NOTICE: Return or renew all Library Materials! The Minimum Fee for each Lost Book is $50.00.

The person charging this material is responsible for its return to the library from which it was withdrawn on or before the Latest Date stamped below.

Theft, mutilation, and underlining of books are reasons for disciplinary action and may result in dismissal from the University.

To renew call Telephone Center, 333-8400

UNIVERSITY OF ILLINOIS LIBRARY AT URBANA-CHAMPAIGN

JAN 2 0 1991

JAN 15 1991

FEB 11 1991

FEB 11 1991

BUILDING USE ONLY

MAR 6 1997

OCT 4 1993

OCT 4 1993

BUILDING USE ONLY

APR 0 1 1995

APR 0 1 1995

APR 0 5 1995

BUILDING USE ONLY

L161—O-1096
Taxonomy of American Species of Linden (Tilia)

GEORGE NEVILLE JONES
ILLINOIS BIOLOGICAL MONOGRAPHS

Volumes 1 through 24 contained four issues each and were available through subscription. Beginning with number 25 (issued in 1957), each publication is numbered consecutively. No subscriptions are available, but standing orders are accepted for forthcoming numbers. Prices of previous issues still in print are listed below, and these may be purchased from the University of Illinois Press, Urbana, Illinois. Microfilm copies of out-of-print titles in the Illinois Biological Monographs are available from University Microfilms, Inc., 313 North First Street, Ann Arbor, Michigan 48107, and reprints can be obtained from the Johnson Reprint Corporation, 111 Fifth Avenue, New York, New York 10003.

Campbell, John M. (1966): A Revision of the Genus Lobopoda (Coleoptera: Alleculidae) in North America and the West Indies. 174 figs. No. 37. $5.75.
Levine, Norman D., and Ivens, Virginia (1965): The Coccidian Parasites (Protozoa, Sporozoa) of Rodents. 2 figs. 48 pls. No. 33. $7.50.
List, James Carl (1966): Comparative Osteology of the Snake Families Typhlopidae and Leptotyphlopidae. 22 pls. No. 36. $3.75.
Morgan, Jeanne (1959): The Morphology and Anatomy of American Species of the Genus Psaronius. 82 figs. No. 27. $3.00.
Raminger, James M. (1962): Taxonomy of Setaria (Gramineae) in North America. 15 maps. 6 pls. No. 29. $3.00.
The person charging this material is responsible for its return on or before the Latest Date stamped below.

Theft, mutilation, and underlining of books are reasons for disciplinary action and may result in dismissal from the University.

University of Illinois Library

OCT 30 1968
Taxonomy of American Species of Linden (Tilia)

GEORGE NEVILLE JONES

ILLINOIS BIOLOGICAL MONOGRAPHS 39
I. INTRODUCTION

Aims

The primary aim of this monograph is to describe and discuss the American species of linden (Tilia). The study is based principally upon morphology, taxonomy, and ecology, that is, upon the study of the structure of preserved specimens in the herbarium, and observation and collection of specimens from living trees in the field. It has been necessary to include a brief survey of the genus as represented in Europe and Asia, where most of the living species occur, and to review the taxonomic history, particularly of American species, with their extensive bibliographies.

One other objective has been as far as possible to coordinate data from different sources, as for example neontological taxonomic data with those pertaining to palaeontology. To approach an understanding of geographical distribution and phylogenetical development of American species, it has been necessary to make a brief excursion into palaeobotany to review the known American fossil species of Tertiary and Quaternary age. At the same time, there has been no intention to overlook the possible practical applications of taxonomic data to those aspects of the study of trees that may be connected with forestry or other phases of applied ecology. Some mention has been made of cer-
tain European and Asiatic species that are found in cultivation in the United States.

Methods

The modus operandi of this monograph is the *taxonomic method*, of which there are several variations. C. R. Ball, the great American salicologist, or willow specialist, outlined in 1946 two methods of taxonomic study which he termed the centripetal and the centrifugal. The centripetal method is followed here.

[This] method is to obtain the largest possible collection of specimens representing all these real, supposed, and/or unadmitted entities. Better still, study living plants in the field, in different habitats in various geographic areas of the total range. Even better yet, do both. Because adequate field study is difficult or impossible for many students, chief dependence must be put on herbarium material. In any case, the specimens should be sorted out by geographical areas without regard to the names which have been applied to them previously. Whether living or dead, complete or fragmentary, they are studied critically for similarities and differences, and the differences are analyzed as to nature, causation, and value, on the basis of the previous precepts. All this is without cross-reference to the previously published descriptions of the species and varieties involved. This is the centripetal method, working from the outside in. It gets to the heart of the matter. It assumes the possibility of specific unity of the material. It challenges the mind to discover if there are differences, and to prove whether discovered differences are inherent or merely the effects of local environment [Ball, 1946: 377-378].

Examples of the centrifugal method are mentioned later in this monograph.

Largely because some botanists have followed other methods of study, American lindens have hitherto been involved in some taxonomic confusion, as shown by the uncertain and varied treatments in recent and current manuals and floras. A curious phenomenon occasionally observed and commented on is a discrepancy between relatively precise knowledge of taxonomy of certain genera of trees in eastern Asia as contrasted with knowledge of their North American counterparts. The genus Tilia furnishes such an example. The relatively complex Tilia flora of eastern Asia has been more clearly defined (Rehder & Wilson, 1915) than its much simpler counterpart in eastern North America.

Names

Tilia is an ancient Latin name. The history of Tilia is of particular botanical interest as it was from this genus that Carolus Linnaeus
(1707-78) acquired his surname. His father based the patronym Tiliander on a famous linden tree, of the species later named *T. europaea* L., that grew near his home in Sweden.

Charles Linnaeus was born on the third of May, 1707, at Råshult, a village in the province of Småland. Nils, or Nicholas Linnaeus, his father, who took birth in the year 1674, held the sacred function of pastor of the village, two years previous to that event. He was joined in the banns of wedlock with Christina Broderson, the daughter of his predecessor in office. His ancestors were peasants. Several of his relatives, who had quitted the plough for the Muses, in the last century, changed their family name with their profession, and borrowed the names of Lindelius, or Tiliander, (Linden-tree-man) of a lofty Linden-tree, which still stood in our time, in the vicinity of their native place, between Tomsboda and Linnhult; a custom not unfrequent in Sweden, to take fresh appellations from natural objects. The father of Linnaeus, as the first learned man of his family, could not withstand following the example which his kindred had set before him. He likewise borrowed of the same tree a name which his son rendered afterwards famous and immortal in every quarter of the globe [Stoever, 1794].

Further commemorating Linnaeus is the genus *Linnaea* (Caprifoliaceae), dedicated originally by J. F. Gronovius (1690-1762) of Holland to Linnaeus at his own request. It was Linnaeus who first pointed out its characters. With him the beautiful circumboreal *L. borealis* L. was a favorite plant. Linnaeus said it “was named by the celebrated Gronovius and is a plant of Lapland, lowly, insignificant, disregarded, flowering but for a brief space — from Linnaeus who resembles it” (Hort, 1938).

“In this indirect fashion one of the tallest trees in Sweden, the linden, the name-tree of the Linnaeus and Tiliander families (cf. A.M. Lindberg, ‘Linden i Jonsboda; det Linneska vortradet’, *Svenska Linne-Sällsk. Arsskr.* 39-40: 95-105, 184; 1957), gave its name to Sweden’s lowliest shrublet, just as earlier the white poplar (the French *aubel* or *aube*) gave its name to the de l’Obel family and so to the genus *Lobelia*” (Stearn, 1959: 62).

The species of *Tilia* in the United States go by the name of basswood or linden. Less frequently they are called whitewood, bee tree, linn, or linnwood, although the last names are mainly applied in the southern states. Other names recorded for these trees are bast tree, monkey-nut tree, white-lind, yellow basswood, wickup, daddy-nuts, spoonwood, and whistle wood. The name lime is infrequently used in this country; it is more commonly applied in Britain, where it is derived apparently as an altered form of lind or linden. Lind or linn was in time corrupted to lyne, line, and later to lime. The usual meaning of the Anglo-Saxon *lind* was shield, i.e., one made of linden wood. The
change from lime to linden seems not to be older than about A.D. 1700. In Canada, the usual names are basswood, Canadian linden, lime tree, and in Quebec, the French bois blanc and tilleul d'Amerique. In Mexico, tilo and sirimo are usual.

Scores of geographical names are derived directly or indirectly from this genus of trees, as, for example, the following towns in the United States: Lind (Wash.), Linden (in 19 states, 3 in Mo.), Lindenhurst (N.Y.), Lindenwold (N.J.), Lindenwood (Ill.), Linn (in 6 states), Linn Creek (Mo.), Linngrove (Ind.), Linn Grove (Iowa), Linnton (Ore.), Linton (6 states), Linville (La., N.C., Va.), Linwood (14 states), and many more.

Citation of Specimens

The number of specimens cited in this study is large. The citations have been selected from among a great many more that have been excluded for lack of space. One of the principal objectives has been to give as extensive geographical information as possible. Specimens have been examined from all or nearly all herbaria that were expected to contain material that would make substantial additions to the distributional data. One specimen to a county or equivalent area has been cited. Preference has been given to widely distributed exsiccate and those bearing collector's numbers. A list of all specimens examined in this study is filed in the Herbarium of the University of Illinois.

The purposes of citing specimens, although obvious to the specialist, are not always clearly understood by others. Properly prepared and preserved herbarium specimens are the best known means of providing basic documentary botanical data. They show the range of morphological variation. Ecological information may be derived from the collection labels. The dates of collection indicate phenology. Frequency of occurrence can often be inferred from the label. Specimens provide the only really definitely documented primary evidence of geographical distribution. Maps, even when based on precise identification of actual specimens, are secondary, rather than primary, sources of information. Citations of specimens enable curators and other users of herbaria to order up their collections for further reference and consultation. "Taxonomists derive their data not only from herbarium specimens, field observation, and literature, but also from the researches of morphologists, geneticists, physiologists, ecologists, cytologists, geologists, and many other groups of colleagues. The numerous cooperative endeavors that have marked the progress of plant science in recent de-
INTRODUCTION

cades point to the value of collaboration; in this collaboration the taxonomist is more than a junior partner, and the herbarium is at least as basic a tool as the greenhouse or the experimental garden" (Smith, 1956: 12).

We have the hope that this study will be of some value to students of local floras. It is, however, intended to supplement rather than to replace that approach. As van Steenis (1957) says, “The local floristic botanist actually observes the populations only in their local facies. Consequently he should realize that his studies will lead only to a local interpretation or evaluation of the polymorphism of entire populations. This is sometimes insufficiently acknowledged by local students.” In this monograph, phytogeographical data are presented on several maps, as well as in citations of specimens. In addition, the states and counties are listed from which one or more specimens have been studied, as it has been possible to cite only a limited selection of representative exsiccateae from the large number of specimens examined.

In most botanical monographs the herbarium in which the specimen is preserved is indicated by name or symbol in order that future investigators may verify the evidence. Following is a list of the herbaria consulted, with their abbreviations according to the International Bureau for Plant Taxonomy and Nomenclature (Lanjouw & Stafleu, 1964).

AA  Arnold Arboretum, Cambridge, Massachusetts.
ACAD  Acadia University, Wolfville, Nova Scotia, Canada.
B  Botanisches Museum, Berlin-Dahlem, Germany.
BREM  Übersee-Museum, Bremen, Germany.
CAN  National Herbarium of Canada, Ottawa, Canada.
CAS  California Academy of Sciences, San Francisco, California.
CM  Carnegie Institute, Pittsburgh, Pennsylvania.
CU  Wiegand Herbarium, Cornell University, Ithaca, New York.
DAO  Department of Agriculture, Ottawa, Canada.
DEN  Denison University, Granville, Ohio.
DS  Dudley Herbarium, Stanford University, Stanford, California.
F  Field Museum of Natural History, Chicago, Illinois.
FKSC  Fort Hays Kansas State College, Hays, Kansas.
FLAS  Florida State University Herbarium, Tallahassee, Florida.
GA  University of Georgia, Athens, Georgia.
GEO  Emory University, Atlanta, Georgia.
GH  Gray Herbarium of Harvard University, Cambridge, Massachusetts.
GOETT  Systematisch-Geobotanisches Institut, Universität Göttingen, Germany.
IA  State University of Iowa, Iowa City, Iowa.
ILL  University of Illinois, Urbana, Illinois.
IND  Indiana University, Bloomington, Indiana.
KANU  University of Kansas, Lawrence, Kansas.
<table>
<thead>
<tr>
<th>Code</th>
<th>Institution Name and Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>KSC</td>
<td>Kansas State College of Agriculture and Applied Science, Manhattan, Kansas.</td>
</tr>
<tr>
<td>KSTC</td>
<td>Kansas State Teachers College, Emporia, Kansas.</td>
</tr>
<tr>
<td>KY</td>
<td>University of Kentucky, Lexington, Kentucky.</td>
</tr>
<tr>
<td>LCU</td>
<td>The Catholic University of America, Washington, D.C.</td>
</tr>
<tr>
<td>LL</td>
<td>Lundell Herbarium, Texas Research Foundation, Renner, Texas.</td>
</tr>
<tr>
<td>LSU</td>
<td>Louisiana State University, Baton Rouge, Louisiana.</td>
</tr>
<tr>
<td>MAINE</td>
<td>University of Maine, Orono, Maine.</td>
</tr>
<tr>
<td>MBG</td>
<td>Missouri Botanical Garden, St. Louis, Missouri.</td>
</tr>
<tr>
<td>MEXU</td>
<td>Herbario Nacional del Instituto de Biología, Universidad de México, México, D.F., México.</td>
</tr>
<tr>
<td>MICH</td>
<td>University of Michigan, Ann Arbor, Michigan.</td>
</tr>
<tr>
<td>MIN</td>
<td>University of Minnesota, Minneapolis, Minnesota.</td>
</tr>
<tr>
<td>MU</td>
<td>Miami University, Oxford, Ohio.</td>
</tr>
<tr>
<td>NCU</td>
<td>University of North Carolina, Chapel Hill, North Carolina.</td>
</tr>
<tr>
<td>NEB</td>
<td>University of Nebraska State Museum, Lincoln, Nebraska.</td>
</tr>
<tr>
<td>NO</td>
<td>Tulane University, New Orleans, Louisiana.</td>
</tr>
<tr>
<td>OC</td>
<td>Oberlin College, Oberlin, Ohio.</td>
</tr>
<tr>
<td>OS</td>
<td>Ohio State University, Columbus, Ohio.</td>
</tr>
<tr>
<td>OWU</td>
<td>Ohio Wesleyan University, Delaware, Ohio.</td>
</tr>
<tr>
<td>PAM</td>
<td>Pennsylvania State Herbarium, Harrisburg, Pennsylvania.</td>
</tr>
<tr>
<td>PH</td>
<td>Academy of Natural Sciences, Philadelphia, Pennsylvania.</td>
</tr>
<tr>
<td>POM</td>
<td>Pomona College, Claremont, California.</td>
</tr>
<tr>
<td>RSA</td>
<td>Rancho Santa Ana Botanic Garden, Claremont, California.</td>
</tr>
<tr>
<td>SMU</td>
<td>Southern Methodist University, Dallas, Texas.</td>
</tr>
<tr>
<td>TAES</td>
<td>Tracy Herbarium, Agricultural and Mechanical College of Texas, College Station, Texas.</td>
</tr>
<tr>
<td>TENN</td>
<td>University of Tennessee, Knoxville, Tennessee.</td>
</tr>
<tr>
<td>TEX</td>
<td>University of Texas, Austin, Texas.</td>
</tr>
<tr>
<td>UARK</td>
<td>University of Arkansas, Fayetteville, Arkansas.</td>
</tr>
<tr>
<td>UC</td>
<td>University of California, Berkeley, California.</td>
</tr>
<tr>
<td>UCLA</td>
<td>University of California, Los Angeles, California.</td>
</tr>
<tr>
<td>UMRO</td>
<td>University of Missouri, Columbia, Missouri.</td>
</tr>
<tr>
<td>USF</td>
<td>University of South Florida, Tampa, Florida.</td>
</tr>
<tr>
<td>USFS</td>
<td>Forest Service Herbarium, U.S. Department of Agriculture, Washington, D.C.</td>
</tr>
<tr>
<td>VDB</td>
<td>Vanderbilt University Herbarium, Vanderbilt University, Nashville, Tennessee.</td>
</tr>
<tr>
<td>WIS</td>
<td>University of Wisconsin, Madison, Wisconsin.</td>
</tr>
<tr>
<td>WJC</td>
<td>William Jewell College, Liberty, Missouri.</td>
</tr>
<tr>
<td>WVA</td>
<td>University of West Virginia, Morgantown, West Virginia.</td>
</tr>
<tr>
<td>YU</td>
<td>Yale University, New Haven, Connecticut.</td>
</tr>
</tbody>
</table>
Acknowledgments

During the course of this study many persons and institutions, too numerous to mention separately, have furnished assistance. It is a pleasure to acknowledge formally their helpful contributions.

To the National Science Foundation I am grateful for financial aid (NSF G-5855) for a short botanical expedition to Mexico, where collections were made of the hitherto mysterious sirimo, *Tilia mexicana*, whose true identity was finally ascertained by studying Mexican collections during the following summer in certain European herbaria.

To the curators of more than 60 herbaria, I should like to express sincere appreciation for assistance of various kinds, particularly in having generously placed at my disposal those parts of the collections under their charge that were essential for my studies.

Finally I am indebted to colleagues at the University of Illinois for many favors, including useful items of botanical information and advice. Among these are Lyle Edward Bamber, Arthur Gibson Vestal, Robert Curtis White, and a former student, David Lellinger. I must acknowledge my debt to my wife, for without her assistance, botanical and clerical, this study would have required an even longer time to be concluded.
II. TAXONOMY

Taxonomic Position of Tilia

Tilia, the type genus of Tiliaceae (Malvales), is the most important extra-tropical genus in this family of predominantly woody plants. The family comprises approximately 500 existing species in about 41 genera (Rendle, 1938: 245). The members of this family are mostly tropical, occurring in two principal regions, one in southeastern Asia and the other in northern South America. Fossil evidence shows that during the Tertiary period the geographical distribution of this family was much different from the present. An Asiatic relationship is suggested by all the Tertiary species of Tilia from North America.

In addition to Tilia, the chief genera are Corchorus, Grewia, Sparmannia, and Triumfetta. The largest genus is the pantropical Grewia with about 240 species. Corchorus has about 70 species of herbs and subshrubs widely dispersed in the tropics. *Corchorus capsularis* L. and *C. olitorius* L., both native in India, furnish the chief supply of the fiber jute or gunny. Sparmannia has 5 or more species of African trees and shrubs, and in the genus Triumfetta there are about 150 species of tropical herbs and shrubs. It is evident that in Tiliaceae, as in many other families of angiosperms, a high proportion of species, in this instance about 75 per cent, belong to a very small number of genera,
the remaining species being distributed among a large number of small genera.

Diagnosis of the Genus


_Tilia_ subgen. Filura Rafinesque, ibid.

Deciduous trees with soft white wood, fibrous tough inner bark, and simple, distichous, alternate, serrate, petiolate, inequilateral leaves; flowers protandrous, bisexual, entomophilous, in a cymose inflorescence whose peduncle is partly adnate to a broad bract; sepals and petals each 5, free; stamens many, free or in bundles opposite the petals, the filaments often forked distally; epipetalous staminodia present in most species; ovary superior, 5-loculed, each locule with two ovules; style simple; stigma 5-lobed; fruit small, indehiscent, unilocular, with 1-3 seeds; endosperm oily; cotyledons broad, 3-5-lobed.


Discussion of Morphology of Tilia

The lindens are widely distributed in the temperate regions of the northern hemisphere, with the exception of western North America, central Asia, and the Himalayan region. On a conservative estimate, there are perhaps 30 existing species, represented chiefly in eastern Asia, about five in Europe, three native in eastern United States and southern Canada, and one extending southward in the highlands of
Mexico. Although Tiliaceae as a family are mostly tropical in their distribution, the genus Tilia is now scarcely represented in tropical climates. If it occurs in a low latitude, as in Mexico, its habitat is always at high altitude.

As a genus, the lindens are readily recognized by their usually cordate leaves, characteristic stalked inflorescences, and roundish fruits appended to elongate bracts. They have yellowish regular flowers with separate petals and numerous stamens. The trees of many species have a marked tendency to develop sprouts from the base of the trunk. On the species level, the lindens are closely related, and the treatments in recent and current manuals are varied.

TWIGS

Lindens have terete, moderately stout branchlets. The twigs are somewhat zigzag, with elongated internodes, in cross-section showing the phloem in fibrous wedges, and a roundish, continuous, pale pith. The buds are solitary, sessile, inequilaterally ovoid with two reddish glossy scales, the outer one shorter. Although the terminal bud is lacking, the topmost axillary bud soon assumes a terminal position and continues the growth of the twig. The leaf scars are alternate, two-ranked, semicircular. The bundle traces are three, or they may be compound and then sometimes scattered. The stipule scars are unequal, one of each pair being much elongated.

LEAVES

The leaves are conduplicate in the bud. They are simple, petiolate, distichous, inequilateral with the larger side next to the branch, cordate or truncate at the oblique base, acute or acuminate at the apex, serrate (or rarely denticulate or nearly entire), deciduous, their petioles in falling leaving large elevated horizontal leaf scars displaying the ends of vascular bundles. Phyllotaxis is 1⁄2, i.e., the buds or leaves are alternate on opposite sides of the stem. The young leaves are in vertical position, with the apex directed downward when they first emerge from the bud. Later, they assume a nearly horizontal position. Each leaf has two narrow, ligulate, caducous, free stipules (bud scales) which fall off as the leaf expands. A peculiarity of the palmate venation of the leaves is that nearly all the lateral veins are branched only on the lower side. The stomata, which are generally confined to the lower surface of the blade, are of the ranunculaceous or anomocytic type, classed by Metcalfe & Chalk (1950: xv) as Type A, in which the
stoma is surrounded by cells that are indistinguishable in size, shape, or form from those of the remainder of the epidermis.

PUBESCEENCE

Much of the practical identification and classification of species of Tilia must be made on the amount and kind of pubescence, particularly on the underside of the leaves. This is often variable, not only according to season, but according to the part of the tree from which the leaves are selected. The lower surface of the blade differs from the upper usually in color and pubescence. With few exceptions, almost all species have the upper surface darker green and glabrous, but the lower surface of many is more or less covered with pubescence. This consists usually of four- or eight-rayed stellate trichomes, or some that are unicellular, or sometimes of both types. Unicellular trichomes are restricted to the veins, while the stellate trichomes may occupy the whole epidermal surface. Young leaves and those of the basal sprouts have the pubescence always connected with the veins. In the young stage, the upper surface is more or less pubescent, but in nearly all species this becomes glabrous soon after unfolding. Pubescence of sprout leaves is usually different from that on leaves of flowering branchlets. Most species of Tilia have small tufts of trichomes in the axils of the principal veins on the lower surface of the blades, particularly toward the base. These tufts have been called barbulae, domatia, or acaradomatia, and have been supposed to be a symbiotic adaptation for mites. These axillary tufts consist usually of simple trichomes, sometimes joined at the base.

INFLORESCENCE AND FLOWERS

All species have similar cymose inflorescences that are more or less flat-topped, with minute caduous bracts at the base of the branches. Depending on the species, the number of flowers ranges from 3 to 80. These appear after the leaves are nearly or quite fully grown. Inflorescences arise from the axils of foliar leaves on short shoots of the current season. The peduncle is more or less commate with the axis of a broad, conspicuous, light green, ligulate, persistent, reticulate-veined bract. Actually, this peduncle is attached to the upper surface of the bract, but the weight of the flowers (and later the fruits) pulls this down so that the positions are soon reversed: the bract is above the flowers with its upper surface turned downward. The resultant inverted or pendent position of the flowers affords protection from rain by the
large leaves. The drops roll off the leaves, so that rarely do any of the flowers become wet at the time the pollen is shed. The inverted position also prevents the pollen from falling directly on the stigmas of the same flower. In any case, self-pollination rarely occurs because the flowers are protandrous, i.e., the anthers open before the stigmas are receptive to pollen.

Each flower has five rather coriaceous, deciduous sepals valvate in aestivation. There are five hypogynous, deciduous petals alternating with the sepals. They are sometimes quinuncially imbricated in aestivation, that is, two being exterior, two interior, and the fifth having one margin exterior, the other interior. The aestivation of the corolla does not furnish a constant taxonomic character as that of the calyx. The stamens are indefinite, 15-80, inserted on a short hypogynous torus. The filaments are filiform, forked near the apex, in most species collected into five groups and more or less united at the base with each other and with a hypogynous spatulate petaloid scale or staminodium opposite each petal, and resembling it except for the smaller size. Staminodia are present in all American species, but are lacking in some European species. The anthers are fixed at the middle, extrose, dithecal, dehiscing longitudinally, the thecae separated or disjoined by the forking of the filament. The ovary is sessile, ovoid, tomentose, five-loculed, the locules opposite the sepals. The slender style is dilated at the apex into five spreading, stigmatic lobes. There are two ovules in each locule, ascending from the middle of its inner angle.

According to Wodehouse (1930: 442), the pollen of Tilia is not a factor in hay fever. The grains are described as tricolpate, with three short furrows equally spaced around the equator. There are three pores, one below the center of each furrow. The exine is finely reticulate. Notwithstanding the fact that its flowers produce nectar and are regularly visited by insects, the linden is an outstanding example of a tree that produces a great abundance of pollen. As many as 32,000 pollen grains have been collected from a single flower of the European Tilia cordata Mill. (Hyde & Williams, 1945: 457). It is found abundantly in postglacial silts. Three fossil species based on pollen have been described from the Green River Eocene formation in Colorado.

There are several reports about the supposed function of the bract of inflorescence. Presumably it serves as a parachute to carry the fruits some distance from the parent tree. Actually, the fruits are almost never carried any considerable distance by the wind. In T. americana and T. heterophylla, and perhaps in some other species, there may be frequently observed a marked tendency for the fruits to be deciduous from the pedicels, leaving the bracts rather conspicuous on
the trees far into the winter. The persistence of the bract and the frequent absence of the fruits can be observed on many hundreds of herbarium specimens. It is in fact so common a phenomenon that complete fruiting herbarium specimens are often a desideratum. The bracts are so variable in size, shape, and degree of pubescence that, in American species at least, they furnish almost no reliable taxonomic characters. There is no evident correlation between variations of the bracts and the characters of flowers, fruits, or leaves.

FRUITS AND SEEDS

The pistil ripens into a woody, subglobose, indehiscent, tomentose, nut-like drupe that is unilocular by the obliteration of the partitions. When dry, the fruits may float on water for several days or weeks. They contain one to three roundish, reddish brown, amphitropous, ascending seeds, with a cartilaginous testa, containing a large, often curved embryo in fleshy endosperm. Their shape and size vary according to the number developing in the fruit. Without special treatment, they require two or more years for germination. The young seedlings are readily recognized in the forest by their two epigeal, palmately three- to five-lobed cotyledons.

BARK AND WOOD

The bark of linden trees may remain smoothish for 20 years or more, but eventually it becomes thick and rough. It is not detached in large pieces but it ruptures by the increasing diameter of the trunk or branches, causing longitudinal fissures. The inner bark is very tough, fibrous, and mucilaginous. The tough phloem fibers have been utilized in the manufacture of cords, fish nets, and similar articles. Mats of this material were formerly a regular article of commerce in some areas of eastern Europe.

