A Phylogenetic Study of the Plant

Family Martyniaceae (Order Lamiales)

by

Raul Gutierrez

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved October 2011 by the
Graduate Supervisory Committee:

Martin F. Wojciechowski, Chair
Leslie R. Landrum
Kathleen B. Pigg
Charlie Butterworth

ARIZONA STATE UNIVERSITY

December 2011

ABSTRACT

Acceptance of the plant group Martyniaceae as a distinct family has long been questioned. Previously placed in the family Pedaliaceae, the Martyniaceae have been allied to numerous other families within the order Lamiales. The objectives of this study include the investigation of the placement of the Martyniaceae within the order Lamiales using molecular data (chloroplast DNA sequences), the further examination of the internal relationships of the Martyniaceae using an expanded nuclear and chloroplast sequences data set, and the construction of a taxonomic treatment of the family that includes all published names and taxa in the Martyniaceae. An analysis of the Lamiales using two chloroplast gene regions (*ndhF* and *rps16*) reveals that the Martyniaceae should be segregated from the family Pedaliaceae, but is not able to support the placement of any of its putatively-related families as sister to the Martyniaceae. Sequences from 151 taxa of the Lamiales are included in the analysis, including six representatives from the Martyniaceae. An analysis of the Martyniaceae using three chloroplast gene regions (*psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron) and the Internal Transcribed Spacer resolves two major clades within the Martyniaceae corresponding to the North American taxa (*Martynia* and *Proboscidea*) and the South American taxa (*Craniolaria*, *Holoregmia*, and *Ibicella*). Sequences from all five genera and 15 taxa were included in the analysis. Results from the molecular phylogenetic analyses are incorporated into a revised taxonomic treatment of the family. Five genera and thirteen species are recognized for the family Martyniaceae.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

Figure	Page

INTRODUCTION

The family Martyniaceae Horan. (1847), some members of which are commonly known as "Devil's claw", "Cat's claw", or "Unicorn plant", consists of thirteen species in five genera (Van Eseltine 1929; Thieret 1977) that are placed within the order Lamiales (Angiosperm Phylogeny Group III 2009). The family is restricted to the New World and found primarily in subtropical and warm temperate areas from the southern half of the United States southward through Central America to Uruguay and Argentina, including many of the islands of the West Indies (Thieret 1977; Benson 1979; Figs. 1, 2). A few species have been introduced to other parts of the world as ornamentals, often escaping cultivation and quickly becoming weeds (Thieret 1977; Gibson 1999; Meyers-Rice 1999b). Genera include *Craniolaria* L., found in South America and the West Indies (Fig. 2), *Holoregmia* Nees, found in the state of Bahia in Brazil (Fig. 2), *Ibicella* Van Eseltine, found in South America (Fig. 1), *Martynia* L., found in Mexico, Central America, and the West Indies (Fig. 1), and *Proboscidea* Keller in Schmidel, found in the United States and Mexico, with disjunct populations occurring in Guatemala and Peru (Figs. 2, 3; Table 1). Plants in this family can typically be found in disturbed habitats in arid and semi-arid areas such as grasslands, deserts, and thornscrub, including in and along washes and arroyos, along roadsides, in pastures and cultivated fields, and along beaches and dunes, at elevations from sea level to about 6000 feet (1850 meters; Van Eseltine 1929; Thieret 1977; Bretting 1981).

Description of the Family – Members of the Martyniaceae are characterized as being annual or short-lived perennial herbs with simple, opposite to sub-opposite leaves (Fig. 3). The size of leaves can vary greatly according to the availability of water, with wetter seasons producing larger leaves. Genera, species, and subspecies can be separated on the basis of their habit, size of the inflorescence, calyx and corolla shape and color, and the shape of the fruits and seeds.

HABIT–*Holoregmia* and *Craniolaria* are usually shrubs, sub-shrubs or herbaceous perennials that can grow to 3 m. *Ibicella*, *Martynia*, and *Proboscidea* are annuals that may be long-lived, with one perennial species occurring in the genus *Proboscidea*. Most species are erect to decumbent and rarely grow taller than 1 m, falling over under the weight of the stems and developing fruits.

VESTITURE–One of the defining characteristics of the family Martyniaceae is the presence of glandular and nonglandular hairs on all above-ground surfaces of the plant, including stems, leaves, all floral parts, and the fleshy exocarp of the fruits. These hairs are multicellular, and the glandular ones give the plant a cold wet feeling and can contribute to the aroma of some species. Not much is known of the chemical composition of the exudate, though it was once thought that the exudate aided in the plant's digestion of the insects it trapped. Although there appears to be some phosphatase activity in the exudate (Plachno et al. 2009), the general consensus is that the Martyniaceae are not carnivorous (Meyers-Rice 1999a; Wallace and McGhee 1999; Rice 2008).

ROOTS–Most species in the Martyniaceae have taproots, except for *Craniolaria integrifolia* Cham. and *Proboscidea althaeifolia* (Benth.) Decne. These exceptions produce tuberous roots from which the aerial portions arise during favorable growing periods (Van Eseltine 1929; Bretting 1981). One specimen examined of *Ibicella parodii* Abbiatti (*Leguiza & Carrizo 67*, CTES) from western

Argentina has portions of a tuberous root attached to the sheet. This is not known from other specimens and may represent an anomaly, a mixed collection, or a new species.

LAMINA–Leaf blades in the Martyniaceae range from obcordate, reniform, and deltoid, to ovate. The outlines can be entire to lobed, with shallow to deep sinuses, and the margins can be entire to denticulate and/or sinuate-undulate. The leaves of *Holoregmia* are the most distinguishable of the family, being densely velutinous and with a darker upper surface. The largest leaves can be found in *Proboscidea parviflora* (Woot.) Woot. & Standl. and *Martynia annua* L., which can often barely fit on standard herbarium sheets. The size of leaves is often a result of available water, with wetter seasons producing larger leaves. The variability of leaf lamina shapes and sizes due to environmental factors does not allow this character to be used for delimitation of the genera.

INFLORESCENCE–The taxa of the Martyniaceae have terminal racemes that occur between the opposite to sub-opposite leaves, and one axillary shoot arises from each of the spaces between the leaves and inflorescence. *Proboscidea spicata* Correll, so named because of its "spicate" inflorescence, technically also has a racemic inflorescence. It is thus named for its short pedicels, which are the shortest in the genus and give the inflorescence a pseudo-spikelike appearance.

FLOWERS–Flowers are perfect, complete, zygomorphic, and pentamerous (Fig. 3), often with a conspicuous spicy or musky aroma. Calyx characters can be very important in the delimitation of genera in the Martyniaceae. Sepals in *Martynia*, *Ibicella*, and one species of *Proboscidea* (*P. sabulosa* Correll) are free or united less than 10% of their length (Table 1). *Craniolaria*, *Holoregmia*, and the rest of the *Proboscidea* have sepals that are united for more than 50% of their length (Table 1). This calyx type is split down to the base of the abaxial side, with the calyx lobes prominent adaxially and more apparent in the genus *Proboscidea* (Fig. 3). The corolla lobes can be imperceptible in some *Craniolaria* and *Holoregmia* specimens, appearing as minute teeth at the apex of the united calyx. The calyces of *Holoregmia* are more inflated or urceolate than the calyces of *Craniolaria.*

The corolla types of the Martyniaceae can be put into two categories. The corollas of *Craniolaria* are the largest flowers of the family, easily reaching over 10 centimeters long in some specimens. These corollas are pale green to pale yellow to white, with an extremely long and narrow tube that opens up into a campanulate throat (Table 1). The lobes are rounded and appear almost radiate. Based on the pale color of the corolla and long narrow tube, these flowers are most likely pollinated by hawkmoths.

The corollas of the rest of the family range from 2 to 6 centimeters. The constricted portion of the tube is shorter or up to 1 centimeter long and opens up into an obliquely campanulate or funnelform throat. Corollas of *Holoregmia* are white to pale yellow with various purple blotches (Table 1). Yellow corollas with orange or brown markings are seen in *Ibicella* and one species of *Proboscidea* (*P. althaeifolia*). All other corollas in *Martynia* and the rest of the *Proboscidea* are white to pink, lavender, or maroon, and have various pink-to-purple dots or splotches and yellow-to-orange nectar guides (Table 1). The lobes on this type of corolla may be variously marked, especially the pinkish corollas of *Martynia*, *Proboscidea triloba* (Schlect. & Cham) Decne., and *P. parviflora*. Based on the size and color of the corollas, the pronounced scent that accompanies the flowers of many of the species, and the nectar guides, these flowers are most likely pollinated by large bees. Bees of the genera *Perdita*, *Melissodes*, *Diadasia*, *Bombus*, *Anthophora*, *Centris*, and *Augochlorella* have been collected from plants of the genus *Proboscidea* (Hurd and Linsley 1963; Thieret 1976; Phillippi and Tyrl 1979; Bretting 1981).

Flowers of the Martyniaceae have four stamens, except for the monotypic *Martynia*, which only has two functional stamens and two rudimentary staminodes. The filaments of the stamens are curved, and the anthers are connivent and dehisce longitudinally. The single pistil is inserted between the two sets of stamens and has two flat stigmas with sensitive lobes. The ovary is superior, unilocular and bicarpellate, with parietal placentae expanded into two broad T-shaped lamellae cohering above to form false partitions. The total number of ovules ranges from four (as in *Martynia*, *Craniolaria*, and *Holoregmia*) to many (as in *Proboscidea* and *Ibicella*).

POLLEN–In general, the pollen is pale yellow-white, apolar, radially symmetrical, spheroidal, and range in size from 43to 133 μm in diameter (Bretting and Nilsson 1988; Harley et al. 2003). Pollen types in the Martyniaceae can be divided into three groups based on their morphology. Pollen of *Martynia* is covered by hexagonal or pentagonal reticulated plates that abut each other and are separated by very narrow grooves. *Ibicella*, *Holoregmia*, and *Proboscidea* all have pollen covered by circular to oval reticulate areoles separated by narrow to wide sulci. Pollen of *Craniolaria* is covered by widely-spaced rings. The space between the rings is filled with numerous tiny finger-like projections that may be shaped like rods, clubs, or cones.

FRUITS–The fruits of the Martyniaceae are the most distinguishing feature of the family (Thieret 1977; Fig. 3, 4), from which the family's common names (unicorn plants, devil's claws, cat's claws) are derived. The fruit is best described as a bivalved capsule with a fleshy dehiscent exocarp and a stony or woody endocarp that is slightly to moderately dehiscent along abaxial and adaxial sutures (Thieret 1977). The body of the fruit can be ovate, rounded, ovate-ellipsoid or ovate-elongate, 2.5 to 10 cm long, and bears the seeds. The fruit is terminated by an incurved hook or beak which can be one to several centimeters long and from shorter than the body to three and a half times its length. The bodies of the fruits of *Martynia*, *Craniolaria*, and *Holoregmia* are ovate to round and may be dorsally flattened. The beak is always shorter than the length of the body in the *Martynia-Craniolaria-Holoregmia*-type fruits, which also only contain four seeds (Fig. 4; Table 1). Fruits of *Proboscidea* and *Ibicella* are ovate-ellipsoid to ovate-elongate and often have a crest along the abaxial and adaxial suture. In the *Ibicella-Proboscidea*-type fruits, the beak is as long or longer than the body of the fruit, which contain more than 20 seeds (Table 1). The fruits of *Ibicella* have echinate or spiny projections along the body of the endocarp. These are lacking in *Proboscidea* (Fig. 3). Due to the nature of the endocarp, the fruits can persist for months and can be found at any time of the year.

SEEDS–Seed type is correlated to fruit type in the Martyniaceae. The seeds can be elongate, rounded, spindle-shaped, or angulate, and can range from 0.6 to 2 cm in length. Seeds from the *Martynia-Craniolaria-Holoregmia*-type fruits are elongate and covered by a papery integument and range in size from 1 to 2 cm long. Seeds from the *Ibicella-Proboscidea*-type fruit are rounded to angulate and 0.6 to 1 cm long. One exception is the species *P. sabulosa*, which has spindle-shaped seeds up to 1.2 cm long.

CHROMOSOMES–Chromosome numbers have been published for four species in three genera in the Martyniaceae (Sugiura 1936a, 1936b; Martini 1939; Srinivasan 1942; Gaiser et al. 1943; Covas and Schnack 1947; Snow 1959; Löve 1977, 1979). Counts range from n=15 to n=18 (Table 2). Sugiura (1936a, 1936b) published chromosome counts of n=15 and drawings of the chromosomes for *Proboscidea fragrans* (Lindl.) Decne. These are the earliest published reports found so far for any member of the Martyniaceae. In addition to embryological data, Martini (1939) published chromosome counts of 2n=30 for *Proboscidea jussieui* Keller (=*Proboscidea louisianica* (Mill.) Thell.) and *Proboscidea lutea* (Lindl.) Stapf (=*Ibicella lutea* (Lindl.) Van Eseltine). Srinivasan (1942) published somatic chromosome numbers of 2n=32 for *M. annua*, but could not verify this number with meiotic counts. He describes the chromosomes as generally small, except for a few larger ones. This description matches Sugiura's (1936a) published drawings of the chromosomes of *P. fragrans*, which show mostly small chromosomes with a few larger ones mixed in. Gaiser et al. (1943) published chromosome counts of n=15 and 2n=30 for *P. louisianica* based on meiotic and somatic counts, respectively. Covas and Schnack (1947) published somatic chromosome counts for *I. lutea* of 2n=32, matching the number of somatic chromosomes published for *M. annua* by Srinivasan (1942). Snow (1959) also published meiotic chromosome counts of n=15 for *P. louisianica*. Löve (1977, 1979) published chromosome counts of n=15 for *P. louisianica* and of n=18 for *M. annua*. It is unclear if these counts represent meiotic or somatic counts. With a few exceptions, the base chromosome number for the Martyniaceae is n=15. There is no evidence of polyploidy, and reasons for anomalous chromosome counts have not been provided.

Habitat and Distribution–Species of the five genera of the Martyniaceae range from the United States south through Mexico to Costa Rica, throughout the West Indies, and south to Argentina, Uruguay and Brazil. Sympatry occurs in central South America between species of *Ibicella* and *Craniolaria*, in Mexico between species of *Proboscidea* and *Martynia*, in the United States between *Ibicella* and *Proboscidea* (the former introduced and not considered part of the native flora), and in the West Indies between *Martynia* and *Craniolaria*. Species of the Martyniaceae are adapted to disturbed areas in arroyos, pastures, and cultivated fields, along roads and beaches, and in dune areas.

The genus *Martynia* is one of the two original genera named by Linnaeus (1753) and has many basionyms attributed to it that are now placed in other genera. It is currently considered monotypic and has one of the largest distributions of any species of the Martyniaceae. It is native from Mexico to Costa Rica and throughout the West Indies, and has been introduced to other parts of the world, including Africa, Asia, and Australia (Fig. 1; Table 1).

The genus *Holoregmia* is also monotypic, though in contrast it has one of the smallest ranges of any species of the Martyniaceae. It is known from a few localities in Brazil in the state of Bahia and is restricted to the valleys of the Rio de Contas and the Rio Paragauçu, both of which arise from the mountains of the Chapada Diamantina (Fig. 2; Table 1).

The two species of *Craniolaria* are completely allopatric, separated by the more mesic Amazon rainforest. *Craniolaria annua* L. occurs on the Greater Antilles in the West Indies and in northern South America in the countries of Venezuela, Colombia, and Guyana. *Craniolaria integrifolia* occurs east of the Andes in the arid and semiarid regions of Argentina, Brazil, Paraguay, and Bolivia (Fig. 2; Table 1).

The two species of *Ibicella* are generally allopatric, though there is some overlap in their ranges. *Ibicella lutea* is found in the grasslands and deserts of Argentina, Brazil, Uruguay, and Paraguay. It has also naturalized in the United States (Munz 1959; Thieret 1977) and Australia (Lawrence 1957; Gibson 1999). *Ibicella parodii* occurs in the eastern Andean foothills of Argentina, Bolivia, and Paraguay. There is a bit of overlap in the ranges of these two species where the foothills level out into the flat plain of central Argentina (Fig. 1; Table 1).

The largest genus in the family, *Proboscidea*, is common in arid and semi-arid areas of the United States and Mexico, with disjunct populations in Guatemala and Peru (Fig. 2; Table 1). *Proboscidea althaeifolia* and *Proboscidea parviflora* exhibit almost identical ranges throughout the southwestern United States (California, Arizona, New Mexico, and Texas) and northwestern Mexico (Baja California, Baja California Sur, Chihuahua, Coahuila, Sinaloa, and Sonora). *Proboscidea triloba* is generally found in Mexico south of the Trans-Mexican Volcanic Belt and in central Guatemala, and *P. fragrans* occurs north of this in central Mexico between the Sierra Madre Oriental and Sierra Madre Occidental. *Proboscidea triloba* ssp. *triloba* is more widespread than its sister subspecies, *P. triloba* (Schlect. & Cham.) Decne. ssp. *diversifolia* (Hevly) Bretting. The distribution of the latter subspecies is limited to fast-draining volcanic soils around Apatzingán in the state of Michoacán. At its northern edge, *P. fragrans* gives way to *P. louisianica*, which occurs north and east of the Pecos River in Texas and northward throughout the southern Great Plains, being most common in Kansas and Oklahoma. *Proboscidea louisianica* has been collected in other states of the United

States, and some of these occurrences may be due to local introductions. *Proboscidea spicata*, which closely resembles *P. fragrans*, is known only from a few collections in West Texas and Coahuila. *Proboscidea sabulosa*, another rare species, is known from deep sand dune habitats of West Texas (Hudspeth, Crane, Wink, and Ward counties) and adjacent southeastern New Mexico (Lea County), central New Mexico (Socorro County), and northern Chihuahua (Samalayuca dune field).

Taxonomic history – The complicated taxonomic history of the family Martyniaceae, beginning with Linnaeus (1753) and ending with Bretting (1981) and Cronquist (1981), is summarized here (Table 3). The first recorded mention of the family Martyniaceae was by Linnaeus in *Species Plantarum* (1753; Table 3), who included two genera in the family, *Craniolaria* and *Martynia*. Lindley (1825) and Brown (1810; Table 3) placed *Martynia* within "natural order" Pedalineae, which consisted mostly of taxa now placed in the Pedaliaceae and were characterized by the presence of hook-like or barb-like structures on the fruits, a character shared by *Martynia*.

De Candolle (1845) followed Brown's (1810; Table 3) taxonomy, but separated the genus *Martynia* into two sections, sectio *Proboscidea* and sectio *Proboscidella*, on the basis of beak length, with sectio *Proboscidea* having a beak longer than the fruit and sectio *Proboscidella* having a beak shorter than the fruit. Around this time, Nees (1821) described a new monotypic genus, *Holoregmia*, from Brazil.

Decaisne (1865) transferred several *Martynia* species into the genus *Proboscidea* on the basis of fruit shape, making the first valid combinations in the genus *Proboscidea*. Those taxa with distinct sepals were kept in *Martynia*, and those with connate calyces were transferred to *Proboscidea*. He also retained the genus *Craniolaria*, distinguished based on the length of the corolla.

Horaninov (1847) was the first person to publish the name Martyniaceae, a name retained by Stapf (1895) when he separated this group from the Pedaliaceae. Within the family Martyniaceae he recognized three genera, *Martynia*, *Proboscidea*, and *Craniolaria,* and created two sections within the genus *Proboscidea*: *Euproboscidea* and *Ibicella*.

Most systematic treatments since then, including those of Van Eseltine (1929), Lawrence (1951), Munz (1959), Kearney and Peebles (1960), Hevly (1962), Taktajan (1969), Benson (1979), and Bretting (1981), have followed Stapf's treatment and retained the Martyniaceae as a distinct family, as did the Angiosperm Phylogeny Group II (APG II 2003). In his treatment of the family, Van Eseltine (1929; Table 3) raised *Proboscidea* section *Ibicella* to the generic level and included the genus *Holoregmia*, bringing the total number of genera to five. Within *Proboscidea*, Van Eseltine recognized two subgenera: *Dissolophia* and *Euproboscidea*. Bretting's dissertation (1981) included a very thorough monograph, though the work only focused on *Proboscidea*. Within the *Proboscidea*, he recognized three informal lineages (Table 3) corresponding to *P. althaeifolia*, *P. sabulosa*, and the "weedy annuals."

Despite the general acceptance of the Martyniaceae as a distinct family throughout the 20th century (Van Eseltine 1929; Lawrence 1951; Munz 1959; Kearney and Peebles 1960; Hevly 1962; Taktajan 1969; Benson 1979; Bretting 1981), Cronquist (1981; Table 3) rejected the Martyniaceae as a distinct family, considering it conceptually more useful to include the Martyniaceae within the Pedaliaceae and recognizing three subfamilies (Pedalioideae, Martynioideae, and Trapelloideae). A detailed description of the taxonomic history of the group is presented in the Taxonomic Treatment (page 75).

Uses of Martyniaceae – The large, showy flowers and distinctive fruits made the Martyniaceae popular in Europe as ornamentals as early as the 1700s (Miller 1768; Bretting 1984). The popularity of these plants spread to other parts of the world, where they have escaped cultivation and become part of the introduced floras in these areas (Van Eseltine 1929; Munz 1959; Thieret 1977; Gibson 1999; Meyers-Rice 1999b; Gutierrez 2007; Kennedy et al. 2010). The dry, mature fruits of *Martynia* are used as pendants in Mexico, and the fruits of *P. louisianica* and *P. parviflora* are often fashioned into caricatures or folk art (Bretting 1984).

Many species of Martyniaceae are important as food sources throughout their native ranges. The roots of *P. althaeifolia* were eaten by the Seri Indians of northwestern Mexico, and the roots are still fed to livestock in Mexico and Peru (Bretting 1984). The roots of *C. annua* are eaten as a sugar-coated confection or as a cooked vegetable in northern South America and the West Indies (Bretting 1984). In Chihuahua, Mexico, the leaves of *P. fragrans* are boiled and consumed as a potherb (Bretting 1984). The immature fruits of *I. lutea*, *P. louisianica*, *P. parviflora* and *P. fragrans* have been eaten as a vegetable, consumed raw or prepared by boiling or pickling (Kearney and Peebles 1960; Hevly 1962; Nabhan et al. 1981; Bretting 1984). Lastly, the oily seeds of *P. fragrans*, *P. parviflora*, and *P. triloba* are eaten fresh throughout their range (Bretting 1984).

Many groups native to the southwestern United States cultivate the domesticated form of *Proboscidea parviflora* (Woot.) Woot. & Standl.ssp. *parviflora*, or did so historically, as a source of fiber for use in basketry (Kearney and Peebles 1960; Nabhan et al. 1981; Bretting 1982; Bretting & Nabhan 1986; Gutierrez 2007). This domesticated variety, *Proboscidea parviflora* (Woot.) Woot. & Standl.ssp. *parviflora* var.

hohokamiana Bretting, can be distinguished from its wild-type, *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *parviflora* var. *parviflora*, by the longer rostrum on the mature fruits. Splints are bundles of lignified fibers that are peeled or stripped from the lateral surface of the rostra and, along with fibers from other native plants, are used as either the coiling elements or for ornamentation (Nabhan et al. 1981; Bretting 1982; Bretting & Nabhan 1986).

In the United States, *P. parviflora* has been evaluated as a potential industrial oil seed crop for arid lands (Berry et al. 1981; Carr et al. 1985), with yields per hectare estimated at 1000 kg of oil and 675 kg of protein (Berry et al. 1981). Seeds of *P. louisianica*, *P. fragrans*, and *P. althaeifolia*, which have oil content of about 40%, have been shown to have fatty acid and sterol compositions that closely resemble soy bean oil (Ghosh and Beal 1979). It is due to this high oil content that seeds of *P. parviflora* and *P. fragrans* are used to polish pottery in Mexico and the southwestern United States (Bretting 1984).

Several plants are used medicinally, though their effectiveness has not been substantiated. Dried fruits of *Martynia* and *Proboscidea* are burned and the ashes used to treat paralysis in Mexico and Central America (Bretting 1984). In Argentina, the seeds of *Ibicella* are used as an eye medicine (Abbiatti 1939; Bretting 1984). The fleshy roots of *C. annua* are used in Colombia and Venezuela as a laxative, sedative, emollient, and to treat menstrual disorders, erysipelas, and syphilis, and in Puerto Rico to relieve heart pains (Bretting 1984). The sticky leaves of *Martynia* are used to remove lice from poultry in Mexico and Central America (Bretting 1984).

Objectives of this study – The objectives of this study include the investigation of the placement of the Martyniaceae within the order Lamiales using molecular data (chloroplast DNA sequences), the further examination of the internal relationships of the Martyniaceae using an expanded nuclear and chloroplast sequences data set, and the construction of a taxonomic treatment of the family that includes all published names and taxa in the Martyniaceae.

A recent study of the family Martyniaceae, utilizing the Internal Transcribed Spacer (ITS) region of nuclear ribosomal DNA (Baldwin et al. 1995; White et al. 1990), included four of the five genera and 12 taxa (Gutierrez 2002). This study found that within the family Martyniaceae, two distinct clades were supported, roughly corresponding to the distribution of the genera in North and South America (Gutierrez 2002). The predominantly North American genera *Martynia* and *Proboscidea* were placed together as sister groups. The predominantly South American genera *Craniolaria* and *Ibicella* were also placed as sister groups (Gutierrez 2002). Within *Proboscidea*, three infrageneric groups suggested by Bretting (1981) were supported by the results of the phylogenetic analyses of the ITS data set. These three lineages correspond to (1) *P. sabulosa*, (2) *P. althaeifolia*, and (3) the rest of the taxa in the genus informally known as the "weedy annual species," which includes *P. fragrans*, *P. louisianica*, *P. parviflora*, and *P. triloba*.

The same study (Gutierrez 2002), which included samples from representatives across the Lamiales, also showed that the sister group to the Martyniaceae was a clade consisting of members of the Lamiaceae, though bootstrap values failed to support this relationship (Gutierrez 2002). While the ITS region was useful in elucidating relationships within the family, it was not as useful across the order due to its high rate of evolution (Schwarzbach and McDade 2002). Several other studies of the order Lamiales included only one (Olmstead et al. 2001; Bremer et al. 2002; Soltis et al. 2011) or two (Oxelman et al. 2005; Rahmanzadeh et al. 2005) samples from the Martyniaceae, and no more than five samples from the closely related families (Acanthaceae, Bignoniaceae, Lamiaceae, Pedaliaceae, and Verbenaceae). There was strong support for the monophyly of these families, but support for the relationships between the families was only present deeper in the trees and disappeared in the more derived lineages to which the Martyniaceae and related families were placed. With the lack of support, these lineages collapsed into a large unresolved polytomy. Other studies that have included representatives from the Martyniaceae were done on the Acanthaceae (McDade and Moody 1999; Manktelow et al. 2001; Schwarzbach and McDade 2002) and Verbenaceae (Marx et al. 2010), though each of these studies included only one representative from the Martyniaceae, which was used as an outgroup.

For the purpose of studying the placement of Martyniaceae within the Lamiales, sequences of the chloroplast *ndhF* and *rps16* genes will be used in the molecular phylogenetic study to be described in this dissertation. These regions have been used in the molecular studies of the order Lamiales that were previously mentioned (Oxelman et al. 1999; Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005) and families and tribes within the order (Acanthaceae – Manktelow et al. 2001; Antirrhineae – Ghebrehiwet et al. 2000; Oleaceae – Wallander and Albert 2000; Plantaginaceae – Albach et al. 2005; Scrophulariaceae – Olmstead and Reeves 1995). For the molecular studies of the Lamiales, these regions appeared to be able to resolve relationships both within families and in the deepest branches of the tree. Support for the branches of the more-recently derived lineages decreased, causing them to collapse into an unresolved polytomy. As for the studies focusing on families and tribes within the Lamiales, the chloroplast genes appeared to have sufficient rates of evolution to resolve relationships within these groups. Common to all of these studies is limited sampling from the Martyniaceae and related families, these often used as outgroups to the groups being studied. For this study, the chloroplast genes *rps16* and *ndhF*, in addition to more thorough sampling of the Martyniaceae and related families, will be used to determine if Martyniaceae is monophyletic, to resolve the relationship between the Martyniaceae and the Pedaliaceae, and to identify the sister group to the Martyniaceae.

Another purpose of this study is to look more closely at relationships within the Martyniaceae, expanding on the previous ITS study (Gutierrez 2002). The previous study included four of the five genera and 12 of the taxa of the Martyniaceae. The study to be described in this dissertation will include ITS sequences from an additional three taxa, including the fifth genus not previously sampled. Chloroplast sequences have also been included to increase the robustness of the results and to compare the utility of nuclear and chloroplast sequences in the phylogenetic reconstruction of the Martyniaceae. The three chloroplast gene regions used in this study include: the $trnH^{(GUG)}$-*psbA* intergenic spacer (Shaw et al. 2005), the $trnQ^{(UUG)}$-5'*rps16* intergenic spacer (Shaw et al. 2007), and the $trnS^{GCU}$-$trnG^{UUC}$-$trnG^{UUC}$ intergenic spacer and intron (Shaw et al. 2005). These regions have been demonstrated to exhibit evolutionary rates similar to the ITS region and are thus appropriate for this analysis (Shaw et al. 2005; Shaw et al. 2007).

The ultimate aim of this work is to revise and reconcile previous treatments of the Martyniaceae to produce a monograph that utilizes new data on phylogenetic relationships from the molecular studies. It will be the first work to include all taxa in the family, and will also reexamine relationships and species concepts in light of results of recent molecular work and the examination of a larger number of herbarium specimens. Thirteen species are recognized in the present treatment. Two of these species, *P. parviflora* and *P. triloba*, are further divided into three and two subspecies, respectively. The category variety has been employed to further distinguish two forms, a domestic and a wild type, of the subspecies *P. parviflora* ssp. *parviflora*. In addition to the taxonomic treatment of the family Martyniaceae, included in this dissertation, as Appendix A, is a regional treatment of the family that has been submitted for the Flora Mesoamericana Project in its originally submitted format.

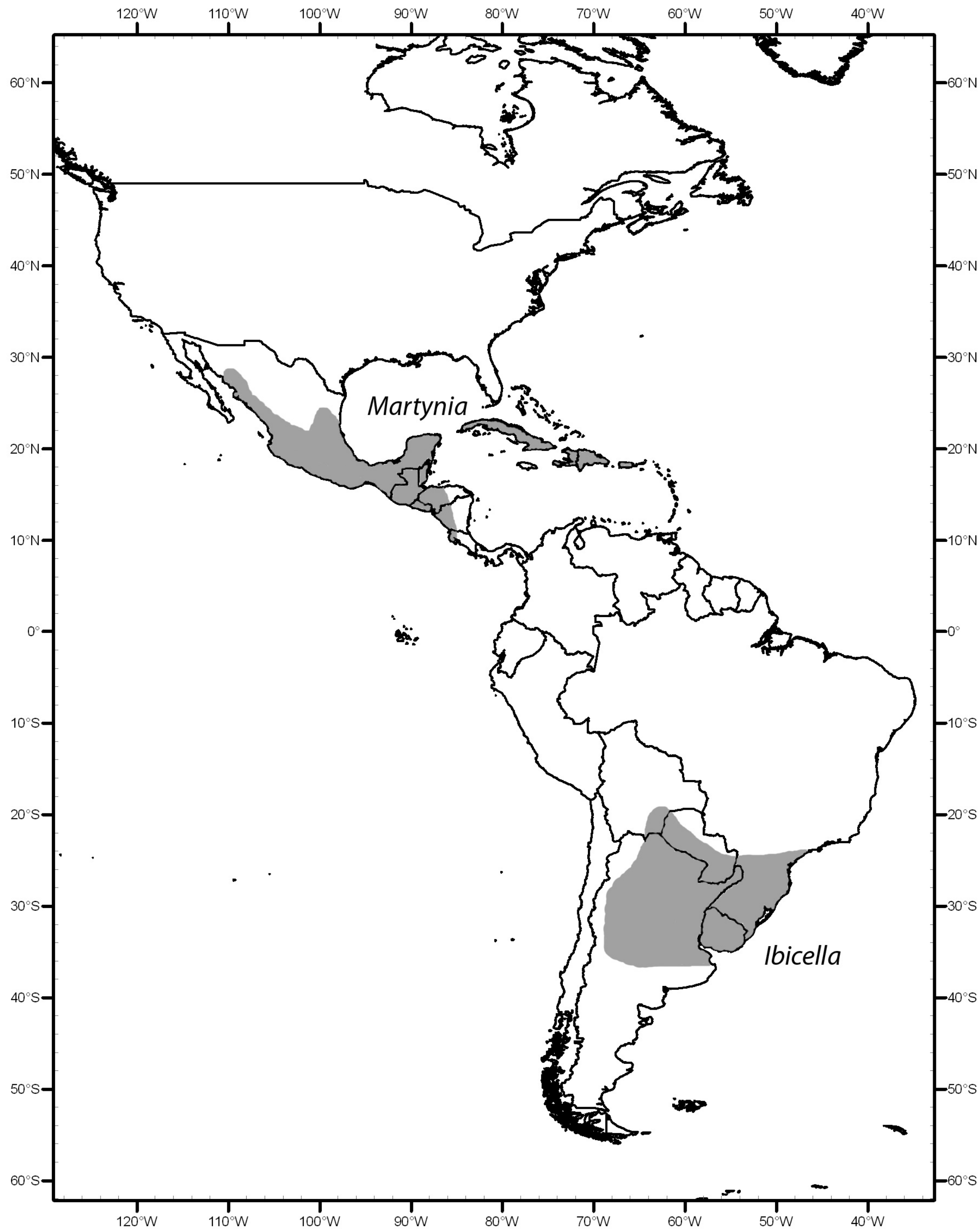

Fig. 1. Distribution of the genera *Martynia* and *Ibicella*.

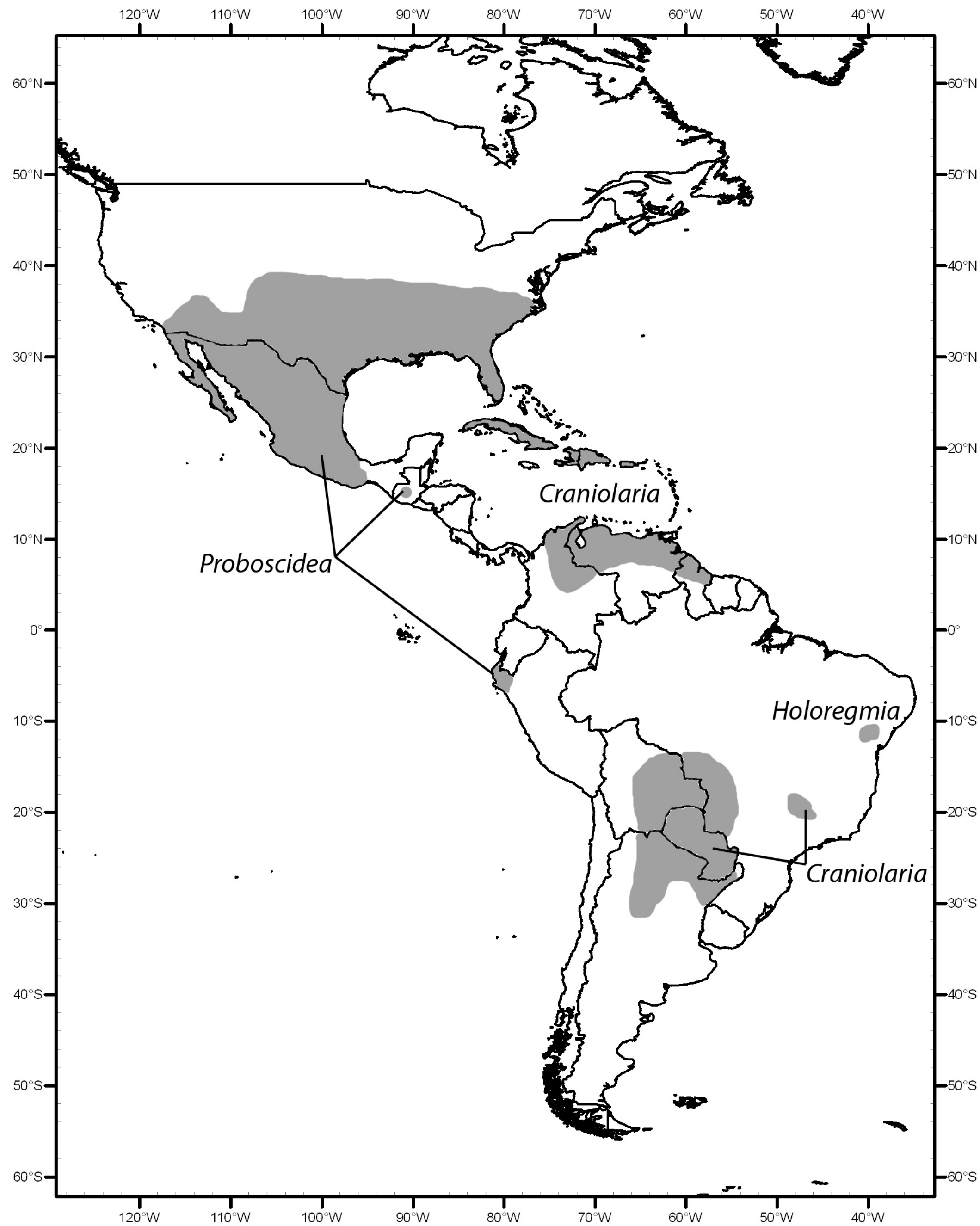

Fig. 2. Distribution of the genera *Craniolaria*, *Holoregmia*, and *Proboscidea*.

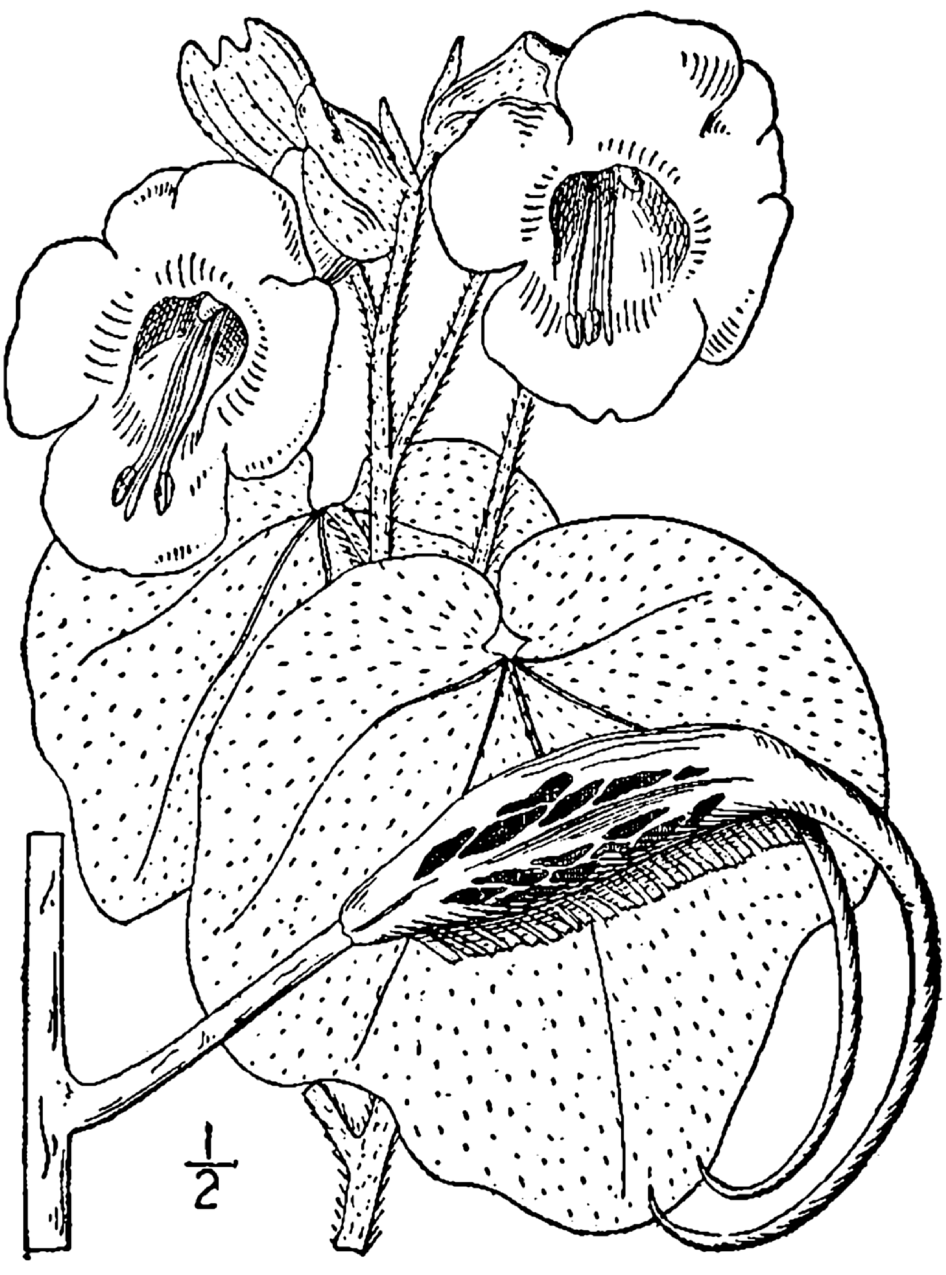

Fig. 3. Illustration of *Proboscidea louisianica*. Courtesy of: USDA-NRCS PLANTS Database / Britton, N.L., and A. Brown. 1913. *An illustrated flora of the northern United States, Canada and the British Possessions. 3 vols.* Charles Scribner's Sons, New York. Vol. 3: 239.

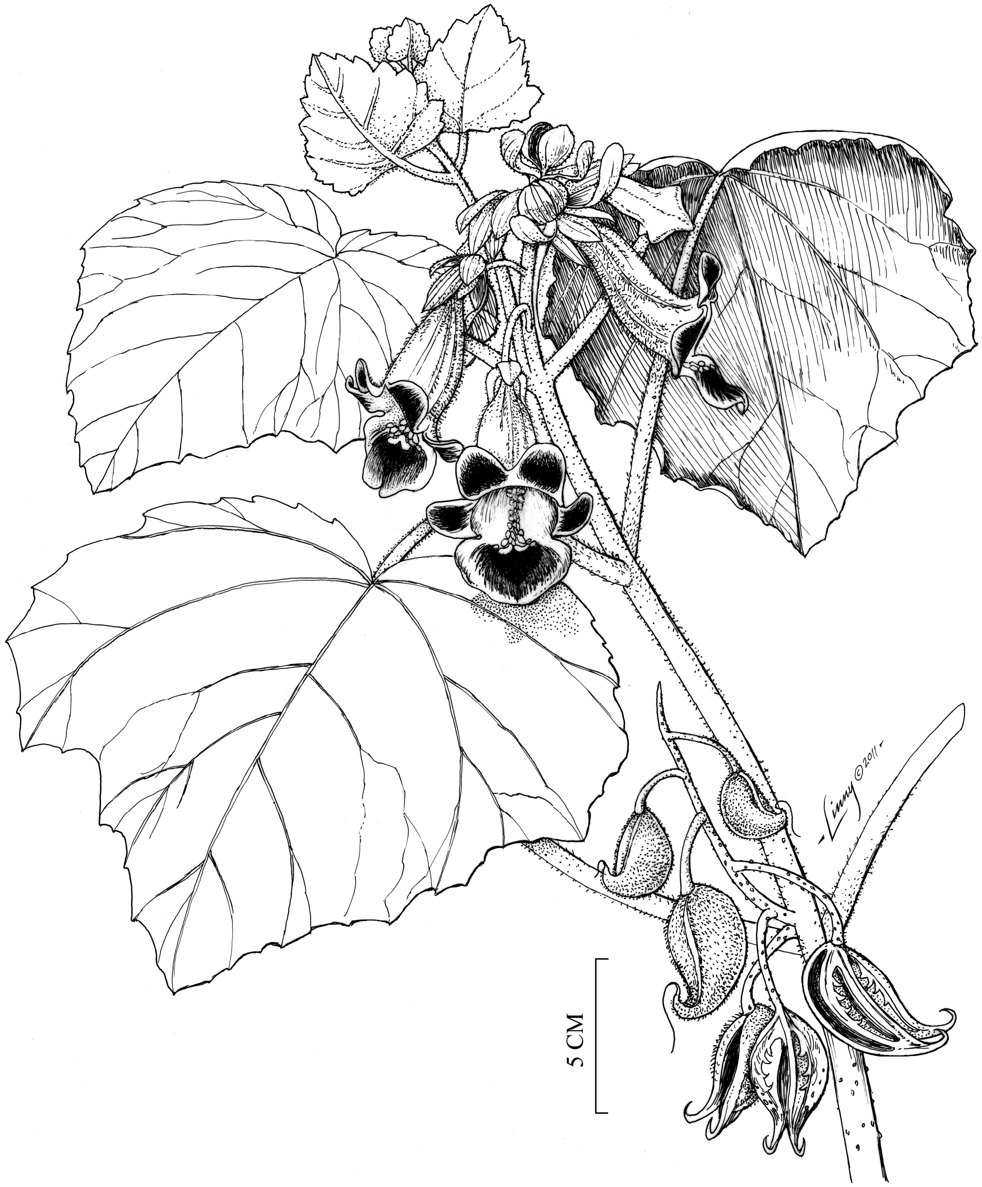

Fig. 4. Illustration of *Martynia annua*. (Art by Linny Heagy © 2011)

Table 1. Distinguishing characteristics of the genera of the family Martyniaceae.

	Craniolaria	*Holoregmia*	*Ibicella*	*Martynia*	*Proboscidea*
No. of species	2	1	2	1	7
Corolla color	Pale yellow to white	Pink	Yellow	Pink	Yellow, pink, white
Sepals	Connate	Connate	Separate	Separate	Connate (separate in *P. sabulosa*)
Length of rostrum on fruit in relation to the body	Shorter than the body	Shorter than the body	Longer than the body	Shorter than the body	Usually longer than the body; equal to the body in *P. triloba*
No. of seeds per fruit	4	4	Many	4	Many
Geographic Distribution	South America, West Indies	Brazil	South America	Mexico, Central America, West Indies	United States, Mexico, Guatemala, Peru

Table 2. A comparison of published chromosome counts for the family Martyniaceae.

Publication	Species	Chromosome Count
Sugiura 1936a, 1936b	Proboscidea fragrans	n=15
Martini 1939	Proboscidea louisianica	2n=30
Martini 1939	Ibicella lutea	2n=30
Srinivasan 1942	Martynia annua	2n=32
Gaiser et al. 1943	Proboscidea louisianica	n=15, 2n=30
Covas and Schnack 1947	Ibicella lutea	2n=32
Snow 1959	Proboscidea louisianica	n=15
Löve 1977, 1979	Proboscidea louisianica	n=15
Löve 1977, 1979	Martynia annua	n=18

Table 3. A review of the taxonomic history of the family Martyniaceae.

Linnaeus (1753) Didynamia Angiospermia genus *Craniolaria* genus *Martynia*	Brown (1810) “natural order” Pedalineae genus *Craniolaria* genus *Martynia*	De Candolle (1845) Pedalineae genus *Craniolaria* genus *Martynia* sectio *Proboscidea* sectio *Proboscidella*
Horaninov (1847) Bignoniaceae s. Martyniaceae Martynieae genus *Craniolaria* genus *Martynia* perennial Pedaliaceae Sesameae annual Pedaliaceae Incarvilleae Bignonieae	Decaisne (1865) Pédalinées “racemic inflorescence” group- martyniaceous taxa genus *Craniolaria* genus *Martynia* genus *Proboscidea* “axillary inflorescence” group- pedaliaceous taxa	Stapf (1895) family Martyniaceae genus *Craniolaria* genus *Martynia* genus *Proboscidea* section *Eu-proboscidea* section *Ibicella*
Van Eseltine (1929) family Martyniaceae genus *Craniolaria* genus *Martynia* genus *Proboscidea* subgenus *Dissolophia* subgenus *Eu-proboscidea* genus *Ibicella* genus *Holoregmia*	Bretting (1981) family Martyniaceae genus *Craniolaria* genus *Martynia* genus *Proboscidea* group 1 – *P. althaeifolia* group 2 – *P. sabulosa* group 3 – “weedy” annuals genus *Ibicella* genus *Holoregmia*	Cronquist (1981) family Pedaliaceae subfamily Pedalioideae subfamily Martynioideae subfamily Trapelloideae

MATERIALS AND METHODS

The molecular phylogenetic methods used to construct the phylogenies of the Lamiales and the Martyniaceae are described below. The phylogeny of the Lamiales will be used to examine the placement of Martyniaceae within the order, and the phylogeny of the Martyniaceae will help to describe internal relationships within the family. Additionally, the methods used to create a taxonomic treatment of the Martyniaceae are described.

***Molecular Phylogenetic Studies*–**TAXON SAMPLING–Sequences of two chloroplast genes (*rps16* and *ndhF*) from 154 taxa, representing nineteen families in the order Lamiales and three outgroup taxa from the related orders of the Solanales (*Solanum* L.), Boraginales (*Borago* L.), and Gentianales (*Gentiana* L.), were included in the study of the placement of the family Martyniaceae within the Lamiales. A query of GenBank (www.ncbi.nlm.nih.gov/genbank/) produced several sequences of *ndhF* and *rps16* that were used as a starting point for this study. Additional sequences were generated for this study, including 46 sequences of *rps16* and 29 sequences of *ndhF*. The list of taxa used in the study of the Lamiales, their collection information, and their GenBank accession numbers are included in Appendix B.

Twenty taxa representing all five genera in the family Martyniaceae and two outgroup taxa from the Verbenaceae (*Glandularia* J.F. Gmel.) and the Thomandersiaceae (*Thomandersia* Baill.), were included in the study of the relationships within the Martyniaceae. Sampling was most extensive in the genus *Proboscidea*, comprising 12 of the 20 samples in the study. *Proboscidea sabulosa*, *P. althaeifolia*, and the monotypic *Martynia annua* each have two sets of sequences represented in these analyses, each from different localities. The *M. annua* samples included a cultivated specimen whose seed originated in Mexico, and a specimen from Puerto Rico. The *P. sabulosa* samples were both from west Texas, with the first coming from near the type locality and the latter from a recently discovered population in far west Texas. The *P. althaeifolia* samples include a sample from Baja California. The other sample, from Texas, belongs to what had previously been accepted as *Proboscidea arenaria* Engelm. Inclusion of a third sample from the Peruvian population, previously accepted as *Proboscidea peruviana* Van Eseltine, was attempted but unsuccessful. Only one representative from the genus *Ibicella* is included, making *I. parodii* and *P. spicata* the only two species missing from this analysis.

The study of the relationships within Martyniaceae utilized the Internal Transcribed Spacer (ITS) region of nuclear DNA and three regions from chloroplast DNA. The three chloroplast regions used in this study were the $trnH^{(GUG)}$-*psbA* intergenic spacer (Shaw et al. 2005), the $trnQ^{(UUG)}$-5'*rps16* intergenic spacer (Shaw et al. 2007), and the $trnS^{GCU}$-$trnG^{UUC}$-$trnG^{UUC}$ intergenic spacer and intron (Shaw et al. 2005). Six of the ITS sequences were used in a previous study (Gutierrez 2002), and the rest of the sequences are new. All of the chloroplast sequences for this part of the study are new. The list of taxa used in the study of the Martyniaceae, their collection information, and their GenBank accession numbers are included in Appendix C.

DNA AMPLIFICATION AND SEQUENCING–Genomic DNAs were isolated from silica-dried and herbarium material using DNeasy Plant Minikits (Qiagen, Valencia, California, USA). Polymerase chain reaction (PCR) amplifications were carried out in 1.1x ReddyMix™ PCR Master Mix (ABgene, Surrey, UK), to which was added the primers and template DNA. The PCR profile was 30 cycles of 30 seconds at 94ºC, 30 seconds at 48ºC, and 45 seconds at 72ºC. The cycles were preceded by 5 minutes of denaturation at 94ºC and were followed by 7 minutes of elongation at 72ºC. Primers flanking the desired regions were used in the PCR amplifications. Amplification products were purified and sequenced using the same primers and resulted in almost complete bidirectional overlap in sequencing the six regions. Additional internal primers were needed for both amplification and sequencing of the *ndhF* region and the *trnS-trnG-trnG* intergenic spacer and intron. The primers used for all of the gene regions are listed in Table 4. DNA sequencing was performed on Applied Biosystems 3730 capillary sequencers (Applied Biosystems, Foster City, California, USA) at Arizona State University (DNA Laboratory, Tempe, Arizona, USA). Sequencer output files were assembled into contigs and edited using the program Sequencher 4.1 (GeneCodes, Ann Arbor, Michigan, USA) before alignment. The sequences were assembled into a data matrix using ClustalW2 (http://www.ebi.ac.uk/Tools/clustalw2/index.html) and then checked by hand. All new sequences have been deposited in GenBank, and the final data matrices have been deposited in TreeBASE (http://www.treebase.org/; http://purl.org/phylo/treebase/phylows/study/TB2:S11991).

For the study of the placement of Martyniaceae within the Lamiales, which included 154 taxa, the resulting alignment was 1413 characters in length for the *rps16* data set, of which 789 were parsimony informative, and the resulting alignment was 2460 characters in length for the *ndhF* data set, of which 1130 were parsimony informative. The *rps16* alignment contained numerous indels, while the *ndhF* alignment contained 36 indels. The combined data set was 3873 characters in length, of which 1919 were parsimony informative. The alignments included 40 indels (ITS), 8 indels (*psbA-trnH* spacer), 12 indels (*trnQ-rps16* spacer), and 24 indels (*trnS-trnG-trnG* spacer and intron). For the study of the relationships within the Martyniaceae, which included 20 taxa, the resulting alignment for the chloroplast data set was 3353 characters and included 151 parsimony informative characters, and the nuclear data had 1549 characters and included 111 parsimony informative characters. The combined (nuclear and chloroplast) data set consisted of 3986 characters, with 262 being parsimony-informative. No characters were excluded from any data set during phylogenetic analysis.

PHYLOGENETIC ANALYSES–For the study of the placement of Martyniaceae within the Lamiales, phylogenetic analyses utilizing maximum parsimony and Bayesian approaches were used. Three parsimony analyses, one using the *ndhF* sequence data set, one using the *rps16* sequences data, and one using a data set that combined both sequences, were performed using *PAUP** (version 4.0b10; Swofford 2002). Heuristic searches were run with stepwise addition, random addition of sequences, TBR branch-swapping, and with 5 trees held at each step, allowing multiple trees to be saved. Nonparametric bootstrap analyses (Felsenstein 1985) were also performed on all three Lamiales data sets (*ndhF*, *rps16*, and combined) and were estimated from 1000 bootstrap replicates incorporating heuristic parsimony searches, simple addition of sequences, TBR branch-swapping, and saving no more than 1000 trees per replicate. Bayesian analyses were performed on the combined nuclear and chloroplast data set using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003) and were run with random starting points for each run. Markov chains of 2,000,000 generations each were sampled every 5000 generations. Stationarity was determined by plotting the log likelihood values of the sampled trees, which stabilized after 30,000 generations. The average standard deviation of split frequencies dropped to less than 0.05 after 650,000 generations. The first 100 trees were discarded as the burn-in, and Bayesian posterior probabilities were estimated as the proportion of the last 100 trees sampled that contained each of the observed bipartitions.

For the study of the relationships within Martyniaceae, phylogenetic analyses utilizing maximum parsimony, maximum likelihood, and Bayesian approaches were performed on all three chloroplast DNA regions sequenced (the *trnH*$^{(GUG)}$-*psbA* intergenic spacer, the *trnQ*$^{(UUG)}$-5'*rps16* intergenic spacer, and the *trnS*^{GCU}-*trnG*^{UUC}-*trnG*^{UUC} intergenic spacer and intron), the nuclear DNA data set consisting of the ITS sequences, and a data set consisting of both chloroplast and nuclear DNA sequences combined. Parsimony, nonparametric bootstrap (Felsenstein 1985), and Bayesian analyses were performed using the same methods as described above for the study of the placement of the Martyniaceae within the Lamiales. For the Bayesian analyses, the log likelihood values of the sampled trees stabilized after 50,000 generations, and Bayesian posterior probabilities were estimated as the proportion of the last 100 trees sampled that contained each of the observed bipartitions. A nucleotide substitution model was selected using Modeltest (version 3.7, Posada and Crandall 1998) using the Jukes and Cantor distance option, equal rates, equal bases, and minimum evolution. The combined chloroplast data set used the F81+ Γ model, the nuclear data set used the TIM+ Γ model, and the combined data set used the GTR+I+ Γ model. These models were incorporated into maximum likelihood analyses run on

*PAUP** (Swofford 2002) using heuristic searches, adding sequences as is, and TBR branch-swapping.

Taxonomic Treatment–This treatment is based on an examination of over 2600 specimens, many of them with duplicates, from the following herbaria: A, ARIZ, ASC, ASU, BRIT, CANB, CR, CTES, DES, E, ECON, F, GH, HUEFS, INB, K, LL, MICH, MNA, MO, ND, NDG, NEBC, NO, NY, SD, SMU, SP, TCD, TEX, UC, US, UTEP, VDB. Digital photographs of the collection from G were also examined. Type collections were studied from ARIZ, F, GH, K, LL, MICH, NDG, NMC, NY, TEX, and UC, as were digital photographs of the type collections from BM-SL, BR, CGE, GH, HAL, IND, LP, MINN, MO, NCU, NY, UC, and US. Specimens collected by the author have been deposited at ASU, with various duplicates sent to the following herbaria: ARIZ, ASC, BRIT, BRY, CANB, CAS, CS, CTES, DES, E, F, GH, HUEFS, ID, K, MBM, MEXU, MICH, MO, MSC, NMC, NO, NY, RM, RSA, SD, SP, SRSC, TEX, UC, US, UTEP, WTS. Where available, information on uses and vernacular names was noted. Herbarium acronyms follow Index Herbariorum (Thiers, continuously updated, http://sweetgum.nybg.org/ih/).

Table 4. Sequences of oligonucleotide primers used for PCR amplification and sequencing.

ndhF		
ndhF_1f	ATGGAACAGACATATCAATATG(C/G)GTGG	A
ndhF_1af	ATGCAACAGACATATCAATACGGGTGGAT	B
ndhF_1bf	ATGGAACA(GT)ACATAT(CG)AATATGC	C
ndhF_274f	CTTACTTCTATTATGTCAATATTAAT	C
ndhF_590f	ATTGGATAACGGGGAGTTTCGAATTT	B
ndhF_972f	GTCTCAATTGGGTTATATGATG	C
ndhF_1201f	AGGTACACTTTCTCTTTGCGGTATTCC	B
ndhF_1318f	GGATTAAC(CT)GCATTTTATATGTTTCG	C
ndhF_1595f	ATCCTTATCCTTATGCCTCAGACAATACTATG	B
ndhF_1603f	CCT(CT)ATGAATCGGACAATACTATGC	C
ndhF_1811f	CAGTCAGTATAGCCTCTTTCGGAAT	B
ndhF_803r	GAAAAATTCCCGCCGCTACCATAG	C
ndhF_953r	CCTCTCTTAATGTCTTTTTGAGCAAGAGCT	B
ndhF_1318r	CGAAACATATAAAATGC(AG)GTTAATCC	C
ndhF_1350r	ATAGATCCGACACATATAAAATGCGGTT	B
ndhF_1603r	GCATAGTATTGTCCGATTCAT(AG)GTTAATCC	C
ndhF_1835r	ATTCCGAAAGAGGCTATACTGACTG	B
ndhF_1955r	CGATTATATGACCAATCATATA	C
ndhF_2110r	CCCCCTA(CT)ATATTTGATACCTTCTCC	C
ndhF_2112r	CCC(CT)A(CG)ATATTTGATACCTTC(GT)CC	A
rps16		
rps16_f	GTGGTAGAAAGCAACGTGCGACTT	D
rps16_2r	TCGGGATCGAACATCAATTGCAAC	D
Internal Transcribed Spacer		
ITS5	GGAAGTAAAAGTCGTAACAAGG	E
ITS4	TCCTCCGCTTATTGATATGC	E
psbA-trnH spacer		
trnH$^{(GUG)}$	CGCGCATGGTGGATTCACAATCC	F
psbA	GTTATGCATGAACGTAATGCTC	F
trnQ-5'rps16 intergenic spacer		
trnQ$^{(UUG)}$	GCGTGGCCAAGYGGTAAGGC	G
rps16x1	GTTGCTTTYTACCACATCGTTT	G
trnS-trnG spacer and *trnG* intron		
3'trnG$^{(UUC)}$*	GAATCGAACCCGCATCGTTAG	G
trnS$^{(GCU)}$*	AACTCGTACAACGGATTAGCAATC	G
5'trnG2G	GCGGGTATAGTTTAGTGGTAAAA	F
5'trnG2S	TTTTACCACTAAACTATACCCGC	F

A – Olmstead & Reeves 1995; B – Oxelman et al. 1999; C – Olmstead & Sweere 1994; D – Bremer et al. 2002; E – White et al. 1990; F – Shaw et al. 2005; G – Shaw et al. 2007

RESULTS AND DISCUSSION

Sequence and Alignment Lengths–The sequences used for the study of the phylogenetic relationships of Martyniaceae within the order Lamiales varied in length from 603 to 919 base pairs for the *rps16* region and 755 to 2256 base pairs for the *ndhF*. The variation in the range of sequence lengths seen in the *rps16* region is mostly due to the non-coding intron. The lower end of the range of sequence sizes for *ndhF* is due to the inclusion of partial *ndhF* sequences from certain taxa so that those groups would be represented in the study, such as the genera *Utricularia* L., *Byblis* Salisb., and *Genlisea* A. St.-Hil. from the family Lentibulariaceae, and the genus *Trapella* Oliv. The resulting alignment for the 154 taxa was 1413 characters in length for the *rps16* data set, of which 789 were parsimony informative, and 2460 characters in length for the *ndhF* data set, of which 1130 were parsimony informative. The *rps16* alignment contained numerous indels, while the *ndhF* alignment contained 36 indels. No characters were excluded from the phylogenetic analyses.

Parsimony analysis of both the *rps16* and *ndhF* data sets produced at least 10,000 most parsimonious trees of 5126 and 9350 steps, respectively, which were each combined into a strict consensus tree (Figs. 5, 6). Bootstrap values greater than 50% are shown on the trees. The combined data set for the Lamiales was 3873 characters in length, of which 1919 were parsimony informative, and produced 690 most parsimonious trees which were combined in a strict consensus (Fig. 7). Bootstrap proportions greater than 50% and Bayesian posterior probability values are shown in the tree. A representative phylogenetic tree constructed using Bayesian methods, with Bootstrap values and Bayesian probabilities, is presented in Figure 8.

The sequences used for the study of phylogenetic relationships within Martyniaceae varied in length from 592 to 606 base pairs for the ITS region, 426 to 494 base pairs for the *psbA-trnH* spacer region, 1172 to 1530 base pairs for the *trnQ-5'rps16* intergenic spacer region, and 1429 to 1530 base pairs for the combined *trnS-trnG-trnG* intergenic spacer and intron region. The resulting alignments for the 20 taxa were 633, 520, 1284 and 1549 characters in length, respectively. No characters were excluded from the analyses. The chloroplast alignments were combined for a total alignment of 3353 characters and included 151 parsimony informative characters, compared with 111 parsimony informative characters for the nuclear data set. The alignments included 40 indels (ITS), 8 indels (*psbA-trnH* spacer), 12 indels (*trnQ-rps16* spacer), and 24 indels (*trnS-trnG-trnG* spacer and intron). The combined (nuclear and chloroplast) data set consisted of 3986 characters, of which 262 were parsimony-informative.

Parsimony analysis of the nuclear and chloroplast data sets each produced 2 most parsimonious trees of 412 and 643 steps, respectively, which were each combined into strict consensus trees (Figs. 9, 10). The combined data set produced 3 most parsimonious trees of 1125 steps. When the trees produced from the combined data set were placed into a strict consensus, most of the family collapsed into a polytomy with 8 lineages. Though the South American taxa remained in one lineage, the trees are presented here in a majority rule tree to provide a better visual representation of the relationships of the North American taxa (Fig. 11). Shown in Figures 12-14 are the three maximum likelihood trees constructed using each of the data sets (chloroplast, nuclear, and combined). Parsimony bootstrap proportions greater than 50% are included on the strict consensus (Figs. 9, 10) and Majority Rule

(Fig. 11) trees, and Bayesian posterior probability values are included on all trees (Figs. 9, 10, 11, 12, 13, 14).

Molecular Phylogenetics of the order Lamiales–The phylogenetic analyses strongly support the monophyly of the Martyniaceae (Figs. 5, 6, 7, 8), but fail to support the placement of any of the closely related families, such as the Acanthaceae (McDade and Moody 1999; Manktelow et al. 2001; Schwarzbach and McDade 2002), Bignoniaceae (Gentry and Tomb 1979; Bretting and Nilsson 1988), Lamiaceae (Gutierrez 2002; Rahmanzadeh et al. 2005), Lentibulariaceae (Soltis et al. 2000; Bremer et al. 2002), Pedaliaceae (Cronquist 1981), or Verbenaceae (Olmstead et al. 2001), as the sister group to the Martyniaceae. Most relationships supported by these analyses were within well-defined families or at the deepest nodes of the tree. Higher order relationships between families were not well resolved or supported, and this lack of support causes the branches to collapse into one large polytomy consisting of several unresolved lineages. This is a problem encountered in other studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011) in which a radiation of families occurs without any resolution in relationships between these families. These studies have suggested that taxon sampling, and the possible absence of characters from extinct taxa that may play a critical role in resolving this relationships, may contribute to the absence of resolution in the core Lamiales. Taxon sampling for this study was greater for the Lamiales, for the core Lamiales, and for the Martyniaceae (Table 5), compared to other similar studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011).

The most basally-branching lineage in the trees resulting from an analysis of the Lamiales was *Plocosperma* Benth. (Plocospermataceae), followed by the Oleaceae. These results, strongly supported by the parsimony and bootstrapping analyses of the *rps16* data set (Fig. 5), and the combined data set (Fig. 7), in addition to the Bayesian analysis of the combined data set (Fig. 8), agree with the results of previous studies that place the Plocospermataceae as the most basally-branching lineage within the Lamiales (Bremer et al. 2002; Soltis et al. 2011), or place the Oleaceae as the most basally-branching lineage when Plocospermataceae is not sampled (Olmstead et al. 2001; Oxelman et al. 2005; Rahmanzadeh et al. 2005). Tetrachondraceae is typically resolved as the sister group to the remaining groups within Lamiales, though this relationship is only moderately supported by bootstrapping of the *rps16* data set (Fig. 5). This support is weak in the analysis of the combined data set (Figs. 7, 8), likely due to the absence of this support from bootstrapping of the *ndhF* data (Fig. 6).

The *rps16* data set (Fig. 5) and the combined data set (Figs. 7, 8) place a clade consisting of the Gesneriaceae and the Calceolariaceae as sister to the rest of the Lamiales, though this is not supported by the *ndhF* data set (Fig.6). The placement of the Gesneriaceae and Calceolariaceae as sisters is itself strongly supported by Bayesian and parsimony analysis of the combined data set, though bootstrapping provides no support (Figs. 7, 8). The phylogenetic placement of Calceolariaceae and Gesneriaceae towards the base of the tree is supported by other studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011), though their placement as sister to each other is demonstrated in only two of the most recent studies (Rahmanzadeh et al.

2005; Soltis et al. 2011). Additionally, the combined data set provides support for the placement of the genera *Sanango* G.S. Bunting and J. A. Duke and *Peltanthera* Benth., traditionally placed in the Buddlejaceae, within the Gesneriaceae clade (Figs. 7, 8), as seen in other studies of the Lamiales (Bremer et al. 2002; Oxelman et al. 2005; Soltis et al. 2011).

Parsimony and Bayesian analyses of the combined data strongly support the placement of the remaining families of the Lamiales (including Acanthaceae, Bignoniaceae, Lamiaceae, Lentibulariaceae, Linderniaceae, Martyniaceae, Orobanchaceae, Paulowniaceae, Pedaliaceae, Phrymaceae, Plantaginaceae, Schlegeliaceae, Scrophulariaceae, Stilbaceae, Thomandersiaceae, and Verbenaceae) into one large clade (Figs. 5, 6, 7, 8). Parsimony analyses of the *rps16* and *ndhF* data sets support the placement of Plantaginaceae as sister to the remaining Lamiales (Figs. 5, 6), with the addition of *Selago* L. from the Scrophulariaceae being included with the Plantaginaceae in the tree formed by the analysis of the *rps16* data. The analysis of the *rps16* data resolves the remaining Lamiales, without support from bootstrapping, into a polytomy consisting of Stilbaceae, Scrophulariaceae, and the core Lamiales (Acanthaceae, Bignoniaceae, Lamiaceae, Lentibulariaceae, Linderniaceae, Martyniaceae, Orobanchaceae, Paulowniaceae, Pedaliaceae, Phrymaceae, Schlegeliaceae, Thomandersiaceae, and Verbenaceae; Fig. 5). The analysis of the *ndhF* data set places Stilbaceae as sister to a polytomy containing the core Lamiales and several lineages of the Scrophulariaceae, though again this lacks support from bootstrapping (Fig. 6). This lack of support is echoed in other studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Soltis et al. 2011), which also place the Plantaginaceae as sister to a clade formed by the Scrophulariaceae and the rest of the Lamiales.

Parsimony analysis of the combined data set creates a polytomy consisting of a strongly supported and monophyletic Stilbaceae, four unsupported clades of Scrophulariaceae, two unsupported clades of Plantaginaceae, and an unsupported clade of the core Lamiales (Fig. 7). Unlike previous studies of the Lamiales that place Plantaginaceae as a basally-branching lineage to the Scrophulariaceae and core Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005), Bayesian analysis of the combined data places Plantaginaceae and Scrophulariaceae as sisters, and this clade is sister to another clade consisting of the Stilbaceae and the core Lamiales (Fig. 8). The placement of the Plantaginaceae and the Scrophulariaceae as sister taxa is supported by Bayesian analysis only, as there is no support from parsimony analysis or bootstrapping. In the results from each of the analyses of the relationships within the Lamiales, the genus *Trapella*, placed in the Pedaliaceae by Cronquist (1981), is consistently resolved as sister to *Gratiola* L., within the tribe Gratioleae of the Plantaginaceae (Figs. 5, 6, 7, 8).

Parsimony analysis of the *rps16* data set places taxa of the core Lamiales into a polytomy (Fig. 5). These lineages include Thomandersiaceae, Schlegeliaceae, a well-supported Pedaliaceae, Paulowniaceae, a well-supported Martyniaceae (with the inclusion of *Jovellana* Ruiz &. Pav. from the Calceolariaceae and *Gloxinia* L'Hér. from the Gesneriaceae), a well-supported Linderniaceae, a moderately-supported Verbenaceae, Lentibulariaceae, a poorly-supported Bignoniaceae, and a clade with Acanthaceae, Lamiaceae, Orobanchaceae, and Phrymaceae (Fig. 5). Monophyly of the Acanthaceae and Lamiaceae is well supported, though the sister relationship between these two families is not. Monophyly of the Orobanchaceae is weakly supported, and Phrymaceae is shown as polyphyletic, with the inclusion of *Chelone* L. from the Plantaginaceae.

Parsimony analysis of the *ndhF* data set places the Scrophulariaceae with the rest of the core Lamiales in a large polytomy of several lineages (Fig. 6). Paulowniaceae is shown as sister to Orobanchaceae, and a well-supported Pedaliaceae is shown as sister to a well-supported Martyniaceae, but neither of these sister group relationships find any support from bootstrapping. Support for the Acanthaceae is poor, and is entirely lacking for the Bignoniaceae. Incomplete *ndhF* sequences from taxa in the Lentibulariaceae may have lead to the placement of *Utricularia* within the Lamiaceae, and *Byblis* and *Genlisea* within the Verbenaceae.

Parsimony analysis of the combined data set also produced a polytomy for the core Lamiales (Fig. 7). Compared to the results of the analyses of the *ndhF* data set, the Acanthaceae and Bignoniaceae are well-supported by bootstrapping and Bayesian analyses. The genus *Avicennia* L. is placed within the Acanthaceae (Figs. 7, 8), a result also shown in previous studies (Bremmer et al. 2002; Schwarzbach and McDade 2002; Rahmanzadeh et al. 2005). Lentibulariaceae and Linderniaceae are also well-supported, but their sister relationship is not. This also occurs between the Martyniaceae and Pedaliaceae, where each family is well-supported, but the sister relationship between them is not. The Lamiaceae and Verbenaceae are each shown as monophyletic, but their monophyly is not supported by bootstrapping or Bayesian analyses. A large clade consisting of several unresolved lineages of taxa from Orobanchaceae, Phrymaceae, and Paulowniaceae is not supported by bootstrapping but well-supported by Bayesian analysis.

The representative tree constructed using Bayesian analysis of the combined data set indicates Linderniaceae is sister to the rest of the core Lamiales (Fig. 8). Within the remaining core Lamiales (Fig. 8), two large clades are formed. One clade consists of the families Acanthaceae, Lamiaceae, Orobanchaceae, Paulowniaceae, and Phrymaceae (ALOPP; Fig. 8). The other consists of the families Bignoniaceae, Lentibulariaceae, Verbenaceae, Martyniaceae, Thomandersiaceae, Schlegeliaceae, and Pedaliaceae.

The lineages within the ALOPP clade are moderately to strongly supported, and are generally internally well-resolved (Fig. 8). Included in Orobanchaceae are two taxa whose familial placement have been in question. These taxa, *Rehmannia* Libosch. ex Fisch. & C.A. Mey. and *Triaenophora* Soler., are sister to each other and form a sister to Orobanchaceae s.s., consisting of the genera *Agalinis* Raf., *Cordylanthus* Nutt. ex Benth., *Pedicularis* L., and *Lindenbergia* Lehm. Xia et al. (2009) also demonstrated that *Rehmannia* and *Triaenophora* are sister to the Orobanchaceae, and suggest either accepting the two genera as a distinct family, or placing them within the Orobanchaceae s.l. *Paulownia* Siebold & Zucc. is sister to the Orobanchaceae s.l., and Phrymaceae is then sister to the Paulowniaceae-Orobanchaceae group, though these relationships are not resolved using parsimony analysis and have no support from parsimony bootstrapping.

Lancea Hook. f. & Thomson and *Mazus* Lour. are two genera currently placed within Phrymaceae, but their inclusion in the family makes Phrymaceae paraphyletic (Figs. 5, 6, 7, 8). Previous studies (Beardsley and Olmstead 2002, Olmstead et al. 2005; Xia et al. 2009) also failed to resolve Phrymaceae, including *Lancea* and *Mazus*, as a monophyletic group. The two genera should be placed in a separate family to make the smaller and redefined Phrymaceae monophyletic and consistent with results of this study and previous studies (Beardsley and Olmstead 2002; Olmstead et al. 2005; Xia et al. 2009).

The large family Lamiaceae is sister to the Orobanchaceae-Phrymaceae-Paulowniaceae clade, a relationship that is also supported in previous studies (Olmstead et al. 2001; Oxelman et al. 2005; Soltis et al. 2011). Relationships within Lamiaceae are well-resolved and supported, as are those of Acanthaceae, which is sister to a clade formed by the Lamiaceae, Orobanchaceae s.l., Paulowniaceae, and Phrymaceae s.l. While each of these lineages is fairly well-supported and resolved internally, deeper relationships within this clade of the core Lamiales fail to garner much support, collapsing and contributing to the unresolved polytomy within the core Lamiales (Fig. 7, 8).

The remaining families in the core Lamiales, including Bignoniaceae, Lentibulariaceae, Verbenaceae, Martyniaceae, Thomandersiaceae, Schlegeliaceae, and Pedaliaceae, are placed into the second large clade (Fig. 8). The monophyly of each of the families is strongly supported, as are the internal relationships within each family. As seen in other areas of the tree, deeper relationships are weakly to moderately supported by Bayesian analysis, but lack support from parsimony bootstrapping (Fig. 8). These relationships also collapse and contribute to the unresolved polytomy within the core Lamiales (Fig. 8). Similar results showing well-resolved lineages collapsing into an unresolved polytomy are characteristic of the core Lamiales that has been seen in other studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011). A group consisting of the Lentibulariaceae and Verbenaceae plus *Scutellaria* L.

of the Lamiaceae is sister to Martyniaceae, and this group is sister to Bignoniaceae. These relationships only have weak Bayesian support (Fig. 8). The basally-branching group in this clade consists of the sister groups Pedaliaceae and Schlegeliaceae-Thomandersiaceae.

Systematic Implications for Pedaliaceae s.l.–Cronquist's (1981) expanded Pedaliaceae contained the three subfamilies Pedalioideae, consisting of the Pedaliaceae sensu Stapf (1895), Martynioideae, consisting of the Martyniaceae sensu Stapf (1895) and APG II (2003), and Trapelloideae, consisting of the genus *Trapella*. The monophyly of the Pedaliaceae and Martyniaceae is strongly supported by parsimony bootstrapping of the *ndhF* (Fig. 6) and combined data sets (Fig. 7), as well as Bayesian posterior probabilities of the combined data set (Fig. 8). Only the monophyly of Pedaliaceae is supported by parsimony bootstrapping of the *rps16* data set (Fig. 5). The parsimony analysis of the *ndhF* data set (Fig. 6) and the combined data set (Fig. 7) resolve the Martyniaceae as sister to the Pedaliaceae, though this is not supported by bootstrapping. The lack of bootstrap support for their sister relationship and the high bootstrap and Bayesian probabilities resolving both of the lineages (100%) does provide some support for the separation of the two lineages into different families.

