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STUDIES OF LEAVES OF MODERN PLATANACEAE, CERCIDIPHYLLACEAE, AND TETRACENTRACEAE AND COMPARISON WITH PLATANUS-LIKE AND CERCIDIPHYLLUM-LIKE LEAVES IN THE BLACKHAWK FORMATION, LATE CRETACEOUS, UTAH

presented by

David Henry Huber

has been accepted towards fulfillment of the requirements for

Master of Science degree in Botany and Plant Patholgy

Kacle V-Major prof

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BY

David Henry Huber

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Botany and Plant Pathology

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ABSTRACT

STUDIES OF LEAVES OF MODERN PLATANACEAE, CERCIDIPHYLLACEAE, AND TETRACENTRACEAE AND COMPARISON WITH PLATANUS-LIKE AND CERCIDIPHYLLUM-LIKE LEAVES IN THE BLACKHAWK FORMATION, LATE CRETACEOUS, UTAH

By

David H. Huber

The assessment of the taxonomic affinities of fossil leaves of Cretaceous or Tertiary age is dependent upon a careful understanding of any morphologically similar extant To understand the familial affinities and leaves. potential infraspecific variability of some platanoid leaves from the Upper Cretaceous Blackhawk Formation of central Utah, the leaves of four extant species, Platanus Xhvbrida, P. occidentalis, P. racemosa, and P. lindeniana were studied. Cercidiphyllum-like leaves from the same formation were compared to leaves of the extant Cercidiphyllaceae and Tetracentraceae. Heterophyllic patterns in the first three <u>Platanus</u> species were identified and quantitatively described. Several gross morphological and architectural characters follow progressive patterns of change in the heterophyllic series. As previous workers have noted, the Platanaceae can be recognized by a combination of several foliar morphological characters. The Blackhawk platanoid fossils show

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platanaceous affinities and are similar to <u>Credneria</u>. The <u>Cercidiphyllum</u>-like leaves have more features in common with the Tetracentraceae.

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I. INTRODUCTION

Considerable paleotaxonomic work on Cretaceous angiosperms was accomplished in the late 19th Century by such pioneers as Leo Lesquereux (e.g. 1883, 1892) and John Newberry (e.g. 1898). Published floras from this time often covered fossil assemblages that are quite difficult in terms of both diversity of taxa and inadequate preservation. Recent Cretaceous angiosperm studies, while benefitting from a wealthy heritage in these extensively published floras, are finding that many of the early taxonomic assignments are generally in need of extensive revision. Dilcher (1974), Schwarzwalder (1986) and others consider the primary shortcoming of these early studies to be methodological: reliance upon too few characters of unproven systematic value, and uncritical lumping of the fossils into modern taxa. In the past two decades renewed activity, new discoveries, and methodological refinement have provided significant advances in our understanding of Cretaceous flowering plants.

Recent approaches to the paleosystematics of fossil leaves have sought more objective and rigorous methods than those commonly employed by early workers. Hickey (1973, 1979) and Dilcher (1974) have provided a base for standardizing foliar characteristics and Hickey and Wolfe (1975) compiled a survey of diagnostically useful foliar architectural features of many extant angiosperm higher

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taxa. Early angiosperm foliar studies have thereby gained more objective taxonomic criteria, and the fruits of these recent studies are now much more empirically appealing.

This study involves two types of fossil leaves from the Blackhawk Formation, of early Campanian age from central Utah. Parker (1976) made a paleoecological study and floristic inventory of this Cretaceous flora. However, his systematic analysis treated only the ferns, gymnosperms, and two species of palms. The diverse dicot assemblage from the Blackhawk was largely untreated systematically although he did assign tentative names to many of the fossil dicots for use in his paleoecological analyses. Two of the most abundant angiosperm leaf types were assigned by Parker to Platanus and Cercidiphyllum. Coarse preservation and the fragmented nature of most of these fossil leaves limits the scope of analysis of their morphologic features, but some of them do show marginal foliar details, and third and fourth order venation. Several nearly whole leaf impressions are also present.

Platanoid and trochodendroid leaf types (i.e. leaf morphologies suggesting alliance with the Platanaceae and Trochodendrales/ Cercidiphyllales, respectively) are among the most common Cretaceous and Paleogene fossils. Unfortunately, even though they are frequent components of fossil floras, typical taxonomic treatments of them have been ambiguous and unparsimonious, rather than biologically realistic. Concerning the platanoids, Brown (1962) Suggests a synonymy for the Paleocene <u>Platanus raynoldsii</u>

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which includes 38 taxa and encompasses previous generic assignments to <u>Acer</u>, <u>Aralia</u>, <u>Cissus</u>, <u>Populus</u>, <u>Ouercus</u>, <u>Sterculia</u>, and others! Perhaps this is not so surprising considering the enormous phenotypic plasticity of the modern genus <u>Platanus</u>. Brown (1962) laments the situation, "after observing the great variation shown by leaves from living species of <u>Platanus</u>, I am amazed that paleobotanists have had the temerity to describe as many fossil species as they have."

The case for the trochodendroids is also confusing because of the uncritical approach of early workers in regard to leaves with actinodromous and acrodromous venation. Genera such as <u>Populus</u>, <u>Smilax</u>, <u>Zizyphus</u>, <u>Ficus</u>, and others have been frequently confused with the trochodendroids. This situation is indeed complex, and Crane (1984) aptly remarked concerning the numerous late Cretaceous and early Tertiary <u>Cercidiphyllum</u>-like leaves that, "although they exhibit a fundamentally uniform pattern of major venation, the variation in shape and the details of venation pose considerable systematic difficulties."

The objectives of this study are to assess the affinities of several Blackhawk leaf morphotypes to extant Platanaceae, Cercidiphyllaceae, and Tetracentraceae based on a detailed morphological examination of the fossils and leaves from representatives of these modern families. The external morphology of leaves of four species of extant

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Platanus were characterized quantitatively. The leaves of several other species were also examined in less detail. Particular attention was focused on the morphological variability present within individuals of three species of Platanus because the physiognomic plasticity of this genus was found to be more pronounced and of greater regularity, and hence more systematically important, than expected. This foliar heteromorphism was treated in greatest detail for one species, <u>Platanus Xhybrida</u>. The foliar morphology of both living species of <u>Cercidiphyllum</u> and the single living species of <u>Tetracentron</u> were characterized and compared with the Blackhawk trochodendroid fossils. It was hoped that studies of the range of variation inherent in the modern taxa would facilitate recognition and interpretation of the platanoid and trochodendroid fossils.

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II. GEOLOGY OF THE BLACKHAWK FORMATION

The exposures of the Blackhawk Formation from which the plant fossils used in this study were collected occur in the Wasatch Plateau of central Utah (Figure 1). Upper Cretaceous and Lower Tertiary rocks form an escarpment along the eastern edge of the Wasatch Plateau which extends from Price River south to Salina Canyon, Utah. The Blackhawk Formation and the Castlegate Sandstone together form the upper part of the Wasatch Plateau escarpment. They also form the major cliffs of the Book Cliffs, a continuous, pronounced escarpment extending for nearly 200 miles from central Utah to Grand Junction, Colorado (Parker Outstanding profiles of the sedimentary facies 1976). deposited by the epicontinental seas are afforded by the Cliffs which, in many places, run approximately normal to the ancient strand line.

The sedimentary facies of the Blackhawk Formation were deposited in response to transgressive--regressive movements of the epicontinental Western Interior Seaway and the associated river systems which flowed eastward from the western highlands into the sea. Young (1966) identified several environmental belts which paralleled the western edge of the epicontinental sea from offshore marine, through coastal margin, and inland to the western highlands. Particularly noteworthy of these paleoenvironments are the swamps which were responsible for the well known economically important coals of the

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Blackhawk. In the region of study, active coal mining occurs in the Blackhawk Formation and Ferron Sandstone.

The stratigraphic relationship of the Blackhawk Formation to related formations is shown in Figure 2. Detailed descriptions of the stratigraphy and geology of the Blackhawk Formation can be found in Fisher et al (1960) and Spieker (1925).



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Figure 1. Fossil plant collection localities in the Wasatch Plateau. The areal extent of the Blackhawk Formation is indicated by stippling (reproduced from Parker, 1976, Figure 1).







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III. TERRESTRIAL PALEOECOLOGY

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The environments of deposition of the plant-bearing sediments of the Blackhawk Formation as described by Parker (1976) are summarized below.

Identification of the Blackhawk environments of deposition was based upon sedimentological and biological Three fluvial environments were inferred from criteria. the amount of organic content of the sediments, grain size, and unique sedimentary and biological features. A swamp environment was identified by high organic content (darker gray color), abundance of clay silt, the presence of aquatic plants, leaf mats, in situ stumps and roots, and the absence of current structures such as ripple marks or cross-bedding. Point bar environments were distinguished as those with little organic material, fine-grained to coarse sandstone, current structures such as ripples and cross-bedding, and high energy deposition features such as water-worn wood and fragmented leaves. The third fluvial environment differentiated was the bottomland that bordered the fluvial channels. Low-energy deposition in a terrestrial environment, less organic content than the swamps, grain size equal to silt but with some sand and clay, raindrop casts, and invertebrate trails were some of the characteristics used by Parker to distinguish bottomland environments. In general, the bottomlands are intermediate in nature between swamps and point bars.

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In addition to the above criteria Parker (1976) relied upon the abundances of the fossil taxa and their presumed equivalence to modern taxa to reconstruct the paleoecology of these three fluvial environments. A fossil plant importance index consisting of relative density plus relative frequency was tabulated for the commonest species in each depositional environment. Both allochthonous and autochthonous depositional settings are represented by the Blackhawk leaf assemblages.

Since Parker's study, quantitative studies comparing the nature and distribution of modern leaf detritus in allochthonous assemblages to source vegetation have shown specific limitations inherent in these leaf assemblages (Spicer, 1981, Spicer and Wolfe, 1987). Specifically, they have shown that the relative abundances of leaf taxa in an allochthonous assemblage are unlikely to directly represent the relative abundances of the same taxa in the source vegetation. However, Spicer and Wolfe (1987) also showed that the distribution of leaves in even high energy depositional environments (e.g. deltaic deposits) does reflect the occurrence of taxa in a wide range of source communities. Those Blackhawk leaf assemblages of an autochthonous origin, such as the swamp assemblages, would have been subjected to different taphonomic constraints. Probably, these assemblages represent the dominant elements in a flora more reliably than low energy allochthonous deposition.

Parker also recognized that some Blackhawk species,

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particularly angiosperms, may be underrepresented for taphonomic reasons. Therefore, while the importance indices probably identify the commonest species and their distribution, they may be limited as an indication of relative abundance in the source vegetation. Importance indices from allochthonous assemblages could be expected to misrepresent the relative frequencies of the taxa in the source communities to a greater degree than indices from autochthonous assemblages.

The fluvial swamps on the Blackhawk floodplain occupied local basins and were quite variable in size. Some that Parker measured varied from about 50m to more than a mile in extent. The dominant trees of the swamps and their importance values are Seguoia cuneata (43.4), Rhamnites eminens (18.1), Protophyllocladus polymorpha (15.0), Brachyphyllum macrocarpum (13.8), and "Platanus" ravnoldsii (10.8). Poor preservation of angiosperm leaves lead Parker to suggest that Rhamnites eminens could be as abundant as Sequoia. Less frequent trees in the swamps include the conifers Androvettia sp., Metasequoia sp., and Widdringtonites reichii, and angiosperms assigned to the genera Cornus, Salix, Drvophyllum, Myrtophyllum, Ficus, and Though an updated systematic study has not Manihotites. been made to verify the identifications to such taxa, there is substantial evidence of the diversity of the flora inhabiting these swamps.

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palm species. <u>Geonomites imperialis</u> was the most common understory shrub and formed local palm thickets. At the Water Hollow locality erect stems spaced about 2 meters apart, apparently buried <u>in situ</u>, are associated with numerous mats of palm leaves. The other two palms, occurring less frequently, are <u>Paloreodoxites plicatus</u> and <u>Sabalites montana</u>.

Herbaceous understory plants are poorly represented in the paleoswamp flora. No angiospermous terrestrial herbs are recognized although two ferns, <u>Cyathea pinnata</u> and <u>Onoclea hebridica</u>, were part of the understory vegetation but they were infrequent. The paucity of herbaceous plants could be due to either their rarity in the flora, poor preservation, or our inability to recognize them. Two aquatic angiosperms, <u>Nymphaeites dawsoni</u> and <u>Trapa paulula</u>, are also known.

The swamp conifers represented a fairly diverse group. In addition to the more common species mentioned above, <u>Nageiopsis</u>, <u>Podozamites</u>, and <u>Moriconia</u> were also present. The shrubby gymnosperm <u>Nageiopsis</u> was found at only one locality where approximately 1000 oval blades were present. Six of the Blackhawk swamp conifers apparently became extinct by the end of the Cretaceous. Parker (1976) suggested that these conifers were restricted to the fluvial and coastal swamps associated with the epicontinental sea and therefore became extinct when the regression of the seas eventually eliminated the swamps.

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developed on land of slightly higher elevation than the swamps. Four arborescent angiosperms were the most common indicated by their taxa as importance indices: "Cercidiphyllum" arcticum (27.3), "Platanus" raynoldsii (21.2), Dryophyllum subfalcatum (19.0), and unknown dicot #2 (13.4). "Cercidiphyllum" arcticum is the most abundant leaf-type in the entire Blackhawk collection and occurs in nearly every bottomland collecting site. Other angiosperms which were common locally in the bottomlands are coloradensis, Manihotites Laurophyllum georgiana, Mvrtophyllum torrevi, and Phyllites vermejoensis. The curious leaf, Manihotites, is most frequent in bottomland sediments. Conifers are much less important in the Blackhawk bottomlands habitats than in the swamps and include Sequoia cuneata, two species of Protophyllocladus Palms apparently were not an and Moriconia cyclotoxon. important understory constituent in the hardwood bottomlands although Geonomites imperialis did occur there. Vines (Menispermum dauricumoides) may have been present in the understory. As in the swamp community, Osmunda hollicki, a fern, appears to have been the primary herbaceous understory plant.

The third paleoenvironment of the Blackhawk floodplain was the point bars. Point bar sandstones are lens shaped and attained thicknesses of 9m or more, and some of those studied by Parker (1976) ranged up to 275 meters in length. Plant fossils in the point bar sediments generally show the

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effects of high energy transport, including water-worn wood pebbles and fragmented leaves originally deposited as flutsam on accretion surfaces of interlayered crosslaminated and horizontally bedded fine to coarse sand. Most of the taxa found in the point bars are also present in the swamp and bottomland sediments. The gymnosperms, Araucarites and Podozamites are an exception and, in fact, were the most abundant taxa represented by megafossils in the point bar environments. Interestingly, the leafy twigs of Araucarites and leaflets of Podozamites are often present in relatively undamaged condition suggesting that these trees might have grown on or near the point bars. Modern araucarians and cycads are not found on such sites, and Parker (1976) suggested the possibility of a piedmont or upper delta origin for these specimens, especially in light of their durability in transport. In situ roots of unknown affinity also occur in the point bars as they do near the surface of point bars of modern meandering streams.

Balsley and Parker (1983) reported an additional type of swamp environment which occurred between the floodplain swamps and the foreshore. These paralic backshore swamps were characterized by brackish groundwater and sea water spray. Of more than 50 paralic swamps observed by Balsley and Parker, one species of <u>Araucaria</u> was the only plant present. It was apparently rooted in sand with little peat development. Similar environmental conditions are tolerated by four modern species of <u>Araucaria</u> which inhabit

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beaches and rocky shorelines of Australia and New Caledonia (Balsley and Parker, 1983).

Unique opportunity for observing the Blackhawk swamp environment is also afforded by local coal mines. The mine roof shales, which overlie the coal, were the result of rapid deposition in the swamp by overbank sediments (Balsley and Parker, 1983). This <u>in situ</u> burial preserved remarkable features of the swamp forest floor which are visible in the roof shales of the mines following coal extraction. Perhaps most impressive of these fossils are the many tree bases and hundreds of dinosaur tracks.

The bases of trees preserved in situ as vitrain are common in some Blackhawk coal mine roofs. Five distinct types of tree bases, distinguished by the size and form of the radiating roots, have been recognized. Palm stumps occur in groups in some mines in conjunction with abundant palm leaf litter (Geonomites imperialis). Balsley and Parker (1983) suggest that the most common types of tree bases may represent several types of conifers. More than 500 of these stumps have been observed and in one section of mapped roof they occurred with a density of about 395 The largest specimen of a stump/root trees per acre. system is an individual with a trunk nearly 3 meters in diameter, roots 1 meter in diameter near the trunk, and a total root spread of 8.5 meters. Tree trunks, lying horizontally on the original peat surface, are also common in certain mine roofs.

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Numerous dinosaur tracks occur in many Blackhawk coal mine roof shales, usually in association with fossil tree stumps (Balsley and Parker, 1983). A five-toed, a fourtoed, and five types of three-toed tracks have been observed. Occasional short trackways of bipedal dinosaurs are obvious although most tracks are too congested to distinguish the movements of one animal. Quadruped tracks may have been present but were not discernable. Balsley and Parker (1983) reported that they had seen several thousand dinosaur tracks and that every observed occurrence of fluvial overbank sediments overlying coal contained tracks.

A paleoclimatic interpretation of the Blackhawk region was proposed by Parker (1976). His interpretation utilized leaf physiognomy and fossil wood rather than the "ecological equivalence" method where climatic tolerances of fossil taxa are inferred from the climatic tolerances of presumed closest living relatives. The Blackhawk leaves primarily fall into the microphyll and notophyll leaf size classes; the majority of species possessed entire margins and about 40% of the species had drip-tips. In addition to leaves, fossil wood from fluvial sediments and coals exhibited distinct growth rings. Parker (1976) concluded that the paleoclimate was probably subtropical and seasonally dry.

An alternative estimation of the climate of the Campanian of the Western Interior has recently been proposed by Wolfe and Upchurch (1987) and Upchurch and

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Wolfe (1987). Using foliar physiognomy and cuticular analysis, these authors inferred that the late Campanian of the Western Interior had a megathermal climate with subhumid conditions. Both of these concurrent papers also suggested a climate of low seasonality although Wolfe and Upchurch (1987) indicate that this interpretation is based on a preliminary assessment of fossil woods. Several occurrences of Paraphyllanthoxylon, a fossil wood which lacks growth rings, as well as other occurrences of woods with weakly developed growth rings (including a dicotyledonous wood from the Campanian of western Wyoming), were cited by them. The low seasonality aspect of their suggested climate is based on a very small sample of wood and requires much more substantial documentation. In addition, Upchurch and Wolfe (1987) indicate that leaves from the Late Cretaceous are typically smaller than the notophyllous size class, and drip-tips and vine habits are represented by low diversity, in low-middle latitude vegetation (ca 30 to 45 degrees N) from both the eastern United States and southern Rocky Mountains. A high equability climate with a latitudinal temperature gradient of about 0.3 C/1 latitude for the Campanian is also suggested (Wolfe and Upchurch, 1987). Modification of these paleoclimatological interpretations, at least with regard to the Blackhawk setting, is probably necessary because of Parker's (1976) observations of Blackhawk leaves and woods, particularly with respect to the larger leaf

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EARLY FOSSIL HISTORY OF THE PLATANOIDS AND TROCHODENDROIDS

Cretaceous angiosperm studies have been the object of intensified research over the past decade or two. Some of the reasons for the mounting interest have been the discovery of new fossil localities with well-preserved reproductive organs (e.g. Friis, 1984), new understanding of previously known fossils (e.g. Crane and Dilcher, 1984), significant new leaf floras (e.g. Spicer, 1981), detailed stratigraphic control of relevant megafossil assemblages (e.g. Doyle and Hickey, 1976) and renewed interest in floral and faunal changes across the K/T boundary (e.g. Hickey, 1984, and Wolfe and Upchurch, 1986). Both magnoliid and non-magnoliid angiosperms have been found in Cretaceous strata of increasing age. Several symposium volumes have recently focused on the early diversification of the angiosperms (Beck, 1976, Dilcher and Crepet, 1984, and Friis, Chaloner, and Crane, 1987) and at least one symposium (University of Reading, 1988) is scheduled for the near future on the origins and evolution of the Hamamelidae. Prominent in discussions of the radiations and early vegetation of the angiosperms in the Cretaceous and early Tertiary are the platanoid and trochodendroid groups (e.g. Crane, 1989 and Spicer, Wolfe, and Nichols, The following section is a brief overview of the 1987). early fossil history of the platanoids and trochodendroids drawn principally from North American sources.

Evidence for the existence of angiosperms in Early

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Cretaceous rocks is based on leaves, reproductive organs However, different types of angiospermous and pollen. structures do not usually cooccur in specific deposits nor do they present a coordinated sequence of evolutionary development: pollen provides the oldest fossil record of the group; leaves appear later in the Cretaceous; and finally reproductive organs appear in still younger Cretaceous strata. Friis and Crepet (1987) are of the opinion that angiospermous affinities have not been adequately demonstrated for any of the approximatley 20 known pre-Albian reproductive organs that have been associated with angiosperms. However, unequivocal evidence of angiosperms from as early as the Hauterivian is known from fossil pollen (Brenner, 1984; Hughes and McDougall, 1987). The abundance and diversity of fossil angiosperm pollen then increases through the Barremian and Aptian intervals (Crane, 1987). Leaves are first known from Zone I of the Potomac Group of the eastern United States which corresponds to the Barremian-Aptian interval. Few leaf types are known from this locality and those present are generally small with less organized venation (Hickey and Doyle, 1977).

Albian strata are the first to show significant diversity in leaves, flowers, fruits, seeds, and pollen. Friis and Crepet (1987) indicate that flowers, fruits, and seeds are known from both North America and Asia at this time and represent both magnolialean and non-magnolialean plants. Potomac Group rocks from Maryland (Upper Albian)

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The se Group of p Which have have yielded more than 20 different taxa representing various dispersed reproductive organs (Friis, Crane, and Pedersen, 1986, and Crane, Friis, and Pedersen, 1986). Three of the six angiosperm subclasses, Magnoliidae, Hamamelidae, and Rosidae, may be present in these Albian sediments (Friis and Crepet, 1987). Among this Potomac Group material and also from the Cedar Mountain Formation of western Colorado (Dilcher and Eriksen, 1983) are the first occurrences of platanoid flowers. The Potomac Group platanoid fossils consist of unisexual, sessile, spherical heads of staminate and pistillate flowers borne on elongated inflorescence axes (Crane, Friis, and Pedersen, These features plus in situ tricolpate, reticulate 1986). pollen, and cuticle from pistillate inflorescences suggest a close relationship to extant Platanaceae. Other characteristics though are distinct from the modern family: a well developed perianth, floral parts in fives, the absence of dispersal hairs subtending each carpel, and smaller pollen size. The Cedar Mountain fossils are infructescences with elongate axes which bear sessile clusters of fruits (Dilcher and Eriksen, 1983). Friis and Crepet (1987) indicate that some other upper Albian inflorescences which may be platanoid were figured by Brown (1933) and named by him as Sparganium aspensis.

The sequence of leaves from the mid-Cretaceous Potomac Group of Maryland provide a varied array of leaf types which have been used to illustrate the early morphological

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diversification of the angiosperms (Hickey and Doyle, 1977. and Doyle and Hickey, 1976). Middle to late Albian leaves possessed greater physiognomic variability than Aptian to early Albian leaves. Leaf types found in the Albian are pinnatifid and pinnately compound leaves (Sapindopsis), cordate, palmately veined leaves with a serrate margin ("Populus" potomacensis and other trochodendroids), and palmately lobed, palinactinodromously veined platanoids. Hickey and Doyle (1977) show what they believe represents a sequence of increasing advancement for these platanoid leaves. Araliaephyllum obtusilobum, from the upper Aptian (middle Subzone II-B), is classified with the lowest (first) rank of the Potomac Group platanoid leaves because secondary veins are only moderately regular. its Stratigraphically higher, upper Subzone II-B contains the platanoid "Sassafras" potomacensis which possesses greater regularity than A. obtusilobum in its secondary and tertiary veins (second rank). Highest in the Potomac sequence (Subzone II-C and Zone III) are the platanoids with percurrent tertiary veins and more ordered quaternary veins (third rank leaves) which are named Araliopsoides cretacea. Hickey and Doyle (1977) note that unlobed, pinnately veined platanoid leaves similar to those from the Dakota Group of Kansas (Protophyllum, Betulites, and in other presumably correlative Populites) occur localities. That some of the Potomac Group platanoids are closely related to extant Platanaceae has been confirmed by the cuticular studies of Upchurch (1984). Although

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considerable attention has been focused on the Potomac Group sequence, significantly greater diversity of platanoids is known from the upper Albian of western Kazakhstan, USSR (Schwarzwalder, 1986). Kutuzkina (1974) reports that these Russian sites contain six species of <u>Platanus</u>, two species of <u>Credneria</u>, and one species each of <u>Protophyllum</u> and <u>Pseudoaspidiophyllum</u>.

By the Cenomanian angiosperms accounted for approximately 75% of the taxa of megafossil assemblages, remaining at about this level through the early Tertiary (Crane, 1987). A major radiation of magnoliids occurred in the Cenomanian, and many of the megafossil floras were dominated by platanoids and related hamamelids (Crane, 1987). Typical of the platanoid-hamamelid group are leaves assigned to Aralia, Betulites, Platanus, Sassafras, and Viburnum from the Dakota Sandstone Flora of central Kansas Indeed, the abundance of platanoid-(Crane, 1987). hamamelid foliage in the mid-Cretaceous is readily seen by a perusal of various published floras such as Berry (1916), Lesquereux (1874, 1892) and Hollick (1930) for North America or Kutuzkina (1974) for the USSR. Schwarzwalder and Dilcher (in press) revised the status of thirty two species of Cenomanian Platanaceae using phenetic analysis and erected or emended five genera (Dischidus, Eurylobum, Eoplatanus, Credneria, and Aspidiophyllum) to better define this highly variable complex.

