

New Andean *Zanthoxylum* (Rutaceae) with Distinctive Vegetative Characters

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ABSTRACT. Three new Andean species of *Zanthoxylum* (= *Fagara*), *Z. gentryi* Reynel, *Z. lenticulare* Reynel, and *Z. lepidopterophilum* Reynel, are described and illustrated. Vegetative characters of taxonomic and practical identification value are briefly discussed. Some of these features relate to insect-plant interactions.

RESUMEN. Tres nuevas especies de *Zanthoxylum* (= *Fagara*), *Z. gentryi* Reynel, *Z. lenticulare* Reynel y *Z. lepidopterophilum* Reynel, son descritas e ilustradas. Se discuten brevemente caracteres vegetativos de utilidad taxonómica y práctica en la identificación de especies en el género. Algunos de estos caracteres tienen relación con interacciones insecto-planta.

The mainly pantropical and subtropical genus *Zanthoxylum* L. s.l. comprises about 200 woody species, mostly trees. Engler (1874, 1896, 1931) regarded *Zanthoxylum* s. str. as separate from *Fagara* L. and proposed a sectional and subsectional scheme for the latter. Waterman (1975a, 1976) combined the two genera and transferred the species from *Fagara* to *Zanthoxylum* s.l.; evidence has accumulated in recent years supporting that unification, on the grounds of floral morphology (Briicky, 1962; Hartley, 1966; Beurton, 1994), floral anatomy (Yamazaki, 1988), wood anatomy (Reynel & Miller, in prep.), and phytochemistry (summarized in Waterman, 1975b, 1977, 1983).

In this paper I describe three new Andean species of *Zanthoxylum* that have distinctive vegetative features: interspaced, short zones of clustered leaf and bud-scale scars (*Z. gentryi*, Fig. 1A, 2B); hollow myrmecophilous apical branchlets (*Z. lenticulare*, Fig. 1B); and twice-revolute basal leaflet margins (*Z. lepidopterophilum*, Fig. 2A, 2C). These new species belong to the group of New World species with 5-merous, differentiated perianths placed in *Fagara* subsection Paniculatae—Neogaeae by Engler (1896).

***Zanthoxylum gentryi* Reynel, sp. nov.** TYPE: Colombia. Valle: Municipio Restrepo, Vereda de Riogrande, abajo del puente, en predios de la familia Reyna, en la vía Pavas-Restrepo, 1200 m, 10 Feb. 1990 (fr), J. Ramos & C. Reyna 2551 (holotype, MO; isotype, CUVC). Figure 1A, 2B.

Haec species *Z. petiolari* A. St.-Hilaire & Tulasne affinis, sed ab eo foliis 15–45 cm longis, interjugis 3.5–9 cm longis, foliolis lateralibus ovatis vel oblongis, sessilibus, (5)7–17 cm longis, marginibus integris, panicula ampla, 7–20 × 6–16 cm (infructescens usque ad 25 × 35 cm); petalis 2.6–3.5 mm longis, coccis 4–7 mm longis et seminibus 4–6 mm longis differt.

Dioecious treelets or trees to 10 m tall; apical branchlets 5–10 mm thick, with interspaced, short zones of clustered leaf and bud-scale scars, also with sparse, straight to incurved, compressed-conical spines to 6 mm long and sparse lenticels to 1 mm long, the branchlets covered with occasional white simple hairs to 0.1 mm long, the periderm usually peeling when dry. Leaves paripinnate or imparipinnate, 4–7(–9)-foliolate, 15–45 cm long, the terminal leaflet in imparipinnate leaves promptly deciduous; petiole 4–13 cm long; rachis terete, 2–3 mm thick, glabrescent, the interjuga 3.5–9 cm long, sometimes with an abaxial spine to 5 mm long; leaflets chartaceous, rigid, usually drying olive green and shiny on both sides, laterals opposite, sessile, terminal leaflet with petiolule 0–3 cm long, ultimate pair usually larger than rest, all leaflets ovate to oblong, (5)7–17 × 3.5–9.5 cm, the apex acuminate, with acumen to 10 × 6 mm, base acute to obtuse or truncate; margin entire or subentire; leaflets glabrescent; midvein adaxially prominulous, secondary veins 10–16 pairs, prominulous on both sides, tertiary veins subreticulate. Inflorescences terminal or subterminal, multiflorous panicles 7–20 × 6–16 cm (–25 × 35 cm in fruit), branched 3–4 times; main axis 2–3 mm thick (–4 mm in fruit), secondary axes to 3–5 cm long (–20 cm in fruit), mostly forming a 60°–90° angle with main axis, the inflorescence axes covered with white, sparse simple hairs to 0.1 mm long; inflorescence bracts ovate to deltoid, 0.6–1(–3) × 0.7–1.2(–2) mm, glabrescent. Flowers 5-merous; floral bracts 1–3 at base of pedicel, deltoid to ovate, 0.6–1 × 0.5–1 mm, covered with indument similar to inflorescence axes or glabrescent; pedicel 0–1 × 1.2–2 mm (–4 mm long in fruit); calyx 0.5–1.4 × 1–3 mm, sepals free or connate to ½ their total length, ovate to deltoid, 0.8–1.2 mm broad, acute, glabrescent; petals saccate, ovate, 2.6–3.5 × 1.2–



