

A new tiny-leaved species of *Raveniopsis* (Rutaceae) from the Pakaraima Mountains of Guyana

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Abstract

Raveniopsis microphyllus K.Wurdack, **sp. nov.**, a new species known only from a single peak in the Pakaraima Mtns. of Guyana, is described and illustrated. This white-flowered shrub adds to the many narrow-endemic Guiana Shield species in the genus, and is unique in bearing small, trifoliate, sclerophyllous leaves. Leaf anatomy and surface micromorphology of the new species were examined to document its montane adaptations. The multiple trichome types of the leaves and flowers of new species were characterized, and the systematics value of the considerable foliar trichome variation in *Raveniopsis* is discussed.

Keywords

Guiana Shield, Guyana, Kamakusa Mtn., leaf anatomy, *Raveniopsis*, Rutaceae, trichomes

Introduction

The Rutaceae of the Guiana Shield region of northern South America contains about 60 species (nearly half endemic) in 20 genera (Kallunki 2005). Of those genera, three (*Apocaulon* R.S. Cowan, *Decagonocarpus* Engl., *Rutaneblina* Steyererm. & Luteyn) are small endemic groups and a fourth, *Raveniopsis* Gleason, is near endemic. *Raveniopsis*, the focus of this study, appears to be a classic Guiana Shield radiation where of its 19 currently recognized species, 16 are narrow montane endemics known from one or a few sandstone mountains (i.e., 13 are known from a single tepui including four species endemic to Sierra de la Neblina and three to Auyán-tepui) in Venezuela (Amazonas,

Bolívar), Brazil (northern Amazonas), and Guyana (Mazaruni-Potaro, described herein). In addition, one species is more widespread and extends to lower elevations across this region, and two species are low-elevation disjuncts further south in Brazil (southeastern Amazonas, Rondônia).

Raveniopsis are attractive shrubs, mostly less than 2 m tall (up to 5 m in *R. stelligera* [R.S. Cowan] R.S. Cowan), with a diversity of leaf, trichome, and floral morphologies. Their leaves can be simple or trifoliate, and can be thin or clearly adapted for montane life in being thickened and well-covered in diverse types of trichomes. Among the species are two strikingly different floral syndromes that presumably reflect pollinator differences, and include: (1) short-tubed white to sometimes pinkish-tinged, or (2) longer-tubed red to orange corollas. The genus is characterized by a combination of pentamorous flowers, subequal and mostly free sepals that are longer than wide, androecia of two fertile anthers with basal appendages and three staminodes, zygomorphic tubular corollas with five lobes, and 5-parted apocarpous gynoecia producing follicular fruit.

Many of those diagnostic features also serve to group *Raveniopsis* with the “Angostura Alliance” (Galipeae subtribe Galipeinae), which includes about 25 genera and 130 species restricted to the neotropics (Kubitzki et al. 2011; Bruniera et al. 2015). Many of the genera are small (13 have 1–2 species), and *Raveniopsis* is the second largest genus after *Conchocarpus* J.C. Mikan (53 species, including *Almeidea* St.-Hil.; Bruniera et al. 2015). Molecular phylogenetic studies have so far indicated that most of the limited Angostura Alliance taxon sampling (10 genera) form a core clade, and that taxonomic adjustments are needed to improve subtribal and generic circumscriptions (Gropo et al. 2008, 2012; Bruniera et al. 2015). Based on floral characters, *Raveniopsis* appears to be closely related to *Ravenia* and a further suggestion has been made that perhaps both genera should be combined (Kubitzki et al. 2011). *Raveniopsis* has not been sampled for any published molecular phylogenetic study, although preliminary evidence indicates that the genera should be kept separate (K. Wurdack unpublished).

While new exploration of montane areas of the Guiana Shield is expected to yield novelties, it was surprising that a very distinct new species of *Raveniopsis* was among collections made during recent botanical exploration of Kamakusa Mtn. in Guyana. The significance of this discovery was not known at the time of collection, although its identity was puzzled over by expedition members including the author. Kamakusa Mtn. is the highpoint of the Merume Mtns., a subrange within the Pakaraima Mtns., and forms part of an escarpment bordering the lowland (<100 m) rainforests of the lower Mazaruni River. This escarpment defines the eastern edge of a broad upland region (mostly >1000 m) within the Guiana Shield that continues westward into adjacent Venezuela and there includes part of the Gran Sabana and numerous scattered tepuis. While the summit of Kamakusa Mtn. apparently had not been botanically explored prior to 2012, an expedition in June–July 1960 led by Stephen Tillett on behalf of The New York Botanical Garden traversed its lower slopes and made many type collections of taxa in diverse families (Wurdack et al. 2013). This richness in novelties suggests a higher degree of local endemism than observed in other mountains in the vicinity except Mt. Ayanganna, although many of those taxa remain poorly collected or studied.

Material and methods

Scanning electron microscopy (SEM) was with a Zeiss EVO MA15 SEM at 10–12 kV after directly mounting dried herbarium specimen fragments, and sputter coating the samples with 25 nm of Au/Pd. For leaf anatomy, a rehydrated fragment was paraffin-embedded, sectioned at 10 μ m, stained with toluidine blue O, and imaged with a Zeiss Universal Compound Microscope. The pollen was only examined and measured with SEM due to the few grains available. Trichome morphology and terminology follows Webster et al. (1996) that treats the great diversity of indument types in *Croton* L. (Euphorbiaceae), which like *Raveniopsis* has considerable variation in branched forms.

Taxonomic treatment

Raveniopsis microphyllus K. Wurdack, sp. nov.

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Figure 1

Diagnosis. Differs from *Raveniopsis breweri* in small trifoliate leaves, indument of small rosulate trichomes, subsessile and few-flowered inflorescences, smaller sepals and corollas, and hirsute anthers.

Type. GUYANA. Cuyuni-Mazaruni Region: Summit of Kamakusa Mtn. (i.e., on top of 4th escarpment of four), impenetrable elfin forest to 3 m, extremely dense and wet, rich in epiphytes, 5°52'51.7"N, 60°6'10.4"W, 1686 m, 7 Jun 2012 (fl), *E. Tripp 3191* with K. Wurdack, A. Radosavljevic, and J. Ralph (holotype: BRG; isotypes: NY, US-3679224).

Description. *Shrub* to 1.5 m, evergreen; leafy ultimate branchlets thin, 0.7–0.9 mm dia., densely pubescent; trichomes rosulate, 0.2 mm wide, sessile to shortly stipitate, with numerous short, uniform-length radii (arms), radii free without coherent edges; bark dark-brown, thin, easily peeled; bark of older twigs with fissures from periderm development, pubescence persistent on strips of remaining epidermis. *Stipules* absent. *Leaves* opposite, 3-foliolate, petiolate; petiole terete, 2.5–3 \times 0.7 mm; leaflets elliptic, subequal, laminar size class leptophyll, margin entire, unlobed; terminal leaflet with petiolule 1–1.5 mm long, lamina 5.5–7.5 \times 3–5.3 mm, length:width ratio 1.32–1.83 (mean=1.63, n=11), base cuneate, symmetric, apex angle acute, apex shape subacute to obtuse; lateral leaflets usually slightly larger than terminal, petiolules 0.3–0.5 mm long, lamina 5–8.8 \times 3–4.5 mm, length:width ratio 1.67–1.97 (mean = 1.84, n = 11; measurements of lateral leaflets from same leaves used in prior terminal leaflet ratio), base subcordate, basal extension asymmetrical, proximal basal extension (outer lobe) 0.3 mm, distal basal extension (inner lobe) 0.1 mm, apex similar to terminal leaflet; adaxial side dark green in life, moderately pubescent, becoming glabrescent with age; adaxial trichomes multiradiate, radii 10–13, free, lateral radii 0.1–0.2 mm long, central radius sometimes differentiated by elongation to 0.6 mm and porrect

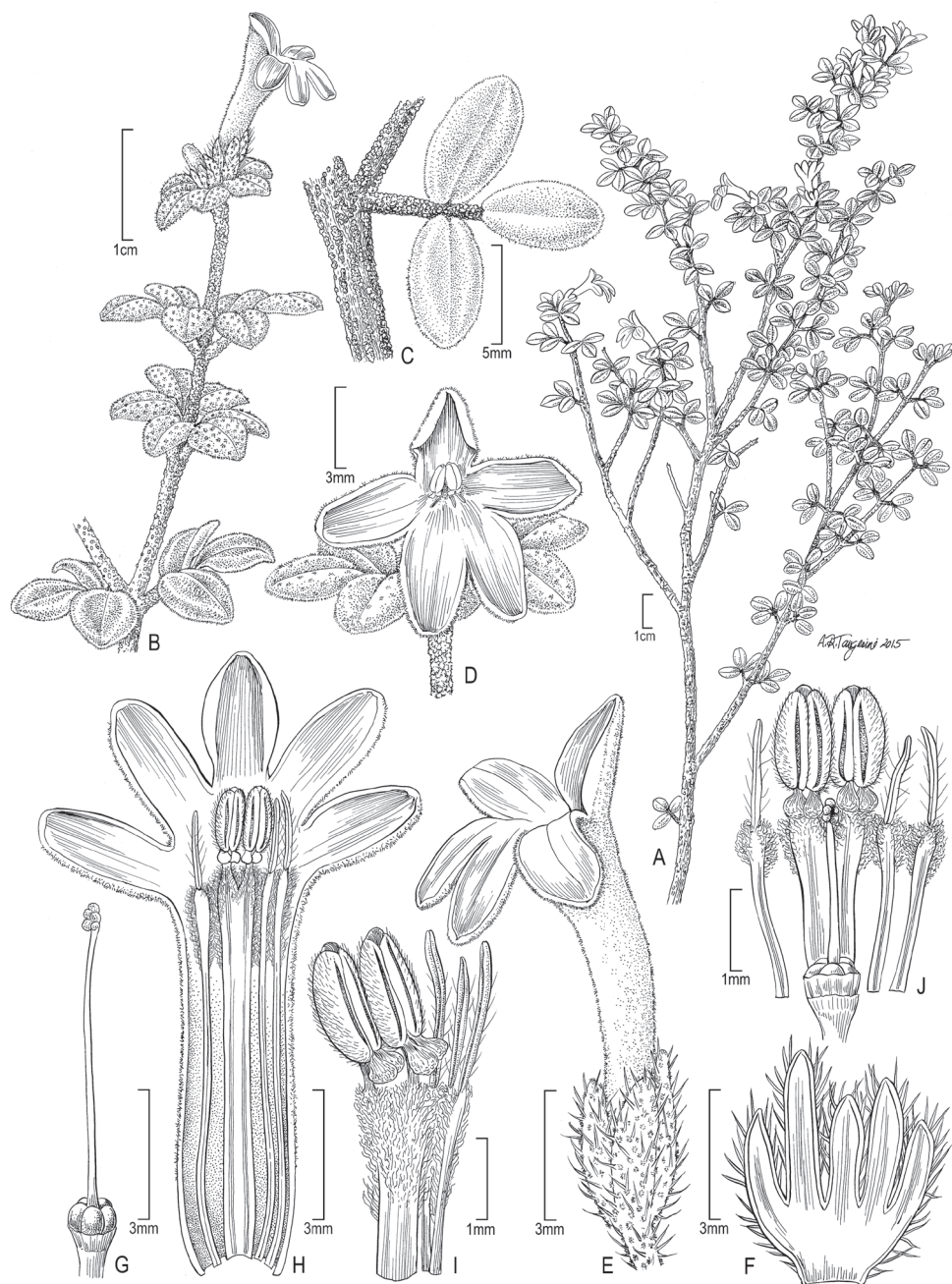


Figure 1. Illustration of *Raveniopsis microphyllus*. **A** Habit **B** Flowering branch **C** Trifoliate leaf **D** Flower (face view) **E** Flower (lateral view) **F** Calyx with five unequal sepals **G** Gynoecium **H** Corolla (split) and androecium **I** Androecium of bud **J** Floral dissection of same bud. (Source: Tripp 3191, US).

(porrect-multiradiate), trichomes near leaf base and margins having the greatest central radius elongation; abaxial side densely pubescent with rosulate trichomes; blade coriaceous, pellucid dots not visible, cross-sectional profile 0.7 mm high including 0.4 mm lamina thickness plus 0.3 mm layer of abaxial trichomes, primary venation pinnate. *Inflorescence* terminal, subsessile, flowers 1(–3) in a reduced monochasium. *Flowers* bisexual, 5-merous, shortly pedicellate, pedicel to 1 mm long. *Calyx* 5-parted, sepals connate at base to 1 mm, separate distally, coriaceous; sepal lobes erect, unequal, in 2 alternating size classes; longer 2, 2–3 × 1 mm, unequal with longest subtending banner petal lobe; shorter 3, 1–2 × 0.5 mm, subequal; externally pubescent with trichomes of both porrect-multiradiate and multiradiate types, internally glabrous and lined with files of dark-content cells. *Corolla* white, tubular-infundibuliform, of 5 connate petals, markedly zygomorphic, 12–15 mm long; tube 8–9 mm long, slightly curved, narrowest point at base 0.9–1.2 mm dia., distally expanded to 1.5–2 mm dia.; lobes 5, imbricate in bud, spreading at anthesis with 4 in 1 plane forming slightly recurved lip and 1 upright banner, 2–3.5 × 1.5–2 mm, subequal, internal pilose band below lobes (zone where androecium is similarly pilose), glabrous elsewhere internally and externally where imbricate petal margins overlap in bud, externally tube otherwise densely multiradiate pubescent becoming porrect-multiradiate towards lobes. *Androecium* of 2 fertile stamens and 3 staminodes, free from corolla. *Fertile-stamens* proximally fused, distally separate but coherent with tangled trichomes, 11.5–12 mm long; filaments 9–10 mm long × ca 0.4 mm wide (per filament) at base, expanding to 0.8 mm wide distally due to asymmetric wings (wider on outer edge, narrower on coherent edge), narrowly oblanceolate, flattened, <0.1 mm thick, central vein prominent; apex of filament abruptly narrowed as 0.3 × 0.1 mm extension connected to anther; fused base and apical extension glabrous, free part pubescent with long crinkled (pilose) trichomes; anthers 2–2.2 mm long, consisting of 1.3–1.5 × 0.9 × 0.5 (thick) mm thecae, 0.5 mm basal saccate appendage, and 0.1 mm acute connective tip, basifixed, free (not laterally coherent along adjacent edges); thecae co-lateral with longitudinal dehiscence slits facing inner side of stamen, hirsute with stiff simple trichomes; basal appendage facing inner (dehiscence) side of stamen, glabrous; connective, tip, and basal appendage darkened and appearing glandular. *Staminodes* 3, free, 11–11.5 mm long; filament portion 9–9.5 mm, flattened and resembling slightly reduced fertile anthers, 0.2 mm wide at base to 0.5 mm distally, distal part pilose; apical tip extension 1.8–2 × 0.2 mm, subulate, undifferentiated with no trace of abortive thecae or distinction between filament apex and connective, glabrous to sparsely hirsute. *Ovary* 0.5 mm (high) × ca 1 mm (wide), 5-lobed (apocarpous), glabrous, surrounded by a thin cupular disc; disc erect, distinctly shorter than ovary, 0.3 mm high, slightly lobed at apex. *Style* single, 6 × 0.1 mm, glabrous; stigma ca 0.3 mm long, obliquely 5-lobed, smooth. Fruit not seen.

Etymology. The specific epithet is derived from *micro-* (Greek, little or small) and *-phyllus* (Greek, -leaved), and refers to the small leaflet size, which is more reduced than in any other species of *Raveniopsis*.

Distribution and ecology. *Raveniopsis microphyllus* is known only from the summit of Kamakusa Mtn. where it was occasional along a transect cut across the north-south

axis of the narrow summit (personal observation). Flowers and young buds, although infrequent, were collected in June. The cold, wet, windswept summit of Kamakusa Mtn. is covered by a relatively low-stature (2–4 m tall) evergreen shrubland on peat overlying sandstone and can be classified in the upper montane life zone (Huber 1995b). The flora contains dense stands of *Bonnetia tepuiensis* Kobuski & Steyer. and *B. roraimae* Oliv. (Bonnetiaceae), along with other montane elements such as *Schefflera monosperma* Maguire, Steyer. & Frodin (Araliaceae), species of *Weinmannia* L. (Cunoniaceae), and at least one other undescribed endemic plant (*Tryssophyton* Wurdack, Melastomataceae). Immediately south of Kamakusa Mtn. along the wet edge of the Pakaraima Mtns. continues an unexplored and poorly mapped montane ridgeline with peaks. This local region includes some other >1500 m elevations, that while lower than the Kamakusa Mtn. summit (1686 m) are still within the 1500–3000 m highlands physiography (Huber 1995a). However, these nearby peaks appear less likely to contain additional populations of *R. microphyllus* due to their small sizes, and lower elevations that tend to support slightly different and taller plant communities. The closest peak (55 km SSE) to reach or exceed the elevation of Kamakusa Mtn. is relatively well-explored Mt. Ayanganna (2041 m), which has so far only yielded *Raveniopsis ruellioides* (Oliv.) R.S. Cowan.

Conservation status. Following the criteria and categories of IUCN (2012), *Raveniopsis microphyllus* is given a preliminary status of Vulnerable (VU D2) due to population very small or restricted (area of occupancy <20km² and number of locations <5). The species has extremely limited suitable montane habitat and coupled with relatively small known population size is vulnerable to climate and land use changes.

The upper part of Kamakusa Mtn. is presently pristine and undisturbed habitat, and the sole known *Raveniopsis microphyllus* population had no evidence of being unhealthy or fluctuating. The region is at risk of habitat destruction due to placer gold mining, although such activity is unlikely to reach the small, inhospitable summit of Kamakusa Mtn. Recent gold mining of moderate scale has occurred along the upper Partang River on the southern edge of Kamakusa Mtn. and its drainage, about 10 km from the type locality. While those mining operations had ceased by 2012, other waves of gold prospecting activities go back decades and have pushed further in. Such activities were noted as “pork-knocker camps” on Tillett et al. herbarium labels of 1960 (e.g., *Aechmea pallida* L.B. Sm. [Bromeliaceae], Tillett 44859, NY), and during the recent fieldwork (personal observation) that encountered old camps (furthest human intrusion was a long overgrown camp at N05°51'44.4", W060°09'20.5", 1019 m, and 6.2 km from the type locality), an abandoned unpaved runway (Partang airstrip), and ATV trails from the nearest village (Imbaimadai), which were constructed to support the recent upper Partang River mining operation.

Discussion

In species keys (i.e., Cowan 1960; Steyermark 1980; Kallunki 2005) *Raveniopsis microphyllus* would quickly group with the three other compound-leaved species, *R. cowani-*

ana Steyerl. & Luteyn, *R. stelligera* (R.S. Cowan) R.S. Cowan (including *R. liesneri* Steyerl.), and *R. trifoliata* R.S. Cowan. However, those taxa are very different from *R. microphyllus* in much larger leaflet size, different types of trichomes, red-orange tubular corollas, and biogeography. They occur in Venezuela at different elevations on Sierra de la Neblina where *R. cowaniana* and *R. trifoliata* are endemic, and slightly broader-ranged *R. stelligera* also extends to Cerro Duida and Cerro Yutajé. Compound leaves aside, *Raveniopsis microphyllus* appears most morphologically similar to *R. breweri* Steyerl. in small, ovate lamina, white flowers, and trichome type (see below). *Raveniopsis microphyllus* has trifoliate leaves with very small leaflets ($5\text{--}8.8 \times 3\text{--}5.3$ mm) that are adaxially pubescent when young (becoming glabrescent), a unique form of small rosulate trichomes, single (to few) flowered subsessile inflorescences, small sepals (largest 3×1 mm), small corollas, and hirsute anthers. In contrast, *R. breweri* has larger ($22\text{--}32 \times 10\text{--}16$ mm), simple leaves that are adaxially glabrous except along the midvein, larger flattened rosulate trichomes, pedunculate 3–7 flowered racemose inflorescences, larger sepals (largest 8×2 mm), larger corollas, and glabrous anthers. In *R. breweri* the suggestion (fig. 1 in Steyermark 1980) that two staminodes are laterally conjoined to the stamens was not confirmed here, although the type collection was not examined. My observations of *R. breweri* (Huber & Medina 8529, US; Prance & Huber 28254, US) are that all three staminodes are free, although distally loosely confluent due to tangled trichomes. In addition, the two anthers are laterally coherent as has been found in some species of *Raveniopsis* and other Angostura Alliance genera (personal observation; Kallunki 1991; El Ottra et al. 2013), but which does not appear to be the case in *R. microphyllus* where the anthers are free in bud and at dehiscence. *Raveniopsis ruellioides*, the only other species in Guyana, differs in larger, simple, pellucid-punctate leaves with exclusively simple trichomes, and long pedunculate inflorescences with red flowers and foliaceous sepals.

The leaves of *Raveniopsis microphyllus* appear well adapted for a montane environment due to their small size, considerable vestiture, thick cuticle, and coriaceous nature. Pellucid dots (oil-containing secretory cavities), which are a characteristic feature of Rutaceae leaves, are not visible in *R. microphyllus*, nor do they appear differentiated anatomically. They are superficially visible in some thinner-leaved species (e.g., *R. necopinata* Kallunki, *R. ruellioides*, and *R. stelligera*) but are not similarly obvious in other coriaceous species. I also did not note them elsewhere in *R. microphyllus* (i.e., floral parts during wet dissections), although some darkened surficial cells on the anthers may be secretory cells. Unfortunately at the time of collection no attention was paid to any presence of citrus or resinous odor that would indicate essential oils. Leaf anatomy (Fig. 2E, F) shows a dorsiventral structure and a thick cuticle (Fig. 2G; $20\text{--}23$ μm at the thinnest point mid-cell and thicker where adjacent cells meet, as measured via SEM) on the large-celled epidermis of the glabrescent adaxial side. The epidermis of the abaxial side is small-celled and lacks the cuticle thickening. Stomata are confined to the abaxial side where they are densely packed under the canopy of stalked trichomes (Fig. 3D) and absent along the slightly raised secondary vein courses. The mesophyll is poorly differentiated into palisade and spongy layers. Elongate styloid crystals are

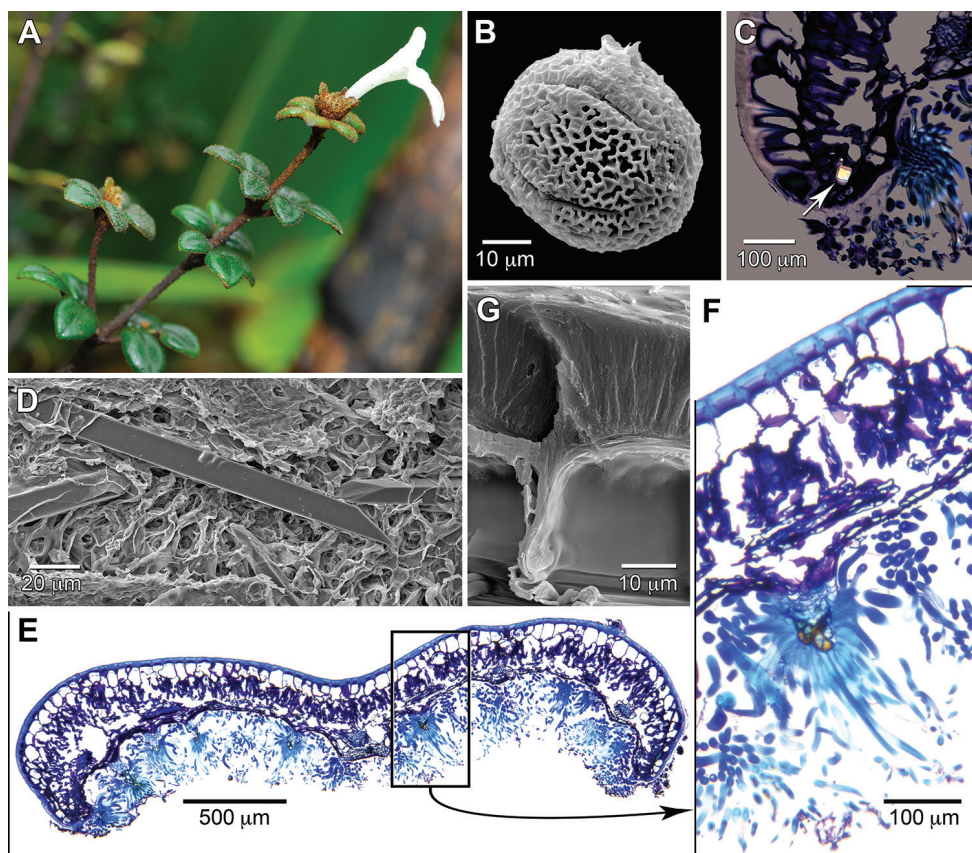


Figure 2. Morphology and anatomy of *Raveniopsis microphyllus*. **A** Life photo of flowering branch showing strongly zygomorphic, white corolla **B** Pollen with mesocolpium-centered equatorial view of whole grain **C** Transverse section of leaflet edge under polarized light, showing bright styloid crystal (at arrow) **D** In-situ styloid crystals near secondary vein **E** Transverse section of entire leaflet (tilled image) **F** Transverse section in closer view showing thick adaxial cuticle, and abaxial trichome with multicelled stalk **G** Adaxial epidermis showing thick cuticle above epidermal cells. (Source: Tripp 3191, US).

sparsely present in the mesophyll and mostly oriented parallel to major veins. The crystals are square in transverse section (Fig. 2C) and have obliquely faceted, needle-like ends (Fig. 2D).

The indument on *Raveniopsis* is very diverse in form (i.e., variations on glandular, simple, dendritic, multiradiate, and rosulate) both among species and often within an individual plant in a location-dependent manner. The interspecific trichome diversity is taxonomically useful (e.g., applied in the species key of Steyermark (1980)) and may be phylogenetically informative, although care is needed to observe homologous plant structures when making fine comparisons. *Raveniopsis microphyllus* bears five different location-specific trichome forms, with some minor intergradation, that can be grouped into three basic types including: (1) simple, (2) rosulate, and (3) multiradiate. While rosulate can

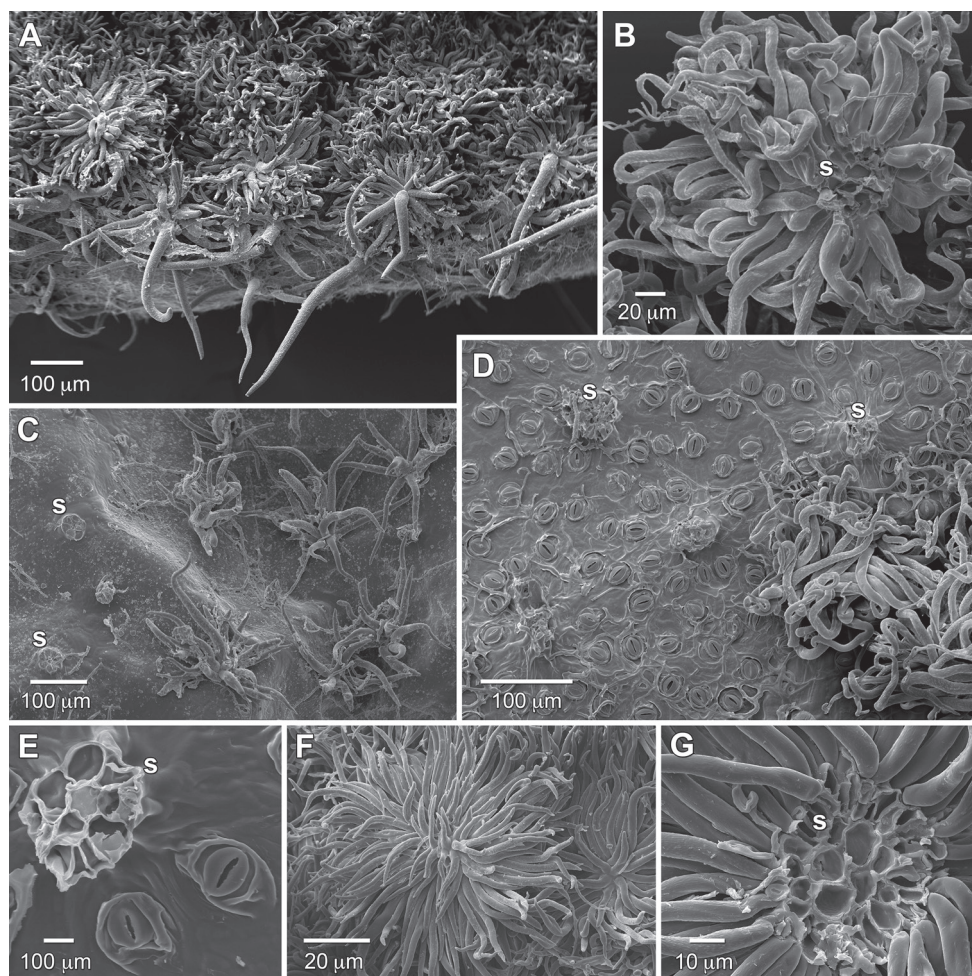


Figure 3. Trichome and leaf surface comparisons of *Raveniopsis microphyllus* (A–E) and *R. breweri* (F–G). **A** Abaxial side of leaflet showing trichomes transitioning from rosulate to porrect-multiradiate with central long radii at margin (sampled from proximal margin of lateral leaflet) **B** Back of rosulate trichome showing central multicellular attachment stalk, and curled free arms **C** Adaxial side of young leaflet showing multiradiate trichomes, and rosette bases of trichomes that have weathered off **D** Abaxial side of leaflet with most trichomes removed to show dense stomata and stalk bases of rosulate trichomes; note fungal hyphae on epidermis **E** Close-up of stomata and stalk base of rosulate trichome **F** *Raveniopsis breweri* abaxial trichome **G** Back of *Raveniopsis breweri* abaxial trichome, showing central multicellular attachment stalk. (Abbreviations: s = stalk. Source: *R. microphyllus*, **A–E** Tripp 3191, US; *R. breweri*, **F–G** Prance & Huber 28254, US).

be considered a subtype of multiradiate (see Webster et al. 1996), the distinction is useful here for descriptive purposes. The simple trichomes are confined to inside the flower, and can be of two forms as either stiff and straight (strigose) on the anthers, or crinkled (pilose) on the filaments and adjacent inner corolla wall. The rosulate trichomes (Fig. 3A–B, D)

are tufts with numerous soft, often twisted radii (arms) and are well developed on the abaxial laminar surface and along stems and petioles. The multiradiate trichomes (Fig. 3A, C) while similar to the rosulate form differ in having fewer and stiffer radii and are often further differentiated into a modified form with an erect longer central radius (porrect-multiradiate); they occur on the adaxial side and margins of the lamina, and outer surfaces of the flower. Both rosulate and multiradiate trichomes are stipitate with a short, fragile (allowing the trichomes to easily detach), non-vascularized multicellular stalk, which in cross section is a rosette of 6–9 cells surrounding a central cell (Fig. 3E). The trichomes and their stalks have differential staining relative to the site of epidermal attachment (Fig. 2F). After the trichomes weather off the adaxial side, the remnants of the stalks are visible as rosette outlines (Fig. 3C). The species of *Raveniopsis* most closely approaching *R. microphyllus* in laminar trichome morphology are *R. breweri*, *R. peduncularis* Pittier & Lasser (but not “appearing lepidote”, fide Kallunki 2005), and *R. jauaensis* Steyermark., that were grouped as “stellate-squamose” in the species key of Steyermark (1980). They share similar tufted rosulate appearance with *R. microphyllus* but are larger and tend to be flattened (i.e., squamose), due to loss or shortening of central radii (Fig. 2F, G). These differences are more pronounced in *R. peduncularis* and *R. jauaensis*, which are further distinguished from *R. breweri* in bearing red flowers on elongate dischasyal inflorescences.

The reticulate pollen of *Raveniopsis* has been shown to have aperture (3, 5, 6-aperturate) and size variation (Morton and Kallunki 1993). Although I had little pollen of *R. microphyllus* available, it appears reticulate, 5-colporate, prolate-spheroidal, and $45\text{--}50 \times 43\text{--}48\text{ }\mu\text{m}$ in size (polar:equatorial ratio 1.05; $n = 3$, via SEM) (Fig. 2B). The pollen of *R. microphyllus* is very similar to other species in details of its reticulate sculpture, and falls in between the two reported size classes (Morton and Kallunki 1993).

The historical biogeography of *Raveniopsis* is likely complex and interesting given the variety of distributional patterns represented by species that are widespread, isolated endemics, sympatric endemics, or Amazonian disjuncts. Moreover, the sympatric species are morphologically diverse and (mostly) not obvious local species complexes. *Raveniopsis microphyllus* is the easternmost member of the 16 tepui species, and separated by 230–250 km from potential Venezuelan close relatives on Auyán-tepui (3 spp.) and Macizo del Chimantá (2 spp.). *Raveniopsis breweri*, which is the most morphologically similar species to *R. microphyllus*, is among the Auyán-tepui endemics. *Raveniopsis ruelioides* is a variable species (especially in leaf shape) that is broadly distributed across the Guiana Shield in southern Venezuela and eastward into the Pakaraima Mtns. It tolerates a broad elevation range (300–2600 m), although is mostly montane (1500+ m) and usually reaches lower elevations along watercourses. In the Pakaraima Mtns. it geographically most closely approaches *R. microphyllus* on Mt. Ayanganna, but as previously noted is morphologically very different and likely distantly related. *Raveniopsis sericea* R.S. Cowan was reported from Guyana (Kallunki 2005; Funk et al. 2007) but this record appears to be incorrect as further documentation could not be found (MO, NY, US, Biological Diversity of the Guiana Shield specimen database; J. Kallunki, personal communication). Otherwise that high altitude (1800–2500 m) species is endemic to the Macizo del Chimantá in Bolívar, Venezuela.

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Novel fern- and centipede-like *Selaginella* (Selaginellaceae) species and a new combination from South America

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Abstract

Two new *Selaginella* species (i.e. *S. altheae* Valdespino and *S. squamulosa* Valdespino) and a novel combination [i.e. *S. philipsonii* (Jermy & Rankin) Valdespino] from South America are proposed. Descriptions, illustrations (line drawings and scanning electron micrographs, SEM, images), discussion on taxonomic affinities and information on habitat, distribution and phenology, as well as on conservation status are provided for each. *Selaginella altheae* is morphologically similar to species with erect, fern-like habit placed in the “*Selaginella flabellata* (L.) Spring group” as defined by Hieronymus, while *S. squamulosa* is allied to a species assembly with centipede-like habit here informally termed the “*Selaginella vernicosa* Baker group;” whereas *S. philipsonii* with its moss-like habit may be associated with species in the “*Selaginella jungermannioides* (Gaudich.) Spring group” or those centered on *S. ovifolia* Baker. All taxa here proposed are classified in subg. *Stachygyndrum*.

Resumen

Dos nuevas especies de *Selaginella* (i.e., *S. altheae* Valdespino y *S. squamulosa* Valdespino) y una nueva combinación [i.e., *S. philipsonii* (Jermy & Rankin) Valdespino] de Sur América son propuestas. Para cada una de ellas se provee una descripción, ilustraciones (i.e. dibujos y microfografías de microscopio electrónico de barrido, MEB), discusión sobre su afinidad taxonómica, información sobre su hábitat, distribución y fenología, así como su estado de conservación. *Selaginella altheae* es morfológicamente similar a las especies con hábito erecto y parecidas a los helechos que se incluyen en el “grupo de *Selaginella flabellata* (L.)

Spring” como fue definido por Hieronymus; *S. squamulosa* es afín a especies con hábito centipediforme que aquí informalmente se denominan “grupo de *Selaginella vernicosa* Baker”, mientras que *S. philipsonii* con su hábito parecido al de los musgos puede estar emparentada con el “grupo de *Selaginella jungermannioides* (Gaudich.) Spring” o a las especies similares a *S. ovifolia* Baker. Por último, todos los taxa aquí propuestos se clasifican en el subg. *Stachygynandrum*.

Keywords

Amazon basin, Guiana Highlands, New World, monomorphic, subgenera, tepuis

Palabras clave

Cuenca del Amazonas, Escudo guyanés, monomórficas, Nuevo Mundo, subgéneros, tepuyes

Introduction

Continued work on South American *Selaginella* leads to the description of two new taxa: *Selaginella altheae* Valdespino and *S. squamulosa* Valdespino and to raise to species level *S. philipsonii* (Jermy & Rankin) Valdespino. These three species are anisophyllous either throughout the stems or shortly below or after the first branches with the leaves arranged in four (i.e. two median and two lateral) distinct ranks and quadrangular strobili composed of monomorphic sporophylls. Accordingly, they can be placed within subg. *Stachygynandrum* (P. Beauv.) Baker following Jermy’s (1986, 1990) morphology-based classification or that of Weststrand and Korall (2016) supported by phylogenetic analysis using molecular and morphological characters. Alternatively, they could each be assigned to two or three subgenera (i.e. *Ericetorum*, *Stachygynandrum* and *Heterostachys*) proposed by Zhou and Zhang (2015). It is believed, however, that placement of these three species in subg. *Stachygynandrum* best reflects their morphology, allows for easy identification and facilitates comparison with other taxa.

Selaginella altheae has a fern-like habit with erect main stems and axillary, ventral, dorsal and, occasionally, lateral rhizophores. Morphologically, this species belongs to the “*Selaginella flabellata* (L.) Spring group” as defined by Hieronymus (1901: 682), which contains ca. thirty-five species in the Americas (Valdespino, unpublished). *Selaginella squamulosa* seems morphologically related to a species group comprising about seven taxa including *S. arrecta* A.R. Sm., *S. marahuacae* A.R. Sm., *S. roraimensis* Baker, *S. scalariformis* A.C. Sm. and *S. vernicosa* Baker and the newly described *S. psittacorrhyncha* Valdespino (Valdespino 2017), which together are herein informally termed the “*Selaginella vernicosa* Baker group”. This group is defined by its centipede-like habit (i.e. plant body elongated and flattened, branching in one plane with leaves suggestive of body segments; overall reminiscent of centipedes), creeping or ascending to suberect stems and coriaceous leaves. *Selaginella philipsonii* has a moss-like habit (i.e. resembling a pleurocarpous moss in its long-creeping main stems and short lateral branches that often bear reproductive structures), axillary and dorsal rhizophores and small leaves. It may be related to species in the “*Selaginella jungermannioides*

(Gaudich.) Spring group”, as circumscribed in Valdespino et al. (2015), or to a species group akin to *S. ovifolia* Baker.

These additions to Neotropical *Selaginella* yield the 100 species estimated by Valdespino (2015, 2016) for Venezuela and raises the number of native Brazilian taxa to 84, including *S. psittacorhyncha* and the recently recorded *S. anaclasta* Alston ex Crabbe & Jermy in Serra do Aracá, Brazil (Barbosa-Silva et al. 2016), based on *Labiak et al.* 5639 (NY!). Thus, Brazil is now the country with the second highest *Selaginella* diversity in the New World. In the case of Colombia, more studies are still needed to ascertain its *Selaginella* diversity. It is likely that the number of Colombian species will be greater than that reported by Alston et al. (1981).

Material and methods

Herbarium studies were carried out by examining specimens from BM, CAS, COL, F, GH, MO, NY, OXF, P, PMA, RB, UC, US and W, as well as digitized images from COL and RB (herbarium acronyms follow Thiers 2017). Scanning electron microscopy (SEM) micrographs were made from selected specimens to document leaf surfaces and mega- and microspores sculpturing patterns, when available, from designated types and paratypes. These studies were conducted according to standard techniques as described by Valdespino (1995) and viewed and digitized at different magnifications using a Zeiss Model Evo 40 SEM at 10–20 kV at the Smithsonian Tropical Research Institute (STRI) in Panama. Digitized SEM images were post-processed and assembled in multipart figures using Adobe Photoshop as explained in Valdespino (2016).

Terminology and measurements of leaves and spores, as well as species conservation status provided in descriptions were assessed following Valdespino (2016 and references therein). Countries, in the additionally examined specimens section, were cited according to geographical order.

Taxonomy

Selaginella altheae Valdespino, sp. nov.

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Figures 1–5

Diagnosis. *Selaginella altheae* differs from *S. lechleri* Hieron. by the main stem leaves becoming obviously dimorphic above or 1–4 cm (vs. 3–6 cm) below the first branches of the stems, its lateral leaves bases oblique with a seemingly inner [actually it is an acroscopic] (vs. lacking) auricle that is tufted with 3–15 hairs (vs. bases glabrous) and the axillary leaves rounded to cordate or truncate with two, distinct, incurved and ciliate (vs. lacking) auricles at least up to the third or fourth branches along the stems.



Figure 1. *Selaginella altheae* Valdespino. **A** Habit, upper surface of stem **B** Close up of section of the upper surface of the stem **C** Habit, lower surface of stem **D** Close up of section of the lower surface of the stem. **A–D** digitized images of holotype, Maguire et al. 60249 (NY).

Type. BRAZIL. Amazonas: Río Negro, Río Cuaburí, along Río Tucano, vicinity of Base Camp, 20 Nov 1965, *B. Maguire, J.A. Steyermark & C.K. Maguire 60249* (holotype: NY).

Description. *Plants* terrestrial. *Stems* erect, stramineous, (20)30–65 cm long, 1.4–3.0 mm diam., non-articulate, usually not flagelliform, stoloniferous, 2–4-branched. *Rhizophores* axillary, ventral and dorsal, borne on lower-most part of the stems and throughout stolons, filiform or stout, 0.2–1.0 mm diam. *Leaves* seemingly monomorphic and strongly appressed to the stem shortly before or after first branches, then dimorphic throughout, coriaceous, upper surfaces dull to shiny green, slightly corrugate, lower surfaces shiny yellowish green to silvery green, striate, the outer bases short- to long-auricled (these tend to disappear on leaves above first branches), the auricle short- to long-ciliate, cilia 2–10, each 0.2–0.5 mm long. *Lateral leaves* on main stem after first branches distant to slightly imbricate, strongly ascending to slightly spreading, ovate-deltate to ovate-oblong, $2.0\text{--}4.2 \times 0.9\text{--}2.2$ mm; bases truncate, on main stem before first branches with an inner, acroscopic bases strongly overlapping stems, rounded, entire, basiscopic bases free from stems, geniculate, usually ciliate, cilia 1–5, each 0.1 to 0.2 mm long; acroscopic margins on main stem leaves after second branches greenish to narrowly hyaline along proximal $\frac{2}{3}$, 1–3 cells wide with the cells elongate, sinuate-walled and glabrous, parallel to margins, otherwise greenish, on branch leaves narrowly hyaline along proximal $\frac{3}{4}$ and cells as those on main stem, otherwise greenish distally, long-ciliate along proximal $\frac{1}{2}\text{--}\frac{3}{4}$, otherwise becoming short-ciliate to dentate distally, basiscopic margins greenish, comprising similar cells as in acroscopic margins, entire along proximal $\frac{2}{3}$, otherwise sparsely denticulate distally; apices gradually tapering, acute to broadly acute, tipped by 1–3 teeth; upper surfaces comprising irregularly shaped, somewhat rectangular to quadrangular, sinuate-walled cells (often difficult to distinguish because of waxy deposits), with some obscure, idioblast-like, short quadrangular to round or elongate and variously papillate cells, without stomata or with some obscure along basiscopic margins, lower surfaces comprising elongate, sinuate-walled cells, with many of these idioblast-like, elongate and papillate, papillae 5–14 in 1 or 2 rows on each cell lumen, stomata on 1–5 rows along midribs. *Median leaves* on main stems after first branches distant to slightly imbricate, ascending, ovate, broadly ovate to ovate-elliptic, $1.4\text{--}3.0 \times 0.8\text{--}1.7$ mm; bases truncate to truncate-oblique, the outer base tufted with (4)6–20 long hairs, without auricles; margins greenish to narrowly hyaline, 1 or 2 cells wide with the cells elongate, slightly sinuate-walled and mostly glabrous or papillate, parallel to margins, the inner margins short-ciliate along proximal $\frac{2}{3}$, denticulate along distal $\frac{1}{3}$, the outer margins entire along proximal $\frac{1}{3}$, becoming short-ciliate along medial $\frac{1}{3}$, otherwise denticulate on distal $\frac{1}{3}$; apices acute to slightly acuminate, the acumen ca. 0.1 mm, tipped by 1–3 teeth; upper surfaces comprising irregular (jigsaw puzzle-like), sinuate-walled cells (often difficult to distinguish because of waxy deposits), some of these papillate, papillae 3–14, irregularly arranged, without elongate idioblasts, stomata in 3–7 rows along the midribs and marginal to submarginal along basiscopic $\frac{1}{3}$ of outer margins, lower surfaces comprising elongate (jigsaw puzzle-like), sinuate-walled cells, without elongate idioblasts and stomata.

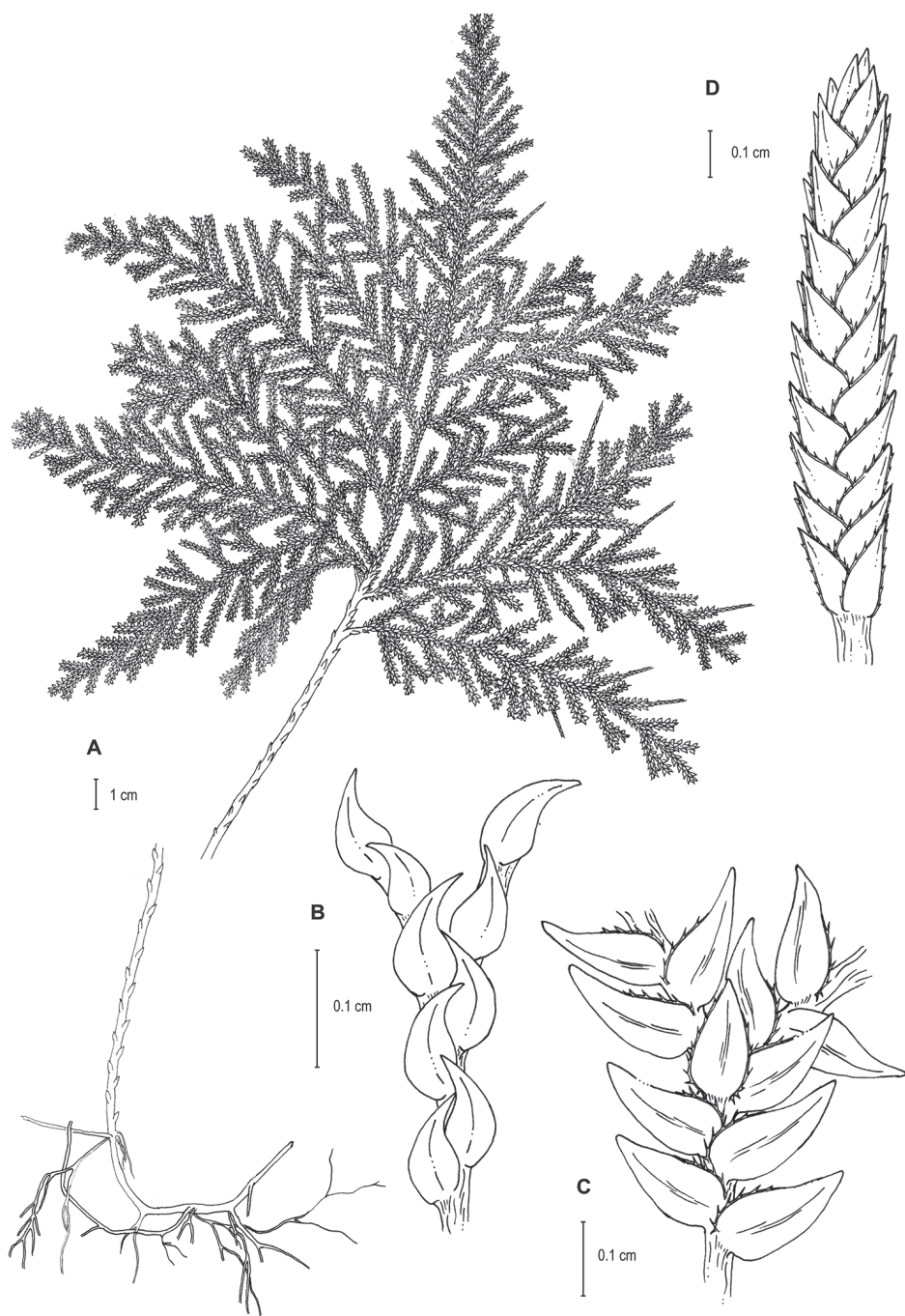


Figure 2. *Selaginella altheae* Valdespino. **A** Habit **B** Section of main stem above first branch showing median leaves, upper surface **C** Section of main stem above first branch showing lateral leaves and axillary leaf, lower surface **D** Close-up of strobilus. **A–D** line drawings of holotype, *Maguire et al.* 60249 (NY). Illustration made by Rubén Lozano.

Axillary leaves on main stem after first branches ovate-lanceolate, $2.0\text{--}3.0 \times 0.9\text{--}1.5$ mm; bases rounded to cordate or truncate, with two small, long-ciliate auricles up to, at least, the fifth branch and then becoming small lobes; margins narrowly hyaline as in median leaves, long-ciliate along proximal $\frac{1}{2}$, otherwise short-ciliate to denticulate distally; apices gradually tapering, acute, tipped by 1–3 teeth; both surfaces as lateral leaves. *Strobili* terminal on main stem and each branch tip, quadrangular, 0.3–1.7 cm. *Sporophylls* monomorphic, without a laminar flap, each with a slightly developed and seemingly glabrous keel along midribs, ovate to ovate-lanceolate, $0.8\text{--}1.0 \times 0.4\text{--}0.6$ mm; bases rounded to truncate; margins narrowly hyaline, 1 or 2 cells wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, short-ciliate along proximal $\frac{1}{2}$, otherwise denticulate to entire distally; apices acute to acuminate, the acumen 0.1 to 0.2 mm, tipped by 3 tooth-like projections; *dorsal sporophylls* with upper and lower surfaces as in vegetative leaves; *ventral sporophylls* with both surfaces, silvery green to hyaline, comprising elongate, papillate, sinuate-walled cells. *Megasporangia* in 2 ventral rows; *megaspores* white, rugulate-reticulate on proximal faces with a slightly developed equatorial flange and microstructure granulate, perforate and sparsely echinate, mostly open to somewhat closely reticulate on distal faces with the microstructure sparse and minutely echinate and perforate, 180–250 μm diam. *Microsporangia* in 2 dorsal rows; *microspores* orange, echinate-rugulate on proximal faces with punctate microstructure, capitate or baculate on distal faces with each caput or bacula and the rest of the surface with echinate microstructure, 20–30 μm diam.

Habitat, distribution and phenology. *Selaginella altheae* grows on lowland and montane rainforests at 140–450 m; it is known from the Amazon basin of Colombia, Venezuela and Brazil and found fertile from April through to November.

Eponymy. I am delighted to dedicate this graceful, fern-like species with shiny idioblasts on leaf surfaces to my mother, Althea Quintero (1939–), whose gentle, selfless demeanor, as well as strength and enlightening life-long support has guided and buttressed my life and professional career. She has adorned my path in life in the same manner as her lovely and resilient namesake flower does in nature.

Conservation status. This is a widely distributed species that grows at low elevations in Tropical rainforests of the Amazon basin; therefore, it is considered here of Least Concern (LC), according to IUCN (2012) categories and criteria.

Additional specimens examined (paratypes). **COLOMBIA.** Amazonas: Río Amazonas, along a road 8–14 km N of Leticia, 450 m, 3–5 Jul 1974, *Breedlove 36331* (CAS). **VENEZUELA.** Amazonas: Rivers Casiquiare, Vasiva [Pasiba] and Pasimoni, 1853–54, *Spruce 3380* (GH, OXF, W); Depto. Río Negro, along river that flows out of the Canyon Grande of Cerro de la Neblina, 2–4 km upriver from base, 10 Feb 1984, *Funk & Liesner 6148* (NY, RB [digital image], US), trail leading N-NE, 28 Feb 1984, *Funk 6419* (MO, NY, US), Río Mawarinuma, 00°50'N, 66°10'W, 140 m, 27 Nov 1984, *Anderson 13372* (CAS, F, UC), Cerro de la Neblina Base Camp on Río Bario (Río Mawarinuma), SE of camp, 00°49'50"N, 66°09'40"W, 140 m, 26 Jan 1985, *Beitel & Buck 85042* (NY), 27 Jan 1985, *Beitel & Buck 85064* (MO, NY, UC), *Beitel & Buck 85068* (NY), 17 Feb 1985, *Beitel & Buck 85210* (NY-2 sheets), 4 Dec 1984, *Bell*

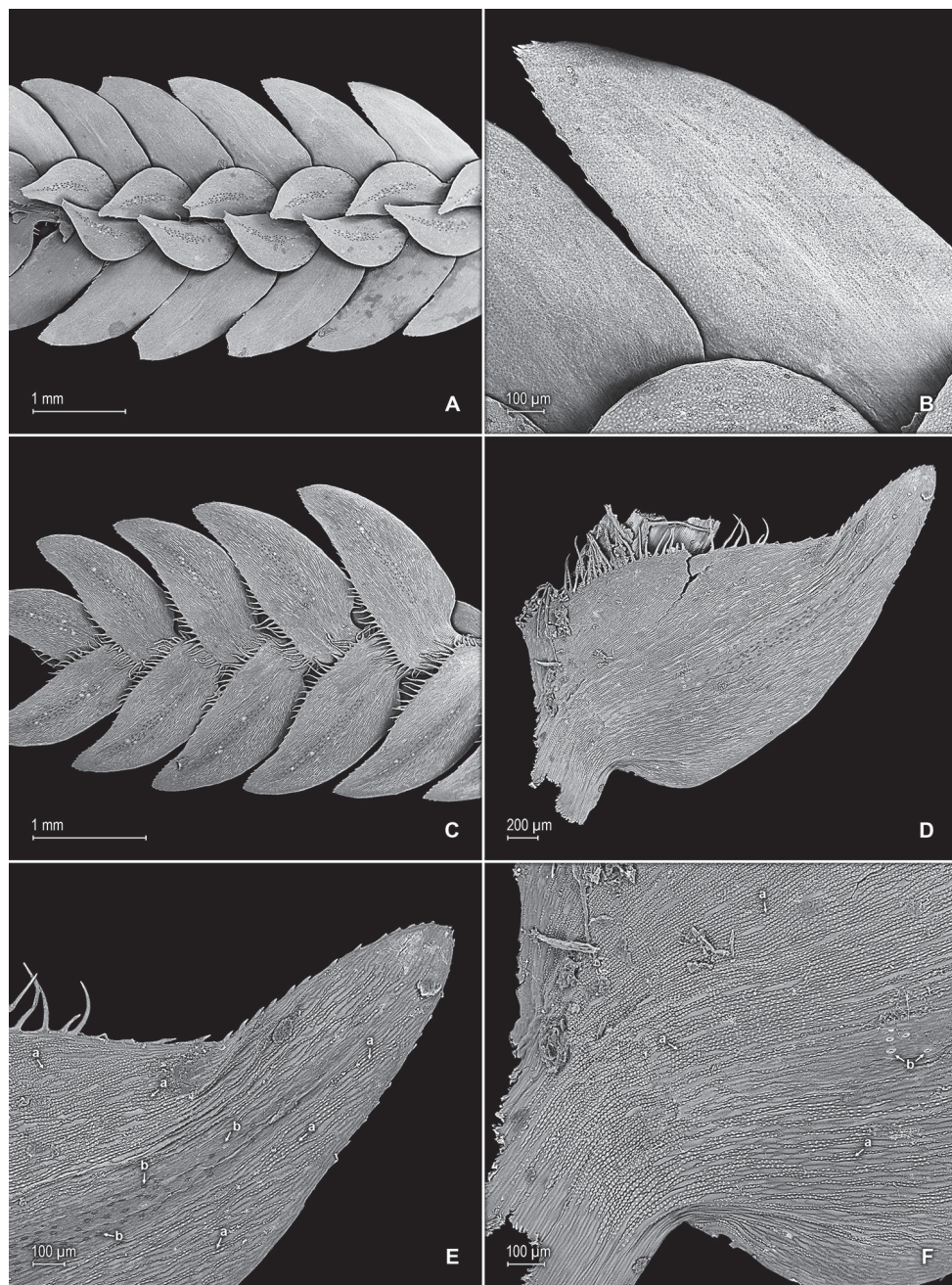


Figure 3. *Selaginella altheae* Valdespino. **A** Section of upper surface of stem branch **B** Close-up of lateral leaf from stem branch, upper surface **C** Section of lower surface of stem branch **D** Close-up of lateral leaf (from branch), lower surface **E** Close-up of distal portion and apex of lateral leaf, lower surface (same leaf shown in **B**); note, elongate and papillate idioblasts (a) and stomata along midrib (b) **F** Close-up of proximal (basal) portion of lateral leaf, lower surface (same leaf shown in **B**); note, elongate and papillate idioblasts (a) and stomata along midrib (b). **A–F** taken from holotype, *Maguire et al.* 60249 (NY).

