, 1–15 mm long, with minute pseudostipules. Calyx 4–5 mm long, the tube 1–2.5 mm long, the lobes 2.5–3.5 × ca. 1.5 mm, ovate-lanceolate to oblong, acute at tips, moderately pubescent, sand punctate; fruiting calyx slightly accrescent, the lobes 4–4.5 × 1.5–2 mm, ovate-lanceolate to oblong. Corolla 0.8–1.5 cm in diameter, 2–6 mm long, pentagonal, white to violet, sometimes with yellow at tips or along the midveins of lobes, flat to strongly reflexed at anthesis, the lobes 1.5–5 × 3–5 mm, acute at apices, glabrous adaxially, moderately to densely pubescent abaxially along midvein of lobes, the trichomes becoming shorter toward the densely pubescent apices of the corolla lobes, the margins densely ciliate apically. Stamens equal, with filaments 0.5–1.5 mm long, nearly free to fused for about ½ their lengths, somewhat broadly flattened, nearly glabrous abaxially, densely pubescent adaxially and on margins; anthers 3–4.5 × 1–1.2 mm, oblong, incurved, connivent, yellow, the pores large, directed distally, opening into latrorse-introrse longitudinal slits with age. Ovary glabrous to sparsely pubescent; style 5–7 × 0.1–0.2 mm, exceeding stamens by 1.5–5 mm, cylindrical, glabrous to papillose in lower ½ to sparsely pubescent with long trichomes in the middle or in the lower ½; stigma capitate. Fruits 2–2.5 × 1.5–2 cm, ellipsoidal, rounded to very slightly obtusely pointed at apex, green with darker mottled striping when immature, orange when mature, glabrous to sparsely pubescent when young. Seeds 3–4.2 × 2–4 mm, flattened, lenticular, rounded to teardrop-shaped, with a 0.2–1 mm wide wing around the margins, the thickened part of the seed 1.8–2.2 × 1.5–2 mm, rounded to reniform, light to medium brown, the surface smooth, the wing yellowish-tan to transparent near the margins, with radial striations.

Distribution and ecology. *Solanum baretiae* is apparently endemic to the Amotape-Huancabamba zone of southern Ecuador and northern Peru and grows in the understory of montane forests and disturbed roadside and pasture vegetation, 1900–3000 m in elevation. The areas where *S. baretiae* has been collected are seasonally dry.

Phenology. Flowering specimens have been collected from Jun–Aug and Oct; fruiting specimens have been collected in May–Jun.

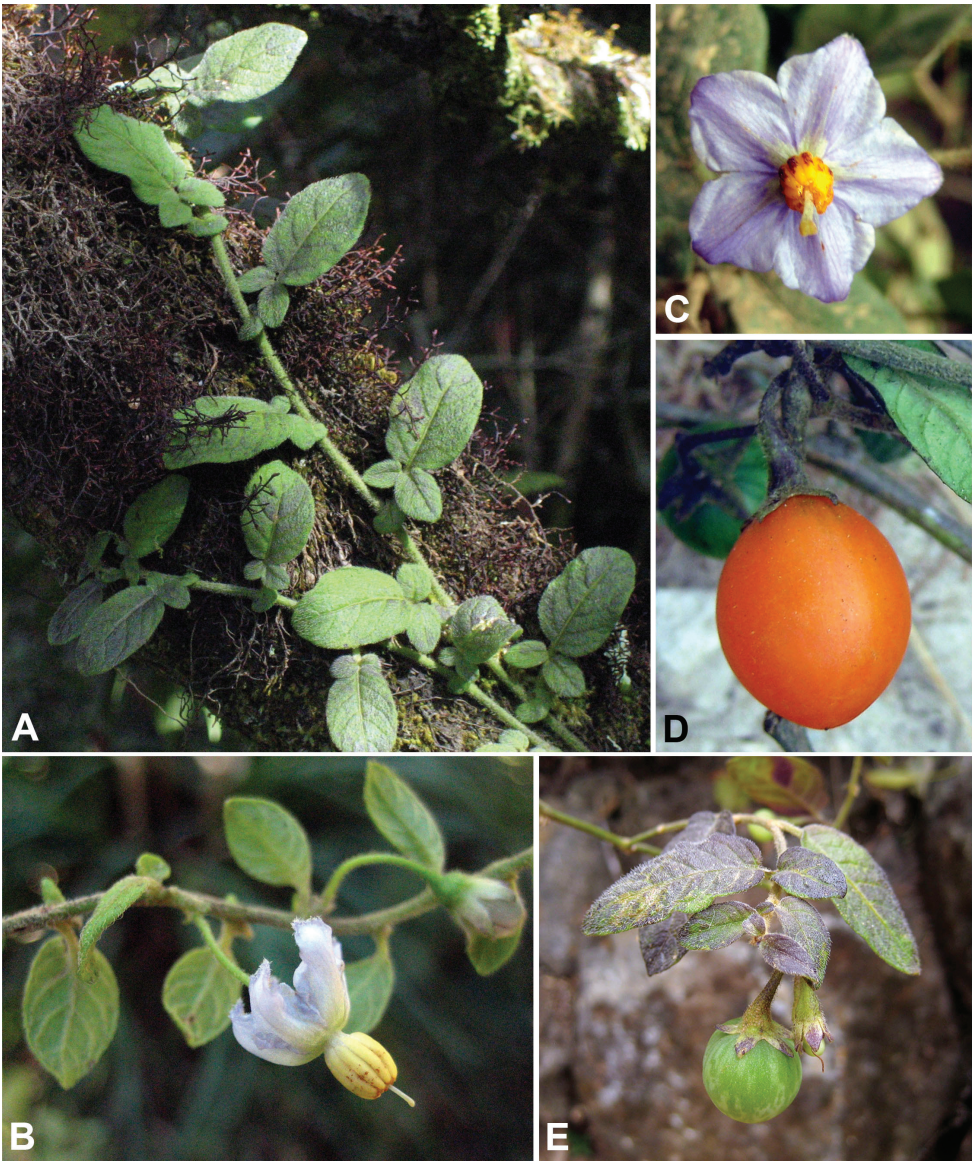

Figure 2. *Solanum baretiae* Tepe. **A** Habit **B** Flower showing reflexed corolla and bud **C** Flower with flat corolla **D** Mature fruit **E** Immature fruit; note mottling, which is absent in the mature fruit. [**A–B** Tepe and McCarthy 3346; **C** Tepe et al. 2885; **D** Bohs et al. 3735; **E** Tepe et al. 2888].

Etymology. *Solanum baretiae* is named in honor of the botanist Jeanne Baret, the first woman to circumnavigate the earth (see below).

Preliminary conservation status. According to the IUCN Red List Categories (IUCN 2011), *S. baretiae* is classified as Data Deficient (DD). Although *S. baretiae* occurs over a broad geographic range (> 60,000 km^2), it has been collected at fewer than 10 localities (localities within a few kilometers of each other have been grouped for this

assessment) and from a narrow elevational band within its range. The relatively small number of collections of this species suggests that it is rare in the habitats where it occurs. Furthermore, these localities are near expanding population centers and habitats in these areas are highly fragmented and degraded. Nevertheless, *S. baretiae* seems to be well suited to habitat change caused by human activities, since EJT and LB observed thriving populations along roadsides and among shrubs between the town of Guzmango (Dept. Cajamarca, Peru) and the cultivated and pasture lands that surround the town. Further data regarding the distribution and abundance of *S. baretiae* are needed before we can make a more solid assessment of its conservation status.

Specimens examined. ECUADOR. Loja: 15 km S of Yangana, 4°25.43'S, 79°8.78'W, 2450 m, 31 Jul 2011 (fl), *E.J. Tepe and M. McCarthy 3346* (BM, MU, NY, QCNE, UT); Gualel, 3°43.5'S, 79°23.0'W, 2900 m, 10 Jun 1995 (fl, fr), *V. van den Eynden & E. Cueva 433* (NY). **PERU. Cajamarca:** Prov. Contumazá, Guzmango, 7°23.12'S, 78°53.73'W, 2600 m, 6 Jun 2010 (fr), *L. Bohs et al. 3735* (photos only); Prov. San Miguel, Miravalles Alto, Bolívar, 2600 m, 25 Aug 1991 (fl), *S. Llatas Quiroz 3021* (NY); Prov. Contumazá, alrededores de Guzmango, 2600 m, 27 Jul 1973 (fl), *A. Sagástegui A. 7711* (HUT, NY); Prov. Cajamarca, Namora–Matra, 2600 m, 16 Aug 1973 (fl), *A. Sagástegui A. 7751* (NY); Prov. San Miguel, entre Calquis y Llapa, 2400 m, 13 May 1977, *A. Sagástegui A. et al. 8863* (HUT, MO, NY); Prov. Contumazá, Contumazá–Ascabamba, 2700 m, 12 Jun 1981 (fl), *A. Sagástegui A. et al. 9991* (MO, NY); Prov. Contumazá, Santiago, 2450 m, 13 Jun 1983 (fl), *A. Sagástegui A. & S. López 10606* (BM, F, MO, NY); Prov. Contumazá, entrada al Bosque Cachil, 2500 m, 29 Jul 1993 (fl), *A. Sagástegui A. et al. 14982* (HUT, MO, NY); Prov. Contumazá, Bosque Cachil, 7°24.38'S, 78°46.88'W, 2500 m, 17 Oct 2010 (st), *E.J. Tepe et al. 2882* (HAO, USM, UT); Prov. Contumazá, ca. 5 km S of tunnel on Contumazá–Bosque Cachil road, , 2625 m, 17 Oct 2010 (st), *E.J. Tepe et al. 2884* (HAO, USM, UT); Prov. Contumazá, ca. 5 km S of tunnel on Contumazá–Bosque Cachil road, 7°24.33'S. 78°46.88'W, 2625 m, 17 Oct 2010 (fl), *E.J. Tepe et al. 2885* (BM, HAO, NY, PLAT, USM, UT); Prov. Contumazá, Contumazá–Guzmango road, 7°22.62'S, 78°53.63'W, 2850 m, 18 Oct 2010 (fl), *E.J. Tepe et al. 2886* (BM, HAO, NY, PLAT, USM, UT); Prov. Contumazá, Guzmango, 7°23.12'S, 78°53.73'W, 2600 m, 18 Oct 2010 (fl, fr), *E.J. Tepe et al. 2888* (BM, CINC, HAO, NY, USM, UT). **Lambayeque:** Prov. Ferreñafe, Bosque de Chiñama, 2300–2700 m, 15 Aug 1988 (fl), *A. Cano 2125* (NY); Prov. Lambayeque, Abra la Porculla, road from Olmos–Pucará, km 45 E of Olmos, 1920 m, 13 Jul 1986 (fl), *T. Plowman et al. 14284* (NY). **La Libertad:** Prov. Otuzco: abajo de Shitahoura (oeste de Salpo), 3000 m, 11 Jun 1992 (fl), *S. Leiva & P. Leiva 582* (NY); Prov. Otuzco: alrededores de San Andrés, 2560 m, 1 Jul 1992 (fl), *S. Leiva & J. Ullilen 646* (MO).

Discussion. *Solanum baretiae* is a striking species with its relatively large, pentagonal corollas in shades of violet, yellow, or white (Fig. 2B), and its soft-pubescent leaves that range from simple to 7-foliolate. Specimens of *S. baretiae* have been previously identified as the Ecuadorian *S. chimborazense* Bitter, from which it differs by its larger corollas (0.8–1.5 cm in *S. baretiae* vs. < 1 cm in diameter in *S. chimborazense*),

styles that are papillose or only sparsely pubescent (vs. densely pubescent with long trichomes in *S. chimborazense*), more flowers per inflorescence (1–8 in *S. baretiae* vs. mostly 1, but up to 3 in *S. chimborazense*), and filaments that are pubescent adaxially, but glabrous abaxially (vs. evenly pubescent on all surfaces in *S. chimborazense*). *Solanum baretiae* is sympatric with the exceedingly rare *S. chachapoyasense* Bitter but the latter species has stellate corollas (vs. pentagonal in *S. baretiae*), long filaments (3–3.5 mm in *S. chachapoyasense* vs. 0.5–1.5 mm in *S. baretiae*), and strictly simple leaves (vs. simple to 7-foliolate in *S. baretiae*). *Solanum baretiae* is also sympatric with several species of *Solanum* section *Basarthrum* (Bitter) Bitter, which can be scandent shrubs with compound leaves and somewhat similar flowers. These species, however, can easily be differentiated by the distinctive two-celled "bayonet" trichomes that characterize *Solanum* section *Basarthrum* (Seithe and Anderson 1982).

The Andean species of *Solanum* sect. *Anarrhichomenum* are typically found in mid- to high-elevation cloud forest habitats that are moist throughout the year. *Solanum baretiae* appears to be an exception to this rule, however, as it occurs in forests and disturbed areas on the western slopes of the Andes which, in the latitudes of the Huancabamba-Amotape zone, experience a marked dry season.

As mentioned above, the number of leaflets in this species is highly variable, with the leaves ranging from simple to compound with seven leaflets. Seedlings and young vegetative shoots typically have compound leaves with five leaflets, whereas the number of leaflets on fertile shoots is much more variable. In general, the number of leaflets, along with the size of the lateral leaflets, decreases along the length of fertile shoots, and the leaves in the proximity of the flowers and fruits are, in many cases, simple or have only one or two tiny lateral leaflets. The number of leaflets is variable in many species of *Solanum* sect. *Anarrhichomenum*, but the range of variability seen in *S. baretiae* is shared only with that of *S. sodiroi* Bitter (Anderson et al. 1999).

This species in named in honor of Jeanne Baret (1740–1807), an unwitting explorer who risked life and limb for love of botany and, in doing so, became the first woman to circumnavigate the world (Ridley 2010).

Jeanne Baret sailed on the ship *L'Étoile* in 1766 and embarked on the first French circumnavigation of the globe under the command of Louis Antoine de Bougainville (1729–1811) as assistant to the botanist Philibert Commerson (1727–1773). Since French naval regulations prohibited women being on board ship, Baret disguised herself as a man to join the expedition, and continued to wear men's clothes during her time on the ship. Baret was Commerson's lover, but was also an accomplished botanist in her own right and evidence suggests that she made some of the expedition's most notable collections, including the showiest, most enduring botanical specimen from the expedition: the vine that would be named in honor of its commander, *Bougainvillea* Comm. ex Juss.

Commerson and Baret (though uncredited) amassed over six thousand specimens that are incorporated into the French National Herbarium at the *Muséum National d'Histoire Naturelle*. In the course of the expedition and the years after its successful completion, over seventy species would be named in honor of Com-

merson using the specific epithet *commersonii.* Expedition records show that Commerson was frequently unable to collect specimens in the field because of his health issues (Vivès 1766-1769) and, at these times, Baret took the part of the expedition's chief botanist. Yet, today, despite the important role she played, not a single species is named after her. Commerson's notes reveal that he intended to name a Malagasy genus *Baretia* (MS 887 of the Commerson archive in the *Muséum National d'Histoire Naturelle*), but it was never published (the species concerned are now placed in *Turraea* of the Meliaceae). The fact that individual plants of this genus that Commerson collected with Baret have leaves that are highly variable in shape perhaps struck him as a neat reflection of the multi-faceted companion who united seemingly contradictory qualities (Monnier et al. 1993): a woman dressed as a man, a female botanist in a male-dominated field, and a working class woman who had traveled farther than most aristocrats. Given the importance of her work and the singular nature of her achievements, Baret has clearly made a sufficient contribution to the field to deserve a species named after her. Following Commerson's example, we believe that this new species of *Solanum*, with its highly variable leaves, is a fitting tribute to Baret.

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Eight new species of *Cestrum* (Solanaceae) from Mesoamerica

Alex K. Monro[1]

1 *Department of Botany, The Natural History Museum, London SW2 5SY, UK*

Corresponding author: *Alex K. Monro* (a.monro@nhm.ac.uk)

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Abstract

As part of the preparation of a taxonomic revision of *Cestrum* (Solanaceae) for Flora Mesoamericana eight hitherto undescribed species from Mexico, Guatemala, Costa Rica and Panama were identified. These eight new species are described and illustrated. Affinities of the species are discussed and Global Species Conservation Assessments presented. The new species are *Cestrum amistadense* A.K. Monro, **sp. nov.** (Vulnerable) which most closely resembles *Cestrum longiflorum* Ruiz & Pav., *Cestrum contrerasianum* A.K. Monro, **sp. nov.** (Vulnerable) which most closely resembles *Cestrum formosum* C.V.Morton, *Cestrum darienense* A.K. Monro, **sp. nov.** (Near Threatened) which most closely resembles *Cestrum morae* Hunz., *Cestrum gilliae* A.K. Monro, **sp. nov.** (Near Threatened) which most closely resembles *Cestrum morae, Cestrum haberii* A.K. Monro, **sp. nov.** (Vulnerable) which most closely resembles *Cestrum poasanum* Donn. Sm., *Cestrum knappiae* A.K. Monro, **sp. nov.** (Near Threatened) which most closely resembles *Cestrum acuminatum* Francey, *Cestrum lentii* A.K. Monro, **sp. nov.** (Near Threatened) which most closely resembles *Cestrum johnniegentrianum* D'Arcy and *Cestrum talamancaense* A.K. Monro (Least Concern) which most closely resembles *Cestrum laxum* Benth.

Keywords

Central America, Conservation Assessments, Costa Rica, Flora Mesoamericana, Guatemala, Mexico, Panama

Introduction

The genus *Cestrum* (Solanaceae) includes ca. 150 species (Nee 1986, 2001; Benítez and D'Arcy 1998) of moth, butterfly and hummingbird pollinated small trees, shrubs, vines and robust herbs from the New World tropics and subtropics. Within the Solanaceae

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Cestrum is characterised by nearly actinomorphic flowers, small, persistent calyces, long-tubular corollas, small longitudinally dehiscent anthers held close to the corolla mouth, superior ovaries (Benítez and D'Arcy 1998) and few-seeded berries. *Cestrum* also frequently has truncated side branches subtended by a leaf at each node which can give the superficial appearance of an opposite arrangement of unequal leaves. Cytologically, *Cestrum*, together with its sister genus *Sessea* is unusual for the absence of typical angiosperm telomeres associated with chromosome ends (Sykorova et al. 2003). With respect to economic value, a number of species are cultivated for their brightly coloured flowers and or fragrance (Beckett 1987) and many represent invasive or potentially invasive species within the tropics, especially on islands in the Pacific Ocean (Mauchamp 1997, Pattison et al. 1998, Space et al. 2003).

The genus *Cestrum* was established by Linnaeus in 1753 (Linnaeus 1753) to accommodate material of two species, *C. nocturnum* L. and *C. diurnum* L. Complete revisions of *Cestrum* have since been undertaken by Dunal (1852) and Francey (1935, 1936). Local treatments exist for the Antilles (Schulz 1909), Guatemala (Gentry and Standley 1974), Nicaragua (D'Arcy 2001), Costa Rica (Standley and Morton 1938), Panama (D'Arcy 1973), Venezuela (Benítez de Rojas and D'Arcy 1998) and Veracruz, Mexico (Nee 1986). As part of this author's preparation of a revisionary treatment for *Flora Mesoamericana*, eight currently undescribed species were discovered.

The taxonomy of *Cestrum* is complicated by a high proportion of synonyms and unidentified collections. Nee (unpublished) encountered ca. 640 valid names for what he considered to be ca. 150 species. In addition, a relatively high proportion of collections in herbaria remain unidentified to species. Of the 2147 collections examined as part of a taxonomic revision for Flora Mesoamericana, 1003 were identified to species at the time of their accession and 266 were identified subsequent to their incorporation, resulting in 737 (ca. 1/3) collections unidentified to species prior to beginning the Flora Mesoamericana treatment.

Materials and methods

Two thousand one hundred and forty-seven collections of *Cestrum* from A, BM, F, G, GH, INB, LL, MO, NY, PMA, TEX and US (http://sweetgum.nybg.org/ih/) were examined. Material examined was assigned to ca. 60 morphospecies. Morphospecies were designated on the basis of a visual sort. Morphological characters used for this were the presence of 'minor' leaves associated with truncated side branches, leaf shape, texture and size, distribution, inflorescence disposition and size, bract size and shape, calyx and corolla morphology and fruit size, shape and colour. Morphospecies were then examined under a Willd M3C binocular microscope and Planapo lens at X64 to × 400 magnification and a maximum of 117 morphological observations were made for each morphospecies. The morphological characters used included those established by Dunal, Francey and D'Arcy together with axillary bud colour, size and pubescence,

position of the petiole, leaf length : width ratio, distribution of the inflorescences on the plant stem, organisation of the flowers in the inflorescence and seed surface morphology. Pubescence was described in terms of hair division, gland association, orientation, shape, size and density. Hair division was classified as simple versus branched and branched hairs were classified as dendritic, stellate etc. Orientation was classified as erect or appressed and shape as straight, curved or crooked. Hair density was somewhat problematic as observations were not taken per square cm but as visual appraisals made using a microscope. Pubescence was arbitrarily classified as dense, sparse or moderate. Modified leaves associated with the inflorescences are described as bracts or bracteoles. Bracts which subtend the pedicel are referred to as bracteoles; those which subtend other parts of the inflorescence are termed bracts.

