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REVISION OF THE MEXICAN AND GUATEMALAN SPECIES OF *PLATANUS* (PLATANACEAE)

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Abstract: A taxonomic treatment of the genus *Platanus* L. in North America is presented, concentrating on the species native to Mexico and Guatemala. Eight taxa are recognized for North America: 3 species with 2 varieties each, and two species without varietal subdivision; all occur in Mexico and/or Guatemala except for one more northern variety. One previously unrecognized species from western Mexico is described, **P. gentryi** Nixon & Poole. Another species from northeastern Mexico, although often called *P. mexicana* Moric., represents an undescribed species because the name *P. mexicana* is correctly applied to a different Mexican species. The resultant new species is **P. rzedowskii** Nixon & Poole. A new variety, **P. mexicana** var. **interior** Nixon & Poole, is described from central Mexico. A key to taxa includes the two Old World species, *P. kerrii* and *P. orientalis,* but complete descriptions of the latter species are not given. A discussion of the morphological characters, biogeography, infrageneric phylogeny and speciation of *Platanus* in North America is presented in light of the greater understanding of the taxa afforded by this study.

Resumen: Se presenta un tratamiento taxonómico del género **Platanus** en Norte América, con un enfoque principal a las especies nativas de México y Guatemala. Se reconocen ocho taxones norteamericanos: 3 especies con 2 variedades cada una, y dos especies sin variedades; todos estan representados en México y Centroamérica con la excepción de una variedad más septentrional. Se describe a **P. gentryi** Nixon & Poole como una especie nueva del oeste de México. Otra especie del noreste de México, frecuentemente identificada como *P. mexicana* Moric., de hecho representa una especie no descrita, ya que el nombre *P. mexicana* es correctamente aplicado a otra especie mexicana. La nueva especie que resulta es **P. rzedowskii** Nixon & Poole. Se describe una nueva variedad para el centro de México, **P. mexicana** var. **interior** Nixon & Poole. Se provee una clave que incluye las dos especies del Viejo Mundo, *P. kerrii* y *P. orientalis,* pero no se presentan descripciones de las mismas. Se presenta una discusión sobre los caracteres morfológicos, la biogeografía, la filogenia infragenérica y la especiación de *Platanus* de Norte América a la luz del mejor entendimiento de los taxones objeto de este estudio.

Keywords: *Platanus,* Platanaceae, taxonomy, systematics.

The genus *Platanus* occurs naturally only in the northern hemisphere. Two species are usually recognized in the Old World, one species in southern Europe and the Middle East (*P. orientalis* L.) and one apparently relictual species in Laos and North Vietnam (*P. kerrii* Gagnep.) The remaining 5 species (as recognized here) have a patchy distribution in North America from northern California and the eastern United States to southern Mexico and adjacent Guatemala. *Platanus* is noteworthy for its generally allopatric species that are apparently highly interfertile and often spontaneously hybridize when brought into cultivation (see Ernst, 1963, for references). Because of this apparent lack of reproductive isolation and poor understanding of the morphology of the species, the taxa have been treated at varying ranks by different authors. Most recent workers have considered the family to be monogeneric, as do we. The many fossils attributed to *Platanus* have generated considerable interest among paleobotanists (see Friis & Crane, 1989). However, no recent taxonomic treatment of

the extant species in North America exists, the taxonomy of Mexican *Platanus* being heretofore especially neglected and confused. During field work in Mexico in the late 1970s and early 1980s, the confusion in the application of names to Mexican *Platanus* became apparent to us, and this study was undertaken to resolve the major taxonomic problems of the Mexican species. Since all taxa except a single variety of one of the North American species (*Platanus occidentalis* L. var. *occidentalis*) occur at least partly in Mexico, we include here a synopsis of all North American *Platanus*. However, we have not treated the variation within *P. occidentalis* var. *occidentalis* in detail nor have we attempted to study the type specimens of the many specific and varietal names which have been proposed for material from the eastern United States. Based on a thorough examination of available material, these infraspecific names all appear to be synonyms of *P. occidentalis* var. *occidentalis*.

Relationships at the Family Level

Over the past century considerable controversy has existed concerning the relationships of the family. Some authors (e.g., Niedenzu, 1881; Boothroyd, 1930) argued for a close alliance with the Rosales, while others preferred to place the family with other wind-pollinated trees in the essentially artificial Apetalae (e.g., Griggs, 1909, argued the Platanales are related to the Urticales). Most recent morphological studies, however, placed the Platanaceae near the Hamamelidaceae in the order Hamamelidales (e.g., Cronquist, 1981; Takhtajan, 1980; Manchester, 1986; Schwarzwalder & Dilcher, 1991). Others (e.g., Ernst, 1963) maintained that the affinities of the family remain uncertain. With the advent of cladistics, most morphological cladistic analyses have continued to place Platanaceae in close association with the Hamamelidaceae (e.g., Hufford & Crane, 1989). Surprisingly, most recent molecular studies position *Platanus* (and therefore Platanaceae) as a sister taxon of modern Proteaceae (see Soltis et al., 2000 and citations therein) in a clade that also includes *Nelumbo* Adans. (Nelumbonaceae), an aquatic perennial that morphologically bears a superficial resemblance to the water lilies (Nymphaeaceae).

In characters of the leaves (Fig. 1) and inflorescences, *Platanus* shows a gross similarity to the subfamily Liquidambaroideae of the Hamamelidaceae, which includes the eastern North American *Liquidambar styraciflua* L. (the subfamily is sometimes recognized as a distinct family, the Altingiaceae). Indeed, some workers (e.g., de Candolle, 1864) placed *Liquidambar* in the Platanaceae. *Platanus* and *Liquidambar* L. are similar in having palmately lobed actinodromous leaves and capitate unisexual inflorescences, but differ in important characters of the flowers, fruit, pollen, and wood. *Liquidambar* has two partially fused multi-ovulate carpels, each splitting like a follicle in its free upper portion when ripe. *Platanus* has a variable number (4–9) of free uni-(rarely bi-)ovulate carpels, each maturing into a unilocular indehiscent achene (technically an achenelet or fruitlet, because more than one occurs in each flower) with a basally attached coma. The wood anatomy of *Platanus* is very dissimilar to that of the Hamamelidaceae (Tippo, 1938; Ernst, 1963; Baas, 1969). *Platanus* has simple vessel element perforations as opposed to scalariform perforations in the Hamamelidaceae *sensu lato*.

In its tricolpate, reticulate pollen (Lieux, 1980; Ludlow-Wiechers & Ayala N., 1982) *Platanus* shows a superficial resemblance to the tricolpate pollen of Hamamelidaceae *sensu stricto* as opposed to the polyforate pollen of *Liquidambar* and *Altingia* Noronha (Bogle & Philbrick, 1980). Fossil pollen similar to that of *Platanus* occurs in the fossil record as *Tricolpites* or *Tricolpollenites* (Ludlow-Wiechers & Ayala N., 1982). Although numerous fossil leaves from the early Cretaceous appear to be pla-

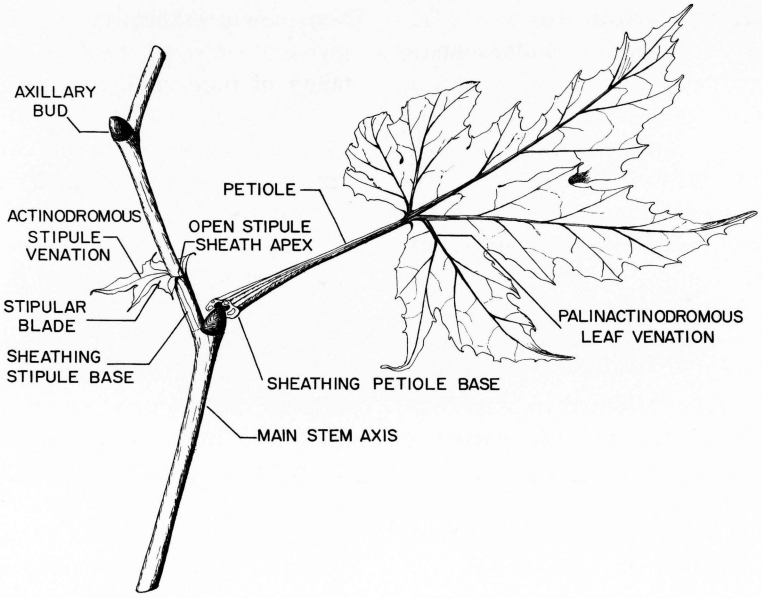

FIG. 1. Vegetative features of *Platanus,* indicating possible homology of the stipule with the leaf. Illustration by J. Larke.

tanoid, these lack unequivocal synapomorphies to place them in the modern crown group of Platanaceae, and no detailed morphological analysis has yet been undertaken. Because it is clear that resemblances between *Platanus* and modern Hamamelidaceae-Altingiaceae are almost entirely superficial, the alternative placement of Platanaceae in a clade with Proteaceae as suggested by molecular analyses (e.g., Soltis et al., 2000) must be accepted as the best working hypothesis at this point.

Cytological evidence is scant in the genus, as for many other trees, and we were not able to contribute chromosome counts for the species occurring in Mexico. Chromosome numbers for *P. occidentalis, P. orientalis* L., and *P.* ×*acerifolia* (Ait.) Willd. and *P. kerrii* have been reported as $2n = 42$ (see Ernst, 1963; Morawetz & Samuel, 1989; ICPN 1994–95, 1992–93).

Platanus is noted for the sweet fragrance of the leaves, which can emanate even from old herbarium specimens of all the North American species. The fragrance apparently arises from volatile terpenoid compounds (Aplin et al., 1963). We know of no attempt to use chemical data to elucidate the relationships of species within *Platanus* or to other genera or families.

TAXONOMIC HISTORY

Platanus was well known to pre-Linnaean botanists (*platanos* is the classical Greek name for *P. orientalis*). Linnaeus (1737; 1753) based his description of the European *P. orientalis* L. and American *P. occidentalis* in part on earlier works. He differentiated the two species mainly on the basis of the depth of the lobing of the leaves, probably still the most commonly used character for distinguishing vegetative material of the two species. After 1753, several species were proposed by European authors that must be referred to *P. occidentalis* or *P. orientalis* (see synonymy below). Mexican or western U.S. material apparently did not come to the attention of European botanists until much later. *Platanus mexicana* Moric. was named in 1830 from material collected by Berlandier with the only locality "Circa Mexico." *Platanus racemosa* Nutt. was named in 1842 from material collected

by Nuttall in Santa Barbara, California. The following year, *P. lindeniana* M. Martens & Galeotti was named based on specimens from the vicinity of Jalapa, in the state of Veracruz, Mexico. Subsequently, this latter name has been applied to most of the Mexican *Platanus* of eastern and southern Mexico south of San Luis Potosí and north and west of Chiapas. *Platanus californica* Bentham (1844) has been considered a synonym of *P. racemosa* by virtually all subsequent authors.

Kuntze (1891) considered all of the *Platanus* known at the time of his treatment to be a single species, and therefore combined *P. occidentalis, P. racemosa, P. mexicana* and *P. lindeniana* as varieties of the European *P. orientalis.* Recent authors have not followed this treatment. Kuntze also named *P. orientalis* var. *palmeri,* based on a Palmer collection from Coahuila. Fernald (1901) later cited the same collection number (*Palmer 1269*) as a syntype of *P. glabrata* Fernald, without reference to Kuntze's varietal name. Sargent (1890) recognized only 3 species in the United States, *P. occidentalis, P. racemosa* and *P. wrightii,* and this treatment has been followed by most workers. Sargent did not treat Mexican *Platanus,* although he later reduced *P. glabrata* to varietal status as *P. occidentalis* L. var. *glabrata* (Fernald) Sargent, recognizing this variety as far north as Oklahoma and Iowa. Sargent did not equate his var. *glabrata* with the earlier varietal name *P. orientalis* var. *palmeri* Kuntze.

Standley (1924) recognized seven species in Mexico, including *Platanus racemosa, P. wrightii, P. glabrata* and *P. lindeniana. Platanus oaxacana* Standl. and *P. chiapensis* Standl. were based on single collections from Oaxaca and Chiapas, respectively. Although subsequent workers have consistently applied the name *P. chiapensis* to material from Chiapas, the name *P. oaxacana* apparently has been applied only to its type specimen. Standley applied the name *P. mexicana* Moric. to a species with solitary capitula from Nuevo León and Tamaulipas. Nee (1981) determined that *P. mexicana* correctly referred to the taxon Standley called *P. lindeniana* and placed the latter name as well as *P. chiapensis* as synonyms of *P. mexicana* Moric. Nee did not address the question of the correct name for *P. mexicana* sensu Standley from northeastern Mexico.

Benson (1943) reduced *Platanus wrightii* to varietal rank as *P. racemosa* Nutt. var. *wrightii* (S. Watson) Benson, citing California specimens that closely approach *P. wrightii* in characters of the inflorescence. Benson included trees from Andreas Canyon, Riverside County, California, in his concept of *P. racemosa* var. *wrightii.*

Leroy (1982) erected *Platanus* subgenus *Castaneophyllum* to accommodate the single Asian species with evergreen pinnate leaves, *P. kerrii.* The remainder of the species (including all the palmately-leaved species in North America) were retained in *Platanus* subgenus *Platanus.* Leroy did not treat *Platanus* at the specific level.

