Isomorphic Polymorphism in the Platanaceae and Altingioideae and the Problem of Their Relationship

N. P. Maslova

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117997 Russia
e-mail: paleobotany_ns@yahoo.com

Abstract—Isomorphic polymorphism is demonstrated by modern and fossil members of the Platanaceae and Hamamelidaceae (subfamily Altingioideae) and is considered as evidence of structural parallelism in the evolution of the Platanaceae and Altingioideae. The supposed relationship between Platanaceae and Altingioideae is discussed from a paleobotanical perspective.

INTRODUCTION

The Platanaceae and Hamamelidaceae have aroused considerable interest among botanists dealing with fossil and extant plants, since in the systems of Takhtajan (1966, 1987) and Cronquist (1981) these families were united in the order Hamamelidales, which occupied a key position in the phylogenetic tree of dicots. A recently proposed system of angiosperm plants based on molecular data (APG, 2003) abolished the order Hamamelidales and assigned the families Platanaceae and Hamamelidaceae to the orders Proteales and Saxifragales, respectively; this excludes any possible close relationship. A discussion of the advantages and disadvantages of the currently existing classifications is beyond the scope of this paper. However it is necessary to point out that the positions of Platanaceae and Hamamelidaceae are here considered according to the systems proposed by Takhtajan and Cronquist, which are better supported by paleobotanical evidence.

Since leaf remains and capitate inflorescences and infructescences that morphologically resemble those of the modern plane tree were widespread in floras of the Northern Hemisphere throughout the Late Cretaceous, and often constituted a significant proportion of assemblages, they have for a long time been the objects of paleobotanical studies. Since Lesquereux, Newberry, Heer, and other European and American paleobotanists of the 19th century, such leaves and reproductive structures were mostly referred to the modern genus *Platanus*. From the works of Krassilov (1973, 1976, 1979) onwards, a new approach to the identification of Cretaceous heads has been developed. The designation of leaves of *Platanus*-like morphology was considered in the context of the morphological system of dispersed leaves of Cretaceous angiosperms, irrespective of the

system of modern plants. The use of names of this system was recently discussed for Cretaceous leaves earlier assigned to the modern genus *Platanus* (Maslova et al., 2005). In the last decades, studies of reproductive structures of platanaceous macromorphology revealed their considerable diversity. In particular, microstructural analysis showed that such structures are assignable either to the Platanaceae (Manchester, 1986; Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006), or Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004), or combine characters of both families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005, 2007).

The study of the taxonomic diversity of fossil *Platanus*-like leaves and heads as well as the analysis of the origin and evolutionary changes of their particular morphological structures (Maslova, 2003) necessitated a detailed comparative study of modern members of the Platanaceae and Hamamelidaceae, in particular, the subfamily Altingioideae, members of which are often compared with fossil *Platanus*-like remains. This study contributed considerably to our knowledge of the widely varying vegetative and reproductive morphological characters of the Platanaceae and Altingioideae and substantiated comparisons between variation series of particular characters, illustrating isomorphic polymorphism, which is characteristic of Platanaceae and Altingioideae. The first instances of isomorphic polymorphism in the modern plane tree, *Liquidambar*, and *Altingia* were observed by Krassilov (1976). Later, they were discussed in more detail (Maslova, 1998, 2003). The present paper continues the consideration of poly-

morphism in morphological characteristics of leaves and heads of modern members of *Platanus* and the Altingioideae, which is treated there as evidence of structural parallelism between the Platanaceae and Altingioideae. The supposed phylogenetic relationships between the Platanaceae and Altingioideae are discussed from a paleobotanical perspective.

TAXONOMIC COMPOSITION OF THE FAMILY PLATANACEAE AND SUBFAMILY ALTINGIOIDEAE, HAMAMELIDACEAE

Platanaceae. The modern family Platanaceae includes only the genus *Platanus*, embracing the subgenera *Platanus* Leroy and *Castaneophyllum* Leroy (Leroy, 1982).

The subgenus *Platanus* includes species with typically lobate leaves and compound inflorescences, consisting of a shortened axis and one to five sessile heads (*P. occidentalis* L., *P. orientalis* L., *P. mexicana* Moricaud, and *P. wrightii* S. Watson). This subgenus is characterized by vessels with predominantly simple perforations; the polar diameter of pollen grains is 18–22 µm.

