

TAXONOMIC SYNOPSIS OF *COLUBRINA* (RHAMNACEAE) IN MEXICO

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ABSTRACT

For the genus *Colubrina* in Mexico, 24 species are recognized — *C. angustior*, *C. arborescens*, *C. asiatica* (adventive), *C. californica*, *C. ehrenbergii*, *C. elliptica*, *C. greggii* (no varieties), *C. heteroneura*, *C. johnstonii*, ***Colubrina lanceolata* Nesom (sp. nov.)**, *C. macrocarpa* (no varieties), ***C. macrocarpoides* (Suess. ex Suess. & Overkott) Nesom (comb. et stat. nov. for *C. macrocarpa* var. *macrocarpoides*)**, ***Colubrina mezquitalensis* Nesom (sp. nov.)**, ***Colubrina neoviridis* Nesom (sp. nov.)**, *C. sordida*, *C. stricta*, ***Colubrina subsessilis* Nesom (sp. nov.)**, *C. tepicana* (= *C. spinosa* var. *mexicana*), ***Colubrina tequila* Nesom (sp. nov.)**, *C. texensis*, *C. triflora*, ***Colubrina villarrealii* Nesom (nom. et stat. nov. for *C. texensis* var. *pedunculata*)**, *C. viridis*, *C. yucatanensis*. Formal typology, photos of representative specimens and pertinent types, and detailed distribution maps are provided. Similar species are separated by keys and diagnostic descriptions/comments.

The taxonomic revision of *Colubrina* by Johnston (1971, recognized 15 Mexican species and 5 varieties other than the typical), and an account of the common names, ethnobotany and geographic distribution of Mexican taxa was published by Fernández Nava (2010, following Johnston's taxonomy). *Colubrina celtidifolia* of southern Mexico and northern Central America has been transferred to the otherwise Asian genus *Hovenia* (Nesom 2023). The present taxonomic update recognizes 24 species in Mexico, with no varieties. Of the 4 species in the western USA (Texas and westward), all occur in Mexico; 7 others occur in southern Florida.

The phylogenetic position of *Colubrina* is unresolved (Hauenschild et al. 2016) — it "might be closely related to Paliureae or could represent an independent section, not yet described." An analysis by Thornhill et al. (2017) suggests that it is closely related to *Ceanothus*. Within the genus, the analysis of Hauenschild et al. included a monophyletic clade of *C. asiatica* (native to India, southeast Asia, Pacific Islands), *C. elliptica* (Florida Keys, West Indies, Mexico, Central America, and Venezuela), *C. glandulosa* (Brazil), and *C. oppositifolia* (Hawaii endemic). The analysis of Hua et al. (2022) added *C. arborescens* (southern Mexico, Central America, West Indies, Florida), *C. javanica* (southeast Asia), *C. spinosa* (Central America, West Indies), *C. triflora* (Mexico, Central America), *C. verrucosa* (West Indies), and their newly described *C. zhaouangii* (China).

Of the 5 *Colubrina* sections recognized by Johnston (1971), only representatives of sect. *Serrataria* (see Map 1) have not been included in a molecular-phylogenetic study. Johnston placed *C. asiatica* in sect. *Serrataria* but the glabrous-glossy leaves with more widely spaced marginal teeth do not have the same appearance as in Mexican members of the section, as recognized here (see Map 1). *Colubrina cubensis* (the type of sect. *Serrataria*) and *C. berteriana* are West Indian species — *C. cubensis* in Florida has been recognized as *C. cubensis* var. *floridana* M.C. Johnston.

The species are described below in alphabetical order. The order of maps and illustrations attempts to place similar species together.

1. **COLUBRINA ANGUSTIOR** (M.C. Johnston) Nesom, *Phytoneuron* 2013-4: 17. 2013. *Colubrina greggii* var. *angustior* M.C. Johnston, *Brittonia* 23: 37. 1971. **TYPE: MEXICO. Tamaulipas.** Vicinity of Tampico, ca. 15 m, 15 Jan 1910, *E. Palmer* 582 (holotype: US; isotypes: K, MO).

Colubrina angustior is distinct from *C. greggii* in a number of morphological features (key couplet below) and has a distinct geography (Map 3; Figs. 4-7). The two are sympatric in part of their range.

1. Leaf blades ovate to lanceolate-ovate or elliptic-ovate, widest below the middle, apex usually distinctly acuminate, commonly long and sharply acuminate; shrubs 2–3 m or trees up to 5 m; leaf blades (4–)6–18 x 3–8(–10) cm; flowers (10–)20–80 per thyrse **Colubrina greggii**
 1. Leaf blades oblong-lanceolate, widest near or at the middle, apex acute to very slightly acuminate; shrubs 1–2.5 m; leaf blades 3–10 x (1–)2–4 m; flowers 6–12 per thyrse **Colubrina angustior**

The northernmost records mapped for *Colubrina angustior* are these: **Nuevo León.** Hda. Vista Hermosa, Cola de Caballo, 6 Mar 1965, *Marroquín* 935 (TEX, Fig. 6). **Tamaulipas.** Mpio. Jiménez: N.C.P. José Silva Sánchez, carr. a Jiménez-Matamoros, arbusto 3 m, canon húmedo con arroyo, riparia y selva baja con *Celtis*, *Bumelia*, *Vallesia*, *Colubrina*, 118 m, 7 Apr 1998, *Mora-Olivo* 6844 (MEXU).

2. **COLUBRINA ARBORESCENS** (Mill.) Sarg., *Trees & Shrubs* 2: 167, pl. 168. 1911. *Ceanothus arborescens* Mill., *Gard. Dict.* ed. 8. 1768. **TYPE:** [Chelsea Garden, grown from seed sent by Catesby from Providence, Bahamas] — *P. Miller s.n.* (holotype: BM).

Rhamnus colubrina Jacq., *Enum. Syst. Pl. Carib.*, 16. 1760. *Ceanothus colubrinus* (Jacq.) Lam., *Encycl. Meth. Tabl.* 2: 90. 1793. *Colubrina ferruginosa* Brongn., *Mem. Fam. Rhamnées.*, 62. 1826 [nom. nov.]. *Marcorella colubrina* (Jacq.) Raf., *Sylv. Tellur.*, 31. 1838. *Colubrina americana* Nutt., *Sylv.* 2: 47, t. 58. 1846 (nom. nov. superfl.). *Colubrina colubrina* (Jacq.) Millsp., *Field Mus. Publ. Bot.* 2: 69. 1900. **TYPE** (holotype): Commelin, Hort. Med. Amst. 1, t. 90. 1697.

Rhamnus ferruginea Nutt., *J. Acad. Nat. Sci. Philadelphia* 7(1): 90. 1834. *Perfonon ferrugineum* (Nutt.) Raf., *Sylv. Tellur.*, 29. 1838. **TYPE: USA. Florida.** Near Key West, *T.R. Peale s.n.* (holotype: PH).

Colubrina obtusata Urban, *Repert. Sp. Nov. Regni Veg.* 18: 116. 1922. **LECTOTYPE** (Johnston 1971): **CUBA. Oriente Province.** Guantanamo (U.S. Naval Station), in rupibus calcareis, 24 Sep 1914, *E.L. Ekman* 2907 (holotype: S).

Colubrina arborescens comprises mostly trees with large, pinnately veined leaves (without 3 veins from the base) with entire margins. Figure 79.

As identified here, following Johnston (1971), it occurs in the West Indies and Veracruz, Chiapas, and the Yucatán Peninsula (Map 14) southward through Central America. Johnston noted that geographic "races" can be identified — (a) Chiapas and southwestern Guatemala, (b) the Yucatán Peninsula, Dept. Petén in Guatemala, and Central America, and (c) the West Indies, including the type of the species. The thick-leaved trees in Veracruz are similar to those of the Yucatán race.

3. **COLUBRINA ASIATICA** (L.) Brongn., *Ann. Sci. Nat. (Paris)* 10: 369. 1827 (Mem. Fam. Rhamnées, 62. 1826). *Ceanothus asiaticus* L., *Sp. Pl.* 196. 1753. *Rhamnus asiatica* (L.) Lam. ex Poir., *Encycl.* 4: 474. 1796. **LECTOTYPE** (Johnston 1971): **SRI LANKA.** Without other collection information, *Hermann Herb. 2.11* (BM). For many synonyms see Johnston (1971).

Similar to *Colubrina triflora* in its prominently 3-veined, broadly ovate leaves abruptly acuminate at the apex. Leaf blades are glabrous adaxially and shiny, usually sparsely silky-strigose abaxially. Leaf margins are regularly and shallowly serrate or serrate-dentate at least on the distal

portion of the blade, and the inflorescence is short-pedunculate (peduncles 1–2 mm long). The plants become sprawling to subsucculent shrubs with long, flexuous branches. Figures 80-82.

Typical *Colubrina asiatica* is native to southeast Asia and is widely naturalized and aggressively invasive — the USA (Florida), Mexico (Map 14), Caribbean, Africa, Madagascar, India, Australia, New Guinea, Hawaii, and other various Pacific islands. *Colubrina asiatica* var. *subpubescens* (Pitard) M.C. Johnston is known only from southeast Asia — because of differences in habitat and morphology, Chen and Schirarend (2007) treated it as a distinct species, *C. javanica* Miquel.

- 4. COLUBRINA CALIFORNICA** I.M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12: 1085. 1924. *Colubrina texensis* var. *californica* (I.M. Johnst.) L.D. Benson, Amer. J. Bot. 30: 630. 1943. **TYPE: MEXICO. Baja California.** Las Animas Bay, gravelly bench in a broad cañon, shrub 7 ft high, 8 May 1921, *I.M. Johnston 3496* (holotype: CAS; isotypes: GH, K, NY, UC, US).

Colubrina californica is native to scattered localities in Arizona, Sonora, southern California, and the two states of the Baja California peninsula (Map 6). Abbreviated short shoots sometimes but not always present. Flowers in pedunculate clusters, peduncles 1–2 mm long, pedicels 2–4 mm long in fruit. Leaf venation sub-brochidodromous, without a pair from the very base; margins entire to shallowly serrulate with few teeth. Figures 33-38.

"Thorns" of *Colubrina californica* (and *C. texensis*, *C. villarrealii*, and others) usually are broken off or senescent tips of stiff, slender branches, lacking a sharp point. Sometimes, however, in *C. californica* the branch tips become sharp-pointed, truly thorn-like — such variants are the only American species with thorn-tipped, meristematic branches. In any case, these thorn tips do not appear to be set in early ontogeny, as they probably are in *Condalia*, where some meristematic branches are thorn-tipped from the outset, with further extension of length apparently originating at the base, at the short shoot.

A group of *Colubrina* species produces axillary, short, needle-like, non-meristematic thorns. Johnston (1971) placed these in sect. *Cowanina* (e.g., *C. heteroneura*, *C. retusa*, *C. tepicana*, *C. verrucosa*), which he characterized as having "branches or inflorescence-axes commonly becoming thorns" or thorns "representing the elongate peduncle of the thyrses." Regardless of their ontogeny, these thorns are non-meristematic or with a node only at the very base.

- 5. COLUBRINA EHRENBERGII** Schlecht., Linnaea 15: 469. 1841. **LECTOTYPE** (Johnston 1971): **MEXICO. Hidalgo.** Inter Amojaque [Santa Maria Amajac, W of Atotonilco el Grande] et el puente de [la Madre de] Dios, Dec 1838, *C.A. Ehrenberg s.n.* (HAL).

A distinctive species, rarely misidentified, in its shrubby habit, lacking short shoots, leaves strongly 3-nerved from the base with margins with relatively few, coarse teeth, prominently tawny-pubescent abaxial leaf surfaces, petioles, and young stems. Style 1 mm long, branches separate to the base. Flowers are produced only on the new year's growth. Figures 56-58.

Colubrina ehrenbergii is a Mexican endemic restricted to eastern states (Map 10). I have seen only one collection from Oaxaca, near the Puebla border and apparently southward disjunct from the main range: Mpio. Tepelmeme: Cuenca Río Hondo Alta Mixteca, Mesa del Calvario, Cerro de El Ramón, NE de el Rodeo, arbusto 4 m, matorral calcicola mixto, 17 Jul 1985, *Tenorio L. 9258* (ASC-Fig. 58, TEX).

A collection noted by Johnston (1971) as a variant of *Colubrina ehrenbergii* from Jalisco is recognized here as a distinct species, *Colubrina tequila* Nesom.

- 6. COLUBRINA ELLIPTICA** (Sw.) Brizicky & Stern, Trop. Woods 109: 95. 1958. *Rhamnus elliptica* Sw., Prodr. 50. 1788. *Rhamnus venosa* Lam. ex Poir., Encycl. [J. Lamarck & al.] 4(2): 474. 1798 [nom. nov. superfl.]. *Diplisca elliptica* (Sw.) Raf., Sylv. Tellur., 31. 1838. **TYPE: JAMAICA.** No other collection information, *Swartz s.n.* (holotype: S; isotype: M).
- Ceanothus reclinatus* L'Hérit., Sert. Angl., 6. 1789. *Colubrina reclinata* (L'Hérit.) Brongn., Ann. Sci. Nat. 1, 10: 369. 1827. **TYPE: JAMAICA.** No other collection information, *W. Wright s.n.* (holotype: P; isotype: K).
- Ziziphus domingensis* Duhamel, Traité Arbr. Arbust. (Duhamel), nouv. éd. 3: 56. 1806. **TYPE:** "hort. Paris," no other collection information (holotype: P).
- Colubrina fermentum* L.C. Rich. ex Brongn., Mém. Fam. Rhamnees, 62. 1826. **TYPE: Protologue:** "2. COLUBRINA FERMENTUM Rich. ined. ex Guyaniá." No other collection information. As a synonym of *Colubrina elliptica*, fide Johnston (1971).
- Rhamnidium moreireanum* Glaziou, Bull. Soc. Bot. France 52 (Mem. 3a): 110. 1905. **TYPE: BRAZIL. Río de Janeiro.** Lagoa de Rodrigo de Freitas, 26 Apr 1887, *A. Glaziou 15898a* (holotype: P).
- Colubrina venezuelensis* Steyerm., Fieldiana Bot. 28: 355, Dec 1952 (not *Colubrina venezuelensis* (Suesseng. & Overkott) Cowan, Oct 1952). *Colubrina pittieriana* Steyerm., Fieldiana Bot. 28: 971. 1957 [nom. nov.]. **TYPE: VENEZUELA. Distrito Federal.** Alrededores de Caracas, 1600-1800 m, *T. Gonzalez s.n.* (holotype: F; isotype: VEN). The VEN label has "Peña de Nord, *T. González 7520.*"
- Colubrina hondurensis* A. Molina, Ceiba 3: 167. 1953. **TYPE: HONDURAS. Dept. Morazán.** Entre Suyapa y Tegucigalpa, márgen de la Quebrada Las Burras, 1050 m, 11 Dec 1948, *A. Molina R. 1801* (holotype: VEN; isotypes: F, GH, US-2 sheets).

Colubrina elliptica occurs in Mexico (Map 13), Central America, the West Indies, and northern South America. The Mexican distribution is primarily in the eastern states, but scattered collections have been made from Michoacán and Colima and the species apparently is abundant in Nayarit (collections as cited below). Plants are thornless and without short shoots, with pinnately veined leaves (without a strong pair from the base) and flowers in a pedunculate thyrse. Figures 75-78.

Nayarit. Mpio. Del Nayar: 12 km NW de Jesús María, camino a La Mesa del Nayar, cerca del Puente en cañada, 22° 10' N, 104° 35' W, arbol 6 m, poco abundante, selva baja caducifolia, 970 m, 28 Sep 1989, *Flores Franco 1507* (MEXU-2 sheets); camino a Cañaveral 3 km N del camino Jesús María-La Mesa del Nayar, 22° 17' N, 104° 40' W, arbol 4 m, poco abundante, selva baja caducifolia, 800-900 m, 29 Sep 1989, *G. Flores Franco 1540* (MEXU); 1-2 km NW de Jesús María, 22° 16' N, 104° 32' W, arbolito 3 m, poco abundante, en cañada, selva baja caducifolia, 500-600 m, 22 Oct 1989, *Flores Franco 1743* (MEXU-2 sheets); 500 m a S de Jesús María, Río Santiago, 22° 16' N, 104° 32' W, en cañada, junto al río, arbusto 2 m, poco abundante, selva baja caducifolia, 500-600 m, 22 Oct 1989, *Flores Franco 1778* (MEXU).

Johnston (1971) noted that a collection from **Colima** identified as *Colubrina elliptica* is unusual not only in the geography but also in its elongate leaves: Ca. 11 mi SSW of Colima on Manzanillo road, mountain summits near pass, tree, abundant in the barrancas, precipitous rocky slopes and ravines of gypsum and slate, 400-500 m, deciduous woodland with *Juliania*, *Bursera*, *Cephalocereus*, *Cyrtocarpa*, *Cassia*, 7-8 Dec 1959, *McVaugh & Koelz 1595* (MICH-Fig. 75, SMU as cited by Johnston). The relative dense abaxial vestiture of the leaves also appears to be unusual for *Colubrina elliptica*, but these differences appear to be qualitative and not outside the concept of the species.

7. **COLUBRINA GREGGII** S. Wats., Proc. Amer. Acad. Arts 17: 336. 1882. **LECTOTYPE** (Johnston 1971): **MEXICO. Nuevo León.** Monterrey, 1846–1849, *J. Gregg 154* (GH).
Colubrina celtidifolia var. *minute-serrata* Susseng., Repert. Sp. Nov. 51: 204. 1942. **TYPE: MEXICO. Tamaulipas.** Cd. Victoria, 320 m, 1907, *E. Palmer 376* (holotype: M, fide Johnston 1971; isotype: MO).

Keys to *Colubrina greggii* and its putatively closest relatives

- 1a. Leaf blades ovate to lanceolate-ovate or elliptic-ovate, widest below the middle, apex usually distinctly acuminate, commonly long and sharply acuminate, short-acuminate to acute in northern Tamaulipas and southern Texas; shrubs 2–3 m or trees up to 5 m; leaf blades (4–)6–18 x 3–8(–10) cm; flowers (10–)20–80 per thyrse; Maps 1, 3 **Colubrina greggii**
- 1a. Leaf blades oblong-lanceolate, widest near or at the middle, apex acute to very slightly acuminate; shrubs 1–2.5 m; leaf blades 3–10 x (1–)2–4 m; flowers 6–12 per thyrse **Colubrina angustior**
- 1b. Leaf blades ovate to lanceolate-ovate or elliptic-ovate, widest below the middle, apex usually distinctly acuminate, commonly long and sharply acuminate; peduncles 5–12 mm **Colubrina greggii**
- 1b. Leaf blades oblong-lanceolate, widest near or at the middle, apex acute to slightly and short-acuminate; peduncles (5–)14–18 m **Colubrina yucatanensis**

See Figures 1-3 for *Colubrina greggii*. Maps 1 and .

8. **COLUBRINA HETERONEURA** (Griseb.) Standl., J. Wash. Acad. Sci. 15: 285. 1925. *Ziziphus heteroneurus* Griseb., Bonplandia 6: 3. 1858. **TYPE: PANAMA. Protologue:** "In litore." No other collection information, *E.P. Duchassaing s.n.* (holotype: GOET).
- Rhamnus spinosa* Hemsley, Diagn. Pl. Nov. 1: 6. 1878 [non Gilib. 1781]. **TYPE: PANAMÁ.** Paraiso Station, a small tree, Oct 1861, *Sutton-Hayes 273* (holotype: K; isotypes: BM [and fide Johnston 1971] E, FI).
- Rhamnus biglandulosa* Sessé & Moc., Pl. Nov. Hisp. 38 (Naturaleza (Mexico City), Ser. 2, 1: App.); ed. 2, 35; Sesse & Moc. Fl. Mexic. ed. 2, 63 (1894) (1888). *Cormonema biglandulosum* (Sessé & Moc.) Standl., Contr. U.S. Natl. Herb. 23: 718. 1923. According to Johnston (1971, p. 22), "No type specimen has been found; the description is designated as the type."
- Cormonema nelsonii* Rose, Contr. U.S. Natl. Herb. 3: 315. 1895. *Colubrina nelsonii* (Rose) Cowan, Brittonia 7: 405. 1952. **LECTOTYPE** (Johnston 1971): **MEXICO. Guerrero.** Near San Marcos, 500 ft, 7 Feb 1895, *E.W. Nelson 2284* (US; isolectotype: GH). The protologue also cited *Palmer 1625* from Sinaloa.
- Rhamnus gonzalezii* Riley, Bull. Misc. Inform. Kew 1923(5): 173. 1923. **TYPE: MEXICO. Sinaloa.** San Ignacio, Cerro de la Nanche, San Agustín, 205 m, May 1921, *J. González Ortega 628* (holotype: K; isotypes: F, US).
- Cormonema multiflorum* Brandeg., Univ. Calif. Publ. Bot. 10: 411. 1924. **TYPE: MEXICO. Veracruz.** [Mpio. Puente Nacional]: Remudadero, Dec 1922, *C.A. Purpus 8863* (holotype: UC; isotypes: F, GH, MO, NY, US).

Colubrina heteroneura is characterized by abbreviated short shoots, stems often with prominent lenticels and with short, axillary, non-meristematic thorns, small, coriaceous, glabrous leaves with entire margins and pinnate venation (without a strongly developed basal pair), and flowers in epedunculate clusters. It usually is correctly identified, especially if thorns are evident. *Colubrina elliptica* is similar but is thornless and has flowers in a pedunculate thyrse. *Colubrina heteroneura* occurs in Mexico (Map 17) and southward to Panama. Figures 88-93.

A collection from Estación Biológica Chamela in Jalisco has been identified as *Colubrina heteroneura*, but the plant seems out of place in that species — it has red stems and thorns at the branch tips and non-meristematic axillary thorns. The collection is sterile, but if it is Rhamnaceae, then it may be an undescribed species of *Colubrina* (or *Ceanothus*?). The relatively small leaves with pinnate venation are similar to those of *C. heteroneura* and *C. elliptica*.

Jalisco. Mpio. La Huerta: Estación Biológica Chamela, 19° 30' N, 105° 03' W, rare shrub, red twigs, densely forested floodplain to more open hillside (selva mediana), 80-100 m, 20-27 Apr 1992, *M.F. Quigley 649* (LSU). Figure 94.

9. COLUBRINA JOHNSTONII T. Wendt, Bol. Soc. Bot. México 44: 83. 1983. **TYPE: MEXICO.**

Veracruz. Mpio. Minatitlán: 13.7 km E de La Laguna, sobre la terracería a Uxpanapa, después 7.2 km N sobre el camino nuevo (no completo) a Belisario Dominguez, en una depresión kárstica donde nace y desaparece un río, arbusto 1.5 m de alto, entre piedras cerca de agua corriente, 120 m, 26 Sep 1980, *T. Wendt 2756* (holotype: MEXU; isotypes: CAS, CHAPA, ENCB, MEXU-Fig. 827, MO, NY-Fig. 86, TEX).