Lindens all have light, soft, white wood that is easily worked and especially adapted for wood-carving. Wood of different species is not distinguishable, and similar structural peculiarities are shared by all. Record & Hess (1943: 533) give the following summary of the characteristics of Tilia wood:

Heartwood creamy white to brownish, not always clearly demarcated from the thick, nearly white sapwood; luster medium; odorless and virtually tasteless. Density low; sp. gr. (air-dry) 0.40 to 0.50; weight 25 to 32 lbs. per cu. ft.; texture rather fine, uniform; grain straight or sometimes curly; easy to season and manufacture; holds its place well; poorly resistant to decay.
The following detailed technical description of the wood of Tilia (Kukachka & Rees, 1943: 25, 26) is based on study of "109 specimens representing 29 species and varieties."

Growth rings distinct; delimited by bands of flattened wood fibers and terminal parenchyma. Wood rays spreading broadly at the limits of the growth layers.

Pores angular in cross-sectional outline; 24 to 112 per square mm., average 59; tangential diameter range from 23 to 106 μ, average 63 μ (S.E. 0.43 μ, S.D. 115 μ); pore walls average 1.5 μ in diameter. Pores mostly solitary (56 per cent) and in radial multiples of 2 to 4 (31 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 2 to 7 pores; distributed without pattern but the pores become somewhat smaller in diameter from one end of the growth ring to the other.

Vessel members very short to medium-sized, average 461 μ in length (S.E. 173 μ, S.D. 91 μ); perforation plates simple, obliquely inclined. Tyloses few to abundant; thin-walled. All vessels with tertiary spirals.

Intervessel pit-pairs round to oval to polygonal; 3 to 8, mostly 3 to 5 μ in diameter, with lenticular, included apertures; alternate.

Vessel-ray pit-pairs and vessel-parenchyma pit-pairs identical; half-bordered; 3 to 5 μ in diameter; round or oval with lenticular included apertures or with large apertures of the same shape as the pit outline; alternate.

Wood parenchyma terminal and reticulate. The terminal parenchyma generally forming a continuous uniseriate band or at times merely interspersed among the flattened wood fibers at the limits of the growth ring.

The reticulate parenchyma forming uniseriate tangential or oblique lines between the wood rays; the individual cells either side by side or staggered. Yellowish-brown contents common. Parenchyma cells average 26 μ in tangential width and 95 μ in length.

Wood rays heterogeneous II B; 3 to 10 per mm., average 6. Multiseriate rays 3 to 4 seriate and commonly 23 to 38 μ in width; height extremely variable, ranging from 265 to 2,265 μ in height but mostly between 750 and 1,500 μ in height. The cells in radial section all tabular. The uniseriate rays generally very low and seldom exceed 300 μ in height. Yellowish-brown contents present; crystals sparse or lacking. Sheath cells extremely sparse; generally lacking in most specimens. Rays unstoried.

Wood fibers very short to moderately long, average 1,086 μ in length (S.E. 10 μ, S.D. 250 μ); middle diameter average of 26 μ and wall thickness of 2 to 2.5 μ. Fibers long to short-tapering; generally sharp-pointed. Pits bordered; round or oval; 5 to 7 μ in diameter; apertures included, lenticular or slit-like, extended.

CHROMOSOMES

H. Derenon (1932) published a list of chromosome counts made on species of Tilia planted in the Arnold Arboretum. These counts were made from buds and root tips. "The number of chromosomes in Tilia was n = 41, making this the highest odd basic number for a genus in plants so far recorded." Some species were reported to be diploids and
TAXONOMY

Table 1

Analysis of Data for Tilia on a Phytogeographical Basis

<table>
<thead>
<tr>
<th>Geographical Origin</th>
<th>Diploids</th>
<th>Tetraploids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td>T. cordata Mill.</td>
<td>T. amurensis Rupr.</td>
</tr>
<tr>
<td></td>
<td>T. platyphyllos Scop.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T. peltiolaris DC.</td>
<td>T. insularis Nakai</td>
</tr>
<tr>
<td></td>
<td>T. europaea L.</td>
<td>T. maximowicziana Shiras.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. tuan Szysz.</td>
</tr>
<tr>
<td>Asia</td>
<td>T. oliveri Szysz.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>America</td>
<td>T. americana L.</td>
<td></td>
</tr>
</tbody>
</table>

Others tetraploids. Dermen includes only one American species, T. americana L.; four are European, although one of these, T. europaea L., is said to be of hybrid origin (T. cordata × platyphyllos V. Engler); of the five Asian species, three are Chinese, one Korean, and one Japanese. Since many cultivated lindens are grown from root grafts, it would be useful to know which chromosome counts were made from root tips. I have seen no supporting herbarium vouchers; none is indicated in the published report. The nomenclature needs revision, as T. americana L. is listed as T. glabra Vent.; T. neglecta Spach is probably T. americana L.; T. vulgaris Hayne is a synonym of T. europaea L.

Chromosome counts for four other genera of Tiliaceae are listed by Darlington & Wylie (1955: 119), with reference to original publication. Corchorus (n = 7); Grewia (n = 9); Clappertonia (n = (9) 18); Triumfetta (n = 16). Among the genera studied, Tilia stands alone with n = 41.


Hybrids

In several contemporary American botanical textbooks and articles, the unqualified assertion is made that in Tilia "numerous hybrids are known." Without analysis, this statement may be misleading. The actual facts are that, except for a few cultivated lindens of hybrid origin, interspecific hybrids are unknown from North America and
only one or two have been recorded from eastern Asia. The conclusion is inescapable that genuine interspecific hybrids are extremely rare.

If we examine the literature, we find the following reports. In his monograph, V. Engler (1909) listed more than a dozen putative hybrids, mostly "Kulturhybriden," one between two Japanese species (japonica × kiusiana), four between European and one American species (T. americana), six between several European species, and three between American species (americana × heterophylla, caroliniana × heterophylla, and caroliniana × mexicana). I have examined the American "hybrids" so far as these are documented by annotated herbarium vouchers cited by Engler, and it is my opinion that these specimens (cited elsewhere in this monograph) fall unequivocally into the range of normal variation of the species concerned. Overemphasis on hybridism seems, at least in part, to be a result of inexact taxonomy.

From 1886 to 1950, the Index Kewensis lists the names of half a dozen authors responsible for the publication of slightly more than 100 putative hybrids, nearly all from Hungary. In Supplement I, published in 1906, there are nine by Simonkai and Borbas, chiefly from Hungary. No other hybrids are listed in Index Kewensis until 1930, when in Supplement VIII there are nine by J. Wagner, also all from Hungary. However, by far the largest eruption of "Bastarden" is to be found in Supplement IX, 1935, where 75 hybrids are listed, all published by J. Wagner and again all from Hungary. In Supplement X, there are seven more from Hungary and one from Japan. In the eleventh supplement published in 1953, there are five more, all by J. Wagner and all attributed to Hungary. These data are impressive. About five times as many named hybrids have been reported as there are species of Tilia on the whole globe, nearly all from Hungary.

Properties and Uses

The smooth, light, close-grained, pale, yellowish or white, soft wood has been used for sounding boards for pianos, various domestic utensils, toys, small boxes, wagon beds, boat paddles, and coffins. For carving it is said to be superior to every other kind of wood. It is not attacked by insects. Formerly, it was used to make excellent charcoal for gunpowder, "even better than alder, and nearly as good as hazel" (Loudon, 1838: 368). Baskets and cradles were formerly made from its twigs. Leaves, both fresh and dried, were used by the Romans for feeding cattle, a custom continued to modern times in northern
Europe. Ropes and mats, shoes and baskets were made from the bark. The sap of the lindens affords a quantity of sugar. The honey produced from the flowers is considered superior to most others. Loudon comments that lindens have long been favorite trees for avenues and public walks, and he quotes Duhamel that the French, “growing tired of the horsechestnut for avenues, adopted the lime for that purpose in the time of Louis XIV and accordingly, approaches to the residences of the French, as well as the English gentry of that date are bordered with lime trees.” Loudon goes on to say:

The fruit of Tilia had long been thought of little use until Missa, a physician of the faculty of Paris, by triturating it, mixed with some of its flowers, succeeded in procuring a butter perfectly resembling chocolate; having the same taste, and giving the same paste, as cocoa. This was in the time of Frederick the Great; who, feeling a greater interest in the discovery than the French, who were in possession of plantations of the cocoa in their colonies, engaged the chemist Maregrafi to prove the observations of Missa, which he did entirely to the satisfaction of Frederick; but, unfortunately, it was found that the lime tree chocolate did not keep. On this Ventenat remarks, that, if the subject had been pursued a little further, and the fruits of some of the American species of limes, taken, the success would probably have been complete. This anecdote is included by Fernald & Kinsey (1958).

Flowering of linden trees may begin at the age of 10 to 20 years. The flowers appear in June after the leaves are fully grown. At flowering time, the surrounding air is heavy with fragrance and noisy with the droning of thousands of bees and other insects. The flowers yield large quantities of nectar and afford an excellent bee pasture. The most excellent honey has made the linden a favorite tree, and we find it mentioned by Theophrastus, Pliny, Virgil, Aristophanes, and other early writers. Lime-flower oil, obtained by distilling the flowers of European species, is used in perfumery. Theophrastus remarks, “The lime hath both ‘male’ and ‘female’ forms, which differ in their general appearance, in that of the wood, and in being respectively fruit-bearing and sterile. The wood of the ‘male’ is hard yellow more branched closer, and also more fragrant; that of the ‘female’ is whiter” (Hort, 1916, 1: 225). It is probable that two species have been confused, possibly the large-leaved $T. \text{platyphyllos}$ and the small-leaved $T. \text{cordata}$.

**Propagation**

Lindens are propagated by seed and by layering. Seeds should be sown immediately after ripening, for if they are allowed to dry, they will often not germinate until the second year (Spaeth, 1934). In
layering, usually the method of "stooling" is employed; this consists of cutting a younger tree close to the ground and of laying down and covering partly with earth the numerous shoots which will appear. Varieties or rarer species are often grafted in spring or budded in August on common stock (Rehder, 1917: 3346).

Age and Size

The extreme limit of age of the large-leaved European linden, T. platyphyllos, has been estimated at 1,000 years. There is a record of a tree of this species in Oldenburg, Germany, 14 m. d.b.h. (diameter breast high), which may have been planted about A.D. 850. Many lindens in Europe are known to be 500 or 600 years old (Hegi, 1925: 444). A tree of T. americana, as it occurred in the valley of the Wabash River in southeastern Illinois, an area notable for the size and number of species (about 90) of deciduous trees, was reported as 17 1/2 feet (about 6 m.) in circumference, and 135 feet (about 45 m.) in height (Ridgway, 1895: 410). Trees of T. americana are mature in 100 to 150 years.

American lindens in present-day forests are often in a decadent condition. The trees (sprouts especially) are subject to attacks by fungi and scale insects. Compound trees of several leaning trunks (sprouts from one or more earlier generations of trunks) are more commonly seen than single erect original stems. The root system may thus be several times as long-lived as the parts above ground. It is also true in many of the old-growth mixed forests that lindens are becoming fewer, apparently as a result of competition with more aggressive species.

Geographical Distribution

The area of geographical distribution of lindens has many features in common with the regions of some other woody plants, such as Acer, Fraxinus, Carpinus, Corylus, and Fagus. In Europe, Tilia cordata Mill. extends farthest north; its boundary coincides approximately with that of the English oak, Quercus robur L. In eastern Asia, T. mandshurica Rupr. & Maxim. reaches the most northerly locations. There is no continuous distribution between the Eurasian and eastern Asian regions. In America, the northern boundary of Tilia (T. americana L.) is approximately that of Pinus strobus L., Tsuga canadensis (L.) Carr., Betula lutea Michx., Quercus rubra L., Acer rubrum L., A. sac-
charum Marsh., and Fraxinus americana L., which extend to Lat. 49°-50° W. in eastern Canada. The most southerly locality of the genus (T. mexicana Schlecht.) lies near the isthmus of Tehuantepec, where Tilia also reaches its highest altitude, up to 2,500 meters.

Table 2 shows the geographical distribution of the principal species of Tilia. The three chief geographical centers of development of the genus are (1) Europe and western Asia, which has few species, (2) the eastern Asian region, with the largest number of species, and (3) the American region of development.


2. The eastern Asian region is the main center of development of the genus, with the following species: T. amurensis Rupr., T. chinensis Maxim., T. dictyoneura V. Engler, T. henryana Szysz., T. insularis Nakai, T. intonsa Rehd. & Wils., T. mandshurica Rupr. & Maxim., T. mongolica Maxim., T. oliveri Szysz., T. paucicostata Maxim., and T. tuan Szysz. Some additional species have been described since 1935. The Japanese islands have a different flora with fewer species: T. japonica (Miq.) Simonk., T. kiusiana Mak. & Shiras., T. miqueliana Maxim., and T. maximowicziana Shiras. Eastern Asia is the connecting link between European and American species. The eastern Asiatic species must be considered the oldest.

It is interesting to note that only *T. cordata*, *T. platyphyllos*, and *T. dasystyla* have the flowers uniformly without staminodia. The others possess staminodia, although in *T. amurensis* these may be rudimentary. On a phytogeographical basis, all species of Tilia in eastern Asia and North America, and two in southeastern Asia, possess staminodia. From a phylogenetic standpoint, it would seem likely that the presence of staminodia should be regarded as a primitive character, while their absence is probably a reduced and derived condition. The traditional classification of Tilia into two groups on the presence or absence of staminodia is not practical and was therefore abandoned by V. Engler in 1909. He substituted a more elaborate classification which is outlined in Table 3.

**Brief Outline of Taxonomic History of American Species**

During the eighteenth and early nineteenth centuries only a few kinds of Tilia were known. Linnaeus in 1753 described two species, *T. europaea*, and a second one, *T. americana*, from eastern North
### Table 3

**ENGLER'S CLASSIFICATION (1909)**

<table>
<thead>
<tr>
<th>Sections</th>
<th>Subsections</th>
<th>Species</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trabeceules</td>
<td>platyphylllos</td>
<td>rubra</td>
<td>Europe, Caucasus</td>
</tr>
<tr>
<td></td>
<td>cordata, sibirica</td>
<td></td>
<td>Europe, Caucasus</td>
</tr>
<tr>
<td></td>
<td>amurensis</td>
<td></td>
<td>Siberia</td>
</tr>
<tr>
<td></td>
<td>mongolica</td>
<td></td>
<td>Continental eastern Asia</td>
</tr>
<tr>
<td></td>
<td>dictyoneura</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>paucicostata</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>japonica</td>
<td></td>
<td>Japan</td>
</tr>
<tr>
<td></td>
<td>kiusiana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anastrae</td>
<td>Reticules</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>tomentosa</td>
<td></td>
<td>Europe, Caucasus</td>
</tr>
<tr>
<td></td>
<td>mandshurica</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>oliveri</td>
<td></td>
<td>Continental eastern Asia</td>
</tr>
<tr>
<td></td>
<td>pendula</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>miqueliana</td>
<td></td>
<td>Japan</td>
</tr>
<tr>
<td>Ebarbulatae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>tuan</td>
<td></td>
<td>Continental eastern Asia</td>
</tr>
<tr>
<td></td>
<td>henryana</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>chinensis</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>maximovoziana</td>
<td></td>
<td>Japan</td>
</tr>
<tr>
<td></td>
<td>caroliniana</td>
<td></td>
<td>Southern U.S.</td>
</tr>
<tr>
<td></td>
<td>pubescens</td>
<td></td>
<td>Mexico</td>
</tr>
<tr>
<td></td>
<td>mexicana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Astrophilyra</td>
<td>Micranthae</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>baroniana</td>
<td></td>
<td>Continental eastern Asia</td>
</tr>
<tr>
<td></td>
<td>americana</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>heterophylla</td>
<td></td>
<td>Eastern U.S.</td>
</tr>
</tbody>
</table>

---

* Nomenclatural notes: *Tilia rubra* Stev., not DC., is *T. dasystyla* Stev.; *T. sibirica* Bayer is probably *T. cordata* Mill.; *T. dictyoneura* V.Engler is probably synonymous with *T. paucicostata* Maxim.; *T. pendula* V.Engler is a synonym of *T. oliveri* Syst.; *T. pubescens* Vent. is a later name for *T. caroliniana* Mill.; and *T. baroniana* Diels is a synonym of *T. chinensis* Maxim.

---

America. In 1768, Philip Miller recognized *T. americana* and added his *T. caroliniana*, described from a tree cultivated in England, where it had been introduced from Carolina by Mark Catesby. With certain variations in nomenclature, this pattern was followed in successive works by several botanists, including Michaux, Persoon, and Pursh.

The first monograph of the genus was published in 1803 by Ventenat, who treated six well-characterized species, three European and three American. In 1824, A. P. DeCandolle, in his *Prodromus*, included ten species, of which four (*T. glabra, T. laxiflora, T. pubescens*, and *T. heterophylla*) are American, the remainder European. In 1834, Spach
wrote a new monograph which included nine species. He divided the
genus into two sections, based, following Linnaeus, on the presence or
absence of staminodia. The monograph by Bayer (1862) reduced the
number of species to six, with many varieties, and, like Spach, divided
the genus into two sections, Haplopetaloideae Bayer (flowers without
staminodia) and Diplopetaloideae (flowers with staminodia). The
American species are discussed: T. heterophylla Vent., T. americana L.
as T. nigra and several other names), T. caroliniana Mill. (as T. laxi-
flora and T. truncata), and T. mexicana Schlecht. In 1817, Rafinesque
published the first of his binomials for American lindens, adding eight
more in 1838. In 1888, Simonkai published a revision in Hungarian
with a Latin summary, treating about 30 species with many varieties
and some hybrids. He kept the genus in two sections, the first, Lind-
nera Reichenb. (Diplopetaloideae of Bayer), having staminodia, and
including 18 species. The American species are described under six
binomials, T. mexicana Schlecht., T. caroliniana Mill., T. heterophylla
The second section, Eutilia Neibr. (1859), includes Haplopetaloideae
Bayer (1862), with a dozen described species, chiefly European, and
all lacking staminodia. In 1900, H. Shirasawa treated the lindens of
Japan, recognizing four species. Tilia japonica (Miq.) Simonk., the
common species throughout Japan, is treated as T. cordata var. japo-
nica. Two are described as new species, T. kiusiana Makino & Shiras.,
of southern Japan, and T. maximowicziana Shiras., the largest of the
Japanese lindens. Tilia miqueliana Maxim. of central Japan is re-
garded as having been originally introduced from China about A.D.
1200, and planted in the temple groves. The flowers of Japanese species
have staminodia. In 1915 a synopsis comprising ten Chinese species of
Tilia, with three described as new, was presented by Rehder & Wilson
(1915) on the basis of collections made by E. H. Wilson for the Arnold
 Arboretum. Since 1915, 18 new species have been described from eastern
Asia, from Siberia to Indochina.

In 1887, Asa Gray summarized the genus for North America, recog-
nizing four species, T. americana, T. pubescens [T. caroliniana], T.
heterophylla, and T. mexicana. Since that time, 118 names have been
applied to these species, but it is clear that Dr. Gray's judgment was
sound and accurate. Nearly all the subsequent nomenclaturizing shows
the futility of emphasizing the study of variations of populations of
trees without a clear concept of the fundamental species involved. Asa
Gray's summary of the taxonomy of American lindens is quoted as follows:

Tilia. Although our species are not absolutely limited, it seems necessary to
restore *T. pubescens* to specific rank, and so to recognize three species, viz.:
—*T. AMERICANA*, L., with ample leaves essentially glabrous, thickish and firm, green on both faces, the upper lucid; floral bract usually tapering into a stalked base (except the uppermost); fruit ovoid, usually lightly costate. *T. PUBESCENS*, Ait., with smaller and mostly thinner leaves, distinctly pubescent beneath, yet often glabrate in age: floral bract usually rounded at base and sessile or hardly stalked; fruit globular. I do not adopt the older name of *T. Caroliniana*, Mill. Diet.; for the original character, as well as that of Marshall and of Wangenheim, points to *T. Americana* rather than to *T. pubescens*. Probably to that species also belongs the *T. pubescens* of the Nouveau Duhamel. The var. *LEPTOPHYLLA*, Vent., is very well marked by its larger and thin leaves. It is hardly possible to combine this form with *T. Americana*, and its habitat is much more southern. *T. HETEROPHYLLA*, Vent., the *T. alba* of Michx., but not of Aiton, is well marked by its ample leaves of ovate outline (not rounded as in the true *T. alba* of S.E. Europe), whitish or silvery beneath; floral bract tapering to a very short-stalked or sessile base, usually elongated, and the peduncles still longer; the fruit globular. It strictly belongs to the Alleghany region, from Southern Pennsylvania to Florida. The original reference of Aiton’s *T. alba* to America was corrected in the second edition of the Hortus Kewensis. But, having been copied by Ventenat, under his *T. rotundifolia*, the mistake has been kept up by Bayer in his Monograph, who places it under his *T. heterophylla-nigra*, and has two forms from Kentucky, both undoubtedly *T. heterophylla*. *T. MEXICANA*, Schlecht., which Bayer makes a variety of *T. pubescens*, is probably a good species. The floral bracts taper to a slender-stalked base.

This summary has stood for 80 years as a sound and practically useful taxonomic statement of the North American species. *Tilia americana* is the common northern species, although the bract characters are less reliable than Gray supposed. The earliest name, *T. caroliniana*, has to be reinstated for the common southern species, with *T. pubescens* relegated to synonymy. In accepting the statement “leaves distinctly pubescent beneath, yet often glabrate in age” allowance must be made for specimens that are glabrescent early in the season. The variety *leptophylla*, with its “larger and thin leaves,” cannot be maintained. *Tilia heterophylla* belongs, as stated, chiefly to the Allegheny region, and *T. mexicana* is a “good species,” although the bracteal character, as in other species, is extremely variable.

In 1909 Camillo Schneider in the first volume of his Illustriertes Handbuch der Laubholzkunde (pp. 367-389) gave a synopsis of the known species, with brief diagnostic descriptions, and analytical dichotomous keys, with major emphasis on vegetative characters. He treated 6 species from Europe and western Asia, 16 from eastern Asia, and 8 from North America. Since that time about two dozen additional binomials have been proposed for Asian species, and several more for the genus in Europe, including many putative hybrids, as well as several more binomials and trinomials indicating American species and
varieties. As it is probable that most of these new names are synonyms, the synopsis of Schneider is still of practical value. He did not accept the schemes of Bayer and V. Engler, neither did he attempt to give a new classification, but instead he arranged the species in a sequence as he thought them to be related: "Da ich weder die alten BAYERschen Sektionen noch ENGLERs neue Gliederung für zutreffend halte, da ich aber nicht in Eile eine neue Gruppierung schaffen will, so gebe ich diesmal einen analytischen Schlüssel für die Arten unter Voranstellung der vegetativen Merkmale und lasse dann die Beschreibungen in der Reihenfolge folgen, wie mir die Arten nahe zu stehen scheinen, ohne aber etwas Definitives sagen zu wollen."

In the same year, a compact dissertation on Tilia by Viktor Engler was published in Breslau. He recognized 25 species in two sections and five subsections, rejecting the hitherto generally accepted scheme of classifying the species in two groups according to presence or absence of staminodia, using instead principally characters of leaf venation and pubescence. Numerous varieties and forms are named, and several hybrids. There is a discussion of taxonomy, morphology, geographical distribution, phylogeny, and paleobotany, with bibliographical references and citation of specimens. He treated the American species under five binomials, T. mexicana, pubescens, caroliniana, heterophylla, and americana. He mentions Schneider’s study, but considers that author to have had too narrow a species concept. He comments (in translation): “In the meantime a treatment of the genus has appeared for the manual of Schneider, who follows in part Simonkai, in part Britton. I cannot agree with the narrow species concept of Schneider as applied particularly to T. rubra, T. mexicana, and T. americana. . . . With respect to a classification of the genus into sections, etc., Schneider, to whom I gave an abstract of my manuscript for reference, believes he cannot agree with me.”

---

1 Viktor Engler, son of Paul Engler, a merchant, was born June 3, 1885, at Thorn (Torun) in Poland, which was at that time German territory. In 1904 he was graduated from the local gymnasium and then, in Breslau, he studied natural science, particularly botany. He was also interested in linguistics and studies of folklore. His doctoral dissertation, “Monographie derGattung Tilia,” was published in Breslau in 1909. His only other publications are “Zwei verkannte Linden” (Mitt. Deutsch. Dendr. Ges., 1907), “Beiträge zur Kenntnis der heimischen Lindenflora” (Jahresber. Schles. Ges. Vaterl. Kult., 1913), and, with H. Winkler, “Über herbstliches Ausdauern von Laubblättern” (Naturwissenschaftliche Wochenschrift, 1913). On the first day of war in 1914, Engler joined the German army as a corporal. He was killed by a bullet near the village of Kanatharei in Bulgaria in 1917 and was buried in the cemetery there. H. Winkler in Ber. Deutsch. Bot. Ges. 36: 137, 1918.
Synopsis of Tilia (after V. Engler)

Section I. Anastraea V. Engler.—Stellate hairs few or none; mature leaves barbulate or glabrous; stamens 15-50.

Subsection 1. Reticulares V. Engler.—Leaves glaucous and glabrous beneath; tertiary nerves not prominent or parallel; pericarp chartaceous, fragile. — Eight species, including T. cordata.

Subsection 2. Trabeculares V. Engler.—Leaves more or less barbulate; nerves more or less pilose; tertiary nerves exactly parallel; stellate hairs none; hairs unicellular; corolla explanate; staminodia none; pericarp ligneous. — T. platyphyllos and T. rubra.

Section II. Astrophylla V. Engler.—Stellate hairs frequent; tertiary nerves always more or less parallel; corolla not explanate; stamens about 50 or more; staminodia always present; pericarp coriaceous or ligneous.

Subsection 1. Ebarbulatae V. Engler.—Leaves ebarbulate, when young pilose above, becoming glabrous, the lower surface stellate-pilose and more or less white-tomentose. — Four species, including T. tomentosa.

Subsection 2. Micranthae V. Engler.—Leaves barbulate, stellate-pilose below; flowers small; buds, branchlets, and petioles more or less pilose. — Seven species, including T. caroliniana and T. mexicana.

Subsection 3. Maeranthae V. Engler.—Leaves barbulate, the lower surface more or less stellate-pilose, or glabrous; flowers large; buds, branchlets, and petioles glabrous. — Three species, including T. heterophylla and T. americana.

The principal modern attempt at a comprehensive analysis of the American species, except for brief summaries in the form of keys and diagnostic descriptions in various manuals, is that of Sargent in 1918. Despite expressions of dissatisfaction (Fernald, 1941: 604, 1950: 999; Bush, in lit.) with the work of Charles Sprague Sargent on the North American species of Tilia, the fact is that he did more work, studied more material, and had more collaborators than any other student of the American lindens before that time. That we cannot accept all his taxonomic conclusions is due mainly to the fact that nowadays we carry our studies along somewhat different lines. Neither Sargent nor his contemporaries approached the study primarily from the standpoint of the monographer. Their basic thesis was the study of variations among specimens. They were interested in analysis rather than syn-
thesis, and in variations of natural populations rather than the underlying similarities. The net result was the recording of quantities of data, competently analyzed, with corresponding multiplication of published binomials and trinomials.

They were following a plan later formulated by C. R. Ball as the centrifugal method.

[This] second method is to study, successively, the descriptions and the cited or supposed material of each of the named species and varieties known or suspected to belong within the broad limits set. When one such has been studied and segregated, another is taken up, and so on until all have been covered. This is the centrifugal method, working from the inside out. It flies out from the center in all directions. It assumes differences, consciously or unconsciously, because others have done so. . . . Others have applied different names, have emphasized different characters or appearances, and have made comparisons to prove that significant differences exist. There is an internal pressure to verify what others have found or decided. All of this influence is present in addition to the urge to father more entities, new or resurrected, especially just before a new edition of a manual [Ball, 1946: 378].