During the course of this study approximately 1500 specimens of *Platanus* from 19 major herbaria were studied (A, ARIZ, BH, BR, CAS, DS, ENCB, F, G, GH, K, LL, MEXU, MICH, MO, NY, PH, TEX, US). Label determinations on these specimens by the collectors and various workers indicate the greatest amount of variability in the application of the names *P. lindeniana, P. mexicana,* and *P. glabrata.*

Vegetative Morphology

Based on characters of leaves, inflorescences, flowers and achenes, two groups can be differentiated morphologically in New World *Platanus* (see also Hsiao, 1973). The three western taxa (Figs. 2 & 4) have more deeply lobed leaves, spicate or racemose carpellate inflorescences, achenes usually glabrous at maturity, and conspicuous peltate staminodia in the carpellate flowers. The five taxa from eastern North American (Figs. 3–5) have generally more shallowly lobed leaves, racemose, spicate or single ca-

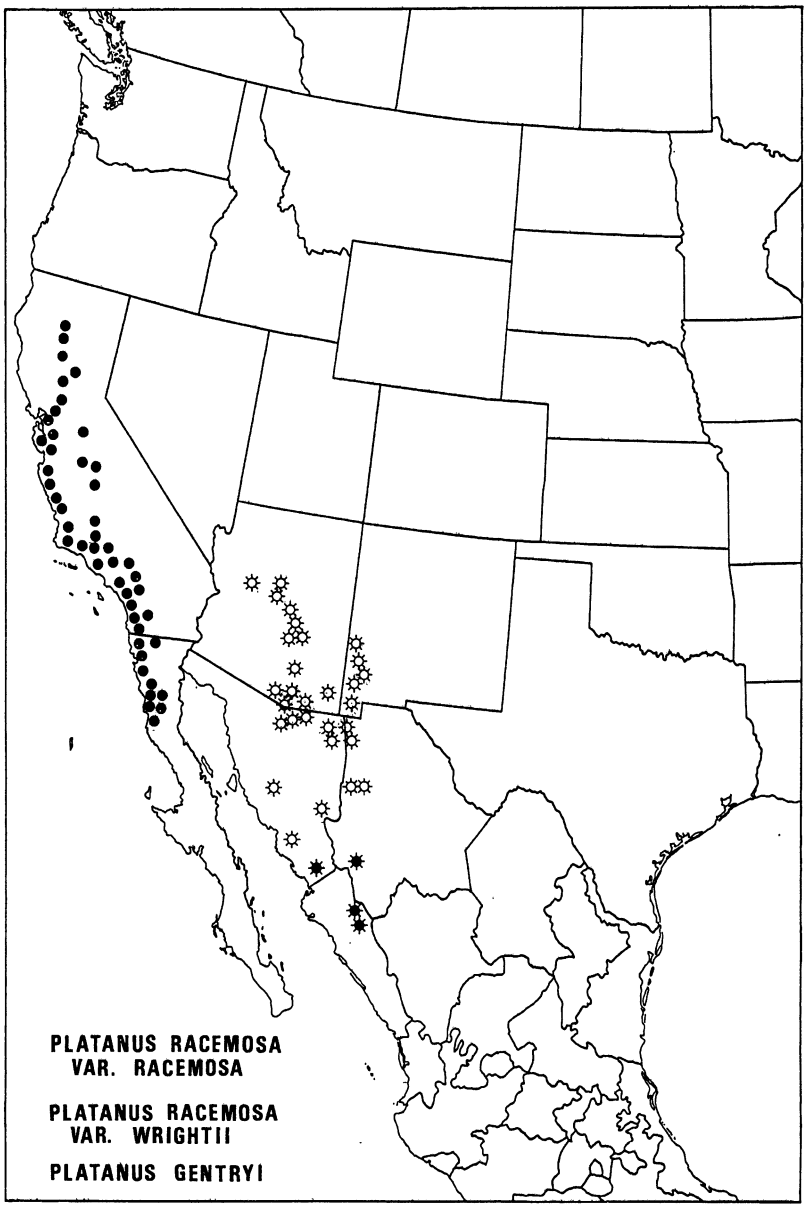

FIG. 2. Distribution of the species and varieties of *Platanus* in western North America. Solid circles, *P. racemosa* var. *racemosa*; solid circles with hairs, *P. gentryi*; open circles with hairs, *P. racemosa* var. *wrightii*.

pitula, achenes distally puberulent to densely tomentose at maturity, and apically flattened glabrescent staminodia. The alliance of *P. mexicana* with *P. occidentalis* and *P. rzedowskii* is weaker than the obviously strong interrelationship of the latter two species. *Platanus orientalis,* the Old World representative of subg. *Platanus,* must be tentatively placed with the western species group, based on its racemose inflorescence and elongate leaf lobes. The observed pattern of variation with mostly allopatric species that intergrade in areas of contact strongly suggests that evolution in North

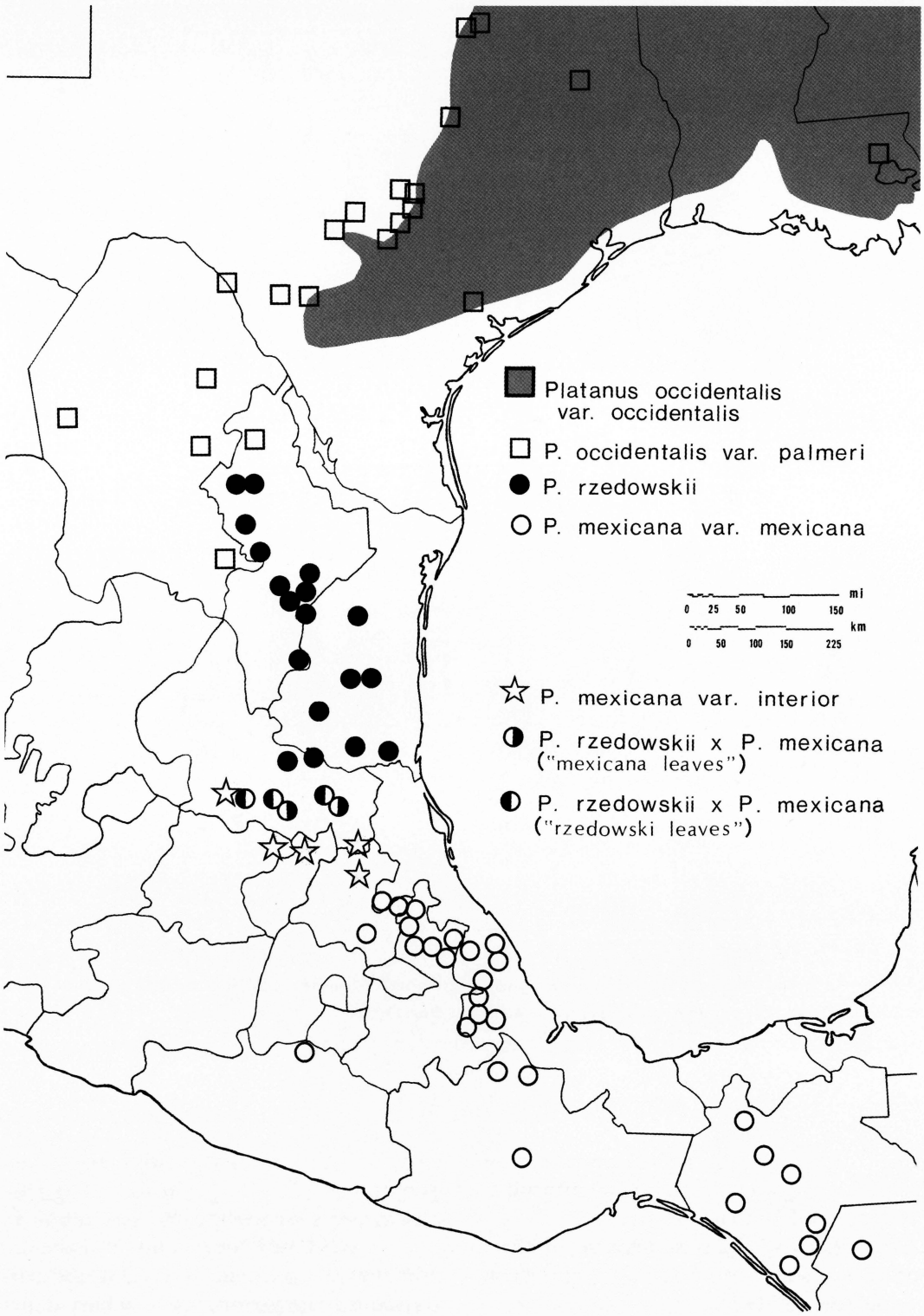

FIG. 3. Distribution of *Platanus* in eastern Mexico and adjacent United States and Guatemala. (Distribution of *P. occidentalis* var. *occidentalis* only partially shown, and adapted from Little (1971), to which the reader is referred for a complete distribution map of that taxon).

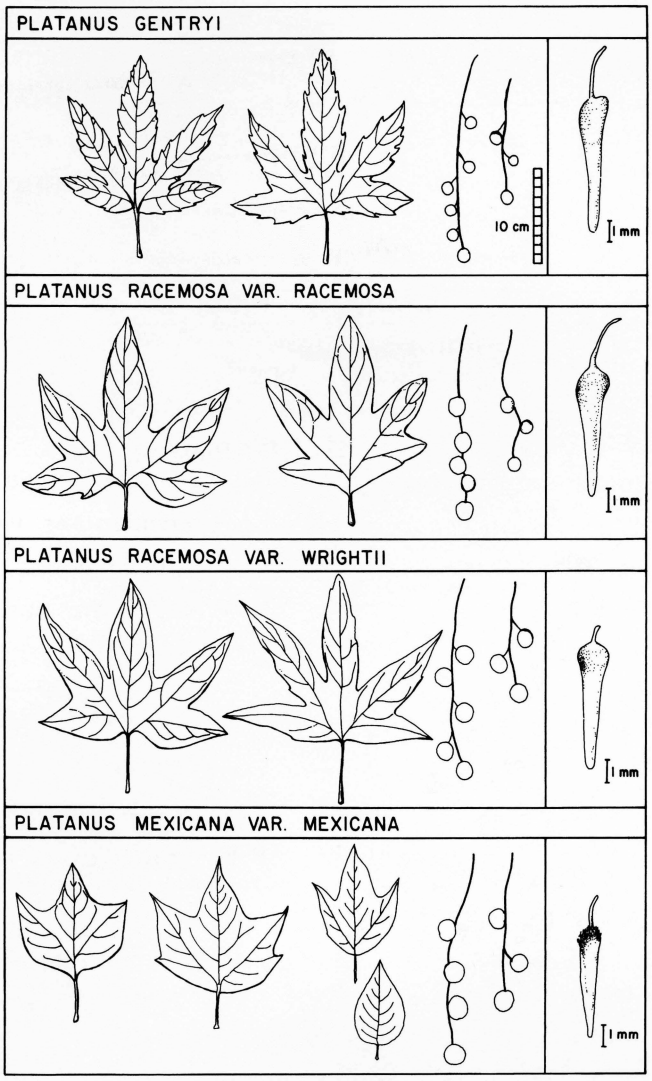

FIG. 4. Representative leaf shape, carpellate inflorescence morphology, and achenes with coma removed of *Platanus* species. Not all variation represented. All leaves and inflorescences to same scale, as indicated; all achenes to separate scale, as indicated.

American *Platanus* was at least in part reticulate. Phylogenetic relationships in groups with past reticulation are difficult to ascertain with confidence using currently available methodologies. Because of these problems, and lack of sufficient and stable qualitative characters to undertake a morphologic cladistic analysis, we have not presented a phylogeny here.

TWIG, BUD AND STIPULE CHARACTERS. Characters of the twigs, buds, and stipules, although useful in delimiting species in some woody plants, were found to be of limited taxonomic value in *Platanus.* Although *P. mexicana* (including the synonymous *P. chiapensis*) tends to have rather brownish twigs as opposed to the reddish twigs of most *Platanus,* this character is var-

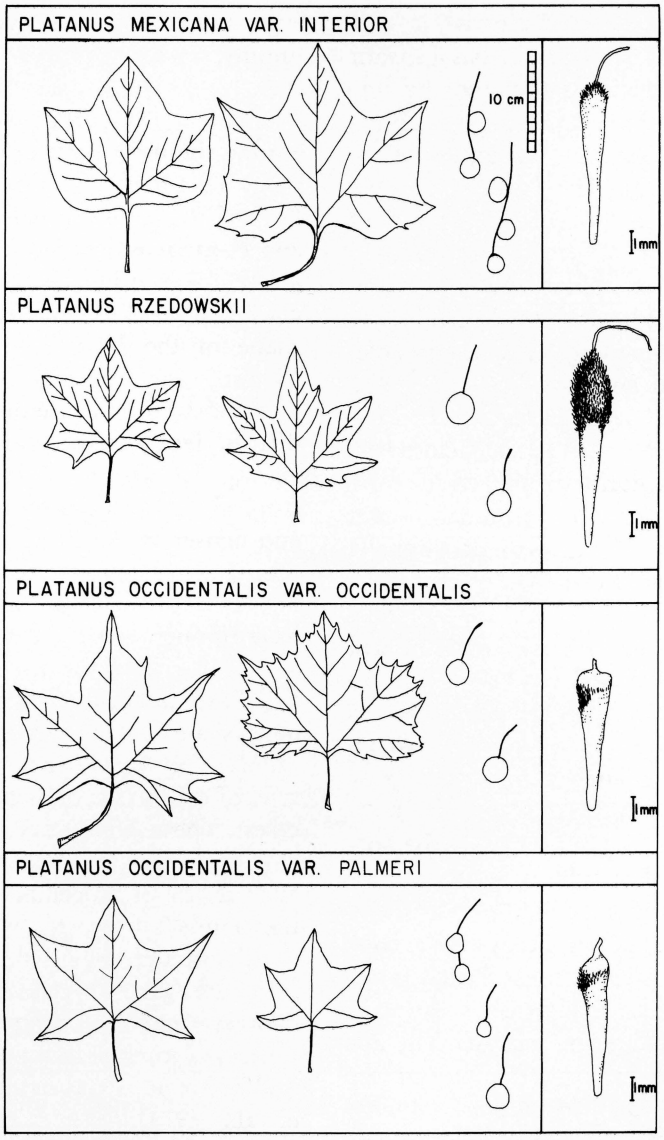

FIG. 5. As Figure 4, to same scales.

iable within species, apparently modified by growing conditions (in general, often strongly affected by exposure to sun) and often difficult to ascertain in very young, densely pubescent, or poorly preserved material. Stipule characters likewise seem to be affected by rapidity of growth, type of branch (juvenile or mature, flowering or not) and environmental factors. This is supported by the studies of McMillan (1974), in which differential stipule production was observed in *P. occidentalis* and *P. rzedowskii* (treated by him as *P. occidentalis*) under varying environmental treatments. Within populations, within trees, and even within herbarium specimens stipules often vary from small membranaceous sheaths with poorly developed blades to those with large, tough foliose blades that are green and apparently photosynthetic. The latter condition seems more prevalent on rapidly growing shoots and regrowth after damage.

Platanus stipules are distinctive in that they consist of a 7- to 9-veined basal sheath that completely encircles the stem (or incompletely in *P. kerrii*) and a peltately attached expanded laminar portion that is often foliose (Fig. 1). The laminar portion usually has 3 to 5 lobes, with prominent actinodromous venation as in the leaf blades. In these characters, the stipule appears to be homologous to the leaf, with the stipular sheath homologous to the petiole, which in the leaf encloses the bud. In the leaf, the petiolar sheath is restricted to the base of the petiole and is apically closed, as opposed to the apically open sheath of the stipule. When precocious summer or fall bud break and shoot growth occasionally occur, the new shoot usually forcibly breaks through the enclosing petiole base, and may damage the petiole (unpubl. obs.). Thus, the incompletely sealed petiolar sheath as found in *P. kerrii* may be an adaptation to an evergreen habit, since without such an opening axillary branches could not grow without either forcing leaf fall or producing damage to the petiole. It should also be noted that *P. kerrii* has axillary inflorescences as opposed to the terminal inflorescences of all other *Platanus* species. Leroy (1982) concluded that the sealed petiolar sheath is ancestral, a conclusion that requires testing in the context of a cladistic analysis. The apparent homology in the structure of the leaves and stipules in *Platanus* also merits further study, and may shed light on the nature of stipules in at least some taxa in the broader tricolpate clade.

Buds of all the American *Platanus* species were found to be externally reddish brown and glabrate, and we could ascertain no distinguishing bud characters in the taxa under study. The inner "bud scales" appear to be stipular, sheathing, and are usually densely brownish-pubescent. This lack of variation, in combination with difficulty in observing buds in herbarium material because they are usually hidden by the sheathing petiole base, makes bud characters of no apparent value in New World *Platanus* taxonomy.

LEAF CHARACTERS. Leaf characters are among the most useful in *Platanus,* and all of the taxa here recognized with the exception of the varieties within *P. occidentalis* and *P. racemosa* can be reliably and consistently differentiated on the basis of the combination of leaf shape, number of lobes, shape of the lobes, degree of secondary toothing, and density, color and persistence of the abaxial vestiture on the blade. In addition, leaf texture varies considerably among the species. In general, the more tropical Mexican species have thicker leaves and denser, more persistent abaxial pubescence, and northern temperate species (*P. racemosa* sensu lato and *P. occidentalis*) have thinner, more glabrate leaves.

