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A REVISION OF *CAPRARIA* (SCROPHULARIACEAE)

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Abstract: Herbarium and field studies of the chiefly neotropical genus *Capraria* have led to the recognition of four species. *Capraria frutescens* and *C. mexicana* are essentially endemic to Mexico. *Capraria biflora* is a widespread species that occurs throughout Mexico, Central and South America, the West Indies, and southern Florida. *Capraria peruviana* grows in northwestern South America and the Galápagos Islands. A complete account of synonymy and typification is provided, along with a key to species, scanning electron micrographs of pollen, stigmas and seeds, photographs, illustrations, and distribution maps.

Keywords: *Capraria*, Caprarieae, Gratioleae, Leucophylleae, Myoporaceae, Scrophulariaceae, SEM.

Capraria L. (Latin = goat, in reference to observations that goats consume the leaves (Sprague (1921)) is a neotropical genus of suffruticose herbs and subshrubs distributed from southern Florida to central South America. *Capraria* is unique within the Scrophulariaceae in having alternate leaves with external punctate glands and oil-secreting cavities. The relationship of *Capraria* within the Scrophulariaceae has been under considerable dispute (see Generic Relations). The species, however, are easily delineated morphologically.

Linnaeus (1753) established the genus with the description of *Capraria biflora* L. Subsequently, 49 names were proposed in *Capraria*. Most of these were transferred or synonymized under other genera (e.g., *Anticharis* Endl., *Freylinia* Colla, *Scoparia* L., and *Stemodia* L.). Sprague (1921), in his treatment of *Capraria*, provided a list of excluded species that is included and expanded at the end of the present article.

A treatment of *Capraria* is pertinent at this time, considering the numerous misidentifications of specimens in various herbaria observed by the present author and the discrepancy in the number of species recognized by various botanists: Lersten and Curtis (2001) considered *Capraria* to be monotypic, Mabberley (1987) recognized four species, Sprague (1921) five species, and Méndez Larios and Villaseñor Ríos

(2001) six species. In this work four species of *Capraria* are recognized; full synonymy, illustrations and detailed exsiccate are presented for all species.

GENERIC RELATIONSHIPS

Throughout its history, the placement of *Capraria* has been under dispute (Table 1). Bentham (1846) placed it in subfamily (his suborder) Rhinanthoideae (with posterior corolla lobes interior in bud), tribe Sibthorpeae (with alternate leaves, and flowers solitary in the leaf axils), along with *Sibthorpia* L., *Hornemannia* Benth., *Hemiphragma* Wall., *Camptoloma* Benth. and *Scoparia*.

Bentham (1876) later reduced the tribe Sibthorpeae to subtribe Sibthorpieae of subfamily (his series) Rhinanthoideae, tribe Digitaleae with *Hornemannia* reduced to a synonym of *Sibthorpia*, and *Camptoloma* repositioned in his subtribe Digitalieae. Bentham's Digitaleae was later viewed as a heterogenous group with no clear definition by Thieret (1967).

Wettstein (1891) essentially followed Bentham's (1876) treatment, differing only in the non-recognition of subtribes for tribe Digitaleae.

Sprague (1921) retained *Capraria* in the tribe Digitaleae, emphasizing that *Scoparia* was its closest relative because both pos-

TABLE 1. Familial, subfamilial, and tribal placement of *Capraria* by various authors.

Author	Family	Subfamily	Tribe
Bentham (1846)	Scrophulariaceae	Rhinanthoideae	Sibthorpeae
Bentham (1876)	Scrophulariaceae	Rhinanthoideae	Digitaleae
Wettstein (1891)	Scrophulariaceae	Rhinanthoideae	Digitaleae
Sprague (1921)	Scrophulariaceae	Rhinanthoideae	Digitaleae
Thieret (1954)	Scrophulariaceae	Rhinanthoideae	Digitaleae
Thieret (1967)	Scrophulariaceae	Antirrhinoideae	Gratiolaeae
Niezigoda & Tomb (1975)	Myoporaceae		Leucophylleae
Barringer (1993)	Scrophulariaceae		Caprariaeae
Méndez Larios and Villaseñor Ríos (2001)	Scrophulariaceae	Antirrhinoideae	Digitaleae
Olmstead (2004)	Scrophulariaceae		Leucophylleae

sessed leaves with punctate glands along the upper leaf surface. Sprague also noted that *Hemiphragma* “has relatively little in common with either” *Capraria* or *Scoparia*, suggesting that its placement near them was artificial, based largely upon a shared possession of alternate leaves.

Thieret (1954) initially followed the treatments of Bentham (1876) and Wettstein (1891), but later transferred both *Capraria* and *Scoparia* into the subfamily Antirrhinoideae, tribe Gratiolaeae (Thieret, 1967). This was based, in part, on the observations of Pennell (1920, 1935), who noted that the posterior corolla lobes are external in bud in both taxa, and that they possess glandular hairs similar to other Gratiolaeae. Thieret also suggested that the scariform-reticulate seeds (his “Bacopa” type) of *Capraria* and *Scoparia* are characteristic of many Gratiolaeae, and that their small 4-valved capsules are similar to those found in the genus *Conobea* Aubl., a native of tropical America with opposite leaves and punctate glands.

Arekal et al. (1971) related *Capraria biflora* to *Scoparia dulcis* L. on the basis of embryological data. This was later negated by Hakki (1975), who noted “no secondary haustoria developed in *C. biflora* as has been reported by Arekal et al. (1975) for *Scoparia dulcis*—the closest relative of our genus.”

Niezigoda and Tomb (1975) showed

that the pollen of *Capraria* is spherical and 3-colpate, as opposed to 4-colpate pollen found in most Scrophulariaceae. They also found 3-colpate pollen in *Leucophyllum* Bonpl., *Eremogeton* Standl. & L. O. Williams (tribe Leucophylleae), and some Myoporaceae. Due to the similarity in pollen structure, Niezigoda and Tomb suggested the placement of *Capraria* close to the Leucophylleae, which they favored placing as a subfamily of the Myoporaceae. Argue (1980), however, observed 3-colpate pollen in *Mimulus* L. (sections *Mimulus* and *Erythranthe*), *Penstemon* Schmidel (tribe Cheloneae), *Celsia* L. (tribe Verbasceae), and selected genera of tribe Gratiolaeae (*Lancea* Hook. f. & Thomson, *Artanema* D. Don, and *Conobea*). Indeed his work vitiates the dramatic placement of *Capraria* in the Myoporaceae, suggesting instead its retention in the Scrophulariaceae tribe Gratiolaeae near *Conobea*, as proposed by Thieret (1967).

Henrickson and Flyr (1985) discussed in detail the systematic position of *Eremogeton* and *Leucophyllum*, concluding that both genera were more closely related to members of the traditional Scrophulariaceae and not to the Myoporaceae. However, they did not study *Capraria*, nor suggest it as a possible relative.

Barringer (1993) did not recognize subfamilies for the Scrophulariaceae and placed *Capraria* in his newly described monotypic

TABLE 2. Morphological variation among the four species of *Capraria*.

	<i>Capraria peruviana</i>	<i>Capraria mexicana</i>	<i>Capraria biflora</i>	<i>Capraria frutescens</i>
Vestiture	none	none	pilose with few glandular hairs (occasionally glabrous)	pilose and glandular
Stems	ramified	ramified	ramified	monopodial
Leaf blades	lanceolate	lanceolate	spatulate-lanceolate	spatulate
Pedicel length	5–25 mm	5–25 mm	5–25 mm	1–4 mm
Sepal shape	lanceolate	lanceolate	lanceolate	oblong
Corolla symmetry	radial	radial	bilateral	bilateral
Corolla tube length	0.8–1.5 mm	2–3 mm	4–6 mm	4–7 mm
Corolla lobes pubescent	no	no	yes	yes
Corolla color	white	light green-white	white with purple blotches on lower surface	white with purple blotches on lower surface
Stamen number	5	5	4–5	4
Stamen arrangement	radial	radial	bilateral	bilateral
Stamens exerted	yes	yes	±yes	no
Style length	0.75–1.5 mm	3–5 mm	3–5 mm	3–5 mm
Style exerted past corolla tube	no	yes	±yes	no
Style pubescent	no	no	no/yes	no
Stigma shape	linear	linear	linear	reniform

tribe Caprarieae, suggesting no close relatives for it.

Lersten and Curtis (2001) noted that *Capraria* and *Leucophyllum* are the only genera of Scrophulariaceae with true secretory oil cavities but noted that these two genera differ in the number and arrangement of these cavities (see Morphology section). They did not propose a systematic placement of *Capraria*; instead, they cited Raman (1991) who, based on a study of trichomes in the Scrophulariaceae, proposed no “taxonomic conclusion” for *Capraria*.

Recently, Olmstead (2004) placed *Capraria* in the tribe Leucophylleae with *Ereмоgeton* and *Leucophyllum*.

The systematic position of *Capraria* within the Scrophulariaceae appears unresolved. I am inclined to recognize *Capraria* in the monotypic Caprarieae as suggested by Barringer (1993). Nevertheless, I acknowledge that *Capraria* shares many char-

acters with various members of the tribes Gratiioleae and Leucophylleae.

MORPHOLOGY

METHODS: The morphological study is based on field observations by the author in Mexico and the examination of approximately 1600 herbarium specimens. Specimens were examined at or borrowed from the following institutions: BM (2 types), F (330 specimens), FLAS (40), K (3 types), MA (1 type), MO (274), NY (445), P (2 types), TEX-LL (96), US (354). There are at least 16 morphological characters (Table 2) that serve to distinguish *Capraria* from other genera and/or the four species from one another as noted below.

For Scanning Electron Microscopy (SEM) studies, the following procedures were followed. Pollen, stigma and seeds of the four species were collected from her-

barium specimens housed at TEX-LL and SHST and the sheets annotated to that effect. These were mounted onto SEM stubs with conductive graphite tape and placed in a silica dessicator for three days. After dehydration the specimens were coated with gold using a LADD sputter coater. Observations of the pollen and stigmas were made with a Vega Tescan 5130 (Department of Biological Sciences, Sam Houston State University) and photographed digitally. Observations of the seeds were made with a Phillips 515 scanning electron microscope (Cell Research Center, University of Texas) and photographed using Polaroid type 55 positive/negative film.

LEAVES: The leaves of *Capraria* are alternate, simple and dentate. They vary in shape from lanceolate to spatulate. Three leaf characters in combination distinguish *Capraria* from other genera of Scrophulariaceae: 1) alternate leaves; 2) punctate glands; 3) oil-secreting cavities. Alternate leaves occur throughout the Scrophulariaceae, as do punctate glands. The possession of oil cavities is the only one of these three characters that does not appear to occur randomly throughout the family. In the Scrophulariaceae, only *Leucophyllum* shares true secretory oil cavities with *Capraria*. Despite the fact that *Capraria* and *Leucophyllum* share alternate leaves and oil cavities, *Leucophyllum* lacks punctate glands along the upper leaf surface and has a different number and arrangement of the oil cavities. *Capraria* has numerous small oil cavities scattered throughout the leaves, while *Leucophyllum* has two large oil cavities paired at the apex of the leaves (Lersten and Curtis, 2001).

COROLLAS: There is a wide range of variation among the corollas of the species of *Capraria* (Fig. 1). *Capraria frutescens* has bilaterally symmetrical, tubular-campanulate corollas pubescent along the base of the throat, and four fertile included stamens as is typical of most Scrophulariaceae. *Capraria mexicana* and *C. peruviana* have glabrous, actinomorphic, rotate corollas with

five distinct petals, five separate fertile stamens, no obvious corolla tube, and exerted stamens. The flowers of *C. biflora* are intermediate between those of *C. frutescens* and *C. mexicana*. The flowers are pubescent, and tubular, with five distinct petals lobes (two posterior and three anterior) that are bilaterally arranged, and exerted stamens. In addition, stamen number in *C. biflora* varies between four and five.

Corolla color ranges from white (*Capraria mexicana* and *C. peruviana*) to white (or pale lavender) with purple splotches running along the ventral internal surface of the tube (*C. biflora* and *C. frutescens*), these probably serving as nectar guides (Henrickson and Flyr, 1985).