An increased diversity and abundance is also true for

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angiosperm reproductive organs from the Cenomanian of North America and Europe (Friis and Crepet, 1987). In addition to apocarpous gynoecia of magnoliidean affinity which already existed, syncarpous gynoecia, cyclically arranged floral parts, and other novel morphologies appeared in the record. Platanoid flowers and other small catkin-like inflorescences were regular elements of the floras; platanoid heads are known from Middle Cenomanian floras in Czechoslovakia (Friis and Crepet, 1987) and elongate axes bearing more than 20 sessile heads (named Platanus primaeva by Lesquereux, 1892) are known from the Cenomanian Dakota Formation (Dilcher, 1979). Friis (1984) reported a remarkably productive site in Sweden where more than 100 angiosperm taxa, consisting of flowers, fruits, seeds and anthers, are present. Among this Swedish material are well-preserved staminate and pistillate platanoid inflorescences identical to those from the Early Cretaceous Potomac Group of Maryland except that the male flowers have thick, conspicuous perianth parts and a unique anther connective (Friis and Crepet, 1987).

The megafossil record of the vegetation of the Cenomanian shows the frequent presence, and occasional dominance, of platanoid and related hamamelid leaves. Major platanoid-containing floras extended across the northern hemisphere from North America to Greenland and Europe and into eastern and central Asia (Schwarzwalder and Dilcher, in press). Hickey (1984) suggests that there may have been two peaks in platanoid diversity in the Late

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Cretaceous. The first peak in diversity occurred in the Cenomanian and included the taxa known as <u>Protophyllum</u>, <u>Aspidiophyllum</u>, <u>Pseudoprotophyllum</u>, and <u>Credneria</u>. The other potential radiation of these leaf types may have occurred in the Maastrichtian. Upchurch and Wolfe (1987), commenting on low-middle paleolatitude megafloras, note only one peak in diversity and abundance for platanoid and inferred platanoid derivatives in the Early Cenomanian.

Platanoid plants probably attained their greatest importance in the vegetation of high latitudes. Alaskan North Slope megafloras, with few exceptions, have been designated as polar broad-leaved deciduous forest (Wolfe and Upchurch, 1987). This unique vegetation type, which has no modern analog, is characterized by low taxonomic diversity, large, thin leaves, low percentages of entiremargined species, some deciduous gymnosperms, and leaf fall controlled by Arctic night (Wolfe, 1985). Temperatures for the North Slope (paleolatitude up to 85 N) during the Cenomanian have been estimated to be about 10 C by Spicer and Parrish (1986). This polar broad-leaved deciduous forest, over the Middle Cenomanian-Late Maastrichtian interval, has low physiognomic diversity with platanoid, "Viburnum", and trochodendroid leaf types (Upchurch and Wolfe, 1987). The platanoid and Protophyllum leaf types attained their greatest diversity in Alaska during the Cenomanian (Spicer and Wolfe, 1987).

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by two taxa known in unusual detail. From the Paleocene of Scotland, Crane et al. (1987) have described a compound leaved plane tree known as <u>Platanites</u> hebridicus. Each leaf is composed of three leaflets: the terminal leaflet is large, trilobed and virtually identical to the leaf blades of extant subgenus Platanus while the lateral leaflets are ovate, asymmetrical and much smaller. Staminate inflorescences have been found associated with Platanites which are also nearly identical to the extant Platanus kerrii except that the achenes differ in being narrowly ellipsoidal rather than obovoid and in lacking dispersal Pollen size and morphology are indistinguishable hairs. from the modern subgenus <u>Platanus</u>. Crane et al. (1987) suggested that similar fossil platanaceous leaves (Platanus appendiculata, Negundo decurrens, Platanus guillelmae, and <u>Cissus marginata</u>) may also be circumscribed by <u>Platanites</u>, but they did not propose any new combinations.

Another early Tertiary plane tree, ranging from the Middle to Late Eocene of Oregon, is currently the most completely documented of any fossil angiosperm taxon. Manchester (1986) described this plane tree on the basis of leaf architecture, stem and petiole anatomy, pistillate and staminate inflorescence morphology, fruit anatomy, and <u>in</u> <u>situ</u> pollen. Reconstruction of the tree is not based on the mutual attachment of organs to one another, but rather on the repeated co-ocurrence of the organs in question. The leaves have palinactinodromous primary venation, deep sinuses separating 5-9 palmately arranged lobes, and were

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originally placed in Aralia (Araliaceae) by Lesquereux Recognition that these leaves belonged to the (1878). Platanaceae was first made by MacGinitie (1941), who reassigned them to <u>Platanophyllum</u>. Recently, Wolfe and Wehr (1987), while retaining the leaves in the Platanaceae, erected a new genus, Macginitiea, for them. Macginitiea angustiloba is the name for the foliage of the plane tree Manchester described from a multiple-organ perspective. Three other species of <u>Macginitiea</u> (<u>M. gracilis</u>, <u>M</u>. whitneyi, and M. wyomingensis) have also been described from the Paleogene of western North America, but the infructescences and dispersed stamen groups found associated with these species are virtually identical to those found with M. angustiloba (Manchester, 1986). Wood of the "M. angustiloba plant" is known as Plataninium haydenii and is nearly identical to modern Platanus wood except for the lack of simple vessel perforations. Pistillate inflorescences and infructescences, consisting of long axes with 10 or more sessile or pedunculate, globose heads, are also guite similar to modern Platanus, but differ in having a well-developed perianth and lacking dispersal hairs on the fruits. An infructescence (Macginicarpa) found associated with M. wyomingensis in the Green River Formation of Colorado contains at least 16 fruiting heads. Staminate inflorescences (Platananthus synandrus) of the "M. angustiloba plant" are similar to Late Cretaceous staminate heads in having 5 stamens per

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floret and a relatively conspicuous perianth. However, <u>Platananthus</u> is distinct from both the Cretaceous platanoids and modern <u>Platanus</u> by having stamens shed in floral clusters held together by intertwining epidermal hairs. Pollen from <u>Platananthus synandrus</u> is distinguishable from modern <u>Platanus</u> pollen only on the basis of its smaller size (Zavada and Dilcher, 1986).

Additional distinct leaf morphologies are also known for other Tertiary Platanaceae. <u>Platanus</u> neptuni has simple, elliptical to obovate leaves with pinnate primary venation which makes it similar to Platanus kerrii, the only extant member of subgenus Castaneophyllum (Walther, 1985, Schwarzwalder and Dilcher, in press). Fruits of P. neptuni, collected from the Miocene of Denmark, are reported by Friis (1985) to be quite similar to modern Platanus achenes. Staminate inflorescences of P. neptuni, although poorly preserved, show features suggestive of both Macginitiea and modern Platanus (Manchester, 1986). Palmately compound leaves are another morphology recently added to the Platanaceae. The genus Dewalguea, from Late Cretaceous and early Tertiary floras, contains several palinactinodromously compound leaf types with suggested affinities to both Fagaceae and Platanaceae (Crane, 1988). Walther (1985) erected <u>Platanus</u> fraxinifolia to accomodate one of the <u>Dewalguea</u> species which closely resembled modern Platanus on the basis of cuticular morphology. Many other species of <u>Platanus</u> from the Tertiary could be mentioned here, including those with leaf morphologies remarkably

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similar to extant <u>Platanus</u>, but such a survey is beyond the scope of this review.

The fossil record of the Cercidiphyllaceae, Tetracentraceae and other members of the Trochodendrales has always been difficult to assess because of the large, heterogeneous, and systematically difficult complex of leaves which require evaluation. The preponderance of leaves known as trochodendroids have been placed in the Cercidiphyllaceae although genera other than Cercidiphyllum are usually erected, especially for Late Cretaceous and Early Tertiary fossils, to accomodate the taxa. The Tetracentraceae have only rarely been recognized as fossils.

Among the new foliar physiognomic types appearing in the Middle-Late Albian interval are trochodendroid leaves which are characterized by a shallowly cordate base, palmate venation, and serrate margins (Upchurch and Wolfe, 1987). Crabtree (1987) reports Trochodendroides from the Middle Albian of the Northern Rocky Mountain region. By Early Cenomanian. the Arctic vegetation, termed "physiognomically stereotyped" by Upchurch and Wolfe (1987), contained a large component of trochodendroids (and platanoids) which had first appeared at middle paleolatitudes. Crane (1989) notes that trochodendroid leaves possibly referable to the Trochodendrales are known from the mid-Cretaceous of Eurasia and North America, including three Potomac Group (mid-late Albian) species,

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"Populus" potomacensis, Populophyllum reniforme, and Menispermites potomacensis. Maastrichtian megafossil floras from the Aquilapollenites province also include significant contributions from the trochodendroids, such as the Nyssidium/Joffrea lineage, the Nordenskioldia lineage, and probable Trochodendrales (Crane, 1987). Muller (1981) places the first occurrence of the Cercidiphyllaceae in the Campanian based upon dispersed pollen. He further noted that only one report of Tertiary <u>Cercidiphyllum</u> pollen is known between the Cretaceous record and the extant genus.

Several fossil Trochodendrales, particularly from the Paleocene, are known from well preserved, multiple organ perspectives. Nordenskioldia, one of the most common reproductive structures from the latest Cretaceous and Early Tertiary of the Northern Hemisphere, is an infructescence consisting of long, branched axes that bear cup-like receptacles which each contain a whorl of about 15 fruitlets (Crane, Dilcher, and Manchester, 1986). Vegetative shoots of the Nordenskioldia plant bear long and short shoots, and the purported leaves of the plant ("<u>Cocculus</u>" flabella) have been identified on the basis of repeated association. Crane (in press) feels that this plant is closely related to the Trochodendraceae.

From the Paleocene and Eocene of Britain, Crane (1984) has reconstructed a member of the Cercidiphyllaceae from several organs which have been found to cooccur repeatedly. The "Nyssidium plant", as he has termed it, is known from leaves, infructescences, fruits, and seeds. The leaves are

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known as <u>Trochodendroides prestwichii</u> and constitute up to 80% of the fossil leaves at several localities. An alliance of this plant to <u>Cercidiphyllum</u> is most strongly suggested by the leaves although they do lack a distinct long- and short-shoot system. The infructescences are named <u>Nyssidium arcticum</u> and are like <u>Cercidiphyllum</u> in general follicle construction, including the free nature of the follicles. The lack of easily definable pistillate flowers, winged seeds, and the distinct course of the raphe further link these two taxa. Dissimilarities with the extant genus include an elongated infructescence and various features of the follicles and seeds; staminate inflorescences, flowers and pollen are yet unavailable for comparison.

Similar fruits from the Paleocene of West Greenland have been named <u>Nyssa arctica</u> by Heer in 1869 (in Crane, 1984). Heer (1870) then went on to name five other species of <u>Nyssidium</u> fruits. Crane (1984) regards both of these genera to be conspecific and closely related to his British Paleocene fossils.

Crane (1984) also notes from the literature several occurrences of <u>Cercidiphyllum</u> wood. Wood has been reported from the London Clay, the Upper Miocene of central Washington State, and the Oligocene of Czechoslovakia.

Another remarkably well known fossil member of the Cercidiphyllaceae is <u>Joffrea</u> <u>speirsii</u> which has been collected from the Late Paleocene of Alberta, Canada (Crane

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and Stockey, 1985). This plant is known from pistillate inflorescences with attached carpels, folliculate infructescences, seeds, seedlings, leaves, shoots and possibly staminate inflorescences. As with the <u>Nyssidium</u> plant, several characters, including inflorescence, follicle, and seed features, distinguish <u>Joffrea</u> from <u>Cercidiphyllum</u>. Particularly noteworthy is the presence of over 8000 seedlings of <u>Joffrea</u> at the Joffre Bridge locality in Alberta (Stockey and Crane, 1983). Associated sediments at this locality also contain <u>Platanus</u> leaves (including seedlings), <u>Glyptostrobus</u>, <u>Metasequoia</u>, <u>Equisetum</u>, and <u>Azolla</u>. It has been suggested that plants of the <u>Cercidiphyllum/Joffrea/Nyssidium</u> complex were opportunistic colonizers on the Paleocene floodplains (Crane and Stockey, 1985).

Other Cercidiphyllum-like leaves have been collected from western Canada by Bell (1949) and Chandrasekharam (1974). Bell assigned the name Trochodendroides arctica to his Upper Cretaceous leaves, while Chandrasekharam recognized three species, <u>Cercidiphyllum</u> genesevianum, <u>C</u>. cuneatum, and C. flexuosum, from the Paleocene Paskapoo Hickey (1977) Formation of Alberta. reported Cercidiphyllum genetrix from the Early Tertiary Golden Valley Formation. He found this taxon to exhibit greater foliar variability than extant <u>C. japonicum</u>. Tanai (1981) has reported both Cercidiphyllum and Tetracentron from the Paleogene of northern Japan, and commented that Cercidiphyllum-like leaves are abundant in the Tertiary of

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MATERIALS AND METHODS

The fossil collections used in this study were made by Parker (1976) and others from the Blackhawk Formation of central Utah. Nearly 7500 specimens were collected by him and utilized in reconstructing the paleoenvironments of the Blackhawk. Precise locality and stratigraphic information can be found in Parker (1976). The Blackhawk "flora" is both large in number of species and diverse, with Parker (1976) recognizing one thalloid-type plant, one club mosslike plant, fourteen ferns, twelve gymnosperms, and eightysix angiosperms of which five are monocots. The fossil leaves designated by Parker as Platanus and Cercidiphyllum are the most abundant of the angiosperm fossils. Additional collections were made in the Blackhawk Formation at several of Parker's previous localities in the summer of 1985 to supplement existing material. Leaves of extant members of the Platanaceae, Cercidiphyllaceae, and Tetracentraceae were examined from individuals collected on the campus of Michigan State University or from specimens in the herbaria of Michigan State University and University of Michigan. Platanus racemosa leaves were collected from native trees in northern California.

The state of preservation of the fossils has been an important limitation in this study. High energy transport and deposition has resulted in the fragmentation of most leaves. In some cases, coarse grain size has not allowed the preservation of very fine features such as ultimate

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venation. In other cases, for example the majority of <u>Cercidiphyllum</u>-like leaves, preservation in siltstone has still generally failed to record ultimate venation. Another problem with the <u>Cercidiphyllum</u>-like leaves is that many of them were buried in mats, so that while they can be identified to morphotype, they are mostly unuseable for detailed systematics.

The evaluation of the taxonomic affinities of the fossil leaves in this study requires critical examination of leaf characters within their putative extant families. Characterization of the extant families is based upon both qualitative and quantitative criteria. Parker's entire collection as well as the material from the 1985 field season failed to yield any reproductive organs resembling known Platanaceae, Cercidiphyllaceae, or Tetracentraceae. Therefore, only foliar features were utilized in this study. The quantitative measurements of the modern leaves were made using a millimeter ruler and clear plastic protractor.

Leaf area and perimeter measurements were greatly facilitated by the VICOM image processing facilities of the Pattern Recognition and Image Processing Lab (PRIP) operated by the Engineering Department at Michigan State University. The VICOM image processor can perform many operations on images it acquires directly through a camera, and therefore is a rapid method for dealing with large quantities of leaves. To enter the image of a leaf into the VICOM, pressed leaves were placed on black construction

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paper on the floor beneath the camera. The camera was a Panasonic WV-CD 50 with a Computar TV Lens (1:1.3, 50mm, f stop at 1.3). The camera lens was positioned 186 cm from the leaves and situated at a right angle to them. First, a leaf would be digitized by the VICOM, then an interactive thresholding operation would be performed on it. This process converts the leaf into an image composed of pixels. The VICOM takes this image obtained through thresholding and reports its area and perimeter in terms of pixels. Each image can be 512x512 pixels in size. The thresholding operation introduced the most significant error into the area and perimeter measurements because of the difficulty of recognizing the point (threshold) at which the borders of the digitized image exactly matched the borders of the This error was typically of minor importance. leaf. Repeated measurements were made on every eighth to tenth leaf to assess the variability in the system and the precision of my thresholding operation. Differences in the area of a single leaf ranged only from .35% to 1.5%; differences in the perimeter values for a single leaf ranged from .67% to 24%, although most perimeter values varied between 1 and 7 percent. Perimeter measurements varied to such a degree because the pixels were rectangular and leaf shape varied greatly, especially with respect to the size and number of teeth.

Another feature of this system which proved extremely helpful was the draw facility. This allowed me to "patch"

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holes in the leaves caused by insects, breakage, or poor thresholding by filling in these portions of the digitized lamina. Missing leaf margins were difficult to reconstruct because of the unpredictability of tooth size and spacing. However, the "patching" always returned the leaf image to a state closer to the undamaged original. Area measurements were converted from pixels to millimeters by a conversion factor of one pixel equaling .30821 mm² (.49mm x .629mm). Perimeter measurements were converted from pixels to millimeters by a conversion factor which was the mean of the two unequal sides of a pixel (.5595mm were said to equal one pixel unit length). The petioles of the leaves were excluded from the image that the VICOM analyzed by covering them with black paper so that they matched the background. Appendix B is a copy of the VICOM command file used for these operations.

The leaf architectural measurements made of the fossil and modern leaves follow the terminology of Hickey (1973, 1979). The macroscopic foliar architecture of four extant species of <u>Platanus</u>, <u>Tetracentron sinense</u>, <u>Cercidiphyllum</u> japonicum, and <u>Cercidiphyllum magnificum</u> were described from personal collections or herbarium material. <u>Cercidiphyllum japonicum</u> and <u>C. magnificum</u> have already been described in great detail by Chandrasekharam (1974). Therefore, to avoid unnecessary duplication, his work should be consulted for detailed descriptions of the individual species. I freely drew upon his work to supplement personal observations for making a summary

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statement of the most important foliar features of the Cercidiphyllaceae. Of the four species of <u>Platanus</u> described in detail, foliar heteromorphism was most thoroughly documented in <u>P. Xhybrida</u>. Some attention was also directed at the foliar heteromorphism found in <u>P. occidentalis</u> and <u>P. racemosa</u>, but sucker shoots and inflorescence-bearing shoots were not collected for <u>P.</u> <u>occidentalis</u>, and shoots of <u>P. racemosa</u> became available too late in the study to make detailed measurements of them. <u>Platanus racemosa</u> and <u>P. lindeniana</u> represent platanaceous leaf forms with rather narrow lobes, commonly numbering five, and <u>P. Xhybrida</u> and <u>P. occidentalis</u> represent broader, predominantly three-lobed forms.

Shoots of P. Xhybrida and P. occidentalis were collected in late summer to ensure that maximum leaf expansion had occurred. A mature tree of both species and the sucker shoots from a recently felled tree were used for sampling. Whole shoots were collected rather than individual leaves because of the pronounced heterophylly and heteroblasty exhibited by these species. Dispersed leaves, canopy shoots, and sucker shoots from the base of trees of P. racemosa were collected by Mr. Patrick Fields in northern California.

Eighteen different measurements were taken of the <u>Platanus</u> species and the fossil platanoids. Thirteen different measurements were taken of <u>Tetracentron</u>, <u>Cercidiphyllum</u>, and the fossil trochodendroids. A

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statistical summary of these data is presented in Appendix C. The original data are on file at the paleobotany laboratory at Michigan State University.

Many of the measurements were straightforward, but some require explanation. Leaf length is the maximum length of the lamina; leaf width is the greatest distance between lateral lobes or teeth. The widest distance between lobes refers to the most distal lateral lobe on each side of the leaf, and may or may not correspond to the leaf width measurement. Sinus incision distance refers to the distance from the most lateral point of a lobe to the center of the lobe sinus. Both lobes were measured on each leaf. The unlobed lamina refers to that portion of the lamina which occurs between the point of lamina--petiole conjunction and the sinuses of the upper lateral lobes.

Angles involving the margin of the lamina were difficult to assess because the margins often lacked uniform curves and usually possessed teeth of highly variable size. The two measurements affected by these irregularities are the angles between central and lateral lobes, and the angle of the lamina base. Both of these cases frequently involved the presence of large teeth which tended to obscure the position of the hypothetical untoothed margin that is needed for consistency in measurements. To include the marginal irregularities caused by large teeth would greatly inflate or deflate the desired angles. This problem was countered by measuring across the base of the first tooth to occur on each side of

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The measurements of the central lobe apex included that portion of the apex prior to a noticeable flaring of the lamina which occurred in many Platanus leaves. <u>Platanus</u> teeth were taken to include marginal projections ranging in size from the very small papillate projections of marginal veins to teeth appearing as incipient lobes. The veins of leaves are identified by terminology taken from Hickey (1979) and other sources. Figure 3 illustrates some of the venation terminology and measurements used Appendix A is a glossary of selected terms. here. Spicer's (1986) use of pectinal veins is incorporated here although it is not totally free from ambiguity in some <u>Platanus</u> leaves. The distance to alpha pectinal departure refers to the distance between the juncture of petiole and lamina and the divergence of the alpha pectinal. The angles of divergence of the pectinal and secondary veins were measured using the course of the vein at a point about five millimeters from the vein origin, and did not include the immediate angle of vein departure when that vein was



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Figure 3. Leaves of <u>Cercidiphyllum</u> japonicum (A) and <u>Platanus</u> occidentalis (B) showing some of the leaf architectural terms used in the text: m, distance to midrib; s, sinus incision distance; u, unlobed lamina; a, angle between central and lateral lobes; b, basal angle.

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decurrent. Two measurements per leaf were made for alpha and beta pectinal departure angles, distance to alpha pectinal departure, angle of secondary departure, secondary spacing, and angle between central and lateral lobes. The secondary veins used for measurement were located in the mid portion of the central lobe. Tertiary vein spacing and angles of departure were taken from veins occurring approximately midway between the midvein and the margin of the central lobe in <u>Platanus</u>. Three measurements were taken of tertiary vein spacing and the angles of departure of the abmedial secondary veins.

Three different ratios were calculated to help describe the systematic variation in lamina shape in Platanus. Length/width (l/w) ratios were made from the maximum length and width dimensions. Distance to sinus/distance to midrib (s/m) ratios refer to the distance from the most lateral point of a lobe to the middle of the base of the sinus, and the distance to the midrib from the same point on the lateral lobe. These distances were measured perpendicularly to the midrib. The unlobed lamina/total lamina (u/t) ratio refers to the length of the unlobed lamina (described above) versus the length of the lamina from the point of lamina base--peticle conjunction (i.e. not maximum lamina length) to lamina apex.
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SYSTEMATICS

Foliar characteristics of <u>Platanus</u> X<u>hybrida</u> Brot. [<u>P</u>. X<u>acerifolia</u> (Aiton) Willd.]

The origin of <u>Platanus</u> X<u>hybrida</u>, the London planetree, is apparently unknown. It may be a hybrid between <u>P.</u> <u>occidentalis</u> and <u>P. orientalis</u>, or it may simply be a cultivar of <u>P. orientalis</u> (Voss, 1985).

Pronounced heterophylly occurs in this taxon and will be described in detail following a general description of the leaves. Heterophyllic variation encompasses both gross shape and architectural features and occurs in all of the shoot types.

The leaves of <u>Platanus</u> Xhybrida are principally three lobed but vary considerably in the extent of the development of the lobes. Canopy shoot leaves often have subsidiary basal lobes produced by the beta pectinal veins. These small basal "lobes" are intermediate in size and aspect between large teeth and the lateral lobes. The first seasonal leaves have either a single lobe or large lateral teeth which appear to be incipient lobes. Each leaf in the heterophyllic succession possesses a greater development of lobation. The average angle of divergence between the central and lateral lobes is about 92.3 degrees (range 44 to 131; SE = 2.54; n= 79). Length/width ratios average .924 (range .777 to 1.31; SE = .0136; n= 48).

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shoot can be interrupted by the initiation of an inflorescence. When a shoot produces an inflorescence, usually after its third or fourth leaf, the succeeding leaves exhibit a dramatic shift in gross morphology. Quantification of this developmental change is presented in detail following this general morphological description. In general, though, the point of inflorescence initiation divides the shoot into two segments.

The first leaf of each segment is small and consists of an unlobed lamina. The second leaf in each series does have lateral lobes, but they are small with shallow sinuses. Well developed lateral lobes then appear in the third and succeeding leaves of each (pre- and postinflorescence) segment of a single shoot. Preinflorescence leaves have few teeth compared to postinflorescence leaves. The first leaf of a shoot can be ovate with an obtuse base, acute apex, and many relatively small teeth (Type II shoots), or it may have few, large teeth, an acute apex, and more or less truncate base (Type I shoots and inflorescence shoots). The first two or three leaves of inflorescence shoots can have a squarish appearance due to laminar margins which are roughly perpendicular to the truncate base. The sinuses between the lobes of pre-inflorescence leaves are broad and rounded, while those of the post-inflorescence leaves are narrow and generally extend more deeply into the lamina. The central lobe of any leaf is always larger than the

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lateral lobes and terminates in an acute, often attenuated apex which has an average angle of divergence of 31 degrees (range 16 to 56; SE = 1.388; n= 47). The bases of the leaves are roughly symmetrical and range from obtuse to truncate to very reflexed, and have an average angle of divergence of 219.3 degrees (range 88 to 316; SE = 7.45; n= 47). Margins of the leaves are always toothed; the number of teeth varies greatly and follows consistent patterns. The mean number of teeth per leaf is 35.4, range 8 to 102 (SE = 3.488; n= 48). Teeth are irregularly spaced and are fed by a centric vein which is derived from either the craspedodromous or semicraspedodromous conditions, or from marginal tertiary or guaternary veins. As in the other Platanus species described above, teeth range in size from small papillate projections on an otheriwse straight margin, to large teeth which form a size continuum with the lobes. On each lobe the size of the teeth tend to decrease Teeth are of the typical platanoid type and distally. conform to Hickey's (1979) types B1, B2, C1, C2, and C3; any individual leaf may possess several of these types. Apices of the teeth are often more or less spinose; scalloped sinuses separate the teeth. Petioles have swollen bases which cover axillary buds.