406 (UC), 2–3 Jul 1984, 00°50'N, 66°10'W, 25 Nov 1984, *Croat 59312* (MO, NY), 2–3 Jul 1984, *Davidse & Miller 26886* (UC), 4–5 Jul 1984, *Davidse & Miller 26972* (MO, UC), ca. 160 m, 27 Nov 1984, *Kral & Liesner 71851* (UC), ca. 180 m, 4 Dec 1984, *Kral 71997* (UC), 0 to 2 km W of Cerro de La Neblina Base Camp, which is on Río Mawarinuma, 140 m, 00°50'N, 66°10'W, 7 Feb 1984, *Liesner 15716* (MO), Río Mawarinuma, below Cerro Neblina Camp, 00°50'N, 66°11'W, 140 m, 16 Apr 1984, *Gentry & Stein 46677* (MO), ca. 2 km S of Base Camp [Cerro Neblina base camp], along Marawanumi River, 00°50'N, 66°10'W, 140 m, 11 Apr 1984, *Thomas & Plowman 3014* (NY), along Río Marawinuma, SE of Base Camp [Cerro Neblina base camp], 00°50'N, 66°09'W, 140 m, 30 Apr 1984, *Thomas & Samuels 3291* (NY, PMA).

Discussion. *Selaginella altheae* is characterized by its erect, fern-like habit, axillary, lateral and dorsal rhizophores, leaves on main stems becoming obviously dimorphic above or 1–4 cm below the first branches and, below this point, the lateral leaf bases oblique with an acroscopic auricle that is tufted with 3–15 stiff hairs and median leaves above first branches in main stems with oblique, not auricled bases, with the outer bases slightly prominent and tufted with (4)6–20 stiff hairs.

Selaginella altheae, *S. lechleri* and other members of the *S. flabellata* group, have microspores distal faces with echinate microstructure. Likewise, *S. altheae* and *S. oaxacana* Spring have dorsal rhizophores, as do other members of the *S. flabellata* group. These two characters, therefore, might represent synapomorphies that define the *S. flabellata* group. Nevertheless, dorsal rhizophores, which are typical of articulate *Selaginella* species, are also found in other taxa such as *S. psittacorbhyncha* (Valdespino 2017) and *S. philipsonii*, suggesting that this character is under-reported and, perhaps, of a wider presence in the genus than hitherto acknowledged. Similarly, different degrees of spore echinate microstructure could occur in other unrelated taxa. Therefore, the occurrence of these characters in morphologically unrelated species warrants further morphological, anatomical and molecular studies throughout the genus to ascertain their evolutionary and phylogenetic implications. Interestingly, a specimen of *S. altheae* (i.e. *Thomas & Samuels 3291*, NY) has flagelliform tertiary branch apices that develop strobilus at their tips.

Selaginella altheae is morphologically close to *S. flabellata* and *S. lechleri*. Their leaves on the main stems below the first branches are seemingly monomorphic and have similar median leaf above the first branches with the outer bases slightly prominent and tufted with either few or many short- to long cilia, as well as submarginal to marginal stomata along the proximal $\frac{1}{3}$ on each outer half of the laminae. Nevertheless, *S. altheae* is set aside from *S. flabellata* by its median leaves on main stems ovate, broadly ovate to ovate-elliptic (vs. broadly ovate to ovate-oblong) with the inner and outer halves on the main stems equal in width or the inner halves slightly wider than the outer halves (vs. usually the outer halves distinctly wider) and lateral leaves acroscopic margins long-ciliate along proximal $\frac{1}{2}$ – $\frac{3}{4}$ (vs. $\frac{1}{4}$ – $\frac{1}{2}$), otherwise distally short-ciliate to dentate (vs. entire or denticulate). It differs further from *S. flabellata* by its megaspores proximal faces rugulate-reticulate (vs. rugulate) with granulate, perforate and sparsely echinate and perforate (vs. tuberculate, mostly psilate to minutely echinate and perfo-

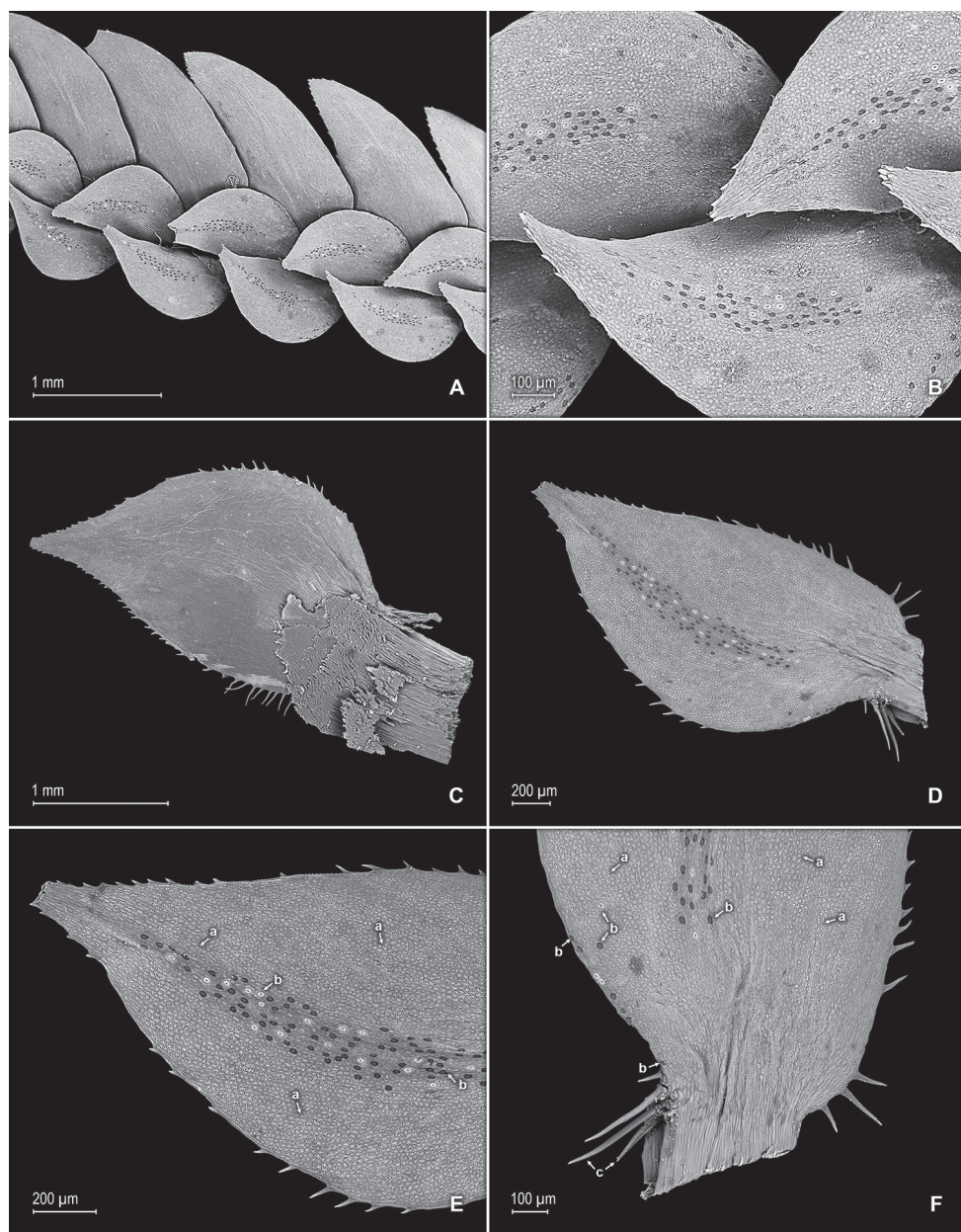


Figure 4. *Selaginella altheae* Valdespino. **A** Section of upper surface of stem branch showing median and lateral leaves **B** Close-up of median leaves from stem branch, upper surfaces **C** Close-up of median leaf from stem branch, lower surface **D** Close-up of median leaf from stem branch, upper surface **E** Close-up of distal portion and apex of median leaf, upper surface (same leaf shown in **D**); note, punctate to shortly elongate and papillate idioblasts (a) and stomata (b) along midrib **F** Close-up of proximal portion and base of median leaf, lower surface (same leaf shown in **D**); note, punctate to shortly elongate and papillate idioblasts (a), stomata (b) along midrib and submarginal and marginal portion near outer base and long cilia (c) on outer base. **A–F** taken from holotype, *Maguire et al.* 60249 (NY).

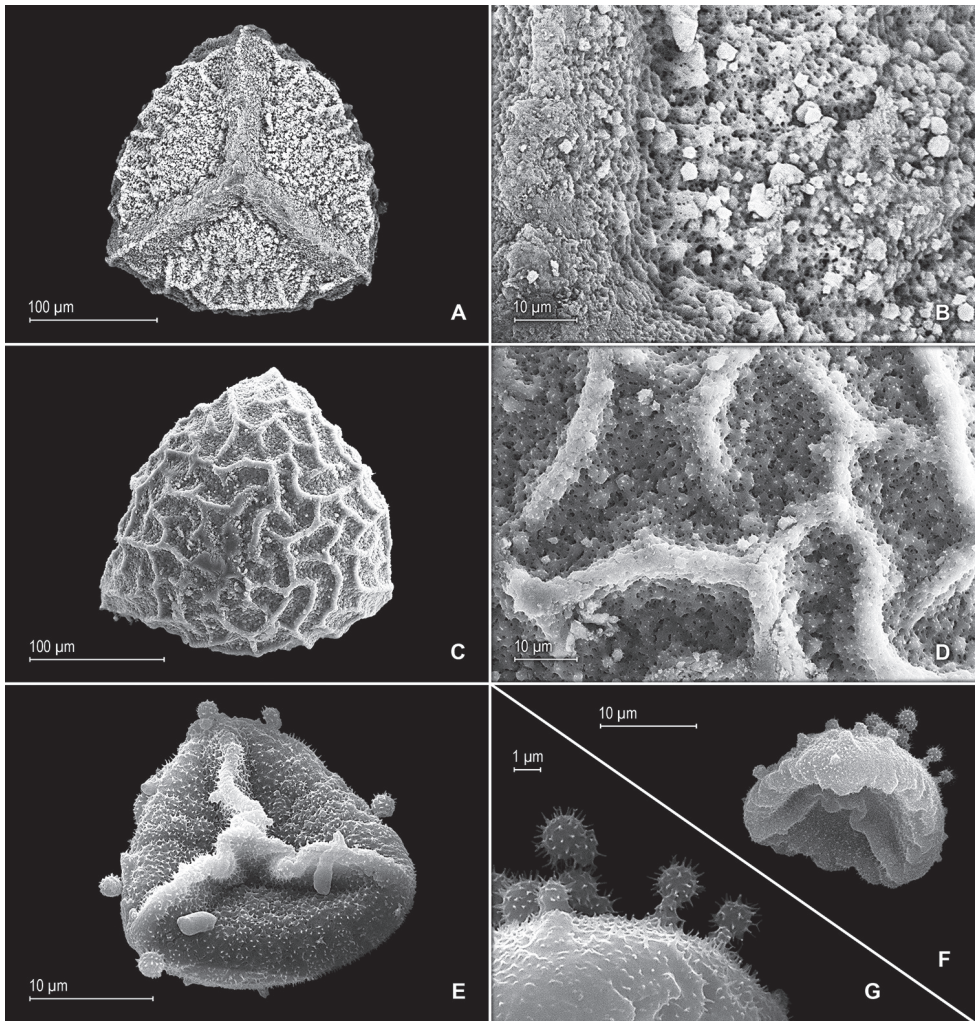


Figure 5. *Selaginella altheae* Valdespino. **A** Megaspore, proximal face **B** Close-up of megaspore, proximal face **C** Megaspore, distal face **D** Close-up of megaspore, distal face **E** Microspore, proximal face **F** Microspore, distal-equatorial-proximal faces **G** Close-up of microspore, distal-equatorial faces; note, capitate projections and echinulate microstructure. **A–G** taken from holotype, *Maguire et al.* 60249 (NY).

rate) microstructures and distal faces mostly open or somewhat closely reticulate (vs. mostly closely reticulate) with minutely echinate and perforate (vs. prominently tuberculate, psilate and perforate) microstructures. *Selaginella altheae* differs from *S. lechleri*, with which it has been confused in the past, by the characters discussed under the diagnosis and by the megaspores proximal faces rugulate-reticulate (vs. reticulate) with granulate, perforate and sparsely echinate (vs. with strongly echinate and perforate) microstructures, while the distal faces are mostly open or somewhat closely reticulate (vs. mostly closely reticulate) with sparse and minutely echinate and perforate (vs. abundantly echinate and perforate) microstructures.

Selaginella altheae may also be confused with the Central and South American *S. anceps* (C. Presl) C. Presl because of their auriculate leaf bases (i.e. auriculae present on lateral leaves of *S. altheae* and on seemingly monomorphic leaves of *S. anceps*) on main stems below the first branches. *Selaginella altheae* is set aside from the latter by its obviously dimorphic leaves immediately above or 1–4 cm below the first (vs. above fourth) branches of the main stems and median leaf bases on main stems above the first branches without auricles (vs. with inner and outer ciliate auricles or only with an outer ciliate auricle). It is further distinguished from *S. anceps* by its megaspores proximal faces with a slightly developed (vs. lacking) equatorial flange, rugulate-reticulate (vs. reticulate) ornamentation with granulate, perforate and sparsely echinate (vs. with perforate and strongly echinate) microstructures, while the distal faces ornamentation is mostly open or somewhat (vs. mostly) closely reticulate with sparse and minutely echinate and perforate (vs. shortly echinate, granulose and perforate) microstructures.

***Selaginella squamulosa* Valdespino, sp. nov.**

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Figures 6–10

Diagnosis. *Selaginella squamulosa* is set aside from similar *S. psittacorhyncha* and *S. vernicosa* by its median leaves upper surfaces with 10 (vs. with 25 in *S. psittacorhyncha* and 35 in *S. vernicosa*) stomata along the midribs. It differs further from *S. psittacorhyncha* by its lateral leaf acute (vs. obtuse) apices and hyaline (vs. greenish) margins and median leaf bases oblique (vs. truncate) and from *S. vernicosa* by the median leaf upper surfaces made up of quadrangular and rectangular (vs. undistinguishable, somewhat appearing quadrangular or elongate) papillate cells and lateral leaf margins on acroscopic side serrate to denticulate (vs. short-ciliate, at least along proximal $\frac{2}{3}$) and on basisopic side sparingly denticulate or entire to slightly denticulate distally (vs. short-ciliate at least along proximal $\frac{1}{3}$).

Type. VENEZUELA – BRAZIL. Venezuelan, Brazilian frontier, Planicie de Zuluaga, Río Titirico, 2300 m, 10–15 Oct 1970, J.A. Steyermark 103872 (holotype: NY; isotypes: MO, PMA).

Description. *Plants* terrestrial, epiphytic or epipetric. *Stems* creeping, stramineous, 10–20 cm long, 0.4–0.8 mm diam., non-articulate, often flagelliform, not stoloniferous, 1–2(3)-branched. *Rhizophores* axillary along proximal $\frac{1}{2}$ of stem, filiform, 0.1 to 0.2 mm diam. *Leaves* dimorphic, coriaceous. *Lateral leaves* distant to imbricate towards stem and branch apices, ascending, broadly deltate-ovate, broadly ovate or ovate-elliptic, (1.0)1.3–1.7 × 0.8–1.7 mm; bases rounded, acroscopic bases overlapping the stem, basisopic bases free from the stem; margins hyaline, made up of a band 2–4 cells wide, the cells elongate and papillate, parallel to margin, papillae in a single row over cell lumen, acroscopic margins serrate to denticulate, basisopic margins sparingly denticulate or entire to slightly denticulate distally; apices broadly acute to acute, tipped by 2–4 teeth; both surfaces without idioblasts, upper surfaces mostly glabrous but with short hairs on submarginal



Figure 6. *Selaginella squamulosa* Valdespino. Holotype, Steyermark 103872 (NY).

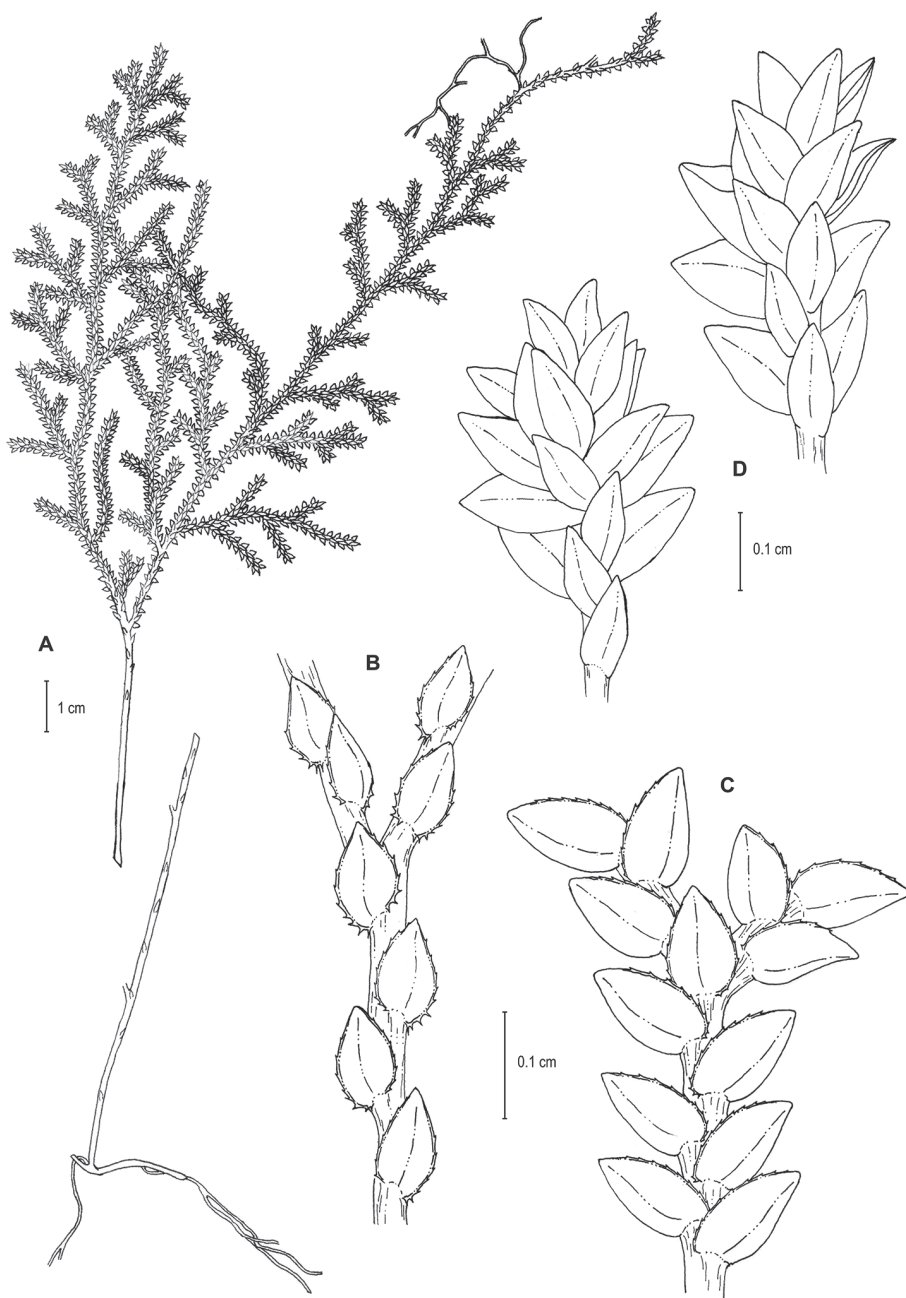


Figure 7. *Selaginella squamulosa* Valdespino. **A** Habit **B** Upper surface of stem showing median leaves **C** Lower surface of stem showing lateral leaves and axillary leaf **D** Close-up of strobili (apices of branches), upper surface. **A–D** line drawings of holotype, *Steiermark 103872* (NY). Illustration made by Rubén Lozano.

and marginal sections of basiscopic half of the lamina, made up of quadrangular to rectangular, irregularly-walled, papillate or not cells, papillae 5–10 over cell lumen arranged in 2 or 3 rows, midribs not prominent, without stomata, lower surfaces glabrous, made up of elongate or asymmetric, straight or slightly sinuate-walled, papillate cells, papillae 8–20 over cell lumen arranged in 2 or 3 rows, midribs raised and prominent at mid-distal section of lamina, stomata concentrated on raised portion of midribs. *Median leaves* distant to imbricate towards stem and branch tips, ascending and, on branches, they may arise at ca. 45° angle, ovate to ovate-deltate, $1.0\text{--}1.5 \times 0.6\text{--}1.0$ mm; bases oblique, inner bases truncate to rounded, outer bases ventricose and often tufted with 2–8 very short hair or teeth; inner margins narrowly hyaline, made up of a band 1 or 2 cells wide, the cells elongate and papillate, parallel to margin, papillae in a single row over cell lumen, serrate to denticulate, outer margins greenish, denticulate at proximal $\frac{1}{4}$, otherwise sparingly denticulate or entire along middle and denticulate at distal $\frac{1}{4}$; apices acute, tipped by 2–4 teeth; both surfaces without idioblasts, upper surfaces mostly glabrous but occasionally with short hairs near marginal, submarginal and submedial section of outer half and on submedial section of inner half near distal $\frac{1}{4}$, made up of quadrangular or with some rectangular, irregularly-walled, papillate cells, papillae 5–10 over cell lumen arranged in 2 or 3 rows, midribs raised and prominent or bevelled specially at mid-distal section of each laminae, stomata concentrated on raised portion of midribs and some marginal on lower $\frac{1}{2}$ of outer margins, lower surfaces glabrous, made up of elongate or asymmetric, straight or slightly sinuate-walled cells, midribs not prominent. *Axillary leaves* similar to lateral leaves. *Strobili* terminal and single on branch tips, quadrangular, 0.5–5 mm long. *Sporophylls* monomorphic, without a laminar flap, ovate to ovate-elliptic, $0.9\text{--}1.3 \times 0.5\text{--}1.3$ mm, with a keel along midrib on upper surfaces; base rounded; margins greenish, minutely denticulate to entire; apices acute; both surfaces without conspicuous idioblasts, both surfaces glabrous; *dorsal sporophylls* with upper surfaces green, except for the half that overlaps the ventral sporophylls where it is hyaline, lower surfaces greenish-hyaline; *ventral sporophylls* with both surfaces greenish-hyaline. *Megasporangia* one or two at the base of ventral rows; *megaspore* yellow, rugulate-reticulate on proximal faces with fissurate microstructure, reticulate-granular on distal faces with granulose and perforate microstructure, 410–445 μm diam. *Microsporangia* in dorsal rows and distal $\frac{3}{4}$ of ventral rows; *microspores* deep orange, proximal and distal faces not studied and not measured.

Habitat, distribution and phenology. *Selaginella squamulosa* grows as a terrestrial, epiphytic or epipetric plant on open slopes to cliff base, in rills and wet depressions of swampy savannas or on scrub dominated forests at 1950–2743 m; it is known from the Guiana Highlands in Cerro de la Neblina, Amazonas State of Venezuela and in Río Cuaburí, Amazonas State of Brazil and found fertile from October through to February.

Etymology. The specific epithet derives from the Latin “*squamulosus*”, meaning minutely scaly and refers to the tiny, stiff leaves that resemble small scales.

Conservation status. *Selaginella squamulosa* is known from two distinct localities at high elevation in isolated tepuis in the Amazon basin of Venezuela and Brazil where

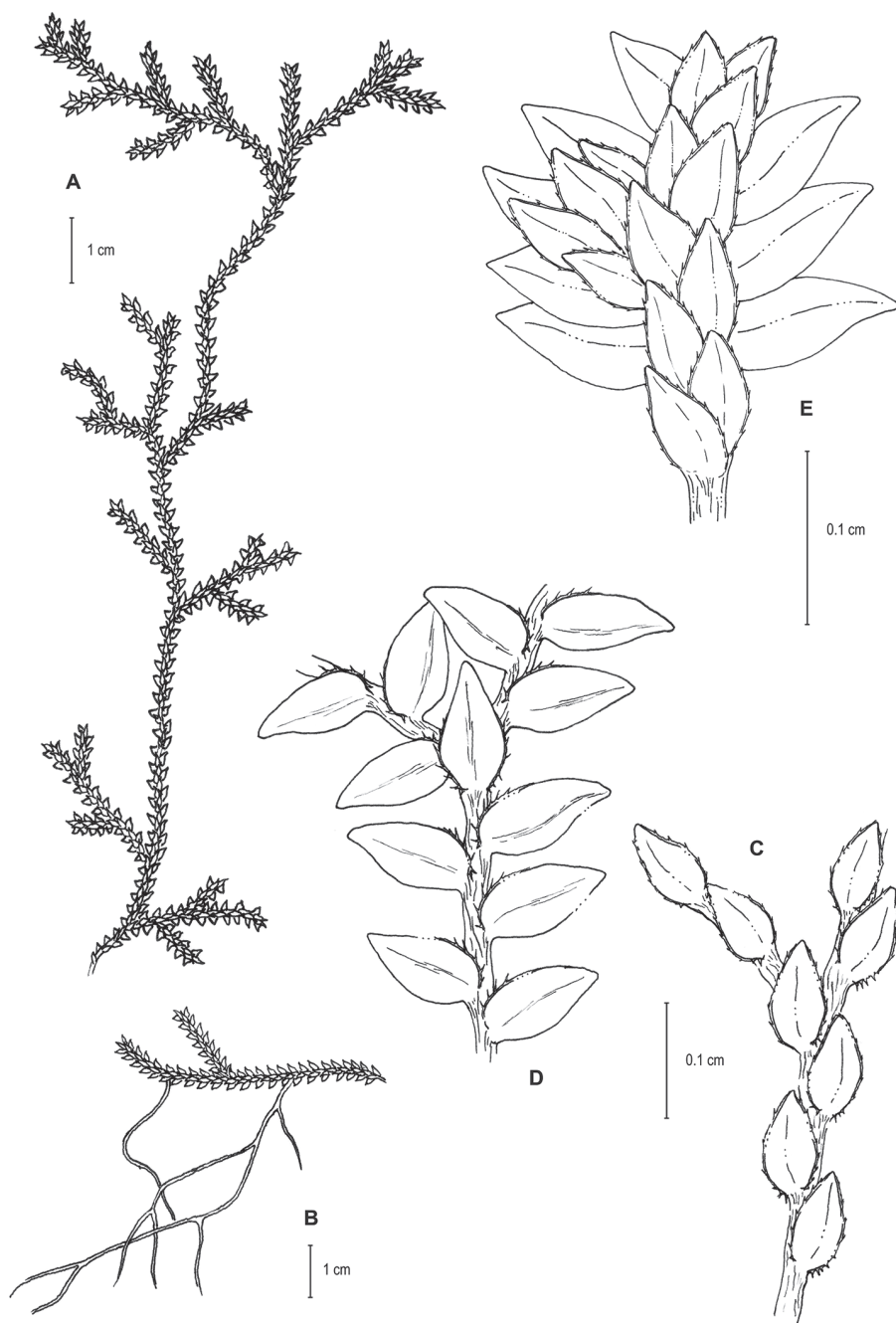


Figure 8. *Selaginella squamulosa* Valdespino. **A–B** Habit **C** Upper surface of stem showing median leaves **D** Lower surface of stem showing lateral leaves and axillary leaf **E** Close-up of distal portion of stem, upper surface. **A–E** line drawings of paratype, *Boom et al. 6011* (NY). Illustration made by Rubén Lozano.

human presence is scarce and immediate threats have not been reported. Therefore, it is tentatively considered of Least Concern (LC) according to IUCN (2012) categories and criteria.

Additional specimens examined (paratypes). **VENEZUELA. Amazonas:** Depto. Río Negro, Camp VII, Cerro de la Neblina, 5.1 km NE of Pico Phelps (= Neblina), 21.5 km E [of] Neblina Base Camp, ca. 2150 m, 5 Feb 1985, *Beitel 85161* (NY–2 sheets, PMA), Neblina Massif, Camp 12, 1950 m, 26–27 Feb 1985, *Boom et al. 6011* (NY, PMA, UC). **BRAZIL. Amazonas:** Río Negro, Río Cuaburí, 8500–9000 ft [2591–2743 m], 2 Dec 1965, *Maguire et al. 60466* (NY).

Discussion. *Selaginella squamulosa* is distinguished by its centipede-like habit with slender and creeping stems, rhizophores restricted to the lower halves of the stems or often present on flagelliform stems and branches (i.e. *Steyermark 103872*, NY), coriaceous, scaly-like leaves with raised and prominent midribs on the lower and upper surfaces of the lateral and median leaves, respectively and acute leaf apices. In addition, the midribs on the upper surfaces of the median leaf are straight to strongly arcuate. In the latter case, the inner half of each leaf lamina becomes slightly wider than the outer one. It is further strikingly distinct by having the lateral leaf acroscopic halves on lower surfaces twice as wide as the basiscopic ones. Furthermore, as noted in other *Selaginella* species, on a duplicate specimen of *S. squamulosa* (i.e. *Steyermark 103872*, MO), a rhizophore becomes a leaf-bearing shoot. Remarkably, *Boom et al. 6011* (NY, PMA, UC) has a more slender habit with the upper leaf surfaces hispidulous. Apparently, these hairs become caducous since they were not observed in a similar collection (i.e. *Beitel 85161*, NY, PMA) or in the more coriaceous form represented by the type.

The holotype and an isotype of *Selaginella squamulosa* at NY and MO, respectively, were originally identified as *S. cruegeri* Jenman vel aff., which is a synonym of *S. minima* Spring. The latter species differs most noticeably from *S. squamulosa* by its ascending (vs. creeping) habit, chartaceous (vs. coriaceous) leaves, median leaf with broadly hyaline margins (vs. inner margins narrowly hyaline and outer margins greenish) and white (vs. yellow) megaspores. A paratype of *S. squamulosa* (i.e. *Boom et al., 6011*, NY, PMA, UC) was determined as *S. rhodostachya* Baker vel aff. Nevertheless, *S. squamulosa* is easily set aside from *S. rhodostachya* by its coriaceous (vs. chartaceous) leaves, oblique (vs. rounded to truncate) median leaf bases with the outer bases ventricose (vs. rounded) and ovate (vs. ovate-elliptic) lateral leaf with its acroscopic margins, as well as both margins of the median leaf serrate to denticulate (vs. often long-ciliate). Another of the paratypes of *S. squamulosa* (i.e. *Maguire et al. 60466*, NY) was determined as *S. brachyclada* Baker. However, it differs from the latter by having the inner and outer margins of the median leaf narrowly hyaline and greenish, respectively (vs. both margins widely hyaline) and serrate to denticulate (vs. faintly denticulate), oblique (vs. truncate) bases, ovate or ovate-elliptic (vs. ovate-cordate) lateral leaf, which is distinctly wider at the middle (vs. at the base), ascending (vs. spreading) and deep yellow (vs. white to light-yellow) megaspores that lack (vs. have) a distinct equatorial flange.

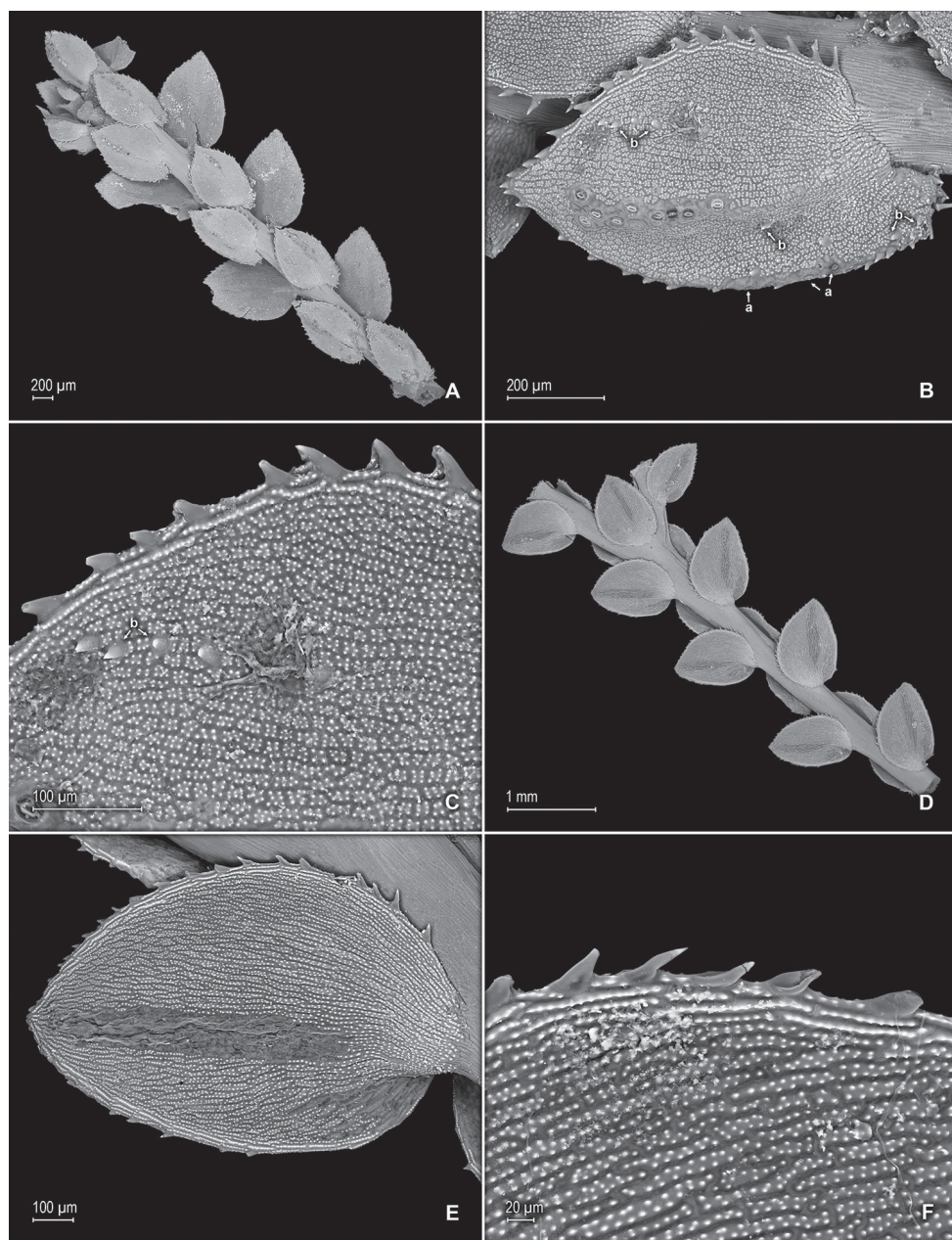


Figure 9. *Selaginella squamulosa* Valdespino. **A** Section of upper surface of stem **B** Close-up of median leaf, upper surface; note, elongate, idioblast-like marginal cells on inner margin and submarginal and marginal stomata (a) along proximal ½ of outer margin and hairs (b) on lamina surface **C** Close-up of mid-distal portion of median leaf, upper surface (same leaf shown in B); note, elongate, idioblast-like marginal cells on inner margin, papillae on each cell lumen and hairs (b) on lamina surface **D** Section of lower surface of stem **E** Close-up of lateral leaf, lower surface **F** Close-up of section of acroscopic half of lateral leaf; note, papillae on cells lumen and marginal, idioblast-like and papillate cells. **A–F** taken from paratype, *Boom et al. 6011* (NY).

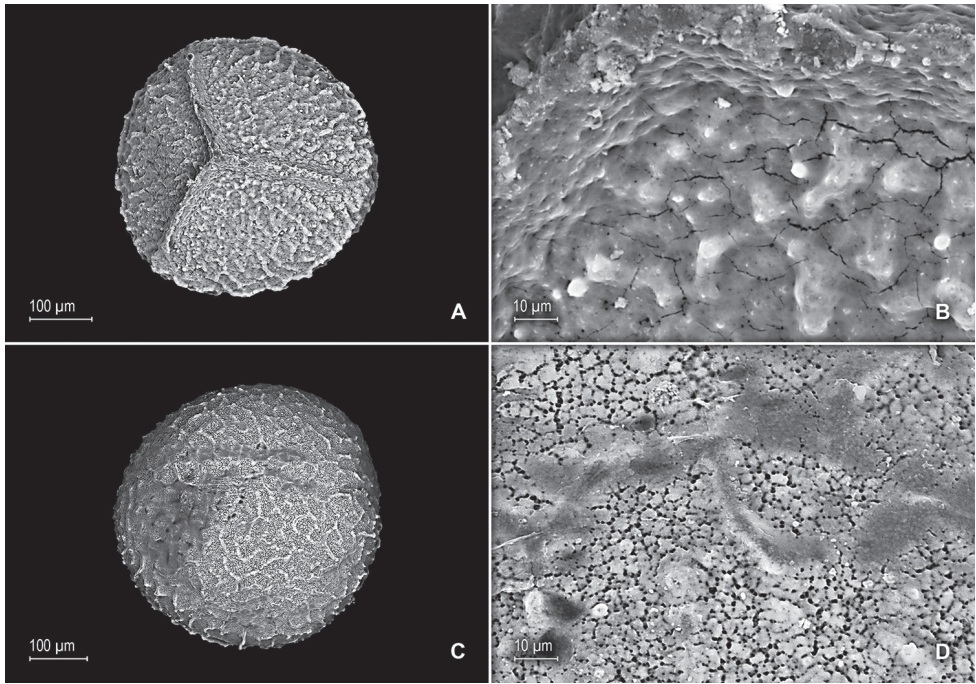


Figure 10. *Selaginella squamulosa* Valdespino. **A** Megaspore, proximal face **B** Close-up of megaspore, proximal face **C** Megaspore, distal face **D** Close-up of megaspore, distal face. **A–D** taken from paratype, Boom *et al.* 6011 (NY).

Selaginella squamulosa is part of the “*Selaginella vernicosa* group” and, amongst these, it is morphologically close to *S. psittacorrhyncha* and *S. vernicosa*. It differs from these two species by the characters discussed under the diagnosis and by its median leaf with the midribs raised at the distal ½ of the laminae but not properly extending into the apices (vs. extending into the apices) with the upper surfaces occasionally puberulent (vs. glabrous). *Selaginella squamulosa* differs from *S. arrecta* by its median and lateral leaf apices broadly acute to acute (vs. long-acuminate to aristate), median leaf inner margins narrowly (vs. widely) hyaline, which consists of 1 or 2 (vs. 3–5) elongate cells wide and ca. 10 stomata on raised midribs (vs. up to 85 stomata, widespread on central portion of lamina). In addition, in *S. squamulosa*, 2–4 teeth tip the acute apices, whereas the acuminate or aristate apices of *S. arrecta* are made of 6–10, narrowly elongate and papillate cells. *Selaginella squamulosa* differs from *S. roraimensis*, *S. marahuacae* and *S. scalariformis* by its narrowly ovate-deltate or ovate (vs. ovate-oblong or oblong in *S. roraimensis* and ovate-elliptic in *S. marahuacae* and *S. scalariformis*) lateral leaves with midribs on lower surfaces distinctly raised (vs. plane in profile). *Selaginella squamulosa* is further separated from *S. roraimensis* by the lateral leaf basiscopic margins extended (vs. slightly reflexed), from *S. marahuacae* by its acute (vs. shortly acuminate) median leaf apices and from *S. scalariformis* by its distant to imbricate and ascending (vs. distant and patent) lateral leaves.

Combination and status novo

***Selaginella philipsonii* (Jermy & Rankin) Valdespino, comb. et stat. nov.**

urn:lsid:ipni.org:names:77173692-1

Figure 11

Selaginella philipsonii (Jermy & Rankin) Valdespino \equiv *Selaginella ovifolia* Baker, subsp. *philipsonii* Jermy & Rankin, Bull. Brit. Mus. (Nat.Hist.) 9(4): 294. 1981. Type: Colombia. Meta / Vaupés: Sierra de la Macarena, Río Guapaya, 03°38'50.72"N, 72°50'45.05"W, 450 m, 29 Nov 1949, W.R. Philipson, J.M. Idrobo & A. Fernández 1607a (holotype: BM barcode BM000905679!).

Description. *Plants* terrestrial or epipetric. *Stems* creeping, stramineous, 6–10 cm long, 0.2 to 0.3 mm diam., non-articulate, not flagelliform, not stoloniferous, 1-branched. *Rhizophores* axillary and dorsal throughout the stems, filiform, 0.05–0.1 mm diam. *Leaves* dimorphic, chartaceous. *Lateral leaves* imbricate, ascending to spreading, ovate, ovate-elliptic or ovate-oblong, (1.0)1.2–1.7 \times 0.6–1.2 mm; bases rounded, acroscopic bases overlapping the stem, basiscopic bases free from the stem; acroscopic margins on upper surfaces greenish to greenish hyaline, made up of a band 1 or 2 cells wide, the cells elongate and papillate, parallel to margins, the papillae in one or two rows over each cell lumen, on lower surfaces hyaline, made up of a band 3–5 cells wide, the cells elongate and papillate, parallel to margin, the papillae in one or two rows over each cell lumen, long-ciliate throughout, the hairs long on proximal $\frac{3}{4}$ and distally smaller, basiscopic margins on upper and lower surfaces greenish, made up of a band 1 or 2 cells wide, the cells elongate and glabrous, parallel to margins, sparsely short-ciliate throughout or seemingly denticulate along proximal $\frac{3}{4}$ and with short hairs along distal $\frac{1}{3}$ and with marginal stomata along proximal $\frac{1}{2}$; apices obtuse to broadly acute or acute, tipped by (1) 2 (4), often divergent, long cilia; upper surfaces with elongate, idioblast-like cells at the base, the idioblasts papillate, the papillae in two rows, otherwise idioblast absent, most of the surface made up of irregular, quadrangular to rectangular, irregularly-walled, papillate cells, the papillae 9–15 irregularly arranged over each cell lumen or some cells glabrous, especially toward basiscopic bases, the laminae pubescent near basiscopic margins, the midrib not prominent, without stomata, the lower surfaces glabrous, made up of elongate, straight-walled, idioblast-like and papillate cells, the papillae 10–30 over each cell lumen, arranged in 2 or 3 rows and often interconnected, midrib not raised or prominent, with stomata in 2 or 3 rows concentrated along raised portion of midrib. *Median leaves* imbricate, ascending, narrowly lanceolate to narrowly lanceolate-elliptic, 0.5–1.2 \times 0.3–0.6 mm; bases oblique to obtuse, glabrous; the inner margins broadly hyaline, made up of a band 2–7 cells wide, the cells elongate, idioblast-like, papillate and parallel to margins, papillae in 1 or 2 rows over each cell lumen and some of these interconnected, proximally entire and short-ciliate along distal $\frac{2}{3}$, the outer margins greenish, made up of 2 or 3 elongate and glabrous cells and with the submarginal portion of the lamina conspicuously hyaline, made up of a band of 8–12 cells wide, the cells elongate,

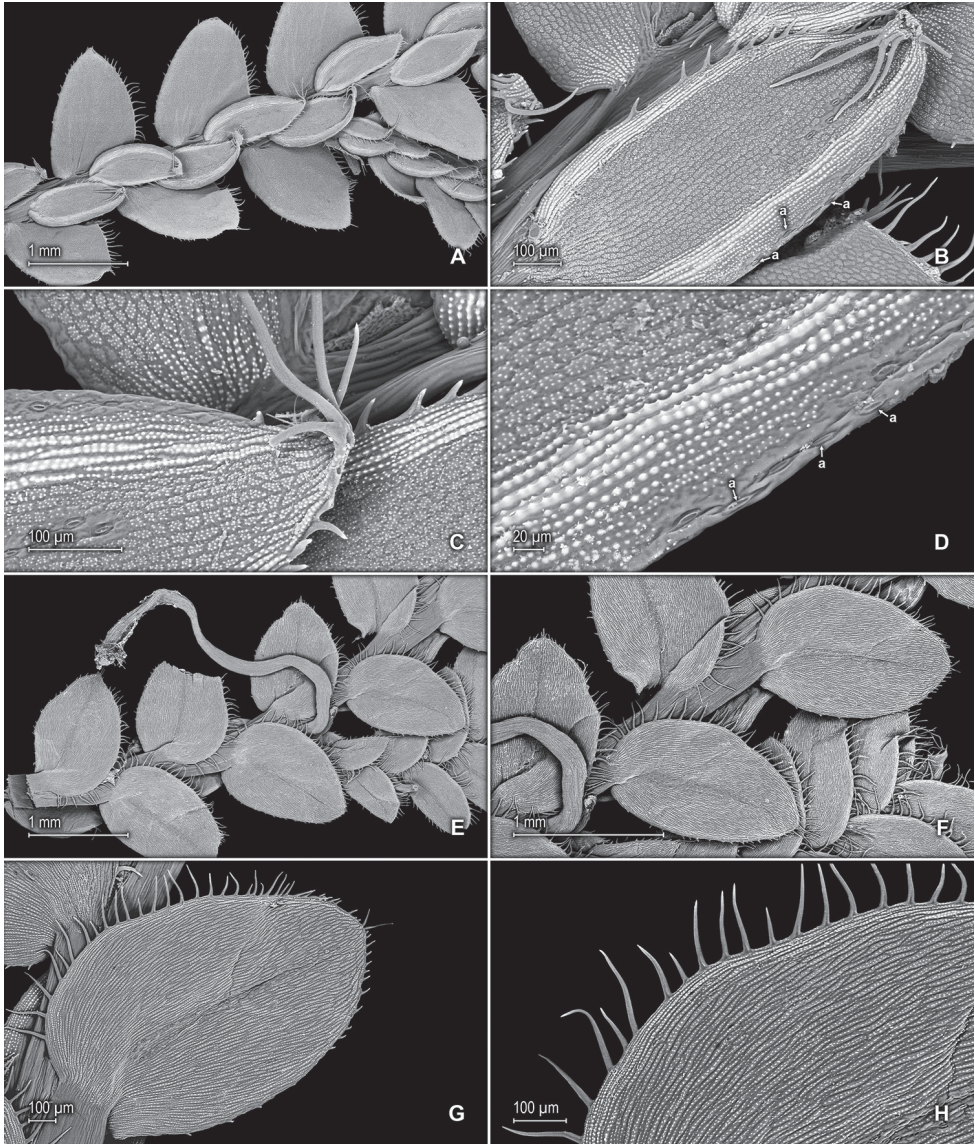


Figure 11. *Selaginella philipsonii* (Jermy & Rankin) Valdespino. **A** Section of upper surface of stem showing median and lateral leaves **B** Close-up of median leaf, upper surfaces; note, inner margin and submarginal portion of outer margin composed of elongate, idioblast-like and papillate cells and stomata (a) along outer margin **C** Close-up of median leaf distal portion, upper surface; note, apex tipped by long, divergent cilia, cells with papillae and stomata along outer margin **D** Close-up of median leaf, upper surface; note, marginal stomata (a), submarginal portion of outer margin composed of elongate, idioblast-like and papillate cells and lumen of lamina cells with multiple papillae **E** Section of lower surface of stem showing lateral leaves, outer halves of median leaves and rhizophore **F** Close-up of (E) **G** Close-up of lateral leaf, lower surface (one of the leaf shown in E) **H** Close-up of lateral leaf, lower surface (same leaf shown in G); note, stomata along midrib, elongate, idioblast-like and papillate cells and long cilia along acroscopic margin. **A–H** taken from Steyermark & Rabe 96652 (GH).

idioblast-like, papillate and parallel to the margins, papillae in 1 or 2 rows over each cell lumen and some of these interconnected; apices acute, attenuate to shortly acuminate, tipped by 1–5 long, divergent cilia or more often by two long, divergent cilia, the acumen or arista 0.1–0.3 mm long; both surfaces without idioblasts, except for the outer margins that have similar hyaline and papillate cells as the inner margins and submarginal portion of outer margins on the upper surfaces, the upper surfaces glabrous, made up of similar cells as the upper surfaces of the lateral leaves, the midrib not prominent and difficult to observe, stomata few, on a single row along distal $\frac{1}{2}$ of each lamina, the lower surfaces glabrous, made up of elongate, straight-walled and papillate cells, papillae 10–30 over each cell lumen, arranged in 2 or 3 rows and often interconnected, midrib on lower surfaces not raised or prominent, stomata absent. *Axillary leaves* absent or, if seemingly present, corresponding to lateral leaves. *Strobili* terminal and single on branch and stem tips, quadrangular, 1.5–6.0 mm long. *Sporophylls* monomorphic, without a laminar flap, ovate-lanceolate, $0.8\text{--}1.2 \times 0.5\text{--}0.6$ mm, with a well-developed, puberulent to shortly ciliate keel along midribs on upper surfaces; bases rounded; margins hyaline, dentate to minutely ciliate; apices acuminate, the acumen 0.1–0.3 mm long; both surfaces without conspicuous idioblasts, glabrous; *dorsal sporophylls* with upper surfaces green, except for the halves that overlap the ventral sporophylls where they are hyaline, lower surfaces hyaline; *ventral sporophylls* with both surfaces hyaline. *Megasporangia* along distal $\frac{1}{8}$ of ventral and dorsal rows; *megaspore* light- to deep yellow, proximal and distal faces smooth to slightly rugulate, the microstructure not observed, 180–200 μm diam. *Microsporangia* on ventral and dorsal rows along proximal $\frac{3}{8}$; *microspores* deep orange, the ornamentation not observed, not measured.

Habitat, distribution and phenology. *Selaginella philipsonii* grows on soil, wet slopes, wet rocks along riverbanks or on shaded bluffs; 100–600 m; it is known from the Meta Department of Colombia and in the State of Mérida, Venezuela and found fertile from February through to November.

Conservation Status. *Selaginella philipsonii* was sporadically collected from 1949 through to 1981 in the Amazon basin of Colombia and Venezuela. No recent collections were seen. This could be, however, due to its being a minute and easily overlooked species. Consequently, based on the lack of reliable information to assign a conservation status, it is considered Data Deficient (DD), according to IUCN (2012) categories and criteria.

Additional specimens examined. **COLOMBIA.** **Casanare:** Tauramena, 600 m, 13 Apr 1963, *Uribe Uribe 4290* (US). **Guaviare:** San José del Guariare [Guaviare], *s.d.*, *Schultes 11120* (GH). **Meta:** Caño Piedra de Candela, 5 km from Remolino, 13 Feb 1969, *Pinto & Sastre 841* (COL, P), Río Guayabero, 10 km below Caño Lozada, 350 m, 18 Jan 1959, *Pinto & Bischler 239* (COL [digital image]). **Vaupés:** Angostura No. 2, Río Guayabero, 23 Feb 1969, *Pinto & Sastre 1024* (COL). **VENEZUELA.** **Mérida:** on slope above dam site on Río Caparo, 31 km ESE of Santa Barbara, $07^{\circ}41'N$, $71^{\circ}28'W$, 100–250 m, 9 Mar 1980, *Liesner & González 9263* (F, PMA); 2–4 km above dam site on Río Guaimaral, $07^{\circ}45'N$, $71^{\circ}29'W$, 200–400 m, 16 Mar 1981, *Liesner & González 10648a* (MO). **Tachira:** W of Ayarí, 200 m, 21 Aug 1966, *Steyermark &*

Rabe 96652 (GH), along old highway, W of Ayarí, 07°32'N, 71°53'W, 250 m, 7 Nov 1979, *Steyermark et al.* 119488 (MO, UC).

Discussion. *Selaginella philipsonii* was originally described as a subspecies of *S. ovifolia* by Jermy and Rankin in Alston et al. (1981: 294). They indicated, however, that Alston considered it a new species, a conclusion with which the author fully concurs and hence its recognition here at that level. According to Alston (1955: 244), *S. ovifolia* is a taxon found in the Dominican Republic, Haiti, Jamaica, Puerto Rico and Belize. Certainly, these two taxa share a moss-like habit and median leaf apices ending in long cilia. Nevertheless, *S. philipsonii* is most distinguished by the median leaves on main stems imbricate, oblong-elliptic with the inner margins hyaline, made up of a band of 2–7, elongate and papillate cells and shortly ciliate and the outer margins greenish, made up of 2 or 3 elongate and glabrous cells and the submarginal portion of the laminae conspicuously hyaline, composed of a band of 8–12 cells wide, with the cells elongate and papillate, parallel to the margins, the papillae in 1 or 2 rows over each cell lumen and some of these interconnected (see Figs 11A–D, 16B in Alston et al. 1981: 296), entire and the apices acute, attenuate to shortly acuminate, tipped by 1–5 (Fig. 11C) or often 2 long, divergent cilia, the acumen or arista 0.1–0.3 mm long. It is further characterized by the lateral leaves acroscopic margins long-ciliate, the basiscopic margins denticulate, the apices obtuse to broadly acute or acute, tipped by (1) 2 (4), often divergent, long cilia (Fig. 11E–G). In addition, SEM images of the median leaves show stomata along the outer margins, as well as on the midribs (Fig. 11B–D). Conversely, *S. ovifolia* is characterized by median leaves on main stems distant, elliptic to ovate-elliptic, the margins sparingly short- to long-ciliate, having the outer margins and the outer submarginal portion of the laminae greenish, composed of rounded cells or the outer margins only slightly hyaline on distal ¼ and made up of only 1 or 2 elongate and papillate cells, while the inner margins are greenish, comprised of roundish cells, the apices long-acuminate, tipped by 2 long cilia, the lateral leaf acroscopic margins long-ciliate, while the basiscopic margins are short- to long-ciliate and the apices acute or short- to long-acuminate, tipped by 1–3 teeth or short cilia.