The only species *P. kerri* Gagnepain belongs to the subgenus *Castaneophyllum*, characterized by simple elliptical leaves and compound inflorescences with an elongated axis bearing at least 12 heads. Unlike species of the subgenus *Platanus*, vessels of *P. kerrii* are with predominantly scalariform perforations, pollen grains are smaller (polar diameter is 16–18 µm).

Kvaček et al. (2001) recently established the third subgenus of *Platanus, Glandulosa,* which consists entirely of extinct members: *Platanus bella* (Heer) Kvaček, Manchester et Guo, *P. fraxinifolia* (Johnson et Gilmore) Walter, and *P. neptunii* (Ettings.) Bůžek, Holý et Kvaček. The new subgenus is distinguished by the presence of, along with simple leaves, compound leaves (with three or five leaflets) with semicraspedodromous or camptodromous venation, large peltate trichomes, and a distinct scar on the stalk of a solitary infructescence.

According to different scientists, the modern *Platanus* includes five to eleven species. Kuntze (1891) expressed the extreme view that the modern flora includes only a single species, *P. orientalis.* Depape (1966) recognized only two modern species, *P. orientalis* and *P. occidentalis*. Recently, Nixon and Poole (2003) performed a detailed taxonomic revision of North American species of this genus.

Paleobotanical research shows that *Platanus* is a small relict of a much larger platanaceous group that occurs in the geological record from the Early Cretaceous. In the fossil state, Platanaceae are known by their leaf and reproductive organs. Numerous fossil leaves from the Upper Cretaceous, macromorphologically similar to leaves of the modern plane tree, are traditionally assigned by many scientists to the genus *Platanus* L. So far the presence of this modern genus in

Cretaceous deposits has not been confirmed by finds of reproductive structures, and Maslova et al. (2005) recently proposed, for Cretaceous and Early Paleogene leaves showing typical morphology of the modern plane tree, the use of the generic name *Ettingshausenia* Stiehler of the morphological system of leaves, with the type species *E. cuneifolia* (Bronn) Stiehler. Entire-margined or weakly lobate leaves with rounded, cordate, or peltate base are assigned to *Credneria, Protophyllum, Pseudoprotophyllum*, and other genera (Lesquereux, 1874; Hollick, 1930), which were later united in platanoids (Vakhrameev, 1976). In the last decades, knowledge of the morphological variations of platanaceous leaves was significantly broadened (Upchurch, 1984; Herman and Golovneva, 1988; Crane et al., 1988, 1993; Johnson, 1996).

To date, 16 fossil species of Platanaceae have been described based on staminate and pistillate inflorescences (Krassilov, 1973, 1976; Manchester, 1986, 1994; Crane et al., 1988, 1993; Friis et al., 1988; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006). Virtually identical at the level of general morphology, they are confidently differentiated micromorphologically. It is pertinent to note that fossil capitate inflorescences and infructescences that are macromorphologically similar to those of the Platanaceae might also belong to the Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004) or combine characters of both families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005, 2007).

Altingioideae, Hamamelidaceae. The taxonomic composition of the modern family Hamamelidaceae has been a matter of discussion for a long time, particularly in relation to *Altingia* Noronha, *Liquidambar* L., and *Semiliquidambar* H.-T. Chang. Some scientists place these genera in a separate family, Altingiaceae, on the basis of seed and vascular anatomy, palynomorphology, chromosome number, and molecular data (Lindley, 1853; Andersen and Sax, 1935; Skvortsova, 1960; Chang, 1964; Takhtajan, 1966, 1987; Melikian, 1971; Rao and Bhupal, 1974; Dahlgren, 1975; Chase et al., 1993; Li et al., 1999; Magallón et al., 1999; Soltis et al., 2000; Shi et al., 2001; APG, 2003).

Based on the morphology, anatomy, and ontogenetic data, other scientists regard *Altingia* and *Liquidambar* as a separate subfamily of the family Hamamelidaceae (Harms, 1930; Makarova, 1957; Schmitt, 1965; Thorne, 1968; Hutchinson, 1969; Meeuse, 1975; Goldblatt and Endress, 1977; Cronquist, 1981; Wisniewski and Bogle, 1981; Uemura, 1983; Bogle, 1986; Goldberg, 1986; Tiffney, 1986; Endress, 1989a, 1989b; Hoey and Parks, 1991, 1994; Zhang and Lu, 1995).

