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THE SYSTEMATICS AND ECOLOGY OF POISON-IVY
AND THE POISON-OAKS
(TOXICODENDRON, ANACARDIACEAE)¹

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(Continued from page 159)

TAXONOMIC TREATMENT

TOXICODENDRON Miller

Toxicodendron Tournefort, Inst. Rei Herb., p. 610. 1700; Miller, Gard. Dict., Abr. ed. 4. 1754, non *Toxicodendron* = *Toxicodendrum* Thunb. in Kongl. Vetensk. Acad. Nya Handl. 7: 188. 1796. (= *Hynaenanche* Lam., Euphorbiaceae), nec *Toxicodendrum* J. Gaertner in Fruct. 1: 207. 1788 (= *Allophylus* L. or *Schmidelia* L., Sapindaceae).

Rhus L., Sp. Pl. 1: 265. 1753, in part as to species 4, 6, and 7.

Vernix Adanson, Fam. Pl. 2: 342. 1763.

Rhus-Toxicodendron Marshall, Arbust. Am., p. 130. 1785.

Pocophorum Necker, Elem. Bot. 2: 226. 1790.

Philostemon Raf., Fl. Ludoviciana, p. 107. 1817; Steudel, Nom. Bot. ed. 2: vol. 2., p. 320. 1841 as *Philostemum*.

Deciduous dioecious trees, shrubs, or woody vines with poisonous effluvium. Leaves alternate, palmately ternate or imparipinnate, estipulate, thin, glabrous to tomentose on the lower surface, glabrous to sericeous on the upper surface; leaflets opposite except for the terminal one. Flowers in axillary, lateral, thyrsoid panicles or racemes, ultimate clusters determinate, of 3 or 4 flowers; bracts of the inflorescence lanceolate, deciduous; fruiting inflorescence

usually pendent, but occasionally erect by lignification of the rachis. Sepals 5, persistent, imbricate in the bud, united at base. Petals 5, ascending, veined, glabrous, imbricate in bud, ovate, usually with reflexed tips, smaller in female flowers than in male. Ovary 1-celled by abortion, sessile or partially buried in the hypogynous disk; style terminal, stigma 3-parted, turning black with age; ovule raised on an elongate ascendent basal funicle. Drupes subglobular or laterally flattened, 2.5-7 mm broad, 1.5-5 mm long, whitish, cream, yellow, to dun-colored, glabrous or pubescent with simple, non-glandular hairs, less than 1.5 mm long, the bony endocarp and mesocarp adhering; mesocarp waxy, striate with black resin canals; exocarp brittle, papery, separating from the mesocarp at maturity; remnant of the 5-lobed disk becoming chartaceous. Stones bony, often with a few ribbon-like longitudinal ridges, endocarp fused to testa; endosperm absent; embryo large, generally transverse with flat foliaceous cotyledons; hypocotyl \pm elongate, incurved upwards toward the hilum. Stamens 5, haplostemonous, inserted below a lobed, annular, patellior, cupuliform, intrastaminal, nectiferous disk, reduced in female flowers; anthers oblong, dorsifixed, usually shorter than the \pm subulate filaments; dehiscence longitudinal, introrse. Pollen tricolpate, finely reticulate, ellipsoidal, with tapering transverse furrows, endexine thickened internally at the edge of the colpus forming a rib; mean length 26.6μ , mean width 23μ . Vessels not clustered in the late wood; resin ducts absent in the xylem rays; septate xylem fibers present; with solid, white. Root ribrous; root hairs dark brown. North America to northern South America, and eastern Asia.

Type species; *Toxicodendron toxicarium* (Salisb.) Gillis (*Rhus toxicodendron* L., Sp. Pl. 1: 265. 1753, lectotype of Barkley, 1937).¹³

¹³Barkley (1937) named *Rhus toxicodendron* L. as lectotype species of sect. *Eutoxicodendron* (= sect. *Toxicodendron*) and equated it with *Toxicodendron radicans*. However, it is now clear that *Rhus toxicodendron* of Linnaeus = *T. toxicarium*, and therefore this is the correct name for the lectotype species of the genus.

KEY TO SECTIONS, SPECIES, AND SUBSPECIES OF
TOXICODENDRON

- a. Large shrub or tree, clonal, but without long stolons; anthers conspicuously exerted, filaments filiform
..... Section Venenata (not treated herein)
- a. Vine, sub-shrub, or shrub with long stolons; anthers included, filaments subulate at the base b.
- b. Leaves simple (Section Simplicifolia) 1. *T. borneense*
- b. Leaves compound c. (Section Toxicodendron)
- c. Leaflets 5 - 9 2. *T. nodosum*
- c. Leaflets 3 d.
- d. Fruits glabrous (or with only occasional hairs); leaflets coarsely toothed, 1-lobed, or entire; if entire, then tufts of hairs concentrated in vein axils on lower surface absent e.
- e. Leaflets with lobed or deeply cut margins
..... 4h. *T. radicans* ssp. *verrucosum*
- e. Leaflets with entire, undulate, notched, or serrate margins f.
- f. Leaflets glabrous to scattered-strigose on the lower surface, or with pubescence confined to the veins, not velvety to the touch; glabrous or with sparse pubescence on the upper surface; pubescence, if any, appressed g.
- g. Most leaves made up of entire or subentire leaflets 4g. *T. radicans* ssp. *divaricatum*
- g. Most leaves made up of notched or serrate leaflets h.
- h. Leaflets suborbicular or broadly ovate; petiole completely glabrous; plant subshrub or shrub 5. *T. rydbergii*
- h. Leaflets ovate or lanceolate; petiole puberulent to densely pubescent; plant shrub or vine 4f. *T. radicans* ssp. *negundo*
- f. Leaflets densely pilose to velutinous on lower surface, velvety to the touch; pubescence on the upper surface; pubescence erect i.
- i. Leaflets serrate; terminal leaflet broadly ovate 4d. *T. radicans* ssp. *pubens*
- i. Leaflets entire or subentire; terminal leaflet elliptic or lanceolate
..... 4e. *T. radicans* ssp. *barkleyi*

- d. Fruits pubescent or papillose; leaflets entire, undulate, or round-lobed; if toothed, then tufts of hairs in vein axils on lower leaflet surface present j.
- j. Leaflets mostly obtuse or rounded at apex; fruits setose or minutely puberulent; tufts of hairs absent from vein axils on lower leaflet surface k.
- k. Leaves glabrous to glabrate 3. *T. diversilobum*
- k. Leaves pubescent l.
 - l. Leaflets deeply incised; leaflet base rounded
..... 4i. *T. radicans* ssp. *eximium*
 - l. Leaflets undulate or lobed; leaflet base cuneate
..... 6. *T. toxicarium*
- j. Leaflets acute or acuminate; fruits puberulent, hispid or scabrous; tufts of hairs present in vein axils on lower leaflet surface m.
- m. Widest part of terminal leaflet blade below centre; tufts of hairs in vein axils usually not red-brown; terminal leaflet blade 2.5-14 cm. long; fruits globose, 3-5 mm. broad; terminal leaflet obtuse or truncate 4a. *T. radicans* ssp. *radicans*
- m. Widest part of terminal leaflet blade at or above centre; tufts of hairs in vein axils usually red-brown; terminal leaflet 6-20 cm. long; fruits flattened, often obliquely deltoid, 5-6 mm. broad; terminal leaflet attenuate or cuneate n.
- n. Fruits short hairy or papillose only; terminal leaflet 1.2-1.7 times as long as broad, cuneate ..
..... 4b. *T. radicans* ssp. *orientale*
- n. Fruits hispid with hairs nearly 1 mm. long; terminal leaflet nearly twice as long as broad, attenuate 4c. *T. radicans* ssp. *hispidum*

Toxicodendron section **Simplicifolia** Gillis, sect. nov.

Vites lignosae deciduae; folia simplicia, subcoriacea; fructus elevatus super vestigium receptaculi et disci.

Deciduous woody vines; leaves simple, subcoriaceous; fruit raised from remnant of receptacle and disk. Northern Borneo (Sabah). Type species: *Toxicodendron borneense* (Stapf) Gillis.

1. **Toxicodendron borneense** (Stapf) Gillis, comb. nov. Fig. 25.

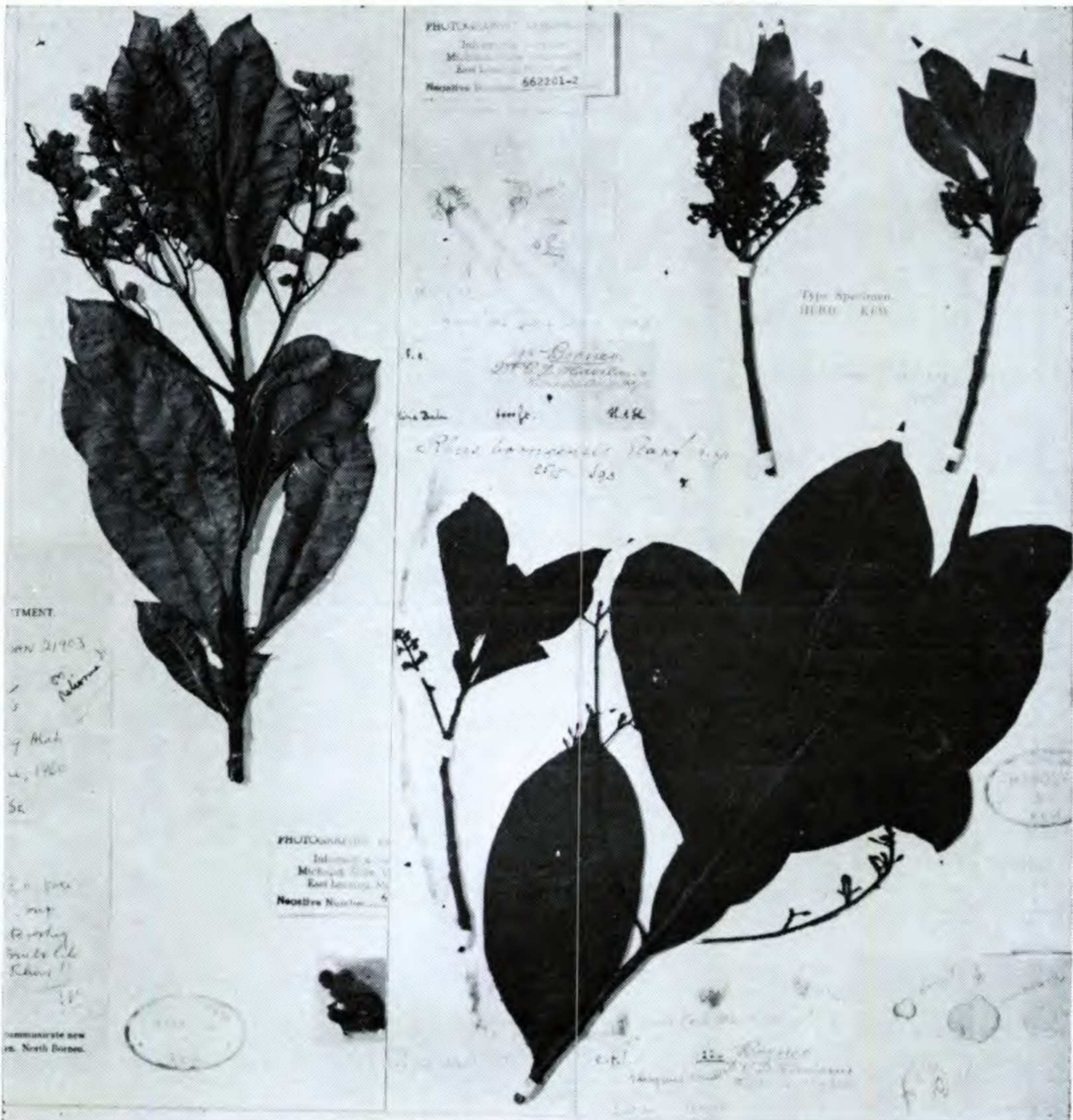


Fig. 25. *Toxicodendron borneense*. Right, above: Holotype of *Rhus borneensis* Stapf, Haviland 1198 (Male). Right, below: Haviland 1224 (female). Left: Fruiting specimen, Meijer.

Rhus borneensis, Stapf in Trans. Linn. Soc. London Bot. 4: 142. 1894. Type: G. D. Haviland 1198, 6000 ft. on Mt. Kinabalu, Sabah, 19 March 1892 (K) male flowering specimen.

Scandent shrub; branches slender, brown, often bearing prominent lenticels. Leaves simple, subcoriaceous, elliptic to oblanceolate, short petiolate, entire with revolute margins, with 14-22 pairs of \pm prominent veins; glabrous, with acuminate to mucronate tips, base attenuate; blade 6-16 cm long, 2.5-6.5 cm broad. Inflorescence a lateral paniculate

thyse, 6-14 cm long, longer in female than in male, generally in verticillate clusters with leaves above and below; flowers clustered often in threes on short, minutely bracteolate pedicels; bracts lanceolate, 1 mm long, 0.2 mm wide, glabrate, gradually tapering to a blunt tip, narrower in female than in male; corolla lobes oblong to oblanceolate, 2.0-2.8 mm long, 1.0-1.5 mm broad, narrower in female than in male, blunt; fertile anthers 1.2 mm long, broadly ovate, filaments 0.5 mm long; in female sterile anthers 0.5 mm long, subulate. Fruiting inflorescence glabrous, erect; fruit obliquely globose-reniform, laterally flattened, 5.5-7 mm broad, 5-6 mm deep at its widest point (through the stigmatic region), glabrous, with mesocarp striate in a white, waxy matrix; fruit raised from remnant of receptacle and disk.

Specimens examined: **Malaysia:** Sabah; Mt. Kinabalu, 6000 ft., *Haviland* 1198, (K); 6600 ft., *Haviland* 1224, (K); Kamberanga, 7040 ft., *Griswold* 118, (A); Gunong Alab, Tambunan, 4000 - 5000 ft. *Meijer* (K, SAN).

Distribution: Province of Sabah (Borneo), Malaysia. Fig. 26.

Toxicodendron borneense is the rarest of the species in the poison-ivy complex. It has been collected only four times. On one occasion, the collector noted that his collection came from a fresh branch found on the ground, no parent plant having been discovered from which it may have come. The range of variation in the species is therefore unknown. Although its type locality is Mt. Kinabalu in the state of Sabah in northern Borneo, a mountain which has been visited by several plant-collecting expeditions, *T. borneense* has been found there only twice.

This species shares with all other *Toxicodendron* species the property of possessing resins which darken with age (presumably poisonous) in addition to their diagnostic fruit and flowers characteristics. It differs markedly in having simple leaves and verticillate inflorescences. The fruits appear to be raised on a remnant of the receptacle and disk, unlike other members of the genus. Because of

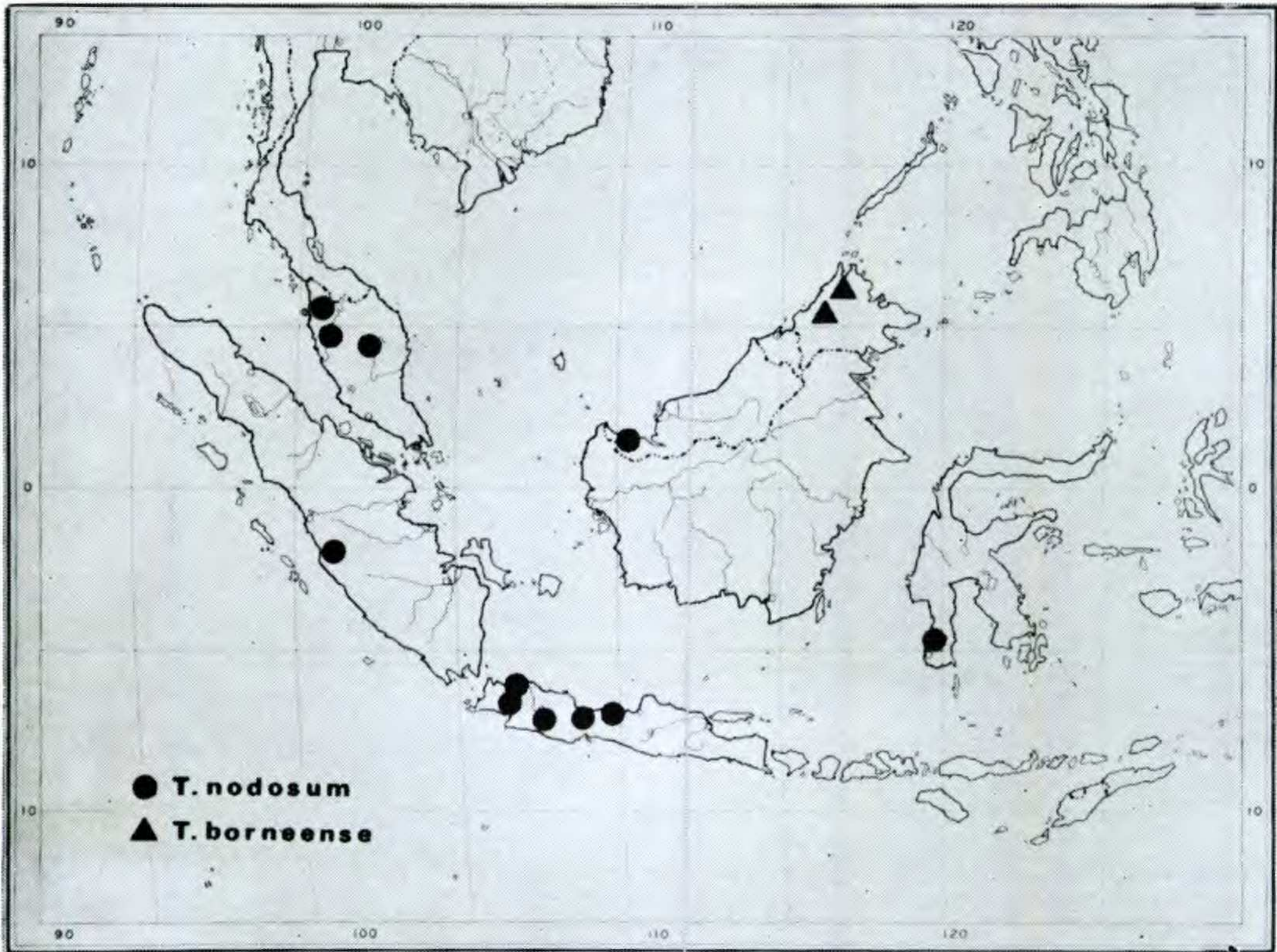


Fig. 26. Distribution of *Toxicodendron borneense* and *T. nodosum*.

these unique characters which set *T. borneense* apart from the rest of the genus, a new section of the genus has been erected for it.

Toxicodendron sect. **Toxicodendron**

Eutoxicodendron Schneider, *Illustr. Handb. Laubholz*. 2: 149. 1907.

Toxicodendron Robinson & Fernald, *Gray's New Manual*, p. 552. 1908, as subgenus.

Sumac DC., *Prodr.* 2: 67. 1825, as sect. in part.

Deciduous woody vines or small shrubs with comparatively slender branches and tendency to proliferate extensive rhizomes. Flowers in small, axillary thyrses; stamens with short subulate filaments and elongate, included anthers; fruits usually pendent. Leaves palmately trifoliolate or pinnately penta- or septi-foliolate, alternate, with phyllotaxy 3/8. North America from Canada to western Guate-

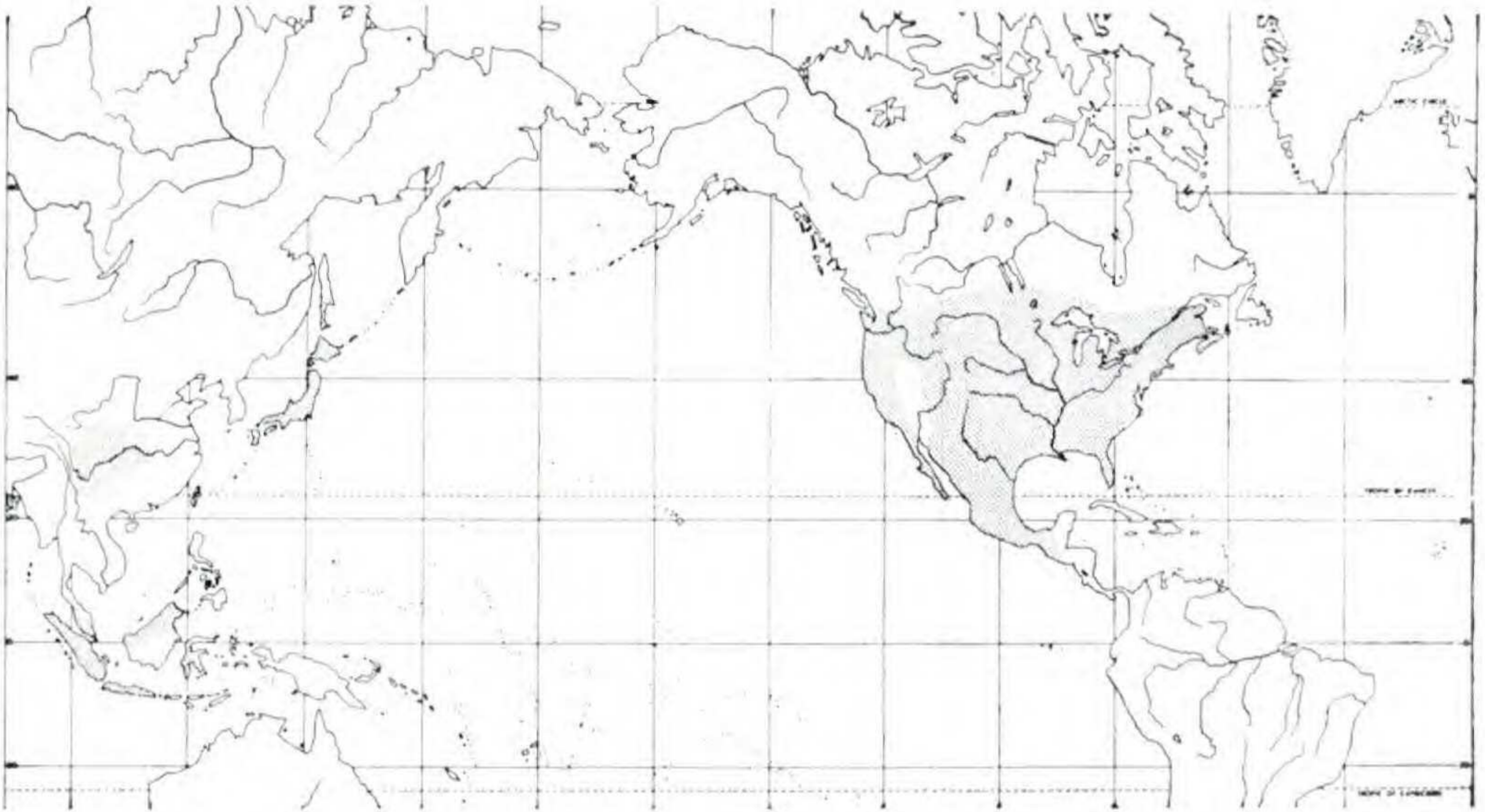


Fig. 27. Distribution of the genus *Toxicodendron* sect *Toxicodendron*.

mala; Asia: Japan, China, Taiwan, Malaysia, Indonesia, and U.S.S.R.: Sakhalin and Kurile Islands. Fig. 27.

2. *Toxicodendron nodosum* (Blume) Gillis, comb. nov. Fig. 28.

Rhus nodosa Blume, Bijdragen tot de Flora van Nederlandsch Indie, 17: 1164. 1826. Type: Java, collector unknown (L, holotype).

Rhus perakensis Scortechini ex King in J. Asiat. Soc. Bengal Pt. 2 Nat. Hist. 65: 500. 1896. Type: *Scortechini* 1668, Perak, Malaya (CAL- 98286, holotype).

Scandent shrub up to 15 meters long with occasional roots; branches slender, red-brown, often bearing prominent lenticels. Leaves imparipinnate; leaflets 5-7 (-9), elliptic-lanceolate to oblong with 14-20 pairs of veins which are \pm prominent beneath, entire, completely glabrous or with occasional hairs, with long acuminate tips, rounded or truncate to obtuse or attenuate at the base, short petiolulate (petiolules less than 1 cm) or sessile except for the terminal leaflet; blade 5-15 cm long, 2.5-5.5 cm

Fig. 28. *Toxicodendron nodosum*. Type of *Rhus nodosa* Blume, Java.



HERBARIUM

PHOTOGRAPHIC SERVICE
 Michigan State University
 East Lansing, Michigan
 Negative Number 662373-1

Herb. Lugd. Batav.

TYPE!

Rhus modata Al.

COMMUNITY

N7899-150

Rhus modata Al.

→ 1200
 Hadong long way
 Rhus sp.



201530 Jara.

broad, generally longer in Bornean than Mayalan or Javan populations; petiole 15-30 cm long, glabrous; petiolule 2-4 mm long, glabrous; terminal petiolule 7-15 mm long, glabrous or exceedingly finely puberulent. Inflorescence a lateral or subterminal thyrse, 15-40 cm long; flowers abundant, tightly clustered on short, minutely bracteolulate, glabrate or puberulent pedicels; bracts oblanceolate, 0.2-0.3 mm long and broad, glabrate, deciduous; calyx 0.5-1.7 mm long, 0.5-1.0 mm broad, narrower in female than in male, glabrous; fertile anthers 1.2 mm long, broadly ovate; filaments linear-subulate, 0.8-1.5 mm long, in female sterile anthers 0.4 mm long, subulate, filament 1.5 mm, pubescent; pollen 20.8-28.5 μ long, 17.5-22.0 μ broad. Fruiting inflorescence puberulent or glabrous, pendent; fruit obliquely globose-reniform, 5.0-8.0 mm across, 3.0-6.0 mm broad, glabrous with mesocarp striate in white waxy matrix; exocarp dun-colored. Buds stalked, naked, mucronate, brown, covered with brown pubescence.

Distribution: Indonesia and Malaysia. At elevations from sea level to 1500 meters growing in shallow soil on limestone, apparently rare. Fl. Aug.-Dec.; fr. Oct.-Mar. Local name: "jahor" (Burkhill, 1935). Fig. 27.

Specimens examined: **Indonesia:** CELEBES; Makassar, collector unknown (BO). JAVA: Batavia Tijanten, *Backer* 25958 (BO); Nirmala, *Backer* 10622 (BO); G. Batoe, *Backer* 25802 (BO); Josoredja en Dara, Pekalongan, *Backer* 16275 (BO); Tjidadap, Bangas, 1000 meters, *Bakhuizen van den Brink* 875 (L); Preanger Regentschappen, Geger Bentang, *Lapün*, s.n. (BO); Preanger G. Karang, *Bakhuizen van den Brink* 833 (BO); locality and collector unknown (Type) (L); SUMATRA: Batang Baroes, *Tegsmain*, s.n. (BO); Sekintjau Belirang, 1400 m., *Rappard* 79 (BO).

