

Lucky morning glory, *Calystegia felix* (Convolvulaceae): a new species from Southern California, with notes on the historical ecology of the Chino ciénega belt

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Abstract

A new morning glory, *Calystegia felix* Provance & A.C. Sanders **sp. nov.** (Convolvulaceae), is described from the Los Angeles, San Gabriel, and Santa Ana River basins. Historical collections of the species, which prior to 2011 had not been seen alive in 94 years, have been misidentified as *Calystegia sepium* (L.) R. Br. subsp. *binghamiae* (Greene) Brummitt. The undescribed species was rediscovered in the City of Chino in April of 2011, a few miles north of the location where the most recent previous collection had been made by I. M. Johnston in 1917. The plants were found just prior to their likely destruction by grading and trenching for an underground power line. Intensive searches have resulted in the discovery of five additional occurrences, all of them in the City of Chino. *Calystegia felix* is at high risk of soon becoming extinct in the wild. All of the known extant occurrences are associated with well-watered landscaping on recently completed industrial, commercial, and residential developments. Every known living occurrence is within the limits of a ciénega belt, which is now mostly historical. Otherwise, the new species is only known only from collections made around the turn of the 20th century in what are now heavily urbanized areas, including one from South Los Angeles and another from Pico Rivera in Los Angeles County. *Calystegia felix* lacks the large bracts that immediately subtend, and enclose the calyx, which are always present in members of the *C. sepium* complex. Affinities to *C. felix* are found among other western US species with graduated sepals and small, often somewhat remote bracts. We discuss the enduring confusion between *C. felix* and *C. sepium* subsp. *binghamiae*, and differentiate the new species from some of its more likely relatives. The taxonomic treatment is supplemented by photos of herbarium specimens and living plants. We also discuss the ecological setting of Chino's ciénega belt, which was a mosaic of palustrine wetlands.

Keywords

alkali meadow, *Calystegia felix*, Chino Basin, ciénega, Convolvulaceae, new species, seep, Southern California, spring, urban landscape, wet meadows

Introduction

Calystegia R.Br. is a genus of about twenty-five species, having a worldwide distribution in temperate zones. Its center of diversity is California, where twelve native species, and thirteen additional native subtaxa, are recognized in the latest Jepson Manual (Brummitt 2012). Although similar to *Convolvulus* L., several characters have been used to differentiate *Calystegia* from *Convolvulus*, including pantoporate pollen, oblong stigma pairs with blunt apices, and a unilocular ovary (Lewis and Oliver 1965). Despite the apparent morphological differences, molecular phylogenetic studies in 2002 (Stefanovic et al. 2002) and 2007 (Carine et al. 2007) suggested that *Calystegia* was nested within *Convolvulus*, making *Convolvulus* paraphyletic with respect to *Calystegia*. However, the studies supported a monophyletic *Calystegia*, but sampled very few members of the genus. Furthermore, the studies did not include species with graduated sepals and small, remote bracts.

In 2011, the first author discovered a morning glory in Chino, California, that could not be differentiated from collections determined by the late R. K. Brummitt as *Calystegia sepium* (L.) R. Br. subsp. *binghamiae* (Greene) Brummitt, or “*Calystegia binghamiae*” (an unpublished name that he had written on one of the specimens years before). Until rediscovered in 2011, this taxon had been widely considered extinct (Brummitt 2012), as the most recently collected specimen authenticated by Brummitt was a specimen collected at Chino Creek in 1917 (*I.M. Johnston 1274*). The site of the rediscovery was along a public walkway in a Southern California Edison (SCE) right-of-way in the City of Chino, roughly four to five miles north of Johnston’s collection locality. This morning glory was confined to an irrigated open-bottom planter at ground level on native soil.

The rediscovery was followed by elevation of *C. sepium* subsp. *binghamiae* to species rank under *Calystegia* (Brummitt et al. 2012) because a reevaluation of the material indicated to them that the taxon warranted species rank. Commendably, their paper drew attention to the astonishing reappearance of a rare taxon in Chino that had been unseen for 94 years. It also completed the lectotypification of *Convolvulus binghamiae* Greene, which had been initiated by Jepson (1939) when he made an earlier combination, *Convolvulus sepium* var. *binghamiae* (Greene) Jepson. Brummitt et al. (2012) noted that more eastern specimens of *Calystegia binghamiae* had more linear to narrowly elliptic bracteoles than were observed in western and more northern populations, and that sepals were at least sometimes inserted significantly below the sepals. They also recognized differences in leaf characters, particularly with regard to basal lobe size and shape. After having received both the lectotype and high-resolution digital images of

all of the other known original material (except an isoelectotype putatively held at F) for closer examination, we are now certain that the Chino material represents a distinct taxon that does not bear a close relationship to *Convolvulus binghamiae* Greene.

The six recent *Calystegia* locations from Chino are a new species. This new species is also known from three historical collections, including one each from South Los Angeles, Pico Rivera, and Chino. *Calystegia felix* Provance & A.C. Sanders, sp. nov., lacks the large bracts that immediately subtend, and clasp the calyx, as are always present in members of the *C. sepium* complex (Brown et al. 2009). We suspect that *C. felix* is more closely related to species of *Calystegia* endemic to the western US that possess graduated sepals, and have relatively small and sometimes remote bracts. Based on data gained from personal observations, herbarium collections, the early literature, and old maps, we think that *C. felix* is restricted to ciénega-wetland complexes in Southern California's alluvial basins. The extant occurrences in Chino must represent either plants that germinated from latent seed banks or are resprouts from the roots of plants that persisted in fields when this was an agricultural area. Either way, they apparently reappeared following the introduction of landscaping practices that have brought about "moist ground" conditions, similar to those that were historically present.

Methods

Recent *Calystegia* specimens from Chino were compared with *Calystegia* and *Convolvulus* collections at RSA-POM and UCR, as well as a selection of specimens from CAS and UC-JEPS, including the lectotype of *Convolvulus binghamiae*. We also obtained high-resolution digital images of *Convolvulus binghamiae* original material held at G-NDG. Scores of *Convolvulus* and *Calystegia* specimen images were evaluated for their relevance to the present study. We obtained images of relevant specimens held at the following herbaria: CAS, DS, E, K, LSU, NA, NY, P, SOC, UC-JEPS, US and WWB. Specimens with little immediate relevance are not listed in the appendices; however, regardless of ultimate relevance, all image sources and their source herbaria, are provided in Appendix I. *Calystegia felix* specimens that were examined are cited in the taxonomic discussion. All specimens of *C. sepium* examined are cited in Appendix II. Species of *Calystegia* that we think could be most easily confused with *Calystegia felix* are compared across a number of characters (Table 1). Specimens that we examined of the species included in that table are cited in Appendix III. Clarifications added to specimen citations appear in brackets. The precisions of the reported geographical coordinates were reduced to ± 300 m for the *C. felix* collections. Only specimens and specimen images that were seen by the authors are cited in the appendices, except in the case of a putative sheet of *Convolvulus binghamiae* at F (Mrs. R.F. Bingham s.n.) cited in the original description, and one specimen of *C. felix* (J.M. Wood et al. 4092). The herbarium code is followed by the word "image" when only an image was examined. Measurements were obtained from specimens conventionally, or from images using Meander V 2.3 (Dixon and Coventry 2008, available at <http://www.fastforwardsw.com/products/>

Table 1. A comparison of floral and vegetative structures in *Calystegia felix* with four similar species of *Calystegia*.

Character	<i>Calystegia felix</i> Provance & A.C. Sanders	<i>C. occidentalis</i> (A.Gray) Brummitt subsp. <i>occidentalis</i>	<i>C. occidentalis</i> subsp. <i>fulcrata</i> (A.Gray) Brummitt	<i>C. peirsonii</i> (Abrams) Brummitt	<i>C. subacaulis</i> subsp. <i>episcopalis</i> Brummitt
habit	clambering to climbing	clambering to climbing	trailing to clambering	tangling subshrub	decumbent to trailing
number of flowers per inflorescence	1, or rarely 2–4	1–4	1	1–2	1
corolla tube width, most proximal visible point (mm)	4–5.9	6–9	5	5.2–6.5	3.3–5.7
sepal shape	narrowly oblong	oblong to oblong-ovate	lanceovate to obovate	oblong to oblong ovate	ovate to narrowly lanceolate
sepal width (mm)	2.5–5	6–9	4–6	5.7	2–4
ovary internal vestiture	glabrous	silky hairy	silky hairy	silky hairy	glabrous
ovary external vestiture	glabrous or obscurely minutely pubescent apically	subglabrous	glabrous	glabrous	glabrous
inflorescence bract length (mm)	5–14	4–16	6.5–18	5–8	5.5–18.5
inflorescence bract shape	entire; narrowly elliptic to obelliptic	entire; narrowly elliptic to elliptic	lobed; triangular-hastate	entire; ovate, oval, or elliptic	entire; ovate to narrowly elliptic
lamina subtending flower, main lobe shape	broadly ovate to oblong ovate	narrowly triangular to broadly ovate	narrowly triangular to ovate	linear lanceolate to triangular	lance-ovate to broadly ovate
lamina subtending flower, basal lobe shape	short, rounded to truncate	short or not, 2-lobed to bipartite,	long, acute to truncate	long	short, somewhat rounded to narrowly lanceolate
lamina subtending flower, basal lobe orientation	barely divergent to parallel	divergent	divergent to parallel	divergent to parallel	strongly divergent
lamina subtending flower, length along midrib (mm)	45–122	32–51	27–46	14–16	23–28
lamina subtending flower, greatest width (mm)	30–96	33–66	35–54	19–22	16–34
lamina subtending flower, margin contour	flat to laxly involute, or with inverted basal lobes	flat	flat, or sometimes slightly wavy (esp. in the San Gabriel Mtns.)	wavy to grotesquely curled, rarely flat	flat

meander/). Cultivated plants were grown in UC mix outdoors in partial shade, at about 250 m elevation, in Riverside, California. The historical ecological setting in Chino was compiled from historical maps, early literature, herbarium specimens, and field observations.

Taxonomic treatment

Calystegia felix Provance & A.C. Sanders, sp. nov.

urn:lsid:ipni.org:names:77134775-1

http://species-id.net/wiki/Calystegia_felix

Fig. 1

Diagnosis. Differs from *Calystegia subacaulis* Hook. & Arn. subsp. *episcopalis* Brummitt, by its clambering to strongly climbing stems (versus decumbent to trailing stems in *C. subacaulis* subsp. *episcopalis*), larger leaves, 45–122 mm long, 30–96 mm wide mm long, subtending the peduncle (versus 23–28 mm long, 16–34 mm wide in *C. subacaulis* subsp. *episcopalis*), with short, rounded, barely divergent to parallel basal lobes, or sometimes nearly without basal lobes, and essentially truncate (versus the basal lobes somewhat rounded to narrowly lanceolate and strongly divergent in *C. subacaulis* subsp. *episcopalis*); Differs from *Calystegia occidentalis* (Gray) Brummitt subsp. *occidentalis* by its narrowly oblong, 2.5–5 mm wide sepals (versus oblong to oblong-ovate, 6–9 mm wide sepals in *C. occidentalis* subsp. *occidentalis*), narrower corolla tube (basally) 4–5.9 mm wide measured at the most proximal visible point (versus 6–9 mm in *C. occidentalis* subsp. *occidentalis*), an ovary that is glabrous on inside walls (versus a silky hairy vestiture inside of the ovary in *C. occidentalis* subsp. *occidentalis*), and larger, 45–122 mm long, 30–96 mm wide, oblong-ovate to broadly ovate leaves subtending the peduncles (versus smaller leaves subtending the peduncle, 32–51 mm long, 33–66 mm wide, narrowly triangular to broadly ovate), and short, rounded, barely divergent to parallel basal lobes, or leaves that are nearly truncate at the base (versus leaves with divergent basal lobes of varying length that are 2-lobed to bipartite).

Type. USA. California: San Bernardino County, City of Chino, SE of intersection of Edison Ave. and Oaks Ave., edge of Chaffey College Chino Campus, public right-of-way along powerlines. 33°59.822'N, 117°40.518'W, 206 m, 19 May 2012, A.C. Sanders, M.C. Provance, & T.A. Provance 40174 (holotype: UCR! [UCR-246125]; isotypes: ARIZ!, CAS!, K!, MO!, NDG!, NY!, RSA!, SBBG!, SD!).

Description. Semi-herbaceous perennial vines, senescing in October, though with some stems and leaves persisting through winter. Aerial stems 1–3 m long, from shallow, creeping rhizomes and stolons (Fig. 2), climbing and twining, or clambering across shrubs, branching frequently, terete, with nonobvious longitudinal ridges, slender, tough and wiry, glabrous to sparsely hairy, in life dull grayish pink to light green with a rosy cast. Leaves alternate, membranaceous to chartaceous, glabrous to sparsely hairy, bicolored when mature green above, paler below, relatively flat and not fold-



Figure 1. *Calystegia felix* Provance & A.C. Sanders, sp. nov. The holotype, A.C. Sanders & M.C. and T.A. Provance 40174 (UCR [UCR-246125]). The flowering branchlets are from a single ramet (Photo M. C. Provance, 2011).



Figure 2. *Calystegia felix* stolons and creeping rootstock. The narrow emergent leaves of this specimen may be atypical; the relatively long petioles are normal (Photo M. C. Provance, 2012).

ing along the midrib, but sometimes the basal half of the lamina slightly involute, and often having the basal lobes abruptly turned upward. Petioles on climbing stems $0.3\text{--}0.5 \times$ length of lamina, e.g. about 14–61 mm long, but often longer relative to lamina length on emergent leaves; lamina of climbing stems 45–115(–122) mm long, 30–80(–96) mm wide, oblong-ovate to broadly ovate, but narrowly oblong on the sterile branchlets and on stems distal to the flowering axils, base cordate, with short, rounded, parallel or barely diverging basal lobes, sometimes essentially without basal lobes and nearly truncate, apex obtusely rounded, sometimes subacute, minutely apiculate; emergent leaves from rhizomes and on trailing stems variable in shape, but usually broadly oblong to oval or orbicular, sagittate, with short lobes, or lobeless and rounded to the petiole, apex broadly rounded; lamina venation obscurely pinnate, but with 2–4 lateral veins from the base. Inflorescences axillary, flowers usually solitary, rarely 2–3(–4)-flowered; pedicels 1–30 mm long, peduncles 18–63 mm long; bracts 2, attached (1–)2–3(–4) mm below the calyx, ascending, subopposite, 5–14 mm long, 1–2.5(–3.5) mm wide, narrowly elliptic to narrowly oblanceolate, obtusely pointed, \pm flat, with a raised midvein, glabrous to scanty puberulent. Flowers perfect; sepals 5,

entire, graduated, narrowly oblong to lanceovate, green with a rosy blush, short-ciliate, inner sepals 11–15 mm long, 3.5–4 mm wide, the lower portion tightly appressed to mature fruit, outer sepals 8–11 mm long, 2.5–5 mm wide, apices \pm acutely rounded, mucronulate; corolla funnelform, 27–45 mm long, base of visible tube 4–5.9 mm wide, white (sometimes appearing light yellow in herbarium specimens), with 5 externally pigmented interplacae (midpetaline bands or longitudinal stripes), these very light-yellow, more rarely reddish-purple (Fig. 3), glabrous externally, or rarely, conspicuously hairy adjacent to pleats in the basal third of the corolla, the hairs yellowish, lobes 5, very short, each with a concentrated area of minute hairs along the margin; stamens 5, equal; filaments 18–21 mm long, fused to the corolla tube \pm 7–9 mm of that length, glandular hairy along the proximal margins; anthers 4–4.5 mm long, white, barely reaching the base of the stigmas; pistil glabrous both internally and externally; style 16–21 mm long, glabrous, or with a few glandular hairs near the base; stigmas 2, cylindrical, \pm 3 mm long, asymmetric, with one axially oriented, and the other ascending; nectary crenate-coronoid. Pollen white to cream, with circular perforations discernible at 60 X. Fruit dry capsule, indehiscent to tardily dehiscent from tip to base, globose, 9–10 mm in diameter, glabrous or obscurely minutely pubescent apically. Seeds 1–4 per capsule, ca. 4 mm in height and 3.5–4 mm in width, \pm angular-ovoid, and depending on the number of developing seeds, nearly black to dark brown and tan-speckled, hilar region purplish, finely granular.

Distribution. *Calystegia felix* is endemic to the inland basins of the Los Angeles, San Gabriel, and Santa Ana river watersheds in Southern California, at between 40 and 208 meters elevation. The species has not been seen in Los Angeles County since 1902. Six occurrences are known, all of them in the City of Chino, in San Bernardino County (Fig 4). The occurrences have a spatial separation ranging from 0.3–2 km. The easternmost occurrence is just west of Euclid Avenue, close to Chino's border with Ontario and Eastvale. The westernmost occurrences are on alluvial terraces above Chino Creek, coming within several meters of the City of Chino Hills.

Phenology. Flowering begins in late March, and is heavy until early August, with flowering thereafter decreasing through late September. In 2011 and early 2012, inflorescences on the only plants known at that time had solitary flowers. During mid-May of 2012, inflorescences at that site were observed to be two or three-flowered, and rarely solitary. It is not certain whether flower number increased as the season progressed, or if flowers during the later visit were originating on vines of a different genet. Only solitary flowers were seen at the sites discovered in 2013. Ripe seeds have been collected from early June until late October. Fruit with small holes indicative of seed predation by bruchid beetles have been found (Provance, pers. obs.). Small, senesced, nodding, sterile, apetalous flowers, mostly near ground level, have recently been noticed on some plants. We observed similar flowers on herbarium specimens of a few other species of *Calystegia*. It is unknown if these flowers are apetalous developmentally, or if the corollas were lost to insect predation. More in-depth study of this condition is needed.



Figure 3. *Calystegia felix* in bloom at the type locality, in a planter bed in Chino. This plant, discovered in 2011, is the only one we have seen that produces corollas with reddish-purple midpetaline stripes. Also, note the blushed sepals (Photo M. C. Provance, 2011).

