

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

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(Continued from page 237)

4g. **Toxicodendron radicans** subsp. **divaricatum** (Greene)
Gillis, stat. nov. Fig. 44.

Toxicodendron divaricatum Greene, Leaf. Bot. Observ. Crit. 1: 122. 1905. *Rhus divaricata* (Greene) McNair, Publ. Field Mus. Nat. Hist. 225, Vol. 4: 69. 1925, non Eckl. and Zeyh., Enum. Pl. Afr., p. 146. 1834. *Rhus greenei* McNair (*ibid.*), insert after page 69. *Toxicodendron radicans* var. *divaricatum* (Greene) Barkley (as *divaricata*), Ann. Missouri Bot. Gard. 24: 433. 1937. *Rhus radicans* var. *divaricata* (Greene) Fernald, Rhodora 43: 596. 1941. Type: *Purpus*, s.n., Mexico, Calmalli, Baja California Norte, 700-900 feet. Jan.-Mar. 1898. (US-383431, lectotype of Barkley, 1937).

Rhus tridentatum Sessé and Moçino, Pl. Nov. Hisp., p. 47. 1887. non Thunb. ex L.f. Suppl. 184. 1781, nec Sond. ex Harv. and Sond., Fl. Cap. 1: 511. 1859, nec Willd. ex Engler in DC., Monogr. Phanerog. 4: 438. 1883. *Rhus saxatilis* DC. Prodr. 71. 1825. Type: "Habitat in calidis Nouae Hispaniae regionibus, et capite Bonae Spei. Floret uere." (MA, lectotype; F-1572884, photograph of type).

Toxicodendron laetevirens Greene, Leaf. Bot. Observ. Crit. 1: 123. 1905. *Rhus radicans* var. *laetevirens* (Greene) Fernald, Rhodora 43: 596. 1941. Type: *J. W. Toumey*, s.n. Arizona, Pima Co., Santa Catalina Mts., 5 May 1894. (US-441725, holotype; A, GH, NY (3 specimens), US-619140, isotypes; MO-144536, photograph of type).

Toxicodendron phaseoloides Greene, Leaf. Bot. Observ. Crit. 1: 123. 1905. Type: *C. V. Hartman* 102. Mexico, Sonora, Turicachi, 5600 feet altitude, 7 Dec. 1890. (US-306157, holotype; GH, NY, isotypes).

Toxicodendron arizonicum Greene, Leaf. Bot. Observ. Crit. 1: 123. 1905. Type: *Edward Palmer* 453a, Arizona,

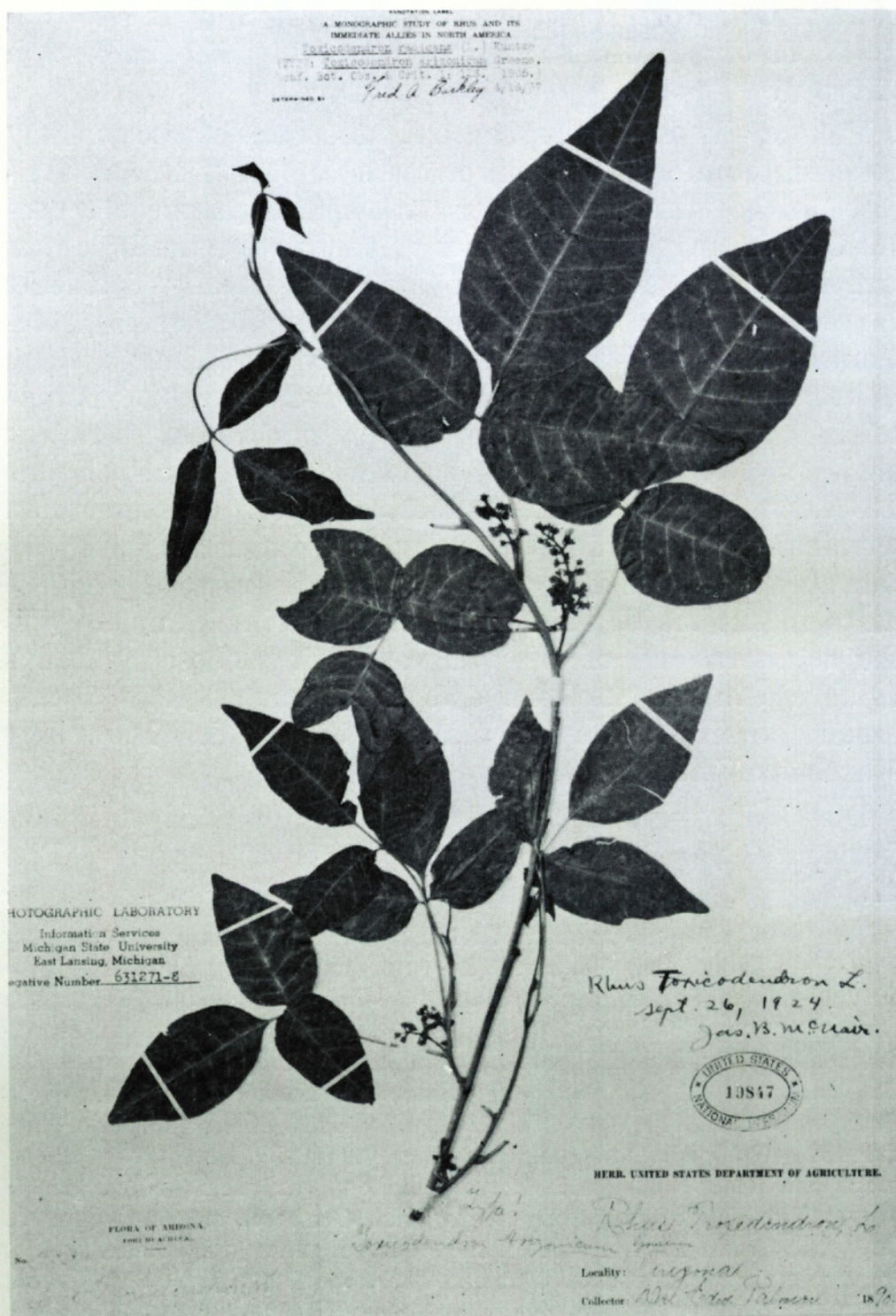


Fig. 44. *Toxicodendron radicans* ssp. *divaricatum*. Holotype of *Toxicodendron arizonicum* Greene, Palmer.

Cochise Co., Fort Huachuca, 26 April-21 May 1890. (US-19847, holotype; GH, NY, isotypes; MO-144549, photograph of type).

Vine or shrub. Leaflets entire, subentire, or occasionally notched, elliptic, lanceolate, or ovate, glabrous, rarely strigose on the lower surface or with sparse pubescence confined to the primary veins, not velvety to the touch; upper leaflet surface glabrous, not lustrous, usually decidedly darker than the lower surface; veins light-colored, prominent on both surfaces. Leaflets usually 1.9-3 times as long as broad with larger leaves southward in the range; petiole 1.5-12.0 cm long, scattered to densely puberulent; terminal blade 1.5-16.0 cm long, 0.6-9.0 cm wide; terminal petiolule 0.2-6.0 cm long; lateral leaflets often as long or longer than terminal. Tip acuminate, usually long tapering; base subcuneate; lower surface with occasional tufts of strigose hairs in the major vein axils, disappearing completely in the southern end of the range. Fruit globose, glabrous (glabrate in the northern end of the range), 3.0-6.0 mm broad, larger southward than in the north. Flowering March to June.

Distribution: Mexico and United States: Sierra Madre Occidental, north to southeastern corner of Arizona. (Fig. 41.)

Representative specimens: UNITED STATES. **Arizona.** COCHISE CO.: Fort Huachuca, *Palmer* 453a (GH, MO, NY, US); Bisbee, *Goodding* 46 (ARIZ); one mile above Paradise, *Blumer* 98a (US); Huachuca Game Reserve, *Goodding* 1104-49 (ARIZ); Chiricahua National Monument, *Clark* 8095 (ARIZ). PIMA CO.: Santa Catalina Mts., *Toumey*, s.n. (A, ARIZ, GH, MO, NY, US); Santa Catalina Mts., Upper Bear Canyon, *Gillis* 6687 (MSC); Santa Catalina Mts., Sabino Canyon, *Rehder* 480 (A), *Jones*, s.n. (RM), *Toumey* 139 (US); Fort Lowell, *Lemmon*, s.n. (MO); Morista Canyon, Baboquivari Mts., *Clark* 11638 (GH); Florida Canyon, Santa Rita Mts., *Graham*, s.n. (NY). SANTA CRUZ CO.: Santa Rita Mts., Sycamore Canyon, *Henly*, *Mason*, & *Stokes* 2257 (ARIZ); Stone Cabin Canyon, *Thorner* & *Griffiths* 139 (ARIZ); Santa Rita Forest Preserve near Amado, *Griffiths* 4222 (MO); vicinity of Nogales, *Rose* 11943 (US); 2.95 miles SW of Patagonia, *Gillis* 6716 (ARIZ, MSC).

MEXICO. **Aguascalientes:** Road to Calvillo, 21 miles west of Aguascalientes, *McVaugh* & *Koelz* 158 (MICH). **Baja California:**

Calmalli, *Purpus*, s.n. (US). El Chorro, *Moran* 7307 (GH). LaLaguna, *Moran* 7431 (ARIZ, GH). **Chiapas:** Paraje of Mahosik, Municipio of Tenejapa, *Breedlove* 14890 (DS, MSC); Pokolom, paraje of Sibanikha, Municipio of Tenejapa, *Breedlove* 11736 (DS). **Chihuahua:** St. Diego, *Hartman* 589 (F, GH, NY, US). Guadeloupe Canyon, *Mearns* 579 (US). Carretos, border of Chihuahua and Sonora, Municipio de Janos, *White* 2551 (GH, MICH, TEX). Loreto near Rio Mayo, *Gentry* 2857 (A, ARIZ, MO). Cajon Creek near US boundary line, *Mearns* 394 (GH, MO, US). **Coahuila:** Sierra de la Gloria, southeast of Monclova, *Marsh* 1973 (F, GH), *Parras, Aguirre & Reko*, s.n. (NY). **Durango:** Cerro Chupadero, 45 miles south of El Salto, west of Pueblo Nuevo, *May-silles* 8211 (MICH). Pueblo Nuevo, *Baker*, s.n. (MSC). Durango, *Palmer* 106 (F). **Guanajuato:** locality unknown, *Dugès* 483 (GH, US). **Hidalgo:** Ixmiquilpan, *Rose, Painer, & Rose* 8950 (NY, US). Barranco de Toliman below Mina Loma de Toro, *Moore* 2599 (GH). **Jalisco:** Sierra del Nayarit, *Diquet*, s.n. (NY). Zahotlan, *Pringle*, s.n. (TEX). Sierra del Halo, *DeJong* 1043 (MSC). Mazamitla, *Donahue* 16 (MSC). Zapotlán, *Salizar*, s.n. (TEX). Vicinity of San Juan Cosalá, north of Lake Chapala, *Puga*, s.n. (MICH). Barrancas of Rio Verde, 20 miles north of Tepatitlán, road to Yahualica, *McVaugh* 17426 (MICH). Ravine bottom in mountains east of Mamantlán, 15 miles SSE of Autlán, *Wilbur & Wilbur* 2074 (MICH). Forested crest of ridge facing Pacific, 10 miles south of Autlán, *Wilbur & Wilbur* (MICH). Summit of volcanic cliffs 8 miles SE of Jalostotitlán, road to San Miguel el Alto, *McVaugh* 17553 (MICH). North slopes Nevado de Colima, near jct. of pack road to Zapotlán, *McVaugh* 14934 (MICH). Sierra del Digre, 3 miles south of Mazamitla, *McVaugh* 13606 (MICH). **México:** Locality unknown, *Sessé & Moçño* 930 (MA). **Michoacán:** Zitacuaro, *Hinton* 13151 (MICH, NY). Mt. Patamban, *Nelson* 6572 (GH, NY, US). Morelia, Loma St. Maria, *Arsène* 2763 (A, GH, MO, US); Morelia, *Arsène* 3011 (A, ILL, MO, NY, US). Apatzingan, Tancitaro Region, Las Barranquillas, *Leavenworth & Hoagstrall* 1817 (F, ILL). Patzcuaro, *DeJong & Longpre* 1081 (MSC). NE of Puenteacillas, north of Ario de Rosales, *Iltis, Koeppen, & Iltis* 865 (WIS). Lava flow east of San Juan Nuevo, 8 miles south of Uruapán, *King & Soderstrom* 4750 (MICH). **Nuevo León:** Hacienda Vista Hermosa, south of Monterrey, *White* 1543 (ARIZ, GH, MICH). Mountains 7 miles east of Iturbide, *McVaugh* 10576 (MICH). **Oaxaca:** Oaxaca Courts motel in Oaxaca, *Beaman* 3660 (MSC). Tamazulapam, *DeJong* 1402 (MSC, MU). **Queretaro:** Tequisquiapan, *Nelson* 3878 (GH). **San Luis Potosí:** 2 km. SE Ahuacatlán, Xilitla, *Rzedowski* 10970 (MICH). Tolen-tino, *Meavry* 7373 (TEX), between San Luis Potosí and Rio Verde, *DeJong* 1571 (MSC, MU). Between Ciudad del Maiz and El Naranjo, *DeJong* 1579 (MSC, MU). El Naranjo, *Donahue* 26 (MSC). **Sinaloa:** Bufa de Surutato, Ocurahui, *Gentry* 6389 (ARIZ, GH, MO, NY, US). East of Mazatlán, *DeJong* 1705 (MSC, MU). **Sonora:** Turicachi, *Hartman* 102 (GH, NY, US). Rancho de la Nacha, *White* 3990 (ARIZ, GH,

MICH, US). Junction of roads to Cananea and Remedios on Rio Magdalena, *Wiggins* 7099 (A, ARIZ, DS, MICH, US). Canyon de los Apaches, north of Aribabi, *White* 2763 (GH, MICH). Region of Cordova, *Borgeau* 2257 (GH). El Rancho del Roble, northeast of El Tigre, *White* 4238 (ARIZ, GH, MICH). Bacoachio near Esqueda, *Wiggins* 11716 (US). Alamo, Mt. Magdalena, *Kennedy* 7106 (US). Canyon of Guadeloupe River, *Smith*, s.n. (NY). Sabino Canyon, Quirocoba, Rio Fuerte, *Gentry* 2246 (A, ARIZ, F, MO, TEX, US). San José Mountains, *Mearns* 1052 (US). Santa Rosa Canyon, near Bavispe, *White* 497 (ARIZ, MICH, GH), Canon International, *White* 3505 (GH, MICH). Sierra Madre Occidental, Sierra Charuca, Canon de Tejas, *Gentry* 6389 (ARIZ, MICH). TAMAULIPAS. Dulces Nombres and east into Tamaulipas, *Meyer & Rogers* 2809 (MO).

Barkley (1937) separated this taxon from others on the basis of a constriction at the side of the seed, a feature often difficult to interpret if it does, indeed, exist. Even the divaricate nature of the inflorescence, which gives the taxon its name, is difficult to see as unique to this plant. When McNair transferred this taxon to *Rhus*, he neglected the Ecklon and Zeyher South African species of that name; so he had a correction slip bound into his article before distribution, changing the name to *Rhus greenei*. So far as I can determine, this name was never affixed to a single specimen.

In citing specimens in connection with *Toxicodendron phaseoloides*, Greene did not designate one of the specimens he saw as type. Barkley (*ibid.*) chose *Hartman* 102. Greene describes his material as having "abruptly acuminate" leaflets, but they are not. Likewise, in his diagnosis of *T. laetevirens*, Greene indicated that the foliage was light green. The type has apparently no brighter green leaves than Greene's twelve other poison-ivy species. Presumably the collections were already dried when Greene affixed names to them, since he was not the collector; therefore, they probably appear today much the same as they did to him.

According to Engler (in DeCandolle, 1883), *Rhus saxatilis* DC. (1825) is a doubtful species and is probably not anacardiaceous. No specimen is known to represent this species in the DeCandolle Herbarium. We would have no idea of what DeCandolle had in mind except for a later

reference to the plant (DeCandolle, 1874). *Rhus saxatilis* was based on one of the Sessé and Moçino paintings (cited as pl. 192 in the Calques des Dessins, DeCandolle, 1874). This is the same plate that was cited as Ic. Fl. Mex. 196 under *Rhus tridentatum* by Sessé and Moçino (1887). Since there is a type specimen for the Sessé and Moçino binomial, we can equate the dubious *R. saxatilis* with a given specimen which is *Toxicodendron radicans* subsp. *divaricatum*. According to Dr. Rogers McVaugh (personal communication), the type locality was in Morelos (Yacapixtla and Cuernavaca).

This taxon flowers from March to June, but chiefly in late April and early May, as distinguished from subsp. *barkleyi*, which flowers from May to August, chiefly in June and early July. Although intergrades between these two subspecies are known, it is likely that their different flowering periods act as a barrier to gene exchange in the regions where their ranges overlap.

Subspecies *divaricatum* is found in southeastern Arizona and western Mexico: the Sierra Madre Occidental and the western portion of the trans-Mexico volcanic belt. It is in this central region of Mexico wherein intergrades, presumed hybrids, have been found between subsp. *divaricatum* and *barkleyi*.

This subspecies is found at moderate elevations, but often is restricted to heavily wooded canyons or south-facing slopes intermixed with tussock grasses. On the one occasion I have had to study it in the field, it was found in moist canyons near creeks or springs. The species of trees making up the dominant vegetation in this locality in southeastern Arizona were *Salix laevigata*, *Fraxinus pennsylvanica* subsp. *velutina*, *Cupressus arizonica*, *Pinus cembroides*, and *Juglans major*. Other species were shrubs such as *Rhus trilobata*, *Rhamnus californica*, *Prunus emarginata*, and *Ceanothus fendleri*. The associated herbs were mostly weeds.

The taxon probably has its closest affinities with subsp. *verrucosum*. The latter subspecies may have been derived from subsp. *divaricatum* after it was isolated from it as a separate population.



Fig. 45. *Toxicodendron radicans* ssp. *verrucosum*. Holotype of *Rhus rhomboidea* Small, Heller 1670.



Fig. 46. *Toxicodendron radicans* ssp. *verrucosum*. Left: Lectotype of *Rhus verrucosa* Scheele, Lindheimer 401. (Right: *Toxicodendron radicans* ssp. *pubens*, Lindheimer 346. These specimens formerly were mounted on the same sheet, see discussion in the text.)

4h. ***Toxicodendron radicans* subsp. *verrucosum*** (Scheele)
Gillis, comb. nov. Figs. 45, 46

Rhus verrucosa Scheele, Linnaea 21: 592. 1848. *Toxicodendron verrucosum* (Scheele) Greene, Leaf. Bot. Observ. Crit. 1: 124. 1905. *Toxicodendron radicans* var. *verrucosum* (Scheele) Barkley, Ann. Missouri Bot. Gard. 24: 435. 1937. (as *verrucosa*). *Rhus radicans* var. *verrucosa* (Scheele) Fernald, Rhodora 43: 596. 1941. Type: *F. Lindheimer* 401. In Hecken auf felsigem Boden auf dem Missionshugel bei Neubraunfels; Lindheimer. May 1845. (GH, lectotype; MO-1774754, isotype).

Rhus rhomboidea Small, Fl. S.E.U.S., 727. 1903. *Toxicodendron rhomboidea* (Small) Greene, Leaf. Bot. Observ. Crit. 1: 125. 1905. Type: A. Arthur Heller 1670. (NY, holotype; E, F-171075, MIN-149968, MO-1774757, MSC-53804, US-213781, isotypes).

Vine or shrub with aerial roots; leaflets rhomboid-ovate, acute to acuminate, usually regularly and deeply incised dentate or acute-angled lobed, glabrous (rarely strigose) above, occasionally with a line of minute curly hairs on the midrib above; glabrous to substrigose below, with hairs confined to the primary and secondary veins, rarely with tufts of hairs in the vein axils; leaflet blade tip sharply acute, base cuneate or obtuse. Petiole glabrous to pilose, rarely short tomentose, 3.2-11.0 cm long; terminal leaflet blade 3-13 cm long, 2-11 cm wide, terminal petiolule 0.5-4.0 cm long. Fruit glabrous 2.5-5.5 mm broad.

Distribution: Texas and Oklahoma: Edwards Plateau and Arbuckle Mts. on limestone. (Fig. 39.)

Representative specimens: UNITED STATES. Texas. BASTROP CO.: Beuscher State Park, *Gillis* 3750 (MSC); Bastrop State Park pine hills, *Duval*, s.n. (TEX); *Gillis* 5161 (MSC). BEXAR CO., Leon Springs *Clemons & Clemons* 830 (RM). COMAL CO.: New Braunfels, *Lindheimer* num. plur. (GH, KSC, MIN, MO, US). CORYELL CO.: 5.6 miles east of Gatesville, *Shinners* 28292 (FSU, SMU). DALLAS CO.: Dallas, Northwest Highway, *Gillis* 5149 (MSC). GILLESPIE CO.: locality unknown, *Jermy*, s.n. (MO). GRAYSON CO.: Denison, *Kohfeldt* 33 (TEX). HARRIS CO.: Houston, *collector unknown* (MO). HARRISON CO.: Marshall, *Gillis* 3772 (MSC). HILL CO.: Hillsboro, *Gillis* 5153 (MSC). KERR CO.: Kerrville, *Heller*, 1670 (ARIZ, E, F, GH, MIN, MO, MSC, NY, US); Turtle Creek, *Bray* 189 (TEX). MEDINA CO.: Castroville, shore of Rio Medina, *Gillis* 5183 (MSC). MENARD CO.: Menard, *Palmer* 11898 (RM). REAL CO.: locality unknown, *Boyles*, s.n. (TEX). Tarrant, Lake Como, *Ruth* 941 (MSC, NY); ravine near Trinity River, *Ruth* 7530 (PH). TOM GREEN CO.: Dove Creek, *Tweedy* 133 (US). TRAVIS CO.: Austin, *Gillis* 3679 (MSC); Bergstrom Air Force Base, *Gillis* 5154 (MSC); Barton Springs, *Krodel* 32 (TEX). UPSHUR CO.: Gladewater, *Gillis* 3766 (MSC). UVALDE CO.: Uvalde along wooded banks of Leana River, *Palmer* 33630 (PH); Uvalde along Frio River, *Gillis* 5193 (MSC). WOOD CO.: Hawkins, *Gillis* 3769 (MSC). LOCALITIES UNCERTAIN: 18 miles SW of View on Edwards Plateau, *Tolstead* 7563 (TEX). Columbia, *Bush* 142 (A). Oklahoma. LOVE CO.: Hickory Creek, *Gillis* 5148

(MSC). MURRAY CO.: Turner Falls, *Gillis* 5142, 5137 (MSC). WOODS CO.: locality uncertain, *White*, s.n. (RM).

