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A SYSTEMATIC STUDY OF *BRAVAISIA* DC. (ACANTHACEAE)

By

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ABSTRACT: A taxonomic treatment of the neotropical genus *Bravaisia* is presented in which three species are recognized: *B. berlandieriana, B. grandiflora,* and *B. integerrima.* The genus belongs to the Trichanthereae where it is allied morphologically with *Trichanthera.* A key to the genera of Trichanthereae is provided. *Bravaisia* is distributed from Mexico and Cuba southward to northern South America, with all three species occurring in southeastern Mexico and northern Central America. Based on an estimate of phylogenetic branching patterns using *Trichanthera* as an outgroup, *B. integerrima* appears to be the sister group of *B. grandiflora* and *B. berlandieriana.* Honey bees are the predominant visitors to flowers of *B. integerrima* in Mexico.

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INTRODUCTION

Bravaisia DC. is a small genus of the predominantly tropical family Acanthaceae. This is the first attempt in this century to delimit all species in the genus. Of the 10 species that have been described in *Bravaisia* and in genera now recognized as congeneric with it, 3 are recognized here. These occur from northeastern Mexico and Cuba southward to Colombia and Venezuela.

Bravaisia is unusual among Mexican and Central American Acanthaceae in that at least two species are commonly mangrove trees. Mangrove plants or mangroves (as distinguished from mangrove communities or mangals) can be defined as tropical or subtropical ligneous plants that occur in intertidal and adjacent communities (modified from Tomlinson 1986). Such plants exhibit various adaptations (e.g., aerial roots in many) to their environment. Although certain other Acanthaceae attain tree size (e.g., species of *Ruellia* L., *Trichanthera* Humb. and Bonpl., and *Louteridium* S. Watson) or exhibit a mangrove habit (e.g., species of *Acanthus* L. in the Old World) mangrove trees are not currently known among other Latin American genera of the family. *Trichanthera gigantea* (Humb. and Bonpl.) Nees, a medium-sized tree that commonly occurs along streams and in swampy regions in northern South America and southern Central America, often has prop roots. It may eventually be shown to occur as a mangrove as well.

The following study provides a taxonomic revision of the genus and offers information on possible phylogenetic relationships and reproductive biology.

MATERIALS AND METHODS

This study is based on information obtained from more than 650 herbarium specimens and

field work in Mexico during 1982 and 1987. The citations of herbaria in the text follow abbreviations of Holmgren et al. (1981). All measurements were made on dried material. Pollen was measured using a compound microscope and a calibrated ocular micrometer. The grains were mounted in Diaphane prior to observation and measurement. Surface features were observed on untreated pollen with a scanning electron microscope. Pollen stainability was determined using analine blue in lactophenol. Pollination of stigmas was determined using a hand lens (10×).

Taxonomic History

The first species described in this genus was attributed to the Verbenaceae as *Amasonia integerrima* (Sprengel 1825). Lacking fruiting material, A. P. de Candolle (1838, 1845) treated his new genus *Bravaisia,* with its sole species, *B. floribunda,* as belonging to the Bignoniaceae. In June of 1847, Lemaire correctly attributed a nonfruiting collection of this genus, which he described as *Androcentrum multiflorum,* to the Acanthaceae. Later that same year, Nees (1847) attributed the two species of this genus described by him, *Onychacanthus cumingii* and *O. berlandierianus,* to the Acanthaceae as well. He did not see material of Lemaire's genus and was therefore unable to compare it to his own genus *Onychacanthus.* In the additions and corrections published with volume 11 of the Prodromus, Nees added a treatment of *Androcentrum.* Based on Lemaire's description, however, Nees was able to place it in tribe Ruellieae near *Onychacanthus.* Subsequently Oersted (1854) described *O. speciosus,* and Karsten (1865) described *O. arboreus.* Bentham (1876) was first to treat *Bravaisia* in the Acanthaceae and to recognize that it is identical to *Onychacanthus.* He did not make new combinations for the various species, however. Additional species of *Bravaisia* were described by Hemsley in 1886 (*B. tubiflora*), Smith in 1902 (*B. grandiflora*), and Blake in 1917 (*B. proxima*). Standley (1926) noted that Sprengel's *Amasonia integerrima* was conspecific with de Candolle's *Bravaisia floribunda.* He included *O. berlandierianus* in the synonymy of this species and suggested that *Androcentrum multiflorum* should likely be considered conspecific here as well. Leonard (1951) included all of the species described in *Onychacanthus* in the synonymy of *B. integerrima.* Gibson (1974) considered *B. proxima* to be conspecific with *B. grandiflora.*

Infrafamilial Relationships

Nees (1847) treated species of *Bravaisia* (as *Onychacanthus*) in his tribe Ruellieae, where they were aligned with *Trichanthera, Macrostegia* Nees, *Sclerocalyx* Nees (=*Ruellia* sp.), *Ophthalmacanthus* Nees (=*Ruellia* spp.), *Whitefieldia* Hook., *Ancylogyne* Nees (=*Sanchezia* Ruiz and Pavón), and *Androcentrum* Lemaire (=*Bravaisia*). After removing *Ophthalmacanthus* and *Whitefieldia,* Bentham (1876) treated this assemblage as tribe Ruellieae subtribe Trichanthereae. The wholly American subtribe was distinguished from other subtribes of Ruellieae by the combination of its *Ruellia*-like corollas; equidistant or subconnate (in pairs) filaments; herbaceous or subcoriaceous, obtuse (except in a few species of *Sanchezia*) calyx lobes; and trichotomously cymose-corymbose, capitate, or rarely spicate inflorescences that are borne at the apices of branches (or sometimes the inflorescence of axillary cymes). These same six genera (the name *Sclerocalyx* was replaced by the earlier name *Gymnacanthus* Nees) were considered by Lindau (1895) as tribe Trichanthereae of his subfamily Acanthoideae. The tribe was distinguished by "Rippenpollen," five-parted calyces, and firm, equally five-parted corollas with contorted lobes. With the exclusion of *Macrostegia,* which was shown to belong to the Verbenaceae (Macbride 1934), Lindau's Trichanthereae were accepted as a tribe of the subfamily Ruellioideae by Bremekamp (1965). He noted that the Trichanthereae differed from other Acanthaceae by their large size and by their pollen. He further noted the following attributes of the tribe: terminal paniculiform or racemiform inflorescences; obtuse calyx lobes; fleshy, actinomorphic corollas with the lobes contorted in bud; and glabrous seeds.

Of the six genera treated by Lindau (1895) in the Trichanthereae, three (*Bravaisia, Sanchezia,* and *Trichanthera*) are currently recognized. Two additional genera, *Trichosanchezia* Mildbr. and *Suessenguthia* Merxm., that would be included in this tribe because of their relationship to *Sanchezia* have been described in this century. *Sanchezia* (including the monotypic *Steirosanchezia* Lindau that was described in 1904) comprises 59 species concentrated in the wet forests of

northwestern South America (Leonard and Smith 1964). *Suessenguthia* consists of four species restricted to Peru and Bolivia (Wasshausen 1970). *Trichosanchezia* is a monotypic genus of Peru (Leonard and Smith 1964). *Trichanthera* consists of two species restricted in distribution to northern South America and southern Central America (Costa Rica and Panama).

Phylogenetic ancestors of the Trichanthereae were likely some part of the typical, four-stamened Ruellioid lineage with corolla lobes contorted in bud. The Trichanthereae differ most conspicuously from this assemblage, which includes *Ruellia,* in features of their pollen (summarized in Raj 1961, although descriptions of pollen have not been reported from either *Suessenguthia* or *Trichosanchezia*). The large size of some Trichanthereae, noted by Bremekamp (1965), is not unique to this tribe. Certain species of *Ruellia* (tribe Ruellieae) and *Louteridium* (tribe Louteridieae) in the Ruellioideae also attain the stature of moderate-size trees.

Despite the relatively large number of species described in *Sanchezia,* the genus remains poorly known. For example, fruits are unknown for most of the species. Likewise, fruits have yet to be described for *Suessenguthia* and *Trichosanchezia.* Therefore a thorough phylogenetic assessment of this tribe will not be possible until *Sanchezia* and its relatives become better known.

Based on data available in Leonard and Smith (1964), information provided by Dieter C. Wasshausen of the Smithsonian Institution (in litt.), and my studies of *Bravaisia* and *Trichanthera* the following key serves to distinguish genera of the Trichanthereae.

