

# *Espeletia praesidentis*, a new species of Espeletiinae (Millerieae, Asteraceae) from northeastern Colombia

Mauricio Diazgranados<sup>1</sup>, Luis Roberto Sánchez<sup>2</sup>

**1** Natural Capital and Plant Health department, Royal Botanic Gardens, Kew, Wakehurst Place Ardingly, West Sussex, RH17 6TN, UK **2** Departamento de Biología y Química. Universidad de Pamplona. Pamplona, Colombia

Corresponding author: *Mauricio Diazgranados* ([m.diazgranados@kew.org](mailto:m.diazgranados@kew.org))

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## Abstract

A new species of *Espeletia* from the Páramo de Presidente in northeastern Colombia is described. The species is named *Espeletia praesidentis* after the name of the páramo, and it is dedicated to the President Juan Manuel Santos, for his persistent efforts in working for peace for Colombia. The new species is closely related to *Espeletia dugandii*, but differs in the shape and colour of the leaves and arrangements of the pubescences. A large population was found, but its total extension is yet to be determined.

## Keywords

Colombia, Compositae, Espeletiinae, *Espeletia*, frailejón, Millerieae, Norte de Santander, Santander, páramos, Presidente

## Introduction

In 1932 the renowned Spanish botanist José Cuatrecasas visited for the first time a páramo in Colombia. From that moment he decided to study the frailejones (common name given to most of the *Espeletia* Mutis ex Bonpl. species), not knowing the taxonomic endeavor he was going to begin. Thirty-four years later he published the classification of the subtribe Espeletiinae Cuatrec. (Asteraceae: Millerieae) (Cuatrecasas

1976), and continued working on the group until his death in 1996. His masterpiece, the systematic study of the subtribe, represents his work for about 64 years, and was finally published in 2013, after almost two decades of further additions. The treatment, however, did not include the genus *Espeletiopsis* Cuatrec., because Cuatrecasas was not able to complete the work on it (Cuatrecasas 2013). The main reason for the delay was the difficulty of working on the group, defying species concepts and challenging collectors and curators to deepen their collecting techniques and studies.

In recent years, several new species have been published, and more new species are foreseen. At the moment the subtribe contains 8 genera, 144 species (including the new species described here), 17 subspecies, 22 varieties and 8 forms (Cuatrecasas 2013; Diazgranados 2012a; Diazgranados and Morillo 2013; Diazgranados and Sanchez 2013). It has been highlighted as one of the examples of the rapid radiations of the páramos (Madriñán et al. 2013), and phylogenetic approaches will bring further reorganizations within the subtribe (Diazgranados 2012b).

There are a number of reasons making the subtribe a difficult group for taxonomist. It is easily identified morphologically, with clear synapomorphies, unique to these plants. However, the variation between and within the species can be astonishing. Despite the notorious morphological variations, characters are often continuous rather than discrete, and species are identified by combinations of character states. This is evident, for example, in Cuatrecasas' dichotomous keys, where paragraphs with various character states are needed to identify the species (Cuatrecasas 2013). There is frequent inter-specific and inter-generic hybridization with introgression. The presence of hybrids with three parental species has even been suggested (Cuatrecasas 2013; Diazgranados 2012a). Hybrid speciation can be also important, as genomic analyses are recently suggesting (Mavárez, J., unpubl. data). Genetic variability between species is very low, and genetic markers are not very useful for separating species (Diazgranados 2012b). Also, populations are very large, dominating the landscape of the páramos. This challenges unexperienced collectors, who collect rare individuals that can be hybrids or just mutants in the population, without reporting the population. Also, collecting frailejones appropriately is time-consuming and samples are bulky. Due to all of this, herbarium samples are often incomplete and can be misclassified and misidentified. Finally, because of the island effect of the páramos and the limited dispersal capability of frailejones, local (geographic) endemism is common (Diazgranados 2013). The previous reasons form together the ingredients for a perfect 'taxonomic storm', inviting review of the species concept for Espeletiinae. In this work we follow the *unified species concept* (De Queiroz 2007), applicable for rapid radiations in early states of divergence, where populations become phenetically distinguishable and diagnosable.

The genus *Espeletia*, as it is currently defined, contains 72 species (including the one described here), distributed from the páramos of Lara (Venezuela) to the páramos of Llanganates (Ecuador). Most of the species grow above the timberline, although some have been identified as pioneer species after disturbance and can grow in ecotones between the high-Andean forest and the páramos, in azonal páramos or in areas with secondary paramisation (Diazgranados 2013).

This genus is diagnosed by being caulirosulas normally monocaulous, with lateral dichasial capitulescences, with branches, leaves, and bracts opposite, at least in the proximal part; leaf bases open, flat; ray corollas yellow, cypselae epappose, and pollen grains with 11–18(–21) spines, (2–)4–7  $\mu\text{m}$  long on equator. Within the genus Cuatrecasas (2013) proposed five sections (*Aristeguietana*, *Bonplandia*, *Badilloa*, *Espeletia* and *Weddellia*) and a dubious group (Aberrantes). However, molecular works have suggested the presence of two clades (one from Venezuela and one from Colombia-Ecuador), which includes other genera (Diazgranados 2012b).

## Methods

The Páramo de Presidente is located 28 km south from Chitagá (Norte de Santander), and it is considered part of the Páramos de Almorzadero-Santurbán complex. It can be reached on the road from Chitagá to Cerrito. For decades this area has been considered unsafe, and the flora of this páramo has not been studied well yet. Material of the new species was collected during an expedition of the authors in 2009, in which they met with left-wing armed members. Duplicates were distributed to COL, ANDES and HECASA. Additional duplicates will be distributed to other Colombian herbaria. 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 and the Smithsonian Institution.

## Taxonomy

### *Espeletia praesidentis* Diazgr. & L.R.Sánchez, sp. nov.

urn:lsid:ipni.org:names:77159581-1

Figures 1–6

**Type.** COLOMBIA, Norte de Santander, Páramo de Presidente. En vía a Chitagá, llegando al páramo. En frailejonal-pajonal típico. Muy abundante. Caulirrósula. Alt. tot.: 0.8 m; alt. de la roseta: 0.4 m; inflorescencias: 2 maduras y 4 secas, con escapo desnudo, con 3–5 capítulos, cada uno de 2.1 cm de diámetro; hojas más angostas que otros individuos simpátricos. Alt. 3503 m,  $-72^{\circ}40.8828'W$ ,  $6^{\circ}59.8362'N$ . 3 Oct. 2009, *M. Diazgranados* & *L.R. Sánchez* 3865 (holotype: COL; isotypes: HECASA and to be distributed).

**Diagnosis.** Caulescent rosette of yellowish-whitish appearance, with leaf laminae linear or linear-obovate, naked scapes with long peduncles and 3(–5) capitula, small in diameter, disc paleae oblong, oblanceolate or narrowly obtusulate, very short yellow ray flowers, and lobes of disc corollas with hairs. Similar to *E. dugandii*, but more yellowish, with much linear and narrower leaf laminae, much longer peduncles, smaller capitula and ray flowers, and disc corolla lobes with more hairs.

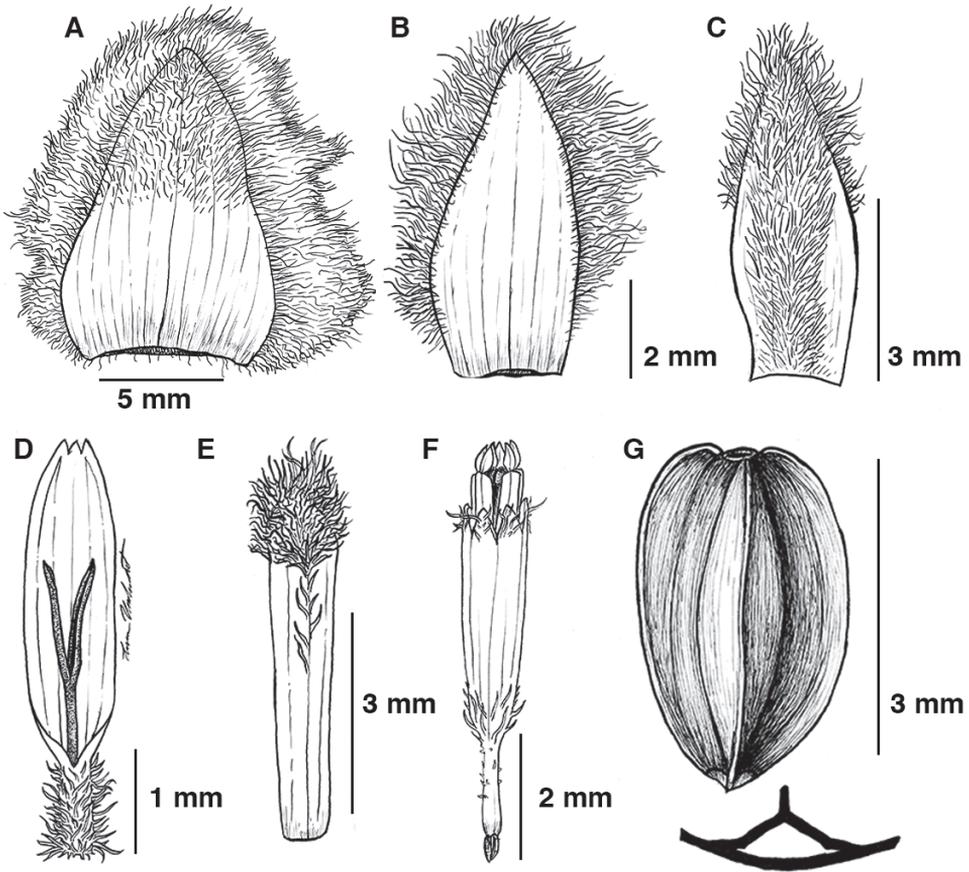


**Figure 1.** *Espeletia praesidentis*: **A** habitat, showing a large population **B** holotype collection (*M. Diazgranados & L.R. Sánchez 3865*), with stemmed rosette habit and very long capitulescences **C** frontal view of capitulum **D** dorsal view of capitulum.

**Description.** Caulescent polycarpic rosette of yellowish-whitish appearance (not cinereous), 0.8–1.5 m tall (including capitulescences), growing in grassland of páramo proper. Excluding reproductive parts, rosette 40–60 cm in diameter, on stems 0–40 cm tall (Fig. 1 A–B).

Leaves firm, coriaceous, rigid, erect; laminae linear or linear-obovate, apex acute to subacute (60–80°), base sessile, slightly pseudopetiole, attenuate, (38–)39–42(–45) cm × (3.0–)3.5–3.6(–4.2) cm, length to width ratio (10–)11–12(–15):1 (Figs 4 E, 5 B). Indumentum pale-yellowish in young leaves, becoming whitish in adult leaves. Adaxial face with indumentum whitish, lanose, costa pale-yellowish, visible, but secondary nerves invisible. Abaxial face with indumentum whitish, lanose, less abundant, costa more prominent, as well as secondary nerves, with deviation angles of 37–45°. Margins entire.

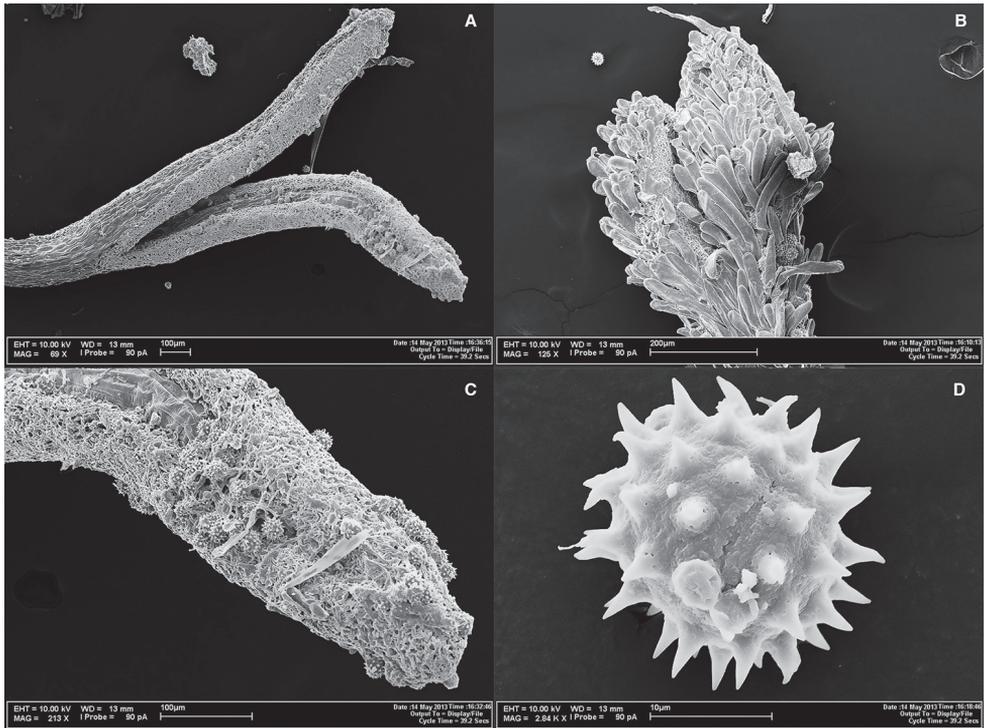
Leaf sheaths open, oblong to trapezoidal, coriaceous, 5–6 cm wide × 7–8 cm long; adaxially glabrescent, whitish, with 10–15 green anastomosing nerves; tawny abaxially, barbate, with hairs up to 15 mm long.



**Figure 2.** Illustrations of *Espeletia praesidentis*. **A** outer phyllary **B** Inner (sterile) phyllary **C** ray flower palea **D** ray flower **E** disc flower palea **F** disc flower **G** dorsal view of cypselae from ray flower. Illustrations made by Lauren Merchant.

Capitulescences 5–15(–18) coetaneous, cymose, dichasial, axillary (lateral), erect, more than twice longer than the leaves, 100–120 cm long; indumentum abundant, villous, white. Scapes erect, firm, 80–100 cm long, 0.8–1.0 mm in diameter; naked, with no sterile bracts. Peduncles terete, 15–18 cm long, curving in the distal end, proximally with a free attachment. One pair of subtending bracts, linear, 8–10 cm long  $\times$  0.9–1.0 cm wide.

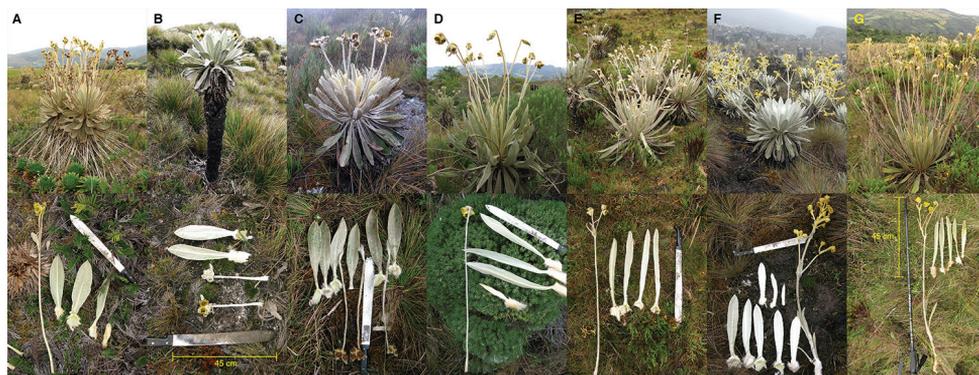
Capitula 3(–5) radiate, subglobose, nodding, 2.0–3.0 cm in diameter (including ray flowers) (Fig. 1 C–D). Involucre 2.0–2.5 cm wide  $\times$  1.0–1.6 cm high. Phyllaries in 2–3 series, ovate to ovate-triangular. Outer phyllaries surpassing the capitulum, 12–13 mm long  $\times$  8.0–9.0 mm wide (excluding hairs), apex obtuse to acute, adaxially glabrous with 10–20 visible nerves, abaxially villous, hairs 2–4.5 mm. Inner phyllaries 6.0–6.5 mm long  $\times$  2.8–3.3 mm wide, with indumentum villous white, hairs 1.0–2.0 mm long.



**Figure 3.** Photomicrographs of *Espeletia praesidentis*. **A** stigmatic branches of ray flower **B** stigmatic branches of disc flower with abundant papillae **C** detail of a stigmatic branch of ray flower with pollen grains **D** Pollen grain.

Ray flowers 80–90 in 2–3 series, yellow, ray corollas 3.5–4.5 mm long (excluding ovary). Ligules 3.0–3.5 mm long, elliptical or oblong, tridentate; tube hirsute, small, 0.2–0.4 mm in diameter and 0.5–1.0 mm long, yellow, the trichomes 0.2–0.3 mm long. Style 2.7–2.9 mm long  $\times$  0.14–0.2 mm in diameter, with stigmatic branches 1.0–1.5 mm long, without papillae in the distal portion. Cypselae oblong, triangular, 3.3–3.5 mm  $\times$  2.0–2.2 mm, glabrous, black. Ray paleae narrowly-ovate, 5.3–5.5 mm  $\times$  long 2.0–2.1 mm wide, brownish, profusely villous.

Discs 1.5–2.6 cm in diameter. Disc paleae oblong, oblanceolate or narrowly obtusulate, 5.0–5.4 mm long  $\times$  0.8–1.1 mm wide, brownish, glabrous becoming villous in the distal portion. Disc flowers 300–400; corolla 5.0–5.2 mm long (excluding anthers and fruit); corolla throat 3.5–3.7 mm long, 1–1.1 mm wide when open, 5-lobed, lobes 0.45–0.55 mm long, with hairs; tube 1.5–2.0 mm long  $\times$  0.2–0.3 mm in diameter, glabrous, with a few hairs; anthers dark yellow, sometimes exceeding the corolla, slightly translucent, approximately 1–2 mm long and 0.3 mm wide. Pollen yellow when fresh, tricolporate, 17.5–19.5  $\mu$ m in equatorial diameter (not counting spines); spines 70–74 total, 14–16 equatorial spines, 3.9–4.5  $\mu$ m long, erect. Style 5.5–7.0 mm long  $\times$  0.14–0.17 mm in diameter, with stigmatic branches 0.6–0.7 mm



**Figure 4.** Comparison of similar *Espeletia* species. **A** *E. brassicoidea* **B** *E. canescens* **C** *E. conglomerata* **D** *E. dugandii* **E** *E. praesidentis* **F** *E. standleyana* **G** *E. steyermarkii*. The hygrophilous and always monocephalous *E. stanislana* was not included because of its very distinctive morphology. Above: plant habit; below: adult leaves with sheaths, and complete capitulescences.



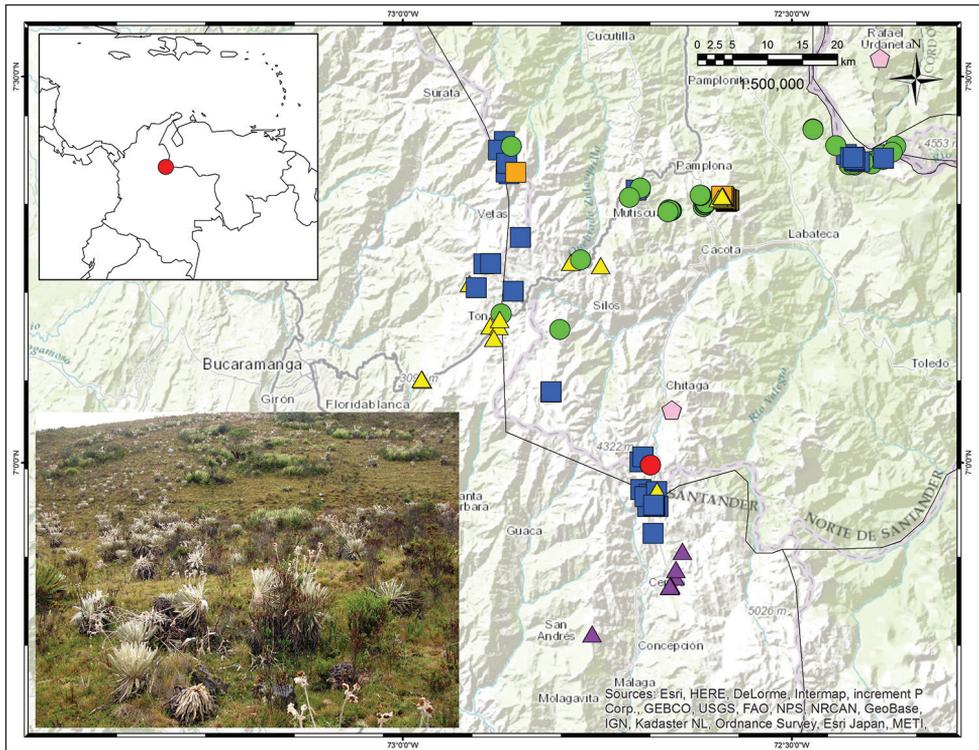
**Figure 5.** Comparison of rosette colours. **A** *E. dugandii* **B** *E. praesidentis*.

long, broadening in the distal portion, 0.20–0.25 mm wide, papillose, papillae to 0.15–0.2(–0.4) mm long.

**Distribution.** Endemic to Colombia. This species has been found only in the Páramo de Presidente (part of the great Páramo de Almorzadero), at elevations of 3400–3600 m (Fig. 6). The known area of distribution is about 2 km<sup>2</sup>.

**Ecology.** A large population of several hundreds of individuals growing in the grasslands of the páramo proper was observed (Fig. 1, 6). Other *Espeletia* species found in the area are: *Espeletia brassicoidea* Cuatrec., *E. canescens* A.C.Sm., *E. conglomerata* A. C. Sm., *E. dugandii* Cuatrec., *E. standleyana* A. C. Sm., and *E. steyermarkii* Cuatrec. (Fig. 6). *E. praesidentis* can be found in slightly humid plains and on relatively drained slopes.

**Etymology.** The specific epithet of this new species, “*praesidentis*”, taken from the locality where the species is found, is dedicated also to the President of Colombia, Juan



**Figure 6.** Distribution map showing the collection locality for *Espeletia praesidentis* (red circle), and collections of other *Espeletia* species found in the area: *E. brassicoidea* (green circles), *E. canescens* (orange squares), *E. conglomerata* (blue squares), *E. standleyana* (yellow triangles) and *E. steyermarkii* (pink pentagons). Topographic map from Environmental Systems Research Institute (Esri), HERE, DeLorme, TomTom, Intermap, Increment P Corp., General Bathymetric Chart of the Oceans (GEBCO), United States Geological Survey (USGS), Food and Agriculture Organization (FAO), National Park Service (NPS), Natural Resources Canada (NRCAN), GeoBase, Institut Géographique National (IGN), Kadaster NL, Ordnance Survey, Esri Japan, Ministry of Economy, Trade and Industry of Japan (METI), Esri China (Hong Kong), Swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community.

Manuel Santos Calderón, for his persistent efforts to achieve peace with the guerillas FARC in Colombia, after 52 years of conflict. The Páramo de Presidente has been one of those places that has been closed to researchers for decades. With the peace agreement this and other places will be open for fruitful botanical explorations during the post-conflict times in Colombia. May this publication inspire the President to continue with further actions for the preservation of Colombian biodiversity.

**Conservation status.** Despite seeing a relatively large population, this páramo area is not under any sort of protection, and there are signs of grazing activity. Also, very close there are extensive potato plantations in areas that were covered by páramo vegetation in the past. This combination of elements suggests that the species is probably *Critically Endangered* (CR, according to the IUCN criteria: extent of occurrence

estimated to be less than 100 km<sup>2</sup>, habitat fragmentation, and likely decline of the extent of the páramo; [http://jr.iucnredlist.org/documents/redlist\\_cats\\_crit\\_en.pdf](http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf)), or *Critically Imperiled* (G1, according to NatureServe; <http://www.natureserve.org/explorer/ranking.htm>).

**Discussion.** The páramos of Santander and Norte de Santander (Colombia) are considered one of the three centres of radiation for the Espeletiinae (Cuatrecasas 2013; Diazgranados 2012b). Probably because of the topographic complexity of these mountains and the longer time for evolution of these plants in this area with respect to other Colombian cordilleras, the overall diversity in the Santanderes is remarkable: 36 species belonging to 7 genera (all but *Carramboa*). New species continue to appear as collectors reach previously unexplored páramos, whilst our taxonomic understanding of the group improves.

In 1926–1927 two American botanists explored the vegetation of these mountains, Ellsworth Paine Killip (1890–1968) and Albert Charles Smith (1906–1999). Smith, who would become later the director of the National Museum of Natural History at the Smithsonian Institution, described years later 10 new species of *Espeletia* from those collections. Since then, no one has really visited the same places that these botanists explored, probably not even Cuatrecasas, who spent decades collecting the Espeletiinae in the páramos. Collectors of Espeletiinae know well that if they miss the slope or the mountain, they can totally miss the species they are looking for, because of the extreme local endemism of the group. As a consequence, Cuatrecasas (2013) made clear in his monographic work that the status of several taxa could be subject to changes with further collections.

*Espeletia praesidentis* exemplifies the lack of collections throughout the páramos of the region, and the challenges taxonomists have to face when studying this group. Cuatrecasas's collections were often limited to the accessibility of roads in those years (1940–1980), and he never found the topolocality where Killip and Smith collected species such as *E. conglomerata* and *E. canescens*. In the remarks for *E. canescens* of his treatment he said “Sometimes I have been inclined to consider *E. canescens* as a local, extreme variation of *E. conglomerata*. However, the scanty, authentic material of *E. canescens* shows features that can justify its specific status [...] On my 1973 trip, I did not have the time to walk from La Baja all the way to the highest spots at the opposite north end of the Páramo del Romeral, where Killip probably collected the type specimens of *E. canescens*. Additional collections from the extreme section of the Páramo del Romeral may clarify the taxonomic status of *E. canescens*” (Cuatrecasas, 2013, pag. 319). In the remarks for *E. conglomerata* he said “*E. conglomerata* as well as *E. canescens* were described with type specimens from Páramo del Romeral between “3800 and 4200” m of altitude. However, according to recent maps, this páramo generally does not exceed 3800 m [...]. My own collections represent several minor variations, as well as the typical form” (Cuatrecasas, 2013, pag. 316). In that moment Cuatrecasas was 70-year old, and clearly did not have time or possibilities to explore close areas were in recent years various new species have been discovered (e.g. *Espeletiopsis sanchezii* S. Díaz & S. Obando

or *E. diazii* Diazgr. & L. R. Sánchez). With no other material than his own collections, he first described morphological variations of his specimens as varieties (*Espeletia conglomerata* var. *macroclada* Cuatrec. and *E. conglomerata* var. *pedunculata* Cuatrec.). Later, he decided to change the status to hybrids, both within *E. conglomerata* × *E. brassicoidea*, and synonymised *E. brassicoidea* f. *contracta* Cuatrec. with *E. conglomerata*. Also, he never published *E. conglomerata* var. *lanceolata* Cuatrec. [*Nom. nud.*, *Carriker 3A*].

*Espeletia praesidentis* differs notably from the type of *E. conglomerata* (Killip *E. P. and Smith A. C.* 18635, see key below), and from the hybrids described from Cuatrecasas (2013). We believe *E. praesidentis* cannot be considered a local variation or hybrid of similar or neighboring species for two reasons: 1) there is a large population of several hundreds of individuals; and 2) there are remarkable morphological differences between *E. praesidentis* and the type collections of other species (as seen in Fig. 4). In this work we do not intend to propose a new categorization for hybrids and/or varieties of *E. conglomerata*, and we recognize that hybrids can be easily spotted when sympatric species occur, but this clearly was not the case.

**Key to *Espeletia praesidentis* and other *Espeletia* species found in an area (*E. brassicoidea*, *E. canescens*, *E. conglomerata*, *E. dugandii*, *E. standleyana* and *E. steyermarkii*)**

The most complete key for the genus has been published by Cuatrecasas (2013) and updated later in various publications (Díaz-Piedrahita and Pedraza 2001; Díaz-Piedrahita and Rodríguez-Cabeza 2008; 2010; Díaz-Piedrahita et al. 2006). This key is a simplification of the updated version of Cuatrecasas' key, for the species of *Espeletia* found in an area of 50 km of radius.

- 1 Proximal vegetative parts of capitulescences naked, completely lacking sterile leaves, occasionally above proximal parts bearing a few leafy bracts originating from the fertile parts and becoming sterile ..... **4**
- 1' Proximal vegetative parts of capitulescences each with from several to 1 pair of sterile opposite leaves ..... **2**
- 2 Leaf laminae somewhat narrowed towards bases, but not obviously pseudopetiolate. Capitulescences with spreading, stout, thick branches and peduncles ..... ***E. standleyana***
- 2' Leaf laminae narrowed toward bases into conspicuous pseudopetioles ..... **3**
- 3 Capitulescences monocephalous; capitula 35–70 mm in diameter ..... ***E. estanislana***
- 3' Capitulescences paniculate, proximal fertile internodes and branches very long (18–44 cm), rather thin, erect, and fastigiated; with numerous capitula (>20), (16–)20–35 mm in diameter ..... ***E. steyermarkii***
- 4 Leaf laminae 7–14 cm wide, length to width ratio 1.3–5(–6):1, elliptic, obovate, oblong-obovate or oblong-elliptic, abruptly or gradually narrowed

- at bases; general appearance white. Capitulescences about 2× longer than leaves ..... *E. brassicoidea*
- 4' Leaf laminae narrow, 3.2–6 cm wide, length to width ratio (5–)6–11(–15):1, oblong-spathulate or oblong-elliptic, occasionally obtrullate, gradually attenuate to bases. Capitulescences longer than 2× the leaves..... **5**
- 5 Leaf laminae (26–)34–40 cm × 4.3–5.5(–6.5) cm; ray corollas 14–18 mm long; tubes 4.5–6 mm long; capitula 3–4 cm in diameter ..... *E. dugandii*
- 5' Leaf laminae shorter or narrower; ray corollas and tubes much shorter; capitula smaller, 2–3.2 cm in diameter ..... **6**
- 6 Plant appearance yellowish; leaf laminae linear or linear-obovate, (38–)39–42(–45) cm × (3.0–)3.5–3.6(–4.2) cm, length to width ratio (10–)11–12(–15):1. Peduncles 15–18 cm long. Ray corollas 3.5–4.5 mm long; tubes 0.5–1.0 mm long..... *E. praesidentis*
- 6' Plant appearance whitish or cinereous; leaf laminae oblong, spathulate or narrowly obovate-oblong, much shorter and wider. Much shorter peduncles (1–6 cm). Ray corollas 7–11(13) mm long; tubes 1.5–2.5 mm long..... **7**
- 7 Leaf laminae more thinly coriaceous, flexible, obtuse or subacute at apex, 22–32(–38) cm × 3.2–5.5 cm; capitula usually glomerate on curled, contracted peduncles (rarely peduncles almost straight); disc corollas hairy and glanduliferous at the middle, at least some of the lobes with a few hairs.....
- ..... *E. conglomerata*
- 7' Leaf laminae rather thickly coriaceous, obtrullate-oblong, angulate and acute at apex, 30–32 cm × 5.3–6.3 cm; capitula drooping or nodding on straight rigid peduncles and pedicels; disc corollas glabrous or subglabrous; lobes only with sparse glands. .... *E. canescens*

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# *Eutrema salsugineum* (Cruciferae) new to Mexico: a surprising generic record for the flora of Middle America

Dmitry A. German<sup>1,2</sup>, Marcus A. Koch<sup>1</sup>

**1** Department of Biodiversity and Plant Systematics, Centre for Organismal Studies (COS) Heidelberg, Heidelberg University, Im Neuenheimer Feld 345, D-69120 Heidelberg, Germany **2** South-Siberian Botanical Garden, Altai State University, Lenin Str. 61, 656049 Barnaul, Russia

Corresponding author: *Dmitry A. German* ([oreoloma@rambler.ru](mailto:oreoloma@rambler.ru))

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## Abstract

The paper reports *Eutrema salsugineum* as a novelty to the flora of Mexico and Middle America in general. The finding stands ca. 1600 km apart from the closest known locality in the Rocky Mountains of Colorado, USA. The species is considered native to NW Mexico and its late discovery in the region is presumably explained by its tiny habit, early flowering time, and subephemeral life cycle. The phylogenetic position of this Mexican population in a haplotype network based on the chloroplast DNA fragment *psbA-trnH* confirms this hypothesis and also suggests, in contrast to the previously held viewpoint, multiple colonizations of North American continent from Asia.

## Keywords

Brassicaceae, floristic finding, geographic disjunction, halophyte, model species, native distribution range, *Thellungiella*

## Introduction

*Eutrema salsugineum* (Pall.) Al-Shehbaz & Warwick, long known as *Thellungiella salsuginea* (Pall.) O.E. Schulz, is, along with *E. edwardsii* R. Br., the most widely distributed representative of the genus *Eutrema* R. Br., occurring in temperate and, to a lesser extent, the Arctic zone of Eurasia and North America. Being an obligatory halophytic annual

related to *Arabidopsis thaliana* (L.) Heynh., it has become a new model for studying abiotic stress (salt, cold, and draught) tolerance in plants (Bressan et al. 2001; Amtmann 2009). As a result, *Eutrema salsugineum* became one of the first representatives of Brassicaceae to have its genome sequenced (Wu et al. 2012). Nevertheless, fundamental (e. g., geographic) information on the species is incomplete (Koch and German 2013). Due to the peculiar ecological requirements of the species, *E. salsugineum* has a highly disjunct distribution in both continents (Korobkov 1975; Ovchinnikova 1994; Rollins 1993; Al-Shehbaz 2010). Despite being described in the 18th century (Pallas 1773) and being noted for its geographic disposition (Schulz 1924), the exact distribution of this species remained unknown, until recently. One of the reasons for the uncertainty was the misidentification of multiple specimens from Russia and Kazakhstan incorrectly referred to as “*Thellungiella salsuginea*”. Of these, all specimens from the western-most part of the range belong to another species, *E. botschantzevii* (D.A. German) Al-Shehbaz & Warwick [*Thellungiella botschantzevii* D.A. German] (German 2002, 2006, 2008). This finding now means that *E. salsugineum* is completely absent from Europe being bounded at the west by the lower reaches of Amu Darya river, Aral Sea, and the Turgai Valley. Our knowledge on the distribution of the species in America had also undergone improvements, and nowadays *E. salsugineum*'s range is known to extend discontinuously from boreal and Arctic Canada (Alberta, Manitoba, Northwest Territories, Saskatchewan, Yukon) down through the Rocky Mountains within British Columbia, and south to Montana and Colorado. Previous reports for other states such as Idaho (Rydberg 1917) and Ontario (Scoggan 1957) were not confirmed by subsequent studies (Al-Shehbaz 2010; Brouillet et al. 2010). Here we report of *Eutrema salsugineum* specimens collected by the second author in 2010 from arid regions in north-eastern Mexico, revealing another highly disjunct and we believe indigenous population. Our findings are supported with additional genetic analyses from which we draw further biogeographic conclusions.

## Materials and methods

The specimen documenting the occurrence of *E. salsugineum* in Middle America is deposited in HEID. For estimation of the newly revealed disjunction in the distribution area of the species, available information regarding the closest occurrence has been used (Weber 1966). Results were interpreted in light of the most recent phylogeographic study of *E. salsugineum* by Wang et al. (2015). In this study various plastid genes (*ndhF1*, *ndhF2*, *psbA-trnH*, *rpoC1*, *rbcL*, *trnD-trnT*, *trnL*, *trnL-trnE*, *trnV*) have been sequenced and DNA polymorphisms have been detected in one marker only. In order to find the inter-species affinity of the Mexican population, its position in the haplotype network based on the respective variable chloroplast DNA fragment, *psbA-trnH*, was determined. For this purpose, representatives of the two geographically closest populations (from Montana and Colorado) not studied molecularly before and one accession from Canada, as internal control, were also sequenced.

Total DNA was extracted from 100 mg of herbarium tissue using the Invisorb Spin Plant Mini Kit (Strattec Biomedical AG, Birkenfeld, Germany). PCR ampli-

fication was performed in a volume of 25  $\mu\text{L}$ , using 10  $\mu\text{M}$  of each primer, respectively, a total of 2.0 mM  $\text{MgCl}_2$  and 0.5 U of Mango-Taq polymerase (Bioline, Luckenwalde, Germany). The primers used for amplification were *psbA*-for: 5'-GTT ATG CAT GAA CGT AAT GCT C-3', and *trnH*-rev: 5'-CGC GCA TGG TGG ATT CAC AAT CC-3'). All primers were extended by the M13 sequence for subsequent sequencing using M13 universal sequencing primers. The amplifications were run on a PTC 200 Peltier Thermal Cycler (MJ Research, Waltham, Massachusetts, USA) under the following conditions: 3 min initial denaturation at 95°C; 30 cycles of amplification with 30s at 95°C, 30s at 50°C, and 1 min at 72°C; and 5 min of final elongation at 72°C. PCR success was checked with electrophoresis in a 1% agarose gel in TAE-buffer. PCR product clean-up was executed using the Wizard SV Gel and PCR Clean-Up System (Promega, Madison, USA). Custom Sanger-sequencing was performed with GATC- Biotech (Konstanz, Germany). The electropherograms were checked and trimmed to the borders of the analysed markers using the program SeqMan DNA-Star Lasergene software package (DNASTAR, Madison, Wisconsin, USA).

DNA sequence variation was compared with cpDNA haplotypes detected by Wang et al. (2015). Haplotype network analysis was conducted with SplitsTree4 vers. 4.14.4 (Huson and Bryant 2006) with gaps treated as additional binary character.

Apart from the Mexican one, the newly sequenced specimens are: 1) USA, Colorado, Park Co., 11 August 1965. *W.A. Weber 12925* (GH); 2) USA, Montana, Beaverhead Co., 20 June 1920. *E.B. Payson & L.B. Payson 1730* (GH); 3) Canada, Saskatchewan, Jameson, 15 miles south of Regina, 15 June 1983. *G.F. Ledingham 7937* (MO).

## Results and discussion

*Eutrema salsugineum* (Pall.) Al-Shehbaz & Warwick, Harvard Pap. Bot. 10(2): 134. 2005. Described from: [NE Kazakhstan], ...circa lacus et lacunas sale praesertim amaro abundantes ad Irtin inter fortalitia Shelesenka et Jamyschewa. Lectotype (designated by German 2011: 52): [Kazakhstan, Pavlodar province, Irtysch valley], "*Sisymb. salsuginosum*. [29 May 1771, *P.S. Pallas s.n.*], Herb. Pallas. Herb. Fischer" (LE!)  $\equiv$  *Sisymbrium salsugineum* Pall., Reise Russ. Reichs 2: 466, 740, tab. V. 1773.  $\equiv$  *Arabidopsis salsuginea* (Pall.) N. Busch, Fl. Sibir. Orient. Extr. 1: 136. 1913.  $\equiv$  *Thellungiella salsuginea* (Pall.) O.E. Schulz in Engler, Pflanzenreich 86 (4, 105): 252. 1924.

As taxonomy/nomenclature is not the focus of the present study, only most frequently used synonyms are given here. For detailed synonymy, Schulz (1924: 252) and Tropicos (tropicos.org) can be consulted.

New locality: "Mexico: Est. Nuevo León, Los Enebros, Cerro el Potosi, Sierra Madre Oriental, saline-sodic soils, limestone. 24°52'35"N, 100°23'38"W, 1882 m a.s.l., 14 March 2010. *Marcus Koch s.n.*" (HEID 501412: <http://gartenbank.cos.uni-heidelberg.de/img/HEID501412>).