Additional support for the recognition of Martyniaceae as a distinct family is provided by chromosome and pollen data. Families within the order Lamiales that are closely related to the Martyniaceae have varying numbers of chromosomes that are similar to those of the Martyniaceae, which range from n=15 to n=18 (Sugiura 1936a, 1936b; Martini 1939; Srinivasan 1942; Gaiser et al. 1943; Covas and Schnack 1947; Snow 1959; Löve 1977, 1979). Published chromosome counts for closely related families include: n=14, 16, 18, 28 for Acanthaceae (Sugiura 1936a, 1936b), n=14, 18, 20 for Bignoniaceae (Covas & Schnack 1947; Löve 1979; Sugiura 1936a, 1936b), n=7, 9, 16, 21 for Lamiaceae (Snow 1959; Sugiura 1936b), n=8, 13 for Pedaliaceae (Sugiura 1936a), and n=5, 10, 14, 18 for Verbenaceae (Covas and Schnack 1947). Though these numbers are similar to those of the Martyniaceae, karyology provides no definitive support for the identification of the closest relative to the Martyniaceae. Additionally, because the variation seen in chromosome counts between Martyniaceae and Pedaliaceae is as great as observed among other putatively related families, karyology provides little support for Cronquist's (1981) taxonomic placement of Martyniaceae within Pedaliaceae.

The pollen of Pedaliaceae does not appear to be similar to the types of pollen found in the Martyniaceae (Bretting and Nilsson 1988). Pollen of *Martynia* is covered by hexagonal or pentagonal reticulated plates that abut each other and are separated by very narrow grooves. *Ibicella*, *Holoregmia*, and *Proboscidea* all have pollen covered by circular to oval reticulate areoles separated by narrow to wide sulci. Pollen of *Craniolaria* is covered by widely-spaced rings. Species of Pedaliaceae are reported to have colpate and oblate-suprolate pollen, appearing cantaloupe-like when magnified. Thus, pollen morphology does not support Cronquist's (1981) placement of the Martyniaceae within the Pedaliaceae. Pollen of the Martyniaceae, in particular the *Ibicella-Holoregmia-Proboscidea* type, are similar to the pollen of *Catalpa* Scop., *Mansoa* DC., and *Delostoma* D. Don in the Bignoniaceae (Gentry and Tomb 1979). Bretting and Nilsson (1988) suggested that the similarities of pollen and floral morphologies of *P. louisianica* and *Catalpa speciosa* (Warder) Engelm. may be due to convergent evolution in response to similar pollinators. Flowers of both species are similar in appearance, and are chiefly pollinated by bumblebees and other large bees (Stephenson and Thomas 1977; Phillippi and Tyrl 1979).

Trapella, which comprises the third subfamily in Cronquist's taxonomic system, appears to be sister to the genus *Gratiola* (tribe Gratioleae, family Plantaginaceae; *Trapella* is indicated by an arrow in Figs. 5, 6, 7, 8). While the fruits of *Trapella* are beaked and similar to those of the Pedaliaceae and Martyniaceae, the habitat and distribution differ markedly. Plants of the Pedaliaceae are limited to southern Africa, Madagascar, and the Indian subcontinent, and grow in arid to semi-arid places. Similarly, the Martyniaceae grow in arid and semi-arid habitats, but they occur in the New World. In contrast, *Trapella* is an aquatic herb with floating leaves and has been recorded in Japan, Korea, China, and eastern Russia. Like the genus *Trapella*, taxa of the tribe Gratioleae also tend to be aquatic to semi-aquatic herbs.

Sister Taxon of Martyniaceae–In the tree resulting from Bayesian analysis of the combined data set (Fig. 8), the family Martyniaceae is placed as sister to a group consisting of the Verbenaceae and the Lentibulariaceae, though there is very weak support from Bayesian probabilities and no support for this relationship from bootstrapping of the *rps16* data set, the *ndhF* data set, or the combined data set (Figs. 5, 6, 7). Placement of these families in a clade agrees with previous studies that place the Martyniaceae as sister to either the Verbenaceae (Olmstead et al. 2001) or Lentibulariaceae (Soltis et al. 2000; Bremer et al. 2002), though the trees in these studies also lack significant support.

Recent analyses of the Bignoniaceae (Olmstead et al. 2009) and Verbenaceae (Marx et al. 2010) suggest that these families evolved in South America and dispersed northward through Central America and the Caribbean into North America. If the sister relationship between Martyniaceae and Verbenaceae was strongly supported by the phylogenetic analyses, then it could be suggested that the Martyniaceae also had an origin in South America and dispersed and diversified in arid and semiarid areas of North America. Without the support of bootstrap or Bayesian posterior probabilities, the direction of dispersal will remain unresolved. While the study of the placement of the Martyniaceae within the Lamiales resolves *P. louisianica* as sister to *Ibicella* (Figs. 5, 6, 7, 8), studies of the relationships within the Martyniaceae show two major clades consisting of North American (*Martynia* and *Proboscidea*) and South American taxa (*Craniolaria*, *Ibicella*, and *Holoregmia*; Figs. 9, 10, 11, 12, 13, 14). The latter will be discussed in greater detail below.

While the family Martyniaceae shares distributional similarities with the Verbenaceae, it also shares morphological similarities with the Lentibulariaceae. Both of these families include species that are covered with sticky, mucilaginous hairs. Hairs of the carnivorous genera *Pinguicula* L. and *Byblis* trap small insects which are then digested and provide a source of nitrogen for the plants. While all taxa within the Martyniaceae are similarly covered in sticky hairs, they do not appear to digest the insects they trap (Meyers-Rice 1999a; Wallace and McGhee 1999; Rice 2008; Plachno et al. 2009). It is possible that this trait has been lost, as the Martyniaceae do not usually inhabit nitrogen-poor habitats, or that glandular trichomes evolved in the most common recent ancestor of the Martyniaceae and Lentibulariaceae, with digestive enzymes later developing in the Lentibulariaceae. The lack of support from bootstrapping and Bayesian posterior probabilities precludes any assessment of polarity in this character.

Molecular Phylogenetics of the family Martyniaceae– Six phylogenetic trees constructed using the nuclear data, the chloroplast data, and the combined data sets are presented in Figures 9-14. The trees are derived from parsimony (Figs. 9, 10, 11) or maximum likelihood analyses (Figs. 12, 13, 14), with parsimony bootstrap values and Bayesian posterior included on all trees. All phylogenetic analyses show two strongly supported clades within the Martyniaceae. One clade consists of the South American taxa and includes the genera *Craniolaria*, *Ibicella*, and *Holoregmia*. The second clade consists of the North American genera *Martynia* and *Proboscidea*.

SOUTH AMERICAN CLADE (CRANIOLARIA + IBICELLA + HOLOREGMIA)–The results of all phylogenetic analyses indicate the two taxa of *Craniolaria* included in this study, *C. annua* and *C. integrifolia*, as sisters to each other (Figs. 9, 10, 11, 12, 13, 14). All parsimony bootstrap and Bayesian posterior probabilities strongly support this, except for the weak support provided by the parsimony bootstrap values for the nuclear data (Figs. 9, 12). Aside from this sister group relationship, the six trees differ in the rest of their internal relationships within the South American clade. The nuclear data suggests *I. lutea* is sister to the genus *Craniolaria*, though this is weakly supported by Bayesian analysis and not supported at all by the parsimony bootstrap analysis, and *Holoregmia* is shown as sister to the *Ibicella-Craniolaria* clade (Figs. 9, 12). Analysis of the chloroplast data resolve *Holoregmia* and *Ibicella* as sister groups to each other, moderately supported by both parsimony bootstrap and Bayesian probabilities, and this clade is then sister to the *Craniolaria* clade (Figs. 10, 13). Analysis of the combined data resolve *Holoregmia* as sister to *Craniolaria*, and this relationship is strongly supported by bootstrapping but lacks support from Bayesian posterior probabilities (Figs. 11, 14). *Ibicella* is then resolved as sister to the *Holoregmia-Craniolaria* clade, with fairly strong bootstrap support (Figs. 11, 14).

The trees reconstructed using the combined data suggest that *Ibicella* is the most basally-branching taxon in the South American clade, and, based on the basally-branching position and the lack of a morphologically comparable outgroup, may display plesiomorphic characters that differ in later-branching taxa (Figs. 11, 14). The beak of the fruit is elongated in *Ibicella*, but reduced in both *Holoregmia* and *Craniolaria*. It has been suggested that the beak is a zoochorous dispersal mechanism (Van Eseltine 1929; Bretting 1981; Taylor 1983; Janzen 1986), and the derivation of a reduced beak could be due to loss of, or change in the type of, animal dispersers. The flower shape in *Ibicella*, a form seen in the North American genera, could also be the plesiomorphic character, later evolving into the larger bee-pollinated flowers of *Holoregmia* and the longer moth-pollinated flowers of *Craniolaria*. Flowers of *Ibicella* are yellow, and color seems to have been lost as flowers of the other two genera are pale yellow to white with a faint green tinge. Additionally, the flowers of *Holoregmia* and *Craniolaria* may be variously marked with purple spots, while *Ibicella* has smaller reddish-orange markings. The degree of unity in the calyx also changes between genera. The sepals are not united in the basally-branching *Ibicella*, but are fused in *Craniolaria* and *Holoregmia*.

NORTH AMERICAN CLADE (*PROBOSCIDEA* + *MARTYNIA*)–The results of all phylogenetic analyses indicate three major lineages within the North American clade (Figs. 9, 10, 11, 12, 13, 14), corresponding to *Martynia*, *P. sabulosa*, and the rest of the taxa within *Proboscidea*. Both samples of *Martynia* are placed together as sisters with excellent support from parsimony bootstrap and Bayesian probabilities. This is also indicated for the two samples of *P. sabulosa*. *Martynia* is the most basally-branching group in the North American clade, forming a sister to *Proboscidea*. Within *Proboscidea*, *P. sabulosa* is sister to the rest of the taxa in the genus. Morphologically, *P. sabulosa* differs from the rest of the genus by having separate sepals, the smallest flowers in the genus, and the longest seeds. The rest of the taxa in the genus have sepals variously united, shorter seeds, and more conspicuous flowers.

Within the rest of the *Proboscidea*, the internal relationships reconstructed by the different analyses vary. Maximum likelihood analysis of the nuclear data shows three clades forming a polytomy within *Proboscidea* excluding *P. sabulosa* (Fig. 12). One lineage corresponds to the two samples of *P. althaeifolia*, the only perennial in the genus. Another represents a subspecies of *P. parviflora*, the taxon *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *gracillima* (Hevly) Bretting. The rest of the "weedy annuals" comprise the third clade. The term "weedy annuals" was penned by Bretting (1981) to represent those taxa within the genus *Proboscidea* not including *P. althaeifolia* and *P. sabulosa*. The "weedy annual" clade is split into two subclades in Figure 12, with the two subspecies of *P. triloba* forming one subclade and the rest of the taxa in the other. Within the latter subclade, the taxon *P. fragrans* is sister to a polytomy of *P. louisianica* , *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *sinaloensis* (Van Eseltine) Bretting and the two varieties of *P. parviflora* ssp. *parviflora*. Parsimony analysis of the nuclear data is able to resolve one of the polytomies that is observed in the maximum likelihood analysis (Fig. 9). In this analysis, *P. parviflora* ssp. *gracillima*, is shown as sister to *P. althaeifolia*, though this is not supported by parsimony bootstrapping or Bayesian analyses. All other relationships indicated by the maximum likelihood analysis (Fig. 12) are also indicated in the strict consensus tree of the parsimony analysis (Fig. 9).

The results of the phylogenetic analyses using chloroplast data resolve a few different relationships for the genus *Proboscidea* excluding *P. sabulosa* (Figs. 10, 13) compared to the phylogenetic analyses using nuclear data (Figs. 9, 12). The two samples of *P. althaeifolia* are not resolved as sister groups to each other, and *P. fragrans* is resolved as the sister group to a clade consisting of the two subspecies of *P. triloba*. *Proboscidea parviflora* ssp. *gracillima* is resolved as sister to a clade consisting of the two varieties of *P. parviflora* ssp. *parviflora*. The rest of the relationships within the *Proboscidea* minus *P. sabulosa* are not well-supported by parsimony bootstrapping, though many show support from Bayesian probabilities (Figs. 10, 13).

The results of the phylogenetic analyses using the combined data (Figs. 11, 14) resolve some of the same relationships for the genus *Proboscidea* excluding *P. sabulosa* that are resolved in the analyses of the nuclear and chloroplast data (Figs. 9, 10, 12, 13). The two samples of *P. althaeifolia* are resolved as sister groups to each other (Figs. 9, 11, 12, 14), and *P. fragrans* is resolved as the sister group to a clade consisting of the two subspecies of *P. triloba* (Figs. 10, 11, 13, 14). *Proboscidea parviflora* ssp. *gracillima* is resolved as sister to a clade consisting of the two varieties of *P. parviflora* ssp. *parviflora* (Figs. 10, 11, 13, 14). The rest of the relationships within the *Proboscidea* minus *P. sabulosa* are not well-supported by parsimony bootstrapping (Figs. 11, 14).

Despite the varying relationships within *Proboscidea*, four lineages are consistently reconstructed and supported. The first, *P. sabulosa*, has already been discussed above. The second group involves the infraspecific taxa within *P. parviflora*.

The two varieties of *P. parviflora* ssp. *parviflora* are consistently resolved as sister groups (Figs. 9, 10, 11, 12, 13, 14), supporting the idea that the domestic Devil's claw, *Proboscidea parviflora* ssp. *parviflora* var. *hohokamiana*, grown for the long fibers of the endocarp that are used in basketry, was developed from local wild-type stocks of *Proboscidea parviflora* ssp. *parviflora* var. *parviflora* (Bretting 1982, 1986). The parsimony and maximum likelihood analyses conducted on the chloroplast and combined data sets strongly support the placement of ssp. *gracillima* as sister to this clade (Figs. 10, 11, 13, 14), which supports the infraspecific classification presented by Bretting (1981). The other subspecies placed in this group by Bretting (1981, 1985), *P. parviflora* ssp. *sinaloensis*, is not resolved with this group by the molecular analyses (Figs. 9, 10, 11, 12, 13, 14). This taxon occurs primarily along coastal areas in the Mexican states of Sinaloa and Sonora, and intergrades with *P. parviflora* ssp. *parviflora.*

Another result consistently supported by parsimony and maximum likelihood analyses of the chloroplast and combined data sets is the group formed by *P. triloba* and *P. fragrans*. The two subspecies of *P. triloba*, ssp. *triloba* and ssp. *diversifolia*, are consistently and convincingly placed together (Figs. 9, 10, 11, 12, 13, 14), supporting Bretting's (1981) treatment of the taxa as subspecies. The chloroplast and combined data sets place *P. fragrans* as sister to *P. triloba*, again with strong support (Figs. 10, 11, 13, 14). *Proboscidea fragrans* has been regarded as a subspecies of *P. louisianica (*Bretting 1981, 1983*)*, but sufficient morphological differences between it and *P. louisianica* coupled with the lack of support from molecular data suggest that *P. fragrans* should be recognized as its own species. *Proboscidea fragrans* has purple to maroon flowers and lobed leaves with denticulate margins. *Proboscidea louisianica* has pale lavender to white flowers and unlobed leaves with an entire margin.

The final lineage supported by the parsimony and maximum likelihood analyses of the chloroplast and combined data sets is the resolution of the two samples of *P. althaeifolia* as sister taxa. This species once consisted of three different and valid taxa (*P. althaeifolia*, *P. arenaria*, and *P. peruviana*; Van Eseltine 1929) that were formally combined into *P. althaeifolia* by Bretting (1981). The type of *P. althaeifolia* was collected in Baja California and considered a perennial. The type of *P. arenaria* was collected near El Paso, Texas, and considered to be annual, though it was later demonstrated to be perennial (Bretting 1981). The morphological variation among and between these two taxa overlaps greatly, so they were combined into *P. althaeifolia*, along with the third taxon, *P. peruviana*. *Proboscidea peruviana* occurs in sandy areas along the coast of extreme northwest Peru. Extraction of DNA was attempted from this taxon but was unsuccessful. Future studies might focus on including this taxon to elucidate its relationship to P. althaeifolia and the rest of the taxa in the family.

***Character Evolution*–**SEPAL CONNATION–The degree of separation or fusion of the calyx seems to convergently evolve into two similar forms. Basally-branching groups in both the North American (*Martynia* and *P. sabulosa*) and South American clades (*Ibicella*) have sepals that are free (Fig. 15). In more derived groups in both of these clades, the tendency is toward connate sepals that are split abaxially. Other than this, the derived calyces of North and South America differ marked in their morphology. The calyces in *Proboscidea* (minus *P. sabulosa*) are prominently lobed and campanulate to funnelform, whereas the calyces of *Holoregmia* and *Craniolaria* are tipped with minute teeth or not lobed at all. Additionally, the calyx of *Holoregmia* is inflated and urceolate, while those of *Craniolaria* are spathelike and campanulate to funnelform.

LENGTH OF ROSTRUM ON FRUIT–The most interesting feature of the family, the distinctive fruits, most likely developed the long beak once, then reduced in length three times (Fig. 14). The converse situation, in which the long rostrum developed three times from an ancestral shorter beak, is also plausible given the phylogeny of the family. The lack of support for the placement of any of the putatively-related families as a sister group to the Martyniaceae (Figs. 5, 6, 7, 8) precludes the use of an outgroup to help discern which evolutionary model seems more appropriate. It has been hypothesized that the beak on the fruit aids in the dispersal of the seeds (Van Eseltine 1929; Bretting 1981; Taylor 1983; Janzen 1986). The beak or hook-like rostrum gets caught either on the feet, fur and feathers of animals. Due to the uniqueness of the beak, it seems more likely that this character evolved once, then reduced in size three times. One reduction in length occurred in the transition from *Ibicella* to the *Holoregmia-Craniolaria* clade. Beaks on the fruits of *Ibicella* are long, while those of *Holoregmia* and *Craniolaria* are reduced in size. Another reduction occurred in the *Martynia* clade, probably in response to the lack of large ungulates in Central America to aid in the dispersal of the fruit. The third reduction in length is possibly still occurring. Some fruits of *P. triloba* exhibit shortened beaks on the fruits. While not reduced to the degree of reduction seen in *Martynia*, *Craniolaria*, or *Holoregmia*, the beaks on *P. triloba* can still be noticeably shorter than those of the other taxa within *Proboscidea*. This lineage may be in the process of losing its long beaks, or it could represent some introgression with *Martynia*, with which they are sympatric.

Biogeography– Molecular phylogenies have been used to infer biogeographical histories and diversification for groups with distributions similar to distribution of the Martyniaceae. *Larrea* Cav. (Zygophyllaceae) is hypothesized to have originated in South America and dispersed into North America (Lia et al. 2001.). *Osmorhiza* Raf. (Apiaceae) originated in temperate Asia, then dispersed through North America into South America (Wen et al. 2002). Other studies of families related to the Martyniaceae suggest that Bignoniaceae (Olmstead et al. 2009) and Verbenaceae (Marx et al. 2010) both originated in South America and dispersed multiple times into North America and other parts of the world.

The results of the phylogenetic analyses presented in this study resolve two major clades within the Martyniaceae representing North American taxa in one and South American taxa in the other (Figs. 9, 10, 11, 12, 13, 14). The lack of support for the placement of any of the putatively-related families as a sister group to the Martyniaceae (Figs. 5, 6, 7, 8) precludes the use of an outgroup to help discern where the family originated from and the direction it dispersed. The most likely sister groups provide numerous options for the origin and dispersal of the Martyniaceae. Bignoniaceae and Verbenaceae both appear to have originated in South America and dispersed into North America multiple times (Olmstead et al. 2009; Marx et al. 2010). Both of these suggest that Martyniaceae may have also originated in South America and dispersed into North America. The origin of Lentibulariaceae has been suggested to be temperate Eurasia or tropical America (Jobson et al. 2003), which may suggest a North American origin for the Martyniaceae (temperate Eurasian hypothesis), or may not provide any support for either a North American or South American origin (tropical American hypothesis).

Within the South American clade of the Martyniaceae, three of the four taxa occur in the central portion of the continent (Figs. 1, 2). *Holoregmia* is found in a few locations in the state of Bahia in Brazil (Fig. 2). Both *C. integrifolia* and *I. lutea* occur in Bolivia, Paraguay, Argentina, and southern Brazil (Figs. 1, 2). *Craniolaria annua* occurs further north in Venezuela, Colombia, Guyana, and the Greater Antilles (Fig. 2). The results of the maximum likelihood analysis of the combined nuclear and chloroplast data suggest this clade developed in central South America, with one species, *C. annua*, crossing the more mesic habitats near the equator and dispersing northwards (Figs. 14, 16).

Like the South American clade, the North American clade shows a general trend toward a northward expansion, at least at the base of the North American clade in the results of the maximum likelihood analysis of the combined nuclear and chloroplast data (Fig. 14). *Martynia* occurs in Mexico and Central America, and, given that the rest of the taxa in the North American clade occur on the mainland, appears to have dispersed to the islands of the Caribbean (Figs. 1, 16, 17). The basally-branching groups within *Proboscidea* are *P. sabulosa* and *P. althaeifolia*, which inhabit sandy areas in northern Mexico and the southwestern United States (Fig. 17). *Proboscidea althaeifolia* probably dispersed southward to Peru, where populations of this species have been found in sandy areas along the northwest coast (Fig. 2). Within the "weedy annuals", the taxa form three unresolved lineages consisting of *P. louisianica*, the *parviflora* lineage, the *fragrans-triloba* lineage, with *P. fragrans* as sister to the two *P. triloba* subspecies (Figs. 14, 17).

Several issues arise from the use of phylogenetic analyses to infer hypothetical dispersal and distribution scenarios. Environmental changes through time and space are most likely to have the largest effects on the distribution of taxa. Also, the phylogenies that resulted from these analyses are evolutionary histories of the genes they were sampled from and may not represent the true evolutionary history of the organisms themselves (Pamilo and Nei 1988; Maddison 1997; Nichols 2001). There are different rates of evolution among and between genes and organisms that must be taken into consideration when inferring biogeographical hypotheses from these analyses.

The ability to date lineages and divergences would help to understand some of the distributions, but the lack of fossil data for the Martyniaceae, the scant fossil record for the Lamiales, and the lack of support from molecular phylogenetic analyses for relationships between families make dating any divergences difficult. Fossils of *Fraxinus* L. (Oleaceae) are known from Eocene (Call and Dilcher 1992; Manchester 1999), Oligocene (Meyer and Manchester 1997), and the Miocene (Chaney and Axelrod 1959) of North America, and from the Miocene of Spain (Barron 1992). A fossil fruit with seeds from the Bignoniaceae has been reported from the Eocene of Washington State (Wehr and Hopkins 1994; Pigg and Wehr 2002; Wolfe et al. 2003), and seeds attributed to *Catalpa* (Bignoniaceae) have been reported from the Oligocene in Oregon (Meyer and Manchester 1997; Manchester 1999, 2000) and the Oligocene in England (Reid and Chandler 1926). Reid and Chandler (1926) also reported seeds from the Oligocene in England from two other genera in the Bignoniaceae, *Incarvillea* Juss. and *Radermachera* Zoll. & Moritzi, and from *Acanthus* L. of the Acanthaceae. Fossils have also been reported in the family Lamiaceae. Wood from *Gmelina* L. has been reported from the Paleogene Deccan

Beds in India (Bande 1986), as have fruits from *Ajuginucula* Reid & Chandler and *Melissa* L. from the Oligocene in England (Reid and Chandler 1926).

Conclusion –Taxon sampling for this study was greater for the Lamiales, for the core Lamiales, and for the Martyniaceae (Table 5), compared to other similar studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011). This study attempted to better resolve the relationships between families within the core Lamiales using increased taxon sampling, but resulted in resolution similar to the previous studies (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011). Since the number of characters (Bremer et al. 2002) nor the number of taxa (this study) alone could significantly increase resolution within the core Lamiales, future studies may have to include both greater numbers of taxa and characters. These unresolved relationships may also represent a rapid diversification that may not be resolvable utilizing current molecular techniques. Nonetheless, like previous studies of the Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Oxelman et al. 2005; Rahmanzadeh et al. 2005; Soltis et al. 2011), the results do support the retention of the Martyniaceae, though they do not provide support for the placement of any of its closely related families as sister to the Martyniaceae.

Within Martyniaceae, the sister relationship between the clades representing the North American (*Proboscidea* and *Martynia*) and South American (*Craniolaria*, *Ibicella*, and *Holoregmia*) taxa agrees with the previous study that used fewer taxa and only one gene region (Gutierrez 2002). This study added data from chloroplast DNA to supplement the nuclear sequences, and it added several new taxa, including the genus *Holoregmia,* which had not been sampled before. Each clade shows a general trend of dispersing northward, and within *Proboscidea*, there was support for the three lineages suggested by Bretting (1981) which he based on morphological data only.

Table 5. Comparison of the number of taxa, the number of characters, and the gene regions included in this and previous studies of the Lamiales.

Publication	No. of taxa from Lamiales	No. of taxa from core Lamiales	No. of taxa from Martyniaceae	No. of informative characters	gene regions
Olmstead et al. 2001	61	28	1	1179	*rbcL*, *ndhF*, *rps2*
Bremer et al. 2002	31	16	1	4930	*rbcL*, *ndhF*, *matK*, *rps16*, *trnL*, *trnV*
Oxelman et al. 2005	71	42	2	1456	*ndhF*, *trnL*, *rps16*
Rahmanzadeh et al. 2005	51	36	2	1038	*matK*
Soltis et al. 2011	22	12	1	1456	17 genes used
current study	151	84	6	1919	*ndhF*, *rps16*

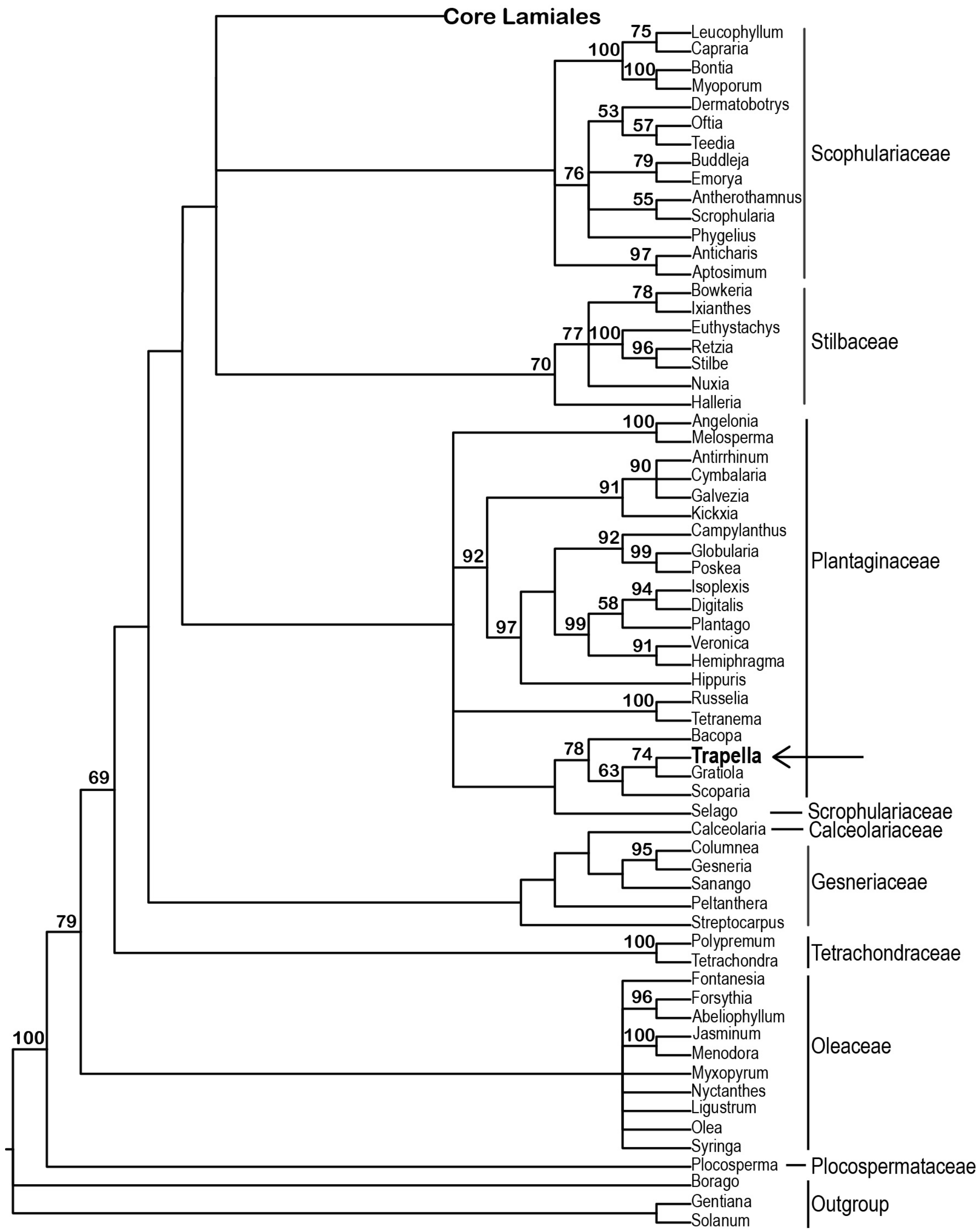

Fig. 5. Strict consensus of 10,000 most parsimonious trees of 5126 steps constructed from an analysis of sequences from the *rps16* region. Numbers represent parsimony bootstrap values.

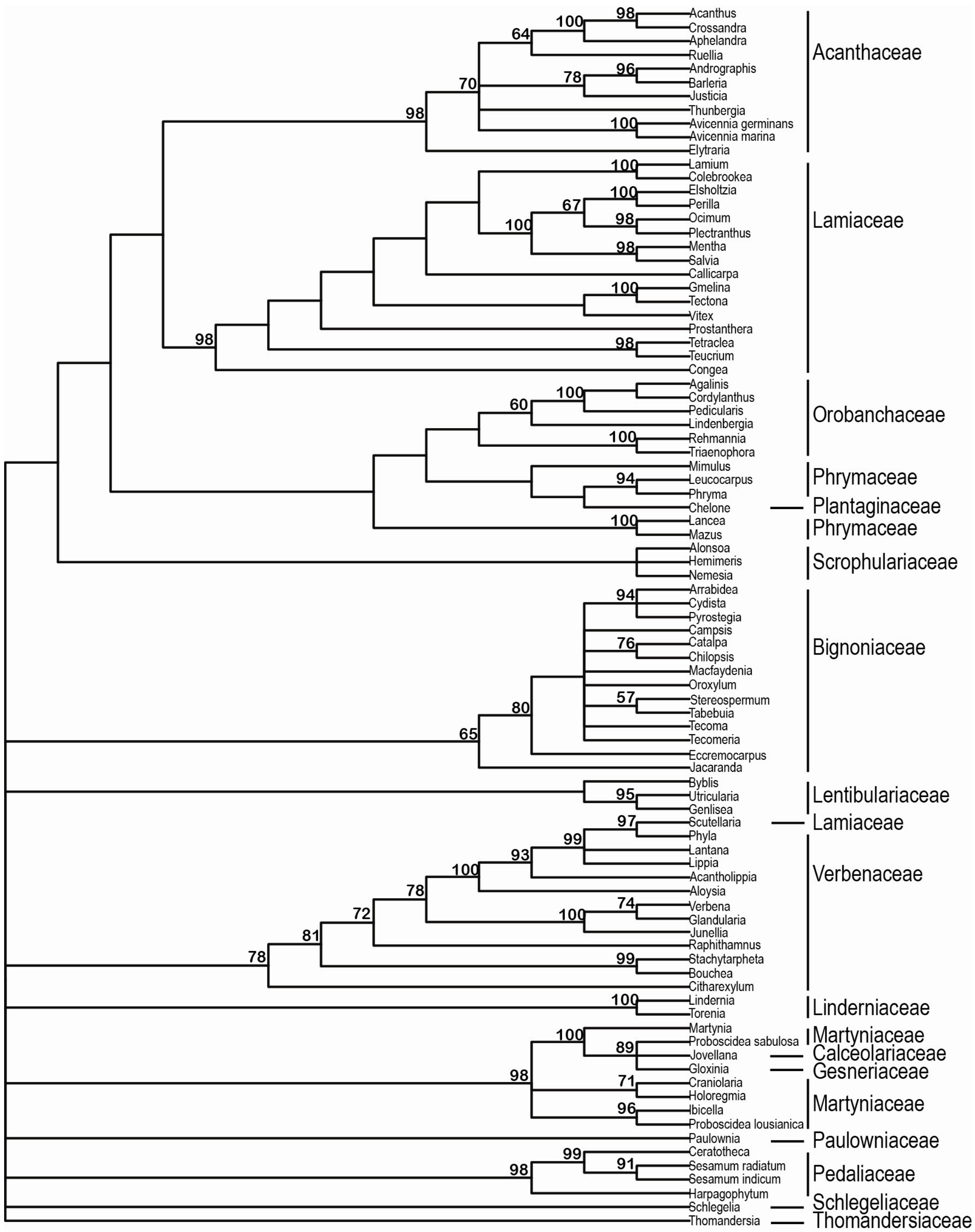

Fig. 5 (cont.). Strict consensus of 10,000 most parsimonious trees of 5126 steps constructed from an analysis of sequences from the *rps16* region. Numbers represent parsimony bootstrap values.

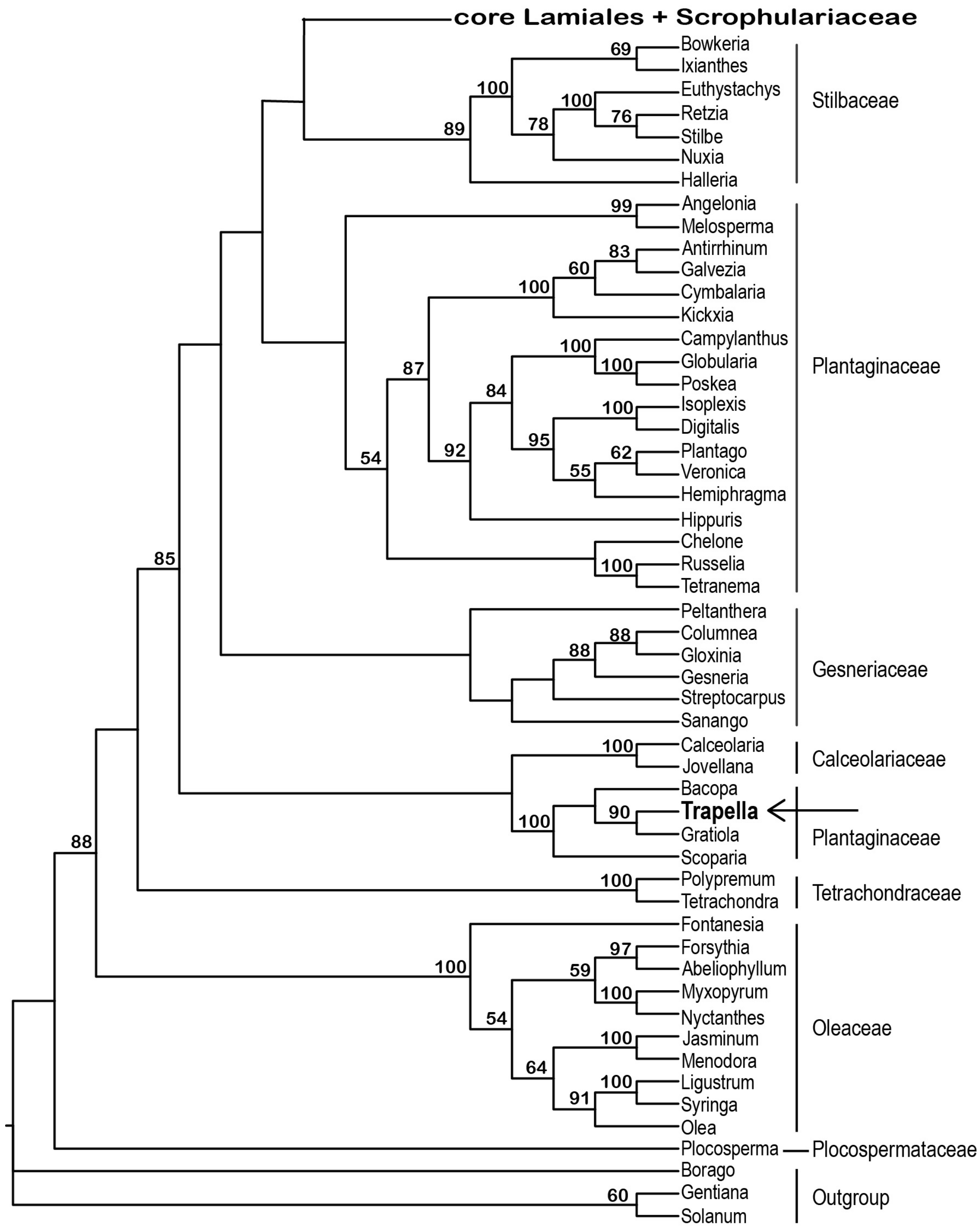

Fig. 6. Strict consensus of 10,000 most parsimonious trees of 9350 steps constructed from an analysis of sequences from the *ndhF* region. Numbers represent parsimony bootstrap values.

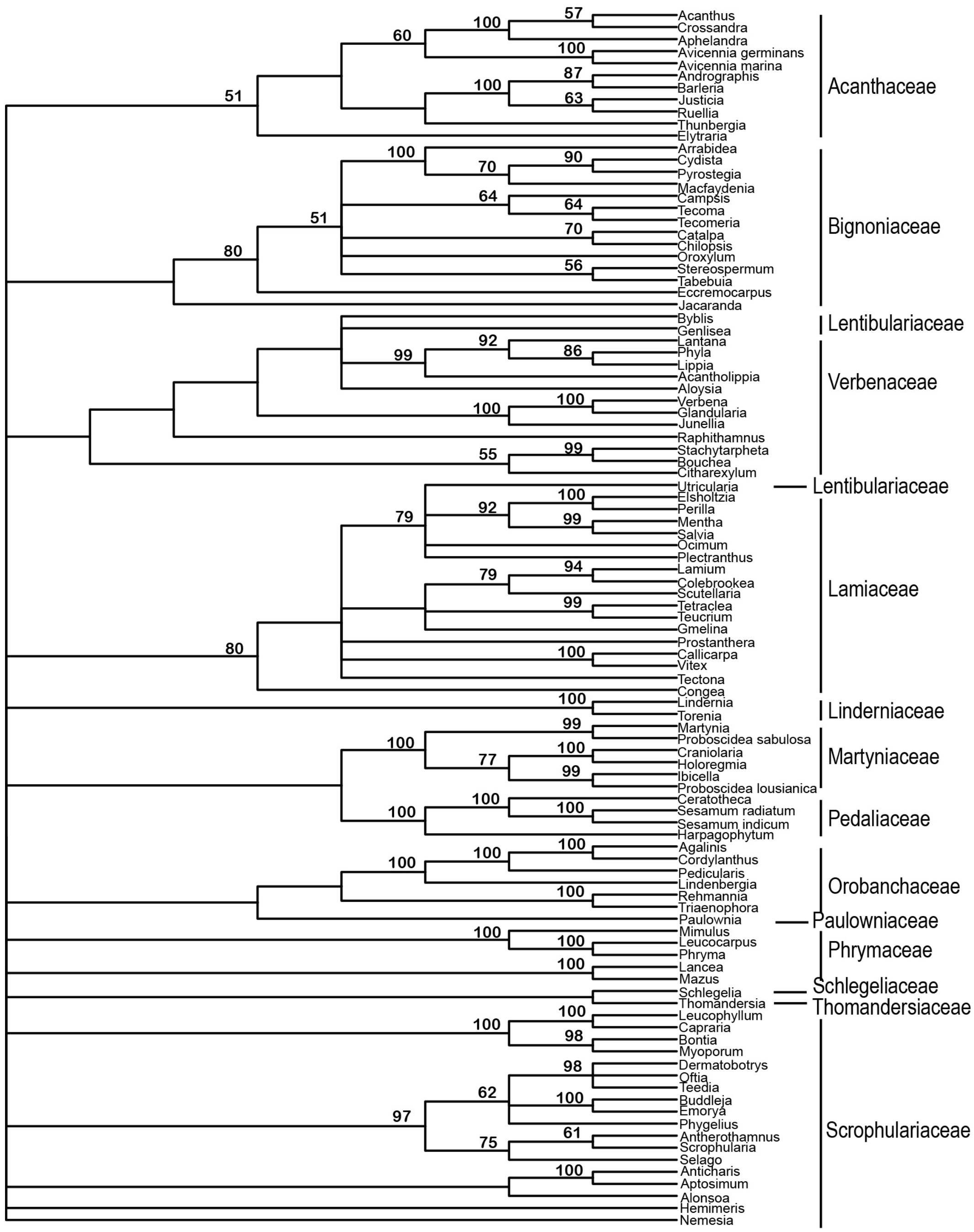

Fig. 6 (cont.). Strict consensus of 10,000 most parsimonious trees of 9350 steps constructed from an analysis of sequences from the *ndhF* region. Numbers represent parsimony bootstrap values.

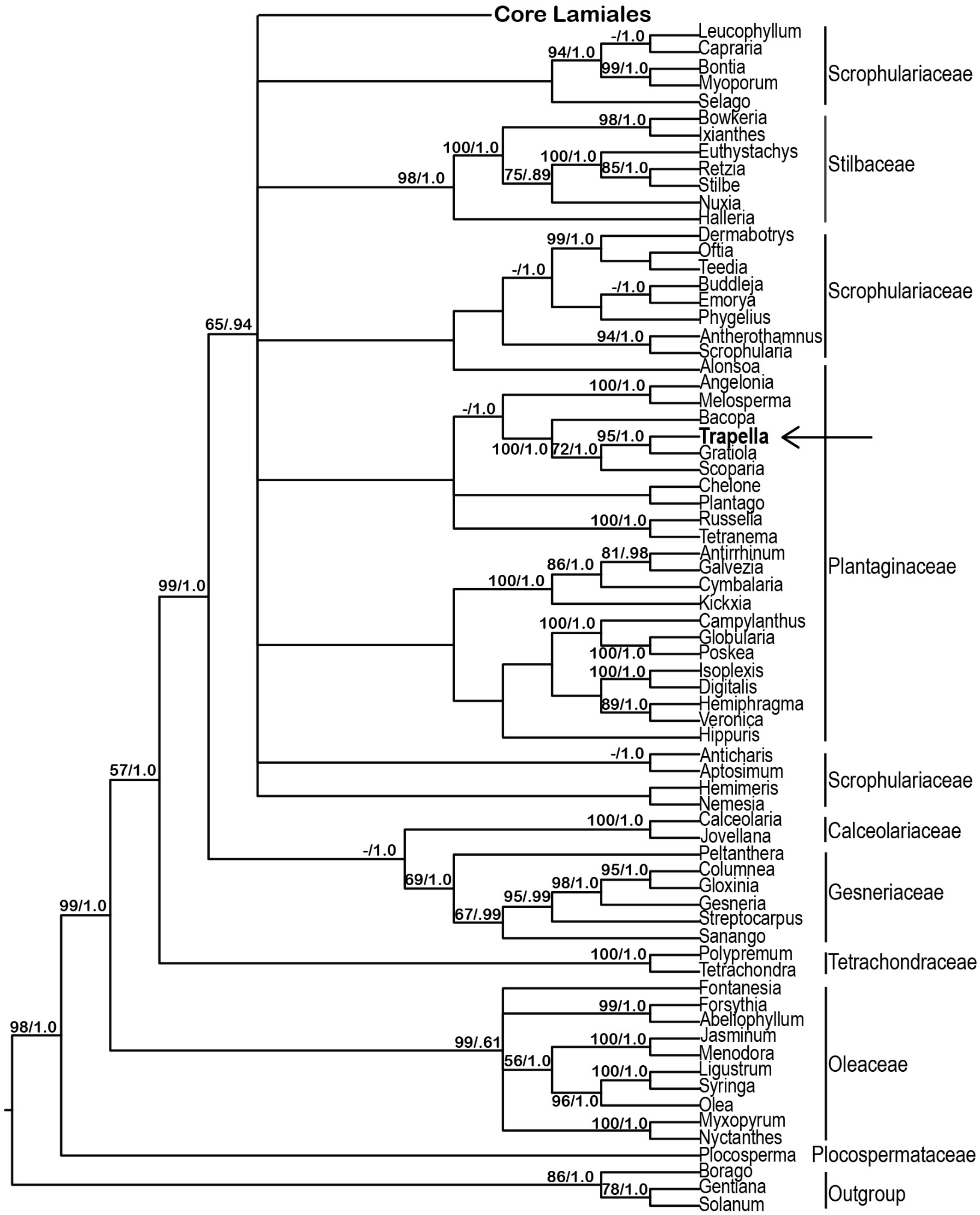

Fig. 7. Strict consensus of 690 most parsimonious trees of 14832 steps constructed from an analysis of sequences from the *ndhF* and *rps16* regions. Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values.

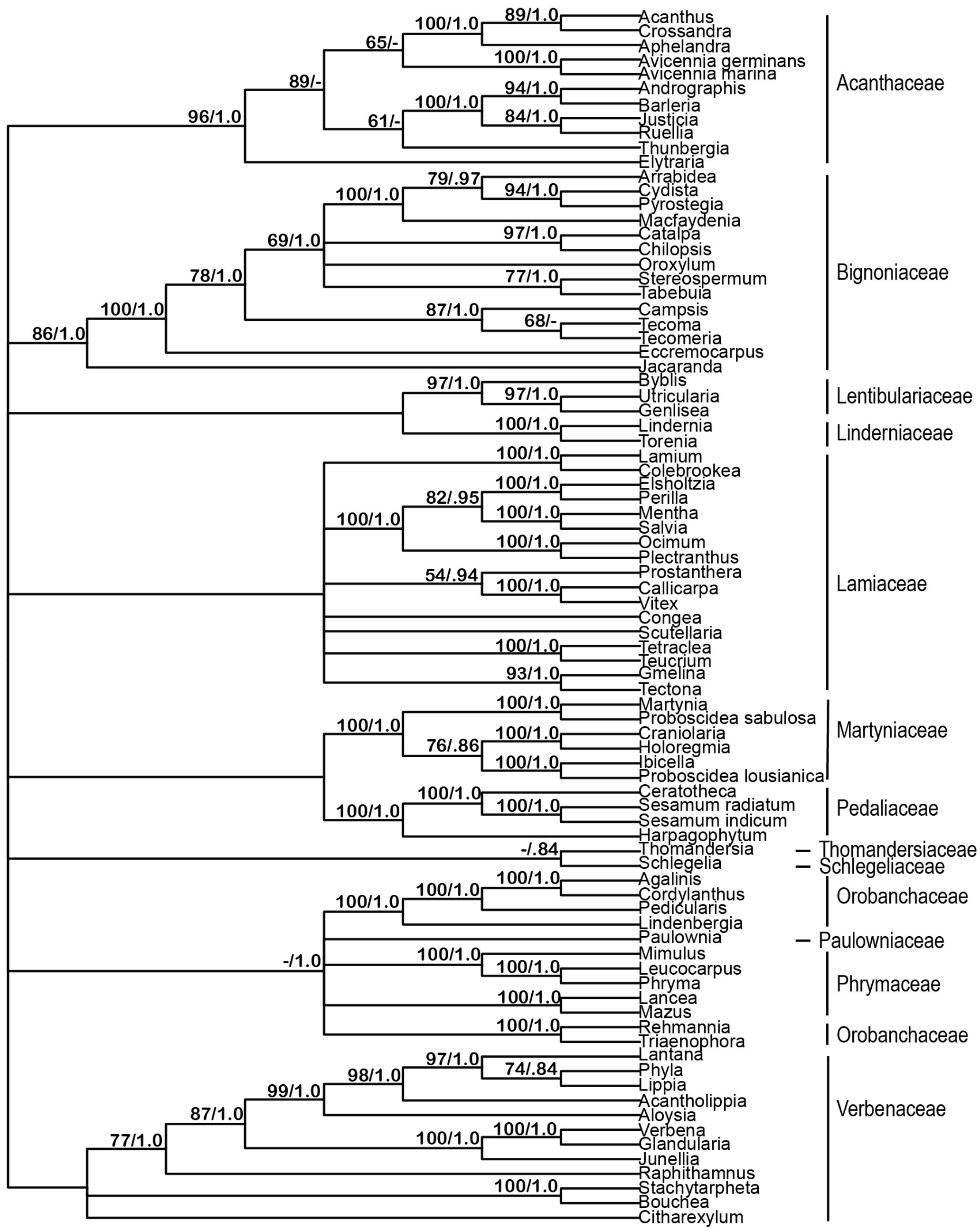

Fig. 7 (cont.). Strict consensus of 690 most parsimonious trees of 14832 steps constructed from an analysis of sequences from the *ndhF* and *rps16* regions. Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values.

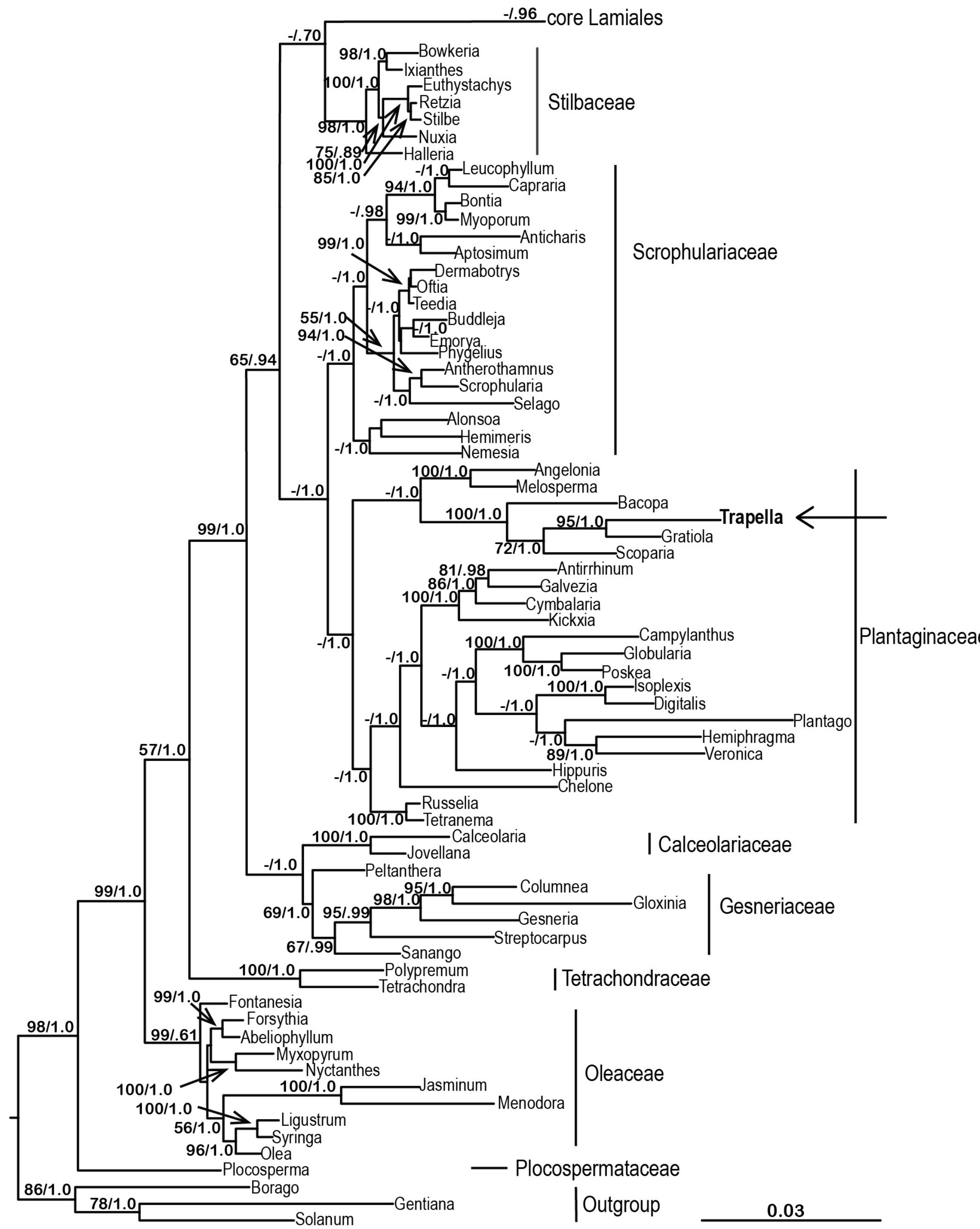

Fig. 8. Representative tree constructed using Bayesian analysis of sequences from the *ndhF* and *rps16* regions (ln=-84970.110). Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values. Scale bar represents 0.03 substitutions per site.

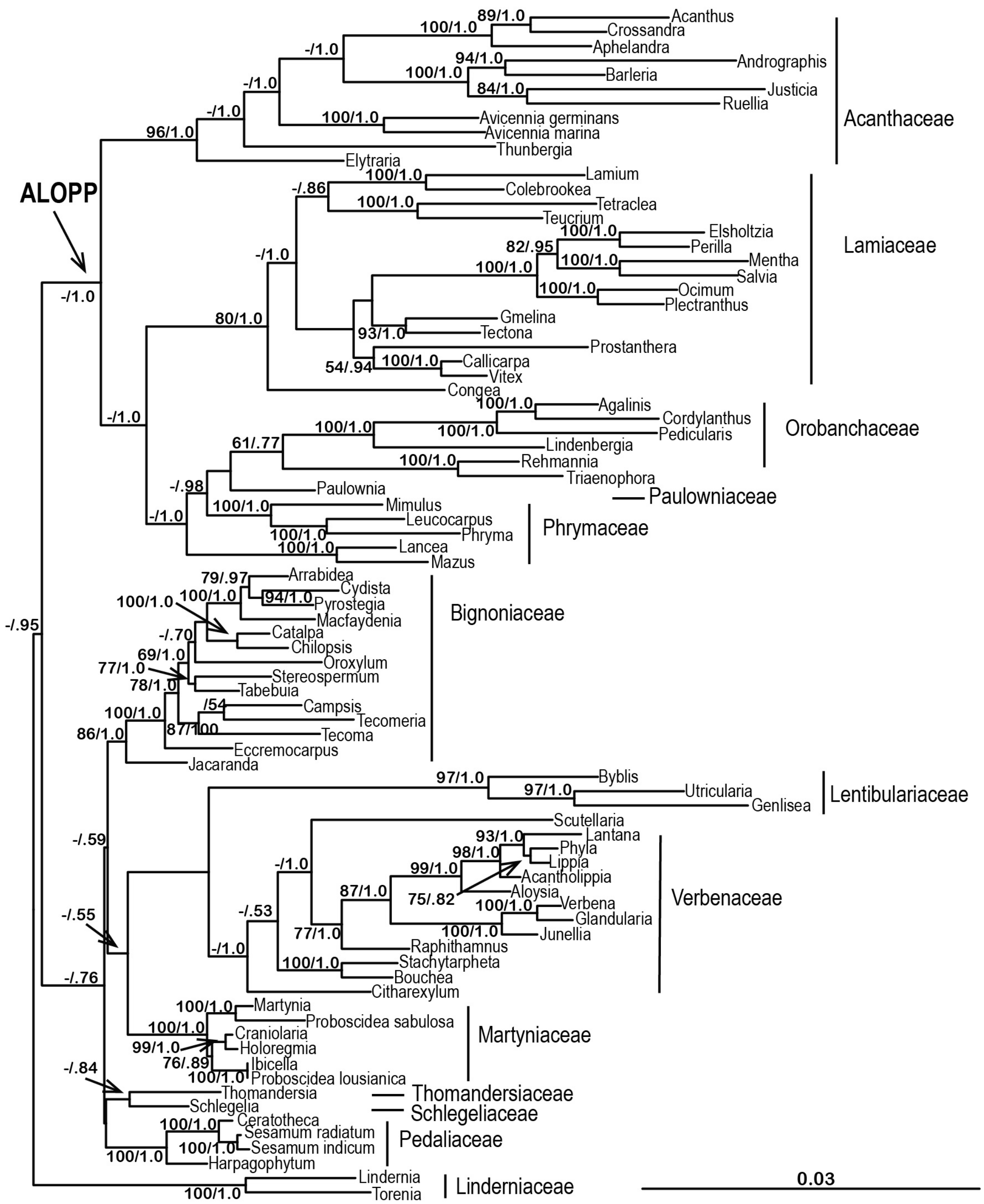

Fig. 8 (cont.). Representative tree constructed using Bayesian analysis of sequences from the *ndhF* and *rps16* regions (ln=-84970.110). Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values. Scale bar represents 0.03 substitutions per site.

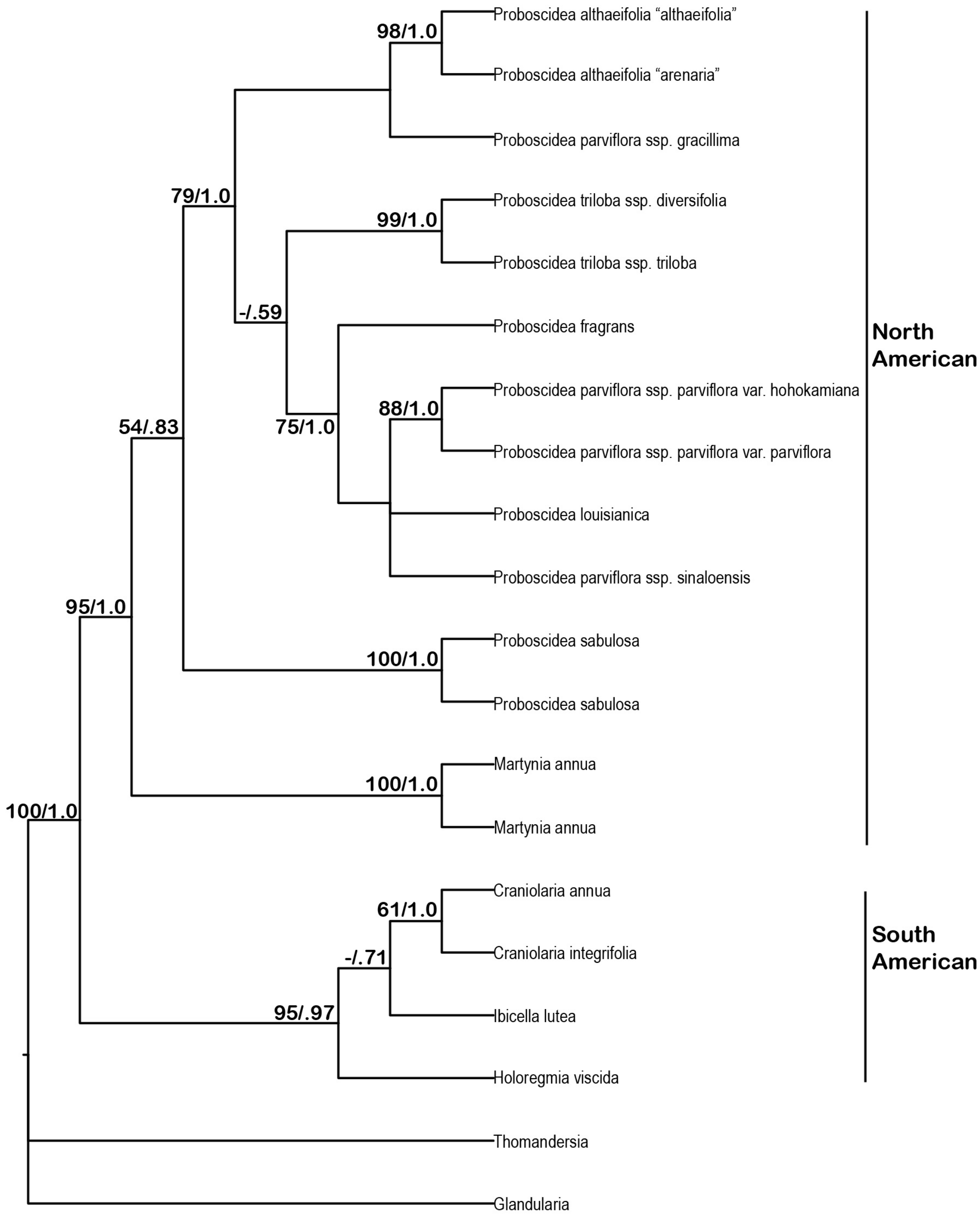

Fig. 9. Strict consensus of two most parsimonious trees of 412 steps based on the analysis of sequences from the ITS region. Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values.

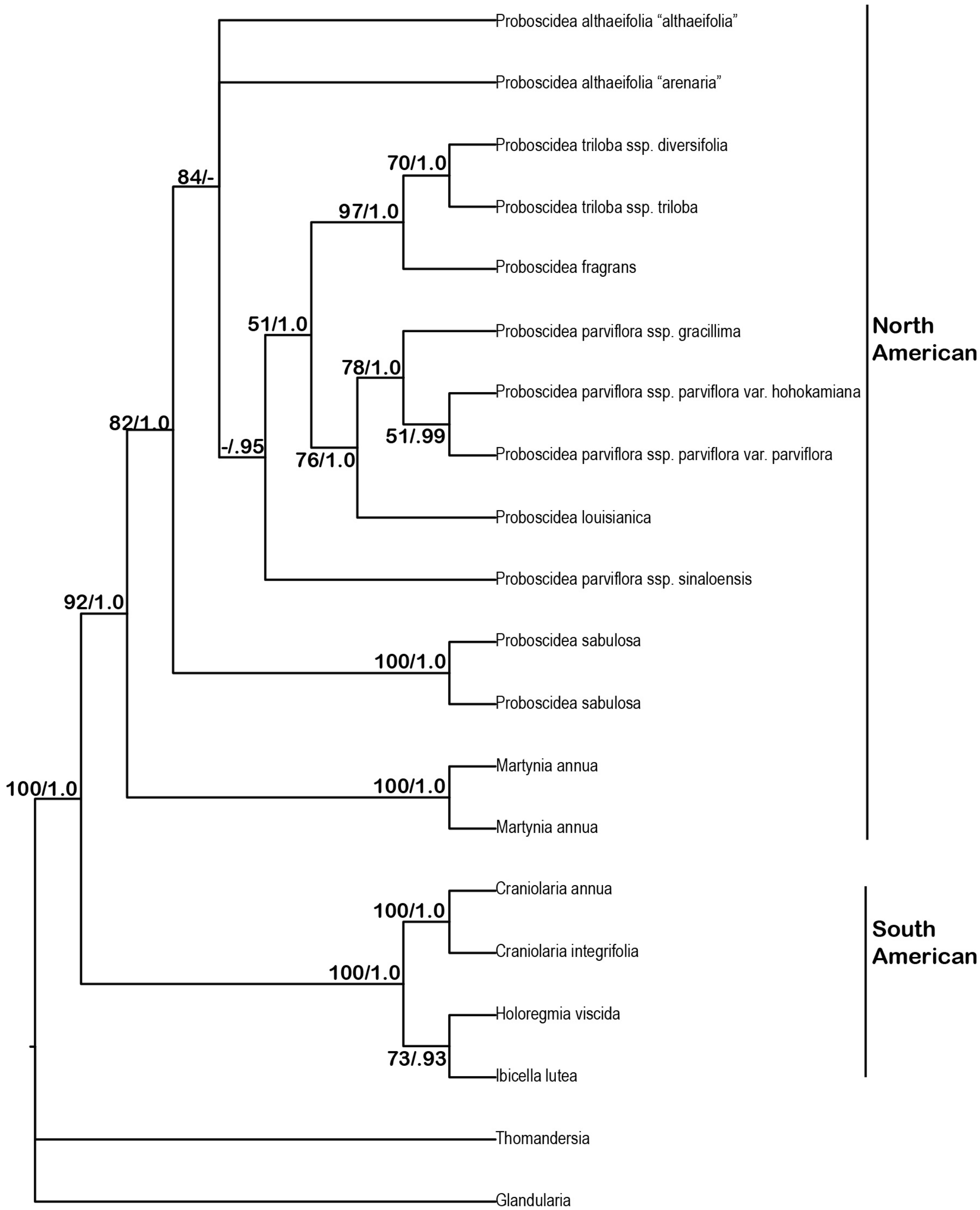

Fig. 10. Strict consensus of two most parsimonious trees of 643 steps based on the analysis of sequences from the *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions. Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values.

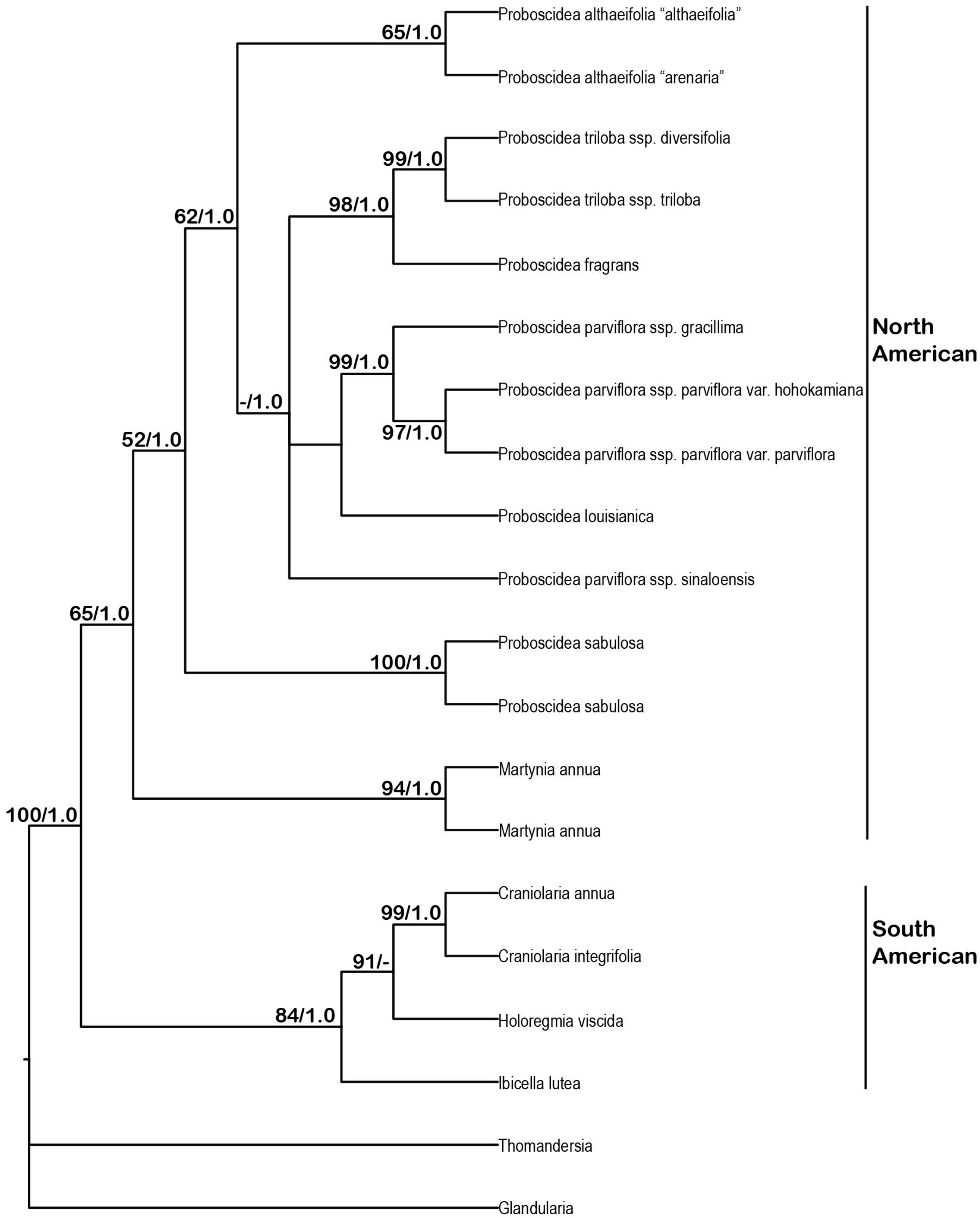

Fig. 11. Majority rule consensus of three most parsimonious trees of 1125 steps based on the analysis of sequences from the ITS, *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions. Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values.

Fig. 12. Maximum likelihood tree of the Martyniaceae based on the analysis of sequences from the ITS region (ln=-2785.578). Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values. Scale bar represents 0.06 substitutions per site.

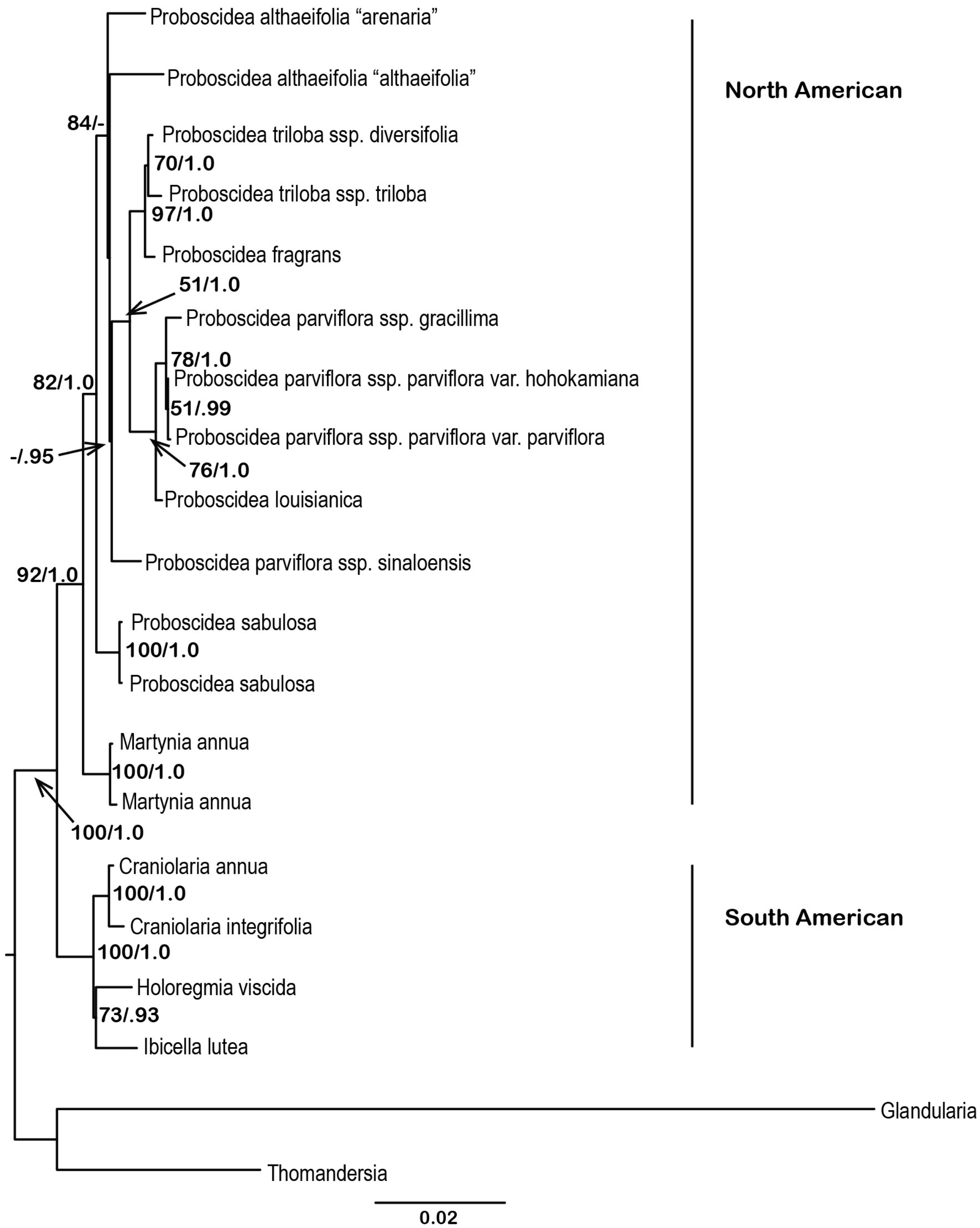

Fig. 13. Maximum likelihood tree of the Martyniaceae based on the analysis of sequences from the *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions (ln=-8117.466). Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values. Scale bar represents 0.02 substitutions per site.

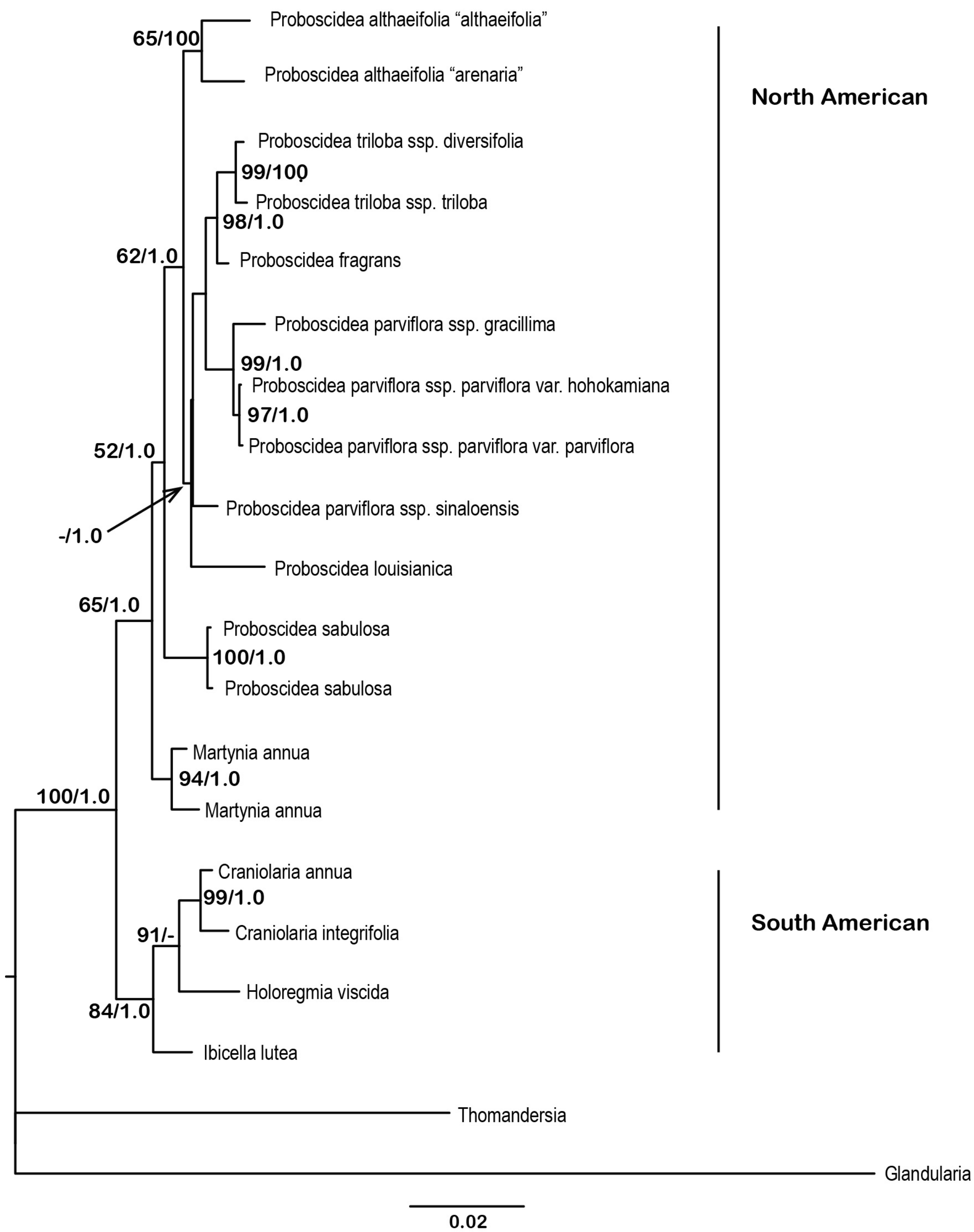

Fig. 14. Maximum likelihood tree of the Martyniaceae based on the analysis of sequences from the ITS, *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions (ln=-11587.643). Numbers to the left represent parsimony bootstrap values. Numbers to the right represent Bayesian values. Scale bar represents 0.02 substitutions per site.