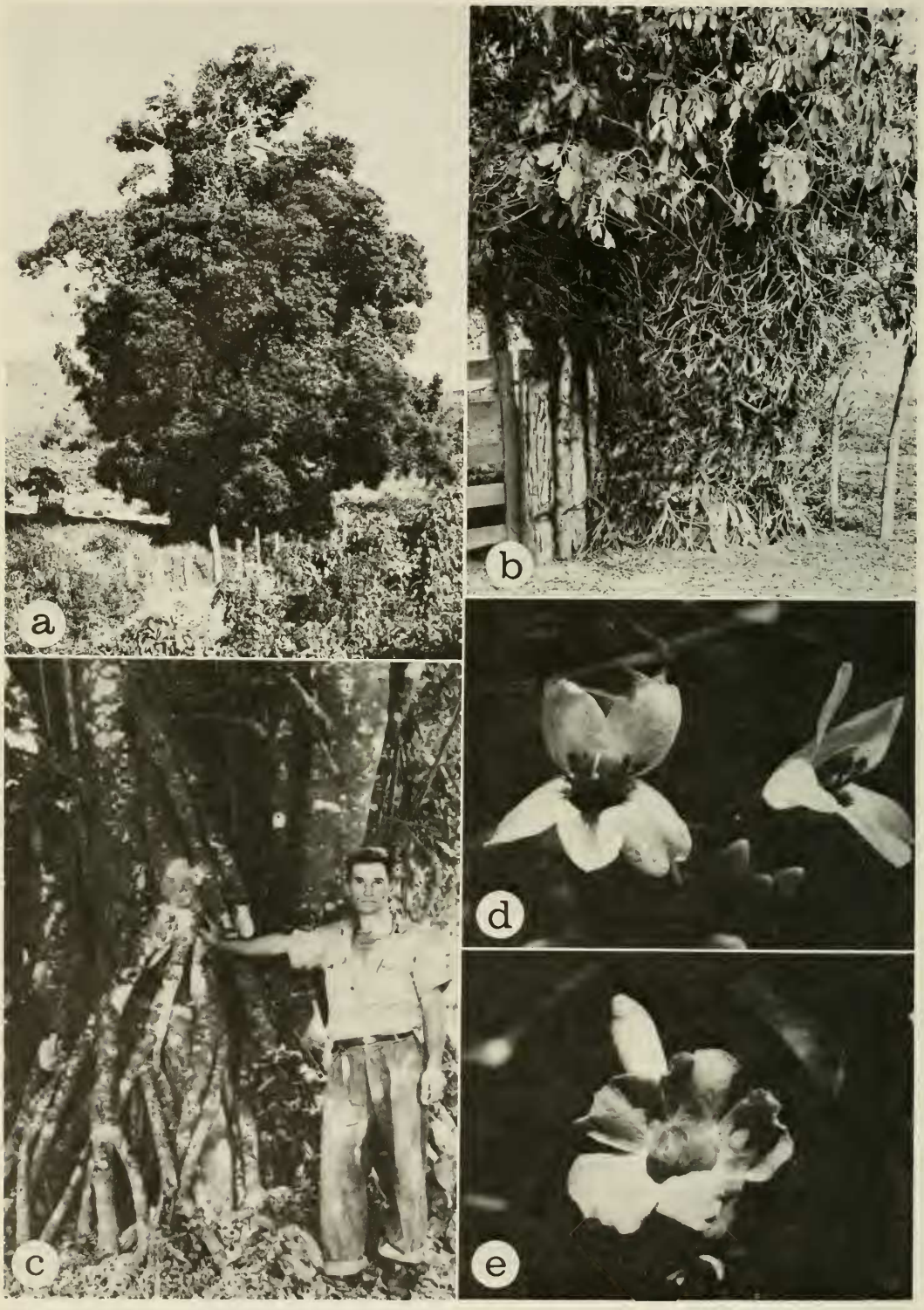
1. Corolla subcylindric; fertile stamens 2 or 4.
   2. Fertile stamens 2 ..... *Sanchezia*
   2. Fertile stamens 4.
      3. Thecae awned at base ..... *Suessenguthia*
      3. Thecae awnless ..... *Trichosanchezia*
1. Corolla campanulate; fertile stamens 4.
   4. Thecae awnless, rounded at base; capsule pubescent at maturity; flowers borne on pedicels 2–11 mm long; stigma elongate, 4.0–4.5 mm long ..... *Trichanthera*
   4. Thecae awned with a single, subulate projection 0.3–1.0 mm long at base; capsule glabrous at maturity; flowers sessile or borne on pedicels to 2 mm long; stigma to 1 mm long ..... *Bravaisia*

Morphology

Habit.—*Bravaisia berlandieriana* and *B. grandiflora* vary in habit from shrubs to small trees to 9 m tall. *Bravaisia integerrima* consists of larger trees, to 20 m in height (Fig. 1a), with expansive, often rounded, crowns and usually numerous stilt or prop roots that extend to 8 m above the ground. The base of mature trees varies in diameter from 8 to 200 cm and usually consists of large prop roots and numerous trunks or large branches (Fig. 1b, c). Bark is usually smooth and light in color. The wood is somewhat soft and varies from white to creamy yellow to grayish. Hess (1946) described wood anatomy in the genus. The young stems are quadrate in cross section with four more or less concave surfaces between the prominent corners. Whitish blister-like protrusions, presumably lenticels, are commonly evident on the corners. The young stems are superficially smooth to wrinkled. The mature stems (i.e., those of previous growing seasons) are usually light-colored and wrinkled.

Leaves.—Leaves of *Bravaisia* are opposite-decussate and consist of a well-defined petiole and blade. The petioles are canaliculate on the adaxial surface. The blades are usually somewhat leathery and shiny. They vary in shape from ovate to broadly elliptic to obovate. The surfaces are either glabrous or sparsely pubescent with eglandular trichomes, especially along the midvein. The abaxial surface is often covered with inconspicuous, sparse to dense, sessile, disk-shaped, glandlike structures to 0.05 mm in diameter. These impressed punctations are especially evident in *B. berlandieriana* but are also encountered in the other species. The margin is entire but often so sinuate as to make it appear crenate. Venation is brochidodromous (i.e., the secondary veins join together toward the margin in a series of prominent arches) with up to five orders of veins observable on dried leaves. Sometimes only two to three orders are observable on the more leathery blades of *B. berlandieriana* and *B. grandiflora.* The veins are flush with, slightly impressed into, or slightly protruding from the adaxial laminar surface. The midvein and second order veins protrude prominently from the abaxial surface.

Vesture and Cystoliths.—Unlike many genera of Acanthaceae in which stipitate glandular trichomes are frequent, *Bravaisia* has eglandular trichomes almost exclusively. In the


a
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genus, readily observable (i.e., with naked eye or dissecting microscope) stipitate glands are found only rarely along styles of *B. integerrima*. The eglandular trichomes are unbranched and consist of 1–4 uniseriate cells. They can occur on most vegetative and reproductive structures. Their presence or absence on the abaxial surface of the corolla is useful in distinguishing the species.

The density of trichomes was found to be somewhat variable within species. Certain specimens of both *B. berlandieriana* (e.g., *Bradburn 1489*) and *B. integerrima* (e.g., *Steyermark 61181*) exhibit a dense pubescence in the inflorescence and on the young stems, whereas in other specimens these structures are largely without trichomes or only sparsely pubescent. Sometimes the young stems of *B. integerrima* are densely pubescent with an even, feltlike vesture consisting of a mixture of eglandular trichomes and sessile glandular punctations. Often as the stems increase in size this covering breaks apart into patches giving the stems a scaly aspect.

In *Bravaisia* cystoliths are best observed on dry, adaxial leaf surfaces. They appear as straight (to slightly curved), protruding, light-colored, lineolate structures up to 0.7 mm long. They are often contiguous with one another, especially when aligned with veins.

Inflorescences.—As in most Acanthaceae, the inflorescence of *Bravaisia* is a thyrse consisting of an indeterminate main axis bearing determinate, lateral axes in the axils of bracts. The determinate, lateral axes are simple dichasia that are usually reduced to a single flower. The number of dichasia per thyrse varies from 3 to 20. In *B. berlandieriana* and *B. grandiflora* the dichasia lack peduncles, and the resulting inflorescence is spicate. In *B. integerrima* the dichasia are borne on distinct peduncles, and the inflorescence is therefore racemose. The modified thyrses of *Bravaisia* are both terminal and axillary from distal leaves; together these form leafy panicles of either spikes or racemes.

Each flower is either sessile or short-pedunculate and subtended by paired, homomorphic bractlets. In *Bravaisia* bractlet form is particularly important because each species can be distinguished by features of the bractlets. The flower(s) and associated bractlets are subtended by a single bract. The bracts are oppositely arranged along the inflorescence.

Flowers.—The calyx is deeply five-lobed. The lobes are imbricate and either homomorphic or sometimes somewhat unequal in length. Although Bremekamp (1965) noted that members of the Trichanthereae have obtuse calyx lobes, those of *Bravaisia* vary from rounded to acute to mucronate to apiculate at their apices.

The corolla is campanulate with a short tube, an ampliate throat, and a bilabiate limb. The upper lip of the limb comprises two lobes, and the lower lip consists of three. The lobes are convolute in bud and rounded to emarginate at their apices. Color of the corolla varies from white to bluish white to pinkish with brown and/or yellow markings on the internal surface of the lower lip and throat. Trichomes can be present on internal and external surfaces as well as along the margins of the lobes.

The androecium consists of four fertile epipetalous stamens that are inserted at the base of the corolla throat. They are either included within the throat or exserted several millimeters beyond it. The anthers consist of two equally inserted, parallel thecae, each with a single awn at the base. Thecae vary from glabrous to pubescent with flexuous eglandular trichomes. Three to 15 subsessile, peltate glands, occurring in a band adjacent to the connective on each side of the theca, are usually evident. Pollen of *Bravaisia* has been erroneously described by many workers (Lindau 1895; Raj 1961; Gibson 1974) as diporate. Lindau (1893) described the pollen as a particular type of "Rippenpollen" which he termed "Trichanthereenpollen." Raj (1961) noted that the Trichanthereae are homogeneous in their pollen. An accurate description of the pollen of *B. integerrima* and *B. berlandieriana* (as *B. tubiflora*) was provided by Vasanthy and Pocock (1986). My examination of pollen from each of the species (Fig. 2) reveals it to be consistently dicolporate. The endoapertures (ora) are as-

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Figure 1. Photographs of *Bravaisia*. a, Remnant individual of *B. integerrima* in coastal region of Michoacán, Mexico; b, Base of pruned tree of *B. integerrima* in coastal Guerrero, Mexico, showing numerous adventitious roots; c, Base of *B. integerrima* with divided trunks and prop roots in southern Central America (from photograph at MO); d, Flowers of *B. integerrima* in Guerrero, Mexico, prior to pollination (flower on right) and after pollination (flower on left) showing orientation of stamens, ×1.4; e, Flower and bud of *B. grandiflora* in Chiapas, Mexico, ×1.