An easily identified species from its morphology and geography. Shrubs or small trees without thorns or well-developed short shoots. **Leaves** mostly glabrous, elongate, elliptic-lanceolate to elliptic-oblongate, margins entire with a single gland near the base of each side, venation pinnate without a strong pair of secondary veins from the base. **Flowers** in pedunculate clusters and fruits relatively large (6.5–8 mm long). Endemic to the Uxpanapa region of Veracruz (Map 16). In its pinnately veined leaves without a strongly developed basal pair, *Colubrina johnstonii* is similar to *C. arborescens*, *C. elliptica*, *C. heteroneura*, and *C. tepicana*.

10. COLUBRINA LANCEOLATA Nesom, **sp. nov.** **TYPE: MEXICO. Aguascalientes.** Mpio. Calvillo: 5 km E of Colomos, ca. 7 km NE of Calvillo, 21° 52.7' N, 102° 38.9' W, solitary tree ca. 15 ft tall, S-facing hillsides with thick tropical deciduous forest, in many areas the overstory quite dense, especially near ephemeral streams on the steepest slopes, with *Cordia*, *Ceiba*, *Manihot caudata*, and *Hintonia latiflora*, 1800 m, 12 Jul 1999, *M. Provanca 1405* (holotype: TEX; isotypes: BRIT, MEXU-Figs. 69-72, UCR).

Similar to *Colubrina triflora* in leaf shape and venation and its axillary inflorescence; different in its thickened, glaucous, tawny leaves with an narrowly attenuate base and its short-pedunculate thyrses. Known only from the type collection.

Trees 15 ft tall, unarmed, branches glabrous. **Leaves** opposite, glabrous, thickened, slightly bicolor, tawny to tawny-brown abaxially, darker adaxially, blades lanceolate, 8–11 cm long, 1.8–2.6 cm wide, prominently 3-veined from the base, with 1–2 pairs of major secondary veins, venation not raised, base acute to attenuate, apex acute, margins shallowly serrate-dentate with 2–5 pairs of teeth, petioles 8–15 mm long. **Flowers** ca. 8–12 in axillary fascicles or thyrses, glabrous, peduncles ca. 1–2 mm long. **Fruits** not seen.

Despite the similarity of *Colubrina lanceolata* to *C. triflora*, it is not clear that they are closest relatives. They occur in close proximity in Aguascalientes (Map 11), where *C. lanceolata* occurs in a tropical deciduous forest, *C. triflora* in matorral. Mpio. Calvillo: 6 km NE de Ojocaliente, ladera riolítica con vegetación de matorral, 1800 m, 25 Aug 1960, *Rzedowski 14061* (MEXU, Figs. 73-74). Map 11.

11. COLUBRINA MACROCARPA (Cav.) G. Don, Gen. Hist. 2: 36. 1832. *Ceanothus macrocarpus* Cav., Icon. Pl. 3: 38, t. 276. 1795. *Ceanothus mocinianus* DC. [nom. nov., illeg.], Prodr. 2: 32. 1825. **TYPE: MEXICO.** Don's protologue cited only the illustration from Cavanilles (holotype: Cavanilles's tab. 276, reproduced here as Figure 16).

Ceanothus alamanii DC., Prodr. 2: 31. 1825. *Colubrina alamanii* (DC.) G. Don, Gen. Syst. Dichlamyd. 2: 36. 1832. **TYPE: MEXICO.** No other collection information, *L. Alaman s.n.* (holotype: G-DC, Fig. 16).

Rhamnus turbinata Sesse & Mociño, Flora Mexicana ed. 2, 62. 1894. Cited by Johnston (1971) as a synonym of *Colubrina macrocarpa*, "ex char."

Colubrina megacarpa Rose, Contr. U.S. Nat. Herb. 8: 50, t. 11. 1903. **TYPE: MEXICO. Puebla.** Near Tehuacan, 1-2 Aug 1901, *J.N. Rose* 5852 (holotype: US; isotype: MEXU).

Colubrina lanulosa Blake, Contr. Gray Herb. 52: 74. 1917. *Colubrina macrocarpa* var. *lanulosa* (Blake) M.C. Johnston, Wrightia 3: 94. 1963. **TYPE: MEXICO. Guerrero.** Tlacotepec, volcanic terrain, 1600 m, 10 Jun 1899, *E. Langlassé* 1053 (holotype: GH; isotypes: P, US).

In Blake's description of *Colubrina lanulosa*, he made this comment: "A species finding its only close ally in *C. megacarpa* Rose, which has somewhat looser fewer-flowered inflorescences, thinner more distinctly toothed leaves, and much less pubescent young branches and under leaf-surfaces." Figures 15-23. In the present study, there does not appear to be a geographic or morphological discontinuity between the Guerrero-Morelos population system (*C. lanulosa*) and that of adjacent Puebla-Oaxaca (*C. macrocarpa* sensu stricto) that would justify recognition of two species (Map 4). Plants from Querétaro previously treated as conspecific with *C. macrocarpa* are recognized here at specific rank, *C. macrocarpoides*.

12. COLUBRINA MACROCARPOIDES (Suesseng. ex Suesseng. & Overkott) Nesom, **comb. et stat. nov.**

Colubrina macrocarpa var. *macrocarpoides* (Suesseng. ex Suesseng. & Overkott) M.C. Johnston, Wrightia 3: 94. 1963. *Colubrina greggii* var. *macrocarpoides* Suesseng. ex Suesseng. & Overkott, Repert. Sp. Nov. 50: 325. 1941. **TYPE: MEXICO. Querétaro.** Mpio. Cadereyta: Between San Juan del Río and Hacienda Ciervo, 19 Aug 1905, *J.N. Rose* 9623 (holotype: B, destroyed; isotypes: A-Fig. 21, GH-2 sheets-Figs. 27-28, MEXU, NY-Fig. 29, US). Johnston (1971) designated the A sheet as lectotype. The US sheet has one branch of *C. macrocarpoides* and one of *C. greggii*.

Additional collections. Querétaro. Mpio. Cadereyta del Montes: KM 5 carretera a San Joaquín, arbol, bosque de pino pincana, 1900 m, 26 Sep 2002, *Rodríguez V. s.n.* (MEXU). **Mpio. Ezequiel Montes:** Del Hacienda Cierva al Cerro de la Mesa, 20 Aug 1905, *Altamirano* 1562 (MEXU, US); El Ciervo, arbusto abundante, 1-2 m, matorral bajo, 2000-2100 m, 25 Sep 1994, *Hernández M.* 10845 (MEXU); El Ciervo, arbusto muy abundante, 1-3 m, matorral bajo, 2100 m, 1 Nov 1994, *Hernández M.* 10970 (MEXU).

Colubrina macrocarpoides is endemic to a small area in Querétaro (Map 4). Unsuccessful searches by Fernández Nava (1996) in the area of the type locality suggest that it may be extinct there.

Fernández Nava (2010) distinguished *Colubrina macrocarpoides* from *C. macrocarpa* as follows (translated):

- | | |
|--|-----------------------|
| 1. Leaves membranous, 1.5–2 times longer than wide, apices acute, venation very conspicuous | macrocarpoides |
| 1. Leaves subcoriaceous, 1.1–1.6 times longer than wide, apices rounded, venation moderately conspicuous | macrocarpa |

13. COLUBRINA MEZQUITALENSIS Nesom, **sp. nov.** **TYPE: MEXICO. Durango. Mpio. Mezquital:** Cerca de la Paura, arbusto ca. 3 m, matorral subtropical, 1490 m, 23 Apr 1985, *S. González* 3108 (holotype: MEXU; isotype: TEX-Fig. 30).

Similar to *Colubrina macrocarpa* in its bicolor leaves densely lanose abaxially, minutely serrulate leaf margins, axillary inflorescence on relatively short peduncles, and large fruits; different in its fewer-flowered inflorescence, longer and straighter hairs on the abaxial leaf surface, and western geography.

Shrubs 1–3 m high, unarmed, without short shoots, branchlets densely lanose, glabrescent. **Leaves** alternate, blades elliptic to elliptic-ovate or nearly rotund, 2–5.5 cm long, (1–)2–4 cm wide, apex obtuse to subacute, base rounded to truncate or subcordate, margins micro-serrulate to dentate-serrulate, "teeth" usually with only a tiny gland and/or tuft of hairs, venation camptodromous, with 4–5 pairs of slightly arching secondary veins, weakly 3-veined from the base, surfaces bicolor, densely lanose abaxially and the epidermis cream-colored, sparsely pubescent adaxially and darker, petioles 2–5 mm long, densely lanose. **Flowers** 4–8 in axillary clusters, primary pedicels 3–5 mm long, thickened and elongating to 5–10 mm in fruit; hypanthium and sepals densely tawny-tomentose; style branches 3, divided about 2/3–3/4 the length. **Fruits** 12–15 mm wide. **Seeds** dark, shiny, slightly elongate, 5–6 mm long. Figures 30–32.

Additional collections. Durango. Mpio. Mezquital: 3 km de Temohaya por el camino a Mezquital, bosque tropical caducifolio, 1400 m, 2 Oct 1984, *M. González & Rzedowski 1616* (MEXU, TEX); 2.5 km al E de Yonora, bosque tropical caducifolio, asoc. *Bursera* spp., *Ipomoea murucoides*, *Hintonia latiflora*, *Myrtillocactus geometrizans*, *Agave angustifolia*, 1500 m, 22 May 1987, *M. González 2190* (MEXU); camino entre Temoaya y La Candelaria, 23° 12' 06" N, 104° 31' 35" W, bosque tropical caducifolio (*Ipomoea murucoides*, *Bursera* spp.), 1280 m, 10 Jun 1999, *M. González 3157* (MEXU). **Mpio. Nombre de Dios:** Berros, matorral de *Opuntia* con *Forestiera*, 29 Apr 1981, *S. Gonzalez 1600* (TEX); Berros, dentro del poblado, matorral de *Prosopis*, 29 Aug 1979, *S. González 1083* (MEXU); village of Nombre de Dios, dominant shrub among large *Opuntia*, 15 Jun 1981, *Scudday 739* (TEX). Map 5.

14. COLUBRINA NEOVIRIDIS Nesom, *sp. nov.* TYPE: MEXICO. Durango. Mpio. Lerdo: 2–4 mi NE of Chocolate, Rte 31, shrub up to 2 ft tall, rocky limestone arroyo, 23 Jul 1958, *D.S. Correll and I.M. Johnston 19991* (holotype: LL, Fig. 51; isotype: ASU).

Similar to *Colubrina viridis* in its intricately branched, shrubby habit with short shoots, small, congested leaves with entire margins and filiform petioles, and flowers 1 or 2–3 in epedunculate fascicles; distinct in its more open venation, shorter pedicels, and its different geography and ecology. *Colubrina viridis* is restricted to coastal and near-coastal localities at 5–450 m in the Sonoran Desert, while *C. neoviridis* is endemic to the Chihuahuan Desert, at 1250–1500 m, separated from *C. viridis* by the Sierra Madre Occidental. Maps 8, 9. Figures 51–55.

Shrubs 2–6 ft high, intricately branched, unarmed, with short shoots. **Stems** not zigzag, thinly and sparsely strigose with short, closely appressed hairs. **Leaves** congested, often in fascicles from short shoots, blades elliptic to elliptic-ovate, 10–25 mm long, 6–15 mm wide, pastel green on both surfaces, glabrous, venation brochidodromous, obscure adaxially, tertiary veins (abaxial) dark, areoles very open, apex obtuse to slightly retuse, base acute to obtuse, margins entire, petioles 2–12 mm long. **Flowers** 1 or in fascicles of 2–3, axillary or usually from short shoots, epedunculate, hypanthium essentially glabrous or with a few tiny hairs (lens); style 3-branched, divided ca. 1/4–1/3 the length. **Fruits** globose to depressed-globose, 5.5 mm wide, fruiting pedicels 7–11 mm long. **Seeds** ca. 5 mm wide, brown.

Additional collections. Durango. Mpio. Cuencamé: 2 mi NE of Pedriceña, Rte 31, shrub up to 4 ft tall, rocky limestone slope, 23 Jul 1958, *Correll and I.M. Johnston 20028* (LL); 4 road mi N of Pedriceña turnoff along Hwy 40, 50 ft N of Microondas Est. Sierra Lorenzo, shrub to 6 ft high, igneous rocky slopes, with *Agave lechuguilla*, *Opuntia*, *Acacia* spp., *Larrea*, *Jatropha*, *Fouquieria*, etc., 4500 ft, 13 Aug 1973, *Henrickson 12313* (ARIZ, LL, MEXU); Velardeña, 23 km al NNE del centro de Cuencamé, 25° 03' 52.6" N, 103° 45' 30.9" W, matorral xerofilo rosetofilo con *Larrea*, *Acacia*, *Jatropha*, 1414 m, 22–23 Jul 2010, *Tejero-Díez 6262* (MEXU). **Mpio. Lerdo:** ca. 24 air mi SW of Torreón, 7.1 mi W of Hwy 40 on road to Presa Francisco Zarco along Rio Nazas, shrub to 3 ft tall, with *Aloysia*, *Larrea*, *Agave*, *Jatropha*, *Leucaena*, *Yucca thompsoniana*, *Hechtia*, etc., vertical limestone in a narrow canyon, 4100 ft, 15 Aug 1973, *Henrickson 12418* (LL, MEXU); ±16 air mi SW of Torreón on upper road to Microondas Saporis, ±5 mi SW of León Guzmán, the road to the Microondas extending from the old Hwy 40, in a saddle ca. 1 road mi below the Mic. towers, openly branched shrubs 3–4 ft, limestone hills, 1400 m, 17 Oct 2002, *Henrickson 23146* (TEX);

Est. Microondas "Sapioris" ca. 30 km SW of Gómez Palacio on hwy toward Durango, matorral desértico micrófilo, *Agave*, *Viguiera*, *Fouquieria*, *Acacia*, steep limestone slopes, 1400-1500 m, 25 Mar 1973, Johnston *et al.* 10405B (MEXU, TEX); just S and SE of Est. Microondas Sapioris ca. 20 km NW of Est. Chocolate, matorral desértico con espinas laterales, steep limestone slopes, 1450-1500 m, *Agave*, *Viguiera*, *Acacia*, *Mimosa*, 13-14 Aug 1973, Johnston *et al.* 12197 (ASU, MEXU, OBI, SD, TEX, UCR); 21 air mi SW of Torreón, 12.3 mi from Mex 40, 5.1 m S of El Refugio, pass through E edge of Sierra del Rosario, E-facing steep mountain cliffs above Rio Nazas, 25° 21' N, 103° 44' W, *Yucca*, *Acacia*, *Jatropha*, *Hechtia*, 4000 ft, 21 Jul 1977, Lehto L21674 (ASU); 16.0 mi S of Nazareno in Rio Aguanaval Valley, E-facing bajada, *Fouquieria*, *Larrea*, *Agave lechuguilla*, 21 Aug 1971, McGill 8032 (ASU, DES); Sierra El Rosaria, camino a la estacion de microondas Sapioris, carr. 49.3 km SE de Lerdo, 25° 24' N, 103° 43' W, Villarreal 5788 (ANSM, CHAPA, as cited by Fernández Nava 2012, not seen). Mpio. Nazas: 3 road mi E of Nazas along hwy, red sandy clay with *Larrea*, *Fouquieria*, *Cordia*, *Opuntia*, *Prosopis*, *Agave*, etc., 4200 ft, 13 Aug 1973, Henrickson 12344 (LL, MEXU). Mpio. Rodeo: 1 km NE de Las Animas, sobre la carretera a Nazas, 25° 08' 36" N, 104° 25' 59" W, arbusto 0.6-1.5 m, abundante, pie de monte, profundo, matorral xerófilo (*Acacia*, *Viguiera*, *Fouquieria*, *Jatropha*), 1340 m, 5 Aug 1997, S. Gonzalez 5904 (MEXU).

Morphological differences between typical *Colubrina viridis* and *C. neoviridis* are few and seemingly qualitative, but their ecological distinction and geographic separation support recognition of each at specific rank.

15. COLUBRINA SORDIDA M.C. Johnston, *Wrightia* 3: 95. 1964. **TYPE: MEXICO. Guerrero.** Sierra Madre del Sur, Dist. Aldama, N of Río Balsas, Temisco, Barranca de la Guacamaya, erect shrub 4 m high, common locally, dry slope above stream, 495 m, 19 Nov 1937, *Y. Mexia* 8854 (holotype: US, Fig. 24; isotypes: CAS, F, G, GH, LL, MO, NY, S, U, UC).

Additional collection. Guerrero. [Mpio. Arcelia]: Ashotla, Aug 1925, *B.P. Reko* 4958 (A, US-Fig. 25). Map 4.

Originally identified (on the label) as *Colubrina macrocarpa*, to which it is similar, especially in its large fruits and leaves 3-nerved from the base, with minutely and evenly serrulate margins and lanose abaxial surfaces. The leaves, however, are larger (blades 8–13 cm long vs. 2–9 cm) than in *C. macrocarpa* and the abaxial vestiture is of longer hairs. The primary peduncles of *C. sordida* are longer than in *C. macrocarpa* (20–25 mm vs. 5–7 mm). Johnston compared *C. sordida* to the large-leaved *Colubrina celtidifolia* (Cham. & Schlecht.) Schlecht., but that species has been transferred to the genus *Hovenia* (Nesom 2023).

16. COLUBRINA STRICTA Engelm. ex Blankinship, *Ann. Rep. Missouri Bot. Gard.* 18: 163. 1907 [non Engelm. ex M.C. Johnston, *Southw. Naturalist* 14: 257. 1969]. **TYPE: USA. Texas.** [Comal Co.]: Comanche Spring, New Braunfels, Jun 1850, *F. Lindheimer* 711 (holotype MO; isotypes A, F-Fig. 18, GH, NY, P, TEX-2 sheets-Fig. 17, US, W). *Lindheimer* 712 (TEX!) has identical collection data but is a paratype; *Lindheimer* 713 and 714 (all from June 1850) also are *C. stricta*, fide Blankinship (1907).

See Figures 15-19 for *Colubrina stricta*.

Additional collections. MEXICO. Coahuila. Mpio. Jimenez: Rancho La Gloria, ca. 6 km S de Jimenez, orilla del Río San Diego, 29° 04' N, 100° 40' W, veg. riparia, 240 m, 26-27 Sep 2000, Carranza C-3800 (MEXU). Mpio. Múzquiz: 47 km N of the Río Sabinas crossing on the Múzquiz-Boquillas hwy near Rancho El Milagro, 28° 15' 04" N, 101° 37' 09" W, roadcut through limestone hills, matorral con espinas varias o sin espinas, *Acacia rigidula*, *Acacia berlandieri*, *Leucophyllum frutescens*, 600 m, 6 Jun 1972, Chiang *et al.* 7531 (MEXU, MO). Mpio. San Juan de Sabinas: Lado N del Río Sabinas, 6.1 km NE de San Juan de Sabinas, bosque riparia de *Carya illinoensis*, *Celtis laevigata*, y *Morus celtidifolia*, 27° 57' 26.29" N, 101° 21' 36.01" W, 7 Apr 2011, Encina D. *et al.* 2841 (TEX). Mpio. Zaragoza: 73 km N of the

Río Sabinas crossing on the Múzquiz-Boquillas hwy, 28° 23' 54" N, 101° 41' 11" W, disturbed roadside through limestone hills, uncommon shrub 2 m high, forming a thicket, matorral, *Acacia*, *Schaefferia*, *Karwinskia*, *Agave lechuguilla*, 625 m, 6 Jun 1972, *Chiang et al.* 7533 (MEXU, MO). **Nuevo Leon.** Mpio. Lampazos: Rancho Résendez, Lampazos, *Edwards* 290 (F, TEX). Mpio. Salinas Victoria: Mamulique Pass, W side of old route Mex 85, ca. 0.2 km N of road to Est. Microondas Mamulique, just S of top of pass, ca. 36 km S of Sabinas Hidalgo, shrub 2 m tall, *Yucca*, *Agave*, *Acacia*, *Colubrina texensis*, *Croton*, *Bauhinia*, *Diospyros*, *Leucophyllum*, *Salvia*, *Fraxinus greggii*, *Opuntia*, 640-660 m, 7 Apr 1990, *Bridges* 13140 (GA, MEXU, MO, TEX). **Tamaulipas.** Mpio. San Nicolas: 1.5 km N de Flechadores, 24° 30' 58" N, 98° 40' 32.5" W, arbusto 1.5 m, matorral alto subinermes, 490 m, 6 May 1988, *Martínez* 4266 (MEXU). Map 2.

17. COLUBRINA SUBSESSILIS Nesom, **sp. nov.** TYPE: MEXICO. Oaxaca. Mpio. Santiago Astata: Al N de Santiago Astata, camino a la torre de TELMEX, 15° 59' 32.1" N, 95° 40' 18.1" W, arbusto 1 m, en ladera, selva baja caducifolia, 230 m, 29 Oct 2002, *M. Elorsa* C. 6274 (holotype: TEX, Fig. 68).

Similar to *Colubrina triflora* in its strongly 3-veined, shallowly dentate-serrate margins, sparsely pubescent leaves with acute-acuminate apex, flowers in epedunculate axillary clusters, and small fruits. Different in its smaller stature, consistently smaller, ovate leaves with subcordate base and tomentose petioles 2–5 mm long, and its pubescent hypanthia.

Shrubs or small trees 1–2 m high, unarmed, without short shoots, young stems tomentose, glabrescent, slightly zigzag. **Leaf blades** ovate, 3.5–8 cm long, 2.5–4.5 cm wide, thin-herbaceous, green on both surfaces, inconspicuously strigose adaxially with fine hairs, sparsely pubescent abaxially with shorter, irregularly oriented hairs, margins shallowly serrate-dentate with 3–5 teeth per side, apex acute-acuminate, base rounded to subcordate, petioles tomentose, 2–5 mm long, venation camptodromous, strongly 3-veined from the base, tertiary veins dark, not raised or impressed. **Flowers** 2–6 flowers in an axillary, epedunculate cluster from an abbreviated short shoot, pedicels 3–6 mm long in fruit, pubescent with orangish, crinkly hairs. **Hypanthium** pubescent with orangish, crinkly hairs. **Fruits** 3.5–4 mm wide. **Seeds** brown, ca. 3 mm wide.

Additional collections. Oaxaca. Mpio. San Pedro Huamelula: 500 m N de Santa María Huamelula, 15° 59' 51.7" N, 95° 42' 10.3" W, arbusto 2 m, sobre el cerro con suelo pedregosa, selva baja caducifolia, en ladera, 115 m, 19 Nov 2002, *M. Elorsa* C. 6301 (TEX). Mpio. Tehuantepec: 12 km E of Tehuantepec, N exposure of the Cerro Guiengola, small tree 2 m tall, low deciduous forest with *Ruprechtia*, *Lonchocarpus*, *Mimosa goldmanii*, *Gyrocarpus americanus*, 320 m, 28 Dec 1986, *Dorado* 1638 (MEXU, TEX); subida al Cerro Guiengola por la ladera S, donde esta la fabrica de cal, arbusto 3 m, selva baja caducifolia, 25 Oct 1986, *Torres* C. 626 (MO).

