

A new species of *Bauhinia* L. (Caesalpinoideae, Leguminosae) from Nakhon Phanom Province, Thailand

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Abstract

A new liana species of the subfamily Caesalpinoideae (Leguminosae), namely *Bauhinia nakhonphanomensis*, collected from the Phulangka National Park, Nakhon Phanom Province, Thailand, is described and illustrated. It is easily recognized by the following combination of characters: tendrilled liana, entire leaves, acuminate or caudate leaf apices, oblong or elliptic floral bud, floral bud 25–35 mm long, raceme or panicle inflorescence, 10–13 mm long hypanthium, anther opening by longitudinal slits. Important comparative morphological characters with some closely related species are discussed.

Keywords

Bauhinia nakhonphanomensis, Thailand, Leguminosae, Caesalpinoideae, new species

Introduction

Bauhinia is a large genus belonging to the subfamily Caesalpinoideae (Leguminosae). It is pantropical and consists of approx. 150–160 species (in the strict sense) and is most abundant in the neotropics (Lewis et al. 2005). The number of species reaches approx. 300 for the genus when treated in a broader sense (Larsen and Larsen 1984, 1996). *Bauhinia* comprises trees, shrubs and tendrilled climbers. Its leaves are simple, entire, emarginated, bi-lobed or divided into free leaflets. Flowers are usually bisexual, with five petals and five sepals; stamens 10, 5, 3, 2 or 1 (Larsen et al. 1984). In Thailand,

Larsen et al. (1984) reported 37 species occurring throughout the country. They also reported that there were six species of tendrilled climbers with entire leaves. During a plant diversity survey carried out in the years 2011–2013 in Phulangka National Park, many specimens of the leaf entire and tendrilled climbers were collected. After careful comparison with known species, it was noted that there was a climber which was quite different from any of the known taxa. Thus, this plant is described here as a new species.

Taxonomy

Bauhinia nakhonphanomensis Chatan, sp. nov.

urn:lsid:ipni.org:names:77131499-1

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

Fig. 1

Type: THAILAND, Phulangka National Park, Ban Pheang District, Nakhon Phanom Province, N 17°57.087', E 104°09.425', alt. 170–240 m, 28 June 2012, W. Chatan 1337 (Holotype: BK; Isotypes: MSUT).

Diagnosis. *Bauhinia nakhonphanomensis* is a tendrilled liana. It differs from other closely similar species by having entire leaves, acuminate or caudate leaf apices, oblong or elliptic floral buds, floral bud 25–35 mm long, raceme or panicle inflorescences, 10–13 mm long hypanthium, and anthers opening by longitudinal slits.

Description. Large tendrilled liana climbing on shrubs or trees or big rocks. Branch glabrous; small young branches straight and the old ones flattened forming “Monkey-Ladders”. Leaves simple; lamina ovate, 7.0–14.5 × 4.0–8.0 cm, palmately netted venation with 5 large veins near the middle and 2 short and small ones marginally; margin entire; apex acuminate or caudate; base rounded to truncate or cordate; both surfaces glabrous excepted for hairs at base of the underside of lamina; young fresh leaves pinkish and green when old. Inflorescences raceme or panicle, terminal or leaf axial; axes greenish and glabrous near base, reddish and covered by densely reddish hairs near apex. Peduncles 35–40 mm long, glabescent. Floral buds oblong or elliptic, 5-ridged, 25–35 × 7–9 mm, apex twisted, reddish-green when fresh and brown when dry. Bracts 1, insert near pedicel base, ovate or lanceolate 8–9 × 4–5 mm, reddish when fresh and brown when dry, sparse minute hairs on abaxial side, dense hairs on adaxial side. Bracteoles 2, insert at the pedicel apex, orbicular or broadly ovate, 10–13 × 9–10 mm, dense reddish-green hairs on adaxial side when fresh and brown when dry, dense hairs on abaxial side when fresh and brown when dry, hairs caducous. Pedicels 28–40 mm long, densely covered with reddish hairs when fresh, the hairs change to be brown when dry. Hypanthium funnel-form, 10–13 mm long, striated. Sepals 5, connate forming an oblong or ellipsoid shape; 5-ridged floral buds, splitting into 5 separated and recurved sepals; each sepal linear, 15–20 × 2–3 mm, abaxial side densely hairy, adaxial side sparsely hairy near apex. Petals 5, pinkish, spatulate, acute to obtuse apex; expanded portion 25–32 × 10–12 mm, sparsely covered by whitish hairs on



Figure 1. *Bauhinia nakhonphanomensis* **A** Habit **B** Habit and inflorescences **C** Large and old stems forming flattened ‘Monkey-Ladders’ **D** Old (green) and young (pinkish) leaves **E** tendril **F** Inflorescence with many reddish bracteoles **G** Inflorescence with many reddish bracteoles and reddish-green floral buds.

both surfaces; margin entire, densely hairy on upper part and sparsely hairy on lower part; petal claw 15–22 mm long. *Stamens* 9–10; fertile stamens 3, filament 55–60 mm long, whitish to pinkish, hairy on lower part and glabrous on upper part; anther pink,

sparserly hairy and 5–6 mm long and opening by longitudinal slits; sterile stamens 6–7, filament 20–24 mm long, anther 2.3–2.5 mm long, hairy and opening by longitudinal slits. *Pistil* flattened, reddish, hairy on the two ridges extending from base to the top of style; stipe 15–17 mm; ovary fusiform, 10–12 mm long; styles 12–14 mm long; stigma capitate, approx. 1 mm diameter, glabrous. *Fruit* not seen.

Flowering and fruiting. flowering April–July and fruiting unknown.

Distribution. This new species is an endemic to Thailand and known from only one location at Phulangka National Park, Ban Pheang District, Nakhon Phanom Province, Thailand.

Ecology. This species grows in a rocky and dense dry evergreen forest at an elevation of 170–240 m. It climbs on small to tall shrubs, trees or on big stones. Some plants grow along the river.

Vernacular name. Thao Khadailing.

Etymology. *Bauhinia nakhonphanomensis* is named after the type locality Nakhon Phanom Province, the northeastern Thailand.

Discussion. In Thailand, *Bauhinia* species can be divided into two groups based upon their habit. The first group is comprised of trees or shrubs, while the other is tendrilled climbers. *Bauhinia nakhonphanomensis* belongs to the latter, but is clearly distinct from the other tendrilled species in having entire leaves with acuminate or caudate leaf apices, oblong or elliptic floral buds, floral bud 25–35 mm long, raceme or panicle inflorescences, 10–13 mm long hypanthium, and the anther opening by longitudinal slits. When comparing the new species to the other Thai species, it seems to closely resemble *B. concreta* Craib, *B. curtisii* Prain, *B. scandens* L., *B. strychnifolia* Craib and *B. tubicalyx* Craib based on their tendrilled climber habit, entire leaves and anther opening by longitudinal slits. *Bauhinia nakhonphanomensis* is distinct from these species by having long floral buds (i.e. 25–35 mm) and longer pedicels (i.e. 28–40 mm), while *B. concreta* Craib, *B. curtisii* Prain, *B. scandens* L., *B. strychnifolia* Craib and *B. tubicalyx* Craib have 12–15 mm floral bud lengths and shorter pedicels (2–20 mm) (Larsen et al. 1984).

When comparing this new species to the entire leaf species of *Bauhinia* in Indo-China, it can be distinguished from the other species based on hypanthium lengths. The hypanthium length of *Bauhinia nakhonphanomensis* is between 10–13 mm, while *B. clemensorum* Merrill has 20–25 mm hypanthium length. Of the other entire leaf species, *B. calycima* Pierre ex Gagnep., *B. cardinalis* Pierre ex Gagnep., *B. championii* (Bentham) Bentham, *B. curtisii* Prain and, *B. scandens* L., all have a short to very short hypanthium less than 5 mm long (Larsen et al. 1980).

Bauhinia nakhonphanomensis closely resembles *B. exurrens* Stapf, known only from Mt Kinabalu Malaysia (Larsen and Larsen 1996). The two species are similar to each other by having entire leaves, anthers opening by longitudinal slits, short hypanthium (approx. 10 mm), petals not recurved and long pedicels more than 25 mm. Further differences between these two species is shown in Table 1.

Table I. The distinguishing features between *B. nakhonphanomensis* and *B. exurrens* Stapf.

Characters	<i>B. nakhonphanomensis</i>	<i>B. exurrens</i> Stapf (from Larsen and Larsen 1996)
1. Floral bud shape	oblong or ellipsoid	clavate-ellipsoid
2. lamina nerve number	7-nerved	9–11-nerved
3. bracteole shape	Orbicular or broadly ovate	subulate
4. bracteole length	10–13 mm	2–3 mm
5. hypanthium size	10–13 mm	approx. 10 mm
6. petal color	pale pink	white?
7. petal surface	covered by whitish hairs on both surfaces	glabrous or subglabrous on both surfaces
8. petal length (including claw)	40–54 mm	approx. 20 mm
9. fertile stamen filament length	55–60 mm	15 mm
10. staminode number	6 or 7	2 or 3
11. staminode filament length	20–24	approx. 2 mm
12. stigma	globose, about 1 mm diameter	Peltate, approx. about 5 mm diameter

Acknowledgements

The author is indebted to Phulangka National Park and Department of National Park, Wildlife and Plant Conservation, for permission to collect and study plants in their National Park, and to my research team for their help. The author is grateful to the National Research Council of Thailand for funding support in the year 2011–2012 (Research Program No. 51593).

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Herbarium of the University of Málaga (Spain): Vascular Plants Collection

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Resource Citation: University of Málaga (2013-). MGC Herbarium of University of Málaga, Spain. 73.351 records. Contributed by García-Sánchez J, Cabezudo B, Pérez-Latorre A, Navarro T, Asensi A, Díez-Garretas B, Salvo E, Nieto JM, Trigo MM, Recio M, Soriguer F and Navas D. Online at http://ipt.gbif.es:8080/ipt/resource.do?r=mgc_cormof, <http://data.gbif.org/datasets/resource/8105/>, http://www.scai.uma.es/servicios/ciencias_vida/herbario/herbario.html, and, version 1.0 (last updated on 2013-04-22), GBIF key: <http://gbif.org/browse/agent?uuid=962ccee-f762-11e1-a439-00145eb45e9a>. Data Paper doi: 10.3897/phytokeys.26.5396

Abstract

The herbarium of University of Málaga (MGC Herbarium) is formed by four biological collections. The vascular plants collection (MGC-Cormof) is the main collection of the herbarium. MGC-Cormof dataset aims to digitize and publish data associated with over 76.000 specimens deposited in the collection, of which 97.2% of the specimens are identified at species level. Since 2011, the University of Málaga's Central Research Service (SCAI) has been responsible for maintaining the herbariums and the dataset. The collection is growing continuously, with an annual intake of about 1.500 specimens. Nearly 96% of the collection is digitized, by Herbar v3.7.1 software (F. Pando et al. 1996–2011), making over 73.000 specimens accessible through the GBIF network (<http://data.gbif.org/datasets/resource/8105/>). At present, 247 families and 8.110 taxa, distributed in angiosperms (93.97%), ferns and fern allies (4.89%) and gymnosperms (1.14%), constitute the MGC-Cormof collection. The families and genera best represented

in the collection are Compositae, Leguminosae, Gramineae, Labiateae, Caryophyllaceae, Teucrium, Silene, Asplenium, Linaria and Quercus. Most of the specimens are from the Western Mediterranean Region, fundamentally Southern Spain (Andalusia: 82% of specimens) and Northern Morocco (2.17%). Approximately, 63% of the specimens are georeferenced. The identification of the specimens in the collection has been carried out by the plant biology department at the University of Malaga and plus 40% of the specimens has been reviewed by experts. The MGC-Cormof dataset has been revised by DarwinTest v3.2 tool (Ortega-Maqueda and Pando 2008) before being published in GBIF. The data included in this database are important for conservation works, taxonomy, flora, cartography, phenology, palynology, among others.

El Herbario de la Universidad de Málaga (Herbario MGC) está constituido por cuatro colecciones biológicas. La colección de plantas vasculares (MGC Cormof) es la colección principal del herbario. La base de datos MGC-Cormof tiene como objetivo la digitalización y publicación de los datos asociados con los más de 76.000 ejemplares depositados en la colección, de los cuales el 97,2% de las muestras se encuentran identificadas a nivel de especie. Desde 2011, los Servicios Centrales de Investigación (SCAI) de la Universidad de Málaga son responsables de mantener el herbario y sus respectivas bases de datos. Esta colección está en continuo crecimiento, con una incorporación anual de unos 1.500 ejemplares. Casi el 96% de la colección está digitalizada, a través del programa Herbar v3.7.1 (F. Pando et al. 1996–2011) por lo que más de 73.000 especímenes son accesibles a través de la red de GBIF (<http://data.gbif.org/datasets/resource/8105/>). Actualmente, la colección MGC-Cormof está constituida por 247 familias y 8.110 taxones, distribuidos en angiospermas (93,97%), helechos y plantas afines (4,89%) y gimnospermas (1,14%). Las familias y géneros mejor representados en la colección son Compositae, Leguminosae, Gramineae, Labiateae, Caryophyllaceae, Teucrium, Silene, Asplenium, Linaria y Quercus. La mayoría de los especímenes provienen de la región del Mediterráneo Occidental, fundamentalmente del sur de España (Andalucía: 82% de las muestras) y del norte de Marruecos (2,17%). Aproximadamente, el 63% de las muestras se encuentran georreferenciadas. La identificación de los ejemplares de la colección ha sido realizada por personal del departamento de biología vegetal de la Universidad de Málaga y además un 40% de los ejemplares ha sido revisado por especialistas. La base de datos MGC-Cormof ha sido revisada mediante la herramienta DarwinTest v3.2 (Ortega-Maqueda and Pando 2008) antes de ser publicada en GBIF. Los datos incluidos en esta base de datos son importantes para trabajos de conservación, taxonomía, flora, cartografía, fenología, palinología, entre otros.

Keywords

MGC, MGC Herbarium, University of Malaga (SCAI), Cormophyta, Spermatophyta, Pteridophyta, Compositae, Leguminosae, Gramineae, Labiateae, Caryophyllaceae, Cruciferae, Scrophulariaceae, Cistaceae, Umbelliferae, Liliaceae, Western Mediterranean Region, Spain, Southern Spain, Southern Iberian Peninsula, Iberian Peninsula, Andalusia (Spain), Malaga province (Spain), Northern Morocco

General description

The MGC-Cormof dataset belongs to the University of Malaga MGC Herbarium, and has been the responsibility of the Central Research Service (SCAI) of the same university since 2011. In addition to that of MGC-Cormof, the MGC Herbarium contains three other datasets, which are not the subject of this paper: MGC-Algae (5.400 sheets), MGC-Briof (1.850 sheets) and MGC-Lichen (350 sheets). The MGC-Cormof collection has nearly 76.000 sheets, of which 97.2% are identified at species level. Most of the plant specimens are collected from Andalusia (Southern

Spain) with 60.456 sheets, which Malaga province is the most important area represented (39.902 sheets). In addition, the herbarium contains plant specimens from Northern Morocco, several other places in Spain, and countries from Europe, Africa and South America

The herbarium collections are the result of several research projects that have been carried out over the last 40 years. This collections are very active and in continual growth, with an annual intake of about 1.500 specimens. The main data contributors are researchers from the Botany Area of the Plant Biology Department of the University of Malaga, which was responsible for administering the herbarium until 2011. Ninety-six percent of the collection is digitalized, by Herbar v3.7.1 software (F. Pando et al. 1996–2011), and so the dataset has 73.156 specimens, which are available on the GBIF data portal (<http://data.gbif.org/datasets/resource/8105/>).

MGC herbarium is one of the reference herbaria for Flora Iberica (Castroviejo 1986–2012) and Vascular Flora in Eastern Andalusia (Flora Vascular de Andalucía Oriental) (Blanca et al. 2009). The journal Acta Botanica Malacitana (B. Cabezudo 1975–2013) (<http://www.biolveg.uma.es/abm/abm.html>) is closely associated with the MGC Herbarium and periodically publishes papers that are based on data included in its dataset.

Project details

Specific projects for computerizing the herbarium specimens, a task that began in 2006, are mentioned below:

Project title: “Informatización del Herbario de la Universidad de Málaga (MGC)”.

Project personnel: Dr. Baltasar Cabezudo Artero

Funding: Digitalisation supported by the Spanish Ministry of Education and Science (ref. CLEG2004-21156-E).

Length: January 2006–September 2009.

Project title: “Realización de una prestación de servicios para el mantenimiento e inclusión de pliegos del proyecto Flora de Andalucía Oriental en el Herbario público de la Universidad de Málaga”.

Project personnel: Dr. Baltasar Cabezudo Artero

Funding: Digitalisation supported by the Regional Government of Andalusia (Junta de Andalucía) (ref. 8.06/03.3353).

Length: February 2010–February 2011.

Project title: “Digitalización y Gestión de las Bases de Datos del Herbario MGC de la Universidad de Málaga”.

Project personnel: Dr. José García Sánchez

Funding: Digitalisation supported by Ministry for Science and Innovation (ref. PTA2011-6046-I).

Length: January 2012–December 2014.

Temporary staff for assisting in the fieldwork were contracted through the Regional Government of Andalusia, Junta de Andalucía (Spain) research group: Biodiversidad, Conservación y Recursos Vegetales; Group code: RNM-115.

Data published through GBIF:

Data from the MGC-Cormof dataset can be consulted in the Spanish GBIF Node IPT and the data resource of the University of Malaga.

http://www.gbif.es:8080/ipt/resource.do?r=mgc_cormof

<http://data.gbif.org/datasets/resource/8105/>

Taxonomic coverage

General taxonomic coverage:

The 76.000 sheets of the MGC-Cormof collection are grouped into 241 families (Figure 1), 1.551 genera (Figure 2), 6.158 species and 8.110 taxa (including infraspecific categories). Most of the specimens are angiosperms (93.97%), followed by ferns and fern allies (4.89%) and gymnosperms (1.14%). The main families in order of abundance are Compositae (10.2%), Leguminosae (9.7%), Gramineae (8.5%), Labiateae (7.5%), Caryophyllaceae (4.8%), Cruciferae (3.8%), Scrophulariaceae (3.5%), Cistaceae (3.1%), Umbelliferae (2.4%) and Liliaceae (2.1%). Main genera in order of abundance are Teucrium (2.48%), Silene (1.62%), Asplenium (1.43%), Linaria (1.20%), Quercus (1.10%), Centaurea (1.08%), Helianthemum (1.02%), Cistus (1.02%), Trifolium (1.01%) and Galium (1.01%).

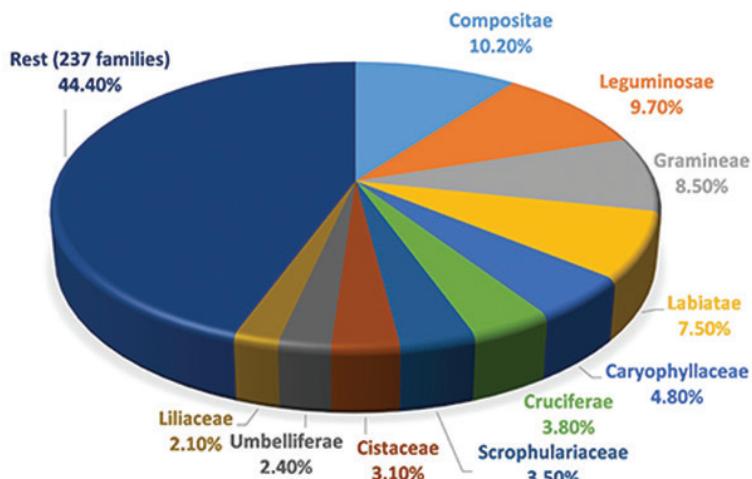


Figure 1. Main families in MGC-Cormof collection

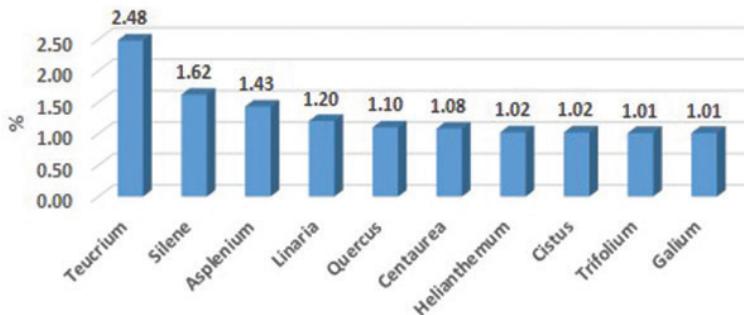


Figure 2. Main genera in MGC-Cormof collection.

It is important to mention that this collection contains a wide representation of plants from several Protected Areas of southern Spain (Cabezudo et al. 2005; Pérez La-torre et al. 1998, 1999, 2002), endemic species (Blanca et al. 2009; Salvo et al. 1983), threatened species (Blanca et al. 1999, 2000, 2009; Cabezudo et al. 2005; Salvo et al. 1983), invasive species (Dana et al. 2005), ornamental species and many weeds.

Taxonomic ranks

Kingdom: Plantae

Phylum: Pteridophyta, Spermatophyta

Class: Magnoliopsida, Liliopsida, Filicopsida, Lycopsida, Coniferopsida, Equisetopsida, Ophioglossopsida, Gnetopsida, Taxopsida, Cycadopsida, Gingkopsida, Psilotopsida.

Family: Acanthaceae, Aceraceae, Adiantaceae, Agavaceae, Aizoaceae, Alismataceae, Alliaceae, Amaranthaceae, Amaryllidaceae, Anacardiaceae, Anemoneaceae, Annonaceae, Apocynaceae, Aquifoliaceae, Araceae, Araliaceae, Araucariaceae, Aristolochiaceae, Asclepiadaceae, Aspidiaceae, Aspleniaceae, Athyriaceae, Azollaceae, Balsaminaceae, Bartramiaceae, Basellaceae, Begoniaceae, Berberidaceae, Betulaceae, Bignoniaceae, Blechnaceae, Bombacaceae, Boraginaceae, Botrychiaceae, Bromeliaceae, Buddlejaceae, Butomaceae, Buxaceae, Cactaceae, Callitrichaceae, Calyceraceae, Campanulaceae, Cannaceae, Capparaceae, Caprifoliaceae, Caricaceae, Caryophyllaceae, Casuarinaceae, Cecropiaceae, Celastraceae, Cephalotaxaceae, Ceratophyllaceae, Chenopodiaceae, Cistaceae, Clethraceae, Clusiaceae, Cneoraceae, Combretaceae, Commelinaceae, Compositae, Convallariaceae, Convolvulaceae, Coriariaceae, Cornaceae, Corylaceae, Crassulaceae, Cruciferae, Cryptogrammaceae, Cucurbitaceae, Culicaceae, Cunoniaceae, Cupressaceae, Cyatheaceae, Cycadaceae, Cynomoriaceae, Cyperaceae, Davailliaceae, Dennstaedtiaceae, Dicksoniaceae, Dioscoreaceae, Dipsacaceae, Dracaenaceae, Droseraceae, Dryopteridaceae, Ebenaceae, Elaeagnaceae, Elatinaceae, Empetraceae, Ephdraceae, Equisetaceae, Ericaceae, Eriocaulaceae, Erythroxylaceae, Escalloniaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Frankeniaceae, Gentianaceae, Geraniaceae, Gesneriaceae, Ginkgoaceae, Gleicheniaceae, Globulariaceae, Gramineae, Grammiti-

daceae, Grossulariaceae, Guttiferae, Haloragaceae, Hamamelidaceae, Hemionitidaceae, Hippochaetaceae, Hippuridaceae, Hydrangeaceae, Hydrocharitaceae, Hydrocotylaceae, Hydrophyllaceae, Hymenophyllaceae, Hypolepidaceae, Iridaceae, Isoetaceae, Juglandaceae, Juncaceae, Juncaginaceae, Labiatae, Lauraceae, Leguminosae, Lemnaceae, Lentibulariaceae, Liliaceae, Linaceae, Lycopodiaceae, Lythraceae, Magnoliaceae, Malpighiaceae, Malvaceae, Marsileaceae, Melastomataceae, Meliaceae, Melianthaceae, Menispermaceae, Molluginaceae, Monimiaceae, Monotropaceae, Moraceae, Musaceae, Myoporaceae, Myricaceae, Myrsinaceae, Myrtaceae, Najadaceae, Nephrolepidaceae, Neuradaceae, Nyctaginaceae, Nymphaeaceae, Oleaceae, Oleandraceae, Onagraceae, Ophioglossaceae, Orchidaceae, Orobanchaceae, Osmundaceae, Oxalidaceae, Paeoniaceae, Pandanaceae, Papaveraceae, Parnassiaceae, Passifloraceae, Phormiaceae, Phyladelphyae, Phytolaccaceae, Pinaceae, Piperaceae, Pittosporaceae, Plantaginaceae, Platanaceae, Plumbaginaceae, Podocarpaceae, Polemoniaceae, Polygalaceae, Polygonaceae, Polypodiaceae, Portulacaceae, Posidoniaceae, Potamogetonaceae, Primulaceae, Proteaceae, Psilotaceae, Pteridaceae, Punicaceae, Pyrolaceae, Rafflesiaceae, Ranunculaceae, Resedaceae, Rhamnaceae, Rosaceae, Rubiaceae, Ruppiaceae, Rutaceae, Salicaceae, Salviniaceae, Santalaceae, Sapindaceae, Sapotaceae, Saxifragaceae, Scrophulariaceae, Selaginellaceae, Simaroubaceae, Sinopteridaceae, Smilacaceae, Solanaceae, Sparganiaceae, Sterculiaceae, Strelitziaceae, Styracaceae, Symplocaceae, Tamaricaceae, Taxaceae, Taxodiaceae, Theligonaceae, Thymelaeaceae, Thymeleaceae, Tiliaceae, Tropaeolaceae, Typhaceae, Ulmaceae, Umbelliferae, Urticaceae, Valerianaceae, Verbenaceae, Violaceae, Viscaceae, Vitaceae, Vivianiaceae, Winteraceae, Woodsiaceae, Zamiaceae, Zannichelliaceae, Zingiberaceae, Zosteraceae, Zygothecaceae

Common names

Tracheophytes, Cormophytes, Vascular Plants, Sunflowers, Legumes, True Grasses, Mints, Pinks, Crucifers or Mustard, Figworts, Rock Roses, Parsley or Carrot family, Lyli family, Germander, Campion, Petalo Rauriki, Spurred Snapdragon, Oak, Knapweed, Rock Rose, Rock Rose, Clover, Bedstraw

Spatial coverage

General spatial coverage

Most of the data refer to the Western Mediterranean Region, mainly Southern Spain (Andalusia 82% of sheets) and Northern Morocco (2.17%). Andalusia is composed of 8 provinces, Malaga province being the most important with 53% of sheets, followed by Cádiz (8.77%) and Granada (8.50%). Moreover, 11% of the data refer to the rest of Spain and 7% from 50 countries of Europe, Africa and South America mainly (Figures 3 and 4).

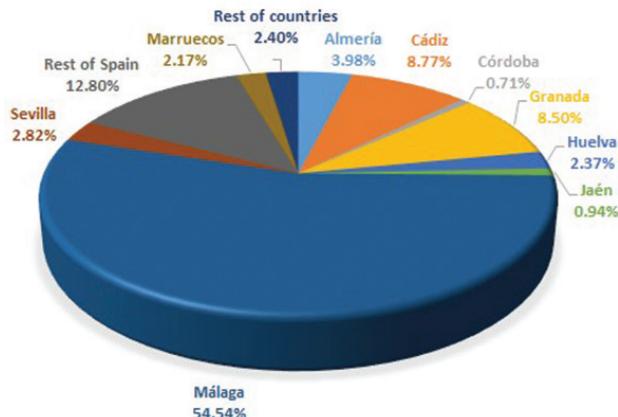


Figure 3. Spatial coverage of MGC-Cormof collection.

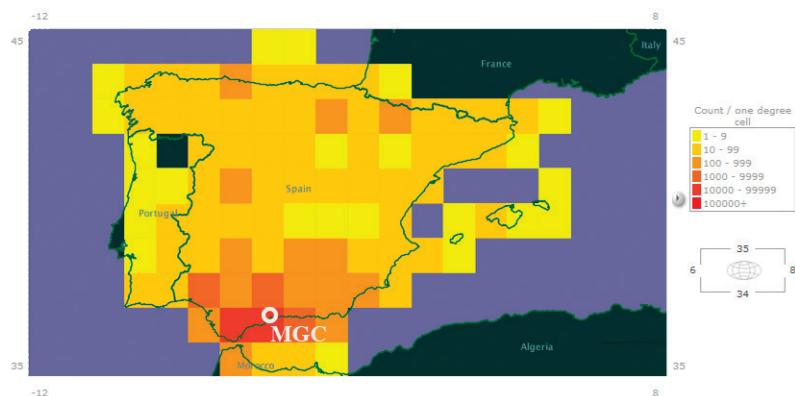


Figure 4. Distribution map of the records from the MGC-Cormof dataset. This map shows most of the records in the dataset (Iberian Peninsula and North of Morocco). Source: GBIF Data Portal (<http://data.gbif.org/datasets/resource/8105/>).

The MGC-Cormof collection has a large number of plants from all the main Protected Areas of Malaga province, including Natural Parks (Sierra de las Nieves, Sierras de Tejeda, Almijara y Alhama, and Montes de Málaga) and Natural Areas (Los Reales de Sierra Bermeja, Torcal de Antequera, and Desfiladero de los Gaitanes), as well as other Protected Areas of southern Spain, some of which are Natural Parks shared with Malaga (e.g. Los Alcornocales, Sierra de Grazalema) and the Protected Landscape Corredor Verde (Green Corridor) del Guadiamar. Table 1 shows the approximate number of sheets from these protected areas. Moreover, many plants considered as agricultural weeds and others taken from roads and cities as well as ornamental plants (910 sheets) from public parks and gardens of the city of Malaga, are included. Sixty-three percent of the specimens are georeferenced. All of them have been referenced by MGRS coordinate system, which have been transformed into geographical coordinate before uploading to the GBIF Portal by Herbar 3.7.1

Table 1. Number of sheets from main protected areas represented in the herbarium.

Protected area	Nº sheets
Natural Park Sierras de Tejeda, Almijara y Alhama	8890
Natural Park Sierra de las Nieves	2545
Natural Park Sierra de Grazalema	1185
Natural Park Los Alcornocales	940
Natural Park Montes de Málaga	680
Natural Area Los Reales de Sierra Bermeja	1700
Natural Area Torcal de Antequera	1180
Natural Area Desfiladero de los Gaitanes	425
Protected Landscape Corredor Verde del Guadiamar	910

software (Pando et al. 1996–2011). The accuracy of the coordinate grids in MGRS system varies from 1 m² to 10 km² and the accuracy in geographical coordinate varies from 1 to 7071 m².

Coordinates

34°0'0"S and 51°42'0"N; 116°2'60"W and 83°25'48"E

Temporal coverage

1837–2012.

Figure 5 represents the year of gather of the sheets incorporated in the MGC-Cormof collection. The sheets prior to 1972 (date of the creation of the MGC Herbarium) and also some of them, along the life of the herbarium, are the result of donations and exchanges with several herbaria. The best represented are The Real Jardín Botánico de Madrid Herbarium (MA Herbarium), Barcelona Botanical Institute Herbarium (BC Herbarium), University of Seville Herbarium (SEV Herbarium), University of Granada Herbarium (GDA Herbarium) and University of Extremadura Herbarium (UNEX Herbarium). The differences observed in the number of sheets along the time are mainly due to develop of research works and post grade studies carried out in the Botany Area of the Department of Plant Biology at University of Malaga.

Natural collections description

Collection name: MGC-Cormof

Collection identifier: 962ccee-a-f762-11e1-a439-00145eb45e9a

Formation period: 1972–2013

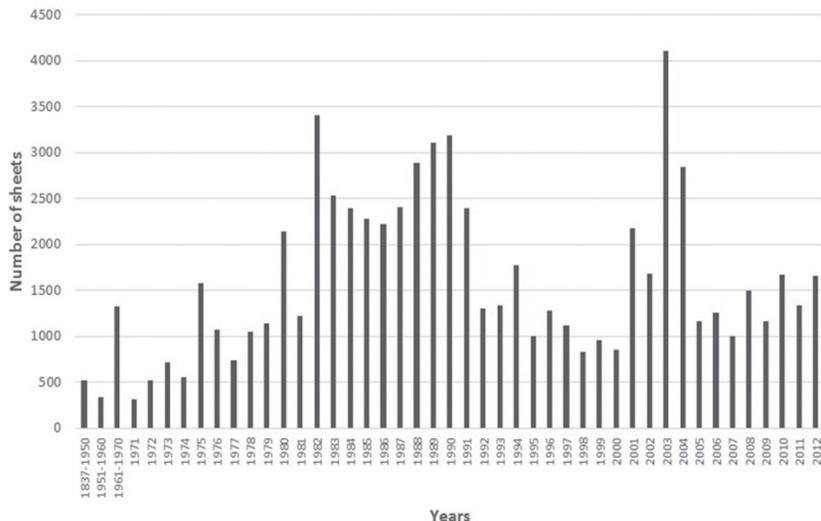


Figure 5. Number of sheets gathered between 1837 and 2012 in the MGC-Cormof collection.

Specimen preservation method: Dried and pressed

Curatorial unit 1: 73.156 with an uncertainty of 0 (Sheets)

Curatorial unit 2: 6.158 with an uncertainty of 0 (Species)

Curatorial unit 3: 1.551 with an uncertainty of 0 (Genera)

Curatorial unit 4: 247 with an uncertainty of 0 (Families)

Methods

Study extent

Most plants are from Southern Spain (Andalusia), Malaga province being the most widely represented area, the aim being to cover the widest degree of plant biodiversity for this territory. In addition, the collection contains plants from Northern Morocco and several places from the rest of Spain and countries from Europe, Africa and South America.

Sampling description

The plants of this collection were mainly gathered by researchers of the Botany Area of the Department of Plant Biology at University of Malaga, as well as by members of the herbarium. A small component of the collection comes from exchanges or donations from other research centres or researchers.

Method step description

Before incorporating new plants in the herbarium, the steps described below are followed.

First, the material is pressed and dried, mounted on double A2 standard size (42 × 59.4 cm) sheets which perfectly cover and protect the specimen. Inside each sheet, an identification label provides the following information: taxonomy, country, province, county, locality, georeference, date, ecology, collectors and determinations. To kill any insects contained in the sheets, they are frozen at -20 °C for 72 hours. Periodically, the herbarium room is fumigated. The specimens are kept in compact shelving cabinets and arranged taking into account three main taxonomic groups: pteridophytes, gymnosperms and angiosperms. Within each group, the specimens are alphabetically arranged by families, genera and species.

Quality control

Every specimen of the MGC-Cormof collection has been identified by researchers of the Botany Area of the Department of Plant Biology at University of Malaga. Moreover, 40% of the specimens of this collection have subsequently been taxonomically revised for regional or national studies of flora or taxonomical revisions. Each taxonomic modification is incorporated into the database.

The dataset is analysed in search of digitalisation errors before uploading to the GBIF Portal. This check is carried out by the DarwinTest v3.2 tool (Ortega-Maqueda and Pando 2008), provided by the Spanish GBIF Node. This tool looks for mistakes in taxonomy, dates, geospatial information, collectors, identifiers, etc.

Datasets

Dataset description

Object name: Darwin Core Archive MGC Herbarium of the University of Malaga (Spain): MGC-Cormof dataset

Character encoding: UTF-8

Format name: Darwin Core Archive format

Format version: 1.0

Distribution: http://www.gbif.es:8080/ipt/resource.do?r=mgc_cormof

Date of metadata creation: 2013-04-04

Metadata language: English

Hierarchy level: Dataset

User license: The MGC-Cormof dataset is made available under the Open Data Commons Attribution License: <http://www.opendatacommons.org/licenses/by/1.0/>

DarwinCore elements: Thirty-two (32) DarwinCore elements (<http://purl.org/dc/terms/>) included in the dataset published through the GBIF network. These are: id, preparations, typeStatus, eventDate, family, specificEpithet, minimumElevationInMeters, decimalLongitude, identifiedBy, occurrenceRemarks, dateIdentified, individualCount, collectionCode, minimumDepthInMeters, kingdom, coordinateUncertaintyInMeters, infraspecificEpithet, institutionCode, country, stateProvince, modified, recordedBy, genus, scientificNameAuthorship, maximumDepthInMeters, locality, recordNumber, catalogNumber, scientificName, maximumElevationInMeters, decimalLatitude, basisOfRecord

External datasets

Dataset description

Object name: Universidad de Málaga: MGC-Cormof

DiGIR information: <http://gbif.cie.uma.es/digir/DiGIR.php>

Character encoding: iso-8859-1

Format name: Darwin Core

Format version: 1.2

Distribution: <http://data.gbif.org/datasets/resource/8105/>

Date of metadata creation: 2009-02-19

Metadata language: English

Hierarchy level: Dataset

Acknowledgments

The authors of this article thank all the people who have contributed, in whatever way, to the creation and growth of the collections of the MGC herbarium, especially all the members of the Department of Plant Biology of the University of Malaga.

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Systematics of *Disakisperma* (Poaceae, Chloridoideae, Chlorideae)

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Abstract

Disakisperma Steud. is a genus of four predominantly perennial C₄ (NAD-ME) species in the Americas, Africa, and Asia. Its species previously were treated in *Eleusine*, *Eragrostis*, *Coelachyrum*, *Cypholepis*, *Leptochloa*, or *Diplachne* by nearly all authors. It includes the widespread North and South American amphi-tropical disjunct *Disakisperma dubium* (type of the genus), *D. eleusine* from southern Africa, *D. obtusiflorum* from central and northern Africa to southern Asia, and *D. yemenicum*, **comb. nov.** from eastern and southern Africa to Yemen. This paper provides a key to the species, geographic distributions, descriptions, including comments on the anatomy of leaves, stems, lemmatal micromorphology, a phylogram based on five molecular markers, and discussions of chromosome numbers. The species are rarely, if at all, known outside of their native ranges and are unlikely to become aggressively invasive. All species are considered Least Concern following IUCN guidelines. Lectotypes are designated for *Diplachne dubia* var. *pringleana* Kuntze, *Disakisperma mexicana* Steud., *Eragrostis yemenica* Schweinf., and *Leptochloa appletonii* Stapf.