GYNOECIUM: The gynoecium in *Capraria* is a superior bi-loculate ovary with a solitary terminal style that varies in length from 3–5 mm (*C. biflora*, *C. frutescens* and *C. mexicana*) to 0.75–1.50 mm (*C. peruviana*). The ovary possesses numerous ovules that are arranged axially. In general, the pistil is glabrous, although the ovary is occasionally glandular in *C. frutescens* (Fig. 2a) and the style is occasionally pubescent in *C. biflora*. The styles are exerted in *C. biflora* and *C. mexicana* but included in *C. frutescens* and *C. peruviana*. Like *Leucophyllum* (Henrickson and Flyr, 1985), *Capraria* exhibits interspecific variation in stigmatic structure. *Capraria biflora*, *C. mexicana* and *C. peruviana* (Figs. 2b, c, d, respectively) all possess stigmas that are elongated and linear in shape, while *C. frutescens* has a stigma that is shortened, bi-lobed and reniform in shape (Fig. 2a). In the subtribe Maurandiyinae, Elisens (1985) proposed that “divergent or lobed stigmas . . . suggest derived character states and evolutionary advancement” from the more primitive conical/linear-shaped stigmas.

POLLEN: Niezgodna and Tomb (1975) described the pollen of *Capraria* as spherical, 3-colpate, and diorate with a reticulate surface (Fig. 3); this contrasts with the 4-colpate pollen found in most Scrophulariaceae. No apparent variation in pollen grain

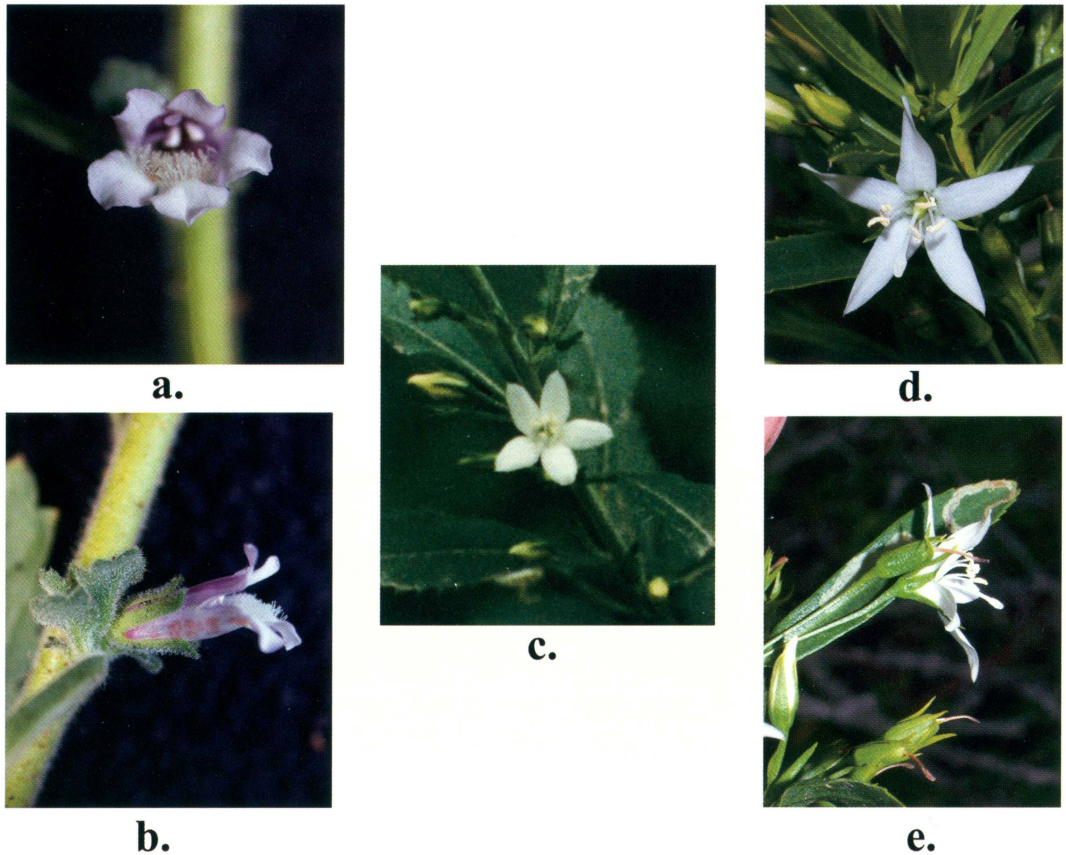


FIG. 1. Flowers of *Capraria frutescens* (a. front view, b. side view); *C. biflora* (c. front view); *C. mexicana*. (d. front view, e. side view). Photos by the author.

sculpturing exists among the four species of *Capraria*.

FRUITS: The capsules (Fig. 4d) of *Capraria* are woody and ellipsoid to ovoid. They dehisce both septicidally and loculicidally to the base, releasing numerous seeds. The capsules are similar in form and structure to those of *Leucophyllum* and *Gratiola*. The structure of the fruits readily separates *Capraria* from the fleshy, 1–10-seeded, indehiscent fruits of the Myoporaceae.

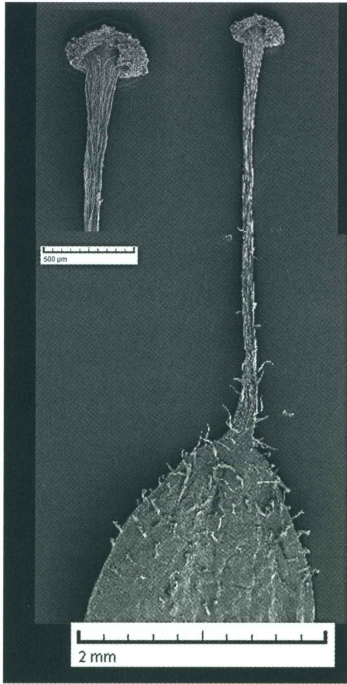
SEEDS: The seeds of *Capraria* are brown and have outer tangential walls forming a scalariform-reticulate surface of square cells (Fig. 5). Their surface structures are very similar to those found in the Gratiolleae (Thieret, 1967; Pastor and Fernández, 2000) and the Leucophylleae (Henrickson and Flyr, 1985), thereby providing no specific

insight into tribal placement. Hakki (1975) described the endosperm as “ab initio cellular.”

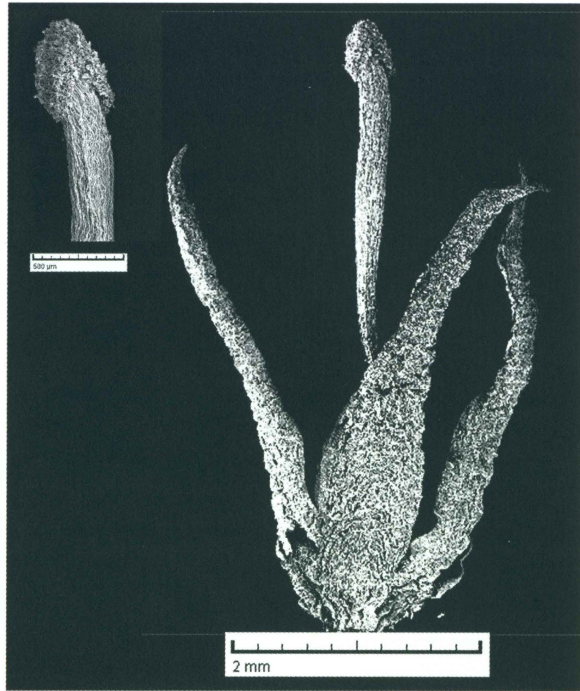
Variation exists in seed size among the four species of *Capraria*. Both *C. biflora* and *C. frutescens* have seeds that ≥ 0.5 mm long while those of *C. mexicana* and *C. peruviana* are ± 0.35 mm.

CHROMOSOME NUMBERS

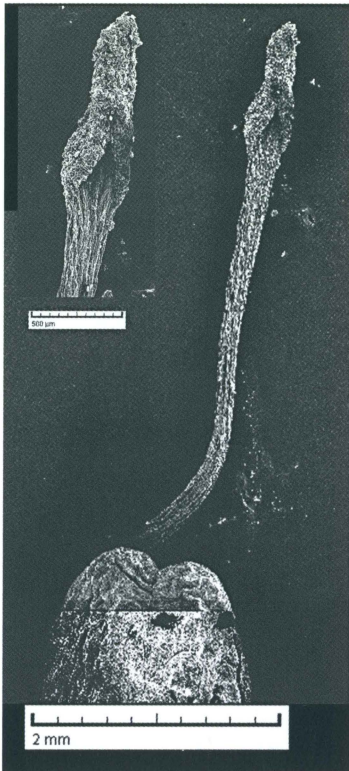
The first chromosome number report for *Capraria* was by Borgen (1980), as a mitotic count of $2n = \text{ca. } 60$ for *C. biflora*. Zhao (1996) reported meiotic counts for *C. biflora* and *C. frutescens* as $2n = \text{ca. } 28$ pairs. These two approximate counts suggest a base number of $x = 14$ or 15 . The latter numbers do not support a relation-



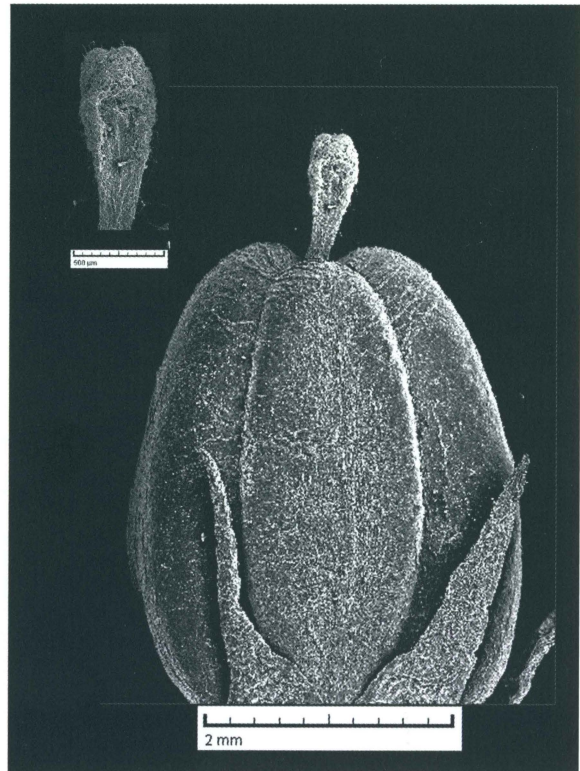
a.



b.



c.



d.

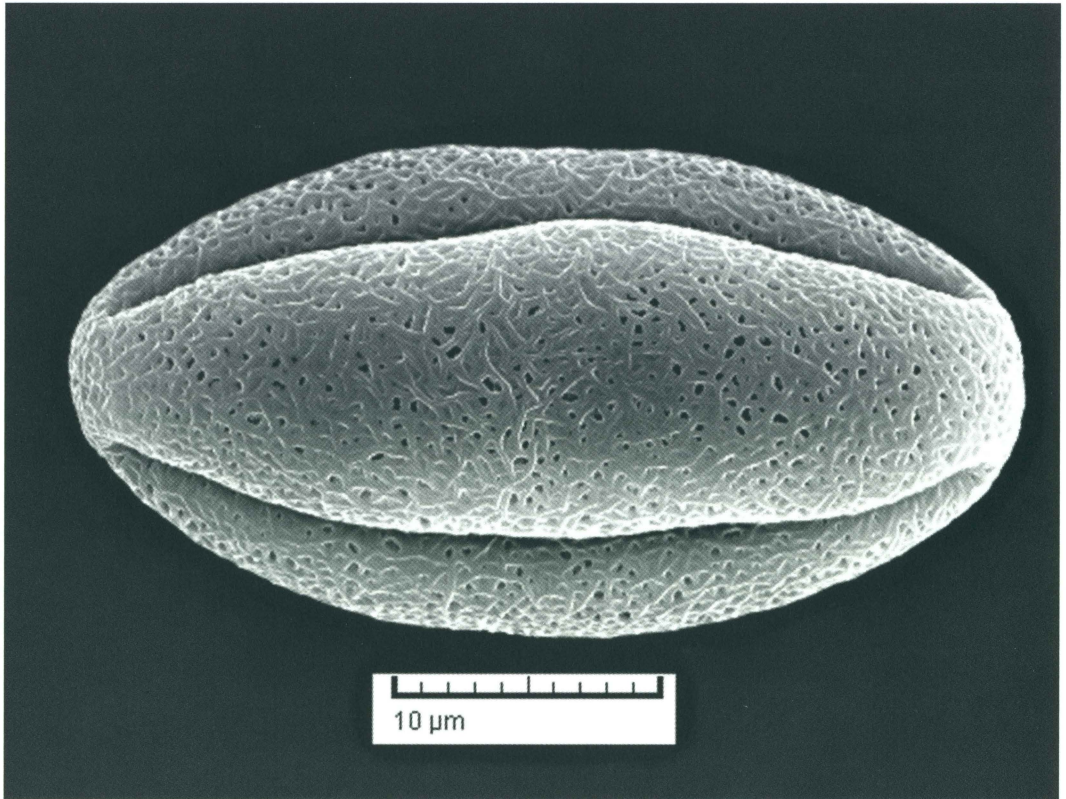


FIG. 3. Scanning electron micrographs of pollen of *Capraria mexicana* (Williams, Plum & Goldman 96-3, SHST). Photo taken at 4.02 kx and 20 kV. Photos by W. Patrick Spencer.

ship of *Capraria* to the Myoporaceae ($x = 27$, Watson and Dallwitz, 1992 and onwards) nor to the genus *Leucophyllum* ($x = 17$; Read and Simpson 1989), as suggested by Olmstead (2004). The genus *Gratiola* has a reported base number of $x = 14$ (Kapoor et al., 1987), thus Zhao's (1996) count of $2n = \text{ca. } 28$ for *Capraria* supports a possible relationship to *Gratiola* as proposed by Thieret (1967).