Additional specimens examined. USA. California. San Bernardino County: Chino Creek south of Ontario, climbing in trees, 500 ft., 30 May 1917 (H), *I.M. Johnston* 1274 (RSA, POM, UC); City of Chino, 33°59.823'N, -117°40.537'W, 206 m, SCE right-of-way, just northeast of Chaffey College, southeast corner of the intersection of Edison Rd. & Oaks Ave., 11 May 2011, *M.C. Provance* 17214 (UCR); same location, 14 May 2011, *M.C. Provance* 17351 (UCR, UC, DAV, NDG); same location, 25 Mar 2012, *M.C., J.M., & T.A. Provance* 17430 (UCR, WIS); West Chino, east

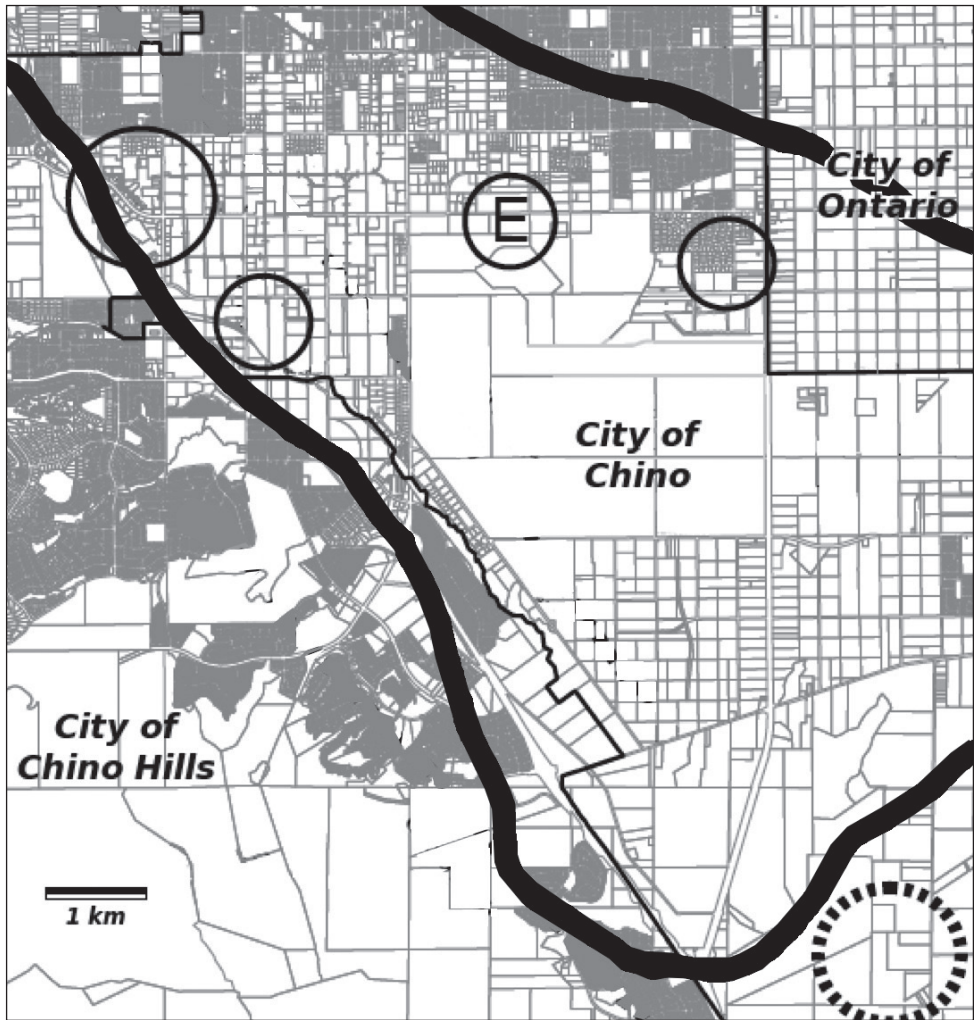


Figure 4. Map of historical and recently discovered *Calystegia felix* occurrences in the Chino Basin. The circled E marks the plant discovered in 2011; normal circles are 2013 occurrences, the largest a cluster of three populations. The broken circle is the approximate location of Johnston's collection in 1917. The perimeter of the Chino artesian belt and "moist land" prior to 1904 is delineated by the thick black line. The street map was adapted from the City of Chino draft general plan EIR, July, 2010, and the artesian belt is based on Mendenhall (1907).

of Chino Creek, 33°59.17'N, 117°42.38'W (\pm 300 m), 190 m, planter bed in public parking area, 31 May 2013, *M.C. Provance* 17525 (UCR, to be distributed); West Chino, east of Chino Creek, 34°00.18'N, -117°43.31'W (\pm 300 m), 208 m, planter bed in public parking area, 3 June 2013, *M.C. Provance* 17526 (UCR, to be distributed); West Chino, Highway 71 – Grand Avenue ramp, 33°59.44'N, -117°43.30'W (\pm 300 m), 205 m, Highway 71 and an adjacent planter bed in a public parking area, 11

June 2013, *M.C. Provance 17527* (UCR, to be distributed); West Chino, 33°59.63'N, -117°43.18'W (± 300 m), 200 m, planter bed in a public parking area, 11 June 2013, *M.C. Provance 17528* (UCR, to be distributed); East Chino, planter bed along public sidewalk near southeast corner of Buckeye Street and Fern Avenue, 33°59.65'N, -117°39.24'W (± 300 m), 206 m, 11 June 2013, *M.C. Provance 17529* (UCR, to be distributed); City of Chino, SE corner of Edison Ave. and Oaks Ave., near entrance to Chaffey college campus, ca. 2.5 mi N of Chino Creek (Prado Basin), irrigated landscaped area adjacent to ruderal grasslands, 17 May 2011, *J.M. Wood et al. 4092* (K not seen, RSA not seen). **Los Angeles County:** Rivera [historic town, later part of Pico Rivera, misspelled “Riveria” on Davidson’s herbarium label, and misspelled “Riviera” in Davidson and Moxley 1923], “Common in most grounds [moist grounds—a phrase Davidson often used on herbarium labels]” (Davidson 1909), “Very common on stream banks [either the Rio Hondo, or a small unnamed stream running through McCampbell and Downey Road, c. 0.5 km west of Rivera] at Riviera [Rivera] and on the Los Angeles and San Gabriel Rivers in that vicinity” (Davidson & Moxley 1923), 1 May 1902, *A. Davidson 1892* (RSA [RSA-394817]); Near University Station [historic train station in S. Los Angeles at 43rd St. and Vermont Ave. (Grace 2007)], Los Angeles, 1899, *A. Davidson 2144* (RSA [RSA-394819] [mixed collection with *C. sepium*]).

Discussion. Taxonomy: Although arguments to maintain *Calystegia* have been weakened by recent molecular studies, we describe this new species as such, pending molecular phylogenetic studies that sample more thoroughly across both *Calystegia* and *Convolvulus*. Although their flowers are not similar, it is noteworthy that few vegetative characters seem to separate *C. felix* from the weed *Convolvulus arvensis* L. The only vegetative feature we currently know that can reliably be used to tell these taxa apart is the cross section of the stem, which is angular in *Convolvulus arvensis*, and terete with weak longitudinal ridges in *C. felix*. There may be differences in leaf venation, but that will require additional study. Unfortunately, *Convolvulus arvensis* is abundant throughout the Chino area, and occurs at several of the *C. felix* sites.

While a definitive treatment of the entire *C. sepium* complex has not been published, the best defining features of this group are the large bracts which immediately subtend, and often enclose the calyx, and have conspicuously netted venation. It is a taxonomically difficult complex that may include over twenty *C. sepium* subtaxa, some additional closely related species, and their subtaxa (Stace 1961, Brown et al. 2009). So defined, all of the original material for *Convolvulus binghamiae*, including the lectotype at UC (Brummitt et al. 2012), is clearly referable to this complex. The epithet *binghamiae* is sometimes applied to specimens from Southern California with clasping bracts that only partly cover the sepals, and have leaves with barely divergent basal lobes, but that are otherwise inseparable from *C. sepium*. All of the original material of *Convolvulus binghamiae* is from a salt marsh that once occurred in Santa Barbara. The lectotype has only one flower (Fig. 5), which has a bract that may be the smallest found on any of the original material. Nonetheless, the corolla has a broad base, as seen in all members of the *sepium* complex. Moreover, leaves from the same sheet (Fig. 5 and Fig. 6) are consistent with many specimens attributable to the *Calystegia sepium* complex. The bracts among the original material range



Figure 5. Lectotype of *Convolvulus binghamiae* Greene, Santa Barbara, July, 1886, R.F. Bingham s.n. (UC335392), with one small bract, and a broad-based corolla.

from 7 to 13.8 mm long and 3.1 to 9.1 mm wide, and in their fully developed state are broadly lanceolate to broadly ovate. Inflorescence bracts in *C. felix* have a similar range in length, but are much narrower at 1 to 3.5 mm in width, and usually lack a conspicuous network of veins. Most bracts in the *Convolvulus binghamiae* original material are in every sense typical of the *C. sepium* complex. Interestingly, some of the largest bracts are associated with flower buds: in one case (Fig. 7), some of the bracts of the flower buds are larger than the bracts of the open flower on the same sheet. Finally, the corolla tubes (measured at the base of the sepal lobes) in the *C. binghamiae* original material are over 8 mm wide. In *C. felix* the lower tube of the corolla is narrow, ranging from 4 mm to about 6 mm in width. *Calystegia felix* is clearly not part of the *Calystegia sepium* complex, and represents a new, unrelated, and previously undescribed taxon.

Specimens of *C. felix* were included in *Convolvulus binghamiae* by Davidson in his list of new records for Los Angeles (1909) and by Davidson & Moxley in their flora of Southern California (1923). When Jepson made the combination *Convolvulus sepium* var. *binghamiae* (Greene) Jepson, he was very particular in his application of the name, stating, “Santa Barbara; a distinct localized variety, rarely collected”. Under *Convolvulus sepium* var. *pubescens*, Jepson (1939) cites a Chino specimen (*Condit s.n.*) that we have seen, and which is equivalent to material typically ascribed to *C. sepium* subsp. *limnophila* in Southern California (and elsewhere). While it is possible that Jepson had



Figure 6. The leaves shown here from *R.F. Bingham s.n.* (UC335392) are consistent with many specimens of *Calystegia sepium*.

seen a collection of *C. felix* at some point, it is not obvious where he would have placed such a collection in his 1939 treatment.



Figure 7. Original material of *Convolvulus binghamiae* Greene, Santa Barbara, 1886, *E.L. Greene s.n.* (NDG [NDG-66275]). Flower buds with large clasp- ing bracts typical of the *Calystegia sepium* complex are noteworthy (a), as is the solitary flower (b) with a broad calyx, broad corolla tube, and a smallish, but otherwise typical clasp- ing bract for the *C. sepium* complex (Image courtesy of Barbara Hellenthal at the Notre Dame Herbarium).

In 1945, Abrams annotated one sheet of Johnston’s *C. felix* collection at RSA as *Convolvulus binghamiae*, probably while preparing his *Illustrated Flora* (1951). The illustration of *Convolvulus binghamiae* in this flora seems to be *C. felix*, which is incongruent with his treatment, since the geographic distribution given by Abrams for *Convolvulus binghamiae* excludes all extant and historic occurrences of *C. felix*. Brummitt (1993) applied *Calystegia sepium* subsp. *binghamiae* (Greene) Brummitt, to plants of the northern and central South Coast between sea level and 20 meters elevation, which excludes collections from Chino. In Brummitt et al. (2012), the author’s recognize the similarity of material we refer to *C. felix* to the illustration in Abrams flora, noting, “A good illustration of the latter may be seen in Abrams (e.g., Fig. 3855, 1951)”. However, they propose that the drawing represents a phenotypic variant of their proposed *Calystegia binghamiae* (Brummitt) Brummitt. The misidentified collections at RSA and the illustration in Abrams of what was actually an undescribed species seems to have influenced the search image of at least some local botanists attempting to rediscover *C. sepium* subsp. *binghamiae*.

Philip A. Munz annotated a Johnston collection at RSA as *Convolvulus purpuratus* Greene in 1931, thus clearly including *C. felix* in his concept of *Convolvulus purpura-*

tus. In his Southern California Manual (Munz 1935) he listed Chino as a locality for this species. Among many differences, *Calystegia purpurata* (Greene) Brummitt subsp. *purpurata* can be readily separated from *C. felix* by its equal, evenly inserted sepals.

The number of flowers per inflorescence, corolla pigmentation, external corolla vestiture, and the vestiture of leaves and stems vary in *C. felix*. Whether this variation is influenced more by genetics or environmental factors remains to be studied. Heterophylly is profound in *C. felix*, and generally manifests as narrower lamina on sterile twining stems, instead of the larger ovate to oblong-ovate leaves of reproductively active stems. There seems to be a tendency towards rounder leaves with longer petioles on emergent stems and sometimes trailing stems. *Calystegia felix* is similar to other species in the genus with small, somewhat remote bracts, and graduated sepals. Several morphological characters are used to compare four of those species with *C. felix* (Table 1). Leaf parameters alone are often insufficient for the identification of *Calystegia*, but fortunately, several other characters in addition to leaf shape, differentiate *C. felix* from other species of *Calystegia*.

At first glance, *C. felix* looks most similar to *C. occidentalis* (Gray) Brummitt subsp. *occidentalis*, since both taxa have a similar clambering or climbing habit, similar bracts inserted approximately the same distance below the calyx, and potentially produce multiple flowers in inflorescences. However, *C. felix* differs from *C. occidentalis* by its narrower sepals, narrower corolla tube, internally glabrous ovary, and larger oblong-ovate to broadly ovate leaves. The leaves subtending peduncles of *C. felix* have short, rounded, barely diverging to parallel basal lobes. Sometimes, *C. felix* leaves are nearly truncate at the base. This easily differentiates *C. felix* from *C. occidentalis*, which has lamina basal lobes that are of varying length, but divergent, and usually 2-lobed or bipartite. *Calystegia felix* also looks like *C. subacaulis* Hook. & Arn subsp. *episcopalis* Brummitt. Both taxa have slender, but tough and wiry stems, corolla tubes that narrow toward the base, narrow sepals, and an ovary that is glabrous both internally and externally. It differs from *C. subacaulis* subsp. *episcopalis* by its strong climbing habit, and much larger leaves that differ considerably in basal lobe morphology.

The similarities between *C. felix* and *C. subacaulis* subsp. *episcopalis* tend to be less readily apparent than the similarities between *C. felix* and *C. occidentalis* subsp. *occidentalis*. However, the characters shared seem not to be widespread in the genus. For example, while ovaries of *C. felix* sometimes have a small number of minute hairs toward the apex, they are essentially glabrous externally. They are also glabrous internally. Though we have had only one specimen of *C. subacaulis* subsp. *episcopalis* upon which we have been able to conduct detailed flower dissections (*F. Bowcutt* 2163 [UCR]), we are especially intrigued by the ovaries of this collection, which are glabrous both internally and externally. We have seen this combination of characters only in *C. felix*, and similarities such as these might indicate that the two taxa are more closely related than their superficial appearances suggest.

Ecology: The six known occurrences are associated with somewhat poorly drained alkali silt loam (SoilWeb 2013), on a floodplain with an average slope of just over 1% (Lewis Publishing Company 1890, SoilWeb 2013). The local soils have developed

primarily from the accumulated granitic alluvium that was washed out of the San Gabriel Mountains during episodic flood events (Hilgard 1902). Historically, there were a number of springs near the *C. felix* occurrences, and the springs of the plains and basins and their accompanying vegetation, typically marshland and wet meadows, were known as *ciénegas* (Schuyler 1880, Mendenhall 1908). In Southern California the use of the word *ciénega* always implied the presence of a spring, unlike in some other parts of the American Southwest (e.g. Hendrickson and Minckley 1985). In the earliest known general description of *ciénegas* in the Chino Basin, Schuyler (1880) emphasized that *ciénega* was the only word commonly used to indicate its springs and associated habitat. In the Chino Basin, there were two (Hall 1888a, 1888b) or three (Tait 1911) main groups of *ciénegas* located a very short distance west to southwest, south, and southeast of Chino (Tait 1911). The perimeter of the Chino Artesian Spring Belt was roughly triangular, and its location in the current landscape is easily derived from the early maps. The east and west vertices were near the Chino Creek and Mill Creek emergences respectively. A third vertex would be near the south side of Prado Basin. These boundaries coincide well with the historical limits of “moist land” as mapped earlier by H. B. Martin (1887–1889). Mendenhall (1908) estimated the area of the artesian belt and associated moist soil as 23 sq. miles prior to 1904. Various aspects of the hydrology and geology of the Chino Basin *ciénegas* have been summarized (e.g. Truman 1874, Schuyler 1880, Hall 1888b, Lewis Publishing Company 1890, Shinn 1898, Mendenhall 1905, 1907, 1908, Hilgard and Loughridge 1906, 1908, Troxell 1957).

Historically, the water table in the vicinity of the artesian spring belt was 6–35 feet below ground (Lewis Publishing Company 1890). The soils within the spring belt, which are largely alkali silt loams, retained moisture throughout much of the year, and as a consequence were extraordinarily important to Southern California agriculture (e.g. Peffer 1894, Shinn 1898, Nelson 1917). Based on soil maps, four of the *C. felix* occurrences are on Chino silt loam. Both of the occurrences that are not on Chino Silt Loam, one on Grangeville fine sandy loam, the other on Hilmar loamy fine sand, are less than 30 feet from Chino silt loam according to soil maps (SoilWeb 2013). While *Calystegia felix* occurrences seem to be strongly associated with Chino silt loam; an analysis of soil at occupied sites has not been performed.

On Edison Rd., *C. felix* was discovered in a sidewalk tree basin on Chino silt loam. In that area, the soil is pale gray, with occasional small patches of fluffy salt crust. Disturbed alkali playa habitat was observed nearby, with *Heliotropium curassivicum* L., *H. europaeum* L., *Cynodon dactylon* (L.) Pers., *Chenopodium berlandieri* Moq., *Malvella leprosa* (Ortega) Krapov., *Convolvulus arvensis* L., and *Amaranthus palmeri* S. Watson. Also nearby was a sparsely vegetated earth-bottom ditch with *Conyza* and *Lepidium strictum* (S. Watson) Rattan, and old fields with *Secale cereale* and a diverse group of weedy native and introduced forbs. Native plant species documented within 400 m of the *Calystegia* site include: *Amaranthus palmeri*, *Ambrosia psilostachya* DC., *Amsinckia* sp., *Atriplex serenana* Abrams, *Baccharis salicifolia* (Ruiz and Pav.) Pers., *Chenopodium berlandieri*, *Epilobium brachycarpum* C. Presl., *Epilobium ciliatum* Raf., *Fraxinus velu-*

tina Torr., *Pseudognaphalium californicum* (DC.) Anderb., *Heliotropium curassivicum*, *Heterotheca grandiflora* Nutt., *Malacothrix saxatilis* (Nutt.) Torr. & A. Gray, *Malvella leprosa*, and *Solanum americanum* Mill.