Colubrina subsessilis has been collected in a small area just east and northeast of Tehuantepec (Map 12). Typical *C. triflora*, to which *C. subsessilis* is most similar, occurs in the same area, e.g., Mpio. San Pedro Huamelula: *Martínez* 32732 (MEXU). Mpio. Santiago Astata: *Martínez* 33147 (MEXU), *Elorsa* C. 871 (MEXU), *Elorsa* C. 845 (MEXU), *Elorsa* C. 2376 (MO).

18. COLUBRINA TEPICANA Standl. [nom. nov., based on *Cormonema mexicanum*], Contr. U.S. Nat. Herb. 23: 1672. 1926. *Cormonema mexicanum* Rose, Contr. U.S. Nat. Herb. 3: 315. 1895 (non *Colubrina mexicanum* Rose 1895). *Colubrina palmeri* Cowan [nom. nov., nom. superfl., based on *Cormonema mexicanum*], Brittonia 7: 405. 1952. *Colubrina spinosa* var. *mexicana* (Rose) M.C. Johnston, Wrightia 3: 93. 1963. *Colubrina glandulosa* subsp. *mexicana* (Rose) Borhidi, Acta Bot. Acad. Sci. Hung. 19: 44. 1973. TYPE: MEXICO. Nayarit. Tepic, 5 Jan-6 Feb 1892, *E. Palmer* 1977 (holotype: US image; isotypes: C, F, GH-Figs. 83-84, MICH-Fig. 85, S). The protologue added this observation to the label locality information: "only 2 trees seen near the mouth of a canyon."

Additional collections. MEXICO. Nayarit. Mpio. Compostela: Mountains 9 mi N of Compostela, locally abundant in moist barranca, steep heavily forested stream valley oak zone, 1000-1200 m, *McVaugh 16519* (MICH). **Mpio. Del Nayar:** Aguamilpa, 4 km antes de la Presa, *Flores 1864* (IEB, MEXU, fide Fernández Nava 2010, not seen). **Mpio. Tecuala:** Las Lumbres, Tecuala, *Vela 1437* (INIF, fide Fernández Nava 2010, not seen). Map 15.

Johnston (1963, 1971) regarded these plants as a variety with *Colubrina spinosa*, but the Mexican plants are distantly separated from the nearest populations of typical *C. spinosa* in Central America (Nicaragua, Costa Rica, Panama — see Pool 2015), and with the morphological differences, there is good reason to regard them as distinct species. *Colubrina tepicana* apparently is rare or uncommon and apparently restricted to Nayarit. The couplet below is based on the comparison by Johnston (1971).

- a. Plants 5–12 m tall; blades narrowly obovate to less commonly obovate-oblong, 8–21 cm long, 3.5–9 cm broad; stipules 3–4 mm long; thyrses sessile; seeds obovate, 5–6 mm long, 4–5 mm broad **Colubrina spinosa**
- a. Plants 3–5 m tall; blades elliptic-oblong to narrowly elliptic-obovate, 6.5–13.5 cm long, 3–6.5 cm broad; stipules 7–10 mm long; peduncles ca. 5 mm long; seeds nearly orbicular, 5–6 mm long, ca. 5.3 mm broad **Colubrina tepicana**

19. COLUBRINA TEQUILA Nesom, **sp. nov.** **TYPE: MEXICO. Jalisco.** [Mpio. Tequila], Salcillo, "fair-sized tree, open branched, bark like the oaks, on rocks and on hillsides," 1 Jun 1892, *M.E. Jones 419* (holotype: US, Figs. 59-62; isotype: MO).

Similar to *Colubrina ehrenbergii* in its lack of short shoots, thick, ovate leaves with relatively few, gland-tipped teeth, tawny vestiture, and sessile to subsessile flowers, but different in its arboreal habit, acuminate leaf apices, shorter styles, and disjunct geography (Map 10). Similar to *C. triflora* in leaf shape and inflorescence but different in the thick leaves, persistent, tawny vestiture, and flowers only on the youngest branches. Known only from the type collection.

Trees, stems stout, without thorns, without short shoots, young stems densely pubescent with tawny-orange hairs, glabrescent. **Leaves** alternate, blades coriaceous, bicolor (darker adaxially), ovate to ovate-lanceolate, 3–7 cm long, 2–3.5 cm wide, glaucous abaxially with a close reticulum of reddish veinlets, sparsely strigose adaxially with fine hairs, evenly pubescent abaxially with yellowish hairs on the epidermis and veins, veins camptodromous to subbrochidodromous with 3–4 pairs of arcuate secondary veins, weakly 3-veined from the base, apex acuminate, base rounded, margins coarsely serrate-dentate with 6–8 pairs of rounded, gland-tipped teeth, petioles 3–7 mm long. **Flowers** sessile to subsessile in epedunculate, axillary clusters of 8–10, only on the youngest branchlets; hypanthium and calyx lobes densely puberulent outside, glabrous within; petals folded around stamens; style ca. 0.3 mm long, the 3 branches hardly distinct from the stigmatic portion. **Fruits** not seen.

20. COLUBRINA TEXENSIS (Torr. & Gray) A. Gray, Boston J. Nat. Hist. 6(2): 169. 1850. *Rhamnus texensis* Torr. & Gray, Fl. N. Amer. 1(2): 263. 1838. **TYPE: USA. Texas.** No other locality information, 1833 or 1834, *T. Drummond II 67* (probable holotype: NY digital image!; isotypes: GH, US digital image!). Further comments on typification are in Nesom (2013).

Shrubs or small trees 1–2(–2.8) m high, unarmed, short shoots present. **Stems** zigzag, white tomentose-sericeous, becoming glabrate. **Leaves** deciduous, sometimes fascicled on short shoots, blades ovate to elliptic, oblong-obovate, or obovate, 1–3(–4) cm, subcoriaceous, apex rounded, often apiculate, base rounded to subcordate, margins shallowly serrate with 10–20 teeth per side, abaxial surface loosely sericeous, adaxial glabrate, pinnately veined, secondary veins (2–)3–4 pairs, arcuate, basal pair prominent, petioles 1–4 mm. **Flowers** solitary or in 2–4(–7)-flowered, epedunculate fascicles. **Fruits** 6–9 mm, fruiting pedicels 5–13 mm. Map 7. Figures 39-41.

In an earlier study (Nesom 2013), I regarded *Colubrina texensis* var. *pedunculata* (here as *C. villarrealii*) as conspecific with *C. stricta* — this was mistaken. *Colubrina stricta*, *C. texensis*, and *C. villarrealii* are distinct species, distinguished by the contrasts below.

- 1a. Short shoots absent; flowers (1–)2–8, in pedunculate thyrses (peduncles ca. 1 mm long) arising from axils of solitary leaves; pedicels 1–2 mm long, elongating in fruit to ca. 5 mm, usually strongly reflexed; branches relatively straight **Colubrina stricta**
- 1a. Short shoots present; flowers 1 or 2–4(–7), pedicellate in fascicles (no peduncle) arising from many-noded short shoots usually with 2 or more clustered leaves; pedicels 2–4 mm long, elongating in fruit to 6–13 mm, usually remaining straight; branches markedly zigzag **Colubrina texensis**
- 1b. Short shoots absent; flowers in a pedunculate cluster, pedicels 2–4 mm long, elongating in fruit to 6–13 mm; short shoots absent; stems relatively straight (vs. zigzag), never white **Colubrina stricta**
- 1b. Short shoots present; flowers sessile to subsessile (no peduncle) clusters; short shoots usually present; stems zigzag, often white when young.
2. Leaf blades with 10–20 teeth per side, and with 1–3 pairs of secondary veins; peduncles absent, pedicels in fascicles from short shoots, 2–4 mm long, elongating in fruit to 6–13 mm, remaining thin, relatively straight **Colubrina texensis**
2. Leaf blades with 15–30 teeth per side, and with 3–5 pairs of secondary veins; peduncles ca. 1 mm long, pedicels 1–2 mm long, thickening and elongating in fruit to ca. 5 mm, often recurving **Colubrina villarrealii**
- 21. COLUBRINA TRIFLORA** Brongn., Ann. Sci. Nat. (Paris) 10: 369. 1827. *Ceanothus triflorus* (Brongn.) Steud., Nomencl. ed. 2, 1: 313. 1840. *Rhamnus triflora* Sesse & Moc., Pl. Nov. Hisp./Naturaleza (Mexico City) ser. 2, 1, app. 68. 1888. **TYPE: MEXICO. [Michoacan].** Protologue: "Habitat in montibus inter oppidum Temascaltepec Coahuayanamque interiectis," Sesse & Mocino 813 (holotype: MA 602456).
- Rhamnus glomerata* Benth., Pl. Hartweg., 9. 1839. *Colubrina glomerata* (Benth.) Hemsley, Biol. Centr. Amer. 1: 200. 1880. **TYPE: MEXICO. Aguascalientes.** No other collection data, *T. Hartweg 40* (holotype: K; isotypes: E-GL, G, LD, P).
- Ziziphus acuminata* Benth., Bot. Voy. Sulph., 78. 1844 [non Royle 1835]. **TYPE: MEXICO. Guerrero.** Acapulco, 1843, *Barclay exs. 124* (holotype: K).
- Barcena guanajuatensis* Dugés, La Naturaleza 4: 281, t. 10. 1879. **TYPE: MEXICO. Guanajuato.** Near Mellada Mine, 1877, *A. Dugés s.n.* (holotype: MEXU fide Johnston 1971)
- Colubrina arborea* T.S. Brandegee, Zoe 4: 401. 1894. **TYPE: MEXICO. Baja California.** La Mesa, 24 Oct 1893, *T.S. Brandegee s.n.* (holotype: UC; isotypes: F, NY, US-2 sheets, YU). The locality is near San José del Cabo (Moran 1952).
- Colubrina mexicana* Rose, Contr. U.S. Natl. Herb. 3(5): 315. 1895. **TYPE: MEXICO. Sinaloa.** Culiacán, rich bottom lands, not common, 27 Aug-15 Sep 1891, *E. Palmer 1526* (holotype: US; isotypes: C, F, GH-Fig. 63, NY, RSA, S, U, W). In the protologue, Rose compared this plant to *Colubrina arborea*, the description of *Colubrina mexicana* immediately following that of *Cormonema mexicanum*, which he considered a different species (here = *C. tepicana*).
- Colubrina guatemalensis* Standl., Field Mus. Publ. Bot. 8: 22. 1930. **TYPE: GUATEMALA. Dept. Chimaltenango.** San Martín J. [Jilotepeque], 1800 m, 1928, *J. Morales-R. 1230* (holotype: F).
- Colubrina ehrenbergii* forma *glomeratoides* Suesseng., Repert. Spec. Nov. Regni Veg. 50: 325. 1941. **TYPE: MEXICO. Veracruz.** [Mpio. Puente Nacional]: Barranca de los Baños, Oct 1918, *C.A. Purpus 8245* (holotype: M? or [fide Johnston 1971] B destroyed; isotypes: MO, S, UC, US). The protologue did not cite a herbarium; Johnston (1971) selected the UC sheet as lectotype.

Colubrina mollis Lundell, Contr. Univ. Michigan Herb. 8: 75. 1942. **TYPE: MEXICO: Chiapas.** [Mpio. Mazapa/Motozintla]: Between Mazapa and Motozintla, tree 12-15 m high, 40 cm in diam., advanced forest, 1200 m, 19 Jul 1941, *E. Matuda 4873* (holotype: MICH; isotypes: A, CAS, F-2 sheets, LL, MEXU-2 sheets, MO, NY). See comments below.

Colubrina montana Rose ex Breedlove, Listados Floríst. México 4: 161. 1986. **TYPE: MEXICO. Guerrero.** Mountains above Iguala, 4000 ft, 3 Oct 1900, *C.G. Pringle 8414* (US, and BM, CM, E, F, K, M, MA, MEXU, MIN, MO, NDG, P-2 sheets, RSA, S, VT). Tropicos notes that this is a "nom. inval., without description, apparently based on herbarium name."

Colubrina triflora is perhaps the most widespread and abundantly collected species of the genus in Mexico (Map 11, Figures 63-67) — it extends southward into Central America as far as Costa Rica. It is variable in leaf morphology but usually correctly identified. *Colubrina subsessilis* is perhaps derived from *C. triflora*.

In the protologue of *Colubrina mollis*, Lundell noted this: "The large thin leaves and persistent soft pubescence of the undersurface of the blade are characteristics by which *C. mollis* may be readily separated from *C. glomerata* (Benth.) Hemsl. [= *Colubrina triflora*], the species to which it apparently has affinity." Standley's description of *C. guatemalensis* (as translated from Latin) — young stems short sordid-pilose, petioles pilose to puberulent, leaf blades abaxially densely tomentose with soft, brownish, often curled hairs. In the southwestern corner of Chiapas and into Guatemala, some plants match the types of *C. mollis* and *C. guatemalensis*, with large leaves and a dense vestiture of soft, orange hairs on the abaxial leaf and petioles. These are distinctive and might be recognized taxonomically, but intermediates exist with typical *C. triflora* -- examples: **Chiapas.** Mpio. Tzimol, *Breedlove 53724* (LL), *Stevens & Martinez 25803* (TEX); Mpio. Tuxtla Gutierrez, *Breedlove 13366* (LL-2 sheets); Mpio. La Trinitaria, *Breedlove 41211* (TEX), *42120* (LL), *47626* (TEX).

Colubrina triflora in the Rio Mayo region (Sonora) tend to produce only a single flower per inflorescence, but the same thing occurs sporadically elsewhere in the range of the species.

22. COLUBRINA VILLARREALII Nesom, **nom. et stat. nov.**. *Colubrina texensis* var. *pedunculata* M.C. Johnston, *Wrightia* 3: 94. 1963 (non *Colubrina pedunculata* Baker f. 1900). **TYPE: MEXICO. Coahuila.** Jimulco, mountains, 27 Apr 1885, *C.G. Pringle 144* (holotype: US; isotypes: A-Fig. 43, BM, BR, CINC, F, G-2 sheets, GH-2 sheets-Fig. 42, GOET, K, NY, PH, RSA, TEX). Johnston (by annotation, and by type citation in the *Colubrina* revision) notes that the collection was made just across the Coahuila border into Durango — Pringle noted in his collection book that he walked in early morning on April 27 four miles westward from the Estación Jimulco RR station (which is on the Coahuila-Durango border) "across the valley and mesa to a great cañon in the mountains" (the mountains there being the Sierra de Guadalupe).

Erect shrubs 1–2 m, unarmed, short shoots present, stems straight or slightly zigzag, loosely sericeous to glabrate. **Leaves** deciduous, alternate, blades ovate to ovate-oblong, 3–7.5 cm, pinnately veined with (3–)4–5 pairs of arcuate lateral veins (basal pair slightly more prominent), sparsely strigose and glabrate adaxially, persistently sparsely villous at least among the veins abaxially, margins serrulate with 40–70 villous-tufted teeth per side, apices rounded to acute, bases rounded to truncate, petioles 3–10 mm. **Flowers** 6–15 in axillary thyrses, peduncles 2–8 mm. **Fruits** 7–8 mm, fruiting pedicels 5–6 mm. Figures 42-45.

Flowering Mar–Jun. Arroyo banks, canyons, hills, usually over limestone or gypseous limestone, chaparral and matorral, commonly with *Larrea-Acacia-Fouquieria* or a combination of *Agave*, *Celtis*, *Dasyliirion*, *Emorya*, *Fraxinus*, *Mimosa*, *Prosopis*, *Rhus*, *Sophora*, *Yucca*; 250–1800 m; Tex.; Mexico (Chihuahua, Coahuila, Durango). Map 7.

The epithet recognizes José A. Villarreal-Quintanilla, Departamento de Botánica, Universidad Autónoma Agraria Antonio Narro in Saltillo, excellent botanist of field and herbarium.

Short shoots in *Colubrina villarrealii* are indeterminate — they can become elongated and often produce additional lengths of stem (e.g., Fig. 44, *Henrickson 13074*). See contrasts under *C. texensis*.

Additional collections. Chihuahua. Mpio. Camargo: 5 km S of jct with rd to Ojinaga on eastern hwy from Jiménez to Camargo, 18.8 km S of Camargo, 27° 36' N, 105° 01' W, *Larrea, Acacia, Fouquieria, Tetracoccus*, 1325 m, 8 Jul 1972, *Chiang et al. 8323* (LL, MEXU, MO). **Mpio. Jiménez:** Canyon del Apache, SE quadrant of Sierra del Diablo, 27° 10' 30" N, 104° 01' W, steep-walled canyon through limestone sierra, matorral desértico con espinas laterales o izotal, *Fraxinus greggii, Yucca carnerosana, Dasylyrion, Mimosa biuncifera*, 1550-1650 m, 30 Aug 1972, *Chiang et al. 9035B* (LL, MEXU); 3 km S of Rancho La Gloria, arroyo in broad valley from W side of limestone Sierra del Diablo, 27° 18' 30" N, 104° 13' W, matorral inerme y con espinas laterales, 1450 m, 29 Aug 1972, *Johnston et al. 8989* (LL, MEXU, MO); Cañon del Rayo, a large canyon on the NE side towards the N end of the Sierra del Diablo, fairly common shrub 1-2 m tall, arroyo banks at canyon mouth, 25-29 Jul 1941, *Stewart 868* (MEXU) and *Stewart 868-A* (LL). **Coahuila. Mpio. Acuña:** 25 km S by winding road from Rancho Chupadero del Caballo toward Las Norias in Cañon del Colorado, 29° 25' N, 102° 02' W, broad valley through limestone hills, matorral inerme, *Emorya, Dasylyrion, Sophora*, 900 m, 12 Sep 1972, *Chiang et al. 9174* (MEXU, MO); Cañon del Colorado in NW quadrant of Serranías del Burro, 27 road km SW of Rancho Chupadero del Caballo, 29° 25' N, 102° 04' W, shrub to 3 m high, bouldery dry arroyo bed thickets, 850 m, matorral, *Rhus, Prosopis, Dasylyrion*, 28 May 1973, *Johnston et al. 11268* (MEXU). **Mpio. Cuatrociénegas:** 1.5 km NE Rancho da San Marcos, on the western edge of the Sierra de San Marcos, 12 Jun 1972, *Chiang et al. 7683* (LL, MEXU, MO); Cañón de la Fora, 7 km W of Estación Socorro on the Cuatro Ciénegas-Esmeralda road, 26° 56' N, 102° 28' W, 3 Sep 1972, *Chiang 9150* (LL, MEXU); Sierra de los Alamitos, 4.3 road mi up the roadway from Hwy 30 (at KM 149), 26° 31.82' N, 102° 26.53' W, limestone rocky canyon, shrubs 5 ft high, with *Acacia, Larrea, Opuntia, Viguiera, Jatropa, Grusonia, Tecoma, Euphorbia antisyphilitica, Hechtia, Croton, Gymnosperma*, 2950 ft, 30 Aug 2004, *Henrickson 23891* (MEXU, MO); Sierra de los Alamitos, 9.6 road mi up the roadway from Hwy 30 (at KM 149), 26° 27' N, 102° 25' W, limestone rocky canyon, shrubs 6 ft high, with *Hechtia, Euphorbia antisyphilitica, Opuntia, Grusonia, Echinocereus, Acacia, Lippia, Randia, Mortonia, Jatropa, Gymnosperma*, 3400 ft, 30 Aug 2004, *Henrickson 23936* (MEXU, MO); Cuatro Ciénegas Basin, Puerto San Marcos, ca. 1.8 mi S of Rancho San Marcos, 10 Jun 1968, *Lehto 5317* (ASU); Cuatro Ciénegas Basin, Sierra San Marcos opposite Laguna Grande, 26.703022 -101.897401, lower canyon and bajada, SW-facing slopes, *Agave, Hechtia, Jatropa, Acacia, Yucca*, 14 Aug 1975, *Pinkava P-13080* (ASU, LL). **Mpio. San Pedro:** ca. 32 (air) mi NE of San Pedro, 1 mi SW of Las Delicias, 26.23333 -102.81667, 27 Aug 1971, *Henrickson 6058* (LL); ca. 15 (air) mi NW of Las Delicias, in broad S-draining arroyo N of Sierra de las Delicias, 26.33333 -102.85, 29 Aug 1971, *Henrickson 6088* (LL); 26 (air) mi W of Cuatro Ciénegas, near Est. Socorro, 26.95 -102.55, 21 Sep 1972, *Henrickson 7923* (LL); 28.3 (road) mi W of Cuatro Cienegas towards Esmeralda, limestone arroyo-canyon along railroad, 26° 55' N 102° 30' W, shrub to 5 ft high, arroyo-canyon along railroad, limestone, 3500 ft, *Chilopsis, Anisacanthus, Acacia*, etc., 7 Aug 1973, *Henrickson 12046b* (ARIZ, MEXU, SRSC); ca. 72 (air) mi SW of Cuatro Cienegas, on E side of Sierra de las Delicias, around spring 1.5 mi SW of Las Delicias, shrub to 12 ft high, below spring, with *Mortonia, Varilla, Acacia*, 3550 ft, 12 Aug 1973, *Henrickson 12258* (MEXU). **Mpio. Jimulco:** ca. 26 (air) mi SE of Torreón, in lower mouth of NE-SW running canyon of Sierra de Jimulco, 4 mi S of La Rosita, 25° 13' N, 103° 13' W, shrub to 4 ft tall, lower limestone alluvial fan of La Rosita, 4500 ft, with *Acacia, Yucca, Agave, Dasylyrion, Celtis, Fouquieria, Cordia, Cassia, Chilopsis, Eysenhardtia, Lantana*, 17 Sep 1973, *Henrickson 13074* (LL, MEXU); ca. 27 (air) mi SE of Torreón, in a broad canyon on N side of Sierra de Jimulco, S of La Rosita, 25° 13' N, 103° 13' W, much-branched thorny shrub, with *Viguiera, Acacia, Forestiera, Dalea, Chilopsis, Opuntia, Anisacanthus, Croton*, 1300-1500 m, 29 Apr 1977, *Henrickson 15869* (LL, MEXU, NMC); Sierra de Jimulco, N side, steep canyon, 1700-2100 m, chaparral, *Dasylyrion, Garrya, Arctostaphylos, Gochnatia, Sageretia, Agave*, 28 Jun 1973, *Johnston et al. 11506* (MEXU, MO); Sierra de Jimulco, E de la mina de San José, 25° 06' N, 103° 13' W, matorral de *Agave, Gochnatia, Acacia, Cercocarpus*, 2100 m, 21 Oct 1989, *Villarreal et al. 5526* (MEXU, TEX). **Mpio. Monclova:** Monclova, 5 May 1939, *Marsh 1690* (TEX). **Mpio. Muzquiz:** Rancho Agua Dulce, [28.4234, -101.9203], 1936, [*Herbario Inst. Biol.*] 4882 (MEXU). **Mpio. Ocampo:** Americanos, [27° 10' 33" N, 103° 17' 10" W], 1937,