Vestiture of the leaves, petioles, twigs and floral structures varies considerably in density and color among the taxa, but the vestiture appears to be based on the same type of distinctive branched trichome in all cases. These trichomes are multicellular, with a central multicellular uniseriate axis and whorls of unicellular rays emerging at the "joints" of the axes, where adjacent cells are connected. This type of trichome falls into the general class of dendritic trichomes, and has been more specifically termed a candelabrum (e.g., Esau, 1965; Radford et al., 1974) or abietiform (Radford et al., 1974). The trichomes are often brownish or yellowish, with what may be glandular contents, and when brownish are termed glandular in this treatment. The branches (rays) of the trichome may be numerous and well-developed, as in the vestiture of leaves and twigs, or the branches may be suppressed, as in trichomes of the comae of the achenes. The latter often have a few small apical branches of one to two cells, indicating the probable derivation of this "unbranched" trichome from a branched type. We were unable to find substantial and consistent differences in trichomes of homologous structures other

than distribution, density, and color. Significant differences in the type of trichome associated with a structure, which have been shown to be of taxonomic value in other families, were not found in *Platanus.*

VENATION CHARACTERS. The venation terminology presented here follows Dilcher (1974). The 3 to 5 veins passing into the major lobes are all considered primary veins; venation in all species is palinactinodromous (the two lateral primary veins branching again) or actinodromous (as in most *P. mexicana*). Variability and overlap of character states at all levels of venation tend to reduce the value of these characters for differentiating species.

Secondary veins in the western species are arcuate as opposed to more or less straight and parallel in the eastern species. There is a tendency to straight or convex percurrent tertiary venation in all the species, but this is most strongly developed in *P. mexicana* and only weakly developed in the three western taxa, in which the tertiary veins are often more highly branched.

REPRODUCTIVE CHARACTERS

INFLORESCENCE CHARACTERS. Inflorescences in *Platanus* are always unisexual, with both staminate and pistillate inflorescences on the same tree. There is no obvious pattern to the distribution of staminate and pistillate inflorescences, although there are generally more staminate than pistillate ones on the same tree. Characters of the pistillate and staminate inflorescences, in particular whether there is a single capitulum or more than one, have been useful in delimiting species. Within a species, the number of capitula is always similar in the staminate and pistillate inflorescences. *Platanus occidentalis* and *P. rzedowskii* are unique in the genus in having usually a single capitulum in each inflorescence. This is clearly a reduction from a racemose or branched inflorescence, since a rudimentary extension of the rachis for a few mm beyond the single capitulum is often present, and rarely two or more capitula are produced in these species. Whether the inflorescence is spicate with sessile capitula, as is usually found in *P. racemosa* var. *racemosa,* or racemose with stalked capitula, as in most *P. racemosa* var. *wrightii,* is of less value. Both sessile and stalked capitula are found throughout the range of *P. mexicana* as well, although material from Chiapas, formerly known as *P. chiapensis,* tends most commonly to have stalked capitula.

FLORAL CHARACTERS. Floral characters are difficult to assay in *Platanus,* mainly because the flowers are small, densely crowded, and variable in the number of parts. Much confusion has occurred in the past as to what structures are present in the carpellate and staminate flowers. The difficulty is compounded by the fact that much of the available material in herbaria is well past anthesis, so for some species scant floral material is obtainable. We agree with Boothroyd (1930) and Ernst (1963) that the minute petals are consistently present in staminate flowers; in fact, in all the American species, these tend to be persistent on the staminate receptacles after the stamens have fallen off. Apparently Griggs (1909) interpreted the staminate petals as pistillodes, but in view of the lack of vasculature in these structures that interpretation is doubtful. We found no characters of taxonomic importance in the staminate petals.

In carpellate flowers, although petals appear to be absent, 3 to 5 staminodia are consistently present. According to Griggs (1909) these structures fold over and protect the carpels prior to anthesis. In the western taxa, these tend to be conspicuous and apically peltate, with some apical pubescence, resembling afunctional stamens. In the three eastern species, although initially peltate, at anthesis these are usually less conspicuous, flattened apically, and glabrate, therefore not resembling stamens as closely as in the western species. We assume that the condition found in the eastern

American species is the more derived condition.

ACHENE CHARACTERS. The fruits of *Platanus* fall as separate single-seeded indehiscent fruitlets each derived from a single carpel, and are commonly called achenes (e.g., Cronquist, 1981; Takhtajan, 1997; Watson and Dallwitz, 1992; Kaul, 1993). However, under some classifications of fruit types, because there is more than one achene per flower, together forming a multiple fruit (although the fruit is never coherent), the individually dispersed achenes are technically called achenelets (e.g., Spjut, 1994). For ease of use and consistency with common usage, we will use the term achene here. Achene characters have proven to be of great value at the species level in the three eastern species, particularly the shape of the achene tip (whether acute and tapered or more or less truncate), whether the styles are persistent or deciduous, and distribution and color of vestiture on the mature achene. In the western American taxa, the achenes are all similar, being usually more or less truncate or rounded and glabrous at maturity, with the styles usually persistent but with a greater tendency to be deciduous in *P. racemosa* var. *wrightii.* The achene characters therefore tend to differentiate the eastern species from each other, and differentiate the western species as a group from the eastern species. The achenes of *P. orientalis* appear to most closely resemble those of *P. rzedowskii* in shape and pubescence. In this treatment, the terms apex and shoulder both are used to refer to the apical part of the achene *below* the style, in other words, the region between the point where the achene begins to narrow significantly and the style begins.

SPECIES CONCEPTS IN *PLATANUS*

Traditionally, species recognized in *Platanus* have been of a more or less geographic and allopatric nature. Attempts to segregate the widespread but patchily distributed *P. occidentalis* into more than one species have met with resistance by most botanists, as have attempts to lump allopatric taxa (e.g., *P. racemosa* and *P. wrightii*). Until the present study, there has been little understanding of the nature of the taxonomic relationships and interactions of *Platanus* as viewed over the whole distribution of the genus in North America. The genus is sometimes cited in discussions of speciation (e.g., Grant, 1981) as an example in which allopatric taxa recognized as species have few or no barriers to hybridization when artificially crossed or grown in common gardens. *Platanus orientalis* and *P. occidentalis* are apparently completely interfertile, the hybrid progeny given the name *P.* ×*acerifolia.*

It seems clear from our study, however, that at least one natural zone of contact between two species of *Platanus* exists in North America. Specimens that have combinations of the characters of *P. mexicana* and *P. rzedowskii* occur in San Luis Potosí, Mexico (see Fig. 3) and are putatively from trees that are the result of hybridization and/or backcrossing between the two species. The zone of intergradation between these two morphologically distinct species appears to be restricted and narrow, probably along a single river drainage. We found no evidence of widespread introgression between the two species.

Because of the documented interfertility of morphologically very different taxa that probably have different phylogenetic relationships, the species concept utilized here is of necessity strictly a morphological one. We have chosen to recognize as species those taxa which are morphologically well-differentiated and show no obvious signs of active introgression, and as varieties taxa which are difficult to separate morphologically, show broad overlap of characters, or clinal intergradation. For example, the morphological differences between and close geographic proximity of *P. gentryi* and *P. racemosa* var. *wrightii* in Chihuahua and Sonora, with no indication of intergradation, argue for the specific distinction of the

two, while the many specimens of *P. racemosa* from California which cannot be distinguished reliably from *P. racemosa* var. *wrightii* argue for varietal instead of specific status of the latter.

The problems associated with species delimitation in *Platanus* are not unique, and in fact are commonly encountered in other woody plants. The species concept implemented here is the same as that used for the genus *Quercus* in the treatment for *Flora of North America* (Nixon, 1993). Unlike *Quercus,* the pattern seen in *Platanus* is one of wholly allopatric species that are presumably interfertile with very limited zones of contact, if any. In contrast, *Quercus* exhibits a far greater range of species patterns and interactions, including species that are sympatric without indications of hybridization, species pairs that hybridize over wide areas, and species that sporadically produce intermediates in some areas of contact, while not producing detectable hybrids in other areas. Although simpler in many respects, the pattern in *Platanus* precludes using sympatry as a test of species status, as is possible in more diverse genera. Thus, our species delimitations in *Platanus* must rely more heavily on morphology in combination with geographic distribution than is the case in many other woody groups.

Species Relationships

The pattern of character variation among *Platanus* species, if considered in light of the high level of interfertility of the taxa, points to past interspecific hybridization and reticulation as possibly important factors in the evolution of the genus. The narrow habitat requirements of all of the species probably contribute greatly to geographical isolation, especially in the western United States and Mexico, producing allopatric populations separated by inhospitable xeric expanses. These same narrow habitat requirements preclude the existence of two different species in the same geographic area without a high likelihood of contact. With changing environmental conditions, adjacent population systems (species) have probably come into contact at various times (as *P. mexicana* and *P. rzedowskii* currently do) and hybridization followed by introgression and eventual stabilization has occurred. Even morphologically well defined species are interfertile (see above). Clinal patterns, such as found between *P. occidentalis* var. *occidentalis* and var. *palmeri,* may be the result of more extensive and/or repeated secondary intergradation on a finer local scale. The weakly differentiated forms of *P. mexicana* with narrower leaves and whiter vestiture from Chiapas (*P. chiapensis* of authors) may be the result of more or less complete swamping of a previously distinct taxon. The low, dry Isthmus of Tehuantepec has probably been sufficiently wet in past times to allow dispersal of *Platanus* freely across this area. These kinds of interactions, followed by isolation and selection, have produced allopatric species of varying amounts of morphological similarity to other species that may be due to common ancestry, or instead may indicate similarity due to periodic reticulation. The interpretation of such patterns undoubtedly will require molecular analyses of extensive samples from throughout the range of each species, which is beyond the scope of the present study. Because of these concerns, we do not present a morphological cladistic analysis here.

Biogeography

In North America there are, as previously noted, two extant geographical clusters of *Platanus* species, a western one (*P. racemosa* and *P. gentryi*) and an eastern one (*P. occidentalis, P. rzedowskii,* and *P. mexicana*). The major event in the biogeography of *Platanus* in North America may have been drying trends of the late Tertiary (Axelrod & Raven, 1985), which either established or accentuated the isolation of the eastern and western species due to increased aridity in the central part of the continent.

Platanus requires abundant moisture to survive and is restricted throughout most of its range to areas of permanent or semi-permanent ground water, mostly in fully riparian situations. The genus is currently absent from the majority of the central part of the continent, although *P. racemosa* var. *wrightii* and *P. occidentalis* var. *palmeri* are found in mesic canyons in the Sonoran and Chihuahuan deserts, respectively. There is some indication that the latter two taxa may have been in contact and hybridized during past periods of higher rainfall, since in some of the characters by which *P. racemosa* var. *wrightii* differs from var. *racemosa* it approaches var. *palmeri* (e.g., leaf vestiture, ultimate venation, tendency to fewer and smaller capitula per inflorescence, deciduous styles). Some material of var. *palmeri* from Coahuila tends to have longer leaf lobes and often has two capitula instead of one per inflorescence, character states that might indicate past introgression with *P. racemosa* var. *wrightii,* or might be an atavistic genetic tendency, assuming a pluricapitulate ancestry.

The majority of *Platanus* species occupy subtropical or montane tropical habitats at present. Of the North American species, only *P. occidentalis* var. *occidentalis* extends into cold north temperate zones. On the basis of leaf morphology and its single capitulum in each inflorescence, *P. occidentalis* is almost surely one of the most highly derived taxa in the genus, which indicates that the genus (and family) is basically montane tropical or subtropical in origin as well as distribution.

Taxonomic Treatment

PLATANACEAE T. Lestib., Botanogr. Elém. 526. June 1826. TYPE: *Platanus* L.

Monogeneric as presently understood.

The following description has been adapted in part from Cronquist (1981).

Trees, monoecious, anemophilous, often large, usually restricted to watercourses, floodplains or swampy ground; Bark exfoliating in irregular smooth plates, appearing mottled cream, grayish, and green, or sometimes on lower portions of trunks and larger branches becoming furrowed and rough; Nodes multilacunar; Twigs usually pubescent with dendritic trichomes, glabrate with age, often noticeably swollen beneath each node in second year; Lenticels evident on younger twigs only, small, round and whitish; Vestiture of leaves and twigs of dendritic abietiform trichomes, sometimes with the rays (branches) reduced or suppressed, and the trichomes then appearing unbranched, e.g., as the achene comae and bud-scale vestiture. Leaves large, deciduous, with strong sweet fragrance, alternately arranged with well developed petioles, actinodromous or palinactinodromous (palmately veined with veins extending to marginal teeth) and 3–5(–7)-palmately lobed or early spring leaves and those on seedlings often pinnately veined and toothed, or (in *P. kerrii*) evergreen, craspedodromous (pinnately veined with veins extending to marginal teeth) with compound teeth; Petioles with expanded base that encloses the axillary bud. Stipules consisting of a single sheathing structure attached opposite each leaf, encircling the twig (called here the stipular sheath), this usually with 7–9 parallel veins, expanding into a 3–5-palmately lobed or merely toothed foliaceous blade that folds around the stem and petiole (called here the stipular blade), or the blade portion essentially absent or membranous, especially on lower nodes. Terminal Buds lacking, due either to abortion or presence of terminal inflorescence; Axillary Buds usually dark brown or reddish, exposed only in dormant season; outer Bud Scale (stipular?) forming a cap, usually enclosing one central and two reduced lateral shoots, true bud scales or perulae not present but each node protected by membranous stipular sheath, next season's inflorescence well developed within

the bud prior to dormancy and usually coated with a resinous yellow exudate. INFLORESCENCES unisexual (rarely bisexual on unusual specimens), terminal on new growth of 2–5 nodes (short terminal or lateral shoots) in spring, or axillary (*P. kerrii*), of spherical, dense, many-flowered capitula, racemosely or spicately arranged along a rachis or solitary on a peduncle, base of each inflorescence with a deciduous stipular sheath and with inconspicuous bracts closely subtending each capitulum, otherwise apparently ebracteate, flowering at vernation. CARPELLATE FLOWERS regular, inconspicuous, densely packed on hard compound receptacle; CARPELLATE PERIANTH of 3–4(–7) free or basally connate sepals, petals usually absent; 3–4 staminodia usually present; GYNOECIUM of (3–)4–9(–11) free carpels, these elongate-clavate with prominent suture and linear style with dry stigmatic surface in a groove from top of ovary to tip, ovary sometimes imperfectly sealed at apex, usually with many straight articulate trichomes from base extending approximately the length of the ovary, forming a coma, and often with shorter highly branched dendritic trichomes on carpel walls and at distal end; OVULES 1(–2) orthotropous, bitegmic, pendent, crassinucellar. STAMINATE FLOWERS in smaller heads without woody receptacle, deciduous following anthesis; STAMINATE PERIANTH similar to carpellate perianth, but petals usually present, petals indistinctly three-lobed, reduced or vestigial and alternating with sepals, persistent after anthesis; STAMENS 4(–9) per flower, tetrasporangiate, dithecal, anther sacs elongate, dehiscing by 1 longitudinal slit, filament very short, connective well developed and forming a (glandular?) cap over anther sacs, contiguous anther-caps of the many stamens of a head completely sealing and protecting the head until time of anthesis; POLLEN binucleate, spheroidal to subprolate, tricolpate, colpus membrane granular, infratectal exine structure columellate, exine semitectate with reticulate sculpturing. FRUIT an achene (achenelet) with attached long articulate hairs, falling separately from the receptacle in autumn or sometimes persistent, receptacles with a reticulate pattern of (4–)5(–6)-sided floral scars, often persistent on the tree through the winter (or dry season). SEED spindle-shaped, 1(–2) per carpel, cotyledons unequal; endosperm scanty.

