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

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INTRODUCTION

An ecological study in which I attempted to germinate seeds of poison-ivy was the forerunner of the present monograph. A study of the literature at that time revealed much confusion as to the application of names to the poison-ivy and poison-oak taxa, not to mention matters relating to its toxicity to man. Thus it appeared that *Toxicodendron* was deserving of a full-scale systematic investigation, even though it had been revised by Barkley (1937). Two of the three sections of the genus are treated herein, section *Venenata* being considered too large and diverse a group to include at the present time.

Barkley (ibid.) provided a taxonomic treatment of poison-ivy and the poison-oaks as part of a larger work on *Rhus (sensu lato)* in North America. His investigation was based chiefly on herbarium material, whereas this one has placed equal emphasis upon field and herbarium studies with a few laboratory experiments where appropriate. Because of the restriction of this investigation to a small segment of what Dr. Barkley monographed, it has been possible to examine the biology, natural history, and ecology of the taxa to a greater extent than he was able to do.

A number of problems had to be confronted in the course of this investigation. The plants are notoriously poisonous to man. The literature relating to *Toxicodendron* is voluminous partly because of its economic importance. The complex includes the most widespread taxa (in terms of native range) within the Anacardiaceae. It is further com-

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plicated by its extreme plasticity. Whereas the leaf and fruit morphology is highly variable, the flower morphology is very conservative. The woody habit and dioecious nature of the taxa complicates experimental studies since at least three years are required for an individual to reach flowering stage from seed. Moreover, in most populations, it is not possible to determine the sex of an individual until it flowers.

Variants have previously been treated as species, subspecies, varieties, or forms without a unifying philosophy or concept of these taxonomic units. Often many of the characters used in differentiating taxa have been inconstant, and combined with one another in various ways, without consideration of the total variation of the plants in nature. Some of the characters which have been used would segregate plants within a single clone into several taxa. Misinterpretation and fractionation of species in the past have been due in part to incomplete knowledge of the range of variation and therefore little concept of which characters were useful taxonomically.

The position of *Toxicodendron* in the tribe Rhoeae is a fortunate one from the standpoint of understanding related genera. If a guide to the variability of plants in this tribe can be found in *Toxicodendron,* then the groundwork has been laid for future study of such vexing genera as *Rhus* and its segregates *Searsia, Melanococca,* and *Lobadium, Comocladia,* and indeed for investigation of the third section of *Toxicodendron,* section *Venenata.*

The present study brings together as much information about *Toxicodendron* (except section *Venenata*) as is now available. It is hoped that this monograph will contribute to a better comprehension of the plants for botanists and for those non-botanists who have need to understand them.

All taxa except *Toxicodendron radicans* subsp. *hispidum, T. nodosum, T. borneense* and *T. magnifolium* were studied in the field, but not all could be investigated with the same intensity. Although I had a considerably larger number of

specimens at my disposal than did Barkley (1937) and, in addition, benefitted from field experience with the plants, various problems remain for future exploration. If this investigation can serve as a reference point for study of problems in population variability, plant migration, modification through evolution, and variability in human sensitivity, then a primary objective will have been met.

ECONOMIC SIGNIFICANCE

The chief importance of members of the poison-ivy complex to man is the dermatitis they cause. More than 350,000 cases of poison-ivy dermatitis are estimated for the United States per year (Turner, 1947). This averaged 2.5 cases per 1,000 persons, 17.7% of which were bed cases (averaging 3.5 days in bed), with 1.7 days of disability, 71.9% attended by professional medical personnel. Of economic impact are the 600,000 man-days of time lost from gainful employment due to the dermatitis and its complications. According to the California State Compensation Insurance Fund, Western poison-oak is the only weed in the state which is responsible for occupational injury (Jones, 1955). Statistics for that state, collected by the Department of Industrial Relations, indicate for 1953 that there were 3,658 cases reported as industrially incurred. Jones (ibid.) estimates the economic loss due to poison-oak dermatitis throughout California as $160,000 per annum. Extrapolation to other states of the Union where *Toxicodendron* species are found is not possible based on these figures alone, due to the differential in distribution of plant and of human population density, but such figures as those above suggest an enormous loss of gainful work by employees, not to mention personal misery, due to these plants.

From a medical viewpoint, members of this complex have had a colorful history. Some of the earliest works on record include a thesis submitted to the Medical Faculty of the University of Pennsylvania by Horsfield (1788), and later, one in Germany by Burse (1811). The reports in the medical literature during the nineteenth and twentieth centuries are legion, many of the significant ones summarized by Rostenburg (1955) and Kligman (1958). A homeopathic approach was prepared by Delestinne (1956), and other summaries of our modern medical knowledge by Epstein (1958). Bewildering and awesome are the lists of "treatments" which Kligman cites as having been used as topical therapy:

"Qualitatively, they range from the preposterous to the fantastic . . .
A brief listing of some of the more interesting agents which have
been thought beneficial clearly reveals the profound emotional effects
of therapeutic desperation: morphine (topically!), bromine, kerosene,
gunpowder (the symbolism here is beautiful), . . . aqua regia (!),
buttermilk, cream and marshmallows (!) . . . strychnine (!), etc."
To this, I must add the preposterous idea of drinking a
pint of photographers' hypo! Kligman continues:
"Throughout, there is a remarkable disregard for a simple biological
fact, namely, that poison-ivy dermatitis is a self-resolving process."

In recent years, there have been attempts to cure or
prevent the dermatitis by use of injections or preparations
taken by mouth of a number of extracts of the poison under
such trade names as Ivyol and Aqua Ivy (Howell, 1947;
Passenger, Spain, and Strauss, 1956; and Gaillard, 1967).
Dr. Kligman (ibid.) comments on these:
"One is confronted with the quixotic fact that many physicians
achieved remarkable results with an extract biologically equivalent
to water!"

Currently a study of oral prophylaxis is under investiga-
tion at the University of Cincinnati under the direction of
Dr. Leon Goldman.

The disease mechanism is basically a delayed hyper-
sensitivity of the contact variety, and is induced by simple
molecular weight haptens rather than proteinaceous anti-
gens (Crowle, 1964). A sensitizing antigenic complex is
presumably created between the poison (3-n pentadecylca-
techol) and skin proteins. The antigens thus are believed
to be chemically-altered autologous skin proteins.

Aside from the medical aspects of the poisoning, poison-
ivy (Toxicodendron radicans) has had other economic sig-
nificances. Unbelievable as it may seem, poison-ivy has
been cultivated in gardens in New South Wales, Australia
(Anonymous, 1908), and in Dunedin, New Zealand (Con-
nor, 1951), and sold as an ornamental by English nursery-
men (Anonymous, 1949), probably as far back as 1640
(Miller and Martyn, 1807).[2] It seems to possess certain

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[2]This is not to be confused with another plant called poison-ivy in
Western Australia which is Tinospora smilacina Benth. (Meni-
spermaceae) (Gardner and Bennetts, 1956).

horticultural values: (1) it has characteristics for the plant connoisseur who likes its autumnal foliage; (2) its autumn leaves have been used to highlight displays of fruit at shows; and (3) it is reported not to escape cultivation (!). Since 1919, poison-ivy has been planted along the dikes of Southwest Friesland Province in the Netherlands in an effort at dike consolidation. One colony has become established along more than 500 meters of one dike (Van der Ploeg, 1966).

Toxicodendron diversilobum is occasionally browsed by horses and cattle without apparent ill effects (Rostenburg, 1955a). Many birds, especially quail, feed on its fruits. Bees are reported to make honey from its flowers, an apparent non-toxic variety (Rostenburg, 1955b). Martin, *et al.* (1951) list a number of birds which eat poison-ivy and poison-oak fruits (not specifying the scientific names for either of the plants they had in mind), particularly in winter when other foods are scarce. Among 55 listed bird species which have been observed eating the seeds, yellow-shafted flickers and wren-tits are claimed to be partial to the fruits of *Toxicodendron* species up to 25% of their diet. Crows have been reported to be fond enough of the fruits to be important disseminators of the species (Burrows, 1895). Poison-ivy fruits in the diet of birds during the winter have been observed by W. R. Overlease in Michigan and Indiana, and by John Verdier for shore birds at Island Beach State Park, New Jersey (both personal communications). Additional relations to wildlife are discussed further under the topic "biological interactions."

Although the lacquer-bearing properties of resins of these plants have been established by Dawson (1956a and b) to be chemically related to those of the lacquer trees of the Orient [*Toxicodendron vernicifluum* (Stokes) Barkley and possibly several other *Toxicodendron* species to a lesser extent], the poisons have never been collected from any member of either section *Toxicodendron* or *Simplicifolia* for commercial use. Only the Pomo Indians of California

ever used the resin for a product: they dyed basket fibers with it (Balls, 1965).

Various American Indian tribes had intriguing uses for poison-ivy and its allies. The Meskwaki, Ojibwe, and Potawatomi used it (presumably *T. rydbergii*) as a poultice on a swelling to make the skin open (Smith, 1928, 1932).

The Ramah Navahoes made an arrow poison from poison-ivy sap mixed with deer's blood and charcoal from a lightning-struck tree, the latter no doubt a connection with black magic (Vestal, 1952). Another version of making this arrow poison added the juices of *Phacelia crenulata* var. *ambigua* Macbr. (Wyman and Harris, 1941). The Navahoes also used poison-ivy *(T. rydbergii)* for good luck in gambling: they chewed a small piece of leaf and gave it to an opponent (Vestal, ibid). The Karok Indians used sticks of *T. diversilobum* to spit salmon steaks while smoking them, and its leaves to cover soaproot (*Chlorogalum pomeridianum* Kunth) when baking it in an earthen oven. The Concow Indians of northern California even mixed the leaves of *T. diversilobum* into their acorn meal when they baked bread. Other northern California tribes simply wrapped their meal in its leaves while baking (Balls, ibid). Some, too, used its supple stems as the warp in weaving baskets (Balls, ibid.).

The Yuki tribe of California used sap from *T. diversilobum* to get rid of warts: they would cut off the wart and apply poison-oak sap to the wound. The same treatment was applied to ringworm and rattlesnake bites (Balls, ibid.). They also used the sap, mixed with mountain hemlock and suet, for tribal markings (John N. Taylor, personal communication). The Yukis also (especially the Tatu or Huchnom branch) used a sprig of poison-oak dipped in water to "keep the women in due subjection." The men, while attempting to conjure up the devil in their meeting-hall, would paint one of their peers, strip him, place a chaplet of leaves over his face to render him incognito, and send him out through the village amid whoops and diabolical

yells. As he cavorted through the village, he would sprinkle
wet poison-oak branches in the squaw's faces. Screaming
with uncontrollable terror, the women would fall prostrate
on the ground. Sworn to silence lest they die while dis-
cussing a spook, they would never realize who had, in fact,
been their attacker (Powers, 1877).

HISTORICAL ACCOUNT OF THE COMPLEX

The first known reference to poison-ivy in written record
dates from the seventh century in China and next from the
tenth century in Japan, according to Toyama (1918). In-
asmuch as the various species do not grow in Europe, the
plants were unknown to Western civilization until explorers
visited the New World, seven centuries after the first writ-
ten record of them in the Orient. Captain John Smith (1609,
1624) is credited with the first reference to the poison-ivy
plant in writings on his findings in North America. It was
he who originated the common name to the plant since he
noted a similarity in its climbing habit of the North Amer-
ican poison-ivy to English ivy (*Hedera helix* L.) or to Bos-
ton ivy (*Parthenocissus tricuspidata* Planch.) in the trifo-
liolate nature of the leaves. He also noted that the plant
produces a dermatitis which "causeth itchynge, and lastly,
blisters." Probably for reasons of Smith's description, the
first published illustration of the plant, and presumably the
first reference to it in a work that is even remotely tax-
onomic, was its appearance in Cornut's "Canadensium
Plantarum" (1635) as *Edera trifolia canadensis*, a name
which implies a true ivy. (The taxon pictured is most likely
not a collection made by John Smith, but a later one from
more northern latitudes, and is *Toxicodendron rydbergii*.
The details of its pre-Linnaean history, including possible
polynomial synonymy, are discussed by Barkley and Bark-
ley (1938).

Toxicodendron is a pre-Linnaean name, not accepted at
the generic level by Linnaeus (1753). Tournefort (1700)
made the following distinction when he first used the name
Toxicodendron: that *Rhus* had unequally pinnate leaves and

a villose berry (sic) with a globular nucleus, and that *Toxi-codendron* had ternate leaves and a striate berry (sic) with a compressed nucleus. By limiting the genus to ternate-leaved plants, Tournefort would have omitted such close relatives of poison-ivy as poison-sumac and the oriental lacquer trees which persumably he did not know. He also knew neither the African *Rhus* species nor *Metopium*. More-over, the compressed nature of the "nucleus" (endocarp and its contents?) is highly variable and certainly not a reliable character. In comparing "villose" to "striated" in reference to the fruit, Tournefort contrasted an exocarp character with a mesocarp character. Boerhaave (1727) followed Tournefort in distributing species in the *Rhus* complex in these genera: *Rhus, Toxicodendron,* and *Co-tinus,* and he lumped the African species in *Rhus*. Dillenius (1732) likewise preserved *Toxicodendron*. He illustrated poison-ivy and referred to it as *Toxicodendron rectum foliis minoribus glabris;* from the illustration and from a speci-men in the Dillenian Herbarium, one can deduce that the taxon which Dillenius had in mind was *T. radicans* subsp. *radicans*. Parkinson (1640), Boerhaave (1727), and Munt-ing (1713) had at one time considered poison-ivy to be a grape (*Vitis*), and Boerhaave (ibid.) referred to its being called an *Apocynum*.

Linnaeus in the Species Plantarum (1753) and Systema Naturae (ed. 10, 1759) recorded 13 species of *Rhus,* al-though probably none of them was known to him in the field. As Barkley (1963) pointed out, 14 more species had been assigned to *Rhus* by the end of the eighteenth century, including species in *Rhus, Toxicodendron, Cotinus, Meto-pium,* and the *Thezera* groups. If priority played a role in keeping species in the genera to which they were originally assigned, then *Rhus* was fast becoming one of the more inclusive of angiosperm taxa.

Engler (1881) divided *Rhus* into four sections: *Tricho-carpeae, Gerontogeae, Venenatae,* and *Melanocarpae*. De-Candolle earlier (1825) had made the following sections: *Sumac* to be roughly equivalent in Engler's concept to *Tri-*

chocarpeae and *Venenatae*; he also recognized Sect. *Loba-
dium* to contain some species which Engler later placed in
Trichocarpeae. The type section *Rhus*, as presently recog-
nized, is equivalent to section *Sumac* DC. = sect. *Tricho-
carpeae* Engl. Blume (1850) erected the genus *Melanococca*
for the black-fruited species of the southwest Pacific region;
it corresponds to Engler's section *Melanocarpae*; Barkley
(1942) raised this to generic rank as *Duckera*, but did not
until 1963 recognize that this name was antedated by
Melanococca. Brizicky (1963) has changed this to a sub-
genus of *Rhus*. Section *Thezera* DC. is the earlier name for
sect. *Gerontogeae* Engl., which Koch (1853) raised to a
subgenus, and Barkley (1942, 1963) renamed as a genus,
Searsia. For the sake of simplicity, I shall refer to the *Rhus*
species of Africa as the *Thezera* group, and those black-
fruited Pacific taxa as the *Melanococca* group. A summary,
with synonymy and designation of types or lectotypes where
needed is given in Brizicky (ibid.) It is further simplified
for reference purposes in Table 1. It is beyond the scope
of this study to make taxonomic judgments concerning
these groups.

Linnaeus described poison-ivy first in the *Hortus Clif-
fortianus* (1737) ; he later edited his description of the plant
to include the climbing habit and added a description of
Eastern poison-oak when he wrote the *Species Plantarum*
(1753). The Clifford specimens include one flowering branch
of *Toxicodendron rydbergii* and a sterile branch of *T. radi-
cans* subsp. *radicans*. Linnaeus apparently did not recognize
poison-ivy to be dioecious, since his symbol for dioecism is
missing from the species descriptions.

Eastern poison-oak presents problems that cannot be
unraveled any farther back than Linnaeus. Several authors
use the same polynomial phrase by which Linnaeus de-
scribes the plant known to him as *Rhus Toxicodendron*, but
the specimen at the Linnaean Herbarium is apparently the
oldest specimen extant, and can be used to verify the Lin-
naean concept of that species.

It is with Michaux that much of the nomenclatural con-

TABLE 1. COMPARATIVE TREATMENT OF *RHUS*

DeCandolle (1825)	Marchand (1869)	Engler (1881)	Barkley (1937, Emended, 1963)	Brizicky (1963)
Rhus	*Rhus*	*Rhus*	*Rhus*	*Rhus*
sect. *Sumac*	sect. *Sumac*	sect. Trichocarpae, in part		subgenus *Rhus*
sect. *Lobadium*	sect. *Lobadium*	sect. *Trichocarpae*, in part	*Lobadium*	subgenus *Lobadium*
sect. *Sumac*, in part	sect. *Sumac*, in part	sect. *Trichocarpae*, in part / sect. *Venenatae*, in part	*Toxicodendron*	subgenus *Toxicodendron*
			Malosma	subgenus *Malosma*
———	———	sect. *Melanocarpae*	*Duckera*	subgenus *Melanococca*
sect. *Sumac*, in part / sect. *Thezera*	sect. *Thezera*	sect. *Gerontogeae*	*Searsia*	subgenus *Thezera*

fusion begins. He made *vulgare, microcarpon,* and *quer-cifolium* varietal names under *Rhus toxicodendron,* whereas *Rhus radicans,* the Linnaean name for poison-ivy, was not used at all. In the several later editions of Miller's *Gardeners' Dictionary, Toxicodendron* and *Rhus* were segregated. In Miller's view, *Rhus* had hermaphrodite flowers and *Toxicodendron* was dioecious. Since both taxa have dioecious members, this character is inappropriate. Miller (1768) discussed ten species of *Toxicodendron,* of which five or six can be referred to the poison-ivy complex. None can be typified by a specimen from the Chelsea Physic Garden, although several can be typified in other ways (see later discussion under the nomenclature of each taxon). A. P. DeCandolle (1825) altered Miller's work by changes in nomenclature, reducing some of his species to varieties, and reverting to *Rhus,* all the while citing Miller as his source.

DeCandolle (1825), Michaux (1803), and later Engler (in DeCandolle, 1883, and in Engler and Prantl, 1897) returned to the use of *Rhus* to the exclusion of *Toxicodendron* as a generic name. It may be significant that in Engler's key to the tribe Rhoideae (1892), *Rhus* is left close to the end where it appears that it might have been a catch-all. Moench (1794) and Rafinesque (1819) recognized *Toxicodendron.*

Engler (1883) aligned the species with essentially the same subdivisions as DeCandolle but, like Michaux, treated all poison-ivies and poison-oaks as varieties of *Rhus toxicodendron,* whereas DeCandolle (1825) made them varieties of *Rhus radicans.* Engler, though attributing his interpretation of this species to an emendation by Torrey and Gray (1838), was nevertheless in error because the Linnaean specimens were extant and would have demonstrated that his several varieties were more closely allied to *Rhus radicans* than to *R. toxicodendron.*

Work in this complex in the nineteenth century began to round out knowledge of distribution. Engler, relying presumably on specimens then at Berlin, had a geograph-

ically very diverse group of specimens at his disposal, for
he cites specimens from localities in Japan, Sakhalin, Can-
ada, Mexico, Texas, California, Central and Eastern United
States, and Bermuda, making a correct assessment of sev-
eral controversial specimens, not correctly interpreted since
(e.g., *Berlandier* 2035). It is tragic that this array of
specimens was destroyed during World War II. The first
nomenclatural separation of Asiatic populations was made
by Lavallée (1877), and the first for those from Mexico by
Sessé and Moçiño (1887).

Otto Kuntze (1891) obliterated the genus *Rhus* as he
made wholesale transfers to *Toxicodendron*. His work has
little value except that it is the first place that a number
of transfers are made from *Rhus* to *Toxicodendron*.

Edward Lee Greene (1905, 1910), as he was wont to
do, named 24 new species in this complex, separating re-
lated populations on superficial grounds. He even anno-
tated isotypes of his own naming years afterward without
recognizing them as the species he had described! He is
known to have assigned different names to flowering and
fruiting collections from the same population along the
Klickitat River in Washington.

Greene, the redoubtable splitter, very sagely pointed out
(1905) that for hundreds of years before Tournefort, there
was only one *Rhus*, i.e., *R. coriaria*, the coriar's (tanner's)
sumac, whose chief use was the source of tannins for the
processing of leather. When *R. hirta* (= *R. typhina*) and
R. glabra were first brought from North America to Europe,
Greene continued, there was no question as to the genus
of these sumacs. But then poison-ivy appeared on the scene.
Presumably the first member of this taxon to reach Europe
was *Toxicodendron rydbergii*, the northern representative
of the complex. It is unquestionably the first member of
the group to be illustrated (as *Edera trifolia canadensis* in
Cornut, 1635). This species is likely to have a subterminal
inflorescence like the terminal one of traditional *Rhus*, and
from the illustrative material that was more commonly
available than herbarium specimens in the eighteenth cen-

tury, likely to have been the source of the *Rhus* myth about poison-ivy (even though Greene incorrectly equates Cornut's illustration with *T. vulgare* = *T. radicans* subsp. *radicans*).[3]

One of the Clifford Herbarium specimens, which were the ones which were instrumental in formulating Linnaeus's early ideas about members of this complex, is *Toxicodendron rydbergii*, a non-climbing sub-shrub which superficially has much in common with the habit of *Rhus* species.

In spite of their penchant for splitting, it is significant that E. L. Greene and John K. Small were the first North American botanists who studied the poison-ivy complex carefully, and among the first who knew it first-hand in the field. Gray, Torrey, and Nuttall apparently did not make an intensive study of this group: Britton changed his mind, using *Rhus* in his earlier publications (1894, 1901) and *Toxicodendron* in his later ones (Britton and Shafer, 1908 and Britton and Brown, 1913).

The work of James B. McNair in the early part of this century on the poison-ivy complex is noteworthy for its volume. There has been no more prolific writer on the broad scope of taxonomy, poison chemistry, medical treatment, etc., of the poison-ivy complex. In 1923, his collected works were republished in book form under the title *Rhus Dermatitis*. In 1925, he published a short treatise on the taxonomy of poison-ivy, an inadequate and fairly incorrect assessment of its taxonomy and nomenclature.

In 1937, Fred A. Barkley wrote his doctoral dissertation on *Rhus (sensu lato)* in North and Central America including the West Indies. His treatment of the *Toxicodendron* group was a conservative approach to species and varieties. However, the nomenclatural decisions which he made have been only partially followed subsequently, largely

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[3]Greene correctly points out that Miller, in using *T. vulgare*, was using the priority of his day: not that related to *Species Plantarum* (1753), but that of Dillenius (1732), who happened not to use the binomial system.

because he chose the unpopular course of action, i.e., to accept *Toxicodendron* as a genus. He later further split *Rhus* into *Schmaltzia* (1940) (= *Lobadium* according to Brizicky, 1963, and Barkley, 1963), *Duckera* (1957) (= *Melanococca*), and *Searsa* (1957, 1963).

Fernald in his intensive examination of the flora of southeastern Virginia (1950), made further nomenclatural additions to the poison-ivy complex. Although Fernald worked from specimens which he himself had collected in the field, he made some errors of judgment (e.g., naming a new form [*Rhus toxicodendron* f. *elobata*] of Eastern poison-oak based on a character which is confined to female plants), therefore not warranting nomenclatural concern.

A comprehensive summary of the *Rhus* vs. *Toxicodendron* problem, with resolution of numerous dilemmas in nomenclature and typification, was published by Brizicky (1963). Barkley (1963) wrote a rebuttal to this discussion, and so the controversy continues.

CHEMISTRY

From a chemical viewpoint, a study of the active poisons began in 1858 with the work of Khittel who thought he was dealing with a volatile alkaloid. Maisch (1866) and Pfaff (1897) isolated the poisons for study, but it was McNair (1916, 1921) who determined the catechol nature of the poisons, and their possession of unsaturated side chains. Majima and Cho (1908) and Majima (1922) recognized the similarity of poisons in poison-ivy and in the Japanese lacquer tree, calling these substances urushiols after *urushi*, the Japanese name for plants of the *Toxicodendron* group. Majima first synthesized a compound like that of urushiol; Hill *et al.*, (1934) isolated some of the pure poison; and Haack (1940) added to our knowledge of the poison chemistry of related toxic Anacardiaceae from the Dutch East Indies. The exact structure of the side chains and of the number of poisons involved in poison-ivy was determined by Dawson and his students at Columbia University (Symes and Dawson, 1954; Dawson, 1954, 1956).