Following the above detailed examination, the morphospecies were reduced to 47 in number. This reduced number of morphospecies were then associated with validly published names or determined to be undescribed species through a comparison with type material. This resulted in the following eight undescribed species being recognised from the 47 morphospecies.

Conservation Assessments were undertaken using IUCN criteria B, 'Geographic range,' in the form of either B1 (extent of occurrence) or B2 (area of occupancy) and A, 'Population reduction' (IUCN 2001). Species distributions were plotted using Google Earth and Extent of Occurrence or Area of Occupancy calculated using the grid and ruler tools. In addition, using Google Earth it was possible to assess the nature of the vegetation cover, urbanisation and road proximity at localities, which were used as indicators of plausible future threats. The risks of doing so (Sheppard and Cizek 2009) were considered low with respect to this application of the Google Earth visualisation system.

Taxonomic treatment

Cestrum amistadense **A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116661-1
http://species-id.net/wiki/Cestrum_amistadense
Figs 1 A–D, 2 A–C

Diagnosis. Most similar to *Cestrum langeanum* D'Arcy from which it can be distinguished by the shiny upper leaf surface that is characteristically shrunken around the primary and secondary veins, the raised quaternary and quinternary veins on the upper leaf surface, the glabrous peduncle and the longer inflorescence.

Type. PANAMA. Bocas del Toro: La Amistad Binational Park, La Pata del Cedro camp, ca. 1750 m, 09°04'27"N, 82°44'17W (DMS), 11 Mar 2004, *A. K. Monro & E. Alfaro 4328* (holotype: PMA; isotypes: BM000849623, INB).

Description. Shrubs, 0.4–2.0 m. Leaf–bearing stems drying brown, yellow–brown or olive green, the internodes 25–55 × 1.375–4.0 mm; young stems glabrous. Axillary

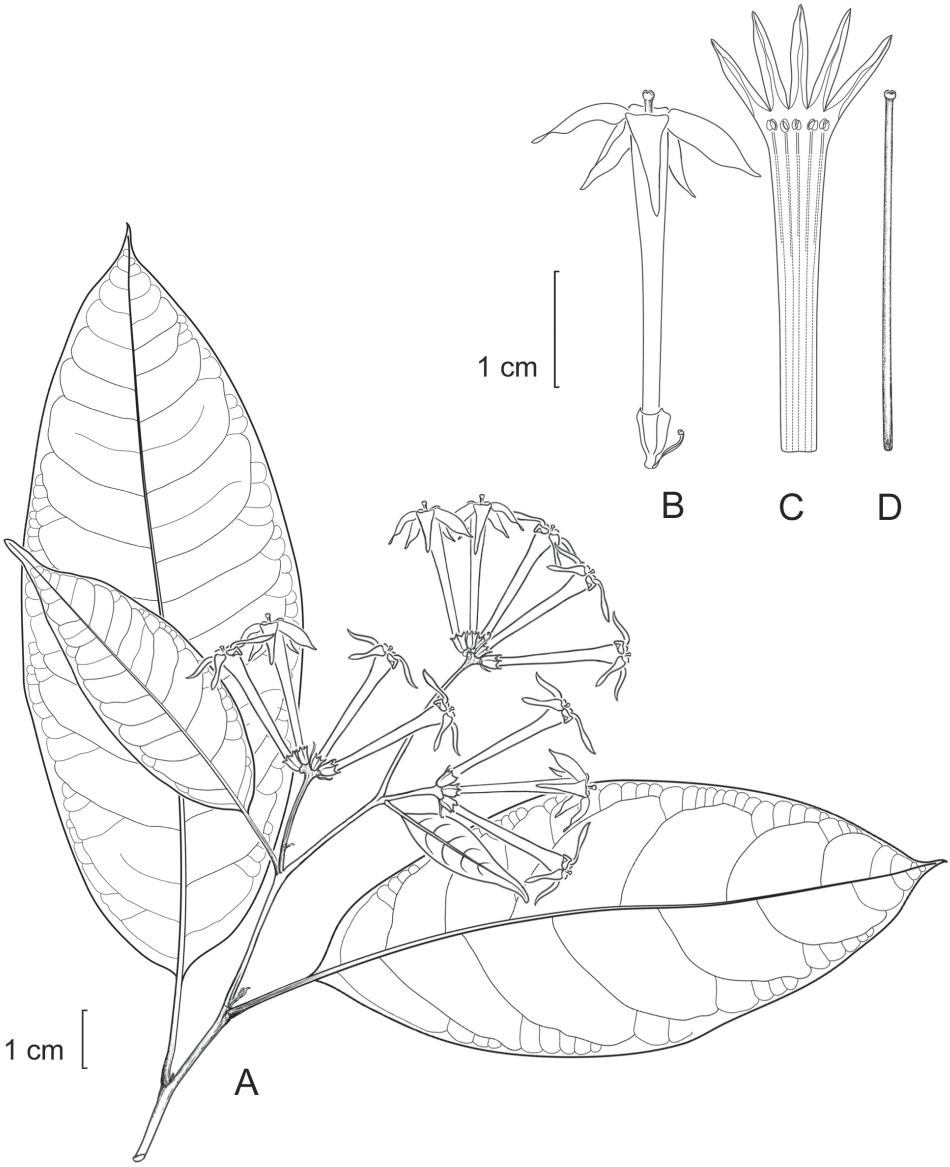

Figure 1. *Cestrum amistadense* A.K.Monro **A** Flowering stem **B** Flower **C** Longitudinal section through the corolla showing stamen arrangement **D** Style. Drawn from *A.K. Monro & E. Alfaro 4328*(BM).

buds 0.5–1.0 mm, drying dark brown to brown, sparsely pubescent or glabrous, not subtended by a minor leaf. Lamina 90–225 × 26–100 mm, length to width ratio 2.1–3.5, oblong–ovate, ovate, ovate–elliptic, elliptic, or lanceolate, coriaceous, drying yellow–green, brown or dull olive green above, paler below; the upper surface glabrous, primary to quarternary veins, (occasionally primary and secondary only) raised and clearly visible to the naked eye; the lower surface glabrous, primary and secondary, pri-

mary to tertiary or primary to quinternary veins raised and clearly visible to the naked eye, secondary veins 6–13 pairs, borne 65–80° to the midrib, irregularly and weakly curved, decurrent, the veinlets visible or not, where visible unbranched or branched; base obtuse to decurrent or asymmetrically acute-cuneate, obtuse, or decurrent; margin entire; apex subcuspidate to cuspidate or acute; petioles 7–25 × 1.25–2.50 mm, drying green, dark brown or yellow–brown, glabrous. Inflorescences 1–3 per herbarium sheet, terminal or subterminal panicles, axillary panicles solitary in each axil, ca. 105 mm long, bearing 7–21 flowers borne in 2–6 clusters, each cluster bearing 3 or 4 flowers; peduncle 25–37 × 1.0–1.5 mm, drying green–brown, yellow–brown or brown, glabrous; bracts 3–100 × 0.75–31.0 mm, leaf–like to bracteole–like; bracteoles 3.0–3.5 mm, linear, glabrous. Flowers pedicellate, the pedicels 0.50–0.75 mm; calyx 3.25–4.50 × 2.0–2.25 mm, the outer surface glabrous, the lobes 5, 0.50–0.675 mm, erect; corolla pale purple to lilac, 26–34 mm long, the tube 26–28 mm long, 3.0–3.5 mm in diameter at the mouth, ca. 1.25 mm in diameter at the base, glabrous, the lobes 5, 6.5–8.0 mm long; stamens 5, the filaments 23.5–26.0 mm long, equal, adnate for 19.0–20.5 mm of their length, glabrous, a lobe–like appendage present at insertion point, the anthers ca. 1 × 0.675–0.750 mm; style 24.5–26.0 mm, the stigma 0.375–0.50 × 0.75–1.25 mm. Infructescences 25-80 mm long, bearing 5–12 fruit; fruiting calyx 3.5–4.0 × 7–8 mm; fruit not seen.

Etymology. From the locality of the holotype, La Amistad Binational Park in Costa Rica and Panama.

Distribution. Premontane, montane, cloud and oak forest from 900 m to 2100 m. Collection notes indicate that this species is restricted to undisturbed or 'high' forest. Existing collection localities suggest that *Cestrum amistadense* is distributed over an area of ca. 7,360 km^2 of the Fila Costeña and the Talamanca Mountains in eastern Costa Rica and western Panama (Google Earth, accesssed April 21 2011, images from 2011).

Discussion. Of the six known collections of *Cestrum amistadense*, none had been previously determined to species. Comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *Cestrum amistadense* as most similar to *C. langeanum* D'Arcy and *C. longiflorum* Ruiz & Pav. It can be distinguished from those species by the presence and distribution of pubescence, leaf surface, venation and inflorescence morphology as summarised in Tables 1 and 2.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum amistadense* is considered Vulnerable based on subcriteria B: Extent of Occurrence <20,000 km^2 (B1), a severely fragmented range and small number of collection localities (B1a) and continuing decline in the area of habitat due to the conversion of forest to agricultural land (B1b).

Paratypes. COSTA RICA. Limón: Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut, siguiendo la fila divisoria entre Ríos Lari y Dapari, cuenca superior de ambos, 09°22'45"N, 83°06'15"W (DMS), 1900 m, 24 Mar 1992, *B. Hammel 5474* (INB, MO); Puntarenas: Cantón de Osa, Río Piedras Blancas, junto a la casa, faldas Cerro Anguciana, Fila Cruces, 900 m, 08°49'02"N, 83°11'23"W (DMS), 9 Dec 1993,

Figure 2. *Cestrum amistadense* A.K.Monro **A** Habit. **B**. Inflorescence **C** Flowers. *A.K. Monro & E. Alfaro 4415* (Photo A.K.Monro 2004).

Table 1.

Characters	*C. amistadense*	*C. langeanum*
Upper leaf surface morphology	shiny and shrunken around primary and secondary veins	matte, not appearing shrunken around primary and secondary veins
Upper leaf surface quarternary and quinternary veins raised	yes	no
Peduncle pubescence	glabrous	pubescent
Inflorescence length in flower	ca. 105 mm	21–55 mm

Table 2.

Characters	*C. amistadense*	*C. longiflorum*
Lower leaf surface pubescence	glabrous	pubescent
Upper leaf surface quarternary and quinternary veins raised	yes	no
Peduncle pubescence	glabrous	pubescent
Bracteole length	3.0–3.5 mm	2.5 mm

R. Aguilar, D. Gómez, M. Grayum & B. Hammel 2732 (BM, INB). PANAMA. Bocas del Toro-Chiriquí border: end of Río Palo Alto road to Chiriquí border with Bocas del Toro, near peak of Cerro Macho, 08°49'N, 082°23'W (DMS), 2200 m, 20 Nov 1978, *B. Hammel 5799* (MO); La Amistad Binational Park, Quebrada by Campamiento Lucio, 09°05'03"N, 082°45'44"W (DMS), 1850 m, Mar 16 2004, *A. K. Monro & E. Alfaro 4415* (INB, MO, PMA); Chiriquí: end of road past Palo Alto northeast of Boquete 2100 m, 8 Feb 1979, *B. Hammel 6062* (MO); trail to Cerro Pate Macho, headwaters of the Río Palo Alto, above Palo Alto, 1700–2100 m, 08°47'N, 82°22'W (DMS), 24 Apr 1982, *S. Knapp & R. Schmalzel 4766* (MO).

***Cestrum contrerasianum* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116662-1
http://species-id.net/wiki/Cestrum_contrerasianum
Fig. 3 A–C

Diagnosis. Most similar to *Cestrum formosum* C.V. Morton from which it can be distinguished by its more compact inflorescences, bearing flowers on shorter pedicels with pubescent calyces and longer corolla tubes.

Type. GUATEMALA. Baja Verapaz: Union Barrios, 15°11'01"N, 090°12'16"W (DMS), 1630 m, 11 Mar 1972, *E. Contreras 11234* (holotype: F-1942896; isotype: MO).

Description. Shrubs, 1–7 m. Leaf–bearing stems drying pale red–brown or tan, the internodes 2–34 × 1.5–3.5 mm; young stems glabrous, occasionally sparsely pubes-

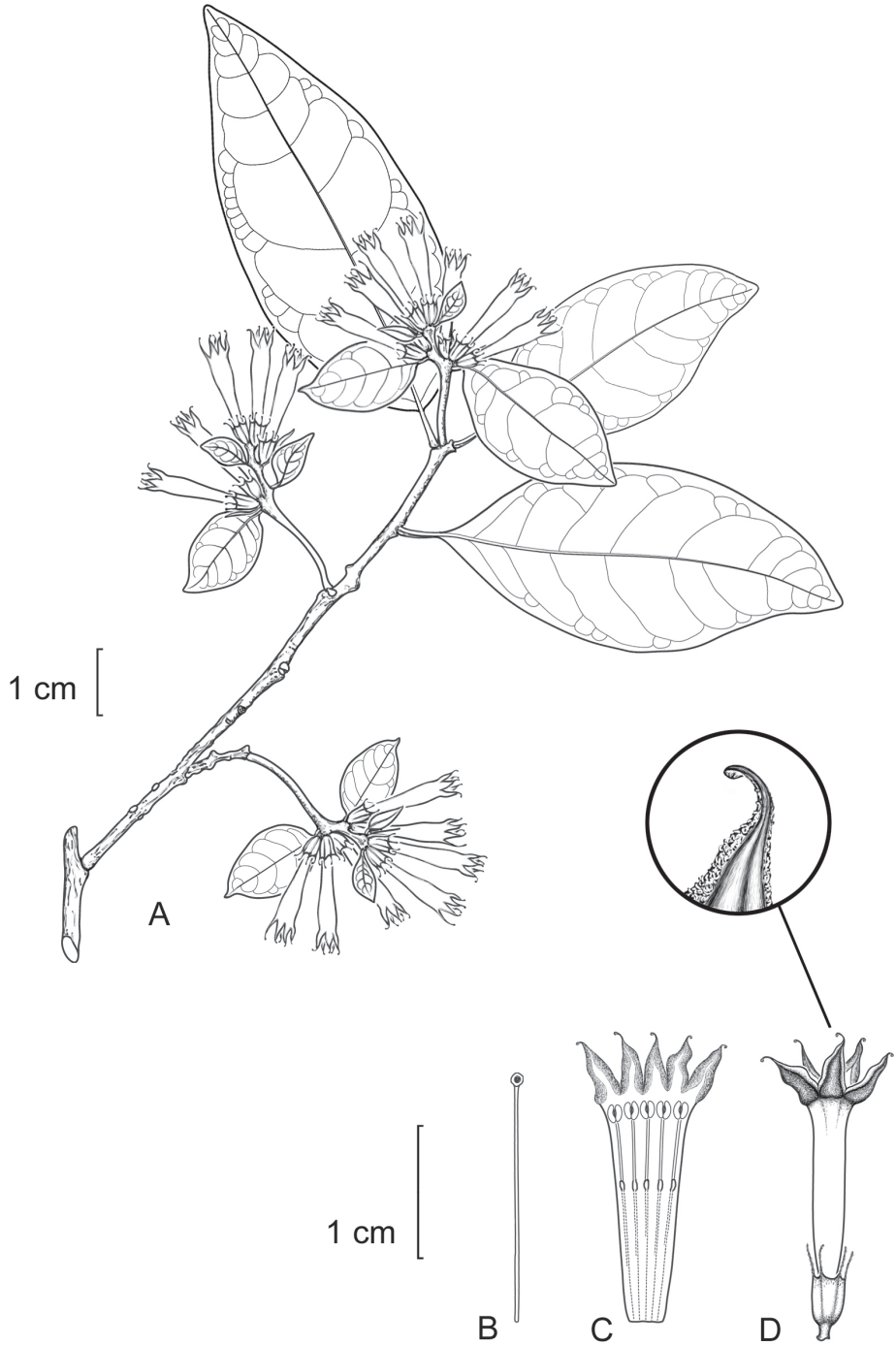

Figure 3. *Cestrum contrerasianum* A.K.Monro **A** Flowering stem **B** Style **C** Longitudinal section through the corolla showing stamen arrangement **D** Flower with apex of corolla lobe highlighted. Drawn from *E. Contreras 11234* (F).

cent, where pubescent the hairs 0.375 mm, simple, appressed, crooked and frequently glandular. Axillary buds 1.25–2.0 mm, frequently absent, drying dark brown, densely pubescent and glandular, not subtended by a minor leaf. Lamina 13–135 × 6–42 mm, length to width ratio 1.5–3.6, obovate, elliptic to ovate, coriaceous, drying olive green, brown or yellow–green above; the upper surface glabrous or very sparsely pubescent, the hairs 0.125 mm, simple, weakly appressed, crooked, occasionally sparsely glandular, primary only or primary and secondary veins clearly visible to the naked eye, only the primary veins raised; the lower surface glabrous, sparsely punctate glandular, primary only, primary and secondary or primary to tertiary veins clearly visible to the naked eye, primary only or primary and secondary veins raised, secondary veins 3–6 pairs, borne 45–75° to the midrib, weakly curved, the veinlets not visible; base decurrent, cuneate, or acute, occasionally asymmetrically so; margin entire; apex acute or subcuspidate; petioles borne on a woody or crescent-shaped spur or regularly from the stem, 5–66 × 0.75–1.25 mm, drying dark purple, dark brown, yellow–green or green, glabrous, occasionally sparsely punctate glandular. Inflorescences 6–13 per herbarium sheet, terminal, subterminal or borne along the full length of the leaf–bearing portion of the stem, axillary panicles solitary in each axil, 25–60 mm long, bearing 1–16 flowers in 1–3 fascicle–like clusters, each cluster bearing 1–5 flowers; peduncle 1.5–20.0 × 0.75–1.75 mm, yellow–brown through orange–brown to dark brown, glabrous tosparsely or very sparsely pubescent, the hairs 0.25 mm, simple, curved or straight, occasionally glandular; bracts 18–43 × 9–13 mm, leaf–like; bracteoles 4–22 mm, ovate, linear, glabrous or sparsely pubescent. Flowers pedicellate, the pedicels 0.5–1.5 mm; calyx 5–6.5 × 2.0–2.5 mm, the outer surface glabrous, the lobes 4–6, 1.25–2.5 mm long, erect; corolla yellow–green or pale yellow to yellow, 4–26 mm long, the tube 9.0–21.5 mm long, 2.5–4.25 mm in diameter at the mouth, 0.75–1.50 mm in diameter at the base, glabrous, the lobes 4–6, 3.5–5.5 mm long; stamens 5, the filaments 16–19 mm, equal, adnate for 6–9 mm, pubescent from insertion point to the base, with a 1–lobed keel–shaped or reduced knee–like appendage present at insertion point, the anthers 1.0–1.5 × 0.675–1.0 mm; style 11–18 mm, the stigma 0.5–1.0 × 1–2 mm. Infructescences 10–65 mm long, bearing 2–6 fruit; fruiting calyx 3.5–7.5 × 6–9 mm; fruit 7–10 × 4–7 mm, subglobose to oblongoid, white when ripe. Seeds 1–10, 3–6 × 1.5–3.5 × 2–3 mm.

Etymology. After Elias Contreras, Guatemalan plant collector and botanist who collected the type and two of the paratype collections of this species.

Distribution. Montane or cloud forest, often undisturbed forest. Existing collection localities suggest that *Cestrum contrerasianum* is distributed along the Pacific drainage of central Guatemala (Baja Verapaz, El Quiche, Huehuetenango) and southeastern Mexico (Chiapas) in an area encompassing ca. 13,400 km^2 (Google Earth, accessed 10 Dec 2010).

Discussion. Of the sixteen known collections of *Cestrum contrerasianum*, ten were previously determined as *C. aurantiacum* Lindl. Comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *C. contrerasianum* as most similar to *Cestrum formosum* C.V.

Morton. It can be distinguished from those species on the basis of inflorescence number and morphology and flower and fruit morphology as summarised in Tables 3 and 4.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum contrerasianum* is considered Vulnerable (VU B1ab(iii)) based on subcriteria B1 based on an Extent of occurrence <20,000 km^2, a severely fragmented range and continuing decline in the area of habitat.