SYSTEMATIC TREATMENT

CAPRARIA L., Sp. Pl. 628. 1753. TYPE SPECIES: *Capraria biflora* L. *Xuarezia* Ruíz & Pav., Prod. 24. 1794. TYPE SPECIES: *Xuarezia biflora* Ruíz & Pav. *Pogostoma* Schrad., Ind. Sem. Hort. Gott. 1831. TYPE SPECIES: *Capraria saxifragifolia* Cham. & Schltldl.

←

FIG. 2. Scanning electron micrographs of the pistil of *Capraria* (insets on the upper left are enlarged photos of the stigma). a. *C. frutescens* (Williams & Siedo 99, SHST). b. *C. biflora* (Contreras 87, TEX). c. *C. mexicana* (Williams, Plum & Goldman 96-3, SHST). d. *C. peruviana* (Leiva & Sagastegui 1991, TEX). Large photos taken at 32 \times and 20 kV; insets taken at 100 \times and 20 kV. Photos by W. Patrick Spencer.



FIG. 4. *Capraria biflora* (Williams & Plum 95-48, SHST). a. Habit. b. Leaf. c. Sepals. d. Capsule. e. Corolla, side view. f. Corolla front view. Figure by Maria Thompson.

PERENNIAL suffrutescent herbs to 2 m high, erect, with one to several stems developing from the basal stem, monopodial or ramified, glabrous to densely glandular-

pubescent. LEAVES alternate, sessile; laminae spatulate or lanceolate; bases cuneate; margins serrate along the upper half with 8-10 teeth along each side at midstem; sur-

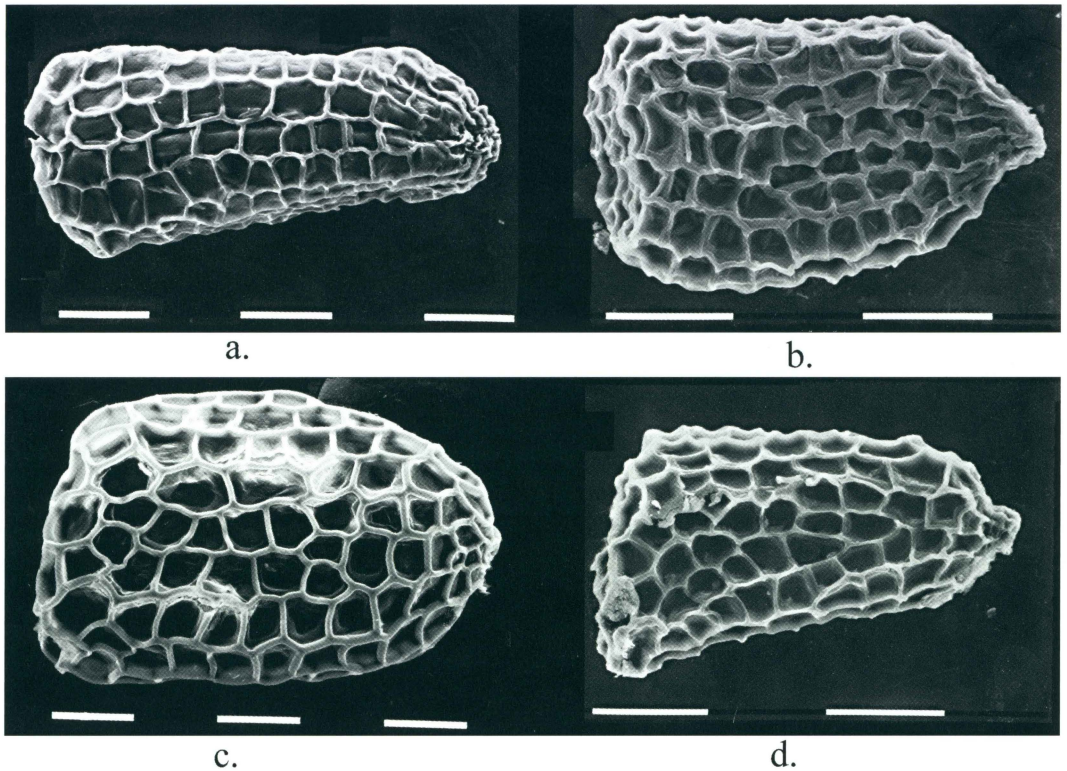


FIG. 5. Scanning electron micrographs of the seeds of *Capraria*. a. *C. biflora* (Contrera 87, TEX). b. *C. mexicana* (King 3879, TEX). c. *C. frutescens* (Hinton 12824, TEX). d. *C. peruviana* (Leiva & Sagastegui 1991, TEX). Scale equals 0.1 mm. Photos by the author.

face with punctate glands and numerous scattered internal secretory oil cavities, with 3 principal nerves arising from or near the base, glabrous or villous. INFLORESCENCE consisting of 2–5 pedicellate flowers in a leaf axil, with 5–20 flowering nodes per stem. PEDICELS 1–22 mm long, glabrous or glandular-pubescent; bracts absent. FLOWERS 4–5-merous, perfect, actinomorphic or zygomorphic. CALYX regular, lobes five, free to the base or nearly so, 3–6 mm long, linear-oblongate to linear-lanceolate, glabrous, villous, or glandular-pubescent. COROLLA white, rotate or bilabiate, tubular-funnelform, glabrous externally. COROLLA TUBE wholly white or white above with purple spots along the ventral side within, glabrous internally or with trichomes along the ventral portion of throat. PETAL LOBES spreading, narrowly triangular or ovate and

apically acute. STAMENS 4 or 5, didynamous or isomerous, included or exerted, alternate or opposite the corolla lobes; filaments glabrous. ANTHERS creamy white, introse, dorsifixed, bithecal, 3 locular with the basal portions of the thecae divaricate, inner locules shorter (0.4–0.7 mm long) with the outer locule longer (0.8–1.4 mm) and confluent across the anther tip. STYLE straight, included or exerted, glabrous or pubescent. STIGMA ellipsoid or reniform. OVARY superior, bilocular, ovoid, glabrous or apically glandular-pubescent; ovules numerous, axially arranged, 4–6 mm long, 3–4 mm wide. FRUIT a glabrous capsule, elliptical, glandular-punctate, loculicidally dehiscent, the placenta and calyx persisting. SEEDS numerous, minute, brown, with outer tangential walls forming a scalariform-reticulate surface of square cells.

The genus contains four species distributed throughout the neotropics, occurring mostly along beaches and moist seepage ar-

reas. Because of its medicinal use, *Capraria biflora* has been propagated in China and Africa.

KEY TO SPECIES

1. Plants hirsute, pilose or glabrous throughout; leaf blades mostly (2-)3-4(-6) times as long as wide; corollas zygomorphic, tubular-campanulate, the tubes 4-7 mm long, villous and with purple markings ventrally within; stamens 4(5), included to occasionally slightly exerted, didynamous.
 2. Stems ramified; calyx lobes not glandular-pubescent, linear-lanceolate, widest well below the middle; pedicels mostly 5-25 mm long; stigmas linear 1. *C. biflora*
 2. Stems monopodial; calyx lobes glandular-pubescent, linear-ob lanceolate, widest at or above the middle; pedicels mostly 1-4 mm long; stigmas reniform 2. *C. frutescens*
1. Plants glabrous throughout; leaf blades mostly 4-6 times as long as wide; corollas actinomorphic, rotate, the tubes 1-2 (-3) mm long, without hairs or colored markings within; stamens 5, exerted, isomerous.
 3. Mature styles 3-5 mm long; corollas 8-10 mm long; Mexico and Belize 3. *C. mexicana*
 3. Mature styles 0.75-1.50 mm long; corollas 5-6 mm long; South America and the Galápagos Islands 4. *C. peruviana*

1. *CAPRARIA BIFLORA* L., Sp. Pl. 875. 1753. TYPE: SWEDEN. Cultivated, Uppsala, (LECTOTYPE: LINN 785.1!; photo-LINN at FI. Howard (1989) reported the type of *C. biflora* as LINN 912348.50. That is actually a specimen of *C. frutescens* collected by Houston and is without location. The correct type of *C. biflora* is LINN 785.1 as selected by D'Arcy (1979)).

Capraria lanceolata Vahl [non. L. f.], Eclog. Amer. 2: 47. 1798. *Capraria semiserrata* Willd., Sp. Pl. 3:324. 1800. TYPE: COLOMBIA. St. Martha, s.d., *Rohr 20* (HOLOTYPE: C n.v.; photo-C at FI, US!). (Willdenow recognized *C. lanceolata* Vahl as a homonym of the earlier *C. lanceolata* L. f. [= *Freylinia lanceolata* (L. f.) G. Don] and renamed it *Capraria semiserrata* Willd.)

Capraria semiserrata Willd. var. *berterii* A. DC. in DC., Prodr. 10: 429. 1846. TYPE: COLOMBIA. St. Martha, 1829, *Bertero s.n.* (HOLOTYPE: G-DC!; photo-G-DC at FI, NY!, US!).

Capraria biflora L. var. *pilosa* Griseb., Fl. Brit. W. I. 427. 1861. TYPE: none designated.

Capraria biflora L. forma *hirsuta* Loes., Bull. Herb. Boissier, Ser. 2, 3: 284. 1903. TYPE:

GUATEMALA. Dept. Chiguimula, San Juan, 7 Jan 1897, *Seler 3314* (HOLOTYPE: B; ISOTYPES: NY!, US!).

Capraria biflora L. subsp. *havanensis* Tzvel-ev, Bot. Zh. (Leningrad) 72: 1663. 1986. TYPE: CUBA. Valle Bacuranao, near Havana, 8 Feb 1984, *Tzvelev 511* (HOLOTYPE: LE).

SUBSHRUBS or suffruticose perennial herbs, stiffly erect to somewhat sprawling, 40-200 cm tall, with several ramified stems emerging from the root stock. STEMS mostly hirsute, occasionally nearly glabrous but always with a few hairs on the emergent part of young branches, 3-5 mm in diameter at midstem. LEAVES spatulate to lanceolate, mostly 3.5-8.0 cm long, 0.5-3.0 cm wide, glabrous to moderately hirsute. PEDICELS 5-22 mm long, glabrous or glandular-pubescent. FLOWERS 5-merous, perfect, zygomorphic to slightly regular, 10-13 mm long. CALYX lobes 4-6(-7) mm long, lanceolate, glabrous to pubescent. COROLLA white, bilabiate, tubular-funnelform. COROLLA TUBE white above with purple spots ventrally within, with villous trichomes along the ventral portion of throat, 4-8 mm long. PETAL LOBES spreading, ovate, apically acute, the tips rolling back after an-

thesis; anterior lobes 3, 3–5 mm long, 1.8–2.2 mm wide; posterior lobes 2, 3–5 mm long, 1.8–2.2 mm wide. STAMENS 4 or 5, didynamous, posterior pair exerted about 0.5–0.8 mm past the tube, opposite with the corolla lobes; filaments glabrous. STYLE included, glabrous to sparsely pilose, 3–5 mm long. STIGMA ellipsoid. OVARY glabrous. SEEDS ca. 0.50 mm long, 0.35 mm wide,

COMMON NAME: Claudiosa (Spanish, *Balick 2304*), Tan-chi (Mayan, *Balick 2116*), Pasmowaxi-uil (Mayan, *Balick 1768*), sabadil (Huave, *D. Zizumbo 63*); Goatweed, Té del País, Hierba Té, Cola de Gallo (D'Arcy, 1979); and many others listed in Sprague (1921).

CHROMOSOME NUMBERS: $2n = \text{ca. } 28$ (Zhao, 1996); $2n = \text{ca. } 60$ (Borgen, 1980).

PHENOLOGY: Flowering August through February with a few specimens flowering in March. Producing mature fruits December through August.