Although seeds and rhizomes can be moved around in many ways, we contend that invoking accidental transport of stem fragments or seed by humans is not the most parsimonious explanation for the presence of *Calystegia felix* in the City of Chino, since the species is known nowhere else. While we have no direct proof, we think the recently discovered *Calystegia felix* populations represent plants that have emerged from latent, long-lived seed banks or roots following a return to “moist soil” conditions (Figs 8, 9), similar to those in the historical record. Buried seeds of *C. sepium* have retained high levels of viability after 39 years (Bond et al. 2007), and *C. felix* may have similar longevity. If changes in soil moisture regimes are occurring (i.e. becoming wetter), horticultural practices within the urban environment are likely the cause. We have not investigated soil moisture in Chino experimentally, but we observed an apparent moisture gradient. The success we have had locating new occurrences of this rare plant in developed areas contrasts sharply with our failure to locate occurrences in undeveloped visually drier areas. While we are not sure of the significance at this point, it seems noteworthy that each of the sites currently supporting *Calystegia felix* were, based on aerial images (Google Earth V.2.1.6014b), completely stripped of their vegetation at some point between 4 and 11 years ago).

Historical information and early herbarium collections suggest that the Chino Basin originally had vegetation of wet meadow and alkali meadows dominated by *Anemopsis californica* (Nutt.) Hook. & Arn., with perennial grasses, such as *Elymus triticoides* Buckley, *Sporobolus airoides* (Torr.) Torr., and *Distichlis spicata* (L.) Greene, and herbs such as *Trifolium willdenovii* Spreng., *Trifolium wormskioldii* Lehm., and *Helianthus annuus* L. In addition, there were small bodies of open water, alkali and freshwater marshes, alkali scrub, alkali grassland, alkali playa, moist stream banks, and willow thickets. There were also phreatophytic woodland communities of *Salix*, *Populus*, and *Platanus racemosa* Nutt. (Truman 1874). The spring-belt wetlands were collectively referred to as “ciénega-lands” (e.g. Hilgard 1889). Common sunflower (*Helianthus annuus*) is frequently mentioned in the early literature as a common species on alkali soils in the Chino Basin, and was considered indigenous (e.g. Davy 1898). The topography just north of the Santa Ana River was reportedly hummocky (Nelson 1917), and may have been supportive of vernal pools. Most fine-scale relief in the basin has probably been lost to disking and grazing cattle, but the north part of the ciénega belt was reportedly rather smooth. Mendenhall (1905) commented:

“The lands just above this [above the ciénega-lands] are flat and often ill drained. The waters rising and evaporating here, under the influence of the effective southern sun, leave behind them their salt content, and thus alkali lands may result”

Thus, much of the landscape represented a mosaic of ciénega and ciénega-creek associated palustrine communities. The historical natural vegetation of the City of Chino cannot easily be envisioned because of past and current development. For example, a satellite of the University of California Agricultural Experiment Station called the “Ten Acre Tract” used to be in Chino and experiments related to growing crops on



Figure 8. *Calystegia felix* climbing upward through urban landscaping in the City of Chino (Photo M. C. Provance, 2013).

alkali soil were conducted there. This property was described as being dominated by *Anemopsis californica* (Hilgard & Loughridge 1896), which indicates that it was likely alkali marsh. The Ten Acre Tract is now occupied by industrial buildings and offices. However, taxa highly indicative of alkaline marsh and alkaline meadow have persisted in unusual places. For instance, we documented a number of *Anemopsis californica* persisting in plantings of *Hedera helix* along a sidewalk in northeast Chino near the Ontario border, just within the mapped historical limits of moist ground. The following



Figure 9. Emergent *Calystegia felix* on crusted, moist, Chino silt loam, amongst urban landscaping. It is unknown if large groups of emergent plants such as these represent one to just a few clones, or many genotypes (Photo M. C. Provance, 2013).

year we found *Calystegia felix* growing in a sidewalk planter across the street from the *Anemopsis* site, in similar urban landscaping. We think other remnants of the ciénega flora may persist in Chino.

Conservation: *Calystegia felix* is endemic to Southern California, extirpated in Los Angeles County, and now likely confined to the Chino Basin in San Bernardino County. It is doubtless at high risk of soon becoming extinct in the wild. This is due to

hydrological changes in the Chino Basin, including the paving of streams, lowering of the water table, and loss of ciénega habitat, including vegetation associated with marshes, meadows, grasslands and alkaline playas; and encroaching commercial, industrial, residential developments, and public works projects. Large areas of habitat have already been transformed. Six extant occurrences are now known, with an estimated 200 ramets emerging in 2013 at a single location near Chino Creek. However, those plants likely represent clones, as do the about 50 ramets at the other sites. Based on there being few known populations, a limited overall distribution, and a small number of individuals in existence, we suggest a conservation status of Critically Endangered (CR). Upon discovering the plants along Edison Road, it was obvious they were in imminent danger of being destroyed by impending grading and trenching for the burial of high-voltage power lines. We initially thought that these plants represented a single clone, but two ramet-specific flower color morphs, seed production, and spatial separation of clusters of emergent stems, suggest that two or more genotypes are present. Over the short term, Rancho Santa Ana Botanical Gardens has been contracted to conduct ex-situ propagation of rhizomes from the Edison Road population, and a few other plants are being cultivated in private and institutional gardens.

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Appendix I

Image databases, internet address, and source herbaria, of specimen images initially examined for this study.

Image database	Location	Herbaria coverage
Herbaria@home	http://herbariaunited.org/atHome/	ABS, BIRM, SLBI, DBC, PTH
Digital specimen images at the Herbarium Berolinense.	http://ww2.bgbm.org/herbarium/	B
Appalachian State University	http://vascularflora.appstate.edu/vps	BOON
California Academy of Sciences, botany collection CAS-BOT	http://collections.calacademy.org/bot/	CAS-DS
George Safford Torrey Herbarium (CONN) database	http://bgbaserver.eeb.uconn.edu/databasesimple.html	CONN
Royal Botanic Garden Edinburgh herbarium catalogue	http://elmer.rbge.org.uk/bgbase/vherb/bgbasevherb.php	E
Botany collections database	http://emuweb.feldmuseum.org/botany/detailed.php	F
Fairchild Tropical Garden, virtual herbarium	http://www.virtualherbarium.org/vh/db/main.php	FTG
Geneva Herbaria Catalogue	http://www.ville-ge.ch/musinfo/bd/cjb/chg/?lang=en	G, G-DC, G-BOIS, G-BU
Kew Herbarium catalogue	http://apps.kew.org/herbar/gotoHomePage.do	K
Virtual guide to the main collections of the LE Herbarium	http://www.mobot.org/MOBOT/Research/LEguide/index.html	LE
The Linnean collections	http://linnean-online.org/view/type/specimen/	LINN, LINN-HS
The Herbarium of Louisiana State University, image gallery	http://www.herbarium.lsu.edu/	LSU
Tropicos Image Search	http://www.tropicos.org/ImageSearch.aspx	MO
US National Herbarium: vascular plant types	http://www.usna.usda.gov/Research/Herbarium/BotType.html	NA
C. V. Starr virtual herbarium	http://sciweb.nybg.org/science2/vii2.asp	NY
Sonnerat – Muséum National d'Histoire Naturelle (Paris, France) Spécimens d'herbier	http://coldb.mnhn.fr/colweb/form.do?model=SONNERAT . www.sonnerat.org	P
Consortium of Pacific Northwest Herbaria	http://www.pnwherbaria.org/	SOC, WWB
Herbarium, Taiwan Forestry Research Institute, specimen data search	http://taif.tfri.gov.tw/search.php?l=Eng	TAIF
Alabama Plant Atlas	http://www.floraofalabama.org/	TROY
Type specimens in UC and JEPS that have high-resolution images	http://ucjeps.berkeley.edu/db/types/imaget_types.html	UC-JEPS
Databased vascular plant types at UC/JEPS	http://ucjeps.berkeley.edu/db/types/types_table.html	UC-JEPS
US Herbarium, type register search	http://collections.mnh.si.edu/search/botany/?ti=3	US
Atlas of Florida vascular plants, herbarium specimen search	http://florida.plantatlas.usf.edu/specimen.aspx	USF
Virtual Herbaria Austria	http://herbarium.univie.ac.at/database/search.php	W, WU, KUFS, HAL

Appendix II

Specimens examined of *Convolvulus binghamiae* Greene, *Convolvulus limnophilus* Greene, and *Calystegia sepium* L.

Original, and possibly original material of *Convolvulus binghamiae* Greene. USA. California. Santa Barbara County: Santa Barbara, “Burton’s Mound” (acc. to the protologue), Aug, 1886 (fl), *Mrs. R.F. Bingham s.n.* (lectotype UC [UC-335392], originally in the Lemmon Herbarium); isolectotype F [not seen], according to Brummitt et al. 2012, photos of a “presumed duplicate” are at K and RSA); same locality, July, 1886 (fl, buds) *E.L. Greene s.n.* (NDG [NDG-66274] image; NDG [NDG-66276] image; NDG [NDG-66275] image [no collection month given on specimen]); Santa Barbara, June, 1887, *Mrs. R.F. Bingham 573* (possible original material NA [NA-0026310] image) (<http://www.usna.usda.gov/graphics/usna/Research/Herbarium/Specimens/0026310.jpg>). *Mrs. R.F. Bingham 573* is labeled “type”, but more study is needed. It was collected the same month and year the description was published. Greene states material used in his description was collected in 1886. Since both Bingham and Greene cultivated native morning glories, and Greene included details based on observations of living plants (e.g. the number of days that flowers persisted). It is possible that *Mrs. R.F. Bingham 573* represents a collection of living material that Greene used in his description.

Original and probably original material of *Convolvulus limnophilus* Greene. USA. California. County unknown: Suisun Bay, Aug 1883, *E.L. Greene s.n.* (probable syntype NDG [NDG-66290] image); “Gxxx Station” [partly illegible], 1883, *E.L. Greene* (probable syntype NDG [NDG-66293] image).

Specimens examined of *Calystegia sepium* L. USA. California. Contra Costa County: levee along Bethel Island, 5 Sep 1954, *I.L. Wiggins 13122, 13123* (DS); Otto’s Black Bass Resort, 8 Jul 1949, *M.A. Nobs & S.G. Smith 941* (DS). **Los Angeles County:** near Los Angeles, May–June 1904, *Pupils of Los Angeles High School s.n.* (UC); SE of Huntington Beach, 15 Jun 1932, *L.M. Booth 1192* (POM). Riveria [Rivera], 1 May 1902, *A. Davidson 1892* [mixed sheet with *Calystegia felix*] (RSA). **Mariposa County:** Martinez, 30 Jul 1893, *J.W. Congdon s.n.* (CAS). **Orange County:** East of Huntington Beach, 5 Aug 1932, *L.M. Booth 1359* (UC); Bolsa Chica, 28 Jun 1932, *L.M. Booth 1214* (POM); Wintersberg, 26 Sept 1926, *Peirson 7086* (UC, RSA). **Riverside County:** Hidden Valley Wildlife Refuge, 28 May 1989, *M. Braun 39* (UCR); Springbrook, Fairmount Park, Riverside, *S.B. Parish 916, 4612, 5334* (DS), *6435* (CAS); same location, Sep 1921, *E. Smith s.n.* (CAS); same location, 31 May 2004, *Clarke s.n.* (UCR); same location, Aug 1901, *Hall s.n.* (UC); same location, 10 Jun 1952, *J.C. Roos 5763* (UCR); same location, 14 Sep 1999, *M.C. Provance & S. Boyd 1780* (UCR, CAS, RSA, SD, UCD); same location, 29 May 2013, *M.C. Provance & R. Richmeier s.n.* (UCR). **Sacramento County:** Sacramento Valley, 1838–1842, *Wilkes 1365* (US image). **San Bernardino County:** San Bernardino, no date, *Wright 1727* (NDG image); two miles SE of San Bernardino, 17 Jul 1924, *P.A. Munz 8690* (UCR);

China Ranch, 7 Aug 1950, *J.C. & A.R. Roos 4919* (RSA); San Bernardino Valley, 7 Sep 1907, *S.B. Parish 6435* (CAS); San Bernardino, Jul 1881, *S.B. & W.F. Parish 916* (DS); E St. Swamp, *S.B. Parish 5334* (DS [2 sheets]); Chino, 16 Jul 1908, *I.J. Condit s.n.* (UC). **San Joaquin County:** Middle River, 22 Aug 1978, *B. Atwater 52* (CAS); Old River, 16 Aug 1978, *B. Atwater 37* (CAS); Holt, 21 Aug 1946, *H.L. Mason & V. Grant 13067* (CAS). **Solano County:** Collinsville, Sep 1921, *E. Smith s.n.* (CAS); Suisun Marshes, 15 Oct 1905, *W.R. Dudley s.n.* (DS); same location, 15 Oct 1905, *W.R. Dudley s.n.* (DS); same location, 28 Oct 1938, *J.T. Howell 14594* (CAS); same location, 28 Aug 1920, *V. Jones s.n.* (CAS); same location, Jul 1913, *A. Eastwood 3451* (CAS).

Appendix III

Herbarium specimens examined of the *Calystegia* species included in Table 1.

Specimens examined. *Calystegia occidentalis* ssp. *fulcrata*. USA. California. Los Angeles County: Big John Flat, 21 Jun 1999, *Swinney 7365* (UCR); Granite Mountain vicinity, 24 July 1991, *T. Ross & S. Boyd 5602* (UCR). **San Bernardino County:** Fredalba, 22 Jul 1902, *Abrams 2780* (E image, P image); N end of Fawnskin, at base of Delamar Mountain, 2141 m, 14 Jul 1993, *S.D. White 1680* (UCR); San Bernardino Mtns., 1880, *J.C. Nevins 417* (P image), Arrowhead Hot Springs and immediate vicinity, 579 m, *A.C. Sanders 13805* (UCR). **Sonoma County:** near Sonoma [according to R. K. Brummitt], *J.M. Bigelow s.n.* (K image, NY image, PH image). **Tuolumne County:** Twain-Harte, *A. Eastwood & J.T. Howell 8618* (CAS image). ***Calystegia occidentalis* ssp. *occidentalis*. USA. California. County unknown:** near San Francisco, date not known, *H. Gibbons* (GH54299 image). **Amador County:** New York Falls, 1500 ft., 3 Jul 1892, *G. Hansen 79* (E image). **Butte County:** no further location provided, 1848, *M. Hartweg 1862* (P image). **Madera County:** Chowchilla, June 1885, *J.W. Congdon s.n.* (P image). **Napa County:** S. of Lake Berryessa, 15 May 1971, *M.J. Minabe 70* (LSU). **Placer County:** Forest Route 13, 1.8 mi south of junction with Forest Hill Rd., 28 Jul 2010, *G. Helmkamp 16643* (UCR); 0.2 mi north of Forest Hill Rd. on unnamed road to Clementine Lake, 14 Jun 2006, *G. & E.A. Helmkamp 10706* (UCR). **Plumas County:** Meadow Valley, 14 Jul 1963, *B. Horn 630714 #10* (UCR). **Shasta County:** Anderson, 20 April 1968, *G.C. Strausbaugh 29* (WWB image); near Middle Creek Station, 3 Jun 1905, *A.A. Heller 7955* [4955 on label apparently in error] (E image). **Siskiyou County:** Little North Fork Public Camp, 1997 ft., *C. Miller 56* (SOC image); Yreka, 8 Jun 1905, *A.A. Heller 7997* (E image). **Oregon. Douglas County:** Mt. Nebo, Roseburg, 900 ft., 22 May 1967, *Godfrey 49* (SOC image). **Jackson County:** Jackson City, 22 May 1981, *F.A. Lang 1412* (SOC image). **Lake County:** Mountains near Lakeview, 19 Aug 1901, *W.C. Cusick 2771* (E image). ***Calystegia peirsonii*. USA. California. Los Angeles County:** Rock Creek, 27 May 1923, *F.W. Peirson 3537* (CAS image); same location, 21 May 1923, *Peirson 7301* (UC image); near Palmdale, 9–24 May 1896, *J.B. Davy 2304* (UC image). Bouquet *C. felix* Road

east of the reservoir, 20 Jun 1979, *T. Krantz s.n.* (UCR); Castaic Mesa, 28 Apr 2003, *A.C. Sanders 26128* (UCR); Mt. Gleason, 20 Aug 1992, *O. Mistretta 761* (UCR); Newhall Ranch, 19 Jun 2002, *A.C. Sanders & M. Elvin 25200* (UCR). ***Calystegia subacaulis* ssp. *episcopalis*. USA. California.** Acad. du San Francisco, *Anonymous* s.n. (P4492495 image). **San Luis Obispo County:** Cambria, 28 Apr 1926, *A. Eastwood 13641* (K image, CAS image). **San Mateo County:** Woodside, 13 May 1932, *L.S. Rose 32248a* (P image). Above Crystal Springs on the Half Moon Bay road, 28 May 1907, *Heller 8557* (P image). **Sonoma County:** Adobe Canyon, just NW of Sonoma, 1200 ft., 24 May 1996, *F. Bowcutt 2163* (UCR).

A new species of *Goniothalamus* (Annonaceae) from Palawan, and a new nomenclatural combination in the genus from Fiji

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Abstract

A new species, *Goniothalamus palawanensis* C.C.Tang & R.M.K.Saunders, **sp. nov.** (Annonaceae), is described from Palawan, Philippines. *Goniothalamus palawanensis* is most closely related to *G. amuyon* (Blanco) Merr., but differs in its shorter inner petals, hairy ovaries, and funnel-shaped stigmas. A new nomenclatural combination, *G. angustifolius* (A.C.Sm.) B.Xue & R.M.K.Saunders, **comb. nov.**, is furthermore validated to reflect the phylogenetic affinities of a Fijian species previously assigned to *Polyalthia*.

