Nesom, G.L. 2023. *Ziziphus* segregates in the USA and Mexico, including *Sarcomphalus*, *Condaliopsis* , and *Conalma*, gen. nov. (Rhamnaceae). Phytoneuron 2023-34: 1–132. Published 6 September 2023. ISSN 2153 733X

ZIZIPHUS SEGREGATES IN THE USA AND MEXICO, INCLUDING *SARCOMPHALUS, CONDALIOPSIS*, AND *CONALMA*, GEN. NOV. (RHAMNACEAE)

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ABSTRACT

Molecular data indicate that Old World (typical) species of *Ziziphus* are more closely related to *Paliurus* than to species identified as *Ziziphus* in the Americas. The New World species are monophyletic but diverse in morphology — molecular data show them to be divided among three clades, each treated here at generic rank. (1) *SARCOMPHALUS* P. Browne is the oldest name at generic rank for the largest New World group (ca. 28 species), which occurs in the West Indies, South America, Central America, and Mexico — 2 species occur in Mexico*: S. amole*, and *S. guatemalensis*. (2) *CONDALIOPSIS* (Weberb.) Suesseng. comprises 7 species of the southwestern USA and Mexico, including **Condaliopsis australis** Nesom, **sp. nov.**, **Condaliopsis chihuahuana** Nesom, **sp. nov.**, **Condaliopsis divaricata** (A. Nels.) Nesom, **comb. nov.** (= *Ziziphus obtusifolius* var. *canescens* from the southwestern USA), *Condaliopsis lloydii* sensu stricto, *Condaliopsis obtusifolia* sensu stricto, *Condaliopsis rigida*, and **Condaliopsis supralloydii** Nesom, **sp. nov.** (3) **CONALMA** Nesom, **gen. nov.**, includes 3 species of southern Mexico: **Conalma mexicana** (Rose) Nesom, **comb. nov.**, **Conalma pedunculata** (Brandegee) Nesom, **comb. nov.**, and **Conalma yucatanensis** (Standl.) Nesom, **comb. nov.** A key, descriptions, typification, and distribution maps are provided for species of the primarily North American genera. *Ziziphus celata*, endemic to Florida, *and Ziziphus parryi*, endemic to the Pacific Coast (California, Baja California), previously have been segregated as the genus *Pseudoziziphus* Hauenschild, which is more closely related to *Condalia* than to New World ziziphoids. Of typical *Ziziphus* (Old World natives), two species are naturalized in the Americas: *Z. jujuba* and *Z. mauritiana*.

Molecular data indicate that American species identified as *Ziziphus* are not in the same clade as typical (Old World) *Ziziphus* P. Mill. and thus should not be regarded as congeneric (Islam & Simmons 2006; Islam & Guralnick 2015; Hauenschild et al. 2016). *Ziziphus celata* (endemic to Florida) and *Ziziphus parryi* (endemic to California and Baja California) have been segregated as the genus *Pseudoziziphus* Hauenschild — molecular data indicated that they are closely related to the American *Condalia* Cav. The remaining American species of *Ziziphus* have been placed in the genus *Sarcomphalus* P. Browne (Hauenschild et al. 2016), where they form three distinct clades, each treated here at generic rank — *Sarcomphalus*, *Condaliopsis* (Weberb.) Suesseng., and a genus described in this paper, *Conalma* Nesom (Fig. 1).

Sarcomphalus (mostly sensu Hauenschild but with modifications) includes 28 species (see accounting below) native to Mexico, Central America, the West Indies, and South America. Five of the species have been included in molecular analyses by Islam & Guralnick (2015) and Hauenschild et al. (2016) – *S. amole*, *S. guatemalensis*, *S. mistol*, *S. taylori*, *S. thyrsiflora*.

Condaliopsis was first recognized as a subgenus of *Condalia* (Weberbauer 1895), then raised to generic rank by Suessenguth (1953), who included *Condaliopsis lloydi*, *Condaliopsis obtusifolia*, *Condaliopsis lycioides* (here = *Condaliopsis obtusifolia*), *Condaliopsis parryi* (now ≡ *Pseudoziziphus parryi*), *Condaliopsis seleri* (here = *Conalma pedunculata*), and *Condaliopsis velutina* (≡ *Condalia velutina*, see Johnston 1962). After Suessenguth's treatment, the only other species to be formally included in *Condaliopsis* has been *C. rigida* (Wiggins) Wiggins — Wiggins treated *Condaliopsis* as distinct from *Ziziphus* in floristic accounts of the Sonoran Desert (1964) and Baja California (1980).

In contrast, Johnston (1962, 1963) concluded that the *Condaliopsis* species should be included within *Ziziphus* and, except for Wiggins and in Schirarend's study of woody anatomy, that is mostly how the group has been treated over the last 60 years (including the FNA treatment, Nesom 2016, where the species were treated as *Ziziphus*). *Condaliopsis* (in the concept here), however, is morphologically discrete. Three of the species have been included in molecular analyses by Islam & Guralnick (2015) and Hauenschild et al. (2016) – *C. divaricata, C. obtusifolia, C. supralloydii*.

All three species of *Conalma* have been included in molecular analyses by Islam & Guralnick (2015) and Hauenschild et al. (2016).

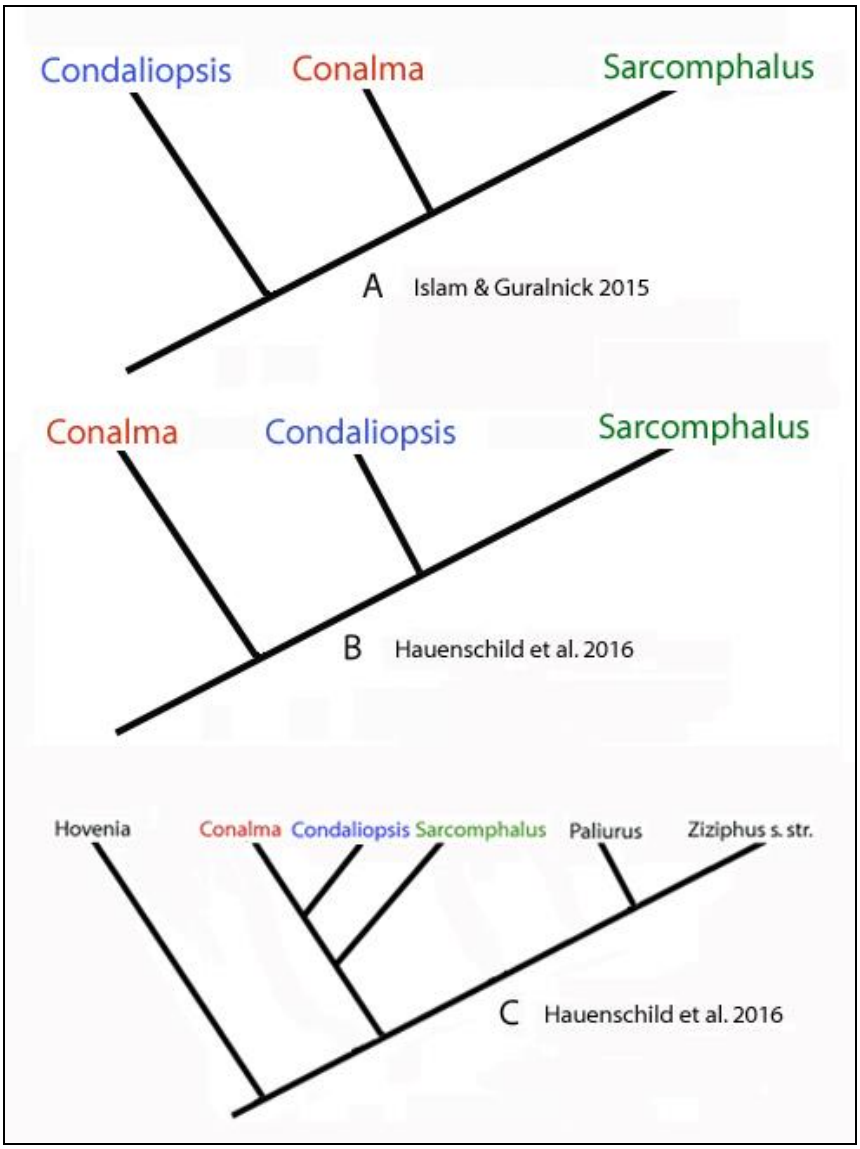


Figure 1. Relative phylogenetic positions of *Condaliopsis*, *Conalma*, and *Sarcomphalus*, based on molecular data. A. From Islam & Guralnick (2015, Fig. 1) — "parsimony simultaneous analysis strict consensus tree." B. From Hauenschild et al. (2016; Electronic Supplement, Fig. S2) — combined nuclear ribosomal transcribed spacer (ITS) and *trnL-trnF* sequence data. Each of the three taxa is monophyletic in both analyses. C. From Hauenschild et al. (2016, Fig. 1) — majority-rule consensus tree based on ITS and *trnL-trnF* sequence data; New World *Ziziphus* sensu lato (*Condaliopsis*, *Conalma*, and *Sarcomphalus*, treated in aggregate by Hauenschild et al. as *Sarcomphalus* sensu lato) is sister to *Paliurus*/*Ziziphus* sensu stricto. *Pseudoziziphus* (*Ziziphus parryi* and *Z. celata*) is most closely related to *Condalia* (not shown).

	SARCOMPHALUS	CONALMA	CONDALIOPSIS
habit	trees or tall shrubs	trees or tall shrubs	low shrubs
wood anatomy (Schirarend 1991)			
ring porous	no	?	yes
oblique/dendritic vessel pattern	no	?	yes
spiral thickenings in vessels	no	?	yes
vascular tracheids	no	?	yes
short shoots present	no	yes	yes
serial buds per node (Tourn et al. 1989, 1990)	3	2	2
thorns with lateral buds (thorns elongating and becoming thorn-tipped lateral branches)	no	yes (or consistently w/o nodes) in *C. yucatanensis*)	yes
paired thorns present (short, non-meristematic thorns at the node	yes (or sometimes only 1 per node)	no	no
leaf/branch position	alternate	mostly opposite to subopposite or fasciculate	alternate or fasciculate
blade thickness	variable — herbaceous or coriaceous with raised subepidermal veins	coriaceous with raised subepidermal veins	herbaceous without raised subepidermal veins
margin	entire to serrulate without glands	gland-tipped teeth sometimes entire	gland-tipped teeth sometimes entire
venation	3-veined (or pinnate to subpinnate in *S. laurinus*)	strongly 3-veined from the base with additional strong 2° veins	pinnate to weakly 3-veined from the base
fruits	9–25 mm red-brown to orangish or yellow	10–20 mm reddish	7–10 mm blue to purple

Table 1. Comparative morphological/anatomical features of *Sarcomphalus*, *Conalma*, and *Condaliopsis*. Differences between *Conalma* and *Condaliopsis* are in leaf position, blade thickness and venation, and fruit size and color. *Sarcomphalus* is distinct from both in its wood anatomy (the anatomy of *Conalma* not known), short shoots (see comments), serial buds per node, thorns without lateral buds, and lack of gland-tipped foliar teeth.

Schirarend's study of wood anatomy (1991) did not include the three species segregated here as *Conalma* — his samples of ziziphoids are as below.

Condaliopsis — *C. obtusifolia* (as *C. lycioides*), *C. divaricata* (as *C. obtusifolia*)
Sarcomphalus — *S. divaricatus* (= *Z. grisebachiana*), *S. domingensis* (= *Z. rignoni*), *S. havanensis*, *S. laurinus*, *S. reticulatus*
Ziziphus group **C** (American species) *Z. amole*, *Z. angolito*, *Z. chloroxylon*, *Z. cinnamomum*, *Z. cyclocardia*, *Z. guatemalensis*, *Z. melastomoides*, *Z. mistol*, *Z. rhodoxylon*, *Z. thyrsiflora*
Ziziphus groups **A** and **B** — 17 Old World species (including *Z. jujuba* and *Z. mauritiana*)
Pseudoziziphus — *P. parryi* (as *Condaliopsis parryi*)

Sarcomphalus is barely differentiated in wood anatomy from *Ziziphus* groups A and B (Old World) as well as from group C (American) but molecular data place group C with Schirarend's *Sarcomphalus* — suggesting that Hauenschild's broad concept of *Sarcomphalus*, even with the removal here of *Conalma* and *Condaliopsis*, should be reexamined. In Schirarend's study, *Condalia* has wood nearly identical to *Condaliopsis*.

The gland-tipped foliar teeth of *Condaliopsis* and *Conalma* are variable in size but apparently characteristic of those clades. I have not seen them in *Sarcomphalus* and they are rare in Old World *Ziziphus* — leaf margins in *Z. borneensis* Merr. sometimes are "finely serrate with minute callosities that dry much darker than the lamina" (see Cahen et al. 2021, description and Fig. 1). The glandular tip of marginal teeth of *Conalma mexicana* is evident only in early stages of leaf ontogeny; the glandular tips of *C. pedunculata* are larger and persistent. The margins of *C. yucatanensis* appear to be completely entire, without glandular tips. The exceptionally large marginal glands of *Condaliopsis chihuahuana* are quickly deciduous, leaving what then appear to be entire margins. Margins in the *Condaliopsis obtusifolia* group usually are entire, but collections have been made of plants with margins coarsely serrate with conspicuously gland-tipped teeth (e.g., see the US isotype of *Paliurus texanus*, Fig. 56). Margins of *C. australis* are persistently "micro-serrulate" with teeth marked essentially only by a dark callosity.

Leaf and branch position in *Conalma* is predominantly opposite but may vary on a single branch from opposite to subopposite and alternate. In *Sarcomphalus* and *Condaliopsis*, the position is consistently alternate.

Thorns in *Conalma* are characteristically short and commonly produce meristematic nodes, though they sometimes are without nodes. *Conalma yucatanensis* apparently is exceptional in that its thorns are short and acicular, consistently non-meristematic, and apparently not often produced. Armament in *Ziziphus* sensu stricto is of stipular spines — stipules in *Sarcomphalus*, *Condaliopsis*, and *Conalma* are herbaceous and early deciduous. The paired spines of *Ziziphus* are not strictly homologous with the paired thorns of *Sarcomphalus* (e.g., Tourn 1985), but their similarity may reflect the same developmental influences.

Short shoots are unequivocally seen and abundantly produced in *Condaliopsis* and *Conalma*, where the cylinder of scaly bracts sometimes elongates for up to a centimeter. Short shoots are said to be produced in *Sarcomphalus* (Tourn et al. 1990, 1992; Islam & Simmons 2006; Islam & Guralnick 2015), where 3 serial buds per node are present, but structures comparable to those in *Condaliopsis* and *Conalma* have not been observed in the present study, thus the scoring in Table 1. In *Sarcomphalus amole* (and *Z. mistol*, Tourn et al. 1992), lateral buds produce one thorn or usually two thorns, thorns and a leaf, thorns and a branch, or commonly just two branches (Figs. 14-24 for *S. amole*). Short shoots in *Pseudoziziphus* are indeterminate in growth (Fig. 79) as in *Condaliopsis* and *Conalma* (*Condaliopsis lloydii*-Fig. 79, *Condaliopsis supralloydii*-Figs. 85, 87), *Conalma yucatanensis*-Fig. 31, and *Conalma pedunculata*-Figs. 42, 44).

KEY TO THE SPECIES OF *ZIZIPHUS* S. STR., *SARCOMPHALUS*, *CONDALIOPSIS*, AND *CONALMA*

1. Armament of stipular, anodal spines; short shoots absent ..... **ZIZIPHUS**

2. Mostly small trees; abaxial leaf surface glabrous to puberulent, green; mature fruits subcylindric to barrel-shaped, 20–35 mm long ..... **Ziziphus jujuba**
2. Large shrubs or small trees; abaxial leaf surface whitish to tawny with dense arachnoid tomentum; mature fruits globose or subglobose to slightly elongate, 8–14 mm long ..... **Ziziphus mauritiana**

1. Armament of axillary thorns, with or without nodes; short shoots clearly present in *Conalma* and *Condaliopsis*, hardly evident (if present) in *Sarcomphalus*.

3. Short shoots absent or at least hardly evident; 3 serial buds per node; thorns often paired, sometimes commonly single or absent, without nodes, branches not thorn-tipped; leaves alternate ..... **SARCOMPHALUS**

4. Leaf margins entire, venation not subepidermal and raised; inflorescence a simple or compound thyrse of 10–25 flowers; mature fruit globose to subglobose, 6–8 mm long ..... **Sarcomphalus amole**
4. Leaf margins shallowly serrate to crenate to subentire, venation subepidermal and raised; inflorescence usually a simple thyrse of 5–10 flowers; mature fruit obovoid, 8–12 mm long ..... **Sarcomphalus guatemalensis**

3. Short shoots clearly present; 2 serial buds per node; thorns present, usually with meristematic nodes, elongating to become lateral branches; stipular spines absent; leaves alternate or mostly opposite but to subopposite or alternate.

5. Leaves opposite to subopposite,alternate, or fasciculate on short shoots, strongly 3-veined, blades coriaceous, with raised subepidermal veins; fruit reddish to brown ..... **CONALMA**

6. Leaves broadly obovate to elliptic-obovate to subrotund, blades 2.5–4 cm long, margins entire; thorns commonly absent or few, axillary, and spine-like; inflorescence a terminal, compound thyrse or panicle, peduncles/main axis 5–11 mm long **Conalma yucatanensis**
6. Leaves oblong to oblong-elliptic or oblong-obovate, 3.5–8 cm long or 1–2.5 cm long, margins entire to minutely toothed; thorns usually present; inflorescence a terminal, compound thyrse or parnicle -or- mostly axillary on lateral branches; peduncles 9–18 mm long.

7. Leaf blades 3.5–8 cm long, petioles 6–12 mm, long; inflorescence mostly terminal as a compound thyrse or panicle, each thyrse with 10–35 flrs, mature peduncles/main axis mostly 9–18 mm long; mature fruits 14–16 mm long ..... **Conalma mexicana**
7. Leaf blades 1–2.5 cm long, petioles 1–2 mm, long; inflorescence mostly axillary, each thyrse with 3–7 flrs, mature peduncles/main axis (3–)6–10 mm long; mature fruits 8–9 mm long ..... **Conalma pedunculata**

5. Leaves alternate or fasciculate on short shoots, pinnately veined or weakly 3-veined (strongly 3-veined in *C. chihuahuana*), blades herbaceous, without raised subepidermal veins; fruit blue to purple ..... **CONDALIOPSIS**

8. Flowers solitary in axils of short shoots; pedicels 3–7 mm long; style 2- or 3-branched; mature fruit elongate.

9. Leaves strongly 3-veined from the base ..... **Condaliopsis chihuahuana**
9. Leaves pinnately to subpinnately veined and weakly 3-veined from the base.

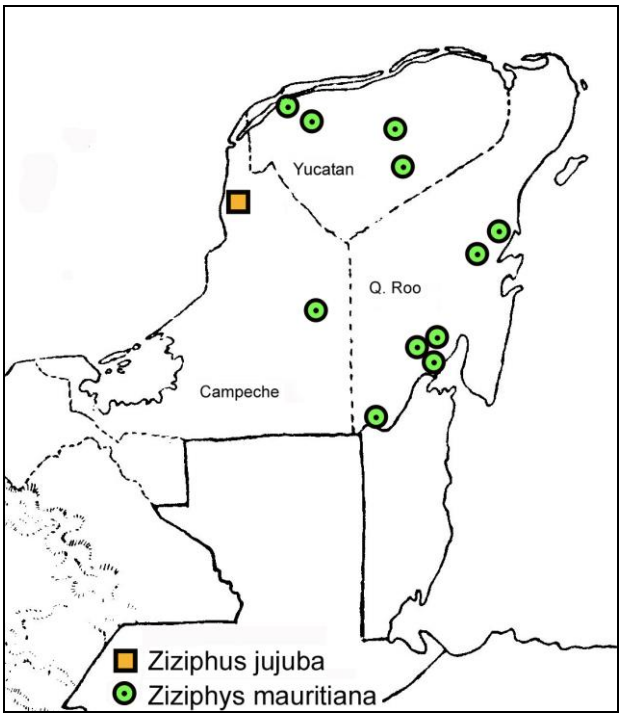
10. Branchlet epidermis pubescent, leaf surfaces sparsely villous; hypanthium hirtellous ..... **Condaliopsis lloydii**
10. Branchlet epidermis and leaf surfaces glabrous; hypanthium glabrous ..... **Condaliopsis supralloydii**

8. Flowers usually in short-pedunculate (0.5–3 mm long) fascicles, rarely solitary; short shoots absent; leaves pinnately or weakly 3-veined; style 2-branched; mature fruit globose to subglobose.

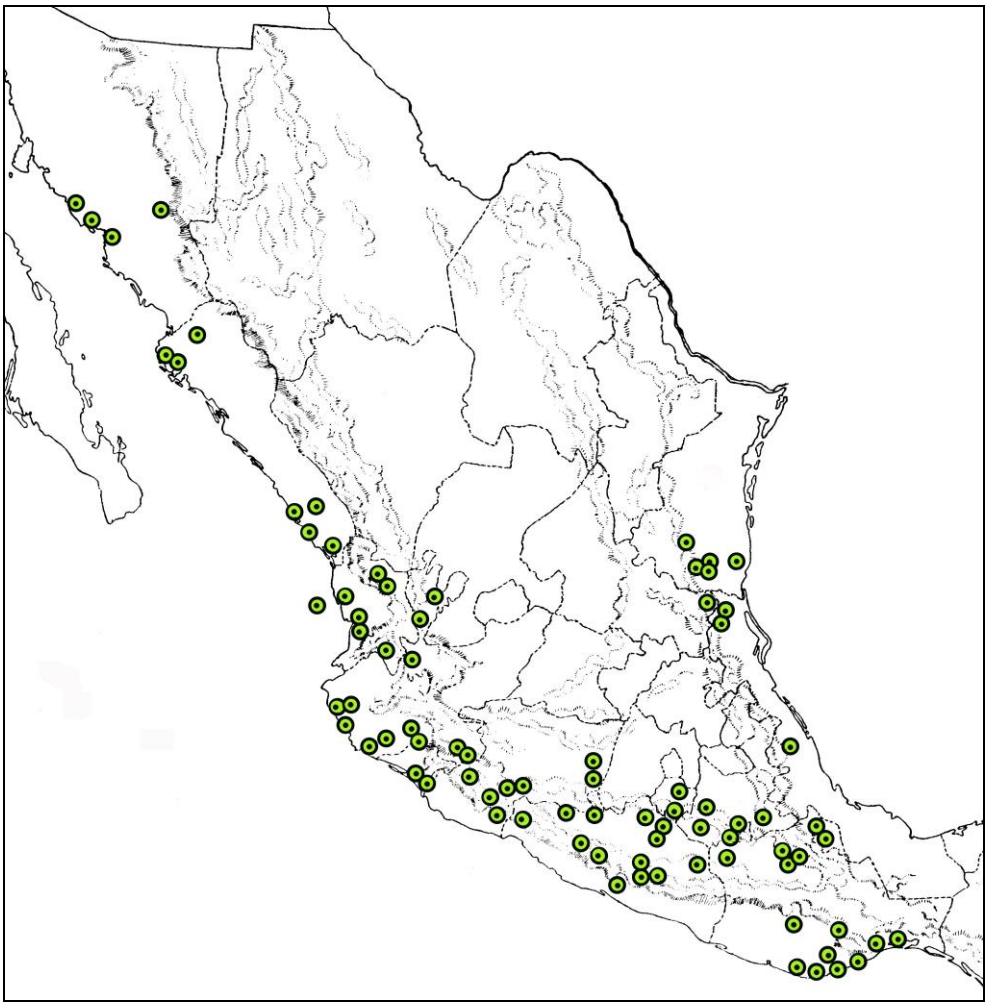
11. Leaf blades mostly elliptic-ovate, 9–16 mm wide, both surfaces hirtellous-puberulent, green on both sides, not glaucous abaxially; style branches divided nearly to the base ..... **Condaliopsis australis**
11. Leaf blades mostly narrowly oblong, 2–10 mm wide, both surfaces glabrous, usually glaucous abaxially; style branches divided nearly to the style base.

12. Stems completely glabrous, without a pruinose covering and without hairs, epidermis olive-green; leaves glabrous; hypanthia glabrous; flowers 14–30 in thyrses 10–20 mm long ..... **Condaliopsis rigida**
12. Stems distinctly pruinose, otherwise glabrous, epidermis greenish gray to white, sparsely short-villous, or densely hirtellous to densely short-villous, epidermis brown; leaves glabrous or hairy; hypanthia sparsely or densely hairy; flowers 1 or 2–15 in thyrses 5–10 mm long.