The venation patterns of the first seasonal non-sucker leaves can be pinnate or actinodromous. When they are pinnate, either of the two lowest secondary veins are more strongly developed than the succeeding secondaries, and terminate in teeth which approximate small lobes in size.

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The first Type II non-inflorescence leaves and the first have pinnate post-inflorescence leaves venation. Beginning, then, with the second leaf in a preinflorescence, post-inflorescence, or non-inflorescence shoot sequence a progressive strengthening of the lowermost secondary vein occurs. This first results in the development of alpha pectinal veins (actinodromy), but further strengthening of these basal lateral veins leads to the development of beta pectinal veins (palinactinodromy). The alpha pectinal veins may be as stout as the midveins in later seasonal leaves, are straight to slightly curved, and diverge from the midvein at an average angle of about 45.5 degrees (range 25 to 64; SE = 1.09; n= 62). These lateral primaries may be either basal or suprabasal, and diverge from the midvein an average of .36 cm (range 0.0 to 1.2 cm; SE = .0357; n= 60) from the base of the lamina.

The superior secondary veins can be either eucamptodromous, brochidodromous, craspedodromous, or semicraspedodromous; all four conditions can occur on the same leaf. The angles of divergence for these veins average about 51.7 degrees (range 36 to 66; SE = .6948; n= 62). Abmedial secondary veins diverge from the alpha pectinals and their marginal behavior is like that of the superior secondary veins. Branching of the noncraspedodromous secondary veins near the margin is common and often results in equal dichotomies. However, craspedodromous secondaries infrequently branch near the

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margin, and those that do rarely form equal dichotomies. The most proximal superior secondary veins may branch near the lobe sinuses and connect with the subjacent admedial secondary veins which are nearest to the sinuses. Alternatively, the most proximal superior secondary may terminate in a tooth and one of its tertiary veins may instead form a connection with the subjacent admedial secondary vein. Inferior secondary veins, when present, are very weak. Intersecondary veins, arising from the midvein or alpha pectinals, are of both the composite and simple types.

Tertiary veins vary from simple percurrent to forked percurrent to reticulate and have an average angle of divergence of about 82.1 degrees (range 62 to 92; SE = .6938; n= 93). Spacing of the tertiaries averages about .33 cm (range .15 to .65cm; SE = .0111; n= 93). Even a cursory inspection of these leaves provides a mental impression influenced by the prominence of the simple and forked percurrent tertiaries. Chevrons are also formed by the tertiaries in the axils of the midvein and alpha pectinals, and in the axils of the midvein and superior secondaries, and to a lesser extent in the axils of the pectinals and ad- and abmedial secondary veins. Because the tertiary veins are approximately perpendicular to the secondary veins, they have a longitudinal orientation in the proximal lamina and an oblique to perpendicular orientation in the distal lamina. Quaternary veins are normal in thickness and orthogonal. Quinternary veins are

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normal in thickness, orthogonal, and form well developed areoles. Areoles are usually four or five sided. The marginal ultimate venation consists of looping of quaternary and quinternary veins.

Foliar heteromorphism in <u>Platanus</u> Xhybrida

<u>Platanus Xhybrida</u> was found to exhibit repetitive patterns of foliar heteromorphism along the nodal sequence of a shoot. Distinctive patterns of gross morphological and architectural change were found to occur in shoots bearing an inflorescence, two types of non-inflorescence shoots, and vigorous crown or basal (sucker) sprouts.

Shoots bearing inflorescences which occur more or less in the open crown possess a pattern of foliar development which could be termed a "reset". The leaves of a shoot that bears an inflorescence can be divided into preinflorescence and post-inflorescence leaves. The postinflorescence morphological sequence, beginning with the leaf at the inflorescence node, repeats some of the trends present in the pre-inflorescence leaf sequence, hence the Several different morphological features term "reset". display such predictable trends. The following measurements were taken of leaves of three inflorescencebearing shoots from the same tree. One of these shoots is illustrated in Figure 4.

The most obvious morphological trend concerns lamina

Figure 4. Leaves from shoot 1, described in Figure 5 (<u>P</u>. X<u>hybrida</u>), numbered from the most basal leaf in the sequence.

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Figure 5. Leaf lamina area of ten sequential leaves (numbered from the most basal leaf in each sequence) on two shoots from a single individual of <u>Platanus Xhybrida</u>. An inflorescence was present at the node of leaf 5 on both shoots.



Figure 6. Leaf lamina perimeter measurements for the shoots described in Figure 5 (P. Xhybrida).



Figure 7. Leaf lamina apical angles for the shoots described in Figure 5 (P. Xhybrida).



Figure 8. Leaf lamina basal angles for the shoots described in Figure 5 (P. Xhybrida).



Figure 9. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from shoot 1 of Figure 5 (P. Xhybrida).



Figure 10. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from shoot 2 of Figure 5 (P. Xhybrida).



Figure 11. Number of teeth on leaves from shoot 1 of Figure 5 (P. Xhybrida). "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.



Figure 12. Number of teeth on leaves from shoot 2 of Figure 5 (P. Xhybrida). "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.

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size. Each fully expanded leaf in a sequence is larger than the preceeding leaf (Figures 4, 5, and 13). An inflorescence shoot bears two size sequences, the second one beginning at the inflorescence node and roughly paralleling the incremental changes in size of the preinflorescence leaves (Figures 4 and 5). The angles of the apices of the leaves and the bases of the leaves follow the same reset pattern. The apex angle of each succeeding leaf becomes smaller until the inflorescence node, at which point the leaf apex broadens again, and then gradually narrows through the remaining leaves of the new sequence (Figures 7, 16, and 20). The basal angles of the laminas follow the opposite trend (Figures 8, 17, and 20). Leaf number one and the inflorescence node leaf often begin with a rather truncated base and weakly developed or absent alpha pectinal veins. When present, the alpha pectinals of these first leaves are approximately perpendicular to the midvein. The successive leaves of both pre- and postinflorescence leaves then develop increasingly large basal angles in conjunction with a strengthening of the alpha pectinal veins, and their progressively more acute angle with respect to the petiole. The abmedial secondary veins branching off of the alpha pectinals also increase in strength. Recurving of the leaf base reaches its greatest extent in late season leaves where the recurved lamina bases can actually overlap, forming a basal angle exceeding 360 degrees.

Lamina shapes were also found to change progressively

in terms of length/width dimensions, the size of the lateral lobes, and the depth of the lobe sinuses (Figures 9, 10, 18, 19, 21). Length/width ratios among successive pre-inflorescence and post-inflorescence leaves tended to decrease; that is, the laminae became proportionately wider than long. This is most evident when comparing the first leaf in a sequence to the last. The first leaf has no or very reduced lateral lobes, while the last leaf has strongly developed lateral lobes. The u/t ratio (unlobed lamina length/total lamina length) between successive preand post-inflorescence leaves also decreases. This means that the base of the lobe sinuses of successive leaves approach increasingly close to the base of the lamina. The s/m ratio (distance to sinus/distance to midvein) tended to increase through successive leaves with a reset occurring at the inflorescence node. This indicates that the sinuses between the central and lateral lobes also became increasingly close to the midvein. Because the first leaf of a shoot and the inflorescence node leaf often lack lateral lobation, the graphs of u/t and s/m ratios often lack data points for these leaves. The measurements of the leaves also do not show changes in lamina symmetry. Preinflorescence leaves are fairly symmetrical with respect to the positioning and "balancing" (i.e. size correspondence) of teeth and lobes on each half of the lamina. In sharp contrast, the post-inflorescence sequence begins with the first two leaves being asymmetrical in terms of tooth size

and placement. Symmetry increases progressively and is restored by about the fourth leaf.

The number of teeth found on the leaves of an inflorescence shoot also follows a characteristic pattern (Figures 11 and 12). Pre-inflorescence leaves bear few teeth of generally large size. Occasionally, the only "teeth" present on a leaf of this early sequence are the lobe apices, the remainder of the lamina margin being entire. A slight increase in the number of teeth among successive leaves of pre- and post-inflorescence sequences occurs although the reset pattern does not appear. The post-inflorescence sequence begins with approximately twice the number of teeth as the last leaf of the preinflorescence sequence. Dramatic variation also occurs in the size range of the teeth. Pre-inflorescence leaves generally bear larger teeth with attenuated apices. Postinflorescence leaves also bear large teeth but they have less attenuated apices, and in addition, they often bear many small teeth, including the very small papillate type. Frequently, the first one or two post-inflorescence leaves and the last one or two leaves of the season have the most papillate teeth. Lamina perimeter measurements are useful in indicating the change in tooth size (Figure 6). For pre-inflorescence leaves the progressive increase in perimeter closely parallels the increase in leaf area because all of the teeth are approximately of the same The same situation obtains for the first three or size. four post-inflorescence leaves. However, a change in tooth

size among the leaves from later in the season is shown by the prominent change in perimeter. For example, Figure 6 shows the eighth leaf of two different shoots with the greatest perimeter although it has a comparable area and fewer teeth than either leaves 7 or 9. This is because leaf 8 has more large teeth than either leaf 7 or leaf 9, with the ninth leaf in particular being notable for its many reduced, papillate teeth (Figures 11 and 12). In general, on the longer shoots the number of large teeth peaks on the second or third leaf from the end. The last leaves of the season may have the most teeth, but they are primarily smaller teeth as revealed by decreasing perimeter measurements.

The last one or two leaves produced on a shoot are usually not fully developed before growth slows and stops at the end of the season. This underdeveloped state is evident in the graphs by a reduction in lamina area, perimeter, and the number and size of teeth as compared to the post-inflorescence leaves showing peak development of these features. Shallower lateral lobe sinuses, a less recurved leaf base, and less attenuated leaf apex are also assumed to be the result of incomplete lamina development. Presumably, if these late season leaves were able to mature, they would continue the trends expressed by the fully developed leaves.

Crown shoots that have not borne an inflorescence can be divided morphogically into two types. Type I shoots

(Figure 13) display some of the same patterns as inflorescence shoots whereas Type II shoots are more similar to stump sprouts. In Type I shoots, gross leaf morphology is similar in many respects to the inflorescence shoots although the dramatic "reset" development does not occur. The first three or four leaves of the shoot may or may not have the squarish aspect seen in pre-inflorescence leaves. When the squarish aspect is present, it is because the lamina base is truncated or only slightly recurved, weak lateral lobes are present with their outer margins roughly perpendicular to the base, and the beta pectinal veins are nearly perpendicular to the midvein. Later leaves lose this squarish aspect when the lamina base becomes progressively reflexed (sometimes with the leaf base angle exceeding 360 degrees), the beta pectinals become stronger and form an acute angle with respect to the midvein, and the margins of the lateral lobes angle toward the petiole. When the first leaf is not squarish, it is due to the lack of lateral lobes, resulting in an ovate shape (an appearance reminiscent of the first postinflorescence leaf though more symmetrical). Lamina area may increase in successive leaves of shorter shoots. In the longest shoots examined (10 or more nodes) the lamina area of successive leaves increases until about the median node where it declines and then remains constant.

The number of teeth varies by as much as a factor of ten (Figures 14 and 15). Interestingly, the number of teeth followed a pattern similar to that of inflorescence

Figure 13. Leaves from shoot 4 (Type I, no inflorescence) from the same individual tree as the leaves of Figure 5 (P. Xhybrida); numbered from the most basal leaf in the sequence.



Figure 13







Figure 14. Number of teeth on leaves from shoot 3 (Type I, no inflorescence) from the same individual tree as the leaves of Figure 5 (P. Xhybrida). "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.







Figure 16. Leaf lamina apical angles for leaves from shoots 3 and 4 (Type I, no inflorescence) from the same tree as the leaves of Figure 5 (\underline{P} . Xhybrida).



Figure 17. Leaf lamina basal angles for leaves from shoots 3 and 4 (Type I, no inflorescence) from the same tree as the leaves of Figure 5 (P. Xhybrida).



Figure 18. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from shoot 3 (Type I, no inflorescence) from the same tree as the leaves of Figure 5 (P. Xhybrida).







Figure 20. Leaf lamina apical and basal angles for leaves from a Type II (no inflorescence) shoot of P. Xhybrida.



Figure 21. Unlobed lamina/total lamina (u/t), length/width (l/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from a Type II (no inflorescence) shoot (same as Figure 20) of \underline{P} . Xhybrida.



Figure 22. Number of teeth on leaves from a Type II (no inflorescence) shoot (same as Figure 20) of P. Xhybrida. "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.



Figure 23. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from a stump sprout of <u>P</u>. Xhybrida(?).

shoots: the first three to five leaves had very few teeth, then the number of teeth suddenly increased by three-fold. This increase is primarily due to papillate teeth fed by tertiary or quaternary veins. Tooth size of Type I leaves varies as greatly as in inflorescence shoots although the greatest number of large teeth (those fed by craspedodromous secondaries) only occurs in the distal half of the shoot. Late season leaves have very few secondary veins that do not directly enter teeth.

The angles of the apices do not show a clear pattern, but increase in one case and appear erratic in another (Figure 16). Basal angles, however, do show a conspicuous increase as the beta pectinals increase in strength and angle of departure, and the lamina base grows increasingly reflexed (Figures 17). The l/w ratios of one long shoot initially decrease and then show little change (Figure 19). The l/w ratios of the shorter shoot show a gradual decline which is consistent with that found in inflorescence shoots (Figure 18). The s/m ratios increase in both Type I shoots examined and the u/t ratios decrease (Figures 18 and 19). This indicates a deepening of the lateral lobe sinuses in successive leaves.

Type II shoots begin with narrower leaves (higher 1/w ratios) than the other canopy shoots (Figure 21). Lateral lobes become pronounced by the third leaf and continue to broaden through the sequence in the usual manner. Similarly to leaves of stump sprouts, the teeth do not follow the customary pattern of increasing in number, but

all the leaves have high numbers of teeth (Figure 22). Additional crown shoots need to be collected to assess whether or not trends in tooth number of these leaves exist. Most of the secondary veins in all of the leaves end in teeth, in distinction to the early leaves of typical canopy foliage. Another distinctive feature of Type II leaves, but characteristic of stump sprouts, is the presence of the minute papillate teeth on all of the leaves, including the first two. The lamina base of the first leaf is not truncate, but sharply angled at nearly 90 degrees. By the fourth or fifth leaf the angle broadens to 180 degrees or more (Figure 20). Apical angles decrease slightly through the series (Figure 20). Length/width ratios decrease through successive leaves; s/m ratios slightly increase; and u/t ratios slightly decrease (Figure 21). These ratios indicate that the leaves become broader and the lateral lobe sinuses become deeper although the sinuses are still not as deep as in Type I leaves or inflorescence shoot leaves.

The foliage most physiognomically distinct from typical crown foliage is that produced as stump sprouts or sprouts from the base of a standing tree. These leaves differ from crown shoots in both gross morphology and the organization of vein architecture. Three sprouts were collected from one stump of unknown age in a parking lot on the campus of Michigan State University. It is not known whether this stump is <u>P</u>. Xhybrida or <u>P. occidentalis</u>

because the standing tree was not observed.

The largest stump sprout does not have the same pattern of progressively increasing lamina area, perimeter, and tooth number as canopy foliage (Figure 24). The lamina area is initially large and decreases through the series (Figure 25). It should be noted that at least the terminal two leaves probably did not complete their expansion so that the ultimate area of these laminae is not known. The number of teeth found on the leaves roughly follows an opposite pattern to that of inflorescence leaves: tooth number is initially high (44) in the first leaf, jumps to 82 and 84 teeth in the second and third leaves, then diminishes (Figure 28). Most of the larger teeth in the first two leaves are broad, but become progressively attenuated through the series. High numbers of small, papillate teeth occur in the early leaves, particularly the first two, but diminish in number in later leaves. Again, this is contrary to the architectural development of Type I and inflorescence leaves. Perimeter measurements reflect the increase in tooth number and size (Figure 27). In conjunction with the narrowing of the teeth, the apical angles also narrow through the series (Figure 26). The base of the lamina is decurrent in all of the stump sprout The first leaves of the largest sprout leaves examined. have an obtuse base; succeeding leaves have progressively broader leaf bases, including the recurved aspect of canopy leaves (Figure 26). Petioles of the first leaves are short and stout, and the lower portion of the primary vein is
I ۷ p d 0 S t i t f tl 0 d: 1 S pę ha pe t? to Þe Be 00 þe :e de much more robust than in canopy leaves. The lower primary vein and petioles show conspicuous vertical striations in pressed specimens. Sprout leaves have large laminae that do not have deep lateral lobe sinuses. In an extreme case, one long narrow leaf has no lateral lobes.

Vein architecture becomes more organized through successive leaves of the stump sprouts. Both secondary and tertiary veins are much less symmetrically organized in the initial two or three leaves than in later leaves. Many of the tertiary veins in the first leaf are reticulate and forked percurrent, but become progressively ordered until the majority are truly percurrent. Intersecondary and composite intersecondary veins, which add to the dissymmetry of early leaves, are less frequent in later leaves. Normally, in <u>Platanus</u> Xhybrida the lowermost strong lateral veins can be unambiguously labeled as alpha pectinal veins. But the first leaf of a stump sprout can have additionally strengthened lateral veins so that the pectinal terminology is difficult to apply. Furthermore, the pectinal terminology is also often difficult to apply to the abmedial secondary veins (that is, to designate beta pectinals) because several of them may be strengthened. Beta pectinal veins can diverge from the alpha pectinals at many points, and only one side of the lamina may have a beta pectinal vein. Inferior secondary veins are relatively well developed because of the suprabasal departure of the alpha pectinal veins and the decurrent

Figure 24. Leaves from a stump sprout (same shoot as Figure 23) of <u>P</u>. X<u>hybrida(?)</u> numbered from the most basal leaf in the sequence.







Figure 25. Leaf lamina area for successive leaves from a stump sprout (same shoot as Figure 23) of \underline{P} . Xhybrida(?).



Figure 26. Leaf lamina apical and basal angles for successive leaves from a stump sprout (same shoot as Figure 23) of P. Xhybrida(?).



Figure 27. Leaf lamina perimeter length for successive leaves from a stump sprout (same shoot as Figure 23) of P. Xhybrida(?).



Figure 28. Number of teeth for successive leaves from a stump sprout (same shoot as Figure 23) of P. Xhybrida(?). "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.



Figure 29. Leaf lamina area of successive leaves from two non-inflorescence shoots (shoots 6 and 7) of Platanus occidentalis.



Figure 30. Leaf lamina perimeter length of successive leaves from two non-inflorescence shoots (shoots 6 and 7) of P. occidentalis.

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Additional shoots which consisted of only two to four leaves were collected from the lower inner crown. These have an obtuse leaf base (some are decurrent) similar to stump sprout and Type II leaves, and the large teeth of Type I and inflorescence leaves. Well developed lateral lobes without deeply incised sinuses are present. The teeth are almost entirely of the large type; small, papillate teeth are usually not present. The teeth are attenuated, and the apices are unique in having long, spinose tips.

Foliar characteristics of Platanus occidentalis L.

The following description is based upon a collection of 17 leaves (three shoots) from one tree, none of which were from an inflorescence-bearing shoot. Twelve additional leaves were measured from herbarium specimens.

The leaves of this plane tree are usually three-lobed although early sucker leaves and leaves with large teeth can have less defined or weaker lobes. The earliest seasonal leaves often lack lateral lobes even though strong basal secondary veins feed large teeth which approach the size of lobes and provide a triangular aspect to the leaf. Length/width ratios for canopy (non-sucker) leaves averages .735 (range .76 to 1.24; n= 36). Newly sprouted trees have ovate to obovate leaves. The texture of the leaves ranges from chartaceous to coriaceous and from glabrous to

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densely pubescent on either surface. Typical P. occidentalis leaves have a more squarish outline than P. Xhybrida, that is, the base of the lamina is closer to 180 degrees and is nearly as broad as the laminar width between lobe apices. The apices of the lobes range from acute to long and attenuated. The average angle of divergence for the apex of the central lobe is about 31.7 degrees (range 16 to 62; n= 26). Sinuses between the lobes are rounded and shallower than P. Xhybrida or P. orientalis. The average angle of divergence between the central and lateral lobes is 116 degrees (range 98 to 149; SE= 1.92; n= 33). The bases of the leaves range from recurved to truncate to obtuse, except in sprout leaves which have acutely tapering bases. The lamina often extends down the petiole in either a decurrent fashion, such as is common in sucker leaves, or in a more obtuse extension, such as is common in typical late season leaves. The mean angle of divergence for the leaf bases is 223.5 degrees (range 122 to 310; n= 29).

A great deal of variation occurs in the size and number of the teeth. The average number of teeth per leaf is 30.3 (range 7 to 71; n= 28). Some leaves have very large teeth which approach the aspect of incipient lobes, particularly those which are fed by the alpha pectinals. The smallest teeth are simply papillate projections formed by veins which extend beyond the margin of the lamina. Shapes of the teeth conform to Hickey's (1979) types B1, B2, C1, and C2, and usually terminate in a spinose tip which may be quite long. Several tooth types may appear on

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one leaf and all of the teeth except the minute papillate type are typical platanoid teeth. The sinuses between the teeth (excluding the papillate type) are scalloped. Petioles have a swollen base covering the axillary buds typical of subgenus <u>Platanus</u>.

The venation of later seasonal leaves is either strongly actinodromous or palinactinodromous. The midrib and alpha pectinal veins are stout and straight to weakly curved. The alpha pectinals diverge from the midrib either basally or suprabasally at a distance ranging from 0.0 to 0.7 cm (mean= .12cm; SE= .033; n= 32) from the lamina base and at an average angle of 52.8 degrees (range 36 to 70; n= 57). The first leaves of the season are pinnately veined and lack alpha pectinals. By the second or third leaf of the shoot beta pectinal veins have developed and diverge off of the alpha pectinals at distance ranging from 0.6 to 1.6 cm from the alpha pectinal--midvein juncture. Superior secondary veins arise from the midrib at an average angle of about 54.4 degrees (range 45 to 72; n= 60). The superior secondaries can be either craspedodromous, eucamptodromous, brochidodromous, or semicraspedodromous. Abmedial secondary veins diverge from the alpha pectinals at an average angle of 56 degrees (range 33 to 77; n= 36). Their marginal course is like that of the superior secondaries. The secondary veins which approach the lobe sinuses may branch and form connecting loops to both the superjacent superior secondary and the admedial secondary

Inferior secondary veins are weak and may either veins. terminate in teeth or form brochidodromous loops. They occur in suprabasally actinodromous leaves, especially where the lamina extends down the petiole. Intersecondary veins are infrequent and most often occur between the alpha pectinals and superior secondaries, or in the upper third of the lamina, or as abmedial veins. Both simple and composite types of intersecondaries are common. As in most <u>Platanus</u> leaves the tertiary veins vary from strongly percurrent to forked-percurrent to reticulate. Chevrons are formed by the tertiaries in the axils of the primary veins, and the axils of the secondary and primary veins. Tertiary veins can join admedial secondary veins and thereby also form chevrons proximal to the lobe sinuses. Tertiaries are orthogonal (average angle of divergence is 84.2 degrees, range 69 to 96; n= 102) and consequently those associated with the abmedial secondaries are longitudinally oriented with respect to the midrib, and those associated with the superior secondaries are obliquely oriented. Tertiary veins are spaced an average of 0.3 cm (range 0.1 to 0.5 cm; SE= .0126; n= 54). The quaternary veins are normal in thickness and approximately orthogonal. Quinternary veins form the areoles and vary from random to orthogonal in course. Well-developed areolation is guadrangular or polygonal in shape. The marginal ultimate venation is looped.

Foliar heteromorphism in <u>Platanus</u> occidentalis

Significant and repetitive trends in the physiognomy of successive leaves on the shoots of <u>Platanus occidentalis</u> were found. Recurring patterns in the leaves were exhibited by both gross morphological and architectural features. The leaves of this species which were examined in greatest detail were from sterile crown shoots. When inflorescences occur, they terminate a shoot; continued apical growth beyond the inflorescence does not occur as it does in <u>P. Xhybrida</u>. Stump sprouts were not included in this study.

The overall change in gross leaf shape between the earliest leaves and the latest leaves is guite pronounced. The first three or four leaves have the squarish aspect seen in the pre-inflorescence leaves of P. Xhybrida: the outer margins of the lobes are roughly perpendicular to the base, and the alpha pectinal veins are nearly perpendicular to the midvein. Change from this morphology is easily followed by noting the increase in the basal angles of the laminae which proceeds throughout the growing season. Initially, the lamina bases are broadly obtuse or truncated, but each succeeding leaf developes a more reflexed base (Figure 32). That is, the beta pectinal veins grow stronger, become acute with respect to the petiole, and develop strong abmedial secondary veins. The apical angles of the laminae did not follow the clear pattern of P. Xhybrida. Figure 31 shows that the apical angles increase along one shoot studied, while another

shoot did not show any clear pattern. Additional sampling is needed to determine whether the increase in apical angles of the distally successive leaves is consistently present or not.

A leaf form has been observed from several trees in which the lamina forms a semi-peltate condition where narrow finger-like extensions of the lamina occur at the petiole-lamina juncture. Schwarzwalder (1986) indicated that this condition is caused by the sycamore anthracnose (<u>Gnomonia veneta</u>), a pyrenomycete. However, such an explanation may be questionable as Agrios (1988) states that this pathogen causes shoot blight and leaf blight, resulting in symptoms that are completely unlike these lamina extensions which occur on otherwise healthy leaves. These laminar basal extensions are quite simiar to some found in fossil platanoid leaves (Ward 1888, 1890).