Malaysia: PERAK: Larut, *King's collector* 6807 (BM, CAL, L); locality unknown, *Scortechini* 1668 (CAL); Tupai, *Wray* 3095 (CAL, SING); Thaipeng, *Wray* 3054 (SING). SARAWAK: Bau, *Haviland* 1965 (CAL); Bau, *Purseglove* 4440 (A, L, SING); Kuching, *Haviland & Hose* 3366 E (BO, L); Mt. Buan, *Haviland* 1962 (SING); Tambusan, HM 12310 (SING); Mt. Dulit near Long Kapa, 400 m., *Richards* 1468 (A, L); Stetapok F. R., 4 miles south of Kuching, limestone hills, *Anderson* S.25131 (MSC).

Toxicodendron nodosum is described (as *Rhus perakensis*) by Corner (1940) as being like one of the "poison ivies of North America." Like poison-ivy, it is a vine or climber; unlike poison-ivy, it has five to seven leaflets. Its inflorescences are longer than those of poison-ivy. As in the case of other members of this complex, *T. nodosum* has been referred to the genus *Rhus* by various authors. It shares with all other *Toxicodendrons*, however, smaller pollen than that of *Rhus* species, toxic effluvium, absence of glandular hairs, buff to tan exocarps, striate mesocarps, and chiefly axillary inflorescences. Some flower clusters occupy a sub-terminal position, but in all specimens that have been examined, there is a vegetative shoot continuing beyond the inflorescences, continuing terminal growth. Because of its scandent habit, anther size, shape, and position, *T. nodosum* has been placed in section *Toxicodendron* of the genus.

Collections made in former Dutch possessions have been called *Rhus nodosa*, while those collected in regions of the British Commonwealth more likely have been named *R. perakensis*. On the basis of herbarium material examined, it is not possible to distinguish between these two taxa.

This is a rarely collected plant, its rarity probably due more to inaccessibility than to actual lack of abundance. It is found in the mountainous areas of northern Perak in the Malay Peninsula, on limestone ridges near Bau and Kuching in the state of Sarawak in Borneo, and scattered throughout Sumatra, Java, and Celebes. Presumably it grows in Indonesian Borneo, but no collections from this region are known. It has been collected only six times since 1920. Label data on herbarium specimens are generally scanty, so that it would not be possible to return to the exact site of a previous collection.

Recent collections were desired to study fresh seeds inasmuch as some important diagnostic characters are found in the fruits of this genus. The *Purseglove* 4440 specimen indicates that the seeds were "red, drying buff," yet the fresh seeds suggest that the exocarps could hardly ever have been red. They certainly are buff, and show the plant to be a *Toxicodendron*. (Acknowledgement is made of Mr.

J. A. R. Anderson, Conservator of Forests in Kuching, who kindly sent fresh material of this species for study.)

Like many other *Toxicodendron* species, *T. nodosum* seems to occur chiefly in limey areas. It is generally found in shallow, rocky soils in open jungle, climbing trees up to 15 meters. Its ecology is incompletely known due to the paucity of collections and collection data, particularly in recent years. Backer and Bakhuizen Van Den Brink (1965) suggest that the plant in Java occupies the wetter sites (up to only three dry months per year, where rainfall greater than 100 mm per month = "wet") at altitudes of 900-1200 m. They, in fact, label it as an "everwet climate" indicator. Flowering season for the plant seems to vary from July to December, possibly just prior to onset of monsoon seasons. It appears not to be a heavy seeder.

Backer and Van Den Brink (*ibid.*) further describe the petiolules as being winged. From all specimens I have examined, I would describe this condition as the attenuate nature of the terminal leaflet base, rather than a true "winged" nature of the rachis as in *Rhus javanica* and *R. copallina*. In the latter, the winged condition extends from the terminal leaflet to the base of the lowest leaflet; in *Toxicodendron nodosum*, it is merely restricted to the base of the terminal leaflet.

From a plant grown from seed in the laboratory, one can see that the young seedling has simple leaves for an appreciable period of time before any compound leaves appear, well after the stem has begun to lignify. The first compound leaves appeared on one such laboratory-grown plant only after 11 simple leaves were produced. Throughout this time, the cotyledons remained on the plant and remained green.

3. ***Toxicodendron diversilobum*** (T. & G.) Greene, *Leafl. Bot. Observ. Crit.* 1: 119. 1905. Figs, 29, 30.

Rhus diversiloba T. & G., *Fl. N. Am.* 1: 218. 1838. *Rhus toxicodendron* subsp. *diversiloba* (T. & G.) Engler in DC.,

Fig. 29. *Toxicodendron diversilobum*. Type of *Rhus lobata* Hook., Douglas.

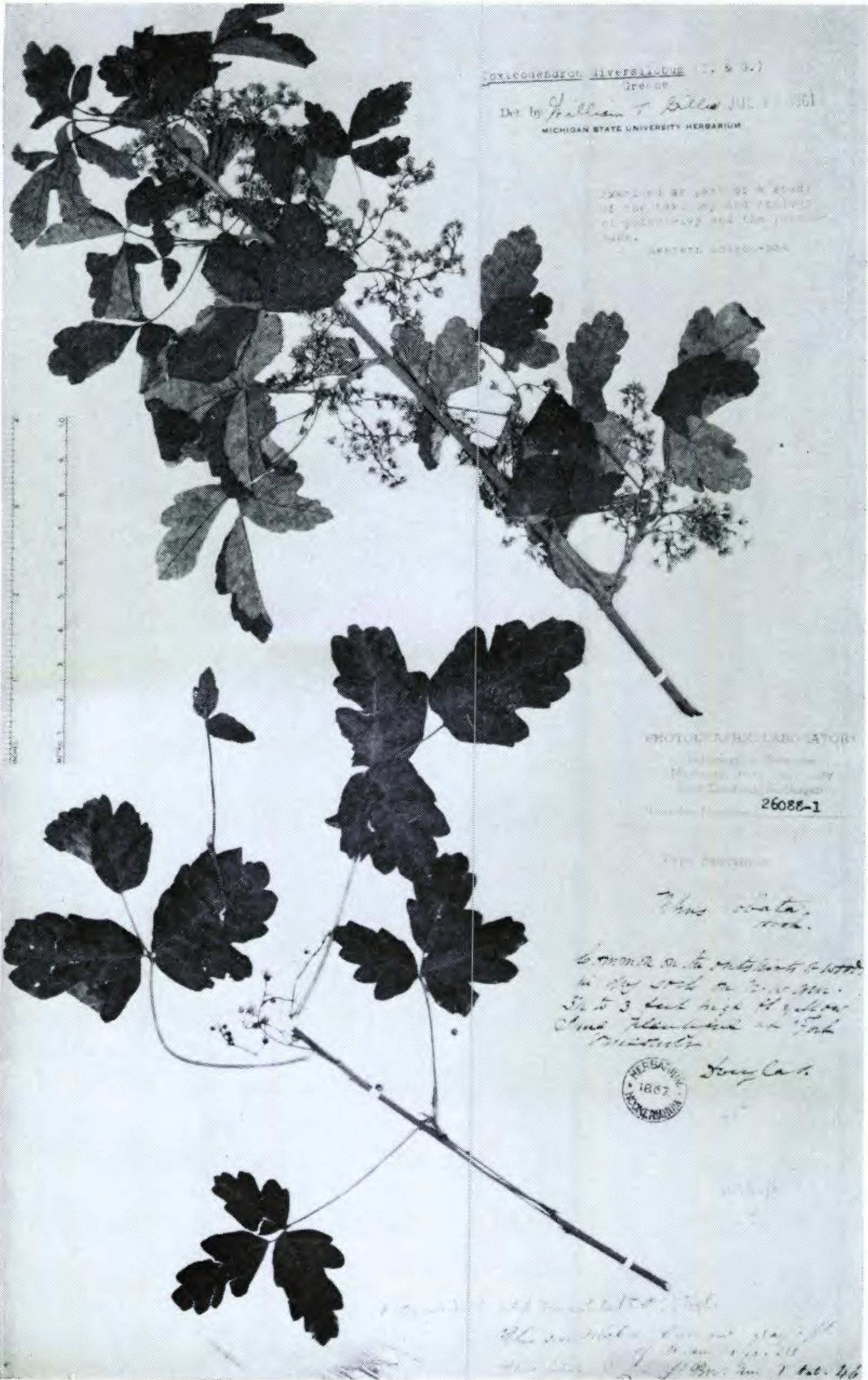




Fig. 30. *Toxicodendron diversilobum*. Type of *T. oxycarpum* Greene, J. Ball.

Monog. Phaner. 4: 395. 1883. *Rhus toxicodendron* var. *diversiloba* (T. & G.) Brandegee, Zoe 2: 345. 1892. *Toxicodendron radicans* subsp. *diversiloba* (T. & G.) Thorne, Aliso 6: 28. 1967 (corrected to *T. radicans* subsp. *diversilobum*, ibid. p. 86.). Type: Nuttall, s.n. "California," (NY, holotype).

Rhus lobata Hook., Fl. Bor. Am., p. 127. 1830, non Poiret, Ency. Meth. Suppl. 5: 264. 1804. *Rhus varielobata* Steudel, Nom. Bot. 2: 452. 1841 (nomen nudum). Type: Douglas, s.n. British Columbia, Fort Vancouver, June, common on the outskirts of woods in dry soils (K, holotype).

Toxicodendron comarophyllum Greene, Leaf. Bot. Observ. Crit. 1: 120. 1905. Type: Palmer 45, California, San Diego Co., Tighe's near San Diego, 1875. (US-19802, holotype; F-302931, isotype; MO-1773737, possible isotype).

Toxicodendron oxycarpum Greene, Leaf. Bot. Observ. Crit. 1: 121. 1905. Type: J. Ball, s.n., California, Santa Cruz Co., Redwood Forest, Santa Cruz, 10 July 1894. (US-292229, holotype).

Toxicodendron isophyllum Greene, Leaf. Bot. Observ. Crit. 1: 121. 1905. Type: John B. Leiburg 3117, California, Riverside Co., river banks near San Jacinto, 600 meters elevation, 9 March 1893. (US-342019, holotype).

Toxicodendron dryophilum Greene, Leaf. Bot. Observ. Crit. 1: 121. 1905. *Rhus diversiloba* f. *radicans* McNair, Publ. Field Mus. Nat. Hist. 225. Vol. 4: 61. 1925. Type: Mrs. R. M. Austin, s.n., Butte Co., climbing oak trees in Little Chico Canyon, May 1896. (ND-G-22098, holotype; MO-1773736, US-28527, isotypes).

Toxicodendron vaccarum Greene, Leaf. Bot. Observ. Crit. 1: 122. 1905. Type: M. S. Baker and Frank Nutting, s.n., 23 May 1894. As *T. vacicarum* McNair, in syn., Publ., Field Mus. Nat. Hist. 225. Vol. 4: 59. 1925. (ND-G, holotype; MO-1114683, photograph of type).

Rhus diversiloba f. *quinquifolia* McNair, Bull. Torrey Bot. Club 63: 476. 1936. Type: A. Wood s.n., 1866 (NY, lectotype).

Vine, shrub, or rarely tree, with slender, glabrous to puberulent branches, usually with brown aerial roots; rhi-

zome creeping; leaves crowded on branches. Bark gray-brown to red-brown on new wood, becoming gray on older wood; leaf scars V- or U-shaped with 6-10 bundle scars; lenticels usually conspicuous. Buds stalked, naked, mucronate, brown, covered with a brown woolly pubescence. Autumn coloration scarlet to red-violet. Leaflets 3, occasionally 5 (-11), ovate, oblong, or suborbicular, entire, undulate, crenate-dentate or bluntly lobed; apex obtuse or rounded; base rounded, truncate, or subcuneate; lateral leaflets mostly inequilateral, 1.0-7.0 cm long, 1.0-6.0 cm broad; short petiolulate or subsessile; terminal leaflet 0.8-13.0 cm long, 0.3-8.0 cm wide, petiole 1.0-10.0 cm long; terminal petiolule 0.1-2.6 cm long; leaflets attached in palmate fashion when trifoliolate, pinnate when more than 3 leaflets; glabrous above, occasionally with a line of minute, curly hairs along the midrib, subpilose below or with trichomes restricted to appressed hairs on major veins. Leaves often mottled when dry. Inflorescences lateral paniculate thyrses up to 1 dm long; pedicels 2.0-8.0 mm long; bracts oblanceolate, 1 mm long, 0.3 mm wide, glabrate, ciliate, deciduous; sepals 5, yellow-green, deltoid-ovate, 1 mm long, 0.5 mm broad; filaments linear-subulate, 1.0-1.8 mm long. Drupe cream-colored, globose-reniform, sometimes obliquely deltoid, sometimes laterally flattened, 4.5-7.5 mm across, 1.5-5.5 mm broad with densely setulose exocarp becoming chartaceous upon ripening and readily separating from the mesocarp; mesocarp black striate in white, waxy matrix; endocarp dun-colored, bony.

Distribution: Northern Baja California, Western California, Oregon, and Washington, Vancouver Island, British Columbia. Common name: Western poison-oak. Fig. 31.

REPRESENTATIVE SPECIMENS

UNITED STATES. California. ALAMEDA CO.: Berkeley, *Greene*, s.n. (ND-G); Oakland, *Drew*, s.n. (F). AMADOR CO.: locality not cited, *Hansen*, s.n. (MO, ND-G, US); Ione, *Eastwood* 10153 (A). BUTTE CO.: Little Chico Creek, *Austin*, s.n. ND-G, MO, US); Big Chico Creek canyon, *Heller* 11211 (A, F, GH, MO, MIN, NY, OSC, ND-G, US); east of Chico, Stilson Canyon, *Heller* 12321 (A, F, MO, NY, OSC, US, WIS); Oroville, *Heller* 10787 (A, F, GH, MO, NY, US). Chico, *Palmer* 2060 (NY).

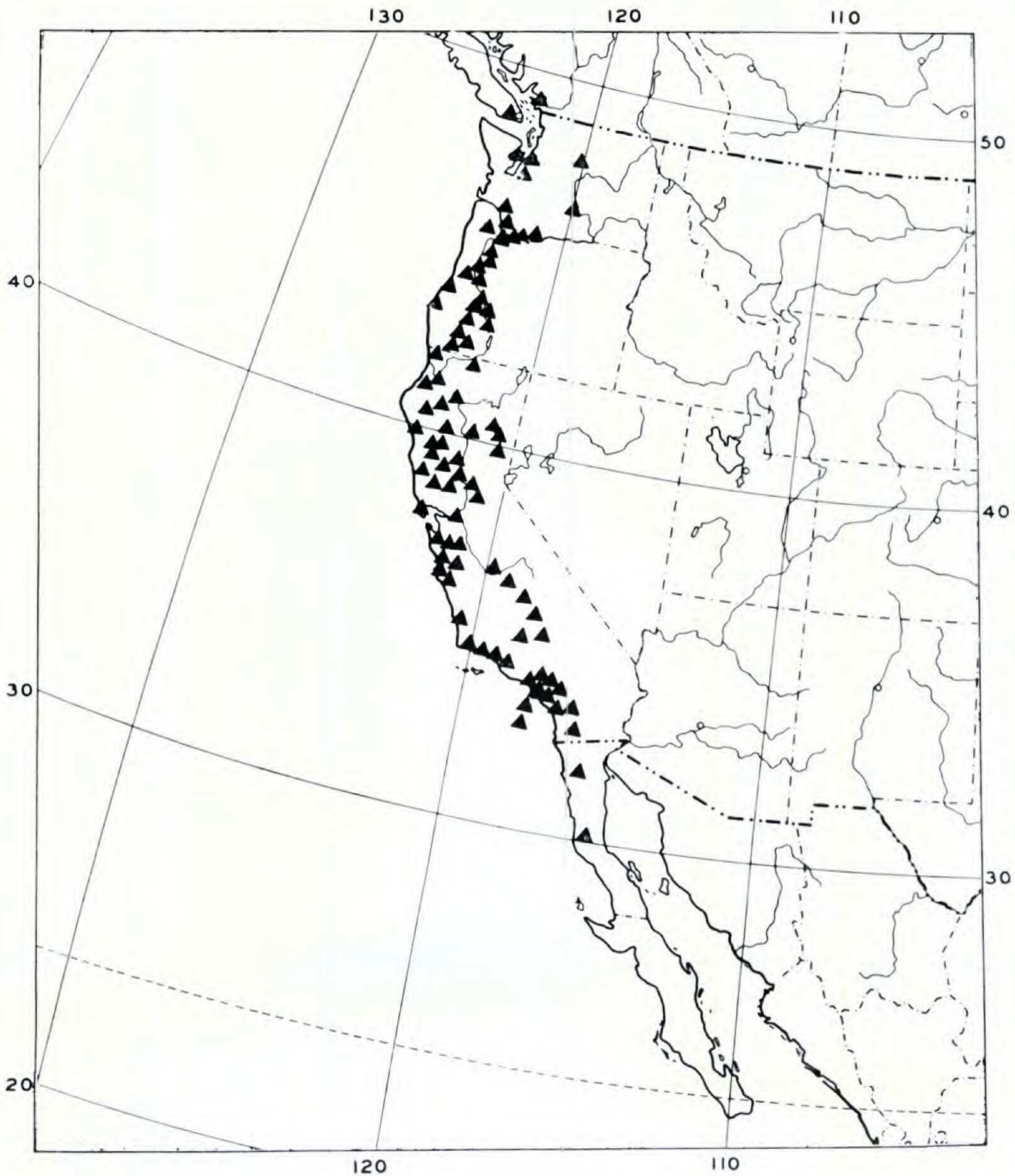


Fig. 31. Distribution of *Toxicodendron diversilobum*.

CALAVERAS CO.: Angels Creek, *Eastwood* 11622 (A); Calaveras River, *Gibbes*, *s.n.* (NY). COLUSA CO.: mountain slopes in chapparral, *Gillis* 4849 (MSC); Colusa, *Eastwood* 10236 (A). CONTRA COSTA CO.: Mt. Diablo, *Brewer* 1068 (GH); Clayton, *Brewer* 1068 (US); DEL-NORTE CO.: Gasquet, *Parks & Tracy* 11188 (GH, US). EL DORADO CO.: east slope of densely vegetated stream bank, 4 miles NE of Aulrun, *Holloway* 47 (ARIZ). GLENN CO.: Stonyford along Stonyford Creek, *Weston*, *s.n.* (MSC); Elk Creek, near Stonyford, *Gillis* 4865 (MSC). HUMBOLDT CO.: Humboldt State Park, *Weston*, *s.n.* (MSC); Willow Creek, *Tracy* 18404 (MO, US); Blacksburg, *Tracy* 15301 (GH, NY). JACKSON CO.: Walker Creek, *Applegate* 2339 (US). KERN CO.: Fort

Tejon, *DeVasey* 19 (GH, NY, US); Havilah, *Grinnell* 362 (US); Caliente Canyon, *Zigmond* 138 (F). LAKE CO.: 1.1 miles east of Middletown on road to Lower Lake, serpentine soil, *Morley* 585 (CAL, MSC); Mt. Konocti, *Blankinship*, s.n. (MO); Middle Creek, 6 miles south of Elk Mountain, between Lake Pilsbury and Lower Lake, *Everett & Balls* 20355 (NY, RM). LOS ANGELES CO.: Santa Catalina Island, *Millspaugh* 4734 (F), Avalon Canyon, *Smith* 5069 (F, US); Hamilton Canyon, *Fosberg* 54301 (A, F, MO, NY, US); Swain's Canyon, *Nuttall* 622 (F, US); Claremont, *Whited* 885 (ND); Topango Canyon, Santa Monica Mountains, *Epling & Ellison*, s.n. (OSC); Pasadena, *Jones* 3206 (A, MSC, MO, NY, US); Mandeville Canyon, Santa Monica Mts., *Epling*, s.n. (A, MO, OSC, US); Temescal Canyon, Pacific Palisades, *Hastings*, s.n. (NY); Bouquet Canyon, San Gabriel Mts., *Templeton* 7702 (NY); Eagle Rock Valley, *Smith* 4904 (F, US). MADERO CO.: North Fork, *Griffiths* 4531 (NO, US). MARIN CO.: Taylor State Park, *Gillis* 4832 (MSC); Reyes Point, *Gillis* 4795 (MSC); 6 miles SE of Lagunitas, west of Fairfax, *Gillis* 4797 (MSC); Rose Valley, *Eastwood*, s.n. (A); Tamalpais, *Kountze* 23146 (NY); Mill Valley, *Eastwood* 6885 (A, NY). MARIPOSA CO.: Mariposa, *Congdon*, s.n. (MIN); Sherlocks, *Congdon*, s.n. (MIN). MENDOCINO CO.: Mendocino, *Brown* 750 (F, MIN, MO, NY, US); Glen Blair, *Eastwood & Howell* 2665 (A); Elk Creek, *Leiberg* 4190 (US). MONTEREY CO.: Salinas Valley, *Vasey* 86 (F, US); Tassajara Hot Springs, *Elmer* 3178 (MIN, MO, US); Carmel Highlands, *C. E.* 8296 (MIN); Big Sur, *Eastwood* 14026 (A); Pacific Grove, *Demaree* 7257a (NY). NAPA CO.: Calistoga, *Greene*, s.n. (ND-G); Napa Valley, *Torrey* 74 (NY); Mt. St. Helena, *Eastwood* 6867 (A). NEVADA CO. 120° 39' W. Long., 39° 20' N. Lat., *collector unknown* (ND-G). ORANGE CO.: Santa Ana Mts., *Rice*, s.n. (MSC). RIVERSIDE CO.: San Jacinto, *Leiberg* 3117 (US). SACRAMENTO CO.: Sacramento, Pocket Road, *Copeland*, s.n. (MSC); Folsom, *Copeland* 1606 (GH). SAN BENITO CO.: Tres Pinos, *Eastwood* 6888 (A, US); The Pinnacles, *Eastwood* 6729 (A). SAN BERNADINO CO.: San Bernadino, *Wright* 207 (GH). SAN DIEGO CO.: San Diego, *Palmer* 42 (G, GH, MO, US); Cuyamaca Peak, *Hitchcock*, s.n. (US); Alpine, *Mearns* 4019 (NY, US); Descanso, *Eastwood* 9075 (GH). SAN FRANCISCO CO.: San Francisco, Lincoln Park, *Eastwood*, s.n. (US). SAN LUIS OBISPO CO.: Morro Bay, *Eastwood* 14254 (A); Avila, *Eastwood* 13788 (A); Cambria, *Eastwood* 13616 (A). SAN MATEO CO.: Higgins Creek Road, east of Half Moon Bay, *Mason*, s.n. (MSC); Corte Madera Creek, *Wiggins*, s.n. (MSC); San Carlos River, *Eastwood* 12414 (A). SANTA BARBARA CO.: *Elmer* 3940 (F, GH, GH, MIN, MO, US, NY); Carpinteria, *Dickover*, s.n. (US); Santa Cruz Island, *Eastwood* 6403 (A); vicinity of Smuggler's Cove, Santa Cruz Island, *Abrams and Wiggins* 204 (A, GH); Montecito Valley, *Bingham* 142 (KSC). SANTA CLARA CO.: Stanford University, *McMurphy* 56 (MIN, MO, ND-G, NY, OSC, GH, US); Gilroy Hot Springs, *Eastwood and Howell*

4304 (A); Clarita Vineyard, Black Mts., *Elmer*, s.n. (MIN, MO, NY, OSC, US); Los Gatos, *Heller* 7327 (A, F, MO, NY, US, GH); Beels Station, *Goldman* 1290 (US); New Almaden, *Torrey* 74 (GH, NY); Saratoga Springs, *Leeds*, s.n. (F); San Jose, *Eastwood* 11238 (A); Mt. Hamilton, *Eastwood* 12420 (A); Mayfield, *Wiggins* 9221 (A); west slopes of Sierra Nevada, east of Palo Alto, *Wiggins*, s.n. (MSC); bank of San Francisquito Creek, Palo Alto, *Wiggins*, s.n. (MSC). SANTA CRUZ CO.: Santa Cruz, *Ball*, s.n. (US). SHASTA CO.: SE slope of Long Valley Mt., *Griffin* 1143 (MSC); gulch north of Pit River, *Griffin* 1156 (MSC); Cow Creek Mts., *Baker and Nutting* (ND-G). SIERRA CO.: locality unknown, *Lemmon* 1032 (GH). SISKIYOU CO.: Hornbrook, Klamath River, *Abrams* 9900 (MO, RM); Shasta Pine, *Butler* 1034 (E); Shasta Springs, *Eastwood* 6694 (A). SONOMA CO.: Petaluma, *Congdon*, s.n. (MIN); Geyserville, *Torrey*, s.n. (NY). SUTTER CO.: Yuba City, Marysville Buttes, *Ferris* 651 (MIN, NY). TRINITY CO.: Tangle Blue and Scott Mt. creeks, *Howell* 12826 (A). TULARE CO.: Eshom Creek, *Clemens* s.n. (RM); Kaweah River, *Woolsey*, s.n. (GH). VENTURA CO.: Foster Park, *Eastwood* 5010 (A); Sulphur Mt., *Abrams & McGregor* 46 (A, ARIZ, GH, NY, OSC, US). YOLO CO.: chamise chapparral along Buckeye Creek, near Dunningan, *Gillis* 4836 (MSC); Putah Canyon, *Dickson* 24 (OSC); Wintere, *Eastwood* 14202 (A). Oregon. BENTON CO.: Corvallis, *Steward* 6863 (NY, OSC); McFadden Marsh, north of Bellfountain, *Steward* 7011 (NY, OSC); MacDonald Forest, *Ishimoto* 3077 (OSC). CLACKAMUS CO.: Willamette Slough, *Howell & Howell*, s.n. (NO); Willamette Hills, *Mulford*, s.n. (GH, MO, NY); COOS CO.: Coos Bay, *House* 4746 (US). DOUGLAS CO.: Umqua River, *Engelmann & Sargent*, s.n. (A, MO); 5 miles south of Roseburg, *Gillis* 4163 (MSC); between Tiller and Drew in foothills of Cascades, 1200 feet, *Gillis* 4169 (MSC); Peel, *Applegate* 2700 (US); Oakland, *Hurst* 44 (A); near Tyee Mt., collector unknown (OSC). GILLIAM CO.: Blalock along Columbia gorge, *Cooke* 12116 (WTU). GRANT CO.: Blue Mts., *Hooker*, s.n. (GH). HOOD RIVER CO.: between Hood River and Mosier, *Suksdorf* 2102 (A); Mt. Hood, *Savage, Cameron, & Lenocker*, s.n. (MO); Hood River, floodplain of Hood River, *Gillis* 4246 (MSC); 2 miles south of Hood River, *Gillis* 5231 (MSC). JOSEPHINE CO.: Grants Pass, *Jack*, s.n. (A); Kerby, *Thompson* 4053 (MO, US). LANE CO.: Cheshire along highway 36, *Gillis* 4156 (MSC); Mapleton, *Gillis* 4159 (MSC). MARION CO.: Jefferson, south slope of Knox Butte, *Gillis* 4151 (MSC); Salem, near Morningside Grade School, *Matthews*, s.n. (OSC). MULTNOMAH CO.: Rocky Butte, collector unknown (F); Bridal Veil, *Smith* 3117, (F, NY); Portland, *Walpole* 44 (US). WASCO CO.: the Dalles, *Gillis* 4222 (MSC). WASHINGTON CO.: Scroggins Creek, *Thompson*, s.n. (MO). UNCERTAIN LOCALITY: *Hall* 82 (A, GH, F, MIN, MO). Washington. CLARK CO.: ½ mile east and ½ mile north of Crawford, *Gillis* 5274 (MSC). COWLITZ CO.: Kalama, *Gillis* 4263 (MSC); Kelso,

Palmer 37961 (A, MO). KING CO.: Seattle, Alki Point, *Gillis* 4251 (MSC); Mercer Island, *collector unknown* (F). KITSAP CO.: Orchard Point, *Piper*, *s.n.* (A). KLUCKITAT CO.: terrace of Klickitat River near confluence with Columbia, *Gillis* 5238 (MSC). PIERCE CO.: between Steilacoom and West Tacoma, *Gillis* 4258 (MSC).