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Figure 1. —A. *Zanthoxylum gentryi* Reynel, apical branchlet with leaf and inflorescence (Ramos 2334). —B. *Zanthoxylum lenticulare* Reynel, apical branchlet with leaf and infructescence (Soejarto et al. 4058).

1.4 mm, the apex rounded to acute, strongly inflexed, usually with an ellipsoid resin gland to 0.2 mm diam., the petals glabrous. *Staminate flowers* with 5 stamens, exserted $\frac{1}{3}$ – $\frac{1}{2}$ their total length; filaments slender, 2.8–4 mm long, anthers 1.2–1.8

mm long, thecae oblong, the connective with an apical ellipsoid gland 0.2–0.3 mm long; nectary discoid to conical-truncate, 5-lobate, 0.4–0.5 × 1–1.3 mm; pistillodes 1–3, distinct to totally connate, elongate-pyriform, 0.7–1.5 × 0.2–0.5 mm. *Pistil-*

late flowers with 0–5 staminodes, membranous, ovate to oblong; gynophore conical, 1.2–1.8 × 0.7–1.6 mm; carpels 3–5, free except in the common stigma, ovaries obovoid, 0.5–0.8 × 1–1.5 mm, styles attached at adaxial upper half of ovaries, to 0.2 × 0.2 mm, stigma discoid, 3–5-lobed, 1.8–2.1 mm diam., 0.2–0.4 mm thick. Fruit apocarpous, (2–)3–4(–5)-follicular, frequently 1–3 follicles aborting; follicles subovoid, slightly laterally compressed, 4–7 mm long, glabrescent; seed ellipsoid to subreniform, 4–6 × 2.5–5 mm, the funicular scar rounded, 1.5–2 × 0.8–1.2 mm.

Distribution. Endemic to the Department of Valle in Colombia, at 600–1100 m, in wet primary or secondary forests.

Within neotropical species of *Zanthoxylum* with differentiated perianths, the presence of interspaced, short zones of clustered leaf and bud-scale scars on apical branchlets (Fig. 2B) is characteristic of a small group: *Z. petiolare* A. St. Hilaire & Tulasne (syn. *Z. naranjillo* Grisebach), a common species from southern Brazil, Bolivia, Argentina, and Paraguay; *Z. pentandrum* (Aublet) R. A. Howard (syn. *Z. hermaphroditum* Willdenow) from northern Brazil, Venezuela, and the Guianas; *Z. verrucosum* (Cuatrecasas) P. G. Waterman from Colombia; and *Z. pucro* from Panama. *Zanthoxylum gentryi* can be distinguished from the species of the *Zanthoxylum petiolare* group by the following key:

KEY TO SPECIES IN THE *ZANTHOXYLUM PETIOLARE* GROUP

- 1a. Leaves with lateral leaflets sessile *Z. gentryi*
- 1b. Leaves with lateral leaflets petiolulate, petiolules 2–10 mm long.
 - 2a. Interjuga 5–12 cm long; leaflets 12–22 cm long.
 - 3a. Leaves imparipinnate, with ovate leaflets; inflorescence axes glabrous; pistillate flowers with petals 3–3.5 mm long; follicles 5–6 mm long *Z. verrucosum*
 - 3b. Leaves paripinnate, with oblong leaflets; inflorescence axes densely and finely pubescent; pistillate flowers with petals 1.7–2.4 mm long; follicles 6–9 mm long *Z. pucro*
 - 2b. Interjuga 1.5–5 cm long; leaflets 3–12(–16) cm long.
 - 4a. Petals 1.3–1.7 mm long; anthers 0.4–0.6 mm long *Z. pentandrum*
 - 4b. Petals 1.9–2.2 mm long; anthers 0.9–1.1 mm long *Z. petiolare*

The new species is named after Alwyn H. Gentry (1947–1993), botanist and ecologist, whose work and knowledge of the Andean–Amazonian flora and its diversity inspired a generation of tropical biologists.

Paratypes. COLOMBIA. Valle: Municipio Toro, quebrada San Lazaro (fr), Devia 328 (MO, TULV); near Yo-

toco, N of Cali, 3°45'N, 76°30'W, Gentry et al. 54073 (COL, MO); El Silencio, Hacienda Himalaya, W of Yumbo, 3°50'N, 76°40'W (fr), Gentry et al. 65516 (COL, MO); Finca El Espinal, 25 km N of Cali (fr), Hughes 129 (FHO, MO); Dagua Valley, 15.5 km below Dagua and 1.5 km below Lobo Guerrero, quebrada de la Chapa, upper end El Boquerón of río Dagua (fl), Hutchinson et al. 3102 (COL, F, G, K, MO, NY, UC, US); Municipio Restrepo, Ramos 2334 (♀), 2281 (♂) (MO, CUVC); Municipio El Cerrito, pueblo de Guabas, cerca de la frontera con Municipio Guacari, Silverstone-Sopkin et al. 2294, 3662 (fr) (CUVC, MO).

***Zanthoxylum lenticulare* Reynel, sp. nov. TYPE:** Colombia. Antioquia: Municipio de Anorí, Corregimiento de Providencia, entre Dos Bocas y Anorí, Buenos Aires, 4 km from Providencia, 400–900 m, approx. 7°N, 75°W, May 1973 (fr), Soejarto et al. 4058 (holotype, COL; isotypes, F, GH, MO). Figure 1B.

Haec species *Z. compacto* (Huber ex Albuquerque) P. G. Waterman affinis, sed ab eo foliis 40–70 cm longis 13–21-foliolatis, foliolis 8–12 cm longis, subcaudatis, marginibus minute crenulatis; paniculis amplissimis congestis 15–35 cm longis, 3(–4)-ramificatis, axibus primariis non fistulosis, axibus secundariis 4–13 cm longis; petalis 1.5–1.9 mm longis; coccis discoideis laevibus 3–4 mm longis, seminibus 2.5–3 mm longis differt.

Dioecious, myrmecophilous treelet or tree to 12 m tall; apical branchlets hollowed, 4–8 mm thick, with sparse, straight, compressed-conical spines to 6 mm long and lenticels to 0.5 mm long, the branchlets covered with sparse to dense, white, simple hairs to 0.1 mm long or glabrescent. Leaves evenly distributed on branchlets, imparipinnate, (11–)13–21(–25)-foliolate, 40–70 cm long; petiole (5.5–)7–10(–15) cm long; rachis terete, narrowly and deeply canaliculate, 2–4 mm thick, interjuga (2.5–)3–4.5 cm long, sometimes with 1(2) abaxial spines to 5 mm long, the rachis covered with indument similar to the branchlets; leaflets chartaceous to submembranaceous, drying pale green to reddish brown above, pale green beneath, laterals opposite to alternate, sessile, terminal leaflet with petiolule 2–10 mm long, ultimate pair or terminal leaflet usually larger than rest, all leaflets oblong to subovate, (2.5–)8–12(–15) × 2–4.5 cm, the apex acuminate to caudate, the acumen to 15 × 5 mm, base acute; margin crenate, the teeth separated 1–1.5 mm at the middle of leaflets; leaflets without hairs; midvein adaxially prominulous; few rounded glands 0.2–0.3 mm diam. usually present on abaxial blade near midvein; secondary veins 16–22 pairs, prominulous on both sides, tertiary veins usually prominulous and subreticulate on both sides. Inflorescences terminal or subterminal, multiflorous, congested panicles (8–)15–35 × (8–)15–22 cm, branched 3(–4) times; main axis 2–4 mm thick, secondary axes 4–13 cm long, mostly forming