Jermy and Rankin in Alston et al. (1981: 294) cited two specimens from Norte de Santander: Catatumbo, Campo Oru, 08°30'30"N, 73°15'52"W, 350–500 m, 13 May 1959, *Bischler* 2397 (COL!) and Campo Tibú, Río Tibú, 08°28'19"N, 72°55'08"W, 200 m, 16 May 1959, *Bischler* 2493 (COL!) as *S. ovifolia* subsp. *philipsonii*. These specimens, however, have soboliferous stems, median leaves narrowly elliptic to ovate-lanceolate, 0.3–0.6 × 0.15–0.3 mm with the inner and outer margins dentate to shortly ciliate, the outer margins and the submarginal portion of the laminae greenish, made of rounded cells or the outer margins only slightly hyaline composed of only 1–3 elongate cells and puberulent bases with 1–3 stiff, short hairs or tooth-like projections. Therefore, the author believes it is best to exclude those specimens from *S. philipsonii*.

Selaginella philipsonii is morphologically close and may be confused with *S. homaliae* A. Braun and *S. schultesii* Alston ex Crabbe & Jermy, which are both from South America, because of their moss-like habit, slender rhizophores, minute leaves and keeled sporophylls with the keel short-ciliate to dentate. *Selaginella philipsonii* differs noticeably from *S. homaliae* and *S. schultesii* by its median leaf outer margins greenish (vs. con-

spicuously hyaline) with the submarginal portion of the laminae conspicuously hyaline (vs. greenish), which is made up of a band of 8–12 elongate and papillate (vs. composed of roundish and glabrous) cells that are parallel to the margins, the apices acute, attenuate to shortly acuminate, tipped by 1–5 (Fig. 11C) or often 2 long, divergent cilia (vs. apices aristate, denticulate with the tip gradually tapering into a long arista and tipped by 1–3 teeth in *S. schultesii* and mucronate to shortly acuminate and tipped by 1 or 2 teeth in *S. homaliae*) and the outer margins entire (vs. long-ciliate in *S. schultesii* and short-ciliate in *S. homaliae*). *Selaginella philipsonii* is set aside further from *S. homaliae* by ovate or ovate-elliptic (vs. oblong) lateral leaves with the leaf apices obtuse to broadly acute or acute, tipped by (1) 2 (4), often divergent, long cilia (vs. truncate to obtuse, not tipped by cilia) and axillary and dorsal (vs. axillary) rhizophores.

Selaginella valdepinosa Baker is another South American moss-like species that could be confused with *S. philipsonii*; however, the former has the lateral leaves broadly ovate-orbicular or broadly ovate-elliptic with the basiscopic bases distinctly, albeit sparsely, short- to long-ciliate and the median leaves broadly ovate-orbicular to ovate-deltate with both margins distinctly long-ciliate and the outer bases noticeably knobbed with the submarginal portion composed of round cells.

Selaginella philipsonii stands out from other moss-like taxa such as *S. achotalensis* Shelton & Caluff, *S. apoda* (L.) C. Morren, *S. armata* Baker, *S. cristalensis* Shelton & Caluff, *S. eatonii* Hieron. ex Small [syn.: *S. armata* var. *eatonii* (Hieron. ex Small) B.F. Hansen & Wunderlin, *S. bracei* Hieron. ex Small], *S. ludoviciana* A. Braun, *S. orbicularifolia* Shelton & Caluff, *S. prasina* Baker (syn.: *S. undata* Shelton & Caluff) and *S. rotundifolia* Spring by its main stems median leaves imbricate, oblong-elliptic and widely hyaline submarginal portion of the laminae, as well as lateral leaves long-ciliate along acroscopic margins. In keeping with Valdespino (1993) by following Buck (1978), Buck and Lucanski (1976) and Somers and Buck (1975) and contrary to Hansen and Wunderlin (2000), *S. eatonii* is considered a different species from *S. armata* as is *S. ludoviciana* from *S. apoda*. Finally, following Valdespino et al. (2015) *S. undata* is considered a synonym of *S. prasina*.

Acknowledgments

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Ex uno, multis: taxonomic revision in *Navarretia divaricata* (Polemoniaceae) and the recognition of four additional cryptic or near-cryptic species

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Abstract

Navarretia divaricata, endemic to western North America and most recently considered a single species with two subspecies, was re-examined in light of field work, DNA sequences, comparative morphology, and a review of herbarium specimens including types. From these studies, we lectotypify the material on which *N. divaricata* is based, elevate *N. divaricata* subsp. *vividior*, which is an allotetraploid, to species rank (as *N. vividior* **comb. et stat. nov.**), and recognize three additional species: *N. modocensis* **sp. nov.**, *N. aeroides* **sp. nov.**, and *N. torreyella* **sp. nov.** *Navarretia modocensis*, the diploid paternal progenitor of *N. vividior*, is morphologically cryptic with respect to its allotetraploid offspring and difficult to distinguish on herbarium sheets. *Navarretia aeroides*, the diploid maternal progenitor of *N. vividior*, is nearly cryptic, but more easily distinguished from both *N. modocensis* and *N. vividior* by its smaller, more glandular inflorescences. *Navarretia torreyella* is readily distinguished from all of these species, but has been generally mistaken for *N. divaricata* subsp. *vividior* given its colored corolla tube and rare co-occurrence with the other *vividior*-like species. Conservation assessments, an identification key, and table of comparative morphological features are provided for each species, emended descriptions for *N. divaricata* and *N. vividior*, and a discussion of the syntypes for *Gilia divaricata* Torr. ex A.Gray.

Keywords

allopolyploidy, California, conservation assessment, exclusivity, species delimitation, taxonomy, unified species concept, western United States

Introduction

Multiple criteria applied to assess the presence of homogenizing gene flow under the framework of the unified species concept (de Queiroz 2007) has provided strong evidence for the existence of previously unrecognized lineages in Polemoniaceae, including in *Navarretia* (Johnson and Cairns-Heath 2010, Johnson et al. 2012, 2013, 2016). Overlooked in the past because they resemble other species, re-examination of morphological variation in conjunction with molecular data has enabled these cryptic or nearly cryptic lineages to be delineated and lifted from obscurity as recognized taxa. In some cases, molecular data provided the first clues as to the uniqueness of these taxa (e.g., Johnson and Cairns-Heath 2010, Johnson et al. 2012), whereas in other cases, morphological variation was recognized first, and the biological significance of this variation confirmed with molecular data (Johnson et al. 2013, 2016). Stimulated by a need for nomenclatural housekeeping along with observations of variation in both morphological and molecular data, we here delimit several near-cryptic species from what previously has been considered a single species, *Navarretia divaricata* Greene.

Within *Navarretia* Ruiz & Pav., *N. divaricata* is one of the more widely distributed species with populations extending from central California (and adjacent Nevada) to Idaho and British Columbia. It is also one of the smallest-flowered *Navarretia*. The taxonomic concept associated with *N. divaricata* has been fairly stable since Greene's treatment of the species in this genus (Greene 1887), and Jepson's subsequent partitioning of "coarser" specimens with more glandular-puberulent bracts and calyces, and blue or blue-lobed corollas into variety *vividior* Jeps. & V.L.Bailey (in Jepson 1943; currently subsp. *vividior* (Jeps. & V.L.Bailey) H.Mason). To preserve this stability, clarification of the type for *N. divaricata* Greene and lectotypification of the basionym upon which Greene's replacement name is based is necessary. Furthermore, stemming from observations that *N. divaricata* subsp. *divaricata* does not form a monophyletic group with *N. divaricata* subsp. *vividior* in comparative DNA sequence analyses (Johnson et al. 2016), that the two taxa co-occur without signs of hybridization, and that material assigned to *N. divaricata* subsp. *vividior* is polymorphic, we initiated fieldwork, a comprehensive review of herbarium specimens, and investigation of morphological and molecular variation across the geographic ranges of these taxa. Results indicate that *N. divaricata* subsp. *vividior* merits recognition at the species level, and that four evolutionarily unique lineages exist in the material heretofore generally referred to subsp. *vividior*. The taxonomy of this group is revised accordingly.

Historical background

Among plants provided to Asa Gray by John Torrey, two *Navarretia* collections are relevant to the present study. The first, labeled simply "*Navarretia*" by Torrey, was collected during his 1865 trip to California. The second, collected by Mr. Shelton, was labeled by Torrey, "*Navarretia divaricata*, n. sp." Gray considered these specimens con-

specific, but having a confused view of generic relationships in Polemoniaceae (Mason 1945), he published this new species, attributed to Torrey, in the genus *Gilia* (i.e., *Gilia divaricata* Torr. ex A.Gray) where *Gilia divaricata* Nutt. (\equiv *Allophyllum divaricatum* (Nutt.) A.D.Grant & V.E.Grant) already existed. Consequently, Gray's action created an illegitimate later homonym that was replaced by Greene (1887). In the protologue, Gray (1870) states, "California, along the foot hills of the Sierra Nevada, coll. Shelton, Rattan, Bolander, Torrey, Mrs. Davis, C. Lee," providing four additional syntypes beyond the two that can be traced to Torrey. The last of these, a specimen attributed to C. Lee, cannot be located and its identity remains unknown to us. The remaining five syntypes represent four distinct taxa. Consequently, the choice of lectotype is critical for maintaining the long-used taxonomic concept for *N. divaricata*.

Gray (1876, 1878) continued to recognize *Gilia divaricata* Torr., using descriptions similar to his original. These descriptions accentuate characteristics of the syntype *Rattan s.n.* (NY!; probable duplicates at UC \times 2 (scan!), US (scan!), KEW (scan!)), which has larger flowers and a more densely pubescent head compared to the other syntypes, and is also a mixed collection from two gatherings. These specimens are today recognized as *N. prolifera* Greene, which has the narrowest distribution of the taxa represented by Gray's syntypes.

Emphasizing the distinctiveness of the calyx in *Navarretia*, Greene (1887) began the work of narrowing Gray's concept of *Gilia* and provided a replacement name for Gray's illegitimate homonym by equating *N. divaricata* Greene with *Gilia divaricata* Torr. ex Gray. There is no indication that Greene viewed the syntypes Gray worked with, and good reason to believe he did not—for example, he described *N. prolifera* as a new species immediately preceding *N. divaricata*, with no reference to any of the *Gilia divaricata* Torr. ex Gray syntypes. Greene characterized *N. divaricata* flowers as "minute" and distributed in the Sierra Nevada from Kern County northward into Oregon; he distinguished this taxon from *N. prolifera* and *N. peninsularis* Greene in part based on smaller flower size. Beyond the description provided for *N. divaricata*, Greene's taxonomic concept can be reconstructed by examining the specimens he worked with. Four sheets with five collections exist at NDG (scans!) labeled "*Navarretia divaricata* Greene", in Greene's hand, with collection dates prior to Greene's publication, and a sixth specimen, also on one of the four sheets, with a preprinted label collected in the year of his publication, labeled "*Gilia divaricata* Torr." Of these, Greene referenced two in his publication.

M. K. Curran s.n. [NDG-40817], from Tehachapi, Kern County, California, was cited as representing the southern extent of the species range, but differs taxonomically from the other specimens and is equivalent to *N. peninsularis*. Interestingly, this collection represents the northern extent of the latter species rather than the southern extent of *N. divaricata*. Greene described *N. peninsularis* based on larger plants from Lower (Baja) California, considerably distant from Tehachapi, so perhaps the Tehachapi plants being more depauperate and proximal to other *N. divaricata* specimens played a role in his misidentification and efforts to circumscribe taxa with little material on hand. The second specimen, *C. F. Sonne s.n.* (Donner Lake) [NDG-40819A], was cited

as a putative hybrid between *N. divaricata* and *N. minima* Nutt. without explanation. This specimen, along with *C. C. Parry s.n.*, (Yosemite) [NDG-40820A], *D. Cleveland s.n.* (Butte County) [NDG-40820B], and *T. Howell s.n.* (near Waldo, Oregon) [NDG-40819B] all correspond to material congruent with Gray's syntypes *Bolander 4908* and *Mrs. Davis 49*, while a second *M. K. Curran s.n.* specimen, from Colusa County, California [NDG-40818], is congruent with Gray's syntype *Torrey 302* discussed further below. Gray's syntypes *Bolander 4908* and *Mrs. Davis 49* have minute flowers and the species represented by them is the most common and widely distributed geographically of Gray's syntypes, as well as the entity to which the name *N. divaricata* subsp. *divaricata* has been applied.

Greene's taxonomic concept influenced nearly all later botanists. For example, Howell (1901) indicated *N. divaricata* occurs from "Washington to California, in the high mountains," with a description that borrowed more from Greene's description of the species than Gray's. Though referencing neither Gray nor Greene, the publication of *Gilia atrata* M.E.Jones with its type and two of three paratypes matching *Bolander 4908* and *Mrs. Davis 49* (and the third a similarly small-flowered entity that would fit within Greene's concept) may stem from Jones' (1908) recognition that Gray's name was illegitimate while disagreeing with Greene in recognizing *Navarretia* as distinct from *Gilia*. *Gilia atrata* has not appeared in print, other than as a synonym, beyond its original publication.

The syntype *Torrey 302* was gathered in Lake County, California, well removed from the Sierra Nevada. Circa 1936, Virginia Bailey began a study of *N. divaricata* and noticed four specimens from Butte, Lake, and Mendocino counties that were stouter of habit, slightly larger flowered, produced more seeds per locule, and possessed blue corollas or corolla lobes (note attached to *Austin 827*, UC!). *Torrey 302*, though not seen by her, fits naturally into the group she was segregating. Jepson (1943) with Bailey, recognized this material as a variety of *N. divaricata* and chose a specimen also from Lake County as the type. Jepson and Bailey's taxonomic concept for the two varieties of *N. divaricata* is clear, with all 17 representative specimens listed for *N. divaricata* var. *divaricata* morphologically congruent with *Bolander 4908* and *Mrs. Davis 49*, and nine representative specimens listed for var. *vividior* (paratypes) that all share the larger flowering heads, more robust habit, and larger/more glandular heads as described by Jepson and Bailey. Thus, in recognizing var. *vividior*, Jepson and Bailey followed a taxonomic concept for the typical variety of *N. divaricata* that matches the syntypes *Bolander 4908* and *Mrs. Davis 49*, despite not examining these syntypes or making reference to them. Mason (1951) treated these varieties as subspecies, but otherwise did nothing to alter the taxonomic concept for them. The description by Cronquist et al. (1984) of *N. divaricata* includes features, such as unequal valves and two of the three stigmas almost entirely fused, that exist only in material congruent with var. *divaricata* as put forth by Jepson and Bailey, and congruent with the syntypes *Bolander 4908* and *Mrs. Davis 49*.

The remaining syntype, *Mr. Shelton s.n.* (NY!), is distinct morphologically from the other syntypes. It has smaller heads and slender branches, like *N. divaricata* subsp.

divaricata, yet has a purple corolla throat and tube, three equal valves, and three equal stigma lobes that readily separates it from that taxon. While material matching this syntype was available to Jepson and Bailey, none of those collections were included in the list of representative specimens for either var. *divaricata* or var. *vividior*. No locality information is provided for Mr. Shelton's collection, though the material that it matches occurs in only a portion of the Sierra Nevada, with known occurrences in close proximity to Sacramento where he lived (Ewan 1981). Mr. Shelton's specimen is of particular interest because it is the only syntype labeled "*Navarretia divaricata* n. sp." in Torrey's hand. An unpublished annotation attached to the sheet at NY, upon which *Mr. Shelton s.n.* and three of the remaining five syntypes are mounted, suggests Shelton's collection is the lectotype—attributing the first step to Jepson (1943) and the second step to Cronquist (1984). We, however, disagree with the inferences made by this annotation. Jepson did not specifically state he was indicating the type, but instead restated the type locality published by Gray with his exact words reading, "type loc. 'foothills of the Sierra Nevada,' Shelton (the first named collector)." This falls short of specifying the Shelton collection as the lectotype, particularly since there is no indication on the sheet that the Shelton collection comes from the Sierra Nevada (even though we have determined, based on morphology, that it does). Jepson (1943) elsewhere explicitly indicates his observation of types, such as the isotype for *N. peninsularis*, but no such indication is provided for *N. divaricata*. It is unlikely Jepson would have specified as lectotype a specimen that varied from the concept he and Bailey defined through extensive specimen citations. Cronquist et al.'s actions also do not constitute a second step lectotypification. The treatment of *N. divaricata* in this work states "Shelton s.n., Sierra Nevada, Calif., is the first specimen cited by Gray, and the only one annotated by Torrey as 'n. sp.'; isotype at NY!" Importantly, the citation above is not an act of lectotypification; the first volume of the *Intermountain Flora* expressly states, "When one of several collections cited in the protologue is obviously the primary basis for a name, we have given it as the type, without further comment. Sometimes the typification is less clear and a more cautious statement is necessary. Our citation is not to be taken as the formal selection of a lectotype, except when specifically so indicated" (Cronquist et al. 1972: 8).

To summarize, for over 125 years, the name *Navarretia divaricata* has been equated with a divaricately branched plant with minute flowers and branches that often arise immediately below a flowering head. Since 1943, the typical variety or subspecies has been associated with specimens having whitish flowers that dry with pink lobes, and a whitish to yellowish lower throat (sometimes streaked with red) and upper tube. Such plants are represented among the syntypes of *Gilia divaricata* Torr. ex Gray by *Bolander 4908* and *Mrs. Davis 49*. Choosing either *Rattan s.n.* (based on Gray's original description, though multiple gatherings is problematic) or *Mr. Shelton s.n.* (based on Torrey's designation) as lectotype would result in needless and confusing nomenclatural shuffling for one of the most recognizable and geographically widespread *Navarretia* species. Similarly, considering *N. divaricata* Greene to represent a new name with Curran's cited specimen as type, independent of *G. divaricata* Torr. ex A.Gray (which was

clearly not Greene's intent), would make *N. divaricata* synonymous with *N. peninsularis*. This action would necessitate a new combination for the entity under consideration based on *Gilia atrata* M.E.Jones, a name buried in obscurity and unused since its original publication. As allowed by the code, we advocate the continued interpretation of Greene's name as a replacement for Gray's, with Gray's syntypes as the original material, and designate one of these syntypes as lectotype to serve as the basionym of *N. divaricata* Greene.

Taxonomic treatment

***Navarretia divaricata* Greene, Pittonia 1(8): 136. 1887 emend. L.A.Johnson & D.Gowen**

Figs 1, 2

Gilia divaricata Torr. ex A.Gray, Proc. Amer. Acad. Arts 8: 270. 1870, non *Gilia divaricata* Nutt. 1848.

Type: United States of America. California: Mariposa County, Yosemite trail, 1866, *Bolander* 4908 (lectotype, designated here: GH scan! [GH-00274983]; isolectotypes: UC scan! [UC-23512], YALE scan! [YU-065402], US scan! [US-322192], KEW, middle of three specimens, flanked on either side by *Rattan s.n.*, scan! [K-000769074]). Replaced synonym.

Gilia atrata M.E.Jones, Contr. W. Botany 12: 55. 1908.

Type: United States of America. Idaho: Washington County, Salmon Meadows, 4000 ft, 22 July 1899, *Jones s.n.* (holotype: POM, top three specimens on sheet, scan! [POM-75127]).

Navarretia prolifera Greene var. *breviflora* M.Peck, Proc. Biol. Soc. Washington 50(24): 94. 1937.

Type: United States of America. Oregon: Douglas County, Diamond Lake, 3 July 1936, *Peck* 19234 (holotype: WILLU! [WILLU-18416]; isotype: OSC scan! [OSC-43592]).

Type. Based on *Gilia divaricata* Torr. ex A.Gray, non *Gilia divaricata* Nutt. 1848.

Emended description. *Taprooted annual herbs* to 15 cm tall and 20 cm wide, sometimes larger, often wider than tall. Primary stem erect, terminating in an inflorescence head 1–5 cm above the cotyledons; generally greatly exceeded by secondary stems, with tertiary, and quaternary stems present on larger plants (these higher order stems may be reduced in length and the inflorescence heads ± congested); higher order branches arise from axils of proximal inflorescence bracts, axils of leaves subtending the primary head, or less commonly, leaves within 1 cm of an inflorescence head; branches ascending to spreading and ± leafless, except for leaves subtending higher order branches or within 1 cm of a head; stem and branches tan to reddish-brown, glabrous or sparsely minutely glandular pubescent to glabrescent, less often villous, the trichomes generally

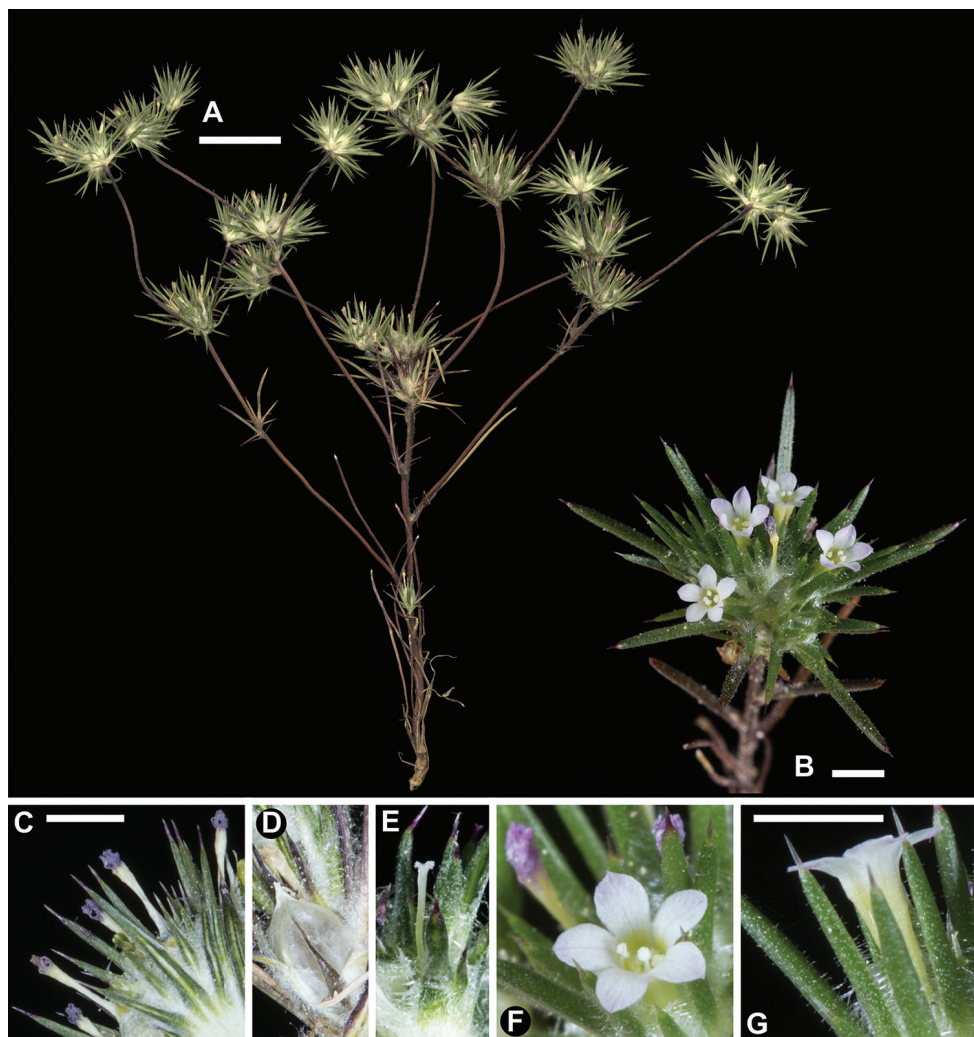


Figure 1. *Navarretia divaricata*. **A** Pressed specimen showing plant habit, scale bar = 1 cm (Johnson 14-143) **B** Flowering head in the field, scale bar = 2 mm (Johnson 15-045) **C–E** Equivalent magnification, scale bar = 2mm **C** Pressed flowering head showing typical coloration of dried flowers (Johnson 16-024) **D** Dried fruit, showing dehiscence from base upward typical in all of the species detailed herein (Johnson 16-024) **E** Fresh flowering head dissected with corolla removed to show style and two-lobed stigma (with third lobe nearly entirely fused to one of the two apparent lobes; Johnson 16-024) **F, G** Fresh flowers showing typical coloration (Johnson 15-045), equivalent magnification, scale bar = 2 mm. All photographs by L. A. Johnson and vouchers deposited at BRY.

less than 0.5 mm long. Cotyledons two, linear, entire, united at base. **Leaves** somewhat finely stipitate-glandular proximally, less so distally; leaves at the lowermost nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more

commonly with 1–3 paired or unpaired linear lateral lobes 1–5 mm long attached along the proximal 3(–15) mm of the leaf, with an elongated, linear terminal segment. **Inflorescences** head-like, generally ≤ 10 mm diameter (exclusive of bract tips; ~ 15 mm with bract tips), mostly less than 15 flowered, villous proximally, obscurely glandular. Inflorescence bracts < 10 (–13) mm long, \pm palmatifid to subpalmatifid; outermost 1–2 bracts with a short achlorophyllous base and 2–3 pairs of lateral lobes flanking an elongate terminal lobe, the distal pair of lateral lobes sometimes shorter and reflexed somewhat out of plane relative to the other lobes; bract bases become larger and clasping centripetally with lateral lobes reduced to a single pair departing from near the apex of the bract base flanking the central terminal lobe, all bract lobes chlorophyllous, entire, long tapering acute. Bracts sparsely villous abaxially, more densely villous adaxially and proximally along the lobes just above their point of attachment, with the distal 1/2 of each lobe more or less glabrous or with a few minute stipitate glands. **Flowers** actinomorphic, **calyces** mostly 4.5–7.5 mm long, tube ~ 1.5 –2 mm; costae entire, long tapering acute, strongly unequal to subequal with typically two costae longer than the other three; costae narrowing proximally, the shorter ones narrower at base than the intercostal membrane and the longer ones subequal with the membrane; calyx tube achlorophyllous, minutely glandular-puberulent on the intercostal membrane with the costae at least somewhat villous, the trichomes longest along the costae at the junction with the intercostal membrane, the free portion of the costae glabrous to very sparsely and minutely glandular distally; intercostal membrane v-shaped at sinus. **Corolla** generally shorter than longest calyx costae at anthesis but exceeding the calyx as fruit matures, narrowly funnelform, glabrous, 3.5–5.0 mm long, lobes 0.6–1.0 mm long \times 0.4–0.9 mm wide, proximal tube white, distal tube and throat yellow, sometimes red-streaked, transitioning to white lobes suffused with pink or lavender at tips (drying pink); tube base expanding and investing the fruit apex. **Stamen** filaments unequal, 0.1–0.6 mm long, inserted unequally to subequally 0.2–1.0 mm below corolla sinuses, included in throat to slightly exserted; pollen white, apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. **Ovary** two-chambered, unequally three-valved with two values bearing a septum and the third valve smaller and lacking a septum entirely or nearly so, stigma obscurely three-lobed, minute, unequally divided with two stigmatic lobes nearly entirely fused, generally included in the corolla throat; capsules mostly 2–2.5 mm long, dehiscent circumcissally around the base with valves splitting upward loculicidally (completely) and septicidally (partially). **Seeds** generally 5–9(–12) per fruit, medium brown, ovoid-angular, mucilaginous when wet. **Nuclear gene** loci showing diploid PCR amplification patterns.

Habitat, distribution, and phenology. *Navarretia divaricata* occurs on a variety of soils from (800)1000–2600 meters in foothill and mountain habitats. It is widely distributed from Santa Barbara and Tulare Counties, California in the south to just within the borders of British Columbia, Canada, in the north, and east to Nevada and Idaho (Fig. 2). Flowering time is (May)June–July(September).

Conservation status. *Navarretia divaricata* has many occurrences throughout its broad range, and is typically abundant when encountered. Occurrences near the periphery of its range (e.g., in British Columbia) may be limited in numbers, but the

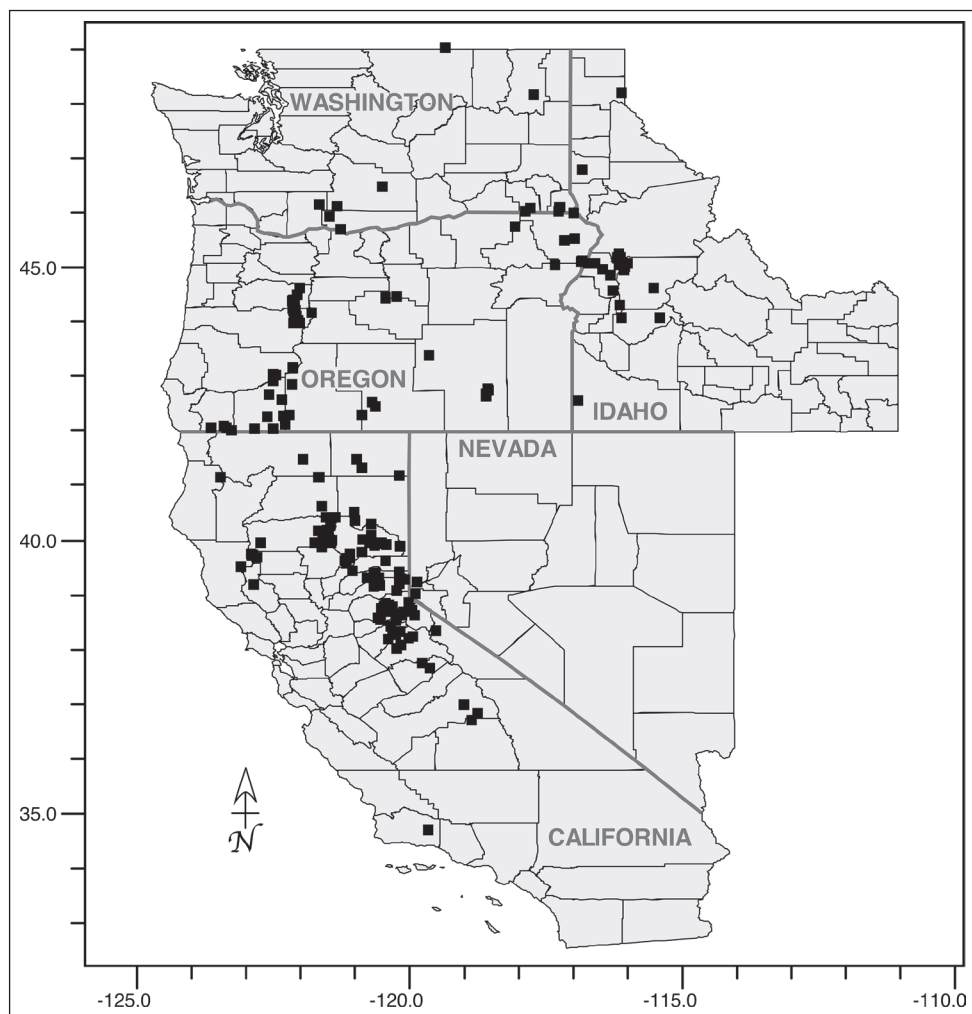


Figure 2. Distribution of *Navarretia divaricata* (black squares) occurrences across its native range in the western United States.

species is otherwise well established. It is a species of Least Concern following IUCN (2012) Red List version 3.1 criteria.

Etymology. From the Latin *divaricatus*, to spread or diverge at a wide angle, which aptly describes the characteristic repeated pattern of nearly leafless stems diverging from under flowering heads to give rise to additional, well-separated flowering heads in this species and its morphological allies.

Representative specimens examined. **CANADA. British Columbia:** Anarchist Mt., 1.6 km north of Hwy 3 rest stop, 6.5 km due east of Osoyoos Lake, 49.0275°N, 119.35°W, 1350 m, 10 July 2000, *Lomer 3838* (UBC Scan); Anarchist Mt., 7 km due east of Osoyoos Lake, 1.5 km due southwest of summit, 200 m northeast of tower, 49.02658°N, 119.34786°W, 1380 m, 9 July 2013, *Lomer 8435* (UBC scan).

UNITED STATES OF AMERICA. All seventeen specimens cited by Jepson (1943) under *Navarretia divaricata* var. *divaricata* (JEPS); **California:** Alpine County, North side of Hwy 88 along an old dirt road, 38.7240°N, 119.9542°W, 2262 m, 10 July 2014, *Johnson 14-179* (BRY); Amador County, down slope from Tragedy Springs Monument, 38.6389°N, 120.1465°W, 2406 m, 8 July 2014, *Johnson 14-159* (BRY); Butte County, ca. 0.7 miles up Humboldt Rd to Butte Meadows from Hwy 32, 40.0407°N, 121.6056°W, 1204 m, 11 June 2015, *Johnson 15-045* (BRY); Calaveras County, at entrance to old lumber road off of Hwy 4 ca. 1.6 miles northeast of Camp Connell Maintenance station, 38.3356°N, 120.2278°W, 1 July 1993, *Johnson 93-112* (BRY); North side of Avery-Sheep Ranch Road ca. 2 miles from Hwy 4, 38.1969°N, 120.4003°W, 1098 m, 4 June 2014, Johnson et al. *14-068* (BRY); El Dorado County, ca. 0.1 mile west of NF-8N55 on Omo Ranch Road, 38.5542°N, 120.5401°W, 1172 m, 29 May 2013, *Johnson 13-189* (BRY); off road to Ice House Reservoir, 6.4 miles from jct. with Hwy 50, 38.7975°N, 120.4028°W, 1596 m, 30 May 2013, *Johnson 13-219* (BRY); Sly Park Vicinity, Park Creek Road 3.7 miles from county road E16, 38.7493°N, 120.4970°W, 1207 m, 8 July 2014, *Johnson 14-141* (BRY); Lassen County, west of county road A21 along dirt road leading to large moist swell, 40.3601°N, 121.0039°W, 1589 m, 2 August 2006, *Johnson 06-129* (BRY); Nevada County, 39.32°N, 120.75°W, 1565 m, 3 June 2014, *Johnson et al. 14-018* (BRY); Placer County, Off Sawtooth Ridge Rd ca. 1.1 mile west of Dawson Spring, 39.21787°N, 120.6226°W, 1670 m, 3 June 2014, *Johnson et al. 14-029* (BRY); Plumas County, south of Cascade and Lava Top, access up FS road 21N22YA, 39.6827°N, 121.1665°W, 1402 m, 10 June 2015, *Johnson & Ahart 15-024* (BRY); Tehama County, two miles south of Hwy 36/89 on Hwy 32, 40.2661°N, 121.4509°W, 4590 ft, *Johnson 04-140* (BRY); Shasta County, off Hwy 89 ca. 1.3 miles north of jct with Hwy A19, 41.1612°N, 121.6609°W, 1257 m, 25 June 2011, *Johnson & Smith 11-058* (BRY); Trinity County, 10.3 miles north along Hastings Tie Road (FS-4N12), 40.5626°N, 123.5236°W, 1577 m, 27 June 2017, *Johnson & Johnson 17-094* (BRY); Tulare County, Rabbit Meadows vicinity off Forest Service road 14S11 near 14S13A, T14S R29E S18, 2300 m, *Johnson 94-065* (BRY); Tuolumne County, Twaine Harte vicinity, north side of highway 108, just west of hairpin in Lava Drive, 38.0266°N, 120.2369°W, 1159 m, 5 June 2014, *Johnson et al. 14-077* (BRY); east of the Punch Bowl, north side of 4N12 ca. 5.4 miles east-northeast from junction with highway 108, 38.2386°N, 119.9496°W, 2178 m, 5 June 2014, *Johnson et al. 14-108* (BRY); **Idaho:** Blaine County, two miles above Alturas Lake, above Alpine Creek, 7400 ft, 23 June 1941, *Cronquist 2661* (IDS); Boise County, at the 62 mile marker of Highway 21, ca. 8 miles south of Lowman, 44.02°N, 115.62°W, 1859 m, 14 July 2003, *Porter & Machen 13772* (BRY); Idaho County, Trail to Lake Serene, 45.1961°N 116.1907°W, 2169 m, 12 July 2013, *Smith et al. 11162* (BRY, SRP scan); Valley County, FR 626, west of Sagehen Reservoir, Sagehen Basin, 44.3196°N, 116.1547°W, 1845 m, 17 July 2011, *Smith 9922* (BRY, SRP scan); Brundage Mt., 7000 ft, 23 July 1940, *Davis 2930* (IDS); **Nevada:** Douglas County, Carson Range, Genoa Peak Road, 2560 meters, 13 August 1974, *Williams 74-D-83* (RENO scan); Nevada, Washoe County, Carson Range, Little Valley, near bridge, 1981 meters, 22

June 1974, *Tiehm s.n.* (RENO scan); **Oregon:** Crook County, Little Hay Creek vicinity, along Forest Service Road 150 0.1 miles north of jct with forest service road 2610, T13S R19E S22, *Johnson 97-133* (BRY); Harney County, Steens Mountain Loop Byway, 1 km below jct with Kiger Gorge turnoff, 42.69°N, 118.59°W, 8251 ft, 21 July 2007, *Johanson 07-76* (WTU scan); Jackson County, Just north of Hwy 66 along Moon Prairie Rd, 42.1263°N, 122.3321°W, 1161 m, 29 June 2017, *Johnson & Johnson 17-147* (BRY); Josephine County, Upper Biglow Lake, 10 July 1949, *Baker & Ruhle 385* (IDS scan, WTU scan); **Washington:** Asotin County, Anatone Butte vicinity ca. 7.2 miles west of highway 129 on West Mountain Road, 1400 m, 2 July 1994, *Johnson & Johnson 94-049* (BRY); ca. 0.5 mile west of Anatone Butte, 10 miles southwest of Anatone, T7N R45E, S2, 4700 ft, 12 June 1949, *Cronquist 5847* (ID scan, WTU scan WS); Chelan County, Rainbow Creek drainage, ca. 4.5 miles north of Stehekin River, 3000 ft, 19 June 1971, *Naas & Naas 851* (WWB scan); Columbia County, Godman Spring campground, 18.5 miles southwest of Dayton, 46.10°N, 117.7861°W, 1753 m, 12 July 2004, *Legler 2014* (WTU scan); Klickitat County, dry hills, Falcon Valley, 18 July 1908, *Suksdorf 168* (WTU ×3 scan).

Notes. By elevating *Navarretia divaricata* subsp. *vividior* to species status, as done below, *N. divaricata* subsp. *divaricata* henceforth is designated simply *N. divaricata*. Fresh *N. divaricata* have no noticeable odor. The reported presence of this species in Montana is based on a single, misidentified specimen collected in an agricultural field; that specimen differs from *N. divaricata* in branching structure, having pinnately divided leaves, and possessing different bract and calyx morphology (our determination is *N. squarrosa* (Eschsch.) Hook. & Arn. [MONT-68910 scan!]). Though the protologue provides no mention of *N. divaricata*, Peck's rationale for recognizing *N. prolifera* var. *breviflora* as distinct from *N. divaricata* can be inferred from the key and species descriptions in the first edition of his Manual of the Higher Plants of Oregon (Peck 1941). Examination of the type reveals it is simply a narrow, more erect *N. divaricata* that fits well within the range of variation observed in this species. Peck, perhaps influenced by Mason (1951), came to realize this and removed *N. prolifera* var. *breviflora* from the second edition of his manual (Peck 1961).

Navarretia divaricata differs from the remaining divaricately branched taxa of *Navarretia* (i.e., those treated below plus *N. crystallina* L.A. Johnson & D.Gowen, *N. miwukensis* D.Gowen & L.A. Johnson, and *N. prolifera*, in having two of its three stigmatic lobes nearly entirely fused, and in having unequal fruit valves with two of the three valves normal sized and bearing a septum, while the third valve is smaller and lacks a septum entirely or nearly so (Cronquist et al. 1984; personal observation). These other species have three lobed stigmas and three equal valves, each bearing a septum. *Navarretia divaricata*'s flowers, ± 4 mm long, are among the smallest in *Navarretia* and typically dry with pink lobes with a white or yellowish throat and tube, though the throat and tube may at times be streaked with red. On herbarium specimens, the contrast between darker, pink lobes and light, whitish or yellowish tube is preserved on many flowers even on specimens 150 years old (Fig. 1). This coloration pattern enables this species to be determined without dissecting flowers to observe the stigma or fruit valves.

***Navarretia vividior* (Jeps. & V.L.Bailey) L.A.Johnson & D.Gowen, comb. et stat. nov.**
urn:lsid:ipni.org:names:60475570-2

Figs 3, 4

Navarretia divaricata var. *vividior* Jeps. & V.L.Bailey, Fl. Calif. 3(2): 156. 1943. *Navarretia divaricata* subsp. *vividior* (Jeps. & V.L.Bailey) H.Mason, Ill. Fl. Pacific States 3: 449. 1951.

Type: United States of America. California: Lake County, Mt. Hanna, 15 July 1897, *Jepson 15045* (Holotype: JEPS! [JEPS-2659]). Basionym.

Type. Based on *Navarretia divaricata* var. *vividior* Jeps. & V.L.Bailey.

Emended description. *Taprooted annual herbs* to 12(–15) cm tall and 20(–25) cm wide, sometimes larger, often wider than tall. Primary stem erect, terminating in an inflorescence head 1–2(–4) cm above the cotyledons; generally greatly exceeded by secondary stems, with tertiary, and quaternary stems present on larger plants; higher order branches arise from axils of proximal inflorescence bracts, axils of leaves subtending the primary head, or less commonly, leaves within 1 cm of an inflorescence head; branches ascending to spreading and \pm leafless, except for leaves subtending higher order branches or within 1 cm of a head; stem and branches reddish-brown, commonly glandular-villous, the trichomes generally greater than 0.5 mm (often \pm 1 mm) long, sometimes glabrescent; distal-most branches generally 0.3–0.5 mm in diameter. Cotyledons two, linear, entire, united at base. **Leaves** somewhat glandular-pubescent proximally, less so distally; leaves at the lowermost nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3(–5) paired or unpaired linear lateral lobes 1–10 mm long attached along the proximal 3–5(–15) mm of the leaf, with an elongated, linear terminal segment. **Inflorescences** head-like, largest generally \geq 12 mm diameter (exclusive of bract tips; \geq 18 mm with bract tips), mostly 10–25-flowered, glandular-pubescent with some minutely-glandular villous trichomes proximally. Inflorescence bracts < 15(–20) mm long, palmatifid to subpalmatifid; outermost 1–2 bracts with a short achlorophyllous base and 2–3(–4) pairs of lateral lobes flanking an elongate terminal lobe, the distal pair of lateral lobes sometimes shorter and reflexed somewhat out of plane relative to the other lobes; bract bases become larger and clasping centripetally with lateral lobes reduced to a single pair departing from near the apex of the bract base flanking the central terminal lobe, all bract lobes chlorophyllous, entire, long tapering acute. Bracts somewhat minutely-glandular villous abaxially, often more densely villous adaxially and proximally along the lobes just above the bract base, glands becoming more prominent and their stipe diminishing in length toward the bract tips. **Flowers** actinomorphic, **calyces** mostly 4–7.5(–8.5) mm long, tube \sim 1.5–2.5 mm; costae entire, long tapering acute, strongly unequal to subequal with typically two costae longer than the other three; costae narrowing proximally, the shorter ones narrower at base than the intercostal membrane and the longer ones subequal with the membrane; calyx tube achlorophyllous, glandular-puberulent

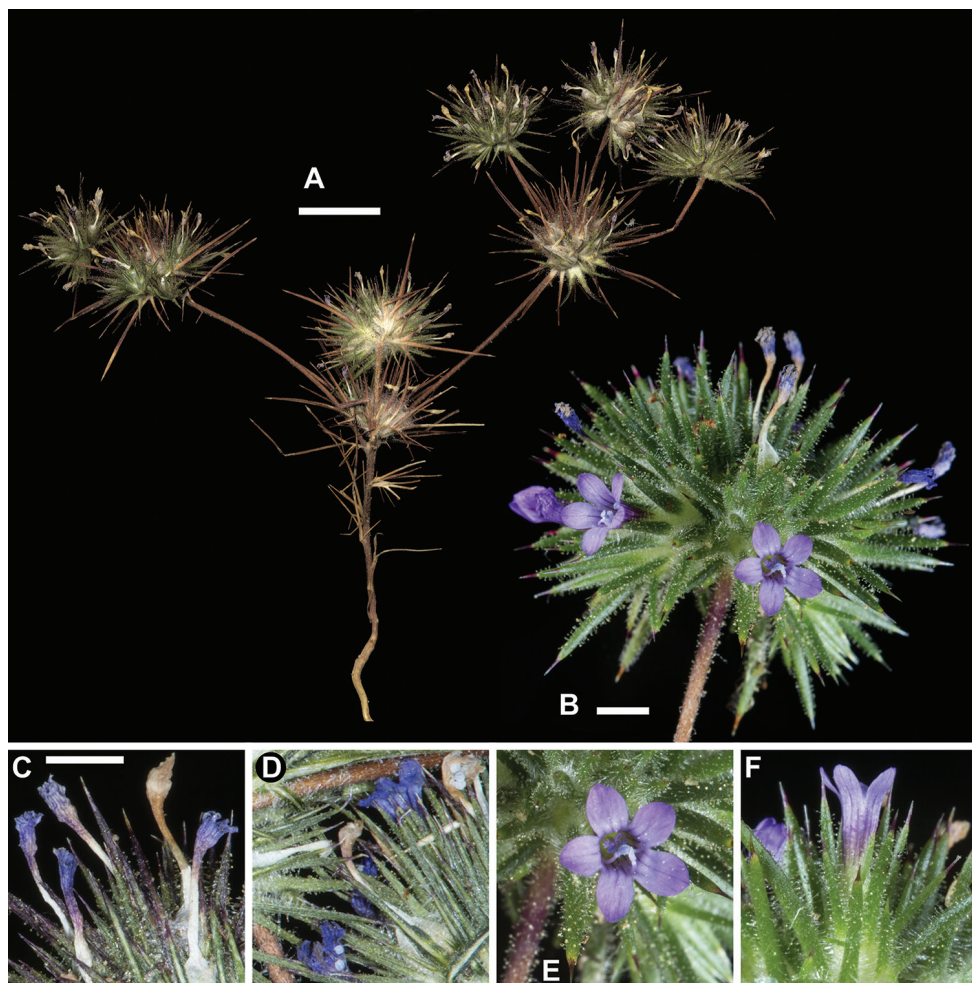


Figure 3. *Navarretia vividior*. **A** Pressed specimen showing plant habit, scale bar = 1 cm (Johnson 16-066) **B** Flowering head in the field, scale bar = 2 mm (Johnson 16-063b) **C–F** Equivalent magnification, scale bar = 2 mm **C, D** Pressed flowering head showing typical coloration of dried flowers and blue pollen (Johnson 16-029, 16-063b, respectively) **E, F** Fresh flowers showing typical coloration (Johnson 16-063b). All photographs by L. A. Johnson and vouchers deposited at BRY.

on the intercostal membrane with the costae at least somewhat glandular-villous, the gland stipes longest along the costae at the junction with the intercostal membrane, diminishing in length toward the chlorophyllous costae tips (may be glabrescent with age); intercostal membrane v-shaped at sinus. **Corolla** generally equal or shorter than longest calyx costae at anthesis but exceeding the calyx as fruit matures, narrowly funnelform, glabrous, 5.0–7.2 mm long, lobes 0.8–1.1(–1.4) mm long \times 0.6–0.9(–1.2) mm wide, tube white proximally, distal tube white or yellow, throat bluish, sometimes streaked with magenta, lobes medium bluish-lavender; tube base expanding and investing the fruit apex. **Stamen** filaments unequal, 0.3–1.2 mm long, inserted unequal-

ly 0.3–1.3 mm below corolla sinuses, anthers \pm included in throat to exerted less than half the length of the corolla lobes; pollen blue (white rarely?), apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. **Ovary** three-chambered, stigmatic lobes three, included in to slightly exerted from corolla throat; capsule \sim 2.3–3.3 mm long, dehiscent circumscissally around the base with valves splitting upward. **Seeds** generally 5–7(8) per locule, medium brown, ovoid-angular, mucilaginous when wet. **Nuclear gene** loci showing allotetraploid PCR amplification patterns.

Habitat, distribution, and phenology. *Navarretia vividior* occurs in soils influenced by volcanic activity with favorable water status such as the edges of ephemeral pools and transient rivulets, to open flats or gentle slopes in forested areas from 300–1600 meters elevation. It occurs predominately in the North Coast Range from Lake and Sonoma Counties, California in the south to Humboldt, Trinity, and the western edge of Shasta County in the north (Fig. 4). A few populations cross the central valley and occur on the western flank of the northern Sierra Nevada/southern Cascade Range in Butte County, California, where they flower in late May–early June, rather than late June–July as is typical for species in the North Coast Range.

Conservation status. As defined here, *Navarretia vividior* is distributed more narrowly than previously considered. Some historical populations have not been revisited for \pm 100 years, though other known occurrences have been revisited multiple times over the past 20 years with no apparent change in local numbers (beyond what may be expected during drought years). Following IUCN (2012) Red List version 3.1 criteria, this species is most accurately characterized as data deficient, though it likely borders between being Vulnerable to a species of Least Concern.

Etymology. This specific epithet is derived from the Latin *vividus*, lively or vigorous, with the comparative ending *-ior*, more so, in reference to the larger, more robust habit and flowering heads this taxon possesses in comparison to *N. divaricata*. Alternative epithets of var. *fertilior* and var. *vividia* were considered by Jepson and Bailey for this entity, as indicated by annotations on the type sheet.

Representative specimens examined. UNITED STATES OF AMERICA. California: Butte County, North of Magalia at Old Coutelenc Site, along Coutelenc Rd, 1.7 miles south of junction with Skyway at Lovelock, 17 June 1980, *Schlising & Banchemo* 3739 (CHSC); Upper Bidwell Park, Chico, on the north rim overlooking Sycamore Creek Canyon about 1.8 miles east of the power lines, 1280 ft, 30 May 1983, *Oswald* 578 (CHSC); South of Cohasset off of Cohasset Highway, T23N R2W S8, 4 June 1979, *Schlising* 3435 (CHSC); Colusa County, Along Pacific Ridge Road (16N06) 0.5 miles east of road to Spanish Ridge and Hough Springs, 39.2236°N, 122.625°W, 3450 ft, 3 July 1998, *Janeway & Isle* 5711 (CHSC); Humboldt County, Waif on river bar, valley of Van Duzen River opposite Buck Mtn, 1000 ft, 27 June–30 July 1908, *Tracy* 2721 (UC); Little Van Duzen River, 23 June 1937, *Eastwood & Howell* 4813 (CAS); Lake County, Mt. St. Helena, 6 June 1915, *Eastwood* 4706; Bartlett Springs, 9 June 1938, *Jepson* 18938 (JEPS); Boggs Lake, at base on Mount Hanna, 29 June 1945, *Mason* 12629 (DS); Margin of Boggs Lake, 3000 ft, 29 June 1945, *Baker* 11088 (CAS); 3.5 miles by road east of Seigler Springs, margin of Snow's Lake, 2150 ft, 26 June 1956, *Crampton* 3646

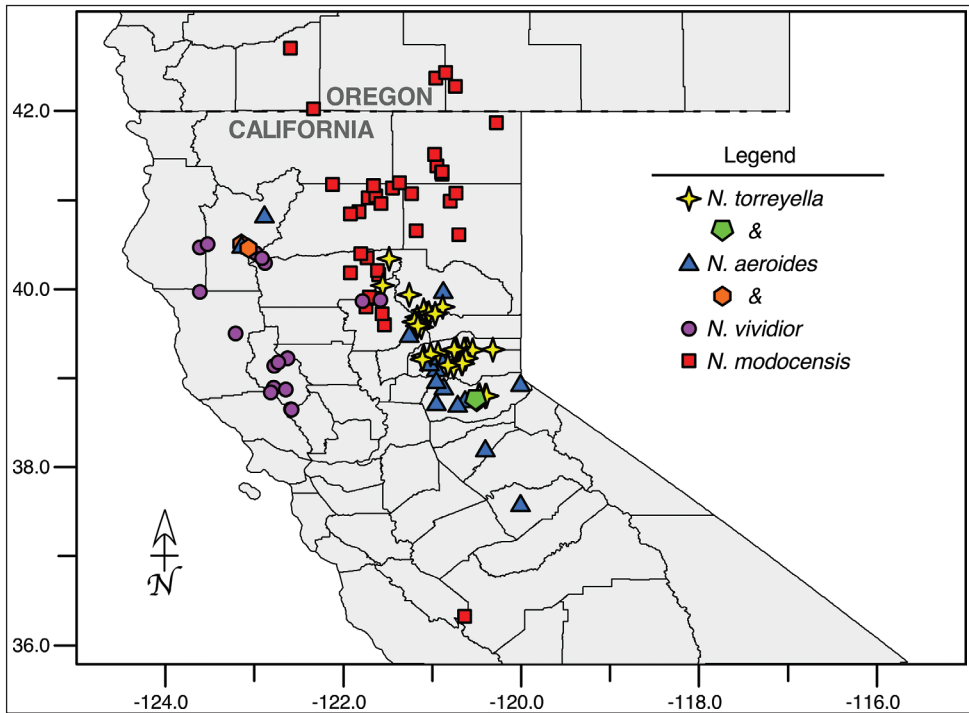


Figure 4. Distribution of *Navarretia vividior* (circles), *N. modocensis* (squares), *N. aeroides* (triangles), and *N. torreyella* (4-pointed stars) occurrences across their native range in California and southern Oregon, United States. Instances of observed syntopy are indicated with the hexagon and pentagon, as defined in the legend.