Paratypes. GUATEMALA. Baja Verapaz: Union Barrios, W of km 154, 15°11'01"N 090°12'16"W (DMS), 1600 m, Aug 17 1975, *C. L. Lundell & E. Contreras 19671* (F); Niño Perdido, La Cumbre de San José Espinero, 15°07'54"N, 090°09'46"W (DMS), 18 May 1977, *C. L. Lundell & E. Contreras 20913* (CAS, F). Huehuetenango: Cerro Huitz, between Mimanhuitz and Yulhuitz, Sierra de los Cuchumatanes, 15°51'18"N, 091°19'28"W (DMS), 1500–2600 m, 14 Jul 1942, *J. A. Steyermark 48657* (F); vicinity of Nucapuxlac, 2500 m, 17 Jul 1942, *J. A. Steyermark 48943* (AA, F). El Quiché: about 7 km SWW of Nebaj, 2200 m, Jun 22 1964, *E. Contreras 5088* (LL). MEXICO. Chiapas: Municipio of San Cristóbal las Casas, 2 miles northeast of Highway 190 along the old road to Huistán, 2300 m, 22 Jan 1965, *D. E. Breedlove & P. Raven 8294* (US); Municipio of Tenejapa, along the river of Chik Ha', barrio of Yashanal, paraje of Matsab, 1700 m, 17 Jul 1965, *D. E. Breedlove 11109* (F); Municipio La Trinitaria, Lagos de Montebello, 42 km northeast of La Trinitaria, 16°07'05"N, 091°42'27"W (DMS), 1300 m, 23 Oct 1971, *D. E. Breedlove & R. F. Thorne 21152* (DS); Municipio of Comitán de Dominguez, 5 km north of Highway 190 on a logging road from Laguna Chamula microwave station, 2400 m, 15 Oct 1976, *D. E. Breedlove & B. Bartholomew 40775* (DS); Municipio of La Independencia, third ridge along logging road from Las Margaritas to Campo Alegre, 2300 m, 24 Oct 1976, *D.E. Breedlove*

Table 3.

Characters	*C. contrerasianum*	*C. aurantiacum*
Inflorescence no. per herbarium sheet	6–13	1–4
Inflorescence length	25–60 mm	58–192 mm
Inflorescence panicle type	compact	not compact
Pedicel length	0.5–1.5 mm	0.5–2.5 mm
Calyx pubescence	sparsely pubescent	glabrous
Fruit size	7–10 × 4–7 mm	ca. 12 × 9.5–10.0 mm

Table 4.

Characters	*C. contrerasianum*	*C. formosum*
Inflorescence panicle type	compact	not compact
Pedicel length	0.5–1.5 mm	2–5 mm
Calyx pubescence	sparsely pubescent	glabrous
Calyx lobe length	1.25–2.5 mm	0.50–0.675
Corolla length	14–26 mm	10–14 mm

41079 (DS); Municipio of Comitán de Dominguez, Laguna Chamula microwave station, 4 km southwest of Highway 190 between Comitán and Amatenango del Valle, 2500 m, 6 Nov 1981, *D. E. Breedlove & G. Davidse 54848* (CAS); San Felipe village, near Ciudad San Cristobal las Casas, Mount Ecatepec, 3 miles W of village, 2400 m, Mar 31 1949, *M. C. Carlson 1614* (F); Municipio of San Cristóbal las Casas, a 200 m del Paraje K'ostic, 16°43'20"N, 092°31'29"W (DMS), 2300 m, 5 Sep 1994, *A. Chamé & A. Luna 352* (CAS); temperate land, 1864–70, *A. B. Ghiesbreght 837* (GH); Municipio of San Cristóbal las Casas, Cerro El Extranjero, 16°39'39"N, 092°34'26"W (DMS), 2350 m, 26 Mar 1992. *M. González E., P. F. Quintana A., M. Martínez I. & N. Ramírez M. 1769* (CAS).

***Cestrum darienense* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116663-1
http://species-id.net/wiki/Cestrum_darienense
Fig. 4 A–D

Diagnosis. Most similar to *Cestrum morae* Hunz. from which it can be distinguished by its thinner, more delicate stems, the lower number of secondary veins in the lamina, the ascendant and shorter inflorescences bearing flowers with shorter corolla tubes and longer corolla lobes.

Type. PANAMA. Darién: Cerro Pirre, valley between between Pirre and next most southerly peak, sloping hillside, 07°40'N 077°42'W (DMS), 1250–1300 m, *J.P. Folsom, R. L. Hartman & R. L. Dressler 4415* (holotype: MO-2620728).

Description. Shrub, occasionally lax, 1.0–2.5 m. Leaf–bearing stems grey–brown, the internodes 16–95 × 1.25–2.75 mm; young stems moderatley pubescent, the hairs 0.125–<0.25 mm, simple, weakly appressed, curved, glandular. Axillary buds 0.675–1.0 mm, red–brown, densely pubescent, not subtended by a minor leaf. Lamina 55–160 × 22–83 mm, length width ratio 1.86–3.0, broad rhombic–elliptic, rhombic–obovate, ovate–rhombic, obovate, rhombic, chartaceous, brown–green to brown; the upper surface glabrous, primary and secondary, primary to tertiary veins clearly visible to the naked eye, primary, primary and secondary raised; the lower surface sparsely pubescent, the hairs ca. 0.125 mm, simple, sessile to subsessile, glandular, weakly appressed, straight, orange–brown, primary to quarternary, primary to tertiary veins clearly visible to the naked eye, primary and secondary, primary to tertiary veins raised, the veinlets visible, unbranched, secondary veins 3–7 pairs, 30–45° to the midrib, straight, weakly curved; base subcordate, asymmetrical, obtuse, cordate-cuneate, cuneate; margin entire to irregularly entire; apex cuspidate, acuminate, subacuminate; petioles bottle-shaped, 3.5–8.0 × 1.375–2.0 mm, dark brown, moderatley pubescent, sparsely pubescent or glabrous, the hairs 0.125–0.25 mm. Inflorescences 2–13 per herbarium sheet, axillary, solitary in each axil, borne along the full length of leaf–bearing stem, 35–48 mm long, bearing 4–6 flowers in a panicle, the bracts forming a loose invo-

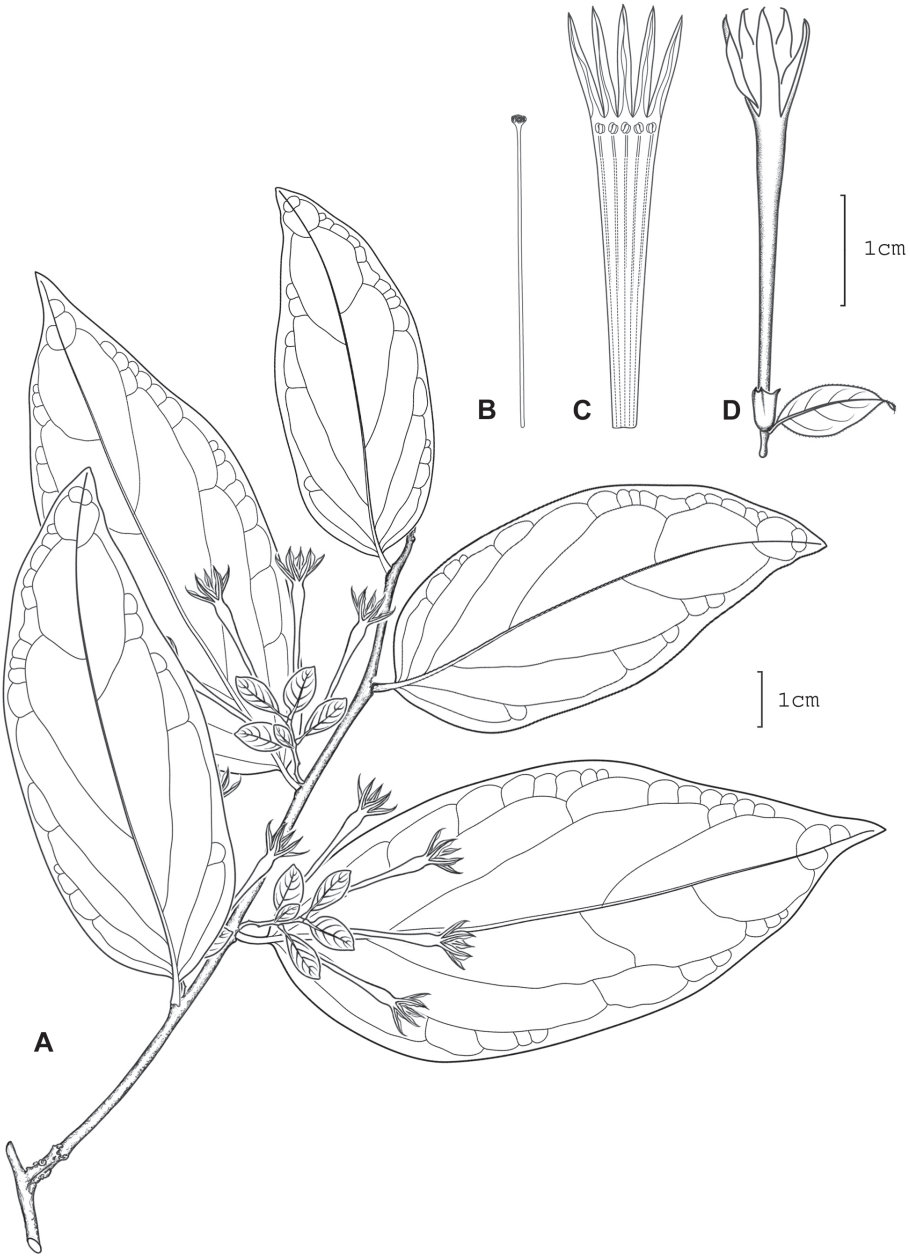

Figure 4. *Cestrum darienense* A.K.Monro **A** Flowering stem **B** Style **C** Longitudinal section through the corolla showing stamen arrangement **D** Flower. Drawn from *J.P. Folsom, R.L. Hartman & R.L. Dressler 4415* (MO).

lucre around 1 or 2 clusters of flowers, each cluster bearing 3–5 flowers; peduncle 3.5–13.0 × 0.5–1.0 mm, dark brown to brown, moderatley pubescent or sparsely pubescent, the hairs 0.125–0.250 mm, glandular; bracts 3.5–10.0 × 2.0–5.5 mm,

leaf–like; bracteoles 6–10 mm, ovate, obovate, rhombic, moderatley pubescent. Flowers subsessile, the pedicels < 0.25 mm; calyx 2.75–3.25 × 1.25–1.75 mm, the outer surface glabrous, the lobes 5, 0.50–0.675 mm long, erect; corolla white, 22–30 mm long, the tube 18.5–24.0 mm long, 1.5–2.0 mm in diameter at the mouth, 0.675–1.0 mm at the base, glabrous, the lobes 5, 7–9 mm long; stamens 5, the filaments 15–22 mm, equal, adnate for 13.5–19.5 mm, glabrous, with a lobe–like appendage present at insertion point, the appendage pubescent, the anthers 0.75 × 0.675 mm; style 17.0–19.5 mm, the stigma 0.675 × 0.75 mm. Infructescences and fruit not seen.

Etymology. This species is named after the Darien province, locality of the type and paratype collections.

Distribution. *Cestrum darienense* is known from two localities in Cerro Pirre and whilst none of the collection labels indicate a forest type, altitude information would suggest that this would be cloud forest. Cerro Pirre covers an area of ca. 50 × 25 km. Using collection label data and Google Earth (accesssed June 7, 2011; images from 2003) the Extent of Occurrence for this species is calculated to be ca. 280 km^2.

Discussion. Of the three collections of *Cestrum darienense* seen, none had been previously determined to species prior to this study. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *Cestrum darienense* as most similar to *C. gilliae* A.K. Monro and *C. morae* Hunz. Together with *C. langeanum* D'Arcy, *C. darienense*, *C. gilliae* and *C. morae* form a coherent morphological and geographical grouping within the genus of species from western Panama and the Chocó in Colombia and Ecuador characterised by broad, nearly three-veined leaves and determinate inflorescences. *Cestrum darienense* can be distinguished from *C. morae* and *C. gilliae* on the basis of stem, leaf, inflorescence and flower morphology as summarised in Tables 5 and 6. The Cerro Pirre mountain range has been noted as a locality for many endemic plant and animal species; this has been attributed to it being a moist forest refugium during dry periods of the Pleistocene (Haffer 1967).

Conservation status. Using IUCN criteria (IUCN 2001), *Cestrum darienense* is considered to be Near Threatened. The Extent of Occurrence is calculated to be ca. 280 km^2 (Criteria B1 <5,000km^2) and there are only two known localities (Criteria B1a ≤5, Endangered). No decline in geographic range or fragmentation of the habitat has been observed, however, and Cerro Pirre is located within the Darién Biosphere Reserve, a UNESCO World Heritage Property. The Darién is vulnerable to factors which may result in future deforestation, e.g. economic development associated with the resolution of the armed conflict in neighbouring Colombia and or an end to narco-trafficking. Any associated decline in geographic range or fragmentation would result in this species being assessed as Endangered.

Paratypes. PANAMA. **Darién:** Serranía de Pirre, trail ca. 1 mi SSW of Cerro Pirre summit, 07°56'N, 077°42'W (DMS), 1200 m, 15 Jul 1977, *R. L. Hartman, J. P. Folsom & R. L. Dressler* 4655 (MO); Cerro Pirre, along stream between Pirre and next southern peak, 07°40'N, 077°42'W (DMS), 10–20 Jul 1977, *J. P. Folsom* 4383 (MO).

Table 5.

Characters	*Cestrum darienense*	*Cestrum morae*
Stem diameter at position of the inflorescences	1.0–2.5 mm	4–6 mm
Leaf lamina width	22–83 mm	105–198 mm
Secondary vein number	3–7 pairs	14–20 pairs
Inflorescence length	35–48 mm	220–320 mm
Inflorescence disposition	spreading to 45°	lax, pendent
Corolla length	22–30 mm	37–39 mm
Corolla lobes	7–9 mm	6–7 mm
Stamen length	15–22 mm	ca. 30 mm
Filament appendage	present, lobe–like	absent

Table 6.

Characters	*Cestrum darienense*	*Cestrum gilliae*
Leaf lamina length	55–160 mm	135–285 mm
Secondary vein no.	3–7	9–15
Inflorescence length	35–48 mm	150–210 mm
Peduncle diameter (basal 1/3)	0.5–1.0 mm	2–3 mm
Calyx length	2.75–3.75 mm	4–6 mm
Corolla lobe length	7–9 mm	4.0–4.5 mm

***Cestrum gilliae* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116664-1
http://species-id.net/wiki/Cestrum_gilliae
Fig. 5 A–D

Diagnosis. Most similar to *Cestrum morae* Hunz. from which it can be distinguished by the fewer secondary nerves, the ascendant inflorescences bearing flowers along a greater proportion of its length, shorter bracteoles and flowers and filaments with a 2-lobed appendage towards its base.

Type. PANAMA. Darien: Rancho Frío to summit of Cerro Pirre, 07°51'N, 077°42'W – 07°58'N, 077°43'W (DMS), 500–1140 m, 30 Mar 1985, *W. G. D'Arcy & G. McPherson 16210* (holotype: MO-4407602).

Description. Robust herb to shrub 1.5–2.0 m. Leaf–bearing stems dark grey–brown, the internodes 15–43 × 4–6 mm; young stems regularly or sparsely pubescent, the hairs 0.25–0.75 mm, branched, dendritic, erect, crooked, not glandular. Axillary buds 1.5–2.5 mm, brown, densely pubescent, not subtended by a minor leaf. Lamina 135–285 × 32–124 mm, length width ratio 2.0–4.2, oblong–elliptic, obovate, elliptic, or oblong–obovate, chartaceous to subcoriaceous, brown or dull green, the upper surface glabrous, sparsely pubescent at the base, the hairs 0.375 mm, branched, erect, crooked dendritic, primary and secondary veins clearly visible to the naked eye, primary or primary and

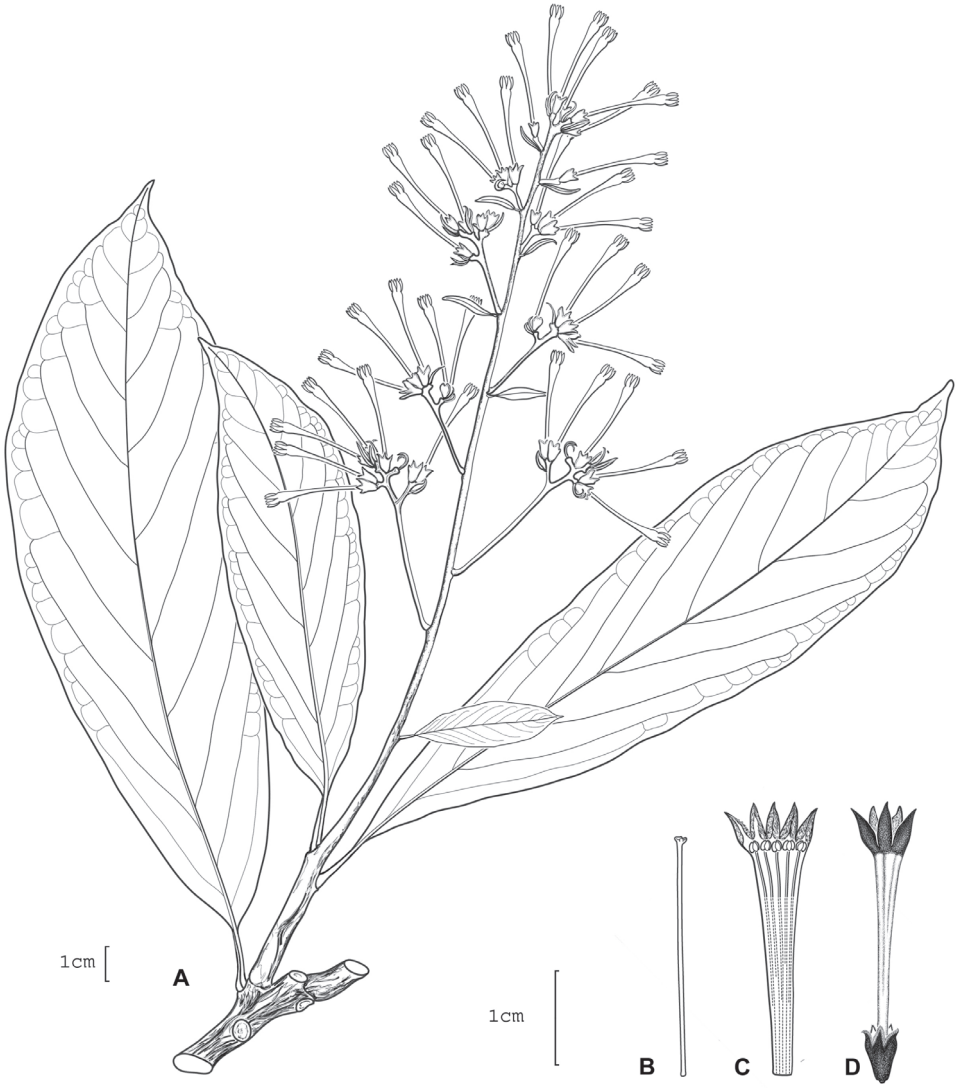

Figure 5. *Cestrum gilliae* A.K.Monro **A** Flowering stem **B** Style **C** Longitudinal section through the corolla showing stamen arrangement **D** Flower. Drawn from *W.G. D'Arcy & G. McPherson 16210* (MO).

secondary raised; lower surface sparsely pubescent on nerves, the hairs 0.125–0.50 mm, branched, glandular, erect, crooked–dendritic, orange–brown; primary and secondary or primary to tertiary veins clearly visible to the naked eye, primary and secondary veins raised, the veinlets not visible, secondary veins 9–15 pairs, 30–45° to the midrib, straight, apically curved; base obtuse, cuneate, asymmetrical, obtuse-cuneate; margin entire; apex subcuspidate to cuspidate; petioles 12–23 × 1.75–3.0 mm, brown to very dark brown, moderatley pubescent when young, becoming glabrous with age or always glabrous, the hairs 0.25–0.75 mm. Inflorescences 1–3 per herbarium sheet, terminal, indeterminate,

solitary, clustered towards the branch tips, 150–210 mm long, bearing 27–36 flowers borne in panicles of 10–16 clusters of flowers, each cluster bearing 1–3 flowers; peduncle ca. 30 × 2–3 mm, brown to very dark brown, sparsely pubescent, the hairs 0.375–0.675 mm, branched, dendritic, eglandular; bracts 7–41 × 1.5–12 mm, leaf–like; bracteoles 6–7 mm, narrow oblong to linear, sparsely pubescent; flowers subsessile or pedicellate, where pedicellate the pedicels 0.25–0.50 mm; flowers yellow–green or white, becoming purple blue; calyx 4–6 × 2.25–3.0 mm, the outer surface glabrous, the lobes 3 or 5, 0.75–1.75 mm, erect or spreading; corolla 26–30 mm long, the tube 23–27 mm long, 2–3 mm in diameter at the mouth, 1–2 mm at the base, glabrous, the lobes 5, 4.0–4.5 mm long; stamens 5, the filaments 22–23 mm long, equal, adnate for 16.5–17.5 mm, pubescent, with a bilobed appendage present at insertion point, the anthers 1.25 × 1.0 mm; style 22–25 mm, the stigma 0.50–0.75 × 0.675–1.0 mm. Infructescences ca. 125 mm long, bearing ca. 14 fruit; calyx 6 × 7.0–7.5 mm; fruit immature, 5–6 × 5 mm, purple–black when ripe. Seeds not seen.