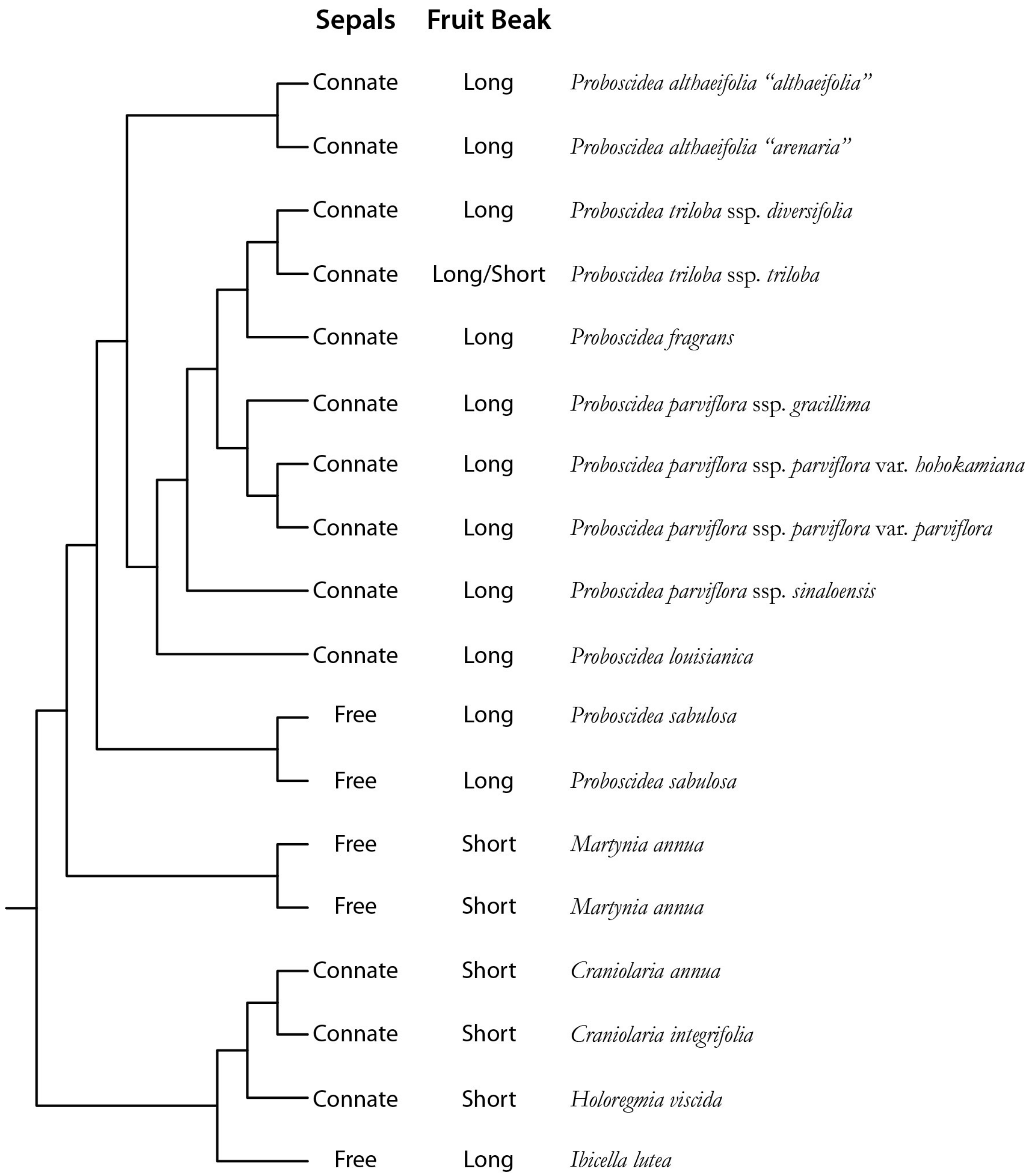

Fig. 15. Character states of the Martyniaceae for sepal unity and the length of beak on the fruits. Tree based on the majority rule consensus of three most parsimonious trees produced by the analysis of sequences from the ITS, *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions.

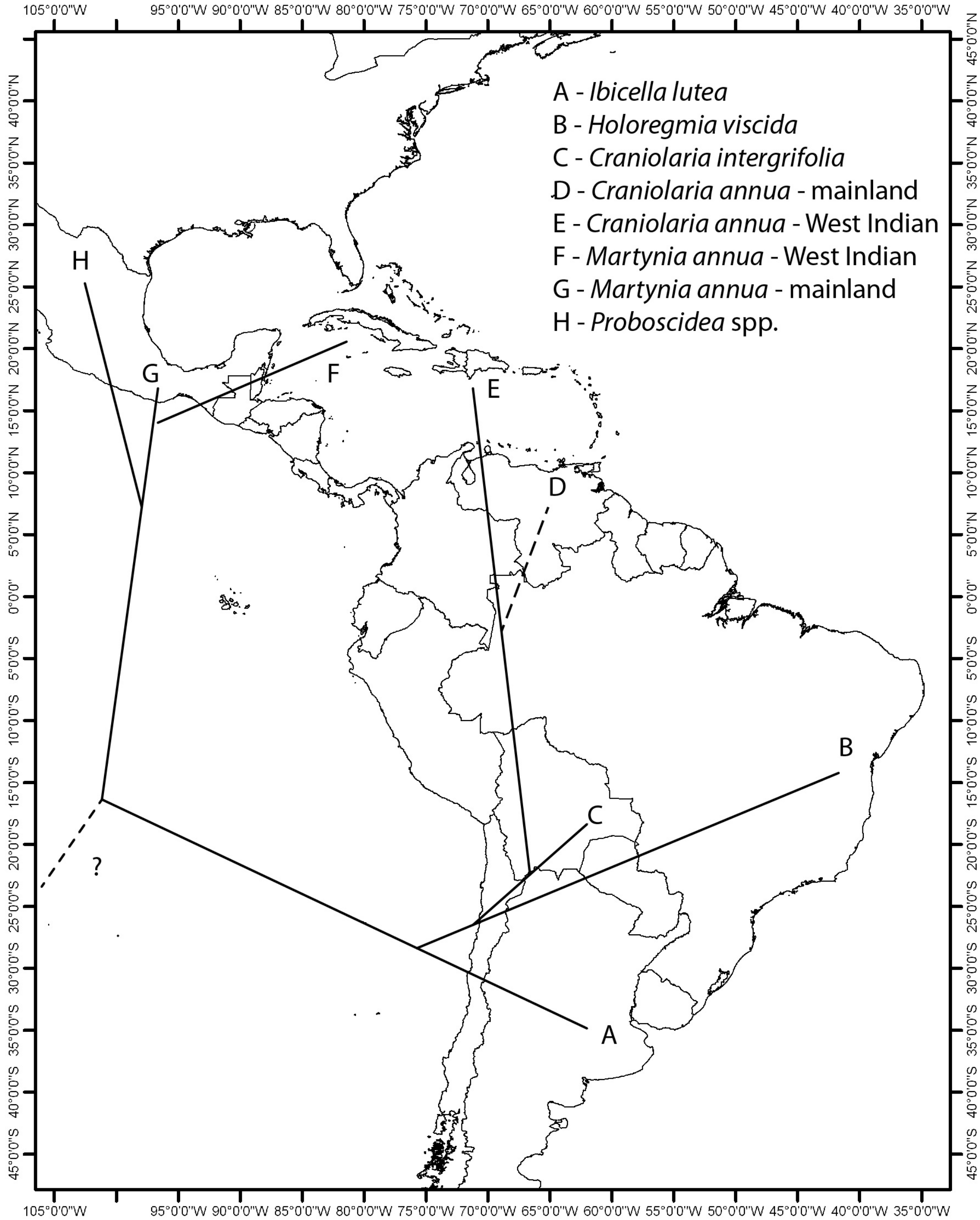

Fig. 16. Hypothetical dispersal of the genera of the Martyniaceae, with emphasis on the South American taxa. Phylogeny based on the maximum likelihood analysis of sequences from the ITS, *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions.

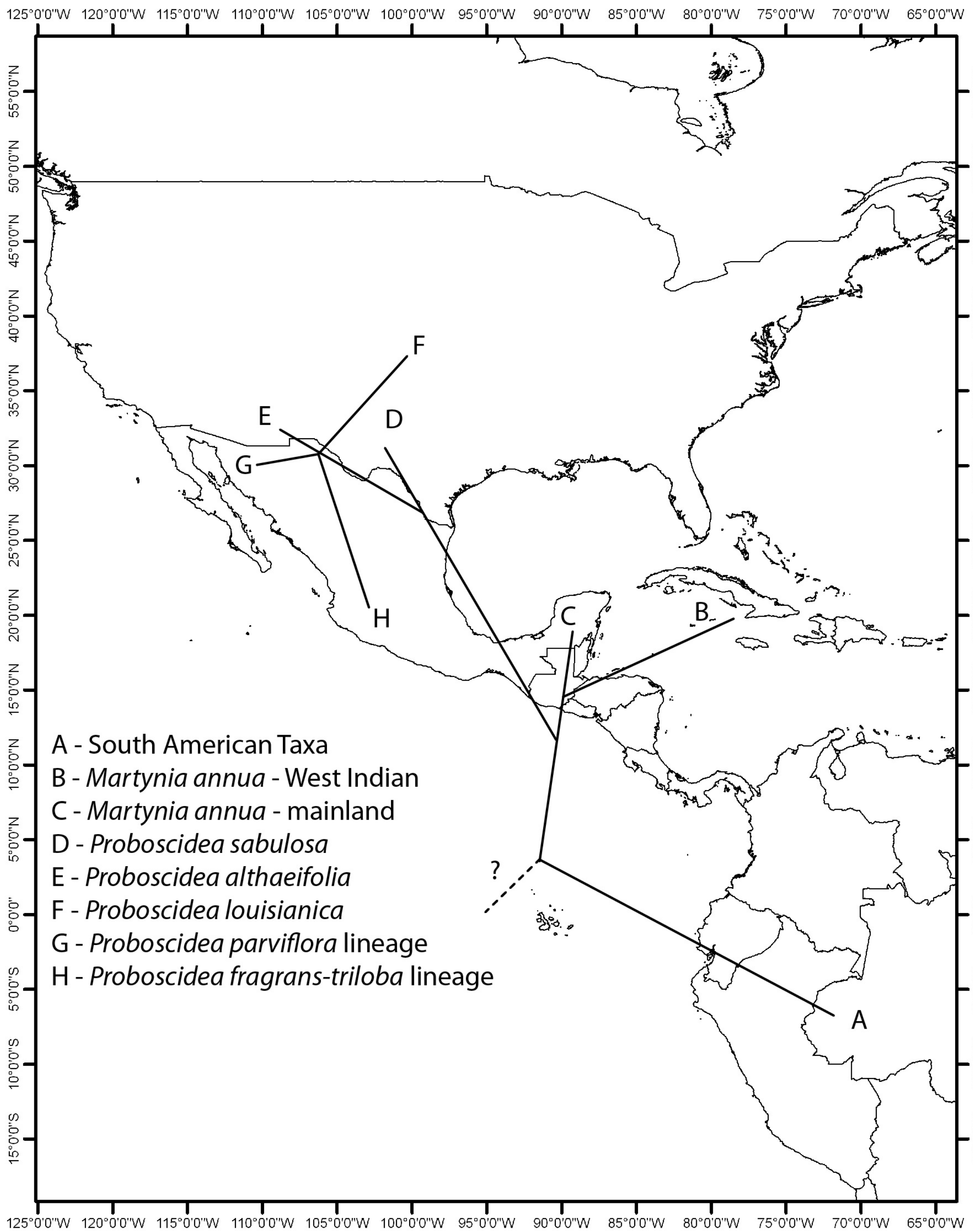

Fig. 17. Hypothetical dispersal of *Martynia* and *Proboscidea* in North America. Phylogeny based on the maximum likelihood analysis of sequences from the ITS, *psbA-trnH* spacer, *trnQ-5'rps16* intergenic spacer, and *trnS-trnG-trnG* spacer and intron regions.

TAXONOMIC TREATMENT

This work aims to revise and reconcile previous treatments of the family Martyniaceae, including those of Van Eseltine (1929), Abbiatti (1939), and Bretting (1981), to produce a treatment that will reexamine relationships and species concepts in light of results of recent molecular work and the examination of a larger number of herbarium specimens. Over 2500 specimens were examined during the course of this study. Genera, species, and subspecies can be separated on the basis of their habit, outline and shape of the lamina, size of the inflorescence, calyx and corolla shape and color, and the shape of the fruits and seeds. Thirteen species in five genera are recognized in the present treatment. Two of these, *Proboscidea parviflora* and *P. triloba*, are further divided into two subspecies each. The category variety has been employed to further distinguish two forms, a domestic and a wild type, of the subspecies *P. parviflora* ssp. *parviflora*.

***Taxonomic history* –** The first recorded mention of the family Martyniaceae was by Linnaeus in *Species Plantarum* (1753; Table 3), who included two members in the family. The first was *Craniolaria annua*, and the genus and species names are still applied to that taxon. The second, *Martynia annua*, was first described by Houstoun (Martyn 1728-1738) based on a plant collected in Veracruz, Mexico, and given the polynomial "*Martynia annua, villosa et viscosa*…" Linnaeus had renamed this plant "*Martynia foliis dentatis*" in the catalogue of Cliffort's Garden (Linnaeus 1737) before adopting his system of binomial nomenclature.

Linnaeus clearly refers to Houstoun's plant in *Species Plantarum*, but descriptions in later publications combine two different plants (Bretting 1981; Hevly

1969). The later Linnaean descriptions of *M. annua* included a plant with dentate-serrate leaves, two fertile stamens, and free sepals. This is accepted as the original *M. annua*, and the name still applies. The other plant included in the descriptions had entire leaves, four fertile stamens, and a lobed corolla. This plant was named *Proboscidea jussieui* by Keller in his revision of Schmidel's *Icones Plantarum* (1762); thus the genus was validly published by Keller. However, the combination of *P. jussieui* cannot be accepted, as Keller used binomial nomenclature inconsistently throughout his publication (Hevly 1969; Lawrence 1957). Miller (1768) later validly renamed this plant *Martynia louisianica*.

Linnaeus (1753) placed the two species he described in the group Didynamia Angiospermia, along with other plants having large, perfect flowers with four stamens arranged in two unequal ranks (Table 3). Lindley (1825) followed Brown's (1810; Table 3) taxonomy when he placed *Martynia* within Brown's "natural order" Pedalineae. The Pedalineae consisted mostly of taxa now placed in the Pedaliaceae and were characterized by the presence of hook-like or barb-like structures on the fruits, a character shared by *Martynia*. De Candolle (1845) also followed Brown's (1810; Table 3) taxonomy, but separated the genus *Martynia* into two sections, sectio *Proboscidea* and sectio *Proboscidella*. De Candolle separated these on the basis of beak length, with sectio *Proboscidea* having a beak longer than the fruit and sectio *Proboscidella* having a beak shorter than the fruit. It is questionable how many, if any, specimens were examined, as some species included in sectio *Proboscidella* have beaks longer than the body of the fruit. Around this time, Nees (1821) described a new monotypic genus from Brazil that he named *Holoregmia viscida* Nees, though he placed this genus in the Bignoniaceae. *Holoregmia* would later be placed in the Martyniaceae by Van Eseltine (1929).

Decaisne (1865) reviewed the group "Pédalinées" which mostly corresponds to Brown's(1810) Pedalineae, and focused on where species were placed within genera, keeping many of the same taxa as Brown but placing many of them into other genera. Decaisne separated the group "Pédalinées" into two informal groups (Table 3); his "racemic inflorescence" group contained the genera now placed in the Martyniaceae, while the "axillary inflorescence" group was comprised of taxa now placed in the Pedaliaceae. Decaisne transferred seven *Martynia* species into the genus *Proboscidea* on the basis of fruit shape. Those taxa with distinct sepals were kept in *Martynia*, and those with connate calyces were transferred to *Proboscidea*. These were the first valid combinations of names in the genus *Proboscidea*, as the combination *P. louisianica* was not published until 1912 by Thellung. Decaisne also retained the genus *Craniolaria*, which he distinguished from *Martynia* and *Proboscidea* on the basis of the elongated corolla tube.

Horaninov (1847) was the first person to publish the name Martyniaceae, though it was possibly included as a synonym, designated as "Bignoniaceae s. Martyniaceae." Within the Bignoniaceae, he recognized four groups. The first, Martynieae, included *Martynia* and *Craniolaria*, as well as a few perennial members that are now placed in Pedaliaceae. The second group, Sesameae, contained the annual members of the Pedaliaceae. The last two groups, Incarvilleae and Bignonieae, contained members that are still placed in the Bignoniaceae. Stapf (1895; Table 3) kept Horaninov's (1847) name for the family, but was the first to separate the Martyniaceae from the Pedaliaceae. Within the family Martyniaceae he recognized three genera, *Martynia*, *Proboscidea*, and *Craniolaria,* and created two sections within the genus *Proboscidea*: *Euproboscidea* and *Ibicella*.

Van Eseltine (1929; Table 3) later raised *Proboscidea* section *Ibicella* to the generic level. He also included *Holoregmia* in his treatment, bringing the total number of genera to five. The genus *Holoregmia* was first mentioned by Nees (1821) in his description of the species and rarely mentioned in subsequent publications due to its limited range and paucity of herbarium specimens. Within *Proboscidea*, Van Eseltine recognized two subgenera: *Dissolophia* and *Euproboscidea*. Ten years later, Abbiatti (1939) published a work on the Argentinian Martyniaceae and recognized four species in two genera. She also published the name *Ibicella parodii* for the first time. The next few decades saw the publication of several new names, and these were included in a dissertation done by Bretting (1981; Table 3). Bretting's dissertation included a very thorough monograph, though the work only focused on *Proboscidea*. Within the *Proboscidea*, he recognized three informal lineages corresponding to *P. althaeifolia* (Benth.) Decne., *P. sabulosa*, and the "weedy annuals."

Despite the general acceptance of the Martyniaceae as a distinct family throughout the 20th century (Van Eseltine 1929; Lawrence 1951; Munz 1959; Kearney and Peebles 1960; Hevly 1962; Taktajan 1969; Benson 1979; Bretting 1981), Cronquist (1981; Table 3) rejected the Martyniaceae as a distinct family, considering it conceptually more useful to include the Martyniaceae within the Pedaliaceae. Plants in both families have herbaceous habits, specialized trichomes on their surfaces, and pod-shaped fruits armed with hooks, horns, or prickles (Cronquist 1981). Thus, Cronquist recognized the two groups as the subfamilies Pedalioideae and

Martynioideae within the family Pedaliaceae, along with a third subfamily, Trapelloideae, whose sole member is *Trapella sinensis* Oliv.

In addition to the Pedaliaceae, other families have been associated with the Martyniaceae. Jussieu (1789) and Kunth (1822-1825) included the Martyniaceae within Bignoniaceae. Pollen morphology (Martin and Drew 1970; Bretting and Nilsson 1988) suggests that Martyniaceae may have a close affinity to Bignoniaceae. Martyniaceae differs from the family Bignoniaceae by the presence of parietal placentation and wingless seeds. Additionally, members of the Bignoniaceae are trees, shrubs, lianas, and rarely herbs, whereas the Martyniaceae are herbaceous annuals and perennials.

Martyniaceae Horan., Char. Ess. Fam.: 130. 1847. –TYPE: *Martynia* L.

Annual and perennial herbs or shrubs, viscid-pubescent throughout except on older woody stems, with taproots or tuberous roots. Stems erect to decumbent, terete or nearly so, hollow, fleshy and green or reddish-green, turning pale brown and woody with age. Leaves simple, opposite or subopposite, exstipulate; petioles long and conspicuous; laminas deltoid, cordate, ovate, suborbicular, or reniform, the margins entire to sinuate, dentate, or lobed, often denticulate or undulate-repand; apices angulate or rounded, acute to obtuse; bases cordate or truncate, sometimes inequilateral. Inflorescences terminal racemes, many-flowered and exceeding the foliage, to few-flowered and equaling or surpassed by the foliage; bracts linear, linear-oblong, or lanceolate, readily deciduous. Flowers perfect, zygomorphic, conspicuous, often with strong scent; pedicel erect in flower, becoming decumbent as the fruit matures and increases in weight; bracteoles 2, oblong, orbicular, oblanceolate or lanceolate, persistent or deciduous; calyx 5-merous, the sepals fused or separate, when separate the sepals oblanceolate, when fused the calyx split abaxially to the base and lobed or unlobed, the lobes mucronate or oblanceolate, equal; corolla maroon, pink, white, yellow, or pale green, sympetalous, 5-lobed, bilabiate to somewhat regular; the tube proximally restricted and distally dilated, the restricted portion cylindrical and surpassed by or surpassing the calyx, the dilated portion campanulate or funnelform, sometimes ventricose, equaling or surpassing the calyx, the interior and exterior surface of the tube with or without purple, maroon, or orange-brownish specks, with or without maroon, orange, or yellow nectar guides along the interior base of the tube; lobes rounded, spreading to reflexed, with or without a single large pink spot or numerous reddish-purple spots, the upper two lobes exterior in bud; stamens 4, didynamous, or 2, the second pair forming staminodes; filaments curved, attached to the corolla; anthers connivent, dehiscing longitudinally; pistil inserted between the two sets of stamens; stigma with 2 flat and sensitive lobes, these equal or unequal; style 1, terminal; ovary superior, unilocular, bicarpellate with 2 parietal placentae expanded into 2 broad T-shaped lamellae cohering above to form false partitions; ovules few to many. Fruits drupaceous capsules, bivalved, ovoid-elliptic to ovoid-elongate, imperfectly 5-celled; exocarp thick, fleshy, deciduous in 2 valves; endocarp dehiscent or indehiscent, woody and persistent, sculptured or echinate, with or without pectinate crests along the adaxial (and sometimes abaxial) suture, terminated by an incurved rostrum that splits into 2-(4)-hooked structures less than to 3 times the length of the body of the capsule. Seeds 4 to many, irregularly compressed, the testa corky-tuberculate or papery.

KEY TO THE GENERA OF THE MARTYNIACEAE

1. Fruit indehiscent or only slightly dehiscent, the rostrum shorter than the seed bearing body; seeds 4, with papery testa.

2. Corolla white, pale yellow, or pale green; sepals connate into a spathe-like sheath, fertile stamens 4.

3. Undilated cylindrical portion of corolla tube 8 cm or longer ..... I. *Craniolaria*

3. Undilated cylindrical portion of corolla tube 4 cm or shorter .. II. *Holoregmia*

2. Corolla white to pale pink; sepals free, fertile stamens 2 .... IV. *Martynia*

1. Fruit dehiscent, the rostrum equal to or longer than the seed bearing body; seeds 8-many, with corky testa.

4. Capsule echinate; sepals free... III. *Ibicella*

4. Capsule sculpted, never echinate; sepals united, or if free then corolla not yellow (in *P. sabulosa*) .... V. *Proboscidea*

I. Craniolaria L., Sp. Pl. 2:618. 1753. –TYPE: *Craniolaria annua* L.

Description. Long-lived annuals, perennials, or subshrubs to 3 m tall. Stems erect. Roots taprooted or tuberous. Leaves palmately lobed, broadly reniform or cordate, opposite, the margins entire to shallowly denticulate; apices acute; bases cordate, equilateral. Inflorescences many-flowered and surpassing the foliage; bracts linear to linear-lanceolate. Flowers: bracteoles narrowly lanceolate, deciduous or persistent; calyx of fused sepals, the lobes tooth-like and mucronate; corolla white, pale yellow, or pale green, somewhat rotate, the restricted portion of the tube surpassing the calyx, the dilated portion campanulate to urceolate, the internal surface of the tube with red or maroon specks; corolla lobes widely spreading to reflexed, the two lobes unmarked; stamens 4; ovules few. Fruits ovoid-elliptic, compressed dorso-ventrally; endocarp indehiscent, sculptured, without pectinate crests along the adaxial suture, rostrum shorter than the body of the fruit. Seeds 4, to 2 cm long, the testa papery.

Species of *Craniolaria* are characterized by their pale flowers having with very narrow and long proximal portion, the ovoid capsules, and the somewhat shrubby habit. *Craniolaria* can be distinguished from *Martynia* and *Holoregmia*, both with similar fruits, on the basis of the noticeably large flowers. *Proboscidea* and *Ibicella* differ both differ from *Craniolaria* in the shape of the fruits and the size, shape and color of the flowers.

The genus *Craniolaria* consists of two species with disjunct distributions. The name refers to the resemblance of the fruits to a cranium or skull.

KEY TO THE SPECIES OF *CRANIOLARIA*

Leaf margins deeply lobate or cleft; root system with a taproot, without tuberous roots; West Indies, northern South America (Colombia, Venezuela, Guyana) ....1. *C. annua*

Leaf margins entire to minutely denticulate; root system without a taproot, with tuberous roots; central South America (Argentina, Bolivia, Brazil, Paraguay).. 2. *C. integrifolia*

1. Craniolaria annua L., Species Plantarum 2:618. 1753. –LECTOTYPE: "*Martynia annua, villosa & viscosa; aceris folio flore albo tubo longissimo*" in Ehret, Pl. Papil.

Rar., t. 1, f. 2, 1748. Lectotype designated by Barrie, Regnum Veg. 127: 38. 1993.

Martynia craniolaria Glox., Obs. 14. 1785. Superfluous illegitimate name; see discussion below.

Martynia spathacea Lam., Encycl. (Lamarck) 2(1): 112. 1786. Superfluous illegitimate name; see discussion below.

Description. Long-lived annuals to 1 m, with taproots. Leaves palmately lobed, margins entire to denticulate. Inflorescences to 40 cm long; bracts to 25 mm long. Flowers to 25 cm long; pedicels about 1.5 cm in length at anthesis, elongating slightly to 2 cm in fruit; bracteoles persistent; calyx to 5 cm long; corolla to 25 cm long, 2 cm wide at throat. Fruits: endocarp to 5 cm long, 2.3 cm wide, rostrum shorter than 1 cm long. Fig. 18.

Phenology. Flowering throughout the year.

Distribution and habitat (Fig. 19). Native to the West Indies (Cuba, Hispaniola, Puerto Rico) and northern South America (Colombia, Guyana, and Venezuela). 0-300 m (0-1000 ft). Disturbed areas along beaches, roads, pastures, and cultivated fields.

Vernacular names. Yuca escorzonera, Escorzonera.

SPECIMENS EXAMINED. **COLOMBIA**. ATLÁNTICO: around Barranquilla, Altos del Prado, 27 May 1953 (fl), *Dugand 4650* (NY, US), region of Barranquilla, Nov 1955 (fl), *Elias 1407* (F). –CASANARE: Orocué, s.d. (fl), *Ariste-Joseph A941* (US). –CESAR: Magdalena Valley, Rincon Hondo, 26 Aug 1924 (fl), *Allen 508* (MO); near

Codazzi, Cesar and Rancheria Valleys, 02 Jun 1944 (fl), *Haught 4188* (F, K, NY). –LA GUAJIRA: no locality given, Oct 1916 (fl), *Dawe 524* (K, US). –MAGDALENA: Santa Marta, open land 5 mi E of Banda, 03 Aug 1898-1899 (fl), *Smith 1159* (E, F, GH, LL, MICH, MO, NY, UC, US); Isla de Salamanca, at km 42 between the highway and the ocean, 04 Dec 1966 (fr), *Romero-Casteñeda 10543* (F, GH, MO, NY). –META: Cabuyaro, Jan 1937 (fl), *García B. 5133a* (US).

CUBA. ISLA DE LA JUVENTUD: roadside at N end of Sierra Las Casas, 28 Apr 1954 (fl), *Killip 44169* (US). –SANTIAGO DE CUBA: Siboney, Santiago, Jul 1948 (fl), *Clemente 6111* (GH); Renté, Santiago, June 1944 (fl), *Clemente 3686* (GH); El Cobre, Santiago, May 1951 (fl), *Alain & Clemente 1984* (GH). –SANCTI SPIRITUS: [Santa Clara], SE of Trinidad, 27 Jun 1931 (fl), *León 14924* (NY).

DOMINICAN REPUBLIC. MONTE PLATA: Santa Cruz, Los Pomos Resort, 7 km NE of Bayaguana, 18°47'N, 69°36'W, 05 Nov 1995 (fl, fr), *Jiménez et al. 1986* (F, MO). –PERAVIA: Llanura Costera, 0.5 km E of Matanzas on the highway to Baní, 18°15'N, 70°24'W, 30 May 1983 (fl, fr), *Zanoni 26048* (MO, NY); Llanura Costera, 0.5 km E of Matanzas on the highway to Baní, 18°15'N, 70°24.5'W, 27 Jun 1983 (fl, fr), *Zanoni & Pimentel 26416* (NY); 300 m E of town of Matanzas, 18°22'00"N, 68°54'00"W, 22 Sep 1996 (fl), *Acevedo-Rodriguez et al. 8486* (NY); 1 km E of Matanzas on road to Baní, 18°15'N, 70°24'W, 07 Aug 1980 (fl, fr), *Mejía & Zanoni 7758* (NY-2). –SANTO CRISTÓBAL: edge of highway to Palenque, 20 Oct 1973 (fl), *Liogier & Liogier 20447* (F, NY). –SANTO DOMINGO: La Cuence, Llano Costero, 13 Aug 1929 (fl), *Ekman 13341* (F). –SAN JUAN DE LA MAGUANA: Valle de San Juan de la Maguana, toward Corral de los Indios, 31 Aug 1929 (fl), *Ekman 13453* (K, NY).

GUYANA. EAST BERBICE-CORENTYNE: Orealla Savannah, 1 mi W of Orealla, 05 Jan 1955 (fl), *Irwin 607* (TEX); Orealla Savannah, Courantyne River, 05 Jan 1955 (fl), *Irwin 371* (US); Orealla Savannah, Courantyne River, 20 Nov 1954 (fl), *Lindeman 6690* (US). –ESSEQUIBO ISLANDS-WEST DEMERARA: St. Cuthbert Mission, Mahaica River, Jan 1967 (fr), *Davis 129* (K). –UPPER DEMERARA-BERBICE: 8 mi along Ituni trail from Waranama along Berbice River, 17 Jun 1958 (fl), *Harrison 1149* (K).

HAITI. CENTRE: Hinche, Massif du Nord, 13 May 1926 (fl), *Ekman 6096* (F).

PUERTO RICO. Manatí to Vega Baja, 14 Jun-22 Jul 1901 (fl, fr), *Underwood & Griggs 929* (NY); Arecibo, 22 Nov 1913 (fl), *Hess & Stevens 5050* (NY); Carolina. Isla Verde, Boca de Cangrejo, 19 Aug 1963 (fl), *Liogier 10185* (GH, NY); Cataño, 26 Aug 1979 (fl), *Woodbury s.n.* (BRIT, MO, NY-2); near Dorado, 16 Jun 1932 (fl), *Britton & Britton 9876* (NY); Humacao; lowlands on W side of Rio de Loiza bridge (Hwy 187) near Loiza, 18º26'12"N, 66º53'20"W, 13 Jul 2002 (fl, fr), *Worthington 31343* (BRIT, UTEP [photo at ASU]); Loiza, Barrio Torrecilla Baja, 0.5-0.6 km W of mouth of Río Grande de Loiza, 14 May 1991 (fl), *Proctor et al. 46838* (NY); Manatí, Barrio Tierra Nuevas Salientes, 18º27.50'N, 66º26'W, 03 Sep 1999 (fl, fr), *Axelrod et al. 10960* (US); Tortuguero, Nov 1972 (fl), *Woodbury s.n.* (BRIT, NY, US); Tortuguero, June 1970 (fl), *Woodbury s.n.* (NY) Quebradillas, Barrio Terranova, La Estación, 18º28.983'N, 66º55.117"W, 22 Dec 1994 (fl, fr), *Acevedo-Rodriguez et al. 7005* (NY, US); Quebradillas, Barrio Terranova, between Rte 4485 & Rte 2, 18º29'N, 66º54-56.5"W, 28 Oct 1994 (fl), *Zanoni et al. 47236* (NY); Quebradillas, 18º29'N, 66º56'W, 04 Nov 1994 (fl, fr), *Atha et al. 713* (NY); San Juan, Río Piedras, Algarroba, 26 Jul 1914 (fl, fr), *Stevenson 2148* (NY, US); Toa Baja, Palo Seco, 12 Oct 1937 (fl), *Otero 59* (MO);

Vega Alta, Cerro Gordo, 01 Dec 1983 (fl, fr), *Liogier & Martorell 34856* (NY); Vega Baja, near Laguna Rica, 02 Feb 1924 (fl), *Britton & Britton 7945* (NY).

VENEZUELA. AMAZONAS: Atures, on E side of road 5.5 km S of Puerto Ayacucho, 2.4 km S of Alcabala, 05°43'N, 67°37'W, 08 Sep 1985 (fl, fr), *Steyermark et al. 131597* (MO, NY, US); Atures, near Puerto Ayacucho, 05°40'N, 67°36'W, 08 Jun 1982 (fl), *Guanchez 1807* (MO). –ANZOÁTEGUI: Freites, Morichal Morichalote, 6-7 km W of Oritupano River, 09°02'N, 63°30'W, 12 Jun 1998 (fl), *Fernandez et al. 12766* (US). –ARAGUA: along Río Limón, 28 Jul 1955 (fr), *Tamayo 4085* (MO, NY). –BOLÍVAR: San Felix, 11 May 1949 (fl), *Curran ZM-7* (NY); near El Paso de la Fortuna 07°8'N, 63°10'W, 29 Jul 1978 (fl, fr), *Liesner & Gonzalez 5793* (MO). –CARABOBO: Hacienda de Cura, near San Joaquin, 05-08 Jul 1918 (fl), *Pittier 7920* (US). –DEPENDENCIAS FEDERALES: Islas Los Testigos, Isla Testigo Grande, 28 Dec 1982 (fl, fr), *Fernandez et al. 276* (MO, NY). –GUÁRICO: El Sombrero-Calabozo Hwy, Jul 1954 (fl), *Aristeguieta & Hernandez 2309* (F); ca 39 km SSW of Calabozo on Hato Masaguaral, 08.56°N, 67.59°W, 28 Feb 1983 (fl, fr), *Rondeau 227* (MO, US); Francisco de Miranda, Calabozo, near Los Llanos Biological Station, 16 Sep 1975 (fl), *Cardenas de Guevara 2237* (F); Francisco de Miranda, Calabozo, Los Llanos Biological Station, 08°56'N, 67°25'W, 20 Mar 1982 (fl), *Ramirez 502* (MO). –MIRANDA: Hacienda El Volcán, near Santa Lucia, 1918 (fl), *Pittier 8247* (GH), Santa Catalina, 1896 (fl), *Rusby & Squires 304* (NY). –MONAGAS: 10 km WSW of Jusepin, 23 Mar 1967 (fl), *Pursell et al. 8512* (NY, US); damned tributary to the Río Guarapiche ca. 9 km WSW of Jusepin, 27 Jun 1967 (fl), *Pursell et al. 9419* (NY, US). –NUEVA ESPARTA: Isla Margarita, El Valle, 12 Jul 1901 (fl), *Miller & Johnston 89* (F, GH, K, NY). –TRUJILLO: Betijoque, ca. 10 km NE of Agua Viva along Maracaibo-Agua Viva Hwy, 34 km SE of La Raya, 31 May 1981 (fl), *Bunting & Clausnitzer 9922* (NY). –ZULIA: San José de Perijá, 23 May 1967 (fl), *López-Palacios 1817* (NY); growing as a weed at Maracibo Botanical Garden, 06 Sep 1977 (fl), *Bunting 5379* (NY); Perijá, ca. 7 km E of Maracaibo-La Fria Hwy (Hwy 6), and ca 4 km N of the Río Aricuaisá, 09°26'N, 72°33'W, 20 Jun 1980 (fl, fr), *Davidse et al. 18343* (MO, NY).

CULTIVATED. *Sargent B53* (US, fl).

Craniolaria annua is distinguished from *C. integrifolia* by the lack of tuberous roots, its shorter life span, its palmately lobed leaves that resemble *Acer* leaves, and its native distribution in the West Indies and northern South America. The epithet is in reference to its somewhat annual habit, though the plant may live for longer than one growing season.

Lamarck (1786) cited the name and illustrations for what is now considered to be the lectotype for *C. annua*, making his name, *M. spathacea*, superfluous and illegitimate. Gloxin (1882) also cited the name and illustrations for the lectotype for *C. annua*, making his name, *M. craniolaria*, superfluous and illegitimate.

2. Craniolaria integrifolia Cham., Linnaea 7: 725. 1832. –TYPE: BRASIL: Brasilia meridionali, 1814-1831, *Sellow s.n.* (Holotype: HAL [photo at ASU!]).

Craniolaria integrifolia fma. *longiflora* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 547. 1903. –TYPE: PARAGUAY: Igatimi, Nov, *Hassler 5527* (syntype: G-Hassler [3 sheets, photos at ASU!]), PARAGUAY: Cordillera de Altos, Oct, *Hassler 3305* (syntype: G-BOIS [4 sheets, photos at ASU!] G-Delessert [photo at ASU!] G-Hassler [photo at ASU!] GH! [photo at ASU!] K! [photo at ASU!] NY! [photo at ASU!] UC!).

Craniolaria argentina Speg., Pl. Nov. Crit. Reipubl. Argent. Decas 3: 3. 1897. – TYPE: ARGENTINA. Salta: La Viña, Jan 1897, *Spegazzini 10449* (syntype: LP [photo at ASU!]), ARGENTINA. Salta: Cafayate, Molinos, Jan 1897, *Spegazzini 10450* (syntype: LP [photo at ASU!]), ARGENTINA. Salta: Cafayate, Dec 1896, *Spegazzini 12556* (syntype: LP [photo at ASU!]).

Description. Perennials to 1 m tall, with tuberous roots. Leaves cordate; margins entire to denticulate. Inflorescences to 30 cm long; bracts to 20 mm long. Flowers to 20 cm long; pedicels about 10 mm in length at anthesis, elongating slightly to 15 mm in fruit; bracteoles deciduous; calyx to 3 cm long; corolla to 20 cm long, 2 cm wide at throat. Fruits: endocarp to 4 cm long, 2 cm wide, rostrum shorter than 1 cm long. Fig. 18.

Phenology. Flowering from October to May (mostly November to February). Fruits are persistent.

Distribution and habitat (Fig. 20). Native to central South America (Argentina, Bolivia, Brazil, and Paraguay). 0-1900 m (0-6000 ft). Sandy soils in disturbed areas.

Common Names. Pico de piraba; Uñas del Diablo.

SPECIMENS EXAMINED. **ARGENTINA**. <u>CATAMARCA</u>: CAPAYÁN, ca. 5 km NW of Chumbicha, 24 Jan 1975 (fl), *Hunziker 22718* (F). CAPITAL, San Fernando del Valle de Catamarca, 12 Nov 1920 (fl), *Castillon 48246* (F). –<u>CHACO:</u> SAN FERNANDO, Colonia Benitez, Dec 1968 (fr), *Schinini 9911* (CTES). –CORDOBA: ISCHILÍN, Quilino, 20 Jan 1947 (fl), *O'Donnell 4544* (TEX). –CORRIENTES: BELLA VISTA, 10 km S of Bella Vista in Arroyo Ribera, 08 Nov 1978 (fl), *Schinini & Ahumada 15899* (CTES, MO). CAPITAL, Riachuelo, 15 Feb 1996 (fl), *Schinini 30426* (ASU, GH); arroyo Riachuelo along Rte 12, 07 Feb 1968 (fl), *Krapovickas & Cristobal 13784* (LL, MO); Paso de la Patria, 19 Nov 1976 (fl), *Seigler et al. 10155* (MO). CONCEPCIÓN, Estancia Palermo, 25 Mar 1967 (fl), *Arbo 88* (UC); Tabay, 01 Nov 1965 (fl, fr), *Krapovickas & Cristobal 11611* (UC). ITUZAINGO, Isla Apipé Grande, ca 5 km from Puerto Arazá, 26 Nov 1988 (fl), *Tressens et al. 3478* (ASU, F, GH, K, MO, TEX); Isla Apipé, Puerto San Antonio, 10 Dec 1973 (fl), *Krapovickas et al. 24150* (CTES). MBURUCUYÁ, Estancia Santa Teresa, 16 Jan 1953 (fl), *Petersen 1925* (GH, MO, NY). PASO DE LOS LIBRES, Paso de los Libres, 11 Jan 1945 (fl), *Ibarrola 2058* (US); Laguna Mansa, 19 Feb 1972 (fr), *Krapovickas & Cristobal 21674* (GH), Bonpland, along Río Uruguay, 19 Jan 1945 (fl, fr), *Ibarrola 2147* (NY-2). SAN COSME, Paso de la Patria, Médano, 25 Nov 1973 (fl), *Lourteig et al. 2977* (US). SAN MIGUEL, 12 km NE of San Miguel, 28 Feb 1990 (fl, fr), *Vanni et al. 1499* (TEX). SAN ROQUE, Campa Anacua, 28º25'30"S, 58º26'17"W, 26 Jun 2001 (fr), *Keller 975* (CTES). –ENTRE RÍOS: CONCORDIA, Ayuí, 31º16'S, 57º59'W, 18 Nov 2003 (fr), *Cocucci et al. 3015* (CTES). –FORMOSA: BERMEJO, 2 km N of Laguna Yema, 12 Dec 1984 (fl, fr), *Schinini & Pire 24242* (CTES, F, UC). PATINO, Las Lomitas, Jan 1928 (fr), *Parodi 8362* (GH). –JUJUY: SANTA BÁRBARA, from Fuerte to Cachipunco, 20 Feb 1985 (fr), *Kielsing et al. 5466* (MO, NY). –LA RIOJA: CHAMICAL [GOBERNADOR GORDILLO], Rte 79, at km 56 between Salina La Antigua and Casa de Piedra, 14 Feb 1984 (fr), *Aguirre 436* (CTES). –MISIONES: SAN IGNACIO, San Ignacio, 22 Dec 1992 (fl), *Rodriguez et al. 383* (CTES); Loreto, camp passing Arroyo Pastora, 27º21'S, 55º31'W, 20 Apr 1996 (fr), *Zuloaga et al. 5669* (MO, NY). –SALTA: CAFAYATE, 7 km S of Cafayate along Rte 40, 02 Jan 1972 (fl, fr), *Krapovickas & Cristobal 20581* (CTES). CHICAOANA, Escopie Trail at bridge over Arroyo Malcante, Rte 33, km 31, 18 Mar 1999 (fr), *Novara et al. 11224* (CTES). LA CANDELARIA, Unquillo, Jan 1933 (fl), *Schreiter 9437* (F). SAN JOSÉ DE METAN, 15 km W of Hickmann, El Milagro Well, Rte 81, 10 Dec 1972 (fl), *Marunak et al. 576* (CTES). –SANTIAGO DEL ESTERO: CAPITAL, Tipiro, 1.7 km NW of access to Los Quiroga, 15 km NW of Route 208, 17 Nov 1994 (fl), *Krapovickas & Cristóbal 46226* (CTES).

BOLIVIA. CHUQUISACA: LUIS CALVO PROV., between La Victoria and Iguabirantí, 31 Jan 1992 (fl), *Saravia T. & Nelson J. 10472* (CTES). OROPEZA PROV., Sucre to Cochabamba at km 80, Apr 1963 (fl), *Cardenas 6110* (US). –POTOSÍ: CHARCAS PROV., Culqui Pampa near Río Caine, 24 Feb 1992 (fl), *Mostacedo 274* (NY). –SANTA CRUZ: CHIQUITOS PROV., 25 km from Aguas Calientes, 55 km E of Roboré along El Carmen road, 18º31'35''S, 59º19'27''W, 02 Feb 1995 (fl), *Mostacedo & Abbot 2817* (NY). CORDILLERA PROV., Bañados de Izozog, between Laguna Negra and Estancia Toborochi, 19º06'S, 62º20'W, 05-15 Jan 1993 (fl, fr), *Vargas C. et al. 1907* (NY, TEX); between El Espino and Saipurú, Feb 1951 (fl, fr), *Cárdenas 4730* (US); San Bernardino, 23 Dec 1936 (fl, fr), *Archer 4735* (US); Izozog-Chaco, Apr 1965 (fl), *Cardenas 6190* (US). FLORIDA PROV., along hwy from Mairana to Mataral, 2 km NE of turnoff to Pampa Grande and 1.5 km SW of bridge in Los Negros, 18º3.8'S, 64º7.2''W, 31 Mar 2002 (fl, fr), *Nee et al. 52095* (NY, TEX). JOSÉ MIGUEL DEL VELASCO PROV., 14 km S of Santa Ana along road to San Rafael, 16º42'28''S, 60º41'26''W, 26 Jan 2004 (fl, fr), *Neffa et al. 1249* (CTES). NUFLO DE CHÁVEZ PROV., along road to dam on Rio Zapocoz, 0-2 km NW of Concepcion, 16º08'S, 62º03'W, 28 Dec 1986 (fl), *Nee 33373* (MO, NY-2, TEX); Concepción, lake W of town, 16º08'S, 62º03'W, 28 Oct 1985 (fl), *Killeen 1322* (F, NY); region of Lomerío, 2 km NW of the San Lorenzo, 16º42'26''S, 61º52'16''W, 22 Nov 1994 (st), *Toledo et al. 479* (NY); San Miguelito, 200 km E of the city of Santa Cruz, 17º04'S, 61º47'W, *Fuentes 1337* (NY). IGNACIO WARNES PROV., 9.5 km NE of Santa Cruz-Warnes Hwy on dirt road to Candelaria, 17º31'S, 63º0.46'W, 21 Mar 2002 (fl, fr), *Nee & Sundue 51907* (NY-2).

BRAZIL. MATO GROSSO: Rio Jauru, 18 Nov 1996 (fl), *Hatschbach et al. 65652* (ASU, MO). –MINAS GERAIS: Campina Verde, 18 Dec 1985 (fl), 20 Mar 1986 (fr), *Macedo 5420* (NY, US). –SAO PAULO: Emas Pirassununga, near the experimental station of the department of Botany of the University of Sao Paulo, 08 Jan 1955 (fl), *Kuhlmann 3529* (K, NY, SP); Emas, 16 Dec 1919 (fl), *Gehrt 3710* (SP); Emas, 22º02'S, 47º30'W, 02 Feb 1995 (fl, fr), *Batalha et al. 306* (SP); Emas, 22º02'S, 47º30'W, 10 Jan 1995 (fl), *Aragaki & Batalha 303* (SP).

PARAGUAY. No locality given, 1885-1895 (fl), *Hassler 1091* (NY). –ALTO PARAGUAY: Chaco, Feb 1989 (fl, fr), *Mereles & Ramella 2627* (CTES). –AMABAY: Bella Vista, ranch of Félix Ocariz, 22º10'S, 56º30'W, 24 Mar 1983 (fl, fr), *Hahn et al. 1327* (MO, NY, TEX). –BOQUERÓN: 40 km S Linea 10, 26 May 1994 (fl), *Mereles & Degen 5705* (CTES); Fortín Nueva Asuncion, forest at N end of military airfield, 20º43'S, 62º56'W, 24 Mar 1986 (fl, fr), *Brunner 1581* (MO). –CAAGUAZÚ: 10-15 km N of Caaguazú, 19 Feb 1994 (fl), *Pedersen 16072* (CTES). –CENTRAL: Itá, along Arroyo Lazarillo, 29 Jan 1966 (fl), *Krapovickas et al. 12203* (CTES, UC); Itá Entamada, Asunción, Nov 1971 (fl), *Schinini 4198* (F); near Asuncion, 02 Nov 1889 (fl), *Morong*

824 (E, MICH, MO, NDG, NY, US). –CORDILLERA: Road from Caacupé to Tobaty, 03 Feb 1978 (fr), *Schinini 14592* (CTES); Altos, Cordillera de los Altos, Oct 1902 (fl), *Fiebrig 307* (E-3, F, GH-2); San Bernardino, 23 Dec 1936 (fl), *Archer 4735* (GH). –ITAPUÁ: Isla Yacyretá, around the military station, 25 Apr 1983 (fr), *Duré 175* (CTES). –PARAGUARÍ: Cerro Mbatoví, 28 Nov 1987 (fl), *Soria & Lardini 1869* (K, MO); n slope of Cerro Mbatoví, 25°25'S, 57°07'W, 26 Jan 1989 (fl), *Zardini & Velásquez 9907* (MO); Parque Nacional Ybycu'í, NE corner of the park on Arroyo Corrientes near Salto Mbocaruzú, 26°03'S, 56°50'W, 21 Dec 1988 (fr), *Zardini et al. 8979* (MO).

Though the margins sometimes have a high degree of undulation and can appear lobed when pressed, the leaves of *C. integrifolia* are entire, whereas *C. annua* has lobed leaves.

The type specimens of *Craniolaria argentina* Abbiatti from the Museo de La Plata (LP) were previously held at the Universidad Nacional de La Plata (LPS), where Abbiatti (1939) examined them for her study of the Martyniaceae of Argentina. In her description of *C. argentina*, she discusses the high levels of overlapping variability within and among *C. integrifolia* and *C. argentina*, suggesting they could be recognized as one taxon. Upon the review of a larger and more widespread set of specimens undertaken for this study, the level of variability in both taxa becomes apparent. This variation does not appear to be geographically correlated, but rather represents the effects of varying microclimatic conditions on growth of the individuals. Until more data are generated to suggest the segregation of these taxa as two separate species, both taxa are here being recognized as one highly variable species.

Additionally, there are some unresolved issues with the type of *Craniolaria argentina*. Three specimens at LP have been stamped in red ink with the word 'Cotypus.' One of these type specimens (*Spegazzini 10449*) comes from La Viña, Salta. There are two other specimens at LP with the exact data as *Spegazzini 10449*, but without both the collector's number and the designation as Cotypus. Another type specimen (*Spegazzini 10450*) comes from Molinos, Salta, with the word 'Cafayate' written in pencil and not part of the typed data. The third one (*Spegazzini 12556*) comes from Cafayate, Salta. In his protologue, Spegazzini (1897) cites the locality in the sandy and gravelly streams of La Viña and Guachipas and in rocky mountainous areas around Cafayate, all in the Province of Salta, Argentina. The origin of the red ink marks on the three syntypes should be investigated to see if Spegazzini himself designated these specimens, or if the designation came at a later time. Other issues to resolve include the omission as types of the other two specimens from La Viña, the lack of any specimens from the stated type locality of Guachipas, and the inclusion as a type of the specimen from Molinos.

Since designations of types on sheets, without publication, are not validly or effectively published, a lectotype should be designated. *Spegazzini 10449* (LP) from La Viña and marked with 'Cotypus' should be designated as the lectotype. Despite the handwritten locality, the data printed on the label for *Spegazzini 10450* includes a locality that is not included in the protologue, and therefore not appropriate for use as a type. Spegazzini (1897) distinguished *C. argentina* from *C. annua* on the basis of floral and leaf characters. Since the lectotype consists of numerous floral parts and no leaves, the third specimen, *Spegazzini 12556* (LP), should be designated as the epitype. This sheet consists of leaves and stems which will help to clarify characters not seen on the lectotype. Both the lectotypification and epitypification will be published separately from this dissertation in accordance with Article 30.5 of the International Code of Botanical Nomenclature (the Code; McNeill et al. 2006).

II. Holoregmia Nees, Flora 4:300. 1821. –TYPE: *Holoregmia viscida* Nees.

Description. Shrubs to 3 m. Stems to 5 cm think, erect, green and fleshy when young, turning pale brown and woody with age. Leaves cordate to deltoid, opposite; petioles to 20 cm long; margins shallowly dentate; apices acute; bases cordate, equilateral; upper surface of the lamina dark green with impressed venation; lower surface paler with prominent veins. Inflorescences many-flowered and surpassing the foliage, to 70 cm long; bracts linear-lanceolate, to 25 mm long. Flowers 4-6 cm long; pedicels to 1.5 cm long at anthesis, elongating slightly to 2cm in fruit; bracteoles narrowly lanceolate, persistent in fruit; calyx fused, spathaceous, the tube inflated, urceolate, circumscissile in fruit, the lobes mucronate, even; corolla to 5 cm long, 2 cm wide at throat, pale yellow to pale green, bilabiate, the restricted portion of the tube surpassed by the calyx, the dilated portion funnelform, surpassing the calyx, the internal surface of the tube with purple to maroon dots coalescing to form nectar guides, the dots fewer on the outside of the tube; lobes with reddish-purple dots; stamens 4, slightly exserted; filaments 2.5 to 2.8 cm long; anthers to 8 mm long; ovules 4. Fruits to 4 cm long, 2.3 cm wide, ovoid-elliptic; endocarp indehiscent, sculptured, with reduced or inconspicuous adaxial crests; capsule indehiscent, the rostrum shorter than 1 cm. Seeds 4, to 2 cm long, elongate, staying within the fruit. Fig. 21.

The genus can be distinguished from the other genera on the basis of its shrubby habit, large bracteoles, inflated-urceolate calyx, pale yellow to pale green flowers with reddish-purple spots, and large indehiscent fruits.

3. Holoregmia viscida Nees, Flora 4: 300. 1821. –TYPE: BRAZIL. Bahia: between Faz. Cachoeira and Jequié, March 1817, *Wied s.n.* (holotype: BR [photo at ASU!]).

Craniolaria unibracteata Nees & Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11:67. 1823. Superfluous illegitimate name; see discussion below. *Proboscidea unibracteata* (Nees & Mart.) Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 325. 1865. Later invalid synonym.

Description. Characters of the genus. Fig. 21.

Phenology. Harley et al. (2003) indicate a long flowering period for this species. Specimens with flowers have been collected from September to March.

Distribution and habitat (Fig. 20). Endemic to the caatinga region of NE Brazil in the state of Bahia (Harley et al. 2003). It is restricted to the valleys of the Rio de Contas and the Rio Paragauçu, both of which arise from the mountains of the Chapada Diamantina.

SPECIMENS EXAMINED. BRAZIL. BAHIA: MPIO. ARACATU, around the city, 14°25'8"S, 41°27'53"W, 08 Feb 2004 (fr), *Harley et al. 54848* (HUEFS). MPIO. IAÇU, Fazenda Lapa, 12°42'S, 39°56'W, 26 Feb 1983 (st), *Bautista 730* (HUEFS). MPIO. ITABERABA, Hwy BA046, 25 km SSE of Itaberaba, 12°43'47"S, 40°12'46"W, 20 Nov

1986 (fl, fr), *de Queiroz 1333* (HUEFS); ca. 9 km E of Itaberaba on Ipirá road, 27 Sept 2001 (fl, fr), *de Queiroz 6642* (HUEFS-2). MPIO. JEQUIÉ, ca. 20 km from Jequié on road to Contendas do Sincorá, 13º45'16"S, 40º16'15"W, 22 Mar 1989 (fl), *de Queiroz & Crepaldi 2157* (HUEFS, NY); Contendas do Sincorá, 20 km L, 21 Nov 1985 (fl), *Hatschbach & Silva 50071* (MO); Chácara Provisao, ca 4 km E of Jequié, 06 May 1979 (fl, fr), *Mori & dos Santos 11844* (US). MPIO. LIVRAMENTO DE NOSSA SENHORA, on right of track leading from main road from Livramento to Rio de Contas going towards the bottom end of the Estrada Real, about 80 m from main road, 13º36'S, 41º48'W, 25 Jan 2001 (fl, fr), *Harley & Giulietti 54073* (HUEFS, K). MPIO. MILAGRES, 3 km NW of Iaçu, 12º44'S, 40º13'W, 20 Nov 1986 (fl), *Webster et al. 25812* (NY).

This species was recently rediscovered by botanists from the Royal Botanical Gardens at Kew and the Universidade Estadual de Feira de Santana (Harley et al. 2003). Prior to that, it was known only from the type specimen. Since then, other specimens have been identified in other collections. In the absence of the capsular fruits, this species may be mistaken for a member of the family Gesneriaceae. Herbaria should check the unidentified specimens filed in Gesneriaceae, under which more unidentified specimens may yet be discovered.

Nees and Martius (1823) cited both the name and illustration for *H. viscida* and in their protologue for *C. unibracteata*, making *C. unibracteata* superfluous and illegitimate. Decaisne (1865) later cites both *C. unibracteata* and *H. viscida* in his protologue for *P. unibracteata*, making *P. unibracteata* an invalid later synonym.

III. Ibicella Van Eseltine, Tech. Bull. N. Y. State Agric. Exp. Stat. 149: 39. 1929. – TYPE: *Ibicella lutea* (Lindley) Van Eseltine.

Proboscidea Keller section *Ibicella* Stapf, Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 269. 1895.

Description. Annuals. Stems erect to decumbent. Roots taprooted. Leaves broadly ovate to suborbicular, opposite to subopposite; margins entire, denticulate; apices angulate to rounded; bases cordate, equilateral. Inflorescences many-flowered and surpassing the foliage; bracts oblong to rhomboidal. Flowers: bracteoles oblong to orbicular, deciduous; sepals free; corolla yellow, bilabiate; the restricted portion of the tube surpassed by the calyx, the dilated portion ventricose to obliquely-funnelform, the internal surface of the tube with orange to maroon specks and orange nectar guides; corolla lobes widely spreading, the lobes lacking any large conspicuous spots; stamens 4; ovules many. Fruits oblong to oblong-ovoid; endocarp moderately dehiscent, with echinate projections and pectinate crests along the adaxial (and sometimes abaxial) suture; rostrum about 1.25 to 2 times as long as the body of the fruit. Seeds many, black or grey, the testa corky.

The genus *Ibicella* is characterized by having yellow flowers, sepals that are free, and spiny, echinate projections on the body of the endocarp. The genus is native to central South America, though one of the species has been introduced to North America, Africa, and Australia. The generic epithet is an allusion to the horns of an *Ibex* (Bovidae) due to a resemblance in the curvature and length of the rostrum of the endocarp.

KEY TO THE SPECIES OF *IBICELLA*

Leaves suborbicular and denticulate, apex rounded; sepals ovate-elliptic; constricted portion of corolla tube 6 mm long; capsule oblong-ovoid, echinate, distal tooth absent, seeds flattened; primarily of the central South American deserts and plains..... .... 4. *I. lutea*

Leaves ovate and entire, apex angulate; sepals elliptic to lanceolate; constricted portion of corolla tube 9-10 mm long; capsule oblong, sparsely echinate, distal tooth present, seeds prismatic; primarily of the Andean foothills............................ 5. *I. parodii*

4. Ibicella lutea (Lindley) Van Eseltine, New York Agric. Exp. Sta. Techn. Bull. 149: 34. 1929. *Martynia lutea* Lindley, Edward's Botanical Register 11: t. 934. 1825. *Proboscidea lutea* (Lindley) Stapf, Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 269. 1895. –LECTOTYPE: "*Martynia lutea*" in Edward's Botanical Register 11: t. 934. 1825. Lectotype to be designated; see discussion below.

Martynia montevidensis Cham. Linnaea 7: 724. 1832. –TYPE: URUGUAY: Cisplatina, *Sellow s.n.* (Holotype: K!).

Ibicella nelsoniana (Barbosa-Rodrigues) Van Eseltine, New York Agric. Exp. Sta. Techn. Bull. 149: 32. 1929. *Martynia lutea* Lindley var. *nelsoniana* Barbosa-Rodrigues, Pl. Nov. Cult. Jard. Bot. Rio de Janeiro 6: 12. 1898. *Martynia nelsoniana* Barbosa-Rodrigues, Pl. Nov. Cult. Jard. Bot. Rio de Janeiro 6: 15. 1898. –LECTOTYPE: "*Martynia nelsoniana*" in Pl. Nov. Cult. Jard. Bot. Rio de Janeiro 6: t. 5. 1898. Lectotype to be designated; see discussion below.

Description. Leaves suborbicular, opposite to subopposite; petioles to 20 cm long; margins denticulate, sometimes undulate; apex rounded. Flowers 2-3.5 cm. in length; bracts oblong to rhomboidal; bracteoles orbicular; sepals ovate-elliptic, to 1.5 cm long; constricted portion of corolla tubes less than 6 mm long. Fruit endocarp body oblong-ovoid, to 8 cm long, densely covered with spiny or echinate projections to 1 cm long, crested along adaxial and abaxial sutures; rostrum 1.25 to 1.5 times as long as the body of the endocarp. Seeds black or grey, flattened. 2n=30, 32. Fig. 22.

Phenology. Flowering as early as October and as late as May in the Southern Hemisphere, but most commonly from December to February. In the Northern Hemisphere, flowering occurs from July to October.

Distribution and habitat (Figs. 23, 24). Native to central South America (Argentina, Brazil, Paraguay, and Uruguay). Introduced to other parts of the world (Algeria, Australia, South Africa, and the United States). Disturbed areas, especially in sandy soils. 0-750 m (0-2500 ft).

SPECIMENS EXAMINED. **ALGERIA**. MASCARA: Mascara, 15 Sep 1923 (fr), *Cesve 4764* (MO).

ARGENTINA. AUTONOMOUS CITY OF BUENOS AIRES: Benavidez, 08 Jan 1945 (fr), *Alvarez 406* (UC); Buenos Aires, 1891 (fl), *Hanthal 636* (NY); Buenos Aires, 11 Dec 1891 (fl), *Kuntze s.n.* (NY); Villa Garibaldi, 05 Feb 1938 (fl, fr), *Cabrera 4237* (NY), Belgrano, Jan-Mar 1867 (fl, fr), *Christison s.n.* (E-3). –BUENOS AIRES: BERISSO DEPT., Berisso, Dec 1944 (fl, fr), *Boffa s.n.* (A, NY, UC). –CATAMARCA: BELÉN DEPT., Los Nacimientos, 28 Feb 1965 (fl), *Cabrera et al. 16763* (GH); Los Nacimientos, 08 Feb 1992 (fl), *Lutz 135* (CTES). EL ALTO DEPT., Balcozna, 15 Jan

1928 (fl), *Venturi 7236* (US). –CHACO: PRIMERO DE MAYO DEPT., Colonia Benítez, 10 Dec 1972 (fr), *Schulz 17929* (CTES). –CÓRDOBA: CALAMUCHITA DEPT., Valle General Belgrano, 31º55'S, 64º15'W, 16 Dec 1978 (fl), *Solomon & Solomon 4163* (MO); La Cruz, 19-21 Feb 1947 (fl, fr), *Gutierrez 124* (TEX). PUNILLA DEPT., La Falda, 22 Mar 1940 (fl), *Rodrigo 2324* (NY). –CORRIENTES: CAPITAL DEPT., Corrientes, 24-28 Jan 1944 (fl, fr), *Meyer 6473* (UC), Corrientes, 11 Feb 1958 (fl, fr), *Pedersen 4812* (GH, US-2), Corrientes, 10 Feb 1977 (fl, fr), *Schinini 14150* (F, MICH, UC). CURUZÚ CUATÍA DEPT., 46 km W of Curuzú Cuatía along Rte 45 at Maria Azucena, 08 Jan 1977 (fl), *Schinini & Ahumada 13950* (F), 10 km N of Curuzú Cuatía along Rte 14, 23 Feb 1979 (fl, fr), *Schinini et al.17608* (K). ITUZAINGÓ DEPT., 17 km NW of San Carlos, Rincon Chico, 14 Feb 1991 (fl, fr), *Tressens et al. 3875* (CTES). –ENTRE RÍOS: COLÓN DEPT., Parque Nacional El Palmar, 23 Jan 1982 (fl), *Cusato 1091* (CTES). –FORMOSA: MATACOS DEPT., Ingeniero G. N. Juárez, 3 km S of the town along road from Bermejo to Belgrano, 23º54'S, 61º51'W, 25 Feb 1983 (fl, fr), *Arenas 2343* (CTES). –SAN LUIS: CHACABUCO DEPT., 5 km W of Papagayos along Provincial Rte 40, 08 Feb 1999 (fl), *Seijo 1849* (CTES, GH). –SANTA FE: CASTELLANOS DEPT., Sunchales, 20 Mar 1999 (fl, fr), *Krapovickas & Vanni 47650* (CTES, GH). –TUCUMAN: CAPITAL DEPT., San Miguel de Tucumán, Parque Nueve de Julio, 22 Oct 1920 (fl), *Schreiter 1376* (F, UC).

AUSTRALIA. NEW SOUTH WALES: 15 mi [24 km] NE of Deniliquin, 35º25'S, 145º05'E, 24 Feb 1966 (fl, fr), *Mulhan & Leigh S430* (CANB-2); Sydney, 18 Mar 1972 (fl, fr), *Michael s.n.* (CANB-2); North Western Plains, ca. 8 km N of Yetman-Texas Road on road to Yelarbon, 28º50'41''S, 150º46'27''E, 11 Dec 1998 (fl), *Lepschi & Connors 4080* (CANB); 3.1 km from Dripstone school towards Burrendong

Arboretum, 15 km SSE of Wellington, 32º41'S, 149º01'E, 07 Mar 1978 (fl), *Coveny & Ingram 10058* (MO).

BRAZIL. CEARÁ: no locality given, 22 Feb 1922 (fl), *Dias da Rocha 62* (SP). –RIO GRANDE DO SUL: Santo Angelo via Cachacira, 13 Feb 1893 (fl, fr), *Malme 598* (MO); São Salvador, Jan 1943 (fl), *Leite 2386* (GH [1 sheet, 1 bagged specimen], NY). –SÃO PAOLO: São Paolo, Butantan, 29 Oct 1918 (fl), *Hoehne 1060* (K, NY, SP); Ipiranga, 25 Feb 1987 (fr), *Toledo & Romaniuc Neto 300* (SP-2).

PARAGUAY. ALTO PARAGUAY: Mayor Pablo Lagarenza, 20ºS, 60º45'W, 11 Apr 1978 (fl), *Schinini & Bordas 15184* (CTES). –CAAGUAZÚ: near Caaguazú, 05 Oct 1905 (fl, fr), *Martius 9145* (K, NY, UC). –CORDILLERA: Cordillera de los Altos, 12 Nov 1902 (fl), *Fiebrig 428* (E, F). –GUAIRÁ: around Villarica, Dec 1931 (fl, fr), *Jorgensen 4529* (F, MO, NY, US).

SOUTH AFRICA. EASTERN CAPE: AMATOLE, King William's Town, 01 Apr 1974 (fl), Richards & Jacot Guillarmod 7442 (TEX). –LIMPOPO: WATERBURG, Naboomspruit, Apr 1936 (fr), *Galpin s.n.* (NY).

URUGUAY. ARTIGAS: bridge over Cuaró, 30º26'13''S, 57º04'41''W, 25 Nov 2001 (fl, fr), *Seijo et al. 2451* (CTES). –COLONIA: Colonia Valdense, Dec 1955 (fl), *Dubugnon 203* (K). –MONTEVIDEO: Montevideo, 22 May 1947 (fr), *Herter 944a* (UC), *Herter 944e* (US).

U.S.A. ALABAMA: CALHOUN CO., no locality data given, s.d. (fl), *Cocks s.n.* (NO). MOBILE CO., Mobile, along Mobile River, Sep 1892 (fl), *McNeil s.n.* (US). –CALIFORNIA: BUTTE CO., along Hwy 149 ca. 1 mi SE of Hwy 99, 11 Aug 1999 (fl, fr), *Gehrung s.n.* (UTEP); 8 mi N of Oroville, 29 Aug 1914 (fl, fr), *Heller 11685* (E, MO, NY); Dry Creek on the Oroville-Chico road, 12 mi from Chico, 20 Aug 1914 (fl, fr), *Heller 11685* (F). COLUSA CO., ca 11 mi SW of Williams along Hwy 20, 29 Aug 1960 (fr), *Thomas 8847* (SMU); near Hwy 20 on the road to Leesville, 03 Aug 1958 (fl, fr), *Snow 671* (NY). CONTRA COSTA CO., Pittsburg, 31 Aug 1937 (fr), *Hoover 2705* (NY). LOS ANGELES CO., introduced at Rancho Santa Ana Botanic Garden, 02 Oct 1973 (fl, fr), *Tilforth 959* (ASU, E, GH, MICH, NY, SD, US, VDB); growing as a weed on the grounds of the Rancho Santa Ana Botanic Gardens, 26 Sep 1992 (fl, fr), *Arnseth 37* (NY-2); weed at Rancho Santa Ana Botanic Gardens, 31 Oct 1968 (fl, fr), *Thorne 37869* (ASU-2). YOLO CO., SW edge of Woodville, 20 Jul 1972 (fl), *Seigler 6322* (BRIT). –FLORIDA: ESCAMBIA CO., Pensacola, Hunter's Wharf, Jul 1895 (fl), *Mohr s.n.* (US). FRANKLIN CO., Apalachicola, Sep 1885 (fl, fr), *Chapman s.n.* (F, MO). –GEORGIA: Hopkins, s.d. (fl, fr), *Chapman 6067* (MO). –MASSACHUSETTS: NORFOLK CO., Wellesley [may have been cultivated], 1890 (fl), *no collector* (NY). –MISSISSIPPI: GRENADA CO., S of Grenada, ca 5 mi W of Elliott, W of Hwy I-55, 11 Nov 2000 (fr), *Winters s.n.* (MO). LEAKE CO., ca 6 mi SW of Carthage, ca 1 mi E of Hwy 25 along MS Hwy 13, 12 Sep 2000 (fr), *Bryson 18058* (MO). MONROE CO., 0.2 mi W of Hwy 45A along Hwy 8, 20 Sep 1996 (fl), *MacDonald 9904* (NY). –PENNSYLVANIA: DELAWARE CO., Chadds Ford, Oct 1914 (fr), *Baldwin s.n.* (US).

CULTIVATED. *Armstrong s.n.* (SD, fl, fr); *Dodson 21510* (fl, fr, NY); *Hoehne 32193* (SP, fl); *Kellogg s.n.* (US, fl, fr); *McClintock s.n.* (fl, fr, SMU); *Nash 921* (fl, fr, NY); *Reitz 1728* (fl, GH); *Schneider 27502* (fl, fr, NY).

NO LOCALITY DATA. *Gillies s.n.* (E, fl), *Tweedie s.n.* (E, fl, fr).

The main distinguishing character between the two species in *Ibicella* is the presence of a strand or residual fiber arising from the rostrum but not dehiscing, creating a distal projection between the two "horns." This projection is present in *Ibicella parodii*. The floral parts of *Ibicella lutea* are larger than those in *I. parodii,* and *I. lutea* is found in the plains and deserts of central South America, whereas *I. parodii* is found in the eastern foothills of the Andes.

The lectotypifications for *M. lutea* and *M. nelsoniana*, which serve as the basionyms for *I. lutea* and *I. nesoniana*, will be published separately from this dissertation in accordance with Article 30.5 of the Code (McNeill et al. 2006).

5. Ibicella parodii Abbiatti, Not. Mus. La Plata, Bot., 4: 458. 1939. –TYPE: ARGENTINA. Santiago del Estero: Chañar Pozo, Estación Gramilla (cultivated at La Plata from seeds sent by F. Ledesma), *D. Abbiatti s.n.* (holotype: LP 30126 with "*Typus*" in black ink [photo at ASU!]).

Description. Leaves ovate, opposite; petioles to 20 cm long; margins entire; apex angulate. Flowers 2-3.5 cm. in length; bracts elliptic-lanceolate; bracteoles linear to orbicular; sepals elliptic to lanceolate, to 1.5 cm long; constricted portion of corolla tubes 9-10 mm long. Fruit endocarps body oblong, to 8 cm long, sparsely covered with spiny or echinate projections to 1 cm long, crested along adaxial and abaxial sutures; rostrum 1.25 to 1.5 times as long as the body of the endocarp, with a distal projection of incompletely dehiscing tissues between both rostral hooks. Seeds black, prismatic. Fig. 22.

Phenology. Flowering from December to April.

Distribution and habitat (Fig. 23). Found mostly throughout the eastern foothills of the Andes in Argentina, Bolivia, and extreme western Paraguay. 200-1600 m(500-5000 ft).

Vernacular Names. Pepino silvestre, cuerno del diablo

SPECIMENS EXAMINED. **ARGENTINA**. CATAMARCA: ANDALGALÁ DEPT., 35 km W of Andalgalá, 15 Feb 1973 (fl), *Cantino 643* (ARIZ, GH); Andalgalá, 20 Dec 1915 (fl), *Jürgensen 1159* (GH, MO, UC, US); km 1537 between Andalgalá and Belén, Feb 1974 (fl), *Turner 9185* (LL). BELÉN DEPT., 8 km from El Eje toward Villavil, 23 Feb 1974 (fl), *Legname & Vervoorst 222* (LL); between El Eje and San Fernando, 31 Mar 1973 (fl, fr), *Cabrera et al. 23771* (CTES). –CORDOBA: SOBREMONTE DEPT., Salinas Grandes, near San José, 18 Sep 1945 (fr), *Hunziker 6146* (GH). –LA PAMPA: RANCUL DEPT., Alpatacal, 15 Feb 1945 (fr), *Fortuna 41* (A). –LA RIOJA: southern end of the Sierra del Famatina, 1 km E of Puerto Alegre on Rte 40, 06 Feb 1973 (fl, fr), *Dillon & Rodriguez 473* (LL). CHAMICAL DEPT., Rte 79 between Chamical and Casa de Piedra, 24 Jan 1990 (fl), *Leguiza & Carrizo 67* (CTES). –MENDOZA: LAS HERAS DEPT., Ramblon, s.d. (fl, fr), *Semper s.n.* (NY, UC). SANTA ROSA DEPT., between Los Catitos and Puerto La Yosefa, 22 Apr 1981 (fr), *Ruiz Leal 31716* (ASU). –SALTA: ANTA DEPT., Joaquín Víctor Gonzalez, 17 Jan 1945 (fl, fr), *Aguilar 228* (A). RIVADAVIA DEPT., km 1692 along Rte 81, 23º4'S, 62º24'W, 15 Jan 2002 (fl, fr), *Neffa et al. 602* (CTES); Misión La Paz, 16 Jan 1984 (fl, fr), *Arenas 2660* (CTES). ROSARIO DE LA FRONTERA DEPT., 13 km S of Antilla along road to Burruyacú, 29 Mar 1975 (fl), *Krapovickas et al. 28043* (CTES). –SAN JUAN: VALLE FÉRTIL DEPT., along Valle Fértil river towards Los Bretes, 30º38'S, 67º29'W, 12 Mar 1998 (fr), *Fortunato et al.*

5983 (ARIZ). VEINTICINCO DE MAYO DEPT., Rte 20 near the border with San Luis, 10 Feb 1984 (fl, fr), *Kiesling 4687* (CTES). –SANTIAGO DEL ESTERO: PELLEGRINI DEPT., Monte Quemado, 03 Apr 1989 (fl, fr), *Pedersen 15382* (CTES).

BOLIVIA. SANTA CRUZ: CORDILLERA PROV., Izozog, Apr 1934 (fl, fr), *Cárdenas 2721* (F). –TARIJA: GRAN CHACO PROV., 3 km E of center of Villa Montes, 21º16’10”S, 63º26’50”W, 09 Feb 2006 (fl, fr), *Nee & Linneo F. 53997* (NY-2 [photos at ASU]).

PARAGUAY. BOQUERÓN [NUEVA ASUNCIÓN]: km 695 along Trans Chaco Route, 20º48’S, 61º54’W, 26 Mar 1986 (fl, fr), *Brunner 1687* (MO).

One specimen from the province of La Rioja in Argentina (*Leguiza & Carrizo 67*, CTES) has segments of a tuberous root attached to it. This has not been seen in other specimens from either of the two species in the genus, and may represent a mixed collection, an anomalous morphological feature, or a new taxon. In the future, plants from this region should be checked for the presence of any tuberous root systems.

The type specimen of this taxon needs to be clarified. The protologue (Abbiatti 1939) states the type is specimen 30126 at the herbarium of the Museo de la Plata (LP). There are six specimens from LP that have the same specimen number, and the collector, Delia Abbiatti, did not assign personal collection numbers to any of these specimens. They all might be considered types, except that there is no explicit designation that the specimen consists of multiple preparations as required by Article 8.3 of the Code (McNeill et al. 2006). Only one of these sheets has the word ‘Typus’ stamped in black ink. To confound the problem, five of the six specimens were collected in March of 1939. The sixth was collected in April of that year. Article 8.2 of the Code states that the types must constitute a single gathering, and the specimen collected in April is a clear violation of this Article. Therefore, the other five specimens may be considered syntypes, or the one specimen designated as the type by the inclusion of the stamped black ink should be somehow distinguished, such as renumbering that specimen as 30126a, and renumbering the other five sheets as 30126b-f.

The distinguishing characteristics of this species are mentioned in the discussion section of *I. lutea*.

IV. Martynia L., Sp. Pl. 2: 618. 1753. –TYPE: *Martynia annua* L., conserved by Green, Prop. Brit. Bot.: 167. 1929.

Disteira Raf., Flora Telluriana 4: 68. 1836. –TYPE: *Disteira angulosa* (Lam). Raf.

Vatkea O. Hoffman, Verh. Bot. Vereins. Prov. Brandenburg 22: 45. 1880. – TYPE: *Vatkea diandra* (Gloxin) O. Hoffman.

Description. Long-lived annuals to 1 m tall. Stems fleshy green turning slightly woody with age. Roots taprooted. Leaves broadly ovate, deltoid, or cordate, opposite; petioles to 25 cm long; blades to 25 cm long and 30 cm wide; margins shallowly lobed to broadly toothed, denticulate; apices acute to subacute; bases cordate to truncate, equilateral. Inflorescences with up to 20 flowers and equaling the foliage; bracts linear-lanceolate. Flowers 4-6 cm long; pedicels to 3 cm long; bracteoles to 1 cm long, oblanceolate, deciduous; sepals free, oblanceolate; corolla white to pale pink, bilabiate, the restricted portion of the tube surpassed by the calyx, the dilated portion ventricose to obliquely-campanulate, the internal surface of the tube with maroon specks and yellow nectar guides; corolla lobes widely spreading to reflexed, the two lobes each with a single large purple spot; stamens 2, staminodes 2; anthers 8 mm long; ovules few. Fruits ovoid-elliptic, compressed dorso-ventrally; endocarp 25 to 40 mm long, slightly dehiscent, sculptured, without pectinate crests along the adaxial suture; rostrum to 1 cm long. Seeds 4, to 2 cm long, the testa papery. 2n=32, 36. Fig. 4.

6. Martynia annua L., Sp. Pl. 2: 618. 1753. –LECTOTYPE: "*Martynia annua, villosa & viscosa; folio subrotundo; flore magno rubro*" in Martyn, Hist. Pl. Rar. t. 42. 1728. –EPITYPE: Miller ex Roy. Soc. No. 476, 1731, (BM-SL [photo at ASU!]). Lectotype and epitype designated by Nafday ex Stearn, Bull. Bot. Soc. Coll. Sci. Nagpur 4: 65. 1963.