DISTRIBUTION (Fig. 6): Southeastern U.S.A. (Florida), Caribbean Islands, Mexico, Central America, Galápagos Islands and South America east of the Andes; sea level to 1250 m. Sanders et al. (1996) reported *C. biflora* as far north as Sonora, Mexico (*Van Devender 95-90*, ARIZ, UCR). Sprague (1921) reported the species from Texas, but to date I have not found additional citations or specimens to verify this account.

ECONOMIC USES: Label data on *Stergios 7773* reports that the plant is used to control hypertension; *Fishlock 270*, used as a tea; *M. Balick 2116*, used for constipation (leaves), kidney stones, and blocked urine flow, when used in conjunction with other species; *M. Balick 2304*, antipyretic (the whole plant, heated in fire and rubbed over body); *M. Balick 1768*, used for bath for feverish infants.

ILLUSTRATIONS: Photo of flower (Fig. 1c); illustration of flower and habit (Fig. 4).

REPRESENTATIVE SPECIMENS: U.S.A. FLORIDA. Collier Co.: 7 mi SE of Naples, road to Briggs Nature Center and Rookery Bay Aquatic Preserve, 23 Nov

1987, *Alcorn 451* (FLAS). Dade Co.: County Sanitary fill, across canal from Coco Palm Drive, ca. 1 mi E of Florida Turnpike, 20 Dec 1980, *Correll 51435* (NY). Lee Co.: Captive Island, 1 Jan 1972, *Brumbach 7790* (FLAS). Monroe Co.: Park Key, S of Park Channel, mile marker 18.1 of Rte. 1, 13 Mar 1984, *Hill 13415* (NY).

MEXICO. CAMPECHE. Mpio. Champotón, beach at Hotel Siho Playa, ca. 38 km S of Campeche on Hwy. 180 (90° 43'W, 19° 35' N), 9 Mar 1990, *Sanders 9564* (TEX); Tuxpefia, 4 Nov 1931, *Lundell 898* (LL, US). CHIAPAS. Mpio. Chiapa de Corozo, Chorreadero de Tuxtla, 5.6 mi E of Chiapa de Corozo along Hwy. 190, 20 Feb 1965, *Breedlove 9098* (LL); Mpio. Ocozocoautla de Espinosa, La Cima, 15 km WNW of Ocozocoautla, 15 Oct 1972, *Breedlove 28999* (NY); Villa Flores, adelante de Monte Cristo, 71.3 km E del entronque Nac 196/Chis 195 sobre Chiapas 195 hacia Suchiapa y 0.8 km S de El Cielito, 790 m, 24 Dec 1984, *Cowan 5016* (TEX); Nuevo Amatenango, 1300 m, 17 Jul 1941, *Matuda 4734* (LL, NY); Mpio. Venustiano Carranza, slope above Finca Carmen, along road from Acala to Pugilitik, 3 Oct 1967, *Ton 2979* (NY). GUERRERO. Dist. Coyuca, Pungarabato, 14 Jan 1934, *Hinton 5474* (NY, US). MEXICO. Dist. Temascaltepec, Naranjo, 4 Oct 1932, *Hinton 1979* (NY, US). NAYARIT. Tres Marias Islands, María Madre, 25 Oct 1925, *Ferris 5731* (US). OAXACA. Tehuantepec, Rincón Moreno, 19 Jan 1971, *MacDougall s.n.* (NY); Puerto Angel, 18 Jul 1910, *Orcutt 5009* (NY). PUEBLA. around San Gabriel Chilac near San Juan Atzingo and San Andrés, 24 Jul 1961, *Smith 4038* (US). QUINTANA ROO. 5 km S of Playa del Carmen, 2 Mar 1985, *Cowan 5078* (TEX); 3 km SSW of Tulum ruins, 7 Jan 1973, *Taylor 12616* (NY, US). SINALOA. Dept. Badiraguato, Tierra Blanca, 4 Mar 1940, *Gentry 5805* (NY); near San Blas, 22 Mar 1910, *Rose 13218* (NY, US); Villa Unión, Dec 1921, *Ortega 4372* (US). SONORA. On riverbank, El Paso on the Río Cuchijaqui (26° 40' 35"N, 108° 49' 30"W), 150 m, 25 Feb 1995, *Van Devender 95-90* (ARIZ). TABASCO. Mpio. Paraíso, road from Nicolás Bravo to Mecoacán, km 15.2, 21 km from road Paraíso-Comcalco, 9 Sep 1980, *Cowan 3188* (NY); Mpio. Nacajuca, Masatepea N of Nacajuca, 17 Jan 1979, *Cowan 1883* (NY). VERACRUZ. 21 mi S of Veracruz, 29 Dec 1970, *Taylor 7391* (NY); Mpio. Chacaltianguis, N side of Río Papaloapan on W side of Benito Juárez and 12 km SW of Cosamalopan (18° 16'N, 95° 54'W), 2 Feb 1984, *Nee 29256* (NY); ca. 5 miles E of Naranjos on dirt road to Tamiahua, 15 Aug 1995, *Williams & Plum 95-48* (SHST, TEX). YUCATÁN. Mpio. Celestún, entrance to Puerto de Celestún, 3 May 1983, *Chan 2240* (TEX); 15 km NW of Humucma, along road Mérida-Sisal, 20 Jul 1985, *Cabrera 9083* (NY); Progreso, along railroad through cleared flat, July 1938, *Lundell 7976* (LL, US).

BELIZE. Dist. Cayo, ca. 15 km SW of San Ig-

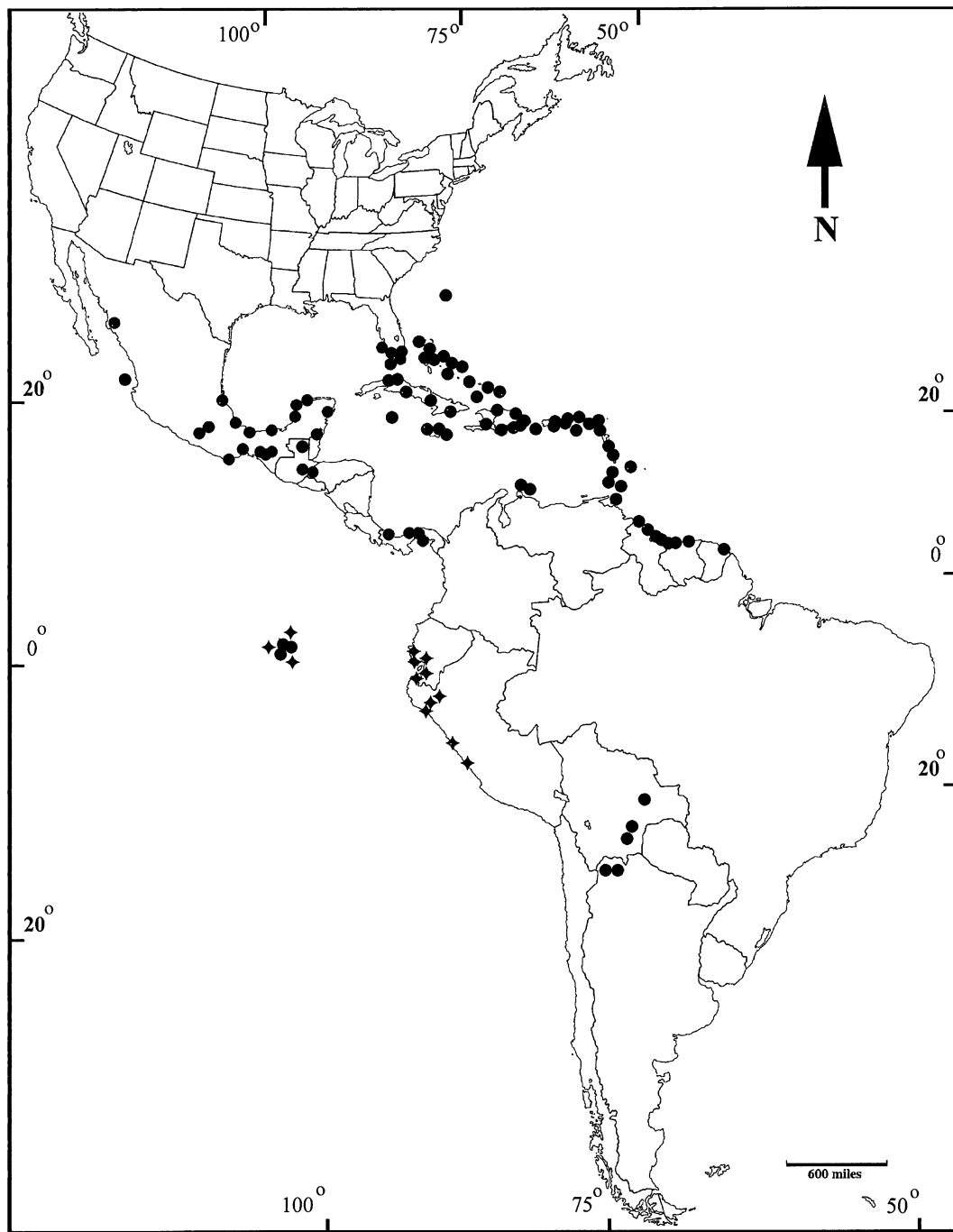


FIG. 6. Distribution of *Capraria biflora* (circles) and *C. peruviana* (diamonds). Note: *C. biflora* and *C. peruviana* are sympatric in the Galápagos Islands.

nacio, near San Antonio (17° 05'N, 89° 00'W), 11 Nov 1987, *Balick 1768* (US); Toll bridge area at New River, 3 mi S of Orange Walk, 25 Jan 1974, *Dwyer 12177* (NY, US); Branch Mouth N of Cayo, 19 Feb 1931, *Bartlett 11944* (NY).

COSTA RICA. Río Higuieron near Taboga (10° 20'N, 85° 12'W), 30 Jun 1977, *Liesner 2764* (NY).

EL SALVADOR. Dept. San Miguel, S side of Lake Olomega (13° 17'N, 88° 04'W), 27 Jan 1942, *Tucker 840* (US); Dept. Sonsonate, Acajutla, 20 Mar 1922, *Standley 21922* (NY, US); Comasagua, Dec 1922, *Calderón 1377* (NY);

GUATEMALA. Dept. El Peten, Tikal Nat. Park, near airfield, 16 Jul 1959, *Lundell 16474* (LL); Tikal, on airfield, 20 Aug 1959, *Contreras 87* (LL, US); Dept. Zacapa, Gualan, 28 Dec 1905, *Kellerman 5734* (LL, US).

HONDURAS. Dept. Copán, matorrales húmedos de Río Copan, cerca de Copan Ruinas, 650 m, 17 Apr 1956, *Molina 6597* (LL); San Pedro Sula, 16 Apr 1984, *Cristoff 190* (NY).

NICARAGUA. Dept. Carazo, S boarder of dept. near boarder of Dept. Rivas (11° 30'N, 86° 10'W), 10 Sep 1982, *Grijalva 1027* (NY); Dept. Chinandega, Ameya, 19 Jun 1923, *Maxon 7118* (US); Calabazas, Rte 1, S of Dario, 25 Dec 1969, *Seymour 2598* (NY); Prov. León, near León, 20 Dec 1975, *D'Arcy 10431* (NY); along shore of Lake Managua, 24 Jun 1923, *Maxon 7255* (US).

PANAMA. Fort Sherman, Torro Point, 28 Feb 1976, *Fosberg 56088* (NY, US); Panamá City, 12 Jun 1923, *Maxon 6951* (NY, US); Bocas del Toro, 6 Feb 1921, *Carleton 150* (NY, US); Isla Taboga, 23 Jul 1938, *Woodson 1492* (NY); Gaeleta Island, 10 Jun 1954, *Ritchie s.n.* (NY); Isla Colón, 19 Nov 1941, *Wedel 2977* (NY); San José Island (8° 15'N, 79° 08'W), 16 Sep 1945, *Harlow 60* (US).

WEST INDIES AND THE CARIBBEAN. ANGUILLA. Road Bay, 9 Jan 1959, *Proctor 18697* (NY, US). **ANTIGUA.** Royals, 11 Sep 1937, *Box 1051* (US).

ARUBA. near Noord, 17 Jan 1953, *Stoffers 1572* (NY).