(AHUC); About 1/4 mile down Harrington Flat Road from Bottle Rock Rd, where access road follows under powerlines, 2850 ft, 7 June 1981, *Knight & Knight 4148* (CAS); Bogg's Lake Vicinity, between Harrington Flat Road and the Bogg's Lake parking area, to the north side of road along the power line corridor, 38.8904°N, 122.7837°W, 862 m, 13 May 2004, *Johnson 04-032* (BRY), and 12 July 2016, *Johnson 16-029* (BRY); Bartlett Mountain Ranger Station, 24 Sept 1949, *Crampton 494B* (AHUC, DAV); About 6.3 miles from Hwy 20 along Bartlett Spring Road, at junction with Pinnacle Rock Road, 39.1345°N, 122.7769°W, 3915 ft, 10 May 2005, *Johnson 05-021* (BRY) and 12 July 2016, *Johnson 16-032* (BRY); Mendocino County, Chamise Mt. north of Bell Springs, 3500 ft, 9 July 1934, *Tracy 13326* (UC); Jeep trail above Bell Springs Rd 11 miles south of jct with Harris Rd, 39.9667°N, 123.6113°W, 1092 m, 28 June 2017, *Johnson & Johnson 17-119* (BRY); Eden Valley Ranch, vernal pool area, north of Hearst, 1249.6 m, 11 July 1978, *Wheeler 506* (CAS); Napa County, Gravelly slope in chaparral, edge of the Crater Country, 13 July 1930, *Howell 5347* (CAS); Robert Louis Stevenson State Park; along trail to Table Rock on East side of Hwy from parking area off Hwy 29, 38.6513°N, 122.5867°W, 802 m, 30 May 2009, *Johnson & Gowen 09-049* (BRY); Shasta County, Harrison Gulch Rd, 2.4 miles north of Hwy 36 west of Platina, T29N R10W S3,

3100 ft, 1 July 1996, *Oswald, Ahart & Ondricek-Fallsheer 7906* (CHSC) and 13 July 2016, *Johnson 16-062* (BRY); 0.3 miles north of Hwy 36 along NF-29, 40.3699°N, 122.9380°W, 893 m, 27 June 2017, *Johnson & Johnson 17-052* (BRY); Sonoma County, Mayacmas Mtns, Caldwell Pines, ca. 3.5 miles west of Glenbrook and Bottle Rock Rd, 38.841°N, 122.815°W, 2350–3000 ft, 27 June 1975, *Neilson & Sholars 3294b* (DAV); Tehama County, West of Red Bluff and south of Platina on Forest Route 45 (Tedoc Mtn. Rd), 6.3 miles south of Hwy 36, 3800 ft, 12 July 1995, *Oswald & Ahart 7022* (CHSC) and 13 July 2016, *Johnson 16-058* (BRY); Trinity County, Along Wildwood Rd north of Hwy 36 between mile post 7 and 8, where drainage crosses and goes under road, 24 June 2005, *Gowen 452* (BRY, JEPS) and 13 July 2016, *Johnson 16-063b* (BRY); 6.2 miles north of Hwy 36 along Hastings Tie Road, 40.5092°N, 123.5041°W, 1597 m, 27 June 2017, *Johnson & Johnson 17-082* (BRY).

Notes. *Navarretia vividior* are mephic when fresh. *Crampton 494B* [AHUC-38375] (collected by McMillan at the Bartlett Mountain Ranger Station) is a voucher for a tetraploid chromosome count from pollen mother cells. Our low copy nuclear gene data indicate this species is an allotetraploid, with *N. modocensis* the paternal diploid parent and *N. aeroides* the maternal diploid parent. Four of the eight paratypes listed for *N. divaricata* var. *vividior* belong here: *Chestnut & Drew s.n.* [UC-52826], *Tracy 2721* [UC-133661], *Tracy 13326* [JEPS-70300], and *Jepson 18938* [JEPS-70299]; a fifth paratype, *Condit s.n.* [UC-455660], is difficult to place with confidence; it was collected from ‘garden soil’ and thus its original source is uncertain, but its smaller corolla features suggest *N. vividior*. The *Torrey 302* syntype of *Gilia divaricata* Torr. ex Gray also belongs here.

Navarretia vividior is readily distinguished from *N. divaricata* with its larger flowering head, larger flowers, equally divided 3-lobed stigma, typically blue pollen, and bluish-lavender corolla lobes and throat (Fig. 3). Stems are typically larger in diameter and invested with long, gland tipped hairs. The evenly 3-lobed stigmas, larger flowers, and some variation in flower color with colored lobes, throat, or both apply to three additional species that have heretofore generally fallen under the umbrella of *N. divaricata* subsp. *vividior*. These species are described and differentiated below.

***Navarretia modocensis* L.A. Johnson & D. Gowen, sp. nov.**

urn:lsid:ipni.org:names:60475567-2

Figs 4, 5

Type. United States of America. California: Shasta County, west side of Hwy 89, ca 10 miles north of junction with Hwy 299. Meadow area adjacent to railroad tracks, 41.0450°N, 121.6326°W, 2992 ft, 17 June 2004, *L.A. Johnson 04-130* (holotype BRY! [BRY-614952]; isotypes JEPS! RSA! and to be distributed).

Diagnosis. A species similar to *Navarretia vividior*, but distinguished by being diploid, rather than allotetraploid, generally being more conspicuously villous in the proximal inflorescence, possessing slightly larger flowers and more exerted corollas



Figure 5. *Navarretia modocensis*. **A** Pressed specimen showing plant habit, scale bar = 1 cm (*Johnson 04-130*) **B** Flowering head in the field, scale bar = 2 mm (*Johnson 16-072*) **C, D** Pressed flowering heads showing range of typical coloration, equivalent magnification, scale bar = 2 mm (*Johnson 04-124, 04-130*, respectively) **E–G** Fresh flowers showing typical coloration and white pollen, equivalent magnification, scale bar = 2 mm. (**E, F** = *Johnson 14-170*; **G** = *Johnson 16-072*). All photographs by L. A. Johnson and vouchers deposited at BRY.

that tend toward pinkish-lavender lobes with darker throat above a yellowish tube rather than bluish to bluish-lavender lobes with darker throat above a yellowish or whitish tube, and having white (rarely blue) rather than blue pollen.

Description. *Taprooted annual herbs* to 12(–15) cm tall and 20(–25) cm wide, sometimes larger, often wider than tall. Primary stem erect, terminating in an inflorescence head 1–2(–4) cm above the cotyledons; generally greatly exceeded by secondary stems, with tertiary, and quaternary stems present on larger plants; higher order branches arise from axils of proximal inflorescence bracts, axils of leaves subtending the primary head, or less commonly, leaves within 1 cm of an inflorescence head; branches ascending to spreading and \pm leafless, except for leaves subtending higher order branches or within 1 cm of a head; stem and branches reddish-brown, commonly glandular-villous, the trichomes generally greater than 0.5 mm (often \pm 1 mm) long, sometimes glabrescent; distal-most branches generally 0.3–0.5 mm in diameter. Cotyledons two, linear, entire, united at base. **Leaves** somewhat glandular-pubescent proximally, less so distally; leaves at the lowermost nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3(–5) paired or unpaired linear lateral lobes 1–10 mm long attached along the proximal 3–5(–15) mm of the leaf, with an elongated, linear terminal segment. **Inflorescences** head-like, largest generally \geq 12 mm diameter (exclusive of bract tips; \geq 18 mm with bract tips), mostly 12–20-flowered, sometimes more, glandular-pubescent, generally with conspicuous, minutely-glandular villous trichomes proximally. Inflorescence bracts < 15(–20) mm long, \pm palmatifid to subpalmatifid; outermost 1–2 bracts with a short achlorophyllous base and 2–3 pairs of lateral lobes flanking an elongate terminal lobe, the distal pair of lateral lobes sometimes shorter and reflexed somewhat out of plane relative to the other lobes; bract bases become larger and clasping centripetally with lateral lobes reduced to a single pair departing from near the apex of the bract base flanking the central terminal lobe, all bract lobes chlorophyllous, entire, long tapering acute. Bracts minutely-glandular villous abaxially, often more densely villous adaxially and proximally along the lobes just above the bract base, glands becoming more prominent and their stipe diminishing in length toward the bract tips. **Flowers** actinomorphic, **calyces** mostly 5–7.5(–12) mm long, tube \sim (1.5–)2–2.5(–3) mm; costae entire, long tapering acute, strongly unequal to subequal with typically two costae longer than the other three; costae narrowing proximally, the shorter ones narrower at base than the intercostal membrane and the longer ones subequal with the membrane; calyx tube achlorophyllous, glandular-puberulent on the intercostal membrane with the costae at least somewhat glandular-villous, the gland stipes longest along the costae at the junction with the intercostal membrane, diminishing in length toward the chlorophyllous costae tips (may be glabrescent with age); intercostal membrane v-shaped at sinus. **Corolla** generally equal to exceeding the calyx costae at anthesis and exceeding the calyx further as fruit matures, narrowly funnelform, glabrous, 6.0–8.2 mm long, lobes (1.0–)1.2–1.5(–1.95) mm long \times 0.8–1.4 mm wide, tube white proximally, yellow distally, throat lavender–purple or purplish streaked, lobes light to dark

pinkish-lavender; tube base expanding and investing the fruit apex. **Stamen** filaments unequal, 0.3–1.3 mm long, inserted unequally 0.3–1.6 mm below corolla sinuses, anthers \pm included in throat to exerted less than half the length of the corolla lobes; pollen white (uncommonly blue), apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. **Ovary** three-chambered, stigmatic lobes three, included in to slightly exerted from corolla throat; capsule \sim 2.6–3.8 mm long, dehiscing circumcissally around the base with valves splitting upward. **Seeds** generally 4–9 per locule, medium brown, ovoid-angular, mucilaginous when wet. **Nuclear gene** loci showing diploid PCR amplification patterns.

Habitat, distribution, and phenology. *Navarretia modocensis* occurs in volcanic influenced soils in forest openings and sagebrush slopes from (390–)800–1700 meters predominately in the Modoc Plateau of northeastern California and adjacent southern Oregon, but extending south to the western flank of the northern Sierra Nevada/southern Cascade Range in Butte County, California, and with a long-distance disjunct occurrence in San Benito County, California. Flowering occurs primarily in (April–)June–July.

Conservation status. *Navarretia modocensis* has many occurrences throughout its range and is often abundant when encountered. It is a species of Least Concern following IUCN (2012) Red List version 3.1 criteria.

Etymology. From the Latin *-ensis*, origin or place, combined with Modoc, in reference to the Modoc Plateau on which this taxon predominantly (but not exclusively) occurs.

Representative specimens examined (paratypes). **UNITED STATES OF AMERICA. California:** Butte County, North east of Forest Ranch, 2.3 miles east and southeast of Hwy 32 along Garland Road, T24N R3E S33, 2960 ft, 13 June 1980, *Schlesinger & Azevedo 3699* (CHSC) and 20 May 2017, *Johnson 17-027* (BRY); Top of North Table Mt, ca 200 meters north of junction of Cherokee Rd and east edge of Mt, T20N R4E S17 NE1/4, 18 May 1979, *Jokerst, Devine, & Greenstein 0462* (CHSC); Ponderosa way on Musty Buck Ridge between Cohasset and Big Chico Creek, T24N R2E S25 SE NW 1/4, 2500 ft, 16 May 1989, *Oswald 3773* (CHSC); About 0.5 mile east of Kunkle Creek, about 2.5 miles south-east of Paradise, 1500 ft, 29 May 1979, *Ahart 1906* (CHSC); Lassen County, Off Hwy 139, up slope and across fence at a pull out area on west side of road, near mile marker 49.5, 40.9833°N, 120.7950°W, 1615 m, 9 July 2014, *Johnson 14-176* (BRY); Murrer Meadow Rd, ca 3 miles east of Eagle Lake Biological Station, 5100 ft, 24 June 1967, *Stern 2418* (CHSC); 100 yards south of Hwy 44, 34 miles northwest of Susanville, 26 June 1974, *Stern 5863* (CHSC); Ash Valley RNA/ACEC, T37N R11E S5, 5100 ft, 29 June 1993, *Schoolcraft 2303* (CAS; mixed collection with *N. divaricata*); Near Bar Springs road, just off Hwy 299 near top of grade, ca. 7.4 miles east of county line, 41.0669°N, 121.2315°W, 1383 m, 14 July 2016, *Johnson 16-075* (BRY); Modoc County, Vicinity of mile maker 9.37 off of Hwy 299, near Roney Flat and Johnson Creek Roads, 41.30602°N, 120.89584°W, 1428 m, 25 June 2011, *Johnson & Smith 11-064* (BRY); Fandango Pass vicinity, helicopter pad 5.1 miles from Hwy 395 on Fandango Pass Road (Rd 9) at south end of Buck

Creek Fire station and intersection with Jack's Rd, 41.8639°N, 120.2849°W, 1586 m, 9 July 2014, *Johnson 14-170* (BRY); About 0.3 miles up 41N25 (Shake Canyon) off of Hwy 139/299, 41.3825°N, 120.9437°W, 1415 m, 9 July 2014, *Johnson 14-173* (BRY); 0.6 miles along Johnson Creek road from jct with Hwy 299/139 about 9.5 miles north of county line, 41.3120°N, 120.8874°W, 1479 m, 14 July 2016, *Johnson 16-083* (BRY); 0.7 miles east of Hwy 139 along road FS 46, 41.5090°N, 120.9750°W, 1519 m, 14 July 2016, *Johnson 16-086* (BRY); Little Hot Spring Valley, 15 June 1894, *Baker s.n.* (UC 23519); San Benito County, Condon Peak vicinity, 36.3205°N, 120.63817°W, 4683 ft, 5 June 2016, *O'Dell s.n.* (BRY; JEPS); Shasta County, Fuller Flat, north side of Hwy 299, just west of mile marker 64.71, about 14 miles west of junction with Hwy 89, 40.86532°N, 121.8238°W, 3792 ft, 17 June 2004, *Johnson 04-124* (BRY, JEPS, RSA) and 14 July 2016, *Johnson 16-072* (BRY); Meadow 0.3 miles past Rock Creek, south side of road 37, 41.0245°N, 121.7164°W, 3180 ft, 17 June 2004, *Johnson 04-137* (BRY); Rock Creek vicinity; north of Summit Lake Road (Forest Route 38N10) ca. 3.5 miles from junction with Clark Creek Road, east of Lake Britton & Hwy 89, 41.0218°N, 121.7217°W, 973 m, 17 June 2005, *Johnson & Zhang 05-157* (BRY); 0.4 miles south of Hwy 299 along Cassel road, 40.9561°N, 121.5772°W, 926 m, 14 July 2016, *Johnson 16-073*; Ahjumawi Lava Springs State Park, 3 miles north of McArthur, along Spatter Cone Trail, 3450 ft, 24 May 2004, *Fischer & Marr 0213* (CHSC); Fall River Springs, 3500 ft, June 1903, *Hall & Babcock 4213* (UC); Montgomery Creek, 27 June 1912, *Eastwood 631* (CAS); Willow Creek Ranch about 6.8 miles south of the intersection of California State Rd 89 and Squaw Valley Rd in McCloud, 2900 ft, 29 May 1995, *Almeda & Eisenhardt 7417* (CAS); Tehama County, High Cascade Range. Along Road 27N08 to Deer Creek and Onion Butte, ca. 4.6 miles from jct with Hwy 32 at sharp hairpin bend (ca. 0.9 miles from Deer Creek), 40.1624°N, 121.5999°W, 994 m, 11 June 2015, *Johnson 15-047* (BRY); North side of Hwy 36 in ecotone gradation between mixed conifer forest and chaparral at mile marker 75.49, about 12.8 miles west of jct with Hwy 89 to Mt. Lassen, 40.34734°N, 121.7299°W, 1138 m, 12 June 2015, *Johnson 15-057* (BRY); Along Ponderosa Way at crossing of Soap Creek; 40.3933°N, 121.8033°W, 2450 ft, 30 May 1997, *Taylor 16013* (BRY, JEPS); North side of Ishi Wilderness at Rancheria Creek Trailhead, 40.2052°N, 121.6141°W, 3210 ft, 31 May 2003, *Hillaire & Elliott 327* (CHSC); 33 meters above Road 27N08, 2.3 km east of major hairpin turn, 40.1586°N, 121.6019°W, 1000 m, 30 May 2004, *Janeway & Castro 8123* (CHSC); North facing slope along Powerline Road just southwest of north fork of Little Antelope Creek, 40.1833°N, 121.9186°W, 1890 ft, 25 April 2009, *Castro & Janeway 1778* (CHSC); **Oregon:** Jackson County, Near trail, 19 June 1931, *Howell 6766* (CAS); 7 miles southwest of Prospect, 2100 ft, 28 June 1939, *Hitchcock and Martin 4992* (IDS; OSC); On Copco Rd., about 1/2 mile south of Ranch, just north of California line, T41S R4E S10 SW1/4, 18 June 1990, *Rolle 237* (OSC); Klamath County, 11 miles east of Blye, 30 June 1937, *Peck 19655* (WILLU); Hwy 140, about 4.7 miles west of Lake County line, to south of highway near old dirt road, 12 July 1995, *Johnson 95-053* (BRY); Lake County, 24 miles northwest of Lakeview, 25 June 1927, *Peck 15226*

(WILLU); jct of FS-3870 and highway 140, 42.2632°N, 120.7197°W, 1529 m, 29 June 2017, *Johnson & Johnson 17-159* (BRY).

Notes. *Navarretia modocensis* are mephic when fresh. Three of the nine paratypes listed for *N. divaricata* var. *vividior* belong here: *Baker s.n.* [UC-23519], *Hall & Babcock 4213* [UC-127856], and *Austin 827* [UC-133706]. A collection from Yosemite National Park, *Mason 12480a* [UC-908393], likely belongs here also, representing a second disjunct population for this species. Pollen is usually white in *N. modocensis*, but blue pollen has been observed.

Navarretia modocensis is the species most likely to be visually confused with *N. vividior*. Though *N. modocensis* can have larger inflorescence heads, calyces, and flowers than *N. vividior*, the range of measurements in these features overlap. We are fairly confident (on fresh flowers) that *N. modocensis* has a yellow corolla tube on fresh flowers, and that populations with blue pollen are uncommon, but we are less certain that *N. vividior* always has yellow on its tube, or that populations with white pollen do not exist (given white results from the absence of pigment; we have collected species in several genera, including *Navarretia* that are characterized by blue pollen but occasionally have populations with white pollen). The more robust features of *N. modocensis* contrast more sharply with *N. aeroides*, which has smaller flowers, smaller inflorescence heads, thinner branches, and is visually much more glandular and less villous in its inflorescence heads. The smaller dimensions and very different corolla coloration patterns also readily distinguish *N. divaricata* and *N. torreyella* from *N. modocensis*.

***Navarretia aeroides* L.A.Johnson & D.Gowen, sp. nov.**

urn:lsid:ipni.org:names:60475568-2

Figs 4, 6

Type. United States of America. California: Calaveras County, west of Avery, at the end of a short forest service road off of Avery Sheep Ranch Road, 38.19488°N, 120.39969°W, 3695 ft, 17 June 2015, *D. Gowen, 1303* (holotype BRY! [BRY-627257]; isotypes JEPS! RSA!).

Diagnosis. A species similar to *Navarretia vividior*, but distinguished by being diploid, rather than allotetraploid, and being less robust in all respects; *N. aeroides* has smaller inflorescence heads that are conspicuously stipitate-glandular throughout (sometimes inconspicuously villous proximally), thinner branches, tends toward smaller corollas, and has stem trichomes mostly 0.5 mm or less rather than mostly ± 1 mm.

Description. *Taprooted annual herbs* to 9(–12) cm tall and 15(–22) cm wide, sometimes larger, often wider than tall. Primary stem erect, terminating in an inflorescence head 1–2(–4) cm above the cotyledons; generally greatly exceeded by secondary stems, with tertiary, and quaternary stems present on larger plants; higher order branches arise from axils of proximal inflorescence bracts, axils of leaves subtending the primary head, or less commonly, leaves within 1 cm of an inflorescence head; branches ascending to spreading and \pm leafless, except for leaves subtending higher



Figure 6. *Navarretia aeroides*. **A** Pressed specimen showing plant habit, scale bar = 1 cm (Gowen 1303) **B** Flowering head in the field, scale bar = 2 mm (Johnson 14-142) **C–F** Equivalent magnification, scale bar = 2mm **C, D** Pressed flowering head showing range of coloration in dried flowers (Johnson 16-070, Gowen 1303, respectively) **E, F** Fresh flowers showing range of coloration (Johnson 16-063a, Johnson 15-065, respectively). All photographs by L. A. Johnson and vouchers deposited at BRY.

order branches or within 1 cm of a head; stem and branches reddish-brown, glandular-pubescent or sparingly so, the trichomes mostly less than 0.5 mm long; distal-most branches filiform, generally no more than 0.3 mm in diameter. Cotyledons two, linear,

entire, united at base. **Leaves** somewhat finely stipitate-glandular proximally, less so distally; leaves at the lowermost nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3(–5) paired or unpaired linear lateral lobes 1–8 mm long attached along the proximal 3–5(–15) mm of the leaf, with an elongated, linear terminal segment. **Inflorescences** head-like, generally ≤ 10 mm diameter (exclusive of bract tips; ~ 15 mm with bract tips), mostly less than 10-flowered, sometimes more, \pm conspicuously glandular. Inflorescence bracts < 10 (–12) mm long, \pm palmatifid to subpalmatifid; outermost 1–2 bracts with a short achlorophyllous base and 2–3 pairs of lateral lobes flanking an elongate terminal lobe, the distal pair of lateral lobes sometimes shorter and reflexed somewhat out of plane relative to the other lobes; bract bases become larger and clasping centripetally with lateral lobes reduced to a single pair departing from near the apex of the bract base flanking the central terminal lobe, all bract lobes chlorophyllous, entire, long tapering acute. Bracts sparsely glandular-villous abaxially, more densely glandular-villous adaxially and proximally along the lobes just above the rachis, with the stipe of each gland diminishing in length toward the bract tips. **Flowers** actinomorphic, **calyces** mostly 4.0–6.0(–8.5) mm long, tube ~ 1.3 –2.2–(2.5) mm; costae entire, long tapering acute, strongly unequal to subequal with typically two costae longer than the other three; costae narrowing proximally, the shorter ones narrower at base than the intercostal membrane and the longer ones subequal with the membrane; calyx tube achlorophyllous, glandular-puberulent on the intercostal membrane and proximal costae, gland stipes lengthen on the costae at the junction with the intercostal membrane, diminishing in length toward the chlorophyllous costae tips; intercostal membrane v-shaped at sinus. **Corolla** generally \pm equal to the calyx costae at anthesis but exceeding the calyx as fruit matures, narrowly funnelform, glabrous, 4.2–6.0 mm long, lobes 0.75–1.3 mm long \times 0.5–0.9(–1.0) mm wide, tube white, transitioning to a bluish throat and lobes in some populations (drying bluish purple, with the distal tube showing hints of magenta or somewhat brownish) or remaining white in others (drying with white or light blue lobes and throat with brownish or magenta distal tube); tube base expanding and investing the fruit apex. **Stamen** filaments unequal, 0.2–0.55 mm long, inserted unequally 0.4–0.9 mm below corolla sinuses, anthers included in throat to slightly exerted; pollen blue or white, generally matching corolla lobe coloration, apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. **Ovary** three-chambered, stigmatic lobes three, included in to slightly exerted from corolla throat; capsule ~ 2.4 –3.4 mm long, dehiscing circumcissally around the base with valves splitting upward. **Seeds** generally 4–8 per locule, medium brown, ovoid-angular, mucilaginous when wet. **Nuclear gene** loci showing diploid PCR amplification patterns.

Habitat, distribution, and phenology *Navarretia aeroides* prefers (reddish) clay soils in forest openings from 400–1350(–1900) meters elevation. Occurrences are widely scattered in the Sierra Nevada from Mariposa County, California in the south to Plumas County in the North, and in the Trinity mountains of the North Coast Range, California. This species flowers primarily June–July.

Conservation status. Many historical collections of this species are sufficiently general in their locality descriptions in areas now populated that our efforts to relocate them, compounded by recent drought years, have been unsuccessful. On the other hand, all but two of our collections were made serendipitously, in the course of looking for other species, suggesting our present knowledge of occurrences is incomplete. Following IUCN (2012) Red List version 3.1 criteria, this species is most accurately characterized as data deficient, though it may be Vulnerable based on the fragmented nature of a limited number of occurrences.

Etymology. From the Latin *aeroides*, like the sky or sky-blue, in reference to the typical color of the corolla.

Representative specimens examined (paratypes). **UNITED STATES OF AMERICA. California:** El Dorado County, Lake Valley, July 1908, *Brandege s.n.* (UC; mixed collection with *N. divaricata*); 3 miles east of Camino at C.C.C. Camp Snowline, 3400 ft, 6 July 1943, *Robbins 1247* (JEPS, UC); 0.1 mi north of Rescue, along deer valley road, 1300 ft, 30 June 1945, *Robbins 2015* (UC); 3 miles southeast of Greenwood, Coloma Canyon, 18 June 1957, *Crampton 4233* (AHUC); 6.4 miles east of Diamond Springs, 6 June 1960, *Crampton 5546* (AHUC); Sly Park Vicinity. Park Creek Road off of county road E16, 38.7493°N, 120.4970°W, 1207 m, 8 July 2014, *Johnson 14-142* (BRY, JEPS); Mariposa County, Telegraph Hill Road, ca. 7 miles from Hwy 140 via E. Whitelock Road, 37.5773°N, 120.0038°W, 809 m, 9 June 2015, *Johnson 15-005* (BRY, JEPS); Nevada County, Colfax, 3 July 1882, *Jones 3417*. (POM, scan); Colfax, 20–22 Jun 1912, *Eastwood 498* (CAS, UC); Rattlesnake Creek, 5 miles south of Grass Valley, 2000 ft, 29 May 1926, *Mason 3279* (UC); Bed of dried pond west of Greenhorn Creek, T16N R9E S24, 3000 ft, 27 August 1954, *Raven 7980* (CAS); Placer County, Nevada City, Hospital Farm, Sierra Nevada Mtns, 5000 ft, 31 July 1915, *Brainerd & Baird 236* (JEPS); 10 miles west of Forest Hill, 15 June 1955, *Crampton 2921* (AHUC); Plumas County, 2.5 miles northeast of Quincy Junction on Mt Hough-Crystal Lake Road, T24N R10E S4, 4200 ft, 24 June 1981, *Barbe, Fuller, & Howell 3181* (CHSC); East of Quincy, about 2.3 miles along Mt. H road from its junction with Quincy Jct Road, at intersection with 25N14, 39.9747°N, 120.8761°W, 1321 m, 12 June 2015, *Johnson 15-065* (BRY, JEPS) and 14 July 2016, *Johnson 16-087* (BRY, JEPS); Trinity County, Hills south above Hayfork, between Kingsbury Rd. and Bridge Gulch Rd, 25 June 2005, *Gowen 462*; East side of Hwy 3 south of Clair Engle Lake, ca 2.3 miles south of Tannery Gulch Road, 40.8225°N, 122.8887°W, 947 m, 16 July 2009, *Johnson 09-109* (BRY); About 7.3 miles up Wildwood Rd (NF-3) from Hwy 36, 40.4514°N, 123.0649°W, 1003 m, 13 July 2016, *Johnson 16-063a* (BRY); South of Hayfork about 3.3 miles along Kingsbury road from jct with Morgan Hill road, 40.5074°N, 123.1469°W, 851 m, 13 July 2016, *Johnson 16-070* (BRY, JEPS); Yuba County, along margin of New York Flat Road, 0.5 miles north from jct with Laporte road (possible waif), 39.4812°N, 121.2606°W, 2255 ft, 18 June 2004, *Johnson 04-150* (BRY).

Notes. *Navarretia aeroides* are mephic when fresh. In 2015, the population first collected by Barbe, Fuller, & Howell in the mountains east of Quincy, California, was

found to have been sprayed with 2,4-D (and blue indicator dye), along with *N. propinqua*, in an area designated for ORV use, perhaps having been mistaken for immature thistle. To date, occurrences in the Trinity Mountains can be distinguished morphologically (white corollas with magenta streaking in the throat and white pollen) from occurrences in the Sierra Nevada (blue to light blue corollas and blue pollen), yet we have resisted recognizing this difference at the subspecific level. As in any species with colored corollas, occasional white flowered individuals are observed in the Sierra Nevada among a sea of blue flowered individuals. The paratype of *Gilia atrata* M.E.Jones from Colfax, California [POM-75128 scan!] belongs here.

Navarretia aeroides is a smaller-featured plant than either *N. vividior* or *N. modocensis*, though its corolla overlaps in size with *N. vividior*. The more conspicuously glandular inflorescence heads (in side-by-side comparisons) contrasts with all of the other species detailed here, and corolla coloration, fresh and dried, readily distinguishes this taxon from *N. divaricata* and *N. torreyella*.

***Navarretia torreyella* L.A.Johnson & D.Gowen, sp. nov.**

urn:lsid:ipni.org:names:60475569-2

Figs 4, 7

Type. United States of America. California: El Dorado County, Peavine Ridge Road, along left fork (11N55) about 4.7 miles from junction with Icehouse Road, 38.7961°N, 120.4770°W, 1480 m, 26 June 2013, *L.A.Johnson, R.L.Johnson, & A. Yankee 13-230* (holotype BRY! [BRY-619469]; isotypes JEPS! RSA! and to be distributed).

Diagnosis. A species similar to *Navarretia divaricata*, but distinguished by having three equal stigmatic lobes and three fully developed fruit valves, and generally larger corollas with a deep maroon distal tube and throat abruptly transitioning to nearly white or less commonly pink lobes, the lobes drying lighter than the much darker throat and tube.

Description. *Taprooted annual herbs* to 7(–10) cm tall and 14(–20) cm wide, sometimes larger, generally wider than tall. Primary stem erect, terminating in an inflorescence head 1–2(–3) cm above the cotyledons; generally greatly exceeded by secondary stems, with tertiary, and quaternary stems present on larger plants; higher order branches arise from axils of proximal inflorescence bracts, axils of leaves subtending the primary head, or less commonly, leaves within 1 cm of an inflorescence head; branches ascending to spreading and ± leafless, except for leaves subtending higher order branches or within 1 cm of a head; stem and branches reddish-brown, sparsely minutely glandular pubescent to glabrescent, less often villous, the trichomes generally less than 0.5 mm long; distal-most branches filiform, generally no more than 0.3 mm in diameter. Cotyledons two, linear, entire, united at base. **Leaves** somewhat finely stipitate-glandular proximally, less so distally; leaves at the lowermost nodes opposite, linear-filiform, and widened at the point of stem at-

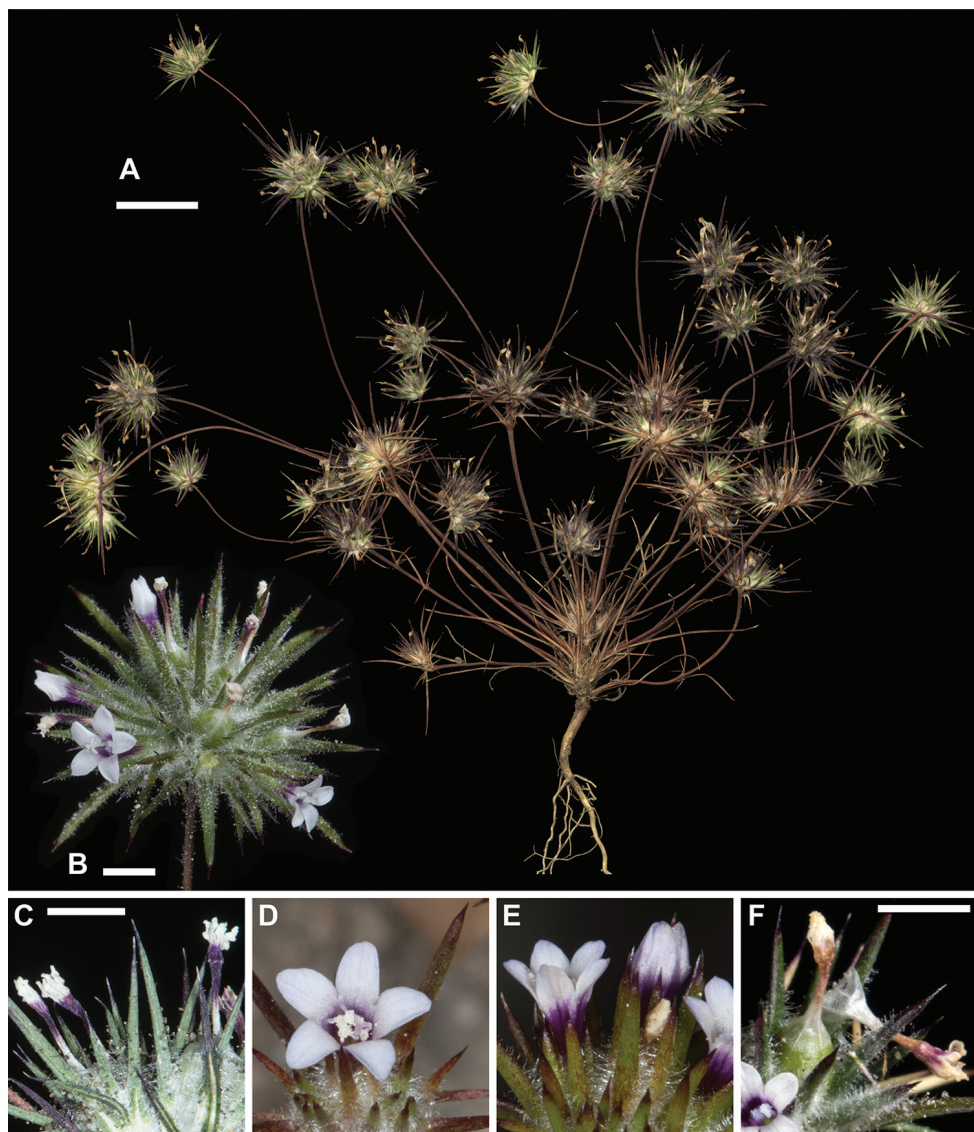


Figure 7. *Navarretia torreyella*. **A** Pressed specimen showing plant habit, scale bar = 1 cm (Johnson *et al.*, 13-230) **B** Flowering head in the field, scale bar = 2 mm (Johnson 16-008) **C–E** Equivalent magnification, scale bar = 2 mm. **C** Pressed flowering head showing coloration of dried flowers (Johnson 16-008) **D, E** Fresh flowers showing coloration (Johnson 13-218) **F** Fresh flowering head with maturing fruit, showing stretched corolla base that typically clings to fruit through maturity common in all of the species detailed herein, scale bar = 2 mm (Johnson 16-008). All photographs by L. A. Johnson and vouchers deposited at BRY.

tachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3 paired or unpaired linear lateral lobes 1–5 mm long attached along the proximal 3(–15) mm of the leaf, with an elongated, linear terminal segment. *Inflorescences* head-like, generally ≤ 10 mm

diameter (exclusive of bract tips; ~15 mm with bract tips), mostly less than 15 flowered, villous proximally, obscurely glandular. Inflorescence bracts < 10(–12) mm long, palmatifid to subpalmatifid; outermost 1–2 bracts with a short achlorophyllous base and 2–3 pairs of lateral lobes flanking an elongate terminal lobe, the distal pair of lateral lobes sometimes shorter and reflexed somewhat out of plane relative to the other lobes; bract bases become larger and clasping centripetally with lateral lobes reduced to a single pair departing from near the apex of the bract base flanking the central terminal lobe, all bract lobes chlorophyllous, entire, long tapering acute. Bracts sparsely villous abaxially, more densely villous adaxially and proximally along the lobes just above the rachis, with the distal 1/2 of each lobe more or less glabrous or with a few minute, stipitate glands. **Flowers** actinomorphic, **calyces** mostly 4.5–7.8 mm long, tube ~ 1.5–2 mm; costae entire, long tapering acute, strongly unequal to subequal with typically two costae longer than the other three; costae narrowing proximally, the shorter ones narrower at base than the intercostal membrane and the longer ones subequal with the membrane; calyx tube achlorophyllous, minutely glandular-puberulent on the intercostal membrane with the costae at least somewhat villous, the trichomes longest along the costae at the junction with the intercostal membrane, the free portion of the costae glabrous to very sparsely, obscurely, and minutely glandular distally; intercostal membrane v-shaped at sinus. **Corolla** generally ± equal to the calyx costae at anthesis but exceeding the calyx as fruit matures, narrowly funnelform, glabrous, 4.0–6.0(–6.8) mm long, lobes 0.7–1.5 mm long × 0.5–1.0 mm wide, proximal tube white, distal tube and throat maroon, abruptly transitioning to white or whitish to uncommonly pink lobes; tube base expanding and investing the fruit apex. **Stamen** filaments unequal, 0.25–1.2 mm long, inserted unequally to subequally 0.2–1.2 mm below corolla sinuses, included in throat to exerted less than half the length of the corolla lobes; pollen white (uncommonly light blue), apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. **Ovary** three-chambered, stigmatic lobes three, included in to slightly exerted from the corolla throat; capsule ~ 2.5 mm long, dehiscent circumscissally around the base with valves splitting upward. **Seeds** generally 2–5 per locule, medium brown, ovoid-angular, mucilaginous when wet. **Nuclear gene** loci showing diploid PCR amplification patterns.

Habitat, distribution, and phenology. *Navarretia torreyella* occurs on basalt flats, pyroclastic rubble, and clay soils from 1000–2100 meters elevation, in Butte, El Dorado, Nevada, Placer, Plumas, and Tehama Counties, California. Depending on latitude and elevation, it blooms from (May) June–July (September), beginning its flowering a little earlier than *N. divaricata*, and about the same as *N. crystallina*, when these taxa co-occur.

Conservation status. *Navarretia torreyella* has many occurrences throughout its range and is typically abundant when it is encountered. It is a species of Least Concern following IUCN (2012) Red List version 3.1 criteria.

Etymology. In honor of John Torrey for the plant he recognized, before others, as distinct at the species level.

Representative specimens examined (paratypes). UNITED STATES OF AMERICA. California: Butte County, about 8 miles east of Feather Falls, 1.5 miles east of Camp 18, yellow pine forest, 1000 meters, 4 June 1982, *Ahart 3533* (CAS, CHSC); About 2 road miles west of Camp Eighteen along La Porte Rd (94), then 0.2 miles north along Frey Ranch Rd, 39.6291°N, 121.1970°W, 1266 m, 10 June 2015, *Johnson & Ahart 15-022* (BRY, JEPS); About 1.2 miles east of Camp Eighteen along Lumpkin Ridge Rd, 39.6277°N, 121.1473°W, 1290 m, 10 June 2015, *Johnson & Ahart 15-028* (BRY, JEPS, RSA); 1.6 miles north of La Porte Road (and 1.8 miles south of south end of Sly Creek Reservoir Dam), T20N R8E S19, 23 June 1980, *Schlising, Ikeda, & Banchero 3765* (CHSC); Lumpkin Ridge, T21N R7E S36, 20 May 1981, *Schlising & Banchero 4059* (CHSC); Near Bull Hill Road, about 3 miles south of Butte Meadows, 1600 m, 16 August 1983, *Ahart 4303* (CHSC); Jackass Flat, Mooreville Ridge, about 1 air mile northwest of the Lost Creek Reservoir Dam, 3800 ft, 20 June 1993, *Ahart 6999* (CHSC); sides of a poor road, east of cow corral, about 200 yards north of the county road, about one mile west of the intersection of county road and Lumpkin Road, about 7 miles northeast of Feather Falls, 39.6294°N, 121.1983°W, 4204 ft, 2 July 2014, *Ahart 19551* (CHSC); Southwest end of Lumpkin Ridge, about 6.75 air miles northeast of town of Feather Falls and 1.3 miles east of the Camp 18 site on topo maps, about 300 ft southeast of USFS Rd 22N27, 2 miles east of its junction with the county road and USFS Rd 22N94 to Fall River, T21N R7E S36 SW1/4 of SE1/4, 4250 ft, 6 June 2005, *Castro 1483* (CHSC); El Dorado County, off road to Ice House Reservoir, 6.4 miles from jct. with Hwy 50, 1596 m, 38.79754°N, 120.40287°W, 30 May 2013, *Johnson 13-218* (BRY, JEPS); Along Park Creek Road, 2.8 miles from junction with Mormon Emigrant Trail, 15 May 2004, *Johnson 04-076* (BRY); Sly Park Vicinity, Park Creek Road off of county road E16, 38.7493°N, 120.4970°W, 1207 m, 8 July 2014, *Johnson 14-143* (BRY); Nevada County, Nevada City, 20–22 June 1912, *Eastwood s.n.* (CAS); Indian Springs Campground, near Cisco, 26 June 1965, *Day 65-146a* (DAV); 1.5 miles west of Cisco Grove, on a western slope above South Fork of Yuba River, 5800 ft, 21 July 1953, *Crampton 1516* (AHUC; mixed collection with *Navarretia divaricata*); Scotts Flat Reservoir on Deer Creek about 5 miles east of Nevada City, 3100 ft, 25 August 1965, *True & J. T. Howell, 2548A* (CAS); Near Grass Valley in red clay in the yellow pine and oak belt, 25 May 1919, *Heller 13197* (CAS, UC); 2 miles west of Grass Valley, gravelly meadow edges, 2350 ft, 5 June 1939, *Rose 39208* (CAS); hills northwest of Grass Valley, 2700 ft, 14 June 1967, *Rose 67134* (BRY); Spur road off north side of Hwy 20, ca. 9–10 miles from I-80 at Yuba Pass, 1565 m, 39.3171°N, 120.7514°W, 3 June 2014, *Johnson et al. 14-017* (BRY); West of meadow under power lines, about 150 yards west of paved road, southwest of Lake Spaulding, 39.3174°N, 120.6400°W, 5160 ft, 23 July 2005, *Ahart 12185* (CHSC); Small meadow near a small wash between the curve and below the bridge on old highway 80, east of Donner Pass and Donner Summit, 39.6521°N, 120.3169°W, 6767 ft, 31 July 2005, *Ahart 12227* (CHSC);

North of Hwy 20 about 8.2 miles west of I-80 ramp at intersection with road 20-16, 39.3171°N, 120.7239°W, 1617 m, 11 July 2016, *Johnson 16-015* (BRY); Placer County, Cisco, 25 June 1910, *Hall 8712* (UC); Rainbow, north of Cisco, 5700 ft, 23 June 1946, *Rose 46201* (UC); Strawberry flat, the Henderson ranch, near Indian Creek, T15N R10E S23 SW1/4 of SW1/4, 3280 ft, 24 May 1969, *Kawahara 870* (CAS); South facing slope of pyroclastic flow overlooking the North Fork of the American River, just off Sawtooth Ridge Road ca. 1.1 mile west of Dawson Spring, 39.2179°N, 120.6227°W, 1670 m, 3 June 2014, *Johnson et al. 14-028* (BRY, JEPS); Along Forest Hill Road, ca. 0.2 miles northeast of NF-66 (Humbug Canyon Rd.), 39.1605°N, 120.6618°W, 1578 m, 3 June 2014, *Johnson et al. 14-048* (BRY, JEPS); Off of Sugar Pine Road (NF10) enroute to Sugar Pine Reservoir, ca. 3.6 miles from Forest Hills Road, 1181 m, 39.1239°N, 120.7588°W, 9 June 2015, *Johnson 15-013* (BRY); 50 yards northeast of the small natural lake, on the east side of the paved road to Lake Valley Reservoir, about 1/4 mile east of Yuba Gap and Highway 80, 39.3158°N, 120.6039°W, 5840 ft, 22 July 2002, *Ahart 9896* (CHSC); Plumas County, south of Cascade and Lava Top, access via FS road 21N22YA, 39.6827°N, 121.1665°W, 1402 m, *Johnson & Ahart 15-023* (BRY, JEPS, RSA); Along Lumpkin Ridge-La Porte Rd, ca. 6.9 miles northeast of junction with Golden Trout Crossing, 39.6982°N, 121.0783°W, 1541 m, 10 June 2015, *Johnson & Ahart 15-030* (BRY, JEPS, RSA); About 1/4 mile north of Lumpkin Ridge Road, on Lumpkin Ridge, about 4 air miles northeast of Camp 18, 39.6856°N, 121.1061°W, 5013 ft, 3 July 2006, *Ahart 12905* (CHSC, JEPS); North side of Onion Valley, east of Quincy La Porte Road, about 1 mile northwest of Pilot Peak, T22N R10E S5 SE1/4, 6000 ft, 13 September 1995, *Ahart 7640* (CHSC); About 100 yards north of the paved basalt road, about 3.75 air miles northwest of Tamarack Flat, about 5.75 air miles northwest of Little Grass Valley Reservoir, 39.7615°N, 121.0980°W, 5507 ft, 9 July 2006, *Ahart 12929* (CHSC); West edge of top of Goat Mountain, 0.7 km southeast of the southeast side of Little Grass Valley Reservoir, 39.7181°N, 120.9664°W, 1721 m, 6 July 2011, *Janeway 10497* (CHSC); Tehama County, across fence on southwest side of Hwy 36 about 5.1 miles west of jct with Hwy 32, 40.3278°N, 121.4735°W, 1459 m, 26 June 2017, *Johnson & Johnson 17-042* (BRY).

Notes. *Hall 8712* (UC) describes this collection as faintly malodorous though we have not detected a scent ourselves in this taxon. The *Shelton s.n.* syntype of *Gilia divaricata* Torr. ex Gray belongs here.

When growing with *N. divaricata*, a subtle difference in habit and coloration is discernable, with *N. torreyella* somewhat more spreading, its primary inflorescence head closer to the ground, and the plants overall more anthocyanic (purple tinged); however, as these features can vary in both taxa, they should not be relied upon for determination. Instead, corolla coloration of both fresh and dried flowers as outlined in the diagnosis distinguishes *N. torreyella* from all of the species treated herein. This taxon also has the thinnest, most filiform branches of the species considered here.

Key to the taxa formerly treated as *Navarretia divaricata*

- 1 Corollas 3.5–5 mm, lobes white or the tips tinged pink to lavender when fresh, drying pink (generally much darker than throat and tube), tube and lower throat yellowish when fresh, similar when dried (sometimes streaked with red); stigmas minute with 2 of 3 lobes fused almost to tips, fruit with 1 (of 3) valves half as wide and lacking a septum..... ***N. divaricata***
- Corollas 4–8(+) mm, commonly with blue, lavender, pink, or whitish lobes and similar or darker maroon throat when fresh, drying with lobes and throat blue to purplish, or whitish lobes with reddish-streaked or dark maroon throat; stigmas equally 3-lobed; fruit equally 3-valved, each bearing a septum..... **2**
- 2 Corollas bicolored when fresh with white or less commonly pink lobes abruptly transitioning to a dark maroon throat, drying in similar manner; distal half (or more) of inflorescence bract lobes and calyx costae glabrous or nearly so ***N. torreyella***
- Corollas variously concolored to bi- or tri-colored when fresh with transition between lobes and throat gradual, bluish, bluish- or pinkish-lavender, or less commonly white, drying in like manner or with darker and/or reddish-streaked throat; distal half of inflorescence bract lobes and calyx costae generally glandular **3**
- 3 Largest inflorescence heads exclusive of bract lobes ≤ 10 mm diameter (≤ 15 mm with bract lobes), conspicuously glandular proximally and distally (some villous trichomes present proximally); branches filiform (± 0.3 mm diameter), trichomes mostly < 0.5 mm, sometimes wanting; corollas 4–6 mm, blue (generally with blue pollen) or whitish (with white pollen) ***N. aeroides***
- Largest inflorescence heads exclusive of bract lobes mostly ≥ 12 mm diameter (≥ 18 mm with bract lobes), \pm villous proximally, glandular distally; branches more robust (± 0.5 mm), trichomes commonly > 1 mm; corollas 5–8(+) mm, bluish-lavender or pinkish-lavender, pollen blue or white..... **4**
- 4 Corolla generally 5–7 mm, bluish or bluish-lavender when fresh distally with whitish to yellowish tube, pollen blue; inflorescence heads often more glandular than villous; plants mainly west of the Central Valley in the North Coast and Klamath Ranges (uncommon in Butte County) ***N. vividior***
- Corolla generally 6–8(+) mm, pinkish-lavender when fresh distally with yellowish tube, pollen white (uncommonly blue); inflorescence heads often more villous than glandular; plants mainly east of the Central Valley in the Modoc Plateau and Cascade Ranges, disjunct in San Benito County ***N. modocensis***

Methods

Herbarium specimens were examined directly or via high resolution scanned images of herbarium sheets; scans are indicated as such in specimen citations. Specimen collections were examined from UC, JEPS, DAV, AHUC, RSA, POM, CHSC, IDS, BRY, HSC, CAS, ORE, OSC, and WTC. Single or small groups of particular specimens of interest were provided by GH, NDG, NY, RENO, US, and UBC. Specimens examined also included material gathered from our own field work (deposited at BRY, JEPS, or both). Working iteratively between herbarium specimens, field work, and laboratory examination, taxonomic hypotheses were refined following the unified species concept (de Queiroz 2007). For *Navarretia divaricata* only, the distribution map (Fig. 2) was compiled by augmenting examined specimens with data obtained from CDA, CIC, DS, HJAEFB, ID, RM, SOC, SRP, WS, and YM as searchable via the Consortium of California Herbaria (<http://ucjeps.berkeley.edu/consortium/>) and the Consortium of Pacific Northwest Herbaria (<http://pnwherbaria.org>). Digital photographs were used to verify determinations of the online records when available, particularly with questionable occurrences in disjunct locations; questionable occurrences were not mapped.

Morphologically, specimens were grouped under the framework of population aggregate analysis/specimen aggregate analysis (Davis and Nixon 1992, Snow et al. 2003). Specimens were examined for qualitative or quantitative features useful for distinguishing among taxa. Digital calipers were used for larger features, while smaller features were measured from digital images taken with an Olympus SZX-12 dissecting microscope using CellSens software (Olympus Soft Imaging Solutions Corp.). All corolla measurements were taken from flowers post-anthesis with expanding to fully mature fruits, after first boiling for ~ 30 seconds and keeping the tissue rehydrated in Pohl's solution (Pohl 1965).

DNA sequences were examined in the context of exclusivity (Brower 1999), with an emphasis on shared patterns across independent loci given that any single locus may violate this principle in recently diverging groups due to lineage sorting or other recognized biological processes. DNA sequence data was initially obtained from 66 accessions representing 10 species as defined herein. This sampling included 11 accessions of *Navarretia divaricata* and 43 accessions representing the various taxa formerly recognized as *Navarretia divaricata* subsp. *vividior* from localities representing the geographic distribution of each taxon. This dataset was simplified a posteriori to include just six accessions of each taxon in the *Navarretia divaricata* complex and a single representative of five related species, selecting accessions that represent the range of genetic variation observed while eliminating much redundancy in the dataset. Focusing on species delimitation rather than phylogenetic reconstruction, the five additional species included in the analyses are morphologically most similar to the focal taxa: *N. crystallina*, *N. filicaulis* (Torr. ex A.Gray) Greene, *N. miwukensis*, *N. peninsularis*, and *N. prolifera*. A concatenated chloroplast matrix was constructed from the 5' *trnK* intron and 5' portion of *matK* (Johnson and Soltis 1995, Johnson and Johnson 2006), *trnL-trnL-trnF* intergenic spacer and intron (Taberlet et al. 1991), *trnS-trnG* inter-

genic spacer (Hamilton 1999), and *rpl16* regions (Small et al. 1998). A matrix from the nuclear ribosomal ITS1, 5.8s, and ITS2 region (White et al. 1990, Porter 1996) was also constructed. For these matrices, amplification primers as described in the papers just cited were used in PCR reactions consisting of 30 cycles of 95°C for 1 min, 52°C for 1 min, and 72°C for 1 min. PCR amplicons were cleaned using PrepEase PCR purification plates (Affymetrix, Santa Clara, California, USA) prior to sequencing with BigDye vs 3.1 (Applied Biosystems/Thermo Fisher Scientific, Waltham, Massachusetts, USA). Sequenced products were cleaned with Sephadex and run on an AB 3730 xl DNA sequencer in the DNA Sequencing Center at Brigham Young University. Three additional matrices from low copy nuclear genes were also constructed: *pistillata* (Johnson et al. 2012) and two paralogs of isocitrate dehydrogenase (Weese and Johnson 2005; Johnson and Johnson 2006). To simplify data acquisition and cloning, new taxon-specific primers were designed for this study to amplify 600–800 bp segments of these low copy regions that included introns and exons: *PIdu1F* 5'-TGGGTACTCAT-AGGTTGGTTGA-3'; *Pidu1R* 5'-TGCAAGGAGAGACTTACCTGA-3'; *idhAdv1F* 5'-AGCAATCAAGTGTGCGACAA-3'; *idhAdv1R* 5'-AGCGGCCACTTCTTCTGATA-3'; *idhBdv354F* 5'-CTGCAGATGAAGCTCGTATGG-3'; *idhBdv1082R* 5'-CGTAAGCTGTGGTCATCGAA-3'. For these low copy nuclear regions, a touch-down PCR protocol was employed starting with a 62°C annealing temperature and decreasing 1°C each cycle until reaching 52°C, then repeating 29 additional cycles with a 52°C annealing. When multiple copies were evident from direct sequencing attempts that made chromatograms unreadable (nuclear regions only), PCR amplicons were first purified using PrepEase PCR purification plates, resuspended in 30 µl water, then cloned via TOPO TA for sequencing kits (Invitrogen/ThermoFisher Scientific, Waltham, Massachusetts, USA), with generally eight colonies per cloning reaction subsequently re-amplified via PCR with standard M13 primers and these amplicons sequenced. Sequences have been deposited in GenBank (Appendix 1). Sequence matrices were aligned by eye using AliView (Larsson 2014). Unweighted parsimony analyses using PAUP* 4.0b10 (Swofford 2003) with 10,000 random addition replications, collapsing branches with minimum length of zero, and assessing support with 100,000 bootstrap replications using fast stepwise addition were performed for each matrix and the results from the separate analyses compared by eye.

Results

The concatenated cpDNA matrix consisted of 35 terminals and 4428 nucleotide characters, of which 51 are parsimony informative. Parsimony analysis of this matrix recovered a single topology of 111 steps (Fig. 8A; CI = 0.96; RI = 0.99).

The nrITS sequence matrix consisted of 37 terminals with two populations of *N. vividior* represented by distinct sequences recovered after cloning the original PCR fragments; the remaining four populations of *N. vividior* provided clean reads from direct sequencing of the original PCR products and were not cloned. This matrix was 631

nucleotide characters in length of which 36 were parsimony informative. Parsimony analysis of this matrix recovered 206052 topologies of 66 steps, which narrowed to eight unique topologies after collapsing branches with a minimum length of zero and then filtering to retain only the shortest trees (still of 66 steps; Fig. 8B; CI = 0.82; RI = 0.95).

The *idh-A*, *idh-B*, and *PI* matrices each contained 41 terminals, with each of the six populations of *N. vividior* represented by two distinct sequences recovered following cloning of the original PCR products. Some cloned fragments were clearly chimeras of the two primary sequences with a single break point in each fragment that varied in location among fragments, indicating these chimeras were generated within the PCR reactions. The *idh-B* matrix contained 729 nucleotide characters of which 55 were parsimony informative. Parsimony analysis of this matrix recovered a single topology of 113 steps (Fig. 8C; CI = 0.95; RI = 0.99). The *idh-A* matrix contained 880 nucleotide characters of which 117 were parsimony informative. Parsimony analysis of this matrix recovered 108 topologies of 220 steps, which reduced to 13 after condensing to remove branches with a minimum length of zero and filtering to retain only the shortest topologies (Fig. 8D; CI = 0.87; RI = 0.96). The *PI* matrix contained 646 nucleotide characters of which 35 were parsimony informative. Parsimony analyses recovered 32 topologies of 83 steps which reduced to nine after condensing to remove branches with a minimum length of zero and filtering to retain only the shortest topologies (Fig. 8E; CI = 0.81; RI = 0.95).