Sargent, then director of the Arnold Arboretum of Harvard University, led all the rest in the observation of these trees in the forest and examination of herbarium material gathered in various parts of the country where lindens grow, much of it collected by E. J. Palmer, T. G. Harbison, R. C. Cocks, W. W. Ashe, and others. The following observations, published nearly 50 years ago, are here given in slightly abbreviated form, largely in his own words (Sargent, 1918: 421-422).

To understand a species of Tilia properly, four collections are needed: the first made in early spring to show the unfolding leaves, the second in early summer when the trees are in flower, the third six or eight weeks later when the fruit is mature, and the fourth in winter for the winter buds. Many of these trees grow in regions where summer collecting presents many difficulties and causes much discomfort; the trees do not always flower every year, and fruit often does not mature or is destroyed in storms before it is ripe. Even with abundant material it is difficult to find characters by which different species and their varieties can be satisfactorily arranged. In most large genera of trees, many species can be distinguished by the bark, but the bark of American lindens varies so little that it has no value in determining species. Branchlets of some species are stouter than others, but stout and slender branchlets are often found on the same tree. Their color is uniform on some species, but on others varies from yellow or pale brown to red; on some species the branchlets are glabrous and on others they are pubescent, but in some species glabrous and pubescent branchlets are found on the same tree. Except in size, there is no con-
constant character in flowers. Fruit, although it varies slightly in size, is always globose or ovoid, these different forms occurring in the same species and often on the same tree. The shape and size of leaves vary on different branches of the same tree, but their serration and venation have sometimes specific importance. "The only constant and reliable character, however, which I have found for distinguishing the species is in the absence or presence of the hairy covering on the surface of the leaves and in the nature of this covering when it exists. . . . When it is possible to make a comparative study of trees growing together in an arboretum where they can be watched through the year, it will probably be found that some characters which now seem constant cannot be depended on and that another arrangement of this group will be necessary."

Like Asa Gray before him, Sargent in 1891 had accepted only three species as native in the United States, *Tilia americana* L., *T. pubescens* Ait., and *T. heterophylla* Vent., but by 1918 he distinguished 15 species, with 14 new varieties, and in his manual (1922) he illustrated 17 of these supposed taxa. As pointed out by Little (1953), the main difference between these numerous supposed additional species and varieties is to be found in pubescence of leaves and twigs, characters which vary among leaves on the same tree as well as according to season. Besides being inconstant, these characters would not be regarded as of specific rank in other genera of trees.

In his Manual of the Trees of North America (1922, reprinted with corrections in 1926), Sargent attributed 15 species (10 described by him) to eastern North America north of Mexico. Each is given a rather full description, statement of geographical distribution, and a reproduction of a line drawing showing a branchlet with flowers and fruits. The taxonomic treatment is furnished with a dichotomous key based almost exclusively on character of pubescence of leaves. *Tilia americana* is named *T. glabra*. The authority for *T. floridana* is given as Ashe (instead of Small), and *T. neglecta* Spach is maintained as a separate species.

During the quarter-century between 1902 and 1928, W. W. Ashe (1872-1932), a pioneer forester of the United States Forest Service, contributed in six articles 16 binomials and trinomials, all of which now fall into synonymy. Nine of these names, standing for three species, one variety, one forma, and four transfers, are synonyms of *T. caroliniana*. Seven others, of which four are for species and three are transfers, belong under *T. heterophylla*. Ashe thus fell short by four names and combinations of the record set by Benjamin Franklin Bush, who was the originator of 20 new names and combinations in *Tilia*. 
In 1927 and in 1929 Bush published two revisional studies, with keys, discussions, bibliographical references, and citations of herbarium specimens, and in 1933 his treatment of the species of southern United States appeared in J. K. Small’s Manual of the Southeastern Flora. In the first study, The glabrate species of Tilia (1927), Bush Treats 11 species and five varieties. Following Sargent, T. americana is treated as T. glabra, but T. neglecta is included as a variety. These are followed by T. leucocarpa with two varieties, T. venulosa and T. littoralis, each with one variety, then come T. crenoserrata, and the newly described T. ashei. The second study, The Mexican species of Tilia (1929), includes 14 binomials for 12 purportedly new Mexican species, but the original species of Mexico, T. mexicana Schlecht., described in 1837, is not understood. In the treatment in Small’s Manual, Bush provides a key and brief descriptions to the 14 species supposed to grow “naturally in Florida, Alabama, Mississippi, eastern Louisiana, Tennessee, North Carolina, South Carolina, and Georgia.” No new names are proposed. Only two species, T. caroliniana and T. heterophylla, appear to be valid; the other 12 names are synonyms. Tilia glabra Vent. is equated with T. venulosa Sarg. and T. fulva Raf. Tilia neglecta is retained as a species that extends southward to North Carolina and northern Mississippi, with the synonym T. americana Marsh., not L.

Probably the most useful and reliable modern taxonomic treatment of Tilia in textbook form is that of Alfred Rehder (1863-1949) in his Manual of Cultivated Trees and Shrubs, of which the first edition appeared in 1927, and a revised, enlarged edition was published in 1940. A workable key and short descriptions are provided for 20 species, with brief reference to two more species, 14 varieties, and half a dozen European hybrids. Of the American species, T. caroliniana and T. mexicana are omitted, probably because they were not recognized as being in cultivation. Tilia floridana Small is included after T. americana as a “closely related species.” This binomial is wrongly ascribed to (V. Engler) Small. The name T. floridana was published by Small in 1903, but in 1909 V. Engler treated it as var. β of T. caroliniana Mill. Much useful information about species of Tilia is included in this manual, such as common name, geographical distribution or origin, references to illustrations, the year when the species was introduced into cultivation, zones of hardiness, and important synonymy. The species are arranged in a sequence beginning with those of Europe, followed by American and eastern Asiatic species. Those with flowers
lacking staminodia are placed first. The genus is not subdivided into subgenera or sections.

A treatment of Tilia in eastern United States, described as "wholly tentative" in Gray's Manual of Botany (Fernald, 1950: 999), includes four species, of which only T. americana and T. heterophylla are valid. Tilia floridana is synonymous with T. caroliniana, which occurs only along the southern edge of the geographical area covered by the manual, and T. neglecta, as there described, seems to be a mixture, or, as Fernald says, "an inconstant and rather nondescript series, perhaps better treated as variations of no. 1 [T. americana]." Viktor Engler is again erroneously cited as parenthetical author of T. floridana. The account by H. A. Gleason in the New Britton & Brown (1952) is quite practical, with the exception that T. monticola should be merged with T. heterophylla.

The most recent synopsis of the United States species of Tilia is that appearing in Check List of Native and Naturalized Trees of the United States by E. L. Little (1953). Four species of Tilia are recognized, T. americana, T. caroliniana, T. floridana, and T. heterophylla. Common names, geographical ranges, bibliographical references, and synonymy are given. The author says "Much detailed field and experimental study of the genus Tilia, particularly of progeny tests, is needed. . . . In this tentative compilation four species are accepted and no varieties are distinguished. The remaining names are grouped in synonymy, though with some uncertainty. Perhaps a few more species may merit recognition, though most trees and specimens probably can be placed satisfactorily in one of these four species until a detailed study of the genus is made."

We can summarize the nomenclatural history of the living American species by noting that a total of 144 names have been applied to the four species of linden recognized in this monograph. These include 70 binomials, 61 trinomials, and 13 quadrinomials. These names and combinations have been made by 38 botanists, but almost half of them have been made by four authors, as follows: 22 by V. Engler, 21 by Sargent, 20 by Bush, and 16 by Ashe.

The present status of the taxonomy of the existing North American species indicates that in the United States there are three, T. americana, T. caroliniana, and T. heterophylla. In Canada there may be two, T. americana and T. heterophylla, and in Mexico there is one more, T. mexicana.
American Fossil Lindens

When dealing with taxonomy and phytogeography of angiosperms we must first of all consider that the study of living genera is so profoundly linked to the fossil representatives that the two fields of research cannot any longer be kept distinct. Instead of writing of fossil and living species it appears more nearly correct to refer to ancient and modern Tiliaceae.

Sometimes the paleobotanist is thought to be working under a disadvantage when he has only leaves or leaf impressions for study, without additional material of reproductive parts of the plant. It is clear, however, that the neobotanical student of certain groups, e.g. the genus Tilia, may be somewhat similarly restricted. In this genus, leaves are on the trees during most months of the year, while flowers are available for scarcely more than a month. Herbarium specimens show about equal proportions of collections with reproductive structures and those consisting entirely of leaves and twigs. Study of living trees in the field will not alter these conditions. It would appear that in this respect the neotaxonomist studying contemporary floras often has only a slight advantage over his paleobotanical colleagues. When studying ligneous plants, both groups of botanists are dependent to a large extent upon vegetative structures to provide key characters for taxonomic discrimination.

OCCURRENCE AND DISTRIBUTION

Ancient fossil linden stock may have originated at high latitudes in the far north, but whether in North America or in Asia it is impossible to say with certainty. All known Tertiary American lindens are from the western part of the continent. The oldest are of Paleocene age, of which three are known, from Alaska, Colorado, and Montana respectively. There are seven Eocene species from Alaska to Colorado and California, and one from southeastern Texas.

There has been some question as to the actual occurrence of Tilia in the Oligocene epoch. LaMotte (1935: 43) says: "There is no known occurrence of Tilia in the North American Oligocene if the Bridge Creek deposits are regarded as lower Mioene." At the time of his report, however, the Florissant beds of Colorado were considered to be Mioene. Subsequent studies by MacGinitie (1953: 4) have assigned the Florissant beds to an Oligocene age, thus providing a record of one species of Tilia in the Oligocene. Mioene records in North America are few, but there are described species from Canada in British Columbia and from the United States in Idaho, Oregon, Washington, Nevada,
### Table 4

**TILIA IN NORTH AMERICA DURING THE CENOZOIC ERA**

<table>
<thead>
<tr>
<th>Mesozoic</th>
<th>Cenozoic</th>
<th>Quaternary</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cretaceous</strong></td>
<td><strong>Tertiary</strong></td>
<td><strong>Quaternary</strong></td>
</tr>
<tr>
<td><strong>Upper Cretaceous</strong></td>
<td><strong>Paleocene</strong></td>
<td><strong>Eocene</strong></td>
</tr>
<tr>
<td>malnigreni Heer, 1866 (Alaska)</td>
<td>grewioides Hollick, 1836 (Alaska)</td>
<td>populifolia Lesq., 1883 (Colorado)</td>
</tr>
<tr>
<td>speciosissima Knowlt., 1918 (Colorado)</td>
<td>notabilis Hollick, 1936 (Alaska)</td>
<td>scudderi (Cock.)</td>
</tr>
<tr>
<td>weedii Knowlt., 1902 (Montana)</td>
<td>R. W. Brown, 1934 (Colorado)</td>
<td>crassipes Wodehouse, 1933 (Colorado)</td>
</tr>
<tr>
<td></td>
<td>tetraforaminites Wodehouse, 1933 (Colorado)</td>
<td>vescipites Wodehouse, 1933 (Colorado)</td>
</tr>
<tr>
<td></td>
<td>inaequalis MacG., 1937 (California)</td>
<td>jacksoniana Berry, 1924 (Texas)</td>
</tr>
</tbody>
</table>
and California. Miocene beds are more frequent in Europe, where more than a dozen different species have been described. "The known Pliocene lindens, owing to the rarity of plant beds of this age in North America, are confined to Eurasia, although the genus was undoubtedly present in North America during the Pliocene, since it is found in the deposits of the immediately preceding and succeeding times" (Berry, 1923: 237).

Lindens are found as fossils in the Pleistocene of both Europe and North America, although the records are not numerous. There is one each from Ontario and New Jersey.

FOSSIL RECORD

The fossil record of Tilia in North America is not extensive, consisting of approximately 20 species (Knowlton, 1917; LaMotte, 1944), ranging from early Tertiary through the Pleistocene. Most species are based on leaf impressions, and a few on the unique bracts of inflorescence characteristic of the genus. Three species have been based on pollen. Because of erroneous identification, a few of the earlier records have been transferred recently to other genera.

The earliest North American record has been named Tilia cretacea Hollick (1930: 106) from the Upper Cretaceous of the Yukon River region in Alaska, but LaMotte (1935) considers it to be a Viburnum (Caprifoliaceae). This leaves Tilia speciosissima Knowlton (1918: 336) from the Paleocene in western Colorado as the earliest seemingly valid record of the genus Tilia in North America. This species, and a second, Tilia weedii Knowlton (1902: 706) from Fort Union deposits of Eocene age on Porcupine Butte near Melville, Montana, are known only from the holotypes. Tilia jacksoniana Berry (1924: 180) has been described from Eocene deposits in Brazos County, Texas. These species have been compared with the living Tilia americana L. of eastern temperate North America, but examination of published photographs of the type material indicates that they show a greater resemblance to certain lindens of eastern Asia which have the leaf blades more nearly symmetrical at the base.

In 1936 Hollick recorded Tilia alaskana Heer, Tilia grewioides Hollick, Tilia malmgreni Heer, and Tilia notabilis Hollick from southeastern Alaska, attributing them to the Tertiary.

Another American collection of fossil leaves that resembles Asiatic rather than living American species is Tilia populifolia Lesq., first recorded from Florissant, Colorado, first considered Miocene in age, but recently referred to Oligocene. It was found later in the Fort Union
<table>
<thead>
<tr>
<th>Mesozoic</th>
<th>Cretaceous</th>
<th>Paleocene</th>
<th>Eocene</th>
<th>Oligocene</th>
<th>Miocene</th>
<th>Pliocene</th>
<th>Quaternary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Cretaceous</td>
<td>malmsgreni Heer, 1866 (Alaska)</td>
<td>grevisoides Hollick, 1936 (Alaska)</td>
<td>populifolia Lesq., 1883 (Colorado)</td>
<td>aspera (Newh.) LaMotte, 1935 (Oregon, Washington, Nevada, California)</td>
<td>penhallow Hollick, 1927 (Brit. Col.)</td>
<td>putulifolia H.V.Smith, 1941 (Idaho)</td>
<td>americana L.; Penhallow, 1899 (Ontario)</td>
</tr>
<tr>
<td></td>
<td>speciosissima Knowl., 1918 (Colorado)</td>
<td>scudderii (Cock.) Knowl., 1902 (Montana)</td>
<td>cordesii R. W. Brown, 1934 (Colorado)</td>
<td>octonaria LaMotte, 1935 (Oregon)</td>
<td>dubia Berry, 1907 (New Jersey)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>tetraforaminifera Wodehouse, 1933 (Colorado)</td>
<td>vesiculifera Wodehouse, 1933 (Colorado)</td>
<td>incertae sedis MacG., 1937 (California)</td>
<td>jacksoniana Berry, 1924 (Texas)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
and California. Miocene beds are more frequent in Europe, where more than a dozen different species have been described. "The known Pliocene lindens, owing to the rarity of plant beds of this age in North America, are confined to Eurasia, although the genus was undoubtedly present in North America during the Pliocene, since it is found in the deposits of the immediately preceding and succeeding times" (Berry, 1923: 237).

Lindens are found as fossils in the Pleistocene of both Europe and North America, although the records are not numerous. There is one each from Ontario and New Jersey.

**FOSSIL RECORD**

The fossil record of *Tilia* in North America is not extensive, consisting of approximately 20 species (Knowlton, 1917; LaMotte, 1944), ranging from early Tertiary through the Pleistocene. Most species are based on leaf impressions, and a few on the unique bracts of inflorescence characteristic of the genus. Three species have been based on pollen. Because of erroneous identification, a few of the earlier records have been transferred recently to other genera.

The earliest North American record has been named *Tilia cretacea* Hollick (1930: 106) from the Upper Cretaceous of the Yukon River region in Alaska, but LaMotte (1935) considers it to be a Viburnum (Caprifoliaceae). This leaves *Tilia speciosissima* Knowlton (1918: 336) from the Paleocene in western Colorado as the earliest seemingly valid record of the genus *Tilia* in North America. This species, and a second, *Tilia weedii* Knowlton (1902: 706) from Fort Union deposits of Eocene age on Porcupine Butte near Melville, Montana, are known only from the holotypes. *Tilia jacksoniana* Berry (1924: 180) has been described from Eocene deposits in Brazos County, Texas. These species have been compared with the living *Tilia americana* L. of eastern temperate North America, but examination of published photographs of the type material indicates that they show a greater resemblance to certain lindens of eastern Asia which have the leaf blades more nearly symmetrical at the base.


Another American collection of fossil leaves that resembles Asiatic rather than living American species is *Tilia populifolia* Lesq., first recorded from Florissant, Colorado, first considered Miocene in age, but recently referred to Oligocene. It was found later in the Fort Union
deposits of Eocene age in Yellowstone National Park. It represents a large-leaved species with the base of the blade almost symmetrical, like that of *Tilia mandshurica* Rupe. & Maxim. of Korea, Manchuria, and northern China. Since its publication by Lesquereaux in 1883, *Tilia populifolia* has been variously interpreted as Alnus, Populus, and Betula, and in 1953, MacGinitie recognized one of its elements as belonging to *Morus symmetrica* Cockerell, pointing to resemblance with the Texas mulberry, *Morus microphylla*. It happens occasionally in dealing with the living flora that specimens of *Morus* and even *Broussonetia* are found in herbaria misidentified as species of *Tilia*.

Another Miocene species, *Tilia aspera* (Newberry) LaMotte, includes *Tilia pedunculata* Chaney from Miocene deposits in north central Oregon and northwestern Nevada, and *Tilia hesperia* Berry from the Latah formation of northeastern Washington. The Miocene species, *Tilia oregona* LaMotte (1935: 47), based on leaves, fruits, and flowers, from Bridge Creek, Oregon, is regarded by its author as most closely related to *Tilia japonica* (Miq.) Simonk. of Japan, and other related species in the temperate forests of Japan, Korea, southern Manchuria, and the northern Chinese provinces.

Three species, *Tilia crassipites*, *Tilia tetraforaminites*, and *Tilia vescipites*, based on pollen of Eocene age from Garfield County, Colorado, were described by Wodehouse in 1933.

As summarized by LaMotte (1935), the Pliocene history of *Tilia* in North America is negative and the Quaternary meager. *Tilia americana* L. is reported from interglacial Pleistocene deposits of the Don Valley near Toronto, Canada (Penhallow, 1899), and *Tilia dubia* (Newberry) Berry from similar deposits in New Jersey "undoubtedly represents a still existing species, either *Tilia americana* L. or *Tilia heterophylla* Vent." (Berry, 1907: 80). On the basis of Newberry's published figure, it seems impossible to tell to which species this may belong, or even whether it is really a member of the genus *Tilia*.

**ORIGIN AND EVOLUTION**

The origin, migrations, and evolution of the species of the genus *Tilia* are little known or at best only partly understood. The living species in North America are restricted to the eastern half of the United States and southermost Canada. In Mexico, one species ranges westward to Long. 108° W., and southward below the Tropic of Cancer almost to the isthmus of Tehuantepec near Lat. 17° N., which is apparently as near the equator as the genus is represented on any part of the earth at the present time.
In times past, however, the pattern of distribution of species of linden was quite different. All fossils of Tertiary age have been found in western North America, where no living species of Tilia occurs. It is possible that during the Cretaceous there may have been a northward migration of floras from the Caribbean region through Mexico into the mountainous parts of western United States (Mason, 1942: 287). This migration contributed little to the floras of eastern North America because of the existence of a great inland Cretaceous sea, dividing the continent into two parts (Pirsson & Schuchert, Textb. II: 557, pl. 42, 1924). It is thought, however, that much of the present flora of southeastern United States may be a direct result of such a migration. It is probable that the coniferous forests of eastern United States which now extend southward in the mountains were also derived from this source, and that certain elements in the present-day flora may have migrated eastward by way of the Ozark Plateau.

During the late Eocene and later, the temperature began to drop, the climate became cooler and drier, and elements of floras migrated southward again. The Pacific Coast coniferous forests, dominated in part by redwoods, came from the north. Whether they originated on the North American continent or in Asia is not certain, but they shifted southward behind retreating angiosperms, making the last major contribution to the present American temperate flora (Chaney, 1936: 55).

What may be the oldest American living species of linden, *T. mexicana*, is part of the ancient Caribbean flora. If it ever migrated northward beyond the present boundary of Mexico, it has left no known trace. The most closely related species, *T. caroliniana*, migrated northward to southern United States and, probably as the result of genetic diversity of the species and its response to climatic and topographic changes, it underwent in its migrations specific differentiation from *T. mexicana*, to which it is closely related phylogenetically and morphologically. A third species, *T. heterophylla*, has diverged even more from the parental stock and is now essentially an Alleghenian tree occupying a geographical range intermediate between but not entirely exclusive of *T. caroliniana* to the south and *T. americana* to the north. The latter is the common widespread northern species, here regarded as probably the youngest, which occupies the areas most recently available since the recession of the Pleistocene ice sheets. This proposed phylogenetical sequence of species (see Diagram 1, p. 36) appears to be supported by available morphological evidence.

The following general theory underlies these suggestions as to the probable phylogenetic relations of the four North American species of Tilia. First, there was a migration of Tilia with other angiospermous
Diagram 1. Probable inter-relationships of American species of Tilia.
enera from Asia to western North America during the Cretaceous. As far as the lindens are concerned, this theory receives some support from the fact that two well-defined species of Tilia, *T. aspera* and *T. oregona* (LaMotte, 1935) in the Miocene of western America, resemble two existing Asian species, *T. mandshurica* and *T. miqueliana* more closely than they resemble any living American species. The forests that included Tilia and other angiospermous genera disappeared from western North America during the Pliocene.

Second, with floristic migrations from Asia, there were also migrations of Caribbean floras into what is now southeastern United States, with the establishment toward the close of the Pleistocene of approximately the present geographical distribution of species of Tilia and some other genera of deciduous trees. Particularly in the Old World, the pattern of distribution of lindens has many features in common with the areas of some other genera of woody dicotyledons, such as Acer, Fraxinus, Carpinus, Corylus, and Fagus.

Following is a systematic and bibliographical list of American fossil lindens.

**ANNOTATED LIST OF SPECIES**

*Tilia alaskana* Heer, 1869: 36, pl. x; Hollick, 1936: 144. Type locality: Port Graham, Kenai, Alaska. It was based on two fragmentary leaf specimens but has never been recognized elsewhere. LaMotte suggests that *T. alaskana* and *T. cretacea* Hollick may be the same or closely similar species, and that it seems likely that *T. cretacea* belongs to the genus *Viburnum*. Eocene.


*Tilia antiqua* Newberry, 1868: 52. North Dakota, Montana, Wyoming. This is *Viburnum antiquum* (Newb.) Hollick ex Newberry in U.S. Geol. Surv. Monogr. 35: 128, pl. 33, 1898. "[Ward] showed conclusively that leaves described by Newberry as *Tilia antiqua* . . . were in fact those of *Viburnum*" (LaMotte, 1935: 41).

*Tilia aspera* (Newb.) LaMotte, 1935: 45, pls. 1, 2. Oregon, Washington, Nevada, California. The figures in plates 1 and 2 compare very favorably with herbarium specimens of *T. mandshurica* Rupr. & Maxim. of northeastern Asia. Type locality: Bridge Creek, Oregon. Miocene. Syn.: *Platanus aspera* Newberry, pro parte; *Tilia pedunculata* Chaney; *Tilia hesperia* Berry; *Vitis chaneyi* MacGinitie.

Tilia cretacea Hollick, 1930: 106, pl. 82. This is a species of Viburnum; vide LaMotte, 1935: 41.


Tilia grewioides Hollick, 1936: 144, pl. 81. Type locality: Admiralty Island, southeastern Alaska. Eocene. According to its author, this species appears to approach most closely T. distans Nathorst from the Tertiary of Japan.

Tilia inaequalis MacGinitie, 1937: 146, pls. 8, 13. Type locality: Trinity Co., California.

Tilia (?) incerta Hollick, 1927: 414, pl. 43. Type locality: Saint Eugene silts, Kootenay Valley, British Columbia. Pleistocene (?)

Tilia jacksoniana Berry, 1924: 180, pls. 63, 64. Type locality: Fayette sandstone, Mossy Creek, 3 miles S.W. of Wellborn, Brazos Co., Texas. Eocene. This is the first fossil Tilia to be discovered in the Coastal Plain Tertiary. Berry compares it with T. americana, but photographic reproductions of the type material show closer resemblance to certain species of eastern Asia; which of the living species it most closely resembles is very difficult to say. In its parallel tertiary venation, the finely toothed margin, and the general configuration of the blade, it perhaps approaches T. oliveri Szysz. of central China.

Tilia malmgreni Heer, 1866; Hollick, 1936: 144, pl. 103. Admiralty Island, southeastern Alaska. Type locality: Spitzbergen. Paleocene. First recorded from Spitzbergen, then Grinnell Land, and later from the Mackenzie region of northern Canada. The closely allied fossil species, T. sachalinensis Heer, has been found on the island of Sakhalin in eastern Asia (Hollick, loc. cit.). The holotype from Spitzbergen appears to be a true linden. According to Berry (1923: 236) the Grinnell Land specimens may belong to a species of Corylus.

Tilia notabilis Hollick, 1936: 145, pl. 82. Type locality: Admiralty Island, southeastern Alaska. Eocene. The fossil species that appears to approach T. notabilis most closely is T. speciosissima Knowl. (Hollick, loc. cit.).

Tilia oregona LaMotte, 1935: 47, pl. 3. Type locality: Bridge Creek, Grant Co., Oregon. Miocene. This species is founded on leaves, fruits, and flowers, but floral bracts are not known. The fossils are said to be comparable to T. japonica (Miq.) Simonk. It is my opinion, however, that the figures in plate 3 show closer resemblance to leaves of herbarium specimens of T. miqueliana Maxim. of eastern China than to the Japanese T. japonica (Miq.) Simonk.
Tilia parvulifolia H.V.Smith, 1941: 519, pl. 13, f. 8. Type locality: Thorn Creek, 10 miles S. of Idaho City, Boise Co., Idaho. Miocene.

Tilia populifolia Lesq., 1883: 179, pl. 34, fig. 8. Yellowstone National Park. Eocene. Florissant, Colorado. Oligocene. MacGinitie (1953: 151, pl. 58, fig. 1) notes that known remains of T. populifolia are extremely rare, being represented by three incomplete leaves and a fruiting bract, and that the leaves resemble certain living Asiatic species such as T. paucicostata and T. japonica rather than those in America. Comparison with herbarium specimens shows little or no resemblance to T. japonica (Miq.) Simonk., but there may be some similarity with the Chinese T. paucicostata Maxim.


Tilia tetraforaminites Wodehouse, 1933: 516, f. 50. Type locality: Parachute Creek, Garfield Co., Colorado. Eocene. Based on fossil pollen.

Tilia vescipites Wodehouse, 1933: 516, f. 49. Type locality: Parachute Creek, Garfield Co., Colorado. Eocene. Based on fossil pollen.

Tilia weedii Knowlt., 1902: 706, f. 1. Type locality: Porecupine Butte, near Melville, Montana. Paleocene. It has been found only once and is represented by a single specimen. According to LaMotte (1935: 41), it resembles Asian rather than American species.

REFERENCES TO FOSSIL RECORDS


III. ANALYTICAL KEYS TO AMERICAN SPECIES OF TILIA

The most useful character for identification of specimens of Tilia is to be found in the kind and distribution of pubescence on the lower surface of the leaf blades. As there is a tendency for this pubescence to diminish or disappear later in the season, flower and fruit characters must be taken into consideration. Specimens consisting solely of sprout leaves are frequently too variable to be “keyed out.”