a 60°–90° angle with main axis, the inflorescence axes covered with sparse to dense, white, simple hairs to 0.05(–0.1) mm long or glabrescent; inflorescence bracts deltoid to ovate, 0.2–0.5(–1) × 0.3–0.5 mm, covered with indument similar to inflorescence axes, usually ciliate. *Flowers* 5-merous; floral bracts (1)2–5 at base of pedicel, ovate to lanceolate, 2–3 × 1 mm, covered with indument similar to inflorescence axes or glabrescent; pedicel terete, 0.2–0.7 × 0.1–0.2 mm (–2.5 × 0.5 mm in fruit), glabrescent; calyx 0.5–0.7 × 0.8–1 mm, sepals connate ½ their total length, ovate, 0.3–0.4 mm broad, rounded to acute, glabrescent; petals saccate, ovate, 1.5–1.9 × 0.8–1.1 mm, the apex rounded, usually apiculate with apiculum to 0.2 mm long, also with an ellipsoid gland to 0.2 mm diam., the petals glabrous. *Staminate flowers* with stamens 5, exserted ⅓ to ½ their length, the filaments slender, 2–3 mm long, anthers 0.8–1 mm long, thecae oblong; nectary conical-truncate, 5-lobate, 0.3–0.4 × 0.3–0.6 mm; pistillodes 1–3, elongate-pyriform, distinct to totally connate, 0.2–0.5 × 0.2 mm. *Pistillate flowers* with no staminodes; gynophore conical, 0.2–0.3 × 0.4–0.6 mm; carpels (2)3, distinct except in the common stigma, ovaries oblongoid, 0.4–0.6 × 0.4–0.6 mm; styles terete, attached at adaxial upper half of ovaries, 0.1–0.2 × 0.1–0.2 mm; stigma discoid. *Fruit* apocarpous, (2–)3-follicular, frequently 1–2 follicles aborting; follicles discoid, 3–4 × 3 mm, glabrous; seed subdiscoid, 2.5–3 × 0.6–0.9 mm, the funicular scar linear, 1–2 × 0.3–0.4 mm. Common name: "Sando."

Distribution. Colombia (Antioquia) and Venezuela (Táchira and Zulia), between 90 and 900 m, in wet primary forests.

Three other New World species of *Zanthoxylum* also have hollow, myrmecophilous apical branchlets, which are very consistent and of practical value for identification. The following key allows the comparison of related species.

KEY TO MYRMECOPHILOUS NEOTROPICAL SPECIES OF *ZANTHOXYLUM*

- 1a. Apical branchlets with enlarged, interspaced zones of clustered leaf scars; panicles clustered at the apex of branchlets . . . *Zanthoxylum setulosum*
- 1b. Apical branchlets uniformly terete; panicles solitary, terminal.
 - 2a. Leaves velutinous-pubescent; leaflets 5–12 cm broad *Zanthoxylum formiciferum*
 - 2b. Leaves glabrous or glabrescent; leaflets 1–5 cm broad.
 - 3a. Panicles compact, 3–10 cm broad; fruit with follicles ovoid to obovoid, 6–9 mm long *Zanthoxylum compactum*
 - 3a. Panicles expanded, 15–22 cm broad; fruit with follicles discoid, 4–4.5 mm long *Zanthoxylum lenticulare*