Discussion

DNA-based inferences. In all DNA sequence-based topologies, using markers representing the chloroplast genome and four putatively unlinked nuclear loci (Fig. 8), *Navarretia divaricata* forms an exclusive group well separated from any of the material previously recognized as *N. divaricata* subsp. *vividior*. Though sequences representing the latter taxon form an exclusive group in chloroplast and nuclear ITS sequences, this larger exclusive group is divided into smaller exclusive groups that also appear, with two exceptions, as exclusive groups in each of the three low-copy nuclear gene data sets (i.e., *idh-B*, *idh-A*, and *PI*; Fig. 8). The two exceptions involve *N. vividior* as defined herein, and *N. torreyella*. Sampled populations of *N. vividior* all contained two homeologs in the low copy nuclear gene data sets: one that clusters with *N. modocensis*, and one that clusters with *N. aeroides*. This is an expected pattern for a plant of allopolyploid origin. The placement of *N. vividior* in the cpDNA tree (Fig. 8A) solely near *N. aeroides* indicates *N. aeroides* (or its ancestral lineage) was the maternal parent in the formation of *N. vividior*, whereas *N. modocensis* (or its ancestral lineage) was the paternal parent. Gene conversion in the nrITS region in some populations of *N. vividior* has fixed, or nearly fixed this locus in favor of the paternal parent (Fig. 8B), which often happens over time in allopolyploids (e.g., Johnson and Johnson 2006). Allopolyploidy in *N. vividior* is consistent with the chromosome count of $2n = 36$ recorded by Crampton for plants collected not far from the type locality (Crampton 494B [AHUC-038375!

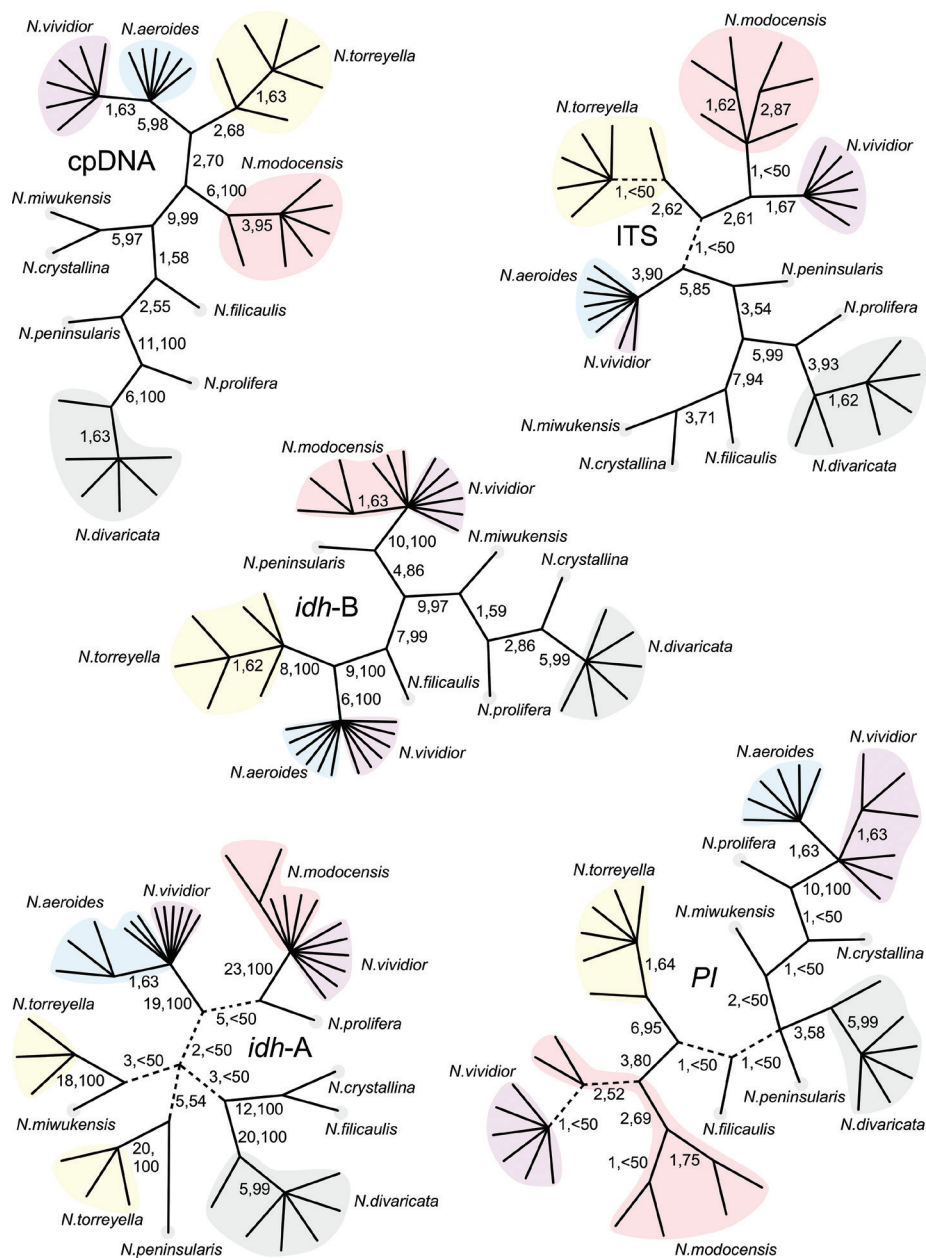


Figure 8. Representative most parsimonious, unrooted trees inferred from analysis of DNA sequence data. Base substitutions are reconstructed along interior branches, followed by bootstrap support values. Shaded regions around terminal branches circumscribe individuals of the same taxon, using colors for *Navarretia vividior*, *N. modocensis*, *N. aeroides*, and *N. torreyella* that correspond with the colors of symbols used in Fig. 4. Branches not found in all most parsimonious topologies for each region are represented by dashed lines. **A** Single topology inferred from concatenated cpDNA sequences **B** One of eight topologies inferred from nrDNA ITS sequences **C** Single topology inferred from nuclear *idh-B* sequences **D** One of 13 topologies inferred from nuclear *idh-A* sequences **E** One of nine topologies inferred from nuclear *PI* sequences.

UCD-36041!]. In the *idh-A* data set (Fig. 8D), *Navarretia torreyella* failed to form an exclusive group, a pattern that may be interpreted as incomplete lineage sorting in this single locus; the two groups do not correlate with geography and though we did not test it specifically, we suspect that both alleles likely reside within single populations given the geographic proximity of plants from which divergent alleles were sampled. In summary, DNA sequence data support the recognition of five distinct species in what has heretofore been considered a single species with two subspecies.

Comparative morphology with similar species. With the exception of *Navarretia filicaulis*, all of the species included in this study share a common branching architecture. They also share features of flower and fruit that distinguish them from other *Navarretia*. The branching architecture consists of a short primary stem terminating in a head-like inflorescence with elongate, more or less leafless secondary stems arising from leaf or outermost bract axils at the base of the inflorescence. Each secondary stem terminates in a head-like inflorescence with tertiary, and even quaternary stems similarly arising from the axils of the outer inflorescence bracts of the higher-order inflorescences, or from leaves that occasionally appear within one cm of an inflorescence (Figs 1, 3, 5–7). When well branched, this pattern gives rise to plants that are typically wider than tall. All species can produce depauperate plants consisting of a single head, and *N. divaricata* sometimes produces plants that are noticeably taller than wide—perhaps when vegetation is dense. Following pollination, it is common in these species for the corolla to detach from the receptacle but remain vested around the upper half of the enlarging fruit, with the corolla base stretched greatly. Spent corollas thus typically adhere to the fruit through maturation rather than being pushed off by the expanding fruit as is common in other *Navarretia*. The fruit detaches circumscissally about its base with the valves separating more or less from the base to the apex. These flower and fruit characteristics are shared by *N. filicaulis* that may even, uncommonly, branch divaricately from the lowermost inflorescence bracts. *Navarretia prolifera* (two subspecies) are distinguished from the species elaborated here by possessing larger flowers with long-exserted stamens. *Navarretia crystallina* and *N. miwukensis*, recently described, vary in their inflorescence architecture by having flowers inserted directly on a common receptacle (Johnson et al. 2016). *Navarretia peninsularis*, at one time placed as a variety of *N. divaricata* (Jepson 1943), is distinguished by having broader terminal lobes to its leaves and bracts and wider calyx costae. Similarity in overall plant size, habit, and diminutive flowers, combined with the absence of analytical study beyond that conducted by Jepson and Bailey (Jepson 1943), have undoubtedly contributed to the view that *N. divaricata* as heretofore defined represents a single species.

Recognition of near-cryptic species. Morphology and one's perception has been the guiding force of species delimitation for centuries. Though some may not admit it, many botanists in the field are sympathetic to Cronquist's (1978) view that "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (often interpreted as a 10× hand lens). That some plants can distinguish their own pollen versus that from a genetically different individual in the same population demonstrates that organisms can perceive what our eyes cannot. It

should not, then, be surprising that different species (i.e., independent evolutionary lineages with distinct trajectories) may be distinguishable genetically by the organisms themselves and biologists with appropriate tools, despite little or no discernable morphological differentiation. This may be inconvenient for field taxonomists, and recognition of such species may be challenging by human eye, yet the taxonomic recognition of biological reality is still merited (Judd et al. 2007; Carolan et al. 2012; Jörger and Schrödl 2013). Withholding taxonomic recognition for cryptic or nearly cryptic species may simplify the placing of a name on an entity by sight, yet also compromises our understanding of diversity via inaccurate estimates of species diversity, superficial understanding of diversification patterns and processes, and inaccurate assessments of species abundance and ecological preferences.

Over several years of field work without observing hybrid swarms or convincing intermediate forms, we suspected that *Navarretia vividior* was a species distinct from *N. divaricata*. In the process of sampling broadly across these species' ranges, the distinctiveness of *N. torreyella* soon came into focus both morphologically and molecularly. Though similar in many respects, it would be inaccurate to characterize *N. divaricata*, *N. vividior*, and *N. torreyella* as truly cryptic—they can be readily diagnosed via observable morphological differences that can be articulated in a dichotomous key. Either *N. modocensis* or *N. aeroides* could replace *N. vividior* in the above three-way species comparison with little to no editing of the dichotomous key (depending on feature choice). The challenge, morphologically, is in distinguishing between *N. vividior*, *N. modocensis*, and *N. aeroides*. Among these latter three species, *N. aeroides* is most distinctive and may be appropriately considered “near-cryptic”; it is discernable from *N. modocensis* in features relating to the corolla and inflorescence size, and inflorescence glandularity. Nevertheless, the morpho-space distinguishing *N. aeroides* from *N. modocensis* is narrow. Consequently, their allopolyploid derivative, *N. vividior*, has a limited morpho-space for intermediacy by which it can be distinguished from its parents, and in that limited space, it lies closer to *N. modocensis*, its paternal parent, than to *N. aeroides*, but overlaps with both. *Navarretia vividior* and *N. modocensis* are the closest of several morphologically similar species pairs we have investigated (e.g., Johnson et al. 2013, 2016) to being truly cryptic. It is not surprising that the distinctiveness of these taxa has been overlooked in the past, and we recognize that difficulty exists in differentiating these species, particularly in their pressed and dried condition on herbarium sheets.

Geographic distribution and syntopy. The taxonomy proposed herein alters our understanding of species distributions and abundance. In its broad distribution that largely encompasses the ranges of the other taxa (compare Figs 2, 4), *Navarretia divaricata* is known to co-occur with *N. modocensis* and *N. torreyella* in many locations, and with *N. aeroides* and *N. vividior* in at least some locations. It can also be found with many other *Navarretia*, including *N. leptalea*, *N. breweri*, *N. capillaris*, *N. linearifolia*, *N. propinqua*, *N. intertexta*, *N. crystallina*, *N. miwukensis*, and *N. prolifera* in portions of its range.

The distribution of *N. vividior* is narrowed to predominantly the North Coast Range, with the exception of apparent occurrences in the foothills of the northern Sierra Nevada/southern Cascade Range in Butte County, California where it may co-

Table 1. Comparison of features among the species treated in this paper. Uncommon variation is listed in parentheses.

	<i>N. divaricata</i>	<i>N. torreyella</i>	<i>N. aevoides</i>	<i>N. vividor</i>	<i>N. modocensis</i>
Stem indumentum	Glabrous to sparingly pubescent, glabrescent; uncommonly pubescent	Glabrous to sparingly pubescent, glabrescent; uncommonly pubescent	Glabrous to pubescent, sometimes glabrescent; trichomes generally less than 0.5 mm	Pubescent; trichomes generally ± 1 mm (glabrescent)	Pubescent; trichomes generally ± 1 mm (glabrescent)
Inflorescence indumentum	Villous; obscurely and minutely glandular; distal half of bract and calyx tips ± glabrous to sparsely minutely glandular	Villous; obscurely and minutely glandular; distal half of bract and calyx tips ± glabrous to sparsely minutely glandular	Conspicuously glandular including distal half of bract and calyx tips; some villous trichomes proximally	Overall more glandular than villous; somewhat villous proximally; distal half of bract and calyx tips ± glandular	Overall more villous than glandular; usually conspicuously villous proximally; distal half of bract and calyx tips ± glandular
Calyx tube pubescence (proximal 3/4)	Puberulent and some villous hairs along costae	Puberulent and some villous hairs along costae	Puberulent	Puberulent and some villous hairs along costae	Puberulent and some villous hairs along costae
Corolla coloration	Proximal tube white, distal tube and throat yellow, sometimes red-streaked, transitioning to white lobes suffused with pink or lavender at tips; lobes drying pink	Proximal tube white, distal tube and throat maroon, abruptly transitioning to whitish (pink) lobes; corolla drying similarly	Tube white, lobes and throat bluish; drying bluish purple—or throat and lobes white; throat and lobes drying white to light blue with brownish to magenta streaked distal tube	Tube white proximally, distal tube white or yellow, throat bluish, sometimes streaked with magenta, lobes medium bluish-lavender; similar or darker when dried	Tube white proximally, yellow distally, throat lavender-purple or purplish streaked, lobes light to dark pinkish-lavender; similar or darker changing toward blue when dried
Corolla length	3.5–5 mm	4–6(–6.8) mm	4.2–6 mm	5–7.2 mm	6–8.2 mm
Corolla lobes	0.6–1.0 mm long × 0.4–0.9 mm wide	0.7–1.5 mm long × 0.5–1.0 mm wide	0.75–1.3 mm long × 0.5–0.9(–1.0) mm wide	0.8–1.1(–1.4) mm long × 0.6–0.9(–1.2) mm wide	(1.0–)1.2–1.5(–1.95) mm long × 0.8–1.4 mm wide
Pistil	2 of 3 stigma lobes nearly entirely fused, one valve partially abortive	3 equal lobes, 3 equal valves	3 equal lobes, 3 equal valves	3 equal lobes, 3 equal valves	3 equal lobes, 3 equal valves
Ovules	5–9 (12)/fruit	2–5/locule	4–8/locule	5–7(8)/locule	4–9/locule
Largest inflorescence head diameter (excluding bracts)	≤ 10 mm	≤ 10 mm	≤ 10 mm	≥ 12 mm	≥ 12 mm
Pollen color	White	White (light blue)	Blue or white, matching corolla	Blue (white rarely?)	White (blue)
Scent (fresh)	Indistinct	Indistinct	Skunky	Skunky	Skunky
Ploidy	Diploid	Diploid	Diploid	Allotetraploid	Diploid

occur with *N. modocensis* (Fig. 4). In Trinity County, California, it co-occurs with *N. aeroides* in at least two locations and at times with *N. divaricata*. We have also collected *N. vividior* growing with *N. atractylodes*, *N. mellita*, *N. squarrosa*, *N. intertexta*, *N. lecucocephala*, *N. subuligera*, and *N. linearifolia*.

Navarretia modocensis' distribution extends beyond the Modoc plateau (Fig. 4). It overlaps with a portion of the range of *N. torreyella* (Fig. 4), though we have not found them co-occurring (both have been collected in the Butte Meadows area). We also have yet to find *N. modocensis* co-occurring with *N. aeroides* or *N. vividior*, though such locations might exist in Butte County, California. We have collected *N. modocensis* with *N. atractylodes*, *N. breweri*, *N. divaricata*, *N. filicaulis*, *N. intertexta*, *N. propinqua*, *N. subuligera*, *N. sinistra*, and *N. linearifolia* in the principle portion of its range, and the disjunct occurrence in San Benito county was co-occurring with *N. mellita*.

The distribution of *Navarretia aeroides* covers considerable geographic area (Fig. 4), yet it has been seldom collected, with over half of the occurrences known only from historical collections over 60 years old. Occurrences appear to be highly fragmented and localized. Awareness of this taxon will undoubtedly aid efforts to better define its abundance. All occurrences in the North Coast Range that we are aware of have been pale (whitish) flowered individuals with white pollen that contrast sharply with the larger and hairier-headed *N. vividior* with its blue flowers and blue pollen when the two co-occur. Besides *N. vividior*, we have observed *N. aeroides* co-occurring with *N. atractylodes* and *N. intertexta* in the North Coast Range, and with *N. divaricata*, *N. filicaulis*, *N. propinqua*, *N. prolifera* subsp. *lutea*, *N. miwukensis*, *N. leptalea* subsp. *leptalea*, in addition to growing near *N. torreyella* in the Sierra Nevada. The latter occurrence, observed in July, found *N. aeroides* on one side of a dirt 4WD road in bloom with *N. divaricata* and *N. prolifera* subsp. *lutea*, while *N. torreyella* occurred completely senesced in monoculture on the opposite side of the road.

Though *N. torreyella* has the smallest geographic distribution of the species considered here (Fig. 4), it occurs abundantly both in number of individuals per occurrence and number of occurrences within its range. It grows intermixed with *N. divaricata* in many locations and herbarium sheets of mixed collections originally determined as either *N. divaricata* subsp. *divaricata* or *N. divaricata* subsp. *vividior* exist. *Navarretia propinqua*, *N. prolifera* subsp. *lutea*, *N. crystallina*, and *N. leptalea* subsp. *leptalea* also co-occur at times, and at least one observation exists of it growing near *N. aeroides* as described above.

Butte County, California collections. Several collections housed at CHSC are intriguing because they compare favorably with either *N. modocensis* or *N. vividior*—and *N. vividior* is otherwise found only on the west side of the central valley. Occurring at somewhat lower elevations, in a hotter environment in the transition between the northern Sierra Nevada and southern Cascade Range, some of these occurrences flower earlier than typical for both *N. modocensis* and *N. vividior*. Because of their parent/offspring relationship and the difficulty at times in distinguishing these two species on herbarium sheets, we have attempted to relocate these populations over the past several years with limited success because of drought, private property access, and possibly invasive species density. For example, in 1980, *Schlising & Azevedo* 3699 col-

lected *N. modocensis* at an ecotone that we visited in 2015; the area was extremely dry and though *N. filicaulis* was found in abundance, a thorough search found no sign of *N. modocensis*. A return visit in 2017, following closer to normal precipitation in the preceding Fall and Winter months (<http://www.usclimatedata.com>) found the area to be lush, and both *N. modocensis* and *N. filicaulis* present in abundance (Johnson 17-027, BRY). On the other hand, no sign of *N. modocensis* could be found at the site of Jokerst et al. 462 in 2017, yet the species was described as common when collected in 1979 growing with *N. tagetina*, which was found in abundance in 2017. Oswald 578 documents what we have determined to be *N. vividior* along the north rim of Upper Bidwell Park in 1983 following a burn. In 2017, *N. intertexta*, *N. pubescens*, *N. tagetina*, and *N. viscidula* were observed in abundance hiking the entire length of the north rim trail without trace of *N. vividior*, but many areas of possible habitat were covered with dense, near monotypic stands of *Centaurea solstitialis* L. growing through considerable plant litter from previous years. Efforts to contact land-owners for property access permission may enable occurrences that have not been recollected (to our knowledge) in the last 30–40 years to be relocated and assessed to see if any represent mixed populations along Cohasset Road (Schlising 3435, Ikeda 383, Oswald 1999), near Paradise (Ahart 1906), and along Ponderosa Way (Taylor 1393, Oswald 3773).

Additional notes on the syntypes for *Gilia divaricata* Torr. ex Gray

Rattan s.n.—Volmey Rattan, a notable student of the California and Pacific Coast flora and accomplished teacher (Jepson 1928) contributed two collections to the California Geological Survey between 1860–1867 of what is now considered *Navarretia prolifera*. Though the syntype at NY (mounted on the same sheet as the syntypes *Mr. Shelton s.n.* and *Mrs. Davis 49*) lacks a collector's number, Rattan did number his collections. *Rattan 7*, collected at Reservoir Hill, Placerville (some labels read “San Francisco” instead of Placerville, an erroneous later labeling by an unknown hand) is equated to *Bolander 6422*, or simply labeled 6422. The number 6422 is Henry N. Bolander's field book number. Bolander served as the state botanist for California for several years beginning in 1864 and played a prominent role in documenting plants as part of the California Geologic Survey (Jepson 1898). In his field notes, Bolander records, “6417–6462 Mr. Rattan's collection It was my intention to renumber his plants; but was obliged to give it up being pressed too much by work” (unpublished field notes courtesy of GH). *Rattan 45* (= *Bolander 6436*) is from an uncertain locality. These specimens were apparently sent first to US, then distributed from there, with some material reaching A. Gray. *Rattan 7* compares favorably with *N. prolifera* subsp. *lutea* (yellow lobed), while *Rattan 45* compares favorably with *N. prolifera* subsp. *prolifera* (blue to purple lobed). Though subsp. *lutea* can dry with bluish lobes, fresh material is distinct. The syntype material at NY! [NY-00336830] appears to have one of each of Rattan's collections, with a note in Gray's hand “Fls. yellow ? & purple”. The material at K [K-000769074] also has one of each, flanking *Bolander 4098*, with a note by Gray indicating “...also

Rattan". We have located isosyntypes (labeled variously as indicated above) at UC (scan!), DS (scan!), KEW (scan!), NY!, and US (scan!).

Torrey 302—In 1865, John Torrey took a joint business and pleasure trip to California to see living specimens of plants he was familiar with only as pressed specimens (Robbins 1968). Among the plants he collected on this trip, we located two sheets [GH-00274982 (scan!) & NY-00336832 (scan!)] of *Torrey 302*, each with one mounted specimen of this collection, though as many as five specimens may have been collected with the intent of one being kept for his own herbarium, one sent to Asa Gray, one for the Smithsonian, one (perhaps) for Kew, and the fifth to be distributed as determined later (Robbins 1968). Both sheets have printed labels with the location and date provided by Torrey. The specimen now at NY was originally part of Torrey's Herbarium and in his hand-writing reads simply, "*Navarretia*", whereas the specimen at GH was left blank by Torrey. Both specimens, in purple ink and Gray's handwriting, are annotated as *Gilia divaricata* Torr. It is possible that Torrey did not consider this plant conspecific with the syntype that follows, which he also had in his possession.

Shelton s.n.—Christopher Shelton was a well-known local botanist credited with bringing the first honey-bees to California. Though his collection is undated and lacking a location, it must have been collected in 1852 or earlier because he was killed aboard the steamboat *Jenny Lind* when it exploded in San Francisco Bay in April 1853 (Ewan 1981). The handwriting denoting the name of this specimen on the type sheet is attributed to Torrey; the indication that the specimen is an isotype was likely added by Cronquist. The lower right corner of the sheet bears the writing "California Mr. Shelton" also in Torrey's hand, with a second note of uncertain authorship written below "Also in Herb. Gray – marked 'Sierra Nevada, Calif. Rattan.'" We interpret this latter note, not in Torrey's hand, as indicating that Rattan's collection (mounted on the same sheet) is to be found in GH, marked Sierra Nevada (though we have not located such a specimen). The common interpretation has been that this second note is referring to the province of Shelton's collection—an interpretation that can be disputed given the reference to Rattan and the uncertain authorship. Nevertheless, as noted above, the morphology of Shelton's collection matches plants known only from the Sierra Nevada. How and when this specimen came into Torrey's possession before being passed on to Gray is unknown to us.

Bolander 4908—Henry Bolander was an important botanist of the California flora in the mid 1800s. He collected this specimen between 14 June and 17 July 1866 in Yosemite Valley as part of his work with the California Geologic Survey, and in the company of Clarence King's survey of Yosemite (unpublished field notes courtesy of GH; Jepson 1898). This collection was widely distributed with specimens located at YALE (scan!), US (scan!), UC!, GH (scan!), NY!, K (scan!).

Mrs. Davis 49—Nancy Jane Davis was principal of the Birmingham School in Pennsylvania for 60 years (Jepson 1934), and collected plants primarily in the eastern United States. This specimen was collected in July 1867 from Nevada County, on the first of three visits to California. The appellation "Mrs." was applied by Gray, who received many of her collections; the original label for the syntype reads, "N. J. Davis," while other collections of hers read, "Miss N. J. Davis."

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Appendix I

Voucher specimens and GenBank accession numbers used in DNA sequence analyses. Information is presented alphabetically by species in two groups (non-focal species, focal species) in the following order: **Taxon:** collector(s) & collection number, nrITS, *PI*, *idh-A*, *idh-B*, *trnK*, *matK*, *trnL*, *trnS*, *rpl16*. For the tetraploid *N. vividior*, where two homeologs were obtained from nuclear regions, the accession numbers for each homeolog are included within parentheses. GenBank numbers prefixed with MG are new to this study; those prefixed with KX are from Johnson et al. (2016). Those prefixed with HQ are from an unpublished thesis from the first author's lab (Green 2010). All vouchers are deposited at BRY.

Non-focal species. *Navarretia crystallina* L.A.Johnson & D.Gowen: Johnson et al. 14-030, KX017878, MG022355, MG022227, MG022268, KX017924, KX017856, KX017946, KX017968, KX017902. *Navarretia filicaulis* (Torr. ex A.Gray) Greene: Johnson 04-068, HQ116860, HQ116921, MG022228, MG022269, HQ117005, HQ116961, HQ117085, HQ117046, KX017897. *Navarretia miwukensis* D.Gowen & L.A.Johnson: Johnson et al. 14-067, KX017881, MG022356, MG022229, MG022270, KX017927, KX017859, KX017949, KX017971, KX017905. *Navarretia peninsularis* Greene: Johnson & Zhang 05-116, HQ116864, HQ116926, MG022230, MG022271, HQ117010, HQ116965, HQ117089, HQ117050, MG022182. *Navarretia prolifera* Greene: Johnson 09-065, KX017873, MG022357, MG022231, MG022272, KX017919, KX017851, KX017941, KX017963, KX017896.

Focal species. *Navarretia aeroides* L.A.Johnson & D.Gowen: Johnson 09-109, MG022309, MG022358, MG022232, MG022273, MG022205, MG022333, MG022394, MG022416, MG022183. Johnson 14-142, MG022310, MG022359, MG022233, MG022274, MG022206, MG022334, MG022395, MG022417, MG022184. Johnson 15-005, MG022311, MG022360, MG022234, MG022275, MG022207, MG022335, MG022396, MG022418, MG022185. Johnson 15-065, MG022312, MG022361, MG022235, MG022276, MG022208, MG022336, MG022397, MG022419, MG022186. Johnson 16-063A, MG022313, MG022362, MG022236, MG022277, MG022209, MG022337, MG022398, MG022420, MG022187. Gowen 1303, MG022314, MG022363, MG022237, MG022278, MG022210, MG022338, MG022399, MG022421, MG022188. *Navarretia divaricata* Greene: Johnson & Johnson 94-049, KX017870, MG022364, MG022238, MG022279, KX017916, KX017848, KX017938, KX017960, KX017892. Johnson 94-065, KX017865, MG022365, MG022239, MG022280, KX017911, KX017843, KX017933, KX017955, KX017887. Johnson 04-140, KX017866, MG022366, MG022240, MG022281, KX017912, KX017844, KX017934, KX017956, KX017888. Johnson 11-029, KX017867, MG022367, MG022241, MG022282, KX017913, KX017845, KX017935, KX017957, KX017889. Johnson 13-219, KX017868, MG022368, MG022242,

MG022283, KX017914, KX017846, KX017936, KX017958, KX017890. *Porter & Machen 13772*, KX017869, MG022369, MG022243, MG022284, KX017915, KX017847, KX017937, KX017959, KX017891. ***Navarretia modocensis* L.A.Johnson & D.Gowen:** *Johnson 95-053*, MG022315, MG022370, MG022244, MG022285, MG022211, MG022339, MG022400, MG022422, MG022189. *Johnson 04-130*, MG022316, MG022371, MG022245, MG022286, MG022212, MG022340, MG022401, MG022423, MG022190. *Johnson 14-170*, MG022317, MG022372, MG022246, MG022287, MG022213, MG022341, MG022402, MG022424, MG022191. *Johnson 15-057*, MG022318, MG022373, MG022247, MG022288, MG022214, MG022342, MG022403, MG022425, MG022192. *Johnson 16-086*, MG022319, MG022374, MG022248, MG022289, MG022215, MG022343, MG022404, MG022426, MG022193. *O'dell s.n.*, MG022320, MG022375, MG022249, MG022290, MG022216, MG022344, MG022405, MG022427, MG022194. ***Navarretia torreyella* L.A.Johnson & D.Gowen:** *Johnson, Johnson, & Yankee 13-230*, MG022321, MG022376, MG022250, MG022291, MG022217, MG022345, MG022406, MG022428, MG022195. *Johnson et al. 14-028*, MG022322, MG022377, MG022251, MG022292, MG022218, MG022346, MG022407, MG022429, MG022196. *Johnson 14-143*, MG022323, MG022378, MG022252, MG022293, MG022219, MG022347, MG022408, MG022430, MG022197. *Johnson & Ahart 15-022*, MG022324, MG022379, MG022253, MG022294, MG022220, MG022348, MG022409, MG022431, MG022198. *Johnson & Ahart 15-028*, MG022325, MG022380, MG022254, MG022295, MG022221, MG022349, MG022410, MG022432, MG022199. *Johnson 16-008*, MG022326, MG022381, MG022255, MG022296, MG022222, MG022350, MG022411, MG022433, MG022200. ***Navarretia vividior* (Jeps. & V.L.Bailey) L.A.Johnson & D.Gowen:** *Johnson 04-032*, (MG022327, MG022328), (MG022382, MG022383), (MG022256, MG022257), (MG022297, MG022298), MG022223, MG022351, MG022412, MG022434, MG022201. *Johnson 05-021*, (MG022329, MG022330), (MG022384, MG022385), (MG022258, MG022259), (MG022299, MG022300), MG022224, MG022352, MG022413, MG022435, MG022202. *Johnson & Gowen 09-049*, KX017885, (MG022386, MG022387), (MG022260, MG022261), (MG022301, MG022302), KX017931, KX017863, KX017953, KX017975, KX017909. *Johnson 16-058*, MG022331, (MG022388, MG022389), (MG022262, MG022263), (MG022303, MG022304), MG022225, MG022353, MG022414, MG022436, MG022203. *Johnson 16-062*, MG022332, (MG022390, MG022391), (MG022264, MG022265), (MG022305, MG022306), MG022226, MG022354, MG022415, MG022437, MG022204. *Gowen 452*, KX017886, (MG022392, MG022393), (MG022266, MG022267), (MG022307, MG022308), KX017932, KX017864, KX017954, KX017976, KX017910.

Four new species of *Cyrtandra* (Gesneriaceae) from the South Pacific islands of Fiji

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Abstract

During fieldwork in Fiji, four new species of *Cyrtandra* (Gesneriaceae) were discovered and are described herein: *C. gregoryi* M.A.Johnson, **sp. nov.**, *C. hispida* M.A.Johnson, **sp. nov.**, *C. longifructosa* M.A.Johnson, **sp. nov.**, and *C. waisaliensis* M.A.Johnson, **sp. nov.** The addition of four new species brings the current number of Fijian *Cyrtandra* to 41 endemic species. Two of the four species are known from only a single locality, and all of the new species are likely endangered or critically endangered. Continued fieldwork in the islands of Fiji is warranted in order to better understand current species distributions and population demographics of *Cyrtandra* in this species-rich and still poorly explored region of the South Pacific.

Keywords

Cyrtandra, Gesneriaceae, Fiji, South Pacific, islands, new species, taxonomy, conservation

Introduction

The Southeast Asian-Pacific genus *Cyrtandra* J.R. Forster & G. Forster (Gesneriaceae) comprises ca. 800 species, with centers of diversity in Borneo, New Guinea, the Philippines, and the Pacific islands (Atkins et al. 2013). Species of *Cyrtandra* are restricted to the understory of rainforests and exhibit high diversity in habit (shrubs, small trees, herbs, or vines), flower color (white, yellow, purple, pink, red), and fruit morphology (indehiscent capsules or berries). In the Pacific, *Cyrtandra* is one of the largest and most

widely distributed genera of flowering plants, with ca. 175 species occurring across a region that extends from the Solomon Islands, east to the Marquesas, and north to the Hawaiian Islands. The vast majority of species are single island endemics, with the entire range of a species often being restricted to a single valley or mountain region.

Recent phylogenetic studies suggest that *Cyrtandra* evolved in Southeast Asia, followed by dispersal to the Pacific islands (Clark et al. 2008, 2009; Johnson et al. 2017), likely via frugivorous birds. The Pacific clade appears to have originated in Fiji ca. 9 mya, with subsequent founder events from Fiji to archipelagos both near (e.g., Samoa) and far (e.g., the Hawaiian Islands) resulting in the current distribution of *Cyrtandra* across the Pacific (Johnson et al. 2017). While Fiji hosts the second highest number of endemic *Cyrtandra* species in the Pacific (second only to the Hawaiian Islands, with 60 spp.), only limited research has been conducted on the genus in this diverse region. Gillett (1967) conducted the only thorough taxonomic review of Fijian *Cyrtandra* to date, with his treatment dividing 35 species among six informal groups. However, upon further study of *Cyrtandra* across the South Pacific, Gillett (1973) acknowledged that these groupings were largely inadequate and that a more accurate treatment of Fijian *Cyrtandra* would require considerably more fieldwork. Smith's treatment of *Cyrtandra* in the Flora of Fiji (1991) was largely drawn from Gillett (1967), although two species were restored from synonymy bringing the number of recognized species to 37.

Botanical explorations in Fiji from 1840–1953 resulted in the description of all 37 currently recognized species of Fijian *Cyrtandra*. Since the 1960s, relatively few collections of Fijian *Cyrtandra* have been made. In the 1970s, a number of new roads were built in Fiji to accommodate the expanding agricultural industry, vastly increasing accessibility into remote regions (e.g., central Vanua Levu, eastern Taveuni; Lin 2012). In 2014 and 2015, I was able to undertake extensive fieldwork across the four largest Fijian islands (Viti Levu, Vanua Levu, Taveuni, and Kadavu), focusing on regions that have been poorly explored in the past. This work resulted in the discovery of four new species that are here described and illustrated.

Methods

Diagnoses of the new species are based on morphological traits and DNA sequence variation in a phylogenetic context. Morphological measurements were taken from live plants in the field, as many characters essential to *Cyrtandra* identification are lost upon drying (particularly floral characters). Information was also taken from liquid fixative-preserved flowers and fruit, as well as from digital photographs. To ensure accurate identification, comparisons were made with all existing species descriptions (Gillett 1967, Smith 1991) as well as with herbarium specimens housed at BISH, GH, K, NY, PTBG, RSA, SUVA, UC, and US. Samples of all four new species were included in a recent molecular phylogeny of the Pacific clade of *Cyrtandra*, which is based on five loci and a dense taxon sampling of 121 species (including 30 Fijian species; Johnson et al. 2017). This study provided the information necessary to identify the closest

relatives of each of the new species based on shared phylogenetic history. Conservation status was assessed in accordance with IUCN Red List Category criteria (IUCN Standards and Petitions Subcommittee 2016).

Taxonomic treatment

Cyrtandra gregoryi M.A.Johnson, sp. nov.

urn:lsid:ipni.org:names:60475584-2

Figs 1, 2

Diagnosis. *Cyrtandra gregoryi* is closely related to *C. ciliata* Seem. (Fig. 2), but differs in its elliptic to ovate leaves up to 39×17 cm (vs. lanceolate to ovate leaves up to 28×12 cm), axillary inflorescences with indument of brown trichomes (vs. cauliflorous inflorescences with indument of white trichomes), pale green calyces 6–13 mm long that are cleft unequally into lanceolate coriaceous lobes (vs. calyces white, 7–10 mm long, cleft nearly to the base into equal linear-lanceolate lobes), these splitting along two to three sutures and recurving after anthesis (vs. remaining erect after anthesis), and corollas with exserted style and stamens (vs. style and stamens included).

Type. FIJI. Taveuni: near the end of the Lavena coastal walk along the Wainibau stream, ca. 3.5 km NW of Lavena Village, $16^{\circ}52.10'S$, $179^{\circ}54.32'W$, 32 m elev., 04 August 2014, *M.A. Johnson 105* with G.J. Hora (holotype: RSA).

Description. Shrub 0.9–2.2 m tall; *stems* unbranched to few-branched, with a dense indument of dark brown uniseriate multicellular trichomes ca. 0.5 mm long. *Leaves* opposite, internodes 2–7 cm long, blades elliptic to ovate to obovate, 22–39 cm long, 7–17 cm wide, upper surface sparsely strigillose, lower surface glabrate except for the densely pubescent 9–13 secondary veins on each side, margins serrulate to subentire, apex acute, base cuneate to rounded, petioles 5–11 cm long, densely pubescent with short brown trichomes; *inflorescence* an axillary cyme with dense brown pubescence on the peduncles and pedicels, 3–22 flowers, cymules 1–4 flowered, peduncle to 31 mm long, terminated by bracts to 6 mm long, narrowly lanceolate, deciduous after anthesis, pedicels to 31 mm long; *calyx* 6–13 mm long, outer surface pale green and moderately pubescent with appressed dark brown uniseriate trichomes, inner surface white and papillate, unequally cleft into 5 lanceolate coriaceous lobes, 3–10 mm long, apex acuminate, upper lobes occasionally connate, often continuing to split along two or three sutures and curl back after anthesis, deciduous; *corolla* white, tube funnelform, slightly curved near mid point, 23–27 mm long, 6–9 mm wide, outer surface glabrate to densely pubescent with short glandular trichomes, inner surface glabrous, upper lobes 5–7 mm long and 5–6 mm wide, lower lobe 7–8 mm long and 5–6 mm wide, lobes recurving after anthesis; *stamens* 2, ca. 9 mm long, becoming exserted from the corolla tube during ovulate phase, base of the filaments bright orange, anthers apically connate, staminodes 3; *nectary disc* cupulate, annular; *gynoecium* (ovary, style, and stigma) 16–24 mm long, ovary glabrous, style pubescent with capitate glandular trichomes, exserted, stigma shallowly bilobed; *fruit* not seen.

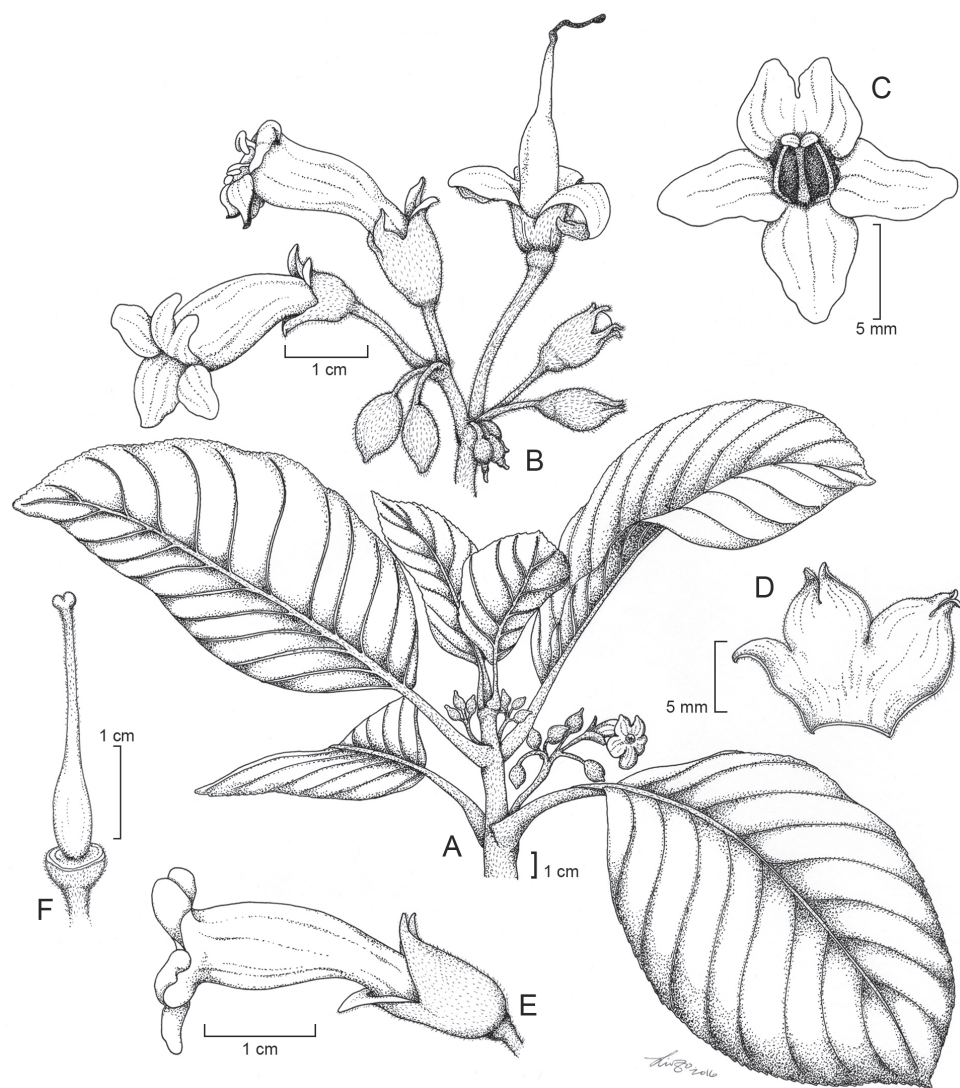


Figure 1. *Cyrtandra gregoryi* M.A.Johnson **A** Habit **B** Inflorescence **C** Corolla, anterior view **D** Calyx **E** Flower, lateral view **F** Gynoecium. Drawn from Johnson 105 (RSA) and field images.

Distribution and ecology. *Cyrtandra gregoryi* is only known from two locations in eastern Taveuni, Fiji, where it grows in lowland forests and along stream banks from ca. 30–50 m (Fig. 3).

Phenology. Individuals of this species were in flower when collected in August and November, with fruits likely becoming mature ca. 5–6 months later.

Etymology. I am pleased to name this new species after my husband, Gregory Hora, to whom I am most grateful for his assistance in collecting this and other species across Fiji.

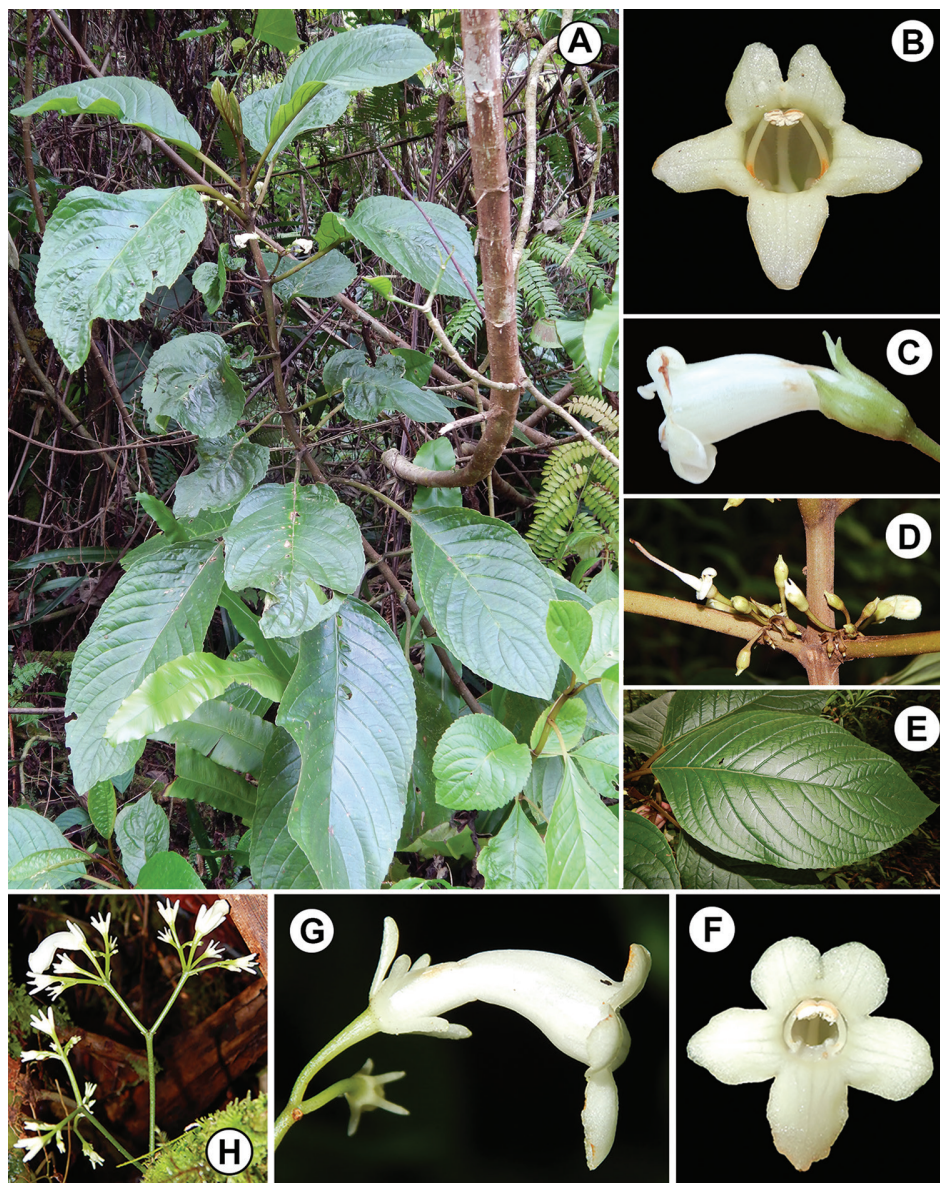


Figure 2. *Cyrtandra gregoryi* M.A.Johnson and closest relative (*C. ciliata*) based on a molecular phylogeny by Johnson et al. (2017). **A** *C. gregoryi* shrub habit **B** *C. gregoryi* corolla, anterior view **C** *C. gregoryi* flower, lateral view **D** *C. gregoryi* axillary cyme inflorescence **E** *C. gregoryi* adaxial leaf surface **F** *C. ciliata* corolla, anterior view **G** *C. ciliata* flower, lateral view **H** *C. ciliata* cauliflorous cyme inflorescence. All photos taken in the field by M. Johnson.

Phylogenetic placement. A recent phylogenetic study by Johnson et al. (2017) placed *Cyrtandra gregoryi* sister to *C. ciliata* with strong support (Fig. 4). *Cyrtandra ciliata* is endemic to the Fijian islands of Vanua Levu, Taveuni, and Koro from 300–1100 m

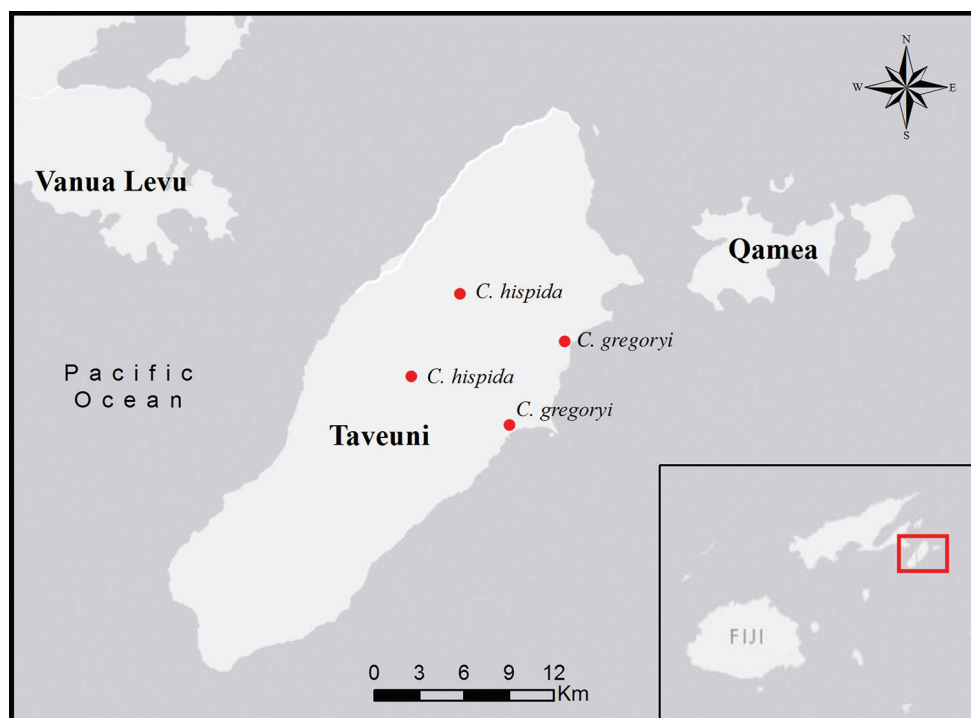


Figure 3. Distribution of *Cyrtandra gregoryi* and *C. hispida* on Taveuni, Fiji.

elevation. These species share a cymose inflorescence and glabrous to glabrate leaves. The key provided in the taxonomic treatment by Gillett (1967) would place *C. gregoryi* in species Group 5 based on the branching cyme inflorescence, non-woody inflorescence axis, deciduous calyx, styles and/or stamens being exserted from the corolla tube, and stamens 8–12 mm long.

Conservation status. Proposed IUCN Red List Category: Endangered (EN) based on an estimated area of occupancy of < 500 km² (criterion B2), known to exist at no more than five locations (B2a), inferred decline in area of occupancy (B2bii), decline in area, extent, and/or quality of habitat (B2biii), decline in number of mature individuals (B2bv), and population size estimated to number fewer than 250 mature individuals (D).

Although Bouma National Heritage Park protects ca. 15,000 hectares of intact rain-forest on eastern Taveuni, indigenous Fijians are permitted to clear land near villages for agriculture. As a result, large areas of coastal forest are increasingly being cleared for dalo (taro, *Colocasia esculenta* (L.) Schott) and yaqona (kava, *Piper methysticum* L.f.), the two main export crops of Taveuni. Given that *C. gregoryi* appears to be restricted to low-elevation forests, it is highly likely that individuals of this species were extirpated during clearing for human settlements and agriculture. Invasive plants are also a major threat to native plants in the area; mile-a-minute vine (kudzu, *Pueraria lobata* (Willd.) Ohwi) may be particularly problematic as it rapidly grows over trees and shrubs and can

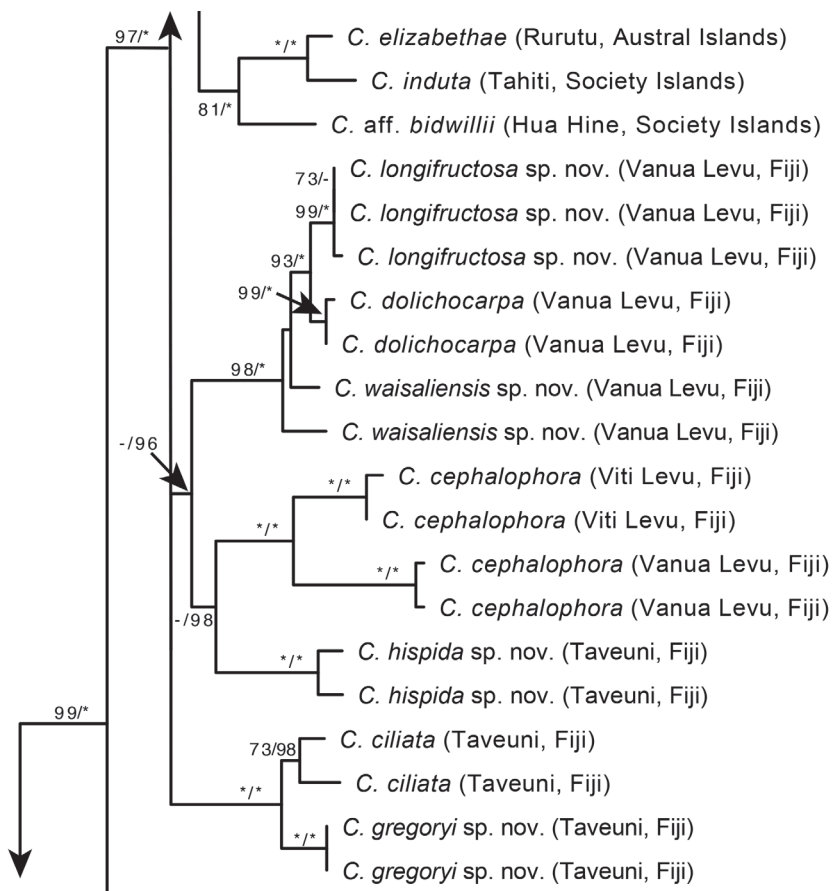


Figure 4. A portion of the Maximum Likelihood phylogram from Johnson et al. (2017) based on three nuclear (ITS, ETS, *Cyrt1*) and two chloroplast (*psbA-trnH*, *rp32-trnL*) loci. Support values shown for each branch are bootstrap and posterior probabilities when $\geq 50\%$ and ≥ 0.50 , respectively. An asterisk indicates 100% BS or 1.0 PP; a dash indicates that the branch was not supported.

kill other plants with heavy shading. Lastly, anthropogenic-induced climate change is a threat to island plant communities. Tropical cyclones are expected to increase in intensity and severity in the coming years (Emmanuel 2005, Knutson 2010), and can have devastating effects on island vegetation due to high winds, flooding, and storm surges (e.g., Cyclone Pam in 2015 caused extensive damage to Vanuatu's forests). Most recently, Cyclone Winston, the strongest tropical cyclone to make landfall in the South Pacific Basin in recorded history, ravaged the islands of Fiji in February of 2016. The coastal regions of eastern Taveuni were inundated by massive storm surges, and much of the vegetation was damaged by winds of up to 185 mph. Although forested regions can often regenerate after a natural disaster if given sufficient time, recent research in the South Pacific suggests that a cyclone can be a catalyst for human-coping strategies that increase pressure on forest ecosystems and exposes them to invasive plant species (Goulding et al. 2016).

Additional specimens examined. FIJI. Taveuni: Tavoro Falls Trail in Bouma National Heritage Park, 19 November 2016, *J.C. Game 16/235* with S. Fawcett (PTBG).

Notes. Eight individuals of *C. gregoryi* were recorded during field surveys along the Lavena coastal trail, with all of these being reproductive. Additional field surveys in the area are likely to reveal more individuals. No other *Cyrtandra* species were observed growing sympatrically with *C. gregoryi* in the Lavena region, although *C. tempestii* Horne ex. C.B. Clarke was collected 0.64 km to the SE. An additional collection was made of a single individual of *C. gregoryi* near the Tavoro Falls in Bouma National Heritage Park, an area that also hosts *C. ciliata*.