There are four toxic substances in poison-ivy, all 3-n penta-decylcatechol. The four differ only in degree of saturation of the side chain.

GENERIC RELATIONSHIPS OF THE COMPLEX

Toxicodendron is most nearly allied to *Pseudosmo-dingium, Comocladia, Metopium*, and the *Rhus* complex, especially *Actinocheita* and *Malosma*. It shares with *Pseudo-smodingium, Comocladia*, and *Metopium* possession of toxic resins (likely all catechols) and odd-pinnate leaves; in the latter two genera, however, the endocarp is thin and layers of the fruits do not separate upon ripening. Furthermore, the flowers of *Comocladia* are trimerous, whereas those of *Pseudosmodingium, Metopium*, and *Toxicodendron* are pentamerous. The drupes of *Pseudosmodingium* share with those of *Toxicodendron* the property of separation of peri-carp layers as the fruits mature; however, the drupes of *Pseudosmodingium* possess two, more or less equal, broad lateral wngs. Engler (1881) and Barkley (1957) separated these two genera on the shape of the fruit, with those of *Pseudosmodingium* being reniform and strongly com-pressed, while those of *Toxicodendron* are subglobose or ovoid and not always strongly compressed. There are sev-eral *Toxicodendron* species however, particularly in Asia, (*T. succedaneum, T. nodosum*, and *T. vernicifluum*), that have drupes which may be more or less reniform and are strongly compressed, although New World species (plus *T. trichocarpum* of Asia) have subglobose fruits. In fruit and flower morphology, *Toxicodendron* is most closely re-lated to *Rhus* and its allies, *Actinocheita* and *Malosma*, but vegetatively it is more similar to *Metopium* and *Pseudo-smodingium*.

The question of whether *Toxicodendron* should be segre-gated at the generic level from *Rhus* has long been prob-lematical, there being so much force of conviction involved that no series of reasonable arguments in support of either view has much hope of victory. It is necessary at this point to choose a taxonomic path and defend its use in this paper.

It would appear that first the taxon *Toxicodendron* needs to be defined. Secondly, *Rhus* needs to be examined as a composite genus made up of several segregates. Thirdly, the reasons pro and con for segregating these components as genera, i.e., what happens to *Rhus (sensu lato)* in each case, must be evaluated.

McVaugh (1945) made eight recommendations to be followed in segregating genera. Because each of these recommendations will be considered in evaluating the status of *Toxicodendron* and *Rhus*, they are rephrased in summary here:

1. Strong morphological characters or presence-absence of distinctive attributes should be emphasized.
2. There should be no segregation of genera on the basis of characters of minor import unless maintained because of long-held botanical tradition.
3. Not the width of the gap between genera but the taxon's own biological unity should be emphasized. Homogeneity, regardless of degree of overlap of characters with those of other genera, is paramount.
4. One should be guided by diagnostic features of more inclusive genera throughout the complete range of the group, and not by local variations.
5. Decisions in regard to the proposed segregate should not be based upon the equality of relationships between it and some other segregate, but upon the relationships between the segregate and the more inclusive genus.
6. Segregate genera should be sharply delimited. Any species intermediate between the segregate and the more inclusive genus should be relegated to the latter.
7. The security of position of any genus increases rapidly in proportion to the number of differentiating characters.
8. The generic position of a segregate group is strengthened if it has a distinctive geographical range together with more or less distinctive morphological features.

With the exception of item 5, with which I am not in complete agreement, these guides will be discussed and observed.

Toxicodendron as a taxon (without rank specified) may be defined as being made up of plants having the properties of the anacardiaceous tribe Rhoeae which have imparipinnate leaves, poisonous effluvium, dark brown root hairs, exocarp wall cream, yellow, tan, or dun-colored, and white mesocarp that is fatty and waxy with black striations which are in reality peripheral resin canals. The plants have axillary, somewhat loose inflorescences which tend to be pendent under the weight of the ripening fruit when the clusters are large. Pubescence of the fruit, if any, is eglandular. These characteristics have been discussed by Barkley (1937, 1965), Brizicky (1963), and others, but these authors have reached diverse conclusions as to the level of separation of this taxon from any near relatives.

Almost all workers agree that there should be a segregation of *Rhus* and *Toxicodendron*, if only at the section or subgenus level. The question then is: are the characters which segregate these two taxa at least as significant as those which segregate other taxa within traditional *Rhus*, so that justification of the segregation can be made at this time? If not, what arguments may be advanced for retaining the genus *Rhus* in its traditional sense with a group of five or six sections or subgenera?

First, let us look at the status of *Rhus* in the traditional sense. The traits which serve to characterize *Rhus (sensu lato)* are: (1) the tendency of the fruit walls to separate in various ways, (2) nonenlarging calyx in the fruiting stage, (3) presence of one basal ovule, (4) apical position of the stigma and style, (5) staminal number the same as the petals, (6) presence of a functionally one-celled ovary with the hypocotyl against the cotyledons, (7) ovary and fruit not deeply buried within the intrastaminal disc, (8) the ring-porous woods with inter-vascular pitting circular or hexagonal, bordered and alternate, and (9) vessel parenchyma and vessel-ray pitting composed of small, round or

slightly oblong pit-pairs. Most students of the Anacardiaceae agree that *Cotinus*, *Metopium*, and *Actinocheita* should be segregated: *Cotinus* on the basis of simple leaves, long fertile and plumose sterile pedicels, lateral styles, and permanently adhering fruit walls; *Metopium* on the basis of permanently adhering fruit walls, more or less united calyx lobes, marked bands of wood parenchyma, and fairly pulpy mesocarp; *Actinocheita* on the basis of the long silky hairs of the fruit and the presence of a gynophore.

What is left of traditional *Rhus* when the foregoing taxa are removed is a genus which occurs in North America, northern South America, Mediterranean eastern Africa, southern Africa, southeastern Europe through southern Asia to China and Japan, Malaysia, and Polynesia. It possesses red, white, black, yellow, or tan fruits which have either glandular or non-glandular hairs or are glabrous. Its mesocarp is either resinous or waxy. Its resins are either benign or dermatitis-producing catechols. Its flowers are either in dense, terminal thyrses, terminal and lateral compound spikes, or loose lateral paniculate thyrses. Its fruit walls separate upon maturity so that there is adhesion of the exocarp and mesocarp, or of the mesocarp and endocarp. Such divergent characters do not unify *Rhus*.

Once segregated (following the splitting off of *Cotinus*, *Metopium*, and *Actinocheita*), then *Toxicodendron* is a group of plants which shares the presence of poisonous resins, axillary inflorescences, pendent clusters of fruit, tan, cream, or dun-colored exocarps, pollen of less than 32μ in length, plus some additional anatomical characters discussed by Heimsch (1940, 1942) that need further study in some Asiatic species. When the fruits of *Toxicodendron* are pubescent, they are not also glandular. What remains of *Rhus* at this point (including the *Thezera* group, the *Lobadium* group, the *Malosma* group, and the *Melanococca* group) is still heterogeneous for a single genus.

The author admits only a cursory acquaintance with the African *Thezera* group and the South Pacific *Melanococca* group. A new look needs to be made of the *Lobadium* and

Malosma groups; the most recent studies (Barkley, 1937, and Brizicky, 1963) involved only herbarium work. To decide the question of splitting or lumping in the *Rhus* complex, one must examine the complex worldwide, complete with cytological, ecological, and comparative anatomical studies. These investigations are beyond the scope of this paper, yet a decision must be made as to the correct names for the poison-ivy complex to be used herein.

Let us explore the kinds of characters which are used to segregate other genera in the Anacardiaceae (Engler, 1883; Barkley, 1957). *Comocladia* is separated from *Metopium* on the characters of sinuate to spinose leaflets and bony seeds vs. entire leaflets and chartaceous seeds. *Actinocheita* is separated from *Rhus* on the basis of presence of a gynophore and long, silky hairs on the exocarp vs. sessile ovary and hairs on the exocarp being short or absent. *Semecarpus* is separated from *Holigarna* on the basis of a half-inferior ovary and intact petiole vs. an inferior ovary and petiole with one to two lateral splits at the base *Harpephyllum* is distinguished from *Koorderisodendron* on the number of locules in the fruit at maturity (two vs. one). *Gluta* is separated from *Swintonia* because the petals of *Swintonia* enlarge in the fruit, whereas *Gluta* petals are deciduous.[4] *Pseudosmodingium* has reniform, strongly compressed drupes, and pinnate leaves, whereas *Rhus* has subglobose, ovoid, or only slightly flattened drupes and trifoliolate, pinnate, or simple leaves. All these separations of genera within the Anacardiaceae seem to suggest that the number of consistent differences between *Rhus* and *Toxicodendron* is certainly greater than, and of at least the same magnitude as, some of these others. In some other families "good" genera have traditionally been made on the basis of a few characters, e.g., *Canavalia* is segregated from closely related genera of the Phaseoloideae because of its

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[4]Current thinking among workers on Flora Malesiana is to unite these two genera into a single genus.

bilabiate calyx (Sauer, 1965), and *Astragalus* from *Oxytropis* on the shape of the tip of the keel petals.

In his revision of the Anacardiaceae, Marchand (1869) poignantly points out: "Personne ne songe, nous le croyons du moins, à rétablir l'indépendance de ces sections pour en faire des genres distincts. Cependant ils sont séparés par les caractères d'une valeur beaucoup plus grande, que ceux qui distinguent encore certains genres de cette famille. Pourquoi cette double maniére d'interpréter la classification? Pourquoi ne pas établir des divisions comparables entre elles? Au moment où le tendance à la division s'accentue à un tel point sur toutes les autres parties de la famille, ici la tendance contraire continue à se manifester. Nous ne comprenons pas pourquoi cette différence existe."

One must be cautious as indicated by Adanson (1757) when he suggested that one cannot choose diagnostic characters of genera when they are incompletely known, because new species might prove to be exceptional. Admittedly, the Far Eastern species of *Rhus* and *Toxicodendron* are incompletely known, but not likely soon to become better known.

The most useful characters for distinguishing *Toxicodendron* from related taxa, in my opinion, are pollen size, presence of poisonous resin in the phloem, exocarp color and pubescence, pendent position of the fruiting inflorescence, and absence of red glandular hairs on pedicels and fruits. There are in addition anatomical differences of lesser importance, but as Barkley says (1963), ". . . an evaluation of the anatomical differences can await more exhaustive studies, and the separation of genera is not dependent on such studies."

The question arises whether the characters which are used to distinguish these genera are consistent in all species. Let us look first at the poisonous nature of the oleoresins.

Literature references to the toxic nature of the various species of *Rhus* are not altogether to be trusted. *Rhus michauxii (Rhus sensu stricto)* of the eastern United States

Coastal Plain and Piedmont has been cited by Sargent (1895) as being highly poisonous, whereas Warren (1909, 1910) correctly disputes this statement. *Rhus trichocarpa* (= *Toxicodendron trichocarpum*) is declared by Rehder and Wilson (1914) to be distinct from *R. vernicifera* (= *T. vernicifluum*) in the "absence of poisonous, varnish-yielding sap." Both of these species have poisonous catechols in abundance. The poisonous nature of *Rhus punjabensis* from India (Chopra, Badhwar, and Ghosh, 1949 and Brizicky, 1963) is still suspect. When I requested of Dr. Chopra a voucher specimen of the *R. punjabensis* which he had in mind when he labeled it toxic, a sample of *R. wallichii* (= *T. wallichii*) was sent. The problem is not uncommon for *Toxicodendron* species of the Far East since they have never been monographed. The best treatment is Rehder and Wilson (1914). Quite recently a seed exchange sent to me from the Soviet Union included a packet labeled "*Rhus silvestris* S. and Z." (= *T. silvestre*) which was in reality *Rhus punjabensis*. It is not enough for an investigator to indicate that a certain species of *Rhus* is toxic; he must verify his determination by a voucher specimen. Otherwise a good case may be made for toxicity among *Rhus* species which are in reality *Toxicodendron* species. Mere reference to the toxicity of *Rhus* in the literature, therefore, need not indicate that they are indeed possessors of the typically poisonous catechols.

The presence of the poisonous sap is easy for susceptible persons to detect in the field, but not so detectable from herbarium specimens. When specimens lack data regarding the toxicity of the plant, one must look elsewhere for suggestion of whether or not the plant was toxic when alive. Inasmuch as the toxic catechols in *Toxicodendron* turn black and generally shiny when allowed to oxidize and polymerize, one may look for evidence of these spots where the leaves and stems have been cut, bruised, or eaten by insects. The tell-tale lacquer-like spots near such wounds may be used to indicate the presence of the toxic substances.

The terminal nature of the *Rhus* inflorescence is open to

some question if the African species are included. In *Rhus*
(*sensu stricto* = subgenus *Rhus*) the inflorescence is strict-
ly terminal. Among the lower pedicels, small leaves or
leaflike bracts may intrude, but the inflorescence is essen-
tially terminal. The occasional pedicels that have leaf-
like structures emerging below them cannot reasonably
be considered axillary. The many *Rhus* species in Africa
(= subgenus *Thezera*) have distinctly axillary flower clus-
ters, these distinguishing them from the *Rhus* species of
North America, southern Europe, and temperate Asia. If
the African species are segregated into a separate genus
(*Searsia*), then *Rhus* indeed may be characterized by ter-
minal inflorescences. The *Rhus* species of the western
Pacific islands (= subgenus *Melanococca*) has a terminal
inflorescence as a rule, but as Brizicky (1963) pointed out,
there are exceptions. All inflorescences appear to be thyrses
with the terminal flower in each tertiary cluster opening
first.

As to fruit color, one must be certain that he is observing
a ripe or (in the case of herbarium specimens) a properly
dried specimen. Brizicky (1963) has examined many fruit-
ing specimens of *Rhus sensu lato*, and suggests that there
is overlap in color between the "brown" fruits of *R. cori-
aria*, *R. copallina*, *R. javanica*, *R. punjabensis*, and *R. (Toxi-
codendron) griffithii*. The decidedly brown fruits of *R.
coriaria* and *R. javanica* have the character of glandular
pubescence linked with the fruit color. The "brown" of the
other true *Rhus* species is red or red-brown, except in slowly
dried material wherein the color deepens to a dark brown.
In the case of *T. griffithii*, the brown is a tan or olive, con-
sistent with the fruit color of *Toxicodendron*.

As will be demonstrated later, the pollen grains of *Toxi-
codendron* are significantly smaller and often more round
(smaller length/width ratio) than those of *Rhus*. Mrs.
Kuprianova (1965) has supported the erection of a whole
family (Pistaciaceae) as a segregate of the Anacardiaceae,
based on pollen grain morphology. It is perhaps not too

extreme to use pollen grain size and shape as yet another set of characters for separating genera.

According to Mr. Joe F. Hennen (personal communication), rusts of the genus *Pileolaria* are genus-specific in the members of the Anacardiaceae which they parasitize. *P. brevipes* and *P. shiraiana* attack only *Toxicodendron* species (*T. radicans* subspp. *orientale* and *hispidum*, *T. silvestre*, *T. succedaneum*, *T. trichocarpum*, and *T. vernicifluum*). *Pileolaria klugskistiana*, on the other hand, finds hosts only in *Rhus hypoleuca*, *R. javanica*, and *R. punjabensis*). Such host specificity seems to support other evidence that these two sumac genera should be recognized as distinct.

The segregation of *Toxicodendron* from *Rhus* appears to be appropriate in view of McVaugh's "laws." There are several strong characters which separate it from all other *Rhus* species, characters which unify the genus throughout its range in both Old and New World. These characters are greater in number and of greater variety than those which separate generally accepted segregates of *Rhus*. One species — admittedly too rare for complete knowledge of it — has the paniculate inflorescence of *Toxicodendron*, yet otherwise possesses *Rhus* characters. It is relegated to the latter as *Rhus paniculata* Wall. Presumably it is not poisonous. There are hybrids and evidences of crossing among species of *Toxicodendron*, but none between *Toxicodendron* and other *Rhus* species, nor even between sections of *Toxicodendron* as herein defined. Their ranges do, however, overlap considerably in Asia and North America. By removing *Toxicodendron* from *Rhus*, each taxon becomes more nearly homogeneous.

TAXONOMIC CONCEPTS

The tendency among taxa in *Toxicodendron* under investigation here is to have allopatric ranges; only two species pairs are sympatric. Among the allopatric taxa, intergrades, representing hybridization or incomplete divergence in the speciation process, occur at the fringes of ranges

where two or more taxa come into contact. Strict genetic isolation does not appear to be operating to the same extent that geographical and ecological barriers do in limiting gene exchange among taxa.

The sections of the genus are recognized chiefly on the basis of vegetative morphology: growth form, phyllotaxy, and nature of the leaves, i.e., simple or compound. The phyllotaxy of section *Toxicodendron* is 3/8, that of section *Venenata* is 5/13, and the leaves of section *Simplicifolia* are whorled. In terms of reproductive morphology, the stamens of section *Venenata* have long filaments and short, globose anthers, but those of sections *Toxicodendron* and *Simplicifolia* have short, subulate filaments and elongate anthers. In the poison-ivy complex, I have recognized as species those populations which are morphologically distinct by more than three characters and which, because of major geographical and ecological barriers to gene exchange, seldom interbreed in the field. Only two sets of species of the complex are sympatric (one barely so), and few interspecific hybrids are known. Fruits have been produced by artificial cross-pollination between *Toxicodendron radicans* and *T. toxicarium*, but *T. toxicarium* possesses a much larger set of unique morphological characters and ecological requirements than does any other species, so that it rarely hybridizes with anything else in nature.

The taxa recognized herein as subspecies of *Toxicodendron radicans* are regarded as geographical segregates with fewer characters distinguishing them from related taxa than were utilized to distinguish species. These subspecies occupy fairly large ranges and seem to intergrade in the area where they come into contact with other subspecies.

The term *subspecies* rather than *variety* is used for the infraspecific units because each of the taxa has a distinctive range, and because there is some variation even within the subspecies. Should a subsequent investigator feel that these variants are worth naming as distinctive taxa, he may assign varietal names as subdivisions of the subspecies. The subspecies group themselves into two distinct categories

according to clusters of characters which they share in common. It was originally my intent to recognize these two groups as subspecies and the individual taxonomic variants as varieties. The group of taxa including *T. radicans* subspp. *radicans*, *orientale*, and *hispidum* would then have been a subspecies divided in range between two hemispheres, whereas other infraspecific taxa with ranges adjacent to subsp. *radicans* in North America have less in common with it and would have been placed in another subspecific cluster.

Because of the relative abundance of these plants and of references to them in both scientific and non-scientific literature, I feel that no good end would be served at this time by adopting a classification with two ranks of infraspecific taxa.

PHYTOGEOGRAPHY AND EVOLUTION

Toxicodendron is primarily a genus of North America and eastern Asia. The range of section *Toxicodendron* (Fig. 26) extends from central China and Japan south to Malaysia and from southern Canada to western Guatemala, Bermuda, and the western Bahamas. The range of section *Simplicifolia* is much more restricted, having been found only in north central Borneo. The range of section *Venenata* (not treated herein) is throughout eastern Asia including Japan and Indonesia with a single species in the United States from southern Quebec to Florida in the eastern third of the country, and a single species in Latin America from Veracruz, Mexico to the highlands of Colombia. The American species of section *Venenata* are *Toxicodendron vernix* (L.) Kuntze and *T. striatum* (Ruiz & Pavon) Kuntze. The former is the well-known poison-sumac which is found in acid bogs and swamps in eastern United States. The latter is an upland tree which occurs in Latin America. The Asiatic members of this section are trees of China, Korea, and Japan, the foothills of the Himalayas, and southeastern Asia. They include the oriental lacquer tree, *T. vernicifluum* (Stokes) Barkley, a tree harvested for the wax in its fruits,

T. succedaneum (L.) Kuntze, and a northern member of the group, *T. trichocarpum* (Miq.) Kuntze, to mention three species. A number of other species are said to occur in China.

It is possible that *Toxicodendron* diverged from *Rhus* in the early Tertiary in China with the rare *Rhus paniculata* Wallich of central China a morphological link between the two genera. This species possesses an inflorescence that is loosely paniculate like *Toxicodendron*, yet terminal like *Rhus*. The color of the fruits on herbarium specimens, which may be misleading, is light brown like *Toxicodendron*. The fruits are also eglandular like those of *Toxicodendron*. The mesocarp is fibrous and barely, if at all, striate, resembling *Rhus*. Due to the paucity of herbarium material in Western Hemisphere herbaria, it has not been possible to test for the presence of catecholic poisons, but lack of lacquer-like spots at breaks in the leaves and lack of similar resin duct striation in the fruit are strongly suggestive of its being benign.

Section *Toxicodendron* with its viney habit appears to be more advanced than section *Venenata*. *Toxicodendron* may well be derived from the common *Rhus* species of Asia, with the multiple leaflet taxa being the older, reduction in leaflets being advanced. On occasion *T. radicans subspp.* produce leaves with more than three leaflets; *T. diversilobum* does so even more commonly. This tendency to produce multifoliolate leaves is interpreted as reversion to an ancestral condition. Section *Simplicifolia* demonstrates reduction to simple whorled leaves, still exemplifying the liana habit, and is interpreted as being highly advanced.

Toxicodendron nodosum may be a link between sections *Toxicodendron* and *Venenata*. This species is scandent, but apparently produces no aerial roots. It will produce leaves composed of as many as seven leaflets, but normally gives rise to only five. In one plant grown in the laboratory leaf primordia initiated during periods of water stress had fewer leaflets than those developing when the plant was abundantly watered. The species appears to combine the multi-

foliolate leaf character and lack of aerial roots of section *Venenata* with the scandent habit and tendency to reduction in leaflet number of section *Toxicodendron*. Because of the importance accorded to habit within the complex, and also the stamen structure, this plant has been placed in section *Toxicodendron*.

Toxicodendron nodosum is found today (Fig. 27) in the Malay Peninsula, Borneo, Java, Sumatra, and Celebes. Backer and Van Den Brink (1965) indicate that Malaya and all the islands of the Sunda Shelf (Java, Sumatra, *et al.*) were a continuous land mass during the Pleistocene and would have permitted a free exchange of disseminules. Presumably *T. nodosum* had a distribution throughout this region during the Pleistocene, its distribution having ebbed and become dissected as the sea rose.

Toxicodendron radicans is a wide-ranging species, having several genetic expressions through North America and eastern Asia. Quoting Asa Gray, J. C. White (1873) notes: "Our *Rhus Toxicodendron*, or poison-ivy, is very exactly repeated in Japan, but found in no other part of the world, although a species much like it abounds in California. Our other poisonous rhus *(Rhus venenata)* is in no way represented in Western America, but has so close an analogue in Japan that the two were taken for the same by Thunberg and Linnaeus, who called them both *Rhus vernix*."

Gray mentions poison-ivy (1846, 1858, 1889) as a typical example of the floristic connection between eastern Asia and North America, especially of the eastern United States. Forbes and Hemsley (1886) felt that the trifoliolate species which Augustine Henry had collected from Ichang on the Yangtze River was "evidently allied to *Rhus toxicodendron* L." Miquel (1867) further recognized the identity of the plant called *Rhus toxicodendron (sensu auctt. plur. non* L.) as being in common with Asia and North America. He further hypothesizes a common ancestor. More complete studies of the poison-ivy complex have served only to confirm this affinity. The Atlantic Coast taxon *(T. radicans*

subsp. *radicans*) is more similar in morphology to the taxa of eastern Asia (*T. radicans* subsp. *orientale* and subsp. *hispidum*) than to any other; the three are thus grouped as morphologically closely related subspecies. Considering the present abundance of *T. radicans* in Japan, it is puzzling that the species is not mentioned in any of the older floras of that country (Thunberg, 1784; Siebold and Zuccarini, 1826-70; Blume, 1849-56).

The North American taxon (*Toxicodendron radicans* subsp. *radicans*) which most closely resembles the oriental and fossil ones perhaps represents populations which have been exposed to relatively little environmental change, except glaciation, since their invasion of this region, presumably during Eocene time or shortly thereafter. Populations in other parts of North America have been exposed to mountain-building, glaciation, and changes in climate which have been accompanied by changes in leaf and fruit morphology, possibly of a non-selective nature. A major change has been in the development of dentate, crenate, and lobed leaflet margins. This latter type of margin is most common in populations of *T. diversilobum* a near relative of poison-ivy. It is this form which represents the greatest departure of the leaflet from the primitive, entire-margined form.