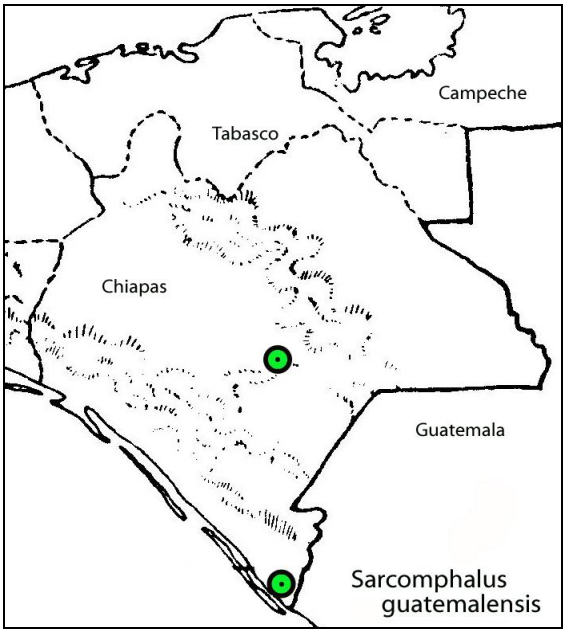
13. Secondary branches usually glabrous, sometimes sparsely pilose; leaf surfaces usually glabrous; hypanthia sparsely strigose with loose, upcurving hairs; inflorescences (1–)2–6-flowered, peduncles (0.5–)1–2 mm, nearly equaling or shorter than pedicels ..... **Condaliopsis obtusifolia**
13. Secondary branches minutely hirtellous to short-villous, usually densely so, glabrescent; at least the abaxial leaf surfaces persistently hirtellous to short-villous; hypanthia densely and persistently hirtellous to hirsute-villous; inflorescences (5–)10–30-flowered; peduncles 2–4 mm, equaling or longer than pedicels ..... **Condaliopsis divaricata**



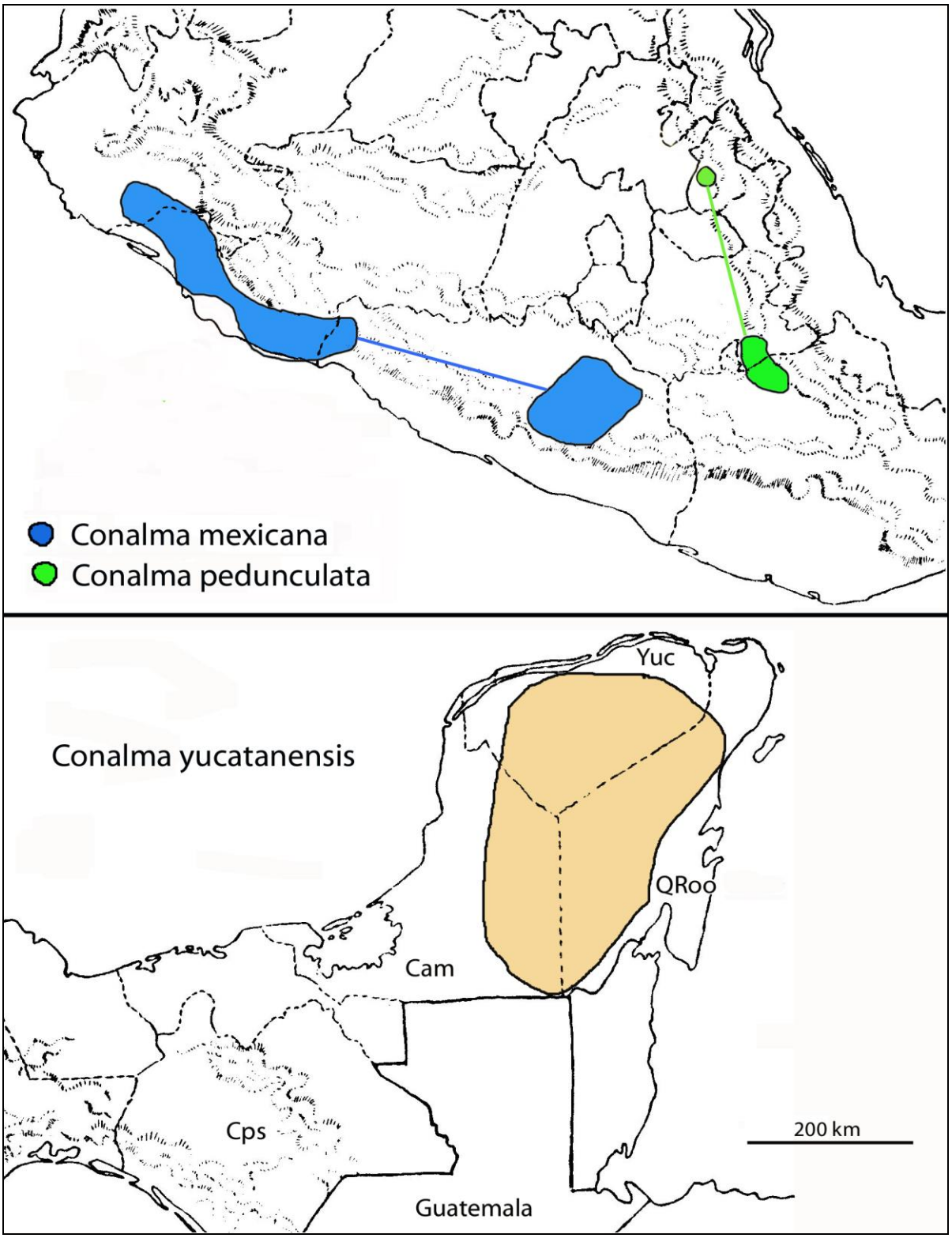
Map 1. Distribution of naturalized *Ziziphus jujuba and Z. mauritiana* in Mexico. Old World natives.



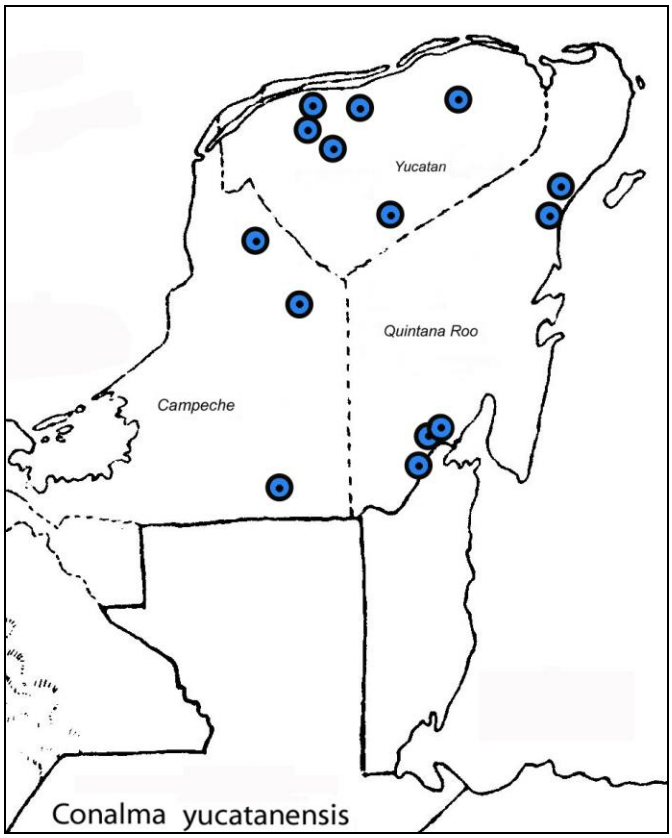
Map 2. Distribution of *Sarcomphalus amole*. Endemic to Mexico.



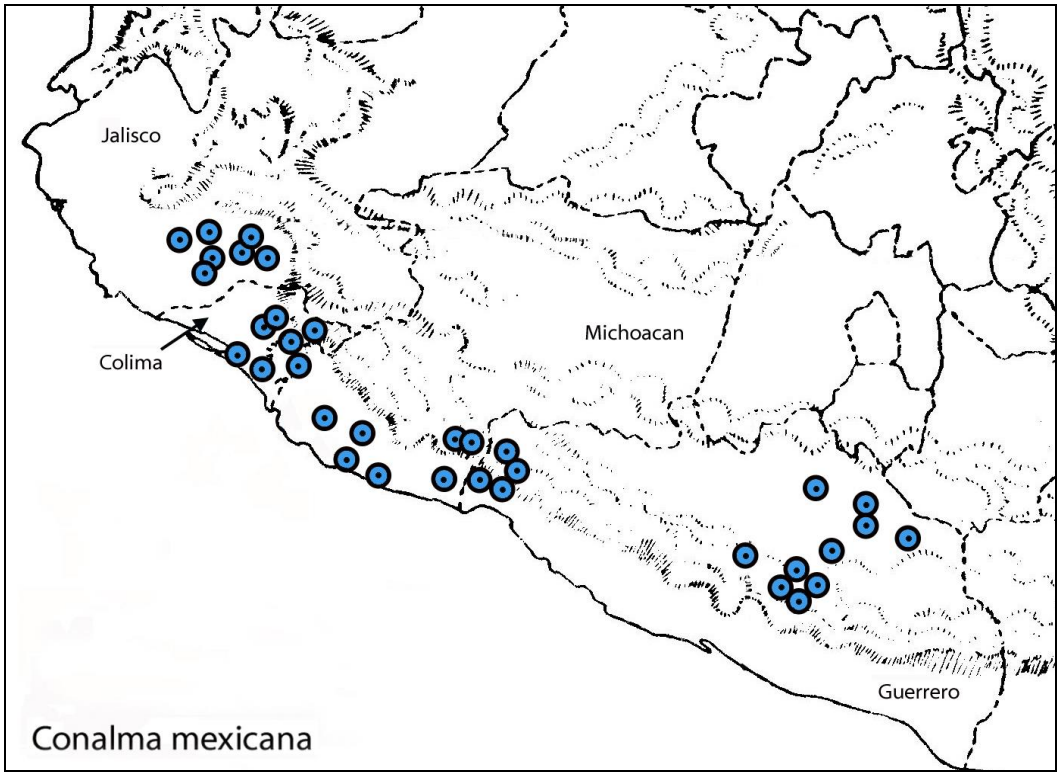
Map 3. Distribution of *Sarcomphalus guatemalensis* in Mexico.



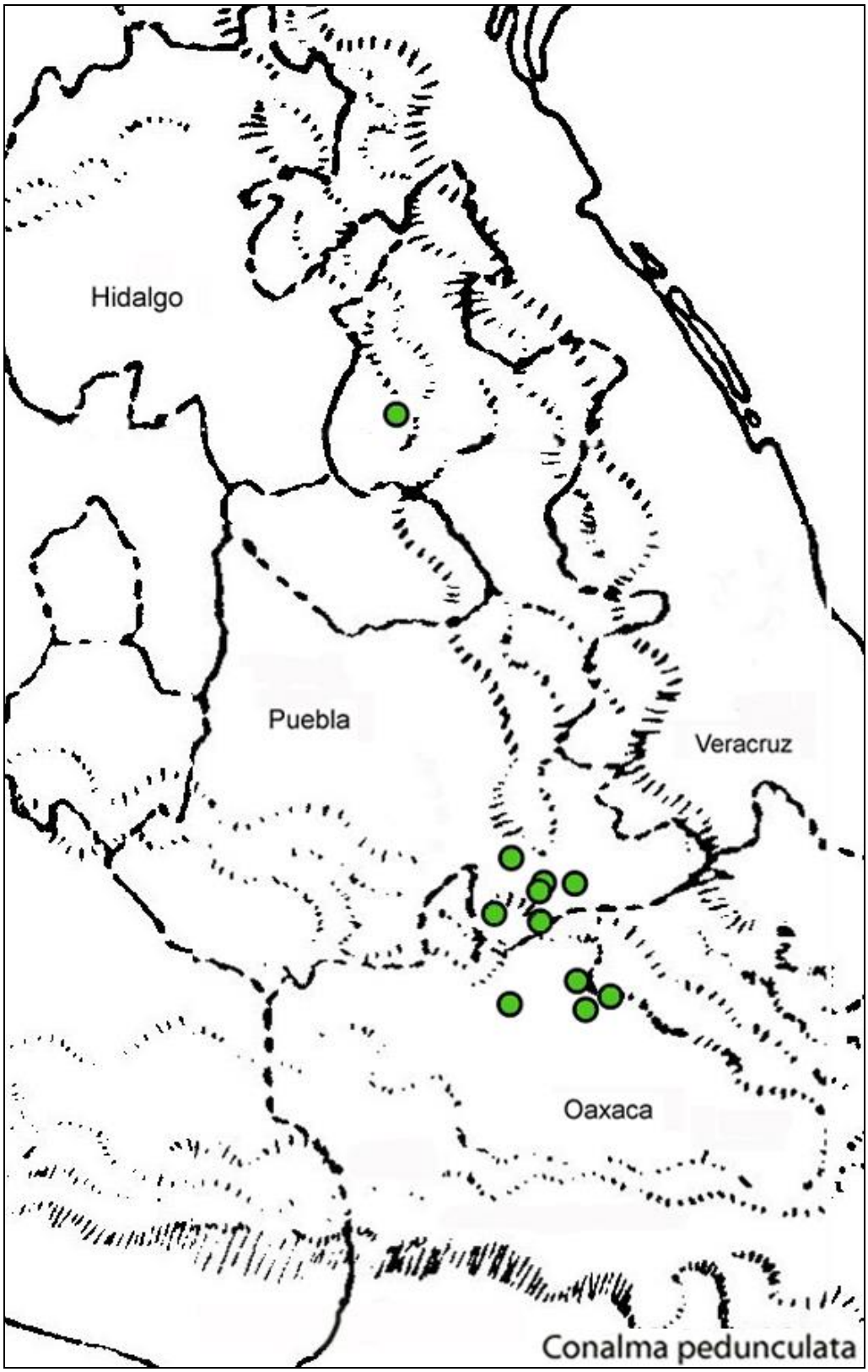
Map 4. Distribution of the genus *Conalma*.



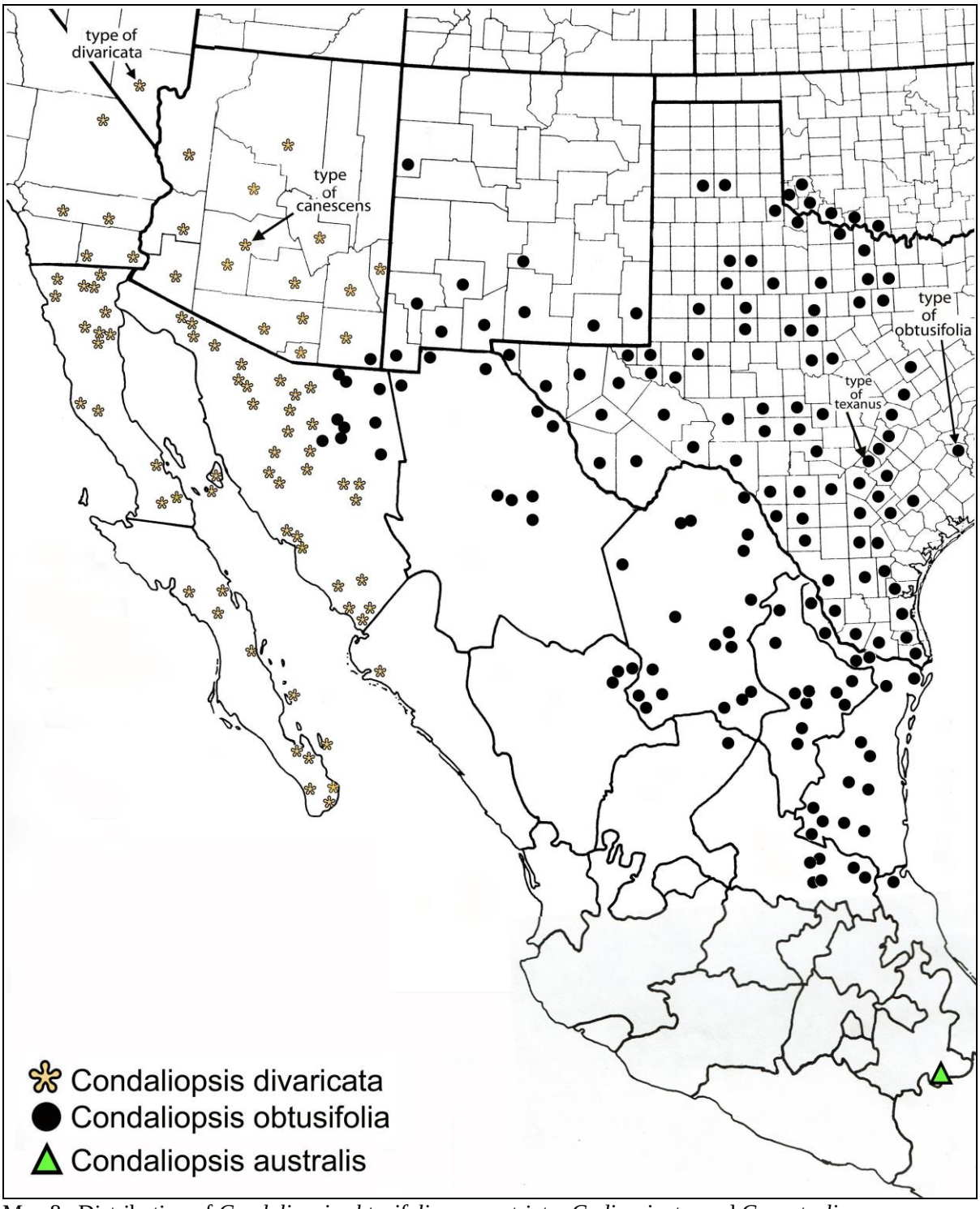
Map 5. Distribution of *Conalma yucatanensis*.



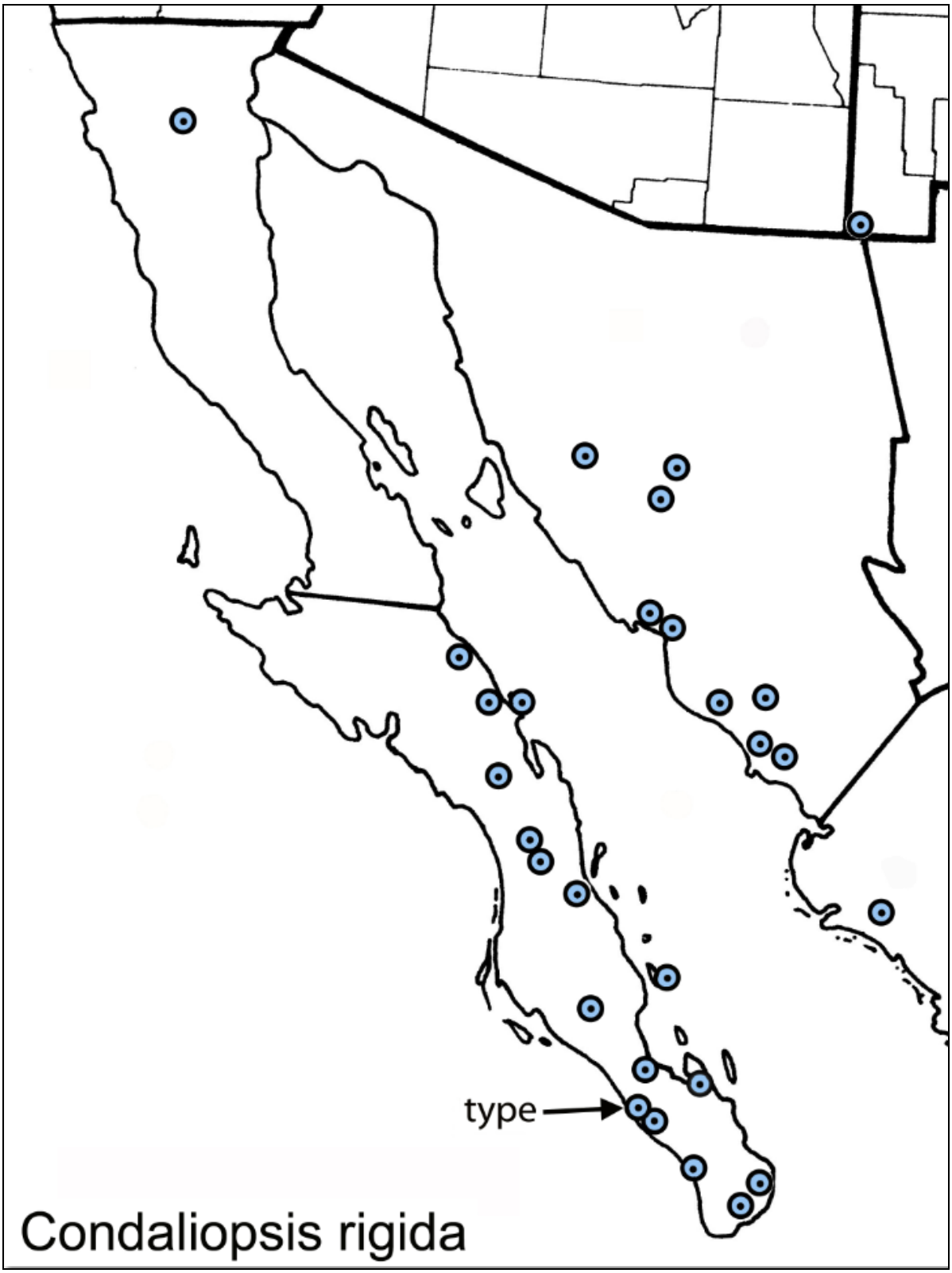
Map 6. Distribution of *Conalma mexicana*.



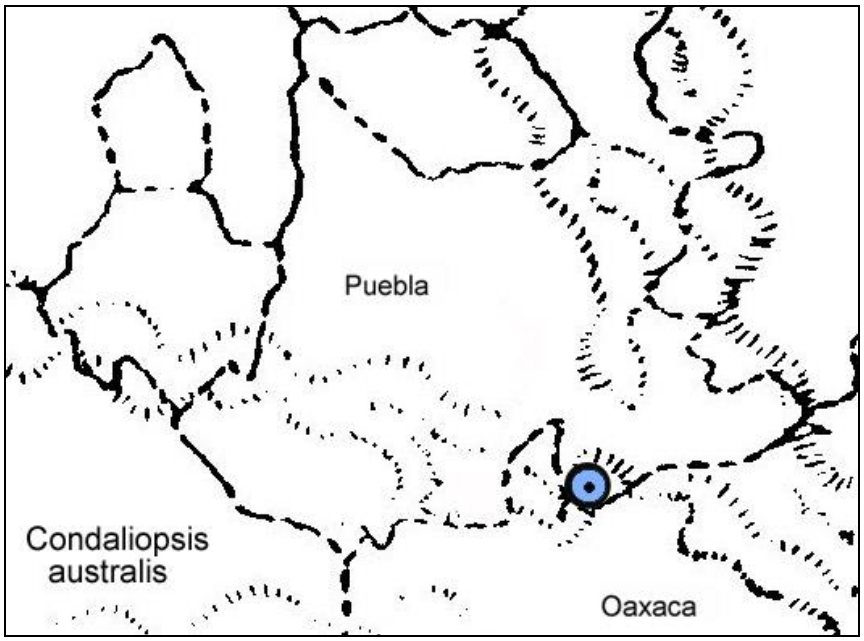
Map 7. Distribution of *Conalma pedunculata*. The record from northern Puebla (Sierra Puebla, N of Zacatlán, *Boege 3122*) is cited in the text. Boege made other collections (MEXU, various taxa) from the same area in May and June of 1974.



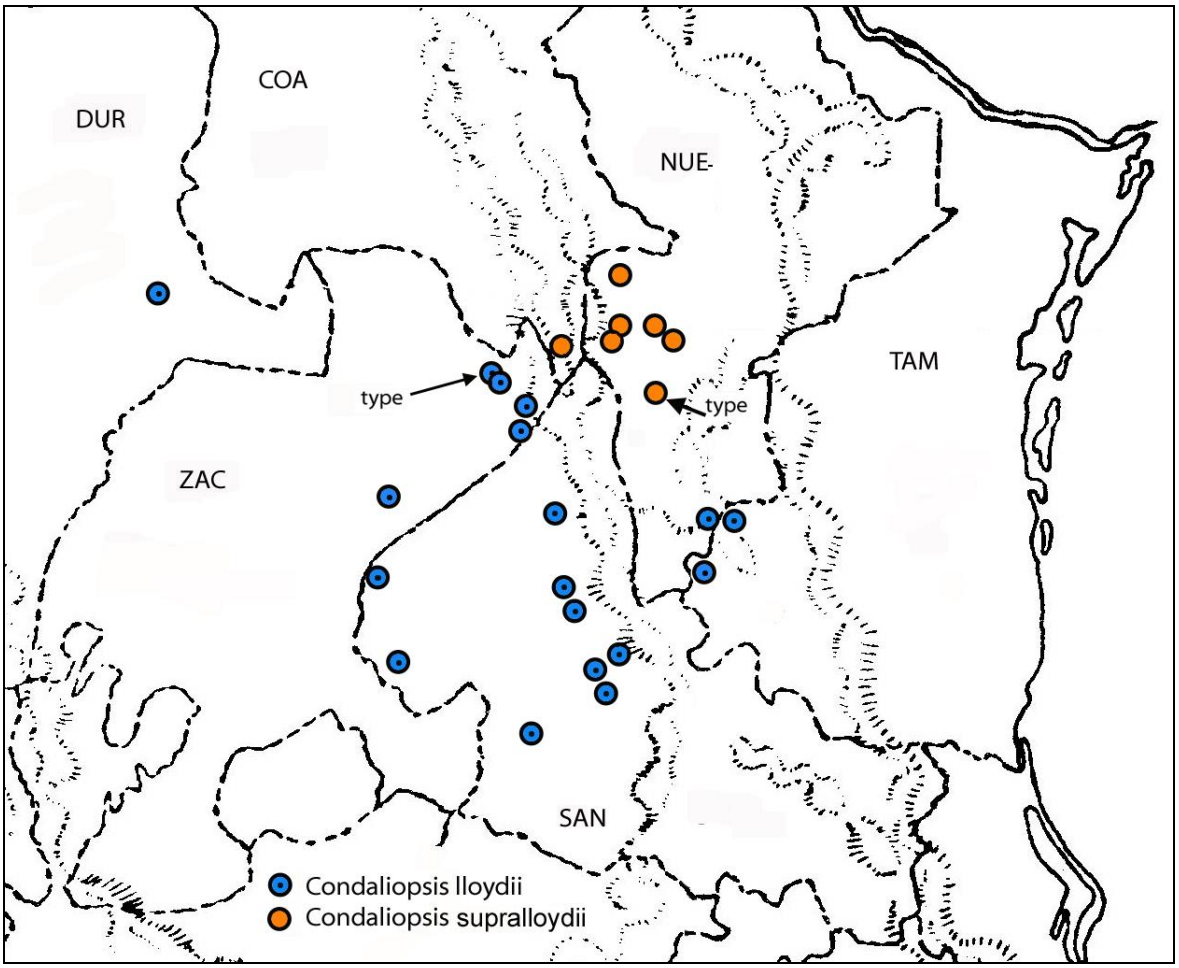
Map 8. Distribution of *Condaliopsis obtusifolia* sensu stricto, *C. divaricata*, and *C. australis*.



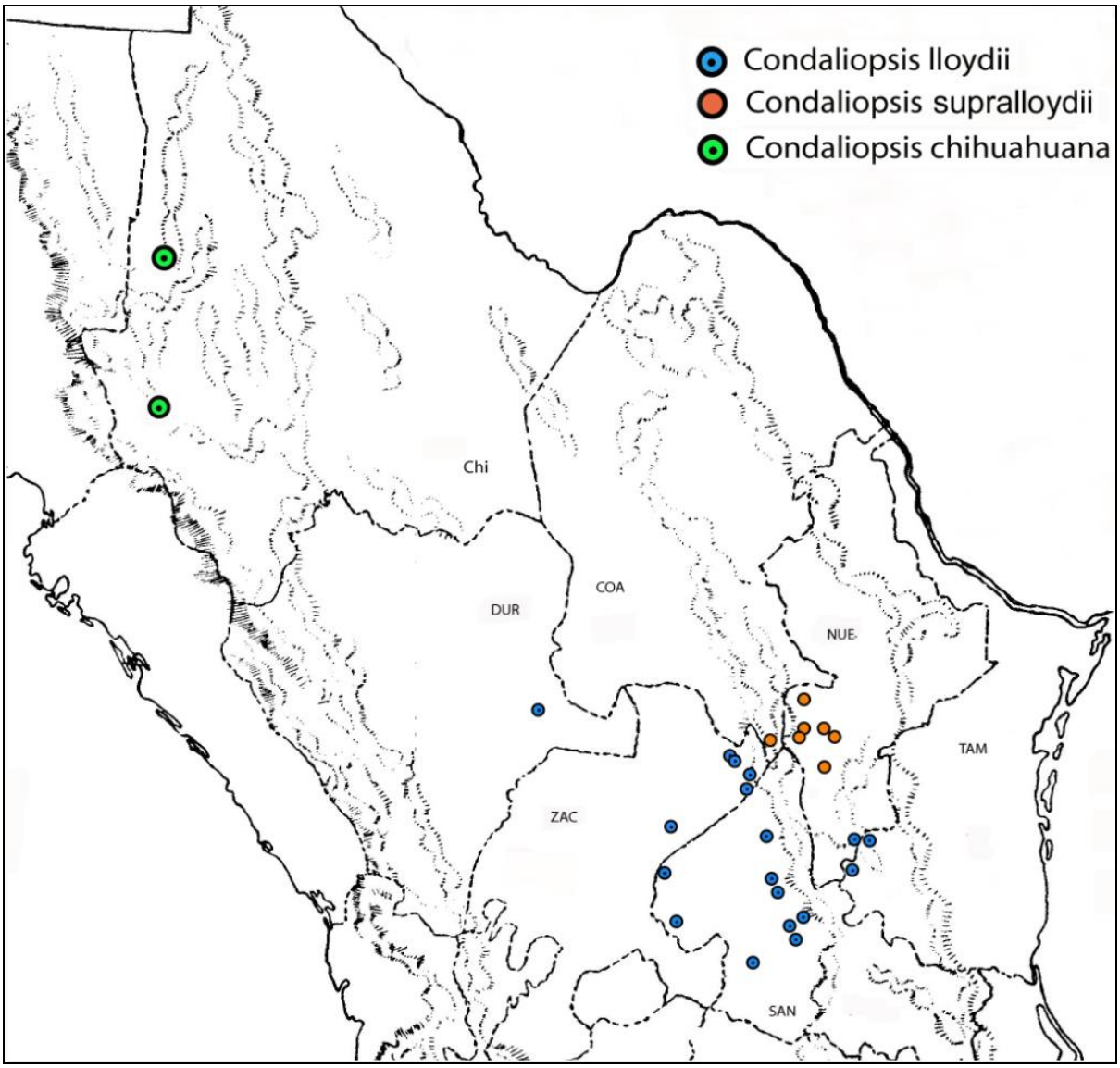
Map 9. Distribution of *Condaliopsis rigida*. The two northern and apparently disjunct records — Baja California and Hidalgo Co., New Mexico — are cited in the text.