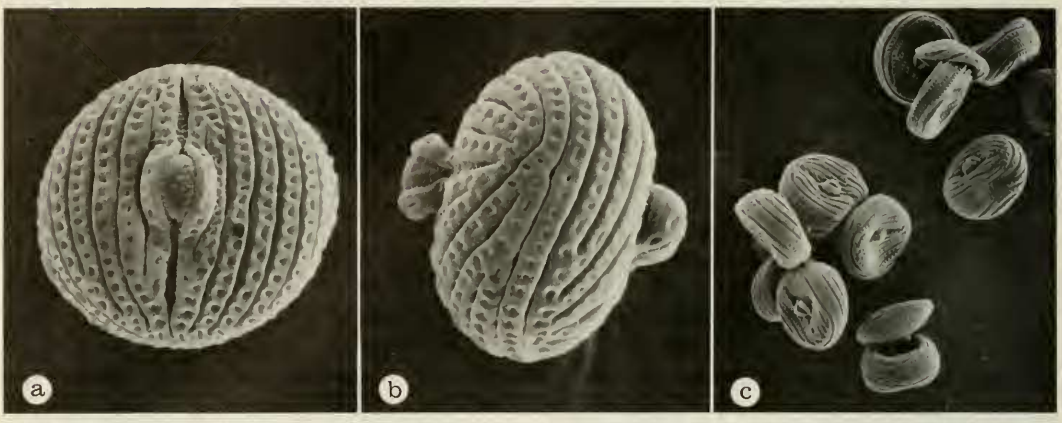

FIGURE 2. Pollen of *Bravaisia*. a, *B. integerrima* (*Daniel 2144*), ×750; b, *B. berlandieriana* (*Cabrera and Ibara 1149*), ×750; c, *B. grandiflora* (*Daniel and Bartholomew 4998*), ×150.

sumed to lie on the equatorial plane of the grain. The grains are partially flattened on the aperturate faces. The compound apertures are centrally positioned on the two flattened faces, 90° out of phase with one another (cf. "rotationally symmetric" in Vasanthy and Pocock [1986]). The pollen might therefore be referred to as "loxodicolporate." The outline of the grain is subcircular to circular when an aperturate face is viewed directly on (Fig. 2a) and elliptical when an inaperturate face is viewed directly on (Fig. 2b). The exine sculpturing consists of a striate pattern of numerous furrows and ridges forming bands of exine oriented in the same direction as the colpi (i.e., perpendicular to one another on the aperturate faces of the grain). Between one and five furrows appear to encircle each grain around its polar periphery. These effectively divide the two identical, but skewed halves of the grain. The ridges, or bands of exine formed by the furrows, each contain a row of centrally positioned foveolae throughout their length. The colpal membranes and the paracolpal furrows are densely studded with granules. Pollen size varies from 54 to 88 μm in diameter (aperturate face). Grains of *B. berlandieriana* and *B. integerrima* are comparable in size (54–66 μm) whereas those of the larger flowered *B. grandiflora* are considerably larger (76–88 μm).

Pollen of *B. grandiflora* from *Daniel and Bartholomew 4998* (Fig. 2c) appears malformed with many of the grains largely or completely collapsed. Three hundred seventy grains of this collection were examined for stainability. Fifty-six (15%) stained completely, 301 (81%) failed to take up any stain, and 13 (4%) took up a small amount of stain. In contrast to the relatively low stainability of pollen from this collection of *B. grandiflora*, 71% of grains examined (364/515) in *B. integerrima* (*Daniel and Bartholomew 4925*) stained completely. Only 29% (151/515) of the grains failed to take up stain; none stained partially.

The gynoecium comprises a bicarpellate, superior ovary, a compound style, and an unlobed, usually curved or coiled stigma. The ovary sits upon a cuplike nectar disc and contains up to 12 ovules.

FRUITS.—The glabrous, explosively dehiscent capsules vary in shape from ovoid to ellipsoid to obovoid. They lack a prominent stalk and have a solid apical beak. Between one and four seeds mature per capsule. These are laterally flattened and subcircular to subellipsoid in outline. Their surfaces are glabrous, smooth, and shiny.

DISTRIBUTION, HABITATS, AND PHENOLOGY

The range of *Bravaisia* extends from western Cuba (ca. 22°30′N), northern Veracruz (ca. 21°30′N) in eastern Mexico, and southern Jalisco (ca. 19°30′N) in western Mexico southward to Colombia and eastern Venezuela (ca. 8°N). The genus is distributed across 44 degrees of longitude, from western Mexico (ca. 105°W) to eastern Venezuela and Trinidad (ca. 61°W). Mexico and Guatemala are the only countries in which all three species are known to occur. *Bravaisia integerrima* is the most widely distributed species and the only one known from South America.

Bravaisia grandiflora has the most restricted distribution, occurring in a region of approximately 24,000 sq. km in southern Mexico, Guatemala, and Belize.

The species occur from sea level to 1,100 m. The plants are usually found along shorelines, streams, and forest edges, or in swamps, marshy areas, and pastures. Each of the species occurs in regions of tropical wet forest. *Bravaisia integerrima* and *B. berlandieriana* also occur in regions of tropical dry forest, mangrove forest (mangal), and other coastal communities. The plants are sometimes a conspicuous, or even dominant, constituent of their biotic communities.

In spite of their similar preferences in habitat, the species of *Bravaisia* appear to be largely allopatric. The ranges of *B. integerrima* and *B. berlandieriana* overlap one another only in southeastern Mexico (Veracruz, Tabasco, and possibly the Yucatán Peninsula). It is not known whether plants of these two species co-occur at any sites. No evidence of hybridization between them was observed based on the collections examined.

Throughout the range of *Bravaisia*, flowering is concentrated during the months of November through April, the dry season in these regions. Fruiting appears to be concentrated during the latter portion of the flowering period.

Infrageneric Relationships

Because the distribution of character states remains unknown for much of the Trichanthereae (see discussion under Infrafamilial Relationships), it is not possible to identify any autapomorphy for *Bravaisia* at present. Therefore, according to strict cladistic principles, monophyly cannot be established for the genus. For purposes of phylogenetic inference, *Trichanthera* is used as the outgroup for determining polarity of character states in *Bravaisia*. *Trichanthera* appears to be *Bravaisia's* closest morphological ally in the Trichanthereae (see under Infrafamilial Relationships). Character state polarities were established for the six characters listed in Table 1. A diagram (Fig. 3) depicting putative phylogenetic branching patterns among the three species was constructed using character compatibility analysis (Meacham 1981). A hypothetical ancestral taxon, X, exhibiting only plesiomorphic character states, was included in the analysis. The largest clique incorporated all characters ex-

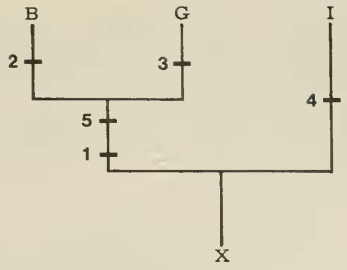

Figure 3. Putative phylogenetic branching patterns within *Bravaisia*. Bars indicate apomorphies with numbers corresponding to those in Table 1. B = *B. berlandieriana*, G = *B. grandiflora*, I = *B. integerrima*, and X = a hypothetical ancestor.

Table 1. Apomorphic and plesiomorphic character states in Bravaisia based on the outgroup Trichanthera. Numbers correspond to those in Figure 3. I = *B. integerrima*, G = *B. grandiflora*, B = *B. berlandieriana*, and X = a hypothetical ancestor.

Plesiomorphy (−)	Apomorphy (+)	I	G	B	X
1. Dichasia pedunculate with peduncles greater than 1 mm long.	Dichasia sessile or borne on peduncles up to 1 mm long.	−	+	+	−
2. Bractlets shorter than calyx.	Bractlets equal to or longer than calyx.	−	−	+	−
3. Bractlets rounded to acute at apex.	Bractlets apiculate to caudate at apex.	−	+	−	−
4. Corolla pubescent on abaxial surface.	Corolla glabrous on abaxial surface.	+	−	−	−
5. Stamens exserted from throat of corolla.	Stamens included in throat of corolla.	−	+	+	−
6. Mean corolla length greater than 25 mm.	Mean corolla length less than 25 mm.	+	−	+	−

cept character 6 (mean corolla length). *Bravaisia integerrima* is hypothesized to be the sister group of *B. berlandieriana* and *B. grandiflora.* The synapomorphy of short corollas (i.e., character 6) in *B. berlandieriana* and *B. integerrima* appears to represent a parallelism.

Reproductive Biology

Bawa et al. (1985) reported a pollination system of medium-size bees for *Bravaisia integerrima* in a lowland rainforest in Costa Rica. Although I did not perform experimental studies on the reproductive biology of *Bravaisia,* observations on pollination biology were made in the field and gleaned from herbarium specimens.