Martynia angulosa Lam., Encycl. (Lamarck) 2(1): 112. 1786. Superfluous illegitimate name; see discussion below.

Disteira angulosa Raf., Fl. Tellur. 4: 68. 1836. Superfluous illegitimate name; see discussion below.

Martynia diandra Gloxin, Obs. 14: t. 1. 1785. Superfluous illegitimate name; see discussion below. *Vatkea diandra* (Gloxin) O. Hoffman, Linnaea 43: 554. 1882. Invalid later homonym.

Description. Characters of the genus. Fig. 4.

Phenology. Flowering throughout the year, though most commonly from June to November, peaking around August.

Distribution and habitat (Figs. 25, 26). Native to southern North America and Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua), and the West Indies (Bahamas, British Virgin Islands, Cuba, Dominica, Dominican Republic, Haiti, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Kitts & Nevis, St. Vincent & the Grenadines, and the Virgin Islands). Naturalized in other parts of the world (Australia, Ghana, India, New Caledonia, Nigeria, Pakistan, Sri Lanka, Thailand). In disturbed areas. 0-1350 m (0-4000 ft).

Vernacular Names. Uñas de Gato, Uñas de gabilan, somberete, toritos, Aguaro, Uñas del Diablo.

SPECIMENS EXAMINED. **AUSTRALIA**. QUEENSLAND: Ookoomba, near Townsville, 17 Oct 1958 (fl, fr), *Everist s.n.* (NY-2); Townsville, 25 Mar 1933 (fl, fr), *White 8827* (NY).

BAHAMAS. NEW PROVIDENCE: no locality given, 09 Mar 1879 (fl), *Brace 245* (NY).

BELIZE. Corozal-Santa Helena road, 09 Aug 1933 (fl), *Gentle 4837* (GH, NY), Corozal-Santa Helena road, 09 Aug 1933 (fl), *Gentle 89* (F). –CAYO: Roaring Creek, Aug 1929 (fr), *Lundell 466* (F, UC). –COROZAL: no locality given, 1931-1932 (fr), *Gentle 203*, 497 (F, K).

BRITISH VIRGIN ISLANDS. TORTOLA: by Huntum Ghut near Main Road, 15 Jun 1965 (fl), *D'Arcy 106* (A-2, MO); waste grounds, 28 Nov 1918 (fl, fr), *Fishlock 482* (NY); Secondary School, Road Town, 28 Jul 1970 (fl), *D'Arcy 4782* (MO).

COSTA RICA. GUANACASTE: CANTÓN DE BAGACES, Guanacaste National Park, Palo Verde Station, along main road and trails at edge of Lake Palo Verde, 10º20'00"N, 85º21'10"W, 05 Aug 1991 (fl), *Chavarria 229* (F); 1 km W of OTS research station (Palo Verde Biological Station), 10º21'09.9"N, 85º19'38.5"W, 27 Jun 2004 (fl), *Moran 7201 & Gutierrez 788* (ASU, CR); Tempisque Valley, Llano de Cortés, 5 km before the entrance to Palo Verde, 10º24'30"N, 85º21'00"W, 22 Aug 1993 (fl, fr), *Zamora et al. 2123* (CR, INB); Guanacaste National Park, Palo Verde Station, around Laguna Palo Verde, 10º20'00'N, 85º21'10"W, 05 Aug 1991 (fl, fr), *Chavarría 229* (CR, INB). CANTÓN DE CAÑAS, around Las Cañas, 24 Jun 1930 (fl), *Brenes 13124* (NY) near Las Cañas via Tilaran, 24 Jun 1930 (fl), *Brenes 12613/13003* (NY). CANTÓN DE LA CRUZ, 3 km SW of La Cruz, 11º4"N, 85º38'W, 29 Jan 1978 (fr), *Liesner 4646* (CR); Cuenca de Salinas, Puerto Soley, 11º3'5.1713"N, 85º39'12.4248"W, 23 Aug 2003 (fl), *Alfaro et al. 5025* (CR, INB); Santa Rosa National Park, Cuenca de Santa Elena, Murciélago, 10º54'6.93"N, 85º43'51.655"W, 08 Jun 2002 (fl), *Kriebel 785* (BRIT, CR, INB); Puerto Soley, Quebrada Tigre, road between La Cruz and Puerto Soley, 11º03'10"N, 85º39'12"W, 05 Oct 1998 (fr), *Gómez-Laurito et al. 13136* (CR); Santa Rosa National Park, Santa Elena Peninsula, Murciélago, 10º55'20"N, 85º44'15"W, 11 Aug 1995 (fl), *Espinoza 1346* (INB). CANTÓN DE LIBERIA, Santa Rosa National Park, Santa Rosa Station, between Bahía Salinas and Santa Cecilia, 10º50'00"N, 85º37'00"W, 15 Jul 1992 (fl), *Espinoza 453* (CR, INB); Santa Rosa, Jul 1971 (fl), *Callaway 175* (CR-3); Santa Rosa National Park, 21 Aug 1973 (fl), *Opler 1840* (F, UC); Santa Rosa National Park, Golfo de Papagayo, 10º50'20"N, 85º37'30"W, 03 Jul 1998 (st), *Vargas et al. 78* (INB). CANTÓN DE

NICOYA, Valle del Tempisque, Estación Barra Honda, Sendero a la Flor, 10º10'00"N, 85º22'00"W, 01 Jul 1994 (fl, fr), *Chavarría 1016* (CR, INB).

CUBA. No locality given, s.d., *Rugel 829* (NY). –CIUDAD DE LA HAVANA: near Havana, 01 Oct 1908 (fl), *Leon 693* (NY); Cojimar, 24 Aug 1910 (fl, fr), *Britton et al. 6277* (NY); near the mouth of the Rio Almendares, 1904 (fl, fr), *Wilson 1388* (F, NY). –CIENFUEGOS: vicinity of Soledad, Aug 1940 (fl, fr), *Hodge & Howard 4130* (GH); vicinity of Soledad, 27 Sep 1941 (fr), *Gonzales 225* (A); Soledad, Limones, 16 Aug 1927 (fl, fr), *Jack 6248* (GH, NY). –MATANZAS: Cardenas, 31 Aug 1903 (fl, fr), *Britton & Wilson 161* (NY). –PINAR DEL RIO: Herradura, 21 Nov 1904 (fl, fr), *van Hermann 299* (F, NY); Mariel, Nov 1902 (fl, fr), *Ames 7784* (ECON-2); San Ramon, 05 Jul 1921 (fl), *Ekman 13004* (NY). –SANCTI SPIRITUS: Lomas de Banao, Aug-Oct 1920 (fr), *Luna 866* (NY). –SANTIAGO DE CUBA: Siboney, Sep 1948 (fr), Bro. Clemente 6258 (GH). –VILLA CLARA: Las Villas, E of Atkins Garden, 17 Jul 1953 (fl), Dressler 1326 (GH, MO, NY, SMU).

DOMINICA. SAINT GEORGE PARISH: Cultivated in Botanic Gardens at Roseau, 03 Sep 1937 (fl), Hodge 1002 (GH); waterfront at Goodwill north of Roseau, 25 Aug 1965 (fl, fr), *Ernst 2145* (GH). –SAINT PETER PARISH: Guele Lion Area, 23 Aug 1965 (fl), *Shillingford & Ernst 328* (MO).

DOMINICAN REPUBLIC. AZUA: Sierra Martin Garcia, entrance to village of Barreras, 18º20'N, 70º56'W, 14 Nov 1984 (fr), *Zanoni et al. 32145* (NY). –BARAHONA: Sierra de Baoruco, in fields along Rio Baoruco, 18º05'N, 71º07'W, 29 May 1987 (fl, fr), *Zanoni et al. 39567* (NY); Barahona, Jun 1910 (fl), *Fuertes 287* (F, GH-2, MO). –DISTRITO NACIONAL: "Haina Arriba", 0.5 km from kilometer marker 12 on the highway from Santo Domingo to San Cristobal on the road to Manresa, 18º26'N, 69°59.5'W, 09 Aug 1983 (fl, fr), Zanoni & Pimentel 26417a (GH, NY). –ELIAS PIÑAS: Between Las Matas and Elias Piña, 10 Sep 1968 (fl, fr), *Liogier 12635* (GH, NY). –MONTE CRISTI: Monción, 16 Oct 1929 (fl), *Valeur 234* (F, MO, NY). –PERAVIA: Bani, 10 Oct 1970 (fl, fr), *Liogier 17574* (F, NY); 1 km E of Matanzas on road to Bani, 18°15'N, 70°24'W, 07 Aug 1980 (fl), *Mejia & Zanoni 7757* (NY); 1 km NW of town of Rio Arriba on road to El Recodo, E side of Rio Bani and 4 km N of Bani to San Cristobal road, 18°18'N, 70°18.5'W, 07 Aug 1980 (fl, fr), *Mejia & Zanoni 7794* (NY). –PUERTO PLATA: Puerto Plata, Cordillera Sepentrional, 21 Mar 1930 (fl), *Ekman 14488* (GH, NY). –SAN CRISTOBAL: near the beach at Playa de Najayo, 22 Sep 1973 (fl), *Liogier & Jimenez 6219* (NY); Santo Domingo, open spaces at Playa Najayo, 18 Aug 1973 (fl), *Liogier & Liogier 19998* (NY); Lake Quita Suena, about 0.3 km W of Rio Haina, Santo Domingo to San Cristobal highway, 18°26'N, 70°01'W, 28 Aug 1981 (fl, fr), *Zanoni & Mejia 16271* (NY). –SAN JOSE DE OCOA: in town of El Pinar NW of La Toronja, 10°33'N, 80°33'W, 08 Aug 1980 (fl, fr), *Mejia & Zanoni 7798* (NY). –SAN JUAN: 11.5 km N of Guanito on road to Arroyo Cano, 01 Jun 1992 (fl), *Judd & Skean 6687* (NY).

EL SALVADOR. –LA LIBERTAD: San Diego, 13°29'N, 89°19'W, 20 Jul 1992 (fl), *Villacorta 1136* (MO). –LA UNIÓN: Laguna de Maquigüe, 18 Feb 1922 (fl), *Standley 20924* (GH, NY). –SAN MIGUEL: Desvio del delirio, 13°21'N, 88°21'W, 20 Sep 1991 (fr), *Villacorta & Montalvo 893* (K, MO). –SONSONATE: Acajutla, Jul 1923 (fl), *Calderon 1651* (GH).

GHANA. Kwahu Region, Hweehwee near Akwaseho, 08 Jun 1979 (fl), *Hall s.n.* (MO).

GUATEMALA. On the route from Guatemala City to Chiquimulilla, 18 Aug 1860 (fl), *Hayes s.n.* (GH). –BAJA VERAPAZ: along road between Salama and Palmar, 02 Oct 1972 (fr), *Molina & Molina 27812* (F); on bank of Salama River 3 km from town of Salama, 01 Oct 1972 (fl, fr), *Molina & Molina 27764* (F). –CHIQUIMULA: no locality given, 08 Jan 1897 (fl, fr), *Seler & Seler 3328* (GH). –EL PROGRESO: 4 km N of El Rancho along road to Cobán, 04 Aug 1988 (fl), *Martínez et al. 23202* (MO-2); 1 km W of El Rancho, 04 Aug 1970 (fr), *Harmon & Dwyer 3524* (MO). –EL QUICHE: no locality given, 1942 (fl), *Aguilar 1390* (F). –GUATEMALA: no locality given, s.d. (fr), *Aguilar 558* (F). –HUEHUETENANGO: Nenton, 07 Sep 1896 (fl, fr), *Seler & Seler 2348* (GH); Nenton, Pozo Arrancado, 25 Nov 1995 (fl), *Castillo & Castillo 2671* (F, MO); vicinity of Cuilco, 17 Aug 1942 (fl, fr), *Steyermark 50753* (F, NY). –JUTIAPA: vicinity of Jutiapa, 24 Oct-5 Nov 1940 (fr), *Standley 75552* (F); along roadbank near bridge on Rio Tamasulapa near Asuncion Mita, 22 Jul 1970 (fl), *Harmon & Dwyer 3301* (MO, NY); 1 km W of San Cristobal, 22 Jul 1970 (fl, fr), *Harmon & Dwyer 3337* (MO). –PETEN: Tikal, on road surrounding El Remate at km 62, 25 Aug 1971(fl, fr), *Ortiz 1867* (F, MO, NY); La Libertad and vicinity, Aug-Nov 1933 (fl, fr); *Aguilar 144* (F, MO). –SANTA ROSA: no locality given, Aug 1892 (fl, fr), *Heyde & Lux 4039* (GH, K, NY); vicinity of Chiquimulilla, 29 Nov-08 Dec 1940 (fr), *Standley 79697* (F). –SUCHITEPEQUEZ: south of Alotenango Farm, 7 miles south of Tiquisate along road within 3 miles of ocean, 19 Jun 1942 (fl), *Steyermark 47743* (F). –ZACAPA: vicinity of Zacapa, 07-16 Oct 1940 (fl, fr), *Standley 73652* (F); near La Fragua, 14 Oct 1940 (fl), *Standley 74790* (F); along railroad near Zacapa railroad station, 05 Oct 1939 (fl, fr), *Steyermark 29053* (F); on road between Zacapa and Chiquimula, 09 Oct 1940 (fl, fr), *Standley 73812* (F).

HONDURAS. Ca. 5 mi E of border checkpoint along CA-1, 30 Jul 1978 (fl, fr), *Dziekanowski et al. 3187* (MO). –CHOLUTECA: Apacilagua, 05 Jul 1970 (fl), *Davidse & Pohl 2268* (F, MO); near Quebrada Tolobre between Morolica & Tolobre, 18 Jun 1964 (fl), *Molina 14225* (F). –COMAYUGUA: road to Ajuterique, 02 Jul 1974 (fl, fr), *Hazlett 1700* (GH, MO); El Taladro, Rio Selguapa, 27 Jun 1964 (fl), *Molina 14319* (F, NY), near Comayaguela, 29 Sep-05 Oct 1951 (fl), *Williams & Williams 18291* (F); at edge of la Quebrada Chucuas, near El Agua Salada, 21 Jul 1962 (fl), *Molina 11015* (F). –COPÁN: between San Antonio and San Gerónimo, 06 Jan 1983 (fl), *Molina et al. 33692* (MO). –CORTES: along Rio Ulua, Pimienta, 27 Aug 1955 (fl, fr), *Molina 5655* (F). –EL PARAISO: Llano de Lizipa, 24 Aug 1948 (fl, fr), *Molina 1088* (F, GH); Vicinity of Danli, 11-23 Feb 1949 (fr), *Standley 16598* (F), 2 km from the town of Oropoli, 10 Jul 1961 (fl), *Molina 10075* (F); 1 km west of Ojo de Agua, 05 Aug 1960 (fl), *Molina 10020* (F). –FRANCISCO MORAZAN: Yeguare river, 16 Jul 1948 (fl), *Glassman 1911* (GH); drainage of the Rio Yaguare, 87ºW, 14ºN, 16 Jul 1948 (fl), *Glassman 1912* (F, NY); along San Antonio road to Zamorano, 03 Aug 1946 (fl), *Williams & Molina 10204* (A, F, MO); Zamorano, along road to San Antonio, 05 Aug 1947 (fl), *Molina 429* (F); El Zamorano, along road toward San Antonio de Oriente, 07 Jul 1949 (fl), *Standley 20967* (F), vicinity of El Zamorano, 03-17 Aug 1947 (fl), *Standley 11680* (F); vicinity of El Zamorano, 26 Nov 1946-09 Jan 1947 (fr), *Standley 870* (F); Zamorano, Dec 1944 (fr), *Rodriguez 2172* (F); near El Jicarito along road toward El Pedregal, 24 Jul 1949 (fl), *Standley 21635* (F); region of Rio de La Orilla, southeast of El Zamorano, 05 Aug 1949 (fl), *Standley 22184* (F). –INTIBUCA: ½ km from La Esperanza, 01 Oct 1983 (fl), *Rodriguez M. 77* (MO). –OCOTEPEQUE: along Lempa River along road to Esquipulas, 29 Aug 1968 (fl, fr), *Molina 22422* (F, NY). –

OLANCHO: Catacamas, E of town on road to river, 11 Sep 1991 (fl), *Chorley 177* (MO).–SANTA BARBARA: between Ceguaca Abajo and Concepcion del Sur, 21 Aug 1968 (fl, fr), *Molina 21950* (F, NY).

HAITI. ARTIBONITE: Vicinity of Ennery, 12 Jan 1926 (fl), *Leonard 8766* (NY,UC); 20 km S of Gonaives and 6 km from the entrance to Dessalines on highway to Dessalines between Hatte Gramont and Dessalines, 19°17'N, 72°33'W, 23 Oct 1983 (fl, fr), *Zanoni et al. 27765* (NY); vicinity of Etang, Etang Saumatre, 04-12 Apr 1920 (fl), *Leonard 3597* (NY). –NIPPES: Miragoane and vicinity, 10 Jul 1927 (fl), *Everdam 34* (GH); Miragoane and vicinity, 08 Jul 1927 (fl), *Everdam 411* (GH); Miragoane and vicinity, 03 Sep 1927 (fl, fr), *Everdam 474* (GH, NY). –NORD: San Michel, 05 Aug 1905 (fl, fr), *Nash & Taylor 1424* (NY); Bayeux, near Port Margot, 15 Jul 1905 (fl), *Nash & Talylor 1014* (NY). –SUD: Port-á-Piment, 13 Aug 1917 (fl, fr), *Ekman 686* (K).

INDIA. Old Delhi Ridge, 15 Sep 1967 (fl), *Lengar 1072* (ASU); northern Bengal, s.d. (fr), *Biswas 2132* (NY); West India, 11 Nov 1875 (fl, fr), *Kuntze 6391* (NY-3); Western India, s.d (fl, fr), *Royle s.n.* (TCD); East India, 1866-1867 (st), *Wight s.n.* (NY); Old Delhi Ridge, Delhi, Nov 1958 (fl), *Sanyal s.n.* (E), Bengal, 20 Jul 1943 (fl), *Sinclair 3062* (E). –ANDHRA PRADESH: CHITTOOR DISTRICT, Tirupathi Hills, 02 Jul 1969 (fl, fr), *Saldanha 13975* (E, MO). –HIMACHAL PRADESH: CHAMBA DISTRICT, no locality given, 14 Aug 1898 (fl), *Lace 1819* (E). KANGRA DISTRICT, no locality given, 04 Sep 1900 (fl), *Hart 180* (E). –JAMMU AND KASHMIR: JAMMU DISTRTICT, Jammu, Aug 1931 (fl), *Stewart 13118* (NY). –KARNATAKA: BIDER DISTRICT, Homnabad, 18 Nov 1978 (fl, fr), *Ramesh & Sreenath KFP4522* (MO). –MAHARASTRA: Juhu, 06 Aug 1966 (fl), *Gupta 85* (MO). –TAMIL NADU: SALEM DISTRICT, Hosur

Taluk, 03 Jun 1933 (fl, fr), *Yeshoda 396* (NY). –UTTARAKAND: DEHRADUN DISTRICT, Dehradun and vicinity, 05 Sep 1928 (fl), *Singh 445* (NY-2).

JAMAICA. No locality data, s.d., *Field Museum Economic Botany Catalog no. 272231-7784* (ECON); no locality data, 20 Nov 1907 (fl), *Harris 154* (K).

MARTINIQUE. No locality given, 1879-80 (fl), *Duss 1874* (F, GH, MO, NY); no locality given, 1899 (fl, fr), *Duss 4048* (NY); road from Cannes to Suire, Jul 1869 (fl), *Hahn 1000* (GH, K).

MEXICO. No locality given, s.d. (fl), *Coulter 1324* (TCD). –CAMPECHE: 4 km W of Tunkasche along Calkini-Punta Arenas road, 19 Sep 1987 (fl), *Cabrera C. & Cabrera 14393* (MO); 11 km south of the Yucatán-Campeche border, near San Antonio Yax-Ché, 20º05'00"N, 89º43'50"W, 20 Sep 1999 (fr), *Carnevali, May & Tapia 5665* (GH, NY). –CHIAPAS: 1 km N of Ocozocoautla, 25 Sep 1971 (fl, fr), Breedlove 19808 (MO); Tonala, Paderon, 17 Sep 1947, *Matuda 16933* (ND); along the streets in Tuxtla Gutierrez, 07 Oct 1971 (fl, fr), *Breedlove 20029* (MO); 14 mi E of Tuxtla Gutierrez along Hwy 190, 14 Aug 1975 (fl, fr), *LeDoux & Torke 2184* (MO); slope above Finca Carmen along road from Acala to Pugiltik, 03 Oct 1967 (fl), Ton 2987 (F); slope above Finca Carmen along road from Acala to Pugiltik, 07 Nov 1967 (fr), Ton 3168 (NY). –CHIHUAHUA: Guasaremos, Rio Mayo, 10 Aug 1936 (fl), *Gentry 2367* (ARIZ, GH, MO); Hacienda San Miguel, near Batopilas, Aug-Nov 1885 (fl), *Palmer 192* (GH, K, NY). –COLIMA: along Hwy 110, 25 Jul 1975 (fl), *Wallace et al. 284* (MO, NY); Colima, on Loma Blanca, Ejido Piscila, 15 Oct 1996 (fr), 19º08'N, 103º42'W, *Cuevas G. et al. 5318* (BRIT); Colima, Aug 1897 (fl), *Palmer 118* (ARIZ, UC); 2 km from Manzanillo, 08 Aug 1938 (fl, fr), *Worth et al. 8622* (ARIZ, UC). –DISTRITO FEDERAL: Town of Tulyehualco, 03 Aug 1979 (fl, fr), *Feine & Nabhan s.n.*

(GH). –DURANGO: No locality given, Aug 1897 (fl), *Rose 2273* (GH, NY). – GUERRERO: El Tibor, 27 Aug 1898 (fl), *Langlasse 308* (GH, K); 0.4 mi from jct of road to Taxco (Hwy 55 & 95), 18 Aug 1972 (fl), *Dziekanowski et al. 1987* (MO); 8 mi E of Acapulco, 25 Jun 1952 (fl), *Rowell & Troublefield 2811* (SMU); 8 mi S of Acapulco, 27 Jun 1952 (fl), *Rowell & Gray 2970* (SMU); Pungarabato, 20 Aug 1934 (fl), *Hinton et al. 6467* (NY); Coyuca-Querencas, 26 Sep 1934 (fr), *Hinton et al. 6663* (MO, NY); Pungarabato, 25 Sep 1934 (fl, fr), *Hinton 6650* (ASU, DES, GH); Jaripo, 23 Aug 1934 (fl), *Hinton 6484* (GH, MO, NY); km 105 of Iguala-Arcelia Hwy (MEX 51) at El Crustal, 18º22'N, 100º8'W, 01 Oct 1982 (fr), *Iltis et al. 28665* (UC); Placeres, 23 Jul 1937 (fl, fr), *Hinton et al. 10525* (GH, NY), Campo Morado-Otatlan, 24 Jul 1939 (fl), *Hinton et al. 14484* (ARIZ, NY); Vallecitos, 12 Jul 1937 (fl), *Hinton et al. 10599* (ARIZ, K, NY); 14 km W of Tecpán, 20 Oct 1977 (fl, fr), *Ladd O. et al. 208* (MO); 3 km SE of Guayameo, 14 Jul 1982 (fl), *Soto N. & Martínez S. 4128* (E). – JALISCO: on mountainside above Acatlán, 23 Aug 1965 (fl), *Barkley 35518* (GH); hills near Guadalajara, 09 Nov 1888 (fr), *Pringle 2181* (GH [1sheet, 1 bagged specimen]); valley near Etzatlan, 02 Oct 1903 (fl, fr), *Pringle 11662* (GH, SMU); near Etzatlan, 02 Oct 1903 (fr), *Rose & Painter 7536* (NY); Mezquitan, 4 miles south of 2nd bridge on Hwy 80, 29 Jul 1990 (fl), *Jack & Sydor 67* (TEX); ca. 36 km southwest of Autlan de Navarro on Mexico Hwy 80, 02 Aug 1971 (fl), *Graham 1333* (NY); 41 km north of Barra de Navidad, 02 Oct 1973 (fl), *Perez 759* (NY); Barranca de Santa Rosa, 45 mi NE of Guadalajara, 14 Sep 1960 (fl, fr), *Templeton 8827* (MO); Rancho Cuixmala, near Gargollo headquarters, 19º23'N, 104º59' W, 01 Aug 1991 (fl), *Rothschild & Upson 324* (ARIZ, BRIT, K, NY); Chamela-Melaque road 1 km N of Chamela Biological Station, 25 Sep 1981 (fl), *Lott 579* (MO); near the UNAM biological station at

Chamela along turnoff from Mex Hwy 200 to Chamela, 19.31ºN, 105.04ºW, 11 Jan 1983 (fl, fr), *Miller et al. 404* (MO); 1 km S of Ayotitlán, 19º28'13''N, 104º11'04''W, 28 Aug 1991 (fl, fr), *Benz K. et al. 1271* (BRIT); Chamela Bay Region, Rancho Cuixmala, 'Cumbres 2' along the Rio Cuitzmala, 19º25'N, 104º57'W, 03 May 1991 (fl, fr), *Ayala 91-92* (ARIZ, K); Mex Hwy 80, ca 1 mi S of Autlan de Navarro, 17 Sep 1962 (fl, fr), *Hevly et al. 2805* (ARIZ); 3 km before Venustiano Carranza on road from Tapalpa, 11 Sep 1991 (fl, fr), *Huerta et al. 151* (TEX); Rancho El Jabali, 20 km N of Colima in the SW foothills of the Volcan de Colima along road to El Canon from La Becerra, 103º43.66'W, 19º27'N, 08 Oct 1991 (fr), *Vazquez 1393* (MO); near Texcueca at km 596 on Mex Hwy 15 on W edge of Lake Chapala, 08 Sep 1962 (fl, fr), *Hevly et al. 2595* (ARIZ). –MEXICO: District of Temascaltepec, Ixtapan, 24 Jul 1932 (fl, fr), *Hinton 1169* (GH, NY); District of Temascaltepec, Ixtapan, 16 Jul 1932 (fl, fr), *Hinton 1069* (DES, NY). –MICHOACAN: 17 miles south of Uruapan, 22 Jul 1966 (fl, fr), *Carr & Barkly 36097* (GH); ca. 16 mi S of Uruapan on Rte. 37 to Puerto Azul,18º50'N, 102º10''W, 16 Aug 1991 (fl, fr), *Soule & Loockerman 2624* (TEX); 5-10 mi SW of Apatzingan, 09 Sep 1962 (fl), *Hevly et al. 2659* (ARIZ); Ostula, 50 mi S of Colima, 16 Jul 1950 (fl), *Turner 2185* (SMU); near La Majada, 09 Aug 1941 (fl), *Leavenworth & Hoogstraal 1405* (GH, MO, NY); Tancitaro Region, open pine forest above Acahuato, 17 Aug 1941 (fl), *Leavenworth & Hoogstraal 1664* (MO); 16 km SE of San Lucas, in El Cajón, 08 Sep 1981 (fr), *Soto N. 3060* (E). –MORELOS: El Progreso, Aug 1946 (fl), *Martínez 15019* (MO); vicinity of Cuernavaca, 1905 (fr), *Lemmon & Lemmon s.n.* (UC); 1 mi SE of Alpoyeca, 12 Aug 1949 (fl), *Duncan 35* (BRIT); Tehuixtla, 16 Aug 1949 (fl), *Duncan 64* (BRIT-2); Alpoyeca, s.d., *Wilhite 1* (BRIT-2). –NAYARIT: Tepic to Calixcillo, 13 Sep 1926 (fl, fr), *Mexia 578* (GH, MO, NY, UC); archaeological zone of

Ixtlán del Río, 21 Aug 1984 (fl), *Hernández M. et al. 9681* (MO); km 5-6 from Cacalután, 21º05'N, 104º17'W, 22 Sep 1989 (fl), *Tellez V. & Salinas 12327* (MO); Paso de los Bueyes, Rio Santiago, 12 km E of Mojarres, 21º29'N, 104º32'W, 28 Oct 1989 (fr), *Tenorio L. & Flores F. 16847* (MO); Jesus Maria, 02 Aug 1977 (fl), *Colunga & Zizumbo 13* (DES); 1 km S of San Juan Peyotán, along road to Rancho Viejo, 22º21'N, 104º25'W, 06 Sep 1991 (fl), *Flores F. 2670* (MO); 3.9 km NE of Jesus Maria along Huejuquilla road, 22º16'N, 104º30'W, 15 Sep 1989 (fr), *Flores F. et al. 1063* (MO); 3 km SE of Tecuitata along Tecuitata-El Cora road, 21º25'N, 105º10'W, 15 Sep 1990 (fr), *Flores F. & Ramírez R. 2316* (MO). –OAXACA: Cuicatlan, 25 Feb 1895 (fl, fr), *Smith 356* (GH); 2 mi E of Tequisistlán, 12 Aug 1962 (fl, fr), *Webster et al. 13001* (GH, MO); along the Pan-American highway (Rte. 190), 2-4 km east of Tehuantepec on the road to Oaxaca (Route 190), 01 Jul 1959 (fr), *King 1164* (NY); 2 km south of the village of Niltepec, 17 Jul 1959 (fl), *King 1772* (NY); ca. 2 km north of the village of Ixhuatan, 23 Jul 1959 (fl), *King 1996* (NY, UC); 14 mi E of La Reforma along MEX 190, 18 Sep 1978 (fl, fr), *D'Arcy 12045* (MO); 2 mi N of jct of Mex 185 & Mex 190 at Tehuantepec, 18 Aug 1971 (fl, fr), *Dwyer et al. 821* (MO); Cerro Coyote, ca. 11 km NW of Tehuantepec, coming from Las Tejas going to Guiengola ruins, 16º21'N, 95º19'W, 30 Aug 1988 (st), *Martinez 1781* (MO); San Juan Bautista Cuicatlan, 1.2 km from El Chilar on the Tehuacán San Juan Cuicatlán, Tilixtlahuaca & Oaxaca road, 17º41'37.2''N, 96º55'56.6''W, s.d., *Calzada JIC 26414* (K); 17.2 km NW of Tehuantepec at entrance to Buenos Aires, 24 Jul 1984 (fl), *Torres C. & Martínez 5550* (NO); on road from Tehuantepec via Totolapan (Mex Hwy 190), 6 mi W of Tehuantepec, 27 Jan 1970 (fr), *Anderson & Anderson 5581* (SD); La Pedrera, 1 km N of Mazahua and 20 km N of La Ventosa along Matías Romero-La

Ventosa highway, 12 Aug 1988 (fl, fr), *Martínez & Abisaí G. 127* (MO); Coastal Region of Oaxaca, jct of Hwy 200 and dirt road to Bahia de San Agustín, 15º45'43''N, 96º16'18''W, 03 Aug 2003 (fl), *Salvato & Provance 335* (BRIT); Rio Seco to Río Santiago SSW of Tecomavaca, 17º54'N, 97º4'W, 05 Dec 1991 (fr), *Salinas T. et al. 6495* (NO); 0.5 km N of Barra de la Cruz, 15º50'31''N, 95º58'26''W, 16 Aug 1999 (fl), *Elorsa 2318* (NY-2); Hierba Santa, 17 km NW of Tehuantepec, 16º21'N, 95º22'W, 24 Sep 1988 (fl, fr), *Torres C. & Martinez 12722* (MO). –PUEBLA: 12 mi east of the junction of Hwy 190 & 160 out of Izucar Matamoros, 02 Aug 1975 (fr), *Torke et al. 361* (MO, NY). –SAN LUIS POTOSÍ: El Salto Falls, 15 Jun 1951 (fl), *Franks & Filer 673* (SMU). –SINALOA: Imala, Sep-Oct 1891 (fl), *Palmer 1737a* (GH, NY); Lodiego, 09-15 Oct 1891 (fr), *Palmer 1537a* (NY);15 km N of Mazatlan at marker 4 ½ on La Noria Road, 08 Sep 1984 (fl, fr), *Walker s.n.* (ARIZ); Culiacan, 24 Sep 1904 (fl, fr), *Brandegee s.n.* (GH); Culiacan, 20 Aug 1904 (fl), *Brandegee s.n.* (UC); 33 mi SW of Rivalcaderos, 12 Aug 1956 (fl), *Waterfall 12732* (GH, SMU); 3 km W of Badiraguato on road to Los Pericos, 08 Sep 1983 (fl), *Anderson 12554* (NY); Mazatlan, 08 Oct 1893 (fl, fr), *Brandegee s.n.* (UC); along road to Micro Ondas La Palma, E of MEX Hwy 15, road jct at km 225, ca. 26 mi S of MEX Hwy 40 jct S of Mazatlán and ca 1.5 mi N of Rosario, 06 Oct 1975 (fl, fr), *Reveal & Harley 4016* (K); Mazatlán, Jul 1934 (fl), *Gonzalez O. 7354* (K); near Escuinapa, 07 Sep 1962 (fl, fr), *Hevly et al. 2575* (ARIZ); near Escuinapa, 07 Sep 1962 (fl), *Hevly et al. 2576* (ARIZ); 19.8 mi E of Villa Union on Mex Hwy 40, 02 Aug 1983 (fl, fr), *Starr 526* (ARIZ); 30 km NE of Villa Union on the Mazatlan-Durango road, 01 Oct 1985 (fl, fr), *Bartholomew et al. 2500* (ASU, GH, NY); Chametla, Coacoyolitos, Oct 1926 (fl, fr), *Ortega 6466* (GH); near Coacoyolitos, Nov 1925 (fl), *Ortega 5839* (MO); road from

Herradura El Alamo to Cerro Yauco, 6 km NE of El Ejido Ponce de Leon, 22º57'N, 105º45'W, 02 Dec 1982 (fr), *Tenorio et al. 2857* (NY). –SONORA: San Bernardo, Rio Mayo, 07 Sep 1935 (fl, fr), *Gentry 1672* (ARIZ, GH, K, MO, UC); San Bernardo, Rio Mayo, 18 Sep 1958 (fl, fr), *Arguelles s.n.* (ARIZ, DES); 8 miles north of San Bernardo, Rio Mayo watershed, 14 Sep 1978 (fl, fr), *Nabhan 951* (DES); Rio Mayo Region, Sierra de Alamos, Rancho las Uvalamas, 26º57.7'N, 108º55-56'W, 25 Aug 1990 (fl), *Martin & McWhorter s.n.* (ARIZ, MO); 1.25 mi NW of Alamos in El Rincon area, 03 Sep 1973 (fl), *Fish 75* (UC); Rio Mayo Region, Las Lajitas crossing of the Rio Cuchujaqui, downstream from Sabanito Sur, 8.9 mi ESE of Alamos, 26º59'N, 108º49'W, 15 Oct 1992 (fl, fr), *Van Devender et al. 92-1364* (ARIZ); Sabanito Sur, 17.5 km from Alamos in the road to upper crossing of Rio Cuchujaqui, 26º59'30''N, 108º48'30''W, 06 Sep 1989 (fl), *Sanders et al. 9416* (ARIZ, SD); Rio Mayo Region, Rio Yaqui drainage, Cerro Verde, SW of San Javier, 28º34'N, 109º43'50''W, 08 Oct 1988 (fl, fr), *Jenkins et al. 88-232* (ARIZ-2); Rio Mayo Region, El Palmarita, Las Llanos, 27º2.3'N, 108º46.6'W, 17 Jul 1990 (fl), *Smith & Rascon s.n.* (ARIZ); Rio Mayo Region, El Rincon Viejo, ca. 4 km N of Alamos, Sierra de Alamos, 27º4'N, 108º56'W, 20 Sep 1994 (fl, fr), *Van Devender et al. 94-630* (ARIZ); Curea, 28º18'42''N, 109º16'42''W, 17 Sep 1998 (fl), *Reina et al. 98-1287* (NY); ca 1 km E of Santa Ana on road to Mex Hwy 16, 28º23'42''N, 109º08'18''W, 09 Sep 1996 (fl, fr), *Reina et al. 96-530* (ARIZ). –TAMAULIPAS: Vicinity of Victoria, 01 Feb-13 Jun 1907 (fr), *Palmer 233* (GH, NY); El Progresso, 18 km NW of Ocampo, 23ºN, 99º30'W, 23 Aug 1941 (fl, fr), *Stanford et al. 1103* (ARIZ, GH, MO, NY). –VERACRUZ: Huasteca, Wartenburg, near Tantoyuca, Jul-Aug 1858 (fl), *Ervendberg 114* (GH); Plan del Rio, E. Zapata, 14 Jan 1973 (fr), *Hernandez & Dorantes 1820* (MO, NY), around Laguna Verde, Alto Lucero, 18 Nov

1975 (fl, fr), *Dorantes et al. 5253* (NY); no locality given, s.d. (fr), *Field Museum Catalog No. 189996* (ECON); Juan Diaz Covarrubias, 01 Sep 1969 (fl), *Calderon 2009* (A); Palmillas, Jul 1920 (fl), *Purpus 8546* (GH, MO-2, NY, UC); 6 km SE of Valladolid along Yalcon road, 21 Jul 1986 (fl), *Cabrera & Cabrera 11545* (MO); no locality given, 1895 (fl), *Gaumer 868* (MO); Cotaxtla Experiment Station, 25 Aug 1962 (fl), *Janzen s.n.* (UC); near Km 385 E of Mexico City, NW of Veracruz, ca 1 mi S of Rinconada, 14 Sep 1962 (fl, fr), *Hevly et al. 2741* (ARIZ); near Rinconada toward Idolos, 19º22'N, 93º33'W, 31 Aug 1982 (fl, fr), *Ortega O. & Ortega O. 2376* (UC); Mesa de Olvera around Jalcomulco, 19º21'N, 96º47'W, 26 Aug 1983 (fl, fr), *Castillo C. & Medina 2834* (UC); Cardel-Veracruz highway, Puente La Antigua, 05 Aug 1987 (fl), *Zamora 538* (NY); 6 km ESE of San Antonio Paso del Toro, 19º34'N, 96º47'W, 14 Jan 1984 (fr), *Nee & Taylor 28807* (NY); San Franciso, May 1894 (fr), *Smith 1950* (GH [1 bagged specimen]). –YUCATAN: along Merida-Sisal road, May-Aug 1938 (fl), *Lundell & Lundell 8145* (GH); Hocaba, 14 Aug 1985 (fl, fr), *Bricker 36* (NO-2); Conkal-Taxkukul road, at the junction with gravel road going to Santa Maria Chi o Nolo, 21º2'55''N, 89º29'00''W, 04 Nov 1997 (fl, fr), *Gonzalez-Iturbe & Tun 330* (NY); Dzibilchaltun ruins 20 km N of Ciudad de Merida, along highway to Progresso, 21º03'31''N, 89º36'24''W, 04 Nov 1980 (fr), *Calzada et al. 6472* (MO, NO); Dzibilchaltun, 17 Jul 1978 (fl), *Thien & Walden 20* (NO); Distrito Ticul, Hacienda Yaxihel, 07 Jul 1911 (fl), *Seler & Seler 5596* (GH); Tixcacaltuyub, 20º29'34''N, 88º54'56''W, 12 Aug 1988 (fl), *Simá 810* (MO). –ZACATECAS: 3 mi N of Santa Rosa along E side of the Rio Juchilipa, 10 Aug 1969 (fl), *Taylor & Taylor 6046* (BRIT, MO, NY).

NEPAL. Chota Nagpur Plateau, 1891 (fr), *Wood s.n.* (E). –BAGMATI ZONE, NUWAKOT DISTRICT, Trisuli Bazar, 27º55'47''N, 85º8'43''E, 13 Jul 1994 (fl), *Suzuki et* *al. 9480002* (E). –<u>BEHRI ZONE</u>, JARJARKOT DISTRICT, 16 Oct 1952 (fr), *Polunin, Sykes & Williams 5696* (E). –<u>KOSHI ZONE</u>, DHANKUTA DISTRICT, E bank of Arun Kosi, near Rithabus, 27°8'14"N, 87°16'8"E, 23 Sep 2001 (fl), *Long et al. ENEP 23* (E); Lagowa, Ramristra, Leguwa, 27°5'45"N, 87°15'16"E, 13 Aug 1997 (fl), *Noshiro et al 9760048* (E). SANKHUWASABHA DISTRICT, 27°19'00"N, 87°12'00"E, 31 Aug 1998 (fl, fr), *Noshiro et al. 9830214* (E). –<u>DHAWALAGIRI ZONE</u>, MYAGDI DISTRICT, Rahagut, 28°20'N, 83°39'E, 08 Aug 1996 (fl), *Hishino et al 9662133* (E); Tatopani, S of Dana, Kali Gandaki Valley, 30 Aug 1954 (fl, fr), *Staintion, Sykes, & Williams 7594* (E).

NETHERLANDS ANTILLES. CURACAO: Wacao, Jul 1969 (fl), *Arnoldo-Broeders 3773* (A-2), St. Rosa, Sep 1964 (fl, fr), *Arnoldo-Broedeers 3121* (K, NY).

NEW CALEDONIA. No locality given, s.d. (fl, fr), *Franc 803* (MO, NY-2).

NICARAGUA. <u>BOACO</u>: NE of Pueblo along Tecolostote River Route 7, San Francisco, 22 Jul 1972 (fl), *Seymour & Robbins 6086* (F, GH, MO, NY, SMU, UC); Jct of Boaco and Chontales highway to Rama, Monte Grande, 12°25'N, 85°45'W, 30 Sep 1980 (fr), *Moreno 3269* (MO). –<u>CARAZO</u>: 10 mi S of Jenotepe, 05 Aug 1971 (fl), *Spellman et al. 509* (MO). –<u>CHINANDEGA</u>: Vicinity of Chichigalpa, 12-18 Jul 1947 (fl), *Standley 11251* (F); E base of Cosiguina Volcano, 07 Jul 1932 (fl, fr), *Howell 10281* (GH). –<u>CHONTALES</u>: around Hacienda Corpus, 13.5 km W of Juigalpa, 12°7'N, 85°29"W, 27 Aug 1983 (fl, fr), *Nee & Miller 27536* (NY); La Pita, along road to Rama, 6.5 km E of Juigalpa, 12°07'N, 85°25'W, 25 Jul 1981 (fl), *Moreno 10094* (MO); road between the highway to Rama and Camalpa, 10 Jul 1980 (fl), *Montiel et al. 334* (MO). –<u>ESTELI</u>: La Trinidad, "Las Animas," 13°01'N, 86°14'W, 23 Jun 1981 (fl), *Moreno 9382* (MO); 6 km NE of La Trinidad, 13°01'N, 86°13'W, 23 Jun 1981 (fl), *Moreno 9353* (MO); San Juan de Limay, Valle San Antonio de los Platanares, 13°12'N, 86°33'W, 01 Sep 1980 (fl), *Moreno 1962* (MO); Hacienda La Grecia, along old road to Limay, 13°10'N, 86°35'W, 02 Sep 1980 (fl, fr), *Moreno 1974* (MO); 2 km from Hacienda La Grecia along old road to Limay, 13°12'N, 86°36'W, 02 Sep 1980 (fl, fr), *Moreno 2042* (MO); Pueblo Nuevo, Matapalo Cally, 6 km NE of Pueblo Viejo, 26 Sep 1980 (fl, fr), *Moreno 3059* (MO). –GRANADA: Near Lake Nicaragua, Vera Cruz, 20 Aug 1976 (fl, fr), *Bockus & Hall 7844* (BRIT, GH, NY, UC); Charco Muerto S of Volcán Mombacho, 11°46'N, 85°57'W, 30 Jun 1981 (fl), *Sandino & Guzmán 758* (MO); Isla Zapatera, S of Hacienda Santa María, 11°45'N, 85°55'30"W, 22 Nov 1982 (fl, fr), *Grijalva 1858* (MO); 5 km along Casa Tejas road from the highway linking Nandaime with Granada, 11°48'N, 86°00W, 21 Jun 1982 (fl), *Moreno 16679* (MO); 5 km S of Paso de Panaloya toward the city of Granada, 12°03'N, 85°54'W, 05 Aug 1981 (fl), *Sandino 1118* (MO); ca. 8.0 km N of Granada on road to Paso de Panaloya on shore of Lake Nicaragua, 12°00'N, 85°55'W, 12 Oct 1977 (fl), *Stevens 4621* (MO); 7 km N of Intécna, 11°59'N, 85°56'W, 24 Jun 1981 (fl), *Sandino 694* (MO); grounds of the Escuela de Física Blas Real Espinales, toward exit to Granada-Masaya highway, 10 Jun 1982 (fl), *Sandino 3030* (MO); Laguna de Apoyo, 11°53'N, 86°01'W, 20 Sep 1981 (fr), *Moreno 11194* (MO); environs of Granada, 1869 (fl), *Lévy 178* (K); shores of Lake Nicaragua near Granada, 01 Jul 1968 (illustration of plant in flower), *Heller s.n.* (F). –JINOTEGA: old road to Jinotega along Río Waswalí, 12°55'35"N, 85°57'58"W, 25 Oct 1983 (fr), *Vega & Robleto 50A* (MO). –LEON: between km 51 & 52 along old highway to León 7 km N of entrance to El Transito, 12°10'N, 86°40'W, 15 Oct 1980 (fl), *Moreno 3524* (MO); km 47.5 along old highway to León, 12°09'N, 86°39'W, 10 Aug 1981 (fr), *Sandino 1189* (MO); Laguna de Asosoca, 12°26'N, 86°40'W, 13 Jul 1981 (fl), *Moreno 9804* (MO); Foot of Cerro Asososca, 12°26'N, 86º40'W, 13 Jul 1981 (fl), *Moreno 9829* (MO); slope and ridge immediately W of Quebrada Las Ruedas and along stream, NW of El Transito, 12º05'N, 86º43'W, 10 Dec 1977 (fr), *Stevens 5433* (MO); slope and ridge immediately W of Quebrada Las Ruedas and along stream, NW of El Transito, 12º05'N, 86º43'W, 16 Oct 1977 (fl), *Stevens 4697* (MO). –MADRIZ: ca. 7 mi S of Ocotal along Highway 15, 6 Aug 1977 (fl), *Croat 42807* (MO). –MANAGUA: grounds of the UCA, 14 Jul 1975 (fl), *Atwood & Neill AN182* (NY, SD); embarcadero de Mateare at Lake Xolotlan, 20 May 1981 (fl), *Sandino 616* (MO, NY); S of Lomas de Villa Fontana on road to Jocote Dulce, 86º16'N, 12º6'30"W, 06 Aug 1982 (fr), *Grijalva 769* (NY); roadside, 10 Sep 1978 (fl, fr), *Vincelli 860* (MO); along Pan-American highway at entrance to Hacienda San Jacinto, 12º21'N, 86º03'W, 16 Jul 1980 (fl), *Moreno 1239* (MO); between Hacienda El Paraiso, and old Managua-Tipitapa Highway (Hwy 1), 12º08-09'N, 86º07'W, 27 Jul 1978 (fl), *Stevens 9517* (MO); Hacienda San Jacinto, 500 m E of the Casa Hacienda, 12º21'N, 86º03'W, 16 Jul 1980 (fl), *Moreno 1202* (MO); along old road between Barrio Cásimiro Sotelo and bypass to U.N.A.N., 18 Jun 1981 (fl), *Sandino 660* (MO); entrance to Salamina along highway to Montelimar in the Valle de Samaria, 12º00'N, 86º33'W, 15 Oct 1980 (fr), *Moreno 3468* (MO); Chiltepe Peninsula, Chiltepe Point, 1 km S of Tamagás, 12º15'N, 86º18'W, 23 Jul 1982 (fl), *Moreno 16926* (MO); El Charco, Río El Carmen, 2 km W of Salamina, 11º59'N, 86º37'W, 07 Sep 1981 (fr), *Moreno 10806* (MO); Chiltepe Peninsula, 1.5 km S of Hacienda El Tamagás, 12º16'N, 86º19'W, 15 Aug 1980 (fl), *Moreno 1779* (MO); 17 km NNE of Tipitapa, 21 Sep 1976 (fr), *Danin 76-12-5* (MO). –MASAYA: Laguna Masaya, 24 Aug 1976 (fl, fr), *Bockus & Hall 7892* (BRIT, GH, NY, UC); Parque Nacional Volcán Masaya, around Casa Taller, 27 Sep 1983 (fl, fr), *Grijalva 2986* (MO); Parque Nacional Volcán Masaya, Piedra Quemada, 2 km E of Volcán Masaya, 22 Jul 1978 (fl, fr), *Neill 4609* (MO). – MATAGALPA: Matagalpa, 22 Jul 1969 (fl), *Zelaya 2305a* (GH, NY, SMU, UC); SW slopes of Cerro El Pilon and adjacent Laguna Tecomapa, 12º37'N, 86º02'W, 20 Jul 1978 (fl), *Stevens 9379* (MO); El Jocote Valley, Hacienda San Roque, 5 km from the Pan-American Highway along highway to León, 12º52'N, 86º13'W, 11 Sep 1980 (fl, fr), *Moreno 2568* (MO); W of Puente de Rio Viejo ca 8 km SE of San Isidro, 12º53'N, 86º90'W, 24 Jun 1982 (fl), *Kral 69078* (VDB). –RIVAS: Isla de Ometepe, 11º29'N, 85º29'W, 14 Sep 1983 (fl), *Moreno 22005* (MO); Isla Ometepe, Volcán Concepción, San José del Sur, 11º29-30'N, 85º38-39'W, 14 Aug 1984 (fl), *Robleto 1107* (MO); Isla de Ometepe, marshes between beach at Finca Santa Cruz and the Isthmus of Istián, 11º29'N, 85º33'W, 17 Jul 1981 (fl, fr), *Sandino 991* (MO); Moyogalpa, Isla Ometepe, road at edge of lake to Point Jesús María, 11º30'N, 85º42'W, 16 Sep 1983 (fl), *Robleto 51* (MO); Las Salinas, 25 Aug 1977 (fl, fr), *Neill 2459* (MO).

NIGERIA. OGUN: Igebu Ode, Ijebi-Igbo, s.d. (fl), *Magbadbeola et al. MAOA.238* (MO-2). ONDO: Akoko South, Epinmi, 25 May 1978 (fl), *Daramola & Ihe BO.499* (MO).

PAKISTAN. AZAD KASHMIR: Kotli Hills, 03 Oct 1956 (fl, fr), *Siddyi s.n.* (SMU).

PUERTO RICO. Guanica, Porto Rico and vicinity, 11-12 Mar 1913 (fl, fr), *Britton & Shafer 1875* (NY); Tortuguero, s.d. (fl, fr), *Woodbury 1972* (BRIT, NY); Penuelas, 01 Aug 1886 (fl, fr), *Sintenis 4892* (MO, NY); Yauco, 03 Oct 1913 (fl, fr), *Hess & Stevens 3267* (NY); Savaneta, near Ponce, 16 March 1915 (fr), *Britton et al. 5493* (NY); on the Adjuntas road seven miles from Ponce, 22 Nov 1902 (fl, fr), *Heller 6100* (E, F, GH, MO, NY); Coamo, 04 Nov 1885 (fl, fr), *Sintenis 2833* (GH, NY);

near Coamo, 19 Sep 1979 (fl, fr), *Liogier et al. 29461* (NY); Coamo, road 14, near Coamo river, 28 Aug 1979 (fl), *del Llano et al. s.n.* (BRIT, NY-2); Coamo, Bo. Cuyon, off Rte 717, km 2.7, NE of road and opposite Las Piedras Chiquitas, 10 Nov 1991 (fl, fr), *Axelrod & Axelrod 3152* (NY); Coarus Springs, 22 Nov 1899 (fl, fr), *Goll et al. 713* (NY); Guayama, Salinas, Rio Nigua at the jct of hwy 712 with 52, 18°02'14''N, 66°14'26''W, 15 Jul 2002 (fl, fr), *Worthington 31408* (UTEP); Guayama, Salinas, jct. of Hwys 1, 712 and 52 at Rio Nigua, 18°2'14''N, 66° 14'26''W, 29 Jul 2005 (fl), *Worthington 33177* (ASU); Guayama, Salinas, Bo. Llano, ca. 1 km E of Rte 706 and S of Rte 712, 04 Nov 1989 (fl), *Taylor & Lodge 9539* (MO, NY); Guayama, Salinas, Section Lima, Camp Santiago, 11 Jun 1992 (fl), *Lopez et al. SAN047* (MO); Lajas, 5.8 km S of jct with Rte 305 along Rte 303, 17°59'N, 67°06'W, 28 Nov 1994 (fl), *Atha & Zanoni 846* (NY); Santa Isabel, Rte 545 at Rte 52, at Lago Coamo Dam, 21 Oct 1989 (fl), *Taylor et al. 9528* (MO); Mayaguez, Sierra Bermeja, 1 mi SE of jct. Hwys 301 and 303, 17°58.96'N, 67°8.61'W, 01 Aug 2005 (fl), *Worthington 33227* (ASU).

SRI LANKA. CENTRAL PROVINCE: MATALE DISTRICT, 36th mi post Dambulla, Matale Road, 14 Jul 1974 (fr), *Waas 375* (MO). –EASTERN PROVINCE: TRINCOMALEE DISTRICT, Trincomalee, main road (A6) before town, 14 Jan 1968 (fl, fr), *Comanor 782* (MO, NY). –NORTH CENTRAL PROVINCE: ANURADHAPURA DISTRTICT, 6 mi N of Dambulla near 5 1/3 mi marker on Dambulla-Anuradhapura road, 30 Oct 1974 (fl), *Davidse & Sumithraarachchi 8157* (MO); Tissa Wewa, 30 Nov 1973 (fl, fr), *Sohmer 8959* (MO); rest house at Anuradhapura, 06 Jun 1972 (fl), *Maxwell & Jayasuriya 795* (NY). POLONNARUWA DISTRICT, grounds at rest house, Polonnaruwa, 07 Oct 1973 (fl), *Sohmer 8226* (MO, NY). –SOUTHERN PROVINCE: HANBANTOTA DISTRICT, Ruhuna National Park, Block I, growing at Patanagala, 18 Nov 1969 (fl), *Cooray*

69111803R (MO, NY); Ruhuna National Park, Block I, Patanagala Beach, 30 Nov 1962 (fl, fr), *Comanor 615* (MO, NY).

ST. KITTS & NEVIS. ST. KITTS: 08 Sep-05 Oct 1901 (fl, fr), *Britton & Cowell 617* (NY).

ST. VINCENT & THE GRENADINES. ST. VINCENT: Mar 1890 (fl), *Smith, Smith & Godman 312* (NY).

THAILAND. [Siam], Sep 1909 (fl, fr), *Kerr 779* (TCD).

VIRGIN ISLANDS. ST. CROIX: Bassin yard, Jul 1896 (fl), *Ricksecker 487* (F, GH, MO, NY, UC); Bassin, 10 Sep 1896 (fl), *Ricksecker 4* (E, F). ST. THOMAS: parade grounds, Nov 1880 (fl), *Eggers 156* (GH, NY); Aug 1881, *Eggers 559* (GH); Roadside along road from New Herruhut to Smith's Bay, 11-22 Feb 1913 (fr), *Britton & Marble 1273* (F, NY); French Hill, 06 Oct 1962 (fl, fr), *Croat 20* (MO).

CULTIVATED. *Damrel 955* (ASU, fl); *Damrel 1024* (ASU, fl, fr).

The monotypic *Martynia* is distinguished from the other genera by the combination of the following characters: sepals that are not united, the presence of only two fertile stamens, the short rostrum on the endocarp of the fruit, and the large purple markings on all petals of the corolla. *Martynia annua* is the most widespread of all the species in the Martyniaceae, having been introduced, most likely as an ornamental, to Africa, Asia, and Australia (Thieret 1977; Gibson 1999).

Lamarck (1786) cited the name and illustrations for what is now considered to be the lectotype for *M. annua*, making his name, *M. angulosa*, superfluous and illegitimate. Gloxin (1882) also cited the name and illustrations for the lectotype for *M. annua*, making his name, *M. diandra*, superfluous and illegitimate. Rafinesque

(1836) incorrectly concluded that all previous names published for the genus *Martynia* belonged as the type species to other genera, leaving the name *Martynia* without a type. Rather than name another species in the genus, he named the plant *Disteira angulosa*, though he cited *M. diandra*, now considered a superfluous name for *M. annua*.

V. Proboscidea Keller in Schmidel, Icones Plantarum [ed. Keller], 49: tt. 12-13. 1762. –TYPE: *Proboscidea louisianica* (Mill.) Thell. (=*Martynia louisianica* Mill.).

Martynia sectio Proboscidea (Schmidel) DC., *pro parte*. DC. Prod. 9: 253. 1845.

Martynia sectio Proboscidella DC., *pro parte*. DC. Prod. 9: 253. 1845.

Proboscidea Keller section *Eu-proboscidea* Stapf, Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 269. 1895.

Proboscidea Keller subgenus *Dissolophia* Van Eseltine. Tech. Bull. N. Y. State Dept. Agric. 149: 12. 1929.

Proboscidea Keller subgenus *Eu-proboscidea* Van Eseltine. Tech. Bull. N. Y. State Dept. Agric. 149: 12. 1929.

Description. Annuals or perennials. Roots taprooted or tuberous. Stems erect to decumbent. Leaves broadly deltoid, ovate-lanceolate, orbicular-reniform, or reniform, opposite to subopposite, the margins entire to deeply palmately lobed with 3-7 lobes, sometimes denticulate, sinuate-undulate, or undulate-repand; apices acute to obtuse, rounded or angulate; bases cordate to truncate, equilateral or inequilateral. Inflorescences many-flowered and surpassing the foliage to few-flowered and surpassed by the foliage; bracts linear-oblanceolate, oblong, rhomboidal, oblanceolate, or obovate. Flowers often with a strong odor; bracteoles ovate, deltoid, oblong, lanceolate, orbicular, oblanceolate, or obovate, deciduous; sepals mostly free or united, when united the calyx lobed, the lobes deltoid; corolla yellow, white, pink, lavender, or maroon, bilabiate; the restricted portion of the tube surpassed by the calyx, the dilated portion ventricose to obliquely-funnelform, the internal surface of the tube with orange, maroon, or dark purple specks and orange or yellow nectar guides; corolla lobes widely spreading, the two adaxial lobes often with large conspicuous purple spots, the other lobes variously marked with specks or streaks; stamens 4; ovules many. Fruits oblong to oblong-ovoid or oblong-ellipsoid; endocarp tan, brown, gray, or black, dehiscent, sculptured and lacking echinate projections, often with pectinate crests along the adaxial and abaxial sutures; rostrum about 1.25 to 3.5 times as long as the body of the fruit. Seeds many, black, brown, grey, or white, spindle-shaped, elliptic, rhomboidal, or ovate; testa corky and tuberculate.

Proboscidea is the largest genus in the family, with seven species recognized in this treatment. It is distinguished from *Craniolaria*, *Holoregmia*, and *Martynia* on the basis of the long beak on the fruit, and from *Ibicella* on the basis of the lack of echinate projections on the body of the fruit. The center of diversity for this genus is in the southwestern United States and Mexico, though some species can be found as far away as Guatemala and Peru. The name was first published by Keller in Schmidel's *Icones Plantarum* (1762), but due to the inconsistent use of the Linnaean binary system, specific epithets in this publication are not valid.

The etymology of the generic name comes from the Greek word *proboskis* in allusion to the long-beaked fruit. Proboscidea is also the name of the Mammalian order that contains the elephants, mammoths, and their relatives. The long-beaked fruit of the plant genus highly resembles the trunk of elephants and mammoths.

KEY TO THE SPECIES OF *PROBOSCIDEA*

1. Plants perennial, arising from a tuberous root; petals yellow .... 7. *P. althaeifolia*

1. Plant annual, taprooted; petals white, pink, lavender, or maroon, never yellow

    2. Sepals free for more than 75% of their length; seeds spindle-shaped, more than three times as long as wide; habitat deep sands .... 11. *P. sabulosa*

    2. Sepals united for more than 25% of their length; seeds ovoid to rhomboid, less than three times as long as wide; habitat various

        3. Inflorescences pseudo-spicate, pedicels shorter than 15 mm at anthesis .... 12. *P. spicata*

        3. Inflorescences racemose, pedicels longer than 15 mm at anthesis

            4. Petals white to pale pink; upper two lobes lacking a single large purple splotch; leaves suborbicular to reniform, margins entire .... 9. *P. louisianica*

            4. Petals pale to dark pink, magenta, or purple; upper two lobes each with a single large splotch; leaves deltate to cordate, margins minutely denticulate

                5. Larger leaves with three prominent lobes; S of the Trans-Mexican Volcano belt in s. Mexico and Guatemala............................ 13. *P. triloba*

                5. Larger leaves unlobed or with five lobes

6. Flowers dark purple to maroon; central Mexico, w Texas, se New Mexico .... 8. *P. fragrans*

6. Flowers pale to dark pink; nw Mexico, sw United States .... 10. *P. parviflora*

7. Proboscidea althaeifolia (Benth.) Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 324. 1865. *Martynia althaeifolia* Benth., Bot. Voy. Sulph. 37. 1844. –TYPE: MEXICO. Baja California del Sur: Bay of Magdalena, 1841, *Hinds s.n.* (holotype: K! [photo at RSA-PO!]; isotypes: BM? NY).

Martynia arenaria Engelm., Wisliz. Tour N. Mex. 100. 1848. *Proboscidea arenaria* (Engelm.) Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 326. 1865. –TYPE: MEXICO. Chihuahua: sandhills below El Paso, 1846, *Wislizenius 92* (holotype MO).

Martynia palmeri S. Wats., Proc. Amer. Acad. 24: 66. 1889. –TYPE: MEXICO. Baja California: Los Angeles Bay, 1887, *Palmer 599* (holotype: GH [1 sheet, 1 bagged specimen, photos at ASU!]; isotypes: NDG! [photo at ASU!] NY [2 sheets, photos at ASU!] US [photo at ASU!]).

Proboscidea peruviana Van Eseltine, N. Y. State Agric. Exp. Stat. Tech. Bull. 149: 17. 1929. –TYPE: PERÚ. Provincia de Paita: Talara, 07 Oct 1925, *Haught 14* (holotype: US [photo at ASU!]; isotypes: F! [photo at ASU!] GH [photo at ASU!] NY [photo at ASU!]).

Description. Perennial herbs. Roots tuberous, large and fusiform. Stems decumbent. Leaves opposite to sub-opposite; petiole 3-18 cm long; lamina reniform, suborbicular, to broadly ovate; apex rounded; base cordate to truncate, equilateral to inequilateral; margins entire to deeply lobed. Inflorescences with 3-16 flowers, surpassing the foliage; peduncles 5-12 cm long; bracts linear. Flowers fragrant; pedicels 2-8 cm long; bracteoles orbicular to broadly ovate; calyx 1-1.5 cm long, sepals free for 30%-50% of their length; corolla 2-3 cm long, yellowish-brown externally, yellow to bronze-orange internally, the tube with pale spots and frequently with maroon, reddish-brown or rust-colored spots forming two rows internally and leading out to the throat and lobes. Fruit endocarp gray, very slender and elongate; endocarp body to 5-6 cm long, 12 mm thick, crested adaxially and sometimes abaxially; endocarp rostrum 1.75 to 2 times the length of the body, with a distal projection of incompletely dehiscing tissues between both rostral hooks. Seeds tan to black, to 8 mm long, oblong and tapering at both ends.

Phenology. Flowering from May to November in the northern and eastern portions of the North American range, with the peak flowering season from July to September. In the southwestern portion of the North American range (Baja California, Baja California Sur), flowering can occur at any time of the year. In Peru, flowering can occur from January to July, occasionally flowering in October and November.

Distribution and habitat (Figs. 27, 28). Disturbed areas such as dunes, arroyos, beaches, and roadsides in soils of pure or high sand content in northwestern Mexico (Baja California, Baja California Sur, Chihuahua, Sonora), Peru, and the southwestern United States (Arizona, California, New Mexico, Texas); 0-1200 m (0-3600 ft).

Vernacular Names. Iispuer (Pima Bajo), ispuel-ga (Pima Bajo), ban ihugga 'Coyote Devil's Claw' (Gila River Pima), campanita, Devil's claw, gatito, yuca de Caballo (Peru).

SPECIMENS EXAMINED. **MEXICO**. Hwy 15 S of Santa Ana, 07 Aug 1957 (fl, fr), *Solbrig & Ornduff 4363* (GH). –BAJA CALIFORNIA: ca. 13 mi N of San Felipe along hwy 5, 03 Jul 1968 (fl, fr), *Henrickson & Hood 2766* (ASU); no locality given, Oct 1959 (fr), *Wiggins 15070* (ASC); Rancho Mesquital, 30 Oct 1946 (fl, fr), *Wiggins 11332* (GH, UC); wash 15 mi N of Bahia de San Luis Gonzaga, 31 Mar 1960 (fl), *Wiggins & Wiggins 16036* (ARIZ, GH); E of Mex Hwy 5, Playa Punta Estrella, 5.5 mi S of San Felipe, 30º55'N, 114º43'W, 26 Feb 1992 (fl), *Baker & Johnson 8660* (ASU); 7 mi SE of Laguna Chapala, 29º21'N, 114º19'W, 18 Oct 1971 (fl, fr), *Moran 18692* (SD, UC); 10-11 mi S of San Felipe off Rte 5, near Sea of Cortes, 25 Apr 1998 (fl, fr), *Hammond 11414* (ASC); 20 km W of Bahia de los Angeles, 19 Oct 1977 (fl, fr), *Gibson & Horak 3309* (ARIZ); 25 mi N of Punta Prieta, 15 Apr 1931 (fl), *Wiggins 5364* (ARIZ); Bahia de Los Angeles, 13 Mar 1992 (fl), *Fritsch et al. 1321* (ARIZ); Ensenada, Cerro Punta Estrella, S of San Felipe, 114º45'N, 30º53'W, 26 Nov 1994 (fr), *Macias et al. 431* (SD); Las Flores, 28º50'N, 113º35'W, 26 Aug 1964 (fl), *Moran 11897* (SD); Los Flores, Los Angeles Bay, 10 Apr 1946 (fr), *Harbison 41746* (SD); Sierra San Borja, Valley of San Juan, 28º45.5'N, 113º37'W, 08 Jun 1962 (fl, fr), *Moran 9748* (SD); 16.1 mi from Bahia de Los Angeles on road to Chapala, 29º02'N, 114º48'W, 25 Sep 1964 (fl, fr), *Howe 3988* (SD); arroyo 2 mi S of El Huerfanito, 30º06'N, 114º39'W, 31 Jan 1973 (fl), *Moran & Reveal 19596* (SD); Valle de Santa Clara, 31º18'N, 115º25'W, 24 Aug 1977 (fl), *Moran 24634* (SD); Delicias, 1-6 km from Bosque Nuevo Mazatlan, 114º46'W, 30º43'N, 16 Mar 1996 (fl), *Macias & Delgadillo 562* (SD); 10 mi N of Catavina, S of El Marmol on Hwy. 1, 12 Aug 1981 (fl), *Mittleman s.n.* (DES); 9.8 km NW of El Arco, 11 Nov 1947 (fr), *Carter et al. 1910* (UC); Arroyo Miramar, 22.3 mi S of Puertocitos, 11 Oct 1963 (fl), *Hastings & Turner 63-146* (ARIZ, SD); 2.2 mi NNE of El Crucero via Bahia San Luis Gonzaga road (El Crucero is 13 mi N of Bahia de Los Angeles via Hwy 1), SW Bajada of Cerro La Gobernadora, on SW side of Sierra La Asamblea, 29º16'N, 114º08'W, 13 Oct 1981 (fl), *Burgess et al 6111* (ARIZ); 29.7 mi SW of Bahia San Luis Gonzaga, 12 Oct 1963 (fr), *Turner & Hastings 63-167* (ARIZ); 2.2 mi S of Hwy to Los Angeles Bay on Mision San Borja Road, 01 Nov 1983 (fl, fr), *Soule & Perrill 1088* (ARIZ). –BAJA CALIFORNIA DEL SUR: beach N of Migriño, 23º03'N, 110º07'W, 27 Nov 1969 (fl), *Moran 16683* (SD); Los Barriles, 26 Nov 1956 (fl), *Harbison s.n.* (SD); dunes 15 mi S of Venancio, 21 Nov 1938 (fl, fr), *Shreve 7193* (ARIZ); Cerro Mechudo, 24º47'N, 110º39'W, 13 Nov 2003 (fl, fr), *Leon de la Luz 10273* (SD); Cape Region, Buenavista, 23º39'N, 109º41'W, 06 Jan 1959 (fl, fr), *Moran 6901* (ARIZ, SD); Cape Region, La Playa, E of San Jose del Cabo, 23º03'N, 109º40'W, 07 Jan 1959 (fl), *Moran 6912* (SD); 9 mi E of San Ignacio, 03 Nov 1946 (fl, fr), *Wiggins 11361* (GH, UC); Bahia de la Ventana at Rancho de la Ventana, 19 Dec 1958 (fl, fr), *Wiggins 14417* (GH, K); 25 mi N of Punta Prieta, 15 Apr 1931 (fl, fr), *Wiggins 5346* (GH); San Jose del Cabo, 16 Oct 1899 (fl), *Brandegee s.n.* (NY); Magdalena Plain near Santo Domingo, 04 Oct 1941 (fl, fr), *Hammerly 188* (GH, MO, NY); San Jose del Cabo, 14 Sep 1930 (fl), *Jones 27438* (MO, NY, UC); San Jose del Cabo, 04 Sep 1890 (fl), *Brandegee 439* (GH); Punta Lobos, 2.1 mi S of Todos Santos and 1 mi W of Todos Santos-Cabo San Lucas Road, 25 Dec 1958 (fl, fr), *Porter 76* (GH); desert flats along Hwy 1, 7.8 mi s of Santa Rosalia, 07 Jan 1983 (fl), *Daniel et al.*

2371 (ASU); Cabo San Lucas, Aug 1859-Jan 1860 (st), *Xantus s.n.* (GH); Cabo San Lucas, 23 Mar 1911 (fl, fr), *Rose 16351* (NY); Cabo San Lucas, 31 Mar 1982 (fl, fr), *Haines 82-47* (NY); Cabo San Lucas, in Bahia San Lucas, 22º50'N, 109º50'W, 22 Dec 1980 (fl, fr), *Edmondson 3619* (ASU); NW of La Paz, just S of the Mogote Peninsula that creates the Ensenada del La Paz, 24º9'N, 110º26'W, 16 Sep 1996 (fl), *Rebman 3423* (ASU, SD); 30.0 km S of Todas Santos along the road down the Pacific Coast toward Cabo San Lucas, 23º10'N, 110º07'W, 15 Dec 1982 (fl, fr), *Sanders et al. 3383* (UTEP); La Paz, Centro de Investigaciones Biologicas de La Paz, near bay, 14-16 May 1984 (fl), *Becvar s.n.* (UTEP); Rancho Los Frailes between La Paz and Cabo San Lucas, 28 Dec 1980 (fl, fr), *Stein 399* (MO); San Jose del Cabo, Jan-Mar 1901 (fl), *Purpus 413* (MO); San Francisco Island, 24º49'N, 110º35'W, 11 Apr 1952 (fr), *Moran 3732* (UC); ca. 9 mi SW from El Arco on road to Banderita, 22 Oct 1959 (fl), *Thomas 8278* (UC); Sierra de la Giganta, Canada del Encinal, S side of Valle de los Encinos, S side of Cerro de la Giganta, 26º3.5-4'N, 111º34'W, 01 Oct 1967 (fl), *Carter & Moran 5363* (UC); 19.2 km SE of San José del Cabo, 17 Dec 1947 (fl, fr), *Carter et al. 2242* (ARIZ, UC); S of La Vigia, Cape San Lucas, 22º52'N, 109º54'W, 20 May 1952 (fl, fr), *Moran 4167* (SD, UC); Cabo San Lucas, 04 Jul 1979 (fl), *Magallanes 1726* (MICH); 15 mi NE of Cabo San Lucas, 04 Nov 1983 (fl, fr), *Starr 697* (ARIZ); 3 mi N of San Jose del Cabo, Santa Rosa, 05 Jan 1974 (fl), *Petryszyn 30* (ARIZ); 30.7 mi W of La Paz, 08 Oct 1964 (fl), *Turner & Hastings 64-194* (ARIZ, SD); Rancho 'La Burrera' near Todos Santos, 23º32'N, 110º04'W, 19 Oct 1985 (fl), *J.L.L.L. 837* (BRIT); Bahia San Lucas, ca. 3.5 km E of Cabo San Lucas, 22º54'N, 109º5.75'W, 13 Jun 1984 (fl), *Dice & Wier 544* (SD); El Salado, dunes N of El Salado lighthouse, 23º16'N, 109º25'W, 20 Feb 1997 (fl), *Perez Navarro 675* (SD); km 160, 4 km W of El Triunfo, 04 Sep 1977 (fl), *Snelling s.n.* (SD); 21.5 km NE of Cabo San Lucas on Mex Hwy 1, 1.5 km SE of Cerro El Biedito near Ensenada del Diablo, 22º59'34''N, 109º45'W, 26 Oct 1990 (fl, fr), *Roberts & Roberts 4752* (SD); 1.5 km SE of Rancho Poza del Leon, 25º21'32.2''N, 111º10'9.6''W, 18 Nov 2003 (fr), *Dominguez Cadena 2867* (SD), San Jose del Cabo, 11 Nov 1952 (fl, fr), *Harbison s.n.* (SD); San Jose del Cabo, 29 Oct 1941 (fl), *Gander 9721* (SD); 5 mi ESE of El Pabellón, 25º55'N, 112º00'W, 13 Feb 1973 (fl), *Moran & Reveal 20067* (SD); Rancho Las Cruces, 24º12'33''N, 110º04'46''W, 14 Oct 2000 (fl, fr), *Rebman & Klavzar 7005* (SD); beach and dune area S of Rancho Dolores, 25º04'28''N, 110º51'11''W, 12 Nov 2003 (fl, fr), *Rebman et al. 9746* (SD); Near La Bocana, W of San Gregorio dunes, 26º3'23''N, 112º17'21''W, 25 Oct 2001 (fl), *Rebman 7769* (SD); Rancho Santa Marta, 25º27'00''N, 111º01'47''W, 20 Oct 2001 (fl), *Rebman & Roberts 7650* (SD). –CHIHUAHUA: La Mesa escarpment along the New Mexico-Chihuahua border 0.9 mi W of Monument No. 3 just across border from T29S R3E Sec. 13, 24 Jul 1986 (fl, fr), *Worthington 14316* (NY, UTEP); 2 mi S of Villa Ahumada, 07 Aug 1956 (fl, fr), *Waterfall 12477* (GH); 8 km. S of Rancho de Encinillas, 06 Jul 1941 (fl), *Stewart 706* (GH); Aug 1851 (fl), *Thurber s.n.* (GH, NY-2); near Juan Jose, 122 miles S of Cd. Juarez, 04 Sept 1974 (fl, fr), *Walker 74-H47* (NY); 45.5 mi N of Villa Ahumada, 27 Aug 1967 (fl, fr), *Oliver et al. 495* (MO). –COAHUILA: El Toro near Morano, Jul 1910 (fl), *Purpus 4546* (GH, MO); road from Zacatosa SE to Puerto Colorado at Tanque Colorado, 31 Aug 1941 (fl, fr), *Johnston 8661* (GH-3); 4.5 km NW of Las Delicias, 04 Oct 1942 (fl), *Stewart & Santos 2837* (GH); 1 km NW of San Jose along road from Guimbalete SE to Acatita via Laguna del Rey, 17 Sep 1942 (fl, fr), *Stewart & Santos 2645* (GH); 8 km NW of Viesca, 25º23'N, 102º51'W, 15 Jun 1972 (fl), *Chiang et al. 7793* (MO, NY). –SONORA:

Sonora Alta, s.d. (fl), *Coulter 1309* (TCD); no collection data, 07 Sept 1851 (fl, fr), *Thurber 1024* (GH-2, NY); Santa Cruz, 7-8 km SSE of San Lazaro (=Miguel Hidalgo) on the road to San Antonio on MEX 2 between Cananea and Imuris, 31º2.47'N, 110º37.156'W, 11 Sep 2002 (fl, fr), *Doan et al. 1333* (ASU, DES); 41 mi S of Agua Prieta, N of Colonia Morelos, 19 Aug 1976 (fl, fr), *Sheridan et al. X-478* (ARIZ, DES); 7.4 mi NE of Mazicahui along road to Moctezuma, 29º35'N, 110º05'W, 01 Sep 1988 (fr), *Hodgson et al. 5170* (DES); San Carlos, 15 Sep 1981 (fl), *Kennedy s.n.* (DES); 21 mi E of Willard between Hermosillo and Colorado, 05 Sep 1941 (fl, fr), *Wiggins & Rollins 299* (ARIZ, GH, MO, ND, NY, UC); 0.5 km E of Macdougal Crater, Pinacate Range, 08 Sep 1964 (fr), *Felger & Lincoln 10459* (NY); ca. 27 mi N of Hermosillo, 16 Jul 1970 (fl, fr), *Lehto 16939* (ASC, ASU); 2.5 mi S of Mexico #2, 32.4 mi W of Sonoita, 22 Mar 1969 (fr), *Pinkava et al. 15509* (ASU); ca. 6 mi N of Alamos, 09 Aug 1980 (fl, fr), *Lehto 24763* (ASU); Camahuiroa, 6.7 km SE of Las Bocas, 32º32'35"N, 109º17'32"W, 20 Jul 1993 (fl, fr), *Friedman 201-93* (ASU); 11 mi W of Hwy 15, on road to San Agustin (and Punta Alesna), NW of Guaymas, 12 Aug 1978 (fl), *Fryxell 3071* (K, NY); road to Tomibabi Hot Springs, between Moctezuma and Granados, 01 Jul 1938 (fl), *White 407* (ARIZ-2, GH); 12 mi S of Agua Prieta on road to Fronteras, 08 Aug 1941 (fl, fr), *White 3850* (GH); El Pilar vicinity, Estero el Soldado, at Condominios Pilar, 4.5 km W on road to San Carlos, 1 km SSE on road to condominium parking area, 27º57.5'N, 110º 58.8'W, 13 Aug 1994 (fl), *Friedman & Espinosa 197-94* (ASU); San Bernardo, Rio Mayo, 12 Jul 1935 (fl, fr), *Gentry 1487* (ARIZ, GH, K, MO, UC); Guaymas, Jul 1887 (fl, fr), *Palmer 114* (GH, NDG, NY-2); Guaymas, 1887 (fl,fr), *Palmer 326* (NDG); Tetasuari, Los Pilares at the edge of the Rio Mayo, 14 Jul 1967 (fl, fr), *Hernandez 430* (GH); Nuevo Guaymas, Bahia de San

Carlos at Creston Motel, 30 Aug 1970 (fl, fr), *Lehto 17028* (ASU); Nuevo Guaymas, at Creston Motel, sand near ocean, 18 Jul 1970 (fl, fr), *Lehto 16980* (ASU, F, NO); Playa Huatabampito, ca. 14 km SSE of Huatabampo, 109º36'W, 26º42'N, 4 Sep 1989 (fl, fr), *Sanders et al. 9199* (ARIZ, SD, UTEP); 18 mi W of Los Arrieros on the road to Tastiota, 02 Sep 1941 (fl, fr), *Wiggins & Rollins 250* (GH); W of Plaza in Huepec, 1.3 N and 0.7 mi W, 01 Jul 1978 (fl), *Vaughn 625* (MO); SW edge of Alamos, 08 Aug 1973 (fl), *Fish 22* (UC); center of MacDougal Crater, Pinacate Range, 08 Sep 1964 (fl), *Felger & Lincoln 10498* (ARIZ); ca. 5 mi W of Mex Hwy 15 on road to Bahia San Carlos, 17 Jul 1964 (fl), *Felger et al. 10133* (ARIZ); Rio Mayo Region, Camahuiroa between Agiabampo and Las Bocas on the Gulf of California, 26º31'N, 109º16'W, 08 Oct 1992 (fl, fr), *Van Devender et al. 92-1066* (ARIZ); Rio Mayo Region, El Rancheria crossing of Rio Cuchujaqui, ca 22.5 km S of Alamos on road to El Chinal, 26º51'N, 108º55'W, 03 Jul 1992 (fl, fr), *Van Devender & Friedman 92-704* (ARIZ); San Bernardo, 15 Aug 1951 (fl), *Gentry 11094* (ARIZ); Rio Mayo, San Bernardo, 15 Sep 1958 (fl), *Arguelles s.n.* (ARIZ); Rio Mayo Region, Loma Chomojabires near Huatabampo, 26º42.7'N, 109º36.3'W, 23 Aug 1990 (fl, fr), *Martin & McWhorter s.n.* (ARIZ); Rio Mayo Region, Estero Santa Barbara, 3 km W of Huatabampito, 26º42'N, 109º38'W, 11 Oct 1988 (fl, fr), *Martin et al. s.n.* (ARIZ); Rio Mayo Region, Las Bocas on the Gulf of California, ca. 52 km S of Navajoa, 26º36'N, 109º20'W, 22 Sep 1994 (fl, fr), *Van Devender & Yetman 94-693* (ARIZ); Pinacate Region, SE slope of Pinacate Peak, 13 Oct 1986 (fr), *Felger & Joseph 86-463* (ARIZ-2); Isla Tiburon, Palo Fierro airfield at E side of island, ca 2 km W of shore, 11 Aug 1964 (fl), *Felger et al. 10321* (ARIZ); ca. 10 mi W of Mazatán, 30 Jul 1959 (fl), *Gentry 17746* (ARIZ); Cerro Colorado, Pinacate Range, 06 Oct 1964 (fl), *Felger & Sherbrooke 10800* (ARIZ);

18.9 mi W of Mex Hwy 15 along Tecolote Road, 1.2 mi N of El Oasis, 29º48’35”N, 111º17’45”W, 07 Aug 1982 (fl, fr), *Reichenbacher 1003* (ARIZ); Pinacate Region, 46 km W of Sonoyta on Mex Hwy 2, 2.8 mi E of Pinacate Junction road to Elegante Crater, 14 Sep 1986 (fl, fr), *Felger & Leigh 86-337* (ARIZ); ca. 5.5 mi downstream from Soyopa on the Rio Yaqui, 21 Jul 1983 (fl, fr), *Van Devender et al. s.n.* (ARIZ); Onavas, 12 Aug 1985 (fl), *Rea 814* (SD); Onavas, 3 June 1984 (fl, fr), *Rea 433* (SD); 82.6 mi W of Sonoyta, 32º00’N, 113º25’W, 22 Sep 1967 (fl, fr), *Howe 4378* (SD); Onavas, 20 Aug 1986 (fl), *Rea 1159* (SD); 2.4 km W of cemetery in Benjamín Hill on road to Rancho El Peñascoso, 30º09’56”N, 111º08’57”W, 17 Oct 2003 (fl, fr), *Reina & Van Devender 2003-1201* (ARIZ); Guaymas, at Estero Soldado, 1.5 km E of Condominios Pilar, 10 km E of Bahia San Carlos, 12 Aug 1985 (fl), *Felger & Dimmit 85-879a* (ARIZ); Rancho la Tinaja Colorada, ca. 15 km NE of Magdalena de Kino, 30º42’10”N, 110º48’20”W, 11 Aug 1996 (fr), *Flores M. et al. 4590* (ARIZ); Arroyo Los Garabullos, 0.5 km SE of Rio Yaqui bridge on Mex 16, 3.3 km S, 1.5 km E of Tonochi, 28º34’10”N, 109º33’00”W, 09 Sep 1999 (fl), *Reina & Van Devender 99-389* (ARIZ); Arroyo Las Tinajas , 3.5 km S of Tónichi, W side of Rio Yaqui, 28º34’03”N, 109º33’25”W, 17 Aug 2006 (fl, fr), *Van Devender & Reina G. 2006-641* (ARIZ); Colonia Lerdo, 31 Mar 1905 (fl), *MacDougal 94* (NY).