CANADA: British Columbia. Fort Vancouver, *Douglas*, *s.n.* (K); Vancouver Island, *Anderson*, *s.n.* (GH).

MEXICO: Baja California Norte: Ensenada, *Wiggins & Gillespie* 3997 (A, GH, MO, NY); El Rosario, *Brandege*, *s.n.* (GH).

The first binomial of *Toxicodendron diversilobum* was *Rhus lobata* Hooker, but this name was a later homonym of Poiret's *Rhus lobata*, a non-toxic sumac from the Canary Islands. Therefore, in searching for the next epithet at the species level, one finds *Rhus diversiloba* to be satisfactory. When the name is transferred to *Toxicodendron*, the epithet *lobatum* appears to have priority, but Arts. 64 and 72 of the Code (Lanjouw et al., 1966) preclude the use of illegitimate epithets, even in combination with another generic name. The earliest, available, legitimate epithet of specific rank, then, is *diversiloba*.¹⁴ Under its name *Rhus diversiloba*, the plant is occasionally found in print as *R. diversifolia*, a misprint probably first published by Engler in DeCandolle (1883, p. 305). Whereas the type specimen of *Rhus lobata* Hook. indicates that the species is "plentiful" on Vancouver Island, the species is rare to the point of being almost unknown in British Columbia today.

Greene did not specify where his type for *Toxicodendron comarophyllum* was located, but most of the type specimens for poison-ivy and poison-oak taxa he described are at the Smithsonian Institution; therefore, the specimen cited as the type is the one located there. A probable isotype at the Missouri Botanical Garden has a different collection num-

¹⁴Initially a combination of *Toxicodendron* with *lobatum* was chosen in connection with this study and all herbarium material examined at that time was so annotated. I am grateful to Dr. Robert Thorne for pointing out this error before this manuscript went to press. Material thus annotated should be considered to be *Toxicodendron diversilobum* (T. & G.) Greene until such time as the corrected annotations shall be made.

ber, but presumably comes from the same gathering; its label data are the same. Jepson (1936) clarified the collection site by indicating that it was "at the foot of Ballena grade, San Diego."

In regard to *Toxicodendron oxycarpum*, Greene places emphasis on the wrinkled nature of the fruits, but this is a common phenomenon of herbarium specimens bearing unripe fruits; when they have not yet reached full growth, the exocarps wrinkle in the drying process. Greene's notation that the branching of the inflorescence is sparse certainly calls attention to a chance character of this single specimen and refers to a character of no genetic significance. Likewise, the importance Greene attaches to the pendulous nature of the fruits is probably not significant.

Greene's choice of specimens for his *Toxicodendron isophyllum* leaves much to be desired. His description and the type specimen do not agree in most characteristics. The leaflets are not "all three sessile"; there is no epicarp present from which to determine that it is "muricate-punctate" and "pubescent." Perhaps it was available when Green described the species.

As with other types, Greene did not indicate the location of the type of *Toxicodendron dryophilum*. Representatives of the type collection are at Notre Dame (Herbarium Greeneanum) and at the Smithsonian. He wrote "type" on the specimen at ND-G even though part of the description ("reported to sustain itself to the height of 20 feet on oak trees") comes from the label data present only on the specimen at US. I have chosen the Notre Dame specimen as the lectotype. Greene's description "never panicled fruits seldom more than 2 or 3 to each raceme" is not borne out by the type collection. The "wrinkling of the epicarp," which seems to have been firmly implanted in Greene's mind as significant in this and several other species of the complex, is typical for dried immature fruits.

The type collection of *Toxicodendron vaccarum* is indicated as having come from Shasta County, California, from the Cow Creek Mountains. In order to locate the site of collection more precisely, I have contacted several persons

in California, especially in Shasta County, to ascertain the precise location of these mountains. No one has been able to give me any information about any mountains of that name in Shasta County. Such mountains are known in Mendocino and Lake Counties, but not in Shasta County.

McNair's name *Rhus diversiloba* f. *radicans* poses some perplexing problems. He indicated that it was synonymous with *Toxicodendron dryophilum* Greene; therefore it should have the same type as *T. dryophilum*, but he proceeded to write on the specimen (*Millspaugh* 4734) at the Field Museum "forma *radicans* McNair type." Although he indicated no type in his publication, he apparently intended the *Millspaugh* specimen to be a representative one. He was attempting to recognize nomenclaturally a form of western poison-oak which had the climbing habit, stating that "taxonomic recognition as a form may be desirable" (McNair, 1925). The ability to climb appears to be general in this species, so that the climbing forms are not genetically different from suffrutescent ones and therefore deserve no nomenclatural recognition.

McNair later (1936) gave a form name to a five-leaflet specimen of Western poison-oak. A type specimen again was not cited. Of the seven specimens which he lists as having the five-leaflet trait, I have chosen the first-mentioned as lectotype: *Wood*, s.n. 1866. This form also deserves no segregate name since there is variability from branch to branch even on the same shrub or vine. Western poison-oak, even more than its eastern counterparts, may frequently have additional leaflets, the author having seen up to eleven (*Gillis* 4874, Glenn Co., California, MSC-165725). *Barkley* (1936) has also described a five-leaflet poison-ivy, but did not give it a name. *Vines* (1943) did assign a name to a five-leaflet form (*Rhus toxicodendron* var. *multifolia*) which he later abandoned (see discussion under *T. radicans* subsp. *pubens*).

Western poison-oak was not among the plants mentioned by the early explorers of the American West. Although the Spanish padres and Conquistadores described the wild life they encountered in California in the fifteen and sixteen

hundreds, poison-oak is not among the species discussed. It is difficult to imagine that this plant could have been as abundant as it is now, and yet escape detection, particularly in view of its toxic properties. A possible conclusion is that the plant was less common several centuries ago. Because *Toxicodendron diversilobum* is a plant which increases in abundance with disturbance, it is likely that it has become more abundant with the activities of man in clearing the countryside, especially changing fire frequency. Its distribution in Baja California, where men's activities have been relatively small, is still sparse, although in that region low rainfall also plays a significant role in its scarcity.

The distribution of the plant is throughout much of California west of the Sierras and the desert. In Oregon and Washington, it is channeled between the Coast Ranges and the Cascades. It is known from only one region on the east flank of the Cascades where James R. Griffin collected it for me in Shasta County, California, on the southeast slope of Long Valley Mountain and on slopes above the Pit River. Local lore in southern Oregon has it that neither poison-oak nor rattlesnakes occur east of the Rogue River. The highest elevation in the Cascades from which *Toxicodendron diversilobum* has been collected is in Douglas Co., Oregon, between Tiller and Drew, at 1200 feet.

Like its counterparts elsewhere in the United States, *Toxicodendron diversilobum* is highly variable, especially in leaflet shape. Its leaflets may be as deeply lobed as are the leaflets of male clones of *T. toxicarium*, thus resembling the leaves of *Quercus alba*, but more often they resemble the leaves of one of the western oaks, such as *Q. agrifolia*. At times, they are even without any evident lobes at all and may be only undulate in leaflet margin. I have been unable to correlate geographical or regional factors with variation in leaflet shape except that sun leaves are normally much larger than shade leaves. The fruits are among the largest of Western Hemisphere *Toxicodendron* species, with deeply furrowed striations in the mesocarp and short, abundant trichomes on the exocarp.

Toxicodendron diversilobum is far less common in Wash-

ington than farther south. In some counties, it is unquestionably scarce. On disturbed sites in the Seattle area (Alki Point, for example), it is abundant enough that municipal authorities have seen fit to erect a sign warning the populace that the hillside is covered with poison-oak, rather than clear away the menace.

In the Columbia River gorge, the ranges of *Toxicodendron rydbergii* and *T. diversilobum* overlap. Intergrades are known from Hood River to The Dalles from the washes and rills of the basaltic hills through which the river has cut; on the Washington side of the river, such intergrades are known from the confluence of the Klickitat and the Columbia east to the vicinity of the John Day Dam. The zones of overlap in range and apparent hybridization between these two species seems to cover about 23 miles along the Oregon shore and about 43 miles along the Washington shore of the Columbia. It was from this region that the type specimens of *T. coriaceum* and *T. lobadioides* came, presumably from the same population (one flowering and one fruiting). In naming these species, Greene recognized that they were different from other named taxa, but did not realize that they might be hybrids, which they probably are (see discussion under section on Hybrids, Crosses, and Intergrades).

Habitats for *Toxicodendron diversilobum* are nearly as catholic as those of any other taxon in this complex. Jepson (1936) described its range of habitats in detail:

"In San Diego County it is associated with characteristic woody species of cismontane Southern California, all of which are wholly different from the associated species in various northern regions, as the Sierra Nevada foothills or Vaca Mountains, these in each case being in the main different from each other yet again from the associated species in the case of the Redwood belt. It has a wider geographic range than any California shrub and grows under a greater variety of soil conditions than any other; though usually preferring good soil or rich loams, it grows in blue adobe, in saline soils, in gray clays, in sandy flats, in heavy gravel deposits and in the crevices of outcropping

rock piles. It is also adapted to a greater range of rainfall and temperature than any other California shrub and is especially remarkable for its extreme shade tolerance and its tolerance of intense insolation. In common with all other woody vegetation it is absent from wide areas on the inner foothills and the plains of the Great Valley. Its preferred habitats are moist slopes in the hills; in such situations it is seldom lacking. It is also curious to add that of all native woody vegetation about the great Keswick smelter on the upper Sacramento River, the species least injured by smelter fumes was *Rhus diversiloba*; at a given station near the smelter it lived in spite of the conditions, while practically all other species were seriously destroyed or in the main destroyed."

"In number of individuals Poison Oak exceeds, in our judgment, any other shrub species in California. While the vast colonies of *Adenostoma fasciculatum* or the mesa growths of *Larrea tridentata* are impressive to the eye, *Rhus diversiloba* occurs over a much larger area than either. It is often an unobtrusive shrub — scarcely noticed in many formations and yet the individuals are really very numerous. When, for example, a Mendocino hillside wooded with *Arbutus menziesii*, *Quercus douglasii* and various shrubs is cleared, the response of Poison Oak by crown-sprouting tells the story of its abundance. It grows in the openly oak-wooded foothills, in Douglas Fir forest, in the Redwood belt, along river banks and "bottoms" and even in salt domes, often in chaparral and rarely in chemisal. In altitudinal distribution the species exists from sea-level to about 5000 feet. In the southern Sierra Nevada it grows as high as 4760 feet, and it is not found on the Yosemite Valley floor, but occurs in Hetch-Hetchy and on the slopes of Francheria Mt. above Hetch-Hetchy at about 4500 feet; in Butte Co. it is found as high as 3800 feet."

No voucher collections have been seen that substantiate some of the extremes to which Jepson alludes, but suffice it to say, *Toxicodendron diversilobum* is very abundant. It is found through central and western California and in the Willamette Valley of Oregon. It is less common, even

scarce, north of the Columbia River except for very local populations. The disturbance due to the activities of European settlers in developing California may account for the tremendous increase in abundance of this plant.

Contrary to the report of Jepson (*loc. cit.*), I have found that it is now quite abundant, at least locally, in the chamise chaparral. It grows well with *Quercus douglasii*, *Ceanothus spp.*, and *Pinus sabiniana*. It also occupies ruderal environments especially those susceptible to fire, provided some moisture is available during the long, dry summer. In Oregon it is abundant in almost any lowland or mesic woods in the Willamette Valley and at elevations up to 1250 meters in the Cascade foothills. Its common associates are *Pseudotsuga menziesii*, *Quercus garryana*, and *Berberis aquifolium*.

4. **Toxicodendron radicans** (L.) Kuntze, Rev. Gen. Pl. Pt. 1, p. 153. Pl. 26, fig. 2. 1891. *Rhus radicans* L., Sp. Pl. 1: 266. 1753.

Vine, shrub, rarely an epiphyte or tree, with slender, glabrous to puberulent branches, often with brown aerial roots; rhizome creeping. Leaflets 3 or rarely 5 (-7), ovate to elliptic, entire or irregularly serrate, dentate, lobed, or deeply incised; acute to acuminate or cuspidate at apex, glabrous to puberulent above, often with minute curled hairs on upper mid-vein near the base, glabrous to velutinous below, often with tufts of hairs in main vein axils below; petiole 2-20 cm long; lateral leaflets mostly inequilateral, 2.5-18 cm long, 1.0-10.0 cm broad, truncate to obtuse, subcuneate or attenuate; petiolules less than 0.1-1.2 cm long; leaflets often sessile; terminal leaflet blade 3.0-20.0 cm long, 1.5-13.0 cm broad, truncate, obtuse, subcuneate, or attenuate at the base, petiolules 0.3-6.0 cm long; leaflets attached in palmate fashion when leaf is trifoliolate, pinnate when leaf is composed of more than 3 leaflets. Inflorescence a lateral paniculate thyrse, up to 1 dm long; pedicels pilose, 2-5 mm long; bracts deltoid to lanceolate, 0.7-10 mm long, 0.5-3 mm broad at the widest point, glabrate, ciliate, deciduous; sepals 5, deltoid-ovate, 1 mm

long, 2-4 mm broad, glabrate; petals 5, cream to yellow-green, pinnately dark-veined, oblanceolate, glabrous, 2-5 mm long, 2-5 mm broad, reflexed in male, recurved in female, larger in male than in female, anthers lanceolate, 1-1.5 mm long, 0.5-1.1 mm broad, filaments linear-subulate, 1.3-1.8 mm long. Drupe hard, cream, yellow, or tan, globose to globose-reniform, sometimes laterally flattened, 0.25-0.7 cm across, 0.15-0.65 cm broad, with exocarp glabrous to bristly, becoming papery upon ripening, readily separating from the mesocarp, later deciduous; mesocarp black-striate in white, waxy matrix; endocarp dun-colored, bony. Bark gray-brown to red-brown on new wood, becoming gray on older wood; leaf scars V- or U-shaped with several bundle scars; lenticels usually conspicuous. Buds stalked, naked, mucronate, brown, covered with a brown wooly pubescence. Autumn coloration yellow to orange, occasionally red or bronze.

Common names: poison-ivy, markweed, poison-mercury, herb à la puce, cow-itch, Gift-sumach.

Toxicodendron radicans is one of two species of the New World (poison-ivy) and of Eastern Asia (tsuta-urushi). It is the most common and most widespread species in the Anacardiaceae. It is distributed from southern Canada to western Guatemala, the eastern third of the United States and throughout Mexico, on Bermuda, and in the western Bahamas, in Japan, western and central China and Taiwan, the Kurile Islands and Sakhalin of the U.S.S.R.

The plant is primarily scandent, but may also grow as a shrub. All taxa within this species produce aerial rootlets but will develop into large shrubs if there is nothing to climb, or if the supporting object upon which the climbing began is removed. Its closest relatives are *Toxicodendron diversilobum* and *T. rydbergii*. The plant is highly variable, much of the literature being replete with names of taxa which have few if any significant genetic differences. Because the nomenclature is very complex, it is discussed with each subspecies recognized in this study. The species consists of nine subspecies.

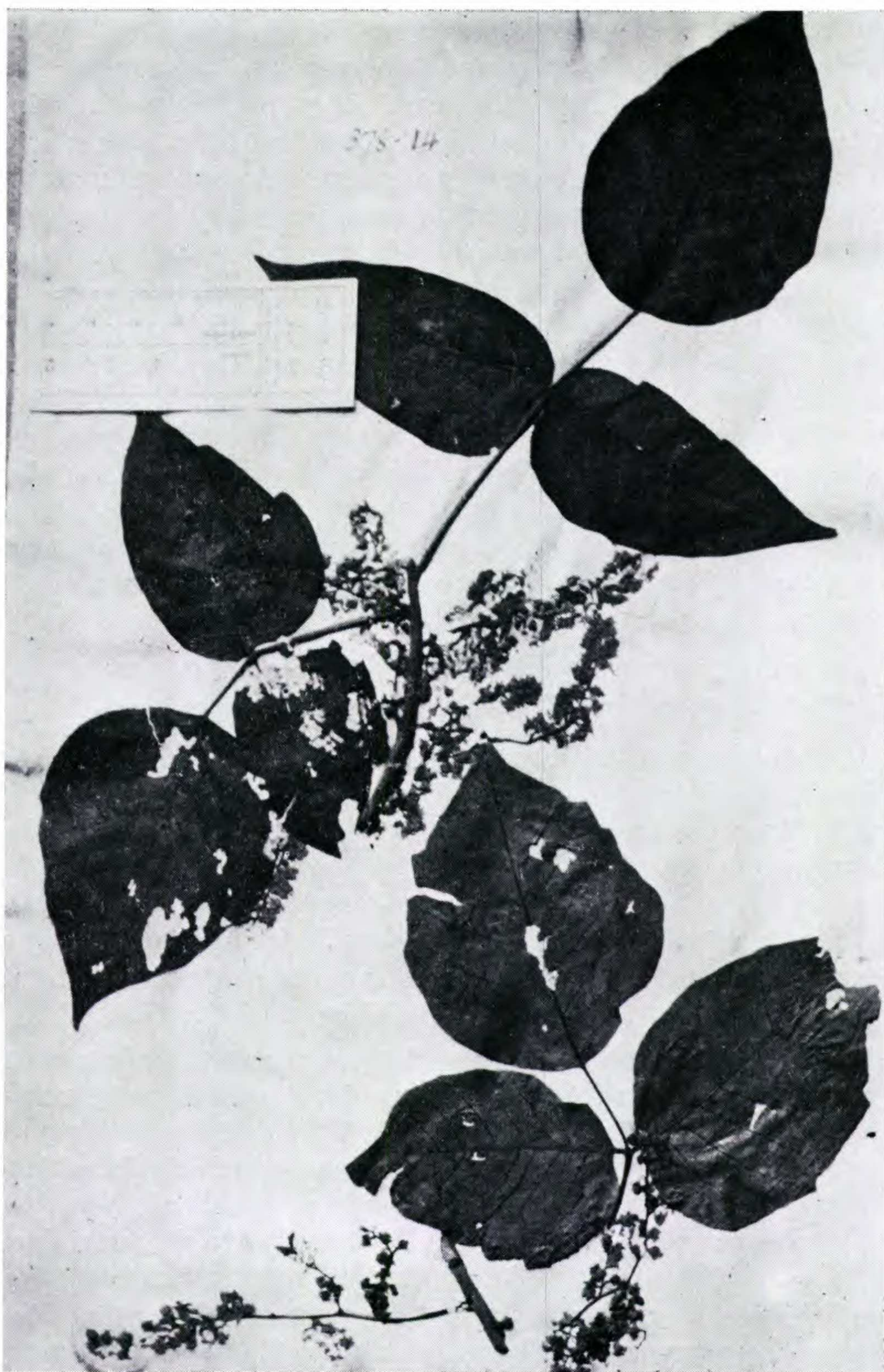


Fig. 32. *Toxicodendron radicans* ssp. *radicans*. Type of *Rhus radicans* L. The Linnaean Herbarium.



Fig. 33. *Toxicodendron radicans* subsp. *radicans*. Type of *Rhus radicans* var. *vulgaris* forma *intercurva* Fernald, Fernald, Long & Smart 5832.

4a. **Toxicodendron radicans** (L.) Kuntze subsp. **radicans**.
Figs. 32, 33.

Toxicodendron radicans (L.) Kuntze, Rev. Gen. Pl. pt. 1, p. 153. Pl. 26, fig. 2. 1891. *Rhus radicans* L., Sp. Pl. 1: 266. 1753. *Rhus radicans opacum* Aiton, Hort. Kew. 1: 367. 1789. *Rhus toxicodendron* var. *radicans* Eaton, Man. Bot., p. 400. 1789. *Rhus scandens* Salisbury, Prodr., p. 170. 1796. *Rhus radicans* var. *toxicodendron* Persoon, Syn. Pl. p. 325. 1805. *Philostemon radicans* Raf., Fl. Ludov., p. 107. 1817. *Rhus toxicodendron radicans* Torrey, Fl. North. Mid. U.S., p. 324. 1824. *Toxicodendron radicans normale* Kuntze, Rev. Gen. Pl. pt. 1, p. 153. 1891. *Rhus toxicodendron a radicans* Dippel, Handb. der Laubholz., p. 376. 1892. *Rhus toxicodendron* f. *radicans* McNair, Publ. Field Mus. Nat. Hist. 225, Vol. 4: 68. 1925. *Rhus toxicodendron* subsp. *radicans* Clausen, Mem. Cornell Univ. Agric. Exp. St. 291: 8. 1949. Type: "Habitat in Virginia, Canada." (LINN 378.14, lectotype of Brizicky, 1963; GH, MSC, photographs of type).

Toxicodendron glabrum Mller, Gard. Dict. Art. *Toxicodendron*, No. 3. 1768, non *T. glabrum* (L.) Kuntze, Rev. Gen. Pl. pt. 1, p. 153. 1891 (= *Rhus glabra* L.). *Rhus humilis* (as *humile*) Salisbury, Prodr., p. 170. 1796. *Rhus radicans lucidum* Aiton, Hort. Kew. 1: 367. 1789. Type: "Dill. Elth., loc. cit." (OXF, lectotype).

Rhus toxicodendron var. *microcarpon* Michx., Fl. Bor.-Am., p. 395. 1803. *Rhus toxicodendron microcarpum* Pursh, Fl. Am. Sept. 1: 205. 1814. *Rhus radicans* var. *microcarpon* (Michx.) DC., Prodr. 2: 69. 1825. *Rhus toxicodendron* subsp. *microcarpon* (Michx.) Engler in DC., Monog. Phaner. 4: 395. 1883. *Rhus microcarpa* Steudel, Nom. Bot. ed. 2: 694. 1841. *Toxicodendron radicans* var. *microcarpon* (Michx.) Farwell, Amer. Midl. Naturalist 12: 125. 1930. Type: "Hab. in Carolina inferiore et Georgia." (P, lectotype).

Rhus blodgettii Kearney, Bull. Torrey Bot. Club 21: 486. 1894. *Toxicodendron blodgettii* (Kearney) Greene, Leaflet Bot. Observ. Crit. 1: 126. 1905. Type: *Blodgett, s.n.*, Pine Key, near Key West, Monroe Co., Florida, (NY, lectotype of Barkley, 1937).

Rhus floridana Mearns, Proc. Biol. Soc. Wash. 15: 149. 1902. Type: *Hitchcock* 39, Hammocks, Alva, Lee County, Florida, A.S. (US-387083, holotype; F-101118, GH, MIN-149688, MO-1773781, NY, isotypes).

Toxicodendron goniocarpum Greene, Leaf. Bot. Observ. Crit. 1: 125. 1905. Type: *Lucia McCulloch* 45, Lake City, Columbia Co., Florida. 25 June 1901. (US-440443, holotype; FLAS-16153, isotype; US-440444, probable isotype).

Rhus toxicodendron f. *malacotrichocarpum* Moore, Rhodora 11: 163. 1909. *Rhus radicans* f. *malacotrichocarpa* (Moore) Fernald, Rhodora 43: 592. 1941. Type: *E. B. Chamberlain* and *G. E. Dinsmore* 832, in and growing over bushes, Pemaquid Beach, Bristol, Lincoln Co., Me. 9 Sept. 1898. (GH, holotype).

Rhus littoralis Mearns, Proc. Biol. Soc. Wash. 15: 148. 1902. *Rhus radicans* var. *littoralis* (Mearns) Deam, Fl. Indiana, p. 651. 1924. *Toxicodendron radicans* var. *littoralis* (Mearns) Barkley, Ann. Missouri Bot. Gard. 24: 434. 1937. Type: *Edgar Mearns* 233, Newport, Rhode Island, Sept. 10, 1901. (US-403300, holotype; US-1317009, US-403299, NY, isotypes).

Rhus radicans var. *vulgaris* f. *intercursa* Fernald, Rhodora 43: 592. 1941. Type: *Fernald, Long, and Smart* 5832, Virginia, deciduous woods, Curles Neck Farm, Henrico Co., June 21, 1936. (GH, holotype; NY, isotype).

Terminal leaflet obtuse, subcordate, or truncate at the base, with widest part generally below center; tufts of hairs in vein axils of leaflets hyaline or straw-colored, occasionally red-brown; blade 2.5-17.0 cm long, 2-13 cm wide, petiole 2.0-20.0 cm long; terminal petiolule 0.5-6 cm long; fruits globose, 3-6.5 mm broad, puberulent, scabrous, or papillose.

Distribution: United States, states bordering on the Atlantic Ocean, southern Maine southwest, west to Appalachians, Ozarks, and East Texas; Bahama Islands; Bermuda. (Fig. 34).