PLATANUS L. TYPE: *Platanus orientalis* L., designated by M. L. Green, Prop. British Botanists, p. 189. 1930.

Characters those of the family.

ARTIFICIAL KEY TO ALL SPECIES AND VARIETIES WORLDWIDE

1. Evergreen trees, leaves pinnately-veined (craspedodromous), base of petiole not completely closed adaxially around axillary bud; inflorescences axillary; distribution in Laos and northern Vietnam . . . . . 1. *P. kerrii*
1. Deciduous trees, leaves palmately-veined and lobed (actinodromous), axillary buds completely enclosed in petiole base (base sometimes splitting to reveal bud late in year); inflorescences terminal on lateral or terminal relatively short new shoots of 3–5 nodes length in spring; distribution in southwest Eurasia, North America from Guatemala to California and eastern Canada.
   2. Carpellate inflorescence a raceme (or spike) of 3 or more (2–12) capitula.
      3. Leaves usually with 5 lanceolate or lanceovate lobes, the lobes longer than their basal width, central lobe often widest above its base, usually near the middle; leaf base often cordate; achenes light yellow and apically glabrous at maturity (or bearded in the Eurasian *P. orientalis*), styles persistent or not; distribution mainly west of the continental divide in southwestern U.S. and northwestern Mexico, and Eurasia.
         4. Vestiture of abaxial leaf surface (of mature leaves) of loose yellowish deciduous or semipersistent trichomes, leaves usually glabrate at maturity; fruiting capitula usually more than 18 mm in diameter.
            5. Prominent antrorse secondary teeth present on lobe margins; achenes usually persistently vestitured at apices; natural distribution in southern Europe and the Middle East; sometimes cultivated in temperate and subtropi-

cal parts of the Americas . . . . . 2. *P. orientalis*

5. Prominent secondary teeth usually absent from lobe margins, glandular teeth sometimes present, especially on "juvenile" growth; achenes usually glabrate apically at maturity; distribution in western United States and northwestern Mexico.
   6. Vestiture of abaxial leaf surface semipersistent or persistent; carpellate capitula usually sessile on inflorescence rachis; achene apex truncate or gradually tapering into usually persistent style; distribution in California and northern Baja California . . . . . 4a. *P. racemosa* var. *racemosa*
   6. Leaves usually glabrate at maturity; carpellate capitula usually attached to rachis by stalks to 5–15 mm long; achene apex usually rounded or truncate, styles usually deciduous; distribution in Arizona, New Mexico, Sonora and western Chihuahua . . . . . 4b. *P. racemosa* var. *wrightii*
4. Vestiture of abaxial leaf surface persistent, whitish, obscuring the surface even on old leaves; capitula usually less than 18 mm in diameter; distribution in southern Sonora and adjacent Sinaloa and Chihuahua . . . . . 3. *P. gentryi*

3. Leaves usually with 3 deltoid-acuminate or narrowly triangular lobes (occasionally unlobed), the lobes usually about equal to or less than their basal width, central lobe usually widest at or near its base, leaf base usually broadly rounded or truncate, typically not cordate (except sometimes in *P. mexicana* var. *interior*); achenes brownish, sparsely puberulent on exposed apex, styles persistent; distribution in eastern and southeastern Mexico, and Guatemala.
   7. Vestiture of abaxial leaf surface dense enough to give a white, cream or yellowish aspect to leaf surface; carpellate capitula usually 3 or more per inflorescence; achenes usually 5–6 mm long excluding style; broadly distributed in eastern and southeastern Mexico and Guatemala . . . . . 5a. *P. mexicana* var. *mexicana*
   7. Vestiture of abaxial leaf sparse or leaves glabrate at maturity; carpellate capitula usually 2–3 per inflorescence; achenes usually 7–9 mm long excluding style; distribution in central Mexico in Querétaro, San Luis Potosí, Guanajuato and Hidalgo . . . . . 5b. *P. mexicana* var. *interior*

2. Carpellate capitulum solitary, terminal on a peduncle from 30–80 mm long, or rarely with 2–3 sessile capitula in spike.
   8. Vestiture of abaxial leaf surface cream or brownish, loose, semipersistent to deciduous, mature leaves glabrate except along primary veins; fruiting capitula yellowish, usually 12–30(–40) mm in diameter (excluding styles); mature achenes with more or less glabrous truncate shoulder (apex), but with glandular dendritic trichomes on apical third of achene sides, styles usually brittle, deciduous.
      9. Major lobes of leaves usually with several secondary teeth, vestiture of abaxial surface semipersistent or deciduous; fruiting capitulum usually more than 20 mm in diameter (excluding styles); eastern to south-central U.S. . . . . 7a. *P. occidentalis* var. *occidentalis*
      9. Major lobes of leaves usually with entire margins or with a few scattered secondary teeth, abaxial leaf surface always glabrate with age; fruiting capitulum usually less than 20 mm in diameter (excluding styles); distribution mostly from Edwards Plateau of Texas to desert ranges of eastern Coahuila and Nuevo León . . . . . 7b. *P. occidentalis* var. *palmeri*
   8. Vestiture of abaxial leaf surface white or cream, tight, persistent, the veins usually with darker brownish trichomes; fruiting capitula (20–)25–35(–40) mm in diameter (excluding styles); mature achenes densely bearded with white or cream trichomes at apex, gradually tapering into the persistent, thin and flexuous styles, these often bearded as well, the capitula appearing whitish and woolly; distribution on lower east slopes of Sierra Madre Oriental of northeastern Mexico . . . . . 6. *P. rzedowskii*

I. *PLATANUS* SUBG. *CASTANEOPHYLLUM* J. F. Leroy in Compt. Rend. Séances Acad. Sci., Sér. 3, Sci. Vie. 295(3): 251, 254. 1982.

Characters of the genus, but differing from subgenus *Platanus* in the following characters: trees evergreen; leaves pinnately veined, craspedodromous, not lobed; petiole base not completely enclosing axillary bud; inflorescences apparently axillary.

1. PLATANUS KERRII Gagnepain, Bull. Soc. Bot. France 86:301. 1939. TYPE: **LAOS** (not seen).

Not treated here. Described from Laos, and more recently discovered in northern Vietnam (Leroy, 1982).

II. ***PLATANUS*** L. SUBG. ***PLATANUS***

Characters of the genus, but differing from subg. *Castaneophyllum* in the following characters: trees with leaves winter-deciduous (but brown leaves sometimes remaining on the tree through the dormant season); mature leaves actinodromous or palinactinodromous, 3–5(–7) lobed (rarely some juvenile or sprout leaves pinnate, unlobed); base of petiole completely enclosing axillary bud, but sometimes splitting adaxially late in the season; inflorescences terminal.

2. PLATANUS ORIENTALIS L., Sp. Pl. 999. 1753. TYPE: **EUROPE.** LECTOTYPE: Herb. Clifford.: 447, Platanus No. 1 (BM). LT designated by Barrie & Nixon, Reg. Veg. 127: 77 (1993).

Not treated here. *Platanus orientalis* resembles our western North American sycamores in the racemose nature of the carpellate inflorescence, more or less glabrate leaves, and relatively narrow leaf lobes, with the central lobe consistently longer than broad. It differs from these species, however, in the overall shape and rather profuse secondary lobing and teeth of its leaves, and in its usually densely bearded achenes, which resemble those of *P. rzedowskii* described below. *Platanus orientalis* is not as commonly cultivated as what is apparently a hybrid derivative of *P. orientalis* and *P. occidentalis* (*P.* ×*acerifolia* (Ait.) Wild.).

3. **Platanus gentryi** Nixon & Poole, sp. nov. TYPE: **MEXICO. Sinaloa:** Mpio. Badiraguato: Sierra Suratato, Canyon Tarahumare, 17–24 Mar 1945, *H. S. Gentry 7154* (HOLOTYPE: GH!; ISOTYPES: MICH!; NY!). Fig. 6.

Arbores cortice exfolianti, folia decidua, laminis lobatis lobis profundis palmatis (3–)5(–7) lanceolatis vel lancei-ovatis subtus dense pubescentibus pilis albis vel canis persistentibus, marginibus saepe dentatis dentibus antrorsis cuneatis interdum nullis, inflorescentiae carpellatae 3–7-capitulatae capitulis 11–18 mm diametro unoquoque pedunculato, achaenia 6–9 mm longa apice ad maturitatem glabra, stylis saepe persistentibus.

TREES to 30 m or more tall, narrowly pyramidal; BARK exfoliating, appearing mottled; TWIGS 2.0–2.5 mm in diameter when young, with dense to sparse vestiture of dendritic trichomes, reddish beneath vestiture, older twigs glabrate, reddish-brown or gray or sometimes persistently dendritic-puberulent. LEAF BLADES to 8–20(–25) cm long by 10–20(–30) cm wide, orbicular to ovate or obovate in outline, deeply lobed, adaxial surface grayish-green, at first sparsely pubescent, soon glabrate, the major veins usually prominent, lighter colored but not raised above the surface, abaxial surface persistently densely white or grayish canescent, the vestiture fine, obscuring the blade surface except in older weathered leaves, major veins raised above the abaxial surface and prominently yellowish or brown due to "glandular" dendritic vestiture; LEAF LOBES usually (3–)5(–7), lanceolate or lance ovate, with tapering apices ending in glandular tips, central lobe 2 to 2 & ½ times as long as broad, to 15 cm long by 5 cm wide, apical lateral lobes ⅔ to $^{9}/_{10}$ the length of central lobe and of similar shape, basal lateral lobes ⅓ to ⅔ length of central lobe, or occasionally lacking, leaves sometimes smaller and unlobed on first node of fertile shoots, margins of lobes with closely spaced gland-tipped teeth, often more than one tooth arising from each branched secondary vein, the teeth to 15 mm long, antrorsely directed, the glandular tips usually 1–2 mm long, or lobes rarely with more or less entire margins and lacking these teeth; SECONDARY VEINS arcuate, anastomosing near margins or passing into marginal teeth; TERTIARY VEINS percurrent but often branched, not prominently straight or convex; LEAF BASES

FIG. 6. Holotype of *Platanus gentryi* (GH). Scale marked in cm.

cordate to truncate, occasionally cuneate, blade usually not decurrent along petiole proximally from axil of major lateral veins, occasionally extending 5–10 mm past this point; PETIOLES at first sparsely to densely clothed with short dendritic trichomes, later glabrate, to (25–)50–70(–86) mm long. STIPULES membranous, usually with brownish trichomes, sometimes (especially on rapidly growing shoots) foliose, lobed, with glandular teeth similar to those of the leaves. AXILLARY BUDS reddish brown, smooth. CARPELLATE INFLORESCENCES lax, racemose or rarely spicate, of (1–)5–7 stalked or subsessile capitula, capitula at maturity (11–)13–15(–18) mm in diameter,

yellowish. CARPELLATE FLOWERS: STAMINODIA conspicuous in young capitula, about as long as ovaries, orange-colored, with peltate cap (to 2.5 mm broad) bearing dendritic and/or unbranched trichomes; CARPELS usually 6 per flower; OVARIES in flowers and young fruit with short "glandular" dendritic trichomes on sides, these deciduous or obscured by the coma of mature achenes; STYLES in flowers and young fruit reddish, apically circinate. STAMINATE INFLORESCENCES of 3–4 subsessile capitula. STAMINATE FLOWERS with connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. MATURE ACHENES 6–9 mm long, truncate or abruptly tapered, asymmetrical at apex, smooth, yellow, glabrous, styles usually persistent, to 3–4 mm long; COMA yellowish, individual trichomes about the length of the achene body; achenes usually falling in autumn (Figs. 4 & 6).

DISTRIBUTION AND HABITAT: At ca. 1000 m elevation in wet subtropical canyons of southern Sonora, northern Sinaloa and adjacent Chihuahua (Fig. 2). Reaching massive proportions, with a narrow, pine-like habit.

The wet subtropical habitat and abundant morphological differences should preclude confusion of this taxon with the typically more glabrate *P. racemosa* var. *wrightii* of the mountains to the north. The species is named in honor of Howard Scott Gentry (1903–1993), who collected the majority of specimens seen of this species, and who contributed so much to the botanical knowledge of the area in which it grows, especially the Río Mayo of Sonora.

In recent treatments, *Platanus gentryi* has been referred to either *P. racemosa* or *P. wrightii* (Martin et al., 1998; Felger et al., 2001). Although *P. gentryi* occurs geographically relatively close to populations of *P. racemosa* var. *wrightii* in Chihuahua, we have seen no indication of intermediate material from this area. This affirms the decision to recognize this taxon at the specific level, since all the taxa we have considered conspecific varieties show closer morphologic similarity and broad or narrow zones of intergradation. We consider this species to be relictual in distribution, and possibly similar to the ancestral type from which *P. racemosa* was derived.

SPECIMENS EXAMINED: **MEXICO. Chihuahua**: Mpio. Batopilas: Above La Bufa, along Arroyo Samachique, *Bye 3387* (MEXU, TEX); W of La Bufa, 30 Jul 1977, *Bye 7768* (CAS, GH, MEXU, MICH, NY, SD); Santa Rosa, *Pennington 283* (TEX); Guaqueybo, 2 Apr 1955, *Pennington 22* (TEX). **Sinaloa**: Mpio. Badiraguato: Sierra Suratato, Canyon Tarahumare, below Jolla, *Breedlove 15606* (ENCB, F, LL, MEXU, MICH); Sierra Suratato, Quebrado de Manzana, 10–14 Sep 1941, *Gentry 6585* (MICH, MO, ARIZ); Los Alisos, 4 Mar 1940, *Gentry 5807* (ARIZ, GH, MEXU, MICH, MO, NY); Tamiapa (Tameapa), *Gentry 5862* (ARIZ, GH, MICH, MO, NY). **Sonora**: Vinata, Rio Mayo, 8 Jul 1935, *Gentry 1477* (MEXU, MO, ARIZ); La Vinatería, 26 Dec 1990, *Felger 90-706* (TEX).

4a. PLATANUS RACEMOSA Nutt. var. RACEMOSA. *Platanus racemosa* Nutt., N. Amer. Sylva 1:47. pl. 15. 1842. *Platanus orientalis* L. var. *racemosa* (Nutt.) Kuntze, Rev. Gen. 2:636. 1891. TYPE: **UNITED STATES. California**: Santa Barbara, Nuttall s.n. (HOLOTYPE: PH!; ISOTYPE: GH!). The specimen at PH, labelled in Nuttall's hand and marked with an asterisk as his designation of a new species, is accepted as the holotype, over the GH specimen similarly marked in Nuttall's hand.