Tatewaki (1958) noted that poison-ivy, like certain other Japanese plants such as *Hydrangea petiolaris*, *H. paniculata*, and *Actinidia kolomikta*, has a distribution throughout Japan, the southern Kuriles, southern Sakhalin, and central China. Nakai (1909) had pointed out earlier that it does not occur in nearby Korea, Manchuria, and Far Eastern Soviet Union.[5] Phytogeographically, poison-ivy's oriental distribution may be described as being in the Temperate Eastern Asiatic and Subarctic regions as defined by Engler. It follows Miyabe's line in the Kuriles, being south, but not

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[5]Its occurrence in the Soviet Union is restricted to the islands east of the Mainland, over which Russia secured mandate following World War II.

north, of the Etorof Strait (Miyabe, 1890), and is south of Schmidt's line in Sakhalin (Schmidt, 1868, and Tatewaki, 1958). *Toxicodendron radicans* subsp. *orientale* is found (Fig. 36) as far south in the Japanese Archipelago as Yaku-sima Island, one of the northernmost islands of the Ryukyus (Masamune, 1934). It skips over the more southerly Ryuk-yus and is replaced in Taiwan by *T. radicans* subsp. *his-pidum* (Fig. 38).

In Japan, poison-ivy is common, not in fields, hedges, and fencerows (of which there are few in that country), but in the forests as a denizen of the old forest vegetation. It is not the common intruder into ruderal sites as it is in North America. It has been collected more often in Hok-kaido and Honshu than in Kyushu and Shikoku, for the former two islands have been studied more intensively than the latter two.

From regions of more rigorous growing conditions in Hokkaido and the Rishiri Islands, a supposedly non-scan-dent form has been described as *Rhus rishiriensis*. For lack of any evidence of a genetic difference between this form and the more typical Japanese poison-ivy, they are treated here in synonymy. It is possible that this sub-shrub is an incipient subspecies.

In the central mountains of Taiwan and in the mountains of central and western China, *Toxicodendron radicans* subsp. *hispidum* occurs as a climber or small bush in rocky places. Its distribution in China follows the Yangtze River drainage system of the Hunnan and Kweichow plateaus and foothills of the Tibetan Plateau in Yunnan, Szechuan, Kweichow, Sikang, and Hupeh Provinces.

The Chinese component of *Toxicodendron radicans* is found in two widely disjunct localities, central China and Taiwan. Taiwan is a continental island probably connected to the mainland until Tertiary times, possibly until the Pliocene (Hosokawa, 1954). The Formosa Straits, separating Taiwan from mainland China, are no deeper than 100 fathoms. The natural initial conclusion of the student of the Chinese flora is that the flora of Taiwan would be more

closely related to that of the East Coast provinces south of
the Yangtze River, but according to Li (1963) the affinity
of Taiwan's mountain flora is with that of central and south-
western China. Even the so-called "endemic" genus of Tai-
wan, *Taiwania*, has been found in northwestern Yunnan.
The phytogeographic link was likely the mountain chain
from China and the Tibetan Plateau through the Malay
Peninsula to Taiwan, a thoroughfare that has been closed
since the Tertiary (Wilson, 1920). According to Hosakawa
(1954), Taiwan was connected geologically with continental
China during the Pliocene. Hypothetically, the distribution
of poison-ivy may have once been continuous from western
China to the mountains of Taiwan, and has shrunk in more
recent times with interruptions by the sea. Long-distance
dispersal cannot be ruled out as the explanation for the dis-
junct distribution of *T. radicans* subsp. *hispidum*, although
no means of transport is suggested at this time.

The mechanism of inter-continental dispersal for *Toxi-
codendron radicans* is now of some importance. One sug-
gestion to account for the present-day distribution is the
shrinking of a once more extensive range with *T. radicans*,
or an ancestor, a member of the Arcto-Tertiary flora. One
may envision a continuous distribution throughout eastern
Asia and North America across a hypothetical connecting
land-bridge in the Tertiary when the climate of the boreal
lands was probably temperate. This hypothesis would ac-
count for the striking similarity between taxa on these two
continents — even greater similarity *between* the inter-con-
tinental populations of *T. radicans* subsp. *orientale* and
radicans than *within* the populations of the various taxa in
North America. The latter have evolved with the evolution
of land forms in North America since the closing of the
land-bridge, eastern North America and eastern Asia hav-
ing remained more stable in the interval than the inter-
vening land mass. No fossils of poison-ivy, however, are
known from this intervening mass except that *T. magni-
folium* has been found in several Oligocene formations in
northern California where *T. radicans* is not found today

(MacGinitie, 1937, and Jack Wolfe, personal communication).

Another possibility for the two-continent distribution of this species is long-distance dispersal, but considering it as part of the Arcto-Tertiary flora is a more logical possibility. The prevailing winds and ocean currents are west-to-east; thus, it is possible that the species may have had its origin in Asia with North America the recipient. However, its closest generic relatives are *Metopium, Pseudosmodingium,* and *Rhus* species which are New World in distribution. It seems, therefore, that *Toxicodendron radicans,* like the horse, may have had a North American origin and later migrated to Asia.

In North America, the possible speciation pattern of the past may be analyzed by present-day distributions. There appear to be, in general, only subtle barriers to gene flow. *Toxicondendron radicans* subsp. *radicans* (Fig. 34) is a lowland subspecies, separated from subsp. *negundo* (Fig. 43) to the west by the Allegheny Ridge in Pennsylvania and New York, and the Blue Ridge and adjoining mountains to the south. Zones of overlap and introgression can be demonstrated in the above-mentioned regions (see discussion under Hybrids, Crosses, and Intergrades.) In the north subsp. *radicans* is separated from *T. rydbergii* (Fig. 49) essentially along the 44th parallel of latitude. This phenomenon is especially evident in Nova Scotia where *T. radicans* subsp. *radicans* is found in the southwest portion of the province, and *T. rydbergii* is found farther northeast above the 44th parallel.

Taken together, *Toxicodendron radicans* subsp. *radicans* and subsp. *negundo* occupy much the same range as such genera as *Nyssa* and *Cornus,* which seem to drop out on their western limit where the rainfall is significantly below the 30-inch annual mark (Dressler, 1954). The northern limit of these taxa (and the southern limit of *T. rydbergii*) also correspond. Moreover, subspp. *radicans* and *negundo,* taken together, have a northern limit almost identical with that of *Panicum miliaceum, Asparagus officinalis, Bromus*

secalinus, and *Arrhenatherum elatius*, as recorded by Hultén (1958-1964) as well as a northern range quite similar to that of a number of others.[6] Presumably when Hultén's work is completed for the dicots, sufficient additional species will be shown to demonstrate a similar distribution to suggest a phytogeographic line at this location in Canada and upper United States.

In further support of the existence of a phytogeographic tension zone here, one might note the southern limit of *Toxicodendron rydbergii*. It is identical with that of *Myrica gale*, *Oxalis acetosella*, and *Goodyera repens*, all of which, like *T. rydbergii*, have an extension of their ranges along summits of the central Appalachians south to Virginia. *Equisetum palustre* has the same southern limit as *T. rydbergii*, and in addition demonstrates a southward continuation along the shore of Lake Michigan as does *T. rydbergii*. Other taxa show a similar, although not identical, southern limit [7] (Hultén, 1958, 1964).

This tension zone as expressed in Michigan has been the subject of several studies involving pollen, plants, animals, and Indian tribes. Potzger (1948) pointed out that climatic factors are less varying over most large geographical distances than they are within the small latitudinal distance of about sixty miles under consideration here. *Quercus* declines in forests north of the zone, whereas *Pinus* does so south of it. Livingston, too (1903, 1905), noted Kent County as the northern limit of many typically southern plants and the southern boundary of the pine forest region. Livingston tends to believe soil factors are controlling in the distribution whereas Potzger (ibid.) feels that the "mas-

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[6]*Bromus japonicus*, *Setaria viridis*, *Poa compressa*, *Holcus lanatus*, *Athyrium filix-femina*, *Phragmitis communis* (sensu lato), *Osmunda cinnamomea* var. *cinnamomea*, *O. claytoniana*, var. *claytoniana*, *Alisma plantago-aquatica*, *Potamogeton nodosus*, *Cyperus flavescens*, *Ruppia maritima*, *Typha latifolia*, and *Carex atherodes*.

[7]*Carex flava*, *Subularia aquatica*, *Asplenium viride*, *Equisteum pratense*, *Carex vaginata*, *C. disperma*, *Calypso bulbosa*, *Eriophorum alpinum*, *Dryopteris fragrans*.

ter control" is climate. "There is every evidence that the forest tension zone is climatically transitional, where a number of climatic factors, especially extremes, are closely spaced latitudinally, and the forest is merely expressing the biological values of these environmental factors."

He cites these dividing lines at the tension zone: average depth of forty inches of frost penetration, the divide of average date of daily normal temperatures above 50°F between 1 April (to the south) and 1 May (to the north), a similar divide of the beginning of daily normal temperatures above 68°F ("beginning of summer") between 15 June (to the south) and 1 July (to the north), boundary of the number of days with temperature constantly below freezing in the shade between 30 and 60, and a difference of a month and a half in length of continuous snow cover.

Cleland (1966) has noted this tension zone as the boundary between the hunter-gatherer livelihood of Indian tribes and the agricultural one. Furthermore, north of the line, no mastodon fossils nor arrowheads have been found. Van Faasen (unpublished) has mapped chromosome patterns in species of *Aster*, showing that within one section of the genus (section *Aster*) with $n = 5$, almost all members occur in the tension zone or south of it: and all species where $n = 9$ (except *A. ciliolatus*) occur in the southern two-thirds of the Lower Peninsula of Michigan, essentially in the tension zone and south of it.

This ecotone extends across the southern lobe of Ontario, upper New York State, and New England at approximately the 44th parallel of latitude. It is possible that the same factors discussed above have contributed to the distribution patterns of poison-ivy taxa, collectively becoming the barriers to gene flow and factors enhancing speciation. Krause and Kent (1944) discuss this zone in New England. The range of *Toxicodendron rydbergii* is in western United States and Canada under similarly rigorous environmental conditions, especially that of reduced rainfall. It occurs west of a tension zone that runs northeastward through western Texas and Oklahoma, central Kansas, and the

southeastern portions of Nebraska, Iowa, and Wisconsin, influenced chiefly by the rainfall which is less than 30 inches west of the zone. Curtis (1959) identifies this tension zone as the boundary between the prairie-forest margin and the northern hardwoods province, noting plant, bird, and fish species which have the edge of their ranges there.

Two of the taxa which occur in Mexico have ranges which follow the major mountain ranges of that country. *Toxicodendron radicans* subsp. *barkleyi* (Fig. 41) is found in the Sierra Madre Oriental, extending south to the Sierra de los Cuchumatanes in western Guatemala and the Isthmus of Tehuantepec. Subsp. *divaricatum*, on the other hand, follows the Sierra Madre Occidental (Fig. 41), although its northern limit continues into the mountains of southeastern Arizona. The two subspecies intergrade in the trans-Mexican volcanic belt, especially in Jalisco and Michoacán.

The taxon which is closest morphologically to *Toxicodendron radicans* subsp. *barkleyi* is subsp. *pubens* (Fig. 39) of the southern Mississippi drainage in the United States. Both forms have pubescent leaves, differing only in that subsp. *pubens* has pronounced notches on the leaflets and broad leaflet bases, whereas subsp. *barkleyi* lacks these features. Non-productive branches of subsp. *barkleyi* revert to a lobed form, although maintaining a narrower leaflet base than does subsp. *pubens*. There have been studies which have noted a phytogeographical connection between plants of the southeastern United States and Mexico (McVaugh, 1943, Crum, 1951, Martin and Harrell, 1957 and Sharp, 1966), especially from the Ozarkian area where subsp. *pubens* is indigenous. I postulate that the ancestors of this pair of taxa (subsp. *barkleyi* and *pubens*) once existed from the south-central United States continuously down the mountain chain of the eastern branch of the Mexican Cordillera. As Dressler (1954) has suggested for disjuncts between Guatemala and the Ozarks, these plants became separated into two distinct populations because of decreased rainfall in Texas and northeastern Mexico in early Pleistocene. The northern portion has expanded its range into

the Lower Mississippi Valley into the former Eocene embayment region, and portions have, in modern times, formed hybrids with taxa in adjacent regions over a large area. The southern population has also expanded its range down from the mountains into various provinces of eastern Mexico.

Highly variable populations of subsp. *barkleyi* in northern Mexico posed problems of interpretation until late in this investigation. They show some variation in degree of leaf pubescence, but more significantly, tend to have leaflets which are broad at the base and more deeply notched on the leaflet margins, both departures from less variable populations to the south. Of these, one population is represented by a large number of herbarium specimens collected by Palmer near Ciudad Victoria (Tamaulipas) in 1907; another I have examined myself on two visits to a site near Galeana (southern Nuevo Léon). These populations are now interpreted as evidences of the common ancestry with subsp. *pubens* to the north, a taxon which has broader leaflets and notched or nearly lobed leaflet margins. Farther to the south in the range of subsp. *barkleyi*, there is greater uniformity in the entire nature of the leaflet margin, dense leaflet pubescence, and elliptical nature of the leaflet margin.

There appears to be a similar tie between the population of poison-ivy from the Edwards Plateau region of Texas (*Toxicodendron radicans* subsp. *verrucosum*, Fig. 39) and the taxon of the western part of Mexico (subsp. *divaricatum*, Fig. 41). Both have completely glabrous leaves and shoots except for an occasional population with small tufts of hairs in major vein axils on the lower leaflet surface, a character which possibly hearkens back to a more distant ancestral type, the Asiatic, Atlantic and Gulf Coast cluster of subspecies. I therefore postulate that there was an original connection in the range of the ancestors of subsp. *verrucosum* and *divaricatum* through the late Tertiary in the province of parallel ridges in northern Mexico, that the population was separated into two phases during Pleisto-

cene submergence of northern Mexico, and southern Arizona (see Eardley, 1962), and that the two populations have evolved *in situ* ever since. The northern Edwards Plateau population has become distinctive by the prominent sharp lobes on the leaflets; the southern (Mexican) population demonstrates narrower, entire leaflets. The southern expression, subsp. *divaricatum*, has in recent times expanded its range along the Mexican Highland into southeastern Arizona; the northern expression, subsp. *verrucosum*, has begun to extend from the limestone of the Edwards Plateau and Arbuckle Mountains into adjoining country to the south and east.

Western poison-oak, *Toxicodendron diversilobum* (Fig. 31), is a likely descendant of the ancestral *T. magnifolium*, or other early form which is known from Western United States. The fossil record shows divergence from other North American taxa at least as far back as the Pleistocene in the western part of the country. Fossil seeds of *T. diversilobum* of Pleistocene age have been found in various parts of California (Potbury, 1932, and Mason, 1934).

Today, all of the North American taxa are denizens of altitudes below 1220 m (or to 1830 m in the Southwest) and are not able to cross high mountain barriers, notably the Cascades. Such populations, which grow west of the Cascade Mountains, the Great Basin, the Sierras, and the Mojave Desert, have been isolated from their eastern counterparts long enough — starting in Miocene time — to have undergone the modification necessary to be recognized as a distinct taxon, based largely on leaf and fruit morphology. The uplift of the Cascades was late Pliocene and early Pleistocene (Williams, 1957); the block faulting of the Great Basin was late Tertiary and Pleistocene (Kay and Colbert, 1965); and the greatest tectonic activity in the Sierras was in the late Miocene (Kay and Cobert, *ibid.*). These landforms thus formed separate *T. diversilobum* and *T. rydbergii* today. Only where the Columbia River cuts through the Pliocene basalts of the Cascade Mountains have Western poison-oak and poison-ivy mingled and inter-

bred. The hybrid progeny show introgressive variation in leaf shape and fruit pubescence ranging from the western to the eastern taxa. (See discussion under "Hybrids, Crosses, and Intergrades.")

The origin of *Toxicodendron toxicarium* (Fig. 51) is open to question. Although the remote ancestry and derivation of this plant remain obscure, its recent history probably can be synthesized from what is known or postulated of other sandhills species. This plant inhabits chiefly the fall-line sandhills of the Carolinas and adjoining states, but also has moved into pine barrens, has reached up the Mississippi Valley to southern Missouri, west to Texas, and north to New Jersey. It has passed freely into the xeric soils of the Piedmont and lower mountains. Duke (1961) describes plants such as these as being indigenous to the sandhills, but not endemic there; rather, they are able to become established in ecologically similar habitats.

The sandhills and pine barrens floras seem to be determined by the inability of roots to grow rapidly enough to penetrate the sterile upper soil horizons to reach the richer soils below (Wells and Shunk, 1931) and to utilize nutrients in the surface decomposition zone. *Toxicodendron toxicarium* is such an example; its roots rarely reach the horizon of illuviation. Plants which comprise these floras were probably the first to colonize the available sandy habitats uplifted after the Cretaceous inundation (Duke, 1961). Where were they before this?

Fernald (1937) postulated a Virginia-centered classification of floral elements that were later distributed throughout the sandhills area of the fall-line. Duke (ibid.) feels that a northern Florida center is more meaningful. For those who believe in the "Orange Island" refugium during the Cretaceous (Woodson, 1947; Vaughan, 1910; Cooke, 1945; Goin, 1958), such a northern Florida center seems most reasonable.

Following late Tertiary uplift, there might have been a dichotomous radiation of migration: northward along the xeric sands of the Cretaceous Tuscaloosa formation to the

middle Atlantic states and west through the xeric sands across the Gulf Coastal Plain. The flora which developed in the sandhills may have evolved along with the development of the sandhills as a geomorphological formation since the late Tertiary.

Toxicodendron toxicarium might well have been one such species. There are a number of examples of plants which share this dichotomous distribution (Duke, 1961, and Gould, 1962) : *Pinus taeda, Prunus angustifolia, Centrosema virginianum, Desmodium strictum, Lespedeza striata, Polygala polygama, Croton glandulosus, Leiophyllum buxifolium, Breweria pickeringii, Ruellia carolinensis, Elaphantopus carolinianum, Eupatorium rotundifolium, Heterotheca subaxillaris, Danthonia sericea, Aristida lanosa, Gymnopogon ambiguus, Panicum aciculare, P. trifolium, Sacciolepis striata, Andropogon ternarius, A. elliottii, Cyperus retrofractus, Carex complanata, Scleria nitida, Smilax glauca,* and *Toxicodendron toxicarium.* As Harper (1906) has noted, those plants whose ranges cross the fall-line (as does *Toxicodendron toxicarium*) nearly all occur in the pine barrens as well as in the sandhills.

If *Toxicodendron radicans* were an ancestor of *Toxicodendron toxicarium,* then *T. toxicarium* was gradually modified for characters of selective advantage in the xeric habitats in which it grew, i.e., pubescent leaves, reduced habit, revolute leaflet margins — all considered at one time or another as water-saving devices. Its ancestry to poison-ivy may be seen in its trifoliolate condition and pubescent fruits, which is a primitive character in the *T. radicans* group.

Part of the clue to the relations of *Toxicodendron toxicarium* might be found in *T. radicans* subsp. *eximium.* Both have narrow ecological requirements. *Toxicodendron toxicarium* inhabits scrub oak forests (often with pine) that are quasi-savannas. The regions are open, seldom with trees more than a foot in diameter, often subject to burning. The soil is generally sand of low nutrient content. The range of *T. toxicarium* is typically the Gulf and Atlantic Coastal Plains, but has extended into adjacent regions

where a sandhills vegetation prevails. *Toxicodendron radicans* subsp. *eximium* (Fig. 41) occurs in mesic canyons in southwestern Texas and northern Mexico, but has the distinction of being the rarest of the taxa here considered.

The affinities of these taxa are obscure. Both have pubescent leaves; both have predominantly lobed leaflets; both have fruits which are pubescent to a greater or lesser degree. Several floras have mistakenly included subsp. *eximium* in *Toxicodendron toxicarium*. These taxa are more like each other than they are like anything else, and have no close affinities with other taxa in the complex. Their chief difference is habit and degree of leaflet lobation. Subsp. *eximium* is completely separated from any taxa in adjoining areas and hence demonstrates no intergrading or hybridization that is known. *Toxicodendron toxicarium*, on the other hand, can form hybrids with *T. radicans* subsp. *radicans*, although such hybrids are rare in nature. It is possible that *T. toxicarium* shared a common ancestor with the poison-ivies because they behave as not distant relatives in their ability to cross, yet their actual relation remains obscure. Perhaps *T. toxicarium* and *T. radicans* subsp. *eximium* are more closely related to each other than either is to other taxa — they do share many morphological similarities — but their present ranges seem difficult to reconcile on the basis of anything but chance long-distance dispersal.

Since the modern distributions of the poison-ivies must be related to Pleistocene glaciation, we must attempt to reconstruct their postglacial history and attempt to account for where the various taxa must have been during the Pleistocene. There is some evidence from present distribution patterns that several of the taxa in question may have resulted from separation by the glaciers of fewer once-widespread ancestral forms into separate populations. At the height of glaciation, subsp. *radicans* was undoubtedly restricted to a region of southern and eastern United States south of the ice sheet. At the same time, subsp. *negundo* might have existed in a refugium in the sand plains of the

central states or in the Ozark region; it may have evolved from subsp. *radicans* during the separation by ice sheet and mountains (Appalachians) at this time. Subspecies *pubens* probably occupied essentially the same pattern as today in the lower Mississippi Valley.

With release from the ice, the *terra nova* was free to be invaded by disseminules of plants such as *Toxicodendron radicans* behind the influx of spruce, fir, willow, and aspen. The northern taxon, *T. rydbergii*, probably invaded from the west through a northern route, coming to occupy land north of the 44th parallel of latitude across eastern United States and Canada. Subspecies *radicans* migrated northward along the Atlantic Coast and lower slopes of the Appalachians while subsp. *negundo* invaded along a northeasterly path through the center of the country into western New York and Pennsylvania. In relatively recent times, *T. rydbergii* may have expanded its range southward along summits of the Alleghenies and the Blue Ridge by long-distance dispersal or inadvertent introduction; several of the southerly outlying populations in mountain areas are associated with road gravels and recent construction. These patterns of post-Pleistocene invasion follow suggestions of migration of many other plants described, for example, by Braun (1950), Fassett (1941), and Iltis (1965, 1966, and personal communication).

In the present Ozarkian region, the systematics of poison-ivy becomes very confusing. The region of southern Missouri, eastern Oklahoma, northwestern Louisiana and most of Arkansas (with the exception of the "Delta" region of cotton-growing country along the Mississippi River) present problems of poison-ivy identity. In this area, which is complex lithologically and pedologically, there appears to be extensive variation over a large area, presumably the result of large-scale introgression among several subspecific taxa. Populations may show a complex of the leaf pubescence of *Toxicodendron radicans* subsp. *pubens*, the entire leaflet margin character of subsp. *radicans* or the lobing on the leaflets of subsp. *negundo* or *pubens*, tufts of hairs

in the vein axils of the lower leaflet surface as in subsp. *radicans* or absence of such hairs as in subsp. *negundo* or *pubens*, the glabrous fruit surfaces of subsp. *negundo* or *pubens*, or the pubescent fruits of subsp. *radicans*, etc. This region has had varieties of poison-ivy indigenous for a longer time than any of the glaciated country, so that there has been a longer time for migration, introgression, and exchange of genes. There appear to be no barriers to gene exchange among the subspecies, neither of the physical environment nor of biological mechanics. The activities of man in altering the landscape will probably enhance this process of gene exchange in the future. No conclusions other than the probability of hybridization between the two subspecies seem to be warranted until experimental studies and additional field work are carried out in this area.

In summary, one might suggest the following as the pattern of development and evolution of the poison-ivy complex in North America. The ancestral form is that which occupies the Atlantic and Gulf Coastal Plain (*Toxicodendron radicans* subsp. *radicans*). The combined forces of the early Cenozoic uplift of the Alleghenies and Pleistocene glacial ice separated this population into two facies which have produced subsp. *negundo* to the west and maintained subsp. *radicans* in the east. The Ozarkian and Mexican populations were continuous until the deserts of the early Pleistocene were formed. Likewise, a western counterpart in subspp. *verrucosum* and *divaricatum* exists with separation in the Pliocene or late Miocene due to faulting and uplift in the American Southwest. The far western populations have been separated into distinct populations since the uplift of the Sierras and Cascades and the block faulting of the Great Basin. In regions of more rigorous growing conditions, the evolution of *T. rydbergii* may have progressed at a more rapid rate so that this taxon possesses more distinctive characters than the others in the complex. The spread of *T. toxicarium* is, no doubt, late Tertiary in age.