***Cyrtandra hispida* M.A.Johnson, sp. nov.**

urn:lsid:ipni.org:names:77174061-1

Figs 5, 6

Diagnosis. *Cyrtandra hispida* is morphologically similar to *C. waisaliensis* sp. nov., but differs in its axillary cyme inflorescence of 2–4 flowers (vs. cauliflorous cyme inflorescence of 2–8 flowers), green bracts and bracteoles 5–9 mm long (vs. white bracts and bracteoles 3–10 mm long), calyx pale green and 29–31 mm long (vs. calyx white and 23–37 mm long), corolla tube 31–34 mm long (vs. corolla tube 23–27 mm long), and staminodes 2 (vs. staminodes 3).

Type. FIJI. Taveuni: Des Voeux Peak, 16°50.48'S, 179°57.97'W, 1109 m elev., 13 July 2014, *M.A. Johnson 91* with G.J. Hora (holotype: RSA; isotype: SUVA).

Description. Shrub 0.6–1.2 m tall; *stems* unbranched or few-branched, with light brown hispid uniseriate multicellular trichomes ca. 5 mm long. *Leaves* opposite, internodes 3–9 cm long, the blades oval to ovate to obovate, 15–22 cm long, 8–10 cm wide, upper and lower surfaces densely strigose with light brown uniseriate trichomes to 2 mm long, 5–7 secondary veins on each side, margins serrate to biserrate, apex acute to acuminate, base oblique or aequilateral and rounded to cuneate, petioles 4–9 cm long, densely pubescent with hispid trichomes ca. 6 mm long; *inflorescence* an axillary cyme, 2–4 flowered, densely hispid throughout, peduncle 10–14 mm long, terminated by green bracts 5–9 mm long, ovate to narrowly lanceolate, densely hispid, pedicels 27–28 mm long, often subtended by bracteoles similar to the outer bracts; *calyx* pale green, cylindrical, 29–31 mm long, unequally cleft into five triangular lobes 4–11 mm long, outer and inner surfaces densely hispid with uniseriate trichomes, persistent on developing fruits; *corolla* white, bilabiate, tube narrowly funnelform, slightly curved near mid point, outer and inner surface glabrous, 31–34 mm long and 8–9 mm wide, upper lobes 12–15 mm long and 10–14 mm wide, lower lobe 13–20 mm long and 10–15 mm wide; *stamens* 2, ca. 7 mm long, anthers apically connate, staminodes 2; *nectary disc* cupulate, annular, deciduous from the fruit; *gynoecium* (ovary, style, and stigma) ca. 22 mm long, ovary and style glabrous, stigma applanate, bilobed; *berries* green when immature, ellipsoid, glabrous, up to 18 mm long and 11 mm wide, tipped by the basal 3 mm of the persistent style, enclosed by the persistent calyx, mature fruit not seen.

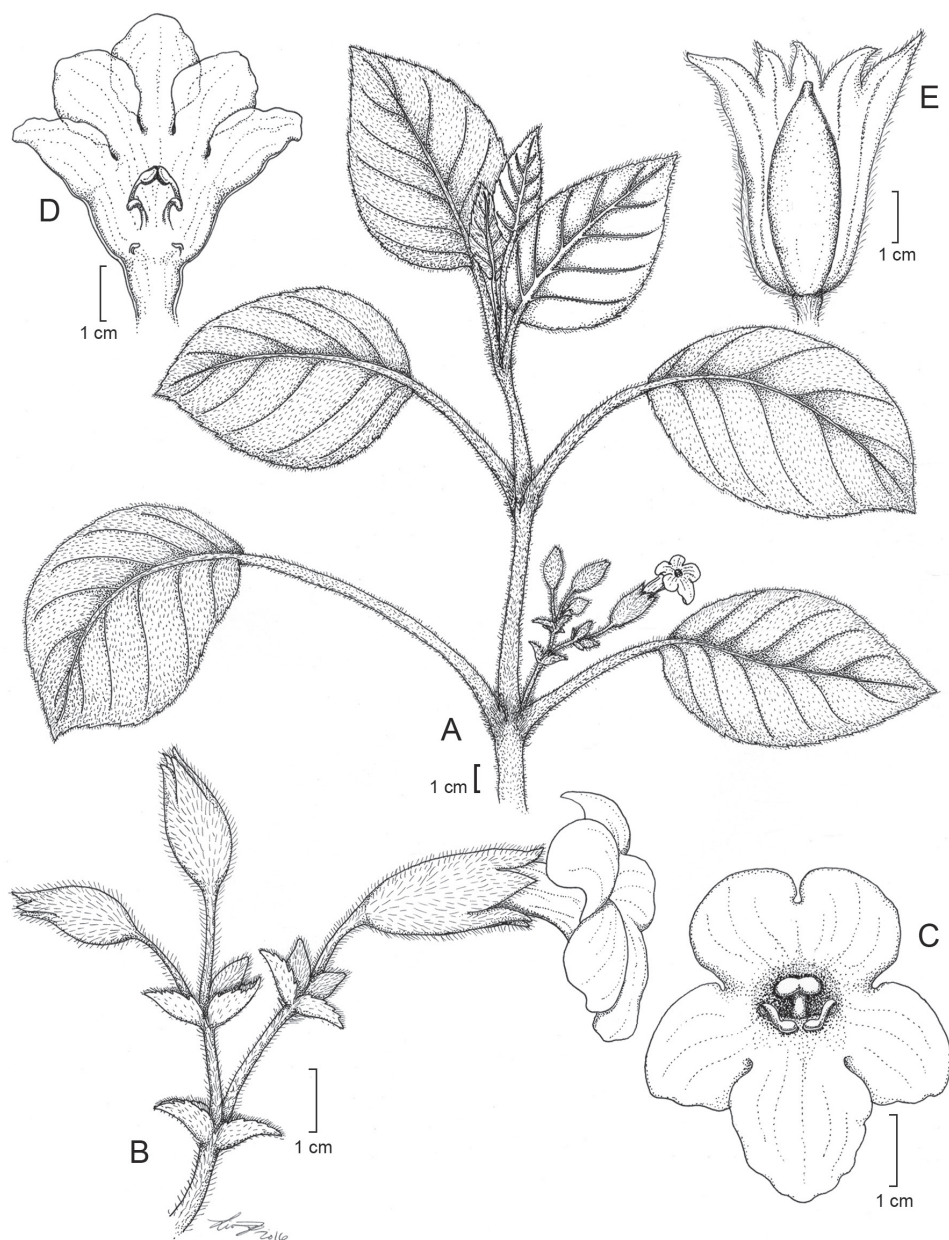


Figure 5. *Cyrtandra hispida* M.A.Johnson. **A** Habit **B** Inflorescence **C** Corolla, anterior view **D** Corolla, longitudinal section **E** Calyx, longitudinal section and young fruit. Drawn from Johnson 91 (RSA, SUVA), Johnson 212 (SUVA), Johnson 215 (RSA), and field images.

Distribution and ecology. *Cyrtandra hispida* is only known from two populations in the upland rainforests of Taveuni, Fiji, where plants occur on exposed hillsides composed of volcanic cinders, and on rocky stream banks from 697–1126 m elevation (Fig. 3).

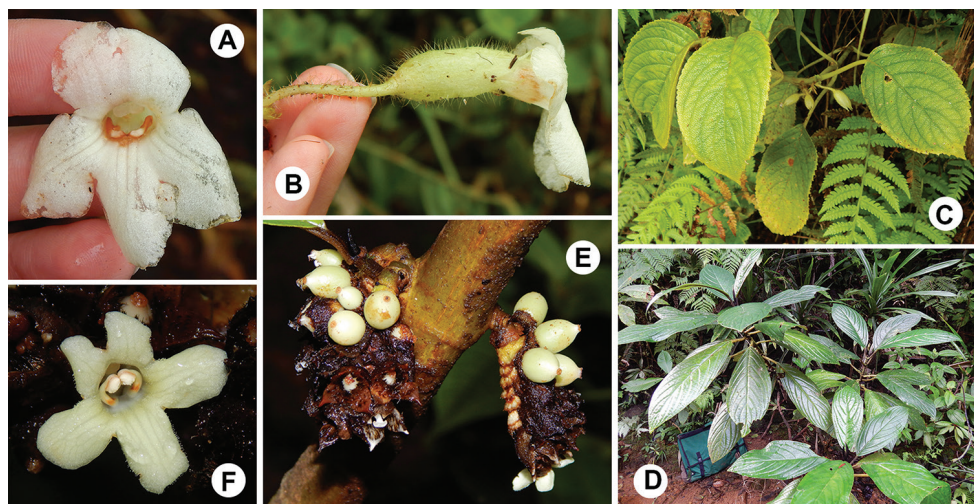


Figure 6. *Cyrtandra hispida* M.A.Johnson and closest relative (*C. cephalophora*) based on molecular phylogeny by Johnson et al. (2017). **A** *C. hispida* corolla, anterior view **B** *C. hispida* flower, lateral view **C** *C. hispida* shrub habit and axillary cyme inflorescence **D** *C. cephalophora* shrub habit **E** *C. cephalophora* capitulate-cylindrical cauliflorous inflorescence and young fruits **F** *C. cephalophora* corolla, anterior view. All photos taken in the field by M. Johnson, with photos of *C. hispida* taken from the type collection.

Phenology. Individuals of this species were in flower when collected in July, with fruits likely becoming mature ca. 5–6 months later (December–January).

Etymology. This species is named for the stiff trichomes that cover the stems, leaves, and inflorescences.

Phylogenetic placement. A recent phylogenetic study by Johnson et al. (2017) placed *Cyrtandra hispida* in a weakly supported clade with four other species (*C. cephalophora* Gillespie, *C. waisaliensis* sp. nov., *C. dolichocarpa* A. Gray, *C. longifructosa* sp. nov.) that are recorded from the Fijian Islands of Viti Levu (*C. cephalophora*) and/or Vanua Levu (*C. cephalophora*, *C. waisaliensis*, *C. dolichocarpa*, *C. longifructosa*) (Fig. 4). Within this clade, *C. hispida* is most similar morphologically to *C. waisaliensis* (sp. nov., described below). Both species have large bilabiate corollas, persistent cylindrical calyces, ovate to obovate leaves, and a dense indument of long stiff trichomes covering the stems, leaves, and inflorescences. Additional sampling of species and of nuclear genic regions may be required to confidently place *C. hispida* with its closest relatives. The key provided in the taxonomic treatment by Gillett (1967) would place *C. hispida* in species Group 2 based on the branching cyme inflorescence and the persistent calyx.

Conservation status. Proposed IUCN Red List Category: Endangered (EN) based on an estimated area of occupancy of < 500 km² (criterion B2), known to exist at no more than five locations (B2a), projected decline in extent of occurrence (B2bi), area of occupancy (B2bii), and area, extent, and/or quality of habitat (B2biii). Although the two areas where this species has been collected are within the Taveuni Forest Reserve, the forest above Somosomo Village is currently being cleared for a hydropower

dam (M. Johnson, pers. obs.). Additional threats include mining for gold and copper, invasion by plant species such as *Clidemia hirta* (L.) D. Don (Koster's curse; M. Johnson, pers. obs), and damage from tropical cyclones. Further surveys are needed in the upland forests of Taveuni (which remain relatively unexplored, exceptions being the area surrounding Lake Tagimoucia and the road to Des Voeux Peak) to determine the extent of occurrence and population demographics of *C. hispida*.

Additional specimens examined. FIJI. Taveuni: mountains above Somosomo, 16°47.67'S, 179°56.10'W, 693 m elev., 24 August 2015, *M.A. Johnson 212* (SUVA), *M.A. Johnson 215* (RSA).

Notes. *Cyrtandra hispida* was observed to grow sympatrically with three species on Des Voeux Peak (*C. leucantha* A.C. Sm., *C. ciliata*, and *Cyrtandra* sp.) and three species in the mountains above Somosomo (*C. leucantha*, *C. ciliata*, *C. taviunensis* Gillespie). Several individuals were observed that appeared to be of hybrid origin in these populations, with the widespread and common *C. ciliata* inferred as one of the parents based on similar floral morphology. While the observation of ongoing hybridization in these populations suggests the possibility of *C. hispida* being of hybrid origin, none of the sympatric species have morphological characters similar to *C. hispida*. Furthermore, *C. hispida* is placed in a clade of species that are endemic to the neighboring islands of Vanua Levu and Viti Levu, and does not appear to be closely related to species endemic to Taveuni.

***Cyrtandra longifructosa* M.A.Johnson, sp. nov.**

urn:lsid:ipni.org:names:77174062-1

Figs 7, 8

Diagnosis. This species is closely related to *C. dolichocarpa* (Fig. 8), but differs in its glabrous elliptic-ovate leaves (vs. moderately pubescent lanceolate-ovate leaves), blades up to 22 × 9 cm (vs. blades up to 17 × 7 cm), petioles 3–9 cm long (vs. petioles 1–4 cm long), deciduous lanceolate bracts (vs. persistent ovate bracts), peduncles 2–4 mm long (vs. 5–10 mm long), pedicels 11–18 mm long (vs. 21–27 mm long), deciduous beaked calyx (vs. persistent cylindrical calyx), and corolla tube 23–29 mm long (vs. corolla tube 36–55 mm long).

Type. FIJI. Vanua Levu: ca. 0.8 km NE of Waisali Village along the Waisali Creek, 16°38.51'S, 179°14.54'E, 110 m elev., 09 July 2014, *M.A. Johnson 65* with G.J. Hora (holotype: SUVA; isotype: RSA).

Description. Shrub 0.9–1.7 m tall; *stems* unbranched to few branched. *Leaves* opposite, internodes 1–5 cm long, the blades narrowly elliptic to elliptic-ovate, 17–22 cm long, 7–9 cm wide, upper and lower surface glabrous, 8–10 secondary veins on each side, these slightly impressed, margins serrulate, apex acuminate, base oblique to aequilateral and attenuate to cuneate, petioles 3–9 cm long, glabrous to glabrate; *inflorescence* an axillary cyme, 1– 2(3–4) flowers, densely pilose with black trichomes ca. 1 mm long throughout, peduncle 2–4 mm long, terminated by green bracts, 3–8 mm long,

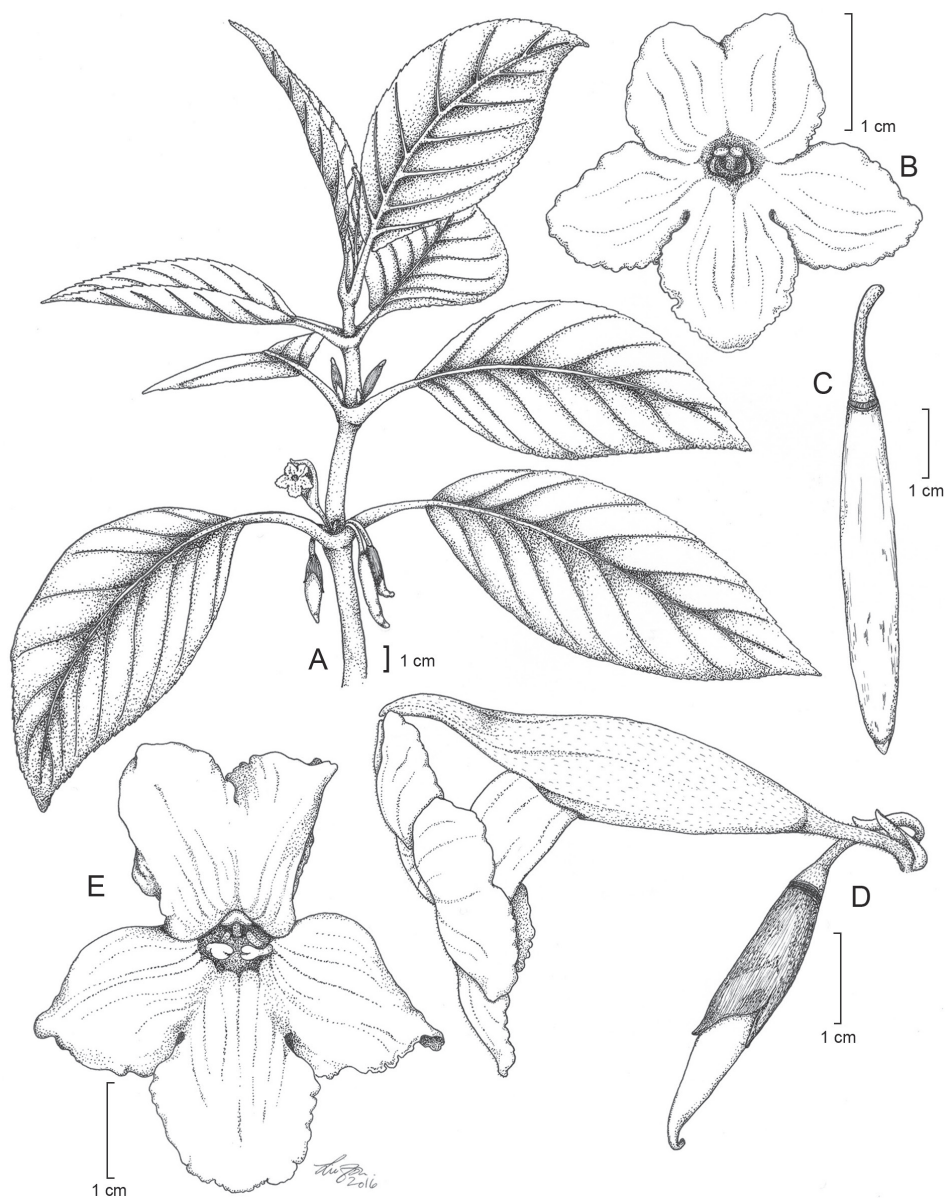


Figure 7. *Cyrtandra longifructosa* M.A.Johnson. **A** Habit **B** Corolla, staminate phase, anterior view **C** Mature elongate cylindrical fruit **D** Inflorescence and young fruit **E** Corolla, ovulate phase, anterior view. Drawn from Johnson 65 (SUVA, RSA), Johnson 59 (RSA), and field images.

lanceolate, deciduous after anthesis, pedicels 11–18 mm long; *calyx* pale green, outer and inner surfaces pubescent with appressed uniseriate trichomes, narrowly fusiform in bud, 28–32 mm long, beaked, the 5 lobes often remaining connivent, splitting along one suture 14–19 mm long, deciduous; *corolla* white, becoming strongly bilabiate in the

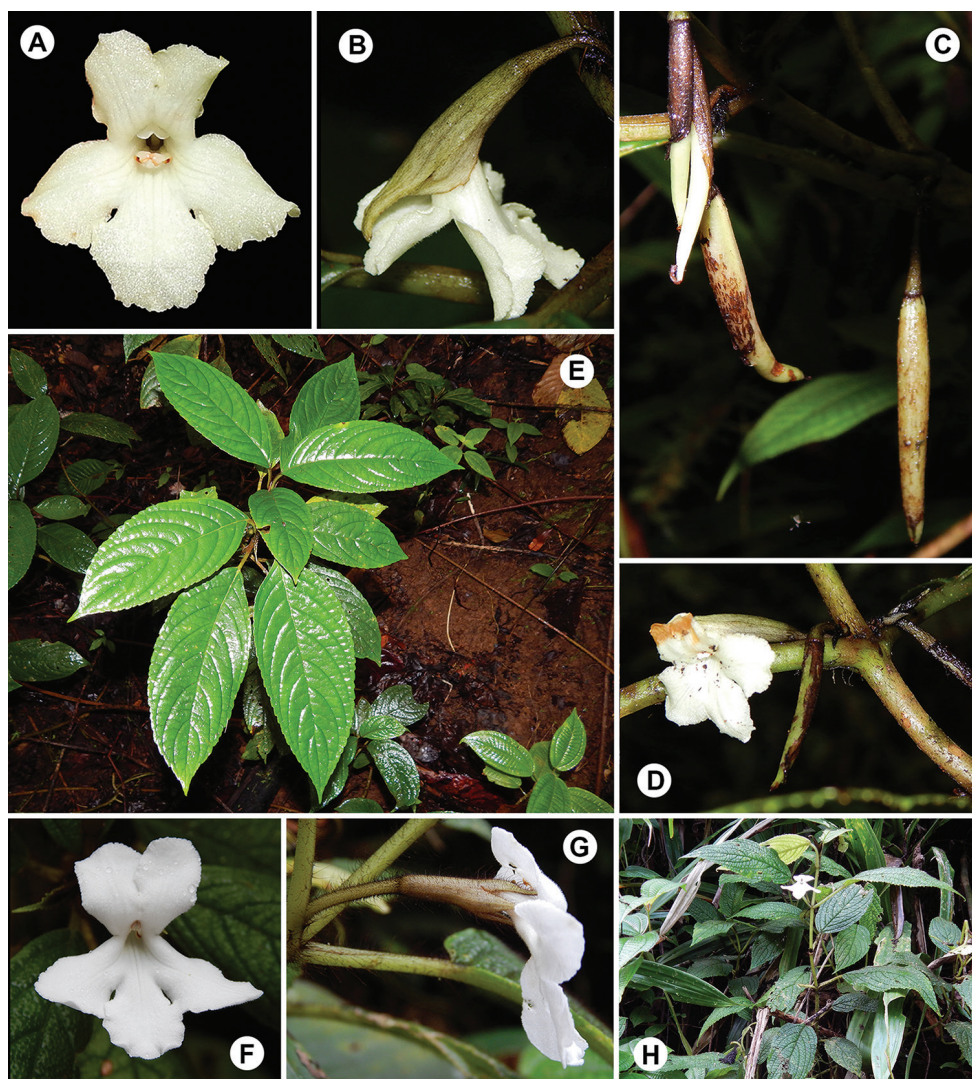


Figure 8. *Cyrtandra longifructosa* M.A.Johnson and closest relative (*C. dolichocarpa*) based on molecular phylogeny by Johnson et al. (2017). **A** *C. longifructosa* corolla, anterior view **B** *C. longifructosa* flower, lateral view **C** *C. longifructosa* elongate cylindrical fruits **D** *C. longifructosa* axillary inflorescence and young fruits **E** *C. longifructosa* shrub habit **F** *C. dolichocarpa* corolla, anterior view **G** *C. dolichocarpa* flower, lateral view **H** *C. dolichocarpa* shrub habit. All photos taken in the field by M. Johnson, with photos of *C. longifructosa* taken from the type collection.

ovulate phase, tube cylindrical, curved near the mid point, outer surface glabrous, inner surface with uniseriate trichomes throughout and short glandular trichomes near the mouth of the tube, the tube 23–29 mm long, 5–7 mm wide, upper lobes 8–12 mm long and 8–11 mm wide, lower lobe 12–14 mm long and 11–14 mm wide; *stamens* 2, ca. 6 mm long, base of the filaments reddish orange, anthers apically connate, staminodes 3;

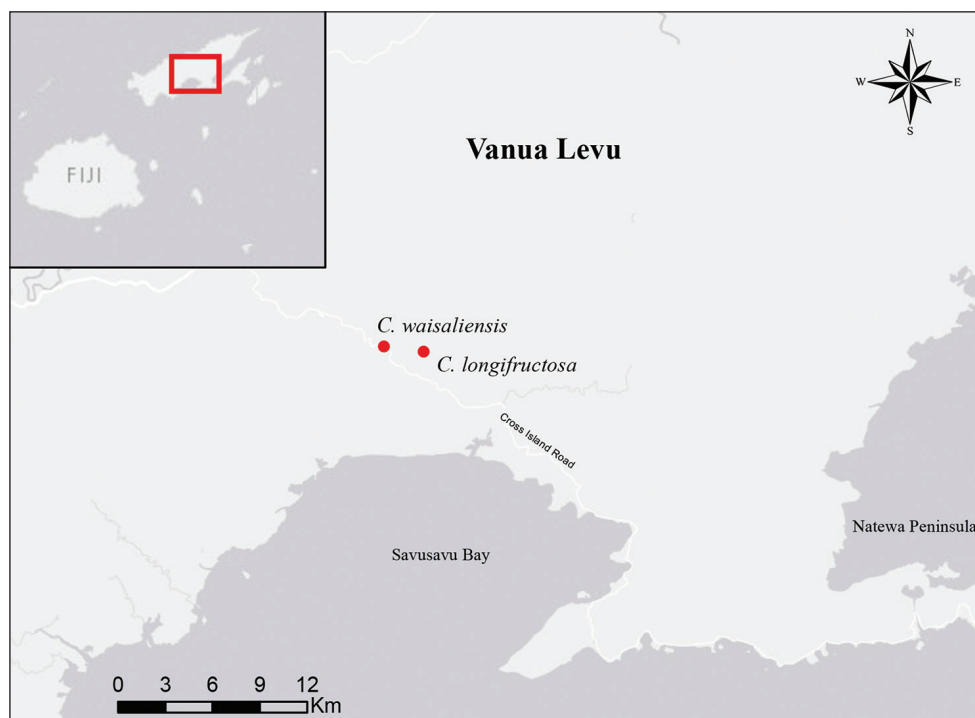


Figure 9. Distribution of *Cyrtandra waisaliensis* and *C. longifructosa* on Vanua Levu, Fiji.

nectary disc cupulate, annular, deciduous from mature fruit; *gynoecium* (ovary, style, and stigma) ca. 24 mm long, ovary glabrous, style pubescent with capitate glandular trichomes along distal $\frac{1}{3}$ of its length, stigma bilobed; *berries* cylindrical, elongate, mature fruit to 40 mm long and 5 mm wide, glabrous, turning white at maturity.

Distribution and ecology. *Cyrtandra longifructosa* is known only from one population in the Waisali region of central Vanua Levu, Fiji, where it occurs in the wet forest understory along a small creek at ca. 110 m elevation (Fig. 9).

Phenology. Individuals of this species had flowers, immature fruits, and mature fruits when collected in July.

Etymology. Named for the elongate cylindrical fruits, one of the diagnostic characteristics of this species.

Phylogenetic placement. The phylogenetic study by Johnson et al. (2017) placed *Cyrtandra longifructosa* as sister to *C. dolichocarpa* (endemic to Vanua Levu and Rabi, Fiji) with strong support (Fig. 4). These species both have large bilabiate corollas and elongate cylindrical berries. The key provided in the taxonomic treatment by Gillett (1967) would place *C. longifructosa* in species Group 3 based on the branching cyme inflorescence, non-woody inflorescence axis, deciduous calyx, inserted anthers and styles, and calyx lobes about the same length as the calyx tube.

Conservation status. Proposed IUCN Red List Category: Critically Endangered (CR): based on an estimated area of occupancy of $< 10 \text{ km}^2$ (criterion B2), known to

exist only at a single location (B2a), projected decline in extent of occurrence (B2bi), area of occupancy (B2bii), and area, extent, and/or quality of habitat (B2biii). This species is only known from one locality in the central mountains of Vanua Levu, warranting additional surveys in areas of Vanua Levu with intact rainforest (e.g., Waisali, the Natewa Peninsula) to determine the full extent of occurrence and population demographics of *C. longifructosa*. Regions with suitable rainforest habitat on Vanua Levu are threatened by logging, mining for bauxite and gold, invasive plant species such as *Clidemia hirta* (Koster's curse; M. Johnson, pers. obs.), and tropical cyclones.

Additional specimens examined. FIJI. Vanua Levu: NE of Waisali Village along Waisali Creek, 16°38.51'S, 179°14.54'E, 110 m elev., 09 July 2014, *M.A. Johnson 59* with G.J. Hora (RSA).

Notes. The population of *C. longifructosa* was observed to contain ca. 20 individuals, many of which were reproductive. No other *Cyrtandra* species were observed growing in the immediate vicinity, although the closely related species *C. dolichocarpa*, *C. waisaliensis*, and *C. cephalophora* were all collected 2.25 km W of the *C. longifructosa* population described here.

***Cyrtandra waisaliensis* M.A.Johnson, sp. nov.**

urn:lsid:ipni.org:names:77174063-1

Figs 10, 11

Diagnosis. The new species is closely related to *C. dolichocarpa* and *C. longifructosa* (Fig. 8), but differs in its dense bristly pubescence on the young stems, leaves, petioles, and inflorescences (vs. moderate appressed pubescence on *C. dolichocarpa*; vs. glabrous on *C. longifructosa*), cauliflorous inflorescences (vs. axillary inflorescences in both *C. dolichocarpa* and *C. longifructosa*), persistent foliaceous ovate white bracts to 10 mm long (vs. non-foliaceous green bracts to 5 mm long in *C. dolichocarpa*; vs. deciduous non-foliaceous lanceolate green bracts to 8 mm long in *C. longifructosa*), and multiple persistent foliaceous white bracteoles (vs. single deciduous non-foliaceous green bracteoles in *C. dolichocarpa*; vs. bracteoles absent in *C. longifructosa*).

Type. FIJI. Vanua Levu: Waisali Forest Reserve along the lower portion of the Savuqoro Creek, 16°38.39'S, 179°13.25'E, 338 m elev., 07 July 2014, *M.A. Johnson 50* with G.J. Hora (holotype: SUVA; isotype: RSA).

Description. Shrub 0.7–2.6 m tall; *stems* few- to many-branched, young stems covered in hirsute trichomes. *Leaves* opposite, those at a node unequal, internodes 2–8 cm long, blades ovate to obovate, 13–24 cm long, 6–12 cm wide, upper and lower surfaces densely hirsute with uniseriate multicellular trichomes, 6–7 secondary veins on each side, margins serrate, apex acuminate, base oblique to aequilateral and attenuate to cuneate, petioles 3–11 cm long, densely hirsute, trichomes ca. 5 mm long; *inflorescence* of cauliflorous cymes, 2–8 flowered, cymules 1–4 flowered, densely hirsute throughout, peduncle 3–8 mm long, terminated by persistent foliaceous white bracts, ovate to lanceolate, 3–10 mm long, outer surface glabrous to glabrate, inner surface densely hirsute, pedicels

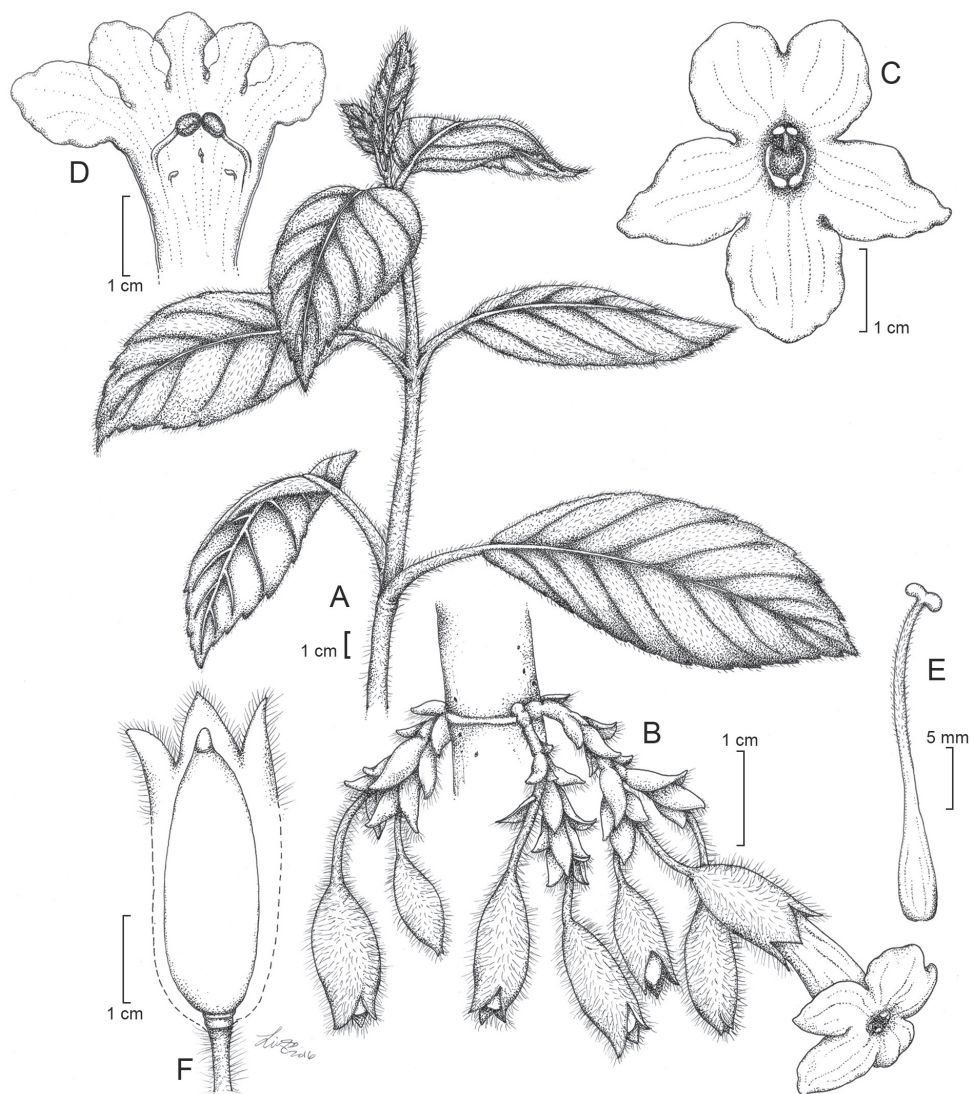


Figure 10. *Cyrtandra waisaliensis* M.A.Johnson. **A** Habit **B** Cauliflorous inflorescence **C** Corolla, anterior view **D** Corolla, longitudinal section **E** Gynoecium **F** Calyx, longitudinal section and young fruit. Drawn from Johnson 48 (RSA), Johnson 50 (SUVA, RSA), and field images.

21–40 mm long, subtended by multiple persistent bracteoles similar to and closely subtended by the outer bracts; *calyx* white, cylindrical, densely hirsute, 23–37 mm long, unequally cleft into 5 triangular lobes, 4–14 mm long, persistent; *corolla* white, bilabiate, tube funnelform, curved near mid point, outer surface glabrous to glabrate, inner surface with capitate glandular trichomes near the mouth of the tube, 23–27 mm long, 6–9 mm wide, upper lobes 11–12 mm long and 8–11 mm wide, lower lobe 13–17 mm long and 10–15 mm wide; *stamens* 2, 3–6 mm long, base of the filaments reddish orange, anthers

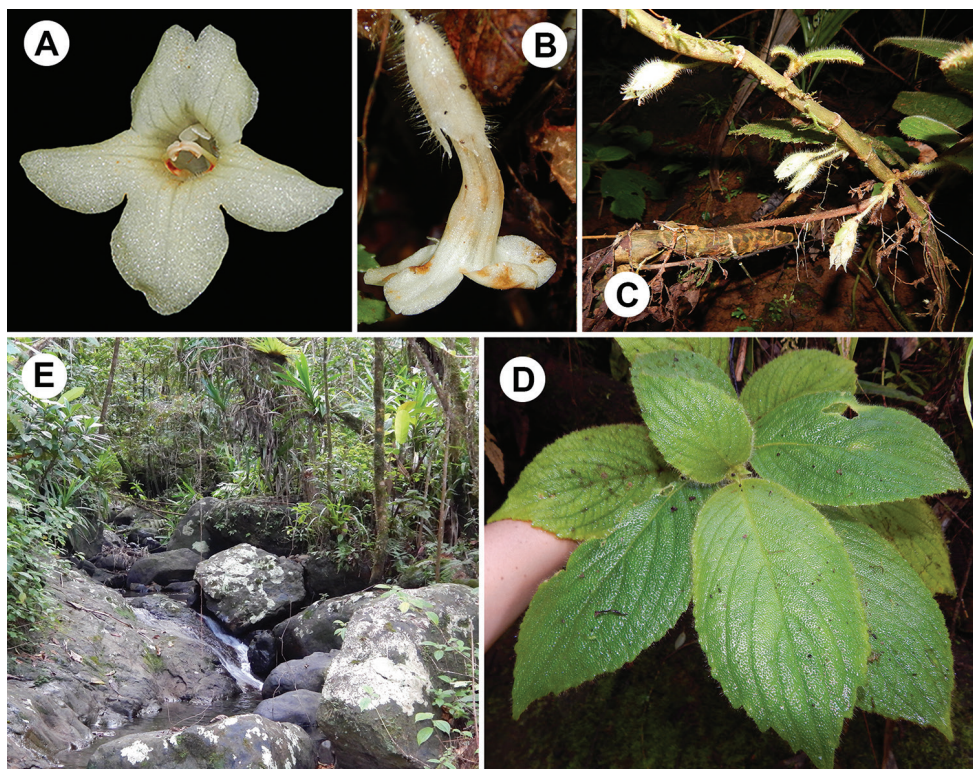


Figure 11. *Cyrtandra waisaliensis* M.A.Johnson. **A** Corolla, anterior view **B** Flower, lateral view **C** Cauliflorous cyme inflorescence **D** Shrub habit **E** Rainforest understory habitat. All photos from the type collection, taken in the field by M. Johnson.

apically connate, staminodes 3; *nectary disc* prominent, annular, 2 mm high; *gynoecium* (ovary, style, and stigma) 16–26 mm long, ovary glabrous, style pubescent with capitate glandular trichomes along distal $\frac{1}{3}$ of length, stigma bilobed; *berries* ellipsoid, green when immature, enclosed by the persistent calyx, mature fruit not seen.

Distribution and ecology. *Cyrtandra waisaliensis* is known only from one population in the Waisali Forest Reserve on Vanua Levu, Fiji at 300–360 m elevation, occurring in the dense forest understory alongside a creek (Fig. 9).

Phenology. Flowers and immature fruits were observed in July, with fruits likely becoming mature ca. 5–6 months later (December–January).

Etymology. The new species is named after the area of Vanua Levu where it was collected, Waisali Forest Reserve.

Phylogenetic placement. A recent phylogenetic study by Johnson et al. (2017) supported the placement of *Cyrtandra waisaliensis* as sister to *C. longifructosa* (endemic to Vanua Levu) and *C. dolichocarpa* (endemic to Vanua Levu and Rabi; Fig. 4). These species all have large bilabiate corollas, and both *C. dolichocarpa* and *C. longifructosa* have elongate cylindrical white fruits. However, *C. waisaliensis* is also morphologically similar to *C. hispida*; these species share bilabiate corollas, persistent cylindrical caly-

ces, and a dense indument of stiff uniseriate trichomes. *Cyrtandra hispida* is currently placed in a polytomy with *C. cephalophora* and the clade comprising *C. waisaliensis*, *C. longifructosa*, and *C. dolichocarpa*. The key provided in the taxonomic treatment by Gillett (1967) would place *C. waisaliensis* in species Group 2, based on the branching cyme inflorescence and the persistent calyx.

Conservation status. Proposed IUCN Red List Category: Critically Endangered (CR) based on an estimated area of occupancy of < 10 km² (criterion B2), known to exist at only a single location (B2a), projected decline in extent of occurrence (B2bi), area of occupancy (B2bii), and area, extent, and/or quality of habitat (B2biii). This species is only known from one locality in the central mountains of Vanua Levu, warranting additional surveys in areas of Vanua Levu with intact rainforest (e.g., Waisali, the Natewa Peninsula) to determine the full extent of occurrence and population demographics of *C. waisaliensis*. Regions with suitable rainforest habitat on Vanua Levu are threatened by logging, mining for bauxite and gold, invasive plant species such as *Clidemia hirta* (Koster's curse; M. Johnson, pers. obs.), and tropical cyclones.

Additional specimens examined. FIJI. Vanua Levu: Waisali Forest Reserve along the lower portion of the Savuqoro Creek, 16°38.34'S, 179°13.18'E, 355 m elev., 07 July 2014, *M.A. Johnson* 48 with G.J. Hora (RSA).

Notes. The observed population of *C. waisaliensis* was comprised of ca. 20 individuals, many of which were reproductive. A single individual appeared to be of hybrid origin, with the putative parents being *C. waisaliensis* and *C. cephalophora* based on morphological characters intermediate between these two species.

Conclusions

The recognition of *C. gregoryi*, *C. hispida*, *C. longifructosa*, and *C. waisaliensis* brings the new total of Fijian *Cyrtandra* species to 41. The four new species of *Cyrtandra* described here demonstrate that the islands of Fiji remain poorly explored botanically, at least in some regions. Of the 28 Fijian *Cyrtandra* species collected during field expeditions in 2014 and 2015, four of these were new to science. An additional four *Cyrtandra* species could not be keyed out to any of the existing species due to a lack of reproductive material. However, with further field study it is possible that these, along with other future collections, may be identified as new species.

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being an excellent field assistant and for providing endless encouragement and moral support. This work would not have been possible without the kind peoples of Fiji, who offered their assistance, expertise and hospitality. The following herbaria graciously allowed the use of their collections for study: BISH, GH, K, NY, RSA, SUVA, UC, US, and WU. John Game provided collection information and photographs of *Cyrtandra gregoryi* for study. Funding for this project was provided by the following: Rancho Santa Ana Botanic Garden; Garden Club of America Award in Tropical Botany; American Philosophical Society Lewis and Clark Fund for Exploration and Field Research; The Gesneriad Society Nelly D. Sleeth Scholarship Endowment Fund; The Gesneriad Society Elvin McDonald Fund; Society of Systematic Biologists Graduate Student Research Award; Sigma Xi Grants-in-Aid of Research; American Society of Plant Taxonomists Graduate Student Research Grant; and Claremont Graduate University. Lastly, I am grateful to my sister, Liv Johnson, for the beautiful line drawings, and to Lucinda McDade, John R. Clark, J. Travis Columbus, J. Mark Porter, David Lorence, and one anonymous reviewer for comments that greatly improved this manuscript.

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Nahuatlea: a new genus of Compositae (Gochnatieae) from North America

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Abstract

In the course of a detailed molecular study of the tribe Gochnatieae (Compositae: Gochnatioideae) it became apparent that the genus *Gochnatia* (sensu Cabrera) was not monophyletic but composed of a number of morphologically, geographically, and molecularly distinct clades. All but one of these clades had previously been recognized at the generic or sectional level and therefore had a name that could be applied. However, one clade, whose members are from Mexico and adjacent parts of the United States, had never been recognized as a distinct taxon. The Mexican clade is the sister group of the Caribbean clade which seems to indicate a dispersal event from Southern South America to Mexico and from Mexico to the Caribbean. Here we provide the Mexican clade with a genus name, *Nahuatlea*, and make the necessary new combinations. The name is derived from Nahuatl, the major indigenous language that is spoken in the area where most of the collections were gathered. A genus description, key to species, images and short descriptions are provided.

Keywords

Asteraceae, *Gochnatia*, Gochnatioideae, Mexico, Texas, Arizona, South American-Mexican disjunct distribution

Introduction

Cabrera (1971) in his comprehensive treatment of *Gochnatia* Kunth recognized six sections in the genus all mainly from the Americas. He placed all known species of *Gochnatia* from Mexico, in the section *Hedraiophyllum* (Less.) DC. along with two southern South American species: *G. palosanto* Cabrera and *G. cordata* Less., which are now part of *Gochnatia* s.s. and *Moquiniastrum*, respectively. Although one species from

Mexico is rather widespread (it has been collected from a number of states in Mexico, a few counties in Texas, and there is one disjunct record from Arizona) all of the species can be found in Mexico (Figs 1, 2).

Cabrera recognized five species of *Gochmatia* from Mexico and adjacent USA: *G. arborescens* Brandegee, *G. hypoleuca* (DC.) A. Gray, *G. magna* M.C. Johnson ex Cabrera, *G. purpusii* Brandegee, and *G. smithii* Robins. & Greenm. *Gochmatia obtusata* S.F. Blake, although accepted by Jervis (1954), was not accepted as a species by Cabrera (1971), instead it was placed as subspecies under the widespread *G. hypoleuca*. According to data from molecular studies (Funk et al. 2014), *Gochmatia* section *Hedraiophyllum* (Cabrera 1971) is not supported but it is interesting to note that Cabrera considered the section *Hedraiophyllum* to be somewhat artificial.

The next comprehensive treatment of *Gochmatia* was by Freire et al. (2002). In this treatment, the authors placed 21 species from South America in section *Hedraiophyllum* but not the Mexican species as Cabrera did (1971); in fact, their concept of this section was very different from Cabrera's (1971). Freire et al. (2002) placed five species in *Gochmatia* sect. *Leucomeris* (D. Don) Cabrera, two of which were from Mexico: *G. hypoleuca* (including *G. obtusata*) and *G. smithii*. The other three species in *G. sect. Leucomeris* were distributed in Brazil, the Andean region of Bolivia and Argentina, and southeastern Asia. Freire et al. (2002) described a new section, *G. sect. Glomerata* S. E. Freire, L. Katinas & G. Sancho, consisting entirely of the final three Mexican species: *G. arborescens*, *G. magna*, *G. purpusii*. Freire et al. (2002) placed the Caribbean species (now in *Anastraphia*) in section *Anastraphioides* Jervis ex S.E. Freire, L. Katinas & G. Sancho. The molecular based study of Funk et al (2014) did not support the arrangement of taxa as proposed by Freire et al. (2002) except for section *Anastraphioides* (the Caribbean species) which formed a strongly supported clade.

In 2004 González-Medrano et al. described a new species of *Gochmatia* from Hidalgo, Mexico: *G. hiriartiana* Medrano, Villaseñor & Medina. It differs from all the other Mexican species because of its few, large heads; and greater number of disc flowers. The authors included a key to seven taxa: six species and the subspecies *G. hypoleuca* subsp. *obtusata*. The authors placed the new species in *G. sect. Glomerata* based on the key in Freire et al. (2002). It seems that González-Medrano et al. (2004) are the only authors to refer to the "Mexican species of *Gochmatia*" but they left them in two groups in different sections and never explicitly said that they thought the taxa formed a closely related group.

The recent molecular study of the tribe Gochnatieae (Funk et al. 2014) showed eight well-supported clades: most species had previously been included in the large genus *Gochmatia*.

All but one of the clades had previously been recognized at the generic or subgeneric level:

- 1) *Gochmatia* Kunth: Eight species from the Central Andes (more or less equal to *G. sect. Gochmatia* of Freire et al. 2002)
- 2) *Pentaphorus* D. Don: Southern Andean clade of two species that, at various times, had been recognized as a genus, subgenus, or section (resurrected by Hind 2007).

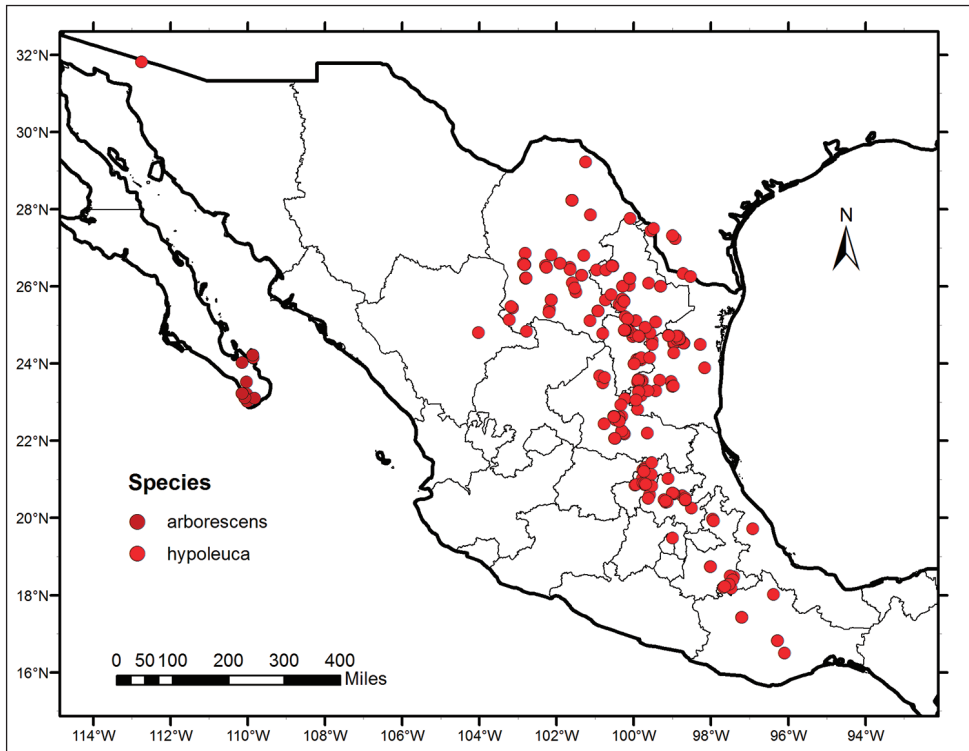


Figure 1. Distribution map of *Nahuatlea arborescens* and *N. hypoleuca*.

- 3) Mexican *Gochnatia*: A group of seven species that had never been recognized as a separate genus nor had they been placed in a section by themselves was recovered as a monophyletic group.
- 4) *Anastrophia*: The 33 Caribbean species fell into one strongly supported clade that had previously been recognized as a genus and a section (re-established as a genus by Ventosa and Herrera 2011a; Robinson and Funk 2012).
- 5) *Moquiniastrium*: The 21 species that form this clade are mainly from central and southern Brazil and previously formed the majority of *Gochnatia* sect. *Moquiniastrium* (Sancho et al. 2013).
- 6) *Richterago* Kuntze: A clade of 16 species, all endemic to the campos rupestres of Brazil (redefined by Roque and Pirani 2001, 2014).
- 7) *Cnicothamnus* Griseb.: A genus of two species found in Bolivia and northwestern Argentina: it has never been included in *Gochnatia*.
- 8) *Cyclolepis* Gilles ex D. Don: A monospecific genus that has never been included in *Gochnatia*: found from Paraguay to the northern Patagonia area of Argentina. This lineage was regarded as “incertae sedis” in Funk et al. (2014) and so it remains.

A key to the genera of Gochnatieae along with additional discussion on the tribe is contained in a upcoming paper (Funk et al. in prep).

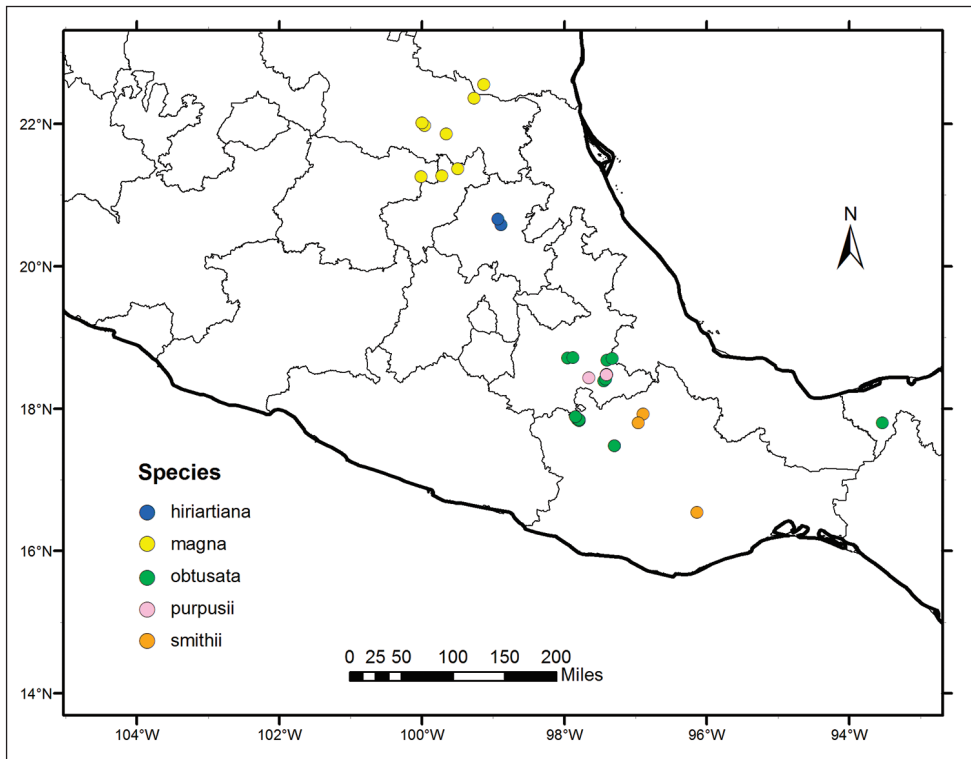


Figure 2. Distribution map of *Nahuatlea hiriartiana*, *N. magna*, *N. obtusata*, *N. purpusii*, and *N. smithii*.

In the Funk et al. biogeographic analysis (2014), it was hypothesized that the tribe had a southern South America origin (including the Central and Southern Andes, Argentina, and southern Brazil). Based on this, plus the fact that the Mexican clade is the sister group of the Caribbean clade (*Anastrophia*) suggests, or is best explained by, a dispersal event from Southern South America to Mexico and from Mexico to the Caribbean. We order the dispersal events in this direction because the Mexican *Gochnatia* are morphologically more similar to the Andean genus *Gochnatia* s.s. than the Caribbean species. This Mexican + Caribbean clade (MCC) is believed to have separated from the rest of the Gochnatieae between 11 and 23 mya at a time when there was a gradual climate warming (early Miocene; Petuch 2003, Zachos et al. 2001). MCC is the sister group of a large clade containing *Richterago* + *Moquiniastrium* (RM) which is mainly from Brazil and Southern South America. The sister groups to these two large clades (MCC + RM) are from the Andes (*Gochnatia* s.s., *Pentaphorus*, *Cnicothamnus*), so just where in southern South America the MCC clade originated is uncertain especially since some of the sister group relationships are not well supported, although all of the segregate genera are individually clearly monophyletic.

The Mexican members of *Gochnatia* clearly do not belong in the genus *Gochnatia* s.s., therefore, we are here describing the genus *Nahuatlea* for these seven species.

Materials and methods

All types and other specimens deposited at LP and US were examined. The remaining types were viewed on line using the JSTOR-GP portal (<http://plants.jstor.org>; Fig 3).

Distributions are based on data derived from databasing and georeferencing the collections at US (available online <http://collections.mnh.si.edu/search/botany/>) with additional records from ARIZ (<http://ag.arizona.edu/herbarium/home>), MEXU (<http://unibio.unam.mx/minero/index.jsp?accion=sc&colecciones=MEXU>, Herbario), MO (<http://www.tropicos.org/Home.aspx>), TEX (http://orchid.biosci.utexas.edu/Texas_list.html), and NY (<http://sciweb.nybg.org/science2/vii2.asp>). When possible, records from GBIF (<http://www.gbif.org/occurrence>) were also added. Figures 1 and 2 were produced using ArcGIS v.10.2 (ESRI 2011).