Platanus occidentalis sensu Hook. & Arn., Bot. Beech. Voy. 160. 1833, non *P. occidentalis* L., Sp. Pl. 999. 1753.

Platanus mexicana sensu Torr. in Sitgreaves, Rep. Exp. 172. 1853, non *P. mexicana* Moric., Pl. Nouv. Amér. 39. 1837.

Platanus californica Benth, Bot. Voy. Sulph. 54. 1844. TYPE: **UNITED STATES. California**: San Francisco (not seen).

TREES to 30 m or more tall; BARK exfoliating, appearing mottled, usually even at base of large trunks; TWIGS densely yellowish tomentose in first year, glabrate and reddish brown or gray in second year, older twigs usually grayish. LEAF BLADES to 8–18(–35) cm long by 10–25(–53) cm wide, orbicular to broadly ovate in outline, deeply palmately lobed, adaxial surface grayish-green, on new leaves usually densely rusty-tomentose, vestiture sparser as blade expands, the surface soon glabrate, major veins usually prominent, lighter colored, but not conspicuously raised above the surface, abaxial surface loosely tomentose with yellowish dendritic trichomes, vestiture semipersistent or persistent, sometimes deciduous with age, usually not completely obscuring the blade surface, the major veins raised above the abaxial surface and prominently yellowish or brown due to glandular dendritic vestiture; LEAF LOBES usually 5(–7), lanceolate or lance ovate, with tapered apices ending in glandular tips, central lobe 1 & ½ to 4 times as long as wide, to 20 cm long by 6 cm wide, apical lateral lobes ca. ⅔ to $^{9}/_{10}$ as long as central lobe and of similar shape, basal lateral lobes ca. ⅓ to ⅔ length of central lobe or occasionally reduced or lacking, margins of lobes entire, smooth, only occasionally with teeth, if teeth are present these usually not more than one per secondary vein; SECONDARY VEINS curved-ascending and anastomosing near margins, or sometimes passing into marginal teeth; TERTIARY VEINS percurrent but often branched, not prominently straight or convex percurrent; LEAF BASES cordate to truncate, occasionally cuneate, blade usually not decurrent along petiole beyond point of branching of major lateral veins (primary vein branching therefore basal) or sometimes decurrent 5–10 mm proximally from primary vein branching, vein branching then suprabasal; PETIOLES usually persistently pubescent, to (25–)30–60(–75) mm long. STIPULES membranous or often foliose, with relatively smooth entire margins. AXILLARY BUDS reddish brown, smooth. CARPELLATE INFLORESCENCES lax, spicate or rarely racemose, to 25 cm long, of 3–7(–8) sessile or stalked capitula, capitula at maturity (12–)14–22(–24) mm in diameter, yellowish. CARPELLATE FLOWERS: STAMINODIA not observed; CARPELS usually ca. 6(–9) per flower; OVARIES in flowers and young fruits with short glandular dendritic trichomes on sides; STYLES in flowers and young fruit circinate, reddish with orangish peltate staminodia (3–4 per flower) appearing to be interspersed among ovaries. STAMINATE INFLORESCENCES spicate, of 2–4(–5) subsessile capitula, usually 8–9 mm diameter. STAMINATE FLOWERS with STAMENS 1.6–2.3 mm long with reddish, peltate connective caps bearing dense short branched and/or unbranched trichomes, these less dense on heads at anthesis, unbranched articulate trichomes to 2 mm long attached to receptacle and often persistent after anthesis, as are grayish "petals." MATURE ACHENES 6–7 mm long, smooth, yellow, glabrous or pubescent on distal third of body, shoulder glabrous, truncate or tapering into the persistent or sometimes deciduous style, style ca. 4–5 mm long, glabrous; COMA of yellowish or brownish articulate trichomes ca. as long as achene body, achenes falling in autumn or sometimes remaining on heads through the winter (Fig. 4).

DISTRIBUTION AND HABITAT: Usually found below 1500 m elevation in cismontane central and southern California and northern Baja California, Mexico (Fig. 2). Restricted to riparian forest, usually along perennial streams, but found in seasonally dry arroyos as well, presumably where high water tables remain through the summer drought. Cultivated widely in California, natural stands often being prominent features of parks and recreational areas, especially in southern California where large na-

tive shade trees are relatively few in number. Flowering from February into March and occasionally as late as April.

The typical variety differs from var. *wrightii* in its generally more densely and persistently tomentose leaves, petioles, and twigs, and carpellate inflorescences that are usually longer (to 25 cm), with usually 4 to 6 capitula. The capitula are usually sessile on the main axis of the inflorescence, but occasionally pedunculate with secondary peduncles up to 5 to 10 mm long, while in var. *wrightii* the capitula are more consistently pedunculate. The achenes tend to be more tapered apically than those of var. *wrightii,* and the styles are usually persistent as opposed to the often deciduous styles of the latter variety. The tertiary venation of var. *racemosa* is usually more prominent than in var. *wrightii,* as is discussed in more detail below. Although the above differences in characters may seem major in the context of differences among other *Platanus* species, there can be little doubt that the two taxa considered here share a common ancestry, and there does not seem to be enough stability in the characters which differentiate the two taxa to maintain them as separate species. Specimens from throughout the range of *P. racemosa* in California can be found which approach var. *wrightii* closely in having various combinations of the following character states: pistillate heads pedunculate, styles deciduous, achenes truncate, and leaves very glabrate with less prominent tertiary venation. These trees are particularly abundant in some Baja California and southern California localities. Trees from Andreas Canyon, Riverside County, California, approach *P. racemosa* var. *wrightii* very closely and were considered that variety by Benson (1943). Similar material occurs sporadically in northern and central California as well. Field studies and common garden analyses of these populations might shed light on the dynamics of the interaction of the two taxa. Since the vast majority of specimens from California are easily separable from var. *wrightii* on the basis of the characters outlined above, taxonomic segregation of the two entities is warranted. We have chosen to follow Benson (1943) and include var. *wrightii* as a variety of *P. racemosa* because this reflects its close relationship to the Californian taxon and the broad overlap in character states of the two taxa. At the same time, we recognize that some workers may prefer to maintain the specific rank of var. *wrightii* (e.g., Kaul, 1993); since species concepts are quite problematic in woody species in general, and cannot easily be standardized, we feel that in the case of this taxon, the decision to recognize it as a variety or a species is somewhat arbitrary. In our experience the characters separating these two taxa are too variable and inconsistent for identification without the help of geographic information. We have chosen the rank that we believe is most consistent with our classification of the remainder of the genus in North America, and best reflects the close relationship of the two taxa included as varieties of *P. racemosa.*

REPRESENTATIVE SPECIMENS EXAMINED: **UNITED STATES. California**: Alameda Co: Mt. Hamilton Range, end of Corral Hollow, *Gould 877* (ARIZ, F, GH, NY, PH, US); Colusa Co: Sycamore Slough, *Stinchfield 395* (A, DS, NY); Kern Co: 6 km above Richbar, *Howell 51794* (CAS, MEXU, NY); Los Angeles Co: Pasadena, 4 Apr 1901, *Grant 1007* (CAS, DS(3), GH, MICH, PH, US); Santa Monica Canyon, *Eastwood 9285* (A, CAS); Rock Creek, San Gabriel Mtns, 2–4 Jul 1908, *Abrams & McGregor 529* (DS, GH, US); Monterey Co: Carmel Valley, 31 Mar 1970, *Howell 46495* (CAS); Jolon, *Eastwood 4164* (GH, A, CAS); Orange Co: Rancho Santa Ana, Dec 1934, *Johnson 6276* (ARIZ); San Benito Co: near San Juan, 11 Mar 1910, *Pieters s.n.* (MICH); San Diego Co: Lakeside, *Carlson s.n.* (A, CAS); Campo road, Sweetwater River Bridge, *Gander 840* (SD); Canyons near San Diego, 31 Oct 1926, *Bailey & Bailey 7911* (BH); San Luis

Obispo Co: San Luis Obispo, *Rose 36071* (A, CAS, DS, F, MICH, NY); Santa Barbara Co: Santa Ynez Mtns, 9 Jul 1959, *Pollard s.n.* (CAS, LL). **MEXICO. Baja California:** Between San Quintín and El Rosario, Arroyo Socorro, *Wiggins & Thomas 22* (DS, ENCB, MEXU, MICH, US); San Ysidro Ranch, *Mearns 3871* (DS, GH, NY, US); 32 km north of Ensenada, *Wiggins & Gillespie 4003* (CAS, DS, F, GH, MICH, MO, SD, US).

4b. PLATANUS RACEMOSA Nutt. var. WRIGHTII (S. Wats.) Benson, Amer. J. Bot. 30:237. 1943. *Platanus wrightii* S. Wats., Proc. Amer. Acad. 10:349. 1875. *Platanus racemosa* Nutt. ssp. *wrightii* (S. Wats.) E. Murray, Kalmia 12:23. 1982. TYPE: **UNITED STATES. Arizona:** Santa Cruz Co: on the Sonoita near Deserta Ranch, 16 Sep 1851, *Wright 1880* (HOLOTYPE: GH!; ISOTYPE: US!). The type collection is apparently Wright's field number 536, but distributed by Gray as number 1880 (fide notation by I. M. Johnston).

Platanus racemosa sensu Watson, Pl. Wheeler 16. 1847, non *P. racemosa* Nutt., N. Amer. Sylva 1:47. 1842.

Platanus mexicana sensu Torr. in Emory, Notes Mil. Reconnois. 151. 1848, non *P. mexicana* Moric., Pl. Nouv. Amér. 39. 1837.

TREES to 30 m or more tall; BARK exfoliating, appearing mottled, usually even at base of large trunks; TWIGS densely yellowish tomentose in first year, glabrate and reddish brown or gray in second year, older twigs usually grayish. LEAF BLADES to (8–)10–25(–35) cm long by (9–)10–30(–50) cm wide, orbicular to broadly ovate in outline, deeply palmately lobed, adaxial surface grayish-green, vestiture at first sparse, soon glabrate, the major veins usually prominent, lighter colored, but not raised above the surface, abaxial surface loosely pubescent with yellowish hairs, pubescence semipersistent or usually glabrate with age, usually not completely obscuring the blade surface, the major veins raised above the abaxial surface and prominently yellowish or brown due to "glandular" dendritic vestiture; LEAF LOBES (3–)5(–7), lanceolate or lance-ovate, with tapering apices ending in glandular tips; central lobe 1 & ½ to 4 times longer than wide, to 15 cm long by 7.5 cm wide, margins of lobes entire, smooth, only occasionally with teeth, if so, then usually not more than one tooth per secondary vein (and usually then only on rapidly growing shoots or "juvenile" growth); SECONDARY VEINS curved-ascending and anastomosing near margins, or sometimes passing into marginal teeth; TERTIARY VEINS percurrent but often branched, often obscure, not prominently straight or convex percurrent, ultimate venation and areolation regular, prominent; LEAF BASES usually cordate or reflexed (to 180°) to truncate, rarely cuneate, blades usually not decurrent along petiole proximally from axil of major lateral veins (veins therefore basal) or occasionally decurrent 5–10 mm past this point (veins then suprabasal); PETIOLES usually persistently pubescent, to (25–)30–50(–75) mm long. STIPULES membranous or often foliose, with relatively smooth entire margins. AXILLARY BUDS reddish brown, smooth. CARPELLATE INFLORESCENCES lax, racemose or spicate, of (2–)3–5(–8) stalked or rarely sessile capitula, capitula at maturity (13–)16–20(–25) mm in diameter, yellowish. CARPELLATE FLOWERS: STAMINODIA 3–4, orangish, peltate, about as long as the ovaries, and appearing interspersed among them; CARPELS ca. 6(–9) per flower; OVARIES in flowers and young fruit with short "glandular" dendritic trichomes on sides; STYLES in flowers and young fruit reddish, circinate. STAMINATE INFLORESCENCES of 2–4(–5) subsessile capitula, connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. STAMINATE FLOWERS with STAMENS (anthers) 2–3 mm long. MATURE ACHENES (5–)6–7(–8) mm long, truncate or abruptly tapering at the apex, smooth,

yellow, glabrous or sometimes with sparse dendritic vestiture on distal third of body, shoulder glabrous, style brittle, usually deciduous, but sometimes persistent and then glabrous; COMA of brown or yellowish straight unbranched articulate trichomes about as long as achene body and attached at its base; achenes falling in autumn or sometimes remaining on heads through the winter (Fig. 4).

DISTRIBUTION AND HABITAT: Typically at higher elevations than var. *racemosa,* at mostly 1200 to 1800 m, and a somewhat smaller, more graceful tree. Montane streams and rivers in southern Arizona, southwestern New Mexico, Sonora and northern and western Chihuahua, Mexico (Fig. 2). Vernation and flowering mainly in April.

This variety differs from var. *racemosa* in the generally more glabrous leaves, petioles, and twigs, the tendency for the carpellate inflorescence to have fewer (often about 3) capitula that are pedunculate on the rachis, and the usually more truncate achenes and deciduous styles. With the exception of the pedunculate capitula, these character trends in *P. racemosa* var. *wrightii* constitute morphologic similarity to *P. occidentalis* var. *palmeri* (see below). This morphological similarity may be due to past contact and introgression, or parallel evolution in response to more xeric desert habitats encountered by the latter two varieties, as compared with *P. racemosa* var. *racemosa* and *P. occidentalis* var. *occidentalis,* respectively.

REPRESENTATIVE SPECIMENS EXAMINED: **MEXICO. Chihuahua**: Mpio. Janos: Carretas, 26–28 Aug 1939, *White 2503* (F, GH, MICH, NY, US); Salto Canyon, Babícora, 23 Jul 1937, *LeSueur 1331* (F, MO). **Sonora**: vicinity of Hermosillo, 8 Mar 1910, *Rose, Standley & Russell 12538* (NY, US); 5 km N of Imuris, 30 Oct 1932, *Wiggins 6210* (DS, US); Cañón de Comajito, 16 km E of Imuris, 7 May 1948, *Wiggins 11654* (DS, SD, TEX, US); Río Gavilán, at Tres Ríos, 26 Aug 1952, *Tucker 2541* (ARIZ, CAS). **UNITED STATES. Arizona**: Cochise Co: Paradise, 16 Oct 1906, *Blumer 1262* (ARIZ, DS, F, GH, MO, NY, US); Chiricahua, Oct 1906, *Blumer 1630* (ARIZ(2), F, GH(2), NY, US); Pima Co: Santa Catalina Mtns, 26 Apr 1939, *Ehlers & Ehlers 6398* (GH, MEXU, MICH); Santa Rita Mtns, 27 Sep 1880, *Engelmann & Sargent s.n.* (A, PH); Pinal Co: Pinal Mtns, Queen Cyn, 16 Jul 1931, *Peebles 7942* (A, NY); Santa Cruz Co: Santa Rita Mtns, Madera Cyn, 25 Mar 1926, *Loomis et al. 1360* (ARIZ); Santa Rita Mtns, 9 June 1884, *Pringle s.n.* (F, NY); Banks of the Rillita, 16 Apr 1881, *Pringle s.n.* (A, F(2), MO, NY, US); Verde Creek beyond Payson, 13 May 1929, *Eastwood 17223* (CAS, MICH). **New Mexico**: Catron Co: Whitewater Canyon, 18 Jun 1966, *Correll & Correll 33071* (LL); Mogollon Mtns, 1 Jul 1887, *Rusby 370* (A, NY(2)); Sierra Co: Animas Creek, 13 Jul 1904, *Metcalfe 1111* (CAS, F, GH, NY, US);

5a. PLATANUS MEXICANA Moric. var. MEXICANA. *Platanus mexicana* Moric., Pl. Nouv. Amér. 39. pl. 29. 1837, non *P. mexicana* sensu Standley. *Platanus occidentalis* L. var. *mexicana* (Moric.) Janko, Bot. Jahr. 11:451. 1890. TYPE: **MEXICO.** "circa Mexico," *Berlandier s.n.* (HOLOTYPE: G!, photo of holotype, A!). The specimen at G, mounted on two sheets but obviously a single collection, matches the illustration accompanying the original description, although one of the leaves of the figured twig has been detached and mounted on the second sheet.