PERÚ. Pariñas Valley, Nov 1928 (fl, fr), *Haught F-114* (F); no locality given, s.d. (fr), *ES22* (MO). –<u>LAMBAYEQUE</u>: LAMBAYAQUE PROVINCE, 28 km W of Olmos, 09 June 1978 (fr), *Gentry, & al. 22544* (F, MO). CHICALYO PROVINCE, Pampas de Reque, 24 May 1971 (fl, fr), *López et al. 7701* (F, NY); km 375 at Cerro Reque, 03 Jul 1972 (fl), *de Ferreyra 5297* (MO); km 712 at Caña Norte, 30 Jun 1972 (fl, fr), *de Ferreyra 5206* (MO); Mocupe (Cayaltí), s.d. (fl), *Llatas et al. 597* (MO); Arenal, 10 Apr 1948 (fl), *Lopez 282* (MO). –PIURA: PIURA PROVINCE, no locality given, s.d. (fl), *Spruce 6370* (E); Alto de la Cruz, 40 km W of Piura, 29 Mar 1939 (fl), *Stork & Horton 11356* (GH, K, UC); 15 km between Piura and Sullana, E of the Pan-American highway, 23 May 1992 (fl, fr), *Vega & Guevara 6184* (F, MO-2, NY); between Piura & Ñomala, Mar 1912 (fl, fr), *Weberbauer 5949* (F, GH, NY); near Piura along highway to Paita, 19 Apr 1953 (fl), *Ferreyra 9100* (MO), near Piura, km 1130-1135 between Piura and Talara, 02 Jun 1972 (fl, fr), *Ferreyra 17998* (MO); near Piura, 16 Apr 1949 (fr), *Ferreyra 5887* (MO); near Piura, 20 Apr 1953 (fl, fr), *Ferreyra 9105* (MO); near Buenos Aires along road to Tambo Grande S of Piura, 30 Apr 1949 (fl), *Ferreyra 6036* (MO); near Piura, 16 Apr 1949 (fl), *Anderson 915* (UC). SECHURA PROVINCE, Sechura, 24 Jan 1984 (fl, fr), *Cisneros s.n.,* (F-2, NY). TALARA PROVINCE, 1 km W of town [Talara], 11 March 1939 (fl), *Beetle 26193* (GH, MO-2, SMU, UC); beach at km 1216 on Panamerican highway SE of Mancora, 21 Feb 1976 (fl), *Plowman 5511* (GH); Talara, 01 Feb 1952 (fl), *Rauh P12* (F); near Talara, 15 Oct 1983 (fl, fr), *Sagastegui 10914* (MO, NY). –TUMBES: TUMBES PROVINCE, Caleta Cruz near Zorritos, 27 May 1957 (fl, fr), *Ferreyra 12219* (MO).

U.S.A. ARIZONA: no locality given, 28 Jul 1920 (fl), *Jones & Hood s.n.* (UC). COCHISE CO., 2 mi W of Texas Canyon, 11 Jul 1926 (fl), *Carter 188* (ARIZ); near Rincon Mts., 31 Jul 1932 (fl, fr), *Peebles & Kearney 8765* (ARIZ); Coronados, 30 Jun 1910 (fl), *Goodding 514a* (ARIZ, NY); Fort Huachuca, Hill Four 11th Brigade Signal Corps site, 4.5 km NW of the confluence of the San Pedro and Graveyard Gulch, 7 km SW of Fairbank, 05 Aug 1992 (fl), *Krohn & Schulz 2548* (DES); 13.2 mi N of Pomerene on Benson-Mammoth Road, 04 Aug 1981 (fl, fr), *Reichenbacher and Van Devender 724* (ARIZ, UTEP); McNeal, 28 Jul 1920 (fl), *Jones 195*, (GH); near Ft.

Huachuca, 1882 (fl), *Lemmon 3060* (GH); W side of San Bernardino Ranch, 18 mi E of Douglas, 24 Jul 1981 (fl), *Marrs-Smith et al. 757* (ASU); Game and Fish Management Area Unit 30A ca. 10 mi SSE of Bowie, 02 Aug 1975 (fl, fr), *Reeves 4088* (ASU); Hwy 181 near Chiricahua National Monument, SE of Wilcox, 01 Sep 1963 (fl, fr), *Deaver 6603* (ARIZ, ASC, ASU); Tombstone, 08 Jun 1950 (fl, fr), *Earle s.n.* (ASU); San Pedro National Conservation Area, Upper San Pedro River floodplain, Escalante Crossing, roadside near Apache Powder station, 31º51'N, 110º12'W, 15 Jul 2002 (fl), *Makings 1109* (ASU); San Pedro National Conservation Area, Upper San Pedro River floodplain, 4-5 mi S of Hwy 82, ca. 1 mi E of San Pedro in Rock Art site just N of BLM interpretive sign, 31º39.729'N, 110º10.508'W, 03 Aug 2002 (fl, fr), *Makings 1150* (ASU); Douglas, 20 Jul 1922 (fl), *Jones s.n.* (UC); W of Bowie, 17 Sep 1960 (fl, fr), *Hevly & Drouet s.n.* (ARIZ); 5-6 mi N of Pomerene, 08 Oct 1958 (fr), *Goodding 612-58* (ARIZ); Zinn Ranch, 02 Sep 1959 (fl), *Goodding 217-59* (ARIZ); ca 5 mi N of Pomerene, 30 Jul 1958 (fl), *Goodding 237-58* (ARIZ); Fordney Ranch Road near Fairbank, 31 Jul 1967 (fl, fr), *Barr 67-269* (ARIZ); 4 mi N of Pearce, 27 Aug 1936 (fl, fr), *Anderson, Rhinehart, & Carter 1337* (ARIZ); US Hwy 666 near Elfrida, 05 Jun 1962 (fl), *Barr 62-366* (ARIZ); Bowie, 07 Sep 1948 (fl), *Gentry 8191* (ARIZ); Elfrida, 01 Aug 1957 (fl), *Jones s.n.* (SD); Government Gap, 08 Aug 1957 (fl), *Jones s.n.* (SD); Paul's Spur, 15 Jun 1944 (fl, fr), *Jones s.n.* (SD). GRAHAM CO., 5.5 mi ESE of Solomon, 30 Jul 1977 (fl), *Minckley et al. s.n.* (ASU, DES, UTEP); near jct of Haekal Road and the Old West Highway, 32º48.209'N, 109º34.835'W, 12 Aug 2003 (fl), *Damrel & Damrel 1954-B* (DES, SD); S of Solomon along cemetery ridge, 27 Aug 1971 (fl), *McLeod et al. 906* (ASU); Frye Canyon Plot, Graham Mountains, 23 Aug 1935 (fl), *Anderson & Rhinehart 430* (ARIZ). LA PAZ CO., near Ehrenberg, 02 Aug

1902 (fl), *Stephens s.n.* (UC). MARICOPA CO., Phoenix Metropolitan area, near Ahwahtukee, near 43rd Street, off North Circle Drive between Chandler Blvd. and Ray Rd., 27 Jul 1990 (fl), *Hodgson & Forster 5850* (ASU, DES, NY); near N boundary of White Tank Mountains Regional Park, ca 1.3 mi N of Peak 2670, 27 Sep 1969 (fl), *Keil 5784* (ASU, UTEP); Scottsdale, E side of Pima Rd., 0.1 mi N of Jomax Rd., 10 Sep 1986 (fl, fr), *Jones 369* (DES); SW Morristown, 30 Jul 1950 (fl, fr), *Barlow s.n.* (DES); McDowell Mtns. Regional Park, 10 May 1975 (fl), *Lane 493* (ASU); ca. 2 ½ mi S of Aguila, 15 Oct 1966 (fl), *Moore, Freeman & Pinkava 2572* (ASU); S of South Mtn. Park, ca. 6 mi E of St. John's Indian School along road between St. John's Indian School and W Chandler along N edge of Gila River Indian Reservation, 22 Jul 1990 (fl), *Landrum 7046* (ASU, UC); Arlington, 12 Aug 1936 (fl), *Stitt & McLellan s.n.* (ASU); Eagletail Mtns., intersection of Courthouse Road and Gas Pipeline road, 24 Sep 2003 (fl, fr), *Newton & Unruh 1* (ASU); rest area ca. 1 mi S of New River along I-17, 01 Aug 1975 (fl), *Lehto et al. L18816A* (ASU); N side of Pinnacle Peak Road E of Scottsdale Road, 20 Jun 1969 (fl), *Lehr 20* (DES); Pinnacle Peak, 10 Aug 1963 (fl, fr), *Lehto 2125* (ASC, ASU, GH); White Tank Mts. Regional Park, road across flats leading to Ford Canyon, 24 Sep 1969 (fl, fr), *Pinkava, Pase & Keil 5625* (ASU, UTEP); 5 mi E of Komatke on Williamsfield Road, 29 Oct 1983 (fl), *Rea 551* (SD), S edge of South Mtns., 5.5 mi E of 51st Ave along Williamsfield Road, 19 Aug 1985 (fl, fr), *Rea 839* (SD). MOHAVE CO., junction of Chicken Springs Rd., and Hwy 93, 3 Jun 1979 (fl), *Parfitt, Butterwick & Hillyard 5058* (ASU, DES); valley 14 mi SW of Kingman, 2 Sep 1942 (fl, fr), *Barneby 5001* (NY); 0.9 mi W of Chicken Springs Road (and Wikieup) along Alamo Lake Road (jct is 0.3 mi W of SR 93), 34°41'00"N, 113°40'W, 26 May 1992 (fl), *Hodgson 6700* (DES, NY); Burro Creek along Hwy 93 NW of

Wickenburg, 08 Jun 1993 (fl, fr), *Atwood & Genz 18060* (ASU); Big Sandy Bridge site ca. 2 mi S of Wikieup on US 93 at mile post 126.5 just SW of the bridge, 04 Aug 1990 (fl, fr), *Rebman & Dempster 90-10* (ASU); S of Wikiup ca 5 mi in Burro Creek along Hwy 93, 19 Sep 1981 (fl), *Back s.n.* (ASC); W of Aquarius Mtns., 09 Aug 1962 (fl), *McCormick s.n.* (MNA). PIMA CO., 1.7 mi S of Why along AZ Hwy 85, 32º14.36'N, 112º44.99''W, 21 Sep 1998 (fl), *Helmkamp & Helmkamp 4453* (TEX); ca. 1 mi S of Three Points, 31 Jul 1992 (fl), *McLaughlin & Hutter 6735* (ARIZ); Santa Rita Experimental Range, 1 mi E of Cattlee, 05 Jul 1978 (fl), *Fay s.n.* (ARIZ); 0.3 mi W of Madera Canyon turnoff along Hwy 89, 31 Jul 1971 (fl, fr), *Brown et al. 589* (ASU); Tumamoc Hill, Tuscson, 17 Aug 1916 (fl), *Harris C16549* (NY); 1 km W of Greasewood Rd on Speedway Blvd, E of the Tucson Mtns., 32º14'08''N, 111º01'57''W, 20 Jul 1999 (fl), *Van Devendar 99-339* (NY); Interstate 19 and Pima Mine Rd., 25 Aug 1971 (fl), *McLeod at al. 630* (ASU); SE end of Coyote Mtns, by mouth of canyon to the N of Mendoza Canyon, 31º59'N, 111º28'W, 7 Sep 2003 (fr), *Salywon et al. 1429* (ASU, NO); S of San Xavier, W of Helmet Peak, 28 Jul 1982 (fl), *Mittleman & Butterwick 162* (ARIZ, ASU, DES); NW Baboquivari Mtns., 25 Jul 1951 (fl, fr), Blakley B-632 (DES); SW of Tucson near Snyder Hill, 16 Sep 1991 (fl, fr), *Fleming 1250* (DES); Upper Altar Valley, 03 Oct 1940 (fr), *Gentry 5968* (DES); Mesas, Tucson, 21 Aug 1903 (fl), *Thornber s.n.* (ARIZ, ASU); Tucson, 25 Sep 1901 (fl), *Thornber s.n.* (ARIZ, UC-2); Wilmot, Small Range Preserve, 15 Aug 1904 (fl), *Thornber 2162* (ARIZ, ASC, GH, K, MO, NY); Range Reserve, Wilmot, 12 Aug 1902 (fl, fr), *Thornber s.n.* (ARIZ); Range Reserve, Wilmot, 22 Aug 1902 (fl, fr), *Thornber s.n.* (ARIZ); Wilmot, 25 Aug 1903 (fl), *Thornber 213* (ARIZ); ca. 2 mi N of Tortuga Ranch, 16 Jul 1959 (fl, fr), *Turner & Yang 59-84* (ARIZ); Tucson, 20 Sep 1891 (fl), *Toumey s.n.* (ARIZ); Canada del Oro ca. 10 mi N of Tucson, 10 Aug 1966 (fl), *Bohrer 1084* (ARIZ); at jct of Brawley Wash and AZ Hwy 289, Buenos Aires National Wildlife Refuge, 10 mi W of Arivaca, 34º45'N, 114º25'W, 29 Jul 1992 (fl, fr), *Ricketson 4686* (MO); W side of Tucson Mtns. near Tucson, 09 Aug 1927 (fl, fr), *Graham 8-9-12* (UC); Wilmot Road 10 mi SE of Tucson, 03 Oct 1938 (fl, fr), *Phillips 59* (ASC); 3 mi N of Ajo Way in Avra Valley, ½ mi W of Cortaro Rd, 08 Aug 1976 (fl), *Nabhan x-454* (ARIZ, ASC); W end of St. Catalina Mtns. near Tucson, 10 Aug 1938 (fl, fr), *Haverty & Hess 130* (ARIZ, ASC); Soldier's Wash, Santa Catalina Mountains, 15 Oct 1962 (fl), *Niering & Whittaker s.n.* (ARIZ); Santa Catalina Mountains, s.d. (fl), *Lemmon & Lemmon s.n.* (UC); Avra Valley, 30 mi W of Tucson, 23 Jul 1953 (fl, fr), *Parker & Nichols 8293* (ARIZ); near mouth of Baboquivari Canyon, 10 Jul 1931 (fl), *Peebles & Swingle 7922* (ARIZ); Papago Indian Reservation, 16 Jul 1938 (fl), *Goodding 6187* (ARIZ); Coyote Mts., 27 Aug 1959 (fl), *Goodding 197-61* (ARIZ); Papago Indian Reservation, yard of Juan Lorenzo Maristo, 31 Jul 1980 (fl), *Nabhan 323* (ARIZ); flats W of Tumamoc Hill, 30 Jul 1982 (fl), *Turner 82-10* (ARIZ); Buenos Aires National Wildlife Refuge, 22.0 mi S of Roble's Jct at Las Delicias Ranch road, 30 Jul 1988 (fl, fr), *McLaughlin 4802* (ARIZ); sandy flats W of Tumamoc Hill, Tucson, 111.0ºN, 32.2ºW, 05 Aug 1983 (fl), *Bowers 2702* (ARIZ, SD); wash 2 mi SE of Walls Well, near N end of Ajo Mts., 30 Aug 1945 (fr), *Gould & Haskell 3217* (ARIZ); 1 mi NE of Organ Pipe Cactus National Monument Boundary on Bates Well Road, E of Growler Mts., 01 Oct 1962 (fl), *Simmons s.n.* (ARIZ); wash near entrance to Organ Pipe National Monument, 08 Oct 1960 (fr), *Hevly & Drouet s.n.* (ARIZ); Organ Pipe Cactus National Monument, 4 mi W of jct of Puerto Blanco Drive & Hwy 85 on S Puerto Blanco Drive, 18 Sep 1988 (fl), *Wilson 198* (ARIZ); Organ Pipe Cactus

National Monument, ca. ¾ mi E of turnoff to Williams Spring, 25 Jul 1978 (fl), *Bowers, Mortensen, & Terhune 1387* (ARIZ); Tucson, Rillito, 19 Aug 1901 (fl, fr), *Thornber s.n.* (ARIZ); Sells, 9 Jul 1931 (fl), *Peebles 7915* (ARIZ); Mesas near Camp Lowell, 29 Jul 1881 (fl), *Pringle 13818* (MO, NY-2). PINAL CO., S Table Top Wilderness Access Road, 08 Aug 1999 (fl), *Mauz 99-85* (ARIZ); Southern Arizona, Camp Grant, 27 July 1867 (fl), *Palmer 155* (GH, MO); Sawtooth Mtns. 6 mi SE from Water tower at Chui Chu on State hwy 93 then along power line road 9 mi then S 0.5 mi to dirt tank, 24 Oct 1971 (fl), *Oxford 279* (ASU); ca. 1 mi E of Sacaton on Gila River flood plain, 18 Sep 1970 (fl, fr), *Pinkava et al. 17114* (ASU, DES); San Tan Mtns. Regional Park, ca. 0.5 mi W of northwest border of park, 14 Aug 2002 (fl), *Damrel et al. 1731-B* (ASU); San Tan Mountains, 0.2 mi W of Thompson Road along Phillips Road, E of San Tan Mountains Regional Park, 33º10'7.6"N, 111º37'20.5"W, 03 Sep 1008 (fl, fr), *Gutierrez 2159* (ASU-2, CANB, CTES, E, F, GH, K, MICH, MO, SP, UC, US, UTEP); Cooper Butte, E of Walnut Canyon, N of Gila River, 29 Jun 1982 (fl, fr), *Mittleman & Butterwick 70* (ARIZ, ASU, DES); 1.5 mi NE of Apache Junction, 04 Sep 1983 (fl), *Cordts s.n.* (DES); Granite Mountain N of Kelvin, 13 Sep 1990 (fl, fr), *Baker & Tress 8038* (ASU); 6 mi NE of Sacaton, 13 Jul 1962 (fl), *Hurd Jr. 102* (UC), near Sacaton, 30 Sep 1925 (fl), *Peebles, Harrison & Kearney 16* (ARIZ); Granite Hills, 20 Aug 1996 (fl), *Reina & Van Devender 96-353* (ARIZ); near Sacaton, 11 Aug 1926 (fl), *Loomis & Peebles 2725* (ARIZ); 10 mi S of Casa Grande, 31 Aug 1940 (fl, fr), *Kearney & Peebles 14921* (ARIZ); Cochran on Gila River S of entrance to Hohokam 'ballcourt' site, 06 Jun 1979 (fl), *Rea 108* (SD); wash behind Olberg trading post, 09 Apr 1985 (fr), *Rea 729* (SD). SANTA CRUZ CO., 2 mi from Pima County line along Tuscon-Nogales hwy, 30 Jul 1946 (fl, fr), *Gould & Robbins 3605* (ARIZ, GH, MO, NY, UC); along the Santa Cruz River Valley about 3 mi S of the Nogales-Patagonia Road, 30 Jul 1946 (fl, fr), *Gould & Robbins 3608* (ARIZ, NY, UC); Patagonia Mtns., 1.1 mi E of Sycamore Canyon and Italian Canyon intersection along FSR 61, 05 Sep 1987 (fr), *Hodgson et al. 4653* (DES), *Hodgson et al. 4654* (DES, NY); Santa Rita Mtns., along main road to Madera Canyon, 0.15 mi N of higway marker 6, 21 Jul 1990 (fl, fr), *Hodgson & Ramsden 5804* (DES); Tumacacori National Historic Park, Calabazas unit, E of Santa Cruz River, 31º27'9.9"N, 110º57'28.3"W, 25 Jul 2001 (fl, fr), *Guertin 317b* (ARIZ). YAVAPAI CO., Verde Mesa, 06 Aug 1866 (fl, fr), *Smart 1* (GH); Santa Maria River, 21 May 1979 (fl), *Parfitt, Butterwick & Hillyard 4930* (ASU); Black Canyon Highway, 07 Jun 1955 (fl), *Wien s.n.* (ASU); Route 71, 3 mi SE of jct with Route 93, 20 Sep 1969 (fl, fr), *McLeod, Keil & Pinkava 6333* (ASU, SD); Agua Fria River bottom at jct with Castle Hot Springs Road, 28 Sep 1969 (fl, fr), *Lehto 16487* (ASU, NY-2); along I-17 10 mi S of Camp Verde, 06 Aug 1993 (fl, fr), *Atwood 18854* (NY); Martinez Wash 1 mi E of Congress, 20 Jul 1978 (fl, fr), *Kepner s.n.* (DES); 0.45 mi N of Route 96 along dirt road to Yava, 33º30'00"N, 113º30'00"W, 28 May 1992 (fl), *Hodgson & Irish 6733* (DES); Agua Fria National Monument, N of Coldwater Guest Ranch, in a wide side wash/flood plain of the Agua Fria River, 34º6.219'N, 112º6.258'W, 28 Sep 2004 (fl, fr), *Damrel et al. 2665* (DES); Yava-Kirkland Wash, 27 Aug 1955 (fl, fr), *Wetherill s.n.* (MNA); 7 mi W of Congress Junction, 11 Aug 1961 (fl, fr), *McCormick s.n.* (MNA); sandy wash at Congress Junction, 11 Nov 1960 (fl, fr), *Hevly, Cameron, & Fischer s.n.* (ARIZ). YUMA CO., Barry Goldwater Air Force Range, Southwestern Copper Mtns., 3.7 km SSW of Coyote Peak, 5.4 km E of Coyote Wash, ca. 12 km NE of Raven Butte, 25 Oct 1993 (fl, fr), *Morrison & Schulz 475* (ASU); 1/4 mi N of McPhaul Bridge, 11 Sep 1967 (fl, fr), *Tate 1043* (ASU); ca. 1 km NE of north end of Mohawk Dunes at north boundary of Barry M. Goldwater Airforce Range, 32º41'71"N, 113º46'50.3"W, 24 Sep 1996 (fl, fr), *Felger & Turner 96-146* (ARIZ, ASU); Roll/Tacna area, S of I-8 near junction with Roll Road, 32º41'N, 114º01'W, 01 Sep 1989 (fl, fr), *Rea 1619* (ARIZ, ASU, SD); Indian Springs N of Salome, 15 Jul 1972 (fl, fr), *Engard & Weber s.n.* (DES); Barry M. Goldwater Military Range, Lechuguilla Valley, Camino del Diablo SE of Raven Butte, 32º23.379'N, 114º4.012'W, 25 Oct 2004 (fl, fr), *Felger & McCasland 04-18 (*ARIZ-2, ASU); along US Hwy 80 near entrance to Marine Corps Air Station, Yuma, 20 Sep 1963 (fl), *Barr 63-482* (ARIZ); ca. ½ mi W of Welton, May 1963 (fl), *Barr 63-242* (ARIZ); 10 mi NE of Yuma in wash along Hwy 95, 13 Nov 1960 (fr), *Hevly, Cameron, & Fischer s.n.* (ARIZ); Yuma, 03 Jul 1905 (fl), *Brown s.n.* (ARIZ); Mohawk Valley, 19 Aug 1996 (fl), *Turner 96-12* (ARIZ); Cabeza Prieta National Wildlife Refuge, Pinacate Lava on Camino del Diablo, 1 mi E of Namer's Grave, 32º06'N, 113º29'W, 15 Sep 1992 (fl), *Felger & Gierlach 92-767* (ARIZ); 6 mi N of Stone Cabin on Hwy 95, 18 Aug 1959 (fl), *Tries s.n.* (ARIZ); Kofa Game Range, Castle Dome Mts., Horse Tank, 18 Aug 1970 (fl), *Furlow 2* (ARIZ); sand dunes S of Airport Loop, 0.3 mi E of intersection with Ave A in Yuma, 32º40'N, 114º40'W, 07 Oct 1989 (fl, fr), *Pitzer & Ballmer 1450* (SD); Yuma Mesa, 10 Oct 1927 (fl, fr), *Peebles, Harrison & Kearney 4956* (ARIZ). –CALIFORNIA: Upper Southern California, s.d. (fl), *Le Conte s.n.*, (NY). IMPERIAL CO., 4 mi S of Palo Verde, 28 May 1941 (fl, fr), *Alexander & Kellogg 2249* (ASC, NY); Ogilby Rd (Hwy S34) where powerlines cross Hwy 1 mi S of Indian Pass Rd, 32º56'N, 114º50.9'W, 19 Oct 1997 (fl), *Pitzer 3323* (SD); Chocolate Mountains Aerial Gunnery Range, ca. 3 km SE of S end of Little Mule Mtns., 1 km W of Dietz Rd., 26 Sep 1989 (fr), *Sanders 9515* (SD). RIVERSIDE

CO., 15 mi W of Blythe, 22 Nov 1951 (fl, fr), *Dressler 1194* (GH); near Red Rock gas station between Desert Center and Blythe, Sep 1931 (fl, fr), *Hutchinson 6882* (NO); Chuckwalla Mtns, 04 Nov 1937 (fl), Rowntree 222 (TEX). SAN BERNARDINO CO., Vallecito, June 1882 (st), *Parish & Parish 1400* (GH); Chemehuevi Valley, road from I-40 to Whipple Mts., passing along W slope of Sacramento Mts., ca 18.5 mi S of I-40, 34º30.6'N, 114º34.7'W, 10 Oct 1997 (fl), *Wear & Moorhatch s.n.* (BRIT). SAN DIEGO CO., N of Sweeney Pass, S of Carrizo Gorge, SH S2, 18 Aug 1984 (fl, fr), *Jonsson & Clemons 873* (SD); Vallecito, 2 Sep 1934 (fl), *Harbison 4749* (SD); Vallecito, 03 Sep 1934 (fl), *Harbison 4750* (SD); E of June Wash, 01 Nov 1987 (fl), *Clemons & Jonsson 1887* (SD); San Felipe Valley, W side of S-2, S of Agua Caliente, 32º57'02''N, 117º17'17''W, 14 Sep 2003 (fl), *Barth s.n.* (SD); W of Vallecito Stage Station County Park, 24 Sep 1986 (fl, fr), *Clemons & Jonsson 1548* (SD). –NEW MEXICO: no collection data, 1851 (fl), *Wright 1448* (GH-3, K, MO, NY, TCD). DOÑA ANA CO., 5.7 mi N of Santa Teresa, 13 Aug 1991, *Hutchins 13142* (UNM); Straus Station, 31º52'N, 106º42'W, 16 Aug 1972 (fl, fr), *Chiang, Wendt, & Johnston 8618* (LL); 14 mi W of Santa Teresa, 13 Aug 1991, *Hutchins 13144* (UNM); ca. 1 mi N of Anthony along I-10 at roadside rest area, 32º00'N, 106º36'W, 17 Jul 1977 (fl), *Lehto et al. L21478* (ASU); Las Cruces, 23 Jun 1897 (fl, fr), *Wooton 58* (E, GH, MO, NY-2, UC); Mesilla Valley, 26 Jul 1895 (fl), *Wooton s.n.* (ARIZ, UC); along NM 273 at entrance to Memory Gardens of the Valley Cemetery, 27 Aug 1978 (fl, fr), *Worthington 3219* (UTEP); NW Anapra, 08 Aug 1974 (fl), *Crouch 16* (UTEP); Anapra Study area, high river terrace S of town along US-Mexico Boundary, 06 Sep 1971 (fl), *Worthington s.n.* (UTEP); 3 mi N of Santa Teresa Golf Course, 0.25 mi W of Southern Pacific railroad tracks, 07 Sep 1979 (fl, fr), *Cordova 23* (UTEP); Potrillo Mts., West Potrillo

Mts., S side of Guzman's Lookout Mtn., 23 Aug 1986 (fl, fr), *Worthington 14738* (UTEP); 3 mi E of Afton, 14 Aug 1930 (fl, fr), *Fosberg S3421* (UTEP); Mesilla Valley, Mesilla, 20 May 1906 (fl), *Standley s.n.* (MO); edge of terrace SW of Pyramid Peak, 01 Aug 1930 (fl), *Fosberg S3576* (MO); Jornada Range Reserve, 25 mi N of Las Cruces, between headquarters and Middle Well, 24 Jul 1929 (fl, fr), *Hellison 762* (K); 8 mi W of Hatch, 28 Jul 1938 (fl, fr), *Shreve 8228* (ARIZ). LUNA CO., Deming, 31 Aug 1895 (fl, fr), *Mulford 1126* (MO, NY); edge of West Potrillo Mts., 15.7 mi E of Columbus, 06 Sep 1997 (fl), *Worthington 27062* (ARIZ, UTEP); Potrillo Mts., West Potrillo Mts., W rim of mtns along Columbus to El Paso road, 29 Aug 1993 (fl), *Worthington 22353* (VDB); Florida Mts., along road to Mahoney Park 0.5 mi W of gate, 9 Sep 1978 (fl), *Worthington 3344* (UTEP); 1.4 mi W of Monument 18 and 30 m N of US/MX border, 01 Aug 1996, *Sivinski & McIntosh 3391* (UNM). –TEXAS: no collection data, s.d. (fl, fr), *LeRoy s.n.* (NY); Western Texas to El Paso, May-Oct 1849 (fl, fr), *Wright 429* (TCD). CULBERSON CO., N of Van Horn on hwy 54, 19 Jul 1988 (fl, fr), *Higgins 17857* (NY); 18 mi E of Van Horn along I-10, 19 Jul 1988 (fl), *Higgins 17877* (NY); 18 mi NE of Van Horn, 10 Sept 1965 (fl, fr), *Correll 31638* (NY); 17 mi NE of Van Horn, 10 July 1943 (fl), *Waterfall 4978* (GH, MO, NY, SMU); Van Horn flats, 10 July 1900 (fl, fr), *Eggert s.n.*, (GH); 13 mi E of Van Horn, 21 Aug 1942 (st), *Waterfall 4172* (ARIZ, GH); near Van Horn, 18 Jun 1905 (fl), *Reverchon 2900* (MO); on road 54 N of Van Horn, 13 Jun 1958 (fr), *Gentry & Gentry 2807* (BRIT). EL PASO CO., El Paso, 11 Sep 1885 (fl, fr), *Jones 4205* (ARIZ, NY, UC); El Paso, mesa along river, 21 June 1921 (fl), *Ferris & Duncan 2378* (MO, NY); ca. 20 mi E of El Paso on Rte 62, 3 Jul 1958 (fl), *Correll & Johnston 19218* (NY); dunes near foothills of Hueco Mtns. 17 mi E of El Paso, 16 Aug 1942 (fl, fr), *Waterfall 3901* (ARIZ, GH); near El Paso, 31 July 1957 (fl, fr), *Knobloch 191* (UTEP); Buford Rd. near Freeway intersection going up to Horizon City, 10 Oct 1966 (fl, fr), *Armendariz R-13* (UTEP); right-of-way at jct between I-10 W and FM 793 (Fabens exit 49) at NW corner next to the on-ramp for I-10 W, 12 Jul 2001 (fl), *Gutierrrez s.n.* (UTEP); 0.8 mi NE of I-10 along FM 1989 (Fabens Exit 49), 13 Aug 2003 (fl), *Gutierrez 202* (ASU); 2.8 mi N jct. I-10 and Mesa, 31º52'106"N, 106º34'30"W, 19 Aug 1978 (fl), *Worthington 3159* (UTEP); Northgate Archaeological Site, N side of Diana St. W of Dyer, 31º53'N, 106º26'W, 27 Jun 1977 (st), *Diaz 9* (UTEP); Hueco Mtns., first hill encountered S of hwy 62-180 traveling E from El Paso, 31º49'12"N, 106º7'11"W, 19 Aug 1979 (fl), *Worthington 5032* (UTEP); along Carlsbad Hwy ca, 16 mi E of El Paso, 28 Jul 1952 (fl), *Warnock 10907* (SMU); I-10 at Clint turnoff ca. 18 mi E of El Paso, 11 Aug 1975 (fr), *Pinkava & Reeves P13001* (ASU); Horizon City exit on I-10 SE of El Paso, 13 Aug 1971 (fl, fr), *McGill & Keil 7660* (ASU); Fabens cutoff, Fall 1969 (fl, fr), *Kretzschmar 50* (UTEP); Ft. Bliss power station waste pond, 31º52'38"N, 106º23'21"W, 12 Jul 1975 (fl), *Mraz & Hiers 1* (UTEP); ca. 3 mi NE of I-10 along FM 1989, 31º32'10.9'N, 106º06'04.4"W, 06 Sep 2005 (fl, fr), *Gutierrez & Gutierrez 1132* (ASU, CAS, UTEP, WTS); Tornillo, Tornillo High School, ca. 500 m W of Baseball Field, 31º27.78'N, 106º5.39'W, 21 Aug 2005 (fl, fr), *Gutierrez & Gutierrez 1097* (ASU, CS, MSC, MEXU); ca. 1 mi S of I-10 along road to Tornillo, 31º27'20"N, 106º04'19.2"W, 21 Sep 2006 (fr), *Gutierrez 1252* (ASU); 0.8 mi NE of I-10 along FM 1989, 13 Aug 2003 (fl), *Gutierrez 202* (ASU); ca. 1.5 mi NE of I-10 along Cattleman's Road (FM 1989), 31º31'53.9"N, 106º6'42.5"W, 21 Sep 2006 (fl, fr), *Gutierrez & Gutierrez 1300* (ASU, UTEP); ca. 1.0 mi E of Hudspeth County line on N side of TX Hwy 20, 31º24'10"N, 106º1'10"W, 14 Aug 2004 (fl), *Gutierrez & Gutierrez 894* (ASU); ca 15 mi SE of El Paso along I-10, 31º40'N, 106º15'W, 05 Sep 1984 (fl, fr), *Bowers et al. 2901* (ARIZ). HUDSPETH CO., ca. 2 mi E of Esperanza, ca. 3 mi W of jct between FM 192 and FM 34, 19 May 2002 (fl), *Gutierrez 32* (UTEP); near McNary, 12 Jul 1943 (fl), *Waterfall 5032* (GH); 32 mi W of Sierra Blanca along Hwy 62 on Pipeline road, 26 Jul 1946 (fl), *Tharp 46135* (K, UC, VDB); Esperanza, ca. 4 mi E of FN 2217, ca. 2 mi W of FM34 along FM 192, 31º09'04"N, 105º41'19"W, 14 Aug 2004 (fl, fr), *Gutierrez & Gutierrez 900* (ASU); 4 mi S of McNary, 10 Sep 1961 (fl, fr), *Fischer 1002* (ARIZ, ASC); Arroyo Diablo E of McNary, 07 Sep 1947 (fl), *Warnock 7327* (ARIZ, SMU); 0.8 mi NE of FM 192 along TX Hwy 20, 31º15'15.7"N, 105º48'08.1"W, 18 Sep 2008 (fl, fr), *Gutierrez 2188* (ASU, E, K, UC, UTEP); 0.3 mi SW of McNary (TX Hwy 20) along FM 192, 31º14'20.4"W, 105º47'48.4"W, 18 Sep 2008 (fl, fr), *Gutierrez 2187* (ASC, ASU, UTEP). PRESIDIO CO., along Cibolo Creek at Presidio, 27 Sep 1937 (fl), *Warnock T97* (ARIZ, GH); near Rio Grande at W end of county, 25 Oct 1941 (fl), *Hinckley 2234* (ARIZ, GH); ca. 1 mi N of Porvenir at mouth of Musgrave Canyon, 02 June 1941 (fl), *Hinckley 1552* (NY-2, SMU); Presidio, 09 Aug 1900 (fl, fr), *Trelease 343* (MO-2).

This is the only perennial and the only yellow-flowered species in *Proboscidea*, and the only species to have any enlarged root. The flowers appear very similar to those of *Ibicella*, but are two to three times larger in size, have calyces of united sepals, and the fruits lack the spiny projections seen on the fruits of *Ibicella*. Even though *Ibicella* has been introduced as a weed to the United States, it has not been found growing in the native range of *P. althaeifolia*.

Over most of its range, *P. althaeifolia* tends to grow during the summer monsoon season. On the peninsula of Baja California, it can flower year round. Its growth here is probably dependent on the presence of moisture that is provided by winter precipitation and the lack of freezing temperatures that can kill this frost-tender perennial.

Van Eseltine (1929) considered *P. arenaria*, *P. althaeifolia*, and *P. peruviana* to be separate species, distinguishable on the basis of leaf, corolla, calyx, and bracteole morphologies. He placed these three species, along with *P. confusa*, in *Proboscidea* subgenus *Dissolophia* Van Eseltine. The distribution of characters varies continuously across *P. althaeifolia* and *P. arenaria*, and the morphological variation in *P. peruviana* falls within this range. Thus, Bretting (1981) considered *P. peruviana* and *P. arenaria* synonyms of *P. althaeifolia*. Given that the placement of representatives of *P. althaeifolia* and *P. arenaria* as sister to each other is resolved by molecular analyses(Figs. 9, 11, 12, 14), the three names (*P. althaeifolia*, *P. arenaria*, and *P. peruviana*) are kept as synonyms, with *P. althaeifolia* having priority. DNA samples were taken from Peruvian specimens, but none of them amplified successfully. Future studies should focus on including Peruvian samples of *P. althaeifolia* to see what phylogenetic relationships are reconstructed.

There is a bagged specimen in the Gray Herbarium containing an immature fruit that has the same collector and collection number of the type of *Martynia palmeri* (*Palmer 599*). This was collected from the vicinity of Durango and has been identified as *P. fragrans*. The identical number may be due to human error, and the type material is easily distinguished on the basis of the other information provided on the labels. There also exists another of Palmer's specimens at UC with the collection number

559, identified as *P. fragrans*, and it may be possible that this is from the same collection as the bagged specimen at GH. A second bagged specimen at GH, also *Palmer 599*, contains a tuber and was collected near Guaymas. This should be regarded as part of the type material.

8. Proboscidea fragrans (Lindl.) Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 326. 1865.

Martynia fragrans Lindl., Bot. Reg. 26: 85. (Misc. Item #206). 1840. *Proboscidea louisianica* (Mill.) Thell. ssp. *fragrans* (Lindl.) Bretting, Southw. Naturalist 28: 448. 1985. –TYPE: MEXICO. Hidalgo: in the vicinity of the Real del Monte mines, *Lindley s.n.* (holotype: CGE [photo at ASU!]).

Martynia violacea Engelm., Wisliz. Mem. Tour N. Mex. 101. 1848. *Proboscidea violacea* (Engelm.) Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 325. 1865. –TYPE: MEXICO. Chihuahua: near Lake Encinillas, north of Chihuahua, *Wislizenius 145* (holotype MO).

Description. Annual. Roots taprooted. Stems decumbent. Leaves opposite to sub-opposite; petiole to 30 cm long; lamina broadly ovate to reniform; apex rounded, obtuse; base cordate or truncate, and equilateral to inequilateral; margins entire to 5-lobed, sinuate-undulate. Inflorescences many-flowered and surpassing the foliage; peduncles to 70 cm long; bracts oblanceolate to obovate. Flowers fragrant, 30-40 per inflorescence; pedicels to 1.8-4 cm long; bracteoles oblanceolate to obovate; calyx 14 to 20 mm long, sepals free for 40%-70% of their length; corolla to 40 mm in length, pale to dark maroon, with yellow, orange, or magenta specks on interior surface and yellow abaxial nectar glands, with a dark purple splotches on each adaxial lobe. Fruit endocarp dark brown or dark gray, oblong-ellipsoid, slightly compressed, the body to 8 cm long and crested adaxially, the rostrum to 18 cm long. Seeds dark gray to black, 7-9 mm long, 4-6 mm wide, rhomboid to ovoid. 2n=30.

Phenology. Flowers from May to November in the United States and Mexico. In Australia, it has been collected in flower in March.

Distribution and habitat (Fig. 29). Disturbed soils in Mexico, southwestern United States (New Mexico and Texas). Naturalized in Australia. 1000-2700 m (3000-6000 ft).

Vernacular Names. Toritos, Cuernito, Cuernitos de Buey

SPECIMENS EXAMINED. **AUSTRALIA**. NEW SOUTH WALES: 9.7 km NNW of Inverell on road to Gramon, 29º43'30"S, 151º05'E, 27 Mar 1987 (fl, fr), *Coveny et al. 12502* (MO).

BRAZIL. RIO GRANDE DO SUL: Porto Alegre, Nov 1897 (fl), *Reineck s.n.* (GH, provenance doubtful).

MEXICO. Cerro de San Cristobal, Valle de Mexico, 02 Jul 1950 (fl), *Matuda 18827* (F, UC); no locality given, s.d. (fl), *Coulter 1325* (TCD); San Andres, 22 Aug 1900 (fl), *Trelease 344* (MO). –CHIHUAHUA: Sierra del Nido complex, 1.3 mi E of Bella Vista, 29º02'N, 106º23'W, 07 Sep 1981 (fl, fr), *Worthington 7738* (UTEP); 2.5 mi NW of Ciudad Camargo, 27º43'N, 105º11'W, 21 Jul 1977 (fl, fr), *Lehto et al. L21647* (ASU); 3.3 mi S of Jimenez on Mex Hwy 49, 25 Aug 1971 (fl), *McGill & Keil 8231* (ASU, DES); 3 mi N of Cd. Jiménez along road to Cd. Camargo, 01 Aug 1939 (fl), *White 2163* (GH); road from Guimbalete W to S end of the Sierra del Diablo, 1 km

NE of Santa Fe, 14 Sep 1942 (fl, fr), *Stewart & Santos 2598* (GH); 37 km NW of Jaco, along road to Victoria, via Temporales de Honorato, 28º00'N, 06 Jul 1941 (fl), *Stewart 688* (GH); at Papalote Las Juntas (Presón de Anteojos) 2 km W of Hacienda El Berrendo on Las Pampas Ranch, 27º21'N, 104º40'W, 25 Aug 1972 (fl), *Chiang C. et al. 8863* (MO); at Papalote Las Juntas (Presón de Anteojos) 2 km W of Hacienda El Berrendo on Las Pampas Ranch, 27º21'N, 104º40'W, 25 Aug 1972 (fl, fr), *Chiang C. et al. 8875* (NY); 19.7 mi E of General Trias on Rte 16, 21 Aug 1979 (fl, fr), *Wagner & Solomon 4354* (MO); valley near Chihuahua, Sep 1886 (fl, fr), *Pringle 1035* (MO, NY-2); Meoqui, 06 Aug 1936 (fl), *LeSueur 33* (UC); Meoqui, 24-30 Aug 1935 (fl), *LeSueur 33* (SMU); Santa Eulalia plains, 06 Aug 1885 (fl), *Wilkinson s.n.* (UC); 20 mi N of Chihuahua, 13 Aug 1961 (fl), *Hevly & Hevly 2265* (ASC); 14 mi NE of Parral, 10 Aug 1961 (fl), *Waterfall 16116* (SMU); km 50 along Chihuahua-Cuauhtémoc hwy, 25 Aug 1995 (fl, fr), *Yen & Estrada 4639* (BRIT-2); 24 km W of Ciudad Chihuahua along hwy to Cuauhtémoc, 11 Aug 1996 (fl), *Yen & Estrada 5303* (BRIT); Guachochic, Basíguare, near Creel-Guachochic road, 11 Oct 1975 (fl), *Bye 7066* (GH). –COAHUILA: 56.6 mi N of Acatita, 0.4 mi E of Rancho El Cinco, 22 Aug 1971 (fl), *McGill & Keil 8099* (ASU); road to Rancho Mesquite, 1.2 mi W of jct with road to Cuatro Cienegas N to Ocampo, 13 Aug 1975 (fl, fr), *Pinkava & Reeves P13018* (ASU, SD); near Mesillas N of Saltillo, 1848-9 (fl, fr), *Gregg 451* (GH-2, MO); 2 km E of Castillon, 28º15'N, 17 Jul 1941 (fl, fr), *Stewart 566* (GH); Valleys NE of Sierra del Pino, 12 km W of San Guillermo, 20 Sep 1941 (fl, fr), *Stewart 1763* (GH); road from Guimbalete SE to Acatita via Laguna del Rey, 2 km SE of Noria de San Juan, 18 Sep 1942 (fl), *Stewart 2659* (GH); Monclova, 20 Jul 1939 (fl, fr), *Marsh 1827* (GH, SMU); 1.3 mi W of Paila, 25º38'N, 102º10'W, 07 Nov 1957 (fl), *Moran 6270* (SD); Ocampo, Rancho El Barranquito, 50 km from Ocampo toward Sierra Mojada, 27º15'N, 102º41'W, 02 Oct 1990 (fl, fr), *Carranza & Carranza 579* (ASU); W from highway 57 ca 75 mi N of Saltillo, 11 Jul 1982 (fl, fr), *Hodgson & Engard H1815* (DES). – DURANGO: Durango, 01 Aug 1898 (fl), *Nelson 4609* (GH, K); city of Durango and vicinity, Apr-Nov 1896 (fl, fr), *Palmer 905* (E-2, MO-2, NY, UC); city of Durango and vicinity, Apr-Nov 1896 (fl, fr), *Palmer 329* (E, GH [bagged specimen], K, MO-2, NY, UC); city of Durango and vicinity, Apr-Nov 1896 (fl), *Palmer 559* (UC); city of Durango and vicinity, Apr-Nov 1896 (fr), *Palmer 599* (GH [1 bagged specimen]); city of Durango and vicinity, Apr-Nov 1896 (fr), *Palmer 906* (GH [1 bagged specimen]); 51 mi S of La Zarca, 14 Aug 1961 (fl, fr), *Hevly & Hevly 2289* (ASC); 3.5 km W of La Soledad, 11 km NW of Santiago Papasquiaro, 25º05'N, 105º32'W, 22 Aug 1983 (fl), *Worthington 11229 & Corral Diaz 485* (MO, UTEP). –GUANAJUATO: Jacal, 20 Aug 1887 (fl), *Schumann 1027* (GH); 10 mi SE of Leon, 16 Aug 1961 (fl), *Hevly & Hevly 2347* (ASU); 12 mi SE of Leon, 16 Aug 1961 (fl, fr), *Hevly & Hevly 2348* (ASC); 15 mi E of Salamanca, 16 Aug 1961 (fl), *Hevly & Hevly 2349* (ASC); between Dolores Hidalgo and city of Guanajuato, 21º00'N, 100º30'W, Jul 1956 (fl, fr), *Coon 114* (GH); vicinity of Guanajuato, 06 Aug 1947 (fl), *Kenoyer 1741* (GH); Guanajuato, 1880 (fl), *Dugès s.n.* (GH), vicinity of Guanajuato, 1897 (fl), *Dugès 116* (GH); Guanajuato, 1895 (fl), *Dugès s.n.* (GH); 12.1 mi N of southern state line along Hwy 57, 22 Aug 1972 (fr), *Dunn et al. 10532* (MO); between San Miguel de Allende & Dolores Hidalgo along Hwy 51, 23 Jun 1971 (fl), *Genelle & Fleming 832* (MO); San Miguel de Allende, 26 Jul 1950 (fl, fr), *Spivey 154* (UC); 34 mi N of Queretaro, 23 Aug 1961 (fl), *Waterfall 16550* (SMU); Abasola, 4 km ESE of Saucillo, 19 Aug 1989, *Galvan & Galvan 3315* (ASU, MO); Cortazar, Canada de Caracheo, 08 Aug 1985 (fl, fr), *Rosas 18* (ASU); 3 km SW of Purísima de Bustos, 20 Jul 1986 (fl), Ga*lván & Galván 1877* (MO). –<u>HIDALGO</u>: vicinity of Zimapán, 22 Jun 1947 (fl), *Kenoyer 1006* (GH); 6 mi N of Ixmiquilpan, 01 Jul 1950 (fl), *Dressler 1172* (MO); 1 km E of Actopan, 13 Sep 1970 (fr), *Diaz M. 139* (NY); Dublán, Aug 1905 (fl, fr), R*ose et al. 9501* (NY-2); 4 mi S of Zimapan, 21 Aug 1961 (fl, fr), *Hevly & Hevly 2458* (ASC); Ajacuba, 2 km E of Tulancalco, 24 Jun 1981 (fl), *Hernández M. et al. 6164* (MO); Poblado Emiliano Zapata, 19 km E of Ajacuba toward San Agustín Tlaxiaca, 20º09'45''N, 99º01'45''W, 22 Aug 1988 (fl), *Díaz V. 71* (ARIZ); N of Emiliano Zapata, S of the Sierra de Chicavasco, 20º09'44''N, 99º01'30''W, 02 Jun 1989 (fl), *Díaz V. 497* (ARIZ); Jacala, 29 Jun 1939 (fl), *Chase 7210* (GH); ca 2 mi W of Jacala off Hwy 85, 17 Aug 1975 (fl, fr), *Dunn & LeDoux 22037* (MO); Portezuelo, 8 km S of Tasquillo, 03 Oct 1980 (fl), *Hernández M. & Rodríguez B. 4983* (MO); Tasquillo, at km 180 on the Mexico-Laredo hwy S of the Río Tula bridge, 08 Oct 1943 (fl, fr), *Gilly & Camp 22* (NY); along MEX 45, 2 km SE of MEX 85, 9 km W of Ixmiquilpan, 20º29'N, 99º19'W, 22 Jul 1982 (fl, fr), *Nee & Diggs 25236* (BRIT); Tasquillo, 01 Jul 1940 (fl), *Booth 16318* (SMU). –<u>JALISCO</u>: Lago Chapala, S & E of Guadalajara on hwy 15 toward Jiquilpan at km 104, 21 Jul 1971 (fl, fr), *Gibson & Gibson 2258* (ASU); 56 mi SE of Guadalajara, 21 Aug 1953 (fl, fr), *Manning & Manning 531210* (GH); ca. 18 mi W of Tuxcueca (SW of Lago Chapala), 26 Jun 1950 (fl, fr), *Dressler 1152* (MO); San Bartolito above Rio Verde on the Yahualica to Guadalajara Road, 1 Jul 1947 (fl, fr), *Sauer 1044* (UC); 16 mi E of Ojuelos de Jalisco, 10 Sep 1960 (fl, fr), *Templeton 8767* (MICH). –<u>MEXICO</u>: Cerro Ahumada, near Rancho Neuvo, 4 km N of Huehuetoca, 11 Aug 1971 (fl), *Rzedowski 28419* (ASU); San Andrés Chiautla, Tepetitlan, 29 Sep 1984 (fl), *Ventura A. 4290* (NY). –<u>MICHOACÁN</u>: Vicinity of Morelia, Punguato, 16 Jul 1909 (fl), *Arsène 2903* (E, GH, MO, NY); along hwy S of Tuxpan, km 190-191 towards Zitacuaro, 23 Jul 1948 (fl), *Moore & Wood 4062* (A); near Morelia, 14 Jul 1941 (fl), *Schery 94* (MO); slopes of Cerro Potrerillos, ca. 5 mi N of Cotija & 22 mi S of Jiquilpan, 05-09 Oct 1961 (fl, fr), *Soderstrom & King 4672* (NY, SMU, UC); Francisco J. Mújica, 9 km NE of Morelia, 10 Aug 1984 (fl), *Soto N. & Román de Soto 6556* (E); 57 mi NW of Zamora near Lake Chapala, 26 Aug 1961 (fl), *Hevly & Hevly 2510* (ASC); along MEX 15 at Los Ejidos, 17 Aug 1966 (fl, fr), *Kral 27678* (VDB-2); Charo, Cerro del Mesquital, 03 Sep 1991 (fr), *Escobedo 2110* (F); between Zitacuaro and San Jose Purua, 21 Jul 1938 (fl, fr), *Hinton 13046* (GH, K, MO, NY, UC). –NUEVO LEON: ca. 24 mi NE of Saltillo along road to Monterrey, 05 Jul 1963 (fl), *Gentry et al. 20015* (ARIZ); 2 mi NW of Monterrey, 15 Nov 1958 (fl, fr), *Rollins & Tryon 5820* (GH-2); Monterrey, Huasteca Canyon, 19 Sep 1937 (fl), *Kenoyer s.n.* (MO); 10 mi W of Monterrey, 07 Jul 1941 (fl), *Schery 20* (MO); 2 km from Icamole toward Villa Garcia, 25°55'N, 100°42'W, *Johnston et al. 11604* (NY). –QUERETARO: 14 mi N of Queretaro, 23 Dec 1970 (fr), *Dunn et al. 17042* (MO); 0.25 mi NW of San Juan del Rio, 10 Aug 1961 (fl), *Cutler 12075* (MO); Queretaro, 1910-1913 (fl), *Aquiel 10399* (MO); Queretaro, Jul 1904 (fl, fr), *Kuntze 23429* (NY-6); Cadereyta, 27 Jul 1952 (fl, fr), *Kelly 705* (UC); near Cerro de la Mesa, ca. 3 mi N of Tequisquiapan, 30 Aug 1965 (fl), *Strother 518* (SMU). –SAN LUIS POTOSI: Cardenas, Nov 1910 (fr), *Orcutt 6944* (ARIZ); Sierra Madre Oriental, 3 km E of Ciudad del Maiz on hwy 80 at km 259, 22°25'N, 99°30'W, 02 Oct 1965 (fl, fr), *Roe & Roe 2349* (F); near city of San Luis Potosí, 1876 (fl, fr), *Schaffner 747* (GH, K); 4 mi E of Ciudad del Maiz, 23 Jul 1953 (fl, fr), *Manning & Manning 53558* (GH); vicinity of San Luis Potosí, 22°N, 1878 (fl), *Parry & Palmer 697* (GH, K, MO, NY); 10-20 mi E of Cd. del Maiz, 23 Jul 1953 (fl), *Manning & Manning 53485* (GH); 5 km S of

Matehuala, 15 Jul 1975 (fl), *Medrano et al. 8122* (MO); 10 mi N of San Luis Potosi, 24 Jul 1958 (fl), *Straw & Forman 1416* (UC); 118 mi N of San Luis Potosi, 17 Aug 1961 (fl), *Hevly & Hevly 2369* (ASC); 6.5 km WNW of Villa de Reyes on road to Bledos, 38 km S of San Luis Potosí, 21°50'N, 100°59'W, 23 Jun 1982 (fl), *Nee & Diggs 24582* (SMU). –TAMAULIPAS: Palmillas, 17 Sep 1942 (fl), *Martinez s.n.* (A); Vicinity of Victoria, 01 May-13 Jun 1907 (fl, fr), *Palmer 455* (GH); E side of Sierra Madre 17 mi SW of Ciudad Victoria, 08 Sep 1978 (fl), *D'Arcy 11847* (MO); Rancho Koronado, 45 km SE of Nuevo Laredo, 09 Nov 1962 (fl, fr), *Casso 4* (SMU). –VERACRUZ: Santiago, 21 Jul 1971 (fl), *Nevling & Gomez-Pompa 1915* (GH). –ZACATECAS: no locality given, s.d. (fl, fr), *Coulter 1326* (GH, TCD); ca. 60 mi SW of Saltillo on Mexico Hwy 54 to Zacatecas, 01 Aug 1975 (fl), *Engard & Gentry 669* (ASU, DES); near El Sauz, 23 Jun 1950 (fl, fr), *Dressler 1134* (GH, MO, NY, SMU); 3 mi N of Fresnillo, 13 Aug 1961 (fl, fr), *Cutler 12091* (MO); 5 mi N of Fresnillo, 15 Aug 1961 (fl), *Hevly & Hevly 2326* (ASC); Mex Hwy 45 bridge over Río Totonilco, 5 km SW of Saín Alto, 25 Jul 1982 (fl, fr), *Diggs & Nee 2993* (SMU).

U.S.A. NEW MEXICO: EDDY CO., Blue Springs near White City, 04 Aug 1967 (fl), *Pinkava 3146* (ASU). –TEXAS: Western Texas to El Paso, May-Oct 1849 (fl, fr), *Wright 429* (GH-2, K, NY, TCD). BREWSTER CO., Chisos Mountains, Lower Green Gulch and the floodplains of the Rio Grande at Johnson Ranch, 05 Sep 1937 (fl, fr), *Marsh 338* (GH, UC); 3.75 mi N of Alpine, 31 Aug 1938 (fl, fr), *Cory 29868* (NY); Boquillas, 19 Oct 1939 (fl), *Jones s.n.* (GH); Alpine Creek, 6.75 mi W of Alpine, 18 May 1946 (fl), *Cory 53198* (NY, SMU); near Fern Canyon N of Alpine, May 1932 (fl), *Striger 1265* (NY); ca. 10 mi S of Alpine, 17 Jul 1952 (fl), *Warnock 10729* (SMU); Terlingua Ranch Estates, ca. 70 mi S of Alpine, then ca. 8 mi E of main hwy on dirt road to Terlingua lodge, 29°32'N, 103°26'W, 19 Jul 1999 (fl), *Turner & Turner 99-483* (TEX). CULBERSON CO., Hwy 54 N of Van Horn, 31°17.269'N, 104°50.184'W, 31 Jul 2003 (fl), *Damrel 1921b* (ASU, DES); W of Van Horn, 22 Jun 1928 (fl), *Cory 2447* (GH); near foot of Sierra Diablos 23 mi N of Van Horn, 20 Jul 1943 (fl, fr), *Waterfall 5170* (GH, MO, NY); flats near Van Horn, 09 Jul 1900 (fl), *Eggert s.n.* (GH, MO); 4 mi W of Van Horn, 19 Aug 1942 (fl), *Waterfall 4070* (MO); ca 26 mi NE of Van Horn, Apache Mountains, 10 Sep 1965 (fl, fr), *Correll 31645* (NY); Hurd's Draw, 10 Jun 1949 (fl), *Janszen 52* (NY); Wallace Ranch, 10 mi S of hwy, 23 Aug 1947 (fl), *Scholl 35* (SMU). HUDSPETH CO., along Green River Road 3 mi N of turnoff to Taylor Ranch, 7.2 mi S of Scott's RR Crossing, 30°51'35"N, 104o55'58"W, 17 Sep 1988 (fl, fr), *Lieb & Anderson 1015* (UTEP). JEFF DAVIS CO., foothills of the Davis Mts. at the jct of Farm Road 505 with Texas Rte 166, 14 Aug 1971 (fl), *McGill & Keil 7697* (ASU); Davis Mts. Resort, Limpia Canyon, McGuire Ranch Site, 30°37'45"N, 104°05'30"W, 11 Jun 1977 (fl), *Worthington s.n.* (UTEP); Davis Mts., 30 Aug 1914 (fl, fr), *Young s.n.* (MO); Loop 118, ca. 1.8 km W of Fort Davis, 30°40'N, 103°59'W, 11 Sep 1994 (fl, fr), *Atha & Ide 592* (NY); ca. 0.5 mi NE of Bloys Campground, 26 Jul 1944 (fl), *Hinckley 3182* (NY); near Fort Davis along Limpia Creek, 11 Jun 1928 (fl), *Palmer 34480* (NY); Davis Mts., 8.5 mi E of FM 505 along TX Hwy 118, 30°32'44"N, 104°08'32"W, 08 Aug 2004 (fl, fr), *Gutierrez & Gutierrez 873* (ASU, HUEFS, UTEP); 1.8 mi SW of TX Hwy 118 along FM 505, 30°32'39"N, 104°17'55"W, 08 Aug 2004 (fl), *Gutierrez & Gutierrez 883* (ASU); on Road 118 ca. 40 mi W of Ft. Davis, 13 Oct 1960 (fl), *Gentry & Bingham 3287* (BRIT); Limpia Canyon, Davis Mts., 1 mi above Ft. Davis, 04 Jul 1948 (fl), *Warnock 7954* (SMU); near Bloys Campground W of Ft. Davis, 30 Jul 1983 (fl), *Rowell 16738* (BRIT); Limpia Canyon, Davis Mts., 20 Mar

1934 (fr), *Ferguson & Ottley 5654* (NY). PRESIDIO CO., 1 mi NW of Saucedo Ranch House (park headquarters), 29º28'N, 103º53'15"W, 25 Sep 1993 (fl, fr), *Worthington 22667* (UTEP); 4.1 mi E of entrance to Ft. Leaton State Historical Site, 0.1 mi E of Casa Piedra Road along hwy 170, 25 Sep 2001 (fl, fr), *Gutierrez s.n.* (UTEP); Marfa, Jul 1936 (fl), *Hinckley 679* (NY-2, SMU); Marfa, 18 Sep 1920 (fl, fr), *Eggleston 17353* (NY); ca. 6 mi E of Presidio along TX Hwy 170, 29º30'59.3"N, 104º15'46.4"W, 02 Sep 2005 (fl), *Gutierrez & Gutierrez 1108* (ASU, CTES, MBM, UTEP); ca. 4.5 mi E of Presidio along TX Hwy 170, 29º31'19"N, 104º16'14.1"W, 02 Sep 2005 (fl, fr), *Gutierrez & Gutierrez 1126* (ASU, DES, UTEP).

Cultivated. *Blake 6459* (UC, fl); *Dressler 1152* (MO, fl); *Hartling 32430* (NY, fl, fr); *James 2873* (E, fl); *Lape 4* (A, fl); *Miller 6398* (MO, fl, fr); *Nash 922* (NY, fl), *Nash s.n.* (NY, fl); *Taylor 119* (GH, MO, NY-2, fl, fr); *Tucker s.n.* (NY, fl, fr).

This taxon has been accepted as a species (Lawrence 1957, Hevly 1962) and as a subspecies of *P. louisianica* (Bretting 1981). Recent molecular work (Gutierrez 2002; Figs. 9, 10, 11, 12, 13, 14) using phylogenetic analyses of nuclear and chloroplast sequences fails to place *P. fragrans* as sister to *P. louisianica*. Thus, they are kept as distinct species in this work, with the main distinguishing morphological characters being color of the corolla and margin of the leaves. In *P. fragrans*, the corolla is purple or magenta, and the margins of the leaves are strongly denticulate. In *P. louisianica*, the corollas are white to pale pink, and the margins of the leaves are entire.

9. Proboscidea louisianica (Mill.) Thell., Mem. Soc. Nation. Sci. Nat. Math. Cherbourg, Ser. 7, 38: 481. 1912. *Martynia louisianica* Mill., Gard. Dict., ed. 8. No. 3. 1768. *Martynia louisiana* Mill. (orthographic variant), Gard. Dict. ed. 8. No. 3. 1768. *Proboscidea louisiana* (Mill.) Woot. & Standl. (orthographic variant), Contr. U. S. Nat. Herb. 19: 602. 1915. –LECTOTYPE: "*Martynia caule ramoso foliis cordato-ovatis pilosis*" in Miller, Gard. Dict., 2: 191, t. 286. 1760. –EPITYPE: Roy. Soc. No. 2024, 1762, (BM-SL). Lectotype and epitype designated by Hevly ex Stearn, Taxon 18: 532. 1969.

Martynia alternifolia Lam., Encycl. (Lamarck) 2(1): 112. 1786. Superfluous illegitimate name; see discussion below.

Martynia proboscidea Glox., Observ. Bot. 14. 1785. Superfluous illegitimate name; see discussion below.

Proboscidea jussieui Keller, Schmidel's Icones 49. tab. 12-13. 1762. Invalid combination. *Martynia jussieui* (Keller) J. T. Howell, Leafl. West. Bot. 1: 40. 1933. Invalid later synonym.–TYPE: tab. 12-13, Schmidel, Icones 49. 1762.

Proboscidea jussieui Steud., Nom. ed. 2, #2: 397. 1841. –TYPE: no type given. Invalid later homonym.

Description. Annuals. Roots taprooted. Stems decumbent. Leaves opposite to sub-opposite; petiole to 30 cm long; lamina broadly suborbicular to reniform; apex rounded, obtuse; base cordate or rounded, equilateral; margins entire and straight. Inflorescences many-flowered and surpassing the foliage; peduncles to 70 cm long; bracts oblanceolate to obovate. Flowers fragrant, 20-30 per inflorescence; pedicels to 2-3 cm long; bracteoles oblanceolate to obovate; calyx 14 to 20 mm long, sepals free for 30%-50% of their length; corolla to 40 mm in length, white to pale lavender, with yellow, orange, or magenta specks on interior surface and orange abaxial nectar glands. Fruit endocarp dark brown or dark gray, oblong-ellipsoid, inflated; endocarp body to 8 cm long and crested adaxially; endocarp rostrum to 18 cm long. Seeds dark gray to black, 7-9 mm long, 4-6 mm wide, rhomboid to ovoid. 2n=30. Fig. 3.

Phenology. Flowering from May to November in the United States. Flowering from February to April in Australia.

Distribution and habitat (Fig. 30). Native to disturbed soils in the United States. Naturalized in Australia, and very rare in the West Indies. 0-1800 m (0-5000 ft).

SPECIMENS EXAMINED. **AUSTRALIA.** AUSTRALIAN CAPITAL TERRITORY: Belconnen, 02 Mar 1978 (fl, fr), *Torssell s.n.* (CANB-2). –NEW SOUTH WALES: 15 mi [24 km] NE of Deniliquin, 35°25'S, 145°05'E, 24 Feb 1966 (fl, fr), *Mulhan & Leigh S430* (CANB); Central Tablelands, Travelling Stock Reserve 10 km directly N of Bigga, 2.5 km along Peach Garden Fire Trail from jct with Greenmantle Road, 39°59'54"S, 149°10'03"E, 16 Apr 1993 (fl), *Taws 144* (CANB); 3.1 km from Dripstone school towards Burendong Arboretum, 15 km SSE of Wellington, 32°41'S, 149°01'E, 07 Mar 1978 (fl), *Coveny & Ingram 10059* (MO). –SOUTH AUSTRALIA: Northern Flinders Range, Wilpena Station, ca. 140 km NE of Port Augusta, 06 Mar 1972 (fl, fr), *Hunt s.n.* (E).

CUBA. HAVANA: Santiago de las Vegas, 18 Jul 1905 (fl), *Baker 5373* (NY).