Paratypes. COLOMBIA. Antioquia: Municipio San Luis, cañón del río Claro (♂), Cogollo 831 (COL, MO); Municipio Tarazá, Río Cauca, right margin on road from El Doce to Barro Blanco, 8°35'N, 75°25'W (fr), Daly et al. 5253 (COL, F, NY); Río Claro, camino al Refugio (♀, fr), Rentería et al. 2855 (COL, MO); Municipio Anorí, Río Anorí valley, near Planta Providencia, 7°30'N, 74°50'W, Shepherd 374 (COL, MO, WIS), 6 Aug. 1977, 913 (COL, MO, WIS); Corregimiento de providencia, entre Dos Bocas y Anorí, Buenos Aires, ca. 7°N, 75°W (♂), Soejarto 3922 (COL, F(2), MO). VENEZUELA. Carabobo: vicinity of Las Trincheras, near Valencia, H. Pittier 7655 (GH). Táchira: ca. 10.5 km NE of La Fría, 90 m, 8°16'N, 72°10'W, 16 Nov. 1979 (♂), J. Steyermark et al. 120511 (MO, NY, VEN). Zulia: Distrito of Colón, aldea Querrequerre, 12–15 km N of Casigua (fr), Bunting et al. 7427 (NY, VEN).

***Zanthoxylum lepidopteriphilum* Reynel, sp. nov.**

TYPE: Peru. Piura: Prov. Huancabamba, Cancagua, between "Chorro Blanco" and "Warwar," 2000–2500 m, 18 Jan. 1989 (fr), C. Díaz, T. D. Pennington & C. Reynel 3192 (holotype, MO; isotypes, K, MOL, USM). Figure 2A, C.

Haec species *Z. mantaro* (J. F. Macbride) J. F. Macbride affinis, sed ab eo foliis 32–45 cm longis, foliolis 9–17(–25), 7–10(–13) cm longis, basibus abaxialibus bis revolutis cylindrum marginalem formantibus 8–10(–14) mm longis; panicula ampla 9–14 cm longa (infructescens usque ad 20 cm longa); petalis 2–3 mm longis; coccis 5–8(–10) mm longis, seminibus 5–6 mm longis differt.

Dioecious trees to 20 m tall; apical branchlets terete, 7–10 mm thick, unarmed, covered with sparse to dense, white or yellow, stellate, bifid and simple hairs 0.2–0.6 mm long. *Leaves* evenly distributed on branchlets, imparipinnate, 32–45 cm long, 9–17(–25)-foliolate; petiole (3.5)–4–10 cm long; rachis terete, obscurely canaliculate, 2–4 mm thick, interjuga 3–5 cm long, the rachis covered with indument similar to branchlets or glabrescent; petiolules 3–5 mm long; leaflets chartaceous, drying olive green to reddish brown on both sides, laterals opposite, ultimate or medial pair larger than rest, all leaflets oblong, 7–10(–13) × 2.5–3(–3.5) cm, the apex emarginate, rounded or acuminate, with acumen to 6 × 4 mm, base acute, oblique in laterals, tubular-twice-revolute 8–10(–14) mm or more along margin, each side of the midvein; margin entire to slightly crenate, with teeth separated 2–3 mm at the middle of leaflets; leaflets covered with sparse to dense, white to yellow, stellate, bifid and simple hairs to 0.2–0.5 mm especially along midvein and abaxial base, or glabrescent; midvein adaxially narrowly and deeply impressed; secondary veins 12–16 pairs, prominulous on both sides, tertiary veins usually prominulous and subreticulate on both sides. *Inflorescences* terminal or subterminal panicles, branched 1–2 times, pauciflorous to submultiflorous, 9–14 × 2.5–5.5 cm (–20 × 20 cm in fruit); main