Etymology. This species is named in honour of Gill Stevens (née Douglas, born 1965), botanist, colleague and close friend who died during the preparation of this manuscript. Gill, an algologist by training, helped pioneer the use of amateur groups in the collection of biodiversity data in the UK.

Distribution. *Cestrum gilliae* is known from three cloud forest localities within the Cerro Pirre mountain range. Cerro Pirre covers an area of ca. 50 × 25 km. Using collection label data and Google Earth (accesssed June 6, 2011; images from 2003) the Extent of Occurrence is calculated to be ca. 260 km^2.

Discussion. Of the three collections of *Cestrum gilliae* seen, only one had been previously determined to species, as *C. langeanum* D'Arcy. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *C. gilliae* most similar to *C. morae* Hunz. and to a lesser extent *C. langeanum* D'Arcy (see Discussion for *C. darienense* above). For this reason *Cestrum gilliae* is contrasted to both *C. morae* and *C. langeanum* on the basis of habit and inflorescence and flower morphology as summarised in Tables 7 and 8 respectively.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum gilliae* is considered to be Near Threatened under IUCN (2001) criteria. The Extent of Occurrence is calculated to be ca. 260 km^2 (Criteria B1, <5,000km^2) and there are only three known localities (Criteria B1a, ≤5). No decline in geographic range or fragmentation of the habitat has been observed and Cerro Pirre is located within the Darién Biosphere Reserve, a UNESCO World Heritage Property. The Darién is, however, vulnerable to factors (see Conservation Status above for *C. darienense*) and any decline in geographic range or fragmentation would result in this species being assessed as Endangered. For this reason *C. gilliae* is considered Near Threatened.

Paratypes. PANAMA. Darién: Cerro Pirre ridge top near Rancho Plastico, 07°57'N, 077°42'W (DMS), 1200 m, 10–20 Jul 1977, *J. P. Folsom* 4253 (MO); Cuasí–Cana Trail between Cerro Campamiento and La Escalera to 'Paramo' east of Tres Bocas, 07°44'N, 077°44'W – 07°46'N, 077°47'W (DMS), 30 Apr 1968, *J. H. Kirkbride & J. A. Duke* 1277 (MO).

Table 7.

Characters	*Cestrum gilliae*	*Cestrum morae*
Habit	robust herb or shrub	shrub, tree or vine
Secondary vein number	9–15 pairs	14–20 pairs
Inflorescence disposition	spreading to 45°	lax, pendent
Flower disposition	flowers borne along the apical 2/3 of the inflorescence length	flowers borne along the apical 1/3 to 1/8 of the inflorescence length
Bracteole length	6–7 mm	11–15 mm
Corolla length	26–30 mm	37–39 mm
Corolla lobe length	4.0–4.5 mm	6–7 mm
Stamen length	22–23 mm	ca. 30 mm
Filament adnation	16.5–17.5 mm of its length	24–25 mm of its length
Filament appendage	bilobed	absent

Table 8.

Characters	*Cestrum gilliae*	*Cestrum langeanum*
leaf shape	oblong–elliptic, elliptic, obovate, oblong–obovate	narrowly ovate, narrowly elliptic, elliptic
Leaf texture	chartaceous to subcoriaceous	coriaceous
Secondary vein angle of insertion	30–45°	60–85°
Leaf apex	subcuspidate to cuspidate	acute to attenuate
Inflorescence length	150–210 mm	21–70 mm
Calyx dimensions	4–6 × 2.25–3.0 mm	3.25–4.5 × 1.75–2.25 mm
Corolla lobe length	4.0–4.5 mm	5.5–7.0 mm
Filament appendage	bilobed	absent

***Cestrum haberii* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116665-1
http://species-id.net/wiki/Cestrum_haberii
Fig. 6 A–D

Diagnosis. Most similar to *Cestrum poasanum* Donn.Sm. from which it can be distinguished by the broader leaves and the shorter pedunculate or sessile inflorescences bearing flowers with usually shorter pedicels.

Type. COSTA RICA. Cantón de Puntarenas, Monteverde, Pacific slope wet forest, 10°18'N, 84°48'W (DMS), 1400–1500 m, 12 Mar 1992, *W. A. Haber 11049* (holotype: MO-3930789).

Description. Trees or shrubs, where shrubs occasionally lax, 1–5 m. Leaf–bearing stems drying pale brown to dark brown, grey–brown, green–grey or grey, the internodes 7–60 × 1.5–8.0 mm; young stems glabrous, sparsely pubescent or moderatley pubescent, where pubescent the hairs 0.25–0.50 mm, branched, erect, dendritic, eglandular. Axil-

Figure 6. *Cestrum haberii* A.K.Monro **A** Flowering stem **B** Style **C**. Longitudinal section through the corolla showing stamen arrangement **D** Flower. Drawn from *W.A. Haber 11049* (MO).

lary buds 0.75–2.50 mm, drying pale brown to dark brown or red–brown or dark grey–brown, densely pubescent to regularly pubescent, not subtended by a minor leaf. Lamina 55–250 × 19–110 mm, length width ratio 1.8–3.3(4.1), ovate–oblong, oblong–obovate,

ovate, obovate, or oblong, chartaceous to subcoriaceous, drying olive green, brown or yellow–brown, upper surface glabrous or sparsely pubescent, minutely pusticulate, where pubescent the hairs 0.250–0.375 mm, branched or simple, appressed, dendritic where branched, straight where simple; primary and secondary veins clearly visible to the naked eye, the primary and secondary raised; lower surface sparsely to very sparsely pubescent, the hairs 0.25–0.50 mm, branched, erect, weakly appressed, dendritic where branched, glandular where simple, dark walled, orange–brown to brown in colour; primary to quarternary veins clearly visible to the naked eye, primary and secondary only or primary to tertiary veins raised, veinlets not visible, secondary veins 6–13 pairs, borne 45–75° to the midrib, curved to weakly curved, strongly ascending; base decurrent or cuneate or asymmetrically obtuse / decurrent or cuneate / decurrent; margin entire, very irregularly and weakly crenate; apex subcuspidate, cuspidate or acute; petioles frequently borne on a crescent shaped short woody spur, 11–43 × 0.75–2.25 mm, brown to very dark brown, sparsely pubescent or glabrous, where pubescent the hairs 0.125–0.50 mm. Inflorescences 3–9 per herbarium sheet, axillary and terminal, solitary, borne along the full length of the leaf–bearing stem, 25–300 mm, panicle occasionally branched to its base, bearing 7–120 flowers in 2–25 clusters, each cluster bearing 1–8 flowers; sessile or peduculate, where pedunculate the peduncle 2–25 × 0.675–1.25 mm, brown to dark brown, densely pubescent or moderatley pubescent, the hairs 0.250–0.675 mm, branched, dendritic, eglandular; bracts (1.5)10–46 × 1.25–14.0 mm, leaf–like; bracteoles 0.5–5.0 mm, frequently caducous, linear, moderatley pubescent or densely pubescent. Flowers pedicellate or subsessile, where pedicellate the pedicels 0.375–0.750 mm; flowers yellow–green, pale yellow, cream, white or dull pink, the lobes occasionally lilac coloured, nocturnally fragrant; calyx 2.75–6.0 × 1.675–2.0 mm long, the tube 11–21 mm long, the outer surface glabrous, the lobes 3–5(6–7), 0.50–2.0 mm, erect; corolla 15–24 mm, 2.0–3.75 mm in diameter at the mouth, 0.5–1.5 mm at the base, glabrous, the lobes 5, 2.5–4.5 mm; stamens 5, the filaments 13.5–19.0 mm long, subequal, adnate for 12.0–16.5 mm, with a lobe–like or bilobed appendage present at insertion point, pubescent from appendage to base, anthers 0.675–1.250 × 0.675–1.0 mm; style 14–20 mm, the stigma 0.675–0.750 × 0.675–1.0 mm. Infructescences 32–100 mm long, bearing 3–15 fruit; fruiting calyx 3.0–4.5 × 4–6 mm; fruit 7.5–10.0 × 5–8 mm, white or cream when ripe. Seeds 7–10, 2.5–4.5 × 1.5–2.0 × 1.5–2.0 mm, the surface minutely verrucate.

Etymology. This species is named after William Haber, US botanist (1946–), who collected the holotype and six of the paratype collections.

Distribution. Wet, cloud and montane forest from (100) 900 to 2200 m. Collection notes indicate that this species is known from undisturbed and disturbed forest. Existing collection localities suggest that the species' Extent of Occurrence is 30,950 km^2 running along the Pacific coast of Costa Rica (Guanacaste, Alajuela, Heredia, Cartago, San José, Puntarenas) and Panama (Chiriquí) (Google Earth, accessed Dec 16 2010, images 2001, 2006).

Discussion. Of the 29 known collections of *Cestrum haberii* most had previously been determined as *C. poasanum* Donn. Sm. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Meth-

ods section recovered *Cestrum haberii* as most similar to *C. poasanum* and *C.rugulosum* Francey. The two species can be distinguished based on leaf, inflorescence and flower morphology as summarised in Tables 9 and 10.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum haberii* is considered Vulnerable (VU, A1c) under criteria A1 (decline in Extent of Occurrence). A current decline in Extent of Occurrence of 27% is inferred from a projection of the locality coordinates on Google Earth (Google Earth, accessed Dec 16 2010, images 2001, 2006). Of the 15 point localities for this species, five remain as undisturbed forest, four (27%) are pasture or crop fields and eight are remnant forest patches. Collection notes indicate that *C. haberii* persists in disturbed or secondary vegetation indicating a tolerance to disturbance. It is therefore assumed that this species will only be lost from a locality where vegetation cover is removed. Using this assumption the extent of decline is estimated at 27% and is assessed as ongoing. It is therefore highly likely that the decline in Extent of Occurrence will exceed 30% in the near future, meeting criteria A1c.

Paratypes. COSTA RICA. Alajuela: Cantón San Ramón, La Palma de San Ramón, 10°07'12"N, 084°33'00" W (DMS), 1300 m, 30 May 1927, *A. M. Brenes 5542* (F); Cantón San Ramón, La Palma de San Ramón, 10°07'12"N, 084°33'00" W (DMS), 1100 m, 27 Jun 1927, *A. M. Brenes 5560* (F); Cantón San Ramón, Los Angeles de San Ramón, Finca Johanson, 10°12'36"N, 084°34'48"W (DMS), 1000 m, 14 Apr 1928, *A. M. Brenes 6130* (F); Cantón San Ramón, Los Angeles de San Ramón, Finca Johanson, 10°12'36"N, 084°34'48"W (DMS), 1000 m, 4 May 1928, *A. M. Brenes 6157* (F); Cantón San Ramón, Piedades Norte, Los Angeles de San Ramón, 10°12'36"N, 084°34'48"W (DMS), 1000 m, 6 Mar 1929, *A. M. Brenes 6713* (F); Cantón San Ramón, Piedades Norte, Los Angeles de San Ramón, 10°12'36"N, 084°34'48"W (DMS), 1000 m, 6 Mar 1929, *A. M. Brenes 6726* (F); Cantón San Ramón, Piedades Sur, 1100 m, 8 Mar 1933, *A. M. Brenes 17167* (F); along road between San Ramón and Balsa, at Angeles Norte, 10°08'24"N, 084°28'48"W (DMS), 1250 m, 2 Feb 1979, *T. B. Croat 46848* (MO); Monteverde Reserve, Atlantic slope, Río Peñas Blancas valley, 10°17'41"N, 084°46'50"W (DMS), 1400 m, 20 Oct 1984, *W. A. Haber 710* (MO); Reserva Biológica Monteverede Río Peñas Blancas, 10°19'N, 84°44'W (DMS), 900 m, 15 Apr 1988, *W. A. Haber & E. Bello C. 8361* (MO); Cantón San Ramón, Rancho La Paz, 10°08'51"N, 084°31'54"W (DMS), 1100 m, 15 Nov 1973, *L. J. Poveda 772* (MO); Cantón Alfaro Ruiz, La Peña de Zarcero, 1400 m, 6 May 1938, *A. Smith H488* (F); Cantón Alfaro Ruiz, La Peña de Zarcero, 1450 m, 11 May 1938, *A. Smith NY568* (F); Cantón San Carlos, Zapote, 22 Apr 1938, 1500 m, *A. Smith H649* (F); Cantón Alfaro Ruiz, El Silencio de Zarcero, 1400 m, 11 Jan 1939, *A. Smith NY1439* (F); Cordillera Central near San Juan de Laja ca. 15 km N of Zarcero, 10°15'00"N, 084°24'36"W (DMS), 1350 m, 7 Feb 1965, *L. O. Williams, A. Molina R., T. P. Williams & D. N. Gibson 29022* (F, MO); Cartago: Cantón de Cartago, Llano Grande, junto a la carretera, cerca del Río Tiribí, 09°57'00"N, 083°55'48"W (DMS), 1400 m, 17 Mar 1993, *Q. Jiménez & L. Poveda 1195* (BM, INB). Guanacaste: Cantón de Tilarán, Zona Protectora Tenorio, Cordillera Tilarán, Tierras Morenas, Río San Lorenzo, 10°36'36"N, 084°59'24" W (DMS), 1000 m, 23 Mar 1993, *G. Rodríguez & Q. Jiménez 123* (BM, INB, MO); Heredia: above San José de la Mon-

Table 9.

Characters	*Cestrum haberii*	*Cestrum poasanum*
Leaf lamina length?	55–250 mm	18–40 mm
Secondary vein no.	6–13 pairs	4–7 pairs
Inflorescence peduncle length	sessile to 2.25 mm	3–60 mm
Pedicel length	0.375–0.750 mm	0.375–2.50 mm
Flower colour (when living)	yellow, yellow–green, pale green or cream, the lobes occasionally flushed purple	white to pale green, occasionally flushed purple

Table 10.

Characters	*Cestrum haberii*	*Cestrum rugulosum*
Stem and lower leaf surface hair type	branched-dendritic	simple
Petiole disposition	borne on a short woody crescent-shaped spur	not borne on a short woody crescent-shaped spur
Peduncle length	sessile to 2.25 mm	2.25-22 mm

taña on W slope of Volcán Barba, 2100 m, 17 May 1966, *F. R. Fosberg, W. H. Hatheway & D. H. Nicolson 47832* (US). Puntarenas: ca. 2 km SE of Monteverde, on the Pacific watershed, 1500–1550 m, 18–21 Mar 1973, *J. L. Gentry & W. C. Burger 2680* (F); San Vito, 08°40'N, 082°59' W (DMS), 1400 m, Jun 1974, *W. A. Haber SV#14* (MO); Monteverde Reserve, 10°18'34"N, 084°48'15"W (DMS), 1500 m, 1 Jun 1985, *W. A. Haber & E. Bello C. 1603* (MO); Cantón de Puntarenas, Monteverde, on Pacific slope, 10°18'N, 84°48'W (DMS), 1400–1500 m, 5 Mar 1992, *W. A. Haber 11036* (MO); Cantón de Golfito, Parque Nacional Corcovado, Finca Alajuela, Piedras Blancas, Sector Esquinas, 08°46'N, 083°15'W (DMS), 100 m, 19 Jun 1994, *F. Quesada 939* (BM, INB); San José: N Cordillera Talamanca, region of Cerro de la Muerte, Carretera Nacional 2, 13.5 km N of San Isidro, 09°27'36"N, 083°42'00"W (DMS), 1600 m, 4 Apr 1978, *C. Davidson 7220* (US); Santo Domingo de Vara Blanca, 2200 m, 22 Feb 1937, *M. Valerio 1552* (F). PANAMA. Chiriquí: Bajo Chorro, 08°51'N, 082°31'W (DMS), 1900–2200 m, 21 Mar 1977, *W.G. D'Arcy 10926* (MO); Boquete District, Chiquero, 08°39'N, 082°20'W (DMS), 1700 m, 11 Apr 1938, *M. E. Davidson 558* (A, F).

Cestrum knappiae **A.K. Monro, sp. nov.**
urn:lsid:ipni.org:names:77116666-1
http://species-id.net/wiki/Cestrum_knappiae
Fig. 7 A–D

Diagnosis. Most similar to *Cestrum acuminatum* Francey from which it can be distinguished by the membranous to subchartaceous leaves, flowers with shorter calyces and the larger fruit.

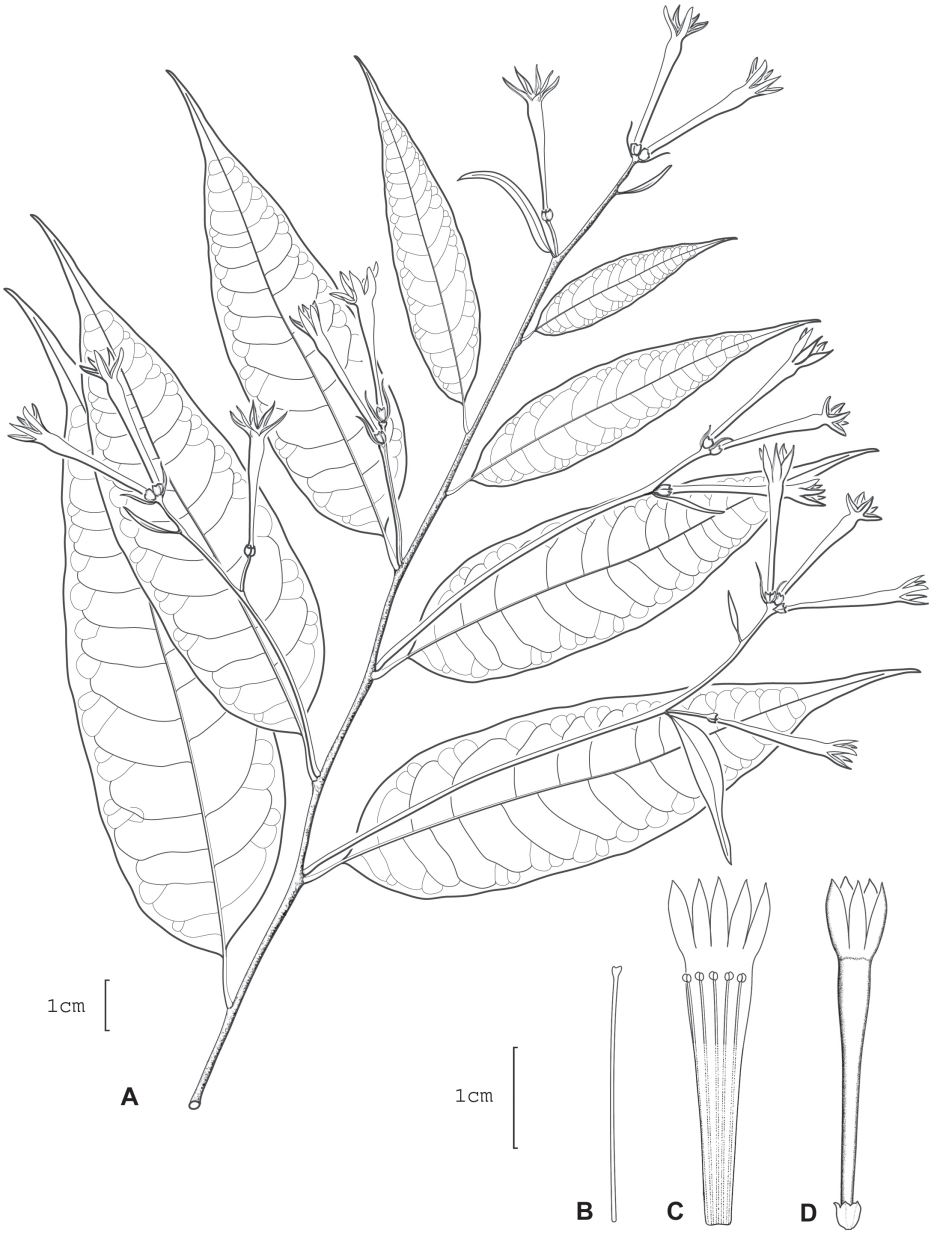

Figure 7. *Cestrum knappiae* A.K.Monro **A** Flowering stem **B** Style **C** Longitudinal section through the corolla showing stamen arrangement **D** Flower. Drawn from *S. Knapp & J. Mallet 9175* (BM).

Type. PANAMA. Chiriquí/Bocas del Toro: along Continental Divide on trail in Zona Protectora Palo Seco, 08°47.1'N, 082°13'W (DMS), 1100–1300 m, 11 Aug 2000, *S. Knapp & J. Mallet 9175* (holotype: BM000648809; isotypes: MEXU, MO-913564, PMA, SCZ).