BAHAMAS. San Salvador, Dec 1973, *Catino 14* (FLAS); Farmer's Hill, Great Exuma, 14 Aug 1975, *Eldridge s.n.* (FLAS, US); Caicos Island, 29 Aug 1974, *Correll 43274* (NY); Icacos Island, 7 Aug 1968, *Woodbury I-67* (NY); Nassau, 8 Jan 1890, *Northop 27* (NY); Andros Island, Nicols Town, 26 Mar 1890, *Northop 381* (NY); Grand Bahama, Pine Ridge, NE of Freeport, 5 Nov 1973, *Correll 40537* (NY); Berry Islands, Great Harbour Cay, 16 Oct 1974, *Correll 43683* (NY); Watling's Island, 27 Nov 1907, *Wilson 7290* (NY); Eleuthera, 21 Feb 1907, *Britton 5581* (NY); Acklin's Island, 21 Dec 1905, *Brace 4318* (NY); Cat Island, near Port Howe, 22 Nov 1975, *Correll 46206* (NY); Long Island, Clarence, 19 Jun 1974, *Hill 2216* (NY); Providence, N side of Island, 3 Sep 1952, *von Reis 249* (NY); Andros Island, 13 Mar 1966, *Dawson 26850* (US). **BARBADOS.** Parish Saint James, 31 Jan

1969, *Andrews 643* (NY). **BERMUDA.** Saint Davis Island, 10 Feb 1908, *Brown 603* (NY, US). **CUBA.** Prov. Camaguey, Camaguey, 15 Mar 1909, *Shafer 792* (NY, US); Prov. Havana, Río Almendares to Playa de Marianao, 22 Dec 1910, *Wilson 9459* (NY); Prov. Matanzas, near San Miguel, 2 Sep 1903, *Britton 218* (NY); Prov. Oriente, Sabana to Maisi, 13 Dec 1910, *Shafer 7889* (NY); Prov. Pinar del Río, Vedado, Habana, Sierra del Jíbaro, 20 May 1955, *Alain 4295* (NY); Prov. Santa Clara, near Soledad, bank of Río Caonao, Jun 1941, *Howard 5122* (NY). **CURAÇAO.** Near Willemstad, 19 Feb 1917, *Curran 78* (NY); Tanchi, 19 Apr 1952, *Arnoldo 2054* (US). **DOMINICAN REPUBLIC.** Prov. Barahona, Río Baoruco, 6 Nov 1979, *Smith 10026* (NY); Prov. Distrito Nacional, La Caleta, 20 m E of Santo Domingo, 25 Sep 1970, *Liogier 17500* (NY); Prov. La Altagracia, 2 km E of Playa de Macaoon, road to Punta Cana Club (18° 45'N, 68° 30'W), 25 Jul 1981, *Watson 1118* (FLAS); Prov. La Romana, Llano Costero, Isla Catalina (18° 22'N, 69° 02'W), 17 Dec 1986, *Zanoni 37229* (FLAS, NY); Prov. Monte Christi, 8 km N of Villa Elisa (19° 44'N, 71° 15.5'W), 21 Aug 1985, *Pimentel 532* (NY); Prov. Peravia, Palmar de Ocoa (18° 18'N, 70° 35'W), 7 Aug 1980, *Zanoni 7769* (NY); Prov. San Pedro de Macpris, Guayacanes, 19 Mar 1965, *Lavastre 1912* (NY); Prov. Puerto Plata, 35 km E of jct with Puerto Plata and Santiago road, 25 Apr 1970, *Burch 2404* (NY). **GRAND CAYMEN.** Center of Island, 14 Feb 1899, *Armour 1364* (NY). **GRENADA.** Parish Saint Patrick, Levera Beach, 20 Jan 1951, *Hunnell 19499* (NY). **HAITI.** Port-au Prince near Mariani, 20 Nov 1927, *Ekman 9344* (LL, US); near Fond Parisien, Etang Saumatre, 5 May 1920, *Leonard 4146* (NY, US); near La Vallée, Tortue Island, 28 Dec 1928, *Leonard 11731* (NY, US). **JAMAICA.** Parish St. Thomas, road from Golden Grove to Morant Point, 56 mi E of Golden Grove, 19 Aug 1965, *Hespenheide 1354* (LL); Saint Ann's Bay, 27 Mar 1908, *Britton 2527* (NY); between Portlan Point and Rocky Point, 5 Mar 1908, *Britton 1932* (NY); Kingston to Port Morant, 28 Feb 1909, *Britton 3902* (NY); Parish Saint Catherine, Port Henderson, 19 Nov 1957, *Yuncker 17475* (NY). **MARTINIQUE.** near Usine Caritan, 24 Jul 1939, *Egler 39-147* (NY). **MONTSERRAT.** N of Plymouth, 21 Jan 1907, *Shafer 88* (NY). **PUERTO RICO.** Mona Island, 20 Dec 1913, *Sterene 6350* (NY); Ponce, 23 Dec 1902, *Heller s.n.* (NY); Caguas, 7 Jan 1899, *Armour 217* (NY); Punta Vacía Talega, 10 Jan 1980, *Liogier 30173* (NY); Isla de Mona, Playa de Sardinera, E side, 27 May 1991, *Acevedo 4287* (NY, US); N of Guayama, 10 Feb 1986, *Taylor 6792* (NY); Mpio. Toa Boja, Sabana Seca, 27 Dec 1984, *Montalvo s.n.* (NY); Vieques Island, near Isabel Segunda, 24 Jan 1914, *Shafer 2433* (NY, US). **SAINT CROIX.** W of Tague Bay, 18 Jul 1970, *D'Arcy 4680* (US); Sandy Point, 28 Feb 1993, *Acevedo 5296* (US). **SAINT KITTS.** Canada Estate, 8 Sep 1901, *Britton 751* (NY). **SAINT VINCENT.** Par-

ish Saint George, Calli-aqua Bay, 12 Jan 1962, *Cooley 8141* (NY). **TABAGO.** Saint Patrick Parish, Bon Accord Lagoon near Pigeon Point, 7 Jan 1989, *Worthington 17695* (NY). **TRINIDAD.** Port of Spain, Jun–Aug 1939, *Almandoz 1* (NY). **TURKS ISLANDS.** Grand Turk, 27 Aug 1905, *Nash 3827* (NY). **VIRGIN ISLANDS.** Tortola, 15 Nov 1965, *D'Arcy 327D* (FLAS); Virgin Gorda, 14 Jan 1919, *Fishlock 270* (NY); Water Island, 8 Nov 1969, *Woodbury WI-26* (NY).

ARGENTINA. Prov. Buenos Aires, Bolívar, 31 Jan 1945, *Perdero 119* (NY); Prov. Cordillera, Santa Cruz, Cabeza, 22 Jan 1945, *Perdero 44* (NY); Prov. Jujuy, Dept. Santa Bárbara, Jinalito, 10 Apr 1945, *Meyer 8512* (NY); Prov. Salta, Dept. Orán, Río Bermejo, 16 May 1945, *Pierotti 1383* (NY).

BOLIVIA. Dept. Santa Cruz, Prov. Andrés Ibáñez, Puerto Pailas (17° 40' S, 62° 47' W), 11 Jul 1991, *Nee 41641* (NY); Dept. Santa Cruz, Prov. Cordillera, Ovai, 6 km NW of Charagua (19° 49.5' S, 63° 14' W), *Quevedo 70* (NY).

BRAZIL. Estado Bahiá, by the Río Cariacã, SW of Monte Santo, 21 Feb 1974, *Harley 16445* (NY, US); Estado Coará, Forrtaleanm 11 Dec 1955, *Duke 2502* (NY); Estado Maranhão, Aleantara, 10 Apr 1954, *Frões 50720* (NY); Estado Paraíba, em regíoes secas, Aug 1959, *Smith 2122* (NY); Estado Portuguesa, Guanare, 31 Dec 1984, *Stergios 7773* (NY); Estado Zulia, km 440 road from Machiques to La Fría, 24 Jul 1976, *Stergios 574* (NY); Mpio. Itiuba, Bahiá (10° 43' S, 39° 50' W), 26 May 1983, *Bautista 765* (NY); Maranhão, Dec 1959, *Carvalho 2* (NY); Saint Paul, Sep 1892, *Glaziou 19734* (NY);

COLOMBIA. Dept. Antioquia, Vuelta de Acuña, Río Magdalena, 14 Jan 1918, *Pennell 3789* (NY, US); Dept. Atlántico, bear Barranquilla, 18 Mar 1961, *Dugand 5625* (NY); Dept. Bolívar, Sincé, 20 Apr 1963, *Romero-Castañeda 9680* (NY); Dept. Bolívar, Mpio. Cartagena, 18 km SW of crossing of Canal Dique at Pasacaballos, Isla Barú (10° 08' N, 75° 42' W), 6 Aug 1985, *Zarucchi 3963* (NY, US); Dept. Cundinamarca, Quebrada Cabaña, Hacienda El Cucharó, between Tocaima and Pubenza, 8 May 1944, *Killip 38366* (US); Dept. Huila, Río Cabrera, 2 km below confluence of Río Ambicá, 3 km WSW of Colombia (3° 22' N, 74° 50' W), 15 Dec 1942, *Fosberg 19316* (NY, US); Dept. La Guajira, 1 km W of Puerto Estrella, 4 Apr 1962, *Saravia 431* (US); Dept. Magdalena, Isla de Salamanca, 20 km along the road from Ciénaga to Boquilla, 10 Dec 1966, *Romero-Castañeda 10500* (NY); Dept. Magdalena, Isla de Santa Marta, 1 Apr 1918, *Pennell 4771* (NY, US).

ECUADOR. Prov. Galápagos, Indefatigable Island, 16 Feb 1939, *Taylor 32* (NY); Prov. Galápagos, Santa Cruz Island, old trail to Bella Vista, 8 Feb 1964, *Fournier 161* (US); Chatham Island, Wreck Bay, Jan 1925, *Stewart 3424* (US).

FRENCH GUIANA. Cayenne, 21 Jul 1985, *de*

Granville 7282 (NY); Maripasoulas, 8 Apr 1990, *Fleury 860* (NY).

GUYANA. Dept. Demerara-Mahaica Region, Atlantic coastline facing leper colony at mouth of Mahaica river (6° 38' N, 57° 55' W), 2 Dec 1986, *Pipoly 9044* (NY, TEX, US); Queen's College, Georgetown, in grasses at edge of drainage trench, 10 May 1956, *Irwin R-97* (TEX); Mahaica-Berbice Region, Abary River mouth and along canals leading into river, between coastal hwy and ocean (6° 35' N, 57° 47' W), 28 Mar 1987, *Pipoly 11248* (NY, US); Pomeroun District, Moruka river, Jul 1927, *de La Cruz 4575* (NY, US); Waini river (8° 20' N, 59° 40' W), 3 Apr 1923, *De La Cruz 3810* (NY).

PERU. Dept. Loreto, San Salvador along the Amazon River, Jul 1929, *Williams 1564* (US); Dept. San Martín, Fundo San Isidro, 13 Feb 1976, *Sagástegui 8312* (NY).

SURINAM. Coronie, 22 Oct 1933, *Lanjouw 1090* (NY); 10 km SW of Paramaribo, 25 May 1961, *Hekking 823* (NY); Nickerie swamp, Schelpenrits Prodobong, 2 Feb 1943, *Geijskes s.n.* (NY); Zandery, 31 May 1916, *Samuels 263* (NY).

VENEZUELA. Estado Aragua, La Trinidad de Maracay, Jan 1913, *Pittier 5823* (NY, US); Estado Bolívar, Río Suapure, 5 Jun 1984, *López-Palacios 4369* (NY); Estado Falcón, Distrito Silva, Cayo Sal, NE of Chichiriviche (10° 58' N, 68° 15' W), 28 Aug 1974, *Steyermark 110325* (NY); Estado Sucre, Península de Araya, 20 km NW of Cariaco (10° 38' N, 63° 40' W), 17 May 1981, *Liesner 11933* (NY); Estado Zulia, near Perijá, 1918, *Tejera 114* (US); Prov., Trujillo, La Concepción, 23 Mar 1931, *Reed 1049* (US); road between Playa El Falucho and Playa El Americano, 5 km de el apostadero naval (11° 50' N, 65° 00' W), 30 May 1986, *Rivero 1052* (FLAS); Maracay, 1928, *Corvelius 286* (FLAS); Guarico, 14 km N of San Fernando de Apure along main hwy to Calaboz, 10 Nov 1973, *Davidse 3952* (NY); road between San Felipe and Barquisiméto km 102, 26 Nov 1952, *Aristeguieta 1100* (NY); Dist. Federal, Mpio. Vargas, Parraquia Catia (10° 36' N, 67° 02' W), 12 Jun 1990, *Ramírez 2715* (NY); Península Paraguana, ca. 1.5 km from Pueblo Nuevo along road to Santa Ana, 19 Dec 1964, *Breteler 4353* (NY, US); Miranda, between Las Canales and El Encanto, Nov 1942, *Lasser 688* (US).

Capraria biflora is the most widespread species of *Capraria* and the only species distributed on both sides of the equator (Fig. 6). The species is readily distinguished by its ramified stems, spatulate leaves, pubescent hairs, lanceolate sepals, bilaterally symmetrical corollas with 4–5 stamens, and linear stigma.