Taxonomy

Nahuatlea V. A. Funk, gen. nov.

urn:lsid:ipni.org:names:60475585-2

Type: *Nahuatlea hypoleuca* (DC.) V.A. Funk

Description. *Shrubs* or trees, monoecious. *Leaves* sessile or with a short petiole of no more than 5 mm long, alternate, chartaceous or coriaceous, entire, margins revolute, usually discolorous (silvery or cinereous-tomentose beneath), clustered near the ends of the branches especially late in the flowering cycle. *Heads* arranged in clusters, rarely solitary, most branches with an apical cluster; sessile or short-pedunculate, peduncles commonly densely scaly-bracted resembling the lowermost involucre bracts, homogamous (flowers bisexual), discoid; involucre obconic (turbinate) or campanulate, shorter than the flowers; phyllaries imbricate, 4–10 seriate, graduate, coriaceous or subcoriaceous. *Flowers* with corollas homomorphic, white or yellow, actinomorphic, deeply 5-lobed, lobes equal or shorter than the tube, revolute; anthers calcarate, caudate, anther apical appendages apiculate, tails 1–3 mm long, entire or fimbriate; styles rounded at apex, glabrous, style branches concave. *Achenes* 5-ribbed sericeous, cuneate-cylindrical, carpopodium conspicuous. *Pappus* of scabrid bristles, uni- or biseriate, graduated (varying in length) and equally wide throughout or rarely flattened at the tips, ca 1 cm long. [7 species]

Remarks. *Nahuatlea*, with some exceptions, is characterized by a combination of characters: short leafy branchlets, entire and revolute blade margins, clusters of sessile or short-pedunculate heads at or near the tips of branches; densely scaly-bracted peduncles (when present); and a pappus that is biseriate, graduated, and equally wide throughout. Most of the exceptions are found in the recently described *Gochnatia hiriartiana* (Medrano, Villasenor & Medina, 2004) which has solitary heads, and a uniseriate pappus with bristles that are flattened at the tips. However, recently produced sequence data including those of *G. hiriartiana* support *Nahuatlea* as monophyletic (Funk, unpublished).



Figure 3. Images of four type specimens: **A** *Nahuatlea arborescens* (UC holotype) **B** *N. smithii* (K lectotype) **C** *N. obtusata* (US holotype) **D** *N. hypoleuca* (G holotype). [Furnished by the respective herbaria.]

Etymology. The genus name was selected to honor the indigenous people of eastern central Mexico by naming it after their language. The name is derived from *Nahuatl*, a language of the *Nahuan* branch of the Uto-Aztecan language family (known informally as Aztec). It is spoken by an estimated 1.5 million people, most of whom live in Central Mexico. *Nahuatl* has been spoken in Central Mexico since at least the 7th century AD and it was the language of the Aztecs who dominated what is now central Mexico during the Late Postclassic period of Mesoamerican history. Today the *Nahuatl* language is spoken in the Mexican states of Durango, Guerrero, Hidalgo, Mexico, Michoacan, Morelos, Oaxaca, Puebla, Tlaxcala, and Veracruz. The distribution of the new genus, *Nahuatlea*, in central Mexico has substantial overlap with the area so it is appropriate to use it for the name of the new genus (<http://en.wikipedia.org/wiki/Nahuatl>).

Key to species of *Nahuatlea*

- 1 Involucre campanulate or broadly obconic, bracts woolly tomentose or puberulous abaxially; corollas yellow **2**
- Involucre narrowly cylindrical or narrowly obconic, bracts glabrous (may be ciliolate); corollas white or yellow (the latter only in *N. arborescens*) **4**
- 2 Heads with 200–230 flowers; involucre 25–35(–40) mm in diameter; corolla 13–22 mm long ***N. biriartiana***
- Heads with 12–50 flowers; involucre 5–12 mm in diameter; corolla 8–12 mm long **3**
- 3 Leaves 5–10 × 4–6.5 cm; involucre 10–12 mm wide; heads with ca. 50 flowers; 3–5 heads per cluster; pappus 9 mm long, bristles uni-seriate; shrub or small tree 2.5–4.5 meters ***N. magna***
- Leaves 1.8–3.0 × 0.5–1.4 cm; involucre 5–6 mm wide; heads with 12–18 flowers; 10–15 heads per cluster; pappus 7.5 mm long, bi-seriate; shrub (no size given) ***N. purpusii***
- 4 Leaves glabrescent abaxially; involucre bracts in 8–10 series; heads 6–8 mm wide; 13–20 flowers per head, corollas yellowish, 12 mm long; trees of 3–8 m, trunks 20–30 cm in diameter ***N. arborescens***
- Leaves tomentose abaxially; involucre bracts in 3–7 series (bracts on peduncle not included); heads ca. 3 mm wide; (3–)5–7 flowers per head, corollas white, 5–12 mm long; shrubs or small trees of 1–7 m, stems less than 10 cm in diameter **5**
- 5 Leaves 4–8 mm × 3–5 mm, broadly ovate; leaves at the glomerule shorter than the heads; involucre bracts usually glabrous ***N. obtusata***
- Leaves 25–50 mm × 15–20 mm, oblong-lanceolate; leaves at the glomerule longer than the heads; involucre bracts ciliolate or ciliolate-tomentose on the margins **6**

- 6 Involucral bracts in 5–7 series; corollas 8.5–9 mm long; anther tails entire; involucre 6–8 mm tall; shrub; blade oblong-lanceolate, apex acute, tomentose below.....*N. smithii*
- Involucral bracts in 3–5 series; corollas 7–12 mm long; anther tails fimbriate; involucre 4–7 mm tall; shrub to small tree; blade narrowly elliptic, apex rounded, mucronate, whitish-tomentose below.....*N. hypoleuca*

1. *Nabuatlea hiriartiana* (Medrano, Villaseñor & Medina) V.A.Funk, comb. nov.

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Fig. 4

Gochnatia hiriartiana Medrano, Villaseñor & Medina. Novon 14: 435–436. 2004.

Type. Mexico. Hidalgo: Municipio Meztlán, 3 km al E de Milpa Grande, barranca sobre el Río Amajac, 19 Sep 1996, *F. González-Medrano, G.G. Hernández & G. Rodríguez 17920* (Holotype: MEXU 00316791; Isotypes, IEB 000177217, MO 3024215, TEX 00208274, XAL 0106702).

Description. *Shrub* 1.0–1.5 m tall; *leaves* coriaceous, blades 1.0–3.5 × 1–2 cm, elliptic to slightly ovate, yellowish-tomentose below; heads sessile, solitary or in clusters of 2–3 at apex of branches, few clusters per plant; *involucre* campanulate, 15–20 mm tall × 25–35(–40) mm wide, bracts in 5–6 series, densely puberulous abaxially; *flowers* 200–230 per head; corollas light yellow, 13–22 mm long; *anther* base caudate, tails 2.0–2.5 mm long, entire; *pappus* ca. 1 cm long, bristles biseriate, broadening slightly at the apex.

Distribution. MEXICO: only known from two collections both in Hidalgo.

2. *Nabuatlea magna* (M.C. Johnst. ex Cabrera) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:60475587-2

Fig. 5

Gochnatia magna M.C. Johnson ex Cabrera, Revista Mus. La Plata, Secc. Bot., 12(66): 147–150. 1971.

Type. Mexico. Tamaulipas: half a mile east of Nuevo Morelos, 25 Oct 1959, *J. Graham & M.C. Johnston 4485* (Holotype: MEXU 01220108; Isotype: TEX 00374383).

Description. *Shrub or small tree* 2.5–4.5 m tall; *leaves* chartaceous, blades 5–10 × 4.1–6.2 cm, widely elliptic, glabrescent adaxially, woolly abaxially; *heads* short pedunculate in clusters of 3–5 at the apex of branches, surrounded by leaves, few clusters per plant; *involucre* campanulate (especially at early flowering), 13–15 mm tall × 10–12 mm wide, bracts in 5–7 series, woolly adaxially; *flowers* ca. 50 per head; *corollas* yellow,

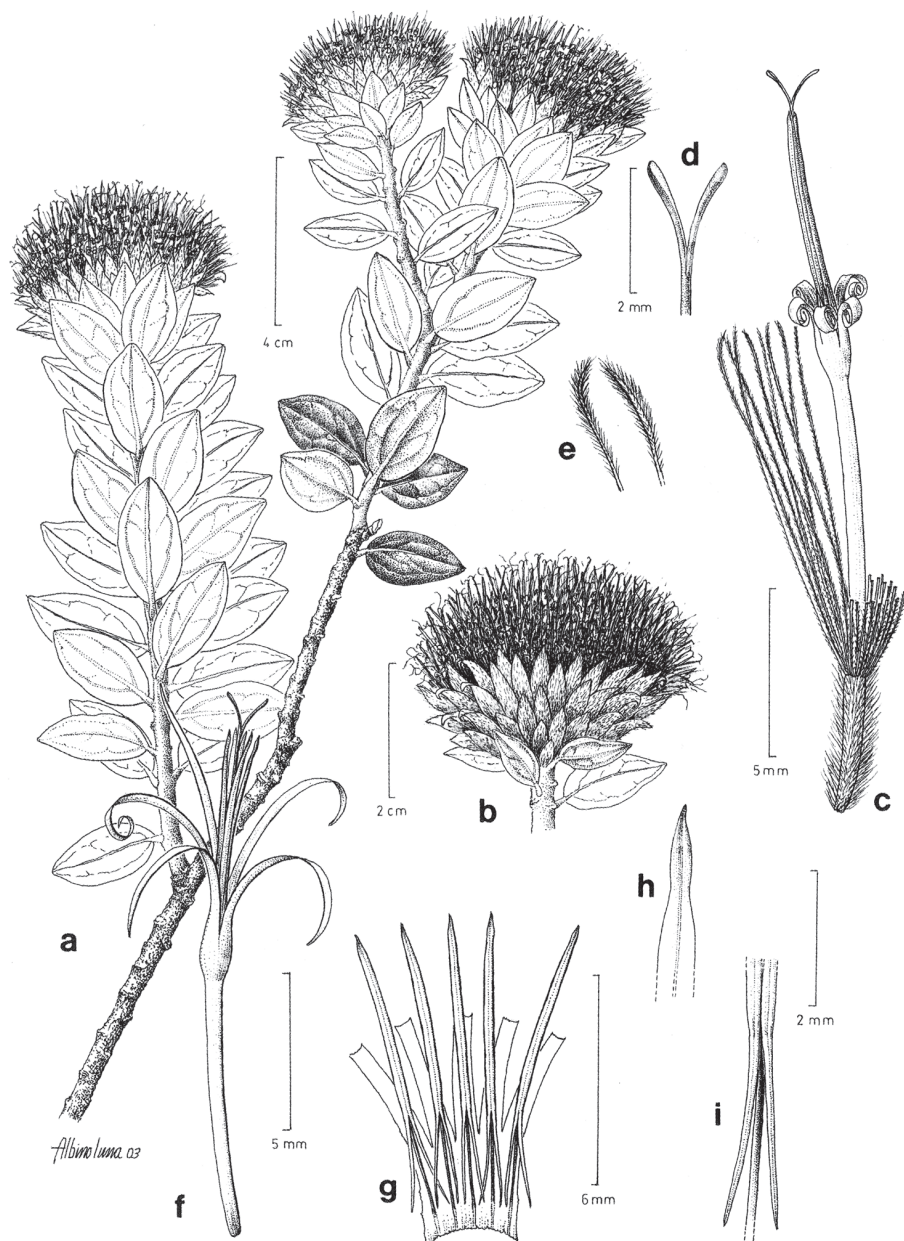


Figure 4. Drawing of *Nahuatlea hiriartiana*. **A** Habit **B** Head **C** Flower with achene **D** Style **E** Apex of pappus bristles **F** Flower **G** Anthers **H** Anther apex **I** Anther tails. [Modified from González-Medrano et al. 2004.]

12 mm long; *anther* base caudate, tails ca. 1 mm long, entire; *pappus* ca. 9 mm long, bristles uniseriate, broadening, flattened, and somewhat darker at the apex.

Distribution. MEXICO: Tamaulipas and San Luis Potosi.

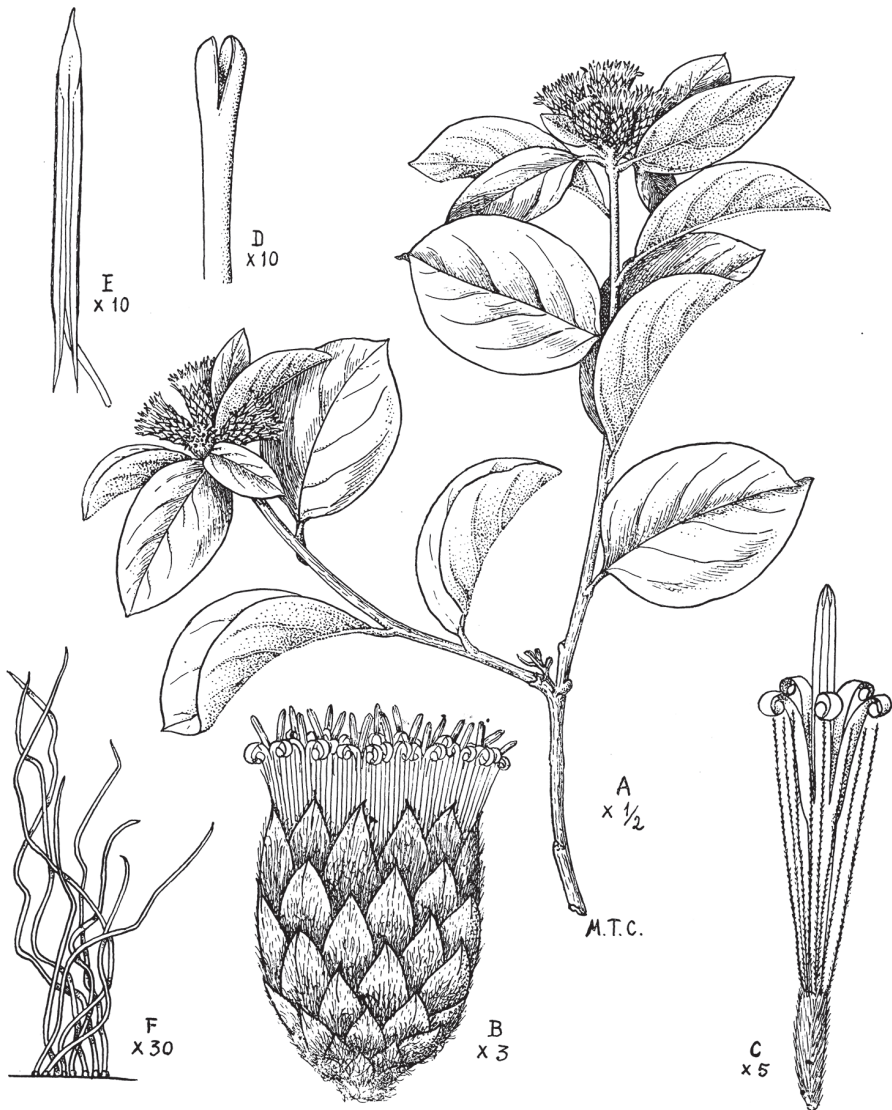


Figure 5. Cabrera's drawing of *Nahuatlea magna*. **A** Habit **B** Head **C** Flower **D** Style **E** Anther **F** Pubescence. [Modified from Cabrera 1971.]

3. *Nahuatlea purpusii* (T.S. Brandege) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:77174064-1

Fig. 6

Gochnatia purpusii T.S. Brandege, Zöe 5(11): 240. 1906.

Type. Mexico. Puebla: Tehuacan, 1800 m, June 1905, *C.A. Purpus 1164* (Holotype: UC 91904; Isotypes: BM 000947904, F 0050268, GH 00008382, NY 00169558,

RSA 0001214). [Specimens at P (P00703338 & P00703339) and E (E00413001) have the correct collecting number but incorrect dates and may or may not be type material; Cabrera (1971) cites isotypes at G, MO, and MEXU that are not found in JSTOR-GP. MO has confirmed that the specimen is not in their collection but there is no information on the others.

Description. *Shrub* of unknown size (one isotype has what appears to be “5–6 m” written on the label); *leaves* coriaceous, petiole minute (1–2 mm), blade 1.8–3.0 × 0.5–1.4 cm, elliptical or slightly lanceolate or oblanceolate, glabrescent adaxially, white flocculent-tomentose abaxially; heads sessile, in few clusters of 8–15, clusters all at apex of branches; *involucre* campanulate (especially at early flowering), ca. 10 mm tall × 5–6 mm wide, bracts in 5–6 series, densely woolly abaxially; *flowers* 12–18 per head; corollas yellowish, ca. 8 mm long; *anther* base caudate, tails ca. 1 mm long, fimbriate; *pappus* ca. 7.5 mm long, bi-seriate with slender bristles.

Remarks. Cabrera (1971) and Jervis (1954) disagree somewhat on the size of the leaf blade: Cabrera lists it as 18–30 mm × 5–14 mm and Jervis has 2.0–2.5 cm × 0.5–1.0 cm. Our measurements, taken from the Holotype, fall within those given by Jervis, however, the isotypes may show the greater range given by Cabrera.

Distribution. MEXICO: known only from four collections all from Puebla.

4. *Nahuatlea arborescens* (Brandeggee) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:77174065-1

Fig. 3B

Gochnatia arborescens Brandeggee, Zöe 5(9): 163. 1903.

Type. Mexico. Baja California: Cañón de Santa María, El Juste, 1 Mar 1898, C.A. Purpus s.n. (Holotype: UC 91900; possible Isotypes: K 000502538; GH 00008379; US 00119526).

Note. Determining what may or may not be type material is difficult; all proposed types are *Purpus* s.n. collections but there are different collection dates and locality information. The Holotype is one of two different collections mounted on the same sheet one of which is annotated as “n. sp.” and “type”. That specimen also has a hand-written note that says “The year doubtless 1901 RM” indicating that the date on the sheet January–March 1898 is not correct. The information found on the three possible isotypes is nearly identical (Lower California, San Felipe, Cape Region Lower California, Jan–Mar 1901) but the information is different from the locality information on the Holotype. All of the “type material” specimens are the same species so there is little doubt that this is the correct name for this entity but someone more familiar with the work of Purpus (who seems to have confusing dates and numbers) and Brandeggee will need to investigate this further to determine if the three listed specimens are actually isotypes.

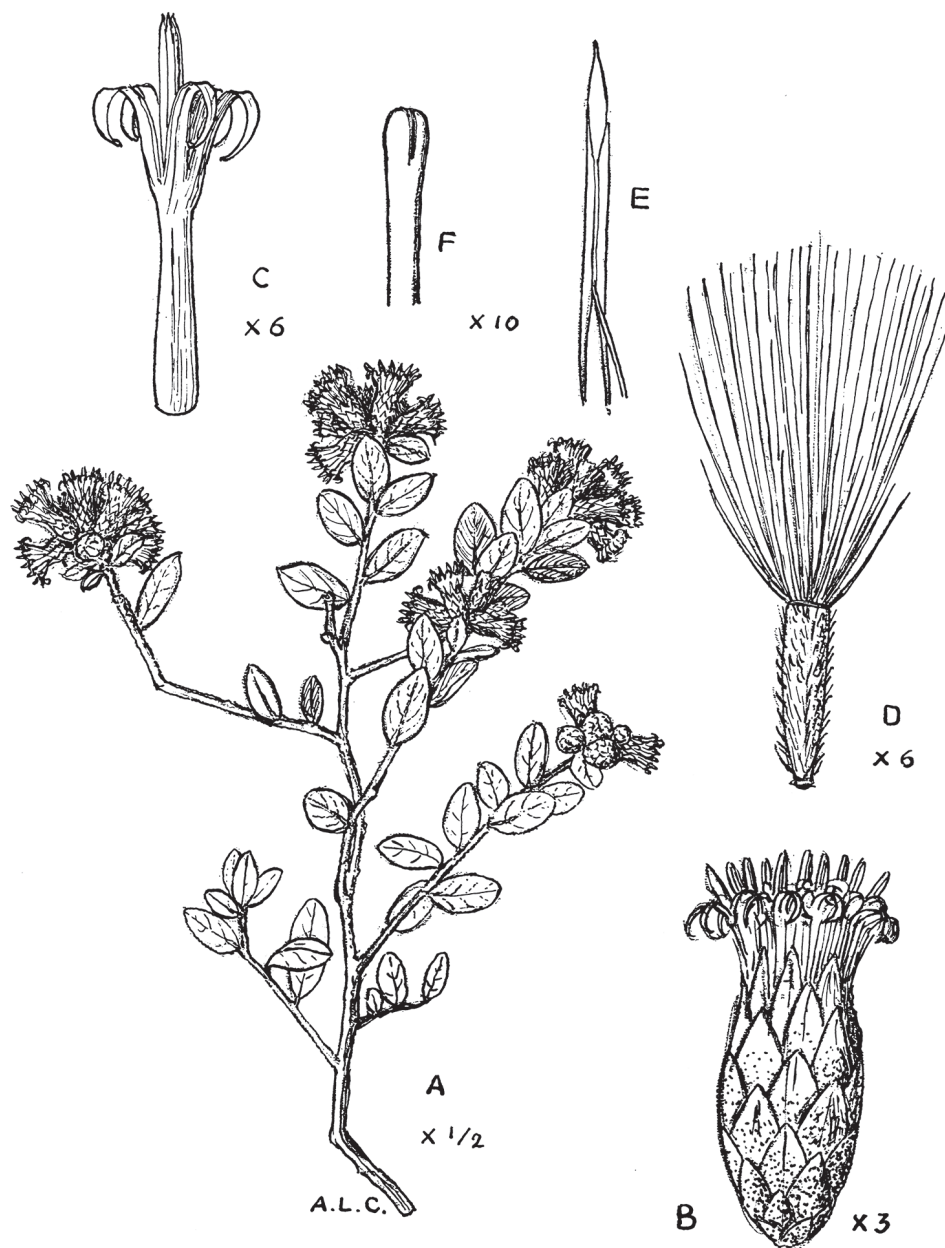


Figure 6. Cabrera's drawing of *Nabuatlea purpusii*. **A** Habit **B** Head **C** Style **D** Achene with pappus **E** Anther **F** Style. [Modified from Cabrera 1971.]

Description. *Tree* 3–8 m tall, trunk 20–30 cm in diameter; *leaves* chartaceous, blades 3.5–6.5 cm × 2.5–4.5 cm, ovate to elliptic, cuneate or rounded at base, glabrescent on both faces; heads short-pedunculate, solitary or more usually in loose clusters of 2–20 at apex of branches, few clusters per plant; *involucre* cylindrical to narrowly ob-

conic depending on age, 10–15(20) mm tall \times 6–8 mm wide at anthesis, bracts in 8–10 series, glabrous; *flowers* 13–20 per head; corollas yellowish, 12 mm long; *anther* base caudate, tails ca. 3 mm long, entire; *pappus* ca. 11 mm long, bristles slender, biseriate.

Remarks. Cabrera (1971) and Jervis (1954) disagree somewhat on the size of the leaf blade: Cabrera lists it as 35–65 mm \times 25–45 mm and Jervis has 5 cm \times 3–4 cm. Specimens available to us agree with the range given by Cabrera.

Distribution. MEXICO: known only from Baja California Sur.

5. *Nahuatlea obtusata* (S.F. Blake) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:77174066-1

Figs 3D, 7

Gochnatia obtusata S.F. Blake, Contributions from the United States National Herbarium 22: 652. 1924.

Type. Mexico. Puebla: dry limestone hills at Tehuacan, 20 Dec 1895, *C.G. Pringle* 6253 (Holotype: US 00119530 [254705]; Isotypes: A 00008380, BM 000947903, BR 0000005318124, CM 2403, E 00413002, JE 00000693, K 000502539, GH 00008381, MEXU 01220107, MO 1544305, NDG 63791, NY 00169557, P 00703351, P 00703352, PH 00025961, S 10-11705, TEX 00000454, US 01100608). [Cabrera (1971) mentions additional specimens at F, G, M, UC, and W but these were not found in JSTOR-GP.]

Description. *Shrub* 1.0–1.5(–2.6) m tall; *leaves* coriaceous, (4.5)5–8(20) \times 3–5 mm, broadly elliptic, apex rounded to obtuse, rounded at base, glabrous adaxially, cinereous-tomentose abaxially; heads short-pedunculate (ca. 2 mm long), in clusters of 10–20 heads, at apices of branches; *involucre* narrowly obconic, 6–8 mm tall \times 2.8–3.2 mm wide, bracts in ca. 5 series, glabrous; *flowers* 5–6 per head; corollas white, 6.5–7.5 mm long; *anther* base caudate, tails ca. 2 mm long, fimbriate; *pappus* 6.0–7.5 mm long, bristles biseriate, broadening slightly at the tips.

Jervis (1954) said that the leaf length is “rarely up to 2 cm” and the width is “less than 1 cm” and Cabrera (1971) lists the length as 4–20 \times 3–13 mm. Both seem to be correct; we found only one specimen that had leaves 20 mm long and all but two were less than 1 cm.

Distribution. MEXICO: Puebla and Oaxaca.

Remarks. *Gochmatia obtusata* was described by S. F. Blake (1924) and accepted as a good species by Jervis (1954). Cabrera placed it as a subspecies of *G. hypoleuca* as did Freire et al. (2002). The difference of opinion is based on the importance one gives to the characters that separate the two entities. Blake stated that *G. hypoleuca* could be separated from *G. obtusata* by the following characters: leaves chiefly elliptic, apex acute or acutish and mucronate, 20–50 mm \times 8–15 mm; involucre 5–6 mm tall, phyllaries obtuse to acute or obtusely acuminate. We have added some additional characters: shrub or small tree 3–7 m; heads arranged in short clusters or panicles; involucre with bracts in 3–5 series; corolla



Figure 7. Cabrera's drawing of *Nahuatlea hypoleuca*. **A** Habit **B** Head **C** Floret **D** Style **E** Anther **F** Pubescence. [Modified from Cabrera 1971.]

10–12 mm long; style branches 0.7–1 mm long; pappus up to 6.5 mm. In contrast, *G. obtusata* has the following: leaves broadly elliptic, apex broadly rounded to obtuse, not mucronate, 4.5–20 mm × 3–13 mm; involucre 6.5–7.5 mm tall, involucre bracts acute to sharply acuminate; style branches 0.5–0.7 mm long. Additional characters for *G. obtusata* include: shrub of 1.0–2.6 m; heads glomerate at tips of branches and in clusters of 1–several in the subterminal axils; involucre with bracts in 5–6 series; corollas 6.5–7.5 mm long; pappus up to 7.5 mm long. In the field the difference is striking with the larger more robust *G. hypoleuca* contrasting with the smaller, more compact *G. obtusata*. Therefore we have chosen to recognize *G. obtusata* as a separate species.

6. *Nahuatlea hypoleuca* (DC.) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:60475588-2

Figs. 3A, 8

Moquinia hypoleuca DC., Prodrum 7(1): 23. 1838.

Gochnatia hypoleuca (DC.) A. Gray, Proceedings of the American Academy of Arts and Sciences 19: 57. 1883.

Type. Mexico. Neuvo León: Monterrey, January 1828, *Berlandier 1391* (Holotype: G 00223915; Isotypes: BM 000947902, GH 00010616, K 000502540, MO 100221306, NY 00230667, P 00703318, P 00703319, P 00703320, US 00119521). [There is a second specimen at NY that is a possible isotype NY 00230666; the specimen from HAL 0112991 may be an isotype but the dates don't match and the number is listed at "1391 s.n."]

Description. *Shrub* or small tree, 2–5(–7) m tall; *leaves* coriaceous, 2–5 × 0.9–1.5 cm, narrowly elliptic, apex obtuse, mucronate, attenuate at base, glabrous adaxially, cinereous-tomentose abaxially; heads sessile or very short pedunculate, in clusters of 5–15 heads at apices and axils of branches, many clusters per plant; *involucre* narrowly obconic, 4–7 mm tall × ca. 3 mm wide, bracts in ca. 3–5 series, ciliolate-tomentose on the margins but otherwise glabrous; *flowers* 5–7 per head; *corollas* white, 10–12 mm long; *anther* base caudate, tails ca. 1 mm long, fimbriate; *pappus* ca. 6.5–7.5 mm long, bristles biseriate, of various lengths and broadening slightly at the tips.

Distribution. MEXICO: Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosi, Queretaro, Hidalgo, and Michoacán. UNITED STATES: Arizona, Texas.

Remarks. According to the Texas A&M University website (<http://aggie-horticulture.tamu.edu/ornamentals/nativeshrubs/gochnatihypole.htm>) the common names for this shrub in Texas are Chomonque and Ocote. The website goes on to say that it is an "attractive, little-known shrub native to extreme South Texas, Chomonque flowers in the winter and has striking bi-colored leaves, very dark green on top and white and feltish underneath. The white flowers that appear from November to February are weakly fragrant and attract bees and many species of butterflies. It grows on gravel and caliche in South Texas shrub lands, and is extremely drought and heat tolerant. A specimen at the San Antonio Botanical Gardens has proved cold hardy and evergreen, but its cold-hardiness farther north is untested." The website lists the USDA hardiness zone 9.

7. *Nahuatlea smithii* (B.L. Robinson & Greenm.) V.A.Funk, comb. nov.

urn:lsid:ipni.org:names:77174067-1

Fig. 3C

Gochnatia smithii B.L. Robinson & Greenm., Proc. Amer. Acad. Arts 32: 50. 1896.

Type. Mexico. Oaxaca: On the hills of Cuicatlan, April 1895, *L.C. Smith 363* (Lectotype: K designated by Cabrera, 1971: 140; Isolectotypes: GH 00008383, MEXU 00525748).



Figure 8. Photos of *Nabuatlea hypoleuca* from southern Texas. Habit photo from La Puerta, Texas; Fruiting photo from Vaquillas Road, Texas; Flowers from Yturria Brush, Texas. [photos by T. F. Patterson.]



Figure 9. Photos of *Nahuatlea obtusata*, all from Oaxaca, Mexico, showing habit and flowering heads of different ages. [photos by V. A. Funk.]

Description. *Shrub* of undetermined size; *leaves* clustered near the ends of the branches, sub-coriaceous, 3–5 × 0.8–1.8 cm, ovate, obtuse, cuneate at base, glabrescent adaxially, cinereous-tomentose abaxially; heads slender, short-pedunculate, in dense clusters at the ends of branches, sometimes several clusters in a dense panicle, many clusters per plant; *involucre* narrowly obconic, 6–8 mm tall × ca. 3 mm wide, bracts in 5–7 series, ciliolate on the margins otherwise glabrous; *flowers* (3–)5–7 per head; *corollas* white, 8.5–9.0 mm long; *anther* base caudate, tails ca. 1.5 mm long, entire; *pappus* ca. 6.5–7.5 mm long, bristles biseriate, not obviously broadened at tips.

Remarks. According to Jervis (1954) the “...small branches are less wooly than most other species.”

Distribution. MEXICO: known only from Oaxaca.

Acknowledgements

No study of this type can be completed without the help of many people. Here we attempt to thank them; we hope we have not missed someone. We thank Thomas F. Patterson (TEX) for making several trips to find *N. hypoleuca* in Texas and for collecting leaf material on silica and taking beautiful photos; Tom Wendt (TEX) for supplying information on both *N. hypoleuca* in Texas and on the isotype of *N. hiriartiana*; Robert McGill (MO) for locating three missing isotypes; G, K, UC and US for providing high resolution images of the type material; JSTOR-GP for the always useful images of types from around the world (<http://plants.jstor.org>); *Revista del Museo de La Plata* for permission to use the drawings from Cabrera (1971); Alice Tangerini (US) for cleaning up the scans of the drawings and making the final plates for the type, photos and illustrations; Sara Alexander (US) for the final maps; Kenia Valesco (SERO) for help in the field searching for the elusive “Mexican *Gochmatia*”. Helpful reviews were provided by Michael Dillon (F) and Sterling Keeley (HAW) and the *Phytokeys* Asterales editor Alexander Sennikov. Of course we are very grateful for the funding provided by the following agencies without which this work would not have been possible: Smithsonian Institution (Peer Reviewed Grants), National Museum of Natural History (small grant program); Department of Botany (US) for providing a Cuatrecasas Travel Award for Roque who spent two months at US; ANPCyT and CONICET to G.S.; CNPq/Pq, REFLORA and PRONEM to N.R. One of the villages we stayed in on our trip to Oaxaca was La Ventosa, very close to Juichitan. The village was heavily impacted by the recent earthquake that hit Oaxaca, Mexico and some of our colleagues lost their homes and the newly opened cultural center was destroyed. If you are interested in helping please contact the corresponding author for information.

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Reduction of the Hawaiian genus *Platydesma* into *Melicope* section *Pelea* (Rutaceae) and notes on the monophyly of the section

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Abstract

Platydesma, an endemic genus to the Hawaiian Islands containing four species, has long been considered of obscure origin. Recent molecular phylogenetic studies have unequivocally placed *Platydesma* within the widespread genus *Melicope* as sister to the rest of the Hawaiian species of *Melicope*. This makes submerging *Platydesma* into *Melicope* necessary. We make the necessary new combinations: *Melicope cornuta* (Hillebr.) Appelhans, K.R. Wood & W.L. Wagner, *M. cornuta* var. *decurrens* (B.C. Stone) Appelhans, K.R. Wood & W.L. Wagner, *M. remyi* (Sherff) Appelhans, K.R. Wood & W.L. Wagner, and *M. rostrata* (Hillebr.) Appelhans, K.R. Wood & W.L. Wagner. An additional species that has been recognized within *Platydesma* should now be recognized under its original name *M. spathulata* A. Gray. All Hawaiian species belong to *Melicope* section *Pelea*. Our molecular phylogenetic studies also showed that in addition to merging *Platydesma* into section *Pelea*, five species described from New Caledonia need to be excluded from the section in order to achieve monophyly of section *Pelea*.

Keywords

Hawaiian Islands, *Melicope*, New Caledonia, *Platydesma*, Rutaceae

Introduction and discussion

The genus *Melicope* J.R. Forst. & G. Forst. is the largest genus within Rutaceae, with approximately 230 species ranging throughout the Malagasy and Indo-Himalayan regions, Southeast Asia, Australasia, and across the Pacific Islands (Hartley 2001). One of the centers of diversity is the Hawaiian Islands, where *Melicope* (including *Platydesma*) is the fourth largest radiation with 54 species after the Hawaiian Lobeliads (Campanulaceae), *Cyrtandra* J.R. Forst. & G. Forst. (Gesneriaceae), and mints (Lamiaceae) (Hartley and Stone 1989, Wagner et al. 1990, Hartley 2001, Wood et al. 2017). It furthermore represents the largest radiation of woody plants on the Hawaiian Islands (Wagner et al. 1990). Hawaiian *Melicope* are an example of an adaptive radiation, as the genus has undergone spectacular morphological and ecological diversification (Stone 1966, Carlquist 1974). Hawaiian *Melicope* taxa, and another rutaceous genus *Platydesma* H. Mann have been widely decimated throughout the Hawaiian Islands due to habitat alteration and introduced organisms; many extant species of *Melicope* and all taxa within *Platydesma* except for *P. spathulata* (A. Gray) B.C. Stone are considered rare, vulnerable, or endangered. At least five species of *Melicope*, namely *M. balloui* (Rock) T.G. Hartley & B.C. Stone, *M. macropus* (Hillebr.) T.G. Hartley & B.C. Stone, *M. nealae* (B.C. Stone) T.G. Hartley & B.C. Stone, *M. obovata* (H. St. John) T.G. Hartley & B.C. Stone and *M. wailauensis* (H. St. John) T.G. Hartley & B.C. Stone, are presumed to be extinct and 11 species are known from 50 or less living individuals in the wild (Wagner et al. 1999, Wood 2011, 2014, Wood et al. 2016).

The immediate relationships of the Hawaiian endemic genus *Platydesma* (Rutaceae) have puzzled taxonomists due to the divergent floral morphology and hermaphroditic breeding system of *Platydesma* (Stone 1962a, Wagner et al. 1990, Funk and Wagner 1995). Engler (1931) placed *Platydesma* between the North American (Mexico and southwestern USA) genus *Choisya* Kunth and the New Caledonian genus *Dutailleya* Baill., while Stone (1962a) hypothesized that the genus was derived from the Australian, New Caledonian and New Guinean genus *Medicosma* Hook. f. Even though *Dutailleya* proved to be part of *Melicope*, and *Medicosma* is the sister genus of *Melicope*, neither of these taxa are immediate relatives of *Platydesma* and the Hawaiian *Melicope* species (Appelhans et al. 2014a). While most *Melicope* species have a dimorphic breeding system (Sakai et al. 1995, Hartley 2001), *Platydesma* is a peculiar taxon for its monadelphous stamens and bisexual flowers (Hillebrand 1888, Kubitzki et al. 2011). In addition, *Platydesma* has unique chemical characteristics; the leaves, bark and wood emit a semeniferous odor due to the unique alkaloid platydesmine (Werny and Scheuer 1963).

Recent molecular phylogenetic studies provided unequivocal evidence for the placement of *Platydesma* within *Melicope*, as sister to the Hawaiian taxa in *Melicope* section *Pelea* (Harbaugh et al. 2009, Appelhans et al. 2014a, 2014b; Fig. 1). These data are consistent with Carlquist's (1974) hypothesis of a Hawaiian origin of *Platydesma*, as well as with Asa Gray's classification of *Platydesma* as *Melicope* taxa (Stone 1962b). This represents an example of divergent evolution in an insular setting. Despite the dif-

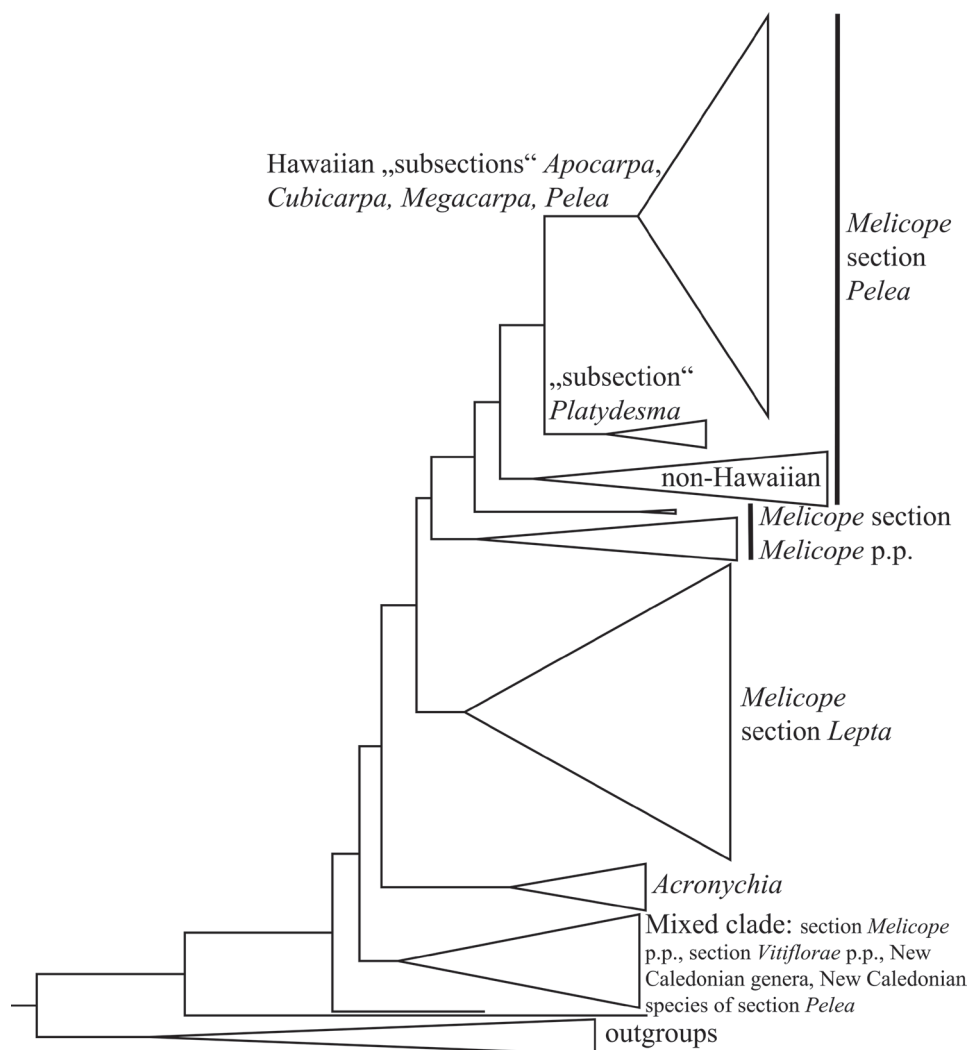


Figure 1. Phylogenetic affinities of Hawaiian *Melicope* section *Pelea* (incl. *Platydesma*) based on five plastid and nuclear markers (modified from Appelhans et al. 2014a). “Subsections” *Apocarpa*, *Megacarpa* and *Pelea* contain exclusively Hawaiian and Marquesan species and “subsection” *Platydesma* includes the former Hawaiian genus *Platydesma*. The New Caledonian species of *Melicope* section *Pelea* are part of the “mixed clade” and we therefore propose to exclude them from section *Pelea*.

ferences in morphology and breeding system, however, the seedling stages of *Melicope* and *Platydesma* are homologous (Stone 1962b).

The Hawaiian Islands have the highest rate of dioecy in the world, evolving *in situ* in at least 12 lineages, possibly as a selective force to avoid inbreeding depression, affect resource allocation, and sexual selection (Sakai et al. 1995). Sakai et al. (1995) hypothesized that Hawaiian *Melicope* and *Platydesma* both arose from separate colonizations; the *Melicope* colonist was dimorphic while the ancestor of *Platydesma* was monomorphic.

The results of molecular phylogenetic analyses (Harbaugh et al. 2009, Appelhans et al. 2014a,b) demonstrate that Hawaiian *Melicope* and *Platydesma* most likely arose from a single ancestor. The ancestor of Hawaiian *Melicope* + *Platydesma* was likely dioecious, because the closest relatives of the Hawaiian species (=the remainder of *Melicope* section *Pelea* excluding species from New Caledonia) are almost exclusively dioecious (Hartley 2001). Only the widespread *M. triphylla* (Lam.) Merr. and the New Guinean endemic *M. conjugata* T.G. Hartley, which are normally dioecious, are in rare cases monoclinal (*M. triphylla*, *M. conjugata*) or andromonoecious (*M. triphylla*). Therefore, *Platydesma* represents a rare reversal from dioecy to synoecy as Carlquist (1974) had hypothesized. Despite the differences in flower, seed and fruit characteristics (*Melicope* has dehiscent fruits while *Platydesma* has indehiscent or tardily dehiscent fruits), Sakai et al. (1995) hypothesized that both genera are insect pollinated, and have undergone long distance dispersal through bird ingestion. Therefore, the mechanisms that may have lead to this reversal in breeding system are unknown, but with discovery of large quantities of nectar produced in the flowers it is likely the breeding system change is part of the shift to bird pollination.

The copious nectar production and the stamens connate into a cup-like structure that holds accumulating nectar in *Platydesma* flowers suggest adaptations to bird-pollination. A similar case of adaptation to bird-pollination can be found in Hawaiian *Schiedea*/*Alsiniidendron* (Caryophyllaceae) (Weller et al. 1998, Golonka et al. 2005, Wagner et al. 2005). Like in *Melicope*/*Platydesma*, adaptation to different pollination vectors has resulted in differences in flower morphology between *Schiedea* and *Alsiniidendron* that are virtually identical to those in *Melicope*/*Platydesma*, which led to the separation of the group into two genera.

To preserve the monophyly of *Melicope* section *Pelea*, *Platydesma* must be merged with *Melicope* and the New Caledonian species of section *Pelea* have to be excluded (Fig. 1). Hawaiian *Melicope* have been subdivided into the four groups *Apocarpa*, *Cubicarpa*, *Megacarpa* and *Pelea*, which were regarded as sections within the genus *Pelea* A. Gray (Stone 1969, Wagner et al. 1990). Now that *Pelea* occupies the rank of a section within *Melicope*, these four groups perhaps should be regarded as subsections. Due to the significant morphological differences between Hawaiian *Melicope* and *Platydesma* (Wagner et al. 1990), a new subsection would need to be created to accommodate *Platydesma*. However, since our molecular phylogenetic studies (Appelhans et al. 2014b) showed low resolution concerning some of the Hawaiian groups, it is premature to establish a new subsectional classification. Instead, we will await the results of our recently initiated Next-Generation Sequencing project focused on Hawaiian *Melicope*.

Hartley (2001) placed the five New Caledonian species of *Melicope* in section *Pelea*. He mentions that their “immediate and broader relationships within sect. *Pelea* are not clear” (Hartley 2001; p. 139) and that they “are probably relicts” (Hartley 2001; p. 31). Hartley listed some characters that might connect the New Caledonian and the Hawaiian species (e.g., persistent petals in three New Caledonian and two Hawaiian species, infertile antepetalous stamens in three New Caledonian species and rare occurrences in Hawaiian species). He also mentioned characters of the New Caledonian species that do not occur in other species of the section or the genus, among which are: abruptly acuminate flower

buds, and persistent and accrescent sepals and/or petals (Hartley 2001; p. 140). Molecular phylogenetic studies (Appelhans et al. 2014a,b; Fig. 1) have shown that the New Caledonian species of section *Pelea* are not directly related to the Hawaiian species and the remainder of section *Pelea*, but that they belong to a clade of taxa from New Caledonia, Australia, New Zealand and the South Pacific, including *Melicope* sections *Melicope* p.p. and *Vitiflorae* (F. Muell.) T.G. Hartley p.p., as well as the genera *Comptonella* Baker f., *Dutailleya*, *Picrella* Baill. and *Sarcomelicope* Engl. (Appelhans et al. 2014b). In line with the results of the phylogenetic reconstruction and the unusual characters mentioned by Hartley (2001), we propose to exclude the New Caledonian species from *Melicope* section *Pelea*.

Taxonomy

With four species of *Platydesma* included and five New Caledonian species excluded, *Melicope* section *Pelea* consists of 86 currently recognized species (Hartley 2001, Wood et al. 2017). The distribution of the section ranges from Borneo, the Philippines, Taiwan and the Ryukyu Islands to the Hawaiian and Marquesas Islands. In the Pacific, the section occurs on the Ryukyu Islands, Pohnpei (Caroline Islands), Bismarck Archipelago, Solomon Islands, Wallis and Futuna, Tonga, Samoa, Niue, Hawaiian Islands, and Marquesas Islands (Hartley 2001; Fig. 2). In the following synopsis sheet numbers, when available are cited for holotype specimens, and barcode numbers are provided for specimens in brackets [].

We propose the following taxonomic changes for *Platydesma*:

***Melicope* sect. *Pelea* (A. Gray). Hook. f., Gen. Pl. 1: 296. 1862.**

Platydesma H. Mann, *Proc. Bost. Soc. Nat. Hist.* 10: 317. 1866. – Type: *Platydesma campanulata* H. Mann (= *Melicope spathulata* A. Gray)

Platydesma sect. *Cornutia* B.C. Stone, *J. Arnold Arbor.* 43: 422. 1962. – Type: *Platydesma cornuta* Hillebr. (= *Melicope cornuta* (Hillebr.) Appelhans, K.R. Wood & W.L. Wagner).

Type. *Pelea clusiifolia* A. Gray (= *Melicope clusiifolia* (A. Gray) T.G. Hartley & B.C. Stone).

***Melicope cornuta* (Hillebr.) Appelhans, K.R. Wood & W.L. Wagner, comb. nov.**

urn:lsid:ipni.org:names:77174269-1

Fig. 3D

Platydesma cornuta Hillebr., *Fl. Hawaiian Isl.* 72. 1888.

Note. As was typical for Hillebrand in the Flora of the Hawaiian Islands, he cited localities for which he saw collections and would only sometimes cite collector information

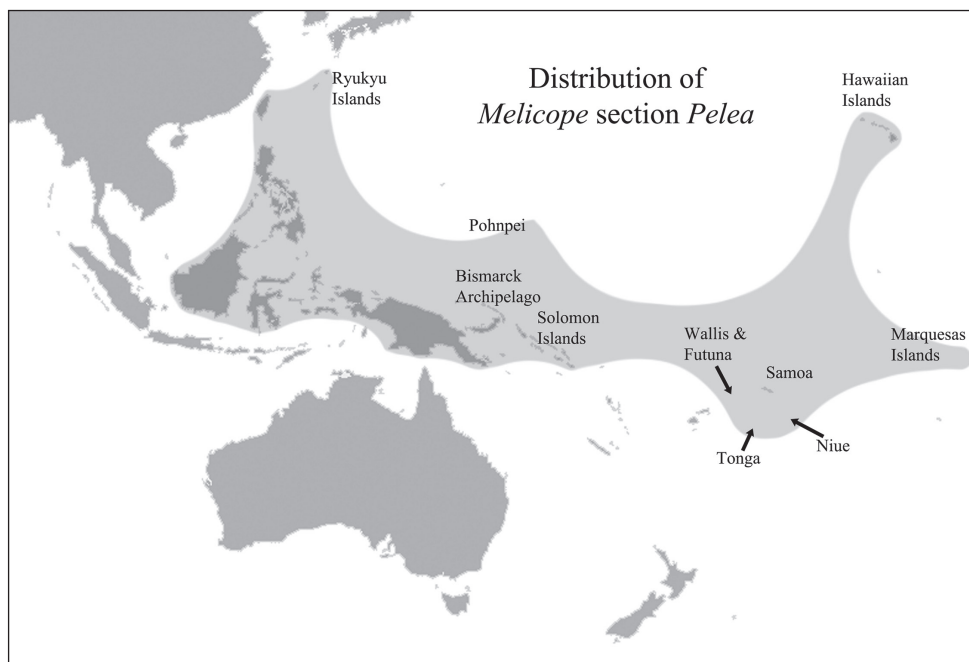


Figure 2. Distribution of the newly circumscribed *Melicope* section *Pelea*.

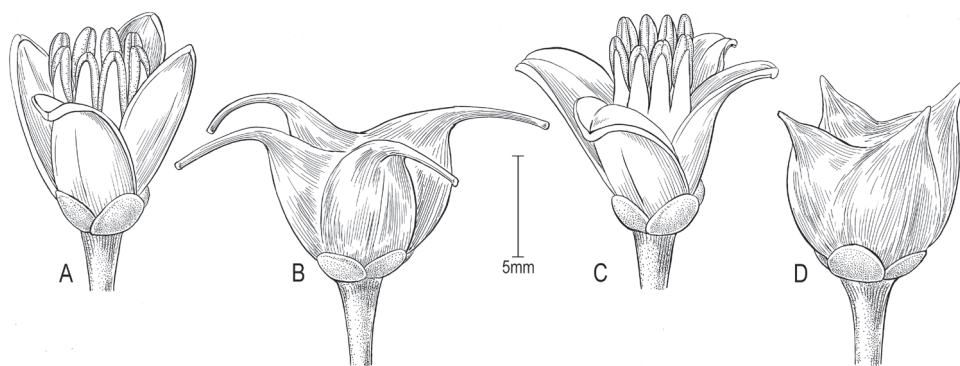


Figure 3. **A, B** *Melicope rostrata*, flower (field images of Appelhans et al. MA683, BISH, GOET), fruit (Wood and DeMotta 14490, US, and Flynn 4626, US) **C** *Melicope cornuta* var. *decurrens* flower (field images by Sebastian Marquez and Dave Fahrenwald in the Wai‘anae Mountains) **D** *Melicope cornuta* var. *cornuta* fruit (field images by Joel Lau in Nui, Ko‘olau Mountains).

(when someone other than himself made the collection). In this case he cited three localities (Halemano, Wailupe, and Pauoa) indicating he collected or saw material from each one of them. As such these collections must be considered syntypes. Stone (1962a) indicated the K sheet and the GH sheet cited below as holotype and isotype. They represent inadvertent selection of a lectotype and isolectotype. A number of additional

syntypes from all three cited localities are known but can with certainty not be considered isolecotypes because the two specimens selected by Stone have no locality on the label other than O‘ahu and Kaua‘i.

Type. O‘AHU: *s. l.*, *W. Hillebrand s.n.* (lectotype, designated by Stone, *J. Arnold Arbor.* 43: 423. 1962: K [K000717606, image!]; isolecotype: GH [GH00044164, image!]. Additional syntypes: O‘ahu, Halemanu, *Hillebrand s.n.* (BISH [BISH1016374, specimen!], US [US00101497, specimen!]); O‘ahu, Pauoa Valley, *Hillebrand & J. M. Lydgate s.n.* (BISH [2; BISH1016375, BISH1016476, specimens!]; O‘ahu, Wailupe (MEL [MEL587728, image!], with a photo at BISH); and a fragment made by J. Rock of B sheet, without locality (BISH [BISH1016377, specimen!]).

***Melicope cornuta* var. *decurrens* (B.C. Stone) Appelhans, K.R. Wood & W.L. Wagner, comb. nov.**

urn:lsid:ipni.org:names:77174270-1

Fig. 3C

Platydesma cornuta Hillebr. var. *decurrens* B.C. Stone, *J. Arnold Arbor.* 43: 423. 1962.

Type. O‘AHU: Wai‘anae Mountains, Munia-Kanehoa trail, wet fern-covered banks by stream in valley just southeast of trail, [200 m], 26 March 1960, *B.C. Stone & G. Pearsall* 3263 (holotype: BISH-579783 [BISH1016373, specimen!]).

***Melicope remyi* (Sherff) Appelhans, K.R. Wood & W.L. Wagner, comb. nov.**

urn:lsid:ipni.org:names:77174271-1

Claoxylon remyi Sherff, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 17: 557. 1939. *Platydesma remyi* (Sherff) O. Deg., I. Deg., Sherff & B.C. Stone, *Fl. Hawaiiensis.* 6: Fam. 179. 1960. *Platydesma campanulatum* H. Mann var. *sessilifolia* Rock, *Indig. Trees Haw. Isl.* 243. 1913. – Type: HAWAII: in dense forests of the summit mountain of the Kohala range, 12 July 1909, *J. F. Rock* 4222 (holotype: BISH, not located; isotype: GH [mounted on two sheets, GH00044160, GH00044161, images!]).

Note. These two sheets are the only type material of this collection located. They were labelled as co-type, which was used at the time Rock published for the equivalent of isotype. Rock stated in his book that most of the specimens mentioned in the text were in the “college of Hawaii Herbarium”, which are now incorporated into BISH. He specifically indicated the type of this new variety to be there, so the presumed holotype should be at BISH, but could not be located.

Type. HAWAII: 1851–1855, *J. Remy* 604, (holotype: P [P00636836, image!]; isotype: P [P00636837, image!]).

***Melicope rostrata* (Hillebr.) Appelhans, K.R. Wood & W.L. Wagner, comb. nov.**

urn:lsid:ipni.org:names:77174272-1

Fig. 3A, B

Platydesma rostrata Hillebr., *Fl. Hawaiian Isl.* 72. 1888.

Note. At the time Hillebrand described this species there was a single specimen known, the type. When Rock brought fragments from B back to BISH the label information was not well transcribed, but all have printed labels indicating they were from the B collection. There were no other collections in the B herbarium so despite the lack of information this must be a fragment of the holotype.

Type. KAUA'I: V. Knudsen 68 (holotype: B-destroyed, fragment BISH-581794 [BISH1016395, specimen!]).