One more case of poison-ivy distribution bears mention-

ing. In the late 1950's, a case of poison-ivy dermatitis showed up in the Union of South Africa near Cape Town. This was anomalous since there was no known poison-ivy on the African continent. It was traced to a specimen of *T. radicans* which was climbing the side of a house in that area, introduced at some time since 1950 (Ross, 1959). The plant has since been removed from South Africa.

CONSTANCY OF CHARACTERS

The constancy and dependability of characters expressed in the poison-ivy complex has relevance to the determination of which characters should be used for taxonomic purposes. One reason for the confusion among taxonomists in the past regarding the number of taxa in the complex has been the profusion of characters which have been used for classificatory purposes. Determination of character constancy has been based herein on uniformity within a region, especially when a character is found (or is absent) in various specimens from a mass collection of a single clone.

Almost all workers have considered the fruits to be of special significance, chiefly in regard to presence or absence of fruit pubescence. Anatomical studies reveal that the trichomes on the fruits are hollow, septate hairs that have been produced by evaginations of the exocarp wall. Small papillae are considered to be incipient or reduced hairs; therefore either trichomes or papillae on the fruit walls are considered an expression of the same character, varying only in degree. Fruits of *Toxicodendron radicans* subsp. *orientale*, for instance, are always either pubescent or papillose, never glabrous.

Fruit pubescence is considered to be primitive in this complex, its greatest expression being found in the populations of China. It may appear secondarily in a few populations in advanced forms which typically have lost their pubescence through evolution, i.e., populations from parts of Indiana and Oklahoma in *Toxicodendron radicans* subsp. *negundo*. It may also become reduced or lost entirely in a

taxon wherein it has been an important character. There appears, for example, to be a cline within this character's expression in *T. radicans* subsp. *radicans*, a taxon normally distinguished by its pubescent fruits. From central Georgia to southern Florida, the fruit hairs appear less and less pronounced and more sparse, until populations from Key West, Florida, are decidedly glabrous. The character of fruit pubescence is still considered of importance within the *T. radicans* group because it helps unify most populations of this taxon. When it does vanish from the population, it does so over a fairly gradual cline. Except for extreme southern Florida populations, then, fruits are pubescent in this subspecies, even though occasionally only sparsely so. Pubescent or papillose fruits are found in all fruiting populations of *T. diversilobum* and *T. toxicarium*.

The fruits of the genus *Toxicodendron* are typically laterally flattened. Only in eastern North American taxa are they globose or subglobose. *Toxicodendron striatum* of Central and South America and *T. diversilobum* show a tendency to flattening, but the other taxa of North America have globose or subglobose fruits. This character then is dependable within species groups.

Habit of the plant and presence or absence of aerial roots are dependable characters. *Toxicodendron toxicarium* and *T. rydbergii* and supposedly *T. nodosum* never produce aerial roots in the wild, the former two being sub-shrubs.

A single leaf does not a taxon make! Although most keys to poison-ivy taxa have been based on fruit characters, more new species have been described on nuances of leaflet morphology than on any other single trait. Many such taxa have been described on the basis of only one or two specimens. Most of these are undependable characters because they vary within as well as among populations.

Number of leaflets is fairly standardized at three in *Toxicodendron radicans*, *T. diversilobum* and *T. toxicarium*. However, a number of populations are known in which additional leaflets are produced year after year (Gillis,

1960). In *T. diversilobum* it is common for a clone to produce a few leaves consisting of five leaflets. As many as eleven leaflets have been found. In subspecies of *T. radicans* the production of multiple leaflets is more sporadic, in *T. toxicarium*, rare. Although multiple-leaflet forms exist, they do not deserve taxonomic recognition. *Toxicodendron nodosum* characteristically has more than three leaflets.

Juvenile leaves are atypical as are shade leaves, and particularly leaves from procumbent stems. Leaves used for diagnostic purposes should always, in erect and liana forms, be chosen from the climbing stems or terminal branches. There is too much variation in shade leaves, those from creeping branches and those buried within the center of a large shrub, for these to be of diagnostic value.

If mature leaves on mature flowering or fruiting branches are selected for diagnostic purposes, then the characters of importance and dependability are: length-to-width ratio, presence or absence of tufts of hairs in axils of vein branches from the midrib on the lower surface of the leaflets, nature of the leaflet apex and base (especially on the terminal leaflet), nature of the leaflet margin (especially on the terminal leaflet), pubescence of the lower surface of the leaflet, and presence or absence of pubescence on the petiole. The length of the petiole and prominence of veins on the leaves are critical in a very few taxa. If a choice of leaves is possible, one should select them from both male and female material, for they often differ in lobation and serration between the sexes in the same population. Young, emergent leaves do not often have all diagnostic characters expressed well enough for accurate determination.

Leaf thickness is of little reliability in determining taxa, since this character is highly variable, often related to the thickness of the cuticle and not to layers of mesophyll tissue. Leaf size is more often than not related to light environment, larger forms being sun (sic) leaves. Notching and serration are good only within certain broad limits. Upper leaflet pubescence is not constant within taxa.

POLLEN MORPHOLOGY

Pollen was examined from species of *Rhus, Toxicodendron, Metopium, Actinocheita,* and *Schinus* to determine the significance of pollen morphology on the classification of *Toxicodendron* and related taxa.

The study was an attempt to determine the degree of variation among genera, species, and subspecies of the tribe Rhoeae, as well as to evaluate pollen characters as a means for distinguishing the taxa.

For most species studied, anthers were removed from materials in the Michigan State University Herbarium (MSC), chiefly from my own collections. Two samples were taken from specimens at other herbaria. Pollen was obtained from the type species of the genus *Rhus* (the south European and western Asiatic *R. coriaria* L.), from the two poison-oak species, from three American species of *Rhus sensu stricto,* and several taxa of poison-ivy from North America and Japan. Two species of *Toxicodendron* sect. *Venenata* and the one of sect. *Simplicifolia* also were examined. One sample each was taken from *Metopium, Actinocheita,* and *Schinus.* The source of the materials used in this study is given in Table 2.

Dried anthers were collected from herbarium specimens and stored in vials of glacial acetic acid. Acetolysis was achieved in the following manner. Pollen and anther material was centrifuged at 1000 rpm; the acetic acid was decanted. Acetic anhydride was added to the mixture and the whole mixture centrifuged. The supernatant liquid was decanted and 5 cc of freshly prepared acetolysis mixture was added (one part conc. H_2SO_4 and nine parts acetic anhydride). The acetolysis mixture was heated quickly over a Bunsen burner to boiling. It was then centrifuged immediately and decanted as close to the residue as possible in order to remove most of the acetolysis mixture. Seven to 10 cc of water were added to reduce the specific gravity of the remaining liquid and to wash the grains.

The washed mixture was centrifuged and decanted. Ten

TABLE 2. SPECIMENS USED FOR POLLEN STUDIES

(MSC Herbarium unless another herbarium is indicated by abbreviation in parentheses)

Species	Locality	Collector and Number
Rhus coriaria	U.S.S.R.	
R. glabra	Oklahoma	DeBarr 349
R. typhina	Ingham Co., Mich.	Gillis 2904
R. copallina var. copallina	Sapelo Island, Ga.	Gillis 3969
R. copallina var. leucantha	Alachua Co., Fla.	Gillis 3936
R. punjabensis var. sinica	Leang Wong Mt., Yunnan, China	McClaren U-614
Toxicodendron diversilobum	San Mateo Co., Calif.	Mason, s.n.
T. toxicarium	Alachua Co., Fla.	Gillis 4315
T. toxicarium	Richland Co., S.C.	Gillis 4558
T. radicans subsp. radicans	Dade Co., Fla.	Craighead, s.n.
T. radicans subsp. radicans	Richland Co., S.C.	Gillis 4569
T. radicans subsp. orientale	Noboribetsu, Japan	Gillis 4743
T. radicans subsp. negundo	Ingham Co., Mich.	Gillis 2464
T. rydbergii	Delta Co., Mich.	Gillis 3645
T. vernix	Ingham Co., Mich.	Gillis 3598
T. trichocarpum	Noboribetsu, Japan	Gillis 4724
T. nodosum	Larut, Perak, Malaya	King 5637 CAL)
T. griffithii	N. Lakhimpur, Assam	Panigrahi 27703
T. borneense	Mt. Kinabalu, Sabah, Malaysia (type)	Haviland 1198 (K)
Metopium toxiferum	Dade Co., Fla.	Gillis 4398
Actinocheita filicina	Tehuacan, Puebla, Mexico	Gillis 3720
Schinus molle	Cuapiaxtla, Puebla, Mexico	Gillis 3714

cc of water were added, the mixture shaken, and the foam broken up with a few drops of methanol. The mixture was again centrifuged, the supernatant liquid decanted, and the residue was suspended indefinitely in glycerin-water mixture (1:1). The pollen was again shaken and centrifuged and then a saturated solution of safranin in ethanol was added for 30 seconds, and the mixture centrifuged. One washing with ethanol, followed by centrifugation, was carried out. A small amount of glycerin jelly (enough to cover the residue) was added and heated to melt (but not boil). By means of a pipette, a portion of the mixture was transferred to each of several clean coverslips. The material was smeared evenly with a toothpick and allowed to dry. The coverslip, when dry, was affixed firmly to a slide by Canada balsam. Ikuse (1956) prefers not to use balsam because he claims the shape of the pollen grain changes as the balsam dries. Inasmuch as all my slides were prepared in the same manner, any change would probably affect all of them more or less uniformly.

Photographs were made under the following conditions: Zeiss research microscope and Exacta camera, full-length tube, optovar at 1.60, iris diaphragm at 4, oil immersion objective (100X), 8X ocular, green and neutral density filters. Because of vibrations due to movement of the shutter, time exposures were employed. Photographs were made with Kodak Plus-X film.

Measurements of acetylated pollen grains were made at a magnification of 1280 X with a calibrated ocular micrometer in the microscope. A total of 15 grains was measured for each "population," three grains on each of five slides. Sets of microscope slides of acetylated grains have been filed in the Herbarium and in the Palynological Laboratory of Michigan State University.

All pollen grains of Anacardiaceae studied are tricolporate (tritreme),[8] finely reticulate (striate-rugulate) with

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[8]Terminology follows Faegri and Iversen (1950), Selling (1952), Erdtman (1952), Erdtman and Vishnu-Mittre (1958), Erdtman and Straka (1961), and Kremp (1965).

Table 3. Summary of pollen measurements — selected Anacardiaceae measurements are in microns, 15 grains per set

	Length		Width		Mean Length-width Ratio
	Range	Mean	Range	Mean	
Rhus coriaria	31.5 - 40.8	34.89	27.5 - 33.1	29.03	1.20
R. glabra	36.5 - 45.6	40.67	25.9 - 35.9	32.45	1.25
R. typhina	38.0 - 43.2	39.70	32.6 - 40.0	34.95	1.14
R. copallina var. copallina	35.1 - 48.0	39.99	27.0 - 39.2	30.93	1.29
R. copallina var. leucantha	37.0 - 45.5	40.31	28.5 - 34.0	31.22	1.29
R. punjabensis var. sinica	30.8 - 34.4	34.43	21.4 - 25.7	25.24	1.36
Toxicodendron diversilobum	25.0 - 29.5	28.14	21.0 - 27.4	24.41	1.16
T. toxicarium (Fla.)	22.5 - 27.8	25.30	18.5 - 26.6	21.53	1.18
T. toxicarium (S.C.)	23.5 - 26.0	25.15	19.5 - 23.8	21.16	1.21
T. radicans subsp. *radicans* (Fla.)	23.0 - 28.0	25.95	20.0 - 23.1	21.22	1.22
T. radicans subsp. *radicans* (S.C.)	22.6 - 28.5	25.08	18.9 - 26.6	20.97	1.20
T. radicans subsp. *orientale*	21.0 - 30.0	27.77	20.0 - 23.5	21.97	1.26
T. radicans subsp. *negundo*	23.0 - 28.5	26.11	19.0 - 25.0	21.75	1.20
T. rydbergii	25.0 - 32.0	27.59	22.5 - 30.0	24.41	1.13
T. vernix	25.7 - 29.0	27.14	25.4 - 27.5	26.16	1.04
T. trichocarpum	25.6 - 32.5	27.95	22.5 - 27.0	26.16	1.13
T. nodosum	20.8 - 28.5	26.38	17.6 - 22.1	19.09	1.31
T. griffithii	21.1 - 24.4	23.38	18.8 - 21.4	20.33	1.15
T. borneense	25.6 - 30.4	27.84	25.6 - 29.6	27.28	1.02
Metopium toxiferum	24.9 - 28.2	25.75	18.4 - 25.1	22.48	1.15
Actinocheita filicina	25.1 - 34.0	28.15	23.2 - 27.6	26.15	1.08
Schinus molle	22.5 - 25.5	24.15	21.0 - 26.1	24.25	1.00

long, tapering, sharply defined transverse furrows (sulci).
The furrows become approximate, but do not meet, at the
poles which are slightly apiculate. In each colpus, there is
a large, oblong germ pore, wider than the furrow, whose
equatorial diameter equals at least two meridional diam-
eters, each possessing a porous vestibulum with centripet-
ally developed lips. The colpi are zonicolporate, i.e., ar-
ranged parallel to the polar axis. The ektexine is slightly
raised above the general surface at the pores; the endexine
is also thickened internally at the edge of the colpus, form-
ing a ridge or rib (distinct costae transversales). The nex-
ine is incrassate toward the apertures. The exine is heavy,
finely reticulate, pitted, or occasionally granular with pits
tending to occur in rows. The reticulum is small-meshed
with irregular and varied anastomoses bearing columellae
conjunctae in the ornamentation. The tegillum is thick; its
edge in cross section is slightly wavy or smooth. The exine
at the edge of the pores thickens from 1.5μ of the mesocol-
pium to about $3.0\text{-}3.5\mu$. Heimsch (1940) describes the exine
as having "elevated portions between the pits . . ." which
"may be reticulate in certain grains, or they may be in
definite ridges or striations with the pits in all stages of
alignment or fusion."

The pollen grains of *Toxicodendron*, *Actinocheita*, and
Schinus are prolate spheroidal (length-width equals 1.01-
1.14) ; grains of *Metopium* are borderline between prolate
spheroidal and subprolate (1/w ratio $=$ 1.14-1.33). Grains
of *Rhus sensu stricto* are subprolate. All have long polar
axes. (See Table 3).

Figures 1-8 show photomicrographs of anacardiaceous
grains. Four views of each sample grain are shown:
(a) plane surface view (Figs. 1-2) showing sculpturing,
(b) longitudinal, equatorial view through costae trans-
versales (Figs. 3-4) showing longitudinal section of a col-
pus, (c) median optical (Figs. 5-6) view showing section
of the exine, and (d) view through the pore (Figs. 7-8)
from the inside (lower surface). Surface sculpturing in
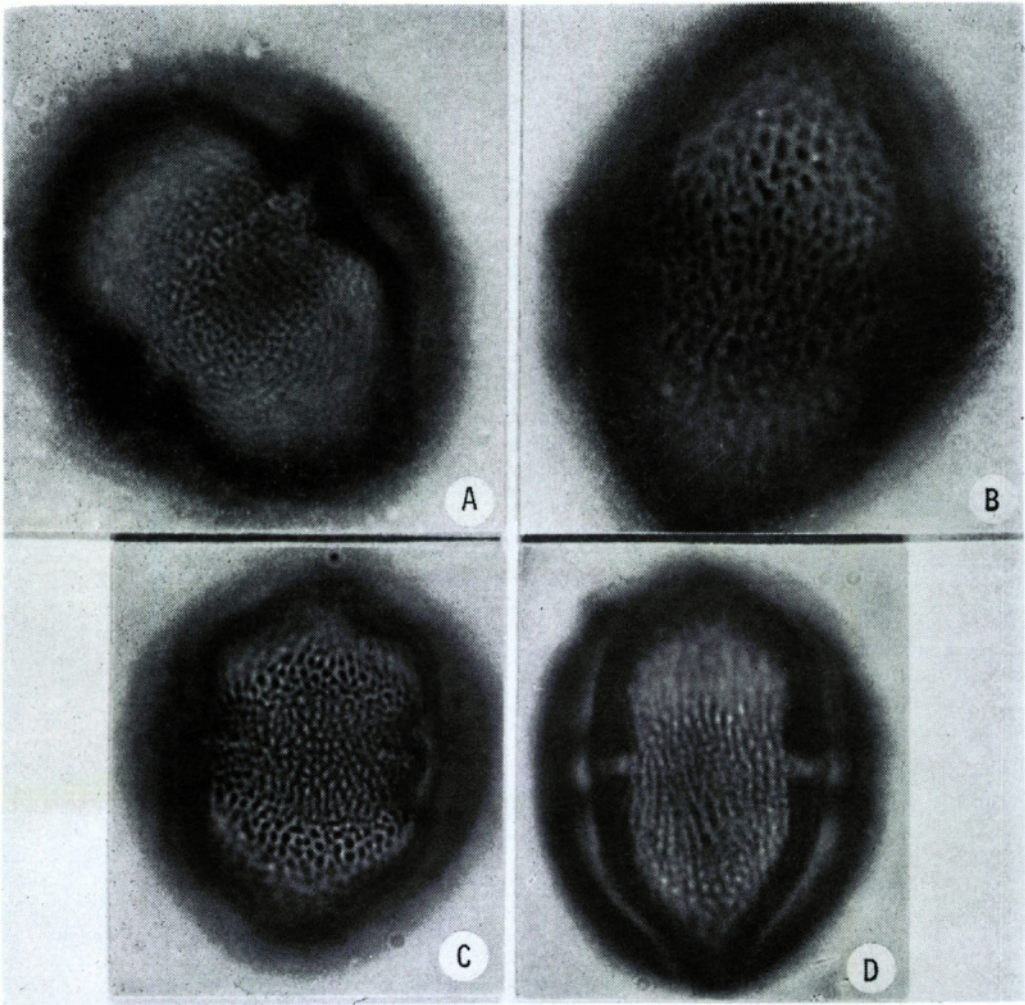
Fig. 1. Anacardiaceous pollen. Surface sculpturing of grains, × 875. A, *Rhus coriaria*. B, *R. copallina* var. *copallina*. C, *Toxicodendron radicans* subsp. *negundo*. D, *T. radicans* subsp. *orientale*.

all grains resembles the surface of a peach pit, seen especially clearly in *Rhus copallina*. (See Fig. 1).

There are few differences among the pollen grains studied which might be useful in classification, except for size (See Table 3). All have similar "peach-pit" sculpturing on the surface. In *Rhus copallina* and *R. glabra* the internal ribs (costae) tend to be more tapering toward the poles of the grain than they do in *R. coriaria* and *R. typhina*, but these differences are only a matter of degree. *Toxicodendron rydbergii* has ribs which arch more broadly toward the poles than do those of other members of the genus which
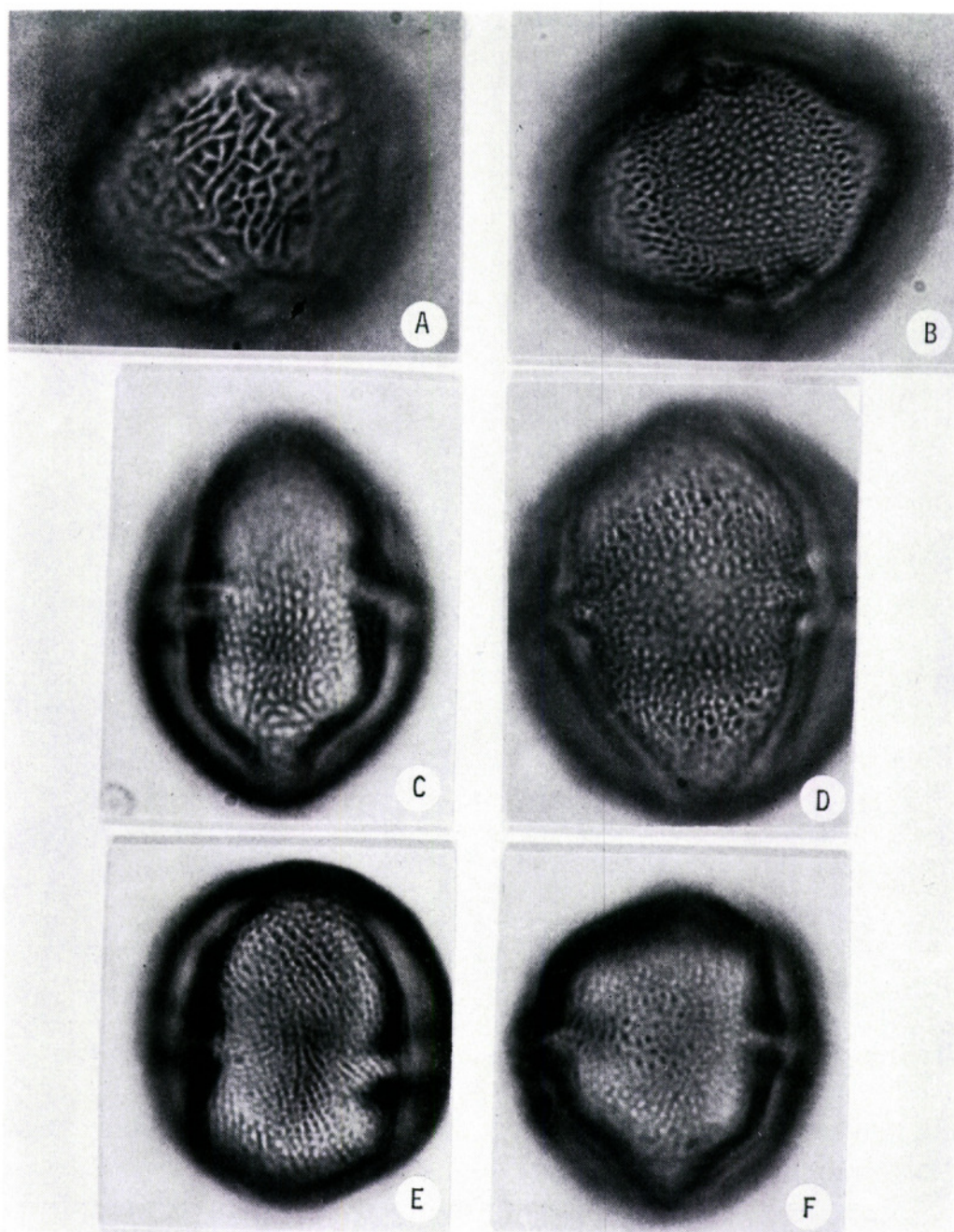
Fig. 2. Anacardiaceous pollen. Surface sculpturing of grains,
× 875. A, *Toxicodendron diversilobum*, aberrant grain. B, *T. diver-
silobum*, normal grain. C, *T. toxicarium* from Florida. D, *T. tricho-
carpum*. E, *T. rydbergii*. F, *Actinocheita filicina*.
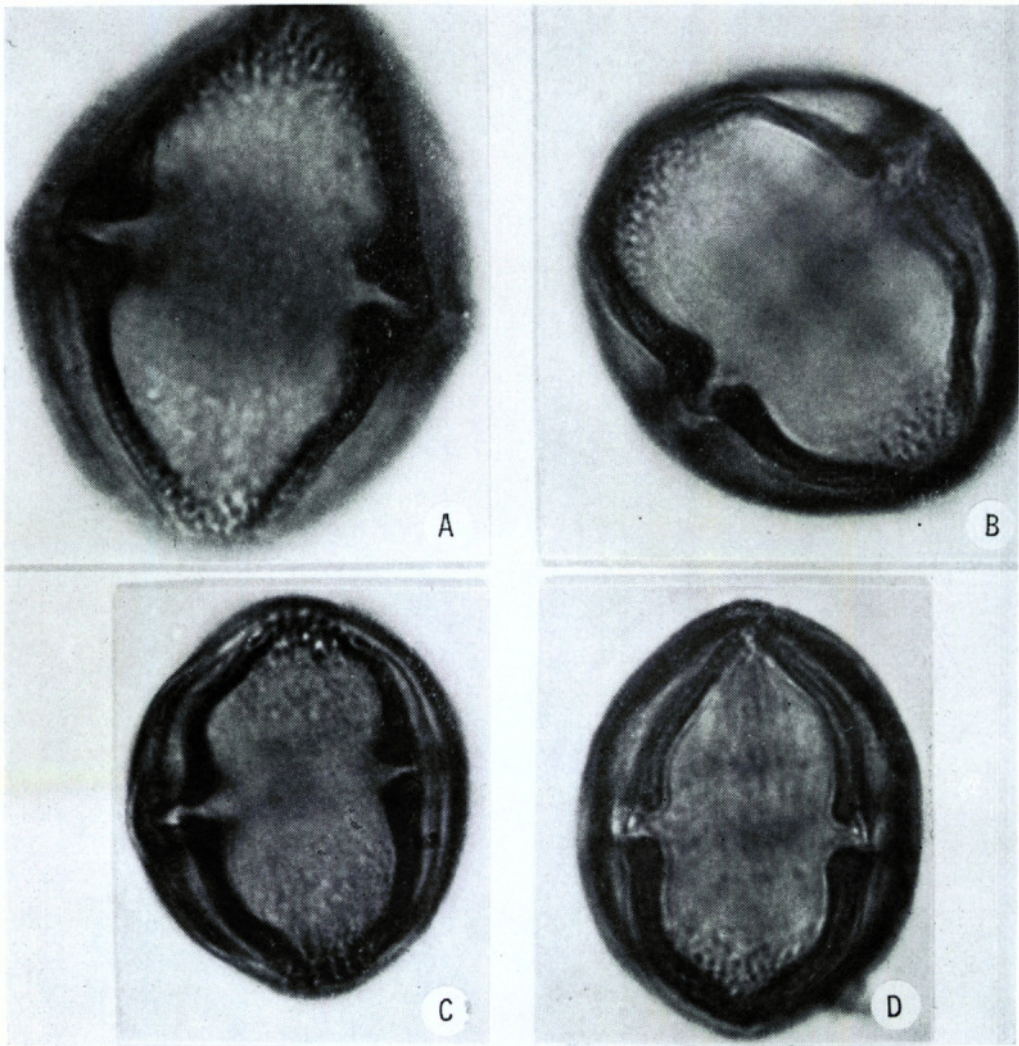
Fig. 3. Anacardiaceous pollen. Section through lateral pores showing costae transversales, × 875. A, *Rhus copallina* var. *copallina*. B, *R. coriaria*. C, *Toxicodendron radicans* subsp. *radicans*. D, *T. radicans* subsp. *orientale*.

were examined. The ribs of *Metopium* appear to arch considerably less (i.e.. more angularly) than those of other genera studied.