Representative specimens. UNITED STATES. Alabama. AUTAUGA CO.: Prattville, *Gillis* 4528 (MSC). BALDWIN CO.: Loxley Research plots, Stapleton, *Grelen*, s.n. (FLAS). CLARKE CO.: Jackson, *Gillis*

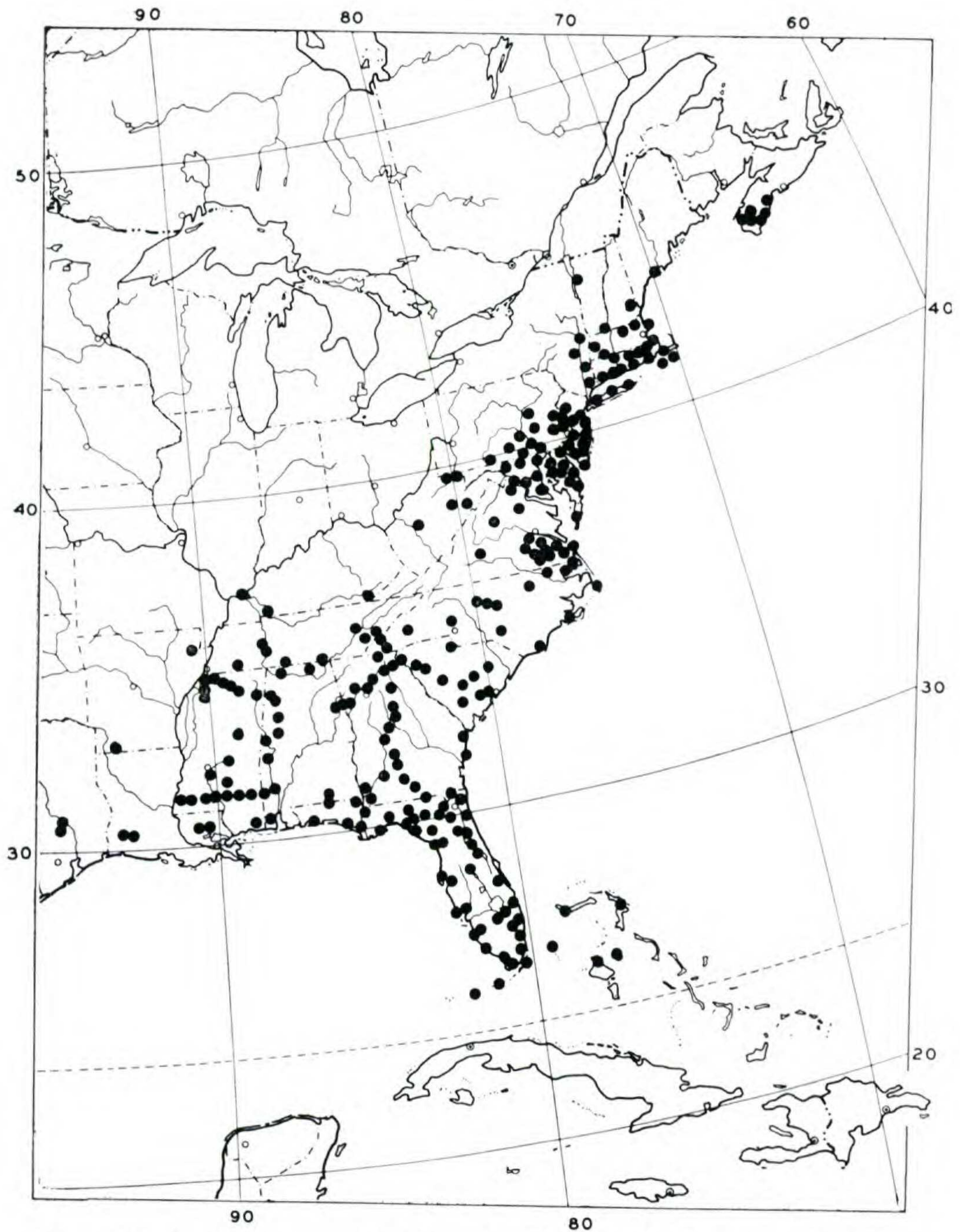


Fig. 34. Distribution of *Toxicodendron radicans* subsp. *radicans*.
 6019 (MSC). CLEBURNE CO.: 6 miles NNW of Edwardsville, *Donahue* 248 (MSC). COLBERT CO.: Sheffield, river bank, *Bartlett* 3370 (MSC, MICH). ELMORE CO.: Elmore, *Gillis* 4525 (MSC). FAYETTE CO.: southern edge of Fayette Experimental Forest, *Gillis* 6037 (MSC). GREENE CO.: 2 miles north of Forkland, *Gillis* 6024 (MSC). HALE CO.: Talladega National Forest, Payne Lake Recreational Area, *Donahue* 246 (MSC). JEFFERSON CO.: flat woods between Mobile Junction and

McCalla, *Bartlett* 3350 (MSC, MICH). LEE CO.: Auburn, *Earle*, s.n. (NY). MACON CO.: Tuskegee, *Gillis* 4506 (MSC). MADISON CO.: Huntsville, *Gillis* 4550 (MSC). MARION CO.: 9.1 miles south of Hamilton, *Gillis* 6039 (MSC). MOBILE CO.: Chunchula, *Shinners* 29301 (SMU). SHELBY CO.: ½ mile SW of Columbiana, *Donahue* 247 (MSC). TUSCALOOSA CO.: Tuscaloosa on river bluff, *Bartlett* 3314 (MICH, MSC). UNION CO.: 6.3 miles SE of New Albany, *Gillis* 6046 (MSC). WASHINGTON CO.: Chatom, *Gillis* 6015 (MSC). **Arkansas.** COLUMBIA CO.: Magnolia, *Demaree* 39203 (SMU). CRAIGHEAD CO.: Jonesboro, *Demaree* 3551 (SMU). DREW CO.: Monticello, *Demaree* 13692 (MO). GARLAND CO.: near Hot Springs, *Runyon* 1211 (NY). HEMPSTEAD CO.: Fulton, *Palmer* 5416 (A, MO, US). HOT SPRINGS CO.: Magnet Cove, *Demaree* 14802 (GH, MO, NY). **Connecticut.** FAIRFIELD CO.: Bridgeport, *Eames*, s.n. (US); Easton, *Johnson* 447 (F). LITCHFIELD CO.: without definite locality, *Weatherby* 5294 (US). MIDDLESEX CO.: Westbrook, *Gillis* 4112 (MSC). NEW LONDON CO.: Groton, *Jansson*, s.n. (OSC); WINDHAM CO.: *Thompson, Churchill & Lane*, s.n. (MO). **Delaware.** KENT CO.: Leipsic, *Laisen* 714 (GH). NEW CASTLE CO.: New Castle, *Tidestrom* 11547 (GH). SUSSEX CO.: *Fogg* 11186 (GH); Milford, *Gillis* 3848 (MSC). **District of Columbia.** Brookland, *Bartlett* 1788, 1789, 1790, 1791, 1793, 1795 (MICH, MSC, SMU). Columbian Formation, *Boettcher* 250 (A, F, GH, MO, RM). **Florida.** ALACHUA CO.: Gainesville, *O'Neill*, s.n. (MO); Gainesville, periphery of golf course on Newberry Road, *Gillis* 3932 (FLAS, MSC); Devil's Millhopper sink-hole, 12 miles NW of Gainesville, *Gillis* 4345 (MSC). BAKER CO.: titi pond, *Manning, West & Arnold*, s.n. (FLAS). BAY CO.: St. Andrew's Bay, *Benker* 3506 (NY). BRADFORD CO.: Santa Fe banks south of Hampton, *West & Arnold*, s.n. (FLAS). BREVARD CO.: Cocoa, *Gillis* 4356 (MSC). BROWARD CO.: Hugh Taylor Birch State Park, Fort Lauderdale, *Roestad*, s.n. (FLAS). CITRUS CO.: Red Level, *West & Arnold*, s.n. CLAY CO.: Goldhead Branch State Park, *West*, s.n. (FLAS). COLLIER CO.: Everglades, Miles City near fire tower, *Gillis* 4480 (MSC); 7.3 miles NW of Copeland, Fahkahatchee Strand, *Ward & Botany Class C-6* (FLAS). COLUMBIA CO.: Lake City, *McCulloch* 45, 46 (FLAS, US). DADE CO.: Homestead, *Small & Wilson*, s.n. (F, NY); Roberts Island, *Small* 7387 (NY); Long Pine Key, *Traverse* 590 (GH); Sykes Hammock, Everglades Keys, *Small & Mosier* 5482 (FLAS, GH, NY, US). DESOTO CO.: Hammock, west edge of Arcadia, *Botany class B-5* (FLAS). DIXIE CO.: Hammock, 1 mile NE of Jena, *Pasture Survey*, s.n. (FLAS). DUVAL CO.: Jacksonville, *Curtiss* 4646 (MO, US). ESCAMBIA CO.: Santa Rosa Island, *Blair*, s.n. (FLAS). FRANKLIN CO.: St. Vincent Island, *McAtee* 17388 (US). GLADES CO.: west of Lake Okeechobee, *Small & DeWinkeler*, s.n. (NY). GULF CO.: Wewahitchka, Dead Lake, *Demaree* 50426 (MSC). HAMILTON CO.: Bayhead 3 miles south of Jennings, *West & Arnold*, s.n. (FLAS). HIGHLANDS CO.: Lake Placid, *Craighead*, s.n. (MSC); Hillsborough, Tampa Bay shore,

Rolfs 247 (F, MO). JACKSON CO.: Blue Springs north of Marianna, *Exploration Party 1937, s.n.* (FLAS). LAFAYETTE CO.: Opposite Bradford on Suwannee River, *West & Arnold, s.n.* (FLAS). LEE CO.: Alva, *Hitchcock* 39 (F, GH, MIN, MO, NY, US); Sanibel Island, *Cooley* 2499 (FLAS, GH, NY, US). LEON CO.: Woodville, *Godfrey & Morrill* 53026 (FSU, GH, NY). LEVY CO.: 2 miles south of Gulf Hammock, *Pasture Survey, s.n.* (FLAS). MADISON CO.: Sirmans, *Palmer* 27268 (A, MO). MANATEE CO.: Long Boat Key, *Gillis* 3939 (MSC); mouth of Manatee River, *Rugel* 79 (BM). MARION CO.: bayhead, 3 miles south of range Springs, *West & Arnold, s.n.* (FLAS); Eureka on Oklawaha River, *Godfrey & Houk* 62806 (MSC); Silver Springs, bank of Silver River, *Gillis* 6594 (MSC). MARTIN CO.: Lake Okeechobee, *Moldenke* 5440 (NY). MONROE CO.: Key West, *Blodgett, s.n.* (NY); Flamingo, *Craighead, s.n.* (MSO); Big Pine Key, *Ward* 4330 (FLAS); NASSAU CO.: Julee, *Gillis* 3958 (MSC). OKALOOSA CO.: Bolton Creek swamp, *Tyson* 314 (FLAS). ORANGE CO.: near Christmas, *Gillis* 6884 (MSC); OSCEOLA CO.: outskirts of Intercession City, *Gillis* 6468 (MSC). PALM BEACH CO.: Palm Beach, *Garvens, s.n.* (F). PINELLAS CO.: St. Petersburg Beach, *Gillis* 6347 (MSC). PUTNAM CO.: west of Mud Springs, Welaka, *Laessle, s.n.* (FLAS). ST. JOHNS CO.: 10 miles west of St. Augustine, *West & Arnold, s.n.* (FLAS); ST. LUCIA CO.: along S-607, 1 mile west of Indio Road, *Gillis* 6894, (MSC). SUMTER CO.: Rutland, hammock near Withlacoochee River, *West & Arnold, s.n.* (FLAS). TAYLOR CO.: Half Mile Rise on Aucilla River, *Exploration Party 1939, s.n.* (FLAS). UNION CO.: Cypress Pond Road, 2 miles south of Raiford, *West & Arnold, s.n.* (FLAS). VOLUSIA CO.: 3 miles west of Stetson University, *Prichard* 533 (FLAS); Cypress hammock about 5 miles NE of Deland, *Rosbach & Prichard* 2039 (FLAS). WAKULLA CO.: 6 miles E of Sopchoppy, *Ward & Ford* 3631 (FLAS). **Georgia.** BIBB CO.: Macon, *Gillespie* 4889 (A, ND, SMU). BRYAN CO.: Richmond Hill, *Gillis* 4000 (MSC). CHEROKEE CO.: SW of Canton, *Donahue* 253 (MSC). CLARKE CO.: Athens, *James, s.n.* (MSC). COOK CO.: south of Lenox near Barneyville Road, *Gillis* 6582 (MSC); CRISP CO.: 0.5 mile north of Turner Co. line, *Gillis* 6578 (MSC). DECATUR CO.: Bainbridge, *Small, s.n.* (A, F, NY). DOOLE CO.: south of Unadilla, *Gillis* 6570 (MSC). DOUGLAS CO.: NE of Villa Rica, *Donahue* 252 (MSC). EARLY CO.: Blakely, *Gillis* 4502 (MSC). EMANUEL CO.: Swainsboro, *Gillis* 4968 (MSC). FLOYD CO.: Rome, Horseleg Mt., *Demaree & Lipps* 50109 (MSC). HABERSHAM CO.: between Clarkesville and Demorest, *Gillis* 6542 (MSC). HARALSON CO.: Tallapoosa, *Donahue* 250 (MSC). HOUSTON CO.: 6 miles north of Henderson, *Gillis* 6567 (MSC). JACKSON CO.: Commerce, *Gillis* 6577 (MSC). LUMPKIN CO.: Chattahoochee National Forest, DeSoto Falls Campground, *Donahue* 255 (MSC). MCDUFFIE CO.: Fall-line sand hills, vicinity of Thomson, *Bartlett* 1509, 1454, 1668, 1667, 1669, 1673, 1674, 1701, 1734, 1747 (MICH, MSC, SMU). MCINTOSH CO.: Sapelo

Island, *Gillis* 3961. MORGAN CO.: 6.6 miles north of Putnam Co. line, *Gillis* 6543A (MSC). PICKENS CO.: 5 miles west of Emma, *Donahue* 254 (MSC). TURNER CO.: 1 mile north of Inaha, *Gillis* 6580 (MSC). UNION CO.: 3 miles NW of Blairsville, *Donahue* 256 (MSC). **Kentucky.** BELL CO.: 0.5 miles NW of Fourmile, weathered rock cliff, *Gillis* 6540 (MSC). TRIGG CO.: 6 miles west of Cadez, *Donahue* 211 (MSC). **Louisiana.** Calcasieu Parish, Lake Charles, *Allison* 320 (US). FRANKLIN PARISH: Gilbert, *Gillis* 5951 (MSC). MOREHEAD PARISH: Jones, *Gillis* 5943 (MSC). NATCHITOCHE PARISH: *Palmer* 7353 (A, MO). RAPIDES PARISH: Valentine Lake, *Thieret* 17945 (MSC). SAINT TAMMANY PARISH: Covington, *Demaree* 50764 (MSC). **Maine.** LINCOLN CO.: Bristol, *Chamberlain* 832 (GH); Boothbay, *Fassett* 28979 (F, MO, SMU, WIS); Monhegan Island, *Churchill*, s.n. (MO). SAGadahoc CO.: Five Islands, *Rehder* 1045 (A, US). YORK CO.: Isle of Shoals, *Howard & Wagenknecht* 5295 (A, MSC). **Maryland.** ANNE ARUNDEL CO.: Annapolis, *Tidestrom* 6639 (A, MO, US). BALTIMORE CO.: Sorrento, *Tidestrom & Bartlett* 7255 (SMU). CALVERT CO.: Cony Point, *Seymour* 17348 (SMU). CAROLINE CO.: Horse Point, Tuckahoe River, *Tidestrom* 11977 (US). FREDERICK CO.: Lewistown, *Gillis* 5695 (MSC); Hunting Creek, *Sullivan* 415 (ND). HARTFORD CO.: Spesukie Island, *Smith*, s.n. (US). MONTGOMERY CO.: Bethesda, *Bartlett* 1820 (MICH, MSC, SMU). PRINCE GEORGES CO.: Beltsville, *Hermann* 10866 (F); Colledge Park, *Tidestrom* 7132 (US). ST. MARYS CO.: St. Mary, *Walker* 3954 (US). TALBOT CO.: Claiborne, *Tidestrom*, s.n. (US). WORCESTER CO.: Ocean City, *Fogg* 11464 (GH). **Massachusetts.** Barnstable Co.: Hyannis, *Fernald, Butters, & St. John* 15269 (GH). BERKSHIRE CO.: Williamstown, *Gillis* 4066 (MSC). BRISTOL CO.: Dighton, *Seymour* 18559 (SMU); Dartmouth, *Knowlton*, s.n. (MIN); New Bedford, *Greene*, s.n. (WIS); DUKES CO.: Oak Bluffs, *Seymour* 1262 (GH, NY, US); Gay Head, *MacKeever* 567 (MSC). ESSEX CO.: Rockport, *Rouleau* 1308 (ARIZ, E, F, FLAS, GH, MIN, MO, MSC, NY, OSC, RM, US, WIS). HAMPDEN CO.: Springfield, *Pillsbury*, s.n. (US). MIDDLESEX CO.: Lowell, *Beattie* s.n. (E, MO, OSC, SMU). NANTUCKET CO.: *Bicknell*, 5591 (NY). NORFOLK CO.: Stoughton, *Blake* 1294 (US); Brookline, *Rohson*, s.n. (A). PLYMOUTH CO.: Middleboro, *Murdoch* 527 (F). SUFFOLK CO.: Boston, *Williams*, s.n. (GH). WORCESTER CO.: Bolton, *Seymour* 6092 (WIS). **Mississippi.** BENTON CO.: near Union Co. line, *Gillis* 6047 (MSC). COVINGTON CO.: pine ridge west of Collins, *Gillis* 6006 (MSC); along route 35 below Bowie River, *Gillis* 6003 (MSC). FRANKLIN CO.: road to Clear Springs, *Gillis* 5975 (MSC); 3 miles from Roxie, *Gillis* 5873 (MSC). ITAWAMBA CO.: between Tremont and Fulton, *Gillis* 6043 (MSC). JACKSON CO.: Magnolia State Park, *Demaree* 31216 (SMU, TEX); Krede, *Demaree* 34912 (SMU). JEFFERSON DAVIS CO.: SE of Prentiss, *Gillis* 6002 (MSC). LAWRENCE CO.: Monticello, *Gillis* 5989 (MSC). LEE CO.: Tupelo, *Gillis* 6045 (MSC). LINCOLN CO.: New Prospect Baptist

Church, *Gillis* 5979 (MSC). MADISON CO.: without definite locality, *McDougall* 1590 (US). MARSHALL CO.: 2.4 miles SE of Holly Springs, *Gillis* 6048 (MSC). OKTIBBEHA CO.: Starkville, *Hill, s.n.* (ILL). PANOLA CO.: Sardis, *Broadhead* 36 (SMU). SMITH CO.: Marathon Lake Recreation Area, *Donahue* 242 (MSC). TATE CO.: Senatobia, *Gillis* 5908 (MSC). UNION CO.: 6.3 miles SE of New Albany, *Gillis* 6046 (MSC). **New Jersey.** ATLANTIC CO.: Mays Landing, *Fogg* 2129 (GH); Hammonton, *Gillis* 5649 (MSC). BERGEN CO.: without definite locality, *Oehler, s.n.* (NY). BURLINGTON CO.: Riverton, *Bassler* 69 (KSC); Mt. Holly, *Gillis* 5650 (MSC). CAMDEN CO.: Chew Road, *MacKenzie* 6912 (NY). CAPE MAY CO.: Cape May Court House, *Gillis* 5632 (MSC). CUMBERLAND CO.: Buena, *Gillis* 5642 (MSC). HUNTERDON CO.: Ellmaker Island, Raven Rock, near Stockton, *collector unknown* (MIN). MERCER CO.: between Princeton and Rocky Hill, roadside, *Gillis* 5089 (MSC). MIDDLESEX CO.: East Millstone, Hutcheson Memorial Forest, *Gillis* 3472 (MSC); Perth Amboy, *Gillis* 5387 (MSC). MONMOUTH CO.: Freehold, *MacKenzie* 7941 (NY). OCEAN CO.: Barnegat Pier, *MacKenzie* 2918 (GH); Island Beach State Park, dominant shrub for 10 miles, *Gillis* 2709 (MSC). SALEM CO.: Penns Grove, *Adams & Adams* 1890 (A, US). SOMERSET CO.: Hillsboro Twp., Sourland Mt., Neshanic-Zion Road, *collector unknown* (NDA). UNION CO.: Rahway, *Gillis* 5090 (MSC). WARREN CO.: Phillipsburg, *Tidestrom* 6009 (US). **New York.** BRONX CO.: Bedford Park, *Edmondson* 1420 (NY). DUCHESS CO.: Brush, *Gillis* 4065 (MSC). GREENE CO.: without definite locality, *Gillis* 3830 (MSC). MANHATTAN CO.: Van Courtlandt Park, *Hastings, s.n.* (NY). NASSAU CO.: Lawrence, *collector unknown*, (ND-G). RENNSELAER CO.: Troy, *Hall, s.n.* (F). RICHMOND CO.: Staten Island, *Dowell* 4641 (MIN). SUFFOLK CO.: Shelter Island, *Wells, s.n.* (MSC); 3 miles south of Montauk Point, *Gillis* 4924 (MSC). WESTCHESTER CO.: Shrub Oak, *Gillis* 4064. **North Carolina.** ALAMANCE CO.: 4.6 miles north of Union Ridge, *Ramseur & Hammond* 2552 (FSU). BRUNSWICK CO.: Long Beach, *Boyce* 1424 (NY). BUNCOMBE CO.: Biltmore, *Bartlett* 2905 (ARIZ, TEX). CAMDEN CO.: Elizabeth City, *Gillis* 3866 (MSC). CATAWBA CO.: east of Conover, *Gillis* 6053 (MSC). CURRITUCK CO.: Currituck Sound, *Randolph & Randolph* 599 (GH). DARE CO.: Pea Island, *Gillis* 4041 (MSC). DAVIE CO.: Farmington, *Gillis* 6066 (MSC). DURHAM CO.: Nelson, *Gillis* 4029 (MSC). FORSYTH CO.: Clemmons, *Gillis* 6072 (MSC). HALIFAX CO.: Enfield, *Ahles* 14917 (GH). HERTFORD CO.: Potecasi Creek, SE of Mapleton, *Ahles* 41517 (FSU). HOKE CO.: 0.2 mile NW of Hoke-Robeson Co. line, *Ahles* 29584 (FSU). MACON CO.: Topten, *Donahue* 257 (MSC). ORANGE CO.: Chapel Hill, *Gillis* 4028 (MSC). PERQUIMANS CO.: Hertford, *Gillis* 3868 (MSC). POLK CO.: Varyhans Gap, *Peattie* 1476 (F); Tryon, *Churchill, s.n.* (MO). SWAIN CO.: SW of Nantahala, *Donahue* 258 (MSC). WAKE CO.: Raleigh, *Hyams s.n.* (US). **Pennsylvania.** ADAMS CO.: East Berlin, *Gillis* 4902 (MSC);

BEDFORD CO.: New Baltimore, *Gillis* 5484 (MSC); 3.5 miles south of Centerville, *Westerfeld* 6568 (FSU). BUCKS CO.: Bowman's Hill, *Gillis* 3840 (MSC); Washington Crossing, *Gillis* 3836 (MSC). DAUPHIN CO.: Harrisburg, *Small*, *s.n.* (F). FRANKLIN CO.: Tuscarora Mountain, *Gillis* 5110 (MSC); MONTGOMERY CO.: Cold Point, *Adams & Adams* 1970 (A). MONTGOMERY CO.: Mausdale, *Adams* 5948 (OSC). NORTHAMPTON CO.: Easton, *Gillis* 4904 (MSC). PERRY CO.: Newport, *Adams & Adams* 3666 (A, GH); PHILADELPHIA CO.: Mermaid, *Adams & Adams* 1883 (A); SNYDER CO.: Selinsgrove, *Moldenke* 2459 (NY); YORK CO.: Dillsburg, *Gillis* 4903 (MSC). **Rhode Island.** BRISTOL CO.: Barrington, *Winslow*, *s.n.* (US). KENT CO.: West Warwick, *Gillis* 4103 (MSC). NEWPORT CO.: Newport, *Mearns* 233, 235, 236 (A, GH, BM, ND-G, NY, US). PROVIDENCE CO.: Grant's Mill, *Palmer* 43426 (MO, NY). WASHINGTON CO.: Wickford, *Williams*, *s.n.* (GH). **South Carolina.** AIKEN CO.: Graniteville, *Eggert*, *s.n.* (MO); ANDERSON CO.: Whitner Park, *Davis* 1710 (MIN, OSC); BAMBERG CO.: Denmark, *Palmer* 39863 (A, MO, NY). BERKELEY CO.: Pineville, *Godfrey & Tryon* 579 (GH, NY, US). FLORENCE CO.: Branch Swamp, *Bartlett* 2372 (MICH). LEXINGTON CO.: Batesburg, *MacGregor* 26 (US). OCONEE CO.: Clemson College, *House* 3103 (NY, US). RICHLAND CO.: north of Columbia along highway 21, *Gillis* 4570 (MSC). WOOD CO.: without definite locality, *Davis* 2041 (US). YORK CO.: Ebenezer, Branch Swamp, *Bartlett* 2373 (MICH, MSC). **Tennessee.** SEVIER CO.: Great Smoky Mountains National Park, 1/2 mile from Gatlinburg, *Gillis* 6541 (MSC). FRANKLIN CO.: Sherwood, *Eggert*, *s.n.* (MIN). HARDEMAN CO.: Bolivar, *Palmer* 17499 (A, MO, US). HENDERSON CO.: Natchez Trace State Park, *Donahue* 212 (MSC). KNOX CO.: Island Home Park, *Ainslie*, *s.n.* (KSC). **Texas.** HARRIS CO.: Houston Memorial Park, *Traverse* 18 (F, GH, SMU); MONTGOMERY CO.: Willis, *Dixon* 292 (F). WALKER CO.: Stubblefield Lake Recreation Area, *Donahue* 235 (MSC). **Vermont.** CHITTENDEN CO.: Charlotte, *Harsford*, *s.n.* (MIN). WINDHAM CO.: Westminster, *Gillis* 4083 (MSC). WINDSOR CO.: White River Jct., *Gillis* 4089 (MSC). **Virginia.** ARLINGTON CO.: Fort Myer, *Mearns* 103 (US). BEDFORD CO.: without definite locality, *Curtiss*, *s.n.* (GH). DINWIDDIE CO.: Burgess Station, *Fernald & Long* 9973 (GH, PH). FAIRFAX CO.: Great Falls, *Bartlett* 1785, 1779, 1787 (MICH, MSC). GREENE CO.: Bear Fence Mt., *Walker* 2951 (US). HANOVER CO.: Mechanicsville, *Adams & Wherry* 2216 (A). HENRICO CO.: Curles Neck Farm, *Fernald, Long & Smart* 5832 (GH, NY). ISLE OF WIGHT CO.: Rushmere, *Fernald & Long* 13066 (GH, MIN, PH); Carrollton, *Gillis* 4043 (MSC). NANSEMOND CO.: South Quay, *Fernald & Long*, *s.n.* (GH, PH). NORFOLK CO.: Ocean View, *Kearney* 1759 (US); Lambert's Point, *Kearney* 1026 (US). NORTHAMPTON CO.: Capeville, *Gillis* 3864 (MSC); Exmore, *Gillis* 3862 (MSC); PRINCE GEORGE CO.: Desputanta, *Fernald, Long & Smart* 5833 (GH, NY, PH, US). PRINCESS ANNE CO.: Virginia Beach, *Britton & Small*, *s.n.* (F, NY, US); SOUTHAMPTON CO.: Oak Grove School, *Fernald & Long* 8351 (GH, MO, PH). SURRY CO.: Chippokes,

Fernald & Long 13064 (GH, NY, PH, US); SUSSEX CO.: Huske, *Fernald & Long* 13067 (GH, PH, US); Jarratt, *Fernald & Long* 13381 (GH, PH, WIS); WARWICK CO.: Hampton, *Churchill, s.n.* (MIN, MO, WIS). WESTMORELAND CO.: Colonial Beach, *Tidestrom & Bartlett* 5962 (A, MO, US). YORK CO.: James River, *Killip* 40122 (US). West Virginia. HAMPSHIRE CO.: Capon Bridge, *Gillis* 5707 (MSC). KANAWHA CO.: Kanawha State Forest, *Donahue* 262 (MSC). MONONGALIA CO.: Morgantown, *Millspaugh* 146 (NY). RANDOLPH CO.: Huttonsville, *Donahue* 264 (MSC). UPSHUR CO.: Bucklin, *Pollack, s.n.* (US). WEBSTER CO.: Hacker Valley, *Smith* 1532 (F).