Flowers of *B. integerrima,* which render the crown nearly white, tend to be abundant for a period of several weeks. Labels on several herbarium specimens indicate that the flowers are somewhat fragrant. *Croat 21533* notes that flowers of this species are visited by small bees and *Hughes and Styles 73* records that the flowers attract bees and hummingbirds. Observations on *B. integerrima* in Colima (*Daniel 2110*), Michoacán (*Daniel 2144*), and Guerrero (*Daniel and Bartholomew 4925*), Mexico during March reveal that the flowers are actively visited by insects. The most abundant visitors in March are honey bees (*Apis mellifera* L.), which use the lower lip as a landing and perching platform while they gather both pollen and nectar. In unpollinated or recently pollinated flowers the didynamous stamens project from the throat, more or less effectively blocking the entrance to the tubular portion of the corolla (Fig. 1d). The style emerges through the upper (dorsal) pair of filaments, overtops them, curves toward the lower lip of the corolla, and positions the stigma directly in front of (distal to) the anthers with the convexly curved and receptive portion facing away from the flower. This arrangement of the androecium and gynoecium would force medium-sized or larger visitors that approach the distal portion of the flower, and follow the colored markings en route to pollen and/or nectar, to contact first the receptive portion of the stigma and then the anthers. Such an arrangement undoubtedly promotes outcrossing. However, geitonogamy likely occurs to a great extent. Bees were observed to visit numerous flowers on a single tree before leaving that individual. In older flowers with pollinated stigmas, the stamens had spread laterally, opening the throat, and the style had curved conspicuously into the throat (Fig. 1d). Pollen removed from hairs on the head and legs of a captured individual of *Apis mellifera* that was visiting *Daniel and Bartholomew 4925* is identical to pollen of *Bravaisia integerrima.* Other visitors to this species in western Mexico include a smaller, native halictid bee, *Halictus* (*Seladonia*) *tripartitus* Cockerell vel aff., on which pollen was not found. Of 10 stigmas observed on flowers of *Daniel and Bartholomew 4925* in Guerrero, seven of them had been pollinated.

In vivo flowers of *B. berlandieriana* were not observed during this investigation. *Bradburn 1476* notes that flowers of this species are frequently visited by hummingbirds.

Bravaisia grandiflora has the largest flowers in the genus. Unlike the androecial arrangement in *B. integerrima,* in this species the stamens are more or less appressed to the dorsal side of the throat and do not block the entrance to the tubular portion of the corolla (Fig. 1e). Nothing is known about visitors to *B. grandiflora.* No visitors to this species were observed in Chiapas, Mexico (*Daniel and Bartholomew 4998*) nor was any fruit production evident. Indeed, only one fruiting collection of this species is known. It remains unknown whether the apparent lack of fruits among individuals of this species is the result of an absence of pollinators or lack of sufficient viable pollen (see discussion under Morphology). However, of 10 stigmas observed on flowers of *Daniel and Bartholomew 4998* in Chiapas, none had adhering pollen.

Taxonomy

Bravaisia DC. Biblioth. Universelle Genève 17: 132. 1838. Type.—*B. floribunda* DC. (=*B. integerrima* (Sprengel) Standley).

Androcentrum Lemaire, Fl. Serrers Jard. Eur. 3:242. 1847 (Jun). Type.—*A. multiflorum* Lemaire (=*B. integerrima*).

Onychacanthus Nees *in* DC. Prodr. 11:217. 1847 (Nov). Type.—*O. cumingii* Nees *in* DC. (lectotype, designated by Leonard [1951]; =*B. integerrima*).

Shrubs to small or medium-sized trees with multiple trunks and usually with numerous stilt roots. Young stems quadrate-sulcate, often with whitish blisters on corners, glabrous or pubescent with eglandular trichomes. Leaves opposite, petiolate; petioles canaliculate; blades usually somewhat leathery, ovate to elliptic to broadly elliptic to obovate, surfaces somewhat shiny, glabrous

or sparsely pubescent with eglandular trichomes, especially along midvein, abaxial surface often covered with inconspicuous, sparse to dense, sessile, disk-shaped glands to 0.05 mm in diameter (punctate-glandular), margin entire to sinuate-crenate, usually somewhat revolute. Inflorescence of axillary and terminal, sessile or pedunculate dichasia (usually reduced to one flower) borne in axil of a bract (or terminal dichasia borne in axil of two bracts) and arranged in short spicate or racemose axes which form terminal panicles; flowers sessile or short-pedicellate in axil of two isomorphic bractlets. Bracts opposite, sessile or petiolate, variously shaped. Bractlets variously shaped, rounded to acute to apiculate to caudate at apex. Calyx deeply five-lobed; tube 0.5–2.0 mm long; lobes imbricate, often turning dark green or brown on dried material, ovate to elliptic to suborbicular to obovate. Corolla white, bluish white, or pinkish, glabrous or pubescent on external surface, sometimes bearded within; tube shorter than throat; limb bilabiate with upper lip two-lobed, lower lip three-lobed, lobes convolute in bud, ovate to elliptic to suborbicular to obovate, rounded to emarginate at apex. Stamens four, didynamous, inserted at base of corolla throat, included or exserted from throat; filaments densely pubescent at base, sparsely pubescent (to nearly glabrous in *B. integerrima*) distally; anthers bithecous, thecae equally inserted, parallel, glabrous to sparsely pubescent with eglandular trichomes, usually with peltate glands 0.1–0.2 mm in diameter evident as well, rounded at apex, awned at base with a single, subulate projection 0.3–1.0 mm long; pollen loxodicolporate, the surface striate-foveolate. Ovary situated on a distinct or indistinct disc 0.7–1.0 mm tall; ovules to 12; style exserted from throat of corolla, glabrous (rarely sparsely pubescent near base); stigma usually coiled or curved, up to 1 mm long. Capsule ovoid to ellipsoid to obovoid, estipitate (i.e., solid basal portion less than 0.5 mm long), with a solid apical beak 1.2–2.1 mm long; retinacula 2–4 mm long. Seeds one to four per mature capsule, brown, strongly laterally flattened and subcircular in outline to only slightly flattened and subellipsoid, glabrous, surface smooth and shiny.

Key to the Species of *Bravaisia*

1. Bractlets apiculate to caudate at apex; corolla 27–47 mm long ..... 2. *B. grandiflora*
1. Bractlets rounded to acute at apex; corolla 15–25 mm long.
   2. Inflorescence racemose, dichasia borne on peduncles (1.0–)1.5–6.0(–13.0) mm long; bractlets linear to triangular to suborbicular, 1.6–5.0 mm long, shorter than calyx; corolla externally glabrous (margins of lobes ciliate, however), tube 1.7–3.2 mm long, usually not well differentiated from throat; style 7–13 mm long; seeds 0.5–1.2 mm thick ..... 1. *B. integerrima*
   2. Inflorescence spicate, dichasia sessile (rarely borne on peduncles to 1 mm long); bractlets obspatulate (i.e., constricted distally) to hourglass shaped (i.e., constricted medially) to spatulate (i.e., constricted proximally), (5–)7–15(–20) mm long, equal to or usually longer than calyx; corolla exernally pubescent, tube 4–8 mm long, clearly differentiated from throat; style 14–21 mm long; seeds 1.8–2.6 mm thick ..... 3. *B. berlandieriana*

1. Bravaisia integerrima (Sprengel) Standley, Contr. U.S. Natl. Herb. 23:1335. 1926.

Amasonia integerrima Sprengel, Syst. Veg. 2:765. 1825. TYPE.—COLOMBIA. "Ad. fl. Magdalen. Bertero." fide protologue; "ex Amer. meridionali h. Bertero Mr Balb. 1822" (G-DC!, photos F, MO, US). Leonard (1951) indicated this specimen as the type material of *A. integerrima* and incorrectly noted its being at G-DEL. Because Sprengel cited a more precise locality for Bertero's collection than that noted on the specimen at G, it is possible that he had a specimen with a different label in his herbarium (i.e., the holotype). The specimen at G is possibly an isotype. A Bertero collection from "Sta. Martha" labelled as *A. integerrima* Spr. at P(!) and as *Bignonia bibracteata* at G-DC(!) and MO ex hb. Bernhardi(!) likely does not represent isotype material since Santa Marta is about 80 km to the northeast of the Río Magdalena. Although the major portion of Bertero's collections are at TO (G. Forneris, in litt.), there are no specimens under either *Amasonia integerrima* or *Bignonia bibracteata* currently at that institution (G. Forneris, in litt.). Sprengel's herbarium was dismembered after his death, and a considerable portion of it was destroyed at B.

Bravaisia floribunda DC. Biblioth. Universelle Genève 17:132. 1838. TYPE.—VENEZUELA. Caracas, *Vargas s.n.* (Holotype: G-DC!; isotype K!). Although initial publication of this species is usually given as occurring in DC. Prodr. 9:240, 1845, de Candolle's earlier treatment fulfills all of the requirements of Article 42 of the ICBN for a *descriptio generico-specifico.* If, in fact, the latter publication were to be accepted as the initial publication of this species, the name would be illegitimate under Article 63.1 of the ICBN since *Amasonia integerrima* Sprengel (the epithet of which ought to have been adopted) was cited as a synonym.

Androcentrum multiflorum Lemaire, Fl. Serr. Jard. 3:242. 1847. TYPE.—MEXICO. Galeotti (Holotype unknown). In the protologue Lemaire drew his description from a dried specimen of a Mexican plant sent by Galeotti. The disposition of Lemaire's herbarium is not known. Galeotti's only known collections of *Bravaisia* came from Oaxaca (one collected at "Tututepeque" in May and numbered *510M* at BR and one collected at "Lacs de Tututepeque" in April and also numbered *510M* at BR, F, GH, MO, NY, UC, US). One of these collections undoubtedly represents the type material.