A major difference in size is noted between grains of *Rhus* and *Toxicodendron*, yet there remains a consistency within each group. The mean length of the *Rhus* grains studied here is 39.11μ, whereas that for *Toxicodendron* is 26.6μ; among 285 grains which were measured, only three had lengths which overlapped the range of grain size in
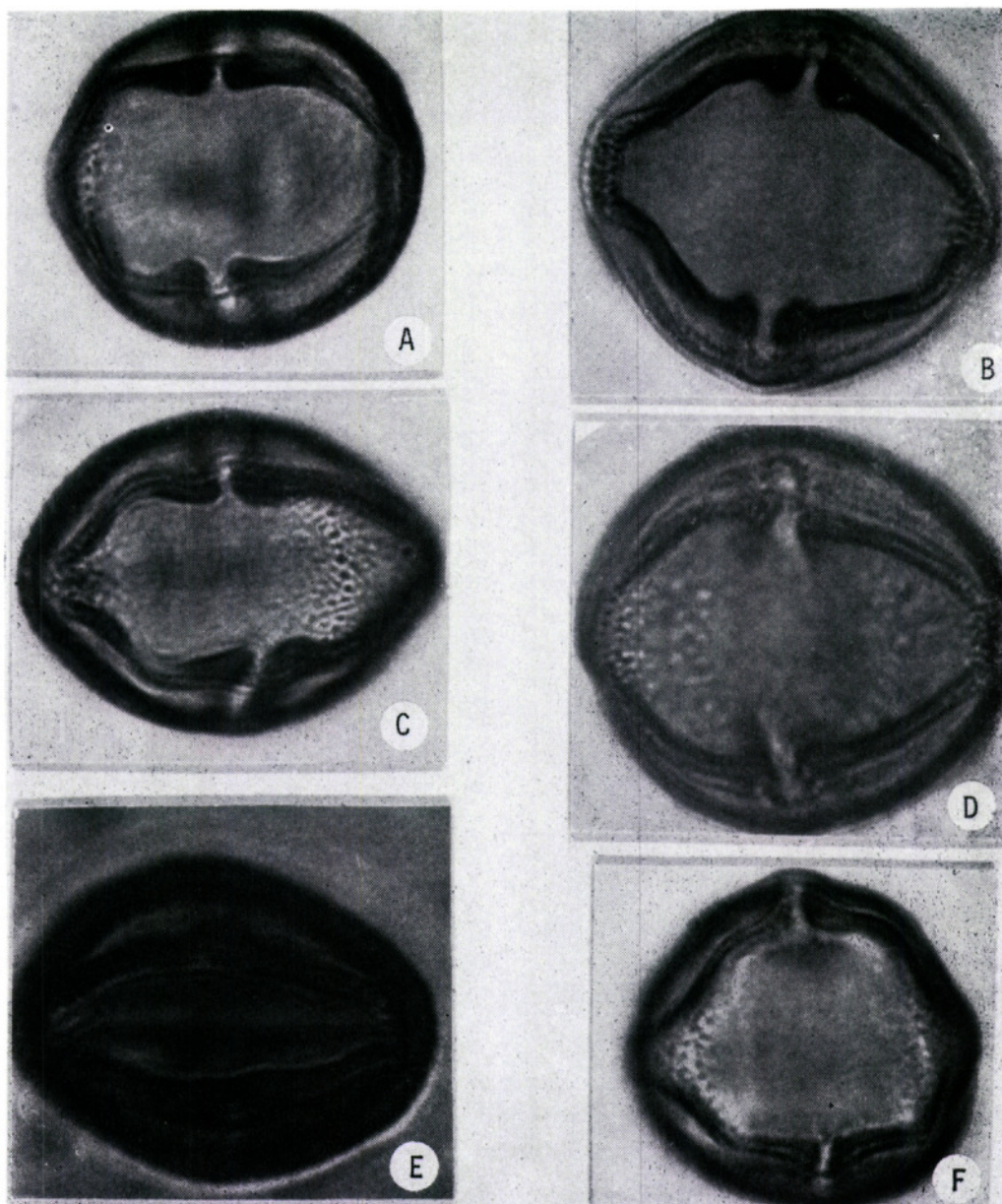
Fig. 4. Anacardiaceous pollen. Section through lateral pore showing costae transversales, × 875. A, *Toxicodendron rydbergii*. B, *T. diversilobum*. C, *T. toxicarium*. D, *T. trichocarpum*. E, *Metopium toxiferum*. F, *Actinocheita filicina*.
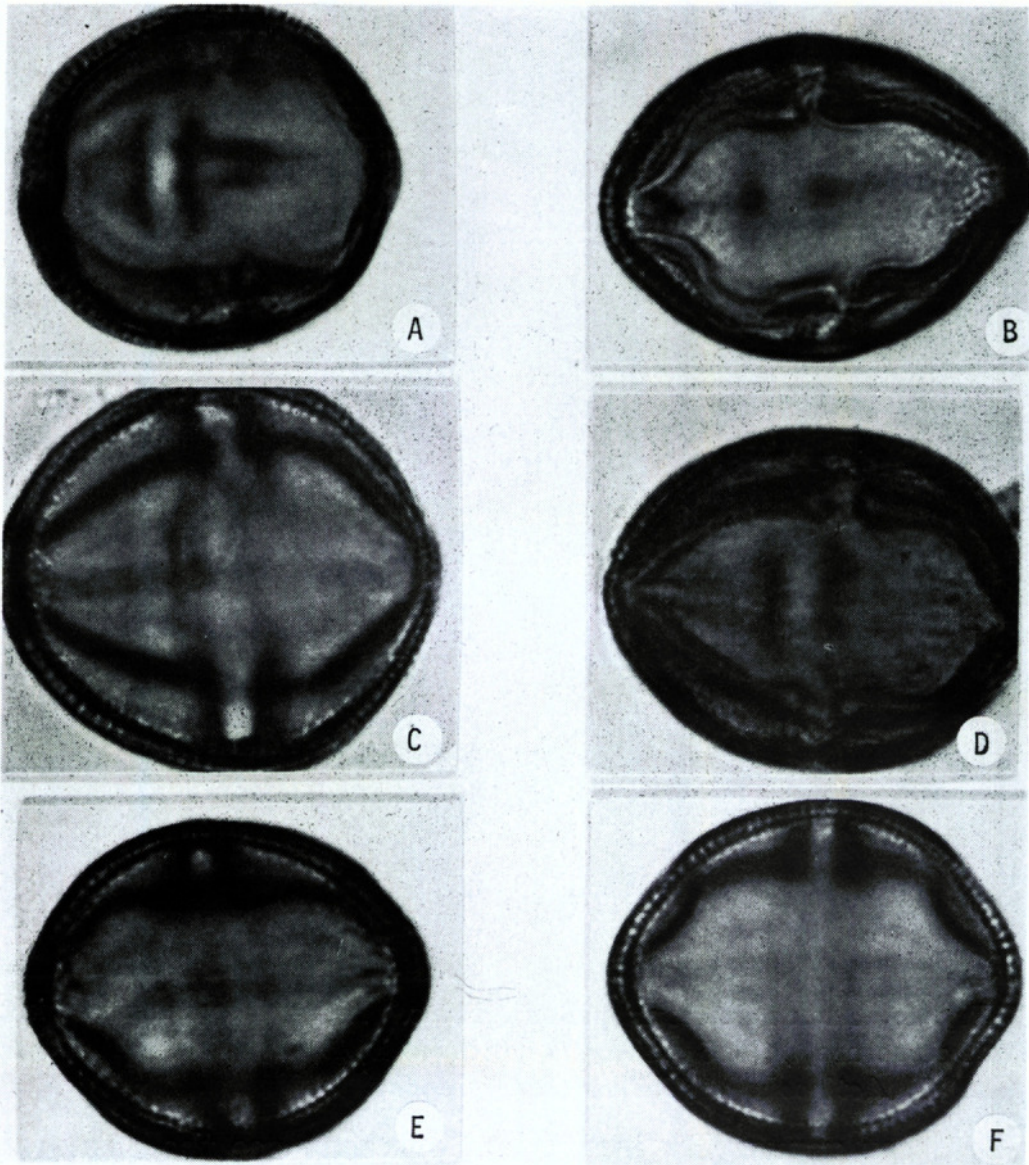
Fig. 5. Anacardiaceous pollen grains. Median section showing wall structure, × 875. A, *Toxicodendron rydbergii*. B, *T. toxicarium* from Florida. C, *T. trichocarpum*. D, *T. radicans* subsp. *orientale*. E, *T. radicans* subsp. *radicans*. F, *T. radicans* subsp. *negundo*.
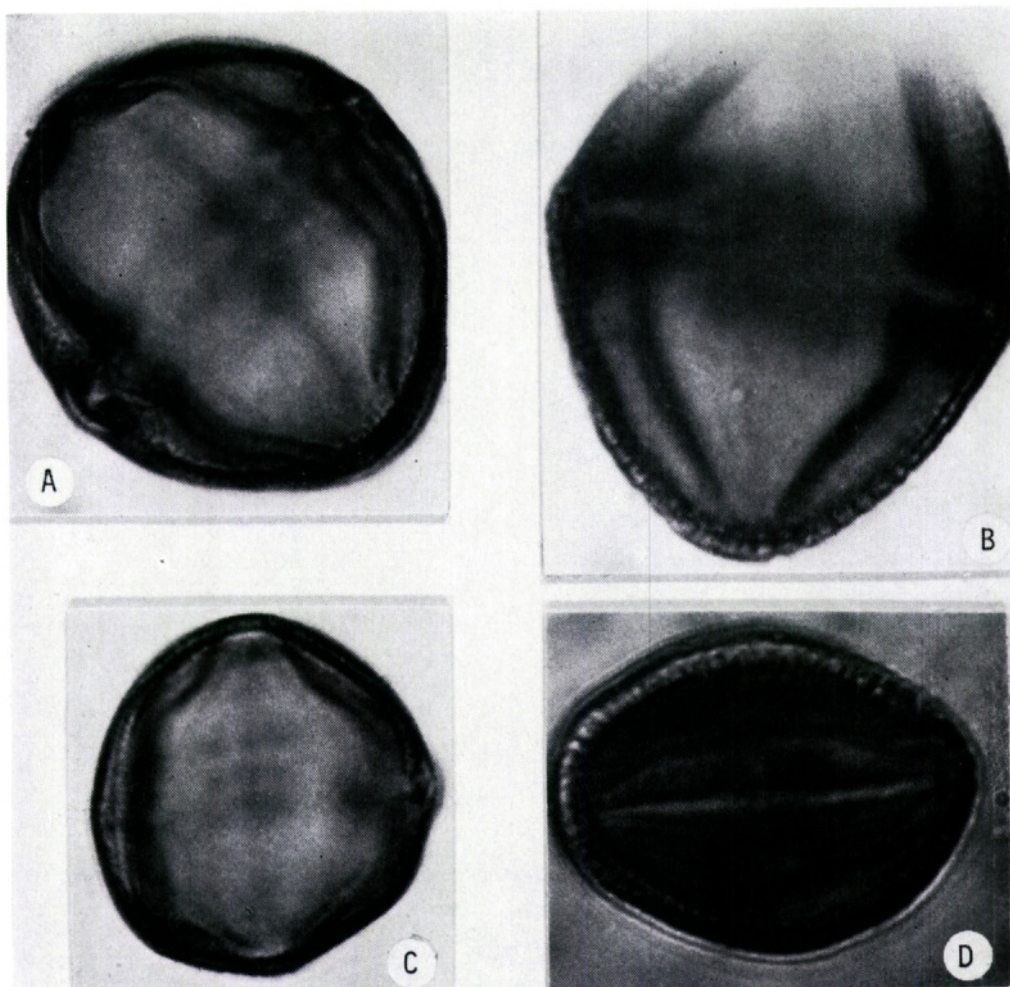
Fig. 6. Anacardiaceous pollen grains. Median section showing wall structure, × 875. A, *Rhus coriaria*. B, *R. copallina* var. *copallina*. C, *Actinocheita filicina*. D, *Metopium toxiferum*.

the other genus. By inspection, one may see the clear-cut separation of the samples. Likewise, the mean width of *Rhus* grains studied is 31.71μ whereas that for *Toxicodendron* is 22.84μ. Here 18 grains overlapped the range of widths, so that the separation, though marked, is not so clear-cut as that for the lengths. Kuprianova (1965) found a specimen of *Rhus semialata* (= *R. javanica*) for which the pollen polar axis was 32.4-43.2μ and the equatorial diameter was 25.2-41.8μ as contrasted with *Toxicodendron orientale* (= *T. radicans* subsp. *orientale*) whose length through the polar axis was 28.8-29.3μ and equatorial diameter was 21.6-28.8μ. Wodehouse (1932) measured *Rhus*
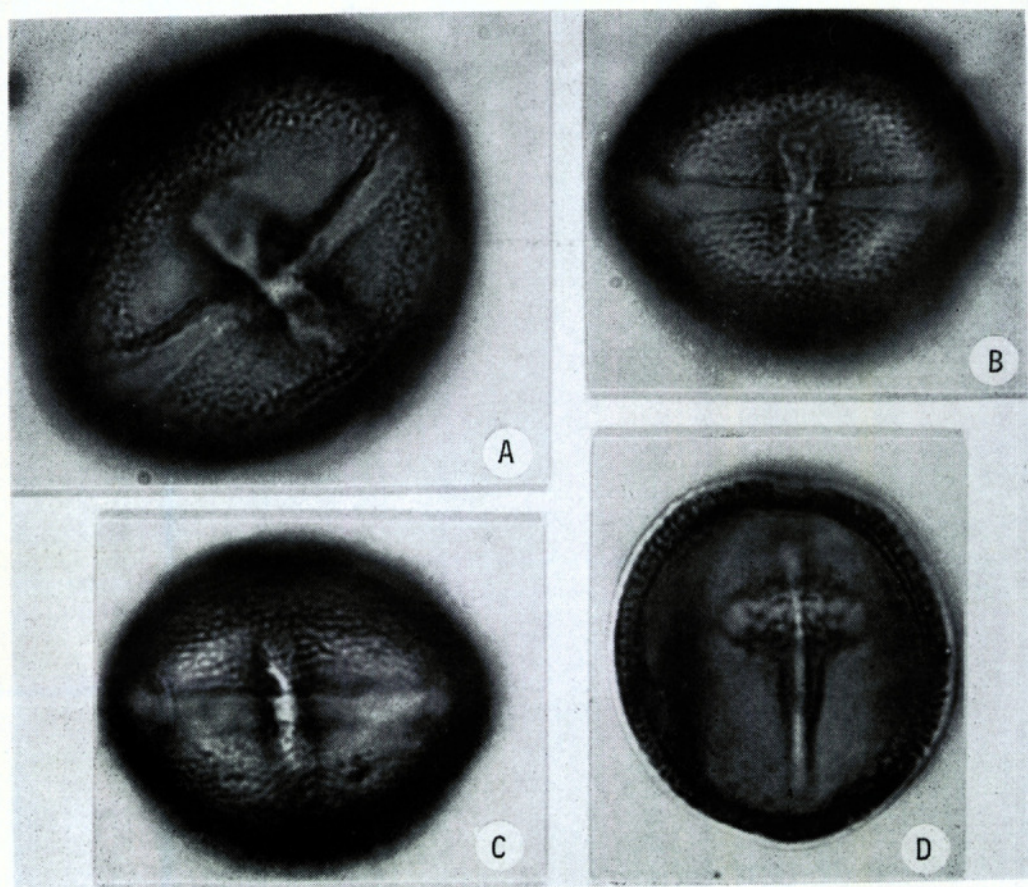
Fig. 7.   Anacardiaceous pollen grains. Surface plan view showing pore and colpus, × 875. A, *Rhus coriaria*. B, *Toxicodendron radicans* subsp. *negundo*. C, *T. radicans* subsp. *radicans*. D, *T. rydbergii*.

typhina pollen length as 37.5-39μ and *R. glabra* as 35.3-40μ. Erdtman (1934) measured *R. typhina* pollen as having length 53μ × width 35μ. Kuprianova (ibid.) further describes *Rhus* pollen as having a slit-type pore vs. the oblong pore of *Toxicodendron*; she also calls the sculpturing of *Toxicodendron* grains more patterned (streaming) than those of *Rhus* ("barely noticeable streaming sculpture"), i.e., there are more likely to be rows of markings.

The fact that these differences are significant is of importance to the question of whether or not *Toxicodendron* should be segregated from *Rhus* as a separate genus. The pollen size is certainly not the major factor in settling this controversy, but it lends some weight to the argument that the two should be recognized as separate genera.
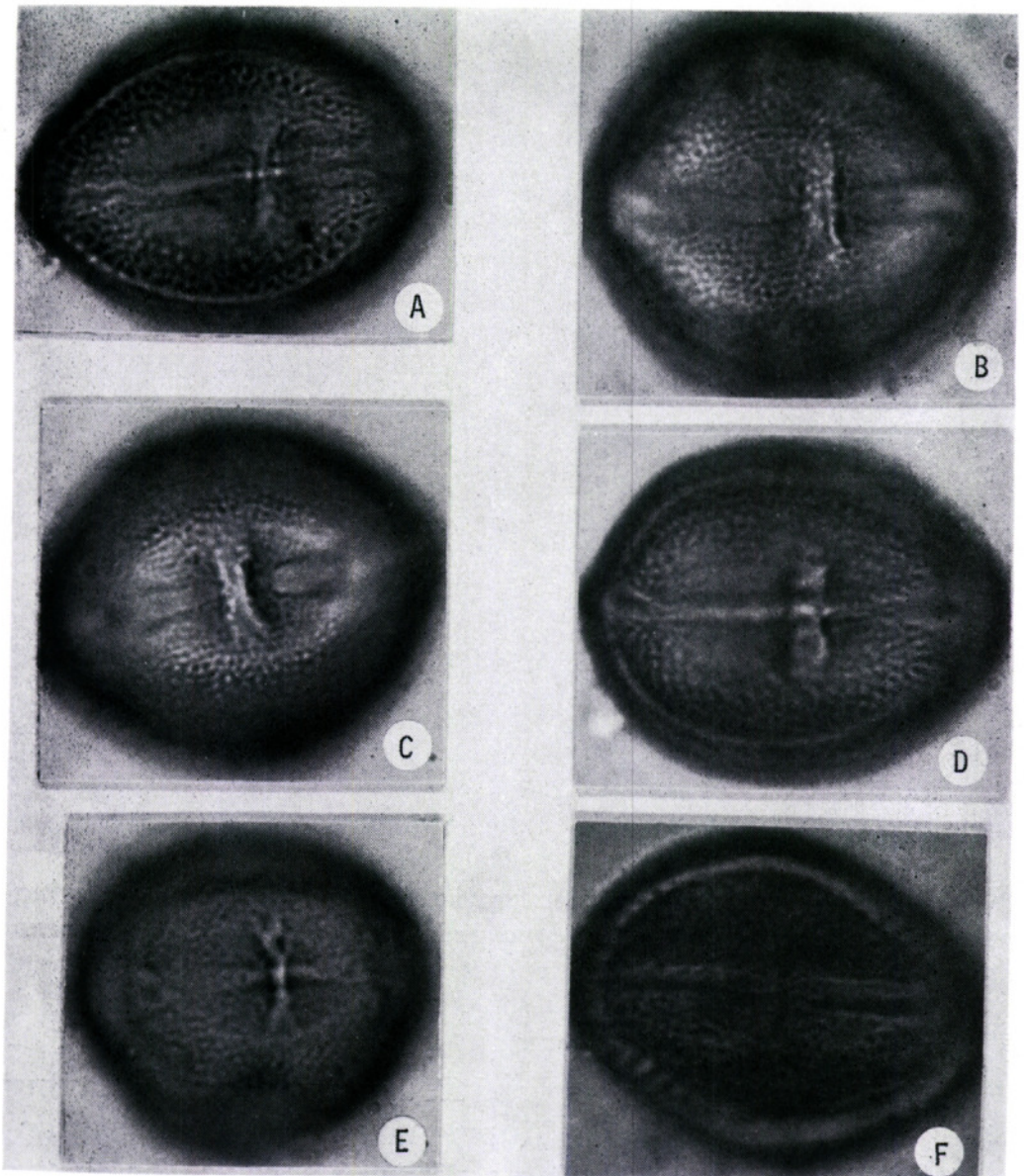
Fig. 8. Anacardiaceous pollen grains. Surface plan view showing pore and colpus. × 875. A, *Toxicodendron toxicarium* from Florida. B, *T. trichocarpum*. C, *T. diversilobum*. D, *T. radicans* subsp. *orientale*. E, *Actinocheita filicina*. F, *Metopium toxiferum*.

Where pollen grains of two different populations of the same taxon were measured (e.g., *Toxicodendron toxicarium*, and *T. radicans* subsp. *radicans*), there was close agreement in size between the two populations. The grains of *T. diversilobum*, *T. vernix*, *T. trichocarpum*, *T. borneense*, *T. radicans* subsp. *orientale*, and *T. rydbergii* are larger

(longer and broader) than grains of other *Toxicodendron* taxa. The smallest grains to be measured were found in *Schinus molle*; these grains are also most nearly spherical (l/w ratio = 1.0). Ikuse (1954) found significantly larger grains of *Rhus ambigua* (= *T. radicans* subsp. *orientale*) than are reported here: $28.5\text{-}32.5\mu \times 27.5\text{-}31\mu$. But Ikuse used glycerin jelly as a mounting medium rather than Canada balsam, claiming that the glycerin jelly caused the grains to swell so that the surface markings might be studied more favorably.

There have been few *Rhus* or *Toxicodendron* pollen grains found in the fossil record. Wodehouse (1932) discovered some *Rhus* pollen in the middle Eocene Green River formation in Wyoming. These grains are very similar to those of *R. typhina* and *R. glabra*, the latter of which grows in that region today. Traverse (1955) described a new species, *Rhus carbogena*, based solely on pollen grains found in the Brandon lignites of Forestdale, Rutland County, Vermont. These were Tertiary (Oligocene?) in age and again resemble those of *R. typhina* and *R. glabra*, both of which currently inhabit that region of Vermont. They are smaller than grains of either extant species, but fall within the range of *Rhus* pollen sizes reported here.

FOSSILS OF TOXICODENDRON

As with most taxa, the fossil record for the poison-ivy complex is incomplete. A study of some fossils from this group of plants and the taxa they represent gives some indication of the past history of the group. The discussion will center around plants listed in Fossilium Catalogus (Edwards and Wonnacott, 1935) and more recently described fossil species. Each will be discussed, evaluated as a member of this complex, and its affinities determined, where possible.