CANADA. Nova Scotia. QUEENS CO.: Port Mouton, *Jack* 3476 (A, F). SHELBURNE CO.: Welshtown (Birchtown) Lake, *Fernald & Long* 24094 (GH). YARMOUTH CO.: Gavelton, *Fernald & Long* 24098 (GH); Argyle Head, *Long & Linder* 21790 (GH); Yarmouth, *Pease & Long* 21785 (GH).

BERMUDA. Paget East, *Hughes, s.n.* (MSC). Tucker's Town, *Brown* 499 (NY). Boaz Island, *Brown & Britton* 1005 (NY).

BAHAMA ISLANDS. Abaco. Marsh Harbor, Great Abaco, *Brace* 1840 (NY); Great Abaco, 3 miles south of Treasure Cay, *Gillis* 6157 (MSC). Andros. North Andros, Staniard Creek, *Small & Carter* 8850 (NY). Bimini. South Bimini, without definite locality, *Howard & Howard* 10061 (NY, SMU). Cat Cay: North Cat Cay, without definite locality, *Millspaugh* 2336 (NY). Grand Bahama. Without definite locality. *Britton & Millspaugh* 2446 (NY); Russell Town near Freeport, *Gillis* (FTG). New Providence. Delaport, *Britton* 3416 (NY); Southwest shore of Lake Cunningham, *Gillis* 6074 (MSC).

This subspecies probably represents the form of poison-ivy which was first encountered by seventeenth century explorers and settlers in the New World. Early collections from North America, made in colonies close to the Atlantic Seaboard, were either of this taxon or, if found north of the 44th parallel, of *Toxicodendron rydbergii*. The designation of a type for *Rhus radicans* L. has presented a dilemma, because of the various specimens known to have been available to Linnaeus.

Linnaeus's first reference to poison-ivy was in the *Hortus Cliffortianus* (1738): *Rhus radicans foliis ternatis: foliolis petiolatis ovatis nudis integerrimis.*" Linnaeus based his early concepts of poison-ivy on the collections other than at Uppsala, such as that of Clifford's. The Clifford specimens are probably the ones upon which Linnaeus based most of his knowledge of poison-ivy. (These specimens, now at BM, are a flowering representative of *T. rydbergii*, and a sterile

branch of *T. radicans* subsp. *radicans*.) They undoubtedly represent Linnaeus's concept of poison-ivy until after the publication of the *Hortus Cliffortianus*. In 1751, however, Peter Kalm returned from his exploring and collecting adventures in North America, bringing with him many specimens which were incorporated into Linnaeus's personal herbarium. Among these was a form of poison-ivy, presumably from the vicinity of Philadelphia (Kalm, 1770), for which Linnaeus must have had some habit data, for he edited his diagnosis of *Rhus radicans* from the *Hort. Cliff.* in *Species Plantarum* (1753) by the insertion of the phrase "*caule radicante*," thus suggesting that he had learned of its habit as a liana. The population represented in the Clifford Herbarium by the flowering specimen (*T. rydbergii*) has no aerial roots and did not climb. Although both the Clifford specimens (already familiar to Linnaeus), and the Kalm specimen (representing a phase of the plant new to Linnaeus), were all under consideration by him at the time of writing of the *Species Plantarum*, the Kalm specimen has been confirmed as the lectotype. It is the specimen which demonstrates the climbing habit, thus the added phrase in the *Species Plantarum*. The Clifford specimen, representing a non-climbing form of poison-ivy, must be excluded as a candidate for the nomenclatural type. Fernald alludes to the LINN specimen as being the type by publishing (1941) a photograph of it labeled "portion of type," but Brizicky (1963) formally designated it as the lectotype. If Linnaeus knew of the non-climbing habit of the Clifford specimen and any other departures from the characteristics represented in the Kalm specimen, he chose not to separate these plants nomenclaturally. This was finally done at the end of the nineteenth century when Rydberg (1900) published Small's name *Rhus rydbergii*.

The type material leaves much to be desired in the way of diagnostic characteristics. After study of the material in the Linnaean Herbarium, I have concluded that the Kalm specimen must represent the Atlantic Coastal population, corroborating the hint in Kalm's records that he collected it near Philadelphia. What has been most influential in

making this decision is the characteristic tufts of hairs in the main vein axils on the lower surface of the leaflets, a characteristic only of Oriental and Atlantic Coast forms. Had the specimen been a fruiting one, the pubescence of the exocarp would have solved the dilemma. Populations from the eastern coastal regions of the United States generally have entire leaflet margins, although not uncommonly with a single lobe or notch each leaflet (two on the terminal) as has the Linnaean specimen. The division of the terminal leaflet into inequilateral halves is a more subtle, although persistently accurate character, and is found in this specimen also. Complicating matters is the additional specimen in the Linnaean Herbarium (sheet 387.15) which has almost glabrous fruit. This specimen is anomalous as to the population which it can represent. It is therefore better to consider that Brizicky has chosen the appropriate specimen for nomenclatural typification.

Curiously enough, most taxonomists, even those who have worked extensively with the poison-ivy problem, have ignored typification of this species and the type subspecies. Many subspecies, varieties, and forms have been described, which all apply to the same taxon as the Linnaean specimen. This is due in part to the fact that the Kalm specimen was collected in flowering condition. Had it been a fruiting specimen with the fruit's characteristic trichomes on the exocarp, the publishing of such epithets as *microcarpon*, *malacotrichocarpum*, and *littoralis* (each used in several combinations) might have been precluded.

The fruits of subsp. *radicans* are generally smaller than the fruits of other subspecies of *Toxicodendron radicans*. This is especially true in populations which are found in Florida and southern Georgia. The small-fruited forms seem to demonstrate some geographical pattern, but otherwise do not differ from other populations of subsp. *radicans*, and therefore do not seem to warrant nomenclatural segregation. The various taxa using the epithet *microcarpon* or its orthographic derivatives are therefore treated in synonymy with subsp. *radicans*.

In regard to the type of *Rhus littoralis* Mearns, there are two sheets and a box of twigs and fruits comprising the type at US, one of the sheets containing a fruiting specimen and one a portion of the stem with abundant aerial roots. Presuming that these all represent a single specimen, thereby fulfilling the requirement of Art. 9 of the Code, these all represent the type specimen. A specimen labeled "isotype" is deposited at GH, but collected 11 days before the type (*Mearns* 232). Furthermore, US-403299 (*Mearns* 235) is probably an isotype. Mearns appears to have numbered each specimen with a separate collection number even though many may be part of the same gathering.

Because the name *Rhus radicans* var. *littoralis* has been applied (Deam, 1940) to populations which do not belong to this taxon, it seems appropriate to discuss the likely reason that this application was made. Some populations of poison-ivy in Indiana, especially from counties bordering the Ohio River, have fruits which are pubescent to a greater or lesser extent; they are, however, dissimilar in other respects to populations from the coastal regions which are truly *Toxicodendron radicans* subsp. *radicans*. This is also true for some populations in Oklahoma (which were named *T. aboriginum* by Greene, 1905). The epithet *littoralis* is misapplied; the populations of Indiana and Oklahoma should be *T. radicans* subsp. *negundo*.

In describing several new varieties and forms, Fernald (1941) described a number of taxa represented in southeastern Virginia. He did not until later (1950) indicate the reasons for his new taxa. He implied that forma *intercursa* (= "running between"), with its supposed pubescent leaf blades and glabrous petioles, was intermediate between forma *vulgaris*, which he said had both leaf surfaces and petioles glabrous, and f. *negundo*, which allegedly had both leaf surfaces and petioles pubescent. These characters in the populations in question, especially petiole pubescence, are highly variable.

We are able to typify *Toxicodendron glabrum* Mill. by Miller's reference to Dillenius's *Toxicodendron rectum foliis minoribus glabris* for which there is a specimen in the

Dillenian Herbarium; this specimen has been designated the lectotype. It was a cultivated specimen, grown in 1727 by Sherard. It is not surprising, its being a cultivated plant, that it is an atypical form of *T. radicans* subsp. *radicans* with very narrow leaflets and almost total lack of the characteristic tufts of hairs in the vein axils on the lower leaflet surface, conditions strongly suggestive of the possibility that the specimen is a juvenile. By reference to this Dillenian citation, *Rhus radicans lucidum* Aiton and *R. humilis* Salisbury¹⁵ (as *R. humile*) can also thus be typified. Greene (1910) interpreted this plant as near his *T. rufescens* or *R. littoralis* Mearns. According to Britten (1900), *T. glabrum* Mill. "is made a synonym of *Rhus glabra* in Ind. Kew. The character 'foliis ternatis' is sufficient to show that this cannot be the case; since we have not Miller's specimens, but the figure which he quotes from Hort. Elth. represents *R. radicans*." *Toxicodendron glabrum* (L.) Kuntze is most likely *R. glabra* L. since Kuntze virtually obliterated *Rhus* by wholesale transfers to *Toxicodendron*.

¹⁵Dillenius (1732) intended that his *Toxicodendron amplexicaule, foliis minoribus glabra* be different from *Toxicodendron rectum, foliis minoribus glabris*. Linnaeus must have agreed, since he quoted the former as synonymous with his variety β , and the latter with his variety γ . The descriptions by Dillenius indicate that he thought *Toxicodendron amplexicaule*. . . . was a climber, and *Toxicodendron rectum* . . . was not. His illustration of *Toxicodendron rectum*. . . , however, appears to be of the climber *Toxicodendron radicans* subsp. *radicans* as herein treated. Moreover, the specimen at the Sherard Herbarium which Dillenius saw demonstrates *Toxicodendron rectum* . . . to be *T. radicans* subsp. *radicans*, despite a written description to the contrary. This becomes of importance when one tries to determine what Salisbury meant by his *Rhus scandens* and *R. humile*.

Rhus humilis must refer to *T. radicans* subsp. *radicans* also, although typified by another specimen (the one at Sherard), even though its description more nearly fits *T. rydbergii* than *T. radicans*. Because a specimen can be found for at least one of these polynomials of Dillenius, we can attribute this one (*Toxicodendron rectum* . . .) to *T. radicans* subsp. *radicans*. Where we have a description, an illustration, and a specimen, the specimen must be granted precedence over all else in typifying, even though it is not correctly defined by the illustration or description. *Rhus scandens*, because of its reference to *Rhus radicans* L., must also be *T. radicans* subsp. *radicans*.

In other words, Miller meant a poison-ivy plant by his use of *Toxicodendron glabrum*; Kuntze did not.

In naming *Rhus blodgettii*, Kearney (1894) described clusters of flowers, but later in the paper admitted that flowers were not seen. His specimen is fairly typical *Toxicodendron radicans* subsp. *radicans*, except for the absence of pubescence on the fruits, but southern Florida populations often have glabrous fruits. Barkley annotated the lectotype as follows:

“Dr. Kearney in the description of the type says, ‘The single specimen which I have seen was collected by Blodgett at Key West, Florida. It is in the Torrey Herbarium.’ As this is the only Blodgett *Rhus* in the Torrey Herbarium and it fits the description, it is probable that it represents the TYPE.”

In regard to *Toxicodendron goniocarpum* Greene, two specimens at US fit Greene’s description of the type. I have chosen the fruiting specimen, *McCulloch* 45 (sheet 440443) as the lectotype. *McCulloch* 46 (sheet 440444) is a probable isotype (presumably *McCulloch* numbered specimens rather than collections). Greene probably had both specimens under consideration since he describes the “rooting freely” of the sterile specimen and the nature of the fruits of the second specimen.

Many specimens of this subspecies are teratological forms, in which the inflorescence proliferates primary and secondary bracts in place of fertile flowers. As I noted earlier (Gillis, 1960), “In these aborted flowers, the bracts grow to several times their normal length (up to 1.4 cm) and were arranged like the flowers, occasionally opposite and occasionally alternate.” This monstrosity has been seen expressed in most taxa of poison-ivy and the poison-oaks, as well as in other *Toxicodendron* and *Rhus* species. Whether this is a response to a virus, insect damage, or some other environmental factor is unknown. It is not genetic in that it does not appear in the same population year after year. It does, however, occur with greatest frequency in *T. radicans* subsp. *radicans*, most especially in the Middle Atlantic and New England States.

One item of periodicity should be noted here. This subspecies is the only member of the poison-ivy complex which digresses from being strictly deciduous. Populations in South Florida retain their leaves until a flush of growth produces new ones, about the time of flowering in February and March. Thus, the plant is never without leaves. Also in South Florida, this subspecies has been seen growing as an epiphyte, rooted not in the ground, but in the old leaf bases of palms in the Everglades.

This subspecies is the most abundant of all poison-ivy taxa, especially in New Jersey, southern New York, and Long Island. Along a stretch of road between the Delaware River and Princeton, New Jersey, poison-ivy forms a roadside carpet for about 15 miles, covering every patch of ground not occupied by some protruding plant, a house, or an intersection, and climbs every tree on both sides of the road! At Island Beach State Park, New Jersey, in the zone protected from salt spray behind the foredunes, poison-ivy forms a dense, shrubby mat, seldom interrupted, between the foredune and the roadway for a distance of 10 miles, about 50-75 meters in breadth. The subspecies becomes less common toward the southern edge of its range, possibly being less able to compete with the more vigorous vines and shrubs in warmer climes.

This subspecies has greatest affinities with Asiatic subsp. *orientale* and *hispidum*. All populations have pubescent fruits, entire leaflet margins (with, at most, only a single notch on each abaxial edge), a characteristic tuft of red-brown or hyaline hairs in the major vein axils on the lower surface of the leaflets, and ovate or elliptic leaflets with acute to acuminate apices. Subspecies *radicans*, however, generally has truncate or obtuse terminal leaflet bases, the broadest portion of the ovate terminal leaflet below center, the tufts of hairs in vein axils generally hyaline or straw-colored rather than red-brown, and small, globose fruits. It is possible that these three subspecies represent disjunction of a taxon that was once contiguous through Eastern Asia and North America.

This subspecies appears to form intergrades with other

taxa where their ranges come into contact. Putative hybrids, intermediate between subsp. *radicans* and *T. rydbergii*, are known from the Berkshire Mountains of western Massachusetts and elsewhere in southern New England. The plant also appears to form hybrids with subsp. *pubens* in Louisiana, Arkansas, and Texas, and with subsp. *negundo* along the Allegheny Ridge (especially Tuscarora Mountain) in Pennsylvania and the Blue Ridge in Virginia, West Virginia, and Maryland. (See discussion under Hybrids, Crosses, and Intergrades; citation of presumed intermediate forms may also be found under that heading.)

Toxicodendron radicans subsp. *radicans* has a broad ecological amplitude. It is most abundant on sand dunes, along fencerows, in floodplain forests, and old fields. It manages to exist marginally as drainage becomes extreme, either with high water table or excessive drainage, such as borders of peat bogs or salt marshes, wet muck, on podzols, or on shallow lithosols. In Nova Scotia, however, one may find it, in addition to sites mentioned above, on gravelly barrens. In the Bahama Islands, it grows in pinelands or hammocks on rocky limestone. In the Florida Everglades, it inhabits leaf mold on potholed limestone.

This taxon has broad community relationships. In its northern reaches, it is closely affiliated with the beech-maple forest and what has evolved from the oak-chestnut woods following the demise of the chestnut. Along the Atlantic and Gulf Coastal Plains, it is often abundant in loblolly pine woods, especially where there is little or no oak present. Farther south, on the Coastal Plain, it is found frequently in liveoak (*Quercus virginiana*) forests and is reported as forming an association with *Persea* in northern Florida (herbarium notes). Along the Gulf Coastal Plain, it is common in southern hardwood forests of *Liquidambar styraciflua*, *Nyssa aquatica*, *Quercus virginiana*, *Fraxinus* spp., and *Acer rubrum*.

On sand dunes it is abundant enough to form an association of its own behind the foredunes where it receives only moderate salt spray (I have observed that a good 2-day northeaster in the Middle Atlantic States and New England

is sufficient to defoliate an entire population in a sand dune association). On the dunes, its frequent associates are *Parthenocissus quinquefolia*, *Myrica pensylvanica*, and *Smilacina racemosa*.

In the Bahama Islands, its chief habitats are relatively dry (no standing water) mangrove swamps associated with *Rhizophora mangle*, *Erithalis fruticosa*, *Blechnum serrulatum*, *Achrostichum aureum*, *Bumelia salicifolia*, *Chrysobalanus icaco*, and *Sabal palmetto*. On some sites, in relatively undisturbed communities, it favors the "blacklands": woods of fairly dense *Pinus caribaea* often associated with *Bumelia*, *Pteridium aquilinum* var. *caudatum*, *Duranta repens*, *Trema lamarckiana*, and *Ilex krugiana*. On New Providence, it is reported from the more open pinelands called "whitelands." At this extreme limit of its range, it appears to compete poorly with other shrubs and vines, being absent from most thickets. I have searched for it on some of the eastern islands in the Bahama Archipelago (San Salvador, Rum Cay, Cat Island) to no avail.

Throughout its range, subsp. *radicans*, as well as subsp. *negundo* and *pubens*, are constantly associated with *Parthenocissus quinquefolia*, *Ulmus* spp., *Fraxinus* spp., and often with *Clematis* spp. and *Ampelopsis arborea*.

4b. ***Toxicodendron radicans* subsp. *orientale*** (Greene) Gillis, comb. nov. Fig. 35.

Toxicodendron orientale Greene, Leaf. Bot. Observ. Crit. 1: 127. 1905. *Rhus orientalis* (Greene) Schneider, Illust. Handb. Laubholz. 2: 151. 1912. Type: *Maximowicz*, s.n. Hakodate, Hokkaido, Japan. 1862. (US-19948, not US-19548 as cited by Greene, 1905, holotype; G-DC, isotype).

Rhus ambigua Lavallée, Arbor. Segrez., p. 54. 1877. Type: unknown, probably a living plant.

Rhus rishiriensis Nakai, Bot. Mag. (Tokyo) 36: 67. 1922. *Rhus ambigua* f. *rishiriensis* (Nakai) Hara, Enum. Sperm. Jap., Part 3, p. 65. 1954. Type: *H. Koidzumi*, s.n. Japan, Rishiri To, Hokkaido, Oshidomari Mts., growing with *Abies sachalinensis*. (TI, holotype).

Leaves bearing tufts of hairs in vein axils on lower surface, generally light-colored to red-brown. Terminal leaflet blade 1.2-1.7 times as long as broad, widest part generally at the middle or above middle, 5-20 cm long, 3-12 cm wide; cuneate at base; petiolule 0.5-3.0 cm long. Petiole 1.5-11.0 cm long. Fruits flattened, obliquely deltoid, 5-6.5 mm broad, short hairy or papillose.

Distribution: Japan, U.S.S.R. (Kurile Islands, Sakhalin).
Common name: tsuta-urushi. Fig. 36.



Fig. 36. Distribution of *Toxicodendron radicans* subsp. *orientale*.

Representative specimens. JAPAN: **Hokkaido.** HIDAKA PROV.: Shoya, Horoizumi-gun, *Tokubuchi*, s.n. (SAP, TI). IBURI PROV.: Noboribetsu on road to Noboribetsu Hot Spring, *Gillis* 4717 (MSC); Mt. Tarumai, *Ito*, s.n. (SAP). ISHIKARI PROV.: Mt. Teine, *Yanagissawa*, s.n. (SAP); Sapparo, *Tokubuchi*, s.n. (GH); Sapporo, *Sugimoto*, s.n. (MSC, TI); Lake Shikotsu, *Gillis* 4743 (MSC); Usakuma National Forest, *Gillis* 4760 (MSC); Asahigawa City, Kamikawa, *Miyabe*, s.n. (SAP). KITAMI PROV.: Shiretoko Peninsula, *Ito* 376 (SAP); Shakubetsu, collector unknown (TI); Shari, *Kanai*, s.n. (TI); Rishiri Islands, Oshidomari, *Suzuki*, *Komiga*, & *Shirahama*, s.n. (SAP); Rishiri Islands, Oniwaki, *Shirahama*, s.n. (SAP). OSHIMA PROV.: Hakodate, *Albrecht*, s.n. (GH, MO, NY); *Maximowicz*, s.n. (GH, NY, US); Yoshioka-mura, *Miyabe* & *Tashiro*, s.n. (SAP); Esashi, *Sasayama*, *Miyabe*, & *Tashiro*, s.n. (SAP). SHIRIBESHI PROV.: along the Tomarikawa, Mt. Shakotan, Shimamaki-bun, *Misumi* & *Igarashi*, s.n. (SAP); Okuskiri Islands, collector unknown (SAP). TESHIO PROV.: Teshio, *Tsujii* & *Kozuka*, s.n. (MSC, SAP). **Honshu.** AOMORI PREF.: Mutsui Horosaki, *Sakurai*, s.n. (A); Mt. Hakkoda, collector unknown (TI). CHIBA PREF.: Awa-Amatsu, 1.3 km. SW of Kameyama, *Gillis* 4678 (MSC); Chiba, *Kanai*, s.n. (TI). ESHIGO PREF.: Mt. of 5 Peaks, collector unknown (TI). FUKUI PREF.: Echizen, Tsuruga, *Kitamura* & *Murata* 2042 (MSC). FUKUSHIMA PREF.: Kashi Hot Spring, *Kanai*, s.n. (TI); Jokogi, *Muramatu*, s.n. (TI); Mt. Bandai, *Koyama*, s.n. (MSC). GIFU PREF. Nakatsugawa, *Kanai*, s.n. (TI); Kisogoe Pass, *Kanai*, s.n. (TI); Mt. Ibuki, *Kanai*, s.n. (TI). GUMMA PREF.: Mt. Tanigawa, *Takeushi*, s.n. (TI); Mt. Hodaka, Kanto District, *Kanai*, s.n. (TI); Oze, *Nishida*, s.n. (TI); Usui Pass, *Kanai*, s.n. (TI). HIROSHIMA PREF.: Mt. Aza, *Kanai*, s.n. (TI). IWATE PREF.: Moichi, *Kanai*, s.n. (TI); KANAGAWA PREF.: Mt. Hakone, *Kanai*, s.n. (TI). Hata, *Bisset* 3890 (E). MIYAGI PREF.: Matushima, *Faurie* 484 (A); Sendai, *Ogina*, s.n. (TI); Okunikawa, collector unknown (TI). NAGANO PREF.: Shimajimadam, *Momose*, s.n. (MSC); Kuzu, Omachi, collector unknown (TI); Nagawado, *Kanai*, s.n. (TI); Mt. Hachibuse, collector unknown (TI); NAGASAKI PREF.: Mt. Yatate, Tsushima Island, *Yabe*, s.n. (TI); Irikan, *Ohki*, s.n. (TI). NARA PREF.: Mt. Odaigahara, *Ohwi*, s.n. (WIS). Niigata Pref.: Mt. Azogi, Sado Island, *Kanai*, s.n. (TI); Niigata, *Yamazaki*, s.n. (TI, US). OKAYAMA PREF.: *Okayama*, *Uno*, s.n. (NY). SHIGA PREF.: near Kyoto, collector unknown (TI); Shiga Highland, *Kanai*, s.n. (TI); Makino, *Kanai*, s.n. (TI). SHIZUOKA PREF.: Mt. Amagi. Izu Peninsula, collector unknown (TI); Mt. Daruma, Izu Peninsula, *Kanai*, s.n. (TI); Mt. Ashitaka, *Kanai* 5847 (TI); Mt. Senmai, collector unknown, (TI); Gotemba, *Hisanchi*, s.n. (MSC, TI). TOCHIGI PREF.: Chuzenji, *Juenberg*, s.n. (A); Nikko, *Kanai* 4030 (TI); Nikko, *Gillis* 4788 (MSC); Chugiyi, *Gillis* 4781 (MSC); Sampeitoge Pass, *Mishida*, s.n. (MSC). TOKYO PREF.: Mitake, *Kanai* 163 (TI); Motohachioji, *Kanai*, s.n. (TI); Asakawa, *Kanai* 3221 (TI); Okutama, *Kanai* 4388 (TI); University Botanical Garden, *Gillis* 4625 (MSC).

WAKAYAMA PREF.: Kii, *Murata* 15138 (MSC); Mt. Koya, *Uno*, s.n. (A). YAMAGATA PREF.: Asahimachi, *Kanai*, s.n. (TI). YAMAGUCHI PREF.: collector and exact locality unknown (TI); YAMANASHI PREF.: Asagoduta, Fuji, *Hayata*, s.n. (TI); Mt. Kenashi, foot of Fuji, *Kanai*, s.n. (TI); Mt. Riugatake, foot of Fuji, *Kanai*, s.n. (TI); Aokihara, *Hayata*, s.n. (MSC). PREFECTURE UNCERTAIN: Lake Chuging, *Wilson* 6876 (A, BM). Ugosakai, *Muramatsu*, s.n. (TI); foot of Mt. Nabekamudi, *collector unknown* (TI). Mt. Azima, *collector unknown* (A, TI). **Kyushu.** FUKUOKA PREF.: Takosara, *Takeda*, s.n. (E). KAGOSHIMA PREF.: Mt. Kirishima, *Wilson*, s.n. (A). KUMAMOTO PREF.: Mt. Asozu, *Kanai*, s.n. (TI); Tuabye Aso-san, *Maximowicz*, s.n. (BM). **Shikoku.** ECHIME PREF.: Mt. Dogo, *Satonii*, s.n. (TI); Uagima, *collector unknown* (TI). KOCHI PREF.: Nanogawa, *collector unknown* (TI); Nanogawa, *Watanabe*, s.n. (GH).