MEXICO. Tamaulipas: Vicinity of San José, Mesa de Tierra, *Bartlett* 10405 (MICH).

Because *Rhus verrucosa* was described by Scheele, in order to typify the species a specimen was sought that he may have seen. McKelvey (1955) indicated that plants collected by Lindheimer in Texas in the middle decades of the eighteen hundreds were intended for Engelmann and Gray; any new species were to have been described by them. A number of specimens, however, went with Roemer to Germany and subsequently were described by Scheele in his series of articles under the title "Beitrage zur Flora von Texas." Unfortunately, no specimen representing *Rhus verrucosa* has been found at Heersum where Scheele was Pastor, nor at nearby Hildesheim, nor has any other specimen been found that could have been the one which Scheele examined.

Gray (1850) claimed that *Lindheimer* 346 (Fascicle iii) represented the species that Scheele (1848) had in mind when naming the plant. Scheele described the plant from New Braunfels whence Lindheimer made several collections, each distributed in several herbaria. It appears that all of the specimens in Table 4 represent Lindheimer's poison-ivy gatherings from New Braunfels.

If we can trust Lindheimer's numbering system, the 1847 and later collections must be excluded from considerations of a type, since, before the 1847 collections were made, Roemer took the specimens to Germany — specimens which Scheele described in 1848 (McKelvey, 1955). As Gray (1850) and Fernald (1941) decided, *Lindheimer* 346 probably represents the collection which Scheele had under consideration, but there are two collections so numbered. The collections given the same number in 1847 (added in longhand on a printed label which reads "fasc. iv. 1847") are probably intended to represent the same population, only a later collection, hence the same number. Since *Lindheimer* 401 of the regularly-numbered series is *Lagenaria vulgaris*, the handwritten labels numbered 401 for a poison-ivy no doubt

fall into the category which Blankinship (1907) indicated were specimens not collected in quantity, nor even in numbered exsiccatae, but are private Lindheimer numbers for the Engelmann Herbarium (now at MO). In Gray's listing, *Lindheimer* 245 of the regular series is *Sedum sparsiflorum* and 246 is miswritten as a typographical error: "346" (it appears in a consecutive list between 245 and 247 and hence must be intended to be 246) ; it is *Galium virgatum*. Hence, 245 and 246 are again examples of private numbers for the Engelmann Herbarium, not to be confused with the series of numbered exsiccatae.

The problem remains as to which specimen should be named lectotype. Lacking Scheele's specimen, a good candidate would be the one which was in Gray's possession at the time, inasmuch as Gray wrote that *Lindheimer* 346 was *Rhus verrucosa* of Scheele. At the Gray Herbarium, there is a pair of specimens which were obviously on the same sheet and separated only in relatively recent years. The sheet had two specimens and three labels on it originally. One specimen was probably part of the May 1845 gathering (according to one of the three labels), and the other a part of a September 1846 gathering. The printed label (associating the plants with Fasc. iii, *Lindheimer* 346) was superfluous originally since neither plant was part of the gathering which was distributed under the 346 number as we shall see. The specimen to which the printed label is affixed is now highly significant because it has been annotated "*Rhus verrucosa* Scheele" in Gray's handwriting. The specimen which has now been detached from Gray's annotation more nearly fits Scheele's description than the specimen which remains attached to it, however, and hence has been chosen lectotype (see Fig. 46.)

The excluded specimen mentioned above (No. 246) has been annotated *Rhus radicans* var. *rydbergii* by Fernald, but is more likely a sparsely pubescent *Toxicodendron radicans* subsp. *pubens*. Among other reasons for this choice is the fact that *T. rydbergii* does not occur in this part of Texas. It is indicated in Gray (1850) by a symbol used to designate specimens which were not distributed. A specimen

TABLE 4. LINDHEIMER COLLECTIONS FROM NEW BRAUNFELS, TEXAS

Collection Number	Stage	Date	Herbaria Where Found
245	sterile	August 1846	MO-1774755
246	fruiting	September 1846	GH, MO-1773729
Fascicle iii 346	fruiting	1846	GH, US-1814899, MO-1774754, MO-1774755
401	fruiting (few flowers)	May 1845	GH, MO-1774754
Fascicle iv 346	fruiting	1847	MIN-460085, MO-1773726
unnumbered	flowering	1850	KSC
unnumbered	fruiting	1851	MO-1774756

in the Engelmann Herbarium has the same printed label marked 346, but also has an attached label in Lindheimer's nearly illegible handwriting giving it collection number 401. The condition of the drupes on both of the 401 specimens suggests that they were not fresh at the time of collection, but had overwintered, thereby confirming their May date of gathering. The fruits of all other 346 specimens are fresher and were no doubt produced during the season of collection. At least one earlier worker at the Missouri Botanical Garden has noted on two specimens the idea that 346 = 401.

It is possible that all poison-ivy specimens that Lindheimer had on hand at the time of making his fascicle iii were included in the distribution under the number 346, whether they were collected in 1846 or before, especially if they were destined for Gray or Engelmann, his employers. Whether Scheele and Gray saw plants from the identical gathering can never be ascertained without an extant Scheele plant. What is assured, however, is that the May 1845 and the 346 gatherings have the insect chewings on the leaves which produced exudations of poison, now hardened into black specks. It was these which Gray maintained were the "verrucae magnae subrotundae atropurpureae lucidae" of Scheele's description, exudations which may have led Scheele to his choice of epithet "verrucosa." There is nothing else verrucose about any of the plants he could have had under consideration. Furthermore, the handwritten labels attached to the specimens which Gray examined declare them to be "small shrub on stony prairies" and "high, in thickets and climbing, N. Braunfels" in Engelmann's handwriting. These phrases agree with Scheele's "In Hecken auf felsen Boden auf Missionshugel bei Neubraunfels: Lindheimer."

I believe that the May 1845 collections (*Lindheimer* 401) distributed in part under exsiccatae number 346 with the date 1846 represent what Asa Gray had before him. The Engelmann Herbarium specimen under the same number is therefore an isolectotype. All other specimens distributed under the number 346 are considered to be topotypes

and therefore of interest, but not of nomenclatural significance.

Greene transferred *Rhus verrucosa* and *Rhus rhomboidea* to *Toxicodendron*. It is curious that he did not note the similarity of these two, both of which came from the same general region of Texas.

This subspecies is found on the Edward's Plateau of central Texas and the Arbuckle Mountains of Oklahoma, reaching its northern limit at Turner Falls, Murray County, Oklahoma. In northeastern and south central Texas, the subspecies is found off the Plateau, but more or less maintains its distinct glabrous and sharply lobed leaflets. There is little apparent intergrading with other taxa, although some is suspected.

Collections of subsp. *verrucosum* have occasionally been confused with subsp. *eximium*, probably because both taxa have lobed leaflets. The latter has pubescent fruits and leaves, whereas the former is glabrous. Furthermore, leaflets of subsp. *verrucosum* have acutely-angled lobes, whereas the lobes of leaflets of subsp. *eximium* are rounded.

This taxon grows in the variety of habitats like those of most of its related subspecies but it is most frequently found in limey soils: lithosols, talus, limestone gravels, limestone bluffs, etc. It is also a roadside weed, found on alluvial banks, forest borders, and even in oak-pine woods on fairly excessively drained acid soils. It has also been reported from thin soil over chalk in Dallas County, Texas. Its community relationships have not been extensively explored.

4i. ***Toxicodendron radicans* subsp. *eximium*** (Greene) Gillis, comb. nov. (Fig. 47.)

Toxicodendron eximium Greene, Leaflet Bot. Observ. Crit. 1: 123. 1905. *Rhus eximia* (Greene) Standley, Contr. U. S. Natl. Herb. 23: 668. 1923. *Rhus toxicodendron* var. *eximia* (Greene) McNair, Publ. Field Mus. Nat. Hist. 225 Vol. 4: 68. 1925. *Toxicodendron radicans* var. *eximium* (Greene) Barkley, Ann. Mo. Bot. Gard. 24: 435. 1937 (as *eximia*). Type: Dr. Edward Palmer 106, Mexico, State of Durango,



Fig. 47. *Toxicodendron radicans* ssp. *eximium*. Above: Large leaves from a shaded branch. Below: Smaller leaves from an unshaded branch of the same plant.

vicinity of the city of Durango. April-November, 1896. (US-305009, holotype; A, F, GH, MO-1774807, NY, isotypes).

Toxicodendron bitermatum Greene, Leaf. Bot. Observ. Crit. 1: 124. 1905. Type: *V. Havard*, s.n., Eagle Nest on Rio Grande River (Presidio), Presidio County, Texas. 1881. (US-156164, holotype).

Vine or shrub with aerial roots; leaflets broadly ovate, deeply-cut, rounded, incised-dentate, sinuate-lobed, sometimes tending to be trilobate; scabrescent to velutinous above, velutinous to tomentose below, veins hirtellous. Terminal leaflet blade 1.1-13.0 cm long, 0.7-11.5 cm wide; petiole hispid, tomentose, or villous; terminal petiolule 0.1-4.5 cm long. Fruits 3-5 mm broad, glabrate, setose, or hispidulous, yellow-cream. Blade tip acute to acuminate, base cuneate.

Distribution: United States: southwestern Texas; Mexico: Coahuila, Durango, Tamaulipas. (Fig. 41.)

Representative specimens: UNITED STATES. Texas. BREWSTER CO.: Big Bend National Park, Chisos Mts., *Warnock* 1212 (ARIZ, GH, TEX); Willow Creek Canyon, *Sperry* 201 (US); *Palmer* 34076 (A, MO, NY); Goode Place, *Young*, s.n. (GH, TEX); Oak Canyon, *Cory* 7010, 18689 (GH); *Mueller* 8063 (F, TEX); Oak Canyon, base of Ward Mt., *Gillis* 5745 (MSC). MAVERICK CO.: Eagle Pass, *Havard*, s.n. (GH). PRESIDIO CO.: Camp Eagle Nest (Presidio), *Havard*, s.n. (US); Fresno Canyon, tributary of Mexican Canyon, *Hinckley* 3596 (SMU, U); Marfa, *Hinckley* 2646 (ARIZ, GH, NY); Shafter, Cibolo Canyon, *Hinckley* 2580 (A, ARIZ, NY, SRSC). VALVERDE CO.: Nueces River near Rio Grande, *Palmer* 33466 (A, MO, NY, US); High bridge of Pecos River, *Pilsbry*, s.n. (PH); Devils River, *Palmer* 13603 (A, MO, WIS); Devils River, *Traverse* 2146 (SMU).

MEXICO. Coahuila: Muzquiz, *Marsh* 1166 (GH); Sierra Hechiceros, *Stewart* 158 (GH). Durango: Near Durango (Nombre de Dios), *Palmer* 106 (A, GH, MO, NY, US). Tamaulipas: Victoria, *Palmer* 154 (US, A, GH, NY). El Rosario, vicinity of Marmolejo, *Bartlett* 10881 (MICH). Nuevo León: San Augustin, Monterrey, *Abbon* 246 (A, F, MO, US).

The type was collected a long distance from any other known stations for this subspecies. Greene (1905) indicates that it was collected at Nombre de Dios, 40 miles southeast of Durango. The type for *T. bitermatum* was collected at Eagle Nest on the Rio Grande River. Barkley (1937) mapped this in Maverick County, Texas, but he

probably confused this locality with Eagle Pass. The actual locality was Camp Eagle Nest, where Havard was post surgeon from August 1880 until June 1881 (McVaugh, 1957). The camp has long since disappeared, but it occupied the present site of the city of Presidio in Presidio County. This flowering specimen must have been collected in the spring of 1881, although the type specimen indicates only "188 ."

This subspecies is one of the more unusual and rare forms of poison-ivy. It is found rarely along the Rio Grande River itself, but is more likely to be found in the washes and tributaries to that river. It apparently had not been collected between 1937 and 1964, at which time Dr. Barton Warnock helped me find a station that was known to him years earlier in Oak Canyon of the Chisos Mountains of Big Bend National Park. This plant is restricted to the canyon bottom where it is abundant, but no trace of it is found anywhere on the walls of the canyon, nor on the ridges above.

The subspecies is distinctive by its peculiarly lobed leaflets which often tend to be trilobate to the extent that they resemble the "club" on a deck of playing cards. The pubescence of the leaves and fruits suggests a relationship of *Toxicodendron toxicarium*, but the climbing habit and aerial roots require its placement in *T. radicans*. As is the case in other taxa, shade leaves are much smaller than sun leaves (sic), as shown in Fig. 47.

Superficially this taxon resembles *Toxicodendron radicans* subsp. *verrucosum* and has frequently been misidentified as such. Earlier maps of its distribution have been in error when they indicated its being found in central Texas, probably because of confusion with subsp. *verrucosum*, a more widely distributed taxon. (See discussion under *T. radicans* subsp. *verrucosum*.)

It is not easy to characterize the niche which is occupied by this plant for there have been few studies of its community associations. The only time that I have studied subsp. *eximium* in the field was in the one canyon bottom mentioned above. There it had the following assemblage of associates:



Fig. 48. *Toxicodendron rydbergii*. Holotype of *Toxicodendron fothergilloides* Lunnell, Lunnell 706.

Quercus gravesii, *Garrya ovata*, *Juniperus flaccida*, *Rhus virens*, *Vitis arizonica*, *Arbutus texana*, and *Ungnadia speciosa*. The soils in which it grew were shallow volcanic lithosols containing calcium concentrations of 1099 ppm.

5. ***Toxicodendron rydbergii*** (Small ex Rydberg) Greene.
Fig. 48.

Rhus rydbergii Small ex Rydberg, Mem. New York Bot. Gard. 1: 268. 1900. *Toxicodendron rydbergii* (Small ex Rydberg) Greene, Leaf. Bot. Observ. Crit. 1: 117. 1905. *Rhus toxicodendron* var. *rydbergii* (Small ex Rydberg) Garrett, Spring Flora Wasatch Range, 3rd. ed., 68. 1917. *Rhus radicans* var. *rydbergii* (Small ex Rydberg) Rehder, J. Arnold Arbor. 20: 416. 1939. *Toxicodendron radicans* var. *rydbergii* (Small ex Rydberg) Erskine, Pl. Prince Edward Island, 190. 1961. Lectotype: *R. S. Williams* 291, Montana, Cascade Co., Great Falls, 1885 (NY). Lectoparatype: *F. W. Anderson*, s.n., northern Montana, Helena, Lewis and Clark Co. (NY).

Rhus toxicodendron var. *vulgare* Michx., Fl. Bor. Am., 183. 1803. *Rhus toxicodendron vulgaris* a. *radicans* Engler in DC., Monogr. Phaner. 4: 394. 1883. *Rhus radicans* var. *vulgaris* Roemer et Schultes, Sys. Veg. Vol. 6. 1820, non *Toxicodendron vulgare* Miller, Gard. Dict., Art. *Toxicodendron*, No. 1. 1768. Type: "Hortus parisiensis," lectotype (P).

Toxicodendron macrocarpum Greene, Leaf. Bot. Observ. Crit. 1: 117. 1905. Type: *C. H. Thompson* 102, Kansas, Hamilton Co., 11 July 1893 (US-265734, holotype).

Toxicodendron longipes Greene, Leaf. Bot. Observ. Crit. 1: 118. 1905. Type: *Lester F. Ward* 212, Canyon south of Glenwood, Sevier Co., Utah, altitude 6300 feet, 12 June 1875 (US-153641, holotype).

Toxicodendron hesperium Greene, Leaf. Bot. Observ. Crit. 1: 118. 1905. Type: *Kirk Whited* 241, Washington, Chelan Co., Wenatchee, 6 August 1893 (1896?) (US-268197, holotype).

Toxicodendron pumilum Greene, Leaf. Bot. Observ. Crit. 1: 124. 1905, non *T. pumilum* Kuntze, Rev. Gen. Pl. pt. 1,

154. 1891. Type: *D. T. MacDougal* 28, Arizona, Coconino Co., vicinity of Flagstaff, altitude 7000 feet, 28 June 1898 (US-334125, holotype; F-69784, GH, NDA, NY, RM-31903, isotypes).

Toxicodendron punctatum Greene, Leaf. Bot. Observ. Crit. 1: 125. 1905. Type: *O. B. Metcalfe* 1088, New Mexico, Sierra Co., Black Range, near Kingston, 9 July 1904 (US-498281, holotype; F-187484, GH, MIN-294394, MO-1773740, NY, US-890258, isotypes).

Toxicodendron desertorum Lunell, Amer. Midl. Naturalist 2: 185. 1912. Type: *J. Lunell*, s.n., North Dakota, McHenry Co., gravelly soil sand hills, 13 July 1899 (MIN-245797, holotype).

Toxicodendron fothergilloides Lunell, Amer. Midl. Naturalist 2: 186. 1912. Type: *J. Lunell* 706, Ramsay Co., North Dakota, thickets at Devil's Lake, 29 June 1902 (MIN-245796, holotype).

Sub-shrub often less than 1 meter high to shrub up to 3 meters. Stem simple or sparsely upright-branched, arising from much branched subterranean stolons; aerial roots absent, plant never climbing. Leaves approximate near summit of stem, often appearing falsely verticillate. Terminal leaflet blade broadly ovate, rhomboid or suborbicular and usually acuminate, 3.0-15.0 cm long, 2.0-11.0 cm wide; petiole glabrous (-glabrate), 1.5-25.0 cm long; terminal petiolule 0.6-5.5 cm long. Leaflet margins dentate or undulate, subtruncate or rounded at the base, glabrous above, often with a line of minute, curly hairs along the midrib, glabrous or appressed strigose below; autumn coloration generally yellow to orange, less often bronze or red. Flowers in small clusters. Fruit globose, cream to yellow, (3-) 4-7 mm broad, glabrous, smooth.

Distribution: Canada: southern provinces north to 52° N. Lat. United States: central Washington, Oregon, Utah south to northeastern Arizona and western Texas, east to central Kansas, Nebraska, Iowa, southern Wisconsin, northern Michigan, New York, New England; few mountain tops,

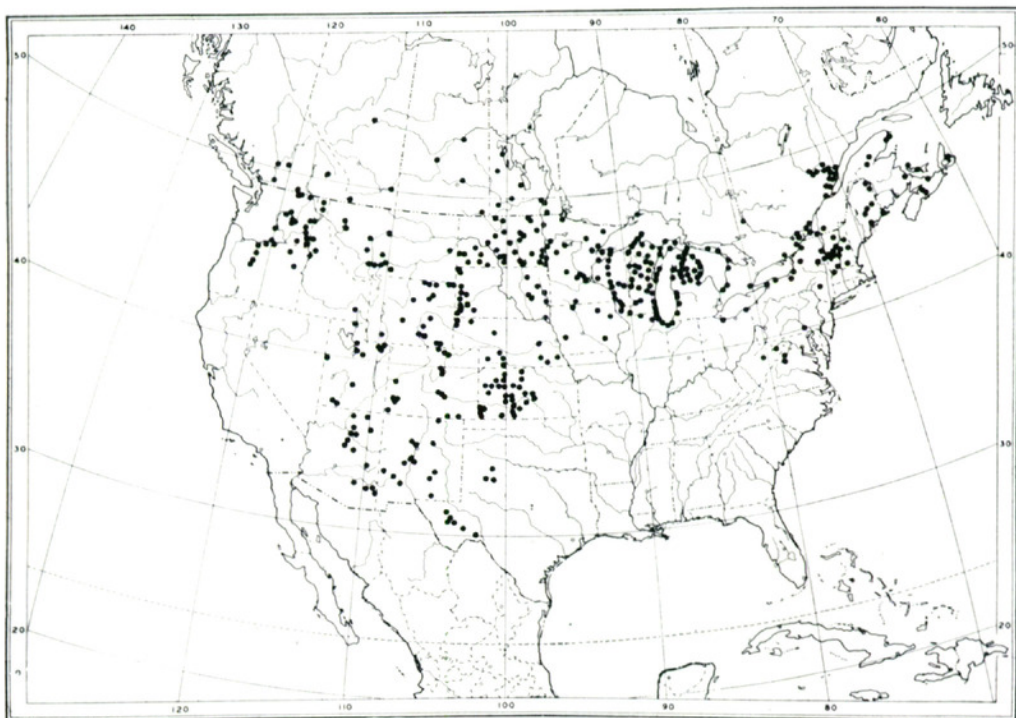


Fig. 49. Distribution of *Toxicodendron rydbergii*.

Appalachian Mountains. Common name: Rydberg's poison-ivy, poison-oak (erroneously). (Fig. 49.)