This is the first record of *Eutrema salsugineum* (and the genus) from Middle America (specifically Mexico) which shifts the southern limit of the distribution of the species



**Figure 1.** Habitat of Mexican accession of *Eutrema salsugineum* (Los Enebras, Cerro el Potosi, Sierra Madre Oriental). **A, B** General view **C–E** Closer look of *E. salsugineum* and co-occurring Brassicaceae species with herbarium numbers of respective specimens: **C** *Descurainia pinnata* (Walter) Britton s. l. (HEID 501409 to 501411) **D** *Eutrema salsugineum* (HEID 501412) **E** *Lepidium alyssoides* A. Gray (HEID 501414, 501415) **F** *Nerisyrenia linearifolia* (S. Watson) Greene (HEID 501413). All images were taken on March 14<sup>th</sup> 2010 by M.A. Koch.

ca. 1600 km to south-southeast from the closest, isolated fragment of the distribution area of the species, confined to Park County, Colorado (Weber 1966). This introduces a hitherto unrecognized disjunction within the New World part of *Eutrema salsugineum*'s range. In Sierra Madre Oriental the plants are found at elevations of ca. 1880 m a.s.l. in a semi-open habitat among halophytic, oak/*Juniperus* (*J. flaccida*)- and grasses-dominated vegetation on alkaline soil which fits well the ecological requirements of the species (Fig. 1). The habitat at the Mexican location of *E. salsugineum* is apparently natural and shows no obvious signs of anthropogenic modification. Having in mind the naturally disjunct biogeography of this species we consider it as a natural element of the flora of Sierra Madre Oriental which was overlooked by previous studies due to

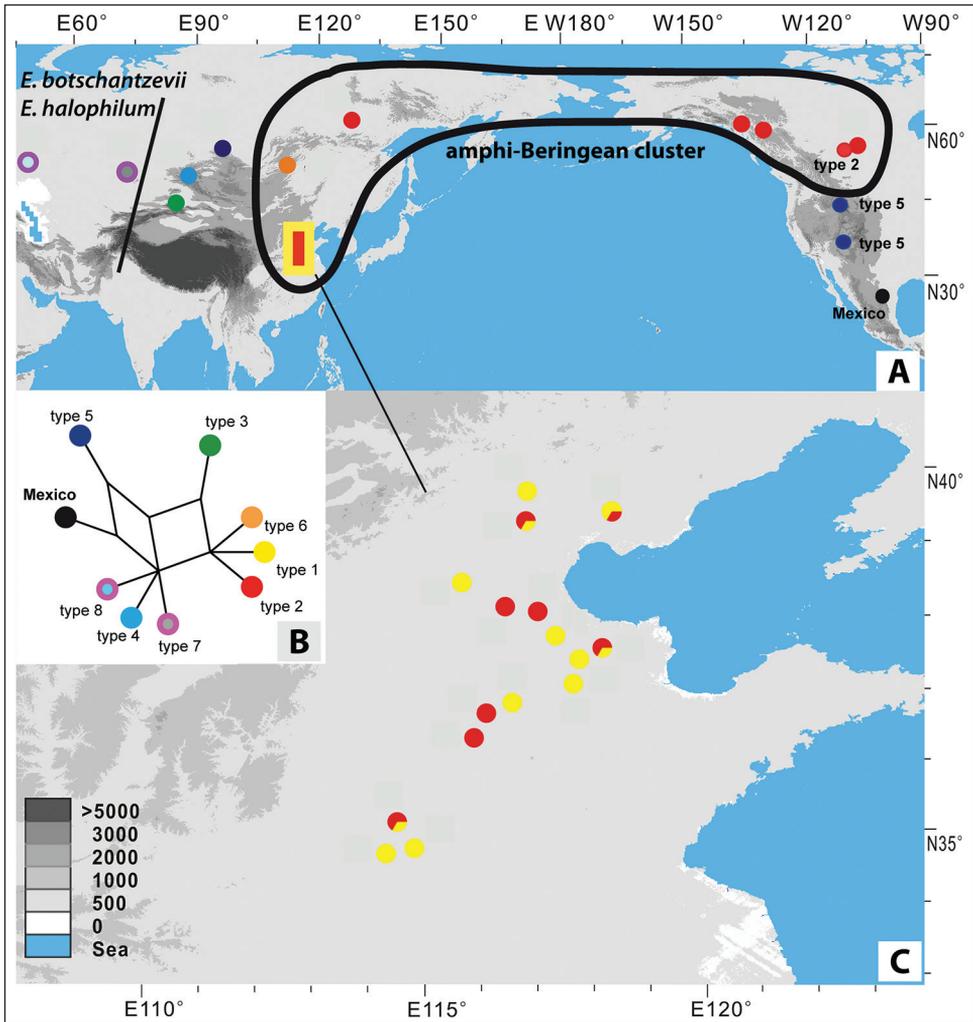
**Table 1.** Variable sites of the polymorphic cpDNA fragment *psbA-trnH* in *Eutrema salsugineum* and closely related species (modified from Wang et al. 2015). GenBank code of the Mexican haplotype is KY073435.

Species	Haplotype	<i>psbA-trnH</i>							
		43	108	129	156	162	208	277	304
<i>E. salsugineum</i>	H1	A	C	TGAATTT	A	TTTCTAT	A	-	C
	H2	A	C	TGAATTT	A	TTTCTAT	A	-	A
	H3	A	C	TGAATTT	A	ATAGAAA	A	-	A
	H4	A	C	TGAATTT	A	TTTCTAT	C	A	A
	H5	A	C	AAATTCA	G	ATAGAAA	A	A	A
	H6	A	T	TGAATTT	A	TTTCTAT	A	-	A
	Mexican	A	C	AAATTCA	A	TTTCTAT	A	A	A
<i>E. halophilum</i>	H7	A	C	TGAATTT	A	TTTCTAT	A	A	A
<i>E. botschantzevii</i>	H8	G	C	TGAATTT	A	TTTCTAT	A	A	A

its tiny habit, trivial appearance, early flowering time, and short, almost ephemeral life cycle. Results of the haplotype analysis (below) apparently confirm this conclusion.

DNA sequence data revealed a new plastid DNA haplotype of Mexican *E. salsugineum* indicating its genetic distinctiveness. The haplotype code is indicated in Table 1 summarizing also haplotypes detected earlier (Wang et al. 2015). The geographic distribution of the various accessions and their plastid haplotypes are given in Fig. 2. SplitTree analysis indicates that the Mexican plastid haplotype is most closely related to haplotype H5 (numbering following Wang et al. 2015), which was originally found only once in Tuva (South Central Siberia) (Fig. 2; Wang et al. 2015). However, the same H5 haplotype was found here in Montana and Colorado, largely representing the mountain regions of the western United States. As expected, the Canadian sample from Saskatchewan analyzed herein carries haplotype H2, which is widely distributed in NE China and the amphi-Beringian region (Fig. 2c).

In their recent phylogeographic study Wang et al. (2015) discovered extremely low level of genetic diversity throughout the whole distribution area of *E. salsugineum*, especially in NE Asia/America, apparently reflecting a very recent (ultimately Late-Pleistocene/very Early Holocene) range expansion. These authors suggested wind to be the main agent mediating the fast and long-distance dispersal of *E. salsugineum* and a single colonization of the New World by the species (Wang et al. 2015). However, a present-day fragmentary sublongitudinal distribution of *E. salsugineum* in the Rocky Mountains along with our finding that relevant populations carry a haplotype (H5) which is identical to a unique haplotype found in South Siberia, suggests that the North American continent has been colonized independently two times. This conclusion is supported by the fact that the newly described accession occurring in Mexico carries a haplotype which most likely derived directly from haplotype H5. This overlapping distribution pattern of an amphi-Beringian group carrying H1/H2 and a disjunct group (South Siberia versus western North America) carrying H5 plus the Mexican type can also be best explained by a first and older immigration of *E. salsugineum*



**Figure 2.** Distribution and relationships of *E. salsugineum* haplotypes. **A** distribution of accessions analyzed herein and in an earlier study (modified from Wang et al. 2015) **B** SplitsTree graph showing genetic relationships among the nine haplotypes (Median-joining network: Bandelt et al. 1999) **C** detailed distribution of haplotypes H1 and H2 in North-West China (modified from Wang et al. 2015).

from Asia predating the last glaciation. During the Last Glaciation Maximum the northern populations in America apparently went extinct and/or migrated southwards. If this scenario is correct, the last latitudinal shift of vegetation belts could enable the species to reach the Middle Americas and subsequently survive there in appropriate habitats at higher elevation. The wide amphi-Beringian distribution of H1 and H2 might reflect postglacial expansion as demonstrated by the phylogeography inferred by Wang et al. (2015) based on nuclear genes. This multiple immigration pattern of various temperate-cold and often draught adapted Brassicaceae taxa between East Asia

and the North America has been documented e.g. also for *Arabidopsis* and *Arabis* L. (Schmickl et al. 2008, 2010; Koch et al. 2010; Koch and Grosser 2017), highlighting the general significance of this spatio-temporal pattern.

## Conclusion

As shown herein, Asian-North American halophyte *Eutrema salsugineum* has a far more southern distribution in the New World than previously considered almost reaching the Northern Tropic. The character of the discovered habitat suggests native rather than human-mediated occurrence of the species in Mexico, a conclusion supported by molecular footprints. A *psbA-trnH*-based haplotype network demonstrates more complicated infraspecific structure and biogeographic history of *E. salsugineum* than previously thought and suggests its multiple invasions to the New World.

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# On the identity and typification of *Solanum brasilianum* Dunal (Solanaceae)

Suelma Ribeiro-Silva<sup>1</sup>, Sandra Knapp<sup>2</sup>, Carolyn E.B. Proença<sup>3</sup>

**1** Centro Nacional de Pesquisa e Conservação da Biodiversidade do Cerrado e Caatinga (CECAT), Instituto Chico Mendes; Prédio do Centro de Excelência do Cerrado; Jardim Botânico de Brasília, SMDB Cj 12, Lago Sul, Brasília, Distrito Federal, 70297-400, Brazil **2** Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom **3** Departamento de Botânica, Instituto de Ciências Biológicas, Universidade de Brasília, C.P. 4457 Brasília, Distrito Federal, 70910-900, Brazil

Corresponding author: *Suelma Ribeiro-Silva* ([suelma.ribeirosilva@gmail.com](mailto:suelma.ribeirosilva@gmail.com))

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## Abstract

*Solanum brasilianum* Dunal was described by Dunal in 1813 with reference only to an illustration in an 18<sup>th</sup> century work by Leonard Plukenet. The plate is difficult to interpret and no explicitly related specimens were available so the name *S. brasilianum* has long been regarded as “unresolved” and has never been used. Material matching the Plukenet plate was discovered in the herbarium of the University of Oxford (OXF) by Stephen Harris during his study of the English privateer William Dampier’s Brazilian collection. The specimen is referable to a common Brazilian *Solanum* that is a member of the Torva clade, *Solanum paniculatum* L., making *S. brasilianum* Dunal a heterotypic synonym. We lectotypify *S. brasilianum* here, and designate an epitype using the Dampier material from OXF.

## Keywords

Brazil, epitype, Leonard Plukenet, nomenclature, *Solanum*, William Dampier, William Sherard

## Introduction

Brazil is one of the hotspots of species richness for the mega-diverse genus *Solanum* L. (Solanaceae), with 272 accepted species (Flora do Brasil 2020, <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB14716>). Much recent work has gone into the resolution of names in the genus (e.g., Knapp et al. 2015), in preparation for the Flora do Brasil 2020 project, and only a few *Solanum* names remain without status in recent updates. Most of these are names attributed to the Italian naturalist Domenico Agostino Vandelli (1735-1816), who worked in Coimbra, Portugal in the mid-18<sup>th</sup> century, where many new plants from Brazil arrived to Europe (Guimarães 2016; see Solanaceae Source <http://www.solanaceaesource.org> or Flora do Brasil 2020 <http://floradobrasil.jbrj.gov.br/> for these names). Another of these unresolved names is Michel-Félix Dunal's (1813) *Solanum brasilianum*, whose identity we resolve here.

## *Solanum brasilianum* Dunal

Michel-Félix Dunal described *S. brasilianum* citing as his only material a figure (“t. 454, f. 4”) from Plukenet's (1705) *Amaltheum botanicum* (Dunal 1813: 239) corresponding to the polynomial “*Solanum Brasilianum*, folio integro mucronato glabro. Papas *Americanui* floribus in summitate caudis.” Plukenet's polynomial appeared in the Appendix to the *Amaltheum botanicum* (Plukenet 1705) along with other Brazilian and Australian plants based on the collections of William Dampier and Chinese plants sent by Jacob Cunningham (“cum multis aliis in hac appendice recensitis, quae ex Hollandia Nova, atque Brasilia a D. Dampier fibi allatae, necnon ex Insula Cheusan a laudatissimo viron Domino Jacobo Cunningham sunt trasnmissae”: Plukenet 1705: pp. 215). Dunal (1813) extended the polynomial with observations he took directly from the figure – “In figura: folia ovate, suminate, inermia; flores corymbosi; corolla pentagona; antherae divaricatae”. He placed *S. brasilianum* amongst his armed species of uncertain status, due to the scarce information available. Plukenet's (1705) figure is extremely diagrammatic, and has none of the diagnostic features that would enable placement in a species group of *Solanum* (Fig. 1); the polynomial however does allow its placement in *Solanum* by reference to its similarity with potatoes (“*Papas Americani*”).

Otto Sendtner, in *Flora brasiliensis* (Sendtner 1846: 112) also treated *S. brasilianum* as a name of uncertain status, and extended Dunal's (1813) description, still only using the Plukenet illustration as his basis for recognizing the species. He compared it to the Mexican species *S. glaucescens* Zucc. (see Clark et al. 2015) based on its curved spines at the leaf bases [“Figura refert RAMULUM (ex habitu fere *S. glaucescentis*) aculeo uno recurvo ad folii basin, FOLIIS petiolatis ovato-lanceolatis acuminatis basi acutiusculis 6-7 nervilis solitariis; INFLORESCENTIAM corymbiformem, subapicalem 8-floram, repetitodichotomam, PEDUNCULO COMUNI breviori quam secundarii; PEDICELLOS graciles; ALABASTRA oblonga obtusa; CALYCEM 5-fidum vel partitum? laciniis acutiusculis, COROLLAM magnam 5-angularem, ANTHERAS longas, angustas, lineares, corollam

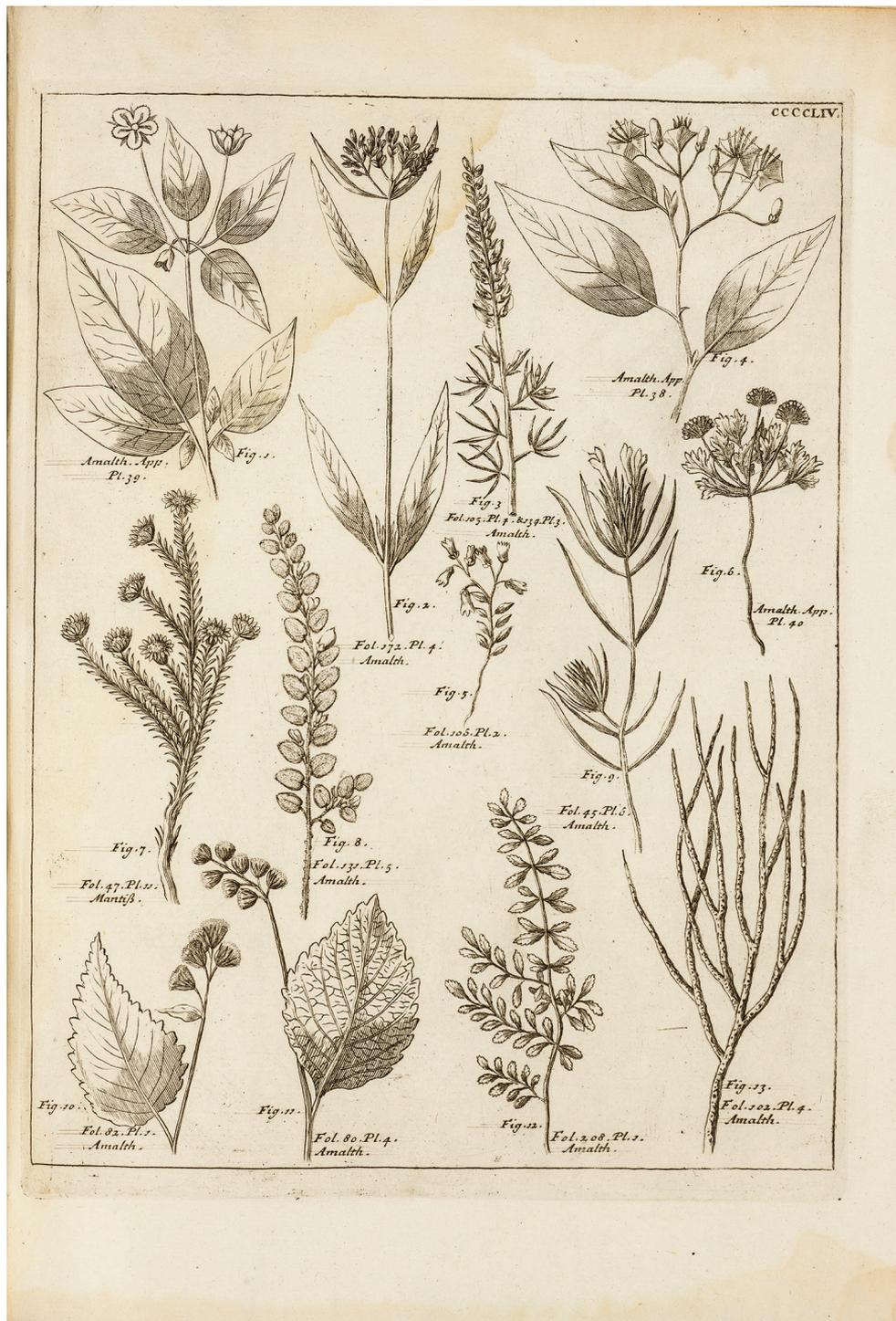


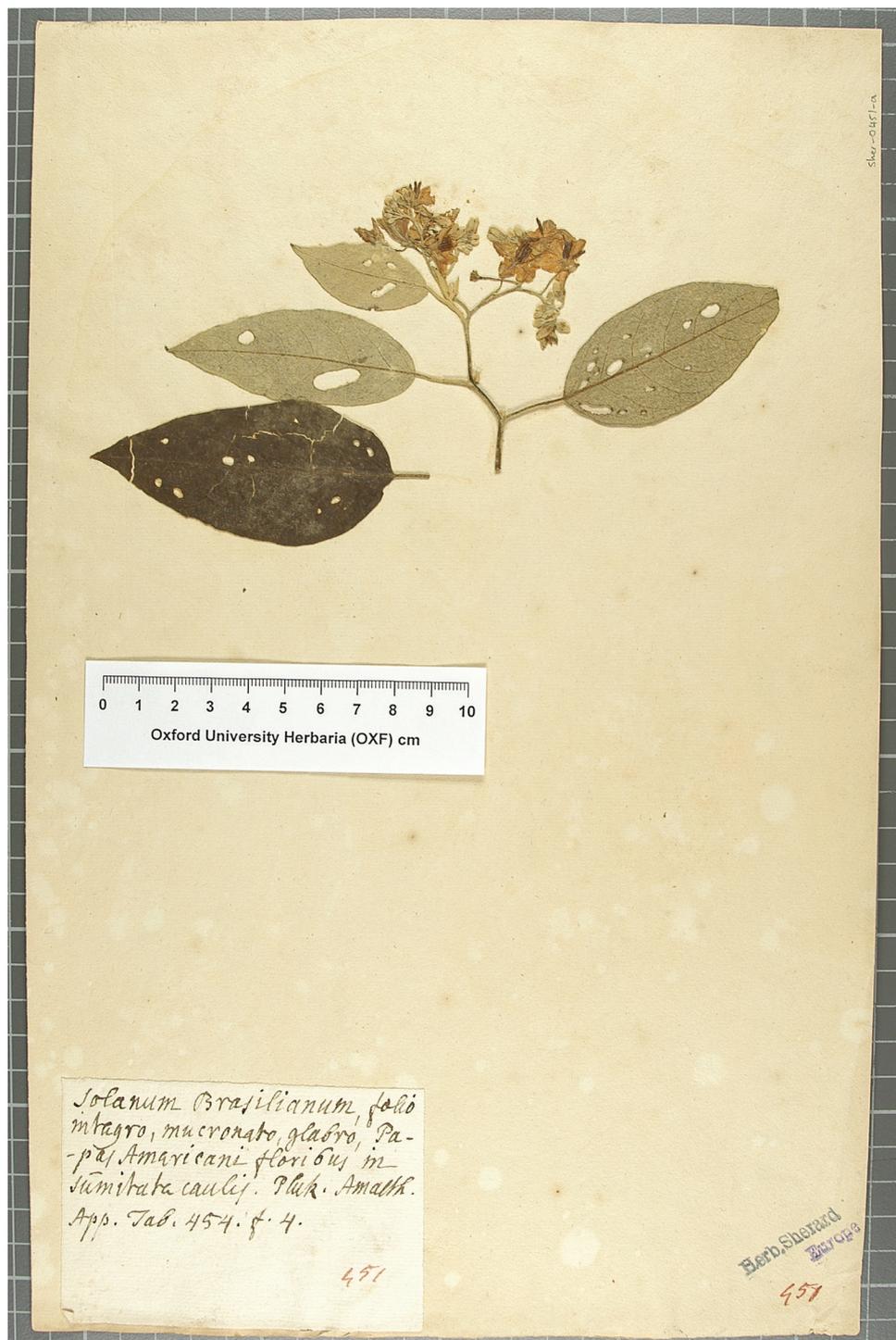
Figure 1. Plukenet, L. 1705. *Amaltheum botanicum* tab. 454, f. 4.

aequantas.”]. He misinterpreted the small axillary leaf shoots for curved spines; the plate is of an unarmed plant as Dunal later recorded in his treatment for the *Prodromus* (Dunal 1852: 372), placing it among unarmed species, but still of uncertain status.

### Dampier’s specimen

William Dampier was an English privateer and navigator who circumnavigated the globe three times between 1686 and 1710 (Preston and Preston 2005). He was a keen observer of nature and during his travels HMS *Roebuck* Dampier collected a handful of plant specimens from Australia and Brazil. These he gave to John Woodward, a professor at Gresham College, who later gave them to the botanist William Sherard, who in turn bequeathed them to Oxford University when he died in 1728 (Harris et al. 2016). They are now kept in the Sherardian Herbarium at OXF. During a study of these historical collections, Stephen Harris (OXF) found a specimen collected by William Dampier in Salvador, Bahia, during his time in Brazil in April–May 1699 (Harris et al. 2016). The sheet is a single specimen with consisting of a small branch with three attached leaves and a single leaf not attached the branch, but clearly belonging to it (Fig. 2). The specimen has a label with the polynomial taken from Plukenet (1705) “*Solanum Brasilianum, folio integro macronato glabro, Papas Americani floribus in summutate caulis. Pluk. Amalth. App. Tab. 454, f. 4*” in Sherard’s hand. The specimen is a good match for the illustration in Plukenet (1705) and is likely to have been the specimen from which that plate was made. Plukenet was based in London at the time the *Amaltheum botanicum* was begin prepared (Jarvis 2007), and he was shown Dampier’s specimens by his “learned friend [*Amicissimus & eruditus Vir*]” John Woodward (Plukenet 1705: 215).

The branch shown in plate 454, fig. 4 of Plukenet’s *Amaltheum botanicum* (1705) is completely unarmed, has leaves with entire margins that are markedly discolourous, and are adaxially glabrescent and abaxially densely stellate-tomentose. The small axillary buds above the lower leaves are likely the elements misinterpreted by Sendtner (1846) as spines at the leaf bases (see Fig. 2). The open flowers have anthers like those of *S. paniculatum* (and other members of the *Torva* clade sensu Stern et al. 2011) that characteristically spread when dry. These morphological characteristics clearly show that the specimen belongs to the taxon currently recognized as *S. paniculatum* L.. *Solanum paniculatum* was described by Linnaeus in his second edition of *Species Plantarum* (1762: 267) based on an illustration “*Jurepeba*” from Willem Piso’s *De Indiae utrisque re naturali et medici libri 14* (Piso 1658; see Knapp and Jarvis 1991). *Solanum paniculatum* is a common small tree or shrub occurring in all phytogeographical areas and regions of Brazil (Flora do Brasil 2020 <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB127325>) and northeastern Argentina and eastern Paraguay (<http://www.solanaceaesource.org>). It is also extremely variable morphologically, with leaf shapes in particular varying from deeply lobed to entire, even on an individual plant (see Fig. 16 in Knapp and Jarvis 1991). The Dampier specimen has four entire leaves, with gla-



**Figure 2.** Brazil. Bahia: Salvador, April-May 1699, W. Dampier “herb. Dampier no. 451” (epitype, designated here: OXF! [Sher-0451-a]).

brescent upper leaf surfaces bearing sparse stellate trichomes, and their shape is almost identical to distal portions of stems from a modern specimen (e.g. *Medeiros Neto 27* at VIES) of *S. paniculatum* from Bahia and, like Dampier's specimen, this very similar plant was collected with flowers in April.

Since Dunal (1813) did not have access to the Dampier specimen when he described *S. brasilianum* the Plukenet image (Fig. 1, upper right hand illustration, "Tab. 454, f. 4") is the only original material (McNeill et al. 2012) and we select it here as the lectotype. Because the illustration is so diagrammatic, and the Dampier specimen is clearly that from which it was prepared, we select the specimen "Herb. Dampier n. 451", collected by Dampier, as the epitype. Thus the discovery of this long-neglected specimen of *S. brasilianum* and its examination have allowed us to elucidate its true identity, and we here recognize *S. brasilianum* as a heterotypic synonym of *S. paniculatum*.

## Taxonomic treatment

***Solanum brasilianum* Dunal, Hist. Nat. Solanum 239. 1813.**

**Type.** Brazil. Sin. loc., no collector cited (lectotype, designated here: Plukenet, L. 1705. *Amaltheum botanicum* tab. 454, f. 4; epitype, designated here: Brazil. Bahia: Salvador, April-May 1699, *W. Dampier* "herb. Dampier no. 451"[OXF! (Sher-0451-a)]).

**Current accepted name.** *Solanum paniculatum* L.

## Acknowledgements

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# A new species of *Erythrostemon* (Leguminosae, Caesalpinioideae) from the western Río Balsas Depression, Mexico

Solange Sotuyo<sup>1</sup>, José Luis Contreras-Jiménez<sup>2</sup>, Gwilym P. Lewis<sup>3</sup>

**1** Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México. Circuito Exterior s/n, Ciudad Universitaria, Copilco, Coyoacán. A.P. 70-367 México, Distrito Federal. C.P. 04510

**2** Facultad de Arquitectura, Benemérita Universidad Autónoma de Puebla. 4 Sur 104. Col. Centro. CP 72000. Puebla, Puebla **3** Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U.K.

Corresponding author: Solange Sotuyo (jssotuyo@ib.unam.mx)

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## Abstract

A new legume species from a seasonally dry forest of the Western Río Balsas Depression, in the states of Guerrero and Michoacán, Mexico, *Erythrostemon guevarafeferii*, is herein described and illustrated. The new species shows morphological affinities with *E. hintonii*, from which it is distinguished in having fewer leaflets per pinna, mature leaflets disposed toward the upper half of the pinnae rachises, long inflorescences on curved slender peduncles, abundant red glands on its flowers and inflorescences, and its fruit glabrous with red stipitate glands at maturity. A taxonomic key to the Río Balsas Depression species of *Erythrostemon* is included.

## Resumen

Una nueva especie de leguminosa de la Depresión Occidental del Río Balsas en los estados de Guerrero y Michoacán, *Erythrostemon guevarafeferii*, se describe e ilustra. La nueva especie muestra afinidades morfológicas con *E. hintonii*, de la que se distingue por tener menos pinnas, folíolos maduros glabros dispuestos hacia la mitad superior de las pinnas, las inflorescencias largas sobre pedúnculos delgados que se curvan y flores con abundantes glándulas; legumbre glabra o con glándulas estipitadas rojas cuando esta madura. Se incluye una clave taxonómica de las especies de *Erythrostemon* que habitan en la Depresión del Río Balsas.

## Keywords

*Caesalpinia* group, Leguminosae, *Erythrostemon*, Fabaceae, Neotropics

## Introduction

*Erythrostemon* was re-circumscribed by Gagnon et al. (2016). The neotropical genus currently includes a total of 31 species of woody shrubs or small to medium-sized trees. Species distributions follow a bicentric amphitropical distribution pattern in México, Central America and the Caribbean, Brazil, Argentina, Bolivia, Chile and Paraguay (Lewis 1998; Gagnon et al. 2013; Gagnon et al. 2016). They grow in a wide range of habitats including seasonally dry tropical forests, caatinga vegetation, deserts, yungas-puna transition zones, and chaco-transition forests.

Species of *Erythrostemon* are distinctive by various combinations of several morphological traits (a reference for this cited here). Leaflets typically are either eglandular or have conspicuous black sessile glands along their margin that renders the margins slightly crenulated. Flowers have sepals that are ovate-lanceolate and their petals bending and either yellow, red, pink or orange, the corolla sometimes laterally compressed. The androecium and gynoecium are free from the calyx and the ovary is eglandular or covered in gland-tipped trichomes. Legumes are typically oblong-elliptic pods with papery to slightly woody valves that are chartaceous or slightly woody, glabrous to pubescent, eglandular or with stipitate glands.

During a revision of *Caesalpinia* sensu lato in Guerrero and Michoacán, several specimens identified in herbaria as *Caesalpinia hintonii* Sandwith (a species recently transferred to the genus *Erythrostemon*, Gagnon et al. 2016) proved to be morphologically distinct. Taking into account the above morphological diagnostic characters of *Erythrostemon*, a detailed study indicated that these specimens belong to that genus, although they do not match the description of any previously described species. The overall morphology of the new taxon most closely resembles *Erythrostemon hintonii* (Sandwith) E. Gagnon & G.P. Lewis, with which it shares a similar distribution area in the Río Balsas Depression. The new species is herein described as *Erythrostemon guevarafeferii*.

## Taxonomy

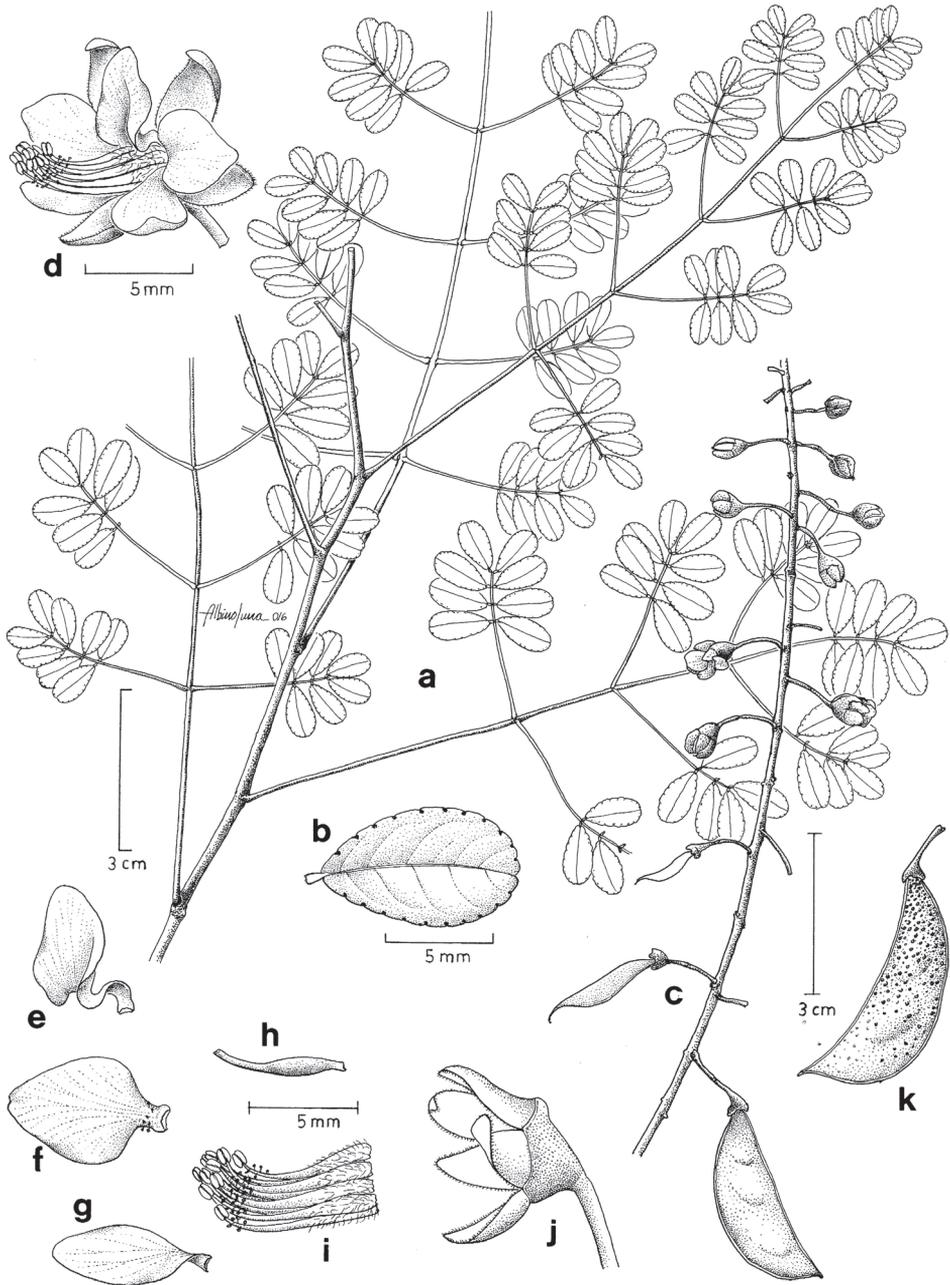
*Erythrostemon guevarafeferii* J.L.Contreras, S.Sotuyo & G.P.Lewis, sp. nov.

urn:lsid:ipni.org:names:77159617-1

Figure 1

**Type.** México, Michoacán. Cerca de la cortina de la presa El Infiernillo J.L. Contreras 3111 (Holotype: MEXU; Isotypes: FCME, K, MEXU).

*Erythrostemon hintonii* affinis sed glabra, structuris floralibus omnino glanduliferis, foliis minoribus cum minus foliolis fasciculatus in dimidio superiore rhachidis pinnae, floribus brevioribus, sepalis laete ochraceis et petalis salmoneis, pedicellis articulatis in dimidio superiore longitudinis, legumine omnino glabro et stipitatis glandulis rubris obducto. Etiam differt inflorescentias arcuatas et pendulas cum pedicellis florum gracilibus, fere horizontalibus vel reflexis, tortis itaque floribus resupinatis.



**Figure 1.** *Erythrostemon guevarafereii*, **a** bipinnate leaves **b** leaflet upper surface showing marginal glands **c** inflorescence with immature fruits developing at base **d** flower **e** adaxial (median) petal **f** lateral petal **g** abaxial petal **h** gynoecium **i** stamens **j** calyx **k** fruit showing the red stipitate glands as black dots. (**a–j** drawn from Contreras-Jiménez et al. 3111, holotype MEXU **k** from Contreras-Jiménez 2860). Drawn by Albino Luna.

Similar to *Erythrostemon hintonii*, but glabrous, all flower structures glandular, leaves smaller with fewer leaflets, flowers shorter, sepals light yellow-ochre and petals salmon coloured, pedicels articulated at, or above, their middle, legume completely glabrous and with stipitate red glands. Also differing in the curved and/or pendulous inflorescences with the flowers on slender, horizontal or reflexed, twisted pedicels that render them resupinate.

**Description.** Small tree or shrub, 2–6 m tall, bark grey pruinose, exfoliating, young branches reddish grey pruinose. Leaves bipinnate, (7.5–) 10–20 (–22) cm long; stipules triangular-acuminate, caducous, 2–3 × 1.2–1.5 mm, margin with red stipitate glands, white hairy on both surfaces; petiole (2–) 3.0–6.5 (–7.3) cm long, pubescent or glabrescent when mature; rachis (3–) 5.0–14.5 (–15.7) cm long, indumentum similar to that of the petiole; pinnae (5–) 7–13 per leaf, (1.6–) 2–6 (–7.7) cm long, densely pubescent when young, glabrescent when mature; leaflets (3) 4–7 (–10) jugate, clustered on the upper half of the pinnae rachises, obovate, elliptic or oblong-elliptic (6–) 10–20 (–25) × (4–) 5–11 (–13) mm, base rounded, slightly oblique, margin entire and lacking glands, or with sunken black punctate glands that render the margin slightly crenulate, apex obtuse to rounded, pubescent or glabrescent at maturity. Inflorescence an erect or pendulous (the peduncles curved downwards), terminal or axillary raceme or panicle (with few branches near the base), (6–) 10–36 cm long, densely white pubescent, and with red glands; bracts ovate-caudate, caducous, (2.5–) 3.2–5.0 (–5.7) × (1–) 1.3–2.0 (–2.3) mm, margin with or without glands, densely white pubescent on both surfaces; pedicels slender, erect-patent, (6–) 7.5–11.0 (–16.5) mm long, articulated at or above the middle, densely white pubescent, sometimes twisted, so that the flowers are resupinate (although then presented with the median petal uppermost on the pendulous inflorescences). Calyx light yellow-ochre, densely pubescent, tube obliquely obconic, laterally compressed, (4.3–) 4.7–6.0 × (2.1–) 2.5–3.5 (–4) mm; adaxial sepals ovate to oblong-ovate, 5.5–7.0 × 2.5–4.1 mm, slightly concave, the lateral sepals oblong-ovate, 5.4–7.0 mm × 2.7–4.0 mm; abaxial sepal cymbiform, (5.7–) 6–7.2 (–7.4) × (3.6–) 3.8–5.0 mm, all sepals with an entire margin, glandular ciliate and with an acute apex, puberulent on adaxial surface; petals salmon-coloured, clawed; adaxial petal ovate, 5.2–7.5 × 3.5–5.5 mm, base cordate, margin entire, apex obtuse, rounded, with stipitate glands near the claw apex on the abaxial surface, pilose on the adaxial surface; claw 1.8–3.0 mm long, sigmoid curved, ciliate, pilose and glandular-stipitate on abaxial surface or glabrous and sparsely stipitate-glandular; lateral petals ovate, 5.6–7.5 (–8) × 4.2–6 (–6.5) mm, base obtuse, margin glandular ciliate up to  $\frac{1}{5}$  of its length, apex rounded or obtuse, stipitate-glandular on abaxial surface, the abaxial petals ovate (6–) 6.5–8.5 × 3.7–5.5 (–5.7) mm, base oblique, margin entire, glandular ciliate from the base up to  $\frac{1}{5}$  of their length, apex obtuse, the claw ciliate and pilose on its abaxial surface; stamens curved, filaments (6.5–) 7.5–9.5 (–10) mm long, flattened at the base, densely villous to  $\frac{3}{4}$  of their length, the upper third with lime green stipitate glands; anthers oblong-elliptic, (1.2–) 1.3–1.8 × (0.8–) 0.9–1.2 (–1.3) mm, erect at anthesis; ovary

(1.7–) 2–3 (–3.5) mm long borne on a stipe 0.5 mm long, densely sericeous and with green cupuliform glands (or these absent); style curved, of different lengths in individual flowers, either short, 2.5–3.5 mm long, or well developed and 4.0–6.5 mm long, pilose for ½ of its length from base; stigma porate laterally; ovules 2 (–3) per ovary. Legume falcate, (3.7–) 4.3–5.7 × 1.1–1.7 cm, chartaceous, brown-yellow to vinaceous, densely to sparsely pubescent or glabrous when mature, with red stipitate glands or these glands absent, sutures densely pubescent, elastically dehiscent; seeds 1–2 (–3) per fruit, obovate, (8.6–) 9.5–10.5 (–11) × 7.5–9.6 × (1.7–) 1.9–2.2 (–2.4) mm, olive-brown, nitid.

**Habitat.** Seasonally dry tropical forest on rocky slopes, locally common in secondary vegetation along roads, on alluvial soils near seasonal or permanent streams.