Lamina size was found to increase through successive leaves, but the seasonal peak in size among different shoots did not necessarily occur at the same node (Figure 29). Leaves from later in the season are progressively smaller. The 1/w ratios showed a slight trend toward increasing, that is, a proportionate increase in lamina length through successive leaves and the u/t ratios decreased through successive leaves, indicating a deepening of the lateral lobe sinuses (Figures 33 and 34). The number of teeth can increase at least five-fold (Figures 35 and 36), and high numbers of teeth can occur by the third



Figure 31. Leaf lamina apical angles of successive leaves from two non-inflorescence shoots (shoots 6 and 7) of P. occidentalis.



Figure 32. Leaf lamina basal angles of successive leaves from two non-inflorescence shoots (shoots 6 and 7) of P. occidentalis.



Figure 33. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from a non-inflorescence shoot (shoot 6) of P. occidentalis.



Figure 34. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves from a noninflorescence shoot (shoot 7) of <u>P. occidentalis</u>.



Figure 35. Number of teeth of successive leaves Ρ. from a non-inflorescence shoot (shoot 6) of "Typical" occidentalis. teeth are those representing extensions of the leaf lamina while teeth represent minute projections papillate without accompanying lamina.



Figure 36. Number of teeth of successive leaves from a non-inflorescence shoot (shoot 7) of <u>P</u>. <u>occidentalis</u>. "Typical" teeth are those representing extensions of the leaf lamina while papillate teeth represent minute projections without accompanying lamina.

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leaf (in contrast to the inflorescence shoots of P. Xhybrida). Tooth size also varies greatly although an abundance of large teeth (those fed by craspedodromous secondaries) only occurs in late leaves. Lamina perimeter lengths reflect both lamina size and tooth size and number (Figure 30). High numbers of teeth in the first three or four leaves are due to minute papillate teeth that are occurring with brochidodromous and semicraspedodromous secondaries. Late season leaves have very few secondary veins that do not directly enter teeth.

Foliar characteristics of <u>Platanus lindeniana</u>

The following quantitative description is based upon a herbarium collection of five leaves; additional leaves also contributed to the non-quantitative aspects of the description.

The leaves are primarily three lobed, less commonly five lobed. Length/width ratios range from 1.03 to 1.46 (SE= .0752; n= 5). Leaf texture is chartaceous to coriaceous with a fine pubescence on the lower side and sometimes on the upper side. The first seasonal leaves have one lobe; the succeeding leaf may have two or three lobes. These lateral lobes are often much weaker than the central lobe. The first seasonal leaves are ovate with an acute apex. Later seasonal leaves have lateral lobes proportionately larger than first seasonal leaves although they remain smaller than the central lobe. Sinuses between

the lobes are rounded. Lobe apices are narrowly to broadly attenuate with an average angle of divergence of 32 degrees (range 24 to 46; SE= 4.83; n= 4). The bases of the laminae are usually symmetrical, occasionally asymmetrical. They are obtuse to cuneate when symmetrical or nearly truncate when asymmetrical. The mean angle of divergence of the bases is about 137.6 degrees (range 118 to 164; SE= 7.49; n= 5). The petioles have swollen bases which cover the axillary buds.

The lamina margins are predominantly entire but do have some irregularly spaced teeth (4 to 10 per leaf; SE= 1.12; n= 5).Teeth are of the typical platanoid type, serrate, and conform to Hickey's (1979) types B1, B2, C1, and C2. An individual leaf may possess all of these tooth types. Tooth size varies greatly from tiny papillate projections on an otherwise entire margin to large coarse teeth which appear to be incipient lobes. The major vein for each tooth is centric and frequently terminates in a spinose tip. The smallest papillate shaped teeth are entered by either fine branches off the ends of the secondary veins, or by a branch off of a series of marginal, abmedial loops on the secondary veins, or less frequently by the semicraspedodromous condition. Some leaves have most of the secondary veins and branches of the secondary veins ending in teeth.

The venation pattern of later seasonal leaves may be either strongly actinodromous or palinactinodromous. The first seasonal leaves have pinnate venation, often with one

pair of lower secondaries strengthened, but not distinctly Primary veins are moderate to stout in actinodromous. thickness, terminate in lobe apices, and vary from straight to slightly curved. The alpha pectinal veins diverge suprabasally from the midvein at an average angle of 39.8 degrees (range 30 to 49; SE= 2.55; n= 10), and are frequently weaker than the midrib. Superior secondary veins arise from the midrib at angles averaging about 45.3 degrees (range 35 to 55; SE= 2.07; n= 10) and are most often eucamptodromous, but may also be brochidodromous, craspedodromous, or semicraspedodromous. Loops formed by the conjoining of superior secondary veins and admedial secondary veins often occur proximally to the lobe sinuses. Abmedial secondary veins diverge from the alpha pectinals at an average angle of about 49.1 degrees (range 35 to 63; SE= 2.197; n= 15). Their marginal behavior is like that of the superior secondaries. Inferior secondary veins are weak and branch near the margin to form festooned Intersecondary veins of the brochidodromous loops. composite type are frequent; larger leaves also have the simple type. Placement of these veins on the laminae is most common near the lobe sinuses, arising from either the midvein or the alpha pectinals. Tertiary veins are a prominent feature of the leaves and vary from simple percurrent to forked percurrent to reticulate. Simple percurrent tertiaries may or may not be the most common condition on an individual leaf. In the axils of the

primary veins, and to a lesser degree in the axils of the superior secondaries and midvein, the tertiaries form chevrons. Because the tertiaries diverge orthogonally from the secondary veins (average angle of divergence 85.5 degrees, range 72 to 90; n= 20) they roughly trend from basally longitudinal to apically perpendicular in relation to the midrib. The quaternary and quinternary veins are normal in thickness and orthogonal. Areolation is well developed and consists primarily of four-sided units. The marginal ultimate venation is looped.

Foliar characteristics of Platanus racemosa Nutt.

The quantitative data in the following description is based upon a collection of thirteen dispersed leaves collected from the ground beneath the parent trees in northern California. The general morphological description is also based upon inflorescence-bearing shoots, noninflorescence shoots, and sucker shoots from trees in the same vicinity.

Heterophyllic variation is present in this taxon in each of the shoot types examined. As in P. Xhybrida, the initiation of an inflorescence is followed by a "reset" pattern in some of the morphological features of the leaves. Inflorescences may be borne terminally on a shoot or they may be followed by additional shoot growth. An internodal shoot segment occurs between the inflorescence node and the first leaf after that node, as distinct from P. Xhybrida, where no apparent internode is present.

The leaves of Platanus racemosa vary from having a single rudimentary lateral lobe on each side of the central lobe to having two subsidiary lobes in conjunction with five strong lobes. Leaf texture varies from chartaceous to coriaceous, and a fine pubescence may be present on both surfaces, or the upper surface may be glabrous. Length/width ratios average .997 (range .717 to 1.327; SE= Early seasonal leaves are three lobed .0424; n= 13).although the lateral lobes may be greatly reduced. Three lobed leaves, in general, have lateral lobes which are smaller (shorter and narrower) than the central lobe, or occasionally nearly equal to it, and sinuses which are either shallow or deep. Five lobed leaves are the result of the palinactinodromous disposition of the alpha and beta pectinal veins. The lateral lobes of the five lobed leaves are also smaller than the central lobe; the most basal lobes (supplied by beta pectinals) are the weakest of all. The average angle of divergence between the central lobe and the largest (distal) lateral lobes is 48 degrees (range 21 to 89; SE= 3.45; n= 25). The leaves of P. racemosa have lobes which are distinctly narrower, and lobe sinuses which are much deeper, than those of P. occidentalis and P. Xhvbrida. Lobe apices for both three and five lobed leaves range from acute to very attenuate and have an average angle of divergence of 43 degrees (range 15 to 77; SE= 6.83; n= 9). The bases of the laminae vary considerably in shape and can be either symmetrical or asymmetrical. They

may be cuneate to obtuse, nearly truncate, cordate, or with a v-shaped sinus, and have an average angle of divergence of 146 degrees (range 68 to 231; SE= 14.29; n= 13). Some of the cuneate leaf bases approach the decurrent condition. Petioles are expanded to cover axillary buds.

Leaf margins may be either entire or toothed. The number of teeth per leaf averages 20.9 (range 3 to 62; SE= 4.83; n= 13). Teeth are of either the typical platanoid type or the minute papillate type, and are similar to the three preceeding species. The papillate teeth are fed by either secondary veins directly, or by branches off of looping secondary veins (semicraspedodromy), or by veins of tertiary or quaternary order which loop near the margin. Less frequent are larger teeth which incorporate a small portion of the lamina (i.e. typical platanoid teeth). When present, these "typical" teeth are usually much smaller than, and without the attenuated apices of, P. Xhybrida and P. occidentalis. Tooth size generally decreases apically along each lobe although to a lesser degree than in either P. Xhybrida or P. occidentalis. Tooth shape conforms to Hickey's (1979) types B1, B2, C1, and C2, and each type may be present on the same leaf. The sinuses between the platanoid teeth are scalloped with the concavity displaced toward the proximal tooth. The laminar margin between the papillate teeth is usually unaffected by the teeth or with only slight scalloping. The major vein for each tooth is approximately centric.

The primary venation consists of a strong midrib and

strong alpha pectinals (actinodromy) or the equivalent architecture with the addition of strong beta pectinals (palinactinodromy). Pectinal veins may be straight or slightly curved. Divergence of the alpha pectinal veins averages 40 degrees (range 27 to 51; SE= 1.10; n= 26) and may be basal or suprabasal; beta pectinal departure is The average distance from the base of the never basal. lamina to the origin of the alpha pectinals is about .84 cm (range 0.0 to 1.9 cm; SE= .128; n= 26).The point of origin of the beta pectinals is about 1.3 cm (range 0.6 to 2.0 cm; n= 19) from the origin of the alpha pectinals. Superior secondary veins occur in the craspedodromous, semicraspedodromous, and brochidodromous conditions. Leaves with the brochidodromous architecture are usually dominated by that condition, while craspedodromous and semicraspedodromous architectures commonly cooccur in the same leaf. The brochidodromous condition is more frequent and better developed in P. racemosa than in P. occidentalis The average angle of departure for the or <u>P. Xhybrida</u>. superior secondary veins is about 57.7 degrees (range 43 to 76; SE= 1.46; n= 26); secondary spacing averages 2.1 cm (range 0.7 to 3.4 cm; SE= .149; n= 26). Abmedial secondary veins present the same architectural variations as the superior secondaries. They diverge from the alpha pectinals at an average angle of about 59 degrees (range 33 to 84; n= 39). In basal sprout (sucker) leaves the first admedial secondary vein can be as strengthened as the beta

pectinal vein which departs very near it. Also, the first superior secondary vein can be unusually strengthened. In both cases the strengthened secondary vein forms an additional small lobe in the sinus between the central and lateral lobes. Simultaneous strengthening of both of these secondary vein types on the same side of the lamina has not been observed, but opposing halves of the lamina can have either vein strengthened. As in the former species, a loop is often formed beneath the lobe sinuses by an adjoining of the most proximal superior secondary and an admedial secondary. This loop is the strongest of a series of loops which begins in the axil of the midvein and alpha pectinal and forms a series of chevrons directed toward the sinus. Inferior secondary veins are weak in small to medium size leaves, fairly coarse in large leaves, and often form brochidodromous loops along the margin which join with the abmedial secondary veins. Composite intersecondary veins of varying strength are present and grade into coarse tertiary veins. Tertiary veins vary from percurrent to forked percurrent to reticulate. Forked percurrent to slightly reticulate tertiary veins are the most common, and the reticulate pattern is exhibited much more frequently than in <u>P. occidentalis</u> or <u>P. Xhybrida</u>. The average angle of departure for the tertiary veins is 87 degrees (range 70 to 99; SE= .945; n= 39); tertiary spacing averages about .53 cm (range .25 to 1.0 cm; SE= .0274; n= 39). Chevrons are formed by the tertiary veins in the axils of the primary veins and also often in the axils of the

primary/secondary vein junctures. Quaternary venation is orthogonal and normal in thickness. Areoles are bounded by quinternary and hexternary venation which is more orthogonal than random, but not as regular as the higher order venation. The marginal ultimate venation is looped.

Foliar heteromorphism in Platanus racemosa Nutt.

The following assessment of heterophyllic trends is based upon six inflorescence-bearing shoots, five noninflorescence shoots, and two basal sprout (sucker) shoots.

The leaves of <u>P. racemosa</u> exhibit broad changes in gross morphology (Figure 37). Some of the heterophyllic patterns of change are similar to <u>P. Xhybrida</u> and <u>P. occidentalis</u> while others are distinct. The lamina area of this species varies greatly (Figure 38), especially among non-sucker shoots where the first seasonal leaf is quite small. Sucker shoot leaves are primarily larger than nonsucker leaves, and the first leaf of the sequence is itself fairly large. Sucker shoots also differ from non-sucker shoots in that the largest leaf of the shoot is the second or third leaf produced.

The number of teeth varied from 3 (lobe apices only) to 62 (Figure 39) and was irrespective of lamina size. The two leaves which represent these extremes are approximately of equal area, and in fact, the leaf with the most teeth has the smaller perimeter. This apparent discrepancy is due to the teeth of the smaller perimeter leaf being the

minute papillate type which do not add significantly to lamina area. Large teeth are only infrequently present in non-sucker leaves, and somewhat more common in sucker leaves.

The s/m and u/t ratios (Figure 40) show that as the primary lateral lobe sinuses extend closer to the midvein they also extend closer to the base of the lamina. Platanus racemosa has the narrowest, deepest lobation of the <u>Platanus</u> species examined. Of the measured leaves, the narrowest one (highest 1/w ratio), leaf number 4, has the shallowest lateral lobe sinuses, while the broadest one (lowest 1/w ratio), leaf number 10, has the deepest The angles of the lamina bases of non-sucker sinuses. shoots follow a trend similar to that found in the corresponding shoots of P. Xhybrida and P. occidentalis. The basal angle of divergence is narrowest for the first leaf of a non-sucker shoot sequence, and broadens through successive leaves. The earliest leaves have acute basal angles and the latest leaves have angles which have broadened to about 180 degrees.

Two of the inflorescence-bearing shoots can also be divided into pre- and post-inflorescence segments, at least upon the basis of a "reset" pattern in basal angles where the first post-inflorescence leaf returns to an acute basal angle, followed again by progressively broadening bases. Lamina bases of sucker shoot leaves follow a different pattern: the first leaf has a rounded base, the next

Figure 37. Selected leaves of <u>Platanus</u> racemosa **Showing** variability in morphology. B - E are crown leaves; **A** and F are from a basal sprout.





Figure 38. Leaf lamina areas of leaves of \underline{P} . racemosa arranged in a size sequence (leaves not from the same shoot). Numbers on the x axis designate individual leaf specimens.



Figure 39. Number of teeth on leaves of Ρ. The numbered leaves the racemosa. are same specimens documented in Figure 38. "Typical" teeth are those representing extensions of the lamina while papillate teeth represent leaf minute projections without accompanying lamina.



Figure 40. Unlobed lamina/total lamina (u/t), length/width (1/w), and distance to sinus/distance to midrib (s/m) ratios for leaves of <u>P</u>. racemosa. The numbered leaves are the same specimens documented in Figure 38.



Figure 41. Leaf lamina apical and basal angles of leaves of P. racemosa. The numbered leaves are the same specimens documented in Figure 38.

several leaves have a straight base, and succeeding leaves develop a cuneate or decurrent extension of the lamina on the petiole while the lamina base becomes broadly obtuse. Apex angles of leaves in growth sequences were not measured, so it is not known if they follow heterophyllic patterns. The angles of the laminar apices and bases are quite variable when related to lamina size, and at least the basal angles do not appear to correlate well with size (Figure 41).

Foliar characteristics of the <u>Platanus</u>-like fossils [Plate 1, Figures 1 to 4] Collection Numbers: 7/11/70 I 020-020, 7/11/70 I 020-021, 7/11/70 I 020-022, 7/11/70 I 020-023, 7/30/70 III 300-308, 8/29/70 060-150, 4/28/68 36-001, P115A-001 Unit I.

Despite the large number of fossil leaf fragments attributable to the <u>Platanus</u>-like morphotype (Parker, 1976, identified 269 pieces of these leaves in his collection), only four or five of them have 75% or more of the lamina intact.

All of the leaves appear to be unlobed, although the margins of many leaves are so tattered that small lateral lobes could remain unrecognized. The maximum lamina length that can be estimated with certainty is 20-23 cm; the maximum estimated width is about 17 cm (specimen no. 7/11/70 I 020-023). One leaf fragment may be from a larger leaf, but it is too incomplete to accurately estimate the size. A smaller lamina which is nearly intact is 14.5 cm

long and 10-11 cm wide (specimen no. 8/29/70 060-150). Portions of smaller leaves are also present. Length/width ratios range from 1.18 to 1.56 (SE= .0869; n= 4). Leaf shape is ovate to elliptic. The leaves were heavy in texture, probably coriaceous, as demonstrated by the stout venation and coarseness of the impressions. Unfortunately, all of the leaves are separated from their branches (the usual situation with fossil leaves) so that sequential heterophylly, if present, could not be observed. Few leaf apices or bases have been preserved. Leaf apices do not appear to be attenuated. They have an average angle of divergence of 97.5 degrees (range 90 to 105; SE= 7.5; n= Leaf bases vary from rounded to bluntly decurrent. 2). Two of the most intact leaves, as well as several fragments, possess a distinct, narrow projection of the leaf base along the petiole for 2-3 cm. Other leaf bases may be only slightly decurrent or simply rounded. The bases of the laminae may be either symmetrical or asymmetrical, and have an average angle of divergence of 140.5 degrees (range 134 to 147; SE= 6.5; n= 2). Although petioles are present it is not clear whether any of them are preserved in their entirety. One short petiole (2 cm) has a slightly expanded base (specimen no. 7/30/70 III 300-308), but it is not clear if the petiole is undamaged.

Leaf margins are rarely preserved and difficult to interpret. Some margins appear to be entire, a few have very small teeth. None of the leaves have conspicuous or
large teeth typical of most living <u>Platanus</u>. Some of the margins that are entire have craspedodromous venation where strong veins appear to end abruptly at the margin. Pectinal, secondary, tertiary, and quaternary veins have all been observed to terminate at the leaf margin without forming visible teeth. In other cases, veins terminate in small papillate/spinose projections similar to those commonly found in living <u>Platanus</u>. In those few instances where small teeth are present they are short, broad and conform to Hickey's (1979) types B2 and C2. Sinuses between these teeth are shallowly scalloped, and the veins feeding these teeth are centric.

The primary venation consists of a strong midrib flanked by two alpha pectinal veins (actinodromy). The alpha pectinals are weaker than the midvein and arise suprabasally or basally from equivalent or staggered points along the midvein. The distance from the base of the lamina to alpha pectinal departure for the large leaves averages 1.49 cm (range 0 cm to 4.8 cm; SE= .697; n= 6). Angle of departure for the alpha pectinal veins has an average of 40.2 degrees (range 25 to 57 ; SE= 1.76; n= 18). The alpha pectinal veins curve toward the apex, are craspedodromous, and may complete their course in a gently recurved fashion. Some also branch dichotomously near the Distinct beta pectinal veins are not common. margin. Often at least two of the abmedial secondaries are strongly developed (i.e., possess their own abmedial branches) and neither could be designated as the beta pectinal. Superior

secondary veins are moderately strong and craspedodromous. These veins are spaced relatively far apart: the distance between the first and second superior secondary veins averages 3.7 cm (range 1.6 to 6.5 cm; SE= .371; n= 14). This results in these leaves having fewer superior secondary veins than in comparably sized <u>Platanus</u> leaves. The average angle of departure for these veins is about 47.6 degrees (range 33 to 59 ; SE= 1.67; n= 20). Abmedial Secondary veins are craspedodromous and have an average angle of departure of 56.8 degrees (range 36 to 82; SE= The abmedial secondary veins frequently 1.97; n= 29). branch dichotomously, usually closer to the margin than to the alpha pectinal vein, but sometimes closer to the alpha pectinal. Inferior secondary veins are not well developed. Those that are strongest occur on the largest leaves which have a greater distance between the lamina base and alpha pectinal departure. The inferior secondary veins may form brochidodromous loops with abmedial branches of the abmedial secondary veins. Intersecondary veins appear to be absent in all of the leaves. Tertiary veins are well developed and guite prominent. They are most commonly percurrent, less commonly forked percurrent, and occasionally reticulate. In the axils of the primary veins, and in the axils of the primary-secondary vein junctures the tertiary veins form either weak chevrons or are straight. The average angle of departure for the tertiary veins is about 84.7 degrees (range 68 to 107 ; SE=

1.3; n= 34); tertiary spacing averages about .57 cm (range .3 cm to .9 cm; SE= .0276; n= 34). Quaternary veins are orthogonal, and percurrent, forked percurrent, or reticulate. Quinternary veins, which are obscurely visible in at least one large leaf, have an orthogonal to reticulate pattern. It is not possible to tell which vein order forms the areoles. The marginal venation was rarely preserved. Marginal brochidodromous loops formed by abmedial branches of the abmedial secondary veins occur in the basal lamina (as mentioned above). Secondary venation, which is normally craspedodromous, may be camptodromous in the apex of one leaf, but inadequate preservation obscures the condition.

Foliar characteristics of <u>Tetracentron</u> <u>sinense</u> Oliver

The following description is based upon one herbarium sheet (specimen no. 514) from the University of Michigan herbarium which had one shoot with ten leaves. Tooth architecture observations were made from the cleared leaf material figured in Tanai (1981).

Tetracentron sinense has both long and short shoot systems. The leaves are somewhat variable in terms of overall shape and the basal lamina shape, but they are not strongly dimorphic as in <u>Cercidiphyllum japonicum</u>. The leaves are simple and symmetrical. Texture of the dry leaves is chartaceous. The lamina has an ovate shape, and varies in size among the specimens examined from a high of

12.1 cm in length and 7.5 cm in width for the largest lamina to 8.7 cm in length and 6 cm in width for the smallest whole lamina. Length/width ratios varied from 1.45 to 1.63 (n= 4). Leaf apices are attenuate to broadly acuminate with an average angle of divergence of 26 degrees (n= 2). From the material seen in this study the leaf bases of short shoot leaves are deeply or shallowly cordate, and the bases of long shoot leaves are truncate. Lamina bases have an average angle of divergence of 254.8 degrees (range 192 to 284 ; n= 6). Petioles ranged in length from 1.7 to 2.4 cm (n= 7). A petiolar (stipular?) flange which encloses the bud extends along the basal half of the petiole and is about 1 mm wide.

Leaf margins are serrate with simple (i.e., not compound) teeth conforming to Hickey's (1979) types A1, B1, The sinuses between the teeth are predominantly and B2. angular, but occasionally rounded. Tooth size varies only slightly and the teeth are fairly regularly spaced at intervals of 6 to 8 teeth per centimeter. Teeth at the base of the lamina may be less closely spaced. Vein configuration and the glandular characteristics of the teeth are of the chloranthoid type. This tooth architecture consists of a dark gland in the apex of the tooth fed by a centric vein, and braced by a vein extending to the apical tooth sinus and a vein extending to the basal sinus. Glands always occur apically on all of the teeth. No teeth occur along the basal sinus of the lamina or along

the basal edge of a truncated lamina.

The primary venation is actinodromous and is composed of 5 or 7 basal radiating veins. Occasionally a delta pectinal vein is present. The midvein is the strongest vein with each succeeding series of pectinal veins becoming weaker than the preceding one. The midvein follows a straight course. Alpha pectinal veins diverge from the base of the midvein at a low angle, then begin to gently curve toward the apex of the leaf until they join a superior secondary vein. Alternatively, the alpha pectinals may approximately parallel the midvein in the upper half of the lamina. Alpha pectinal veins depart from the midvein at angles averaging 19.4 degrees (range 14 to 26; n= 16). These veins do not extend to the apex of the lamina, but join superior secondary veins at a point threequarters or more of the distance to the apex. Obtuse angles that are close to 90 degrees are formed by the juncture of the alpha pectinals and superior secondaries. The beta pectinal veins extend one-quarter to one-half of the lamina length, and then join alpha abmedial secondary veins (here called alpha abmedials) at obtuse angles that are near to 90 degrees. The course of the beta pectinals gradually curves apically, and it may parallel the first alpha abmedial vein, but it does not parallel the alpha pectinals. These veins depart from the midvein at an average angle of 47.4 degrees (range 40 to 52; n= 14). Reduction of the beta pectinals occurs in the smaller leaves so that they are no more robust than the alpha

abmedial veins. Gamma pectinal veins are also present in the larger leaves and they diverge from the midvein at an average angle of 87.8 degrees (range 75 to 103; n= 10). Their configuration is similar to that already noted for the beta pectinals: they form a loop by joining the beta abmedial secondary veins (here called beta abmedials) at obtuse angles that are close to 90 degrees, and behave as simply the first vein in the beta abmedial loop series. The strong superior secondary vein which joins the alpha pectinal vein has an average angle of departure from the midvein of 42.3 degrees (range 32 to 56 ; n= 18). The secondary veins which depart from the midvein proximally to this strong superior secondary (termed weak secondaries in Cercidiphyllum) depart from the midvein at an average angle of 49.7 degrees (range 41 to 59 ; n= 18). Alpha abmedial veins depart from the alpha pectinals at an average angle of 41.7 degrees (range 33 to 62 ; n= 13). Beta abmedial veins depart from the beta pectinals at an average angle of 48.1 degrees (range 40 to 56 ; n= 7). Secondary veins, therefore, are associated with all four types of primary venation: secondaries diverge from the midvein (i.e. superior secondaries); secondaries diverge from the alpha pectinal veins (i.e. alpha abmedials); secondaries diverge from the beta pectinals (i.e. beta abmedials); and very weak secondaries (or tertiaries?) diverge from the gamma pectinals (i.e. gamma abmedials). The succession of superior secondary veins which depart from the midvein

become progressively strengthened apically until the strongest one is the one joined by the alpha pectinal. Apically of this point they become weaker. Beginning with the superior secondary joined by the alpha pectinal, the upper superior secondaries form angular brochidodromous loops ascending toward the leaf apex. Alpha and beta abmedial veins also form angular brochidodromous loops.