Description. Shrub or small tree to 1–7 m. Leaf–bearing stems yellow–brown, pale brown to tan, the internodes 8–25(33) × 0.75–5.0 mm; young stems glabrous. Axillary buds 0.75–6.0 mm, very dark green, green–brown, orange–brown, sparsely pubescent or glabrous, not subtended by a minor leaf. Lamina 27–210 × 8–43 mm, length width ratio 2.6–8.4, narrowly lanceolate, lanceolate, narrowly ovate or narrowly oblong, membranous to subchartaceous, occasionally chartaceous, green, dull green, yellow–green; the upper surface glabrous, primary, primary and secondary veins clearly visible to the naked eye, primary and secondary raised; the lower surface glabrous; primary, primary to tertiary or primary to secondary veins clearly visible to the naked eye, primary, primary and secondary veins raised, the veinlets visible or not, secondary veins 7–20(27) pairs, 75–90° to the midrib, weakly curved; base obtuse, acute, asymmetrical, acute / obtuse, obtuse / subcordate, acute / attenuate, acute / cuneate, obtuse / decurrent; margin entire, occasionally irregularly so; apex acuminate, subcaudate to caudate; petioles regular, 3–21 × 0.675–1.0 mm, dark green, brown or yellow–green, glabrous. Inflorescences 5–9 per herbarium sheet, axillary on apical portion of the stem, terminal, pendant, 55–150 mm long, bearing 3–10 flowers in a compact panicle of 2–7 clusters of flowers, each cluster bearing 1, 2 or 4 flowers; peduncle 15–70 × 0.50–0.75 mm, straw coloured or orange–brown, glabrous; bracts 16–60 × 3–14 mm, leaf–like; bracteoles 4.0–7.5(14.0) mm, linear, spathulate, narrowly ovate, 1 or 2 per flower, glabrous. Flowers pedicellate or subsessile, where pedicellate the pedicels 0.25–1.0 mm; calyx 2.0–2.5 × 1.75–2.675 mm, the outer surface glabrous, the lobes 5, 0.125–0.675 mm, erect; corolla pale green, white or yellow–green, 28–35 mm, the tube 20–28 mm long, 2.5–3.5 mm in diameter at the mouth, 0.75–1.0 mm at the base, glabrous, the lobes 5, 6–10.0 mm long; stamens 5, the filaments 21–25 mm long, equal, adnate for 17–21 mm, with a lobe–like appendage present at insertion point, pubescent at insertion point, the anthers 0.675–1.0 × 0.5–0.75 mm; style 21–26 mm, the stigma 0.375–0.750 × 0.674–2.0 mm. Infructescences 27–110 mm long, bearing 2–4 fruit; fruiting calyx 2.0–2.5 × 3.0–4.0 mm; fruit 7–14 × 7–12 mm, white when ripe. Seeds (2)6–10, 4.5–7.5 × 1.5–5.0 × 2.5–4.5 mm, the surface smooth.

Etymology. This species is named after Sandra Knapp (1956–), Anglo–US botanist and Solanaceae specialist who collected the holotype and three of the paratype collections.

Distribution. Tropical wet, premontane and montane forest from 1100 to 1600 m. Collection notes indicate that this species is known from primary or undisturbed forest. Existing collection localities suggest that *Cestrum knappiae* is restricted to an area of the Main Divide (river drainage between the Caribbean Sea and Atlantic Ocean) of the Talamanca Mountains ca. 270 km in extent that runs from Parque Nacional Tapantí in W in Costa Rica to the Fortuna Forest Reserve and Palo Seco Protected Areas in the E in Panama. The Extent of Occurrence is calculated to be 5,400 km^2 (Google Earth, accesssed June 2 2011, images 2001 to 2006).

Discussion. Seven of the 15 collections of *Cestrum knappiae* examined had been previously determined as *Cestrum fragile* Francey. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the

Materials and Methods section recovered *Cestrum knappiae* as most similar to *C. acuminatum* D'Arcy, *C. fragile* and *C. cristinae* D.A.Soto. It can be distinguished from those species based on size, leaf, flower and fruit morphology as summarised in Tables 11, 12 and 13.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum knappiae* is considered Near Threatened (NT). *C. knappiae* meets criterion B1 (Extent of Occurrence <20,000 km^2) and one subcriterion, a (number of localities <10). The full extent of the species' Extent of Occurrence, however, is located within protected areas. There is considerable pressure for copper and gold mining within Costa Rica and Panama within the Extent of Occurrence which may present a threat of fragmentation or decline in the near to medium term future. If mining were to take place within this area then it is likely that *C. knappiae* would be classified as Vulnerable.

Paratypes. COSTA RICA. Cartago: Cantón de Paraíso, Tapantí Nacional Park, Río Reventazón water basin, Tapantí station, Arboles caidos trail, 09°44'53"N, 083°46'55"W (DMS), 1600 m, 10 Jan 1997, *A. Rodríguez, S. Salas & A. Soto 1874* (BM). PANAMA. Bocas del Toro: Fortuna Dam area, Continental Divide, ridge trail to unnamed peak to E of Oleoducto road, 08°46'19"N, 082°11'51"W (DMS), 1200 m, 1 Aug 1984, *H. W. Churchill 5861* (MO); 12 miles beyond Campamento Chami (12+12 mi from Río San Félix), 08°33'N, 081°48'W (DMS), 1400–1470 m, 20 Jun 1986, *W. G. D'Arcy 16274* (MO); ca. 5 km ENE of Cerro Pate Macho near Finca Serrano, NE of Boquete, in forest along trail downhill from Finca Serrano, 08°50'24"N, 082°19'18"W (DMS), 1500 m, 12 Feb 1979, *B. Hammel 6162* (MO); on gravel road branching N from main Fortuna Dam–Chiriquí Grande road, 1.1 miles from junction, 08°47'18"N, 082°14'00"W (DMS), 1200 m, 11 Mar 1985, *G. McPherson 6801* (MO); along trail on divide separating Chiriqui and Bocas del Toro, 08°46'42"N, 082°12'48"W (DMS), 1150 m, 22 Oct 1985, *G. McPherson 7203* (MO); along trail on divide separating Chiriqui and Bocas del Toro, 08°46'42"N, 082°12'48"W (DMS), 1150 m, 22 Oct 1985, *G. McPherson 7205* (MO); N of Fortuna Dam on road to Chiriquí Grande, forested slopes along divide–trail, 08°46'36"N, 082°13'00"W (DMS), 1150 m, 18 Jan 1986, *G. McPherson 8095* (MO); vicinity of Fortuna Dam. Trail along continental divide, 08°46'12"N, 082°09'00"W (DMS), 1300–1400 m, 6 Feb 1987, *G. McPherson 10384* (MO); Bocas del Toro–Chiriquí: along Continental Divide on trail in Zona Protectora Palo Seco, 08°47'N, 082°13'W (DMS), 1100–1300 m, 11 Aug 2000, *S. Knapp & J. Mallet 9182* (BM, MO, PMA, SCZ); along Continental Divide on trail in Zona Protectora Palo Seco, 08°47'N, 082°13'W (DMS), 1100–1300 m, 11 Aug 2000, *S. Knapp & J. Mallet 9188* (BM, MO, PMA, SCZ); Chiriquí: Distrito de Guanaca, Cordillera Central, Trocha, 08°47'N, 082°14'W (DMS), ca. 1000 m, 27 Aug 1993, *M. Correa, E. Montenegro, H. Navarrete & E. Hidalgo 9836* (PMA); ridges above and W of Quebrada Aleman, trail to town of Fortuna, 08°45'N, 082°13'W (DMS), 1200–1500 m, *S. Knapp & J. Mallet 9224* (BM, PMA); Cordillera Central, 7 Dec 1996, *E. Montenegro 1595* (BM); Fortuna, Trocha Cordillera Central close to the Continental Divide, 28 Oct 1997, *E. Montenegro 1799* (INB, BM).

Table 11.

Characters	*Cestrum knappiae*	*Cestrum fragile*
Stem pubescence	glabrous	sparsely pubescent or moderatley pubescent
Minor leaves borne on truncated side branches	absent	present, occasionally absent
Secondary veins	borne at 75-90° to the midrib	borne at 45-75° to the midrib
Peduncle pubescence	glabrous	pubescent
Bracteoles	4.0-7.5(14.0) mm	1.25-4.0 mm
Infructescence fruit no.	2-4	12-36
Fruiting calyx length	2.0-2.5 mm	3.0-5.5 mm

Table 12.

Characters	*Cestrum knappiae*	*Cestrum acuminatum*
Plant height	1–7 m	1–2 m
Leaf length	27–210 mm	42–107 mm
Leaf length : width ratio	2.6–8.4	2.4–3.5
Leaf texture	membranous to subchartaceous	Chartaceous to subcoriaceous
Inflorescence flower no.	3–10	4–31
Calyx length	2.0–2.5 mm	5–7 mm
Calyx lobe length	0.125–0.675 mm	1–3 mm
Fruiting calyx diameter	3.0–4.0 mm	4.5–5.5 mm
Fruit size	7–14 × 7–12 mm	5.0–6.5 × 4.5–6.0 mm

Table 13.

Characters	*Cestrum knappiae*	*Cestrum cristinae*
Leaf texture	membranous to chartaceous	subchartaceous to subcoriaceous
Peduncle diameter	0.5–0.75	ca 1.5
Bracteole pubescence	glabrous	apically pubescent
Pedicel colour	pale yellow-brown, dull yellow or dull yellow-green	brown to dark brown almost black
Calyx length	2.0–2.5 mm	4.0–4.75 mm
Calyx lobe length	0.125–0.675 mm	1.25–2.25
Corolla lobe length	6–10 mm	4.75–7.0 mm
Calyx in fruit length and diameter	2.0–2.25 × 3–4 mm	4.5–6.5 × 5–7 mm

***Cestrum lentii* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116668-1
http://species-id.net/wiki/Cestrum_lentii
Fig. 8 A–D

Diagnosis. Most similar to *Cestrum johnniegentrianum* D'Arcy from which it can be distinguished by the secondary nerves of the lower leaf surface which are dark relative

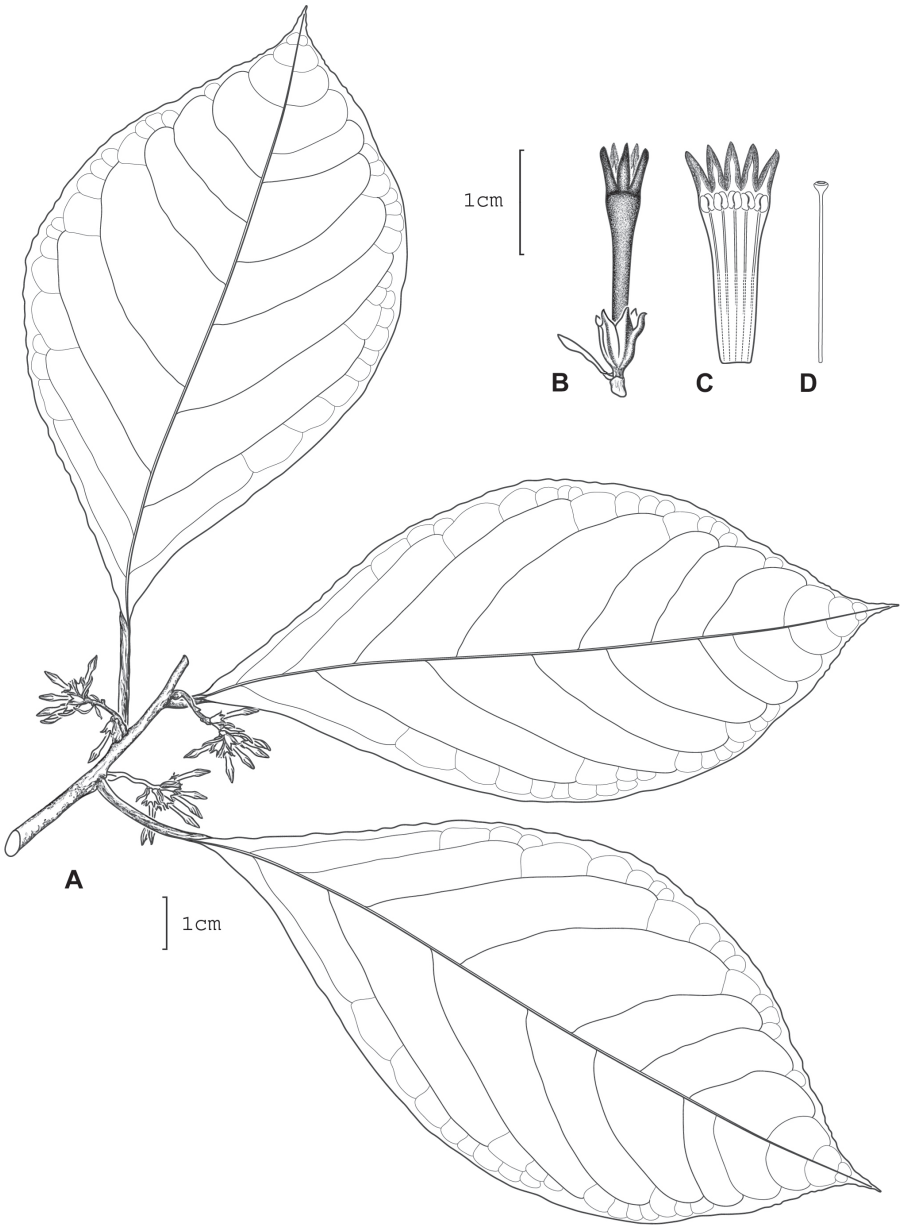

Figure 8. *Cestrum lentii* A.K.Monro **A** Flowering stem **B** Flower **C** Longitudinal section through the corolla showing stamen arrangement **D** Style. Drawn from *R.W. Lent 1051* (MO).

to the leaf lamina, the longer inflorescences bearing larger bracteoles and flowers with larger calyces.

Type. COSTA RICA. Cartago: 8 km SE of Tapantí, 09°43'54"N, 083°46'43"W (DMS), 1500 m, 18 Jun 1967, *R. W. Lent 1051* (holotype: MO-3279022).

Description. Unbranched shrub to 1.0–1.5 m. Leaf–bearing stems grey–tan to pale brown, the internodes 20–67 × 3.5–8.0 mm; young stems glabrous. Axillary buds 2.5–7.0 mm, brown, densely pubescent, not subtended by a minor leaf. Lamina 130–200 × 70–98 mm, length width ratio 1.7–2.4, broadly ovate, elliptic or broadly obovate, chartaceous or subcoriaceous, brown, green–grey; upper surface glabrous, primary and secondary veins clearly visible to the naked eye, primary and secondary raised; the lower surface glabrous, primary to quarternary, primary to quinternary veins clearly visible to the naked eye, primary and secondary veins raised, the veinlets visible, unbranched, secondary veins 7–10 pairs, 45–60° to the midrib, curved, weakly curved, ascending; base decurrent, cuneate–obtuse, cuneate–decurrent; margin irregularly entire, minute crenate to sinutae; apex cuspidate, subcuspidate; petioles decurrent on the stem, 17–30 × 1.5–2.5 mm, dark brown, yellow–brown, tan–cream, glabrous. Inflorescences 4–15 per herbarium sheet, axillary, panicles solitary in each axil, along the full length of leaf–bearing stems and below, 25–30 mm long, bearing 5–9 flowers borne in a panicle of 2–3 clusters of flowers with reduced branches, each flower cluster bearing 1, 3–6 flowers; peduncle 3–12 × 0.75–1.0 mm, dark brown, sparsely pubescent, the hairs 0.250–0.375 mm, branched, dendritic, eglandular; bracts absent; bracteoles 3–6 mm, linear, spathulate, sparsely pubescent. Flowers pedicellate, the pedicels 0.50–0.75 mm; calyx 4.0–4.5 × 2.0–3.5 mm, the outer surface glabrous, the lobes 5, 1.25–1.75 mm long, weakly spreading; corolla green (in bud), 15–17 mm long, the tube ca. 13.5 mm long, ca. 1.5 mm in diameter at the mouth, 0.75 mm at the base, glabrous, the lobes 5, 4 mm long; stamens 5, the filaments ca. 13 mm long, equal, adnate for 12 mm, with a lobe–like appendage present at insertion point, pubescent from insertion point to the base, the anthers ca. 1.375 × 1.0 mm; style ca. 13 mm, the stigma ca. 0.75 × 1.0 mm. Infructescences 15–25 mm long, bearing 5–8 fruit; fruiting calyx ca. 3 × 4 mm; fruit immature, colour when ripe unknown. Seeds 6, mature seeds not seen.

Etymology. This species is named after the US collector of the holotype Roy Lent (1931–), who worked for F in Costa Rica.

Distribution. Wet premontane forest from 1100 to 1700 m on Pacific and Caribbean drainage of the Talamanca Mountains, Costa Rica and Panama. *Cestrum lentii* is known from two localities ca. 210 km apart at the eastern (La Fortuna, Chiriquí, Panama) and western (Tapantí, Cartago, Costa Rica) ends of the Talamanca Mountains. It is likely that populations of *C. lentii* connect these localities and that the absence of records is a reflection of sampling effort. Assuming that *C. lentii* is found throughout the Talamanca Mountains between altitudes of 1100 to 1700 m then an estimated Area of Occupancy for this species is 5,880 km^2 (Google Earth, accessed June 17, 2011, images 2001, 2003, 2006, 2009).

Discussion. None of the four known collection of this species had been determined to species prior to this study. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *C. lentii* as most similar to *C. johnniegentrianum* D'Arcy. It can be easily distinguished from this species based on leaf and inflorescence morphology as summarised in Table 14.

Table 14.

Characters	*Cestrum lentii*	*Cestrum johnniegentrianum*
Leaf colour when dry	brown	olive green
Lower surface secondary vein colour	darker than the lamina	equal or paler than the lamina
Inflorescence length	25–30 mm	10–21 mm
Bracteoles	3–6 mm	1.5–2.0 mm
Calyx length × diameter	3.5–3.75 × 2.0–3.5 mm	ca. 2 × 1.0–1.5 mm
Calyx lobe length	1.25–1.75 mm	0.5–0.75 mm
Filament pubescence	pubescent from the appendage to the base	glabrous
Filament appendage	present, lobe–like	absent

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum lentii* is considered to be Near Threatened (NT) under IUCN (2001). The Extent of Occurrence for *Cestrum lentii* is calculated to be 5,880 km^2 (criteria B1, <20,000km^2, Vulnerable) and it is known from only two localities (B1a, ≤5) both of which are protected. Field experience at these localities suggests that the habitat of this species is not under any imminent threat. Illegal mining activity and planned hydroelectricity dam projects in the area may, however, result in habitat loss in the medium–term to long–term which would result in this species being assessed as Vulnerable. For this reason *C. lentii* is considered Near Threatened.

Paratypes. COSTA RICA. Cartago: Tapantí Hydroelectric Reserve, trail along Río dos Amigos, 09°41'24"N, 083°47'24"W (DMS), 1600–1700 m, 23 Jun 1976, *T. B. Croat 36199* (MO). PANAMA. Chiriquí: Fortuna Dam area, between Quebrada Los Chorros and Quebrada Hondo, to N of reservoir, in forest N of road, 08°45'N, 082°14'W (DMS), 1100 m, 20 Sep 1984, *H. W. Churchill & A. Churchill 6172* (MO); Fortuna Dam area, between Quebrada Los Chorros and Quebrada Hondo, to N of reservoir, in forest N of road, 08°45'N, 082°14'W (DMS), 1100 m, 20 Sep 1984, *H. W. Churchill & A. Churchill 6179* (MO).

***Cestrum talamancaense* A.K.Monro, sp. nov.**
urn:lsid:ipni.org:names:77116669-1
http://species-id.net/wiki/Cestrum_talamancaense
Fig. 9 A–D, Fig. 10 A

Diagnosis. Most similar to *Cestrum laxum* Benth. from which it can be distinguished by the absence of a minor leaf subtending axillary buds, flowers with shorter calyces that are pale pink or purple in colour.

Type. PANAMA. Bocas del Toro: Cerro Fábrega, 09°04'81"N, 82°54'35"W (DDM), 3000 m, 10 Mar 2003, *A. K. Monro, B. B. Klitgaard & J. DeGracia 4054* (holotype: PMA; isotypes: BM000811836, SCZ).