One specimen from Oaxaca, Mexico

(Orcutt 5009) and several in Panama (Hayes 322, 745, and 876) are glabrous and have linear-lanceolate leaves that are only 4–6 mm wide, superficially resembling *Capraria mexicana* and *C. peruviana*, while the flowers are zygomorphic as in *C. biflora*. In addition, occasional specimens from Florida, the Caribbean islands and the Atlantic coast of both hemispheres have lanceolate leaves; these appear to be largely confined to areas that are at or near sea level. However, sporadic plants of a similar nature occur throughout the range of *C. biflora*, and consequently such plants do not appear to merit varietal status.

I follow Wiggins and Porter (1971) who noted that because plants that are subglabrate and densely pubescent intergrade, "it seems futile to recognize var. *pilosa* Griseb."

2. *CAPRARIA FRUTESCENS* (Mill.) Britton, J. Bot. 45: 315. 1907.

Erinus frutescens Mill., Gard. Dict. ed. 8. 1768. *Capraria cuneata* R. Br. in W. T. Aiton, Hortus Kew., ed. 2, 4: 45. 1812. TYPE: MEXICO. VERACRUZ: 1730, *Houston s.n.* (HOLOTYPE: BM!; photo-BM at NY!, US!)

Capraria hirsuta Kunth in H.B.K., Nov. Gen. Sp. 2: 355. 1817. TYPE: MEXICO. GUERRERO: "Crescit locis exustis inter La Venta del Exido et portum Acapulci," 200 m, 1802–1804, *Humboldt & Bonpland* 3892. (HOLOTYPE: P!; ISOTYPES: B; photo-B at F!, US!) Sprague (1921) treated *Capraria hirsuta* as a synonym of *C. biflora*. Examination of the type, however, indicates it to be a specimen of *C. frutescens*.)

Capraria saxifragifolia Cham. & Schltld., Linnaea 5: 105. 1830. *Pogostoma saxifragifolia* (Cham. & Schltld.) Schrad., Ind. Sem. Hort. Gotting. 1831. TYPE: MEXICO. VERACRUZ: Jul 1828, *Schiede s.n.* (HOLOTYPE: B; photo-B at F!, NY!, US!)

PERENNIAL herbs, stiffly erect to somewhat sprawling, 40–200 cm tall, with several

monopodial stems emerging from the root stock. STEMS pilose, 2–4 mm in diameter at midstem, the vestiture 1–2 mm long. LEAVES oblanceolate, mostly 4–8 mm long, 1.5–4.0 cm wide, moderately hirsute. PEDICELS 1–4 mm long, glandular-pubescent. FLOWERS zygomorphic, 6.5–8.5 mm long. CALYX lobes 3.0–4.5 mm long, linear-oblong, variously pubescent with glandular or eglandular hairs (these often intermixed), the apices acute. COROLLA white to pale lavender, bilabiate, tubular-funnelform. COROLLA TUBE white with purple spots ventrally within, with villous trichomes along the ventral portion of the throat, 4–7 mm long. PETAL LOBES spreading, ovate, apically acute, tips rolling back after anthesis; anterior lobes 3, 3.5–5.0 mm long, 1.8–2.2 mm wide; posterior lobes 2, 2.5–4.0 mm long, 1.8–2.2 mm wide. STAMENS 4, didynamous, included, opposite the corolla lobes; filaments 2.5–3.0 mm long, glabrous. STYLE included, glabrous to sparsely pilose, 3–5 mm long. STIGMA reniform. OVARY pubescent apically, the hairs extending up the style shaft near its base but not much beyond. SEEDS ca. 0.5 mm long, 0.35 mm wide,

COMMON NAME: Claudiosa (Yucatán; Sprague, 1921).

CHROMOSOME NUMBERS: $2n = \text{ca. } 28$ (Zhao, 1996).

PHENOLOGY: Flowering August through December with a few specimens flowering in January. Producing mature fruits December through September.

DISTRIBUTION (Fig. 7): Central Mexico southwards to Honduras, 0–1000 m.

ILLUSTRATION: Photo of flower (Fig. 1 a & b); illustration of flower and habit (Fig. 8).

REPRESENTATIVE SPECIMENS: MEXICO. CAMPECHE. near the caves of Xtacumbilxunam, 3 km W of Bolonchen de Rejón, 29 Sep 1985; *Cabrera* 9525 (MO). CHIAPAS. Mpio. Chiapa de Corzo, steeped walled canyon with tropical deciduous forest, above El Chorreadero, 800 m, 9 Jul, 1972, *Breedlove* 26004 (LL); Ocozocuatla, 16 km W of Ocozocuatla and 3.2 km from El Aguacero, 24 Dec

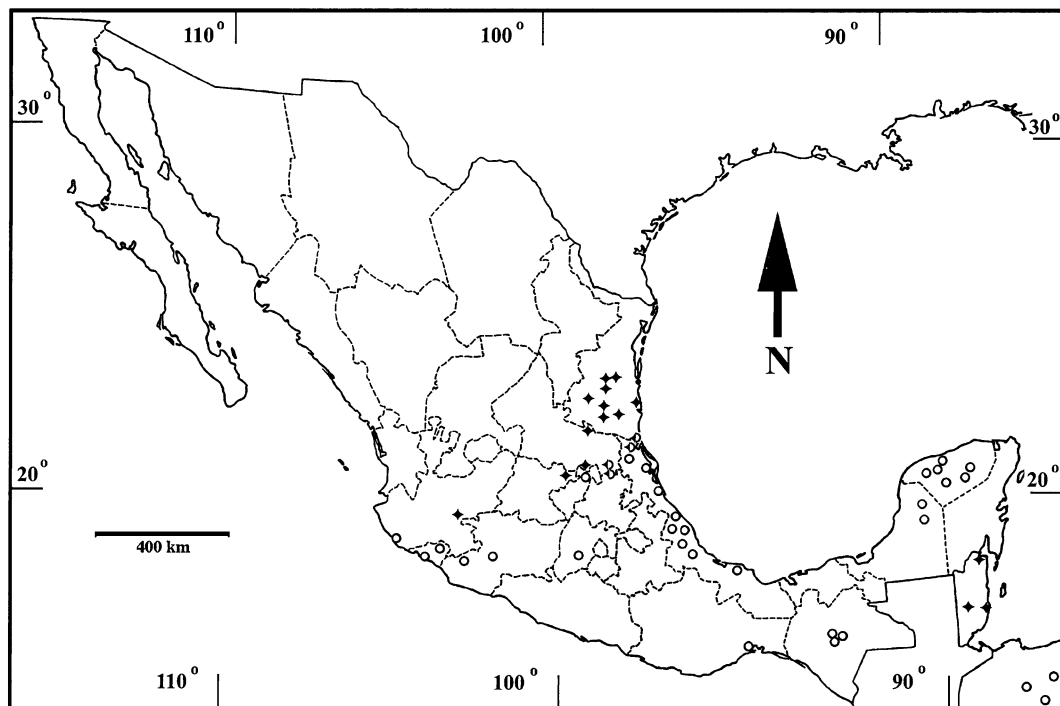


FIG. 7. Distribution of *Capraria frutescens* (open circles) and *C. mexicana* (diamonds).

1984, *Cowan 5020* (TEX); Mpio. Tuxtla Gutiérrez, S of Tuxtla Gutiérrez on Hwy. 195 (to Villaflores), 4.7 mi from jct. with bypass, on top of escarpment in roadside brush in rocky limestone soil, 860 m, 1 Nov 1980, *Fryxell & Lott 3265* (F, NY, TEX). **COLIMA.** Manzanillo, 1 Dec 1890, *Palmer 917* (NY, US); Colima, 20 Oct 1910, *Orcutt 4522* (F). **GUERRERO.** near Acapulco, Oct 1894, *Palmer 567* (US). **JALISCO.** Tuxpan, 4 Nov 1926, *Mexia 1041* (US); Chamela Biological Station, along main road about 50 m from the entrance to preserve headquarters (19° 30'N, 104° 50'W), 31 Dec 1996, *Williams, Siedo & Wood 99* (SHST). **MÉXICO.** Dist. Temascaltepec, Bejucos, 13 Feb 1933, *Hinton 3383* (F, NY). **MICHOACÁN.** Dist. Coalcomán, Coalcomán, 1000 m, Dec 28 1938, *Hinton 12824* (LL, NY). **OAXACA.** Tehuantepec, Potrero Villalobos, 20 Nov 1970, *Dougall s.n.* (NY). **QUERÉTARO.** Mpio. Jalpan, 7 km SE of Tancoyol, 800 m, 8 Nov 1986, *Fernández 3685* (NY, TEX). **SAN LUIS POTOSÍ.** Mpio. San Antonio, San Antonio, disturbed ground near abandoned house, 5 Sep 1978, *Alcorn 1559* (TEX); Tamazunchale, 28 Nov 1937, *Kenoyer 765* (F); Tamagundarb, 19 Jan 1947, *Aguirre & Reko 309* (NY). **SINALOA.** near Mazatlan, 31 Mar 1910, *Rose 13772* (US); Pueblo de las Trancas San Ignacio, 30 Oct 1917, *Montes 22* (US). **TAMAULIPAS.** near Tampico, 15 m, 1–31 Jan 1910, *Palmer 43* (F, NY). **VERACRUZ.** Mpio. Axocuapán, road Coetzalán-Cueva del Abono

(19° 18'N, 96° 42'W), 11 Jun 1983, *Robles 362* (NY); Mpio. Coatepec, 2 km antes de Jalcomulco, 30 Jul 1980, *Castillo & Tapia 1085* (F); ladera NE of Cerro Monte de Oro, 22 Jun 1972, *Dorantes et al. 920* (F); Mpio. Dos Rios, Cerro Gordo, 550 m, 14 Oct, 1970, *Ventura 2613* (F, NY); Mpio. Tantoyuca, Silosuchil, dooryard, 22 Dec 1978, *Alcorn 2296* (TEX); Mpio. Santiago Tuxtla, Acahual, 30 m, 29 Jul 1967, *Martínez-Calderón 1472* (F, LL, NY); Lagos Tamiahua, 25 mi S of Tampico, 3 Mar 1939, *LeSueur 378* (F, TEX, US); near Palma, 3 Sep 1935, *MacDaniels 456* (F); ca. 5 miles E of Naranjos on dirt road to Tamiahua, 15 Aug 1995, *Williams & Plum 95-49* (SHST; TEX). **YUCATÁN.** Chichen Itzá, 27 Feb 1899, *Mills-paugh 1625* (F); in wet places near Sayil, 35 km SE of Oxkutzcab, 19 Jul 1985, *Cabrera 9006* (TEX); Mpio. Santa Elena, 0.55 km SW of entrance road to Kabah archeological site on Hwy. 261, between Holpelchen and Mérida (89° 40'W; 20° 15'N), 100 m, 11 Mar 1990, *Sanders 9628* (TEX); Chankon, 22 Jun 1929, *Bequaert 78* (F); near the caves of Balancanché, 32 km W of Valladolid, 29 Jun 1985, *Cabrera 8778* (MO).

HONDURAS. Dept. Comayagua, near Comayagua, 600 m, 12–23 Mar 1947, *Standley 5312* (F); Dept. El Paraíso, vicinity of Danlí, 700–800 m, 11–23 Feb 1949, *Standley 17042* (F); Dept. Olancho, near Juticalpa, 380–480 m, 5–16 Mar 1949, *Standley 17953* (F).