Keywords

Goniothalamus, *Polyalthia*, Fiji, Malesia, Melanesia, Palawan, new combination, new species

Introduction

The Annonaceae are a species-rich early-divergent angiosperm family, consisting of ca. 108 genera and ca. 2500 species of trees, scandent shrubs and woody climbers (Chartrou et al. 2012), forming an important component of tropical lowland forest ecosystems. The genus *Goniothalamus* (Blume) Hook. f. & Thomson (subfam. Annonoideae Raf., tribe Annoneae Endl.) is one of the largest genera in the family, with more than 130 species (Nakkuntod et al. 2009). The genus is widely distributed in lowland and submontane forests of tropical South-east Asia, with a centre of diversity in western Malesia, particularly Borneo (34 species: Mat-Salleh 2001; Turner and Saunders

2008), Sumatra (14 species: Saunders 2002) and Peninsular Malaysia/Thailand, south of the Isthmus of Kra (22 species: Saunders 2003; Saunders and Chalermglin 2008).

Goniothalamus species are small to large trees, with generally solitary, axillary and pendent inflorescences, and are often cauliflorous or ramiflorous. Individual flowers possess one whorl of three sepals, and two whorls of three petals each, with the outer petals larger than the inner. The three inner petals form a distinctive mitriform dome over the reproductive organs, with three lateral apertures at the base of the dome allowing access to beetle pollinators (Saunders 2010, 2012). The flowers are hermaphroditic, with numerous free stamens and carpels. The stamens have broad connectives that cover the thecae; these connectives vary in length and are taxonomically important. The carpels are variable in ovary indument and the size and shape of the stigmatic head. The fruits are apocarpous, with “monocarps” (derived from individual carpels after fertilisation) that are either sessile or borne on stipes.

Fieldwork in Palawan has revealed a previously unknown *Goniothalamus* species, which is formally described here as *G. palawanensis* C.C.Tang & R.M.K.Saunders. The present research also validates a new nomenclatural combination arising from the transfer to *Goniothalamus* of a Fijian species that was formerly classified in *Polyalthia*.

New species description

Goniothalamus palawanensis C.C.Tang & R.M.K.Saunders, sp. nov.

urn:lsid:ipni.org:names:77134790-1

http://species-id.net/wiki/Goniothalamus_palawanensis

Figs 1, 2

Diagnosis. Similar to *Goniothalamus amuyon* (Blanco) Merr. except with shorter inner petals (11–16 mm), hairy ovaries, and filiform pseudostyles with funnel-shaped stigmas.

Type. Palawan: Puerto Princesa, Corrigutor, 31 May 2012, C.C. Tang TCC10 (holotype: L; isotypes: PNH).

Description. Small trees, to 5 m tall, to 3 cm d.b.h. Young shoots (densely) hairy. Leaf laminae 18–31 cm long, 5.8–11 cm wide, length/width ratio 2.3–3.5, broadly elliptic or oblong elliptic, apex (long) acuminate, base acute, papyraceous to coriaceous, 50–100 µm thick, glabrous both ab- and adaxially; midrib slightly pubescent and very prominent abaxially; secondary veins 8 to 10 pairs per leaf, prominent adaxially; tertiary veins reticulate (sometimes slightly percurrent towards base of leaf), distinct; petioles 8.5–15.5 mm long, 1.5–2.8 mm in diameter, hairy. Flowers axillary, solitary, on young branches, pendent; pedicels 8–13(–16.5) mm long, 0.8–1.2(–1.7) mm in diameter, (sparsely) hairy; bracts 2 to 5. Sepals 3–4(–5) mm long, 3.5–4.5(–6.5) mm wide, length/width ratio 0.6–0.9, generally not reflexed at anthesis, not connate, triangular, 170–250 µm thick, (sparsely) hairy abaxially, glabrous to very sparsely hairy adaxially, green, venation indistinct. Outer petals 20.5–34 mm long, 5.5–13.5 mm wide, length/width ratio 2.4–4.9, broadly to elongated lanceolate, 450–1100 µm

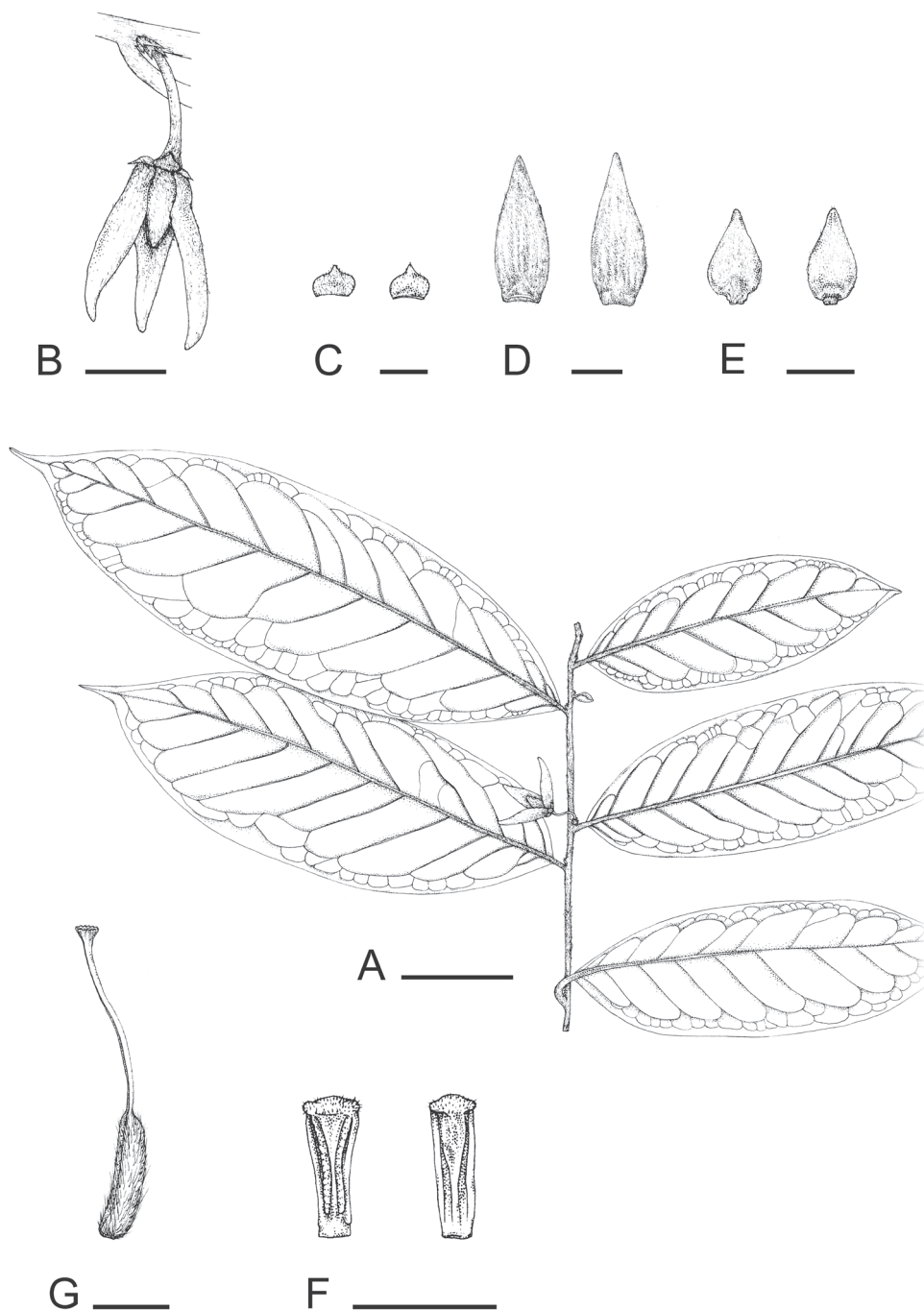


Figure 1. *Goniothalamus palawanensis*, sp. nov. **A** Flowering branch **B** Flower **C** Sepal (ab- and adaxial) **D** Outer petal (ab- and adaxial) **E** Inner petal (ab- and adaxial) **F** Stamen (ab- and adaxial) **G** Carpel. Scale bars: **A** = 5 cm; **B**, **D**, **E** = 1 cm; **C** = 5 mm; **F** = 2 mm, **G** = 1 mm; **A** from *C.C. Tang 10* (HKU); **B–G** from *C.C. Tang 14* (HKU); drawing by Caren Pearl Shin.

thick, (densely) hairy both ab- and adaxially, with glabrous region at base of adaxial surface, greenish yellow, venation indistinct. Inner petals 11–16.5 mm long, 5–9.5 mm wide, length/width ratio 1.6–2.5, with 2.3–3.4 mm wide basal claw, 330–800 μm thick, densely hairy abaxially, sparsely hairy adaxially, greenish yellow; apertures between inner petals 3.5–4.5 mm long, 3.5–5 mm wide. Stamens ca. 100 per flower, 1.9–2.2 mm long, 0.3–0.5 mm wide; connectives rounded, 0.2–0.5 mm long, papillate-hairy. Carpels 10 to 15 per flower; ovary 0.8–1.8 mm long, 0.4–0.7 mm wide, densely hairy with long golden-brown hairs; stigmas and pseudostyles 2.4–4 mm long; pseudostyles 0.1–0.3 mm wide, glabrous; stigma funnel-shaped, glabrous. Fruits unknown.

Phenology. Flowering specimens collected in May and June; fruiting specimens unknown.

Distribution and habitat. Endemic to Palawan (Fig. 3), in mixed dipterocarp and limestone forests; 50–120 m.

Etymology. The specific epithet reflects the geographical distribution of the species in Palawan.

Additional specimens examined (paratypes). Philippines. PALAWAN: Bloomfield, St. Pauls Bay, Mt. Bloomfield, lowlands to the SSE, 4 May 1984, *A. C. Podzorski SMHI2012* (K, L); Iraan Mountains, Aborlan, 29 May 1950, *M. D. Sulit 14792* (L); Puerto Princesa, Corrigutor, 31 May 2012, *C.C. Tang TCC06* (HKU), *C.C. Tang TCC09* (HKU), *C.C. Tang TCC11* (HKU), *C.C. Tang TCC14* (HKU), *C.C. Tang TCC17* (HKU).

Discussion. Phylogenetic analysis of chloroplast DNA sequence data (C.C. Tang et al., unpubl.) indicates that this new species, *G. palawanensis*, is sister to *G. amuyon* (Blanco) Merr. with moderate to strong support (posterior clade probability = 0.97 and bootstrap support = 74%), and more distantly related to *G. costulatus* Miq., *G. rufus* Miq., *G. sawtehii* C.E.C.Fischer, *G. tomentosus* R.M.K.Saunders, *G. undulatus* Ridl. and *G. velutinus* Airy-Shaw. These species are all characterised by a distinct indument of rusty-red hairs on the young shoots and petals. Amongst these species, *G. amuyon* and *G. palawanensis* are distinct in possessing fewer secondary veins per leaf (8 to 11, compared with 11 to 25 in the other species, with the exception of *G. rufus*), and in having indistinct sepal venation (although similar venation is observed in *G. velutinus*). *Goniothalamus palawanensis* is furthermore geographically close to *G. amuyon*, which occurs in Luzon, Visayas and Mindanao (Guzman et al. 1986). Morphological differences between *G. palawanensis* and *G. amuyon* include: inner petal length (11–16.5 mm vs 15–29 mm, respectively: Ying 1991; Liao 1996); ovary indument (hairy in *G. palawanensis* [Fig. 1G] vs glabrous in *G. amuyon*); and pseudostyle/stigma shape (filiform pseudostyle with small, funnel-shaped stigma in *G. palawanensis* [Fig. 1G], vs relatively enlarged, fleshy pseudostyle with entire stigma in *G. amuyon*).

The flora of Palawan shows close biogeographical affinities with Borneo, reflecting the extensive connectivity that existed between the two regions (Hall 2009). Two of the species listed above as close relatives of *G. palawanensis* occur in Borneo, viz. *G.*

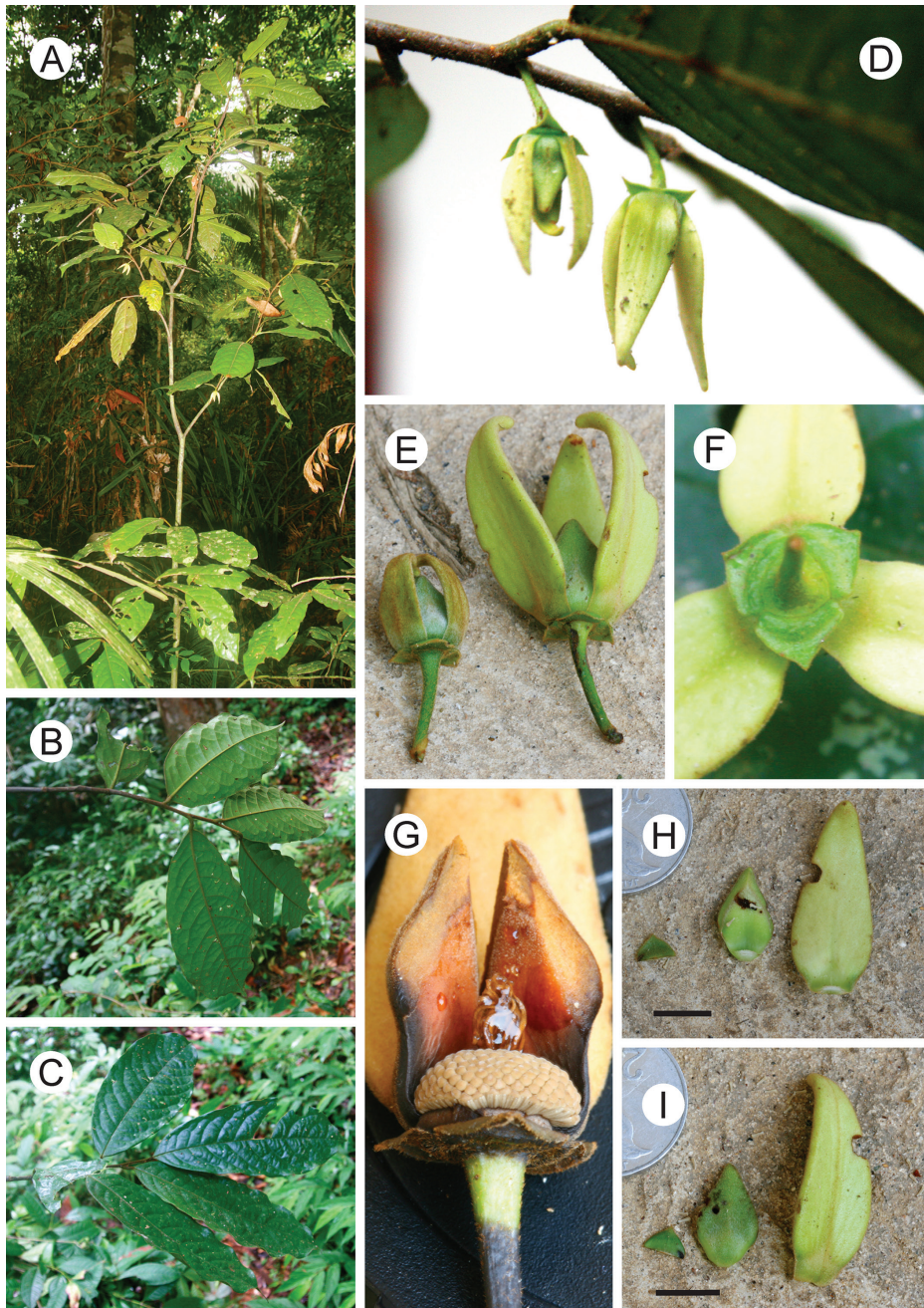


Figure 2. *Goniothalamus palawanensis*, sp. nov. **A** Habit (mature individual with flowers) **B** Branch with leaves (abaxial) **C** Branch with leaves (adaxial) **D, E** Flower **F** Sepals (abaxial) **G** Very mature flower with two outer petals and one inner petal removed, showing stamens and stigmas **H** Perianth parts (abaxial; left to right: sepal, inner petal, outer petal) **I** Perianth parts (adaxial; left to right: sepal, inner petal, outer petal). Scale bars: **H, I** = 1 cm; **A, D** from *C. C. Tang 09* (HKU); **B, C, F, G** from *C. C. Tang 06* (HKU); **E, H, I** from *C. C. Tang 14* (HKU). Photos by C.C. Tang.

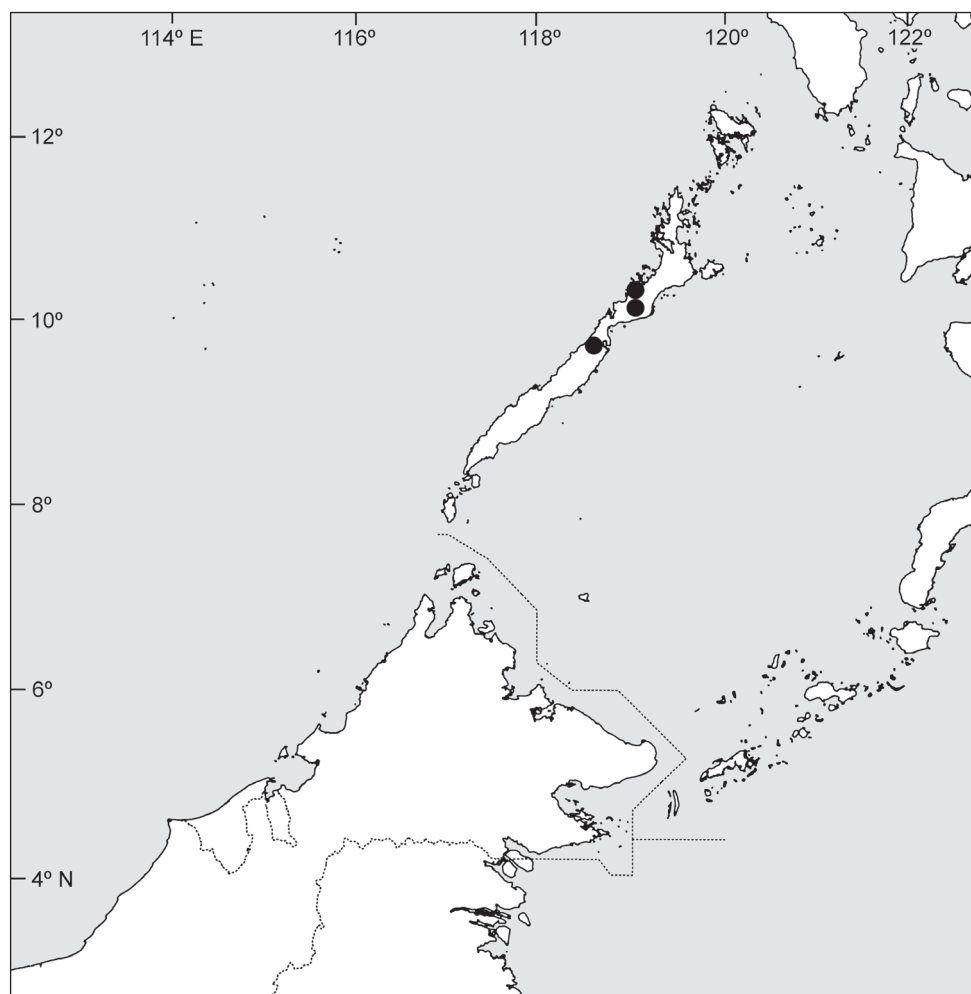


Figure 3. Distribution of *Goniothalamus palawanensis*, sp. nov., in Palawan.

rufus and *G. velutinus*. In addition to the differences in leaf and sepal venation alluded to above, these species differ from *G. palawanensis* in possessing greatly enlarged and warty pseudostyles/stigmas (Mat-Salleh 1993).