Map 10. Distribution of *Condaliopsis australis*.



Map 11. Distribution of *Condaliopsis lloydii* and *C. supralloydii*, with type localities for each. The disjunct record in Durango is cited in the text.



Map 12. Distribution of *Condaliopsis lloydii*, *C. supralloydii*, and *C. chihuahuana*.

Hauenschild et al. (2016) chose lectotypes for *Ziziphus sonorensis* S. Wats., *Rhamnus obtusifolia* Hook. ex Torr. & Gray, *Ziziphus lycioides* var. *canescens* A. Gray, *Condalia divaricata* A. Nels., and *Condalia pedunculata* Brandegee. These choices were superfluous, however, since in each case a collection at the author's home herbarium can be regarded as the holotype (St. Louis Code Rec. 9A.4, but not repeated in the Shenzhen Code) — **T.S. Brandegee** in 1909 (UC), **A. Gray** (GH), **Hooker ex Torrey & Gray** (GH), **A. Nelson** (RM), **S. Watson** (GH).

I. ZIZIPHUS Gard. Dict. ed. 4., alphabetical–not paginated. 1754. **LECTOTYPE (**Britton & Wilson 1924**)**: *Ziziphus jujuba* P. Miller (nom. conserv.). Britton and Wilson cited *Rhamnus zizyphus*, which is now a synonym of *Ziziphus jujuba*, as the type.

1. **ZIZIPHUS JUJUBA** P. Miller, Gard. Dict. Abr. ed. 8., Ziziphus No. 1. 1768 [nom. conserv.; Kirkbride et al 2007; Brummitt et al. 2009]. *Rhamnus zizyphus* L., Sp. Pl. 1: 194. 1753. *Ziziphus zizyphus* (L.) H. Kart., Deut. Fl. 870. 1882 [nom. rej.; Brummitt et al. 2009]. **TYPE**: Herb. Burser XXIII: 50 (UPS), fide Index Nominum Genericorum.

Two nontypical varieties have been recognized with *Ziziphus jujuba*, both apparently endemic to China, and are treated in the Flora of China (Chen & Schirarend 2007): var. *inermis* (Bunge) Rehder and var. *spinosa* (Bunge) Hu ex H.F. Chow. Other synomyms are *Z. sativa* Gaertn. (1788), *Z. sinensis* Lam. (1789), and *Z. vulgaris* Lam. (1789). Figures 1-4.

2. **ZIZIPHUS MAURITIANA** Lam., Encycl. [J. Lamarck & al.] 3: 319. 1797. **LECTOTYPE** (Johnston 1972, following Trimen 1887): **FRANCE**. Isle de France (Mauritius), *P. Sonnerat s.n.* (P-LAM; isolectotype: G-DC). See further comments in Kellerman (2019). Protologue: "Ce *Jujubier* croit à l'Isle de Franc, & nous a été communiqué par M. Sonnerat. h (v.s.)."

Rhamnus jujuba L., Sp. Pl. 1: 194. **LECTOTYPE** (Kellerman 2019): **CEYLON** (**SRI LANKA).** "*Herb.. Hermann 3.14 no. 89* (BM 00621844 and BM 00621467)," as cited by Kelleman. *Ziziphus jujuba* (L.) Gaertn., Fruct. Sem. Pl. 203. 1788 [nom. superfl., non P. Mill. 1768]. *Ziziphus jujuba* (L.) Lam., Encycl. 3: 318. 1797 [nom. superfl., non Gaertn. 1788; non P. Miller 1768]. Protologue: "Habitat in India. ♄" BM 00621844 and BM 00621467 apparently are branches from the same collection but have been given separate barcode numbers.

Figures 5-8.

I. SARCOMPHALUS P. Browne, Civ. Nat. Hist. Jamaica 179. 1756. **TYPE**: *Rhamnus sarcomphalus* L., Syst. Nat., ed. 10, 2: 937. 1759. **Sarcomphalus retusus** Raf., Sylva Tell., 29. 1838 [nom. nov. for *Rhamnus sarcomphalus*]. *Sarcomphalus laurinus* Griseb., Fl. Brit. W. Indies, 100. 1859 [nom. nov. for *Rhamnus sarcomphalus*]. *Ziziphus sarcomphalus* (L.) M.C. Johnston, Amer. J. Bot. 50: 1021. 1963.

The lectotype of *Rhamnus sarcomphalus* (fide Johnston 1964) is *Browne 179* (LINN 262.11) from Jamaica. Twenty-eight species are included, as follow.

West Indies: *Sarcomphalus acutifolius* Griseb.; *S. bidens* Urb.; *S. chloroxylon* (L.) Hauenschild; *S. crenatus* Urb.; *S. domingensis* (Spreng.) Krug. & Urb. (incl. *Sarcomphalus rignonii* Delponte); *S. havanensis* (Kunth) Griseb.— 2 varieties, fide Hauenschild et al. (2016); *S. laurinus* Griseb. (≡ *Ziziphus sarcomphalus* (L.) M.C. Johnston; *Sarcomphalus retusus* Raf.) — 2 varieties, fide Hauenschild et al. (2016); *S. microdictyus* Urb. & Ekm.; *S. obovatus* Urb.; *S. parvifolius* Urb. & Ekman (≡ *Ziziphus urbanii* M.C. Johnst.); *S. reticulatus* (Vahl) Urb.; *S. rhodoxylon* (Urb.) Hauenschild; *S. taylori* Britton

South America: *Sarcomphalus cinnamomum* Triana & Planch.) Hauenschild; *S. cyclocardius* (Blake) Hauenschild; *S. divaricatus* Griseb. (≡ *Ziziphus grisebachianus* M.C. Johnst.; *S. glazovii* (Warm.) Hauenschild; *S. joazeiro* Mart. (Hauenschild) (incl. *Ziziphus cotinifolia* Reiss., *Ziziphus pseudojoazeiro* Mansf.); *S. mistol* (Griseb.) Hauenschild (incl. *Ziziphus oblongifolius* S. Moore; *Ziziphus weberbaueri* Pilg.); *S. piurensis* (Pilg.) Hauenschild; *S. platyphyllus* (Reiss.) Hauenschild; *S. saeri* (Pittier) Hauenschild (incl. *Ziziphus angolito* Standl.); *S. strychnifolius* (Triana & Planch.) Hauenschild; *S. thyrsiflorus* (Benth.) Hauenschild; *S. undulatus* (Reiss.) Hauenschild

Central America/Mexico: *Sarcomphalus amole*; *S. cinnamomum*; *S. guatemalensis*; *S. strychnifolius*. The ranges *of S. cinnamomum* and *S. strychnifolia* extend from South American into Central America (Pool 2015).

1. SARCOMPHALUS AMOLE (Sessé & Moc.) Hauenschild, Taxon 65: 55. 2016. *Rhamnus amole* Sessé & Moc., Pl. Nov. Hisp., 38. 1887. *Ziziphus amole* (Sessé & Moc.) M.C. Johnst., Amer. J. Bot. 50: 1021. 1963. **TYPE**: **MEXICO**. No other locality data, *Sesse & Mocino 817* (MA 602482). Johnston (1963), followed by Hauenschild et al. (2016), cited this collection as the lectotype but a 2008 annotation by MA staff notes that it is the holotype.

Ziziphus sonorensis S. Wats., Proc. Amer. Acad. Arts 25: 44. 1889. **LECTOTYPE** (designated here): **MEXICO**. **Sonora**. "Common about Guaymas, near brackish water" [protologue], alkali sands, Jul 1887, *E. Palmer 124* (GH; isotypes: ARIZ, BM, E, K).

Watson's protologue for *Ziziphus sonorensis* cited two collections, *Palmer 124* and *Palmer 659*. Hauenschild et al. (2016) cited the E sheet of *124* as the lectotype, but the material studied by Watson is at GH. The E sheet was annotated by M.C. Johnston in 1969 as an isotype.

Ziziphus endlichii Loes., Feddes Repert. Spec. Nov. Regni Veg. 8: 296. 1910. **TYPE**: **MEXICO**. **Sinaloa**. Cerca de Topolobampo, Hacienda Correrepe, Endlich 696 (B?, not seen).

Ziziphus sonorensis forma *brevipedunculata* Suess., Repert. Spec. Nov. Regni Veg. 50: 332. 1941. **TYPE**: **MEXICO**. **Guerrero**: Xochipala, 800 m, 24 May 1899, *E. Langlassé 1035* (holotype: M?, not seen; isotypes: P-2 sheets, images).

Figures 14-24.

2. SARCOMPHALUS GUATEMALENSIS (Hemsl.) Hauenschild, Taxon 65: 56. 2016. *Ziziphus guatemalensis* Hemsl., Diagn. Pl. Nov. Mexic. 1: 6. 1878. **LECTOTYPE** (Hauenschild et al. 2016): **GUATEMALA**. No other collection data, *G.U. Skinner s.n.* (K 531808; isolectotype: K 531807). Hauenschild et al. cited K 531808 as the holotype, but the protologue does not specify which of the K sheets is the type, thus his choice is taken here as the lectotype.

The occurrence of *Sarcomphalus guatemalensis* in Mexico is known to me from two collections: **Chiapas**. Mpio. Mazatán: Barra San Simón, bosque, terreno plano, 12 Aug 1985, *Ventura & López 2213* (MEXU). **Oaxaca**. Distr. Juquila: Parque Nacional de Chacahua, arbol 8 m alto, selva mediana perennifolia con *Brosimum*, 80 m, 22 Jun 1982, *Cedilla Trigos 1508* (MO).

Figures 9-13.

II. CONDALIOPSIS (Weberb.) Suess., Natürl. Pflanzenfam. (ed. 2) 20d: 134. 1953. *Condalia* subg. *Condaliopsis* Weberb., Natürl. Pflanzenfam. 3(5): 404. 1895. **LECTOTYPE** (Sussenguth 1953): *Condaliopsis lycioides* (A. Gray) Suess. (= *Condaliopsis obtusifolia*).

Shrubs with zig-zag or right-angled branches; secondary branches first appearing as short to long axillary thorns, branches/thorns with (0–)1–6 nodes, nodes meristematic, producing a few small leaves and tertiary thorns or short shoots and inflorescences; stipular spines absent; branchlets glabrous or hairy, sometimes pruinose. **Leaves** persistent, alternate, sparse and solitary on short shoots, or fascicled; petiole present; blades mostly elliptic to oblong or oblanceolate, herbaceous to subcoriaceous, margins entire to serrate or crenate with gland-tipped teeth, apex rounded to obtuse or retuse, surfaces glabrous or hairy, not gland-dotted; pinnately nerved (brochidodromous), 1-veined from the base; stipules herbaceous, narrowly triangular, deciduous. **Inflorescences** axillary, flowers (1–)2–30 in sessile fascicles or pedunculate thyrses; bracts (bracteoles) present. **Flowers** bisexual, pedicellate; hypanthium shallowly cupulate; sepals 5, greenish or greenish white to yellowish, sometimes purple- or orange-tinged, ovate-triangular to deltate, adaxially keeled; petals yellow to pale yellow, limb cucullate and at first surrounding the anthers, base clawed; nectary disc shallow, fleshy, 10-angled, filling the hypanthium and covering 1/2–3/4 of the ovary in early anthesis but not adnate to it; stamens 5; ovary broadly attached to receptacle, free from disc, 2-loculed; ovules 1 per locule; style 1, 2-fid (rarely 3-fid) 1/8–7/8 of the length. **Fruits** fleshy drupes, blue to purplish or red to pink, globose to oblong-ellipsoid, obovoid-ellipsoid, or ellipsoid-cylindric, 5–10 mm long; stones 1. **Seeds** 2 per stone, or sometimes 1 by abortion of 1 ovule. **Chromosome number** not reported.

Weberbauer's *Condalia* subg. *Condaliopsis* included 3 taxa: *C. lycioides*, *C. obtusifolia*, and *C. parryi*. Suessenguth (1953) added *C. lloydii* and *C. velutina* (I.M. Johnst.) Suess., but Johnston (1962) observed that the latter indeed does belong with typical *Condalia* (where it was originally placed) despite its production of petals (several other North American taxa of *Condalia* also are petaliferous, see Henrickson 2003 and Nesom 2023). As treated here, *Condaliopsis* comprises seven species: *C. obtusifolia*, *C. divaricata*, *C. rigida*, *C. lloydii*, *C. supralloydii*, *C. chihuahuana*, and *C. australis*.

1. CONDALIOPSIS OBTUSIFOLIA (Hook. ex Torr. & Gray) Suess., Natürl. Pflanzenf. (ed. 2) 20d: 135. 1953. *Rhamnus obtusifolia* Hook. ex Torr. & Gray, Fl. N. Amer. 1: 685. 1840. *Ziziphus obtusifolia* (Hook. ex Torr. & Gray) A. Gray, Gen. Amer. Bor. 2: 170. 1849. *Condalia obtusifolia* (Hook. ex Torr. & Gray) Weberb., Natürl. Pflanzenf. 3(5): 404. 1895 (basionym not given). *Sarcomphalus obtusifolius* (Hook. ex Torr. & Gray) Hauenschild, Taxon 65: 56. 2016. **TYPE**: **USA**. **Texas**. [Austin Co.:] San Felipe de Austin, 1835, *T. Drummond 45* (holotype: K image; isotype: GH image).

The handwritten label by Drummond on the GH sheet says "Hooker misit 1835" (i.e., sent to Hooker in 1835). Leaves of *Drummond 45* are larger than characteristic for the species — perhaps juvenile leaves and leaves on a damaged shoot.

Paliurus texanus Scheele, Linnaea 21: 594. 1848. **TYPE**: **USA**. **Texas**. [Comal Co.:] Protologue: "Im bottomwalde des ohern Guadeloupe: Lindheimer. Juni bis September." 1846, *F. Lindheimer 364* (Fasc. III) (holotype: not located; isotypes: US image, MO-3!). Figure 56.

Each of the Lindheimer sheets at MO has a handwritten label with "Comale Creek, Juni 1845, Texas, F. Lindheimer 607." A printed label shows "Flora Texana exsiccata 364 Fasc II, leg. F. Lindheimer 1846."

Leaves of this collection are larger than characteristic for the species — they perhaps are juvenile leaves and leaves on a damaged shoot.

Ziziphus lycioides A. Gray, Bost. J. Nat. Hist. 6 [Pl. Lindh. 2]: 168. 1850. *Condalia lycioides* (A. Gray) Weberb. (basionym not given in protologue), Natürl. Pflanzenfam. 3(5): 404. 1895. *Condaliopsis lycioides* (Gray) Suesseng., Natürl. Pflanzenfam. (ed. 2) 20d: 135. 1953. **TYPE**: **MEXICO**. **Coahuila**. Label: "Matamoros to Mapimi," [1847], *J. Gregg s.n.* (holotype: GH 51528; isotype: NY "Pozo Patos .. Garambullo "; probable isotype: GH 51529; isotype: MO).

The MO sheet has a printed label with "Pozo, Mexico, 13 Apr 1847, J. Gregg 707" and a handwritten label with "707" and "Pozo, April 13 & Patos May 19/47 (from Matamoros to Mapimi)." Patos is in Mpio. General Cepeda; Garambullo is about 35 miles to the south in Mpio. Parras.

Condalia lycioides var. *microphylla* Loes., Repert. Sp. Nov. Regni Veg. 8: 296. 1910. **TYPE**: **MEXICO**. **Coahuila**. Protologue: "Strauchsteppen auf der Hacienda 'La Tortuya'," [shrubby vegetation around Hacienda 'La Tortuya,'] 1000 m, May [1904 or 1905], *R. Endlich 497a* (not seen, not available through JSTOR Global Plants).

Var. *microphylla* was distinguished by Loesener only by the brief protologue: "Foliis parvis tantum usque 1 cm longis et circ. 2 mm latis, disco obsolete 5-lobo a typo recedens." Johnston (1963, p. 1025) noted that he had "not seen the collection. The description say that the leaves are small, about 1 cm broad and 2 mm broad. This characterizes one of the small-leaved forms common in scattered parts of the Chihuahuan desert" (e.g., Fig. 58). Christie et al. (2006) noted that in Arizona "leaf size [in *Ziziphus divaricata*] is dependent upon climate, habitat and season."

Johnston (1963) cited var. *microphylla* as a synonym of *Ziziphus obtusifolia* but (as here) he did not see the type. Ejido La Tortuga is located in Mpio. Ramos Arizpe along Hwy 114, about 30 miles NW of Saltillo in southeastern Coahuila, just to the east of Sierra de la Paila, at about 3300 feet elevation.

Shrubs, 0.5–1(–2.5) m, stems densely and stiffly branched at right angles, branches gray-green to white, usually distinctly pruinose, glabrous to sparsely short villous-strigose-sericeous, secondary branches thorn-tipped, axillary thorns single, 2–10 mm, with (0–)1–4(–6) nodes, sclerified thorn tips abruptly differentiated. **Leaves** deciduous, alternate or fascicled, blades dull green adaxially, glaucous abaxially, both surfaces persistently villous, usually glaucous abaxially, sometimes sparsely short-villous to short-strigose adaxially, ovate, oblong, or elliptic to nearly linear, 0.5–2.5(–5) cm long, relatively thin-herbaceous, pinnate to subpinnate, sometimes weakly 3-veined from the base, base rounded to truncate, margins entire or broader leaves shallowly serrate or crenate, young leaves with gland-tipped teeth, apex rounded to slightly retuse; petioles 1–2 mm long. **Flowers** 1 or 2–6 in short-pedunculate thyrses 5–10 mm, peduncles (0.5–)1–2 mm; pedicels 1.5–2.5 mm, short-villous; hypanthium purple, sparsely to moderately to densely strigose-villous with appressed to loose, upcurving hairs, sepals yellow to orangish or slightly purple; style branches 2, divided ca. 1/4-1/5 of the style length; petals yellow to pale yellow or nearly white. **Fruit** globose to slightly elongate, 5–10 mm long, dark blue to purplish, rarely (immature?) reddish. Figures 48-61.

Flowering (Mar–)Apr–Jun. Silty and sandy flood plains and washes, stream banks, gravelly slopes, brushy hills, sand and clay dunes, plains, gypsum roadsides and outcrops, desert grasslands, scrublands; (10–)100–1600(–1800) m; Ariz., N.Mex., Okla., Tex.; Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora, Tamaulipas, Veracruz, Zacatecas).

In Arizona, *Ziziphus obtusifolia* sensu stricto occurs only in the southeasternmost corner of Cochise County, just to the east of Douglas. **Representative collections**: Cochise Co.: Old Douglas Gypsum mine, 10 mi out of town on Geronimo trail, [no date], *Harris s.n.* (ASU); 7.2 mi E of corner of Airport road and 15th Street in Douglas on road to San Bernardino Valley, 2 May 1988, *Landrum 6043* (ASU); San Bernardino Ranch, 18 mi E of Douglas, 1159 m, 11 Apr 1981, *Marrs-Smith 450* (ASU); San Bernardino Ranch, 18 mi E of Douglas, 25 Jun 1981, *Marrs-Smith 626* (ASU); 10 mi E of Douglas, 1249 m, 26 May 1935, *Peebles 11703* (ARIZ).

Fernández Nava (1986) cited only one collection of *Ziziphus obtusifolia* from Veracruz — e.g., Mpio. Pánuco: 1 km N of Hwy 70, gravel road toward Est. Méndez, 6.2 km W of Canoas jct and 12 km NNW of Pánuco, shrub 2 m high, brushy roadsides and pasture, 50 m, 24 Oct 1981, *Nee 22339* (TEX, also F and XAL as cited by Fernández Nava). It also is the only Veracruz collection I have seen.

Ziziphus obtusifolia has been recognized to comprise two entities, beginning with the description of *Z. lycioides* var. *canescens* by Asa Gray in 1879. The recognition of *Condalia rigida* Wiggins in 1950 has not been accepted (except by Wiggins) until now, although Johnston (1963) noted that *Z. rigida* could be regarded as a weakly distinguished geographical race. These three taxa constitute the *Condaliopsis obtusifolia* group, as referred to here.

Johnston (1963) recognized two varieties but, like Gray, gave no explicit rationale for the taxonomic arrangement. Nor, as far as I can find, has anyone provided even a brief comment regarding a putative evolutionary relationship or interaction between the two. Presumably they have been regarded as conspecific because of their similarity in morphology and relatively northern distribution compared to other native species. Morphology and geography suggest that typical *Z. obtusifolia* and *Z. obtusifolia* var. *canescens* have a cladistic sister relationship, but as implied by Johnston's descriptions and distribution map and as corroborated in the present review, the two appear to be discontinuously distinct and parapatric in Cochise Co., Arizona, and southward into Sonora (Map 1), without evidence of hybridization and introgression. This suggestion of reproductive isolation supports the recognition of *Ziziphus obtusifolia* var. *canescens* at specific rank.

Schirarend (1991) observed significant differences in wood anatomy between *Condaliopsis obtusifolia* (voucher from Nuevo León, identified by him as *Condaliopsis obtusifolia*) and *C. divaricata* (vouchers from Arizona, identified by him as *Condaliopsis lycioides*) — in vessel frequency, diameter, and member length and ray frequency and height.

Johnston (1966) reported the occurrence of *Condaliopsis* (as *Ziziphus*) *obtusifolia* just south of Tehuacán in Puebla, disjunct southward from the range of the latter, but this collection instead is a plant of *Conalma pedunculata* with mostly alternate to subopposite leaves: 2 mi SW of Zapotitlán, alluvial flat of big arroyo, desertic area, 30 Aug 1965, *Johnston & Johnston 7272* (TEX).

Collections of *Condaliopsis obtusifolia* (as identified here) with smooth, dark brown stems, reminiscent of *C. rigida*, have been made from two localities in relatively close proximity — **Nuevo Leon**. Mpio. Gral. Bravo: Rancho La Encantada [24.39, -97.95], 30 km al SW de Reynosa, camino a China N.L., matorral alto espinoso, arbusto de 2 m, 14 May 1985, *González-Medrano 14582* (MEXU). **Tamaulipas.** Mpio. San Fernando: 2 km al WSW de Punta de Alambre, 24° 32' 35" N, 97° 44' 58" W, 19 Jul 2007, *Martínez S.* 39367 (MEXU, IDed on the label as *Ziziphus lloydii*).

2. CONDALIOPSIS DIVARICATA (A. Nels.) Nesom, **comb. nov**. *Condalia divaricata* A. Nels., Bot. Gaz. 47: 427. 1909. *Ziziphus divaricata* (A. Nels.) Davidson & Moxley, Fl. S. Calif., 226. 1923. **TYPE**: **USA**. **Nevada**. Clark Co.: Las Vegas, 5 May 1905, *L.N. Goodding 2300* (holotype: RM image; isotypes: GH image, MO!).

Ziziphus lycioides A. Gray var. *canescens* A. Gray in Rothr., Rep. U.S. Geogr. Surv., Wheeler 6: 82. 1879. *Condalia lycioides* var. *canescens* (A. Gray) Trel. in A. Gray, Synopt. Fl. N. Amer. 1(1): 403. 1897. *Condaliopsis lycioides* var. *canescens* (A. Gray) Suess., Natürl. Pflanzenf. (ed. 2) 20d: 135. 1953. *Ziziphus obtusifolia* var. *canescens* (A. Gray) M.C. Johnston, Brittonia 14: 367. 1962. *Sarcomphalus obtusifolius* var. *canescens* (A. Gray) Hauenschild, Taxon 65: 57. 2016. **TYPE**: **USA**. **Arizona**. [Maricopa Co.:] Valley of the Gila, 3080 ft, Jul 1874, *J.T. Rothrock 331* (holotype: GH image; isotypes: F image, US image, YU).

Shrubs or small trees, 1–3(–4) m, stems densely and stiffly branched at right angles, branches gray-green to white, distinctly pruinose, minutely hirtellous to short-villous, usually densely so, glabrescent; secondary branches thorn-tipped, axillary thorns single, 2–10 mm, with (0–)1–4(–6) nodes, sclerified thorn tips abruptly differentiated, tertiary thorns 1–3 mm. **Leaves** deciduous, alternate or fascicled; blade dull greenish adaxially, glaucous abaxially, both surfaces hirtellous to short-villous with persistent vestiture, ovate, oblong, or elliptic to nearly linear, 0.3–2(–2.5) cm, subcoriaceous, base rounded to truncate, margins entire or broader leaves with few shallow distal teeth, apex rounded to slightly retuse. **Flowers** 1 or 2–5 in a short-pedunculate thyrse, peduncles 1–2(–3) mm; pedicels 1–1.5 mm; hypanthium purplish, sepals yellow to orangish or slightly purple, densely puberulent-canescent; style branches 2; petals light green to white. **Fruit** globose to slightly elongate, 7–10 mm long, dark blue to purplish. Figures 62-65.

Flowering Apr–Jul(–Sep). Washes, basin edges, roadsides, desert grasslands, mesquite and tamarisk thickets; (20–)200–1500 m; Ariz., Calif., Nev., Utah; Mexico (Baja California, Sonora).

3. CONDALIOPSIS RIGIDA (Wiggins) Wiggins, Veg. Fl. Sonoran Des. 2: 861. 1964. *Condalia rigida* Wiggins, Contr. Dudley Herb. 4: 20. 1950. **TYPE**: **MEXICO**. **Baja California Sur**. Just beyond Rancho Arroyo Seco, lat. 24° 10', 7 Apr 1930, *D.A. Johansen 601* (holotype: CAS image).