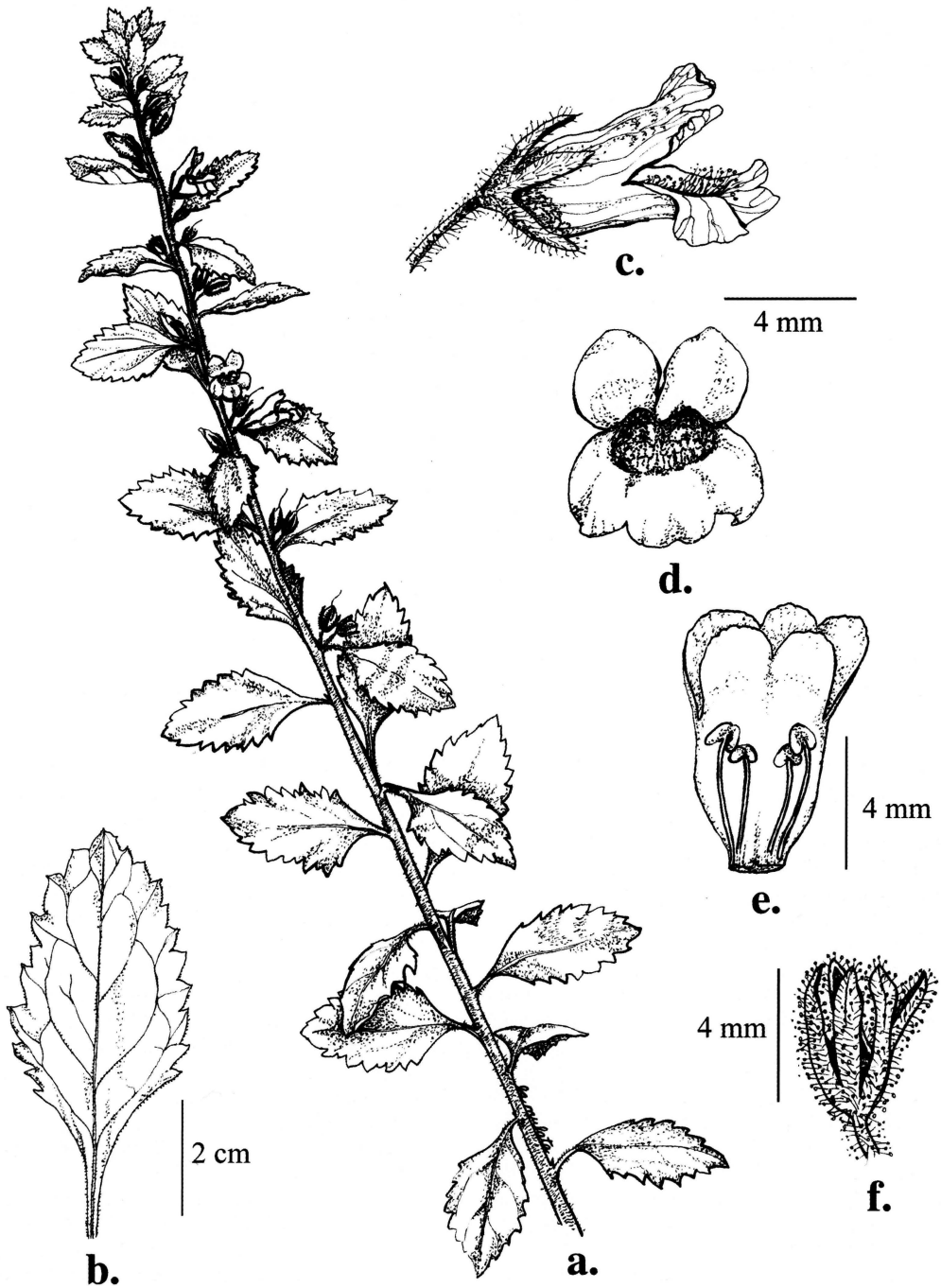


FIG. 8. *Capraria frutescens* (Williams & Siedo 99, SHST). a. Habit. b. Leaf. c. Corolla, side view. d. Corolla, front view. e. Corolla, top view. f. Sepals, note glandular hairs. Figure by Maria Thompson.

Capraria frutescens is a very distinct species. It is readily distinguished by its monopodial stems, glandular-pilose vestiture, oblong sepals, bilateral corolla and reniform stigma (Fig. 2a). Due to its distinctiveness, the species has been recognized as the monotypic genus *Pogostoma*. However, because of the suite of characters it shares with *C. biflora* (Table 2) and because it has alternate leaves with punctate glands (like the other species of *Capraria*) I retain it in *Capraria*.

3. CAPRARIA MEXICANA Moric. ex. Benth. in DC., Prodr 10: 429. 1846. TYPE: MEXICO. TAMAULIPAS: Tampico, s.d., *Berlandier s.n* (LECTOTYPE: K!, designated by Sprague (1921)).

SUBSHRUBS or suffruticose perennial herbs, stiffly erect to somewhat sprawling, 50–200 cm tall, with several ramified stems emerging from the root stock. STEMS glabrous, 2–4 mm in diameter at midstem. LEAVES lanceolate, mostly (3–) 4–10 (–11) cm long, 0.6–2.2 cm wide, glabrous. PEDICELS 5–12 mm long, glabrous. FLOWERS 5-merous, perfect, actinomorphic, 8–10 mm long, 8–10 mm broad when open. CALYX lobes 3–5 mm long, 0.8–1.2 mm wide, lanceolate, glabrous. COROLLA white, rotate. COROLLA TUBE light green to white, glabrous internally, 2–3 mm long. PETAL LOBES spreading, lanceolate, 4–7 mm long. STAMENS 5, isomerous, exerted about 0.8–1.0 mm past the corolla tube, alternate with the corolla lobes; filaments glabrous. STYLE exerted, glabrous, 3–5 mm long. STIGMA ellipsoid. OVARY glabrous. SEEDS ca. 0.35 mm long, 0.2 mm wide.

COMMON NAME: Tamaulipan Tea (Ideker, 1996).

CHROMOSOME NUMBERS: None reported.

PHENOLOGY: Flowering November through April. Producing mature fruits February through August.

DISTRIBUTION (Fig. 7): Northern Mex-

ico with disjunct populations south into Belize, mainly eastern Mexico with one population in south Texas (Ideker, 1996). Sea level to 650 m elevation.

ILLUSTRATION: Photo of flower (Fig. 1 d & e); illustration of flower and habit (Fig. 9).

REPRESENTATIVE SPECIMENS: MEXICO. GUANAJUATO. Mpio. San Luis de la Paz, paso Macuala del Realito, 8 Nov 1990, *Ventura 9003* (F). JALISCO. volcanic soil on mountain side near Lake Chapala, 12 Aug 1947, *Webster 7652* (F, TEX, US). QUERÉTARO. Mpio. Arroyo Seco, Puente Concá, 4 km SE of Concá, 18 Mar 1985, *Fernández 2777* (NY). SAN LUIS POTOSÍ. MPIO. TANQUIAN, BETWEEN TAMUIN PYRAMIDS AND SAGRADA FAMILIA, 29 MAY 1979, ALCORN 3107 (TEX); MPIO. SAN ANTONIO, TANJASNEC, 8 MAR 1979, ALCORN 2515 (TEX); ALONG ROAD BETWEEN RÍO VERDE AND SAN CIRO, 1000 M, 12 AUG 1954, RZEDOWSKI 4509 (F, TEX). TAMAULIPAS. Barra del Tordo, ca. 45 km east of Aldama, marshy area 1.5 mi inland from beach, 18 Mar 1996, *Williams, Plum & Goldman 96-03* (SHST); Juamave, 1931, *Rozynski 333* (F, NY, US); Rancho Calabazas, on the Río Sabinas, across from the village Azteca, 3 mi W of Rte. 85, at a point 20 m N of Ciudad Mante, 30 Mar 1975, *Harriman et al. 10831* (F); 30 mi S of Ciudad Victoria, 4 Apr 1947, *Smith & Barkley 17M191* (F, LL, MO); 14 mi E of Victoria jct on road to Casas, 4 Feb 1960, *Johnston 5020* (TEX); low shrub Oak forest 2 mi NE of Altamira, 3 Mar 1961, *King 4039* (F, NY, TEX, US); Las Adjuntas, 24 Jan 1970, *Gómez-Pompa 4721* (LL, MO); Mpio. Gomez Farias, NW of Gomez Farias in Sierra de Guatemala, on cretaceous limestone (23° 06' N, 99° 12' W), 17 Mar 1987, *Woodruff 157* (TEX); near Tampico, 27 Apr 1910, *Palmer 320* (F, NY); shores of Laguna Anda la Piedra, 2 Nov 1939, *LeSueur 585* (F, US). VERACRUZ. 6 km from Panuco toward Tampico (22° 07' N, 98° 09' W), 20 Mar 1971, *Chiang 418* (F, NY).

BELIZE. Dist. Corozal, between Sarteneja and Chunox (18° 17' N, 88° 15' W), 18 Mar 1987, *Davidse 32632* (MO); Stann Creek, 10 Jun 1932, *Schipp 945* (F, NY); El Cayo, Mar 1933, *Chanek 138* (F).

Capraria mexicana is readily distinguished by its glabrous condition, branching stems, and regular corollas with five isomerous stamens (Fig. 1d.).

One population of *Capraria mexicana* has been reported in Texas and the species has been listed as endangered by the Texas Organization for Endangered Species (Idek-

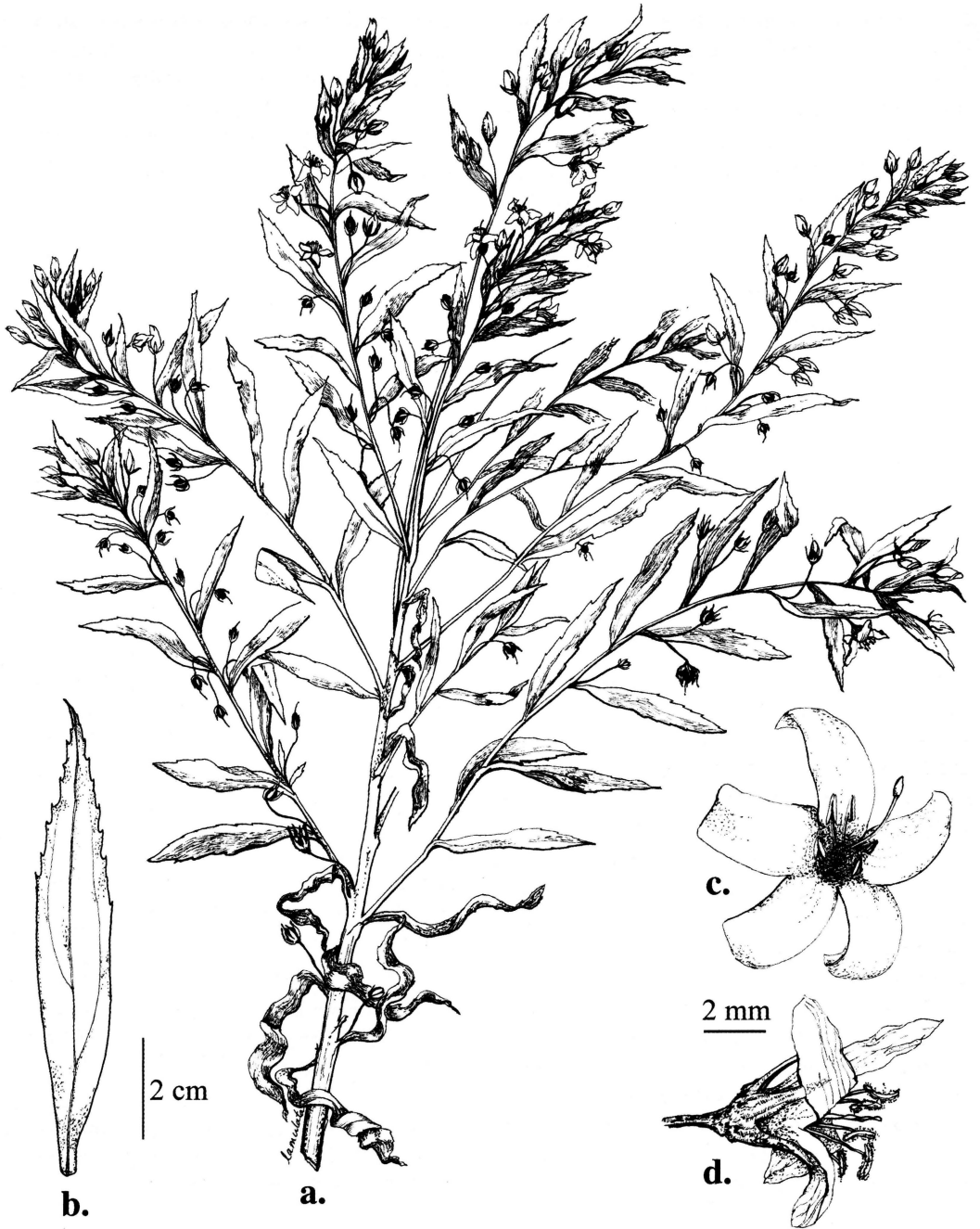


FIG. 9. *Capraria mexicana* (Williams, Plum & Goldman 96-3, SHST). a. Habit. b. Leaf. c. Corolla, front view. d. Corolla, side view. Figure by Maria Thompson.

er, 1996). Although Ideker reported the location of the population (Falcon Reservoir, Zapata Co., Texas), he did not cite a specimen.

4. *CAPRARIA PERUVIANA* Benth. in DC., Prodr. 10: 430. 1846. TYPE: **ECUADOR**. Guayaquil, s.d., *Hinds s.n.* (LECTOTYPE: K!, designated here. Of the paratypes listed by Bentham I could only locate *Hinds s.n.*, hence its selection as the lectotype.).