A. Key to Flowering Specimens

1. Leaves of flowering branches glabrous or essentially so on both surfaces at flowering time except for tufts of trichomes in the axils of the veins on the lower surface; pericarp of mature fruit 0.5-0.6 mm. thick.

2. Leaves green on both sides, chiefly obliquely cordate at base, sharply serrate with incurved teeth; young expanding leaves glabrous or nearly so from the beginning; pedicels usually glabrous or nearly so; petals 7-9 mm. long; staminodia 5-7 mm. long; style stout, hispidulous at the somewhat thickened base; fully developed cymes usually exceeding the bracts; northern species.....................................................1. *T. americana*

2. Leaves chiefly obliquely truncate or sometimes broadly cuneate
at base, the lower surface often pale or glaucous, or commonly olive green; margins with ovate teeth; young expanding leaves densely whitish tomentose, this indument soon disappearing; pedicels stellate-tomentulose; petals 5-6 mm. long; staminodia 4-5 mm. long; style slender, glabrous throughout or tomentose at base; cymes equaling or scarcely longer than the bracts; southern species.........................3. *T. caroliniana*

1. Leaves beneath more or less pubescent with stellate trichomes; axillary tufts usually less conspicuous.

3. Pubescence of the lower surface of the leaves of the flowering branches typically dense, appressed, firmly attached, whitish stellate-tomentulose or pannose, the foliage therefore appearing pale or whitish beneath, or on some specimens the trichomes are sparser and looser, or less commonly the surface nearly glabrous; petals 8-9 mm. long; anthers 1 mm. long; style 6-7 mm. long, hispidulous below the middle; pericarp on mature fruit 0.8-1 mm. thick..........................2. *T. heterophylla*

3. Pubescence of the lower surface of the leaves of the flowering branches grayish or brownish, loose, frequently copious, easily detached, usually deciduous, the stellate trichomes often scattered, or some specimens with glabrescent leaves, the foliage appearing green beneath; style 5-6 mm. long; pericarp of the mature fruit 0.5-0.6 mm. thick.

4. Sepals finely grayish stellate-pannose on the back; inflorescence relatively small with slender pedicels and peduncle; trees of southeastern United States.........3. *T. caroliniana*

4. Sepals copiously stellate-villosulous in the back; inflorescence becoming relatively large, coarse, the cymes usually exceeding the bracts; Mexico..................4. *T. mexicana*

B. **Key to Fruiting Specimens**

1. Fruiting pedicels usually glabrous or nearly so.........1. *T. americana*

1. Fruiting pedicels more or less pubescent.

2. Pedicels stellate-tomentulose; fruits closely tomentulose.

3. Pericarp of the mature fruit

0.8-1 mm. thick............................2. *T. heterophylla*

3. Pericarp not more than 0.6 mm. thick........3. *T. caroliniana*

2. Pedicels and fruits densely villosulous, the pericarp not more than 0.6 mm. thick..................4. *T. mexicana*
IV. DESCRIPTION AND DISCUSSION OF AMERICAN SPECIES

Tilia americana L.: American Basswood
(Plates 1-4)


Miller (1768) No. 8; Marshall (1785) 154; Wangenheim (1787) 55; Willdenow (1799) 2: 1162; Persoon (1806) 2: 66; F. A. Michaux (1813) 3: 311; Watson (1825) 134; Torrey & Gray (1838) 239; Loudon (1838) 373; Torrey (1843) 116; Wood (1845) 85, (1847) 210; Emerson (1846) 511; Gray (1849) 92; Chapman (1860) 59; Koch (1869) 480; Wood (1870) 64; Gray (1887) 305; Simonkai (1888) 321; Sargent (1891) 1: 52, pls. 24, 25; Gray (1897) 343; Britton (1901) 617; Dame & Brooks (1901) 153; Small (1903) 761; Hough (1907) 350; Britton (1908) 684; Robinson & Fernald (1908) 565; Schneider (1909) 381; V. Engler (1909) 136; Britton & Brown (1913) 512; House (1924) 487; Wiegand & Eames (1926) 297; Rosendahl & Butters (1928) 283; Illick (1928) 208; Rydberg (1932) 537; Dean (1940) 665; Braun (1943) 91; Hyland & Steinmetz (1944) 43; Jones (1945) 181, (1950) 193; Fernald (1950) 999; Stevens (1950) 204; Gleason (1952) 2: 523; Little (1953) 418; Jones & Fuller (1955) 318; Rosendahl (1955) 309; Strausbaugh & Core (1959) 624; Jones (1963) 79; Steyermark (1963) 1042; Gleason & Cronquist (1963) 461.

*Tilia glabra* Ventenat in Anal. Hist. Nat. [Madrid] 2: 62 (1800), Mem. Inst. Nat. Sci. France 4: 9, t. 2 (Monogr. Tilleul) (1803). Duhamel (1801) 1: 228; Poiret (1806) 681; Pursh (1814) 362; Nuttall (1818) 2: 3; Elliott (1824) 2: 2; DeCandolle (1824) 513; Hooker (1831) 108; Sargent (1818) 424, (1922) 733, fig. 650; Bush (1927) 235; Dean (1932) 271; Bush (1933) 845; Marie-Victorin (1935) 382; Palmer & Steyermark (1935) 597; Munns (1938) map 156; Steyermark (1940) 353.


*Tilia nigra* Borkhausen, Theor.-Prakt. Handb. Forstbot. 2: 1219 (1803); Watson (1825) pl. 45; Spach (1834) 340; Walpers (1842) 358; Bayer (1862) 52.


*Tilia neglecta* Spach in Ann. Sci. Nat. II. 2: 341, t. 15 (1834). “Habitat verosimiliter in America septentrionali. Hospitatur in ambulaeris Horti Parisiensis, ubi codem tempore ac *Tilia nigra* floret (V. v. e.).” Walpers (1842) 359; Simonkai (1888) 322; House (1924) 488; Ashe (1926) 32; Bush (1933) 843; Braun (1943) 91; Coker & Totten (1945) 314; Dimitri & Alberti (1948) 30, f. 10; Fernald (1950) 999, pro parte.

*Tilia nigra* var. *a* densiflora Spach in loc. cit.; Walpers (1842) 359. A variety with more compact cymes and umbonate fruits.

*Tilia nigra* var. *b* laxiflora Spach in loc. cit.; Walpers (1842) 359. A variety with fewer-flowered cymes and more pointed fruits.

*Tilia nigra* var. *vestita* A.Braun in Doell, Rhein. Fl. 674 (1843).


*Tilia nigra* var. *glauca* (Schweinitz) A.Braun ex Bayer in loc. cit. “Bracteae multae subsessiles; folia subtus glauca (ut *T. parvifoliae*), pilis stellatis inspersa,—Kentucky (Hooker). Orig. in herb. Berolin.”


*Tilia americana* var. *pubinata* Tausch ex Bayer in loc. cit. “Folia basi obliquecordata, plura oblique-truncata, cyma multiflora — In America septentrion.”

*Tilia americana* 3. *laxiflora* Kirchner in Petzold & Kirchner, Arb. Museov. 195 (1864).

*Tilia longifolia* dentata Hort. ex Kirchner in op. cit. 160.

*Tilia americana* var. *pubescens* sensu Macoun (1883) 88. Non (Ait.) Loud.


Tilia michauxii sensu Sargent, Man. Trees N. Am. 673, fig. 549 (1905); Robinson & Fernald (1908) 565. Non Nuttall (1842).

Tilia americana var. densiflora (Spach) V.Engler, Monogr. Gatt. Tilia 137 (1909).

Tilia americana var. densiflora f. cyclophylla V.Engler, op. cit. 138. “Folia quam in typo latiora, subsymmetra.” The first specimen cited is from “Comtney” (Courtney, Jackson Co.), Missouri, B. F. Bush 1147.

Tilia americana var. densiflora f. macrophylla (Fischer) V.Engler, op. cit. 139.

Tilia americana var. densiflora f. megalodont a V.Engler, loc. cit. “Folia majora, irregulariter et grosse dentata, non lobata.” Based on specimens with large, coarsely toothed leaves. Middletown, Connecticut, S. B. Buck ley; American Bottom near St. Louis, Missouri, G. Engelmann; Cleveland, Ohio, Krebs 319.

Tilia americana var. densiflora f. rosenthalii (Dippel) V.Engler, loc. cit. A cultivar with variegated leaves.

Tilia americana f. macrophylla (Fischer) V.Engler, loc. cit.

Tilia macrophylla hort. ex V.Engler, loc. cit., pro syn. Non Merat (1821), nec Kirchner (1864).

Tilia americana var. densiflora f. laxiflora (Spach) V.Engler, op. cit. 140. This is T. americana, except for the Polk Co., North Carolina, collection, which is a glabrate form of T. heterophylla.


Tilia velutina Mackenzie ex V.Engler, loc. cit., pro syn. T. americana var. vestita.

Tilia americana var. densiflora f. pedunculata V.Engler, loc. cit. “Cymae saepissime divaricatae bracteam non abbreviatam longe superantes.” A cultivar, occasionally spontaneous, as, for example, Broad River, North Carolina, Rugel.

Tilia americana var. vestita f. divaricata V.Engler, loc. cit. “Cymae divaricatae.” Spontaneous and cultivated. Easton, Pennsylvania, Tyler 82; Buckhannon, West Virginia, Pollock.

Tilia americana var. mississippiensis hort. ex Rehder in Bailey, Stand. Cycl. Hort. 3: 3347 (1917), pro syn.


Tilia americana var. scabra f. microphylla Farwell in op. cit. 368. “Frequent at Rochester [Michigan] and vicinity, July 13, 1918, Farwell 5062; October

Tilia americana var. heterophylla sensu Wiegand & Eames (1926) 298.


Tilia glabra f. dentata Rehder in loc. cit. Based on European specimens of T. americana with “rather larger deeply and incisely often nearly doubly serrate leaves.”

Tilia laxiflora hort. ex Rehder, Man. Cult. Trees Shrubs 616 (1927), pro parte; pro syn.


Tilia americana f. dentata (Kirechn.) Rehder in loc. cit.

Tilia palmeri Bush ex F. C. Gates in Trans. Kans. Acad. Sci. 41: 100 (1938), nom. nud.; ibid. 42: 135 (1939) [1940]. Type: B. F. Bush 12656, from Clay Co., Missouri, without definite locality, June 15, 1933 (MBG). Isotypes, AA, KSC, UMO. Clearly T. americana, although three sheets (not paratypes) from Geary Co., Kansas, Gates 21086, 21087 (KSC), and one from Mound City, Linn Co., Kansas, collector unknown, June 17, 1887 (paratype of T. palmeri) consist of very vigorous sprout leaves more pubescent beneath than usual in T. americana, resembling in this respect T. caroliniaina, or what has often been labeled T. neglecta.

Tilia floridana sensu E. L. Braun (1943) 91. Non Small (1903).

Tilia americana var. neglecta (Spach) Fosberg in Castanea 20: 58 (1955); Steyermark (1963) 1042.

A large tree attaining a maximum height of 40 m., with a diameter of 1-1.5 m., frequently growing in clusters of two or more trunks, and with several or many basal sprouts; bark on old trunks firm, dark gray, with deep longitudinal furrows; branches and young trunks remaining for a short time smooth and gray; twigs slender, reddish or green, glabrous and glossy, usually somewhat zigzag; winter buds ovoid or ellipsoid, 2-ranked, the 2-3 visible scales glabrous except the ciliolate margins; terminal bud absent; leaf sears alternate, conspicuous, raised, containing few to many bundle sears arranged in a ring or a single curved line, or scattered; stipule sears distinct, one narrow, the other broad; leaves of the flowering branches broadly ovate to orbicular, unequally obliquely cordate or truncate at the base, abruptly acuminate at apex, 6-16 cm. long, 5-13 cm. wide, palmately veined, the
primary veins somewhat prominent on the lower surface of the blade, the median vein continuing from the petiole stronger than the laterals, the secondary veins about 7-8 pairs, tertiary cross-veins about 15-18 between each pair of secondaries; upper surface dark green, glabrous and glossy; lower surface somewhat paler and glabrous except for small tufts of hairs in the axils of the main veins (these tufts sometimes small or absent), rarely with a few scattered simple trichomes along the main veins; margins sharply serrate, the curved teeth usually about 2 mm. long, gland-tipped; petiole one-third to one-half the length of the blades, glabrous; stipules oblong, prominent on the young growth but soon deciduous; flowers yellowish white, very fragrant, 12-15 mm. in diameter, appearing in midsummer in pendulous cymose clusters from the axils of the leaves, each cluster subtended by a membranous bract to which the peduncle is fused for half its length; bract spatulate, 7-10 cm. long, veiny, the stalk very short; sepals lanceolate, acuminate, 4-6 mm. long, 2-3 mm. wide, densely pubescent within and slightly pubescent on the outside; petals about one-third longer than the sepals, elliptical, obtuse, yellowish, 7-9 mm. long, 3 mm. wide at middle, the claw about 1 mm. long; staminodia spatulate, 5-7 mm. long, about two-thirds the length of the petals, and somewhat longer than the approximately 60 stamens; style stout, exserted, hispidulous at the somewhat thickened base, otherwise glabrous; fruit a subglobose or ellipsoid woody, nut-like drupe 6-9 mm. in diameter, covered with short, gray, stellate pubescence, occurring singly or in small clusters of 5-7, often persisting on the tree into the winter; pedicels glabrous or nearly so, 7-11 mm. long; seeds brown, smooth; cotyledons lobed to the middle, the lobes subequal, glabrous above, sparsely pubescent to glabrous beneath; hypocotyl glabrous or nearly so.


RANGE: Growing chiefly in rich loamy soil from New Brunswick and Maine to southern Quebec, Ontario, northern Michigan, southern Manitoba, eastern North Dakota, eastern Nebraska, eastern Kansas, Missouri, Kentucky, New York, and New Jersey. Flowering from June 1 to July 20 (−August 15); fruits July-September.

SIGNIFICANT COLLECTIONS

Canada

MANITOBA. Cornwallis: Brandon, H. J. Scoggan 11451 (CAN).
Map 3. *Tilia americana* L.


UNITED STATES


DELWARE. New Castle: Mount Cuba, A. Commons in 1875 (PH).

DISTRICT OF COLUMBIA. Washington, R. P. Hayes 103 (OS).


In addition, the Iowa State University Herbarium (IA) contains specimens from the following counties: Adams, Allamakee, Bremer,


In addition, the herbarium of the University of Minnesota contains specimens from the following counties: Beltrami, Benton, Blue Earth, Brown, Carlton, Clay, Cook, Cottonwood, Douglas, Houston, Itasca, Kanabec, Kandiyohi, Kittson, Lake, Le Sueur, Lincoln, Martin, Mille Lacs, Mower, Nicollet, Olmsted, Pine, Polk, Pope, Red Lake, Rice, Roseau, Scott, Sibley, Steele, Waseca, Wilkin, Wright.

DESCRIPTION AND DISCUSSION OF AMERICAN SPECIES 55


RHODE ISLAND. Providence, E. J. Palmer 43441 (MBG, NY).


TENNESSEE. Tipton: Brighton, G. N. Jones 31062 (ILL).


In addition, the University of Wisconsin Herbarium (WIS) contains specimens from the following counties: Ashland, Clark, Columbia, Crawford, Dane, Dunn, Eau Claire, Florence, Fond Du Lac, Grant, Green, Green Lake, Iowa, Iron, Jefferson, Juneau, Lafayette, Marathon, Monroe, Oconto, Oneida, Outagamie, Pierce, Price, Racine, Richland, St. Croix, Sawyer, Sheboygan, Taylor, Vilas, Washburn, Waukesha, Waupaca, Waushara, Winnebago, Wood.

In the Species Plantarum (1753: 514) Linnaeus recognized two species of Tilia, i.e., T. europaea, “Tilia floribus nectaris destitutis. . . . Habitat in Europae pratis,” with five varieties, and an American tree, T. americana, characterized as “Tilia floribus nectaris instructis. Kalm. . . . Habitat in Virginia, Canada.” Sargent (1918: 424) attempted to discard the name Tilia americana for the common northern linden with usually glabrous leaves, and to substitute the much later name Tilia glabra Vent. He expresses the opinion that the quoted synonym “Tilia foliis majoribus mucronatis. Gron. virg. 58,” referring to a collection by John Clayton and indicated by Gronovius as having come from Virginia, cannot be applied to T. americana because that species is not known to grow in Clayton’s region. While this is quite true, there is, however, no reasonable doubt as to the identity of Tilia americana L., although Sargent, stating that T. americana was based by Linnaeus upon a specimen from Kalm “not in the Linnaean Herbarium,” rejected the name because “both T. neglecta and T. heterophylla michauxii are more common in the part of the country which Kalm visited than the tree which some recent botanists have called T. americana.”

The identity of Kalm’s specimens can hardly be doubted (Fernald, 1941: 605). “It is certainly not without significance that in September, 1748, in an enumeration of the trees of the Philadelphia region, Kalm listed as no. 52 ‘Die Linde, in guter Erde.’ This could have been only T. americana as regularly interpreted.” The name Tilia glabra Vent. therefore goes out except as a synonym of Tilia americana L. This subject has been discussed at greater length by L. Croizat (1937), who concludes that “T. americana is valid and rules out the later T. glabra Vent.”

In the United States this species is an important forest tree in the northern and middle states, growing in fertile soil and sometimes at-
taining a height of 125 feet and a diameter of three to four feet near the base. When growing apart from other trees, it develops symmetrically and reaches a large size. Trees of this species are readily recognized in winter by the robust appearance of the trunks and branches, and by the dark brown bark on the younger shoots. This latter character is probably the reason for the English name "black lime" and the binomial *T. nigra* Borkh. It was cultivated in England as early as 1752 by Philip Miller. The American basswood is a dominant tree in the northern maple-basswood forest region, where it and *Acer saccharum* are frequent species, with *Quercus rubra* as an associate. Its usual habitats are rich woods and along streams and in bottom lands. It is common in most parts of its range, and in the Adirondacks ascends to a 2,500- or 3,000-foot altitude.

Distributional maps of American basswood (Munns 1938: 156; Schmucker 1942: 192) are more nearly maps showing the total distribution of most American species than maps showing the actual distribution of only one, *T. americana*. The southern area extends much too far south. *Tilia americana* does not range south of Nebraska, Missouri, Kentucky, and New Jersey. Nova Scotia should be excluded. Although the species is in cultivation there, it is not native in that province. It is native, however, in western New Brunswick, but not common there. A more accurate map showing the distribution of *Tilia americana* is given by Harlow & Harrar (1958: 478, pl. 64). In Canada, this species ranges from western New Brunswick to southern Quebec, across southern Ontario to the north shore of Lake Superior to the southern edge of Manitoba. A map of the Canadian distribution of this species is given by the Dominion Forest Service (1949).

Leaves of *T. americana* have been usually described as glabrous, and as is shown by nearly all specimens, this is the most nearly glabrous or least pubescent of American species. However, the fact should not be overlooked that *T. americana* is not always completely glabrous. On the lower surface of the blades, there are usually some, perhaps as few as half a dozen or as many as 20 to 30, small tufts of trichomes in the axils of the principal veins, although these tufts are sometimes absent. In addition to the small tufts, sometimes the lower surface of the blade shows more or less pubescence or puberulence. Sprout leaves are almost always pubescent on the lower surface, particularly along the veins, with chiefly straight, simple, unicellular hairs, but some specimens show branched hairs. Occasional specimens of flowering branches show some pubescence on the lower surface of the leaves, as, for example, a collection from Jackson County, Missouri, by K. K. Mackenzie, which he named *T. velutina*, and which V. Engler called *T. ameri-
TAXONOMY

Most trees, especially in the northern and eastern part of the range, have leaves glabrous on the lower surface from the first; in others, the leaves are pubescent when first expanded but soon become glabrous, while still others may retain a sparse pubescence to maturity. Flowers and fruits of all these variants are remarkably uniform.

Other specimens supposed to represent pubescent varieties of *T. americana* have turned out to belong to some other species, particularly the European *T. platyphyllos*, when the collector neglected to state on the label that the specimen came from a cultivated tree, or the identifier did not notice the source where it had been given. Pubescence of leaves of *T. americana*, except sprout leaves on vigorous shoots, where it may be copious, is seldom noticeable without magnification not less than that provided by a pocket hand-lens. However, if a careful search is made with a binocular microscope giving a magnification of 20-30×, it is seldom that a few trichomes cannot be found on the lower surface of the blade. Most of these are usually simple trichomes growing from the tertiary veins, but branched trichomes sometimes can be found. These are small, widely separated, sometimes bifurcate, or sometimes with four branches.

In addition to the variable pubescence, the blades, often being large and thin, vary considerably in size and shape, and several varieties and forms have been proposed on the basis of these variations. *Tilia americana* varies also somewhat in size of flowers and shape of the bract, but these variations appear to be in no way correlated with pubescence of leaves.

Specimens of *Tilia americana* showing pubescence have often been labeled *T. neglecta* Spach, which almost from its first definition has been a source of confusion and misunderstanding. It was described from a tree in the botanical garden in Paris ("Hospitatur in ambulacris Horti Parisiensis") as having originated in North America, being closely related to *T. americana*, but with "folia subtus puberula." American botanists during the past century have interpreted it variously as a separate species, or as a variety of *T. americana*, and in actual practice so naming specimens of *T. heterophylla* ("T. heterophylla michauxii"), and sprout leaves of *T. americana*. Some of the less pubescent states of *T. caroliniana* have been labeled *T. neglecta*. One of the most striking peculiarities of series of specimens named *T. neglecta* is that they usually consist almost entirely of sprout leaves, and in the majority of herbaria only rarely does one encounter a flowering or fruiting specimen that is labeled unequivocally *Tilia neglecta* Spach. Fernald has commented on these specimens as follows:
"As to Tilia neglecta (T. Michauxii sensu Sargent, not Nutt.), it is a baffling series with little constancy. Theoretically it should have the leaves green or merely grayish beneath, with loosely scattered stellate hairs and simple pilosity. In fact, however, few different collections can be closely matched with another. It seems to be a series very close to T. americana, but with some stellate or mixed pubescence. As now interpreted it is surely not a satisfactory species" (Fernald, 1941: 606-607). In Gray's Manual, the author says, T. neglecta is "An inconstant and rather nondescript series, perhaps better treated as variations of no. 1 [T. americana]." Perhaps the most unusual attempt to account for T. neglecta has been made by J. Wagner (1933: 44), who describes it as "Bastarde der T. americana L., and T. argentea Desf.," the silver linden, correctly named T. tomentosa Moench, a native of southeastern Europe. In the same article there are 48 "hybr. nov.," with 23 of these (including several "tripelbastarde") attributed to T. americana. According to Dermen (1932: 49) Tilia neglecta and T. americana are both diploids. The original description of T. neglecta Spach follows:

Tilia neglecta Nob.

T. foliis serratis, cuspidato-acuminatis, subtus molliter pubescentibus: inferioribus cordatis, v. cordato-ovatis, subrotundisve; superioribus e basi hinc dimidiato-cordata v. rotundata, illine oblique trunca, vel utrinque trunca ovatis v. ovata-elliptieis, petiolo dimido — duplo longioribus; cymis laxe 5-12-floris; petalis oblongis v. spathulato-oblongis, obtusis, apice obsolete crenulatis; stylo post anthesin exserto; nuce subglobosa, v. obovata, v. ovata, v. turbinata, umbonata, subpentagona: costis prominulis.


Habitat verosimiliter in America septentrionali. Hospitatur in ambulaeris Horti Parisiensis, ubi codem tempore ac Tilia nigra floret. (V. v. e.) [Spach, 1834: 341-342, pl. 15].

The holotype of Tilia neglecta Spach is not available at the Museum National d'Histoire Naturelle (P) in Paris, and is probably nonexistent. Through the courtesy of the director, however, who most kindly arranged to send to me for study certain collections under his charge, I have been able to examine one sheet labeled by Spach as T. neglecta. This bears the collection label "269. Tilia nigra Borkh. Bords des rivieres 1841 an Julliet. W. Riehl. St. Louis, Missouri" and is of par-
ticular interest as it has been labeled "T. neglecta Spach" in Edouard Spach's handwriting. While this is, of course, not type material, it presumably represents Spach's concept of his T. neglecta, which was supposed to be a species of North American origin. It consists of a specimen with leaves and bracts, but lacking flowers or fruits. On the basis of observation of all visible characteristics, this specimen belongs unequivocally to T. americana L.

A suggestion has been offered (Braun, 1960) that Tilia neglecta may be a "hybrid swarm" supposed to have come about as a result of past migrations of two or more species. Although the pattern of variability in vegetative characters would agree well with the assumption that introgression from one species into another may be occurring, evidence that such phenomena do occur has not yet been produced. The fact remains, as already noted, that almost all herbarium specimens labeled T. neglecta consist of sprout leaves.

Because the geographical ranges of T. americana and T. caroliniana generally do not coincide, there is seldom any difficulty in separating these two species. However, glabrous-leaved specimens of T. caroliniana (sometimes labeled T. floridana) may resemble those of T. americana, but the pubescence of the lower surface of the sprout leaves of the latter species consists of simple trichomes along the veins and veinlets, while that of T. caroliniana usually or often consists of small stellate trichomes appressed to the principal veins. Tilia americana has somewhat larger flowers than T. caroliniana, with glabrous pedicels, the sepals sparsely tomentulose on the back, and the bracts usually nearly glabrous. T. caroliniana has stellate-pubescent pedicels, sepals closely tomentulose on the back, and the bract sparsely stellate to essentially glabrous. In T. caroliniana, the leaves have broader teeth, the base of the blade is characteristically obliquely truncate, and the base of the style is glabrous or nearly so. The petals are usually erose at the apex. The fruits are somewhat smaller, 5-6 mm. in diameter, with a thin pericarp, and the peduncle is joined to the bract more than half its length. Both T. caroliniana and T. americana have the summer-shoot leaves thinly pubescent on the lower surface. This condition often has been named T. neglecta. Tilia americana is usually distinguished from T. caroliniana by the sharper teeth of the leaves, the blades obliquely cordate, the base of the style villous, and the pedicels glabrous or nearly so. The petals are usually entire; the fruits are 6-7 mm. in diameter, with a relatively thick pericarp, and the peduncle divergent from the bract below its middle. In T. americana, the first leaf above the cotyledons is slightly pilosulous beneath, while that of
T. caroliniana is densely tomentulose beneath. This parallels the condition in the young unfolding leaves of the flowering branches, which in T. americana are glabrous or essentially so, while those of T. caroliniana are densely whitish stellate tomentose.

Sterile specimens of Tilia americana sometimes have been misidentified as Morus alba L., but leaves of the white mulberry have quite different venation and serration.

Very young leaves (3-4 cm. long) of Tilia americana are bright green and nearly glabrous on both sides, but on the lower surface there are at first some trichomes, mostly simple and unicellular, forming a fine ciliation along the serrations of the margin, and with some scattered sparsely along the veins. There are sometimes a few slender stellate four-branched trichomes. Minute ellipsoidal multicellular glandular trichomes may be observed on the petiole and along the veins. Tufts of axillary trichomes, characteristic of older leaves, are not evident at this stage.

Even while the leaves are young, the pattern of venation can be clearly discerned. There are usually five principal palmate veins from the base, with the central one longest and extending as a continuation of the petiole into the caudate apex. There are seven to nine pairs of opposite primary lateral veins, or the shorter ones toward the apex of the blade are alternate. The secondary veins branch only from the proximal or lower side of the lateral veins, and then chiefly from the first pair and from near the apices of the others. The tertiary cross-veins are numerous, conspicuous, somewhat curved, or nearly straight. Trichomes, when present, arise from veins. The intervals between the tertiary veins are always glabrous. There are 50-80 ciliate curved teeth on each margin, each tooth with one veinlet. The apex of the blade is caudate and the base obliquely cordate or truncate.