Shrubs, 1–2.5 m, stems densely and stiffly branched at right angles, without hairs or white wax, sometmes a waxy epidermal layer peeling off to green stems; secondary branches bright green, thorn-tipped, axillary thorns single, 7–25 mm, with 1–5(–8) nodes (more if becoming a long branch), sclerified thorn tips abruptly differentiated. **Leaves** alternate or fascicled; blades green to gray-green, glabrous on both surfaces, glaucous abaxially, narrowly to broadly elliptic to obovate, 1.5–2.5 cm, subcoriaceous, base rounded to truncate, venation pinnate, margins entire, apex rounded to retuse. **Flowers** (5–)14–30 in pedunculate thyrses 10–20 mm long, peduncles 0.5–2.5(–5) mm; pedicels 1–2.5 mm; hypanthium glabrous to minutely puberulent, purple, style branches 2; hypanthium and sepals yellow to orangish or slightly purple; petals pale yellow. **Fruit** broadly obovoid-ellipsoid, 6–8 mm long, dark blue to blue-black. Figures 66-74.

Flowering (Feb–) April–Jun and sporadically through the year. Hillsides, rocky benches, arroyo bottoms, matorral, palm grove thickets; 5–400(–1200) m; Mexico (Baja California, Baja California Sur, Sonora), USA (Hidalgo Co., New Mexico).

Johnston (1963) viewed *Ziziphus obtusifolia* var. *canescens* as comprising two "weakly distinguished sorts of plants, somewhat geographically segregated ... ." The atypical form is completely glabrous and (as noted by Johnston) had been described as *Condalia rigida* Wiggins (1950) = *Condaliopsis rigida* (Wiggins) Wiggins. "Plants with intermediate pubescence [i.e., intermediate between rigida and obtusifolia = canescens] are rather numerous" according to Johnston (1963) but he mapped the two expressions with separate ranges, essentially contiguous in Sonora, and did not indicate the occurrence or location of putative intermediates. Here, *C. rigida* and *C. divaricata* are seen as widely sympatric. *Condaliopsis rigida* occurs in southern Sonora and Baja California Sur and was formally recognized in floristic studies of both areas (Wiggins 1964, 1980), with no suggestion of intermediacy. Its distinction is confirmed here.

Some collections of *Condaliopsis rigida* have sparsely white-puberulent young stems and might be identified as *C. divaricata*, but the vestiture is quickly lost. Leaves of *C. rigida* are typically glabrous, compared to *C. divaricata*, where at least the abaxial surface is persistently hairy. Hybrids may shown intermediate morphology.

Representative collections. **MEXICO**. **Baja California**. Sierra Juárez, 6 km NW of El Rodeo, 31° 35.3' N, 115° 51' W, 1010 m, few on flat with *Juniperus* and *Prosopis*, 28 Jul 1979, *Moran 27913* (SD). **Baja California Sur**. San Gregorio, 4 Feb 1889, *Brandegee s.n.* (UC); SE of Comondú, Rancho Quiñi, bottom of deep arroyo on old mission trail, 310 m, 20 Apr 1955, *Carter & Ferris 3420* (DS, UC); low hills W of cemetery, 26° N, 111° 21 W, 5 m, 13 Jun 1965, *Carter 4953* (UC); 10 mi S of Comondú, wash in arroyo, 6 Aug 1955, *Chambers 794* (UC); Las Lomas de Anita, NW of Loreto, 27 Mar 1976, *Fuerte O. 152* (UC); La Paz, rocky bench, 11 Apr 1921, *Johnston 3025* (CAS); Bajia de La Paz, El Comitán, matorral sarcocaule, 2 May 2010, *Leon de la Luz 10_10* (MEXU); NE side of San José Island, Arroyo de Aguada, near beach, 5 m, 11 Apr 1962, *Moran 9396* (RSA); 2 mi W of San José del Cabo, roadside arroyo bank, 175 ft, 30 May 1948, *Peters 272* (UC); Comondú, 27 Apr 1931, *Wiggins 5500* (UC); Arroyo Aguada, E side of Isla San Jose, Gulf of California, 26 Jun 1964, *Wiggins 19079* (DS). **Sinaloa**. 8 mi SE of Guasave, 12 Mar 1973, *Johnson 507-73* (ASC). **Sonora**. Ejido Sahuaral, 5 km E del Mpio. Etchojoa, junto al canal de riego de campo agricola, 12 m, 2 Sep 2012, *Aceves et al. 2012-001* (USON); San Carlos Bay ca. 8 mi N of Guaymas, thicket in palm grove 1/2 mi back from water, 19 Mar 1934, *Ferris 8737* (DS); Bachoco, 12 mi NE of Cajeme, mesquite valley, 12 Mar 1937, *Gentry 3047* (MO, UC); 7-9 mi W of Navajoa, thorn forest, 50-150 ft, 12 Apr 1948, *Gentry 7963* (RSA); Guaymas, 26 Jan 1927, *Jones 22890* (POM, UC); 7 mi E of jct with Mex Rte 15 along Masiaca-Alamos road, ca. 200 ft, thorn scrub, occasional shrub to 2 m tall, 13-14 Jan 1983, *Keil 16873* (OBI); Loma de Moroncarit, 2 km W of Etchoropo, 26° 45' N, 109° 40' W, remnant of thorn forest, 10 m, 11 Oct 1988, *Martin et al. s.n.* (MO); Mpio. Hermosillo, Colonia La Manga, Hermosillo, a un costado del represo Sifón, a orilla de aquas negras, 212 m, 27 Jan 2013, *Molina R. & Coronado 2013-01* (USON); S of Etchojoa por la carr. Navajoa Huatabampo, llanura cercanías del Rio Mayo, poca vegetación con alamos, 13 m, 25 Sep 2009, *Moran Palacio & Zomara A. LBT-04* (USON); Guaymas, 15-17 Feb 1890, *Palmer 162* (UC); San Bernardino, 20 Apr 1894, *Price s.n.* (DS); Mpio. Moctezuma, Ciénega de Tonibabi, a 11.9 km (linea recta) ENE de Moctezuma, comun en los alrededores de la ciénega, 785 m, 27 Jun 2011, *Sanchez E. 2011-451* (USON); near Guaymas, 28 Feb 1933, *Shreve 6124* (RSA); just N of Corall on Hwy 15, 16 Apr 1968, *Smith 4728* (US-2 sheets); hillsides near Guaymas bathing beach at Miramar, 28 Feb 1933, *Wiggins 6360* (DS, POM, UC); 4.5 mi N of Empalme along road to Ortiz, 5 May 1948, *Wiggins 11636* (DS, UC). **USA. New Mexico**. Hidalgo Co.: Guadalupe Canyon, 15 mi E of jct with Douglas Arizona road, very SW corner of state, *Juniper-Agave-Yucca* zone, 4200 ft, shrub 10 ft tall, smooth green bark, 20 Apr 1968, *Hess 1805* (NMC, SMU).

4. CONDALIOPSIS LLOYDII (Standl.) Suess., Natürl. Pflanzenf. (ed. 2) 20d: 135. 1953. *Condalia lloydii* Standl. Contr. U.S. Natl. Herb. 23: 714. 1923. *Ziziphus lloydii* (Standl.) M.C. Johnst., Brittonia 14: 367. 1962. **TYPE**: **MEXICO**. **Zacatecas**. Hacienda de Cedros, Garapata, foothills, 1908, *F.E. Lloyd 71* (holotype: US image; isotypes: DS, F image, UC!). Figs. 77-78, 80.

Shrubs 1–5 m, longer secondary branches gray, glabrous or sparsely hirtellous, not waxy or pruinose, not thorn-tipped, thorns axillary, often from short shoots, short with 0–1(–2) meristematic nodes, sclerified thorn tips abruptly differentiated. **Leaves** deciduous, alternate or usually fascicled, blades oblong to elliptic-oblong, 4–10 mm long, 2–3 mm wide, herbaceous, margins entire or sometimes (in young leaves) pauciserrulate with gland-tipped teeth, apex rounded, base rounded to attenuate to a very short petiolar region, both surfaces sparsely villous, not abaxially glaucous, venation pinnate (brochidodromous), 1-veined from the base or weakly 3-veined. **Flowers** solitary, usually from short shoots, sessile or on short peduncles (sessile and pedunculate commonly on the same plant); pedicels 1–3 mm; hypanthium yellow-brown, hispidulous to puberulent-hirtellous, style branches 2 or rarely 3, divided 1/2–2/3 of the style length; petals white, 1 mm long; style branches 2 or rarely 3, divided nearly to the base. **Fruit** red to pink, ovoid to ellipsoid or ellipsoid cylindric, ca. 4.5–9 mm long, short-beaked, often with persistent style branches. Figures 75-78, 80-83.

Flowering (Mar–) May–Oct (–Nov). Hills and flats, matorral with *Agave*, *Yucca*, mesquite, *Hechtia*, *Larrea*, *Flourensia*; 1150-2150 m. Coahuila, Durango, Nuevo León, San Luis Potosi, Tamaulipas, Zacatecas.

Additional collections. Coahuila. Torreón, 3740 ft, 10 Jul 1944, *Johnston 44161* (MO); Torreón and vicinity, 13-20 Oct 1898, *Palmer 470* (MO); 11 km NE of Jimulco, rolling hills covered with *Agave*, *Yucca*, and low mesquite, plants 2-4 ft tall, 2100 m, 27 Jun 1941, *Stanford et al. 7* (MO). **Durango**. Mpio. Cuencamé, Ejido las Mercede, campo experimental de Zonas Aridas, ca. 19 km al N de Cuencamé, carr. 40 Durango-Torreón, 8 May 1992, *Rodriguez 1513* (MEXU-2 sheets); Bolson de Mapimí, matorral xerófilo, Mar 1987, *Zurita N. s.n.* (MEXU). **Nuevo León**. Specimen seen but not recorded. **San Luis Potosí**. Mpio. de Ramos, camino al Toro, en las inmediaciones de Santa Maria, matorral desertico microfilo, 2020 m, 1973, *Banda 1137* (MO); 14.4 km S of Warley on road to Charcas, with *Larrea*, *Flourensia*, *Lophophora*, 1600 m, 3 Jul 1972, *Chiang et al. 8237* (CAS, LL, MEXU); 7.7 km S of Warley on road to Charcas, with *Larrea*, *Flourensia*, 1600 m, 3 Jul 1972, *Chiang et al. 8240* (LL, MEXU); 3 mi E of Huizache Jct and 3 mi W of El Huizache on the Cd. del Maiz hwy, 20 Sep 1960, *Crutchfield & Johnston 5657* (TEX); ca. 2 km airline SE of Huizache Jct and ca. 5 km WSW of El Huizache near the SLP-Cd. del Maiz hwy, 19 May 1973, *Johnston et al. 11123* (CAS, LL, MEXU); Charcas, Jul-Aug 1934, *Lundell 5353* (CAS, DS, F, GH, MICH, US); 5 km S de Matehuala, matorral, 1300 m, 15 Jul 1975, *Medrano et al. 8126* (MO); Charco Blanco, carr. San Luis-Antiguo Morelos, llano con vegetacion de mezquite y gobernadora, 1 May 1955, *Rzedowski 5809* (MEXU); Mpio. Santo Domingo, Laguna de Sta. Clara, 2100 m, 2 Jun 1956, *Rzedowski 7637* (MEXU); Mpio. San Luis Potosí, Mantequilla, alrededores del poblado, 2 Jun 1957, *Rzedowski 8876* (MEXU); Guadalcázar, 1 km al SE de Palos Altos, carr. a Cerritos, matorral xerófilo, 9 Oct 1996, *Torres C. 14620* (MEXU); Guadalcázar, Cerro Calvo o Cerritos Malpaisitos (Antena de Microondas) o 7.3 km al NE del Huizache, hacia Santa Rita del Rucio, matorral xerófito de *Hechtia*, *Agave*, *Myrtillocactus*, 13 Nov 1996, *Torres C. 14719* (MEXU). **Tamaulipas**. Mpio. Miquihuana: 6 km E del Llano entre Dr. Arroyo y Miquihuana, matorral rosetofilo, 22 May 1974, *González Medrano 6980* (MEXU); 2.5 mi N of Rancho La Alberca (ca 15 mi SE of Mier y Noriega, NL), 26 May 1974, *Wendt & Chiang 195* (TEX). **Zacatecas**. Mpio. Mazapil, 9 km E de San Tiburcio por la carretera a Matehuala, 1666 m, 24° 7' 32" N, 101° 24' 49" W, matorral xerofilo de *Larrea* con *Yucca* y *Flourensia*, 8 Jul 2003, *Balleza C. 16165b* (MEXU); 6 mi E of San Tiburcio, mesquite-*Larrea*-*Flourensia* plain, 6400 ft, 3 Aug 1975, *Engard 700* (ASU, DES, LL); Mpio. Villa de Cos, Calabacillas, KM 114 de la carretera Zacatecas-Saltillo, matorral microfilo, 2150 m, frecuente en un llano, 7 May 1977, *García P. 318* (MEXU); hills just SE of Cedros, matorral desertico, 1810 m, 1 Jul 1973, *Johnston et al. 11543* (CAS, LL, MEXU, MO, SD); no other locality, Jun 1908, *Kirkwood 110* (GH); Hacienda de Cedros, Garapata, foothills, May 1908, *Lloyd 72* (UC); no other locality data, 1908, *Lloyd 131* (GH).

The Durango collection (*Rodriguez 1513*) appears to be widely disjunct from the main range of typical *Condaliopsis lloydii*. The petioles of those plants are more distinct (Figs. 81-83) and the hypanthum glabrous — they may prove to warrant formal recognition.

5. CONDALIOPSIS SUPRALLOYDII Nesom, **sp. nov. TYPE**: **MEXICO**. **Nuevo León**. Mpio. Dr. Arroyo, ca. 3.5 km S of San Vicente, Matehuala-Saltillo hwy, low limestone hills just W of Mesa de Gonzales, matorral desertico, 1900 ft, 24 May 1973, *Johnston et al. 11202* (holotype: LL; isotypes: ASU, MEXU, MO, SD). Figures 84-87.

Similar to *Condaliopsis lloydii* in most features but distinct in its fewer lateral thorns, glabrous stems, leaves, and flowers, and northern geography.

Shrubs 1–5 m, longer secondary branches gray, glabrous, not waxy or pruinose, not thorn-tipped, lateral thorns from axils of short shoots, short and needlelike, mostly nonmeristematic but sometimes with 1–2 nodes; sclerified thorn tips abruptly differentiated. **Leaves** deciduous, opposite or usually fascicled, blades oblong to elliptic-oblong, mostly 6–10 mm long, 2–4 mm wide, herbaceous, margins entire or sometimes (in young leaves) pauciserrulate with gland-tipped teeth, apex rounded, base rounded to attenuate, petiole or petiolar region 1–3 mm long, both surfaces glabrous, not abaxially glaucous, venation pinnate (brochidodromous), 1-veined from the base or weakly 3-veined. **Flowers** mostly from short shoots, solitary, sessile or on short peduncles (sessile and pedunculate commonly on the same plant) pedicels 1.5–6 mm long; hypanthium glabrous, yellow-brown, style branches 2 or rarely 3, divided 1/2–2/3 of the style length; petals white, ca. 1 mm long; style branches 2 or rarely 3, divided nearly to the base. **Fruit** red to pink, ovoid to ellipsoid, ca. 7–9 mm long, short-beaked, often with persistent style branches. Figures 84-88.

Flowering May–Nov). Hills, flats, limestone and gypsum, matorral and izotal with *Yucca*, *Larrea*, *Flourensia*; 1900-2150 m. Coahuila, Nuevo León.

Additional collections. MEXICO. Coahuila. 3 mi S of La Ventura, 12-13 Sep 1938, *Johnston 7630* (GH). **Nuevo León.** 2 km SE of Canelito on road to San Juan de Dios, 24°37' N, 100°42' W, low, flat valley bottom between gentle hills, izotal de *Yucca filifera*, understory of *Flourensia cernua* and *Larrea tridentata*, 1925 m, 19 Jun 1972, *Chiang et al. 7983* (LL, MEXU, MO); 0.5 km NW of Rancho Zaragoza, 4 km E of El Barrosito, 24° 36' N, 100° 36' W, rocky hills, *Yucca* and *Larrea*, 2050 m, 19 Jun 1972, *Chiang et al. 8026* (CAS, LL, MEXU); 7 km W of Hwy 57 on road to El Carmen, near Cerro de la Conformidad, 24°43' N, 100°23' W, 2150 m, limestone hillside, *Larrea*, *Condalia fasciculata*, *Yucca torreyi*, 19 Jun 1972, *Chiang et al. 8034* (CAS, MEXU, MO); 13 km N of San Roberto Jct on hwy to Saltillo, at turnoff to Rancho La Luz, 24° 47' N, 100° 20' W, 1875 m, gypseous soil, *Haplopappus rhizomatus*, *Sartwellia* sp., *Isocoma veneta*, 4 Jul 1972, *Chiang et al. 8259A* (CAS, LL, MEXU, MO); 5 mi S of the Coahuila boundary on the Saltillo-Matehuala hwy, 1 Oct 1960, *Crutchfield & Johnston 5865a* (TEX); 39 mi S of San Roberto, 7 Nov 1960, *Crutchfield & Johnston 6041b* (TEX); Iturbide -> La Purísima, 25 Oct 1991, *Hinton 21679* (TEX); 6 km S of San Roberto Jct on the Matehuala-Saltillo hwy, 24°37' N, 100°17' W, 1900 m, with *Yucca filifera*, *Larrea*, *Flourensia cernua*, shrubs to 2 m, 17 May 1973, *Johnston et al. 11060* (CAS, LL, MEXU, MO).

Condaliopsis supralloydii and *C. lloydii* sensu stricto are allopatric and they are discontinuous in features of vestiture. Although they probably are sister entities, they appear to be evolutionarily distinct. Treatment of the northern entity (glabrous "C. lloydii") as a separate species is consistent with the recognition here of *C. divaricata* and *C. rigida* as distinct from *C. obtusifolia*. The 2 samples of *Ziziphus lloydii* studied by Islam & Guralnick (2015) — *Johnston et al. 11202*, *Chiang et al. 7983* — are identified here as *C. supralloydii*.

6. CONDALIOPSIS CHIHUAHUANA Nesom, **sp. nov. TYPE**: **MEXICO**. **Chihuahua**. Mpio. Madera: Cuesta de la Borrego, 8 km al SE de Madera, 2100 m, bosque de pino-encino, suelo amarillo forestal, arbusto de 30-40 cm, flores blancos, muy abundante, 29 Sep 1982, *P. Tenorio L. 1854* (holotype: MEXU, image not availabe; isotype: MO!). Figures 89-90, 93-100.

Distinct among all Mexican species of *Ziziphus* sensu lato, and among species of *Condaliopsis*, in its combination of shrubby habit, thorn-tipped branches (meristematic thorns), alternate, strongly 3-veined leaves, flowers solitary on short shoots, sometimes in sessile fascicles, long pedicels, and style with 2–3 short branches. Similar to *C. lloydii* and *C. supralloydi* in its relatively short lateral thorns (intermediate length between *C. lloydii* and *C. obtusifolia*), solitary flowers, and 3-branched styles; distinct in its larger leaves, strongly 3-veined leaves, and foliar teeth with large glands.

Shrubs 30–40 cm high, young branches and thorns closely and minutely puberulent; lateral branches thorn-tipped; thorns 10–35 mm long, without a sharply demarcated apex, with 4–8(–10) meristematic nodes and producing leaves and flower clusters. **Leaves** apparently deciduous, alternate or fascicled on short shoots, blades mostly oblong elliptic to elliptic-ovate, 6–13 mm long, 3-veined from the base with raised veins, secondary venation a close reticulum of dark, non-raised veinlets, apex rounded to truncate or shallowly retuse, margins minutely crenate or becoming essentially entire, teeth tips with black, gland-like, early-deciduous appendages, adaxial surface glabrous or sparsely strigose along the 3 main veins, abaxial surface sparsely strigose, with hairs mostly concentrated along the 3 main veins; petioles 1–1.5 mm long, closely and minutely puberulent and strigose. **Flowers** solitary, often appearing crowded in epedunculate fascicles on short shoots, usually near branch tips, pedicels 3–7 mm long; hypanthium glabrous, yellow-brown, 1.4–1.5 mm wide; style branches 2–3, divided only near the very apex, stigmas slightly bilobed. **Fruit** not seen. Figures 89-100.

Additional collection examined. **Chihuahua**. Ca. 27 mi S of Creel on road to La Bufa, 6 Jul 1969, *Soule 521* (MO, apparently a unicate collection). Figs. 91, 92.

The only other *Condaliopsis* species with solitary flowers are *C. lloydii* and *C. supralloydii*, which also rarely produce 3-branched styles and relatively short lateral thorns, but the Chihuahua plants are otherwise similar to those of the *C. obtusifolia* complex.

Map 13. *Condaliopsis chihuahuana*. Nearly 150 miles between these two collections and the comment by Tenorio that the plants were abundant suggest that *C. chihuahuana* is undercollected.

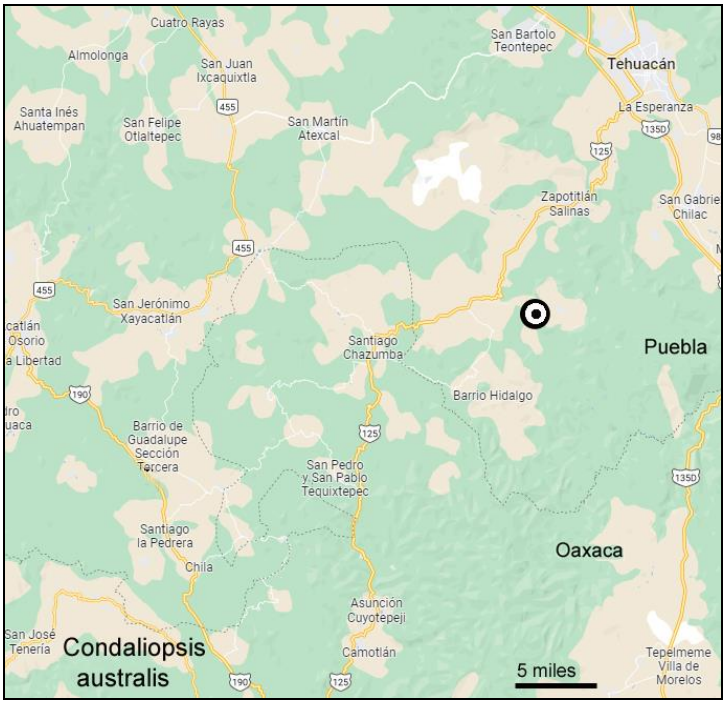
7. CONDALIOPSIS AUSTRALIS Nesom, **sp. nov. TYPE: MEXICO. Puebla**. Mpio. Zapotitlán Salinas: 2.5 km por la desviacion a los Reyes Metzontla de la carr. Tehuacán-Huajuapan de León, arbusto 3 m alto, con flores verdosas y fruto café-naranja, 1550 m, 16 May 1981, *F. Chiang et al. F-1903* (LL, MO, PH). Figures 101, 102.

Distinct from *Condaliopsis obtusifolia* in its leaf blades mostly elliptic-ovate, 9–16 mm wide, both surfaces hirtellous-puberulent, green on both sides, not glaucous abaxially, its 4–15-flowered inflorescence with peduncles mostly 3 mm long, hypanthium 2 mm wide, and style branches divided nearly to the base. Known only from the type collection.

Shrubs ca. 3 m high, lateral branches becoming zigzag, thorn-tipped; young stems green or sometimes with a white, waxy cover, sparsely puberulent, glabrescent. **Leaves** alternate, relatively thin-herbaceous, green on both surfaces, blades mostly elliptic-ovate, 17–25 mm long, 9–16 mm wide, apex acute to obtuse, base rounded to truncate, venation camptodromous but 3-veined from near the base with 2–4 additional, well-developed secondary veins, dark reticulum prominent abaxially, veins not subepidermal and raised, margins micro-serrulate, wih teeth marked essentially only by a small orange gland, both surfaces sparsely hirtellous-puberulent with soft hairs, not glaucous abaxially, petioles 4–6 mm long, pubescent. **Flowers** in axillary, 4–5 flowered thyrses, peduncles mostly 3 mm long; hypanthium 1.5–2 mm wide, sparsely pubescent, disc and calyx (within) glabrous, hypanthium (outside) and calyx lobes sparsely puberulent; petals white; style branches 2, divided nearly to the style base. **Fruit** globose to slightly elongate, 7–8 mm long, red; seeds 2, 6 mm long. In the type collection, only a single fruit per inflorescence has matured.

1. Leaf blades mostly narrowly oblong, 2–10 mm wide, both surfaces glabrous, usually glaucous abaxially; inflorescence 1–6(–8)-flowered, peduncles mostly 1 mm long; hypanthium 1.5 mm wide; style branches divided only near the style apex; fruit blue ..... **Condaliopsis obtusifolia**

1. Leaf blades mostly elliptic-ovate, 9–16 mm wide, both surfaces hirtellous-puberulent, green on both sides, not glaucous abaxially; inflorescence 4–15-flowered; peduncles mostly 3 mm long; hypanthium 2 mm wide; style branches divided nearly to the style base; fruit red ..... **Condaliopsis australis**



Map 14. *Condaliopsis australis*. Known only from the type locality in south-central Puebla.

EXCLUDED SPECIES

Condaliopsis velutina (I.M. Johnst.) Suess., Naturl. Pflanzenf. (ed. 2) 20d: 135. 1953. = ***Condalia velutina*** I.M. Johnst., J. Arnold Arb. 20: 236. 1939. **TYPE**: **MEXICO**. **Guanajuato**. Campo Santo de San Sebastian, ville de Guanajuato, 1897, *A. Dugès s.n.* (holotype: GH).

Condaliopsis parryi (Torr.) Suess., Mitt. Bot. Staatssamml. München 1: 354. 1953. *Ziziphus parryi* Torr., Rep. U.S. Mex. Bound., Bot. [Emory] 46. 1859. = ***Pseudoziziphus parryi*** (Torr.) Hauenschild, Taxon 65: 53. 2016. **TYPE**: **USA**. **California**. [San Diego Co.]: Near San Felipe, gravelly ravines, Jun 1850, *C.C. Parry s.n.* (holotype: NY; isotypes: GH, P, PH). Hauenschild (2016) designated the GH specimen as lectotype, but that from NY appears to be the one before Torrey when he described the species.

III. CONALMA Nesom, gen. nov. **TYPE**: *Conalma pedunculata* (Brandegee) Nesom

Distinct from *Sarcomphalus* in its production of short shoots, 2 serial buds per node, lack of stipular spines, thorn-tipped lateral branches with meristematic nodes, and opposite to subopposite leaves often with gland-tipped teeth at least when young. Distinct from *Condaliopsis* in its opposite to subopposite leaves (vs. leaves alternate or fasciculate on short shoots), leaves thickened with raised subepidermal venation, strongly 3-veined from the base, and more southern geographical distribution. Indicated by molecular data (*C. mexicana*, *C. pedunculata*, *C. yucatanensis*) to be a monophyletic clade distinct from *Sarcomphalus* and *Condaliopsis*.