Platanus lindeniana M. Martens & Galeotti, Bull. Acad. Roy. Bruxelles 10:342. 1843. *Platanus orientalis* var. *lindeniana* (M. Martens & Galeotti) Kuntze, Rev. Gen. 2:636. 1891. *Platanus occidentalis* L. var. *lindeniana* (M. Martens & Galeotti) Jaen., Nova Acta Acad. C. L. C. G. Nat. Cur. 77:118 & 121. 1899.—TYPE: **MEXICO. Veracruz:** Xalapa, *Linden 9* (LEC-

TOTYPE (here designated): GENT! ISOLECTOTYPE: BR!). Martens and Galeotti clearly cited *Linden 9* in the original publication. The specimen of *Linden 9* at BR bears the label of the Wesmael herbarium, indicating that it was probably obtained by BR sometime after the original publication. It is fragmentary, and consists of a a single detached leaf and a single detached capitulum. The specimen of *Linden 9* at GENT is a complete specimen, consisting of a twig with a leaf and a complete inflorescence, and therefore matches the protologue more closely than the specimen at BR. We therefore choose the GENT specimen as lectotype.

Platanus chiapensis Standl., Contr. U. S. Natl. Herb. 20:212. 1919. TYPE: **MEXICO. Chiapas:** Zinacantán, 16 May 1904, *E. A. Goldman 993* (HOLOTYPE: US!; ISOTYPE: NY!).

Platanus oaxacana Standl, Contr. U. S. Natl. Herb. 20:213. 1919. TYPE: **MEXICO. Oaxaca:** San Miguel Alborrados, 2 Jul 1894, *E. W. Nelson 540* (HOLOTYPE: US!).

TREES to 35 m tall; BARK exfoliating, appearing white-mottled; TWIGS tomentose with whitish or yellowish dendritic trichomes when young, usually brown or reddish-brown beneath vestiture, older twigs brown or gray, glabrate or sometimes persistently dendritic-puberulent. LEAF BLADES to (3–)8–20(–25) cm long by 10–20(–30) cm wide, broadly to narrowly ovate in outline, shallowly to deeply lobed, thick and leathery, adaxial surface grayish-green, at first with sparse vestiture of dendritic trichomes, soon glabrate, the veins usually slightly impressed, abaxial surface with very dense, fine, interlocking white, grayish or yellowish vestiture obscuring blade surface except in older weathered leaves, the major veins raised above the abaxial surface and prominently yellowish or brown due to "glandular" dendritic vestiture; LEAF LOBES usually (0–)3(–5), broadly deltoid to narrowly triangular, but usually broadest at or very near the base, broadly acuminate at tips, entire or with sessile marginal glands, occasionally with triangular teeth, apices glandular or not, central lobe ½ to 2 times as long as broad, to 20 cm long by 6 cm wide, two lateral lobes usually ⅓ to ⅔ the size of the central lobe and of similar shape, or the lateral lobes poorly developed or lacking, especially in the first leaf of a fertile shoot; LEAF BASES broadly rounded to truncate, but usually decurrent along petiole from major vein axil for 10–20 mm and then abruptly cuneate, primary vein branching therefore suprabasal, blade often minutely peltate at juncture with petiole, the primary vein usually branching only twice to form two lateral primary veins, occasionally each of these again branching to form two lateral veins on each side, these then passing into rudimentary basal lobes; SECONDARY VEINS of a given primary vein usually more or less parallel, extending to marginal glands, teeth, or anastomosing near the margins; TERTIARY VEINS usually prominent, straight or convex-percurrent, ultimate venation obscured abaxially by dense tomentose vestiture; PETIOLES at first tomentose, later glabrate, to (25–)30–55(–90) mm long. STIPULES usually foliose, with sharply pointed lobes, sometimes with teeth similar to those of the leaves. AXILLARY BUDS at first yellowish or rusty pubescent with unbranched trichomes, later glabrate, reddish brown, smooth. CARPELLATE INFLORESCENCES lax, racemose or spicate, of (3–)5–7 stalked or sessile capitula, overall length 100–260 mm or more, length to first capitulum 40–50(–80) mm, capitula at maturity (14–)18–25(–30) mm in diameter, brownish. CARPELLATE FLOWERS: STAMINODIA 3–4, reddish, strap-shaped, apically ampliate but not usually peltate, glabrous, about as long as ovaries, not conspicuously visible in young capitula without dissection, but often persistent on capitulum receptacle after achenes are shed; CARPELS (4–)6(–9) per flower; OVARIES in flowers and young fruit with short glandular branched trichomes on sides and apex; STYLES in flowers and young fruit circinate, reddish. STA-

MINATE INFLORESCENCES of 2–4 subsessile capitula. STAMINATE FLOWERS with stamens 2–3 mm long, connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. MATURE ACHENES (3–)5–7 mm long, brownish-yellow, rounded at apex or abruptly tapered into the persistent style (to 3–5 mm long), apically puberulent with detachable short-branched cream or yellowish dendritic trichomes, usually glabrate on sides; COMA of brownish straight ascending unbranched articulate trichomes usually about two-thirds the length of the body attached at its base; achenes falling in late summer or autumn or rarely remaining on heads through the winter (Fig. 4).

DISTRIBUTION AND HABITAT: Occurring along streams from 150 to 1850 m, mostly at 900 to 1650 m, surrounded by vegetation generally considered tropical forest (various types), oak, oak-pine, or cloud forest, in eastern Mexico from Veracruz to Chiapas and also in Guatemala.

The typical variety differs from the following variety by its denser and more persistent abaxial leaf vestiture, its narrower leaves often with narrower lobes, and in a tendency to have three or more capitula per carpellate inflorescence as opposed to 1 to 3.

The bulk of the material from Veracruz has been previously placed in *P. lindeniana.* Our examination of type materials supports placing *P. lindeniana* in synonymy under *P. mexicana* var. *mexicana,* as was independently concluded by Nee (1981). The leaf and achene characters of both the lectotype and isolectotype specimens of *P. lindeniana* cited above are completely consistent with *P. mexicana* var. *mexicana* as circumscribed here, and the racemose inflorescence of the lectotype further supports the conspecificity of these types with the type of *P. mexicana.* The type locality of *P. lindeniana* is well known, with much additional material of *P. mexicana* var. *mexicana* collected in the general vicinity in recent years.

Platanus oaxacana appears to be based on a somewhat aberrant specimen in terms of the degree of toothing of the leaves, but otherwise is consistent with *P. mexicana* var. *mexicana* in all important diagnostic characters. Based on the single collection from the type locality, we must consider this a synonym of *P. mexicana.*

We were not able to find consistent differences between material from Chiapas (as *P. chiapensis* in most herbaria) and other parts of the range of *P. mexicana.* However, some morphological trends in the southern material are apparent. A greater portion of trees from Chiapas tend to have narrower, more acute leaf lobes, a whiter leaf vestiture, and more leathery leaves than trees from Veracruz and adjacent areas. Nevertheless, both forms are found intermixed in Chiapas and Veracruz, and the characters do not appear to hold together in suites as would be expected if two well defined taxa were interacting. There are likewise some trends in number and size of capitula, but these trends break down quickly when large numbers of specimens are examined. Trees with both pedunculate and sessile capitula occur in Chiapas as well as to the north. These characters do not seem to be strongly correlated, and we have observed all combinations of the characters which at first might seem to separate the two putative taxa. In our opinion the extreme forms previously called *P. chiapensis* do not show the degree of consistent differences found in the extremes of the other varietal taxa we are recognizing. More field work, observation of flowering times, and possibly crossing experiments in eastern and southern Mexico are necessary before a final decision can be made, but the evidence at present argues strongly against recognizing *P. chiapensis* at either specific or varietal rank. If *P. chiapensis* were in fact a distinct species, it must occur sympatrically with *P. mexicana* over a broad area, a situation which would be unique within the generally allopatric species pattern in *Platanus.*

REPRESENTATIVE SPECIMENS EXAMINED: **GUATEMALA. Quiché**: Finca San Francisco, Cotzal, 5 Dec 1934, *Skutch 1839* (A, F, NY, US); same locality, 9 Feb 1945, *Sharp 45154* (F, MEXU). **MEXICO. Chiapas**: Mpio. Ángel Albino Corzo, Río Cuxtepec, 7 Apr 1981, *Breedlove 50734* (LL, TEX); near Siltepec, 4 Mar 1945, *Matuda 5124* (LL (2)); Mpio. Ixtapa, 20 Apr 1966, *Laughlin 717* (DS); Mpio. Tenejapa: Tanate River, 13 Jul 1964, *Breedlove 6348* (ENCB); Río Cachinula, 2 Mar 1951, *Miranda 7076* (MEXU); Tierra Colorada between Chiapa & Las Casas, 1941, *McBryde s.n.* (F(2)); Rincón Chamula, 12 km NW of Pueblo Nuevo Solistahuacán, 23 Jan 1965, *Raven & Breedlove 19783* (ENCB, F, MICH). **Hidalgo**: Río (Cueva los Caliches), San Bartolo Tutotepec, 3 Jun 1972, *Leyva 648* (ARIZ, CAS, ENCB, MICH). **Oaxaca**: Mpio. Teotitlán del Camino, 8 km NW de Huautla de Jiménez, 27 Apr 1978, *Sousa, Soto & Zárate 9344* (MEXU); Huautla de Jiménez, 23 May 1963, *Vela 1334* (ENCB); Base of Teotitalpam, 1 Jul 1939, *Schultes 773* (GH); Mpio. Tuxtepec, Río Usila, 27 Sep 1973, *Hill 1784* (A, NY). **Puebla**: Mpio. Ahuacatlán, 3.6 km S of Ahuacatlán, 14 Apr 1985, *Tenorio 8768* (TEX); River below Huauchinango toward Xilocuanutla, 23 Mar 1945, *Sharp 45303* (GH, MO, NY); Río Apulco, N. of Zacapoaxtla, 21 Jun 1977, *Martínez & Ibarra 81* (ENCB); Mpio. Hueytamalco, Rancho Las Margaritas, 20 Aug 1975, *López-Forment 89* (MEXU) and *López-Forment 91* (MICH). **Veracruz**: Mpio. Atzalán, Tomata, 25 Feb 1970, *Ventura 596* (DS, MICH); Mpio. Coatepec: La Florida, 28 Jan 1971, *Ventura 3019* (DS, ENCB, F, MICH, NY); 1 km N of Coatepec, 2 Jul 1980, *Nee & Hansen 18760-a–e* (F, MEXU), *18760-f* (F); road from Coatepec to Teocelo, below bridge "Puente Texelo", 22 Apr 1986, *LaFrankie 1001* (TEX); Huatusco, Sep 1841, *Liebmann 1880* (NY, US); Huatusco, Río Jamapa, 11 Oct 1964, *Rzedowski 19058* (ENCB, MEXU); Mpio. San Juan Coscomatepec, Barranca de Cliapa, 16 Apr 1971, *Ventura 3452* (DS, ENCB, MICH); Orizaba, 1856, *Botteri 859* (A, F, GH, NY, US(3)); Mpio. Teocelo, Santa Rosa, 10 Apr 1970, *Ventura 873* (DS, ENCB, F, MICH); Mpio. Xalapa: streams near Xalapa, 10 Apr 1899, *Pringle 8107* (A, BH, ENCB, F, GH, MO, NY, PH, US(2)); Maltrata, 12 May 1937, *Matuda s.n.* (A, DS, MEXU, MICH, MO, NY).

5b. **Platanus mexicana** Moric. var. **interior** Nixon & Poole var. nov. TYPE: **MEXICO. Querétaro:** El Trapiche, 17 km al NW de Jalpan, 8 Apr 1971, *Rzedowski 28109* (HOLOTYPE: F!; ISOTYPES: DS!, ENCB!, MICH!, NY!, TEX!). Fig. 7.

Arbores cortice exfolianti, folia decidua, laminis lobatis lobis non profundis palmatis 3(–5) deltoideis vel late acuminatis subtus glabratis vel sparse pubescentibus marginibus integris vel irregulariter dentatis; inflorescentiae carpellatae (1–)2–3(–4)-capitulatae capitulis 16–30 mm diametro unoquoque sessili, vel pedunculato; achaenia (5–)7–10 mm longa, ad apicem puberula, stylo persistenti.