There is only one *Goniothalamus* species, *G. obtusifolius* Merr., that is sympatric with *G. palawanensis* in Palawan. These two species are clearly distinct, however, as *G. obtusifolius* has much smaller (15–18 × 6–8 cm) coriaceous leaves, and large (ca. 5 × 3.5 cm) membranous outer petals (Merrill 1906).

IUCN conservation status. EN B1ab(iii) (IUCN, 2001). *Goniothalamus palawanensis* is endemic to Palawan, with an extent of occurrence of ca. 1,800 km². The species is only known from three periods of collection (1950, 1984 and 2012), and from fewer than five localities. The region is subject to continuing habitat decline due to logging of low altitude forests (DENR/UNEP 1997), hence the endangered red list category recommendation.

New nomenclatural combination

***Goniothalamus angustifolius* (A.C.Sm.) B. Xue & R.M.K.Saunders, comb. nov.**

urn:lsid:ipni.org:names:77134791-1

http://species-id.net/wiki/Goniothalamus_angustifolius

Basionym. *Polyalthia angustifolia* A.C.Sm., Bull. Torrey Bot. Club 70: 538. 1943. Type: FIJI: Viti Levu, *J.W. Gillespie 2198* (holotype: A!; isotypes: BISH, GH!).

Discussion. The historical delimitation of the genus *Polyalthia* has been shown to be highly polyphyletic, and large-scale taxonomic realignment and recognition of new genera has been undertaken to ensure strict monophyly of genera (Mols et al. 2008; Saunders et al. 2011; Xue et al. 2011, 2012, in press; Chaowasku et al. 2012). As part of this series of taxonomic revisions, chloroplast DNA regions were sequenced from eight species from the Melanesian island of Fiji (Xue, 2013) that had previously been assigned to *Polyalthia*. Phylogenetic analysis of this data revealed that most of these species align with either *Hubera* (Chaowasku et al. 2012; Xue 2013) or *Meiogyne* (Xue 2013; Xue et al. in press), although one species, *Polyalthia angustifolia* A.C.Sm., which was sequenced from the type material, is nested within the *Goniothalamus* clade (Xue 2013). *Polyalthia angustifolia* was originally described from fruiting material (Smith 1943), and it is likely that its incorrect generic affiliation was due to the absence of flowers, which are very different in *Polyalthia* and *Goniothalamus*. Subsequent phylogenetic analyses with a larger taxon sampling (C.C. Tang et al., unpubl.) have revealed *P. angustifolia* as sister to the Fijian species *Goniothalamus monospermus* (Baill.) R.M.K.Saunders with strong support (posterior clade probability = 1; bootstrap support = 96%); these two species are morphologically distinct, as *P. angustifolia* seeds lack the broad lateral testa wings that are diagnostic of *G. monospermus* (Van Setten and Koek-Noorman 1992: pl. 39i). The transfer of the name *P. angustifolia* to *Goniothalamus* is accordingly validated here.

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A new species of *Espeletiopsis* (Milleriaceae, Asteraceae) from Colombia

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Abstract

A new species of *Espeletiopsis* was found in two small páramos of Norte de Santander, Colombia. The species is named *Espeletiopsis diazii* honoring the contributions of Santiago Díaz-Piedrahita in recognition of his vast knowledge of the Compositae in Colombia. This is a very distinctive species, markedly different from most of the *Espeletiopsis* present in Colombia. The new species is closely related to *Espeletiopsis caldasii* and *E. santanderensis*, but differs in having (1–)4–6(–7) capitula, with very short peduncles, and capitula arranged in a compact or densely glomerate cyme. With a total distribution area of less than 75 km², this species is probably critically endangered or imperiled.

Keywords

Cáchira, Colombia, Compositae, Espeletiinae, *Espeletiopsis*, frailejón, Milleriaceae, Norte de Santander, páramos

Introduction

At the high elevations of the tropical Andes, typically above 3600 m, trees and shrubs disappear gradually, opening the space for the páramo. With an estimated age of 2–4 million years (Van der Hammen et al. 1986), the páramo ecosystem is relatively young and yet is widely regarded as the world's most diverse high-elevation ecosystem (Lu-

teyn 1999; Rangel-Ch. 2000; Sklenář et al. 2005), and probably the fastest evolving biodiversity hotspot (Madriñán et al. 2013). One of the unique characteristics of the páramo is the presence of frailejones, the name being generally used to refer to all the species within the subtribe Espeletiinae Cuatrec. (Asteraceae: Millerieae).

The subtribe Espeletiinae Cuatrec. (Millerieae, Asteraceae) includes eight genera and at least 141 species (Cuatrecasas 2013; Diazgranados 2012a). In the monograph of Espeletiinae, Cuatrecasas (2013) treated seven of these genera in detail, but *Espeletiopsis* remained untreated. This genus is diagnosed by axillary, monochasial, corymbiform-paniculate capitulescences, with branches, leaves and bracts spirally alternate, and involucre with gradual transition from sterile outer phyllaries to fertile inner phyllaries (Cuatrecasas 1976). Currently the genus contains 22 species, two varieties, three forms and three described hybrids (Diazgranados 2012a).

The genus *Espeletiopsis* is distributed from the central Andes of Venezuela to the Cordillera Oriental (Eastern Cordillera) in Colombia, approximately from 70.8°W and 8.9°N to 74.3°W and 4.1°N). Only five species are found in Venezuela (four of them endemic to the country), whereas Colombia has 18 species. According to Cuatrecasas (2013), *Espeletiopsis* represents a derived line of evolution within Espeletiinae, being mainly adapted to lower elevations. Twenty species are found at elevations of 3200–3400 m in the subpáramo belt, two species grow as low as 2200 m, and one reaches 4500 m.

Most of the species are restricted to one continuous páramo and have relatively narrow distributions (<1000 km²). Seven species have distributions of 2500–4750 km², six species are distributed in areas of less than 20 km², and six species are known from less than seven collections, including two with only the type collection (Diazgranados 2012a; b). In the last ten years four new species of *Espeletiopsis* have been described from Colombia (Díaz-Piedrahita and Obando 2004; Díaz-Piedrahita and Rodríguez-Cabeza 2008; 2010; Díaz-Piedrahita et al. 2006), and it is not surprising that more new species will be discovered in uncollected páramos.

Species of *Espeletiopsis* have not been studied thoroughly. In addition to general morphology and reports in inventories and floras, six species have studies on anatomy (Carlquist 1958; Ortega 1982; Rock 1972; Torres de Ricardi 1979), six on chemistry (Bohlmann et al. 1980; Ramírez et al. 1998; Ramírez et al. 2000; Usubillaga et al. 2003; Meccia et al. 2010), two on physiology (Bayona et al. 2005; Coba de Gutiérrez 2005; Rache and Pacheco 2009), one on demography (Chaves and Bonilla 2007), one in ethnobotany (Báez et al. 1999), three in animal-plant interactions (Berry and Calvo 1989; Sturm 1989; 1990a, b), one in mycorrhizae (García Romero et al. 2004) and 12 have chromosome counts (Cuatrecasas 2013; Rondón et al. 2013). The most studied species are *E. corymbosa* (Humb. & Bonpl.) Cuatrec., *E. muiska* (Cuatrec.) Cuatrec., *E. angustifolia* (Cuatrec.) Cuatrec. and *E. pannosa* (Standl.) Cuatrec., all relatively close to major cities in Colombia and Venezuela. Several species in more pristine páramos remain largely unstudied. Unfortunately, páramos are shrinking rapidly as a consequence of climate change, and several species are predicted to become extinct in the following decades (Diazgranados 2012b).

Methods

The Páramo de Cáchira (also called Páramo de Guerrero; see Fig. 4) and the adjacent Páramo de los Ranchos are located in a region of Norte de Santander (Colombia) of very difficult access. North from the Páramo de Arboledas, these are probably the last páramos of the Eastern Cordillera before the Ocaña depression. For decades the area was unsafe, and the only road that reaches these páramos was almost impassable. Still now, the area is floristically poorly known. Material of the new species was collected during an expedition in 2009, and duplicates distributed to COL, ANDES and HECASA. Additional duplicates will be distributed to other herbaria, including US and MO. Micrographs were taken by the first author at the Scanning Electron Microscopy Laboratory of the National Museum of Natural History, in Washington DC. Lauren Merchant from Saint Louis University provided the illustrations, which were funded by the Missouri Botanical Garden.

Taxonomy

***Espeletiopsis diazii* M. Diazgranados & L.R. Sánchez, sp. nov.**

urn:lsid:ipni.org:names:77134808-1

http://species-id.net/wiki/Espeletiopsis_diazii

Figures 1–4

Type. COLOMBIA, Norte de Santander, Municipio de Cáchira, Páramo de Cáchira o de Guerrero, vía Alto Chiquito (desde Villa Caro) a Cáchira, alto del páramo, a los lados de la vía antes de comenzar el descenso a Cáchira, en comunidad de pajonal-frailejónal dominado por esta especie. Alt. 3394 m, 73.00173°W, 7.7655°N. *M. Diazgranados & L.R. Sánchez* 3898 (holotype: COL; isotypes: COL, HECASA and to be distributed). Paratypes: same locality, *M. Diazgranados & L.R. Sánchez* 3897 (COL, HECASA and to be distributed); *L.R. Sánchez* 10113 (HECASA!), 12714 (HECASA!).

Diagnosis. Sessile rosette of whitish appearance, related to *Espeletiopsis santanderensis*, but with smaller leaves, capitulescence compact with a dense glomerate cyme of (1–)4–6(–7) capitula and short peduncles, and disc flowers with corolla lobes glabrescent.

Description. Acaulescent (sessile) polycarpic rosette of whitish appearance, 40–50(–100) cm tall (including capitulescences), growing in grassland of páramo proper. Excluding reproductive parts, rosette 20–30(–50) cm tall.

Leaves firm, coriaceous, erect; laminae linear or narrowly oblanceolate, apex acute, base without pseudopetiole, (15–)16–19(–21) cm × (0.6–)0.65–0.7(–0.8) cm, length to width ratio 26:1; margins strongly revolute. Adaxial face with indumentum whitish or silvery-sericeous, hairs 1 mm long, very abundant in young leaves, becoming less dense and almost tomentose-velutinous in old leaves, giving them a greener appearance; costa prominent but secondary nerves invisible. Abaxial face with loose indumentum, silvery or whitish, with hairs up to 2 mm long; costa more prominent than from adaxial face,



Figure 1. *Espeletiopsis diazii*: **A** acaulescent (sessile) habit **B** whitish rosette from top **C** lateral view of capitulescence showing a dense glomerate cyme of capitula **D** capitulum of the holotype collection (M. Diazgranados & L.R. Sánchez 3898) **E** paratype collection (M. Diazgranados & L.R. Sánchez 3897) **F** holotype collection (M. Diazgranados & L.R. Sánchez 3898) **G** capitulescence showing the alternate bracts along the scape.

secondary nerves invisible. Leaf sheaths narrowly-oblong, (2.5–)2.7–3.1(–3.3) cm × (0.5–)0.7–0.9(–1.1) cm; white adaxially, glabrescent in the proximal portion, with 10–15 anastomosing nerves; white abaxially, tomentose-velutinous, with hairs up to 0.9 mm long.

Capitulescences 2–5, corymbiform, more or less coetaneous, axillary, emerging from the upper nodes, twice longer than the leaves, (15–)25–45(–60) cm long; indumentum abundant, lanose-sericeous white towards the base, becoming lanose whitish-yellowish towards the distal portion. Scapes erect, firm, 5–6 mm in diameter; 5–10-bracteate basally, subcoriaceous, alternate, linear with acute apex and without pseudopetiole, up to 13 cm long × 0.5 cm wide; 2–5 sterile bracts in the first 2/3 of the scape, alternate, linear, shorter, 5–6 cm long × 0.5 cm wide. Capitula (1–)4–6(–7), arranged in a compact or dense glomerate cyme in the distal 3–4 cm of the capitulescence; peduncles terete, short, 1(–3) cm long or less; with indumentum lanose

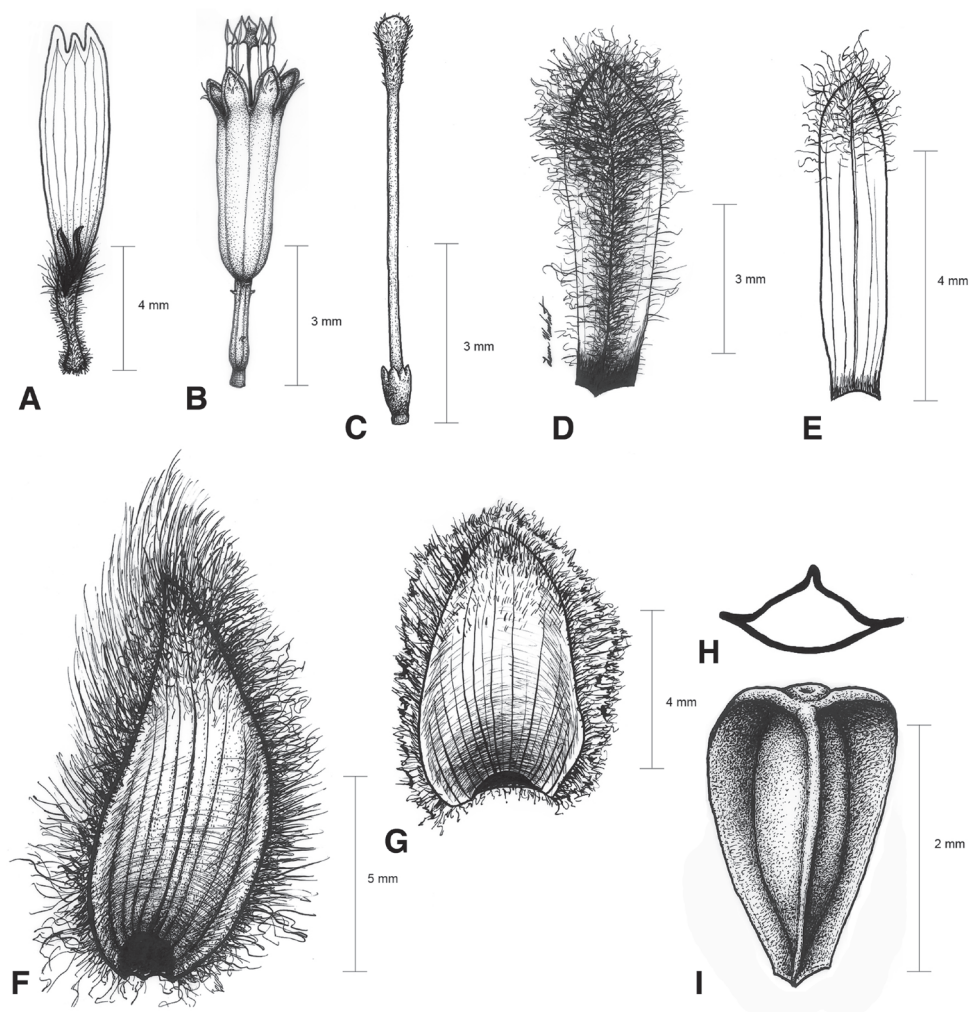


Figure 2. Illustrations of *Espeletiopsis diazii*. **A** Ray corolla **B** disk flower **C** disk flower style **D** ray flower palea **E** disk flower palea **F** outer phyllary **G** inner (sterile) phyllary **H** transversal view of cypsela **I** dorsal view of cypsela.

whitish-yellowish, and portions of epidermis reddish. Fertile bracts linear or narrowly triangular, 2–2.5 cm long \times 0.4–0.5 cm wide.

Capitula radiate, subglobose, 2.0–3.0 cm in diameter (including ray flowers). Involucre 1.2–1.4 cm wide \times 0.8–1.2 cm high; phyllaries in 2–3 series, oblanceolate or triangular, the outer phyllaries 10–12 mm long \times 3.0–5.0 mm wide (excluding hairs), the inner phyllaries 6.5–7.2 mm long \times 4.0–4.3 mm wide, with indumentum villous white and epidermis green, turning red when older.