Tall shrubs or small trees; branches and leaves primarily opposite but to subopposite or alternate; short shoots present; secondary branches usually first appearing as short to long axillary thorns, branches/thorns with 0–3 nodes, nodes meristematic (except in *C. yucatanensis*), producing a few small leaves and tertiary thorns or short shoots and inflorescences; stipular spines absent; branchlets glabrous or hairy. **Leaves** persistent; petiole present; blades mostly elliptic to oblong or oblanceolate, coriaceous, margins entire to serrate or crenulate with gland-tipped teeth, apex rounded to obtuse or retuse, surfaces glabrous, not gland-dotted; venation brochidodromous, usually with 2, well defined veins from the base, veins subepidermal and raised; stipules herbaceous, narrowly triangular, deciduous. **Inflorescences** axillary, flowers 3–35 in pedunculate thyrses or terminal and thyrsoid-paniculate in *C. yucatanensis*; bracts (bracteoles) present. **Flowers** bisexual, pedicellate; hypanthium shallowly cupulate; sepals 5, greenish or greenish white to yellowish, ovate-triangular to deltate, adaxially keeled; petals 5, yellow to pale yellow, limb cucullate and surrounding the anthers when first opening, base clawed; nectary disc shallow, fleshy, 10-angled, filling the hypanthium and covering 1/2–3/4 of the ovary in early anthesis but not adnate to it; stamens 5; ovary superior, broadly attached to receptacle, free from disc, 2-loculed; ovules 1 per locule; style 1, 2-fid nearly to the base, ca. 1/2 of the length, or only near the very apex. **Fruits** fleshy drupes, reddish to brownish, globose to depressed-globose, 10–15 mm long (*C. yucatanensis*), 14–16 mm long (*C. mexicana*), or 8–9 mm long (*C. pedunculata*), reddish to brown; stones 1. **Seeds** 2 per stone. **Chromosome number** not reported.

The inflorescence of *Conalma mexicana* and *C. yucatanensis* is characteristically a terminal compound thyrse or panicle similar to *Sarcomphalus amole*. Flowers of *Conalma pedunculata* and *C. hidalgoensis* are mostly produced in an axillary, short-pedunculate thyrse, rarely reduced to a single flower.

Conalma yucatanensis is distinct from its congeners in its lack of thorns with meristematic nodes, but sometimes a single, short, stipule-like spine is produced at a node (e.g., Fig. 28, *Martinez 30891*, MEXU) — the presence of opposite leaves, short shoots, and 2 serial buds per node place it with *Conalma*, as does molecular evidence. The short, spine-like lateral thorns are not paired and apparently do not develop meristematic nodes — secondary branches are developed from lateral buds on the primary axis.

"Con Alma" is the name of a beautiful jazz standard by Dizzy Gillespie and serves here to position the genus in alphabetic proximity to the closely related *Condaliopsis*.

1. CONALMA MEXICANA (Rose) Nesom, **comb. nov.** *Ziziphus mexicana* Rose, Contr. U.S. Natl. Herb. 1: 315. 1895. *Sarcomphalus mexicanus* (Standl.) Hauenschild, Taxon 65: 56. 2016. **TYPE**: **MEXICO**. **Colima**. Hills about Armeria, 15 Feb 1891, *E. Palmer 1278* (holotype: US; isotypes: A, GH-2 sheets, K).

Trees (2–)4–9 m or tall shrubs, glabrous throughout; short shoots present, lateral branches sometimes thorn-tipped, more commonly thorns short (mostly 8–10 mm long) and non-meristematic, 1–2 per node. **Leaves** opposite, blades oblong-elliptic to oblong-ovate, 3.5–8 cm long, coriaceous, prominently 3-veined from the base, primary abaxial veins green or slightly darkened, secondary and reticulate venation subepidermal and raised, apex obtuse to rounded or retuse. base obtuse or cuneate to truncate, margins barely serrulate, minutely gland-tipped when young, petioles 6–12 mm long. **Inflorescence** mostly terminal as a compound thyrse or panicle, each thyrse with 10–35 flrs, mature peduncles or inflorescence axis mostly 9–18 mm long. **Flowers**: pedicels 2–4 mm long; style 2-branched, divided half the length. **Fruits** globose, 14–16 mm long, reddish to brown. Figures 33-37.

Flowering February–April, sporadically through the year. Bosque tropical caducifolio, selva baja caducifolia, thorn scrub, matorral crassicaule espinoso; 100–1200 (–1750) m.

Representative collections. Colima. Mpio. Coquimatlán, Ejido El Alcomún (Luis Echeverría Álvarez), 5 km ENE de Madrid, arborescente 4.5 m, bosque tropical caducifolio, con *Jacquinia*, *Gossypium*, *Plumeria*, *Ceiba*, *Swietenia*, 460-500 m, 28 Apr 2001, *Carrillo R. 1683* (MEXU); 3 km de Juluapan a Campo Cuatro, Comala, 3 km de Juluapan a Campo Cuatro, Comala, en faldas de un cerro, arbusto ca. 3 m alto, selva baja caducifolia, 500 m, 22 Jul 1994, *García T. 170* (MEXU-2 sheets); Mpio. Colima, Ixtlahuacán-Angeles de Los Infiernos, arbol hasta 5 m, en terrenos de cultivo de sorgo, 200 m, 16 Oct 1998, *García 908* (MEXU); Mpio. Colima, 3.7 km en linea recta NW de Tepames, camino a Trapichillo, selva baja caducifolia, arbol 5 m, 22 Nov 2001, *Ibarra-M. 5828* (MEXU, MO); Mpio. Colima, camino a la torre de microondas "La Cumbre," ca. 10 km directos al SE de Colima, 480-780 m, arbol 3 m alto, 4 Oct 1987, *Koch et al. 87111* (TEX); 11 mi SSW of Colima on Manzanillo road, 12 Jul 1959, *McVaugh & Koelz 1574* (MICH); Mpio. Colima, Junto al Canal Grande, ±5 km NE de Las Ortices, arbol 4 m, 11 Sep 1980, *Megallanes 2521* (MEXU); ca. 5 km N of Rincon de Lopez, Armeria, Manzanillo, open selva baja on steep basalt slopes, 220 m, 9 Nov 1999, *Pendry 911* (MO); between Armeria and Colima, tall shrub or small tree 8-12 ft high, 22 Sep 1960, *Templeton 8975* (MO). **Guerrero**. Mpio. Eduardo Neri (Zumpango del Rio), Ameyaltepec, between Ameyaltepec /Ahuehuepan, Tlacuitlapa, 880 m, 11 Oct 2001, *Amith 334* (MO); Mpio. Coahuayutla, 1.3 km al N de Matamoros de Guerrero, arbusto 2 m, bosque tropical caducifolio, 3 Nov 1998, *Calónico S. 11855* (MEXU); Mpio. Coahuayutla, 7.18 km al NO Matamoros de Guerrero, arbusto 2 m, bosque tropical caducifolio, 240 m, 4 Nov 1998, *Calónico S. 11963* (MEXU); Mpio. Coahuayutla, 6.31 km al N de Matamoros de Guerrero, arbol 5 m, bosque tropical caducifolio, 200 m, 25 Jul 1999, *Calónico S.* 15505 (MEXU); Mpio. Coahuayutla, 0.91 km al O de La Corva, arbol 5 m, bosque tropical caducifolio, 240 m, 16 Nov 1999, *Calónico S. 187694* (MEXU); Mpio. Coahuayutla, 2.41 km al E de La Corva, arbol 5 m, bosque tropical caducifolio, 360 m, 16 Nov 1999, *Calónico S. 18718* (MEXU); Mpio. Cuilpan, San Juan Totolcintla, between "Ayawanthli," arbol 3 m, 571 m, 25 Jan 2004, *Ceuterick MC012* (MO); Mpio. Martir de Cuilpan, San Juan Totolcintla, between Amatitlan and SJT, arbol 4 m, 564 m, 29 Jan 2004 ("flowers in Sep"), *Ceuterick MC036* (MO); Mpio. Zumpango del Rio, 2 km W de Milpillas, sobre el camino Milpillas-Xochipala, Filo de Caballo, arbusto 3 m, selva baja caducifolia, 800 m, 12 Jun 1982, *Martínez S. 663* (MO); Mpio. Zumpango del Rio, 8 km al SO de Xochipala, arbol espinoso, veg. secundario de selva baja caucifolia con *Brahea dulcis*, 1 Jul 1989, *Soto Núñez 13161* (MEXU). **Jalisco**. 22 km N of Autlán de Navarro on Hwy 80, tree 6 m tall, deciduous forest on steep rocky hillsides, 1200 m, 7 Oct 1985, *Bartholomew 2736* (MEXU, MO); Mpio. Juchitlán, cañada rocosa en las afueras de los corrales rumbo a los guajes, arbolito, bosque tropical caducifolio, 1200 m, 3 Apr 1992, *Cházaro 6924* (MO); Mpio. Tuxcacuesco, 2 km W de Tuxcacuesco, arbusto 1-3 m alto, veg. baja, espinosa, caducifolia, 900-1000 m, 7 Oct 1982, *Hernández M. 9113* (MEXU); Santa Cruz, 6 Jun 1892, *M.E. Jones 82* (MO, RSA); Mpio. Venustiano Carranza, 2 km de Acapulco, 22 km NW de Venustiano Carranza, carr. El Grullo, arbol 5 m, pendiente rocosos de caliza con selva baja caducifolia perturbado y matorral espinoso de *Mimosa brongniartii*, *Spondias*, *Wimmeria*, 1770 m, 1 Jul 1981, *Lott*

433 (MEXU, MO, TEX); 2 mi NW of Totolimispa, road to Apulco, open thorn scrub, gentle grassy slopes, 1000 m, tree to 8 m, 35 cm dbh, 31 Oct 1962, *McVaugh 21987* (LL, SD); 6.5 mi NE of Autlan, near hwy pass, 925 m, small tree, 24 Nov 1959, *McVaugh & Koelz 1033* (MICH); Mpio. Tuxcacuesco, ca. 5 km E de Tuxcacuesco y 500 m S de la carr. San Gabriel-Tuxcacuesco, selva baja caducifolia con tepenisquite *Lysiloma divaricata*, 900 m, 12 Sep 1995, *Navarro M. 1366* (MEXU); Mpio. Tolimán, camino hacia Chachahuatlán, 2 km de Paso Real, arbusto 2-3 m, bosque tropical caducifolio, 700 m, 26 May 1990, *Rodríguez C. 2026* (MEXU); Mpio. Tonaya, 4 km al NW de Tonaya, por la carretera a El Grullo, arbol 5 m, bosque tropical caducifolio con elementos espinosos, 800 m, 1 Sep 1987, *Santana M. 2980* (MEXU); Mpio. Venustiano Carranza, La Croix, arbolito 4-5 m alto, bosque tropical deciduo, 1180 m, 10 Aug 1986, *Zamudio 4296* (MEXU). **Michoacan**. Dto. Coalcoman, Huizontla, 1 Dec 1941, *Hinton 16210* (LL); carr. Playa Azul-Nueva Italia, 2 km N de Rancho Viejo, y a 6 km S de El Guayabito, arbusto 3 m, 24 Oct 1977, *Ladd et al. 359* (MEXU); 1 km S of turnoff to Infiernillo from Mex Hwy 37 (between Nueva Italia and Playa Azul), tree 5 m tall, thorn scrub with *Acacia*, *Bursera*, *Jacquinia*, 360 m, 13 Jun 1987, *Miller 3078* (MO, TEX); en la desviacion al Infiernillo, carr. Nueva Italia-Playa Azul, 375 m, arbusto 3-6 m, selva baja caducifolia, 17 Sep 1979, *Soto Núñez 1623* (MO); Mpio. Aquila, en Ostula, 100 m, arbol 4-5 m alto, frecuente en terrenos aluviales, selva baja caducifolia, 20 Dec 1984, *Soto Núñez 7104* (MO); Mpio. Aquila, 4 km al SE de Cachán y 21 km al SE de Maroata, carr. Tecomán-Lázaro Cárdenas, arbol 4-6 m, selva baja caducifolia primaria, 240 m, 5 Feb 2003, *Soto Núñez 14966* (MEXU); Mpio. Arteaga, 8.1 km S de la desviación a Infiernillo, arbusto decumbente 3 m alto, matorral crassicaule espinoso, 230 m, 20 Oct 1982, *Torres C. 1602* (MO).

2. CONALMA PEDUNCULATA (Brandegee) Nesom, **comb. nov.** *Condalia pedunculata* Brandegee, Univ. Calif. Publ. Bot. 3: 384. 1909. *Ziziphus pedunculata* (Brandegee) Standl., Contr. U.S. Natl. Herb. 23: 713. 1923. *Sarcomphalus pedunculatus* (Standl.) Hauenschild, Taxon 65: 57. 2016. **TYPE**: **MEXICO**. **Puebla**. San Luis Tultitlanapa (now San Luis Atolotitlán in Mpio. Caltepec), Barranca de Tlacuilosto, Jun 1908, *C.A. Purpus 3173* (holotype: UC!; isotypes: F, GH, NY, US).

Condalia seleri Loes., Repert. Spec. Nov. Regni Veg. 9: 355. 1911 [not *Ziziphus seleri* Loes. 1909 = *Ziziphus amole*]. *Condaliopsis seleri* (Loes.) Suess., Nat. Pflanzenfam., ed. 2 20d: 135. 1953. **TYPE**: **MEXICO**. **Oaxaca**. Distr. Teotitlán del camino, im Busch (Trockenwald) bei Tecomavaca, [1906], *E.G. Seler 5228* (holotype: Berlin, not seen). The locality is within the range of *Conalma pedunculata* and the description (particularly the opposite leaves) indicates that *Condalia seleri* is a synonym of *Conalma pedunculata*. Loesener noted that (as translated here) "With the absence of the fruits, the genus affiliation is still somewhat doubtful. If the species does belong to *Condalia*, it belongs in the subgen. *Condaliopsis* and is perhaps best placed near *C. obtusifolia*. But because of the relatively large flowers, it would occupy a fairly isolated position."

Trees or shrubs (2–)3–4 m tall; short shoots present, branches glabrous, lateral branches thorn-tipped, sometimes also with short, axillary, non-meristematic thorns (or rarely with a single node), stems usually with evident lenticels. **Leaves** opposite to subopposite or alternate, blades oblong to oblong-elliptic or elliptic, 1–3 cm long, 0.5–1.4 cm wide, coriaceous, strongly to weakly 3-veined from the base, secondary and reticulate venation subepidermal and raised, apex rounded to retuse, base cuneate to rounded or truncate, glabrous on both sides or lightly puberulent abaxially along the veins, margins entire to minutely serrate to crenulate-serrate (at least when young), each tooth terminated by a minute, orange, glandlike appendage, petioles 1–2(–3) mm long. **Inflorescence** mostly an axillary, pedunculate thyrse, each thyrse with 3–12 flrs, mature peduncles/main axis (3–)6–10 mm long. **Flowers**: pedicels 1–4 mm long, glabrous; hypanthium and calyx lobes puberulent abaxially (outside), disc and calyx adaxially (inside) glabrous; style branches 2, separate to near the base. **Fruit** globose to depressed globose, 8–9 mm long, reddish at maturity. Figures 38-47.

Flowering January–June. Matorral with cacti, matorral crassicaule, matorral espinoso, desert thorn forest, selva baja caducifolia, riparian, roadsides, hillsides, arroyos, barrancas; 2000–5100 ft (600–1550 m).

Collections examined. Oaxaca. Dto. Cuicatlán, Tecomavaca, Río Salado, a 4.8 km de Tecomavaca, carr. Tehuacán-Oaxaca, 11 Aug 1988, *Campos V. 2126* (ARIZ, TEX); Mpio. Tecomavaca, Dto. Cuicatlán, Rio Salado, a 4.8 km de Tecomavaca, carr. Tehuacan-Oaxaca, 17° 41' N, 97° 00' W, 630 m, riparia en matorral xerófilo, 11 Aug 1988, *Campos V. 2111* (MEXU); 5 km N de Tecomavaca, carr. Oaxaca-Tehuacan, por Tlaxlixtlahuco, arbol 5 m, matorral con cactaceas, 28 Sep 1982, *Cedillo T. 1884* (MO); 3 km NW de Teotitlán del Camino, arbol 3 m, selva baja caducifolia en laderas calizo-gipsiferas, 1000 m, 25 Jul 1979, *Chiang et al. F141* (MO); Dept. Cuicatlán, Cuesta Quiotepec, 700 m, 21 Jun 1909, *Conzatti 2414* (F, MEXU-2 sheets); Mpio. Cuicatlán, 11 km E de Cuicatlan, camino a Valerio Trujano, 615 m, selva baja caducifolia, 9 Jan 2001, *Martinez S. 33512* (MEXU); NW de Cuicatlán, 17 Sep 1948, *Miranda 4669* (MEXU); Tomellin Canyon, 17 Aug 1929, *Runyon 1349* (US). Dist. Teotitlán, 7 km S de Ignacio Mejía, por la brecha que va al Río Xiquila, 800 m, 16 Nov 1987, *Salinas T. 4510* (MO); Mpio. Tepelmeme de Morelos, E del KM 93 carr. Tehuacan-Oaxaca, ca. 250 m en linea recta, arbol 6 m, manchon verde en esta época, dado por especies de *Brahea dulcis*, *Tecoma stans*, *Morkilia mexicana* en selva baja caducifolia, 1625 m, 9 Apr 2001, *Tenorio L. 20004* (MO); Dto. Coixtlhuaca, Mpio. Tepelmeme de Morelos, El Paraje, Cerro Verde, 18° 6' N, 97° 12' W, 935 m, selva baja caducifolia en la barranca, 27 May 2001, *Tenorio 20164* (MEXU); 10 km N de Tecomavaca, arbusto 1.8 m, veg. secundario de matorral xerófito, 680 m, 5 Aug 1983, *Torres C. 3484* (MO). **Puebla**. Mpio. San Gabriel Chilac, poblado San Juan Atzingo, arroyo intermitente al N del poblado, 1200 m, bosque tropical caducifolio, secundario, 10 Jul 2002, *Alvarado C. 152* (MEXU); Mpio. Coxcatlan, Cueva del maiz, conglomerado 67597 del Inventario Nacional Forestal y de Suelos, arbol 4.6 m, selva baja caducifolia, 994 m, 23 Apr 2013, *Alvarado F. MAF21* (MO); 2.8 km NE de San Jose Tilapa, selva baja caducifolia, 20 Sep 2011, *Arellanes 744* (MEXU); Mpio. Coxcatlan, km 56 SE of Tehuacan on the toad to Teotitlan del Camino and ca. 2 km NW of the Oaxaca border, desert thorn forest, 960 m, 19 Oct 1985, *Bartholomew 3144* (MEXU); antes de Coxcatlán, 1000 m, matorral crassicaule, 1000 m, 15 Sep 1977, *Chazaro 661* (MEXU); 3.2 km NNE de Zapotitlán (carr. Huajuapan-Tehuacán), 12 Jun 1979, *Chiang 852* (MEXU); 3.5 km al NE de Zapotitlán de las Salinas, por la carretera a Tehuacán, a lo largo de lecho seco del Río Salado, 1500 m, matorral crasicaule de *Neobuxbaumia tetetzo*, *Ceiba*, *Acacia*, *Echinocactus*, arbusto de 3 m, 17 May 1981, *F. Chiang C. 1984* (ASU, RSA, TEX); 10 km al N de Zapotitlán de las Salinas, rumbo a Tehuacán, 2 km antes de Texcala, arbol de 3 m, flores verdosas, 25 Mar 1982, *F. Chiang C. 2304* (RSA, TEX, US); 3 km al SE de Calipan, por la carretera rumbo a Coxcatlán, en borde de arroyo seco, matorral espinoso con *Prosopis*, *Cercidium*, *Stenocereus*, *Escontria*, 4 Jun 1985, *Chiang 2440* (MEXU, MO); 7 km SE de Sinacaltepec, por la carr. rumbo a Oaxaca, 18° 17' N, 97° 10' W, matorral espinoso, con *Prosopis laevigata*, *Cercidium praecox*, *Mimosa polyantha*, *Opuntia*, 1150 m, 30 Sep 1985, *Dorado R. & Salinas T. F-2976* (DES); Cerro Tepetroja, a 13 km al SO de Axuxco, 1300 m, selva baja caducifolia y matorral crasirosutifolio espinoso, 28 Jun 1987, *Martínez S. 21733* (MEXU); 0.5 mi NW of Calipan, 3900 ft, 27 Jun 1969, *Maslin 121* (COLO); 1 km W de Cozcatlán, matorral xerofilo perturbado, 1100 m, 25 Aug 1980, *Medrano et al. F-1452* (MEXU, MO, TEX); 7 km SW of Tehuacan, matorral, 8 Jan 1981, *Medrano et al. BC-94* (MEXU); vicinity of San Luis Tultitlanapa, Barranca de Tlacuilosto, Jun 1908, *Purpus 3173* (MO); 4 km NW de Calipán sobre la carr a Tehuacán, 26 Jun 1971, *Rzedowski 28159* (TEX); alrededores del Cerro Petlanco, 15 May 1986, *Salinas T. F-3282-A* (TEX-2 sheets); Cerro Tepetroje, ca. 6 km SSW de Axusco, 4 Oct 1986, *Salinas T. F-3579* (MEXU); Mpio. San Jose Miahuatlán, 3 km SE de Axusco por la terraceria rumbo a Puebla Nuevo, lugares abiertos y cultivos, 900 m, 17 Apr 1987, *Salinas T. F3909* (MO); Mpio. San Jose Miahuatlán, Cerro Tepetroje, ca 6.5 km al SW de Axusco, selva baja caducifolia con crasi-rosulifolius, *Fouquieria purpusii*, *Echinopterys*, *Opuntia*, *Hechtia*, *Ceiba*, *Jatropha*, *Bursera*, *Cercidium*, arbole de 2 m, flores amarillentas, 27 Jun 1987, *Salinas T. 4076* (RSA); 1.5 km W de Tomellín, arbol 2 m, veg. riparia, 1000 m, 30 Jun 1987, *Salinas T. 4145* (MO); near Coxcatlan on Cerro Ajuereado and in the adjacent valley, thorn-scrub-cactus, ca. 1000-1800 m, tree to 2 m on hilltop, Jul 1961, *Smith et al. 3551* (US); 1 km de Ajalpan, 25 Sep 1983, *Tenorio 10* (MEXU); San Jose Miahuatlán, Barranca Seca SW de Axusco, 16 Aug 1984, *Tenorio L.* 6900 (MEXU); Caltepec, Santa

Lucía, Río Hondo, 19 Oct 1984, *Tenorio L. 7815* (TEX); San Jose Miahuatlan, Axusco, 27 May 1985, *Tenorio L. 8853* (MEXU); Mpio. Ajalpan, Comeallo, arroyo seco NE de Ajalpan, selva baja caducifolia, primaria, 1260 m, 18 Oct 1986, *Tenorio 12033* (MEXU); Dept. Puebla, 17 mi from the Oaxaca border on Hwy 190, dry arroyo, thorn forest with tree cacti, 4600 ft, 20 Jul 1979, *Trott et al. 161* (USF); 1.9 mi N of San Jose Tilapa or 4.3 mi N of Teotitlan del Camino, tree to 5 m, dry hillside with abundant *Hechtia*, *Agave*, and numerous cactus species, 31 Jul 1981, *Utley 6630* (MO).

Puebla, disjunct. [Mpio Zacatlán]: N de Zacatlán, Sierra de Puebla, [elev. ca. 6000 ft], 2 Jun 1974, *Boege 3122* (MEXU). Figures 46, 47.

3. CONALMA YUCATANENSIS (Standl.) Nesom, **comb. nov.** *Ziziphus yucatanensis* Standl., Trop. Woods 32: 16. 1932. *Sarcomphalus yucatanensis* (Standl.) Hauenschild, Taxon 65: 57. 2016. **TYPE: MEXICO. Yucatan.** Progreso, 1932, *R.S. Flores s.n.* (holotype: F!).

Trees 4–12 (–20) m tall; short shoots present, thorns usually absent, rarely a short (4–6 mm), axillary, non-meristematic thorn. **Leaves** opposite, single or fascicled on short shoots, blades broadly obovate to elliptic-obovate to subrotund, 2.5–4 cm long, coriaceous, prominently 3-nerved from the base, primary abaxial veins often orange, secondary and reticulate venation subepidermal and raised, apex rounded to retuse, base obtuse, glabrous on both sides, often bicolor (orange-brown adaxially), margins entire, petioles 3–6 mm long. **Inflorescence** terminal or axillary from distalmost nodes, thyrsoid to paniculate, main axis 5–11 cm long with shorter lateral branches. **Flowers**: pedicels 1–1.5 mm long, puberulent; hypanthium and calyx lobes puberulent abaxially (outside), disc and calyx adaxially (inside) glabrous; style 2-branched, divided only near the apex. **Fruits** globose to depressed-globose, 10–15 mm long, reddish at maturity, usually described by collectors as green, but drying reddish or "café." Figures 25-32.

Flowering (January–) May–July (–October). deciduous woods, woods with cactus, roadsides; 40–100 m.

Conalma yucatanesis is unusual among its congeners in producing only short, acicular, non-meristematic thorns (see Figs. 28 and 29, *Martinez 30891*-MEXU and *Simá 1245*-MEXU). With its distinct morphology and geography, the species is consistently identified correctly.

ACKNOWLEDGEMENTS

I am grateful to the herbaria of MO, TEX-LL, and SMU-BRIT, to Walter Fertig for examining ASU collections of *Condaliopsis divaricata* from Cochise County, to George Yatskievych for photos of TEX,LL specimens, and to MO library staff for help with literature.

LITERATURE CITED

Brandegee, T.S. 1889. A collection of plants from Baja California, 1889. Proc. Calif. Acad. Ser. 2. 2: 117–216.

Britton, N.L. and P. Wilson. 1924. Scientific Survey of Porto Rico and the Virgin Islands, Volume 5, part 2. New York Academy of Sciences.

Brummitt, RK., J. McNeill, S.A. Redhead, and J.H. Wiersema. 2009. Report of the Nomenclature Committee for Vascular Plants: 60. Taxon 58: 280–292.

Cahen, D., J. Rickenback, and T.M.A. Utteridge. 2021. A revision of *Ziziphus* (Rhamnaceae) in Borneo. Kew Bull. 76: 767–804.

Chen, Y. and C. Schirarend. 2007. Rhamnaceae. Pp. 115–168, in Flora of China, Vol. 12. Science Press, Beijing.

Christie, K., M. Currie, L.S. Davis, M.-E. Hill, S. Neal, and T. Ayers. 2006. Vascular Plants of Arizona: Rhamnaceae (Buckthorn family). Canotia 2: 23–46.

Fernández Nava, R. 1986. Rhamnaceae. Flora de Veracruz 50: 1–65.

Hauenschild, F., S. Matuszak, A.N. Muellner-Riehl, and A. Favreh. 2016. Phylogenetic relationships within the cosmopolitan buckthorn family (Rhamnaceae) support the resurrection of *Sarcomphalus* and the description of *Pseudoziziphus* gen. nov. Taxon 65: 47–64.