Tertiary veins form angular loops exmedially from the upper superior secondaries, alpha abmedials, and beta abmedials. Generally, these loops form across the sinus formed by the adjoining of secondary vein loops, or several tertiary loops may also occur along a single secondary loop. Occasional quaternary vein loops situated exmedially to the tertiary loops may be present. Teeth are fed by veins branching off of either the secondary loops, tertiary loops, or quaternary loops. The secondary and tertiary veins which bridge the midvein to the alpha pectinals may form crude apically directed chevrons in conjunction with lateral branching, or they may extend apically a short distance, giving off lateral branches. In the other portions of the lamina the tertiaries connect the other primary and secondary veins via a similar weak chevron/reticulate pattern.

Foliar characteristics of Cercidiphyllum Sieb. and Zucc.

Detailed descriptions of the leaves of both Cercidiphyllum japonicum Sieb. and Zucc. and <u>C. magnificum</u>

(Nakai) Nakai have been prepared by Chandrasekharam (1974). To avoid unnecessary repetition the reader is directed to this source for more complete descriptions of the individual species. Chandrasekharam (1974) also summarized the foliar architectural characteristics which he found to be diagnostic for the genus <u>Cercidiphyllum</u>. These diagnostic traits and my own observations are incorporated in the description below. Terminology used here differs somewhat from that used by Chandrasekharam.

Because extant <u>Cercidiphyllum</u> has polymorphic foliage, Chandrasekharam separately described short shoot leaves, long shoot leaves, and sucker leaves. The following description does not include separate data for sucker leaves. A sample size of 400 leaves of both extant species were used by Chandrasekharam to obtain his quantitative and qualitative data. Those morphological features which I measured, but he did not, are followed by the number of measurements upon which they are based (i.e., "n="). Figure 42 shows an example of long and short shoot leaves of <u>C. japonicum</u>.

Two basic leaf types occur in this genus: those produced by short shoots and those produced by long shoots. Sucker shoot leaves are intermediate in aspect between short and long shoot leaves, but share more features with long shoot leaves. Short shoot leaves vary from cordate to broadly ovate while long shoot leaves are generally elliptic, ranging to ovate. Length/width ratios vary from

0.7 to 2.0. The leaf base of the short shoot leaves is cordate; the base of the long shoot leaves is cuneate, or rounded obtuse, or truncate. Short shoot leaves of <u>C.</u> japonicum occasionally have a morphology like long shoot leaves, but long shoot leaves have not been observed that possess the broadly ovate shape, deeply cordate base, and venation patterns of short shoot leaves. The average angle of divergence for the leaf base of <u>C</u>. japonicum is 215.4 degrees (range 140 to 280; n= 16); leaf base angles of <u>C</u>. magnificum average 265.8 degrees (range 242 to 301; n= 5). Leaf tips are retuse to rounded obtuse with a gland at the tip or in the notch in short shoot leaves. The leaf tip may be acute, acuminate or retuse, and is gland-tipped, in long shoot leaves. Average leaf tip angles for \underline{C} . <u>japonicum</u> are 107.6 degrees (range 66 to 160; n= 16); <u>C</u>. magnificum averages 133.2 degrees (range 119 to 148; n= 5).

The leaf margin of short shoot leaves is variable: teeth may be crenate throughout the lamina, or they may be rounded-serrate at the base and grade into crenate teeth apically. The leaf margin of long shoot leaves may be serrate, rounded serrate, serrate-crenate, or glandularentire. The teeth in <u>C. magnificum</u> may become larger distally; <u>Cercidiphyllum japonicum</u> generally has larger basal and lateral teeth. Both leaf types have globular glands that may be either emergent or non-emergent and normally occupy the apical position on the teeth, but also occur in the sinuses. Vascularization of the teeth is at times "loosely" chloranthoid. That is, some of the apical



Figure 42

glands are connected to both adjacent sinuses by a bracing vein, but others are connected to the sinus region by a series of loops, or the bracing veins may not connect to the gland, or only a central vein may be present. Tooth sinuses may be angular or rounded, and the glands may be emergent or nonemergent. Chandrasekharam (1974) notes, and my observations of one shoot concur, that the distinction between long and short shoot leaves in <u>C</u>. <u>magnificum</u> is less pronounced than in <u>C</u>. japonicum. In addition, the short shoot leaves of <u>C</u>. <u>magnificum</u> have a more deeply crenate, sometimes irregular, margin, exclusively apical glands on the teeth, and a deeply cordate base (average angle of divergence is 265.8 degrees; n = 5).

The primary venation is actinodromous in both species and all leaf types, and consists of 5 radiating veins in long shoot leaves and 5 or 7 radiating veins in short shoot leaves. The midvein is the strongest vein with each succeeding pectinal vein being weaker than the previous The midvein is straight until the strong superior one. secondary veins begin in the upper half of the lamina, at which point it angles away from the secondary departure points in a zig-zag fashion. The alpha pectinal veins depart from the midvein at angles ranging from 25 to 52.5 Short shoot and long shoot leaves differ in the dearees. course followed by the alpha pectinals. In short shoot leaves the alpha pectinals curve only slightly toward the apex. In long shoot leaves the alpha pectinals have a more pronounced apically directed curvature, especially in the

last one-half to one-third of their course. In C. <u>iaponicum</u> they do not normally parallel the midvein for any of its course. In <u>C. magnificum</u> the alpha pectinals may parallel the midvein in the last guarter of their course. The alpha pectinals do not extend to the apex of the leaf in either species. When the alpha pectinal veins join the first superior secondary veins directly, as in the long shoot leaves of <u>C.</u> japonicum, they form obtuse, or occasionally acute, angles with them. However, in <u>C.</u> magnificum and short shoot leaves of C. japonicum the alpha pectinals may not directly join the superior secondaries, but instead may be connected to them by branching or reticulate tertiary veins. Alpha pectinal departure is basal in short shoot leaves and may be basal or suprabasal in long shoot leaves. When it is suprabasal, the veins are commonly decurrent. The beta pectinal veins have an average angle of departure from the midvein of 63 degrees (range 41 to 80; n=45). These veins are strongest in the short shoot leaves where they extend half way to the apex. In long shoot leaves the beta pectinals are much weaker and do not extend beyond one-third of the lamina length. The beta pectinals may either form an angular loop by joining with the superjacent alpha abmedial vein, or they may not directly connect to alpha abmedials. Looping of the beta pectinals to join directly with alpha abmedials is most regular in long shoot leaves, and most obscured in large short shoot leaves where terminal branching of the beta

pectinals and alpha abmedials occurs. Gamma pectinals are usually present in short shoot leaves and form an angular loop with the superjacent beta abmedial vein.

Secondary veins form exmedially directed angular loops off of the midvein, and the alpha, beta, and gamma pectinals. Or, the secondaries of short shoot leaves may branch and not directly connect with the superjacent secondary. However, at no time do the secondaries ever directly enter teeth (i.e. craspedodromy). The first strong superior secondary veins (those joined by the alpha pectinals) diverge from the midvein at angles ranging from 40 to 75 degrees. Looping of the secondary veins is more consistent in long shoot leaves than in short shoot leaves, at least in <u>C. japonicum</u>. Secondaries can also bridge primary veins via a straight course, chevrons, or most commonly, branching. Alpha abmedial secondary veins diverge from the alpha pectinals at angles ranging from 40 to 90 degrees. Weak secondary and tertiary veins may be present between the midvein and pectinals, or nearly absent in the lower half of the lamina. Weak secondary veins depart from the midvein at angles ranging from 40 to 90 degrees. Beta abmedials diverge from beta pectinals at an average angle of 67.8 degrees (range 47 to 82; n= 25). Foliar characteristics of the trochodendroid fossils [Plate 2, Figures 1 to 4]

Collection numbers: 7/30/70 I 062-300, 7/30/70 I 93-176, 7/30/70 I 93-173, 7/30/70 II 007-24, 7/30/70 II 31-75,

7/30/70 II 45-103, 7/30/70 II 43-101, 7/30/70 II 43-200, 7/30/70 III P382-300, 7/30/70 III P382-301, 7/30/70 III P382-302, 7/30/70 III P382-303, 7/30/70 III P382-304, 7/30/70 III P382-305, 7/30/70 III P382-306, 7/30/70 III P382-307, 6/30/85 001-001A and B, 6/30/85 001-002A and B, 6/30/85 002-003, 6/30/85 003-004, 6/30/85 004-005, P34-001, P510-001, P510-002, P16-001.

Although these fossil leaves are the most abundant type in the Blackhawk (Parker, 1976, counted 354 individual specimens in his collection), most of the impressions are not sufficiently preserved for detailed study. Many of the impressions reveal no more than lamina shape and the distinctive pectinal veins (which I believe are adequate for identifying this morphotype).

The leaves are simple and symmetrical. The lamina shape varies from ovate to elliptic with a greater percentage of the larger leaves being ovate, and a greater percentage of the smaller leaves being elliptic. The dimensions of the largest whole lamina (specimen no. 6/30/85 001-001A) are 8.4 cm length and 4.4 cm width; the dimensions of the smallest whole lamina (specimen no. 7/30/70 III P382-306) are 2.5 cm length and 1.4 cm width. Length/width ratios range from 1.7 to 1.91 (n= 4). Leaf apices vary from acute to acuminate, and have an average angle of divergence of 33.5 degrees (range 27 to 47; n= 8). Leaf bases are obtuse, sometimes rounded, and have an average angle of divergence of 129.4 degrees (range 112 to 146; n= 5). Petioles are preserved in only a small

percentage of the leaves. It is not known whether any of the petioles are preserved in their entirety, but their length ranges from .8 cm to 1.9 cm. Most of the petioles are of normal width, but several are slightly wider than the others. It is not clear if these wider petioles are undamaged.

Leaf margins are serrate with the teeth conforming to Hickey's (1979) types A1, B1, B2, and C1. The teeth generally have rounded sinuses; a small number of sinuses are angular. Irregular spacing separates the teeth which may be either simple or compound. When the teeth are compound, they occur in pairs with the distal tooth being larger. The number of teeth varies from 3 to 6 per centimeter (mean= 4.2; n= 9). Teeth are of the chloranthoid type (see Figure 43) and terminate in what appears to be a dark gland. The basal margin of the lamina is free from teeth.

The primary venation is actinodromous and has five basal radiating veins. The midvein is the strongest vein; the alpha pectinal veins are pronounced; and the beta pectinal veins are usually quite weak. The midvein follows a straight course while the alpha and beta pectinals curve toward the apex of the leaf. Alpha pectinal veins depart from the midvein at an average angle of 26.4 degrees (range 18 to 34; n= 36). The alpha pectinal veins do not extend to the apex of the lamina, but join superior secondary veins at a point approximately three-quarters of the



Figure 43. Camera lucida drawings of the fossil trochodendroid leaves from the Blackhawk Formation. Note tooth and gland shape and chloranthoid architecture. Specimen numbers: A. 7/30/70 III P382-300 C. 6/30/85 001-001A D. 6/30/85 001-001A.

distance to the apex. They usually form acute or rarely obtuse angles with the superior secondaries that are close to 90 degrees. The beta pectinal veins depart from the midvein at an average angle of 52 degrees (range 39 to 61; n=15). At a point about one-third of the distance to the apex of the leaf, the beta pectinal veins join alpha abmedial secondary veins (alpha abmedials) which are departing from the alpha pectinals at acute or obtuse angles which approach 90 degrees. In some leaves the beta pectinals are reduced to the point where they are identical to the other alpha abmedial veins with which they form brochidodromous loops. The beta pectinal veins are weakest in the smaller leaves. Gradual, apically directed curvature characterizes both the alpha and beta pectinal veins until they join a superjacent secondary vein.

Secondary veins are associated with all three types of primary venation: secondaries depart from the midvein (called superior secondaries); secondaries depart from the alpha pectinals (alpha abmedials); and secondaries depart from the beta pectinals (here called beta abmedials). Very weak secondary (or tertiary?) veins arise from the midvein and appear to form chevrons in the axils of the midvein and alpha pectinals, but it is not clear if they join the alpha pectinals or not. A secondary vein of much greater strength arises from the midvein about three-quarters of the distance to the leaf tip and joins the subjacent alpha pectinal vein. The average angle of departure for this

strong secondary vein is 57.1 degrees (range 47 to 67; n= 8). Weak superior secondary veins (those departing the midvein proximally to the strong secondaries) have an average angle of divergence of 70.75 degrees (range 62 to 94; n= 4). Moderately sized alpha abmedial veins form relatively large brochidodromous loops, beginning with the beta pectinal vein. The average angle of departure for the most proximal alpha abmedial vein is 59.8 degrees (range 54 to 67; n = 9). The beta abmedial veins also form brochidodromous loops near the margin. Branches from the beta abmedial veins feed the teeth in the lower third of the leaf, and branches from the alpha abmedials feed the teeth where these veins occur. Teeth in the apical third of the leaf are fed by branches off of brochidodromous superior secondary veins.

Tertiary venation appears to run between primary veins, superior secondary veins, and alpha abmedial veins, but it is so faintly preserved that course pattern is difficult to recognize. Indeed, as mentioned above, the distinction between weak secondary and tertiary veins is not clear. However, some faintly visible tertiary veins between the midvein and alpha pectinals appear to form apically directed chevrons and a reticulate pattern, both of which may be the result of branches of apically directed tertiary veins. Fourth order and any higher order venation cannot be seen except for the fine veins which enter the teeth. The type of areolation is unknown.

DISCUSSION

THE PLATANOIDS

Platanaceae

The extant family Platanaceae consists of a single genus but there is no consensus on the total number of species. Cronquist (1981) suggests 6 or 7 species while Schwarzalder (1986) bases his study on 11 species and one variety. Traditionally, leaf characters have played the major role in delimiting the species. As this study and others have noted, leaf morphology is highly variable within individuals, to say nothing of entire species, so that taxonomies dependent on leaves could be expected to be disharmonious. Leroy (1982) has separated the extant genus into two subgenera where subgenus <u>Castaneophyllum</u> consists solely of <u>Platanus kerrii</u>, and subgenus <u>Platanus</u> contains the remaining species.

Extant Platanaceae are distributed from the eastern Mediterranean region to the Himalaya Mountains, and southeast Asia, and from Mexico to eastern Canada in North America. Subgenus <u>Platanus</u> has its center of diversity in the southwestern United States and Mexico; the only species of subgenus <u>Castaneophyllum</u> occurs in tropical Laos and Vietnam.

The foliar physiognomy of the Platanaceae is fairly diverse, especially if the fossil representatives are

considered. Late-season leaves of the extant species which I have examined are generally pinnately veined and unlobed, or palmately veined with three to five or more lobes. Tn this study, Platanus occidentalis and P. Xhybrida are examples of the three-lobed morphology, and P. racemosa and P. lindeniana represent the five-lobed morphology. The single living species in subgenus Castaneophyllum, P. kerrii, is exceptional in having elliptic, non-lobed, pinnately veined leaves that lack platanoid teeth (Leroy 1982, Baas 1969). In this study, unlobed leaves with pinnate venation are also noted in the case of the first leaf of the heterophyllic shoots of the four species examined in subgenus <u>Platanus</u>. Some fossil representatives of the Platanaceae from the Cretaceous (Aspidiophyllum and Eoplatanus) and, more commonly, Tertiary Platanus, are quite similar to extant three- and five-lobed forms. Other Late Cretaceous platanoids, such as Credneria, have broad, unlobed laminas. Paleogene representatives of the genus Macginitiea, which contains four species, bear from five to nine narrow lobes. The Paleocene genus Platanites has compound leaves with one large, shallowly three-lobed central leaflet, and two small, ovate, asymmetrical lateral leaflets. Another unlobed, pinnately veined species is Platanus neptuni from the Tertiary. It has elliptic to obovate laminas, but differs from the extant P. kerrii in having craspedodromous secondaries. A palinactinodromously compound leaf with three to five oblanceolate leaflets, known as Platanus fraxinifolia, is another unusual

morphology.

A review of foliar heteromorphism

The Platanaceae are notable for diverse leaf morphologies among different taxa, ranging from pinnate to palmate venation and simple to compound leaves, as well as for a wide range of developmentally based infraspecific Foliar heteromorphism has been recognized variability. from the Platanaceae and various other woody genera, and is a complicating factor in the taxonomy of both living and Spach (1841; in Depape and Brice, 1966) fossil taxa. observed that individual species of <u>Platanus</u> are polymorphic in terms of different developmental stages of canopy leaves and leaves from shoots arising from the base Two types of foliar heteromorphism, known as of trees. heteroblasty and heterophylly, have been distinguished to accomodate this foliar variability (Critchfield, 1960). Heteroblasty is the condition where juvenile individuals bear foliage which is morphologically distinct from that of Heterophylly refers to morphological variability adults. that can be noted in leaves from a single shoot.

The concept of heteroblastic development in plants was formulated by Goebel in 1900, and was apparently prompted by Haeckel's then widely accepted biogenetic "law" (Kaplan, 1980). One of the best known examples of heteroblasty is found in the phyllodineous species of <u>Acacia</u>. Kaplan (1980) examined several species of <u>Acacia</u> in great detail

and pointed out the dramatic replacement of pinnatifid leaves in juveniles by simple leaves or phyllodes in the adults. Eckenwalder (1980) reported that heteroblasty is present to some degree in all species of <u>Populus</u>, and two Mexican species exemplify a pronounced heteroblasty. <u>Populus mexicana</u>, for example, has willow-like, narrowly oblong juvenile leaves, and long-acuminate, broadly ovate adult leaves. Details of the margin and major and minor venation are also distinct. <u>Acer</u> is another common genus exhibiting this phenomenon (Critchfield, 1971).

Examples of heterophylly have been well documented for several extant woody taxa. The genus Populus is known for heterophyllic, as well as heteroblastic, development (Eckenwalder, 1980). Populus monticola has late leaves which are more narrowly ovate and have more regularly shaped, and more numerous, teeth than early leaves. The most striking example of seasonal heterophylly among the extant poplars is in Populus alba where late leaves are palmately lobed, but early leaves are ovate. Critchfield (1960) discussed leaf dimorphism in Populus trichocarpa and noted that short shoots bear only early leaves, long shoots bear early leaves proximally and late leaves distally, and adventitious shoots bear only late leaves. Morphological differences between these two leaf types involved petiole length, presence and size of marginal glands, vein coarseness, leaf thickness, and stomatal distribution. Critchfield suggested that the early leaf--late leaf

distinction may be the consequence of differing ontogenies. He found that early leaves overwinter as embryonic leaves and therefore have a prolonged and interrupted period of development. In contrast, the first two or three late leaves and adventitious shoot leaves overwinter as arrested primordia, allowing for continuous rather than interrupted development during one growing season.

Critchfield (1971) also reported that heterophylly is present in some species of <u>Acer</u>, associated with long and short shoot systems. Early leaves of <u>Acer pensyslvanicum</u> have three nearly equal lobes in contrast to the late leaves (especially the first pair) which have very reduced lateral lobes, an elongated central lobe, and a narrow lamina. <u>Acer rubrum</u> also has late leaves with smaller, more exmedially divergent lateral lobes.

Parthenocissus tricuspidata exhibits both seasonal heterophylly and heteromorphism associated with short and long shoot systems (Critchfield, 1970b). Early leaves have three nearly equal lobes while late leaves have quite reduced lateral lobes and fewer teeth. Leaves transitional between these two types generally do not occur except in aberrant shoots.

Dancik and Barnes (1974) investigated the foliar heteromorphism within single individuals of <u>Betula</u> <u>alleghaniensis</u> and found dimorphism corresponding to short and long shoots as well as variation among short shoot leaves within a single crown.

<u>Ginkgo biloba</u>, which does not show a sharp

morphological distinction between early and late leaves, does bear somewhat different leaf types on short and long shoots: leaves are undivided or slightly bilobed on short shoots, and deeply dissected into two or more lobes on long shoots (Critchfield, 1970a).

Heterophylly in extant <u>Platanus</u>

Foliar heteromorphism of a quite pronounced nature was found in all four of the extant species of <u>Platanus</u> examined for this study. In particular, heterophylly and differences between shoot types are greatly developed in <u>Platanus Xhybrida</u>, <u>P. occidentalis</u>, and <u>P. racemosa</u> (see Figures 4, 13, 24, and 37). Heterophylly, as used here, refers to the changing morphologies of successive leaves along a single shoot.

Fundamental differences occur in the foliar heteromorphic patterns present in inflorescence-bearing shoots, two types of non-inflorecence shoots, and sucker shoots (basal sprouts) of <u>P. Xhybrida</u>. Inflorescence shoots display what I have termed a "reset" pattern of development where the morphological patterns expressed by the leaf sequence prior to an inflorescence node are repeated after such a node. Non-inflorescence shoots from the same tree do not show such a "reset" pattern but do follow other heterophyllic patterns common to the other three shoot types. Sucker shoots, which also lack a "reset" pattern, follow a developmental pattern that is markedly different, at least in the initial leaves, from

most crown shoots. Consistent and predictable patterns of change in various morphological features can be followed through successive leaves on each of these four types of shoots.

Repetitive patterns of change are exhibited by lamina size and gross shape in P. Xhybrida and P. occidentalis. Lamina area was found to increase in successive leaves of non-inflorescence crown shoots of both species until about the middle leaf, after which the size would progressively decrease or remain relatively constant. The leaves of shoots of P. Xhybrida that bear an inflorescence increase in size until the inflorescence node, at which point they become small again and resume a progressive increase. Sucker shoots may (though not always) begin with much larger leaves than any type of crown shoot, diminishing in size by about the third leaf.

Gross morphological variations were partially quantified by measuring the angles of leaf apices, angles of divergence of lamina bases, angles between central and lateral lobes, and by calculating ratios relating length to width (1/w), sinus incision distance to width (s/m), and sinus incision distance to length (u/t).

The angles of the leaf apices showed a narrowing trend in both pre- and post-inflorescence shoot sequences, but showed less consistency in the other types of shoots. In terms of apical angles, considerable variation (16 to 56 °; mean= 31° ; n= 47) was found in <u>P. Xhybrida</u>. <u>Platanus</u> <u>racemosa</u> varied to an even greater extent ranging from 15

to 77° (mean= 43° ; n= 9). The normal foliage of <u>Platanus</u> <u>occidentalis</u> was less variable (20 to 42° ; mean= 26.7° ; n= 15) than the others except for an unusual orbicular leaf form which had an average apex angle of 142° (range 130- 160° ; n= 3).

The angles of divergence of the base of the laminae of P. Xhybrida, P. occidentalis, and to a lesser extent, P. racemosa, produce a conspicuous pattern of seasonal heterophylly. In all cases the base of the lamina grows increasingly reflexed through successive leaves, even to the extent of occasionally overlapping basal "lobes". Inflorescence shoots which display a reset pattern in lamina size also show a reset in lamina basal angles. Inflorescence shoots, Type I non-inflorescence shoots of P. Xhvbrida, and the non-inflorescence shoots of P. occidentalis, begin a leaf sequence with roughly truncated leaf bases; Type II non-inflorescence shoots and sucker shoots begin with cuneate to decurrent leaf bases. **A**11 types of shoots of these two species eventually produce leaves with basal angles exceeding 180°. The basal angles of <u>P. racemosa</u> follow the same general pattern except that the maximum basal angle is smaller.

<u>Platanus occidentalis</u> has been noted as having narrow projections of the lamina around the lamina-petiole juncture since at least the late 19th Century (Ward 1888, 1890). These are also evident in this study. Ward (1890) named <u>Platanus basilobata</u> from the Upper Cretaceous on the

basis of similar basal projections and suggested that this feature supports an affinity between the fossil taxon and the modern genus <u>Platanus</u>.

Additional variations also occur in the base of the lamina of <u>P</u>. Xhybrida and <u>P</u>. occidentalis. As noted previously, lamina bases can range from cuneate to truly decurrent, particularly in sucker shoot leaves. Additionally, lamina bases can also extend across the petiole, forming a peltate condition. Ward (1888) noted that the lamina of the Upper Cretaceous <u>Aspidiophyllum</u> <u>trilobatum</u> is constructed in this manner, and he compared it to modern <u>Platanus</u> leaves with the basal laminar projections, but not to the more strictly comparable modern peltate leaves.

Changes in the depth of the lateral sinuses contributed to the gross morphological variation in leaves of seasonally heterophyllic shoots. S/m and u/t ratios show that the sinuses between central and lateral lobes became deeper relative to the midvein and relative to the lamina base for successive leaves. The angles between the lobes also decreased with the broadest sinuses present in the first leaves of a sequence, unless that leaf lacked lobes, and the narrowest sinuses in the most distal leaves. Inflorescence shoots displayed reset patterns with respect to sinus depth.