Resumen

Disakisperma Steud. es un género de cuatro especies perennes C₄ (NAD-ME), las cuales que son de las Américas y África y Asia. Sus especies previamente fueron tratados en *Eleusine*, *Eragrostis*, *Coelachyrum*, *Cypholepis*, *Leptochloa*, o *Diplachne* por casi todos los autores. Incluye la generalizada del Norte y América del Sur amfitropical disjunta *D. dubium* (tipo del género), *D. eleusine* desde el sur de África, *D. obtusiflorum* del centro y el norte de África hasta el sur de Asia, y *D. yemenicum*, **comb. nov.** del este y sur África a Yemen. Este documento proporciona una clave para las especies y las descripciones completas, incluidos los comentarios sobre la anatomía de las hojas, tallos, micromorfología lemmatal, una filograma basado en cinco marcadores moleculares y las discusiones de los números de cromosomas. Las especies son rara-

mente, si acaso, conocida fuera de sus áreas de distribución natural y es poco probable para convertirse en invasora agresiva. Todos las especies se consideran la designación de Least Concern sigue IUCN. Se designa lectotipos para *Diplachne dubia* var. *pringleana* Kuntze, *Disakisperma mexicana* Steud., *Eragrostis yemenica* Schweinf. y *Leptochloa appletonii* Stapf.

Keywords

Conservation, *Coelachyrum*, *Cypholepis*, *Disakisperma*, grasses, ITS, leaf anatomy, lectotypification, *Leptochloa*, phylogeny, plastid DNA sequences, stem anatomy, systematics, taxonomy, Thysanoptera

Introduction

Recent molecular studies by Peterson et al. (2010, 2012) determined *Leptochloa* P. Beauv. s.l. (Snow 1997) to be polyphyletic, with its sampled species partitioned into five strongly supported clades. Peterson et al. (2012) analyzed 22 of the 32 species of *Leptochloa* and a wide representation of taxa from related genera in subfamily Chloridoideae, tribe Chlorideae. *Disakisperma* Steud. was one of the proposed segregate genera (Peterson et al. 2012), but that generic name has not been used widely since its description by Steudel (1854). Nearly all authors have placed *Disakisperma* in *Leptochloa* or *Diplachne* (see summaries in Valls 1978; McNeill 1979; Snow 1997).

The clade in Peterson et al. (2012) that we recognize as *Disakisperma* included *Leptochloa dubia* (Kunth) Nees, *L. eleusine* (Nees) Cope & N. Snow, and *L. obtusiflora* Hochst. These were the first molecular results to suggest a close relationship among these species, although based on overall morphology Steudel (1841: 30) placed *Leptochloa obtusiflora* Trin. ex Steud. (nom. inval.) as a synonym of *L. dubia*, suggesting their affinity. In a paper documenting C₄ origins in the grasses, Aliscioni et al. (2012) presented a summary tree for Chloridoideae derived from *rbcL*, *ndhF*, and *trnK/matK* sequences, which united *Leptochloa dubia* and *Coelachyrum yemenicum* (Schweinf.). S.M. Phillips in a clade with moderate bootstrap support. For this study we included two samples of *Coelachyrum yemenicum* to test its relationship with other members of *Disakisperma*.

The genus *Disakisperma* was first described by Steudel (1854) based on *Disakisperma mexicana* Steud.; the latter name probably first placed in synonymy of *Leptochloa dubia* by Chase and Niles (1962). The biology and taxonomy of *Disakisperma dubium* (Kunth) P. M. Peterson & N. Snow have been studied in some detail by Valls (1978), albeit with different interpretations of how many infraspecific taxa to recognize (Nicora 1995; Snow 1997, 2012), whereas knowledge of the African species is more limited (Phillips 1974a; Gibbs Russell et al. 1991; Snow 1997). Historically, the classification of the four species included in our study has been disparate. *Disakisperma dubium* was first described as *Chloris dubia* by Kunth (1816); *Disakisperma eleusine* (Nees) P.M. Peterson & N. Snow was first recognized as *Diplachne eleusine* by Nees von Esenbeck (1841); the basionym of *Disakisperma obtusiflorum* (Hochst.) P.M. Peterson & N.

Snow is *Leptochloa obtusiflora*, first described by Hochstetter (1855); and *Coelachrysum yemenicum* was first described by Schweinfurth (1894) as an *Eragrostis*, placed in the monotypic *Cypholepis* by Chiovenda (1908), who transferred it to *Eleusine* (Chiovenda 1912), and finally Phillips (1982), who transferred it to *Coelachrysum*.

The purpose of this paper is to present a systematic account of *Disakisperma* as part of a series of papers separating *Leptochloa* s.l. (Snow 1997) into monophyletic genera (see also Snow and Peterson 2012). In addition, we include a phylogram derived from analysis of combined plastid and ITS sequences that suggests evolutionary relationships among the four species of *Disakisperma*.

Materials and methods

We viewed over 1500 herbarium specimens from nearly 60 herbaria for this revision (see Acknowledgements). However, we estimate that less than half of the existing specimens of *Disakisperma dubium* have been cited, particularly in the southwestern USA and northwestern Mexico, given the large numbers of collections deposited in the larger herbaria (e.g., ARIZ, ASU, MEXU, TAES, TEX) and in many smaller herbaria that we have not visited in North America and southern South America. The first author has collected a dozen specimens of *D. dubium* in the USA and parts of Mexico and *D. eleusine* in South Africa, whereas the second author has collected 85 specimens of *D. dubium* across much of its native range, and *D. obtusiflorum* (3) and *Coelachrysum yemenicum* in Tanzania. Geographic range abbreviations follow Brummitt (2001) and herbarium abbreviations follow Thiers (2013).

Fresh leaf and stem material was preserved for anatomical analysis and studied for (but not summarized) in Snow (1997). Leaf anatomy terminology follows Ellis (1976). Characters of lemmatal micromorphology were studied using scanning electron microscopy (Snow 1996), and caryopsis features were viewed using simple light microscopy (Snow 1998b).

The phylogram (Fig. 1) was generated with existing data from Peterson et al. (2012) but with six new samples added: three of *D. obtusiflorum*, two of *Coelachrysum yemenicum*, and one of *D. eleusine*. Voucher information and GenBank numbers for the new samples are given in Table 1. The methods for DNA extraction, amplification, sequencing, and phylogenetic analysis are given in Peterson et al. (2012). We estimated the phylogeny among members of *Disakisperma* based on the analysis of six molecular markers (nuclear ITS 1&2 and plastid *rpl32-trnL*, *ndhA* intron, *rps16* intron, and *rps16-trnK* DNA sequences). To make the phylogram smaller some clades are depicted at a higher level (subtribe or tribe) and the number of species in each is: Aeluropodinae (1), Boutelouinae (1), Centropodieae (1), Eragrostideae (9), Hilariinae (2), Monanthochoiniae (3), Muhlenbergiinae (2), Orcuttiinae (2), Pappophorinae (2), Scleropogoninae (3), Traginae (3), Triodiinae (2), Tripogoninae (4), Triraphideae (2), and Zoysieae (5).

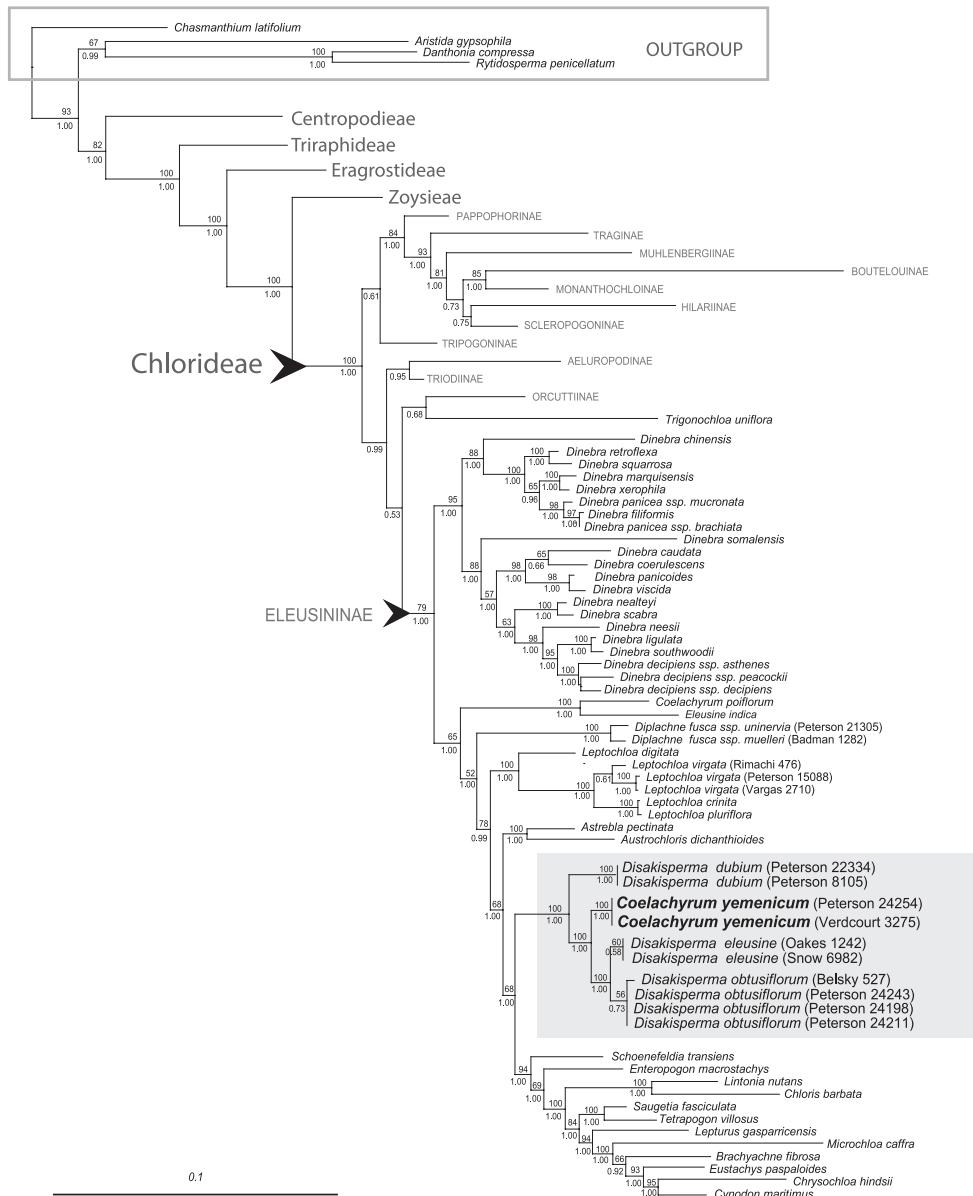


Figure 1. Phylogram of maximum-likelihood tree from analysis of combined plastid (*rpL32-trnL*, *ndhA* intron, *rps16* intron, and *rps16-trnK*) and ITS sequences. Numbers above branches represent bootstrap values; numbers below branches represent posterior probabilities; gray highlighted area is the *Disakisperma* (incl. *Coelachyrum yemenicum*) clade. Scale bar = 10% sequence divergence.

Table 1. Specimens sampled in the *Disakisperma*–*Coelachrysum yemenicum* clade, vouchers (MO = Missouri Botanical Garden; US = United States National Herbarium, Smithsonian Institution), country of origin, and GenBank accession numbers for DNA sequences. All accessions marked in **bold** are newly submitted sequences to GenBank.

Taxon	Voucher	Country	rpl32-trnL	ndhA intron	rps16 intron	rps16-trnK	ITS
<i>Disakisperma dubium</i> (Kunth) P.M. Peterson & N. Snow	Peterson 22334 & Saarela (US)	Mexico	GU359811	GU359442	GU360416	GU360695	GU359145
<i>Disakisperma dubium</i> (Kunth) P.M. Peterson & N. Snow	Peterson 8105 & Annable (US)	Mexico	JQ345332	JQ345214	JQ345290	JQ345247	JQ345179
<i>Disakisperma eleusine</i> (Nees) P.M. Peterson & N. Snow	Snow 6982 (MO)	South Africa	JQ345333	JQ345215	JQ345291	JQ345248	JQ345180
<i>Disakisperma eleusine</i> (Nees) P.M. Peterson & N. Snow	Oakes 1242 (US)	South Africa	KF574410		KF574416	KF574422	KF574399
<i>Disakisperma obtusiflorum</i> (Hochst.) P.M. Peterson & N. Snow	Peterson 24243, Soreng & Ronaschenko (US)	Tanzania	KF574413	KF574407	KF574419	KF574425	KF574402
<i>Disakisperma obtusiflorum</i> (Hochst.) P.M. Peterson & N. Snow	Belsky 527 (MO)	Kenya	JQ345340		JQ345298	JQ345255	JQ345187
<i>Disakisperma obtusiflorum</i> (Hochst.) P.M. Peterson & N. Snow	Peterson 24198, Soreng & Ronaschenko (US)	Tanzania	KF574411	KF574405	KF574417	KF574423	KF574400
<i>Disakisperma obtusiflorum</i> (Hochst.) P.M. Peterson & N. Snow	Peterson 24211, Soreng & Ronaschenko (US)	Tanzania	KF574412	KF574406	KF574418	KF574424	KF574401
<i>Disakisperma yemenicum</i> (Schweinf.) P.M. Peterson & N. Snow	Peterson 24254, Soreng & Ronaschenko (US)	Tanzania	KF574414	KF574408	KF574420	KF574426	KF574403
<i>Disakisperma yemenicum</i> (Schweinf.) P.M. Peterson & N. Snow	Verdcourt 3275 (US)	Kenya	KF574415	KF574409	KF574421	KF574427	KF574404

Results and discussion

Phylogeny. A total of 29 sequences from six species are newly reported in GenBank (Table 1). Total aligned characters for individual regions are noted in Table 2. We combined the plastid–ITS sequences in our analysis since there were acceptable levels of congruence between the majority of the data sets in Peterson et al. (2012).

The maximum-likelihood tree from the combined analysis of four plastid regions (*rpL32-trnL*, *ndhA* intron, *rps16* intron, and *rps16-trnK*) and ITS is well resolved, with strong to moderate support for the tribes and most subtribes of the Chloridoideae (Fig. 1). The Chloridoideae is composed of five tribes; followed by, in order of divergence: Centropodieae, Triraphideae, Eragrostideae, Zoysieae, and Chlorideae (Peterson et al. 2010, 2011, 2012). Within the subtribe Eleusininae, species of *Leptochloa* s.l. form four major clades: *Dinebra*, *Diplachne*, *Leptochloa* s.s., and *Disakisperma* (including *Coelachyrum yemenicum*). *Trigonochloa*, a genus with only two species (formerly placed in *Leptochloa*) is sister to the Orcuttiinae; and together these are sister to the Eleusininae (Peterson et al. 2012; see also Snow and Peterson 2012). In the *Disakisperma* clade (incl. *Coelachyrum yemenicum*; bootstrap: BS = 100, posterior probability: PP = 1.00), *D. eleusine* and *D. obtusiflorum* are sister (BS = 100, PP = 1.00); *C. yemenicum* is sister to these (BS = 100, PP = 1.00); and *D. dubium* is sister to all three species (BS = 100, PP = 1.00) [Fig. 1].

Morphology. *Disakisperma* (including *Coelachyrum yemenicum*) can be recognized by its paniculate inflorescence (=synflorescence) composed of several unilateral racemes that are racemosely to subdigitally inserted along a central axis, spikelets with multiple florets (4–14), mostly 3-nerved lemmas and 1-nerved glumes, and dorsally flattened, mostly elliptical caryopses that are shallow to broadly concave on the hilar surface with a pericarp weakly adnate to endosperm.

Lemmal micromorphology. The four species share a similar but not identical suite of lemma micromorphological traits, including the presence of silica cells, cork cells, long cells and short cells, and bicellular microhairs. The lemmatal hairs of *Disakisperma eleusine*, *D. obtusiflorum* and *D. yemenicum* are clavicorniculate (apically club-shaped with a pointed tip), whereas those of *D. dubium* are acute or rounded apically (Snow 1996). These four species form a strongly supported clade in the phylogram (Fig. 1).

Caryopsis morphology. The hilar profile of the caryopsis in *Disakisperma* is elliptic, with the most common length:width ratio being approximately 2:1 (Snow 1998b). However, an elliptic hilar profile occurs in many genera of Chloridoideae (Snow 1998b). Variation in hilar profile shape and length was noted for *D. dubium* (Valls 1978), which reflects its wide geographical range and considerable variation in vegetative and reproductive morphology (Valls 1978; Snow 1997, 2003, 2012). For example, the hilar profile of *Gould 12183* (K) from Baja California Sur in Mexico was widely obovate (Snow 1998b). In contrast, a narrowly elliptic hilar profile of *D. dubium* was observed for *Warnock 46783* (NCU) from Pecos County, Texas. Variation in hilar profiles also was observed for *D. eleusine* (Snow 1998b), which also sometimes had an obovate profile (i.e., broadened towards the apex; e.g., *Drège s.n.* (S) and *Extension Officer 16419 PRE*). The hilar profile of *Coelachyrum yemenicum* is elliptic (Snow

Table 2. Summary of the four plastid and nrDNA ITS regions used in the maximum likelihood and Bayesian searches indicated by Akaike's Information Criterion (AIC).

Characteristic	<i>rpl32-trnL</i>	<i>ndhA intron</i>	<i>rps16 intron</i>	<i>rps16-trnK</i>	Combined plastid data	ITS	Overall combined dataset
Total aligned characters	1233	1323	1074	1040	4670	832	5502
Maximum likelihood scores (-lnL)	9567.4667	8778.3245	6732.027	8265.2405		20947.0843	
Number of substitution types	6	6	6	6		6	
Model for among-site rate variation	gamma	gamma	gamma	gamma		gamma	
Substitution rates	0.9361 1.8439 0.4825 1.4468 1.5696 1.0000	1.3591 2.8338 0.5457 2.2589 2.9694 1.0000	1.0865 1.4745 0.3367 1.3805 2.2541 1.0000	1.1338 2.6853 0.5231 1.7173 2.4576 1.0000			
Character state frequencies	0.3836 0.1431 0.1295 0.3436	0.3767 0.1249 0.1430 0.3552	0.3925 0.1047 0.1636 0.3390	0.3066 0.1341 0.1407 0.4184		0.2495 0.1914 0.2496 0.3093	
Proportion of invariable sites	0.0774	0.2175	0.1551	0.1303		0.2365	
Substitution model	GTR+I+G	TVM+G	TIM3+I+G	TIM3+G		GTR+I+G	
Gamma shape parameter (α)	0.9636	1.2427	1.1594	1.6560		0.9959	

1998b). Valls (1978) noted considerable variation in caryopsis morphology among the cleistogenous spikelets of *D. dubium* that occur within the leaf sheath, but Snow (1998b) did not measure variation among cleistogamous spikelets.

In transverse section the caryopsis of *Disakisperma* is usually transversely elliptic (Snow 1998b). This shape accords with many previous observations that the spikelets are strongly flattened dorsally in species now treated in *Diakisperma* (Parodi 1927; McNeill 1979; Lazarides 1980; Phillips 1982; Jacobs 1988; Nowack 1994; Nicora 1995). Snow (1998b) also reported “rounded shallowly obtriangular” for *D. eleusine*, but in reviewing his original notes for that project, now considers that report erroneous.

In addition to its transversely elliptic shape, all four species typically (but not always) have caryopses that are concave on the hilar surface (Snow 1998b). For example, in *D. dubium* the broad shallow concavity was noted for *Warnock* 46783 from Texas (NCU), *Kral* 51801 from Florida (MO), and *Hernández & Mathia* N-2066 from San Luis Potosí, Mexico (GH). The depression was not noted specifically for *Mearns* 1213 (US) from Kinney County, Texas; *Gould* 12183 (K) from Baja California Sur, or *Castillon* 43560 (GH) from Tucumán, Argentina, although it probably was shallow in these. Broad to shallow concavities were noted to characterize the caryopses of some species for all specimens observed by Snow (1998b) for *D. eleusine* and *D. obtusiflorum* (and, newly noted here for the latter, *Blesky* 433 (BH) from Kenya). However, broad to shallow depressions were noted for many specimens of species treated by Snow (1997) in *Leptochloa* s.l., including: *Dinebra aquatica* (Scribn. & Merr.) P.M. Peterson & N. Snow: *Pringle* 6664 (US); *Dinebra chinensis* (L.) P.M. Peterson & N. Snow: *Davidse* 7471 (MO) from Sri Lanka; *D. decipiens* (R. Br.) P.M. Peterson & N. Snow subsp. *decipiens*: *Lazarides* 5634 (US) from Queensland, Australia; *Dinebra decipiens* subsp. *peacockii* (Maiden & Betche) P.M. Peterson & N. Snow: *R. Johnson* 713 (CANB) from Queensland, Australia; *Dinebra panicoides* (J. Presl) P.M. Peterson & N. Snow: *Francoer & Williams* 47 (ENCB) from Oaxaca, Mexico; *Dinebra viscosa* (Scribn.) P.M. Peterson & N. Snow: *Palmer* 1789 (GH) from Sinaloa, Mexico; *Leptochloa digitata* (R. Br.) Domin.: *Blake* 6320 (CANB) from Queensland, Australia; *Leptochoa longa* Griseb.: *Davidse* 2612 (MO) from Trinidad; and *Coelachyrum yemenicum*: *Schweickerdt* 2011 (S) origin not recorded.

The pericarp is weakly adnate among species of *Disakisperma* and disassociates relatively quickly in water at room temperature (Snow 1998b). This is a homoplastic trait within Chlorideae given its recurrence in *Diplachne* s.s. (Snow 1997, 1998b; Peterson et al. 2012), *Dinebra panicoides*, and *D. viscosa*, the latter two of which form a distinct clade in the combined plastid and ITS phylogram (Fig. 3 in Peterson et al. 2012). *Leptochloa chloridiformis* (Hack. ex Stuck.) Parodi, in the newer and narrower circumscription of *Lepotchloa* (Peterson et al. 2012), was the only species in which the pericarp readily disassociated in water (Snow 1998b). Valls (1978: 104) also reported a freely disassociating pericarp for the rarely collected *Leptochloa longa* Griseb., of which we have not yet obtained molecular data.

The hilum is uniformly punctiform and highly conspicuous among species historically treated in *Leptochloa* s.l. (including Snow 1997). Thus hilar shape is of little if any value in the generic reconfiguring of *Leptochloa*.

To summarize, when used with other characters, species of *Disakisperma* generally can be characterized by the dorsally flattened caryopses that are broadly to shallowly concave on the hilar side, with pericarps that detach readily from the seed wall of the caryopsis in water. However, since some species in closely related chloridoid genera also share these homoplastic traits, features of the caryopsis by themselves are insufficient to diagnose *Disakisperma*. This observation echoes Vavilov (1922) and his “Law of Homologous Series in Variation”. However, the term homologous is a misnomer as presently used by evolutionary biologists, given that such traits are now considered non-homologous (homoplastic).

Taxonomic treatment

***Disakisperma* Steud., Syn. Pl. Glumac. 1: 287. 1854.**

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

Type species. *Disakisperma mexicana* Steud. = *Disakisperma dubium* (Kunth) P.M. Peterson & N. Snow.

Description. Plants perennial, rarely annual in a few populations, occasionally stoloniferous. Culms 30–200 cm long, solid, decumbent or clambering to erect; nodes glabrous. Leaf sheaths half as long to slightly longer than internodes, glabrous or ciliate apically along margins; ligule membranous, 0.5–1.5 mm long, ciliate or fimbriate apically; leaf blades caudine, linear. Inflorescence apical and exserted at maturity or cleistogamous in lower leaf sheaths, a panicle composed of several to numerous unilateral racemes, racemose or subdigitately scattered along a central axis; branches at maturity slightly reflexed to ascending or steeply erect. Spikelets sessile to subsessile, dorsally rounded to flattened, typically overlapping, disarticulation above the glumes; florets 4–13; glumes 2, 1-nerved or occasionally with remnants of two additional nerves near base, mucronate or emarginate; lemmas 3-nerved, rarely with remnants of two additional nerves near base, sometimes cartilaginous towards the base, macrohairs acute, obtuse, or clavicorniculate; paleas often somewhat cartilaginous towards base. Stamens 3. Lodicules 2, flabellate. Caryopses dorsally flattened, broadly concave on the hilar surface; pericarp weakly adnate to endosperm. $2n = 40, 60, 80$ (Snow 1997).

Vernacular name. In light of its only recent resurrection from generic synonymy (Peterson et al. 2012), no common name exists for *Disakisperma*. We suggest Jacobgrass to honor the memory of Dr. Surrey W. L. Jacobs (1946–2009), an Australian friend, colleague, and chloridoid specialist (e.g., Jacobs 1988).

Key to the species of *Disakisperma*

- | | | |
|---|---|---|
| 1 | Panicles 1–3 cm wide; branches mostly erect or steeply ascending, stiff, 2–10.5 cm long | 2 |
| – | Panicles 3–25 cm wide; branches ascending but not steeply so, usually reflexed (towards tips) and somewhat flexuous, (−1.5) 3–19 cm long..... | 3 |

- 2 Lemmas membranous throughout, margins not involute near base; adaxial leaf blades surfaces without long hairs; anthers 0.9–1.0 mm long..... *D. eleusine*
- Lemmas cartilaginous below, margins involute near base; adaxial leaf blade with scattered, delicate, straight hairs near the base, the hairs 3–5 mm long; anthers 0.2–0.3 mm long..... *D. yemenicum*
- 3 Lemmas 3.5–5.0 mm long with round- to acute-tipped hairs along margins and sometimes the midnerve below; glumes 3.3–6.0 mm long; cleistogamous spikelets hidden in lower leaf sheaths; anthers 1.0–1.6 mm long; native to the Americas..... *D. dubium*
- Lemmas 2.2–2.8 (–3.0) mm long with clavicorniculate (club-shaped) hairs along the margins and midnerve below; glumes 1.5–2.9 mm long; cleistogamous spikelets absent in the lower leaf sheaths; anthers about 0.7 mm long; native to Africa and Asia *D. obtusiflorum*

***Disakisperma dubium* (Kunth) P.M. Peterson & N. Snow, Ann. Bot., 109: 1327. 2012.**
http://species-id.net/wiki/Disakisperma_dubium

Figure 2A–P

Chloris dubia Kunth, Nov. Gen. Sp. 1: 169. 1816. *Leptostahys dubia* (Kunth) G. Mey., Prim. Fl. Esseq. 74. 1818. *Leptochloa dubia* (Kunth) Nees, Syll. Pl. Nov. 1: 4. 1824. *Festuca obtusiflora* Willd. ex Spreng., Syst. Veg. 1: 356. 1825. *Diplachne dubia* (Kunth) Scribn. Bull. Torrey Bot. Club 10: 30. 1883. *Rabdochloa dubia* (Nees) Kuntze ex Stuck., Anales Mus. Nac. Buenos Aires 11: 121. 1904. *Sieglungia dubia* (Kunth) Kuntze ex Stuck., Anales Mus. Nac. Buenos Aires 11: 128. 1904.

Schismus patens J. Presl. Reliq. Haenk. 1(4–5): 269. 1830. *Leptochloa patens* (J. Presl) Kunth, Enum. Pl. 1: 271. 1833. *Diplachne patens* (J. Presl). TYPE: Chile, *Hab. in Cordilleris chilensis*, T. Haenke s.n. (holotype: PR; isotype: US-A78816!).

Disakisperma mexicana Steud., Syn. Pl. Glumac. 1: 287. 1854. (“1855”). TYPE: Mexico, Vallee de Mexico, Aug 1827, J.L. Berlandier 758 (lectotype: P ex herb. Drake barcode P02295597 seen digitally!; isolectotypes: MO-134708 seen digitally!, US-90594, US-865873 frag. ex CN!).

Uralepis brevicuspidata Buckley, Proc. Acad. Nat. Sci. Philadelphia 1862: 93–94. 1862. TYPE: U.S.A., Northern Texas, Wright 767 (lectotype: PH! designated by Hitchcock Man. Grass. U.S. 877. 1935 but without designating a herbarium; isolectotype: US-2786821-photo!).

Ipnum mendocinum Phil., Anales Univ. Chile 36: 211. 1870. *Diplachne mendocina* (Phil.) Kurtz, Bol. Acad Ci. (Córdoba) 15: 521. 1897. *Eragrostis mendocina* (Phil.) Jedwabn., Bot. Arch., 5(3–4): 192. 1924. TYPE: Argentina, Mendoza (holotype: SGO; isotype BAA-1452!).

Leptochloa pringlei Vasey ex Beal, Grass. N. Amer. 2: 436. 1896. *Diplachne pringlei* Vasey ex Beal, Grass. N. Amer. 2: 436. 1896. nom. inval. pro syn. *Leptochloa pringlei*

Beal. TYPE: USA, Arizona, Pima Co., Arizona, Sierra Tucson, 27 Apr 1884, C.G. Pringle 13 (holotype: MSC-8177 seen digitally!; isotypes: GH, US-78806!, VT).

Diplachne dubia var. *kurtziana* Kuntze, Révis. Gen. Pl. 3 (2): 349. 1898. TYPE: Argentina, Córdoba, F. Kurtz 6647 (holotype: NY, fragment US-86574!).

Diplachne dubia var. *pringleana* Kuntze, Revis. Gen. Pl. 3 (2): 349. 1898. *Leptochloa dubia* var. *pringleana* (Kuntze) Scribn. & Merr., U.S.D.A. Div. Agrostol. Bull. 24: 27. 1901. TYPE: Mexico, Chihuahua, Hills and plains near Chihuahua, Pringle 422 (lectotype: NY! here designated, barcode 00019500; duplicates of lectotypes: GH!, MSC, NY-19498!, NY-19500!, P!, PH!, PR!, RSA!, US-899043!, VT).

Type. MEXICO. F. Humboldt & A. Bonpland 4172 (lectotype: P! barcode P032678 designated by Snow et al., J. Bot. Res. Inst. Texas 2: 863. 2008; isolectotypes: B-Willd. barcode 02095-010! seen digitally May 2013, HAL-107044! seen digitally May 2013, K, K-microfiche, US-865876 frag. ex P!).

Description. Perennials (or infrequently annuals; see below). Culms (5–)30–110 cm tall, 1.0–4.5 mm wide at base, round or flattened below, mostly erect or infrequently decumbent or sprawling, arising from fibrous roots, culms unbranched or only as tillers from very base; nodes glabrous; internodes 3–11 cm long, soft, solid or occasionally hollow with age. Leaf sheaths longer or shorter than internodes, sparsely pilose, especially below, and occasionally pilose (sometimes densely so) near the collar, the hairs occasionally with papillose bases, the margins glabrous or somewhat pilose; collars green or tan; ligules (0.5–)1.0–1.5 mm long, membranous, truncate, ciliate apically; blades (2–)8–35 cm long, 2–8 mm wide, cauline, mostly linear or somewhat narrowly ovate, flat but drying involute, scabrous above at base or sparsely pilose, glabrous to minutely scabrous below, midrib mostly prominent. Panicles of two types, the apical ones generally exserted at maturity and the lateral ones cleistogamous and completely hidden in lower leaf sheaths; apical panicles mostly 10–45 cm long, (2–)3–25 cm wide; branches (2–)5–15, (1.5–)3–19 cm long, alternate or infrequently subdigitate, ascending to reflexed, usually somewhat flexuous, minutely scabrous, the axils pilose or merely scabrous. Spikelets 4.0–12.0 mm long, most nearly sessile, imbricate to distant, 4–13-flowered; callus glabrous or with a few short hairs; lower glumes (1.6–)2.3–4.8 mm long, membranous, narrowly triangular or ovate, scabrous along midnerve, sometimes papillate on sides, acute; upper glumes 3.3–6.0 mm long, membranous, ovate to narrowly ovate, scabrous on midnerve (and sometimes with 1 or 2 additional nerves at least basally) and papillate on edges, acute; lemmas 3.5–5.0 mm long, 3-nerved (or infrequently 4- or 5-nerved above base), membranous, ovate to obovate or widely obovate, lateral nerves usually prominent but sometimes not so, sericeous at least along lower portions and sometimes on midnerve and between nerves, the hair tips rounded, apex usually bifid, broadly acute, obtuse, or truncate, awnless or mucronate; paleas membranous above and sometimes cartilaginous near base, subequal to lemma, narrowly ovate, distinctly ciliate on edges, sometimes sericeous between nerves, apex acute to obtuse. Anthers 1.0–1.6 mm long, yellow. Lodicules about 1 mm long. Caryopses 1.5–2.3 mm long, 0.7–1.0 mm wide.

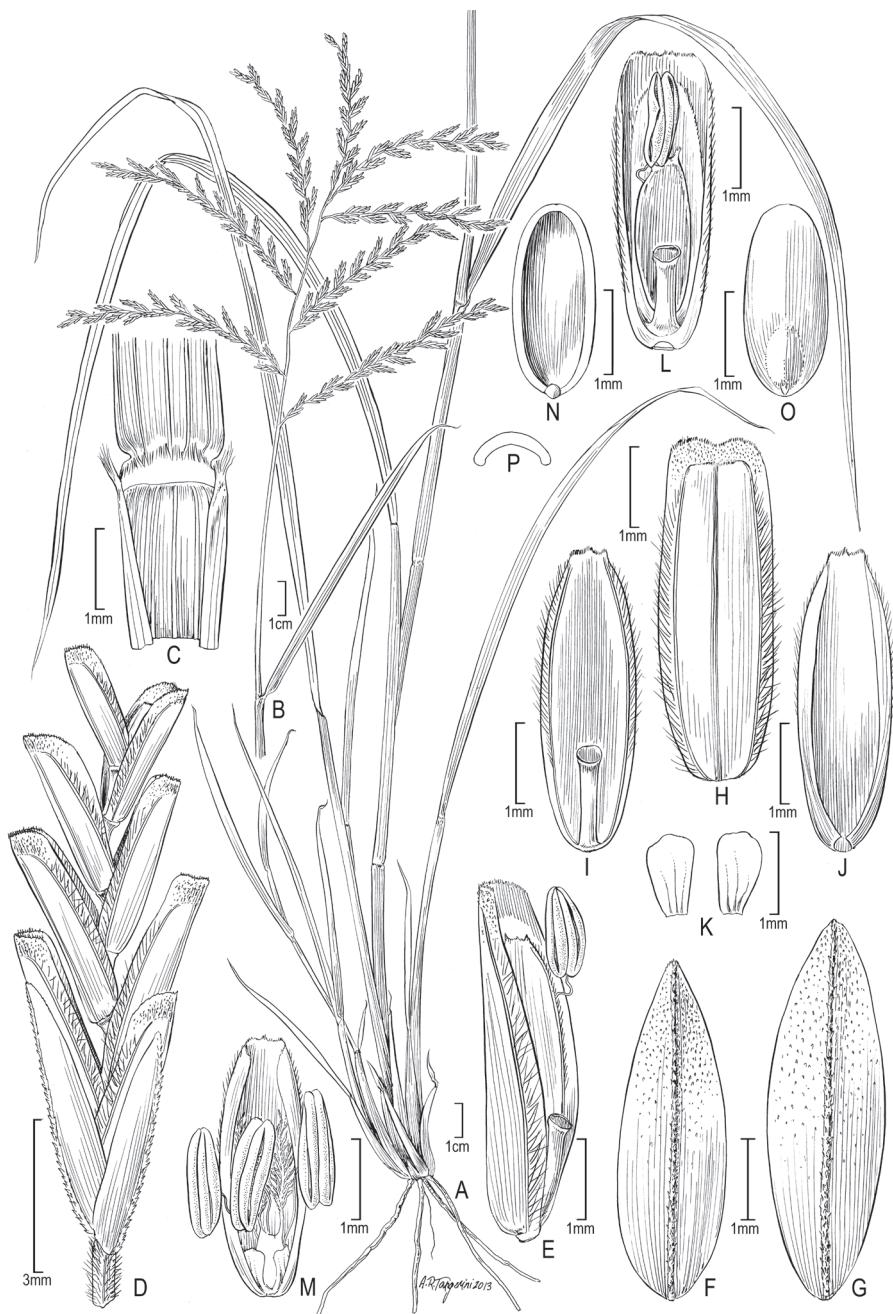


Figure 2. *Disakisperma dubium* (Kunth) P.M. Peterson & N. Snow **A** habit **B** culm and inflorescence **C** sheath, ligule, and blade, ventral view **D** spikelet **E** floret **F** lower glume **G** upper glume **H** lemma, dorsal view **I** palea, dorsal view **J** palea, ventral view **K** lodicules **L** floret, ventral view **M** perfect flower with lodicules, pistil, and stamens enclosed in palea **N** caryopsis, ventral view **O** caryopsis, dorsal view **P** caryopsis, cross section. A–C, M drawn from Peterson & Annable 5387 (US); D–L, N–P drawn from Peterson & Lara-Contreras 19890 (US).

Leaf anatomy. Previous authors discussed aspects of cross-section laminar anatomy of *D. dubium* (Brown 1960, Black and Mollenhauer 1971, Gutierrez et al. 1974, Valls 1978), whose collective data agree with our findings of the C₄ NAD-ME photosynthetic pathway.

Midrib absent, or if present then lacking associated lacunae. Primary bundles (metaxylem elements present) separated from one another by up to five secondary bundles (metaxylem elements absent). Primary and secondary bundles projecting little if at all adaxially or abaxially in fresh material. Outer primary bundle sheath cells continuous or interrupted adaxially but typically interrupted abaxially. Primary and secondary bundles often with colorless extension cells and sclerenchyma girders associated above and below. Colorless cells lacking between adjacent bundles; chlorenchyma always continuous. Bulliform cells present between primary and secondary bundles [Vouchers: *Snow 5865* (MO), *Snow 6673* (MO)].

Stem anatomy. The culm anatomy of *D. dubium* was discussed briefly by Canfield (1934) and Brown et al. (1959). The cross-section shown in Valls (1978, see fig. 21) is indented on one side where an axillary cleistogamous inflorescence likely was located.

Culm solid. Outer sclerenchyma ring (subjacent to epidermis) present and sometimes surrounding outermost vascular bundles. Assimilatory (=assimilation) tissue (chloroplast-bearing and lightly staining parenchyma tissue (Pée-Laby 1898; Metcalfe 1960) often present between outermost vascular bundles. Additional vascular bundles scattered in outer ca. 1/3 of cortical tissue. Inner sclerenchyma ring absent or present (Valls 1978). [Voucher: *Snow 5865* (MO)].