Representative specimens: UNITED STATES. **Arizona.** APACHE CO.: Bog Creek, 8 miles east of McNary, *Deaver* 6391 (ARIZ). COCHISE CO.: Big Emigrant Canyon, *Blumer*, s.n. (ND-G, NY); Chaperon Canyon, *Blumer* 1325 (ARIZ, E, F, GH, KSC, MIN, MO, ND-G, NY, RM, US); Cabeyas Mts., *Simmon* 160 (GH); Fort Huachuca, *Wilcox* 215 (US); Chiricahua National Forest, *Burrall* 2029 (US). COCONINO CO.: bottom, West Fork Canyon, Oak Creek Canyon, near Sedonia, *Demaree* 41258 (ARIZ); Bright Angel Canyon, *Nelson* 125 (US). GILA CO.: Parker Creek Branch Station, *Little* 4007 (ND). NAVAJO CO.: Beta-takin ruins, *Howell* 24569 (ARIZ); Fort Apache, *Mayerhoff* 47 (F). PIMA CO.: Coronado National Forest, *Clark* 4852 (SMU). SANTA CRUZ CO.: Santa Rita Forest Reserve, *Griffiths* 4222 (US). YAVAPAI CO.: Montezuma Well near Camp Verde, *Gillis* 6602 (MSC, US). **Colorado.** BOULDER CO.: Gregory Canyon near Boulder, *Robbins* 1607 (RM). DENVER CO.: Denver, *Smith*, s.n. (KSC). EL PASO CO.: Pikes Peak, *Ball*, s.n. (US); Williams Canyon, *Harper & Harper*, s.n. (A). LARIMER CO.: Canyon of the Thompson near Forks, *Osterhout* 3631 (RM). LAS ANIMAS CO.: Region of the Mesa de Maya, Troy, *Rogers* 6025 (TEX, US). MESA CO.: Grand Junction, *Eastwood* 7217 (A). SAN MIQUEL CO.: Norwood Hill, *Walker* 498 (GH, MIN, NY, RM, US). MONTEZUMA CO.:

Navajo Canyon, Mesa Verde, *Cary* 181 (US). WELD CO.: Windsor near river, *Osterhout* 1725 (ND-G, RM). **Idaho.** BONNER CO.: Big Potlatch River, *Christ* 4275 (NY). VANNOCK CO.: Inkom, *Jack* 1142 (A). BONNER CO.: Lake Pen D'Oreille, *Christ* 11181 (NY). BOUNDARY CO.: Bonner's Ferry, *Epling* 10465 (MO). IDAHO CO.: Cottonwood, *Christ* 10062 (NY). KOOTENAI CO.: Coeur d'Alene, *Christ* 19126 (NY). LATAH CO.: Julietta, *Christ* 10157 (NY). LEMHI CO.: Indianola Ranger Station, *Hitchcock & Muhlick* 14324 (NY). **Illinois.** COOK CO.: Glencoe, shore of Lake Michigan, *Churchill*, s.n. (MIN). DU PAGE CO.: Wheaton, *Moffatt* 594 (WIS). LAKE CO.: Waukegan, *Steyermark & Standley* 28186 (F). **Indiana.** BENTON CO.: Pine, *Merner* 14907 (WIS). LAKE CO.: Gary, *Thieret* 1505 (F). LAPORTE CO.: wooded dunes 2 miles west of Michigan City, *Deam* 8854 (IND). MARSHALL CO.: Lake Maxinkuckee, *Evermann* 833 (US). PORTER CO.: Dunes State Park, *Tryon* 1071 (F). **Iowa.** CERRO GORDO CO.: Mason City, *Shimek*, s.n. (NY). CLAYTON CO.: Giard, *Grether* 8136 (WIS). DICKINSON CO.: Spirit Lake, *Evermann*, s.n. (F). JOHNSON CO.: Lake Macbride State Park, *B.C.G.* 64763 (FSU). **Kansas.** (All Hitchcock collections are without definite locality.) COMMANCHE CO.: *Hitchcock*, s.n. (KSC). COWLEY CO.: locality unknown, *Clothier & Whitford*, s.n. (KSC). DECATUR CO.: *Hitchcock*, s.n. (KSC). DICKINSON CO.: *Westgate*, s.n. (KSC). DOUGLASS CO.: *Hitchcock*, s.n. (KSC). ELLSWORTH CO.: Ellsworth, *Palmer* 21289 (US). HAMILTON CO.: Syracuse, *Thompson* 102 (GH, KSC, MO, US). KEARNEY CO.: *Hitchcock*, s.n. (KSC). KIOWA CO.: *Hitchcock*, s.n. (KSC). LEAVENWORTH CO.: *Hitchcock*, s.n. (KSC). LOGAN CO.: *Hitchcock*, s.n. (KSC). MARSHALL CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). MCPHERSON CO.: Lindsberg, *Bodin*, s.n. (MIN). MEADE CO.: *Hitchcock*, s.n. (KSC). MORTON CO.: *Hitchcock*, s.n. (KSC). NESS CO.: *Hitchcock*, s.n. (KSC). OSBORNE CO.: Osborne City, *Shear* 226 (RM, US). PAWNEE CO.: *Hitchcock*, s.n. (KSC). POTTAWATOMIE CO.: St. George, *Kellerman*, s.n. (MO). PRATT CO.: without definite locality, *Van Vranken* 183 (KSC). RENO CO.: *Hitchcock*, s.n. (KSC). REPUBLIC CO.: without definite locality, *Smith*, s.n. (KSC). RUSH CO.: *Hitchcock*, s.n. (KSC). RUSSELL CO.: without definite locality, *Hutchinson* 278 (KSC). SALINE CO.: Salina, *Hancin* 2426 (KSC). SHERIDAN CO.: *Hitchcock*, s.n. (KSC). STANTON CO.: *Hitchcock*, s.n. (KSC). SUMNER CO.: without definite locality, *Clothier & Whitford*, s.n. (KSC). THOMAS CO.: *Hitchcock*, s.n. (KSC). TREGO CO.: *Hitchcock*, s.n. (KSC). WALLACE CO.: *Hitchcock*, s.n. (KSC). WEBSTER ROCK CO.: without definite locality, *Griebel*, s.n. (KSC). WICHITA CO.: *Hitchcock*, s.n. (KSC). **Maine.** AROOSTOOK CO.: Fort Fairfield, *Fernald* 1995 (GH). KENNEBEC CO.: Winthrop, *Sturtevant*, s.n. (MO). LINCOLN CO.: Boothbay, *Fassett* 28979 (SMU). SOMERSET CO.: Fairfield, *Fernald & Long* 14017 (GH). WASHINGTON CO.: Ox Cove, *Fernald* 1993 (GH). **Massachusetts.** BERKSHIRE CO.: Berkshire, *Churchill*, s.n. (MO). **Michigan.** ALCONA CO.: Crooked Lake, *Gillis* 4136 (MSC). ALGER CO.: Au Train Lake, *Gillis* 3643 (MSC); Devil's Slide, *Gillis* 5549

(MSC). ALLEGAN CO.: Old Baldy Dune near Saugatuck, *Gillis* 3523 (MSC). ALPENA CO.: Long Rapids Twp., *Gillis* 4123 (MSC). ANTRIM CO.: Eastport, *Gillis* 3629 (MSC). BARAGA CO.: Sturgeon River, *Gillis* 3114 (MSC). BENZIE CO.: Point Betsie, *Gillis* 6511 (MSC). CHARLEVOIX CO.: Charlevoix on dunes, *Gillis* 2940 (MSC); Beaver Island, *Ries*, s.n. (BLH). CHEBOYGAN CO.: University of Michigan Biological Station, *Gillis* 2943 (MSC). CHIPPEWA CO.: De Tour, *Gillis* 4117 (MSC); Drummond Island, *Hiltunen* 1809 (MSC, WUD); Sugar Island, *Hiltunen* 261 (WUD). CRAWFORD CO.: Lake Margrethe, *Gillis* 3074 (MSC); Wakeley Bridge, *Gillis* 5513 (MSC). DELTA CO.: base of Burnt Bluff, *Gillis* 3645 (MSC). DICKINSON CO.: Quinnesec, *Gillis* 3069 (MSC); EMMET CO.: Mackinac City, *Gillis* 3073 (MSC). GOGEBIC CO.: Gogebic Lake, *Darlington*, s.n. (MSC). GRAND TRAVERSE CO.: East Bay near Acme, *Gillis* 2802 (MSC); mixed woods below Brown Bridge Dam on bank of Boardman River, *Dieterle* 1722 (MICH). HOUGHTON CO.: Bear Lake, *Richards* 3996 (MICH, MIN, NY). IOSCO CO.: Nissikone Camp for Boys, *Gillis* 3532 (MSC). IRON CO.: Horserace Rapids, *Gillis* 3041 (MSC). KENT CO.: Ross, *Jones*, s.n. (MO). KEEWENAW CO.: Anich, *Farwell*, s.n. (MSC). LAKE CO.: Pine River, Dover Twp., *Gillis* 3620 (MSC). LEELANAU CO.: Seeping Bear Dune, base of pinnacle, *Gillis* 3489 (MSC); South Manitou Island, morainic bluff, *Voss* 9878 (MICH). LUCE CO.: Manistique Lake shore, *Gillis* 3639 (MSC). MACKINAC CO.: St. Ignace, *Gillis* 3638 (MSC); Thuja forest, Mackinac Island, *Potzger*, 7308 (ND). MANISTEE CO.: Portage Park dunes, *Umbach* 8401 (MICH). MARQUETTE CO.: Tankowa Lake, *Gillis* 5473 (MSC). MASON CO.: Ludington, dunes, *Chase* 12553 (ILL, NY). MENOMINEE CO.: shore of Lake Michigan along highway, *Waterman* 372 (MSC). MISSAUKEE CO.: Hopkins Creek, *Gillis* 3538 (MSC); Goose Lake, *Gillis* 3537 (MSC). MONTMORENCY CO.: West Twin Lake, *Gillis* 5517 (MSC). MUSKEGON CO.: near Coast Guard Station near North Muskegon, *Gillis* 5398 (MSC). OCEANA CO.: Pentwater dunes, *Chase* 12713 (ILL). OGEMAW CO.: Piper Lake, *Gillis* 3534 (MSC). ONTONAGON CO.: Escarpment overlooking Lake-of-the-Clouds, *Gillis* 3152 (MSC). OSCODA CO.: Mio, *Gillis* 4140 (MSC). OTSEGO CO.: Otsego Lake, *Gillis* 3631 (MSC). OTTAWA CO.: Ferrysburg dunes, *Gillis* 3528 (MSC). PRESQUE ISLE CO.: Rogers City, *McVaugh* 9228 (BLH, MO, MICH). ROSCOMMON CO.: Roscommon, *Gillis* 3536 (MSC). SCHOOLCRAFT CO.: Hiawatha National Forest, shore of Clear Lake, *Waterman* 361 (MSC). WEXFORD CO.: Greenwood Twp., above Manistee River on High Roll Way, *Gillis* 3626 (MSC). **Minnesota.** BECKER CO.: Detroit, *Woladron*, s.n. (NDA). CARLTON CO.: Thompson, *Sandberg* 541, (KSC, MISC). CARVER CO.: without definite locality, *Anthony & Waconia*, s.n. (WIS). CLAY CO.: Buffalo State Park, *Schuette* s.n. (GH). DAKOTA CO.: without definite locality, *Moore & Moore* 16214 (BRY). ITASCA CO.: Bena *Gillis* 3176 (MSC); Sand Lake, *Johnson* 2122 (MO). JACKSON CO.: Kilen Woods State Park, *Moore & Huff* 19341 (SMU). LAKE OF THE WOODS CO.: without definite

locality, *Moore & Moore* 12166 (NDA). MARSHALL CO.: Warren, *Gillis* 3177 (MSC). NORMAN CO.: Frenchman's Bluff, *Stevens*, s.n. (NDA). RAMSEY CO.: St. Paul, St. Anthony Park, *Lugger*, s.n. (NDA). ST. LOUIS CO.: Duluth, *Lakela*, s.n. (F, NY, US); STEARNS CO.: Paynesville Twp., *Moore & Phinney* 12639 (A). WINONA CO.: Winona, *Holzinger*, s.n. (GH). **Montana.** CASCADE CO.: Great Falls, *Williams* 291 (NY, US). DAWSON CO.: Glendive, *Ward*, s.n. (US). FLATHEAD CO.: Flathead Lake, *Clemens*, s.n. (F). GALLATIN CO.: Bozeman, *Blankinship* 106 (F, MO, US). LAKE CO.: Swan Lake, *Jack* 2377 (A). LEWIS AND CLARK CO.: Helena, *Anderson*, s.n. (NY). MADISON CO.: Upper Madison River, *Lenz*, s.n. (MO, ND). PARK CO.: Livingston, *Booth* 3802 (NDA). STILLWATER CO.: Absarokee, *Hawkins*, s.n. (WIS). **Nebraska.** BROWN CO.: Columbus, *Palmer* 36060 (MO, NY). DIXON CO.: Newcastle, *Clements* 2606 (NY, US). FRANKLIN CO.: Franklin, *Laybourn* 47 (M). GAGE CO.: without definite locality, *Knight*, s.n. (RM). KEARNEY CO.: Minden, *Hapeman*, s.n. (ARIZ, FLAS, MIN, MO, RM, SMU). OTOE CO.: Syracuse, *Osborn* 762R (MO). SALINE CO.: Crete, *Diehl*, s.n. (BRY). SHERIDAN CO.: Metcalf Public Hunting Grounds, 13 miles north of Hay Springs, pine forest, *Nixon* 53 (RM). SIOUX CO.: Monroe Canyon, *Baker*, s.n. (MO). STANTON CO.: Stanton, *Lindbo*, s.n. (US). THOMAS CO.: Helsey sand hills, *Bréneckle*, s.n. (NDA). **New Hampshire.** CARROLL CO.: Intervale, between Conway and Bartlett, *Rehder* 997 (A, US). COOS CO.: Shelburne, *Moore* 4171 (GH). GRAFTON CO.: Thornton along railroad, *Gillis* 4098 (MSC); Warren, *Williams*, s.n. (GH). HILLSBORO CO.: Fox State Forest, *Baldwin*, s.n. (MSC); **New Mexico.** BERNALILLO CO.: Capelin Canyon, Sandia Mts., *Ellis* 245 (MO, NY, US). CATRON CO.: Gila River west fork, *Metcalf* 339 (GH). COLFAX CO.: Ute Park, *Standley* 14036 (US). LINCOLN CO.: Gray, *Earle & Earle* 485 (NY); Ruidosa Creek on Mescalero Reservation, 7 miles west of Ruidosa, *Hinckley* 780 (ARIZ, F, GH, NY, SRSC, TEX). SANDOVAL CO.: Tijeras Canyon, Sandia Mt. north end, *Stoutamire* 3979 (MSC). SAN MIQUEL CO.: Pecos River Division, Santa Fe National Forest, *Standley* 4011 (GH, NY, RM, US). SIERRA CO.: Kingston, *Metcalf* 1088 (F, GH, MIN, MO, NY, US). SOCORRO CO.: Gila River, Mogollon Mts., *Metcalf* 339 (ARIZ, E, MIN, MO, ND-G, NY, RM, US); **New York.** ESSEX CO.: Port Henry, *Britton*, s.n. (NY). MONROE CO.: Inspiration Pt., *Matthews* 2131 (WIS). NIAGARA CO.: Niagara Falls at base of Bridal Veil Falls, *Gillis* 6316 (MSC). ONONDAGA CO.: near Syracuse, *Underwood*, s.n. (E). OSWEGO CO.: Selkirk, *Fernland, Eames, & Wiegand* 14374 (GH). ST. LAWRENCE CO.: Lisbon, *Phelps* 642 (GH, NY). ULSTER CO.: Lake Mohonk, *Gillis* 4061 (MSC). WARREN CO.: The Glen Pack Forest, *Gillis* 5378 (MSC). WASHINGTON CO.: Pilot Knob Lake George, *House* 28972 (TEX). **North Carolina.** CUMBERLAND CO.: Fayetteville, *Miles*, s.n. (US). **North Dakota.** BARNES CO.: Valley City, *Bergman* 393 (NDA). BENSON CO.: Butte, *Lunell*, s.n. (NY); Pleasant Lake, *Lunell*, s.n. (MIN). BILLINGS CO.: Medora in ravine,

Bergman, s.n. (NDA). BOTTINEAU CO.: Lake Metigoshe, *Stevens*, s.n. (NDA). BURLEIGH CO.: Bismarck, Apple Creek, *Stevens*, s.n. (NDA). CASS CO.: Fargo along Red River, *Bergman*, s.n. (NDA). CAVALIER CO.: Tongue River, *Stevens*, s.n. (NDA). DUNN CO.: Killdeer Mts., *Stevens & Moir*, s.n. (NDA). EDDY CO.: Hamar, *Stevens*, s.n. (NDA). EMMONS CO.: Linton, *Stevens*, s.n. (NDA). GOLDEN VALLEY CO.: Sentinel Butte, *Bergman*, s.n. (NDA). GRAND FORKS CO.: Turtle River State Park, *Stevens*, s.n. (NDA). GRANT CO.: Wade, *Bell*, s.n. (NDA). KIDDER CO.: Dawson State Game Refuge sand flat, *Stevens*, s.n. (NDA). LOGAN CO.: Napoleon, *Stevens*, s.n. (NDA). LAMOURE CO.: Kulm, *Brenckler*, s.n. (NDA). MCHENRY CO.: Sand Hills, *Lunell*, s.n. (MIN). MCLEAR CO.: T. 48, R. 91 woods, *Heidenreich*, s.n. (NDA). MORTON CO., Mandan, *Bergman*, s.n. (NDA). OLIVER CO.: Fort Clark, *Hayden*, s.n. (MO). PEMBINA CO.: Walhalla stream bank, *Bergman* 1965 (NDA, OSC). PIERCE CO.: Lake Girard, lower edge of prairie coulee, *Stevens*, s.n. (NDA). RAMSAY CO.: Devil's Lake, *Lunell* 706 (MIN, RM, WIS). RANSOM CO.: McLeod, *Stevens*, s.n. (NDA). RICHLAND CO.: Hankinson, lake shore, *Bergman* 804 (NDA); Kindred, sandy prairie, *Stevens* 2465 (NDA). ROLETTE CO.: Duneith, *Stevens*, s.n. (NDA). SARGENT CO.: Milnor, *Stevens*, s.n. (NDA). SHOPE CO.: Black Butte in coulee, *Stevens & Moir*, s.n. (NDA). STARK CO.: Hebron, side of butte, *Stevens & Moir*, s.n. (NDA). WARD CO.: Minot, *Lakela* 389 (MIN). WELLS CO.: NE slope of Coteau, *Stevens*, s.n. (NDA). WILLIAMS CO.: Williston, *Bell* 191 (NDA). **Ohio.** ASHTABULA CO.: Geneva-on-the-Lake, *Rood* 2484- (MIN). **Oklahoma.** BEAVER CO.: Knowles, *Stevens* 516 (MO). **Oregon.** BAKER CO.: Wallowa National Forest, *Peterson* 236 (OSC). BONNER CO.: Kootenay, *Lyall*, s.n. (GH). DESCHUTES CO.: Redmond, *Whited* 122 (ND). GRANT CO.: Canyon City, *Peck* 10174 (NY). JEFFERSON CO.: west of Culver on bank of Crooked River, *Gillis* 5215 (MSC); Warm Springs, *Gillis* 4218 (MSC). SHERMAN CO.: Rufus, *Gillis* 4227 (MSC). UMATILLO CO.: Pendleton, *Henderson* 29 (GH). WALLOWA CO.: Snake River Canyon, Eureka Creek, *collector unknown*, (WTU); College Creek Ranger Station, *Ingram* 2940 (ND). WASCO CO.: Maupin, *Gillis* 4217 (MSC). **Pennsylvania.** LANCASTER CO.: Lancaster, *Ely*, s.n. (MIN). **South Dakota.** BROOKINGS CO.: Brookings, *Moore* 59 (MIN). CLAY CO.: floodplain of Brule Creek, 12 miles east of Vermilion, *Over* 7020 (SDU). CUSTER CO.: Hermosa, *Rydberg* 594 (NY, US); Jewel Cave National Monument, *Stoutamire* 4004 (MSC). DAVISON CO.: Mitchell, *Small*, s.n. (F). FALL RIVER CO.: Edgemont, *Visher* 2569 (F, RM, SDU); Hot Springs, *Thatcher* 129 (MIN). HANSON CO.: Alexandria, *Weber*, s.n. (FLAS). HARDING CO.: Cave Hills, *Moore* 1823 (MIN). KINGSBURY CO.: Spirit Lake, *Thornber*, s.n. (ARIZ). LAWRENCE CO.: Deadwood, *Carr* 83 (F, MIN, MO, NY, SDU, US, WIS). MEADE CO.: Ft. Meade, *Forwood* 60 (US); Piedmont, *Pratt* 6116 (F, MIN, RM, WIS). MINNEHAHA CO.: Sand Hills, *Duncan*, s.n. (MIN). PENNINGTON CO.: Rockerville, *White*, s.n. (MO); Dark Canyon, 7

miles west of Rapid City, *McIntosh* 676 (SDU). SHANNON CO.: White River Valley, *Visher* 2184 (NY). SPINK CO.: Mellette, *Brenckle* 41-28 (FLAS, MO, NY). STANLEY CO.: Cedar Pass, *Over* 6081 (SDU). Texas. ARMSTRONG CO.: Gamble's Ranch, *Palmer* 13928 (GH, MO). BREWSTER CO.: Alpine, *Warnock* 8409 (SMU); Pine Peak, Davis Mts., *Hinckley* 1107 (ARIZ, F). BRISCOE CO.: Lubeck, *Demaree* 7629 (MO). CULBERSON CO.: McKittrick Canyon, *Hinckley* 4484 (SRSC). FLOYD CO.: between Floydada and Emma, *Coville* 1879 (US). JEFF DAVIS CO.: 10 miles SE of Fort Davis, *Cory* 53563 (SMU, US); Elbow Canyon near Pine Peak, *Hinckley* 1107 (ARIZ, GH, NY, TEX). Utah. CACHE CO.: Logan, *Cotten*, s.n. (MIN). DAGGETT CO.: Grouse Creek Canyon, *Graham* 8115 (GH, MO). DAVIS CO.: Farmington, *Clemens*, s.n. (A, GH). JUAB CO.: without definite locality, *Maguire & Holmgren*, s.n. (GH, NY). SALT LAKE CO.: City Creek Canyon, Salt Lake City, *Palmer* 38032 (M). SEVIER CO.: Glenwood, *Ward* 212 (US). SUMMIT CO.: Wahsatch, *Watson* 218 (US). UTAH CO.: Ashley Creek near mouth of Dry Fork, *Graham* 6766 (MO); Split Mt. Gorge, Dinosaur National Monument, *Welsh* 367 (BRY). WASHINGTON CO.: Springdale, *Jones* 5249 (MIN, MSC, MO, US); Zion National Park, springline on Cathedral Mt., *Gillis* 6632 (MSC, US). Vermont ADDISON CO.: Leicester, *Dutton*, s.n. (FLAS); CALDEONIA CO.: Barnet, *Blanchard*, s.n. (MIN, MO, US). CHITTENDEN CO.: Charlotte, *Hosford*, s.n. (F). LAMOILLE CO.: Cambridge Junction, *Donahue* 272 (MSC). ORANGE CO.: Bradford, *Gillis* 4092 (MSC). ORLEANS CO.: Willoughby Lake, *Churchill*, s.n. (GH, MIN, MO). RUTLAND CO.: Proctor, *Banker* 247 (NY). WINDHAM CO.: Westminster, *Gillis* 4081 (MSC). Virginia. GREENE CO.: summit of Rocky Mount near Skyline Drive, *Ewan* 17205 (TEX). PAGE CO.: Luray, *Steele & Steele* 151 (E, GH, MIN, MO, NY, US). Washington. CHELAN CO.: Chelan, *Muenschner & Muenschner* 11224 (A); Wenatchee, *Whited* 241 (US). GRANT CO.: Dry Falls, Coulee City, *Thompson* 9115 (GH, MO, ND, NY); Grand Coulee, Soap Lake, *Eyerdam* 625 (A, F, MO). KLIKITAT CO.: near John Day Dam on bluffs overlooking Columbia River, *Gillis* 5245 (MSC). OKANOGAN CO.: Epsom Lake, Kruger Mt. Oroville, *St. John, Courtney, & Parker* 5478 (WTU). SPOKANE CO.: Hangman Creek, *Suksdorf* 264 (GH); STEVENS CO.: Northport, on Columbia River, *Rogers* 640 (MO, NY, SMU). WALLA WALLA CO.: Waitsburg, *Horner* 129 (GH, US). WHITMAN CO.: Revere, *Eastwood* 13271 (A); Wawawai, *Elmer* 778 (A, ILL, MIN, MO, US, NY); YAKIMA CO.: N. Yakima, *Mosier*, s.n. (US). West Virginia. MINERAL CO.: Allegheny Front Mt., *Gillis* 5717 (MSC). UPSHUR CO.: Buckhannon, *Pollock*, s.n. (MO). Wisconsin. BARRON CO.: Poskin Lake, *Cheney*, s.n. (WIS); BAYFIELD CO.: Tomahawk Lake, *Fassett* 9814 (WIS); Port Wing, *Cheney* 7168 (WIS); BROWN CO.: Green Bay, Brannery Hill Creek, *Khuschke*, s.n. (MIN). BUFFALO CO.: near Fountain City, *Smith* 7147 (MIL, WIS). BURNETT CO.: Viola Lake, *Fassett* 9891 (WIS). CLARK CO.: Neillsville, *Goessl* 1493 (MIL). COLUMBIA CO.: near Prairie du Sac Bridge, *Smith* 8043