[*Herbario Inst. Biol.*] 759 (MEXU); 25 mi E of Americanos, 22 Aug 1937, Wynd 759 (MO). Mpio. Parras: Sierra de Parras, ca. 15 km WNW de Menchaca rumbo al Amparo, 14 Apr 1981, *Rodríguez s.n.* (LL). Mpio. San Pedro: ca. 32 (air) mi NE of San Pedro, 1 mi SW of Las Delicias, 26.23333 -102.81667, 27 Aug 1971, *Henrickson 6058* (LL); ca. 15 (air) mi NW of Las Delicias, in broad S-draining arroyo N of Sierra de las Delicias, 26.33333 -102.85, 29 Aug 1971, *Henrickson 6088* (LL); 26 (air) mi W of Cuatro Ciénegas, near Est. Socorro, 26.95 -102.55, 21 Sep 1972, *Henrickson 7923* (LL); 28.3 (road) mi W of Cuatro Cienegas towards Esmeralda, 26° 55' N 102° 30' W, shrub to 5 ft high, arroyo-canyon along railroad, limestone, 3500 ft, *Chilopsis*, *Anisacanthus*, *Acacia*, etc., 7 Aug 1973, *Henrickson 12046b* (ARIZ, MEXU, SRSC); ca. 72 (air) mi SW of Cuatro Cienegas, on E side of Sierra de las Delicias, around spring 1.5 mi SW of Las Delicias, shrub to 12 ft high, below spring, with *Mortonia*, *Varilla*, *Acacia*, 3550 ft, 12 Aug 1973, *Henrickson 12258* (MEXU). Mpio. Torreón: NW flank of Sierra del Venado ca. 12 km airline or 16.5 km by winding road NE of Las Margaritas, side canyon in W side of a gypseous-limestone sierra, 26° 33' N, 102° 43' 30" W, 1000 m, 23 Sep 1972, *Chiang et al. 9487* (LL, MEXU, MO); 12.6 km NNE of Las Margaritas in a large canyon in the E face of the Sierra de las Margaritas, 26° 34' N, 102° 51' W, steep limestone and gypseous slopes, 1150-1350 m, 24 Sep 1972, *Chiang et al. 9506* (MO). Mpio. Viesca: 11 km N of Ahuichila, Cañón de Ahuichila, 25° 12' N, 102° 39' W, *Sericodes*, *Yucca*, *Larrea*, *Acacia*, 1250-1500 m, 15 Jun 1972, *Chiang et al. 7813* (LL, MEXU); San Lorenzo de Laguna, 70 mi SW of Parras, 1-10 May 1880, *Palmer 169* (MO); Sierra El Número, 33 km S de Viesca, 25° 08' N, 102° 39' W, matorral de *Acacia crassifolia*, *Agave lechuguilla*, *Agave scabra*, *Viguiera*, *Larrea*, 1160 m, 9 Aug 1994, *Villarreal 7765* (MEXU-2 sheets). Durango. Mpio. Cuencamé: Cuencamé, arroyo El Trejo, camino a Guadalupe Victoria, carretera 40, 24° 46' 47" N, 103° 44' 42" W, arbusto, orilla de arroyo, matorral xerófilo, 1800 m, 24 May 1999, *M. González 3044* (MEXU); 23.3 road mi by Hwy 45 S of jct Hwys 45 and 30 (La Zarca), 6.2 road mi N of Alamillo (25° 30' N, 104° 40' W), desert scrub, 1800 m, 20 Aug 1983, *Worthington 11097* (MO, UTEP). Mpio. Mapimí: NW third of Sierra del Rosario, steep limestone sierra, 25.7 -103.95, *Lindleya*, *Garrya*, *Rhus virens*, *Arctostaphylos*, *Agave macroculmis*, *Agave parrasana*, 25 Jun 1973, *Johnston et al. 11462* (LL, MEXU, MO); W foot of Sierra del Rosario, 4 km E of Rancho Santa Rita, 6 km N of Santa Ines, 7 km S of Ejido Santa Librada, 3 Jul 1986, *Sanders 101* (TEX); W foot of Sierra del Rosario, 4.0 km E of Rancho Santa Rita, 6.0 km N of Santa Ines, 7.0 km S of Ejido Santa Librada, 25.7 -103.96667, uncommon, alluvial fan cut by a large arroyo, with *Larrea*, 1676 m, 3 Jul 1986, *Sanders 6722* (SD, UCR). Mpio. Rodeo: 3 km N de Linares del Río, 25° N, 104° W, arbusto 1.5 m, 18 Jun 1997, *García 3.2* (MEXU); 6 km NW de Las Higueras, arbusto 1 m, matorral espinoso con *Brahea*, *Cnidosculus*, 4 Sep 1983, *Torrecillas 176* (MEXU). [Mpio. ??]: 95 mi NE of Durango, 8 Aug 1957, *Waterfall 13332* (TEX).

23. COLUBRINA VIRIDIS (M.E. Jones) M.C. Johnston, *Wrightia* 3: 93. 1964. *Phyllanthus viridis* M.E. Jones, *Contr. W. Bot.* 18: 47. 1933. **TYPE: MEXICO. Baja California Sur.** [Mpio La Paz]: Cacachilla Mountains [Sierra de la Cacachilas], 2 Oct 1930, *M.E. Jones 27503* (holotype: RSA; isotypes: CAS, NY, US).

Colubrina glabra S. Wats., *Proc. Amer. Acad. Arts* 24: 44. 1889 (non Nutt. 1846). **TYPE: MEXICO. Sonora.** Ravines about Guaymas, *E. Palmer 200* (holotype: GH; isotypes: C, MEXU, NY, P, S).

Shrubs with short shoots, without thorns. **Leaves** relatively small, pastel green on both sides, elliptic to obovate-elliptic or obovate, pinnate-veined without a pair from the very base, margins entire, petioles often filiform. **Flowers** in epedunculate clusters from the short shoots, pedicels usually elongating in fruit. See *C. neoviridis* for comments. Map 9. Figures 46-50.

24. COLUBRINA YUCATANENSIS (M.C. Johnston) Nesom, *Phytoneuron* 4: 20. 2013. *Colubrina greggii* var. *yucatanensis* M.C. Johnston, *Wrightia* 3: 95. 1963. **TYPE: MEXICO. Yucatán.** Chichen Itza, near Sacred Cenote, in low second growth, 29 May 1938, *C.L. Lundell & A.A. Lundell 7310* (holotype: LL digital image!; isotype: US-digital image!).

Shrubs 1–4 m or trees up to 12 m, trunks up to 4 inches in diam., without short shoots, without thorns. **Leaves:** blades oblong-lanceolate, widest at the middle, 6–12 x 3–7 m, lateral veins 5–7(–9)

pairs, apex acute to slightly and short-acuminate, base rounded to truncate. **Peduncles** (5–)14–18 mm. **Flowers** yellow-green to greenish, 30–80 per thyrse.

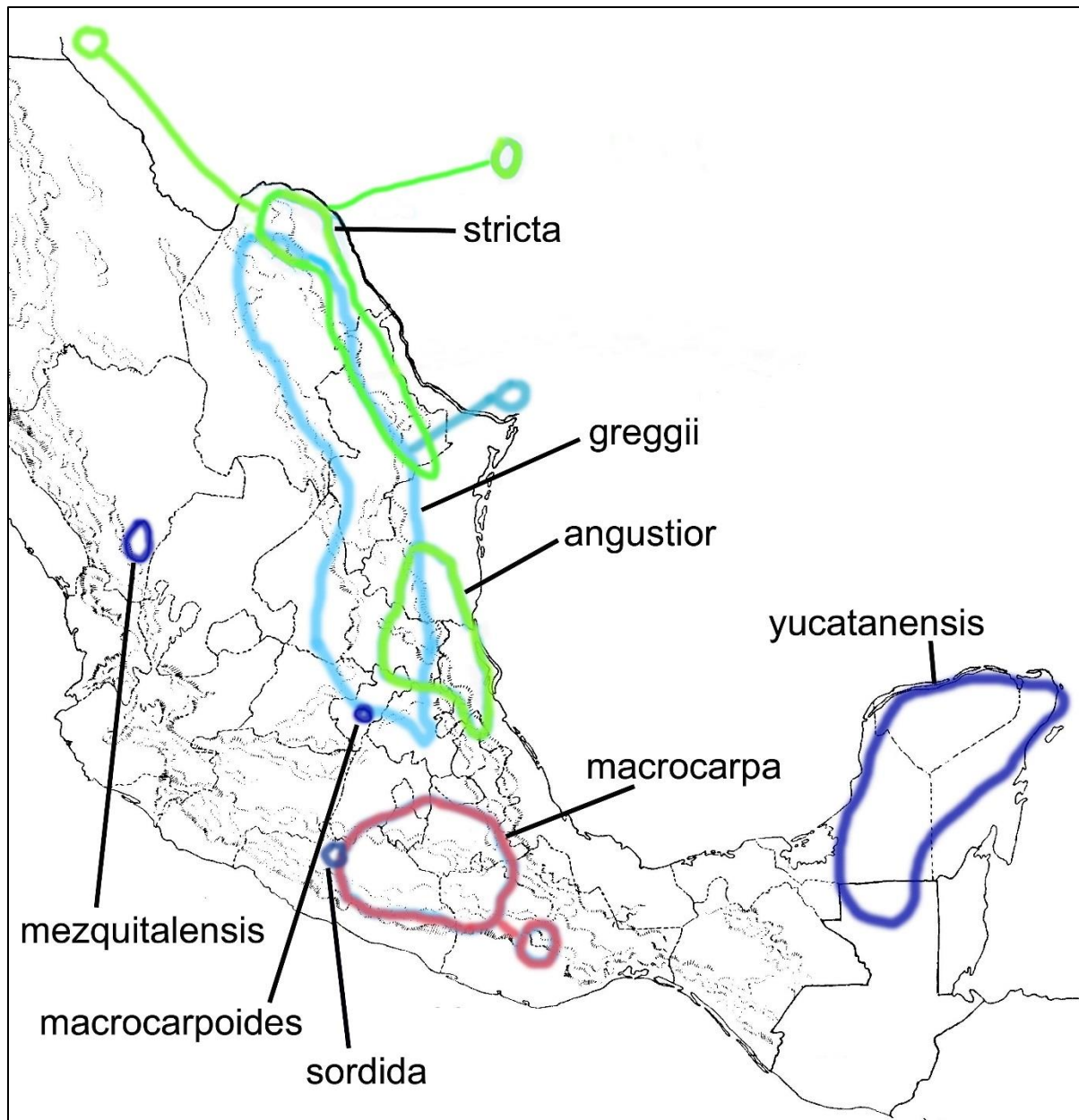
These plants are morphologically distinct and distantly separated in geography from typical *Colubrina greggii*, with which it has been considered conspecific. Map 3.

ACKNOWLEDGEMENTS

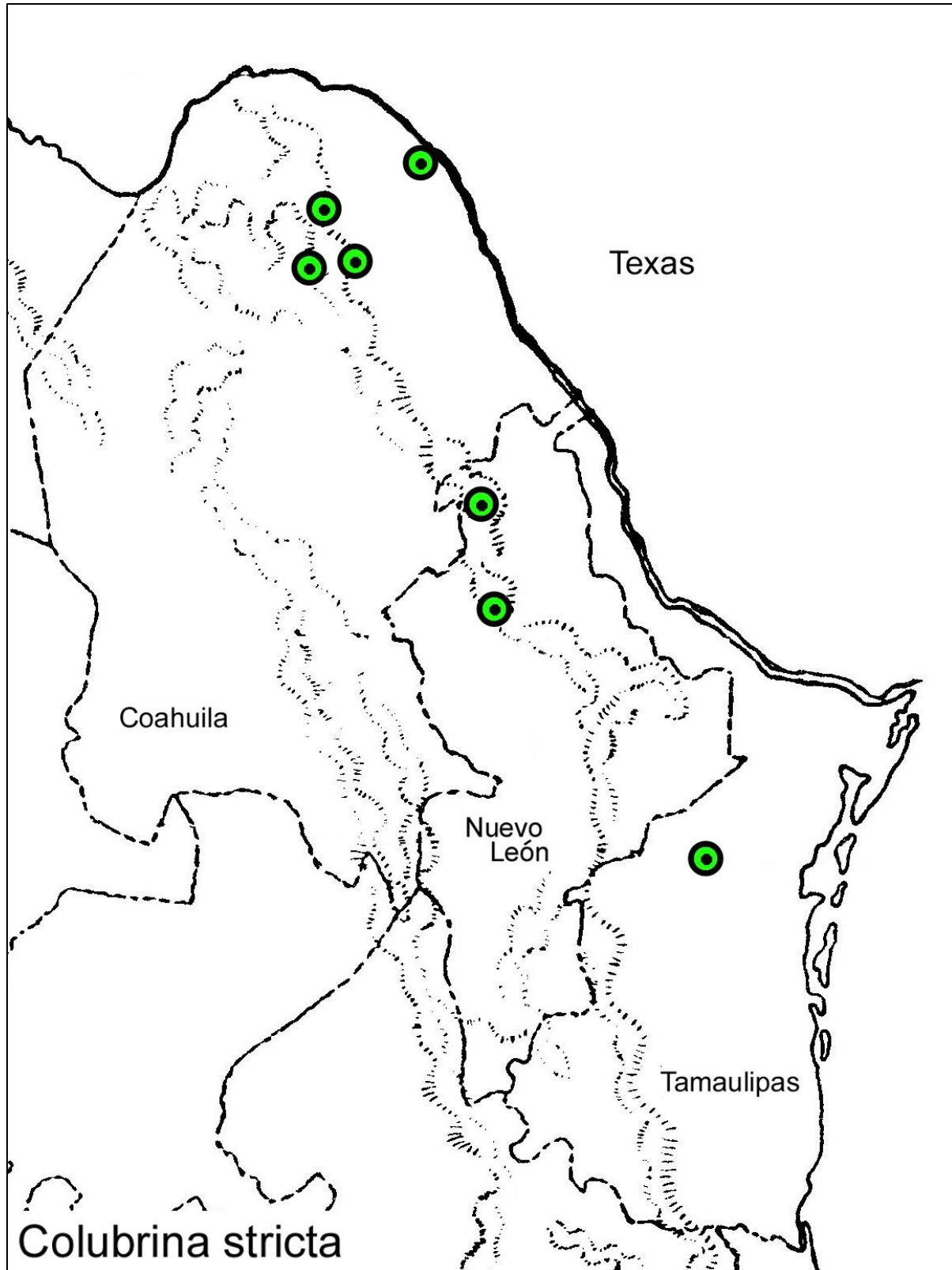
Dr. Pablo Reyes searched in IBUG for additional collections of *Colubrina lanceolata*, *C. tequila*, and the anomalous red-stemmed plant referred to under *C. heteroneura* but was unable to find any. Many thanks to George Yatskievych (TEX, LL) for various hi-res photos and to Andy Sanders (UCR) for comments on the distribution of type specimens of *C. lanceolata*.

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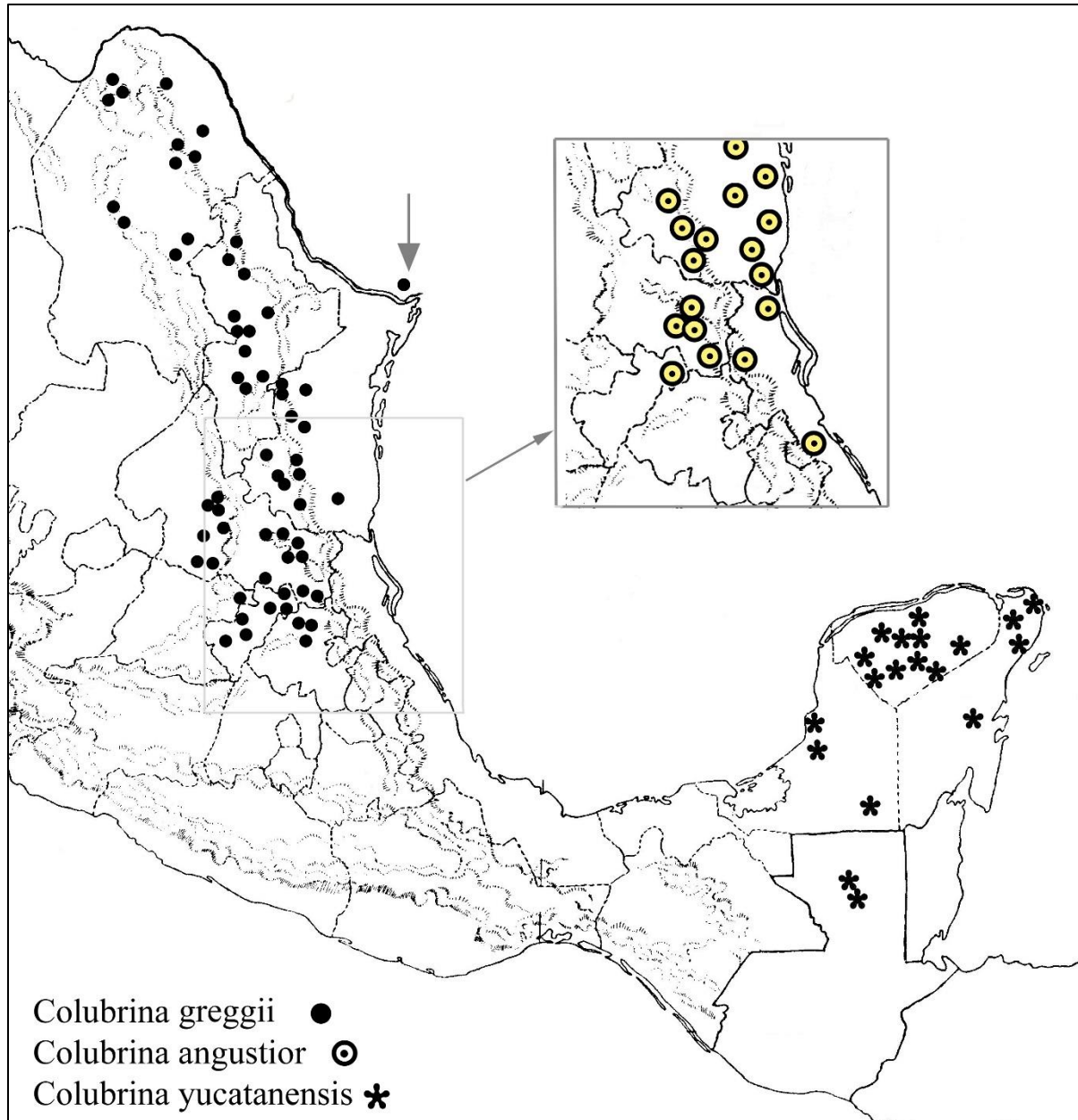
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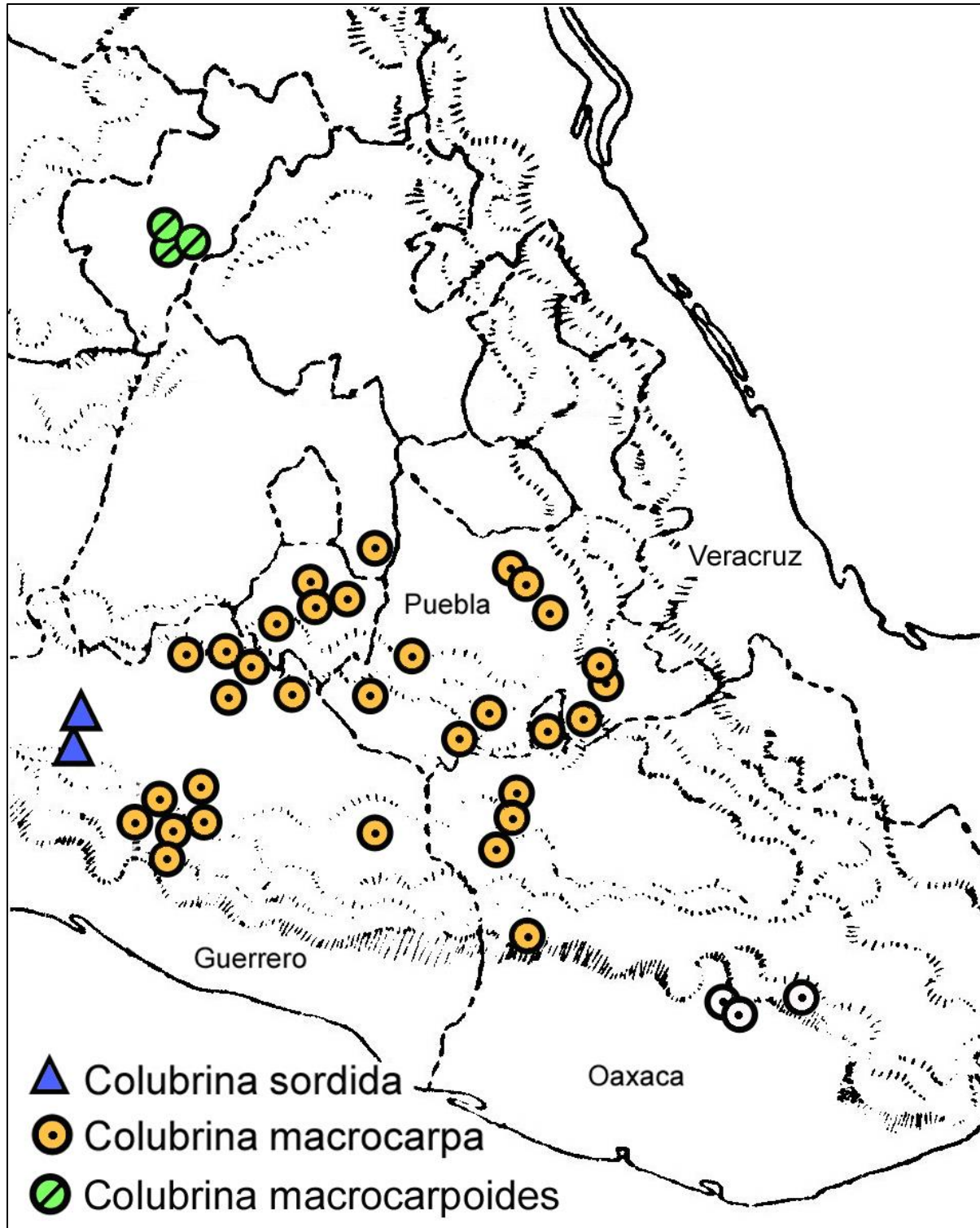
Map 1. The *Colubrina greggii* group — *Colubrina stricta*, *C. greggii*, *C. angustior*, *C. yucatanensis*, *C. macrocarpa*, *C. macrocarpoides*, and *C. mezquitalensis*. Outliers are shown for *C. stricta*, *C. greggii*, and *C. macrocarpa*. These species are members of sect. *Serrataria*, as defined in Johnston (1971). Johnston also included *C. californica*, *C. texensis*, and *C. texensis* var. *pedunculata* (= *C. villarrealii*), but these are distinct in their production of short shoots and their phylogenetic position needs to be further investigated. The Caribbean species *C. cubensis* (the type of the section) and *C. berteroana* were also placed by Johnston in sect. *Serrataria* — they lack short shoots and otherwise fit well with the Mexican species. The Asiatic species *C. anomala*, *C. asiatica*, *C. beccariana*, *C. pedunculata*, and *C. travancorica*, with large, glabrous, and thickened leaves and tropical to subtropical habitats, seem out of place in the section.