Islam, M.B. and M.P. Simmons. 2006. A thorny dilemma: Testing alternative intrageneric classifications within *Ziziphus* (Rhamnaceae). Syst. Bot. 31: 826–842.

Islam, M.B. and R.P. Guralnick. 2015. Generic placement of the former *Condaliopsis* (Rhamnaceae) species. Phytotaxa 236: 25–39.

Johnston, M.C. 1962. Revision of *Condalia* including *Microrhamnus* (Rhamnaceae). Brittonia 14: 332–368.

Johnston, M.C. 1963. The species of *Ziziphus* indigenous to United States and Mexico. Amer. J. Bot. 50: 1020–1027.

Johnston, M.C. 1964. The fourteen species of *Ziziphus* including *Sarcomphalus* (Rhamnaceae) indigenous to the West Indies. Amer. J. Bot. 51: 1113–1118.

Johnston, M.C. 1966. *Condalia fasciculata* and *Ziziphus obtusifolia* (Rhamnaceae) near Tehuacan, southern Puebla. Southwestern Nat. 11: 126.

Johnston, M.C. 1972. Rhamnaceae. Flora of Tropical East Africa 114. Royal Botanic Garden, Kew.

Kellerman, J. 2019. Nomenclatural notes and typifications in Australian species of Paliureae (Rhamnaceae). Swainsonia 33: 43–50.

Kirkbride, J.H., Jr., J.H. Wiersema, and N.J. Turland. 2006. Proposal to conserve the name *Ziziphus jujuba* against *Z. zizyphus* (Rhamnaceae). Taxon 55: 2049–2050.

Nesom, G.L. 2016. Rhamnaceae. Pp. 43–110, in Flora of North America North of Mexico, Vol. 12. Oxford Univ. Press, New York and Oxford.

Nesom, G.L. 2023. Taxonomic synopsis of *Condalia* (Rhamnaceae) in Mexico and the USA. Phytoneuron 2023-24: 1–115.

Pool, A. 2015. Rhamnaceae. Pp. 55–88, in Ulloa U., C., G. Davidse, M. Sousa S., S. Knapp, and F. Chiang (eds.). Flora Mesoamericana, Vol. 2, part 3.

Richardson, J.E., M.F. Fay, Q.C.B. Cronk, D. Bowman, and M.W. Chase. 2000a. A phylogenetic analysis of Rhamnaceae using rbcL and trnL-F plastid DNA sequences. Amer. J. Bot. 87: 1309–1324.

Schirarend, C. 1991. The systematic wood anatomy of the Rhamnaceae Juss. (Rhamnales). I. Tribe Zizipheae. IAWA Bulletin 12: 359–388.

Standley, P.C. 1923. Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb. 23. Govt. Print. Office, Washington, D.C.

Suessenguth, K. 1953. Rhamnaceae. Natürl. Pflanzenf. (ed. 2) 20d: 7–173.

Tourn, G.M. 1985. La naturaleza caulinar de las espinas de *Ziziphus mistol* (Rhamnaceae) y su comparación con otras especies de la familia. Bol. Soc. Argent. Bot. 24: 71–79.

Tourn, G.M., D. Medan, and R.D. Tortosa. 1989. Yemas múltiples en Ramnáceas: Organización del complejo axilar en *Ziziphus* y *Paliurus*. Kurziana 20: 101–111.

Tourn, G.M., R.D. Tortosa, and A. Bartoli. 1990. El complejo axilar de las especies de *Ziziphus* (Rhamnaceae) del Nuevo Mundo. Bol. Soc. Argent. Bot. 26: 215–220.

Tourn, G.M., R.D. Tortosa, and D. Medan. 1992. Rhamnaceae with multiple lateral buds: An architectural analysis. Bot. J. Linn. Soc. 108: 275–286.

Trimen, H. 1887. Hermann's Ceylon herbarium and Linnaeus's "Flora Zeylanica." J. Linn. Soc. Bot. 24: 129–155.

Weberbauer, A. 1895. Rhamnaceae. Natürl. Pflanzenf. 3(5): 393–427.

Wiggins, I.L. 1964. Rhamnaceae. Pp. 856–869, in F. Shreve and I.L. Wiggins. Vegetation and Flora of the Sonoran Desert, Vols. 1 and 2. Stanford Univ. Press, Stanford, California.

Wiggins, I.L. 1950. Taxonomic notes on plants from the Sonoran Desert. Contr. Dudley Herb. 4: 15–31.

Wiggins, I.L. 1980. Flora of Baja California. Stanford Univ. Press, Stanford, California.

Figure 1. *Ziziphus jujuba*. Texas, *Sanchez 3814* (BAYLU).

Figure 2. *Ziziphus jujuba*. Texas, *Sanchez 3814* (BAYLU). Detail from Fig. 1.

Figure 3. *Ziziphus jujuba*. Edwards Co., Texas, *Cory 53655* (GH). Single and paired stipular spines.

Figure 4. *Ziziphus jujuba*. Arizona, *Hodgson 3748* (DES).

Figure 5. *Ziziphus mauritiana*. Guyana, *Hill 27178* (VT). Single stipular spines.

Figure 6. *Ziziphus mauritiana*. Florida, *Sellers s.n.* (FLAS). Single and paired stipular spines.

Figure 7. *Ziziphus mauritiana*. Florida, *Howell 1075* (USF).

Figure 8. *Ziziphus mauritiana*. Florida, *Garcia E2012-625* (FLAS).

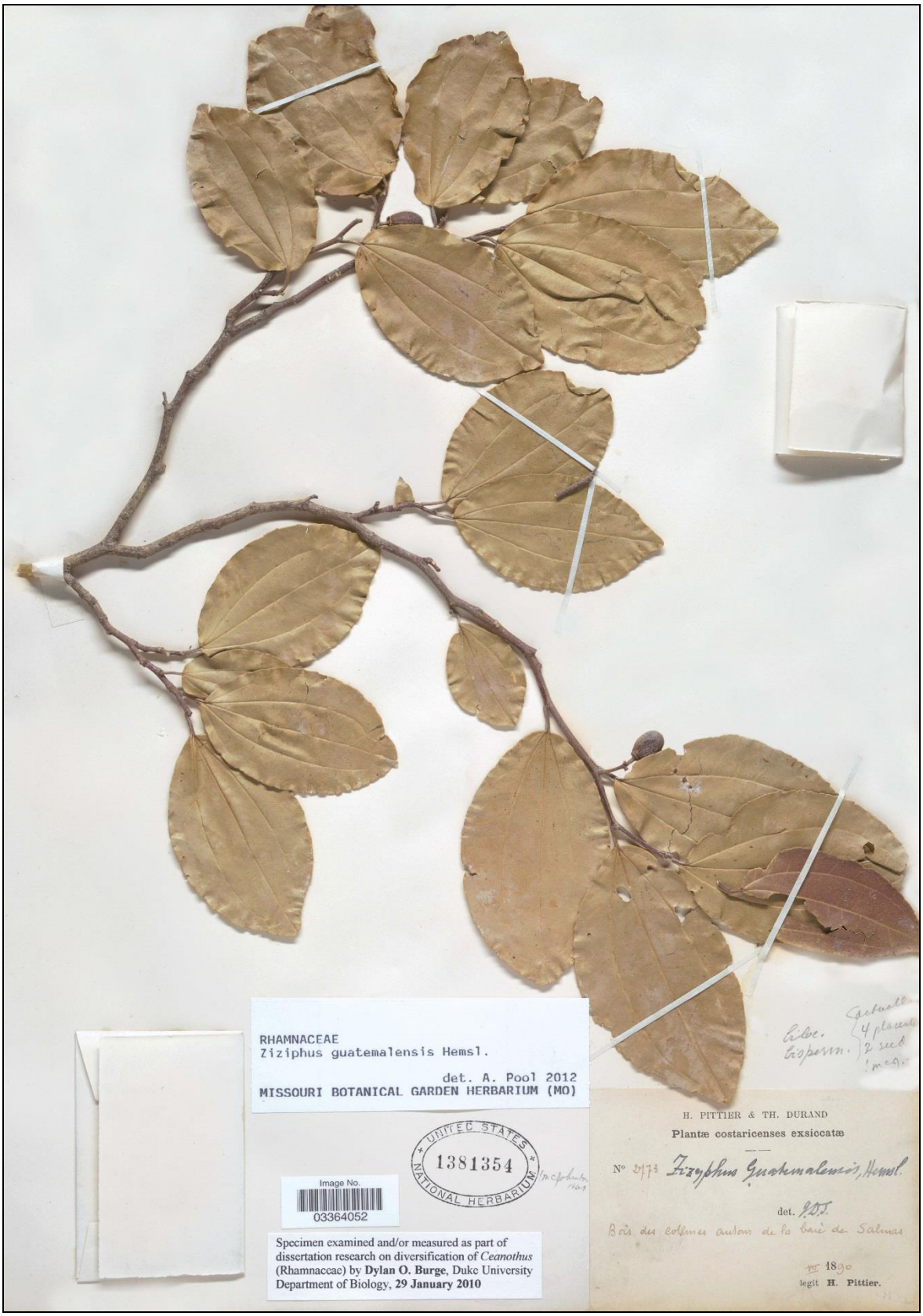


Figure 9. *Sarcomphalus guatemalensis*. Costa Rica, *Pittier 2773* (US).

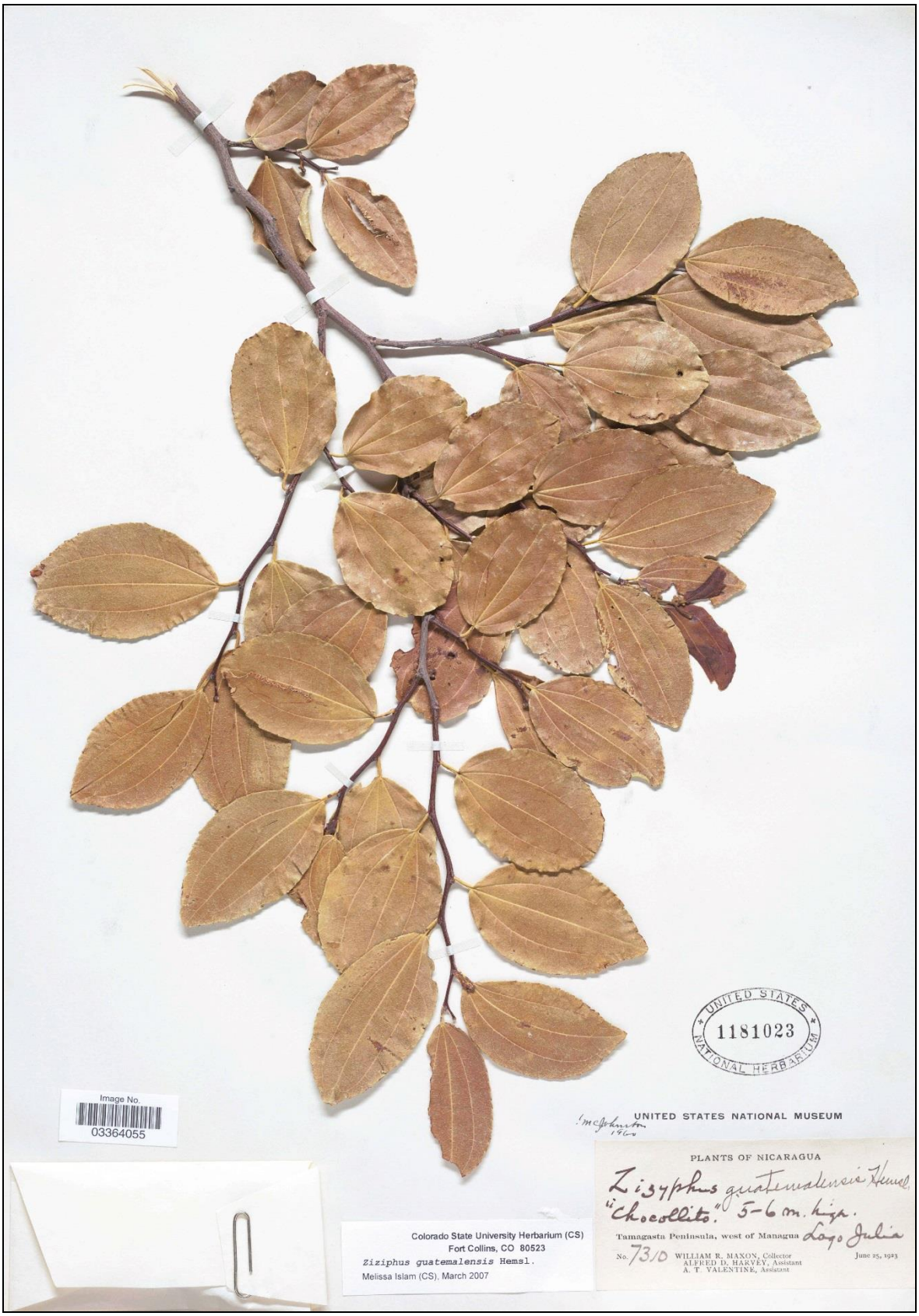


Figure 10. *Sarcomphalus guatemalensis*. Nicaragua, *Maxon 7310* (US).

Figure 11. *Sarcomphalus guatemalensis*. Costa Rica, *Chavarría 578* (MEXU).

Figure 12. *Sarcomphalus guatemalensis*. Nicaragua, *Grijalva 2387* (MEXU).

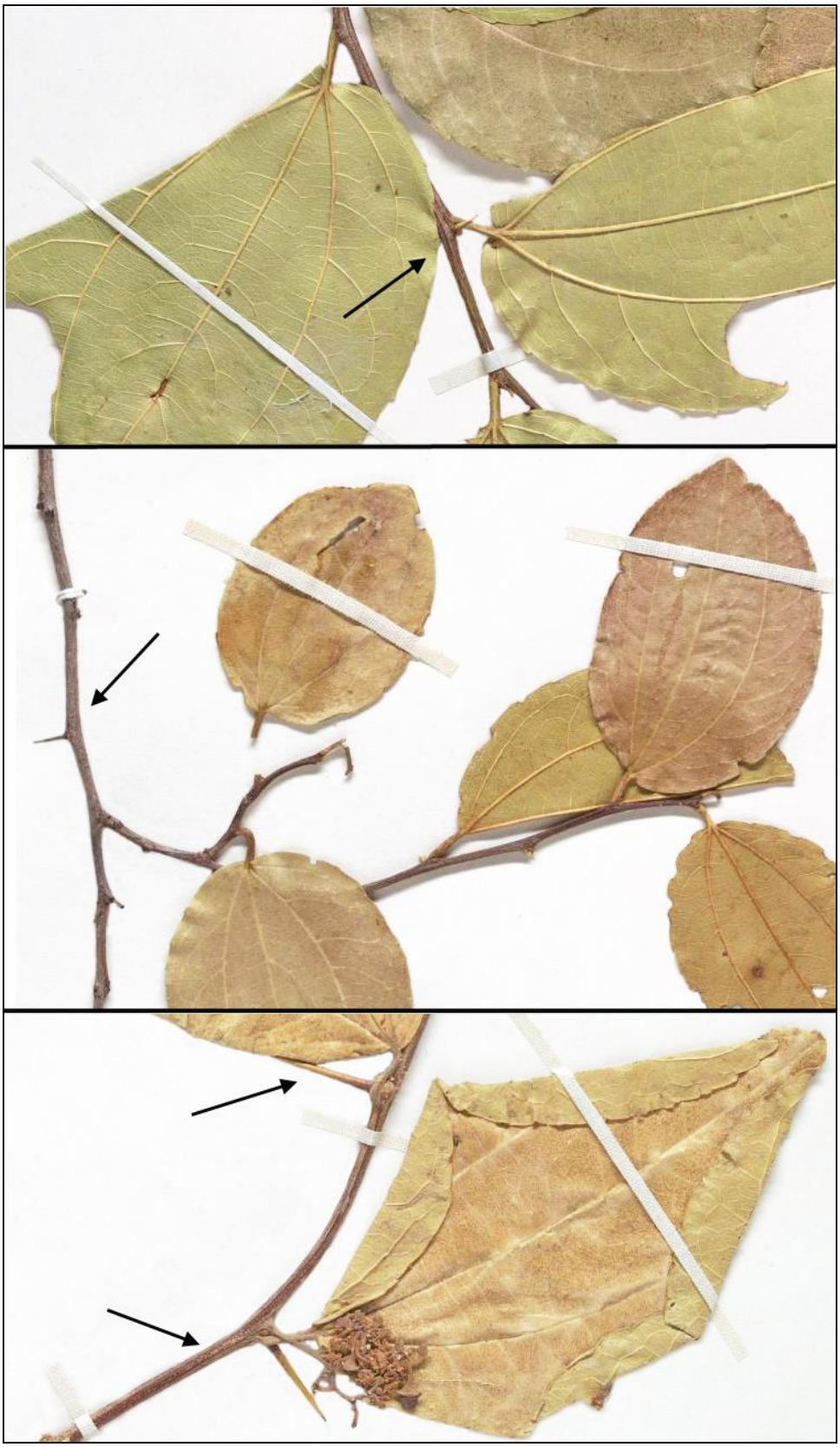


Figure 13. *Sarcomphalus guatemalensis*. Acicular thorns. Top: Nicaragua, *Maxon 7561* (US). Middle: El Salvador, *Williams 16726* (US). Bottom: Nicaragua, *Garnier A956* (US).

Figure 14. *Sarcomphalus amole*. Sonora, *Palmer 124* (GH).

Figure 15. *Sarcomphalus amole*. Sonora, *Palmer 124* (GH). Detail from Fig. 14. Acicular thorn.

Figure 16. *Sarcomphalus amole*. Paired acicular thorns. Tomellin Canyon, Oaxaca, *Rose 10085* (US).

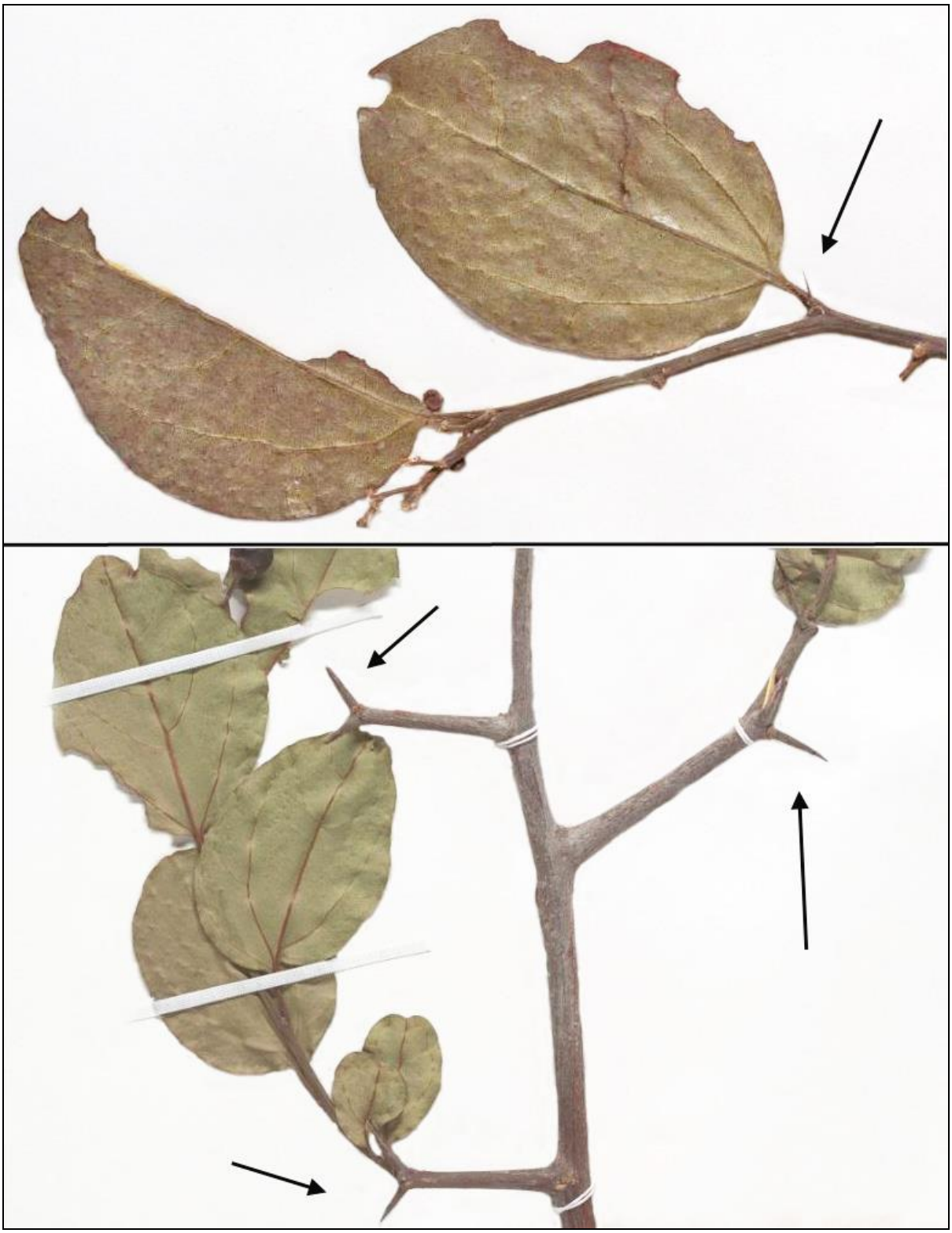


Figure 17. *Sarcomphalus amole*. Paired acicular thorns. Top: Sinaloa, *Ortega 4682* (US). Bottom: Oaxaca, *Salinas 5523* (US).

Figure 18. *Sarcomphalus amole*. Paired acicular thorns, the upper node with two thorns and a leafy branch. Sinaloa, *Rose 1352* (US). Details.

Figure 19. *Sarcomphalus amole*. Lateral buds (short shoots?), each producing two leafy branches. Oaxaca, *Sanchez 712* (US).

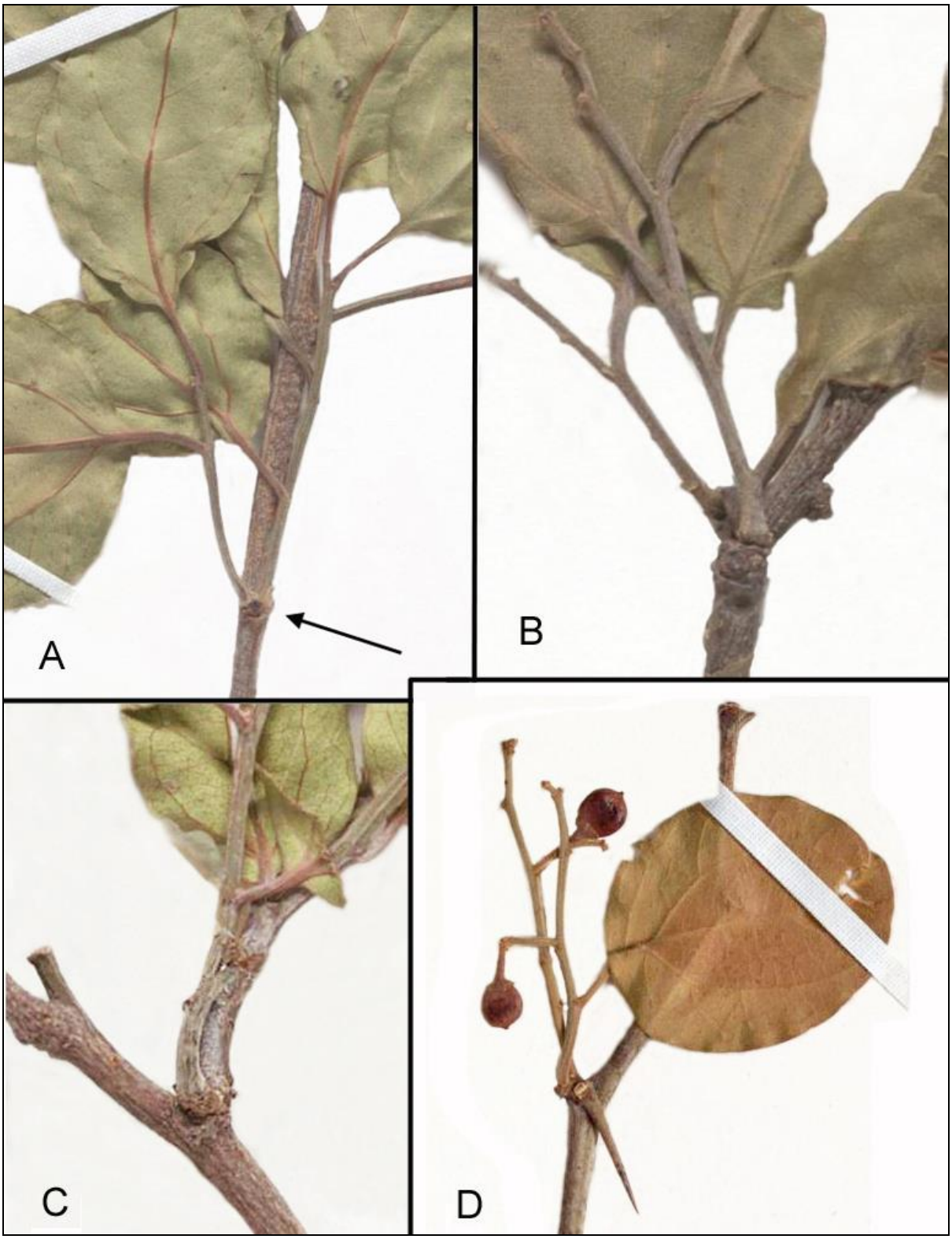


Figure 20. *Sarcomphalus amole*. Lateral buds, each producing two branches. A. Oaxaca, *Salinas 5523* (US). B. Oaxaca, *Torres 9839* (US). C. Oaxaca, *King 1719* (US). D. Two flowering branches and one thorn, Oaxaca, *Hansen 1578* (US).