More than 30 years ago Bush (1927: 238) wrote that he had examined specimens collected by Miss A. I. Mulford at Santa Fé, New Mexico, labeled Tilia. "These specimens are certainly T. glabra [T. americana], and judging by the labels were collected from wild trees; but it seems so very improbable that T. glabra should be found in New Mexico that I have refrained from citing these specimens as collected in the known range of this species." These specimens have been distributed to several herbaria; they belong certainly to T. americana L.; but if they were collected in New Mexico, they came from cultivated trees, as no trees of any species of Tilia are known to grow wild in New Mexico.
Tilia heterophylla Vent.: White Basswood

(Plates 5-6)


6. TILA HETEROPHYLLA folis ovatis, argute serratis, basi nune cordatis, nunc oblique aut aequaliter truncatis, subtus tomentosis: nuce globosa, multineriosa.

Fraser y Michaux encontraron esta especie en la baxa Carolina, y creo debo crecer en Marilandia, porque he visto en el herbario del ciudadano Lamarck varios exemplares de ella cogidos en esta última provincia: ella debe distinguirse de la precedente por muchos caracteres. Porque sus ramos tiernos y sus yemas son lampiñas, y de un púrpura tirante al negro. Las hojas aovadas con punta, unas casi acorazonadas en la base, y otras truncadas allí obliquamente ó con igualdad, aserradas con dientes muy finos, lisas, y de un verde obscuro por arriba, borrosas y canas por abajo: tienen un copito de pelos bermejos en el punto de donde salen los nervios laterales. Los pedúnculos, que son casi tan largos como las hojas, son tres veces mayores que los del Tilia rotundifolia. Los frutos son globulosos, del tamaño de quisantes, con cinco nervios algo protuberantes, entre los cuales se ven otros, aunque menos sensibles. El ciudadano Michaux me ha hecho saber, que este árbol crece con especialidad en las partes marítimas de la Virginia y de la Carolina; pero que solo se levantaba a la altura de nuestros árboles frutales.

Duhamel (1801) 1: 229; Poirret (1806) 683; Pursh (1814) 363; Nuttall (1818) 2: 3; De Candolle (1824) 513; Spach (1834) 345; Torrey & Gray (1838) 1: 239; Walpers (1842) 359; Nuttall (1842) 90; Chapman (1860) 60; Bayer (1862) 51; Wood (1870) 64; Gray (1887) 305, (1897) 344; Simonkai (1888) 320; Watson & Coulter (1890) 101; Sargent (1891) 57, pl. 27; Mohr (1901) 613; Britton (1901) 617; Small (1903) 761; Hough (1907) 449; Robinson & Fernald (1908) 566; Britton (1908) 686; V. Engler (1909) 133; Schneider (1909) 387; Britton & Brown (1913) 512; Sargent (1922) 745; Ashe (1926) 30; Illick (1928) 209; Deam (1932) 271, (1940) 666; Bush (1933) 544; Braun (1943) 91; Coker & Totten (1945) 322; Jones (1945) 181, (1950) 193; Fernald (1950) 999; Gleason (1952) 523; Little (1953) 420; Jones & Fuller (1955) 319; Gleason & Cronquist (1963) 461; Jones (1963) 50; Steyermark (1963) 1042.

Tilia caroliniana sensu Marshall (1785) 154; Du Roi (1772) 469. Non Miller (1768).


\(^1\)“Ventenat’s paper on Tilia was read in 1799 and published in 1802 [1803] in the fourth volume of the Memoires de l’Acad. Sci. Paris. A separate of this paper with the same pagination appeared the same year, but a Spanish translation without the illustrations was published in Madrid in May 1800 with the title Monografía del genero Tilo in the second volume of the Anales de Historia Natural” (Sargent, 1918: 425).
binomial has eleven years' priority over *T. heterophylla* Vent. (1800), Croizat, writing on this subject (1938), concludes that in view "of the uncertainty attaching to the type and of the indifferent use of the binomial, it seems best to reject altogether *T. alba* Ait., accepting in its stead *T. tomentosa* Moench, and *T. heterophylla* Vent. . . . which can be attributed to species of reliable typification, and are well established in taxonomic and horticultural usage." F. A. Michaux (1813) 3: 315, t. 2; Torrey & Gray (1838) 240; Wood (1847) 210.


*Tilia michauxii* Nuttall, Sylva 1: 92 (1842). "The TILIA ALBA, White Lime of Michaux, plate 132, not being the *T. alba* of Kitaibel and Aiton, (Hort. Kew. l.c.) which is a native of Hungary, it is necessary to change his name, and we propose to call it TILIA MICHAUXII. (Michaux's Lime), if his plant should indeed prove to be anything more than a smoother variety of our *T. heterophylla*." Small (1903) 761; Hough (1907) 449; Britton (1908) 688; Schneider (1909) 387; Britton & Brown (1913) 513; House (1924) 488; Ashe (1926) 28; Bush (1933) 844.

*Tilia rotundifolia* sensu Bayer in Verh. Zool. Bot. Ges. Wien 12: 52 (1862). Non Vent. (1800). "The original reference of Aiton's *T. alba* to America was corrected in the second edition of the Hortus Kewensis. But, having been copied by Ventenat, under his *T. rotundifolia*, the mistake has been kept up by Bayer in his Monograph, who places it under his *T. heterophylla*-nigra, and has two forms from Kentucky, both undoubtedly *T. heterophylla*."

Gray, 1887: 305.

*Tilia heterophylla* var. *alba* (Aiton) Wood, Fl. Atlantica 64 (1870). "Lvs. whitish and minutely tomentous beneath, serratures fine and long-mucronate, Ky. and South along the mountains."

*Tilia eburnea* Ashe in Bot. Gaz. 33: 231 (1902). "*Tilia eburnea* is found from middle North Carolina to northern Georgia between 200 m. and 700 m. elevation, on rich moist soil near small streams or on steep cool slopes." No type is cited, but a sheet in NCU is marked "*Tilia eburnea* Ashe, sp. nov. Type, Polk Co., N.C., near Esmeralda Inn, No. 142, July 11, 1895," and one in NY has the label: "near Esmeralda Inn, Rutherford Co., N.C., along the Hickorynut Creek, July 10, 1895, W. W. Ashe 142." Both of these collections belong evidently to *Tilia heterophylla*. Small (1903) 761; Britton (1908) 687; Schneider (1909) 387; Bush (1933) 844.


*Tilia pubescens* var. *aitonii* f. *truncata* (Spach) V. Engler, op. cit. 129. "A typo differt in folii minus. Selten spontan, in der Kultur früher anscheinend ziemlich verbreitet.—Zwischen Stone Mountain und Tricuem, de [De] Kalb Co., 350 m. (SMALL. Pl. Middle Georgia!)." This is clearly *T. heterophylla*. However, the second collection cited by V. Engler, "Wrights-
ville, New-Hannover [New Hanover] Co., N.C. (BILTMORE Herb. no. 4699a!);” belongs to *Tilia caroliniana*.

*Tilia caroliniana × heterophylla* V.Engler, op. cit. 151. “Hybrida *T. heterophyllae* similior quam *caroliniana*e, illius praebens vestimentum formam magnitudinem foliorum, hanc floribus parvis solum atque pedunculis subpilosellis daeaequans. River bottom, River Junction, Flo. (CURTISS' second Distrib. Pl. South. U.S. no. 5875!).” This fine collection, distributed to several herbaria, evidently represents typical *Tilia heterophylla* Vent., with no evidence of influence from or transition toward *Tilia caroliniana* Mill.

*Tilia apposita* Ashe in Bull. Charleston (S.C.) Mus. 13: 27 (1917). “A small tree about 20 m. high on the banks of streams in the mountains of northern Georgia at altitudes of 400 m. to 600 m. This tree is probably most closely related to *T. pubescens* Ait. [*T. caroliniana* Mill.] though the fruit is considerably larger and it is further separated from this species by having more copious light gray and not tawny pubescence. From *T. eburnea* Ashe it differs in having much denser and more permanent pubescence.” No specimens cited or type designated, but the type locality, as inferred from specimen labels, is Wiley, Rabun Co., Georgia. Although *T. apposita* is compared to *T. caroliniana*, topotypes collected by Ashe, and others, belong to *T. heterophylla*. A collection from “probably the type tree,” Sept. 5, 1933, H. R. Totten & T. G. Harbison (GA), near “Wylie,” Rabun Co., Georgia, belongs certainly to *T. heterophylla*.

*Tilia tenera* Ashe in loc. cit. “A small tree 15-20 m. high on the banks of streams from North Carolina to Alabama in the Piedmont and upper coastal plain. Type material from near Jessup, Moore County, N.C. This tree is undoubtedly related to *T. leptophylla* (Vent.) Small. . . .” However, *Tilia leptophylla* (Vent.) Small (1903), not Simonkai (1888), is a synonym of *T. caroliniana*, and *T. tenera* is a synonym of *T. heterophylla*, to which the type collection belongs.

*Tilia lasioclada* Sargent in Bot. Gaz. 66: 502 (1918), (1922) 744; Bush (1933) 845; Coker & Totten (1945) 328. Type from rich wooded slopes near the Savannah River, 3 miles below Augusta, Georgia, June 17 and Aug. 23, 1916 (no. 8 type), T. G. Harbison (AA). “From all other American lindens this species differs in the straight hairs on the lower side of the midribs and veins of the leaves, on the peduncle and branches of the inflorescence and on the branchlets, and similar to those of the European *T. platyphyllus* Scopoli. The number of these hairs varies on different individuals, and on some trees the branchlets become nearly glabrous by the middle of June, while on others the hairs are present for 2 or 3 years.” *Tilia lasioclada* is clearly a minor variant of *T. heterophylla*. Similar tendencies in the type of pubescence may be observed occasionally on certain specimens of *Tilia caroliniana*.

*Tilia monticola* Sargent in op. cit. 508. Type not designated, but the first cited specimens are “NORTH CAROLINA. — Highlands, Macon County, at an altitude of about 600 m., T. G. Harbison (many specimens), June, July, and September 1915; Busbee Mountain near Biltmore, July 5, and September 16, 1897 (ex herb. Biltmore 1030 B).” Sargent (1922) 747; Braun (1943) 91; Coker & Totten (1945) 320; Gleason (1952) 523; Gleason & Cronquist (1963) 461.

*Tilia heterophylla* var. amphibola Sargent in op. cit. 507. Type from River
Trees usually 15-20 m. tall, but sometimes reaching a height of 30 m. with a d.b.h. of 1-1.2 m.; bark on old trunks thick, firm, longitudinally furrowed; branchlets stoutish, almost always glabrous, silver-gray or reddish brown; winter buds glabrous or nearly so, reddish, 5-8 mm. long, the outer scales slightly ciliolate at apex; leaves of the flowering branches variable in outline, of firm texture, 8-15 (or the longest 15-20) cm. long, 6-12 cm. wide, ovate, thin, the apex gradually or abruptly acuminate, the base obliquely truncate or rarely slightly cordate; the side of the blade nearest the branch larger; principal veins 7-9 pairs, the connecting veins prominent on the lower surface of the blade; upper surface at maturity smooth, dark green, lustrous, and glabrous, the lower surface nearly always covered with thick, firmly attached, pale or silvery pannose tomentum, varying occasionally to nearly glabrous; trichomes commonly 8-rayed (or 6-, or 4-), the rays 0.2-0.3 mm. long; margins serrate with incurved, apiculate, gland-tipped teeth; petioles slender, glabrous, or rarely pubescent, 4-7 cm. long, about one-fourth the length of the blade; bracts linear-elliptic to oblanceolate or spatulate, narrowed and rounded at the apex, asymmetrically cuneate at base, finally glabrous, 10-15 cm. long, 2-3 cm. wide, nearly sessile or decurrent; peduncle slender, glabrous, the free portion 2-4 cm. long;
pedicels stout, sparingly pubescent with stellate trichomes; flowers 7-12 mm. long, in mostly 8-20-flowered cymes; sepals pale pubescent outside, villous within, acuminate, triangular-lanceolate or deltoid, 5-6 mm. long, 3 mm. wide at base; petals 8-9 mm. long, 2-3 mm. wide, elliptical, cuneulate, the apex obtuse and erose, longer than the sepals; staminodia spatulate, erose, 5-6 mm. long, 1-1.5 mm. wide above the middle, the claw about 2 mm. long, anthers about 1 mm. long; filaments about 2 mm. long; style 6-7 mm. long, hispidulous below the middle, otherwise glabrous, about as long as the petals; stigma 5-lobed; fruits subglobose, apiculate, tomentulose, 7-10 mm. in diameter, single or usually 5 or 6 together; fruiting pedicels closely stellate, eventually glabrescent; seeds brown, glabrous; cotyledons lobed to below the middle, the central lobe one-third longer than the others, hispidulous with simple trichomes along the veins, strongly so on the lower surface; hypocotyl retrorsely strigose.

TYPE LOCALITY: "Cet arbre, qui se trouve plus particulièrement dans les parties maritimes de la Virginie et de la Caroline. . . ."

RANGE: In moist soil or on rich wooded slopes from south central New York and southeastern Canada to Pennsylvania and West Virginia, westward along the Ohio River through southern Ohio to the southern tip of Illinois, southward from Kentucky to Alabama, northwestern Florida, and North Carolina. Flowering in June and July; fruits maturing in July-October.
SIGNIFICANT COLLECTIONS

Canada

ONTARIO. Stormont: Ile Cornwall, Fr. Marie-Victorin et al. 56828 (DAO, MOAR).

QUEBEC. Chambly: Longueuil, Fr. Rolland-Germain 30504 (CU, MOAR).

United States


TAXONOMY and OCCURRENCE

76

BERKELEY: 1736 (NCU). Wythe: Reed Creek, J. K. Small (F, MBG, NY, OC, PENN).


The white basswood is typically a southern species, attaining a height of 60-80 feet and a d.b.h. of 20-30 inches. It is a common tree from western New York to southern Illinois and northern Arkansas, reaching its largest size and greatest beauty in the forests which cover the slopes of the mountains of North Carolina, Tennessee, and Kentucky. It is common throughout the state of West Virginia, usually more abundant at lower elevations. The leaves appear somewhat larger than those of other American species. They are commonly ovate or elongate-ovate, obliquely truncate at the base, usually whitish or silvery white on the lower surface and pendent on long petioles.

In one of the best of the early descriptions of *Tilia heterophylla*, Thomas Nuttall (1842: 91) says:

This is one of the rarest [i.e., choicest] and most ornamental trees of the whole genus, and as far as my own observations go, it is almost wholly confined to the shady forests of the Ohio and its tributary streams, to which Pursh also adds the banks of the Mississippi... In descending the Ohio, late in autumn,
(about the year 1816) I got out of the boat... to walk round Le Tart's Rapids above Cincinnati, here I observed almost an exclusive forest of this fine linden, on a rather elevated alluvial platform, in a light, rich, calcareous soil. Most of the trees were tall and rather slender, 60-80 feet in height, and the ground was thickly strewed with their large and singular leaves, almost as white as snow beneath. The young branches are purplish and somewhat glaucous. The largest leaves I have seen are about 6 or 7 inches long, and 3 to 5 broad. In the young state, the white pubescence beneath is most conspicuous when the leaves are thinly covered, the hairs are stellate, the serratures strong and sharp, with acuminated rigid points, the upper surface is dark green; the base of the leaf varies considerably, sometimes it is sinuated, at other times perfectly flat and truncated; the leaves are always very oblique at the base. The flowers are somewhat larger than those of T. americana, and the fruit is villous, nearly spherical, and certainly always without any ribs.

Toward the northern part of its range, some trees tend to have leaves with thinner pubescence; such trees, often identified as T. michauxii, might represent hybrids with T. americana, but T. heterophylla shows a wide range of variation in pubescence, although in this respect it is possibly somewhat less variable than T. caroliniana and T. mexicana. While the majority of specimens show the characteristic dense, appressed, firmly attached, whitish stellate tomentum, others have the lower surface nearly glabrous except for a few scattered stellate trichomes, and in a few specimens the surface is glaucous. Tilia caroliniana has usually tawny, stipitate, looser trichomes. Sparsely pubescent specimens of T. heterophylla, especially of sprout leaves, are sometimes labeled T. neglecta or T. michauxii. The leaves tend to be larger than those of T. americana and T. caroliniana, often 15-20 cm. long, dark green above, acute or acuminate. Flowers are slightly larger and often fewer than in T. americana. The globose fruits are about 1 cm. in diameter, larger than those of T. caroliniana, and with a thicker pericarp.

Occasional specimens of T. heterophylla have the leaves so nearly glabrous beneath that a close scrutiny is necessary to see the fine stellate pubescence. The lower surface of leaves should be studied through a binocular microscope to be sure of the pubescence character, which, although usually evident, may be in certain specimens somewhat elusive. The pubescence of T. heterophylla is more firmly attached, flatter, denser, and less frequently deciduous than that of T. caroliniana. Leaves of sprouts are, as in other species, extremely variable in size, shape, and pubescence, sometimes varying to nearly glabrous and somewhat glaucous on the lower surface. It is an interesting fact that the sprout leaves of T. heterophylla are usually less pubescent than those of the flowering branches, while in T. americana the reverse is true, the pubescence of the lower surface of the leaves, if any, being
always more evident on the sprout leaves. The usual and typical condition of the lower surface of the blades of flowering branches of *T. heterophylla* is whitish stellate pubescent with a compact, often pannose tomentum consisting of very numerous, flattened, usually eight-rayed trichomes covering the surface not only along the veins and veinlets but in the interstices as well. The blades are usually ample, typically longer than wide, abruptly acuminate, darker, smooth, glabrous on the upper surface, and the base of the blade is characteristically obliquely truncate.

A collection from River Junction, Gadsden County, Florida (A. H. Curtiss 5875) has been named *T. caroliniana × heterophylla* V. Engler, hybr. nov. Both species occur in Gadsden County, and interspecific hybrids are possible on the basis of geography, although none has yet been discovered. In this instance, however, both flowering and fruiting specimens, distributed by Curtiss as *T. pubescens*, belong clearly to *T. heterophylla*. It is interesting to note that this collection is also a paratype of *T. heterophylla* var. *nivea* Sarg., which is said to differ from the type in "the whiter tomentum on the lower surface of the leaves, the glabrous styles, in the tomentum on the lower side of the bract of the peduncle at the time the flowers open, the slightly pubescent gray or pale reddish brown branches, and in the puberulous winter-buds." None of these characters is diagnostic.

In 1926, *Tilia lata* Ashe was at first contrasted with *T. heterophylla*, but later (1931) Ashe said that it is clearly allied to *T. caroliniana*. Study of type collections including topotypes confirms relationship with *T. heterophylla*, with which it is identical in leaf pubescence and from which on other characteristics it cannot be distinguished.

The difference between the white stellate-tomentose or stellate-pannose pubescence of *T. heterophylla* and the loose, usually darker colored stellate pubescence of *T. caroliniana* is chiefly quantitative. The structure of the trichomes, the number and length of branches, and the diameter of the whole trichome are essentially the same in both species. The conspicuous and usually unmistakable difference in the pubescence is caused chiefly by the number and arrangement of trichomes. In *T. heterophylla* they are more numerous, closer together, characteristically so compact as to present a nearly unbroken surface of tomentum, producing a panniform surface, that is, having the appearance of felt or woolen cloth. This is the usual condition. A few specimens are found from which the tomentum has all but vanished, leaving only white, scattered, stellate trichomes, and, rarely, occasional leaves are seen that are almost glabrous, with only an occasional trichome to be found here and there.
Very young leaves (3-4 cm. long) of *Tilia heterophylla* are pubescent on both sides, the bright green and glossy upper surface at first sparsely and finely pubescent with short, chiefly branched trichomes, but soon glabrescent. The lower surface is pale or whitish with a copious pubescence of both simple or bifurcate trichomes about 1 mm. long on the veins, and a copious, minute, dense, soft pannose covering over the surface between and along the tertiary veins. Minute, ellipsoid, multicellular glandular trichomes are abundant along the veins and the petiole. The characteristic axillary tufts are not evident at this stage.

The pattern of venation shows several veins from the base of the blade with the central one longest and strongest and extending into the apex of the blade as a continuation of the petiole. There are eight to ten pairs of opposite or subopposite primary lateral veins, although the short ones in the apex of the blade are alternate. As in other species, the secondary veins branch only from the proximal or lower side of the lateral veins, and then chiefly from the first pair and from the apices of the others. Tertiary cross-veins are numerous, conspicuous, somewhat curved or nearly straight, with the intervals densely pubescent.

There are 100-120 ciliate curved teeth, each with one veinlet. They are finer, narrower, less curved, and more numerous than those of *T. americana*.

**Tilia caroliniana** Mill.: Carolina Basswood

(Plates 7-16)

*Tilia caroliniana* Miller, Gard. Dict., ed. 8, Tilia No. 4 (1768). Described from a tree cultivated in England, where it had been introduced from Carolina by Catesby. The type is in the herbarium of the British Museum, the name written on the sheet in Miller’s handwriting. The lower surface of the leaves is clearly and definitely stellate-pubescent, particularly along the veins. This specimen is also the type of Aiton’s *T. pubescens*. Du Roi (1772) 2: 469; Wangenheim (1787) 50; Simonkai (1888) 316; Engler (1909) 131; Sargent (1918) 496, (1922) 740; Bush (1933) 543; Coker & Totten (1945) 334; Hunt (1947) 735; Little (1953) 419; Brown (1956) 66.

*Tilia americana* sensu Walter, Fl. Carol. 153 (1788); Curtis (1860) 79; Coulter (1891) 46; Mohr (1901) 613; Lewis (1915) 140; Brown (1945) 180, f. 109. Non L. (1753). Walter’s specimen (British Museum) has the lower leaf surface stellate-tomentose and the young branchlet pubescent. It is evidently *Tilia caroliniana*.

Tilia americana \( \beta \) caroliniana (Miller) Castiglioni, Viag. negli Stati Uniti 2: 389 (1790).

Tilia grata Salisbury, Prodr. 367 (1796). This is a renaming of \( T. \) pubescens Ait.

\textit{Tilia pubescens} var. \textit{leptophylla} Venentan in Anal. Hist. Nat. [Madrid] 2: 64 (1800); Pursh (1814) 363; DeCandolle (1824) 513; Elliott (1824) 3; Watson (1825) 135; Torrey & Gray (1838) 240; Chapman (1860) 59; Bayer (1862) 56; Koch (1869) 479; Gray (1857) 305, (1897) 343; Sargent (1891) 55, pl. 26; Britton (1901) 617; Small (1903) 761; Britton (1908) 689; V. Engler (1909) 128; Schneider (1909) 384; Small (1913) 70; Britton & Brown (1913) 2: 512.

\textit{Tilia americana} \( \beta \) caroliniana (Miller) Castiglioni, Viag. negli Stati Uniti 2: 389 (1790).

\textit{Tilia pubescens} var. \textit{leptophylla} Venentan in Anal. Hist. Nat. [Madrid] 2: 64 (1800); Pursh (1814) 363; DeCandolle (1824) 513; Loudon (1838) 375; Torrey & Gray (1838) 240; Gray (1887) 305, (1897) 344.

\textit{Tilia multiflora} hort. ex Venentan in op. cit. 64.

\textit{Tilia laxiflora} Michaux, Fl. Bor. Am. 1: 306 (1803). “\( T. \) foliiis cordatis, sensim acuminatis, rareris dentatis, membranaceis: paniculis laxifloris: stylo petalis longiores. \textit{Hab.} in maritimis Caroliniae, Virginiae.” Poiret (1806) 683; Persoon (1806) 2: 66; Pursh (1814) 363; Hayne (1822) 113; DeCandolle (1824) 513; Elliott (1824) 2; Don (1831) 553; Spach (1834) 343; Dietrich (1839) 237; Walpers (1842) 359; Bayer (1862) 55.

\textit{Tilia stenopetala} Rafinesque, Fl. Ludov. 92 (1817). “\( T. \) foliiis base obliquis denti- culatis glabris, petalis oblongis acutis integris. \textit{Raf. Tilleul de la Louisiane.} Rob. p. 484. Large tree over 60 feet high, and two feet in diameter, bark thin and rough, wood soft and light, peduncles long and slender on a bractea, flowers small, very fragrant.” This name is usually placed as a synonym of \( T. \) americana (Merrill, 1949: 165). The statement in the original publication quoted above that the leaves are glabrous supports this, but \( T. \) americana does not extend southward to the present state of Louisiana. Rafinesque’s name must apply to glabrous-leaved \( T. \) caroliniana Mill.

\textit{Tilia mississippiensis} Bose ex Spach in Ann. Sci. Nat. Bot. II. 2: 340 (1834). Type locality: New Orleans, Louisiana. DeCandolle (1824) 513, pro syn. \( T. \) pubescens \( \beta \) leptophylla Vent.; Spach (1834) 340, pro syn. \( T. \) nigra \( \beta \) laxiflora Spach; Bayer (1862) 54; Rebder (1949) 455, pro syn. \( T. \) americana L.


\textit{Habitat in Carolina atque Georgia.} — In Herto Parisiensi sub dio culta floret julio, fructus autem maturos rarissime perficit. (\textit{V.} \textit{sp. in herb. Michx. et Vent. atque v.c.}).” Dietrich (1839) 237; Walpers (1842) 359; Bush (1933) 844.


\textit{Tilia americana} var. \textit{pubescens} (Aiton) Loudon, loc. cit.

\textit{Tilia americana} var. \( \beta \) \textit{walteri} Wood, Flora Atlantica 64 (1870). “\( T. \) pubescent (but green) beneath. A large tree. \textit{Va. to Fla.”}

\textit{Tilia leptophylla} (Venentat) Simonkai, Rev. Til. Hung. 323 (1888); Small (1903) 762, 1335; Britton & Brown (1913) 512; Lewis (1915) 141. Simonkai says: “\( T. \) foliiis ... subitus glauco vel pallide virentibus, junioribus saltam stellato pubescentibus, adultis saepe glabriuscelus. . . .” This is clearly the form of \( T. \) caroliniana with the pubescence quickly deciduous from the
underside of the leaves that Small described as *T. floridana*. This frequently
has the lower surface of the leaves pale or glaucous. *T. leptophylla* (Vent.) Simonkai is erroneously listed as a synonym of *T. americana* L. by V. Engler (1909: 136) and by Rehder (1949: 455).


*Tilia floridana* Small, Fl. Se. U.S. 761, 1335 (1903). In rich woods, Jackson Co., Florida, A. H. Curtiss 401*, NY, type; AA, F, KANU, MBG, NEB, US, isotypes. Britton (1908) 686; Schneider (1909) 382; Small (1913) 60; Sargent (1918) 431, (1922) 737, the binomial wrongly ascribed to Ashe; Standley (1923) 735; Bush (1927) 245, (1929) 549, (1933) 845; Palmer & Steyermark (1935) 597; Steyermark (1940) 353; Fernald (1941) 604; Coker & Totten (1945) 330; West & Arnold (1946) 140; Fernald (1950) 999, wrongly ascribed to (V.Engler) Small; Little (1953) 419.