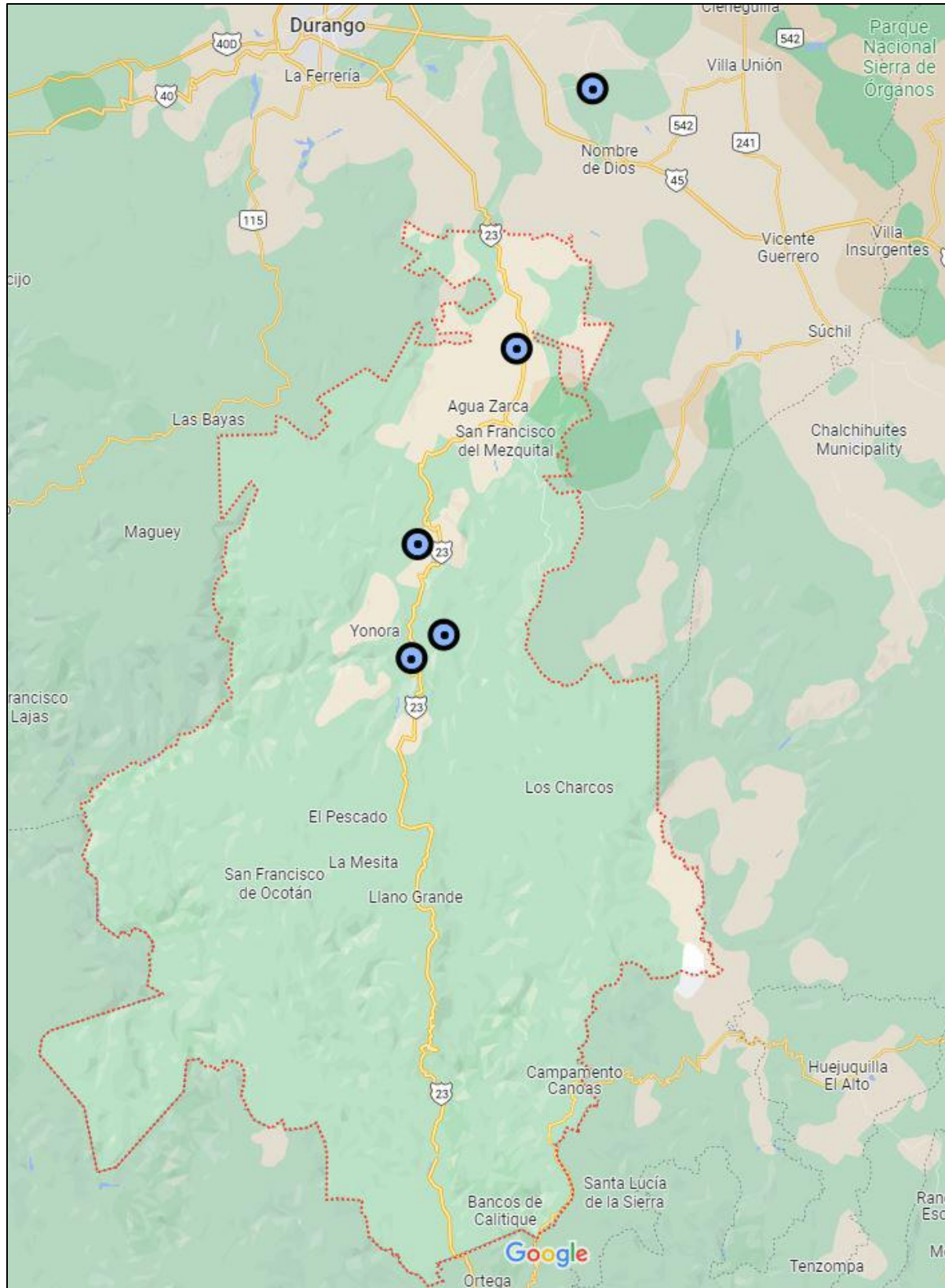
Map 2. Distribution of *Colubrina stricta* in Mexico. It also occurs in Texas in two widely separated localities — El Paso County and Comal County.



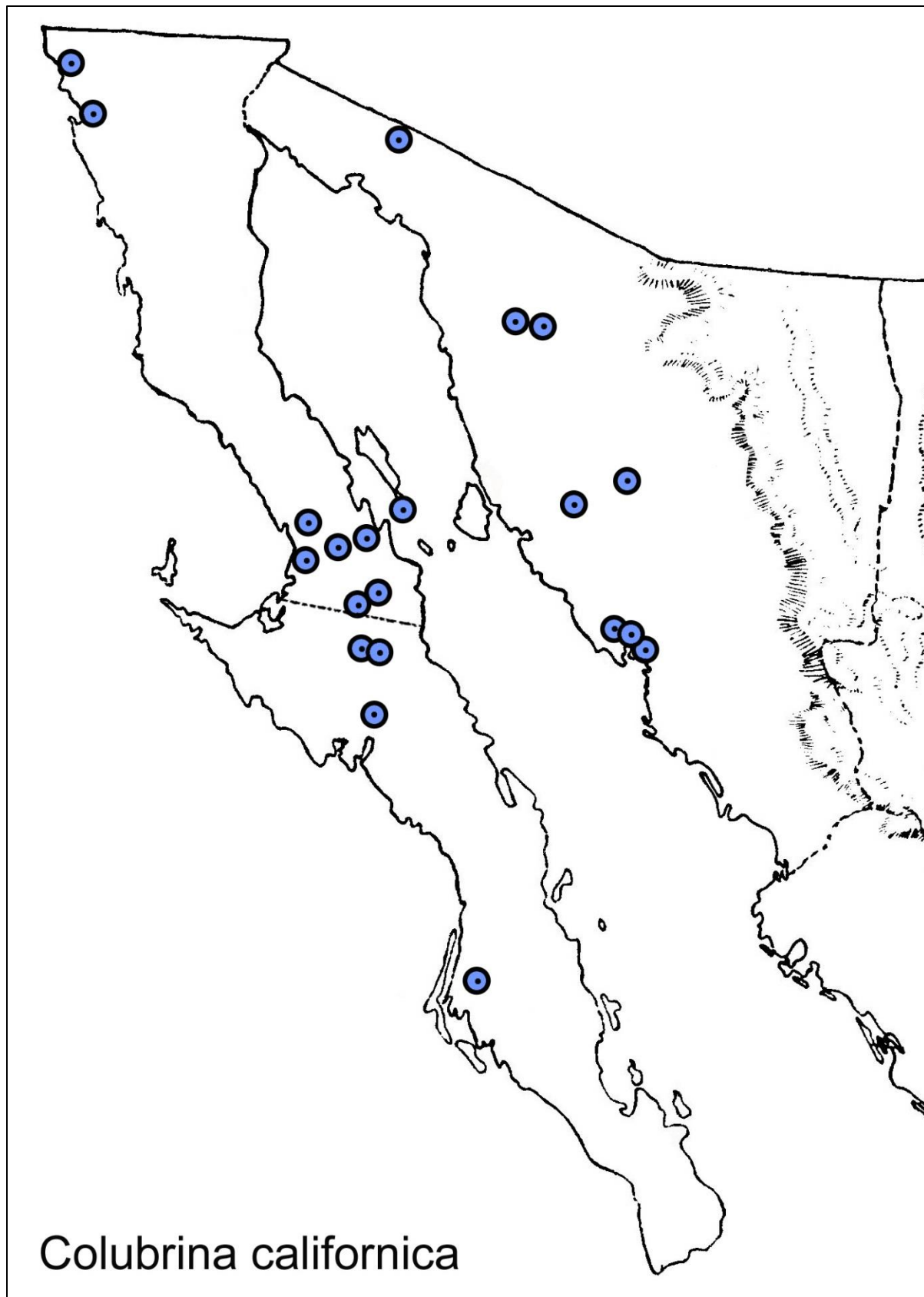
Map 3. Distribution of *Colubrina greggii*, *C. angustior*, and *C. yucatanensis*. *Colubrina greggii* and *C. angustior* are sympatric in east-central Nuevo León, Tamaulipas, and central San Luis Potosí. The downward arrow points to the locality in Cameron Co., Texas (see Fig. 3).



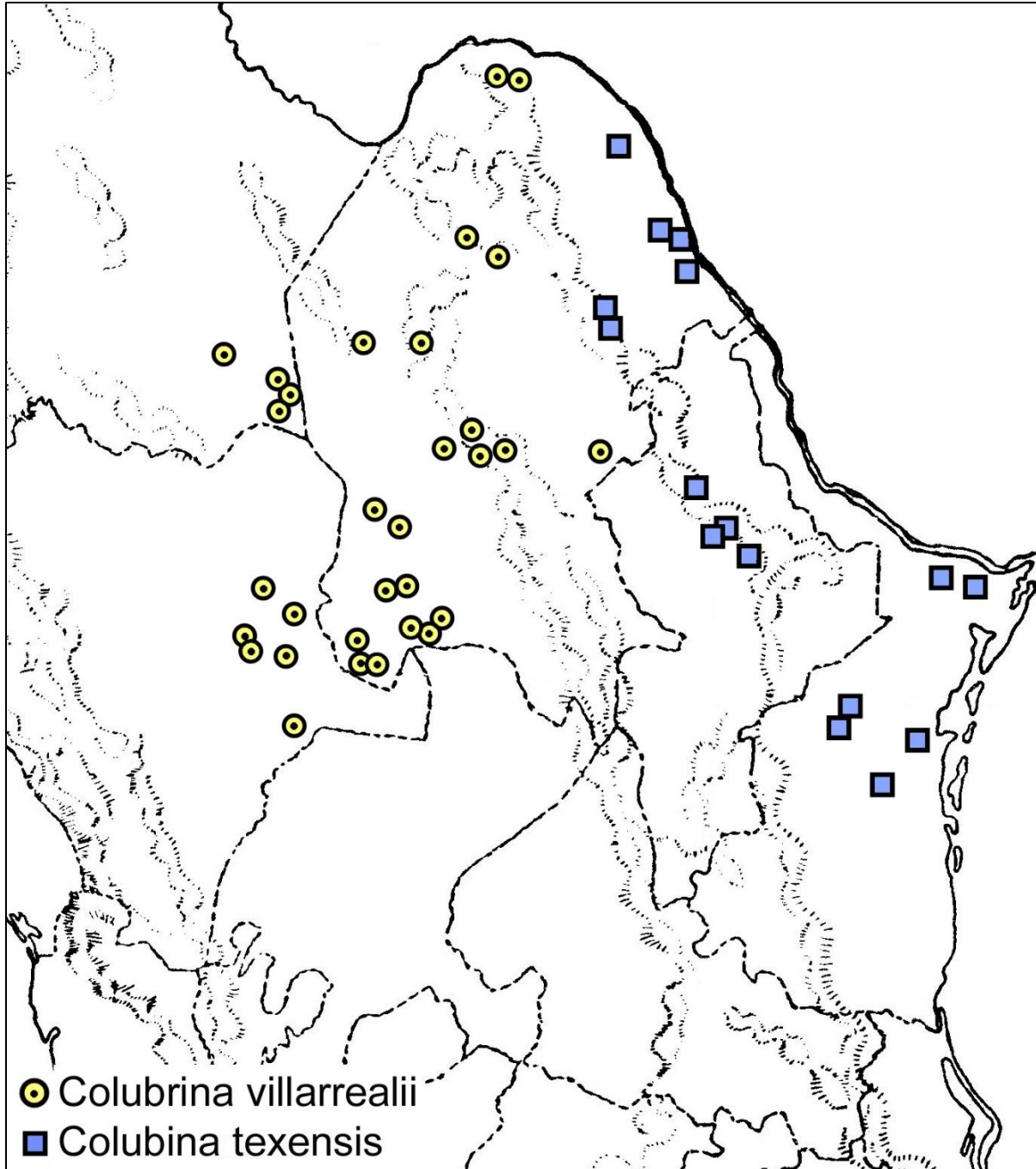
Map 4. Distribution of *Colubrina sordida*, *C. macrocarpa*, and *C. macrocarpoides*.



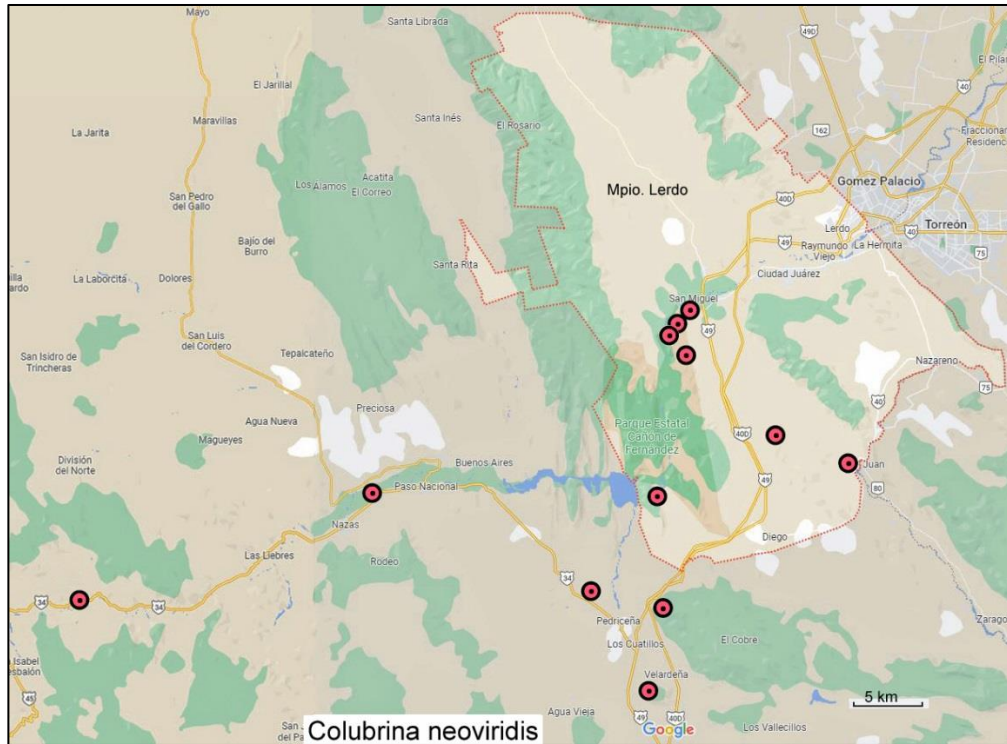
Map 5. Distribution of *Colubrina mezquitalensis*. Mpio. Mezquital, Durango, is outlined in red.



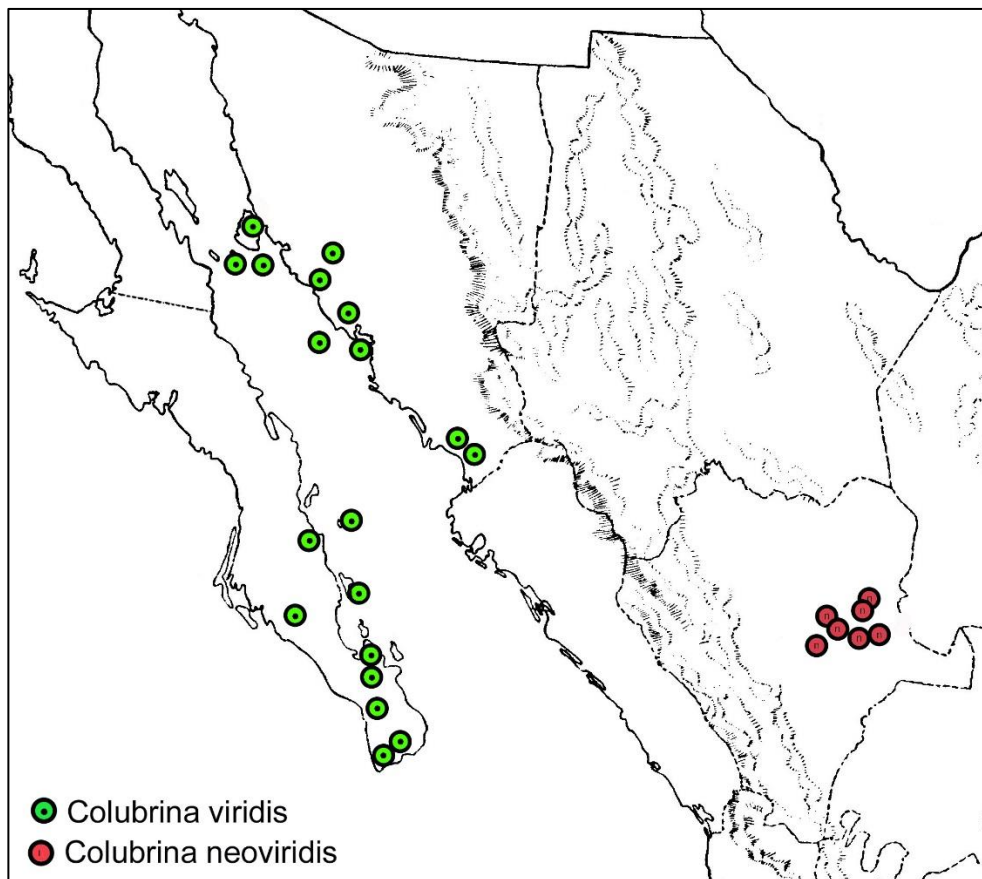
Map 6. Distribution of *Colubrina californica* in Mexico.



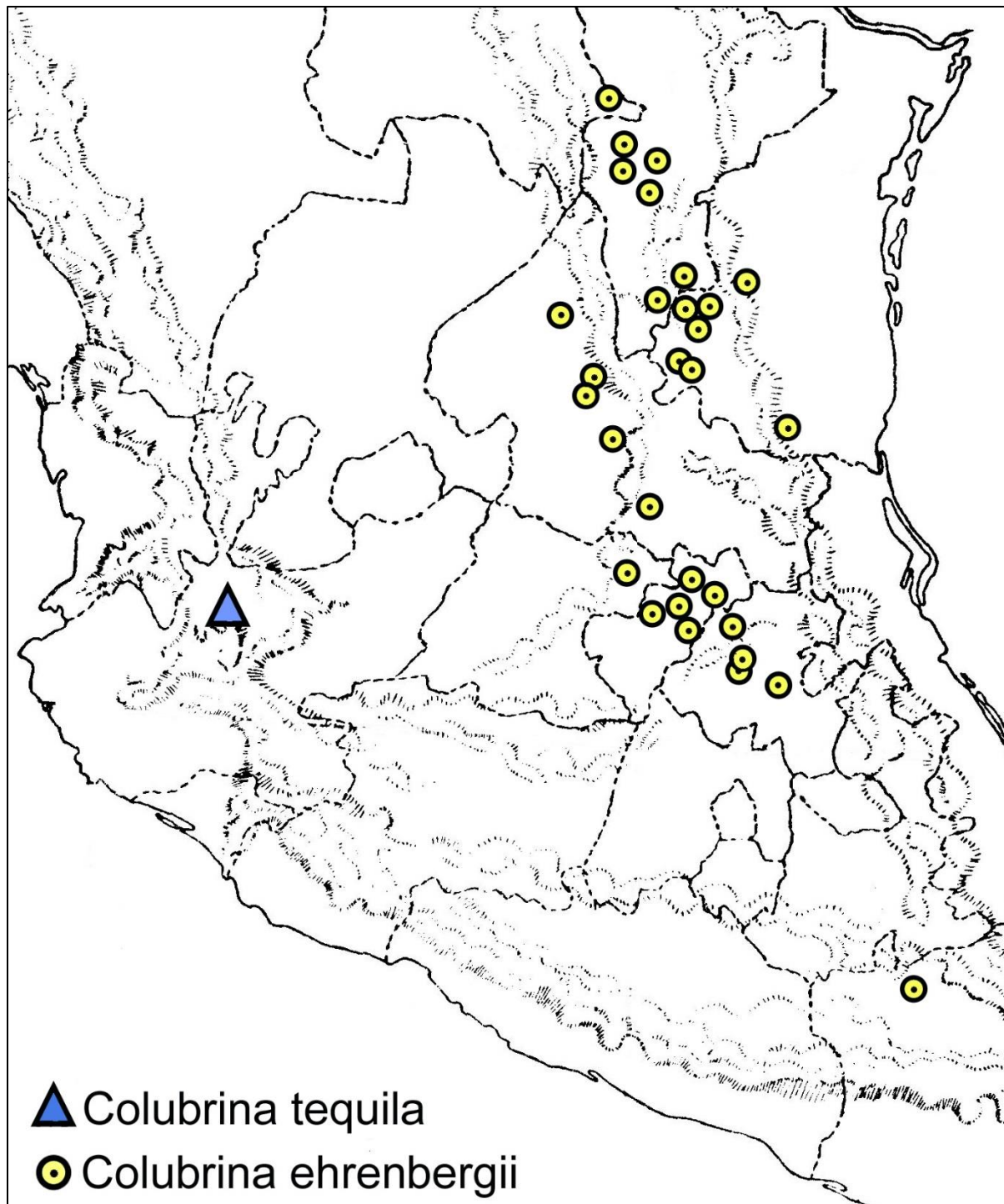
Map 7. Distribution of *Colubrina texensis* and *C. villarrealii*.