TREES to 30 m or more tall; BARK exfoliating, appearing mottled; TWIGS reddish-brown or gray when older, glabrate or sometimes persistently dendritic-puberulent. LEAF BLADES to 8–20(–25) cm long by 10–20(–30) cm wide, broadly to narrowly ovate in outline, shallowly to deeply lobed, thick and leathery, adaxial surface grayish-green, at first with sparse vestiture of dendritic trichomes, soon glabrate, the veins usually slightly impressed, abaxial surface at first with dense to rather sparse white or grayish trichomes, the vestiture fine, becoming sparse or often glabrate in older leaves, the major veins raised above the abaxial surface and prominently yellowish or brown due to "glandular" dendritic vestiture; LEAF LOBES usually 3(0–5), broadly deltoid or acuminate, broadest at or very near the base, apices glandular or not, central lobe ½ to 1 times as long as wide, to 15 cm long by 15 cm wide, margins entire or rarely the lobes with closely spaced gland-tipped teeth; LEAF BASES broadly rounded to truncate, but usually decurrent along petiole for 10–20 mm and then cu-

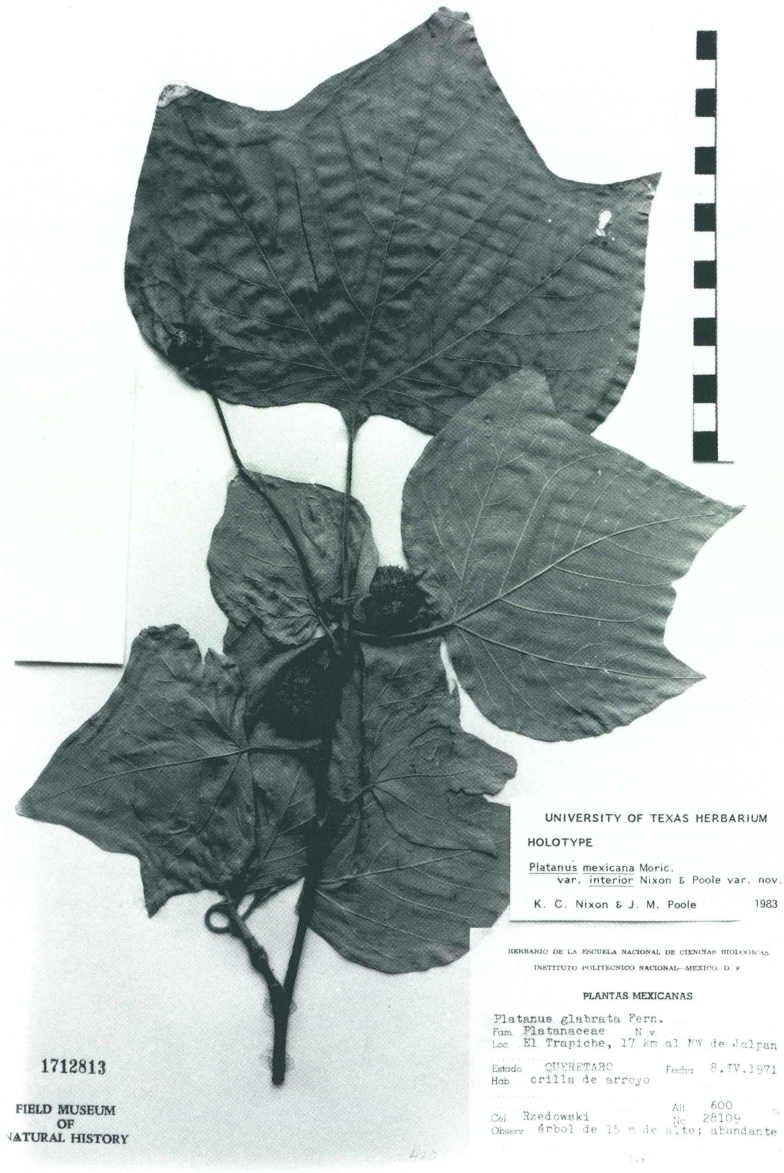

FIG. 7. Holotype of *Platanus mexicana* var. *interior* (F). Scale marked in cm.

neate; PETIOLES at first tomentose, later glabrate, to (25–)30–55(–86) mm long. STIPULES usually foliose, with sharply pointed lobes, sometimes teeth similar to those of the leaves. AXILLARY BUDS at first yellowish or rusty dendritic-puberulent, later glabrate, reddish brown, smooth. CARPELLATE INFLORESCENCES lax, spicate or racemose, of (1–)2–3(–4) sessile or pedunculate capitula, overall length 10–15 cm or more, length to first capitulum 40–50(–80) mm, capitula at maturity (16–)18–22(–30) mm in diameter, brownish. CARPELLATE FLOWERS: STAMINODIA not observed; CARPELS ca. 6; OVARIES in flowers and young fruit with short glandular branched

trichomes on sides; STYLES in flowers and young fruit reddish. STAMINATE INFLORESCENCES of 2–4 subsessile capitula. STAMINATE FLOWERS with STAMENS 2–3 mm long, connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. MATURE ACHENES (5–)7–10 mm long, apically rounded or abruptly tapering into the persistent style (style 3–6 mm long), apically yellowish dendritic-puberulent, sometimes puberulent on sides as well, occasionally completely glabrous; COMA of brownish-yellow unbranched ascending articulate trichomes about ⅔ the length of the achene body, attached at its base; achenes falling in autumn or sometimes remaining on heads through the winter (Figs. 5 & 8).

DISTRIBUTION AND HABITAT: Rather restricted in distribution in central Mexico in the states Querétaro, Guanajuato, San Luis Potosí and Hidalgo (Fig. 3), inhabiting streamside habitats typical of all species in the genus, at 600 to 1500 m altitude.

This variety differs from var. *mexicana* in the larger, more loosely tomentose and usually eventually glabrescent leaves, often fewer (2 to 3) capitula per pistillate inflorescence, and generally longer achenes. It is otherwise similar to the typical variety in leaf shape, venation, achene shape, and achene vestiture.

The varietal epithet was chosen to reflect the distribution of this variety in the interior central highlands of Mexico. We feel the taxon merits recognition because of its distinctive suite of character-states within the general pattern found in *P. mexicana.* Some of the material has been previously identified as *P. glabrata* (here treated as a synonym of *P. occidentalis* var. *palmeri*), apparently because of the glabrate leaves. The distribution of this taxon in the drier, more interior part of the range of *P. mexicana,* as well as its more glabrate leaves and reduced number of capitula, might indicate past contact with and introgression from *P. occidentalis* var. *palmeri.* Alternatively, these trends might indicate only parallel characters derived from similar selection pressures. We have chosen to place it as a variety of *P. mexicana* both because of its marginal geographic distribution relative to *P. mexicana* var. *mexicana* and the great morphologic similarity of the two taxa.

REPRESENTATIVE SPECIMENS EXAMINED: **MEXICO: Guanajuato**: Xichú, 19 Aug 1947, *Kenoyer 2330* (GH); Hidalgo: Mpio. Molango, alrededores de Chinameca, 13 Sep 1964, *Quintero 1607* (DS, ENCB, MICH). **Querétaro**: km 10 del camino que va a San Pedro Escaneia, 17 Oct 1972, *Ochoa 617* (ENCB); Mpio. Pinal de Amoles, 4 km al SW de Ahuacatlán, 17 Sep 1970, *Rzedowski 27739* (ENCB, MICH); 20 km de Pinal de Amoles, sobre el camino de Jalpan, 2 Sep 1965, *Vela & Martínez 1705* (ENCB). **San Luis Potosí**: Álvarez, 13–23 Jul 1904, *E. Palmer 235* (NY(2)); Tamazunchale, 12 Jul 1937, *Edwards 536* (ARIZ, MO, TEX).

6. **Platanus rzedowskii** Nixon & Poole sp. nov. TYPE: **MEXICO. Nuevo León:** Mpio. Iturbide, 11.9 km W of Iturbide, 16 May 1981, *Poole, Hinton, & Nixon 2292* (HOLOTYPE: TEX; ISOTYPES: ENCB!, MEXU!). Fig. 8.

Arbores cortice exfolianti, folia decidua, laminis lobatis lobis non profundis palmatis (3–)5(–7) late acuminatis deltoideis, subtus dense pubescentibus pilis albis vel canis persistentibus, marginibus integris vel irregulariter dentatis, inflorescentiae carpellatae l(raro-2)-capitulatae capitulo 20–40 mm diametro achaenia (4)8–10(l2) mm longa ad apicem dense barbata, styli tenues flexuosi persistentes.

TREES to 25 m or more tall, narrow to broadly spreading; BARK exfoliating in large plates, appearing mottled; TWIGS sparsely tomentose when young, reddish beneath vestiture, older twigs reddish-brown or gray, glabrate or sometimes persistently dendritic-puberulent, 2–3 mm in diameter. LEAF BLADES (3–)7–15(–25) cm long, to 10–20(–25) cm wide, broadly ovate to del-

FIG. 8. Holotype of *Platanus rzedowskii* (TEX). Scale marked in cm.

toid in outline, shallowly lobed, adaxial surface deep green or sometimes yellowish-green, at first with sparse vestiture of dendritic trichomes, soon glabrate, the major veins not usually prominent above, often lightly impressed, abaxial surface persistently densely white or grayish tomentose, the vestiture fine, obscuring the blade surface except in older weathered leaves (sometimes young juvenile or second-growth leaves glabrate), the major veins raised above abaxial surface and prominently yellowish or brown due to glandular dendritic vestiture; LEAF LOBES usually (3–)5(–7),

deltoid to narrowly triangular, the central lobe broadly acuminate, tips glandular or eglandular, central lobe $^7/_{10}$ to 1 & ½ times as long as wide, to 15 cm long by 11 cm wide, apical lateral lobes usually ⅔ or less length of central lobe, basal lateral lobes usually ⅔ length of apical lobes, margins of lobes usually smooth, entire, but sometimes with secondary teeth, these usually not obviously gland-tipped; LEAF BASES truncate to attenuate-decurrent, blade usually decurrent proximally on petiole from axil of major lateral veins for ca. 5–7(–10) mm (vein branching therefore suprabasal) or sometimes not decurrent (vein branching then basal); PETIOLES at first puberulent, later glabrate, to (25–)50–70(–80) mm long, the expanded basal sheath 5–6 mm long by 3–5 mm broad. STIPULES foliaceous or membranous, mostly entire and greenish, usually with brownish unbranched trichomes, 12–18 mm across blade. AXILLARY BUDS reddish brown. CARPELLATE INFLORESCENCES lax, of a single capitulum (rarely 2), capitula at maturity (20–)25–35(–40) mm in diameter, usually with a definite overall whitish color due to whitish achene vestiture. CARPELLATE FLOWERS: STAMINODIA not observed; CARPELS ca. 6 per flower; OVARIES in flowers and young fruit densely bearded with whitish dendritic trichomes; STYLES in flowers and young fruit 4–7(–8) mm long, apically circinate, reddish. STAMINATE INFLORESCENCES of 1 capitulum. STAMINATE FLOWERS with STAMENS (anthers) 2.5–3 mm long, connective caps reddish with dense short dendritic and/or unbranched trichomes, these mostly deciduous at anthesis. MATURE ACHENES (4–)8–10(–12) mm long, the upper portion of the achene gradually tapering into the persistent style, densely bearded with whitish dendritic trichomes at least on distal ⅓, in some specimens the entire achene densely tomentose, vestiture often extending onto the style as well; COMA of yellowish articulate ascending unbranched trichomes about the length of the achene body or somewhat shorter and attached at its base; achenes usually falling in late summer or autumn or rarely remaining on heads through winter (Figs. 5 & 8).

DISTRIBUTION AND HABITAT: A large tree, restricted to streams, arroyos and rivers, from 450 to 1800 m elevation, mainly on the eastern side of the Sierra Madre Oriental in Nuevo León, Tamaulipas, and northern San Luis Potosí (Fig. 3). Of potential ornamental value, cultivated in northern Mexico and occasionally in Texas, this species might do well in cultivation in California and Florida.

Although this species has been well known to botanists at least from the time of Standley's treatment (1924), the generally applied name *Platanus mexicana* correctly belongs to a different species from eastern and southern Mexico, as previously discussed. *Platanus mexicana sensu* Standley therefore needs to be named, since no existing names apply to it. We are pleased to name this species in honor of the Mexican botanist Jerzy Rzedowski, especially due to his considerable work on the taxonomy of Mexican woody plants. Redowski's many collections of *Platanus* throughout Mexico were of great value during the course of this study.

Platanus rzedowskii is one of the most distinctive and beautiful of the species of *Platanus.* It is easily distinguished from *P. mexicana* and the western species of *Platanus* by its typically unicapitulate inflorescence, apically tapered achenes with dense whitish vestiture, and broadly 5-lobed leaves. These same achene characters, persistent styles, large size of the capitula, and densely white tomentose leaves separate it from *P. occidentalis* var. *palmeri* and these characters as well as the often entire lobes of its leaves separate it from *P. occidentalis* var. *occidentalis.*

Although *Platanus rzedowskii* and *P. occidentalis* var. *palmeri* occur in close proximity on some of the same river systems in Northeastern Mexico, we know of no areas

of complete sympatry of the two species, and no zones of putative hybridization as discussed for *P. rzedowskii* and *P. mexicana* var. *interior* below. Occasional specimens of *P. rzedowskii* show sparse leaf vestiture, which is nevertheless persistent, and sometimes smaller capitula (less than 25 mm diameter) but in all cases the majority of the achene and leaf characters are indisputably those of *P. rzedowskii* and do not indicate morphological intermediacy with *P. occidentalis* var. *palmeri.* We have observed that stump sprouts, regrowth following insect damage (which can be especially heavy in Nuevo León and Tamaulipas) and shade growth of this species tends to produce leaves which are less tomentose, with narrower lobes and often with a great degree of toothing. Other leaves from the same trees and populations show characteristics typical of the majority of *P. rzedowskii* specimens. We interpret these specimens as juveniles, exhibiting responses to unusual growing conditions, and feel that care should be taken in the identification of such specimens, especially when fertile material is not available.

McMillan (1974) reported on a study of habitat response in what he considered to be *Platanus occidentalis.* The provenances of McMillan's plants included two populations from Illinois, two populations from Kentucky, four populations from Texas, and two Mexican populations, from Monterrey and Linares, Nuevo León. The latter two populations were actually of *P. rzedowskii,* verified by an examination of material still growing in experimental gardens at the University of Texas at Austin in the late 1980's. The study included growing seedlings in four controlled temperature-photoperiod regimes for 85 days, and measuring overall height, leaf area, and stipule production under these four regimes. The data were reported as mean values for each population. These results suggest a distinctive physiological response of *P. rzedowskii* and further support its recognition as a species distinct from *P. occidentalis.*

REPRESENTATIVE SPECIMENS EXAMINED: **MEXICO. Nuevo León**: Aramberri, 2 May 1994, *Hinton 24096* (TEX); Iturbide, 17 Sep 1991, *Hinton 21543* (TEX); Mpio. Galeana: Alamar, 2 Jun 1934, *Mueller & Mueller 684* (A, MICH); Mpio. Iturbide: Canyon de Santa Rosa, 4 Jul 1934, *Pennell 17247* (PH); ~ 8 mi E of Iturbide, 22 Jul 1981, *Poole 2372* (MEXU, TEX-2); ~11.9 km W of Iturbide, 16 May 1981, *Poole 2292* (TEX); Mpio. Linares: ~18 mi W of Linares, 23 Oct 1981, *Poole 2430b,c,d,e,f,g* (TEX); Mpio. Monterrey: spring, 3.2 km E of Chipinque, May 1961, *Smith M535* (TEX); Cerro de La Silla, 4 Sep 1937, *White & Chatters 157* (GH, MEXU, MICH); Mountains near Monterrey, 27 Aug 1889, *Pringle 2678* (F, MEXU); Diente Canyon, 12 Aug 1939, *Muller 2690* (LL, MICH); Mpio. Villa Santiago: Cola de Caballo, 22 Oct 1981, *Poole, et al. 2402* (MEXU, TEX); same locality, 28 Jun 1948, *Moore & Wood 3620* (A, BH, MICH); same locality, 20 Jun 1984, *Villarreal et al. 2782* (TEX). **San Luis Potosí**: near El Salto, 20 Feb 1961, *King 3900* (F, MICH, NY, TEX, US). **Tamaulipas**: Mpio. Victoria: Canyon above Ciudad Victoria, 11 Aug 1942, *Gentry 6710* (DS, GH, US), Ciudad Victoria, 15 Jul 1933, *Fisher 3330* (US); 12.5 km SE of Ciudad Victoria, 7 Mar 1983, *Nee & Taylor 25785* (BH, NY); 11 km S of Ciudad Victoria, 21 Jun 1980, *Hansen & Nee 7303* (F); Hidalgo, Cuatro Caminos, 5 Jun 1994, *Hinton et al. 24183* (NY); Victoria, *Palmer 66* (F, GH, NY, US); Mpio. González: between Torrecillas and Pénjamo, 30 May 1974, *Guevara, Flores & Ayala 7285* (MEXU); Villa Mainero: Arroyo La Oveja, a unos de 10 km del Pueblo, May 1970, *González-Medrano et al. 2919* (MEXU); Villa Mainero, 11 May 1995, *Hinton 25239* (TEX); La Vegonia, 2 Jul 1930, *Bartlett 10025* (DS, ENCB, F, GH, LL, MICH(2), US); Mpio. Villa de Casas: Cañón del Diablo, 12 Mar 1969, *Puig 4170* (ENCB).