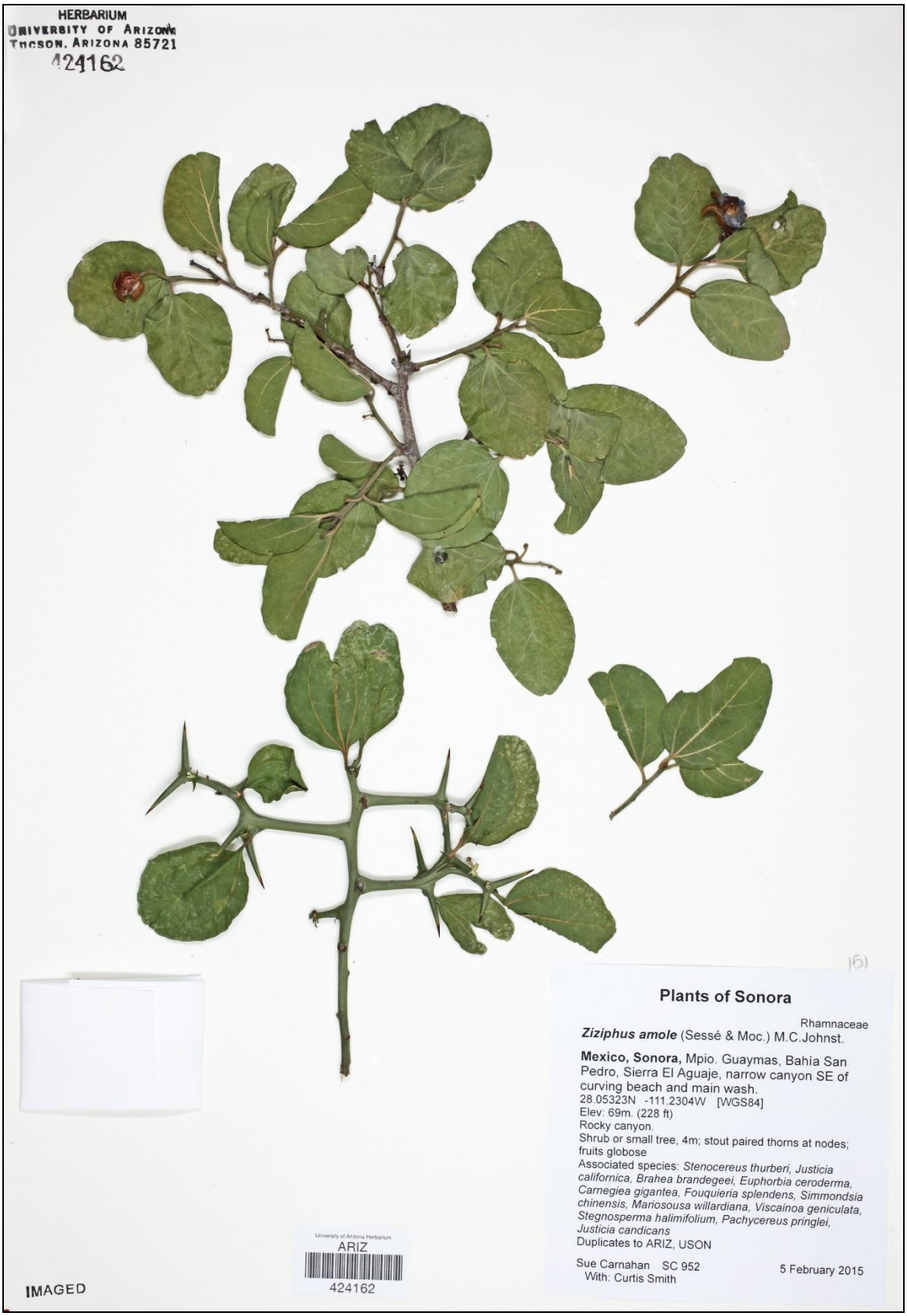


Figure 21. *Sarcomphalus amole*. Sonora, *Carnahan SC952* (ARIZ). Unusually stout paired thorns.

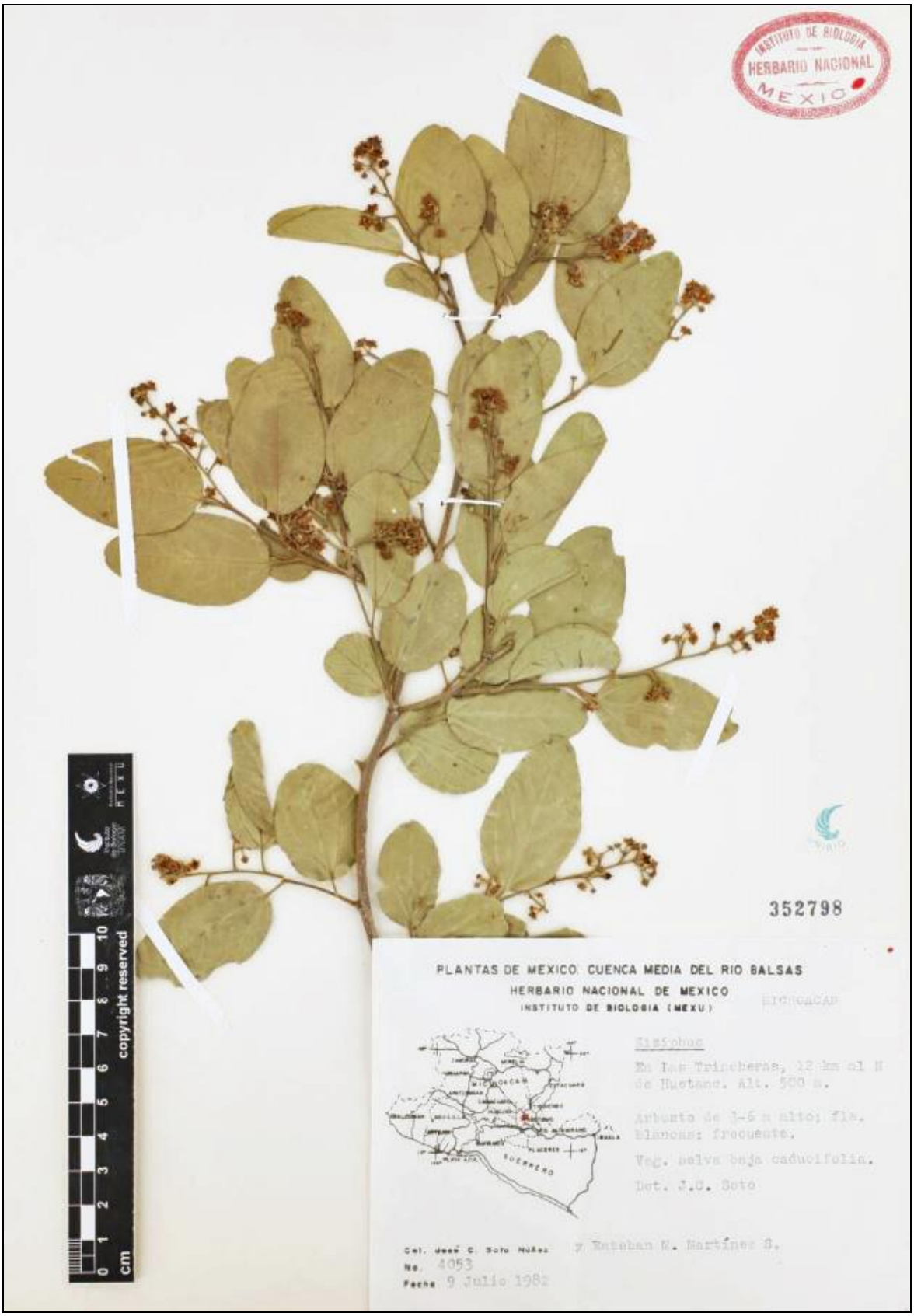


Figure 22. *Sarcomphalus amole*. Guerrero, *Soto Nuñez 4053* (MEXU).

Figure 23. *Sarcomphalus amole*. Tamaulipas, *Hernandez 1095* (MEXU).

Figure 24. *Sarcomphalus amole*. Sonora, photo by T.R. Van Devender.

Figure 25. *Conalma yucatanensis.* Campeche, *Alvarez 8956* (MEXU).

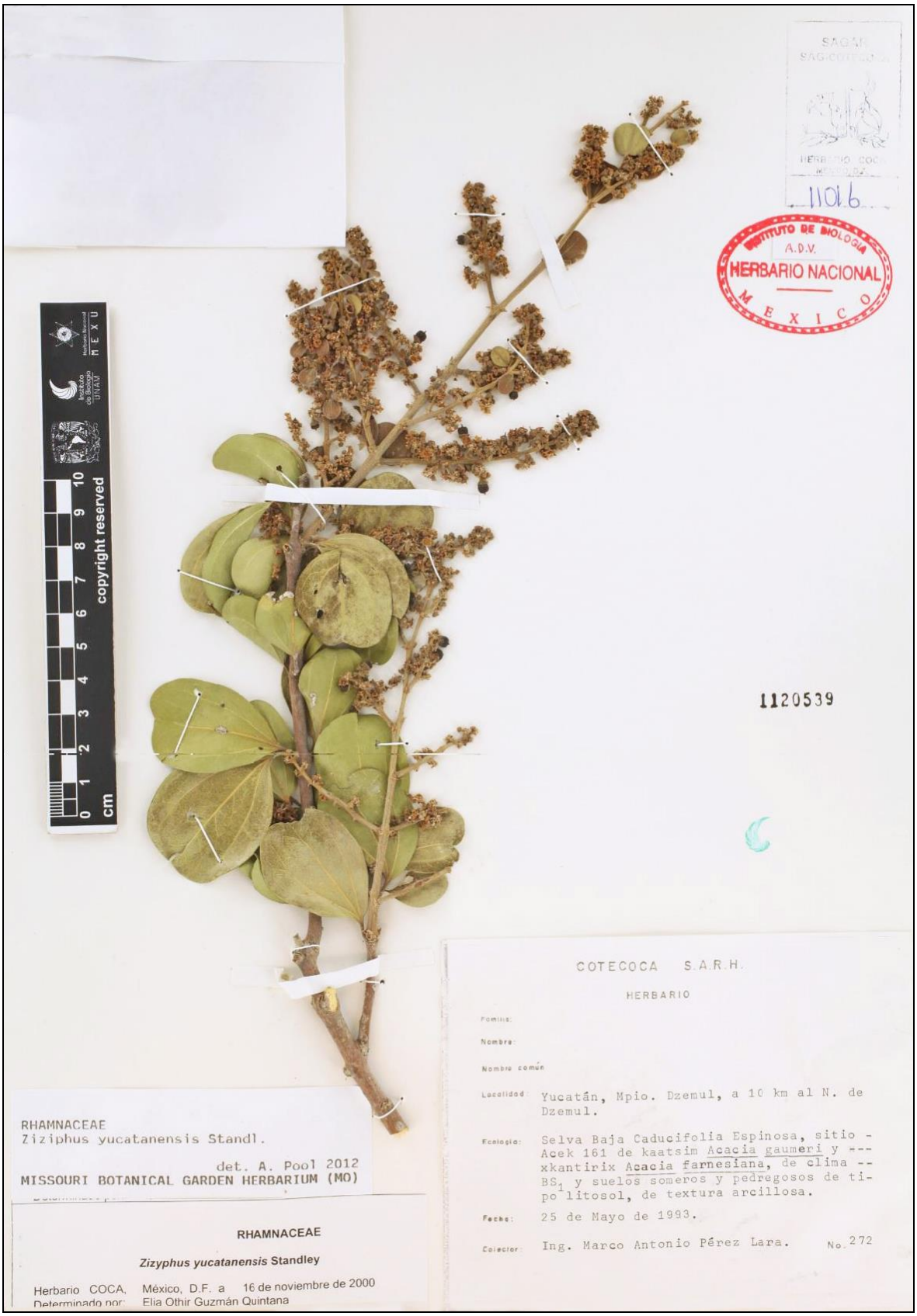


Figure 26. *Conalma yucatanensis.* Yucatán, *Pérez L. 272* (MEXU).

Figure 27. *Conalma yucatanensis.* Yucatán, *Simá & Campos Rios 1360* (MEXU).

Figure 28. *Conalma yucatanensis.* Campeche, *Martínez 30891* (MEXU). Arrows point to acicular thorns.

Figure 29. *Conalma yucatanensis.* Yucatán, *Simá 1245* (MEXU). Arrow points to an acicular thorn.

Figure 30. *Conalma yucatanensis.* Yucatán, *Simá & Campos Rios 1360* (MEXU).

Figure 31. *Conalma yucatanensis.* Quintana Roo, *Cabrera 2589* (MEXU). Indeterminate short shoots are evident.

Figure 32. *Conalma yucatanensis.* Yucatán, *Lundell 7984* (US).

Figure 33. *Conalma mexicana*. Colima, *Palmer 1278* (GH).

Figure 34. *Conalma mexicana.* Michoacan, *Miller & Tellez 3078* (LL). Single, short thorns. Leaves alternate to subopposite.

Figure 35. *Conalma mexicana.* Michoacan, *Hinton 16210* (US). Axillary inflorescence, young branch without short shoots.

Figure 36. *Conalma mexicana*. Guerrero, *Delgado S. 183* (US).

Figure 37. *Conalma mexicana.* Guerrero, *Martínez 663* (US). Short shoots with clustered leaves. Inflorescence from a short shoot.

Figure 38. *Conalma pedunculata*. Oaxaca, *Pringle 10254* (US).

Figure 39. *Conalma pedunculata.* Oaxaca, *Pringle 10254* (US). Detail from Fig. 38 — coriaceous leaves with raised, subepidermal venation.

Figure 40. *Conalma pedunculata*. Puebla, *Chiang 2304* (US). Single, very short thorns.

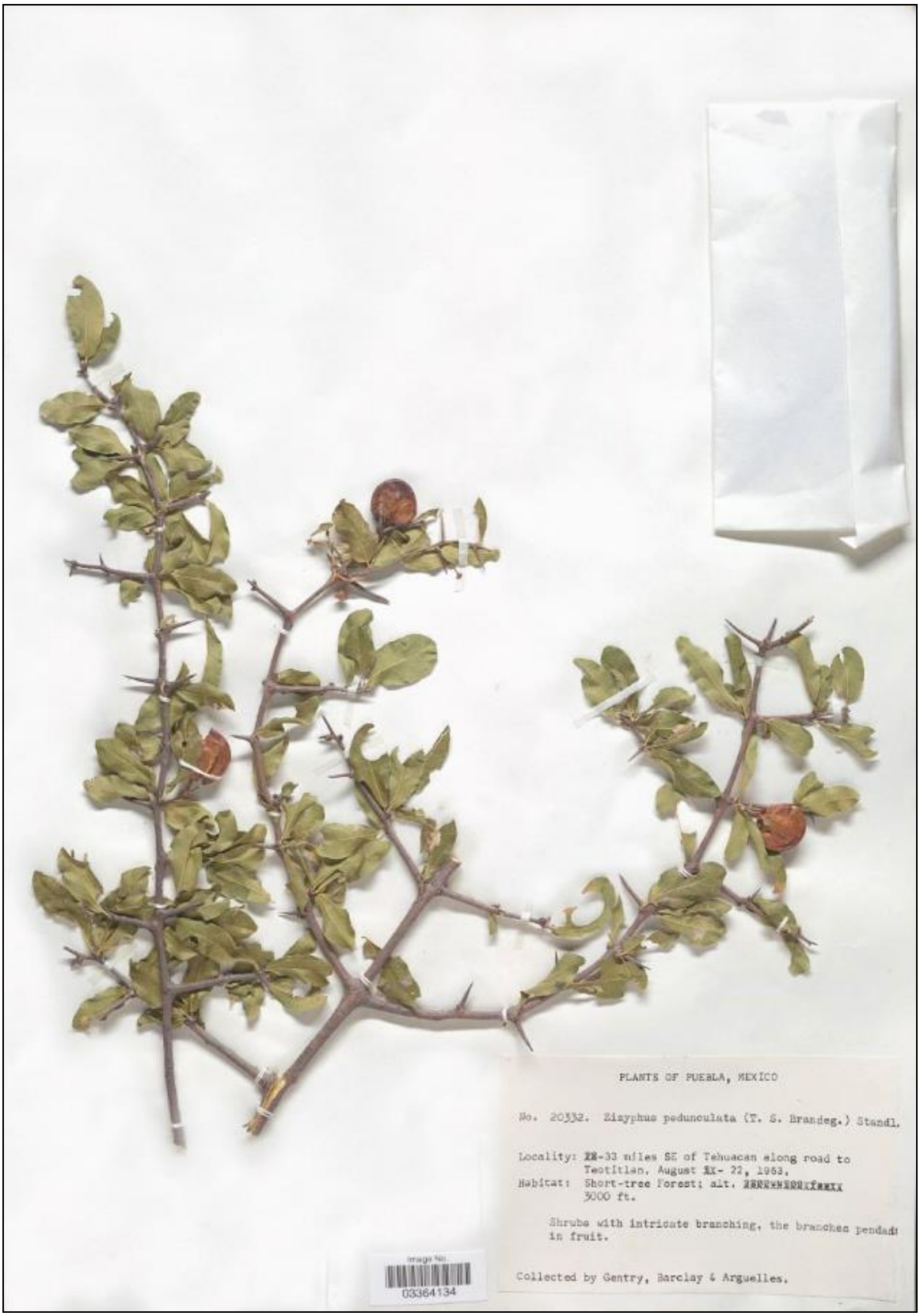


Figure 41. *Conalma pedunculata*. Puebla, *Gentry et al. 20332* (US). Short thorns, some elongating and becoming meristematic.

Figure 42. *Conalma pedunculata*. Puebla, *Chiang 1984* (ASU). Short thorns. Indeterminate short shoots.

Figure 43. *Conalma pedunculata*. Puebla, *Chiang 1984* (ASU). Detail from Fig. 42.

Figure 44. *Conalma pedunculata*. Puebla, *Chiang 852* (MEXU). Detail. Indeterminate short shoots with elongating apical meristem producing a branch.

Figure 45. *Conalma pedunculata*. Puebla, *Chiang 2440* (MEXU). Detail.

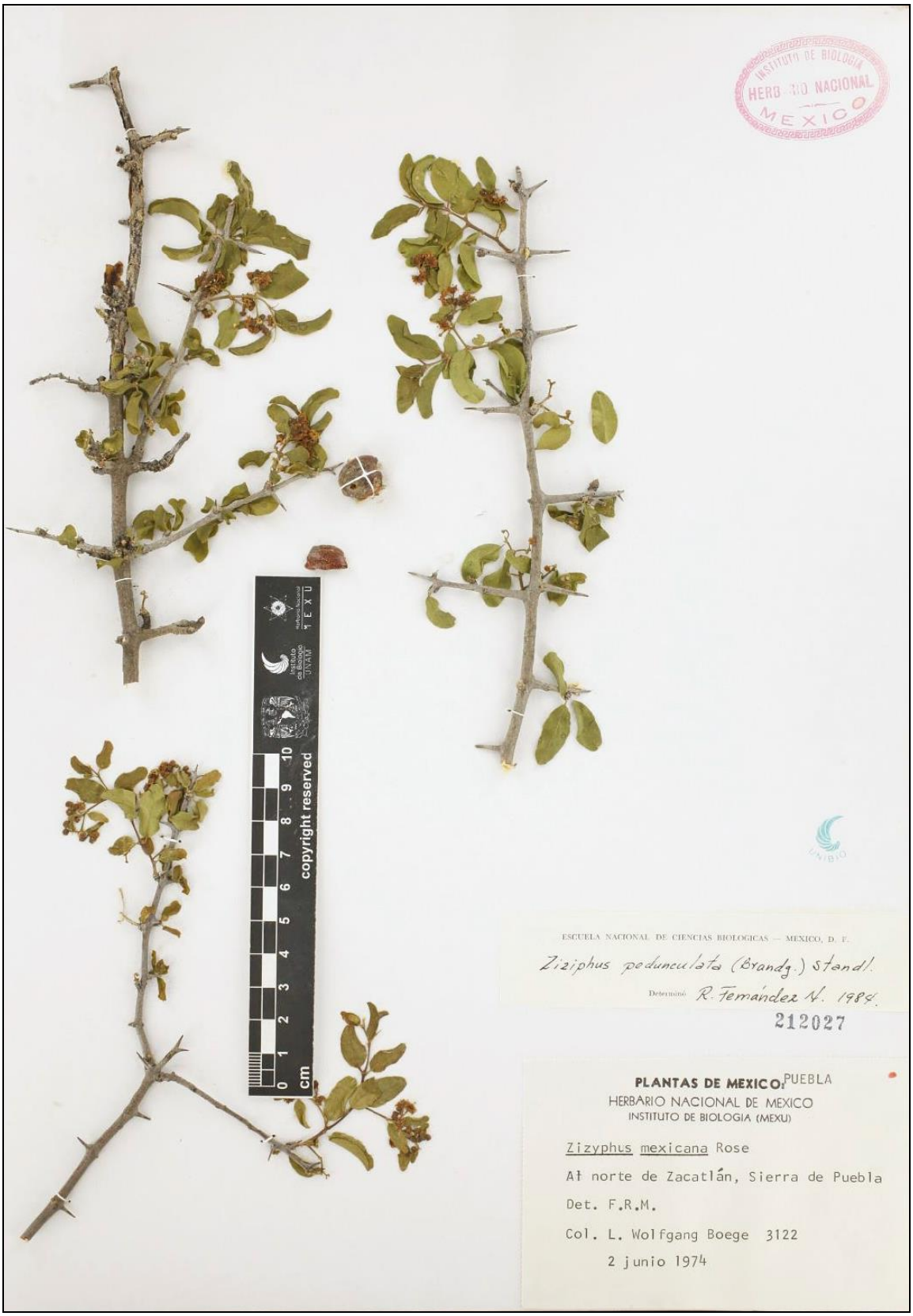


Figure 46. *Conalma pedunculata*. Puebla, north of Zacatlán, *Boegge 3122* (MEXU). Short thorns and thorn-tipped branches.

Figure 47. *Conalma pedunculata*. Puebla, north of Zacatlán, *Boegge 3122* (MEXU). Detail from Fig. 46 — arrows point to a thorn (short, thorn-tipped branch) with short shoot and a newly produced thorn-tipped branch.

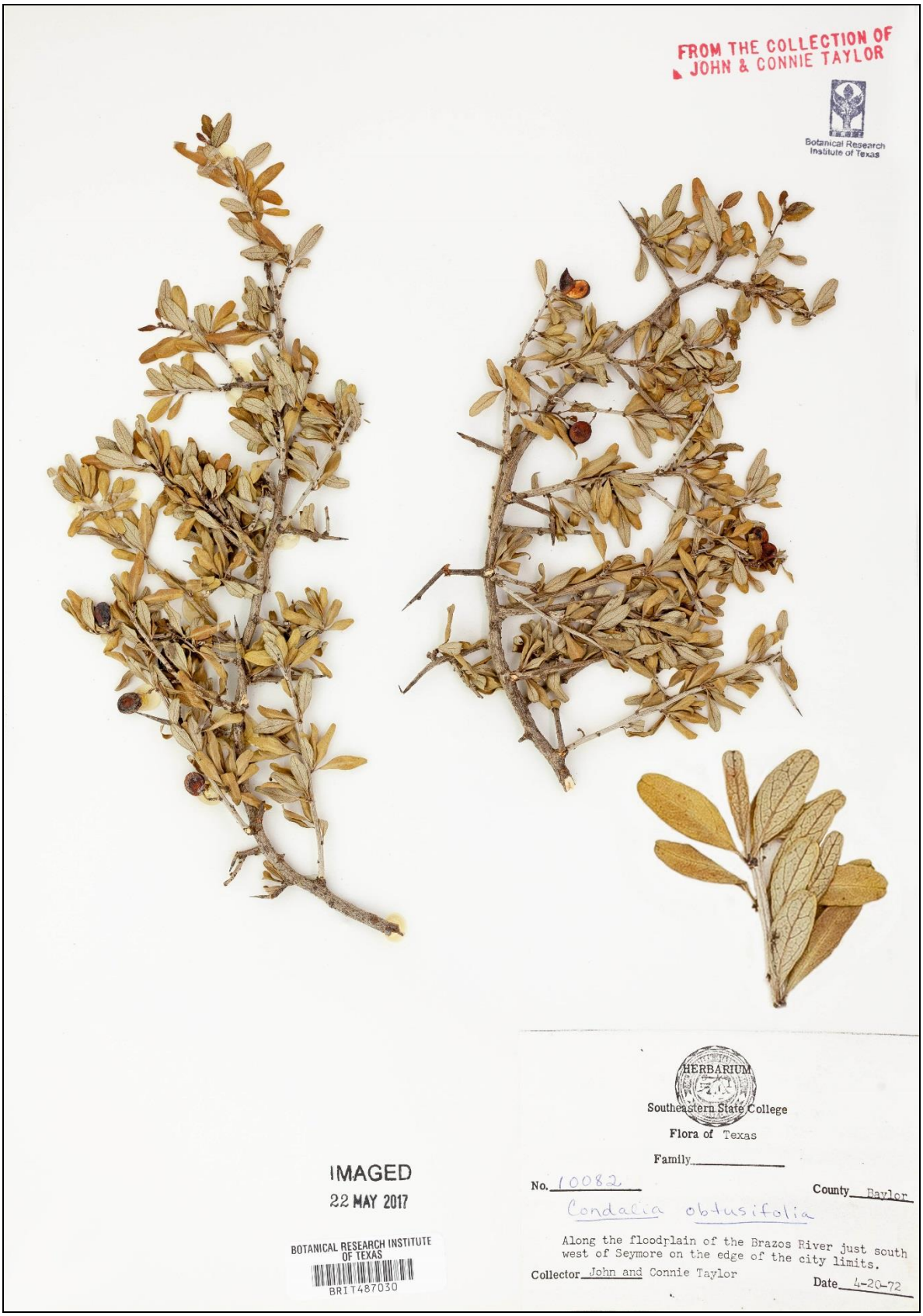


Figure 48. *Condaliopsis obtusifolia*. Baylor Co., Texas, *Taylor 10082* (BRIT).

Figure 49. *Condaliopsis obtusifolia*. Brewster Co., Texas, *Whitehouse 19683* (SMU).

Figure 50. *Condaliopsis obtusifolia*. Pecos Co., Texas, *Whitehouse 25162* (SMU).

Figure 51. *Condaliopsis obtusifolia*. Chihuahua, *Gentry & Engard 23205* (US).

Figure 52. *Condaliopsis obtusifolia*. Randall Co., Texas, *Taylor 10102* (BRIT).

Figure 53. *Condaliopsis obtusifolia*. Presidio Co., Texas, *Muller 8317* (SMU).

Figure 54. *Condaliopsis obtusifolia*. Wilbarger Co., Texas, *Whitehouse 10924* (SMU).

Figure 55. *Condaliopsis obtusifolia*. Throckmorton Co., Texas, *Cornelius 1521* (BRIT).

Figure 56. *Condaliopsis obtusifolia*. Texas, *Lindheimer 364* (US). Isotype of *Paliurus texanus*.

Figure 57. *Condaliopsis obtusifolia*. Tom Green Co., Texas, *Whitehouse 19521* (SMU).

Figure 58. *Condaliopsis obtusifolia*. Sierra Paila, Coahuila, *Hinton 16529* (US). Detail. This specimen was annotated by M.C. Johnston in 1961 as *C. obtusifolia* var. *microphylla*, but in his 1963 revision he recognized var. *microphylla* only as a synonym of *C. obtusifolia*.

Figure 59. *Condaliopsis obtusifolia*. Tamaulipas, near Tula. iNaturalist-Mexico photo by Lex Garcia, 2015.

Figure 60. *Condaliopsis obtusifolia*. iNaturalist photo.

Figure 61. *Condaliopsis obtusifolia*. Brewster Co., Texas. iNaturalist photo by silversea_starsong, 2022.

Figure 62. *Condaliopsis divaricata*. La Paz, Baja California Sur. Photo by Jon Rebman, 2017.

Figure 63. *Condaliopsis divaricata*. Pima Co., Arizona, *Hodgson H206* (DES).

Figure 64. *Condaliopsis divaricata*. Pima Co., Arizona, *Lehr 1568* (DES).

Figure 65. *Condaliopsis divaricata*. Sonora, *Anonymous s.n.* (RSA).

Figure 66. *Condaliopsis rigida*. Baja California Sur, *Johansen 601* (CAS). Holotype, detail.