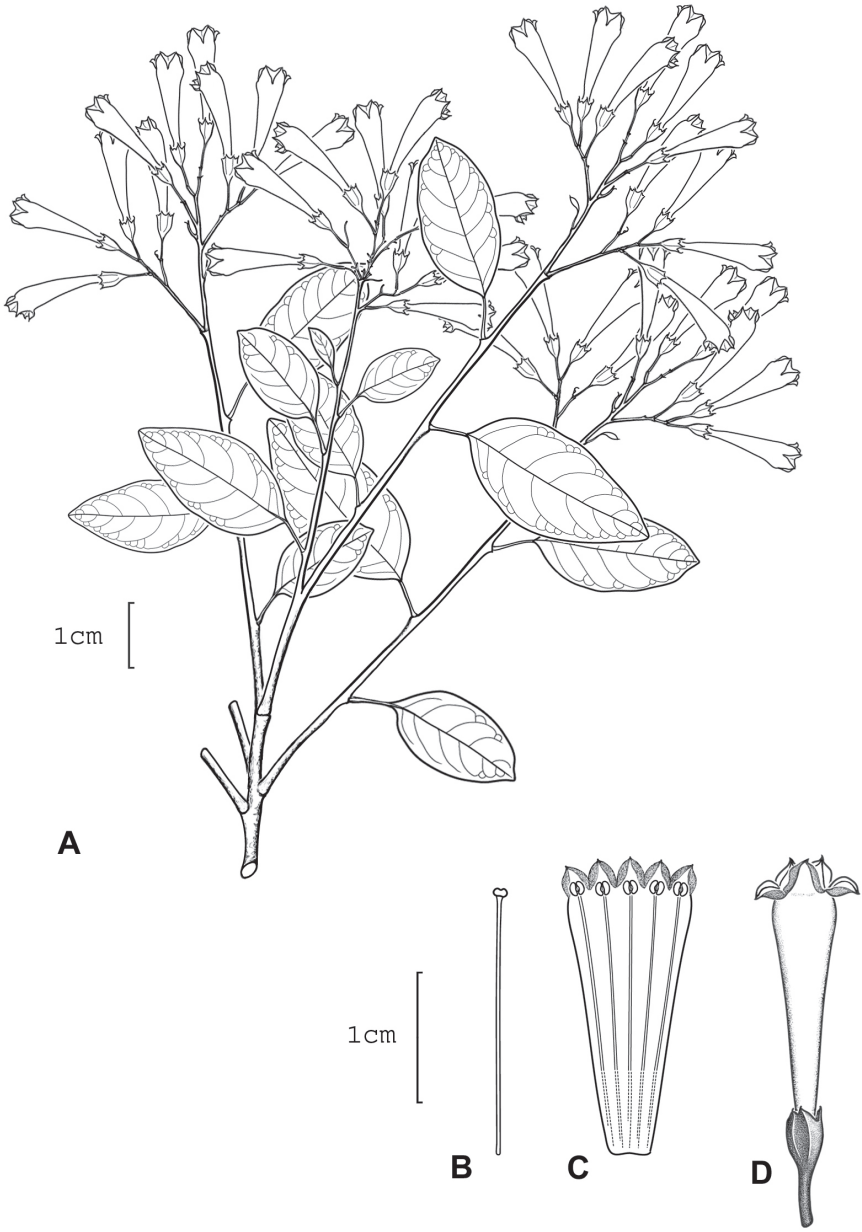

Figure 9. *Cestrum talamancaense* A.K.Monro **A** Flowering stem **B** Stamen **C** Longitudinal section through the corolla showing stamen arrangement **D** Flower. Drawn from *A.K. Monro, B.B. Klitgaard & J. DeGracia 4054* (BM)

Description. Lax shrub to 1–2 m. Leaf–bearing stems brown, the internodes 8–20 × 1–2 mm; young stems glabrous to sparsely pubescent, the hairs 0.5 mm, simple, erect, curved, not glandular. Axillary buds 0.5–1.5 mm, black, very dark brown, sparsely pu-

Figure 10. *Cestrum talamancaense* A.K.Monro **A** Inflorescence and flower. *A.K. Monro, B.B. Klitgaard & J. DeGracia 4054* (Photo A.K.Monro 2003).

bescent, not subtended by a minor leaf. Lamina 31–80 × 15–26 mm, length width ratio 2.6–3.1, ovate, lanceolate, or obovate, chartaceous tosubchartaceous or subcoriaceous, brown; the upper surface glabrous, primary and secondary, primary veins clearly visible to the naked eye, primary and secondary, primary raised; the lower surface glabrous, sparsely pubescent, the hairs 0.25 mm, simple, erect, curved, apparently glandular, orange–brown; primary to quarternary, primary to tertiary veins clearly visible to the naked eye, primary veins raised, veinlets not visible, secondary veins 5–8 pairs, 45–60° to the midrib, weakly curved; base decurrent, asymmetrical, decurrent–cuneate; margin irregularly entire; apex acute or subcuspidate; petioles borne on a woody or crescent shaped spur, 4–13 × 0.675–1.5 mm, dark brown, glabrous. Inflorescences 6 or 7 per herbarium sheet, axillary and indeterminate terminal, solitary, clustered towards the branch tips, 40–130 mm long, bearing 6–75 flowers in a panicle of 3–12 clusters, each cluster bearing 1 or 2 flowers; peduncle 22–25 × 0.675–0.750 mm, brown, moderatley pubescent, the hairs ca. 0.5 mm, branched, dendritic, eglandular; bracts 9–19 × 2–16 mm, leaf–like; bracteoles 1.5–2.5 mm, linear, glabrous. Flowers pedicellate, the pedicels 1.25–5.0 mm; calyx 2.5–4.0 × 2.0–2.25 mm, the outer surface glabrous, the lobes 5, 3, 0.5–1.0 mm long, erect; corolla pink to pale pink, 12–23 mm long, the tube 14–18.5 mm long, 3.0–4.5 mm in diameter at the mouth, 1.0–1.5 mm at the base, glabrous, the lobes 5, 2–3 mm long; stamens 5, the filaments 7.5–16.0 mm long, equal, adnate for 4.5–8.0 mm, with a reduced swelling-like to knee-like appendage present at insertion point, pubescent from insertion point to the base, the anthers 1.0–1.25 × 0.75–1.0 mm; style 7.5–18.0 mm, the stigma 0.75 × 1.25 mm. Infructescences not seen.

Etymology. From the Talamanca mountains, the locality of all known collections of this species.

Distribution. *Cestrum talamancaense* is known from three locations which span the entire range of the Talamanca Mountains from Chirripó, Costa Rica in the west to La Fortuna, Panama in the east. The altitude range for this species is believed to be 2000–3200 m. This and collection label data suggest that *C. talamancaense* is restricted to oak forest and subparamo vegetation. Given the small number of collections this should be considered provisional. Using this altitude range and the location of the three known localities the Area of Occupancy is calculated to be 2,300 km^2 (Google Earth, accessed June 20, images from 2003, 2004, 2006).

Discussion. Of the four collections of *Cestrum talamancaense* seen none had previously been identified to species. A comparison of the holotype and paratype material with type specimens from the herbaria listed in the Materials and Methods section recovered *C. talamancaense* as most similar to *C. laxum* Benth. and *C. irazuense* Kuntze. *Cestrum laxum* and *C. irazuense* occupy a similar altitudinal range. Cestrum irazuense occupies an overlapping but broader geographical range whilst *C. laxum* has a distinct and much broader geographical range being known from Mexico, Guatemala, El Salvador and Honduras. The species can be distinguished based on axillary bud, petiole and flower morphology as summarised in Tables 15 and 16.

Conservation status. Using IUCN criteria (IUCN 2001) *Cestrum talamancaense* is considered Least Concern. *C. talamancaense* has an Area of Occupancy of 2,300

Table 15.

Characters	*Cestrum talamancaense*	*Cestrum laxum*
Axillary bud pubescence	sparsely pubescent	densely pubescent or moderatley pubescent
Axillary bud subtended by a minor leaf	not subtended by a minor leaf	subtended by a minor leaf or not
Petiole pubescence	glabrous	moderatley pubescent, occasionally glabrous
Calyx length	2.5–4.0 mm	4–15 mm
Corolla lobe length	2–3 mm	3–5 mm
Corolla colour when fresh	pale pink	yellow, pale green to yellow–green

Table 16.

Character	*Cestrum talamancaense*	*Cestrum irazuense*
Stem and lower leaf surface pubescence	glabrous or sparsely pubescent	glabrous
Peduncle length	22–25	2–12
Peduncle pubescence	pubescent	glabrous
Calyx diameter	2–2.5 mm	0.75–1.75 mm
Flower colour	pink to pale pink, or purple	pale green, pale to dark purple
Corolla tube base width	1–1.5 mm	0.5–1 mm
Corolla tube mouth width	3-4.5 mm	2–3.5 mm

km^2 (Criteria B2, >2000 km^2) and meets a single subcriteria for criteria Ba (number of localities less than 5). In addition the whole of the range of this species is currently not fragmented and within protected areas both in Costa Rica and Panama. Should current attempts at illicit mining within the Area of Occupancy persist, however, the threat status may need to be revised to Near Threatened.

Paratypes. COSTA RICA. San José: Parque Nacional Chirripó, Cuenca Térraba–Sierpe, Sabana, Chirripó, 09°25'12"N, 083°30'36"W, 3200 m, 6 Nov 1996, *E. Alfaro, B. Gamboa & A. Picado* 895 (BM, INB). PANAMA. Bocas del Toro: Parque Nacional La Amistad, Cerro Fabrega, 09°06'56"N, 82°52'15"W (DDM), 3200 m, 16 Mar 2003, *B. B. Klitgaard, A. K. Monro & J. E. DeGracia* 818 (BM, INB, MO, PMA, SCZ).); Chiriquí: Proyecto Fortuna, Valle de Hornito, 08°38'N, 082°13'W (DMS), ca. 2000 m, 13 Feb 1981, *J. J. Him & I. O. Gordon* 50 (PMA).

Acknowledgements

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An explosive innovation: Phylogenetic relationships of *Solanum* section *Gonatotrichum* (Solanaceae)

Stephen Stern[1,2], Lynn Bohs[1]

1 *Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, Utah, 84112-0840, USA*
2 *Department of Biology, Colorado Mesa University, 1100 North Ave., Grand Junction, CO, 81501, USA*

Corresponding author: *Stephen Stern* (sstern@coloradomesa.edu)

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Abstract

Solanum is one of the largest plant genera and exhibits a wide range of morphological diversity. *Solanum* section *Gonatotrichum*, the focus of this study, is unique within the genus because of its fruits that swell with turgor pressure and explosively dehisce to disperse the seeds. We infer phylogenetic relationships within section *Gonatotrichum* using DNA sequence data from two nuclear regions (ITS and the granule-bound starch synthase gene [GBSSI or *waxy*]) and the chloroplast region *trnT-F*. The resulting phylogenetic trees support the monophyly of the section with the inclusion of *S. lignescens*, a species not previously thought to belong to the group due to the presence of stellate hairs. This inclusion of this species in section *Gonatotrichum* suggests that the simple, often geniculate hairs of species in the group may represent reduced stellate hairs. The presence of heterantherous flowers appears to be derived in the section, but this character is largely lost in *S. parcistrigosum*.

Keywords

explosive fruit dehiscence, Neotropics, *Solanum,* phylogeny

Introduction

Solanum (Solanaceae), with approximately 1500 species, is one of the 10 largest flowering plant genera (Frodin 2004; Bohs 2005). Recent species-level taxonomy (Knapp et al. 2004; http://www.solanaceaesource.org) and numerous molecular phylogenetic

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studies (e.g., Bohs 2005; Weese and Bohs 2007) have helped to define infrageneric groups within the genus, some of which correspond to formally named subgenera or sections. Weese and Bohs (2007) recognized 12 to 15 major clades in *Solanum*, one of which they called the Brevantherum clade. This large clade includes species with short, broad anthers that lack spines but commonly have stellate hairs or lepidote scales. It encompasses members of the formally named sections *Brevantherum* Seithe, *Extensum* D'Arcy, *Lepidotum* Seithe, *Stellatigeminatum* A. Child, and *Gonatotrichum* Bitter. *Solanum* section *Cernuum* Carvalho & G. J. Sheph. belongs to the clade on the basis of morphological data, but no sequence data have been available to place it in a molecular phylogeny.

Solanum section *Gonatotrichum* is morphologically unusual within the Brevantherum clade because the species traditionally placed within it have simple rather than stellate hairs and unique fruits with explosive dehiscence (see below; Bitter 1912; Nee 1989, 1999; Weese and Bohs 2007). Prior to molecular studies, its affinities were thought to be with the Morelloid clade of the non-spiny Solanums, not with the Brevantherum clade (D'Arcy 1972, 1991; Nee 1999; Child and Lester 2001). The taxonomy of section *Gonatotrichum* has been poorly understood and its sectional limits have been unclear. Until recently, this section was thought to contain two species (Nee 1989). A forthcoming revision (Stern et al. in review) and this contribution recognize eight species within it: *S. adscendens* Sendtn., *S. deflexum* Greenm., *S. evolvuloides* Giacomin & Stehmann (recently described, see Giacomin and Stehmann 2011), *S. hoffmanseggii* Sendtn., *S. lignescens* Fernald, *S. manabiense* S.Stern, *S. parcistrigosum* Bitter, and *S. turneroides* Chodat. The purpose of this study is to clarify the circumscription of section *Gonatotrichum* and to investigate the phylogenetic relationships of the species of the section as well as its placement within the larger Brevantherum clade.

Species in section *Gonatotrichum* are native to North, Central, and South America. They are herbs or small, woody shrubs with short inflorescences and simple hairs (except *S. lignescens*, which has stellate pubescence; see below). Flowers in the section have corollas ranging from 1–2.5 cm in diameter. The largest flowers are those of *S. turneroides* and *S. evolvuloides*, which also exhibit marked heteranthery, in which one filament is nearly double the length of the other four. The fruits of species in section *Gonatotrichum* are unique within the genus. They have a thin pericarp with a watery mesocarp held under pressure until they explosively dehisce. The fruits are white, yellow, or green, nearly transparent, and turgid before explosive dehiscence and deflated and shriveled after dehiscence.

Some species within section *Gonatotrichum* are relatively widespread (*S. deflexum, S. parcistrigosum,* and *S. turneroides*), whereas others are narrowly distributed and relatively inconspicuous, making them among the least collected species of *Solanum.* As Bitter (1912) noted in the original description of the section, the group has a large geographic disjunction, with species found in the southwestern USA, Mexico, and Central America as far south as Costa Rica and then again in southern South America (Bolivia, Paraguay, northwestern Argentina, and southern Brazil). The recent description of *S. manabiense* from coastal Ecuador (Stern and Bohs 2009) and identification

of previously undetermined specimens, particularly those of *S. hoffmanseggii* from Pará and Tocantins states in Brazil, has lessened the area of this disjunction; however, the section is absent from large areas of South America. This is likely due to the preference of the species for lower-altitude, dry habitats that are widely spaced on the continent.

Species placed in section *Gonatotrichum* have been subjected to two previous phylogenetic studies. Bohs (2005) and Weese and Bohs (2007) obtained sequence data for three species of the section (*S. deflexum*, *S. turneroides*, and "*S. adscendens*," later reidentified as *S. parcistrigosum*). In both studies they formed a strongly supported monophyletic group sister to the remaining sampled members of the Brevantherum clade. Concurrently, morphological and field studies of the group identified two new species, *S. manabiense* (Stern and Bohs 2009) and *S. evolvuloides* (Giacomin and Stehmann 2011), and clarified species limits and nomenclatural problems in the section. The presence of explosively dehiscent fruits in the Mesoamerican *S. lignescens* suggested that it also belongs to the group despite its stellate rather than simple pubescence (Stern et al. in review).

In this paper we use molecular phylogenetic methods to 1) examine the phylogenetic relationships of section *Gonatotrichum* with other members of the genus, 2) test the monophyly of section *Gonatotrichum*, 3) test the monophyly of species within the section and examine selected species-level relationships, and 4) examine geographical distributions and morphological patterns within the section.

Materials and methods

Taxon sampling

Seven of the eight recognized species of section *Gonatotrichum* were sampled. We were unable to obtain high quality genomic DNA for *S. hoffmanseggii*, an undercollected species from Amazonian Brazil. Multiple accessions were sampled for four species, with four accessions sampled for *S. parcistrigosum*, and two each for *S. evolvuloides*, *S. manabiense*, and *S. deflexum.* In addition to the species of section *Gonatotrichum*, we included members of *Solanum* as outgroups guided by results from previous studies showing other members of the Brevantherum clade to be sister to the section (Bohs 2005; Weese and Bohs 2007). Members of section *Geminata* (G. Don) Walp. were included as a more distant outgroup and the tree was rooted with *S. betaceum*, a member of section *Pachyphylla* (Dunal) Dunal. All taxa, along with voucher information and GenBank accession numbers, are listed in Appendix 1.

DNA Extraction, amplification and sequencing

Total genomic DNA was extracted from fresh, silica gel-dried, or herbarium material using the DNeasy plant mini extraction kit (Qiagen, Inc., Valencia, California). PCR

amplification for each gene region followed standard procedures described in Taberlet et al. (1991), Bohs and Olmstead (2001), and Bohs (2004) for the *trnT-L* and *trnL-F* intergeneric spacer regions; Levin et al. (2005) for *waxy*; and Levin et al. (2006) for ITS. The ITS region was amplified as a single fragment using primers ITSleu1 (Bohs and Olmstead 2001) and ITS4 (White et al. 1990) using PCR conditions described in Bohs and Olmstead (2001). When possible, *trnT-F* and *waxy* were amplified as single fragments using primers a and f for *trnT-F* (Taberlet et al. 1991) and primers waxyF and waxy2R for *waxy* (Levin et al. 2005). PCR conditions for *trnT-F* followed Bohs and Olmstead (2001); conditions for *waxy* followed Levin et al. (2005). When necessary, overlapping fragments were amplified and assembled, using primers a with d and c with f to amplify *trnT-F*, and primers waxyF with 1171R, and 1058F with 2R to amplify *waxy*.

PCR products were cleaned using the Promega Wizard SV PCR Clean-Up System (Promega Corporation, Madison, Wisconsin). The University of Utah DNA Sequencing Core Facility performed sequencing on an ABI automated sequencer. Sequences were edited in Sequencher (Gene Codes Corp., Ann Arbor, Michigan) and all new sequences were submitted to GenBank; accession numbers are listed in Appendix 1.

Sequence alignment and analysis

Sequence alignment for all of the gene regions was straightforward and performed visually using Se-Al (Rambaut 1996). The aligned dataset is available as Appendix 2 (see Appendix 2: Aligned Dataset).

Parsimony analyses

Parsimony analyses were performed on each dataset separately and on the combined dataset using PAUP*4.0b10 (Swofford 2002). All characters were weighted equally in analyses that implemented TBR branch swapping with 1,000 heuristic random addition replicates, each limited to 1,000,000 swaps per replicate. Gaps were treated as missing data. Bootstrapping (BS; Felsenstein 1985) was used to evaluate branch support with 1,000 random addition replicates and TBR branch swapping limited to 1,000,000 swaps per replicate.

Bayesian analyses

Prior to Bayesian analyses, a general model of nucleotide evolution was selected for the separate and the combined datasets using the AIC criterion identified in Modeltest 3.7 (Posada and Crandall 1998). MrBayes 3.1 (Hulsenbeck and Ronquist 2001) was used to analyze each of the separate and combined datasets. For each analysis, five million generations were run using eight Markov chains, each initiated from a random tree and

sampled every 1,000 generations. Each of the analyses reached a standard deviation below 0.01 between the chains and all parameters from each analysis were visualized graphically to determine the trees discarded as burn-in prior to achieving stationarity.

Results

Phylogenetic analyses

The parsimony strict consensus and Bayesian majority rule consensus trees of all datasets differed only in the degree of resolution, with Bayesian tree topologies more resolved than parsimony trees (Table 1). Clades with low posterior probabilities, typically those below 0.90 PP but occasionally those with up to 1.0 PP in Bayesian analyses were often collapsed in parsimony strict consensus trees. Descriptive statistics for individual and combined genes are provided (Table 1). More nodes were strongly supported by combining the data than were obtained in any of the separate analyses.

Table 1. Descriptive statistics for each data set analyzed. Strongly supported nodes for parsimony indicate those with ≥ 90% BS; Bayesian strongly supported nodes are those with ≥ 0.95 PP.