UNION OF SOVIET SOCIALIST REPUBLICS. **Kurile Islands.** Kunashir, Rebansa, *Shisahama & Takehashi*, s.n. (SAP); Kaikaramur, *Tatewaki*, s.n. (SAP); locality unknown, *Vorobjov* 92 (LE); Kinakai, *Pobedimova*, s.n. (MSC). Shakotan, Mt. Shakotan, *Ohwi* 526 (SAP). Sikotan, Sikotan-yama, *Vorobjov*, s.n. (MSC). **Sakhalin:** South Sakhalin Preserve, Nevelsky Region Kuznepovo, *Kravchenko* 49 (LE); locality uncertain, *Glehn*, s.n. (LE).

In naming a Maximowicz collection from Hakodate, Greene (1905) expressed the idea that his *Toxicodendron orientale* was sufficiently different from "any and all New World species that it forms a fair subgenus." The type has both flowering and fruiting stems, but suggests two inaccuracies in Greene's description. He indicated that the Japanese poison-ivy differs from North American poison-ivy by its petals not being "nervose and epicarp thinner . . ." These characters are, however, not borne out on the type specimen.

The first poison-ivy from eastern Asia with which one might be concerned nomenclaturally was described as *Rhus ambigua* Lavallée, a nomen nudum. Dippel (1892) supplied the diagnosis. The name was used in connection with *Ampelopsis japonica*, a supposed synonym. Presumably Lavallée studied a living plant in the arboretum and therefore the name cannot be typified. Because the description is so brief, the name is frequently — and erroneously — attributed to Dippel (1892) whose description is more detailed. Masamune (1934) erroneously equated this name with *Rhus succedanea* var. *japonica* Engl. in DC. For

those who would recognize this taxon as a species of *Rhus*, the combination *Rhus ambigua* may not be used in any case since it was first published by Unger (1849) for an Eocene fossil of Italy, a plant not similar to the one under consideration here, but rather of the genus *Zanthoxylum* of later authors (Edwards and Wonnacott, 1935).

Nakai (1916b) felt that the poison-ivy called *Rhus toxicodendron* by Miquel (1865, and often attributed to Miquel as author of the binomial in Japanese literature) and *Rhus toxicodendron* var. *vulgaris* (sensu Engler, 1883) should be *R. ambigua* Lav. In his opinion, *R. orientalis* or *Toxicodendron orientale* should be reserved for Chinese or Hokkaido poison-ivy (Nakai, 1916b and Tanaka, 1916).¹⁶ Nakai (*ibid.*) went on to say that Japanese poison-ivy was not poisonous, had larger flowers, more brown trichomes in the vein axils, and more nearly entire leaflet margins in comparison to American poison-ivy. His concept of *R. toxicodendron* was essentially that of Linnaeus, and therefore he felt that the binomial could not be used for any of the climbing forms in Japan.¹⁷

Hara (1939) compared Chinese and Japanese poison-ivy and arrived at the conclusion that they are the same species. He recognized that fruit pubescence is a critical character, but pointed out that this feature is variable even among specimens collected in the same area. He indicated that Chinese specimens are occasionally found to be nearly glabrous. It is likely that he was examining immature fruits when he made this observation, for the mature fruits are hispid in all Chinese poison-ivy specimens I have seen. Although Hara did not believe that the narrowness of the leaflets could be used to separate the two taxa, I feel that the ratio of length-to-width of the terminal leaflet is of taxonomic significance, and not narrowness (i.e., width)

¹⁶Schneider (1901) suggested that *Ampelopsis orientalis* Planch. in DC. is synonymous with *R. orientalis*, but this plant is most likely *Parthenocissus tricuspidata*.

¹⁷The common name of Japanese poison-ivy, tsuta-urushi ("climbing urushi") attests to the fact that the plant is a liana member of the lacquer tree group.

alone. This ratio is reasonably uniform within each of the two populations and therefore of importance in separating the two. The terminal leaflet in the Japanese populations is always less than twice as long as broad (1.2-1.7), whereas the Chinese populations are characterized by terminal leaflets closely approaching a length twice the breadth (1.9-2.0 times). The more subtle difference of a cuneate leaflet base in Japanese forms as opposed to an attenuate base in Chinese forms is less useful, but nevertheless seems to be a consistent character.

Nakai (1922) described a new species of poison-ivy from northern Hokkaido and the Rishiri Islands which he called *Rhus rishiriensis* (tachii-tsuta-urushi). Hara (1954) reduced this species to a form: *Rhus ambigua* f. *rishiriensis*. Koidzumi (1924) described its habitat as being the conifer forest of the Oshidomari Mountains of Rishiri To at 1050 meters. The taxon's only distinguishing character is that it does not appear to be scandent. Whereas the habit is generally considered to be reliable in poison-ivy taxonomy, in this case it is considered suspect. At the moment there seems to be little to verify its restricted growth on genetic grounds. The holotype (at TI) is indistinguishable from all other Japanese poison-ivies. It is most likely not cognate to *Toxicodendron rydbergii* of North America which, like its Japanese counterpart, does not climb and curiously similarly, does not grow south of the 44th parallel of latitude (Gillis, 1962). Forma *rishiriensis* appears impossible to characterize outside of the field, has not been proven to be a non-climbing plant at all times, and is inadequately collected. For the present it must be regarded as an ecological form from the windswept insular areas of northern Japan and far eastern U.S.S.R., not to be recognized nomenclaturally.

Toxicodendron radicans subsp. *orientale* grows in dense forests in Japan where it apparently sprouted when the forest was young, simply growing up with the forest. Reproduction within the forest is probably mostly restricted to individuals with some foliage in good light situations. From central Japan northward, it is often found in fir

forests. It is far less of a weedy species than its North American counterparts. Rather, it is a denizen of forest communities of the hills and mountains. Where there has been disturbance, such as a road cut, it becomes more abundant.

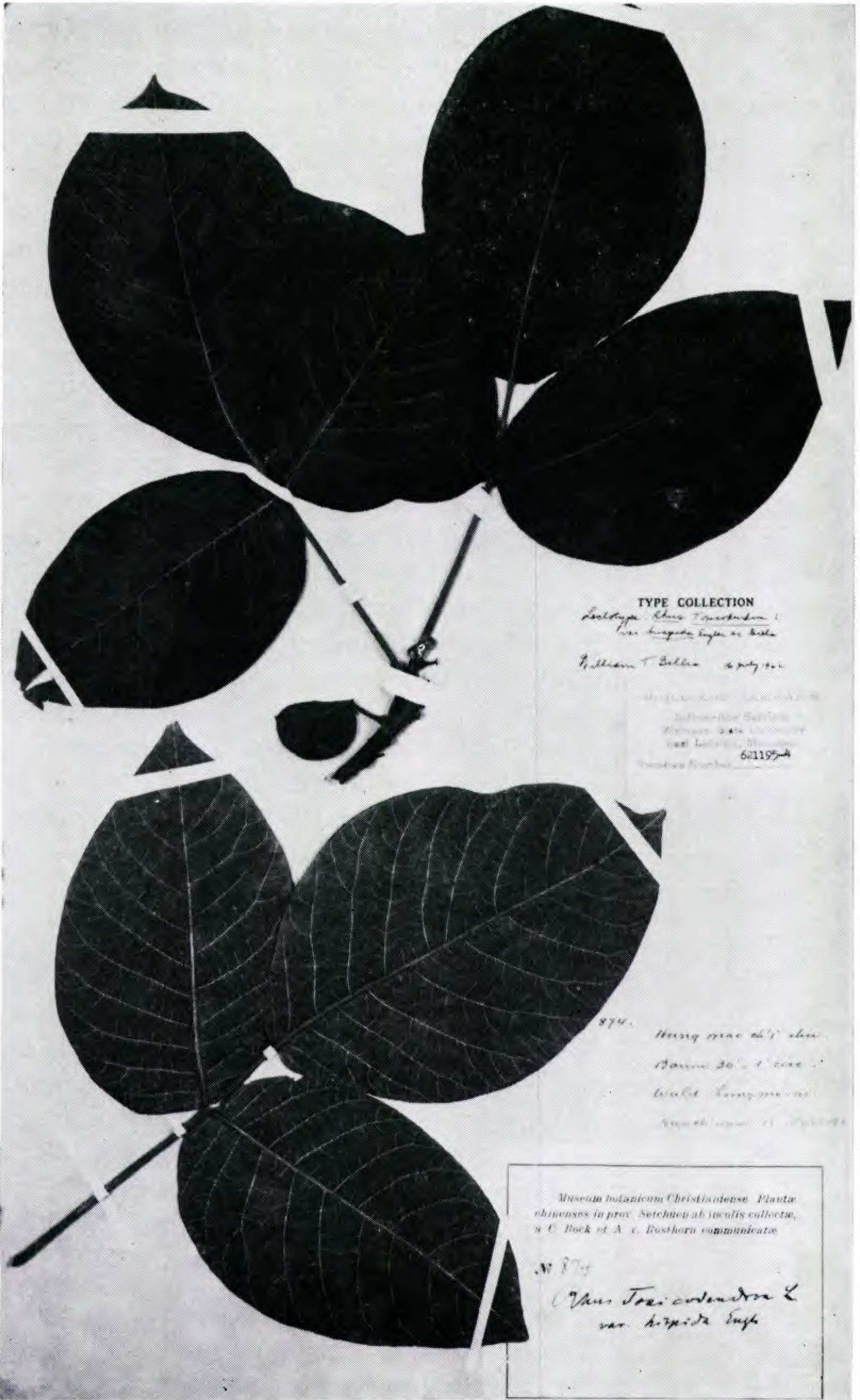
In northern Japan and the Kuriles, it is common in the forests of *Picea jesoensis* and *Abies sachalinensis* along with another liana, *Actinidia kolomikta*. In central Honshu where *Chosenia bracteosa* forms large forests, it is also a common woody climber (Tatewaki, 1950). Elsewhere in Japan, it is found in the pine-fir-redwood woods (*Pinus densiflora*, *P. thunbergii*, *Abies sachalinensis*, *Cryptomeria japonica*). In addition, Tatewaki (1958) has reported it as a typical inhabitant of the associations characterized by either *Aesculus turbinata*, *Fagus crenata*, *Pterocarya rhoifolia*, *Cercidophyllum japonicum*, *Acer mono*, or *Quercus crispula*. Its chief associates in most of these associations are also vines: *Vitis coignetiae*, *Hydrangea petiolaris*, *Actinidia arguta*, and *Schizophragma hydrangeoides* primarily, and secondarily *Celastrus orbiculatus* var. *papillosus*, *Schisandra chinensis*, and *Euonymus fortunei*. In the woods of the Boso Peninsula highlands (Chiba Pref.) the most common trees of the forests in which *T. radicans* subsp. *orientale* grows are *Quercus serrata*, *Castanea crenata*, *Lithocarpus edulis*, *Abies firma*, and *Pinus thunbergii*.

4c. **Toxicodendron radicans** subsp. **hispidum** (Engler in Diels) Gillis, comb. nov. Fig. 37.

Rhus toxicodendron var. *hispidum* Engler in Diels, Bot. Jahrb. Supt. 29: 433. 1900. Type: C. Bock and A. V. Rothorn 874. "Bamm (sic) 30', 1" circ., Wald. Lung mo-ai. Nanch'uan, China (Szechuan), 11 Sept. 1891." (o, lectotype).

Rhus intermedia Hayata, J. Coll. Sci. Imp. Univ. Tokyo 23 (art. 19): 73. 1908. Type: T. Kawakami and U. Mori 2024. Taiwan, Nantou County, Mt. Morrison, 7500 feet elevation, (TI, lectotype).

Widest part of the terminal leaflet blade generally at the middle or above the middle, nearly twice as long as broad,



TYPE COLLECTION

Rhodora chinensis Sieb. & Zucc.
var. *hispida* Sieb.

William T. Sullivan April 1911

Herbarium Christianiense
Museum Botanicum
Christianiense
No. 1, Christianiense, Szechuen
Provincia Szechuen
621195-4

874.

Herbarium Christianiense
Museum Botanicum
Christianiense
No. 1, Christianiense, Szechuen
Provincia Szechuen

Museum botanicum Christianiense. Planta chinensis in prov. Szechuen ab incolis collecta, a C. Bock et A. v. Rothorn communicata.

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Rhodora chinensis L.
var. *hispida* Sieb.

attenuate at the base, 6-20 cm long, 4-9 cm wide; petiole 3-11 cm long, terminal petiolule 0.3-3 cm long; tufts of hairs in vein axils below light-colored to red-brown. Fruits flattened, obliquely deltoid, 5-6.5 mm broad, hispid with hairs nearly 1 mm long.

Distribution: Western and central China and Taiwan.
Common name: Taiwan tsuta-urushi. Fig. 38.

Representative specimens. PEOPLES REPUBLIC OF CHINA: **Hupei.** Fang Hsien, *Wilson* 284. (A, E, GH, US). Changyang, *Wilson* 1128 (A, E, NY, US). Patung District, Ichang, *Henry* 4861 (K, NY), Locality unknown, *Henry* 6448 (A, E, BM, GH, MSC, US). **Sikang.** Huping, Paohing, *Wilson* 4647 (A). **Szechuan.** Nanchuan, *Bock & von Rosthorn* 874 (O); *Fang* 895 (A, E, MSC); *Hwang* 48 (A). Mt. Wa, *Wilson* 284a (A). Tachienlu, *Pratt*, s.n. (K). Cheng-Tu Plain,



Fig. 38. Distribution of *Toxicodendron radicans* subsp. *hispidum*.

Fig. 37. *Toxicodendron radicans* subsp. *hispidum*. Lectotype of *Rhus toxicodendron* var. *hispidum* Engel. ex Diels, *Bock & Rosthorn* 874.

Wang 22065 (GH). Yunnan. Liang-shan I'cho, Tsai 51280 (A). Locality unknown. Henry 2005 (K).

REPUBLIC OF CHINA (TAIWAN). Chiayi Co.: Mt. Arisan (also spelled Alishan), collector unknown (TAI); Wilson 10804 (US). Linsley-Gressitt 132 (BM, NY, U); Hayata (MSC); Liu, Liao, Kuo 2021 (MSC). Ilan Co.: Mt. Oobi, collector unknown (TAI). Mt. Bombon, Eizi, s.n. (TI). Nantou Co.: Saramao, Eizi 224 (TI); Mt. Taiheizan, Suzuki, s.n. (UC). Taichung Co.: Pai-koo-shan, collector unknown (TAI); Sing San, Liu, Liao, Kuo, s.n. (MSC). Taipei Co.: Taikoku-syu, collector unknown (TAI); Taitung, Pa-Hsien-shan, collector unknown (TAI). Locality unknown: Niitaka (TAI).

A type was not designated by Engler for *Rhus Toxicodendron* var. *hispidula*, although several specimens were cited in the original description. These were all destroyed by the 1943 bombing of the Berlin Herbarium. The only known extant duplicate of any of the cited specimens is the one at Oslo, hereby designated a lectotype.

Poison-ivy in Taiwan was named *R. intermedia* by Hayata (1908), who thought it was intermediate between sect. *Trichocarpae* and sect. *Venenata* of the genus *Rhus* (sensu Engler), due to the resemblance of the bristly trichomes of the Taiwan poison-ivy fruits to those of *Toxicodendron trichocarpum* (Miq.) Kuntze of Engler's sect. *Trichocarpae*. Even those who would retain this taxon as a species segregate of *Rhus* cannot use *Rhus intermedia* since this combination has been antedated by *Rhus intermedia* Ettingshausen (1888) for a Miocene fossil of Styria, Austria, a plant not conspecific with the taxon under consideration here.

In China poison-ivy is known from the central and western mountains, bordering on the Yunnan and Kweichow Plateaus and the foothills of the Tibetan Plateau in the provinces of Szechuan, Hupeh, Sikang, Kweichow, and Yunnan. There is a hiatus in the distribution of Chinese poison-ivy between these western mountains and the highlands of Taiwan, with none known in the intervening hills and plains. As Li (1963) has noted, there are phytogeographic links between the mountains of Taiwan and those of central and western China. In Taiwan, the plant is found growing on the Paleozoic slates of the central mountains.¹⁸

¹⁸Attempts on the part of the writer to study the poison-ivy com-

The ripe drupes of *Toxicodendron radicans* subsp. *hispidum* possess striking hispid hairs, often nearly 1 mm in total length, the longest fruit hairs in the genus. *Toxicodendron radicans* subsp. *orientale* has fruit with far shorter trichomes, often no longer than those of fruits of eastern North American taxa. On occasion, the fruits are papillose, rather than pubescent. As mentioned elsewhere, the papillose condition is interpreted as a form of incipient pubescence, the papillae being evaginated or reduced hairs. More than likely, mature fruits will be pubescent. The tufts of hairs in the vein axils on the lower surface are red-brown in about 60% of the specimens examined, hyaline or straw-colored in the remainder.

The closest relative of this subspecies is *Toxicodendron radicans* subsp. *orientale* of the Japanese Archipelago, which was probably derived from it. The three foregoing taxa, *T. radicans* subsp. *radicans*, *orientale*, and *hispidum*, are very similar morphologically, almost enough to form a separate cluster of taxa from all the other subspecies. All these plants have pubescent fruits, entire leaflet margins (with at most a single notch on each abaxial edge), the characteristic tufts of hairs that are red-brown or hyaline in the major vein axils on the lower surface of the leaflet, and ovate or elliptic leaflets with acute or acuminate apices.

They differ, however, by several reliable characters. The North American taxon has truncate or obtuse terminal leaflet bases; the broadest portion of the terminal leaflet is below center making the leaflet ovate; the tufts of hairs in the vein axils are generally hyaline or straw-colored rather than red-brown; the fruits are globose, 3-5 mm

plex in China have been frustrated by the current political feud between the United States and the Peoples Republic of China. Correspondence, both in English and in Chinese, has been sent to the several botanical gardens and herbaria in China listed in *Index Herbariorum* (Lanjouw and Stafleu, 1964), all to no avail. A professor of biology at Nanking University was willing, but unable, to be of help. Even intercession on my behalf by journalist Edgar Snow with Premier Chou En-Lai yielded no specimens nor information. Because of these political difficulties, no specimens from any herbarium in the Peoples Republic of China were examined.

broad. The two Asiatic subspecies, on the other hand, have attenuate or cuneate terminal leaflet bases; the broadest portion of the elliptic or obovate terminal leaflet is above the mid-point; the flattened fruits are often obliquely deltoid as in the fruits of other *Toxicodendron* species in the Far East; the fruits are 5-6 mm broad; and the hairs in the vein axils are generally red-brown. The leaflets are generally smaller in subsp. *radicans* than those in the Oriental subspecies, although there is considerable overlap in size.

4d. ***Toxicodendron radicans* subsp. *pubens*** (Engelm. ex Watson) Gillis, comb. nov.

Rhus toxicodendron var. *pubens* Engelm. ex Watson, Bibliog. Index, p. 185. 1878. *Rhus radicans* var. *pubens* (Engelm. ex Watson) Fernald, *Rhodora* 43: 596. 1941. Type: *F. Lindheimer* 247. High in thickets, not climbing, fl. odorous. New Braunfels, Comal Co., Texas. August 1846. (GH, lectotype; MO-1773730, MO-1773731, US-19858, isotypes).

Rhus toxicodendron var. *multifolia* Vines, Trans. Texas Acad. Sci. 26: 75. 1943. Type: *Robert A. Vines* B-3092. Bray's Bayou, Houston, Harris Co., Texas. 50 feet. July 1939. (SMU, holotype; MSC-190169, isotype).

Vine or shrub with aerial roots. Leaflet blade ovate, serrate, notched, or occasionally with one lobe on each edge; scabrous or rarely glabrous on the upper surface, often with a line of minute, curly hairs on the midrib, densely strigose, hirsute, or velutinous on the lower surface, velvety to the touch; without tufts of hairs concentrated in the vein axils. Terminal leaflet 3-20 cm long, 3-11 cm wide, acuminate; petiole 2-13 cm long, hispid, villos, or tomentose; terminal petiolule 0.3-5.0 cm long; veins on lower surface light in color, usually prominent and raised above the surface. Fruits glabrous, often glaucescent, rarely with incipient papillae or hairs, 3.0-4.5 mm broad.

Distribution: Former Eocene Embayment region of



Fig. 39. Distribution of *Toxicodendron radicans* subsp. *pubens* and subsp. *verrucosum*.

Lower Mississippi Valley west to East Texas, states of Mississippi, Louisiana, Arkansas, Missouri, Texas, southeastern Kansas. Fig. 39.

Representative specimens. UNITED STATES: **ARKANSAS**. ARKANSAS CO.: Arkansas Post, *Demaree* 21046 (MO, NY, SMU); St. Charles, White River National Wildlife Refuge, *Demaree* 48889 (MSC). CHICOT CO.: along US-82 adjacent to Ditch Bayou, *Gillis* 5939 (MSC). CRITTENDEN CO.: West Memphis, *Demaree* 11118 (GH). DREW CO.: Bayou Bartholomew, Tillar, *Demaree* 14665 (MIL, MIN, NY, SMU). FAULKNER CO.: Conway, *Moore*, *s.n.* (MSC). GARLAND CO.: Hot Springs National Park, Thousand Dripping Springs, *Demaree* 45564 (MSC). HEMPSTEAD CO.: Fulton, *Demaree* 42707 (SMU). HENRY CO.: Windsor Spring, *Hitchcock*, *s.n.* (MO). HOWARD CO.: Ouachita Region, Baker Springs near Umpire, *Demaree* 55705 (MSC). LEE CO.: La Grange,

Mariana-Helena Recreational Area, *Demaree* 47848 (MSC). LOGAN CO.: base of Magazine Mountain, near Blue Mountain, *Palmer* 24810 (A). MARION CO.: Yellville, *Demaree* 47910 (MSC). MONTGOMERY CO.: Mount Ida, *Demaree* 47235 (MSC); Norman, *Demaree* 45436 (MSC). POINSETT CO.: Marked Tree, edge of river, *Demaree* 57252 (MSC). POLK CO.: Big Fork, *Moore, s.n.* (MSC). PULASKI CO.: Arkansas River bottom below Natural Steps, *Demaree* 8569 (A, GH, MO, NY). SCOTT CO.: Mill Creek Recreation Area, 5 miles east of Y City, *Donahue* 228 (MSC). SEARCY CO.: Marshall, *Gillis* 3786 (MSC). **Kentucky.** FAYETTE CO.: Lexington, *Hille* 2, (MSC). **Louisiana.** AVOYELLES PARISH: *Bunkie, Thieret & Williams* 17663 (MSC). BOSSIER PARISH: Bossier City, *Gillis* 3773 (MSC). CADDO PARISH: Shreveport, *Coty, s.n.* (A). CATAHOULA PARISH: Sicily Island, *Gillis* 5954 (MSC). IBERIA PARISH: Jefferson Island, *Thieret* 17425 (MSC). LAFAYETTE PARISH: Lafayette, *Thieret* 17413 (MSC); MADISON PARISH: Tensas River terrace, Tensas Gun Club Refuge, *Ewan* 17578 (MO). MOREHOUSE PARISH: 4.8 miles north of Oak Ridge, *Gillis* 5946 (MSC). NATCHITOCHE PARISH: small creeks near Clarence, *Demaree* 47360 (MSC). ORLEANS PARISH: New Orleans, *Fendler, s.n.* (MO); New Orleans, *Drummond* 74 (E). PLAQUEMINES PARISH: Pilottown, Delta Wildlife Refuge, *Ewan* 17486 (SMU). RAPIDES PARISH: Alexandria, *Ball* 429 (F, GH, MIN, MO, NY, US). RICHLAND PARISH: north of Girard, *Gillis* 5949 (MSC). ST. LANDRY PARISH: Bayou Carron, near Plaisance, *Thieret & Williams* 17538 (MSC). ST. MARTIN PARISH: St. Martinsville, *Langlois, s.n.* (MIN); Lake Martin, *Thieret* 17402 (MSC). ST. MARY PARISH: Cote Blanche Island, *Thieret* 17443 (MSC). WEBSTER PARISH: locality unknown, *Brown* 5339 (A). WEST FELICIANA PARISH: Catalpa, *Pennell* 4270 (NY). **Mississippi.** ADAMS CO.: 6 miles east of Natchez, *Gillis* 5968 (MSC). LEFLORE CO.: 3.7 miles NE of Itta Bena, *Gillis* 5927 (MSC). QUITMAN CO.: north of Marks, *Gillis* 5919 (MSC). SUNFLOWER CO.: Moorhead, *Gillis* 5932 (MSC); shore of Sunflower River between Moorhead and Indianola, *Gillis* 5935 (MSC). WASHINGTON CO.: east of Leland, *Gillis* 5936 (MSC). **Missouri.** CARTER CO.: Big Spring State Park, *Gillis* 3795 (MSC); west side of Current River north of Big Spring State Park, *Houk & Redfearn* 333 (FSU). HENRY CO.: Windsor Spring, *Hitchcock, s.n.* (MO). IRON CO.: Vulcan, *Smith* 441 (F). JACKSON CO.: Courtney, *Bush* 13892 (A, MIN, MO, ND, NY). ST. LOUIS CO.: Kirkwood, *Woodson* 738 (MIN). **Oklahoma.** LEFLORE CO.: Page, *Palmer* 20948 (A, US). **Tennessee.** RUTHERFORD CO.: Rockvale, limestone glades, *Demaree* 47568 (MSC). SHELBY CO.: Capeville, *Gillis* 5901 (MSC); south of Memphis, *Gillis* 5903 (MSC). **Texas.** ARANSAS CO.: 3 miles NE of Rockport, *Jones* 895 (SMU); Aransas National Wildlife Refuge, *Traverse* 1303 (F, SMU, US). BEXAR CO.: San Antonio, *Jermy, s.n.* (GH, NY). BRAZORIA CO.: Columbia, *Bush* 142 (A, MO, US). BRAZOS CO.: College Station, *Parks* 20714 (SMU); CHEROKEE CO.: Larissa, *Bush* 5589 (A). COLORADO CO.: 5 miles NE of Columbus

on stream bank, *Shinners*, 14612 (SMU). COMAL CO.: New Braunfels, *Lindheimer* 247 (GH, MO, US). COOKE CO.: Gainesville, *Cory* 56120 (SMU). HARDIN CO.: Sour Lake, *Lundell & Lundell, s.n.* (NY). HARRIS CO.: Houston, *Fisher* 33147 (US); North Shore Development, Lake Houston, *Traverse* 1007 (F, US); Bray's Bayou, Houston, *Vines* 242, B-3086, B-3092 (SMU, MSC, US). SAN PATRICIO CO.: Sinton, *Jones* 966 (SMU); Sinton, *Traverse* 1236 (F, SMU, US). WILSON CO.: SE of Floresville, *Parks* 48746 (NY).