Chromosome number. Individuals of *Disakisperma dubium* are tetraploid (Covas 1949; Valls 1978, voucher not seen), hexaploid (Brown 1950, voucher confirmed by Valls 1978), or octaploid (Gould 1960, 1965, vouchers confirmed by Valls 1978). Variation in ploidy number has not been shown to correspond with morphological variation or have a clear geographical pattern (Valls 1978), although sampling has been limited.

Phenology. Flowering commencing after the dormant season and continuing several months thereafter, or year-round in tropical climates at lower altitudes.

Distribution. Native: In the USA from Arizona to Oklahoma and Texas, and disjunct in southern Florida, in much of Mexico, sporadically in the Caribbean and in Mesoamerica to Bolivia and Chile east to Paraguay, Uruguay, and Argentina; in a variety of vegetation and soil types (including limestone), but most frequently on well-drained slopes, mostly 100–2500 m, to 3150 m in the Andes of South America (e.g., *Vargas 13770* [US]). (TDWG: AGE-CD, AGE-CN, AGW-JU, AGE-LP, AGW-CA, AGW-LR, AGW-ME, AGW-SA, AGW-SE, AGW-SJ, AGU-TU, BOL, CLM, ECU, MXC-DF, MXC-PU, MXE-AG, MXE-CO, MXE-CU, MXE-DU, MXE-GU, MXE-HI, MXE-NL, MXE-QU, MXE-SL, MXE-TA, MXE-ZA, MXN-BS, MXS-MI, MXT-CI, PER, PUE, ARI, FLA, NWM, OKL, TEX.) **Non-native:** USA in California, Hawaii (Snow and Davidse 2011), Kansas, and Missouri (TDWG: CAL, KAN, MSO). Its occurrences in the high Andes of Colombia, Ecuador, Bolivia, and Peru may be as introductions.

Conservation status. Least Concern (IUCN 2010).

Etymology. The Latin *dubium* means wavering or doubtful, which may refer to Kunth's uncertainty about its inclusion in *Leptochloa* at the time of its description, but the intention behind the specific epithet is uncertain.

Vernacular names. Green sprangletop; Texas crowfoot (Valls 1978), Zacate gigante (Beetle et al. 1991). Suggested name: American Jacobsgrass.

Comments. The combination of its perennial habit, cleistogamous inflorescences inserted in the sheath near the base of the culms, short ciliate ligules, typically notched lemma apices, frequently (but not always) widely diverging florets during anthesis, and typically racemose to subdigitately arranged panicle branches, generally distinguish *Disakisperma dubium* from others in its geographical range. Among former components of *Leptochloa* s.l. (Snow 1997), *Disakisperma dubium* is sometimes confused with *Diplachne fusca* (L.) P. Beauv. ex Roem. & Schult. subsp. *uninervia* (J. Presl) P.M. Peterson & N. Snow, which also has truncate to (usually) emarginate lemma apices. However, *D. fusca* subsp. *uninervia* is an annual (that sometimes is weakly perennial), has much longer and apically attenuated (and often lacerated) ligules, lacks hairs on the outer edges of the collar, lacks cleistogamous inflorescences, and grows most frequently in disturbed areas in heavier and more poorly-drained soils, often in disturbed habitats or along watercourses.

The root hair formula of *Disakisperma dubium* is P-I-I (Row and Reeder 1957), whereas its embryo formula (Reeder 1957) is P+PP (Valls 1978). Branching, if present, usually occurs only at the basal most nodes (Valls 1978). The cleistogamous lateral inflorescences (Parodi 1927; Gould 1975; Valls 1978), which correspond to subtype 1b of Campbell et al. (1983), do not occur in the *D. eleusine*, *D. obtusiflorum*, or *D. yemenicum*. Obligate cleistogamy by means of inserted inflorescences in Eragrostideae (sensu Clayton and Renvoize 1986) also occurs in some species of *Muhlenbergia* Schreb., *Triplasis* P. Beauv., and *Cleistogenes* Keng (Clayton and Renvoize 1986; Peterson and Annable 1991; Chen and Phillips 2006). Species formerly placed in *Lepthochloa* s.l. (Snow 1997) in which basal panicle branches typically are not completely exserted, and for which some degree of cleistogamy likely occurs, include *Dinebra viscosa*, *Diplachne fusca* subsp. *fascicularis* (Lam.) P.M. Peterson & N. Snow, and *D. fusca* subsp. *muelleri* (Benth.) P.M. Peterson & N. Snow.

Disakisperma dubium exhibits considerable morphological variation across its range, which is expected given its wide geographical distribution. Some populations of *D. dubium* are somewhat distinct locally and might be found to be genetically distinct. For example, the life cycle of some specimens from Baja California is annual (Valls 1978; e.g., Rebman 7548 et al. and Dominguez L. 3062 (both at ARIZ)). In the Baja and Sonora states of Mexico some specimens [e.g., Gould 12183 (K, TAES), Felger et al. 92–966 (MEXU), Carter & Moran 5317 (GH), Carter 4781 (GH)] are atypical in having some combination of the following characters: palea with appressed hairs between the nerves, caryopses widely to very widely ovate, and lemmas obovate to widely obovate with very wide apical lobes (Valls 1978). Many specimens from Kenedy and Cameron counties in south Texas, an area where sandy soils are common, are characterized by relatively thin, short, densely cespitose culms having short, few-branched

panicles, an overall growth form that also occurs in some plants from Argentina. The short stature, however, may be a phenotypic response to frequent grazing by cattle (Valls 1978) or due to lower levels of soil moisture typical of sands. Variation in lemmatal shape and spikelet shape also can be considerable (Valls 1978; Nicora 1995; Snow 1997, 2012). For example in Argentina, where the species is cultivated (Nicora 2006), specimens may have either exceptionally wide lemmas or acute, unnotched lemmatal apices. The lemmas and upper glumes occasionally have indistinct additional nerves at the base. The palea is atypical and somewhat cartilaginous and flared outwards near the base, thereby surrounding the adjacent rachilla segment. Since morphological variation intergrades more or less continuously, we feel that recognition of infraspecific taxa is unwarranted.

Snow (1997) included *Leptochloa digitatiformis* Beetle (1982) as a synonym of *D. dubium*, which merits additional explanation. The original description by Beetle (1982) was sparse, who for reasons unknown compared the species to *Leptochloa chloridiformis*, a non-persisting South American species collected for a brief period in North America during the 1940s in Cameron County, Texas (Snow 2003). Beetle's concept of *L. digitatiformis* was a combination of *D. dubium* and *Chloris submutica* Kunth, the latter of which is sometimes perceived as immature *D. dubium* and misidentified as such. The basis for this conclusion is a result of the first author having seen numerous specimens of *D. dubium* and *C. submutica* annotated in Beetle's hand as *L. digitatiformis* (e.g., White 3606 [MEXU], Cervera 90 [SARH], Carranco & Brito 59 [SARH], Murrieta 17 [SARH], Banks 1832 [WYAC], Llmeida et al. 121 [WYAC]). This name is now excluded (see Excluded name, below) from *Disakisperma*.

The species apparently provides moderate forage quality for livestock (Valls 1978; Nicora 2006) although it rarely occurs in dense stands in native vegetation. Marone et al. (1998) reported that the caryopses of *D. dubium* constitute a significant component of the seed mass consumed by granivorous birds in the Monte Desert of Argentina.

Valls (1978: 144) reported thrips (Thysanoptera) in the spikelets of *D. dubium*.

Specimens examined. Argentina. Catamarca: Dpto. Belén, Laguna Blanca, Cabrera et al. 32526 (SI); Dpto. Belén, Quebrada del Belén, Cabrera et al. 16758 (LP); Dpto. Andalgala, Jörgensen 1352 (GH, MO, NY, UC, US); W base of Cuesta La Chilca, 14 road km E of Andalgala jct, Hwy 46 on Hwy 365/48, Peterson, Soreng, Solariato & Panizza 19418 (US); Sierra de Belén, NW of Condor Huasi, ca. 14 air km NW of La Puerta de San Jose, jct Hwy 40 N of Belén Peterson, Soreng, Solariato & Panizza 19407 (K, US); Dpto. Belén, Las Mansas, Schreiter 698 (GH); Valle Cata-marca, Parodi 13983 (BAA); Balcones, Sierra Ambato, Parodi 14072 (BAA); Dpto. Andalgalá, El Ingenio, Cabrera et al. 24723 (LP); Dpto. Belén, Quebrada de Belén, Cabrera et al. 23773 (LP). Dpto. Paclín, 19 km E of Catamarca on Hwy 42 towards Puesto del Portezuelo, Peterson & Annable 11641 (AAU, GH, K, MO, P, NY, RSA, TAES, UC, US, UTC). Córdoba: Plaz Colón, Kurtz 8866 (NY); Bei Córdoba in Argentinien, Stuckert 378 (PR); Dpto. Capital, Quinta en los alrededores de la Ciudad de Córdoba, Stuckert 11187 (MO, NY); Dpto. de San Javier, San Javier, Bridarolli 1270 (LP); Camino de Casilla del Monte a San Marcos, Nicora 2435 (MICH); Valle

de los Reartes, Parodi 166 (BAA); Capilla de Remedios, Parodi 6476 (BAA); Ciudad de Córdoba, Dpto. Capital, Stuckert 5725 (MO, NY, US). Corrientes: Dpto. Prim. de Mayo, Colonia Benítez, Schulz 17291 (SI). Jujuy: On open rocky Mt. slope, Alfarcito, E of Tilcara, Correll et al. A669 (US); Dpto. Tumbaya, El Moreno, Cabrera et al. 22441 (LP); Dpto. Tilcara, Pucara, Cabrera et al. 23553 (LP); Dpto. Tumbaya, camino de Purmamarca a Abra de Pives, Cabrera 18523 (LP); Volcán, Cabrera & Frangi 20645 (LP). Dpto. Humahuaca, Azul Pampa, Cabrera et al. 21410 (LP); Dpto. Purmamarca, subida a Tascal, Cabrera et al. 15082 (LP); Maimará, Sierra de Zenta, Budin 1510 (BAA). La Pampa: Dpto. Sierra Lihuel-Calel, Sierra Lihuel-Calel, Peterson & Annable 11233 (K, MO, US). La Rioja: Dpto. Famatina, Los Corrales, Cabrera et al. 27223 (SI). Dpto. General Lavalle, Sierra de Sanogasta, W side of Cuesta de Miranda ca. 20 km W of Miranda on Hwy 40, Peterson & Annable 11566 (K, MO, RSA, US). Dpto. Rosario Vera Peñaloza, Chelcos, Stuckert 18788 (MO, NY); Sierra Velazco, Morello 5087 (LP); Dpto. Chilecito, Guanchin, Cabrera et al. 24626 (LP); Puerta de Miranda, Parodi 7837 (BAA); Sierra de Famatina, Camino a La Mejicana, Parodi s.n. (BAA); Sierra de Sanogasta, 43 air km due E of jct Villa Union, jct with Hwy 76, 1 road km W of Cuesta Miranda, Peterson, Soreng, Solariato & Panizza 19332 (GH, K, MO, NY, RSA, US, UTC). Mendoza: Dpto. Las Heras, Capdevila, Covas 3593 (SI); Prov. de La Rioja, Ruiz Leal 16724 (ARIZ); 10 km N of Uspallata on Hwy 39 towards Calingasta, Peterson & Annable 11456 (K, MO, RSA, US); 25 km N of Uspallata on road towards Calingasta, Peterson & Annable 11472 (GH, K, MO, NY, RSA, US, UTC). Dpto. Santa Rosa, Nicora et al. 8367 (MO, SI); Dpto. Godoy Cruz, Cacheuta, O'Donell 1115 (MO); Villavicencis, Beetle 699 (GA); Cerro de la Gloria, Contardi 13 (LP); Dpto. Lujan, Dist. Chacras de Coria, Bartlett 19195 (MICH); Dpto. San Rafael, San Rafael, Otamendi 17184 (BAA); San Rafael, Schulz 6183 (LP); 35 km SW of San Rafael on Hwy 144 and 4 km W of road, Peterson & Annable 11347 (K, MO, NY, US). Dpto. Tupungato, N of Rio de la Carrara on Hwy 89 at jct to Estancia La Carrera, 6.3 road km NW of San Jose, jct. Hwy 86, Peterson, Soreng, Solariato & Panizza 19240 (K, MO, NY, RSA, US). Salta: Dpto. Santa Victoria, Santa Victoria, Meyer 4999 (NY, UC); Dpto. Poma, Canguejillos, Cabrera 8826 (LP); Nevada de Cachi, 15 km NW of Cachi just below the Ruinas Las Pailas, Peterson, Annable & Morrone 10192 (K, MO, US); Valles Calchaquies, ca 66 air km N of Cachi, Hwy 40, 68 rd km N of jct of Hwy 38, N of La Quesera, S of Abra del Acay, Peterson, Soreng, Solariato & Panizza 19511 (GH, K, MO, NY, RSA, US, UTC). Dpto. Tupungato, 3 km NW of San Jose on Hwy towards La Carrera, Peterson & Annable 11391 (K, MO, NY, RSA, US); Dpto. La Poma: Malpaso, ca. 25 km E of Súsques along rte 40, Taylor et al. 11243 (MO, US). San Juan: Dpto. Zonda, Camino a Estancia Maradona, Kiesling 4348 (SI); Dpto. Ullún, Hualilán, Kiesling 7858 (SI); A Carpineria on dry sterile banks in rocky hills at 2500 m in central Andes, Beetle 657 (GA); 48 mi E of Cachi on Hwy 40 to Salta and 2 km W of turnoff to Amblayo and Iszona, Peterson & Annable 10213 (K, MO, RSA, US); 40 mi SW of Zonda at Agua Pinto (Estación Maradona), Peterson & Annable 11505 (K, MO, NY, P, RSA, US). Dpto. Iglesia, 25 km W of Las Flores on Hwy 150 towards Puerto del Agua Negra, Peterson & Annable 11538 (K,

US); Valle de Pismanta, along Hwy 150 to Porto del Agua Negra, 16 road km W of jct Hwy 150 in Las Flores, Peterson, Soreng, Solariato & Panizza 19279 (K, MO, NY, RSA, US). Santiago del Estero: Dpto. Guasayán, Ea. "El Mangrullo", Kunst & Perez 4 (UC). Tucumán: Dpto. Tafi, Los Sauces, Peirano 276 (NY); Dpto. Grancas, Vipos, Venturi 1675 (GH, US); Tafi del Valle, Region Montañosa entre San Javier, cumbres calchaquies y Amaicha (Valle Calchaqui), Parodi 10978 (BAA); Dpto. Tafi, Tafi del Valle, Türpe 704 (M); Ca. 12 km W of Amaicha del Valle on Hwy 307 towards Tafi del Valle, Peterson & Annable 11613 (K, MO, US); Tapia, Venturi 2338 (US). Bolivia. Campero: Cochabamba, localidad alreadedores de Pasorapa, Saravia 659 (MO); Cochabamba, Parodi 10199 (BAA); La Paz, Murillo (Valencia/Mecapaca); Stony slopes above the village, Renvoize & Cope 4234 (US); La Paz, Murillo, Mecapaca, Rocky slope above village, Renvoize & Cope 4240 (MO, US). Potosí: Approximately 8 km S of Tupiza on Hwy 702 towards Villazon, Peterson & Annable 11860 (US). Tarija: Ab. loco, Fries 1094 (US). Columbia. Nariño: Río Guaitara valley near jct of Pan Americana and road to Tuquerres, Wood 5326 (COL, K, US). Mun. Imúes, corregimiento El Pedregal, Pilcuán, B. Ramírez 1259 (COL, PSO). Carretera Pasto-Túquerres, C. Saravia & R. Jaramillo 1869 (COL). Ecuador. Azuay: 11 km N of Ona on the Pan Am. Hwy near the Río Leon, Peterson, Annable & Poston 8907 (MO, US); 80 km SW of Cuenca on road to Loja, 3 km N of Río León, Peterson & Judziewicz 9374 (US). Loja: Km 13.5 Catamayo-Catacocha, Lægarrd & Kullberg 71178 (NY). Pinchicha: El Pisque, Acosta Solis 16300 (US). Mexico. Aguascalientes: 11 mi N of Rincon de Romos, Shreve 9246 (ARIZ); 7 mi S of Aguascalientes, Soderstrom 712 (ARIZ); 6.4 m E of Aquascalientes on MEX Hwy 70 to San Luis Potosi, Peterson 9672 (BISH, K, MO, US); Hwy to Ojuelos, Jal., 9 mi E of Aguascalientes, McVaugh 16641 (NY); Mpio. Palo Alto, Mesa de Preñadas, Palo Alto, Gutiérrez 89 (ENCB). Baja California Sur: Ca. 2 mi E of Route 1, along road to San Basilio, between Loreto and Mulege, Rebman 7548 et al. (ARIZ, ASU); Aguaje Los Tules, San Jaun de la Costa Municipio de La Paz, Dominguez L. 3062 (ARIZ); One mi SW of Jct of road to Huatomote along Hwy Mex. 1, Reeder & Reeder 6717 (ARIZ); 54 mi NW of La Paz, Gould 12200 (US); 7 mi W of Loreto on road to Las Parras, Reder & Reeder 6649 (RM); Cape St. Lucas, Xanthus 119 (GH); Isla del Carmen, lado W de la isla, Puerto Balandra, a 100 m de la playa, Sousa 136 (MO); 15 mi SE of San Antonio, Gould 12159 (TAES); Cañon del Cayuco, E base of Cerro de la Giganta, Carter & Kellogg 3107 (ARIZ, GH, LL, UC, US); S of La Paz, km 100 near San Bartolo, Beetle M-2561 (NA, RSA, TAES); Mts. E of Loreto, Jones 27624 (POM); 14 mi E of San Ignacio, Wiggins 11370 (GH, POM, UC); 3 mi SW of San Pedro on La Paz-Todos Santos Rd., Gould 12183 (MICH, TAES, TEX, UC, US); 5 mi W of Loreto, Beetle M-2428 (TAES); Peaks south of Portezuelo de la Cuesta de los Dolores, Sierra de la Giganta, Carter 4781 (ARIZ, GH, MEXU, MICH, MO, TAES, UC); Mouth of Cañada del Aguaje, Valle de Los Encinos, S side of Cerro Giganta, Sierra de la Giganta, Carter & Moran 5317 (GH, MICH, TAES, UC); Just W of summit peak of Mesa San Gerónimo, northerly from Rancho Viejo, Carter 5028 (TAES, UC). Chiapas: Mpio. San Cristóbal, NE edge of San Cristóbal Las Casa, Breedlove 51440 (CAS),

MO, NY). Chihuahua: Km 1918 carretera Cd. Juarez, Hernandex & Mathus N-1906 (RM); 50 km SW of Coyame of Mex 16 between Presidio, Texas and Chihuahua, Peterson & Annable 5761 (US); Nuevo Majalca; Ca. 14.5 km W of HWY 45, N of Chihuahua, Peterson and Annable 5769 (US); 58 km N of Parral on MEX 24 towards Chihuahua, Peterson & Annable 8095 (BISH, US); 87.7 km N of Parral on MEX 24 towards Chihuahua, Peterson & Annable 8105 (BISH, K, MO, US); Sierra El Nido, 6.1 mi W of Hwy 45 on dirt road towards Santa Clara, Peterson & Annable 12581 (US); 10 mi N of Ciudad Camargo, Reeder & Reeder 2612 (MEXU); Sierra Madre Occidental, 11 mi SE of Balleza on road to Parral, Peterson, Knowles, Deitrich & Braxton 13525 (K, US); Sandstone hill 8 mi NW of Cruces, Shreve 8911 (MICH); Km 11 entre San Buenaventura y El Carmen, carretera Nuevo Casas Grandes, Hernández & Mathus N-1940 (GH); 7 mi NE of Janos at top of Mt. with radio tower, Luckow et al. 13239 (TEX); 7.4 km W of Balleza on road to Guachochi, Peterson, Annable & Valdes-Reyna 10727 (ANSM, BISH, US); Ca. 31 (air) mi NW of Julimes in a SW-facing canyon above Rancho El Recuerdo in Sierra de Carrasco, Henrickson 12924 (LL); 17 (road) mi NE of Aldama along Hwy 16 at Puerto de Gomez, Henrickson 7544 (LL); 13.3 (road) mi NE of Aldama along Chih. Hwy 16, Henrickson 7524 (LL); Canyon La Campana, near Encinillas, Knobloch 613 (TAES); Along Chihuahua Hwy 0, ca. 57 mi S of Mexico Hwy 16 at Ojinaga and ca. 40 mi N of turnoff to La Perla, and 30.9 mi S of Lan Mula, Reveal & Atwood 3310 (NY, TEX); W of Buenaventura along Hwy 28, 7.4 mi W of jct Hwy 10 in Buenaventura, Mayfield et al. 114 (ARIZ, TEX); Hills and plains near Chihuahua, Pringle 422 (GH, NA, NY, P, RSA, US); Carretas, White 1115 (ARIZ, MICH); Near boundary with Durango at 10 mi SW of El Ojito, Peterson Sánchez-Alvarado & Gómez-Ruiz 20026 (BISH, K, MO, US); Santa Eulalia, Velardeña arroyo, Hewitt 238 (GH); Mpio. Hidalgo del Parral, 10 km al sur de Parral, Blanco-Aguirre 2108 (ENCB); Rancho Carretas, Harvey 1620 (MO, US); Ca. 8 mi S of Ixmiquilpan, Reeder 1615 et al. (ARIZ). Coahuila: Saltillo, Hitchcock 5631 (RM); 12 mi S of Saltillo, Reeder & Reeder 2912 (ARIZ); 5 mi S of Castanos, Reeder 3284 et al. (ARIZ); 9 km S of Parras on Sierras Negras, Standord 2400 et al. (ARIZ); 30 km al Pte. de G. Cepeda, carretera a Parras, Valdés VR-1577 et al. (ARIZ); N side of Canon de la Fragua, ca. 25 mi SW of town of Cuatro Cienegas on Mexico Hwy 30, Van Devender 84-601 et al. (ARIZ); 12 mi W of San Buenaventura, Reeder & Reeder 3932 (ARIZ); Approximately 32.2 km SE of Saltillo on road to Los Lirios, Peterson & Annable 6248 (US); ca. 6 km S of Saltillo, owned by Univer. Autónoma Agraria “Antonia Narro”, Peterson & Valdes-Reyna 8341 (BISH, K, MO, US); 85.4 km NW of Muzquiz, on Hwy 53 towards Boquilla del Carmen, via La Rosita, Peterson & Annable 10573 (BISH, US); Madera del Carmen; 9.7 mi NE of Las Pilares, Peterson, Saarela, Lara Contreras & Reyna Alvarez 20940 (ANSM, US); N of Los Pilares, Peterson & Romaschenko 24472 (ANSM, US); Madera del Carmen, road between Campo Cinco and Campo Uno, Peterson & Romaschenko 24554 (ANSM, US); 135.4 km NW of Muzquiz, on Hwy 53 towards Boquilla del Carmen, Peterson & Annable 10580 (BISH, GH, K, MO, NY, RSA, US); Sierra El Pino, 18.8 km SW of Rancho El Cimarron, Peterson & Annable 10646 (BISH, K, MO, US);

Sierra Zapalinamé, along camino “El Cuarto”, E of Saltillo, Peterson & Valdes-Reyna 18803 (BISH, K, MO, US); Sierra del Carmen, Ejido San Francisco, near small cabin, Peterson, Valdes-Reyna & Sifuentes 18823 (BISH, K, MO, US); Sierra El Jardin, Peterson & Lara-Contreras 19918 (K, MO, US); Sierra El Jardin, slopes above Canyon del Diablo, Peterson & Lara-Contreras 19890 (BISH, GH, K, MO, NY, RSA, US, UTC); Sierra El Jardin, Canyon del Diablo, at 8 miles from jct of road towards Boquillas, Peterson & Lara-Contreras 19871 (K, MO, US); 99.6 mi N of Melchor Muzquiz at Cuesta de Malena on Hwy 25 towards Boquillas del Carmen, Peterson & Laras-Contreras 19832 (US); Cañon de Madera, W side of Sierra de los Guajes, ca. 4 km E of Rancho Buena Vista, Stewart 1506 (GH, US); Ca. 18 (air) mi NE of Tlahualilo, 9 (rd) mi NW of Los Charcos de Risa, Henrickson 13698 (ARIZ); Cuesta Zozaya, ca. 38 km de Ocampo rumbo a Sierra Mojada, Carranza & Carranza C-680 (MO); Sierra de la Madera, vicinity of “La Cueva”, Johnston 9103 (GH, MO, US); Sierra de la Paila (Lado Norte) Cañada becerros, Villareal et al. 5449 (ANSM); 11 km W of Saltillo, Mick & Roe 24 (TAES); Rancho “El Porvenir”, located N of “La Bahía”, Huss 39–69 (TAES); 10 mi SE of Saltillo on old road to Argeaga, Gould 8691 (TAES, UC); Sierra de la Gavia, Valdés-Reyna et al. 1710 (TEX); 4.6 mi W of Rancho Ganadero, Los Angeles, Peterson, Saarela, K Romaschenko & Valdés-Reyna 23120 (ANSM, US); Buenavista, a 6 km al sur de Saltillo por la carretera Saltillo-Zacatecas, carr. 54, en Universidad A. A. “Antonio Narro”, Snow & Valdés-Reyna 6675 (ANSM, MEXU, MO); Entroque Derramadero, a 20 km al Sur de Saltillo por la carretera Saltillo-Zacatecas, carr. 54, Snow & Valdés-Reyna 6696 (ANSM, MEXU, MO); Entrada de la Carretera 54 a Rancho Los Angeles, 52 km al Sur de Saltillo, Snow & Valdés-Reyna 6710 (ANSM, MEXU, MO); Sierra de Arteaga, Rancho “El Chorro”, Carretera 57, casi 0.5 km pasando el entronque a Los Lirios, cerca de encampamiento “El Chorro”, Snow & Carranza 6764 (ANSM, MEXU, MO); Mpio. de Arteaga, Sierra de Arteaga, Bella Union, ca. 2 km al E de Arteaga, Carretera 57, Snow & Carranza 6765 (ANSM, MEXU, MO); 1 km E of San Antonio, Mpio. Arteaga, Peterson & Romaschenko 24566 (ANSM, US); Santa Rosa Mts., Marsh 1449 (TEX); Norias de Guadalupe, 100 km al SW de Acuña, Cabral 954 (TEX); Sierra de los Organos, Wendt & Lott 1396 (LL); 9 km S of Parras on Sierras Negras, Stanford et al. 189 (GH, MO, NY, UC); Del Carmen Mts., Marsh 723 (GH, TEX); Cuatro Ciénelgas, Puerto del norte, Harvey 1226 (MICH); 2 mi W of Saltillo, road to Torreón, Harvey 1092a (GH, MICH, MO, US); Serranías del Burro Mts., Rancho Margareta headquarters, ca. 65 mi NW of Sabinas, Gould 10623 (MICH, TAES, UC); La Escuela Superior de Agricultura, Buena Vista, ca. 5 mi SE of Saltillo, Gould 6387 (MICH, RSA, TAES, TEX, UC); 1 mi SE of San Antonio de las Alazanas (SE of Saltillo), Gould & Watson 10516 (MICH, TAES, TEX, UC, US); Sierra de las Cruces, eastern foothills 8 mi N of Santa Elena Mines, Johnston & Muller 1029 (GH, LL, US); Sierra del Pino, vicinity of La Noria, Johnston & Muller 493 (GH, LL, NA); Vicinity of La Noria, Steward 1201 (GH, TEX, US); 13 km N of Rancho El Jardin on winding road to Mina El Popo, Johnston et al. 11854A (LL); La Cuesta del Plomo on the Músquiz-Boquillas Hwy, Johnston et al. 9199 (LL, MEXU); Mina El Popo, ca. 2 km S of

Cañon del Diablo on dissected E slope of Sierra del Carmen, ca. 19 km by winding road N of Rancho El Jardin, Johnston et al. 11912 (LL, MO, NY); 3.7 (road) mi S of Parras, Henrickson 6177b (LL); Ca. 45 (air) mi W of Cuatro Cienegas, 4 mi SW of Hacienda Zacatosa, Henrickson 12056 (LL); Ca. 35 (air) mi SSW of Cuatras Cienegas in northern slope of limestone Sierra de Los Alamitos, ca. 9.2 road mi S of El Hundido, in Izotal, Henrickson 13677b (ARIZ, LL); Ca. 12 (air) mi E of Boquillas, Henrickson 11553 (LL); Ca. 27 (air) mi SE of Torreon in Sierra de Jimulco, ca. 6 (air) mi SSW of La Rosita, ca. 1/2 mi along rail beyond road's end, Henrickson 13235 (LL); Ca. 18 (air) mi NE of Tlahualilo, 9 road mi NW of Los Charcos de Risa, Henrickson 13698 (LL); Ca. 54 (air) mi SE of Big Bend N.P. Basin in S end of Sierra Maderas del Carmen in the Cañon de la Fronteriza, 2 mi NE of Rancho San Isidro, Henrickson & Prigge 15046 (LL); Serranias del Burro, Rancho El Bonito, Mpio. de Villa Acuna, Riskind et al. 2187 (ANSM, TEX); 15 mi W of Saltillo on Hwy to Torreon, Gould 11556 (TAES); 0.5 mi N of Las Vacas, Ely 156 (TAES); Cañon del Agua, 1.3 mi S of ranchito, Valdés-Reyna & Wendt 1016 (TAES); S end of Puerto San Lázaro (Cuesta La Muralla), 0.5 mi N of San Lázaro along Rte. 57, Valdés-Reyna & Wendt 1106 (ANSM); Sierra de Zapaliname Mts., 5 km S of Saltillo, Hatch et al. 4489 (TAES); 53 km S of Saltillo along Hwy 54, S of Concepcion del Oro, Hatch et al. 5412 (TAES). Distrito Federal: Pedregal de San Angel, 1 km S of UNAM, Nee 238 (MEXU); Sierra de Santa Catarina, parte alta Delegación de Ixtapalpa, Rzedowski 33862 (ANSM); San Angel, Orcutt 3691 (GH, MICH, MO, NY, TEX); Sierra de Guadalupe, Balls 5612 (MICH, UC); Tacubaga, St. Pierre 872 (MICH, US); Del. Coyoacan: Pedregal de San Angel, Sharp & Gilly 180 (MICH); Del. Ixtapalapa, Partes altas del Cerro Estrella, Koch 77203 (ENCB, TAES, US); Pedregal de San Angel, Fernández 9 (ENCB, TEX); Lomas, Lyonnet 1735 (CM, ENCB, MEXU, MO, UC, US); Around Coyoacan, Antipovitch 40 (CM); Vicinity of México, Hitchcock 5892 (US); Mixcoac, Olivar, Arsene 8283 (GH, US); Mixcoac, St. Pierre 2250 (MICH); Sierra de Santa Catarina, parte alta, Del. de Ixtapalapa, Rzedowski 33862 (ENCB); San Gregorio, Del. de Xochimilco, Ventura 2105 (ENCB, MEXU, TAES); Sierra de Guadalupe, Ticomán, Bopp 38 (ENCB). Durango: 35.5 km N of Durango on MEX Hwy 45, Peterson 9647 (BISH, K, MO, US); A 11 km de Nombre de Dios, sobre la carretera a Durango, Herrera 692 (MEXU, NY); Ca. 18 km al E de Durango, carretera a México, Herrera 438 (MEXU); Hwy 49, 1.5 mi N of Rancho Grande, ca. 15–20 mi S of Rio Grande, Spellenberg 2935 (NMC, NY); Ca. 18 km al E de Durango, carretera a México; Herrera 438 (ANSM); 1.3 mi SE of San Jose del Molino, Peterson, Saarela, Rosen & Reid 21170 (CIIDIR, US); Estacion Microondas "Sapioris" ca. 30 km SW of Gomez Palacio on Hwy toward Durango, Johnston et al. 10399 (LL, NY); 3 mi N of Donato Guerro, Emery 342 (TEX); ca. 35 mi N of Rodeo, Emery 357 (TEX); Mpio. Súchil, al SE de Súchil, González 2023 (TEX); Mpio. Mapini, Top of Perto de la Cadena, Sanders et al. 6689 (ARIZ, RSA); Santiago Papasquiaro, Palmer 468 (BAA, MICH, MO, UC, US). Guanajuato: 79 mi N of Queretero (1 mi S of San Luís Potosí state line), Waterfall 16563 (UC); About 5 mi E of Silao along the road to Guanajuato, Reeder & Reeder 2287 (GH); 5 km E of Jofre, Peterson, Saarela & Romaschenko

23422 (CIIDIR, US); 10 km al N de León, Mpio. León, Galván & Galván 3039 (MO); Rancho Las Adjuntas, Mpio. de San José Iturbide, Ventura & López 9473 (ANSM); La Angelita, Beetle et al. M-1723 (NA, TAES); Cerro Capulin, just E of Mexico 43, ca 0.8 km NNE of Vriangato on road to Salamanca, Iltis & Doebley 147 (TAES); 20 mi NW of Irapuato, Barkley et al. 764 (TEX); Mpio. Jerequerro, near Fresno, Beetle M-7166 (RSA); 39 km al SW de Cuerámaro, sobre el camino a la Barranca del Chilar, Rzedowski 47214 (ENCB); Ca. 22 mi NE of San Luis de la Paz, Reeder & Reeder 2257 (GH); Mpio. San Luis de la Paz, El llano 1 km de la comunidad de San José de jofre, González s.n. (ENCB); Mpio. Santiago Papasquiaro, grounds of Escuela José Ramon Valdés, Díaz 611 (TAES). Hidalgo: Cerro Ventoso, entre Pachuca y Real del Monte, Rzedowski 20578 (GREE, MEXU); Pachuca, Orcutt 3917 (MO, US); 10 km al NNW de Ixmiquilpan, Gonzalez Quintero 2735 (RM); 7 km al NNE de Tasquillo, González 2966 (TAES); Tailings dam from Loreto Mill, Santa Julia near Venta Prieta, Dsto. Pachuca, Moore 3165 (GH, US); 8 km al SSW de Al-fajayacun, González 3027 (TAES); Durango, Mpio. Hidalgo, El portento (Rancho las Iglesias), Ríos 12 (TAES); Ca. 8 mi S of Ixmiquilpan, Reeder et al. 1615 (RSA); 8 mi S of Ixmiquilpan, Gould 9302 (MICH, TAES); 11 mi N of Ixmiquipan, Gould 9566 (TAES); Cerca de los pitos, Matuda 21519 (MEXU, MICH); Cerca de los pitos, Matuda 21496 (MEXU, MO, TEX); Cerro Ventoso, entre Pachuca y Real de Monte, Rzedowski 20561 (ENCB, NY, US); Mpio. Zempoala, Sierra de los Pitos, Tlaquilpan, Benítez 122 (ENCB). Jalisco. Lagos de Moreno, Beetle M-5623 & Guzman M. (ARIZ); El Jalocotal, 2-3 km W de El Jalocote, Santana 8729 (BRIT); Barranca of Río Verde, ca 20 mi N of Tepatitlán on road to Yahualica, McVaugh 17431 (NY); 7 mi SE of the junction of Hwys 80 and 45 at Lagos de Moreno, Davidse & Davidse 9937 (MO); 11 mi N of Ciudad Guzman, Gould 9638 (TAES, TEX); 48 mi SW of Aguascalientes on Hwy 45, Pratt 630 (TEX); 10 mi E of Tepatitlan, Gould 9653 (TAES, TEX, UC); 8 mi NE of Lagos de Moreno, Gould 9657 (TAES); Cerro de los Gallos (ca. 15 mi S of Aguascalientes, McVaugh 17126 (TAES); Barranca of Río Verde, ca. 20 mi N of Tepatitlán on road to Yahualica, McVaugh 17431 (TAES). Mexcio D.F.: Mpio. Texcoco, Poblado de Huexotla, Teresea Licona 14 (MO); Old Hwy 190 between turnoff to Chalco (Hwy 115) and Santa Barbara ca. 30 mi above Azotla, Mick & Roe 288 (TAES); Mpio. Ajapusco, Cerro de Jaltepec, Ventura 168 (FLAS, MEXU); Mpio. Ajapusco, Terrenos de Jaltepec, Ventura 1997 (ANSM, TAES); Satelite (NW edge of Mexico City on Hwy 57), Gould 10190 (TAES); San Vicente Chicoloapan, Mpio. Texcoco, Ventura 4103 (TAES); 16 mi N of Cuautitlan, Gould 10205 (TAES, TEX); Huehuetoca, Matuda 26647 (MEXU, MO, TEX); Cercanías de Tultepec, Matuda et al. 29336 (MEXU, MICH, NY); Pegregal de Tlalpan, Matuda 21376 (MEXU, MICH, MO); Mpio. Huehuetoca, Cerro Mesa La Ahumada ladera Oeste, Romero-Rojas 1612 (ENCB); Mpio de Temascalpa, 1 km al oeste de Temascalpa, Espinosa 786 (ENCB, MEXU); Cerro Buenavista, Temascalapa, Castilla & Tejero 765 (ENCB); Mpio. de Axapusco, 12 km al NE de San Martín de las Piramides, por la carretera a Tulancingo, Hgo, Koch 77170 (ENCB, TAES, US); San Juan Teotihuacan, Fisher s.n. (CM). Michoacán: Ca. 1.7 mi NW of Tuxpan, near km post 129 on