6a. PLATANUS RZEDOWSKII × P. MEXICANA var. INTERIOR

In a small region near Ríoverde, San

Luis Potosí, the ranges of *Platanus rzedowskii* and *P. mexicana* var. *interior* overlap. Material from the rivers and arroyos of this area is extremely variable, with various combinations of the characters of the two putative parental taxa expressed. It is interesting that there appears to be segregation of characters, with two major classes of specimens observed: those with leaves similar to *P. rzedowskii,* but racemose inflorescences and brownish, apically puberulent achenes resembling *P. mexicana,* and those with leaves similar to *P. mexicana* var. *interior* in lobing and vestiture, but single massive capitula with large, apically tomentose achenes as are found in *P. rzedowskii.* We interpret this kind of variation as perhaps indicative of hybridization and backcrossing between individuals of two species with a low level of reproductive isolation. We have seen no material that we would interpret as "blended" or intermediate in the majority of characters, as would be expected in F1 offspring.

REPRESENTATIVE SPECIMENS EXAMINED: **MEXICO. San Luis Potosí**: Mpio. Ríoverde: 15 km SW of Ríoverde, 26 Aug 1964, *Medellín s.n.* (ENCB); El Zapote, *Puig 6786* (ENCB); Grutas de la Catedral, 22 Mar 1958, *Medellín 621* (ENCB, MEXU); vicinity of San Dieguito, 7–10 Jun 1905, *Palmer 642* (F, GH, MO(2), NY, US); Mpio. Tamasopo: San Nicolás de los Montes, 28 May 1959, *Rzedowski 10648* (ENCB); Mpio. Zaragoza: La Salitrera, 8 July 1955, *Rzedowski 6102* (LL, US).

7a. PLATANUS OCCIDENTALIS L. var. OCCIDENTALIS. *Platanus occidentalis* L., Sp. Pl. 999. 1753. *Platanus orientalis* L. var. *occidentalis* (L.) Kuntze, Rev. Gen. 2:636. 1891. TYPE: **UNITED STATES.** North Carolina or Virginia (HOLOTYPE: LINN, photograph of holotype! as IDC microfiche 1133-5).

Platanus lobata Moench., Meth. 358. 1794. *Platanus occidentalis lobata* Bommer, Les Platanes 17. 1869.

Platanus vulgaris angulosa Spach, Ann. Sci. Nat. Bot. (ser. 2) 15:293. 1841.

Platanus occidentalis hispanica Wesmael, Mém. Soc. Sci. Hainaut (ser. 3) 1:12. 1867.

Platanus excelsa Salisb., Prod. Stirp. 393. 1796.

Platanus integrifolia Hort. ex C. Koch, Dendrologie 2(1):469. 1872.

Platanus pyramidalis Hort. ex Dippel, Handb. Laubholzk. 3:279. 1893.

TREES to 45 m tall, often with massive trunks, branches ascending to broadly spreading; BARK exfoliating, appearing mottled, but often rough and scaly on older, larger trunks; TWIGS reddish-brown or gray when older, glabrate or sometimes persistently puberulent. LEAF BLADES 7–20(–35) cm long by 10–20(–40) cm wide, broadly ovate to deltoid in outline, shallowly lobed, adaxial surface deep green or sometimes yellowish-green, at first with sparse dendritic vestiture, soon glabrate, the veins not impressed above, abaxial surface of blade at first loosely yellowish or grayish tomentose, the hairs persistent or sometimes the blade eventually glabrate except along the veins, the major veins raised above the abaxial surface and prominently yellowish due to "glandular" dendritic vestiture; LEAF LOBES usually 5, broadly deltoid, the central lobe broadly acuminate, tips glandular or eglandular, central lobe ½ to 1 times as long as broad, to 20 cm long by 20 cm wide, margins of lobes usually with several secondary lobes and teeth, these usually not obviously gland-tipped; LEAF BASES truncate and attenuate-decurrent for 5–15 mm proximally from first major vein axil, or sometimes the lateral lobes reflexed, forming a cordate base; SECONDARY VEINS of a given primary vein usually parallel, usually anastomosing and not extending to margins; TERTIARY VEINS often strongly convex or straight percurrent; PETIOLES at first vestured, later glabrate, to (25–)40–75(–86) mm long. STIPULES foliaceous or membranous, mostly entire and greenish, usually with brown-

ish vestiture. AXILLARY BUDS reddish brown, smooth. CARPELLATE INFLORESCENCES of a single capitulum (rarely 2), capitula at maturity (18–)23–33(–40) mm in diameter, yellowish in color due to achene vestiture. CARPELLATE FLOWERS: STAMINODIA ca. as long as ovary, flattened at apex or subpeltate, usually purplish; CARPELS usually 6–9(–11) in each flower; OVARIES in flowers and young fruits with yellowish trichomes on distal one third; STYLES in flowers and young fruit reddish, circinate distally, 4–5(–8) mm long. STAMINATE INFLORESCENCES of 1 capitulum. STAMINATE FLOWERS with STAMENS (anthers) 2.5–3 mm long, connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. MATURE ACHENES (6–)8–11(–12) mm long, yellowish, the upper portion of the achene truncate or abruptly tapering, styles early deciduous, exposed apex of achene usually completely glabrous or sometimes sparsely puberulent with yellowish dendritic trichomes near apex, upper third of ovary usually with some sparse puberulence; COMA of straight ascending unbranched articulate yellowish trichomes about the length of the achene and attached at its base; capitula usually remaining on trees and conspicuous through winter season, achenes falling from autumn to spring (Fig. 5).

DISTRIBUTION AND HABITAT: *Platanus occidentalis* var. *occidentalis* is the common sycamore of the eastern United States, and is found mainly in bottomlands, riparian forests and swampy areas, from Maine south to central Texas and Florida (Fig. 3). It is one of the largest hardwood trees of the eastern deciduous forest (Ernst, 1963) and the lumber was used extensively in the past for items which required extremely hard wood resistant to splitting, such as butcher's blocks and wagon wheels. Although *P. occidentalis* is cultivated as a shade tree, the somewhat similar *P.* ×*acerifolia* is cultivated more commonly both in the eastern and the western United States.

We have not addressed the considerable variation in leaf shape, lobing, and toothing which occurs in *P. occidentalis* in eastern North America, but our study of representative material from throughout the range of the species provides no basis for recognition of varieties other than var. *palmeri* as discussed below.

REPRESENTATIVE SPECIMENS EXAMINED: **UNITED STATES. Arkansas**: Pope Co: Nogo, 24 Aug 1932, *Merrill 14* (NY); Sharp Co: Hardy, Spring River, 18 May 1947, *Demaree 26102* (TEX). **Georgia**: Athens, 3 Oct 1936, *Univ. Georgia School Forestry 8285* (TEX). **Kentucky**: Jefferson Co: Brown's Lane, 5 Sep 1955, *Gunn J142* (LL; this specimen shows pinnate venation of seedling *Platanus* leaves). **Louisiana**: Urania, 24 Jul 1936, *Bickford 8219* (TEX). **Massachusetts:** Norfolk Co: Stoughton, 22 Sep 1929, Blake 11028 (LL). **New York**: Cardiff, Jun 1936, *Brown 8267* (TEX). **North Carolina**: Stokes Co: along Dan River, W of U.S. 311, 1 Jul 1969, *Leonard & Russ 2555* (LL). **Oklahoma**: Cherokee Co: 6.4 km N of Ft. Gibson, *Wallis 309* (TEX); Payne Co.: 2 mi E of Stillwater, 11 Aug 1963, *Pearce 1014* (TEX). **Tennessee**: Anderson Co: 21 Nov 1936, *Kline 8231* (TEX). **Texas**: Bandera Co: Sabinal Canyon, Nov, *Owens 1897* (TEX); Fayette Co: LaGrange, 29 Mar 1964, *Peterson 121* (TEX); Galveston Co: Dickinson, 8 Jul 1974, *Waller 2903* (TEX); Gillespie Co: ca. 6.5 km W of jct of hwy 87 & West Cherry Spring rd, 18 Jul 1981, *Poole & Watson 2353* (TEX); McClennan Co: Crawford, rock quarry, 5 May 1947, *Smith 574* (TEX); Travis Co: 10 km NW of Hwy 620 on Hwy 71, 17 Jul 1981, *Poole & Watson 2351* (TEX); Williamson Co: Brushy Creek, N of Round Rock, 20 Jul 1946, *York 46206* (BH, TEX).

8b. PLATANUS OCCIDENTALIS L. var. PALMERI (Kuntze) Nixon & Poole ex Geerinck,

Belg. Journ. Bot. 130(2):127. (1998). *Platanus orientalis* L. var. *palmeri* Kuntze, Rev. Gen. Pl. Vasc. 2: 636. 1891. TYPE: **MEXICO. Coahuila:** Monclova, 23–31 Aug 1880, E. Palmer 1269 (HOLOTYPE: K [not seen]; ISOTYPES: A!, GH(2)!, NY(2)!, US!).

Platanus glabrata Fern., Proc. Amer. Acad. 36:493. 1901. *Platanus occidentalis* L. var. *glabrata* (Fern.) Sarg., Bot. Gaz. 67: 230. 1919. LECTOTYPE (here designated): **MEXICO. Coahuila:** Monclova, 23–31 Aug 1880, *E. Palmer 1269* (GH!; ISOLECTOTYPES: A!, GH!, K, NY(2)!, US!). We have chosen as lectotype the collection from the original syntypes which is most representative of Fernald's description. As this collection number was cited by Kuntze as the type of *P. orientalis* var. *palmeri,* this lectotype firmly establishes the synonymy of these names.

Platanus densicoma Dode, Bull. Soc. Dendr. France 7:67. 1908. TYPE: **UNITED STATES. Iowa:** Jackson Co., Maquoketa River (not seen).

TREES to 25 m or more tall, narrow to broadly spreading; BARK exfoliating, appearing mottled, but often rough and scaly on older, larger trunks; TWIGS reddish-brown or gray when older, glabrate or sometimes persistently dendritic-puberulent. LEAF BLADE to 4–15(–20) cm long by 6–15(–20) cm wide, broadly ovate to deltoid in outline, shallowly to moderately lobed, adaxial surface deep green or sometimes yellowish-green, at first tomentose or with sparse vestiture of dendritic trichomes, soon glabrate, the veins not impressed above, abaxial surface of blade at first loosely yellowish or grayish tomentose, soon glabrate or sometimes the veins persistently tomentose, the major veins raised above the abaxial surface; LEAF LOBES usually 5, broadly deltoid, the central lobe broadly acuminate, the tips glandular or eglandular, central lobe largest, to 12 cm long by 10 cm wide, basal lateral lobes often weakly developed, margins of lobes usually entire or with a few teeth, these usually not obviously gland-tipped; LEAF BASES truncate and attenuate-decurrent for 5–15 mm proximally from first major vein axil, or the vein axil sometimes basal, lateral occasionally reflexed, forming a cordate base; SECONDARY VEINS of a given primary vein usually parallel, usually anastomosing and not extending to margins; TERTIARY VEINS often strongly convex or straight percurrent; PETIOLES at first puberulent or tomentose, later glabrate, to (25–)40–75(–70) mm long. STIPULES foliaceous or membranous, mostly entire and greenish, usually with brownish trichomes. AXILLARY BUDS reddish brown, smooth. CARPELLATE INFLORESCENCES of a single capitulum (rarely 2), capitula at maturity (12–)20–30(–40) mm in diameter, yellowish in color due to achene pubescence. CARPELLATE FLOWERS: STAMINODIA reddish, ca. as long as ovary, flattened and ampliate but not usually peltate at distal end, sparsely puberulent; CARPELS usually 6–9 in each flower; OVARIES in flowers and young fruit with yellowish dendritic trichomes on distal one third; STYLES in flowers and young fruit reddish, circinate distally, 4–5(–8) mm long. STAMINATE INFLORESCENCES of 1 capitulum. STAMINATE FLOWERS with STAMENS (anthers) 2.5–3.0 mm long, connective caps reddish with dense short dendritic trichomes, these less dense on heads near or at anthesis. MATURE ACHENES (4–)6–10(–11) mm long, the upper portion of the achene truncate or abruptly tapering, styles deciduous, achene sparsely puberulent with yellowish pubescence near apex, exposed apex usually sparsely puberulent or sometimes glabrate late in the season; COMA of straight yellowish articulate trichomes about the length of the achene and attached at the base; capitula usually remaining on trees and conspicuous through dormant season, achenes falling from autumn to spring (Fig. 5).

DISTRIBUTION AND HABITAT: The core distribution of this variety (but see below) is from central Texas to northeastern

Mexico, in the state of Coahuila, along streams and gullies surrounded by relatively dry habitat and various scrub and forest types.

Although the extremes of *Platanus occidentalis* var. *palmeri* in northern Mexico are distinctive, the trends in characters which do exist (smaller, more entire-margined, more glabrate leaves, and smaller capitula) appear to be clinal from Texas into northern Mexico. Most of the material from the Edwards Plateau of central Texas is referable to *P. occidentalis* var. *palmeri*, as is all of the material from Coahuila. Material referable to both varieties occurs at wetter sites on the plateau, and along its east escarpment, as at Austin, Texas. To the east of this zone, most material is referrable to var. *occidentalis*. However, material which approaches var. *palmeri* occurs sporadically through east Texas into Oklahoma, Iowa, Arkansas, and Louisiana, and even rarely in the eastern coastal states.

REPRESENTATIVE SPECIMENS EXAMINED: **MEXICO. Coahuila**: streams near Díaz (Piedras Negras), 24 Apr 1900, *Pringle 8319* (syntype: A, GH(2), MEXU, MO, NY, PH, US(3); Mpio. Mélchor Múzquiz, 61 km N of Múzquiz, 18 Sep 1999, *Villarreal 8757* (TEX); Hacienda Mariposa, near Puerto Santa Ana, 24 Jun 1936, *Wynd & Mueller 657* (A, MICH, MO, NY, US); Hacienda San Rafael, Sabinas River, 18 Aug 1937, Wynd 702 (A, GH, MEXU, MO, NY, US); Saltillo, 5 Apr 1887, *Sargent s.n.* (syntype: A). **UNITED STATES. Texas**: Anderson Co: 14 mi SW of Jacksonville, 1 Apr 1982, *Poole & Watson 2522* (TEX); Burnett Co: 9 km NW of spur 191 on Hwy 71, *Poole & Watson 2352* (TEX); Kerr Co: Kerrville: 19–25 Apr 1894, *Heller 1622* (PH); 18 Jul 1981, *Poole & Watson 2354* (TEX); Travis Co: Austin, 30 May 1974, *Nee & Whalen 11846* (LL, WIS); 25 Mar 1982, *Nixon 3624* (TEX); Uvalde Co: along Rio Frio, Garner State Park, 16 Apr 1957, Correll, et al. 15935 (LL); Val Verde Co: 16 km NW of Del Rio, 8 Apr 1951, *Warnock & Cameron 9907* (LL).

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