(A, MIL, WIS); DANE CO.: Beeche's Woods between Sauk City and Mazomanie, *Fassett* 21549 (MIN, WIS). DOOR CO.: Washington Island, *Fuller* 1429 (MIL); Sturgeon Bay, *Goessl* 3717 (MIL). DOUGLAS CO.: upper St. Clair Lake, *Museum Expedition*, s.n. (MIL). DUNN CO.: Menomonie, *Goessl* 9226 (MIL). EAU CLAIRE CO.: Eau Claire, *Goessl* 1715 (MIL); FLORENCE CO.: bank of Menominee River near Menominee, Michigan, *Gillis* 3061 (MSC); Fond du Lac, Moon Lake, *Smith & Fuller* 1810 (MIL). GRANT CO.: Bascobel, *Sylvester*, s.n. (MIL). IOWA CO.: Arena, *Bullamore*, s.n. (WIS); JACKSON CO.: Black River Falls, *Smith* 6894 (MIL, WIS). LACROSSE CO.: Mormon Coulee, *Harmon* 531 (WIS); LAFAYETTE CO.: near Belmont, *Smith* 7761 (A, MIL, WIS). LANGLADE CO.: Hollister, *Seymour* 10776 (WIS); LINCOLN CO.: Pine River Twp., *Seymour* 14055 (WIS); MARATHON CO.: Wassau, *Goessl* 2848 (MIL). MARINETTE CO.: east of Amberg, *Martz* 226 (WIS). MILWAUKEE CO.: Wauwatosa, *Finger*, s.n. (MIL). OCONTO CO.: Pensaukee, *Goessl* 4017 (MIL). ONEIDA CO.: Rainbow Rapids, *Cheney* 1351 (MIL, WIS). OZAUKEE CO.: Saukville Twp., *Kruschke* K-60-40 (MIL). PIERCE CO.: Prescott, *Museum Expedition*, s.n. (MIL). PRICE CO.: Fifield, *Graenicher*, s.n. (MIL). RACINE CO.: Horlicksville, *Wadmond* 466 (MIN); RICHLAND CO.: Richland, *Fassett* 22498 (GH, MO, WIS). SAUK CO.: Ableman, *Palmer* 27657 (A, MO); SHAWANO CO.: Shawano, *Goessl* 4760 (MIL). SHEBOYGAN CO.: Sheboygan, *Goessl*, s.n. (WIS); VERNON CO.: Genoa, *Museum Expedition*, s.n. (MIL); WASHBURN CO.: Minong, near Bass Lake, *Fassett* 8528 (A, GH, WIS, US). WAUSHARA CO.: Plainfield, *Fassett* 21637 (MO, WIS). WOOD CO.: Remington, *Fassett, Catenhusen, Grange, & Oehmeke* 20321 (WIS). **Wyoming.** ALBANY CO.: Pole Creek Canyon, *Nelson* 154 (GH, MIN, ND-G). CARBON CO.: Freezecut Hills, *Nelson* 4857 (MO, NY, RM); Seminole Dam, N. Platte River, *Porter & Porter* 8525 (RM). CROOK CO.: Hulett, *Ownbey* 556 (RM). FREMONT CO.: 10 miles west of Lander, middle fork of Popo Agrie Creek, *Porter* 5569 (RM). HOT SPRINGS CO.: Wind River Canyon, south of Thermopolis, *Jones* 23840 (MSC). LARAMIE CO.: Pole Creek near Table Mt., *Nelson* 154 (RM). NATRONA CO.: Casper Mt., Garden Creek Falls, *Joswik* 301 (RM). PLATTE CO.: 15 miles west of Wheatland, Palmer Canyon, *Porter* 4415 (RM, SMU, TEX). SHERIDAN CO.: Big Horn, *Tweedy* 2289 (NY); Sheridan, *Rollins* 558 (GH, MO, NY). UINTA CO.: Evanston, *Pannel & Blackwood* 3630 (MO). WASHAKIE CO.: north end of Tensleep Canyon, Big Horn Range, *Porter & Porter* 8247 (RM).

CANADA. **Alberta.** Fort Saskatchewan, *Turner*, s.n. (ALTA). Medicine Hat, *Dore*, 11956 (MSC). **British Columbia.** International boundary between Kettle and Columbia Rivers, *Macoun* 63750 (ND-G), Spence's Bridge, *Macoun*, s.n. (NY). Fort Vancouver, *Hooker*, s.n. (K). **Manitoba.** Grand Rapids, *Scoggan* 4751 (MIN). Arveme, *Cridle*, s.n. (A). Vorette, Chainaie, St. Boniface, *Boivin* 6434 (MSC). Winnipegosis, *collector unknown* (WIN). Big Grass Marsh, south-

ern Lake Winnipeg, *collector unknown* (WIN). **New Brunswick.** CARLETON CO.: Woodstock, *Dore & Gorham* 45894 (US). VICTORIA CO.: Aroostook River, *Williams*, s.n. (GH). WESTMORELAND CO.: Cap Brulé, *Knowlton*, s.n. (GH). **Nova Scotia.** HALIFAX CO.: Shubenacadie Grand Lake, *Fernald & Bissell* 21787 (GH). HANTS CO.: Five Mile River, *Pease & Long* 21789 (GH). LUNENBURG CO.: Bridgewater, *Fernald & Long* 24093 (A, GH). PICTOU CO.: Ferrona Junction, *Robinson* 522 (NY). VICTORIA CO.: Port Bevis, *Fernald & Long* 21792 (GH). **Ontario.** ALGOMA CO.: Batchawana Falls, *Taylor et al.* 914 (GH). BRUCE CO.: Sydney Bay, *DeJong* 1355 (MSC); Stokes Bay, *Krotkov* 9193 (MO, NY). CARLETON CO.: Ottawa, *Marshall*, s.n. (MSC). FRONTENAC CO.: Westbrook, *Gillis* 5373 (MSC). Lambton, Pinery Provincial Park near Grand Bend, *Gillis* 5389 (MSC). LENOX CO.: Newburgh, *Baker*, s.n. (F). MANITOULIN CO.: Manitoulin Island, *Grassl* 5745 (NY). REN-FREW CO.: Cobden, *Gillis* 3442 (MSC). STORMONT CO.: Longue Sault Rapids, *Dore & Cody* 15087 (MSC). PARRY CO.: Island in French River, *Dewey* 39 (US). THUNDER BAY CO.: Sibley Peninsula, *Boivin* 2614 (MIN). WENTWORTH CO.: 1/2 mile from Lincoln Co. line, 2 miles from Winoma, *Gillis* 6317 (MSC). TIMISKAMING CO.: Dawson Point, Lake Timiskaming, *Morton & Le Page* 11687 (US). **Prince Edward Island.** Malpeque, *Fowler* 22104 (WIS). **Québec.** ARGENTEUIL CO.: Chatham Twp. Cushing, *Jenkins* 9036 (MSC). BELLECHASSE CO.: Beaumont, *Chabot & Verret* A-2204 (QUE). BERTHIER CO.: Berthier en Bas, *Rousseau* 22077 (GH). CHAMBLY CO.: Longueuil, *Marie-Victorin*, s.n. (ND). CHARLEVOIX CO.: Baie-des-Rochers, *Cayouette & Brassard* 5847 (QUE); Port-aux-Quilles (part of town of Cap-aux-corbeaux), *Cayouette & Barassard* 5846 (QUE). CHICOUTIMI CO.: Anse St. Jean, *Brassard*, s.n. (QUE). DEUX MONTAGNES CO.: Oka-sur-le-lac, *Cartier*, s.n. (QUE); La Trappe, Pinière Sablonneuse du lac, *Louis-Marie*, s.n. (OSC). GASPÉ CO.: Rivière Petit-Pabos, *Marie-Victorin, Jacques, & Rolland-Germain* 44919 (GH). GATINEAU CO.: Grand Remous, *Louis-Marie & Lamarre* 294 (GH). HEFFORD CO.: Granby, *Fabius* 373 (NY). HULL CO.: Hull, *Macoun* 427 (GH). IBERVILLE CO.: Iberville, *Cinq-Mars & Samoisette*, s.n. (QUE). LAC SAINT-JEAN CO.: Saint Gédéon, *Cayouette & Brisson* 6149 (QUE). LAVAL CO.: Saint Leonard, *Ricard & Boivin* 1020 (GH, MO); Mount Royal along railroad tracks, *Gillis* 3444 (MSC). MATAPEDIA CO.: Routhierville, *Cayouette & Cayouette* 6295 (QUE). MONTGOMERY CO.: Isle of Orleans, *Jack*, s.n. (A). MONT-MORENCY CO.: Montmorency, *Marie-Victorin, Rolland-Germain, Raymond, & Champagne* 56889 (MSC). NAPIERVILLE CO.: Napierville, *Voss* 9085 (MSC). QUÉBEC CO.: Plaines d'Abraham, *Cinq-Mars & Barabé*, s.n. (QUE). ROBERVAL CO.: Pointe-Bleue, *Lalonde & Cayouette* 5691 (QUE). SAGUENAY CO.: Albert, *Cayouette* 840 (QUE); Petites Bergeronnes, *Cayouette & Brassard* 5863 (QUE). ST. JEAN CO.: St. Jean, *Cinq-Mars & Samoisette*, s.n. (QUE). **Saskatchewan.** South ridge of

Qu'Appelle River, *Shumovich, Selleck, & Gellata* 67 (RM). Moon Lake near Saskatoon, *Boivin, Russel, & Breitung* 6709 (MSC).

Toxicodendron rydbergii is the most northerly ranging species in the Anacardiaceae. It is a taxon which is easily separated from related taxa by a number of constant characters, yet forms morphological intermediates on the fringes of its range where it apparently intergrades with neighboring taxa. At least eight species have been described by writers who apparently did not know its range of variation; at least three other taxa have been described which are probably intermediates between this species and other taxa, and represent populations from the edges of its range.

Prior to 1900 any specimens of this taxon were called by the names of other taxa—their collectors not being aware of any distinctions between them. It is possible that Linnaeus had such differences in mind in the *Species Plantarum* since he described three forms of poison-ivy, but his references are to the older literature and refer to names which cannot be typified.

The species is distinct from all other poison-ivy taxa in not producing aerial roots in the wild, thus always remaining a sub-shrub or, at best, a shrub of dimensions not more than several meters high. Its fruits tend to be larger and lighter in color than those of other taxa, its petioles always glabrous and usually quite long, and its leaflets very broad, often suborbicular. Because of the size and shape of the leaflets, they are difficult to press intact and therefore will often be folded along the midrib in herbarium specimens. In the field, this character is expressed by a spoon shape to the leaflets. The leaves are usually clustered near the top of the aerial stem, borne on petioles that are sometimes short, but more often than not, are more than one and a half times as long as the blade. Because the petiole length seems to be somewhat related to the degree of sunlight received by the plant, the length of petiole alone is not a definitive character; its glabrous nature is. The short pedicels bearing fruits larger than other members of the complex make the fruiting inflorescence much more compact

and tightly clustered than those of other taxa, hence the ability of the infructescence to stand erect.

In describing *Toxicodendron hesperium*, Greene distinguished the taxon by its wrinkled fruits, apparently unaware that unripe fruits of all members of this group become wrinkled upon drying. In regard to *T. pumilum* Greene, a different situation exists. *Toxicodendron pumilum* Kuntze (1891) is meant to refer to *Rhus pumila* Michx. (= *R. michauxii* Sargent) which is a homonym of *R. pumila* Meerb. *Toxicodendron pumilum* Greene therefore is also a homonym, having been published 14 years after Kuntze's name. Greene felt that this species was characterized by nodding inflorescences, but confused the issue by his statement describing the type: "In higher mountains of northern Arizona, . . . labeled *R. diversiloba*, though the plant, despite its inclining panicles, is strictly of the Atlantic type of the genus." The type is a collection from early in the growing season with new leaves barely opened and fruits dating from the preceding season.

In regard to *Toxicodendron punctatum* Greene, isotypes at NY and at US were annotated by Greene himself (after publication of this species) as *Rhus rydbergii*! Greene's description mentioned "tufts of hairs in and near axils of midveins" as a definitive character, but this trait does not characterize the type.

J. Lunell collected two forms in North Dakota, naming them *Toxicodendron fothergilloides* from the same locality which, even though given the same collection number, were collected two years apart. Barkley (1937) chose "type no. 1" as the type inasmuch as the Code provides only for a single specimen to serve as the nomenclatural type. It is a flowering specimen with a separate sprig of fruits attached to the sheet.

The range of this species extends throughout western United States roughly from the 100th meridian to the Great Basin and the Cascade Mountains. It is also the sole representative of the complex in North America found north of the 44th parallel of latitude. It is the taxon which inhabits the dunes of the Great Lakes and so follows the

shorelines of Lakes Michigan, Ontario, and Erie which extend south of the 44th parallel. A disjunct population is found on mountain crests in the central Appalachians from Pennsylvania, West Virginia, and Virginia. Except for the southern lobe of Ontario which bounds Lakes Huron, Erie, and Ontario, and for Nova Scotia, *Toxicodendron rydbergii* is the sole taxon of poison-ivy found in Canada from the Gaspé Peninsula to the east flank of the Cascade Mountains.

In garden plots at Michigan State University, where poison-ivy populations were grown experimentally, plants of *Toxicodendron rydbergii* maintained their distinctiveness especially in regard to the non-climbing habit. A specimen from the Davis Mountains of southwestern Texas, however, demonstrated a different behavior in a growth chamber. After several months at high relative humidity, aerial roots were produced. It appears that a response to moisture may induce aerial root formation even in this taxon, as a reversion to the stock from which it was derived. In the wild, it is this ability to produce roots which presumably permits the stolons to root upon stimulus by soil moisture, thus expanding a clone spatially.

Because of the apparent range limits at the 44th parallel in eastern United States, a study area was sought along a north-south river valley whose floodplains and terraces would likely be hospitable for the climbing forms to the south (*Toxicodendron radicans* subsp. *radicans* and *negundo*), yet a river valley which would cross the 44th parallel. The Connecticut River Valley, both in New Hampshire and Vermont, was explored. As I searched southward through New Hampshire, the first place where climbing poison-ivy was encountered was on a stream bank at the West Thornton-Woodstock city line in Grafton County at 44° N. This collection appears to be an intergrade between *T. rydbergii* and *T. radicans* subsp. *radicans*.

There is a cognate form of poison-ivy in Japan, also restricted north of the 44th parallel, and reported to be a sub-shrub. This taxon, named *Rhus rishiriensis* Nakai, is discussed under *Toxicodendron radicans* subsp. *orientale*,

and treated herein as an ecotype without being recognized nomenclaturally.

Plants of *Toxicodendron rydbergii* grow on sandy or rocky lakeshores, floodplains, river terraces, talus, precipices, railroad rights of way, and other ruderal sites, sand dunes, and cutover woods. It is frequently found with *Pteridium aquilinum* whereas most other poison-ivy taxa do not occur with bracken fern. It is seldom found in deep woods or old forests, having been shaded out, if it ever did occur there. When it is found on sand dunes, it is missing from the adjacent dune forest, being replaced, within their geographic ranges, by *T. radicans* subsp. *radicans* and subsp. *negundo*. In Nova Scotia and the Gaspé region it inhabits gypsum cliffs, slaty ledges, and the cobbly upper beach. It produces stolons that intertwine the chinks and crevices in stone walls of northern New England farms. Although often in wet places like rills, ravines, and near waterfalls, it is reported from sub-alpine rocks on Pike's Peak (Colorado). It is also reported as forming an "association" with *Shepherdia* in Dinosaur National Monument, Utah. In growth form, it is usually a sub-shrub, generally achieving no more stature than a meter. When it is undisturbed for several decades and the site conditions are favorable, it may reach two or more meters in height and be a genuine shrub. I have collected it under such conditions, from moist washes along the Columbia River in Washington and Oregon, and at the outlet of Montezuma Well in Yavapai County, Arizona.

Habitats for this taxon are many and varied. Because the taxon reproduces by rhizomes, it is difficult to assess the true abundance and ease of establishment of this species. The many stems appearing on a single site may all be of a single individual, or of several. It is not usually abundant, but may find its niche in the more mesic and better illuminated portions of the hemlock-white-pine-northern hardwoods association, the spruce-fir forest formation, the maple-basswood formation, or in a disturbed woods of pine, cherry, and red maple. In southern Ontario, *Toxicodendron rydbergii* inhabits woods of elm, oak, and ironwood (*Os-*

trya). It inhabits some of the more mesic habitats in the prairies and moist valleys in the Rocky Mountains. The ruderal nature of this plant permits invasion along roads, railroads, lakeshores, floodplains, fencerows, etc., where there are many weedy associates. It is probably safe to say that the plant's ecological amplitude is such that it will grow in situations too varied to characterize. Rather, the need for moisture and sunlight likely determines in large measure where it occurs.

6. **Toxicodendron toxicarium** (Salisb.) Gillis, comb. nov.
Figs. 50, 52.

Rhus toxicodendron L., Sp. Pl. 1: 266. 1753. *Rhus toxicarium* Salisb. Prodr. 170. 1796. *Toxicodendron magnum* Bert. (sic) ex Steudel, Nom. Bot. 2: 694. 1841. (*nomen nudum*). *Rhus toxicodendra* St. Lager, Ann. Soc. Bot. Lyon 7: 133. 1880. *Toxicodendron toxicodendron* (L.) Britton in Britton and Brown, Ill. Fl. U. S. 2: 484. 1913. Type: "Habitat in Virginia, Canada." (LINN 378.16, lectotype, specimen on left).

Rhus toxicodendron var. *quercifolium* Michx., Fl. Bor.-Am., 183. 1803. *Rhus quercifolia* (Michx.) Steudel (in synonym.), Nom. Bot. 1: 689. 1821, non *R. quercifolia* Goepert, Die Tertiäre von Schossnitz in Schlesien, 37. 1855. *Toxicodendron quercifolium* (Michx.) Greene, Leaf. Bot. Observ. Crit. 1: 127. 1905. Type: "Virginie et Carolines." (P, lectotype).

Rhus acutiloba Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 612. 1863. Type: *Berlandier* 2035, Mexico (actually Texas), (KW, lectotype, G-DC, GH, MO-1773755, isotypes).

Toxicodendron monticola Greene, Leaf. Bot. Observ. Crit. 1: 126. 1905. Type: *Albert Ruth* 356, Georgia, Lookout Mt., July 1898, (US-345540, holotype; ND-G, MO-1773749, NY, presumed isotypes).

Toxicodendron compactum Greene, Leaf. Bot. Observ. Crit. 1: 126. 1905. Type: *William Hunter*, s.n., Virginia, Carroll Co., Woodlawn, August 1899, (US-364942, holotype; GH, isotype).

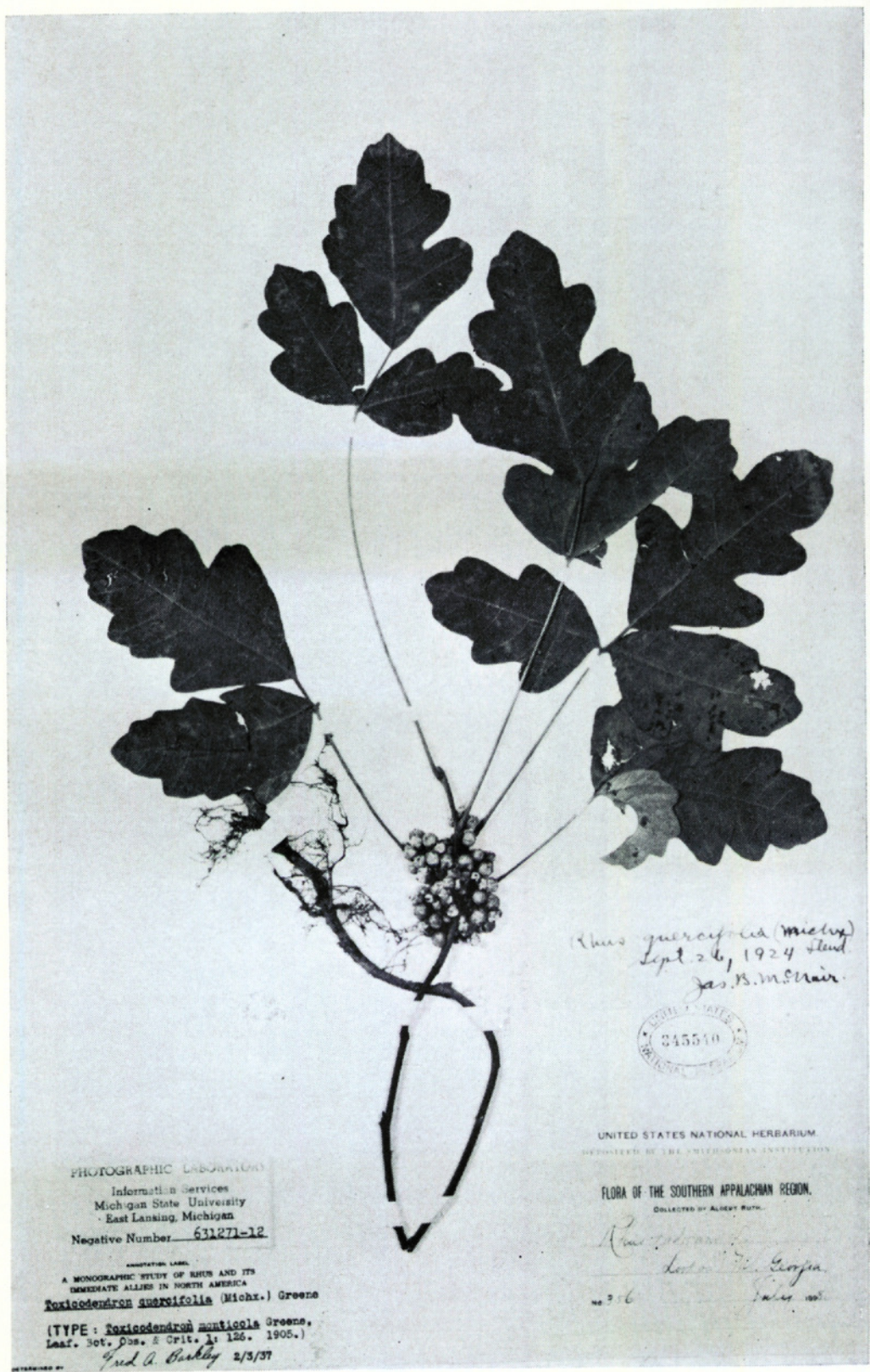


Fig. 50. *Toxicodendron toxicarium*. Holotype of *T. monticola* Greene, Ruth 356.