Hwy 15 to Morelia, Davidse & Davidse 9816 (MO); 4 km E of San José Coapa along MEX 14, Steinmann & Steinmann 1933 (ARIZ); Cerro del Bao, cerca de Tzurumutaro, Mpio. Pátzcuaro, Escobedo 1668 (ANSM); 2 km al N de Catedral Porvenir, Mpio. Tarímbaro, Zamudio 4413 (ANSM); Hills of Lake Cuitzeo, on road from Morelia to Cuitzeo del Porvenir, Sohns 741 (TAES, US); Ca. 5 mi SW of Quiroga, Barkley et al 2725 (TEX); 6 mi E of Ciudad Hidalgo on Hwy 15, Pratt 741 (TEX). Nuevo Leon: 1 mi E of San Marcos, ca. 13 mi SE of Galeana, Gould 10725 (MICH); Mpio. Galeana, Chase 7742 (ARIZ); Along the big arroyo W of Galeana, Hwy no. 60, Cummins s.n. (RM); Monterey, Tateoka 1100 (TAES); Sierra Madre Oriental, El Salero, Peterson and Valdes-Reyna 15817 (BISH, US); Sierra Madre Oriental, 6.5 mi S of Border of Coahuila and Nuevo Leon on Hwy 57 towards Matehuala, Peterson & Knowles 13285 (BISH, K, MO, RSA, US); 5.2 mi S of Zaragoza on road towards Ejido La Encantada, Peterson, Valdes-Reyna & Sosa-Morales 16752 (US); 9.4 mi W of San Antonia de Peña Nevada and 0.4 mi E of Jtn of Hwy 2 to Or, Peterson, Valdes-Reyna & Sosa-Morales 16788 (US); 4.3 mi E of Hwy 57 on Mex 31 towards Linares, Peterson, Saarela & Romaschenko 23182 (US); 0.1 mi W of Once de Marz, Peterson, Saarela & Romaschenko 23611 (CIIDIR, US); 14.4 mi S of Casas Blancas, Peterson, Saarela & Romaschenko 23686 (CIIDIR, US); 5 km E of San Roberto on Hwy 62 towards Galeana, Peterson, Romaschenko & Valdés-Reyna 24453 (ANSM, US); 7.5 km E of Puentes on dirt road, Peterson, Valdes-Reyna & Sosa-Morales 17852 (US); 14 mi S of San Roberto along Hwy 57, McGregor et al. 472 (KAU, NY, TAES, US); 7 mi E of San Roberto along Hwy 60, McGregor et al. 439 (KANU, TAES, US); 25 km E of San Roberto along Hwy 58, Hatch et al. 4566 (TAES); 12 mi N of Matehuala, 0.5 mi N of SLP state line, Gould 10654 (TAES, UC); Ca. 10 mi NW of Rancho Margareta headquarters, 75 mi NW of Sabinas, Gould 10705 (TAES); 5 mi S of Monterrey on road to Chipinque, Gould 6312 (MICH, TAES, UC); Between Old Mexico City Hwy and El Diento, Monterrey, Smith M558 (TEX); 11 mi NW of Linares, Johnston 4644A (TEX); Galeana, Rancho Aguililla, Hinton et al. 19639 (TEX); Galeana, bank of steam, Chase 7742 (GH, MICH, MO, NA, NY, US); Monterrey, Hitchcock 5517 (US); Rancho Aguililla, Hinton et al. 19556 (ENCB, TEX); Sierra Madre Oriental, El Salero, Peterson & Valdes-Reyna 15817 (US). Oaxaca: Along ditch between Tule and Oaxaca, Hitchcock 6186 (BISH); Cerro La Torrecilla al W de El Enebro, Mpio. Concepción Buenavista, Tenorio & Romero 9374 (TEX); road leading from Hwy 190 to nativity site of Benito Juárez, Sierra de San Felipe, Soderstrom 436 (US); Cerro La Torrecilla al W de El Enebro, Mpio. Concepción Buenavista, Tenorio & Romero 9374 (ANSM); 13 km E of Mitla on MEX Hwy 179 towards Ayutla, Peterson & Annable 9875 (BISH, K, US); 9 mi S of San Cualimojoyas, Peterson & Saarela 22334 (SERO, US). Puebla: Camino de Cholula a Acatepec, después de una curva doble en la salida sur de Cholula, Vibrans 3163 (MEXU); Rio de San Francisco, Puebla, Purpus 4079 (UC); 5 km al E de Santa Catarina Tehuixtla, ca. 5 km al E de Tepoztlán, Medrano et al. F-1372 (MO); Tehuacan, Purpus 1465 (RM); vicinity of San Luis Tultitlanapa, Puebla, near Oaxaca, Purpus 3591 (MO, NY, UC, US); 9 km NW of San Lorenzo on the Tehuacán-Tecamachalco Hwy (No. 150), Davidse &

Davidse 9305 (MO, NY); 5 km carretera Tehuacán-Teotitlán, Mpio. Tehuacán, Morales 16 (MO); Afuera de Tehuacán, Puebla, por la carretera a Esperanza, González et al. F-312 (ANSM); Near Tehuacan, Pringle 9552 (GH, MO, TAES, US); Just over the Puebla-Veracruz boundary on Hwy 150, Gould 14904 (TAES); Mpio. Azumbilla 10 km al NE de Azumbilla, carretera a Esperanza, Tenorio 15209 (ARIZ, TEX); Oriental, Mpio. Oriental, Ventura 4148 (KANU, MICH); Vicinity of Puebla, Arsène 231 (CM, GH, MO, US). Querétaro: Querétaro, Escamilla 3 (MEXU); Mpio. Cadereyta, along MEX 120, ca. 3.5 km S of Vizarrón, Steinmann 3682 et al. (ARIZ); Ladera oriental de Cerro de la Tembladera, 6 km al N de Peña Blanca, Mpio. Peñamiller, Zamudio 3455 (ANSM); 8 mi SE of Queretaro, Gould 10235 (TAES, UC); 5 mi N of Queretaro, Gould 11597 (TAES, TEX); 11 mi N of Ixmiquilpan, Gould 9566 (TEX); 1 km al S de Vizarrón, Mpio. Cadereyta de Montes, Zamudio 3367 (MO, TEX); Near San Juan del Rio, Rose et al. 9587 (US); 4 km E of San Javier, Peterson, Romaschenko & Zamudio Ruiz 24742 (CIIDIR, IEB, US). San Luis Potosí: El Huizache, 11 mi E along Hwy 80, McGregor 748 et al. (KANU); Matehuala, 9 mi S along Hwy 57, McGregor 527 et al. (KANU); San Luis Potosí, 10 mi E along Hwy 86 to Rio Verde, McGregor 660 et al. (KANU); San Luis Potosí, 12 mi N along Hwy 57, McGregor 551 et al. (KANU); 32.2 km SW of San Luis Potosí on Hwy 70 to Aguascalientes, Peterson & Annable 6199 (BISH, US); 30 km SW of San Luis Potosí on Hwy 70 to Aguascalientes, Peterson & Annable 6212 (US); Sierra Madre Oriental, 2.5 mi E of Hwy 57 on road towards Guadalcazar, Peterson & Knowles 13389 (BISH, K, US); Estación San Bartalo, Mpio de Rio Verde, Bravo 16 (MEXU); On border N of Saldana, Beetle et al. M-1768 (UC); San Francisco, 20 km al NE de Rioverde, Rzedowski 5150 (US); 12 km al W de la Est. Berrendo, Mpio. de Charcas, Rzedowski 6570 (US); 10 km al S de Cárdenas, Rzedowski 4598 (US); just S of Nuevo Leon/San Luis Potosí border on Hwy 57, Peterson, Saarela & Romaschenko 23233 (CIIDIR, US); 5.7 mi E of Wadley, Peterson, Saarela & Romaschenko 23275 (CIIDIR, US); 4.1 mi E of Charco Blanco on road towards Guadalcázar, Peterson, Saarela & Romaschenko 23338 (CIIDIR, US); 10 mi W of Guadalcázar, Peterson & Romaschenko 24665 (CIIDIR, US); 6.1 mi N of Lazaro Cardenas, Peterson & Romaschenko 24601 (CIIDIR, US); 7.1 mi W of Santo Domingo, Peterson & Romaschenko 24905 (CIIDIR, US); Peñasco, Rzedowski 3424 (US); Cerro al W de Villa Hidalgo, Rzedowski 3776 (US); Ca. 3 km E of Laguna Seca on NW slope of the Sierra de Alvarez, Sohns 1089 (P, TAES, US); On boarder N of Saldana, Beetle et al. M-1768 (FLAS); Valley of the Rio Verde and in the Sierra de Cuates, Sohns 1262 (P, TAES, US); 2 km S of Venados, on road to Moctezuma, Chiang et al. 8219B (LL, MEXU, NY); Mpio. Matehuala, Ejido Cerrito Blanco, 10 km al E de Matehuala, Lemus 123 (TAES); 10.4 mi E of El Huizache along Hwy 80 at K182, Henrickson 6533a (ARIZ, LL); 6.5 road mi S of Arista, Henrickson 6431 (LL); Carretera de S. L. Potosí a la Presa de San José, Gómez-Lorence 57 (ANSM); 3 km S of Jct with Hwy to Villa de Reyes, Reeves 6325 (LL); Cerro al W de Villa Hidalgo, Rzedowski 3776 (GH, LL); Hills above San Luis Potosí ca. 5 mi SW of the city, Reeder et al. 1370 (RSA); 18 km al E de San Luis Potosí, sobre la carretera a Rioverde, Rzedowski 11214 (MICH); Cerro Ventoso, 5 km al

NE de Pachuca, sobre la carretera a Real del Monte, Rzedowski 19968 (MICH); 1 km al S de Cerro Godo, Mpio. Zaragoza, Rzedowski 11253 (MICH, TAES); Charcas, Whiting 486 (MEXU, MICH, US); Mpio. Villa de Arriaga, 2 km al W de La Placa, Gómez 878 (ENCB); Entroque a Derramaderos, Mpio. Ahualulco, Gómez s.n. (ENCB); Cárdenas, Hitchcock 5739 (US); Charcas, Whiting 957 (ARIZ, MICH, US); Charcas, Whiting 779 (MICH, US); Guascama, Purpus 5434 (GH, MO, NY, UC, US); Mpio. Villa de Arriaga, Rancho “El Palmar”, Potrero “Tortugas”, al SO del Edo., Rivas & González 197 (TAES); 41 mi S of San Luis Potosí, Gould 11579 (TAES, UC); 4.1 mi E of Hwy 57, 1.2 mi W of El Aguije, Hatch et al. 4878 (TAES); 5 mi SE of San Luis Potosí, Gould 11565 (TAES, UC, US); 24.1 km NE of San Luis Potosí on MEX 57 towards Matehuala, Peterson & Annable 11125 (BISH, K, MO, NY, US). Sonora: 51.6 km E of Agua Prieta on Hwy 2 towards Janos, Peterson & King 8138 (US); Sierra la Mariquita, 9.4 im (air) NNW of Cananea, Reina-G. 2010-852 et al. (ARIZ); Sierra San Luis, Arroyo Las Cabañas, Rancho Los Pinitos, 61.3 km (air) ESE of Agua Prieta, Reina-G. 2009-1221 et al. (ARIZ); Isla Tiburon, E side of the island, 1 km inland Zozni Quimpla, at base of N side of Punta San Miguel, Bilder 06-371 et al. (ARIZ); Mpio. Yecora, 19 km, al W de Yecora, Carr. a Cd. Obregón, Tenorio et al. 4561 (MEXU); La Vega Azul, SW of Colonia Morelos, Vera Santos 2171 (GH, TAES, TEX); Isolated hill NE of Sierra Anibacacachi, Rancho La Calera, ca. 10 km (by air) SW of Agua Prieta, Reinga G. 2003-1258 & Van Devender (ARIZ); Pinacate Region, arroyo half way between Tinaja de los Papagos and small “jungle-like” playa, ca 15 km S of MacDougal Crater, Eacurra s.n. (ARIZ 270781); Along Mex. Hwy 2, 16.6 km E of Agua Prieta, Reeder & Felger 8080 (ARIZ, MEXU, TEX); Valle de Teras, near La Angostura, White 3547 (GH, MICH, US); Horconcitos, Arroyo del Salto, White 3750 (GH, MICH); Cañon del Agua Amarga, White 3606 (GH, MEXU, MICH, NA); El Cañón de la Mescalera, Sierra de la Cabellera, Vera Santos 2116 (MICH); Agua Zarca, S of Colonia Morelos, Vera Santos 2010 (MICH, NY); El Puerto del Molino Quemado, E of Colonia Morelos, Vera Santos 2043 (MICH); La Vega Azul, SW of Colonia Morelos, Vera Santos 2171 (MICH, US); Guaymas, Palmer 273 (US); Nogales to Cocospora ranch, Griffiths 6804 (US); 6 km W of Los Vidrios on Mex. Hwy 2, Felger et al. 92-966 (MEXU). Tamaulipas: Mpio. Tula, 30 km al SW de Tula, cerca de límite de estados (SLP y Tamps.), González-Medrano 4432 (MEXU); El Canelo Ranch, 24 mi N of San Fernando on the Matamoros Hwy, Johnston 4879 (MICH, TEX); 5 km from San Fernando on the Victoria Hwy, Martínez and Borja F-2406 (TEX); 35 km from Victoria on the road to Casas and Soto la Marina, Martínez & Borga F-2347 (MEXU, TEX, US). Zacatecas: 45.5 km NW of Fresnillo on MEX Hwy 45 to Durango, Peterson 9661 (BISH, K, MO, US); 5 mi N of Cardona, Johnston 7371 (GH, US); 22 km N of Fresnillo rumbo a Durango, Beetle M-7483 & Yatskievych (ARIZ); 20 km N of Fresnillo, rumbo a Durango, Beetle M-7474 (ANSM); Intersection of Mexico 54 and the Tropic of Cancer, Brunkin & Perino 476 (MO, TAES); 40 km N of Fresnillo rumbo a Durango, Beetle M-7504 (ENCB, TAES); 76 mi NE of Zacatecas (road junction with Hwy 45), Gould 12347 (TAES, US); 15 (air) mi NE of Estacion Camacho on NW slopes of Pico de

Teyra, Henrickson 13424 (LL); 81 mi SE of Durango on Hwy 45, Pratt 614 (TEX); 71 mi SE of Durango on Hwy 45, Pratt 606 (TEX); 15 km al N de Fresnillo, Diaz Luna 988 (RSA); Near Conception del Oro, Palmer 268 (GH, NY, UC, US); Mpio. Concepción del Oro, Ej. Neria de Guadalupe, Del Rio s.n. (ENCB); Along Hwy 54, 0.4 road mi S of Hwy 60 turnoff towards Fresnillo, at junction of dirt road leading (unmarked) to Ranchito San Ramon, Snow 6673 (MO, MEXU); Near Sombrerete, Peterson, Saarela, Flores Villegas 21282 (CIIDIR, US); 20 km N of Fresnillo rumbo a Durango, Beetle M-7466 (MO); 10 mi E of Zacatecas at Guadalupe, Beetle et al. M-1793 (UC); 0.3 mi N of Chiripe, Peterson & Romaschenko 24845 (CIIDIR, US); Nombre de Dios, 48 mi SE, Marsh 1898 (KANU). Yucatán. About 17 mi SW of Mendoza, Reeder & Reeder 2017 (ARIZ). Peru. Ancash, Corongo, Peterson & Soreng 21791 (US, USM); Urubamba: Alturas de Tarapata, Vargas 13770 (US); Laderas de Muyock, Vargas 14109 (US). Puerto Rico. Río Piedras, Garcia M. 352 (UPR). United States of America. Arizona: Apache Co., Big Canyon, Ft. Apache, Goodding & Schroeder 387–41 (RSA). Cochise Co., Ca. 14.3 mi NE of Douglas, along US Hwy 80, ca. 50 m N of mile marker 384, Snow 5857 (MO); 17 mi E of Douglas, Gould & Haskell 4518 (ARIZ); 10 mi E of Benson, Anderson & Collins 478 (TAES); Tombstone, along First St., between Toughnut St, and Old Charleston Rd, Reeder & Reeder 8674 (ARIZ); 16 mi SW of Tombstone, Gould 7970 (TAES, UC); Southwestern Research Station, Chiricahua Mts, “Chiricahua Veg. Team” 59-798 (ARIZ); 1 mi W of Chiricahua Nat. Monument, 45 mi SE of Tucson, Deaver 6613 (TAES); AVA Ranch, Portal, Barr 67-319 (ARIZ); 9 mi S of Fry, Gould 2411 et al. (ARIZ); Pearce, Griffiths 1943 (ARIZ); Bisbee, Deaver 6625 (TAES); Entrance to Cave Ck. Canyon, Barkley 14A671 (RSA) and Barkley 14A678 (TEX, US); 6 mi S of Ft. Huachuca, Benson 11497 (POM); Ft. Huachuca, Wilcox 384 (POM); Ft. Huachuca, Gooding 853 (ARIZ); 9 mi S of Fry, Gould et al. 2411 (POM, UC); Triangle Tree Rd.-Dragoon Turnoff from I-10, ca. 13 mi E of Benson, Davidson 6430 (POM); Dragoon Summit, Tornber s.n. (ARIZ 139150); 10 mi E of Benson, Collins 478 (ARIZ); Dragoon Mts, ca. 1 mi SE of Sheepshead Pass, Yatskievych 85-293 & Windam (ARIZ); Dragoon Mts, Griffiths 1859 (ARIZ); Cave Creek, Chiricahua Mtns, Shreve 6351 (ARIZ); Arizona Hwy 181, 2.5 mi W of Chiricahua National Monument Headquarters, Strandberg 344 (ARIZ); Ditto, 4 mi W of Chiricahua N.M. Hqrs, Strandberg 348 (ARIZ); Hwy 181, 1 mi W of Chiricahua N.M., Wilcox 6613 (ARIZ); El Coronado Ranch, Turkey Ck, Chiricahua Mts, Miller G-470 (ARIZ); Near Marble Canyon (1 mi SE of Marble Camp), Dos Cabezas Mtns, Kaier s.n. (ARIZ 20544); San Pedro Riv., ca. 1 km E of Benson, Baker 10173 (ARIZ, RSA); San Pedro Riparian National Conservation Area, “Palominas-3” site, ca. 1 mi S of Palominas Rod, Makings 513 (ARIZ); Tinker Canyon 11th Brigade Signal Corps site, 0.3 km NW of mouth of Tinker Canyon, 3 km E of the mouth of Garden Canyon, Schulz & Krohn 2496 (ARIZ); West Gate 11th Brigade Singal Corps site, 0.5 km NW of Kino Springs, Kronh & Shulz 2106 (ARIZ); Ditto, 1.0 km N of the mouth of Huachuca Canyon, Morrison & Popolizio 1194 (ARIZ); Ditto, immediately SW of Buffalo Soldier Road, 2.4 km S of Main Gate, 2.5 km NE of Stone Ridge, Schulz & Krohn 2667 (ARIZ);

Along AZ-90 ca. 17 km S of jct with I-10, Reeder & Reeder 9750 (ARIZ); Carr Peak, Benson 10487 (RSA); AVA Ranch, Portal, Barr 67–319 (NCU); Gate 7 at Saddle above Scotia Canyon and Boundary of Fort Huachuca Military Reservation, ca 2.5 mi NE of Sunnyside, Peterson & Annable 5476 (US); Chiricahua Mts., 10 mi S of Rucker Canyon Rd. on Tex Canyon Rd. and 6 mi NE of HWY 80, Peterson & Annable 5524 (BISH, US); Rucker Canyon, Gould & Haskell 4556 (ARIZ); Rucker Canyon, Chiricahua Mts, Jones & Thornber s.n. (ARIZ 139157); Ramsey Canyon Nature Preserve, Miller Peak Quad, T23S, R20E, SE1/4 of SW1/4 of Sect. 9, Adams 203-83 (ARIZ). Coconino Co., Prescott, Purchase 416 (MICH) and Purchase 3383 (ARIZ); Prescott, Benham 846 (ARIZ); Highway above Jerome, Goodding 72-46 (ARIZ); Sycamore Canyon Wilderness Area, Pinkava et al. 5902 (NCU); Ditto, 150 m N of Yavapai County line, Maker 10128 (ARIZ). Gila Co. 3 Bar Study Area, Tonto National Forest, Pase 1173 (ARIZ); Lower Parker Ck. Canyon, near south end of Natural Drainages Experimental Area A., Sierra Ancha Mts., Gould & Hudson 3837 (ARIZ, US); Parker Creek Exp. Stn., Hendricks 2052 (RM); Branch of Pinto (Riv.), Read 16 (RM); Sierra Ancha Wilderness Area, along FSR 203 ca. 6.2 mi S of Board Tree Saddle (jct with Hwy 288), Imdorf 1017 & Rebman (ARIZ); Sierra Ancha Wilderness Area, just N of Bull Canyon trailhead (trail 128) at end of FSR 203A, Imdorf 1045 & Dow (ARIZ); Pinal Ranger Stn., Sec. 22, T1S, R15E, Kirby P-2 (RM). Graham Co. Frye Mesa, Graham Mts., Kessler 500 (NY, TAES); 16 mi S of Safford near the highway, Gould & Haskell 3994 (ARIZ); BLM Wilderness, Black Rock, Buegge 622 (ARIZ); Swift Trail Rd, Maguire et al. 12099 (ARIZ, RM); Frye Mesa, Graham Mts, Kessler 500 (ARIZ); Sec. 10, T9S, R23 E, Christensen MG-32 (RM). Greenlee Co. Benton Creek near Baseline R.S., Sizer 30 (RM); 5 km NE of Greenlee-Graham Co. line along US-191, Reeder & Reeder 9176 (ARIZ) and 9621 (ARIZ); Along US-191; Big Lue Range, near Hwy 78 ca. 7 mi from the state line, Gould & Haskell 4109 (ARIZ, UC); Honeymoon, Eagle Creek, Pase 2270 (RM). La Paz Co., Eagletail Mts., side of Indian Spring Canyon, Newton 10 (ASU). Maricopa Co. US Hwy 60, 2.6 mi E of Queen Ck. Tunnel, Pinkava et al. L18913 (ASU, FLAS); Hassayampa River Preserve, ca 2 mi SE of Wikenburg on Hwy 89, Woldon 607 & Richter (ARIZ); Tonto National Forst, ca. 0.1 mi S of Seven Springs campground along road, Doan 931 (ARIZ); Sonoran Desert National Monument, Sand Tank Mts, north-facing slope ca 50 m eastward from summit of small peak, 730 m (air) NW of Bender Spring, 250 m northward from end of Bender Spring road, 1.05 km (air) NNW of Squaw Tit Peak, Felger 01-384 et al (ARIZ); Agua Fria River bottom near Cold Water, Harrison 1813 (ARIZ). Pima Co., Molina Canyon, Santa Catalinea Mts, R.S. Felger 668 (ARIZ); Stone Cabin Canyon above McClearys Camp, Hill 356 (RM); Santa Rita Range Reserve, Southwest Pasture no. 6, Culley 54 (RM); ditto, Pasture 2b, Streitz S-56 (RM); Canille Ranger Station, Rodgers 2 (RM); Near Florida Station in Canyon, Magee 385 (RM); Oracle Ranger Stn., T10S, R15E, Read 37 (RM); Rincon Ranger Stn. pasture, Galer 2 (RM); Santa Catalina Mts, 3.6 mi S of General Hitchcock Campground on Mt. Lemmon Hwy, Peterson & Annable 5656 (US); Santa Rita Mts, 2.1 mi W of Hwy 83 on Forest Service road 92 up Gardener Canyon, NW of Sonoita, Peterson & Annable

5684 (US); Santa Rita Mts. 0.4 mi W of Hwy 83 on FS 231 towards Rosemont Springs, Peterson & Annable 12235 (K, US); Santa Rita Mts, Thornber Griffiths 77 (ARIZ); Santa Rita Mt, J.W. Toumey s.n. (17 Jul 1894) (ARIZ); Tanque Verde Ck., 7 mi below Italian Ranch, 18 mi E of Tucson, Tanque Verde Mts., Parker 7164 (ARIZ, MICH); Southern Comobabi Mts., near Comobabi, Gould & Haskell 3206 (ARIZ, GH, NY, UC); SW slopes of Santa Catalina Mts., near Mt. Lemmon Rd., Gould 3451 (ARIZ, TAES); Nolina Basin Recreation Area, Sta Catalina Mts., Parker 7087 (ARIZ, RSA); Crest of Gates Pass, Tucson Mountain Park, Van Devender 88-798 (ARIZ); Tucson Mountains, Oeste Wash; Van Devender et al. 88-595 (ARIZ); Tucson Mountains, near radio towers on crest, nw of Trails End Canyon, Van Devender & Van Devender 88-698 (ARIZ); Cienega Creek Natural Preserve, next to train tracks at Three Bridges, near parking area below Marsh Station Road, Mauz 24-097 (ARIZ); Tucson, in roadside ditch 4 mi N of Tucson on Campbell Ave, Gould 2523 (ARIZ); Tucson, Sta Cruz Riv., Benson 8935 (POM); 61 mi SSE of Tucson, the Research Ranch, Elias 8976 (NY, RSA); 5 mi W of State Hwy 83 on Greaterville-Madera Canyon Rd, McLaughlin 61 (ARIZ); Sabino Canyon, Sta. Catalina Riv., Benson 9829 (RSA); Florida Canyon, Santa Rita Range, Benson 8974 (POM); Santa Rita Experimental Range, Galt s.n. (ARIZ 168258); Ca. 4.0 mi W of SR 83 along Greatville-Box Canyon Rd, Gutierrez 1756 (ARIZ); Baboquivari Cañon, Peebles et al. 575 (ARIZ, US); Baboquivari Canyon, Peebles et al. 346 (ARIZ) & 575 (ARIZ, US); Baboquivari Mts, Goodding 844 (ARIZ); Baboquivari Canyon, W side of Baboquivari Mountains, 2 mi from end of road that leads in from highway, Leader & Leader 375 (ARIZ); Thomas Canyon, E side of Baboquivari Mts., Toolin 398 (ARIZ); Mendoza Canyon, Coyote Mountains, Kurt & Haskell 45 (ARIZ); Ajo Mountains, main canyon N of Alamo Canyon, Gould & Darrow 4690 (ARIZ); Molina basin, Catalina Mts., King 229 (NCU); Rincon Peak, 20 km SE of the edge of Tucson, 2.5 km WSW of Papago Spring, Baker 16350 (ARIZ); Ragged Top Peak, ca. 4 mi N of Silver Bell, Wiens et al. 89-RT-43-02 (ARIZ); Arivaca Cienega, Buenos Aires Natioanl Wildlife Refuge, McLaughlin 6033 (ARIZ); Brown Wash, McLaughlin 4914 (ARIZ). Pinal Co., Pinal Mts. in pass S of Globe, Shreve 7459 (MICH); Oracle Road, Santa Catalina Mountains, Niering & Whittaker 388 (ARIZ); Above Oracle, Peebles 2559 et al. (ARIZ); Oracle, Thornber s.n. (ARIZ 139146); Ditto, Thornber s.n. (ARIZ 139160); West end of Holy Joe Peak, Galiuro Mtns, Darrow s.n. (ARIZ 14848); Peppersauce Canyon, Control Road, Santa Catalina Mtns foothills, Leader & Leader 332 (ARIZ); Sun Space Ranch, along arroyo WSW of production complex on north-facing slope, Burges 7139 (ARIZ); Pinal Mts, in pass south of Globe, Shreve 7459 (ARIZ). Santa Cruz Co., Sonoita Creek State Park Natural Area, saddle along ridgetop, McLaughlin 8421 & Lewis (ARIZ); San Rafael State Park, along E boundray fence, McLaughlin 8582 et al. (ARIZ); Ditto location, McLaughlin 8575 (ARIZ); Ditto location between Sharp and Heron Springs, McLaughlin 8707 & Lewis (ARIZ); The Research Ranch, drainage leading to East Tank, McLaughlin 10054 (ARIZ); Ruby Road 2 mi W of US Hwy 89, Barr 60-279 (ARIZ); San Rafael State Natural Area, San Rafael Valley to im-mediate W of Santa Cruz Riv., 0.5 mi N of Mexico border, Reif 10478 (ARIZ, RM);

W slope of Atascosa Mts., Sycamore Canyon, Franklin 5356 (NY, RM); Nogales, Peebles & Harrison 4674 (ARIZ, US); Patagonia Nature Conservancy Wildlife Sanctuary, Correll & Correll 39284 (LL); Patagonia-Sonoita Creek Sanctuary, Along Sonoita Ck, less than 1 mi S of Patagonia, Rogers 30 & Fassuliotis (ARIZ); Coronado National Forest, ca. 4.0 air mi N of Mexico border, Jct of USFS roads 39 and 115, Snow 5865 (MO); 9.3 mi NE of Patagonia along AZ Hwy 82, Snow 5867 (MO); Madera Canyon, Parker 7077 (ARIZ, RSA); Nogales, Thornber s.n. (ARIZ 139153) Nogales, Jones 22760 (POM); Appleton Whitehall Research Ranch, near Elgin, ca. 61 mi SSE of Tucson, Lyle Canyon, near S boundary of Ranch, Thomlinson et al. 747 (NY, RSA); Ditto, northeast of headquarters, McLaughlin 7334 & Plemons-Rodriguez (ARIZ); Ca. 5 mi N of Elgin, Reeder & Reeder 6955 (ARIZ); Monkey Springs Area, Gooodding 150–62 (ARIZ, NCU); Patagonia, Hitchcock 3651 (US); Along the road from Canelo Pass to Patagonia, ca 3 mi SW of the Pass, in the north end of the San Rafael Valley, Toolin 1133 & Reichenbacher (ARIZ); 5 km E of Washington Camp, Reeder & Reeder 7418 (ARIZ); 3.3 mi W of HWY 289 and Pena Blanca on Forest Service Rd. 39 towards Sycamore Canyon, Peterson & Annable 5320 (BISH, K, US); O'Donel Canyon, N of Knipe Cienega, Yatskievych 80-514 (ARIZ); Patagonia Mts, 1.7 mi SE of Patagonia on Harshaw Ck., Peterson & Annable 5387 (US); Ophir Gulch, 4 mi N and 2 mi W of Sonoita, Ptarmontano T 91 (ARIZ); Sycamore Canyon, Pajarito Mountains, Van Devender s.n. (ARIZ 201184); Sycamore Canyon, Pajarito Mountains, on east-facing slope immediately W of Hank & Yank ruins, Toolin 2128 & Buhrow (ARIZ). Yavapai Co., 2 mi N of Mingua Mt. Pass, Prescott to Jerome, Benson 14223 (POM); Tributary of Little Shipp Wash, ca. 9 mi SE of Bagdad, ca. 3.5 mi W of Santa Maria River, 1.5 mi N of AZ 96, Van Devender 91-798 et al. (ARIZ); Santa Maria River, canyon on W side of crossing, Darrow & Gould 3656 (ARIZ). Yuma Co., Ten Ewe Canyon, Kofa Mts, Monson 5 (ARIZ); Wire Corral, 13 Mile Rock Allotment, Julander 113 (RM). Florida. Collier Co., Collier City (Caxambas) on Marco Island, Deam 65392 (US); Marco Island, beach and hammock N of Caxambas Pass off US 92, Lakela 29242 (GH); Goodland, Godfrey 65552 (FSU); Caxambas, Garber 33 (GA, GH, MO, NY, US); In sand dunes, Caxambas, Moldenke 999 (MO, NY, US). Lee Co., Pointybel, Sanibel Island, Brumbach 5809 (FLAS, GH); Darling Sanctuary, Sanibel Island, Brumbach 7294 (NA, FLAS, US); Vicinity of Fort Myers, Standley 18946 (US); Sanibel Island, Cooley 2659 (US); Western Sanibel Island, Wulfert, Brumbach 8666 (GA, NCU, NY, US); Lower Camtiva Island, Brumbach 9280 (GA, GH, NCU, US); Sanibel Island, waste land near entrance to Sawgrass Rd., Cooley 2309 (FLAS, GA, NCU). Monroe Co., Key Largo, Phillips 588 (ARIZ); North Key Largo ca 3 mi from left turn of US Hwy 1, Cooely et al. 9257 (FSU); Vaca Keys, Small & Carter 2860 (FLAS, GH, US); Everglades N.P., Northwest Cape Sable, Avery & Russell 2138 (FLAS); Big Pine Key, Swallen 10670 (US); Big Pine Key, Small et al. 3572 (US); Big Pine Key, Killip 40685 (US); Big Pine Key, Killip 41238 (US, VPI); Big Pine Key, Killip 41715 (GA, GH, US); Big Pine Key, Radford 46083 (NCU); Big Pine Key, Martin 1323 (NA, NY, UC); Big Pine Key, Killip 32092 (UC, US); Sugarloaf Key, Sargent 6693 (GA); Key Largo, Hitchcock 675 (LL, GH, MO,

RM, UC, US); N end of Key Largo, Kral 51801 (MO, TEX); West Summerland Key, Godfrey 74051 (FSU, NCU); Key Largo, Atwater GS-182 (NCU). Sarasota Co., Longboat Key, south end, beach hammock overlooking Gulf of Mexico, Long & Lakela 27563 (FLAS, GA). Hawaii. Maui Co., Molokai: Molokai Project – Transect 9, Makakupa’ia Ridge, Char et al. 82.046 (HAW); Kawela, east of Road TRA, A-1300 plot, Jacoby s.n. (BISH). Kansas. Douglas Co., Lawrence, Booth s.n. (KANU, MONT 38814). Missouri. Crawford Co., In test plot, Pickle 150 (UMO). St. Clair Co., Tony s.n. (UMO 147246). New Mexico. Chaves Co.: Along U.S. Hwy 82, ca. 20 mi E of Mayhill, Henderson 69–314 (FSU, MO, NCU). Dona Ana Co., Foothills of Organ Mts., Barneby 2464 (NY); South end of Bishop’s Cap, Van Devender s.n. et al. (ARIZ 192727); On US Hwy 70–82 2.7 mi E of San Augustin Pass, Spellenberg & Spellenberg 3684 (NY); Bishop Cap, 2 air km NNW of the top of Bishop Cap, Worthington 17281 (NY); Mesa W of the Organ Mountains, Wooton 3198 & Standley (ARIZ); Aguirre Springs, Hwy 70, 15 mi from NMSU in Las Cruces, Adeola 37 (TAES); 4 mi from Organ Mt., on the way to White Sands Nat. Museum, Dashe 3 (TAES); 13 mi E of Las Cruces, ca. 1/4 mi SE of Hayner Ranch, Dunn 8576 (RSA); Canyon in S end of Organ Mts., Fosberg 53671 (POM); Organ Mts., Wooton 418 (GH, NMC, NY, P, POM, RM, UC, US); Dripping Springs in Organ Mts., Archer 499 (MICH); Dona Ana Mts., S end of College Ranch, 15 mi N of Las Cruces, Hatch 2336 (TAES); Filmore Canyon, Organ Mts., Hitchcock 3798 (MICH); Jornada Range Reserve, below Goldenburg Spring, Copple 328 (RM). Eddy Co.: Guadelupe Mts near Queen, Hitchcock 676 (RM); Jornada R.R., 1.5 mil W of Ropes House, Pasture 11, Schoeller & Hough 417 (RM); Carson Seep Ranger Station Pasture, Chapline 452 (RM). Grant Co.: Mangas Cañon, 16 mi WNW of Silver City, Barkley 14653 (TEX, US); 18 mi NW of Silver City, Metcalfe 641 (ARIZ, GH, NMC, NY, RM, US). Guadalupe Co., Vicinity of Santa Rosa, Arsène & Benedict 16973 (P). Hidalgo Co.: Little Hatchet Mts., Granite Pass, Worthington 12604 (NY); Apache Hills, slopes about the Apache Mine, Worthington 13498 (NY); Animas Mts., ca. 7 air mi SE of Animas, Worthington 14788 (NY); Guadalupe Canyon, ca. 1 mi E of AZ state line, Allred 4282 (TAES); Box Canyon near Lynch Camp, Turner & Felger 98-133 (ARIZ); Saddle in Spring Canyon Range, Pigott 7a (RM). Lincoln Co., N side of Capitan Mts., New Mexico route 48, 12 airline miles E of Encinosa, Holmgren & Holmgren 7416 (KANU, NY, NMC, RSA); Corona, Hershey s.n. (GREE). Luna Co.: Tres Hermanas Mts., canyon on NE side of South Peak, Worthington 19818 (RSA). Otero Co., 9 mi S of Alamogordo on W face of Sacramento Mts, S slopes of mouth of Dog Canyon, Spellenberg & Spellenberg 4296 (NY); McKittrick Canyon, Patterson 610 (TEX); N McKittrick Canyon, Patterson 537 (LL); Road to Rinconada, Humphrey 59 (ARIZ). San Miguel Co., Conchas Canyon below Crystal Pasture, 8.5 mi due W of Trujillo, Hill & Levandoski 12214 (TAES); Cuevas Canyon Rd. cut at Conchas Canyon below Crystal Pasture, 8.5 mi due W of Trujillo, Hill and Levandoski 12214 (GH, NY). Sierra Co.: 6 mi NW of Hillsboro off Hwy 90, Milestone 37 (TAES); W slope of the Caballo Mts., 6.7 mi by winding road E of Caballo Dam on the Rio Grande, Spellenberg 3920 (NMC, NY); San Andres Mtns, White Sands Missile Range, Rhodes Canyon, 0.1 mi