There is no generally accepted opinion about the validity of these genera. Some researchers combine *Alt-*

ingia and *Liquidambar* in one genus *Liquidambar* based on their morphological and anatomical similarities (Lindley, 1836; Oken, 1841; Bentham and Hooker, 1865; Blume, 1928) and molecular data (Shi et al., 2001).

In the present paper, I use the supergeneric classification proposed by Endress (1989a, 1989b) as a well-substantiated system later confirmed by paleobotanical evidence: the genera *Altingia, Liquidambar*, and *Semiliquidambar* are considered within the subfamily Altingioideae of the family Hamamelidaceae. At the same time, the uniting of these three genera into one genus appears to be uncertain.

Modern members of the subfamily Altingioideae belong to three genera: *Altingia, Liquidambar*, and *Semiliquidambar*. The first comprises eight species of two sections, *Altingia* and *Oligocarpa*, distinguished by reproductive characters (Chang, 1979). The section *Altingia* is characterized by compact globular inflorescences of about 25 flowers; the section *Oligocarpa* slightly differ in the shape of inflorescences (conical) and the smaller number of ripening fruits (up to nine).

Two sections of the genus *Liquidambar*, *Liquidambar* and *Cathayambar* (Harms, 1930), differ in the inflorescence macromorphology. Currently, the genus embraces eight species, but there is no consensus about its species composition (Ferguson, 1989; Shi et al., 2001; Ickert-Bond et al., 2005).

Three species of *Semiliquidambar* are endemic to China (Chang, 1979). This genus is considered to be transitional between *Altingia* and *Liquidambar* (Chang, 1962, 1973). Geographically, it occupies a transitional territory between the ranges of *Altingia* and East Asian *L. formosana* in southeastern China and Hainan Island (Chang, 1962). Bogle (1986) hypothesized that *Semiliquidambar* is a hybrid between modern *Altingia* and *Liquidambar*. The interfertility between three species of *Liquidambar* was shown experimentally (Santamour, 1972). However, no data are available about possible hybridization between species of *Altingia* and between *Altingia* and *Liquidambar*.

Among members of the Altingioideae, *Liquidambar* is the genus most often reported in the fossil state. It played a significant role in Tertiary floras of the Northern Hemisphere and was a permanent component of broad-leaved forests. Since the Eocene, leaves of *Liquidambar* have been known from North American, European, and Asian floras (MacGinitie, 1941; Uemura, 1983; Maslova, 1995; Meyer and Manchester, 1997). The situation with fossil leaves of *Liquidambar* is reminiscent of that of *Platanus*; quite often, possible polymorphism in characters of fossil leaf blades is not taken into account, and, as a result, any at least slightly deviating specimen is described as a separate species. Consequently, in my opinion, the number of ancient species of *Liquidambar* described on leaf remains is significantly overestimated. Keeping in mind the known high polymorphism in leaves of modern *Liq-*

uidambar, the high number of fossil species of *Liquidambar* seems unjustified. The analysis of the original material and published data allowed me to distinguish two groups of fossil members of *Liquidambar* (Maslova, 2003). These groups differ in the following characteristics: the lobe outline (short, triangular, and widest in the basal region in the first group and narrow, elongate, and parallel-margined in the second); the number of secondary veins (about six–eight pairs in the first group and about eight–ten pairs in the second); and the marginal teeth (larger and hooklike teeth in the second group). These groups might correspond to two species, *L. miosinica* and *L. pachyphylla*. However, this problem remains unsolved in lack of additional data on the associated reproductive structures and epidermal morphology of these leaves.

Although fossil leaves of *Liquidambar* are widespread in the Neogene, they are virtually unknown from pre-Tertiary floras. However, reproductive structures assignable to the Altingioideae are known since at least the Late Turonian (Zhou et al., 2001). What leaves might have belonged to parent plants with such reproductive structures is still an open question. The co-occurrence of leaves of *Ettingshausenia*, previously determined as *Platanus louravetlanica* Herman et Shczepetov (Herman, 1994), and infructescences of *Anadyricarpa* N. Maslova et Herman, referred to as a member of the Altingioideae on the basis of its microstructural characters (Maslova and Herman, 2004), is noteworthy. There are also cases of co-occurrence of leaves with the *Platanus*-like morphology of the *Ettingshausenia*-type and capitate reproductive structures assigned to different platanaceous genera (Krassilov and Shilin, 1995; Maslova and Kodrul, 2003; Maslova and Herman, 2006), and reproductive structures combining characters of both families (Maslova et al., 2005, 2007).