The epithet *pubens* is attributed to Engelmann in Watson's Bibliography (1878). It is accompanied by a reference to Gray (1850) who supplied a description in Latin. No type specimen is cited. After Gray's discussion of Lindheimer's collection of *Rhus verrucosa* (see treatment on that topic under *Toxicodendron radicans* subsp. *verrucosum*), he discussed a specimen which he called only "*Rhus toxicodendron* var.". A specimen at the Gray Herbarium fits his description and furthermore was probably seen by Gray. It is labeled "*Rhus toxicodendron* var. *pubens*" in Engelmann's handwriting, probably the source of Watson's attribution of the name to Engelmann. It is the one specimen most likely seen by Watson, the publishing author. Fernald (1941) felt that this specimen was "either the type or isotype." I herewith designate it as the lectotype.

The type comes from the western end of the range of this subspecies where its range overlaps that of subsp. *verrucosum*. The specimen on the lower right of the type sheet has been annotated as *Rhus radicans* var. *verrucosum* (sic) by Fernald, but it is too pubescent for that taxon. It is more likely an intergrade between subsp. *pubens* and subsp. *verrucosum*, bearing the pubescence of the former and the lobing of the latter.

The name *R. toxicodendron* var. *multifolia* Vines is not validly published (no Latin diagnosis), ungrammatically named (should be *multifoliata*), and later abandoned by its author (Vines, 1960). Extra leaflets occur sporadically on individuals in the poison-ivy complex, but are not of population significance, chiefly since plants with extra leaflets generally possess the normal trifoliolate condition as well. The type specimen indicated by the author comes from a park in the city of Houston, Texas, although it was not

marked as the type. It was cited as being in Vine's personal herbarium at the time of the publication of the name, but this herbarium has subsequently been incorporated into the SMU Herbarium.

Subspecies *pubens* is distinguished from subsp. *negundo* by its pilose leaves which are broad, the terminal leaflets often being as wide or wider than long. It occurs in the western Gulf Coastal Plain where subsp. *radicans* is also found. It may be distinguished from subsp. *radicans* by its glabrous fruits and pubescent leaves. Furthermore, the leaflets of subsp. *pubens* usually have coarse teeth on the margins, whereas those of subsp. *radicans* are entire. In Arkansas and Missouri, this subspecies appears to form hybrids over a large area with subsp. *negundo* and to some extent with subsp. *radicans*. At least there is significant diversity over a large area. (See discussion under Hybrids, Crosses, and Intergrades.)

The subspecies is most distinctive in the former Eocene Gulf Embayment, particularly in what is locally called the "delta" region of northwestern Mississippi, southeastern Arkansas, and the eastern part of Louisiana, i.e., the cotton-growing region. From the Mississippi River eastward, the subspecies is replaced abruptly by subsp. *radicans* in the pine region of southern Mississippi. The transition to other taxa is more blurred to the north and west in Tennessee, Arkansas, Missouri, Louisiana, and Texas.

This plant inhabits the southeastern evergreen forest of the Mississippi alluvial plain. Its tree associates are most often *Liquidambar styraciflua*, *Quercus virginiana*, and *Ulmus crassifolia*. Because of the tendency of the plant to be weedy, it often occupies a host of ruderal sites, regardless of the plant associations involved. E. Lucy Braun (1950) describes it as a shrubby component of the oak-hickory forest of the Mississippi embayment section. Its soil preferences are those of terraces of the Old Mississippi Valley south to the present delta. In a few instances it is known from highly calcareous lithosols.

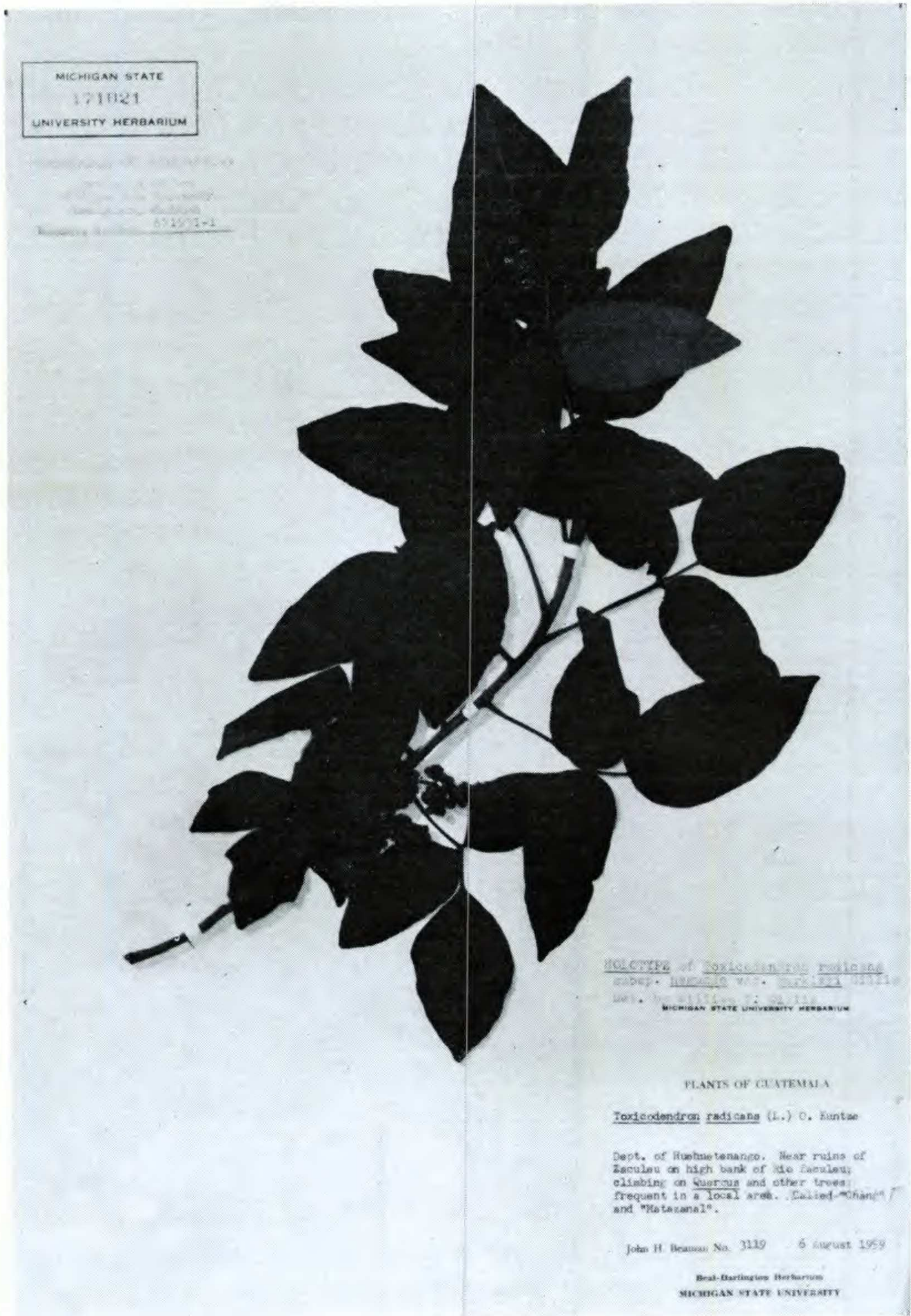


Fig. 40. Type of *Toxicodendron radicans* subsp. *barkleyi* Gillis, Beaman 3119.

4e. **Toxicodendron radicans** subsp. **barkleyi** Gillis, subsp. nov. Fig. 40.

Type: *John H. Beaman* 3119. Guatemala, Department of Huehuetenango. Near ruins of Zaculeu on high bank of Rio Zaculeu, 1850 m elevation. Climbing on *Quercus* and other trees; frequent in a local area. Called "Chang" and "Matazanal." 6 August 1959. (MSC-171021, holotype; DUKE, ENCB, GH, NY, TEX, UC, US, isotypes).

Rhus villosum Sessé and Moçino (as *uillosum*), Pl. Nov. Hisp., p. 47. 1887, non *Rhus villosa* L.f., Suppl. p. 183. 1781, nec Hochet ex A. Rich., Tent. Fl. Abyss. 1: 145. 1847, nec E. Mey. ex Engl. in DC., Monogr. Phaner. 4: 427. 1883, nec Engler, Bot. Jahrb. Supt. 24: 501. 1898. Type: *Sessé and Moçino, Castillo et Maldonado, 1787-1795-1804, No. 856*. "Habitat in Ayahualtempam prope Chilpam et in capite Bonae Spei." (MA, lectotype).

Vitis vel frutex radicellibus aeribus. Folioli integri vel subintegri aut incisuribus interdum, glabrati usque velutini pagina supera folioli, strigosi, pilosi dense, vel tomentosi pagina inferna. Fructi glabri aut puberuli. Differt a subsp. *divaricato* foliis pubescentibus et foliolis aliquantum latioribus, et a subsp. *pubenti* foliolis integribus vel subintegribus et foliolo terminali elliptico seu lanceolato.

Vine or shrub with aerial roots. Leaflets entire or subentire or with occasional notches, ovate to elliptic or elliptic-lanceolate, glabrate to velutinous on the upper leaf surface, strigose, tomentose, or densely pilose on the lower surface. Terminal leaflet blade 3-14 cm long, 1-10 cm broad, petiole 2-12 cm long; terminal petiolule 0.5-5 cm long. Fruits glabrous or puberulent, 3.0-5.0 mm broad. Stem of the season pilose to wooly.

Distribution: Mexico and Guatemala. Fig. 41.

Representative specimens: MEXICO. **Chiapas**: 1 mile north of Jitotol on road to Pueblo Nuevo Solistachuacán, *Breedlove, s.n.* (DS). **Distrito Federal**: Chapultepec Park, Ciudad México, *Bourgeau* 94 (GH); *Gillis* 3726 (MSC). **Durango**. North of Coyotes, Quebrado de San Juan, *Maysilles* 7194 (MICH, US). **Guerrero**: Ayahualtempam near Chilapa, *Sessé and Moçino* 930 (MA). Omilteme, *Nelson* 7059

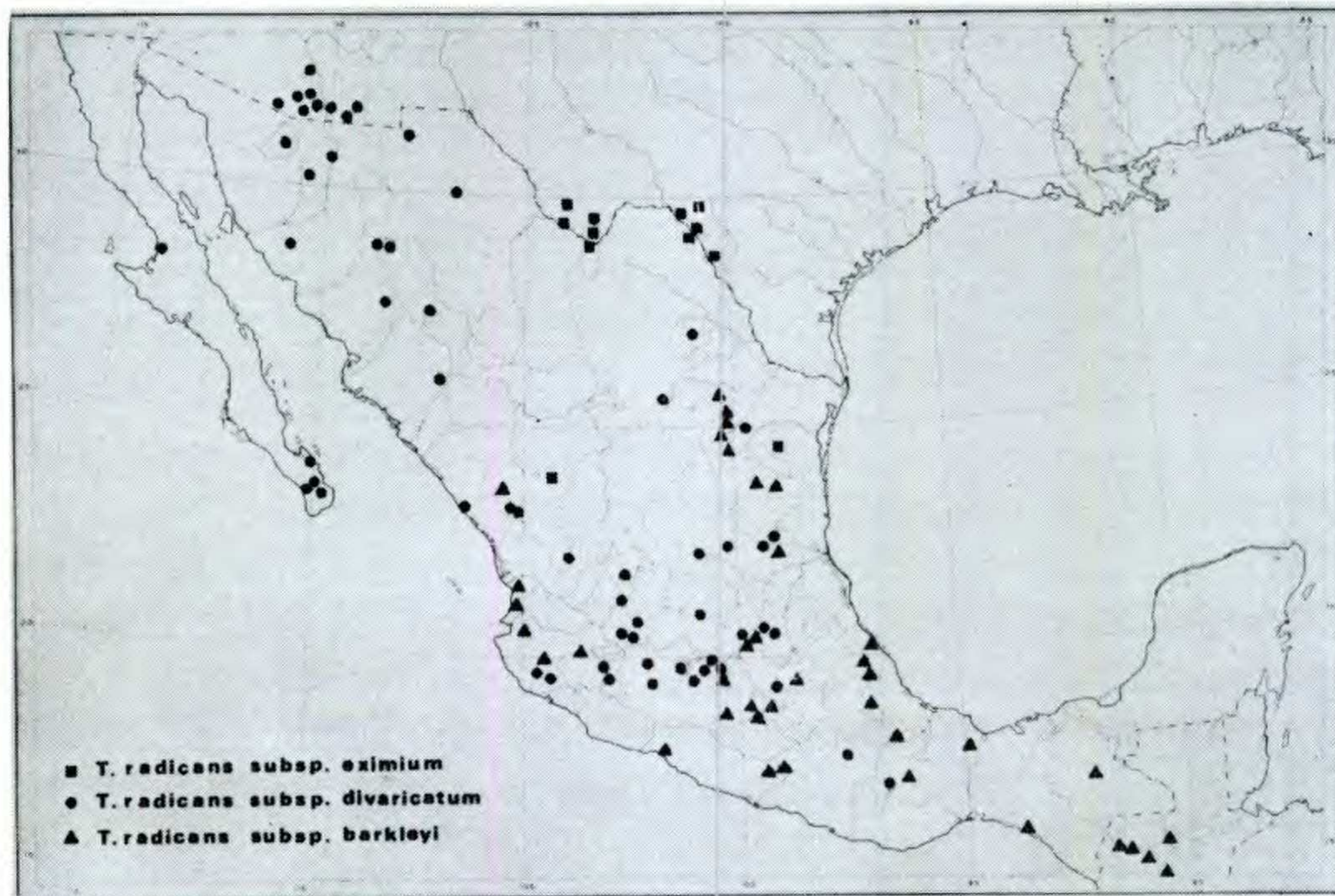


Fig. 41. Distribution of *Toxicodendron radicans* subsp. *barkleyi*, subsp. *divaricatum* and *eximium*.

(US). Vallecitos, Montes de Oca, *Hinton* 10551 (ARIZ, F, GH, NY). Mina, *Hinton* 10492 (A, MO, NY). Hidalgo: Rancho Viejo, Municipio de la Misión, *González Quintero* 1002 (MICH, MSC). Tecozantla, *Salazar*, s.n. (US). Jalisco: Headwaters of Rio Mascota, 4-7 miles south of El Rincón, road to sawmill called LaCumbre, *McVaugh* 21490 (MICH). Summit of plateau and steep mountainsides above Amacueca, road to Tapalpa, *McVaugh* 20660 (MICH). Summit of pass 7-8 road miles NW of Los Volcanes, between Ayutla and Mascota, *McVaugh* 12195 (MICH). México: Tenancingo, *Salazar*, s.n. (TEX). Iztaccihuatl, *Purpus* 269 (MO). Morelos: Cuernavaca, *Trelease* 106 (ILL). Tetecala, *Urbino*, s.n. (TEX). Valle del Tepeite, *Lyonnet* 987 (US). Nayarit: Oak forest 9 miles north of Compostela, *McVaugh* 18737 (MICH). Arroyo 3.5 miles SW of Jalisco, road to El Malinal, *McVaugh* 14917 (MICH). Nuevo León: Alamar about 15 miles SW of Galeana, *Mueller and Mueller* 750 (A, F, TEX). 10 miles south of Monterrey, *Hennen* 67-21 (MSC). Horsetail Fall, SW of El Cercado, 24 miles south of Monterrey, *DeJong* 1818 (MSC, MU). Cerro del Silla, near Monterrey, *Nelson* 6688 (US). Oaxaca: San Miquel Alborrados, *Nelson* 534 (US). Cuyamecales, Distrito de Cuicattan, *Conzafta and Gomer*, s.n. (TEX). San Luis Potosí: 1.5 miles east of El Plantanito, 20 miles east of Ciudad del Maíz, *McVaugh* 10482 (MICH). Tamaulipas: Victoria, *Palmer* 228 (F, GH, MO, NY, US). Veracruz: Orizaba, *Botteri*, s.n. (US). Colipa, *Liebman*, s.n. (NY).

Encinal, Matrata, *Matuda* 1368 (A, F). Jalapa, *Smith* 1897 (GH). Other: Valle de La Lagima. *Martinez*, s.n. (TEX).

GUATEMALA. Alta Verapaz: Coban, *Turchheim* 111784 (GH, NY, US). El Quiche: Between San Francisco and Cotzal, *Sharp* 45178 (F). Guatemala: San Juan Sacatepequez, *Lewis*, s.n. (F). Huehuetenango: Paso de Boquerón along Río Trapichillo below La Libertad, *Steyermark* 51123 (F, TEX). Los Pintos, SW of Huehuetenango, *Steyermark* 48166 (TEX). Near ruins of Zaculeu on bank of Rio Zaculeu, *Beaman* 3119 (DUKE, ENCB, GH, MSC, NY, TEX, UC, US).

This subspecies differs from subsp. *divaricatum* by its pubescent leaves and its somewhat broader leaflets, and from subsp. *pubens* by its entire or subentire leaflets and its elliptic or lanceolate terminal leaflet. The subspecies is named for Dr. Fred A. Barkley, a long-time student of the Anacardiaceae, whose earlier (1937) monographic studies in the poison-ivy complex have been a valuable source of information to this study. Distribution: Mexico: moderate elevations in Sierra Madre Oriental south to Sierra de los Cuchumatanes in Guatemala.

This subspecies is found in the Sierra Madre Oriental, the Sierra Madre del Sur of Mexico, and the Sierra de los Cuchumatanes of western Guatemala. It forms intergrades with subsp. *divaricatum* in the trans-Mexican volcanic belt as far west as southern Jalisco. It is the eastern Mexican counterpart of subsp. *divaricatum*, which occurs in western Mexico although subsp. *barkleyi* was probably not derived from subsp. *divaricatum*, but rather from an ancestral population of subsp. *pubens*. The eastern subspecies has very pubescent leaves, whereas the western one is characterized by glabrous leaves. The leaflet shape and prominence of veins are shared by both subspecies.

The Sessé and Moçiño name *Rhus villosum* is an enigma. It has been thought to be a misprint for *villosum* because of the frequent interpolation of u's and v's in earlier writing. This suspicion is especially cogent since the leaves are often villous. The name is herein considered to be an orthographic variation of *villosum*.

This subspecies grows chiefly on soils high in calcium, such as the limestones of the Cuchumatanes Mountains and other limestone and calcareous outcroppings of Mexico. It



Fig. 42. *Toxicodendron radicans* subsp. *negundo*. Type of *Toxicodendron negundo* Greene, Norton 73.

was found to be abundant on the edge of an orchard in Galeana, Nuevo León, Mexico, where the soil calcium was higher than in any other soil studied: up to 5700 ppm.

4f. **Toxicodendron radicans** subsp. **negundo** (Greene) Gillis, comb. nov. Fig. 42.

Toxicodendron negundo Greene, Leaf. Bot. Observ. Crit. 1: 117. 1905. *Rhus toxicodendron* (subsp.) *negundo* (Greene) Gates, Trans. Kansas Acad. Sci. 41: 106 (nomen nudum), 1938, republished legitimately, Trans. Kansas Acad. Sci. 42: 13. 1939. *Rhus radicans* var. *vulgaris* f. *negundo* (Greene) Fernald, Rhodora 43: 594. 1941. Lectotype: *J. B. Norton* 73. Low woods in Riley County, Kansas. 28 September 1895 (in fruit). US-352742. Isotypes: GH, KSC, MO-1773717, NY, RM-18888. Paratype: *Norton* 73a, same locality, 1896, (in flower). US-352743. Isoparatypes: GH, KSC, MO-1773718, NY, RM-19505.

Toxicodendron aboriginum Greene, Leaf. Bot. Observ. Crit. 1: 125. 1905. Type: *J. M. Bigelow*, s.n., Indian Territory (Oklahoma), Choctaw Agency, 1853. (US-19845, holotype).

Vine or shrub with aerial roots. Leaflet blade ovate to elliptic, generally notched or serrate, often lustrous in sun forms; glabrate to strigose on the lower surface or with pubescence confined to the veins, not velvety to the touch; no tufts of hairs concentrated in the vein axils below; glabrous on the upper surface with a line of minute curly hairs for several cm along the mid-vein base. Terminal leaflet blade 3.0-20.0 cm long, 1.0-12.0 cm wide, petiole 2.0-16.0 cm long, glabrate, puberulent, hispid, or villous; terminal petiolule 0.5-6.5 cm long. Leaflet tip acute or acuminate; base obtuse or truncate. Fruits glabrous or with a few scattered hairs, 2.5-5.5 mm broad, cream-colored to tan. Branches glabrate to densely puberulent.

Distribution: Canada: southern lobe of Ontario: United States: Great Lakes States south to West Virginia, Kentucky, Tennessee, Arkansas, Oklahoma, west to eastern Kansas, Nebraska, Iowa. Fig. 43.

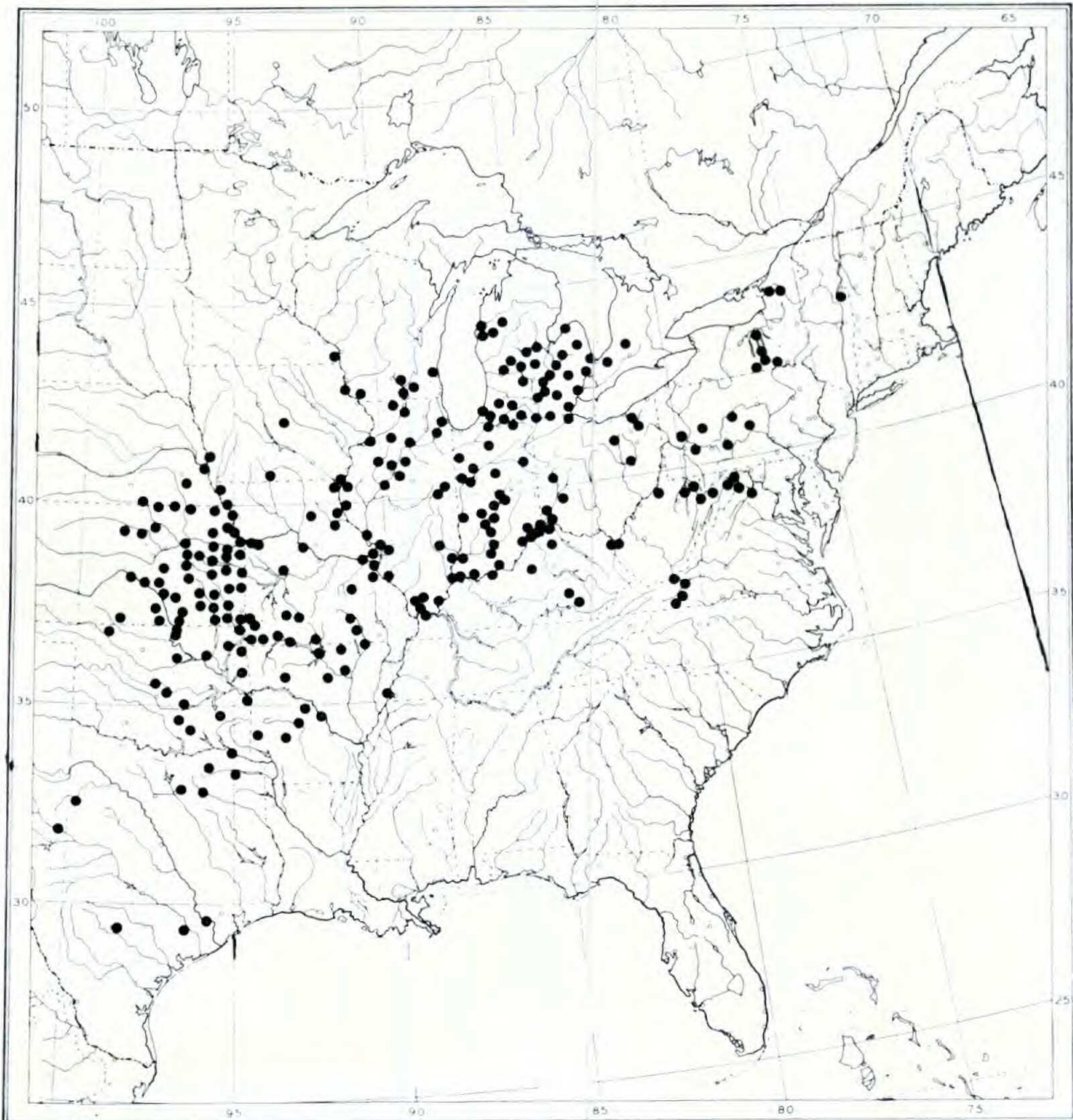


Fig. 43. Distribution of *Toxicodendron radicans* subsp. *negundo*.