SW of Bearden Canyon Rd, just above Granite Gap, Van Devender & Toolin 1903 (ARIZ); Ridge N of Trujillo Canyon, Chapline 377 (RM); Gottom [of] south Percha Creek, Chapline 623 (RM). Oklahoma. Cimarron Co., Side of Mesa de Maya (Black Mesa), 3.5 mi N of Kenton, Rogers 6411 (MICH, TEX, US). Murray Co., On rocky bank of mt. stream, Arbuckle Mts., Hopkins 1109 (GH, MO, US); Arbuckle Mts., Cowpen Canyon, Hopkins et al. 715 (GH, RM); Ca. 0.5 mi W of Honey Ck., Arbuckle Mts., Robbins 3175 (TAES, UC); Igneous canyon wall along creek 8 mi W and 3 S of Davis, Waterfall 6743 (MO, VPI). Texas. Aransas Co., Cape Carlos, Tharp 9125 (TEX); Goose Island State Park, Brown 53–252 (TEX); Near seashore, Metz 3318 (NY). Armstrong Co., Claude, 15 mi S, 6 mi SW, Stephens 57414 (KANU). Bandera Co., Lost Maples State Park, confluence of Sabinal Riv. and Can Ck., Smith 698 (TEX). Bastrop Co., Bastrop State Park, Lybarger 100 (CM). Bee Co., 7 mi E of Beeville, Gould 6057 (TAES, TEX, UC). Bell Co., 8 mi N of Belton, Wolff 1308 (TAES); Near Moffat, Wolff 2681 (BRIT, TAES); Prairie near Schwertner, Wolff 2551 (US). Bexar Co., Leon Springs, Clemens & Clemens 75 (MO, MONTU); 15 mi NW of San Antonio, Burr 292 (TEX); US Hwy 45, 4 mi N of Richland Springs, England & McCart 9135 (TEX); San Antonio, Silveus 865 (US). Blanco Co., Pedernales Falls State Park, 7 mi N on Ranch Rd. 3232 off of US 290, E of Johnson City, Hill 3744 (TAES); 1 mi S of Johnson City, Francis 77 (TAES). Brewster Co., 1.5 mi E of Alpine, Gould 8317 (BRIT); Paisano Pass, 12 mi W of Alpine, Shreve 8354 (ARIZ); 7.9 km E of Alpine on U.S. 90, Van Devender 2003-841 & Reina (ARIZ); Glass Mountains, Warnock 20872 (US); Paradise Canyon, 4 mi W of Alpine, Warnock 20195 (BRIT) and 20196 (BRIT, KANU); Kokernot Lodge Road, Alpine, Warnock 20197 (BRIT); Leonard Mt., Warnock 20750 (BRIT); Rio Grande at Mariscal Canyon, Warnock 811 (BRIT); Big Bend N.P., Inner Basin, Chisos Mts., Kruckeberg 4737 (UC); 13 mi S of Marathon, Wood Hollow Mts., Wallmo 5341 (TAES); Chisos Basin, Big Bend N.P., Gould 9722 (TAES); 18 mi S of Marathon, Parks 30155 (TAES); Along Hwy 90, 5 mi W of Alpine, Morden 69 (TAES); Del Norte Pass, Berkman 46208 (TAES); N slope of Elephant Mesa, ca 35 mi S of Alpine, Johnston 6435 (LL, NY); Big Bend N.P., Upper Green Gulch, Chisos Mts., Warnock & Tharp 6839 (BRIT, LL); Hwy between Alpine and Fort Davis, Teague T31 (BRIT, LL); Boot Canyon, Correll 13721 (BRIT); Big Bend N.P., in Oak Canyon below the “Window”, Correll & Correll 30618 (LL); Chisos Mts., lower slopes of Basin, Lundell 13279 (LL); Kobernath Lodge Rd., Warnock 20197 (LL, POM); 9 mi NE of Alpine on O 6 Ranch, Warnock 21734 (TEX, US); N Side of Leonard Mt., Warnock 20750 (TEX, US); Paradise Canyon, Warnock 20195 (US); Glass Mts, Green Valley, Warnock W361 (US); Mt. slopes 12 mi W of Alpine, Shreve 8352 (MICH, US); Leonard Mt., Warnock 20750 (NY); Honeysuckle Canyon, Glass Mts., Warnock 21062 (TEX); Sul Ross College Campus, Alpine, Sperry T718 (UC); Chisos Mts, Upper Blue Ck., Mueller 7876 (GH, MICH, MO, NY, US); North Sunny Glen, Chisos Mts., Sperry T-491 (TAES, UC); Blue Ck. Canyon, Chisos Mts., Wolff 4476 (TAES). Briscoe Co., 9–12 mi N of Turkey on the Breaks of the Little Red Riv., Higgins 8263 (NY). Brooks Co., Near Huesos Camp, Encino Division, King Ranch, Morrow &

Nord 30 (TAES). Brown Co., Brownwood, Palmer 29519 (MO, NY) and Palmer 26986 (GH). Burnet Co., 1 mi E of Bertram, Rogers & Webster 6467 (KANU, RM, TEX); Marble Falls, Biltmore 4155a (S, US). Caldwell Co., Edge of Wilcox farm site, Tharp & Tyson 52–540 (TEX); TX Hwy 80, 5.6 mi E of junction with FM 20, Breckenridge 549 (TEX). Cameron Co., Los Fresnas to Brownsville, Swallen 1427 (US): 14 mi E of Brownsville on Hwy 14, Lonard 2825 (TAES); 10 mi W of Port Isabel on Hwy 100, Lonard 4988a (TAES); Laguna Atascosa Nat. Wildlife Ref., 2 mi from North Point, Fleetwood 7042 (TEX); Laguna Atascosa NWR., Unit 1, Fleetwood 7039 (TEX); Levee of Resaca de la Gringa, Johnston 542187 (TEX); Levee of Resaca de la Gringa in Laguna Atascosa NWR, Johnston 542176 (TEX); Laguna Atascosa NWR, along gunnery range, Fleetwood 3322 (TEX); Laguna Atascosa NWR, Fleetwood 3736 (TEX); Laguna Atascosa NWR, Unit 2, near impoundment 1, Fleetwood 8131 (TEX); near Brownsville, Point Isabel Rd., Runyon 132 (TEX); 8.2 mi from Boca Chica, NE of Brownsville, Lundell and Lundell 14712 (GA, LL, TEX); New Barreda, on the R.R. right of way, Runyon 4073 (BRIT, TEX); Los Fresnos, Swallen 1440 (US). Comal Co., Near Canyon Lake Dam, Davies 97 (TAES); Payne's Ranch on Smithson Valley Rd., 2 mi off of Hwy 46 W of New Braunfels, Fey 82 (TAES); 3 mi W of Hwy 281 N on Hwy 46, Edwards Plateau, Coltman 7 (TAES). Concho Co., 2 mi E of Eden, Gould 9528 (TAES). Crockett Co., Ca. 3 mi W of Ozona, along Texas FM 2398, Snow 5891 (MO). Culberson Co., 4 mi S of New Mexico State line on Hwy 62, Whitehouse 16941 (BRIT); About 4 mi NE of Pine Springs, Waterfall 5755 (BRIT); 6 mi NE of Pine Springs, Waterfall 5748 (GH, NY); Guadalupe Mts National Park, mouth of Pine Spring Canyon ca. 0.1 km NE of campground, Burgess 2321 (ARIZ); 7 mi N of Pine Springs, Davis et al. 243 (TAES); 9K Ranch, vicinity of Gray Tank on Willow Draw, 4.0 mi S, 6.5 mi W 9K headquarters, Burgess 653 (TAES); 9K Ranch, 1.8 mi E Ranch Rd. 1108, 2.8 mi N, 0.4 E 9K headquarters, Burgess 756 (TAES); Apache Mts., ca. 28 mi NW of Kent, Correll 31666 (LL); Guadalupe Mts., Pine Canyon, Standley 40611 (US); Creek, 7 mi NE of Pine Springs, Smith & Robertson 243 (US); Limestone hillsides approaching the Guadalupe Mts., ca. 4 mi NE of Pine Springs, Waterfall 5755 (GH, MO, NY); Pine Springs Canyon Trail near the Summit, Guadalupe Mts. N.P., Higgins 17468 (NY); Bear Canyon, Guadalupe Mts. N.P., Higgins 17428 (NY); Bear Canyon, Mount Lemmon Hwy, Santa Catalina Mts, Van Devender & Eiber s.n. (ARIZ); Upper Pine Springs, Guadalupe Mts, Turner & Warnock 85 (GH, LL). Duval Co., Texas Route 44, ca. 5 mi E of Duvall County Line near Freer, Seigler et al. 15326 (BRIT); 1 mi W of San Diego, Gould 10998 (TAES); 3 mi S of Freer, Tharp & Johnston 541817 (TEX); 9 mi SW of Freer on road no. 202, Tharp & Johnston 542023 (BRIT, RM, TEX). Edwards Co., Sonora Experimental Station, Gibbens 36 (TAES); Sonora Experiment Station, Nolen 34 (BRIT); Substation No. 14, Cory 52478 (BRIT, MICH, NY, RM, TAES); 14.5 mi SE of Rocksprings, Cory 35637 (TAES); T.A.E.S. Substation 14, ca. 25 mi S of Sonora, Gould 8391 (BRIT, TAES, UC); 1.1 mi N on the entrance road along limestone ledges on Kickapoo State Park, Keeney 7424 (BRIT); Ca. 1/4 mi S of the dam on the W bank of Hackberry Ck. near Deadman's Hollow, Smith & Butterwick 247

(LL); Substation No. 14, Cory 53478 (UC). El Paso Co., McKelligan Canyon, Franklin Mts., Shinners 9001 (BRIT); Franklin Mts., 0.9 air mi WNW jct. Trans-Mt. road & Gateway South, Worthington 9186 (BRIT, NY); El Paso, Jones 25a (US); McKelligan Canyon, Franklin Mts., Warnock 7373 (BRIT, LL, TEX); McKelligan Canyon, Franklin Mts., Correll 13834 (BRIT, LL, US); Mt. Franklin, Warnock 10354 (BRIT, LL); 5 mi W of El Paso, Warnock 7246 (TEX); El Paso, Jones 4210 (NY, POM, US); El Paso, Stearns 182 (US). Fannin Co., Ca. 1 mi NW of center of Honey Grove, Nee 44047 (BRIT, NY, TEX). Garza Co., 2.8 air mi SW of Post, Hutchins 939 (BRIT, LL). Gillespie Co., Kast Ranch, 18 mi N of Fredericksburg, Kast 9 (TAES). Goliad Co., McNamara Ranch, 2.8 mi SW of Goliad, Hill 6307 (TAES); 5.6 mi SW on US 59 from its jct. with FR's 2957 & 2506 in Fannin, Jones & Jones 5931 (GA, NY); 3.5 mi N of Eckert (17.5 mi NE of Fredericksburg), Shinners 31085 (BRIT). Harris Co., Intersection of Underwood St. & Fairmont Parkway in Deer Park, Brown 8100 (TAES). Haskell Co., Ca. 3 mi W of Rochester, Grayum 46 (TAES). Hays Co., 6 mi W of San Marcos, Niemann 19–62 (TAES); Outside San Marcos, on Ranch Rd. 12 in the Devils Backbone, Caeser 19 (TAES); Blanco Riv., 7 mi NW from Kyle, Tharp 47 (LL, TEX); 7 mi W of San Marcos, Gould 6696 (BRIT, TAES, TEX); 5 mi S of Wimberly, Emery 806 (TEX); 2 mi SE of Wimberly across road from entrance to Hidden Valley Ranch, Johnson 422 (TEX). Hidalgo Co., Railroad crossing, Sprague Street, Edinburg, Lonard 5010 (TAES); Donna, alley by Post Office, Fleetwood 8044 (TEX); 5 mi N of Edinburg, Runyon 1892 (LL); 10 mi W of Mission, Lundell & Lundell 9969 (LL); S. O. Johnson home south of Alamo, Clover 1481 (US); Santa Ana National Wildlife Regue, Fleetwood 7059 (TEX). Hood Co., 2 mi E of Tolar on US Hwy 377, Vest 6 (TAES); Top of Comanche Peak, near Granbury, Palmer 6529 (MO). Howard Co., Big Spring, Tracy 8219 (CM, GH, MO, TAES, TEX, US). Hudspeth Co., Ca 30 mi E of El Paso (Hwy 180), Warnock 13819 (LL, TEX); 5 mi W of Van Horn, Beach Mts., Warnock 13635 (LL, TEX). Humble Co., Jesse Jones County Park N off of Hwy 1960 W of Humble, Rolling s.n. (BRIT). Jeff Davis Co., 10 mi NW of Valentine on US Hwy 90, Spellenberg & Spellenberg 3690 (NY); Valentine, Gooodding A-9747 (ARIZ); 12 mi NW of Ft. Davis, Gould 7657 (BRIT, MO, TAES); 5 mi NE of Juno, Warnock & McBryde 15066 (LL); Mitre Peak Girl Scout Camp at Fern Canyon, Keough 58 (TEX); Limpia Canyon, 10 mi N of Fort Davis, Innes & Moon 1107 (TEX, US); Frazier Canyon, Davis Mts., Cory 12074 (GH); Davis Mts., 7 mi from cut-off to McDonald Observatory, Hwy 118, Lundell & Lundell 14227 (LL, US); Davis Mts., Little Aguja Canyon, Palmer 34549 (NY); 0.25 mi below McDonald Observatory turnoff along Hwy 118 NW of Ft. Davis, Hatch & Morden 4330 (MO, UC); Along Hwy 118 by rest stop; 1/4 mi E of turnoff to McDonald Observatory, Morden & Hatch 77 (TAES); 19.3 km NW of Ft. Davis on TX 118 & 61.3 km S of Kent, Peterson & Annable 10407 (BISH, K, US). Jim Wells Co., 5 mi S of Alice on Hwy 281 & 7 mi W of Ben Bolt, La Capita Research area, Coffey 806 (TAES); ditto, Coffey 820 (RM); NE side of SE arm of Naval Auxillary Landing Field, Orange Grove, Carr 11459 (TEX); 5.0 mi S of Alice & 7.0 mi W of Ben Bolt at the La Copita research area, Whitley 33 (US). Karnes Co., Cemetery Rd., Karnes

City, Johnson 1051 (TAES); 2.3 mi NE of Karnes City, Johnson 991 (TAES, TEX). Kenedy Co., King Ranch, Norias Division, Lundell 14985 (LL, UC, US); Just N of Mifflin, Kenedy Ranch, Johnston 541575 (TEX); SW of El Toro Island, Tharp 48348 (TEX); El Toro Island, Tharp 49233 (NY, TEX); El Toro Island, Atnip 48–407 (TEX); 3 mi S of Norias, off Hwy 77, Lundell 14958 (ARIZ, LL, UC, US). Kendall Co., Boerne, Palmer 10860 (MO). Kerr Co., Kerr Wildlife Mgmt. Area, East Bobcat Pasture, Sanchez 4077 (BRIT); Mt. Tivy, Kerrville, Cory 50473 (BRIT, MICH, NY, US); 10 mi N of Hunt on Kerr Wildlife Mgmt. Area, Coffey 40 (TAES); 3 mi W of Kerrville, May 5517 (BRIT, TAES); 11 mi W of Hunt on FM 1340, Hyman 56 (TAES); Kerr Wildlife Mgmt. Area, Copeland 20 (TAES); Kerr Management Area, Hendley 33 (TAES). Kimball Co., 8 mi SE of Junction, Gould 9681 (BRIT, TAES, TEX, UC). King Co., 7 mi E of Guthrie along the South Fork of the Wichita Riv., Higgins 6255 (NCU, NY); South Llano River State Park, 0.1 mile S of park headquarters along gravel road leading into Buck WMA, near plot #3, Sanchez 1035 (BRIT). Kinny Co., Kickapoo State Park, Keeney 8708 (BRIT). Kleberg Co., Along Hwy 141 ca 3 mi W of Kingsville, Riherd 52–2 (TAES); 8.3 mi NE of Riviera, Parks & Cory 16968 (TAES); 1 mi N of Kingsville, Brothers 69 (TAES); King Ranch, Kingsville, Perdue 1623 (ISC, LL); 3.2 mi SE of Kingsville, Cory 16969 (GH, TAES). Live Oak Co., 7.6 mi S of George West, Johnston 542072 (BRIT, TEX). Llano Co., 17.4 mi W of Llano, Gould 8380 (TAES, UC); Enchanted Rock State Park, 19 mi N of Fredericksburg, Kast 78 (TAES); 4 mi S of Llano on Hwy, Heinemann 63–21 (TAES); Black Rock Park, Box 113 (TAES); Lower slopes of Enchanted Rock, Butterwick & Lamb 3360 (TEX); Just W of Enchanted Rock, Butterwick & Lamb 3089 (TEX); Ca 1 mi NE of Enchanted Rock, just W of Sandy Ck., Butterwick & Lamb 3296 (TEX); Enchanted Rock, Tharp s.n. (TEX). Lubbock Co., Lubbock, Texas Tech grass garden, Caddell s.n. (BRIT); Lubbock Lake Landmark State Historic Park, Launchbaugh s.n. (BRIT). Mason Co., Ca. 6 mi N of Mason on old Katemcy Rd., Waller 2156 (TAES); Katemcy, Ruegner s.n. (TAES); 13 mi W of Mason near road to Junction, Gould 5702 (TAES). Maverick Co., 8 mi N of Quemado, Gould 11319a (UC); 8 mi N of Quemado, Gould 11319b (TAES, UC, US). McMullen Co., Off Hwy 5.2 mi W of Tilden, Swallen 10008 (US); 9 mi W of Tilden on Rd. No. 63, Tharp & Johnston 541771 (TEX); 2.5 mi S of Tilden on Rd. no. 173, Tharp & Johnston 541779 (TEX). Nueces Co., Corpus Cristi, North Beach, Jones 1336 (FSU); 5 mi NW of Corpus Cristi, Parks & Cory 16970 (TAES); 2.5 mi S of Violet, Bockholt 52–22 (TAES); 0.4 mi W of junction roads 666 & 624 N of Banquete, Johnston 542329 (TEX); vacant lot on North Beach, Corpus Cristi, Jones 1336 (BRIT). Mitchell Co., Caliche Hill, NE 1/4 sec. 17, S.P.R.R. Block 18, Pohl 4622 (BRIT). Oldham Co., Adrian, waste area & ditches bordering Hwy on N side, Brooks & McGregor 16524 (GA, KANU, RM). Palo Pinto Co., Mineral Wells, Reed 34873 (TAES); Possum Kingdom State Park, near headquaters, Correll & Correll 24120 (LL, MO). Pecos Co., 6 mi W of Longfellow, Sanderson Canyon, Warnock 11848 (BRIT, LL); 29 mi W of Sheffield, Gould 7215 (TAES, TEX); Ca 6 mi N of Ft. Stockton, Warnock 46783 (BRIT, NA, TAES, TEX); “Roadside”, Tharp 43A71 (GH, MO, RM, UC, US). Presidio Co.,

Along US Hwy 67 11.2 mi S of Marfa, Spellenberg & Spellenberg 3695 (NY); 1/4 mi N of Solitario Peak, Johnston 3435 (TEX); Ridge just W of mouth of Musgrave Canyon, Tierra Viejas, Hinckley 1940 (GH, TEX); Ca. 1 mi W of mouth of San Antonio Canyon, Butterwick & Lott 3845 (LL); Along Cibolo creek near large Hwy bridge at Presidio, Warnock 96 (TEX, US); About 10.5 mi SE of Valentine on US Route 90, Van Devender s.n. (ARIZ 238886). Randall Co., Palo Duro Canyon, ca. 2 mi NE of Canyon off Interstate-87, Higgins 11374 (NY); S of Canyon, along creek bottom & breaks, Higgins 18579 (NY); Just E of Canyon near the water tower, Higgins 16974 (NY); Coyote Springs, Palo Duro State Park, Cory 50325 (BRIT). Reeves Co., Along US Hwy 290, 1 mi E of jct of US Hwy 80, Johnston 3285 (TEX); Balmorhea, Bayles 15420 (GH, TAES). Refugio Co., 8.5 mi SW of Woodsboro, Hill 7824 (TAES); Along Hwy 77, 0.7 mi N of the Aransas Riv. Crossing, Hill 7837 (TAES). San Patricio Co., Near entrance to Lake Corpus Cristi State Park, Gould 10971 (TAES); 7 mi S of Taft, Jones 1049 (BRIT); Lake Corpus Cristi State Park near Mathis, Brown 9525 (ARIZ). San Saba Co., 2 mi S of San Saba, Smith 24 (TAES); 20 mi SW of San Saba on Hwy 501, Hatch & Briggs 1206 (TAES); US Hwy 45, 4 mi N of Richland Springs, England & McCart 9135 (LL, TAES); Coleman Ranch, 3 airline miles SE of San Saba, Cory 58254 (BRIT). Schleicher Co., 11–3/4 mi N of Eldorado, Cory 52507 (BRIT, MICH). Scurry Co., 5 mi N of Fluvana, Correll & Johnston 17200 (LL, US); Caprock, ca. 4 mi N of Fluvana, Correll 15170 (BRIT, LL, MO, NY). Shackelford Co., Fort Griffin State Park, 9/10 mi W of south entrance, Cory 58428 (BRIT). Starr Co., 0.7 mi E of Rd. No. 755 on the side road to McCook (Hidalgo Co.), Tharp & Johnston 541895 (TEX). Sterling Co., Hill, Tharp s.n. (ARIZ 31152). Stonewall Co., 13 mi S of Aspermont & 3 mi S of Double Mt. Fork of Brazos Riv., on road to Hamlin, Johnston & Walker 6772 (LL). Sutton Co., Sonora branch of TAMU Experimental Station, Tunnell 53 (TAES); 13 mi W of Sonora, Gould 9691 (BRIT, TAES, UC). Tarrant Co., US Hwy 287 X Eden Rd., Snowden 915308 (TAES); Arlington, US Hwy 287 N-bound access road, between Eden & Sublett overpasses, Snowden 915218 (TAES). Taylor Co., Buffalo Gaps Estates ca 12 mi S of Abilene, Henderson 61–912 (FSU); Camp Barkeley, Tolstead 5812 (BRIT, TAES); 4 mi NE of Lawn, Mahler 4115 (TAES); Abilene State Park, ca. 20 mi S of Abilene, Henderson 63–988 (BRIT, TEX). Terrell Co., 9 mi N of Dryden, Gould 9709 (TAES, UC); 6 mi E of Sanderson, Warnock 6817 (BRIT, LL, TEX); Blackstone Ranch, rocky mesa slopes 15 mi S of Sheffield, Webster 172 (TEX); 26.5 km NW of Lantry, 37.0 km SE of Dryden on U.S. 90, Reinga 2004-740 et al. (ARIZ); 4 mi W of Sanderson, Shinners 17380 (BRIT). Throckmorton Co., W. Matthews' Lambshead Ranch, ca. 20 km S and 15 km N of Throckmorton, Cornelius 1168 (BRIT); Ca. 2 km S and 17 km E of Throckmorton (Jimmy Mieng's Elm Valley Ranch), Cornelius 1704 (BRIT). Tom Green Co., Hwy 2288, 5 mi from intersection with Hwy 87, Hoover 70 (TAES). Travis Co., NE of intersection of FM 2222 & Lakewood Drive, Carr 4001 (TAES); 0.1 mi W of Oasis Bluff Rd. from its junction with Bullock Hollow near the community of Marshall Ford, Jones & Jones 1860 (TAES); Brackenridge Field Station, Austin, Baird 3772 (KANU); Near Bull Ck. Lodge, along FM 2222, Mears 997 (TEX); ca. 1.5

airmiles due N of W end of Tom Miller (Lake Austin) Dam, Carr 6161 (BRIT); McDonald Ranch, Higdon 121 (TEX, US); Onion Ck., Moon 134 (TEX); Watkins Ranch, Tharp et al. 49033 (KANU, TEX); Colorado Riv. flood plain, Armer 5301 (TEX); Mt. Barker, Austin, Innes 171 (GH). Uvalde Co., Montell, Palmer 13016 (UC, MO). Val Verde Co., 5 mi E of Comstock on Hwy 90, Zuberbueler 73 (TAES); 11.2 mi W of Comstock on US Route 90, Van Devender 84-653 et al. (ARIZ); 9-1/4 mi N of Del Rio, Parks & Cory 20831 (TAES); 3 mi N of Juno, Gould 9954 (TAES); Seminole Canyon State Historical Park, Labus 4 (TEX); Devil's Riv., Tharp 43072 (TEX); Devil's Riv. bridge on Hwy US 90 (W of Del Rio), Gould 9748 (TAES, TEX); 5 mi E of Juno, Warnock 15066 (TEX). Webb Co., N of Laredo, Silveus 7557 (ARIZ, BRIT). Williamson Co., 0.5 mi N of Round Rock, Gould 8420 (TAES, UC). Winkler Co., Along Concho Bluff, 20 mi NE of Kermit, Collins 667 (BRIT). Young Co. Graham, Reverchon 3451 (GH, MO, NY, US). Zapata Co., 15 mi N of San Ygnacio, Cory 35815 (TAES).

***Disakisperma eleusine* (Nees) P. M. Peterson & N. Snow, Annals Bot. 109: 1327. 2012.**
http://species-id.net/wiki/Disakisperma_eleusine

Figure 3A–P

Diplachne eleusine Nees, Fl. Afr. Austr. 255. 1841. *Uralepis eleusine* (Nees) Steud., Syn. Pl. Glumac. 1: 248. 1854. *Tridodia eleusine* (Nees) T. Durand & Schinz, Consp. Fl. Afr. 5: 877. 1894. *Leptochloa eleusine* (Nees) T. A. Cope & N. Snow, Novon 8: 78. 1998.

Type. SOUTH AFRICA, Katrivierspoort, JF Drège 3906 (lectotype: B!, designated by Snow (1998a); isolectotype: P!).

Description. Perennials. Culms 50–130 cm tall, 2.5–4.0 mm wide at base, round, erect, rarely geniculate and rooting from lower nodes, arising from fibrous roots or sometimes from a knotted crown, branching or not; nodes glabrous; internodes 5–30 cm long, soft, hollow. Leaf sheaths longer or shorter than the internodes, round or slightly flattened, glabrous on the sides and margins; collar green or tan; ligules 0.8–1.4 mm long, membranous, often dark brown near base, apically truncate, erose or fimbriate; blades (3–) 15–30 cm long, 5–7 mm wide, caudate, linear, flat but becoming involute on edges, glabrous to minutely but densely scabrous above, nearly glabrous to moderately scabrous below, not disarticulating at base, midrib prominent. Panicles to 65 cm long, 1.5–3.0 cm wide, exserted at maturity; branches (1–) 3–9, (3–) 5.5–10.5 cm long, alternate along rachis, steeply ascending to erect, rigid, minutely scabrous, the axils glabrous or with a few short hairs. Spikelets 4.7–9.2 mm long, pedicels mostly less than 0.5 mm long, usually imbricate, 5–8 (–10)-flowered; callus glabrous; lower glumes 2.8–4.1 mm long, membranous, narrowly ovate, scabrous on midnerve, acute; upper glumes 2.9–5.3 mm long, membranous, ovate, scabrous on midnerve, acute; lemmas 3.2–4.2 mm long, 3- or sometimes 4–5 nerved (at least basally), membranous,



Figure 3. *Disakisperma eleusine* (Nees) P.M. Peterson & N. Snow **A** habit **B** culm and inflorescence **C** sheath, ligule, and blade, ventral view **D** branch of inflorescence **E** spikelet **F** floret, ventral view **G** clavicorniculate hairs **H** lower glume **I** upper glume **J** lemma, dorsal view **K** palea, ventral view **L** palea, dorsal view **M** stamens and pistil **N** lodicules **O** caryopsis, dorsal view **P** caryopsis, ventral view. Drawn from Schweickert 1896 (US).

ovate, smokey white, bronze, light green, lateral nerves distinctly raised, sericeous along lower half of lateral nerves, midnerves and often between nerves, the hair tips clavicorniculate, apex obtuse and sometimes bifid, awnless and often erose, hyaline; paleas subequal to lemma, elliptic to ovate, membranous, with short clavicorniculate or nonswollen hairs between lateral nerves, apex broadly acute. Anthers 0.9–1.0 mm long, brown or yellow. Lodicules 0.7–0.8 mm long. Caryopses 1.7–2.0 mm long.

Leaf anatomy. Ellis (1977) reported C₄ NAD-ME anatomy for *Diplachne eleusine*, which we confirm here. Primary, secondary, and occasionally (e.g., Snow & Burgoyne 7021 [MO]) tertiary bundles are evident. Midrib present but lacking associated lacunae. Primary bundles easily distinguished from secondary bundles; tertiaries separable from secondaries based on much smaller diameter and absence of associated sclerenchyma girders. Primary and secondary bundles in fresh material projecting somewhat adaxially but not abaxially. Outer bundle sheath cells of primary and secondary bundles interrupted adaxially and abaxially. Extension cells occurring adaxially above primary and secondary bundles but more so over primaries. Sclerenchyma girders present adaxially and abaxially above primaries and secondaries (more so adaxially) but lacking from tertiaries. Colorless cells lacking between adjacent bundles; chlorenchyma continuous between all bundles. Bulliform cells between primary and secondary bundles but adaxial (above) to tertiary bundles [Vouchers: Snow & Burgoyne 6941 (MO), 7021 (MO); photographs of cross sections seen by the first author and housed at PRE: Ellis 2057, 2058, 2059, 2106, 3546, 3868].

Stem anatomy. Outer (subepidermal) ring of sclerenchyma present. Broadly triangular sclerenchyma girders (broadest near epidermis) arising from outer ring and projecting inwardly to connect with outermost ring of vascular bundles. Assimilatory tissue present, partially ringed by Kranz-like cells, in distinct patches between adjacent vascular bundles and associated triangular girders. Inner ring of sclerenchyma present, continuous, and several layers thick. Inner ring of vascular bundles scattered in the remaining cortical tissue but these mostly close to but not touching inner sclerenchyma ring. Cortical vascular bundles surrounded by sclerenchyma at least around their xylem-bearing portion [Voucher: Halse 29 (MO)].

Chromosome number. Not known.

Phenology. Flowering year-round.

Distribution. **Native:** Africa south of about latitude 20°S and most common in South Africa; growing in heavy clays to sandy soils, in rocky open sites or disturbed woodland or bushveld, infrequent to common. Elevation ca. 300 to 2000 m. (TDWG: BOT, MOZ, NAM, CPP-WC, CPP-EC, CPP-WC, TVL-GA, TVL-MP, TVL-NP, NAT-OO, SWZ). **Non-native:** None known.

Comments. *Disakisperma eleusine* resembles the partially sympatric *D. yemenicum*. Both species have relatively few and erect panicle branches that bear moderately to tightly overlapping spikelets, florets with distinctly raised lateral nerves, lemmas and upper glumes occasionally with basal remnants of extra nerves, clavicorniculate hairs and similar caryopsis morphologies (Phillips 1982; Snow 1996, 1998b). *Disakisperma yemenicum* is distinguished by having lemmas that are cartilaginous below with invo-

lute margins, leaf blades with scattered delicate, long hairs (3–5 mm long), smaller anthers 0.2–0.3 mm long, and shorter paleas (1/2–2/3 as long as the lemma). The base of the ligule is often dark brown in *D. eleusine*.

Conservation status. Least Concern (IUCN 2010).

Etymology. The epithet *eleusine* probably was used to suggest that the species resembles *Eleusine* Gaertn.

Vernacular name. South African sprangletop (Snow 1997). Suggested name: Southern African Jacobsgrass.

Specimens examined. Botswana. Central: Seleka Ranch, Hansen 3373 (GABS). Mozambique. Lourenco Marques: Maputo, regiao de Changalane, próx. da Cabeca do Elefante, Myre & Carvalho 1847 (K). Maputo: Semi-riverine thicket, Hornby 2609 (K). Sul do Save: circ. Magude, entre Macaena e Panjano, Myre & Balsinhas 1572 (CANB, K); Prox. da povoacao da Moamba, Myre & Balsinhas 1628 (I); between Moamba & Boane, Schweichert 1896 (B, K, S, US); Entre Moamba & Ressano Garcia, Marques 2209 (K); Maputo, arredores de Catuanac, Myre & Carvalho 1434 (K). Namibia. Ausdauernde, aufrechte bis 1.30 m hohe Horste, Giess 8422, (M); ca. 25 mi E of Sesfontein, De Winter & Leistner 5884 (PRE). South Africa. Cape Districts, Sekoekoienland, Stellenbosch, langs Olifansrivier, du Toit 124 (PRE); Dist. Kingwilliamstown, Kei Rd., Ranger 109 (PRE); Ft. Beaufort, Giffen 1630 (MO); Haha Haha Lagoon, Ellis 2106 (PRE); Fort Beaufort Distr., Killians's grave, 5 mi NW of Fort Beaufort, Story 3875 (K); Dist. Queenstown, 38 mi SE by E of Queenstown, Acocks 17946 (K); Near Riv. Kei, Swallen 10575 (US); Albany [now merged with Cacadu], Lindsleath (sp.?) s.n. (US). East Cape District: Transkei, near the Kekau River, Drège 1840 (K). Kwazulu–Natal: Umzivulu, Schlechter 6424 (K); Ngotshe Distr., Farm Welcome, 42 km from Pongola on the road between Magudu & Candover, Koekemoer 125 (PRE); Louwsburg Distr., Itala Nature Reserve, Rangers house, Brown & Shapiro 166 (PRE); at False Bay, Godfrey & Bayer SH–1472 (PRE, US); Vryheid, Pole Evans 2641 (US); Slopes of Umkomas Valley near Josephine Bridge, Otto 19993 (PRE); Ca 8.2 km S of Golela along hwy to Pongola, before "T" junction, Snow & Burgoyne 6954 (MO, PRE); Mkuze Game Reserve, A.J. Oates 1242 (US); Mkuze Game Reserve, Mahlobeni area, Snow et al. 6982 (MO, PRE); Ca 300 m from "T" intersection along dirt road leading to headquarters of Mkizi Game Reserve, from dirt road leading S from town of Mkizi, Snow & Burgoyne 6963 (MO, PRE); Zululand, Umfolozi Game Reserve, Guy & Ward 7 (PRE); Zululand, Prinshof Experimental Station, Pretoria, Phillips & Goossens 8785 (MEL, PRE, US); Zululand, Hluhluwe Game Reserve, Huntley 1735 (MO); Umtambanana, Halse 29 (MO, U); Nkansini, Tugela Valley, Smook 1817 (K, MO); N Weenen on Muden Rd, Acocks 13458 (BM, K); Inguavuma Dist., Ndumu Game Reserve, Pooley 1040 (K). Limpopo: Kruger N.P., Schÿff 3968 (K); Lebowa, Blouberg Mt., Farm Buffelshoek 261 on the SW side of the massif on the Blouberg geological series, Smook 7371 (PRE); Kruger N.P. 13 mi E of Skukuza, de Winter & Codd 529 (BM, K); Kruger N.P. 8 mi E of Skukuza, de Winter & Codd 524 (BM); Kruger N.P., 10 km east of Satara on Satara–Nwanedzi Rd. near Msasane Windmill, Ellis 3546 (PRE); Blaauwberg Tin Mine, Schweickerdt

2011 (B, BM, US); Lebowa: Stellenbosch, 56 km van Burgersfort op Pietersburg pad, draai NO af vir 10 km, du Toit 1001 (PRE); Noordelike kant van Soutpansberg, Nel 320 (PRE). Mpumalanga: Loskopdam Nature Reserve, along dirt road leading west from administration buildings, ca 2 km along road, Snow et al. 6941 (MO, PRE); Loskop Dam Nature Reserve, Ellis 2058 (PRE); Blyde Riv. Canyon Nature Reserve, north end of nature reserve, just off of Hwy R532, Snow et al. 7021 (MO, PRE); Bellevue, SO van Steilloopbrug, du Toit 161 (PRE); Distr. Potgietersrust, Springbuck Flats, de Winter 2331 (PRE). Swaziland. Farm Mlawula, below western edge Lubombo Mts, Upper Nkumbane Valley, small dam near Cyrildene fence, Culverwell 298 (PRE); 2–3 mi W of Border (with Natal) at Cecil Mack Pass, Maguire 8398 (M); Mlawula Nature Reserve, SARA campsite, Braun 119 (PRE).

***Disakisperma obtusiflorum* (Hochst.) P. M. Peterson & N. Snow, Annals Bot. 109: 1327. 2012.**

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

Figure 4A–O

Leptochloa obtusiflora Hochst. Flora 38: 203. 1855. *Eleusine obtusiflora* (Hochst.) Blatt., Rec. Bot. Surv. India 8: 505. 1936.

Type. ETHIOPIA, W. Schimper in Herb. Buchinger 1204 (holotype: STR; isotypes: B!, P!, S! co-mounted with a specimen of *Trigonochloa uniflora* (Hochst. ex A. Rich) P.M. Peterson & N. Snow).

Description. Perennials. Culms 45–200 cm tall, 1.2–5.0 mm wide at base, round, erect to sprawling, from fibrous or knotted root crowns sometimes bearing short cataphylls (rhizomatous in the opinion of some, e.g. Chiovenda 2585 [US]), often branching (sometimes abundantly so; e.g., Glover & Gilliland 298 [US]); nodes glabrous; internodes (1.5–) 3–35 cm long, soft, hollow. Leaf sheaths longer or shorter than the internodes, mostly round, glabrous or sparsely hairy near apex, the margins glabrous; collar tan or maroon; ligules 1.7–2.2 mm long, membranous, often somewhat lacerate, apically truncate and erose; blades 7–37 cm long, up to 12.5 mm wide, caudine, linear, flat but drying involute, mostly glabrous but sometimes sparsely pilose at the base of blade to minutely but densely scabrous above, nearly glabrous to minutely but densely scabrous below, not disarticulating at base, midrib prominent. Panicles 28–65 cm long, 3–8 (–12) cm wide, exserted at maturity; branches (4–) 9–18, (2.5–) 9–13 cm long, alternate along the rachis, steeply ascending to erect, somewhat flexuous, minutely scabrous, the axils shortly pilose. Spikelets 3.7–6.5 (–8.5) mm long with 5–10 (–15)-flowered, pedicels to 1.2 mm long, imbricate about halfway near base of branches to tightly at branch tips; callus glabrous; lower glumes 1.5–2.9 mm long, membranous, narrowly ovate or occasionally ovate, scabrous on midnerve, acute; upper glumes 1.8–2.9 mm long, membranous, ovate, scabrous on midnerve, acute; lemmas 2.2–2.8 (–3.0) mm long, 3-nerved (rarely 4–5-nerved above base), membranous,



Figure 4. *Disakisperma obtusiflorum* (Hochst.) P. M. Peterson & N. Snow **A** habit **B** culm and inflorescence **C** sheath, ligule, and blade, ventral view **D** branch of inflorescence **E** spikelet **F** floret, ventral view **G** lower glume **H** upper glume **I** palea, dorsal view **J** lemma **K** lodicules and stamens enclosed in palea **L** palea, dorsal view **M** lodicules and stamens **N** caryopsis, dorsal view **O** caryopsis, ventral view. Drawn from Shantz 791 (US).

ovate, light brown, green, or maroon, the lateral nerves distinctly raised and usually bright green, sericeous along the lower ¾ of the nerves and between the nerves, the hair tips clavate or clavicorniculate, apex obtuse and sometimes bifid; paleas 2.0–2.3 mm long, membranous, ovate, sparsely short pubsecant on lower half between nerves or nearly glabrous, apex broadly acute. Anthers ca 0.7 mm long, yellow. Lodicules 0.2–0.3 mm long. Caryopses 1.4–1.5 mm long, 0.7–0.8 mm wide.

Leaf anatomy. Midribs are always present and the diameter of primary bundles exceeds that of the secondaries.

Stem anatomy. Culms with outer (subepidermal) and inner (cortical) sclerenchymatous rings. Other details uncertain [Voucher: *Harris & Tadres 2151* (MO)].