U.S.A. ALABAMA: LAWRENCE CO., no locality given, 20 Jul 1899 (fl), *Eggert s.n.* (MO). PICKENS CO., near Aliceville, 20 Aug 1978 (fl, fr), *Kral s.n.* (VDB-2). – ARKANSAS: PULASKI CO., marsh places, s.d. (fl, fr), *Hasse s.n.* (NY). –CALIFORNIA: BUTTE CO., Chico-Hamilton Road 6 miles from Chico, 30 May 1914 (fl), *Heller 11467* (E, GH, MO, NDG, NY); ca. 6 mi N of Chico, 08 Sep 1978 (fl, fr), *Taylor 1902* (MO); ca. 1.5 mi NE of Hwy 99 and Pentz Road, ca. 14.5 mi N of Oroville, 10 July 1983 (fl, fr), *Ahart 4192* (TEX). GLENN CO., N end of Stony Gorge Resevoir SE of Elk City, 21 Oct 1989 (fl), *Ertter et al. 8881* (NY, SD). LAKE CO., Kelseyville, 11 Sep 1929 (fr), *Blankinship s.n.* (MO). RIVERSIDE CO., ca. 3 miles NE of Murrieta, Jun-Jul 1948 (fl, fr), *Gentry 8181* (ASU, DES); Jurupa Mtns., Jurupa Mtns. Cultural Center, 0.25 mi SE of peak 1411, 34º01'N, 117º26'W, 28 Oct 2000 (fl, fr), *Provance 2282* (SD). SAN BERNARDINO CO., San Bernardino Valley, Fontana/Bloomington, S side of Slover Ave., ca. 0.5 mi E of the corner of Slover Ave. and Sierra Blvd., 34º01'N, 117º25'W, 11 Sep 2000 (fl), *Provance & George 2223* (SD). SAN DIEGO CO., Deerhorn Valley, 13 Jul 2001 (fl), *Bell 426a* (SD); Deerhorn Valley, 21 Aug 2001 (fr), *Bell 426b* (SD); Warner Springs, SE of Warner Springs Ranch on E side of Los Coyotes Road, 2 mi from its intersection with Hwy 79, 32.2678ºN, 116.6164ºW, 05 Sep 2005 (fl, fr), *Nenow & Glacy 206* (SD); San Diego, 11 Oct 1939 (fl), *Perry s.n.* (SD). SAN JOAQUIN CO., San Joaquin Valley, Dogtown, ca 12 mi NE of Lodi, Collier Road at Mackville Road, 1.1 mi W of CA-88, 38º12'47''N, 121º05'15''W, 09 Oct 2008 (fl), *Helmkamp & Helmkamp 14240* (ASU). SHASTA CO., Kennet, 26 Jul 1912 (fl), *Eastwood 1479* (MO). SOLANO CO., 3 mi S of Davis, 01 Oct 1954 (fl, fr), *Crampton 2284* (NY). SONOMA CO., along US Hwy 101, 2.1 mi N of jct to Skagg's Springs, 23 Jul 1958 (fl), *Raven & Snow 13681* (GH). STANISLAUS CO., Little Salado Creek drainage, west of I-5 on Crow's Landing Road ca. 5 mi W of Crow's Landing, 04 Jul 1982 (fl, fr), *Sanders 2782* (UTEP). SUTTER CO., Pass Road W of South Butte, Sutter Buttes, 04 Aug 1983 (fl, fr), *Ahart 4267* (TEX). YOLO CO., along Putah Creek W of Davis, 14 Jul 1958 (fl), *Snow 605-1* (NY). –COLORADO: BACA CO., S of Walsh, S side of Road M between Road 46 and Road 49, 12 Jul 1991 (fl, fr), *Weber & Wittmann 18222* (NY); confluence of Sand and Gallinas Canyons, tributary to Cimarron River, vicinity of Wilson Ranch, 27 mi S of Pritchett, 06 Aug 1948 (fl), *Weber 4326* (ARIZ); Wilson Ranch, 27 mi S of Pritchett at confluence of Sand and Gallinas Canyons in a tributary to the Cimarron River, 06 Aug 1948 (fl), *Weber 4326* (TEX). BOULDER CO., along Foothills Hwy at N edge of Boulder W of Broadway, 13 Aug 1970 (fl), *Weber & Grove 14110* (SD). FREMONT CO., Canon City, 14 Sep 1874 (fl), *Brandegee 6399* (MO); South Canon, 14 Sep 1874 (fr), *Brandegee 1034* (UC). KIOWA CO., 15 mi E of Eads along US 287, 17 Jul 1982 (fl), *Walter & Walter 8045* (MO); 1.5 N, 5.5 M E of Eads, 38°30'32"N, 102°40'33"W, 24 Aug 2000 (fl, fr), *Freeman & Morse 16601* (NY). KIT CARSON CO., along US 385 at mile marker 174, 22.8 mi N of Cheyenne Wells, 39°07'N, 102°18'W, 13 Aug 1991 (fl, fr), *Miller et al. 6676* (MO). PROWERS CO., 3.6 mi S of Lamar along US Hwy 287, 07 Aug 1994 (fl, fr), *Sylvester 2261* (BRIT); 2 mi N of Baca County line, 17 Aug 1968 (fl), *Tomb 340* (TEX). RIO GRANDE CO., Valley of Del Norte, 1846 (fl), *Emory s.n.* (NY). WASHINGTON CO., vicinity of Akron, 14 Sep 1937 (fr), *Ramaley & Ewan 16321* (MO, NO). –CONNECTICUT: MIDDLESOX CO., Middleton, s.d. (fl), *Barratt s.n.* (NY). WEST HAVEN CO., Oxford, 22 Sep 1901 (fl, fr), *Harger 2091* (NEBC). –DELAWARE: no locality given, s.d. (fl), *Bernhard s.n.* (MO); no locality given, s.d. (fl, fr), *Beyrich s.n.* (MO). –FLORIDA: LEVY CO., Morriston, 28 May 1979 (fl-2), *Kral 63805* (VDB-2). MADISON CO., no locality given, Jun-Jul 1898 (fl), *Hitchcock s.n.* (MO). –GEORGIA: No locality given, 1833 (fl), *Chapman s.n.* (NY). BALDWIN CO., Milledgeville, 16 Aug 1884 (fl), *Smith s.n.* (GH). HABERSHAM CO., Henderson Falls, 30 Aug-03 Sep 1894 (fl, fr), *Small s.n.* (NY-2). –ILLINOIS: CHAMPAIGN CO., Urbana, 12 Jul 1880 (fl), *Seymour 3577* (MO). HENDERSON CO., Oquawka, 6 Sep 1873 (fl), *Patterson s.n.* (MO, NY). JACKSON CO., Grand Tower, 17 Aug 1900 (fl), *Gleason 1764* (GH). MACOUPIN CO., Shipman, 06 Jul 1932 (fl), *Ledman s.n.* (MO). MENARD CO., Athens, 1861 (fl, fr), *Hall s.n.* (NY). MERCER CO., Keithsburg, banks of the Mississippi River, s.d. (fl), *Horner s.n.* (GH). ROCK ISLAND CO., Cordova, 12 Sep 1877 (fl, fr), *Monell s.n.* (MO). ST. CLAIR CO., Cahokia, 08 Jun 1874 (fl), *Eggert s.n.* (MO-2, NY). WOODFORD CO., S of Spring Bay, 07 Aug 1948 (fl, fr), *Chase 10038* (TEX). –INDIANA: JEFFERSON CO., Hanover, 1877 (fl, fr), *Barnes 8292* (NY). MARION CO., 16th & Wilcox, 15 Jul 1933 (fl), *McCoy 1110* (NY). MONTGOMERY CO., Bechtel garden on Union St., Crawfordsville, 15 Aug 1950 (fl, fr), *Bechtel 17190* (NY). –KANSAS: NW Kansas, 1878 (fl), *Rusby s.n.* (GH). BARBER CO., near Medicine Lodge, 22 Jul 1933 (fl), *Palmer 41841* (GH); 4 mi E of Kiowa, 05 Jul 1929 (fl, fr), *Rydberg & Imler 653* (NY); ca. 4.5 mi S and 1 mi E of Sun City in Bear Creek Valley, 22 Aug 1991 (fl), *Freeman 4075* (UC). CHEYENNE CO., 1.5 mi W of St. Francis, 16 Aug 1960 (fl, fr), *Harms 1232* (NY); ca. 1 mi SW of St. Francis, 07 Sep 1936 (fl, fr), *Steller 94* (NY). CLARK CO., 5 mi W of Ashland, 27 Aug 1957 (fl), *Wagenknecht 4676* (SMU). COMANCHE CO., Winfield, 09 Sep 1898 (fl), *White s.n.* (NY). EDWARDS CO., 3 mi E and 8 mi S of Kinsley, 19 Jun 1951 (fl), *Horr 4003* (NY). ELLIS CO., rock quarry 3 mi W of Hays, 19 Jul 1929 (fl), *Rydberg & Imler 1175* (NY); 1 mi E of Ellis, 26 Jun 1969 (fl), *Dutt 156* (MO); no locality given, 1908-1911 (fl, fr), *Zeller s.n.* (MO). FRANKLIN CO., ca. 10 mi SE of Ottawa along old US 50, 05

Aug 1994 (fl), *Henderson 94-657* (MO); 2 mi E of Pomona along Kansas State Hwy 68, 25 Aug 1965 (fl), *Hall s.n.* (ASC). GRANT CO., Ulysses, 24 Jun 1893 (fl), *Thompson 4* (GH, MO, NY, UC). HAMILTON CO., Syracuse, 07 Jul 1893 (fl), *Thompson 88* (MO, NY); vicinity of Syracuse, 14 Sep 1912 (fl, fr), *Rose & Fitch 17028* (NY). HODGEMAN CO., 1 mi E of Hanston, 28 Aug 1963 (fl, fr), *Anderson 2582* (BRIT). KIOWA CO., 21 mi W of Pratt, along Hwy 54, 9 mi E of Greenburg, 2 Sep 1961 (fr), *Mason 2056* (ARIZ). LEAVENWORTH CO., along KS Hwy 92 3.5 mi S, 2.25 mi E of Easton, 39º17'41"N, 95º03'53"W, 24 Jul 2003 (fl), *Morse 9763* (VDB). LOGAN CO., Oakley, 31 Aug 1915 (fl), *LMD s.n.* (GH). MEAD CO., Park, 14 Sep 1944 (fl), *Horr 3318* (GH). MORTON CO., 3 mi W of Elkhart along the Cimarron River, 8 Jul 1961 (fl, fr), *Richards 2907* (SMU). OSBORNE CO., within 5 mi of Osborne City, 22 Jun 1894 (fl), *Shear 129* (GH, NY); no locality given, 20 Jul 1885 (fl, fr), *Kellerman s.n.* (VDB). PRATT CO., 3 mi S of Stafford-Pratt County line on US 281, 05 Aug 1969 (fl), *Tomb & Tomb 545* (TEX). REPUBLIC CO., SE ¼ of NE ¼ of Sec 13, T2S, R3W, 11 Jul 1960 (fl, fr), *Morley 463* (NY, SMU, UC). RICE CO., 0.5 mi E of Raymond, 22 Jul 1969 (fl), *Stephens & Brooks 34563* (ASU). RILEY CO., Manhattan, 25 Jul 1892 (fl, fr), *Clothier s.n.* (NY-2); Manhattan, Aug 1893 (fl), *Horton s.n.* (NY). SEWARD CO., Liberal, 1892 (fl), *Hitchcock s.n.* (MO). SMITH CO., along US 36 E of Smith Center, 29 Aug 1933 (fl, fr), *Gates 17466* (MO). WYANDOTTE CO., Murray, 15 Aug 1897 (fl), *Mackenzie s.n.* (NY). –KENTUCKY: HICKMAN CO., Columbus, 24 Aug 1923 (fl), *McFarland & Anderson 198* (MO). WARREN CO., Bowling Green, Aug 1890 (illustration), *Price s.n.* (MO); Bowling Green, Jul 1899 (fl, fr), *Price s.n.* (MO). – LOUISIANA: no locality given, 1840 (fl, fr), *Short s.n.* (GH); no locality given, s.d. (fl), *Riddell 1255* (NY). NATCHITOCHES PARISH, no locality given, Jul 1930 (fl), *Dormon* *s.n.* (NY). ORLEANS PARISH, New Orleans, s.d. (fl), *Drummond s.n.* (E). – MASSACHUSETTS: ESSEX CO., Lawrence, 14 Sep 1932 (fl), *Collins s.n.* (GH, NEBC). SUFFOLK CO., Boston, 1877 (fl), *Perkins 382* (NEBC). –MINNESOTA: WINONA CO., Pleasant Valley, Jun 1901 (fr), *Holzinger s.n.* (NY). –MISSOURI: CAPE GIRARDEAU CO., Cape Girardeau, Jul 1925 (fr), *Wagner s.n.* (MO). CITY OF ST. LOUIS, 08 Jun 1874 (fl), *Eggert 955* (ND); Jul 1838 (fl, fr), *Buckley s.n.* (GH, NY); s.d. (fl), *Engelmann s.n.* (MO); 1833 (fl, fr), *Engelmann 331* (MO); s.d. (fl), *Drummond s.n.* (E, TCD). DUNKLIN CO., Walden, 12 Sep 1893 (fl, fr), *Bush s.n.* (MO); 1235 Kraft Street, Sep 1920 (fr), *Dickerson s.n.* (MO). FRANCOIS CO., Bonne Terre, 03 Jul 1892 (fl), *Eggert s.n.* (MO-2). JACKSON CO., Courtney, 22 Sep 1913 (fl, fr), *Bush 7075* (MO, NY). JEFFERSON CO., Bushberg, 26 Jun 1883 (fl), *Prince s.n.* (GH); De Soto, Jul 1887 (fl, fr), *Hasse 10* (NY). OZARK CO., Gainesville, 23 Jul 1913 (fl, fr), *Emig 7* (MO). ST. CHARLES CO., US Army Corps of Engineers Riverlands Environmental Demonstration Area, just S of Alton on W bank of Mississippi River, E of US Hwy 67, 38°51'40"N, 90°51'40"W, 28 Jul 1996 (fl), *Yatskievych & Harris 96-63* (MO). ST. LOUIS CO., no locality given, 27 Aug 1936 (fl), *Kellogg s.n.* (MO); Osage Hills, 15 Jun 1930 (fl), *Christ s.n.* (MO); Valley Park, 13 Jul 1938 (fl), *Layton s.n.* (MO); Allenton, 10 Jul 1898 (fl), *Letterman s.n.* (MO); Kirkwood, 19 Sep 1936 (fl, fr), *Chandler 1162* (MO). STODDARD CO., Bernie, 20 Jul 1917 (fl), *Shaw s.n.* (MO). WASHINGTON CO., Curtois Creek 2 mi S of Brazil, 19 Aug 1936 (fl), *Steyermark 21045* (MO). –NEBRASKA: FURNAS CO., S of Beaver City, 02 Sep 1941 (fl, fr), *Tolstead 411122* (UC). KEARNEY CO., Minden, 25 Jul 1933 (fl, fr), *Hapeman s.n.* (ARIZ, ND, UC); Minden, 30 Aug 1937 (fl, fr), *Hapeman s.n.* (SD); Minden, 24 Sep 1937 (fr), *Hapeman s.n.* (ARIZ). KEYA PAHA CO., N of Norden at Fred Egelhoff Farm, 27 Aug 1982 (st), *Egelhoff s.n.* (NY-2). RED WILLOW CO., near

Bartley on shores of Republican River, 28 Aug 1941 (fl, fr), *Tolstead 411121* (UC). – NEVADA: CLARK CO., Logan, 10 Jun 1912 (fl), *Heller s.n.* (NY). –NEW HAMPSHIRE: STRAFFORD CO., Dover, Dover Point, Albert Gage Farm, 17 Sep 1938 (fr), *Hodgdon et al. 3701* (NEBC). –NEW JERSEY: CAPE MAY CO., Cape May, 5 Aug 1915 (fl, fr), *Brown 10693* (GH). MONMOUTH CO., Sandy Hook, Aug 1884 (fl, fr), *Canby s.n.* (NY). –NEW MEXICO: BERNALILLO CO., Albuquerque, 305 Elm St., 30 Jul 1990, *Mactavish 95* (UNM). CHAVES CO., 20 mi S of Roswell, 19 Aug 1900 (fl, fr), *Earle & Earle 315* (E, K, MO-2, NY), Two Rivers Reservoir, 7 mi S of Hwy 380, 13 mi W of Roswell, 15 Jul 1968 (fl), *Averett & Tomb 326* (TEX). COLFAX CO., Lower Spring, Cimmarron, 1847 (fl, fr), *Fendler 554* (MO-2). CURRY CO., Cannon Air Force Base, 24 Jun 1993, *Bleakly & De Bruin 222* (UNM). GUADALUPE CO., E bank of Pecos River, Catfish Falls Quadrangle, 24 Jul 1979 (fl, fr), *Tschaikowsky 321* (ARIZ); E bank of Pecos River, Catfish Falls Quadrangle, 9 Jul 1979 (fl), *Tschaikowsky 227* (ARIZ); Vaughn, 30 Jul 1933 (fl, fr), *Degener 4516* (NY); near San Ignacio, 12 Aug 1949, *Gordon & Norris 512* (UNM). HARDIN CO., W of Mills, 18 Sep 1981, *Martin 5809* (UNM). LEA CO., 16 mi W of Hobbs on the Carlsbad Highway, 19 Aug 1967 (fl), *Pearce 2889* (ARIZ); 1-11 mi N of Hobbs, 31 Aug 1966 (fl), *Pearce 2553* (ARIZ). ROOSEVELT CO., Melrose Air Force Range, 2 mi SW of Steele Ranch, 06 Oct 1993, *Bleakly & De Bruin 520* (UNM). SAN MIGUEL CO., Trujillo Hill, 33 mi E of Las Vegas on Rte 65, 21 Sep 1955, *Castetter 10166* (UNM); 2 mi S of Rte 104, 20 mi E of Las Vegas, 21 May 1982 (fr), *Hill & Cress 11331* (GH [bagged specimen]). UNION CO., along Cimarron River ca. 10 mi W and 4 mi N of Kenton, Oklahoma, 27 Jul 1961, *Findley s.n.* (UNM). – NEW YORK: ALBANY CO., Albany, s.d. (fl), *no collector data* (NY). NIAGARA CO., Niagara Falls, Sep 1880 (fl), *Britton s.n.* (NY). ONTARIO CO., Geneva, s.d. (fl, fr), *Le*

Roy s.n. (NY). –NORTH CAROLINA: NEW HANOVER CO., Wilmington, 1879 (fl, fr), *Canby s.n.* (NY); Wilmington, 1892 (fl), *Williamson s.n.* (LL). –OKLAHOMA: BEAVER CO., 5.8 mi W of Turpin, 38 mi NE of Guyman, 16 Jul 1970 (fl, fr), *Bohrer 1385* (ARIZ). BECKHAM CO., Cedar Tops in SE part of county, 18 Oct 1936 (fl, fr), *Eskew 1510* (GH, NY); 6.3 mi E of Texas state line on US 66, 20 Aug 1970 (fl, fr), *Semple 277* (MO). CIMARRON CO., Kenton, 27 Jul 1936 (fl, fr), *Demaree 13312* (GH); 6.3 mi E of Kenton town limits on road to Boise City, 05 Sep 1985 (fl), *Yatskievych & Windham 85-321* (ARIZ). COMANCHE CO., Fort Sill, 07 Jul 1916 (fl, fr), *Clemens 11780* (GH). COTTON CO., 4 mi N and 1.75 mi E of Temple, 27 May 1985 (fl), *Lipscomb & Lipscomb 3421* (SMU). CUSTER CO., 0.5 mi W of Weatherford, 10 Jul 1937 (fl, fr), *Waterfall 728* (NY). GREER CO., near Granite, 17 Jun 1913 (fl, fr), *Stevens 1033* (GH, K, MO). HARMON CO., near Hollis, 20 Jun 1913 (fl, fr), *Stevens 1060* (GH); 4 mi W of Hollis, 09 Jul 1976 (fl, fr), *Taylor 22590* (BRIT). HARPER CO., 1 mi N and 4.5 mi E of Laverne, 02 Jul 1977 (fl, fr), *Springer 180* (SMU). MARSHALL CO., S of Madill, 1.8 mi N of Texas border along OK 99, 11 Aug 1979 (fl), *Rich & Rich 1383* (NY); Lake Texoma, Island No. 2, 25 Jul 1950 (fl), *Basler s.n.* (SMU). MCCURTAIN CO., 8 mi S and 2 mi E of Idabel near Hwy 259 along Waterfall Creek, 11 Sep 1979 (fr), *Taylor 28175* (BRIT). PAYNE CO., Stillwater, 12 Jul 1937 (fl, fr), *Ress 83* (TEX). TILLMAN CO., Frederick, 29 Jun 1903 (fl), *Duncan 95* (MO). WOODS CO., near Hopeton, 12 Jul 1913 (fl, fr), *Stevens 1701* (GH, MO, NY). –PENNSYLVANIA: BUCKS CO., Telford, 30 Aug 1921 (fr), *Benner s.n.* (GH, NY). –RHODE ISLAND: BRISTOL CO., Bristol, Aug 1887 (fl), *Leland s.n.* (NEBC). –SOUTH CAROLINA: ABBEVILLE CO., Abbeville District, Jul 1855 (fl, fr), *Hexamer & Maier s.n.* (GH, NY). ANDERSON CO., Anderson, 23 Jul 1919 (fl, fr), *Davis 7132* (MO). –SOUTH DAKOTA: STANLEY CO., Fort Pierre, Jun 1854 (fl), *Hayden 410* (MO). –TENNESSEE: DAVIDSON CO., Nashville, s.d. (fl, fr), *Gattinger s.n.* (GH); Nashville, Green Hills District, 04 Sep 1971 (fl, fr), *Kral 43881* (BRIT, VDB-2). FRANKLIN CO., Cowan, Cumberland Mts., 18 Jul 1898 (fl, fr), *Ruth 588* (MO); Cumberland Mts., Jul 1898 (fl, fr), *Ruth 555* (NY). –TEXAS: Fort Smith [Arkansas] to the Rio Grande, 1853-4 (fl, fr), *Bigelow s.n.* (GH); no locality given, s.d. (fl, fr), *Jermy s.n.* (MO, NY); Bed of the Brazos River, Camarkle Crossing, 09 Jul 1903 (fl), *Reverchon s.n.* (SMU). ANDREWS CO., no locality given, Sep 1957 (fl, fr), *Scudday s.n.* (LL). ARCHER CO., Archer City, 28 Sep 1934 (fl, fr), *Burke s.n.* (TEX). ARMSTRONG CO., in Palo Duro Canyon, 17 Jun 1952 (fl), *Gentry 1323* (BRIT). BAILEY CO., Coyote Lake, 25 Aug 1921 (fl, fr), *Ferris & Duncan 3464* (MO, NY). BASTROP CO., no locality given, 20 Aug 1928 (fl), *Duval s.n.* (TEX). BELL CO., Camp Hood, 27 Jul 1943 (fl, fr), *Cohn T8* (ND, NY, TEX); 1 mi S of Pendleton, 05 Oct 1930 (fl, fr), *Powers 2611* (ND, SMU); 2.1 mi NW on FM 485 from its jct with FM 1915, SE of Temple, 24 Jun 1989 (fl), *Jones & Jones 3262* (ARIZ); Upper Tennessee Valley, near Leon River, 21 Jun 1954 (fl), *York & York 54493* (SMU, TEX). BEXAR CO., 8-12 km ENE of Shavano Park between US 281 and FR 2968 N of FR 1604 on E. E. Voight Ranch, 04 Jul 1981 (fl, fr), *Lieb 123* (UTEP); 4.6 mi SE of Texas Hwy 16 along FM 1560, 0.2 mi N of FM 471, 02 Jun 2003 (fl, fr), *Gutierrez 210* (UTEP-2); San Antonio, 11 Jul 1911 (fl, fr), *Clemens & Clemens 864* (MO); San Antonio, s.d. (fl), *Jermy 124* (MO). BLANCO CO., ca 0.4 mi S of Pedernales River by US Hwy 281, 28 Jul 1969 (fl, fr), *Smith 1301A* (SMU); Candlin Farm, Cox Road, 30 Jul 1960 (fr), *Baird s.n.* (TEX). BROWN CO., Adams Branch, Brownwood, 12 Sep 1965 (fl), *McCart 9161* (ARIZ, LL); 10 mi N of Brownwood, Lake Brownwood, below dam, 16 Oct 1965 (fl, fr), *Rahtke et al. 9191* (SMU); Brownwood, 15 Jun 1966 (fl, fr), *Purvis 18* (LL, SMU); Camp Bowie Training Site, 31º39’58”N, 98º55’37”W, 27 Jun 1995 (fl, fr), *Carr, Wolfe, & Liu 14745* (TEX). BURNET CO., Marble Falls, Jul 1912 (fl, fr), *Young s.n.* (MO); Burnet, 22 Sep 1934 (fl), *Fisher B15517* (BRIT); 1 mi E of Bertram along Hwy 29, 21 Sep 1948 (fl), *Webster & Rogers 6464* (TEX). CALDWELL CO., 5 mi S of Lockhart, 10 May 1964 (fl), *Chesser s.n.* (TEX). CAMERON CO., Brownsville, 10 Jul 1923 (fl, fr), *Runyon 264* (SMU). CARSON CO., Texas Technological College Research Farm, 5 Jul 1965 (fl), *Trlica & Sellars 103* (SMU). COKE CO., ca. 5 mi E of Robert Lee, 11 Sep 1965 (fl, fr), *Corell 31728* (LL, NY). COLEMAN CO., 5 mi S of Santa Anna, 04 Jun 1966 (fl), *Bible 16* (LL, SMU, VDB); Grady Laws Ranch 1.5 mi N of Valera, 02 Jul 1976 (fl), *Nixon 440* (BRIT). COLLIN CO., NW corner of jct between FM 2514 and FM 1378, 33º03’16.2”N, 96º34’08.7”W, 18 Jul 2003 (fl), *Rich & Dunkle 3669* (BRIT). CORYELL CO., Fort Gates, 3 mi S of Gatesville, 09 Oct 1965 (fl, fr), *Baize 16* (SMU). CROCKETT CO., ca. 2.5 km NE of Fort Lancaster Ruins picnic area along US Hwy 290, 30º40’40”N, 101º40’23”W, 26 Jul 1987 (fl), *Lieb 894* (UTEP); Ozona, 03 Aug 1933 (fl), *Degener 5085* (NY); 9 mi S of Ozona, 12 Jul 1941 (fl, fr), *Tharp s.n.* (TEX). CROSBY CO., Walker Tank, 22 Jun 1925 (fl), *Erlanson 1137* (SMU). DALLAM CO., 8 mi E of Texline at Thompson Grove Picnic Area, 14 Jul 1956 (fl), *Gould & Thomas 7139* (SMU). DALLAS CO., Dallas, s.d. (fl, fr), *Reverchon s.n.* (MO); Dallas, s.d (fl, fr), *Letterman s.n.* (MO). DENTON CO., 6.7 mi E of Denton, at head of Lake Dallas, 21 Aug 1954 (fl, fr), *Shinners 19099* (SMU). DICKENS CO., 1.8 mi SW of US Hwy 82 on Co Rd 371, 33º35’27”N, 100º34’52”W, 03 Sep 2000 (fl), *Wendt & Collins 7132* (TEX). DONLEY CO., near Clarendon, 23 Jun 1978 (fl), *Nabhan et al. s.n.* (ARIZ). DUVAL CO., ca 6 mi N of Hebbronville, ca 2 mi N of county line, ca 0.5 mi W of Hwy 16, 06 Nov 1979 (fl), *Ajilvsgi 6501* (BRIT); 6.5 mi E of Bruni along Tx

Hwy 359, 04 Nov 1962 (fl), *Vergara et al. 8573* (TEX). ECTOR CO., 9 mi S of Odessa on Rte 385, 06 Aug 1966 (fl, fr), *Correll 33321* (LL). EDWARDS CO., ca. 25 mi S of Sonora, 18 Sep 1958 (fl), *Gould 8385* (SMU); Pasture R, Substation No. 14, 15 Jun 1944 (fl), *Cory 44580* (TEX). ELLIS CO., 3 mi N of Italy, 04 Jul 1957 (fl, fr), *Correll & Johnston 17361* (LL, NY-2). ERATH CO., no locality given, 05 Sep 1927 (fr), *Gough s.n.* (TEX). GARZA CO., Post, 31 May 1918 (fl), *Palmer 13824* (MO); 14.8 mi SE of Post along Hwy 84, 18 Jun 1965 (fl), *Hutchins 616* (LL, SMU). GILLESPIE CO., Pedernales Creek, s.d. (fl, fr), *Jermy 508* (MO); Pedernales, s.d. (st), *Jermy 691* (MO); Fredericksburg, 755 S. Washington, ca. 0.1 mi N of Friendship Lane along Hwy 87, 30º15'45"N, 98º52'20"W, 07 Aug 2008 (fl, fr), *Gutierrez et al. 2126* (ASU, BRIT, UTEP); LBJ National Historic Park, Ranch Unit, along Pedernales River at Ranch House (Texas White House), below dam, 30º15"N, 98º37'W, 22 Aug 2002 (fl), *Sanders 5447* (BRIT). GRAY CO., along Rte 66 in SW corner of county, 30 Jun 1966 (fl, fr), *Correll & Correll 33294* (LL). HALL CO., N of Estelline, ca. 4 mi from Hwy 287 E of Newlin near dunes of Red River, 06 Sep 1945 (fl, fr), *Whitehouse 10737* (NY, SMU). HARDEMAN CO., Chillicothe, 31 Aug 1906 (fl), *Ball 993* (LL). HARDIN CO., 0.7 mi S of Silsbee, 08 Jul 1949 (fl, fr), *Cory 56629* (SMU). HARRIS CO., Houston, 22 Aug 1910 (fl), *no collector data* (MO); Houston, 1509 Cortlandt Street, 16 Jul 1943 (fl), *Boon 132* (TEX). HARTLEY CO., 5 mi S of Dalhart, Aug 1949 (fl), *York & Rodgers 278* (TEX). HASKELL CO., Haskell, 1898 (fl), *Morton s.n.* (MO). HILL CO., 6 mi S of Whitney, 07 May 1939 (fl), *Rogers 17* (SMU). HAYS CO., ca. 0.75 mi NNW of Wimberly near juncture of Cypress Creek and Blanco River, 09 Aug 1961 (fl), *Walker 14* (TEX). HEMPHILL CO., 5 mi E of Canadian, Gene Howe Wildlife Management Area, 10 Jun 1955 (fl), *Rowell 4063* (TEX). HOOD CO., Granbury, 16 Sep 1914 (fl, fr), *Palmer 6548* (MO). HOWARD CO., 1.9 km W, 12.5 km S of Big Spring, 2 Jul 2003 (fl), *Cerda 376* (BRIT); 11.2 km N of Big Spring, 16 Jul 2003 (fl), *Woods 44* (TEX). HUTCHINSON CO., Lake Meredith National Recreation Area, Spring Creek picnic and fishing area, NE side of Sanford Dam, NE side of lake along park boundary, 35º43'06-09''N, 101º32'54-55''W, 24 Jun 2002 (fl), *Nesom & O'Kennon LAMR516* (BRIT); Phillips, 1121 Gulf St., 18 Jun 1965 (fl), *Drake 139* (TEX). JACK CO., 6 mi NW of Jacksboro, 16 Aug 1960 (fl), *Caddell 989* (BRIT). KERR CO., Verde Creek, 20 Jun 1946 (fl), *Correll & Correll 12819* (SMU). KIMBLE CO., Junction, 20 Jul 1949 (fl), *Fisher 49216* (ARIZ). LAMB CO., 11.9 mi N of Spade, 29 Jul 1967 (fl, fr), *Wall 45* (ASU). LOVING CO., between Wink and Mentone, 13 Jul 1952 (fl, fr), *Warnock 10707* (LL, SMU). LUBBOCK CO., Lubbock, 900 block of East Marlboro Street, 13 Jul 2002 (fl, fr), *Gutierrez 24* (UTEP); 2.0 miles east of I-27 (Hwy 87) on FM 1729 at road to Pheasant Ridge Winery, 13 Jul 2002 (fl), *Gutierrez 21* (UTEP), *Gutierrez 22* (UTEP). MARTIN CO., 18 mi N of Midland on Hwy 349, 12 Jul 1977 (fl, fr), *Higgins 10327* (NY). MASON CO., Mason Wildlife Management Area, Spring Pasture, 20 Aug 2005 (fl, fr), *Sanchez 4018* (BRIT). MCLENNAN CO., Brazos Valley N of Childress Creek, 25 Jul 1947 (fl, fr), *Smith 964* (TEX), Waco, Power Plant Control Center, Baylor University campus, 26 Jul 2004 (fl), *Holmes 13028* (TEX-2). MCMULLEN CO., Lively Ranch, ca. 20 mi SW of Tilden, 31 May 1949 (fl), *Rogers, Albers & Webster 6813* (TEX). MIDLAND CO., ca. 2 mi SW of Midland, 12 Sep 1967 (fl, fr), *Correll 35000* (LL). MILLS CO., 8.5 mi SW of Goldthwaite along Hwy 16, 27 Sep 1950 (fr), *Cory 58203* (SMU). MONTGOMERY CO., Willis, s.d. (fl), *Warner s.n.* (MO). NOLAN CO., Sweetwater, 20 Sep 1927 (fl, fr), *Stanfield 7194* (TEX). OCHILTREE CO., Wolf Creek 12 mi SE of Perryton along US Hwy 83 and 5 mi E of hwy, 13 Jul 1957 (fl, fr), *Wallis*

4888 (SMU); 3 mi S of Farnsworth, 08 Jul 1963 (fl), *Correll & Ogden 28354* (LL). OLDHAM CO., 2 mi W of Vega, 07 Jul 1936 (fl), *Howard s.n.* (TEX). PALO PINTO CO., Brazos, Sep 1930 (fl, fr), *Wadsworth s.n.* (TEX). PARKER CO., 1.5 mi SE of Springtown, 05 Jun 1949 (fl), *Hennen 434* (SMU); Millsap, 06 Nov 1927 (fl), *Wadsworth s.n.* (TEX). POTTER CO., Alibates National Monument, 05 Jun 1971 (fl), *Higgins 4380* (ASU); Rte 1061, ca. 2 mi W of Amarillo, 08 Jul 1963 (fl), *Correll & Ogden 28403* (LL); N bank of the Canadian River, ca. 20-25 mi N of Amarillo on US 87, 16 Jul 1968 (fl), *Averett & Tomb 352* (TEX). REAL CO., 1.5 km NW on Ranch Rd 337 from TX 55, 29º41'N, 99º56'W, 24 Sep 1994 (fl, fr), *Ada & Ide 567* (TEX). REEVES CO., Pecos, 19 Jul 1919 (fl), *Hanson 750* (GH). RANDALL CO., Palo Duro Canyon, ca. 2 mi NE of Canyon off Interstate 87, 02 Sep 1977 (fl), *Higgins 11375* (NY). REAL CO., 1.5 km NW of Ranch Road 337 from its intersection with TX 55, 29º41'N, 99º56'W, 24 Sep 1994 (fl, fr), *Atha & Ide 567* (NY). ROBERTSON CO., along US190 6 mi SE of the Spring Creek bridge, 30º47.78'N, 96º30.22'W, 04 Aug 2001 (fl), *Worthington 30669* (UTEP); Brazos River, 29 Jun 1982 (fl, fr), *Starbuck 2574* (BRIT-2). SAN PATRICIO CO., 4 mi S of Taft, 10 Jun 1950 (fl, fr), *Jones 275* (SMU). SAN SABA CO., 3 mi NW of Richland Springs, 13 Jul 1976 (fl, fr), *Burleson 467* (BRIT). SHERMAN CO., North Canadian River, 9 mi N of Straford, 08 Oct 1964 (fr), *Correll 30314* (LL). STARR CO., spillway of Falcon Dam, 21 Jul 1974 (fl), *Butterwick & Strong 1166* (TEX); 3 mi W of Roma, 16 Jul 1932 (fl), *Clover 120* (TEX); 10 mi E of Rio Grande City, 10 Jul 1923 (fl), *Runyon 264* (TEX); 9 mi W of La Gloria on Hwy 1017, 13 Aug 2005 (fl, fr), *Richardson & King 3282* (TEX); Rio Grande City, 29 Sep 1951 (fl), *Runyon 4409* (TEX), La Joya, 08 Jun 1941 (fl), *Runyon 3282* (TEX). STEPHENS CO., 8 mi N of Caddo, 28 Jul 1961 (fl, fr), *Correll & Correll 24135* (LL).

TARRANT CO., no locality given, 15 Jul 1923 (fl, fr), *Ruth 145* (GH, NY); Fort Worth, 12 Sep 1910 (fr), *Ruth 123* (TEX). TAYLOR CO., Abilene, 06 Jun 1943 (fl, fr), *Pride 20295* (GH); along Little Elm Creek, ca. 1 mi W of jct of Hwy 20 & 277, NW of Abilene, 15 Aug 1963 (fr), *Mahler 3613* (MO, SMU); Abilene, 25 May 1902 (fl, fr), *Tracy s.n.* (MO, TEX); Abilene, 13 Aug 1948 (fl), *Fosberg 30006* (NY); Abilene, 15 May 1900 (fl), *Williams s.n.* (LL); Abilene, 19 Jun 1946 (fl, fr), *Warnock 46348* (TEX-2). TERRELL CO., Independence Creek near Pecos River, 19 Jul 1964 (fl), *Demaree 50905* (NO-2); Blackstone Ranch, Gravel Springs, 20 mi S of Sheffield, 11 June 1948 (fl), *Webster 225* (TEX); Independence Creek at Dryden-Sheffield Road, 03 July 1949 (fr), *Hinckley & Hinckley 168* (TEX); N side of Chandler irrigation channel on N side of Independence Creek, ca 0.2 mi W of Chandler fence, 30º27.562'N, 101º44.963'W, 25 June 2002 (fl), *Carr 21111* (TEX). TOM GREEN CO., Concho River ca. 10 mi W of San Angelo, 31 Aug 1953 (fl, fr), *Warnock 11547* (SMU). TRAVIS CO., along Colorado River bank near dam in Austin, 22 Aug 1935 (fl), *Metz 2189* (ND, NY); along Onion Creek, 8.5 mi S of Colorado River, 21 Jul 1964 (fl), *Correll & Correll 29936* (LL); Austin, 03 June 1974 (fl, fr), *Whalen 1* (LL-2); Austin, Oct 1935 (fl, fr), *Smith s.n.* (TEX); Barton Springs, 03 Oct 1908 (fl), *York & Wolf 79* (TEX); Austin, 15 Aug 1941 (fl, fr), *Tharp s.n.* (TEX); Pace Bend County Park, 800-1000 ft E of RM 2322 from Davis Cove, ca 6.1 mi NE to NNE of jct of State Rte 71 and RM 2322, 22 Aug 1996 (fr), *Carr 15658* (TEX); Colorado River at Barton's Creek, 11 Nov 1954 (fl), *Tharp s.n.* (TEX); 3 mi SSE of St. Ed's Univ, 05 July 1954 (fl, fr), *Lynch s.n.* (TEX). VAL VERDE CO., Devil's River and Hwy 90, 01 Jul 1968 (fl, fr), *Lewis s.n.* (ASU); 48 mi S of Ozona on Comstock Road, 27 Jun 1921 (fl, fr), *Ferris & Duncan 3010* (MO); along San Felipe Creek, near Del Rio, 08 Oct 1952 (fr), *Correll 14968* (LL, SMU);

Amistad National Recreation Area, N of campground on Spur 406 (NE of US 90 SE of Constock), 18 May 1984 (fl, fr), *Ertter 5407* (TEX). WEBB CO., Laredo, Aug 1879 (fl, fr), *Palmer 2027* (GH-2); near Laredo, 06-07 Aug 1906 (fl, fr), *Rose & Rose 11025* (NY); Laredo, Del Mar Addition, 02 Nov 1962 (fl, fr), *Solis 5* (SMU); Fort McIntosh, 30 Oct 1961 (fl, fr), *Fernandez & Fernandez 32* (SMU, TEX); Laredo, s.d. (fl, fr), *Solis 5* (TEX); Rio Grande near International Bridge, 14 Nov 1961 (fl), *Ruiz 31* (TEX); Fort McIntosh, W of Laredo Junior College, 08 Nov 1961 (fl, fr), *Bruni & Cardenas 29* (TEX); Ratamosa Ranch, 10 mi N of Aguilares, 27 Oct 1963 (fr), *Vergara 2* (TEX). WILLIAMSON CO., N bank of Lake Creek, SE corner of US Rte 183 and RM 620, 09 Sep 1988 (fl), *Carr 9227* (TEX). WISE CO., LBJ Grasslands Unit 12, 07 Sep 2002 (fl), *O'Kennon & McLemore 17211* (BRIT). –VERMONT: CHITTENDEN CO., Burlington, 16 Oct 1970 (fl, fr), *Waddell s.n.* (NEBC).

CULTIVATED. *Armstrong s.n.* (SD-2, fl, fr); *Christ 918* (NY, fl); *Freeman 281* (UTEP, fl); *Hartling s.n.* (NY, fl, fr); *Keefe s.n.* (NY, fl); *Kellogg s.n.* (MO, fl); *Moffatt s.n.* (NY, fl); *Moldenke 3113* (NY, fl); *Nash 923* (NY, fl, fr); *Nash 924* (NY, fl); *Nash 7921* (NY, fr); *Nash 9220* (NY, fl, fr); *Plowman 2950* (ECON, fl, fr); *Sartwell s.n.* (NY, fl); *Schneider 22381* (NY, fl, fr); *Schneider 22382* (NY, fl, fr); *Schultes et al. 34* (ECON-2, fl, fr); *Sharples s.n.* (GH, fl); *Spellman 869* (ASU, fl); *Stehlé 1818* (A, fl); *Thomas 126355* (MO, NY, fl); *Vincent 7991* (F, fl); *Worthen 7794* (ECON; fl, fr).

This species is believed to be native to the West Indies, though very rare. It is not inconceivable for fruits to travel from the mainland United States, where it is native and common, to islands in the West Indies. Two specimens are known from this region, one from Cuba (*Baker s.n.*, NY!) and a second, not seen for this study, from Guadeloupe (*Stehle 1818*, MICH). In North America, this is the taxon with the farthest range north. Its native range is most likely the south-central Great Plains, and may have spread to other parts of the country via cultivation in the ornamental plant industry.

Lamarck (1786) cited the name and illustrations for what is now considered to be the lectotype for *P. louisianica*, making his name, *M. alternifolia*, superfluous and illegitimate. Gloxin (1785) also cited the name and illustrations for what is now considered to be the lectotype for *P. louisianica*, making his name, *M. proboscidea*, superfluous and illegitimate. While *Proboscidea jussieui* holds priority over other names in the genus, it was first published in a work that inconsistently used the Linnaean binary system, thus rendering the name invalid. See the notes under *P. fragrans* for a discussion of the relationship between these two taxa.

10. Proboscidea parviflora (Woot.) Woot. & Standl., Contr. U. S. Nat. Herb. 19: 602. 1915. *Martynia parviflora* Woot., Bull. Torrey Bot. Club 15: 453. 1898. – TYPE: U.S.A. New Mexico. Doña Ana Co., San Agustin Ranch, Organ Mts., 30 Aug 1897, *Wooten 580* (holotype: US [photo at ASU!], isotypes: MO [photo at ASU!] MINN [photo at ASU!] NMC! [photo at ASU!] NY US [photo at ASU!]).

Description. Annual. Roots taprooted. Stems erect to decumbent. Leaves opposite to sub-opposite; petiole to 35 cm long; lamina broadly deltate-ovate to suborbicular-ovate; apex acute to obtuse, rounded to angulate; base cordate, equilateral to inequilateral; margins entire to 3-to 7-lobed, sometimes denticulate.

Inflorescences few-flowered and equaling the foliage or many-flowered and surpassing the foliage; peduncles to 9 dm long; bracts obovate to oblanceolate. Flowers 5-50 per inflorescence; pedicels to 1.5-9cm long cm in flower; bracteoles ovate, elliptic, or oblong; calyx 1-1.5 cm long, sepals free for 25%-50% of their length; corolla to 2.5-4 cm in length; corolla tube reddish-purple, pink, or white, with a bright yellow band extending along the lower portion of tube and out onto lower lobe; corolla lobes the same color as the tube but the upper lobes frequently with a single large purple or reddish-purple blotch, the upper and lateral lobes wide-flaring or reflexed. Fruit endocarp black or gray, ellipsoid; the endocarp body 5-10 cm long, strongly keeled abaxially, the endocarp rostrum 1 to 3.5 times the length of the body. Seeds black or white, to 9 mm long, 4-6 mm wide, ovate.

This species can be distinguished from other *Proboscidea* on the basis of its light pink flowers with a united calyx and leaves with denticulate margins and inequilateral bases.

KEY TO THE SUBSPECIES OF *PROBOSCIDEA PARVIFLORA*

1. Peduncle shorter than 15 cm; mature inflorescence with fewer than 15 flowers; pedicels shorter than 32 mm; anthers shorter than 4.2 mm ....10a. *P. parviflora* ssp. *parviflora*

1. Peduncle longer than 15 cm; mature inflorescence with more than 15 flowers; pedicels longer than 32 mm; anthers longer than 4.2 mm

2. Apex angle of leaf lamina greater than 90°; Baja California....................................
....10b. *P. parviflora* ssp. *gracillima*

2. Apex angle of leaf lamina less than 90°, Sinaloa and Sonora.................................
.... 10c. *P. parviflora* ssp. *sinaloensis*

10a. Proboscidea parviflora ssp. **parviflora**

Description. Leaves opposite to sub-opposite; petioles to 25 cm long; apex obtuse, rounded; margins entire to shallowly 3- to 7-lobed, often denticulate. Inflorescences equaling the foliage; peduncles to 1.5 (-1.8) dm long. Flowers 2-4 cm long, fewer than 15 per inflorescence; pedicels 1.5-3 cm long; anthers to 4.2 mm long. Fruit endocarp body 5-10 cm long; the endocarp rostrum 1-3.5 times the length of the body. Seeds black or white.

The subspecies can be distinguished on the basis of having a peduncle shorter than 15 cm, pedicels shorter than 32 mm, and fewer than 15 flowers per inflorescence. Bretting's (1981) acceptance of two varieties for this subspecies is supported by molecular data (Gutierrez 2002).

KEY TO THE VARIETIES OF *PROBOSCIDEA PARVIFLORA* SSP. *PARVIFLORA*

Anthers shorter than 2.8 mm, style shorter than 10 mm; mature capsules shorter than 9 cm, fruit crests shorter than 5 cm and lower than 5 mm, rostra shorter than 18 cm; seeds black......................................10a(i). *P. parviflora* ssp. *parviflora* var. *parviflora*

Anthers longer than 2.8 mm, style longer than 15 mm; mature capsules longer than 9 cm, fruit crests longer than 5 cm and higher than 5 mm, rostra longer than 18 cm; seeds white. ....10a(ii). *P. parviflora* ssp. *parviflora* var. *hohokamiana*

10a(i). Proboscidea parviflora ssp. **parviflora** var. **parviflora.**

Proboscidea crassibracteata Correll, Madroño 19: 190. 1968. –TYPE. U.S.A. Texas: Presidio Co., on clay flats near Adobes, Rte. 170, 25 Sep 1966, *Correll 33900* (holotype: LL! [photo at ASU!], isotype: LL! [photo at ASU!]).

Description. Flowers: anthers shorter than 2.8 mm; style shorter than 10 mm. Fruits: endocarp bodies shorter than 9 cm, fruit crests shorter than 5 cm and lower than 5 mm; rostrum shorter than 18 cm. Seeds black.

Phenology. Flowers from June to October, rarely as early as May and as late as November, and in February on the Baja California Peninsula.

Habitat and Distribution (Fig. 31). Disturbed soils in arid and semiarid lands in Mexico, and the southwestern United States; 0-2200 m (0-4500 ft).

Vernacular Names. Devil's Claw, Aguaro.

SPECIMENS EXAMINED. **MEXICO**. BAJA CALIFORNIA: Rancho Viejo, 31º35'N, 115º51'W, 03 Oct 1971 (fr), *Moran 18658* (SD, UC); ca. 9 mi W of Ejido San Matias, 31º22.5"N, 115º41'W, 15 Nov 1983 (fr), *Thorne & Wisura 57660* (SD); Agua Flores, 31º42'N, 115º56'W, 18 Sep 1977 (fl), *Moran 24946* (SD); 6 km WNW of San Matías Pass, 31º21.5'N, 115º38'W, 17 Sep 1977 (fl), *Moran 24907* (SD). –BAJA CALIFORNIA SUR: Purisima to Comondu, 16 Feb 1889 (fl, fr), *Brandegee s.n.* (UC). –CHIHUAHUA:

Batopilas, 19 Sep 1957 (fl, fr), *Knobloch & McVaugh 538* (UTEP); 8.4 mi S of Moctezuma along Hwy 45, 30º04'N, 106º19'W, 15 Jul 1981 (fl, fr), *Worthington 7287* (UTEP); Corralitos to El Paso, Aug 1852 (fl, fr), *Thurber s.n.* (GH); old ruin area in Urigue, 31 Jul 1971 (fl, fr), *Bye 1699* (GH-2); ca. 2 mi SE of Conejos Station, 26º12'N, 103º50'W, 13 Sep 1976 (fl, fr), *Webster & Armbruster 21238* (LL); Meoquí, 24-30 Aug 1935 (fl), *Le Sueur MEX-33* (TEX); Laguna de Palomas, 31º42'30"N, 107º35'W, 18 Aug 1972 (fl, fr), *Chiang et al. 8653* (LL); 7 mi N of Colonia Juárez in "The Tinaja," 30º22'N, 108º07'W, 28 Jul 1972 (fl), *Wilson et al. 8429* (LL); 9.4 mi W of Hwy 45 along Hwy 10, ca 15 mi SW of Ciudad Juárez, 31º37'N, 106º39'W, 18 Aug 1971 (fl, fr), *Henrickson 5699* (LL); Batopilas, La Bufa, 10 Oct 1973 (fl, fr), *Bye 5357* (ECON); Batopilas region, S side of Barranca de Batopilas, 03 Aug 1973 (fl, fr), *Bye 4488* (ECON); 0.75 mi S of Mata Ortiz, 13 Jul 1997 (fl), *Atwood & Spencer 22886* (ARIZ). –SINALOA: San Blas, 24 Mar 191? (fr), *Rose et al. 13417* (NY). –SONORA: Sonora Alta, s.d. (fl, fr), *Coulter s.n.* (TCD); SE of Empalme, near Guaymas, off old highway 0.3 mi W of marker km 111, 27º50'N, 110º45'W, 19 Aug 1995 (fl), *Snow & Prinzie 6531* (MO); 7.4 miles NE of Mazocahui, along road to Moctezuma, 29º35'N, 110º05'W, 01 Sep 1988 (fl, fr), *Hodgson et al. 5169* (DES); ca. 200 yards SW of El Coyote along road from Huasabas, 20 Jul 1988 (fr), *Hodgson et al. 5113* (DES); 6 mi S of Nogales, 07 Aug 1965 (fl), *Matthews & Matthews 494* (ASU, TEX, VDB); ca. 27.9 mi NE of Alamos, 09 Aug 1980 (fl, fr), *Lehto 24749* (ASU); 2 mi NE of airport on road to Bahia de Kino NW of Hermosillo, 18 Sept 1971 (fl, fr), *McLeod et al. 951* (ASU); Onavas, Aug 1968 (fl), *Pennington 336* (TEX); Rancho El Palmar, 20 km E of Onavas, 28º29-30'N, 109º23'W, 19 Apr 1992 (fr), *Joyal 1965* (ASU, boxed); San Bernardo, Rio Mayo, 15 Sep 1958 (fl, fr), *Arguelles s.n.* (ARIZ, LL); Mouth of Arroyo

Masiaca, Las Bocas on the Gulf of California, ca. 52 km by air S of Navajoa, 26º35'55"N, 109º20'04"W, 22 Sep 1994 (fl, fr), *Van Devender & Yetman 94-706* (ARIZ); Rio de Bavispe, Colonia Morelos, 15 Sep-04 Oct 1941 (fl, fr), *White 4459* (GH); locality illegible, 31 Sep 1851 (fl, fr), *Thurber 913* (GH, NY-2); Rio de Bavispe, Cañón de Huépari, Rancho de Babidianchi, 03 Sep 1940 (fr), *White 3683* (GH); San Bernardo, Rio Mayo, 14 Jul 1935 (fl, fr), *Gentry 1495* (GH, MO, UC); La Concepcion, 29º19'25"N, 109º02'20"W, 17 Jul 1997 (fl, fr), *Trauba s.n.* (ARIZ); along Hwy 14 NE of Hermosillo, ca 37.5 km SW of Ures, 29º18'N, 110º50'W, 21 Aug 1995 (fl, fr), *Snow & Prinzie 6575* (MO); S edge of Alamos, 19 Sep 1973 (fl, fr), *Fish 125* (UC); along Oputo-Angostura road, 7 mi from jct with Agua Prieta-Nacozari road, 13 mi S of Curicachi, 07 Sep 1961 (fr), *Mason et al. 2082* (UC); near Las Casitas on Hwy 15 between Magdalena and Nogales, 24 Jun 1977 (fr), *Nabhan & Morton 650b* (MNA); Onavas, 25-29 Oct 1979 (fl, fr), *Rea 217* (SD); Yecora, Arroyo Santa Ana at SON 12 (Tepoca-Cd. Orbergon Hwy), 2.3 km SW of turnoff to La Quema, 8.5 km W of Guadalupe Tayopa, 28º21'06"N, 109º15'42"W, 14 Aug 1998 (fl, fr), *Reina et al. 98-856* (NY).

U.S.A. ARIZONA: Verde River, 20 Sep 1866 (fl), *Smart 41* (GH); Southern Arizona, 1867 (fl), *Palmer 154* (MO); Monroe, 22 Jul 1921 (fr), *Jones s.n.* (UC). APACHE CO., Canyon de Chelly National Monument, Canyon del Muerto near bottom of Many Skulls Route, 04 Nov 2001 (fr), *Rink 1108* (ASC); Navajo Nation, Canyon de Chelly National Monument, Black Road Canyon, 10 Oct 2006 (fr), *Roth & Remucal 1903* (ASC). COCHISE CO., 18 mi NE of Douglas on US Hwy 80 to Rodeo, New Mexico, 04 Oct 1942 (fr), *Wolf & Everett 11356* (DES, NY, UC); 3 mi E of Portal, 05 Sep 1981 (fl, fr), *Emslie s.n.* (ASC); ca. 6 mi W of jct between Turkey

Creek Rd and Hwy 181, 01 Sep 1980 (fl), *Hodgson 1052* (DES); Texas Canyon, 18 Aug 1963 (fl), *Lehto 2136* (ASC, DES); 4.0 mi W of Arizona-New Mexico state line, 4.8 miles west of NM Hwy 80 on NM 533 (Portal Rd.), 21 Sep 2002 (fl, fr), *Gutierrez & Gutierrez 43* (UTEP); 6 mi E of Portal, 27 Aug 1955 (fl), *Cazier s.n.* (A); 15 mi S of Benson on Rte 90, Sep 1969 (fl, fr), *Harris s.n.* (ASU); 2 mi N of Portal, 27 Aug 1964 (fr), *Lehto 3972* (ASU); Skeleton Canyon in Peloncillo Mountains, 30 Aug 1966 (fl), *Cazier 794* (ASU); 5 mi N of Paradise, 27 Aug 1966 (fl, fr), *Cazier 536* (ASU); 1.5 mi E of RR crossing in Dragoon, 25 Aug 1970 (fl, fr), *McLeod et al. 244* (ASU); San Pedro Riparian National Conservation Area, Upper San Pedro River floodplain, ca 2 km S of Charleston Road, 200-300 m E of San Pedro River, 31º37.35'N, 110º10.148'W, 15 Aug 2002 (fl, fr), *Makings 1219* (ASU); San Pedro Riparian National Conservation Area, Upper San Pedro River floodplain, ca 2.5 mi S of Hwy 82, 300 m S of Boquillas Ranch, 100 m E of San Pedro River, 31º41.5'N, 110º10.5'W, 23 Aug 2002 (fl), *Makings 1247* (ASU); San Pedro Riparian National Conservation Area, Upper San Pedro River floodplain, Palominas Road, ca. 200 m W of San Pedro River, 31º21.464'N, 110º07.508'W, 01 Sep 2003 (fl, fr), *Makings 1599* (ASU); Southern Huachuca Mountains, Coronado National Monument, east entrance, 30 Aug 1989 (fl), *Parfitt et al. 4091* (ASU); Southern Huachuca Mountains, Coronado National Monument, N of east entrance, 15 Sep 1990 (fl), *Parfitt & Christy 4646* (ASU); Sulfur Springs Valley, NW end of Willcox Playa, 0.2 mi SE of Exit 336 of I-10 (W of Willcox), 32º13.1'N, 109º52.5'W, 19 Sep 2002 (fl, fr), *Helmkamp & Helmkamp 7683A* (ASU); Riggs Ranch, 1 mi W of Chiricahua National Monument, mouth of Pickett Canyon, 08 Sep 1974 (fl, fr), *Reeves R1645* (ASU); Chiricahua National Monument, Residential Area, 06 Sep 1975 (fr), *Reeves R4463* (ASU);

Chiricahua National Monument, Residential Area, 02 Aug 1975 (fl, fr), *Reeves & Jandrey R4048* (ASU); Chiricahua National Monument, Residential Area, 22 Aug 1975 (fl), *Reeves R3665* (ASU); San Bernardino Ranch, 17 mi E of Douglas, 25 May 1981 (fl, fr), *Marrs 334* (ASU); San Bernardino Ranch, 18 mi E of Douglas, 26 Jul 1981 (fl), *Marrs-Smith 839* (ASU); San Bernardino Ranch, 18 mi E of Douglas, 26 Jul 1981 (fl), *Marrs-Smith 825* (ASU); San Bernardino Ranch, 17 mi E of Douglas, 24-26 Sep 1981 (fr), *Daniel & Marrs 1794* (ASU); floodplain of Black Draw and adjacent desert grassland along Geronimo Trail ca. 3 mi NE of jct with road to San Bernardino Ranch, ca 16.5 mi E of Douglas, 20 Aug 1983 (fl), *Daniel & Butterwick 2984* (ASU); along Silver Creek, AVA Ranch near Portal, 26 Aug 1964 (fl, fr), *Barr 64-480* (ARIZ); Elfrida, 3 Sep 1954 (fr), *Jones s.n.* (SD); Sulfur Springs Valley, 14 Aug 1947 (fl, fr), *Jones s.n.* (SD); Sanson Valley, Cave Creek Canyon, 26 Sep 1944 (fl, fr), *Barkley 14A535C* (TEX). COCONINO CO., Havasu Canyon, 18-25 Oct 1940 (fr), *Whiting 1047/4505* (ASC, ECON, MNA); near Navajo Falls, Havasu, 03 Oct 1953 (fr), *Deaver 4454* (ASC, ASU); below Navajo Falls, Havasu, 05 Aug 1950 (fr), *Deaver 2950* (ASC); Cataract Canyon, 23 Oct 1997 (fr), *Rink s.n.* (ASC); Grand Canyon Havasupai Indian Reservation, Supai Village, 19 Aug 1978 (fl, fr), *Nabhan 889* (LL, SD). GILA CO., Payson, 26 Aug 1940 (fr), *Hubert 1047/4190* (MNA); Young, 15 Oct 1977 (fr), *Pierce s.n.* (ASC); 7 mi SE of Payson, 0.5 mi N of Pocket Cabin (Old Rock House on 1973 quad.) along FSR 454, near 34°10'N, 111°13'45"W, 22 Aug 1990 (fl, fr), *Hodgson & Ecker 5958* (DES, UTEP); Reynolds Creek, 9 Sep 1932 (fl, fr), *Siltbank 159* (DES); Little Acres, ca 1 mi N of Tonto National Forest boundary on FR55, ca 2 mi S of jct between St Rte 88 and US Rte 60, 33°23.553'N, 110°49.148'W, 02 Nov 2003 (fr), *Gutierrez & Bills 441* (ASU, CS, UTEP); Intersection of Salt River and Cibecue, 27

Sep 1968 (fr), *Pinkava et al. 14189* (ASU-2); Three Bar Game Management Area, 29-30 Aug 1968 (fl, fr), *Keil 3765* (ASU); Salt River and Salt River Draw, ca. 6 mi W of Salt River Canyon bridge, 27 Sep 1968 (fr), *Pinkava et al. 14234* (ASU); Tonto National Forest, S of Pine at jct of Hwy 87 and road to Tonto Natural Bridge, 18 Sep 1977 (fr), *Parfitt 2342* (ASU); E side of Mt. Ord, Slate Creek bed, ca 0.2 mi W of Hwy 188, 09 Sep 2006 (fl, fr), *Price & Porter 518* (ASU); ca. 2.9 mi W of Reno Creek road (FS409), 02 Sep 2006 (fl, fr), *Price 509* (ASU). GRAHAM CO., Santa Teresa Mountains, BLM wilderness, along jeep trail off FR 292, NW of Black Rock, 05 Sep 1999 (fl), *Buegge 1100* (ASU); Santa Teresa Mountains, Coronado National Forest, Cottonwood Canyon, below Sand Tank, 19 Aug 1999 (fl, fr), *Buegge 1021* (ASU); 14.3 mi SW of US Hwy 70 on Aravaipa Road, 19 Oct 1968 (fr), *Pinakava et al. 15000* (ASU); 1.8 mi N of Well on road to Van Valor Spring, W of Pinaleno Mountains, 19 Oct 1968 (fr), *Pinkava et al. 15315* (ASU). GREENLEE CO., 2.6 mi W of Blue along Blue River, 14 Aug 1974 (fl), *Pinkava et al. P12432* (ASU, NY); SE of Clifton, 06 Sep 1942 (fl, fr), *Barneby 5117* (NY). MARICOPA CO., Eagle Eye Road and Tiger Wash, near Hummingbird Springs Wilderness, 07 Oct 2006 (fr), *Lester 389* (ASU); Glendale, ASU West campus, SE corner of Thunderbird and 43rd Ave, 33º36'33.3"N, 112º9'13.2"W, 19 Sep 2007 (fl, fr), *Gutierrez 1767* (ASU, CANB, CTES, UC, UTEP); Tonto National Forest, Mazatzal Mountains, along/in Sycamore Creek just E of Route 87, 33º47.828'N, 111º29.421'W, 23 Oct 2002 (fr), *Hodgson et al. 15994* (DES); Phoenix, 08 Aug 1952 (fl, fr), *Blakley 1561* (DES); 3 mi E of Scottsdale, 30 Jul 1950 (fl, fr), *Blakley 569* (DES); Fish Creek Canyon, 06 Oct 1939 (fr), *Kearney & Peebles 14889* (UC); ca. 1.5 mi S of Cave Creek Road, ca. 11 mi N of Loop 101 on Pima Road, 33º47.847'N, 111º53.482'W, 31 Oct 2003 (fr), *Gutierrez 422* (ASU); 1.5 mi E of

White Tank Mountains Regional Park, turnoff from Greenway Road to road to old quarry at NE end of park, 27 Sep 1969 (fl), *Keil 5788* (ASU); Tonto National Forest, Seven Springs Recreational Area, 33º57.974'N, 111º51.788'W, 09 Oct 1991 (fr), *Johnson & McNeill 204* (ASU); Tonto National Forest, W side of Seven Springs road on FS 2049, 33º56.75'N, 111º49.682'W, 21 Aug 2001 (fl, fr), *Doan & Damrel 954* (ASU); Sierra Estrella Regional Park, Salt River Bed, 1 mi E of park entrance, 09 Sep 1973 (fl, fr), *Sundell & Sundell 347* (ASU); corner of Hawes and Baseline Road, 19 Sep 1999 (fl, fr), *Damrel & Mejia 2525* (ASU); Hassayampa River Preserve, ca. 2 mi SE of Wickenburg on Hwy 89, 10 Aug 1989 (fl), *Wolden 255* (ASU). MOHAVE CO., Whitmore Canyon, just N of the Bar 10 Ranch, 10 Oct 2000 (fl), *Higgins & Atwood 21788* (NY); E side of Hualapai Mts., near Blake Ranch Road (formerly Peacock Mt Road) along Timber Wash, 12 Aug 1986 (fr), *Butterwick & Daniel 9045* (ASU); Hualapai Mts., E side of foothills; lower Moss Road at Stokes Well, ca. 0.5 mi E of Blakes Ranch Road, 26 Aug 1998 (fl, fr), *Anderson 98-65* (ASU); 5.3 mi SE of Burro Creek Bridge along Rte 93, 20 Sep 1969 (fl, fr), *Keil et al. 6338* (ASU); Cerbat Mountains, 20 Jul 1977 (fl), *Jorden 301* (MNA). NAVAJO CO., Hopi Indian Reservation, near Araibi, 08 Sep 1937 (fr), *Whiting 854/2821* (MNA). PIMA CO., Rte. 86, 0.75 mi from jct of Hwys 386 & 86, 02 Sep 1979 (fl, fr), *Hodgson 546* (DES); Santa Catalina Mountains, s.d. (fr), *Lemmon & Lemmon s.n.* (UC); Coronado National Forest, Santa Rita Mountains foothills, along Arizona Trail where it intersects FSR 62 (Box Canyon or Greaterville Road), 31º47.862'N, 110º44.839'W, 23 Aug 2002 (fl), *Hodgson et al. 15601* (DES); Coronado National Forest, Santa Rita Mountains foothills, along Arizona Trail where it intersects FSR 62 (Box Canyon or Greaterville Road) near Road 4072, 31º48.541'N, 110º44.123'W, 23 Aug 2002 (fl, fr), *Hodgson et al.*

15649 (DES); Garcia Ranch, Garcia Represo, E of Sasabe, 19 Aug 1981 (fl, fr), *Van Devender s.n.* (UTEP); Santa Cruz Valley near Tucson, 29 Jul 1881 (fl, fr), *Pringle s.n.* (GH, NY-2); Tanque Verde Creek Bridge, between Tanque Verde Road and Speedway Blvd, along Houghton Road, Tucson, 27 Oct 1992 (fr), *Ricketson & Schmidt 4981* (MO); road to Greaterville, 3.6 mi E of jct to Madera Canyon, 11 Oct 1968 (fr), *Pinkava et al. 14530* (ASU, NY); Tucson, 25 Sep 1892 (fl, fr), *Toumey s.n.* (NY); Tucson, 27 Jul 1894 (fl, fr), *Toumey s.n.* (UC); near Fort Lowell, 15 Sep 1900 (fr), *Griffiths 1561* (NY-2); Tucson, 10 Sep 1903 (fl, fr), *Thornber 3* (MO, NY-2, UC); Santa Rita Experimental Station, Pasture #9, 0.3 mi W of E boundary along Greaterville-Continental Road, 7 Oct 1967 (fl), *Keil et al. 9664* (ASU, NY); W of Tucson, 13 Jul 1908 (fr), *Sherff s.n.* (K); Greaterville Rd turnoff, ca. 0.25 mi E of Greaterville, 25 Aug 1971 (fl, fr), *Pinkava et al. 669* (ASU); bottomlands of Cienega Creek, S side of Pantano Interchange E of Tucson along I-10, 31º50.035'N, 110º34.04'W, 29 Sep 2001 (fr), *Rainey et al. 163* (ASU); wash along Arivaca Road ca. 8 rd mi W of I-19, late Sep 1992 (fl, fr), *Christy 1173* (ASU); Canada del Oro ca. 10 mi N of Tucson, 10 Aug 1966 (fl), *Bohrer 1084* (ARIZ); ca 2.5 mi W of SR 83 along Greaterville-Box Canyon Road, 31º46'36.7"N, 110º43'20.3"W, 07 Sep 2007 (fl, fr), *Gutierrez 1755* (ASU, F, GH, MICH, MO, SP, US, UTEP); ca 4.0 mi W of SR 83 along Greaterville-Box Canyon Road, 31º46'59.1"N, 110º44'34.7"W, 07 Sep 2007 (fl, fr), *Gutierrez 1757* (ASU, TEX, UTEP). PINAL CO., Burns, 16 Jul 1921 (fl, fr), *Jones s.n.* (UC); Aravaipa Canyon, 17 Aug 1970 (fl, fr), *Correll & Correll 39367* (LL); 0.6 mi S of Akimel Road, N of Cottonwood, 33º04'6.5"N, 111º40'7.8"W, 21 Sep 2007 (fl, fr), *Gutierrez 1768* (ASU, UTEP); 17.8 mi NW of Hwy 77 along Hwy 79 between Oracle Junction and Florence, 32º45'32.3"N, 111º08'39.7"W, 11 Sep 2008 (fl, fr), *Gutierrez 2234* (ASU, BRIT, ID, NO, OS, UTEP); San Pedro River Floodplain S of San Manuel, 01 Sep 2000 (fr), *Bagstad 169* (ASU); San Manuel, 23 Sep 1973 (fl, fr), *McIver 19* (ASC); Tonto National Forest, Superstition Wilderness Area, Miles Ranch Trailhead, Pinto Creek turnoff from Hwy 60 on FR 287 past Magma Copper Mine ca. 12 to end of Rd 278A, 20 Sep 1992 (fr), *Rice et al. 1478* (ASU); Oracle Junction, along road to Biosphere II, 24 Sep 1994 (fl, fr), *Landrum & Bye 8310* (ASU); 3 mi SE of Maricopa Hwy and Goodyear Road, 28 Sep 1971 (fl, fr), *Oxford 115* (ASU); Sacaton, Gila River bed on flats N of main channel, 24 May 1991 (fr), *Rea & Cassa 1747* (SD); Maricopa Road just S of Gila River, 25 Oct 1985 (fr), *Rea 968* (SD); 2.5 mi S of Hunt Highway along SR 87, 33º10'45.8"N, 111º48'15.2"W, 21 Sep 2007 (fl, fr), *Gutierrez 1774* (ASU-3, ARIZ, ASC, BRIT, BRY, DES, F, GH, MO, NY, SD, UTEP-3); 17.8 mi NW of Hwy 77 along Hwy 79 between Oracle Junction and Florence, 32º45'32.3"N, 111º08'39.7"W, 11 Sep 2008 (fl, fr), *Gutierrez 2234* (ASU, BRIT, ID, NO, OS, UTEP). SANTA CRUZ CO., Calabasas Picnic Area, 6.9 mi W of I-19 along Rte 289, 10 Sep 1985 (fl, fr), *Hodgson & Quirk 3828* (DES); Coronado National Forest, Santa Rita Mountains foothills, along Arizona Trail SE of Kentucky Camp and N of Fish Canyon, near FSR 163, 31º44.3'N, 110º44.3'W, 10 Sept 2000 (fl,fr), *Hodgson et al. 12796a* (DES); Coronado National Forest, Santa Rita Mountains foothills, Agua Caliente Wash, 31º41.566'N, 110º57.383'W, 21 Sep 2002 (fl, fr), *Hodgson et al. 15794* (DES); 1 mi W of Elgin-Canelo Road along SR 83, 31º36'28.9"N, 110º35'03.7"W, 07 Sep 2007 (fr), *Gutierrez 1746* (ASU); Pena Blanca Canyon, 17 Aug 1966 (fl), *Tate 334* (ASU); Pena Blanca Canyon, 0.5-1 mi S (upstream) from creek's entrance into Pena Blanca Lake, 29 Aug 1966 (fl, fr), *Tate 487* (ASU); SE of Patagonia, 5.2 mi NW of Santa Cruz River crossing, 12 Oct 1968 (fr), *Pinkava et al. 14790* (ASU); SE of

Patagonia, 0.6 mi S of Boy Scout Camp, 12 Oct 1968 (fr), *Pinkava et al. 14851* (ASU-2); Coronado National Forest, FR 61 at Lochiel, between Nogales and Coronado National Memorial, 14 Aug 1989 (fl), *Austin & Austin 7566* (ASU); Sycamore Canyon, 6 Oct 1967 (fr), *Keil et al. 9920* (ASU); San Rafael State Natural Area, Arizona Game and Fish Department Monitoring Site, vicinity of jeep trail in San Rafael Valley to immediate W of Santa Cruz River, 0.5 mi N of Mexico Border, 17 Sep 2006 (fl, fr), *Reif 10474* (ASC); Coronado National Forest, SR 87 at Turkey Creek Crossing, 31º32'49.1"N, 110º30'58.1"W, 07 Sep 2007 (fl, fr), *Gutierrez 1742* (ASU, CANB, E, K, UTEP); 1 mi W of Elgin-Canelo Road along SR 83, 31º36'28.9"N, 110º35'3.7"W, 07 Sep 2007 (fl, fr), *Gutierrez 1746* (ASU). YAVAPAI CO., Agua Fria National Monument, Agua Fria riverbed, SE of mouth of Little Sunset Canyon, 34º10.21'N, 112º06.77'W, 14 Oct 2005 (fr), *Damrel et al. 3402* (DES); Agua Fria National Monument, road to Richinbar Mine, 34º12.624'N, 112º6.491'W, 05 Oct 2004 (fl, fr), *Damrel et al. 2733* (DES); 0.9 mi S of Rte. 89A, on road to state hwy 69, 29 Aug 1971 (fl), *Weber s.n.* (DES); Soda Springs on Beaver Creek, 13 mi above Camp Verde, 30 Jun 1928 (st), *Wolf 2397* (GH); Fort Verde, 26 Aug 1887 (fl), *Mearns 215* (NY); Fort Verde, 29 Sep 1887 (fl, fr), *Mearns 215* (NY); Fort Verde, 14 Sep 1887 (fl, fr), *Mearns 215* (NY); at bridge between Congress and Yarnell, 1.2 mi NE of Congress, Hwy 89 and Hwy 71, 26 Sep 1994 (fl, fr), *Landrum & Bye 8322* (ASU); Chino Valley, 27 Aug 1990 (fl, fr), *Baker 7949* (ASU); 1.3 mi inside Prescott National Forest just N of Wilhoit, 30 Sep 1967 (fr), *Keil 2747* (ASU); between Bumblebee and Cleator (FR 259) SE of Prescott National Forest, 09 Aug 1989 (fl, fr), *Austin & Austin 7559* (ASU); Bradshaw Mountains, SSW of Prescott, 1 km N of Johnson Flat at The Clements, 34º09.8'N, 112º26.5'W, 03 Oct 2002 (fl, fr), *Baker*

14982.1 (ASU); Dry Creek Road and Thunder Mountain Road, 34°52'3.7"N, 111°49'13.6"W, 18 Aug 2005 (fl, fr), *Licher 1433* (ASC); Red Rock State Park, visitor center, 34°48'39.2"N, 111°49'37.2"W, 23 Sep 2005 (st), *Licher 1508* (ASC); Wet Beaver Creek 1 km from Ranger Station, McGuireville, 02 Sep 1979 (fl), *PDE s.n.* (ASC); Verde Valley, confluence of Oak and Spring Creeks, 08 Sep 1979 (fl), *Peper s.n.* (ASC); John Babbitt Farm No. 2, 0.5 mi N of Camp Verde, 02 Aug 1961 (fl, fr), *Van Gorder 183* (ASC); Beaver Creek, 4 mi N of Camp Verde, 10 Sep 1978 (fl, fr), *McKusick s.n.* (ASC); near Wet Beaver Creek Ranger Station, s.d. (fl, fr), *Hevly s.n.* (ASC); 1.5 mi NE of Clarkdale across from Tapco in Verde River floodplain, 14 Oct 1972 (fl), *Trune s.n.* (ASC). Cornville Quadrant, Aug 1979 (fl, fr), *Jeffers s.n.* (ASC); 15 mi NE of Camp Verde in fallow fields of Verde Park School, 3 Oct 1976 (fl, fr), *Kalafarski s.n.* (ASC); Dry Beaver Study Plot, 7 mi S of Sedona, 20 Aug 1971 (fl), *Hall 767* (MNA); 2 mi N of Prescott, 11 Aug 1961 (fl), *McCormick s.n.* (MNA); Fort Whipple, Verde River, 07 Sep 1865 (fl), *Coues & Palmer 525* (MO). –CALIFORNIA: SAN DIEGO CO., N side of Hwy 78, lower Banner Grade, 19 Sep 1988 (fl, fr), *Clemons & Jonsson 2186* (SD); N side of Hwy 78, 1.3 mi E of Banner, 13 Nov 1987 (fl, fr), *Armstrong 1282* (SD); Otay Mesa, 09 Oct 1939 (fl), *Osborne s.n.* (SD); Otay Mesa, 19 Oct 1939 (fr), *Osborne s.n.* (SD). –NEVADA: CLARK CO., Moapa Indian Reservation, 06 Jun 1938 (fl), *Train 1917* (NY). –NEW MEXICO: no locality data given, 1851 (fl, fr), *Wright 1448* (GH); no locality given, s.d. (fl), *Le Roy s.n.* (NY). BERNALILLO CO., Albuquerque, Indian School Road E of Tramway Blvd., 19 Sep 1987 (fl, fr), *Clemons 1808* (SD). CATRON CO., Gila National Forest, San Francisco Hot Springs, 1 mi SE of jct of US Hwy 260/180 at end of USFS Road 519 along the E bank of the San Francisco River, ca 35 mi NW of Silver City, 28 Aug 1988 (fl), *Ricketson & Raechal*

4277 (ASC, MO); 4 mi W of Alma, Vigil Canyon, 05 Jul 1984 (fl), *Doolittle 10* (TEX). DOÑA ANA CO., Bishop Cap Hills, S side of South Hill on Ft. Bliss Military Reservation, 21 Aug 2008 (fl), *Worthington 35387* (ASU); near southern boundary of Ft. Bliss, 4 km S of Main Post, 29 Aug 1991 (fl, fr), *Anderson 5112* (TEX); Potrillo Mts., West Portillo Mts., S side of Guzman's Lookout Mtn., 23 Aug 1986 (fl), *Worthington 14716* (UTEP); Organ Mts., 2.1 mi S US 70 by road to Aguirre Springs, 20 Sep 1980 (fl, fr), *Worthington 6502* (UTEP); 2 km NNW of top of Bishop Cap, 05 Sep 1988 (fl, fr), *Worthington 17283* (UTEP); White Sands Missile Range, 30 Sep 2005 (fl), *Corral-Diaz s.n.* (ASU). EDDY CO., S of Carlsbad at jct of Dark Canyon Road with US 62-180, 32º17.208'N, 104º17.116'W, 16 Sep 2007 (fl, fr), *Worthington 34975* (ARIZ, ASU). GRANT CO., Little Hatchet Mts, 1.0 mi SE of top of Playas Peak, 27 Sep 1997 (fl), *Worthington 27167* (UTEP); Mangas Canyon 16 mi WNW of Silver City, 25 Sep 1944 (fr), *Barkley 14744b* (TEX); City of Rocks State Park, 5 mi E of jct of US Hwy 260/180 via NM Hwy 61 along the park service road W of Table Mtn, ca. 28 mi N of Deming, 28 Aug 1988 (fl, fr), *Ricketson & Raechal 4249* (MO); Fort Bayard, Aug 1895 (fl), *Mulford 947* (MO, NY). HIDALGO CO., Peloncillo Mountains, Clanton Draw at E National Forest Property Line, 31º31.56'N, 108º58.62'W, 05 Sept 2003 (fl), *Worthington 32261* (ASU); Peloncillo Mountains, Tank Mtn., ca 10 mi SSW of Animas on S end of Tank Mtn., 09 Aug 1986 (fl, fr), *Worthington 14629* (ASU, NY); Big Hatchet Mountains, N end of mtns. in the Hatchet Gap area, 19 Sep 1993 (fl, fr), *Worthington 22514* (UTEP); Little Hatchet Mountains, Granite Pass, 05 Sep 1994 (fl, fr), *Worhtington 23518* (UTEP); Apache Hills, 4.5 mi S of Hachita at W end of the Apache Hills, 18 Sep 1994 (fr), *Worthington 23644* (UTEP); Cienega Lake, 24 Aug 1966 (fl), *Cazier 496b* (ASU); Alamo Hueco Mts., 1.8 mi N of Alamo Hueco

Ranch HQ, 10 Aug 1986 (fl, fr), *Harris s.n.* (UTEP); Guadalupe Canyon, ca 25 mi E of Douglas, Arizona, 17 Aug 1971 (fl), *Hess 2792* (BRIT); Playas Valley, Vitorio Cattle Co. Ranch, 9.7 mi S of Cienegas Ranch House on road to Cloverdale, 31º30'N, 108º30'30''W, 17 Aug 1972 (fl, fr), *Chiang, Wendt, & Johnston 8639* (LL). LUNA CO., Florida Mtns., Mahoney Park, 01 Oct 1978 (fl, fr), *Worthington 3652* (UTEP); Florida Mtns., ca 0.5 mi NW from top of Baldy Peak, 25 Aug 1990 (fl, fr), *Worthington 18637* (NY); Florida Mtns., Florida Gap, 25 Aug 1984 (fl, fr), *Worthington 12472* (NY); Victorio Mtns., 3 mi S of I-10 (Gage exit), 25 Aug 1984 (fl, fr), *Worthington 12395* (UTEP, NY); Tres Hermanas Mtns., 5 mi NW of Columbus in Rascon Canyon, 29 Aug 1993 (fl, fr), *Worthington 22322* (NY, UTEP); Cedar Mts., N side of Cedar Mtn., ca 8.5 air mi NE of Hachita, 7 Sep 1996 (fl, fr), *Worthington 25840* (UTEP); 9 mi E of Deming, 05 Oct 1944 (fr), *Hershey 3473* (GH); Deming, 31 Aug 1895 (fl, fr), *Mulford 1126a* (K, MO, NY). OTERO CO., Jarilla Mtns, 0.3 mi SE of Orogrande Range Camp entrance (ca. 3 air mi NW of Orogrande), 32º23.33'N, 106º07.77'W, 22 Oct 2005 (fr), *Worthington 33899* (ASU); Fort Bliss Military Reservation, North Training Area, Jarilla Mtns., tank at N end of Elephant Mtn., 32º23.76'n, 106º08.4'W, 22 Oct 2005 (fl, fr), *Worthington 33902* (ASU). SANDOVAL CO., 15 mi W of Albuquerque on Hwy 44, 29 Aug 1974 (fl), *Shultz & Shultz 1319* (NY). SOCORRO CO., E of San Antonio (ca 13 mi), then S 3 mi of Hwy 525 to N boundary of White Sands Missile Range, collected in field as seedling on 12 Aug 2001, pressed 19 Sep 2001 (fl), *Freeman 292* (UTEP); 3.4 mi S of NM 380 on NM 525, 19 Aug 2001 (fl, fr), *Gutierrez 35* (UTEP); San Antonio, Bosque del Apache National Wildlife Refuge, Spring 1958 (fl), *Fleetwood 877* (US); San Antonio, Bosque del Apache National Wildlife Refuge, Spring 1958 (fl), *Fleetwood 840b* (US).