Onychacanthus cuningii Nees *in* DC. Prodr. 11:217. 1847. TYPE.—Nees cited the following syntypes: a Pavón collection from Peru (in de Candolle's herbarium), *Cuming 1307* from Central America (in the herbaria of Bentham and Hooker), and a specimen labelled as *Ruellia arborescens* Pavón (in Moricand's herbarium). Leonard (1951) effectively lectotypified this species when he indicated that the type was collected in Peru by Pavón and deposited in the de Candolle herbarium. I was unable to locate this collection at G-DC; however, isolectotypes were seen at BM and P. The specimen at P is attributed to Peru. One of the labels on the isolectotype at BM gives the "name" *Ruellia arborescens* and the locality "NE" (i.e., Nueva España or Mexico). This "name" was applied to a Mexican specimen (at MA) of what is here considered to be *B. integerrima* by Sessé and Mociño. The lectotype material was undoubtedly collected by Sessé and Mociño in Mexico and wrongly attributed to Peru, from which region the plant is not known to occur. See McVaugh (1987) for a discussion of certain Sessé and Mociño collections erroneously believed to have been collected in Peru.

Onychacanthus speciosus Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:131. 1854. TYPE.—COSTA RICA. Puntarenas: La Barranca near Puntarenas, Feb. 1847, *A. Oersted 10624* (Lectotype: C!). In the protologue Oersted mentions collections from Costa Rica and Nicaragua. At C there are three Oersted collections of this species, two from La Barranca in Costa Rica and one from Volcán Mombacho in Nicaragua. From among these syntypes, the collection cited above is here chosen as the lectotype.

Onychacanthus arboreus Karsten, Fl. Columb. 2:111. 1865. TYPE.—VENEZUELA. "Habitat regiones montuosas calidas Venezuelae in provincia Caracas prope oppida Victoria et San Sebastian observata." The location of Karsten's herbarium is unknown. I have not seen any specimens that might represent type material of this species. Stafleu and Cowan (1979) note that important sets of plants collected by Karsten are to be found at LE and W. Neither of these herbaria reports having material with the above name and locality. The illustration provided in the protologue pertains to *B. integerrima*.

Tree to 20 m tall; numerous stilt or prop roots often present around the base; main trunk divided at or above the base into several prominent trunks; bark light gray to dark gray-brown, sometimes mottled, smooth or slightly warty; crown spreading, often somewhat rounded. Younger stems glabrous, farinose-puberulent with trichomes to 0.05 mm long, or pubescent with flexuose to ascendant-appressed or retrorse-appressed trichomes 0.1–0.5 mm long, the youngest growth sometimes densely pubescent with flexuose to appressed trichomes up to 1.5 mm long. Leaves with petioles to 90 mm long; blades ovate to elliptic to broadly elliptic to obovate-elliptic, 30–305 mm long, 11–157 mm wide, 1.4–3.6 times longer than wide, rounded to acute to attenuate at base, (rounded to) acute to acuminate at apex, surfaces glabrous or with scattered trichomes along veins on abaxial surface, abaxial surface usually punctate-glandular, adaxial surface somewhat darker than abaxial surface. Inflorescence racemose; dichasia (3–)6–10(–20) per raceme, borne on peduncles (1.0–)1.5–6.0(–13.0) mm long; flowers sessile (or borne on pedicels to 2 mm long); rachis densely pubescent with eglandular trichomes 0.05–0.5(–1.0) mm long. Bracts linear to linear-subulate to triangular to ovate, lowermost rarely petiolate, 2–14 mm long, 0.7–4.0 mm wide, abaxial surface pubescent like rachis, sometimes punctate-glandular. Bractlets linear to triangular to suborbicular, 1.6–5.0 mm long, shorter than calyx, 1.0–2.5 mm wide, rounded to acute at apex, abaxial surface pubescent like rachis to glabrous, sometimes punctate-glandular, margin ciliate with straight to flexuose trichomes to 0.3 mm long. Calyx 3–10 mm long; lobes sometimes unequal in length, ovate to elliptic to suborbicular to obovate-elliptic, 2–8 mm long, rounded to acute at apex, pubescent like bractlets, sometimes punctate-glandular. Corolla white with brown and yellow markings on inner surface of lower lip, 15–22 mm long, externally glabrous; tube 1.7–3.2 mm long (usually not well differentiated from throat); throat 5.5–10.0 mm long, 5.5–11.0 mm in diameter near midpoint; limb 17–27 mm in diameter with lobes 6–12 mm long, lobes sparsely ciliate on margin. Stamens exserted from throat, shorter pair 7–9 mm long, longer pair 9–11 mm long; filaments maroon; thecae maroon, 2.1–3.2 mm long including basal awn, sparsely pubescent to glabrous; pollen 53.9–61.3 μm in diameter. Style white, 7–13 long, glabrous (rarely sparsely pubescent near base with eglandular trichomes to 0.7 mm long and occasionally with stipitate glands up to 0.1 mm long as well). Capsule ellipsoid to obovoid, 5–13 mm long, glabrous at maturity (rarely sparsely pubescent near apex when immature); retinacula to 3.5 mm long. Seeds one (to four), subcircular, strongly laterally flattened, 3–5 mm long, 2.8–4.0 mm wide, 0.5–1.2 mm thick, surfaces glabrous, smooth, shiny (Fig. 4).

PHENOLOGY.—Flowering and fruiting September through May, also in July.

FIGURE 4. *Bravaisia integerrima* (*McVaugh 22884*). a, Habit, ×½; b, Bractlets and calyx, ×3.5; c, Corolla cut open showing epipetalous, didynamous stamens, ×2; d, Distal portion of filament and anther, posterior side, ×5; e, Distal portion of filament and anther, anterior side, ×5; f, Distal portion of style and stigma, ×5; g, Dehiscing capsule with subtending calyx and bractlets, ×3.5. Drawing by Karin Douthit for McVaugh's *Flora Novo-Galiciana;* copyright reserved to the University of Michigan Herbarium, used with permission.

FIGURE 5. Distribution of *Bravaisia integerrima.*

DISTRIBUTION.—West-central through southeastern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, and Trinidad (Fig. 5). The plants occur along streams and forest edges, in pastures, and in swamps in regions of tropical dry forest, tropical wet forest, and mangrove forest, at elevations from near sea level to 1,100 m; most collections were made at elevations below 300 m. Associates include species of *Brosimum, Bursera, Dialium, Ficus, Guazuma, Heliocarpus, Inga, Lonchocarpus, Ocotea, Orbignya, Pithecellobium,* and *Spondias.* The plants are often abundant and sometimes become the most common understory tree.

All of the names listed above as synonyms of *B. integerrima* were similarly treated by Leonard (1951) with the exception of *Androcentrum multiflorum.* Standley (1926) noted that specimens referred to *A. multiflorum* that he had seen appeared to be conspecific with *B. integerrima.* Although the holotype of this species is not known with certainty, probable type material (i.e., *Galeotti 510M*) is referable to *B. integerrima.*

Bravaisia integerrima differs from the other species of the genus by its externally glabrous corollas, exserted stamens, and racemose inflorescences with the dichasia borne on peduncles 1–13 mm long.

Considering the wide distribution, arboreal nature, unusual form, and occasional local abundance of *B. integerrima,* it is not surprising that numerous local names have been recorded for this species. These are: "árbol de lluvia" (*Elias 974*), "charote" (*Lopez-Palacios 1810*), "chorote" (*Bunting 9150*), "cien patos" (*Wendt et al. 3114*), "cien-pied" (*Williams 8913*), "cintopie" (*M.A.M.A. 677*), "curta" (*Smith 123, 270*; *Pittier 7760*), "curte" (*Pittier 7727*), "jigger tree" (*Britton et al. 1099*), "jigger wood" (*Chalmers s.n.*; *Marshall 12474*), "mangle" (*Steyermark 62161*), "mangle blanco" (*Alexander 74-16*; *Brenes 6600, 6600a*; *Chaves 184*; *Englesing 147*; *Hartshorn 1172, 1294*), "mangle de agua" (*Cooper and Slater 269*), "mangle llanero" (*Molina R. 2130*), "naranjillo" (*Bernardi 1174, 6311, 6903*; *John 335*; *Pittier 7727, 11449*; *Steyermark 89202*; *Williams 12341, 12904*; *Wurdack and Monachino 39712*), "palo blanco" (*González T. 46*; *Langlassé 831*; *Villegas 247*), "palo de agua" (*Brenes 6660a*; *Dugand 13, 412, 542, 580*; *Dugand and Jaramillo 4094*; *Dunlap 23*; *Elias 444, 487, 1265, 1507*; *Jiménez L. 367*; *Romero 34*; *Soto and Ramón de Soto 759*), "pata de gallo" (*Cedillo T. 736*), "sancarano" (*Curran 222*), "sancho-araña" (Curran 1929), "white mangue" (*Chalmers s.n.*), "yaga-zee" (*Seler and Seler 1609*).

Bravaisia integerrima does not appear to have significant economic value. Hess (1946:17) reported that "the wood has no special uses but appears suitable for cheap construction lumber or box boards." Curran (1929:18) noted that some of the main branches "are large enough to be utilized for timber. Wood nearly white, odorless and tasteless, moderately soft, easy to work, not readily discolored or attacked by insects when left on the ground after logging." Curran (1929) further notes that the wood is appropriate for packing crates. Others (Record 1929; *Williams 12904*) report that the wood is not used. *Steyermark 61181* indicates that the root is cooked in guarapo (a fermented beverage made from either sugar cane or pineapple) and used by the "curiosos" for pains. *Chazaro B. and Dominguez 2158* note that the flowers are melliferous. The species is sometimes cultivated in tropical botanic gardens (e.g., Martinique and Caracas) and is reported to be planted along streets in South America.