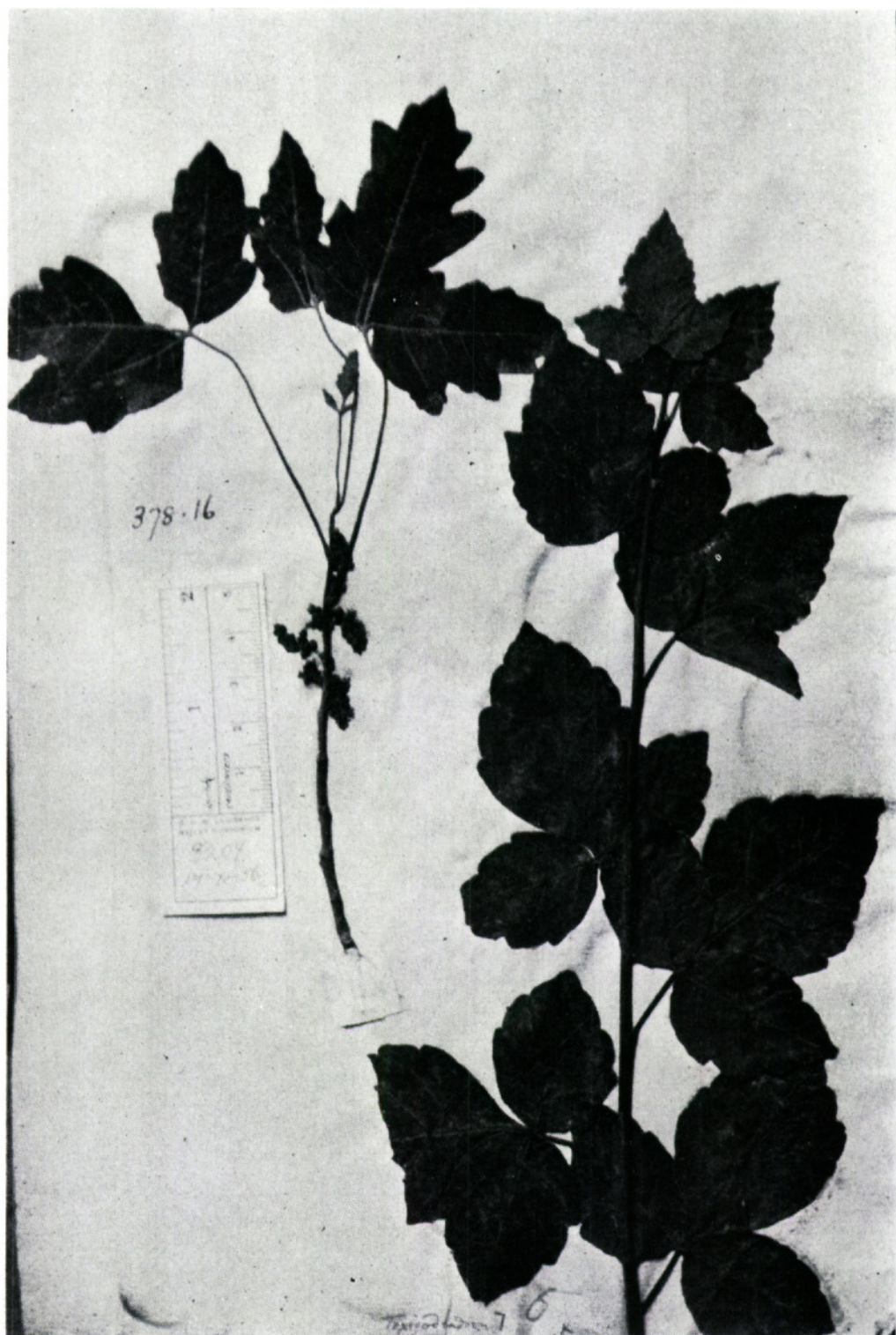


Fig. 52. *Toxicodendron toxicarium*. Upper left: Lectotype of *Rhus toxicodendron* Linn. Right: *Lobadium aromaticum* (Ait.) Steudel, P. Kalm.

Rhus toxicodendron f. *elobata* Fernald, *Rhodora* 43: 598. 1941. Type: *S. S. Van Pelt*, s.n., Bridgeton, Cumberland Co., New Jersey, 1 1/2 miles s.e., by N. J. Central R.R., 20 July 1909. (GH, holotype).

Rhus toxicodendron f. *leiocarpa* Fernald, *Rhodora* 43: 599. 1941. Type: *M. L. Fernald & Bayard Long* 8347, dry open sandy pine and oak thickets near the county line, south of Jarratt, Sussex Co., Virginia, June 8, 1938, (GH, holotype, NY, US, isotypes).

Small shrub or subshrub with slender, pubescent branches and branching subterranean stolons. Leaflets often subcoriaceous, 3 (-5), ovate to oblong or oblong-obovate, lobate-dentate or lyrate, sinuate-pinnatifid with 3-7 rounded, blunt or rarely subacute lobes, occasionally just undulate; often more deeply lobed in male than in female clones; apex rounded, subacute or acuminate, base obtuse or cuneate. Petiole hispid or villous, 1.4-12.5 cm long, terminal leaflet blade 0.7-3.2 cm long. Leaves pilose, strigose, hirsute, or velutinous above, strigose, velutinous, or woolly below, often drying brown. Lateral leaflets inequilateral, subsessile or with petiolules up to 2.5 cm long; leaflets attached in palmate fashion when trifoliolate, pinnate when more than 3 leaflets. Inflorescence a lateral paniculate thyrse, up to 1 dm long; bracts deltoid to lanceolate, 0.6-10 mm long, 0.3-3 mm broad at the widest point, glabrate, ciliate, deciduous; sepals 5, deltoid-ovate, 1-2 mm long, 0.5-1.5 mm broad, glabrate; petals 5, cream to yellow-green, dark-veined, oblanceolate, glabrous, 2-4 mm long, 2-3 mm broad, reflexed in male, recurved in female, larger in male flowers than in female. Anthers lanceolate, 1-1.5 mm long, 0.5-1.1 mm broad, filaments linear-subulate, 1.0-1.8 mm long. Drupe hard, yellow-brown to tan, globose-reniform, sometimes depressed-globose, pubescent (rarely glabrate), exocarp becoming papery upon ripening and readily separating from the mesocarp; mesocarp 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; young branches villous. Buds stalked, naked,

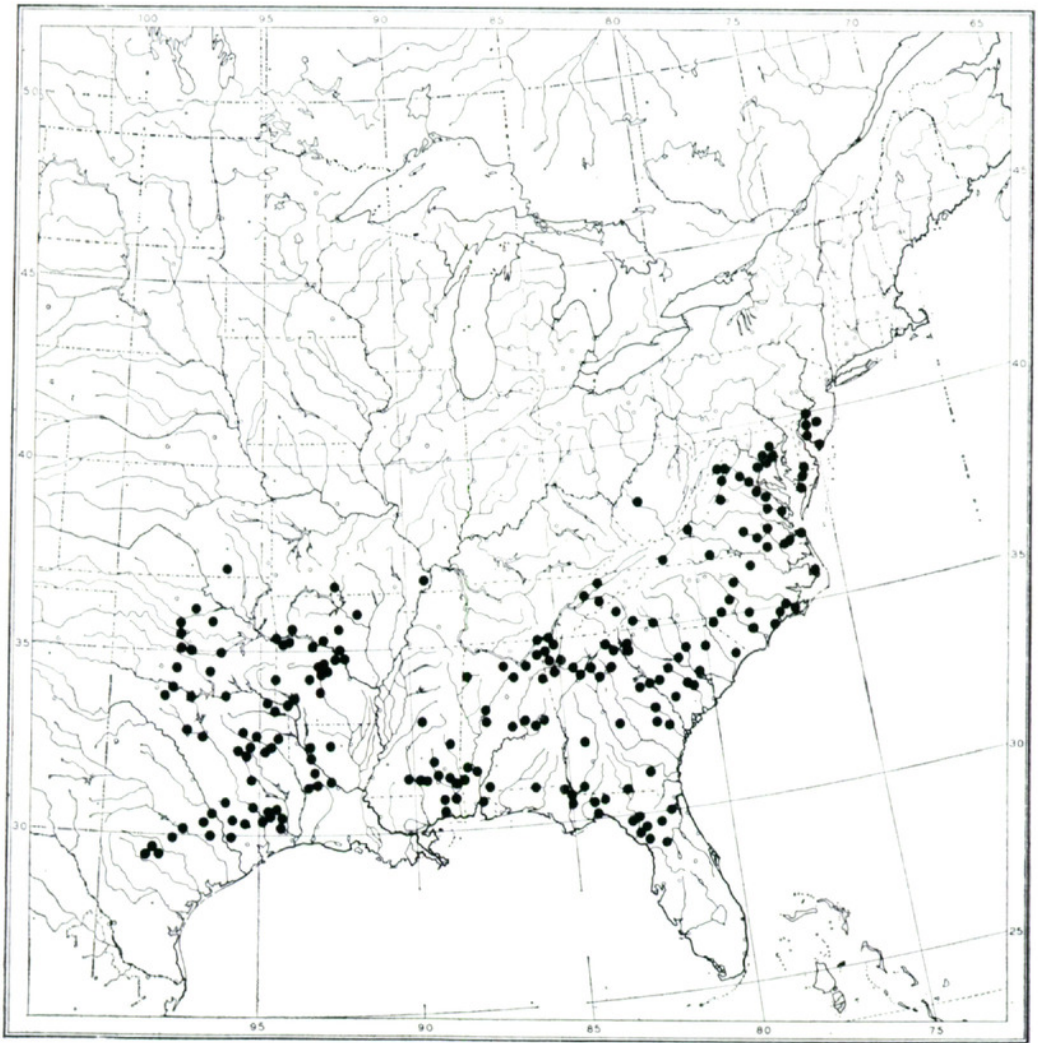


Fig. 51. Distribution of *Toxicodendron toxicarium*.

mucronate, brown, covered with a brown woolly pubescence. Autumn coloration red-bronze or brown.

Distribution: southeastern United States, New Jersey to Florida, west to Texas, north to southeastern Kansas. Common name: Eastern poison-oak. (Fig. 51.)

Representative specimens: UNITED STATES. **Alabama.** AUTAUGA CO.: Booth, *Gillis* 4530 (MSC). BALDWIN CO.: Loxley Research Plots, Stapleton, *Grelen* 5/59-46 (FLAS). BLOUNT CO.: *Eggert*, s.n. (MIN, MO, NY). CHOCTAW CO.: Bladonsprings, *Mohr*, s.n. (US). CLARK CO.: Jackson, *Gillis* 6021 (MSC). CLEBURNE CO.: north of Edwardsville, *Donahue* 249 (MSC); waterfall, Che-a-ha Mt., *Mohr*, s.n. (ALU). CULLMAN CO.: St. Bernard *Wolf*, s.n. (MO). DEKALB CO.: Ft. Payne, *Sherman* 298 (SMU). ELMORE CO., Wetumpka, *Gillis* 4524 (MSC). ESCAMBIA CO.:

Atmore, *Ahles* 7279 (ILL). HALE CO.: Payne Lake Recreation Area, Talledega National Forest, *Donahue* 245 (MSC). LEE CO.: Auburn, *Earle & Baker*, s.n. (F, KSC, MIN, MO, NY, RM); Auburn University, *Gillis* 4504 (MSC). MACON CO.: Tuskegee, *Gillis* 4509 (MSC). MARION CO., north of Hamilton, *Gillis* 6040 (MSC). TUSCALOOSA CO.: 3 miles south of Fosters, *Gillis* 6032 (MSC); Tuscaloosa, *Mohr* 231a (ALU). WASHINGTON CO.: 1 mile east of state line, *Gillis* 6012 (MSC). ARKANSAS. CLARK CO.: Arkadelphia, *Demaree* 17824 (A, MO, SMY); Graysonia, *Demaree* 21940 (A, ND-N, NY, SMU). CLEBURNE CO., Heber Springs, rim of Round Mt., *Demaree* 56274 (MSC). CONWAY CO., Petit Jean Mt., Morrilton, *Moore* 400 (SMU). DREW CO.: Ladelle, *Demaree* 22007 (A, MO); Monticello, *Demaree* 25409 (SMU). FAULKNER CO.: Cove Creek, *Demaree* 70 (MO); Greenbrier, *Gillis* 3777 (MSC). FRANKLIN CO.: north slope of Altus Hill, *Donahue* 225 (MSC). GARLAND CO.: Hot Springs, *Demaree* 17856 (MO, NY, SMU); Hot Springs, *Palmer* 24520 (A). GRAND PRAIRIE CO.: Hazen, *Wheeler* 78 (F). GRANT CO.: Poyen, *Demaree* 11052 (SMU). HEMPSTEAD CO.: Fulton, *Bush* 5677 (A, F, PH, MO). HOT SPRINGS CO.: Magnet Cove, Cook Mt., *Demaree* 19531 (MO, NY, SMU); Bismarck, *Demaree* 17405 (MO, WIS); Butterfield, *Demaree* 14519 (MO, NY); Malvern, *Palmer* 30361 (A). LAWRENCE CO.: Strawberry, *Demaree* 26212 (MU, TEX). LOGAN CO.: West Mt., *Palmer* 24520 (MO); east side of Magazine Mt., *Donahue* 227 (MSC). LONOKE CO.: Carlisle, *Demaree* 17570 (A, GH, MIN, MO, NY, SMU). MILLER CO.: Texarkana, *Demaree* 24476, (MO, NY, SMU). OUA-CHITA CO.: Camden, *Demaree* 16782 (A, MO, NY). PRAIRIE CO.: Hazen, *Palmer* 25052 (A, MIL). PULASKI CO.: Little Rock, *Palmer* 22943 (A). SALINE CO.: Bauxite, *Moore* 480198 (SMU). SCOTT CO.: 3 miles east of Y City, *Donahue* 229 (MSC). SEBASTIAN CO.: Mansfield, *Demaree* 18149 (SMU); Arkansas National Forest, *Palmer* 39315 (ND). SEIVER CO.: DeQueen, *Fassett & Watts* 19737 (GH, NY, WIS); Mineral, *Brinkley* 219 (F, TEX). YELL CO.: Dardanelle, *Demaree* 22769, 20055 (MIN, MO, NY, SMU). Delaware. SUSSEX CO.: Laurel, *Commons*, s.n. (GH, MO, NY). District of Columbia: Fort Totten, *Holm*, s.n. (MO). Woods near Sligo Creek, *Moffatt*, s.n. (ILL). Terra Cotta, *Holm*, s.n. (ILL, LCU, MO). Woodley Park, *Steele*, s.n. (A, F). Without locality, *Hitchcock* 12962 (US). Florida. ALACHUA CO.: Gainesville, *Gillis* 4315 (FLAS, MSC); oak-pine-hickory forest, University of Florida campus, *Wiggins & Wiggins* 19855 (FLAS); Wacahoota West, s.n. (FLAS). CLAY CO.: Goldhead Branch State Park, *West*, s.n. (FLAS). DIXIE CO.: 5.5 miles north of Oldtown, *Pasture Survey*, s.n. (FLAS). GADSDEN CO.: Aspalaga, *collector unknown* (MO). GILCHRIST CO.: Fort White, *Cooley & Brass* 8108 (SMU); *Wilcox, Martin, DeVall, & Arnold*, s.n. (FLAS). JACKSON CO.: west side of Apalachicola River, north of Victory Bridge, *Exploration Party* 1937 (FLAS); Marianna, *Godfrey* 60771 (MSC, SMU). JEFFERSON CO.: Wacissa and Capps, *Godfrey* 60640 (FSU, MSC, SMU). LAFAYETTE CO.: north of Mayo, *West & Arnold*, s.n.

(FLAS). LEON CO.: Tallahassee, *Godfrey* 53105 (FSU, GH, NY, SMU, VDB); Hammock, *Small, DeWinkeler, & Mosier*, s.n. (NY). LEVY CO.: locality unknown, *Hitchcock* 335 (F). LIBERTY CO.: pineland near Bristol, *West & Arnold*, s.n. (FLAS); 5.5 miles north of Bristol, *Godfrey & Henderson* 62875 (FLAS, FSU, MSC); MARION CO.: 2 miles south of Silver Springs *Gillis* 4487, 6867 (MSC). OKALOOSA CO.: Laurel Hill, *Godfrey* 61315 (FSU, MSC). SUWANEE CO.: locality unknown, *Hitchcock* 332 (F, MO); pineland 8 miles west of O'Brien, *West & Arnold*, s.n. (FLAS). WAKULLA CO.: Wakulla, *Godfrey* 60730 (MSC, NY, SMU). **Georgia.** BARTOW CO.: Cartersville, *Rhoades*, s.n. (WIS). BULLOCH CO.: locality unknown, *Harper* 948 (F, GH, MO). CLARKE CO.: Athens, *James*, s.n. (MSC). COBB CO.: Kenesaw Mt., *Rhoades*, s.n. (WIS). DADE CO.: Lookout Mt. *Ruth* 356 (MO, ND-G, US). DECATUR CO.: Bainbridge, *Gillis* 4500 (MSC). DEKALB CO.: Stone Mt., *Miller, Perry, Myers, & Boyel* 542 (GH); Lithonia, *Perry & Myers* 927 (GH). EMANUEL CO.: Swainsboro, *Gillis* 4966 (MSC). FLOYD CO.: Rome above Cossa River, *Demaree & Lipps* 50134 (MSC). GWINNETT CO.: Thompsons Mill, *Allard* 146 (US). HABERSHAM CO.: Currahee Mt., *Small*, s.n. (MSC, NY). HARALSON CO.: Tallapoosa, *Donahue* 251 (MSC). JEFFERSON CO.: locality unknown, *Hopkins*, s.n. (NY). LOWNDES CO.: 4 miles north of Clyattville, *Gillis* 6583 (MSC). MCDUFFIE CO.: near Sweetwater and Thomson, *Bartlett* 1702, 1703, 1704 (MICH, MSC). PEACH CO.: near Byron, 1.5 miles north of jct. I-75 and Ga-49, *Gillis* 6551 (MSC). RANDOLPH CO.: Shellman, *Sandlin*, s.n. (BLH). RICHMOND CO.: Augusta, *Sargent*, s.n. (A); Augusta, *Gillis* (MSC). WALTON CO.: Loganville, *Wiegand & Manning* 1862 (GH). WARE CO.: Waycross, *Gillis* 4975 (MSC). WHITFIELD CO.: Taylor's Ridge, *Wilson* 155 (E, F, GH). **Kansas.** CHAUTAQUA CO.: locality unknown, *Hitchcock*, s.n. (KSC). **Louisiana.** BIENVILLE PARISH: Castor, *Moore* 6407 (GH). JACKSON PARISH: Indian Village, *Moore & Marman* 5913 (GH). NATCHITOCHE PARISH: *Chopin* 7326 (A, F, MO). RAPIDES PARISH: Valentine Lake, *Thieret* 17923 (MSC). VERNON PARISH: LaCamp, *Donahue* 241 (MSC); 4 miles SE Ft. Polk, *Kral & Ricks* 16788 (FLAS). **Maryland.** ANN ARUNDEL CO.: Severn Run, *Reed* 29949 (FLAS, FSU, MO, NY, US). Baltimore, *Forman*, s.n. (NY). MONTGOMERY CO.: north end of Rock Creek Park, *Bartlett* 2243 (MICH, MSC). PRINCE GEORGES CO.: Clinton, *Holm*, s.n. (GH, KY, LCU). WICOMICO CO.: Salisbury, *Chickering*, s.n. (F, NY). WORCESTER CO.: Snow Hill, *Norton*, s.n. (MO). **Mississippi.** ATTALA CO.: locality unknown, *McDougall* 1615 (US). COVINGTON CO.: Collins, *Gillis* 6005 (MSC). GEORGE CO.: Lucedale, *Cooley, Pease, & Demaree* 3374 (GH). HARRISON CO.: DeSoto National Forest, *Diener* 905 (ILL). JEFFERSON DAVIS CO.: between Lucas and Prentiss, *Gillis* 6000 (MSC). JONES CO.: Laurel, *Teer* 64 (SMU, WIS). LAUDERDALE CO.: Meridian, *Rhoades*, s.n. (GH, RM). SMITH CO.: Marathon Lake, *Donahue* 243 (MSC). STONE CO.: McHenry, *Demaree* 33379 (FSU, GH, SMU, VDB). WAYNE CO.: Beat Four School along