**Distribution and phenology.** Known only from the western region of the Río Balsas Depression, in the states of Guerrero and Michoacán. Flowering from February to April and in fruit from February to May.

Selected specimens examined. MÉXICO. **Michoacán:** Municipio de Arteaga: El Infiernillo, cerca de la cortina de la presa: *Nuñez & Silva 3905* (MEXU); *J.C. Soto 1331 & S. Zárate* (MEXU); *J.C. Soto 3694* (MEXU); *Sotuyo et al. 41, 46, 47, 48* (K, MEXU); 23 km por el camino a Infiernillo a partir de la carretera Apatzingan-Lázaro Cárdenas: *J.L. Contreras 2060, 2838* (MEXU). Municipio de Nocupétaro: San Antonio de los Muertos; *J.C. Soto 3905 & G. Silva* (MEXU). **Guerrero:** Municipio de la Unión: 5 km al S de Colmeneros, camino a Coahuayutla: *J.L. Contreras 2371, 2372* (FCME); Cerro Prieto, 12 km al E de la Garita: *J.L. Contreras 2388* (FCME); Zihuatanejo, 85 km aprox. NW, on road 22 km to N of La Unión and 7 km to N of Las Juntas del Río towards Santa María: *D.J. Macqueen & A. Nileshwar 446* (K).

**IUCN Red List category.** We recommend that *Erythrostemon guevarafeferii* be given a conservation assessment of Vulnerable [VU (B1b-iii)], in accordance with IUCN (2012) categories and criteria. The extent of occurrence (EOO) of *E. guevarafeferii* is estimated to be over 2424.18 km<sup>2</sup>, well below the 20,000 km<sup>2</sup> upper limit for Vulnerable status under criterion B1, but its area of occupancy (AOO) is estimated to be less than 10 km<sup>2</sup> (the limit for Endangered status under criterion B2). The species is currently known from three discontinuous populations in the states of Michoacán and Guerrero, these separated by differing habitat type, human settlement and agricultural land. *Erythrostemon guevarafeferii* is known in only one protected area, the Reserva de la Biosfera Zicuirán-Infiernillo in Michoacán. The preferred habitat of the species is potentially threatened by future settlement and agricultural activities, as well as by environmental problems associated with drug trafficking organizations.

**Etymology.** The species epithet is dedicated to Fernando Guevara Fefer who recently passed away. Friend, botany teacher and researcher at the Universidad Michoacana de San Nicolás de Hidalgo, he was interested in the genus *Bursera* and in floristic and vegetation studies within Michoacán, particularly in the Infiernillo region where the type specimen was collected.

## Discussion

*Erythrostemon guevarafeferii* differs from *Erythrostemon hintonii* in being glabrous at maturity and by sometimes having glands on floral structures and fruits. It has smaller leaves with (5–) 7–13 pinnae per leaf and leaflets (3–) 4–7 (–10) jugate, these on the upper half of the pinna rachis. Flowers are smaller (1.2–1.6 cm long, including the calyx) with light yellow-ochre sepals and salmon-pink petals, its pedicels are articulated at or above their middle. Its legume is glabrous when mature and sometimes has red stipitate glands.

*Erythrostemon hintonii* differs by having leaves with 3–9 pinnae per leaf and leaflets 4–6 jugate, these distributed along the length of the pinna rachis, flowers 2 cm long (including the calyx) with red-purple sepals and purple-red petals, pedicels that are articulated near the base of the calyx tube, and a legume that is pubescent and has dark red-brown sessile glands. Some individual plants of *E. guevarafeferii* have glandular fruits while others in the same locality do not. The species is characterized by its arched and pendulous inflorescences, with slender, nearly horizontal pedicels (or these reflexed and sometimes twisted, so that the flowers are resupinate). Resupinate flowers on a pendulous inflorescence renders them, once again, in their usual position with the median (standard) petal uppermost.

Field and laboratory observations reveal two kinds of flower, with either a short or long pistil, as also observed in *Erythrostemon epifanioi* (J.L. Contr.) E. Gagnon & G.P. Lewis (as *Caesalpinia epifanioi* J.L. Contr.; Lewis, 1998) and in another legume genus, *Tylosema esculentum* (Burch.) A. Schreib., which displays functional heterostyly (Hartley et al. 2002). Flowers with short pistils are functionally male and flowers with long pistils are hermaphrodite. We hypothesise that the occurrence of both flower forms in the same inflorescence ensures that not too many flowers on each inflorescence set fruit (which would put a strain on maternal resources, as well as mechanically over-loading the peduncle) and that pollinators continue to move pollen throughout or between populations of the species, thus promoting cross-pollination. Andromonoecy, with a labile sex change of flowers from hermaphrodite to functionally male (the gynoecium development is suppressed in flowers higher up an inflorescence only if the lower flowers are successfully pollinated and fruits are set) has been observed in *Erythrostemon calycina* (Benth.) L.P. Queiroz (as *Caesalpinia calycina* Benth.) in Brazil (Gibbs et al. 1999).

## Taxonomic key to the species of *Erythrostemon* in Rio Balsas Depression

- 1 Shrubs or herbaceous plants; leaflets without black glands along margin; flowers deflexed; glandular stamen filaments curved, twice the length of the petals; legume 4.7–7.1 cm long; Sierra Madre del Sur, Guerrero and Oaxaca, 1400–2000 m elevation ..... *E. laxis*
- Trees; leaflets with black glands along margin; flowers reflexed; stamen filaments falcate or curved, equalling the length of the petals; legume 3–6 cm long; seasonally dry forest of the Río Balsas Depression, 100–1200 m elevation..... 2

- 2 Leaves with 3–5 pairs per pinnae, leaflets 2–6 pairs per pinna; inflorescence a raceme, on a short woody brachyblast..... **3**
- Leaves with 7–13 pairs per pinnae, leaflets 4–11 pairs per pinna; inflorescence a terminal or axillary raceme or panicle, peduncles branched near base ..... **4**
- 3 Leaflets 2–3 pairs per pinna; pedicels 6.5–12.5 mm long, pubescent; eastern region of Río Balsas Depression (Ozomatlán, Guerrero)..... *E. epifanioi*
- Leaflets 4–6 pairs per pinna; pedicels c. 7 mm long, densely stipitate-glandular; Valle de Tehuacán-Cuicatlán (Puebla and Oaxaca)..... *E. melanadenius*
- 4 Pedicels articulated below the middle; petals yellow; leaflets oblong-elliptic....  
..... *E. macvaughii*
- Pedicels articulated at or above the middle; petals pink, red or scarlet; leaflets ovate or oblong..... **5**
- 5 Fruit with red cupuliform glands or these absent; standard petal red or salmon coloured, stamen filaments pubescent on basal  $\frac{1}{2}$  to  $\frac{3}{4}$ , sometimes stipitate-glandular; western part of Río Balsas Depression (Guerrero and Michoacán).. **6**
- Fruit with green pixie-cup (or doughnut-shaped) glands; standard petal pale pink with a red blotch at the lamina base on the inner surface; stamen filaments with green glands; western Río Balsas Depression (Guerrero, Oaxaca and Puebla)..... *E. oyamae*
- 6 Leaflets obovate to elliptic, inserted along the pinna rachis; bracts erect or incurved; stamen filaments 13–15 mm long; legume with red cupuliform glands; seasonally dry forest in Guerrero and Michoacán ..... *E. hintonii*
- Leaflets oblong-elliptic, inserted on the upper half of the pinna rachis; bracts ovate-caudate; stamen filaments 6.5–10 mm long; legume with or without red cupuliform glands; Infernillo region in the Río Balsas Depression (Guerrero and Michoacán)..... *E. guevarafeferii*

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# Synoptic taxonomy of *Cortaderia* Stapf (Danthonioideae, Poaceae)

Daniel Testoni<sup>1</sup>, H. Peter Linder<sup>2</sup>

**1** Herbario BBB, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, CP-8000 Bahía Blanca, Argentina **2** Department of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland

Corresponding author: Daniel Testoni ([daniel.testoni@uns.edu.ar](mailto:daniel.testoni@uns.edu.ar))

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## Abstract

*Cortaderia* (Poaceae; Danthonioideae) is a medium-sized genus of C3 tussock grasses, widespread in the temperate to tropic-alpine regions of South America. It is particularly important in the subalpine and alpine zones of the Andes. We revised the classification of the genus, and recognize 17 species grouped into five informal groups. We describe one new species, *Cortaderia echinata* H.P.Linder, from Peru. We provide a key to the groups and the species, complete nomenclature for each species including new lectotypes, and notes on the ecology, distribution and diagnostic morphological and anatomical characters.

## Keywords

Leaf anatomy, key, nomenclature, South America, taxonomy

## Introduction

*Cortaderia* Stapf (Danthonioideae, Poaceae) is best known for the pampas-grass, *Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn., which is globally cultivated as a garden ornamental (Grounds 1979), but which is also an aggressive invader in many warm-temperate regions (Gadgil et al. 1990; Harradine 1991; Lambrinos 2001;

Okada et al. 2007; Robinson 1984). However, the genus is also a major component of the temperate C3 grasslands of South America, from Tierra del Fuego in the south to Venezuela in the north, and from the Atlantic coastal mountains near Rio de Janeiro to the Equadorian Andes, and from sea level at the southern extreme to over 4500 m at the equator.

The genus was erected by Stapf (1897), initially to include only the large tussocks allied to *Cortaderia selloana*, which until then had been classified under *Gynerium* Bonpl. In the first decades of the 20<sup>th</sup> century Pilger (1906) and Hackel (in Dusén 1909) transferred four species from *Gynerium* into *Cortaderia*. During the second half of the last century five new species were described by Swallen (1948; 1956). Recently, Linder et al. (2010) segregated five New Zealand species into *Austroderia* N.P.Barker & H.P.Linder and a New Guinean species into *Chimaerochloa* H. P. Linder on the basis of morphology and molecular data, and included *Lamprothyrsus* Pilg., a genus of two species distributed in South America, in *Cortaderia*.

The taxonomy of the genus has never been reviewed in total, from a global perspective. The *Cortaderia selloana* group was revised by Acevedo de Vargas (1959) and Testoni and Villamil (2014), and *Lamprothyrsus* by Conert (1961), Bernardello (1979) and Testoni (2016). In addition, there have been numerous regional treatments in diverse South American floras, including Ecuador, Peru and Bolivia (Hitchcock 1927), Patagonia (Nicora 1978), Peru (Tovar 1993), Argentina (Astegiano et al. 1995), Ecuador (Laegaard 1997), Bolivia (Renvoize 1998) and Venezuela (Davidse 2004).

There are several taxonomic problems in the genus. Species delimitations of the three species closely related to *C. selloana* present a major challenge, as already noted by Stapf (1897). These have recently been revised by Testoni and Villamil (2014), based on field and herbarium studies. Similar species delimitation problems are also evident in some of the Andean tussock species. There are several very local species, apparently known only from the type localities – the validity of these species could be questioned. As well, there are several apparent segregates from currently accepted species; these may be due to “over-splitting” of taxa. Finally, in 2008 Paul Peterson and Rob Soreng collected a putatively new species of *Cortaderia* from Peru, which needs a formal description.

The reproductive biology of *Cortaderia* is complex, with apparently hermaphrodite, dioecious, gynodioecious and apomictic species. Connor (1965) showed that gynodioecy, rather than dioecy, is the common and widespread condition in *Cortaderia*. The variation in reproductive structure in the genus was explored in detail in Connor (1973). He showed several syndromes. Only *C. sericantha* (Steud.) Hitchc. was monomorphic, with the reproductive organs in the male and bisexual plants scarcely differentiated. Testoni and Villamil (2014) established that species of the Selloana group (Sect. *Cortaderia* sensu Conert 1961) are gynodioecious and apomictic (e.g. *C. selloana* can form extensive clonal populations, one of which gave rise to *C. selloana* subsp. *jubata* (Lemoine) Testoni & Villamil) or only apomictic species (e.g. *C. speciosa*

(Nees & Meyen) Stapf), whereas the species in the rest of the genus are dimorphic and dioecious, except for *C. hieronymi* (Kuntze) N.P.Barker & H.P.Linder, which Connor and Dawson (1993) showed to be apomictic. The genetics of the gynodioecism was explored for *C. selloana* by Connor and Charlesworth (1989), who showed that it was probably controlled by a male-sterility gene, expressed in the female-only plants of the species. The reproductive system influences the patterns of variation in the species, and might account for the taxonomic complexity of some species.

The phylogeny of *Cortaderia* is as yet incompletely known. Phylogenetic analyses have been published by Barker et al. (2003) and Pirie et al. (2008), based on which the New Zealand and New Guinean species were separated into the genera *Austroderia* and *Chimaeorochloa*, whereas the South American *Lamprothyrsus* was included in the genus *Cortaderia* (Linder et al. 2010). *Cortaderia* in its current circumscription is monophyletic, and most closely related to the “danthonioid” clade of the Danthonioideae (Pirie et al. 2009).

This paper presents a critical review of the species limits in *Cortaderia* based on leaf anatomical features, investigation of field populations and the study of herbarium specimens. We also clarify the nomenclature and typification of all names in the genus, and provide a key to the species. A descriptive monograph of the whole subfamily is in preparation, and full descriptions will be published in that account, as well as the full lists of specimens examined.

## Materials and methods

The morphological descriptions were compiled from the analysis of the available herbarium material at B, BA, BBB, CONC, CORD, K, LOJA, M, NY, P, RB, SI, SGO, QCA, US, W, Z and ZT (acronyms follow Thiers (continuously updated)). Where sufficient material was available, spikelets were dissected, sketched and measured. The lemmas were mounted in glycerine, and drawn using a camera lucida. Anatomical investigation was based on leaf fragments of herbarium specimens (Table 1). Fragments ca. 1 cm long, from near the middle of blade, were first softened and reconstituted in warm, soapy water for 20–40 min. Transverse sections were hand-cut at 20–40  $\mu\text{m}$ , and epidermal scrapes were prepared of the abaxial surface. Sections and scrapes were differentially stained with a combination of Safranin Red and Alcian Blue (Tolivia and Tolivia 1987), dehydrated in an alcohol series, and mounted in Histomount. In addition, for *Cortaderia selloana*, *C. speciosa* and *C. vaginata* samples were fixed in formalin-acetic acid-alcohol, dehydrated in an ethyl alcohol-tertiary butyl alcohol series and embedded in Paramat. The study plant sections (20  $\mu\text{m}$ ) were stained with safranin-fast green and mounted in Canada balsam. The anatomy of each species was described using the characters and character states proposed by Ellis (1976; 1979).

The assignation of holo- and lectotype status follows the analysis and recommendations of (McNeill 2014).

**Table 1.** Vouchers for anatomy.

Species	Voucher	Country
<i>araucana</i>	Testoni, D., 656 (BBB)	Chile
<i>araucana</i>	Werdermann, E., 1360 (K)	Chile
<i>bifida</i>	Beck, S.G., 1816 (US)	Bolivia
<i>bifida</i>	Renvoize, S.A.; Cope, T.A.; Beck, S., 4202 (K)	Bolivia
<i>bifida</i>	Smith, D.N. & Canabilla, J., 7167 (US)	Peru
<i>bifida</i>	Testoni, D., 477 (BBB)	Ecuador
<i>boliviensis</i>	Beck, S.G., 21266 (K)	Bolivia
<i>boliviensis</i>	Beck, S.G., 11273 (K)	Bolivia
<i>boliviensis</i>	Renvoize, S.A., 5342 (SI)	Bolivia
<i>columbiana</i>	Schultes, R.E., 7251 (K)	Venezuela
<i>columbiana</i>	Schultes, R.E., 7226 (K)	Colombia
<i>columbiana</i>	Schulz, J.P. & Rodri, L., 318 (US)	Venezuela
<i>egmontiana</i>	Green, S.W., 42385 (K)	Falkland/Malvinas
<i>egmontiana</i>	Moore, D.M., 1697 (K)	Argentina
<i>egmontiana</i>	Peterson, P.M., Soreng, R.J. & Refulio-Rodriguez, N., 17465 (US)	Argentina
<i>egmontiana</i>	Pisano, E. & Henriquez, M., 8802 (CONC)	Chile
<i>egmontiana</i>	Testoni, D., 634 (BBB)	Argentina
<i>echinata</i>	Peterson, P.M. & Soreng, R.J., 21587 (Z)	Peru
<i>hapalotricha</i>	Laegaard, S., 53805 (K)	Ecuador
<i>hapalotricha</i>	Renvoize, S.A. & Laegaard, S., 5023 (K)	Peru
<i>hieronymi</i>	Asplund, E. 11971 (K)	Peru
<i>hieronymi</i>	Garcia, Beck, S.G. & Michel 563 (K)	Bolivia
<i>hieronymi</i>	Testoni, D., 386 (BBB)	Argentina
<i>hieronymi</i>	Testoni, D., 496 (BBB)	Ecuador
<i>modesta</i>	Carauta, P., 927 (RB)	Brazil
<i>modesta</i>	Chase, A., 8288 (US)	Brazil
<i>modesta</i>	Glaziou, A.F., 17913 (K)	Brazil
<i>modesta</i>	Luetzelburg, 6368 (M)	Brazil
<i>nitida</i>	Laegaard, S., 53121 (K)	Ecuador
<i>nitida</i>	Testoni, D. 516 (BBB)	Ecuador
<i>nitida</i>	Soderstrom, T.R., 1350 (K)	Colombia
<i>nitida</i>	Steyermark, J. & Dunsterville. G.C.K., 101134 (US)	unknown
<i>roraimensis</i>	Farney, C. 885 (RB)	Brazil
<i>roraimensis</i>	Magire, B., Pires, J.M. & Magire, C.K., 60448 (US)	Venezuela
<i>roraimensis</i>	Steyermark, J., 103836 (US)	Venezuela
<i>speciosa</i>	Renvoize, S.A., 5341 (K)	Bolivia
<i>selloana</i> ssp. <i>selloana</i>	Linder, H.P., s.n.	South Africa
<i>selloana</i> ssp. <i>selloana</i>	Villamil, CB., 11738 (BBB)	Uruguay
<i>selloana</i> ssp. <i>jubata</i>	Testoni, D., 435 (BBB)	Ecuador
<i>sericantha</i>	Laegaard, S., 55066 (K)	Ecuador
<i>sericantha</i>	Laegaard, S., 55728 (P)	Ecuador
<i>sericantha</i>	Ramsay, P.M.; Merrow-Smith, P.J., 967 (K)	Ecuador
<i>sericantha</i>	Testoni, D., 438 (BBB)	Ecuador
<i>speciosa</i>	Renvoize, S.A.; Flores, G.; Peca, C., 5272 (K)	Bolivia
<i>speciosa</i>	Testoni, D., 644 (BBB)	Chile
<i>vaginata</i>	Reitz, P.R., 2672 (US)	Brazil
<i>vaginata</i>	Smith, L.B., Reitz, P.R. & Klein, R., 7761 (B)	Brazil
<i>vaginata</i>	Zanin 1654 (BBB, FLOR)	Brazil

## Taxonomic treatment

### *Cortaderia* Stapf, Gard. Chron. ser. 3. 22: 378 (1897) nom. cons.

*Cortaderia* Stapf, Gard. Chron. ser. 3. 22: 378 (1897) nom. cons. Type species: *C. selloana* (Schult.) Asch. & Graebn. (Syn. Mitteleur. Fl. 2(1): 325. 1900) (Basionym *Arundo selloana* Schult.).

*Moorea* Lem., Ill. Hort. 2: Misc. 14 (1855) nom. rej., non Rolfe (1890). Type species: *M. argentea* (Nees) Lem. (*C. selloana*).

*Lamprothyrus* Pilg., Bot. Jahrb. Syst. 37 (Beibl. 85): 58 (1906). Type species: *L. hieronymi* (Kuntze) Pilg. (Basionym *Triraphis hieronymi* Kuntze).

**Description.** Gynodioecious, dioecious, hermaphrodite or apomictic perennials, ranging from rounded vegetable hedgehogs less than 0.5 m tall to erect 4 m tall tussocks; innovations intravaginal; spreading stolons rare. Leaf sheaths variable: persisting intact, or fragmenting transversely, or decaying into a tangled mass of fibres, or occasionally persisting as burnt-off sheaths; glabrous or more rarely covered in a dense indumentum. Ligule of one or many rows of cilia, to 5 mm long. Leaf blades to 2 m long, tough, expanded, rolled or folded, occasionally pungent, usually persistent but occasionally disarticulating above the ligule, sometimes with an adaxial weft of hairs directly above the ligule; margins sometimes roughly scabrid and cutting. Inflorescences paniculate, sometimes compact but usually plumose, to 1 m long, many-spikeleted, pedicels and pulvini glabrous, scabrid or villous. Spikelets to 30 mm long, with 2–10 florets, disarticulating above the glumes, male spikelets usually less hairy than female spikelets and glabrous in the Selloana group; glumes glabrous, often papery or membranous, 4–30 mm long, usually 1-veined and rarely with no veins, upper and lower glumes similar. Lemmas (Fig. 1) 3–7 nerved, mostly with the central three nerves continuing into a more or less twisted awn; the lateral nerves sometimes terminating in lateral bristles, the lemmas often continuing up the awns, consequently with the bristles apparently borne on the awn, in *C. selloana* the lemma continues to the tip of the awn and so obscures the awn; lemmas usually long-villous on the back, rarely glabrous. Palea membranous, linear, often longer than the lemma, keeled, sometimes variously villous on the back. Lodicules two. Anthers three, fertile or sterile, to 3.5 mm long. Ovary stalked, styles two. Caryopses 1.5–3.5 mm long, variable in shape, glabrous, embryo mark from  $\frac{1}{4}$  to more than  $\frac{1}{2}$  length of caryopsis, hilum linear, from  $\frac{1}{4}$  to  $\frac{3}{4}$  caryopsis length.

**Leaf anatomy.** Leaf in transverse section sclerophyllous, leaves varying from expanded to setaceous, margins not thickened but with a sclerenchyma cap. Adaxial furrows vary from deep and cleft-like to absent; abaxial ribs sometimes present. Vascular bundles differentiated into two, rarely three, orders; primary vascular bundles 6–30, symmetrically distributed in the two leaf sections; either ad- or abaxially or centrally positioned, circular or elliptical, sometimes with sclerosed phloem; outer bundle sheath cells always distinct from the chlorenchyma and sometimes lignified, entire or interrupted by bundle sheath; adaxial sclerenchyma as narrow girders, as

trapezoidal girders, as T-shaped girders or inversely anchor-shaped girders; abaxial sclerenchyma as small strands, as narrow girders, as wide girders, as trapezoidal girders, or as massive linked girders forming a continuous subepidermal layer; tertiary vascular bundles 1-several between the primary vascular bundles, adaxial sclerenchyma as small strands, as narrow girders, as trapezoid girders narrowing towards vascular bundles, as T-shaped girders or inversely anchor-shaped girders; abaxial sclerenchyma absent, as small strands, as narrow girders, as broad girders, as trapezoidal girders or as massive linked girders forming a continuous subepidermal layer. Mesophyll of small, angular isodiametric chlorenchyma cells with small air spaces; mesophyll islands of colourless cells usually absent, sometimes with colourless collenchyma cells connecting the adaxial and abaxial furrows and so partitioning the chlorenchyma. Abaxial subepidermal layer sometimes with collenchymatous or non-chlorophyllous cells in 1-several layers only along the margins, or flanking the midrib, and sometimes with this layer extending over the whole width of the leaf. Abaxial epidermal zonation present or absent; microhairs or macrohairs absent; silica bodies absent, or tall and narrow, or round and single. Adaxial epidermis sometimes with papillae, prickle-hairs, and microhairs.

**Distribution and ecology.** Widespread in South America, from Tierra del Fuego (Argentina) to Venezuela, from Brazil to Peru, from sea level to the Páramo.

## Systematics

We arranged the species into five informal groups, which are coherent morphologically and anatomically.

### Key to the species (anatomical characters in brackets)

- 1 Lemma body continued up the awn, for at least the same length as the expanded portion of the lemma; plants forming massive tussocks to 4 m tall, inflorescences plumose (leaves with abaxial grooves (Fig. 2a–c)) ..... **Selloana group...2**
- Lemma body not continued up the awn, lemmas consequently acute or obtuse or lobed, usually obviously awned; plants and inflorescences various (leaves rarely with abaxial grooves).....**5**
- 2 Glumes 9–17 mm long, ca. ½ length of basal lemmas; basal lemmas 14–25(–30) mm long; plants of southern (austral) Andean region..... **2. *C. araucana***
- Glumes 5–14 mm long, almost as long as or longer than the basal lemmas; basal lemmas 6–15 mm long; plants from southern Brazil, Uruguay, and Argentina northwards to Colombia.....**3**
- 3 Lemma awn present above the insertion of the lateral setae (these often lost on herbarium material); spikelets 8–15 mm long; lemmas 7.0–12.5 mm

- long; glumes 6–8 mm long; plants from desert regions of the Andes.....
- ..... **3. *C. speciosa***
- Lemma awn absent; spikelets 10–20 mm long; lemmas 6–15 mm long; glumes 5–14 mm long; widely distributed in South America..... **4**
- 4 Gynodioecious plants, exceptionally populations exclusively pistillate; panicles pyramidal to fusiform, dense to lax, included or not in the foliage; southern Brazil, Uruguay and Argentina ..... **1a. *C. selloana* subsp. *selloana***
- Only pistillate plants; panicles pyramidal, lax, much exerted above the foliage; northwest Argentina to Colombia..... **1b. *C. selloana* subsp. *jubata***
- 5 Glumes without veins; lemmas with awns 14–35 mm long; sheaths always intact (primary vascular bundles with lignified sheaths and girders, tertiary vascular bundle sheaths and girders collenchyma) .....
- ..... **Lamprothyrsus Group: 5. *C. hieronymi***
- Glumes with 1 (rarely 2) vein; lemmas awnless or with awns up to 17 mm long; when longer than 13 mm the basal sheaths are lacerated, sheaths and girders of all vascular bundles similar .....
- 6**
- 6 Lemmas acute, at most with vestigial lobes, mostly without awns; from southern and eastern South America (leaves with large bulliform cells – Fig. 3A–C) .....
- Egmontiana group...7**
- Lemmas lobed, often with setae on the lobes, mostly with awns; from the Andes and the tepui (bulliform cells absent or poorly developed)..... **9**
- 7 Inflorescence compact with the branches shorter than the spikelets; leaf blades disarticulating from a persistent sheath; southern South America (leaf anatomy with adaxial ribs, phloem-pole usually intact)..... **5. *C. egmontiana***
- Inflorescences plumose with the branches longer than the spikelets; leaf blades persistent on the sheath; eastern Brazil (leaf anatomy with hardly any ad- or abaxial grooves and with the phloem-pole split)..... **8**
- 8 Glumes 8–12 mm long; lemma back villous; basal sheaths burnt off, ensheathing the tiller bases .....
- 6. *C. modesta***
- Glumes 4–6 mm long; lemma back glabrous; basal sheaths breaking up into fibres..... **7. *C. vaginata***
- 9 Old leaf sheaths intact, or shattering transversally, rarely some lacerated (sometimes in *C. boliviensis*); (leaves, except in *C. echinata*, with a multilayered wide collenchyma below the adaxial epidermis and no sclerenchyma girder connecting the vascular bundle to the epidermis, Fig. 3(1)) .....
- ..... **Nitida group...10**
- Old leaf sheaths lacerated (leaves never with a multilayered collenchyma below the abaxial epidermis, or when present then interrupted by a sclerenchyma girder connecting the vascular bundle to the epidermis)..... **Bifida group...14**
- 10 Plants caespitose, at least 0.5 m tall (leaf anatomy with adaxial ribs, and the adaxial surface papillate) .....
- 11**
- Plants usually forming vegetable hedgehogs (spiny cushions), rarely caespitose, up to 0.5 m tall..... **12**

- 11 Tussocks up to 2.3 m tall; old sheaths remaining intact; inflorescence branches nitid to scaberulous, nodes villous; lemmas villous overall with callus indumentum longer than lemma hairs ..... **8. *C. nitida***
- Tussocks up to 1.5 m tall; old sheaths shattering transversely; inflorescence branches and nodes scabrid; lemma indumentum sometimes only basal with callus indumentum only as long as the lemma hairs..... **9. *C. boliviensis***
- 12 Leaves densely pilose (leaves folded double, no adaxial ribs)..... **10. *C. sericantha***
- Leaves glabrous (leaves expanded, with adaxial ribs)..... **13**
- 13 Plants caespitose; sheaths remaining intact; inflorescence branches villous; glumes less than 15 mm long; lemma setae, excluding lobes, to 1.5 mm long; from marshlands in Colombia (anatomy not known) ..... **11. *C. pungens***
- Plants cushion-forming; sheaths splitting transversely; inflorescence branches scabrid; glumes more than 15 mm long; lemma setae, excluding lobes, at least 2 mm long; from epilithic habitats in Peru (leaves without abaxial collenchyma) ..... **12. *C. echinata***
- 14 Leaf upper surface, directly above the ligule, glabrous (leaves abaxially shallow grooves with collenchyma in the grooves (Fig. 3(2))..... **15**
- Leaf upper surface, directly above the ligule, villous (leaves abaxially not grooved, with a weakly developed sclerenchyma layer below the abaxial epidermis) ..... **16**
- 15 Leaves not pungent, more than 20 cm long, when dry expanded, disarticulating from the sheath; inflorescences plumose, pedicels not obscured by spikelets; lemma awn 6–17 mm long..... **13. *C. bifida***
- Leaves pungent, to 20 cm long, when dry folded double, persistent on sheath; inflorescence contracted, pedicels obscured by spikelets; lemma awn 4–8 mm long (anatomy not known) ..... **14. *C. planifolia***
- 16 Glumes 10–22 mm long; lemma setae 1–3 mm long; from Andes..... **15. *C. hapalotricha***
- Glumes 5–13 mm long; lemma setae 0–2 mm long; from Andes or tepuis ... **17**
- 17 Lemma indumentum 3–4 mm long; setae 3–9 mm; from Andes..... **16. *C. columbiana***
- Lemma indumentum 4–6 mm long; setae 0–2 mm; from tepuis ..... **17. *C. roraimensis***

## Notes on species

### Selloana group

In this group three morphologically and anatomically similar species, with both gynodioecious and apomictic breeding systems, are included. They are easily distinguishable from other species in the genus: they form big tussocks 1.5 to 3 m in diameter and

up to 4 m in height, and the leaf edges are strongly cutting. The panicles are large and plumose, very showy, and much larger than in most of the other species. The spikelets have 1-veined glumes, the lemmas are long-acuminate, with or without evident awns, unlobed, 3-veined and with long hairs only in female plants (hermaphrodites glabrous).

The leaf, in transversal section (Fig. 2A–C), is ribbed, with moderately deep square ribs on adaxial and ribbed on abaxial surface. Colourless chlorenchya cells occur between the vascular bundles on the abaxial epidermis. Aerenchyma is sometimes present (Fig. 2B) in all species.

**1. *Cortaderia selloana* (Schult. & Schult. f.) Asch. & Graebn., Syn. Mitteleur. Fl. 2(1): 325. 1900.**

*Arundo dioeca* Spreng., Syst. Veg. (ed. 16) 1: 361. 1825 [1824], nom. illeg. (non Lour. 1790); *Cortaderia dioeca* (Spreng.) Speg., Anales Mus. Nac. Buenos Aires 7: 194. 1902; *Arundo selloana* Schult. & Schult. f., Mant. 3(1): 605. 1827; *Gynerium argenteum* Nees, Agrost. Bras. 462. 1829, nom. illeg.; *Moorea argentea* (Nees) Lemaire, Ill. Hort. 2: 14. 1855; *Cortaderia argentea* (Nees) Stapf, Gard. Chron. ser. 3, 22: 396. 1897, nom. illeg.

Type. Uruguay. Montevideo, I-1836, *F. Sellow 570* (lectotype, designated here: B 10 0185657! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100185657>); isolectotypes: BAA frag. ex B!, FR photo!).

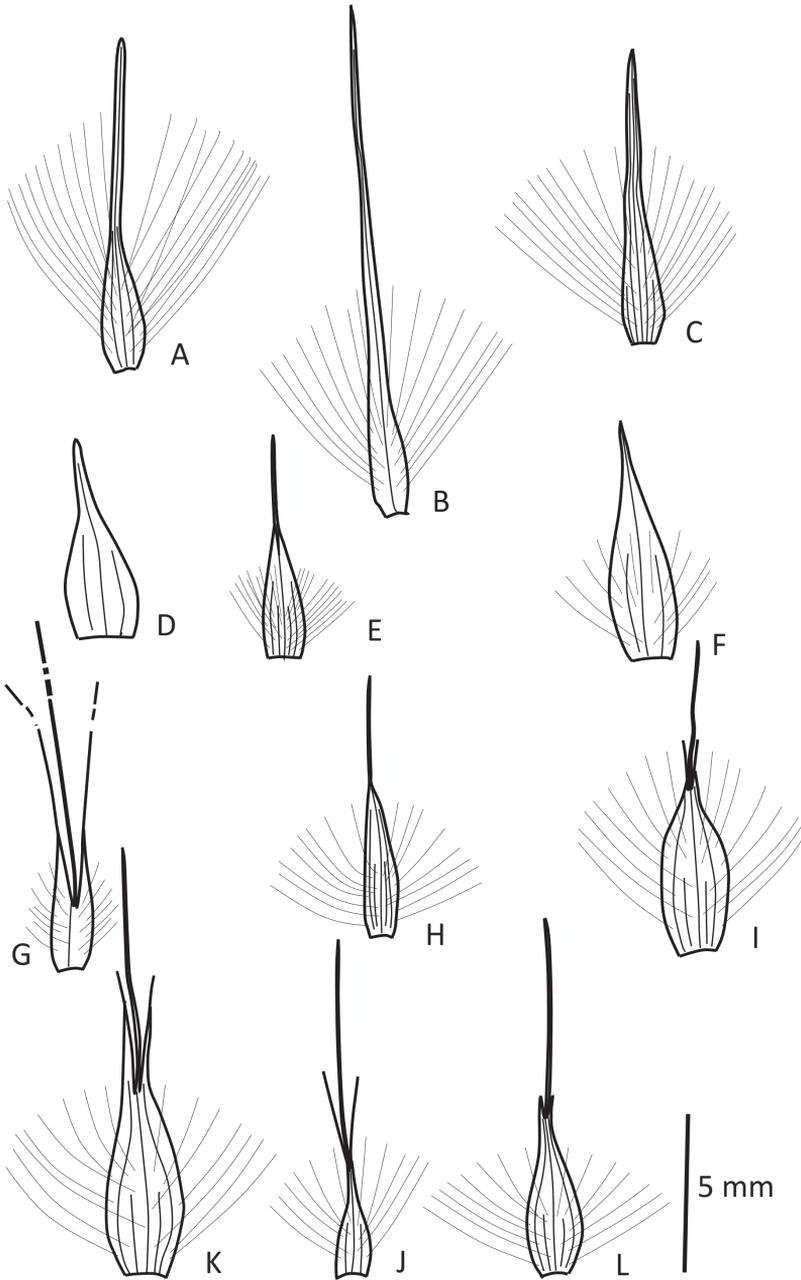
**Etymology.** *selloana*: In honour of Friedrich Sellow (1789–1831), German botanist, a major collector of Brazilian flora.

**Nomenclatural comments.** *Arundo dioeca* Spreng. is a later homonym of *Arundo dioica* Lour. (1790) from Indochina, and is consequently illegitimate. *Arundo selloana* Schult. & Schult.f. is a new name for *A. dioica* Spreng.; *A. dioeca* Spreng. is cited in the protologue, and the diagnoses are identical. Furthermore, both description cite a Sellow collection, without number, from Montevideo. It is most likely that the type is *Sellow 570* from Montevideo, which is in B, and is designated here as lectotype. Curiously, Conert (1961) proposed *Sellow 396* from Brasilia as holotype of *A. dioica*, although Sprengel explicitly mentions that the type is from Monte Video. *Gynerium argenteum* Nees is also based on the same collection as *Arundo dioica* Spreng., plus some additional material. All three names are based on the same type.

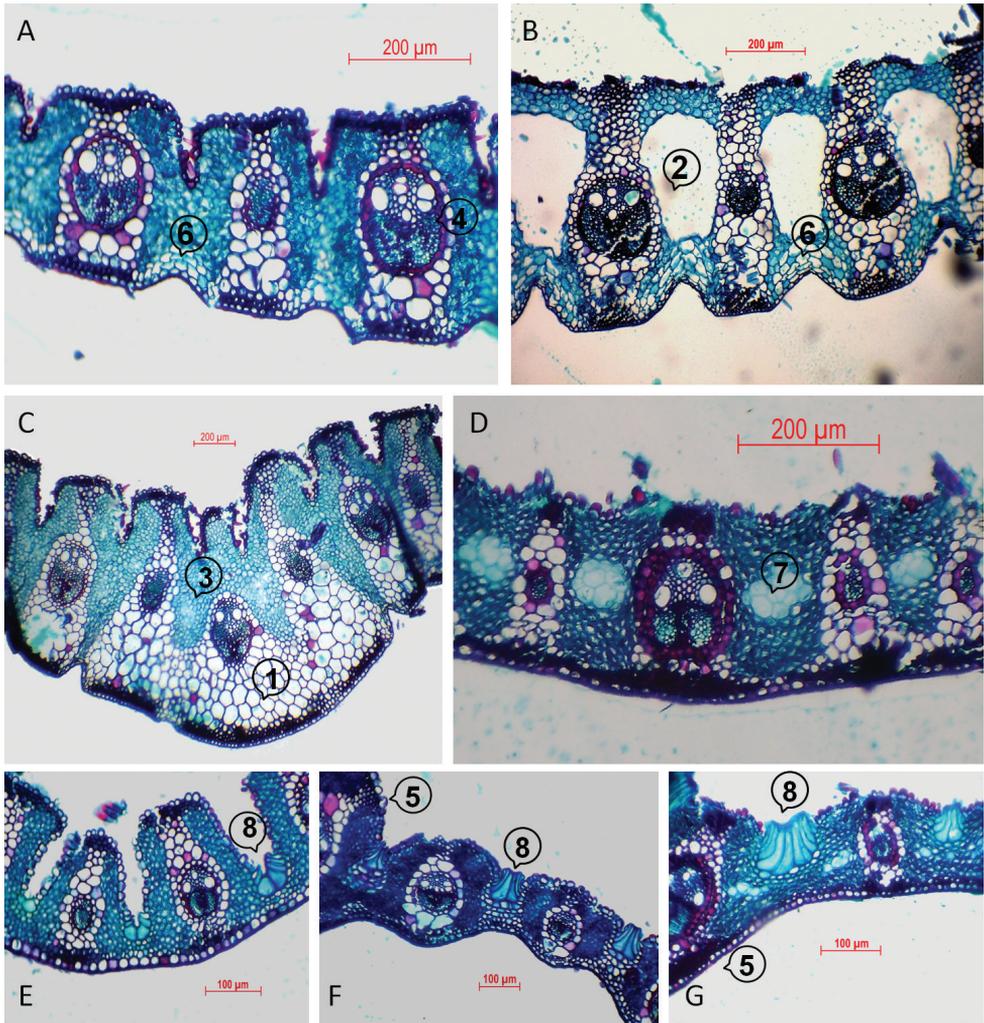
**1a. *C. selloana* subsp. *selloana***

Figs 1A, 2A–B

**Common names.** pampas grass, cortadera, cola de zorro, carrizo de las pampas. The origins of the popular name “pampas grass” are somewhat obscure, and do not reflect the ecology of the species (Stapf 1897).