VALENCIA CO., I-25 at Exit 190 overpass, 0.2 mi N of mile marker 190 and 6.2 miles N of Socorro Co. line, 15 Aug 2001 (fl, fr), *Freeman 286* (UTEP-2). –TEXAS: EL PASO CO., Franklin Mountains, 1.1 mi W jct Trans-Mountain Road and Gateway South, 31º53'49"N, 106º27'35"W, 07 Oct 1978 (fl, fr), *Worthington 3696* (UTEP); 1.8 mi NE of jct at I-10 and Mesa, 31º51'30"N, 106º33'30"W, 28 Oct 1978 (fl, fr), *Worthington 3778* (UTEP); Franklin Mountains, McKelligon Canyon, 26 Sep 1963 (fl, fr), *Wells 8* (UTEP); Franklin Mountains, 1.2 mi SE from top of North Franklin Mt., 31º53'25"N, 106º28'53"W, 18 Sep 1977 (fl, fr), *Worthington s.n.* (UTEP 6447); Three Sisters Hills in El Paso, ca. 1.5 mi N of jct of I-10 with North Mesa, 31º52'N, 106º33'30"W, 24 Aug 1997 (fl, fr), *Worthington 26982* (UTEP); Three Sisters Hills in El Paso, ca 1.5 air miles N of jct of I-10 with North Mesa, 31º52'N, 106º33'30"W, 15 Sep 1988 (fl, fr), *Worthington 17407* (UTEP); El Paso, 0.3-0.4 mi N of Kolhberg School along El Paso Natural Gas pipeline and on W bajada of the Franklin Mts., 31º53.30'N, 106º33.42'W, 27 Oct 2006 (fr), *Worthington 34496* (ASU); 5 mi NE of El Paso, 31 Aug 1948 (fr), *Warnock 8209* (LL, SMU); El Paso, 24 Oct 1931 (fr), *Whitehouse s.n.* (TEX). HUDSPETH CO., Indio Mountains, Indio Ranch Research Area, near Peccary Tank, 30º45'20"N, 105º00'15"W, 22 Sep 1990 (fl, fr), *McGolderick & Lieb 41* (UTEP); 0.6 mi NE of TX Hwy 20 along Acala Road, 31º20'09.6"N, 105º54'07.3"W, 18 Sep 2008 (fl, fr), *Gutierrez 2173* (ASU-2, BRIT, BRY, NY, SD, UTEP); 5.6 mi E of FM 234 along FM 192, 27 Jul 2003 (fl, fr), *Gutierrez 247* (UTEP); ca. 1 mi N of TX Hwy 20, ca. 0.5 mi E of Acala Road, 31º20'02"N, 105º54'16.4"W, 20 Sep 2006 (fl), *Gutierrez & Gutierrez 1224* (ASU, HUEFS, UTEP); Esperanza, ca. 4 mi E of FM 2217, ca. 2 mi W of FM 34 along FM 192, 31º9'4"N, 105º41'19"W, 14 Aug 2004 (fl, fr), *Gutierrez & Gutierrez 901* (ASU); Esperanza, ca. 2 mi E of FM 2217, ca. 3.5 mi W of FM 34 along FM 192, 31º09'53"N, 105º42'50"W, 14 Aug 2004 (fl, fr), *Gutierrez & Gutierrez 899* (ASU-2); 1.4 mi SW of McNary (TX Hwy 20) along FM 192, 31º13'34.9"N, 105º48'19.4"W, 18 Sep 2008 (fr), *Gutierrez 2180* (ASC, ASU, UTEP); 0.8 mi NE of FM 192 along TX Hwy 20, 31º15'15.7"N, 105º48'08.1"W, 18 Sep 2008 (fl, fr), *Gutierrez 2189* (ASU, E, K, UC, UTEP); 0.6 mi NE of TX Hwy 20 along Acala Road, 31º20'9.6"N, 105º54'7.3"W, 18 Sep 2008 (fl, fr), *Gutierrez 2173* (ASU, BRIT, BRY, NY, SD, UTEP); ca. 2 km E of Quail Tank in the SE Hueco Mtns, 24 Aug 1976 (fl), *Butterwick & Lamb 3235* (TEX). JEFF DAVIS CO., Miller Ranch, 03 Jul 1948 (fl), *York 48269* (TEX); Lower Madera Canyon, N of Timber Mtn, 21 Jun 1977 (fl), *Weedin & Crabtree 657* (TEX). PRESIDIO CO., San Antonio Canyon, S side of Chinati Mtns, 13 Jun 1977 (fl, fr), *Butterwick & Lott 3841* (TEX); Chinati Mtns State Natural Area, 29º53'10"N, 104º30'02"W, 19 Sep 2004 (fr), *Lott, Rankin, & Butterwick 5369* (TEX). –UTAH: WASHINGTON CO., Lytle Ranch, Beaver Dam Wash, 26 Sep 1985 (fr), *Welsh & Baird 23669* (GH); Beaver Dam Wash, Lytle Ranch, 19 Aug 1985 (fl, fr), *Baird 1815* (NY); Lytle Ranch Preserve, 22 Oct 1998 (fr), *Higgins 19946* (NY); Beaverdam Mtns., jct of Hwy 91 and Gunlock road, 3 Aug 1966 (fl), *Higgins 812* (NY).

CULTIVATED. *Burris s.n.* (ASU, fl, fr); *Gutierrez 02* (UTEP, fl); *Gutierrez 34* (UTEP, fr); *Gutierrez 42* (UTEP-2, fl, fr); *Johnsen s.n.* (MNA, fl, fr).

This variety can be distinguished by the shorter anthers, styles and capsule bodies and rostra, and the presence of black seeds. The type specimen for *P. parviflora* needs clarification and possible lectotypification. In his protologue for *Martynia parviflora*, Wooton (1898) gives two localities where he collected this species, but only gives a collection number for the first locality (*Wooton 580*). He then gives a discussion of other specimens that "should be referred here," including *Thurber 913*, *Mearns 215*, and *Wright 429*. It is debatable whether Wooton meant to typify this species with his first specimen (*Wooton 580*), or if all of the specimens should be regarded as syntypes because of the lack of an explicit designation of type. Two different species have been identified on specimens of *Wright 429* (*P. althaeifolia* and *P. fragrans*), and Article 9.9 of the Code (McNeill et al. 2006) could arguably be invoked if all the specimens are to be regarded as syntypes. Article 9.9 states that "when the material designated as type is found to belong to more than one taxon, a lectotype…as a substitute for it may be designated." Wooton and Standley (1915) later placed *M. parviflora* into the genus *Proboscidea*, and explicitly cited one type specimen (*Wooton 580*). Since *Wright 429* is problematic, and Wooton and Standley later intended *Wooton 580* to be the type, its status should be clarified with a lectotypic designation. Additionally, since there exist at least five known specimens of *Wooton 580*, one of the two sheets at US, where both Wooton and Standley worked extensively, should be regarded as the second-step lectotype. Lectotypification will be done in another publication so as not to call into question the validity and effectiveness of this dissertation under Articles 7.10 and 30.5 of the Code (McNeill et al. 2006).

One specimen at ASU (*Keil et al. 9920*) appears to be introgressed with the domesticated variety *Hohokamiana*. Seeds are white, black and various shades of gray. It is placed in var. *parviflora* because the fruits do not exhibit the long beak characteristic of the domestic variety, and the locality, Sycamore Canyon in Santa Cruz County, is not known to be a site typically cultivated by indigenous peoples.

10a(ii). Proboscidea parviflora (Woot.) Woot. & Standl. ssp. **parviflora** var. **Hohokamiana** Bretting, Amer. J. Bot. 69: 1537. 1982. –TYPE: U.S.A. Arizona. Pima Co., Sells, Papago Indian Reservation, cultivated as a field crop in the houseyard of Inez Francisco, *Bretting 305c*, also numbered *Nabhan X462* (holotype: ARIZ [2 specimens, photos at ASU!], isotype: IND [photo at ASU!]).

Description. Flowers: anthers longer than 2.8 mm; style longer than 15 mm. Fruits: endocarp bodies longer than 9 cm, fruit crests longer than 5 cm and higher than 5 mm; rostrum longer than 18 cm. Seeds white.

Phenology. Flowering from July-August.

Distribution and habitat (Fig. 31). Cultivated by Native Americans for basketry fiber in the southwestern United States.

Specimens examined. **U.S.A.** CALIFORNIA: INYO CO., abandoned field below mouth of Hunter Canyon, Saline Valley, 23 Jul 1955 (fl, fr), *Roos & Jaeger 6516* (SD). –ARIZONA: COCONINO CO., Havasu Canyon, 18-25 Oct 1940 (fr), *Whiting 1047/4504* (ECON, MNA); Havasu Canyon, 14 Jul 1948 (fr), *Clover 5104* (SMU). GILA CO., Fort Apache Indian Reservation, Cibecue, irrigated field by Cibecue Creek, 09 Aug 1977 (fl, fr), *Nabhan 665* (MNA); Hopi Land, Lower Moenkopi, 15 Aug 1978 (fl, fr), *Nabhan 884* (SD). MARICOPA CO., Pima garden field near Komatke, 19 Aug 1985 (fl, fr), *Rea 861* (SD). PIMA CO., E edge of landfill, Tumamoc Hill, 13 Sep 1983 (fr), *Bowers 2727* (SD). Mohave Co., Kaibab southern Paiute Reservation, Kaibab Village, 24 Aug 1979 (fr), *Reichardt & Nabhan 1106* (LL). –NEVADA: CLARK

CO., near Moapa Indian Agency, 27 Sep 1937 (fr), *Murphey 675* (UC). –UTAH: WASHINGTON CO., Virgin City, 27 Sep 1894 (fr), *Jones 6086* (MO-2, NY-3, UC); Beaver Dam Wash, Terry's Ranch, 5 Oct 1969 (fr), *Welsh et al. 9522* (NY).

CULTIVATED. *Armstrong s.n.* (SD, fl, fr); *Bohrer 1257* (ASU, fr); *Damrel 954* (ASU, fl, fr); *Gutierrez 007* (UTEP, fr), *Gutierrez 1763* (ASU-2, DES-2, fl, fr); *Mittleman s.n.* (ASU, fl, fr); *Plowman 13830* (MO, NY, fl); *Plowman 13866* (MO, NY, fr).

This variety can be distinguished by the longer anthers, styles and capsule bodies and rostra, and the presence of white seeds. The epithet *Hohokamiana* commemorates the Hohokam, an extinct culture that pre-dated, and most likely gave rise to, the Pima and Papago of southern Arizona and northwestern Mexico. These tribes cultivated the variety for the fiber from the fruits, the strips of which are woven into baskets. Cultivation of the variety continues today in many of the tribes across the southwestern United States.

10b. Proboscidea parviflora (Woot.) Woot. & Standl. ssp. **gracillima** (Hevly) Bretting., Southw. Naturalist 30: 150. 1985. *Proboscidea gracillima* Hevly, Madroño 20: 392. 1970. –TYPE: MEXICO. Baja California Sur: Mesa de San Javier (NE of Misión San Javier), *Carter 4993* (holotype: UC [photo at ASU!], isotype: MEXU US [photo at ASU!]).

Description. Leaves opposite; petioles to 15 cm long; apex obtuse, rounded; margins entire, sometimes denticulate. Inflorescences surpassing the foliage;

peduncles to 2.5 dm long. Flowers 2.4-4 cm long, 15-24 per inflorescence; pedicels 4-5 cm long; anthers 4.2-4 mm long. Fruit endocarp body 5-10 cm long; the endocarp rostrum 1-2 times the length of the body. Seeds black.

Phenology. Flowers from August to November.

Distribution and habitat (Fig. 31). Disturbed soils in arid lands near Sierra de La Giganta, Baja California del Sur, Mexico; 200-850 m.

Vernacular Names. Espuela del Diablo.

SPECIMENS EXAMINED. **MEXICO**. BAJA CALIFORNIA SUR: El Llanito, E end of Valle de Los Encinos on S side of Cerro Giganta, 26º04'N, 111º33'W, 28 Sept 1967 (fl, fr), *Moran & Carter 5289* (ARIZ, SD, UC); Mesa de la Higuera, NE of Cerro Giganta along trail to Arroyo Hondo, 26º08'N, 111º33'W, 30 Aug 1971 (fl), *Carter 5628* (GH [1 sheet, 1 bagged specimen])); N of Comondú, 03 Oct 1941 (fl), *Hammerly 179* (UC); N of Rancho del Cayuco, trail to Rancho San Francisco, NE of Cerro de la Giganta in the Sierra de la Giganta, 26º08'N, 111º33'W, 08 Oct 1951 (fl, fr), *Carter & Kellogg 3137* (UC); Tinaja de Naucojoa, Cerros de Naucojoa W of Llanos de San Juan, 26º16'N, 111º38.5'W, 24 Nov 1962 (fl, fr), *Carter 4478* (UC); ca. 50 mi E of Ciudad Constitución, E of Rancho Tijuana, 25º12'01''N, 111º01'45''W, 22 Oct 2001 (fl), *Rebman 7688* (SD); Sierra Guadalupe, between San José de Magdalena and San Sebastian, 27º05'N, 112º21'W, 21 Sep 1997 (fl, fr), *Rebman & Roberts 4303* (SD); 1.6 mi E of Comondú, 26º03'N, 111º47'W, 06 Oct 1967 (fl, fr), *Howe 4444* (SD); Loreto, near Agua Verde, 14 Sept 2000 (fl), *Dominquez 2808* (ARIZ).

This subspecies can be distinguished on the basis of having unlobed leaves with an apex angle less than 90º, a peduncle longer than 15 cm, pedicels longer than 32 mm, and more than 15 flowers per inflorescence. It does not intergrade with either of the other two subspecies, though a specimen of ssp. *parviflora* (*Brandegee s.n.* [UC]) has been collected within 15 km of ssp. *gracillima*.

10c. Proboscidea parviflora (Woot.) Woot. & Standl. ssp. **sinaloensis** (Van Eseltine) Bretting., Southw. Naturalist 30: 150. 1985. *Martynia sinaloensis* (Van Eseltine) Wiggins & Rollins, Contr. Dudley Herb. 3: 271. 1943. *Proboscidea sinaloensis* Van Eseltine, Tech. Bull. N. Y. State Agr. Exp. Stat. 149: 24. 1929. –TYPE: MEXICO. Sinaloa: Topolobampo, 15-25 Sep 1897, *Palmer 230* (holotype: US [photo at ASU!]: isotype MICH! [photo at ASU!]).

Description. Leaves opposite to sub-opposite; petioles to 30 cm long; apex acute, angulate; margins 3- to 7-lobed, denticulate. Inflorescences many-flowered and surpassing the foliage; peduncles to 4-7 dm long. Flowers 2.5-4 cm long, 20-40 per inflorescence; pedicels 3.5-9 cm long; anthers 4.2-5 mm long. Fruit endocarp body 5-10 cm long; the endocarp rostrum 1-2 times the length of the body. Seeds black.

Phenology. Flowering from July to November, occasionally in January and February.

Distribution and habitat (Fig. 31). Disturbed soils along roads and arroyos of arid and semiarid lands in northwestern Mexico (Nayarit, Sinaloa, and Sonora); 0-200 m (0-500 ft).

Common names. Aguaro, Aguaro sin camote, Las cinco llagas, toloache, cuernos.

SPECIMENS EXAMINED. **MEXICO**. NAYARIT: near Jesus Maria, 26 Jul 1970 (fl, fr), *Norris & Taranto 13929* (MICH). –SINALOA: El Tres Rios Motel, 07 Aug 1960 (fl), *Arms et al. s.n.* (ARIZ); Cerro Llano Redondo, W of Caimanero, 08 Oct 1944 (fl, fr), *Gentry 7090* (ARIZ, F, GH, NY, UC); Guasave, Sep 1932, *Smith s.n.* (F); 5-10 mi N of Los Mochis at km 1726, 18 Sept 1962 (fl, fr), *Barr 62-830, with Dennis & Hevly 2839* (ARIZ, SD); ca. 75 mi N of Mazatlan near Espinal at km 1321, 18 Sept 1962 (fl, fr), *Barr 62-828, with Dennis & Hevly 2837* (ARIZ); 19 mi N of El Burrion, 106 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2546* (ARIZ); 13 km S of ISST Clinic, Culiacan, along Hwy 15, 15 Aug 1977 (fl, fr), *Bretting & Johnson 363* (ARIZ); Imala, 03 Feb 1940 (fl), *Gentry 5465* (ARIZ-2, GH, MO, NY); Espinal, 08 Oct 1964 (fl, fr), *Barr & Barr 64-562* (ARIZ); 27 mi N of Mazatlan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2531* (ARIZ); 134 mi N of Mazatlan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2536* (ARIZ); 9 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2538* (ARIZ); 22 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2540* (ARIZ); 38 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2541* (ARIZ); 47 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2543* (ARIZ); 61 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2544* (ARIZ); 69 mi N of Culiacan, 28 Aug 1961 (fl, fr), *Hevly & Hevly 2545* (ARIZ); La Noria foothills, 08 Oct 1925 (fr), *Mexia 191* (MO, UC); Culiacan, 19 Aug 1904 (fl, fr), *Brandegee s.n.* (UC-2). –SONORA: 16 mi S of Hermosillo on the road to La Palma, 01 Sept 1941 (fl, fr), *Wiggins & Rollins 197* (ARIZ, GH, MO, ND, NY); 26 km S of Navajoa on Mex 15, 28 km by air from Huatabampo, 26°51'13"N, 109°22'15"W, 16 Aug 1994 (fl), *Friedman & Espinosa 251-94* (ASU); 9.8 km W of Mex

15 on Las Bocas Road, 5 km N of Las Bocas Road, 37 km by air SE of Huatabampo, 5.6 km E of Las Bocas, 26º39'10"N, 109º19'30"W, 19 Jan 1995 (fl, fr), *Friedman & Zittere 120-95* (ASU); Alamos-Navajoa Highway, 25 Sep 1986 (fl), *CICTUS 1450* (ARIZ); 17 mi S of Hermosillo, 29 Aug 1961 (fl, fr), *Hevly & Hevly 2551* (ARIZ); 7.0 mi N of Guirocoba, 04 Aug 1988 (fl, fr), *Salmon s.n.* (ARIZ); 3 mi N of Navajoa, 29 Aug 1961 (fl), *Hevly & Hevly 2548* (ARIZ); S of Navajoa, 06 Sep 1962 (fl, fr), *Barr 63-553, Dennis and Hevly 2561* (ARIZ); 4 mi S of Navajoa, 07 Nov 1958 (fl, fr), *Gentry 17630* (ARIZ, LL); Guaymas, 29 Aug 1961 (fl), *Hevly & Hevly 2550* (ARIZ); Guaymas, Oct 1887 (fl, fr), *Palmer 326* (GH [1 sheet, 1 bagged specimen], K, NY-2); 10 mi W of Alamos, 08 Aug 1957 (fl), *Solbrig & Ornduff 4399* (GH, NY); Huerigo, 18 Oct 1890 (fl, fr), *Lumholtz 175* (GH); ca. 2.2 mi NE of Hwy 15 (toward a microwave tower), ca. 6.9 mi SE of Cuidad Obregon, 12 Sep 1973 (fl, fr), *Stevens & Fairhurst 2053* (GH, SD, TEX); ca. 4 mi N of Onavas, 28º28'N, 109º32'W, 20 Aug 1986 (fl, fr), *Rea & Levin 1160* (SD); Canyon 2 mi NW of San Carlos Bay (near Guaymas) on the old road to Rancho La Manga at the 'Club Med' beach, 27º58'N, 111º04'W, 03 Sep 1989 (fl, fr), *Sanders et al. 9185* (SD); Huatabampo, 5 mi N of Estación Don along Mex Hwy 15, 07 Oct 1970 (fl, fr), *Breedlove & Thorne 18629* (MO); Navajoa, Teachive de Masiaca, Arroyo Masiaca, 26º47'10"N, 109º14'W, 21 Sep 1994 (fl, fr), *Van Devender & Yetman 94-674* (ARIZ).

CULTIVATED. *Gutierrez 31* (UTEP, fl).

This subspecies can be distinguished on the basis of having lobed and denticulate leaves with an apex angle greater than 90º, a peduncle longer than 15 cm, pedicels longer than 32 mm, and more than 15 flowers per inflorescence. This taxon intergrades extensively with ssp. *parviflora* as you head north along the coast of Sinaloa into Sonora.

11. Proboscidea sabulosa Correll, Rhodora 68: 426. 1966. –TYPE: U.S.A. Texas: Crane Co., on shinnery oak dunes along ranch road #1233 about 1.5 miles west of U.S. Rte. 385, north of Crane, 06 Aug 1966, *D. S. Correll 33328* (holotype: LL [photo at ASU!]; isotypes: ENCB GH [photo at ASU!] NCU [photo at ASU!] TEX [photo at ASU!] UC [photo at ASU!] US [photo at ASU!]).

Description. Annual. Roots taprooted. Stems decumbent. Leaves opposite to sub-opposite; petiole to 15 cm long; lamina ovate to broadly sub-reniform; apex rounded; base cordate and equilateral to inequilateral; margins entire to sinuate-undulate. Inflorescences few-flowered and surpassed by the foliage; peduncles to 5 cm long; bracts linear-oblanceolate. Flowers: pedicels to 1 cm in flower and 2 cm in fruit; bracteoles deltoid; calyx 7 to 13 mm long, sepals free for 90% of their length; corolla to 27 mm in length, cream-colored on the inside with purple specks proximally, solid purplish-red distally, with yellow-orange nectar guides. Fruit endocarp tan or gray, oblong-ellipsoid, laterally compressed, the body to 8 cm long and crested adaxially, the rostrum to 17 cm long. Seeds silvery-gray, 14-17 mm long, 4-6 mm wide, oblong and tapering at both ends.

Phenology. Flowers from August to September.

Distribution and habitat (Fig. 32). This edaphic endemic is found in deep sand dunes from the southwest edge of the Great Plains in Texas and southeastern

New Mexico, west to the Pleistocene lakeshore remnants of Lake Coronado in West Texas and northern Mexico, and north to the sand hills along the Rio Grande and its tributaries in central New Mexico.

SPECIMENS EXAMINED. **MEXICO**. CHIHUAHUA: 6 mi S of Samalayuca in open dune area along Hwy 45, 30º16'N, 106º29'W, 13 Sept 1972 (fr, fl), *Henrickson 7497* (LL).

U.S.A. NEW MEXICO: CURRY CO., Army Corps of Engineers biological survey of Melrose Bombing Range, 11 Oct 1990, *Barlow & Clark s.n.* (UNM). EDDY CO., 11 mi E of NM 34 along NM Hwy 128 between Loving and Jal, 15 Oct 1971 (fl, fr), *Thomas 26842* (VDB); Los Medanos Site, 21 Jul 1978, *Marley et al. s.n.* (UNM); Los Medanos Site near Carlsbad, 12 Jun 1978, *Martin et al. 310* (UNM); Los Medanos Site near Carlsbad, 21 Jul 1978, *Martin et al. 327* (UNM); Los Medanos Site near Carlsbad, 21 Jul 1978, *Martin et al. s.n.* (UNM). LEA CO., 50 mi E of Carlsbad, 21 Oct 1935 (fr), *Vaughan 2066* (ARIZ). SOCORRO CO., W of Bingham, 04 Jul 1949, *Castetter & Dittmer 6112* (UNM); Sevilleta, on Rio Salado near jct with I-25, 14 Sep 1975, *Manthey 305* (UNM). –TEXAS: CRANE CO., 3.5 miles south of Ector County line, 10.0 miles south of I-20 on FM 1601, 01 Aug 2002 (fl), *Gutierrez 17* (UTEP); 10 miles NW of Crane toward Penwell, 28 June 1957 (fr), *Warnock 15423* (LL); 13.6 miles south of I-20, 7.1 miles south of Ector County line along FM 1601, 6 Aug 2004 (fl), *Gutierrez & Gutierrez 847* (ASU); 11 miles NW of Crane on Rte. #1601 to Penwell, 6 August 1966 (fl, fr), *Correll 33332* (LL). HUDSPETH CO., ca. 1.0 mi N of Tx Hwy 20 and 0.5 mi E of Acala Road, 31º20'0.20"N, 105º54'16.4" W, 20 Sep 2006 (fl, fr), *Gutierrez & Gutierrez 1225* (ASU, BRIT, CAS, DES, NMC, NY, RM, RSA, SRSC, UTEP); ca. 1.0 mi N of Tx Hwy 20 and 0.5 mi E of Acala Road, 31º20'0.20"N, 105º54'16.4" W, 1

Nov 2006 (fr), *Gutierrez & Gutierrez s.n.* (ASU, DES, NY, UTEP; each specimen at these herbaria consists of ca. 20 seeds stored in a packet that is mounted on 1 sheet and 1 box with fruits). LOVING CO., deep sandy soil along hwy between Wink and Mentone, 13 Jul 1952 (fr), *Warnock 10708* (SMU). WARD CO., 3 mi E of Monahans, 15 Sept 1948 (fr), *Turner & Warnock 65* (GH). WINKLER CO., N side of FM 874, 1.6 road miles W of FM 1218, 31º56'32"N, 103º01'05"W, 23 Oct 1990 (st), *Carr and McNeal 10880* (TEX).

The species is characterized by having the smallest flowers of the genus and a calyx of sepals that are not united. The spindle-shaped seeds are adapted to sandy habitats. The specimens collected in November from Hudspeth County in Texas (*Gutierrez & Gutierrez s.n.*) consist of ca. 20 seeds stored in a packet that is mounted on a sheet and an accompanying box containing fruits. Seeds were removed from these fruits and are stored at the Desert Botanical Garden in Phoenix, Arizona.

12. Proboscidea spicata Correll, Wrightia 4: 77. 1968. –TYPE: U.S.A. TEXAS: Presidio Co., along route 170 east of Fort Leaton, in dry, sandy soil, 14 June 1967, *D. S. Correll and Helen B. Correll 34211* (holotype: LL [photo at ASU!]; isotype: GH [photo at ASU!]).

Description. Annuals. Roots taprooted. Stems decumbent. Leaves opposite to sub-opposite; petioles to 10 cm long; lamina widely ovate to 12 cm long; apex rounded, base cordate, equilateral to inequilateral, margins entire to sinuate-undulate. Inflorescences many-flowered and exceeding the foliage; peduncles to 20 cm long;

bracts narrowly oblong. Flowers: pedicels to 15 mm long; bracteoles lanceolate and 5 mm long; calyx 12 to 14 mm long, sepals free for 30% of their length; corolla to 45 mm in length, pink on the inside of the tube, purple externally, with magenta specks in two rows along the bottom on the inside of the tube and yellow nectar guides. Fruit morphology unknown. Seed morphology unknown.

Phenology. Flowering June and July.

Distribution and habitat (Fig. 32). Disturbed areas in West Texas and northern Mexico.

SPECIMENS EXAMINED. **MEXICO**. COAHUILA: 25 mi W of El Oro, road to Guimbalete, 24 Jul 1939 (fl), *White 2021* (GH).

U.S.A. TEXAS: BREWSTER CO., Altuda Pass, Glass Mtns, 08 Aug 1940 (fl), *Warnock W308* (TEX). JEFF DAVIS CO., Madera Canyon, 10 mi N of Observatory, Davis Mtns, 25 Jun 1947 (fl), *Warnock 6051* (TEX).

This species is known only from the type and a few additional specimens of questionable identification. This species is distinguished by the short pedicels, but otherwise resembles *Proboscidea fragrans*, which has been collected in the type locality. Until more specimens can be collected or discovered to determine if this species should be synonymized with *P. fragrans*, this treatment will continue to recognize it as a distinct species.

13. Proboscidea triloba (Schlect. & Cham.) Decne., Ann. Sci. Nat., Bot. sér 5, 3: 321. 1865. *Martynia triloba* Schlect. & Cham., Linnaea 5: 121. 1830. –TYPE:

MEXICO. Veracruz: “prope Vera-Cruz,” *Scheide & Deppe 82*, Jul 1828 (holotype: HAL [photo at ASU!]).

Description. Annual. Roots taprooted. Stems erect to decumbent. Leaves opposite to sub-opposite; petiole 15 to 30 cm long; lamina deltoid to widely ovate; apex acute; base truncate or cordate and equilateral, margins entire or shallowly trilobed to deeply palmatifid, the depths of sinuses ranging from 0%-90%, often sinuate-undulate. Inflorescences many-flowered and surpassing by the foliage; peduncles to 50 cm long; bracts linear-oblanceolate. Flowers with a strong musky odor; pedicels to 2-4 cm long; bracteoles ovate to lanceolate; calyx 10 to 24 mm long, sepals free for 50%-75% of their length; corolla to 45 mm long, lavender internally, with rusty to dark purple specks scattered in the interior, nectar guides bright yellow, adaxial lobes each with a large purple splotch, mid and abaxial lobes lavender with dark purple streaks and speckles. Fruit endocarp dark gray or black, oblong-ellipsoid and inflated; endocarp body to 6 cm long; rostrum to 7 cm long. Seeds dark brown to black, 7.5-10 mm long, 4-6 mm wide, elliptic to ovate.

This species is the only species in *Proboscidea* with trilobed leaves. It is most similar in appearance to *P. fragrans* and can be distinguished from it by its shorter capsules and rostra and geographic distribution, with *P. triloba* generally being found south of the Trans-Mexican Volcanic belt. The two subspecies of *P. triloba* are allopatric and do not overlap morphologically and could conceivably be considered separate species. Molecular evidence suggests the two subspecies are most closely related to each other (Figs. 9, 10, 11, 12, 13, 14), supporting Bretting’s (1981) treatment of the two taxa.

KEY TO THE SUBSPECIES OF *PROBOSCIDEA TRILOBA*

Leaves entire or trilobed with denticulate margins; mature inflorescences with more than 15 flowers, peduncles longer than 15 cm; seeds 8.5-9.7 mm long...........................
....13a. *Proboscidea triloba* ssp. *triloba*

Leaves deeply incised-palmatifid with smooth margins; mature inflorescences with less than 15 flowers, peduncles shorter than 15 cm; seeds 7.5-8.0 mm long. ....
.... 13b. *Proboscidea triloba* ssp. *diversifolia*

13a. Proboscidea triloba ssp. **triloba**.

Proboscidea botteri Decne., Ann. Sci. Nat., Bot. sér. 5, 3: 327. 1865. *Martynia botteri* (Decne.) Hemsley, Bio. Cent. Amer. 2: 499. 1882. –TYPE: MEXICO. Veracruz: "circa Orizabam," *Botteri 797* (holotype: P, isotypes: CGE [photo at ASU!] K).

Proboscidea confusa Van Eseltine, Tech. Bull. N. Y. State Agric. Exp. Stat. 149: 15. 1929. *Martynia confusa* (Van Eseltine) Standl. & Steyerm., Field Mus. Pub. Bot. 23: 86. 1944. –TYPE: MEXICO. Puebla: Teocali de Cholula, vicinity of Puebla, 26 Aug 1907, *Arsène s.n.* (holotype: US [photo at ASU!], isotype: MO).

Description. Stems erect to decumbent. Leaves shallowly to deeply trilobed, depths of sinuses 0%-30%; margins entire to denticulate. Inflorescences with 15-35 flowers; peduncles to 50 cm long. Flowers: calyx 10 to 24 mm long. Seeds 8.5-10 mm long, 4-6 mm long, ovate. Fig. 33.

Phenology. Flowering June-September, occasionally as late as December.

Distribution and habitat (Fig. 34). Disturbed soils in arid zones in southern and central Mexico and central Guatemala; 1170-1750 m.

Vernacular Names. Uñas de gato, torito.

SPECIMENS EXAMINED. **COLOMBIA**. CUNDINAMARCA: near Bogota, 06 Aug 1903 (fl, fr), *Apollinaire* s.n. (E, provenance doubtful).

GUATEMALA. CHIMALTENANGO: Chimaltenango, s.d. (fl, fr), *Johnston 761* (F). –GUATEMALA: Lago Aurora, 1940 (fl), *Aguilar 528* (F).

MEXICO. No locality given, s.d. (fl), *Bates s.n.* (K). –GUERRERO: Coyuca-Querendas, 26 Sept 1934 (fl, fr), *Hinton et al. 6661* (GH, NY); Taxco, 28 July 1937 (fl, fr), *Abbott 293* (GH); Tepoztitlan, 07 Aug 1945 (fl, fr), *Alexander & Hernandez 2022* (NY, UC); Zumpango del Rio, 1 km S of jct of the road to Filo del Caballo with the Mexico-Acapulco Hwy (Rte 95), 33 km N of Chilpancingo, 17.48ºN, 99.35ºW, 25 Aug 1984 (fl, fr), *Barrie et al. 967* (TEX). –JALISCO: 15 mi S of Guadalajara on Hwy 54, 25 July 1975 (fl, fr), *Wallace et al. 252* (MO-2, NY). –MEXICO: 4 mi S of Ixtapan on Hwy 55, 16 Aug 1972 (fl, fr), *Dunn et al. 20447* (MO); Temascaltepec, Vigas, 30 July 1932 (fl), *Hinton 1202* (GH, K, MO, NY-2). –MICHOACÁN: Vicinity of Morelia, Punguato, 16 Jul 1909 (fl), *Arsène s.n.* (E). –MORELOS: Northern edge of Cuernavaca, 28 June 1950 (fl, fr), *Dressler 1164* (GH, MO); town of Hualzurco on the road to Amayuca, 06 Aug 1979 (fl, fr), *Feine & Nabhan s.n.* (GH); Cuautla, Jul 1930 (fl), *Lyonnet 665* (NY); near Cuernavaca along the Mexico City-Cuernavaca road, 28 Aug 1935 (fl, fr), *MacDaniels 309* (F); E of Hwy 60 near Cuautla, 01 Aug 1975 (fr), *LeDoux et al. 2089* (MO); Alpuyeca, 10 Aug 1949 (fl), *Russell 71* (BRIT-2); Tepalcingo, 4 km N of El Limón along road to Huitchila, 15 Oct 1986 (fl), *Cabrera C. et al. 12095*

(MO); Tlaquiltenango, between Juan Garcia and Terreplen, 03 Jul 1978 (fl), *Vasquez T. 693* (MO). –OAXACA: no locality given, 1844 (fl), *G. 1061* (TCD); Molinos Valley, ENE of Oaxaca, 1844 (fl), *Liebmann 471* (TCD); 18 miles SW of City of Oaxaca, 02 Oct 1894 (fl), *Nelson 1490* (GH); near Oaxaca, 24 Nov 1894 (fl), *Smith 357* (GH); Oaxaca, 30 June 1947 (fl), *Johnston s.n.* (TEX); Santa Maria del Tule, 18 Aug 1907 (fl,fr), *Conzatti 1960* (F-2); E side of Mex Hwy 190 on northern outskirts of Huajapan de Leon, 29 Dec 1973 (fl, fr), *Reznicek et al. M273* (MICH); Distrito del Centro, Cerro San Antonio, 06 Sept 1908 (fl, fr), *Conzatti 2243* (F); Distrito Huajuapan, 10 km N of Huajuapan de Leon and 2 km N of Luz Nagore on Huajuapan-Tehuacan hwy, 17 July 1982 (fl), *Torres et al. 756* (ARIZ, GH); Distrito Teposcolula, 5 km NE of Chilapa de Diaz, 02 July 1977 (fl), *Rzedowski 34816* (ARIZ, NY); 3 km S of Tamazulapan, 25 Aug 1983 (fl), *Mendoza 1248* (MO); Cerro El Peñasco S of Teposcolula, 09 Sep 1988 (fl, fr), *Torres C & Torres C. 12349* (MO). –PUEBLA: Teyuca, along Hwy 190, 24 July 1971 (fl), *Gibson & Gibson 2335* (ASU); Manzanilla, 20 Aug 1911 (fl, fr), *Nicolas s.n.* (NY); near Tehuacan, June 1888 (fl), *Seler & Seler 54* (GH); San Martin, 14 July 1929 (fl), *Mexia 2659* (E, MO, NY, UC); ca 2 mi NE of Atlixco on Mexico Rte 190, 23 July 1964 (fl), *Mickel 1387* (NY), 12.6 mi SE of Tehuitzingo along Hwy 190 (fl), *Torke et al. 376* (MO, NY); 76 miles NW of Huajuapan de Leon on Hwy 190 to Matamoros, 09 Aug 1978 (fl, fr), *McCarten et al. 2995* (ARIZ); 17 mi from Oaxaca border along Hwy 190, 20 Jul 1979 (fl), *Thurm et al. 148* (MO); 40 mi S of Atlixco, 19 Aug 1971 (fl), *Dwyer et al. 871* (MO); 13 mi W of Acatlán along Hwy 190, 08 Aug 1978 (fl), *Dunn et al. 23066* (MO); 42 mi S of Acatlán along MEX 190, 16 Sep 1978 (fl, fr), *D'Arcy 11952* (MO-2); 5 mi S of Matamoros, near Terpene, 02 Jul 1977 (fl), *Dwyer 14277* (MO); vicinity of San Luis Tultitlanapa, Aug 1908 (fl), *Purpus 3267* (UC); Acaltepec, 5 km from jct for San Juan Trujapan on gravel road towards Sabina Farol along federal road Santiago Chazumba-Huajapan de Leon, 18º10'26.8"N, 97º38'38.6"W, 25 Dec 2004 (fl, fr), *Calzada JIC 24471* (K); 3 km from Zapotitlan Salinas, road to Los Reyes Metzontla, 18º17'56"N, 97º30'56"W, 30 Nov 2001 (fr), *Calzada & Flores 23078* (K); Caltepec, La Laguna, foothills of Cerro El Gavilán, 2 km E of Caltepec, 14 Jul 1986 (fl), *Salinas et al. F-3440* (MO); 3 mi E of Tepexco, 18.36ºN, 98.30ºW, 09 Aug 1976 (fl, fr), *Webster & Armbruster 20731* (TEX); 1 km N of Zapotitlán del las Salinas, 23 Aug 1988 (fl, fr), *Salinas T. & García 4918* (K). –TAMAULIPAS: between Victoria and Antiguo, 20-23 Jun 1937 (fl), *Happ 68* (MO, provenance doubtful).

CULTIVATED. *Gutierrez 4* (UTEP, fl).

The subspecies is distinguished from *Proboscidea triloba* ssp. *diversifolia* by the degree of lobation of the leaves, the size of the peduncle and seeds, and the number of flowers on the inflorescence. The subspecies *triloba* has leaves with shallow or no sinuses, larger seeds and peduncles, and more than 15 flowers per mature inflorescence.

This taxon is generally found south of the Trans-Mexican Volcanic Belt and west of the Coastal ranges of Puebla and Oaxaca. Bretting (1981) noted the paucity of plant collections in western central Mexico contributes to the uncertainty of the western limits of the taxon, which still remains true. The disjunct populations in Guatemala occur more than 800 km away from the southern-most populations in Oaxaca.

Proboscidea confusa, now considered a synonym of *P. t.* ssp. *triloba*, consisted of five specimens that have all been placed in three separate taxa. Two are now placed in *P. t.* ssp. *triloba*, including the type of *P. confusa*. Additionally, two are placed in *P. fragrans*, and one in *P. p.* ssp. *sinaloensis*.

13b. Proboscidea triloba (Schlect. & Cham) Decne. ssp. **diversifolia** (Hevly) Bretting, Southw. Naturalist 30: 150. 1985. *Proboscidea diversifolia* Hevly, Brittonia 21: 311. 1969. –TYPE: MEXICO. Michoacán: 13.3 mi SW of Apatzingán, *Hevly et al. 2662*, 09 Sept 1962 (holotype: ARIZ [photo at ASU!], isotypes: ARIZ [photo at ASU!] MEXU UC US)

Description. Stems decumbent. Leaves deeply incised-palmatifid, depths of sinuses to 90%, margins entire and smooth, apex acute. Inflorescences with 8-15 flowers; peduncles less than 15 cm long. Flowers: calyx 10 to 18 mm long. Seeds 7.5-8 mm long, 4-6 mm long, elliptic. Fig. 33.

Phenology. Flowering August to September.

Distribution and habitat (Fig. 34). Volcanic soils of disturbed areas in the xeric thorn scrub vegetation of the Rio Tepalcatepec in Michoacán; 300-500 m.

SPECIMENS EXAMINED. **MEXICO**. MICHOACÁN: 1 mi S of Apatzingán, 06 Aug 1940 (fl, fr), *Leavenworth 485b* (ARIZ, F, GH, MO, NY).

Bretting (1981) suggested the distinguishing characters of this subspecies, mentioned under the discussion section of *P. triloba* ssp. *triloba*, may be adaptive to selective pressures of the Apatzingán region of Michoacán. The need for the seeds to be excised from the fruit and rinsed for a prolonged period of time, coupled with the time seedlings spend growing underground prior to emergence of the hypocotyls and cotyledons suggest that these may be adaptations to the hot, fast-draining volcanic soils of the Apatzingán region. The highly dissected leaves, smaller seeds, and shorter peduncles with fewer flowers may be additional adaptations to this environment.

Dubious or Excluded Names

Craniolaria fruticosa L., Sp. Pl. 618. 1753. =*Gesneria fruticosa* Kuntze, Revis. Gen. Pl. 2: 473. 1891. (Gesneriaceae).

Martynia capensis Glox., Obs. 13. =*Rogeria longiflora* J. Gay, in Ann. Sc. Nat. Ser. I. i. 457. 1824. (Pedaliaceae).

Martynia caulescens Desf. ex Steud, Nomencl. Bot., ed. 2 (Steudel) ii. 104. =*Sinningia speciosa* Hiern, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 91. 1877-1878. (Gesneriaceae).

Martynia fruticosa Glox., Obs. 15. =*Pentarhaphia craniolaria* Decne., Ann. Sci. Nat., Bot. sér. 3, 6: 99. 1846. (Gesneriaceae).

Martynia hirsuta Desf. ex Steud, Nomencl. Bot., ed. 2 (Steudel) ii. 104. =*Ligeria hirsuta* Decne. ex Hanst., Fl. Bras. (Martius) 8(1): 386. (Gesneriaceae).

Martynia lanceolata Macrae ex Nees, Prod. (DC.) 11: 174, 182. =*Strobilanthes lanceolatus* Hook. ex Nees, Prod. (DC.) 11: 181. (Acanthaceae).

Martynia lanceolata Moon, Cat. Pl. Ceyl. 45. =*Chirita moonii* Gardn., Calc. Journ. Nat. Hist. vi: 479. 1846. (Gesneriaceae).

Martynia longiflora L., Syst. ed. XII. 412. =*Rogeria longiflora* J. Gay, in Ann. Sc. Nat. Ser. I. i. 457. 1824. (Pedaliaceae).

Martynia perennis L., Sp. Pl. 2: 618. 1753. =*Gloxinia perennis* Fritsch, Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 174. 1894. (Gesneriaceae).

Martynia spathacea Spreng., Syst. Veg. (ed. 16) [Sprengel] 4(2 Cur. Post.): 238. 1827. (citation could not be located; name remains unresolved).

Martynia speciosa Loisel., Herb. Amat. t. 225. =*Sinningia speciosa* Hiern, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 91. 1877-1878. (Gesneriaceae).

Martynia zanguebaria Lour., Fl. Cochinch. ii. 386. =*Pretrea zanguebaria* (Lour.) J. Gay ex DC., DC. Prodr. ix. 256. 1845. (Pedaliaceae).

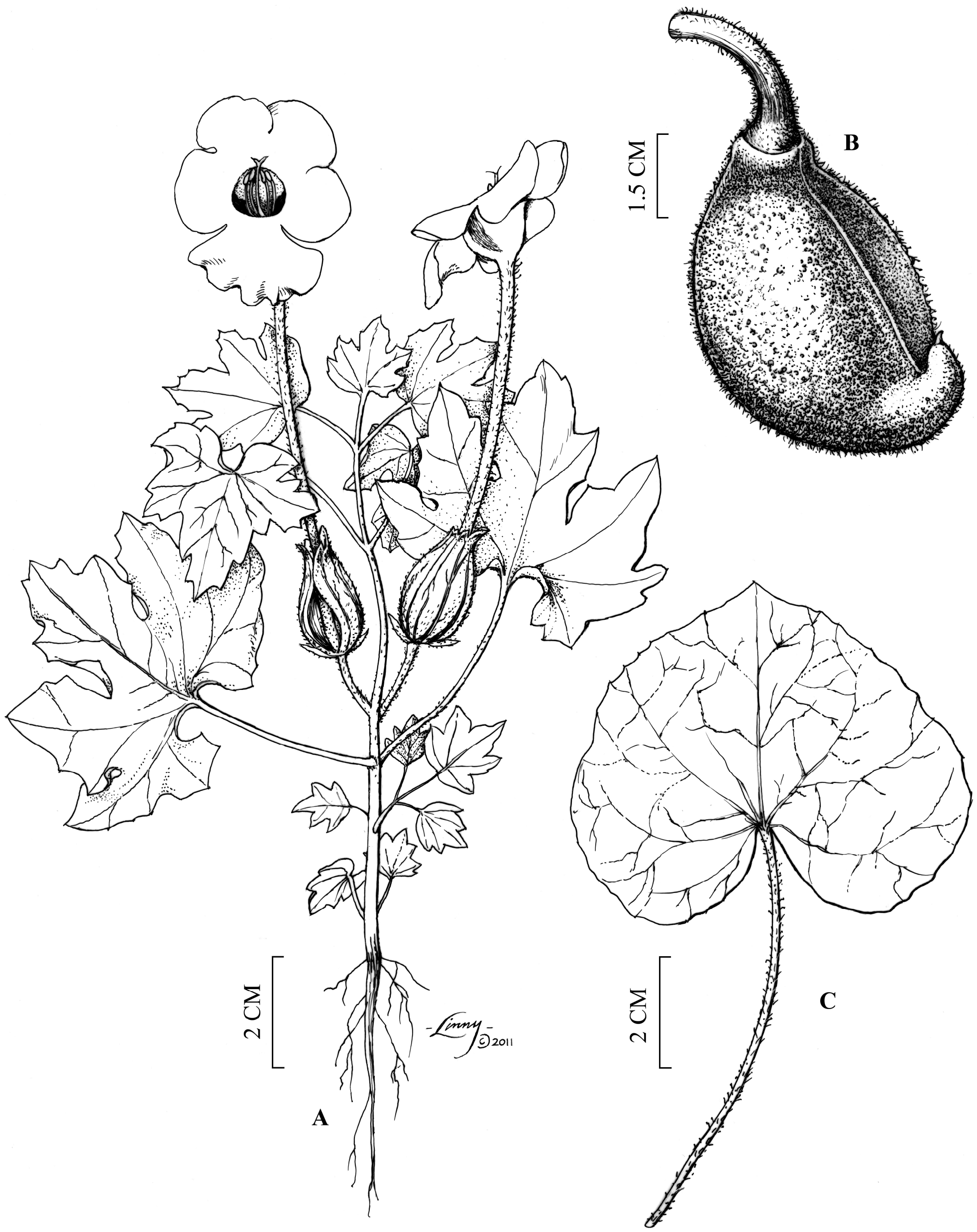

Fig. 18. Illustration of *Craniolaria annua* and *Craniolaria integrifolia*. A. Full plant of *Craniolaria annua*. B. Close-up of immature fruit of *Craniolaria annua*. C. Leaf of *Craniolaria integrifolia*. (Art by Linny Heagy © 2011)

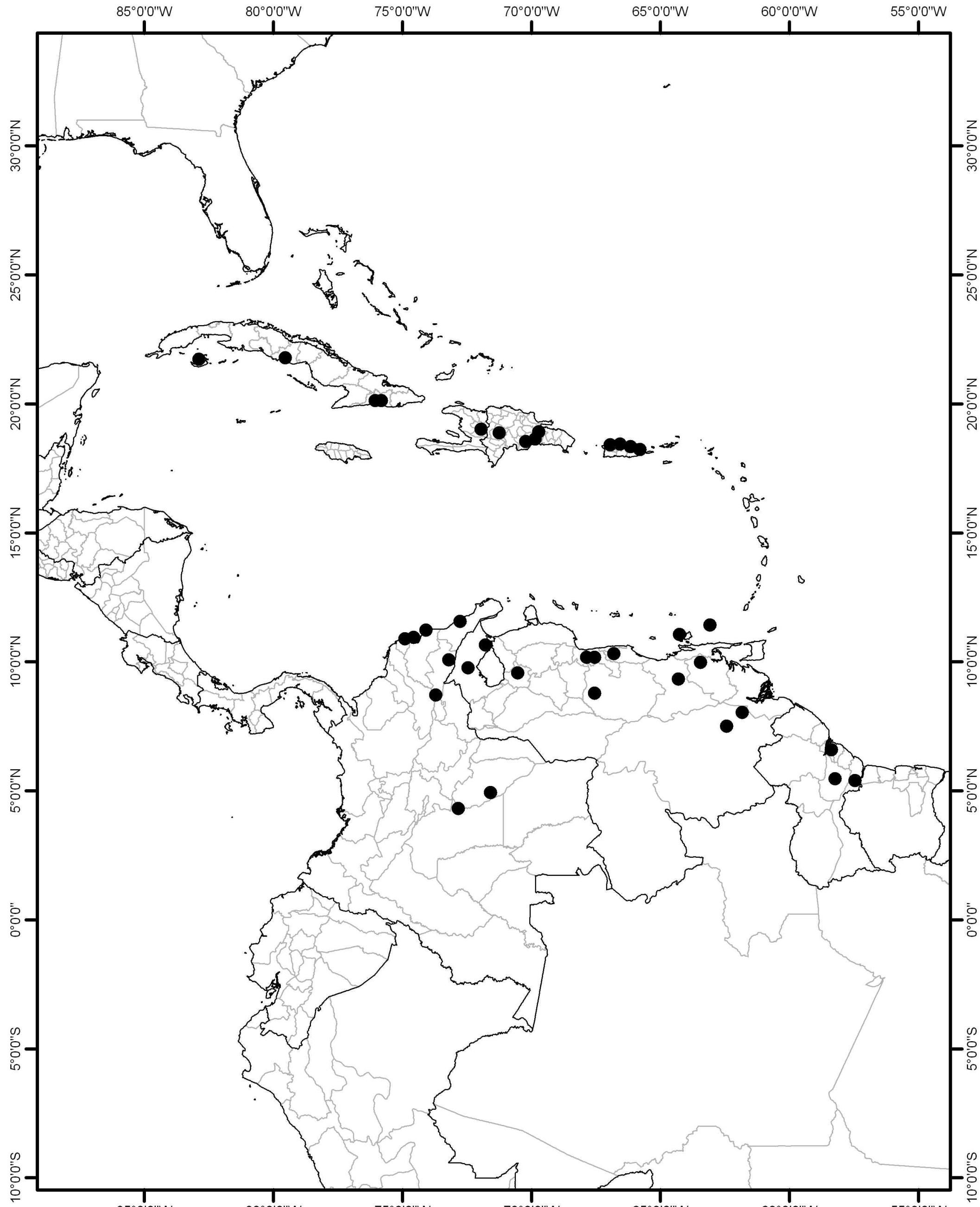

Fig. 19. Distribution of *Craniolaria annua*.

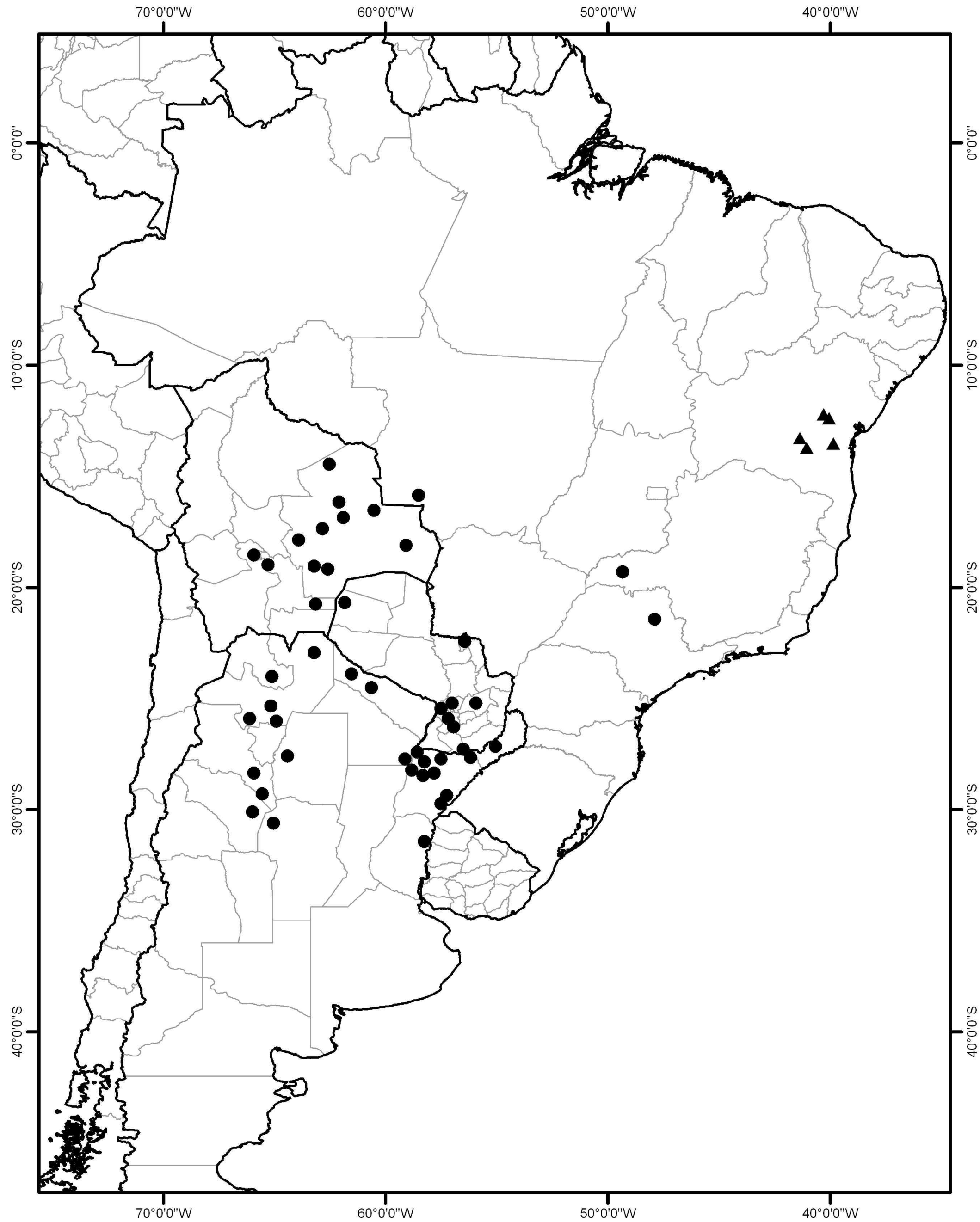

Fig. 20. Distribution of *Craniolaria integrifolia* (●) and *Holoregmia viscida* (▲).

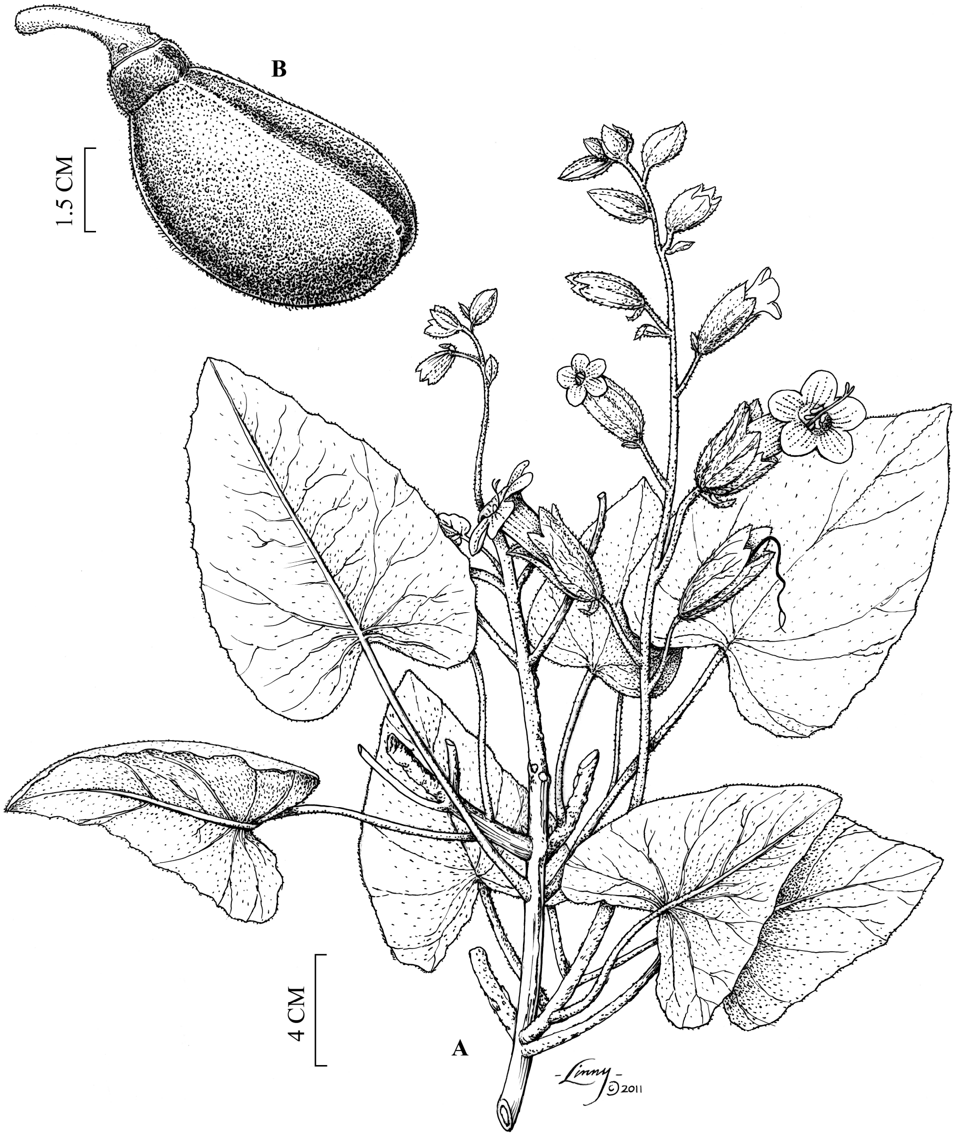

Fig. 21. Illustration of *Holoregmia viscida*. A. Upper branch with leaves and inflorescences. B. Close-up of immature fruit. (Art by Linny Heagy © 2011)

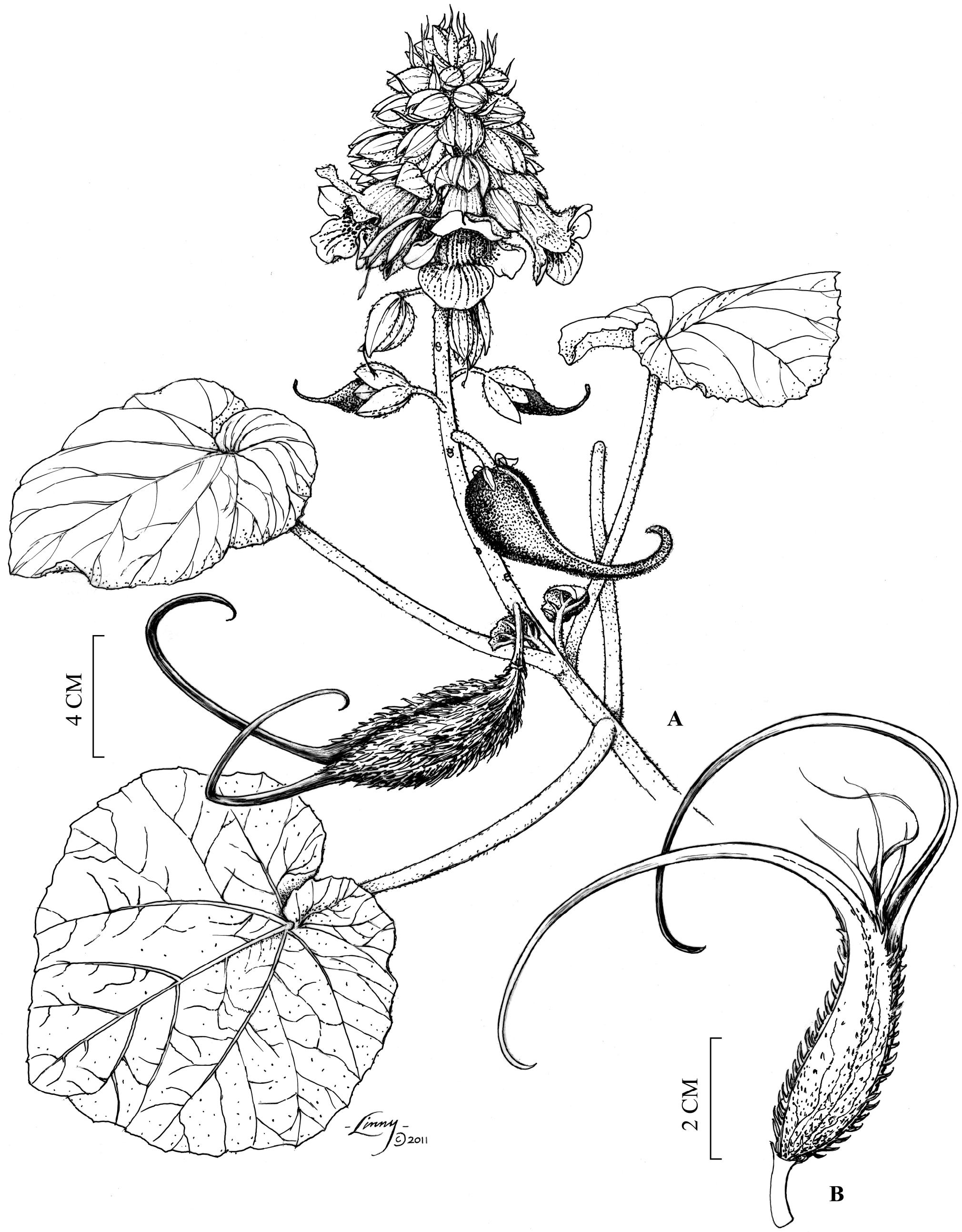

Fig. 22. Illustration of *Ibicella lutea* and *Ibicella parodii*. A. Upper branch of *Ibicella lutea* with leaves and inflorescence. B. Fruit of *Ibicella parodii*. (Art by Linny Heagy © 2011)

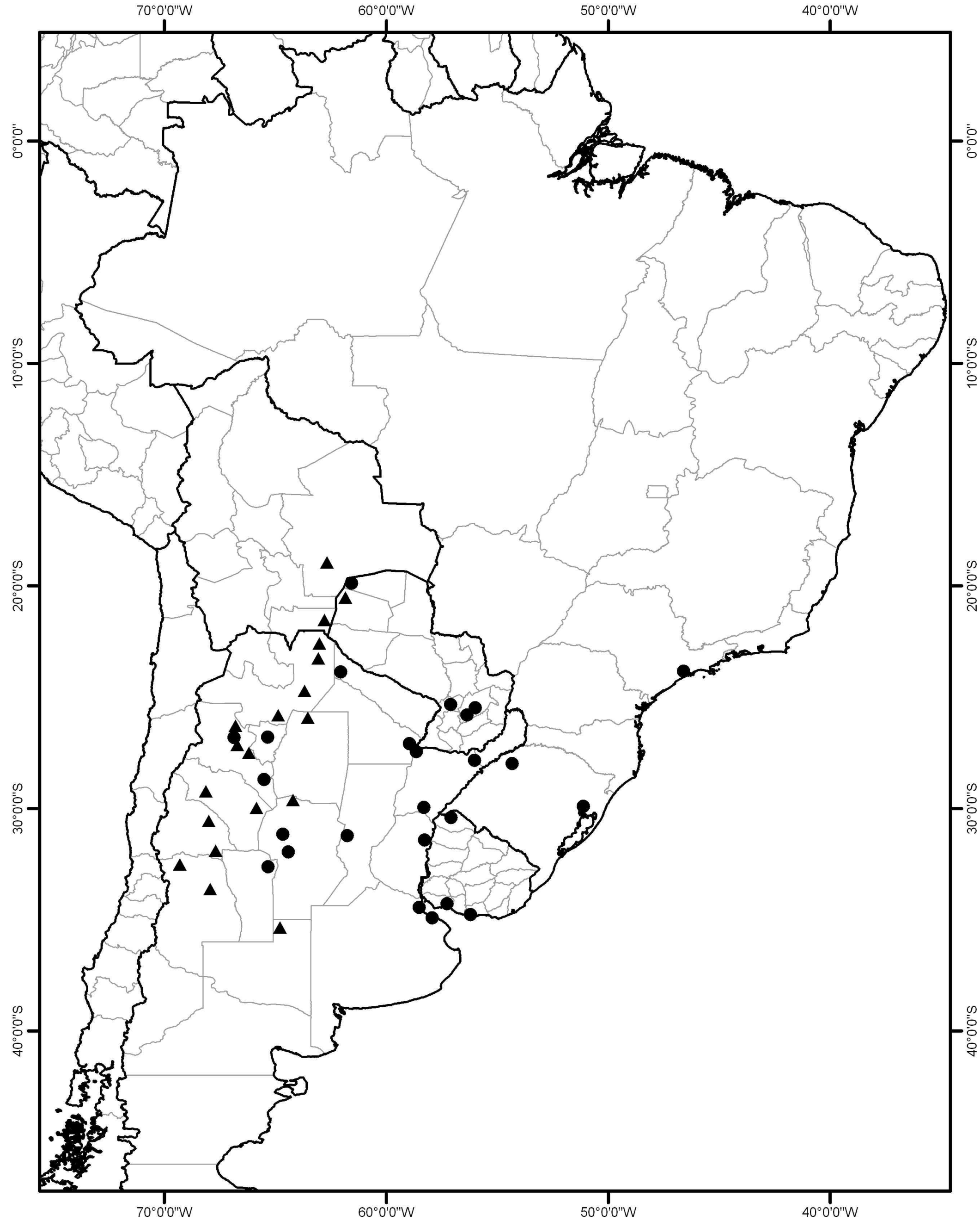

Fig. 23. Distribution of *Ibicella lutea* (●) and *Ibicella parodii* (▲).

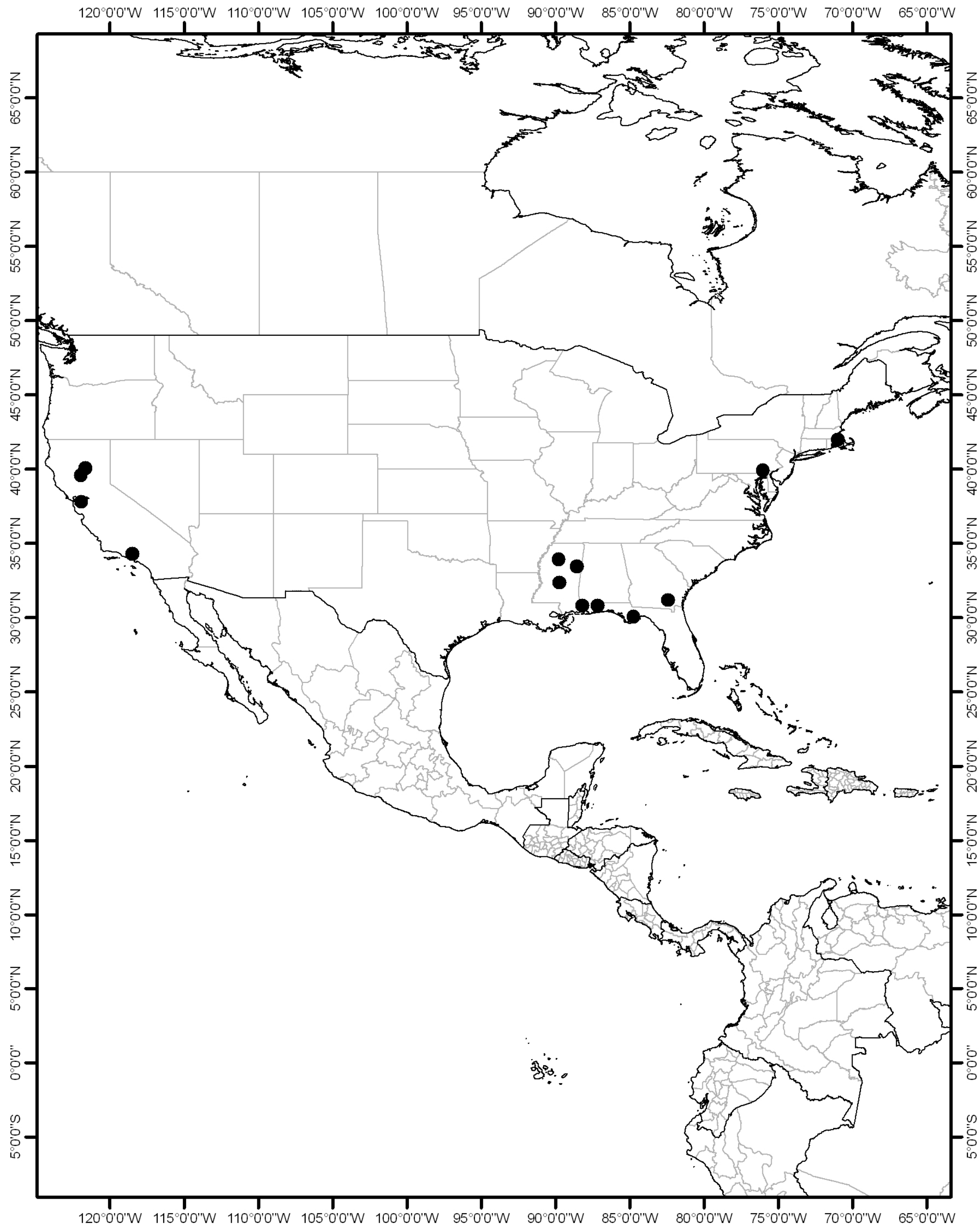

Fig. 24. Distribution of *Ibicella lutea* in North America.

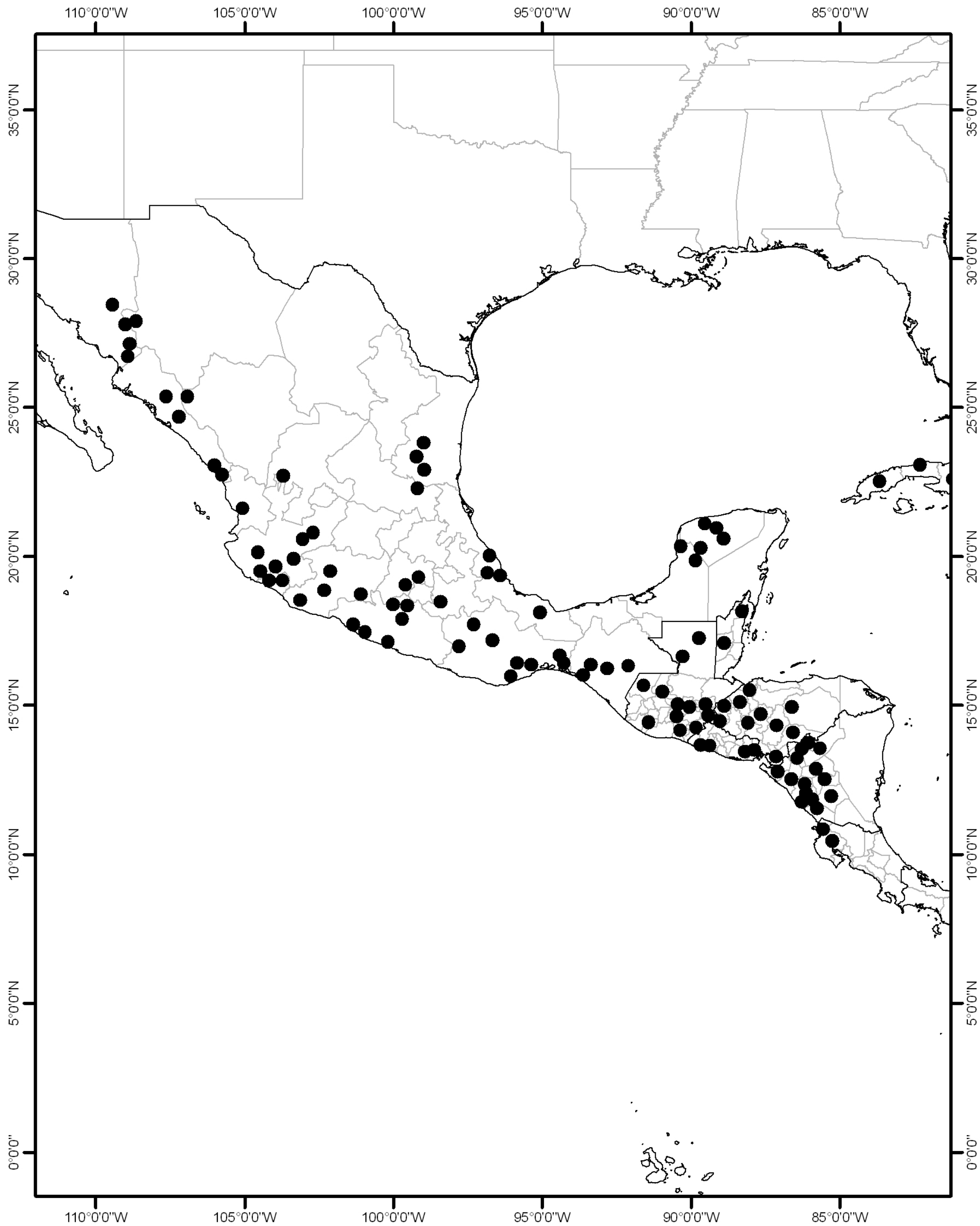

Fig. 25. Western distribution of *Martynia annua*.

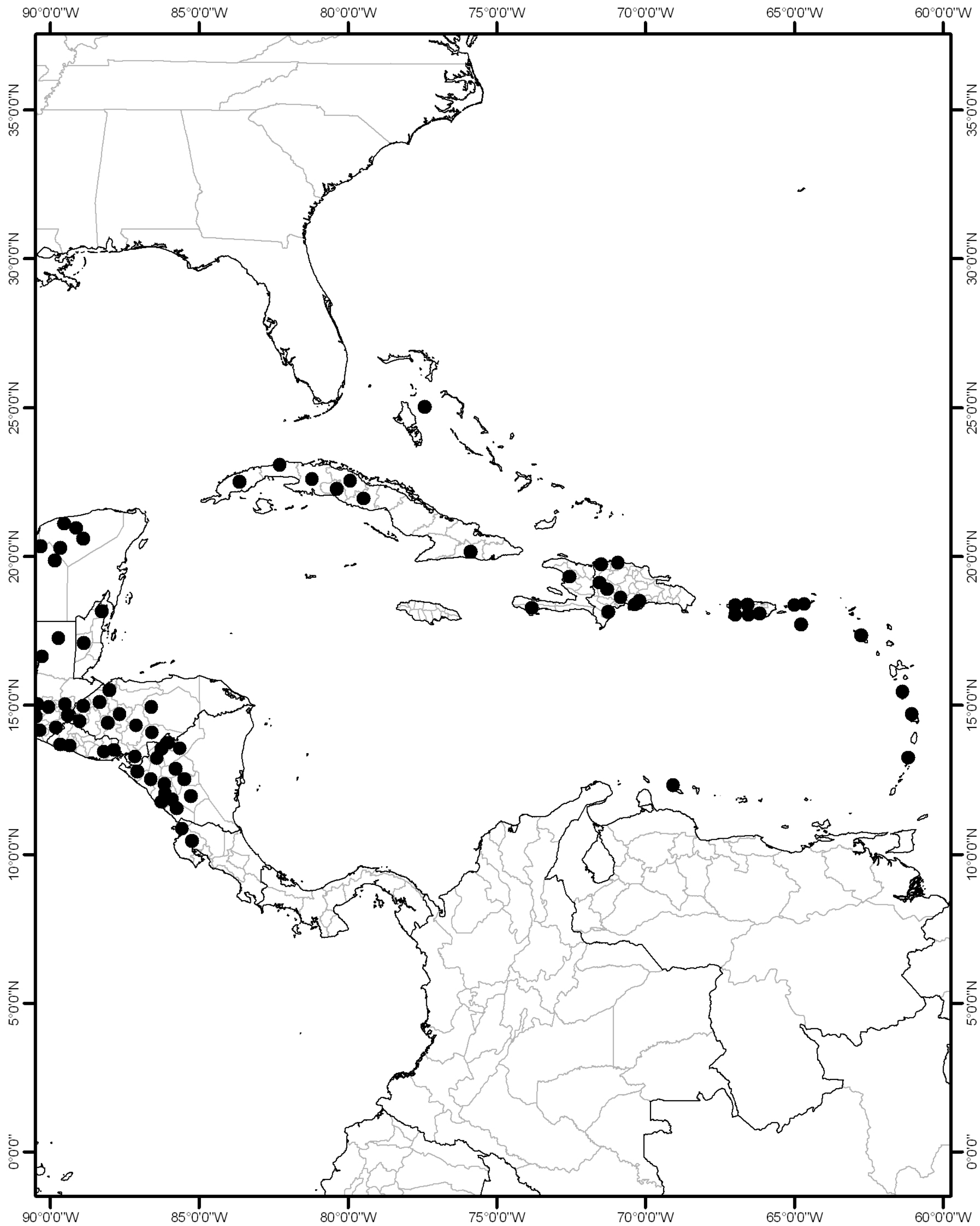

Fig. 26. Eastern distribution of *Martynia annua*.