*Tilia australis* Small, loc. cit. On wooded hillsides, Blount Co., Alabama, H. Eggert. June 20, 1897, NY, type; MBG, isotype, distributed as *T. heterophylla*. This is based on glabrous specimens of *T. caroliniana*, with unusually broad bracts and the lower surface of the leaves glaucous and essentially glabrous. An additional character adduced by Bush (1933: 843), the entire or erose staminodia, seems to depend on the magnification. Although the type collection appears distinctive, it is matched by collections from other parts of the range of *T. caroliniana*, distributed as *T. floridana*, *T. lenocarpia*, *T. nuda*, and under other names. Britton (1908) 685; Schneider (1909) 382; Bush (1927) 244, (1933) 846.


*Tilia pubescens* var. *aitonii* f. *heteromorpha* V.Engler, loc. cit. “Folia diversiforma, minor a typo vix diversa, apice satis obtusa, majora numerosiora manifeste grosse serrata, longe acensis acuminata, in axillis pedunculos elongatos atque cymas squarrosas gerentia. Spontan; selten. — Lake City, Columbia Co., Fla. (NASH, Pl. Flo. no. 2188!)”. The lower surface of the leaves shows the characteristic loose stellate pubescence of *T. caroliniana*.


*Tilia pubescens* var. *ventenatii* f. *gymnophylla* V.Engler, op. cit. 130. “Natech,
Taxonomy of American Species of Linden (Tilia)

Miss. (B. SHIMEK!), Blanco, Tex. (BUSH, Pl. Tex. no. 9931). — College Station (REVERCHON, Pl. Tex. no. 4345! 1915!" One collection from Natchez, Mississippi, June, 1898, B. SHIMÈK (F), is a sterile specimen of Morus rubra L.; the MBG sheet is a shade form of T. caroliniana.

Tilia caroliniana var. floridana (Small) V. ENGLE, op. cit. 132.

Tilia caroliniana var. vagans V. ENGLE, ex parte, loc. cit. "Hanmoek, Columbia Co. (HITCHCOCK, Flo. pl.!) — Flussufer des oberen Georgia (BEYRICH!)." The label gives the habitat of the Hitcheock collection as "hammock." This was mistaken by V. ENGLE for the name of the locality. There is no such place as "Hammoek."

Tilia alabamensis Ashe in Bull. Charleston (S.C.) Mus. 14: 31 (1918, Oct. 24). Described from Tombigbee River and its tributaries in Greene, Hale, and Sumpter counties, Alabama, the type from Boligee Swamp, Greene Co., Alabama, W. D. Johnson, August, 1918 (NCU). Bush (1927) 247; Coker & Totten (1945) 316, say there has been considerable confusion as to the systematic position of this kind of tree. Ashe described it as T. alabamensis but later decided that as the flowers were so much like those of T. floridana, it was only a long-leaved variety of that "species."


Tilia nuda Sargent in Bot. Gaz. 66: 425 (1915, Nov. 15); Sargent (1922) 734. Rich woods and river bluffs near Natchez, Adams Co., Mississippi, June 2 and Sept. 24, 1915, Miss C. C. Compton 12 (AA). This appears to be a phase of T. caroliniana, although in the key preceding the original description it is contrasted with T. americana, from which it is said to differ by the leaves "usually without tufts of axillary hairs," but some specimens, e.g. Compton 2 (AA) from the type collection, show traces of axillary pubescence, and Sargent (op. cit. 427) points out that "the absence of the axillary tufts cannot always be depended on...."

Tilia nuda var. glaucescens Sargent in op. cit. 427. Bluffs of the Alabama River, Berlin, Dallas Co., Alabama, June 11 and July 20, 1915, R. S. Cocks 786 (AA). The label on one sheet is inscribed "Cocks' Place, Sardis, Ala.," and on the other "Ala. River near Sardis."

Tilia nuda var. brevipedunculata Sargent in loc. cit. Flat wet woods subject to overflow, San Augustine, San Augustine Co., Texas, June 5, 1915, E. J. Palmer 7889 (AA). This is clearly to be referred to T. caroliniana.

Tilia venulosa Sargent in op. cit. 428. "Rocky 'coves' in rich soil, Hickory Nut Gap, in the Blue Ridge, North Carolina, W. W. Ashe, April, May and October 1916 (distributed as T. eburnea Ashe), T. G. Harbison, July 5 and September 21, 1917 (no. 2 type for flowers, no. 3 type for fruit); near Saluda, Polk County, North Carolina, T. G. Harbison, July 4, 1917 (nos. 1, 2, 4, 5, 7)." This appears to be a northern phase of T. caroliniana. Under side of leaves of a sterile specimen (part of syntype) collected by Ashe, numbered 7a (ILL), shows clearly the remnants of the characteristic scattered stellate pubescence of T. caroliniana.

Tilia venulosa var. multinfervis Sargent in loc. cit. "Differing from the type in its obliquely truncate, not cordate, leaves with 12 or 13 pairs of more crowded primary veins, ellipsoidal fruit, slender branchlets, and smaller winter buds. A single tree near Saluda, Polk County, North Carolina, T. G. Harbison, July 4 and September 29, 1907 (no. 6 type)."
Tilia littoralis Sargent in op. cit. 429. Shore of Colonel’s (formerly Bermuda) Island on Dyke’s Creek, an ocean inlet near the mouths of the North Newport and Medway rivers near Dunham, Liberty Co., Georgia, Aug. 1, 1916, Miss Julia King, and June 18, 1917, T. G. Harbison 15 (AA). Sargent (1922) 736; Bush (1927) 241, (1933) 845; Coker & Totten (1945) 327, who say: “Bush considered the twigs of the summer shoots glabrous, but they are quite tomentose. The summer shoots of T. littoralis var. discolor Sarg., in which the leaves are nearly white (glaucescent) on the under surface, are also tomentose. This plant is closely related to T. crenoserrata.”


Tilia floridana var. australis (Small) Sargent in op. cit. 435.


Tilia floridana var. hypoleuca Sargent in op. cit. 436. Arkansas: “At the foot of a high bluff growing on the rock margin of White River or on talus sloping to the foot of the bluff in rich soil across the river (i.e. in Marion Co.) from Cotter, Baxter County, E. J. Palmer, June 12, 1914 (no. 5943 type), July 24, 1916 (nos. 10555, 10559).” Bush (1927) 244; Palmer & Steyermark (1935) 597. Sargent says “The unusual whiteness of the under surface of some of the leaves of this variety is due to a thick bloom. When this is rubbed off, the surface left is pale green. This bloom appears to be most common on leaves near the ends of branches and is often entirely wanting from those lower down on the branches and from the leaves of young vigorous shoots.” From this it would appear that T. floridana var. hypoleuca and T. floridana var. floridana may be found on the same branch.

Tilia cocksii Sargent in op. cit. 437. Bank of the Calcasieu River, West Lake Charles, Calcasieu Parish, Louisiana, March 23, 1917, C. S. Sargent & R. S. Cocks 4922, July 12, 1918 (type for flowers), R. S. Cocks 4949 (type for fruit) (AA). Sargent (1922) 738; Bush (1927) 245. “From other American lindens T. Cocksi differs in the thicker dark green lustrous leaves, in the peculiar bluish color of their lower surface in early spring, and in the pubescence during the summer on the leaves and branchlets of leading shoots in a species which, except when the leaves unfold and the inflorescence first appears in early spring, is otherwise glabrous. It is most closely related to T. floridana, from which it differs in the texture, color, and venation of the more finely serrate leaves, in the more compact inflorescence, and in the much shorter portion of the peduncle. I take much pleasure in associating with this handsome tree the name of Professor Reginald Woodhouse Somers Cocks, professor of botany in Tulane University and for many years my companion in annual journeys of exploration through the forests of Louisiana” (Sargent, 1915: 438).

Tilia neglecta sensu Sargent (1918) 494, (1922) 739. Non Spach (1834).

Tilia caroliniana var. rhoophila Sargent in Bot. Gaz. 66: 498 (1918). Type:
Tilia texana Sargent in op. cit. 500. Type from Kerrville, Kerr Co., Texas, E. J. Palmer 10887, 10888 (fruit), others for flowers. Sargent (1922) 742.

Tilia texana var. grosseserrata Sargent in op. cit. 501. "Differing from the type [i.e. T. texana] in the coarse serration of the leaves, in the absence of lateral lobes on the leaves and on the bracts of the peduncles, and in the constantly pale, never rusty pubescence of the branchlets and winterbuds. . . . In rocky soil at the foot of a limestone bluff by a small stream forming the head of the Sabinal River, near Utopia, Uvalde County, Texas, E. J. Palmer, June 17, 1916 (no. 10227 type), April 10 and October 6, 1917 (nos. 11522, 12937)." Foliage of rather distinctive appearance but specimens show complete intergradation to Tilia caroliniana from other parts of its geographical range. Some specimens collected by Mr. Palmer were distributed to several herbaria as "T. grosseserrata Sarg.," an unpublished combination.


Tilia phanera var. scabrida Sargent in op. cit. 502. Type: Blanco, Texas, July, 1885, J. Reverchon 1500. "Differing from the type in the seaboard lower surface of the leaves." These are glabrous above and "roughened below by the persistent bases of fascied hairs. . . ."

Tilia georgiana Sargent in op. cit. 510. Type: Brunswick, Glynn Co., Georgia, T. G. Harbison 6, 7 (AA). Sargent (1922) 748; Bush (1933) 844; Coker & Totten (1945) 336.

Tilia georgiana var. crinita Sargent in op. cit. 511. Type not designated, but the first cited collection is from sandy woods, Bluffton, Beaufort Co., South Carolina, May 28, 1887, J. H. Mellichamp (AA). "To the most hairy form Sargent has given the name T. georgiana var. crinita but fast growing branches are very hairy and could easily mislead one" (Coker & Totten, 1945: 337).

Tilia perplexa Harbison, ined. This name has been applied to specimens collected in Jackson, Hinds Co., Mississippi, June 26, 1916, and May 17, 1915, T. G. Harbison (NCU). These are sterile twigs of T. caroliniana, with the underside of the leaves more sparsely pubescent than usual.


Tilia porracea Ashe in loc. cit. "Separated from all other species by its small pubescent foliage, narrow terminal leaves, often cuneate at base. Hickory Head, Okaloosa County, Florida, W. W. Ashe . . . April 1923; Oct. 1923, and Nov. 1924" (Bush, 1933: 843). Type material of T. porracea Ashe consists of small-leaved twigs of T. caroliniana, probably a shade form, or as Ashe says on one sheet, "a depauperate branchlet." Stellate trichomes persist on
the lower leaf surface at least until flowering time. At first glance, specimens distributed as *T. porracea* appear to be a distinct species, but the peculiar foliage is duplicated in many collections from other parts of the range. Nearly identical specimens of this thin-leaved form have been collected in North Carolina (Moore Co., W. B. Fox 2540, 3598) and in other parts of the geographical range of *T. caroliniana*. It is evidently not confined to the type locality in Okaloosa Co., Florida.

*Tilia floridana* var. *alabamensis* (Ashe) Ashe in op. cit. 32. “Since the flowers of this form seem much like those of *floridana*, it at present seems best to consider this as a long-leaved variety of that species, notwithstanding its different habitat, growing in swamps, whereas *floridana* is a tree of well drained sites.”


*Tilia ashei* Bush in op. cit. 241. Florida: Hickory Head, Okaloosa Co., W. W. Ashe, April 25 and June 20, 1923, and Nov. 7, 1924, from the same tree (no. 3 type). The leaves are said to be “essentially glabrous as they unfold,” but a sheet of the type collection shows young leaves densely pubescent, as in other specimens of *T. caroliniana*. Coker & Totten (1934) 332.

*Tilia alabamensis* var. *oblongifolia* (Sargent) Bush in op. cit. 248. “The ovate-oblong leaves, the more prominent tufts of axillary hairs, the slender glabrous reddish-brown branchlets seem to separate it from *floridana*; but that it is a variety of *T. alabamensis*, I am not sure, and further observations and collections may prove that it is only a form of *T. floridana*.”

*Tilia leucocarpa* glaucescens (Sargent) Sudworth, Check List Forest Trees U.S. 201 (1927); Bush (1927) 239.


*Tilia crenoserrata* var. *acuminata* Ashe in Bull. Torr. Club 55: 465 (1928). “This differs from the type [i.e., the type of *T. crenoserrata*] in the acuminately pointed leaves and like the type it often has summer shoots which are velvety pubescent. Type: *Prof. M. D. Cody and W. W. A[she]* near Gainesville, Fla., June 9, 1925.”

*Tilia pallida* Bush, ined. Hillside woods, San Augustine, San Augustine Co., Texas, June 5, 1915, E. J. Palmer 7882, in flower (AA). Sheet annotated “T. pallida Bush 3-13-29. TYPE.” A second sheet, from wet woods, same locality and date, E. J. Palmer 7883 (AA), bears a branchlet with leaves only. It is marked by Bush “Co-type.” These specimens belong to *T. caroliniana*. The leaves are pale and glabrous beneath; the axillary tufts of trichomes are small and inconspicuous, or absent.

*Tilia leucocarpa* var. *cocksii* (Sargent) Ashe in Torreya 31: 39 (1931). “The chief character presented by Dr. Sargent for the separation of *T. cocksii*
from *T. leucocarpa* Ashe (*T. nuda* Sarg.) is the pubescent summer shoots of the former species. It is now known, however, that *T. leucocarpa* also develops pubescent summer shoots. The only other evident difference between these trees seems to be that the leaves of *T. leucocarpa* are sharply serrate and those of *T. cocksi* are finely and distantly dentiulate."


*Tilia floridana* var. *porracea* (Ashe) Coker & Totten, Trees Southeast. States 331 (1937). “Except for more abundant and more persistent hairs, the leaves generally remaining tomentose through the summer, and for narrower, nearly linear bracts, the description of this plant would be practically identical with that of *T. floridana.*"

Trees 10-20 m. tall and 30-50 cm. in diameter, with furrowed bark and slender glabrous reddish brown or somewhat yellowish branchlets; winter buds ovate, obtuse, glabrous or pubescent, 3-4 mm. long; leaf scars alternate, conspicuous, raised, containing few to many bundle scars arranged in a ring or a single curved line, or scattered; stipule scars distinct, one narrow, the other broad; leaves tomentose especially beneath when unfolding, those of the flowering branches ovate, acuminate, 6-15 cm. long, 5-12 cm. wide, the base unsymmetrical, truncate or cordate or variously oblique; apex abruptly acuminate; margins coarsely serrate with apiculate teeth; primary veins 5-8 pairs; lower surface of mature leaves of flowering branches often pale and somewhat glaueous, or coated with a rusty or pale, easily detached pubescence of fascicled hairs, soon becoming glabrous, with small tufts of trichomes in the axils of the primary veins, or these small tufts sometimes lacking; trichomes commonly 8-rayed (or 6-, or 4-), the rays 0.2-0.3 mm. long; upper surface of blades smooth, glabrous, dark green, or sometimes somewhat glossy; petioles slender, glabrous, 2-4 cm. long, usually shorter than the blades; bracts elliptical to ligulate or oblanceolate, obtuse, glabrous, often falcate, 7-15 cm. long, 1.5-2 cm. wide, sessile or nearly so; peduncle slender, pubescent, the free portion 2-5 cm. long; cyme mostly shorter than the bract; flowers 6-7 mm. long, on slender, pubescent pedicels, in small, stout-branched, pubescent, mostly 8-30-flowered cymes; sepals lanceolate, acuminate, 4-5 mm. long, conca
evate, 2-3 mm. wide at the base, pale pubescent on the outer surface, with long whitish hairs inside; petals pale yellowish, narrowly elliptical, 5-6 mm. long, 2 mm. wide; staminodia 4-5 mm. long, spatulate, much exceeding the stamens and about two-thirds the length of the petals; style slender, glabrous throughout or pubescent only at the very base; stigma 5-lobed; fruit subglobose, densely and finely grayish tomentose, 5-8 mm. in diameter; fruiting pedicels tomentulose; seed commonly one, brownish, subglobose, glabrous, about 4 mm. in diameter; seedlings unknown.
DESCRIPTION AND DISCUSSION OF AMERICAN SPECIES

DESCRIPTION AND DISCUSSION OF AMERICAN SPECIES


**TYPE LOCALITY:** “Carolina,” described from a tree cultivated in England. “The seeds . . . were brought from Carolina by the late Mr. Catesby” (Miller, 1768). Type in the British Museum. This certainly represents the species as currently interpreted.

**RANGE:** North Carolina to central Florida, eastern and central Texas, eastern Oklahoma, and southern Missouri. Flowering from May 5 to June 20; fruits ripening from June to September.

**SIGNIFICANT COLLECTIONS**


TAXONOMY


DESCRIPTION AND DISCUSSION OF AMERICAN SPECIES


A brief commentary on Miller’s publication of *T. americana* and *T. caroliniana* may be in order here, as some authors have professed inability to interpret these species satisfactorily. Miller’s “3. TILIA (Americana)” is clearly *T. americana* L. as commonly interpreted. It “was brought back from New England by the title of Black Lime.” It is the only species that grows naturally in New England. The leaves are said to be “a little hairy on their underside,” a condition not incompatible with the assignment to that species.

Miller’s *T. caroliniana* is clearly characterized: “4. TILIA (Caroliniana) foliis cordatis obliquis glabris subserratis cum aequmine, floribus nectario instructis. Lime-tree with heart-shaped smooth leaves, which are oblique to the foot-stalk, etc. . . . Carolina Lime-tree with a long-pointed leaf. . . . The seeds of the fourth sort were brought from Carolina by the late Mr. Catesby.” It will be noted that the leaves are “smooth.” Assuming this to mean glabrous on both surfaces, no problem presents itself, as it means simply that a glabrous-leaved form of *T. caroliniana* was being described. I have studied collections with both glabrous and pubescent leaves growing on the same twig, or in another instance of specimens from two adjacent trees, one with glabrous leaves, the other with stellate-pubescent leaves, and there are several examples of different specimens bearing the same collection number but having different foliar indument. The significant fact is that the holotype of *T. caroliniana* in the British Museum shows unequivocally the characteristic stellate pubescence of *T. caroliniana*.

*Tilia caroliniana* most resembles *T. mexicana* and is probably
closely related to that species. They occupy different geographical areas. Specimens of *T. caroliniana* may usually be identified by a combination of characters outlined in the key. These include the finely grayish stellate-pannose pubescence of the sepals obvious in the buds as well as the flowers, as contrasted with the usually copious stellate-villosulous pubescence of the calyx of *T. mexicana*. The ovary of *T. caroliniana* is densely whitish tomentose, versus the brownish short villosity of the Mexican species. In *T. caroliniana* the inflorescence is usually relatively small, with slender pedicels and peduncle, and the petioles of the leaves of the flowering branches are sparsely pubescent to glabrous, while those of *T. mexicana* are usually densely and copiously short villous-pubescent with stellate trichomes, although this condition, as shown in some specimens, has a tendency to diminish with age, and is not evident on the type collection.

In the Gulf region of Texas Tilia is generally known as linn, and apparently no other vernacular name is employed. The trees are not common. They occur chiefly in the bottom lands, associated with species of oak (*Quercus*), sweet-gum (*Liquidambar*), sycamore (*Platanus*), and pine (*Pinus*), their branches often heavily festooned with the bromeliaceous epiphyte Tillandsia, commonly known as Spanish moss. It is likely that these trees were formerly more frequent than they are now. With other deciduous trees, they tend to be crowded out by the more rapidly growing pines. When a tree is cut for lumber, the stump, as in many other species of Tilia, may sprout vigorously, but these sprouts are said to have a tendency to die as the stump rots away. The largest trees may be two feet or more in diameter. The lumber is valuable commercially, although it is rather scarce. In Louisiana, and elsewhere, boat paddles are made from linn wood.

The type collection of *T. floridana* Small consists of flowering branchlets collected by A. H. Curtiss in June, the year not stated. According to the label, the type region is “Rich woods, Jackson County, N. W. Florida.” No more definite locality is given either on the label or with the original publication, but it is near the central part of northern Florida adjacent to the states of Alabama and Georgia, a region occupied by *T. heterophylla* as well as *T. caroliniana*. Specimens with printed labels were distributed as “Curtiss, North American Plants,” and named “*Tilia Americana* L., var. *pubescens* Gray,” a varietal combination that should be attributed to Loudon. The leaves are ovate, sharply serrate, thin, abruptly acuminate, obliquely truncate at base, dark green and glabrous above, and pale green or glaucous beneath, covered early in the season on the under surface with fascicled hairs that soon disappear, so that when the flowers open,
they are almost glabrous, or with some remnants of stellate tomentum along the veins and toward the base, and with small tufts of hairs in the axils of the veins. The flowers are 5-6 mm. long, borne on tomentose pedicels in few-flowered, rather compact, pubescent corymbbs. The nearly glabrous bracts are 7-8 cm. long and 1.5-2 cm. wide. In the shape of the leaf blades, the type of marginal serration, the acuminate apices, the relative length of blade and petiole, and in the shape and size of the bracts, the type collection of *T. floridana* Small is evidently a very good match for the type of *T. caroliniana*.

For several years, I have tried to discover evidence to maintain *T. floridana*, first as a species and later as a subspecies or variety. Hundreds of specimens have been so labeled. But I am forced to the conclusion that *T. floridana* Small is specifically or even varietally indistinguishable from the variable and widespread *T. caroliniana*. The type collection shows the characteristic pubescence of *T. caroliniana* on the underside of the leaves. There are no other tangible characters than the “glabrous” leaves of *T. floridana* to define it, and this does not hold. Viktor Engler treated *T. floridana* as a variety of *T. caroliniana*. However, as *T. caroliniana* and *T. floridana* form a continuum with no tangible lines of demarcation, there appears to be no practical possibility of attempting to maintain *T. floridana* as a variety.

Specimens with the leaves covered below with a rusty or pale, easily detached pubescence of fascielled hairs show a positive mark of identification of *T. caroliniana*, as no other species in the United States shows this character, but the absence of this pubescence does not signify that it necessarily must belong to some other species, as this character is variable in *T. caroliniana*, as in other species. On different leaves of the same specimen from Kendall County, Texas (*Palmer 9879*, May 25, 1916, AA, DS), the condition is glabrous, nearly glabrous, sparsely stellate, and copiously stellate-pubescent, respectively. A characteristic of *T. caroliniana* not observed in other species is that the lower surface of the leaves, when glabrous or glabrescent, often shows a distinctive minutely tessellated pattern. The axillary tufts of trichomes are sometimes small or absent.

Loudon (1838: 374) says of *T. caroliniana* (under *T. americana* var. *pubescent*): “The leaves are most pubescent after their first expansion: as they increase in size, a part of the pubescence falls off, and the hairs which remain form little starry tufts. . . . It is the only variety found in the maritime parts of Carolina and Georgia. Michaux found it principally in the neighborhood of Charleston. . . . Seeds of this variety were brought to England by Catesby in 1726. . . . In New York, the price is 50 cents a plant.”
Specimens with apparently glabrous leaves, if examined under a binocular dissecting microscope, will often show traces or vestiges of the typically ephemeral stellate pubescence characteristic of this species, particularly on the lower half of the under surface of the leaf blades, usually near the midvein or midrib.

Some specimens show a tendency for the pubescence to disappear late in the season, leaving lines or patches of stellate tomentum along the main veins on the under surface of the leaf, and on the small veins there may be observed the "stumps" of the stellate trichomes, resulting in a scabrid condition observable under the binocular microscope. Such specimens were described from Texas by Sargent as T. phanera var. scabrida. Leaves of other specimens become later in the season nearly or completely glabrous.

Sargent's statement, "As here understood the range of T. caroliniana is remarkable, as there is no evidence that it occurs between the coast of Georgia and western Louisiana" (1918: 498), is no longer valid, as since that time collections have been made in a dozen or more counties in Georgia, Alabama, and Mississippi.

A sheet of T. caroliniana (Ashe 27, MBG), from Gainesville, Florida, collected on June 9, 1925, with the inscription on the label: "Note: tomentose summer shoot & leaves," shows a twig six or seven inches long, bearing four small leaves, the two upper ones with the characteristic stellate pubescence of T. caroliniana, the two lower ones with the lower surface perfectly glabrous except for tufts of hairs in the axils of the principal veins. Hence, on the conventional interpretation, we have two species represented on a single twig!

Concerning Tilia australis, which is here regarded as one of the numerous forms of T. caroliniana, Bush (1927: 244) says:

Restricted to the rough mountainous region of middle Alabama. It is very common there, and may occur in the mountainous parts of the adjacent states. The summer-shoots are glabrous (tomentose in T. floridana); flowers very large (very small in T. floridana); inflorescence not widely spreading in fruit (wide-spreading in T. floridana); pedicels glabrous or glabrate at flowering time (permanently tomentose in T. floridana and T. alabamensis); bracts glaucous; leaves large, thick, glaucous beneath. Sargent, in his Tilia paper and in his Manual of Trees, does not recognize this as a species, but in this he has done the species a great injustice, as it is better separated from T. floridana than is his T. nuda (T. leucocarpa Ashe).

I cannot concur that "the species has been done a great injustice," as all the names mentioned above stand for the trivial and inconstant variations of one species, Tilia caroliniana Mill.

On the theory that the occurrence and distribution of foliar indument might possibly be found to conform to some geographical pattern, ap-
approximately 1,000 specimens of \textit{T. caroliniana} were examined from 11 states over a range of about 700,000 square miles, from North Carolina to Arkansas and southern Oklahoma, and from Florida to central Texas, an area including every type of habitat or ecological niche in which the species occurs.

No significant correlations were discernible. Leaves generally tend toward glabrescence in age, but the leaves of some trees retain the stellate pubescence until autumn. Retention of pubescence on the lower surface of the leaf blades of flowering branches is probably not to any considerable extent determined by environmental factors. Following is a list showing percentage of specimens by states with leaves stellate pubescent beneath at flowering time.

\begin{tabular}{|l|c|}
\hline
\textbf{State} & \textbf{Per cent} \\
\hline
South Carolina & 82 \\
Georgia & 80 \\
Texas & 54 \\
North Carolina & 50 \\
Missouri & 42 \\
Louisiana & 40 \\
Florida & 25 \\
Arkansas & 25 \\
Alabama & 10 \\
Mississippi & 8 \\
Oklahoma & 0 \\
\textbf{Average} & 38 \\
\hline
\end{tabular}

With regard to the tendency of the lower surface of leaf blades of \textit{T. caroliniana} to be glaucous, it may be observed that specimens with noticeably glaucous leaves have been given several different names and have been described as new species or varieties. However, certain obvious facts stand out clearly. All leaves have a cuticle. The epidermal cells of some leaves secrete more cutin than others; the thickness or density of the cuticular layer determines the degree to which the lower surface of the blade appears glaucous. This character is not evidently related to other characters. It is interesting to note that conspicuously glaucous-leaved specimens of \textit{Tilia} may be less frequently deposited in herbaria since the custom of drying plants over "artificial heat" has become widespread.

Very young leaves of \textit{Tilia caroliniana} differ from those of \textit{T. americana} and \textit{T. heterophylla} in having the lower surface densely chiefly homotrichous with a copious tomentum of loose mostly six-rayed stellate trichomes giving such a uniformly dense indument that the primary and secondary veins are visible only as dark lines among the copious whitish pubescence, and with the tertiary veins being com-
pletely obscured, the numerous small regular nearly glabrous teeth protruding from the margin.