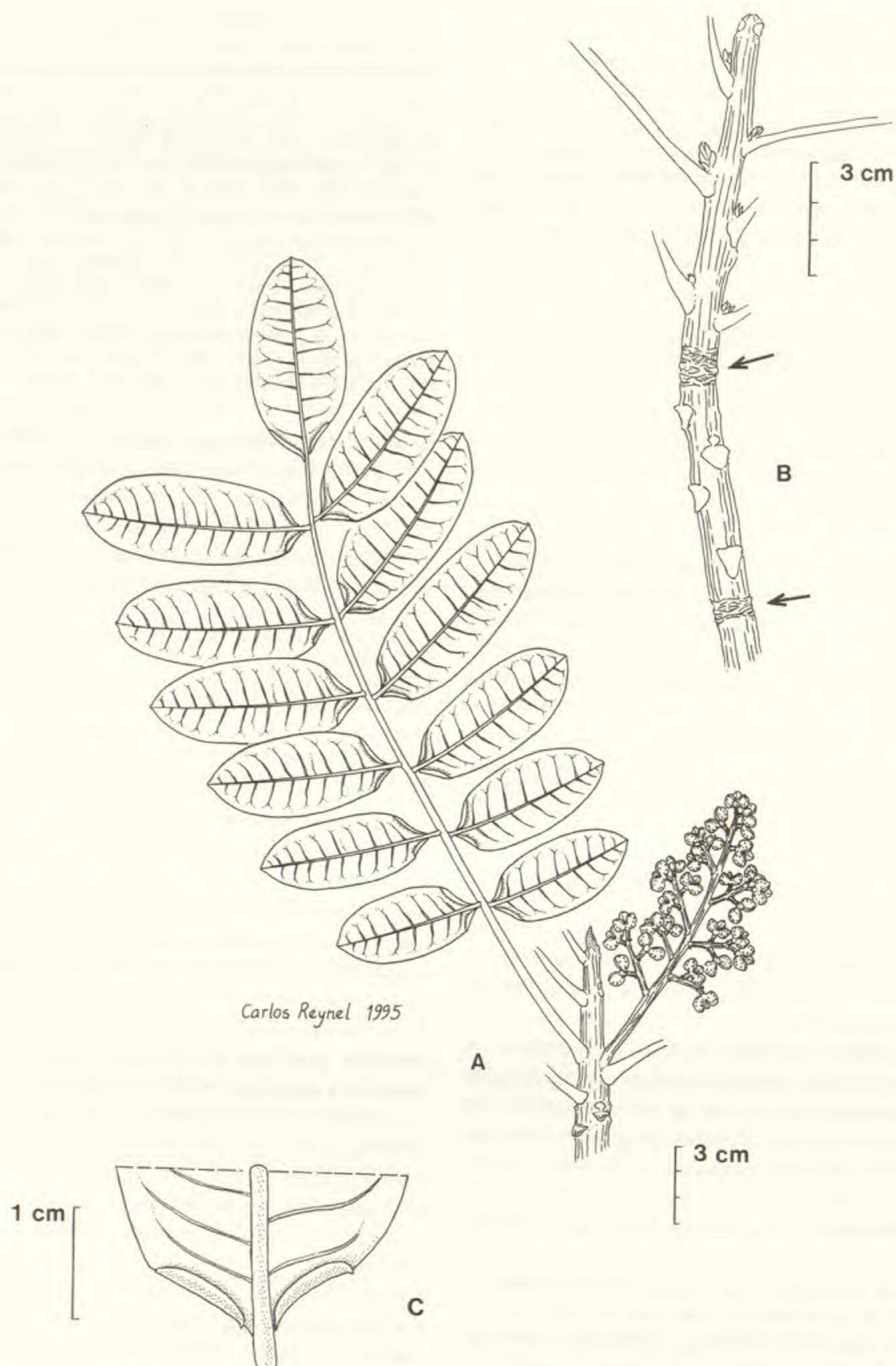


Figure 2.—A. *Zanthoxylum lepidopterophilum* Reynel, apical branchlet with leaf and infructescence (Díaz et al. 3192).—B. *Zanthoxylum gentryi* Reynel, apical branchlet showing short zones of clustered leaf and bud-scale scars (arrows) (Silverstone-Sopkin et al. 2294).—C. *Zanthoxylum lepidopterophilum* Reynel, leaflet showing the basal margin abaxially tubular-revolute each side of the midvein (Díaz et al. 3192).