Representative Specimens Examined.—Colombia. Atlántico: near Puerto Colombia, *Dugand 13* (F); "Convento" near Galapa, *Dugand 412* (F); Arroyo de Piedras, *Dugand 580* (F, US); Juanmina, *Dugand and Jaramillo 4094* (US); Galapa, *Elias 444* (US); Sabanalarga, *Elias 487* (US); region of Barranquilla, *Elias 1265* (A, F, US), *1507* (F, US). Bolívar: vicinity of Estrella, Caño Papayal, Lands of Loba, *Curran 308* (GH, US); 1 km de Buenavista, camino entre Carrizal y Buenavista, *Forero and Jaramillo 500* (F, MO, NY, US); Morrocoquiel, on Río Sinú, *Pennell 4697* (F, GH, K, MO, NY, US). Guajira: near Barrancas, on Río Ranchería, *Haught 3989* (F, K, NY, P, US). Magdalena: vicinity of Santa Marta, *Romero 34* (MO), *Smith 1869* (A, BM, BR, F, G, GH, K, LL, MICH, MO, NY, P, PH, UC, US); Ciénaga, *Romero 980* (US). Department not determined: Sabanilla lagoon, *Dugand 83* (F); El Pajar forest, *Dugand 542* (F, G). Costa Rica. Alajuela: San Francisco y San Pedro de San Ramón, *Brenes 6600* (F); Santiago de San Ramón, *Brenes 6660a* (NY); llanura de San Carlos, near Los Angeles, *Molina R. et al. 17645* (F, GH, NY); Aguas Claras, 40 km N of Pan Am. Hwy., *Utley and Utley 3987* (CAS, F, MICH, MO, NY, WIS). Guanacaste: ca. 11 km N of La Cruz, *Liesner 4847* (F, MO); above Río Las Cañas, H. Granadilla, *Dodge and Thomas 6393* (GH, MO); Colonia Carmona, *Jiménez L. 367* (US); Río Congo, entre Río Lagarto y Limonal, *Jiménez M. 301* (F, G, US); bords des chemins a Nicoya, *Tonduz 13884* (G, K, P). Heredia: slopes of Volcán Barba, *Bawa 305* (MO); Puerto Viejo, *Biolley 7368* (BM, US); along Sarapiquí rd., ca. 10 km N of San Miguel, *Hartshorn 1172* (MO). Puntarenas: vicinity Palmar Norte de Osa, *Allen 5714* (BM, DS, F, GH, US); entre playas Jacó y Herradura, *Jiménez M. 1702* (BM, F, US, WIS); La Barranca, *Oersted 10633* (C). San José: Turubares près de San Mateo, *Biolley 7105* (BM, P, US), *16134* (G, MEXU, MO, US). El Salvador. La Libertad: coastal hwy. W of La Libertad, *Allen 7201* (F, LL, MICH, NY, US). San Miguel: W of Hacienda San Román, ca. 13 km S of Lake Olomega, 13°10′N, 88°04′W, *Tucker 864* (F, K, MICH, UC, US). Usulután: La Concordia, *Calderón 2138* (GH, US). Guatemala. Department not determined: Guaumitul (sp?), *Bernoulli and Cario 2042* (K, MO). Honduras. Choluteca: 4 km SO de Marcovia, *Alexander 74-16* (MO). Comayagua: along Río Humuya, 1 km SE of Comayagua, *Hazlett 1189* (MO). Mexico. Chiapas: cerca de Pichucalco, *Gómez-Pompa 711* (MEXU); 20 km NO de Randales, *González Q. 3496* (ENCB, MICH); Mt. Ovando, Escuintla, *Matuda 16218* (MEXU, US). Colima: along Hwy. 200, Club Santiago Golf Course, 3.0 mi (4.8 km) NW of Santiago, *Daniel 2110* (ASU, CAS, ENCB, MEXU, MICH, NY); environs de Cuyutlán, *Diguet s.n.* (MICH, P); Mpio. Tecomán, 5 km O de Chenchopa, *Rzedowski 15397* (ENCB, MEXU, TEX); Costa Rica, 15 km SE de Manzanillo, *Soto and Ramón de Soto 759* (CAS, MEXU, RSA). Guerrero: along Hwy. 200 between Petatlán and Tecpan, just SE of Juluchuca, *Daniel and Bartholomew 4925* (CAS, DUKE, K, MEXU, MICH, NY); Rives du Rio Coyaquilla, *Langlassé 831* (G, GH, K, MICH, P, US); La Lagunilla, *Nelson 7001* (GH, NY, US). Jalisco: 10 km antes de La Huerta, *Ramirez V. 19* (IBUG); Barra de Navidad a 123 kms, *Puga 2916* (ENCB, IBUG). Michoacán: along Hwy. 200 between turns to Coahuayana and Aquila, 2.5 mi (4.0 km) N of Río El Ticuiz, *Daniel 2144* (ASU, CAS, ENCB, MEXU, MICH, NY); ca. 8 km W of Apatzingán, *McVaugh 22884* (ENCB, MICH); alrededores de El Habillal, 15 km O de Playa Azul, *Villegas 247* (ENCB). Oaxaca: near Huilotepec, *Alexander 268* (MEXU, MICH, NY); Distr. Juchitán, cerca de Bernal, al NE de Chahuites, *Cedillo T. 736* (MEXU); from Jamiltepec to Río Verde, *Nelson 2375* (GH, US); 15 km de Puerto Escondido en el camino a Puerto Angel, *Pennington and Sarukhan K. 9491* (A, K, MEXU, NY); Huilotepec, *Seler and Seler 1609* (GH). Tabasco: Mpio. Cárdenas, KM 21 de la carretera Cárdenas-Coatzacoalcos, *Magaña and Zamudio 128* (CAS, ENCB, IBUG, MEXU, MO); Mpio. Cárdenas, Escuela, *M.A.M.A. 677* (MEXU). Veracruz: ca. 40 mi (64 km) N of Chachalacas, *Davis and Kincaid 55-7* (TEX); Mpio. Hidalgotitlán, 1 km al S del Poblado 7, 17°19′N, 94°31′W, *Wendt et al. 3114* (CAS, DAV, ENCB, F, MICH, NY, TEX, WIS); Fortuño, Coatzacoalcos River, *Williams 8913* (A, CAS, DS, F, GH, MICH, UC, US). Yucatán: without locality, *Johnson s.n.* (NY). State not determined: without locality, *Haenke 1439* (F), *Sessé, Mociño et al. 275* (F), *2147* (F). Nicaragua. Boaco: along carretera 7, between Boaco cutoff, Dept. Chontales, and Tipitapa, Dept. Managua, *Bunting and Licht 740* (F, NY, US). Chinandega: Palo Blanco, *Shannon 5005* (F, G, GH, K, NY, US). Chontales: between Santo Tomás and Villa Somozo, near border with Depto. Zelaya, *Bunting and Licht 1101* (BM, F, WIS). Granada: Volcán Mombacho, *Baker 2363* (A, F, G, GH, K, MO, POM, UC, US); *Oersted 10634* (C). Jinotega: al NE de Wiwilí, camino entre El Carmen y Wamblán, a lo largo del Río Coco, *Araquistain and Castro 1883* (TEX). León: KM. 52, carretera vieja a León, La Paz Centro, 12°20′N, 86°42′W, *Moreno 6595* (MO). Managua: Managua, *Chaves 184* (US); 5 km SE of San Francisco NE of Lago de Managua, *Hughes and Styles 73* (MEXU); Cuesta del Coyol, Pan Am. Hwy., ca. 60 mi (96 km) N of Managua, *Williams et al. 25070* (F, LL, NY, US). Zelaya: bank of Morcielago Creek, region of Braggman's Bluff, *Englesing 147* (F, K); La Esperanza, Río Grande, *Molina R. 2130* (F). Department not determined: Sierra de Managua, *Garnier 1003* (US); without locality, *Wright s.n.* 1853–56 (GH, P, US). Panama. Bocas del Toro: vicinity of Almirante, *Cooper 25a* (F, GH, MO, NY, US); Changuinola Valley, *Dunlap 23* (F); 10–15 mi (16–24 km) inland (S) from mouth of Río Changuinola, *Lewis et al. 886* (MO, US, WIS). Chiriquí: Progresso,