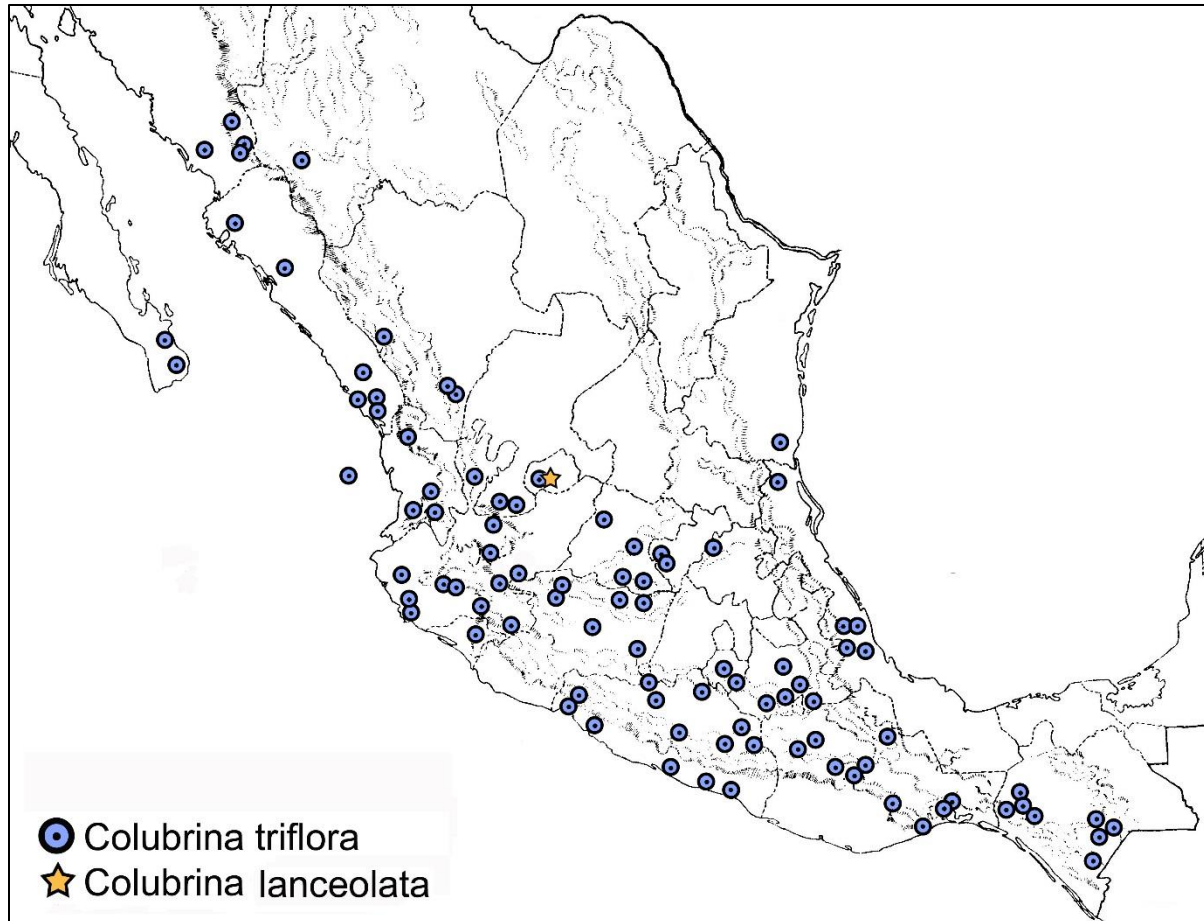
Map 8. Distribution of *Colubrina neoviridis*. The red outline shows Mpio. Lerdo in Durango.



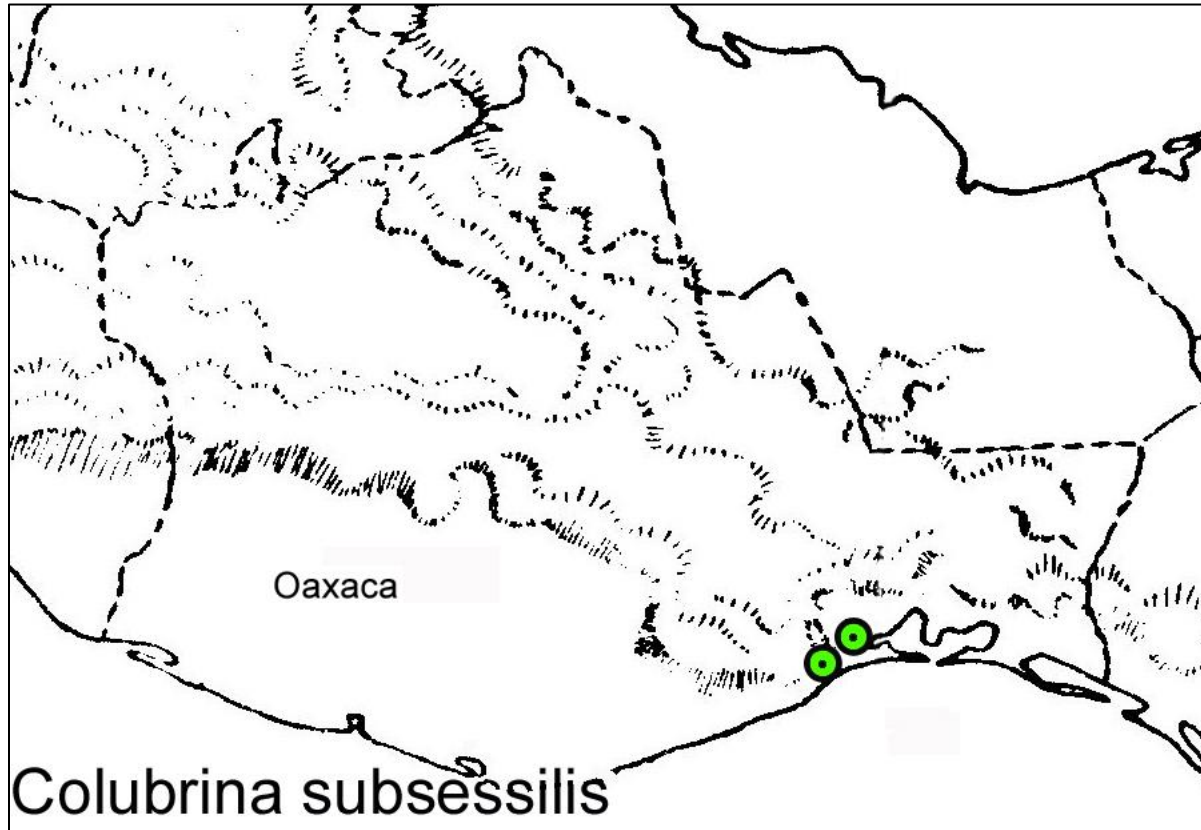
Map 9. Distribution of *Colubrina viridis* and *C. neoviridis*.



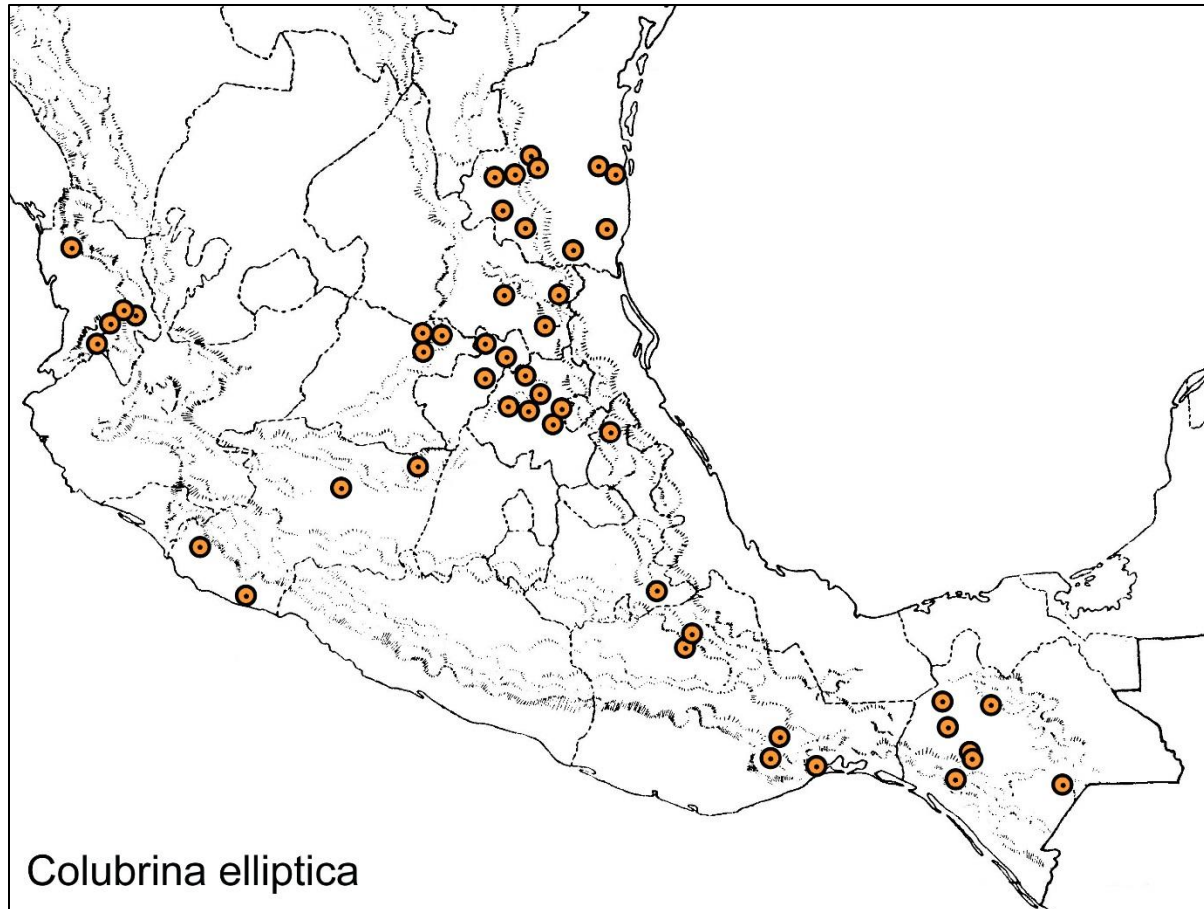
Map 10. Distribution of *Colubrina ehrenbergii* and *C. tequila*. The Oaxaca record, a collection of typical *C. ehrenbergii*, is cited in the text.



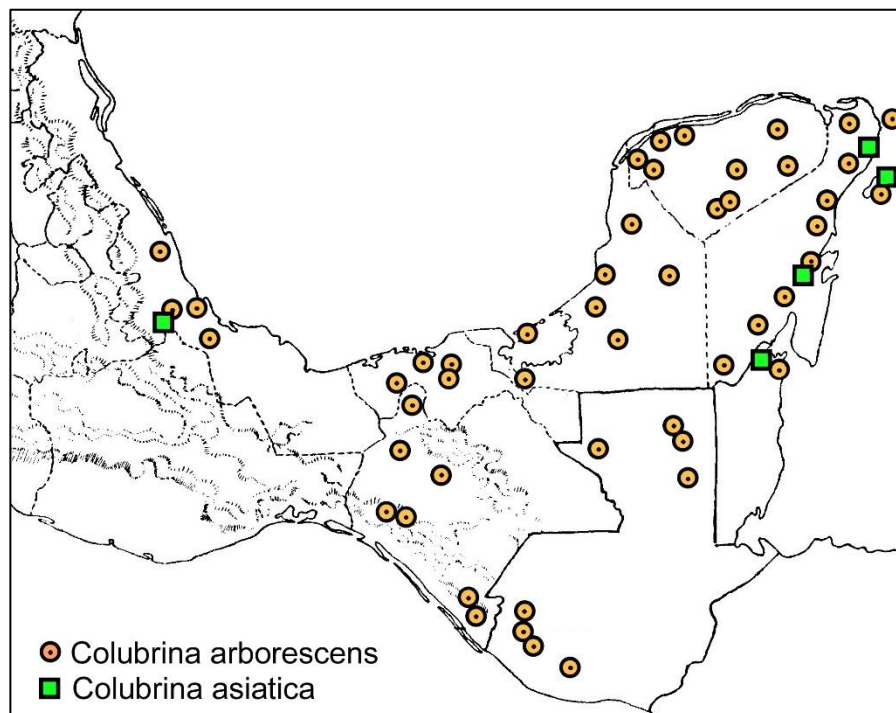
Map 11. Distribution of *Colubrina triflora* in Mexico and *C. lanceolata* (Aguascalientes). The two species occur in close proximity in Aguascalientes (bottom map).



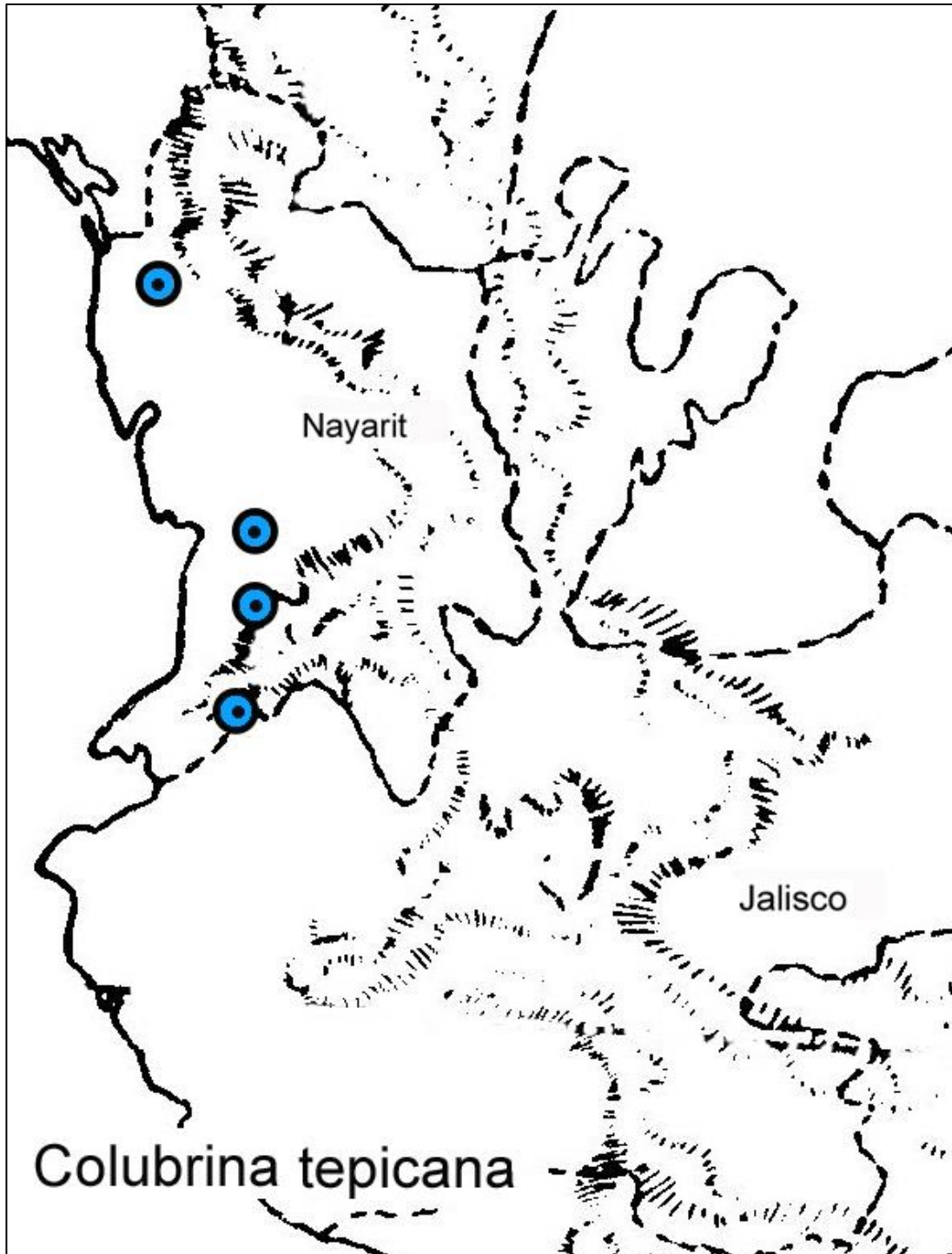
Map 12. Distribution of *Colubrina subsessilis*. The red outline shows Mpio. Tehuantepec.



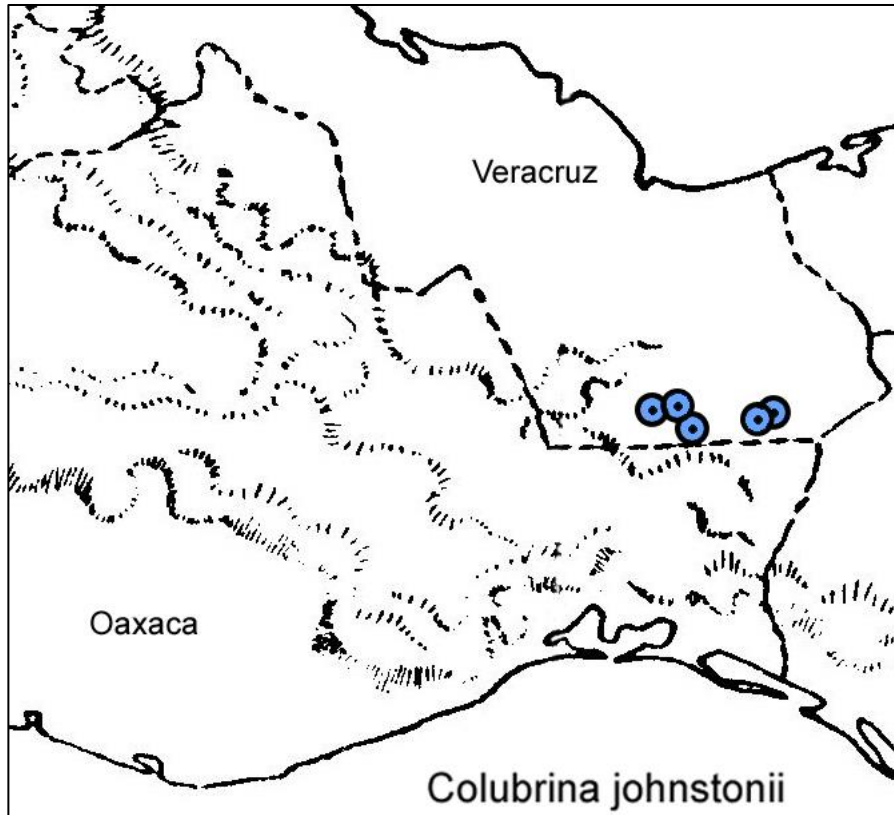
Map 13. Distribution of *Colubrina elliptica* in Mexico.



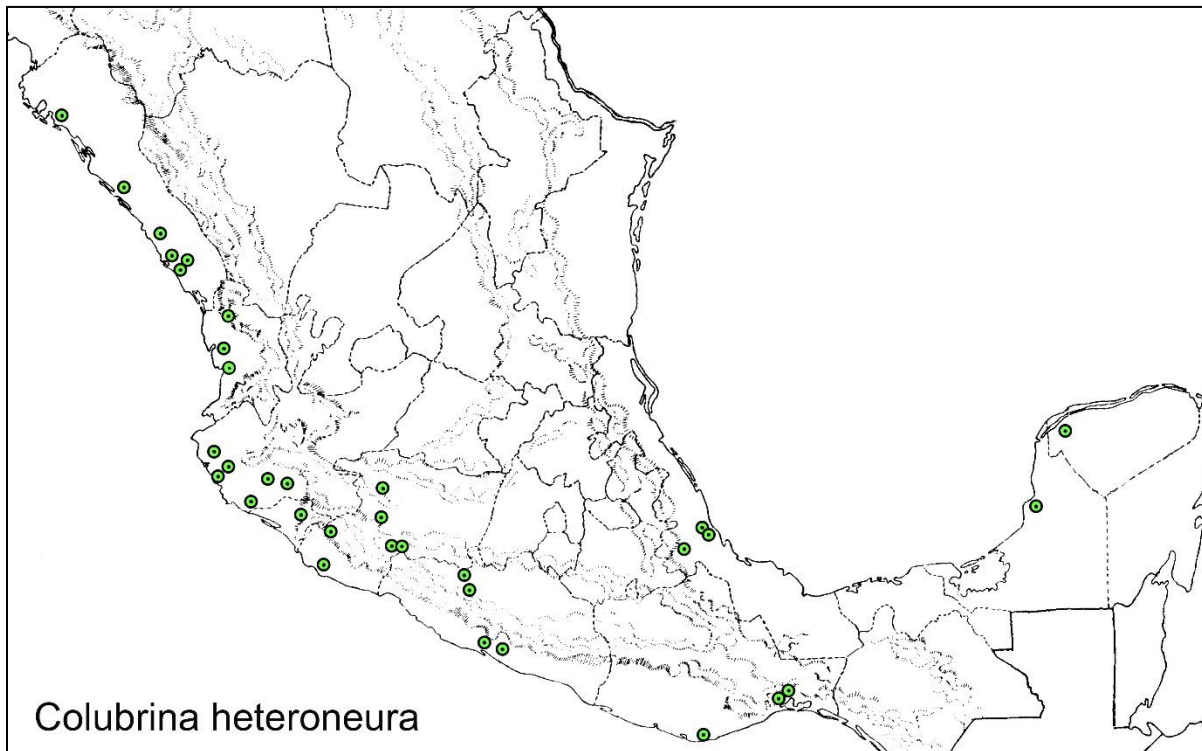
Map 14. Distribution of *Colubrina arborescens* and *C. asiatica* in Mexico.



Map 15. Distribution of *Colubrina tepicana*, known only from the state of Nayarit.



Map 16. Distribution of *Colubrina johnstonii*, endemic to the Uxpanapa region of Veracruz.



Map 17. Distribution of *Colubrina heteroneura* in Mexico.



Figure 1. *Colubrina greggii*. Nuevo León, Villarreal et al. 2742 (TEX).



Figure 2. *Colubrina greggii*. San Luis Potosi, McVaugh 10430 (US).

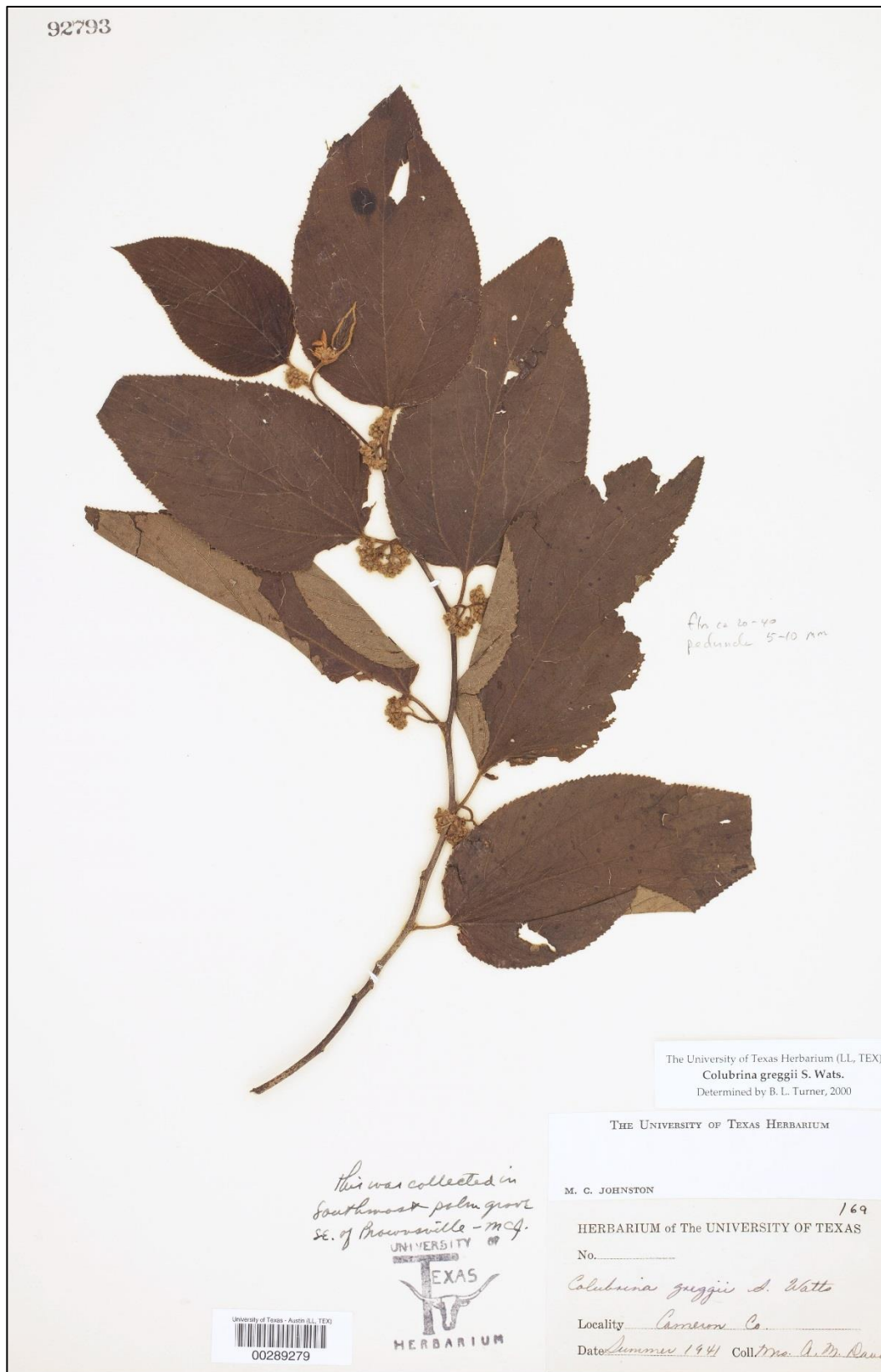


Figure 3. *Colubrina greggii*. Cameron Co., Texas, Davis s.n. (TEX). Note by M.C. Johnston: "collected in southmost palm grove SE of Brownsville."