Specimens of the native American red mulberry, *Morus rubra* L., without flowers or fruits have been sometimes named *Tilia caroliniana*, or as other species of *Tilia*, including *T. americana*, *T. floridana*, *T. heterophylla*, *T. phanera*, *T. platyphyllos*, and *T. texana*, but usually they can be distinguished at a glance by the different pubescence and serration. The buds also are dissimilar. As an example of how easily *Tilia* and *Morus* can be confused, I cite a sheet from the George Engelmann herbarium in the Missouri Botanical Garden labeled *Tilia americana* L., from River de Pere, July 15, 1860, “6 m. from St. Louis,” later annotated as “*T. americana* var. *pubescens*” in the handwriting of William Trelease, director of the garden, also bearing the annotation label *Tilia platyphyllos* Scop. var. *cordifolia* (Bess.) V.Engler, the monographer of the genus, yet the specimen belongs certainly to *Morus rubra* L.! *Morus* differs, *inter alia*, from *Tilia* in showing three or more bud scales, as well as in the less zigzag twigs. Milky sap exudes from fresh specimens of twigs and petioles if cut or wounded. The terminal bud is absent in both genera. I have seen several American specimens of the paper-mulberry, *Broussonetia papyrifera* (L.) Vent. (Moraceae), native of eastern Asia, labeled in herbaria as species of *Tilia*. It is not surprising that several Tertiary fossil lindens have been confused with *Morus*, *Viburnum*, and *Populus*.

**Tilia mexicana** Schlcht.: Mexican Basswood

*(Plates 17-30)*

Tomento canescens, omnino ecosatus. Gemmæ parvae glabrae.” Bentham (1839) 35; Walpers (1842) 360; Bayer (1862) 57; Hemsley (1879) 141; Gray (1887) 305; Simonkai (1888) 315; V. Engler (1909) 125; Schneider (1909) 382; Standley (1923) 735; Bush (1929) 54S.

*Tilia floridana* sensu Sarg (1918) 434; Standley (1923) 735. Non Small (1903).


*Tilia houghii* Rose in op. cit. 318 (1905). “Distinguished from *T. occidentalis* by its larger broader leaves, which are much paler beneath and covered with a finer pubescence.” Collected by J. N. Rose and Walter Hough in a mountain canyon above Cuernava, Morelos, May 27-30, 1899 (no. 4398, US). Schneider (1909) 384, t. 275 c-d; Standley (1923) 736; Bush (1929) 555; Martínez (1956) 44.


*Tilia mexicana* var. *houghii* (Rose) V. Engler, op. cit. 126.


*Tilia caroliniana* var. *vagans* V. Engler, ex parte, op. cit. 132. “Folia subitus tomentosa, basi magis obtusata quam truncata. Cymae paeclfiorae. Veracruz (SUMICHRAST no. 988!); el Chico (EHRENBerg no. 1289!).”


*Tilia ambiguа* Sarg. ex Bush in loc. cit. Type from Orizaba, Veracruz, Botteri 62 (US).

*Tilia rotunda* Bush in op. cit. 552. Type from vicinity of Morelia, Michoacán, *G. Arsène* 2664, April 11, 1909 (AA), distributed as *T. heterophylla*.

*Tilia coahuilana* Bush in loc. cit. (as “Milia”). Type from Monclova, Coahuila, E. Palmer 118. Type, AA; isotypes, US.


*Tilia longipes* Bush in op. cit. 554. Type from “Orizaba, Veracruz, Botteri 63, p. p., about 1855-57, Field Museum 118976, the plant marked 2 on this sheet, TYPE.” Isotypes, AA, GH, NY, US.

*Tilia moreliana* Bush in op. cit. 547. Published with diagnosis (in the key), but the name changed on p. 557.

*Tilia patzcuaroana* Bush in op. cit. 557. In the key this is named by Bush as *T. moreliana*. Type: hills of Patzcuaro, Michoacán, C. G. Pringle 3578, Nov. 21, 1890 (AA).

*Tilia sargentiana* Bush in loc. cit. Type from wet mountain canyon above

*Tilia roseana* Bush in op. cit. 559. Type from “wet bluffs of the barranca below Honey Station, Hidalgo, September 21, 1908, C. G. Pringle 10500,” holotype said by Bush to be in the Deam Herbarium (Indiana University). Isotypes, GH, MICH, US, YU.


*Tilia arsenei* Bush in loc. cit. Type from vicinity of Morelia, Michoacán, G. Arsène 2534, May 5, 1909 (AA). This collection has nearly full-grown leaves, retaining the typical copious pubescence of *T. mexicana* in this stage of growth. The young inflorescence consists of unopened flower buds. To the printed label has been added, in the handwriting of Arsène, “Rincon, alt. 2950 m.”

Tree 10-20 m. tall, the trunk with a diameter of 25-50 cm.; bark firm, dark gray, developing deep longitudinal furrows; twigs of the season slender, densely villosulous-pubescent, soon glabrescent, usually somewhat zigzag; winter buds ovoid or ellipsoid, 2-ranked, the outer scales glabrous, the inner pubescent; terminal bud absent; leaf scars alternate, conspicuous, raised, containing few to several bundle scars arranged in a ring or a single curved line, or scattered; stipule scars distinct, one narrow, the other broad; leaves ovate, oblique and truncate or unequally cordate at base, abruptly acuminate at apex, 8-16 cm. long, 5-13 cm. wide, palmately veined, the median vein stronger than the rest, the secondary veins connected by numerous cross-veins; upper surface dark green, glabrous and glossy; pubescence of the lower surface of the leaves of the flowering branches grayish or brownish, loose, easily detached, and eventually deciduous, consisting of numerous, stellate, commonly 8-rayed (or 6-, or 4-) trichomes with divergent or erect branches 0.5-0.9 mm. long; late-season leaves on the fruiting branches sometimes nearly or quite glabrous, often showing vestiges of loose stellate pubescence; margins sharply serrate; petioles about one-half (to one-fourth) the length of the blades; densely pubescent to glabrate; stipules prominent on the young growth but soon deciduous; flowers yellowish or cream, fragrant, 12-15 mm. in diameter, appearing from April to July according to latitude and altitude, in pendulous cymose clusters from the axils of the leaves, each cluster subtended by a membranous bract to which the peduncle is fused for half its length; bract pubescent, spatulate, 7-10 cm. long, veiny, the stalk very short; fruiting bracts retaining some pubescence, at least on the peduncle and midrib; inflorescence widely branching, the pedicels densely white-tomentulose; cymes usually exceeding the bract; sepals lanceolate,
acutish, thick, concave, curved, villous, 6-8 mm. long, 2-3 mm. wide; petals slightly exceeding the sepals, elliptical, concave, entire, pale yellow, obtuse, 6-8 mm. long, 2-3 mm. wide at middle, the claw about 1 mm. long; staminodia elliptical, erose or dentate, 6-7 mm. long, about two-thirds the length of the petals and somewhat longer than the approximately 60 stamens; pistil about 1 cm. long, the style stout, exserted, hispidulous below the middle, otherwise glabrous, about three times the length of the densely pubescent ovary; stigma 5-lobed; fruit a woody, globose drupe, about 8 mm. in diameter when fully grown, densely velvety villosulous, occurring in clusters of 6-12, often persisting until December, the pedicels pubescent; seeds in the material examined 1 or 2, brown, ellipsoid, 5 mm. long, 4 mm. wide; seedlings unknown.

**TYPE LOCALITY:** Cuesta Grande de Chiconquiaco, Veracruz, Mexico. Collected by C. J. W. Schiede, Sept. 29, 1829. Holotype: Botanisches Museum, Berlin-Dahlem (B), presumably destroyed in 1943. Isotypes from Übersee-Museum, Bremen (BREM), Universitét Göttingen (GOETT), and the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE), have been examined, and the latter designated as the lectotype of T. mexicana Schlecht.

The type locality is given erroneously by Viktor Engler as Nuevo León, and by Sargent as Hidalgo, but the type collection was made in the Sierra Madre Oriental, state of Veracruz, in the mountains northwest of the city of that name, probably near 20° N. Lat. and 97° W. Long.

**SIGNIFICANT COLLECTIONS**

**CHIHUAHUA:** 27 miles S. of Creel, Aug. 5, 1960, R. M. Straw & M. Forman 1880 (ILL); Guayanopa Canyon, Sierra Madre, alt. 5,000 ft., Sept. 23, 1903, M. E. Jones (US); Cas equal de Basaseachic, headwaters of Rio Mayo, July 6, 1936, H. LeSueur 649 (F, GH, MBG,

---

2 "Christian Julius Schiede (1798-1836), a German, studied natural science, especially botany, at Berlin and Goettingen, and, as a means of assistance in his proposed botanical explorations, medicine. Accompanied by another botanist, Deppe, he reached Mexico in 1828. The two spent about a year in exploring the State of Veracruz, and obtained large collections of plants and other objects. Schiede then took up the practice of medicine, which gave him means to explore other regions of Mexico. His collections were studied chiefly by Schlechtendal and Chamisso, who published numerous papers dealing with them in Linnaea. Schiede himself published descriptions of some of the new plants he discovered, as well as letters dealing with the general aspects of Mexican vegetation. He died in the City of Mexico in 1836. His plants were widely distributed, the most complete series being in Berlin; a few are in the U.S. National Herbarium" (Standley, 1920: 81).
TEX, US), at about 108° W. and 28° N., the most westerly known locality for Tilia in North America.


DURANGO: moist ravines in oak-pine forest, elev. 2,100-2,300 m., along highway from Durango to Mazatlan, 50-54 miles W.S.W. of El Salto, March 25, 1951, R. McVaugh 11579 (MICH).


JALISCO: barranca in pine-oak-fir forest, elev. 2,400-2,600 m., about 15 miles S.E. of Autla in mountains near trail from Chante to Rancho Manatlan, April 13, 1949, R. McVaugh 10265 (ILL, MICH); abundant in barranca on steep mountainsides in pine-oak forest, elev. 2,250-2,550 m., northeast slopes of the Nevado de Colima below Canoa de Leóncito, Oct. 11-13, 1952, R. McVaugh 13428 (ILL, MICH); northwestern slopes of Nevado de Colima in pine-fir zone above Jazmin, in deep heavily wooded barranca 1 km. above El Isote, elev. 2,500-2,600 m., March 25, 1949, R. McVaugh 10013 (ILL, MICH);
north side of Nevado de Colima, near summit of road from Atenquique to Jazmin, elev. ca. 2,100 m., in barrancas among pines and oaks, scarce, June 21, 1957, R. McVaugh 14946 (ILL, MICH); barrancas in
fir zone on steep slopes, abundant up to about 2,200 m. elev., Sierra
de Cuale, S.W. of Talpa de Allende southwest of the prominent peak
called Piedra Rajada, Nov. 19-21, 1952, R. McVaugh 14378 (ILL, MICH);
early Ciudad Guzman, alt. 1,900 m., June 1, 1939, O. Nagel
8058 (GH); occasional tree in woods in mountains east of Mamantlan
about 15 miles S.S.E. of Autlan by way of Chante, alt. 8,300 ft., July

MEXICO: barranca, Calera, alt. 770 m., Temascaltepec, Oct. 8,
1932, G. B. Hinton 2030 (AA, GH, NY); on cliff in upper oak belt,
Cajones, Temascaltepec, Sept. 8, 1935, G. B. Hinton 8277 (AA, F, GH,
NY, US); barranca, alt. 1,200 m., Plaza de Gallos, Temascaltepec, June
14, 1933, G. B. Hinton 4120 (AA, F, GH, MBG, US); Tequisquiapan,
east of Temascaltepec, alt. 2,480 m., May 31, 1932, G. B. Hinton 820
(MEXU, NY), 1340 (MEXU, NY).

MICHOACÁN: Campanario, alt. 2,100 m., vicinity of Morelia,
December, 1910, G. Arsène 5355 (AA, GH, US); 6 miles from road
junction near Capaeuaro on the road to the volcano Paricutín, Nov. 4,
1959, G. N. Jones 22527 (ILL); wooded ravine 8 miles E. of Carapan,
Nov. 3, 1958, G. N. Jones 22526 (ILL); 4 miles E. of Carapan, Nov. 3,
1958, G. N. Jones 22523 (ILL); moist ravine in hardwood-conifer
forest, Nov. 6, 1958, G. N. Jones 22525 (ILL); wooded ravine 2 miles
N.W. of Cheren, Nov. 6, 1958, G. N. Jones 22537 (ILL); 4 miles S. of
Cheren, between Cheren and Paracho, near the locality of no. 22524,
Nov. 6, 1958, G. N. Jones 22536 (ILL); barranca 4 miles S. of Cheren
on road to Uruapan, Nov. 3, 1958, G. N. Jones 22524 (ILL); south-
facing slopes between Rio del Salto and La Polvilla, 18 miles E. of
Morelia, November, 1961, R. M. King & T. R. Soderstrom 5127 (ILL);
mountainside near stream, El Salto, 18 miles E. of Morelia, Nov. 7,
1958, G. N. Jones 22521 (ILL); along stream at edge of field, 13 miles
E. of Morelia, Nov. 7, 1958, G. N. Jones 22522 (ILL); wooded canyon
near road, 2 miles N. of Opopo between Patzcuaro and Ario, Oct. 31,
1958, G. N. Jones 22535 (ILL); hills of Patzcuaro, Nov. 21, 1890, C. G.
Pringle 3378 (AA, GH), type coll. of T. patzcuaroana; mountains
about Patzcuaro, July 22, 1892, C. G. Pringle 4126 (AA, GH, MBG,
MEXU, MICH, US), type coll. of T. occidentalis; Rincon, alt. 1,950
m., vicinity of Morelia, May 5, 1909, G. Arsène 2534 (AA, GH, ILL,
MBG, NY, US), type coll. of T. arsenei Bush, April 11, 1909, G. Arsène
2664 (AA, GH, MBG, NY, US), type coll. of T. rotunda Bush; by
stream in pine forest, Tancitaro, alt. 2,150 m., near Uruapan, Nov. 7, 1940, G. B. Hinton 15480 (US); rather common along watercourses on trail up Mt. Tancitaro, elev. 7,500 ft., Aug. 19, 1940, W. C. Leavenworth 721 (F, GH, ILL); in ravine in cloud forest, elev. 7,200 ft., Tancitaro, June 28, 1941, W. C. Leavenworth & H. Hoogstraal 4012 (F, ILL, MBG); north slope of Mt. Tancitaro, alt. 7,000-8,500 ft., Feb. 23, 1903, E. W. Nelson 6874 (GH, US); near Uruapan, June, 1940, M. Martínez (DAO, GH, MEXU, MICH, US), October, 1940, M. Martínez (MEXU); moist ravine at western edge of Mil Cumbres, alt. 8,000 ft., June 18, 1945, A. J. Sharp 45541 (TENN).

MORELOS: on bank of stream in mixed pine and broad-leaf woods on mountain slope at Km. 61 along road from Mexico City to Cuernavaca, Aug. 11, 1929, Ynez Mexia 2706 (AA, F, GH, MBG, MICH, US); 7 miles N. of Cuernavaca, Nov. 11, 1958, G. N. Jones 22538 (ILL); Cuernavaca, May 27-30, 1899, J. N. Rose & W. Hough 4398 (US), type of T. houghi Rose; wet mountain canyon above Cuernavaca, alt. 6,500 ft., July 30, 1906, C. G. Pringle 10264 (F, GH, MBG, MEXU, MICH, NY, SMU, US, YU), type coll. of T. sargentiana, toptype of T. houghi Rose; Valle des Tepeite, May 25, 1938, E. Lyonnet 2098 (US).


OAXACA: Santa Maria Yavesía, H. Galeotti 4158 (K, US); La Parada, alt. 7,500-8,500 ft., Aug. 16, 1894, E. W. Nelson 999 (GH, US); Manzanar, east of Oaxaca on road through San Augustín toward Natividad, alt. 7,550 ft., March 11, 1949, Margery Carlson 1390 (F); en bosque de Quercus en laderas de barrancas, carretera de Ixtlácn de Juárez a Capulalpan, Oct. 26, 1956, F. Miranda 8395 (MEXU).

PUEBLA: on slopes above Río Necaxa toward Huaucheinango, alt.
4,700 ft., March 27, 1945, A. J. Sharp 45378 (TENN); norte de Huauchinango, F. Miranda & A. J. Sharp 3432 (MEXU).


SINALOA: oak-pine forest, alt. 4,000-5,000 ft., 30 miles E. of El Batel on the road to Durango, June 22, 1955, L. I. Davis 55-80 (TEX).


VERACRUZ: Orizaba, about 1855-57, M. Botteri 63 (AA, F, GH, NY, US), type coll. of *T. ambigua* Bush and *T. longipes* Bush; limestone hills, mountains of Orizaba, in 1856, M. Botteri 988 (K, NY); along bank of river, alt. 5,800 ft., below Atzalán, March 13, 1946, A. J. Sharp 46157 (ILL, TENN) (this locality is near the type region of *T. mexicana*); Cuesta Grande de Chiconquiaco, Sept. 29, 1829, Schiede (BREM, GOETT), isotypes of *T. mexicana* Schlecht., lectotype (LE).

STATE UNKNOWN: Chaparro, Sept. 20, 1902, F. Altamirano 524 (US); “near Mexico,” Bustamente & Rocher (NY); El Chico (Engler [p. 132] says Veracluz [state]), C. A. Ehrenberg 1289 (MBG, NY, US, ex Museo Botanico Berolinsen); “Ahuareo (?),” March, 1848, Dr. Halstead (probably NY); between Angangueo and San Andreia, acc. to V. Engler (p. 126) [probably Michoacán], in 1840, K. T. Hartweg 276 (NY); without locality, F. M. Liebmann 502 (F, NY, US).

*Tilia mexicana* is the oldest name applied to any linden in Mexico. The original description by Schlechtendal, based on specimens without flowers, clearly states “foliiis . . . glaberrimus,” but for 100 years no collections of Tilia in Mexico were recognized as agreeing with this description, particularly in the glabrous leaves; Standley (1923: 735) noted that *T. mexicana* was “known only from the type locality,” and that he had seen no material agreeing with the original description in which the lack of pubescence of the leaves is emphasized, although most Mexican specimens had been referred previously to this species. In
December, 1958, Dr. Faustino Miranda\(^3\) showed me in the Herbario Nacional del Instituto de Biología in Mexico City specimens that he had collected near the type locality of *T. mexicana*. The leaves of these specimens are definitely pubescent, and resemble closely those of dozens of other specimens of *Tilia* collected in 16 or more different states in Mexico. We thought that an error had been made in the original description, and that the problem might be insoluble because Schiede had sent his collections to Willdenow in Berlin and that herbarium was nearly destroyed in 1943. In the summer of 1959, however, isotypes were discovered in two European herbaria, one at Bremen and the other at Göttingen. These collections, bearing the original label of Schiede in his handwriting, are late-season specimens with old, thickish leaves that are glabrous or nearly so, the pubescence being nearly completely deciduous at that season in the mountains. These specimens are perfectly matched by many other Mexican collections, notably several by McVaugh from Jalisco. During the past half-century specimens with pubescent leaves have been given between 15 and 20 different names, while glabrous plants have been referred to *T. floridana* as by Sargent (1918) and Standley (1923), in both instances it would seem on insufficient evidence.

The following descriptive notes are based on study of part of the type collection (BREM, GOET, LE) which was evidently made late in the season (Sept. 29) at high altitude (probably 6,000 feet). It consists of a twig with several large, coarse, tough leaves, and a few bracts. The fruits have disappeared. There are, of course, no flowers.

The leaves are dark green, glabrous above and probably glossy, the lower surface pale and nearly completely glabrous. The axillary tufts are lacking, or are small and inconspicuous. The petioles, buds, and twigs are essentially glabrous, but examination under \(10 \times\) or higher magnification reveals the presence of small scattered stellate trichomes on the twigs of the season. The blades are obliquely truncate at the base, acute or abruptly acuminate at the apex, and serrate on the margin. The petioles are about one-fourth the length of the blades.

The bracts are 9-10 cm. long, 1-2 cm. wide, obtuse at the apex, cuneate at the nearly sessile or shortly stipitate (4-6 mm.) base, essentially glabrous, but there are on both surfaces a few small, appressed, scattered, stellate trichomes visible under magnification. The peduncle is adnate to the bract for somewhat less than half its length.

The first attempt to clarify the status of *Tilia* in Mexico was made by Rose in 1905, who described *T. occidentalis*, on the basis of a col-

lection by Pringle in the mountains about Patzuaro, Michoacán, in 1892, this published with the comment "Perhaps nearest T. mexicana, but certainly with very different leaves," a comparison based in all probability on the original description of T. mexicana. At the same time Rose attempted to segregate a second species, T. houghi, "by its larger broader leaves." Both of these were promptly reduced to varietal status by V. Engler in 1909. In 1929, Bush applied 13 names to the Mexican Tiliae, thus bringing to an end, for the time at least, further attempts to describe new species of Tilia from Mexico. In 1933, Bush summarized his ideas on species of Tilia in Small's Manual of the Southeastern Flora, but as none of these was said to range farther south than Texas, this treatment need not be discussed here. Of the 14 Mexican species included in his key (1929), to be distinguished by such characters as thickness, size, pubescence of leaves, without supporting characters of flowers or fruits, the only one that stands is the original T. mexicana.

*Tilia mexicana* is exclusively Mexican. It is known to occur in 16 states, southward into Guerrero and Oaxaca, and on the east to Vera-cruz. In the United States, no species of Tilia extends its range west of about Long. 100° W., but in Mexico, *T. mexicana* goes west to Long. 110° W., where it has been collected in Sierra Madre Occidental, at the headwaters of Río Mayo in Chihuahua. This species is probably no more variable than are others of this genus, but the fact that the late-season extreme form was described first and not recognized again for more than a century, with the additional factor of the description of more than a dozen nonexistent species in the meantime, has contributed to the slow progress in understanding this hitherto somewhat mysterious species.

I am informed by Professor M. Martínez⁴ that Tilia (sirimo) trees are sought by Mexicans for the wood, which they prize highly and work into bowls and other wooden utensils. When the trees are cut down, they sprout freely from the stumps as in other species of Tilia; hence, the periodic cuttings do not exterminate the trees, although they are often severely pruned by browsing livestock, particularly goats and burros.

---

V. REFERENCES

List of Numbered Exsiccate\textsuperscript{1}

Adams, J. W. — 3615, 5536, 5929, 9313 (AM); 8114 (HET)
Adams, J. W., & Wherry, E. T. — 2364 (HET)
Adams, J. W., & Adams, M. L. T. — 1394 (HET)
Aikman, J. M. — 1803, 1804 (AM)
Albertson, F. W. — 202 (AM)
Allison, A. — 322 (CAR)
Altamirano, F. — 524 (MEX)
Anchors, G. B. — 8, 71 (CAR)
Arsène, G. — 2534, 2664, 5355 (MEX)
Arthur, J. C. — 9015 (AM)
Ashe, W. W. — 43, 97, 181, 193a (HET); 2, 7a, 9, 27, 32, 35, 37, 41, 43, 60, 111, 138 (CAR)
Auer, B. — 3028 (AM)
Bailey, J. A. — 520 (AM)
Barnhart, J. H. — 1586 (AM)
Bartholomew, Elizabeth A. — 40, T-36 (AM); 040, 205, 919, W-3213 (HET)
Bartholomew, Elizabeth A., & Fry, Mildred C. — B-156 (AM); B-216 (HET)
Bartley, F., & Pontius, L. L. — 793 (HET)
Bauer, B. — 2686 (AM)
Beckett, Mary R. — 482 (HET)
Bell, F. H. — 396 (HET)
Benke, H. C. — 4936 (AM)

\textsuperscript{1}AM: \textit{Tilia americana}; CAR: \textit{T. caroliniana}; HET: \textit{T. heterophylla}; MEX: \textit{T. mexicana}. 

106
REFERENCES

Benner, W. M. — 6765 (AM)
Bergman, H. F. — 972, 1907, 2851 (AM)
Berkheimer, D. — 3256, 5069, 14141, 16196 (AM); 5457, 13952 (HET)
Berkley, E. E. — 1555, 1717 (HET)
Bicknell, E. P. — 5743 (AM)
Biltmore Herbarium — 3571a (HET); 4699a, 4699d (CAR)
Bissell, C. H. — 4401 (AM)
Blair, E. — 10-102 (AM)
Blakley, O. W. — 3449 (AM)
Boone, W. — 175 (HET)
Botteri, M. — 95 (MEX)
Bovce, S. G. — 1003 (CAR)
Boynton, C. S., & Harbison, T. G. — 3571a (CAR)
Brannon, M. A. — 278 (AM)
Bray, W. L. — 110 (CAR)
Brinker, R. — 1225 (AM)
Brinkley, Elizabeth — 218 (CAR)
Brown, C. A. — 2135, 5793, 6556 (CAR)
Brown, H. P. — 5158 (AM); 8343 (HET)
Brown, S. — 4128 (AM)
Brubaker, Ethel — 595 (AM)
Buchholz, J. T. — 957 (CAR)
Buell, J. H. — 70 (HET)
Bush, B. F. — 101, 3211, 5530, 6351, 9283, 12647, 12656, 13575 (AM); 659, 1062, 5977 (CAR)
Byhouwer, J. T. P., & Kobuski, C. E. — 140 (AM)
Calef, R. T. — 541, 569 (AM)
Capelnor, D. — 551 (HET)
Carlson, Margery — 1390 (MEX)
Chase, V. H. — 661, 1854, 3134, 9017, 11390 (AM)
Clark, H. B. — 8, 23 (AM)
Clarkson, R. B. — 149 (HET)
Clements, F. E. — 2576 (AM)
Cocks, R. S. — 836 (HET); 6, 10, 2528, 4010 (CAR)
Cody, W. J. — 279, 9496 (AM)
Combs, R. — 574 (AM)
Cook, C. C. — C-41, C-110, C-189 (AM)
Core, E. L. — 5264, 5376, 6155 (AM); 5455, 6046, 6515 (HET)
Correll, D. S. — 14180, 15273 (CAR)
Cory, V. L. — 14431, 34754, 54589 (CAR)
Cory, V. L., & Parks, H. B. — 10911 (CAR)
Coulter, T. — 790 (MEX)
Crane, R. — 3034 (AM)
Crookshanks, D. R. — 175 (AM)
Crowl, C. S. — 14 (AM)
Curtiss, A. H. — 5875 (HET); 401a, 401b, 401* (CAR)
Davis, H. A. — 4656 (AM)
Davis, J. — 607, 2216, 2374, 2463, 3156, 3501, 3847 (AM); 1679 (HET)
Davis, L. I. — 55-80 (MEX)
Dayton, W. A. — 803 (HET)
TAXONOMY OF AMERICAN SPECIES OF LINDEN (Tilia)

Deam, C. C. — 1200, 7687, 7779, 7803, S344, S876, S880, 9213, 9651, 9910, 11298, 11306, 11923, 14352, 14491, 14981, 15491, 16128, 16129, 16597, 16871, 20607, 21531, 23753, 31360, 31414, 31462, 32051, 32062, 32202, 34466, 36905, 51911, 52279, 52477 (AM); 13794, 13808, 16050, 16304, 16314, 16475, 16505, 16522, 16575, 16689, 18603, 20607, 21531, 23753, 31360, 31414, 31462, 32051, 32062, 32202, 34466, 36905, 51911, 52279, 52477 (MEX); 13794, 13808, 16050, 16304, 16314, 16475, 16505, 16522, 16575, 16689, 18603, 20607, 21531, 23753, 31360, 31414, 31462, 32051, 32062, 32202, 34466, 36905, 51911, 52279, 52477 (HET)

DeForest, H. P. — G103 (AM)

Demaree, D. — 11450 (AM); 6728, 9506, 9859, 15353, 16124, 17621 (CAR)

DePue, P. — 41 (CAR)


Dieterle, Jennie — 1793 (AM)

Dix, W. L. — 689 (HET)

Dix, W. G. — 479 (AM)

Dore, W. G. — 9177 (AM)

Dreissbach, R. R. — 1411 (AM)

Duncan, W. H. — 1185, 2327, 2776, 2906, 3600, 3655, 5080, 6179, 6462, 7025, S357, S417, S502, S895, 13538 (HET); 5866, 11645 (CAR)