Variation in the number and size of teeth proved to be considerable, although generally predictable. Inflorescence and Type I non-inflorescence shoots of <u>P</u>

Xhvbrida bore leaves which had very few teeth on the first three to five leaves, but many teeth in succeeding leaves. The shift from few teeth to many teeth was usually, though not always, abrupt. In inflorescence shoots the large increase in tooth number occurred at the inflorescence node, and thereby added to the distinctive appearance of the "reset" leaves. A slight increase in the number of teeth typically occurs in each succeeding leaf in both preand post-inflorescence sequences. Much of the increase in the number of teeth is often due to the minute papillate teeth which do not normally occur in pre-inflorescence leaves, but which are common in post-inflorescence leaves. Normal platanoid teeth of quite variable size also increase in number with the inflorescence node leaf. Type I noninflorescence leaves abruptly acquire papillate teeth and greater numbers of typical platanoid teeth midway along the shoot. This is notable because this same pattern is associated with the reset phenomenon in inflorescence shoot leaves. Type II non-inflorescence shoots and sucker shoots were unique in having papillate teeth on each leaf. In fact, tooth number was much higher, including platanoid teeth, on all of the leaves of these shoots, particularly the first leaves. Teeth generally diminish in size distally along each lobe of each leaf for each shoot type. Large teeth are always fed by craspedodromous secondaries while smaller teeth can be fed by secondaries, branches of secondaries, tertiaries, or quaternaries. <u>Platanus</u>

<u>racemosa</u> is also highly variable in tooth number, though less so in tooth size. Some leaves are entire margined while others can have both platanoid and papillate teeth, or simply large numbers of papillate teeth.

Venation patterns demonstrated consistency in some features and variability in others, including some repetitive patterns of variability. Secondary venation of the first leaves of both segments of inflorescence shoots, and non-inflorescence shoots, usually was pinnate. Sometimes these first leaves would clearly have strengthened basal secondaries, but in either case the succeeding leaves would develop increasingly strengthened alpha pectinal veins (lateral primaries). The second or third leaf of a series would have clearly developed alpha pectinals and rudimentary, or moderately developed beta pectinal veins. It should be noted that the development of unambiguous pectinal veins may not be evident until the second or third leaf in a shoot sequence, so that designating some of these early transitional veins as being pectinals is a matter of judgment. Platanus Xhvbrida, P. occidentalis, P. lindeniana, and P. racemosa all have the palinactinodromous condition present in late leaves, and the actinodromous condition as intermediate to the initial pinnate venation. The point of departure for the alpha pectinals can be either suprabasal or basal for all four species, and at least in P. Xhvbrida, P. occidentalis, and P. racemosa different leaves from the same shoot can show both conditions. Little difference is shown in the angle

of departure of the secondary veins in the central lobe as compared to the alpha pectinal veins from the same shoot, although the secondary angles are usually slightly larger. In sucker shoots of <u>P</u>. Xhybrida, and the morphologically similar Type II non-inflorescence shoots, the secondary angles of departure are significantly broader than the alpha pectinal departure angles.

Each of the four species in this study can have craspedodromous, semicraspedodromous, brochidodromous, and eucamptodromous secondary venation. Individual leaves may even exhibit all of these patterns. Patterns in the change of course of secondary veins are also a prominent feature of the heterophyllic sequences of some species of Platanus. The pre-inflorescence leaves of Platanus Xhybrida and the non-inflorescence leaves of this species and Platanus occidentalis are primarily characterized by brochidodromous and eucamptodromous venation. As successive leaves of both inflorescence-bearing and non-inflorescence shoots acquire more teeth they also gain more craspedodromous secondaries and lose those types of secondary veins which do not enter teeth. Consequently, post-inflorescence leaves and middle season to late season non-inflorescence leaves become primarily craspedodromous. A somewhat intermediate condition of semicraspedodromy is found most commonly in the leaves of P. occidentalis that occur between the initial non-craspedodromous leaves and later craspedodromous leaves, and in the non-sucker foliage of P.

racemosa.

The tertiary venation of the extant Platanaceae maintains a great deal of uniformity across different species and through the leaves of the heterophyllic sequences of <u>P. Xhybrida</u>, <u>P. occidentalis</u>, and <u>P. racemosa</u>. Variability in this venation type ranges, in order of increasing regularity, from reticulate to forked percurrent to percurrent. Forked percurrent and percurrent courses are generally the most frequent type in any leaf, except for early sucker shoot leaves (as discussed below). Sequential patterns of change through the heterophyllic series were not observed. It is worth noting that the highest percentage of percurrent tertiaries occurred in the central lamina region and not in the distal regions of the lobes.

The source of greatest infraspecific variability in leaf morphology observed in this study was exhibited by basal sprouts (sucker shoots) of both <u>Platanus Xhybrida(?)¹</u> and <u>P. racemosa</u>. These shoots arise from the base of a standing tree or from the base of stumps. Sucker shoot leaves, principally those from early shoot growth, varied considerably in gross morphology and vein architecture from typical canopy foliage. It should be noted that, occasionally, vigorous sprouts do arise from the main limbs of the canopy or crotches between the main limbs that are

¹As noted in the systematics section, the stump suckers reported as <u>P</u>. Xhybrida may be <u>P</u>. <u>occidentalis</u>.

quite similar to sucker shoots. However, by convention, reference to "crown" foliage in this discussion excludes these vigorous crown sprouts which were not sampled.

Heterophyllic sequences characterized by changes in the same morphological features as those that varied in crown shoots were found in sucker shoots. The greatest divergence from typical crown foliage occurred in the first leaf of the season and was followed by progressive change in several morphological features through successive leaves that eventually lead to morphologies identical to the general crown type. The first leaves of sucker shoots of both species are large and the sinuses between lobes are not deeply incised, relative to crown leaves. After the first two or three leaves, development through the remainder of the season results in smaller leaves with deeper incisions between the lobes. The lamina bases of the sucker shoot leaves of P. Xhybrida are notably decurrent throughout the heterophyllic series even after the laminae have developed the reflexed bases typical of most crown leaves. Platanus racemosa differs in that these same leaves are initially rounded basally and become truncate.

Tooth shape and number change through the heterophyllic series found on basal sprouts. The earliest leaves of <u>P</u>. Xhybrida have the most teeth, many of which are the papillate type. The number of papillate teeth diminishes in later leaves of both species. Tooth shape

changes from broad in early leaves of both species to attenuated in later leaves of <u>P</u>. Xhybrida and to narrower, serrate teeth or an entire margin in <u>P</u>. racemosa.

In addition to distinctive gross morphologies, sucker shoot leaves of both species differ in the organization of the lower orders of venation. Primary venation remains relatively constant in sucker shoots except for unequal points of divergence of the lateral primaries in individual early leaves of shoots of P. Xhybrida. Additional strengthened basal, lateral veins may also be present in at least the first sucker leaf of Ρ. Xhybrida. Palinactinodromy appeared gradually in <u>P. Xhvbrida</u> as the alpha pectinal veins differentiated from the other abmedial secondary veins. <u>Platanus racemosa</u>, which has a five lobed leaf, acquires palinactinodromy more quickly in sucker shoot leaf sequences. Leaves of this species that fall midway between the early "disorganized" leaves and the late season crown-type leaves are some which possess "accessory" lobes in the sinuses between the central and lateral lobes. These unusual lobes are smaller than the normal, subjacent lateral lobes and are formed by a strengthened superior secondary or admedial secondary vein.

Secondary and tertiary venation is much less organized in the initial sucker shoot leaves of both species than in later leaves and crown leaves. Less regularity in course and wider spacing characterize the secondary venation of both species, while <u>P</u>. Xhybrida also has greater bifurcations of the secondaries in these early leaves.

Dissymetry is further enhanced by frequent intersecondary veins which grade into tertiary veins. The secondary and tertiary venation of the early sucker shoot leaves of <u>Platanus racemosa</u> exhibit greater dissymetry than <u>P</u>. Xhybrida.

Diagnosis of the Platanaceae

Many of the Tertiary fossil leaves belonging to the family Platanaceae can be readily associated with the family because of their close correspondence to the gross morphology of the leaves of extant subgenus <u>Platanus</u>. Unfortunately, the situation does not remain so straightforward when infraspecific variability, "atypical" morphologies of extant taxa, and the fragmentation of leaves, are considered.

Various authors have commented on family level foliar diagnostic traits for the Platanaceae, but Schwarzwalder and Dilcher (in press) have done the most thorough treatment that I have found. They indicate that no single morphological feature is unique to the family, but several characteristics, used together, are highly significant for recognition of the family. The most important characteristics are: the suprabasal actinodromous or palinactinodromous pattern of primary venation, the convergence of secondary veins upon superadjacent secondaries in the lobes through a series of loops that culminate in the "platanoid tooth", the formation of

chevrons by tertiary veins in the axils of primary veins, the percurrent to reticulate nature of the other tertiary veins, and highly orthogonal higher orders of venation. Schwarzwalder and Dilcher also indicate that cuticle of the Platanaceae has distinct protruding trichome bases. They found the atypical <u>Platanus kerrii</u> to be like subgenus <u>Platanus</u> in its higher order venation and epidermal features, but pinnate venation, unusual tooth vasculature, marginal venation and secondary venation clearly segregate it from the remainder of the extant family.

This study concurs with the judgments of Schwarzwalder and Dilcher (in press) as to the systematic usefulness of these morphological characters (except cuticular traits which I have not examined). However, other morphological features can also indicate platanaceous affinities for fossil leaves and leaf fragments. Of primary importance in this regard is the heteromorphism and sequential heterophylly present in the extant subgenus Platanus. The high degree of foliar variability and the heterophyllic are themselves a diagnostic patterns of change characteristic of subgenus Platanus and can be expected in extinct taxa of the Platanaceae as well. Suites of leaves that have tertiary and higher order venation consonant with the above characteristics, but show variability in number of lobes, depth of lobe sinuses, numbers of teeth, size and shape of teeth, spacing, course, and regularity of secondary veins, course and regularity of tertiary veins (as represented by sucker shoots), and particularly in the
shape of the lamina base, bear significant resemblance to the highly heteromorphic modern Platanaceae.

Lamina bases can be particularly valuable in identifying the family. Their uniqueness lies in the great variability they display both in hetrophyllic series, where they can vary from acute to strongly reflexed (basal angle >360 degrees), and in the decurrent or loosely peltate condition found in some canopy leaves and most sucker shoot leaves of some species. Other taxa which superficially resemble platanaceous leaves, such as the Vitaceae and Viburnum, can be eliminated by their foliar regularity and lack of decurrent or peltate lamina bases. As Ward (1888, 1890) observed, the presence of narrow basilar projections of the lamina around the petiole is also an indication of this family. Schwarzwalder and Dilcher (in press) refer to the lamina bases of Aspidiophyllum, Credneria, Eurylobum and stump sprouts of <u>Platanus occidentalis</u> as being perfoliate. However, I question whether this term is appropriate. Perfoliate refers to leaves which are sessile and have the stem passing through them. This morphology would be highly unusual for the Platanaceae. I have never seen a stump sprout of P. occidentalis, P. Xhybrida, or P. racemosa with this morphology, nor have any figured platanoids that I have seen convincingly show this condition. Those figured fossil platanoids with apparent peltate lamina bases and no visible petiole may simply have the petiole curving downward into underlying sediments.

Schwarzwalder and Dilcher (in press) report that the multidimensional scaling and cluster analysis tended to separate leaves with a perfoliate (peltate?) base into distinct groups based upon other morphological characters. As they note, this would be expected based upon the present state of <u>Platanus</u> variability.

Tooth architecture is usually of the platanoid type, but this feature too, is not consistent throughout the family. <u>Platanus kerrii</u> has unique marginal venation which includes unusual tooth architecture consisting of vascularization by branches of an inner marginal vein, and bracing on either side by an outer marginal vein (Schwarzwalder and Dilcher, in press). Wing (1981) also found <u>Platanus guillelmae</u> from the Eocene to have violoid teeth.

The presence of extensive heteromorphism also suggests significant applications in the systematics of fossil species already identified as belonging to the Platanaceae. Workers with platanoid leaves should strongly consider the potential that their suites of variable leaves represent heterophyllic shoots, including sucker shoots, derived from single taxon (or even a single individual). a Characteristics such as, the presence or absence of alpha and beta pectinal veins, highly ordered versus dissymmetrical venation, lobe number, tooth number and size, angles between lobes, and shape of the lamina base, have all been used to distinguish fossil form-species, but all of these can be highly variable within even a single

modern species.

The possibility that different fossil <u>Platanus</u> species represent adult and sapling foliage of a single species has been suggested by Wing (1981) for two sets of taxa. He suggested that <u>Platanus guillelmae</u> may be the sapling foliage of <u>P. brownii</u> which occurs in the same locality because <u>P. guillelmae</u> has characteristics similar to those of the sapling foliage of <u>P. occidentalis</u>. He also suggests that <u>P. raynoldsii</u> and <u>P. nobilis</u> may have a similar relationship.

Fossil leaf taxa that fall into the general category of the platanoids have been consistently confused with taxa morphologically and architecturally similar to the Platanaceae. Several points can be made here concerning some of the families and genera that are easily mistaken for unlobed platanaceous leaves. The following observations are not based upon complete surveys of the families and genera in question, but they are valid for at least portions of these groups.

The Vitaceae, <u>Viburnum</u>, and the Menispermaceae are some of the most potentially difficult taxa, especially the unlobed forms. All three of these taxa have members with actinodromous primary venation and percurrent tertiary veins (which also often form chevrons in the axils of primary and secondary veins). These features are conspicuous and shared with the Platanaceae (subgenus <u>Platanus</u>) so that they have frequently been a source of

misidentifications. However, none of these taxa has platanoid teeth. The majority of the Vitis herbarium material which I examined commonly has teeth that conform to Hickey's (1979) types A1 (convex-convex) and B2 (straight-straight). These tooth types are uncommon in Platanus. Some Viburnum species do have dimorphic foliage (unlobed and three-lobed leaves) as well as primary, secondary, and tertiary venation similar to Platanus, but lack platanoid teeth. Some members of the Menispermaceae are similar to Platanus; Menispermum canadense even bears unlobed, three-lobed and five-lobed leaves. In addition, Ruffle (1968) considers the Cretaceous Credneria cuneifolia to be menispermaceous rather than platanaceous on the basis of gross leaf morphology. He also states that the cuticle of this fossil bears similarities to some the Menispermaceae. However, Hollick (1930), Brown (1962), Depape and Brice (1966), Kutuzkina (1974), and Schwarzwalder and Dilcher (in press) all regard Credneria as belonging to the Platanaceae. Wolfe (1977) indicates that the Menispermaceae can be identified by the presence of marginal (fimbrial) veins, and irregularly branching intercostal tertiaries. Finally, none of the representatives of the above taxa that I have examined possess the heteromorphic variability found in subgenus <u>Platanus</u>: the variability in secondary venation, tooth size and number, and particularly the lamina base. Large suites of fossil platanaceous leaves would be expected to demonstrate considerable heteromorphism (unless, of course,

the fossil taxon is more similar to extant subgenus <u>Castaneophyllum</u> which has simple, unlobed leaves).

The status of Cretaceous platanoids

The identification of angiosperm leaf megafossils in the Cretaceous, as well as other time periods, is impeded by several difficult problems. Two of the problems are especially significant if the goal of the inquiry is the reconstruction of "whole plants" from the fossils. The first problem concerns the high degree of intraspecific foliar variability in modern taxa and the recognition of such variability in fossil taxa. Foliar heteromorphism is present in varying degrees in many woody taxa, and some, such as the extant Platanus examined in this study, and Acacia, are remarkably heteromorphic. Others, such as <u>Cercidiphyllum</u>, members of the Aceraceae, and <u>Ginkgo</u>, are at least dimorphic if not polymorphic. If pronounced intraspecific variability is present in extant taxa, the possibility of similar variability in related fossil taxa must be considered.

Among the fossil angiosperms, Cretaceous and Paleogene platanoids and trochodendroids are notorious for forming what are often called "complexes" where the intergradation of leaf morphologies obscures taxonomic boundaries. This intergradation of leaves in the fossil record could have several sources. Spicer (1986) suggests that Cretaceous leaf fossils may be exhibiting extensive morphological

intergradation because of evolutionary radiation, overlapping population samples, hybridization, polyploidy, or phenotypic plasticity. Surprisingly, he devotes the least consideration to plasticity when, in fact, the Cretaceous platanoid leaves which form a significant part of his data base, are today represented by <u>Platanus</u> which exhibits tremendous foliar plasticity. How can questions concerning hybridization, polyploidy, and evolutionary radiations be addressed prior to thorough considerations of heteromorphic variability in the highly plastic modern equivalents?

The second problem is the practical side of the first: How are the leaves and leaf fragments of taxa with suspected high intraspecific variability to be identified and named? If the leaves of a modern Platanus Xhybrida were preserved in a sedimentary basin, what could the "fossil" record look like? First, it should be emphasized that sucker shoot leaves would be expected to constitute a very small percentage of the total <u>Platanus</u> Xhvbrida leaves in a deposit. But at least leaves from four shoot types, each of which bears a somewhat distinct heterophyllic pattern, could potentially be found. It is probable that when the entire melange of leaves was sorted out, four or even five (due to the "reset" phenomenon) distinct heterophyllic sequences might be recognized. In addition, because of the rarity of sucker shoot leaves and the inevitable gaps in the morphological transitional series among leaves and shoot types, the situation that would

emerge is a "complex" of leaves showing much intergradation, but also apparent morphogical discontinuities.

To what extent should individual taxa be segregated from this assemblage of leaves? This is a difficult question and it has been approached from both "splitting" and "lumping" perspectives. Many of the older workers such as Lesquereux (e.g. 1892) and Hollick (1930) opted for a high degree of taxonomic "splitting". Hollick (1930) named new fossil <u>Platanus</u> species which, on morphological criteria, could certainly have come from the same tree. He also named new platanoid genera (e.g. <u>Pseudoprotophyllum</u> and <u>Pseudoaspidiophyllum</u>) on the basis of relatively minor differences.

Some modern approaches to dealing with fossil leaves showing high variability and intergradation of morphologies have sought a more realistic method for identifying and naming the fossils. One approach is that of Spicer (1986) who suggests a preliminary taxonomic framework for Cretaceous leaves which groups specimens into forms that are broad morphological categories prior to assignment to formal names. The utility of this approach is that it seeks a larger data base to accomodate the variability of populations of leaves and thereby hopefully avoid excessive taxonomic revisions necessitated by premature conclusions. However, these same goals are inherent in the traditional form species and genus concepts. A careful approach to the

naming of Cretaceous angiosperms using form species and genus names attendant upon a critical assessment of the variability of suites of both fossil and modern leaves would accomplish the same goals. Eleven different forms were used by Spicer (1986) to accomodate Alaskan Cretaceous leaves. Most of these categories are subdivisions of, or equivalent to, Krassilov's (1977) earlier foliar morphological types.

The recent quantitative approach of Schwarzwalder and Dilcher (in press) is another attempt to delimit Cretaceous fossil leaf taxa in light of foliar variability. They conducted a phenetic analysis of Cenomanian Platanaceae utilizing cluster analysis and multidimensional scaling, and erected or emended thirty-two species in five genera using methods which utilized all of the available data, deemphasized morphologically plastic characters, eliminated or minimized overlap between taxa, and were broadly defined for ease in identification.

Mid-Cretaceous and Upper Cretaceous angiosperm leaf fossils have been grouped under informal descriptive names by Crabtree (1987) in a manner like that of Spicer (1986) and Krassilov (1977). Crabtree's categorization of platanoid leaves is worth reporting here because of its bearing on the Blackhawk platanoids. Three morphotypes of what can be loosely called platanoid leaves were distinguished by Crabtree from mid-Cretaceous floras of western North America.

The pentalobaphyll leaf type is characterized by

Crabtree as having 3-5 lobes, palinactinodromous primary venation with a suprabasal departure, eucamptodromous, weakly developed secondary veins, reticulate to transverse tertiary veins, an entire margin, and a more or less cuneate base. He indicates that although Doyle and Hickey (1976) include Araliaephyllum obtusilobum in their platanoid line, he believes that it falls within a nonplatanaceous pentalobaphyll type because of the entire margins, eucamptodromous secondaries, weak tertiary venation, and absence of orthogonally branching tertiary and quaternary veins. Crabtree does not believe that palmate lobing and palinactinodromous venation are alone sufficient to regard a leaf as platanoid, especially when they are accompanied by other "nonplatanaceous" morphological characteristics (as in Araliaephyllum obtusilobum). Other examples of the pentalobaphylls bear a lauralean affinity as suggested by cuticle morphology, sinus bracing, mesophyll secretory glands, and possible basilaminar secondary veins. A rosid affinity is also apparently suggested by the secondary and tertiary venation of this leaf type.

The second leaf type is termed the platanophylls because of their obvious similarity to subgenus <u>Platanus</u>. These are characterized by lobed or unlobed leaves, entire or serrate margins, palinactinodromous venation with several pectinal secondaries on laterals, and straight secondaries that fork or branch exmedially. Also, the

secondaries may be either craspedodromous with teeth, or brochidodromous with an entire margin; tertiaries and quaternaries form an orthogonal network. The teeth are of the platanoid type and have glandular processes that are often papillate.

The protophylls are another variation of the platanoid leaf type. The leaves are sometimes lobed, and have entire or dentate margins. Venation is pinnate where the basal secondaries are sometimes strengthened and bear pectinal veins. Secondary and higher order venation is similar to the platanophylls. The protophylls are distinguished by Crabtree from the platanophylls by pinnate venation and a more consistent craspedodromy in the protophylls, and a greater tendency toward lobation in the platanophylls. Similarities between the two groups are well-defined, orthogonl-reticulate, tertiary and quaternary venation and an intergradation of the two morphotypes in "many cases" such that "recognition is difficult." Crabtree proposes that the platanophylls are closer to the platanaceous line of the Hamamelidales than are the protophylls.

Neither Spicer (1986), Schwarzwalder and Dilcher (in press), nor Crabtree (1987) comment on the extensive foliar heteromorphism found in extant species of the Platanaceae. While each of these treatments of Cretaceous platanoids is a vast improvement over previous studies which often defined the fossil taxa too narrowly, none of them treat the range of foliar heteromorphism/heterophylly within the modern family. As they currently stand, Spicer's three

platanoid leaf types could all be found in a single individual of Platanus occidentalis. Crabtree's distinction between the platanophylls and protophylls on the basis of lobation and secondary vein architecture should be reconsidered in view of high infraspecific And some of the architectural characters variability. measured by Schwarzwalder and Dilcher among different taxa show less variability than within single individuals of This is not to say that their phenetic modern Platanus. analysis was too discriminating, but the study could only benefit from a similar phenetic analysis of the foliar heteromorphism in the living taxa. It is possible that a single individual of <u>Platanus</u> Xhybrida would produce distinct clusters in the same phenetic analysis that could be interpreted as different species, if not distinct genera.