US-84, *Gillis* 6011 (MSC). **Missouri.** MISSISSIPPI CO.: Charleston, *Palmer & Steyermark* 41516 (A, MO). OZARK CO.: Tecumseh, *Palmer* 33025 (A, MO); Gainesville, Bald Jesse, *Palmer* 43891 (MO, NY); *Palmer* 33068 (A, MIN, NY). **New Jersey.** CAMDEN CO.: Cooper Creek, *Long* 18963 (GH); Somerdale, *Meredith*, s.n. (GH). CAPE MAY CO.: Goshen, *Gillis* 5631 (MSC); Locust Grove, West Medford Branch of railroad, *Long*, s.n. (MICH). CUMBERLAND CO.: Bridgeton, *Van Pelt*, s.n. (GH); Millville, *Gillis* 5634 (MSC). GLOUCESTER CO.: Woodbury, *Long*, s.n. (GH); Malaga, shore of Lake Malaga, *Gillis* 4044 (MSC). **North Carolina.** BLADEN CO.: Tackeel, *Ahles* 29161 (GH). BUNCOMBE CO.: Asheville, *Schneck*, s.n. (ILL). CARTERET CO.: Longleaf, *Gillis* 3883 (MSC). CUMBERLAND CO.: Fayetteville, *Miles*, s.n. (US); Cedar Creek, *Ahles & Hammond* 24447 (NY). DARE CO.: Manteo near old fort, Roanoke Island, *Churchill*, s.n. (MSC). DURHAM CO.: Nelson, *Gillis* 4030 (MSC). FRANKLIN CO.: Nash, *Ahles* 16514 (SMU). MOORE CO.: Carthage, *Fox, Godfrey & Campana* 1381 (FLAS, GH, SMU). ONSLOW CO.: Gum Branch, *Boyce & Moreland* 640 (GH). PENDER CO.: 4 miles south of Wallace, *Kral* 10091 (FSU). POLK CO.: Tryon, *Millsbaugh* 4060 (F). RICHMOND CO.: locality unknown, *Wiegand & Manning* 1861 (GH). **Oklahoma.** ATOKA CO.: 12 miles south of Atoka, *Hopkins & Nelson* 1103 (RM). CLEVELAND CO.: Norman, *Woodward* 92 (MO). CREEK CO.: Bristow, *Gillis* 5123 (MSC). GARVIN CO.: Davis, *Palmer* 57 (NY). LOGAN CO.: Guthrie, *Carleton*, s.n. (ILL). LOVE CO.: Hickory Creek north of Marietta, *Gillis* 5144 (MSC). OKLAHOMA CO.: Oklahoma City, *Campbell*, s.n. (MIN). PAYNE CO.: Stillwater, *Waugh* 124 (F, KSC). PITTSBURG CO.: McAlester, *Palmer* 6402 (A, F, MIN). POTTAWATOMIE CO.: St. Louis, *Faulkner* 66 (GH). **South Carolina.** AIKEN CO.: Mt. Pleasant, *Gillis* 4614 (MSC); north of Augusta, Ga., *Gillis* 4930 (MSC); Graniteville, *Eggert*, s.n. (MIN, MO); Aiken, *Harbison* 1159 (A, E). ANDERSON CO.: Anderson, *Davis* 1435 (US). BARNWELL CO.: Williston, *Palmer* 39870 (A, MO). CHEROKEE CO.: Draytonville Mt., ESE of Gaffney, *Ahles* 26988 (FLAS). CLARENDON CO.: Paxville, *Godfrey & Tryon* 1011 (GH, NY). DARLINGTON CO.: Darlington, *Rehder* 966 (A). GREENVILLE CO.: near Greenville, *Small*, s.n. (NY). HORRY CO.: locality unknown, *Weatherby & Griscom* 16583 (GH). KERSHAW CO.: Camden, *Palmer* 42394 (A, MO, NY). LEXINGTON CO.: Gaston, *Gillis* 4002 (MSC); Pleasant Hill, *Gillis* 4611 (MSC). OCONEE CO.: Tomassee, *House* 2051 (US). ORANGEBURG CO.: Eutawville, *Godfrey & Tryon* 829 (G, GH, MO, NY). PICKENS CO.: Clemson, *House* 3354 (NY). RICHLAND CO.: Columbia, *BARTRAM*, s.n. (NY); north of Columbia along highway 21, *Gillis* 4582 (MSC); Fort Jackson, *Gillis* 4014 (MSC). **Tennessee.** GRAINGER CO.: Rutledge, *Norton*, s.n. (ND-G). HAMILTON CO.: Chattanooga, *Churchill*, s.n. (GH); Lookout Mt., *Sharp & Hesler* 1060 (SMU). KNOX CO.: Knoxville, *Lamson-Scribner*, s.n. (US). SEVIER CO.: Sevierville, *Palmer* 42509 (A, MO). **Texas.** BASTROP CO.: Bastrop, *Lundell & Lundell* 10334 (F, NY, SMU); Bastrop

State Park, *Gillis* 3694 (MSC). BEXAR CO.: near Rio Medina, *Berlandier* 2035 (KW, G-DC, GH, MO). BOWIE CO.: 8.8 miles NNE of Sulphur River, *Donahue* 231 (MSC). BRAZOS CO.: 12 miles NE of Bryan, *Donahue* 234-A (MSC). BURLESON CO.: Somerville, *Shinners* 14694 (SMU). CALDWELL CO.: locality unknown, *McBryde*, s.n. (TEX). DALLAS CO.: Dallas, *Reverchon* 154, (A, F, GH, MO). GRAYSON CO.: Denison, *Reverchon*, s.n. (MIN, MO). HARDIN CO.: Kountze, *Demaree* 55416 (MSC). HARRIS CO.: Hickley, *Thuron*, s.n. (US). HARRISON CO.: Marshall, *Palmer* 5288 (A, MIN). HENDERSON CO.: NNE of Frankston, *Donahue* 232 (MSC). HOUSTON CO.: WNW of Ratcliff, Davy Crockett National Forest, *Donahue* 233 (MSC). JASPER CO.: Bouton Lake Recreation Area, Angelina National Forest, *Donahue* 240 (MSC). LAMAR CO.: Arthur City, *Demaree* 12006 (A). MONTAGUE CO.: St. Joe, *Shinners* 13272 (SMU). MONTGOMERY CO.: Conroe, *Palmer* 33331 (A, MO, NY). POLK CO.: Livingston, *Palmer* 5228 (A, F, MIN); NE of Camden, *Tharpe, Turner & Johnston* 54738 (TEX). RUSK CO.: Henderson, *Shinners* 14036 (SMU); Tatum, *Cory* 56464 (SMU). SMITH CO.: western Tyler, north of Pine Bluff Rd. *Cory* 56191 (F, NDA, SMU). TARRANT CO.: locality unknown, *Ruth* 550 (F, US). UPSHUR CO.: Big Sandy, *Shinners* 14380 (SMU). WALKER CO.: Huntsville, *Palmer* 12049 (A, MO). WALLER CO.: Hempstead, *Hall* 78 (F, ND-G, NY, MO). WILSON CO.: Ted Cover Road, *Cory* 55405 (SMU). WOOD CO.: Mineola, *Shinners* 14360 (SMU). COUNTY UNKNOWN: between Bejar and Trinidad Rivers, *collector unknown* (G-DC). Virginia. ARLINGTON CO.: Oakcrest, *Hotchkiss* 5861 (ND-G, NY); Naucks, *Steele*, s.n. (A). AUGUSTA CO.: locality unknown, *Caro* 466 (GH). CAROLINA CO.: Milford, *Fernald & Long* 7518 (GH, PH). CARROLL CO.: Woodlawn, *Hunter*, s.n. (GH, US). CULPEPPER CO.: Buzzard Mt., *Allard* 20851 (US). DINWIDDIE CO.: Carson, *Fernald, Long, & Smart* 5834 (GH, PH); Petersburg, *Fernald & Long* 8346 (GH, MO, NY, PH). FAIRFAX CO.: Great Falls, *Bartlett* 1784 (MICH, MSC, SMU). FAUQUIER CO.: western slope of Bull Run Mt., *Allard* 10006 (GH, US). GREENSVILLE CO.: Orion, *Fernald & Long* 13675 (GH, PH, US). NANSEMOND CO.: South Quay, *Fernald & Long* 10322 (GH, PH, US). PAGE CO.: Kimball, *Miller*, s.n. (US). PRINCE EDWARD CO.: Farmville, *Fosberg* 15541 (GH). PRINCESS ANNE CO.: Cape Henry, *Egler* 40-151 (NY); Richmond, University of Richmond Campus, *Clarke* 996 (GH); *Churchill*, s.n. (GH). ROANOKE CO.: Hanging Rock, *Wood* 3094 (GH). SHENANDOAH CO.: Massanutten Mt., *Allard* 6618 (F, MO, NY, US); South of Elizabeth Furnace Forest Camp, *Chrysler* 3027 (CHRB). SPOTSYLVANIA CO.: Fredericksburg, *Iltis* 220 (SMU). SUSSEX CO.: Jarrett, *Fernald & Long* 8347 (GH, NY, US); Williamsburg, *Grimes* 3667 (GH). West Virginia. KANAWHA CO.: Pine Top Ridge, Loudon District, *Fletcher*, s.n. (MSC).

The Tournefort name *Toxicodendron*, which has been used for this generic segregate of *Rhus*, was chosen by

Linnaeus as the specific epithet for Eastern poison-oak. Tournefort (1700), Barrelier (1714), and Gronovius (1743) may have had this plant in mind when they described *Toxicodendron triphyllum folio sinuato pubescente*, for its leaves are characteristically sinuate or lobed and pubescent. Linnaeus included this polynomial phrase in synonymy under his *Rhus toxicodendron*. However, no specimens representing this species which were probably seen by these early authors appear to be extant to confirm their identity. Furthermore, in the Michaux Herbarium, there is a specimen labeled with this same polynomial phrase that is *T. rydbergii*. It is with Michaux that much of the nomenclatural confusion begins, as mentioned earlier. The point to be made herein is that authors before and after Linnaeus have had different taxa in mind in their use of *Rhus toxicodendron* as a name, or polynomial phrases associated with it. Typification of the Linnaean name is therefore exceedingly important.

The lectotype sheet at LINN (sheet 378.16 Fig. 52) bears two plants; the one on the left represents the taxon here recognized; the other is aromatic sumac [*Rhus aromatica* Aiton = *Lobadium aromaticum* (Ait.) Raf. ex Steudel]. The specimen on the left, then, is chosen as the lectotype of *Rhus toxicodendron*. This species name has been used indiscriminately for poison-oak (both *Toxicodendron diversilobum* and *T. toxicarium* and poison-ivy (*T. radicans* and *T. rydbergii*). Of the infraspecific names proposed for various members of the complex using *Rhus toxicodendron* as a base, one has been applied to Western poison-oak, three to Eastern poison-oak, and twelve to poison-ivy!

Many persons have used the name *Rhus toxicodendron* in preference to *R. radicans* because it is perhaps more euphonious and more suggestive of the toxic nature of the plant. A rough count of herbarium specimens examined shows that it has been used more frequently (and carelessly) than any other binomial with reference to either poison-ivy or poison-oak. It was not even spelled in full by Linnaeus until the publication of *Systema Naturae*, ed.

11 (1760). A good discussion of the orthography is given in Fernald (1941, pp. 597-599).

Michaux (1803) published the epithet *quercifolium* without rank indicated, but variety implied. It was Eaton (1818) who designated the rank as *Rhus toxicodendron* var. *quercifolium*. Steudel (1871, p. 689) made the combination *R. quercifolia*, but lists it in synonymy and should not, according to the Code (Lanjouw *et al.*, 1966), be cited as author of the combination. Robinson and Fernald (1908) made the combination legitimately, although they attribute it to Steudel. In the meantime, however, this combination was validly published as a fossil species, *Rhus quercifolia* Goeppert from the Tertiary of Bohemia (Goeppert, 1855).

To give some idea of the nomenclatural "mess" (to quote Fernald's well-chosen word regarding this complex) involving the epithets *toxicodendron* and *radicans*, some combinations are listed below. Where their true identity can be correlated with a known species, the names are listed in the appropriate synonymy in the taxonomic treatment; where they are not, such names are listed in a group of doubtful species.

Rhus toxicodendron L. (1753, p. 266)

R. radicans var. *toxicodendron* Persoon (1805, p. 325)

Rhus-Toxicodendron radicans Marshall (1785, p. 131)

Rhus-Toxicodendron toxicodendron Marshall (1785, p. 131)

R. toxicodendron var. *radicans* Eaton (1818, p. 400)

R. toxicodendron forma *radicans* McNair (1925, p. 68)

R. toxicodendron subsp. *radicans* Clausen (1949, p. 8)

Toxicodendron toxicodendron (L.) Britton (1913, p. 484)

All of these have been cited by other authors. Also, *Rhus toxicodendron radicans* (without rank specified) has been attributed in the literature to Torrey, Dippel, Miquel, and to "Farr." (sic) (Dodge, 1911), and *R. toxicodendron* attributed both to Linnaeus and to Small by McNair (1925). McNair (*loc. cit.*) also mentions a var. *typica* which has no nomenclatural status according to the Code.

With respect to *Toxicodendron vulgare* Miller (Gard. Dict., ed. 8, Art. *Toxicodendron*, No. 1, 1768), confusion

of a different sort pertains. It was not Miller's custom to cite Linnaean binomials when transferring species to other genera, or when providing new epithets for them, but to give a reference at the beginning of the account which established a connection with the earlier literature. He used Linnaean epithets where appropriate; in other cases, he used pre-Linnaean names, citing the source of the original publication. A synonym which Miller (and others) frequently cited as "*Toxicodendron triphyllum folio sinuato pubescente*" (Tournefort, Inst. Rei, Herb. 611) links the name *T. vulgare* Mill. with *Rhus toxicodendron* L., being a polynomial phrase shared in the two descriptions. The lectotype of the Linnaean name accordingly typifies the name substituted for it by Miller. This is the species which herein is called *T. toxicarium*.

Should not the epithet *vulgare* of Miller (1768) have priority over *toxicarium* first applied as a species epithet by Salisbury (1796)? It probably would if Miller's Latin and English diagnoses accurately described Eastern poison-oak, but they do not. He described the "foliolis" as: "obcordatis, glabris, integerrimis," and adds further, "caule radicante." Still further, he continues, "with roundish, heart-shaped, smooth, entire, trifoliate (sic) leaves, and a stalk putting out roots." Eastern poison-oak has leaflets which are not obcordate, not glabrous, and are lobed, not entire. The stem is not climbing; the stalk never produces aerial roots. Inasmuch as the species which Miller named as *Toxicodendron vulgare* is too inaccurately described to be Eastern poison-oak, even though indirectly linked with that species in the literature (thus satisfying Art. 32 of the Code), this binomial must be rejected under Art. 69 of the Code.

A specimen at Kiev representing *Rhus acutiloba* Turcz., was collected in Texas by Berlandier. At the time of Berlandier's explorations in Texas (1827-1830), this region was part of Mexico, hence the word "Mexico" on the label. This taxon is not found in present-day Mexico. It was presumably collected in Southeastern Texas (McKelvey, 1955). An isotype at the Gray Herbarium completes

the story: the specimen was collected near the Medina River in July 1829. According to McKelvey (*loc. cit.*), this would have been 15-16 July, just south of present-day San Antonio in Bexar County. Another specimen cited by Turczaninov (at KW) is *Mathes* 160 from Taylor County, Texas. This is a mixed collection; the two large specimens on the sheet are *Toxicodendron radicans* subsp. *verrucosum*, but the small sprig in the upper right corner is *T. toxicarium*.

There are many populations of Eastern poison-oak in which leaflets of the male clones differ from the leaflets of female clones. Most often, the leaflets on male plants are more deeply lobed than those of female clones. In fact, some of the leaflets in female plants may be elobate or with undulating leaflet margins. Fernald named the form *Rhus toxicodendron* f. *elobata*, separating it simply on the basis of sexually dimorphic characters, apparently unaware that this was the case.

In collecting material which later became the type for *Toxicodendron monticola*, Ruth apparently numbered specimens, rather than gatherings. Hence, the specimens at ND-G, NY, and MO are presumed isotypes. Greene did not clearly cite a type specimen, but indicated *Ruth* 356 as representative. This specimen is therefore designated lectotype. Because of the uncertainty with which Greene deals with *Percy Wilson* 155 from Taylor's Ridge, Georgia, this specimen is not considered a syntype. Greene's diagnosis described the leaves as bright green, yet the leaves of the type have dried brown, and he probably saw it after the plant was dried.

Often used in connection with this species is the epithet *pubescens*. Philip Miller originally published the name *Toxicodendron pubescens* (Gard. Dict., ed. 8, Art. *Toxicodendron*, No. 2, 1768). His description fits *T. toxicarium* which has pubescent leaves and fruits, but not to the exclusion of all other taxa. Apparently no specimen upon which this name could be based is extant. Thunberg (1794) published the epithet again, this time as *Rhus pubescens* for a plant from the Cape of Good Hope, not a member of the poison-ivy complex, but a *Rhus* sect. *Thezera*. *Rhus pubescens* Engelm. ex Engler in DC. (1883) was a new name

(and a homonym) published for a plant that is likely to be *T. radicans* subsp. *radicans*, which has pubescent fruits. Type specimens — designated or implied — are known for none of these. In 1900, Farwell published another *Rhus pubescens*, indicating that he was transferring the name from Miller, although, judging from the region covered by his work (Michigan), not to represent the same species. As was his custom, he named a "type specimen" (sic) which is at BLH with a duplicate at ND-G. Farwell's "type" is *T. radicans* subsp. *negundo*.

The formal epithet of *R. toxicodendron* f. *leiocarpa* means "smooth-fruited," but the holotype has pubescent fruits (although the sheet bears the notation "glabr. fr."); furthermore, the fruits are immature and shriveled, not readily demonstrating any papillose condition. The glabrate or glabrous nature of the fruit might be due in part to their immaturity (their having been collected early in June) and therefore should not be considered diagnostic. The holotype has some aborted ovary tissue such as that described for New Jersey poison-ivy by Gillis (1960). Isotypes at NY and US were annotated by Fernald as a form of *Rhus radicans* (sic) in error.

Toxicodendron toxicarium clearly is the most misunderstood species in the poison-ivy complex. The common name, poison-oak, is related to the typical leaflet shape, which resembles the leaf of a species of the white oak group. This common name has been used in different senses by physicians, Boy Scouts, extension agents, botanists, and others until it has lost its meaning. Most often it is used to represent *T. rydbergii* or a shrubby or arborescent form of *T. radicans*. The plant is seldom encountered in the wild by non-botanists because of its habitat requirements. It is practically restricted to low-nutrient sands of the Atlantic and Gulf Coastal Plains, generally in association with scrub-oak and pine woods (sandhills vegetation) that have little economic value. It is seldom abundant. Although it produces aerial stems from its stolons, it does so at far greater intervals than its counterparts *T. radicans* or *T.*

diversilobum. In habit, it resembles the sub-shrub *T. rydbergii* more than any other member of the complex.

This plant is found most often in scrub-oak and pine woodland savanna that has an understory of ericaceous shrubs and bunch grasses, chiefly *Aristida*, *Stipa*, and *Andropogon*, characteristically found in the sandhills of the Carolinas. In Oklahoma, where the same general vegetation type, minus the pine, may be found, *Toxicodendron toxicarium* occurs also. The soils in which it grows are most often coarse sands, generally low in calcium, magnesium, and potassium. In fact, the Lakewood and Norfolk sands in which it has been found most often are the soils with the lowest nutrient values of any along the Atlantic Seaboard. For this reason, its requirements are such that it seldom occurs in the same association with any other taxa of the complex, all of which generally prefer richer soils.

In a very few instances, putative hybrids between *Toxicodendron toxicarium* and *T. radicans* subsp. have been found. The former is contained within the combined ranges of *T. radicans* subsp. *radicans*, *pubens*, and *verrucosum*. It might be expected, given the environment intermediate between that restricted one required by *T. toxicarium* and the rather broad one permitted by subspecies of *T. radicans*, that some gene interchange might take place. In the field, although such situations are comparatively rare, several have been found. One from Bastrop County, Texas, suggests crossing between *T. radicans* subsp. *verrucosum* and *T. toxicarium* in a region where both are abundant. Several collections have been made in New Jersey, Georgia, and South Carolina which seem to be intermediate between *T. toxicarium* and *T. radicans* subsp. *radicans*. Other putative hybrids have been seen among herbarium specimens. A more complete discussion of putative hybrids is discussed in the section on "Hybrids, Crosses, and Intergrades."

The relative rarity of intermediate forms throughout the southeastern states where both of these species are frequent, if not common, has been a guiding factor in recognizing them as distinct species. Although hybridizing can appar-

ently occur, it is not an important factor in the genetics of these populations.

Part of the difficulty in recognizing the species *Toxicodendron toxicarium* in the field is the degree of lobation of the leaflets. Leaflet margins may be undulate or almost entire varying through degrees of lobing to crenate or deeply lobed. Often, as mentioned before, one sex may have leaflets more distinctly lobed than the other, all within the same population. It is usually the male which has more deeply lobed leaflets than the female, but the converse may also be true. The most significant morphological features, then, are the pubescent nature of the leaves and fruits, the non-climbing habit, and the rather impoverished habitat.

In published keys, one finds that some previous workers have considered thickness of the leaves to be a major factor separating *T. toxicarium* from related taxa. From anatomical sections, I have measured a number of leaves of various of these species, and found no consistent difference. The leaves of *T. toxicarium* are also described as leathery. They perhaps have a slightly thicker cuticle, a possible evolutionary result of the plant's being found on drier sites than is poison-ivy, but otherwise, this character is variable. The thickness or leathery nature of the leaflets is hardly conducive to field determination in such a dermatitis-producing plant!

HYBRIDS, CROSSES, AND INTERGRADES

A study of naturally-occurring suspected hybrids found in the field was made, and an attempt was made to produce hybrids artificially. Difficulty in obtaining germination precluded the latter's being wholly successful, but nevertheless some data of significance were accumulated. Suspected natural hybrids have been found and are herein described along with ecological and geographical considerations.

FIELD STUDIES

Because several subspecies of *Toxicodendron radicans* and *T. toxicarium* overlap in range, a search was made for natural hybrids between them. As will be discussed later,

these two species rarely exist in the same vegetation association or soil type. Even on the few occasions where one finds them occurring together, there is a paucity of intermediate forms. Several of these associations were investigated in detail.