Cooper and Slater 269 (F, NY, US); Burica Peninsula, Rabo de Puerco, 8 km W of Puerto Armuelles, *Croat 21966* (CAS, DAV, F, MO, NY). TRINIDAD AND TOBAGO. St. Patrick: Erin, *Broadway 2555* (BR, F, MICH, US). Victoria: Moruga, La Fortune Trace, *Broadway 7919* (K, NY). County undetermined: Southern Watershed Reserve, *Britton et al. 1099* (GH, NY, US), *Marshall 12474* (K, NY); Belmont, *Broadway s.n.* (NY); Catshill Reserve, *Chalmers s.n.* 29.3.63 (K, US). VENEZUELA. Anzoátegui: Cantaura, *Smith 123* (US); vicinity of confluence of Río León with Río Zumbador, NE of Bergantín, *Steyermark 61181* (F, K, US). Aragua: between Maracay and S. Mater., *Alston 6057* (BM, F, K, NY, US); Maracay, *Linden 441* (G, P); La Trinidad de Maracay, *Pittier 5807* (F, MO, NY, P, US); Magdalena y El Tocorón, *Williams 12341* (F, US). Barinas: La Libertad, bosques del Cachicamo, *Bernardi 1174* (G, NY); orillas del Río Masparro, *Bernardi 6311* (G). Bolívar: SE of Cerro Pichacho, N of Las Nieves, 45 km N of Tumeremo, *Steyermark 89202* (NY, US); El Palmar, *Williams 12904* (A, F, K, UC, US). Carabobo: between Valencia and Maracay, *Pittier 7727* (GH, US). Delta Amacuro: Serranía Imataca, 2–6 km SE of Río Guanamo, *Wurdack and Monachino 39712* (NY). Distrito Federal: vicinity of Caracas, *Bailey and Bailey 1107* (US), vicinity of Maiquetía, *Gentry and Morillo 10325* (MO, NO, NY, US); Puerto La Cruz, *John 335* (US); El Paují, road Caracas-La Guaira, *Pittier 13358* (G, NY, PH). Guárico: vicinity of El Sombrero, along rd. to Calabozo, *Pittier 11449* (A, G, GH, K, NY, P, US). Lara: between Humocaro Alto and Humocaro Bajo, *Steyermark 55551* (F, US). Miranda: between Carenero and Chirimena, along Quebrada del India, *Steyermark and Carreño E. 106903* (F, P, US). Monagas: ca. 7.5 km SSE of San Felix, *Pursell et al. 8446* (NY, US); Caicara, *Smith 270* (NY, US); Caripe, N side of Río Caripe, coffee hacienda, *Steyermark 62161* (F, MO, NY, US). Sucre: Sabilar (Carr. Cumaná-S. Juan Macarapana), *Cumana C. 248* (MEXU); Distr. Benítez, along Caño Ajíes, N of Ajíes, 10°28'N, 63°05'W, *Steyermark et al. 121317* (MO). Trujillo: Alcabala de La Concepción, *Delgado 349* (US); between Motatan and Valera, *Alston 6391* (BM). Yaracuy: Colonia Yumare, *Bernardi 6903* (G, K, NY). Zulia: Dtto. Perijá, KM 25 al SE de San José, *Bunting 5544* (NY, US); Dtto. Bolívar, entre Campo Lara y Piedras Blancas, *Bunting 9150* (NY, US); Dtto. Mara, alrededores de Campamento Carichuano (de Carbozulia), *Bunting 10009* (US); vicinity of Perijá, *Tejera 113* (GH, US). State undetermined: without locality, *Funcke and Schlim 441* (BM), *Otto 538* (K, P). COUNTRY UNDETERMINED. Central America (printed label on specimen at F ex K says western South America; date of collection given as 1831 on specimen at K; label on specimen at BM notes collection in Costa Rica in 1832), *Cuming 1307* (BM, CGE, F, K).

2. Bravaisia grandiflora J. D. Smith, Bot. Gaz. 33:255. 1902. TYPE.—GUATEMALA. Alta Verapaz: "In silvis ad Sachicha," Apr. 1901, *von Tuerckheim 7924* (Holotype: US!).

Bravaisia proxima S. F. Blake, Contr. Gray Herb. 52:96. 1917. TYPE.—BELIZE: upper Moho River, 16 Mar. 1907, *M. E. Peck 730* (Holotype: GH!; photo: NY!).

Shrub to understory tree to 9 m tall; trunk to 20 cm in diameter; bark light-colored, smooth. Younger stems glabrous or sparsely pubescent with flexuose to retrorse- or antrorse-appressed trichomes to 1.4 mm long. Leaves with petioles to 40 mm long; blades elliptic to obovate, 30–190 mm long, 10–75 mm wide, 2.1–4.5 times longer than wide, attenuate at base, acuminate to acute (sometimes aristate) at apex, surfaces glabrous or pubescent along veins on abaxial surface, abaxial surface sometimes punctate-glandular. Inflorescence spicate; dichasia one to five (commonly three) per spike, sessile; flowers sessile; rachis pubescent with flexuose to ascendant-appressed, sometimes golden trichomes 0.1–1.1 mm long, sometimes punctate-glandular. Bracts petiolate or narrowed at or near base and abruptly expanding into lanceolate to narrowly elliptic to oblanceolate lamina, lowermost sometimes ovate to elliptic and uppermost sometimes widest at base and narrowed distally, 2.5–15.0(–23.0) mm long, 1–8 mm wide, pubescent like rachis near base, often glabrous above, sometimes punctate-glandular. Bractlets triangular to orbiculate to somewhat squarish, 3–8 mm long, shorter than calyx, 1.5–4.0 mm wide, prominently apiculate to caudate at apex, the abaxial surface pubescent like rachis (often only sparsely so) and sometimes punctate-glandular, margin ciliate (at least near the apex) with mostly straight trichomes 0.05–0.5 mm long. Calyx 5.0–10.5 mm long; lobes obovate to elliptic, mucronate to apiculate at apex, abaxial surface densely puberulent with ascendant trichomes 0.05–0.20(–0.50) mm long and sometimes punctate-glandular, margin densely ciliate with straight to flexuose trichomes to 1 mm long. Corolla purplish white or pinkish with yellow markings in throat, 27–47 mm long, externally pubescent with trichomes 0.3–0.7 mm long; tube 6–13 mm long; throat 12–22 mm long, 7.5–13.0 mm in diameter near midpoint; limb 22–40 mm in diameter with lobes 7–18 mm long, lobes ciliate. Stamens included in throat or the longer pair slightly emergent, shorter pair 9–14 mm long, longer pair 11–19 mm long; thecae 3.0–4.5 mm long including basal awn, pubescent with flexuose or twisted trichomes; pollen 75.9–88.2 μm in diameter. Style 20–29 mm long, glabrous. Capsule ovoid, 10 mm long, glabrous. Seeds not seen (Fig. 6).

PHENOLOGY.—Flowering January through April; fruiting in June.

DISTRIBUTION.—Southern Mexico, northern Guatemala, and southern Belize (Fig. 7). The plants occur along streams and at the edges of forests in regions of tropical wet forest at elevations from 90 to 1,000 m.

FIGURE 6. *Bravaisia grandiflora* as illustrated by figure 75 in Gibson's treatment of Acanthaceae in *Flora of Guatemala;* copyright Field Museum of Natural History, used with permission.

Gibson (1974) was the first to synonymize *B. proxima* with *B. grandiflora.* The species is readily distinguishable by its large, pubescent corollas and apically apiculate to caudate bractlets. The local name "boc-ché" (Quecchí dialect) has been noted from Guatemala (*Johnson 187*) for this species.

ADDITIONAL SPECIMENS EXAMINED.—BELIZE. Toledo: Bolo Camp, upper reach of Golden Stream River, *Gentle 4555* (LL); along Temash River, *Lamb 58* (F); Blue Creek, *Whiteford 3219* (BM, MEXU, MO, NO). District undetermined: Jacinto Hills, *Schipp 1259* (A, BM, F, G, GH, MICH, MO, NY). GUATEMALA. Alta Verapaz: Chama, along Río Salba, *Johnson 187* (US); 8–10 mi (13–16 km) NW of Cubilguitz, *Steyermark 45031* (A, F, LL, US); Yaxcabnal, *von Tuerckheim 8259* (A, GH, K, MO, NY, US). Petén: Santa Isabel, *Contreras 6694* (K), *6695* (K, US); La Cumbre, KM 155 of Cadenas Rd., Chacalte Abajo, *Contreras 10563* (ENCB, LL, RSA); Dolores, en la orilla del Río Machaquilla a Km. 93, *Tún Ortíz 1642* (F, MO, NY, US). Izabal: El Estor, *Contreras 11383* (US); between Cienaga and Pto. Méndez along Petén-Río Dulce Hwy., *Tún Ortíz 2351*

FIGURE 7. Distribution of *Bravaisia grandiflora* (triangles) and *B. berlandieriana* (dots).

(BM, F, MICH, US). Department undetermined: eastern portions of Vera Paz and Chiquimula, *Watson 240* (F, GH, US). MEXICO. Chiapas: Mpio. Palenque, Agua Azul, *Breedlove 49859* (CAS), *Daniel and Bartholomew 4998* (ASU, CAS, DUKE, ENCB, F, K, MEXU, MICH, MO, NY, TEX, US), *Ventura A. 20001* (CAS).

3. **Bravaisia berlandieriana** (Nees) T. F. Daniel, comb. nov.

Onychacanthus berlandierianus Nees *in* DC. Prodr. 11:217. 1847. TYPE.—MEXICO. Veracruz: vicinity of Laguna de Tamiahua, S of Tampico, Tamaulipas, *J. L. Berlandier 108* (Holotype: G!; isotypes: BM!, P!).

Bravaisia tubiflora Hemsley *in* Hook. Icon. Pl., ser. 3, 16: t. 1516. 1886. TYPE.—MEXICO. Quintana Roo: Cozumel Island, 25 Apr. 1885, *G. Gaumer 52* (K!).