Data Partition	Aligned Sequence Length	# Parsimony Informative Characters	# MP Trees	Tree Length	CI	RI	# Strongly Supported Nodes Parsimony	Model Selected	# Strongly Supported Nodes Bayesian
ITS	709	127	14	435	0.632	0.683	4	GTR+I+G	15
waxy	2090	173	40	403	0.893	0.942	10	TIM+G	21
trnT-F	1953	71	>135,000	178	0.944	0.960	8	TVM+G	12
combined	4752	371	14	1031	0.779	0.847	13	GTR+I+G	25

Topological conflicts

Our discussion will largely be based on the parsimony strict consensus tree of the combined data set, which is a conservative hypothesis of phylogenetic relationships, but areas of the tree that receive strong support in the Bayesian analysis that are less strongly supported in the parsimony analysis will be noted (Fig. 1). The parsimony strict consensus trees for the individual markers are also presented (Fig. 2–4). In parsimony analyses, each DNA sequence region consistently identified the same major, well-supported groups corresponding to the Brevantherum clade and section *Gonatotrichum* comprising identical species, but relationships within these major clades were often not strongly supported (BS values < 90 %), or were unresolved, and thus cannot be considered conflicting under Wiens' (1998) criteria. Within section *Gonatotrichum*, one incongruence of note among the various datasets is the placement of *S. adscendens*, *S. lignescens*, and *S. deflexum*. In the plastid (Fig. 3) and combined trees

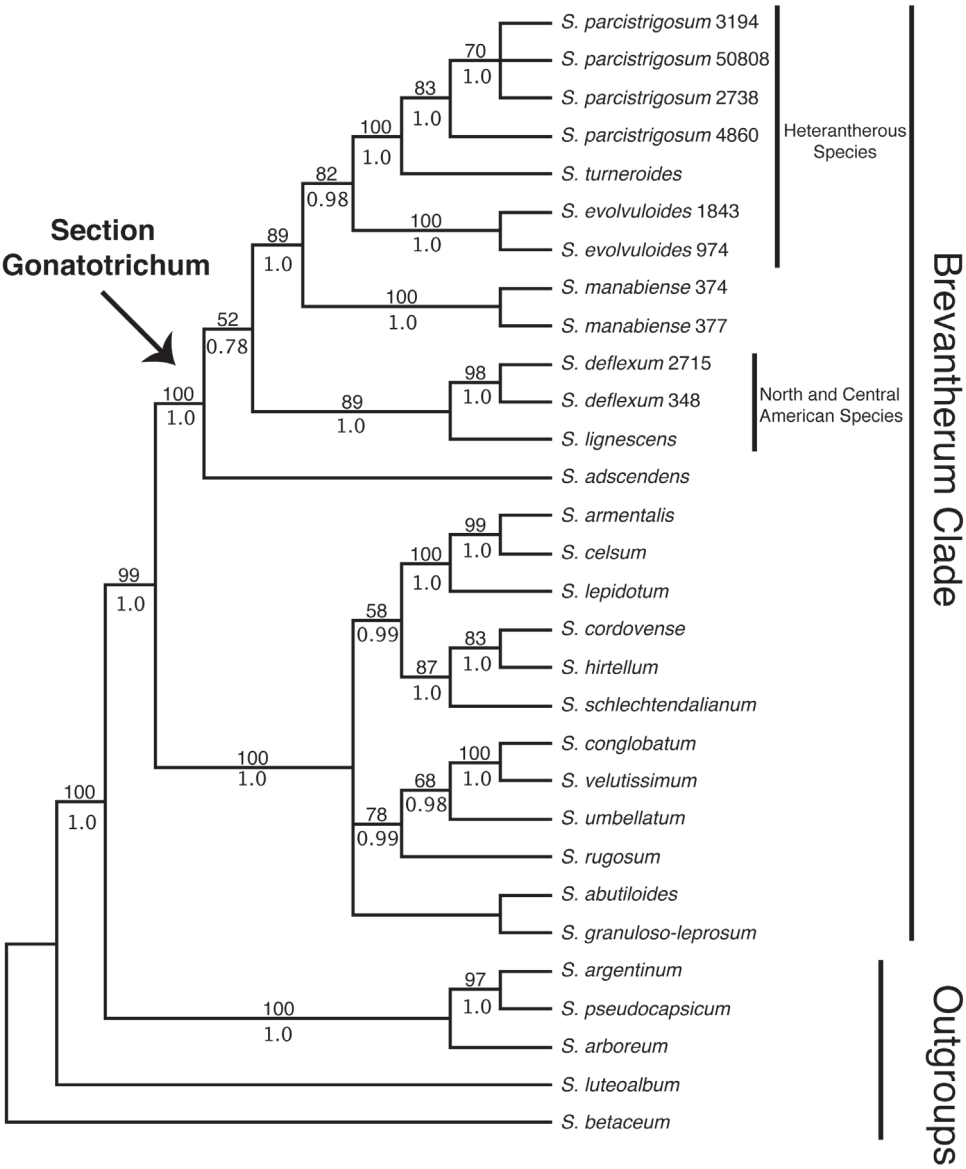

Figure 1. Strict consensus of the 14 most parsimonious trees from the concatenated MP analysis of ITS, *trnT-F*, and *waxy* data. Bootstrap values > 50% and posterior probabilities are shown above and below the branches, respectively. Numbers after species names indicate collector numbers listed in Appendix 1 for multiple accessions of a single species.

(Fig. 1), *S. adscendens* is sister to the remainder of the species in the section (98% BS, 1.0 PP in the *trnT-F* tree, 52% BS, 0.78 PP in the combined tree). In the ITS tree, *S. lignescens* is sister to the remaining species in section *Gonatotrichum*, but this relationship is unsupported (Fig. 2). In the *waxy* tree, *S. adscendens*, *S. lignescens*, and *S.*

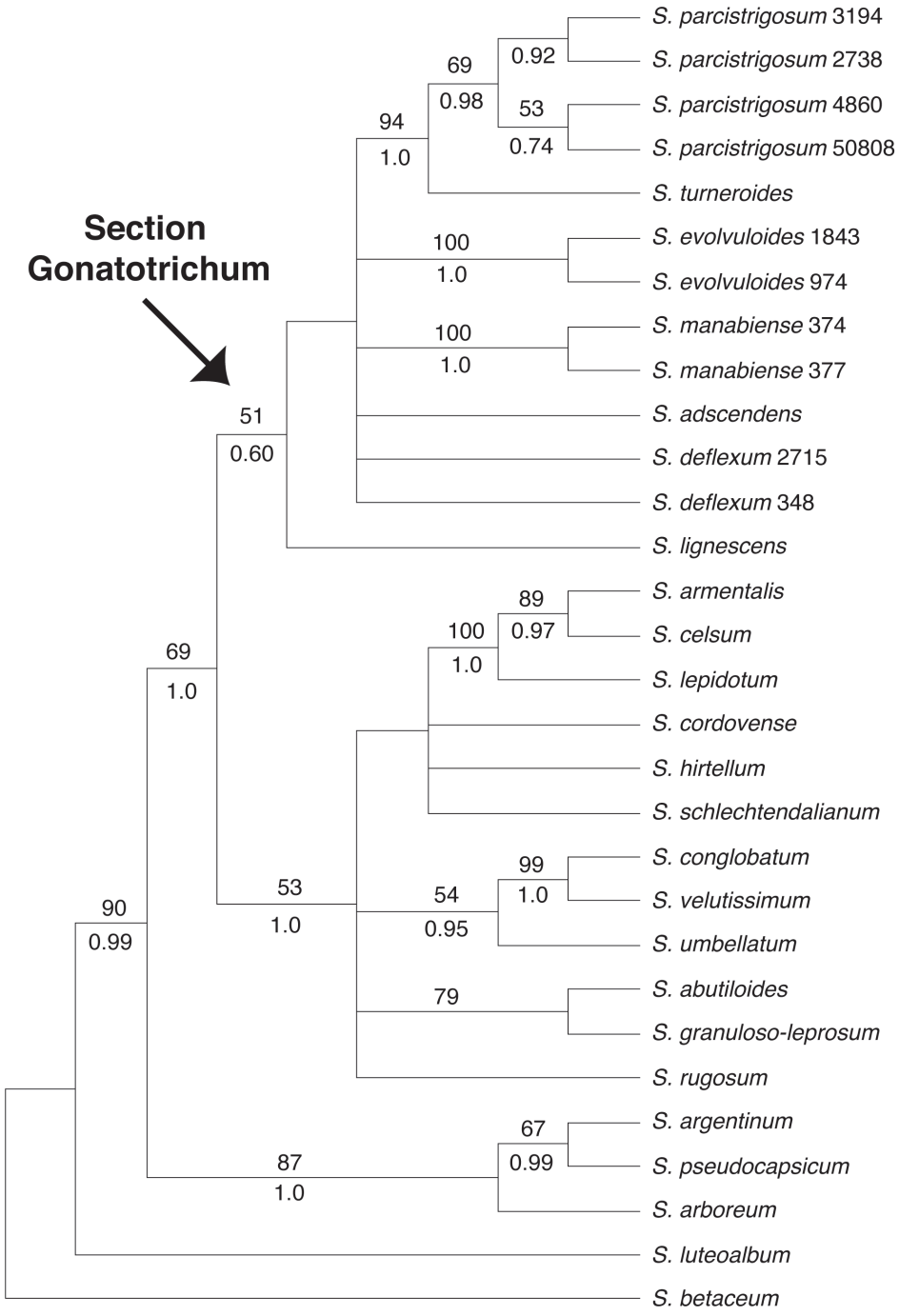

Figure 2. Strict consensus of the 14 most parsimonious trees from the MP analysis of the ITS dataset. Bootstrap values > 50% and posterior probabilities are shown above and below the branches, respectively.

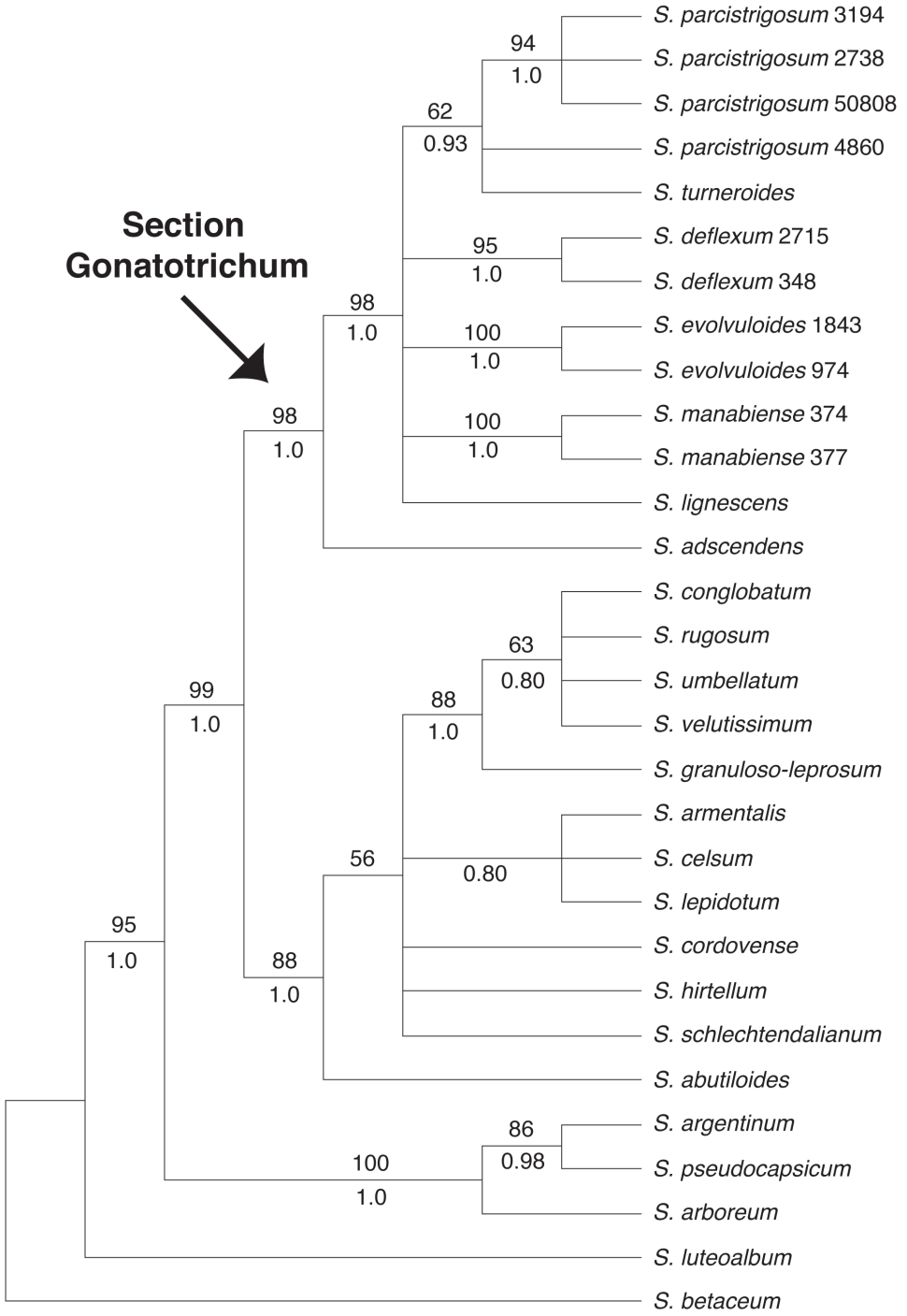

Figure 3. Strict consensus of the more than 135,000 most parsimonious trees from the MP analysis of the *trnT-F* dataset. Bootstrap values > 50% and posterior probabilities are shown above and below the branches, respectively.

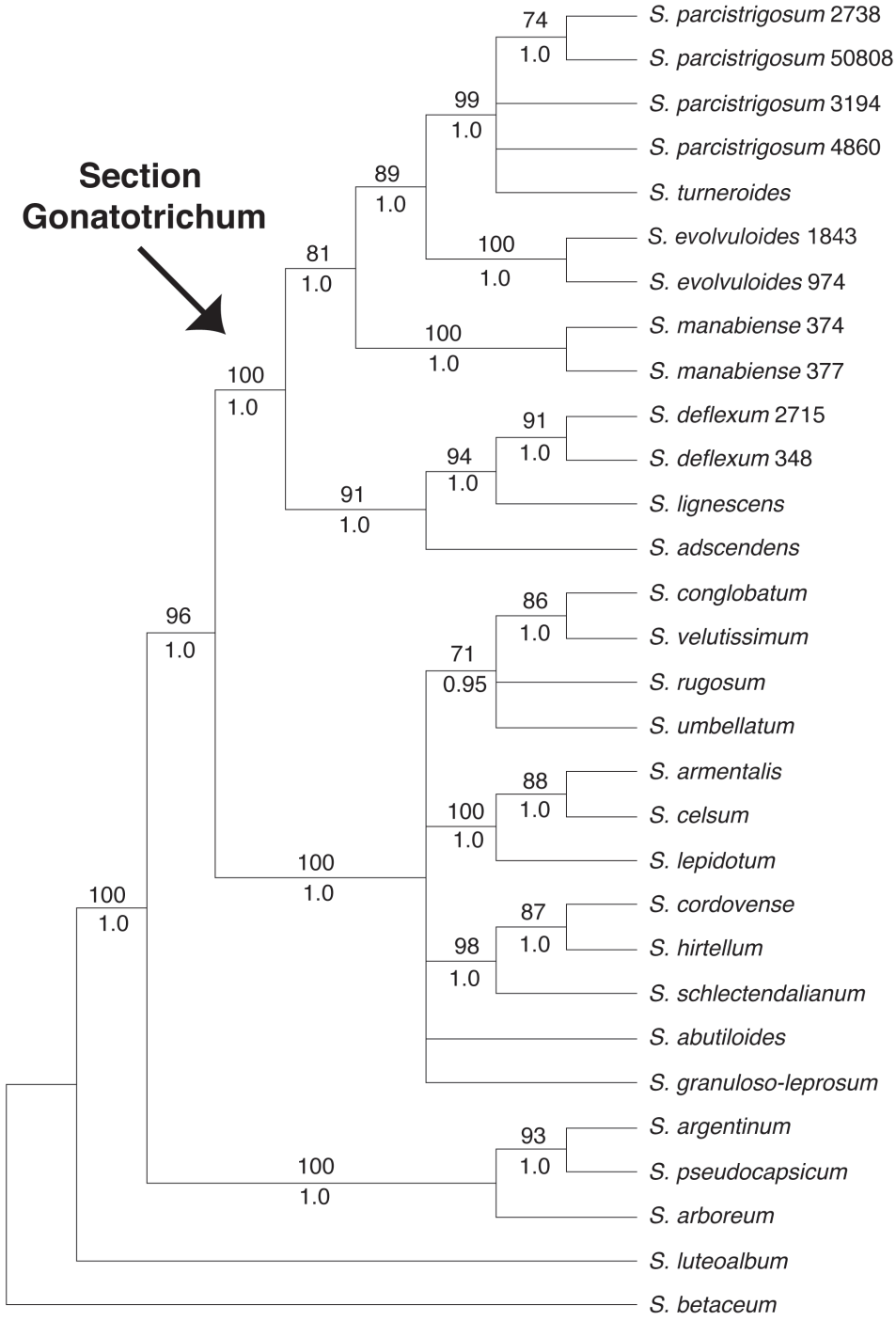

Figure 4. Strict consensus of the 40 most parsimonious trees from the MP analysis of the *waxy* (GBSSI) dataset. Bootstrap values > 50% and posterior probabilities are shown above and below the branches, respectively.

deflexum form a well-supported clade (91% BS, 1.0 PP) sister to the remaining species of section *Gonatotrichum* (Fig. 4).

Phylogenetic relationships

Solanum section *Gonatotrichum* emerges as monophyletic in all analyses and strongly supported in all except the ITS-only tree. The section is strongly supported (99% BS, 1.0 PP in the combined tree) as sister to the remainder of the species sampled from the Brevantherum clade, which form a monophyletic group in all analyses (100% BS, 1.0 PP in the combined tree; for sampling of Brevantherum clade see Fig. 1). Species with duplicate accessions sequenced (*S. parcistrigosum*, *S. evolvuloides, S. manabiense,* and *S. deflexum*) were all monophyletic in the combined tree. Within section *Gonatotrichum*, *S. turneroides* is strongly supported as sister to *S. parcistrigosum* in the combined tree (100% BS, 1.0 PP), and *S. evolvuloides* is sister to this clade (82% BS, 0.98 PP). *Solanum manabiense* from coastal Ecuador is resolved as sister to this clade (89% BS, 1.0 PP). *Solanum deflexum* and *S. lignescens* form a clade (89% BS, 1.0 PP). The final species, *S. adscendens*, is sister to the remainder of the species of section *Gonatotrichum* in the combined tree, although this relationship is poorly supported (52% BS, 0.78 PP) and, as noted above, is not recovered in the ITS and *waxy* trees.

Discussion

Our data, like those of previous studies, show that *Solanum* section *Gonatotrichum* belongs to the Brevantherum clade (sensu Bohs 2005; Weese and Bohs 2007). This clade consists of approximately 60 species of herbs, shrubs and trees found in tropical and subtropical regions of the New World (Bohs 2005). Centers of diversity occur in the Andes and in eastern Brazil, where many species are common in secondary vegetation and disturbed habitats. All members of the clade lack prickles and have relatively short, broad anthers. However, members of section *Gonatotrichum* are strikingly different from the rest of the species of the Brevantherum clade. Traditionally, the section included small annuals or perennials with reduced inflorescences and simple hairs, whereas the remainder of the Brevatherum clade includes shrubs to sizable woody trees with stellate or lepidote pubescence and often large, branched inflorescences. The explosively dehiscent fruits of section *Gonatotrichum* differ from those of the rest of the Brevantherum clade, which are variously colored, fleshy in texture, and not dehiscent at maturity.

These results indicate that section *Gonatotrichum* forms a monophyletic group including the Mesoamerican *S. lignescens*. This species had not been considered to be a member of the section *Gonatotrichum* in previous taxonomic treatments (Bitter 1912, 1913; Nee 1989). Nee (1999) placed *S. lignescens* in section *Brevantherum* due to its shrubby habit and stellate hairs, although he indicated that it had no obvious close relatives within the section and suggested that perhaps it might belong in section

Gonatotrichum. Our molecular data place *S. lignescens* within section *Gonatotrichum* and, in the combined and *waxy* trees, as sister to *S. deflexum*, a species with exclusively simple hairs found from the southwestern USA to Mexico and Central America. The fruits of *S. lignescens* are explosive berries like those of the rest of the section, indicating that fruit morphology may be a synapomorphy for section *Gonatotrichum*, but that habit and hair morphology may be somewhat variable within it.

Hairs have been used extensively for identification of species and sections in *Solanum* and have their own standardized terminology in the genus (see Roe 1971 for a overview). While the presence of specific hair types can be diagnostic, many groups or even species can have multiple hair types. Section *Brevantherum* sensu Roe (1972), placed in the Brevantherum clade by Bohs (2005) and Weese and Bohs (2007), exemplifies this complexity, with some species having up to six different hair types (see Table 1, Roe 1972). Section *Gonatotrichum* was previously distinguished within the genus due to the presence of simple, geniculate hairs with a short basal cell and a 90° bend between this and the second cell in at least some of its members (Bitter 1912, 1913; Nee 1989). Geniculate hairs are present in some species in the section (*S. hoffmanseggii* and *S. parcistrigosum*) but absent in other species (*S. adscendens, S. deflexum, S. evolvuloides,* and *S. manabiense*) with one species (*S. turneroides*) having intermediate hairs that are flattened along the stem but lack a 90° bend between the basal and second cells. Our results show that a species with stellate hairs, *S. lignescens*, also belongs in section *Gonatotrichum*, which previously was thought to contain only simple-haired species. The placement of *S. lignescens* as sister to the simple-haired *S. deflexum* in some analyses suggests that simple hairs may have evolved from branched hairs in the latter species and perhaps in the four species sister to the *S. lignescens*/*S. deflexum* clade in the combined and *waxy* trees. Further morphological, developmental, and phylogenetic study of various species of the Brevantherum clade may clarify the patterns of hair evolution throughout the group and distinguish between simple hairs that are pleisiomorphic versus those derived via ray reduction from branched-haired ancestors.

We sampled multiple accessions per taxon in four of the seven species of section *Gonatotrichum* included in the phylogeny (*S. evolvuloides*, *S. deflexum*, *S. manabiense*, and *S. parcistrigosum*). In the combined and *waxy* trees, all four species were monophyletic. The four accessions of *S. parcistrigosum* were not monophyletic in the *trnT-F* tree, and the two accessions of *S. deflexum* did not form a clade in the ITS tree. However, neither of these cases of species non-monophyly were strongly supported. It appears that species limits, at least within these four taxa, are fairly distinct.