**Figure 1.** Lemmas of selected species of *Cortaderia*. **A** *C. selloana*, Jürgens 40 (B) **B** *C. araucana*, Borchers s.n. (US) **C** *C. speciosa*, P.M. Peterson 12766 (US) **D** *C. vaginata*, L.B. Smith, P.R. Reitz & R. Klein 7761 (B) **E** *C. egmontiana*, P.M. Peterson, R.J. Soreng & N. Refulio-Rodriguez 17508 (US) **F** *C. modesta*, A. Chase 8288 (US) **G** *C. hieronymi*, A. Burkart et al. 30395 (P) – note that awn and setae are much longer than illustrated **H** *C. nitida*, S. Laegaard 52786 (K) **I** *C. sericantha*, E. Asplund 17175 (B) **J** *C. bifida*, D.N. Smith & J. Cabanillas 7167 (US) **K** *C. hapalotricha*, J.C. Solomon & R. Chevalier 16620 **L** *C. columbiana*, J.P. Schulz 318 (US). All at same magnification.



**Figure 2.** Leaf anatomy of *Cortaderia*, as evident from transverse sections. **A–B** *C. selloana* (Villamil 11738) **C** *C. speciosa* (Testoni 644) **D** *C. vaginata* (Zanín 1654). Comparison of bulliform cells in Egmontiana group: **E** *C. egmontiana* (Testoni 634) **F** *C. modesta* (Carauta 927) **G** *C. vaginata* (Zanín 1654). Structures referred to in the descriptions are labelled as follows: 1, multi-layered abaxial sub-epidermal collenchyma layer; 2, aerenchyma; 3, chlorenchyma; 4, primary vascular bundle; 5, midrib; 6, colourless cells; 7, empty cells; 8, bulliform cells.

**Taxonomy.** *Cortaderia selloana* ssp. *selloana* can be diagnosed by the glumes about as tall as the basal lemma, and lemma without a distinct awn. The plants are generally larger than those of *C. araucana* and *C. speciosa*, and the panicles are larger (0.5 to 1 m long), more lax, and coloured white, pink or yellowish. The similar size of basal lemmas and glumes (6–15 mm) further separates it from *C. araucana* (glumes 9–17 mm long, ca.  $\frac{1}{2}$  length of basal lemmas), whereas the larger glumes separate it from *C. speciosa* (glumes 6–8 mm, ca.  $\frac{3}{4}$  length of basal lemmas). The large size may also

lead to confusion with *C. nitida*, but it is easily separated by the larger and laxer panicles, 3-veined, awnless lemmas that are glabrous on hermaphrodite plants; and female plants with tiny staminodes. For the distinction from ssp. *jubata* see below.

*Cortaderia selloana* ssp. *selloana* was originally described as dioecious, but Astegiano et al. (1995) showed that it is gynodioecious, and Testoni and Villamil (2014) recorded several populations with only pistillate individuals (so presumably apomictic) in central and northern Argentina. This subspecies presents the greatest morphological variability and geographical range in the genus. The morphological characterization is also complicated by interbreeding between natural populations and cultivated plants.

**1b. *C. selloana* subsp. *jubata* (Lemoine) Testoni & Villamil, *Darwiniana, nueva serie* 2(2): 272. 2014.**

*Gynerium jubatum* Lemoine, Rev. Hort. 50: 449. 1878; *Cortaderia jubata* (Lemoine) Stapf, Bot. Mag. 124: t. 7607. 1898.

Type: Ecuador, “sent by Lemoine of Nancy and collected at Chimborazo by the botanical collector Roez!”, sine data, B. Roez! s.n. (lectotype designated by Connor & Edgar, *Taxon* 23: 598 (1974): K 000307978!).

**Etymology.** *jubata* (Lat.): Having mane, crest, in allusion to the panicle.

**Common names.** pink pampas grass, jubata grass, cortadera

**Taxonomy.** This subspecies is generally similar to ssp. *selloana*, and includes all the morphologically homogenous apomictic populations of the Yungas region. It can be separated from ssp. *selloana* by the inflorescences which extend far beyond the foliage, and the pink, 75–90 cm long, very lax, pyramidal and nodding panicles. In Ecuador it is sympatric with *C. nitida*, from which it can be separated by its larger size and its spectacular pink panicles. They can also easily be distinguished by the leaves: in subsp. *jubata* they are flat and folded V-shaped, while in *C. nitida* leaves are inrolled from both margins.

**2. *Cortaderia araucana* Stapf, *Gard. Chron. ser. 3, 22: 396. 1897.***

Fig. 1B

*Moorea araucana* (Stapf) Stapf, *Gard. Chron. ser. 3, 34: 400. 1903.*

Type: Chile, llanos de Valdivia, 20-XII-1852, W. Lechler 613 (lectotype designated by Connor & Edgar, *Taxon* 23: 598 (1974): K 000308157!; isolectotypes: P photo!, W photo!, US! fragm. ex K).

*Cortaderia quila* var. *patagonica* Speg., *Anales Mus. Nac. Buenos Aires* 7: 194. 1902.

Type: Argentina, Chubut, “non rara in rupestribus secus Carren-leofú, aest. 1899-900”, N. Illín s.n. (lectotype, here designated: LP!).

*Cortaderia longicauda* Hack., Repert. Spec. Nov. Regni Veg. 10 (243–247): 169. 1911.

Type: Chile, Valdivia, “Potrero Coihue, I-1861”, R. A. Philippi s.n. (lectotype designated as holotype by Connor & Edgar, Taxon 23: 598 (1974): W-1916-0039626 ([http://jacq.nhm-wien.ac.at/djatoka/jacq-viewer/viewer.html?rft\\_id=w\\_19160039626&identifiers=w\\_19160039626](http://jacq.nhm-wien.ac.at/djatoka/jacq-viewer/viewer.html?rft_id=w_19160039626&identifiers=w_19160039626)); isolectotype: BAA!).

*Cortaderia araucana* var. *fuenzalidae* Acevedo, Bol. Mus. Nac. Hist. Nat. Santiago de Chile 27(4): 239. 1959.

Type: Chile, Curico, Potrero Grande, 5-XI-1943, M. Espinosa s.n. (lectotype, here designated: SGO photo!).

*Cortaderia araucana* var. *skottsbergii* Acevedo, Bol. Mus. Nac. Hist. Nat. Santiago de Chile 27(4): 240. 1959.

Type: Chile, provincia Chiloé, región del Corcovado, sine data, C. Reiche s.n. (lectotype, here designated: SGO photo!).

**Etymology.** *-ana*, indicating connection. From the Araucania region of Chile.

**Common names.** cortadera

**Taxonomy.** In the *Selloana* group, *C. araucana* is readily diagnosed by the basal lemmas longer than 12.5 mm and much longer than the glumes. The spikelets are 20–35 mm long and the lemma of the basal floret 14–25 (30) mm long (including awn of 5–11 mm long). The species is found in the southern (austral) Andean region.

*Cortaderia araucana* includes extensive morphological variation, and both gynodioecious and apomictic populations. This variability led Acevedo Vargas (1959) to recognize three varieties, which are no longer maintained. In northern Patagonia *C. araucana* and *C. selloana* are sympatric, but the plants of *C. araucana* are somewhat smaller, with less lax panicles and flowering in the austral spring (late November and early December), whereas *C. selloana* flowers in the austral summer (January and February). Further, the spikelets are different: the glumes are shorter than the basal floret, the lemma may terminate in an awn that arises between two lower lateral setae. The leaf anatomy of both species is similar.

### 3. *Cortaderia speciosa* (Nees & Meyen) Stapf, Gard. Chron. Ser. 3(22): 396. 1897. Fig. 1C

*Gynerium speciosum* Nees & Meyen, Nov. Act. Nat. Cur. 19 suppl. 1: 153. 1843; *Gynerium argenteum* var. *strictum* E. Desv., Fl. Chile. 6: 328. 1854; *Moorea speciosa* (Nees & Meyen) Stapf, Gard. Chron. Ser. 3, 34: 400. 1903.

Type: Chile, ad flumen Copiapo dictum circa Nantoco in provincia Copiapó reipublicae Chilensis, III-1831, F. J. F. Meyen s.n. (lectotype designated by Connor & Edgar, Taxon 23: 603 (1974): B 10 0217503! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217503>); isolectotype: K! frag. ex B).

*Gynerium quila* Nees & Meyen, Nov. Act. Nat. Cur. 19 suppl. 1: 153. 1843; *Cortaderia quila* (Nees & Meyen) Stapf, Gard. Chron. Ser. 3: 22: 396. 1897; *Moorea quila* (Nees & Meyen) Stapf, Gard. Chron. Ser. 3, 34: 400. 1903.

Type: Chile, ad Copiapó fluvium circa Nantoco, sine data, F. J. F. Meyen s.n. (syntype: B!); Perú, ad lacum Titicacam et ad pedem vulcani Arequipensis. Femina planta. Mascula ignota est., 1000 m, Maio, F. J. F. Meyen s.n. (syntype: B 10 0217504 (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217504>; isosyntype: BAA! frag. ex B).

*Gynerium quila* var. *pygmaeum* Meyen, Nov. Act. Nat. Cur. 19 Suppl. 1: 153. 1843.

Type: Perú, “ad lacum Titicacam. ♀”, IV-1841, F. J. F. Meyen s.n. (lectotype, designated here: B 10 0217506! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217506>)).

*Gynerium argenteum* var. *parviflorum* E. Desv., Fl. Chile. 6: 328. 1854.

Type: Chile, Mal Paso, cordillera de Guanta, a la orilla de los arroyos, 2490 m., en donde forma copas apretadas de un metro y más, sine data, C. Gay s.n. (lectotype, designated here: P 00506920!).

*Gynerium atacamense* Phil., Linnaea 33: 289. 1865. *Cortaderia atacamensis* (Phil.) Pilg., Bot. Jahrb. 37: 374. 1906.

Type: Chile, prope San Pedro de Atacama, I-1854, R. A. Philippi s.n. (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 597 (1974): SGO photo!; isolectotype: BAA! frag. ex SGO, W!).

*Cortaderia rudiuscula* Stapf, Gard. Chron. Ser. 3, 22: 396. 1897. *Moorea rudiuscula* (Stapf) Stapf, Gard. Chron. Ser. 3, 34: 400. 1903.

Type: Chile, Santa Rosa de los Andes, V-1882, J. Ball s.n. (lectotype, designated by Connor & Edgar, Taxon 23: 601 (1974): K!; isolectotype: BAA! frag. ex K).

**Etymology.** *speciosus* (Latin), beautiful, showy.

**Nomenclatural comments.** The binomials *Gynerium speciosum*, *G. neesii* and *G. pygmaeum* – mentioned as new species by Meyen (1834), from Copiapo (Chile) and Lake Titicaca (Peru), respectively – are synonyms of *Cortaderia speciosa*, but are invalid (*nomina nuda*) as no descriptions were published. Their identity can be determined, because the specimens in B! were annotated with the Meyen names. *Gynerium speciosum* was validated by Nees in 1943. Tropicos (Downloaded 14 December 2016) lists the species as described by Nees in 1841 (Nees ab Esenbeck 1841), but this is erroneous. Conert (1961) designated *Philippi 1024* (B photo!) from Chile (“Atacama oppidum, 1824”) as lectotype of *Gynerium atacamense* Phil. However, the type has been found in the herbarium SGO (Connor, 1983) and, therefore, the lectotype designated by Conert should not be taken into account. The binomial *Arundo quila* Molina is a synonym of *Chusquea quila* Kunth (Bambusoideae). In some works, it has been confused *Gynerium quila* Nees & Meyen (basionym of *Cortaderia quila* Nees & Meyen) Stapf, therefore, the binomials *Gynerium quila* (Molina) Nees & Meyen and *Cortaderia quila* (Molina) Stapf are invalid.

**Common names.** cortadera

**Taxonomy.** In the Selloana group, *C. speciosa* can be diagnosed by the short basal lemmas, which are less than 13 mm long. The spikelets are 8–15 mm long and the basal lemma 7.0–12.5 mm long (including awn, 1–4 mm). It differs from other species in the group by its very compact, bright brown panicles with ascending, short and stiff

branches. The species is readily distinguished by the small floret sizes. The leaf anatomy is also somewhat different from the other species of the group (Fig. 2C): the midrib is rounded and somewhat lower; the outer sheath of the central vascular bundle without projections to the adaxial epidermis; and with a massive abaxial sub-epidermal collenchyma layer, only in the middle part of the leaf. The latter occurs in the Nitida group but along the leaf. It is known only by pistillate plants from desert regions (the Puna) of Argentina, Bolivia and Chile.

This species is completely apomictic, and several morphological subgroups can be recognized. As these are all apomicts, it is presumed that they derive from the same ancestral sexual population. The material previously separated as *C. rudiuscula* has longer (9–12 mm) and more slender lemmas, than the material previously separated as *C. speciosa* (lemmas ca. 8 mm), but there is no clear separation between these two forms.

### Lamprothyrsus group

This group is very distinct within *Cortaderia*. Morphologically, it differs by the long, filiform awns, 14–35 mm long; glumes without veins; and by the sheaths which are always intact. Furthermore, the leaf anatomy differs by the primary vascular bundles with lignified sheaths and girders, tertiary vascular bundle sheaths and girders collenchyma (Fig. 3C). The group includes only one species. The enormous variation with this species complex could be due to its apomictic reproduction (Connor and Dawson 1993).

#### 4. *Cortaderia hieronymi* (Kuntze) N.P.Barker & H.P.Linder, *Ann. Missouri Bot. Gard.* 97(3): 342. 2010.

Figs 1G, 3C

*Triraphis hieronymi* Kuntze, *Revis. Gen. Pl.* 3(3): 373. 1898; *Danthonia hieronymi* (Kuntze) Hack., *Anales Mus. Nac. Buenos Aires ser.* 3, 6: 484. 1906; *Lamprothyrsus hieronymi* (Kuntze) Pilg., *Bot. Jahrb. Syst.* 37 (Beibl. 85): 58. 1906.

Type: Argentina, Córdoba, “prope urbem”, 6 Nov. 1881, G. H. E. W. Hieronymus s.n. (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 128 (1961): B!; isolectotype: K!).

*Triraphis hieronymi* var. *jujuyensis* Kuntze, *Revis. Gen. Pl.* 3(3): 374, 1898; *Danthonia hieronymi* var. *jujuyensis* Kuntze, *Anales Mus. Nac. Buenos Aires ser.* 3, 6: 486 (1906); *Lamprothyrsus hieronymi* var. *jujuyensis* (Kuntze) Pilg., *Bot. Jahrb. Syst.* 37 (Beibl. 85): 59, 1906.

Type: Argentina, Jujuy, sine data, O. Kuntze s.n. (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 130 (1961): B!).

*Lamprothyrsus hieronymi* var. *pyramidatus* Pilg., *Bot. Jahrb. Syst.* 37 (Beibl. 85): 59. 1906.

Type: Bolivia, ad Toldos prope oppium Bermejo, 2000m, 8 Dec. 1903, K. A. G. Fiebrig 2372 (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 128 (1961): B 10 0249138! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100249138>); isolectotypes: K, US).

*Lamprothyrus hieronymi* var. *nervosus* Pilg., *Bot. Jahrb. Syst.* 37 (Beibl. 85: 59. 1906. Type: Argentina, Cordoba, Sierra Achala, 11 Nov. 1878, G. H. E. W. Hieronymus 43 (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 129 (1961): B 01 0272938! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100272938>); isolectotype: W).

*Lamprothyrus hieronymi* var. *tinctus* Pilg., *Bot. Jahrb. Syst.* 37 Beibl. 85: 59. 1906. Type: Bolivia, Bermejo, 1400m, 16 Nov. 1903, K. Fiebrig 2099 (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 129 (1961): B 10 0249137! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100249137>); isolectotypes: K, L, US!).

*Lamprothyrus peruvianus* Hitchc., *Proc. Biol. Soc. Washington* 36: 195. 1923; *Cortaderia peruviana* (Hitchc.) N.P.Barker & H.P.Linder, *Ann. Missouri Bot. Gard.* 97(3): 342. 2010.

Type: Peru, Yanahuanca, 16–22 Jun 1922, J. F. Macbride & W. Featherstone 1205 (lectotype, designated as holotype in F: F-V0040645F, photo F-50163 (<http://emuweb.fieldmuseum.org/web/pages/common/imagedisplay.php?irn=39615&ref table=efmnh&refirn=257048>); isolectotypes: US photo!, K!).

*Lamprothyrus venturi* Conert, *Syst. Anat. Arundineae* 130. 1961.

Type: Argentina, prov. Tucuman, Famailla, Villa Nougues, 21-10-1923., S. Venturi 2534 (lectotype, designated as holotype by Conert, *Syst. Anat. Arundineae* 131 (1961): K; isotype: US!).

**Etymology.** In honour of George Hans Emmo Wolfgang Hieronymus (1846–1921), German botanist, sometimes resident of Argentina.

**Common names.** Seringuilla, sivinga (Tucuman).

**Taxonomy.** This species contains substantial variation in the robustness of the plants. Conert (1961) partitioned this variation into three species (*L. peruvianus*, *L. venturi* and *L. hieronymi*) and Pilger (1906) recognized varieties in his *L. hieronymi*. Study of the herbarium material suggests that this is most likely all one taxon (Bernardello 1979), but an analysis of variation within natural populations in the field would be useful to understand the range of variation possible. *Cortaderia hieronymi* differs from the other species in *Cortaderia* by the very long hair-like lemma awns and setae, the glumes without veins, and the small flowers with relatively short and sparse lemma hair.

Only apomictic populations are known, but a few fertile staminate specimens with long hairs on the lemmas were found (Bernardello 1979). It is not known if they can form viable caryopses, and if the species is dioecious or gynodioecious.

In the central and northern Argentina to Ecuador *C. hieronymi* is sympatric with the two subspecies of *C. selloana*, but it is easily separated by its smaller panicles, spikelets with glumes without veins, and 5-veined, 3-awned lemmas. In Peru and Ecuador it



**Figure 3.** Leaf anatomy of *Cortaderia*, as evident from transverse sections. **A** *C. egmontiana* (Moore 2677) **B** *C. modesta* (Glaziou 17913) **C** *C. hieronymi* (Garcia 563) **D** *C. nitida* (Laegaard 53121) **E** *C. boliviensis* (Beck 11273); **F** *C. sericantha* (Ramsay 967); **G** *C. echinata* (Peterson 21587) **H** *C. bifida* (Renvoize 4202) **I** *C. hapalotricha* (Laegaard 53305) **J** *C. roraimensis* (Maguire 60448). Structures referred to in the descriptions are labelled as follows: 1, multi-layered abaxial sub-epidermal collenchyma layer; 2, adaxial islands of collenchyma in the abaxial grooves; 3, chlorenchyma; 4, primary vascular bundle; 5, midrib.

is sympatric with *C. bifida*, with which it is often confused: in both species the old leaf sheaths are lacerated and the spikelets have long awns, but the spikelets of *C. hieronymi* are bigger, and the lemmas with longer and robust central awns.

## Egmontiana group

This group includes three quite distinctive species. *Cortaderia vaginata* and *C. modesta* have an unusual (for *Cortaderia*) leaf anatomy lacking ribs, and with deeply split phloem poles (Fig. 3B), and large bulliform cells (Fig. 2E–G), which are rare in the other groups.

### 5. *Cortaderia egmontiana* (Roem. & Schult.) M.Lyle ex Connor, *Darwiniana* 49: 90. 2011.

Figs 1E, 2E, 3A

*Arundo egmontiana* Roem. & Schult., *Syst. Veg.*, ed. 15 b [Roemer & Schultes] 2: 511. 1817. *Phragmites egmontiana* (Roem. & Schult.) Trin. ex Steud., *Nomen. Bot.* (ed. 2) 2: 324. 1840.

Type: Falkland / Malvinas Islands, Port Egmont, R. J. Schuttleworth s.n. (type: BM photo!).

*Arundo pilosa* d'Urv., *Mém. Soc. Linn. Paris* 4: 603. 1826; *Cortaderia pilosa* (d'Urv.) Hack. ex Dusén, *Bol. Acad. Nac. Ci.* 16: 253. 1900; *Gynerium pilosum* (d'Urv.) Macloskie in Scott, *Rep. Princeton Univ. Exped. Patagonia, Botany* 8, part 1: 213. 1904; *Phragmites pilosa* (d'Urv.) Macloskie & Dusén in Scott, *Rep. Princeton Univ. Exped. Patagonia, Botany* 8, suppl. bot.: 50. 1915. *Ampelodesmos australis* Brongn. in Duperrey, *Voy. Monde* 2(2): 31. 1829, nom. illeg.

Type: Falkland / Malvinas Islands, 1825, J. S. C. D. D'Urville s.n. (central inflorescence designated as lectotype by Connor & Edgar, *Taxon* 23: 600 (1974): P 00740221! (<http://mediaphoto.mnhn.fr/media/1443644100310dGB3ZqFqm8JGPDaz>; isolectotype: B!).

*Calamagrostis patula* Steud., *Syn. Pl. Glumac.* 1(6): 422. 1854.

Type: Chile, Huiti, sine data, W. Lechler 760 (lectotype, selected here: P-00740220 (<http://mediaphoto.mnhn.fr/media/1443644088798jsLY8AS29Euj4oHx>); isolectotypes: GOET; W photo!).

*Poa phragmites* Phil., *Anales Univ. Chile* 43: 576. 1873.

Type: Chile, volcan de Osorno, 1872, C. Juliet s.n. (holotype: SGO photo! (<http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.sgo000000667>); isotype: BAA! frag. ex SGO);

*Gynerium nanum* Phil., *Anales Univ. Chile* 94: 155. 1896.

Type: Falkland / Malvinas Islands, Dec. 1884, C. Martin s.n. (lectotype, designated as holotype by Connor & Edgar, *Taxon* 23: 600 (1974): SGO 065328!; isolectotype: BAA!).

*Calamagrostis scirpiformis* Phil., *Anales Univ. Chile* 94: 20. 1896.

Type: Chile, ad lacum Llanquihue, I-1866, F. Philippi s.n. (lectotype, designated here: SGO 37097; isolectotypes: US, BAA!)

*Cortaderia minima* Conert, *Syst. Anat. Arundineae* 119. 1961; *Cortaderia pilosa* var. *minima* (Conert) Nicora, *Darwiniana* 18(1–2): 80. 1973.

Type: Chile, Andes, Villarrica, “in feuchten Schluchten nahe der Waldgrenze”, 1897, F. W. Neger s.n. (lectotype, designated as holotype by Conert, Syst. Anat. Arundineae 119 (1961): M; isolectotypes: W5945! B! fragm. ex M).

**Etymology.** *egmontiana*: called after Port Egmont in the Falklands / Malvinas Islands.

**Nomenclatural comments.** Brongniart (1829) described *Ampelodesmos australis*, and explicitly included *Arundo pilosa* D’Urville as a synonym, noting that this species is better placed in *Ampelodesmos*.

**Taxonomy.** The species can be readily diagnosed by the combination of compact inflorescences, almost glabrous leaves, and either no, or poorly developed, awns and setae on the lemmas. The habit and dense inflorescences are as in *C. sericantha*, but *C. egmontiana* differs by the absence of setae, and by the almost completely glabrous leaves. The lemma and spikelet morphology (reduced or absent awns and setae) suggests an affinity to the eastern Brazilian species *C. vaginata* and *C. modesta*. From these two species *C. egmontiana* can be separated by the compact inflorescences and the tendency of the leaf blades to disarticulate from the sheaths. It is the only *Cortaderia* species in southern South American temperate zone. The leaf anatomy (Figs 2E, 3A) does not show any distinctive peculiarities.

There is remarkable intraspecific variation in the spikelet and floret sizes, and Conert (1961) separated the forms with smaller spikelets as *C. minima*. Moore (1983) suggested that the two taxa were latitudinally separated, with the southern populations constituting *C. pilosa*, and the northern *C. minima*. On the available material, there is indeed a break in the glume length variation. However, this fits no ecological or geographical pattern, and both small and large-glume forms occur in both the Falkland / Malvinas islands and Tierra del Fuego. Further north, indeed, only the small-glume form is found. This suggests that this size variation has no biological significance, accordingly it is ignored here.

## 6. *Cortaderia modesta* (Döll) Hack., Ark. Bot. 9(5): 4. 1909.

Figs 1F, 2F, 3B

*Gynerium modestum* Döll, Fl. Bras. [Martius] 2(3): 240. 1880.

Type: Brasil, near Rio de Janeiro, Serra dos Órgãos, au Frade (2 ou 3 mois après l’incendie de la forêt), 11-X-1869, A. F. M Glaziou 4352 (lectotype, designated by Connor & Edgar, Taxon 23: 600 (1974): W 10406!; isolectotypes K!, NY!).

*Gynerium ramosum* Hack., Arq. Mus. Nac. Rio de Janeiro 13: 73. 1903. *Gynerium modestum* f. *ramosa* (Hack.) Hack., Ark. Bot. 9(5): 4. 1909.

Type: Brasil, Campo 2100 m, 18 Dec. 1895, P. K. H. Dusén s.n. (lectotype, designated here: W!).

**Etymology.** *modesta* (Latin) = moderate, presumably referring to the culms of average height.

**Nomenclatural comments.** The locality information given by Connor and Edgar (1974) is incorrect. Note that Glaziou made several collections of the same species from the same area.

**Common names.** cabeça de negro, capim-de-anta.

**Taxonomy.** Some specimens show a poorly developed axillary inflorescence developed at the penultimate node of the flowering culm. The almost awnless lemmas, with the paleas as long as the lemmas, and the very dense callus hairs compared to the short lemma back hairs, are almost unique in the genus. Its closest relative might be *C. vaginata* from Santa Catarina, further south along the Brazilian Atlantic coast. It is readily distinguished from *C. vaginata* by the persistent leaf sheaths and the awnless lemmas. According to herbarium labels the plant forms massive tussocks with persistent red, burnt sheaths.

### 7. *Cortaderia vaginata* Swallen, *Sellowia* 7: 9. 1956.

Figs 1D, 2D,G

**Type.** Brasil, Santa Catarina, Bom Retiro, Campo dos Padres, 16 Dec. 1948, R. Reitz 2398 (lectotype, designated as holotype by Connor & Edgar, *Taxon* 23: 603 (1974): US 00133444!; isolectotype: HBR).

**Etymology.** *vagina* (Latin) = sheath. Possibly referring to the conspicuous leaf-sheaths, a feature that is common to most of the genus.

**Common names.** Penacho, Capim-Penacho.

**Taxonomy.** According to Swallen (1956) this species resembles *C. parviflora*, but differs by the glabrous lemmas and long-villous calli. It is unusual among the species assigned to *Cortaderia* by the glabrous lemma, and the almost glabrous pedicels and inflorescence axes. This species may be a local endemic, and might be quite rare. It is probably most closely related to *C. modesta*, which also has a reduced awn, but differs by the sheaths which are lacerated, lax panicles (without axillary panicles), and the glabrous lemma. Geographically it can be immediately identified as the only *Cortaderia* species from Santa Catarina in southern Brazil.

The leaf anatomy is identical to that of *C. modesta*, except that all sections appear to have large empty cells in the middle of the leaf (Fig. 2D), between the vascular bundles. These were seen on some sections of *C. modesta*, but rarely.

## Nitida group

The Nitida group can be characterized by the leaf sheaths which generally remain intact, and the leaves which, in transverse section, show a massive abaxial sub-epidermal collenchyma layer. *Cortaderia nitida*, *C. pungens* and *C. boliviensis* are very similar, whereas *C. sericantha* is quite distinct by the villous, folded leaves with no adaxial ribs. The distinction of *C. pungens* is not clear, and needs fieldwork. The new *C. echinata* is also included in here although anatomically it fits into the next group. Leaf anatomically, *C. nitida* and *C. boliviensis* are very similar, with papillate adaxial surfaces, deep adaxial grooves, and a well developed abaxial collenchyma layer. The leaf anatomy of *C. pungens* is not known.

**8. *Cortaderia nitida* (Kunth) Pilg., Bot. Jahrb. Syst. 37: 374. 1906.**

Figs 1H, 3D

*Arundo nitida* Kunth in Humb. et Bonpl., Nov. Gen. Sp. [H.B.K.] 1: 149. 1816; *Gynerium nitidum* (Kunth) Pilg., Bot. Jahrb. Syst. 27: 31. 1899.

Type: Colombia, inter Guachucal et Tuqueres, sine data, A. J. A. Bonpland s.n. (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 600 (1974): B; isolectotypes: BM, K!).

*Cortaderia sodiroana* Hack., Oesterr. Bot. Z. 52: 238. 1902.

Type: Ecuador, in reg. silvat. suband., 1872, L. Sodiro s.n. (lectotype, designated by Connor & Edgar, Taxon 23: 600 (1974): W 25246!; isolectotype: US!). A second Sodiro collection, same date and place, on the same sheet as the lectotype [W 25245], does not belong to *C. nitida*, and does not fit Haeckel's description.

**Etymology.** *niteo* (Latin) = shine. It may refer to the persistently intact, more or less white, leaf sheaths.

**Common names.** "Sigse de Páramo".

**Taxonomy.** *Cortaderia nitida* is a distinctive grass. It is the tallest and most robust species of this group. The lamina margins are inrolled. The basal sheaths gradually become shorter with age, but do not become lacerated, the leaf blades are scabrid in the upper half but not the lower, and the inflorescence branches which are scaberulous while the pulvini often have a few long hairs (the latter seems to be unique in the genus). The callus usually has very long spreading hairs (more than 2 mm, almost equivalent to the lemma hairs), and the setae are less than 2 mm long. The other tall *Cortaderia*, *C. bifida*, has central awns that are longer than 8 mm, and very well developed setae. The lemma shape is similar to *C. columbiana*, but the inflorescence branches are scaberulous in *C. nitida*, and villous in *C. columbiana*.

This species also approaches the Selloana group by its large size, big plumose inflorescences, and especially by the lemma shape. It is easy to confuse the lemmas of the two groups, but in the Nitida group the lemmas are 5–7 veined, hairy in both sexes, while in the Selloana group the lemmas are 3-veined, hairy in female plants and glabrous in hermaphrodite plants. The plastid sequence data also places this species as sister to the Selloana group, but this is not corroborated by the ITS-based phylogeny.

Laegaard (1997) mentions a distinct form of smaller and more delicate plants from the province of Azuay in Ecuador, and with three-nerved glumes, but we have not seen any material of it.

The leaf anatomy (Fig. 3D) is similar to that of *C. boliviensis*, and approaches that of *C. sericantha*. A well-developed layer of collenchyma is found below the abaxial epidermis, and overall there is little evidence of lignification. It differs from *C. sericantha* by the well-developed adaxial grooves and the not quite so massive collenchyma, and by the presence of adaxial papillae.

**9. *Cortaderia boliviensis* M.Lyle, *Novon* 6(1): 72. 1996.**

Fig. 3C

*Cortaderia bifida* Pilg. var. *grandiflora* Henrard, *Meded. Rijks-Herb.* 40: 67. 1921.

Type: Bolivia, Departamento Cochabamba: “Charactergrass der Andenwiesen über Tablas, feuchte Stellen, 3400 m, Mai 1911, T. C. J. Herzog 2194 (holotype: L; isotypes: S, US!, W!, Z!).

**Etymology.** *-ense* (Latin), denoting origin. From Bolivia.

**Taxonomy.** This species is very similar to *C. nitida*, with which it shares the (usually) non-lacerated, entire leaf sheaths and the shape of the lemmas, as well as largely similar leaf anatomy. However, neither chloroplast nor nuclear genome indicates such a relationship for *C. boliviensis* (Pirie et al. 2009). It differs by the horizontally shattering sheaths. More inconsistent differences are in the indumentum of the floret, with the callus indumentum of *C. boliviensis* being shorter than in *C. nitida*. Lyle (1996) diagnosed *C. boliviensis* against *C. bifida*, under which it was originally described as a variety by Henrard in 1921. Mostly it is very different from *C. bifida*: the latter has much longer lemma setae and the basal sheaths are lacerated and not shattered. The type collection, however, is easily confused with *C. bifida* due to the long awns and setae, and somewhat fragmented leaf sheaths. The leaf anatomy is also quite different.

The leaf anatomy (Fig. 3E) is like that of *C. nitida*, with adaxial grooves and a well-developed abaxial collenchyma layer. There are differences in detail, and wider sampling may well indicate that this is within-species variation.

**10. *Cortaderia sericantha* (Steud.) Hitchc., *Contr. U.S. Natl. Herb.* 24: 348. 1927.**

Figs 1I, 3F

*Danthonia sericantha* Steud., *Syn. Pl. Glumac.* 1(3): 246. 1854.

Type: Ecuador, Quito “On boggy plains on the eastern Cordillera at 13000 feet above sea level”, sine data, W. Jameson 93 (lectotype designated by Connor & Edgar, *Taxon* 23: 602 (1974): K!; isolectotypes: K! - frag US!, OXF!, TCD!).

*Danthonia jubata* Sodiro, *Revista Colegio Nac. Vicente Rocafuerte* 12: 91. 1930.

Type: Ecuador, Pinchincha, sine data, A. S. J. Mille s.n. (NY, MO photo!, US!).

**Etymology.** *serios* (Greek) = silken + *Anthos* (Greek) = flower. Presumably this refers to the silky-haired leaves, a diagnostic trait for this species.

**Taxonomy.** This species is very distinctive in *Cortaderia* by its very villous leaves, which are rolled rather than flat, and quite pungent; the compact inflorescences with short inflorescence branches; the glumes with three veins and which are much longer than the packet of florets; and the tuft of hair at the base of the spikelets. The inflorescences are similar to those of *C. egmontiana*, but the villous leaves immediately distinguish our species from *C. egmontiana*. The intact leaf sheaths, pungent leaf tips,

and compact growth form related this species to *C. pungens* and *C. echinata*. The remarkably large glumes, much overtopping the packet of florets, are shared with *C. echinata*.

The leaf anatomy (Fig. 3F) could be unique in the genus. The abaxial half of the leaf, in cross-section, consists of colourless collenchyma. The vascular bundles are very slender, and the girders taper towards the adaxial epidermis. Adaxially the leaves are only very slightly grooved.

### 11. *Cortaderia pungens* Swallen, *Contr. U.S. Natl. Herb.* 29: 251. 1948.

*Danthonia confusa* L.B.Sm., *Phytologia* 22(2): 89. 1971, non *D. pungens* Cheeseman, 1906.

Type: Colombia, Dept. Santander, Páramo de Santurban, near Vetas, 17 Jan. 1927, E. P. Killip & A. C. Smith 17467 (lectotype, designated as holotype by Connor & Edgar, *Taxon* 23: 600 (1974): US 00133443!; isolectotype: K!).

**Etymology.** *pungens* (Latin): piercing, terminating in a sharp point. This describes the leaf tips.

**Taxonomy.** This species is often placed with *C. hapalotricha*, from which it differs by (a) shorter growth-form (less than 1 m tall); (b) the intact leaf bases; (c) the rolled, pungent leaves; and (d) deeply lobed lemmas. The two species have much in common (leaf anatomy, spikelet and inflorescence structure). It is possible that they are ecotypes of each other, and the problem needs critical field work. We keep them separate on the very different growth-form. The intact leaf bases and pungent leaves suggest a relationship to *C. sericantha* and *C. echinata*, but the species is readily separated from these two by the much shorter glumes.

The leaf anatomy was not studied.

### 12. *Cortaderia echinata* H.P.Linder, *sp. nov.*

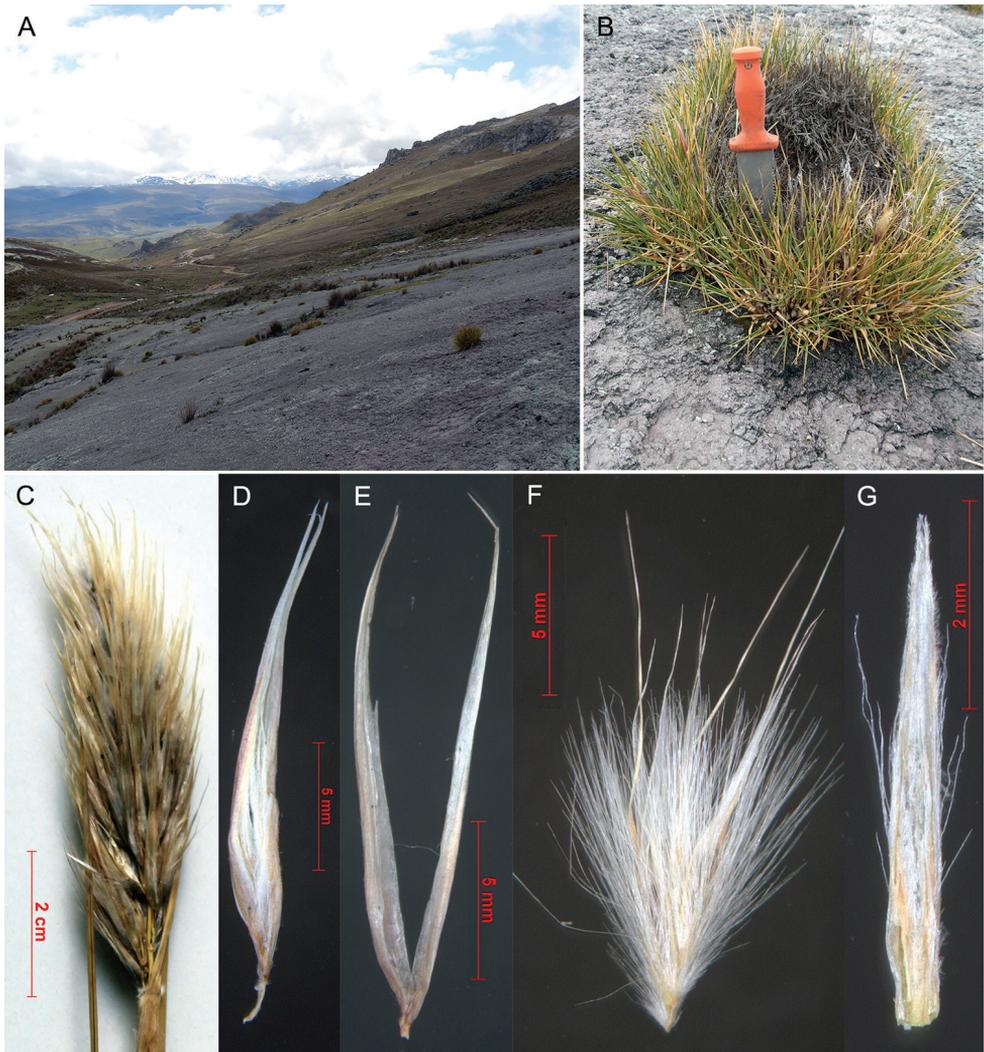
urn:lsid:ipni.org:names:77159701-1

Figs 3G, 4A–G

**Type.** PERU, vicinity of Cerro Ayrhananca pass ca. 1 km E of Lugo Ututo on road between Cataparaco and Utcuyau, 4223 m. Rocky slopes, 11 Mar 2008, *P. M. Peterson, R. J. Soreng, M. I. la Torre & J. V. Rojas Fox* 21587 (holotype: Z!, isotype: US!).

**Diagnosis.** Similar to *C. pungens* by the small compact habit and pungent leaves, but differing by the shattering leaves and the longer spikelets.

**Description.** Plants forming tough, perennial cushions (vegetable hedgehogs) to 30 cm in diameter and to 30 cm tall. Basal sheaths white, shiny, persistent, when old splitting transversely into segments, puberulous between the veins. Ligule a dense ring of hairs 2–3 mm long, sheath mouth glabrous. Leaf blades 80–150 × 2–3 mm;



**Figure 4.** *Cortaderia echinata* (all from Peterson 21587). **A** habitat on bare rock slabs **B** habit, forming a vegetable hedgehog **C** inflorescence **D** spikelet, somewhat squashed (all very compact in the inflorescence) **E** glumes **F** floret package, with three florets, note long lemma indumentum **G** palea with sparse indumentum on the lateral palea flaps. **A** and **B** were photographed by Paul Peterson and Robert Soreng.