Affinities of the Blackhawk platanoids

Both the question of familial affinity and the question of applying the appropriate form-species name need to be considered for the Cretaceous leaves of this study. Table 1 compares certain morphological characters of the Blackhawk platanoid to the corresponding characters in the leaves of <u>Platanus Xhybrida</u>, <u>P. occidentalis</u>, <u>P. lindeniana</u>, and <u>P. racemosa</u>. The Blackhawk platanoid fossils do possess structural characters which are normally suggestive of alliance to the Platanaceae. The fossil

	the Blackhawk plata	noid. All angles ar	e in degrees. MD, mi	issing data. NA, no	t applicable. SE, s	tandard error.
		<u>Platanus</u> X <u>hybrida</u>	<u>Platanus</u> occidentalis	<u>Platanus</u> lindeniana	<u>Platanus</u> racemosa	Blackhævk platanoid
Ι.	lobation	1 - 3	1 - 3	1 - 5	3 - 5 (7)	1
2.	lamina base morphology	obtuse-truncate to reflexed; decurrent in sucker shoots	acute-truncate to reflexed; basal appendages sometimes present	obtuse to truncate	cuneate, obtuse, nearly truncate, cordate, or V-shaped sinus	rounded or decurrent
e.	"reset" pattern in inflorescence shoots	present	absent	£	present	£
4.	l/w ratio	mean = .924 range .777-1.31 SE = .0136	mean = .8 59 range .76943 SE = .0119	mean = 1.18 range 1.03-1.46 SE = .0752	mean = .994 range .717-1.327 SE = .0424	mean = 1.413 range 1.18-1.56 SE = .0869
5.	tooth morphology	platanoid and papillate	platanoid and papillate	platanoid and papillate	platanoid and papillate	papillate?
.	number of teeth	mean = 35.4 range 8-102 SE = 3.488	mean = 24.2 range 7-47 SE = 3.453	mean = 6.4 range 4-10 SE = 1.122	mean = 20.9 range 3-62 SE = 4.827	£
٦.	angle between central and lateral lobes	mean = 92.3 range 44-131 SE = 2. 542	mean = 116 range 98-149 SE = 1.922	£	mean = 47.8 range 21-89 SE = 3.45	NA
.	apical angle	mean = 31 range 16-56 SE = 1.388	mean = 26.7 range 20-42 SE = 1.617	mean = 32 range 24-46 SE = 4.83	mean = 42.9 range 15-77 SE = 6.83	mean = 97.5 range 90-105 SE = 7.5
9.	basal angle	mean = 219 range 88-316 SE = 7.45	mean = 222.5 range 132-306 SE = 12.19	mean = 137.6 range 118-164 SE = 7.49	mean = 146 range 68-231 SE = 14.29	mean = 140.5 range 134-147 SE = 6.5
10.	l venation architecture	pinnate, actinodromous, palin- actinodromous	pinnate- actinodromous- palin- actinodromous	pinnate, actinodromous, palin- actinodromous	actinodromous, palin- actinodromous	actinodromous

Table 1. Comparison of foliar morphological characters of <u>Platanus Xhybrids, P. occidentalis, P. lindeniana, P. racemosa</u>,

		<u>Platanus</u> Xhybrida	<u>Platanus</u> occidentalis	<u>Platanus</u> lindeniana	<u>Platanus</u> racemosa	Blackhavk platanoid
11	 pectinal departure angle 	mean = 45.5 range 25-64 SE = 1.09	mean = 54.1 range 36-70 SE = 1.674	mean = 39.8 range 30-49 SE = 2.55	mean = 39.9 range 27-51 SE = 1.10	mean = 40.2 range 25-57 SE = 1.76
12	. distance from lamina-petiole juncture to pectinal origin	mean = .363 range 0-1.2 SE = .0357	mean = .117cm range 07cm SE = .0333	£	mesn = .84cm range 0-1.9cm SE = .128	meetn = 1.49cm range 0-4.8cm SE = .697
13	. 2 venation (superior) architecture	eucamptodromous brochidodromous semi- craspedodromous craspedodromous	eucamptodromous brochidodromous semi- craspedodromous craspedodromous	eucamptodromous brochidodromous semi- craspedodromous craspedodromous	eucamptodromous brochidodromous semi- craspedodromous craspedodromous	eucamptodromous? craspedodromous
14	. 2 venation (superior) departure angle	mean = 51.7 range 36-66 SE = .6948	mean = 54.6 range 45-64 SE = .7962	mean = 45.3 range 35-55 SE = 2.07	mean = 57.7 range 43-76 SE = 1.46	mean = 47.6 range 33-59 SE = 1.67
15	. distance between superior 2 veins	mean = 1.91 range .7-3.2 SE = .0678	mean = 1.53cm range .9-2.3cm SE = .0641	Ð	mean = 2.1cm range 0.7-3.4cm SE = .149	mean = 3.7cm range 1.6-6.5cm SE = .371
16	. Intersecondary veins	present	present	present	present	absent
17	. 3 venation architecture	percurrent to reticulate	percurrent to reticulate	percurrent to reticulate	percurrent to reticulate	percurrent to occasionally reticulate
18	. 3 venation angle of departure	mean = 82.1 range 62-92 SE = .6938	mean = 86.4 range 70-97 SE = .6819	Ð	mean = 87 range 70-99 SE = ,945	mean = 84.7 range = 68-107 SE = 1.3
19	. distance between 3 veins	mean = .334 range .1565 SE = .0111	mean = .3cm range .15cm SE = .0126	mean = 85.5 range 72-90 SE = 1.06	mean = .527cm range .25-1.0cm SE = .027	mean = .569 range .39 SE =.028
20	. chevrons formed by 3 veins in axils of primary veins	vell developed	well developed	well developed	vell developed	weakly developed or straight
21	. 4 venation architecture	orthogonal	orthogonal	orthogo na l	orthogonal	orthogonal

Table l continued

leaves are suprabasally actinodromous, and have prominent secondary and tertiary venation. Orthogonal departure angles for the tertiary and quaternary veins, and a tertiary vein course which is predominantly percurrent (but varying to forked percurrent and reticulate) and forms weak chevrons in the axils of primary and secondary veins are also, in concert, distinctly platanaceous. Leaf apices are not well-preserved. However, lamina bases are preserved in a number of leaves and show variability similar to that found in several extant <u>Platanus</u> species: variability ranges from truncated to slightly rounded, and most significantly, several bases have distinct decurrent extensions. In some instances where the lamina margin is visible and bears small spinose/papillate teeth it is slightly scalloped. All of the above characters are important diagnostic traits of the extant subgenus Platanus, and therefore represent, albeit incompletely, the family Platanaceae.

Some of the structural features of the fossil leaves are different from the modern family. The large unlobed leaves have few secondaries that are quite widely spaced as opposed to much narrower spacing in unlobed leaves of <u>Platanus mexicana or P. lindeniana</u>. The secondary veins commonly bifurcate well before the margin. In extant subgenus <u>Platanus</u> bifurcations of the secondary veins occur less frequently and closer to the margin of the leaf. One of the most conspicuous differences is that while the secondary veins of the fossils are craspedodromous, they do

not end in platanoid teeth, or even teeth that simply include portions of the lamina. The few visible teeth are small spinose/papillate projections of the craspedodromous secondary veins, which are superficially similar to the papillate teeth in <u>Platanus</u>. However, the papillate teeth in extant <u>Platanus</u> are generally vascularized by the semicraspedodromous condition or other marginal tertiary or quaternary veins, whereas the fossil leaves have the secondaries ending at the margin or forming the small teeth. The Blackhawk leaves also lack intersecondary veins which are consistently present, to varying degrees, in the extant <u>Platanus</u> species examined. In both of these last features the fossils more closely resemble Actinidia. However, Actinidia lacks orthogonal quaternary venation and decurrent leaf bases. The tertiary venation forms weak chevrons in the axils of primary and secondary veins, but many of these veins are also straight to nearly straight.

The fossil taxon most similar to the Blackhawk platanoids that I have seen is <u>Credneria</u>. Crabtree (1987) includes <u>Credneria</u> in his concept of the protophylls which he suggests are more similar to mainline Hamamelidales than are the platanophylls. But Schwarzwalder and Dilcher (in press) who have recently emended <u>Credneria</u> as a result of their study of Cenomanian platanoids using multidimensional scaling and cluster analysis place it within the family Platanaceae. Included within their revised concept of the genus are some fossil taxa previously assigned to <u>Cissites</u>,

Populites, Pterospermites, and Platanus, as well as the synonymizing of Protophyllum. The Blackhawk platanoids and typical <u>Credneria</u> are similar in having an unlobed lamina, a broad apex (>60 degrees), suprabasally actinodromous primary venation, percurrent to reticulate tertiary veins, and orthogonal guaternary and guinternary veins. The emended description (Schwarzwalder and Dilcher, in press) indicates that the lamina base is variable, sometimes cordate, and ranges from petiolate to slightly perfoliate (peltate?); secondary veins are primarily craspedodromous and diverge from the midvein at angles ranging from >25 to >50 degrees. <u>Credneria</u> <u>pseudoguillelmae</u> (Krass.) Schwarzwalder and Dilcher bears many similarities to the Blackhawk leaves, especially the course and bifurcating nature of the secondary veins. The Blackhawk leaves are always petiolate and some of them have a prominent decurrent extension of the lamina, others have a more rounded base, but none are perfoliate or peltate; the secondary veins are also craspedodromous, but their departure angles range from 31 to 57 degrees (X = 40.2). The secondary veins are also more widely spaced in the To accommodate the Blackhawk leaves Blackhawk leaves. within the generic circumscription of Credneria the generic diagnosis would have to be further emended to account for these variations.

It is recognized that interpretations of family boundaries become especially difficult when considering the historical roots of a family and the potential extent of

the diversity of extinct members of that family. The Platanaceae, whose extensive geological range spans the mid-Cretaceous to the present, is an example of this problem. As described earlier in this paper, the morphological range of the leaves of known fossil Platanaceae exceeds that found in the extant family (subgenus Platanus and subgenus Castaneophyllum). To is, those whose include "atypical" species, that morphologial characters diverge from the known extent of variability, in a higher taxon, there should be either additional characters which are shared with the known taxon, or the divergent characters should lay in a transitional series that provides some amount of continuity with the known taxon. In the case of the Blackhawk platanoids, even though some morphological characters are different from the living species, many foliar architectural features of the fossils are found in the extant family so that an alliance with the Platanaceae is compelling. Indeed, when the range of variability of extinct members of the Platanaeae is considered in conjunction with the extant species, a broader concept of the family unfolds which is even more amenable to inclusion of the Blackhawk platanoids.

Although the Blackhawk fossils can be placed into the family Platanaceae, they do bear many differences with the extant genus <u>Platanus</u>, as ennumerated above. In Parker's (1976) preliminary investigation of the Blackhawk

angiosperms he tentatively assigned the platanoid leaves to the genus <u>Platanus</u>. However, this study has shown that it is more appropriate to place these leaf fossils into a form-genus rather than the extant genus.

Consideration must also be given to the number of form-species that should be recognized for the Blackhawk fossils. Parker (1976) divided the specimens into two form-species and assigned to them the names Platanus ravnoldsii and Platanus alata. Hollick (1930) erected the name P. alata for two figured specimens each of which is only a portion of the basal half of a lamina. The characteristic upon which Hollick based his diagnosis is the presence of a decurrent leaf base. Several other formspecies are also placed in the genus Platanus and figured by him in the same monograph. Taken together, some of these form-species show an intergradation of morphology, including leaves intermediate between the decurrent P. alata and those with more truncated leaf bases. As already noted, several of these figured specimens are also reminiscent of the leaves of stump sprouts and vigorous crown sprouts. Based upon Hollick's (1930) figured specimens, I doubt whether P. alata should remain a distinct form-species. However, the question remains as to whether the Blackhawk platanoid specimens should be segregated into two form species. As with Hollick's (1930) material, the only significant difference between the two forms is the presence or absence of a decurrent leaf base. Unfortunately, few lamina bases are preserved intact.

Those that are preserved do not form a clear transitional sequence between the bluntly decurrent lamina extensions and the truncated to rounded lamina bases. In addition, these extinct members of the Platanaceae may not possess the same type of variability as the extant species. Therefore, although I consider these two forms to constitute a single form-species, I recommend retaining them as two form-species, pending additional collections that demonstrate a greater degree of morphological continuity.

THE TROCHODENDROIDS

As used here, the term trochodendroids refers to fossil morphotypes with actinodromously or acrodromously veined leaves and entire, serrate, or crenate margins. Some of these fossils are known to be members of the Cercidiphyllaceae or Tetracentraceae while others have leaf morphologies suggesting alliance to these families.

Cercidiphyllaceae and Tetracentraceae

The Cercidiphyllaceae is an east Asian family of trees consisting of one genus and two species. <u>Cercidiphyllum</u> <u>japonicum</u> Siebold and Zuccarini is native to Japan and central and western China; <u>Cercidiphyllum magnificum</u> (Nakai) Nakai is endemic to Honshu, Japan (Spongberg, 1979). The two species are very similar but can be

distinguished by minor leaf, stipule, follicle, and seed characters, and the length of the short shoots. Concerning the taxonomic placement of the family, Cronquist (1981) says that it "is generally regarded as related on the one hand to the Hamamelidaceae (especially <u>Disanthus</u>) and on the other to the Trochodendrales and Magnoliales".

The Tetracentraceae is a monotypic family, native to Nepal, central and southwestern China, and northern Burma (Cronquist, 1981). <u>Tetracentron sinense</u> Oliv. and the only species of the Trochodendraceae, <u>Trochodendron aralioides</u> Siebold and Zuccarini, constitute the order Trochodendrales. Cronquist (1981) regards the order as "the most archaic surviving group of Hamamelidae"; both families also have been associated with the Magnoliidae, particularly on the basis of vesselless wood.

The status of fossil trochodendroids

The assessment of the taxonomic affinities of fossil taxa is clearly dependent upon a thorough understanding of the potentially related living taxa. However, it is at this fundamental level that problems first arise when the works of modern authorities are consulted. Not only have the familial affinities of the fossil trochodendroids been elusive, but disagreement has existed over the diagnosis of the relevant living families. In commenting on the ability to distinguish between <u>Tetracentron</u> and <u>Cercidiphyllum</u> in the fossil record, Bailey and Nast (1945) remarked that the

leaves of these extant genera are so distinct that differentiating them as fossils could only be difficult if hypothesized overlap actually existed. Wolfe (1977), on the other hand, stated that "the leaves of extant <u>Tetracentron and Cercidiphyllum</u> are indeed difficult to distinguish." Disagreements among modern workers might be a telltale sign that the separation of these extant taxa does include some pitfalls, but perhaps not so many as Wolfe implies.

In recent years several authors have considered the foliar morphological criteria for recognizing the Cercidiphyllaceae. Chandrasekharam (1974) and Tanai (1981) have been the most thorough in discussing the modern To understand the <u>Cercidiphyllum</u>-like leaves leaves. dominating the Paleocene Genesee flora, Chandrasekharam (1974) made extensive quantitative and qualitative observations of select foliar architectural features of living <u>Cercidiphyllum</u>. However, although he utilizes an extensive data base from the extant species to provide criteria for the segregation of his Genesee material into three species of <u>Cercidiphyllum</u>, and at various points contrasts the Cercidiphyllaceae with Tetracentron, Smilax, Populus, and other genera, he does not provide family-level diagnostic criteria. Tanai (1981) in revising the Cercidiphyllum-like leaves from the Paleogene of northern Japan does provide a family level foliar diagnosis. He distinguished extant Cercidiphyllum leaves from Populus on the basis of smaller areoles, thicker freely-ending

veinlets, larger marginal glands with pointed setae, and thicker tertiary veins in <u>Populus</u>. <u>Tetracentron</u> is distinguished upon the basis of marginal gland morphology. He characterizes the marginal glands of <u>Cercidiphyllum</u> as being globular in shape and sometimes projecting out of the teeth, while glands of <u>Tetracentron</u> are capped by undetached setae, gradually expand toward the tooth apex in a conical fashion, and do not protrude beyond the margin. He notes similarities between these two taxa to be size and shape of the areolation, and veinlets with two or three freely-ending branches.

Among the trochodendroids, the foliar morphological and architectural differences between Cercidiphyllum and Tetracentron are the thorniest because of their many similarities and the attending difficulties in determining fossil material. Chandrasekharam (1974) reported that Tetracentron is distinct in having serrate margins with glandular tips and acuminate apices. An examination of fifty leaves showed that the average angles of departure for the alpha pectinal veins is approximately 15⁰, for the first strong superior secondary vein is approximately 17.5°, and for the alpha abmedials is approximately 20° . In addition, vein islets are regular and intruded by once or twice branched veinlets. Wolfe (1973) distinguishes Cercidiphyllum on the basis of six orders of venation, and intercostal venation which is "formed primarily by closely spaced veins directly connecting the secondaries." Wolfe

(1973) considers some of Brown's (1939) Eocene <u>Cercidiphyllum</u> leaves, and some of MacGinitie's (1941) <u>Cercidiphyllum</u> elongatum to be <u>Tetracentron</u>, but he does not explicitly explain his reasoning for this judgment. In his subsequent paper on the Paleogene floras of Alaska, Wolfe (1977) separates the two taxa by the more elongated larger, more equally sided teeth leaves, and of Tetracentron. But his most definitive criterion is the apical glands of the teeth which are connected by veins to the adjacent sinuses (i.e. chloranthoid teeth of Hickey and Wolfe, 1975) in <u>Tetracentron</u>, but not in <u>Cercidiphyllum</u>. However, a consensus is lacking concerning tooth architecture as Crane (1984) regards both of these taxa to have chloranthoid teeth. Tanai (1981) notes Wolfe's criterion of unbraced marginal glands in Cercidiphyllum, and states that the same condition is sometimes present in C. magnificum.

Apparently, Heer (1876; in Crane and Stockey, 1985) the first to note the similarity of was some actinodromously veined fossil leaves to the genus Cercidiphyllum. The first erection of a form genus, Trochodendroides, to accomodate leaves that resembled Cercidiphyllum was by Berry in 1922 (Crane, 1984). In 1939 Brown reported on the cooccurrence of Trochodendroides and similar leaves with Nvssidium infructescences and seeds at 30 separate North American localities and suggested that they belonged to the same plant. Four species of Cercidiphyllum were erected by Brown from this suite of

leaves on morphological and stratigraphical grounds, but later he found difficulty in maintaining some of them (Brown, 1962).

Despite the ground gained in recent years in understanding fossil Cercidiphyllum-like leaves the situation remains complex. Wolfe (1966) revised Brown's 1939 classification and split Brown's Cercidiphyllum arcticum into five separate species which he felt might even represent five families. His principal criterion for the splitting was variable ultimate venation. These five taxa are Cocculus flabella (Newberry) Wolfe, Trochodendroides serrulata (Ward) Wolfe, Dicotylophyllum <u>richardsonii</u> (Heer) Wolfe, and two undescribed species. In part, Wolfe's impetus for initially suspecting that these taxa were not Cercidiphyllaceae was Chandler's (1961) conclusion that the Nyssidium considered by Brown to be cercidiphyllaceous, was, in fact, not. However, Crane (1984) reexamined the <u>Nyssidium</u> reproductive material and found it to belong to the Cercidiphyllaceae although not the modern genus. Criticism of Wolfe's treatment of <u>C</u>. arcticum has also come from Chandrasekharam (1974) who found that ultimate venation was a tenuous taxonomic character in light of the amount of variability in the two Hickey (1977) uses the phrase, extant species. "Cercidiphyllum arcticum complex" to refer to the five taxa segregated by Wolfe plus others of similar morphology. His use of this term is strictly morphological, though, as he

includes within it "<u>Cocculus</u>" <u>flabella</u> and <u>Menispermites</u> <u>parvareolatus</u>, which he assigns to the Menispermaceae. Current opinion, however, has again come full circle, and "<u>Cocculus</u>" <u>flabella</u> is now regarded as belonging to the Trochodendrales because of its repeated association with the infructescence <u>Nordenskioldia</u>, now known to be in the Trochodendrales (Crane, 1989). Another fossil leaf, formerly thought to belong to the Vitaceae, "<u>Ampelopsis</u>" <u>acerifolia</u> (Newberry) Brown, is now thought to be a trilobed form of the Trochodendrales (Crane, 1989).

An extensive collection of leaves from the Paleocene of western Canada was incorporated by Chandrasekharam (1974) into the modern genus and divided into three species, <u>C</u>. <u>genesevianum</u> Chandrasekharam, <u>C</u>. <u>cuneatum</u> (Newberry) Chandrasekharam, and <u>C</u>. <u>flexuosum</u> (Hollick) Chandrasekharam. This treatment of these three taxa is especially significant because he based their delimitation upon a statistical assessment of a large population of the leaves of both extant species. However, Crane and Stockey (1985) remark that these three fossil species are "extremely difficult to separate."

Recently, two partial "whole plant" reconstructions of cercidiphyllaceous plants from the early Tertiary bear foliage remarkably similar to that of the living genus. Leaves from southern England, <u>Trochodendroides prestwichii</u> (De la Harpe) Crane, are very close to extant <u>Cercidiphyllum</u> (although dimorphic foliage is unknown) but were kept in the form genus because the "reconstructed

plant", called the "Nyssidium plant" for associated infructescences, bears some organs that are distinct from the modern genus (Crane, 1984). The most thoroughly known Cercidiphyllum-like plant is Joffrea speirsii Crane and Stockey from the Late Paleocene of Alberta, Canada. Crane and Stockey (1985) apply this single binomial to several organs, including pistillate inflorescences, shoots, and seedlings, which they have found in intimate association. The leaves of Joffrea are "strikingly similar" to extant Cercidiphyllum, and the reproductive organs are also similar to previously described taxa, but they apply a new name because this plant is known from considerably greater detail than any other. Based primarily on reproductive organs, both the "Nyssidium plant" and Joffrea are considered to be extinct genera within the Cercidiphyllaceae.

Diagnosis of the Cercidiphyllaceae and Tetracentraceae

Gross leaf architecture similar to the Cercidiphyllaceae and Tetracentraceae, that is, elliptic to broadly ovate leaves with actinodromous and acrodromous venation, is fairly common among a diversity of extant woody taxa such as <u>Populus</u>, <u>Cercis</u>, <u>Smilax</u>, <u>Disanthus</u>, <u>Zizyphus</u>, and other genera. Leaves of this general architecture also often share similarities in the courses of their secondary veins. These commonalities can, and frequently do, obfuscate the identity of fossil leaves bearing this general morphology. However, the extant

Cercidiphyllaceae and Tetracentraceae can be distinguished from each other and from similarly appearing taxa upon the basis of leaf morphology.

Leaves of the Cercidiphyllaceae can be identified by several features. Foliar dimorphism, with respect to the leaves borne on long and short shoots, is a characteristic of both extant species. However, its utility in diagnosing the family is limited since Crane (1984) has not found Trochodendroides prestwichii (the "Nyssidium arcticum plant from the Paleocene of England) to be dimorphic. However, Joffrea speirsii (from the Paleocene of Canada) is dimorphic, and it is reasonable to expect other extinct members of the family to bear dimorphic foliage. Generally, in the extant taxa, short shoot leaves are quite broad, even to the point of being orbicular, and they have a cordate base; long shoot leaves are distinctly narrower, that is, ovate and have a truncate to rounded or cuneate base. Short shoot leaves normally have 7 primary veins, and long shoot leaves usually have 5 primary veins. The alpha pectinal veins are much more divergent (50-105 degrees) than in Tetracentron. Wolfe (1973) has noted that Cercidiphyllum has six orders of venation.

Among the more helpful diagnostic traits is the morphology and architecture of the leaf margin. Margins vary from crenate to rounded serrate to entire. In all cases, the leaves bear globular glands that may be either emergent or non-emergent, and occur both on tooth apices and in the sinuses between teeth. Tooth architecture has

been termed chloranthoid by Crane and Stockey (1985) and Wing (1981), but I prefer to call it "mixed chloranthoid" because of the differences between it and the classical chloranthoid type of Hickey and Wolfe (1975). In standard chloranthoid teeth, such as in Chloranthus and Tetracentron, the apical gland is connected to both adjacent sinuses (or sinus regions) by a "bracing" vein. As noted by Tanai (1981), some <u>Cercidiphyllum</u> leaves are like this. Others, however, have the apical gland connected to the sinus by a series of loops, or a vein may extend from a sinus toward the gland but not connect to it, or the gland may only be fed by a central vein, entirely lacking bracing veins. When the glands occur in the sinuses between teeth, as they frequently do, the chloranthoid terminology obviously cannot apply.

The Tetracentraceae can also be recognized on the basis of foliar morphology and architecture. Bailey and Nast (1945) regard the uniformity in gross morphology of the leaves to be diagnostic in relation to the dimorphism of extant <u>Cercidiphyllum</u>. Uniformity is seen in the generally ovate shape and attenuate to broadly acuminate apices. However, the leaves do exhibit some variability in their bases which range from cordate to truncate. Primary, secondary, and tertiary veins also exhibit less variability than they do in <u>Cercidiphyllum</u>. Primary venation consists of two or three pairs of lateral primary veins, of which the inner pair is more steeply ascending (i.e. narrower

angle between alpha pectinals), and is more nearly parallel to the upper midvein, than in <u>Cercidiphyllum</u>. In the course followed by the alpha pectinal veins, Tetracentron is more like certain species of Zizyphus than Cercidiphyllum. Chandrasekharam (1974) reported the inner primary angle to be about 30 degrees. The beta pectinal veins (second pair of lateral primaries) are much weaker than the alpha pectinals, and correspond in size to the first vein in the series of loops formed by alpha abmedial secondary veins. Secondary veins depart abmedially from all primary veins, ascend steeply, and consistently form strong brochidodromous loops. Cercidiphyllum also has secondaries which form brochidodromous loops, but they are not as strong, nor do they possess the regularity of Tertiary veins also Tetracentron. form strong brochidodromous loops exmedially to the secondary loops. Chandrasekharam (1974) and Crane (1984) have used the terminology, "strong superior secondary and weak secondary", to aptly refer to the pattern in Cercidiphyllum where weak secondary veins departing from the lower midvein abruptly increase in strength along the upper midvein. This condition has not been observed in Tetracentron. Instead, the secondary veins departing from the midvein progressively increase in strength distally and are generally more uniform. All of the primary and secondary vein departure angles that were measured were smaller than the corresponding angles in <u>Cercidiphyllum</u>.

Two additional characteristics are especially helpful

in distinguishing <u>Tetracentron</u> leaves from similarly appearing taxa. One of the most unique features of the leaves is the presence of petiolar (stipular?) flanges that are connected to the petiole and cover the axillary bud. I have never seen purported fossil <u>Tetracentron</u> in the literature which was reported to have petiolar flanges. Distinct marginal teeth are also diagnostically important. Leaf margins have teeth with nearly equal sides (slightly serrate), approximately equal size and evenly spaced. Teeth always bear apical glands which, as Tanai (1981) noted, are broader at the apex and narrow proximally. Vasculature of the teeth is chloranthoid, as described above.

Affinities of the fossil Cercidiphyllum-like leaves

The fossil <u>Cercidiphyllum</u>-like leaves have characteristics found in several extant taxa as well as characteristics unshared with known Tetracentraceae and Cercidiphyllaceae. Table 2 compares the foliar morphology of these leaves with Tetracentron sinense, extant Cercidiphyllum, Joffrea, and Trochodendroides prestwichii. Leaves of the Blackhawk fossils are actinodromously veined with strong alpha pectinal veins and quite weak beta pectinal veins. The alpha pectinal veins have a narrow angle of departure and their course approximately parallels the midvein in the upper half of the lamina. These features are consonant with both <u>Tetracentron</u> and <u>Zizvphus</u>,

and quite distinct from the short shoot leaves of <u>Cercidiphyllum</u>.