Within section *Gonatotrichum*, the phylogeny from the combined data exhibits clear geographic patterns. The species ranging from North to Central America (*S. lignescens* and *S. deflexum*) form a strongly supported clade, as do the southern South American species (*S. evolvuloides, S. parcistrigosum*, and *S. turneroides*) with the Ecuadorian *S. manabiense* sister to the southern South American species. The position of the Brazilian *S. adscendens* as sister to the rest of the clade in the combined and *trnT-F* trees does not fit this biogeographic pattern and is confounded by the incongruence between

the *trnT-F* and *waxy* datasets indicated above, although neither of these datasets place *S. adscendens* with the remainder of the southern South American species. Future molecular studies should attempt to include *S. hoffmanseggii*, a poorly known species from Amazonian Brazil and the only member of section *Gonatotrichum* for which sequence data are not available. Based on morphology, particularly the geniculate hairs that lay flat along the stem, the similar sized flowers and fruits, and the overall distribution, we speculate that *S. hoffmanseggii* will likely be closely related to the southern South American species *S. parcistrigosum*. Sequence data is needed to confirm this relationship and determine its phylogenetic affinities to the rest of the South American taxa of the clade.

Although buzz pollination is virtually universal in *Solanum*, heteranthery is an unusual trait in the genus and has been shown to have evolved multiple times independently within it (Bohs et al. 2007). It has been particularly well studied in the temperate spiny weed, *S. rostratum* Dunal, a member of *Solanum* section *Androceras* (Nutt.) Marzell in the subgenus *Leptostemonum* (Dunal) Bitter (Bowers 1975; Vallejo-Marín et al. 2009). This species has four yellow stamens that serve a "feeding" function, providing pollen that is used as food for the bee pollinator. Pollination is achieved by an elongate, brown lower stamen that is specialized for placing pollen on areas of the insect where it cannot be easily removed and used for food (Vallejo-Marín et al. 2009). In section *Gonatotrichum*, *S. evolvuloides* and *S. turneroides* are both strongly heterantherous, with the lowermost filament extending to 2-5 mm, thereby reaching double the length of the other stamens. These two species also have flowers that open during the morning hours and close by midday (Nee 1989; S. Stern and L. Giacomin pers. obs.) with the flowers of *S. turneroides* also strongly fragrant, an unusual trait in the genus. The pollinators of these species are unknown and it is also unknown whether the upper stamens are modified for "feeding" and the lower stamen modified for "pollinating" as described for *S. rostratum* above. The third member of this clade, *S. parcistrigosum,* has flowers that are only weakly heterantherous with the filament of the lowermost stamen only ca. 1 mm longer than the other stamens.

Future work on section *Gonatotrichum* should include sequencing of more gene regions and species accessions, especially targeting *S. hoffmanseggii* and *S. adscendens*, to clarify biogeographic patterns in the group. Nothing is known about chromosome numbers or potential hybridization among taxa, and the function of heteranthery in pollination of several species within the group is unclear. Detailed studies of the development and morphology of hairs in *Solanum* and in section *Gonatotrichum* in particular may reveal that simple hairs may have arisen by two different evolutionary pathways, either from plesiomorphically simple hairs or by reduction from branched hairs. Finally, more in-depth studies of the entire Brevantherum clade are needed to clarify its species limits, phylogenetic relationships, and morphological and biogeographical patterns.

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Appendix 1

Summary of species, collection location, vouchers, herbarium acronym, and GenBank accession numbers for taxa used in this study provided in the order ITS, *trnT-F,* and *waxy*. BIRM samples have the seed accession number for the Solanaceae collection at the University of Birmingham, UK (now transferred to the Botanic Garden of the University of Nijmegen, Nijmegen, The Netherlands, http://www.bgard.science.ru.nl/solanaceae/).

Species	Collection Location	Voucher and Herbarium Acronym	Genebank Accession Number for ITS	Genebank Accession Number for *trnT-F*	GenBank Accession Number for *waxy*
Solanum abutiloides (Griseb.) Bitter & Lillo	BIRM S.0655	*Olmstead S-73* (WTU);	AF244716	AY266236	AY562948
Solanum adscendens Sendtn.	Brazil	*Stehmann 6001* (BHCB)	JN542580	JN661818	JN661835
Solanum arboreum Dunal	Costa Rica	*Bohs 2521* (UT)	AF244719	DQ180424	AY996381
Solanum argentinum Bitter & Lillo	Argentina	*Bohs 2539* (UT)	,AF244718	DQ180425	AY996382
Solanum armentalis J.L. Gentry & D'Arcy	Costa Rica	*Bohs 2593* (UT);	JN542581	JN661819	JN661836
S. betaceum Cav.	Bolivia	*Bohs 2468* (UT)	AF244713	DQ180426	AY996387
Solanum celsum Standl. & C.V. Morton	Costa Rica	*Bohs 2592* (UT)	JN542582	JN661820	JN661837
Solanum conglobatum Dunal	Bolivia	*Bohs 2740* (UT)	JN542583	JN661821	JN661838
Solanum cordovense Sessé & Moc.	Costa Rica	*Bohs 2693* (UT)	AF244717	DQ180480	AY996401
Solanum deflexum Greenm.	Costa Rica	*Bohs 2715* (UT)	JN542584	DQ180427	DQ169025
Solanum deflexum Greenm.	Mexico	*Smith & Rojas 348* (NY)	JN542585	JN661822	JN661839
Solanum evolvuloides Giacomin & Stehmann	Brazil	*Jardim 1843* (NY)	JN542586	JN661823	JN661840
Solanum evolvuloides Giacomin & Stehmann	Brazil	*Giacomin 974* (BHCB)	JN542587	JN661824	JN661841
Solanum granuloso-leprosum Dunal	Paraguay	*Bohs 3190* (UT)	JN542588	JN661825	JN661842
Solanum hirtellum (Spreng.) Hassl.	Paraguay	*Bohs 3166* (UT)	JN542589	JN661826	JN661843
Solanum lepidotum Dunal	Costa Rica	*Bohs 2621* (UT)	JN542590	DQ180486	DQ169035
Solanum lignescens Fernald	Mexico	*Linares 3536* (MEXU)	JN542591	JN661827	JN661844
Solanum luteoalbum Pers.	BIRM S.0042	*Bohs 2337* (UT)	AF244715	DQ180433	AY562957

Species	Collection Location	Voucher and Herbarium Acronym	Genebank Accession Number for ITS	Genebank Accession Number for *trnT-F*	GenBank Accession Number for *waxy*
Solanum manabiense S. Stern	Ecuador	*Stern & Tepe 377* (UT)	JN542592	JN661828	JN661845
Solanum manabiense S. Stern	Ecuador	*Stern & Tepe 374* (UT)	JN542593	JN661829	JN661846
Solanum parcistrigosum Bitter	Bolivia	*Bohs 2738* (UT)	JN542595	DQ180431	DQ169013
Solanum parcistrigosum Bitter	Argentina	*Nee & Bohs 50808* (NY)	JN542597	JN661832	JN661849
Solanum parcistrigosum Bitter	Paraguay	*Bohs 3194* (UT)	JN542594	JN661830	JN661847
Solanum parcistrigosum Bitter	Brazil	*Aparecida et al. 4860* (NY)	JN542596	JN661831	JN661848
Solanum pseudocapsicum L.	BIRM S.0870	no voucher	AF244720	DQ180436	AY562963
Solanum rugosum Dunal	Costa Rica	*Bohs 3011* (UT)	JN542598	DQ180490	DQ169046
Solanum schlechtendalianum Walp.	Costa Rica,	*Bohs 2915* (UT)	JN542599	DQ180491	DQ169047
Solanum turneroides Chodat	Bolivia	*Nee 51716* (NY);	JN542600	DQ180439	DQ169051
Solanum umbellatum Mill.	Costa Rica	*Bohs 2560* (UT)	JN542601	JN661833	JN661850
Solanum velutissimum Rusby	Bolivia	*Nee 51780* (NY)	JN542602	JN661834	JN661851

Appendix 2

Aligned dataset. (doi: 10.3897/phytokeys.8.2199.app) File format: NEXUS matrix file.

Explanation note: Aligned dataset; alignment performed visually using Se-Al (Rambaut 1996).

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RESEARCH ARTICLE

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Amomum nilgiricum (Zingiberaceae), a new species from Western Ghats, India

V. P. Thomas[1], M. Sabu[1], K.M. Prabhu Kumar[1]

1 *Department of Botany, University of Calicut, P. O. Calicut University 673 635, Kerala, India*

Corresponding author: *M. Sabu* (msabu9@gmail.com)

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Abstract

A new species of *Amomum* Roxb. from Western Ghats of Kerala is illustrated and described. *Amomum nilgiricum* VP.Thomas & M.Sabu, **sp. nov.** shows similarity with *A. masticatorium* Thwaites in having long drying ligule with an acuminate apex, pubescent anther and echinate capsules, but differs in clump forming habit with non-stoloniferous rhizomes, tomentose lamina beneath, long corolla tube, obovate to rhomboid labellum with clefted apex and without any colour design, emarginate anther crest and reduced staminodes. Detailed description, illustration, photographs, conservation status, and distributional details are provided.

Keywords

Amomum, Zingiberaceae, Western Ghats, Kerala, India

Introduction

Intensive botanical explorations for the revision of Indian *Amomum* have resulted in the collection of an interesting species with long membranous ligule from the Silent Valley National Park on the Western Ghats of Kerala. The family Zingiberaceae (ginger family) consists of 53 genera and over 1200 species (Kress et al. 2002). *Amomum* Roxb. is the second largest genus after *Alpinia* Roxb. within Zingiberaceae with about 150-180 species, widely distributed in Southeast Asia (Xia et al. 2004). In India the genus is represented by 22 species, mostly restricted to North-East India and South India

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(Thomas et al. 2010). Sabu (2006) reported 6 species of *Amomum* from South India and Thomas et al. (2009) raised the number species to 7 by reporting new distribution record of *A. fulviceps* Thwaites.

The new species, *A. nilgiricum,* shows similarity with *A. masticatorium* Thwaites in having long drying ligule with an acuminate apex, pubescent anther and echinate capsules, but differs in clump forming habit with non-stoloniferous rhizomes, tomentose lamina beneath, long corolla tube, obovate to rhomboid labellum with clefted apex, emarginate anther crest and reduced staminodes (Table 1). *A. nilgiricum* shows some morphological affinities with *A. villosum* group in the phylogenetic grouping of Xia et al. (2004).

Table 1. Distinguishing morphological characters of *A. masticatorium* and *A. nilgiricum*

Attributes	*mAmomum masticatoriu*	*m nilgiricumAmomu*
Habit	slender, spreading	robust, clump forming
Rhizome	slender and stoloniferous	stout and non-stoloniferous
Lamina	oblong-lanceolate, 15–30 × 3–7.5 cm	lanceolate to elliptic-lanceolate, 32–41 × 6.5–8 cm
Petiole	0–2 mm long	2–8 mm long
Leaves	glabrous to puberulous beneath	tomentose beneath
Ligule	2.5–4.5 cm long and half deciduous	4.5–9 cm long and persistent
Corolla tube	shorter than labellum	longer than labellum
Labellum	3–3.5 × 2.3–2.8 cm, trilobed, maroon stripes on yellow ground	1.4–1.5 × 1–1.2 cm, not trilobed, uniformly yellow
Lateral staminodes	2–5 mm long	absent
Stamen	1.7–2.1 cm long, crest truncate, 1.5–1.6 × 0.3–0.4 cm	1.1–1.2 cm long, crest emarginate, *c.* 0.3 × 0.1 cm

Taxonomic affinities

***Amomum nilgiricum* V.P. Thomas & M. Sabu, sp. nov.**
urn:lsid:ipni.org:names:77116671-1
http://species-id.net/wiki/Amomum_nilgiricum
Figs 1–2

Diagnosis. The species shows similarity with *A. masticatorium* Thwaites in having long drying ligule with an acuminate apex, pubescent anther and echinate capsules, but differs in clump forming habit with non-stoloniferous rhizomes, tomentose lamina beneath, long corolla tube, obovate to rhomboid labellum with clefted apex and without any colour design, emarginate anther crest and reduced staminodes.

Type. INDIA. Kerala: Palakkad District, Silent Valley National Park, 1.5 km from Walakkad towards Sispara, 1200 m elevation, 3 April 2009, *V.P. Thomas & M.C. Shameer 115574* (holotype: CALI; Isotype, MH, CAL).

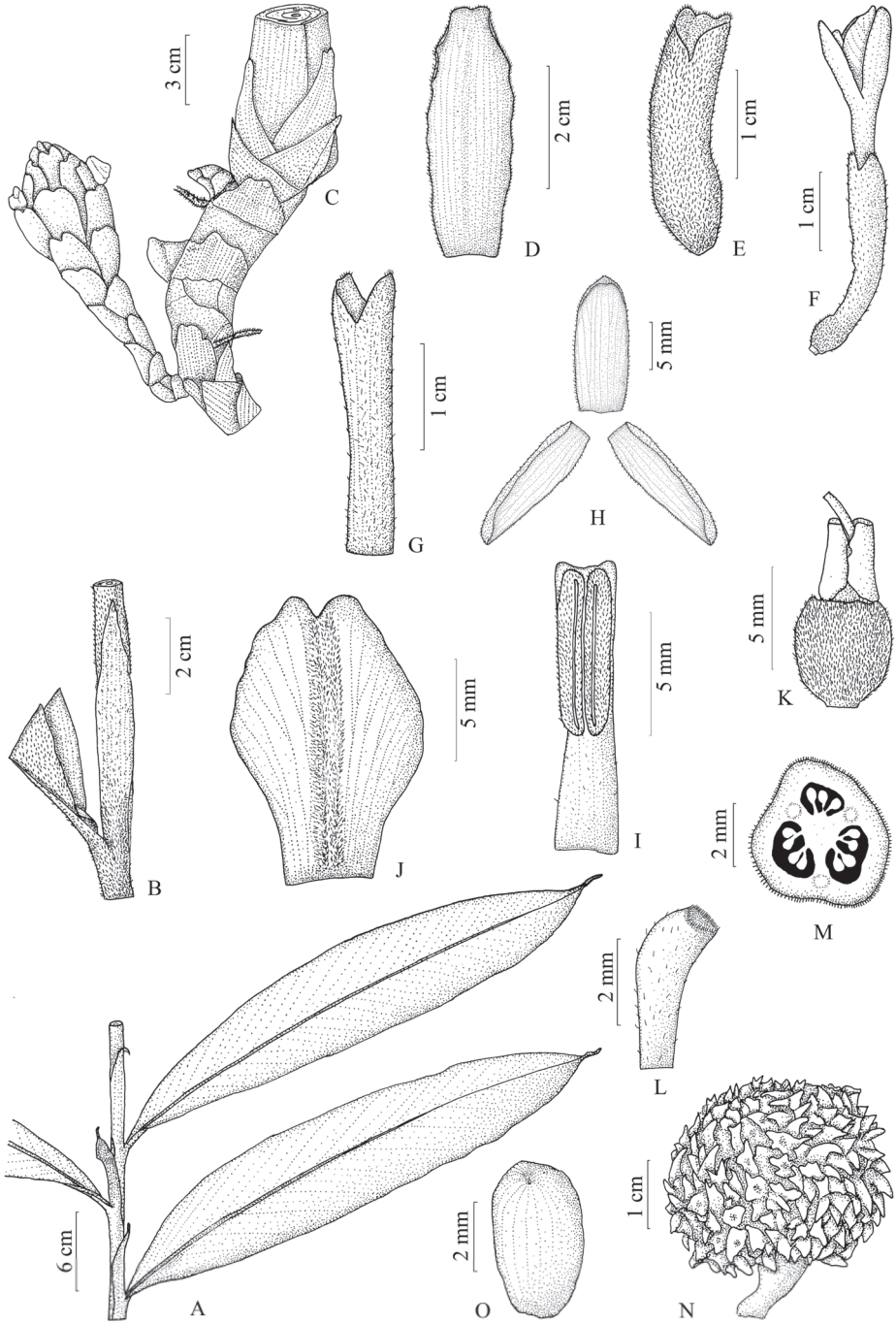

Figure 1. *Amomum nilgiricum* **A** a part of leafy shoot **B** ligule **C** inflorescence **D** bract **E** bracteole **F** flower **G** calyx **H** corolla lobes **I** stamen **J** labellum **K** ovary with epigynous glands and style **L** stigma **M** c.s. of ovary **N** fruit **O** seed.

Description. Clump forming herb. Rhizome non-stoloniferous, stout, robust, 2–4 cm thick, robust, creamy-white inside, sheathed with scales; scales ovate to triangular, chartaceous, c. 1.8 × 2 cm, apex nearly rounded, pubescent externally. Leafy shoots 200–400 cm tall, robust, clump forming; sheath 2.5–4.5 cm wide at base, green, densely pubescent externally. Leaves 14–20 per leafy shoot; lamina lanceolate to elliptic-lanceolate, 32–41 × 6.5–8 cm, base cuneate, margin slightly straight, apex acuminate to 3 cm long, puberulous to glabrous and green on upper surface, tomentose and pale beneath; midrib hispid beneath; veins appressed above; petiole 2–8 mm long, pale green, wooly tomentose. Ligule entire, lanceolate, 4.5–9 cm long, chartaceous, drying, persistent, apex acute, pubescent to tomentose externally, glabrous within. Inflorescence 7–15 cm long, many flowered, arise from the rhizome under soil; peduncle 3.5–7.5 cm long. Bract oblong, 3–4.7 × 1.6–2.1 cm, coriaceous, red, margin ciliate, apex slightly emarginate, pubescent externally, glabrous internally. Bracteole tubular, 2-lobed, 2.2–2.5 × 0.5–0.6 cm, unequally split, membranous, red, margin ciliate, apex acute, pubescent externally, glabrous within. Flower 4.7–5.2 cm long, yellow; pedicel 5 mm long. Calyx 2 or 3-lobed, 2.4–2.8 × 0.4 cm, pale red, membranous, split nearly equal, margin ciliate, apex acute, pubescent externally, glabrous within. Corolla tube 2.5–3 cm long, c. 4 mm wide at mouth, pale yellow, pubescent externally, glabrous internally except near mouth; dorsal corolla lobe oblong, 1.4–1.6 × 0.7–0.8 cm, yellow, margin ciliate, apex hooded, ecuspidate, pubescent externally, glabrous within; lateral corolla lobes oblong, 1.4–1.6 × 04–0.6 cm, yellow, margin ciliate, apex nearly rounded, one side slightly folded, pubescent outside, glabrous within. Labellum obovate to rhomboid, 1.4–1.5 × 1–1.2 cm, uniform yellow, margin entire, apex clefted, pubescent inside along the median part. Lateral staminodes absent. Stamen 1.1–1.2 cm long; filament 4–5 × 2.5–3 mm, pale yellow, broader towards base, rarely minutely pubescent; connective rarely pubescent externally; crest inconspicuous, c. 3 × 1 mm, yellow, apex emarginate, rarely puberulous; anther thecae oblong, 6–7 mm long, creamy-white, base nearly rounded, apex rounded, pubescent; dehiscing throughout their length. Epigynous glands 2, oblong, 3–4 mm long, cream coloured, apex truncate, rarely puberulous. Ovary globose, 4–5 × 4 mm, densely pubescent externally; locules 3; ovules many on axile placentae; style 3.4–3.7 cm long, pubescent towards tip, glabrous towards base; stigma, tubular, c. 1 mm across, pale yellow, mouth ciliate, opening terminal. Capsule 8–10 per spike, globose, 2–3 × 2–3 cm, red, echinate, spines stout, pubescent externally, calyx not persistent. Seeds many, slightly oblong, 4–5 × c. 3 mm, black, aromatic, arillate, glabrous; aril white.

Flowering and fruiting. March–November.

Distribution. Known only from type locality, Silent Valley National Park, Western Ghats, Kerala in the evergreen forest above 1210 m.

Etymology. the specific epithet *nilgiricum* indicates the place of collection Nilgiri Hills, a part of Western Ghats.

Conservation status. Critically endangered (CR B1ab(ii,iii)+B2ab(i,ii)). The taxon has been evaluated against the criteria as described in IUCN (2001). The area of occupancy is estimated to be less than 10 Km^2 and its habitat is severely fragmented,

Figure 2. *Amomum nilgiricum* **A** habit **B** ligules **C** inflorescence **D** rhizome with inflorescences **E** bract **F** bracteole **G** flower with a bract **H** calyx **I** corolla lobes **J** stigma **K** ovary with epigynous glands and style **L** stamen **M** labellum **N** infructescence.

and known to exist only in a single location. A continuous decline in quality of habitat and extent of occurrence is noticed. Major threat to the population are forest fire and clearing of trekking path in the forest which cause damage to the existing population.

Specimens examined. INDIA, Kerala: Palakkad District, Silent Valley National Park, 3 km from Walakkad towards Sispara, 24 September 2008, *V.P. Thomas & K.M. Prabhu Kumar 115504* (CALI); 2 km from Walakkad towards Sispara, 1 March 2009, *V.P. Thomas & A.V. Prasanth 115540* (CALI).

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