C-shaped at base and margins incurved towards apex, forming a rolled, viciously pungent tip; disarticulating from the persistent sheath at the ligule. Inflorescence paniculate, contracted, ovate, 60–100 × 15–25 mm, with 100–300 spikelets; branches and pedicels shorter than and obscured by the spikelets, scaberulous. Female-fertile spikelet 16–22 mm long; with ca. 3 florets. Glumes 16–22 × 0.6–0.8 mm; twice as long as the packet of florets; 1 veined, acute, glabrous, straw to almost white, upper and lower glumes similar. Callus ca. 0.75 mm long; indumentum 2–2.5 mm long, overtopping the base of the lemma hairs length; rhachilla 0.75 mm long. Second

lemma ca. 4 mm long, 5 veined, indumentum scattered on lower half of lemma back, about as long as the lemma lobes, 5–6 mm long; lemma-lobes acute, 3–4.5 mm long, setae 2–3 mm long, distinctly shorter than lemma lobes, included in the glumes; awn simple, 8.5–10 mm, longer than setae. Palea linear, 5 × 0.5 mm, obscurely bilobed, keels sinuose; scabrid, with hair-tufts along mid-margins. Lodicules obtriangular and with bristles.

**Leaf anatomy.** Leaf in transverse section expanded, sclerophyllous; margins gently tapering, sclerenchyma caps well-developed; adaxial furrows located between all vascular bundles, the same over primary and tertiary vascular bundles, about half depth of leaf, forming narrow clefts, ribs flat-topped; abaxial ribs and furrows present. Vascular bundles closer to abaxial surface, 3 primary vascular bundles in half a leaf section, with 1–2 tertiary vascular bundles between the primary vascular bundles. primary vascular bundles elliptical; phloem without lignified cells; metaxylem vessels narrower than outer bundle sheath cells; outer bundle sheath clearly distinct from chlorenchyma, cells larger and colourless, with adaxial and abaxial interruptions; inner bundle sheath walls thickened anticlinally, cells smaller than outer bundle sheath cells; adaxial sclerenchyma as inversely anchor-shaped girders; abaxial sclerenchyma as trapezoidal girders. tertiary vascular bundles outer bundle sheath cells distinct from and larger than chlorenchyma cells, walls thickened anticlinally or all round; with abaxial interruption only; adaxial bundle sheath extension present with cells smaller than outer bundle sheath cells; adaxial sclerenchyma inversely anchor-shaped girders; abaxial sclerenchyma as trapezoidal girders; phloem without lignified cells or with only the inner bundle sheath lignified. Mesophyll of small, angular isodiametric chlorenchyma cells with small air spaces. Abaxial epidermal cells all larger than adaxial ones; outer wall twice as thick as inner wall; walls equal to mesophyll walls. Subepidermal layer of sclerified fibres only in marginal regions of leaves, absent from the middle of the leaf (directly next to leaf margins), 2–3 cells thick; with large clear parenchymatous cells below abaxial furrow present, connected via collenchyma cells to the adaxial furrow to the epidermis and so partitioning the chlorenchyma. Bulliform cells absent; abaxial epidermal zonation present (Fig. 3G).

**Etymology.** *echinus* (Latin) = hedge-hog or sea-urchin. The plant is spiny like a hedgehog.

**Distribution and ecology.** South America, Peru.

**Altitude.** 4220–4230 m.

**Habitat.** Rock ledges (bedrock slabs); moisture regime: in soil pockets on rock. Forming cushions on almost flat rock slabs, in pockets of soil.

**Conservation status.** Known only from the type collection.

**Phenology.** Flowering month March or April.

**Taxonomy.** The small compact hedgehog form with pungent leaves is similar to *C. pungens*, from which it differs by the shattering leaves and the longer spikelets (glumes 15–25 mm long). The shattering leaf-sheaths link the species to *C. boliviensis*, but it differs by the very different growth form. The compact inflorescences are reminiscent of *C. egmontiana*, but the pungent leaves provide a simple diagnostic difference.

The leaf anatomy is reminiscent of that of *C. bifida*, but the outer bundle sheath is not lignified, and form an extension adaxially on the vascular bundles, connecting them to the lignified anchor-shaped girders.

### Bifida group

The leaf sheaths of this group are highly lacerated and form a tangled mat around the base of the plant. Anatomically there is nothing unusual about these species. The distinction between *C. columbiana* and *C. roraimensis* needs critical investigation.

### 13. *Cortaderia bifida* Pilg., Bot. Jahrb. Syst. 37: 374. 1906.

Figs 1J, 3H

*Cortaderia bifida* Pilg., Bot. Jahrb. Syst. 37: 374. 1906.

Type: Peru, “zwischen den Tambo Yuncacoya und Ramospata (Weg von Sandia nach Chunchusmayo), 2000–2400m”, 27 Jul. 1902, A. Weberbauer 1328 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 597 (1974): B-100217561! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217561>); isolecotype: US!).

*Cortaderia aristata* Pilg. Bot. Jahrb. Syst. 37: 375. 1906.

Type: Peru, Prov. Huamali, Dep. Huanuco, “Berge südwestlich von Monzon, 3400–3500m”, 11 Jul. 1903., A. Weberbauer 3349 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 597 (1974): B-100217562! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217562>); isolecotypes: K!, US!).

*Cortaderia trianae* Stapf ex Conert, Syst. Anat. Arundineae 100. 1961.

Type: New Granada, February 1892, J. Triana 289 (lectotype, designated as holotype by Conert, Syst. Anat. Arundineae 100 (1961): K!).

**Etymology.** *bis* (Latin) = twice + *fidu*, divide, this presumably refers to the lemma setae.

**Taxonomy.** This species can be diagnosed by the combination of the lacerated sheath bases, the long awns and especially the long setae. The shape of the lemmas with lobes and setae are shared with *C. hapalotricha*, and the curly fibrous leaf remains are similar to *C. roraimensis*. It is separated from *C. roraimensis* by the hairy lemmas and by the much longer awns and setae. It differs from *C. hapalotricha* by the glabrous adaxial surface above the ligule and the scaberulous inflorescence branches. From the other tall species, *C. nitida*, it can be separated by the longer awns (more than 8 mm long). The long awns and setae result in the inflorescences looking similar to those of *C. peruviana*, but the bases of the plants are quite different. Consequently, it can be difficult to determine collections which consist only of inflorescences.

The leaf anatomy (Fig. 3H), in transverse section, shows shallow abaxial groves and deep adaxial clefts. Adaxially there appear to be no papillae (different from the

*C. hapalotricha* anatomy). Abaxially below the epidermis are large colourless cells. The outer bundle sheath of the primary vascular bundles are completely lignified. Thus broadly similar to the *C. halalotricha* anatomy, but differing in a number of traits.

**14. *Cortaderia planifolia* Swallen, Contr. U.S. Natl. Herb. 29: 253. 1948.**

**Type.** Colombia, Dept. Valle del Cauca, Cordillera Occidental, extremo N, vertiente NW, entre Alto del Buey y Quebrada de los Ramos, 12 Oct. 1944, J. Cuatrecasas 18059 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 601 (1974): US 00133442!).

**Etymology.** *planus* (Latin) = flat + *folium* (Latin) = leaf. Leaf-blades flat.

**Taxonomy.** *Cortaderia planifolia* has many similarities to *C. pungens*, but is separated by the flat or folded, but not rolled, leaves; somewhat taller tussocks (0.5-1 m, compared to 0.2-0.5m); adaxial leaf surface above the ligule glabrous; glumes 8-15 mm long, compared to 12-16 mm; lemmas 4-8 mm, compared to 3-4 mm long; lemma awn less than 8 mm long, compared to more than 9 mm in *C. pungens*. These numerous small differences suggest that these are two species.

It has also been grouped with *C. hapalotricha*, from which it differs by the smaller size, the flat leaves glabrous above the ligule, the shorter lemma awn and setae.

Leaf anatomy not investigated.

**15. *Cortaderia hapalotricha* (Pilg.) Conert, Syst. Anat. Arundineae 102. 1961.**

Figs 1K, 3I

*Danthonia hapalotricha* Pilg., Bot. Jahrb. Syst. 25: 715. 1898.

Type: Colombia, Páramo between Usme and Pasca, Cudinamarca, June 1868, M. A. Stübel 111C (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 598 (1974): B, frag. US!).

*Cortaderia scabriflora* Swallen, Contr. U.S. Natl. Herb. 29: 252. 1948.

Type: Ecuador, near Treador, between Molleturo and Quinoas, Province of Azuay, along lake shore, 15 June 1943, J. A. Steyermark 53188 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 602 (1974): US 00027057!; isolectotype: NY!).

**Etymology.** *hapalos* (Greek) = soft + *thrix* (Greek) = hair. It presumably refers to the densely pubescent rhachilla.

**Nomenclatural comments.** The type specimen of *Cortaderia scabriflora* is intermediate between *C. hapalotricha*, *C. pungens* and *C. planifolia*. It has the lemma structure of *C. pungens*, the folded leaves typical of *C. planifolia*, the pungent leaves typical of both, but the size of *C. hapalotricha*. Overall, it approaches *C. hapalotricha*.

**Taxonomy.** Connor and Edgar (1974) note “The golden brown panicles with very hairy branches are obvious characteristics of this species.”, but these characters

are variable in the species. *Cortaderia hapalotricha* is morphologically very close to *C. columbiana*, especially by the inner leaf surfaces directly above the ligule being densely and finely woolly. Genetically, the two species are strongly supported as sister species. *Cortaderia hapalotricha* can be separated from *C. columbiana* by the longer glumes, which are much longer than the spikelets, by the denser inflorescences, and by the lemmas which have well developed setae. It is also similar to *C. bifida*, but the lemmas are longer and the setae shorter. Most convincing might be anatomical differences, these need to be corroborated with more sections. The leaf anatomy and spikelet structure indicate a very close relationship with *C. pungens*, and the two might just be ecological variants of each other. However, the growth form is quite different, and we keep them separate on this basis.

Leaf anatomically (Fig. 3I) this species is very similar to *C. columbiana*, with well developed adaxial ribs, and girders linking the vascular bundles to both surfaces, as well as well developed adaxial epidermal papillae. The only difference may be the absent or poorly developed abaxial subepidermal sclerenchyma layer.

**16. *Cortaderia columbiana* (Pilg.) Pilg., Bot. Jahrb. Syst. 37 (Beibl. 85): 65. 1906.**  
Fig. 1L

*Gynerium columbianum* Pilg., Bot. Jahrb. Syst. 27: 31. 1899.

Type: Colombia, Merida, sine data, J. W. K. Moritz 1558 & 1559 (lectotype, designated by Connor & Edgar, Taxon 23: 597 (1974): B 10 0217508! (<http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B100217508>); isotype: US! frag. ex B). Note: The other sheet collected by Moritz (B 10 027507) is *C. hapalotricha* (Connor and Edgar 1974).

*Cortaderia parviflora* Swallen, Contr. U.S. Natl. Herb. 29: 253. 1948.

Type: Venezuela, between La Trampa and Casadero, State of Merida, 28 April 1944, J. A. Steyermark 56182 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 600 (1974): US 00133441!).

**Etymology.** *-ana*, indicating connection. From Republic of Colombia.

**Taxonomy.** Connor & Edgar (1974) imply a similarity to *C. hapalotricha*, but note that the panicle is longer, more laxly flowered, and dull brown, and that this separates the two species. *Cortaderia columbiana* is superficially similar to *C. hapalotricha*, and also has short felty hair on upper leaf surface above the ligule, but is different by the shorter setae. Leaf anatomically they can be separated by the presence of a continuous lignified sub-epidermal layer on the abaxial side. It is also very similar to *C. roraimensis* by the lemma shape, in particular with the very short setae. However, the plant bases differ: in *C. roraimensis* the leaf bases are lacerated and curly, a feature less well developed in *C. columbiana*. Possibly the best way to separate the two species might be by the much more villous leaf margins, and often the villous adaxial leaf surface of *C. columbiana*. Geographically, the two species are also adjacent.

The leaf anatomy is like that of *C. hapalotricha*, but differs by a continuous sclerenchyma layer below the abaxial epidermis.

**17. *Cortaderia roraimensis* (N.E.Br.) Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 6: 112. 1914.**

Fig. 3J

*Arundo roraimensis* N.E.Br., Trans. Linn. Soc. London, Bot. ser. 2, 6: 74. 1901.

Type: British Guiana, summit Mt. Roraima, autumn 1898, F. V. McConnel & J. J. Quelch 673 (lectotype, designated as holotype by Connor & Edgar, Taxon 23: 601 (1974): K!).

**Etymology.** *-ensis* (Latin), denoting place of origin. From Mt Roraima, Guyana.

**Taxonomy.** This is the only *Cortaderia* species from the tepuis. It is very similar to *C. columbiana*. It shares with *C. columbiana* and *C. bifida* a base of dense clustered lacerated sheaths. From the similar *C. columbiana* it is separated by the almost absent indumentum on the leaf margin directly above the simple ligule. From *C. bifida* it is distinct by the lobed lemma, where the lobes are not extended into slender setae.

The leaf anatomy (Fig. 3J) follows the same basic plan as that of *C. hapalotricha*.

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# Reproductive biology and variation of nuclear ribosomal ITS and ETS sequences in the *Calligonum mongolicum* complex (Polygonaceae)

Wei Shi<sup>1,2</sup>, Jun Wen<sup>3</sup>, Yanfeng Zhao<sup>1,2</sup>, Gabriel Johnson<sup>3</sup>, Borong Pan<sup>1,2</sup>

**1** Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China **2** Turpan Eremophytes Botanic Garden, Chinese Academy of Sciences, Turpan 838008, China **3** Department of Botany, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

Corresponding author: Jun Wen (WENJ@si.edu)

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## Abstract

To explore the biosystematics of the *Calligonum mongolicum* complex (Polygonaceae), the flowering phenological period, breeding and pollination characters and seed set of the complex (*C. Mongolicum* Turze, *C. chinense* A. Los., *C. gobicum* A. Los., *C. pumilum* A. Los. and *C. zaidamense* A. Los.) were documented in the Turpan Eremophyte Botanical Garden, China. The sequences of the nuclear ribosomal ITS and ETS region were employed to differentiate the *C. mongolicum* complex and other species in sect. *Medusae*. The results showed species of the *C. mongolicum* complex occupied overlapping flowering periods and had consistent pollination agents. Their breeding systems are all self-compatible, tend to be out-crossing and they interbreed amongst each other (out-crossing index, OCI = 4). The crosses within and amongst species had high seed sets (44 - 65%). Phylogenetic analyses of *Calligonum* sect. *Medusae* and the network analysis of nrDNA (ITS and ETS) in the complex suggest interbreeding amongst “species” within the complex and provide evidence for taxonomically merging the five species in the complex. The detected hybridisation, occurring within the complex, suggests the need to improve traditional methods of *ex situ* plant conservation in botanical gardens for maintaining genetic diversity of *Calligonum* within and amongst species from different geographic areas.

## Keywords

*Calligonum mongolicum* complex, Phenology, Breeding System, Crossing experiments, Phylogeny, ETS, ITS

## Introduction

*Calligonum* L. is widely distributed in Northern Africa, Southern Europe and Western and Central Asia (Bao and Alisa 2003). It is the only genus in Polygonaceae that contains  $C_4$  species (Pyankov et al. 2000) with rapid rates of evolution and diversification (Mabberley 2008). The taxonomy of this genus is complex (Xu 1998) and that of the *Calligonum mongolicum* Turcz. complex is especially difficult. *Calligonum mongolicum* Turcz. is widely distributed from Xilinhote-Inner Mongolia in the east, Kyzyl Kum Desert in Uzbekistan in the west, Milan in Xinjiang in the south, Baitashan, Qitai and Karamay in Xinjiang in the north, with a longitudinal range of about  $30^\circ$  (Pavlov 1936; Drobov 1953; Baitenov and Pavlov 1960; Sergievskaya 1961; Kovalevskaja 1971; Shi et al. 2011). *Calligonum pumilum* A. Los., *C. gobicum* A. Los., *C. chinense* A. Los., *C. alashanicum* A. Los., *C. zaidamense* A. Los. and *C. roborowskii* A. Los. (1927) of the complex occur within the geographic range of *C. mongolicum* (Losinskaja 1927; Bao and Grabovskaya-Borodina 2003). All of these more narrowly ranged species were merged into *C. mongolicum* based on the variation of their fruit characters and the chromosome numbers (Soskov 1975a, 1975b). However, these species are currently recognised in the Flora of China treatment according to their fruit morphology (Bao and Grabovskaya-Borodina 2003; Mao et al. 1983). Nevertheless the fruits are overall similar, making it difficult to distinguish the species of the complex (Soskov 2011, Mao and Pan 1986, Shi et al. 2011; Table 1). Analyses of the reproductive biology of the complex are important for resolving the taxonomy and exploring the evolutionary processes (Stebbins 1950; Grant 1992, 1994; Oldfield 2009).

Studies on the reproductive biology of *Calligonum* are rare. Kang et al. (2011) assessed information from four taxa (*Calligonum calliphysa* Bunge, *C. rubicundum* Bge., *C. densum* Borszcz and *C. ebinuricum* Ivanova) which were selected from each section (four sections in *Calligonum*) and revealed that all the investigated species were self-compatible but there was no hybridisation amongst them. A few examples of hybridisation were mentioned such as between *Calligonum dubjanskyi* Litv. and *C. bubuyri* B. Fedtsch. ex Pavl., between *C. acanthopterum* and *C. leucocladum* and between *C. acanthopterum* Borszcz. and *C. leucocladum* (Schrenk) Bunge (Soskov 1975b). These reported hybrids occurred between species within a section, including sect. *Peterococcus* and sect. *Medusae*. The taxonomic relationships of the genus have been tested by the applications of several molecular techniques, such as the RAPD markers (Ren et al. 2002) and other chloroplast DNA markers (*trnL-F*, *matK*, *atpB-rbcL*, *psbA-trnH*, *psbK-psbI* and *rbcL*) (Tavakkoli et al. 2010; Sanchez et al. 2011; Abdurahman and Sabirhazi 2012; Sun and Zhang 2012; Li et al. 2014), but the markers employed so far have been inefficient for resolving the taxonomic problems in *Calligonum*. It was expected that reproductive biology and faster-evolving nuclear DNA sequences (Sang 2002; Zimmer and Wen 2012) might shed some light on the taxonomy of the genus.

The *Calligonum mongolicum* complex is almost exclusively diploids with  $2n$  ( $2x$ ) = 18, except *C. roborowskii* with  $2n$  ( $4x$ ) = 36 (Wen et al. 2016), although a polyploid count was reported as  $2n$  ( $3x$ ) = 27 (Shi et al. 2013) in an individual of *C. mongolicum*.

**Table 1.** Differences in fruit characters among species of the *Calligonum mongolicum* complex according to the treatment in Flora of China, the monograph of Soskov (2011) and the observations by Shi et al. (2011). \* NRR = Number of rows of bristles in each rib.

	<i>C. mongolicum</i>			<i>C. pumilum</i> (syn. <i>C. rubescens</i> )			<i>C. chinense</i> (syn. <i>C. litwinowii</i> Drob.)			<i>C. gobicum</i> (syn. <i>C. litwinowii</i> Drob.)			<i>C. zaidamense</i> (syn. <i>C. litwinowii</i> Drob.)		
	Flora of China	Soskov (2011)	Shi et al. (2011)	Flora of China	Soskov (2011)	Shi et al. (2011)	Flora of China	Soskov (2011)	Shi et al. (2011)	Flora of China	Soskov (2011)	Shi et al. (2011)	Flora of China	Soskov (2011)	Shi et al. (2011)
<b>Fruit morphology</b>															
Fruit length (mm)	8-12	8-12	5-15	7-12	12-22 mm	5-17	10-15	9-12	8-13	11-18	9-12	10-12	10-17	9-12	11-18
Seta length (mm)	-	3.5-5	1-5	-	(3)5-8(10) mm	1-5	-	3.5-5	2-7	-	3.5-5	2-4	-	3.5-5	3-6
NRR*	2 or 3	(1)2(3)	2 or 3	1	(2)3	1 or 2	3	2 or 3	2 or 3	2	2 or 3	2	2	2 or 3	2
Ribs flat or elevated	prominent or not	flat	prominent or not	-	elevated	prominent or not	flat	little elevated	flat	flat	little elevated	flat	flat	little elevated	flat
Seta texture & branching	soft, thin, 2 or 3 -branched	soft, thin, 2-branched	soft, thin, 2, 3 or 4 branched	soft, thin, 2 or 3 -branched	soft, 3-4 -branched	soft, thin, 2, 3 or 4 branched	thick, stiff, 2 or 3 branched	thick, 3 or 4 branched	thick, stiff	thick, breakable, 2-branched	thick, 3 or 4 branched	thick, breakable	thick, breakable, 2-branched	thick, 3 or 4 branched	thick, breakable
Seta distance (mm)	-	moderately dense	0.2-2	-	0.7-1	1-2	-	0.5-1.2	0.5-2	-	0.5-1.2	0.1-1.8	-	0.5-1.2	1.2-2.3
Nutlet length (mm)	-	9-10	5-10	-	7-10	5-12	8-11	6-10	1.5-9.2	-	6-10	6.7-8.2	-	6-10	7.2-12
Nutlet width (mm)	-	2.8-3	2-6	-	3-3.5	2-5	3-5	4-5	3.6-9.8	-	4-5	3.0-4.1	-	4-5	3.1-7.2
Nutlet coiled or not and its form	not coiled, ellipsoid	not coiled	coiled or not	coiled, ovoid	coiled	coiled or not	coiled, ellipsoid	coiled	coiled, ellipsoid	not coiled, oblong	coiled	not coiled, ellipsoid	not coiled, broadly ovoid or ellipsoid	coiled	not coiled, broadly ovoid or ellipsoid

The situation is markedly different in other species of the *Calligonum* sect. *Medusae* which are polyploids with the most frequent chromosome number  $2n$  ( $4x$  or  $6x$ ) = 36 or 54 (Wang and Yang 1985; Wang and Guan 1986; Shi and Pan 2015). The above chromosomal data indicate the significant role of polyploidy in the evolution of the sect. *Medusae* of *Calligonum*. The flowering phenology, characters of breeding systems and pollination and fruit set of the *C. mongolicum* complex (*C. mongolicum*, *C. pumilum*, *C. chinense*, *C. alashanicum* and *C. zaidamense*) have been documented by the authors, leaving out the tetraploid *C. roborowskii* (see also Wen et al. 2016). The phylogeny of *Calligonum* sect. *Medusae* has been reconstructed using nuclear ribosomal markers (ITS and ETS). The new data will be used to discuss the taxonomic implications of the species complex and the conservation strategy of *Calligonum* in botanical gardens.

## Materials and methods

Five species of the *Calligonum mongolicum* complex (*C. mongolicum*, *C. pumilum*, *C. chinense*, *C. alashanicum* and *C. zaidamense*) were selected by the authors, leaving out the tetraploid *C. roborowskii*. These selected species were brought to Turpan Eremophytes Botanical Garden (TEBG) from their natural habitats during 2011 to 2013 and were planted in the germplasm garden of *Calligonum* (Table 2, Qi and Pan 2010; Shi et al. 2013).

## Collection of phenological information

Phenological information of the *Calligonum* species was collected from field investigations. The phenological observations were made once every two days during the growing period, according to the method of the Chinese Phenological Observation Standard (Zhu and Wan 1973). The investigated flowering phenological periods included flower bud appearance, beginning of flowering, flower blooming, end of flowering and fruit maturity. The starting date of a species' growing period was expressed in the day of year (calculated from 1 January of the current year and thereafter).

Five plants from each species in the field were randomly selected to document the flowering phenology and they were observed every day in the blooming and fruiting periods from 2011 to 2013.

## Pollen morphology

Scanning electron microscopy (SEM) was used to document the micromorphology of pollen. Samples were dehydrated and were then placed on aluminium stubs using double-sided adhesive tape and sputter coated with gold in a Hitachi E-1010 Ion

**Table 2.** Voucher information for the samples used in the study.

Species	Pop.	individuals (flowers in an individual)	Location	Num. in DNA analysis	Coordinates	
					ITS	ETS
<i>C. mongolicum</i>	M1	3(25)	Erlianhaote, Neimeng, China E112°03' N43°45' 898 m	M1–2	KU050839	KY316968
				M1–3	KU050840	KY316961
	M2	3(25)	Qingtongxia, Ninxia, China E105°55' N38°01' 1134 m	M2–1	KU050847	KY316966
				M2–2	KU050853	KY316970
	M3	3(25)	Erjinaqi, Inner Mongolia China E100°26' N41°27' 1002 m	M3–1	KU050846	KY316971
				M3–2	KU050848	KY316973
				M3–3	KU050838	KY316979
	M4	3(30)	Wuerhe, Kelamayi, Xinjiang, China E 85°45' N 46° 9' 521 m	M4–1	KU050849	KY316969
M4–3				KU050850	KY316972	
<i>C. pumilum</i>	P1	3(50)	Hami, Xinjiang, China E091°32' N43°23' 1038 m	P1–1	KU050851	KY316974
				P1–2	KU050852	*
				P1–3	KU050841	KY316960
	P2	3(25)	Hami, Xinjiang, China E091°23' N43°20' 1273 m	P2–3	KU050843	KY316962
	P3	3(25)	Liuyuan, Gansu, China E095°28' N95°28' 1744 m	P3–1	KU050844	KY316963
P3–2				KU050845	KY316975	
<i>C. chinense</i>	C1	3(100)	Zhangye, Gansu, China E100°18' N39°28' 1458 m	C1–2	KY316981	KY316977
<i>C. gobicum</i>	G1	3(100)	Mingqing, Gansu, China E102°52' N38°34' 1369 m	–	–	–
<i>C. alashanicum</i>	A1	3(100)	Erjinaqi, Inner Mongolia China E100°27' N41°43' 969.8 m	A1–2	KY316980	KY316967
<i>C. zaidamense</i>	Z1	3(100)	Zhangye, Gansu, China E100°18' N39°03' 1458 m	Z1–1	KY316982	KY316978
				Z1–2	KY316983	KY316965
<i>C. calliphysa</i>	–	1	–	<i>C. calliphysa</i>	KX186585	KY316976
<i>C. arich</i>	–	6	–	–	KC585438	–
					KC585446	
					KC585445	
					KC585444	
					KC585477	
<i>C. comosum</i>	–	2	–	<i>C. comosum</i>	KC585417	–
					KC585430	
<i>C. caput-medusae</i>	–	1	–	–	JB187106	–
<i>C. ebinuricum</i>	–	1	–	<i>C. ebinuricum</i>	JQ731664	–
					JQ731665	
					JQ731663	
<i>C. molle</i>	–	1	–	–	GQ206245	–
<i>C. crinitum</i>	–	1	–	–	AB542776	–
<i>C. junceum</i>	–	1	–	<i>C. junceum</i>	GQ206243	–
					AB542774	
					JX987230	
<i>C. polygonoides</i>	–	1	–	–	AB542776	–

Species	Pop.	individuals (flowers in an individual)	Location	Num. in DNA analysis	Coordinates	
					ITS	ETS
<i>C. mongolicum</i>	–	1	–	<i>C. mongolicum</i>	JX259384	–
					JX259385	
<i>C. roborowskii</i>	–	1	–	<i>C. roborowskii</i>	JX259386	–
					JX259387	
<i>C. takemakanense</i>	–	1	–	<i>C. takemakanense</i>	JX259390	–
<i>C. persicum</i>	–	1	–	<i>C. persicum</i>	AB542777	–

Sputter Coater, following Wen and Nowicke (1999). The materials were subsequently observed and photographed under a Hitachi S-4800 scanning electron microscope. Pollen sizes from both polar view (P) and equatorial view (E) were measured using 10 grains of each sample.

### Controlled crossing experiments and observations on fruit and seed sets

The breeding systems of the *C. mongolicum* complex were examined by a hand-pollination test. More than 1600 buds were marked and bagged before opening during the period 2011 to 2013. Each flower of an individual plant was randomly assigned to one of the following treatments with each treatment, except hybridisation, including about 30 flowers in each taxon: i) autonomous pollination: no treatment but just bagging to test self-pollination naturally; ii) selfing: test for self-compatibility by bagging and undertaking pollination from the same flower; iii) geitonogamous selfing: emasculation, bagging and pollination in the same individual but using different flowers, to test for self-compatibility; iv) crossing: emasculation, bagging and pollination from another individual that was located more than 2m from the recipient v) apomixis: emasculation, bagging but no pollen; vi) natural pollination: emasculation, no bagging; vii) autonomous pollination via geitonogamy: bagging the whole branch; viii) hybridisation: emasculation and cross-pollinations with four other species, each species included 100 flowers. The stigma receptivity time was about 12 hours; and the pollen viability was about 12-24 hours (XS Kang, W Shi and BR Pan, unpublished data).

### DNA extraction, amplification and sequencing

Nineteen (19) individuals of six species, *C. mongolicum*, *C. pumilum*, *C. chinense*, *C. alashanicum*, *C. zaidamense* and *C. calliphysa* were sequenced and 24 ITS sequences of *Calligonum* from GenBank were downloaded (Table 2). Young green branches of each species were collected from natural populations in China (Table 2). The samples were collected from adult individuals with green healthy branches (with no signs of parasitism or of drought stress). They were dried in silica gel and kept in a freezer at

-25°C. Voucher specimens of the studied material were deposited in the Herbarium of Institute of Ecology and Geography in Xinjiang (XJBI).

Total genomic DNAs were extracted from fresh or silica gel dried assimilating branches following the protocol of Doyle and Doyle (1990). In this study, the protocols were followed for obtaining ITS sequences in plants by Wen and Zimmer (1996), Stanford et al. (2000) and Feliner and Rossello (2007). The ETS primers were newly designed for the study with the forward primer ETS<sub>calli1</sub>: 5'-GTTACTTACACTCC-CCACAACCCC-3' and the reverse primer as18SIGS: 5'-GAGACAAGCATATGACTACTGGCAGGATCAACCAG-3'. The DNA amplifications via a polymerase chain reaction (PCR) were performed using 10 ng of genomic DNA, 4 pmol of each primer, 0.5 U Taq polymerase (Bioline, Randolph, MA, USA) and 2.5 mM MgCl<sub>2</sub> in a volume of 25 µL using a PTC-225 Peltier thermal cycler. The PCR cycling parameters were as follows: 95 °C initial heating for 5 min, 40 cycles of 94 °C for 30s, 55°C for 45s for ITS (60°C for 40s for ETS) and 72°C for 60s and 72 °C for 10 min for final extension. The PCR products were purified using EXO-SapIT (US Biological, Swampscott, MA, USA) and sequenced in both directions using PCR primers. The ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, CA, USA) was carried out for cycle sequencing with mixing in a 10 µL reaction volume including 5 ng of primer, 1.5 µL of sequencing dilution buffer and 1 µL of cycle sequencing. The conditions were as follows: 35 cycles of 96 °C for 30s denaturation, 50 °C for 30s annealing and 60 °C for 4 min elongation. An ABI 3730xl DNA analyser (Applied Biosystems, Foster City, CA, USA) was used for separating the sequencing products. Both strands of DNA with overlapping regions ensured that each base was double-checked. We assembled the electropherograms and generated the consensus with Sequencher 4.5 (GeneCodes, Ann Arbor, MI, USA).

Sequences were initially aligned using MUSCLE 3.8.31 (Edgar 2004), followed by manual adjustments using GENEIOUS 8.1.2 (Kearse et al. 2012). The newly generated sequences from the 20 samples of *Calligonum* were deposited in GenBank (Table 2). The jModeltest 2.1.7 (Posada 2008, Darriba et al. 2012) was used to show the best-fit model of sequence evolution for each data. The Bayesian inferences were run according to the model chosen by the Akaike information criterion (AIC) method. Phylogenetic relationships were inferred using both maximum-likelihood estimation (ML) in RAxML (Stamatakis 2006) and Bayesian inference (BI) in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Bayesian analyses were conducted using the combined ITS and ETS data sets, using partitions of the respective models from the jModeltest. The ML analyses also used the partition of the two markers. The bootstrap analysis (Felsenstein 1985) was executed with 1000 replicates, with a maximum of 100 trees saved per replicate. The Bayesian inference was run with 2,000,000 generations and the Markov chain Monte Carlo (MCMC) run had one cold and three incrementally heated chains. For each dataset, all Bayesian analyses produced split frequencies of less than 0.01 and convergence between the paired MCMC runs were repeated twice to avoid spurious results. The remaining trees were used to construct majority-rule consensus trees after discarding the first 2000-5000 trees as burn-in before stationary conditions were

established. A neighbour-net analysis was conducted using the uncorrected p-distance between individuals and the programme SplitsTree 4.13.1 (Huson and Bryant 2006). Branch support was tested using bootstrapping with 1000 replicates.

## Results

### Phenological data

The bisexual flowers occur in groups of two to four in assimilating branches of the *Calligonum* species. The perianth has five tepals, which are green or red with a broad white margin abaxially, ovate, unequal and persistent in fruits. The flower has 12–18 stamens and the filaments are connate at the base. The pollen presentation pattern is gradual and, when pollen is viable, the stigmas also have receptivity (no dichogamy) (BR Pan, unpublished data).

The five *Calligonum* species flower from mid-April to mid-May in the field. The duration of *C. mongolicum* and *C. gobicum* for flowering was generally from mid-April to early May, whereas that of *C. pumilum*, *C. chinense* and *C. zaidamense* was from late April to mid-May; individual species of *C. mongolicum* continued to flower sporadically until late May. Thus the blooming period was similar for *Calligonum* both in field and in TEBG (Figure 1).

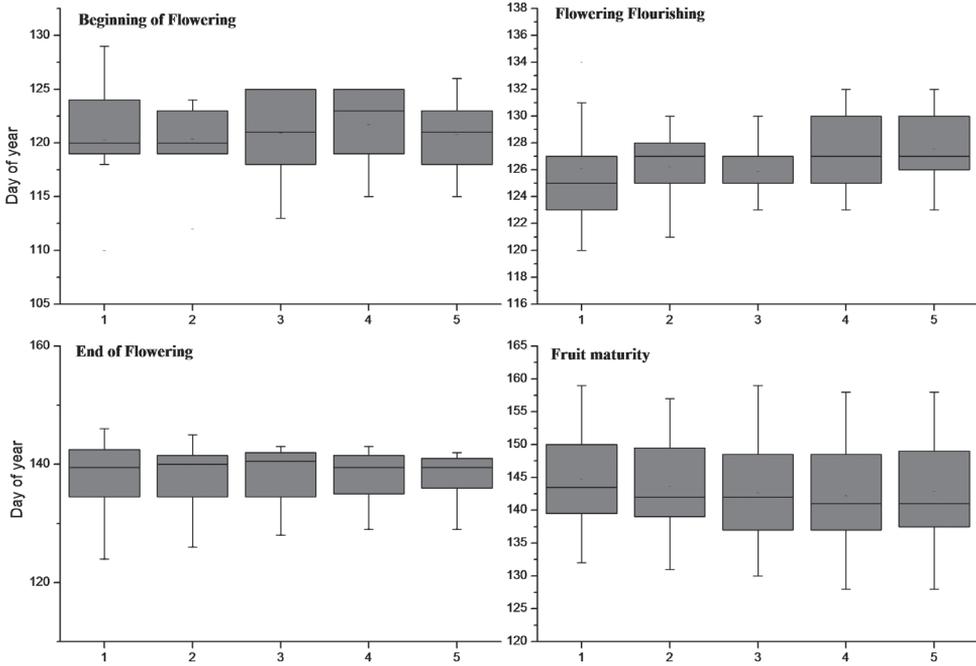
The blooming periods of the complex overlapped and the percentage overlap was about 80–100% (Figure 1). The peak flowering periods of *C. mongolicum* complex occurred at the same time in early May. Although flowering was generally ending in early May, flowering in some individuals of *C. mongolicum* was still at its peak until mid-May.

### Floral visitors

The major pollinators for collecting pollen and nectar were *Apis mellifera* L. and *Halic-tus* sp., both of which collected pollen in pollen baskets on their third legs and, occasionally, pollen also adhered to their chests and then contacted with the stigmas whilst feeding. These species frequently visited nearby flowers on the same plant individual and frequent visits on the same flowers were also undertaken. Other recorded species were nectar thieves including some flies (*Lasioticus* sp., *Musca domestica* and *Calliphoravicina*), butterflies (*Plebejusargus*) and others in Formicidae.

### Breeding systems

The results of the pollination experiment suggested that species in the complex had analogous mating systems (Tables 3 & 4), as both geitonogamy and cross-pollination conducted by hand yielded better fruit sets compared with natural pollination. They



**Figure 1.** The phenological phases of the *Calligonum mongolicum* complex. **1** *C. mongolicum* **2** *C. chinense* **3** *C. gobicum* **4** *C. pumilum* and **5** *C. zaidamense*.

**Table 3.** Comparison of actual fruit set of species in the *Calligonum mongolicum* complex under each pollination treatment in 2011 to 2013 (n = the total number of flowers manipulated in each treatment, data shown are mean ± SE).

Treatment	Species				
	<i>C. mongolicum</i>	<i>C. gobicum</i>	<i>C. chinense</i>	<i>C. pumilum</i>	<i>C. zaidamense</i>
No emasculatum, bagged, self-pollination	0	0	0	0	0
Emasculatum, bagged, hand geitonogamy	2.00±1.00	1.67±0.58	1.00±1.00	1.00±1.00	1.00±1.00
Emasculatum, bagged, hand cross pollination in same individual	15.12±1.00	16.58±1.22	17.24±1.31	17.32±1.23	14.42±1.25
Emasculatum, bagged, no pollination	0.00	0.00	0.00	0.00	0.00
Emasculatum, unbagged, natural pollination	11.21±2.13	9.15±2.54	12.48±2.41	12.47±1.21	13.56±2.15
Unemasculatum, unbagged, natural pollination	11.23±1.23	15.45±1.58	8.35±3.35	14.28±3.69	10.25±2.36

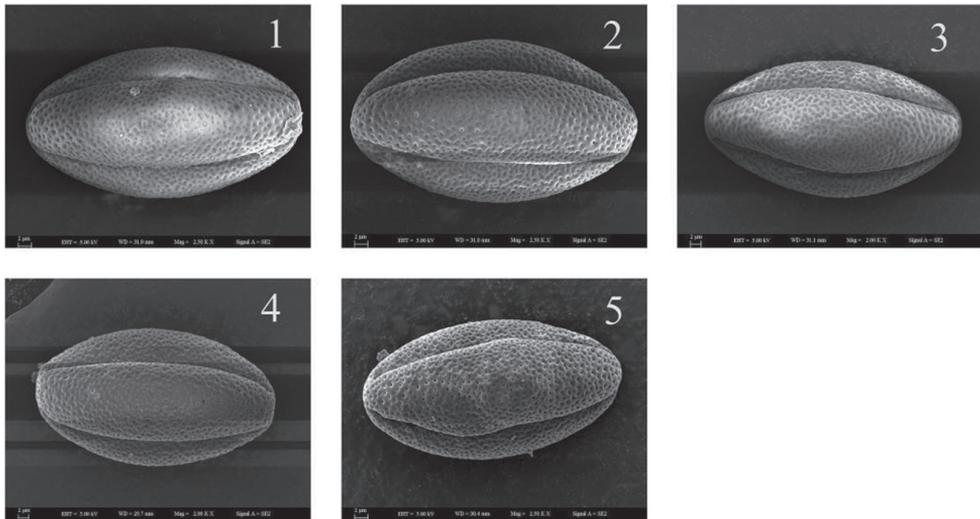
also had similar pollen characters and indices (P & E) (Table 5 & Figure 2). They interbred amongst each other (OCI = 4). The spontaneous self-pollination did not occur because when pollinators were excluded in the bagging treatment, no fruits were produced. It resulted in a very low (if any) fruit set in the self-pollination treatment.

**Table 4.** Fruit set (%) for the five *Calligonum* species under different cross-pollination treatments (n = the total number of flowers manipulated in each treatment, mean ± SE).