Shrub to tree to 7.5 m tall; trunk to 8 cm in diameter. Younger stems pubescent with ascendant-appressed to ascendant to erect to flexuose trichomes 0.1–1.0 mm long or nearly glabrous. Leaves with petioles to 35 mm long; blades ovate-elliptic to elliptic to broadly elliptic to obovate-elliptic, 15–159 mm long, 9–75 mm wide, 1.3–2.8 times longer than wide, acute to attenuate at base, acute to acuminate at apex, adaxial surface glabrous or with trichomes along midvein, abaxial surface glabrous or sometimes sparsely pubescent and usually punctate-glandular. Inflorescence spicate; dichasia 3–7(–11) per spike, sessile (rarely borne on peduncles to 1 mm long); flowers sessile; rachis pubescent like younger stems (or with the trichomes denser), usually punctate-glandular. Bracts petiolate or narrowed at base and abruptly expanding into an elliptic to orbiculate lamina, 7–15(–30) mm long, 3.0–10.0(–14.5) mm wide, pubescent like leaves and punctate-glandular on abaxial surface. Bractlets obspatulate (i.e., constricted distally) to hourglass shaped (i.e., with a prominent medial constriction), rarely spatulate (i.e., constricted proximally), (5–)7–15(–20) mm long, equalling or usually longer than calyx, 1–5 mm wide, rounded to acute at apex, abaxial surface pubescent like rachis and punctate-glandular, margin ciliate with flexuose trichomes to 0.5 mm long. Calyx 4.5–9.0 mm long, lobes ovate-elliptic to obovate, rounded to acute to mucronate at apex, abaxial surface puberulent with trichomes 0.05–0.10 mm long and sometimes with ascendant-appressed trichomes to 0.8 mm long along midvein, punctate-glandular, margin ciliate like bractlets (or

FIGURE 8. *Bravaisia berlandieriana* (as *B. tubiflora*) as illustrated by plate 1516 in *Hooker's Icones Plantarum* in 1886. 1, Bud; 2, Pair of stamens; 3, Stamen, anterior side; 4, Stamen, posterior side; 5, Gynoecium; 6, Longitudinal section of ovary; 7, Developing capsule with subtending calyx and bractlets. Magnifications were not provided. Copyright Bentham-Moxon Trustees, used with permission.

the trichomes sometimes denser). Corolla white to pinkish with purplish and yellow markings within, 15–25 mm long, pubescent on external surface of the lobes and upper portions of the throat with dense trichomes 0.2–0.5 mm long; tube 4–8 mm long; throat 6–11 mm long, 6–11 mm in diameter near the midpoint; limb 15–22 mm in diameter with lobes 5–9 mm long. Stamens included in throat or longer pair slightly emergent, shorter pair 7–10 mm long, longer pair 10–14 mm long; thecae 2.5–4.0 mm long including basal awn, pubescent; pollen 56.4–66.2 μm in diameter. Style 14–21 mm long, glabrous. Capsule ovoid to ellipsoid, 6.5–11.0 mm long, glabrous. Seed usually one, subellipsoid, slightly flattened laterally, 3.5–4.3 mm long, 3.0–3.5 mm wide, 1.8–2.6 mm thick, surface glabrous, smooth, shiny (Fig. 8).

Phenology.—Flowering November through April; fruiting March through May (to July).

Distribution.—Northeastern through southeastern Mexico, western Cuba, northern Belize, and northern Guatemala (Fig. 7). The plants occur, often abundantly, on sand dunes (with *Coccothrinax*) along shorelines, beside streams, and in swamps and seasonally marshy areas in regions of coastal scrub, mangrove forest (with *Conocarpus, Rhizophora, Laguncularia,* and *Archosticum*), deciduous and subdeciduous forest, and tropical wet forest at elevations from sea level to 80 m. The plants grow in clayey to sandy, moist to wet soils, some of which are subject to salt water inundation.

Leonard (1951) included *Onychacanthus berlandierianus* in the synonymy of *Bravaisia integerrima.* Examination of the holotype and two isotypes of *O. berlandierianus* reveal Berlandier's early nineteenth-century collection to possess the diagnostic features of what has hitherto been known as *B. tubiflora.* The type collection from the vicinity of Laguna de Tamiahua in northern Veracruz represents the northernmost extent of the distribution of both *B. berlandieriana* and the genus in Mexico. The species has been recollected at Laguna de Tamiahua as recently as 1967. *Bravaisia integerrima* is not known to occur in northeastern Mexico.

The species is easily recognized by its relatively small, pubescent corollas and distinctive bractlets. The bractlets of *B. berlandieriana* usually have a prominent medial constriction and thus appear hourglass shaped. Bractlets that are obspatulate (i.e., constricted distally; e.g., *West 5/2*) can appear similar to those of *B. grandiflora* that have apiculate to caudate apices. At least some bractlets on every specimen of *B. berlandieriana* examined exhibited a prominent medial constriction, however. These two species can be further distinguished by features of the flowers.

Local names noted on herbarium specimens of *B. berlandieriana* are: "chilat" (*Arnason and Lambert 17152*), "hoo-loop" (*Winzerling VIII-14*), "hulaba" (*Gentle 380, 1193*), "hulu" (*Mell 2001*), "hulub" (*Crane 321*), "hulu-bal" (*Stevenson 1*), "hulup" (*Crane 47*), "julub" (*Chan V. 1291*), "julube" (*West 5/2*), "julubo" (*Orozco-Segovia and Gallegos 436*), "kulub" (*Enriquez 398*), and "xulub" (*Vela G. 3046*). Most of these appear to represent variations of a single Mayan name. *Ucan et al. 921* notes the usage of this species as a green dye in Quintana Roo, Mexico. Mendieta and del Amo R. (1981) record the use of poultices made from stems of this species for treatment of mammary abscesses in the Mexican state of Yucatán.

Representative Specimens Examined.—Belize. Belize: Maskall, *Gentle 1193* (A, BM, F, G, GH, K, LL, MICH, MO, NY, US); ca. 12 mi (19 km) W of Belize, *McDaniel 13080* (MO). Corozal: Cerros Maya Ruins, Lowry's Bight, *Crane 47* (LL), *321* (LL); without locality, *Gentle 380* (CAS, F, MICH, US); Freshwater Creek, *Stevenson 1* (F). Orange Walk: Indian Church, *Arnason and Lambert 17152* (MO); without locality, *Winzerling VIII-14* (US). District undetermined: without locality, *Campbell 1* (K), *Stevenson s.n.* (US). Cuba. Pinar del Río: Carabela Grande, *Ruig 3194* (GH, NY, US). Matanzas: Boca de Canasí, *León 13236* (GH), *13679* (US), 14205 (GH, US), *16549* (NY). Province undetermined: without locality, *de la Sagra 679* (P). Guatemala. Petén: Dos Lagunas, *Contreras 8369* (US). Mexico. Campeche: E side of Río San Pedro y San Pablo mouth, *Barlow 17/3* (F, MEXU, WIS); Mpio. Hopelchen, 10–50 km de Xpujil, 18°12′N, 89°26′W, *Chan V. 1291* (F); Canasayab, *Lundell 1414* (GH, MICH, NY); Cd. del Carmen, *Mell 2001* (US); Distr. Champoton, Mokel, *Seler and Seler 4938* (GH); Laguna Atasta, near Isla del Carmen, *West 8/2* (GH, WIS). Quintana Roo: 1 km al S de Akumal, carretera Cancún-Tulum, *Cabrera and Ibarra 1149* (BM, CAS); directly W of Puerto Morelos, *Davidse et al. 20039* (BM, MEXU, MO); Cozumel, *Gaumer 52* (GH); Laguna Guerrero a 20 km N de Chetumal, *Lot and Novelo 799* (GH, MEXU); Cozumel Island, east shore, *Millspaugh 1580* (F); Isla Mujeres, central east coast, *Sauer and Gade 3242* (WIS); 36 km NE de F. Carrillo Puerto, 20 km SW de Vigía Chico, *Tellez and Cabrera 1462* (BM, MEXU); Mpio. Othon P. Blanco, orilla del Río Hondo en Juan Sarabia, 18°30′N, 88°29′W, *Ucan et al. 921* (F). Tabasco: near Playa Azul, ca. 20 km WNW of Paraíso, *Barlow 1/1* (BM, GH, WIS); Balancan, *Mendez et al. 439* (CAS, K, MEXU, MO); Mpio. Centla, a 12 km de Frontera rumbo a La Pera, *Orozco-Segovia and Gallegos 436* (MEXU); Camino Escárcega-Sabankuy, *Vela G. 3046* (ENCB, MEXU); lower Río Naranjeno, Laguna Machona region, *West 5/2* (F, MICH, UC, WIS). Veracruz: Tlacotalpan, *Hahn s.n.* (MO); Laguna Tamiahua, 25

mi (40 km) S of Tampico, *LeSueur 433* (F, GH, TEX); orilla sur del Estero Cucharas cerca de su desembocadura en la Laguna de Tamihahua, *Varquer Y. 23* (MEXU). Yucatán: vicinity of Progreso, *Seler and Seler 3819* (A, F, G, GH, K, US); vicinity of Sisal, *Gaumer et al. 23227 (A, BM, F, G, GH, MO, NY, US); Lake Chichankanab, Gaumer et al. 23662* (F, G, GH, NY, US); Becanchen, *Enriquez 398* (MEXU); Port Silam, *Gaumer 618* (BM, F, MO, US); Chichankanab, *Gaumer 1547* (F), *1872* (A, BM, F, GH, K, MO, NY, US); 4 km E de Celestum, *Lot H. 2603* (GH, MEXU); beach ridge near Chicxulub, *Saunders 93* (ENCB); Mpio. El Cuyo, camino de las Coloradas rumbo al Cuyo, *Ucan and Espejel 788* (F).

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Appendix A

Index to Collections Examined

The numbers in parentheses refer to the corresponding species in the text.

Alexander, E. 268 (1), 74-16 (1).
Allen, P. 5714 (1), 7201 (1).
Alston, A. 6057 (1), 6391 (1).
Araquistain, M. and D. Castro 1883 (1).
Arnason and Lambert 17152 (3).
Bailey, L. 606 (1).
Bailey, L. and E. Bailey 1107 (1).
Baker, C. 2363 (1).
Barlow, F. 1/1 (3), 8/2b (3), 17/3 (3).
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