Figure 4. *Colubrina angustior*. San Luis Potosí, Fryxell 3428 (ASU).



Figure 5. *Colubrina angustior*. San Luis Potosí, Fryxell 3428 (TEX).



Figure 6. *Colubrina angustior*. Nuevo León, Marroquín 935 (TEX).



Figure 7. *Colubrina angustior*. Querétaro, Zamudio & Carranza 6494 (TEX).



Figure 8. *Colubrina yucatanensis*. Quintana Roo, Davidse et al. 20101 (TEX).



Figure 9. *Colubrina yucatanensis*. Guatemala (Petén), Contreras 899 (ASU).

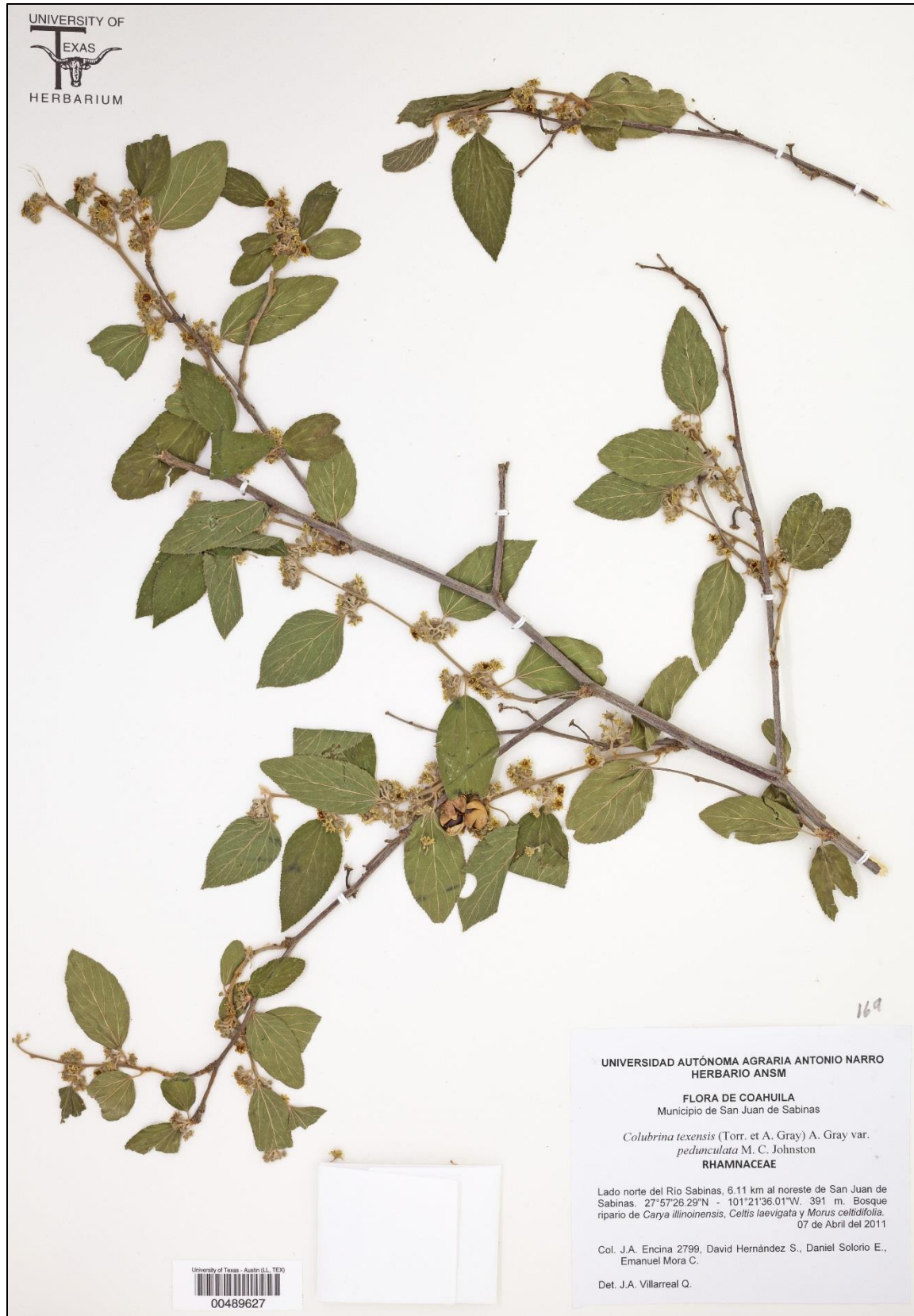


Figure 10. *Colubrina stricta*. Coahuila, Encina 2799 (TEX).



Figure 11. *Colubrina stricta*. Nuevo León, Bridges 13140 (GA).



Figure 12. *Colubrina stricta*. Texas, Lindheimer 712 (TEX). Isotype, detail.



Figure 13. *Colubrina stricta*. Texas, Lindheimer 712 (F). Isotype, detail.



Figure 14. *Colubrina stricta*. Coahuila, Carranza C-3800 (MEXU). Detail.

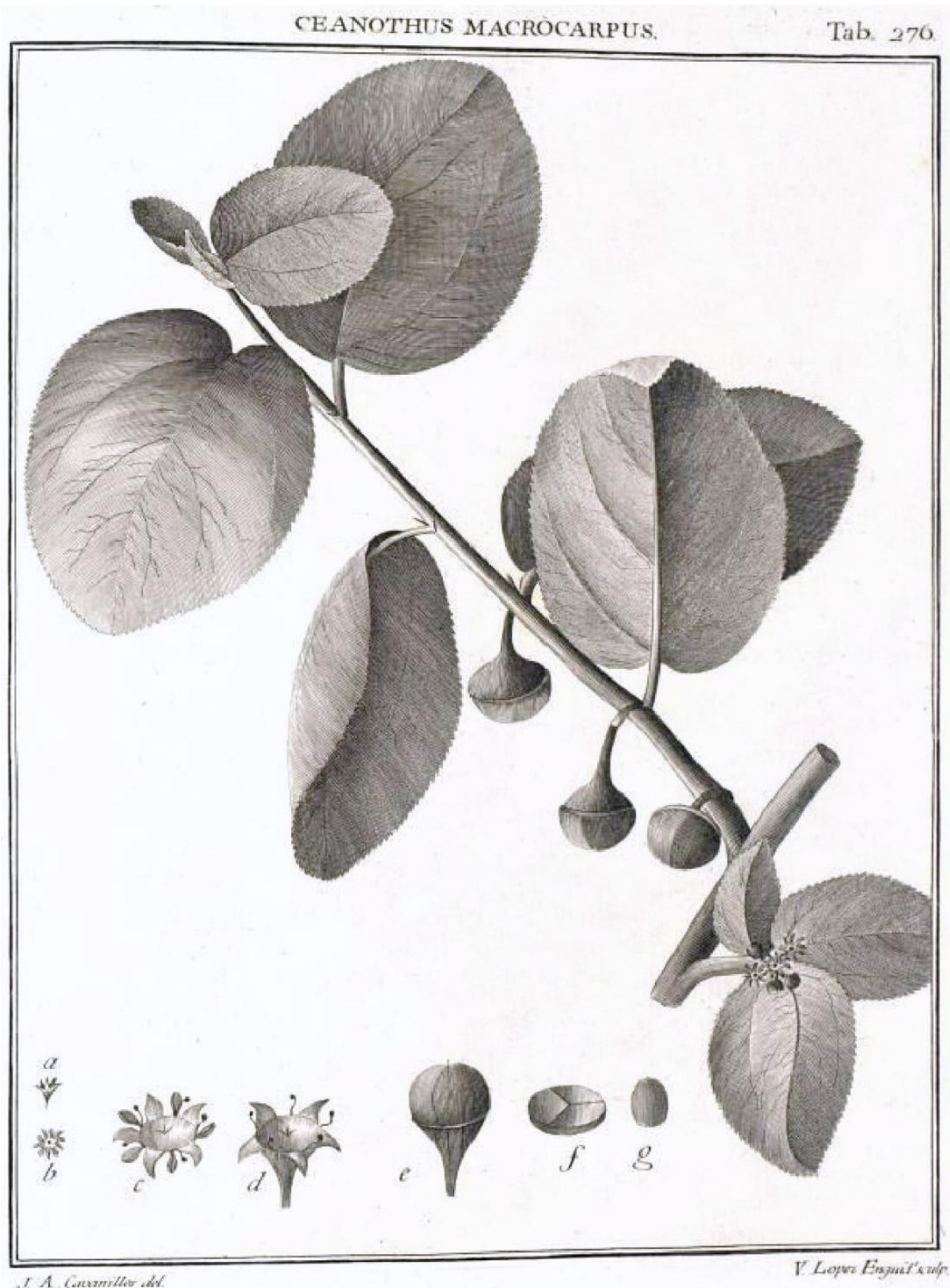


Figure 15. *Colubrina macrocarpa*. Illustration of *Ceanothus macrocarpus* Cav., *Icones et descriptiones plantarum* 3: 38, t. 276. 1795. Holotype.



Figure 16. *Colubrina macrocarpa*. Holotype (G-DC) with detail of *Ceanothus alamanii* DC.



Figure 17. *Colubrina macrocarpa*. Puebla, Pringle 6761.



Figure 18. *Colubrina macrocarpa*. Oaxaca, Chiang 1983 (US).



Figure 19. *Colubrina macrocarpa*. Puebla, Nava 214 (MEXU).



Figure 20. *Colubrina macrocarpa*. Guerrero, *Langlassé 1053*. Isotype (US) of *Colubrina lanulosa*.

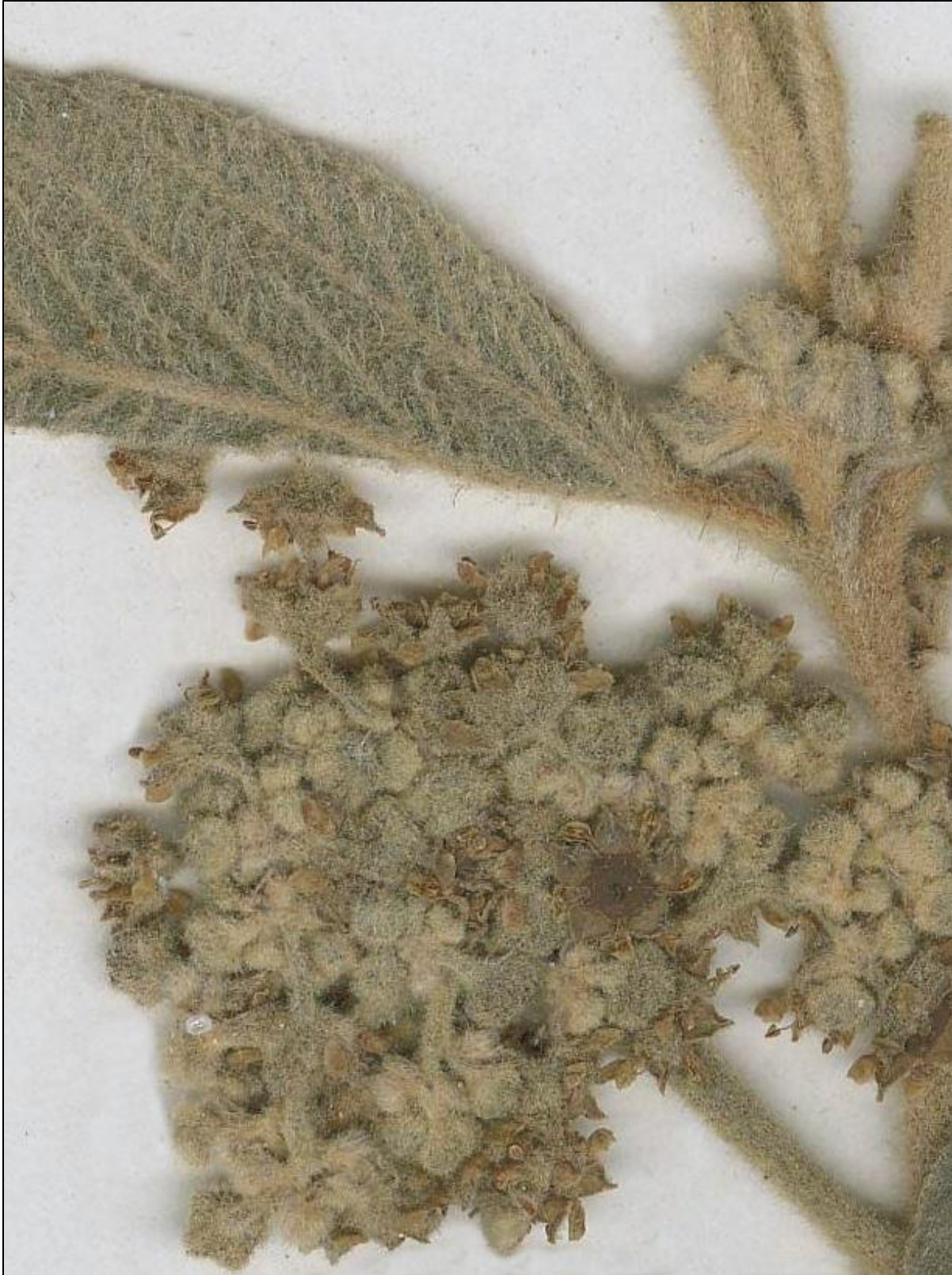


Figure 21. *Colubrina macrocarpa*. Detail from Figure 9.



Figure 22. *Colubrina macrocarpa*. Guerrero, Soto Nuñez 8758 (MEXU).



Figure 23. *Colubrina macrocarpa*. Guerrero, Mpio. Taxco, Martínez S. 1204 (MEXU).

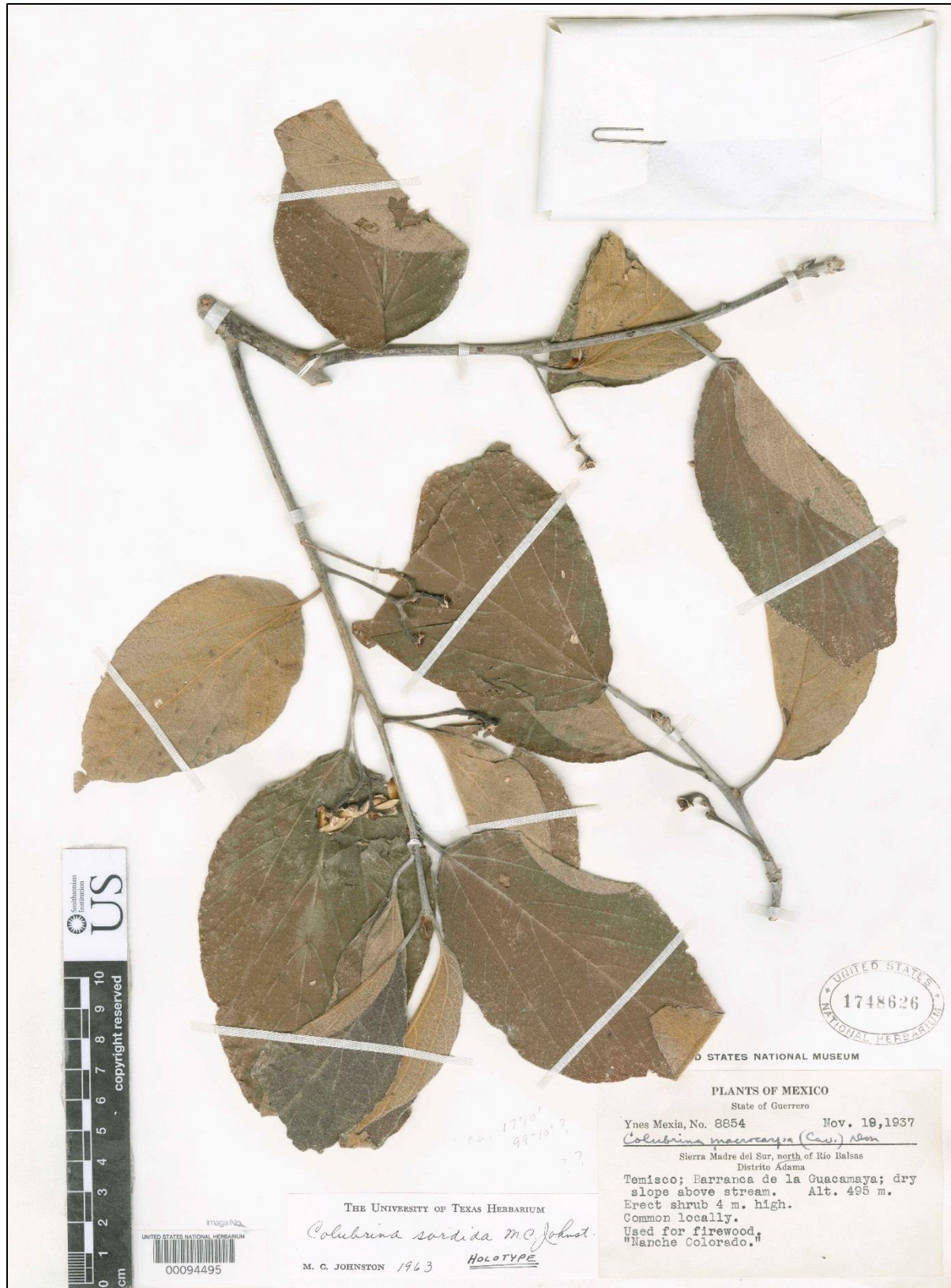


Figure 24. *Colubrina sordida*. Guerrero, Mexia 8854 (US-holotype).



Figure 25. *Colubrina sordida*. Guerrero, Reko 4958 (US).



Figure 26. *Colubrina macrocarpoides*. Querétaro, Rose 9623 (A). Isotype of *Colubrina greggii* var. *macrocarpoides*.



Figure 27. *Colubrina macrocarpoides*. Querétaro, Rose 9623 (GH). Isotype of *Colubrina greggii* var. *macrocarpoides*.



Figure 28. *Colubrina macrocarpoides*. Querétaro, Rose 9623 (GH). Detail from isotype of *Colubrina greggii* var. *macrocarpoides* (Fig. 22).



Figure 29. *Colubrina macrocarpoides*. Querétaro, Rose 9623 (NY). Detail from isotype of *Colubrina greggii* var. *macrocarpoides* (Fig. 22).



Figure 30. *Colubrina mezquitalensis*. Durango, M. González 1400 (TEX, holotype).



Figure 31. *Colubrina mezquitalensis*. Durango, M. González 2190 (MEXU).



Figure 32. *Colubrina mezquitalensis*. Durango, S. González 3108 (MEXU).



Figure 33. *Colubrina californica*. Baja California Sur, Hodgson 9525 (DES).

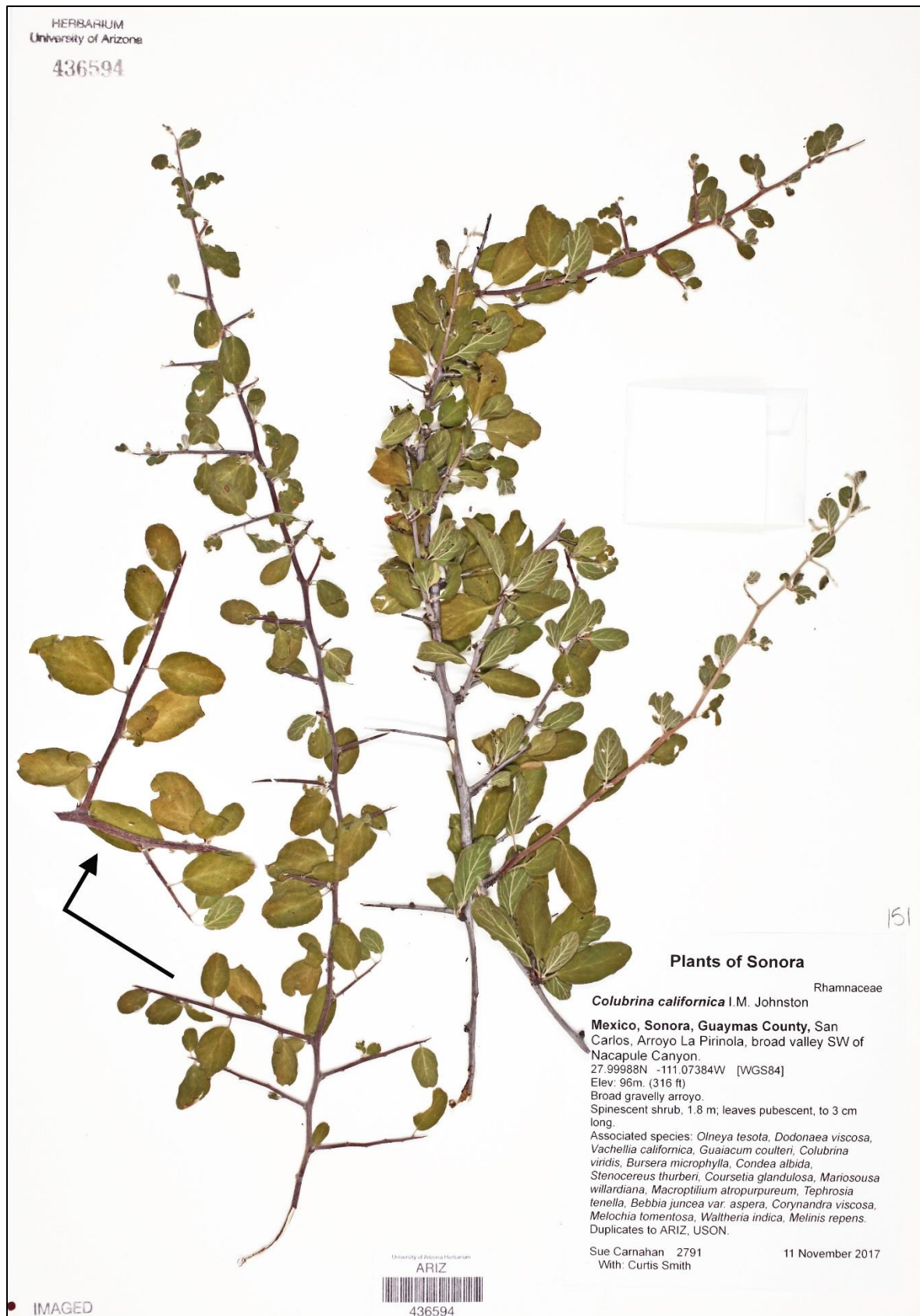


Figure 34. *Colubrina californica*. Sonora, Carnahan 2794 (ARIZ).