Species cross	<i>Calligonum mongolicum</i> ♂	<i>Calligonum gobicum</i> ♂	<i>Calligonum chinense</i> ♂	<i>Calligonum pumilum</i> ♂	<i>Calligonum zaidamense</i> ♂
<i>Calligonum mongolicum</i> ♀	65±1.25	54±3.21	41±1.15	47±1.68	45±1.25
<i>Calligonum gobicum</i> ♀	47±2.34	44±2.47	59±4.21	57±1.51	47±2.36
<i>Calligonum chinense</i> ♀	58±1.21	46±2.11	59±4.18	66±2.12	48±3.25
<i>Calligonum pumilum</i> ♀	48±2.24	59±4.56	54±3.06	65±2.14	52±2.48
<i>Calligonum zaidamense</i> ♀	44±2.14	58±1.63	47±1.85	60±1.23	51±4.21

**Table 5.** The characteristics of the pollen grains of five species of the *Calligonum mongolicum* complex.

Species	Shape	Length (µm)	width(µm)	P/E	Aperture	ornamentation
<i>Calligonum mongolicum</i>	Prolate	38.90	23.20	1.68	tricolporate	reticulate
<i>Calligonum gobicum</i>	Prolate	38.35	19.51	1.97	tricolporate	reticulate
<i>Calligonum chinense</i>	Prolate	33.45	21.15	1.58	tricolporate	reticulate
<i>Calligonum pumilum</i>	Prolate	31.52	22.40	1.41	tricolporate	reticulate
<i>Calligonum zaidamense</i>	Prolate	37.79	20.04	1.89	tricolporate	reticulate



**Figure 2.** Equatorial view of pollen grains of the *Calligonum mongolicum* complex under SEM micrographs. **1** *C. mongolicum* **2** *C. chinense* **3** *C. gobicum* **4** *C. pumilum* and **5**. *C. zaidamense*.

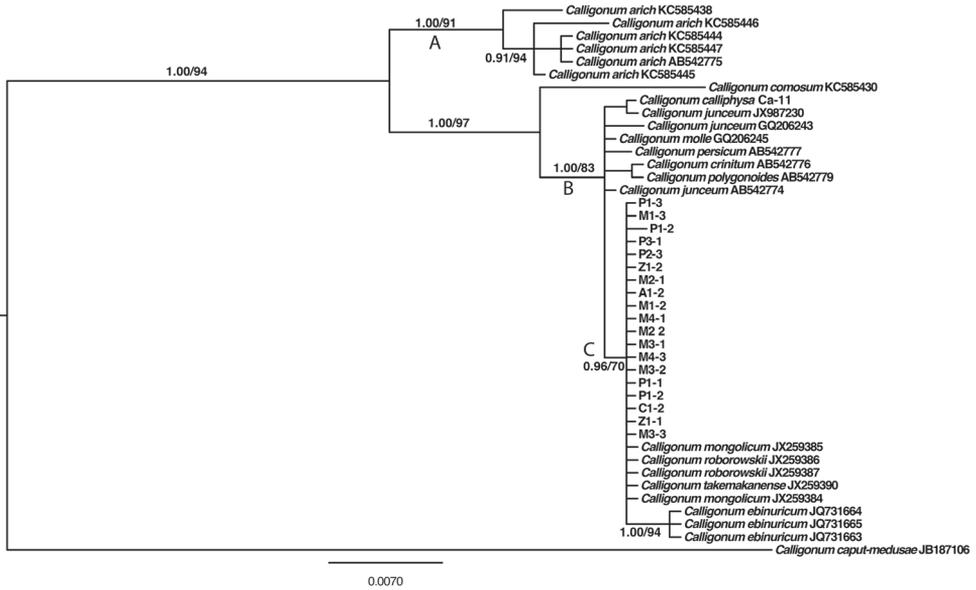
The fruit set using geitonogamy treatment shows self-compatibility within each species. The apomixis did not occur in these species as exclusion of both pollinators and emasculation did not result in any fruit set.

Hybridisation experiments in the complex resulted in a fruit set and the results (in percentage terms) are shown in Table 4. The flowering of the complex was synchronised. The pollen morphology of the five species showed similarities in major pollen characteristics such as shape, size and exine characters (Figure 2, Table 5). The hybridisation experiments and interspecific hand pollination yielded some viable seeds (Table 5). The maximum of the fruit set is amongst the *C. mongolicum* ( $65 \pm 1.25$ ) and the *C. pumilum* ( $65 \pm 2.14$ ) themselves; the minimum is that between *C. chinense* and *C. mongolicum* ( $41 \pm 1.15$ ). In general, the fruit set amongst the five species is similar ( $p > 0.05$ ).

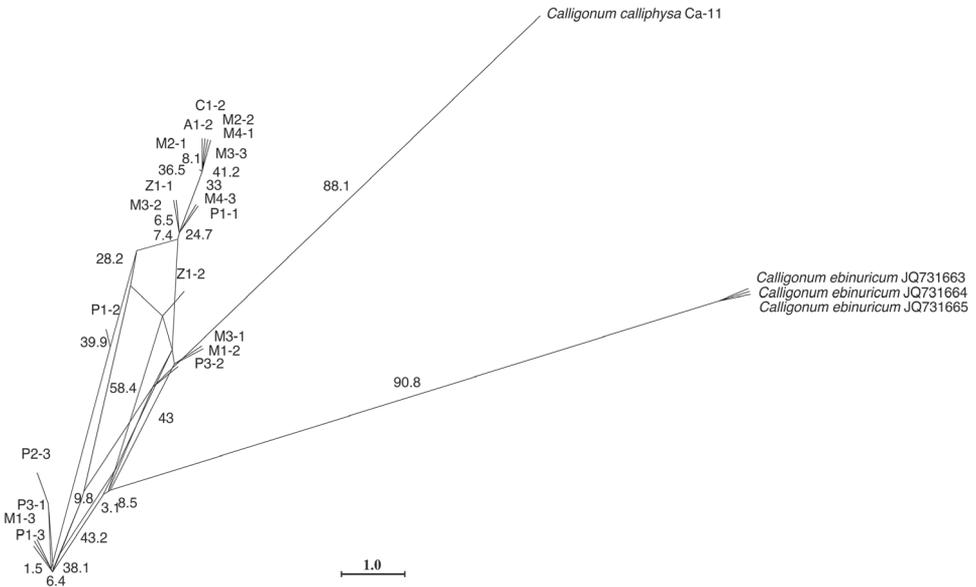
### Phylogenetic analysis

The aligned matrix with 45 accessions of nrITS and ETS is 807bp long. The Phi test did not find statistically significant ( $p = 0.0323$ ) evidence for the presence of chimeric sequences in the nrITS and ETS data matrix. The nrITS and ETS sequence alignment used for phylogenetic tree reconstruction included 44 sequences: 43 from the in-group and one of *C. caput-medusae* as the out-group. The data sets included 20 newly generated nrITS, 23 ITS sequences from GenBank and 20 new ETS sequences (Table 2).

The model test suggested F81 for ETS (nucleotide frequencies A = 0.2023, C = 0.3494, G = 0.2778, T = 0.1706) and TPM2uf for ITS (nucleotide frequencies A = 0.1873, C = 0.3265, G = 0.3277, T = 0.1586; substitution rates: RAC = 0.3484, RAG = 3.4478, RAT = 0.3484, RCG = 1.0000, RCT = 3.4478, RGT = 1.0000). The Bayesian inference used the partition of ITS and ETS based on the respective models. The ML analyses used GTR+G as the model. Topologies inferred by the two phylogenetic tree reconstruction methods were congruent (Figure 3). The most morphologically distinctive *C. caput-medusae* from Central Asia was used as the out-group, the first diverged clade in the analyses being *C. arich* (six accessions included, PP 1.00, BS 92) from western Asia, the remaining species forming a large clade A. Of interest, all species from the *C. mongolicum* complex formed a clade. The five species of the *C. mongolicum* complex, *C. ebinuricum* and two other species *C. roborowskii* and *C. taklamakan* were distributed within the broad geographic region of the *C. mongolicum* complex, but *C. roborowskii* and *C. taklamakan* were of a more restricted distribution in the Taklamakan Basin of Xinjiang province, China. The three individuals of *C. ebinuricum* which form an independent clade, have specific fruit characters different from the complex. The individuals of *Calligonum mongolicum* and *C. pumilum* each did not form a clade, but they were intermixed with *C. alashanicum*, *C. zaidamense* and *C. chinense*, *C. roborowskii* and *C. taklamakan*, forming a large clade C (Figure 3). It is of interest to note that the p-distance amongst taxa of *Calligonum* for the ITS and ETS region is as high as 11.364% between the out-group species *C. caput-medusae* and *C. mongolicum* JX259384. Within the clade C, the p-distance was as high as 0.564% between *C. ebinuricum* and *C. mongolicum* JX259384. A neighbour-net was constructed for the *C. mongolicum* complex using ITS and ETS sequences which also supported the complex in one branch (Figure 4).



**Figure 3.** Maximum likelihood tree for 43 (in-group) *Calligonum* nrITS and ETS sequences produced with RAxML. Numbers adjacent to (relevant) nodes represent maximum likelihood value and Bayesian posterior probabilities. Branches marked with an asterisk collapse on the maximum likelihood strict consensus tree of the same dataset. The branch marked with a number sign collapses on the Bayesian majority rule consensus tree of the same dataset.



**Figure 4.** Neighbour-net analyses of the *Calligonum mongolicum* complex, *C. ebinuricum*, *C. calliphysa* and closely related taxa based on uncorrected p-distances. Numbers indicate bootstrap values over 1000 replicates.

## Discussion

### Evidence for interbreeding of species in the *Calligonum mongolicum* complex

Species isolation is frequently caused by the temporal heterogeneity of blooming amongst sympatric species (Levin 1971; Adams 1983; Grant 1992, 1994). The flowering periods of five species in the complex showed a high degree of overlapping, with some differences in peak blooming periods (also see cases in Wilson 1983; Burd 1995).

These five diploid species of *Calligonum* have similar pollen characters in both with spheroidal shape and tricolporate apertures with each other (Figure 2). The other species in *Medusae* also have the similar pollen characters but without specific pollen indexes (P&E) analysis (Qiu 1988; Gulinuer 2008). The hand-pollination tests suggested the five species are self-compatible (geitonogamous, not autophilous). Furthermore, pollinators were necessary for the sexual reproduction in the complex, although some fruit sets were resulted with exclusion of pollinators. The results of test crosses suggest the existence of a strong internal hybridisation potential in each of these species.

Crossing compatibility between the species of the *C. mongolicum* complex is largely the same as that between individuals within the same species (Table 4). The crossing behaviour amongst them is consistent with the view from Soskov (1975a, 1975b) by treating these various segregate species as one variable biological species of *C. mongolicum*.

### Lack of phylogenetic structure and nrDNA sequence variation as indirect evidence for interbreeding in the *C. mongolicum* complex

Although phylogenetic inference based on nrITS needs to be considered carefully (Alvarez and Wendel 2003, Feliner and Rossello 2007), some conclusions may be drawn based on the ITS and ETS analyses of the target species. As shown by the ML and Bayesian trees of nrITS and ETS sequences (Figure 3), a striking divergence exists between *C. arich* (clade A) and other species. Yet species of the *C. mongolicum* complex had very similar or identical sequences (Clade C in Figure 3). The nrITS and ETS tree together with the network of ribotypes (Figure 4) suggest the lack of phylogenetic structure within the complex. Excluding *C. arich* (5 individuals), *C. ebinuricum* (3 individuals) can be easily differentiated from the *C. mongolicum* complex (13 individuals) (Figures 3 and 4). The intermixed patterns of sequences from different “species” of the *C. mongolicum* complex may indicate past or present introgressive potential of the *C. mongolicum* complex and argues for the existence of hybridisation or interbreeding (if these “species” represent the same taxon).

### Implications on taxonomy and conservation of *Calligonum*

*Calligonum* is one of the medium-sized genera of Polygonaceae with approximately 60–80 species and represents a rapid diversification in the hot and arid deserts of Central Asia

to western China (Mabberley 1990). Molecular analyses of both nrDNA ITS and some cpDNA sequences (*trnL-F*, *matK*, *atpB-rbcL*, *psbA-trnH*, *psbK-psbL* and *rbcL*) have not resolved relationships amongst species of *Calligonum* (Sanchez et al. 2011, Sun and Zhang 2012, Li et al. 2014). Our study showed that *C. ebinuricum* possesses highly distinct nrITS sequences (Figures 3 & 4); yet the ITS and ETS sequences of the *C. mongolicum* complex generated a topology with the species of the complex highly intermixed with each other in the tree. The authors' results both in this paper and in their previous studies (Shi et al. 2011, 2012, 2013, 2016, Shi and Pan 2015) argue for the merging of *C. chinense*, *C. gobicum*, *C. pumilum* and *C. zaidamense* with *C. mongolicum* as proposed by Soskov (1975a, 1975b). Detailed evidence was also recently presented on merging *C. pumilum* with the more widespread *C. mongolicum* (Shi et al. 2016). Detailed morphological comparisons of the other species in the complex will be pursued by the authors as was done for *C. pumilum* and *C. mongolicum* (Shi et al. 2016) and the phylogeographic structure of the complex will be further explored with phylogenomic methods (Wen et al. 2015, Zimmer and Wen 2015).

Distributional ranges of some species in clade C (Figure 3) do not overlap but are geographically close or adjacent to each other. *Calligonum roborowskii* ( $2n=36$ ) grows at the edge of Taklamakan basin; *C. taklamakan* occurs in the central part of the basin; and the other species in the complex except *C. mongolicum* are confined to the south-eastern edge of the basin and *C. ebinuricum* is in North Xinjiang and also in Mongolia but never in South Xinjiang. According to their morphological comparisons (Gulinuer 2008, Kang et al. 2008), the taxonomic relationship of *C. ebinuricum* and *C. taklamakan* with other species needs further analyses. The fact that most of the collected seeds can germinate without any pre-treatment suggests that the five *Calligonum* species produce enough seeds to renew the populations. On the other hand, the *ex-situ* conservation of genetic diversity for the long-term survival of species of *Calligonum* needs a new management strategy due to their reproductive biology and the potential for hybridisation/interbreeding (Kramer and Havens 2009, Swarts and Dixon 2009). Special efforts are needed to ensure isolation of genetic sources in *ex situ* conditions.

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The authors declare that they have no conflict of interest.

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# Two new species and a new combination in *Protium* (Burseraceae) from Costa Rica

Daniel Santamaría-Aguilar<sup>1</sup>, Laura P. Lagomarsino<sup>2</sup>

**1** Current address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, USA **2** Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, USA, and University of Missouri–St. Louis, Biology Department, One University Blvd., Research Building, St. Louis, MO 63121, USA

Corresponding author: Daniel Santamaría-Aguilar ([daniel.santamaria366@gmail.com](mailto:daniel.santamaria366@gmail.com); [Daniel.Santamaria@mobot.org](mailto:Daniel.Santamaria@mobot.org))

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## Abstract

Two new species of *Protium* (Burseraceae) are described and illustrated: *Protium aguilarii* **sp. nov.**, from the Pacific slope of the Osa Peninsula, Puntarenas Province, Costa Rica; and *P. hammelii* **sp. nov.**, from wet forests on the Caribbean slopes of Nicaragua and Costa Rica. In addition, *Protium brenesii* **comb. nov.**, is proposed as a new combination based on *Trichilia brenesii*, a name that was based on a specimen collected with flowers in the mountains near San Ramón, Alajuela Province, Costa Rica. It is compared with *P. costaricense*, a similar species with which it has been confused for more than 90 years. Finally, illustrations and specimen citations are provided for all the aforementioned taxa, and some others with which they have been confused.

## Resumen

Se describen e ilustran dos nuevas especies de *Protium* (Burseraceae): *Protium aguilarii* **sp. nov.**, de la vertiente del Pacífico en la Península de Osa, provincia de Puntarenas, Costa Rica; y *P. hammelii* **sp. nov.**, de los bosques húmedos de la vertiente del Caribe en Nicaragua y Costa Rica. Además, se propone la combinación *Protium brenesii* **comb. nov.**, basada en *Trichilia brenesii*, un nombre que fue descrito en base en un ejemplar con flores recolectado en las montañas de San Ramón, provincia de Alajuela, Costa Rica. Se compara con *P. costaricense*, especie similar, con la cual se confundió por más de 90 años. Finalmente, se proveen ilustraciones y listas de los ejemplares examinados para todos los taxones antes mencionados, y además algunos otros similares.

## Keywords

Burseraceae, Costa Rica, Nicaragua, *Protium*, Sapindales, taxonomy

## Introduction

The genus *Protium* (Burseraceae), with approximately 160 species, is nearly pantropical in distribution, though absent from continental Africa. Twelve species (including those described in this paper) have been recorded from Costa Rica, making this the largest of the five native genera in the country. *Protium* is distributed in Costa Rica from sea level to 1500 m, mainly in humid lowland forests, though some species occur in montane forest or (more rarely) relatively dry areas [e.g., *P. tenuifolium* Engl. subsp. *sessiliflorum* (Rose) D. M. Porter on the Pacific slope]. The genus is characterized in general by its arborescent or less often shrubby habit; resin that is usually aromatic; imparipinnately compound, trifoliolate, or rarely unifoliolate leaves, with petiolules that are commonly pulvinate at both ends, (3) 4–5-merous flowers with distinct or weakly connate petals and 8–10 stamens inserted outside the base of the nectary disk, and dehiscent fruits with 1–5 pyrenes.

The two new species described below and the need for a new combination in *Protium* were discovered during preparation of the Burseraceae treatment for the *Manual de Plantas de Costa Rica*. This study was based on an examination of *Protium* specimens deposited at A, CR, F, GH, MO and USJ (acronyms according Thiers 2016, continually updated), along with consultation of digital images in national and international virtual herbaria and relevant literature on *Protium* (e.g., Rose 1911; Standley 1937; Swart 1942; Standley and Steyermark 1946; Cuatrecasas 1957; Porter 1970; Daly 1987, 1989, 1997, 1999, 2002, 2014, 2016; Porter and Pool 2001). Additional field collections were conducted in Costa Rica in February through March 2016. The distribution map was generated using the program SimpleMappR (Shorthouse 2010) from coordinates reported on specimen labels; specimens whose label data did not indicate coordinates are shown in brackets.

## Taxonomy

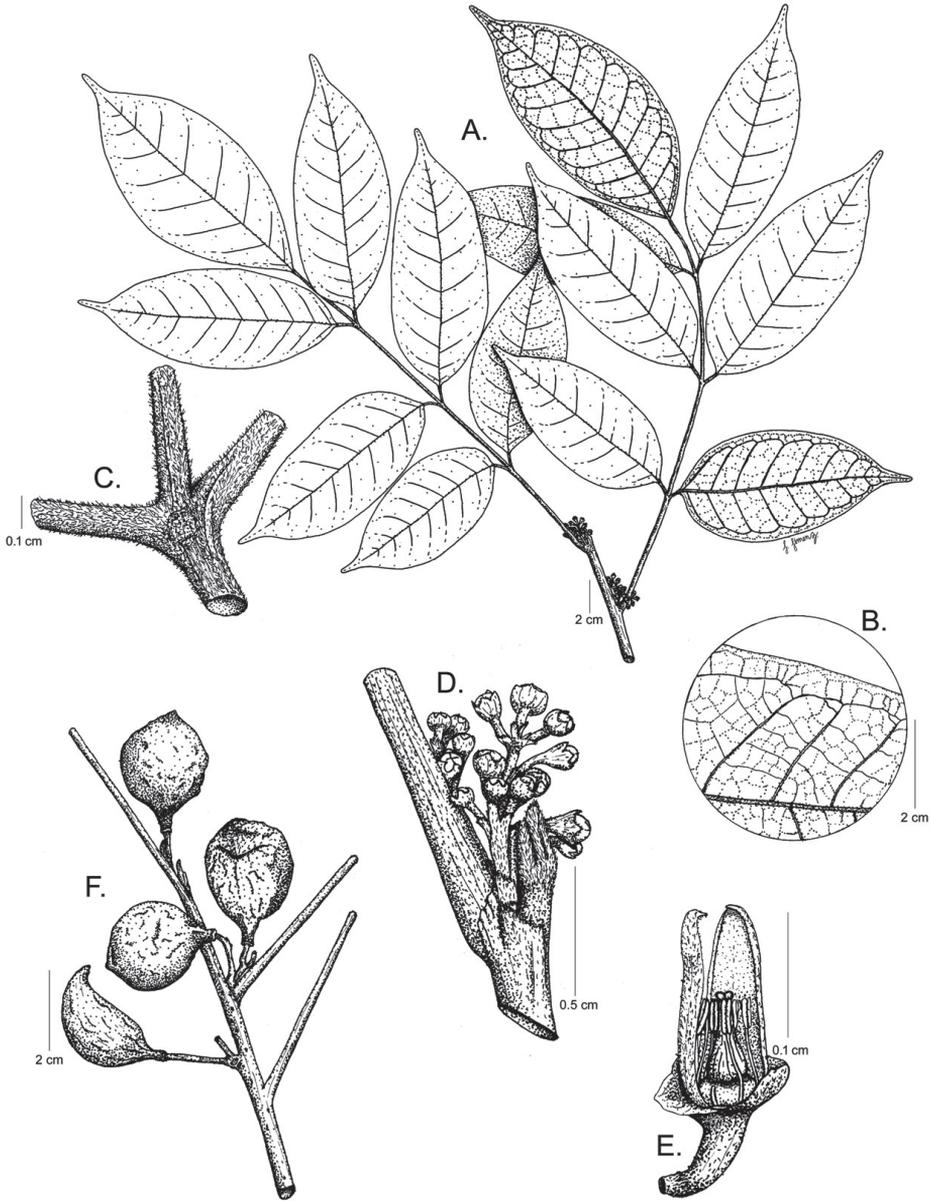
### *Protium aguilarii* D.Santam., sp. nov.

urn:lsid:ipni.org:names:77159804-1

Figs 1, 2, 3

**Diagnosis.** *Protium aguilarii* most closely resembles *P. costaricense* (Rose) Engl. and *P. pilosissimum* Engl., for their leaves with petiole, rachis, and leaflets that are hispidulous on the abaxial side and leaflets of comparable in size and coloration in herbarium material, but differs from both for its glabrous pistil and fruits (vs. pubescent).

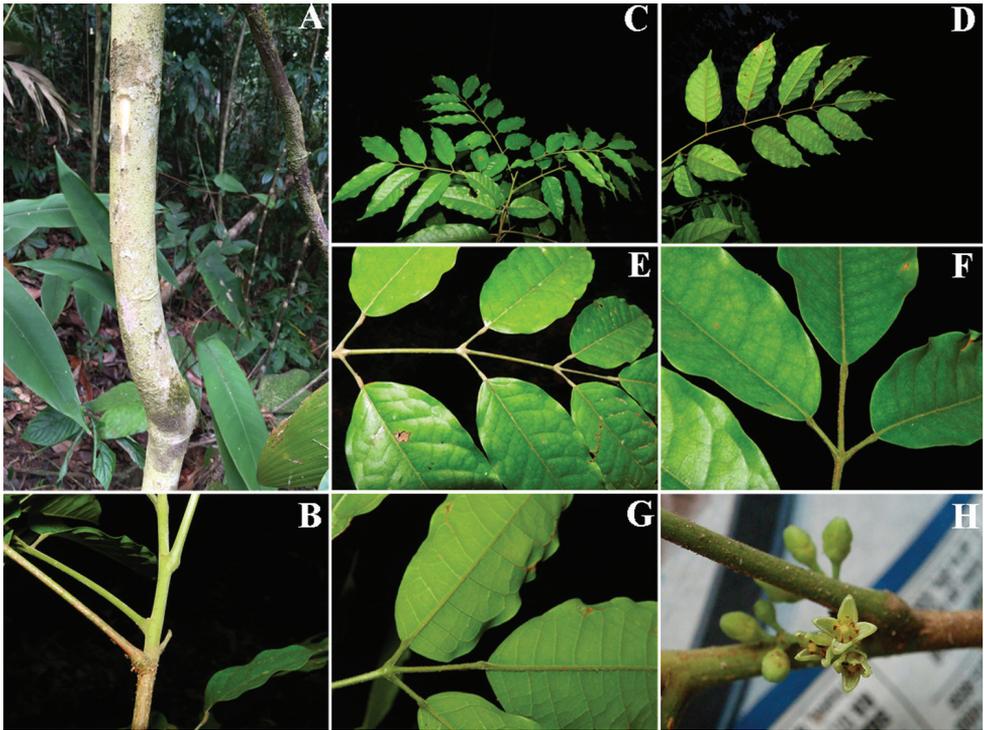
**Type.** COSTA RICA. Puntarenas: Reserva Forestal Golfo Dulce, Osa Peninsula, Rancho Quemado, ca. 15 km W of Rincón, on forested slopes at NW end of valley, near Fila Ganado, 08°33'N, 083°34'W, 300–400 m, 29 May 1988 (fr), B. Hammel, G. Herrera, M. M. Chavarria & Á. Solís 16885 (holotype: MO-6664125!; isotypes: CR-51404! [ex-INB], NY-01189275, digital image!).



**Figure 1.** *Protium aguilarii*. **A** Branch with inflorescences **B** Venation **C** Pubescence on the leaf rachis and petiolules **D** Inflorescences **E** Female flower, with perianth partially removed **F** Fruits. **A–D** from *R. Aguilar* 4593, CR **E** from *R. Aguilar* & *X. Cornejo* 11115, CR **F** from *K. Thomsen* 226, CR. Drawing by Jessica Jiménez.

Tree, 8–15 m tall × 6–18 cm DBH, lacking stilt roots; external bark white (*D. Santamaría et al.* 9851). Resin transparent when fresh, a little sticky, aromatic. Twigs 2–4 mm diam, appressed-pubescent with simple or malpighiaceous, pale brown tri-

chomes 0.05–0.6 mm long, sparsely lenticellate, solid, never stained white. Leaves 2–4-jugate, (12.5–) 19.5–33.8 cm long; petiole (2.3–) 3.3–6.3 cm long, 0.2 cm diam, semi-terete, smooth or slightly striate; rachis (2.6–) 3.5–11.8 cm long, terete, smooth or slightly striate; petiole and rachis hispidulous with simple, pale brown trichomes 0.1–0.5 mm long; lateral petiolules 0.3–1.7 cm long, with pulvinuli evident on both ends, smooth or slightly striate on both sides, rounded, hispidulous with yellowish brown trichomes; terminal petiolule 1.9–4.1 cm long, pulvinulus conspicuous; basal pair of leaflets 5.2–10 × 2–4.3 cm, elliptic to ovate, obtuse at the base; other lateral leaflets 6.7–13.2 × 2.6–5 cm, elliptic to ovate, obtuse to subcuneate at the base (with one side sometimes asymmetric); the terminal leaflet 7.3–14.2 × 2.7–5.8 cm, ovate, elliptic, base obtuse to subcuneate and symmetrical; apex acuminate, the acumen 0.7–1 cm long; margin entire; leaflets drying dark brown or olivaceous above and pale brown or olivaceous below; secondary venation brochidodromous, secondaries in 7–10 pairs of secondary veins, ascending, weakly arcuate, the spacing irregular, perpendicular intersecondaries sometimes present, intercostal tertiaries alternate or mixed percurrent tertiary; on abaxial side the midrib prominent, dense hispidulous, with trichomes 0.06–0.55 mm long, yellowish brown, the secondary veins prominent, with trichomes similar to the midrib, the higher-order veins prominulous, with scattered trichomes, the rest of the surface with scattered trichomes, not papillae; on adaxial side the midrib lightly prominent to flat, hispidulous, secondary veins flat, scattered hispidulous to almost glabrous, the higher-order veins flat almost glabrous, the rest of surface nearly glabrous. Inflorescences fasciculate, axillary (sometimes at leafless nodes), staminate inflorescences unknown, pistillate inflorescences ca. 0.6 cm long (0.9–1.2 cm in fruits), much shorter than the petiole, branching at the base, not flexuous, all axes densely pubescent with simple, yellowish brown or whitish trichomes; bracts subtending the inflorescences ca. 1.3 mm long, lanceolate, acuminate to obtuse at the apex, densely pubescent abaxially; those on primary axes ca. 0.6 mm long, broadly ovate, obtuse at the apex, densely pubescent abaxially; bracteoles subtending flowers ca. 0.8 mm long, triangular, acuminate at the apex, pubescent abaxially. Flowers 4-merous, the pedicel ca. 2.2 mm long (ca. 3 mm in fruit), sparsely pubescent with trichomes ca. 0.2 mm long. Staminate flowers unknown. Pistillate flowers with calyx 1–1.16 × 2.3 mm, sparsely pubescent on abaxial side with trichomes ca. 0.1 mm long, the lobes ca. 0.4 mm long, rounded to depressed-deltate, much taller than the disk, often persistent in fruit; petals white, ca. 2.6 × 0.9 mm, distinct, suberect at anthesis, lanceolate, sparsely appressed-pubescent on abaxial side with yellowish brown to whitish trichomes ca. 0.1 mm long, glabrous but papillose on the adaxial side, papillose and involute marginally, inflexed-apiculate at the apex (the apiculum ca. 0.2 mm long); disk ca. 0.4 tall × 0.2 mm thick, glabrous; staminodes 8, 1.66–1.8 mm long, the antepetalous almost equaling than antesepalous, the filaments ca. 0.9 mm long, flat, the anthers ca. 0.6 mm long, lanceolate, subcordate at the base; pistil ca. 1.5 × 1 mm (at the base), ovoid, glabrous, the style ca. 0.8 mm long, stigma lobes 4, globose, densely papillose. Fruits 1.6–1.8 × 1.2–1.4 cm, subglobose to slightly obliquely ovoid, green (possibly immature), obtuse



**Figure 2.** *Protium aguilarii*. **A** Trunk and bark **B** Twigs **C** Branch with leaves **D** Leaves showing abaxial side of leaflets **E** Leaf showing adaxial side **F** Leaflet bases **G** Venation **H** Flower. Photo credits: Reinaldo Aguilar (**A–G**) from *D. Santamaría et al.* 9851; and Xavier Cornejo (**H**) from *R. Aguilar & X. Cornejo* 11115.

at the base, acuminate at the apex, sometimes weakly curved, smooth and glabrous, stipitate (the stipe ca. 0.2 cm long); pseudoaril present, color unknown; pyrenes, 1 or 2 usually developing, 1.1–1.4 × ca. 1.2 cm, smooth, broadly ovate, obtuse at the base, acuminate at the apex, bony, the wall ca. 0.75 mm thick, yellowish; funicular scar ca. 0.7 cm long, usually not very deep, without a rib in the middle.

**Habitat and distribution.** *Protium aguilarii* is endemic to Costa Rica, where it is restricted to the Osa Peninsula, on the southern Pacific coast in Puntarenas Province. It occurs in primary forest, at 150–400 m elevation. In Aguabuena, Rincón de Osa, this species occurs in well-drained forest on undulating terrain, with many palms and large lianas; here, it co-occurs with *Brosimum utile* (Kunth) Oken (Moraceae), *Carapa Aubl.* (Meliaceae), and *Symphonia* L. f. (Clusiaceae) (see, for example, *K. Thomsen* 226). In Rancho Quemado, *P. aguilarii* is a small, infrequent tree on mountain ridges, where it is sympatric with tree species that are not very common in the area, or even the country as a whole, including *Fareamea permagnifolia* Dwyer ex C. M. Taylor (Rubiaceae), *Hirtella papillata* Prance and *Licania corniculata* Prance (Chrysobalanaceae), *Oecopetalum greenmanii* Standl. & Steyerf. (Metteniusaceae), and *Ruptioncarpon caracolito* Hammel & N. Zamora (Lepidobotryaceae).

**Phenology.** *Protium aguilarii* is known from only six fertile collections (one of these with flowers in bud). Pistillate flowers have been collected in April, and fruits in February, May, June, and December.

**Common name.** Copalillo (Spanish; Costa Rica, *K. Thomsen* 683).

**Etymology.** The epithet of this new species honors Reinaldo Aguilar Fernández for his important contributions to botany and his dedicated study and devoted collection of the plants of the Osa Peninsula for more than 25 years. He has become the world's expert in the flora of this remarkably species-rich and beautiful corner of the world. This species is further dedicated to him in appreciation of his support and intellectual stimulation.

**Discussion.** *Protium aguilarii* can be recognized by the combination of leaves with 5–9 leaflets with hispidulous pubescence on the petiole, rachis, petiolules, abaxial side of the leaflets, and inflorescence axes; leaflets with a distinct marginal vein that is visible on the abaxial side; short inflorescences and infructescences; flowers that are 4-merous, with the petals appressed-pubescent on the abaxial side and glabrous on the adaxial side; and glabrous pistils. The new species resembles, and has been confused with, *P. costaricense*, which, as treated here, is known only from the Caribbean slope of Nicaragua, Costa Rica, and Panama. Both species share hispidulous pubescence on the leaflets and inflorescences, but *P. aguilarii* has a glabrous pistil (vs. densely pubescent in *P. costaricense*), short inflorescence (ca. 0.6 vs. 1.6–6.5 cm long), petals that are glabrous on the abaxial side (vs. sparsely pubescent), and secondary venation brochidodromous (vs. eucamptodromous). *Protium aguilarii* also has usually shorter (non-basal) leaflets than *P. costaricense* (6.7–13.2 vs. 10.5–17.5 cm), and glabrous fruits (vs. minutely pubescent with scattered trichomes), with a stipitate base, the stipe ca. 0.2 cm long (vs. sessile or with stipitate ca. 0.1 cm long). Additionally, *P. aguilarii* differs from *P. costaricense* by its smooth (vs. rugose) pyrene. In Costa Rica, others species with glabrous pistils or pistillodes are *P. aracouchini* Marchand, *P. hammelii* (described here), *P. panamense* (Rose) I. M. Johnst., and *P. ravenii* D. M. Porter. Unlike *P. aguilarii*, these species have nearly glabrous leaves and other vegetative parts. *Protium aguilarii* also shares some similarities with the South American *P. pilosissimum* including short inflorescences and pubescent leaflets but it differs by its pubescent pistil or pistillode and fruit (vs. glabrous in *P. aguilarii*).

**Additional material examined.** COSTA RICA. **Puntarenas:** Osa, Bahía Chal, La Parcela, 08°43'50"N, 083°27'17"W, 150 m, 25 Jul 1996 (fl bud), *R. Aguilar 4593* (CR-2 sheets, F); Bahía Chal, La Parcela, 08°43'50"N, 083°27'17"W, 150 m, 12 Dec 1996 (fr), *R. Aguilar 4746* (CR); Rancho Quemado, camino a Drake, parte mas elevada del camino, 200 m al Este de la torre del ICE, en una trocha que lleva al Tierra de Conservación de Rancho Quemado, 08°41'33"N, 083°35'35"W, 350 m, 04 Apr 2008 (♀ fl), *R. Aguilar & X. Cornejo 11115* (MO, NY-digital image, USJ); Rancho Quemado, siguiendo a fila Ganado, 08°43'30"N, 083°35'30"W, 200–450 m, 26 Nov 1991 (st), *J. Marín & G. Herrera 306* (CR-2 sheets); Sierpe, Península de Osa, subiendo hacia el Cerro Chocuaco, desde el Bajo de San Juan, 400 m, 12 Jan 1991 (st), *C.O. Morales 262* (USJ); Distrito de Sierpe, Península de Osa, entre Rancho Quemado y Drake, trocha al sur, sobre la fila, antes de llegar a la torre, 08°41'30"N, 083°35'28"W,



**Figure 3.** Distribution of *Protium aguilarii* and *P. hammelii*.

375 m, 21 Mar 2016 (st), *D. Santamaría et al.* 9851 (CR); Península de Osa, Aguabuena, 3.5 km W of Rincón, 1 km N of BOSCOA station, 08°43'N, 083°31'W, 350 m, 09 Jan 1993 (fr), *K. Thomsen* 226 (CR, NY-digital image, USJ); Península de Osa, Aguabuena, 3.5 km W of Rincón, 1 km N of BOSCOA station, 08°43'N, 083°31'W, 350 m, 13 Nov 1992 (st), *K. Thomsen* 683 (CR); Península de Osa, Aguabuena, 3.5 km W of Rincón, 1 km N of BOSCOA station, 08°43'N, 083°31'W, 350 m, 30 May 1993 (st), *K. Thomsen* 707 (CR); Península de Osa, Aguabuena, 3.5 km W of Rincón, 1 km N of BOSCOA station, 08°43'N, 083°31'W, 350 m, 18 Jun 1993 (fr), *K. Thomsen* 807 (CR, NY-digital image).

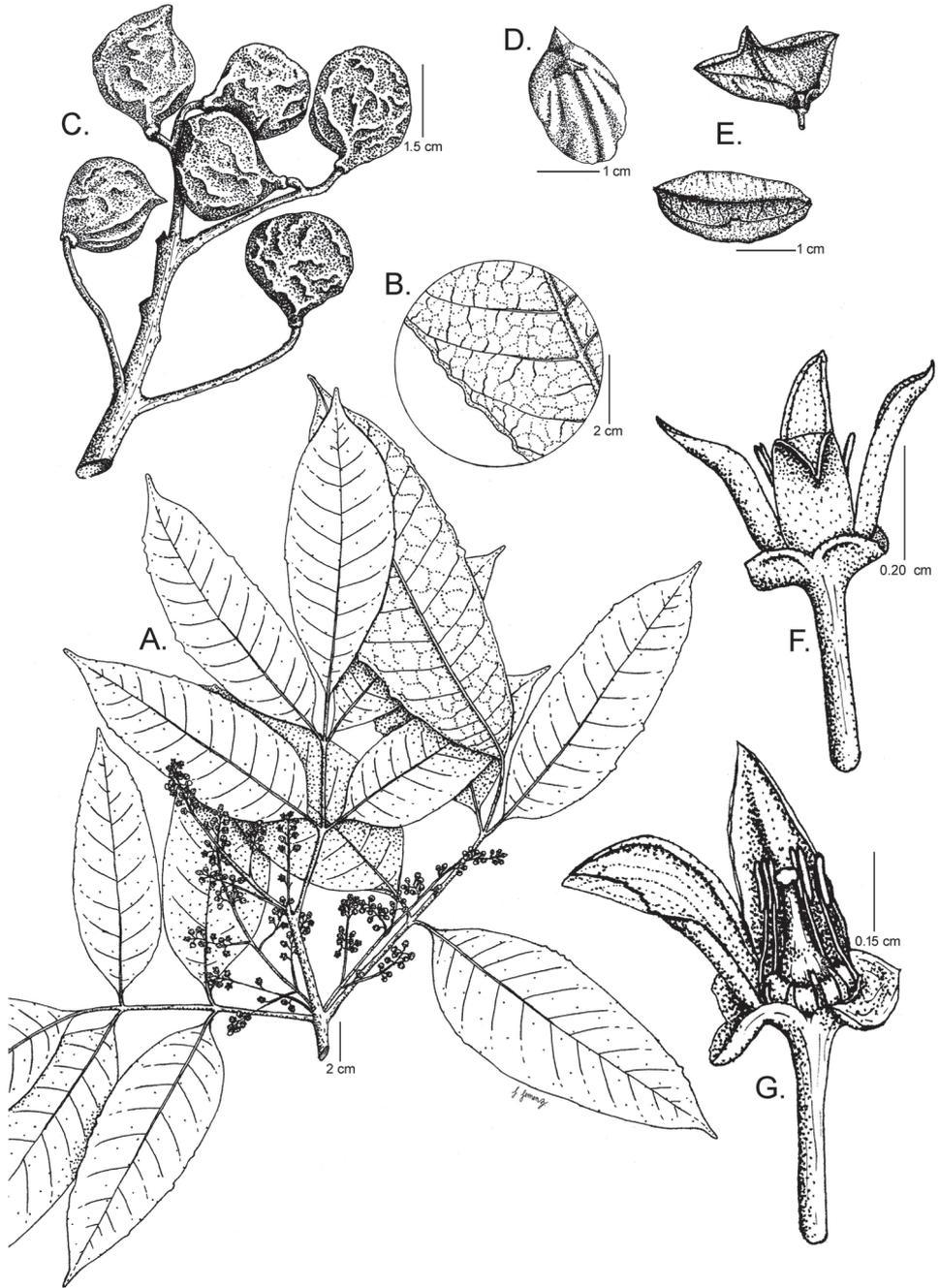
***Protium hammelii* D.Santam., sp. nov.**

urn:lsid:ipni.org:names:77159805-1

Figs 3, 4, 5, 7A

**Diagnosis.** *Protium hammelii* is similar to *P. multiramiflorum* Lundell and *P. panamense* for their nearly glabrous leaves, petals, and usually pistil or pistillode (always glabrous in *P. panamense*; sometimes glabrous in *P. multiramiflorum*). However, the new species it is distinguished from *P. multiramiflorum* by the short calyx in both sexes (0.7–1.3 vs. 1.4–2 mm long), pyrenes with thick walls (0.6–1.1 vs. 0.3–0.5 [–0.6] mm thick), and a short and shallow scar (0.3–0.45 [–0.5] vs. 0.4–0.7 cm long). It is distinguished from *P. panamense* by its smaller lateral (11–22.2 × 3.3–6.4 vs. 16–32.5 × 6.7–10.3 cm) and terminal (11.2–17.7 × 3.9–8.5 vs. 15–28.3 × 7–13.6 cm) leaflets and shorter petiolules.