Rhus and its relatives are found frequently in the fossil state in various periods of the Tertiary (Saporta, 1888).

They are never represented by more than detached leaflets and are therefore difficult to determine accurately. The fossils suspected of belonging to this group, or for which discussion is relevant, will be discussed.

Rhus quercifolia Goeppert (1855). Fig. 9.

This name is probably synonymous with *R. aegopodiifolia* Goeppert, Fig. 9. The fossil specimens come from the Tertiary of Bohemia and southwestern Russia (Kryshtofovich, 1914). The material illustrated does not resemble anything in the modern poison-ivy complex, especially that which has previously been called *Rhus quercifolia auct. pl.* and which is herein called *Toxicodendron toxicarium*. The palmate venation shown in Goeppert's illustration reveals five main veins with the lowest two leading to a pronounced lobe on each lateral leaflet, unlike present-day poison-ivy or poison-oak. Specimens which were presumably deposited in Breslau have not been located and are presumed to have been destroyed during World War II.[9]

Kräusel (1919), however, throws some light on the subject. He discusses Goeppert's plants (while citing his own name as author of the binomial) from Silesian collections by Perusch. His illustration (See Fig. 10) is more suggestive of Eastern poison-oak *(Toxicodendron toxicarium)* than is any illustration by Goeppert. The rounded lobes of the terminal leaflet very closely resemble those on leaves of modern Eastern poison-oak, as do the cuneate leaflet bases. The venation also agrees with patterns on modern leaves.

Kräusel felt that his fossil plant was not conspecific with the plant of North America. Until his specimens can be studied more thoroughly, one must consider this fossil as a doubtful member of the poison-ivy complex.

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[9]Personal communication from Dr. Bohnslav Fott, Head of Katedra Botaniky Prirodovedecke Fakulty University Karlovy, 1963.
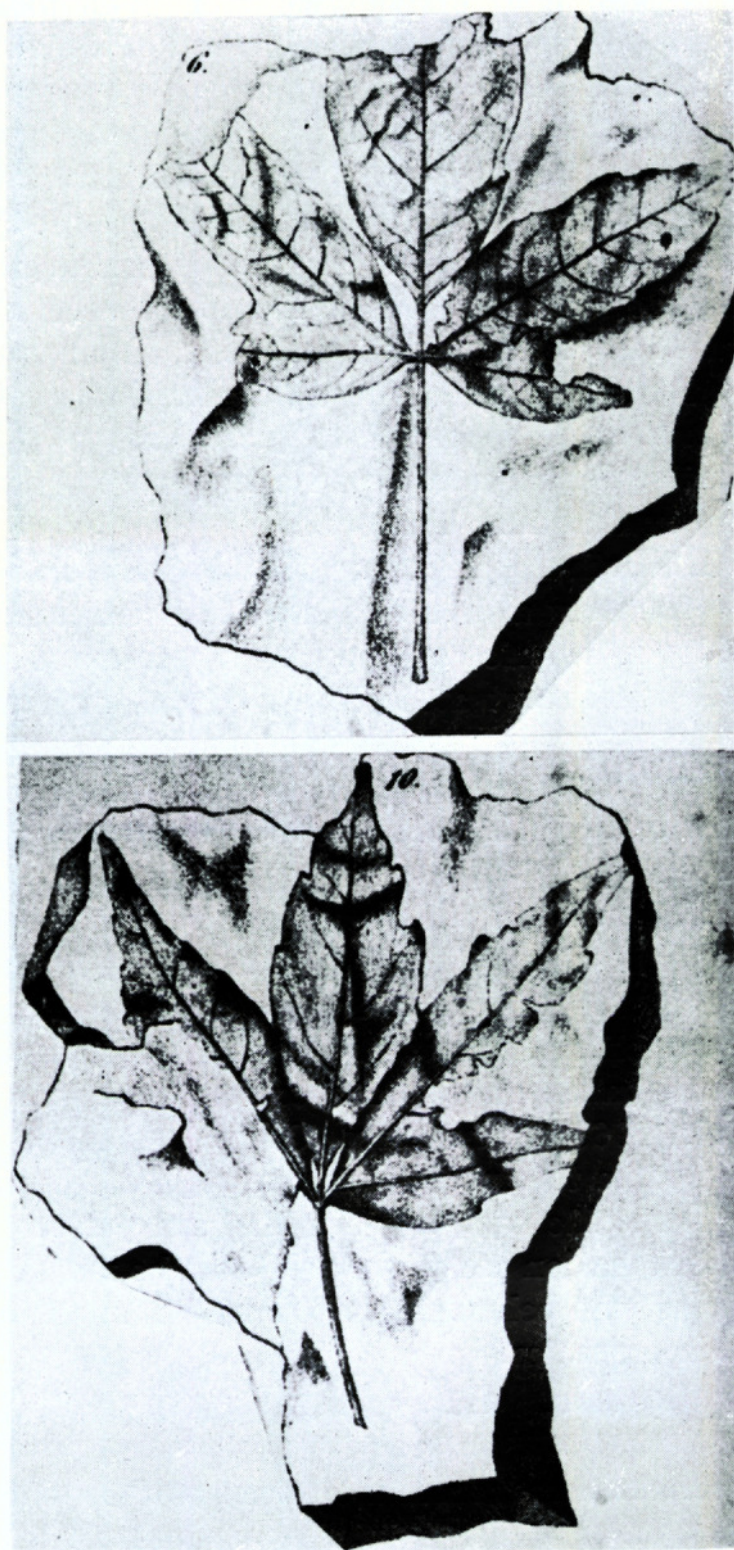
Fig. 9. Fossil species: *Rhus quercifolia* Goepp. (upper) and *R. aegopodiifolia* Goepp. (lower), (Goeppert, 1855).

There are a number of genera which presumably occupied the region of the Tethys Sea, several of which also extended to eastern Asia (e.g., *Liquidambar, Juglans, Salix,* and *Diospyros*). Some genera of these floras apparently vanished with the tectonic activity that was associated with the uplift of the Alps. The Pliocene vegetation of western Europe is distinguished by the occurrence of a large number of elements no longer a part of European vegetation, but identical with species now living in China, Japan, and North America (Seward, 1931). The close morphological link of *Rhus coriaria* of Europe and *R. michauxii* of the southeastern United States may be an example of plants in the *Rhus* complex that may have once had a range which included both North America and southern Europe. Section *Toxicodendron* may also have shared a distribution in Europe and North America at this time, represented by a fossil which Kräusel illustrated (Fig. 10), a plant now extinct in Europe, possibly as a result of mountain building. Current thinking among European paleobotanists, however, places *Rhus quercifolia* Goeppert in the fossil genus *Monopleura* (Aceraceae). Whether this plant is really the same one which Kräusel had under consideration is not certain.

The binomial *Rhus quercifolia* was listed in synonymy by Steudel (1821) for Eastern poison-oak, earlier than Goeppert's publication; but publication in synonymy does not constitute valid publication according to the Code (Lanjouw, *et al.*, 1966). Therefore, Goeppert's name is valid and is ascribable to him. Unless one regards the Goeppert fossil as conspecific with modern Eastern poison-oak, this binomial combination cannot be used for the modern plants, even by those who believe them to be *Rhus* species and not *Toxicodendron* species.

Rhus toxicodendroides Pilar (1883)

This specimen comes from the Miocene of Croatia. Pilar's plate shows but a single lanceolate acuminate leaf (leaflet?) that is irregularly dentate and slightly asymmetrical. He described it as recalling the form and venation of "*Rhus*

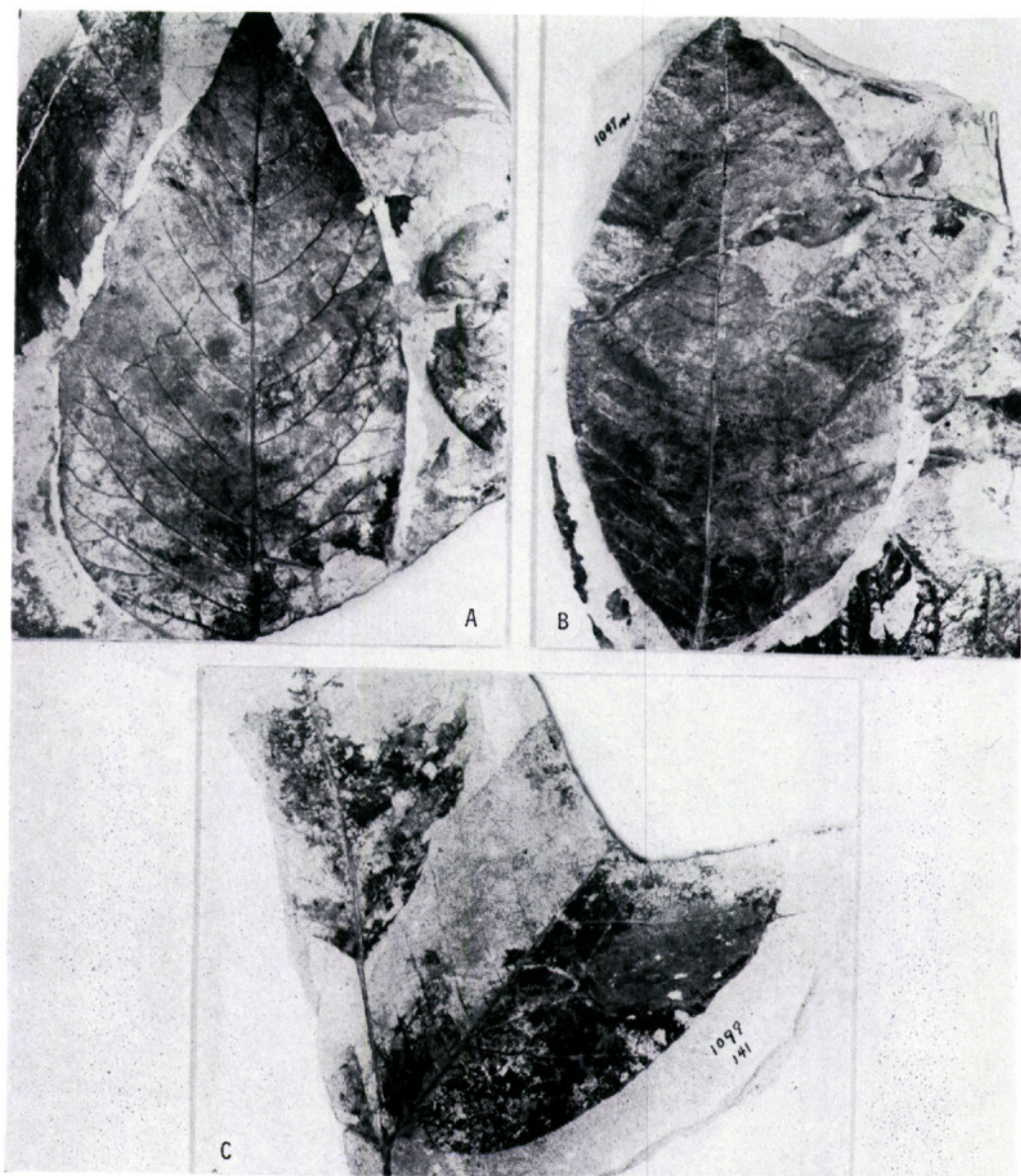Fig. 10. *Rhus quercifolia* Goepp. from specimens shown in Kräusel (1919).

Fig. 11. *Toxicodendron magnifolium* (MacGinitie) Gillis from the Weaverville flora at Redding Creek, California. Specimens at the University of California, Dept. of Paleontology. A, Holotype of *T. magnifolium*, based on *Rhus magnifolia*. Presumably the right lateral leaflet. B, Left lateral leaflet of *T. magnifolium*. C, Specimen showing three leaflets.
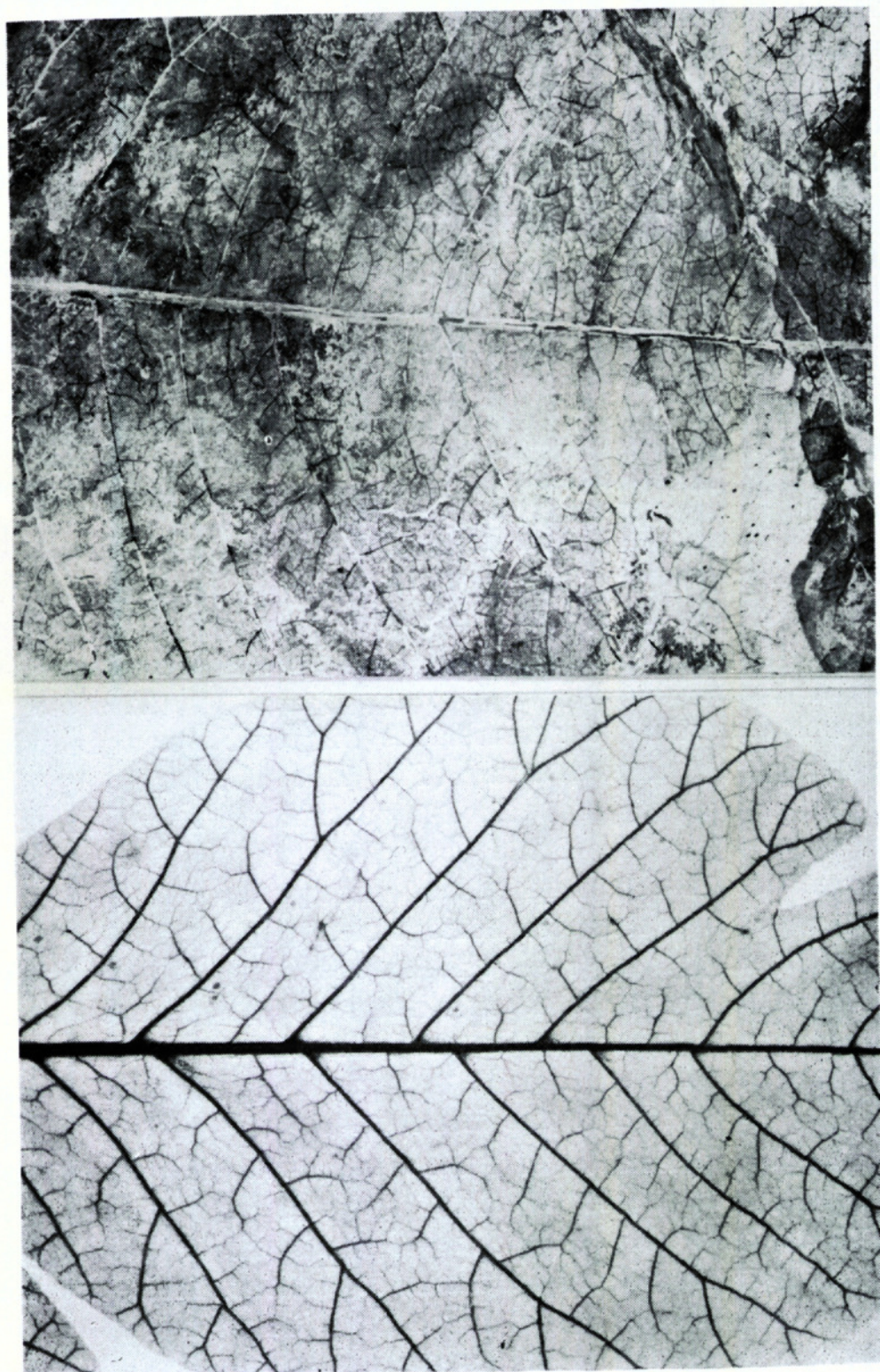
Fig. 12. Comparison of fossil and modern poison-ivy. Upper: Close-up view of venation pattern of *Toxicodendron magnifolium* (from holotype). Lower: Close-up view of venation pattern of *T. radicans* subsp. *orientale* (from Gillis 4691, Japan).

Toxicodendron L. of North America." It probably is not related to any extant *Toxicodendron* and is difficult to place even in the Anacardiaceae. The type cannot be found at the Geological Paleontological Museum at Zagreb where Pilar's specimens are located. although other *Rhus* species described at the same time are there.[10]

Toxicodendron magnifolium (MacGinitie) Gillis, comb. nov. Fig. 11.

Rhus magnifolia MacGinitie, Publ. Carnegie Inst. Wash. 465: 144. 1937. Type: *Harry D. MacGinitie s.n.*, California, Trinity County, Oligocene beds at Redding Creek; Weaverville flora. (University of California, Dept. of Paleontology, holotype; several isotypes).

This fossil plant shares with modern poison-ivy (especially the group including *Toxicodendron radicans* subsp. *radicans*, *hispidum*, and *orientale*) several morphological characteristics. Dr. MacGinitie noted the close resemblance of the fossil to leaves of Japanese poison-ivy (*T. radicans* subsp. *orientale*), a resemblance that is closer than with North American taxa today (Fig. 12). The fossil suggests a link between Asiatic poison-ivy and North American populations. Aside from the possibility of long-distance dispersal as a mechanism of accounting for poison-ivies in Asia and North America, some ancient population may have existed continuous across the Alaskan-Siberian land bridge during the Paleocene-Eocene interval. There are unfortunately no fossils from the northern Orient, the Aleutians, Alaska, or western Canada to sustain the hypothesis that the plants really had this distribution.

The fossil associates of *Toxicodendron magnifolium (Ilex, Nyssa, Juglans,* and *Taxodium)* are similar to poison-ivy's present-day associates in the southeastern United States, and it may actually represent an organism whose ecological requirements are little changed now. The fossil specimen,

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[10]Personal communication from Dr. Ivan Crnolatac, Curator of the Geological Paleontological Museum, Zagreb, Jugoslavia, 1962.

however, was found in a region not presently inhabited by poison-ivy, but rather by western poison-oak, *T. diversilobum*. Because of the great separation in time and distance between the fossil and modern plants, I choose to recognize the taxon named by MacGinitie as distinct from the modern plants, but nevertheless to transfer the species from *Rhus* to *Toxicodendron* to place it with the toxic sumacs.

Toxicodendron lobatum, the western poison-oak, has been found also in fossil forms.

Rhus diversiloba first reported by Potbury (1932) in Pleistocene deposits at San Bruno, California. Her specimens are seeds with obtuse ends and irregular nodules 5.5 × 3 mm. (Univ. Cal. Coll. Pal. Bot. Plesiotype 437). The modern seed measures 5-6 × 3.4-4 mm. Fruit characters of taxonomic significance are all found in the evanescent exocarp which is not available in the fossils. Wood fragments were reported by Mason and Chaney (1933) from Carpinteria, California, in asphalt sand. The accompanying fossil vegetation was a Monterey pine forest. Such forests are now found 200 miles farther north, suggesting that the plant grew during a glacial (vs. interglacial) epoch when the lower latitudes were colder than they are today. The wood fragments are rare. Both those records were too fragmentary to determine the materials with certainty.

More seeds were reported by Mason (1934) in the Tomales formation of the Pleistocene near Inverness Bay (Mason's locality 609). The soft mesocarp and exocarp were lost, but the hard endocarp persisted (Univ. Cal. Coll. Pal. Bot. Plesiotype 514). Other plants found with it (*Rubus spectabilis, Symphoricarpos, Pseudotsuga,* and *Acer macrophyllum*) are frequent associates of *T. diversilobum* today in northern California, Oregon, and Washington. Based on fossil invertebrates also present, this plant must have grown during an interstadial period warmer than today, in a vegetation related to the closed-cone pine forests now discontinuously relict along the coast (Mason, 1934).
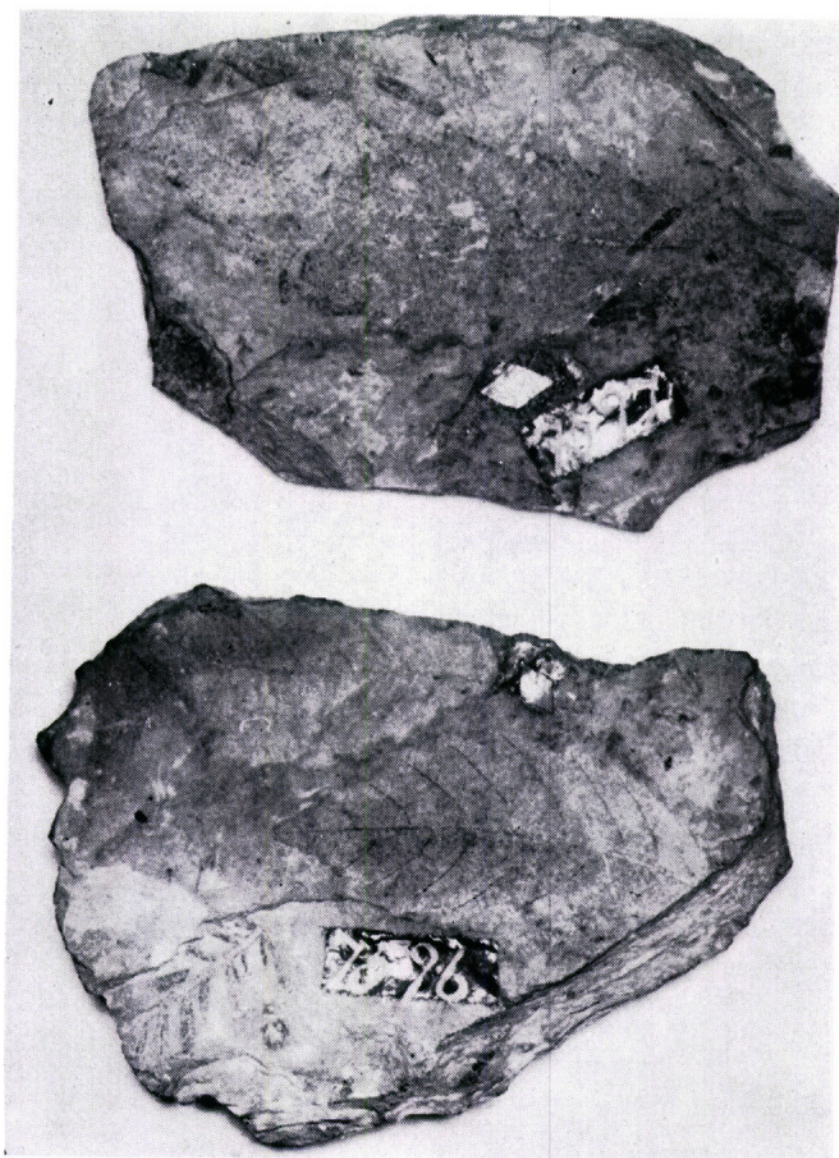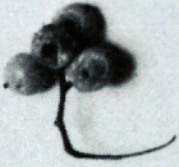
Fig. 13. *Quercus applegatei* Knowlton (1900) (from type collection, United States National Museum).

Fig. 14. Archeological remains. Upper: *Toxicodendron rydbergii*, from Mesa Verde, ca. A.D. 1200 (right), from Wexford County, Michigan, 1961, for comparison (left). Lower: Roots and stems from cliff dwellings at Mesa Verde National Park, Colorado (specimens courtesy of the Wetherill Archaeological Project, Douglas Osborne, Director), see text.

Michigan poison-ivy
A.D. 1961
seed cluster

Mesa Verde poison-ivy
about A.D. 1200
seed cluster 35821/709

Poison-ivy - A.D. 1200
Mesa Verde National Park, Colo.
34251/709

Quercus applegatei Knowlton (1900). Fig. 13.

This species has been mentioned as a possible Anacardi-
aceous plant related to *Toxicodendron diversilobum*. A
careful examination was made of specimens from the type
collection (at the Department of Paleobiology, Smithsonian
Institution) from the Tertiary Ashland beds in Oregon.
Most specimens are not Anacardiaceae and probably are
Quercus (except for one which appeared to be neither
Anacardiaceae nor *Quercus*). The leaflet margins of the
fossil appear to be bristle-tipped; the lobes are somewhat
pointed; there is no evidence that the leaves were compound.
This species therefore cannot be recognized to be a *Rhus*,
i.e., *Rhus applegatei* (Knowlton) Chaney ex Potbury
(1932).

Archeological Remains. Fig. 14. Special note is made of a
unique group of specimens which are barely fossils in the
strictest sense. They are, however, a group of fruits and
stem and root fragments estimated by the Wetherell Project
using radiocarbon methods to be about 700 years old, found
in adobe dwellings at Mesa Verde National Park, Colorado.
The dry desert air and freedom from disturbance have
permitted complete preservation of the plant fragments,
so that they are still recognizable today. Poison-ivy plant
parts are known to be used by modern Indian tribes in
various ceremonial ways, customs originating perhaps as
far back as 700 years ago.