Figure 35. *Colubrina californica*. Arizona, Ahles 8917 (ASC).



Figure 36. *Colubrina californica*. Baja California Sur, Carter 4903 (US).



Figure 37. *Colubrina californica*. Arizona, Fish Creek Canyon, Harrison & Kearney 5685 (GH).



Figure 38. *Colubrina californica*. Arizona, Hodgson 11302 (DES).



Figure 39. *Colubrina texensis*. Texas, Lindheimer 424 (K).



Figure 40. *Colubrina texensis*. Texas, Brewster Co., Butterwick & Lott 3696 (TEX)



Figure 41. *Colubrina texensis*. Nuevo León, near Mamulique Pass, Bridges 13137 (MEXU)



Figure 42. *Colubrina villarrealii*. Coahuila, Pringle 144 (GH, isotype of *C. texensis* var. *pedunculata*).



Figure 43. *Colubrina villarrealii*. Coahuila, Pringle 144 (A, isotype of *C. texensis* var. *pedunculata*).



Figure 44. *Colubrina villarrealii*. Coahuila, Sierra Jimulco, *Henrickson 13074* (MEXU). Indeterminate short shoots and short, thick pedicels.



Figure 45. *Colubrina villarrealii*. Chihuahua, Chiang et al. 8323 (MEXU).



Figure 46. *Colubrina viridis*. Sonora, Isla San Pedro Nolasco, *Felger 08-142* (MEXU).



Figure 47. *Colubrina viridis*. Sonora, Isla Almagre Chico, *Suarez G. 2006-71* (MEXU).



Figure 48. *Colubrina viridis*. Sonora, Isla Mellizas (Norte), Suarez G. 2006-42 (MEXU).



Figure 49. *Colubrina viridis*. Sonora, Isla Mellizas (Sur), Suarez G. 2006-48 (MEXU).



Figure 50. *Colubrina viridis*. Sonora, Cañon Nacapuli, Felger 85-864 (MEXU).



Figure 51. *Colubrina neoviridis*. Durango, Correll & Johnston 19991 (LL, holotype).

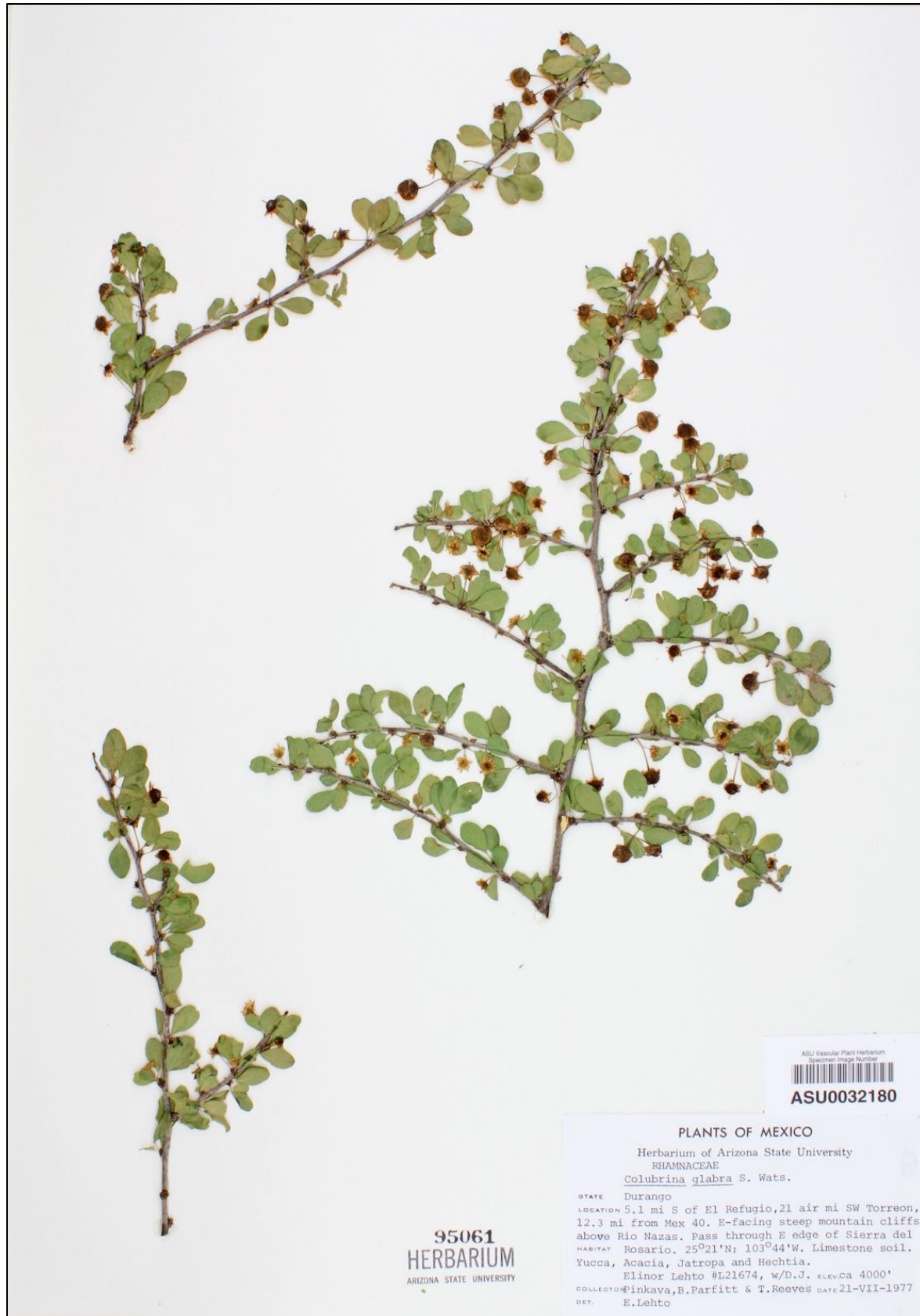


Figure 52. *Colubrina neoviridis*. Durango, Lehto L21674 (ASU).

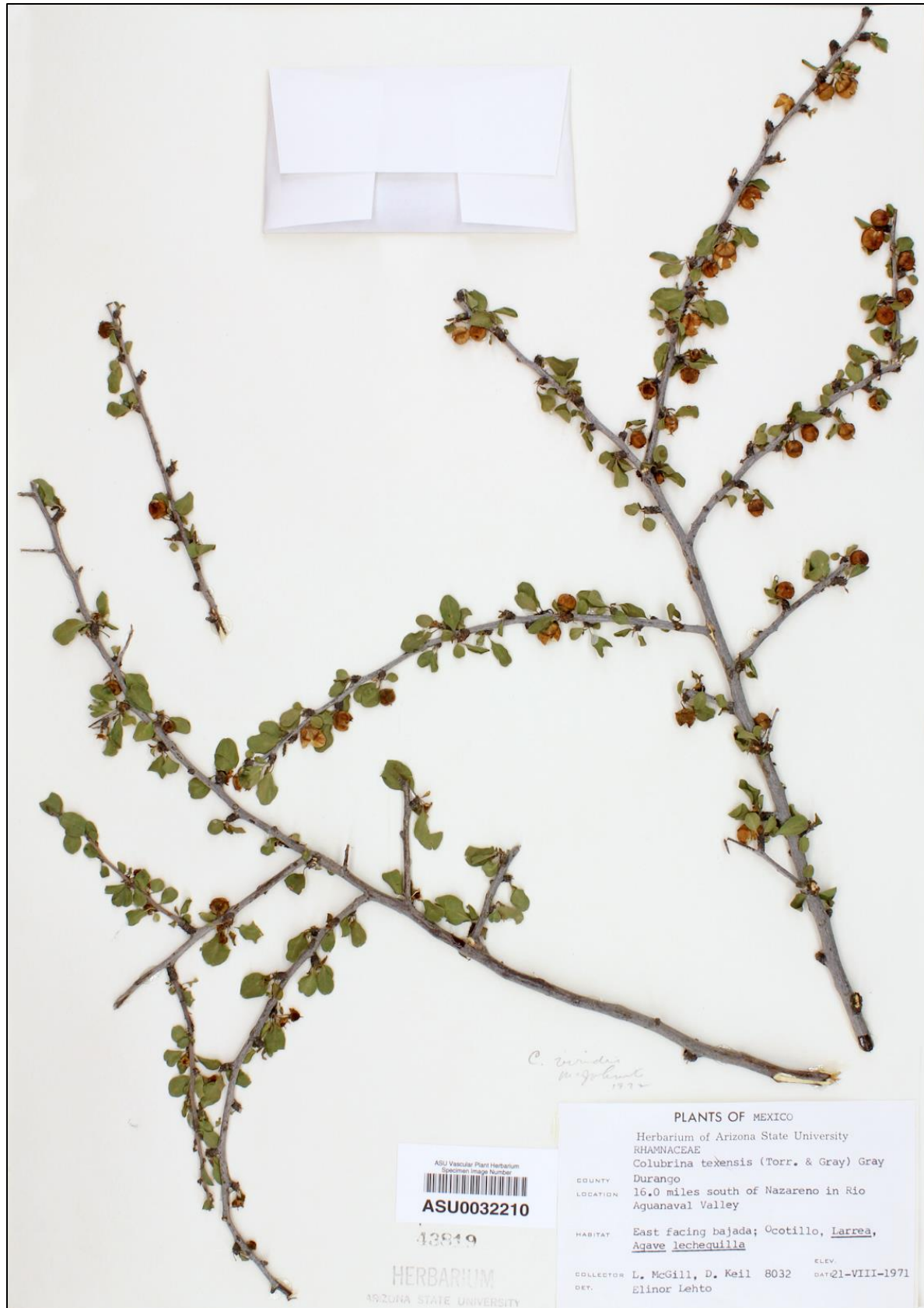


Figure 53. *Colubrina neoviridis*. Durango, McGill 8032 (ASU).



Figure 54. *Colubrina neoviridis*. Durango, McGill 8032 (ASU). Detail from Figure 48.



Figure 55. *Colubrina neoviridis*. Durango, Mpio. Torreón, Lehto L21674 (MEXU).



Figure 56. *Colubrina ehrenbergii*. San Luis Potosí, Pringle 3189 (COLO).



Figure 57. *Colubrina ehrenbergii*. Nuevo León, Hinton 24502 (MEXU).



Figure 58. *Colubrina ehrenbergii*. Oaxaca, Mpio. Tepelmeme, Tenorio L. 9258 (ASC).



Figure 59. *Colubrina tequila*. Jalisco, Mpio. Tequila, M.E. Jones 419 (US, holotype).



Figure 60. *Colubrina tequila*. Detail from holotype (Fig. 59).



Figure 61. *Colubrina tequila*. Detail from holotype (Fig. 59).



Figure 62. *Colubrina tequila*. Detail from holotype (Fig. 59).



Figure 63. *Colubrina triflora*. Sinaloa, Palmer 1526 (GH). Isotype of *Colubrina mexicana*.



Figure 64. *Colubrina triflora*. Colima, McVaugh & Koelz 1446 (MICH).



Figure 65. *Colubrina triflora*. Sonora, Felger 90-718B (MEXU).



Figure 66. *Colubrina triflora*. Sonora, Durango, Mpio. Mezquital, M. González 1604 (MEXU).



Figure 67. *Colubrina triflora*. Zacatecas, *Enríquez E. 26* (MEXU). Unusually rotund leaves.



Figure 68. *Colubrina subsessilis*. Oaxaca, Elorsa 6274 (TEX). Holotype.



Figure 69. *Colubrina lanceolata*. Aguascalientes, Mpio. Calvillo, Provance 1405 (MEXU). Isotype.



Figure 70. *Colubrina lanceolata*. Aguascalientes, *Provance 1405* (MEXU). Detail from isotype (Fig. 69).



Figure 71. *Colubrina lanceolata*. Aguascalientes, *Provance 1405* (MEXU). Detail from isotype (Fig. 69).



Figure 72. *Colubrina lanceolata*. Aguascalientes, *Provance 1405* (MEXU). Detail from isotype (Fig. 69).



Figure 73. *Colubrina triflora*. Aguascalientes, Mpio. Calvillo, typical morphology near the collection site of *Colubrina lanceolata*. Rzedowski 14061 (MEXU).



Figure 74. *Colubrina triflora*. Aguascalientes, Mpio. Calvillo, Rzedowski 14061, detail from Figure 73.



Figure 75. *Colubrina elliptica*. Colima, McVaugh & Koelz 1595 (MICH).

Figure 76. *Colubrina elliptica*. Oaxaca, Sánchez 924 (US).



Figure 77. *Colubrina elliptica*. Oaxaca, Sánchez 924 (US). Detail from Figure 76.



Figure 78. *Colubrina elliptica*. San Luis Potosí, *Hernandez-Sandoval 8810* (QMEX). The long-attenuate leaf apices are unusual.



Figure 79. *Colubrina arborescens*. Veracruz, Martinez C. 1355 (US).



Figure 80. *Colubrina asiatica*. Florida, Chevalier 64 (USF).



Figure 81. *Colubrina asiatica*. Quintana Roo, Duran 560 (MEXU).



Figure 82. *Colubrina asiatica*. Jamaica, Chrysler 1997 (MEXU).



Figure 83. *Colubrina tepicana*. Nayarit, Palmer 1977 (GH). Isotype of *Cormonema mexicanum*.



Figure 84. *Colubrina tepicana*. Nayarit, Palmer 1977 (GH). Isotype of *Cormonema mexicanum*, detail from Figure 83. Arrows point to non-meristematic thorns.



Figure 85. *Colubrina tepicana*. Nayarit, Palmer 1977 (MICH). Isotype of *Cormonema mexicanum*).



Figure 86. *Colubrina johnstonii*. Veracruz, Wendt 2756 (NY). Isotype.



Figure 87. *Colubrina johnstonii*. Veracruz, Wendt et al. 3678 (MEXU).



Figure 88. *Colubrina heteroneura*. Michoacan, Martínez 4511 (MEXU).



Figure 89. *Colubrina heteroneura*. Michoacan, Martínez 4511 (detail from Fig. 88).

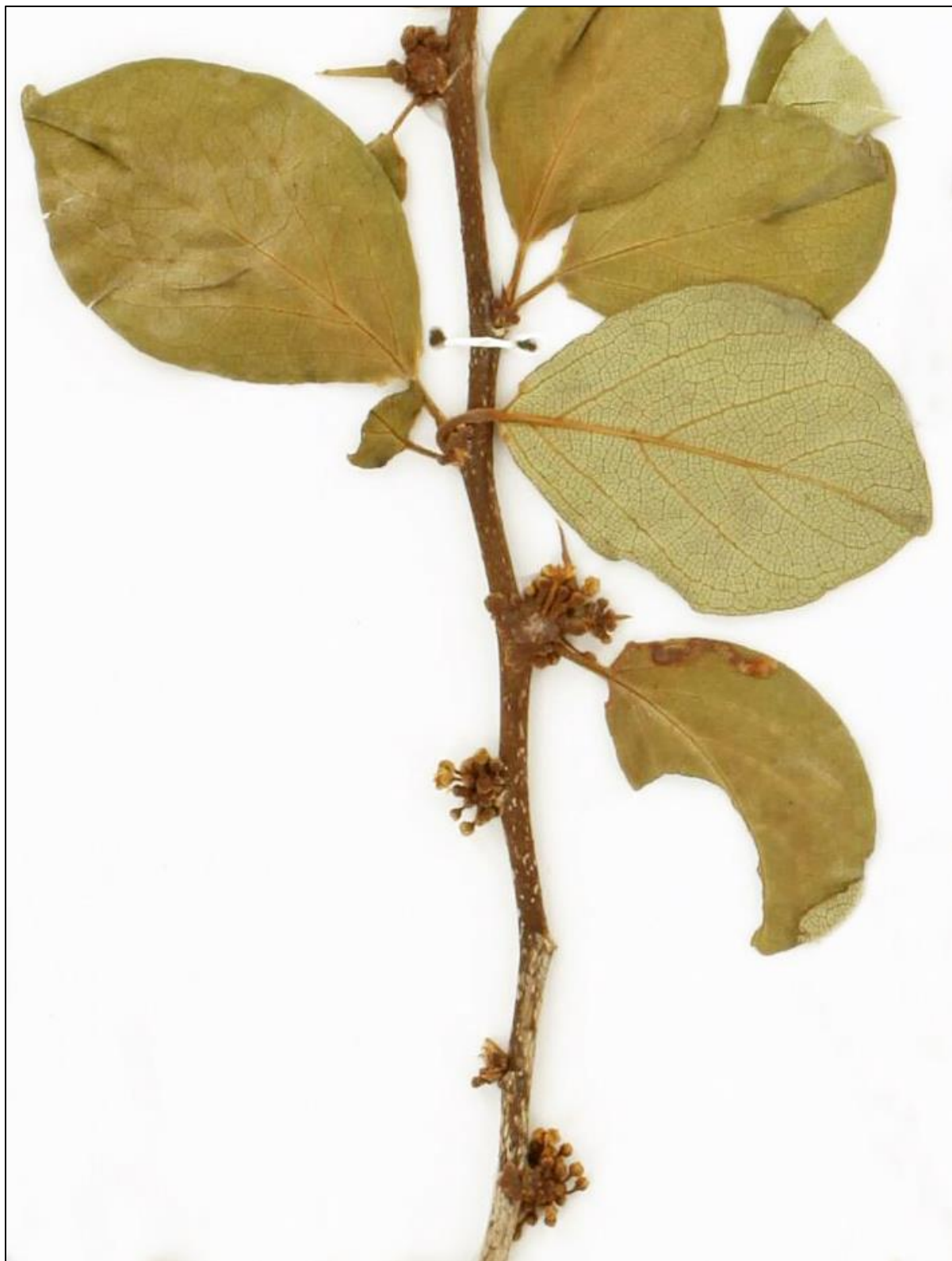


Figure 90. *Colubrina heteroneura*. Michoacan, Martínez 4511 (detail from Fig. 88).

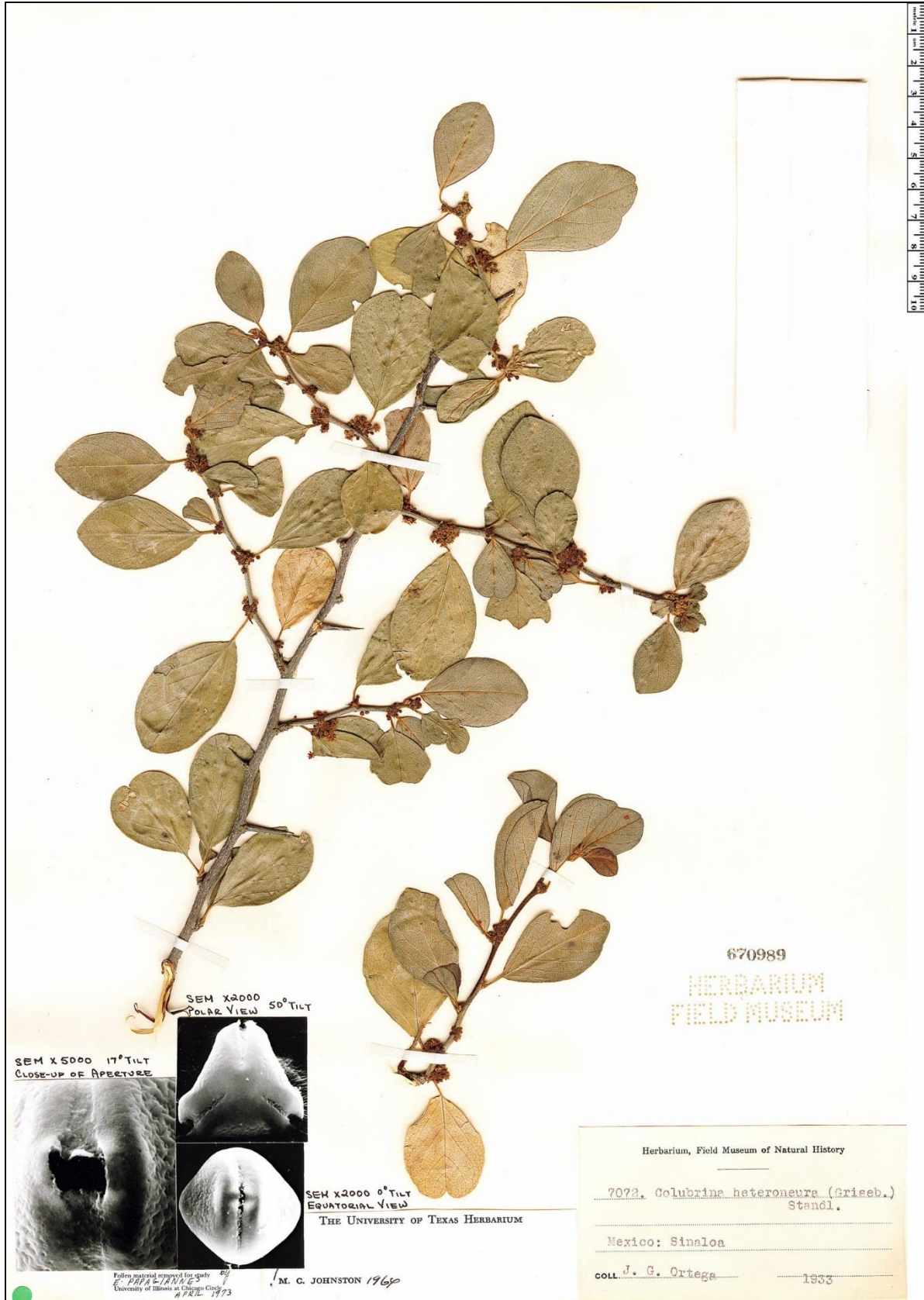


Figure 91. *Colubrina heteroneura*. Sinaloa, Ortega 7072 (F).



Figure 92. *Colubrina heteroneura*. Nayarit, Flores F. 1818 (MEXU).



Figure 93. *Colubrina heteroneura*. Sinaloa, Beltran 827 (MEXU).



Figure 94. *Colubrina*? Estación Biológica Chamela, Jalisco, Quigley 649 (LSU). See text (p. 6) for comments.