In the San Felasco area of Alachua County, Florida, there is an extensive tract (T. 9S., R. 19 E., Sec. 21) of mixed community of hammock and sandhills vegetation (Monk, 1960), where both *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* grow abundantly side by side. Despite intensive searching, I was unable to find any intermediate forms between these two readily distinguishable species. Both flower at the same time (early April) and are pollinated by honey bees, although few female flowers of *T. radicans* were found in the population.

In a study area north of Columbia, Richland County, South Carolina, in a narrow band of overlap between poison-ivy and Eastern poison-oak (c. 10 meters), there was only one individual with intermediate characters found (Gillis 4582). This individual has some of the leaflet shape, notching and color of *Toxicodendron radicans* subsp. *radicans*, but the pubescence and growth form (sub-shrub) of *T. toxicarium*. The cited specimen is a female in flower.

In another study area in Bastrop County, Texas, between Beuscher and Bastrop State Parks, one finds pockets of *Toxicodendron radicans* subsp. *verrucosum* and others of *T. toxicarium*, the latter growing on the poorer soils. Only one suspected hybrid was discovered, a sterile specimen which possessed the leaf pubescence of *T. toxicarium* but the climbing habit of *T. radicans* subsp. *verrucosum* (Gillis 5167). The lobing is intermediate between the rounded lobes of *T. toxicarium* and spreading, sharp lobes of *T. radicans* subsp. *verrucosum*.

A suspected hybrid clone (between *Toxicodendron toxicarium* and *T. radicans* subsp. *radicans*) was found in Jefferson County, Georgia, in a loblolly pine and sassafras woods (Gillis 4965). It shared with poison-ivy the climbing habit and the tendency to have entire leaflet margins, but had the pubescence of Eastern poison-oak.

Artificial crosses were made between *Toxicodendron radicans* subsp. *radicans* and *T. toxicarium* in Alachua County, Florida, and in Richland County, South Carolina, in the areas mentioned above during the spring of 1961. Because of a dearth of female flowering poison-ivy plants, reciprocal crosses were not possible in the Florida experimental plots. Crosses which were made in South Carolina were each replicated in three inflorescences and bagged to prevent contamination by insects. Pollen was transferred from anther to stigma by means of a loblolly pine needle. The population of Eastern poison-oak had sexually dimorphic leaves, so that the male clones could be distinguished from the females even when only unopened flowers were present. Flowers which had not yet opened, but for which flowering appeared imminent, were chosen exclusively. Results were considered successful if fruits were produced.

Where *Toxicodendron radicans* was the female parent, the fruits were small (3.5-4.0 mm broad), whereas the fruits were more typically the size of *T. toxicarium* fruits (5.5-6.5 mm broad) where this plant was the female parent. The hybrid seeds were indistinguishable from normal seeds whose parentage represents but a single species. It is to be noted that no fruits at all developed from unpollinated controls, thus making it unlikely (but not impossible) that apomixis might be taking place. Germination of the hybrid seeds was attempted, but no seedlings resulted. But then, I have succeeded in germinating only two seeds of *T. toxicarium* in trials numbering more than 200 seeds of pure parentage.

Results, as shown in Table 5, suggest that there is no apparent difference in percentage of successful crosses between open-pollinated flowers and artificial hybrids, at least not in the South Carolina series. In the Florida trials, however, the number of interspecific crosses producing fruits was half that of open-pollinated poison-ivy flowers.

In the gorge of the Columbia River between Oregon and Washington, there is overlap in range of *Toxicodendron diversilobum* from the west and *T. rydbergii* from the east. In studies made in late summer and early autumn of 1960

TABLE 5. INTERSPECIFIC CROSSES BETWEEN TOXICODENDRON RADICANS SUB-
SP. RADICANS AND T. TOXICARIUM. CROSSES WERE MADE IN ALA-
CHUA COUNTY, FLORIDA, ON 6 APRIL 1961 (lettered) AND IN RICHLAND
COUNTY, SOUTH CAROLINA ON 12 MAY 1961 (numbered). RESULTS WERE
GATHERED IN EARLY SEPTEMBER 1961 AT BOTH SITES

Cross Number	Repli- cation	Male Parent	Female Parent	Number of Flowers Pollinated	Number of Resulting Fruits	Percentage Successful Crosses	Mean Per Cent
Y	A	<i>T. toxicarium</i>	<i>T. radicans</i>	38	21	55	
	B			41	16	39	41
	C			20	6	30	
Z	A	<i>T. radicans</i>	<i>T. radicans</i>	56	45	80	
	B			63	51	84	82
1	A	<i>T. toxicarium</i> ¹	<i>T. toxicarium</i>	22	6	27	
	B			10	7	70	52
	C			32	19	59	
2	A	<i>T. toxicarium</i> ²	<i>T. toxicarium</i>	18	10	55	
	B			20	10	50	57
	C			50	32	64	

3	A	<i>T. radicans</i>	<i>T. toxicarium</i>	34	15	44	58
	B			41	22	54	
	C			20	16	75	
4	A	open-pollinated	<i>T. toxicarium</i>	44	23	52	47
	B			55	16	29	
	C			34	20	60	
5	A	unpollinated	<i>T. toxicarium</i>	38	0	0	0
	B			27	0	0	
	C			42	0	0	

¹Source of pollen was from different populations.

²Source of pollen was from same population.

and 1962, the populations of these two were examined and samples collected from along the two sides of the gorge. The zone of overlap produced an apparent introgressive series between these two taxa. The zone of apparent hybridization extends in Washington from the confluence of the Klickitat and the Columbia Rivers eastward 43 miles to the vicinity of the John Day Dam, and in Oregon from the Hood River eastward 23 miles to the vicinity of The Dalles. There is evidence that this zone of overlap is restricted to the gorge because populations immediately south of Hood River appear to be genetically pure *T. diversilobum* (Gillis 5231 from 2 miles south of Hood River city limits). Furthermore, neither taxon grows above 1275 meters in the Cascades which rise to the north and south of the gorge.

In a roadside park at the confluence of the Klickitat and Columbia Rivers there is a large shrub of *Toxicodendron diversilobum* surrounded by a clone of suspected hybrids. These populations were seen late enough in the season to demonstrate their autumn coloration. The difference between the two taxa was therefore striking. From this location, each population of the taxa was studied as I collected eastward through the gorge. Each population in the zone of overlap was sampled until populations appeared to be fairly constant as typical *T. rydbergii*. It is in the same region that flowering and fruiting material were collected by Suksdorf in the late 1800's. The latter collections were the basis for two new species names by Greene (1905). Presumably these collections represent hybrid populations.

Eastward through the gorge from Hood River in Oregon or from the Klickitat River in Washington, fruits of the *Toxicodendron* species become smaller, less pubescent, more nearly globose, and on shorter pedicels. The inflorescence becomes more compact and more erect than pendent. The leaves progressively become less crowded at the summits of branches, lose the pubescence of the petioles, assume a more yellow-orange (less red-brown) autumn coloration, lose the tendency for the peculiar mottling of the dried leaves of *T. diversilobum* and tend to have the broadest

part of the leaflet below the midpoint, becoming ovate rather than elliptic. (Fig. 53.)

HERBARIUM STUDIES

In the course of examination of populations in the field plus examination of herbarium specimens, I have determined a number of these to be intergrades between taxa. In several cases, the situation indicates that these intergrades are very likely hybrids. In others, the nature of the intergrades is less certain, possibly examples of incomplete divergence among taxa. *Toxicodendron diversilobum* and *T. rydbergii*, for example, occupy completely separate ranges except for a zone of overlap in the Columbia River gorge, as mentioned above. It seems justified to interpret the intergrades in the gorge as putative hybrids. The rather blurred separation between *T. radicans* subsp. *negundo* and subsp. *radicans* in the Allegheny Mountains may be interpreted as hybridization, but, on the other hand, may also be looked upon as intergrading due to current speciation. The Alleghenies are not a completely effective barrier to gene exchange between subsp. *radicans* to the east and subsp. *negundo* to the west. They are treated here as hybrids, but the case of incipient speciation cannot be ruled out.

HYBRIDS OF SUBSPECIES OF *T. RADICANS*

***Toxicodendron radicans* subsp. *barkleyi* × subsp. *divaricatum*. Table 6.**

The two Mexican subspecies of poison-ivy are not abundant in comparison with taxa found farther north. It is not surprising therefore that apparent intergrades between the two taxa are scarce. Only a few populations from the trans-Mexico volcanic belt or an extension of this mountain region seem to show traits intermediate between the two parental types. Such populations have been found in Jalisco, Guerrero, the Distrito Federal, Michoacan, and Oaxaca. (Fig. 55.) Characters which have been used to demonstrate the suspected hybrid nature of the populations are few. They are listed in Table 6.

It may be noted from Fig. 55 that these two subspecies

TABLE 6. CHARACTERS OF PARENT TOXICODENDRON RADICANS SUBSP. BARKLEYI, SUBSP. DIVARICATUM, AND OF THEIR PUTATIVE HYBRID OFFSPRING

<i>Toxicodendron radicans</i> subsp. <i>divaricatum</i>	Putative Hybrid	<i>T. radicans</i> subsp. <i>barkleyi</i>
Lower leaflet surface glabrous or with scattered erect strigose trichomes	Lower leaflet surface with scattered pubescence; essentially prostrate pilose hairs	Lower leaflet surface pilose to velutinous
Upper leaflet surface glabrous	Upper leaflet surface glabrate or with scattered hairs	Upper leaflet surface pubescent
Fruits usually glabrous, pubescent only in northern end of range	Fruits with scattered pubescence or nearly glabrous	Fruits always glabrous

appear to be sympatric in several regions. The concept of sympatric subspecies is an anathema to some taxonomists or evolutionists, because, by definition, subspecies have distinct geographical ranges. The Mexican populations of poison-ivy, however, bring to the fore some possible explanations for this phenomenon. One possibility is that the two subspecies evolved in separate regions, separated from one another by any of the traditional barriers to gene flow. Then, in relatively recent times, perhaps assisted by the activities of man, the two have expanded their ranges to overlap. Thus, only recently have they become sympatric and share genes. Another possibility is that they are not strictly sympatric in that they do not occupy the same communities as do, for example, *Acer nigrum* and *A. saccharum* in eastern North America. There has been no location found where they are growing close to one another. It is, then, their gross ranges which overlap, but not the refined patterns too small to show on a standard political map; that is to say, they are ecologically different, occupying the same overall range, but not the same communities.

A third possibility, not likely to be valid here, is that the two subspecies are just now speciating and exist relatively close together only as relicts of populations which existed prior to the erection of a barrier to gene flow. As interpreted herein, the two subspecies under consideration here were not derived from one another, but both have their closest relatives farther to the north of Mexico. A fourth possibility is also unlikely in this case, i.e., that either or both of the subspecies is apomictic and unable to share genetic information, yet have come to occupy portions of the same range.

Representative specimens: MEXICO. **Guerrero:** Barranca, Mina, Hinton 9488 (MICH, NY). **Jalisco:** Nevado de Colima, Beaman 2388 (MSC); Sierra del Halo, lumber road leaving Colima Highway, 7 miles SSW of Tecalitlan toward San Isidro, 2000 m., McVaugh 16229 (MICH). **Michoacan:** east of Morelia between Rio del Salto and La Polvilla, King & Soderstrom 5082 (MICH, SMU). **Nayarit:** Mountains 9 miles south of Compostela, heavily forested stream valley in oak zone, 1000-1200 m., McVaugh 16484 (MICH). **Oaxaca:** Reyes, Nelson 1789 (GH, US).

Toxicodendron radicans subsp. **negundo** × subsp. **pubens**.
Table 7.

Toxicodendron radicans subsp. **pubens** × subsp. **radicans**.
Table 7.

Considerable taxonomic difficulties are encountered in the region of overlap where *Toxicodendron radicans* subsp. *pubens*, subsp. *radicans*, and subsp. *negundo* intergrade. The number of specimens available for study which combine characters of these taxa is numerous, but not enough specimens are available from the most significant area, i.e., the second and third tiers of counties west of the Mississippi River in northern Louisiana, southern Missouri, and the intervening region of Arkansas. Perhaps it is due to active divergence among the taxa. More likely this large-scale variation is attributable to three-way hybridization among the taxa.

This region of the foothills of the Ozarks represents the western edge of the range of subsp. *radicans*, the northern edge of the range of subsp. *pubens*, and the southern edge of the range of subsp. *negundo*. No conclusions other than the probability of hybridization among these subspecies seem to be warranted at this time. Further field work in this area is desirable for resolution of the true nature of these populations. It is possible that the region in question is the center of diversity of a rapidly evolving species, but more likely a region which the three subspecies have been invading for a considerable period of time, perhaps since the Pleistocene.

For the time being, specimens from this region have been classified by the combination of several key characters. Pubescent fruits and tufts of hairs in the vein axils on the lower surface of the leaves have been interpreted as indicative of the presence of genes of subsp. *radicans*. The presence of dense, erect hairs in the interveinal area on the lower surface of the leaves is interpreted as indicative of the presence of genes of subsp. *pubens*. The presence of appressed hairs on the lower leaflet surface is indicative of the presence of genes of subsp. *negundo*. These clusters of

TABLE 7. CHARACTER CLUSTERS REPRESENTED IN VARIOUS POPULATIONS OF TOXICODENDRON RADICANS IN THE OZARKIAN REGION

subsp. <i>radicans</i>	subsp. <i>negundo</i>	subsp. <i>pubens</i>	subsp. <i>radicans</i> × <i>pubens</i>	subsp. <i>pubens</i> × <i>negundo</i>
Fruits pubescent	Fruits glabrous	Fruits glabrous	Fruits somewhat pubescent	Fruits glabrous
Tufts of hairs in vein axils present	Tufts of hairs absent	Tufts of hairs absent	Tufts of hairs present	Tufts of hairs absent
Hairs on lower leaf surface scattered	Hairs on lower leaf surface scattered	Hairs on lower leaf surface dense	Hairs on lower leaf surface dense	Hairs on lower leaf surface dense
Pubescence appressed	Pubescence appressed	Pubescence erect	Pubescence mixed appressed and erect	Pubescence mixed appressed and erect
Leaflets mostly entire	Leaflets mostly notched	Leaflets all notched or serrate	Some leaflets notched; some entire or subentire	Leaflets all notched or serrate
Leaflets ovate to lanceolate	Leaflets ovate	Leaflets broadly ovate	Leaflets broadly ovate	Leaflets broadly ovate

characters and the taxa they represent are shown in Table 7.

Toxicodendron radicans subsp. *negundo* × subsp. *pubens*.

Representative specimens: UNITED STATES. **Arkansas.** BENTON CO.: Twin Mountain, *Demaree* 4579 (F, MO, WIS). FULTON CO.: Salem, *Demaree* 26305 (SMU). WASHINGTON CO.: Lake Weddington Recreation Area, *Donahue* 224 (MSC). **Iowa.** POTTAWATTAMIE CO.: Council Bluffs, *Demaree* 23666 (MO, SMU). **Kansas.** POTTAWATOMIE CO.: St. George, *Kellerman*, s.n. (KSC). SUMNER CO.: Geuda, *Gassler*, s.n. (MIN). **Missouri.** OREGON CO.: Pine, on country road J., *Donahue* 219 (MSC). OZARK CO.: Tecumseh, *Palmer* 32912 (A, MO, NY).

Toxicodendron radicans subsp. *pubens* × subsp. *radicans*.

Representative specimens: UNITED STATES. **Arkansas.** CONWAY CO.: Morrillton, Petit Jean State Park, *Demaree* 22801, 36876 (GH, MO, NY, SMU). CRAIGHEAD CO.: Lake City, *Demaree* 7218 (GH, SMU, TEX, WIS). GARLAND CO.: Hot Springs *Demaree* 22056 (A, MIN, MO, NY); Hot Springs, *Palmer* 23098 (A, MIN). HEMPSTEAD CO.: Fulton, *Bush* 5647 (A, US). MONTGOMERY CO.: Norman, *Demaree* 9563 (GH, MO, SMU). POPE CO.: Hector, *Merrill* 52 (A, MIN, NY); Nogo, *Merrill* 332 (MIN, MO). PULASKI CO.: Little Rock, *Gillis* 3776 (MSC). STONE CO.: Ozark National Forest, rocky creek above Blanchard Springs, Allison, *Demaree* 52504 (MSC). **Louisiana.** New Orleans, *Cocks* 67 (A); 3 miles north of Maurepas, *Seibert* 703 (MO); Hammond, 13 miles east of city, *Rose-Innes & Warnock* 721 (GH, TEX). **Mississippi.** DESOTO CO.: 3 miles north of Nesbitt, *Gillis* 5906 (MSC). JACKSON CO.: Ocean Springs, *Demaree* 28099 (SMU). **Oklahoma.** LEFLORE CO.: Stapp, creek banks, *Demaree* 15732 (MO, NY, SMU).

Toxicodendron radicans subsp. *negundo* × subsp. *radicans*.

Table 8.

Rhus radicans forma *hypomalaca* Fernald, *Rhodora* 43: 592. 1941. Type: West Virginia, Ritchie Co., Berea, dry upland woods. *L. F.* and *F. R. Randolph* 1385, 23 August 1922. (GH, holotype).

Representative specimens: UNITED STATES. **Arkansas.** DREW CO.: Monticello, *Demaree* 13692 (A, NY). GARLAND CO.: Starlight Bay, Hot Springs National Park, *Demaree* 54056 (MSC). JOHNSON CO.: Knoxville, *Demaree* 19943 (MIN). PERRY CO.: Ouachita National Forest, *Demaree* 37842 (SMU). PULASKI CO.: Galloway near Little Rock, *Demaree* 53848 (MSC). **District of Columbia:** Washington, Hunting Creek, *Ward*, s.n. (US); Giesboro Road, *Steele*, s.n. (US). **Kentucky.** BREATHITT CO.: Robinson Forest, *Smith* 1717 (KY). OLDHAM CO.: 3 miles SE of Westport, *Duncan* 22750 (KY). **Louisiana.** MADISON PARISH: Tensas Gun Club Refuge, *Ewan* 17578 (MO). ORLEANS

PARISH: New Orleans, *collector unknown* (E). PLAQUEMINES PARISH: Pillottown, *Ewan* 17486 (MO). ST. MARY PARISH: Cote Blanche Island, *Thieret* 17443 (MSC). **Massachusetts.** BERKSHIRE CO.: without definite locality. *Milligan*, s.n. (ARIZ). BRISTOL CO.: Nunquit, part of Dartmouth, *Sturtevant*, s.n. (MIN). ESSEX CO.: Bradford, part of Haverhill, *Churchill*, s.n. (MIN). NORFOLK CO.: West Quincy, *Churchill*, s.n. (MIN). **Mississippi.** DESOTO CO.: 3 miles north of Nesbit, *Gillis* 5906 (MSC). **North Carolina.** BUNCOMBE CO.: Asheville, *Donahue* 259, (MSC). SWAIN CO.: Alarka, *Ahles & Bell* 14210 (FLAS). **Pennsylvania.** BEDFORD CO.: without definite locality, *Westerfield* 6568 (SMU). CHESTER CO.: Berwyn, Darby Creek, *Stone*, s.n. (RM). HUNTINGDON CO.: Rays-town Branch, 1 mile NE of Entriken Bridge, *Wahl, Handwerk, & Westlake* 5627 (FLAS). JUNIATA CO.: Port Royal, *Fogg* 16858 (NY). ADAMS CO.: South Piney Mt., *Gillis* 5112 (MSC). FRANKLIN CO.: east slope of Tuscarora Mt., *Gillis* 5110 (MSC); near summit, east slope of Tuscarora Mt., *Gillis* 5114 (MSC). **Tennessee.** FRANKLIN CO.: without definite locality, *Eggert*, s.n. (MO). **Texas.** BEXAR CO.: Rio Medina, *Berlandier* 2475, 1045 (E, GH); SMITH CO.: Tyler, *Moore* 580 (GH). **Virginia.** BEDFORD CO.: without definite locality, *Curtiss*, s.n. (GH). FREDERICK CO.: Winchester, *Gillis* 5702 (MSC). FLOYD CO.: State highway near Blue Ridge Parkway, *Donahue* 260 (MSC). JAMES CITY CO.: Toano, *Menzel*, s.n. (GH). MONTGOMERY CO.: East Bradford, *Adams & Wherry* 2263 (GH). SMYTH CO.: Marion, *Britton & Wail*, s.n. (F, NY). **West Virginia.** GREENBRIER CO.: Blue Bend Recreation Area, *Donahue* 263 (MSC). MORGAN CO.: near B. & O. Railroad and Potomac River, *Donahue* 266 (MSC). TAYLOR CO.: Thornton, *Gillis* 5723 (MSC).

Whereas *Toxicodendron radicans* subsp. *radicans* is primarily an Atlantic Seaboard taxon and subsp. *negundo* is a land-locked taxon of the Midwest and the Ohio River Valley, their ranges come into contact in the Piedmont, the lower Appalachians and west in Arkansas. Characters separating these taxa are more subtle than those separating many others; it is therefore not always easy to determine with assurance what may be an extreme form of one of the parents, or what may actually be a hybrid. It is on the basis of certain key characters, however, that determinations of suspected hybrid origin have been made. These characters are listed in Table 8.

Although Fernald intended to differentiate forma *hypomaloca* from others by the pilose lower leaf surfaces, the type specimen actually represents an intermediate between Coastal poison-ivy (subsp. *radicans*) and the midwestern taxon (subsp. *negundo*). The pilosity of the lower leaf sur-

TABLE 8. CHARACTERS OF PARENTS TOXICODENDRON RADICANS SUBSP. NEGUNDO AND SUBSP. RADICANS

<i>Toxicodendron radicans</i> subsp. <i>radicans</i>	Putative Hybrid	<i>T. radicans</i> subsp. <i>negundo</i>
Petioles sparsely pubescent	Petioles puberulent to sparsely strigose	Petioles strigose
Leaflets entire	Leaflet margin with prominent notches, or undulate or serrate	Leaflets notched or serrate
Lower leaflet surface with tufts of hairs in vein axils	Lower leaflet surface with a few hairs concentrated in vein axils	Lower leaflet surface without tufts of hairs in vein axils
Fruits pubescent	Fruits with scattered hairs or incipiently papillose	Fruits glabrous

faces is interpreted as a local variation. It is perhaps the result of the proper "dose" of additive genes. The fruits have a few scattered hairs and papillae, suggestive of *Toxicodendron radicans* subsp. *radicans*, but the leaflets are notched and acuminate in the fashion of subsp. *negundo*. Since the specimen comes from the mountains of West Virginia which form part of the barrier between these two taxa, it is not unlikely that intermediate forms should be found. (Fig. 54.)