Ray flowers (30–)44–46 in 2(–3) series, yellow, 10.5–11.5 mm long (excluding ovary). Ligules 7.6–8.0 mm long, elliptical or oblong, tridentate; tube hirsute, small, 0.35–0.5 mm in diameter and 2.5–3.0 mm long, without linguiform appendages, yel-

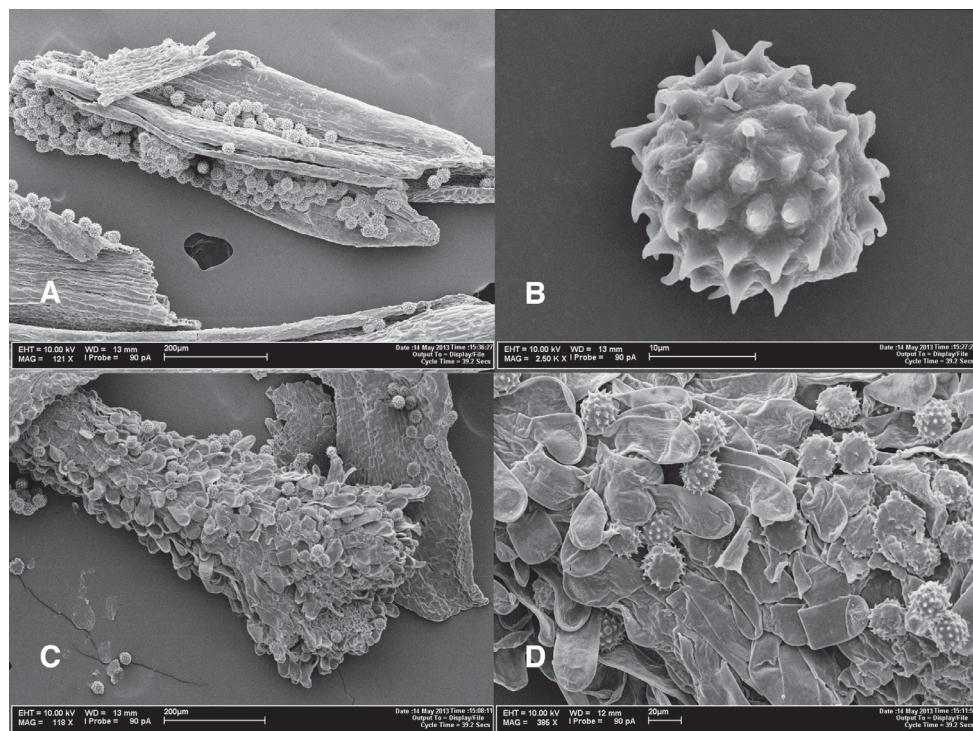


Figure 3. Photomicrographs of *Espeletiopsis diazii*. **A** Fragment of anther with pollen grains **B** pollen grain **C** disc flower style with pollen grains **D** papillae of outer side of stigmatic branches, showing pollen grains.

low becoming brown distally, the hairs 0.2–0.3(–0.7) mm long. Style 6.5–7.0 mm long \times 0.16–0.2 mm in diameter, with stigmatic branches 1.0–1.5 mm long, broadening in the distal portion, 0.25–0.28(–0.5) mm wide, papillose, papillae to 0.1 mm long.

Discs 1.0–1.5 cm in diameter; disc flowers (72–)100–108; corolla 6.2–7 mm long (excluding anthers and fruit); corolla throat 4.4–4.6 mm long, 2–2.2 mm wide when open, 5-lobed, lobes 1–1.1 mm long, glabrescent or with a few hairs; tube 1.8–2.4 mm long \times 0.3–0.5 mm in diameter, glabrous, with a few hairs; anthers dark yellow, sometimes exceeding the corolla by 2 mm, slightly translucent, approximately 1 mm long and 0.3 mm wide; disc paleae 5.2–5.5 mm long \times 1.0–1.1 mm wide, brownish, with 3 main nerves, glabrescent but becoming villous in the distal third.

Cypselsae oblong, triangular, 2.3–2.4 mm \times 1.5–1.6 mm, glabrous, black. Paleae 6.4–6.8 mm long, 1.8–2.0 mm wide, brownish, profusely villous. Pollen yellow when fresh, tricolporate, 20.56–21.08 μ m in equatorial diameter (not counting spines); spines 68–80 total, 14–16 equatorial spines, (2.8–)3.6–4.06 μ m long, erect.

Distribution. Endemic to Colombia. This species has been found only in the Páramo de Cáchira (or Páramo de Guerrero), and in a smaller adjacent páramo, called Páramo de los Ranchos, at elevations of 3300–3500 m (Fig. 4). The area of distribution is less than 75 km².

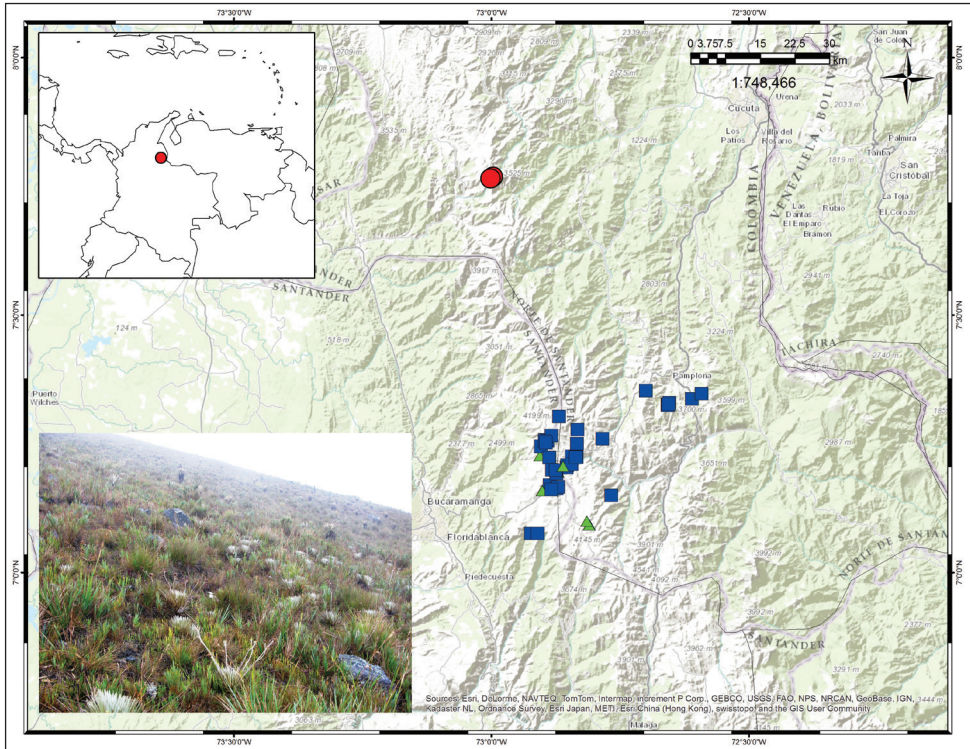


Figure 4. Distribution map showing collections for *Espeletiopsis diazii* (red circles), *E. santanderensis* (blue squares) and *E. caldasii* (green triangles). Photograph of the Páramo de Cáchira, with a population of *E. diazii*.

Ecology. A large population of several hundreds or thousands of individuals growing in the grasslands of the páramo proper was observed (Fig. 4). Other Espeletiinae found in the area are: *Espeletia brassicoidea* Cuatrec., *E. conglomerata* Cuatrec. and *Libanothamnus occultus* ssp. *oroquensis* Cuatrec.

Etymology. The specific epithet of this new species, “diazii”, is dedicated to Santiago Díaz-Piedrahita, Colombian botanist, for his vast contributions to the knowledge of the Compositae of his country.

Conservation status. The preservation of this species is linked to the preservation of the Páramo de Cáchira and the Páramo de Los Ranchos. These are both very small páramos (70–80 km² of total area), likely sensitive to climate and land use change, with substantial fragmentation, and without any legal measures of protection. Therefore, *E. diazii* is probably *Critically Endangered* (CR, according to the IUCN criteria: extent of occurrence estimated to be less than 100 km², habitat fragmentation, and likely decline of the extent of the páramo; http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf), or *Critically Imperiled* (G1, according to NatureServe; <http://www.natureserve.org/explorer/ranking.htm>).



Figure 5. *Espeletiopsis santanderensis*: **A** acaulescent (sessile) habit **B** lateral view of a section of the capitulescence, showing the long peduncles of the capitula **C** rosette from the top **D** capitulescence spreading and rosette (M. Diazgranados 3841).

Discussion

Espeletiopsis diazii is a very distinctive species. The laminae lack pseudopetioles and the sheaths are oblong, rectangular, not broadening toward the base, the features being rare in *Espeletiopsis* but characteristic of *Espeletia* sect. *Weddellia* Cuatrec. (8 species) of the páramos of Apartaderos, Piñango and Timotes in Mérida, Trujillo and Lara, Venezuela. However, monochasial capitulescences with several alternate bracts along the scape place this species within *Espeletiopsis*.

The new species is probably related to a group of 10 species of *Espeletiopsis* with sessile caulirosula habit (sensu Cuatrecasas 2013) from the páramos. Two of these (*E. angustifolia* (Cuatrec.) Cuatrec. and *E. pannosa* (Standl.) Cuatrec.) also have an indumentum that is silvery-sericeous, but differ from the rest in having white-purple ligulae. The remaining eight species, all from Colombia, have yellow ligulae: *E. betancurii* Rodr.-Cabeza, S. Díaz & Gal.-Tar., *E. caldasii* (Cuatrec.) Cuatrec., *E. colombiana* (Cuatrec.) Cuatrec., *E. funckii* (Sch. Bip. ex Wedd.) Cuatrec., *E. muisca* (Cuatrec.) Cuatrec., *E. petiolata* (Cuatrec.) Cuatrec., *E. pozoensis* (Cuatrec.) Cuatrec., and *E. santanderensis* (A. C. Sm.) Cuatrec. However, only two of them (i.e., *E. santanderensis* and

E. caldasii) have a reduced silvery-sericeous indumentum and reduced oblong sheaths. *Espeletiopsis caldasii* has capitulescences monocephalous, and *E. santanderensis* has capitulescences spreading (Fig. 5). Both species grow in the páramos of Santander-Norte de Santander, but relatively distantly from the population of *E. diazii* (Fig. 4).

Key to *Espeletiopsis diazii*, *E. caldasii* and *E. santanderensis*

A key for the genus was initially published by Cuatrecasas (1996) and updated later by Díaz-Piedrahita and Rodríguez-Cabeza (2010). This key is an extension of the updated version of Cuatrecasas' key.

- 4 Leaf lamina up to 25 cm long \times 0.3–1.5 cm wide, with indumentum dense, appressed, silvery-sericeous.
- 5 Leaf lamina 4–6 cm long \times 0.3–0.9 cm wide. Capitulescence monocephalous.....***Espeletiopsis caldasii***
- 5' Leaf lamina 15–25 cm long \times 0.6–1.5 cm wide. Capitulescence polycephalous.
- 6 Capitulescence spreading, of 15–20 cm in diameter, with 20–40 capitula, peduncles 3–7 cm long. Disc flowers with corolla lobes \pm pilose. Leaf lamina 15–25 cm long \times 0.8–1.5 cm wide***Espeletiopsis santanderensis***
- 6' Capitulescence compact, with a dense glomerate cyme of (1–)4–6(–7) capitula, peduncles up to 1(–3) cm long. Disc flowers with corolla lobes glabrescent or with a few hairs. Leaf lamina (15–)16–19(–21) cm long \times (0.6–)0.65–0.7 (–0.8) cm wide.....***Espeletiopsis diazii***

Acknowledgements

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Toward a monophyletic *Cheilanthes*: The resurrection and recircumscription of *Myriopteris* (Pteridaceae)

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Abstract

The fern genus *Cheilanthes* (Pteridaceae) has perplexed taxonomists for more than two centuries. Complex patterns of evolution involving rampant morphological convergence, polyploidy, hybridization, and apomixis have made the taxonomy of this group especially difficult. Fortunately, recent phylogenetic analyses have helped to clarify relationships among cheilanthoid taxa. Based on these findings, we here formalize an updated taxonomy for one monophyletic clade comprising 47 primarily North and Central American taxa usually included in *Cheilanthes*. Because the type species of *Cheilanthes* (*C. micropteris*) is only distantly related to this clade, we resurrect the genus *Myriopteris* to accommodate these taxa, and present a revised circumscription for the group, including 36 new combinations.

Keywords

Cheilanthes, cheilanthoid, myriopterid, myriopteroid, nomenclature, taxonomy

Introduction

A “practical and natural” generic classification of cheilanthoid ferns (Pteridaceae) has eluded taxonomists for more than 200 years and was viewed by Tryon and Tryon (1982) as one of the most contentious issues in fern systematics. Central to the problem is the circumscription of the large genus *Cheilanthes*, which all molecular studies with sufficient sampling indicate is polyphyletic (see Gastony and Rollo 1998; Kirkpatrick 2007; Prado et al. 2007; Schuettelpelz et al. 2007; Zhang et al. 2007; Rothfels et al. 2008; Eiserhardt et al. 2011). Since the initial description of *Cheilanthes* (Swartz

1806) encompassing 16 species, various authors have moved hundreds of taxa into (e.g., Domin 1913; Mickel 1979) and out of (e.g., Fée 1852; Smith 1875; Ching 1941) the genus. Of the ca. 500 validly published species names in *Cheilanthes*, some 60% have, at some point, resided in other genera. The lack of definitive taxonomic characters in this group often is attributed to widespread convergent evolution in the drought-prone habitats occupied by these ferns (Tryon and Tryon 1973, 1982), and the problem is likely insoluble based on morphology alone. However, the same genetic evidence that highlights shortfalls in the current classification provides a key to solving this puzzle. As DNA sequence data proliferate and morphological features are reexamined in light of molecular phylogenies, it eventually becomes possible to recognize monophyletic assemblages of species that can be circumscribed as genera. We now have reached this point with certain groups of cheilanthoid ferns, at least in terms of removing taxa and clades that cannot reasonably be included within *Cheilanthes* (Link-Pérez et al. 2011; Li et al. 2012).

Here, we focus on the primarily New World lineage previously referred to as the “American *Cheilanthes*” (Kirkpatrick 2007), myriopteroid (Rothfels et al. 2008), or myriopterid (Windham et al. 2009; Eiserhardt et al. 2011) ferns. Limited sampling in each of those analyses indicated that these ferns might represent a well-supported, monophyletic group, an assumption fully supported by the more complete (85%) taxon sampling of Grusz et al. (in review). In addition to suggesting the monophyly of the myriopterid lineage, the analyses of Rothfels et al. (2008) and Eiserhardt et al. (2011) conclusively demonstrated that this clade was quite distantly related to the type species of *Cheilanthes*, *C. micropteris* (results summarized in Fig. 1). This improved understanding of phylogenetic relationships among cheilanthoid ferns necessitates a taxonomic revision that can be achieved by one of two options: 1) all taxa derived from the most recent common ancestor of *C. micropteris* and the myriopterid ferns could be assigned to a single genus (which would not be called *Cheilanthes* because of the priority of *Hemionitis*), or 2) myriopterid ferns could be transferred to a different genus, reflecting their phylogenetic distinction from *Cheilanthes* s.s. The first option would require 400+ new combinations in *Hemionitis* (or the conservation of *Cheilanthes* against it followed by more than 100 new combinations in that genus). It would also subsume a number of cohesive, well-characterized genera that are clearly distinct based on morphological, molecular, and cytological grounds, including *Adiantopsis* (Link-Pérez et al. 2011), *Argyrochosma* (Windham 1987; Sigel et al. 2011), *Astrolepis* (Beck et al. 2010), *Doryopteris* (Yesilyurt 2004), *Gaga* (Li et al. 2012), and *Notholaena* (Rothfels et al. 2008). This approach would maximize the number of nomenclatural changes while simultaneously obscuring well-documented phylogenetic relationships, resulting in the inclusion of all but six cheilanthoid species in one genus. Because we consider this option untenable, we have, instead, chosen to remove the myriopterid ferns from *Cheilanthes*.

When any species or clade is removed from *Cheilanthes*, the first issue that must be addressed involves their relationship to *Allosorus pusillus* (Willd. ex Bernh.) Bernh. [= *Cheilanthes pteridioides* (Reich.) C. Chr.]. This species was designated the lectotype

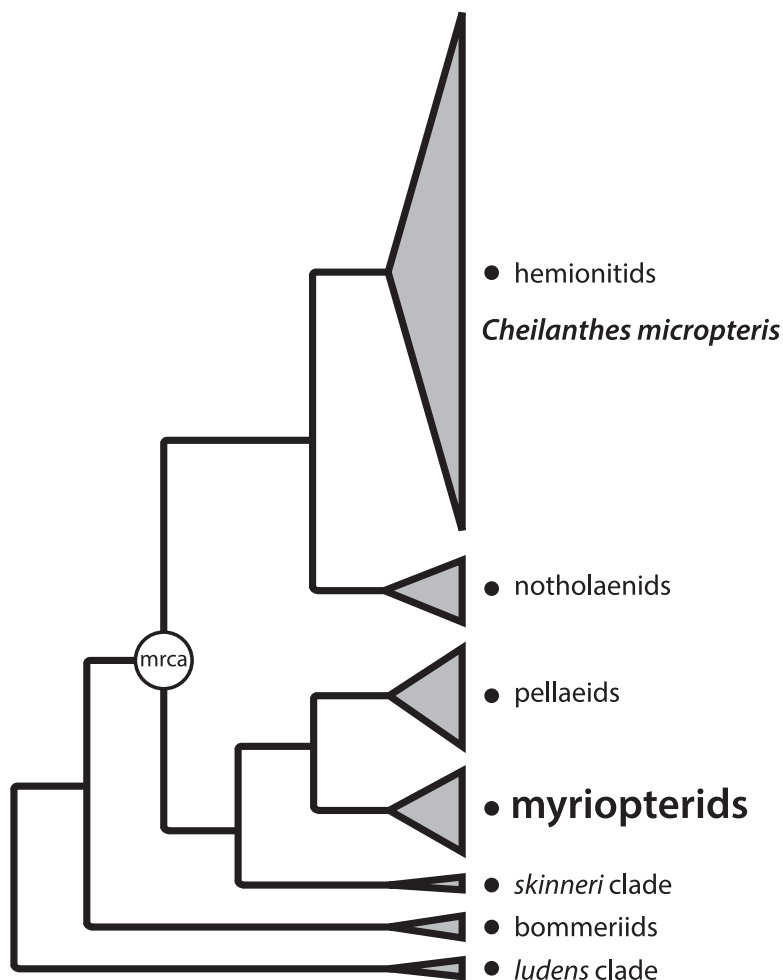


Figure 1. Summary phylogeny for cheilanthoid ferns, indicating the placement of *Cheilanthes micropteris* (the type species for *Cheilanthes*) within the hemionitid clade—only distantly related to the myriopterid clade. The six major clades of cheilanthoid ferns are shown with tips roughly proportional to clade size. The most recent common ancestor (mrca) of *C. micropteris* and the myriopterid clade is indicated. Modified with permission from Windham et al. (2009).

of *Allosorus* Bernh. by Pichi-Sermolli (1953), a choice subsequently validated by the ICBN when *Cheilanthes* was conserved over *Allosorus* (Appendix II of the Montreal Code, Stafleu et al. 1961). The only phylogenetic study published to date that includes the type species of both *Allosorus* and *Cheilanthes* is that of Eiserhardt et al. (2011). In that analysis, it is unclear whether the divergence between *C. maderensis* (= *C. pteridioides*; see Nardi and Reichstein 1985; Rothfels et al. 2012) and *C. micropteris* is sufficient to justify the recognition of two genera. The two taxa appear in distinct, well-supported clades (clade A vs. clade C in fig. 2B of Eiserhardt et al. 2011), but

deeper relationships are poorly resolved and both clearly belong to the rapidly diversifying hemionitid lineage (clade H). The unequivocal assignment of *Allosorus* to the hemionitids by Eiserhardt et al. (2011) does, however, prevent the application of this generic name to the myriopterid clade. Any attempt to expand *Allosorus* to include myriopterids would encompass both *Cheilanthes* (conserved over *Allosorus*) and *Hemionitis* (which has priority over both).