Dimorphism is not present in this population of fossil leaves although some variation in gross shape does occur. Leaf shape varies from ovate to elliptic (usually in the smaller leaves); leaf bases are obtuse to rounded, and leaf apices are acute to attenuate. Although long shoot leaves of <u>C</u>. japonicum are often ovate with a rounded base, the attenuated apex and narrow lamina of the fossils are more Long shoot leaves of both Tetracentron like Tetracentron. and <u>C</u>. japonicum are more similar to the fossils than the short shoot leaves of either. Weak beta pectinal veins are similar to Tetracentron and long shoot leaves of Cercidiphyllum in being the first in a series of brochidodromous loops formed by the alpha abmedial (secondary) veins. These veins form loops which parallel the alpha pectinal veins, in contrast to the usual condition of greater divergence and rounder loops of Tetracentron and Cercidiphyllum. Some long shoot leaves of both extant species, though, are similar to this condition. The superior secondary vein to which the beta pectinal vein connects is much stronger than the secondaries proximal to it, which also occurs in Cercidiphyllum. The course of the tertiary veins between the midvein and alpha pectinals is only faintly visible in several leaves, but it appears to be apically directed with lateral branches, some of which form chevrons. Better preserved leaves need to be

Character	Blackhawk trochodendroid	<u>Tetracentron sinense</u>	<u>Gercidiphyllun</u> (extant)	<u>Joffrea speirsii</u>	<u>Trochodendroides</u> <u>prestwichia</u>
Shoot worphology	2	Long and short shoots	Long and short shoots	Long and short shoots	Tiong shoots only
Last types	Probably monomorphic	Monomorphic	Dimorphic	Righly variable	Variable
Leef shape	Ovate or elliptic	Ovate	Ovate to elliptic to nearly circular	Ovate, obovate to nearly circular	B lliptic or ovate
Land apex	Attemmate to acute	Attenuate to acuminate	Acute, obtuse or retuse	Obtune to rounded	Obtuse, acute to
Leaf here	Obtuse or rounded	Cordate to truncate	Rounded, obtuse, cuneste, truncate, or cordate	Nounded, truncate, cordate, acute (rare)	Rounded or cordate
Petiolar flanges	2	Present	Absent	2	Absent
Locf mergin	Berrate	Berrate	Crepate, serrate, glandular-entire	Creante	Crenate
Tooth architecture	Chlorent hold	Chlor anthoid	Mixed chlorenthoid	Chlor m thoid	Chlor anthoid
Tooth gland placement	Apical	Apical	Apical or sinuses	Apical	Apical or simuses
Reaber of primery veine	3 or 5	5 or 7	5 or 7	3 or 5	3 or 5
Pectinal (a) placement	base]	Beesl	Basel or suprabasel	Beeel	2
Pectinal (a) course	Parallels uidvein distally	Parallels midvein distally	Diverges from midvein	Sometimes perallels midvein distally	Sometimes parallel midvein distally
Righest order of branching	2	5	v	s	2
Veinlet branching	2	1 or 2 orders	Several orders	2 or 3 orders	8
Vescular tissue	2	Yessels absent	Vessels present	2	2
Inner primary angle	X = 33 (range 3 8 6 1; N = 18)	30	30-105	50-70	(30-) 40-70 (-100)
Pectinal (8) departure angle	X = 52 (r ange 39-6 1; W = 15)	II = 47 (range 40-52; H = 14)	X = 63 (range 41-80; M = 45)	65-85	(20-) 40-80 (-110)
First strong superior secondary angle	X = 57 (range 47–67; H = 8)	35	40-75	9	(30-) 40-80 (-60)
Weak secondary angle	X = 71 (range 62-94; H = 4)	X = 50 (range 41-59; H = 18)	06-07	30-65	(40-) 60-100 (-110
Abmedial (a) secondary	X = 60 (range 54-67; H = 9)	X = 42 (range 33-62; H = 13)	06-07	30-65	(30-) 40-80 (-110)

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* Duta for extant plants based upon Chandrasekharam (1974), Wolfe (1973), Crame and Stockay (1965), and personal observation. Duta for <u>Joffren</u> based upon Crame and Stockay (1965); <u>Irochodentroiden</u> based upon Crame (1964). Data reported as mean, range, and number of measurements (N =) were collected by Ruber; other numerical data are reported as they appeared in publication. MD, missing data.

consulted to characterize the tertiary venation, but this architecture is found in both extant taxa. Petioles are missing or broken in many leaves so that it is not known whether the petioles bore flanges, in the fashion of <u>Tetracentron</u>.

The margins of the leaves and tooth architecture are preserved in a number of specimens and provide an important reference for taxonomic judgments. The teeth are serrate, sometimes bluntly so, and usually occur in pairs where a larger sinus separates every other tooth. Some leaves possess a larger pair of teeth that flank each side of the upper one-quarter of the lamina, and thereby provide a "shouldered" Tooth appearance. architecture is chloranthoid. Some teeth clearly show marginal glands which expand toward the tooth apex as Tanai (1981) noted for <u>Tetracentron</u>. However, the teeth do not have the consistency of size and shape that are found in extant Tetracentron. In summary, tooth architecture and glands are like those found in Tetracentron rather than Cercidiphyllum, but tooth shape and placement are unlike the extant members of these families.

The fossil <u>Cercidiphyllum</u>-like leaves from the Blackhawk formation do not fall clearly into any extant family that I have investigated. The leaves were tentatively assigned by Parker (1976) to <u>Cercidiphyllum</u> <u>arcticum</u> based upon a cursory examination. But, despite a superficial resemblence to <u>Cercidiphyllum</u>, leaf morphology and architecture are sufficiently distinct from this taxon

that it cannot be placed in the Cercidiphyllaceae without evidence from reproductive organs that would show the leaves to be, indeed, atypical to the family. Those fossil leaves from the Paleocene known to belong to the Cercidiphyllaceae, Joffrea, Trochodendroides prestwichii, and the Cercidiphyllum from western Canada, are also distinct from the Blackhawk leaves. The leaves are quite distinct from Zizyphus in terms of tooth architecture.

The case for a tetracentraceous placement of the fossils is the most compelling due to the overall shape, primary and secondary vein courses, relatively narrow vein departure angles, chloranthoid teeth, and nature of the marginal glands. Hickey and Wolfe (1975) regard tooth architecture in angiosperm leaves to be relatively more conserved evolutionarily than other morphological features. If this is true, the chloranthoid nature and apically expanded marginal glands of the teeth are strong evidence in favor of alliance with the Tetracentraceae.

The question raised earlier concerning the recognition of unknown variability in the fossil representatives of a higher taxon is relevant to the problems of these trochodendroid fossils. How far can a fossil taxon morphologically diverge from an extant monotypic family and still be considered as an historic part of the family? In the case of the Platanaceae, several living species and numerous Tertiary form-species provide a good representation of familial foliar morphological diversity,

and therefore a good basis for judging the conservability of architectural features. A monotypic family, on the other hand, does not possess such variability, especially if unequivocal fossil representatives are unknown. <u>Tetracentron sinense</u>, the only extant member of the Tetracentraceae, may be the final representative of a historically diverse family. Judgments concerning the placement of fossil taxa, especially Cretaceous forms, into the Tetracentraceae (or other extant families), must be based upon foliar architectural characters that are thought to be evolutionarily conservative. In addition, the presence of fossil reproductive organs would, of course, greatly enhance the recognition of the historical members of a monotypic family.

A collection of better preserved leaves from the Blackhawk Formation that fully display tertiary and quaternary venation, and cuticle, is needed for further confirmation of the tetracentraceous alliance of these fossil trochodendroid leaves.

SUMMARY

The determination of the systematic affinities of fossil leaves is improved with a thorough understanding of potentially related extant taxa. Likewise, the assessment of infraspecific variability in fossil taxa, particularly among morphotypes whose modern representatives are known to be heteromorphic, should proceed from an understanding of the ranges of the modern variability. Upper Cretaceous platanoid and trochodendroid leaf fossils are known to commonly exhibit intergradations in morphologies that make the systematic boundaries difficult to ascertain. The purpose of this study was to document the patterns of variability in modern Platanus, Cercidiphyllum, and Tetracentron leaves in order to evaluate the systematic affinities of Platanus-like and Cercidiphyllum-like leaf fossils from the Upper Cretaceous Blackhawk Formation of central Utah. The following conclusions can be made from this study:

1. Foliar heteromorphism was found to characterize <u>Platanus Xhybrida, Platanus occidentalis, Platanus</u> <u>racemosa, and Platanus lindeniana</u>. Shoots from all of these species bear leaves showing heterophyllic patterns of development.

2. The variability in <u>Platanus</u> X<u>hybrida</u> was examined in the greatest detail. Three types of crown shoots can be distinguished by differences in their heterophyllic patterns: inflorecence-bearing shoots, Type I non-
inflorescence shoots, and Type II non-inflorescence shoots. Several morphological characters followed progressive patterns of change through successive leaves of these shoots. Lamina area and perimeter lengths increased through successive leaves, except for a tapering-off later in the season, presumably from incomplete development. Lamina basal angles increased in the leaves along a shoot and the lamina bases often became guite reflexed in the Leaf apices generally became more late-season leaves. The number and size of teeth are highly attenuated. variable; tooth size generally decreased distally along each leaf lobe and the number of teeth increased through successive leaves on a shoot. The leaves of shoots bearing an inflorescence and Type I shoots initially have very few teeth and eucamptodromous and brochidodromous secondary venation. Successive leaves acquire more teeth, both the typical platanoid type and minute papillate teeth. The papillate teeth are accompanied by semicraspedodromous secondary venation. As the number of platanoid teeth increases so do the craspedodromous secondary veins which Type II non-inflorescence shoots are enter these teeth. distinct by having the lamina base of the first leaf acute to obtuse and broadly decurrent (rather than truncate as in the other two shoot types); in addition, many teeth, including papillate teeth, occur on the first leaf. The first leaf of all three shoot types generally lack lateral lobes, but succeeding leaves progressively develop these

lobes. Sinuses between the lateral lobes become more deeply incised through the heterophyllic series.

3. Inflorescence-bearing shoots of <u>Platanus Xhybrida</u> display a "reset" phenomenon where leaves developed after the inflorescence node repeat some of the heterophyllic patterns present in the pre-inflorescence leaves. Morphological features which follow this pattern are lamina size, lamina base angle, lateral lobe sinus incision depth, and the first leaf in the sequence has an unlobed form and pinnate venation.

4. One type of non-inflorescence canopy shoot of <u>Platanus</u> <u>occidentalis</u> was examined and found to display the same heterophyllic trends as <u>P</u>. Xhybrida Type I shoots. Inflorescences terminate shoots in <u>P</u>. <u>occidentalis</u> so that "reset" sequences do not occur.

Shoots from a stump of <u>P</u>. Xhybrida or <u>P</u>. occidentalis 5. and shoots from the base of P. racemosa trees display heterophyllic trends similar to, but differing in some essential details from, the heterophyllic sequences of the respective canopy shoots. The initial leaves are large with shallow lobe sinuses, many teeth, and dissymetrical arrangements of secondary and tertiary venation. Higher numbers of intersecondary veins and reticulate tertiary veins add to the less-organized aspect of these early Lamina bases from the same stump shoot are leaves. conspicuously decurrent. The development of lobation increases in successive leaves of both taxa. The leaves of Platanus racemosa that occur midway along a sucker shoot

possess small "accessory" lobes in the sinuses between the central and adjacent lobes. The heterophyllic patterns in leaves from the sucker shoots of both species converge upon a morphology quite similar to canopy shoot leaves.

6. The family Platanaceae can be recognized by a suite of foliar characters although no single character is uniquely diagnostic. The extant subgenus <u>Platanus</u> is characterized by basally or suprabasally actinodromous or palinactinodromous primary venation, percurrent to reticulate tertiary veins, chevrons formed by tertiaries in the axils of the primary veins, orthogonal quaternary veins, platanoid teeth, swollen petiole bases that cover the axillary bud, and heteromorphism, particularly heterophyllic patterns of development. The subgenus <u>Castaneophyllum</u> is, however, quite distinct in having elliptic leaves, pinnate venation, different marginal venation, and exposed axillary buds (Schwarzwalder and Dilcher, in press). Platanus kerrii, the only species in the subgenus, was not studied and it is not known if its leaves are heteromorphic.

7. The <u>Platanus</u>-like leaves from the Upper Cretaceous Blackhawk Formation can be placed within the Platanaceae based upon their possession of most of the above characters. They differ from extant subgenus <u>Platanus</u> in having craspedodromous secondary veins that generally appear to terminate at an entire margin; some do terminate in minute papillate/spinose teeth, but platanoid teeth are

The tertiary veins form very weak chevrons or absent. simply a straight bridge in the axils of the primary veins. Previous preliminary work on the Blackhawk platanoids assigned the leaves to two separate <u>Platanus</u> form species based upon the presence or absence of a decurrent lamina This study has shown that such variability is both base. diagnostic for the family Platanaceae and commonly occurs as infraspecific variability in some extant species. Α treatment of the Blackhawk platanoids as a single species is therefore considered to be a more biologically realistic The Upper Cretaceous form genus most closely approach. resembling the Blackhawk platanoids is Credneria.

The leaves of the Cercidiphyllaceae and Tetracentraceae 8. are quite similar to each other in some features of gross morphology and vein architecture, but some morphological characters do exist that can be used to distinguish them. This study concurs with previous studies that separation of the leaves of these two families may be based upon the following characteristics: foliar dimorphism in Cercidiphyllum; attenuated leaf apices and smaller departure angles of the primary and secondary veins in Tetracentron. Tooth shape, gland shape and placement, and tooth architecture are also distinct between these two In addition, this study has noted that the primary, taxa. secondary, and tertiary venation of Tetracentron is less variable than in <u>Cercidiphyllum</u>, and that successive secondary veins which depart from the midvein gradually become strengthened distally in <u>Tetracentron</u> rather than an

abrupt strengthening as in <u>Cercidiphyllum</u>.

9. The fossil <u>Cercidiphyllum</u>-like leaves from the Blackhawk Formation can be placed into the Tetracentraceae rather than the Cercidiphyllaceae based upon the following leaf morphological characters: a narrow angle of departure for the alpha pectinal veins, attenuated leaf apices, chloranthoid tooth architecture, and marginal glands which become broader toward the tooth apex and always occur at tooth apices, never in sinuses. APPENDICES

APPENDIX A

GLOSSARY OF SELECTED TERMS¹

acrodromous - two or more primary or strongly developed secondary veins running in convergent arches toward the leaf apex.

actinodromous - three or more primary veins diverging radially from a single point. See figure 4a.

brochidodromous - secondaries joined together in a series of prominent arches. See figure 5, b and c.

craspedodromous - secondary veins terminating at the margin. See figure 4b.

eucamptodromous - secondaries upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops. See figure 38.

intersecondary vein - thickness intermediate between that of the second and third order veins; generally originating from the medial primary vein, interspersed among the secondary veins, and having a course parallel to, or nearly so, to them. See figure 4 c and d.

palinactinodromous - primaries diverging in a series of dichotomous branchings, either closely or more distantly spaced. See figure 14, c through k.

pectinal vein - a vein which subtends abmedially a distinct series of more or less parallel branches as thick as, or thinner than, themselves, in a similar manner to teeth of a comb. Pectinal veins are normally primary or secondary although they may be of any vein order; they may be basal or suprabasal in origin, and they may bear admedial branches in addition to the abmedials. See figure 4.

percurrent - tertiaries from the opposite secondaries joining. See figure 4 or 13.

semicraspedodromous - secondary veins branching just within the margin, one of the branches terminating at the margin, the other joining the superadjacent secondary. See figure 37 a and d.

¹ Definitions of the leaf architectural terms presented here are taken verbatim from Hickey (1979), except for the definition of pectinal veins which is taken from Spicer (1986).

APPENDIX B

VICOM COMMAND FILE

* Program: 8000.&.LEAVES.VC David Huber April 14, 1988 Vicom 1800 CIM command file for digitizing a leaf, thresholding it * interactively, optionally patching holes (#DRA 2), then taking the area * and perimeter measurements. CALL 0.&.CCD Repeat loop begin REP CAM **GRE (OFF)** * * Prepare next leaf for digitization * * * Pause until user is ready to continue pause * Digitize the next leaf DIG 1 Perform an interactive thresholding operation * on the leaf image #THR 1 Turn on the graphics mode GRE Shift the data into the graphics bits for AREA and perimeter measurements to be possible LSH 1>2 (13) Call up #DRA for optional manual leaf filling in **#DRA 2** * Get AREA measurement ARE 2 Get PERIMETER measurement PER 2 Pause so numbers can be written down PAUSE

ERE

APPENDIX C

Table 3. Statistical summary of foliar morphological data of <u>Platanus</u> X<u>hybrida</u> and <u>Platanus occidentalis</u>. All angles are in degrees. N, number of data. SE, standard error. MD, missing data.

	u/t ratio	s/m ratio	l/w ratio
 Pre-inflorescence leaves <u>P</u>. Xhybrida 	mean = .459 min. = .395 max. = .532 SE = .0182 M = 7	mean = .49 min. = .388 max. = .554 SE = .0253 N = 7	mean = .924 min. = .791 max. = 1.05 SE = .0301 W = 8
 Post-inflorescence leaves <u>P</u>. Xhybrida 	<pre>mean = .405 min. = .322 max. = .534 SE = .0242 N = 9</pre>	mean = .616 min. = .477 max. = .722 SE = .0295 N = 9	mean = .909 min. = .833 max. = 1.01 SE = .0186 W = 11
 Mon-inflorescence shoot (Type I) <u>P. Xhybrida</u> 	mean = .461 min. = .335 max. = .562 SE = .016 N = 16	mean = .548 min. = .391 max. = .694 SE = .0203 N = 16	mean = .908 min. = .813 max. = 1.12 SE = .0173 M = 17
 Mon-inflorescence shoot (Type II) <u>P</u>. Xhybrida 	mean = .562 min. = .53 max. = .597 SE = .0139 N = 4	nean = .485 nin. = .452 nax. = .522 SE = .0158 N = 4	mean = .995 min. = .777 max. = 1.31 SE = .0957 W = 5
5. Stump shoot leaves <u>P</u> . X <u>hybrida</u> (?)	<pre>mean = .614 min. = .512 max. = .719 SE = .0218 W = 12</pre>	<pre>mean = .394 min. = .271 max. = .51 SE = .0211 W = 12</pre>	mean = 1.16 min. = .828 max. = 2.11 SE = .1075 W = 12
 Total for inflorescence plus non-inflorescence shoots of <u>P. Xhybrida</u> 	<pre>mean = .454 min. = .322 max. = .597 SE = .0113 W = 42</pre>	mean = .54 min. = .386 max. = .722 SE = .0139 N = 43	mean = .924 min. = .777 max. = 1.31 SE = .0136 W = 48
7. Non-inflorescence shoot <u>P. occidentalis</u>	mean = .526 min. = .417 max. = .632 SE = .0176 W = 17	mean = .439 min. = .205 max. = .546 SE = .0198 W = 17	mean = .859 min. = .76 max. = .943 SE = .0119 N = 18

	Basal angle	Apical angle	Number of teeth	Angle between central and lateral lobes
1.	mean = 232 min. = 180 max. = 267 SE = 9.803 N = 8	mean = 29.4 min. = 17 max. = 41 SE = 3.156 N = 8	mean = 10.8 min. = 8 max. = 16 SE = 1.031 N = 8	<pre>mean = 105 min. = 69 max. = 129 SE = 4.303 N = 14</pre>
2.	mean = 228 min. = 180 max. = 276 SE = 9.157 N = 11	<pre>mean = 37.4 min. = 23 max. = 56 SE = 3.186 N = 11</pre>	<pre>mean = 37.1 min. = 29 max. = 55 SE = 2.23 N = 11</pre>	<pre>mean = 66.6 min. = 44 max. = 98 SE = 4.36 W = 15</pre>
3.	mean = 242 min. = 145 max. = 316 SE = 11.66 N = 16	mean = 25.6 min. = 16 max. = 32 SE = 1.369 N = 16	<pre>mean = 47.3 min. = 10 max. = 102 SE = 7.606 N = 17</pre>	mean = 99.7 min. = 56 max. = 131 SE = 3.288 N = 31
4.	mean = 116	mean = 33.8	mean = 50.8	mean = 97.9
	min. = 88	min. = 23	min. = 41	min. = 79
	max. = 164	max. = 46	max. = 63	max. = 119
	SE = 14.46	SE = 4.641	SE = 3.734	SE = 4.969
	N = 5	N = 5	W = 5	N = 7
5.	mean = 142	mean = 52.5	mean = 54.8	mean = 118
	min. = 56	min. = 25	min. = 30	min. = 81
	max. = 228	max. = 107	max. = 84	max. = 148
	SE = 17.35	SE = 7.829	SE = 5.445	SE = 3.895
	N = 12	W = 12	N = 12	W = 22
6.	mean = 219	mean = 31	mean = 35.4	mean = 92.3
	min. = 88	min. = 16	min. = 8	min. = 44
	max. = 316	max. = 56	max. = 102	max. = 131
	SE = 7.45	SE = 1.388	SE = 3.488	SE = 2.542
	N = 47	M = 47	N = 48	M = 79
7.	mean = 222.5	mean = 26.7	mean = 24.2	mean = 116
	min. = 132	min. = 20	min. = 7	min. = 98
	max. = 306	max. = 42	max. = 47	max. = 149
	SE = 12.19	SE = 1.617	SE = 3.453	SE = 1.922
	W = 17	W = 15	N = 17	W = 33

	Distance from lamina-	Angle of	Angle of	
	petiole juncture to	pectinal	secondary vein	
	pectinal origin	departure	departure	
1.	nean = .113cn	ne an = 46.4	mean = 49.8	
	m in. = 0.0cm	m in. = 34	m in. = 38	
	nax. = .3cm	max. = 60	max. = 58	
	SE = .026	SE = 1.94	SE = 1.32	
	N = 16	N = 16	W = 16	
	n 10	A 20		
2.	n ean = .453cm	n ean = 49.5	mean = 52.8	
	min. = 0.2cm	m in. = 38	m in. = 46	
	max. = 1.1cm	max. = 64	max. = 62	
	SE = .041	SE = 1.38	SE = .908	
	X = 20	N = 22	N = 22	
3.	mean = .285cm	mean = 48.6	mean = 52.5	
	min. = Ocm	m in. = 33	m in. = 44	
	max. = .45cm	max. = 65	max. = 66	
	SE = .0262	SE = 2.18	SE = 1.19	
	N = 20	N = 22	N = 22	
4.	m ean = 0.725cm	mean = 34.1	mean = 51.2	
	min. = 0.3cm	m in. = 25	min. = 36	
	max. = 1.2cm	max. = 44	max. = 59	
	SE = 0.092	SE = 1.946	SE = 2.169	
	W = 10	N = 10	M = 10	
5.	n ean = 2.38cm	mean = 41.1	mean = 49.3	
	m in. = 0.9cm	m in. = 24	min. = 28	
	nax. = 3.4cm	max. = 51	max. = 65	
	SE = 0.17	SE = 1.36	SE = 1.7	
	N = 21	N = 21	N = 24	
6.	mean = 0.36cm	n ean = 45.5	mean = 51.7	
	min. = 0.0cm	m in. = 25	min. = 36	
	max. = 1.2cm	max. = 64	max. = 66	
	SE = 0.036	SE = 1.091	SE = 0.695	
	$\mathbf{N} = 60$	N = 62	X = 62	
7.	mean = 0.117cm	mean = 54.06	mean = 54.58	
	min. = 0.0cm	m in. = 36	min. = 45	
	Bax. = 0.7	max. = 70	max. = 64	
	SE = 0.033	SE = 1.674	SE = .796	
	W = 32	X = 34	N = 36	

	Distance between	Angle of	Distance between
	secondary vein	departure of	tertiary vein
	departures	tertiary veins	departures
1.	mean = 1.91cm	mean = 80.75	mean = 0.398
	min. = 1.2cm	min. = 70	min. = 0.2
	max. = 3.2cm	max. = 90	max. = 0.65
	SE = 0.141	SE = 1.399	SE = 0.025
	N = 16	N = 24	N = 24
2.	<pre>mean = 2.02cm min. = 1.2cm max. = 2.9cm SE = 0.085 N = 22</pre>	mean = 81.73 min. = 62 max. = 90 SE = 1.328 N = 33	mean = 0.294 min. = 0.2 max. = 0.4 SE = 0.012 N = 33
3.	<pre>mean = 2.44cm min. = 1.0cm max. = 3.5cm SE = .1297 N = 22</pre>	mean = 81.3 min. = 60 max. = 90 SE = 1.298 N = 33	mean = MD min. = max. = SE = N =
4.	mean = 2.27cm	mean = 84.7	mean = 0.363
	min. = 1.4cm	min. = 75	min. = 0.15
	max. = 3.2cm	max. = 90	max. = 0.6
	SE = 0.175	SE = 1.337	SE = 0.033
	N = 10	N = 15	W = 15
5.	mean = 2.31cm	mean = 76.7	mean = 0.449
	min. = 0.8cm	min. = 56	min. = 0.2
	max. = 5.9cm	max. = 90	max. = 0.8
	SE = 0.271	SE = 1.282	SE = 0.0267
	N = 24	N = 36	N = 36
6.	<pre>mean = 1.91cm min. = 0.7cm max. = 3.2cm SE = 0.0678 W = 62</pre>	mean = 82.1 min. = 62 max. = 92 SE = 0.694 N = 93	mean = 0.334 min. = 0.15 max. = 0.65 SE = 0.0111 N = 93
7.	mean = 1.53cm	mean = 86.4	mean = 0.3
	min. = 0.9cm	min. = 70	min. = 0.1
	max. = 2.3cm	max. = 97	max. = 0.5
	SE = 0.0641	SE = 0.682	SE = 0.0126
	N = 36	N = 54	N = 54

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PLATES

PLATE 1

Figure

1.	Blackhawk platanoid leaf. 8/29/70 060-150
2.	Blackhawk platanoid leaf. The bar line indicates 2 cm. 4/28/68 36-001B
3.	Blackhawk platanoid leaf. 7/11/70 I 020-023
4.	Blackhawk platanoid leaf. 7/30/70 III 300-308

PLATE |



PLATE 2

Figure

- 1. Blackhawk trochodendroid leaf. Natural size. 6/30/85 001-001A
- 2. Blackhawk trochodendroid leaf. 7/30/70 II 47-112
- 3. Blackhawk trochodendroid leaf. 7/30/70 III P382-300
- 4. Blackhawk trochodendroid leaf. P510-001

PLATE 2