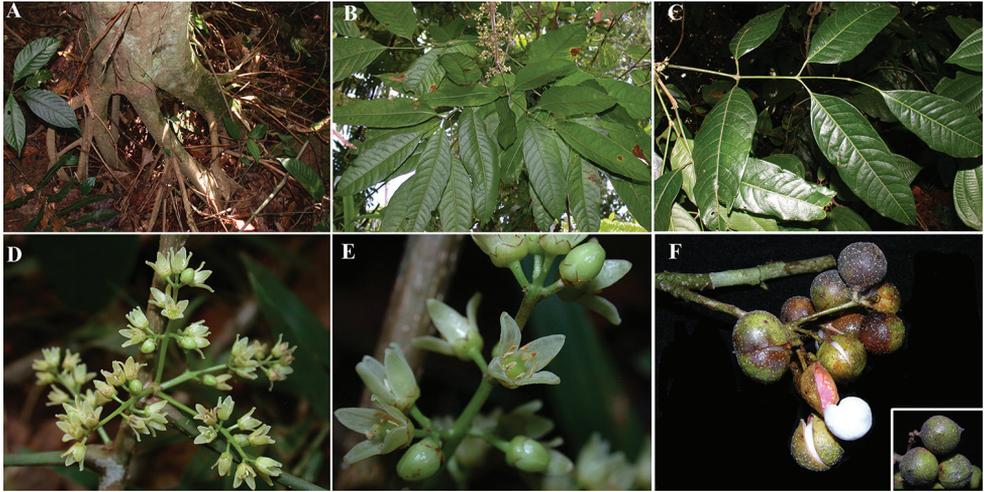
**Type.** COSTA RICA. Limón: Parque Nacional Tortuguero, 5 km N de La Aurora, Guápiles, límite sur del Parque, junto río Sierpe, 10°22'00"N, 083°31'00"W, 30 m,



**Figure 4.** *Protium hammelii*. **A** Branch with inflorescences **B** Venation on the abaxial side and marginal teeth of leaflets **C** Fruits **D** Pyrene **E** Fruit valves **F** Flower **G** Staminate flower with two petals removed, showing the pistillode and stamens. **A** and **B** from *J. Solano 77*, CR **C–E** from *J. Gómez-Laurito et al. 10998*, CR **F, G** from *W.D. Stevens 23769*, CR. Drawing by Jessica Jiménez.

11 Apr 1990 (♂ fl), *J. Solano* 77 (holotype: CR-152860!; isotypes: CR-51496! [ex-INB], F-2 sheets 2081330!, 2127441!, MO-6664125!, NY-01189417, digital image!).

Tree, 4–30 tall × 9–40 cm DBH, sometimes with stilt roots; external bark grayish. Resin transparent when fresh, aromatic. Twigs 2–5 mm diam, appressed-pubescent with simple or malpighiaceus, whitish yellow trichomes 0.1–0.5 mm long, to glabrescent, sparsely lenticellate, solid, never white-stained with resin that crystallizes on the stem (except weakly in *W.D. Stevens* 31653; also on the fruits). Leaves (2–) 4–6 jugate, 21.5–43.5 cm long; petiole (2.7–) 4.7–7.4 (–8.2) cm long, 0.1–0.3 cm diam, semi-terete except weakly sulcate at the base, striate; rachis 4–8.2 (–9) cm long or absent, terete, striate on both sides; petiole and rachis nearly glabrous or sparsely pubescent with simple and malpighiaceus, usually whitish yellow trichomes 0.1–0.3 mm long; lateral petiolules 0.7–2.1 cm long, with pulvinuli evident on both ends, striate, canaliculate adaxially, glabrous or minutely pubescent with whitish yellow trichomes; terminal petiolule 1.8–4.3 (–5.5) cm long, pulvinulus conspicuous; basal pair of leaflets 10.1–19 × 3.7–6.7 cm, ovate or lanceolate, obtuse to subcuneate at the base (sometimes asymmetric); other lateral leaflets 11–22.2 × 3.3–6.4 cm, lanceolate, oblong, ovate or elliptic, obtuse to subcuneate at the base; the terminal 11.2–17.7 × 3.9–8.5 cm, broadly elliptic to obovate, lanceolate, obtuse or subcuneate at the base (usually with both sides equal); apex acuminate, the acumen 0.7–1.3 cm long; margin entire or much more commonly sparsely denticulate; leaflets drying more or less pale brown, olivaceous to amber on both sides; secondary venation eucamptodromous or slightly brochidodromous, secondaries in 12–17 pairs of secondary veins, ascending, weakly arcuate, sometimes discolored on abaxial side, ascending, the spacing irregular, perpendicular intersecondary veins often 1 per pair of successive secondary veins or absent, intercostal tertiaries alternate or mixed percurrent tertiary; on abaxial side the midrib prominent, glabrous or minutely pubescent, with trichomes ca. 0.03–0.6 mm long, whitish yellow or reddish, secondary veins prominent, with trichomes similar to the midrib or glabrous, the higher-order veins prominulous with scattered trichomes or glabrous, the rest of surface almost glabrous to glabrous, not papillate; on adaxial side, the midrib prominent, minutely and scattered pubescent, secondary veins impressed to flat with trichomes similar to the midrib or glabrous, the higher-order veins flat to lightly impressed, with scattered trichomes, the rest of surface with scattered trichomes to glabrous. Inflorescences axillary (sometimes at leafless nodes), generally branching at the base, not flexuous, the staminate inflorescences 3.4–8.5 cm long, shorter or exceeding the petiole, minutely pubescent with simple and malpighiaceus, whitish trichomes on all axes, the pistillate inflorescences 1–1.8 cm long [(1.4)– 2.5–12.5 cm in fruit], much shorter than the petiole; bracts subtending the inflorescences 1–1.7 mm long, triangular, acuminate at the apex, densely pubescent abaxially; those on primary axes 0.6–1.3 mm long, triangular, acuminate or obtuse at the apex, densely pubescent abaxially; bracteoles subtending flowers 0.3–0.8 mm long, triangular or broadly ovate, obtuse to acuminate at the apex, pubescent or nearly glabrous abaxially. Flowers 4(5)-merous, the pedicel 1.5–2.8 mm long (2–6 mm in fruit), generally glabrous. Staminate flowers with calyx 0.7–1.3 × 1.3–2.4 mm, much



**Figure 5.** *Protium hammelii*. **A** Stilt roots **B** Branch with inflorescences **C** Adaxial side of the leaflets **D** Inflorescences **E** Flower **F** Fruits. Photo credits: Orlando Vargas (**A–E**); and N. Zamora (**F**).

taller than the disk, the lobes 0.4–1 mm long, rounded to depressed-deltoid, glabrous on abaxial side, papillate marginally, often persistent in fruit; petals variously reported as green, greenish yellow or white, 3–4 × 1.4–1.8 mm, distinct, erect to suberect at anthesis, lanceolate or ± triangular, glabrous on the abaxial side, glabrous but papillose on the adaxial side, papillose and weakly involute marginally, inflexed-apiculate at the apex (the apiculum 0.15–0.25 mm long); disk 0.23–0.46 tall × 0.26–0.5 mm thick, glabrous; stamens 8, (sub) equal, the antesealous 1.8–2.4 mm long, the antepetalous 1.5–2 mm long, exceeding the pistillode, the filaments more or less flat, papillate, the anthers 0.7–0.9 mm long, lanceolate, obtuse to subcordate at the base, apiculate at the apex; pistillode 0.5–0.83 × 0.5–0.8 mm at the base, ovoid, globose or conical, glabrous, the style 0–1.5 mm long, stigma lobes 4, subglobose to weakly angulate, densely papillose. Pistillate flowers with calyx 1–1.2 × 2–2.5 mm, the lobes ca. 0.8 mm long, all parts similar to that of the staminate flowers; petals green, greenish yellow or white, distinct, 3–3.5 × 1.16–1.5 mm, suberect to reflexed at anthesis similar to those of the staminate flowers; disk 0.4–0.5 tall × ca. 0.3 mm thick, glabrous; staminodes 8, (sub) equal, the antesealous 1.5–1.7 mm long, the antepetalous 1.3–1.5 mm long, shorter or longer than the pistil, the filaments flat, not papillate, the anthers 0.6–0.8 mm long, lanceolate, cordate at the base; pistil 1.16–1.3 × 1–1.23 mm (at the base), ovoid or conical, glabrous, the style 0.3–0.8 mm long, stigma lobes 4, globose, densely papillose, each lobe sulcate on the middle (± as an inverted “C”). Fruits 1.6–2.4 × 1.1–2.1 cm, globose to ovoid, reddish or green (*M. Ballestero* 71) when ripe, obtuse at the base, the apex generally conspicuously apiculate at the apex, smooth or (more commonly) lenticellate, glabrous, stipitate [the stipe (0.1–) 0.2–0.5 cm long]; pseudoaril white; pyrene 1(2), 1.3–1.6 × 0.9–1.2 cm, smooth, ovoid to very widely ovate, obtuse at the base, apiculate at the apex, the wall 0.6–1.1 mm thick, whitish or yellowish; funicular

scar 0.3–0.45 (–0.5) cm long, usually not very deep, without a rib in the middle or the rib inconspicuous.

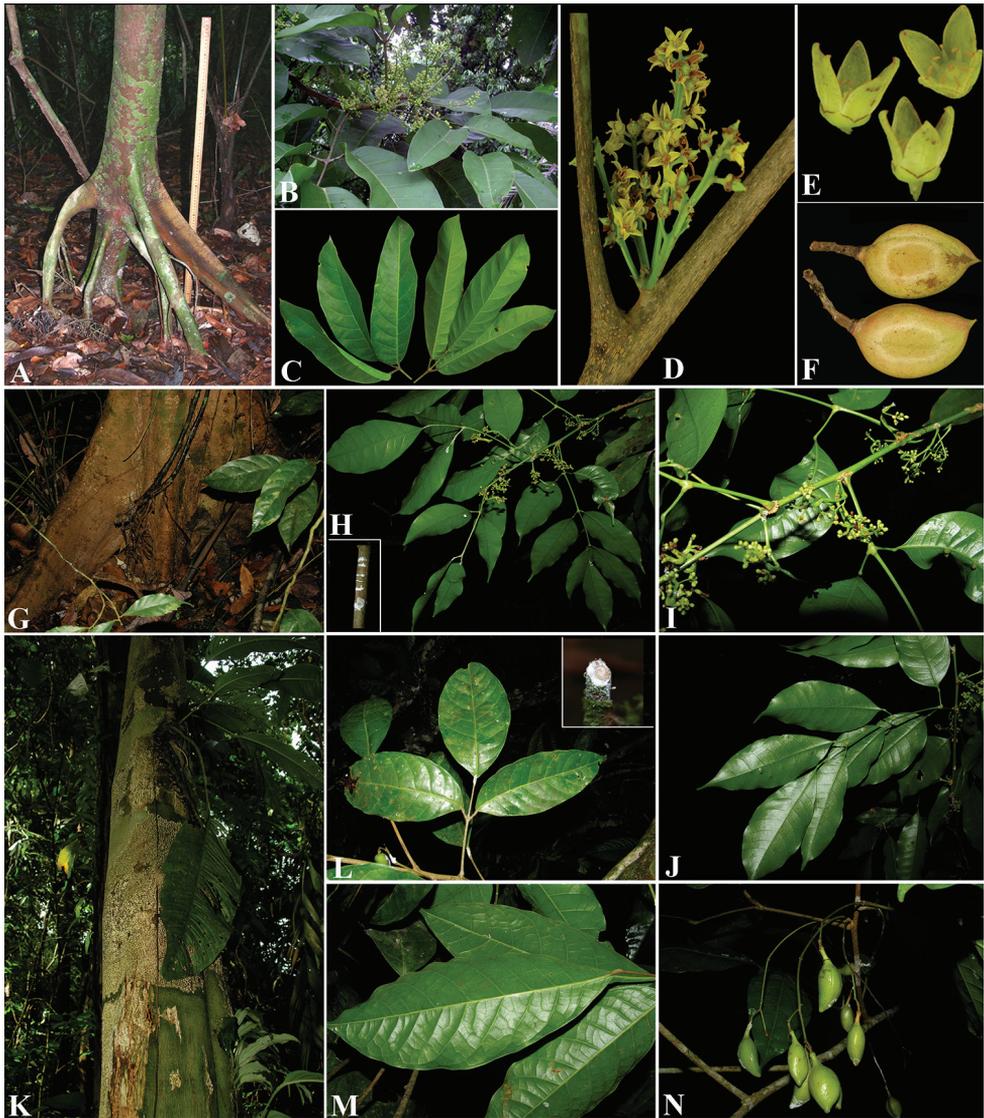
**Habitat and distribution.** This species is known so far only from wet forest on the Caribbean slope of Nicaragua and Costa Rica. It occurs mainly between 10 and 200 m in elevation, although some collections were made between 300 and 700 m. In Costa Rica, this species is common in the Sarapiquí region, where it seems to prefer alluvial soils on flat or relatively flat ground, sometimes on river banks. In this area, *Protium hammelii* grows sympatrically with the following species: *Carapa guianensis* Aubl. (Meliaceae), *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Euterpe precatoria* Mart. (Arecaceae), *Minquartia guianensis* Aubl. (Coulaceae), and *Pentaclethra macroloba* Kuntze (Fabaceae), among others species (N. Zamora, pers. comm.; May 2016).

**Phenology.** In Nicaragua, *Protium hammelii* has been collected with fruits in January, February, from May to July, and in October, but never in flower. In Costa Rica, it has been collected with staminate flowers in January, February, April, and December; pistillate flowers in January and February; and fruits in January, March, April, June, from August to October, and in December.

**Common name.** Alcanfor (Spanish; Nicaragua, *R. Rueda et al.* 2642, 2701; *J.C. Sandino* 3424).

**Etymology.** The specific epithet honors Barry E. Hammel, curator at the Missouri Botanical Garden and co-editor of the *Manual de Plantas de Costa Rica*, in recognition of his extensive work on the Costa Rican flora, as well as his personal support and motivation.

**Discussion.** *Protium hammelii* is recognizable by its almost glabrous vegetative parts, leaves with 5–7 leaflets, commonly with a sparsely denticulate margin, prominent tertiary veins on the abaxial side, 4(5)-merous flowers with glabrous petals, pistils, and pistillodes, the pistillate flowers with globose stigma lobes that are sulcate in the middle, and glabrous, usually lenticellate fruits that are stipitate and apiculate at the apex. Specimens of *Protium hammelii* have frequently been identified as *P. glabrum* (Rose) Engl., a species that is widespread from Belize to Panama, or *P. panamense*, from Costa Rica, Panama, and Colombia. The first of these is common in Costa Rica, while the second is quite rare (Fig. 6A–F); both have leaflets that are always entire. *Protium hammelii* differs from *P. glabrum* by its consistently glabrous petals on both sides, pistil, and pistillode (vs. petals on the adaxial side, pistil, and pistillode always pubescent). Fruiting material can usually be distinguished by the apiculate apex of the fruits of *P. hammelii* (vs. obtuse or rounded), and the glabrous (vs. with very small trichomes). *Protium panamense* shares occasional stilt-roots, glabrous flowers and fruits that are apiculate at the apex with *P. hammelii*, but *P. hammelii* usually has smaller lateral (11–22.2 × 3.3–6.4 vs. 16–32.5 × 6.7–10.3 cm), and terminal leaflets (11.2–17.7 × 3.9–8.5 vs. 15–28.3 × 7–13.6 cm) that are also usually thinner, as well as thinner lateral and terminal petiolules that are also shorter (1.8–4.3 [–5.5] vs. 5.2–8.7 cm); *P. hammelii* further has smaller (1.6–2.4 × 1.1–2.1 cm), globose to ovoid fruits (vs. usually 2.2–3 × 0.9–1.7 cm lanceolate. *Protium multiramiflorum* from Mexico to



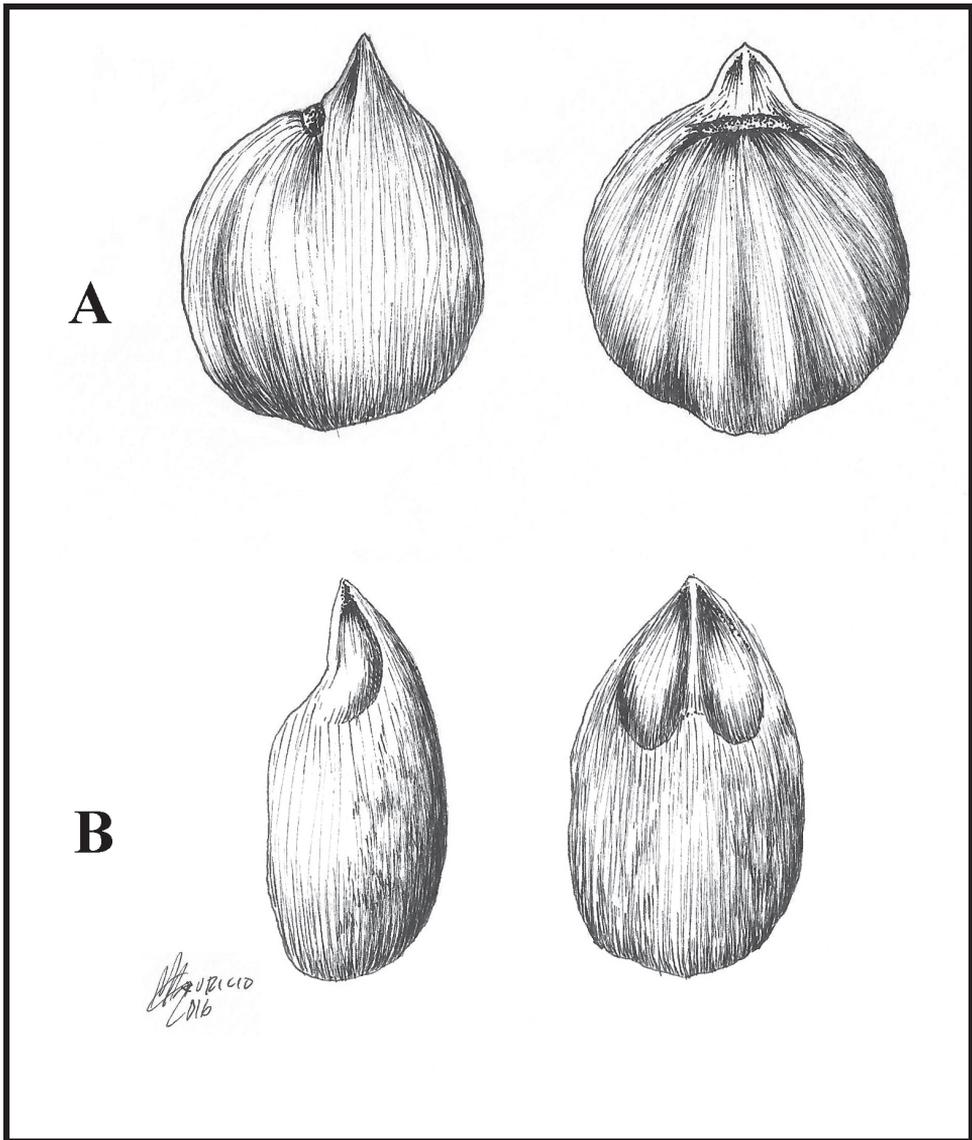
**Figure 6.** *Protium panamense*. **A** Stilt roots **B** Branch with inflorescences **C** Leaflets **D** Inflorescences **E** Staminate flowers **F** Fruits. *Protium aracouchini* **G** Trunk base **H** Branch with inflorescences; inset showing dry resin on cut twig **I** Inflorescences; also see the suberose petiole base **J** Abaxial side of the leaflets. *Protium ravenii* **K** Trunk **L** Adaxial side of the leaflets; inset dry resin on cut twig **M** Abaxial side of the leaflets **N** Fruits. Photo credits: Rolando Pérez (**A**); Carmen Galdames (**B**); Steven Paton (**C–F**). **G–J** photos by Reinaldo Aguilar, from *D. Santamaria & R. Aguilar* 9836 **K–N** photos by Reinaldo Aguilar, from *R. Aguilar* 12067, except **L**, inset by Orlando Vargas.

Honduras is similar to *P. hammelii* in its nearly glabrous leaves, petals, and sometimes pistil or pistillode. (Although the pistil of *P. multiramiflorum* was originally described as glabrous [Lundell 1937], almost all collections studied, including one of the isotypes

[Lundell 6212, GH-2 sheets!] and the paratype [Schipp 1021; A!, F!, GH!, MO!], have the pistil or pistillode with tiny, scattered trichomes). The new species differs in its short calyx in both sexes (0.7–1.3 vs. 1.4–2 mm long), stigma lobes that are sulcate (vs. not sulcate), and pyrenes with thick walls (0.6–1.1 vs. 0.3–0.5 [–0.6] mm thick) and short scar (0.3–0.45 [–0.5] vs. 0.4–0.7 cm long) (Fig. 7B). Others species in Costa Rica with glabrous pistils or pistillodes are *P. aracouchini* (Figs 6G–J), *P. ravenii* (Figs 6K–N), and *P. aguilarii*. The first two species can be distinguished from *P. hammelii* by their flexuous inflorescences and twigs and abundant exuding resin that becomes whitish and chalky (Figs 6H and L, inset), while *P. aguilarii* can be distinguished by its petals that are pubescent abaxially.

Fruit dispersal by birds and mammals has been reported at the La Selva Biological Station for *P. panamense* (Vargas 2000), but the observation likely corresponds to *P. hammelii*.

**Additional material examined. NICARAGUA. Atlántico Norte** [Zelaya]: Reserva Bosawas, Mpio. de Bonanza, Cerro Cola Blanca, entre el cacerío de Vitinia y empalme de la Comarca de Panamá, 14°04'N, 084°34'W, 200 m, 02 Jun 1997 (fr), *R. Rueda & I. Coronado 6595* (MO). **Atlántico Sur** [Zelaya]: área de la Bahía de Bluefields, río Escondido, camino entre El Pool y Abardeen Hills, 0–30 m, 22 Mar 1949 (st), *A. Molina 1899* (F); Monkey Point, Caño El Pato, 1.5 km sobre la ribera del Caño, 11°35'N, 083°42'W, 10 m, 25 Oct 1981 (fr), *P.P. Moreno 12411* (MO); Caño Montecristo, al este del Campamento Germán Pomares, 11°36'N, 083°52'W, 60–90 m, 08 Feb 1982 (fl bud), *P.P. Moreno 15132* (MO); Mpio. de Rama, Loma Buena Vista, 12°08'N, 084°12'W, 100–150 m, 23 May 1984 (st), *W. Robleto 613* (MO); a lo largo del río Maíz, 11°16'N, 084°07'W, [25–50 m], 08 Jan 1995 (fr), *R. Rueda et al. 2642* (MO); Mpio. Laguna de Perla, río Wawanshang, 12°40'N, 083°42'W, 50 m, 15 Feb 2002 (fr), *R. Rueda & R. Dolmus 16851* (MO); 1 km de Colonia Serrano, río Serrano, 11°34'N, 084°22'W, 70–80 m, 31 Jul 1982 (fr), *J.C. Sandino 3424* (MO). **Chontales**: Along road from Ciudad Sandino toward El Guabo, 0.7 km SW of El Porvenir, 12°09'02"N, 084°52'43"W, 345 m, 17 May 2011 (fr), *W.D. Stevens 31653* (MO). **Matagalpa**: Falda norte del Cerro Musún, frente a trocha a Wanawás, [13°02'N, 085°15'W], 200–500 m, 16 May 1980 (fr), *M. Araquistain & P.P. Moreno 2789* (MO). **Río San Juan**: Mpio. de San Juan del Norte, del Delta 1 km al este y después 2 km al norte, 10°46'N, 083°46'W, [40–80 m], 08 Jun 1995 (st), *R. Rueda et al. 2701* (MO). **COSTA RICA. Alajuela**: Los Chiles, Finca La Urraca, Los Lirios, camino a los Chiles, ca. 100 m, 11 Dec 1985 (fr), *J. Gómez-Laurito et al. 10998* (CR, F, USJ). **Heredia**: Sarapiquí, OET, La Selva, 14 Jun 2004 (fr), *R. Aguilar et al. 8337* (LSCR-digital image); Parque Nacional Braulio Carrillo, frente al Puesto La Ceiba, 10°19'47"N, 084°04'48"W, 400–700 m, 23 Dec 1988 (fr), *M. Ballester 71* (CR, MO); about 5 km north of Puerto Viejo along the road to El Muelle, 10°28'N, 083°58"W [10°30'36"N, 084°00'36"W], 100 m, 08 Jan 1967 (♂ fl), *W.C. Burger & G. Mata 4307* (F-2 sheets, MO); about 5 km north of Puerto Viejo along the road to El Muelle, 10°28'N, 083°58"W [10°30'36"N, 084°00'36"W], 100 m, 08 Jan 1967 (♀ fl, fr), *W.C. Burger & G. Mata 4315* (F, MO, NY-digital image); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río



**Figure 7.** Comparison between the pyrenes of *Protium hammelii* (**A**) and *P. multiramiflorum* (**B**). **A** from G. Davidse & G. Herrera 30879; and **B** from G.M. Aguilar et al. 4754. Drawing by Alex M. Campos.

Sarapiquí, Southwest trail, 1600 m line, 100 m, 16 Feb 1981 (♂ fl), *J.P. Folsom 8965* (F, MO); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, central trail to Holdridge Trail 3000 m line, 100 m, 08 Mar 1981 (immat fr), *J.P. Folsom 9279* (MO); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the Río Sarapiquí, junction South Boundary and Western Boundary, 21 Mar 1981 (immat fr), *J.P. Folsom 9435* (CR); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the Río Sarapiquí,

El Swampo Trail, 100 m, 27 Apr 1981 (fr), *J.P. Folsom* 9882 (F, MO, NY-digital image); Magsasay, near La Selva, 10°24'N, 084°03'W, 150 m, 16 Jul 1990 (st), *A.H. Gentry* 71766A (MO); La Selva, río Sarapiquí near Puerto Viejo, junction SSO and LOC Trails, 10°26'N, 084°01'W, 100 m, 05 Jan 1993 (all st), *A.H. Gentry et al.* 78485 (CR, MO), 78507 (CR, MO), 78522 (CR, MO), 78543 (CR, MO); La Selva, río Sarapiquí near Puerto Viejo, junction SSO and LOC Trails, 10°26'N, 084°01'W, 08 Jan 1993 (st), *A.H. Gentry & R. Ortiz* 78630 (CR, MO); Parque Nacional Braulio Carrillo, fila Carrillo, 700 m, 30 Mar 1984 (fr), *L.D. Gómez et al.* 21135 (CR); Parque Nacional Braulio Carrillo, estación El Ceibo, 10°20'00"N, 084°04'00"W, 450–500 m, 13 Mar 2003 (fr), *J. González* 3147 (CR); Parque Nacional Braulio Carrillo, estación El Ceibo, 10°20'00"N, 084°04'00"W, 450–500 m, 14 Mar 2003 (immat fr), *J. González* 3176 (CR, MO, USJ); Chilamate, Cerros de Sardinal, finca propiedad de Isaías Alvarado, 100 m, 26 Aug 2007, *J. González et al.* 9326 (LSCR-digital image); Finca La Selva, Arboretum tag #522, 10°26'N, 084°01'W [10°25'53"N, 084°00'13"W], [40 m], 30 Dec 1970 (♂ fl bud), *G.S. Hartshorn* 968 (F, MO-2 sheets); Finca La Selva, 10°26'N, 084°01'W, [100 m], 25 Jan 1973 (fr), *G.S. Hartshorn* 1108 (CR); Finca La Selva, Holdridge Arboretum tag #119, 10°26'N, 084°01'W, [100 m], 22 Aug 1975 (fr), *G.S. Hartshorn* 1476 (CR, F, LSCR-digital image, MO); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, quebrada El Sura, 100 m, 06 Jun 1984 (fr), *B. Jacobs* 2148 (CR); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, camino circular Lagano, at bridge across Q. [Quebrada] Salto, 100 m, 15 Jun 1928 (fr), *B. Jacobs* 2362 (F); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, vicinity Sendero Jaguarunda and Lindero Sur intersection, [10°25'53"N, 084°00'13"W], 100 m, 28 Jun 1984 (fr), *B. Jacobs* 2644 (MO); río Sarapiquí, 125 m, 18 Jan 1966 (fl bud), *A. Jiménez* 3602 (F-2 sheets, CR); Finca Hermanos Vargas, 1 km al Suroeste de Puerto Viejo, 125 m, 04 Feb 1966 (♂ fl), *A. Jiménez* 3602 (CR); Estación Biológica La Selva, LOC 600, 10°25'47"N, 084°01'00"W, 55 m, 29 Jul 2004 (st), *S. Letcher* 77 (USJ); Finca La Selva, the OTS Field Station on the río Puerto Viejo just E of its junction with the río Sarapiquí, Far Loop Trail at about 350 m, [10°25'53"N, 084°00'13"W], 100 m, 11 Feb 1996 (♂ fl bud), *R.L. Wilbur* 65080 (F, MO); Parque Nacional Braulio Carrillo, El Ceibo, 10°22'29"N, 084°02'10"W, 200–300 m, 24 Aug 2004 (fr), *R. Kriebel et al.* 4857 (CR); Estación Biológica La Selva, 10°26'00"N, 084°00'30"W, 0–100 m, 05 Feb 2004 (st), *A. Rodríguez* 8395 (CR, USJ); OET La Selva, a orillas del río Sarapiquí, [10°25'53"N, 084°00'13"W], [100 m], 30 Oct 2005 (fr), *N. Zamora* 3871 (LSCR-digital image, MO). **Limón:** Bosque Lluvioso [finca propiedad de INBio], 10°11'28"N, 083°51'28"W, 350 m, 16 Aug 2005 (st), *L. Acosta et al.* 3550 (CR); Pococí, 300 m al sur del Hotel Vista Al Mar, Tortuguero, 10°35'51"N, 083°31'40"W, 10 m, 22 Oct 2011 (fr), *M. Argueta* 107, 109 (USJ); Guápiles, La Leona, 10°09'45"N, 083°49'37"W, 478 m, 31 May 2005 (fr), *C. Benavides & A. Chacón* 160 (USJ); North shore of the mouth of the río Colorado at Barra del Colorado, 10°47'40"N, 083°35'30"W, 1–5 m, 12 Sep 1986 (fr), *G. Davidse & G. Herrera* 30879 (CR, F, MO); Guápiles, Cariari, El Zota, Finca El Progreso, 10°30'35"N, 083°44'39"W, 40 m, 11 Jun 2011 (fr), *M. Díaz s.n.*

(USJ-99607); Parque Nacional Tortuguero, Cerro Tortuguero, 10°35'37"N, 083°31'31"W, 5–120 m, 22 Oct 2011 (fr), *J. Gómez-Laurito 15689* (USJ); near río Parismina, 8 km W of Dos Bocas, [10°14'46"N, 083°27'21"W], 8 m, 31 Mar 1972 (fr), *R.W. Lent 2457* (CR, F, MO); Matina, Colonia Puriscaleña, Sendero Cerro Azul, 09°59'44"N, 083°23'08"W, 400–500 m, 15 Mar 2000 (fr), *E. Mora 984* (CR); Parque Nacional Tortuguero, Estación Agua Fría, rumbo Noreste, a orillas del río Agua Fría, 10°27'N, 083°33'W, 40 m, 02 Feb 1988, *R. Robles 1586* (CR, MO, NY-digital image); Llanura de Santa Clara, Chiporrisito, 10°36'10"N, 083°47'20"W, 400 m, 30 Jan 1995 (fl bud), *A. Rodríguez 507* (INB); Parque Nacional Tortuguero, Estación Agua Fría, Sendero El Aguacate, a 500 m de la entrada, 10°26'40"N, 083°34'40"W, 20 m, 11 Jan 1990 (fr), *J. Solano 62* (CR, MO, NY-digital image); Caño Chiquero, Tortuguero, 31 Jan 1986 (♂ fl), *R. Soto 2758* (CR); Cerro Coronel, E of Laguna Danto, 10°41'N, 083°38'W, 20–170 m, 16–13 Jan 1986 (♂ fl), *W.D. Stevens 23769, 23770* (CR, MO); Cerro Coronel, along río Colorado at and below outflow of Laguna Danto, 10°42'N, 83°39'W, 5–10 m, 25 Jan 2016 (fr), *W.D. Stevens 24002* (CR, MO); Cerro Coronel, E of Laguna Danto, 10°41'N, 083°38'W, 16 Mar 1987 (st), *W.D. Stevens et al. 24912* (MO); Monte Verde, 300 [ft?], 25 Apr 1928 (fr), *H.E. Stork 1682* (F); Zapota Dos, ca. 20 NW of Tortuguero village, on farm of Ronulfo Vargas, 10°38'N, 083°41'W, 90–110 m, 16 Mar 1995 (st), *K. Thomsen 1377* (CR); Parque Nacional Tortuguero, Agua Fría, 10°26'35"N, 083°34'38"W, 32 m, 14 Jun 2007 (fr), *L.D. Vargas et al. 2379* (CR); Parque Nacional Tortuguero, Agua Fría, 10°26'20"N, 083°34'47"W, 30 m, 18 Oct 2007 (fr), *L.D. Vargas et al. 2813* (CR).

***Protium brenesii* (Standl.) D.Santam., comb. nov.**

urn:lsid:ipni.org:names:77159806-1

Figs 8A, 9

Basionym: *Trichilia brenesii* Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 583. 1937.

Type. COSTA RICA. [Alajuela:] colinas del Tremendal (San Pedro) de San Ramón, [09] Apr 1935 [♂ fl], *A.M. Brenes 20510* (holotype: F-866066!; isotypes: CR-2 sheets! [Hb. Brenes 20009, both with the same herbarium number], NY-00054791, digital image!).

**Habitat and distribution.** *Protium brenesii* is only known from Costa Rica, where it grows mainly in the Cordilleras de Guanacaste, de Tilarán and Central on both the Caribbean and Pacific slopes, though it also has been collected in the Cordillera de Talamanca (Dota region) and the Valle del General. It is found in primary forest and along roads and rivers between 640 and 1500 m elevation. *Protium brenesii* is found at the highest elevations of any species of its genus in Costa Rica.

**Phenology.** Collections with male flowers have been made from March to May, and December; female flowers in February; and fruits in March and April, and from June to December.



**Figure 8.** Types of *Protium brenesii* (A) and *P. costaricense* (B). Images courtesy of Museo Nacional de Costa Rica.

**Common name.** Copal (Spanish; Costa Rica, *E. Bello* 473).

**Discussion.** In the course of examining material identified as *Protium costaricense*, a notable number of collections from Costa Rica, mainly from 640–1500 m elevation in the Cordilleras de Guanacaste, de Tilarán and Central, were identified that differed from the rest. This material has twigs and leaflets with inconspicuous pubescence on the abaxial side; leaves with more numerous and usually narrower leaflets; and longer inflorescences and infructescences. *Protium costaricense*, as interpreted here, is a species of the lowlands of the Caribbean slope in Nicaragua, Costa Rica, and Panama, while the other collections represent a distinct montane taxon. An appropriate name already exists, and had been applied to some material collected in the Costa Rican cordilleras: *Trichilia brenesii* Standl. (1937: 583). Therefore, a new combination is proposed here, transferring *T. brenesii* to *Protium*.

The first known collection of *Protium brenesii* was made by Alberto M. Brenes (1870–1948) in the mountains near San Ramón, Alajuela Province, Costa Rica, in May 1923 (*Brenes* 19953). This species is similar in some aspects to *P. costaricense*, with which it has been confused for more than 90 years. These two taxa share the following morphological characteristics: twigs and leaves with dense pubescence; entire leaflets; 4(5)-merous flowers with pubescent petals, pistil, and pistillode; and rugose pyrene. The leaflets and fruits of the two species are also more or less similar in shape and size,

but tend to be narrower in *P. brenesii*. However, *P. brenesii* can be distinguished from *P. costaricense* by its longer inflorescences [(5–) 7–11.5 vs. 1.6–6.5 cm], with malpighiaceous and simple trichomes (vs. only simple) on the axes, and male and female flowers with the disk equal or taller than the calyx (vs. shorter), a feature that is also evident on collections with fruits. Additionally, the terminal leaflets of *P. brenesii* are smaller (6.8–10.7 × 2.5–3.7 vs. 10.5–17.5 × 4.5–7.7 cm) and have shorter petiolules (1.5–2.5 vs. 2.8–3.5 [–5] cm). Importantly, *P. brenesii* is a species of montane forests at elevations of 640–1500 m, while *P. costaricense* is most frequent in lowland wet forests from 0–200 m. Some collections of *P. brenesii* have been confused with *P. confusum* (Rose) Pittier (or its synonym, *P. schippii* Lundell), the latter distinguished by its distally undulate or serrulate leaflets (vs. entire), inflorescences usually with a mixture of malpighiaceous, reddish trichomes and apparently glandular, whitish trichomes (vs. yellowish to pale brown malpighiaceous and simple trichomes), and flowers with the petals, pistil, and pistillode densely covered by dark red trichomes (vs. with whitish or pale brown trichomes).

In the checklist of Plantas Vasculares de Monteverde (Haber 2014), *Protium* sp. A. (7508 [W. Haber & E. Cruz]) and *P. costaricense* (E. Bello 473) correspond to *P. brenesii*; the same applies to the collection cited by Gómez-Laurito and Ortiz (2004) (*J. Gómez-Laurito et al.* 12278).