HYBRIDS WITH *T. RYDBERGII*

Toxicodendron diversilobum × *rydbergii*. Table 9.

Toxicodendron lobadioides Greene, Leaf. Bot. Observ. Crit. 1: 119. 1905. Type: Washington, Western Klickitat County along the Columbia River, rocky places. *W. N. Suksdorf*, s.n., July 1885. (US-47202, holotype; F-155984, F-255875, isotypes in part).

Toxicodendron coriaceum Greene, Leaf. Bot. Observ. Crit. 1: 120. 1905. Type: Washington Territory, *W. N. Suksdorf*, s.n., 6 May 1885. (US-19803, holotype; DS-85511, F-155984 (in part), F-255875 (in part), MO-1773719, NY, isotypes).

Representative specimens: UNITED STATES. **Oregon.** HOOD RIVER CO.: Hood River, near mouth of river on floodplain, *Gillis* 5237 (MSC); same, *Whited* 1117 (ND); same, rocky bluffs, *Henderson* 305 (MO). WASCO CO.: The Dalles, *Howell*, s.n. (GH), *Gillis* 4222 (MSC); Seufert, *Gillis* 4232 (MSC). SHERMAN CO.: east of Rufus, *Gillis* 4230 (MSC). **Washington.** KLICKITAT CO.: western part of county, *Suksdorf*, s.n. (DS, F, GH, MO, NY, US); roadside park near confluence of Klickitat and Columbia Rivers, *Gillis* 5240 (MSC); 11.2 miles east of Klickitat River confluence with Columbia, *Gillis* 5241 (MSC); 11.3 miles east of confluence of Klickitat and Columbia Rivers, *Gillis* 5242 (MSC); Murdock, east of bridge, *Gillis* 5343 (MSC); savanna valley, T. 2N., R. 15E., SW 1/4 Sec. 11, *Gillis* 5244 (MSC).

Presumably the two Greenean species are hybrids between *Toxicodendron rydbergii* and *T. diversilobum* for they were collected in the region where the two species overlap in range. They are probably part of the same population, from the basaltic washes in the hills near the confluence of the Columbia and Klickitat Rivers in western Klickitat County, Washington.

TABLE 9. CHARACTERS OF PARENTS, TOXICODENDRON DIVERSILOBUM AND T. RYDBERGII, AND THEIR PUTATIVE HYBRID OFFSPRING

<i>T. diversilobum</i>	Putative Hybrid	<i>T. rydbergii</i>
Petiole glabrate or puberulent	Petiole glabrate	Petiole glabrous
Leaves 7-10 per 10 cm twig	Leaves 4-10 per 10 cm twig	Leaves 4-5 per 10 cm twig
Leaflets serrate, undulate, or lobed	Leaflets entire, or with undulating margin	Leaflet margins undulate
Leaflets broadly elliptic, obovate, or suborbicular	Leaflets broadly ovate	Leaflets broadly ovate to suborbicular
Leaflets glabrous below, or with few scattered hairs	Leaflet glabrate to strigose below	Leaflets glabrous or appressed strigose below
Leaflet tips obtuse	Leaflet tips acute to slightly acuminate	Leaflet tips acute or acuminate
Fruits 6-7 mm broad	Fruits 5-6.5 mm broad	Fruits 4.5-5.5 mm broad
Fruits flattened, obliquely deltoid	Fruits slightly flattened, subglobose	Fruits globose
Fruits glabrous	Fruits setulose or papillose	Fruits globose

Data on an isotype of *Toxicodendron coriaceum* and of *T. lobadioides* at F suggests that one population which was sampled by Suksdorf on two different occasions furnished the type material for two of Greene's species! This sheet has both a fruiting and a flowering specimen and bears a printed label indicating the date of collection as "May 6, July 1885." The holotype of *T. coriaceum* at US is a match for the fruiting representative except that it bears a handwritten label. The type of *T. lobadioides* at US is a match for the flowering representative on the sheet at F, but bears copies of both the handwritten and printed labels. Also, the isotypes of *T. coriaceum* at NY and at MO have the printed label with the May date crossed out.

Presumably the flowering specimen dates from May, and the fruiting one from July, both from the same general area, representative of the same or closely related populations. The two type specimens mentioned above appear to be intermediate in morphology between *Toxicodendron diversilobum* and *T. rydbergii*. Whereas *T. diversilobum* has densely short-pubescent fruits and *T. rydbergii* has glabrous fruits, these intermediates have scattered hairs, or in one instance, a crown of hairs at the base of the fruit. Table 9 shows the diagnostic characters used in analyzing these intergrades.

Because of the already burdensome collection of names that the poison-ivy complex has acquired, I have preferred to use a formula to designate this hybrid, rather than use either of the Greene names, or some other at the subspecies level. Moreover, no one population possesses the same cluster of intermediate characters nor the whole array of them, so that a hybrid taxon would be difficult to circumscribe. The formula seems to be a better means to indicate a specimen or population that demonstrates intermediate characters anywhere along the spectrum between one parental form and the other.

***Toxicodendron radicans* subsp. *divaricatum* × *T. rydbergii*.**

Table 10.

These two taxa are relatively uncommon throughout their

TABLE 10. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. DIVARICATUM AND T. RYDBERGII, AND THEIR PUTATIVE HYBRID OFFSPRING

<i>T. radicans</i> subsp. <i>divaricatum</i>	Putative hybrid	<i>T. rydbergii</i>
Aerial roots present; plant often climbing	Aerial roots present; plant climbing to 3 meters	Aerial roots absent; plant never climbing
Petiole thinly to thickly puberulent	Petiole glabrous or puberulent	Petiole always glabrous
Petiole shorter than terminal leaflet	Petiole about the same length or longer than terminal leaflet	Petiole usually very long; usually much longer than terminal leaflet
Leaflets 1.9-3 times as long as broad	Leaflet 1.3-1.6 times as long as broad	Leaflets broadly ovate to suborbicular, 1.1-1.5 times as long as broad
Leaflet margins entire	Leaflet margins dentate	Leaflet margins dentate or undulate
Fruits glabrate in northern part of range (Arizona)	Fruits with scattered pubescence	Fruits always glabrous

respective ranges, but especially so in the arid and semi-arid regions of southern Arizona and northern Sonora. Suspected intermediates have been found in only three places: in the Chiricahua Mountains and the Santa Rita Mountains of Arizona and the San José Mountains of Sonora. The characteristics which appear to intergrade are listed in Table 10.

Representative specimens: MEXICO. Sonora: San José Mountains, *Mearns* 1052 (US). UNITED STATES. Arizona: SANTA CRUZ CO.: Florida Canyon, Santa Rita Mountains, 4000 feet, *Graham*, s.n. (NY). COCHISE CO., above Portal, Chiricahua Mountains, 5000 feet elevation. *Stoutamire* 3986 (BLH, MSC).

Toxicodendron radicans subsp. negundo × **T. rydbergii**.
Table 11.

Toxicodendron rufescens Greene, Leaf. Bot. Observ. Crit. 2: 46. 1910. Type: Indiana, Marshall County, vicinity of Lake Maxinkuckee, *H. Walton Clark* 2, 14 September 1906 (US-645163, holotype).

Representative specimens: UNITED STATES. Illinois. WILL CO.: Romeoville (formerly Romeo), *Umbach*, s.n. (F, WIS). Locality uncertain: *Gates* 745 (F). Indiana. MARSHALL CO.: Lake Maxinkuckee, *Clark* 2 (ND-G, US). Michigan. GLADWIN CO.: Sage Twp., shore of Wiggins Lake, *Gillis* 3602 (MSC). LAPEER CO.: Imlay City, *Farwell* 6693 (BLH). OSCODA CO.: south of Oscoda, *Hagenah* 2365 (BLH). ST. CLAIR CO.: Port Huron, *Dodge*, s.n. (MIN). Minnesota: Spring Grove, *Rosendahl* 280 (GH). New York. CHEMUNG CO.: without definite locality, *Lucy* 1694 (F, RM, WIS). LEWIS CO.: Harrisville, *Gillis* 5377 (MSC). Oklahoma. BEAVER CO.: Knowles, *Stevens* 516 (GH, MIN, MO, NY). South Dakota. UNION CO.: Ravine, T. 92N., R. 49W., *Eslick*, s.n. (SDU). West Virginia. KANAWHA CO.: Quick, *Reed*, s.n. (CHRB). Wisconsin. SAUK CO.: *Smith* 7984 (A, MIL, WIS).

CANADA Ontario. WATERLOO CO.: Hamburg, river banks. *Merner* 15031 (WIS); Québec. LAVAL CO.: St.-Laurent, *Adrien* 1088 (A, GH).

Greene (1900) thought his species *Toxicodendron rufescens* to be near *T. glabrum* Mill. or *Rhus littoralis* Mearns (= *T. radicans* subsp. *radicans*). It appears rather to be an intermediate between *T. radicans* subsp. *negundo* and *T. rydbergii*, with fruits and petiole length in common with the former and leaflet shape, habit, and absence of aerial rooting of the latter. Both taxa are known from this general region of Indiana.

The two parental taxa are very different from one another when they show the most definitive characters, but not all specimens seen in the field, or worse yet, in the herbarium, demonstrate the most important diagnostic characters. A fruiting specimen with tight, erect inflorescences, fruits greater than 0.5 cm broad, very long, glabrous petioles, and suborbicular leaflets is unquestionably *Toxicodendron rydbergii*. A flowering male specimen with puberulent petioles and broadly ovate leaflets is not so easily pigeon-holed. It has been mentioned earlier that subsp. *negundo* is difficult to characterize because it has much in common with several other taxa and is characterized more because of what striking characters it does *not* possess, than because of those it does. Along the zone of overlap in the ranges of *T. rydbergii* and *T. radicans* subsp. *negundo*, the characters which distinguish these taxa become blurred. A number of populations in this tension zone look suspiciously like intergrades between the two parental forms.

The regions where the two ranges meet are: the southern lobe of Ontario, the central part of the Lower Peninsula of Michigan, areas around the southern half of Lake Michigan, and an irregular line cutting southwest across Illinois, Iowa, Nebraska, and Kansas, and through parts of Oklahoma. Suspected intermediates have been examined in the herbarium and a few in the field from this region. (Fig. 54.) The suspected hybrids show their intermediate nature as indicated in Table 11.

***Toxicodendron radicans* subsp. *radicans* × *rydbergii*. Table 12.**

Toxicodendron rydbergii and *T. radicans* subsp. *radicans* have ranges which meet in the northern United States and bordering Canada east of the Appalachian Mountains and the Laurentian Plateau. Where their ranges overlap, there appears to be some introgression. A number of specimens have been seen from Quebec, Nova Scotia, the Berkshire Mountains, and other places in southern New England which appear to be intergrades between these two taxa. (Fig. 54.) The characters upon which their hybrid nature has been suspected are listed in Table 12.

TABLE 11. CHARACTERS OF PARENTS, *T. RADICANS* SUBSP. *NEGUNDO* AND *RYDBERGII*, AND THEIR PUTATIVE HYBRID OFFSPRING

<i>T. radicans</i> subsp. <i>negundo</i>	Putative Hybrid	<i>T. rydbergii</i>
Shrub or vine with aerial roots	Sub-shrub or climbing vine; aerial roots may or may not be present	Sub-shrub
Petioles puberulent or strigose	Petioles glabrous, puberulent, or scattered hairy	Petioles glabrous
Petioles averaging less than 10 cm long	Petioles averaging about 15 cm long	Petioles 8-18 cm long
Leaflets ovate	Leaflets broadly ovate	Leaflets suborbicular
Leaflets coarsely toothed	1-2 teeth on leaflets	Leaflets with 1-8 pairs of notches or serrations
Fruits averaging less than 0.45 cm in diameter	Fruits ranging between 0.4 and 0.5 cm in diameter	Fruits averaging 0.5 cm in diameter

TABLE 12. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. RADICANS, AND T. RYDBERGII AND THEIR PUTATIVE HYBRID OFFSPRING

<i>Toxicodendron rydbergii</i>	Putative Hybrid	<i>T. radicans</i> subsp. <i>radicans</i>
Sub-shrub	Sub-shrub; few plants climbing by aerial roots	Shrub or climbing vine
Petioles averaging more than 15 cm	Petioles averaging 12 cm	Petioles averaging less than 10 cm
Petioles glabrous	Petioles glabrous or becoming puberulent distally	Petioles glabrate or puberulent
Leaflets broadly ovate to suborbicular	Leaflets broadly ovate	Leaflets ovate or elliptic
Lower leaflet surface with no concentration of hairs in vein axils	Lower leaflet surface with few hairs in vein axils	Lower leaflet surface with concentration of hairs in vein axils
Upper leaflet surface glabrous	Upper leaflet surface glabrous	Upper leaflet surface glabrate
Leaflet margins serrate or undulate	Leaflet margins undulate or entire	Leaflet margins entire
Fruits averaging 0.5 cm in diameter	Fruits variable in size, but averaging 0.45 cm in diameter	Fruits averaging 0.4 cm in diameter
Exocarp glabrous	Exocarp incipiently papillose; some with scattered hairs, or glabrous	Exocarps pubescent or papillose

Representative specimens: UNITED STATES. **Connecticut.** LITCHFIELD CO.: 2.5 miles SE of Washington, *Donahue* 267 (MSC); near Massachusetts line, *Fernald*, s.n. (GH). **Maine.** KNOX CO.: Rockland, *Fernald* 1994 (GH). **Massachusetts.** BERKSHIRE CO.: Hoosac Valley, Lanesboro, *Churchill* 552 (IN). ESSEX CO.: Bradford, part of Haverhill, *Churchill*, s.n. (MO). SUFFOLK CO.: Dorchester, section of Boston, *Churchill* 552 (MO). **New Hampshire.** STRAFFORD CO.: NE of Durham, *Donahue* 268 (MSC). GRAFTON CO.: West Thornton, *Gillis* 4097 (MSC). MERRIMACK CO.: Concord, *Gillis* 4100 (MSC). **Pennsylvania.** MIFFLIN CO.: without definite locality, *Rothrock*, s.n. (F). **Rhode Island.** PROVIDENCE CO.: Diamond Hill, *Palmer* 46188 (A). **Tennessee.** BLOUNT CO.: Walland, *Hudson*, s.n. (RM). **Vermont.** CALEDONIA CO.: Barnet, *Blanchard*, s.n. (MIN, MO, NY, US). LAMOILLE CO.: without definite locality, *Grout*, s.n. (F). WINDSOR CO.: Ascutney, *Gillis* 4088 (MSC). **Virginia:** 1 mile north of Hopewell Gap, western slope of Bull Run Mts., *Allard* 462 (GH, US). **West Virginia.** HAMPSHIRE CO.: Slanesville, *Donahue* 265 (MSC).

CANADA. **Nova Scotia.** HALIFAX CO.: Fall River, *Jack* 3317 (MO). LUNENBERG CO.: East Bridgewater, *Macoun* 81289 (F). **Québec.** BROME CO.: Glen Sutton along the Missiquoi River, *Marie-Victorin, et al.* 56209 (GH, F, MO, NY).

HYBRIDS WITH T. TOXICARIUM

Toxicodendron radicans subsp. **radicans** × **toxicarium**. Table 13.

Suspected hybrids between these two species have been found along the American Atlantic Seaboard where their ranges overlap. Because their habitat requirements are generally quite different, it is not often that a pollinating vector will visit one parent plant while carrying pollen from the other. Criteria which were employed for determination of these forms as hybrids are given in Table 13.

Representative specimens: UNITED STATES. **Alabama.** COVINGTON CO.: edge of titigum—magnolia bay, 17 miles SSW of Andalusia, *Hardin & Duncan* 15010 (GA). **Arkansas.** CONWAY CO.: Morrilton, *Demaree* 23089 (GH, MIN, MO, NY, SMU). LOGAN CO.: Blue Mountain, *Palmer* 24810 (MO). **Georgia.** BIBB CO.: savanna woodland, *Gillis* 6575 (MSC). WALKER CO.: rocky area below Harrisburg, 10.3 miles SW of Lafayette, *Hardin, Humphrey & Duncan* 13872 (GA). **North Carolina.** FORSYTH CO.: Kernersville, *Ahles & Britt* 40711 (NY). STANLEY CO.: Yadkin River, southeast of Badin, *Ahles & Radford* 11936 (SMU). **South Carolina.** PICKENS CO.: Clemson College (MO). RICHLAND CO.: north of Columbia on highway 21, pine woods, *Gillis* 4582 (MSC). **Virginia.** FAUQUIER CO.: Bull Run Mts., *Allard* 9941 (GH).

TABLE 13. CHARACTERS OF PARENTS, TOXICODENDRON RADICANS SUBSP. RADICANS AND T. TOXICARIUM, AND PUTATIVE HYBRID OFFSPRING

<i>Toxicodendron toxicarium</i>	Putative Hybrid	<i>T. radicans</i> subsp. <i>radicans</i>
Sub-shrub	Shrub or vine	Shrub or vine
Petioles hirsute or tomentose	Petioles hirsute or strigose	Petioles sparsely pubescent
Leaflet with lobed or undulating margins	Leaflet with sharp lobes, or with coarsely serrate or crenate margins	Leaflet with entire margins, or rarely notched
Leaflets ovate to oblong or oblong-obovate	Leaflets rhomboid to broadly ovate or elliptic	Leaflets ovate or elliptic
Upper leaflet surface scabrous or hispid	Upper leaflet surface sparingly pubescent	Upper leaflet surface glabrate
Lower leaflet surface hirsute or velutinous	Lower leaflet surface velutinous	Lower leaflet surface glabrous or glabrate
Fruit pubescent and often papillose	Fruits rare	Fruits pubescent
Leaflet margins ciliate	Leaflet margins ciliate	Leaflet margins not ciliate
Lower leaflet pubescence uniformly distributed or perhaps heaviest along midrib	Lower leaflet with tufts of hairs in vein axils	Lower leaflet with tufts of hairs in vein axils

Toxicodendron radicans subsp. **verrucosum** × **toxicarium**.

Table 14.

This hybrid is likely to be a limited one because the two parental types are sympatric for only a small portion of their total range. Moreover, *Toxicodendron toxicarium* tends to be found in rather acidic soils and *T. radicans* subsp. *verrucosum* is generally found in more alkaline soils or in shallow lithosols derived from limestone. Several populations in Texas, however, have produced suspected hybrids, plants which are intermediate in morphology between the two taxa. (See Table 14.)

Representative specimens: UNITED STATES. Texas. ARANSAS CO.: *Cory* 49016 (GH). BASTROP CO.: climbing post oak in Bastrop State Park, *Gillis* 5167 (MSC). BEXAR CO.: San Antonio, *Jerry* 326 (GH); MCLENNON CO.: Robinson, *Cory* 55710 (SMU). RED RIVER CO.: Clarkville along Red River, *Cory* 5604 (SMU). White Oak Bayou, collector and county unknown (MIN).

UNCERTAIN OR EXCLUDED SPECIES

Rhus-Toxicodendron radicans Marshall, Arbust. Am. p. 131. 1785. This name probably refers to *Toxicodendron radicans*, but there is neither citation of previous published names nor of any specimens.

Rhus-Toxicodendron toxicodendrum Marshall, Arbust. Am. p. 131. 1785. This name probably refers to *Toxicodendron toxicarium*, but there is neither citation of previous published names nor of any specimens.

Toxicodendron vulgare Mill. Gard. Dict. ed 8, Art. *Toxicodendron*, No. 1. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

Toxicodendron pubescens Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 2. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

Toxicodendron crenatum Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 5. 1768. The description can apply to a number of taxa. No specimen to represent this name can be found.

TABLE 14. CHARACTERS OF TOXICODENDRON RADICANS SUBSP. VERRUCOSUM
AND T. TOXICARIUM AND THEIR PUTATIVE HYBRID OFFSPRING

<i>Toxicodendron toxicarium</i>	Putative Hybrid	<i>T. radicans</i> subsp. <i>verrucosum</i>
Sub-shrub	Small shrub or vine	Shrub or vine
Aerial roots absent	Aerial roots present	Aerial roots present
Leaflet lobes rounded	Leaflet lobes obtuse	Leaflet lobes angular
Lower leaflet surfaces pilose to velutinous	Lower leaflet surfaces pilose	Lower leaflet surfaces glabrous or glabrate
Fruits pubescent or papil- lose	Fruits with scattered pubes- cence and papillae	Fruits glabrous

Toxicodendron volubile (as "*volubilis*") Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 6. 1768. *Rhus radicans* var. *volubile* (Mill.) DC. Prodr. p. 69. 1825. *Rhus toxicodendron* subsp. *vulgaris* var. *volubilis* Engler in DC. Monog. Phaner. 4: 394. 1883. *T. radicans* var. *volubile* Farwell, Amer. Midl. Naturalist 12: 125. 1930. All uses of the epithet *volubilis* refer to Miller or DC, the former of whom equates his species to *Toxicodendron amplexicaule* . . . of Dillenius. None of these plants can be typified. They probably refer to some kind of *T. radicans*, but which subspecies is uncertain. Engler cites "*Rh. Toxicodendron* L. Spec. 381 sensu stricto" but describes it as "*caule scandente, vix radicante*" which does not accurately describe *Rhus Toxicodendron* sensu stricto. He further cites a large number of specimens, some at Kew and some presumably then at Berlin, but these specimens represent almost every taxon in the poison-ivy complex.

Toxicodendron serratum Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 7. 1768. No specimen to represent this name can be found.

Toxicodendron arborescens Mill. Gard. Dict. ed. 8, Art. *Toxicodendron*, No. 9. 1768. The description can fit most taxa in the poison-ivy complex. No specimen to represent this name can be found.

Rhus pumilum Pursh, Fl. No. Am. 1: 205. 1814. (= *R. michauxii* Sarg.).

Rhus variifolium DC. Prodr. 2: 73. 1825. Nomen nudum.

Rhus bahamensis D. Don. 1832. A General System of Gardening and Botany, p. 72. London. 1832. Nomen nudum. This is possibly *Toxicodendron radicans* subsp. *radicans*, the only member of the *Rhus* complex known from the Bahamas.

Rhus quercifolia Goeppert, Tert. Fl. Schosnitz. 1855 (= *Monopleura* in Aceraceae).

(To be concluded)



Gillis, William Thomas. 1971. "THE SYSTEMATICS AND ECOLOGY OF POISON-IVY-D AND THE POISON-OAKS-D TOXICODENDRON-D ANACARDIACEAE-D." *Rhodora* 73, 370–443.

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