Chromosome number. $n = 20$ (Ammal 1955; voucher not seen).

Phenology. Flowering July through December.

Distribution. **Native:** India west to Saudi Arabia, Yemen and Somalia; south through Tanzania, and Angola; in a variety of semi-open or disturbed habitats in rocky areas or sandy to heavy soils, from sea level to 1900 m. (TDWG: ANG, BUR, CON, ERI, ETH, KEN, SAU, SOM, SUD, TAN, UGA, YEM. **Non-native:** IND (see comment below).

Conservation status. Least Concern (IUCN 2010).

Etymology. The epithet probably refers to the obtuse lemma apex.

Vernacular name. North African sprangletop. Somalia: Buldorle, Rareh. Suggested: African Jacobsgrass.

Comments. Herbarium specimens (and label descriptions) often indicate the panicle as nodding or pendulous, which contrasts with the more nearly erect panicle of the related *D. eleusine*, which *D. obtusiflorum* closely resembles, but which occurs farther. The collection of *Jackson 3977* (K) differs in its short stature, profuse branching, and short panicles that bear only 1–2 branches, which may reflect local grazing selection. Over ninety collections have been seen from Uganda, although not all are reported below.

The species evidently may occur in nearly pure stands and is known in abandoned cultivated areas. The label of *Greenway 2213* (US) indicates the species is “A useless fodder as it causes dysentery in cattle according to the Wapares.” Boonman (1993) reports that *D. obtusiflorum* is a potential species for reseeding denuded pasture.

Hooker (1896) clearly included *Poa maysorensis* Rottler ex Hook. f., nom. inval., in synonymy of *D. obtusiflorum*, and merely cited the Rottler name as being in manuscript. Hooker (1896) suggested that the presence of the species in southern India in Kochi (“Cochin”) was an introduction due to heavy trade between that port and Africa.

Specimens examined. Angola. Loanda: Maianga d’El Rei, Welwitsch 7282 (BM); On the rocky banks of Riv. Long at Capolo, Gossweiler 8281 (K, US). Burundi. Bubanza: Rugombo, Reekmans 6486 (B, MO, PRE). Bujumbura: Gitaza, Reekmans 4010 (MO). Democratic Republic of the Congo. Sud-Kivu. Kabare, Bequaert 5348 (K); Parq. Nat. Albert [=Virunga Nat. Park], Rurindi, Lebrun 7943 (K, M, MO) & Rurindi, Lebrun 7784 (MO, NY). Orientale. Terr. Mahagi, Plaine Iswa—village Awo-ra, Taton 1246 (MO). Eritrea. Northen Red Sea: Lungo il Torrente Haddas, Pappi 2585 (G, MO, P, US). Ethiopia. Harrar: 35 km along the road from Dire Dawa to

Erer Gota, De Wilde 6449 (M, MO). Gamu Gofa: 72 km S of Soddu on road to Arba Minch, 50 km from Arba Minch, Gilbert et al. 8860 (K). India. Kerala: Cochin (=Kochi), Rottler s.n. (K). Tamil Nadu: Coimbatore, Narayana 1929 (NY); On the way to Areakhaldi, Raju & Napanatham 4763 (K). Madras [Chennai], Janaki Ammal 1154a (K); Masanagudi, The Niligris, Barber 2656 (US). Kenya. Coast Province, Kwale, near Taru, between Samburu & Mackinnon Rd., Drummond & Hemsley 4192 (B); Tsavo N.P. West, 7 km S of Mtito Andei, Belsky 527 (BH); Kitovo, Taveta, Nye 42 (BM); Mtwapa, Thorold 2002 (K); Vipingo 20 mi N of Mombasa, Verdcourt 1101 (K, MO). Mombasa, Napier 6370 (K, PRE); Tsavo N.P. East, Greenway & Kanuri 12836 (K, P); Tsavo N.P., N end, Heady 1759 (UC); Gazi, along coast, Heady 1376 (MO, UC); Galole [=Hola], Makin 128 (P). Eastern Province, Kiboko Range Research Stn., near Makindu, Ndegwa 579 (MO); Near Makindu Riv.,... Kiboko Range Research Stn., Ndegwa 474 (MO); Kibwezi, McCallum Webster K164 (K); Kilifi Distr., N of & just below Jilore Forest Station, Perdue & Kibuwa 10124 (K, NA); Maktau, Hitchcock 24697 (K, US). Nairobi Province, Nairobi, Hitchcock 24822 (US); Nairobi, Lyne Watt 18 (US). Nyanza Province, Kisumu, Hitchcock 24865 (K, US). Rift Valley Province, K1, Mathew's Range [=Lenkiyio Hills], Gachathi 440 (B); Southern Turkana at Namorutung'a near Lokori, Mwangangi & Gwynne 1161 (MO); Kitale grass nursery, Heady 1474 (MO, UC); Turkana Distr., Oropoi Valley, Liebenberg 27 (MICH, PRE, US). Saudi Arabia. Wadi Maraba, foot of Raidah Escarpment, Collenette 8764 (K); Jizan–Abha Rd., ca. 20 km from Abha, Chandhanj 7262 (K). Somalia. Government House grounds, Hargeisa, Glover & Gilliland 17 (BM, K); Within a radius of ca. 5 mi of the Hargeisa Stn, Farquharson 29 (K); 29 km SW on coast road from Mogadishu airport, then inland 2.5 km, Kuchar 17708 (K); Burran, Erigavo Distr., McKinnon S122 (BM, US); Between Wasdere & Walwal, Glover & Gilliland 398 (BM, P, US); Wobleh, Gillett 4584 (K, P); Tugdheer region, 6 km NW of Borao, Hansen & Heemstra 6105 (K). Hargesia, Gillett 4059 (K, P, S). Sudan. Kurdufan Province, Rahad, 1 hour S of J. Hadadiad, Taganor Wilderness, Michelmore s.n. (K). Red Sea Province, Slopes Jebel Hamoyet, Red Sea Hills, Jackson 3977 (K). Tanzania. Arusha Region, Lake Manyara N.P., Near Mbagaya Riv.-Ndabash, Greenway & Kanuri 11280 (K, PRE); Serengeti N.P., Serengeti Research Institute, Belsky 144 (BH, MO). Kilamanjaro Region, Moshi, GB Wallace 1190 (NY); Mwanga District, Peterson, Soreng & Romaschenko 24198 (DSM, US). Lindi Region, Lutamba–See, 40 km westlich Lindi, Schlieben 5945 (M, S); Lindi, H J Schlieben 5945 (M). Man-yara Region, Mbagaya Riv.-Ndabash, Lake Manyara N.P., Greenway & Kanuri 11280 (PRE). Mara Region, T1, Klein's Camp to Bologonja Riv., Greenway 10666 (K); Musoma Distr., Seronera, Greenway 9971 (K, US). Moshi Region, Pangani Distr., Kikokwe area, Bond 84 (P); Pangani Distr., Jassini in sandy hollow, Milne–Redhead & Taylor 7297 (K, US); Moshi, Hitchcock 24557 (US); Vicinity of Moshi, Kiboscho Rd., Piemeisel & Kephart 405 (US); Moshi Town, B Mhoro 1868 (MO); Moshi Kilimanjaro, Shantz 791 (K, US). Mwanza Region, Lake Prov., Nyegezi, Bunegeji Chiefdom, Tanner 1060 (K, MICH, NY, UC). Tanga/Kilimajaro Region, Pandani River, Peterson, Soreng & Romachenko 24243 (DSM, US). Tanga Region, Korogwe Distr.,

Magunga Estate, Faulkner 961 (A, K); 5 km W of Tonibombo, Peterson, Soreng & Romaschenko 24211 (DSM, US); Muheza, Hitchcock 24540 (US); Mkaramo, Mkwaja Subchiefdom, Pangani Distr., Tanner 2346 (K, NY, UC). Zanzibar Central/South Province, Kisuani [Airport], Greenway 2213 (K, US). Unknown Province: T3, Kwamarukanga, Magogo 344 (K); Saira, HG Faulkner 3775 (K, P). Uganda. Central Region, Mengo-Kisenyi, Kyadondo, W. Mengo District, Rwaburindore 2134 (MO). Eastern Region, Buyonjo, Lake side, Busogo, Maitland 1100 (US); Serere, at Robori, Maitland 1345 (B, K, US). Western Region, Katwe Ruwenzori, Maitland 963 (B); Butiala, Lake Albert, Thomas 4086 (K); Mohokya Toro, AS Thomas 2757 (K). Yemen. Between Beni Omer & Barakain, Hoogariah, Wood 1407 (BM, K); Between Taiz & Sharab (Roona), Wood Y/75/966 (BM); Hadia, Wood Y/75/797 (BM).

***Disakisperma yemenicum* (Schweinf.) P.M. Peterson & N. Snow, comb. nov.**

urn:lsid:ipni.org:names:77131997-1

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

Figure 5A–Q

Eragrostis yemenica Schweinf., Bull. Herb. Boissier 2 (App. 2): 41. 1894. *Cypholepis yemenica* (Schweinf.) Chiov., Annuario Reale Ist. Bot. Roma 8(3): 357–358. 1908.

Eleusine yemensis (Schweinf.) Chiov., Ann. Bot. (Rome) 10: 410. 1912. *Coelachyrum yemenicum* (Schweinf.) S.M. Phillips, Kew Bull. 37(1): 159. 1982.

Leptochloa appletonii Stapf, Bull. Misc. Inform. Kew 6: 223. 1907. TYPE: SOMALIA.

Golis Range, Drake-Brockman 147 (lectotype: G (photo!), designated here).

Eragrostis diplostachya Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 100, t. 58, f. 1. 1929. TYPE: TANZANIA. Lushoto District, Buiko, Peter 11083 (lectotype: B designated by S.M. Phillips, 59. *Cypholepis*, Gramineae, part 2, Fl. Trop. E. Africa 250. 1974; K-photo!).

Type. YEMEN. Arabia Felici, 2 Feb 1889, G.A. Schweinfurth 1332 (lectotype: G-photo! designated here, S.A. Chaudhary, Grasses of Saudi Arabia 274. 1989, earlier cited no specific herbarium). We are choosing the G specimen as the lectotype because it is easily seen (electronically), was previously selected by Chaudhary (1989), and the original collection at B was destroyed.

Description. Perennials. Culms 30–100 cm tall, 1–2 mm wide at base, usually flattened, erect, infrequently decumbent or sprawling, arising from fibrous roots, culms unbranched or only as tillers from very base; nodes glabrous; internodes 4–14 cm long, soft, hollow. Leaf sheaths longer or shorter than the internodes, round or slightly flattened, glabrous on the sides and margins; collar green or tan; ligules 0.5–1 mm long, membranous, erose or lacerate, apex truncate; blades 7–32 cm long, 2.5–5.5 mm wide, caudine, linear, flat but becoming folded to loosely involute, scaberulous with scattered, delicate, straight hairs near base above, the hairs 3–5 mm long, glabrous to scaberulous below, often disarticulating at base, midrib prominent.



Figure 5. *Disakisperma yemenicum* (Schweinf.) P.M. Peterson & N. Snow **A** habit **B** sheath, ligule, and blade, ventral view **C** branch of inflorescence with glumes **D** spikelet **E** lower glume **F** upper glume floret, ventral view **G** floret, lateral view **H** floret, central view **I** lemma **J** palea with rachilla joint **K** palea, ventral view **L** pistil and stamens **M** caryopsis, lateral view **N** caryopsis, dorsal view **O** caryopsis, cross section **P** caryopsis, ventral view. Drawn from Peterson, Soreng & Romaschenko 24254 (US).

Panicles 3.5–19 cm long, 1.0–3.0 cm wide, exserted at maturity, composed of 2–8 racemosely arranged branches; branches 2–7 cm long, alternate along rachis, rachis often somewhat zig-zaged from each spikelet insertion to the next, steeply ascending to erect, rigid, axis scabrous. Spikelets 5–10 mm long, pedicels mostly less than 0.5 mm long, usually imbricate, 7–12-flowered; callus glabrous; glumes 2–3.8 mm long, subequal, 1-nerved, membranous, lanceolate to narrowly ovate, scabrous on midnerve, the midnerve dark green; apex acute to obtuse; rachilla joint cartilaginous and expanded above; lemmas 2.5–4.7 mm long, usually 3-nerved, membranous above, lower margins cartilaginous and involute, ovate, pale green with dark green nerves, often tinged with dark or olive-green, glabrous above and appressed pilose on lower half, the hairs clavicorniculate, apex obtuse to subacute, awnless; paleas 1/2–2/3 as long as the lemma, ovate, longitudinally bowed-out, the keels ciliolate, dorsal surface glabrous or with appressed clavicorniculate hairs on the lower half, apex obtuse. Anthers 0.2–0.3 mm long, yellowish. Lodicules about 0.2 mm long. Caryopses 1.2–1.5 mm long, 0.7–0.9 mm wide.

Leaf anatomy. Watson and Dallwitz (1992) reported C₄, XyMS+ anatomy with centripetal chloroplasts. Midribs conspicuous with colorless cells, having a conventional arc of bundles (a large bundle, flanked on each side by two smaller bundles). All vascular bundles accompanied by sclerenchyma (Watson and Dallwitz 1992; Snow unpublished). Bulliforms present in simple fans.

Stem anatomy. Not known.

Chromosome number. Not known.

Phenology. Flowering July through December.

Distribution. Native: Saudi Arabia, Oman, Yemen, Eritrea, Ethiopia, Somalia, Kenya, Tanzania, and South Africa; growing in *Acacia* and miombo woodlands on dry, shallow, often stoney soils among rocks, often in disturbed habitats (Phillips 1974b). Elevation 250–2100 m. (TDWG: CPP, ERI, ETH, KEN, OM, SAU, SOM, TAN, YEM.)

Non-native: Not known.

Conservation status. Least Concern (IUCN 2010).

Etymology. The epithet refers to Yemen, the geographical origin of the holotype.

Vernacular name. Suggested: Yemen's Jacobsgrass.

Comments. *Disakispermum yemenicum* most closely resembles *D. eleusine* by virtue of the ascending to erect panicle branches, but the base of the lemma of *D. yemenicum* is cartilaginous, the base of the leaf blade adaxially has delicate straight hairs mostly 3–5 mm long, and its anthers are less than 0.5 mm long (vs. 0.9–1.0 mm in *D. eleusine*). We have examined relatively few specimens of *D. yemenicum* given that initial herbarium studies did not believe it was a part of *Leptochloa* s.l. (Snow 1997).

Specimens examined. Eritrea. Assaorta, A. Pappi s.n. (US); Ocule, A. Pappi 5239 (US). Kenya. 6 mi SW of Nairobi, Nairobi National Park, S.L. Hatch 4220 (TAES, US). Somalia. Buramo, J.B. Gillett 4872 (US); Daganyado, P.E. Glover & H. Gilliland 745 (US). South Africa. Cape Province, Boetsap Barkly West, A. Brueckner 143 (US);

Kimberley Div. M. Wilman s.n. (US); Farm Rosenthal Mopane, L.E.W. Codd 4455 (US); North Cape, A. Brueckner 1032 (US). Tanzania. Shinyanga Region, Serengeti National Park, Naabi Hill, Peterson, Soreng & Romaschenko 24254 (DSM, US).

Excluded names

Leptochloa digitatiformis Beetle, Phytologia 52: 14. 1982. TYPE: Mexico, Sonora, Mpio. Fronteras, ejido km 47 km, Bernal & Cuadra s.n. (holotype: SARH, A. Beetle pers. comm. to N. Snow in 1993, but not found there by Snow).

Comment. The status of this taxon is not entirely certain since we cannot locate the type for study (see comments above under species).

Diplachne dubia var. *humboldtiana* Kuntze, Revis. Gen. Pl. 3(2): 349. 1898. *Leptochloa dubia* var. *humboldtiana* (Kuntze) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico.

Comment. We have been unable to locate a type for this name (but not at NY; P.M. Peterson, pers. obs., 2013).

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A new species of *Licania* (Chrysobalanaceae) from Cordillera del Cónedor, Ecuador

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Abstract

A new mid altitude species of the predominantly lowland genus *Licania*, *L. condoriensis* from Ecuador is described and illustrated.

Keywords

Chrysobalanaceae, *Licania*, Cordillera del Cónedor, Ecuador

Introduction

A worldwide monograph of the Chrysobalanaceae was published in 2003 (Prance and Sothers 2003a, b). Some recent collections from Ecuador made in 2005 are of an undescribed species of *Licania*. This genus of 218 species is predominantly a lowland one and all three collections of this new species, *L. condoriensis*, are from an altitude of over 1,100 m. Table 1 lists 14 montane and submontane species of *Licania* that occur mainly at altitudes of over one thousand metres.

Description

Licania condoriensis Prance, sp. nov.

urn:lsid:ipni.org:names:77132009-1

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

Fig. 1

Ab *L. compacta* foliis subcoriaceis, haud nitidibus, haud dense brunneo-tomentosis, staminibus 7–8 differt.

Type. Ecuador. Zamora-Chinchipe, El Pangui, Cordillera del Cónedor, plateau of Contrafuerte, Tres Patines, W of main Cónedor ridge above Jardín Botánico of EcuaCorriente Copper Company, 03°37'48"S, 78°26'50"W, 1685 m. 2 Dec 2005, D. Neill & W. Quizhpe 15076 (holotype K; isotypes, MO, QCNE).

Small tree 3–7 m tall, young branches appressed puberulous, soon glabrous. Leaf lamina broadly ovate, 2.5–6 × 1.5–3.5 cm, subcoriaceous, acute or with short blunt acumen at apex, rounded to subcuneate at base, margins entire, glabrous and dull with densely reticulate prominulous venation above, with well-developed stomatal cavities beneath, the venation flattened around slit-like apertures of cavities, the venation glabrous and the cavities filled by a mass of white, unicellular simple hairs; veins 13–15 pairs, plane above, prominulous beneath; petioles glabrous, 3–10 mm long, rugose, with two sessile glands near apex. Stipules lanceolate, early caducous. Inflorescences short once-branched panicles 3–5 cm long, lateral branches borne at 90 degrees to rachis, the rachis and branches densely yellowish-brown tomentose. Flowers c 2 mm long, sessile or subsessile on primary branches of inflorescence; bracteoles oblong-triangular, acute, 1–1.5 mm long, tomentose on exterior and with ciliate margins. Receptacle campanulate, 1.5 mm long, yellowish-brown tomentose on exterior; calyx-lobes c. 1 mm long, acute, triangular, densely tomentose on exterior, tomentose within; petals absent; stamens 7–8, included, filaments equaling or shorter than the calyx lobes in length, c. 0.8 mm long. Ovary inserted at base of receptacle, unilocular with 2 ovules; style pubescent at base. Young fruit only seen, puberulous, glabrescent, unilocular.

Additional specimens examined. Ecuador. Morona-Santiago: Limon Indanza, Cordillera del Cónedor, Centro Shuar Yunkumas, Cerro Chuank Naint, 03°03'31"S, 78°14'48"W, 1,130 m, 19 Dec 2005, A. Wisum & Grupo Shuar de Conservación 326 (K, MO, QCNE); same locality, Asociación Nunkui, 03°3'34"S, 78°14'45"W, 1,150 m, 19 Dec 2005, C. Morales, A. Wisum & C. Kajekai 1593 (K, MO, QCNE).

This distinct mid-altitude *Licania* belongs to Section *Licania* of the genus and is probably most closely related to *L. compacta* Fritsch from Roraima in Guyana, but differs from *L. compacta* in the much less coriaceous, more acute leaves with a dull rather than shiny upper surface and in lacking the dense pubescence that covers the stomatal cavities of the latter and in the greater number of stamens. The leaves of *L. condoriensis* are very similar to those of *L. octandra* (Hofmanns. ex Roem & Schultes) Kuntze sub-

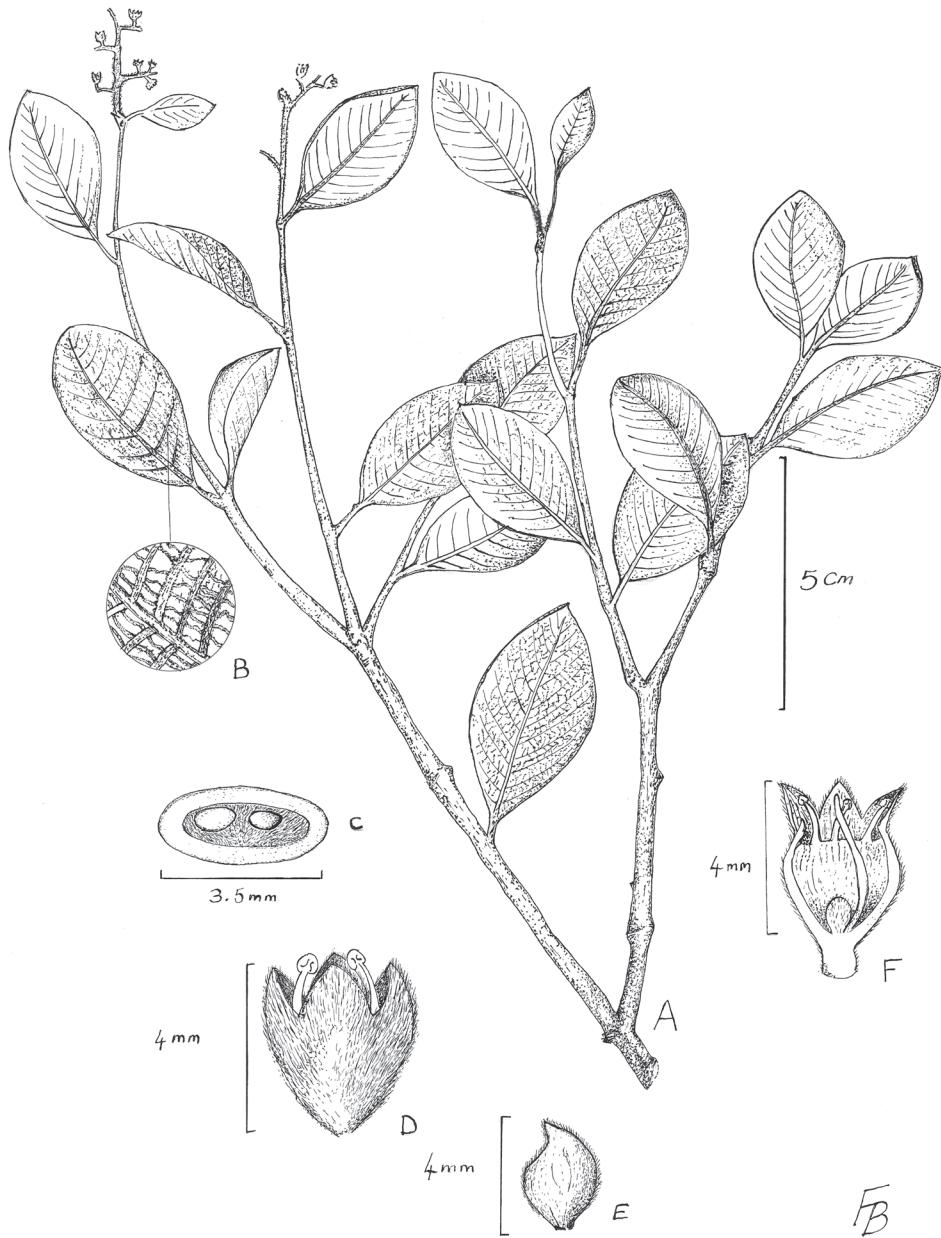


Figure 1. *Licania condoriensis* Prance: A habit B leaf undersurface showing reticulation from the deep stomatal cavities C ovary cross section D flower E bracteole F flower section. (Drawn from Neill & Quizhpe 15076 by Flora Bamford).

sp. *octandra*, but it differs in the fewer stamens (7-8 vs 9-12) that are included rather than far exserted. All collections of *L. condoriensis* are from the Cordillera del Cónedor for which this species is named.

Table 1. Species of *Licania* (Chrysobalanaceae) occurring mainly at above 1000 m.

Species	Locality	Altitude
<i>Licania</i> subgenus <i>Moquilea</i> section <i>Moquilea</i>		
<i>L. durifolia</i> Cuatr.	Colombia, Ecuador, Peru	500–2000 m
<i>L. cabreriae</i> Prance	Colombia: Antioquia	2200–2550 m
<i>L. montana</i> Prance	Venezuela: Lara	1300–1500 m
<i>L. hedbergii</i> Prance	Ecuador: Napo	1600 m
<i>L. longicuspidata</i> Prance	Ecuador: Carchi	650–1800 m
<i>L. cariae</i> A. Cardozo	Venezuela: Aragua	1100–2000 m
<i>L. chiriquiensis</i> Prance	Panama: Chiriquí	1007–1200 m
<i>Licania</i> subgenus <i>Moquilea</i> section <i>Leptobalanus</i>		
<i>L. jefensis</i> Prance	Panama: Chiriquí	1007 m
<i>Licania</i> subgenus <i>Licania</i> section <i>Hymenopus</i>		
<i>L. pakaraimensis</i> Prance	Venezuela: Bolívar	1400 m
<i>Licania</i> subgenus <i>Licania</i>		
<i>L. subrotundata</i> Maguire	Venezuela: Dist. Federal	1200–2000 m
<i>L. aracaensis</i> Prance	Brazil: Amazonas	1000 m
<i>L. pittieri</i> Prance	Venezuela: Aragua	1100–2200 m
<i>L. tepuiensis</i> Prance	Venezuela: Bolívar	1350 m
<i>L. condoriensis</i> Prance	Ecuador: Zamora-Chinchipe	1130–1685 m

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Leaflet anatomy verifies relationships within *Syagrus* (Arecaceae) and aids in identification

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Abstract

The current investigation was carried out to examine how palm anatomy may coincide with the current molecular analysis including the three recognized clades of *Syagrus* Mart. and to justify the splitting of acaulescent *Syagrus* species (e.g. *S. petraea* (Mart.) Becc.) into several species. Free-hand cross-sections of leaflets were made and the comparison of these verifies the relationships suggested by the molecular data. Free-hand leaflet sections were also found to be useful in the identification of otherwise difficult-to-identify acaulescent *Syagrus* species. The result and conclusion is that anatomical data is valuable in helping to verify molecular data and that splitting the acaulescent species of *Syagrus* is justified by the differences discovered in their field habit and anatomy. These differences were used to produce an identification key that is based on the anatomy.

Keywords

leaflet anatomy, identification, Arecaceae, *Syagrus*, acaulescent

Introduction

Syagrus is part of the largest subfamily of palms, Arecoideae (Dransfield et al. 2005, 2008; Gunn 2004). Recent construction of a supertree using a supermatrix consisting of DNA sequence data, plastid restriction fragment length polymorphism data and morphological data further supports that *Syagrus* belongs to the Cocoseae (Baker et al. 2009). Within the Arecoideae there is strong support via the phylogenetic analyses of the low copy genes PRK and RPB2 that it belongs to the RRC (Roystoneeae, Re-

inhardtieae, Cocoseae) clade and specifically to the Cocoseae and Attaleinae (Baker et al. 2011). Attaleinae include genera like *Allagoptera*, *Attalea*, *Beccariophoenix*, *Butia*, *Cocos*, *Jubaea*, *Jubaeopsis*, *Lytocaryum*, *Parajubaea*, *Syagrus*, and *Voanioala* or in other words all of the non-spiny palms with small hard coconut-like fruits.

Palm leaflet anatomy has been useful in identification and has been used to suggest systematic relationships. Tomlinson (1961) examined and described the leaflet anatomy of some 250 species of palms in 137 genera and suggested some systematic relationships among genera. Horn et al. (2009) took it a step farther and mapped out the lamina anatomy using the data matrix for the palm family resulting from a phylogenetic analysis by Asmussen et al. (2006) in order to understand the lamina anatomy evolution. Tomlinson's "brief survey" (Tomlinson 1961) inspired Glassman (1972, 1987) to examine *Syagrus* and its closely related genera in greater detail. Glassman (1972) emphasized that his survey of the genus was "based on mostly one collection for each taxon." However by the time he completed his revision (Glassman 1987), slides of two or more specimens were made for most taxa. His key was written as a convenient tool for identification and was not intended to show close relationships. Meerow et al. (2009) showed how leaflet anatomy further supported the molecular relationships between *Allagoptera*, *Parajubaea* and *Polyandrococos* (now synonym of *Allagoptera*). Tomlinson et al. (2011) expanded his original work and presented information on 183 palm genera (out of 185 now recognized) and suggested relationships based on anatomy and the use of modern phylogenetic approaches.

Glassman (1972) emphasized the following anatomical characters: (1) nature of adaxial and abaxial surfaces (straight, wavy or furrowed), (2) number of cell layers comprising both adaxial and abaxial hypodermis, (3) relative frequency and location of larger veins and whether they bulge at the laminar surfaces, (4) frequency and location of intermediate and minor veins (whether they are abaxial, in the middle or both) and whether they are attached to nonvascular fibers (5) relative abundance, shape and location (adaxial and abaxial, or adaxial only) of clusters of nonvascular fibers (N.V.F.), called fiber bundles by Tomlinson et al. (2011), (6) relative frequency and location of stomata (abaxial surface only or both leaf surfaces) and whether they are sunken or not, (7) size of midrib and its shape in transection (truncate, rounded or pointed), (8) size and shape of expansion cell tissue (E.C.T.), (9) relative frequency of dark staining bodies (probably groups of cells containing tannins) in mesophyll and midrib, (10) number and relative size of fiber clusters and veins at extremities of pinna.

Tomlinson et al. (2011) suggested that the following anatomical features vary in *Syagrus*: (1) abundance and distribution of trichomes; (2) adaxial epidermal cells varying from rectangular, with distinctly sinuous anticlinal walls to rhombohedral, obviously extended cells with straight or at most undulate walls; (3) the thickness of the outer epidermal wall, varying from very thick with the cell lumen scarcely one tenth its depth, to thinner walls only 2-3 times thicker than the remaining walls, the cell lumen large; (4) the abundance and location of adaxial non-vascular fibers, varying from an almost continuous layer within the hypodermis to few fibers; (5) the extent and location of abaxial non-vascular fibers; (6) the extent to which the minor abaxial veins are

in contact with the abaxial hypodermis; (7) the degree to which the inner sheath of major veins develop fibrous extensions to the upper surface layers.

The first part of this paper investigates leaflet anatomy to see how it coincides and possibly even verifies the relationships supported by the molecular analysis of Meerow et al. (2009). Leaflet anatomy was useful in producing valuable anatomical characters for a phylogenetic analysis of the Attalinae palms based purely on morphological and anatomical characters (Noblick et al. 2013). Some of these anatomical characters were found to coincide with the molecular analysis of the Attaleinae (Meerow et al. 2009) as previously mentioned above. Using seven low copy nuclear WRKY genes, Meerow et al. (2009) inferred that the coconut (*Cocos nucifera*) was sister to new world *Syagrus* species and that the genus *Syagrus* was composed of at least three distinct clades: Rain Forest, Eastern Brazilian and Cluster-stem (Fig. 1). The three clades were examined anatomically to see if their anatomy supported these relationships.

The second part of this paper deals with the problem of identifying the “acaulescent” species of *Syagrus*. Most of these palms grow in Brazilian savannas (*cerrados*) and high altitude rocky fields (*campo rupestre*). Many species of *Syagrus* are described as acaulescent and Tomlinson et al. (2011) admitted that based on the low number of collections, especially of *Syagrus*, there was a great need for more detailed studies within this group. In fact, about 25 out the 54 currently recognized species of *Syagrus* are acaulescent or short stemmed (Table 1) and their identification remains challenging with many having formerly been dismissed as *Syagrus petraea* (Noblick and Lorenzi 2010). Palms that do not have visible above ground stems are often referred to as acaulescent meaning “without a stem.” In fact all palms have a stem, whether it is suberect, short-stemmed with the crown remaining at ground level, persistent juvenile which remains at ground level or rhizomatous stems that remain horizontal at ground level (Tomlinson et al. 2011). *Syagrus lilliputiana* (Barb. Rodr.) Becc., *S. itacambirana* Noblick & Lorenzi, *S. pleiocladoides* Noblick & Lorenzi and *S. procumbens* Noblick & Lorenzi are suberect and short-stemmed. *Syagrus microphylla* Burret, *S. vagans* (Bondar) A. Hawkes, *S. werdermannii* Burret and *S. duartei* Glassman usually have rhizomatous stems that remain horizontal at ground level and which are not always apparent. *Syagrus pleioclada* Burret usually has a very short, vertical aboveground stem. Over half of the acaulescent *Syagrus* species have similar looking simple spicate inflorescences (an unbranched inflorescence) and similar looking flowers and fruits. Many herbarium specimens of these acaulescent *Syagrus* look alike, but in the field they display characters that are not well preserved on herbarium sheets or that are not reported on the labels (Table 1), like deflexed pinnae (leaflets that are bent or turned abruptly or sharply downwards) or petioles that bend strongly downwards causing the leaf to lie parallel or flat on the ground (prostrated) as opposed to having leaves that are strongly ascending with straight petioles. The second part of this paper will therefore confirm, add to and hopefully correct some of the work already started by Glassman (1972, 1987). Not counting the two acaulescent *Butia* that Glassman (1987) included in the *Syagrus* portion of the leaflet anatomical key for his revision, Glassman only includes about half or 12

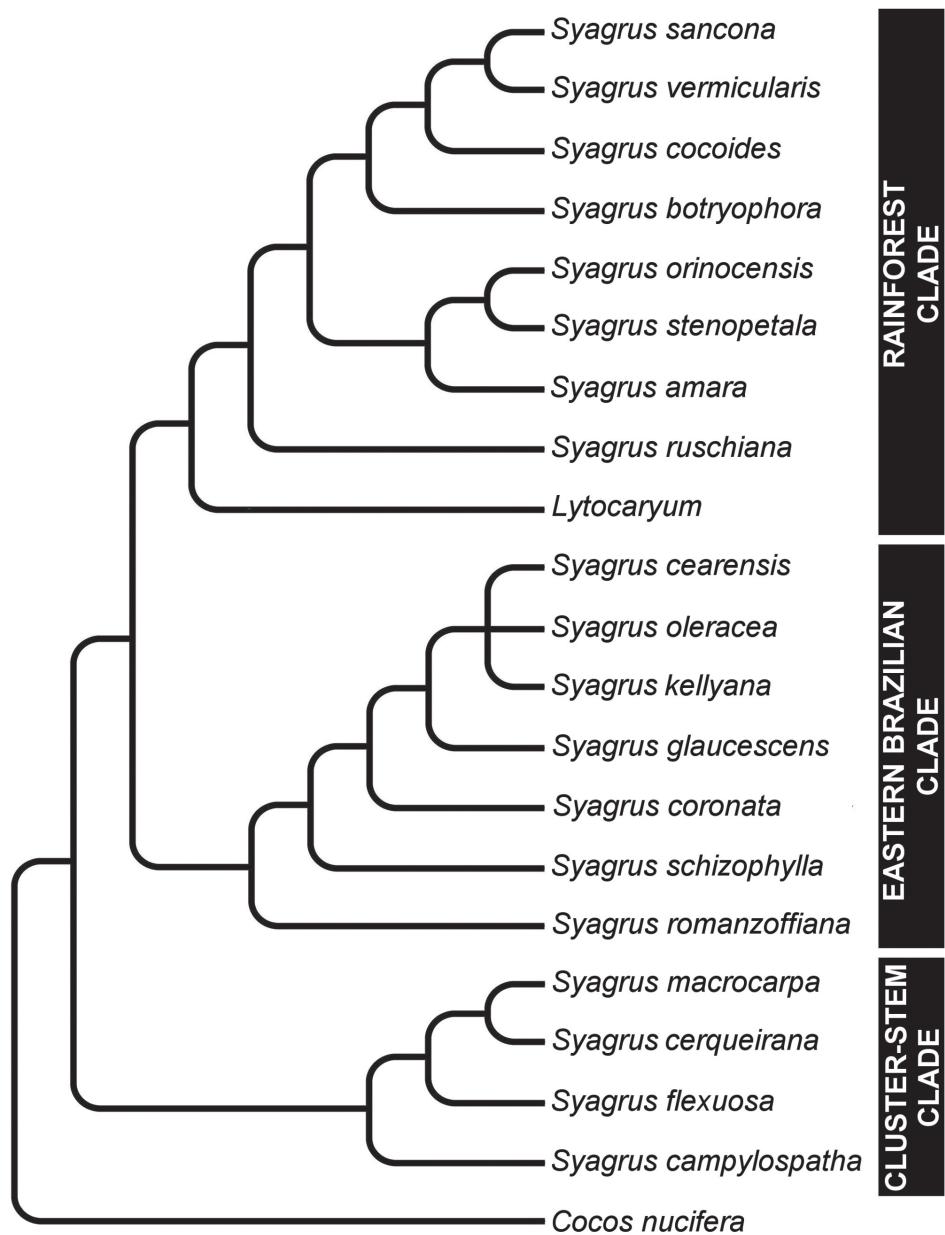


Figure 1. Cladogram showing major relationships in *Syagrus* (adapted from Meerow et al. 2009). Three major clades of *Syagrus* have been identified through analysis of low copy nuclear genes: the Rain Forest Clade, the Eastern Brazilian Clade, and the Cluster-stem Clade.

of the 26 currently recognized acaulescent *Syagrus* taxa. In addition, he misidentified some of the specimens used in that key. For his anatomical studies, he sometimes neglected to use specimens collected in the vicinity of their holotypes. *Syagrus*

Table 1. Visible morphological field characters of “acaulescent” *Syagrus* species. x = normally present and s = sometimes present.