**Additional material examined. COSTA RICA. Alajuela:** Cantón de Grecia, Cordillera Central, Los Ángeles, camino de Los Ángeles a la Laguna de Hule, 10°17'55"N, 084°12'20"W, 740–900 m, 28 Oct 1995 (fl bud), *J. González & G. Perera* 995 (CR-2 sheets, MO, NY-digital image); Cantón de San Ramón, Reserva Biológica Monteverde, río Peñas Blancas, parcela de los Enanos, 10°18'00"N, 084°43'48"W, 850 m, 02 Sep 1988 (fr), *E. Bello* 332 (CR-2 sheets, F, MO, NY-digital image, USJ); Reserva Biológica Monteverde, río Peñas Blancas, 10°19'N, 084°43'W, 850 m, 06 Sep 1988 (fr), *E. Bello* 353 (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°19'N, 084°43'W, 820 m, 10 Oct 1988 (fr), *E. Bello & E. Cruz* 458 (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, parcela de Badilla, 10°19'N, 084°43'W, 850 m, 22 Oct 1988 (fr), *E. Bello* 473 (F, MO, NY-digital image, USJ-2 sheets); Reserva Biológica Monteverde, río Peñas Blancas, 10°18'36"N, 084°43'12"W, 900 m, 21 Apr 1993 (♂ fl), *E. Bello* 5014 (CR-2 sheets); San Pedro de San Ramón, 1000 m, 06 May 1923 (♂ fl), *A.M. Brenes* 19953 [Hb. Brenes 3883], (CR, F, NY-digital image); Colinas de San Pedro de San Ramón, 1050–1075 m, 27 May 1925 (fl bud), *A.M. Brenes* 19955 [Hb. Brenes 4222], (CR, F, NY-digital image); Colinas de San Pedro de San Ramón, 04 Jul 1925, 1075 m, *A.M. Brenes* 4827 [612], (F); Colinas de San Pedro de San Ramón, 19 May 1927 (♂ fl), *A.M. Brenes* 19954 [Hb. Brenes 5445], (CR, NY-digital image); Bajos del Jamaical, Reserva de San Ramón, 700–1000 m, 10 May 1985 (♂ fl), *I. Chacón* 1800 (CR-4 sheets); Reserva Forestal de San Ramón, Colonia Palmareña, 800–950 m, 19–22 Sep 1985 (fr), *J. Gómez-Laurito* 10528 (CR, USJ); Reserva Forestal de San Ramón, sendero a la fila al S. O. de la Estación, 10°13'N, 084°37'W, 05 Sep 1992 (fr), *J. Gómez-Laurito* 12278 (CR, F, USJ); Barranquilla, Falda Noroeste del Cerro Jabonal,



**Figure 9.** Distribution of *Protium brenesii* and *P. costaricense*.

10°09'40"N, 084°39'30"W, 1500 m, 04 Nov 1997 (fr), *J. González et al. 2081* (CR-2 sheets, MO); Monteverde Reserve, Peñas Blancas river valley, Eladio Cruz farm, 10°20'N, 084°43'W, 800 m, 01 Nov 1986 (fr), *W. Haber & E. Bello 6176* (CR, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°20'N, 084°43'W, 850 m, 13 Mar 1987 (♂ fl), *W. Haber & E. Bello 6801* (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°20'N, 084°43'W, 800 m, 14 Apr 1987 (♂ fl), *W. Haber & E. Cruz 6979* (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°18'N, 084°45'W, 900 m, 21 May 1987 (fl with galls), *W. Haber & E. Bello 7169* (MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°20'N, 084°43'W, 820 m, 10 Jun 1997 (fr), *W. Haber & E. Cruz 7248* (CR, MO); Reserva Biológica Monteverde, río Peñas Blancas, Finca Wilson Salazar, 10°18'N, 084°43'W, 800–900 m, 20 Aug 1987 (fr), *W. Haber & E. Cruz 7391* (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, Finca Wilson Salazar, 10°18'N, 084°43'W, 860 m, 20 Oct 1987 (fr), *W. Haber & E. Cruz 7508* (CR-2 sheets), *7509* (MO); Reserva Biológica Monteverde, río Peñas Blancas, Finca Wilson Salazar, 10°18'N, 084°43'W, 800 m, 06 Nov 1987 (fr), *W. Haber & E. Cruz 7691* (CR, MO, NY-digital image); Reserva Biológica Monteverde, río Peñas Blancas, 10°18'N, 084°44'W, 900, 15 Dec 1987 (fr), *W. Haber & E. Bello 7914* (CR, MO); Reserva Biológica Monteverde, río Peñas Blancas, 10°19'N, 084°43'W, 800 m, 14 Dec 1987 (♂ fl), *W. Haber & E. Bello 7899* (CR, MO, NY-digital image); San Ramón, Bosque Eterno De Los Niños, 4 km SW of La Tigra de San Carlos, valley of río La Esperanza, finca Araya Ledezma, 10°18'N, 084°37'W, 600–800 m, 01 Jul 1992 (fr), *W. Haber et al. 11232* (CR-2 sheets, MO); Reserva Forestal de San Ramón, 10°12'53"N, 084°36'28"W, 03 May 1987 (♂ fl), *G. Herrera 617* (CR, F, MO); San Ramón, Los Ángeles, Reserva de San Ramón, 2 km al Norte de la Estación, 10°12'40"N, 084°36'20"W, 1000 m, 18 Oct 1993 (fr), *G. Herrera 6604*

(MO); area of the Reserva Biológica Alberto M. Brenes, 10°13'N, 084°36'W, 1010 m, 29 Apr 2001 (st), *J. Homeier & A. Wolter 723* (USJ); area of the Reserva Biológica Alberto M. Brenes, 10°13'N, 084°36'W, 1010 m, 29 Apr 2001 (st), *J. Homeier & A. Wolter 1010* (USJ); Reserva Forestal Arenal, río Peñas Blancas, Quebrada Agua Gata, Finca Francisco, 10°20'N, 084°42'W, 1200 m, 19 Sep 1990 (fr), *N. Obando 122* (CR-2 sheets, MO, NY-digital image); Reserva Biológica Monteverde, Estación Eladio's, 10°18'30"N, 084°43'10"W, 820 m, 02 Oct 1990 (fr), *N. Obando et al. 187* (CR-2 sheets, MO, NY-digital image); San Rafael de San Ramón, 20 Oct 1969 (fr), *S. Salas et al. 1378* (USJ); Reserva de San Ramón, 13 May 1985 (♂ fl), *L. Umaña s.n.* (USJ-026360); Cantón de Upala, Bijagua, El Pilón, Cabeceras del río Celeste, 10°49'N, 084°57'W, 700 m, 21 Apr 1988 (fr), *G. Herrera 1852* (CR, MO, NY-digital image); Volcán Tenorio, Pilón, 19 Nov 1987 (fl bud), *P. Sánchez & L.J. Poveda 1282* (CR, F); Parque Nacional Guanacaste, Sector San Ramón, Dos Ríos, sendero a Nispero y Argentina, 10°52'50"N, 085°24'30"W, 550 m, 04 Mar 1995 (fr), *R. Espinoza et al. 1298* (CR-2 sheets, MO, NY-digital image); Parque Nacional Guanacaste, Nueva Zelândia, Estación San Ramón, La Campana, Dos Ríos, río Colón, 10°52'50"N, 085°24'05"W, 550 m, 23 Mar 1994 (♂ fl), *D. García 196* (CR-2 sheets, MO, NY-digital image); Cantón de San Carlos, hacia Quebrada "Corella" San Carlos, 650 m, 23 Jun 1966 (fr), *A. Jiménez 4045* (CR, F, MO, NY-digital image); La Fortuna, Finca El Jilguero, Sendero La Lava, río Aguas Calientes 0.5 km aguas arriba, 10°26'35"N, 084°42'20"W, 700 m, 23 Nov 1992 (fr), *G. Herrera 5625* (CR-2 sheets); North side Arenal Volcano, 10°28'N, 084°42'W, 800 m, 11 Apr 1974 (fr), *R. Lent 3862* (CR, F, NY-digital image). **Guanacaste:** Cantón de La Cruz, Parque Nacional Guanacaste, Estación Pitilla, al noroeste de la estación, 11°01'48"N, 085°25'12"W, 550 m, 16 Jun 1989 (fr), *B. Hammel 17495* (CR, F, MO, NY-digital image); Parque Nacional Guanacaste, Estación Pitilla, 9 km al S de Santa Cecilia, 10°59'25"N, 085°25'40"W, 700–1000 m, 06 Mar 1991 (fr), *C.O. Moraga 315* (CR-2 sheets); Parque Nacional Guanacaste, Estación Pitilla, Sendero El Mismo, Finca La Pasmompa, 11°02'00"N, 085°24'30"W, 700 m, 09 Dec 1990 (♂ fl), *P. Ríos 216* (CR, MO); Parque Nacional Guanacaste, Estación Pitilla, Fila Orosilito y Sendero El Mismo, 10°59'26"N, 085°25'40"W, 700 m, 02 Mar 1991 (fr), *P. Ríos 310* (CR-2 sheets, MO, NY-digital image); Parque Nacional Guanacaste, Estación Pitilla, Sendero El Mismo, 10°59'26"N, 085°25'40"W, 700 m, 15 Jun 1991 (♂ fl), *P. Ríos 364* (CR-2 sheets, MO); Cantón de Bagaces, Parque Nacional Rincón de la Vieja, Sendero de la toma de agua, a 3 km de la estación, 10°46'05"N, 085°17'40"W, 1000 m, 17 Sep 1990 (fr), *G. Rivera 546* (CR-2 sheets, MO, NY-2 sheets, digital image); Parque Nacional Rincón de la Vieja, Colonia Blanca, 10°48'20"N, 085°17'50"W, 1300–1600 m, 08 Nov 1990 (fr), *G. Rivera 847* (CR-2 sheets); Parque Nacional Rincón de la Vieja, Sector Santa María, Sendero La Plantación, cabeceras Quebrada Zopilote, 10°46'48"N, 085°17'24"W, 950–1100 m, 14 Aug 1996 (fr), *J. F. Morales 5667* (CR-2 sheets); Guatuso, Lago Coter, 5 km norte, Hotel Ecolodge, 10°35'20"N, 084°55'50"W, 700 m, 28 Apr 1997 (♂ fl), *G. Rivera 3005* (CR). **San José:** Reserva Forestal Los Santos, quebrada Bomba, cruce a Fila Mona y La Bomba, 09°30'00"N, 083°56'45"W, 500 m, 28 Feb 2005 (fl bud), *D.*

*Santamaría* ♂ J.F. Morales 751 (CR); Reserva Forestal Los Santos, Dota, Fila Vega, Sendero a Fila Seca, 09°29'40"N, 083°57'30"W, 800–950 m, 03 Mar 2005 (fl bud), *D. Santamaría* ♂ J.F. Morales 900 (CR); Cantón de Pérez Zeledón, vicinity of El General, [09°23'42"N, 083°38'26"W], 1040 m, Feb 1936 (♀ fl), *A.F. Skutch* 2620 (A, GH, MO, NY-digital image); Pérez Zeledón, vicinity of El General, [09°20'48"N, 083°39'27"W], 640 m, Mar 1939 (♂ fl), *A.F. Skutch* 4244 (A, MO, NY-digital image); Pérez Zeledón, vicinity of El General, [09°22'20"N, 083°39'12"W], 675–900 m, Mar 1940 (♂ fl), *A.F. Skutch* 4849 (A, CR, F-2 sheets, MO); basin of General, 675–900 m, 10 Feb 1942 (fl), *A.F. Skutch* 5024 (F).

In view of the long history of confusion involving *Protium brenesii* and *P. costaricense*, the following information is provided to clarify some important parameters of the latter species, as it is here interpreted:

***Protium costaricense* (Rose) Engl., Nat. Pflanzenfam., ed. 2 [Engler & Prantl] 19a: 414. 1931.**

Figs 8B, 9

*Icica costaricensis* Rose, N. Amer. Fl. 25(3): 259. 1911.

Type. COSTA RICA. [Alajuela:] Santa Clara: Las Delicias, [500 m], Jan 1897 [♀ fl], *P. Biolley* 10665 [*T. Biolley* (sic), in the protologue] (holotype: US-digital image! [herbarium of Capt. John Donnell Smith, in the protologue]; isotypes: CR!, F!).

**Habitat and distribution.** *Protium costaricense* it is known from wet forests on the Caribbean slopes of Nicaragua (Atlántico Sur and Río San Juan Departments), Panama (Colón and Panamá Provinces), and Costa Rica. In Costa Rica, it is known from throughout the Caribbean coastal plain in Alajuela and Limón Provinces. It grows in primary forest and along river or forest edges, from 0 to 200 m in elevation (reportedly up to 500 m, according to the label of the type).

**Phenology.** Collected with staminate flowers in February and June; pistillate flowers in February, July, and August; and fruits in January and from June to December.

**Common name.** In Nicaragua, this species is known as alcanfor (*A. Laguna* 73; *R. Rueda et al.* 5338). In Costa Rica and Panama, it goes by copal, chutra, kerosín and alcanfor (Condit et al. 2011).

**Additional material examined.** NICARAGUA. **Atlántico Sur** [Zelaya]: Santa Fe, unión del Caño Agua Fría y Quebrada La Capilla, [11°41'N, 084°28'W], [100–200 m], 02 Oct 1982 (fr), *A. Laguna* 73 (MO). **Río San Juan:** Sábalo, 1 km al norte de río San Juan, 11°02'N, 084°27'W, [100 m], 09–10 Jul 1985 (fr), *P.P. Moreno* 26057 (MO); sobre el río Indio, entre San Juan del Norte Nuevo y La Casa de Narciso Orozco, incluyendo Caño Negro, 10°58'N, 083°44'W, 0–100 m, 01 Jul 1994 (♀ fl), *R. Rueda et al.* 1612 (MO); Reserva Indio-Maíz, Mpio. de San Juan del Norte, Laguna de Silico, 10°51'N, 083°46'W, 0–10 m, 02 Aug 1996 (fr), *R. Rueda et al.* 4850 (MO); Reserva Indio-Maíz, Mpio. de El Castillo, a lo largo del río Bartola entre el caño la Lar-

garta y la cabecera del río Bartola, 11°16'N, 084°16'W, [50–100 m], 29 Dec 1996 (fr), *R. Rueda et al.* 5127 (MO); Reserva Indio-Maíz, Mpio. de El Castillo, a 8 km de la cabecera del río Bartola, en dirección al Cerro el Diablo, 11°01'N, 084°14'W, 120 m, 04 Jan 1997 (fr), *R. Rueda et al.* 5338 (MO); Reserva Indio-Maíz, Mpio. de El Castillo, 3 km al norte de la desembocadura del Caño Chontaleño, 11°05'N, 084°15'W, 24 Feb 1997 (♂ fl), *R. Rueda et al.* 6285 (MO); Mpio. El Castillo, Reserva Indio-Maíz, río San Juan, entre la desembocadura del río Bartola y el Caño Sarnoso, 10°56'N, 084°20'W, 100 m, 04 Dec 1998 (fr), *R. Rueda et al.* 9462 (MO). **COSTA RICA. Alajuela:** along road between Cañas (Guanacaste) and Upala, near río Zapote, 1.8–2.7 km south of río Canalete, ca. 100 m, 25 Jun 1976 (♂ fl), *T.B. Croat* 36355 (MO, NY-digital image); San Carlos, San Luis de Cutris, 23 Sep 1983 (fr), *L.J. Poveda* 3663 (USJ). **Limón:** cantón de Pococí, Refugio Nacional de Fauna Silvestre Barra del Colorado, Sardinas, 10°38'24"N, 083°43'48"W, 15 m, 25 Nov 1992 (fr), *F. Araya* 61 (CR, MO, NY-digital image); Refugio Nacional de Fauna Silvestre Barra del Colorado, Puerto Lindo, 10°41'24"N, 083°39'00"W, 200 m, 24 Jul 1995 (fr), *F. Araya & J. Corrales* 803 (MO, NY-digital image); Southwestern-most ridge of Cerro Coronel, NW-facing slope, just S of the río Colorado, 10°40'30"N, 083°39'30"W, 10–80 m, 17–18 Sep 1986 (fr), *G. Davidse & G. Herrera* 31469 (MO); Hacienda Tapezco-Hds, La Suerte, 29 air km W of Tortuguero, 10°30'N, 083°47'W, 40 m, 20 Aug 1979 (♀ fl), *C. Davidson & J. Donahue* 8514 (MO); Parque Nacional Tortuguero, Estación Agua Fría, 3 km al Sur, Sendero Real, 10°27'N, 083°34'W, 40 m, 18 Jan 1988 (fr), *R. Robles* 1624 (MO, NY-digital image); Refugio Nacional de Fauna Silvestre Barra del Colorado, sector Cocorí, 30 km N de Cariari, 10°35'40"N, 083°48'00"W, 100 m, 15 Jun 1991 (fr), *E. Rojas* 227 (CR, MO, NY-digital image); río Santa Clara, 1 ½ mi NW. of Los Diamantes, ne. of Guápiles, ca. 980 ft [298 m], 18 Aug 1961 (fr), *G.B. Rossbach* 3823 (GH); Cerro Coronel, E of río Zapote, 1 km of río Colorado, 10°40'N, 083°40'W, 10–40 m, 13–14 Sep 1986 (fr), *W.D. Stevens & O.M. Montiel* 24333 (MO); Pueblo Nuevo, 17 km NE of Guácimo, 10°20'N, 083°36'W, 100 m, 07 Sep 1994 (fr), *K. Thomsen* 1112 (CR, NY-digital image). **PANAMA. Colón:** Donoso, río Hoja, UTM: E544656; N985023 [08°54'39"N, 080°35'38"W], 23 Aug 2009 (fr), *B. Araúz & J. De Gracia* 2118 (MO). **Panamá:** Zona del Canal: Barro Colorado Island, Frank Drayton Trail, [09°09'15"N, 079°51'05"W], [10–150 m], 22 May 1968 (fl bud), *T.B. Croat* 5769 (MO); Barro Colorado Island, William Morton Wheeler Trail, [09°09'20"N, 079°51'10"W], [10–170 m], 22 Sep 1968 (fr), *T.B. Croat* 6295 (MO); Barro Colorado Island, Drayton House, [09°08'29"N, 079°50'35"W], [10 m], 28 Feb 1969 (st), *T.B. Croat* 8262 (MO); Barro Colorado Island, Drayton House, [09°08'29"N, 079°50'35"W], [10 m], 16 Jul 1970 (fr), *T.B. Croat* 11337 (F, MO); Drayton House, [09°08'29"N, 079°50'35"W], [0–5 m], 28 Aug 1970 (fr), *T.B. Croat* 11939 (MO); Barro Colorado Island, James Zetek Trail, [09°09'31"N, 079°52'05"W], [10–100 m], 07 Jun 1971 (♂ fl), *T.B. Croat* 14926 (F, GH, MO-2 sheets); Barro Colorado Island, Drayton House, 06 Jul 1969 (fr), *R. Foster* 1093 (F, GH); Pipeline Road, 4 mi. N of Gamboa, [09°10'N, 079°46'W], [50–100 m], 21 Dec 1971 (st), *A.H. Gentry* 3230 (MO); Pipeline Road, [09°10'N, 079°46'W], 100 m, 10 Aug 1971 (fr), *E. Lao et al.*

16 (GH, MO-2 sheets); Pipeline Road, 16.6 km from beginning of road, N along río Agua Salud, [09°14'38"N, 079°48'57"W], 0–100 m, 22 Sep 1974 (fr), *S.A. Mori & J.A. Kallunki 2039* (GH, MO); along río Mendosa near Pipeline Road, 8 km NW of Gamboa, [09°09'36"N, 079°44'44"W], 95 m, 01 Nov 1973 (fr), *M. Nee 7743* (MO); Isla Barro Colorado, 120 m, 12 Oct 2006 (fr), *R. Pérez & S. Aguilar 1632* (MO); Barro Colorado Island, W of Drayton House, [09°08'29"N, 079°50'35"W], [0–10 m], 16 Feb 1932 (♀ fl), *R.H. Woodworth & P.A. Vestal 605* (A, MO).

The pseudarils of *Protium costaricense* are reported to have a pleasant flavor (*L.J. Poveda 3663*, USJ).

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# *Athyrium haleakalae* (Athyriaceae), a new rheophytic fern species from East Maui, Hawaiian Islands: with notes on its distribution, ecology, and conservation status

Kenneth R. Wood<sup>1</sup>, Warren L. Wagner<sup>2</sup>

**1** National Tropical Botanical Garden, 3530 Papalina Road, Kalāheo, HI 96741, USA **2** Department of Botany, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

Corresponding author: Kenneth R. Wood ([kwood@ntbg.org](mailto:kwood@ntbg.org))

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## Abstract

*Athyrium haleakalae* K.R. Wood & W.L. Wagner (Athyriaceae), a small lithophytic fern from East Maui, Hawaiian Islands, is described and illustrated. Notes on its distribution, ecology, and conservation status are also presented. The new species appears to be an obligate rheophyte, preferring sites of fast moving water along concave walls of streams and waterfalls. *Athyrium haleakalae* differs from the only other known Hawaiian *Athyrium*, *A. microphyllum* (Sm.) Alston, in having rhizomes 1–3 cm long and lanceolate blades 1- to 2-pinnate-pinnatifid, 3–8(–11) × 1–3(–4) cm, as compared to *A. microphyllum* having rhizomes (10–)15–30 cm long and ovate to ovate-triangular blades 3-pinnate-pinnatifid to 4-pinnate, 30–82 × 20–50 cm.

## Keywords

Athyriaceae, *Athyrium*, new species, rheophyte, Hawaiian Islands, East Maui endemic, Critically Endangered

## Introduction

*Athyrium* Roth, in the family Athyriaceae Alston, is a genus composed of ca. 230 species of terrestrial or epilithic plants with mostly erect or occasionally creeping or ascending rhizomes. Primary centers of *Athyrium* diversity are found in the Sino-Himalayan region where ca. 91 species are recorded from Southwest China, Sichuan Basin, Tibet-Yunnan Plateau and Nepal (Kramer and Green 1990, Fraser-Jenkins 1997, Wang 1999, Mabberley 2008, Liu et al. 2009) and with secondary centers of diversity in the Western

Pacific islands where ca. 54 species are known from the Japanese Archipelago, the Ryukyu Islands, Taiwan, and the Philippines (Salgado 1990, Kato 1995, Liu et al. 2009).

Concepts in the classification of *Athyrium* continue to change and evolve with recent molecular phylogenetic studies (Smith et al. 2006, Christenhusz et al. 2011, Rothfels et al. 2012, Sundue and Rothfels 2014, PPG I 2016). Smith et al. (2006) published a revised fern classification based on both morphological and molecular evidence placing *Athyrium* into Woodsiaceae (Diels) Herter, yet state that its placement was tentative and in need of a more refined analysis. Subsequently Christenhusz et al. (2011) placed *Athyrium* into Athyriaceae along with four other genera, namely *Anisocampium* C. Presl, *Cornopteris* Nakai, *Deparia* Hooker & Grev., and *Diplazium* Sw. Furthermore, they report the need for continued research, referring to the monophyly of *Athyrium* and *Diplazium*. In 2016 the Pteridophyte Phylogeny Group (PPG) published the most current understanding of lycophyte and fern phylogeny and in their community-derived classification they limit Athyriaceae to three genera, namely *Athyrium*, *Deparia*, and *Diplazium*, with an estimated 650 species.

There are nine other athyroid fern species endemic to the Hawaiian Islands, namely *Athyrium microphyllum* (Sm.) Alston, *Deparia cataracticola* M. Kato, *Deparia fenzliana* (Luerss.) M. Kato, *Deparia kaalaana* (Copel.) M. Kato, *Deparia marginalis* (Hillebr.) M. Kato, *Deparia prolifera* (Kaulf.) Hook. & Grev., *Diplazium arnottii* Brack., *Diplazium molokaiense* W.J. Rob., and *Diplazium sandwichianum* (C. Presl) Diels (Palmer 2003, Vernon and Ranker 2013). This recent discovery and present publication of *Athyrium haleakalae* K.R. Wood & W.L. Wagner brings the total number of Hawaiian Athyriaceae to ten, and represents the second *Athyrium* species in the archipelago.

## Methods

All measurements were taken from dried herbarium specimens and field notes and are presented in the descriptions as follows: length × width, followed by units of measurements (mm or cm). The authors have examined all specimens cited. The extent of occurrence and area of occupancy for *Athyrium haleakalae* was calculated by using ArcMap 10.2 in relation to coordinates recorded while collecting herbarium specimens or making field observations

## Taxonomic treatment

*Athyrium haleakalae* K.R. Wood & W.L. Wagner, sp. nov.

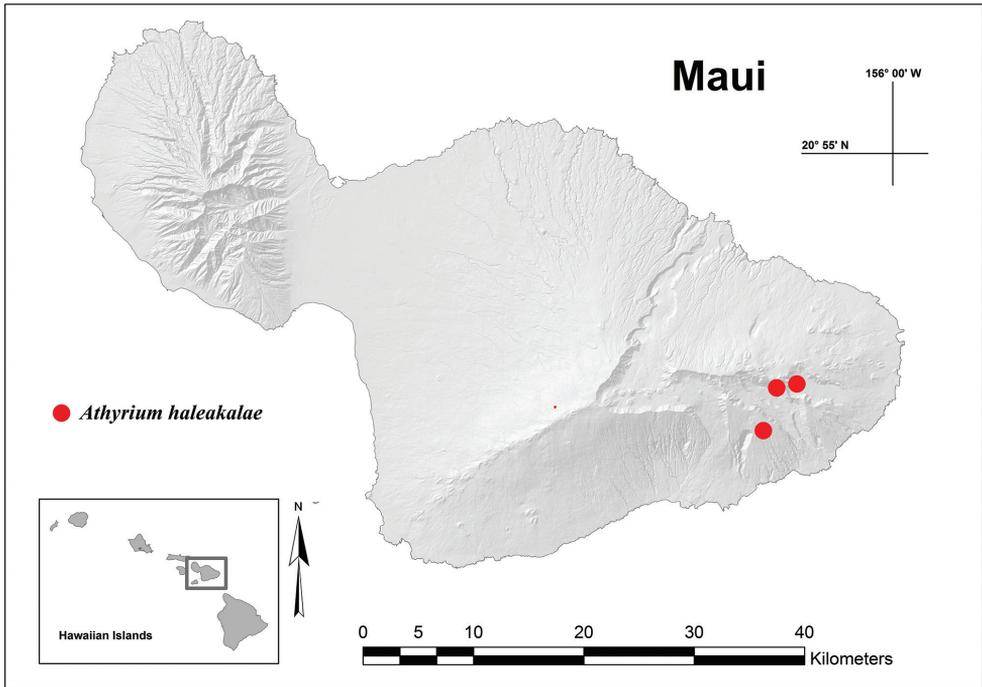
urn:lsid:ipni.org:names:77159814-1

Figs 1, 4A

**Diagnosis.** *Athyrium haleakalae* differs from the only previously known Hawaiian *Athyrium*, *A. microphyllum*, in having rhizomes 1–3 cm long and lanceolate blades



**Figure 1.** *Athyrium haleakalae* K.R. Wood & W.L. Wagner. **A–B** habit **C** detail of adaxial pinnule showing venation and fleshy spines **D** detail of abaxial pinnule showing range of sori shapes **E–F** lower stipe scales **G** rhizome scale. **A–G** from *Perlman et al.* 23964 (BISH, PTBG, UC, US) (Illustration by Alice Tangerini).



**Figure 2.** Map showing known distribution of *Athyrium haleakalae*, East Maui, HI, with upper right red dot indicating colonies in the headwaters of Kawakoe and Mokulehua, upper left in Helele'ike'oha, and lower red in Kīpahulu, near Palikea.

1- to 2-pinnate-pinnatifid, 3–8(–11) × 1–3(–4) cm, as compared to *A. microphyllum* with rhizomes (10–)15–30 cm long and ovate to ovate-triangular blades 3-pinnate-pinnatifid to 4-pinnate, 30–82 × 20–50 cm.

**Type.** UNITED STATES OF AMERICA. Hawaiian Islands, East Maui: Ko'olau Forest Reserve, west fork of Helele'ike'oha Stream, 20°45'14.58"N; 156°5'23.496"W, 1247 m elev., 28 May 2014, *Perlman et al. 23964*, (holotype: PTBG-070914; isotypes: BISH, UC, US).

**Description.** *Lithophytic ferns.* *Rhizomes* slender, erect to suberect, unbranched, radial, dark brown, 1–3 × 0.5–1.0 cm, closely set with roots and persistent, densely clothed by old stipe bases; scales covering rhizome tips, stramineous to dark brown, 2–4 × 1.0–1.5 mm, lanceate, margins entire, attenuate toward apex. *Fronds* 3–7 per rhizome; *stipes* medium brown, 20–50(–70) × 0.3–0.7 mm, swollen bases proximally thickened to 1 mm, well clothed with stramineous to dark brown basal scales 3.0–4.5 × 0.5–1.0 mm, sparser distally, thinning to glabrous; *blades* medium green, 1- to 2-pinnate-pinnatifid, 3–8(–11) × 1–3(–4) cm, lanceolate, *rachises* medium green to dark brown, glabrous, apex pinnatifid, acute, lobed ½ toward costae, *pinnae* 10–12 pair, lanceolate, alternate, petioled 1–2 mm, sessile near apex, fleshy spines 0.3–1.0 mm long on adaxial surface at bases of costae and costules, basal pinnae spaced 2–5(–8) mm, distal pinnae more closely spaced, not overlapping, lowest pinnae slightly re-

duced, second lowest pair usually largest, 0.7–2.0(–2.5) × 0.3–0.5(–0.8) cm, *pinnules*, lower with 6–8 pair, reduced distally, ovate to lanceolate, near alternate, serrate to lobed, veins 2–4 pairs in basal lobe, fewer pairs distally. *Sori* short linear, oblong, or J-shaped, 1.0–1.4 mm long, along acroscopic base of veinlets, 1(–2) per ultimate segment, *indusia* tan or brown, same shape as sori, entire, persistent.

**Etymology.** The new species is named after Haleakalā, East Maui, a massive, dormant shield volcano (3,057 m tall) and the only known location of *Athyrium haleakalae*.

**Specimens examined. United States. Hawaiian Islands, East Maui:** Hana Forest Reserve, Mokulehua drainage basin, *Metrosideros-Cheirodendron-Dicranopteris* montane wet forest, dissected by riparian vegetation, 1195 m elev., 21 Aug 2013, *Wood & Oppenheimer 15624* (BISH, PTBG, US); *loc. cit.*, 1161 m elev., 21 Aug 2013, *Oppenheimer et al. H81332* (BISH, PTBG); Hana Forest Reserve, Kawakoe headwaters, 1183 m elev., 22 Aug 2013, *Wood et al. 15637* (PTBG); *loc. cit.*, 1164 m elev., 22 Aug 2013, *Wood et al. 15639* (PTBG, UC); Ko‘olau Forest Reserve, west fork of Helele‘ike‘oha Stream, 1326 m elev., 28 May 2014, *Oppenheimer et al. H51415* (NY, PTBG); *loc. cit.*, 1367 m elev., 28 May 2014, *Oppenheimer et al. H51418* (MO, PTBG); *loc. cit.*, 1204 m elev., 29 May 2014, *Oppenheimer et al. H51426* (PTBG, UC); Haleakalā National Park, Kīpahulu Valley, south of Palikea Camp, 1280 m elev., 28 Aug 2014, *Welton et al. 2359* (HALE).

### Key to *Athyrium* in the Hawaiian Islands

- 1 Plants lithophytic; blades lanceolate 1- to 2-pinnate-pinnatifid, 3–8(–11) × 1–3(–4) cm.....*Athyrium haleakalae*
- Plants mostly terrestrial; blades ovate to ovate-triangular 3-pinnate-pinnatifid to 4-pinnate, 30–82 × 20–50 cm.....*Athyrium microphyllum*

**Distribution and ecology.** *Athyrium haleakalae* has only been documented on the mountain of Haleakalā, East Maui, the third highest prominence in the Hawaiian archipelago at 3,057 m. The volcanic island of Maui is ca. 1.2 million years old (Price and Elliott-Fisk 2004) and has an area of ca. 1,884 km<sup>2</sup>. Hawaiian flowering plants on Maui include 518 plant taxa, with 422 endemic and 99 of those being single-island endemics (Sakai et al. 2002). Estimates on the number of endemic fern and lycophyte taxa on Maui vary only slightly (Palmer 2003, Vernon and Ranker 2013) and the present authors estimate there are 115, including five single-island endemics. *Athyrium haleakalae* now represents the sixth single-island endemic fern or lycophyte taxon found on Maui. It is the tenth endemic athyrioid species in the Hawaiian Islands, and the second in that group that is restricted to a single island, the other being *Deparia cataracticola* M. Kato, of Kaua‘i.

Since its discovery in August of 2013 ca. 300 plants of *Athyrium haleakalae* have been observed in several headwater drainage systems of East Maui, namely Mokulehua and Kawakoe in the Hana Forest Reserve, Helele‘ike‘oha in the Koolau Forest Reserve, and Kīpahulu, near Palikea in Haleakalā National Park (Figure 2). Perhaps the com-



**Figure 3.** Typical habitat of *Athyrium haleakalae* around stream plunge pools, Hana Forest Reserve, East Maui, HI. Photo by K.R. Wood, 21 Aug 2013.

bination of its small size, remoteness of preferred habitat, and the extreme physical geography of its surroundings can explain why *A. haleakalae* has been overlooked to date. Modern access by helicopter and careful floristic inventories around large waterfalls and rugged plunge pools have led to its recent discovery by botanists of the National Tropical Botanical Garden (NTBG), the Maui Nui Plant Extinction Prevention Program (PEPP), and Haleakalā National Park. It is believed that the extent of occurrence for *A. haleakalae* may be greater than the four drainages reported here, and further research into similar habitats along adjacent drainage basins could lead to the discovery of additional colonies.

The current distribution of *Athyrium haleakalae* has an elevational range of 1,161–1,326 m. The dominant plant community of those regions is a *Metrosideros* Banks ex Gaertn. (Myrtaceae)-*Cheirodendron* Nutt. ex Seem. (Araliaceae) montane wet forest. Large colonies of matting ferns such as *Dicranopteris linearis* (Brum. f.) Underw. and *Diplopterygium pinnatum* (Kunze) Nakai (both Gleicheniaceae) are associated with these forests, being especially expansive near forest borders where steep slopes drop down to deep dissecting streams. Observations to date indicate that *Athyrium haleakalae* is an obligate rheophyte which prefers concave moss-matted basalt walls along the waterline of perennial streams, forming colonies over wet basalt rock faces especially under and around the ledges of waterfalls and hollows of large plunge pools



**Figure 4. A** Mature plants of *Athyrium haleakalae*, showing habitat preference along concave hollow of stream, Hana Forest Reserve, East Maui, HI (22 Aug 2013, *Wood & Oppenheimer 15639*) **B** Mature plant of *Athyrium microphyllum*, showing terrestrial habitat preference, erect rhizome, and large size, Mohihi, Kaua'i, HI (18 Dec 2014, *Wood & Flynn et al. 16175*). Photos by K.R. Wood.

(Figures 3, 4A). These stream sites average ca. 10–15 m broad and have exposed basalt bedrock and large strewn boulders. Associated ferns occurring with *A. haleakalae* include *Athyrium microphyllum*, *Cyclosorus sandwicensis* (Brack.) Copel. (Thelypteridaceae), *Selaginella arbuscula* (Kaulf.) Spring (Selaginellaceae), and *Hymenasplenium unilaterale* (Lam.) Hayata and *Vandenboschia davallioides* (Gaudich.) Copel. (both Hymenophyllaceae). Significantly, *A. haleakalae* grows in association with one of the rarest Hawaiian endemic rheophytes, *Cyclosorus boydiae* (D.C. Eaton) W.H. Wagner.

Adjacent riparian angiosperm vegetation, usually outside the rheophyte zone, includes *Broussaisia arguta* Gaudich. (Hydrangeaceae), numerous species of *Clermontia* Gaudich. and *Cyanea* Gaudich. (both Campanulaceae), several species of *Cyrtandra* J.R. Forst. & G. Forst. (Gesneriaceae), *Deschampsia nubigena* Hillebr. (Poaceae), *Dubautia plantaginea* Gaudich. and *D. scabra* (DC.) D.D. Keck (both Asteraceae), *Gunnera petaloïdea* Gaudich. (Gunneraceae), *Kadua affinis* DC. and *K. axillaris* (Wawra) W. L. Wagner & Lorence (both Rubiaceae), *Labordia venosa* Sherff (Loganiaceae), *Machaerina angustifolia* (Gaudich.) T. Koyama (Cyperaceae), *Melicope clusiifolia* (A. Gray) T.G. Hartley & B.C. Stone and *M. molokaiensis* (Hillebr.) T.G. Hartley & B.C. Stone (both Rutaceae), *Myrsine sandwicensis* A. DC. (Primulaceae), *Nertera granadensis* (Mutis) Druce (Rubiaceae), *Phyllostegia ambigua* (A. Gray) Hillebr. (Lamiaceae), *Polyscias oahuensis* (A. Gray) Lowry & G.M. Plunkett (Araliaceae), *Scaevola chamissoniana* Gaudich. (Goodeniaceae), and *Vaccinium dentatum* Sm. (Ericaceae).

Pigs (*Sus scrofa* L.), landslides, and invasive weeds such as *Ageratina adenophora* (Spreng.) R.M. King & H. Rob. (Asteraceae), *Axonopus fissifolius* (Raddi) Kuhlmann and *Paspalum urvillei* Steud. (both Poaceae), *Juncus planifolius* R. Br. (Juncaceae), *Hedychium gardnerianum* Ker Gawl. (Zingiberaceae), and *Tibouchina herbacea* (DC.) Cogn. (Melastomataceae) threaten the immediate habitat of *Athyrium haleakalae*.

**Conservation status.** *IUCN Red List Category.* When evaluating the conservation status of *Athyrium haleakalae* utilizing the World Conservation Union (IUCN) criteria for endangerment (IUCN 2001), *A. haleakalae* falls into the Critically Endangered (CR) category, which designates this species as facing the highest risk of extinction in the wild. Our formal evaluation can be summarized by the following IUCN hierarchical alphanumeric coding system of criteria and subcriteria: CR B1ab(i,ii,iii,v)+2ab(i,ii,iii,v), which reflects a wild population of ca. 300 individuals, an Extent of Occurrence (EOO) of 4.3 km<sup>2</sup>, and an Area of Occupancy (AOO) of less than 1 km<sup>2</sup>. Ecosystem trends on the mountain of Haleakalā also indicate that *A. haleakalae* is subject to an inferred decline in its area of occupancy, in addition to a decline in the extent and quality of its habitat and number of mature individuals. It should be noted that *A. haleakalae* is currently being cultivated by the Hawai'i State Division of Forestry and Wildlife at their Olinda Rare Plant Facility on East Maui.

## Discussion

*Athyrium microphyllum*, previously thought to be the only member of the genus in the Hawaiian Islands, is widely distributed and endemic on all the major high islands, ranging from 500 to 2,320 m (Figure 4B). Hawaiians called this species 'ākōlea and it is commonly found in native forest understory where it can occasionally become a co-dominant in healthy forests, especially just above the riparian edges of both mesic and wet forest habitats. *Athyrium microphyllum* is almost always terrestrial, averaging 50–100 cm tall, and having strait narrow rhizomes of up to 30 cm. Although *A. microphyllum* is occasionally lithophytic around streams, its large form eventually gets dislodged from the walls that enclose fast moving waters especially during flash floods.

In great contrast, *Athyrium haleakalae* is quite unique and has adapted itself to a very specific habitat with the ability to withstand flooding torrents that cascade through the deeply carved drainages of East Maui. With its tenacious rhizomes 1–3 cm long, small recumbent lanceolate blades 1- to 2-pinnate-pinnatifid, 3–8(–11) × 1–3(–4) cm, and stipe scales of up to 4.5 mm long, *A. haleakalae* can easily be distinguished from *A. microphyllum* which has rhizomes (10–)15–30 cm long, ovate to ovate-triangular blades 3-pinnate-pinnatifid to 4-pinnate, 30–82 × 20–50 cm, and stipe scales of up to 15 mm long (Figures 1, 4A,B).

Currently there are no extra-Hawaiian species of athyrioid ferns naturally occurring in the Hawaiian archipelago, although there are two historical introductions that have naturalized, namely *Deparia petersenii* (Kunze) M. Kato and *Diplazium esculentum* (Retz.) Sw. In our review, no previously described *Athyrium* was comparable to *A.*

*haleakalae*, and with hopes for its conservation and habitat protection we report this newly discovered, critically endangered, narrow endemic rheophyte as the latest addition to the pteridophyte flora of the Hawaiian Islands.

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