Several of the stem and root fragments were examined
by Dr. Charles Heimsch of Miami University, and deter-
mined possibly to be poison-ivy, based on anatomical detail.
Most of them, however, were decidedly not poison-ivy. The

Fig. 15. Flowering *Toxicodendron radicans* subsp. *radicans*, from
south Florida (Drawn by Priscilla Fawcett). A, Habit sketch, × 0.33.
B, Female flower, × 3.3. C, Male flower, × 3.3. D, Male flower,
× 3.3. E, Female flower, × 3.3. F, Ultimate branch of inflorescence,
× 3.3. G, Longisection of female flower, × 3.3. H, I, Floral diagrams
of alternate forms of aestivation of female flower. J, K, Floral
diagrams of alternate forms of aestivation of male flower.
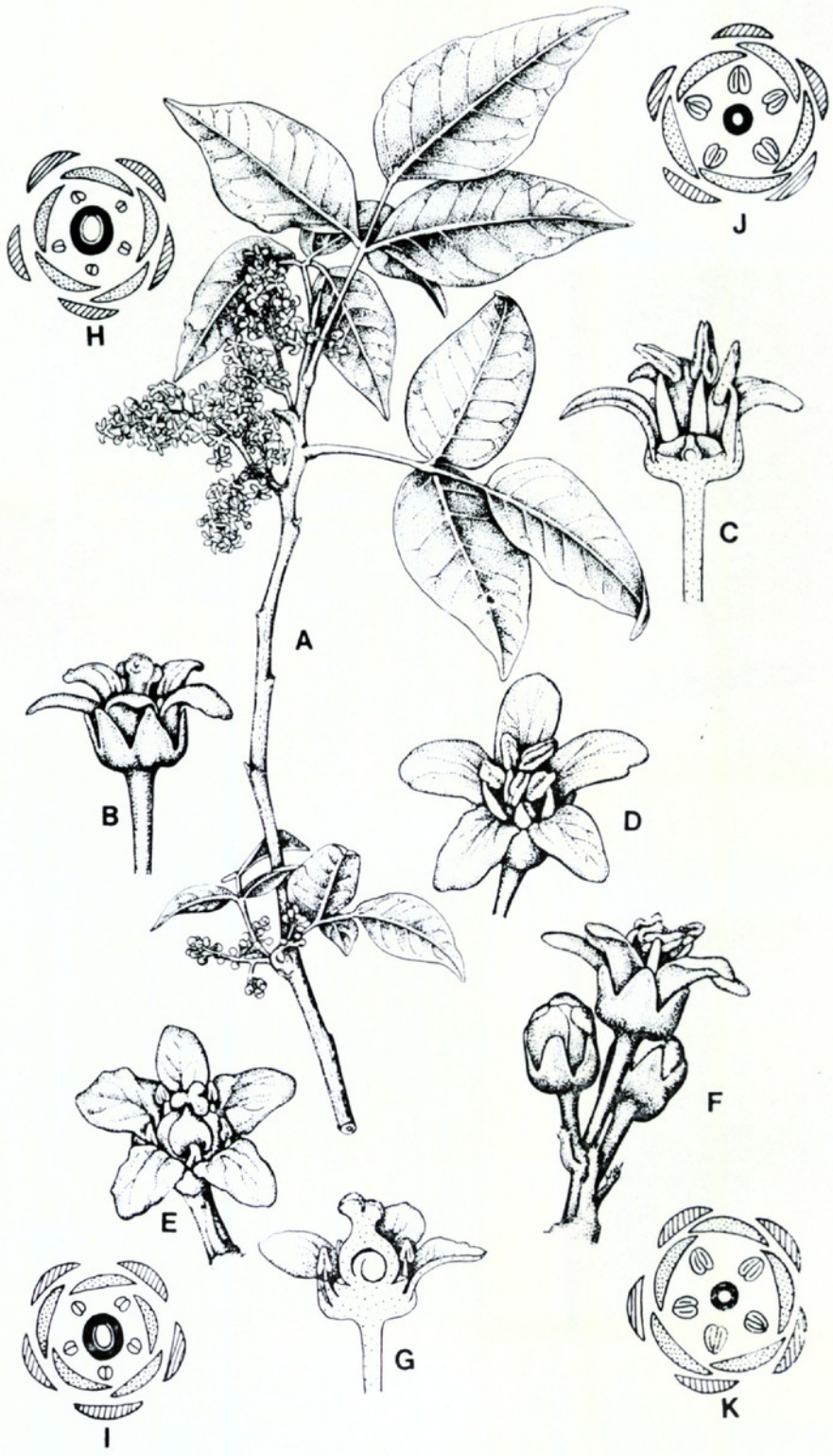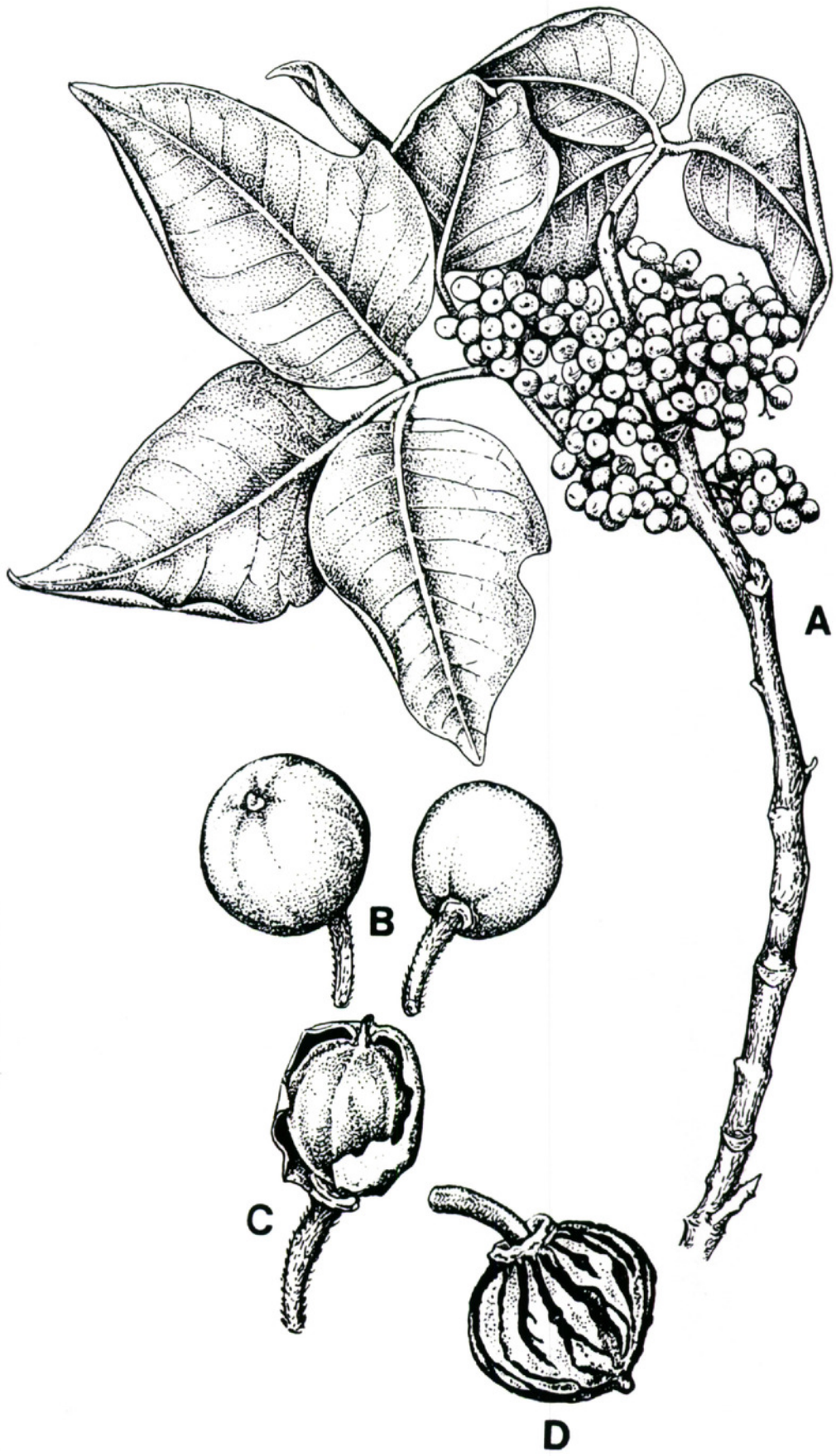
fruits, on the other hand, are unquestionably *Toxicodendron rydbergii*, a taxon which still grows in that vicinity of Colorado.

FLOWER AND FRUIT MORPHOLOGY

Inflorescence. Figs. 15-16.

The flowers of the genus *Toxicodendron* are borne in paniculate or racemose thyrses in the axils of leaves. The ultimate clusters are determinate, of three or four flowers each. The inflorescences are variable in number of flowers; when large, the clusters are pendulous. In fruiting condition, the inflorescence of a few taxa may be erect in small, tight clusters, but will become pendulous in those taxa wherein the inflorescence is large and loose, bending under the weight of the developing fruits. Lignification of the fruiting rachis enables even a heavy cluster to stand erect in some taxa (*T. rydbergii* and *T. toxicarium*). The bracts of the inflorescence are lanceolate and deciduous. Inflorescences vary from a few cm in length in *T. rydbergii* to over 40 cm in *T. nodosum*.

Flowers. Figs. 15, 17-19.

The entire genus has relatively small, pentamerous flowers which differ more markedly between the sexes of a single species than they do within the same sex throughout the genus. That is to say that one cannot use the flowers for key taxonomic characters except for separating section *Toxicodendron* from *Venenata* on stamen characters.[11] Miller and Martyn (1807) maintained that the male flowers of poison-ivy smelled like lily-of-the-valley, and that the female flowers bore no scent, but I find no evidence to substantiate this.

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[11]See discussion of the androecium.

Fig. 16. Fruiting *Toxicodendron radicans* subsp. *radicans*, from south Florida (Drawn by Priscilla Fawcett). A, Habit sketch, × 0.75. B, Intact fruits, × 5.5. C, Fruit with portion of exocarp removed, × 5.5. D, Fruit with exocarp removed, showing striated endocarp; the form of the usual propagule, × 5.5.
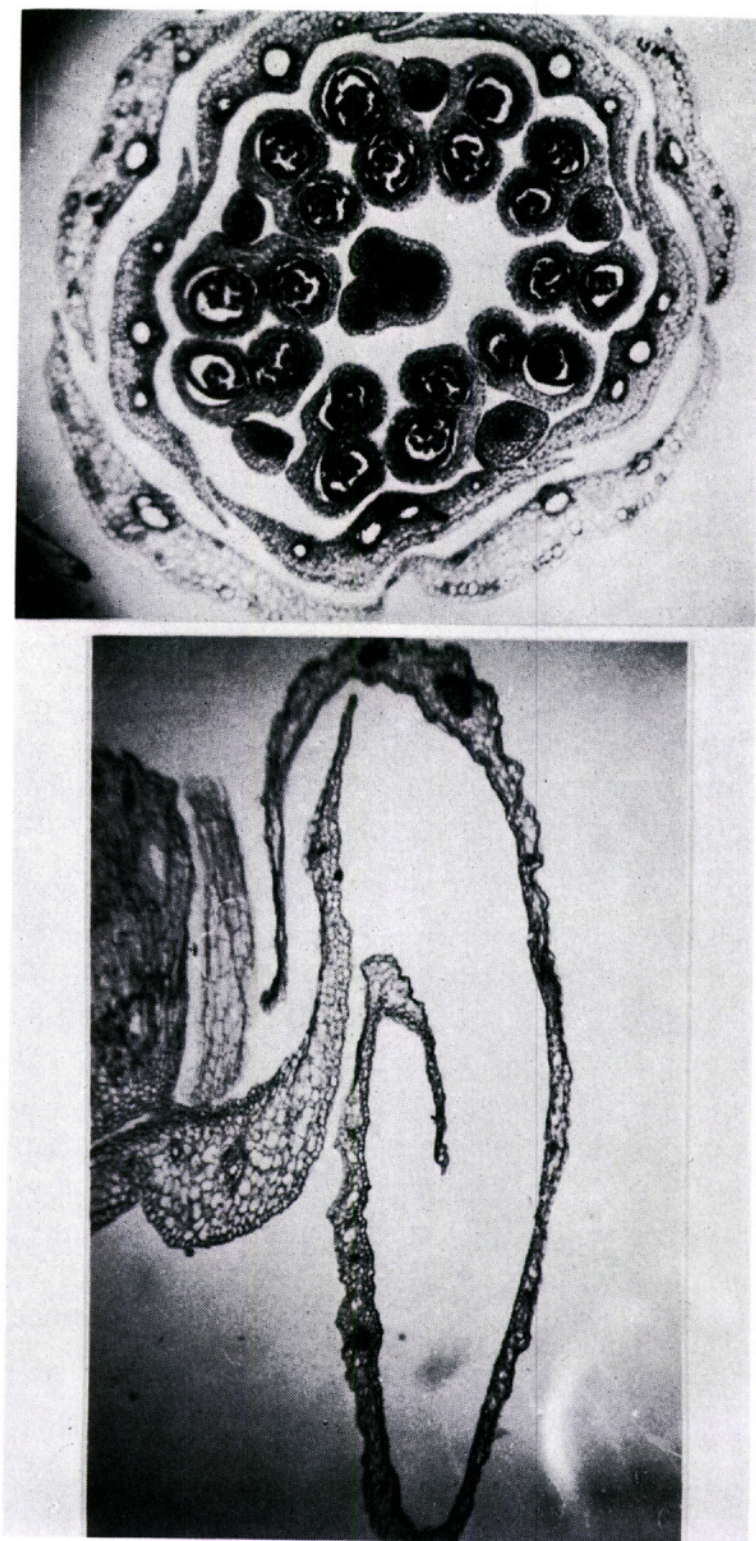
Fig. 17. Flowers of *Toxicodendron radicans*. Upper: Cross section of subsp. *negundo*, taken just below midpoint of flower, $\times$ 30. Lower: Longisection of subsp. *orientale*, showing perianth parts (note the long reflexed petal), $\times$ 80.
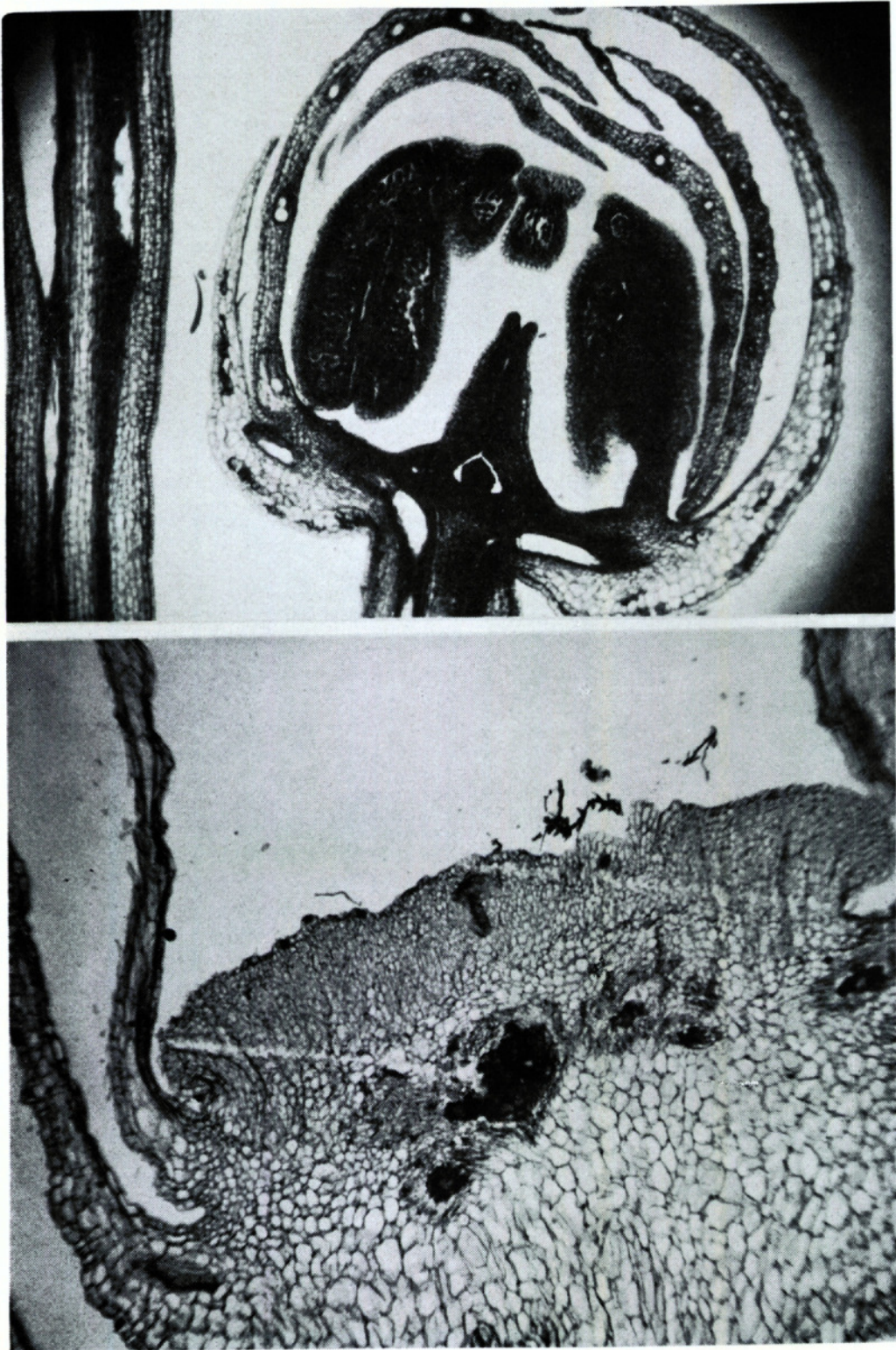
Fig. 18. Longisection of the flower of *Toxicodendron radicans* subsp. *negundo*. Upper: Flower in bud showing stamens, staminal disk and sterile ovary, × 35. Lower: Open flower, showing attachment of petal and sepal to staminal disk, × 90.
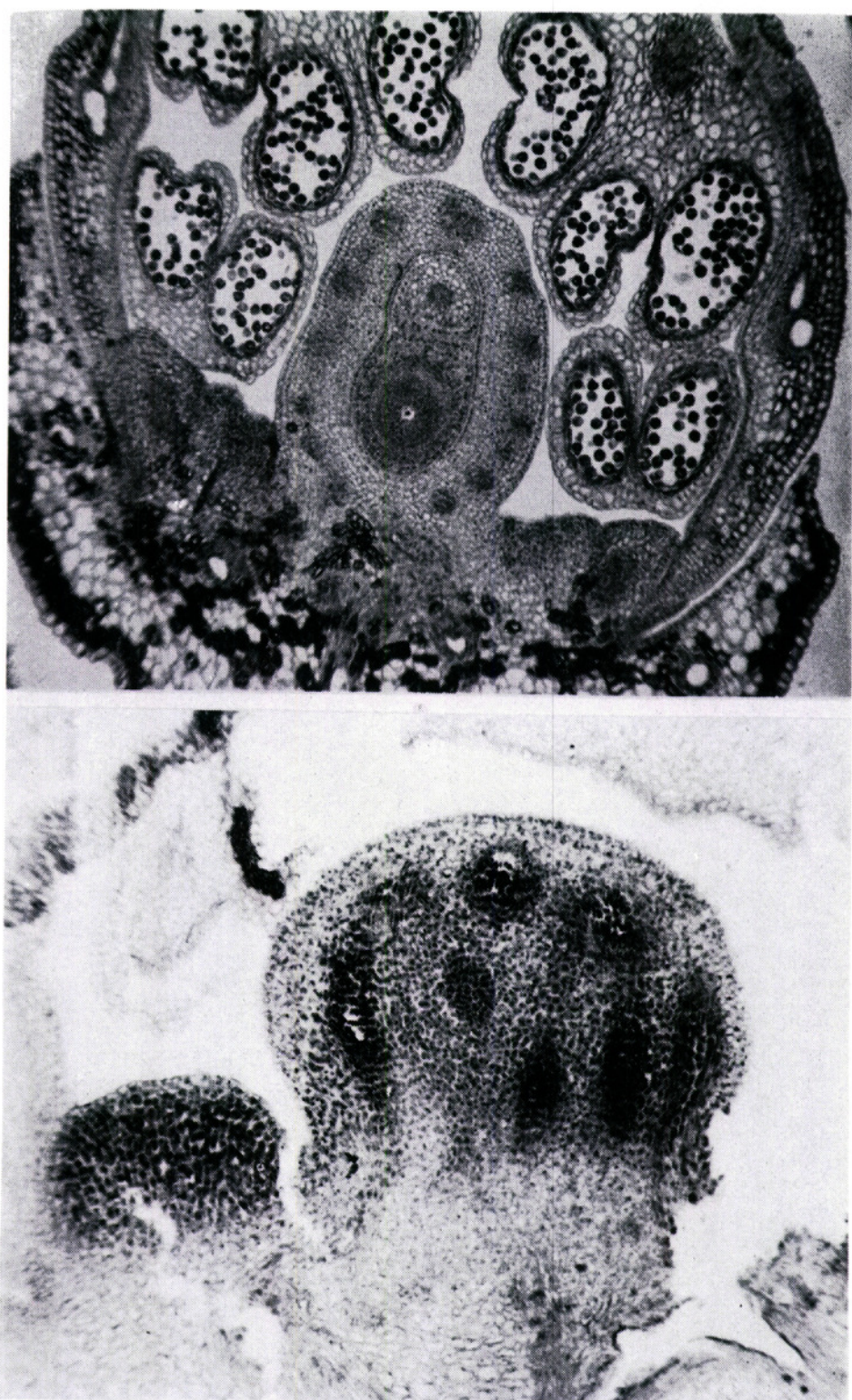
Fig. 19. Longisection of flowers of *Toxicodendron radicans* subsp. *negundo*. Upper: Male flower, showing fertile stamens and developing rudimentary ovary × 85. Lower: female flower, sectioned after petals had fallen, showing enlarging disk and ovary. Dark stained cells in the ovary are incipient resin canals × 65.

Calyx

The five sepals are united only immediately above their insertion below the disk. They are broadly lanceolate or ovate, imbricate in the bud, and do not enlarge significantly once the flowers open. The bases are green, but the upper half is cream-colored like the petals, often with prominent purplish veins. They alternate with the petals. There is a thicker epidermis on the abaxial surface of the sepals than on the adaxial surface, and the outer surface may be slightly pubescent at the base. Resin ducts pervade the phloem of the sepals as they do also in other floral organs. The sepals shrink to dark brown vestiges in fruit, but remain at the base of the staminal disk, and are disseminated with the fruits.

Corolla

The five petals are cream-colored, ascending, glabrous, free, and imbricate in the bud, often with prominent purplish veins. They are obtuse, ovate to lanceolate, always smaller in the female than in the male flowers. In male flowers of Asiatic subspecies of *Toxicodendron radicans* the tips are longer and more prominently reflexed — to over half the total length — than elsewhere in the genus. The shorter petals in female flowers may be slightly recurved, but never reflexed. Poison-carrying resin ducts are found in the phloem of the petals. There is a thick epidermis on both surfaces of the petals. The corolla is attached to the under side of the staminal disk.

Androecium

The five stamens are borne on a glabrous, substaminal disk, typical of Anacardiaceae and related families and orders. Anatomy texts do not treat the origin of this disk, but it appears to have its origin as an outgrowth of the torus. The disk surrounds the ovary, being present to a greater or lesser degree even in female flowers, and is attached to the ovary base. In ripened fruits, the disk and attached calyx remain intact, although shriveled, at the proximal end.

In flowers of sect. *Toxicodendron* the stamens possess

subulate filaments with large, elongate anthers, 4-celled at maturity. They are borne on the edge of the cushion-like disk, alternating with the petals and lobes of the disk. The anthers are oblong, dorsifixed, nearly as long as the filaments, with only the anthers projecting beyond the corolla. Dehiscence is longitudinal and introrse.

Male flowers may be used diagnostically to separate sect. *Toxicodendron* from sect. *Venenata*. The former has stamens included within the perianth at maturity, elongated anthers, and subulate filaments. The latter has stamens exserted at maturity with globose anthers only about one-fourth as long as the enlarged-based filaments. In other characters, the anthers of this section are like those of sect. *Toxicodendron*.