#	Name	Inflorescence branched	Inflorescence a spike	Pinnae whitish / silver beneath	Pinnae silvery blue
1	<i>S. allagopteroides</i> Noblick & Lorenzi	x			
2	<i>S. angustifolia</i> Noblick & Lorenzi	x			x
3	<i>S. caerulescens</i> Noblick & Lorenzi	x		x x	x
4	<i>S. campylospatha</i> (Barb. Rodr.) Becc.		x		x
5	<i>S. cerqueirana</i> Noblick & Lorenzi		x		x
6	<i>S. duartei</i> Glassman		x		x
7	<i>S. evansiana</i> Noblick	x		x x	x
8	<i>S. glazioviana</i> (Dammer) Becc.		s x		x
9	<i>S. gouveiana</i> Noblick & Lorenzi		x		x
10	<i>S. graminifolia</i> (Drude) Becc.		s x x		x
11	<i>S. graminifolia</i> var. <i>glazioviana</i> (Dammer) Becc.		s x		x
12	<i>S. harleyi</i> Glassman	s x			x
13	<i>S. itacambirana</i> Noblick & Lorenzi	s		x	x
14	<i>S. liliiputiana</i> (Barb. Rodr.) Becc.	x		x	x
15	<i>S. loefgrenii</i> Glassman			x x	x x
16	<i>S. longipedunculata</i> Noblick & Lorenzi	x		x	x
17	<i>S. mendanhensis</i> Glassman			x	x
18	<i>S. microphylla</i> Burret	x		x x	x
19	<i>S. minor</i> Noblick & Lorenzi	x x	x x		x
20	<i>S. petraea</i> (Mart.) Becc.		x x		x x
21	<i>S. pleioclada</i> Burret	x	x		x
21	<i>S. pleiocladoides</i> Noblick & Lorenzi	x x			x
23	<i>S. procumbens</i> Noblick & Lorenzi	x		x	x
24	<i>S. rupicola</i> Noblick & Lorenzi			x x	x x
25	<i>S. vagans</i> (Bondar) A. Hawkes		x		x
26	<i>S. werdermannii</i> Burret			x	x

petraea (Fig. 6M) whose Bolivian holotype is now believed to be a local endemic is just such an example. His anatomical leaflet drawing of Glaziou 22254 (Glassman 1987) from central Brazil in the state of Goiás matches *S. glazioviana* (Dammer) Becc. anatomy (Fig. 7E) more than it does the Bolivian *S. petraea* (Fig. 6M). Also instead of Glassman’s simple drawings of the middle portion of the lamina, I believe the images of leaflet marginal cross-sections to be more useful and more informative. Therefore, the second intent of this paper is to facilitate the identification of these difficult acaulescent *Syagrus* species by (1) making use of poorly recorded field characters (Table 1) that are not easily interpreted from a flattened dried specimen and (2) their leaflet anatomy (Table 2) making use of digital images of the cross-sections of leaflet margins.

Table 2. List of anatomical descriptors or characters for each of the species of acaulescent *Syagrus*. X = present, S = sometimes.

Descriptors or Characters	Major veins	Intermediate veins	Minor veins
<i>S. campylospatha</i>			
	Huge major vein adjacent to or nearly adjacent to leaflet margin		
	Normal-sized major vein near the margin but not adjacent to it (separated by a fiber bundle adaxially and/or a minor vein abaxially).		
	Major vein usually unattached separated from the abaxial and adaxial hypodermis by another cell layer or more	X	
	Major veins attached to the adaxial hypodermis but separated from the abaxial hypodermis by an additional cell layer or layers	X	
	Major veins mostly attached to the adaxial surface often by a short or long fibrous sheath extension (girdle)		
	Major veins are usually attached to both the adaxial and abaxial hypodermis.	X	
	Intermediate veins		
	Intermediate veins unattached		
	Most intermediate veins attached adaxially by a fibrous sheath extension	X	
	Intermediate veins attached to both surfaces by a fibrous sheath extension	X	
	Minor veins		
<i>S. graminifolia</i> var. <i>glaziioviana</i>			
<i>S. graminifolia</i>			
<i>S. mendoncensis</i>	X		
<i>S. pleiollada</i>			
<i>S. petricoloides</i>			
<i>S. wendrmanii</i>			
<i>S. vagans</i>			
<i>S. microphylla</i>			
<i>S. glazioviana</i>			
<i>S. evansiana</i>			
<i>S. rupestris</i>			
<i>S. carrelessii</i>			
<i>S. duartei</i>			
<i>S. gueretiana</i>			
<i>S. petreana</i>			
<i>S. procumbens</i>			
<i>S. procumbens emasensis</i>	X		
<i>S. taicambariana</i>			
<i>S. angustifolia</i>			
<i>S. longipetiolata</i>			
<i>S. loegei</i>	X		
<i>S. minor</i>			
<i>S. littoralis</i>			
<i>S. allagopetiolata</i>			
<i>S. coryneiformis</i>			
<i>S. barreya</i>			

Materials and methods

Plants examined

Both live material and preserved herbarium material (Table 3) were used in this project. The living material used in this study came from the collections at Montgomery Botanical Center (MBC, Miami, FL). The dried material was from collections made while doing fieldwork in Brazil, from the garden and herbarium at Jardim Instituto Plantarum (HPL, Novo Odessa, São Paulo, Brazil) and from dried collections at the Fairchild Tropical Botanic Garden herbarium (FTG, Miami, FL) and a few specimens from the following herbaria: G, IBGE, IPA, K, MO, NY and US.

Anatomical preparation

Two methods were employed for expedient identification. First, one side of the middle section of a middle leaflet was folded back and forth on itself in accordion fashion; the folded leaflet was then held down on a cutting board, while using a double-edged razor blade to cut thin cross-sections. The sections were rinsed into a watch glass with water and a thin brush was used to select the thinnest sections under a dissecting scope and then placed on a microscope slide in a droplet of 1:1 glycerin/water solution. A cover glass was placed over the specimen and the slide was placed under a compound light microscope and photographed under the 10 \times objective (100 \times magnification). Most of the sections were unstained, but in rare cases toluline blue (0.01%) was tested to see if it made it easier to view certain characters, which it did not (Fig. 3C, 6D).

In the second method, better suited when material is limited, a small square of carrot of the appropriate size is cut to fit in an inexpensive hand-held student microtome. I purchase my hometrainingtools hand-held microtome online. A vertical slit is cut in the carrot and a small piece of leaflet is inserted in the appropriate orientation. The carrot is clamped into the hand-held microtome. The microtome is screwed to the appropriate level and an ordinary folding straight edge razor, the kind used for shaving, is utilized to cut the cross-sections and honed occasionally to keep it sharp. Sections are handled the same way as above. Scale was later added using a stage micrometer. Dried material can also be sectioned and photographed after rehydrating in a 5% solution of Contrad 70° (Decon Labs, King of Prussia, Pennsylvania) for a period of 24 hours (Tomlinson et al. 2011).

Characters utilized

This paper is focused mainly on characters of the more easily sectioned marginal and laminal portions of the leaflet and not so much on the harder to section midrib. Trichomes, epidermis and dark staining bodies were also not looked at.

Table 3. Selected specimens examined.

SYAGRUS Martius
<i>S. allagopteroides</i> Noblick & Lorenzi, Lorenzi et al. 6792 (HPL, FTG, NY, K, CEPEC, R, SP).
<i>S. angustifolia</i> Noblick & Lorenzi, Lorenzi et al. 6636 (HPL, R, SP, BHCB, NY, K); Oliveira et al. 1082 (IBGE).
<i>S. caeruleascens</i> Noblick & Lorenzi, Lorenzi et al. 6649 (HPL, NY, K, R, SP); Tsuji & Franco 2622 (HPL).
<i>S. campylospatha</i> (Barb. Rodr.) Becc., Hassler 1733 (G [holotype]), K, NY; Pedersen 14638 (G); Noblick et al. 5128 (FTG, PY, MBC96103).
<i>S. cearensis</i> Noblick, Noblick et al. 4951 (EAC, FTG, RB, MBC94652); Noblick et al. 4953 (EAC, FTG, TEPB, MBC94654); Noblick et al. 5132 (IPA, MBC97262, MBC97263).
<i>S. cerqueirana</i> Noblick & Lorenzi, Noblick et al. 5126 (FTG, NY, PY, MBC96100); Schinini & Bordas 20288 (MO); Schinini & Bordas 20291 (CTES); Swallen 9520 (US).
<i>S. cocoides</i> Mart., Fischer s.n. (MBC96363); Froes 11622 (GH, MO, NY); Henderson et al. 337 (NY); Henderson & Pardini 1503 (NY); Kruckoff 1221 (F); Noblick 4954 (FTG, MBC94795); Plowman et al. 8267 (NY); Taylor et al. E1049 (NY).
<i>S. coronata</i> (Mart.) Becc., Noblick & Soeiro 4694 (CEPEC, F, FTG, HRB, NY); Noblick & Soeiro 4704 (CEPEC, F, FTG, HRB); Noblick & Queiroz 4833 (FTG, HUEFS, MBC92146, MBC92196); Noblick et al. 4975 (FTG, IPA, MBC94473).
<i>S. duartei</i> Glassman, Glassman & Gomes 8033 (F); Glassman 8035 (FTG); Hatschbach & Ferreira 35324 (MBM, F); Noblick 4854 (BHCB, FTG, MO, NY).
<i>S. evansiana</i> Noblick, Tsujiet et al. 2703 (HPL, R, BHCB, FTG, K, NY); Lorenzi 4269 (HPL); Lorenzi 4276 (FTG, HPL).
<i>Syagrus flexuosa</i> (Mart.) Becc., Noblick & Lima 4632 (BAH, CEPEC, CPATSA, F, FTG, NY, RB); Noblick & Lima 4633 (CEPEC, CPATSA, F, FTG); Noblick & Lima 4661 (CEPEC, CPATSA, F, FTG, NY); Noblick 4850 (BHCB, FTG, K); Noblick 4852 (BHCB, F, FTG, K, NY, US); Noblick & Ferreira 4869 (FTG, UFG); Noblick & Cropper 5108 (CEN, FTG, MBC96136); Noblick & Behr 5165 (IPA, MBC97800); Noblick & Behr 5166 (IPA, MBC97801); Noblick 5166 (IPA, MBC97801, MBC971463).
<i>S. glaucescens</i> Glaziou ex Becc., Brown s.n. (MBC20030758); Glassman & Gomes 8112 (SP); Glassman 13002 (F, FTG); Noblick 4843 (BHCB, F, FTG, K, NY, US); Noblick 4845 (BHCB, FTG).
<i>S. glazioviana</i> (Dammer) Becc., Noblick & Lobo 4527 (CEPEC, F, FTG, HRB, HUEFS, K, NY, RB, SP); 4617 (BAH, CEN, CEPEC, CPATSA, F, K, MICH, MO); Noblick & Lima 4643 (CEN, CEPEC, CPATSA, F, NY); Noblick & Lima 4659 (CPATSA, F, FTG), 4662 (CEPEC, CPATSA, F, FTG); Tsuji et al. 2681 (HPL).
<i>S. gouveiana</i> Noblick & Lorenzi, Lorenzi 6537 (HPL, R, SP, BHCB, NY, K).
<i>S. graminifolia</i> (Drude) Becc., Belem 2029 (UB); Burchell 5956 (K), holotype for <i>Cocos graminifolia</i> Drude; Davis & Shepherd 60024 (NY); Glassman 13093 (F); Noblick 5164 (FTG).
<i>S. graminifolia</i> var. <i>glazioviana</i> (Dammer) Becc., Glaziou 22252 (G, K); Glaziou 22253 (G, K), isotype for <i>Cocos graminifolia</i> var. <i>glazioviana</i> Dammer; Lorenzi et al. 6791; Tsugi et al. 2682 (HPL).
<i>S. harleyi</i> Glassman, Noblick 2867 (CEPEC, F, HUEFS, MO); Noblick & Lima 4380 (CEPEC, F, GH, HUEFS, MBM, SP); Noblick 4387 (BH, CEPEC, F, HUEFS, NY); Noblick 4389 (CEN, CEPEC, F, FTG, HRB, HUEFS, IPA, K, NY, RB, SP, US); Noblick & Lobo 4517 (AAU, ALCB, CEN, CEPEC, F, FTG, HRB, HUEFS, K, U).

***SYAGRUS* Martius**

- S. itacambirana* Noblick & Lorenzi, Andrade-Lima 68-5425 (IPA); Tsuji et al. 2706 (HPL, R, SP, BHCB, NY, K).
- S. kellyana* Noblick & Lorenzi, Noblick & Cline 5156 (IPA, FTG, MBC97289, MBC97290).
- S. lilliputiana* (Barb. Rodr.) Becc., Hassler 9519 (G); Lorenzi et al. 2805 (HPL).
- S. loefgrenii* Glassman, Noblick & Lima 4634 (AAU, BAH, BH, CEPEC, CPATSA, F, FTG, K); Noblick & Lima 4660 (CPATSA, F, FTG); Noblick & Lima 4669 (ALCB, CEPEC, CPATSA, F, K, U); Lorenzi 6642 (HPL); Noblick & Buzeiro 4888 (BHCB, FTG, K, MO, US).
- S. longipedunculata* Noblick & Lorenzi, Lorenzi et al. 6790 (HPL, R, SP, BHCB, NY, K); Oliveira et al. 588 (IBGE).
- S. macrocarpa* Barb. Rodr., [No Collector] (MBC20080848, MBC20080849, MBC20080850); Noblick & Abrahao 4841 (BHCB, FTG, NY); Noblick & Abrahao 4842 (BHCB, FTG); Noblick 4857 (CESJ, F, FTG, IPA, NY, US).
- S. mendanhensis* Glassman, Archer 4086 (BH [holotype], US); Glassman 13003 (FTG); Noblick 4844 (BHCB, F, FTG, MO, NY, K, US); Noblick 4846 (BHCB, FTG, NY, US); Noblick 4847 (BHCB, FTG).
- S. microphylla* Burret, Glassman 13018-031 (F, SP); Noblick & Clodoaldo 3508 (F, FTG, GH, HUEFS, MO, RB, SP); Noblick 4534 (ALCB, CEPEC, F, FTG, HUEFS, RB); Noblick & Lima 4612 (BAH, BH, CEPEC, CPATSA, F, FTG, K, NY, US); Noblick 4835 (FTG, MO).
- S. minor* Noblick & Lorenzi, Lorenzi et al. 6639 (HPL, R, SP, BHCB, NY, K).
- S. orinocensis* (Spruce) Burret, Balick et al. 1192 (NY); Betancur 1315 (NY); Bomm & Wentzel 6616 (NY); Davidse & Huber 15286 (BH); Mejia et al. 1258 (NY); Noblick et al. 4946 (FTG, MBC94586); Noblick et al. 4948 (FTG, PORT, MBC94588).
- S. petraea* (Mart.) Becc., H. Lorenzi et al 6835 (HPL); Moreno 246 (JBSC); Saldias et al. 953 (NY).
- S. pleioclada* Burret, Glassman & Gomes 8037-042 (F, FTG [8037], SP [8041, 8042]); Hatschbach 35313 (F, MBM); Heringer & Castellanos SP80005 (SP); Martinelli & Smith 6333 (MO); Noblick 4853 (BHCB, FTG, MO, NY); Smith 6699 (US).
- S. pleiocladoides* Noblick & Lorenzi, Lorenzi et al. 6583 (HPL, R, SP, UB, UFMT, NY, FTG, K, AAU, CTES).
- S. procumbens* Noblick & Lorenzi, Lorenzi et al. 6583 (HPL, R, SP, UB, UFMT, NY, FTG, K, AAU, CTES); Lorenzi 4752 (HPL); "emasensis" Noblick & Ferreira 4868 (FTG, UFG); Tsuji et al. 974 (HPL); Lorenzi et al. 6787 (HPL).
- S. rupicola* Noblick & Lorenzi, Lorenzi et al. 6647 (HPL, R, SP, UB, NY, K).
- S. stenopetala* Burret, Liesner & Gonzalez 11928 (NY); Noblick & Smith 4936 (FTG, PORTO, MBC94576); Noblick & Smith 4938 (MBC94577); Pittier 9154 (NY, US); Steyermark et al. 102432 (MO); Steyermark & Manara 110614 (BH).
- S. vagans* (Bondar) A. Hawkes, Carvalho 2409 (CEPEC); Glassman & Medeiros-Costa 8725-726 (F); Lima & Noblick 140-147 (CPATSA); Mori 10066 (CEPEC, NY); Noblick 3161 (HUEFS); Noblick et al. 3253 (HUEFS); Noblick & Clodoaldo 3537 (HUEFS); Noblick 3609 (HUEFS); Noblick 3846 (F, HUEFS).
- S. vermicularis* Noblick, Fischer s.n. (MBC96364); Noblick & Feitosa 4971 (FTG, IPA); Noblick & Feitosa 4974 (FTG; MBC94690).
- S. werdermannii* Burret, Carvalho 1790 (CEPEC, US); Glassman & Medeiros-Costa 8728-739 (F); Noblick & Clodoaldo 3769 (BH, F, HRB, HUEFS); Noblick & Lobo 4519 (BAH, CEN, CEPEC, F, FTG, HUEFS, K, MO, NY, RB).

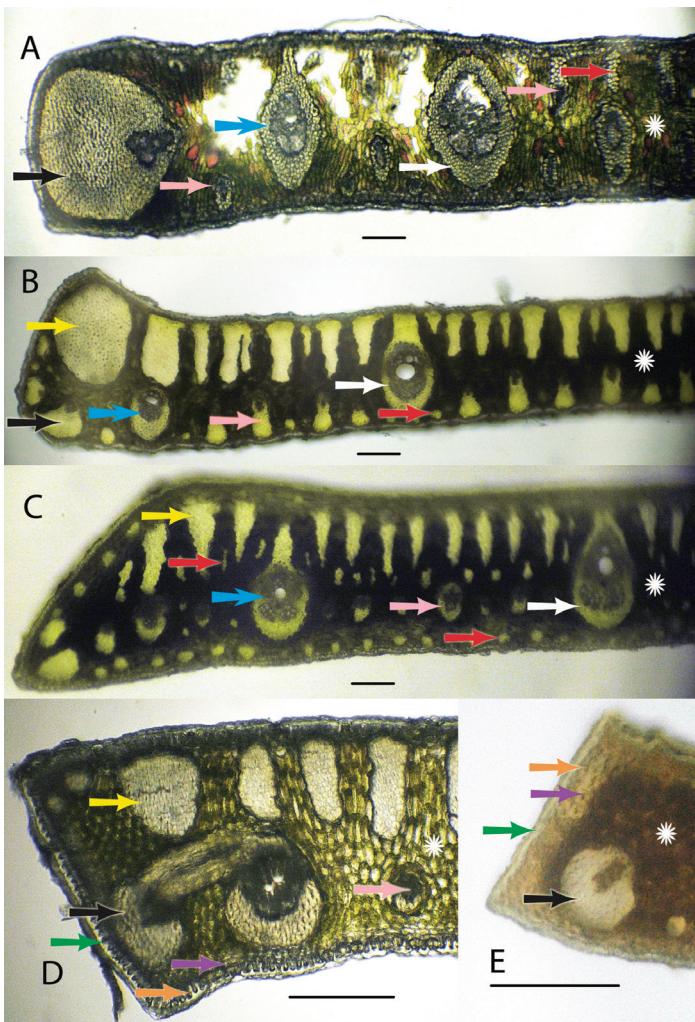


Figure 2. Anatomical characters. White arrows = major veins; Blue arrows = intermediate veins; Pink arrows = minor veins; Black arrows = vein with an exaggerated fibrous sheath; Yellow arrows = major fiber bundles; Red arrows = minor fiber bundles; Green arrows = Cuticle; Orange arrows = epidermis; Purple arrows = hypodermis; White star = mesophyll **A** *S. allagopteroides* illustrates a large marginal vein with an exaggerated fibrous sheath (black), an unattached major vein (white), the presence of minor veins on both the adaxial and abaxial surfaces (pink) and an occasional minor adaxial fiber bundle (red) **B** *S. caerulescens* illustrates a large marginal fiber bundle (yellow), a major vein attached to the adaxial surface by a fibrous extension (white), a small vein with an exaggerated fibrous sheath (black), minor veins (pink) sometimes alternating with minor fiber bundles (red) along the abaxial surface, and adaxial fiber bundles reaching nearly $\frac{1}{2}$ the distance across the mesophyll (white star) **C** *S. vagans* illustrates the first or second fiber bundle as being the largest along the adaxial surface (yellow) and minor fiber bundles (red) scattered throughout the mesophyll (white star), minor veins located near the middle or just slightly below **D** *S. gouweiana* illustrates the cuticle (green), epidermis (orange), hypodermis (purple) **E** *S. harleyi* illustrates a protective layer of thick-walled hypodermal cells (purple) on the margin, which is characteristic of this species. **A, B, C** Scale = 0.1 mm; **D, E** scale = 0.2 mm.

Characters examined during this study follow some of Glassman's 4, 5 and 10 characters listed above and Tomlinson's characters 4, 5, 6, and 7 listed above. Figure 2 will clarify much of the terminology and characters used in this paper. In each leaf cross-section the upper or superior side of the lamina is called the adaxial surface, meaning "towards the axis", since this side of the leaf faces towards the axis or center of the plant as it grows out. The lower or inferior side is called the abaxial, meaning "away from the axis", since this side faces away from the center of the plant (Dransfield et al. 2008, Esau 1977). The outer most layer of the leaf is the cuticle (Fig. 2D, 2E green arrow), a non cellular waxy layer produced by epidermis (Dransfield et al. 2008). The cuticle is followed by the epidermis, "outer skin" (Fig. 2D, 2E orange arrows), followed by the hypodermis, "under skin" (Fig. 2D, 2E purple arrows), which is finally followed by the mesophyll, "middle leaf", region (Fig. 2 white stars). Within the mesophyll are vascular bundles, or fibrovascular bundles or veins of various sizes (Tomlinson et al. 2011) that will be referred to as major veins (Fig. 2 white arrows), intermediate veins (Fig. 2 blue arrows), and minor veins (Fig. 2 pink arrows). Some major and intermediate veins are often attached to the adaxial hypodermis and sometimes to both the surfaces by fibrous sheath extensions. If the attachment extends to both surfaces via a fibrous sheath extension, the vein becomes girder-like and is indeed referred to as a girder (Tomlinson et al. 2011) (Fig. 5A). In some veins the fibrous sheath becomes so enlarged with fibers that such veins are referred to as veins with exaggerated fiber sheaths (Tomlinson et al. 2011) (Fig. 2 black arrows). In addition to the veins, the laminal tissues are supported by nonvascular fibers or fiber bundles of various sizes. Some have major fiber bundles adjacent to or near their margins (Fig. 2 yellow arrows). Many fiber bundles are adaxial and may reach close to $\frac{1}{2}$ the distance across the mesophyll (Fig. 2B, 2D). Minor, intermediate and major fiber bundles can be found adaxially (Fig. 2A red arrows; 2B, 2C yellow arrows). Most minor fiber bundles are mainly abundant abaxially (Fig. 2B, 2C red arrows) and occasionally scattered throughout the mesophyll (Fig. 2C red arrows).

To keep things simple for field examination, the following qualitative characters were examined: (1) location, attachment or lack of attachment of the major veins to one or both surfaces and method of attachment (fiber sheath extension or not); (2) location, attachment or unattachment of intermediate veins to one or both surfaces and method of attachment (e.g. sheath extensions, formation of girders); (3) location of the minor veins (e.g. adaxial, abaxial, abaxial and adaxial, middle, marginal); (4) presence, size and location of veins with an exaggerated fibrous sheath (large ones often located on the leaflet margin); (5) presence, location, size and sometimes cross-sectional shape of fiber bundles and the extent they reach across the mesophyll. These characters can also be further summarized as follows:

- (1) Major vein location {adjacent to the margin; near the margin but not adjacent to it (this means that along a horizontal plane there is a maximum of one minor vein or one fiber bundle separating it from the actual margin); not adjacent to nor near the margin}

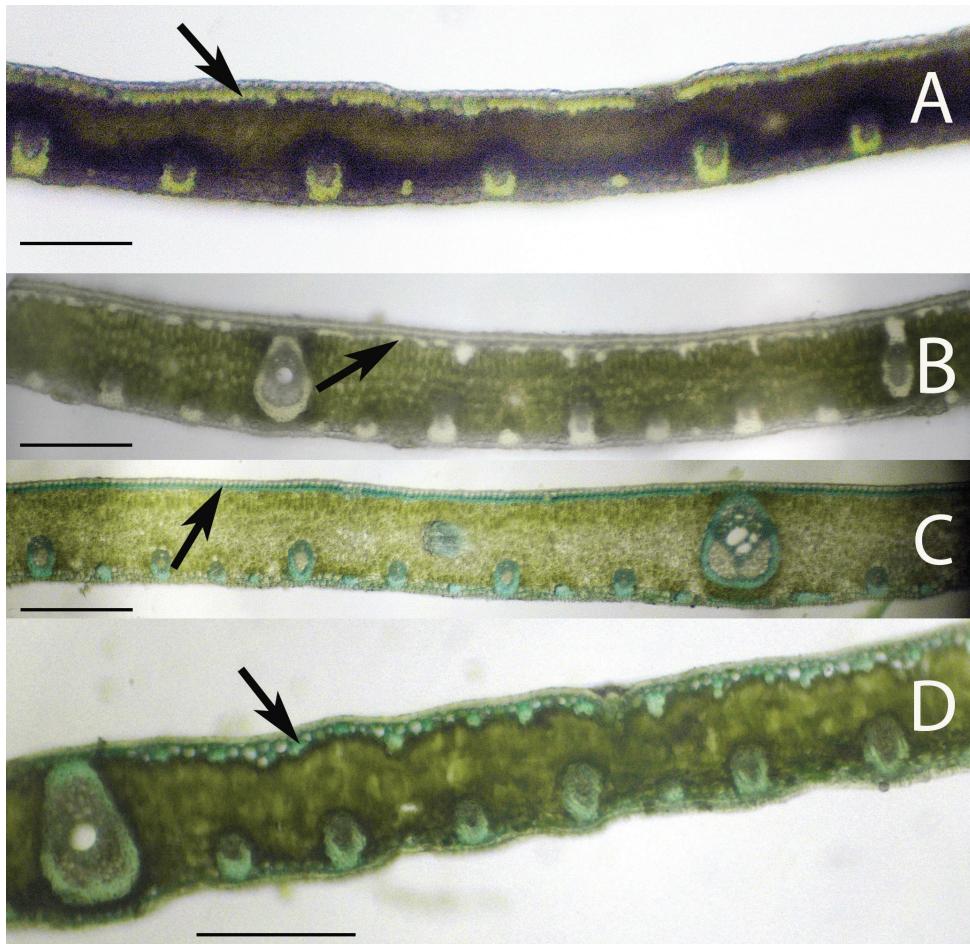


Figure 3. Leaflet cross-sections of the Rain Forest Clade of *Syagrus* species with arrows pointing out the 1–2 cell thick fibrous sheet just below the epidermis that is a defining character of species of this clade: **A** *S. vermicularis* Noblick **B** *S. stenopetala* Burret **C** *S. sancona* (Mart.) Becc **D** *S. cocoides* (Mart.) Mart. Scale = 0.2 mm.

- (2) Major vein attached where {unattached; attached to adaxial hypodermal surface only; attached to both adaxial and abaxial hypodermal surfaces}
- (3) Major vein attachment how{attached by a short or long fibrous sheath extension; attachment not by a fibrous sheath extension}
- (4) Intermediate veins attached {unattached; attached to adaxial surface only; attached to both surfaces}
- (5) Intermediate vein attachment {to both surfaces by fibrous sheath extension (girders); attached to adaxial surface only by fibrous sheath extension; attached but without fibrous sheath extension}

- (6) Minor vein location {adjacent to both the adaxial and abaxial surface; a few adjacent to the adaxial but most on the abaxial surface; near the middle of the mesophyll; adjacent to the abaxial surface or at least in the lower third of the mesophyll; only adjacent to the abaxial surface}
- (7) Presence of major marginal vein with large exaggerated fibrous sheath {absent; present}
- (8) Presence of minor marginal vein with exaggerated fibrous sheath {absent; one present; two or more present}
- (9) One major rounded fiber bundle adjacent to the margin {absent; present}
- (10) First fiber bundle on the adaxial surface the largest {absent; present}
- (11) Adaxial fiber bundles size if present {reach 1/3 to 1/2 across the mesophyll; reach 1/5 to 1/4 across the mesophyll}
- (12) Fiber bundles shape {mostly long and skinny: mostly long and thick: mostly short and thick}
- (13) Fibers or minor fiber bundle locations {adaxial only; adaxial and abaxial only; adaxial, abaxial and scattered in the mesophyll}
- (14) Minor fiber bundles adjacent to the margin {absent; present}.
- (15) Minor fiber bundles abundance {none; few along the adaxial and abaxial surface; only a few along the abaxial surface alternating with the minor veins; many along the abaxial surface}
- (16) Thick walled hypodermis protecting the margin {absent; present}

The key was designed for field use, which means minimal equipment, no staining, and low magnification and the use of simple characters. Refer to the characters in the methods for clarification of terminology. By using the methods listed above and following many of the simple techniques mentioned by Tomlinson et al. (2011), rapid results can be achieved in a laboratory provided with only the simplest equipment. This simple approach was also successfully used in a significant study of palm leaf development by Nowak et al. (2007).

Results

Anatomical characters observed on marginal palm leaflet cross-sections have been found to verify the Rain Forest and Eastern Brazilian clades and to some extent the Cluster-stem clade found within *Syagrus* (Fig. 1). In the Rain Forest clade, there is a continuous hypodermal layer of fibrous to thick-walled cells, one to two layers thick just below the adaxial epidermis (Fig. 3A, 3B, 3C, 3D). In the Eastern Brazilian clade, there are many thick, closely-spaced, multicellular fiber bundles running along the adaxial surface of the leaflet (Fig. 4A, 4B, 4C, 4D). Finally the Cluster-stem clade is usually characterized by minor sparsely spaced fiber bundles on the adaxial side and minor veins adjacent to the abaxial surface (Fig. 5B, 5C) or with

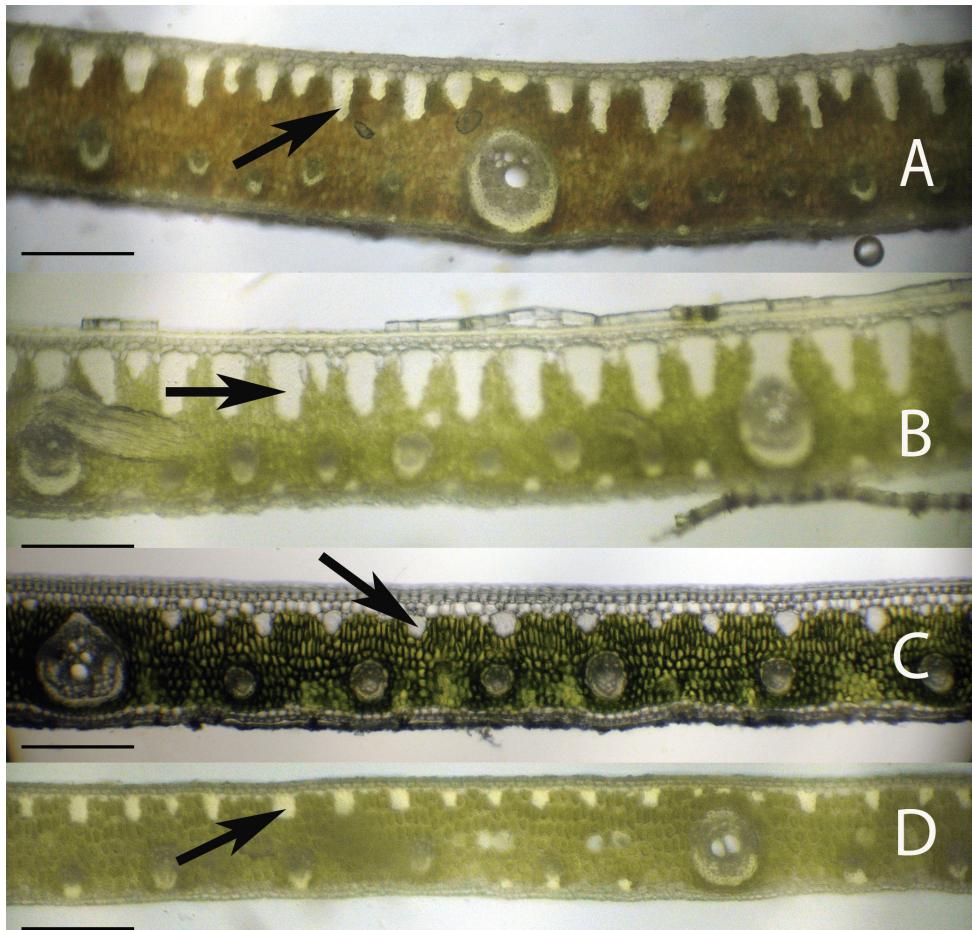


Figure 4. Leaflet cross-sections of the Eastern Brazilian Clade of *Syagrus* species with arrows showing the multicellular fiber bundles that are a defining character of species of this clade: **A** *S. coronata* (Mart.) Becc. **B** *S. glaucescens* Glaziou & Becc. **C** *S. kellyana* Noblick & Lorenzi **D** *S. cearensis* Noblick. Scale = 0.2 mm.

minor veins on both surfaces (Fig. 5D) that make the anatomy of *S. macrocarpa* Barb. Rodr. *S. flexuosa* (Mart.) Becc. and *S. cerqueiriana* look interestingly similar to one another.

After examining many leaflet hand sections of various acaulescent palm specimens, it was discovered that many had very different leaflet anatomy. The presence and absence of the anatomical characters in all 25 species is recorded in Table 2. Useful anatomical characters were found to separate the 25 known species of acaulescent and short-stemmed *Syagrus* and an identification key was developed. Several acaulescent *Syagrus* specimens frequently identified as *Syagrus petraea* were found to have distinctive field habits and leaflet anatomies (Table 1 and 2).

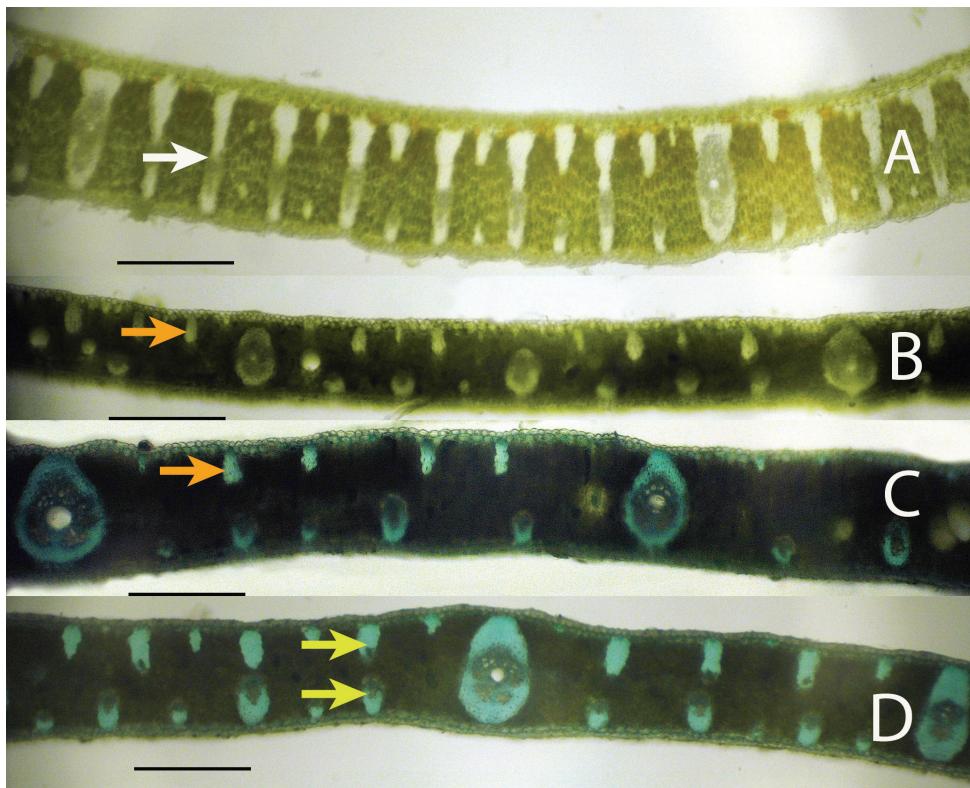


Figure 5. Leaflet cross-sections of the Cluster-stem Clade of *Syagrus* species. (A) *S. campylospatha*, white arrow pointing at an intermediate vein with fibrous sheath extensions to both surfaces forming a girder type vein **B** *S. macrocarpa* Barb. Rodr., orange arrow indicating a minor fiber bundle **C** *S. flexuosa* (Mart.) Becc. orange arrow indicating a minor fiber bundle **D** *S. cerqueirana*, yellow arrows indicating minor veins on both surfaces of the leaflet. Scale = 0.2 mm.