Dreesbach, R. R. — 1411 (AM)

Dunn, W. H. — 1185, 2327, 2776, 2906, 3600, 3655, 5080, 6179, 6462, 7025, S357, S417, S502, S895, 13538 (HET); 5866, 11645 (CAR)

Eames, A. J. — 10289 (AM); 12462 (HET)

Eames, A. J., & Wiegancl, K. M. — 12443, 12445 (AM); 12450 (HET)

Ehrenberg, C. A. — 1289 (MEX)

Elmore, Helen — 4272 (AM)

Erlanson, C., & Erlanson, E. — 1569 (AM)

Evers, R. A. — 1380 (AM)

Fairchild, S. — 7610 (HET)

Fassett, N. C., & Wilson, L. R. — 10016 (AM)

Fender, Flora S., & Ludwig, E. H. — 3672 (AM)

Fernald, M. L., & Long, B. — 14072, 14073, 18742 (AM); S365, 13082 (HET)

Fishe, T. R. — 1623 (AM)

Fogg, J. M. — 12318, 12495, 14905, 15933, 20622 (AM)

Fosberg, F. R. — 16002 (AM)

Fox, W. B. — 308, 634, 675, 736, 741, 788 (HET); 538, 709, 1358, 1397, 2540, 3598 (CAR)

Fox, W. B., & Whitford, L. A. — 3850 (HET)

Friesner, R. C. — 7555, 22615 (AM)

Fuller, A. M. — 1533 (AM)

Fuller, G. D. — 8975 (AM)

Galeotti, H. — 4158 (MEX)

Gates, F. C. — 3898, 13744, 17525 (AM)

Gates, F. C., & Gates, M. T. — 10345, 10762 (AM)

Gillespie, J. W. — 4871 (HET)

Gillett, J. M., & Calder, J. A. — 6296 (AM)

Gillett, J. M., & Van Rens, L. J. — 9563 (AM)

Gleason, H. A. — 9357 (AM)

Glowenke, S. L. — 5244 (AM); 2921, 4136 (HET)

Glowenke, S. L., & Langman, Ida K. — 2394 (AM)

Godfrey, R. K. — 54967 (HET)

Godfrey, R. K., & O'Connell, J. E. — 51979 (CAR)
REFERENCES

Godfrey, R. K., & Tryon, R. M. — 1153 (CAR)
Goodrum, P. — 76 (CAR)
Graham, H. W. — 27 (AM)
Grasl, C. O. — 2151 (AM)
Gray, A., Redfield, J. H., Canby, W., & Sargent, C. S. — 103 (HET)
Greenman, J. M. — 850, 2406 (AM)
Gress, E. M. — 73, 604, 780 (HET)
Grove, J. H. — 509 (AM)
Grover, F. O., & Horsey, R. E. — 578 (AM)
Guest, Katherine R. — 145 (AM); 340 (HET)
Guttenberg, G. — 401 (AM)
Hambv, H. J. — 1549 (CAR)
Harbison, T. G. — 8, 10, 12, 19, 29, 46, 1552, 1736, 3505, 6418, 7220 (HET); 2, 3, 5, 6, 7, 8, 16, 25, 35, 45, 1908, 2357, 2391, 14319, H-1478 (CAR)
Harper, F. — 1442 (CAR)
Harper, Jean S. — 199 (AM)
Harper, R. M. — 167, 211, 1049, 1302 (HET); 211 (CAR)
Hartweg, K. T. — 276 (MEX)
Haugt, O. — 339 (AM)
Hayden, Ada — 873, 874 (AM)
Hayes, R. P. — 103 (AM)
Hills, Alice — 3402 (AM)
Hinton, G. B. — 820, 1340, 2030, 4120, 8277, 10405, 10475, 15480 (MEX)
Hodgdon, A. R. — 5429 (AM); 3934 (HET)
Horsey, R. E. — 264, 266, 281, 306, 311, 342, 556, 568, 1037, 2089 (AM); 532, 539, 1063, 1118, 1330, 1575, 1606, 1948, 2089, 2314, 2401 (HET)
Horr, W. H. — 4469 (AM)
Jenkins, L. — 8201, 8228 (AM)
Johnstone, P. — 578 (AM)
Jones, G. N. — 12061, 13490, 14929, 18222, 24202, 29982, 31062 (AM); 22530, 22532, 33102 (CAR); 22521, 22522, 22523, 22524, 22525, 22526, 22527, 22534, 22535, 22536, 22537, 22538 (MEX)
Kellogg, J. H. — 25654, 25878, 26001 (AM)
King, R. M., & Soderstrom, T. R. — 5127 (MEX)
Kniepe, Florence — 2610 (AM)
Krotkov, P. V. — 9211 (AM)
Kunz, O. — 2441 (AM)
Lane, H. C. — 114 (CAR)
Langlois, A. B. — 39 (CAR)
Lansing, O. E. — 1603, 4143 (AM)
Lathrop, E. W. — 3119 (AM)
Leavenworth, W. C. — 721 (MEX)
Leavenworth, W. C., & Hoogstraal, H. — 4012 (MEX)
Leeds, A. N. — 2183 (HET)
Le Sueur, H. — 649 (MEX)
Liebmann, F. M. — 502 (MEX)
Little, E. L., & Olmsted, C. E. — 523 (CAR)
Lloyd, C. G. — 1385 (HET)
Long, B. — 6917, 33824, 45740, 4S336 (AM); 1S947, 49207 (HET)
Long, B., & Brown, S. — 112 (AM)
Loughridge, G. A. — 2419 (AM)
Lucy, T. F. — 401 (AM)
Luttman, J. — 608 (HET)
Lyonnet, E. — 2098 (MEX)
MacDaniels, L. H., & Eames, A. J. — 190 (AM)
Mackenzie, K. K. — 532 (HET)
Marie-Victorin, Fr. — 28307 (AM); 56828 (HET)
Marsh, E. G. — 1956, 2305 (MEX)
Martin, P. S. — 39 (MEX)
Martin, R. F. — 252 (AM)
McCoy, Pearl — 1031 (AM)
McDaniel, S. — 1028 (CAR)
McFarlin, J. B. — 5328 (CAR)
McGregor, R. L. — 2449, 10147, 10481 (AM)
McVaugh, R. — 55, 1291, 8803 (AM); 10013, 10265, 10453, 11579, 13428, 14378, 14946 (MEX)
Mexia, Ynez — 2706 (MEX)
Meyer, F. G., & Rogers, D. J. — 2644, 2694 (MEX)
Miller, E. S. — 9016 (AM)
Mills, R. G. — 30 (AM)
Montgomery, F. H. — 658 (AM)
Moore, D. M. — 32343 (HET); 4399, 32514, 51069 (CAR)
Moore, H. E. — 1744 (MEX)
Moore, J. A. — 6540 (CAR)
Moore, J. W. — 13718, 16669 (AM)
Moore, J. W., & Hall, R. B. — 16704 (AM)
Morrison, J. L. — 1096 (AM)
Moyle, J. B. — 561 (AM)
Mueller, O. E. — 4112 (HET)
Nagel, O. — 8058 (MEX)
Nelson, E. W. — 999, 6874, 7044 (MEX)
O'Dell, Louise — 267 (AM)
O'Neill, H. — 1482 (CAR)
Overfield, R. — 28 (AM)
Palmner, E. J. — 6126, 6175, 6180, 6246, 10572, 14877, 15043, 15225, 15250, 15251, 17014, 17085, 17819, 17845, 17986, 18928, 19538, 20329, 20417, 23648, 25379, 25416, 25480, 25720, 27385, 27939, 28502, 28089, 29035, 29980, 30283, 33100, 34844, 35041, 35721, 35733, 35744, 35800a, 35852, 36623, 36901, 39196, 39211, 40584, 40587, 43441, 43628, 43772, 43974, 44555 (AM); 6287,
REFERENCES

Palmer, E. J., & Steyerman, J. A. — 40584 (AM)
Palmer, E[dward] — 118 (MEX)
Pammel, L. H. — 246, 264, 410, 1523 (AM)
Pammel, L. H., & Fisk, V. C. — 248 (AM)
Parks, H. B. — 10726 (CAR)
Parks, H. B., & Cory, V. L. — 23151 (CAR)
Pennell, F. W. — 16378 (AM)
Pohl, R. W. — 5412 (HET)
Potzger, J. E. — 11164 (AM)
Pretz, H. W. — 7253, 7561a, 7886 (AM); 7755 (HET)
Price, D. G. — 36 (AM)
Pringle, C. G. — 3578, 4126, 10185, 10264, 13845, 15610 (MEX)
Quarterman, Elsie, & Keever, Catherine — 58-28 (HET); 4779, 57-163, 57-3054 (CAR)
Raup, H. M. — 7889 (AM)
Ray, J. D. — 6066, 6525, 7069, 8353, 8430 (CAR)
Redfield, J. H. — 5544 (HET)
Rehder, A. — 984 (AM)
Revere, J. — 1915 (CAR)
Richards, D. — 351a (AM)
Richards, E. L. — 54, 623, 935, 3539 (AM)
Ridgway, R. — 544 (AM); 3162 (HET)
Rolland-Germain, Fr. — 30504 (HET)
Rood, A. N. — 2 (AM)
Rood, A. N., & Simon, W. — 487 (AM)
Rose, J. N., & Hough, W. — 4398 (MEX)
Rosendahl, C. O. — 7361 (AM)
Rossbach, G. B. — 1046 (AM)
Roy, E. — 1784, 1966, 3205 (AM)
Ruth, A. — 2593 (HET)
Schaeffer, R. L. — 2150, 6373, 49128 (AM); 26507 (HET)
Schallert, P. O. — 21185 (CAR)
Schuster, R. M. — A-7130 (HET)
Seoggan, H. J. — 10559, 10670, 11451 (AM)
Senn, H. A. — 1805, 1994 (AM)
Senn, H. A., & Zinck, M. N. — 477 (AM)
Seymour, F. C. — 28, 15753 (AM)
Shacklette, H. T. — 102 (HET)
Shanks, R. E. — 16099 (HET)
Shantz, H. L. — 120 (AM)
Sharp, A. J. — 3245, 3763 (HET); 41536, 45378, 45541, 45841, 46157, 46210, 46212 (MEX)
Sherff, E. E. — 1941 (AM)
Shields, J. K. — 135 (AM)
Shinners, L. H. — 15368 (CAR)
Shirley, J. C. — 1638 (AM)
Simkins, G. D. — 932 (AM)
Skeels, H. C. — 390 (AM)
Skinner, H. J. — 37 (AM)
Small, J. K., & Wherry, E. T. — 11970 (CAR)
Smith, E. C. — 15872 (AM)
Smith, H. H. — 787, 6919, 7314 (AM)
Smith, R. H. — 7283 (HET)
Soper, J. H., & Burcher, R. P. — 2002 (AM)
Soper, J. H., & Dale, H. M. — 4042 (AM)
Spangler, R. C. — 219 (HET)
Sparling, S. — 880b (AM)
Spike, B. — 8285 (AM)
Steele, E. S. — 78, 230 (HET)
Stevens, G. W. — 2171, 2669 (AM)
Steyermark, J. A. — 9861, 12023, 12584, 21393, 24126, 24676, 27484, 27840, 28961, 41367 (AM)
Stone, W. — 1596, 1752, 3242, 8617 (AM); 6659, 7084, 8542 (HET)
Straw, R. M., & Forman, M. — 1880 (MEX)
Svenson, H. K. — 10373 (HET)
Taylor, Mary — 254 (MEX)
Taylor, N. — 993 (AM)
Thomason, G. L. — 9 (CAR)
Thone, F. — 221 (AM)
Thorne, R. F. — 7283 (HET); 6668a (CAR)
Thorne, R. F., & Muencher, W. C. — 8610 (HET)
Tidestrom, I. — 4835 (HET)
Tolstead, W. L. — 541 (AM)
Tosh, J. P. — 87 (HET)
Totten, H. R. — 2 (HET)
Travis, Mildred T. — 1690 (HET)
True, R. H. — 6011 (AM)
Turner, L. M. — 241 (AM)
Twining, A. — 25 (HET)
Volle, L. D. — 326 (AM)
Wade, D. E. — 962 (HET)
Wagner, P. R. — 693, 8559 (AM); 5487, 8742 (HET)
Wahl, H. A. — 2701, 5153, 14362, 15970 (AM); 3959, 6218, 16S34, 17S34 (HET)
Ward, D. B. — 863 (AM)
Weatherby, C. A. — 5074 (AM)
Webber, H. J. — 5479, 5480 (AM)
Webber, C. — 45 (AM)
Wehmeyer, L. E. — 709 (HET)
Welch, Winona — 333a, 4884 (AM)
Welch, Winona, & Price, Gladys — 3948 (AM)
Westerfeld, W. F. — 1241 (AM)
Wharton, Mary E. — 1037, 192S, 98S0, 10S13, 10S70 (AM); 4530, 5094, 63S6, 9223, 10091, 10900 (HET)
REFERENCES

Wheeler, H. E. — 1362 (CAR)
White, S. S. — 1482 (MEX)
Wilbur, R. L., & Wilbur, C. R. — 1830 (MEX)
Williams, R. M. — 7 (CAR)
Williams, T. A. — 27, 151 (AM)
Wilson, D. — 142 (AM)
Wolf, W. — 36 (CAR)
Woodson, R. M. — 7 (CAR)
Yuncker, T. G. — 531 (AM)

Bibliographic References

Braun, E. Lucy. 1943. An annotated catalog of the spermatophytes of Kentucky. Published by the author, Cincinnati.
—. 1907. Third edition.
—. Letter from Bush to J. K. Small in herbarium NY.
—. 1934. Trees of the southeastern states including Virginia, North Carolina, South Carolina, Georgia and northern Florida. Chapel Hill, N.C.
REFERENCES

Elliott, S. 1824. A sketch of the botany of South Carolina and Georgia, vol. 2. Charleston, S.C.
Green, Charlotte. 1939. Trees of the South. Chapel Hill, N.C.
———. 1907. Handbook of the trees of the northern United States and Canada east of the Rocky Mountains. Lowville, N.Y.
REFERENCES


Miller, P. 1768. The gardener's dictionary, ed. S. London.


—. 1940. Second edition, revised and enlarged.

Robinson, B. L., & M. L. Fernald. 1908. A handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada (Gray’s New manual of botany, ed. 7). New York.
—. 1926. Third edition.
REFERENCES


Stevens, O. A. 1950. North Dakota plants. Fargo, N.D.


TAXONOMY OF AMERICAN SPECIES OF LINDEN (TILIA)

Plate 1

*T. americana* L., Horseshoe Bottom Overlook, Peoria Co., Illinois, V. H. Chase 17391, ILL.
Plate 2
*T. americana* L., Princeton, Bureau Co., Illinois, V. H. Chase 16644, ILL. (Lower surface of leaf.)
Seedlings of *T. americana* L., showing cotyledons. Lodge Park, near Monticello, Piatt Co., Illinois, G. N. Jones 32972, ILL.
Plate 4

*T. palmeri* Bush ex F. C. Gates, Junction City, Geary Co., Kansas, F. C. Gates 21236, KSC.
Plate 5

*T. heterophylla* Vent., 4 miles E. of Raven Fork, Qualla Indian Reservation, North Carolina, W. B. Fox 788, ILL.
Plate 6

*T. heterophylla* Vent., same collection data as Pl. 5. (Lower surface of leaf.)
Plate 7
*T. caroliniana* Mill., Hot Springs National Park, Arkansas, D. Demaree 47638, ILL.
Plate 8
Isotype of *T. floridana* Small, Jackson Co., northwestern Florida, A. H. Curtiss 401*, KANU.
Plate 9

Isotype of *T. australis* Small, Blount Co., Alabama, H. Eggert, MBG.
Plate 10
Type of *T. pubescens* var. *aitonii* f. *heteromorpha* V.Engler, Lake City, Columbia Co., Florida, G. V. Nash, NEB.
Plate 11
Topotype of *T. leucocarpa* Ashe, Greensboro, Hale Co., Alabama, S. A. Dew 42, MBG.
PLATE 12
Isotype of *T. crenoserrata* Sarg., Oviedo, Florida, T. L. Mead, 1910, MBG.
Plate 13
Isotype of *T. floridana* var. *hypoleuca* Sarg., near Cotter, Marion Co., Arkansas, E. J. Palmer 5943, F. (Lower surface of leaf.)
Plate 14
Type of *T. cocksii* Sarg., Lake Charles, Calcasieu Parish, Louisiana, C. S. Sargent & R. S. Cocks 4922, NY. (Lower surface of leaf.)
Plate 15
Isotype of *T. phanera* Sarg., Boerne, Kendall Co., Texas, E. J. Palmer 10325, MBG.
Plate 16
Isotype of *T. leucocarpa* f. *attenuata* Ashe, Greensboro, Hale Co., Alabama, S. A. Dew et al. 41, ILL.
Plate 17

Lectotype of *T. mexicana* Schlecht., Mexico, Schiede, LE.
Plate 18
Isotype of T. mexicana Schlecht., Chiconquiaco, Mexico, Schiede, GOETT.
Plate 19

*T. mexicana* Schlecht., Nevado de Colima, Jalisco, Mexico, R. McVaugh 14946, ILL.
Plate 20

*T. mexicana* Schlecht., 7 miles S. of Patzcuaro, Michoacán, Mexico, G. N. Jones 22535, ILL.
Plate 21

*T. mexicana* Schlecht., same collection data as Pl. 20. (Enlargement of section of sheet.)
Type of *T. houghi* Rose, Cuernavaca, Morelos, Mexico, J. N. Rose & W. Hough 4398, US. (Lower surface of leaf.)

Cotype of *T. occidentalis* Rose, Patzcuaro, Michoacán, Mexico, C. G. Pringle 4126, NY. (Lower surface of leaf.)
PLATE 23

*T. houghi* Rose, Cuernavaca, Morelos, Mexico, C. G. Pringle 10264, SMU.
Plate 24
*T. pringlei* Rose, Monterrey, Nuevo León, Mexico, C. G. Pringle 15610, MICH.
Plate 25
Type of *T. ambigua* Sarg. ex Bush, Orizaba, Veraeruz, Mexico, M. Botteri 63, US. (Lower surface of leaf.)
Type of *T. rotunda* Bush, vicinity of Morelia, Michoacán, Mexico, G. Arsène 2664, AA. (Lower surface of leaf.)

Isotype of *T. sargentiana* Bush, Cuernavaca, Morelos, Mexico, C. G. Pringle 10264, N.Y. (Lower surface of leaf.)
Type of *T. patzcuaroana* Bush, Patzcuaro, Michoacán, Mexico, C. G. Pringle 3578, AA. (Lower surface of leaf.)

Type of *T. coahuilana* Bush, Monclova, Coahuila, Mexico, E. Palmer 118, US. (Lower surface of leaf.)
Type of *T. roseana* Bush, Chico, Mexico, C. A. Ehrenberg, NY. (Lower surface of leaf.)
Plate 29

*T. cordata* Rose (isotype of *T. roscana* Bush), Honey Station, Hidalgo, Mexico, C. G. Pringle 10800, MICH.
PLATE 30
Isotype of *T. arsenei* Bush, Rincón, vicinity of Morelia, Michoacán, Mexico, G. Arsène 2534, AA.
INDEX TO PLANT NAMES

Acer, 18, 37  
rubrum, 18  
saccharum, 18, 61  
Alnus, 34  
Betula, 34  
lutea, 18  
Broussonetia, 34  
papyrifera, 96  
Carpinus, 18, 37  
Clappertonia, 15  
Corehors, 8, 15  
capsularis, 8  
olitorius, 8  
Corylus, 18, 37, 38  

*Diplopetaloidae*, 22  
*Entilia*, 22  

Fagus, 18, 37  
Fraxinus, 18, 37  
americana, 19  

Grewia, 8, 15  

*Haplopetaloidae*, 22  

*Lindnera*, 9, 22  
*Linnaea*, 3  
*borealis*, 3  
Liquidambar, 92  
Lobelia, 3  
Morus, 34, 96  
*alba*, 65  
*microphylla*, 34  
rubra, 82, 96  
symmetrica, 34  

Pinus, 92  
strobus, 18  
Platanus, 92  
*aspera*, 37  
Populus, 34, 96  
*balsamoides latifolia*, 39  
*scudderii*, 39
TAXONOMY OF AMERICAN SPECIES OF LINDEN (TILIA)

Quercus, 92
- robur, 18
- rubra, 18, 61

Sparmannia, 8

Tilia
- subgen. Filura, 9
- subgen. Nepara, 9
- sect. Anastreae, 21, 25
- sect. Astrophilyra, 21, 25
- subsect. Ebarbulatae, 21, 25
- subsect. Macranthae, 21, 25
- subsect. Reticulare, 21, 25
- subsect. Trabeoculares, 21, 25
- alabamensis, 82, 85, 94
- var. oblongifolia, 85
- alaska, 33, 37
- alba, 23, 66, 67, 115
- ambigua, 97, 103, 146
- americana, 28, 79
- americana, 12, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 27, 28, 29, 30, 32, 33, 34, 35, 36, 37, 38, 41, 42, 43, 44, 45, 46, 48, 60, 61, 62, 63, 64, 65, 77, 79, 80, 81, 82, 91, 95, 96, 106, 113, 115, 116, 122, 123, 124
- var. scabra, 45
- f. microphylla, 45
- var. β vestita, 45
- var. vestita, 45, 60
- f. divaricata, 45
- var. β walteri, 80
- amurensis, 15, 19, 20, 21
- antiqua, 37
- apposita, 68
- argentea, 63
- arsenei, 98, 101, 151
- ashei, 28, 85
- aspera, 32, 34, 37
- australis, 81, 94, 130
- baroniana, 21
- canadensis, 44
- caroliniana, 66
- caroliniana, 19, 20, 21, 22, 23, 24, 25, 27, 28, 29, 30, 35, 36, 42, 46, 62, 64, 65, 68, 69, 77, 78, 79, 80, 81, 82, 84, 85, 91, 92, 93, 94, 95, 96, 106, 128
- var. floridana, 82
- X heterophylla, 16, 68, 71, 78
- var. lata, 69
- X mexicana, 16
- var. rhoophila, 83
- var. vagans, 82, 97
- chinensis, 19, 21
- coahuiliana, 97, 148
- cocksii, 83, 85, 86, 135
- cordata, 98, 150
- var. japonica, 22
- cordata, 12, 15, 17, 18, 19, 20, 21, 25, 98
- X platyphyllos, 15
- crassipilosa, 32, 34, 37
- crassipilosa, 28, 83, 85, 89, 133
- var. acuminata, 85
- cretacea, 33, 37, 38
- dasyphylla, 19, 20, 21
- dictyoneura, 19, 21
- distans, 88
- dubia, 32, 34, 38
- eburnea, 67, 68, 82
- lasioclada, 69
- europaea, 3, 9, 15, 19, 20, 60
- floridana, 27, 28, 29, 46, 64, 81, 82, 83, 84, 85, 86, 88, 92, 93, 94, 96, 97, 104, 165, 129
INDEX TO PLANT NAMES

var. alabamensis, 85
var. australis, 83
var. floridana, 83
var. hypoleuca, 83, 134
var. oblongifolia, 83
var. porracea, 86
fulva, 28
georgiana, 84
var. crinita, 84
var. macrophylla, 46
var. macrophylla, 46
var. neglecta, 46
glauca, 44
gratia, 80
grewioides, 32, 33, 38
grosseserrata, 84
henryana, 19, 21
hesperia, 34, 37
heterophylla, 12, 19, 20, 21, 22, 23, 24, 25, 27, 28, 29, 30, 34, 35, 36, 42, 45, 62, 66, 67, 68, 69, 76, 77, 78, 79, 81, 92, 95, 96, 97, 106, 126, 127
var. alba, 67
var. amphibola, 68
var. michauxii, 60, 62
var. michauxii, 60, 86
var. microdonta, 67
nigra, 23
var. nivea, 69, 71, 78
tenerea, 69
houghi, 97, 102, 105, 143, 144
hypoleuca, 84
maequisalis, 32, 38
incerta, 32, 38
insularis, 15, 19
intonsa, 19
jacksoniana, 32, 33, 38
japonica, 19, 21, 22, 34, 38, 39
× kinsiana, 16
kiusiana, 19, 21, 22
lasiocladia, 68
lata, 69, 78
latifolia, 44
laxiflora, 21, 22, 46, 80
leptophylla, 22, 68, 80, 81
leucocarpa, 28, 81, 82, 85, 86, 94, 132
f. attenuata, 85, 87, 137
brevipedunculata, 85
var. brevipedunculata, 85
var. cockii, 85
glaucescens, 85
littoralis, 28, 83
var. discolor, 83, 89
longifolia dentata, 44
longipes, 97, 103
macrophylla, 45
malungreni, 32, 33, 38
mandshurica, 18, 19, 21, 34, 37
maximowicziana, 15, 19, 21, 22
var. houghi, 97
f. pringlei, 97
var. occidentalis, 97
michauxii, 45, 63, 67, 77
miqueliania, 19, 21, 22, 37, 38
mississippiensis, 80
mongolica, 19, 21
monticola, 29, 68
moreliana, 97
multiflora, 80
neglecta, 15, 22, 27, 28, 29, 44, 46, 60, 62, 63, 64, 69, 77, 83
nelseni, 97, 100, 103
nigra, 22, 44, 60, 63
β barbata, 45
var. α densiflora, 44
var. glauca, 44
var. heterophylla, 67
var. β laxiflora, 44, 80
var. macrophylla, 44
var. vestita, 44
notabilis, 32, 33, 38
nuda, 81, 82, 86, 94
var. brevipedunculata, 82
var. glaucescens, 82
occidentalis, 97, 101, 104, 143
oliveri, 15, 19, 21, 38
oregona, 32, 34, 37, 38
pallida, 85
palmeri, 46, 52, 54, 55, 125
parvulifolia, 32, 39
patzcuaroana, 97, 101, 148
paucicostata, 19, 21, 39
pedunculata, 34, 37
pendula, 21
perplexa, 84
pertomentosa, 98
petiolaris, 15, 19
phauera, 84, 96, 136
  var. scabra, 84, 94
platyphyllos, 15, 17, 18, 19, 20, 21, 25, 62, 68, 96
  var. cordifolia, 96
populifolia, 32, 33, 34, 39
porracea, 84, 85, 88
pringlei, 97, 102, 145
pubescens, 21, 22, 23, 24, 27, 44, 68, 78, 79, 80
  var. aitonii. 81
    f. glabrata, 81
    f. heteromorpha, 81, 131
    f. truncata, 67
  var. leptophylla, 23, 80
  var. venenatii, 81
    f. gymnuophylla, 81
roseana, 98, 100, 149, 150
rotunda, 97, 101, 147
rotundifolia, 23, 66, 67
rubra, 21, 24, 25
sachalinensis, 38
sargentiana, 97, 102, 147
scudderi, 32, 39
sibirica, 21
speciosissima, 32, 33, 38, 39
stenopetala, 80
tenusa, 68
tetraforaminites, 32, 34, 39
texana, 84, 96
  var. grosseserrata, 84
tomentosa, 19, 21, 25, 63, 66, 67
truncata, 22, 80
tuan, 15, 19, 21
velutina, 45, 61
venulosa, 28, 82, 84, 89
  var. multinervis, 82
vescipites, 32, 34, 39
vulgaris, 15
  × vulgaris, 15
weedii, 32, 33, 39
Tiliaephyllum dubium, 38
Tillandsia, 92
Triumfetta, 8, 15
Tsuga canadensis, 18
Viburnum, 33, 37, 38, 96
  antiquum, 37
Vitis chaneyi. 37