***Melicope spathulata* A. Gray *Bot. U.S. Expl. Exped.* 1: 352. 1854. *Platydesma spathulatum* (A. Gray) B.C. Stone, *Madroño*. 16: 165. 1962.**

Fig. 4

Melicope? *grandifolia* A.Gray *Bot. U.S. Expl. Exped.* 1: 354. 1854. – Type: HAWAII: forests of Mauna Kea, 1840, *U.S. Expl. Exped. s.n.* (holotype: US-15033 [US00101457, specimen!]; isotype: GH [GH01153097, image!]).

Platydesma campanulata H. Mann, *Proc. Bost. Soc. Nat. Hist.* 10: 317. 1866. – Type: O'AHU: on the mountains behind Honolulu, at middle heights, *H. Mann & W. T. Brigham* 94 (holotype: CU, not located; isotypes: BISH [4 sheets, BISH1016385, BISH1016386, BISH1016388, BISH1016390, specimens!], G [G00380101, image!], GH [2 sheets, GH00044158, GH00044159, images!], MASS [MASS00320396, image!], MO [MO-251520, specimen!], NY [NY00067067, specimen!], US [US00101498, specimen!]).

Platydesma campanulata f. *coriaceum* Rock, *Indig. Trees Haw. Isl.* 243. 1913. – Type: HAWAII: Kohala Mts., [W of] Honokanenui gorge, June 1910, *J. F. Rock* 8367 (holotype: BISH-586927 [BISH1016394, specimen!]; isotypes: BISH [BISH1016441, specimen!], GH [2 sheets, GH00044162, GH00044163, images!]).

Platydesma campanulata var. *macrophylla* Hillebr., *Fl. Hawaiian Isl.* 71. 1888. – Type: KAUA'I: V. Knudsen *s.n.* (holotype: B-probably destroyed, fragment of holotype BISH-581799 [BISH1016383, specimen!]).

Platydesma campanulata var. *pallida* Hillebr., *Fl. Hawaiian Isl.* 71. 1888. *Platydesma spathulatum* var. *pallidum* (Hillebr.) B.C. Stone, *Madroño*. 16: 165. 1962. – Type: O'AHU: Ka'ala, *Hillebrand s.n.*; E. MAUI, Hamakua, *Lydgate s.n.* (syn-types: B-destroyed); MAUI: along pipe-line trail, Olinda, in dark forest, 29 July 1927, *O. Degener & L. Topping* 8615 (neotype [designated by Stone, *J. Arnold Arbor.* 43: 420. 1962]: BISH-68071 [BISH1016379, specimen!]; isoneotypes: B [B_10_0296003, image!], BH [BH000121710, image!], K [K000342164, image!], MASS [MASS00320397, image!], NY [NY02859241]).



Figure 4. *Melicope spathulata* **A** habit with flower (Wood 15091, Kaua'i, Kohua Ridge, US) **B** flower, lateral view (Ishikawa 302, Kaua'i, Koke'e, US) **C** flower, top view (Ishikawa 302, US) **D** flower, longitudinal section (Ishikawa 302, Kaua'i, Koke'e, US) **E** fruit (Herbst & Mull 5507, Hawai'i, Ola'a, US and Takeuchi et al. 1997, O'ahu, Ko'olau Mountains, US).

- Platydesma campanulata* var. *pubescens* Skottsbl., *Acta Horti Gothob.* 15: 388. 1944. *Platydesma spathulatum* var. *pubescens* (Skottsbl.) B.C. Stone, *Madroño*. 16: 165. 1962. – Type: O‘AHU: Wai‘anae Mountains, slope of Ka‘ala, 25 September 1938, O. Selling 3710 (holotype: GB [GB-0048636, image!]; isotype: S [S08-7736, image!]).
- Platydesma oahuensis* H. Lév., *Repert. Spec. Nov. Regni Veg.* 10: 154. 1911. – Type: O‘AHU: Punalu‘u, May 1910, U. Faurie 243 (holotype: not located; isotypes: A [A00044165, image!], BM [BM000798124, image!], P [P00639232, image!]).
- Platydesma spathulatum* f. *kalalauense* O. Deg. & I. Deg., *Fl. Hawaiiensis*. 7: Fam. 179. 1960. – Type: KAUA‘I: east rim of Kalalau Valley, 16 Nov 1960, O. Degener, I. Degener, & W. Cadenhead 27150 (lectotype [designated here]: US-2604492 [US00101496, specimen!]).
- Platydesma spathulatum* f. *stonei* O. Deg. & I. Deg., *Fl. Hawaiiensis*. 7: Fam. 179. 1960. – Type: O‘AHU: Ko‘olau range. Punalu‘u, summit of Castle trail, B.C. Stone 3551 (holotype: BISH, not located; lectotype [designated here]: fig. 2, Stone, J. Arnold *Arbor*. 43: 418. 1962).

Type. KAUA‘I: mountains, 1840, *U.S. Expl. Exped. s.n.* (holotype: US-15031 [US00101445, specimen!]).

Names excluded from *Platydesma*

Platydesma auriculifolia (A. Gray) Hillebr., *Fl. Hawaiian Isl.* 72. 1888. *Pelea auriculifolia* A. Gray, *Proc. Amer. Acad. Arts* 3: 50. 1853. – Type: HAWAI‘I: forests of Mauna Kea, *U.S. Expl. Exped., s.n.* (holotype: US-15020 [US00101488, specimen!]). [= *Melicope clusiifolia* (A. Gray) T.G. Hartley & B.C. Stone]. – Note: Hillebrand cited the second source of the name in *Pelea* by Gray (*U.S. Expl. Exped.*, Phan. 343. 1854) and also used part of the description (fruit). Hillebrand cites among the three collections the type of *Pelea auriculifolia* A. Gray as well as a specimen of *Platydesma* (Hillebrand *s.n.*), and the third one can’t be located (Lydgate *s.n.*). So his cited collections are a mixture as is the description. This Hillebrand name must be taken as a new combination. The critical facts are: Hillebrand cited the basionym, used the same epithet, and did not exclude the holotype of the basionym. It does not matter that Hillebrand cited a later publication of the cited basionym. Since this is a pre-1953 publication, it is not mandatory to cite the original publication of the basionym.

Platydesma fauriei H. Lév., *Repert. Spec. Nov. Regni Veg.* 10: 153. 1911. – Type: O‘AHU: Punaluu [Punalu‘u], May 1910, U. Faurie 242 (Isotypes: BM [BM000994065, image!], P [P00311275, image!]). – Note: The holotype was expected to be stored at E but no specimen could be located there. [= *Nothocestrum longifolium* A. Gray].

Insert for existing keys to Hawaiian Rutaceae and *Melicope*

The identification keys included in the “Manual of the Flowering Plants of Hawaii” (Wagner et al. 1990) need to be slightly modified in order to incorporate the taxonomic changes proposed here.

Key to the genera of Rutaceae (p. 1175 in Wagner et al. 1990)

- 1 Leaves simple, opposite or whorled **2. *Melicope***
- Leaves pinnately compound, opposite, or alternate (2).
- 2 Leaves alternate; seeds not winged **3. *Zanthoxylum***
- Leaves usually opposite; seeds winged **1. *Flindersia***

Key to the species of *Pelea*/*Melicope* (p. 1178 in Wagner et al. 1990)

- 1 Shrubs, shrubby trees, or with palmoid habit; flowers perfect; petals slightly imbricate; filaments nearly completely connate into a staminal tube; ovules 5–8 per carpel; fruit a subglobose or cruciate capsule, indehiscent or tardily dehiscent **use original key for *Platydesma*** (p. 1209 in Wagner et al. 1990)
- Trees, shrubs, or subscandent; flowers functionally unisexual (and the plants polygamous) or rarely perfect; petals valvate; stamens in 2 whorls, distinct, reduced but always present in functionally pistillate flowers, longer fertile stamens equal to or exserted from corolla; ovules 2 per carpel; fruit composed of 4 nearly distinct follicles or a 4-lobed, 4-valved, cruciate or cuboid capsule, dehiscent **use original key to species of *Pelea*/*Melicope*** (p. 1178 in Wagner et al. 1990)

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Morphological and anatomical evidence support a new wild cassava: *Manihot fallax* (Crotonoideae, Euphorbiaceae), from Mato Grosso, Brazil

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Abstract

During the preparation of the taxonomic treatment of *Manihot* in the Midwest Region of Brazil, a new species was found. *Manihot fallax* M.J. Silva & L.S. Inocencio is described, illustrated and morphologically compared with similar simple-leaved species. The conservation status, geographic distribution (including map), ecology, phenology and notes about leaf anatomy of the new species are given. The synonymisation of *M. robusta* M. Mend. & T. B. Cavalc. under *M. attenuata* Müll. Arg. and lectotypes for *M. attenuata* and *M. brachystachys* Pax & K. Hoffm are also proposed. An emended description of *M. attenuata* is proposed as the original description is incomplete as it lacks information on the pistillate flowers, fruits and seeds.

Keywords

Central Brazil, leaf anatomy, nomenclature, typification, Manihoteae

Introduction

The taxonomy of *Manihot* was studied by Rogers and Appan (1973), who recognised 98 species distributed into 19 sections. The genus is monophyletic and has a complex taxonomy (Duputié et al. 2011, Silva 2014). In Brazil, it is represented by over

80 species, especially growing in the Cerrado region, in rocky fields and grasslands (Silva 2014, Silva et al. 2017).

Despite the revision of *Manihot* (Rogers and Appan 1973), taxonomic studies about this genus in Brazil are scarce. *Manihot* is cited in floristic surveys of Euphorbiaceae (Cord-eiro 1992, Sátiro and Roque 2008) or as an isolated genus (Allem 1997, Rodrigues 2007, Carmo-Júnior et al. 2013, Orlandini and Lima 2014). In the last four years, a number of species of *Manihot* have been described in Brazil in the coastal sand plains of the state of Sergipe (Martins et al. 2011), in the semi-arid region of the state of Bahia (Martins et al. 2014) and in Cerrado *sensu lato* of the state of Goiás (e.g. Mendoza et al. 2015, Silva et al. 2013, 2016, 2017, Silva 2014, 2015, Silva and Sodré 2014).

Considering the species of *Manihot* present in the Midwest Region of Brazil, the knowledge about the genus is scarce mainly in the states of Mato Grosso and Mato Grosso do Sul, where BFG (2015) reported 17 and 6 species respectively. However, taking into consideration that the flora of these states is relatively poorly known, that *Manihot* has its main diversity centre in the Brazilian Cerrado and also that these states have their areas covered predominantly by Cerrado vegetation, it is plausible to conclude that the number of species of the genus has been underestimated in Mato Grosso and Mato Grosso do Sul.

During the preparation of the taxonomic treatment of *Manihot* in the Midwest Region of Brazil, some collections were found from Serra Azul, Serra do Roncador, Serra do Taquaral and neighbouring areas in the state of Mato Grosso, which could not be assigned to any known species. One of these species, with entire and unlobed leaves and habit slender and virgate, is hereby illustrated, described as new and designated as *M. fallax*. The new species is compared with *M. attenuata* Müll. Arg. and *M. weddelliana* Baill., the taxa most morphologically similar to it and its phenology, conservation status and geographic distribution are also presented. The leaf anatomy of the new species and the species most morphologically similar to it were also compared because leaf anatomy constitutes an important tool for delimiting taxa in *Manihot* (e.g. Vannucci 1982, Cunha Neto et al. 2014, Cunha Neto et al. 2017 and Graciano-Ribeiro et al. 2016). Additionally, as part of these studies on *Manihot* of the Cerrado flora, *M. robusta* as a synonym of *M. attenuata* Müll. Arg. is proposed and *M. attenuata* and *M. brachystachys* Pax & K. Hoffm are lectotypified. An emended description of *M. attenuata* is provided, as the original description is incomplete as it lacks information on the pistillate flowers, fruits and seeds.

Materials and methods

Morphological and taxonomic studies

The morphological description of the new species is based on field observations, conducted by the authors during expeditions to the state of Mato Grosso and on morphological analyses of 34 collections from the authors and 10 collections from herbaria (UFMT/ICLMA and IAC). The emended description of *Manihot attenuata* and the nomenclatural revision for all taxa associated with it, resulted from analysis of all pro-

tologues, type and historical collections (17 exsiccatae) of the same and also of extensive field work in their areas of occurrence, as well as analyses of 30 collections from herbaria (BR, CEN, F, G, HRCB, HUEFS, IBGE, K, MG, MO, NY, P, RB, S, SP, UB and UFG). The terminology used in the description of both species is based on specific literature such as Pohl (1827), Pax (1910) and Rogers and Appan (1973); the last was employed mainly for the inflorescence types and venation pattern. All the samples used in the description of the new species, including the holotype, were deposited in the UFG herbarium and the isotypes will be sent to K, NY and MO. The acronyms of herbaria previously cited follow Thiers (2017, continuously updated)

The conservation assessment of both the species was based on field observations and applying the IUCN Red List Categories and Criteria (IUCN 2014). The geographic distribution map was made using the software QGIS (Quantum GIS Development Team) version 2.8.1, which was used for the geographic coordinates obtained both during the collection expeditions and from the labels of the collections examined. The extent of occurrence (EOO) was calculated with the Geospatial Conservation Assessment Tool (GeoCAT - <http://geocat.kew.org>), (Bachman et al. 2011).

Anatomical studies

Leaves of the type collection of the new species (i.e. L. S. Inocencio, A. O. Souza, L. L. C. Antunes and C. C. Oliveira 293) and *M. attenuata* (M. J. Silva 4063/UFG) with fully expanded leaf blades were fixed in FAA (formaldehyde/glacial acetic acid/ethanol 50% at 1:1:18 v/v/v) for 48h and transferred to 70% ethanol (Johansen 1940). Freehand sections of the median portion of the leaf blade and petiole of the samples were cleared in sodium hypochlorite solutions (20%), rinsed with distilled water, stained with aqueous 1% astra blue and aqueous 1% Safranin (Bukastch 1972) and mounted in aqueous glycerine solution (1:1). For epidermal analysis, classification and observation of stomata distribution, leaf blade segments were dissociated using a hydrogen peroxide and acetic acid solution (Franklin 1945). Sections were examined and photographed using a Leica ICC50 camera coupled with a Leica DM500 microscope (Leica Microsystems, Heerbrugg, Switzerland).

Taxonomic treatment

***Manihot fallax* M.J. Silva & L.S. Inocencio, sp. nov.**

urn:lsid:ipni.org:names:77174267-1

Figs 1, 2

Type: BRAZIL. Mato Grosso: Município de Barra do Garça, BR-158, na altura do km 726, margem esquerda da estrada no sentido Nova Xavantina, campo cerrado em encosta, 15°17'9.7"S, 52°11'15.5"W, 385 m a.s.l., 26 Jan 2014, fl., L. S. Inocencio, A. O. Souza, L. L. C. Antunes, and C. C. Oliveira 293 (holotype: UFG; isotypes: K, MO, NY).

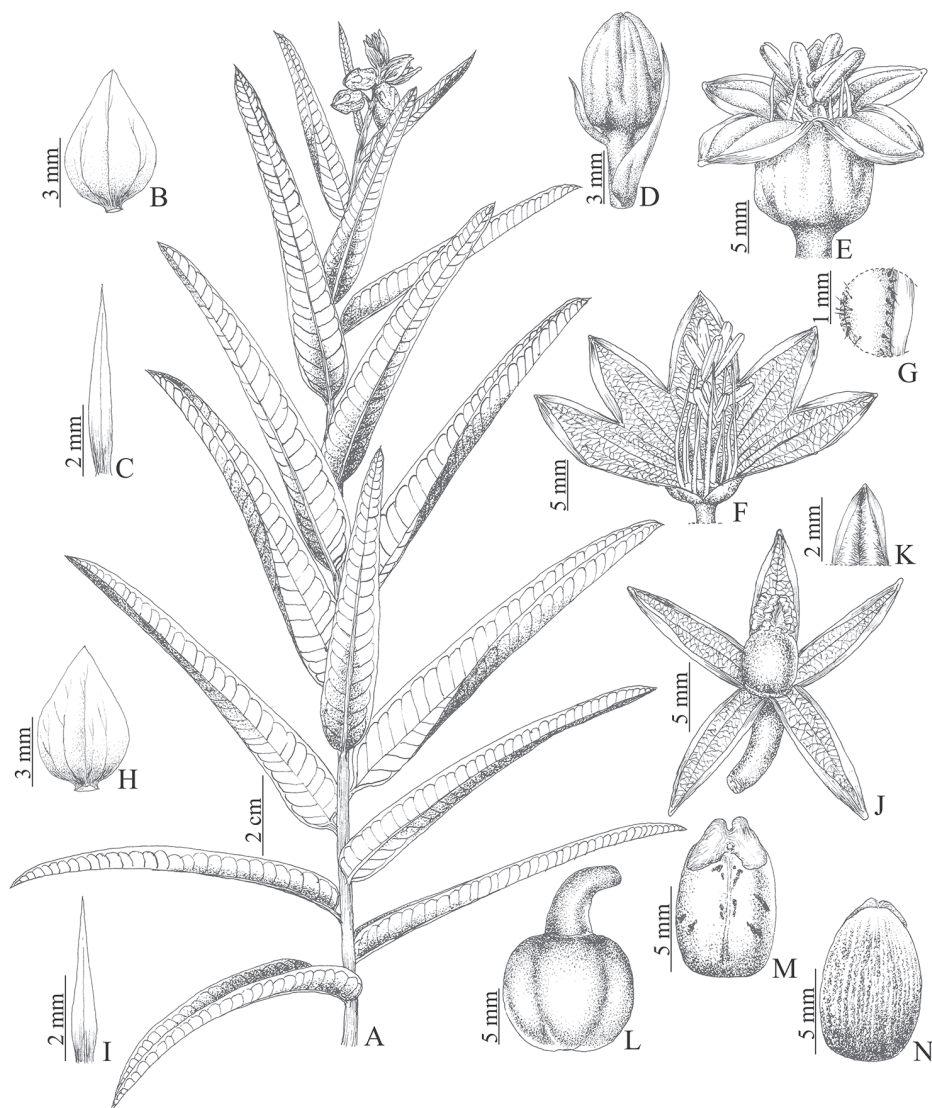


Figure 1. *Manihot fallax*. **A** Habit **B** Staminate bracts **C** Staminate bracteole **D** Staminate bud **E** Staminate flower **F** Staminate flower with calyx split and open **G** Inner surface of the staminate calyx showing the trichomes **H** Pistillate bracts **I** Pistillate bracteole **J** Pistillate flower **K** Inner surface of the pistillate calyx showing the trichomes **L** Fruit **M** Seed, ventral side **N** Seed, dorsal side. Drawn by Cristiano Gualberto from the holotype.

Diagnosis. Shrubs slender and virgate, up to 1.9 m tall; leaves light green, entire, unlobed, with secondary veins perpendicular to the midvein. Stipules 1–3 × 0.2–0.3 mm, setaceous, entire, early caducous; racemes 2.5–6 cm long, solitary, subspicate, staminate buds obovoid, stamens with filaments pubescent, pistillate calyx dialisepalous and fruits light green, without wings.



Figure 2. *Manihot fallax*. **A** Habit **B** Leaves; note the spiral phyllotaxy **C** Inflorescence; note the showy bracts **D** Staminate flower, frontal view **E**. Pistillate flowers in the inflorescence, lateral view; note the free sepals **F** Fruit.

Description. Shrubs 1–1.9 m tall, slender and virgate, monoecious, glabrous. Stem solid in cross section, greenish to reddish, glossy and waxy in young parts; latex clear, abundant; roots fibrous. Stipules $1-3 \times 0.2-0.3$ mm, setaceous, margins entire, early caducous; petiole 0.3–0.7 mm long, angulate, greenish. Leaves alternate spiral, sparsely distributed along the branches, but more concentrated near apex, blades $8-14 \times 1-2$ cm, lanceolate, narrowly elliptic or linear, entire, unlobed, non-peltate, base obtuse, apex obtuse with a short mucro, firmly membranaceous to chartaceous, glabrous on both surfaces, adaxial surface dark green, abaxial surface glaucous, the latter with a smooth wax pattern, venation camptodromous-brochidodromous, primary and secondary veins impressed on both surfaces, the secondary veins perpendicularly arranged in relation to the midvein, all of them pinkish to yellowish. Racemes 2.5–6 cm long, staminate or bisexual, solitary, terminal or arising from dichotomy of the branches, glabrous, angulate, glaucous to cinereous, waxy. Staminate flowers: buds $5.8-6 \times 3.9-4$ mm, obovoid, yellowish-green, without purplish pigmentation; bracts $6-6.1 \times 3.9-4$ mm, widely elliptic, foliaceous, apex acuminate, persistent; bracteoles situated along the lower third up to half of the pedicel, $4-4.1 \times 0.4-0.5$ mm, lanceolate, foliaceous, persistent, subopposite; pedicels 0.5–0.7 mm long, cylindrical, glabrous, light green; calyx $13.2-14 \times 5.9-6$ mm, campanulate, yellowish, without purplish pigmentation, shortly tomentose internally, lobes widely triangular, ovate to oblong, apex obtuse, base truncate; stamens 10, in two whorls of five, filaments pubescent near apex, the longer 12.5–12.6 mm long, the shorter 8.4–8.5 mm long, both thickened; anthers 5–7 mm long, oblong, dorsifixed, bright yellow; disc 10-lobed, intrastaminal, dark yellow. Pistillate flowers: buds $6-9 \times 4-6$ mm, ovoid, green-yellowish, without purplish pigmentation; bracts $6.4-7 \times 2.9-3$ mm long, widely ovate, margin entire, glabrous; bracteoles $3.7-3.8 \times 0.8-0.9$ mm, lanceolate, foliaceous, persistent, margin entire, apex acuminate, opposite along the lower third of the pedicel, glabrous; pedicels 4–6 mm long, cylindrical-clavate, glabrous, green; sepals $10-12 \times 5-7$ mm, lanceolate, apex acute, shortly tomentose externally, yellowish, without purplish pigmentation; ovary $4-6 \times 3-4$ mm, globose to ovoid, glabrous, green, disc patelliform, lobed, yellow; styles 3, shortly united at the base, stigmatic surface 2–3 mm long, densely papillose. Capsules $0.9-1.5 \times 0.8-1.2$ cm, oblong, light green, smooth, glabrous, without wings, dehiscence septicidal and loculicidal; columella (carpophore) persistent, $0.9 \times 2-2.2$ mm (width at narrowest point in middle), narrowly alate. Seeds $0.7-1 \times 0.39-0.4$ cm, oblong-ellipsoid, dark grey, with black spots; caruncle triangular, prominent, apex bilobed, cream to yellowish.

Distribution and ecology. *Manihot fallax* appears endemic to the state of Mato Grosso (Fig. 3), where it grows in Cerrado *sensu stricto* on flat or slope areas and also in grasslands, on clayey and sandy soils, between 385 m and 642 m elevation.

Phenology. The species has been collected with flowers and fruits from October to March.

Etymology. The specific Latin epithet “fallax” refers to deceptive and was chosen due to the false similarity of the new species to *M. attenuata* and *M. weddelliana*.

Conservation status. According to the IUCN (2014), *M. fallax* can be considered preliminarily as an endangered species (EN-B2a), because it grows in disturbed areas subject to fires and human pressure and has an extent of occurrence of 175 km².

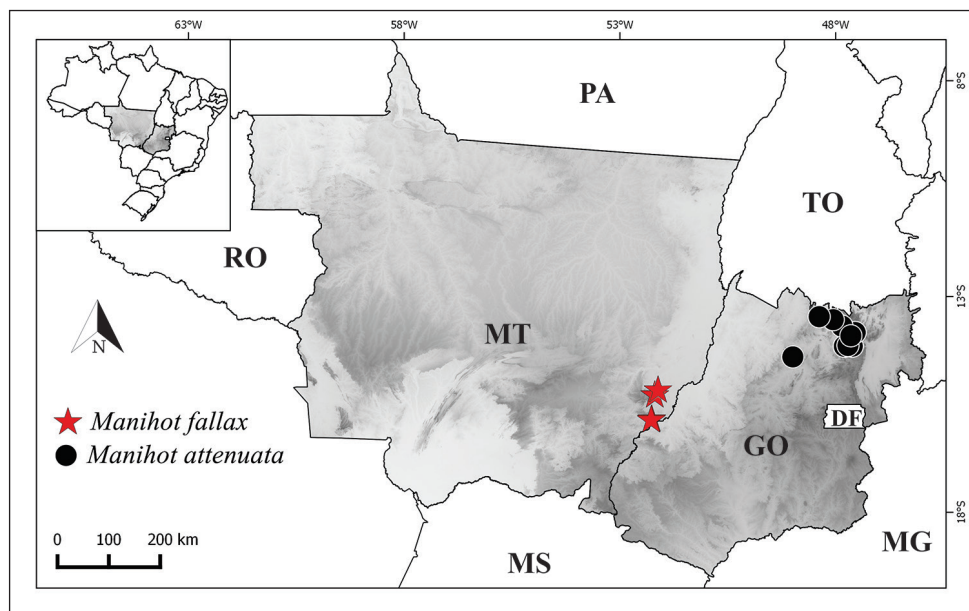


Figure 3. Distribution map of *Manihot fallax* sp. nov. and *M. attenuata*.

Specimens Examined. Brazil. Mato Grosso. Barra do Garças, Serra Azul, trilha as usina, próximo a sede da Moçonaria, 17 Mar 1990, fl., fr., *L. Santos s.n.* (UFMT/ICLMA 00856); próxima da cidade, nas imediações da antena do Cristo, 09 Mar 1991, fl., fr., *L. Santos s.n.* (UFMT/ICLMA 00866); Serra do Taquaral, Cerrado, 23 Nov 1997, fl., fr., *L. C. Bernacci & G. Arborech* 2525 (UFMT, IAC); cerrado do Marcello, 15°50'50.9"S, 52°15'54.7"W, 14 Nov 2005, fl., fr., *I. Faria & M. L. Mayer* 339 (UFMT/ICLMA); gruta do pezinho, 15°50'29.6"S, 52°16'50"W, 28 Dec 2005, fl., *I. Faria, M. L. Mayer & Moisés* 517 (UFMT/ICLMA); Parque Estadual da Serra Azul, 15°51'S, 52°16'W, 21 Oct 2005, fl., *M. Sanchez* 2216 (UFMT/ICLMA); *ib.*, 21 Feb 2006, fl., fr., *I. Faria, M. L. Mayer & M. S. M. Ramos* 787 (UFMT/ICLMA); *ib.*, 15°52'S, 52°16'W, 04 Oct 2006, fl., *R. Freitas & M. L. Mayer* 145 (UFMT/ICLMA); *ib.*, 13 Feb 2007, fl., *R. Freitas & M. L. Mayer* 404 (UFMT/ICLMA); *ib.*, 1 Mar 2007, fl., fr., *R. Freitas & M. L. Mayer* 445 (UFMT/ICLMA); BR 158 na altura do km 726, margem esquerda, sentido Nova Xavantina, adjacências da Serra do Roncador, 15°17'21.8"S, 52°11'38.7"W, 389 m a.s.l., 28 Jan 2014, *L. S. Inocencio, A. O. Souza & G. H. Silva* 68, 69, 70, 71, 72 and 73 (UFG); *ib.*, 15°17'9.7"S, 52°11'15.5"W, 385 m a.s.l., 26 Jan 2015, fl. fr., *L. S. Inocencio, A. O. Souza, L. L. C. Antunes & C. C. Oliveira*, 290, 291, 292 and 294 (UFG); BR 158, na altura do km 726, margem esquerda, sentido Nova Xavantina, 15°17'9.8"S, 52°11'22.3"W, 422 m a.s.l., 1 Feb 2015, fl. fr., *L. S. Inocencio, A. O. Souza, L. L. C. Antunes & C. C. Oliveira* 363, 364, 365, 366, 367, 368, 369, 370, 371, 372, 373, 374, 375, 376, 377, 378, 379, 380, 381, 382, 383, 384, 385, 386, 387 and 388 (UFG); Serra do Roncador, ca. 60 km a norte da cidade pela BR-158 e 5 km a esquerda desta rodovia em direção a Xavantina a partir do povoado

Vale dos Sonhos, 52°13'54"S, 15°20'54"W, 642 m a.s.l., 24 Mar 2016, R. C. Sodré, T. P. Mendes & J. A. Oliveira 2174 (UFG).

Discussion. *Manihot fallax* stands out from the other species of the genus with entire and unlobed leaves (Silva 2015) by its shrubby, slender, virgate habit up to 1.9 m tall, leaves ascendant and in a spiral arrangement along the branches. It morphologically resembles *M. weddelliana* and *M. attenuata*, especially the latter, in the aspect of the leaves, racemes conspicuously pedunculate, bracts of flowers of both sexes showy and foliaceous and calyx internally shortly tomentose. However, *M. fallax* differs from *M. weddelliana* in its shrubby, slender and virgate habit (vs. subshrub up to 0.5 m tall in *M. weddelliana*), leaves without repand margins (vs. leaves with repand margins) and bracts of both staminate and pistillate flowers ovate, with margins entire and apex acute or obtuse (vs. widely elliptic, with margins very serrated and apex conspicuously acuminate). The combination of the characters listed in table below serve to differentiate *M. attenuata* from *M. fallax*.

Regarding leaf anatomical features, *M. fallax* differs from *M. attenuata* in having the vascular cylinder with arch-shaped collateral vascular bundles surrounded by pericyclic fibres in the midvein (Fig. 4A), uniseriate epidermis in the median portion of both surfaces of the leaf blade (Fig. 4B), at the edge (Fig. 4C) and petiole with collateral vascular bundles discontinuous in the vascular cylinder (Fig. 4N). In *M. attenuata*, the vascular cylinder has collateral vascular bundles in a flattened arc, not surrounded by pericyclic fibres in the midvein (Fig. 4D), epidermal cells without papillae in the median portion of the abaxial surface of the leaf blade (Fig. 4E), but with druses in the

Table 1. Morphological characters useful in separating *M. fallax* from *M. attenuata*.

Character	<i>M. fallax</i>	<i>M. attenuata</i>
Leaves	8–14 × 1–2 cm, lanceolate, narrowly elliptic or linear, adaxial surface dark green, abaxial surface glaucous	17.5–24 × 4–4.5 cm, widely elliptic, ovate-lanceolate, oblong-elliptic or sometimes lanceolate, adaxial surface dark purple or greenish purple, abaxial surface glaucous or cinereous
Arrangement of secondary veins in relation to the midvein	Perpendicular	Diagonal
Stipules	Margin entire, early caducous 2.9–3 mm long	Margin serrulate, persistent, 10–11 mm long
Inflorescence	Racemes subspicate, 2.5–6 cm long	Racemes with well developed pedicels, 4.5–10.5 cm long
Bracts on flowers of both sexes	Glabrous, widely ovate with entire margin	Pubescent, widely elliptic with denticulate margin
Lobes of staminate calyx	Triangular with apex acuminate	Ovate-oblong with apex obtuse or rounded
Staminate buds	Obovoid	Ovoid
Filaments	Pubescent	Glabrous
Pistillate bracts	5–9 mm long, margin entire	6.4–7 mm long, margin irregularly serrate
Pistillate bracteoles	Lanceolate, margin entire	Oblong-elliptic, margin denticulate
Pistillate calyx	Dialisepalous	Gamosepalous
Caruncle shape	Triangular with bilobed apex	Widely triangular with entire apex

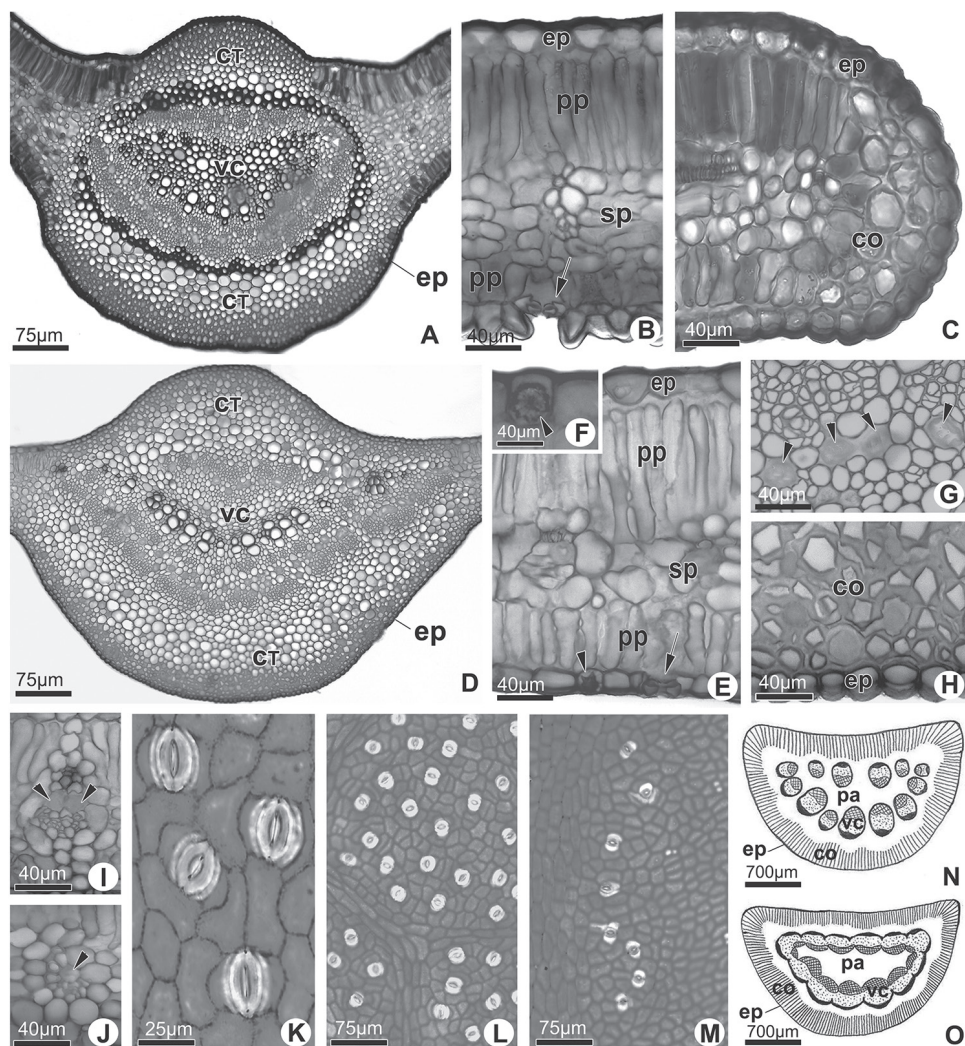


Figure 4. Leaf anatomy of species. **A–J** Cross section of the leaf blade. *Manihot fallax* (**A–C**): **A** Median portion of the midvein **B** Median portion of the leaf blade; abaxial epidermis papillose and stomata indicated by arrow **C** Edge. *Manihot attenuata* (**D–J**): **D** Median portion of the midvein **E** Median portion of the leaf blade; note stomata (arrow) and epidermal idioblast with druse (arrowhead) **F** Detail of epidermal idioblast with druse (arrowhead) **G** Laticifers in the midvein phloem (arrowheads) **H** Detail of the epidermis and collenchyma in the midvein **I** Vascular bundles with parenchymatous sheath in the median portion of the leaf blade (arrowheads correspond to laticifers) **J** Vascular bundles in the median portion of the leaf blade (arrowheads correspond to laticifers) **K–M** Dissociated epidermis of both species. *Manihot fallax*. **K**. Paracytic stomata. *Manihot attenuata* (**L–M**): **L** Stomata distribution in the abaxial surface of the leaf blade **M** Stomata distribution in the adaxial surface of the leaf blade lateral to midvein **N** and **O** Schematic representation of the petiole in cross section **N** *Manihot fallax* **O** *Manihot attenuata*. CT: cortex; VC: vascular cylinder; co: collenchyma; ep: epidermis; pp: palisade parenchyma; sp: spongy parenchyma; pa: medullar parenchymatic.

protoplast (Fig. 4E, F), as well as petiole with collateral vascular bundles continuous in the vascular cylinder (Fig. 4O).

Both *M. fallax* and *M. attenuata* have midveins with angular collenchyma on both surfaces, ground parenchyma surrounding the vascular cylinder (Fig. 4A, D, H), isobilateral mesophyll (Fig. 4B, E), edges with annular collenchyma (Fig. 4C), parenchymatic sheath surrounding the secondary veins towards the epidermal cells on both surfaces of the leaf blade (Fig. 4I) and other veins without sheath (Fig. 4J). Laticifers are also found in both species distributed along the phloem cells in the midvein, petiole and median portion of the leaf blade (Fig. 4G). Additionally, the petiole has epidermal cells and cortex similar to those of the midvein (Fig. 4N, O). The stomata are paracytic in both species (Fig. 4K), evenly distributed on the abaxial surface of the leaf blade (Fig. 4L) and in a parallel and continuous band on each side of the midrib (Fig. 4M). Due to the stomatal pattern, both species have amphistomatic leaves.

Amongst the anatomical features that differ between *M. fallax* and *M. attenuata*, the presence the fibres in the vascular cylinder in the midvein, the papillae in the epidermal cells and the arrangement and number of collateral bundles in the petiole have been cited by Allem (1984), Cunha Neto et al. (2014) and Graciano-Ribeiro et al. (2016) as characters that help differentiate species in *Manihot*.

***Manihot attenuata* Müll. Arg. (1874: 442) emend. M.J. Silva**

Figs 5, 6

Manihot brachystachys Pax & K. Hoffm., Pflanzenr. (Engler) 4, Fam. 147, II: 97. 1910.

Type. Brazil. Südbrasilianische Provinz, Staat Goiaz, 8 Jan 1898, fl., *Glaziou* 22126 (lectotype, designated here: P [P04786133!]; isolectotypes: BR [BR000005101320!], G [G00441911!], K [000600417!], P [P04786134!], P04786135!], S [S-R-9076!]).

Manihot robusta M. Mend. & T. B. Cavalc. Arneloia 22(2): 297, 2015.

Type. BRAZIL. Alto Paraíso de Goiás, Parque Nacional Chapada dos Veadeiros, ca. 0.3 km da GO-239, sentido sede alojamento do ICMBio (lado direito), 14°09'55.92"S, 47°47'25.62"W, 1046 m a.s.l., 31 Oct 2014, *M. Mendoza, J.B.A. Bringel, A.A. Santos and T. Reis* 4343, **syn. nov.** (holotype: CEN!; isotypes: HRCB!, HUEFS!, K!, MG, MO!, NY!, RB!, SP!, UB!).

Type. BRAZIL. Goiás: inter Goyaz et Cavalcante, *Burchell* 7865 (lectotype, designated here: K [K000600418!]; isolectotypes: BR [BR510866!], G!).

Emended description. Shrubs 0.5–1.2 m tall erect or decumbent, in which case the stem to 0.6 m tall with lateral branches to 1.3 m long, monoecious, glabrous. Stems and branches angulose, glossy, brownish, the bark exfoliating when adult and purplish, greenish or combinations of these when young; latex yellow or clear. Stipules 10–12 × 0.5–0.1 mm, lanceolate, sparsely serrate, persistent; petiole 3–4 mm long, greenish. Leaves alternate, spiral, sparsely distributed along the branches, but

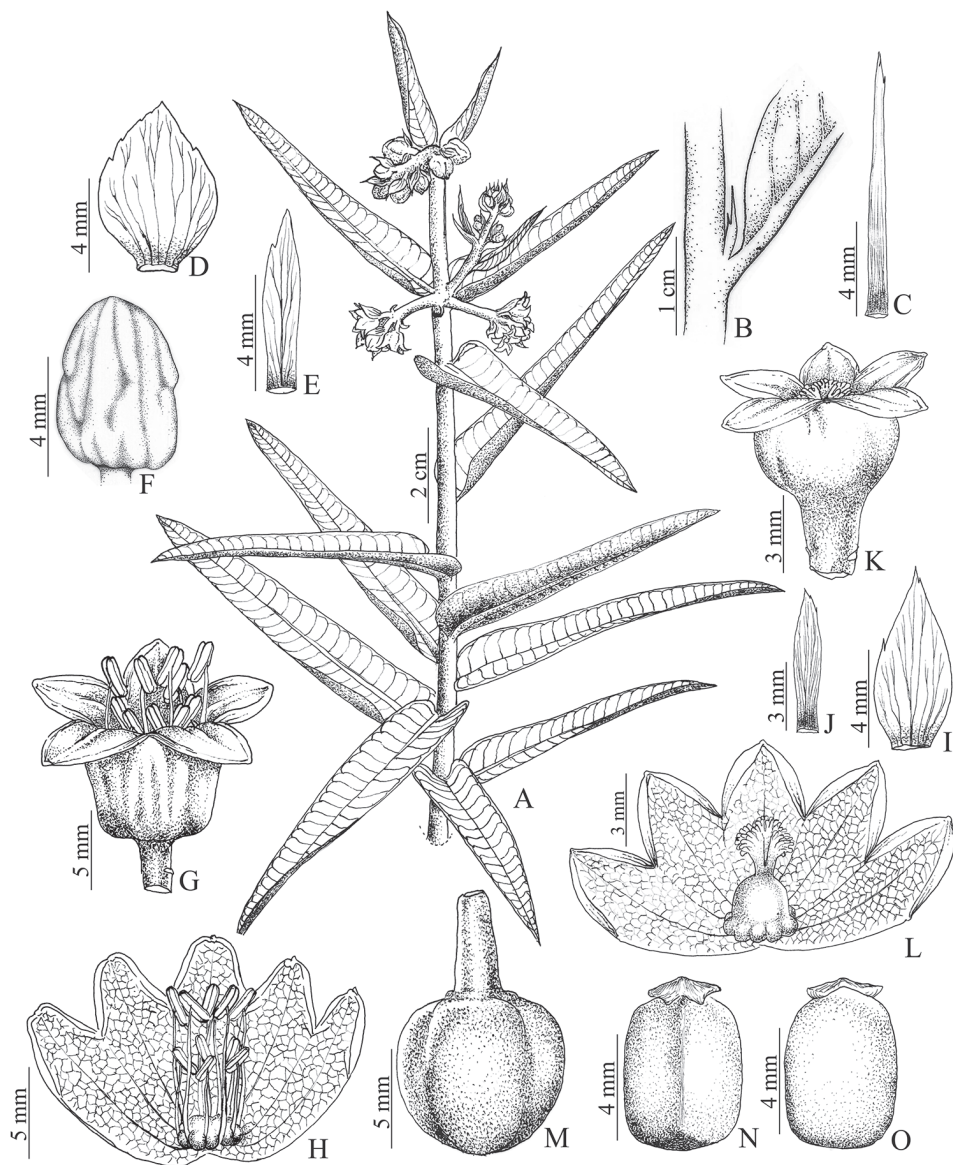


Figure 5. *Manihot attenuata*. **A** Habit **B** Details of the branch showing the persistent stipule **C** Stipule **D** Staminate bracts **E** Staminate bracteole **F** Staminate bud **G** Staminate flower **H** Staminate flower with calyx split and open **I** Pistillate bracts **J** Pistillate bracteole **K** Pistillate flower, note the gamosepalous calyx **L** Pistillate flower with calyx split and open **M** Fruit **N** Seed, ventral side **O** Seed, dorsal side. Drawn by Cristiano Gualberto from the holotype.

more concentrated near apex; blades $17.5\text{--}24 \times 4\text{--}4.5$ cm, elliptic, widely elliptic, ovate-lanceolate, oblong-elliptic or sometimes lanceolate, entire, unlobed, non-peltate, base obtuse or attenuate, apex acute and mucronulate, chartaceous, glabrous on

both surfaces, adaxial surface dark purple or greenish purple, abaxial surface glaucous to cinereous, the latter with a smooth wax pattern, venation camptodromous-brochidodromous, primary veins prominent on both surface, secondary veins impressed on both surfaces, diagonally arranged towards the midvein, all pinkish to purplish. Racemes 4.5–10.5 cm long, staminate or bisexual, solitary, terminal or arising from dichotomy of the branches, erect or pendent, congested, glabrous, angulate, glaucous to cinereous, waxy. Staminate flowers: buds 4–7 × 3–6 mm, widely ovoid, yellowish, without purplish pigmentation; bracts 10–15 × 3–7 mm, widely ovate, foliaceous, apex acuminate, margins sparsely and irregularly denticulate, persistent; bracteoles situated along the lower third up to half of the pedicel, 4–4.6 × 1–1.5 mm, ovate or ovate-lanceolate, foliaceous, persistent, subopposite; pedicels 3–3.2 mm long, cylindrical, glabrous, light green; calyx 7–15 × 5–10 mm, campanulate, green-yellowish, without purplish pigmentation, shortly tomentose internally, lobes ovate-oblong with apex obtuse or rounded, base truncate; stamens 10, in two whorls of five, glabrous, the longer 7.5–7.6 mm long, the shorter 4.5–4.6 mm long, both thickened, anthers 3–4 mm long, oblong, bright yellow, dorsifixed; disc 10-lobed, intrastaminal, dark yellow. Pistillate flowers: buds 6–8 × 4–6 mm, ovoid, green-yellowish, without purplish pigmentation; bracts 5–9 × 1.5–5 mm long, widely ovate, entire, apex acuminate, margin irregularly serrate, glabrous, persistent; bracteoles 4–6 × 1–3 mm, oblong-elliptic, foliaceous, persistent, margin denticulate, apex acuminate, opposite along the lower third of the pedicel, glabrous; pedicels 4–5 mm long, cylindrical-clavate, glabrous, green; calyx 7–9 × 5–7 mm, campanulate, yellowish green, without purplish pigmentation, glabrous externally, shortly tomentose internally, lobes triangular, base truncate; ovary 5–7 × 2–3 mm, ovoid to oblong, glabrous, green, disc patelliform, lobed, yellow; styles 3, shortly united at the base, densely papillose lobed. Capsules 0.8–1.8 × 0.7–1.2 cm, oblong, light green, smooth, glabrous, without wings, waxy, dehiscence septicidal and loculicidal; columella (carphophore) persistent, 0.78–0.8 × 1.2–1.3 mm (width at narrowest point in middle), dilating to 2–2.2 mm at both tip and base, narrowly alate. Seeds 7–10 × 5–6 mm, oblong, dark grey or cinereous, with black spots; caruncle prominent, widely triangular with entire apex, cream.

Morphological relationships and characterisation. *Manihot attenuata* is easily recognised by its shrub habit; erect or decumbent habit; large leaves (17.5–24 × 4–4.5 cm) that are purplish; sparsely serrate, persistent stipules; bracts and bracteoles of both staminate and pistillate flowers widely ovate, pubescent externally and acuminate at the apex; usually pendent inflorescences; and pubescent stigmatic branches. It is morphologically similar to *M. fallax*. However, it differs by the set of characters cited in Table 1 and also according the anatomical characters previously discussed.

Distribution and ecology. A species endemic to the northern portion of the state of Goiás, Chapada dos Veadeiros and neighbouring regions (municipalities of Niquelândia and Minaçu) (Fig. 3). It grows in cerrado rupestre, cerrado *sensu stricto*, near to rocky outcrops and in rocky fields, in flat sites, slopes or hilltops on clay-sandy soils, or in rock cracks, at altitudes from 440 and 1477 metres.



Figure 6. *Manihot attenuata*. **A** Habit **B** Inflorescence; note the ovoid staminate bud and showy bracts **C** Portion of inflorescence showing the staminate flowers, lateral view **D** Staminate flower, frontal view **E** Pistillate flowers in the inflorescence, frontal view; note the campanulate calyx **F** Fruit.

Phenology. The species has been collected with flowers from November to March, with the flowers more common from September to December and with fruits from December to March.

Conservation Status. *Manihot attenuata* is here classified as Vulnerable (VU) according to the IUCN Red List Categories and Criteria (IUCN 2014) because it has an extent of occurrence of ca. 9850 km². However, the species has populations with more 20 individuals and it grows in environments inappropriate for farming and habitations, as well as in protected areas such as the Chapada dos Veadeiros National Park.

Typification. Müller (1874) described *M. attenuata* in Flora Brasiliensis based on Burchell 7865 from Goiás state. Pax (1910) recognised *M. attenuata* as a good species without comment about its typification and established *M. brachystachys*. Rogers and Appan (1973) subordinated *M. brachystachys* Pax & K. Hoffm. as a synonym of *M. attenuata* without comment or typification of the latter. Analysing all type collections of both species confirmed that both species need to be lectotypified. The collection Burchell 7865 (Fig. 7) deposited in the herbarium K (K000600418) as lectotype of *M. attenuata* was designated here because it complies with the protologue and has flowers. Based on this same principle, the collection Glaziov 21126 at P (P04786133) was proposed as a lectotype of *M. brachystachys*; isolectotypes are BR (BR0000005101320), G (G00441911), K (K000600417), P (P04786134, P04786135) and S (S-R-9076). *M. brachystachys* was also recognised as a synonym for *M. attenuata* because the characters used by Pax (1910) to differentiate them (e.g. leaf type, habit, fusion of floral parts) overlap and are variable within populations.

Recently, Mendoza et al. (2015) published *M. robusta* as a new species from Chapada dos Veadeiros region in Goiás state. Reviewing all collections used by the authors in the description of *M. robusta*, based on the images provided by them and the characters cited to differentiate *M. robusta* from *M. attenuata* (e.g. habit and aspect of growth, secondary vein numbers, inflorescence position and numbers, bract shape and length), it is concluded that the characters cited by the authors overlap and are variable within populations. Furthermore, all collections of *M. robusta* are from the same location as the type of *M. attenuata*. It is therefore considered that *M. robusta* is a synonym of *M. attenuata*.

Additional specimens examined. BRAZIL. Goiás: Alto Paraíso de Goiás, Chapada dos Veadeiros, estrada GO 327, aproximadamente 1800 metros antes da Vila São Jorge, 14°09'00"S, 47°37'00"W, 1000 m a.s.l., 29 Mar 1988, I. R. S. Costa et al. 19 (UFG); entrada do Parque Nacional da Chapada dos Veadeiros, 14°10'5"S, 47°47'25"W, 27 Jan 1996, fl., fr., W. L. Werneck 706 (CEN); entrada do Parque Nacional da Chapada dos Veadeiros (a esquerda), estrada Alto Paraíso-Colinas, 34 km da GO 118, 14°09'49"S, 47°47'8"W, 1250 m a.s.l., 22 Jan 1997, fl., B. M. T. Walter et al. 3644 (CEN); Parque Nacional Chapada dos Veadeiros (PNCV) área queimada com relevo plano, 15°44'14"S, 47°54'54"W, 1477 m a.s.l., 25 Sep 1995, fl., M. L. Fonseca et al. 549 (IBGE); *ib.* Cerca de 1 km acima do alojamento dos brigadistas, 20 Jan 2012, fl. fr., M. J. Silva et al. 4063, 4065 (UFG); *ib.*, Proximidades do alojamento dos brigadistas, 25 May 2012, fr., L. C. S. Almeida et al. 42 (UFG); *ib.*, final do acesso da trilha que



Figure 7. Specimen selected as the lectotype of *M. attenuata*, Burchell 7865 (K000600418). Image used with permission and provided by the Royal Botanic Gardens, Kew.

leva ao Cânion I, entre fendas de rocha, 14°09'6.55"S, 47°48'0.74"W, 1114 m a.s.l., 29 Sep 2012, fl., *M. J. Silva et al.* 4421 (UFG); 2.5 km em direção ao rio Preto, 26 Oct 2012, fl., *M. J. Silva et al.* 4502 and 4506 (UFG); na subida para o alojamento dos brigadistas do PNCV, 22 Oct 2011, fl., *M. J. Silva et al.* 3885 (UFG); Parque Nacional Chapada dos Veadeiros, estrada que leva ao alojamento dos brigadistas, 14°9'53.6"S, 47°47'25.7"W, 1034 m a.s.l., 31 Oct 2014, fl., *L. S. Inocencio et al.* 180, 181, 182 and 183 (UFG); *ib.*, segundo morro a nordeste do alojamento principal dos brigadistas do PNCV, 27 Oct 2012, fl., *M. J. Silva et al.* 4503 and 4507 (UFG); topo da serra à direita da estrada que leva ao Cânion I, 14°09'05.7"S, 47°48'00"W, 1130 m a.s.l., 23 Nov 2012, fl., *L. C. S. Almeida & I. A. M. Watanabe* 67 and 69 (UFG); estrada para Vale da Lua, 24 Nov 2012, fl., *M. J. Silva et al.* 4589 (UFG); trilha a partir do dos alojamentos do PNCV em direção ao Cânion I, 14°08'S, 47°43'W, 1086 m a.s.l., 29 Nov 2012, fl., *L. C. S. Almeida et al.* 50 (UFG); afloramento rochoso à nordeste do Cânion I, 14°9'S, 47°48'W, 1082 m a.s.l., 29 Nov 2012, fl., *L. C. S. Almeida et al.* 51, 52 and 56 (UFG); subida de acesso ao alojamento dos brigadistas do PNCV, 14°09'37.6"S, 47°57'2.3"W, 1034 m a.s.l., 22 Feb 2014, fl., fr., *M. J. Silva et al.* 5921 (UFG); cerca de 500 m do alojamento dos brigadistas, 14°9'22.4"S, 47°47'38.9"W, 1089 m a.s.l., 13 Dec 2014, fl., *L. S. Inocencio et al.* 278 (UFG); Parque Nacional da Chapada dos Veadeiros, estrada que leva ao alojamento principal do Parque, 04 Jan 2015, fl., *R. C. Sodré, M. J. Silva & C. H. G. M. Filho* 1636 (UFG). Cavalcante, exatos 8 km a noroeste de Cavalcante ao longo da estrada de terra que leva à Colinas do Sul, 13°50'S, 47°33'W, 12 Dec 1986, fl., fr., *A. C. Allem et al.* 11307 (CEN); estrada Minaçu-Cavalcante passando pela balsa Serra Branca (COTERRA), à cerca de 126 km do rio Tocantins, 13°41'07"S, 47°51'22"W, 740 m a.s.l., 10 Nov 2000, fl., *G. P. Silva* 4421 (UFG); cerca de 4 km da Vila Veneno, na direção do rio São Félix, cerca de 12 km da Balsa da Coterra, 13°32'10"S, 48°03'29"W, 380 m a.s.l., 25 Jan 2001, fl., *B. M. T. Walter et al.* 4807 (UFG). Chapada dos Veadeiros, imediações da Serra do Ministro, a aproximadamente 500 m da estrada entre Cavalcante e Colinas do Sul, 13°54'34"S, 47°38'55.4"W, 20 Jan 2014, fr., *R. C. Sodré et al.* 1193 (UFG). Minaçu, 7 km após a entrada norte do canteiro de obras, 13°28'00"S, 48°23'00"W, 920 m a.s.l., 10 Mar 1992, fl., fr., *T. B. Cavalcanti et al.* 1112 (CEN). Niquelândia, Reservatório em formação do AHE Serra da Mesa, região na margem direita do rio Maranhão, próximo ao rio das Almas, 14°34'50"S, 48°59'07"W, 440 m a.s.l., 16 Oct 1997, fl., *B. M. T. Walter* 3924 (CEN).

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