One potentially viable option for generic placement of the myriopterid clade would be to include it within a revised circumscription of *Pellaea* Link. All recent phylogenetic studies with adequate sampling of the two groups (e.g., Kirkpatrick 2007; Rothfels et al. 2008; Eiserhardt et al. 2011) strongly support the position of myriopterids as the sister group of the pellaeid clade, which includes *Pellaea atropurpurea*, the lectotype of the oldest generic name applicable to that clade. We are not in favor of expanding the definition of *Pellaea* to encompass the myriopterids for a variety of reasons. First, the two are quite distinct, both in terms of phylogenetic divergence and morphology. The myriopterids have substantially smaller ultimate segments, pubescent and/or scaly (vs. mostly glabrous) leaf blades, and sporangia that are confined to vein tips (vs. distributed along the veins near the segment margins). Because of these differences, the two groups generally have not been considered closely related, and most myriopterids would require new combinations in *Pellaea*. Adding to this nomenclatural upheaval is the fact that other well-defined genera, including *Argyrochosma* (Sigel et al. 2011) and *Astrolepis* (Beck et al. 2010), would be subsumed within such a circumscription of *Pellaea*, which would require additional new combinations and serve only to further undermine the distinctions among the major genera of cheilanthoid ferns.

If the expansion of *Pellaea* is ruled out, there remain three other generic names typified by species belonging to the myriopterid clade: 1) *Myriopteris*, described by Fée (1852) and typified by *M. marsupianthes* Fée; 2) *Cheilosoria*, named by Trevisan (1877) and lectotypified by Copeland (1947) based on *C. allosuroides* (Mett.) Trev.; and 3) *Pomataphytum*, published by Jones (1930) and typified by *P. pocillatum* M. E. Jones (= *M. lendigera*). Phylogenetic reconstructions (Grusz et al. in review) confirm that the type species of *Myriopteris* and *Pomataphytum* fall within a single, well-supported clade. In fact, the diploid species *M. marsupianthes* is thought to be one of the parents of sexual tetraploid *M. lendigera* (see Mickel and Smith 2004). Thus, the generic name *Pomataphytum* is appropriately considered a taxonomic synonym of the earlier described *Myriopteris* and can be eliminated as a potential name for the myriopterid clade. Copeland's (1947) lectotype of *Cheilosoria* belongs to the well-supported and morphologically distinctive alabamensis clade that diverges earlier in the myriopterid phylogeny (Grusz et al. in review), and the name *Cheilosoria* could be used for this particular group if the myriopterids were subdivided into two or more genera. However, *Myriopteris* predates *Cheilosoria* by 25 years and, when these species are assigned to a single genus (our preferred approach), *Myriopteris* is the correct generic name for the inclusive myriopterid clade.

Historical use of the name *Myriopteris*

The original concept of *Myriopteris* (Fée 1852) included 11 species, these split between two sections (*Eumyriopteris* and *Cheilanthesastrum*) distinguished by the presence or absence of a well-developed, inframarginal false indusium. The Latin and French descriptions of the genus are only partly overlapping; shared elements include the highly divided fronds, the small, orbicular ultimate segments with recurved margins (“formant un bourrelet très-contracté”), and a tendency to be covered by hairs and/or scales. *Myriopteris* was accepted and significantly expanded by J. Smith (1875: 280) who stated “the genus consists of about 20 species, distinguished from *Notholaena* and *Cheilanthes* by their small, concave, lenticular segments.” The segregation of *Myriopteris* from *Cheilanthes* was, however, rejected by most subsequent authors (e.g., Christensen 1906; Copeland 1947; Lellinger 1965; Tryon and Tryon 1982; Kramer et al. 1990), with two notable exceptions. Pichi-Sermolli (1977) advocated a narrowed circumscription of the genus, including only the two species with prominent false indusia, viz., *M. marsupianthes* and *M. lendigera*. As shown by Grusz et al. (in review), this definition of *Myriopteris* is phylogenetically indefensible because it excludes *M. mexicana*, the apparent maternal progenitor of allotetraploid *M. lendigera*. About the same time Pichi-Sermolli was narrowing the definition of *Myriopteris*, Löve and Löve (1977) expanded it slightly by proposing a new combination for the species known as *Cheilanthes covillei* Maxon. This was done without explanation, though almost certainly reflects the fact that this species has the small, bead-like ultimate segments emphasized in earlier circumscriptions of the genus.

Although this “microphyllous” leaf morphology is common within *Myriopteris*, it does not characterize the entire clade (Grusz et al. in review) and has evolved independently in other cheilanthoid lineages. Thus, the possession of small, bead-like ultimate segments does not constitute a synapomorphy for the genus as defined herein. In fact, our list of excluded names (see Taxonomic Treatment) includes seven taxa with bead-like segments previously ascribed to *Myriopteris* but more closely related to *Cheilanthes* s.s. (Windham et al. unpublished). Because all morphological characters used by previous authors to define *Myriopteris* are subject to strong, positive selection in xeric-adapted cheilanthoid lineages (Hevly 1963), it is not surprising that none of them uniquely define the genus. The totality of evidence, however, indicates that the myriopterids represent a deeply divergent clade that cannot reasonably be combined with any other in a single genus. Therefore, we propose to resurrect *Myriopteris* and recircumscribe it to encompass the entirety of this well supported cheilanthoid lineage.

Distinguishing *Myriopteris* Fée emend. Grusz & Windham from *Cheilanthes* s.s.

Ideally, morphological and/or cytological synapomorphies would substantiate phylogenetic relationships inferred from DNA sequence data. However, easily observed synapomorphies distinguishing the various clades of cheilanthoid ferns are few, and

homoplastic characters abound. To paraphrase Sir William Hooker (1852: 75), “Vain is the attempt to form a definite character which shall decide the limits of [*Cheilanthes*],” a statement that applies equally well to *Myriopteris*. Highly divided (decompound) leaf blades with small ultimate segments are scattered across the cheilanthoid tree and, indeed, are characteristic of ferns in general, and an indument of hairs and/or scales is one common strategy among plants used to reduce water loss in xeric habitats (Hevly 1963). Other characters useful for species-level identification within myriopterids, such as vernation, are, without exception, shared with other distantly related cheilanthoid ferns.

Molecular analyses spanning the diversity of cheilanthoid species (Windham et al. unpublished) illuminate one particularly useful character distinguishing *Myriopteris*, as defined herein, from *Cheilanthes* s.s. The taxa most closely related to the type species of the latter [*C. micropteris* plus all Australian *Cheilanthes* and a group of South American species including the *C. scariosa* (Sw.) C. Presl complex of Tryon and Tryon (1982), *C. obducta* Mett. ex Kuhn, and *C. fractifera* R. M. Tryon] have 32 small spores per sporangium when sexual, and 16 large spores per sporangium when apomictic. This intriguing cytological synapomorphy results from the elimination of a premeiotic mitosis in the cell lineages generating the sporocytes (Windham et al. unpublished). Aside from a few species of the distantly related genus *Notholaena*, all other cheilanthoid ferns so far examined (including every *Myriopteris* species; Grusz et al. in review) produce 64 small spores per sporangium in sexual individuals and 32 large spores per sporangium in apomicts. This character appears to provide an absolute separation between *Myriopteris* and *Cheilanthes* s.s., and is easily observed using a dissecting microscope. In combination with differences in spore ornamentation (see Tryon and Lugardon 1991), leaf venation (Pryer et al. 2010), and geographic distribution, this feature provides a clear distinction between the two genera. For diagnostic purposes, then, *Myriopteris* Fée emend. Grusz & Windham differs from *Cheilanthes* s.s. (i.e., *C. micropteris* and its close relatives) in its production of 64 small or 32 large (vs. 32 small or 16 large) spores per sporangium; mostly cristate or rugulose (vs. echinate, granulose, or verrucate) spore ornamentation; a lack of obvious vein endings near the margins of the ultimate segments (vs. often prominent hydathodes), and a largely North and Central American (vs. exclusively South American/Old World) distribution.

Taxonomic treatment

Myriopteris Fée emend. Grusz & Windham

<http://species-id.net/wiki/Myriopteris>

Type. *Myriopteris marsupianthes* Fée, Mém. Fam. Foug. 5: 149, t. 12A. f. 1. 1852

Description. Plants rupestral or terrestrial. Rhizomes compact to long-creeping, ascending or horizontal, scaly. Rhizome scales lanceolate to acicular, concolorous (tan

to dark brown) or bicolorous (with dark central stripe and brown margins). Leaf veneration non-circinate to circinate. Petioles castaneous to black, scaly and/or pubescent, rarely almost glabrous. Rachises terete or flattened or grooved adaxially, with indument similar to that of the petioles. Blades 2- to 4-pinnate (rarely pinnate-pinnatifid), lanceolate to ovate-deltate, occasionally linear or pentagonal; adaxial surfaces glabrous or pubescent; abaxial surfaces scaly and/or pubescent or rarely glabrous. Ultimate segments round to oblong-ovate, minute to >1 cm long, the veins obscure and not ending in prominent hydathodes. Segment margins usually recurved, with a poorly differentiated false indusium (strongly differentiated in *M. lendigera* and *M. marsupianthes*). Sori usually partly to completely covered by the recurved segment margins, the sporangia clustered at vein tips. Sporangia 64-spored (in sexual species) or 32-spored (in apomicts). Spores globose-tetrahedral, tan to brown, cristate to rugulate. Chromosome numbers $n = 29, 30, 58, 60$ (sexual species); $n = 2n = 87, 90$ (apomictic triploids); $n = 2n = 120$ (apomictic tetraploids).

Distribution. Species of *Myriopteris* range from southern Canada through the Caribbean and Central America to southern Chile, with one species (*M. rawsonii*) endemic to Namibia and South Africa. Mexico is the center of species diversity for the genus; 34 of the 44 species can be found in Mexico, and seven of these are endemic.

New and resurrected combinations in *Myriopteris*

- 1) *Myriopteris aemula* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes aemula* Maxon, Contr. U.S. Natl. Herb. 10: 495. 1908. Type: Mexico. Tamaulipas: Victoria, in river canyon, under overhanging rocks, altitude about 320 meters, February 1 to April 9, 1907, Palmer 187 (holotype: US; isotype: US). urn:lsid:ipni.org:names:77134841-1
- 2) *Myriopteris alabamensis* (Buckley) Grusz & Windham, **comb. nov.** *Pteris alabamensis* Buckley, Amer. J. Sci. Arts 45: 177. 1843. *Cheilanthes alabamensis* (Buckley) Kunze, Linnaea 20: 4. 1847. Type: USA. Alabama: Growing in tufts on limestone rocks that form the banks of the Tennessee River, at the foot of Muscle Shoals, Buckley s.n. (holotype: PH; isotypes: MO, NY). urn:lsid:ipni.org:names:77134842-1
- 3) *Myriopteris allosuroides* (Mett.) Grusz & Windham, **comb. nov.** *Cheilanthes allosuroides* Mett., Abh. Senckenberg. Naturf. Ges. 3: 78. 1859. *Pellaea allosuroides* (Mett.) Hieron., Hedwigia 62: 18. 1920. Type: Mexico, Schmitz s.n. (holotype: location unknown). urn:lsid:ipni.org:names:77134843-1
- 4) *Myriopteris aurea* (Poir.) Grusz & Windham, **comb. nov.** *Pteris aurea* Poir. Encyclopédie Méthodique, Botanique 5: 710. 1804. Type: Peru. Elle a été recueillie au Pérou par Joseph de Jussieu s.n. (sheet 1333 in hb. Jussieu; holotype: P). urn:lsid:ipni.org:names:77134844-1

Acrostichum bonariense Willd., Sp. Pl., ed. 4, 5(1): 114. 1810. *Notholaena bonariensis* (Willd.) C. Chr., Index Filic. 459. 1906. *Cheilanthes bonariensis* (Willd.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 15. 1953.

In *Cheilanthes*, this has been called *C. bonariensis* (Willd.) Proctor because use of the oldest applicable epithet (based on *Pteris aurea* Poir.) was blocked by the earlier publication of *Cheilanthes aurea* Baker (Proctor 1953). With the transfer of this species to *Myriopteris* we revert to the older epithet and thus avoid the typification difficulties associated with the basionym *Acrostichum bonariense* Willd. (Ponce and Zimmer 2011).

- 5) *Myriopteris chipinquensis* (Knobloch & Lellinger) Grusz & Windham, **comb. nov.** *Cheilanthes chipinquensis* Knobloch & Lellinger, Amer. Fern J. 59: 8. 1969. Type: Mexico. Nuevo Leon: Chipinque Mesa, outside Monterey, Knobloch 1996B (holotype: MSC; isotypes: F, GH, MEXU, MICH, UC, US). urn:lsid:ipni.org:names:77134845-1
- 6) *Myriopteris cinnamomea* (Baker) Grusz & Windham, **comb. nov.** *Notholaena cinnamomea* Baker in Hook. & Baker, Syn. Fil. ed. 2. 515. 1874. *Cheilanthes cinnamomea* (Baker) Domin., Biblioth. Bot. 20: 133. 1913. *hom. illeg. non* *Cheilanthes cinnamomea* D. C. Eaton, Proc. Amer. Acad. Arts 18: 186. 1883. Type: Guatemala. Mo[n]tagua, 1862, Salvin & Goodman s.n. (holotype: K; isotype: BM). urn:lsid:ipni.org:names:77134870-1
Cheilanthes tryonii T. Reeves, Brittonia 32: 504. 1980.
 In *Cheilanthes*, this species has been called *C. tryonii* T. Reeves because use of the oldest applicable epithet (based on *Notholaena cinnamomea* Baker) was blocked by the earlier publication of *Cheilanthes cinnamomea* D. C. Eaton (Reeves 1980). With the transfer of this species to *Myriopteris*, we revert to the older epithet.
- 7) *Myriopteris clevelandii* (D. C. Eaton) Grusz & Windham, **comb. nov.** *Cheilanthes clevelandii* D. C. Eaton, Bull. Torrey Bot. Club 6: 33. 1875. Type: USA. California: Growing on a mountain about forty miles from San Diego at an elevation of about 2500 feet, Cleveland s.n. (holotype: YU; isotypes: GH, P, US). urn:lsid:ipni.org:names:77134846-1
- 8) *Myriopteris cooperae* (D. C. Eaton) Grusz & Windham, **comb. nov.** *Cheilanthes cooperae* D. C. Eaton, Bull. Torrey Bot. Club 6: 33. 1875. Type: USA. California: near Santa Barbara, Mrs. Ellwood Cooper (syntype: YU); Sierra Valley, Lemmon s.n. (syntype: YU). urn:lsid:ipni.org:names:77134847-1
- 9) *Myriopteris covillei* (Maxon) Á. Löve & D. Löve, Taxon 26: 325. 1977. *Cheilanthes covillei* Maxon, Proc. Biol. Soc. Wash. 31: 147. 1918. Type: USA. California: Surprise Canyon, Panamint Mountains, 13 April 1891, 1550 meters, Coville & Funston 593 (holotype: US). urn:lsid:ipni.org:names:77134848-1
- 10) *Myriopteris cucullans* (Fée) Grusz & Windham, **comb. nov.** *Cheilanthes cucullans* Fée, Mém. Fam. Foug. 7: 39, t. 25, f. 4. 1857. Type: Mexico, ad vallem Mexicanum, Schaffner 82 [holotype: RB; isotypes: K, US (fragment)]. urn:lsid:ipni.org:names:77134873-1

- 11) *Myriopteris fendleri* (Hook.) E. Fourn., Mex. Pl. 1: 125. 1872. *Cheilanthes fendleri* Hook., Sp. Fil. 2: 103, p. 107b. 1852. Type: USA. New Mexico, 1847, Fendler 1015 [holotype: K; isotypes: GH, MO, NY, US (fragment)].
- 12) *Myriopteris* × *fibrillosa* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes lanuginosa* var. *fibrillosa* Davenp., Bull. Torrey Bot. Club 12: 21. 1885. *Cheilanthes fibrillosa* (Davenp.) Davenp., Bull. Torrey Bot. Club 15: 225. 1888. Type: USA. California: San Jacinto Mountains, June 1882, Parish & Parish s.n. (holotype: GH). urn:lsid:ipni.org:names:77134880-1
- 13) *Myriopteris fimbriata* (A. R. Sm.) Grusz & Windham, **comb. nov.** *Cheilanthes microphylla* (Sw.) Sw. var. *fimbriata* A. R. Sm., Amer. Fern J. 70: 19, 21., f. 9–10. 1980. Type: Mexico. Chiapas: Munic. Frontera Comalapa, 6–8 km east of Frontera Comalapa, Breedlove 39018 (holotype: DS). urn:lsid:ipni.org:names:77134881-1
Cheilanthes fimbriata (A. R. Sm.) Mickel & Beitel, Mem. New York Bot. Gard. 46: 112. 1988. *hom. illeg., non Cheilanthes fimbriata* Vis., Fl. Dalmat. 1. 42 t. 1 f. 1. 1842.
- 14) *Myriopteris gracilis* Fée, Mém. Fam. Foug. 5: 150, t. 29, f. 6. 1852. *Cheilanthes gracilis* (Fée) Mett. ex Riehl, Abh. Senckenberg. Naturf. Ges. 80. 1859. *hom. illeg., non Cheilanthes gracilis* (Michx.) Kaulf., Enum. Filic. 209. 1824. Type: USA. Missouri: Jefferson County, Habitat ad rupes circa Hillsboro, America septentr., Riehl 529 (isotypes: MO, US).
Cheilanthes feei T. Moore, Index Fil., 38. 1857.
Myriopteris lanuginosa J. Sm. Hist. Fil. 280. 1875. [*non M. lanuginosa* (Mart. & Gal.) E. Fourn. Mexic. Pl. 1: 125. 1872.]
In *Cheilanthes*, this has been called *C. feei* T. Moore because use of the oldest applicable epithet (based on *Myriopteris gracilis* Fée) was blocked by the earlier publication of *Cheilanthes gracilis* (Michx.) Kaulf. With the transfer of this species to *Myriopteris*, we revert to the original name published by Fée in 1852.
- 15) *Myriopteris gracillima* (D. C. Eaton) J. Sm., Hist. Fil. 280. 1875. *Cheilanthes gracillima* D. C. Eaton, Rep. U.S. Mex. Bound. Botany 2: 234. 1859. Type: USA. Oregon: Cascade Mountains, 7000 feet of altitude, latitude 44°, Bigelow s.n. (lectotype: YU).
- 16) *Myriopteris intertexta* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes covillei* Maxon subsp. *intertexta* Maxon, Proc. Biol. Soc. Wash. 31: 149. 1918. *Cheilanthes intertexta* (Maxon) Maxon in Abrams, Ill. Fl. Pacific States 1: 28. 1923. Type: USA. California: Santa Clara County, Santa Cruz Mountains, collected at the top of Black Mountain, 6 July 1903, Dudley s.n. (holotype: DS). urn:lsid:ipni.org:names:77134849-1
- 17) *Myriopteris jamaicensis* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes jamaicensis* Maxon, Contr. U.S. Natl. Herb. 24: 51. 1922. Type: Jamaica. Below Cinchona, 28 February 1919, Harris 12905 (holotype: US; isotypes: GH, MO, NY). urn:lsid:ipni.org:names:77134850-1
- 18) *Myriopteris lanosa* (Michx.) Grusz & Windham, **comb. nov.** *Nephrodium lanosum* Michx. Fl. Bor.-Amer. 2: 270. 1803. *Cheilanthes lanosa* (Michx.) D.