axis 2–3 mm thick (~5 mm in fruit), secondary axes 1–2 cm long (~6 cm in fruit), the inflorescence axes covered with sparse to dense, stellate, bifid and simple hairs 0.2–0.8 mm long; inflorescence bracts deltoid to lanceolate or ovate, 0.5–1.3 × 0.5–0.7 mm, covered with indument similar to inflorescence axes. *Flowers* 5-merous; floral bracts 1(–3) at base of pedicel, ovate to deltoid, 0.4–0.6 × 0.3–0.6 mm, with indument similar to inflorescence axes; pedicel subterete, 0.6–1.2 × 0.6–0.8 mm; calyx with sepals basally connate to $\frac{1}{3}$ their total length, ovate to deltoid, 0.8–1.2 × 0.5–0.8 mm, covered with sparse, stellate, bifid and simple hairs 0.3–0.5 mm long, usually ciliate; petals oblong to ovate, 2–3 × 1.2–1.6 mm, saccate, the apex inflexed, rounded, usually apiculate, with apiculum 0.2–0.4 mm long, petals covered with scattered, stellate, bifid or simple hairs 0.2–0.4 mm long, subciliate. *Staminate flowers* with 5 stamens, exserted to $\frac{1}{3}$ their total length, filaments slender, 2.5–3.8 mm long, anthers oblongoid, 0.8–1 mm long, the connective with an obscure apical gland 0.1–0.2 mm diam.; nectary conical-truncate to discoid, basally 5-lobed, 0.4–0.6 × 0.9–1.2 mm; pistillodes 2–3, distinct to connate, pyriform-elongate, 0.6–0.9 × 0.3–0.4 mm. *Pistillate flowers* with staminodes 0–5, membranous, ovate to oblong, 0.4–0.6 × 0.2–0.3 mm; gynophore conical, 0.6–1.2 × 0.7–1.4 mm; carpels 3–5, free except in the common stigma, ovaries obovoid, 0.7–1.3 × 0.8–1.3 mm; styles attached at adaxial upper half of ovaries, 0.3–0.5 × 0.2–0.3 mm, stigma discoid, 3–5-lobed, 1.5–2.1 mm diam., 0.2–0.4 mm thick. *Fruit* apocarpous, 2–3(–5)-foliolar, frequently 1–3 follicles aborting; pedicel 3–5 × 1.7–2.3 mm, with indument similar to inflorescence axes; follicles globose to obovate-compressed, 5–8(–10) mm long, glabrescent; seed globose to ovoid-compressed, 5–6 × 4–5 mm, the funicular scar linear, 4–5 × 0.4–0.7 mm.

Distribution. Ecuador (Imbabura, Loja, Pichincha) and Peru (Piura, Cajamarca), 1000–2500 m, in montane cloud forests.

The New World species of *Zanthoxylum* with differentiated and 5-merous perianths, placed in *Fagara* subsection *Paniculatae–Neogaeae* by Engler (1896), frequently have lateral leaflets with basally slightly to strongly revolute margins. *Zanthoxylum lepidopterophilum* is unique in having the basal margin twice-revolute, forming a conspicuous cylinder 8–10(–14) mm long along the margin on each side of the midvein (Fig. 2C). The larvae of an unidentified lepidopteran have been found to inhabit the interior of this marginally formed cylinder. *Zanthoxylum lepidopterophilum* is similar to *Z. mantaro* (J. F. Macbride) J. F. Macbride in its apical bran-

chlets and leaves with indument of simple, bifid and stellate hairs and 5-merous, 3–5-carpellate flowers, but differs in its markedly larger terminal buds, leaves, leaflets, and inflorescences; sizes of these organs for both species compare as follows (first measurement for *Z. lepidopterophilum*, second for *Z. mantaro*): leaves 32–45 cm long vs. 9–15 cm long; leaves 9–17(–25)-foliolate vs. 5–7(–9)-foliolate; petioles 4–10 cm long vs. 1.5–3.5 cm long; leaflets 7–10(–13) cm long vs. (2–)3–6(–9) cm long; and inflorescences 9–14 cm long (~20 cm in fruit) vs. (2.5–)4–6 cm long (~9 cm in fruit).

Paratypes. PERU. Cajamarca: San Miguel, Distrito La Florida, Agua Azul (fr), Díaz 2095 (MO, MOL, TEX, USM). Piura: Cerro Aypate, 49 k E of Ayabaca, in disturbed dry cloud forest, 4°35'S, 79°32'W, Gentry et al. 75045 (MO, USM). ECUADOR. Imbabura: Cantón Urquí, Balneario Cachimbio, 0°27'N, 78°14'W (♂), W. Palacios 5241 (MO, QCA). Loja: Cantón Sozoranga, slope of San Fernando, exiting Las Cochas, 4°18'S, 79°57'W (fr), Palacios 3321 (MO, QCA). Pichincha: Reserva Geobotánica Pululahua, between La Reventazón and Pululahua, 0°05'N, 78°30'W, (♀, fr) C. Ceron et al. 5673 (MO, QCA).

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