In female flowers, reduced, sterile stamens are present. Microscopic sections show that there is active nuclear division (meiosis?) in progress in these anthers, but they produce no pollen.

Gynoecium

The ovary is tricarpellate, with but one carpel fertile. It is sessile or partially buried in the hypogynous disk. The style is terminal on the ovary, branching near the tip into three parts. The stigma is captitate, simply an expanded portion of the style just above a slight constriction. It may be rough and minutely pitted, but is never pubescent. It turns black when it ceases to function in receiving pollen. This color change from white to black is useful in indicating whether a flower can still be pollinated. The single ovule is anatropous and parietal, seemingly basal, raised on a short, ascending basal funicle.

In male flowers, there is a rudimentary ovary complete with ovule, style, and stigma, although all are reduced in size. The ovary in male flowers begins to develop apparently fertile tissue for a time and even produces rudimentary fruit characteristics such as a thickened ovary wall complete with resin ducts. These parts are deciduous with the flowers when pollination is complete.

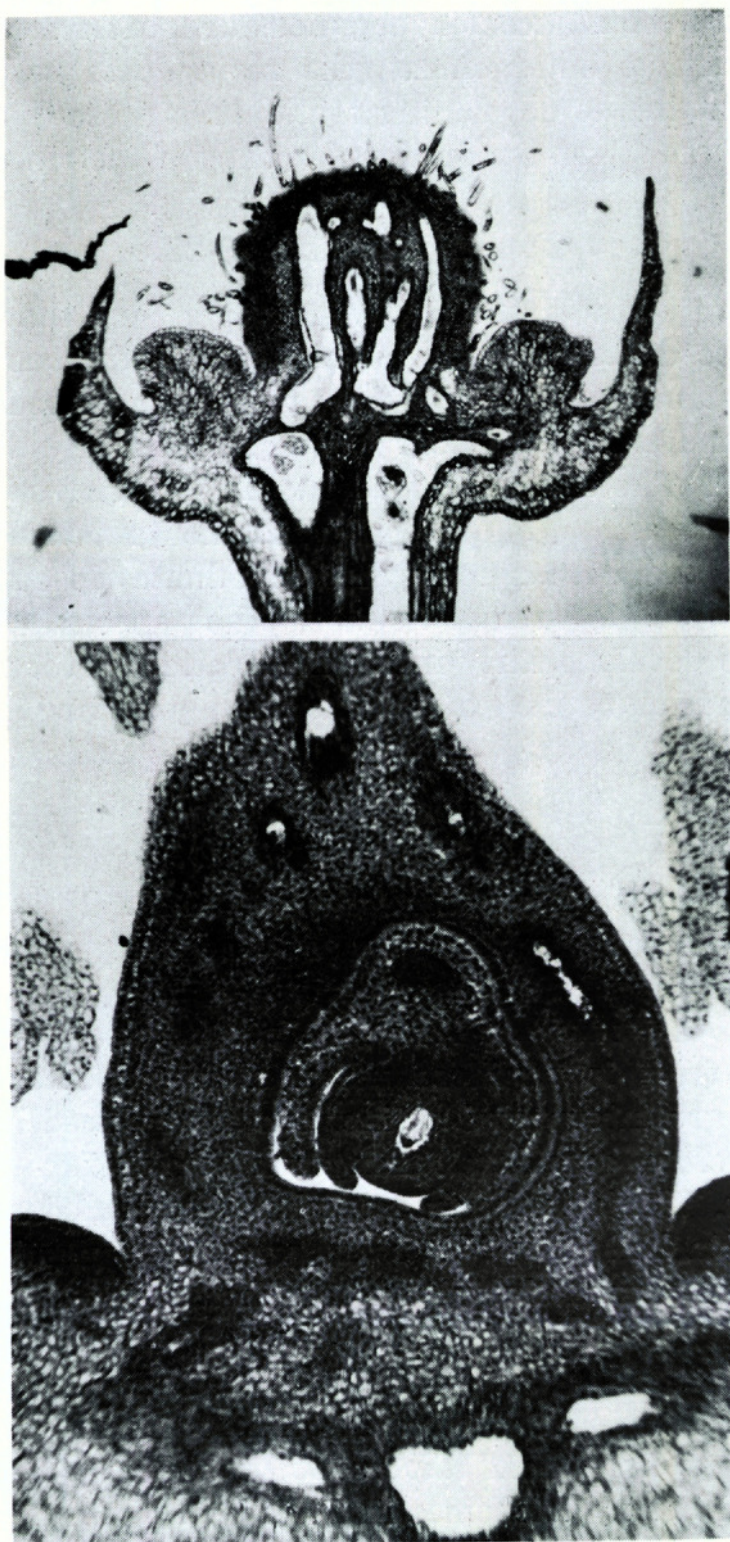In functional female flowers, the ovary wall will enlarge

Fig. 20. Longisection of young fruit of *Toxicodendron*. Upper: *T. toxicarium*, showing enlarged disk, calyx remnant, resin canals and hairs on the outer surface, × 25. Lower: *T. radicans* subsp. *negundo*, showing ovule development, × 100.

along with the adjacent hypogynous disk after fertilization. In addition to enlargement, the resin ducts become very prominent in the developing fruit. It is these ducts which make up the striations on the mesocarp of the ripened fruit.

Fruit. Figs. 16, 20-22.

The fruit is a dry drupe with a pericarp that matures into three distinct layers: a brittle, chartaceous exocarp, a fibrous and waxy mesocarp in which are embedded resin canals, and a bony endocarp to which is firmly affixed the seed wall. The drupe is globose in *Toxicodendron radicans* and *T. toxicarium*, but laterally flattened, bilaterally asymmetrical, and with a somewhat acuminate tip culminating in the stigmatic surface in most other species. The bony endocarp develops early in the maturation of the fruit, but the separation of the exocarp occurs only in the later stages of ripening.

The exocarp is green until late stages of development when it turns yellow, straw-, dun-, or cinereous-colored (deep brown in *Toxicodendron wallichii*). It is glabrous in a number of taxa, but may produce non-glandular hairs in others. Any hairs that are produced begin as evaginations of the outer cell layer. In some populations the ripened fruit is papillose rather than pubescent. These papillae are interpreted as incipient or reduced hairs, and are therefore considered along with hairs for taxonomic purposes. The hairs begin as multi-celled, bulbous evaginations, attached by stalk cells, appearing glandular, but developing ultimately into unbranched, multicellular, elongate, bristle-like hairs of varying length. The hairs are scattered to dense in *T. radicans* subsp. *orientale*, subsp. *radicans*, and in *T. toxicarium*. There are much finer, almost setose hairs in *T. diversilobum* but very dense, elongate, and bristly trichomes in *T. radicans* subsp. *hispidum*, reaching a length of nearly a millimeter in the latter taxon. The trichomes appear to be hollow at maturity, unlike the leaf trichomes which often appear to be filled with a dark-
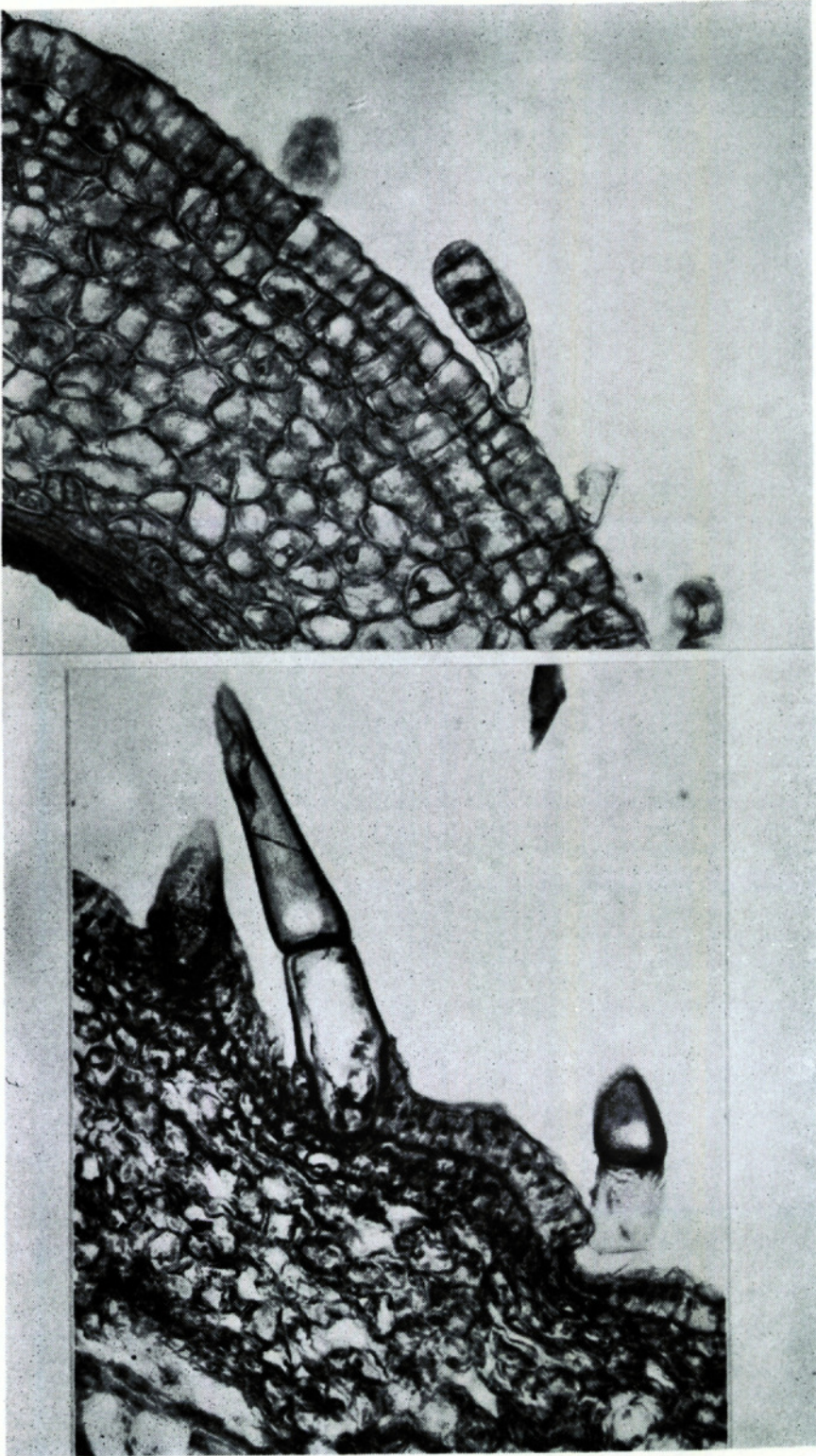
Fig. 21.   Cross section of fruit wall of *Toxicodendron toxicarium*. Upper: Developing wall, showing emerging trichomes, × 90. Lower: Later stage of development than in A, showing mature exocarpal hairs, × 90.
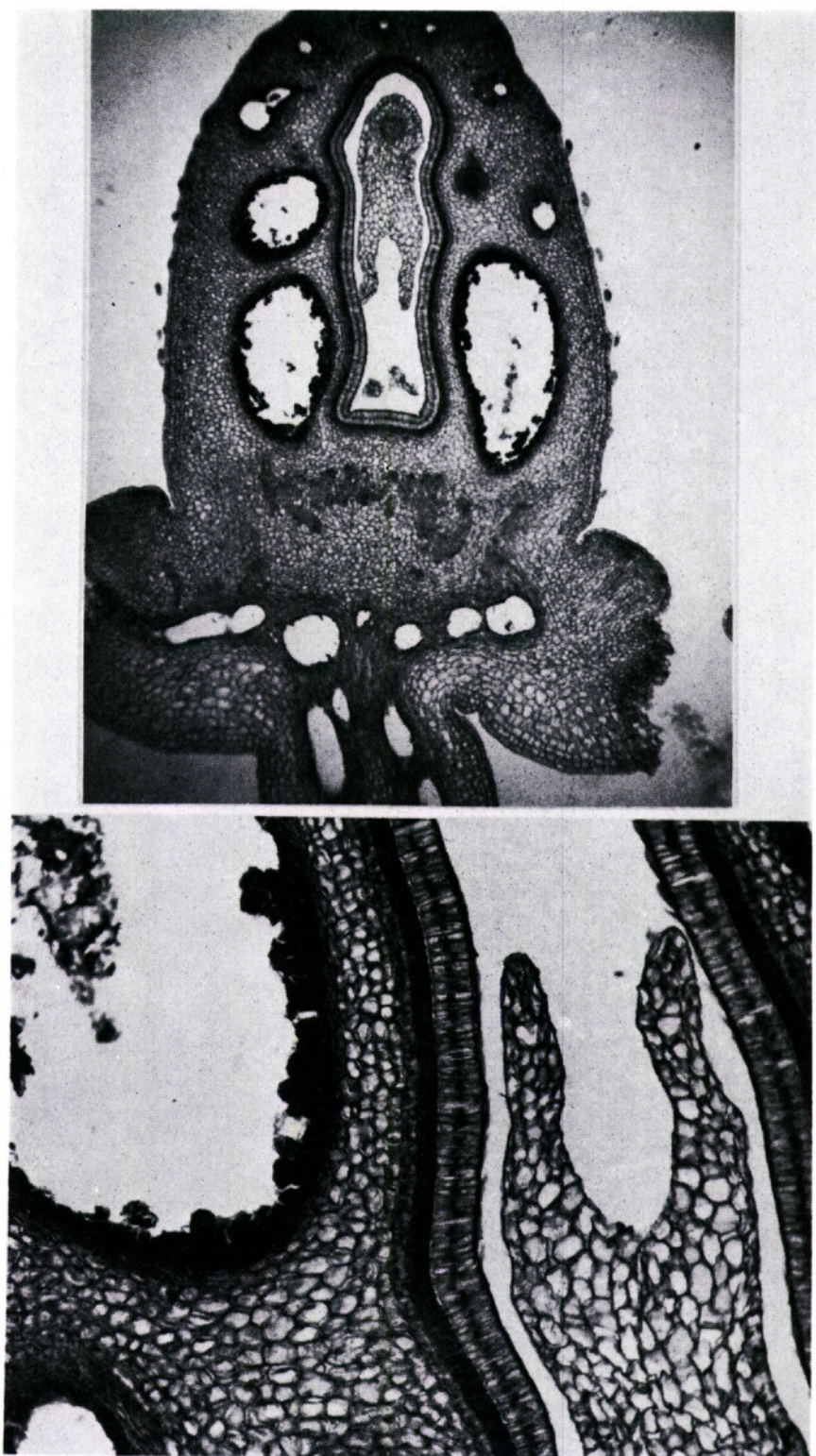
Fig. 22. Longisection of nearly mature fruit of *Toxicodendron toxicarium*. Upper: Functional resin ducts, beginning of endocarp sclerification, elongating embryo, $\times$ 75. Lower: Tissues of seed coat and endocarp, $\times$ 190.

colored substance at maturity.[12] Wrinkled exocarp, often seen in herbarium material, is merely an indication that the fruits are not ripe; the wrinkling occurs due to differential shrinking in the drying process.

The endocarp is a triple-layered tissue, consisting of a single basal layer of small, thick-walled cells, and a double layer of smaller, isodiametric, very thick-walled cells. Perpendicular to this endocarp layer is a single layer of thinner-walled elongate seed coat cells. Entire fruits with shrunken calyces and disks attached constitute the functional disseminules, although overwintering fruits clinging to the pedicels often lose their exocarps before dispersal. References in the literature to "seed" characters are interpreted as references to the mesocarp and its contents. The endocarp may separate from the mesocarp to some extent in some taxa, but never from the testa.

CHROMOSOME NUMBERS

Chromosome numbers were determined from observations of pollen mother cells. *Toxicodendron* species flower for a relatively brief period each year; hence, it was not possible to collect cytological material for chromosome counts in most of the taxa in this group. Counts were made for *T. radicans* subsp. *negundo* (Fig. 23), *T. rydbergii*, and *T. toxicarium* (Fig. 24). In all taxa for which counts were available, meiosis appeared regular and the chromosome number was the same. This figure of $2n = 30$ agrees with published counts of $n = 15$ for *T. diversilobum* by Copeland and Doyel, coroborated by the work of Raven, Kyhos, and Hill (1965), and for *Rhus toxicodendron* by Grimm (1912). In the latter case, we have no way of knowing which taxon was under study; from the context of the article, it might have been *T. radicans* subsp. *radicans*. Because of the small size, relative uniformity in size

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[12]The fruit trichomes of *T. trichocarpum* are unique in the genus. Their bases anastomose all over the surface of the fruit and finally project outward as hollow, curved, bristly hairs.
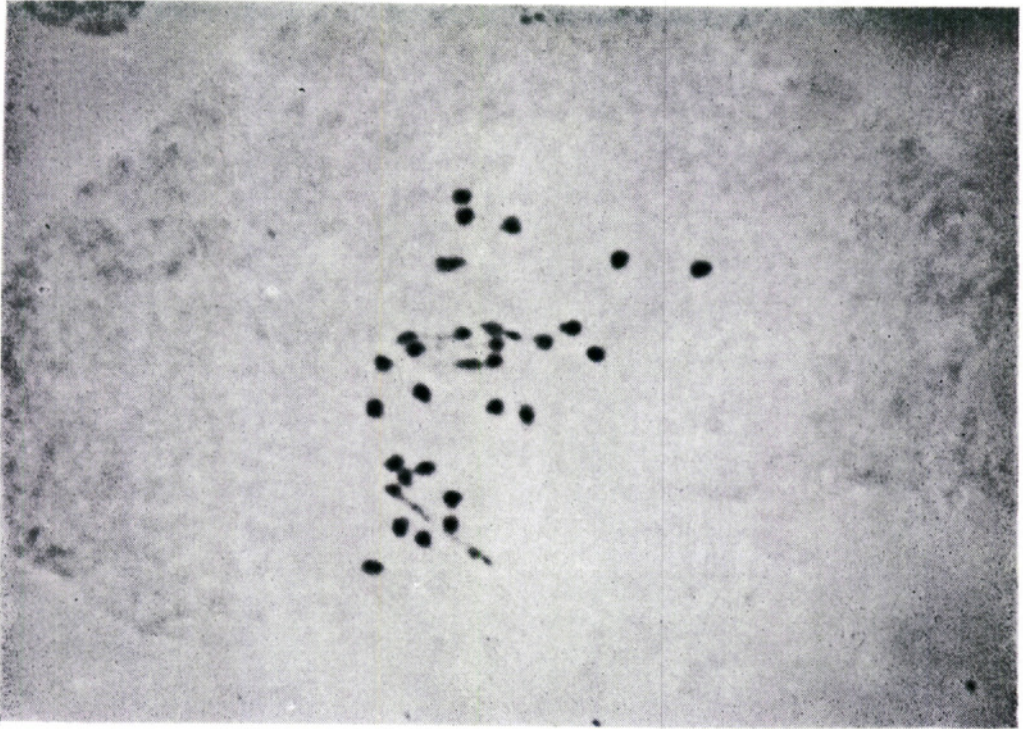
Fig. 23. Meiotic chromosomes in anther of *Toxicodendron radicans* subsp. *negundo*, × 200.

of the chromosomes, and difficulty in differentiating the kinetochore, karyotype analyses were not undertaken. In one pair of chromosomes in *T. toxicarium*, however, there appear to be satellites.

Material of *Toxicodendron* used in cytological investigations: *Toxicodendron radicans* subsp. *negundo*, *Gabriele Mühling s.n.*, Michigan, Oakland County, 5 miles north of Farmington on 12-Mile Road between Halstead and Haggerty, 11 May 1959. *Toxicodendron rydbergii*, *Gillis* 5549, Michigan, Alger Co., T. 49N., R. 14W., SW 1/4 Sec. 7. Devil's Slides on high sand dune overlooking Lake Superior. 17 June 1964. *Toxicodendron toxicarium*, *Gillis* 4315, Florida, Alachua County, T. 9S., R. 19E., Sec. 13, 12 miles NW of Gainesville, San Felasco area. Turkeyoak-pine Woods. 6 April 1961.

SPECIMENS EXAMINED

In the citation of specimens, herbarium abbreviations in the fifth edition of "Index Herbariorum" (Lanjouw and Stafleu, 1964) have been used. Those herbaria which are not included in the Index have been assigned provisional abbreviations marked with a plus (+). The herbaria and

Fig. 24. Chromosomes of *Toxicodendron*. A, *T. toxicarium*, Alachua county, Florida, Gillis 4315. B, *T. rydbergii*, Alger county, Michigan, Gillis 5549.

their abbreviations are: Arnold Arboretum of Harvard University (A); University of Alberta (ALTA); Mohr Herbarium, Alabama Museum of Natural History (ALU); University of Arizona (ARIZ); Arizona State College (ASC); Cranbrook Institute of Science (BLH); British Museum (Natural History) (BM); Herbarium Bogoriense, Lembaga Biologi Nasional (BO); Brigham Young University (BRY); Central National Herbarium, Calcutta (CAL); Chrysler Herbarium, Rutgers University (CHRB); Plant Research Institute, Canada Dept. of Agriculture, Ottawa (DAO); Dayton Museum of Natural History (DMNH +); Dudley Herbarium, Stanford University (DS); Duke University (DUKE); Royal Botanic Garden, Edinburgh (E); Escuela Nacional de Ciencias Biologicas, Mexico City (ENCB +); Chicago Natural History Museum (F); Florida Agricultural Experiment Station (FLAS); Florida State University (FSU); Conservatoire et Jardin Botaniques, Geneva (G); University of Georgia (GA); Gray Herbarium of Harvard University (GH); University of Illinois (ILL); Herbarium, Kew (K); Kansas State University (KSC); Botanical Institute, Kiew, Ukranian S.S.R. (KW); Rijksherbarium, Leiden (L); Catholic University of America (LCU); Komarov Botanical Institute, Leningrad (LE); Linnaean Society (LINN); University of Michigan (MICH); Public Museum, City of Milwaukee (MIL); University of Minnesota (MIN); Missouri Botanical Garden (MO); Michigan State University (MSC); Universite de Montreal (MT); University of Notre Dame (ND); Greene Herbarium, University of Notre Dame (ND-G); North Dakota State University (NDA); New York Botanical Garden (NY); Botanisk Museum, Oslo (O); Oregon State University (OSC); Fielding Herbarium, Oxford University (OXF); Muséum National d'Histoire Naturelle, Paris (P); University of Pennsylvania (PENN); Philadelphia Academy of Natural Sciences (PH); Rocky Mountain Herbarium, University of Wyoming (RM); Hokkaido University (SAP); South Dakota State College (SDC); University of South Dakota (SDU); Botanic Gardens, Singapore (SING); Southern Methodist University (SMU); Sul Ross

State College (SRSC); National Taiwan University (TAI); University of Texas (TEX); Botanical Institute, Tokyo University (TI); Botanical Museum, Utrecht (U); University of California, Berkeley (UC); United States National Museum (US); University of Manitoba (WIN); University of Wisconsin (WIS); and Wayne State University (WUD).

(To be continued)

DIPLACRUM AFRICANUM NEWLY FOUND IN TROPICAL AMERICA: A small tropical sedge, *Diplacrum africanum* C. B. Clarke, previously known as an endemic to Africa, has been collected from southern Suriname near the Brazilian border. The collection is: SURINAME. Sipaliwini savanna area on Brazilian frontier, 1.5 km NNW of 4-Gebroeders Mountains, 300 m alt., on plain in wet valley near a Mauritia-swamp, ON 152, *F. H. F. Oldenburger, R. Norde & J. P. Schulz,* Sept. 1968 (BBS, NY, U). This particular specimen was found growing in sandy soil with an impeded water table through the rock pavement at a depth of ca. 50 cm. Among the associated plants from the same locality were *Philodice hoffmanseggii, Syngonanthus glandulosus, S. gracilis* var. *koernickeanus, Bacopa monierioides, Centunculus pentander, Polygala paludosa, Utricularia adpressa* and *Eleocharis nana.*

Diplacrum africanum belongs to the section *Sphaeropus* of the genus bcause of its fruits, which fall off apart from the subtending glumes, and the spongy thickened receptacle below the upper glumes. Such thickenings are presumed to be formed by the adnation of abortive staminate spikelets to the base of the reduced glumes, and are seen also in a few species of the genus *Becquerelia,* showing the close taxonomic affinity between *Diplacrum* and *Becquerelia* (cf. T. Koyama, in Mem. N. Y. Bot. Gard. 17: 23-79. 1967).

Diplacrum section *Sphaeropus* involving two other Asiatic species has hitherto been noted from tropical Africa