Discussion

Distinguishing Major Clades

Species of the Rain Forest clade (Fig. 1), which includes many Amazonian species, are distinguished anatomically by an almost continuous adaxial fibrous layer, one or a few cells thick just under the epidermis (the hypodermal layer) (Fig. 3A, 3B, 3C, 3D). I speculate that perhaps this nearly continuous fibrous layer strengthens the lamina while maintaining its flexibility (Vincent 1982), helps the leaf shed water and discourages fungus infection. Species of the Eastern Brazilian clade (Fig. 1) are distinguished by thicker and stiffer leaflets reinforced by many adaxial, thick, multicellular fiber bundles along the adaxial side of the leaf and these fiber bundles may extend as far as $\frac{1}{2}$ the distance across the mesophyll (Fig. 4A, 4B, 4C, 4D). Fibers assume much of the load-bearing capacity of the lamina (Horn et al. 2009, Vincent 1982). These fibers and



Figure 6. Leaflet cross-sections of acaulescent *Syagrus* species found in the key: **A** *S. campylospatha* **B** *S. harleyi* **C** *S. procumbens* “emasensis” **D** *S. cerqueirana* **E** *S. minor* **F** *S. allagopteroides* **G** *S. lilliputiana*, arrow indicates a rounded minor fiber bundle **H** *S. cerqueirana*, arrow indicate an elongated, longer than wide minor fiber bundle **I** *S. loefgrenii* **J** *S. longipedunculata*, arrow indicates a minor vein located in the middle of the mesophyll **K** *S. angustifolia* **L** *S. itacambiran* **M** *S. petraea* **N** *S. procumbens*, note major vein near but not adjacent to the margin. Scale = 0.2 mm.

fiber bundles help the leaflet to retain its shape, flexibility and form when leaf turgidity wanes during the periodic dry spells that frequent the seasonally dry forests, *cerrados* and *caatingas* of Eastern Brazil. The Cluster-stem clade (perhaps a misnomer, since not

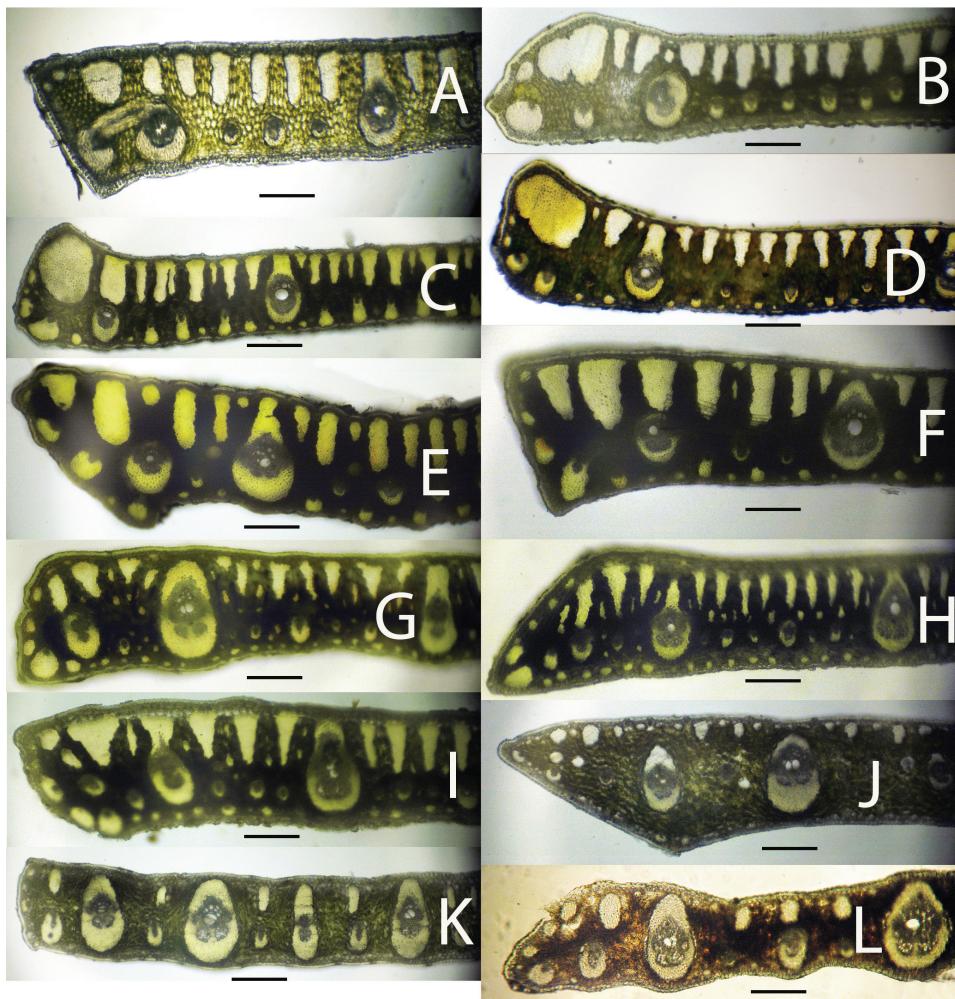


Figure 7. Leaflet cross-sections of acaulescent *Syagrus* species found in the key: **A** *S. gouveiana* **B** *S. drudei* **C** *S. caerulescens* **D** *S. rupicola* **E** *S. glazioviana* **F** *S. evansiana* **G** *S. werdermannii* **H** *S. vagans* **I** *S. microphylla* **J** *S. pleiocladoides* **K** *S. pleioclada* **L** *S. graminifolia* **M** *S. mendanhensis* **N** *S. graminifolia* var. *glazioviana*. Scale = 0.2 mm.

all are cluster-stemmed) is not as clear. *Syagrus campylospatha* (Figs. 5A, 6A) appears anatomically different from the rest of the group having girder type intermediate veins that are attached to both sides of the leaf by fibrous sheath extensions. *Syagrus flexuosa* and *S. macrocarpa* have nearly identical anatomies with minor, sparsely spaced fiber bundles running along the adaxial surface (Fig. 5B, 5C) and *S. cerqueirana* (formerly identified as *S. petraea*) has a similar aspect but replaces these adaxial fiber bundles with minor veins, which are found on both sides of the leaf (Fig. 5D).

Most acaulescent *Syagrus* exhibit the Eastern Brazilian pattern (e.g. *S. gouveiana*; Fig. 7A) with the large, multicellular fiber bundles running along the adaxial side of

the leaflet and the Cluster-stem pattern, similar to that of *S. cerqueirana* (Fig. 5D, 6D, 6H), with minor veins on both surfaces (e.g. *S. lilliputiana*, Fig. 6G), each attached to either the adaxial or abaxial surface by short, fibrous extensions. Since most acaulescent palms grow in seasonally dry areas (*cerrados*) that require stiffer leaflets, it is perhaps understandable why the Rain Forest pattern is not seen among them.

Acaulescent species

Some of the problems of identifying acaulescent *Syagrus* species were covered previously in the introduction concerning the lack of good label information in relation to how leaves and leaflets are displayed or arranged on the plant before pressing and drying. Having observed most of these variations personally in the field has led me to the challenging process of trying to straighten out this much neglected complex of species. For me, it started in Bahia, Brazil with the misidentification of the acaulescent *cerrado* palm, *S. glazioviana*. Many palm taxonomists, including Glassman and myself (Noblick 1991), have erroneously identified it as *S. petraea*. Initially, Glassman (1965) placed it in synonymy with *S. petraea*, based on the shape and size of their female flowers. A few years later, he considered them distinct species (Glassman 1968) after he had seen the lectotype for *S. glazioviana* due to differences in the width of the leaflets and shape of the leaflet tips (symmetrical versus asymmetrical). Finally in his revision (Glassman 1987), he synonomized it once again with *S. petraea*, concluding that the differences seen must have been due to favorable versus unfavorable growing conditions. In western Bahia it is often used to make brooms. It has meter-long leaves with long, regular to loosely clustered pinnae and a spike inflorescence. In the same *cerrados*, one will encounter another acaulescent, spicate palm with shorter leaves and tightly clustered pinnae that are unsuitable for broom making, which I had previously identified as *S. petraea* as well. I currently believe that the smaller western Bahian one is *S. loefgrenii*, which has also been proposed as a synonym of *S. petraea* (Henderson et al. 1995), but the leaflet anatomy of *S. petraea* (Fig. 6M) is very different from the anatomy of both *S. loefgrenii* (Fig. 6I) and *S. glazioviana* (Fig. 7E). It has been an unfortunate fact that most acaulescent, spicate *Syagrus* have gotten automatically classified as *S. petraea*. In truth, acaulescent palms with a sparsely branched inflorescence have also been classified as *S. petraea* (i.e. *S. cerqueirana* from Paraguay). However *Syagrus petraea* is not the only problematic acaulescent *Syagrus*. In his anatomy paper (Glassman 1972), Glassman misidentified *S. cerqueirana* (Swallen 9520 from Mato Grosso) as *S. graminifolia*. He then proceeded to use the anatomy of that misidentified specimen to represent *S. graminifolia* in his publications (Glassman 1972, 1987). When I examined the anatomy of collections of *S. graminifolia* from Goiás I discovered that they had a very different anatomy from what Glassman had published, but I resolved the issue by comparing the anatomy of my specimens with that of a leaflet fragment borrowed from the original 1827 holotype (Burchell 5956) and found them to be a match. In addition, Glassman mistakenly reported Burchell's collection from the state of Piauí,

but Burchell's field notes and itinerary (Smith and Smith 1967) clearly place him in southern Goiás at the time.

Many of the *S. petraea*-types have very different leaflet anatomies. Their visible field characters (Table 1) and their distinctive anatomy has justified splitting up the complex (Noblick and Lorenzi 2010; Lorenzi et al. 2010) by resurrecting formerly synonymized names (e.g. *Syagrus glazioviana*, *S. loefgrenii*) and by describing several new species (e.g. *S. allagopteroides*, *S. angustifolia*, *S. caerulescens*, *S. cerqueirana*, *S. evansiana*, *S. gouveiana*, *S. itacambirana*, *S. minor*, *S. pleiocladoides*, *S. procumbens*, *S. rupicola*). Currently, there are about 26 taxa of *Syagrus* without visible above ground stems or with very short stems and it is strongly suspected that there will be several more based on the anatomy that has so far been observed. As a disclaimer, I feel that this key is still not the final word and will need further revision as new species are discovered and others get reworked. The same species grown under different growing conditions or adult and juvenile forms may look slightly different, but the anatomy maybe an important tool in helping us to resolve these issues. I suspect that some species which appear to be morphologically different but anatomically similar may turn out to be the same species (e.g. *S. allagopteroides* and *S. minor* are suspicious).

In conclusion, leaflet anatomy has been found to be useful in helping to confirm or verify relationships discovered through the molecular analysis and in identifying some of the difficult acaulescent *Syagrus* species.

Anatomical key to acaulescent *Syagrus*

- 1 Many large intermediate veins with fibrous extensions to both adaxial (upper) and abaxial (lower) surfaces forming girders across the leaflet (Fig. 5A, 6A) .. *S. campylospatha*
- No such girders formed 2
- 2 Margin of leaflet protected by a layer of thick-walled cells (Fig. 2E, 6B) *S. harleyi*
- Margin of leaf lacking protective layer with few fibers, veins with exaggerated fibrous sheaths, large fibrous bundles 3
- 3 Margin with a huge fully functional major vein with a somewhat exaggerated fibrous sheath at or near the margin (Fig. 6C) ... *S. procumbens* "emasensis"
- Margin with a vein with an exaggerated fibrous sheath, fiber bundles or anything other than a major vein..... 4
- 4 Minor veins adjacent to both the adaxial and abaxial surface (Fig. 6D-H) ... 5
- Minor veins mostly present adjacent to the abaxial surface and few if any on the adaxial surface 9
- 5 A minor to intermediate vein with an exaggerated fibrous sheath adjacent to the margin and occupying less than half of the margin (Fig. 6D)... *S. cerqueirana*
- A major vein with an exaggerated fibrous sheath adjacent to the margin and occupying more than half to nearly the entire margin (Fig. 2A) 6

- 6 Marginal vein with exaggerated fibrous sheath occupies over half of the margin but not the entire margin (Fig. 6E) *S. minor*
- Marginal vein with exaggerated fibrous sheath occupies the entire margin .. 7
- 7 Major vein usually unattached separated from the hypodermis by another cell layer or two (Fig. 2A, 6F) *S. allagopteroides*
- Major vein usually attached to the adaxial hypodermis but separated from the abaxial by an additional cell layer or two 8
- 8 Minor fiber bundles along the adaxial nearly round in shape (Fig. 6G)
..... *S. lilliputiana*
- Minor fiber bundles along the adaxial elongated, longer than wide (Fig. 6H)
..... *S. cerqueirana*
- 9 Vein with a very large exaggerated fibrous sheath adjacent to the margin .. 10
- Margin without such a vein but with or without minor veins, and/or minor or major large fiber bundles 13
- 10 Minor veins near the middle of the mesophyll (Fig. 6J) ... *S. longipedunculata*
- Minor veins adjacent to the lower abaxial surface 11
- 11 Most large adaxial fiber bundles reaching less than 1/4 to 1/5 across the mesophyll (Fig. 6I)
..... *S. loefgrenii*
- Most large adaxial fiber bundles reach 1/3 to ½ across the mesophyll 12
- 12 A few minor veins near or attached to the adaxial surface and veins often alternating with the minor fiber bundles adjacent to the abaxial surface (Fig. 6K)
..... *S. angustifolia*
- No minor veins near or attached to the adaxial surface and minor veins but no fiber bundles present on the abaxial surface (Fig. 6L) *S. itacambiraniana*
- 13 Large major vein near the margin but not adjacent to it (Fig. 6N)
..... *S. procumbens*
- Major veins neither near the margin nor adjacent to it 14
- 14 Margin with one very large fiber bundle or the first or second adaxial fiber bundles are larger than the rest 15
- Margin with no significantly large fiber bundles 24
- 15 Adaxial fiber bundles long and skinny and reaching less than 1/5 to ¼ across the mesophyll (Fig. 6M)
..... *S. petraea*
- Adaxial fiber bundles long and usually fat and reaching 1/3 to ½ across the mesophyll 16
- 16 No minor fiber bundles scattered throughout the mesophyll 17
- Minor fiber bundles scattered throughout the mesophyll 22
- 17 Minor fiber bundles usually absent from the abaxial surface 18
- Minor fiber bundles usually present either along the abaxial surface and/or margin 19
- 18 Major veins are usually attached adaxially (Fig. 2D, 7A) *S. gouveiana*
- Major veins are usually unattached (Fig. 7B) *S. duartei*
- 19 One major fiber bundle adjacent to the margin 20

- No major fiber bundle adjacent to the margin 21
- 20 Minor veins all attached to the adaxial hypodermis (Fig. 2B, 7C) *S. caerulescens*
- Some adaxial minor veins attached but many unattached (Fig. 7D)....*S. rupicola*
- 21 Major vein attached to adaxial surface by a fibrous sheath extension (Fig. 7E) *S. glazioviana*
- Major vein usually unattached (Fig. 7F) *S. evansiana*
- 22 Major veins surrounded by a very thick fibrous sheath (Fig. 7G) *S. werdermannii*
- Major veins surrounded by a thin to medium fibrous sheath 22
- 23 Adaxial fiber bundles mostly long and skinny in cross-section (Fig. 2C, 7H) *S. vagans*
- Adaxial fiber bundles mostly long and thicker (Fig. 7I).....*S. microphylla*
- 24 Most adaxial fiber bundles reach less than 1/5 across the mesophyll (Fig. 7J) *S. pleiocladoides*
- Most adaxial fiber bundles reach 1/3 to ½ across the mesophyll.....25
- 25 Leaflets deflexed, adaxial fiber bundles more rounded (Fig. 7L)...*S. pleioclada*
- Leaflets straight or erect, adaxial fiber bundles long and skinny.....26
- 26 Leaflets silvery blue color, very small minor fiber bundles between the veins and intermediate fiber bundles adaxially, and a few minor fibers abaxially (Fig. 7L) *S. graminifolia*
- Leaflets green in color, no or few small minor fiber bundles between the veins and intermediate fiber bundles adaxially and none abaxially27
- 27 Leaflets with many minor fibers adjacent to the margin (Fig. 7M) *S. mendanhensis*
- Leaflets with one to no minor fiber bundles adjacent to the margin (Fig. 7N).....*S. graminifolia* var. *glazioviana*

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Appendix

Numerical list to *Syagrus* taxa and numbered collections. (doi: 10.3897/phytokeys.26.5436.app) File format: Microsoft Word file (doc).

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A new species from Thailand and Burma, *Dracaena kaweesakii* Wilkin & Suksathan (Asparagaceae subfamily Nolinoideae)

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Abstract

A morphologically distinct element of the group of *Dracaena* species from Thailand and Burma with undifferentiated leaf sheaths, no leaf blade central costa, free tepals and free thickened filaments known as *Chan nuu* or *Chan pha krai* in Thai is shown to be a distinct species, *Dracaena kaweesakii* Wilkin & Suksathan based on habit, leaf base and margin, inflorescence axis indumentum and floral characters. It is described and illustrated. Ecological and conservation status assessment information are provided.

Keywords

Dracaena L., dragon trees, Thailand, Burma, taxonomy, morphology, conservation

Introduction

The taxonomy of the “dragon tree” group of *Dracaena* L. species in mainland South-East Asia was summarised in Wilkin et al. (2012). The species possess an undifferentiated leaf sheath, lack a leaf blade central costa and have free tepals and free thickened

filaments. Three species with this set of characters are recognised in the World Checklist of Monocotyledons (WCM, Govaerts et al. 2011), *Dracaena cambodiana* Pierre ex Gagnep., *Dracaena cochinchinensis* (Lour.) S.C.Chen and *Dracaena yuccifolia* Ridl. The WCM suggests that there are a total of 15 species of *Dracaena* in Thailand. A further “dragon tree” species occurs in South-East Asian and Pacific islands, *D. multiflora* Warb. ex Sarasin (Wong et al. 1999).

In addition to the three accepted names in Govaerts et al. (2011) and *D. jayniana* Wilkin & Suksathan that was described in Wilkin et al. (2012), a further element of the “dragon tree” group of species usually known as *Chan nuu* or *Chan pa krai* in Thai appeared distinct in its macromorphology from all other related taxa. Thus it was investigated more closely to discover if it represented an undescribed taxon.

Materials and methods

This research involved comparative morphological study of living plants of the “dragon tree” group of *Dracaena* in the field and in cultivation in Thailand and of the specimens cited below. Further specimens of *Dracaena* from the herbaria BM, BK, BKF, QGB, C, K, L, P and WAG were examined. In order to test the hypothesis that *Chan nuu/Chan pa krai* represented a distinct taxon it was compared directly with *D. yuccifolia* (Ridley 1896) and with *D. cambodiana*, *D. cochinchinensis*, *D. jayniana* and *D. multiflora*. The principal characters used are listed in Table 1.

Results

Both *Dracaena yuccifolia* and *Chan nuu/Chan pa krai* differ from other taxa of the Asian “dragon tree” group of *Dracaena* species in their much-branched habit (there may be several hundred branches in large mature trees of *Chan nuu*), with spreading and dividing branches usually borne on a short, unbranched basal trunk. They also possess narrow terminal branches, usually less than 2 cm in diameter near the leafy apices. The other taxa, *D. cochinchinensis*, *D. cambodiana*, *D. jayniana* and *D. multiflora* (Gagnepain 1934, Wong et al. 1999, Chen and Turland 2000) usually have not more than 10 erect or ascending stems bearing few erect to decumbent branches which are not spreading. Their terminal branches are more robust, being at least 2.4 cm in diameter. The latter taxa also possess thicker leaf blades with stronger longitudinal costae than *D. yuccifolia* and the entity under study, in which the leaf blades are relatively thin and soft.

Table 1 shows the main morphological differences between *D. yuccifolia* and *Chan nuu/Chan pa krai*. It is clear that the habit, vegetative and reproductive morphology of the latter are distinct from that of the former species. Thus it is described as a new species below.

Table I. A summary of the main morphological character state differences between *Dracaena kaweesakii* and *D. yuccifolia* Ridl.

Character	<i>Dracaena kaweesakii</i>	<i>D. yuccifolia</i>
Habit	To 12 m tall, branches to several hundred	To 6 m, usually not more than 3 m in coastal forms; branches to ca 80.
Leaf blade dimensions (mm)	110–605 × 9–31	90–735 × 7–35
Leaf blade texture	Thickly chartaceous to thinly coriaceous	Thinly coriaceous
Leaf base colour	White, when fresh, pale to mid brown when dry	Often yellow-hued or brown in living and dried material
Leaf margin	Dark to mid green with a ca 1–2 mm white margin when fresh	Pale to mid green, margin concolorous
Inflorescence axis indumentum	Tuberculate-villous, often dense, sometimes crisped, to 0.15 mm long	Absent to microaculeate, trichomes ca 0.01 mm long
Floral stalk dimensions (above articulation at pedicel apex)	Floral stalk absent (i.e. flower inserted directly on articulation at pedicel apex)	0.5–0.8 × 1.1–1.3 mm
Tepal colour	Cream with a green or yellow hue, paler and more translucent towards margins, greener towards apex and along costa	Bright white
Filament length (mm)	2.2–3.8	3.3–4.9
Filament colour	Intense orange	Bright white
Filament orientation	Erect	Spreading
Anther length (mm)	1.7–2.2	1.0–1.4
Style length (mm)	2.5–3.3	3.4–5.5
Ovary dimensions (mm)	2.3–3.3 × 1.3–2.0	1.8–3.2 × 0.5–1.1
Fruit colour at maturity	Brown, becoming orange just before or after falling from infructescence	Dull red on infructescence
Distribution	Thailand (Saraburi to Chiang Rai) and adjacent eastern Burma.	Thailand (Ratchaburi) to Malaysia (Langkawi)

Description

Dracaena kaweesakii Wilkin & Suksathan, sp. nov.

urn:lsid:ipni.org:names:77132456-1

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

Figs 1–3

Diagnosis. *Dracaena kaweesakii* differs from *Dracaena yuccifolia* Ridl. in its habit, with up to several hundred branches, white (brown when dry) leaf sheaths lacking yellow or dark brown pigmentation and blades with a narrow white margin when fresh. The inflorescence axis of *D. kaweesakii* is tuberculate-villous, and the species lacks a floral stalk above the pedicel articulation. The tepals are cream-green or cream-yellow and



Figure 1. The habit, vegetative, inflorescence and seedling of *Dracaena kaweesakii*. **A** Trunk base showing the pattern of branching and corky, fissured surface **B** Habit **C** Branch apex with erect inflorescence **D** Leaf sheath and blade **E** Seedling with rosulate leaves. Scale bar: **A** 50 cm; **B** 125 cm; **C** 6 cm; **D** 3 cm; **E** 4 cm. From Maxwell 96-379 (**C**), Geesink et al. 8122 (**D**) and photographs. Drawn by Lucy Smith.

the filaments intense orange. The anthers are 1.7–2.2 mm long and the style 2.2–3.3 mm. The ovary is 1.3–2.0 mm broad and develops into and fruits that largely remain brown on the infructescence, turning orange only just before or after falling.

Type. Thailand; Central, Lop Buri, Lam San Ti, Khao Wong Chan Daeng, 15°03'45.2"N, 101°27'17.1"E, fr. 26 May 2009, Wilkin, Suksathan, Phonsena, Truboun, Keeratikiat & Plataan 1500 (holotype QBG!; isotypes BKF!; K!); Figs 1–3.

Description. *Underground organs* unknown. *Indumentum* absent except for inflorescence axes and pedicels with tuberculate-villous trichomes to 0.15 mm long, often dense, sometimes crisped; similar trichomes on margins of leaves and tepal bases and margins. *Habit* treelike, 3–6 m(–12) m in height at maturity with an approximately equivalent crown diameter; usually much-branched, branches spreading and dividing, with up to several hundred terminal branches in large mature trees, branches rarely as few as ca 10 (mainly in high altitude forms such as those on Doi Chiang Dao). *Trunk* base to 1 m in diameter, sometimes markedly thicker than where branching begins, usually at ca 30–100 cm above the soil surface, epidermis brown, grey or ash-white, corky and fissured except at branch apices, enclosing cream-coloured, densely fibrous parenchyma, less dense towards centre, denser and heavier than that of *D. jayniana*. Leaf scars present in apical 30–50 cm of branches where diam. is 1.3–2.4 cm (to 4.2 cm some cultivated plants e.g. Wilkin et al. 1521 perhaps due to increased nutrient availability), epidermis grey to light brown with tightly packed scars. *Leaves* in dense clusters of ca 20–50 leaves at shoot apices, clusters ca 30–120 cm in diam., 7–10 youngest leaves ascending to spreading, older recurved-pendent; divided into a basal sheath and blade, not pseudopetiolate; sheaths 8–16 × 17–32 mm, ovate to ovate-triangular, white (pale brown to mid brown when dry) sometimes with some irregular red markings from dried sap, sheath base clasping stem apex for ca 180°; leaf blades 11–60.5 × 0.9–3.1 cm, lorate-acuminate to linear-acuminate, not or weakly thickened above sheath, softer in texture than other Thai *Dracaena* species occurring on limestone, dark to mid green, thickly chartaceous to thinly coriaceous with a weak longitudinal central costa that is barely visible in apical half of the blade, primary venation parallel, dense sometimes denser in costa than elsewhere, secondary venation not visible; margins ca 1 mm broad and white when fresh, 0.1–0.3 mm wide when dry, to 0.5 mm on sheath, translucent white or pale brown, entire to bearing scattered trichomes, sometimes quite dense on sheath, often concealed by rolling of margins during drying; apex acuminate, terminated by a ca 1.5 mm long blunt, angular apiculus, translucent white to pale brown when dry, similar in appearance to margins. *Inflorescence* terminal on shoot, apical, erect or ascending relative to shoot growth direction in flower but can become pendent in fruit due to their mass, with 4 levels of branching; peduncle (0.8–)3.2–15.5 cm long, primary fertile axis ca 25–38 cm long; partial inflorescences racemose, with a primary axis and flowers in glomerular clusters or solitary towards axis apex; peduncular bracts to 8.7 cm long, foliaceous but with a reduced sheath, lower primary axis bracts to 7.5 cm long, foliaceous, becoming smaller towards apex, ovate-acuminate to broadly so and increasingly brown and scarious towards axis apex, morphologically continuous with bracts of secondary and tertiary axes



Figure 2. Reproductive organ morphology of *Dracaena kaweesakii*. **A** Part of partial inflorescence bearing solitary flowers **B** Flower in side view showing tepal shape and orientation and stamens **C** Flower with 2 tepals removed showing filaments shape and insertion and gynoecium **D** Branch apex showing infructescence in development and peduncular bracts **E** Branch apex with infructescence rendered pendent by weight of fruit **F** Submature fruit containing two seeds **G** The same fruit in cross-section **H, J** seed in dorsal and side view respectively. Scale bar: **A, F, G** 1 cm; **B, C, H, J** 7 mm; **D** 4 cm; **E** 10 cm. From Siriponamat 2 (**A**), Siriponamat 3 (**D**), Geesink et al. 8122 (**F-J**) and photographs. Drawn by Lucy Smith.

and glomerular bracts, secondary branches 3.4–19.1 cm long, tertiary branches 1.9–6.2 cm long; glomerules (fourth level of inflorescence branching) composed of 1–3 flowers, internodes between glomerules to 10 mm in length, glomerular bracts 1.2–1.6 × 0.6–1.5 mm, ovate to broadly so, acuminate to acute, pale brown, scarious, clasping glomerule base, floral bracts like glomerular bracts but smaller and tending to be acute rather than acuminate, clasping pedicel base. Flowers patent to axis to ascending on a 1.2–2.0 × 0.3–0.7 mm, terete-angular pedicel, expanded and articulated at its apex; floral stalk absent, with 0.5–0.8 × 1.0–1.4 mm receptacle inserted directly on pedicel apex; tepals 6.0–8.5 × 1.2–2.6 mm long, narrowly oblong to oblong-elliptic or oblong-lanceolate, free almost to base, erect, with apical half recurved, cream with a green or yellow hue, paler and more translucent towards margins, greener towards apex and along thickened longitudinal costa, apex cucullate, acute to rounded, margins towards apex bearing a fringe of translucent trichomes; filaments 2.2–3.8 × 0.4–0.7 mm (free part), erect, narrowly lanceoloid, thickened, intense orange, green at base and where fused to tepal base, orange colour derived from bundles of heavily pigmented cells in translucent matrix; anthers dorsifixed, before anthesis 1.7–2.2 × 0.4–0.7(–1.0) mm, pale yellow, oblongoid; ovary 2.4–3.3 × 1.3–2.0 mm, ellipsoid to narrowly obovoid, pale green, 3-locular, with an apical swelling at the apex of each vertical loculicidal dehiscence line, swelling minutely verrucate and surrounding point of style insertion, style 2.5–3.3 mm long, erect, terete, white, stigma 0.5–0.8 mm in diam, 3-lobed, capitate. Inflorescence usually with most bracts fallen, trichomes substantially persistent. Fruit a berry, tepal remains persistent at base, each berry bearing 1–3 seeds, 6.6–8.3 × 7–8.5 mm and (sub)globose (where 1-seeded), 7.0–8.2 × 9.9–11.3 mm (2-seeded) or 8.3–8.8 × 11.2–12.0 mm (3-seeded) and lobed, light to mid brown, becoming orange at maturity but most orange fruit already fallen, when dry with a paler cap around point of style base insertion sometimes bearing stylar remains. Seeds ca 6–7 mm in diam., globose to broadly triquetrous, pale brown, smooth but microreticulate.

Distribution. Specimens seen from northern, northeastern and central Thailand, but anecdotal evidence exists as to extensive distribution in adjacent Burma (Fig. 4) through oral reports of the Burmese workers at Doi Ang Khang, which is on the Thailand/Burma border.

Specimens examined. Thailand. Northern; Chiang Rai, Mae Sai, Doi Pha Mi/Doi Nang Non/Khun Nam Nang Non, 20°22'18.8"N, 99°51'12.9"E, old infructescence 1 June 2009, Wilkin, Suksathan & Wongnak 1507 (BKF!; K!; QBG!); Mae Sao, Doi Ang Khang Royal Project, cultivated bonsai garden nursery, 19°54'09.1"N, 99°02'30.2"E from a branch brought from a limestone ridge ca 2 km away (in Burma), sterile 30 May 2009, Wilkin, Suksathan, Wongnak & Sumit 1505 (BKF!; K!; QBG!); Chiang Mai, Doi Chiang Dao, sterile 28 Jan. 1913 Kerr 2870 (BM!; K!); Doi Chiang Dao, fr. 3 Nov. 1922, Kerr 6542 (BM! K!); Doi Chiang Dao (Chiengdao), fr. 22 April 1940, Garrett 1189 K!); Doi Chiang Dao, fr. 27 Sep. 1971, Vidal 5245 (AAU!; BKF!; L!; P!); Doi Chiang Dao, fr. 6 Jan. 1975, Geesink, Hiepko & Phengklai 8122 (K!, L!); Doi Chiang Dao Wildlife Sanctuary, north cliffs of Doi Nahng limestone mountain, fl. 17 March 1996, Maxwell 96-379 (BKF! CMU); Doi Chiang Dao, Doi



Figure 3. Photographs of *Dracaena kaweesakii* showing its habit and reproductive morphology. **A** Trunk base of large individual showing and coky, fissured surface **B** habit of relatively small individual **C** habit viewed from below showing the rich branching **D** Fertile shoot apex showing the white leaf margins and bearing an inflorescence **E** Branch apex with infructescence rendered pendent by weight of fruit, narrow branch diameter and leaf scars **F** Flowers on partial inflorescence showing tepal, stamen and gynoecium orientation, shape and colour and axis indumentum. Photographs by Warakorn Kasempankul/Parinya Siriponamat (**A, B, D, F**) and Paul Wilkin (**C, E**).

Chiang Dao Wildlife Sanctuary, ridge to closest peak to ranger station, 19°23'02.3"N, 98°51'04.4"E, sterile 12 November 2011, *Wilkin, Suksathan, Trias Blasi, Clark & Phitak* 1525 (BKF!; K!; QBG!); Mae Sa, Queen Sirikit Botanic Garden Botanical Resort, near restaurant, cultivated plant of unknown origin, fr. 8 June 2009, *Wilkin, Suksathan & Sumit* 1521 (BKF!; K!; QBG!). Northeastern; Loei, Nong Hin, near Ban Suan Hom, 17°01'45.2"N, 101°44'28.8"E, fr. 5 June 2009, *Wilkin, Suksathan, Phonsena, Keeratikiat & Tot* 1517 (BKF!; K!; QBG!). Central; Saraburi, Muak Lek, Lam Phaya Klang, Si U-tumpon temple, fl. 23 Mar. 2009, *Sriponamat* 2 (BKF!); Saraburi, Muak Lek, Lam Phaya Klang, Si U-tumpon temple, fl. 7 May 2009, *Sriponamat* 3 (BKF!).

Vernacular names. *Chan nuu* (Saraburi, Lop Buri, Loei) *Chan pa krai* (Chiang Mai, Chiang Rai), *Chan ku on* (Shan, Chiang Rai and Burma)

Ecology. On limestone rocks from 550–2000 m altitude. In higher mountains on ridge tops (*Chan pa krai* form) and on the slopes and/or summits where they occur on lower limestone mountains in Loei and Lop Buri Provinces of Thailand. Higher altitude forms tend to be smaller, with fewer branches, a more open crown and smaller leaves, especially when in more exposed habitats. However, trees to ca 8 m in height and diam. and 50 cm DBH can be found in dense montane forest on limestone ridges at high altitude in northern Thailand.

Conservation status. As indicated in Fig. 4, there are two groups of lowland populations of *Dracaena kaweesakii*, in Saraburi and Lop Buri (Central Thailand), where we have reports supported by photographs of seven populations in addition to the localities represented by *Wilkin et al.* 1500 and *Sriponamat* 2 and 3. It is found near Nong Hin in Loei Province (northeastern Thailand). There are three known localities in northern Thailand; at Doi Chiang Dao and near Doi Ang Khang and Mae Sai. These population locations were imported into GeoCAT (Bachman et al. 2011; <http://geocat.kew.org/>) and extent of occurrence (EOO) was calculated to be 73, 657 km², while area of occupancy (AOO) was calculated to be 44 km² based on a cell width of 2 km. However, anecdotal reports suggest the species is also distributed well into Burma on limestone ridges. The authors have seen populations of 10s to 100s of individuals and we have received reports of seven populations with sizes from eight to 150 mature plants in Saraburi and Lop Buri Provinces, suggesting that there are likely to be a few hundred plants in central Thailand. There appear to be few plants of *Chan pa krai* on Doi Chiang Dao. Thus it is likely that even including its distribution in Burma there would be less than 2, 500 mature individuals, the threshold for criterion C of EN (IUCN 2001).

Dracaena kaweesakii is extracted from the wild for use in horticulture in Thailand and is one of the more popular taxa due to its extensive branching. A number of populations are protected by proximity to temples or having been transplanted into their gardens. There is no evidence yet of over-extraction but sustainability studies are needed at population level; the authors have, for example, encountered an alley of vegetation being cleared to remove *D. kaweesakii* from a limestone karst in Loei Province. Limestone habitats are generally threatened in Thailand by extraction for concrete manufacture, especially those closest to cities such as Bangkok; the populations in Saraburi and Lop Buri are the most vulnerable to this threat. Fires can also be

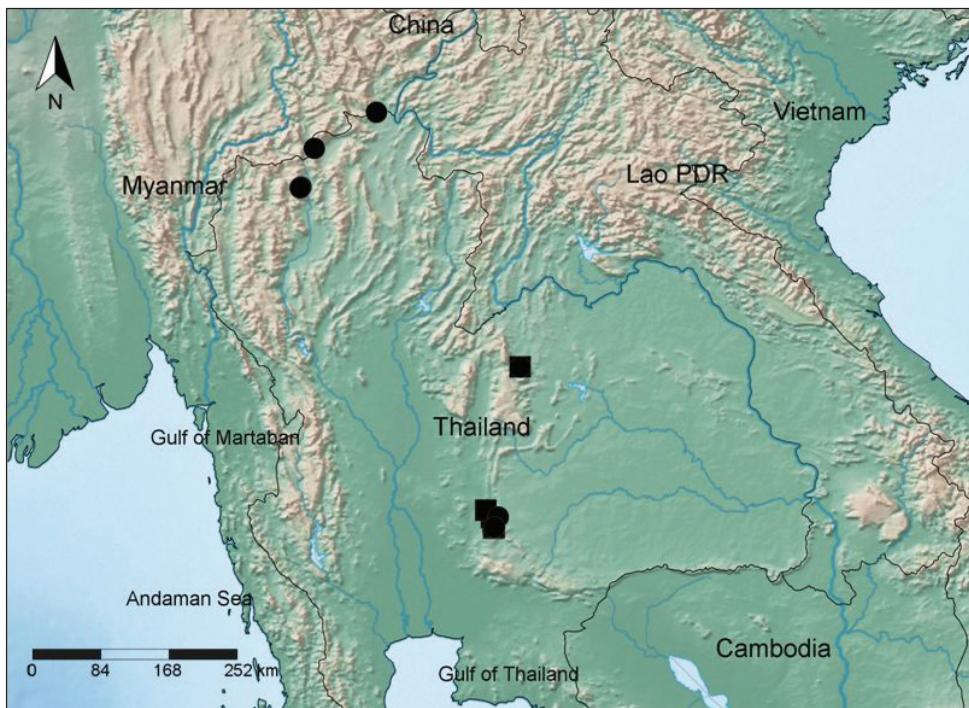


Figure 4. A map showing the distribution of *Dracaena kaweesakii* in northern, northeastern and central Thailand based on both specimen data (●) and observations (■). Map Created with SimpleMappr, <http://www.simplemappr.net> (Shorthouse 2010).

problematic. Thus a preliminary assessment of Endangered (EN B2b (ii, iii, iv, v) C1) based on the criteria of IUCN (2001) is indicated.

Uses. Used in horticulture in Thailand.

Etymology. This species is named for our collaborator, friend and co-author Toi (Keeratkiat Kaweesak) to recognise of his extensive knowledge of *Chan* diversity.

Notes. As indicated in Table 1, *Dracaena kaweesakii* differs from *Dracaena yuccifolia* in both vegetative and reproductive characters. It has up to several hundred branches, while the latter does not exceed about 80. The leaf sheaths are white (brown when dry) and lack the yellow or dark brown pigmentation found in *D. kaweesakii*. The leaf blades of *D. kaweesakii* possess a distinctive a narrow white margin when fresh. The inflorescence axis of *D. kaweesakii* is tuberculate-villous not glabrous to microaculeate, and it lacks a floral stalk above the pedicel articulation; thus the flower is inserted directly at the pedicel apex. The tepals of *D. kaweesakii* are cream-green or cream-yellow, with intense orange filaments (as opposed to bright white tepals and filaments), the anthers 1.7–2.2 mm long (as opposed to 1.0–1.4 mm) and the style 2.2–3.3 mm long (as opposed to 3.4–5.5 mm). The ovary is broader (1.3–2.0 versus 0.5–1.1 mm) and fruits that largely remain brown on the infructescence, turning orange only just before or after falling (dull light red on the infructescence in *D. yuccifolia*).

Two specimens collected on Hainan Island, *How* 70949 & *Lau* 225 may belong to an expanded concept of this species or a morphologically distinct close relative. Both have relatively thin leaves with pale margins and narrow terminal shoots; floral colour and dimensions also appear similar to those of *D. kaweesakii* (e.g. tepals ca 6.5 mm long), although there are no flowers at anthesis on those specimens. They both differ in possessing glabrous inflorescence axes, up to 5 flowers per glomerule and a stalk above the point of articulation of the pedicel. Neither is *D. cochinchinensis* as they have been determined. Both specimens possess a few leaves and an inflorescence with a few closed flowers. The taxonomy of *Dracaena* with free tepals in Hainan needs urgent revision including field-based study of fertile plants, not least to provide conservation status information.

The fruits of *D. kaweesakii* were said to be dispersed by squirrels at Nong Hin in Loei Province. This may explain the late transition from brown to orange in colour around the time of fruit fall. Other species in Thailand have dull red fruits on the infructescence, bird dispersal appears likely. Field studies are needed to test these hypotheses.

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