- C. Eaton, Rep. U.S. Mex. Bound., Botany 2: 234. 1859. Type: USA. Tennessee (sic) et Carolinae septentrionalis (non designatus). urn:lsid:ipni.org:names:77134851-1
- Myriopteris vestita* (Sw.) J. Sm., Cul. Ferns 29. 1857. (fide C. Chr. 1906.) *Adiantum vestitum* Spreng., Anleit. Kenntn. Gew. 3: 122. 1804.
- 19) *Myriopteris lendigera* (Cav.) Fée, Mém. Fam. Foug. 5: 149. 1852 (as *M. lentigera*). *Pteris lendigera* Cav., Descr. Pl. 268. 1801. *Cheilanthes lendigera* (Cav.) Sw., Syn. Fil. 128, 328. 1806. Type: Mexico. Hidalgo: Ixmiquilpan en la Nueva España, Nee s.n. [syntype: MA, US (fragment)]; Ecuador. Bolivar: junto á Guaranda en el Reyno de Quito, Nee s.n. (syntype: MA).
Cheilanthes minor Mart. & Gal. Mém. Act. Brux. 75, pl. 21, f. 1. 1842. *Myriopteris minor* (Mart. & Gal.) Fée, Mém. Fam. Foug. 5: 150. 1852.
Cheilanthes lanuginosa Mart. & Gal. Mém. Act. Brux. 75, pl. 20, f. 2. 1842. *Myriopteris lanuginosa* (Mart. & Gal.) E. Fourn. Mex. Pl. 1: 125. 1872.
Myriopteris villosa Fée, Mém. Fam. Foug. 5: 149. t. 28, f. 1. 1852.
Cheilanthes frigida Linden ex T. Moore, Gard. Chr. 772. 1857. *Myriopteris frigida* (Linden ex T. Moore) J. Sm. Cat. Cult. Ferns 28. 1857.
Myriopteris lendigera (Cav.) J. Sm., Cat. Cult. Ferns 28. 1857. *hom. illeg.*
Pomatophytum pocillatum M. E. Jones, Contributions to Western Botany 16: 12. 1930.
- 20) *Myriopteris lindheimeri* (Hook.) J. Sm., Bot. Voy. Herald. 340. 1856. *Cheilanthes lindheimeri* Hook., Sp. Fil. 2: 101, t. 107a. 1852. Type: USA. Western Texas, 1847, Lindheimer 744 [lectotype: K; isoelectotypes: GH, P (2 sheets), SD, US, YU].
- 21) *Myriopteris longipila* (Baker) Grusz & Windham, **comb. nov.** *Cheilanthes longipila* Baker, Ann. Bot. (Oxford) 5: 211. 1891. Type: Mexico. San Luis Potosí, 22°N Lat., 6000–8000 ft., Parry & Palmer 989 [holotype: K; isotype: US (fragment)]. urn:lsid:ipni.org:names:77134852-1
- 22) *Myriopteris longipila* subsp. *brevipila* (Mickel) Grusz & Windham, **comb. nov.** *Cheilanthes longipila* var. *brevipila* Mickel, Mem. New York Bot. Gard. 88: 198–199, f. 84N–Q, 87J–M. 2004. Type: Mexico. Guerrero: 2 km al SE de Amatitlán, 1600 m, 13 August 1994, Soto 1052 (holotype: NY; isotype: FCME). urn:lsid:ipni.org:names:77134882-1
- 23) *Myriopteris marsupianthes* Fée, Mém. Fam. Foug. 5: 149, t. 12A, f. 1. 1852. *Cheilanthes marsupianthes* (Fée) T. Reeves ex Mickel & A. R. Sm. Mem. New York Bot. Gard. 88: 201, f. 83M–P. 2004. Type: Mexico. Veracruz: Pic d'Orizaba, Martens & Galeotti 6256 (holotype: P; isotype: BR).
- 24) *Myriopteris maxoniana* (Mickel) Grusz & Windham, **comb. nov.** *Cheilanthes maxoniana* Mickel, Mem. New York Bot. Gard. 88: 201, f. 87A–D. 2004. Type: Mexico. Tamaulipas: San Lucas, Viereck 76 (holotype: US). urn:lsid:ipni.org:names:77134853-1
- 25) *Myriopteris mexicana* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes mexicana* Davenp., Bull. Torrey Bot. Club 15: 227. 1888. Type: Mexico. Chi-

- huahua: on the verge of a high cliff near the summit of Potrero Peak (Santa Eulalia Mts.), October 1886, 7300 ft., Pringle 827 (holotype: GH; isotypes: MO, BR, DS, NY, P, UC, US, YU). urn:lsid:ipni.org:names:77134854-1
- 26) *Myriopteris mickelii* (T. Reeves) Grusz & Windham, **comb. nov.** *Cheilanthes mickelii* T. Reeves, Brittonia 32: 502, f. 1–5. 1980. Type: Mexico. Oaxaca: Distr. Yautepec, Mickel 4210 (holotype: NY; isotypes: MO, UC). urn:lsid:ipni.org:names:77134855-1
- 27) *Myriopteris microphylla* (Sw.) Grusz & Windham, **comb. nov.** *Adiantum microphyllum* Sw., Prodr. 135. 1788. *Cheilanthes microphylla* (Sw.) Sw., Syn. Fil. 127. 1806. Type: Jamaica, Swartz s.n. (holotype: S). urn:lsid:ipni.org:names:77134856-1
- 28) *Myriopteris moritziana* (Kunze) Grusz & Windham, **comb. nov.** *Cheilanthes moritziana* Kunze, Linnaea 23: 307. 1850. Type: Venezuela. Caracas: La Guayra, Moritz 263 (lectotype: B; isoelectotype: GH). urn:lsid:ipni.org:names:77134857-1
- 29) *Myriopteris myriophylla* (Desv.) J. Sm., Bot. Voy. Herald, 340. 1856. *Cheilanthes myriophylla* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 328. 1811. Type: South America. Anon. s.n. (holotype: P). *Cheilanthes elegans* Desv. Ges. Naturf. Freunde Berlin Mag. 5: 328. 1811. *Myriopteris elegans* (Desv.) J. Sm., Cat. Cult. Ferns 29. 1857. *Cheilanthes paleacea* Mart. & Gal., Mém. Foug. Mexique 76, pl. 21, f. 2. 1842. *Myriopteris paleacea* (Mart. & Gal.) Fée, Mém. Fam. Foug. 5: 149, t. 29, f. 6. 1852. *Myriopteris intermedia* E. Fourn., Bull. Soc. Bot. Fr. 27: 328. 1880. *hom. illeg., non* Fée, Mém. Fam. Foug. 5: 149. 1852.
- 30) *Myriopteris newberryi* (D. C. Eaton) Grusz & Windham, **comb. nov.** *Notholaena newberryi* D. C. Eaton, Bull. Torrey Bot. Club 4: 12. 1873. *Cheilanthes newberryi* (D. C. Eaton) Domin, Biblioth. Bot. 20: 133. 1913. Types: USA. California: San Diego, 9 November 1857, Newberry 1352 (syntype: MO, YU); San Diego, 1866, Wood s.n. (syntype: YU); Southern California: S. W. corner of San Bernardino County, rocks in the Temescal range, 22 January 1861, W. H. Brewer s.n. (syntype: YU). urn:lsid:ipni.org:names:77134858-1
- 31) *Myriopteris notholaenoides* (Desv.) Grusz & Windham, **comb. nov.** *Pteris notholaenoides* Desv., Mém. Soc. Linn. Paris 6: 299. 1827. *Cheilanthes notholaenoides* (Desv.) Maxon ex Weath., Contr. Gray Herb. 114: 34. 1936. Type: Hispaniola, Anon. s.n. (holotype: P). urn:lsid:ipni.org:names:77134859-1
- 32) *Myriopteris* × *parishii* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes parishii* Davenp., Bull. Torrey Bot. Club 8: 59. 1881. Type: USA. California: San Diego County, W. J. Parish s.n. (holotype: GH; isotypes: GH, YU). urn:lsid:ipni.org:names:77134860-1
- 33) *Myriopteris parryi* (D. C. Eaton) Grusz & Windham, **comb. nov.** *Notholaena parryi* D. C. Eaton, Amer. Naturalist 9: 351. 1875. *Cheilanthes parryi* (D. C. Eaton) Domin, Biblioth. 85: 133. 1913. Type: USA. Utah: C. C. Parry 263 (holotype: YU; isotypes: GH, US, YU). urn:lsid:ipni.org:names:77134861-1

- 34) *Myriopteris peninsularis* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes peninsularis* Maxon, Contr. U.S. Natl. Herb. 10: 496. 1908. Type: Mexico. Baja California, T. S. Brandegees s.n. (holotype: US). urn:lsid:ipni.org:names:77134862-1
- 35) *Myriopteris peninsularis* subsp. *insularis* (Weath.) Grusz & Windham, **comb. nov.** *Cheilanthes peninsularis* (Maxon) var. *insularis* Weath., Amer. Fern J. 21: 25. 1931. Type: Mexico. Socorro Island, Mason 1616 (holotype: CAS). urn:lsid:ipni.org:names:77134884-1
- 36) *Myriopteris pringlei* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes pringlei* Davenp., Bull. Torrey Bot. Club 10: 61, t. 34. 1883. Type: USA. Arizona: C. G. Pringle s.n. (holotype: GH; isotypes: DS, MO, NY, US, YU). urn:lsid:ipni.org:names:77134863-1
- 37) *Myriopteris pringlei* subsp. *moncloviensis* (Baker) Grusz & Windham, **comb. nov.** *Cheilanthes moncloviensis* Baker, Ann. Bot. (Oxford) 5: 210. 1891. *Cheilanthes pringlei* var. *moncloviensis* (Baker) Mickel, Mem. New York Bot. Gard. 88: 207–208, f. 79J–M. 2004. Type: Mexico. Coahuila: Soledad, E. Palmer 1378 (holotype: K; isotypes: MO, NY, US). urn:lsid:ipni.org:names:77134864-1
- 38) *Myriopteris rawsonii* (Mett. ex. Kuhn) Grusz & Windham, **comb. nov.** *Cheilanthes rawsonii* Mett. ex. Kuhn, Filices Africanæ 75. 1868. Type: Africa. Cape Province: Namaqualand, between Specktakel and Komaggas, Whitehead s.n. (holotype: BM; isotype: K). urn:lsid:ipni.org:names:77134878-1
- 39) *Myriopteris rufa* Fée, Mém. Fam. Foug. 8: 77. 1857. Type: Mexico. Veracruz: Volcan de Orizaba, Schaffner 83 (holotype: P?; isotype: RB?).
Cheilanthes eatonii Baker in Hook. & Baker, Syn. Fil. 140. 1867.
Cheilanthes castanea Maxon, Proc. Biol. Soc. Wash. 32: 111. 1919.
 In *Cheilanthes*, this has been called *C. eatonii* Baker. Examination of putative type specimens of *Myriopteris rufa* housed at RB (digital image) and P indicates that the latter name very likely represents the same species as broadly defined by recent authors (e.g., Mickel and Smith 2004). Because *M. rufa* (published in 1857) has priority over *C. eatonii* (1867), we take up Fée's original name for this taxon in *Myriopteris*.
- 40) *Myriopteris scabra* (C. Chr.) Grusz & Windham, **comb. nov.** *Pellaea scabra* C. Chr., Index Filic. 483. 1906. Type: USA. Texas: crevices of rock on hills, Turkey Creek, 25 June 1849, Wright 824 (holotype: K; isotypes: GH, NY, US).
Cheilanthes aspera Hook., Sp. Fil. 2: 111, t. 108A. 1852. *hom. illeg., non Cheilanthes aspera* Kaulf., Linnaea 6(1): 186. 1831. urn:lsid:ipni.org:names:77134865-1
Cheilanthes horridula Maxon, Amer. Fern J. 8: 94. 1918.
 In *Cheilanthes*, this has been called *C. horridula* Maxon because use of the oldest legitimate epithet (based on *Pellaea scabra* C. Chr.) was blocked by the earlier publication of *Cheilanthes scabra* H. Karst. (Maxon 1918). With the transfer of this species to *Myriopteris*, we revert to the older, exceedingly appropriate epithet.
- 41) *Myriopteris tomentosa* (Link) Fée, Mém. Fam. Foug. 5: 149. 1852. *Cheilanthes tomentosa* Link, Hort. Berol. 2: 42. 1833. Type: Mexico. Anon. s.n. [holotype: B; isotypes: PH, US (fragment)].

- Cheilanthes bradburii* Hook., Sp. Fil. 2: 97, t. 109b. 1852. *Myriopteris bradburii* (Hook.) J. Sm. Hist. Fil. 280. 1875.
- 42) *Myriopteris viscida* (Davenp.) Grusz & Windham, **comb. nov.** *Cheilanthes viscida* Davenp., Bull. Torrey Bot. Club 6: 191. 1877. Types: USA. California: Eastern slope of the Sierra Nevada near San Gogorio Pass, April 1876, Parry & Lemmon 427 (syntype: NY); California/Nevada: Downieville Buttes and bluffs of White Water River on the Colorado Desert, April–May, Lemmon s.n. (syntype: NY). urn:lsid:ipni.org:names:77134866-1
- 43) *Myriopteris windhamii* Grusz, Amer. Fern J. 103: 113. 2013. Type: USA. Arizona: Huachuca Mountains, Windham 4165 (holotype: DUKE; isotypes: ARIZ, ASC, ASU, GH, MO, NMC, NY, TEX/LL, UNM, US, UT).
Cheilanthes villosa Davenp. ex Maxon, Proc. Biol. Soc. Wash. 31: 142. 1918. In *Cheilanthes*, this has been called *C. villosa* Davenp. ex Maxon. Because transfer of the epithet *villosa* to *Myriopteris* is blocked by the earlier publication of *M. villosa* Fée (= *M. lendigera* fide Reeves 1979), we use the replacement name for this distinctive taxon published by Grusz (2013).
- 44) *Myriopteris wootonii* (Maxon) Grusz & Windham, **comb. nov.** *Cheilanthes wootonii* Maxon, Proc. Biol. Soc. Wash. 3: 146. 1918. Type: USA. Arizona: Santa Rita Mountains, Wooton s.n. (holotype: US). urn:lsid:ipni.org:names:77134867-1
- 45) *Myriopteris wrightii* (Hook.) Grusz & Windham, **comb. nov.** *Cheilanthes wrightii* Hook., Sp. Fil. 2: 87, t. 110A. 1858. Type: USA. Texas–New Mexico: Wright 823 (holotype: K; isotypes: GH, NY, US). urn:lsid:ipni.org:names:77134868-1
- 46) *Myriopteris yatskievychiana* (Mickel) Grusz & Windham, **comb. nov.** *Cheilanthes yatskievychiana* Mickel, Mem. New York Bot. Gard. 88: 212–213, f. 74F–K. 2004. Type: Mexico. Sonora: Sierra del Aliso, A. Búrquez M. 96-302 (holotype: MO). urn:lsid:ipni.org:names:77134869-1
- 47) *Myriopteris yavapensis* (T. Reeves ex Windham) Grusz & Windham, **comb. nov.** *Cheilanthes yavapensis* T. Reeves ex Windham, Contr. Univ. Michigan Herb. 19: 32. 1993. Type: USA. Arizona: Yavapai County, Windham 202 (holotype: UT; isotypes: ASC, ASU, US). urn:lsid:ipni.org:names:77134879-1

Name of uncertain application

Myriopteris cheiloglyphis Fée, Mém. Fam. Foug. 8: 77. 1857.

Excluded names

Myriopteris contracta (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = *Cheilanthes contracta* (Kunze) Mett. ex Kuhn

Myriopteris hirta (Sw.) J. Sm., Ferns Brit. and For. 174. 1866. = *Cheilanthes hirta* Sw.

Myriopteris induta (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = *Cheilanthes induta* Kunze

- Myriopteris intermedia* (Kunze) Fée, Mém. Fam. Foug. 5: 149. 1852. = *Cheilanthes hirta* Sw. fide Christensen (1906)
- Myriopteris macleanii* J. Sm., Hist. Fil. 280. 1875. = *Cheilanthes pilosa* Goldm. fide Christensen (1906)
- Myriopteris scariosa* (Sw.) Fée, Mém. Fam. Foug. 5: 149, t. 29, f. 6. 1852. = *Cheilanthes scariosa* Sw.
- Myriopteris szovitzii* (Fisch. & Meyer) J. Sm., Hist. Fil. 281. 1875. = *Cheilanthes persica* (Bory) Mett. ex Kuhn fide Christensen (1906)

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