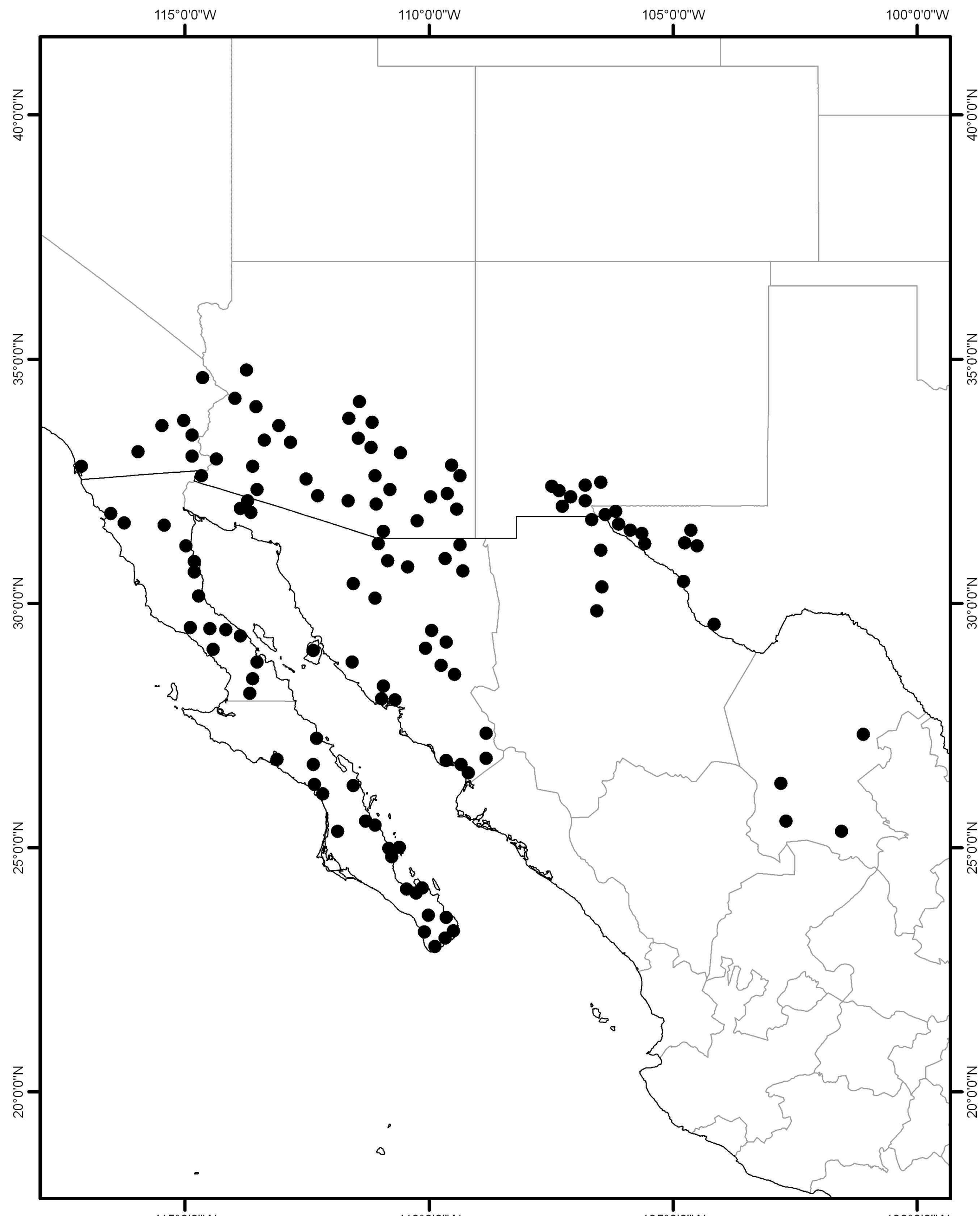

Fig. 27. Distribution of *Proboscidea althaeifolia* in North America.

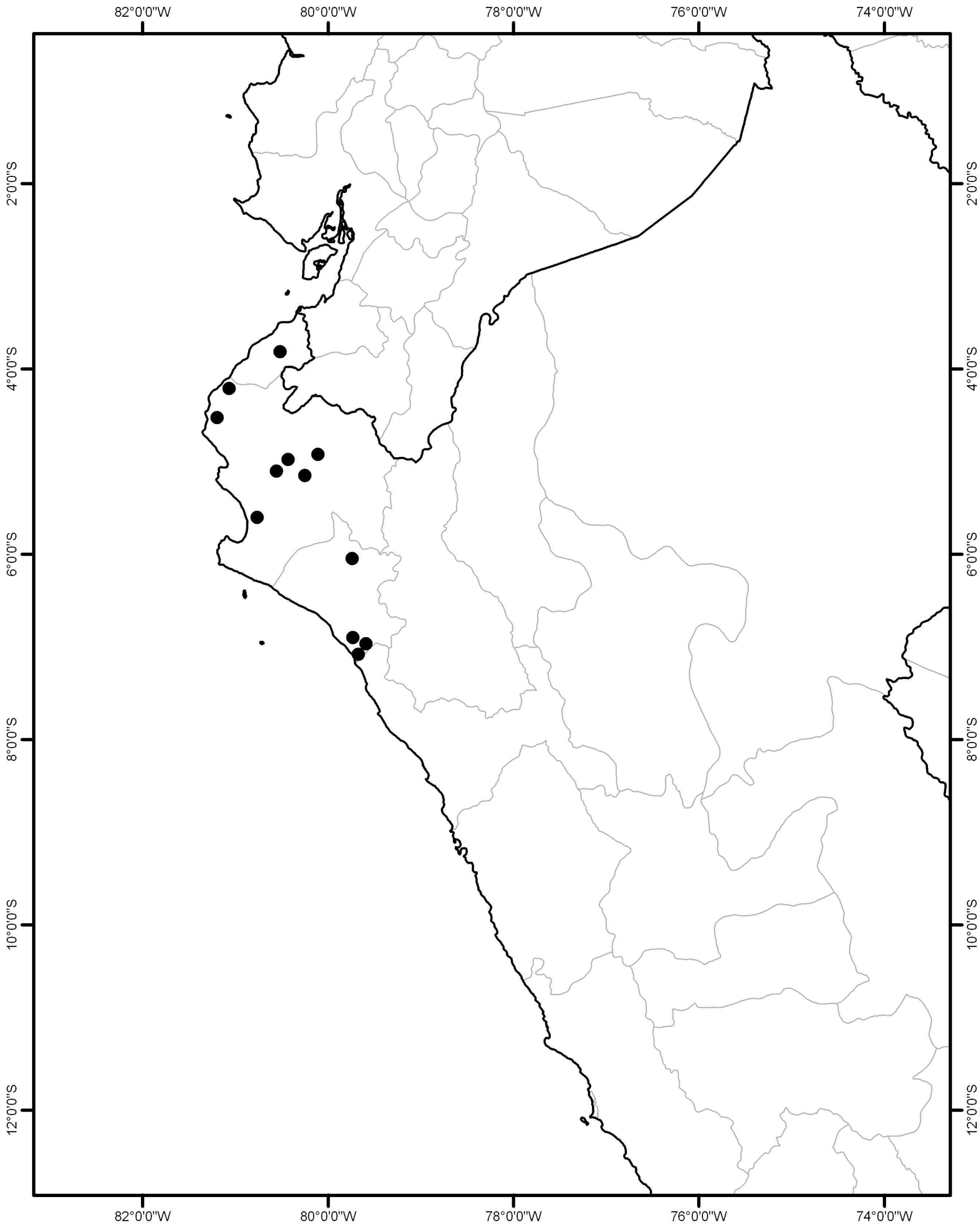

Fig. 28. Distribution of *Proboscidea althaeifolia* in South America.

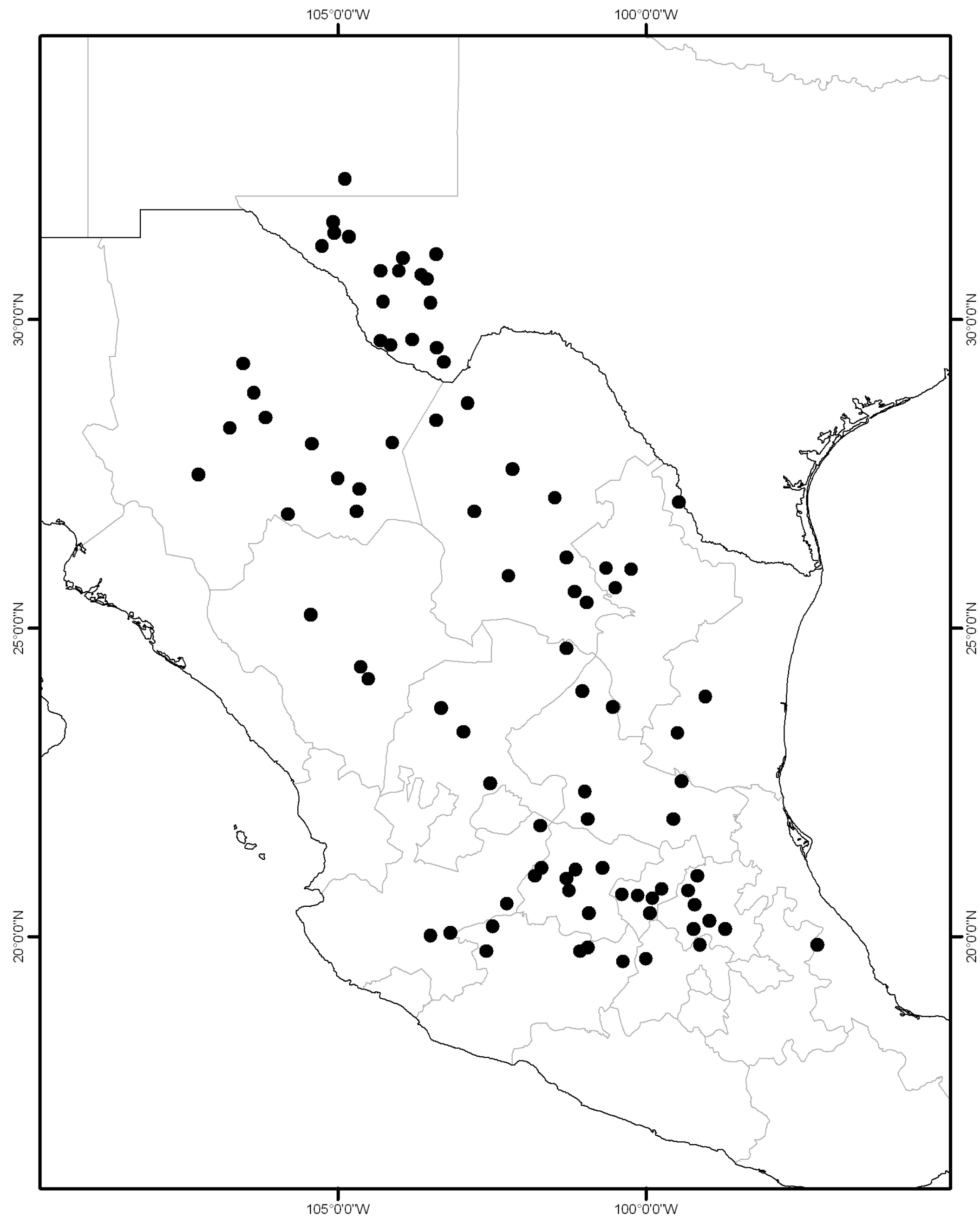

Fig. 29. Distribution of *Proboscidea fragrans*.

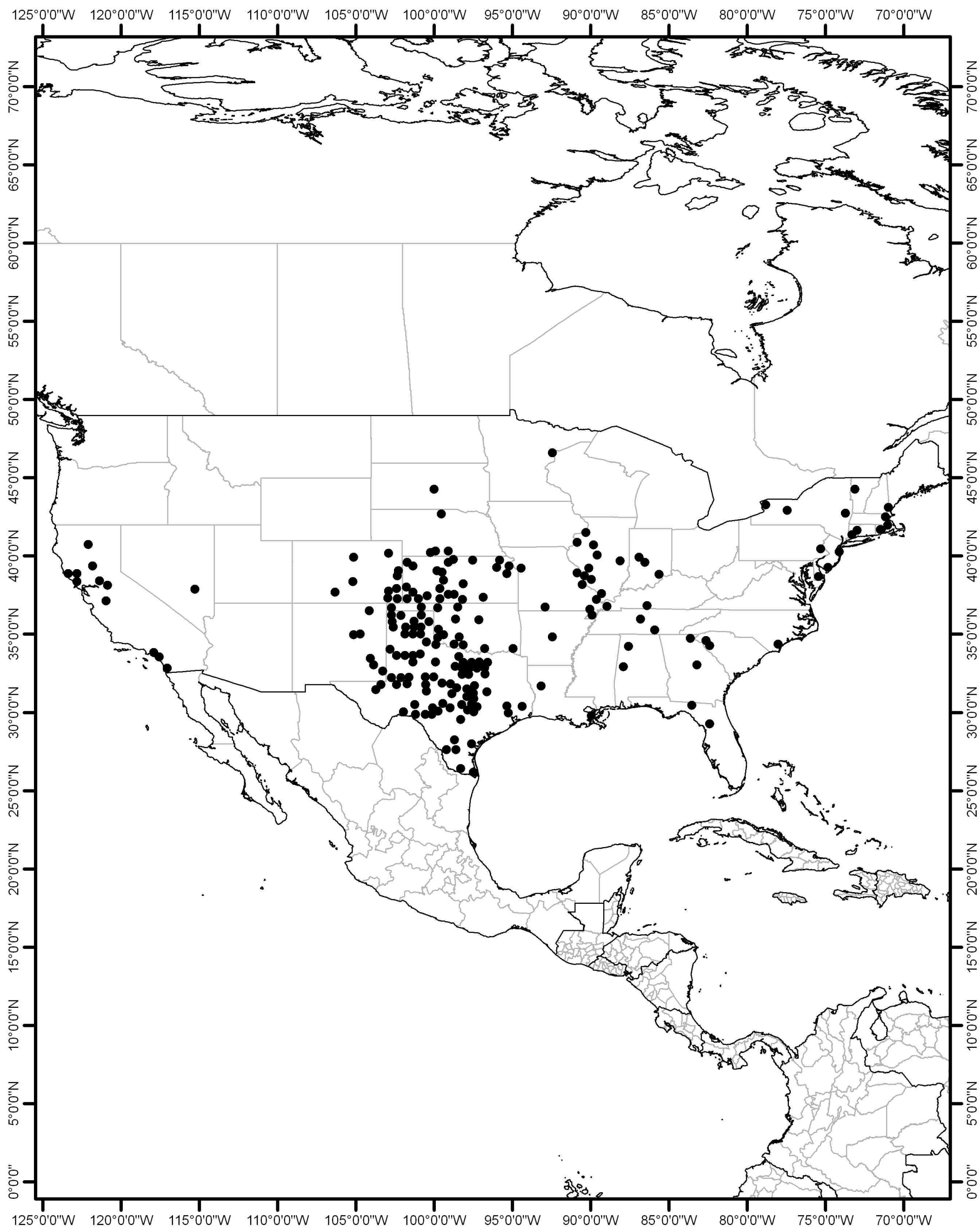

Fig. 30. Distribution of *Proboscidea louisianica*.

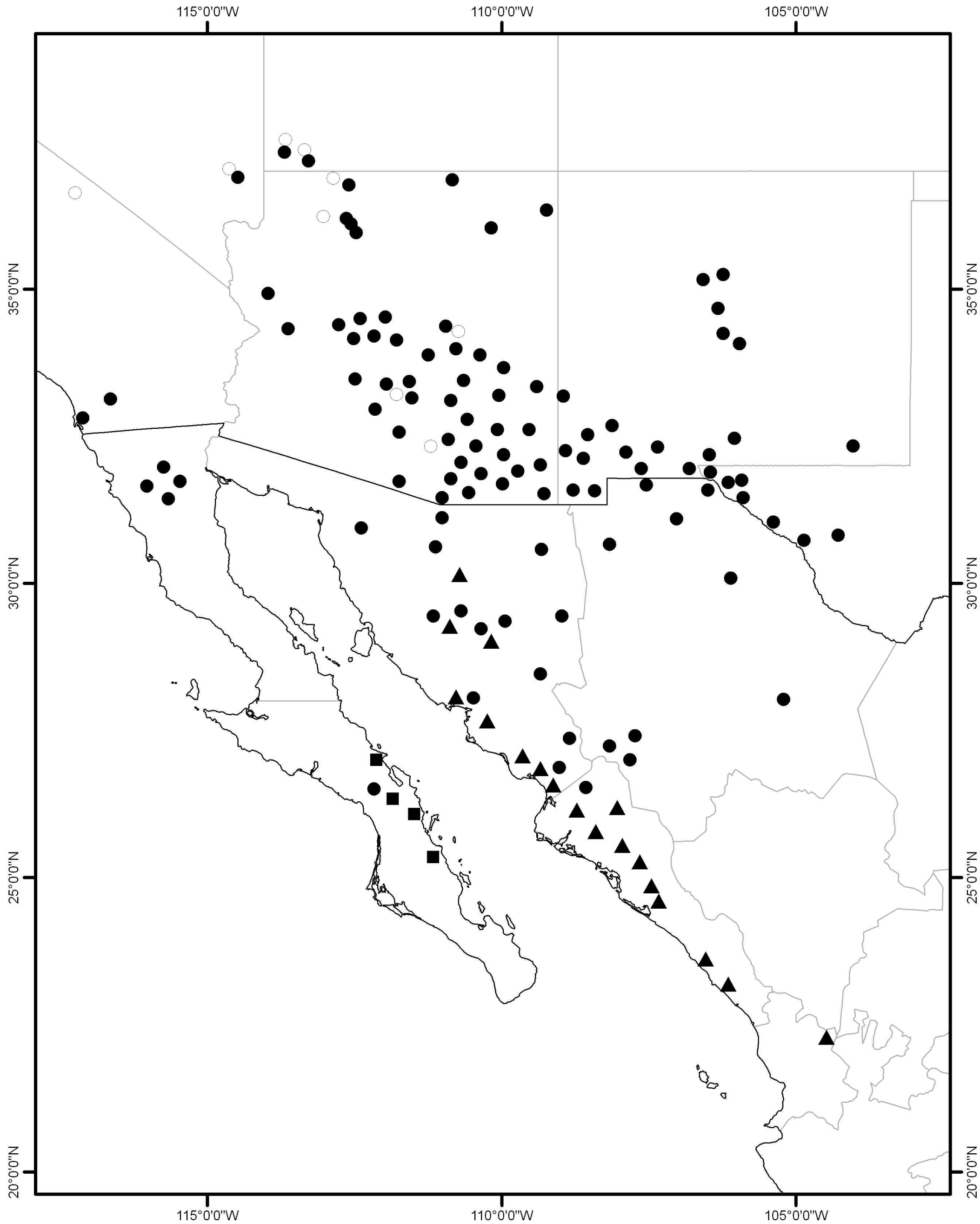

Fig. 31. Distribution of *Proboscidea parviflora* ssp. *parviflora* var. *parviflora* (●), *Proboscidea parviflora* ssp. *parviflora* var. *hohokamiana* (○), *Proboscidea parviflora* ssp. *gracillima* (■), *and Proboscidea parviflora* ssp. *sinaloensis* (▲).

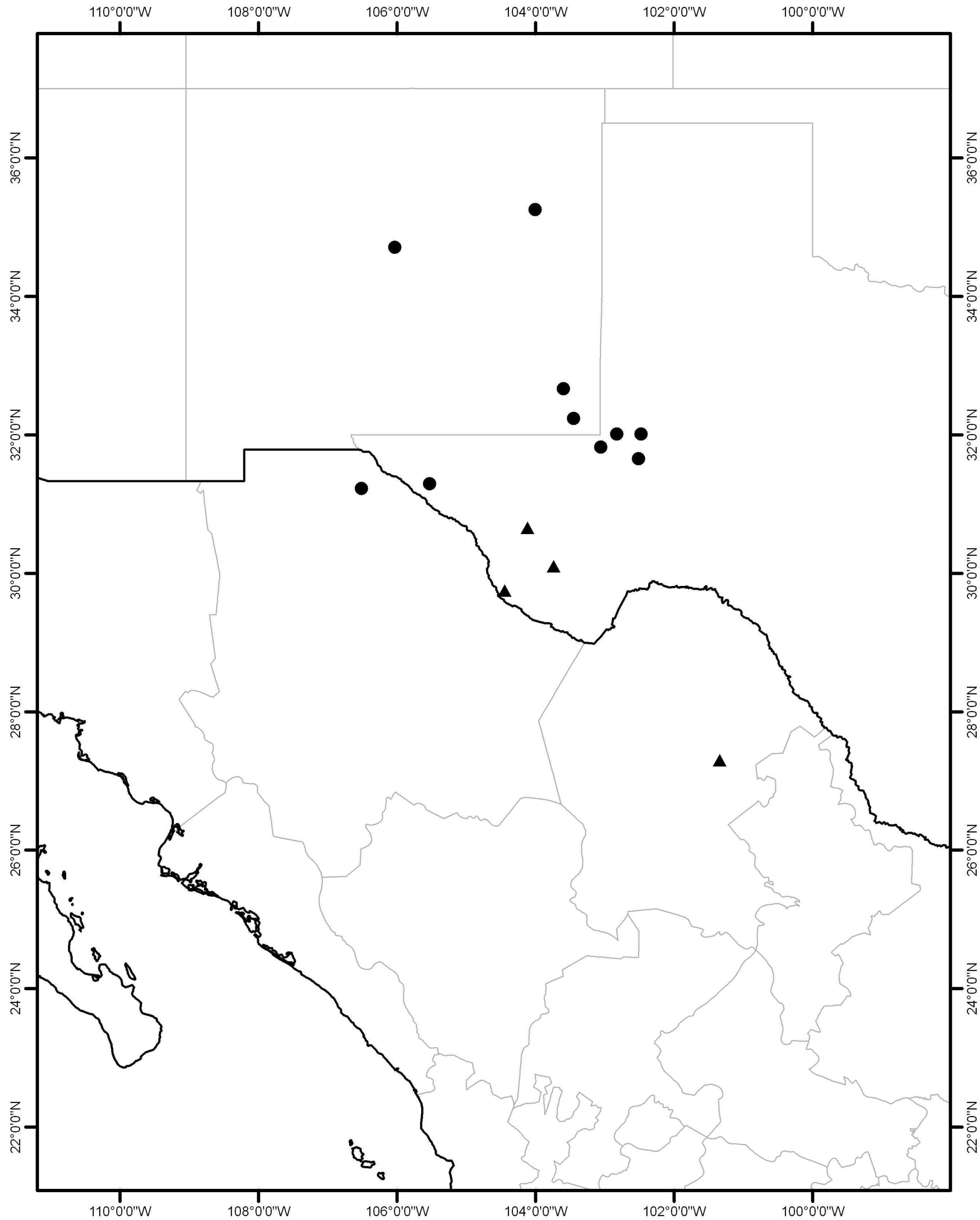

Fig. 32. Distribution of *Proboscidea sabulosa* (●) and *Proboscidea spicata* (▲).

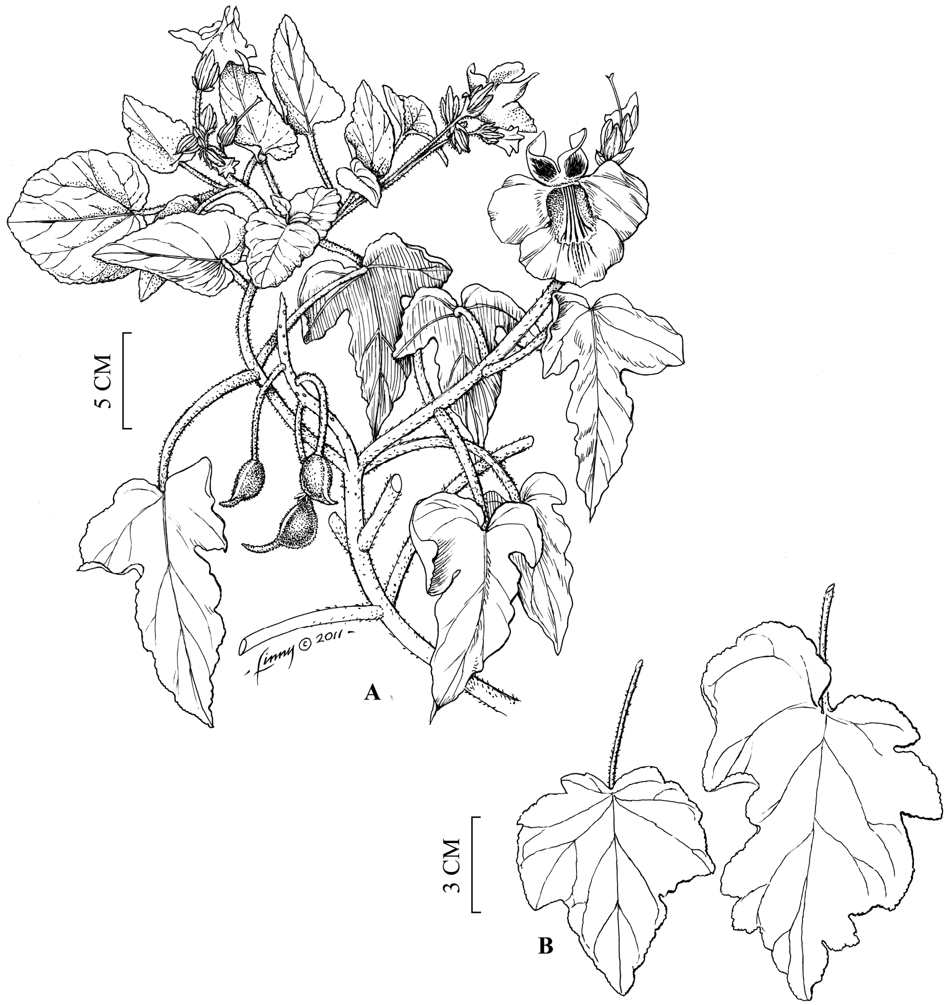

Fig. 33. Illustration of *Proboscidea triloba*. A. Upper branch of *P. triloba* ssp. *triloba* with leaves and inflorescence. B. Leaves of *P. triloba* ssp. *diversifolia*. (Art by Linny Heagy © 2011)

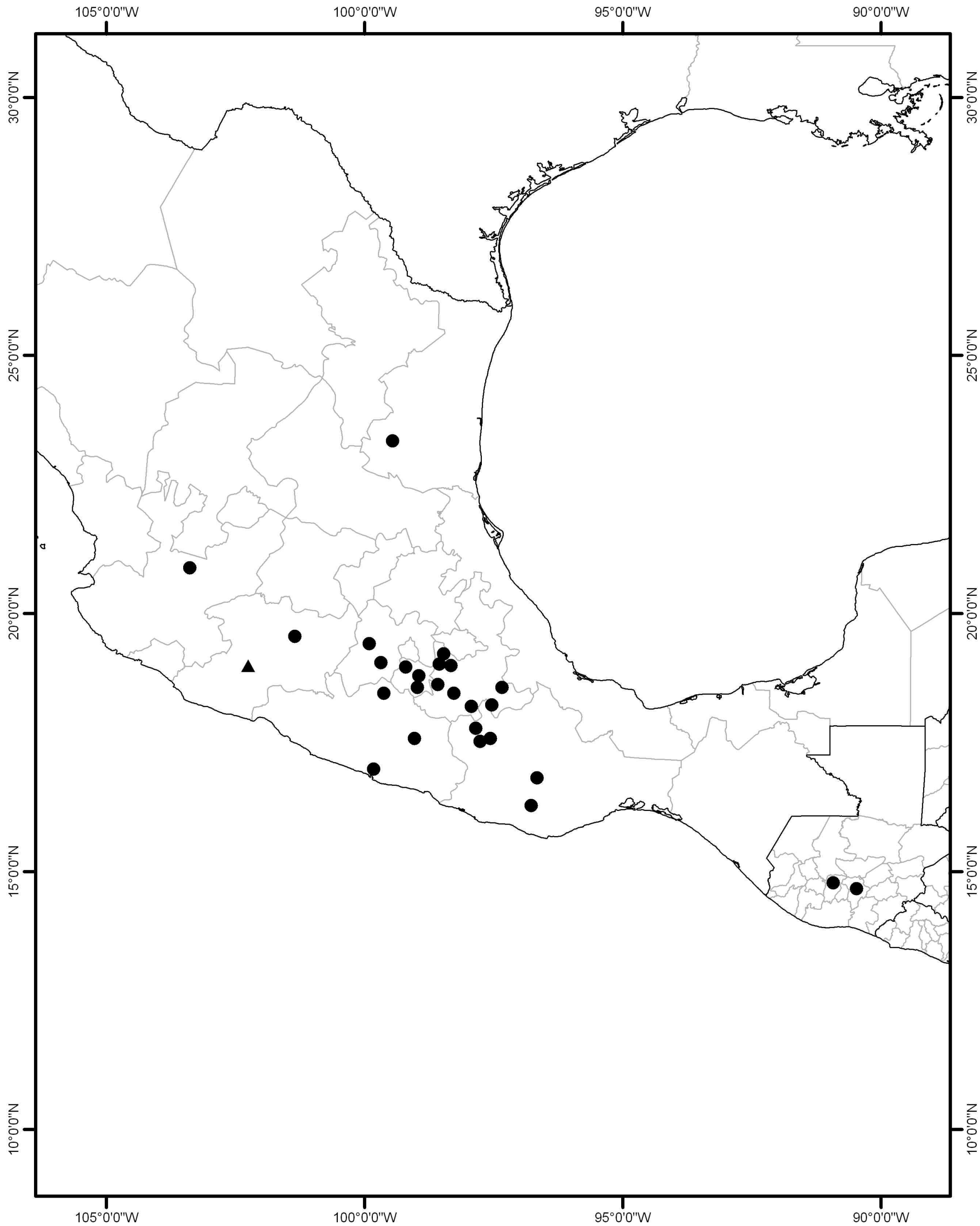

Fig. 34. Distribution of *Proboscidea triloba* ssp. *triloba* (●) and *Proboscidea triloba* ssp. *diversifolia* (▲).

LITERATURE CITED

Abbiatti, D. 1939. Las Martiniáceas Argentinas. *Notas del Museo de La Plata (Botánica)* Tomo 4, #29: 443-473.

Albach, D. C., H. M. Meudt, and B. Oxelman. 2005. Piecing together the "new" Plantaginaceae. *American Journal of Botany* 92: 297-315.

Angiosperm Phylogeny Group II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141: 399-436.

Angiosperm Phylogeny Group III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell, and M. J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247-277.

Bande, M. B. 1986. Fossil wood of *Gmelina* Linn. (Verbenaceae) from the Deccan Intertrappean Beds of Nawargaon with comments on the nomenclature of Tertiary fossil woods. *The Palaeobotanist* 35: 165–170.

Barron, E. 1992. Presencia de *Fraxinus excelsior* Linne (Oleaceae, Gentianales) en el Mioceno superior de la depresión Ceretana; implicaciones tafonómicas y paleoecológicas. *Revista Española de Paleontología* 7: 101–108.

Beardsley, P. M., and R. G. Olmstead. 2002. Redefining Phrymaceae: the placement of *Mimulus*, tribe Mimuleae, and *Phryma*. *American Journal of Botany* 89: 1093-1102.

Benson, L. 1979. *Plant Classification*, 2nd ed. D.C. Heath & Co.

Berry, J., P. K. Bretting, G. P. Nabhan, and C. Weber. 1981. *Proboscidea parviflora*: a potential oilseed crop for arid lands. *Journal of Arid Environments* 4: 147-160.

Bremer, B., K. Bremer, N. Heidari, P. Erixon, R. G. Olmstead, A. A. Anderberg, M. Källerjö, and E. Barkhordarian. 2002. Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. *Molecular Phylogenetics and Evolution* 24: 274-301.

Bretting, P.K. 1981. *A systematic and ethnobotanical survey of Proboscidea and allied genera of the Martyniaceae*. Ph.D. Thesis, Indiana University, Bloomington, Indiana.

Bretting, P. K. 1982. Morphological differentiation of *Proboscidea parviflora* ssp. *parviflora* (Martyniaceae) under domestication. *American Journal of Botany* 69: 1531-1537.

Bretting, P. K. 1983. The taxonomic relationship between *Proboscidea louisianica* and *Proboscidea fragrans* (Martyniaceae). *The Southwestern Naturalist* 28: 445-449.

Bretting, P. K. 1984. Folk names and uses for martyniaceous plants. *Economic Botany* 38: 452-463.

Bretting, P. K. 1985. Geographical intergradation in Proboscidea parviflora ssp. sinaloensis (Martyniaceae). *The Southwestern Naturalist* 30: 343-348.

Bretting, P. K. 1986. Changes in fruit shape in *Proboscidea parviflora* ssp. *parviflora* (Maryniaceae) with domestication. *Economic Botany* 40: 170-176.

Bretting, P. K., and G. P. Nabhan. 1986. Ethnobotany of devil's claw (*Proboscidea parviflora* ssp. *parviflora*: Martyniaceae) in the greater southwest. *Journal of California and Great Basin Anthropology* 8: 226-237.

Bretting, P. K. and S. Nilsson. 1988. Pollen morphology of the Martyniaceae and its systematic implications. *Systematic Botany* 13(1): 51-59.

Britton, N.L., and A. Brown. 1913. *An illustrated flora of the northern United States, Canada and the British Possessions. 3 vols.* Charles Scribner's Sons, New York.

Brown, R. 1810. *Prodromus Florae Novae Hollandieae et Insulae Van Dieman*. London.

Call, V. B., and D. L. Dilcher. 1992. Investigations of angiosperms from the Eocene of southeastern North America: samaras of *Fraxinus wilcoxiana* Berry. *Review of Palaeobotany and Palynology* 74: 249– 266.

Carr, M. E., B. S. Phillips, and M. O. Bagby. 1985. Xerophytic species evaluated for renewable energy resources. *Economic Botany* 39: 505-513.

Chaney, R. W., and D. I. Axelrod. 1959. Miocene floras of the Columbia Plateau. *Carnegie Institution of Washington Publication* 617: 1–231.

Covas, G., and B. Schnack. 1947. Estudios cariológicos en antófitas, II parte. *Revista Argentina de Agronomia* 14(3): 224-231.

Cronquist, A. 1981. *An integrated system of classification of flowering plants*. Columbia University Press, New York.

de Candolle, A. P. 1845. *Podromus Systematis Naturalis Regni Vegetabilis*. Fortin, Masson. Paris. vol. 9.

Decaisne, J. 1865. Revue du Groupe des Pedalineés. Annales Science Natural Series V, #3.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using bootstrap. *Evolution* 39: 783-791.

Gaiser, L. O., M. Sutherland, and R. Moore. 1943. Cytological studies in *Martynia louisiana*. *American Journal of Botany* 30(7): 543-551.

Gentry, A. H. and A. S. Tomb. 1979. Taxonomic implications of Bignoniaceae palynology. *Annals of the Missouri Botanical Garden* 66(4): 756-777.

Ghebrehiwet, M. B. Bremer, and M. Thulin. 2000. Phylogeny of the tribe Antirrhineae (Scrophulariaceae) based on morphological and *ndhF* sequence data. *Plant Systematics and Evolution* 220: 223–239.

Ghosh, L. and J. L. Beal. 1979. Seed lipid constituents of three species of *Proboscidea*. *Journal of Natural Products* 42: 287-292.

Gibson, R. 1999. Carnivorous plants of New South Wales, Australia. *Carnivorous Plant Newsletter* 28: 59-69.

Gloxin , B. P. 1882. Martynia annua, villosa et viscosa, folio subrotundo, flore magno rubro, D. Houston: historia et analysis plantae. *Observationes Botanique* 14: 1-15.

Gutierrez, Jr., R. 2002. *A molecular phylogeny of the family Martyniaceae (order Lamiales) based on nrDNA Internal Transcribed Spacer sequences*. Master's Thesis, University of Texas at El Paso, El Paso, Texas.

Gutierrez, R. 2007. Vascular plants of Arizona: Martyniaceae. *Canotia* 3: 26-31.

Harley, R. M., A. M. Giulietti, and F. A. R. dos Santos. 2003. *Holoregmia* Nees, a recently discovered genus of *Martyniaceae* from Bahia, Brazil. *Kew Bulletin* 58: 205-212.

Hevly, R. H. 1962. Martyniaceae. *in* Correll, D.S. and M. C. Johnston. *Manual of the Vascular Plants of Texa*s. Texas Research Foundation, Renner, Texas.

Hevly, R. H. 1969. Nomenclatural history and typification of *Martynia* and *Proboscidea* (Martyniaceae). *Taxon* 18: 527-534.

Horaninov, P. F. 1847. *Characteres essentiales familiarum ac tribuum regni vegetabilis et amphorganici ad leges tetractydis naturae conscripti accedit enumeratio generum magis notorum et organographiae supplementum, auctore Paulo Horaninow*. Typis K. Wienöberianis, Petropoli.

Hurd, P. D., and E. A. Linsley. 1963. Pollination of the unicorn plant (Martyniaceae) by an oligolectic corolla-cutting bee (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 36: 248-252.

Janzen, D. H. 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. *Annual Review of Ecology and Systematics* 17: 595-636.

Jobson, R. W., J. Playford, K. M. Cameron, and V. A. Albert. 2003. Molecular phylogenetics of Lentibulariaceae inferred from plastid *rps*16 intron and *trn*L-F DNA sequences: implications for character evolution and biogeography. *Systematic Botany* 28: 157-171.

Jussieu, A. L. 1789. *Genera Plantarum, secundum ordines naturales disposita juxta methodum in Horto Regio Parisiensi exaratam*. Paris.

Kearney, T. H., and R. H. Peebles. 1960. *Arizona Flora*. Ed. 2. Berkeley: University of California Press.

Keller, J. C. (ed.) 1762. Icones Plantarum (original author: C. C. Schmidel). Nuremberg, Germany.

Kennedy, B. H., S. A. James, and C. T. Imada. 2010. New Hawaiian plant records from *Herbarium Pacificum* for 2008. *Bishop Museum Occasional Papers* 107: 19-26.

Kunth, C. S. 1822-1825. *Synopsis plantarum, quas in itinere ad plagam aequinoctialem orbis novi, collegerunt Al.* De Humbolt et Am. Bonpland. 4 vols. Paris.

Lamarck, J. B. P. 1786. *Martynia*. *Encyclopedie Methodique, Botanique* 2: 112.

Lawrence, G. H. M. 1951. *Taxonomy of Vascular Plants*. Macmillan Co., New York. 823 pp.

Lawrence, G. H. M. 1957. *Proboscidea* and other unicorn plants (Martyniaceae). *Baileya* 5: 127-132.

Lia, V. V., V. A. Confalonieri, C. I. Comas, and J. H. Hunziker. 2001. Molecular phylogeny of *Larrea* and its allies (Zygophyllaceae): reticulate evolution and the probable time of creosote bush arrival to North America. *Molecular Phylogenetics and Evolution* 21: 309-320.

Lindley, J. 1825. *Martynia lutea*. *Edward's Botanical Register* 11: t. 934.

Linnaeus, C. 1737. Hortus Cliffortianus. Amsterdam.

Linnaeus, C. 1753. Species Plantarum (1st ed.). Stockholm.

Löve, Á. 1977. IOPB chromosome number reports LVIII. *Taxon* 26(5/6): 557-559.

Löve, Á. 1979. IOPB chromosome number reports LXIV. *Taxon* 28(4): 391-395.

Maddison, W. P. 1997. Gene trees in species trees. *Systematic Biology* 46: 523-536.

Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86: 472–522.

Manchester, S. R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. Oregon Geology 62: 51-63.

Manktelow, M., L. A. McDade, B. Oxelman, C. A. Furness, and M. J. Balkwill. 2001. The enigmatic tribe Whitfieldieae (Acanthaceae): Delimitation and phylogenetic relationships based on molecular and morphological data. *Systematic Botany* 26: 104-119.

Martin, P.S., and C. M. Drew. 1970. Additional scanning electron photomicrographs of Southwestern pollen grains. *Journal of the Arizona Academy of Science* 6: 140-161.

Martini, E. 1939. Ricerche embriologiche sulle Martyniaceae. *Nuovo Giornale Botanico Italiano* 46(2): 197-226.

Martyn, J. 1728-1738. Historia Plantarum Rariorum. London.

Marx, H. E., N O'Leary, Y. Yuan, P. Lu-Irving, D. C. Tank, M. E. Múlgura, and R. G. Olmstead. 2010. A molecular phylogeny and classification of Verbenaceae. *American Journal of Botany* 97(10): 1647–1663.

McDade, L. A., and M. L. Moody. 1999. Phylogenetic relationships among Acanthaceae: evidence from noncoding *trnL-trnF* chloroplast DNA sequences. *American Journal of Botany*: 86: 70-80.

McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, and N. J. Turland. (eds.) 2006. International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005. Regnum Vegetabile 146. Gantner Verlag, Ruggell, Liechtenstein.

Meyer, H. W., and S. R. Manchester. 1997. The Oligocene Bridge Creek Flora of the John Day Formation, Oregon. *University of California Publications in Geological Science* 141: 1–195.

Meyers-Rice, B. 1999a. Testing the appetities of *Ibicella* and *Drosophyllum*. *Carnivorous* Plant *Newsletter* 28: 40-43.

Meyers-Rice, B. 1999b. On cultivating *Ibicella lutea* (Martyniaceae). *Carnivorous Plant Newsletter* 28: 47-48.

Miller, P. 1768. Gardener's Dictionary (8th ed.). London.

Munz, P. A. 1959. *A California flora*. Berkeley: University of California Press.

Nabhan, G., A. Whiting, H. Dobyns, R. Hevly, and R. Euler. 1981. Devil's claw domestication: evidence from Southwestern Indian fields. *Journal of Ethnobiology* 1:135-164.

Nees von Esenbeck, C. G. D. 1821. Reise des Prinzen von Neuwied. *Flora* 4: 294-304.

Nees von Esenbeck, C. G. D. and K. F. P. Martius. 1823. *Craniolaria unibracteata*. *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum* 11: 67.

Nichols, R. 2001. Gene trees and species trees are not the same. *Trends in Ecology and Evolution* 16: 358-364.

Olmstead, R. G. and P. A. Reeves. 1995. Evidence for the polyphyly of the Scrophulariaceae based on chloroplast *rbcL* and *ndhF* sequences. *Annals of the Missouri Botanical Garden* 82: 176-193.

Olmstead, R. G. and J. A. Sweere. 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in Solanaceae. *Systematic Botany* 43: 467-481.

Olmstead, R. G., C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. T. Elisons, and P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. *American Journal of Botany* 88: 348-361.

Olmstead , R. G. , M. L. Zjhra , L. G. Lohmann , S. O. Grose , and A. J. Eckert . 2009 . A molecular phylogeny and classification of Bignoniaceae. *American Journal of Botany* 96: 1731 – 1743 .

Oxelman, B., M. Backlund, and B. Bremer. 1999. Relationships of the Buddlejaceae s.l. investigated using parsimony jackknife and branch support analysis of chloroplast *ndhF* and *rbcL* sequence data. *Systematic Botany* 24: 164-182.

Oxelman, B., P. Kornhall, R. G. Olmstead, and B. Bremer. 2005. Further disintegration of the Scrophulariaceae. *Taxon* 54: 411-425.

Pamilo, P., and M. Nei. 1988. Relationships between gene trees and species trees. *Molecular Biology and Evolution* 5: 568-583.

Phillippi, A. and R. J. Tyrl. 1979. The reproductive biology of *Proboscidea louisianica* (Martyniaceae). *Rhodora* 81: 345-361.

Pigg, K. B., and W. C. Wehr. 2002. Tertiary flowers, fruits and seeds of Washington State and adjacent areas, part III. *Washington Geology* 30: 3–16.

Plachno, B. J., L. Adamec, and H. Huet. 2009. Mineral nutrient uptake from prey and glandular phosphatase activity as a dual test of carnivory in semi-desert plants with glandular leaves suspected of carnivory. *Annals of Botany* 204: 649-654.

Posada, D., and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Rafinesque, C. S. 1836. *Disteria*. *Flora Telluriana* 43: 68.

Rahmanzadeh, R., K. Müller, E. Fischer, D. Bertels, and T. Borsch. The Linderniaceae and Gratiolaceae are further lineages distinct from the Scrophulariaceae. *Plant Biology* 2005: 1-12.

Reid, E. M., and M. E. J. Chandler. 1926. *Catalogue of Cainzoic plants in the Department of Geology: the Brembridge Flora*. Vol. 1. London, UK: British Museum (Natural History).

Rice, B. 2008. Reassessing commensal-enabled carnivory in *Proboscidea* and *Ibicella*? *Carnivorous Plant Newsletter* 37: 15-19.

Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.

Schwarzbach, A. E., and L. A. McDade. 2002. Phylogenetic relationships of the mangrove family Avicenniaceae based on chloroplast and nuclear ribosomal DNA sequences. *Systematic Botany* 27: 84-98.

Shaw, J, E. B. Lickey, J. T. Beck, S. B. Farmer, W. Liu, J. Miller, K. C. Siripun, C. T. Winder, E. E. Schilling, and R. L. Small. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142-166.

Shaw, J., E. B. Lickey, E. E. Schilling and R. L. Small. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American Journal of Botany* 94(3): 275–288. 2007.

Snow, R. 1959. Chromosome numbers of California plants, with notes on some cases of cytological interest. *Madroño* 15: 81-89.

Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* 133: 381-461.

Spegazzini, C. 1897. *Plantae Novae v. Criticae, Republicae Argentinae, Decas 3*. Tallares-Solá, Sesé y Cia, La Plata, Argentina.

Srinivasan, A. R. 1942. Contribution to the morphology of *Pedalium murex* Linn. and *Sesamum indicum* D.C. Proceedings of the Indian Academy of Science, Sect. B. 16(5): 155-164.

Stapf, O. 1895. Martyniaceae. *in* Engler, A., and K. Prantl. Die Natürlichen Pflanzenfamilien. 4(3b): 265-269.

Stephenson, A. and W. W. Thomas. 1977. Diurnal and nocturnal pollination of *Catalpa speciosa* (Bignoniaceae). *Systematic Botany* 2: 191-198.

Sugiura, T. 1936a. Studies on the chromosome numbers in higher plants, with special reference to cytokinesis, I. *Cytologia* 7: 544-596.

Sugiura, T. 1936b. A list of chromosome numbers in angiospermous plants. II. *Proceedings of the Tokyo Imperial Academy* 12(5): 144-146.

Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods), version 4.0b10. *Sinauer, Sunderland, Mssachusetts, USA.*

Takhtajan, A. 1969. *Flowering plants: Origin and dispersal.* Smithsonian Institution Press, Washington, DC. 310 pp.

Taylor, K. R. 1983. Martyniaceae. *Flora of Veracruz* 30: 1-11.

Thellung. A. 1912. La flora adventice de Montpelier. Memoires de la Societé Nationale des Sciences Naturelles Mathématiques de Cherbourg. Tome 38. Quatrieme Serie-Tome VII.

Thieret, J. W. 1976. Floral biology of *Proboscidea louisianica* (Martyniaceae). *Rhodora* 78: 169-179.

Thieret, J. 1977. The Martyniaceae in the southeastern United States. *Journal of the Arnold Arboretum* 58: 25-39.

Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/

Van Eseltine, G. P. 1929. A preliminary study of the unicorn plants (Martyniaceae). *New York State Department of Agriculture Technical Bulletin* 149: 1-41.

Wallace, J. and K. McGhee. 1999. Testing for carnivory in *Ibicella lutea*. *Carnivorous Plant Newsletter* 28: 49-50.

Wallander, E. and V. A. Albert. 2000. Phylogeny and classification of Oleaceae based on *rps16* and *trnL-F* sequence data. *American Journal of Botany* 87: 1827-1841.

Wehr, W. C., and D. Q. Hopkins. 1994. The Eocene orchards and gardens of Republic, Washington. *Washington Geology* 22: 27–34.

Wen, J., P. P. Lowry II, J. L. Walck, and K. Yoo. 2002. Phylogenetic and biogeographic diversification in *Osmorhiza* (Apiaceae). *Annals of the Missouri Botanical Garden* 89: 414-428.

White, T. J., J. Bruns, S. Lee, and J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. in PCR Protocols: A Guide to Methods and Applications, M. Innis, D. Gelfand, J. Sninsky, and T. White (eds.). pp. 308-322. Academic Press, San Diego.

Wooton, E. O. 1898. New plants from New Mexico. III. *Bulletin of the Torrey Botanical Club* 25: 451-456.

Wooton, E. O. and P. G. Standley. 1915. Flora of New Mexico. *Contributions of the United States National Herbarium* 19: 1-794.

Xia, Z., Y. Wang, and J. F. Smith. 2009. Familial placement and relations of *Rehmannia* and *Triaenophora* (Scrophulariaceae s.l.) inferred from five gene regions. *American Journal of Botany* 96: 519-530.

APPENDIX A

A KEY FOR THE FLORA MESOAMERICANA PROJECT

MARTYNIACEAE

Viscid-pubescent herbs, annual or perennial, usually strongly scented. Leaves simple, opposite to sub-opposite, entire to sinuate, dentate, or lobed, margins entire to denticulate, base cordate; stipules absent. Inflorescence a terminal raceme. Flowers perfect, zygomorphic, pentamerous, bibracteolate; calyx composed of 5 free or united sepals, if united then the calyx split abaxially to base; corolla sympetalous, the tube cylindrical at base and equaling or surpassing the calyx, the throat campanulate or infundibular, the upper lobes exterior in bud; stamens 4, didynamous, or 2, the second pair forming staminodes, the filaments attached to the corolla, the anthers with two divergent cells; ovary superior, unilocular, bicarpellate with 2 parietal placentae expanded to form false partitions; ovules few to many. Fruit a drupaceous capsule, dehiscing longitudinally, terminated by an incurved 2-horned beak or rostrum; exocarp thick, fleshy, deciduous in 2 valves; endocarp woody, sculptured. Seeds 4 to many, often somewhat irregularly compressed, the testa corky or papery. 5 genera. Native to arid and semi-arid regions in the U. S., Mexico, West Indies, Central and South America, naturalized in other parts of the world.

Bibliography: Van Eseltine, G.P. *NY St. Agr. Exp. Sta. Tech. Bull.* 29:1-41 (1929).

1. Sepals free; fertile stamens 2; rostrum of fruit shorter than the capsule; seeds with papery seedcoat **1. Martynia**

1. Sepals united more than 50% of the length of the calyx; fertile stamens 4; rostrum of fruit longer than the capsule; seeds with corky seedcoat **2. Proboscidea**

1. **Martynia** Linnaeus
By Raul Gutierrez

Annual herb. Stems viscid-pubescent when young, becoming glabrate with age. Leaves broadly ovate to deltoid, base cordate, margins dentate, apex acute. Inflorescences racemose, the peduncle densely viscid-pubescent. Flowers 40-60 mm; pedicels densely viscid-pubescent, upright at anthesis and hanging in fruit; bracteoles 10 mm, oblong; calyx composed of 5 free sepals; corolla obliquely campanulate with 5 widely-spreading lobes, white to pink with a large purple blotch on each of the petals; fertile stamens 2, staminodes 2. Fruit ovoid, compressed dorso-ventrally; exocarp viscid-pubescent; endocarp woody with a rostrum shorter than the length of the capsule, the fruit dehiscing only to base of rostrum. Seeds few and enclosed within the fruit. 1 species. Mexico, Central America and the West Indies. Naturalized worldwide.

Bibliography: Van Eseltine, G.P. *NY St. Agr. Exp. Sta. Tech. Bull.* 29:1-41 (1929).

1. Martynia annua Linnaeus, *Sp. Pl.* 2: 618 (1753). Lectotype (designated by Nafday, 1963): Martyn, *Hist. Pl. Rar.* t. 42 (1728). N.v.: uña de gato, uña de diablo.

Disteira angulosa Raf., *Martynia angulosa* Lam., *M. diandra* Glox., *Vatkea diandra* (Glox.) O. Hoffman.

Annual herb. Stems viscid-pubescent. Leaves opposite; petioles 5-25 cm; lamina 5-25 x 10-30 cm. Inflorescences with up to 20 flowers. Flowers 40-60 mm; pedicels

30 mm, densely viscid-pubescent; bracteoles 1 cm; calyx composed of 5 free sepals; corolla obliquely campanulate with 5 widely-spreading lobes, white to pink with a large purple blotch on each of the petals; fertile stamens 2, staminodes 2. Fruit 60 mm, ovoid; exocarp separating from the endocarp at maturity; endocarp woody, the rostrum 10 mm. Seeds with papery testa. Flowering Jun-Oct, occasionally at other times of the year. *Disturbed areas along roads, lakes, and rivers*. Ch (*Ton 3168*, NY); Y (*Seler & Seler 5596*, GH); C (*Carnevalli, May & Tapia 5665,* NY); B (*Lundell 466, F*); G (*Steyermark 50753, NY*); H (*Molina 22422, NY*); ES (*Calderon 1651, GH*); N (*Nee & Miller 27536*, NY); CR (*Chavarria 229, F*). 10-1400m. (Native from Mexico to Costa Rica and the West Indies.)

2. **Proboscidea** Schmidel
By Raul Gutierrez

Erect viscid-pubescent annuals. Leaves simple, opposite, orbicular-reniform to ovate-lanceolate, sometimes inequilateral at base, margins entire to palmately or pinnately lobed. Inflorescences terminal racemes exceeding the foliage. Flowers 20-70 mm; pedicels erect to spreading but lengthening, thickening and becoming deflexed in fruit; calyx 10-25 mm, 5-lobed, split abaxially to the base, deciduous, with 2 bracts at the base; corolla sympetalous, tubular-cylindric to campanulate or infundibular; stamens 4, didynamous, included in the throat of the corolla, the abaxial pair of fertile stamens longer; filaments arcuate and attached to the corolla; pistils about as long to longer than stamens; style slender, about three times as long as ovary; stigma lobes 2, sensitive, obovate-oblanceolate; ovary 1-celled, ovate to lanceolate. Fruit exocarp viscid-tomentose, deciduous; endocarp woody, reticulate-sculptured, with a suture on both dorsal and ventral median lines, terminated by an upcurved beak about 1.25 to 3.5 times as long as the capsule that splits into two elongate, sharp-pointed "horns." Seeds 6-8 mm, black, angled, with a thick corky tuberculate testa. 6 species. USA, Mexico, Guatemala, & Peru.

Bibliography: Bretting, P.K. *A systematic and ethnobotanical study of Proboscidea and allied genera of the Martyniaceae*. Ph.D. thesis, Indiana University, Bloomington, Indiana (1982).

1. Proboscidea triloba (Chamisso & Schlectendahl) Decaisne, *Ann. Sci. Nat. 5*. 3: 321 (1865). *Martynia triloba* Schlect. & Cham., *Linnaea* 5: 121. 1830. Holotype: Mexico, Veracruz, *Scheide & Deppe 242*, July 1828, (HAL-43262). N.v.: uña de gato, uña de Diablo, toritos.

Martynia botteri (Decne.) Hemsley, *M. confusa* (Van Eseltine) Standl. & Steyerm., *Proboscidea botteri* Decne., *P. confusa* Van Eseltine.

1a. ssp. **triloba**.

Viscid-pubescent annual. Stems procumbent. Leaves opposite; petiole 15-30 cm; lamina trullate, entire to shallowly trilobed, depths of sinuses ranging from 0%-30%, base equilateral to slightly inequilateral, margins entire to denticulate, apex acute. Inflorescences racemic, peduncles 10-50 mm with 15-35 flowers and exceeding the foliage. Flowers with strong musky odor; pedicels 20-40 mm, persistent, and thickening in fruit; bracteoles ovate to lanceolate; calyx 10-24 mm; corolla 45 mm, lavender internally, with rusty to dark purple specks scattered in the interior, nectar guides bright yellow, adaxial lobes each with a large purple splotch, mid and abaxial lobes lavender with dark purple marks; stamens 4. Fruit dark gray or black, oblong-ellipsoid and inflated, capsule 60 mm, rostrum 75 mm long. Seeds, 8.5-10 x 4-6 mm, ovate, dark brown to black. Flowering Jun-Sep. *Disturbed areas, especially along roads.* G (*Aguilar 528*, F). 800-2200m. (Native to Mexico and Guatemala.)

Index of plant names

Bibliography

Bretting, P.K. A systematic and ethnobotanical study of *Proboscidea* and allied genera of the Martyniaceae. Ph.D. thesis, Indiana University, Bloomington, Indiana (1982).

Nafday, U.R. Studies in the Tubiflorae of Nagpur V: Martyniaceae. *Bull. Bot. Soc., College of Sci., Nagpur* 4: 58-71 (1963).

Van Eseltine, G.P. A preliminary study of the unicorn plants (Martyniaceae). *NY St. Agr. Exp. Sta. Tech. Bull.* 29:1-41 (1929).

APPENDIX B

LIST OF SEQUENCES USED IN THE PHYLOGENETIC ANALYSES OF THE LAMIALES.

Data listed includes: Family: taxon [locality data and voucher information if sequence is new], *ndhF* GenBank accession number, and *rps16* GenBank accession number. Underlined GenBank accession numbers denote new sequences that were generated for this study. An asterisk (*) denotes that the sequence from that taxon was not used but combined with the sequence of another species in the same genus to provide a complete data set.

Acanthaceae: *Acanthus montanus* T. Anderson, AJ429115, DQ059146; *Andrographis paniculata* Nees [Jamaica, *Keil 16415* (ASU)], JN686620, JN686514; *Aphelandra squarrosa* Nees, AJ249405, DQ059200; *Avicennia germinans* (L.) Stearns [Mexico: Baja California Sur, *Rebman 3425* (ASU)], JN686621, JN686517; *Avicennia marina* (Forssk.) Vierh., AJ429116, AJ431038; *Barleria micans* Nees [Mexico: Nayarit, *Daniel 2035gh* (ASU)], *, JN686515; *Barleria prionitis* L., U12653, *; *Crossandra nilotica* Oliver, U12656, *; *Crossandra strobilifera* (Lam.) Benoist, *, DQ059176; *Elytraria crenata* Vahl, U12657, *; *Elytraria imbricata* (Vahl) Pers. [U.S.A.: Arizona, *Makings 1239* (ASU)], *; JN686516; *Justicia adhotada* L., *, DQ059214; *Justicia americana* (L.) Vahl, U12663, *; *Ruellia ciliosa* Pursh, U12664, *; *Ruellia humilis* Nutt., *, AF482538; *Thunbergia alata* Bojer ex Sims, U12667, AJ609131.

Bignoniaceae: *Arrabidaea selloi* (Spreng.) Sandwith, DQ222560, *; *Arrabidaea selloi* (Spreng.) Sandwith [Brazil, *Kegler 152* (ASU)], *, JN686518; *Campsis radicans* (L.) Bureau, AF130144, *; *Campsis radicans* (L.) Bureau [U.S.A.: Texas, *Gutierrez 2127* (ASU)], *, JN686519; *Catalpa* sp., L36397, *; *Catalpa speciosa* Warder ex Engelm., *, AJ609197; *Chilopsis linearis* (Cav.) Sweet [U.S.A.: Texas, *Gutierrez 364* (ASU)], JN686617, *; *Chilopsis linearis* (Cav.) Sweet, *, DQ532492; *Cydista aequinoctialis* (L.) Miers, DQ222577, *; *Cydista aequinoctialis* (L.) Miers [Puerto Rico, *Salywon 806* (ASU)], *, JN686520; *Eccremocarpus scaber* Ruiz & Pav., AF102630, *; *Eccremocarpus scaber* Ruiz & Pav. [Chile, *Landrum 10050* (ASU)], *, JN686521; *Jacaranda mimosifolia* D. Don [Cultivated, *Gutierrez 958* (ASU)], JN686638, JN686522; *Macfadyena unguis-cati* (L.) A. H. Gentry [Cultivated, *Gutierrez 712* (ASU)], JN686639, JN686523; *Oroxylum indicum* (L.) Benth. ex Kurz, AF102635, *; *Oroxylum indicum* (L.) Benth. ex Kurz [Thailand, *Anderson 6135* (ASU)], *, JN686524; *Pyrostegia venusta* Miers, DQ222633, *; *Pyrostegia venusta* Miers [Brazil, *Wasum 12137* (ASU)], *, JN686525; *Stereospermum nematocarpum* DC., EF105025, *; *Sterospermum neuranthum* Kurz [Thailand, *Anderson 5456* (ASU)], *, JN686526; *Tabebuia chrysantha* (Jacq.) G. Nicholson, EF105030, *; *Tabebuia ochracea* (Cham.) Standl. [Costa Rica, *Gutierrez 786* (ASU)], *, JN686527; *Tecoma stans* (L.) H.B.& K., AF130145, *; *Tecoma stans* (L.) H.B.& K. [Cultivated, *Gutierrez 1573* (ASU)], *, JN686528; *Tecomeria capensis* (Thunb.) Spach, DQ222642, *; *Tecomeria capensis* (Thunb.) Spach [Cultivated, *Gutierrez 519* (ASU)], *, JN686529.

Calceolariaceae: *Calceolaria* sp., AF123679, *; *Calceolaria mexicana* Benth., *, AJ609202; *Jovellana* sp., AF123684, *; *Jovellana violacea* G.Don [Chile, *Landrum 7966* (ASU)], *, JN686507.

Gesneriaceae: *Columnea* sp., *, AF482535; *Columnea oblongifolia* Rusby, AF013696, *; *Gesneria pedunculata* Fritsch [Puerto Rico, *Salywon et al. 1216* (ASU)], *, JN686508; *Gesneria ventricosa* Sw., AY623167, *; *Gloxinia perennis* Fritsch [Ecuador, *Landrum 10672* (ASU)], *, JN686509; *Gloxinia sylvatica* (Kunth) Wiehler, U62157, *; *Peltanthera floribunda* Benth., AF027281, AJ431041; *Streptocarpus caulescens* Vatke, *, AJ431043; *Streptocarpus holstii* Englem., L36415, *; *Sanango* sp., AF027283, AJ431042

Lamiaceae: *Callicarpa japonica* Thunb., AF130148, AJ505413; *Colebrookea oppositifolia* Sm., U78688, *; *Colebrookea oppositifolia* Sm. [India, *Inderjeet 52* (ASU)], *, JN686531; *Congea tomentosa* Roxb., U78689, AJ505411; *Elsholtzia stauntonii* Benth., U78690, AJ505406; *Gmelina hystrix* Schult. ex Kurz, U78692, AJ505407; *Lamium purpureum* L., U78694, AJ609175; *Mentha* x *rotundifolia* (L.) Huds., U78696; *; *Mentha suaveolens* Ehrh., *, AJ505418; *Ocimum americanum* L. [Cultivated, *Damrel 2144* (ASU)], JN686623, *; *Ocimum basilicum* L., *, AJ505351; *Perilla frutescens* (L.) Britton, [U.S.A.: Missouri, *Rebman 709* (ASU)], JN686622, JN686530; *Plectranthus barbatus* Andrews, U78698, AJ505378; *Prostanthera petrophila* B.J. Conn, *, AJ505404, *Prostanthera rotundifolia* R.Br., U78702, *; *Salvia divinorum* Epling & Jativa, U78703, *; *Salvia guarantica* A.St.-Hil. ex Benth, *; AJ505421; *Scutellaria baicalensis* Georgi [Cultivated, *Schmidt 1* (ASU)], *, JN686532; *Scutellaria bolanderi* A.Gray, U78704, *; *Tectona grandis* L.f., U78705, AJ505408, *Tetraclea coulteri* A.Gray, U78706, *; *Tetraclea coulteri* A.Gray [U.S.A.: Arizona, *Makings 1208* (ASU)], *, JN686533; *Teucrium fruticans* L., U78686, *; *Teucrium laciniatum* Torr. [U.S.A.: New Mexico, *Worthington 33155* (ASU)], *, JN686534; *Vitex agnus-castus* L., U78707, *; *Vitex trifolia* L., *; AJ505416.

Lentibulariaceae: *Byblis gigantea* Lindl. [Australia, *Chase 2159* (K)], JN686614, JN686511; *Genlisea aurea* A.St.-Hil. [Brazil, *Kummrow et al. 3356* (ASU)], JN686616, *; *Genlisea aurea* A.St.-Hil., *, AF482540; *Utricularia alpina* Jacq., *, AF482556; *Utricularia subulata* L. [U.S.A.: Alabama, *Diamond 14350* (ASU)], JN686615, *.

Linderniaceae: *Lindernia brevidens* Skan, *, AY492213; *Lindernia dubia* (L.) Pennell, EF527446, *; *Torenia baillonii* Godefroy ex André, AJ617583, AY492227.

Martyniaceae: *Craniolaria integrifolia* Cham. [Bolivia, *Nee 52095* (NY)], JN686625, JN686536; *Holoregmia viscida* Nees [Brazil, *Webster 25812* (NY)], JN686611, JN686505; *Ibicella lutea* (Lindl.) Van Eselt. [U.S.A.: California, *Gehrung s.n.* (UTEP)], JN686626, JN686537; *Martynia annua* L. [Cultivated, *Damrel 1024* (ASU)], JN686624, JN686535; *Proboscidea louisianica* (Mill.) Thell. [Cultivated, *Gutierrez 001* (UTEP)], JN686627, JN686538; *Proboscidea sabulosa* Correll [U.S.A.: Texas, *Gutierrez 017* (UTEP)], JN686628, JN686539.

Oleaceae: *Abeliophyllum distichum* Nakai, DQ673262, AF225216; *Fontanesia phillyreoides* Labill., DQ673263, AF225226; *Forsythia europea* Degen & Baldacci, DQ673264, *; *Forsythia suspensa* Vahl, *, AF225231; *Jasminum mesnyi* Hance, DQ673267, AF225248; *Ligustrum vulgare* L., AF130164, AF225257; *Menodora integrifolia* (Cham. & Schltdl.) Steud., *, AF225259; *Menodora longiflora* A.Gray, DQ673273, *; *Myxopyrum hainanense* L.C.Chia, DQ673265, *; *Myxopyrum nervosum* Blume, *, AF225260; *Nyctanthes arbor-tristis* L., DQ673266, AF225272; *Olea europaea* L., DQ673278, AF225275; *Syringa vulgaris* L., DQ673277, AF225292.

Orobanchaceae: *Agalinis peduncularis* (Benth.) Pennell [Mexico: Sonora, *Van Devender et al. 2001-1080* (ASU)], *, JN686540; *Agalinis tenuiflora* Raf., AY563927, *; *Cordylanthus laxiflorus* A.Gray [U.S.A.: Arizona, *Gutierrez 300* (ASU)], JN686629, *; *Cordylanthus ramosus* Nutt. ex Benth., *, EF103803; *Lindenbergia philippinensis* Benth., AF123686, AJ609169; *Pedicularis attollens* A. Gray, *, EF103821, *Pedicularis foliosa* L., AF123689, *; *Rehmannia chingii* H.L. Li, EF522187, DQ856488; *Triaenophora rupestris* Soleneder, EF522186, EF522183.

Paulowniaceae: *Paulownia tomentosa* (Thunb.) Steudl., L36406, AJ431051.
Pedaliaceae: *Ceratotheca triloba* E. Mey. ex Bernh., AY919281, AF482534; *Harpagophytum procubens* DC. ex Meisn. [South Africa, no voucher specimen], JN686630, JN686541; *Sesamum indicum* L., L36413, AJ431052; *Sesamum radiatum* Schumach. & Thonn. [Cultivated, no voucher specimen], JN686631, JN686542.
Phrymaceae: *Diplacus aurantiacus* (W.Curtis) Jeps., AF188186, AJ609163; *Lancea tibetica* Hook. f. & Thomson, AJ617599, AJ609174; *Leucocarpus perfoliatus* (Kunth) Benth., AJ617600, *; *Leucocarpus perfoliatus* (Kunth) Benth. [Mexico, *Gonzalez Medrano 17394* (ASU)], *, JN686543; *Mazus stachydifolius* Maxim., AJ619559, AJ609167; *Phryma leptostachya* L., AJ617586, AJ431053.
Plantaginaceae: *Angelonia pubescens* Benth., AF123675, AJ609214; *Antirrhinum majus* L., L36392, AJ431054; *Bacopa monnieri* (L.) Pennell, EF527447, AY492196; *Camplyanthus salsoloides* Roth, AJ619556, AY492199; *Chelone obliqua* L., AJ245814, AJ609220; *Cymbalaria muralis* G.Gaertn, B.Mey. & Scherb., AJ250382, AY492202; *Digitalis purpurea* L., AF130150, AY492203; *Galvezia fruticosa* J.F.Gmel., AJ250383, *; *Galvezia limensis* Domb. ex Chav., *, AY492205; *Globularia cordifolia* L., AF027282, AJ431055; *Gratiola pilosa* Michx., AF188183, AJ609182; *Hemiphragma heterophyllum* Wall., AF123683, AY492207; *Hippuris vulgaris* L., L36401, AY492208; *Isoplexis canariensis* (L.) Loudon, AJ617597, AJ609177; *Kickxia elatine* (L.) Dumort., AJ245816, AY492210; *Melosperma andicola* Benth., AJ617602, AY492216; *Plantago coronopus* L., *, AY218801; *Plantago lanceolata* L., L36408, *; *Poskea socotrana* (Balf.f) G.Talyor, AJ617585, AJ609147; *Russelia retrorsa* Greene, AJ619567, AJ609143; *Scoparia dulcis* L., EF527450, AY492223; *Tetranema mexicanum* Benth., AF123692, AJ609132; *Trapella sinensis* Oliv. [Japan, no voucher specimen], JN686619, JN686513; *Veronica persica* Hort. ex Poir., L36419; *Veronica tauricola* Bornm., *, AF482531.
Plocospermataceae: *Plocosperma buxifolium* Benth., AJ011985, AJ431026.
Schlegeliaceae: *Schlegelia parviflora* (Oerst.) Monach., L36410, AJ431057.
Scrophulariaceae: *Alonsoa unilabiata* Ruiz & Pav. ex Steudl., AF188184, AJ609217; *Antherothamnus pearsonii* N.E.Br., AJ401392, AJ609213; *Anticharis glandulosa* Asch., AJ619553, AJ609212; *Aptosimum* sp., AF123676, AJ609210; *Bontia daphnoides* L., AJ617613, AJ609219; *Buddleja davidii* Franch., L36394, AJ609204; *Capraria biflora* L., AJ617610, AJ609198; *Dermatobotrys saundersii* Bolus, AJ617592, AJ609191; *Emorya suaveolens* Torr., AF027278, AJ609187; *Hemimeris sabulosa* L.f., AF123682, AJ609227; *Leucophyllum frutescens* (Berland.) I. M. Johnst., AF123685, AJ609172; *Myoporum mauritianum* A.DC., L36403, AJ609161; *Nemesia strumosa* Benth., AF123688, AJ609159; *Oftia africana* Bocq. ex Baill., AJ617606, AJ609156; *Phygelius capensis* E.Mey. ex Benth., AJ617608, AJ609149; *Scrophularia* sp., L36411, *; *Scrophularia arguta* Soland., *, AJ431061; *Selago thomsoni* Rolfe ex Oliver, *, AJ431060; *Selago thunbergii* Choisy, L36412, *; *Teedia lucida* Rudolphi, AJ617582, AJ609127.
Stilbaceae: *Bowkeria verticillata* Druce, AJ617589, AJ609206; *Euthystachys abbreviata* A.DC., AF147715, AJ609185; *Halleria lucia* L., AJ550569, AJ609180; *Ixianthes retzoides* Benth., AJ617598, AJ609176; *Nuxia* sp., AF027280, AJ609157; *Retzia capensis* Thunb., AF027289, AJ609144; *Stilbe albiflora* E.Mey., AF027287, *; *Stilbe ericoides* L., *, AJ431062.

Tetrachondraceae: *Polypremum procumbens* L., AJ011986, AJ431063; *Tetrachondra patagonica* Skottskb., AF027272, AJ431064.

Thomandersiaceae: *Thomandersia laurifolia* Baill., AY919285, *; *Thomandersia laurifolia* Baill. [Gabon, *Bradley et al. 1052* (MO)], *, JN686550.

Verbenaceae: *Acantholippia* sp. [Argentina, *Landrum & Landrum 8361* (ASU)], JN686632, JN686544; *Aloysia gratissima* (Gillies & Hook.) Troncoso [U.S.A.: Texas, *Worthington 32415* (ASU)], JN686613, JN686510; *Bouchea prismatica* (L.) Kuntze [U.S.A.: Arizona, *Makings 1613a* (ASU)], JN686633, JN686545; *Citharexylum scabra* Moc & Sessé ex D.Don [Mexico: Sonora, *Friedman & Freeh 371-94* (ASU)], JN686612, JN686506; *Glandularia wrightii* (A.Gray) Umber [U.S.A.: Arizona, *Gutierrez 423* (ASU), JN686636, JN686548; *Junellia tridens* (Lag.) Moldenke [Chile, *Landrum & Landrum 8404* (ASU)], JN686618, JN686512; *Lantana camara* L., *, AF225294; *Lantana horrida* H.B. & K., AF130152, *; *Lippia macrophylla* Cham. [Brazil, *Stapf et al. 477* (ASU)], JN686637, JN686549; *Phyla nodiflora* (L.) Greene [U.S.A.: Arizona, *Makings 1858* (ASU)], JN686634, JN686546; *Rhaphithamnus spinosus* (Juss.) Moldenke [Chile, *Landrum & Donoso 7597* (ASU)], JN686635, JN686547; *Stachytarpheta dichotoma* (Ruiz & Pav.) Vahl, L36414, AJ299259; *Verbena bracteata,* L36418, *; *Verbena rigida* Spreng., *, AJ431065.

Outgroups: *Borago officinalis* L., L36393, AJ431019; *Gentiana procera* T.Holm, L36400, *; *Gentiana purpurea* L., *, AJ431034; *Solanum physalifolium* Rusby, U47421, AY727449.

APPENDIX C

LIST OF SEQUENCES USED IN THE PHYLOGENETIC ANALYSES OF THE MARTYNIACEAE.

Data listed includes: Taxon [locality data and voucher information], Internal Transcribed Spacer GenBank accession number, *psbA-trnH* intergenic spacer GenBank accession number, *trnQ-5'rps16* intergenic spacer GenBank accession number, and *trnS-trnG-trnG* intergenic spacer and intron GenBank accession number. Underlined GenBank accession numbers denote sequences that were generated for a previous study (Gutierrez 2002).

Martyniaceae: *Craniolaria annua* L. [Puerto Rico, *Worthington 31343* (UTEP)], <u>AY182834</u>, JN686593, JN686573, JN686553; *Craniolaria integrifolia* Cham. [Bolivia: Santa Cruz, *Nee 52095* (NY)], JN686496, JN686599, JN686579, JN686559; *Holoregmia viscida* Nees [Brazil: Bahia, *Webster 25812* (NY)], JN686495, JN686598, JN686578, JN686558; *Ibicella lutea* (Lindl.) Van Eseltine [U.S.A.: California, *Gehrung s.n.* (UTEP)], <u>AY178640</u>, JN686601, JN686581, JN686561; *Martynia annua* L. [Cultivated, *Damrel 1024* (ASU)], JN686498, JN686602, JN686582, JN686562; *Martynia annua* L. [Puerto Rico, *Worthington 33177* (ASU)], JN686499, JN686603, JN686583, JN686563; *Proboscidea althaeifolia* (Benth.) Decne. [Mexico: Baja California Sur, *Daniel 2371* (ASU)], JN686491, JN686591, JN686571, JN686551; *Proboscidea althaeifolia* (Benth.) Decne. [U.S.A.: Texas, *Freeman 288* (UTEP)], <u>AY178641</u>, JN686592, JN686572, JN686552; *Proboscidea fragrans* (Lindl.) Decne. [Mexico: Guanajuato, *Rosas 18* (ASU)], JN686493, JN686595, JN686575, JN686555; *Proboscidea louisianica* (Mill.) Thell. [U.S.A.: Texas, *Worthington 30669* (UTEP)], JN686497, JN686600, JN686580, JN686560; *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *gracillima* (Hevly) Bretting [Mexico: Baja California Sur, *Rebman 7688* (SD)], JN686494, JN686596, JN676576, JN686556; *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *parviflora* var. *hohokamiana* Bretting [cultivated, seed from Native Seed/SEARCH (Tucson, Arizona), *Gutierrez 07* (UTEP)], <u>AY178643</u>, JN686597, JN686577, JN686557; *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *parviflora* var. *parviflora* [cultivated, seed from U.S.A., Texas, *Gutierrez 34* (UTEP)], <u>AY178644</u>, JN686604, JN686584, JN686564; *Proboscidea parviflora* (Woot.) Woot. & Standl. ssp. *sinaloensis* (Van Eseltine) Bretting [Mexico: Sonora, *Van Devender 94-674* (ARIZ)], JN686501, JN686607, JN686587, JN686567; *Proboscidea sabulosa* Correll [U.S.A.: Texas, *Gutierrez 17* (UTEP)], <u>AY178646</u>, JN686605, JN686585, JN686565; *Proboscidea sabulosa* Correll [U.S.A.: Texas, *Gutierrez 1225* (ASU)] JN686500, JN686606, JN686586, JN686566; *Proboscidea triloba* (Schlect. & Cham.) Decne. ssp. *diversifolia* (Hevly) Bretting [Mexico: Michoacán, *Bretting 390* (IND)], JN686492, JN686594, JN686574, JN686554; *Proboscidea triloba* (Schlect. & Cham.) Decne. ssp. *triloba* [Mexico: Oaxaca, *Rzedowski 34816* (NY)], JN686502, JN686608, JN686588, JN686568.

Outgroup: *Glandularia bipinnatifida* Nutt. [U.S.A.: Arizona, *Gutierrez 423* (ASU)], JN686504, JN686610, JN686590, JN686570.; *Thomandersia laurifolia* Baill. [Gabon, *Bradley et al. 1052* (MO)], JN686503, JN686609, JN686589, JN686569.