Xuaresia biflora Ruiz & Pav., Fl. Peruv. 2: 13. 1794. pl. 123. TYPE: **ECUADOR**. Prov. of Bolívar, Guaranda, 72 mi NE of Guayaquil, s.d., *Née s.n.* (LECTOTYPE: MA! spec. # 488144, designated here. Although the name *Xuaresia biflora* Ruiz & Pav. pre-dates *Capraria peruviana* by 52 years, its placement within *Capraria* would create an illegitimate homonym of the earliest name, *C. biflora* L.)

Witheringia salicifolia Hook. [non Salisb.], Bot. Misc. 2: 231. 1831. TYPE: **PERU**. Prov. Lurin, near Lima, s.d., *Cruckshanks s.n.* (HOLOTYPE: K! Although the name *Witheringia salicifolia* Hook. pre-dates *C. peruviana* by fifteen years, its placement within *Capraria* would be illegitimate as it would be a later homonym of *Capraria salicifolia* Salisb. [= *Freylinia lanceolata* G. Don].)

SUBSHRUBS or suffruticose perennial herbs, stiffly erect to somewhat sprawling, 50–200 cm tall, with several ramified stems emerging from the root stock. STEMS glabrous, 2–4 mm in diameter at midstem. LEAVES lanceolate, mostly (3–) 4–10 (–11) cm long, 0.6–2.2 cm wide, glabrous. PEDICELS 5–22 mm long, glabrous. FLOWERS 5-merous, perfect, actinomorphic, 5.0–6.0 mm long, 6–8 mm broad when open. CALYX lobes 3.0–4.0 mm long, 0.8–1.2 mm wide, lanceolate, glabrous. COROLLA white, rotate. COROLLA TUBE light green to white, glabrous internally, 0.8–1.5 mm long. PETAL LOBES spreading, lanceolate, 3–4.5 mm long. STAMENS 5, isomerous, exerted

about 0.8–1.0 mm past the corolla tube, alternate with the corolla lobes; filaments glabrous. STYLE included, glabrous, 0.75–1.50 mm long. STIGMA ellipsoid. OVARY glabrous. SEEDS ca. 0.35 mm long, 0.2 mm wide.

COMMON NAME: Té del Perú, Té de Lima (Sprague, 1921). Smooth capraria (McMullen, 1999).

CHROMOSOME NUMBERS: None reported.

PHENOLOGY: Flowering August through January. Producing mature fruits January through August.

DISTRIBUTION (Fig. 6): South America on the western side of the Andes (Peru and Ecuador) and the Galápagos Islands. Sprague (1921) and D'Arcy (1979) identified specimen *Hayes 375* as *C. peruviana* and consequently reported the taxon as growing in Panamá. Unfortunately, I was unable to locate *Hayes 375*. I have examined other *Capraria* collections by Hayes (322, 745, 876) from the same region of Panama and I note that these specimens are rather narrowed leafed, glabrous individuals of *C. biflora*, which superficially resemble *C. peruviana*.

ECONOMIC USES: Sprague (1921) reported that the leaves of this species are brewed as a tea in Peru.

ILLUSTRATIONS: A detailed line drawing is provided in Wiggins and Porter (1971) and McMullen (1999) has a beautiful color photo of the species.

REPRESENTATIVE SPECIMENS: **ECUADOR**. Prov. Chimborazo, Canyo of the Río Chanchan, from Naranjapata to below Huigra, 19 Jun 1945, *Camp E-3854* (NY, US); Prov. El Oro, Santa Rosa, 11 Mar 1955, *Asplund 15665* (LL, NY); Prov. Galápagos, Albejarle Island, Villamil, 27 Apr 1932, *Howell 8950* (US); Prov. Galapagos, Charles Island, Black Beach, 3 Apr 1930, *Svenson 177* (F); Prov. Galapagos, Santa Cruz Island, Academy Bay, 4 Mar 1960, *Léveque 118* (US); Prov. Guayas, Guayaquil, Jan 1938, *Mille 1064* (F); Prov. Esmeraldas, in and near Esmeraldas, 12 Sep 1974, *Hudson 738* (NY); Prov. Guayas, 4 km S of Punta Blanca (N of Santa Elena), gallery vegetation in desert (80° 49'W, 02° 10'S), 300 m, 22 May 1973,

Holm-Nielsen et al. 2459 (F, MO, NY); Prov. Manabí, 1.5–3 km W of Leonidas Plaza (00° 36' S, 80 27' W), 25–75 m, 16 Sep 1993, *Webster* 30652 (TEX).

PERU. Dept. Cajamarca, 30 km E of bridge over Río Maichil (79° 10' W, 06° 30' S), 1450 m, 9 Feb 1988, *Gentry* 61402 (F, MO); Prov. Casma, ca. 48 km N of Pativilca on Pan Am Hwy., coastal desert dunes, 10 m, 13 Oct 1984, *Dillon* 4011 (NY, TEX); Prov. Lambayeque, 12 km (via Pan Am Hwy) N of Olmos, 29 May 1978, *Barbour* 2117 (MO, NY); Prov. Santa Cruz, Lurin, 4 Jan 1925, *Pennell* 12209 (NY); Prov. Trujillo, Ladera, 26 Jun 1986, *Mostacero* 1105 (F, NY); Prov. Tumbes, Dept. Tumbes, La Cruz, 28 May 1992, *Sagástegui* 14611 (F, NY).

Except for the consistently smaller styles (1–2 mm long; Fig. 2d) and somewhat smaller greenish white corollas, this species is almost identical to *C. mexicana* (Table 2).

EXCLUDED NAMES

Below is a list of names in *Capraria* that are presently referable to other genera. The six *Capraria* names highlighted in bold are those not accounted for in Sprague's (1921) study.

- Capraria aegyptiaca* Steud. & Hochst. ex Endl., Nov. Strip. Dec. 23. 1839. = **Anticharis Arabica** (Steud. & Hochst. ex Endl.) Endl. (*vide* Sprague, 1921)
- Capraria annua* (Cham. et Schltld.) Kuntze, Rev. Gen. Pl. 2: 459. 1891. = **Scoparia annua** Cham. et Schltld. (*vide* Sprague, 1921)
- Capraria arabica* Steud. & Hochst. ex Endl., Iconogr. Gen. Pl. pl. 7. 1837. = **Anticharis arabica** (Steud. & Hochst. ex Endl.) Endl. (*vide* Sprague, 1921)
- Capraria calycina* A. Gray, Proc. Am. Acad. Arts. 6: 49. 1862. = **Myoporum debile** R. Br. (*vide* Sprague, 1921)
- Capraria crustacea* L., Mant. Pl. 87. 1767. = **Lindernia crustacea** (L.) F. Muell. (*vide* Howard, 1989)
- Capraria diffusa* Roxb., Hort. Bengal. 47. 1814. = **Ebermaiera thysoidea** Wall. (*vide* Sprague, 1921)
- Capraria dissecta* Delile, Descr. Egypte, Hist. Nat., 95. t. 32. fig. 3. 1812. = **Sutera glandulosa** Roth. (*vide* Sprague, 1921)
- Capraria dulcis* (L.) Kuntze, Rev. Gen. Pl. 2: 459. 1891. = **Scoparia dulcis** L. (*vide* Sprague, 1921)
- Capraria durantifolia* L., Syst. Nat., ed. 10. 1116. 1759. = **Stemodia durantifolia** (L.) Swartz (*vide* Turner & Cowan, 1993)
- Capraria elliptica* (Cham.) Kuntze, Rev. Gen. Pl. 2:

459. 1891. = **Scoparia elliptica** Cham. (*vide* Sprague, 1921)
- Capraria ericacea* (Cham. & Schltld.) Kuntze, Rev. Gen. Pl. 2: 459. 1891. = **Scoparia ericacea** Cham. & Schltld. (*vide* Sprague, 1921)
- Capraria gratioloides* L., Syst. Nat., ed. 10. 1117. 1759. = **Ilysanthes gratioloides** (L.) Benth. (*vide* Sprague, 1921)
- Capraria gratissima* Roxb., Hort. Bengal. 47. 1814. = **Limnophila roxburghii** G. Don. (*vide* Sprague, 1921)
- Capraria humifusa* Buch.-Ham. ex Wall., Cat. n. 3883. 1831. = **Centranthera humifusa** Wall. (*vide* Sprague, 1921)
- Capraria humilis* Solander in W. T. Aiton, Hortus Kew., ed. I. 2: 354. 1789. = **Stemodia verticillata** (Miller) Hassler (*vide* Turner & Cowan, 1993)
- Capraria integerrima* Miq., Linnaea, 22: 476. 1849. = **Sesamum indicum** L. (*vide* Sprague, 1921)
- Capraria integrifolia* Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles, 12: 20. 1845. TYPE: MEXICO. OAXACA. Oaxaca, 1840, *Galeotti* 653 (HOLOTYPE: BR!). = **Nama jamaicense** L. (In his treatment of *Capraria*, Sprague (1921) recognized this as a valid species of *Capraria*. Examination of the type material, however, reveals that this is, in fact, a species of *Nama*.)
- Capraria lanceolata* L. f., Suppl. Pl. 284. 1781. = **Freylinia lanceolata** (L. f.) G. Don. (*vide* Sprague, 1921)
- Capraria longiflora* Thunb., Mus. Nat. Acad. Upsal. 17: 150. 1794. = **Freylinia undulata** (L. f.) Benth. (*vide* Sprague, 1921)
- Capraria lucida* W. T. Aiton, Hortus Kew., ed. I. 2: 353. 1789. = **Teedia lucida** (W. T. Aiton) Rudolphi (*vide* Sprague, 1921)
- Capraria monnieria* Roxb., Hort. Bengal. 47. 1814. = **Herpestis monnieria** (Roxb.) H.B.K. (*vide* Sprague, 1921)
- Capraria montevidensis* Kuntze, Rev. Gen. Pl. 2: 459. 1891. = **Scoparia montevidensis** (Kuntze) R. E. Fries; **S. flava** Cham. & Schltld. (*vide* Sprague, 1921)
- Capraria multifida* Michx., Fl. Bor.-Amer. 2: 22. t. 35. 1803. = **Conobea multifida** (Michx.) Benth. (*vide* Sprague, 1921)
- Capraria multiflora* Steud., Nom. ed I. 149. 1820. = **Conobea multifida** (Michx.) Benth. (*vide* Sprague, 1921)
- Capraria oppositifolia* L., Fl. Jamaic. 380. 1759. = **Stemodia durantifolia** (L.) Swartz (*vide* Turner and Cowan, 1993).
- Capraria pinnatifida* Kuntze, Rev. Gen. Pl. 2: 459. 1891. = **Scoparia flava** Cham. & Schltld. (*vide* Index Kewensis)
- Capraria pusilla* Torr., Ann. Lyceum Nat. Hist. New York, 1: 36. 1824. = **Mimulus floribundus** Dougl. (*vide* Sprague, 1921)

- Capraria rigida* Buch.-Ham. ex Hook. f., Fl. Brit. India 4: 301. 1884. = *Centranthera hispida* R. Br. (fide Sprague, 1921)
- Capraria rigida* Thunb., Prodr. Pl. Cap. 103. 1800. = *Ehretia rigida* (Thunb.) Druce (fide Sprague, 1921)
- Capraria salicifolia* Link & Otto, Icon. Pl. Rar. Hort. Berol. 11. t. 4. = *Freylinia cestroides* Colla (fide Index Kewensis)
- Capraria salicifolia* Salisb., Prodr. Strip. Chap. Allerton 94. 1796. = *Freylinia lanceolata* (L. f.) G. Don. (fide Sprague, 1921)
- Capraria ternifolia* Sessé & Moç., Fl. Mexic., ed. 2, 145. 1894. = *Stemodia tenuifolia* Minod (fide McVaugh, 2000)
- Capraria undulata* L. f., Suppl. Pl. 284. 1781. = *Freylinia undulata* (L.f.) Benth. (fide Sprague, 1921)
- Capraria uniflora* Burm. f., Fl. Indica 133. fig. 3. 1768. = *Lysimachia* sp. (fide Sprague, 1921)
- Capraria verticillata* Sessé & Moç., Pl. N. Hispan., ed. 1, 98. 1887–90. = *Russelia* sp. (fide McVaugh, 2000)

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NUMERICAL LIST OF TAXA

- 1 = *C. biflora* 3 = *C. mexicana*
 2 = *C. frutescens* 4 = *C. peruviana*

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The exsiccate listed below is for all specimens examined during this study and includes those listed and those not listed in the representative specimens above. The numbers in parentheses refer to the corresponding taxa in the Numerical List of Taxa presented above.

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