Representative specimens: UNITED STATES. **Arkansas:** BAXTER CO.: Norfork, rocky bluffs above Norfork River, *Gillis* 3789 (MSC). BENTON CO.: War Eagle, *Demaree* 6742 (GH, NY, TEX, US). CLARK CO.: Okolona, *Demaree* 17201 (MIN, MO, NY). CLEBURNE CO.: Heber Springs above Greer's Ferry Dam, *Demaree* 45064 (SMU). CRITTENDEN CO.: West Memphis, *Demaree* 11118 (SMU). GARLAND CO.: Hot Springs, *Demaree* 17856 (MO); Magnet Cove, *Palmer* 26617 (A). INDEPENDENCE CO.: Batesville, *Demaree* 17085 (MO, NY). JOHNSON CO.: Knoxville, *Demaree* 19943 (SMU); PERRY CO.: Nimrod, *Demaree* 39638 (MSC). PHILLIPS CO.: Helena, *Palmer* 25097 (A). POLK CO.: base of Rich Mt., *Hopkins & Nelson* 595 (RM); PULASKI CO.: Pulaski Heights, *Demaree* 17319 (MIN); Boyle Park, Little Rock, *Gillis* 3776 (MSC); RANDOLPH CO.: 4 miles SSW Maynard, *Donahue* 216 (MSC). ST. FRAN-

CIS CO.: Forrest City, *Demaree* 47842 (MSC). SEVIER CO.: Bluffs over Little River, Brownstown Ben Lomond, *Demaree* 54004 (MSC). SHARP CO.: Hardy, *Demaree* 27730 (RM, SMU, TEX). **Illinois.** ADAMS CO.: Quincy, *Holton* 174 (F). BUREAU CO.: Ohio, *Ruhl*, s.n. (MO). CALHOUN CO.: Kampsville, *Turner* 467 (F). CHAMPAIGN CO.: Urbana, *Jones* 12640 (MIN, MO, ND, NY). COOK CO.: River Forest, *Eifrig*, s.n. (F); DUPAGE CO.: Naperville, *Powell* 17788 (WIS). HANCOCK CO.: Hancock Twp., *Gates*, s.n. (F). JOHNSON CO.: Tunnel Hill, *Palmer* 15168 (A, MO). KANKAKEE CO.: Kankakee, *Schneider* 671 (F). KNOX CO.: Abingdon, *Batis*, s.n. (A). LAKE CO.: Lake Bluff, *Hutchinson*, s.n. (F). LASALLE CO.: Starved Rock State Park, *Greenman, Lansing, & Dixon* 66 (F, GH, NY); MASON CO.: Bishop, *Chase* 10397 (G). PEORIA CO.: Peoria Heights, *Chase* 9089 (MIN, TEX, WIS). POPE CO.: Golconda, *Palmer* 15390 (A, MO, US). PULASKI CO.: Mounds, *Palmer* 15072 (A, MO, US). RANDOLPH CO.: Red Bud, *Pammel*, s.n. (MO). RICHLAND CO.: Olney, 1818 (F, US); ROCK ISLAND CO.: Park Bryan, *Harper & Harper*, s.n. (A). ST. CLAIR CO.: Cahokia, *Eggert*, s.n. (MO). SANGAMON CO.: Stephenson, Freeport, *Johnson*, s.n. (MIN). TAZEWELL CO.: Kerfoot, *Chase* 10957 (F); VERMILION CO.: between Oakwood and Collison, *Jones* 15599 (MO, WIS); WILLIAMSON CO.: Pittsburg, *Douglass*, s.n. (MO). WOODFORD CO.: south of Spring Bay, *Chase* 12250 (TEX). **Indiana.** CRAWFORD CO.: Milltown, *Deam* 16414 (A); DEARBORN CO.: Aurora, *Deam* 16111 (A). GIBSON CO.: Mt. Carmel, *Tryon* 2805 (F); HARRISON CO.: Elisabeth, *Deam* 16349 (A). HENRY CO.: Mt. Summit, *Kriebel*, s.n. (SMU). HOWARD CO.: Kokomo, *Ek* 57 (US). HUNTINGTON CO.: Huntington College campus, *Henderson*, s.n. (FSU). JEFFERSON CO.: Hanover, *Coulter*, s.n. (F). JOHNSON CO.: Edinburgh, *Deam* 19079 (A). LAGRANGE CO.: Wolcottville, *Deam*, s.n. (SMU). LAWRENCE CO.: Rivervale, *Dean* 17302 (A). MADISON CO.: Ingalls, *Smith* 5619 (F, GH). MONROE CO.: north of Bloomington, *Hawkins*, s.n. (FLAS). NEWTON CO.: Kankakee River State Park, *Thieret* 1295 (F). ORANGE CO.: West Baden, *Deam* 17336 (A). OWEN CO.: McCormack Creek, *Deam* 17519 (A). PERRY CO.: Cannelton, *Deam* 16618 (A). POSEY CO.: Shelton, *Heiser*, s.n. (MSC). PUTNAM CO.: Green Castle, *Grimes* 531 (US). RIPLEY CO.: Laugherty Creek, east of Versailles, *Deam* 16132 (A); ST. JOSEPH CO.: South Bend, *Nieuwland*, s.n. (MO). SWITZERLAND CO.: Cross Plains, *Deam* 16183 (A). TIPPECANOE CO.: West Point, *Gillis* 4274 (MSC). VANDERBURG CO.: Evansville, *Deam* 16781 (A). VERMILLION CO.: Blanford, *Freisner* 19505 (NY). WARRICK CO.: Yankee-town, *Deam* 16711 (A). WELLS CO.: Harrison Twp., *Deam*, s.n. (GH, MIN, MO, US, WIS). WHITE CO.: Furnessville, *Johnson*, s.n. (NY). **Iowa.** CLAYTON CO.: McGregor, *Shimek*, s.n. (WIS). DECATUR CO.: without definite locality, *Anderson*, s.n. (MIN, MO, RM). FAYETTE CO.: Fayette, *Fink*, s.n. (MIN). JOHNSON CO.: Iowa City, *Hitchcock*, s.n. (MIN.). LEE CO.: Keokuk, Jackson Twp., *Hayden* 9364 (GH, MIN, MO, NY). STORY CO.: Ames, *Hitchcock*, s.n. (MO). **Kansas.** ALLEN CO.: without

definite locality, *Hitchcock*, s.n. (KSC). ANDERSON CO.: without definite locality, *Hitchcock*, s.n. (KSC). BARBER CO.: Hardtner, *McGregor* 14822 (SMU). BARTON CO.: without definite locality, *Hitchcock*, s.n. (KSC). BROWN CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). BUTLER CO.: White Water, *Hitchcock*, s.n. (KSC). CHASE CO.: without definite locality, *Hitchcock*, s.n. (KSC). CHEROKEE CO.: Elm Branch, *Jacobs*, s.n. (KSC); COFFEY CO.: LeRoy, *Dunfield*, s.n. (KSC). CONCORDIA CO.: without definite locality, *Hitchcock*, s.n. (KSC). COWLEY CO.: Arkansas City, *Palmer* 22101 (A, US). CRAWFORD CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). DOUGLAS CO.: Lawrence, *Gillis* 6484A (MSC). ELK CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). ELLSWORTH CO.: Terra Cotta, *McGregor* 12644 (US); FRANKLIN CO.: without definite locality, *Hitchcock*, s.n. (KSC). GEARY CO.: Alida, *Gates* (KSC). JACKSON CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). JEFFERSON CO.: Perry, *Clothier*, s.n. (KSC). JOHNSON CO.: without definite locality, *Pinchomb*, s.n. (KSC). KIOWA CO.: without definite locality, *Hitchcock*, s.n. (KSC). LABETTE CO.: Montana, *Rydberg & Imler* 305 (KSC, NY). LINCOLN CO.: without definite locality, *Hitchcock*, s.n. (KSC). LINN CO.: Pleasanton, *Hitchcock*, s.n. (KSC). MARION CO.: without definite locality, *Hitchcock*, s.n. (KSC). MITCHELL CO.: Beloit, *Hitchcock*, s.n. (KSC). MONTMORENCY CO.: without definite locality, *Hitchcock*, s.n. (KSC). MORRIS CO.: Kelso, *Good* 29 (KSC). NEMAHA CO.: Aenida, *Hitchcock*, s.n. (KSC). NEOSHO CO.: without definite locality, *Hitchcock*, s.n. (KSC). OSAGE CO.: Burlingame, *Hitchcock*, s.n. (KSC). OSBORN CO.: Downs, bank of Solomon River, *Palmer* 21335 (A). OTTAWA CO.: without definite locality, *Hitchcock*, s.n. (KSC). POTTAWATOMI CO.: Floersh, *Haymaker*, s.n. (KSC); Onaga, *Day*, s.n. (KSC). REPUBLIC CO.: T. 4S., R. 3W., SW 1/4 Sec. 27, *Morley* 308 (SMU). RICE CO.: without definite locality, *Hitchcock*, s.n. (KSC). RILEY CO.: without definite locality, *Norton* 73, 73a, (GH, KSC, MO, NY, RM, US); ROOKS CO.: Rockport, *Bartholemew*, s.n. (MO). SALINE CO.: Gypsum City, *Palmer* 21329 (A, US). SEDGWICK CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). SHAWNEE CO.: Topeka, *Popenoe*, s.n. (KSC). SMITH CO.: without definite locality, *Hitchcock*, s.n. (KSC). SUMNER CO.: Belle Plaine, *Gates* 19279 (KSC). Wabaunsee, *Gates* 21617 (KSC). WASHINGTON CO.: Linn, *Dodd*, s.n. (KSC). WILSON CO.: Neodesha, *Palmer* 21152 (A); Roper, *Haller*, s.n. (KSC). WYANDOTTE CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). WOODSON CO.: without definite locality, *Lathrop* 391 (US). **Kentucky.** BALLARD CO.: without definite locality, *Anderson*, s.n. (GH, MO). BOYD CO.: Catlettsburg, *McCoy*, s.n. (GH). CHRISTIAN CO.: Pennyriple Forest State Park, *Donahue* 210 (MSC). FAYETTE CO.: 8 miles north of Kentucky River, *Gillis* 6534 (MSC). JEFFERSON CO.: Louisville, N.G.R.R., *Mueller* 447 (HY). KENTON CO.: 2 miles south of Erlanger, *Gillis* 6315 (MSC). LAUREL CO.: 0.6 mile north of high-

way 30, *Gillis* 6538 (MSC). NELSON CO.: 4 miles south of Bardstown, *Donahue* 274 (MSC). ROCKCASTLE CO.: 0.6 mile north of Roundstone Creek, 7.9 miles north of Mt. Cernon, *Gillis* 6535 (MSC). SCOTT CO.: 1.5 miles north of Georgetown, *Gillis* 6532 (MSC). **Maryland.** MONTGOMERY CO.: Plummer's Island in Potomac River, *Kearney*, *s.n.* (US). **Michigan.** ARENAC CO.: Au Gres Twp., *Gillis* 3599 (MSC). BARRY CO.: Maple Grove Twp., *Gillis* 3575 (MSC); Wall Lake, *Gillis* 3595 (MSC). BERRIEN CO.: Three Oaks Twp., Warren Woods, *Gillis* 3510 (MSC); Grand Beach, *Nieuwland*, *s.n.* (ND, MSC). BRANCH CO.: Coldwater, *Gillis & Wetmore* 2871 (MSC). CALHOUN CO.: Athens, *Gillis* 3503 (MSC); Bedford Twp., *Gillis* 2804 (MSC). CASS CO.: Vandalia Twp., *Gillis* 3509 (MSC); CLARE CO.: Clare, *Flicke*, *s.n.* (MSC). CLINTON CO.: Rose Lake Bog, *Howell & Roberts*, *s.n.* (MSC); EATON CO.: Thornapple River bank, *Gillis* 4273 (MSC). GENESSEE CO.: Montrose, *Gillis* 3483 (MSC). GRATIOT CO.: Bethany Twp., *Gillis* 5487 (MSC). HILLSDALE CO.: intersection of Custer and Grace Roads, *Gillis* 4141 (MSC). HURON CO.: Charity Island, Saginaw Bay, *Dodge*, *s.n.* (GH). INGHAM CO.: Haslett, *Gillis* 2850 (MSC); East Lansing, bank of Red Cedar River, *Gillis* 2517 (MSC). IONIA CO.: Morrison Lake, *Muma*, *s.n.* (MSC). ISABELLA CO.: Mt. Pleasant, *Gillis* 3075 (MSC). JACKSON CO.: Jackson 2558 (MSC). KALAMAZOO CO.: adjacent to Gull Creek, *Fischer*, *s.n.* (MSC). KENT CO.: Cascade Twp., along Thornapple River, *Hoffman, Swan, & Sarkissian* 338 (MSC); LENA WEE CO.: Seneca Twp., *Gillis* 3548 (MSC); LIVINGSTON CO.: SW of Pinckney, *Hiltunen* 2096 (WUD); Hamburg, *Farwell* 8343 (BLH). MACOMB CO.: Washington, *Cooley*, *s.n.* (MSC). MASON CO.: Scottville, *Gillis* 3546 (MSC). MECOSTA CO.: Colfax Twp., *Gillis* 3591 (MSC). MIDLAND CO.: Midland, *Erbisch* 1 (MSC). MONROE CO.: Clark Island, *McDonald*, *s.n.* (MSC). MONTCALM CO.: Stanton, *Gillis* 3574 (MSC). MUSKEGON CO.: North Muskegon, *Gillis* 5427. NEWAYGO CO.: Ashland Twp., *Gillis* 3583 (MSC). OAKLAND CO.: Proud Lake Recreation Area, *Gillis* 2586 (MSC); Farmington, *Mühling*, *s.n.* (MSC). OGEMAW CO.: West Branch, *Gillis* 3533 (MSC). OSCEOLA CO.: Sylvan Twp., *Gillis* 3480 (MSC). ST. CLAIR CO.: Port Huron, *Dodge* 3784 (SMU, BLH, NY, TEX, E). ST. JOSEPH CO.: Mendon, *Gillis* 3506 (MSC). SHIAWASSEE CO.: Woodhill Twp., *Gillis* 3479 (MSC). TUSCOLA CO.: Vassar, *Gillis* 5000 (MSC). VAN BUREN CO.: Bangor Twp., *Gillis* 3521 (MSC). WASHTENAW CO.: Ann Arbor, *Sudworth*, *s.n.* (US). WAYNE CO.: Belle Isle, *Farwell* 1492 (BLH). **Minnesota.** HOUSTON CO.: Houston Village, *Butters & Rosendahl* 3014 (GH). **Missouri.** ADAIR CO.: Novinger, *Palmer* 25504 (A, MO). ATCHISON CO.: Watson, *Palmer* 18912 (A, MO, US). BARRY CO.: Roaring River State Park, *Donahue* 222 (MSC). BENTON CO.: Cole Camp, *Palmer* 30035 (A, MO). CARTER CO.: Big Spring State Park, *Donahue* 220 (MSC); CLARK CO.: Dumas, *Palmer* 21882 (A). GREENE CO.: Springfield, *Standley* 8627 (US). HENRY CO.: Windsor, *Hitchcock*, *s.n.* (MO). HOLT CO.: Forest City, *Palmer* 25402 (A, MO). JACKSON

co.: Kansas City, *Bush* 10103 (MO). JASPER CO.: LaRussel, *Palmer* 1517 (MO). JACKSON CO.: Independence, *Bush* 9365 (A, F, MO). JEFFERSON CO.: Kemmswick, *Wislizenus*, *s.n.* (MO). JOHNSON CO.: Columbus, *Palmer* 36615 (A, MO). MARION CO.: Hannibal, *Davis*, *s.n.* (A, MO). MCDONALD CO.: Noel, *Bush* 5757 (A, US). OZARK CO.: Pontiac, *Palmer* 34792 (A, MO). PHELPS CO.: Jerome, *Kellogg* 310 (MINN, MO). RALLS CO.: Bear Creek, *David*, *s.n.* (MO). ST. LOUIS (city); *Emig* 287 (MO). ST. LOUIS CO.: Allenton, *Letterman*, *s.n.* (MIN, MO, NY, US). SHANNON CO.: Montier, *Bush* 144 (M). STONE CO.: Galena, *Palmer* 23879 (A). TANEY CO.: Branson, *Palmer* 4714 (A, E, MO). WEBSTER CO.: Seymour, *Donahue* 221 (MSC). **Nebraska.** CHERRY CO.: Lancaster, wooded banks of Salt Creek, *Turrell*, *s.n.* (ARIZ). SARPY CO.: Bellevue, *Eastman*, *s.n.* (NY). WEBSTER CO.: Red Cloud, *Bates*, *s.n.* (MIN). **New York.** BROOME CO.: Mount Glenwood Ravine, Binghamton, *Millspaugh*, *s.n.* (F). CAYUGA CO.: Montezuma, *Eames*, *Wiegand*, & *Randolph* 12399 (GH). CHEMUNG CO.: East Elmira, *Johnson*, *s.n.* (NY). FRANKLIN CO.: Brushton, *Cutler*, *s.n.* (MSC). JEFFERSON CO.: Plessis, *Gillis* 5376 (MSC); MURRAY CO.: Price's Falls, *Demaree* 12891 (MIN). SENECA CO.: Magee, *Gillis* 3804 (MSC). TIOGA CO.: without definite locality, *Millspaugh*, *s.n.* (US). TOMPKINS CO.: Ithaca, Cascadilla Creek, *Palmer* 768 (GH). **Ohio.** BUTLER CO.: Oxford, *Overholts*, *s.n.* (MO). COSHOCTON CO.: Coshocton, *Moldenke* 12788 (SMU). GREENE CO.: Yellow Springs, *Demaree* 11455 (A, GH, MIN, MO, NY, SMU, WIS). HAMILTON CO.: Cincinnati, *Lloyd*, *s.n.* (MIN). LUCAS CO.: Sylvania, *Wilson* 1512 (WIS). SANDUSKY CO.: Cedar Point, *Jennings & Jennings*, *s.n.* (ND-G). SHELBY CO.: 2.9 miles north of McCartyville, *Gillis* 5431 (MSC). SUMMIT CO.: Cuyahoga River, Akron, *Folz*, *s.n.* (MIN, US). **Oklahoma.** ADAIR CO.: Watts, *Wallis* 8171 (SMU). CADDO CO.: False Washita River between Fort Cobb and Fort Arbuckle, *Palmer* 58 (NY, US). CANADIAN CO.: Yukon, *Palmer* 22120 (A). CHEROKEE CO.: limestone escarpments 8 miles north of Talequah, *Hopkins* 3127 (TEX). CLEVELAND CO.: Norman, *Goodman*, *s.n.* (MSC). COMMANCHE CO.: West Cache Creek, Wichita Mts., *Nagle*, *s.n.* (US). CREEK CO.: Sapulpa, *Bush* 57 (MO). DELAWARE CO.: Dripping Springs, *Wallis* 8180 (SMU). JOHNSTON CO.: Tishomingo, *Palmer* 6412 (A, MO, US). KAY CO.: without definite locality, *White*, *s.n.* (NY). LEFLORE CO.: Choctaw Agency (Skullyville), *Bigelow*, *s.n.* (US). MCCURTAIN CO.: Boss, *Houghton* 3718 (GH, MO, NY). MURRAY CO.: Platt National Park, *Merrill & Hagen* 1124 (F). OTTAWA CO.: Commerce, *Bush* 10142 (A, GH, MO, NY). PAYNE CO.: 2 miles west of Stillwater, *Cockrell* 43 (TEX). PONTOTOC CO.: Ada, *Robbins* 2500 (SMU). PUSHMATAKA CO.: Clayton, *Waugh* 124 (MO). SEQUOYAH CO.: Gore, *Wallis* 8430 (SMU). Woods CO.: without definite locality, *White*, *s.n.* (MIN, RM). **Pennsylvania.** ALLEGHENY CO.: Mt. Lebanon Twp., along creek in Kennedy's wood, *Churchill*, *s.n.* (MSC). DAUPHIN CO., Harrisburg, *Small*, *s.n.* (F, US). FULTON CO.: between Tuscarora and Sideling Mountains, *Gillis* 5113

(MSC); Knobsville, *Gillis* 5116 (MSC). INDIANA CO.: Homer City, *Wahl* 1725 (SMU). MIFFLIN CO.: Reedsville, *Fogg* 16790 (NY). **South Dakota.** CLAY CO.: river bottom, *Taxonomy Class of 1955* (SDU). **Tennessee.** DAVIDSON CO.: Nashville, near confluence of Mill Creek and River, *Bartlett* 3381 (MICH, MSC). **Texas.** BEXAR CO.: without definite locality, *Parks*, B-50, B-66 (MO, MSC). COOKE CO.: Gainesville, *Shinners* 13236 (SMU). DALLAS CO.: Dallas, *Reverchon*, s.n. (GH). FORT BEND CO.: Richmond, *Bray* 80 (US). HARRIS CO.: Houston, *Eggert*, s.n. (MO); San Jacinto, *Boon* 20002 (MO). HUNT CO.: Commerce, *Shinners* 12265 (SMU). JACKSON CO.: Ganado, *Palmer* 9233 (A, MO). KARNES CO.: Panna Maria, *Johnson* 1300 (SMU). KAUFMAN CO.: Terrell, *Tyler*, s.n. (US). RED RIVER CO.: Clarksville, *Cory* 56041 (US). TAYLOR CO.: Abilene, *Talstead* 7657 (GH). TOM GREEN CO.: San Angelo, *Palmer* 11137 (A, MO). WOOD CO.: Hawkins, *Gillis* 3769 (MSC). **Virginia.** FREDERICK CO.: Chambersville, *Gillis* 5705 (MSC). GILES CO.: Pembroke, *Fogg* 14773 (GH, MIN, MO). LOUDOUN CO.: 1 mile down Limestone Branch from highway 15, *Allard* 21392 (US). MONTGOMERY CO.: Blacksburg, *Adams & Wherry* 2230 (A, GH, US). WESTMORELAND CO.: Colonial Beach, *Tidestrom & Bartlett* 5938 (US). **West Virginia.** CABELL CO.: Milton, *Williams* 379 (GH); Huntington, *Gilbert* 186 (GH). GRANT CO.: Mt. Storm, east flank, *Gillis* 5720 (MSC). JEFFERSON CO.: Charles Town, Byrd roadside park, *Gillis* 5701 (MSC); Harper's Ferry, *Gillis* 5700 (MSC). MINERAL CO.: Burlington along Patterson Creek, *Gillis* 5714 (MSC). PRESTON CO.: Erwin on Wolf Creek, *Gillis* 5721 (MSC). RITCHIE CO.: Berea, *Randolph & Randolph* 1385 (GH). TUCKER CO.: Blackwater River, *Moore* 2115 (GH). UPSHUR CO.: Buckskin, *Pollock*, s.n. (KSC). **Wisconsin.** DANE CO.: Mazomanie, *Seymour* 11500 (WIS). GRANT CO.: Rockville, *Wunderlin*, s.n. (WIS). MASON CO.: Bath, *Guther* 7517 (WIS). MILWAUKEE CO.: without definite locality, *Russell*, s.n. (GH). RACINE CO.: Racine, *Hale*, s.n. (WIS). ROCK CO.: Avon, *Fassett* 28113 (WIS). SAUK CO.: *Smith* 53928 (MIL).

CANADA. Ontario. CARLETON CO.: March Twp., *Dore & Breitung* 8516 (E). GRENVILLE CO.: Prescott, *Dore* 18622 (MSC). MIDDLESEX CO.: Poplar Hill, *Gillis* 5370 (MSC). NORFOLK CO.: *Williams*, s.n. (A), *Richardson*, s.n. (A). WATERLOO CO.: Galt, *Montgomery* 893 (GH). Baden, *Gillis* 5581 (MSC).

Gates published the trinomial *Rhus toxicodendron negundo* in a species list in 1938, followed it a year later with a formal description. He did not clearly designate a rank for the epithet *negundo*, but included this enigmatic statement: "The trinomial in botany is usually referred to as a variety, although the designation subspecies would appear to be more reasonable." Even though no rank is clearly stated, it would appear that Gates intended the rank

of subspecies. His 1939 publication should be considered the legitimate and valid publication because it refers to a previously and effectively published name (*Toxicodendron negundo* Greene). Greene described the fruits of his taxon, *Toxicodendron negundo*, as "uncommonly small . . . the length distinctly greater than the thickness," neither character being borne out by the type material.

The type for *Toxicodendron aboriginum* was collected at Choctaw Agency, Indian Territory by J. M. Bigelow on the Whipple Expedition. Although there is no Choctaw Agency today, Gaspare Signorelli (personal communication), philatelic history specialist, informs me that this locality was a small settlement now known as Skullyville, Oklahoma. It was "Choctaw Agency West," just across the border from Arkansas Territory in what is now northern LeFlore County. Greene's description "abruptly apiculate" for the leaflets does not fit the type material which has acuminate leaflets. The fruits have a scattered pubescence which will be discussed later.

It seems strange that this common plant of the mid-western United States should have no formal subspecies or variety name until now. Most manual writers presume that the typical variety is this one and that the Atlantic Coast subspecies must be one which was described later, rather than the other way around. Such presumptions, of course, fly in the face of the historical evidence that the earliest collections in America were from the Coastal regions, and not the interior.

It has been difficult to characterize this subspecies, largely because of the distinctive characters it does *not* have. It does not have the lobed margins of subsp. *eximium* nor of subsp. *verrucosum*, nor the consistently entire or subentire margins of subspp. *radicans*, *orientale*, *hispidum*, *barkleyi*, nor *divaricatum*, nor the pubescent fruits of subspp. *radicans*, *eximium*, etc. Rather, it possesses a variable and moderate degree of pubescence on the leaflets, occasionally scattered-pubescent fruits, some notching on the leaflets, which are clusters of characters found to some degree in other subspecies.

Miller (Gard. Dict. Art. *Toxicodendron*, No. 6, 1768) may have had reference to this taxon in his *Toxicodendron volubilis* (sic). The description of "trifoliate leaves whose lobes are oval, smooth, and cut into sinuses" does not wholly apply, and could relate to other taxa, but also might fit this one. Miller's reference to Dillenius's *Hort. Elth.* seems to provide a lead, but it is to *Toxicodendron amplexicaule, foliis minoribus glabris*, which cannot be typified. There is sufficient doubt as to whether Miller's plant refers to subsp. *radicans* or to subsp. *negundo* that the basionym *volubile* cannot be used. In all likelihood, evidence suggests that, since most specimens available to eighteenth century England were coastal forms, Miller had probably never seen this subspecies.

This subspecies intergrades with *Toxicodendron rydbergii* at its western and northern limits and along Lake Michigan. It intergrades with subsp. *radicans* in the Appalachians, especially the Allegheny ridge and the Blue Ridge Mountains. It seems to form large populations of intergrades with subsp. *pubens* in Arkansas and southern Missouri where the infraspecific boundaries become obscured.

Although subsp. *negundo* and subsp. *radicans* have been confused because of their similarity, the closest relationship of subsp. *negundo* seems to be with subsp. *pubens*. These two subspecies are sympatric in Arkansas and Missouri. Subspecies *pubens* is possibly a specialized, pubescent form from more generalized *negundo* stock. The differences are mainly quantitative ones in degree of pubescence, length-to-width ratio of leaflets, and degree of notching or serration of leaflets.

Some populations of subsp. *negundo* possess a slightly pubescent fruit, reminiscent of the fruits of subsp. *radicans*, under which name Barkley (1937) included them. These populations appear in a few places in northwestern Indiana, the Ohio River counties of Indiana (Deam, 1940), and a few places in eastern Oklahoma. In no way, other than the slightly pubescent fruits, do these plants seem to diverge from the more typical subsp. *negundo*, and they do not

possess the entire leaflets, nor tufts of hairs on the lower leaflet surface characteristic of subsp. *radicans*.

Toxicodendron radicans subsp. *negundo* is frequent in beech-maple, elm-ash, elm-maple, and weedy plant associations. In southeastern Wisconsin, at the northwestern extent of its range, it has been described from the mesic and lowland southern forests (Curtis, 1959). Farther to the south it is a constant species in the northern Appalachian highland division of the hemlock-white pine-northern hardwoods of the Alleghenies and the mixed mesophytic forest and western mesophytic forest of the central states (Braun, 1950), but it is not found in similar forests in the northern reaches of the country such as upper Michigan, Wisconsin, New York, and New England. There it is replaced by the less abundant *T. rydbergii*.

Whereas its related taxon, subsp. *pubens*, is a component of the oak-hickory woods, this subspecies and its other relative, subsp. *radicans*, are seldom found in the dry, undisturbed oak-hickory forest of the northeastern or central United States. Although it is difficult to prove negative associations, more than 58 oak-hickory stands have been examined in the northeastern United States in only four of which poison-ivy has been found. It was usually in a marginal state of existence as a chance invader. Its existence is also marginal in scrub-oak and pine woods of the Coastal Plain or the jack-pine plains of Michigan. It is generally replaced on open dunes by *Toxicodendron rydbergii*, but may appear in the dune forests. Other than these habitat preferences, it occupies habitats similar to those in which subsp. *radicans* occurs.

(To be continued)