Figure 67. *Condaliopsis rigida*. Sonora (just N of Corrall), *Smith 4728* (US).

Figure 68. *Condaliopsis rigida*. Sinaloa, *Johnson 507-73* (ASC).

Figure 69. *Condaliopsis rigida*. Sonora, *Delgado 2011-052* (USON).

Figure 70. *Condaliopsis rigida*. Sonora, *Sanchez E. 2011-451* (USON).

Figure 71. *Condaliopsis rigida*. Baja California, *Daniel 1366* (ASU).

Figure 72. *Condaliopsis rigida*. Hidalgo Co., New Mexico, *Hess 1805* (NMC).

Figure 73. *Condaliopsis rigida*. La Paz, Baja California Sur. iNaturalist-Mexico photo by Gerardo Marron, 2023.

Figure 74. *Condaliopsis rigida*. La Paz, Baja California Sur. iNaturalist-Mexico photo by Fernandez Reza, 2023.

Figure 75. *Condaliopsis lloydii*. Zacatecas, *Engard 700* (ASU).

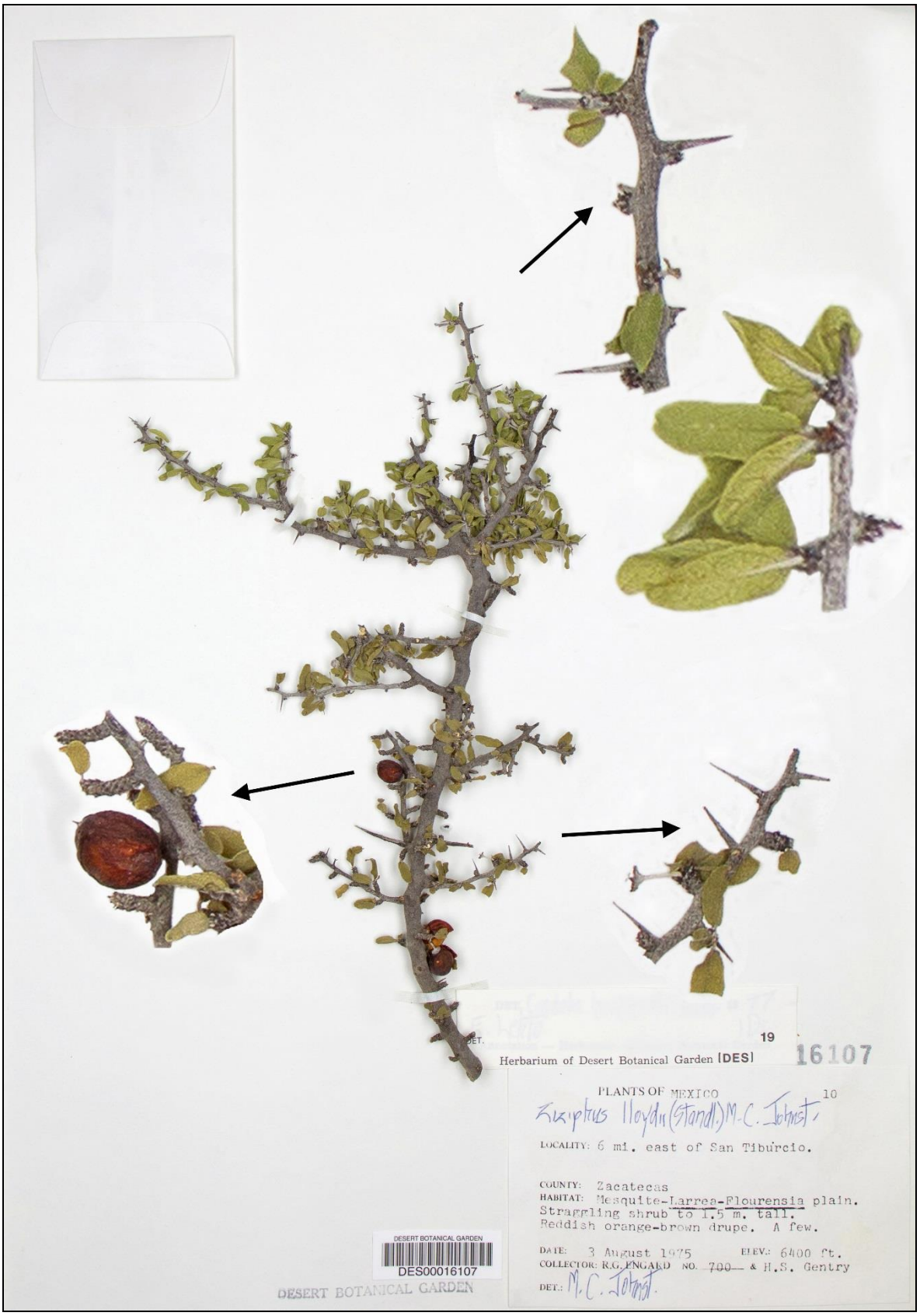


Figure 76. *Condaliopsis lloydii*. Zacatecas, *Engard 700* (DES).

Figure 77. *Condaliopsis lloydii*. Zacatecas, *Lloyd 71* (F, isotype). Details.

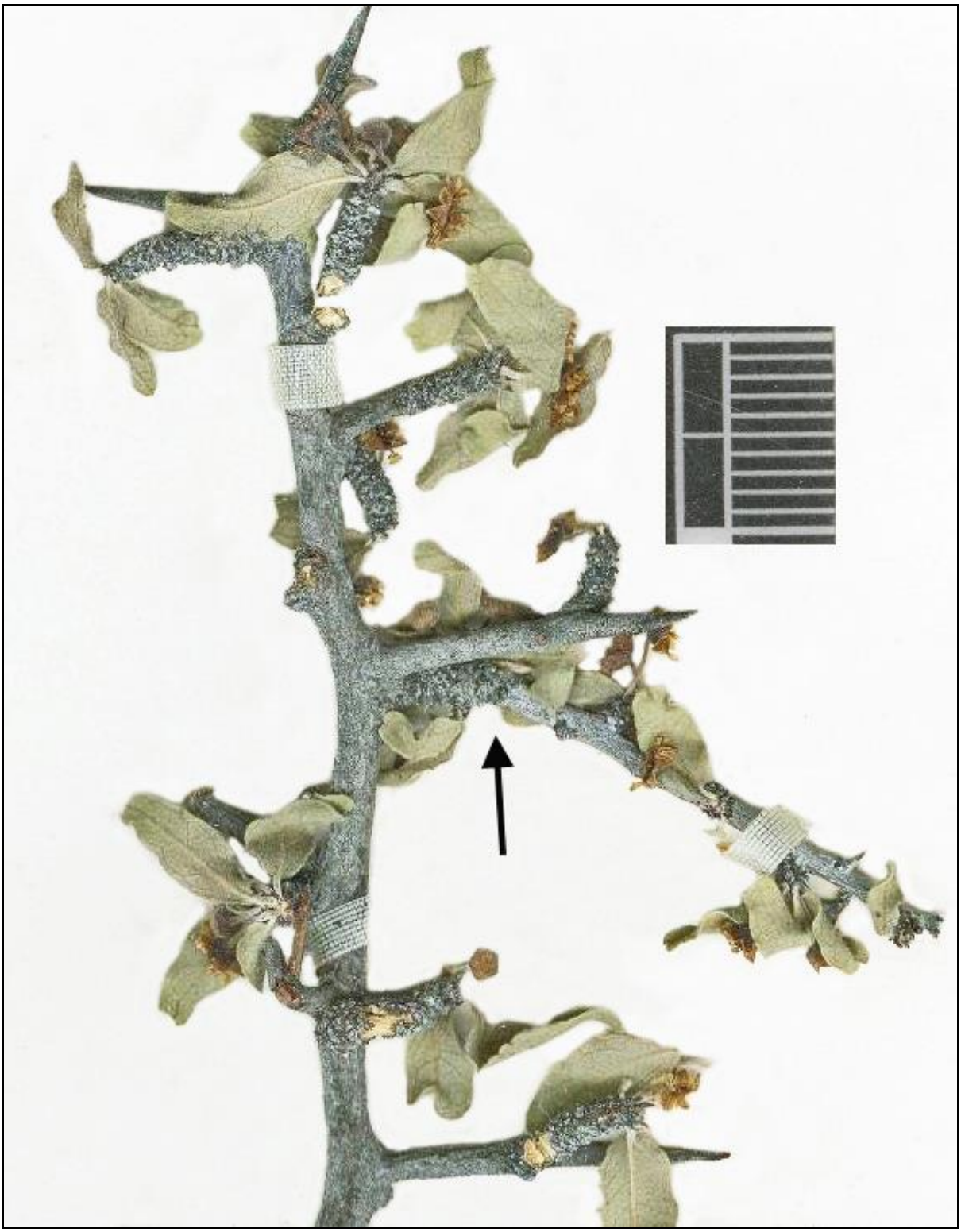


Figure 78. *Condaliopsis lloydii*. Zacatecas, *Lloyd 71* (US, isotype). Cylindric short shoots with pronounced elongation are produced sporadically through the range of the species. Arrow points to a short shoot with indeterminate growth.

Figure 79. *Pseudoziziphus parryi*. Cedros Island, Baja California (ASU). Solitary flowers also are produced in *Condaliopsis lloydii*, but the terminal bud of short shoots in *P. parryi* remains active (indeterminate) and is capable of producing a branch (see arrow). See similar examples of branch-producing short shoots in *Condaliopsis lloydii* (Fig. 79), *Condaliopsis supralloydii* (Figs. 85, 87), *Conalma yucatanensis* (Fig. 31), and *Conalma pedunculata* (Figs. 42, 44).

Figure 80. *Condaliopsis lloydii*. Zacatecas, *Lloyd 71* (UC, isotype).

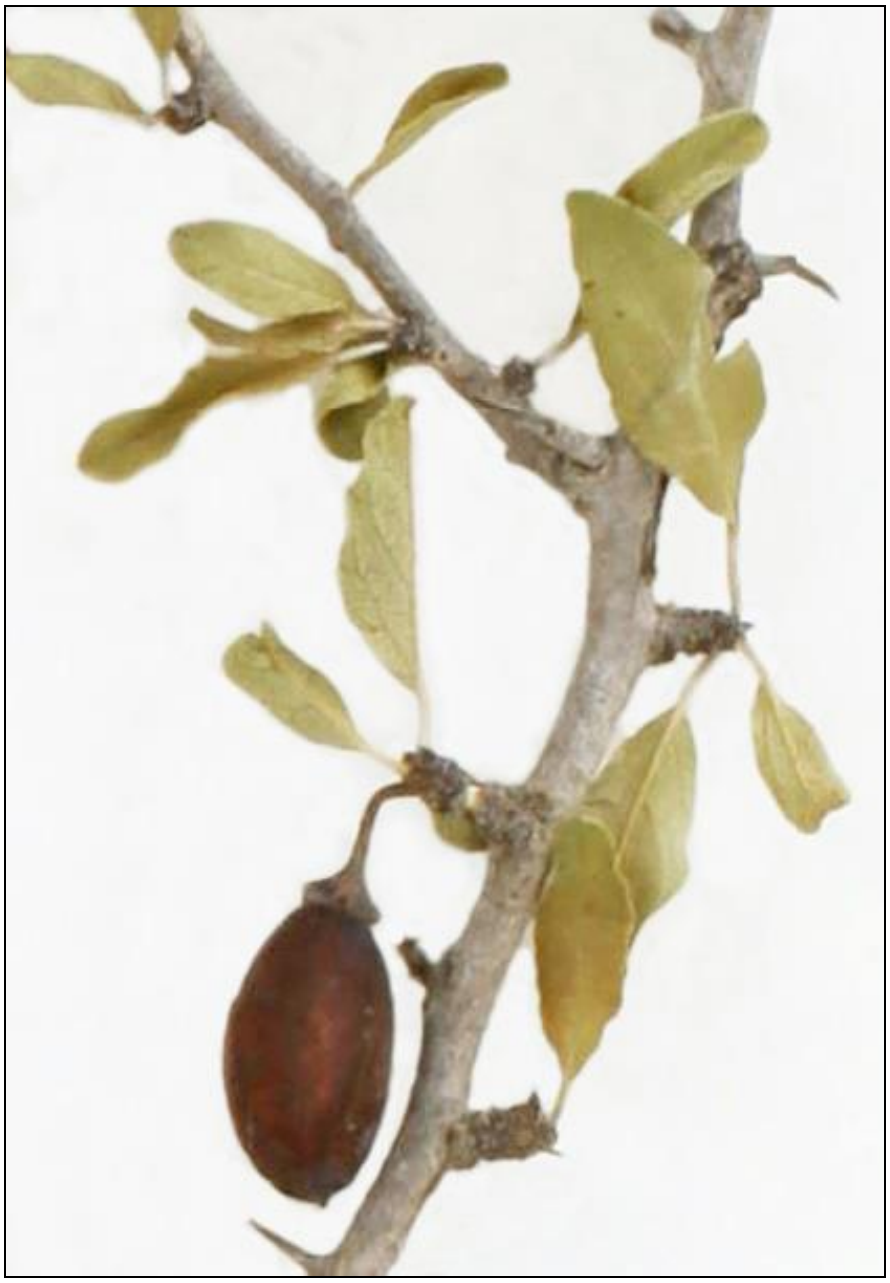


Figure 81. *Condaliopsis lloydii*. Durango, *Rodriguez G. 1513* (MEXU).

Figure 82. *Condaliopsis lloydii*. Durango, *Rodriguez G. 1513* (MEXU). Arrow points to a leafy branch apparently produced from a lateral bud of the short short.

Figure 83. *Condaliopsis lloydii*. Durango, *Rodriguez G. 1513* (MEXU).

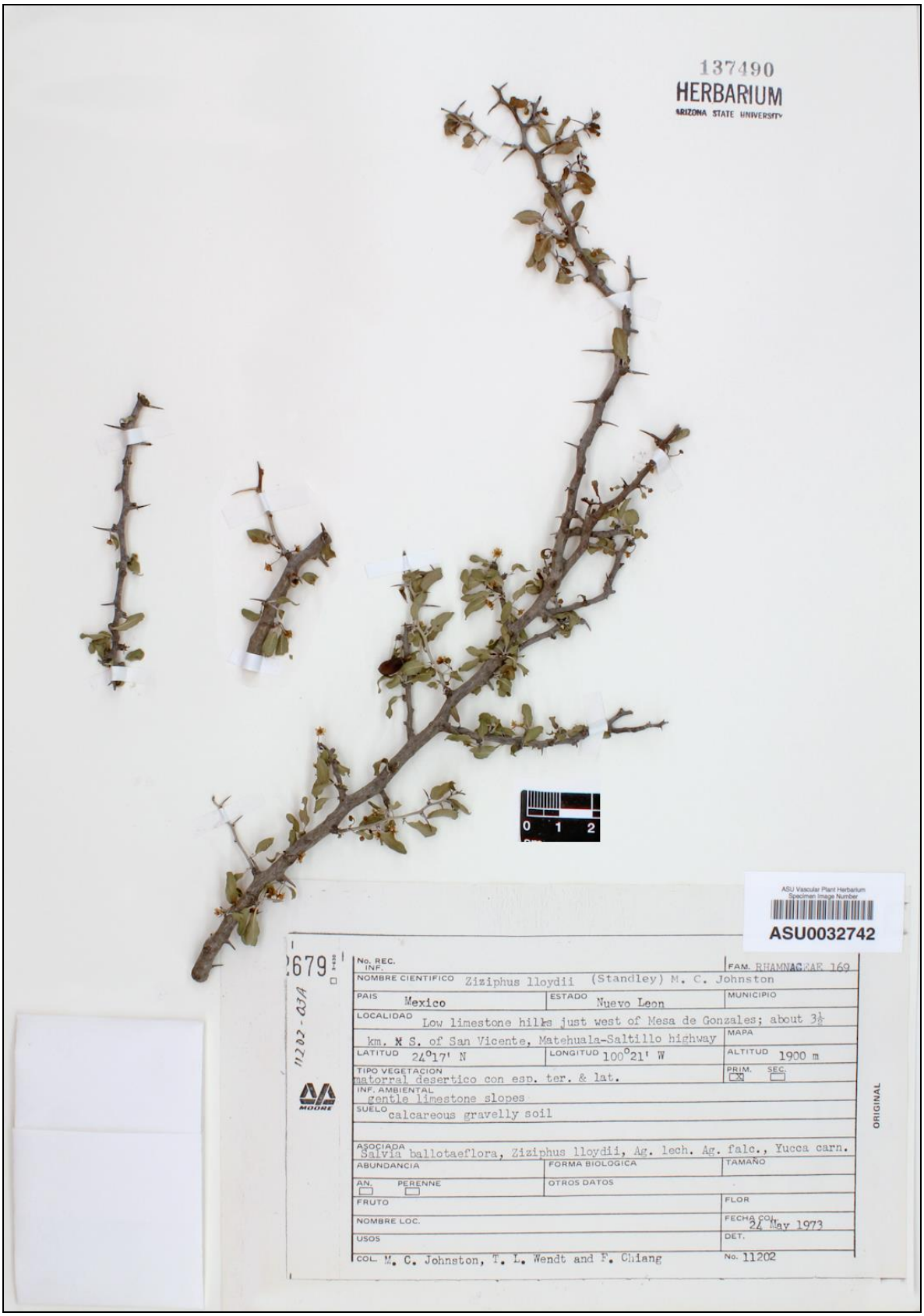


Figure 84. *Condaliopsis supralloydii*. Nuevo León, *Johnston et al. 11202* (ASU), isotype.

Figure 85. *Condaliopsis supralloydii*. Nuevo León, detail from *Johnston et al. 11202* (ASU) in Fig. 84.

Figure 86. *Condaliopsis supralloydii*. Nuevo León, *Johnston et al. 11202* (SD), isotype.

Figure 87. *Condaliopsis supralloydii*. Nuevo León, *Johnston et al. 11202* (MEXU), isotype. Arrow points to a short shoot with indeterminate growth.

Figure 88. *Condaliopsis supralloydii*. Mpio. Galeana, Nuevo León. iNaturalist-Mexico photo by Miguel González B., 2011.

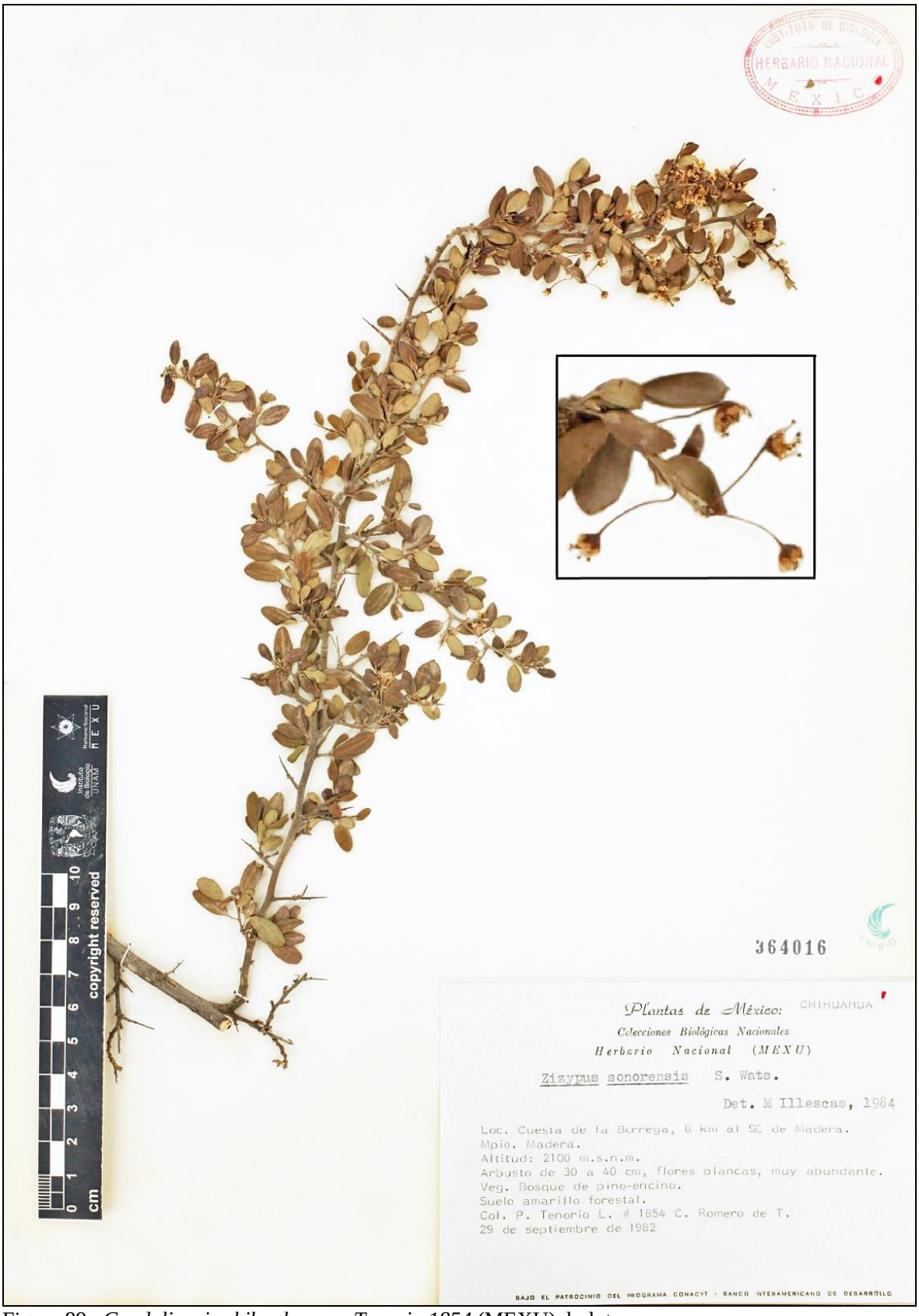


Figure 89. *Condaliopsis chihuahuana*. *Tenorio 1854* (MEXU), holotype.

Figure 90. *Condaliopsis chihuahuana*. *Tenorio 1854* (MO), isotype.

Figure 91. *Condaliopsis chihuahuana*. *Soule 521* (MO), paratype.

Figure 92. *Condaliopsis chihuahuana*. Detail from *Soule 521* (MO).

Figure 93. *Condaliopsis chihuahuana*. Puberulence on young stem. Detail from *Tenorio 1854* (MO).

Figure 94. *Condaliopsis chihuahuana*. Young thorn. Detail from *Tenorio 1854* (MO).

Figure 95. *Condaliopsis chihuahuana*. Detail from *Tenorio 1854* (MO). Bud scales.

Figure 96. *Condaliopsis chihuahuana*. Detail from *Tenorio 1854* (MO). Marginal glands on young leaves are quickly deciduous and the margins then appear entire.

Figure 97. *Condaliopsis chihuahuana*. Details from *Tenorio 1854* (MO). Mature leaves.

Figure 98. *Condaliopsis chihuahuana*. Detail from *Tenorio 1854* (MO).

Figure 99. *Condaliopsis chihuahuana*. Detail from *Tenorio 1854* (MO). Styles 2-parted.

Figure 100. *Condaliopsis chihuahuana*. Detail from *Tenorio 1854* (MO). Style 3-parted near the apex.

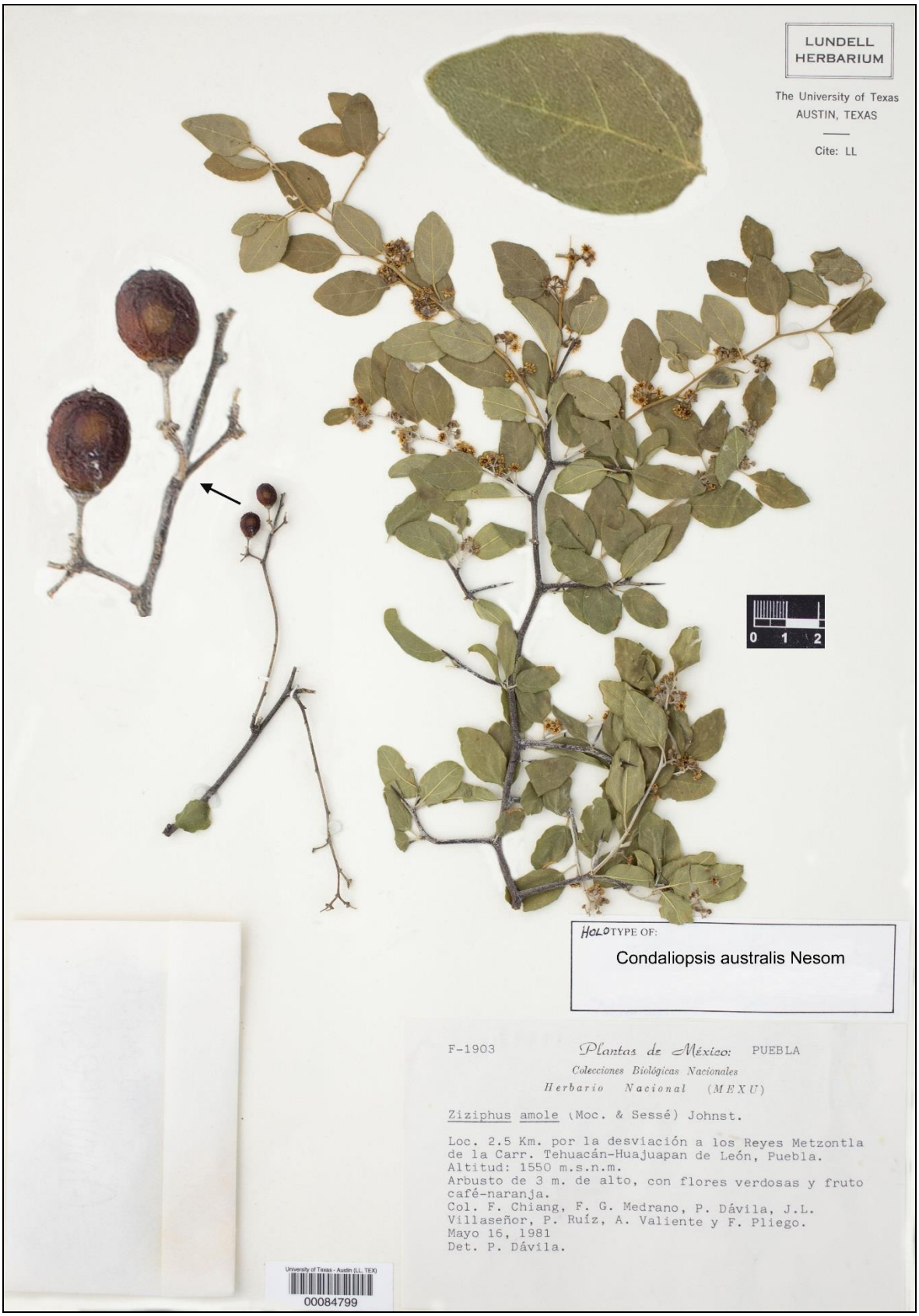


Figure 101. *Condaliopsis australis*. Puebla, *Chiang 1903* (TEX, holotype).

Figure 102. *Condaliopsis australis*. Detail from holotype.