The mosaicism in characters of the Altingioideae and Platanaceae is expressed in reproductive structures of the genus *Microaltingia* Zhou, Crepet et Nixon (Zhou et al., 2001), in which the major diagnostic features of the Altingioideae are combined with the tricolpate palynotype, which is a character of the Platanaceae (as well as some hamamelidaceous genera of other subfamilies).

To date, six genera have been described on the basis of reproductive remains that are assigned or more or less definitely related to the Altingioideae (Kirchheimer, 1943; Mai, 1968; Krassilov, 1976, 1989; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a; Zhou et al., 2001; Maslova and Herman, 2004; Pigg et al., 2004). All genera but *Steinhauera*, which possesses an infructescence of a relatively unusual morphology, have capitate reproductive structures. Infructescences and seeds from the Eocene–Pliocene of North America, Europe, and Asia were assigned to the modern genus *Liquidambar* (Uemura, 1983; Friis, 1985; Ferguson, 1989; Manchester, 1999; Pigg et al., 2004).
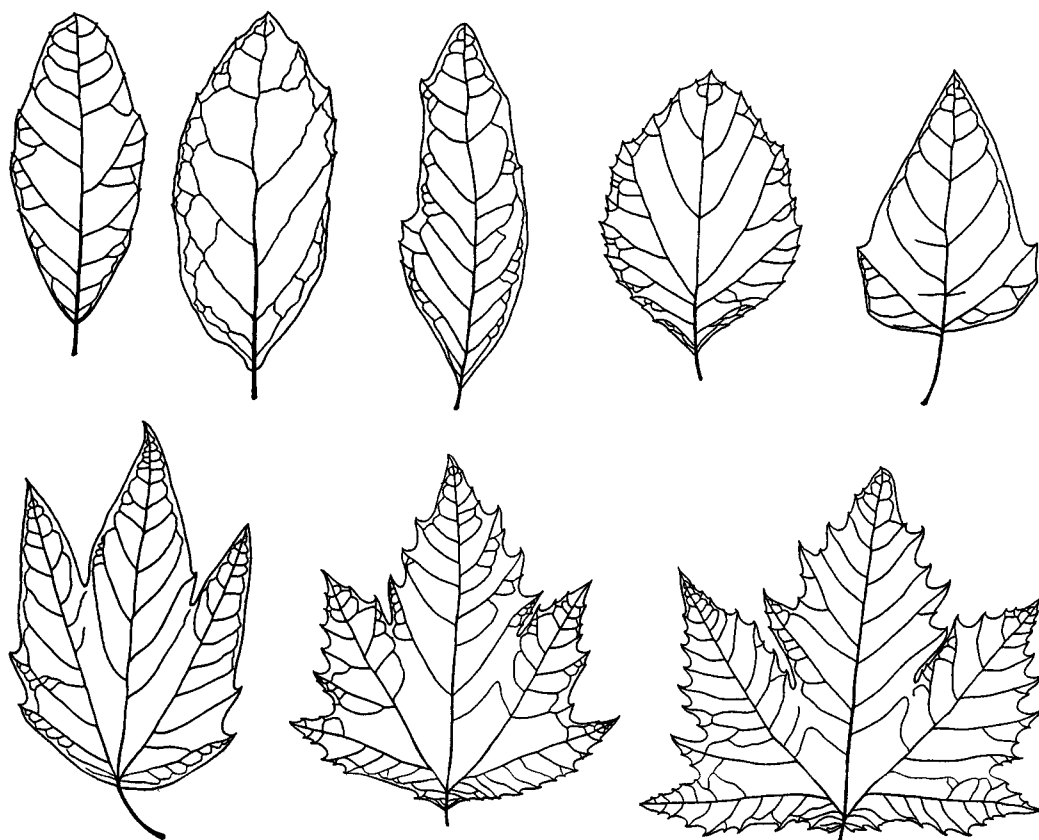
Fig. 1. Polymorphism of leaf blades in modern *Platanus acerifolia* Willd., all leaves collected from one tree; not to scale.

LEAF BLADE MORPHOLOGY IN MODERN MEMBERS OF *PLATANUS*

Leaf blade outline. The outline of the leaf blade varies widely in members of the genus. In general, lobate leaf blades dominate (from weakly to deeply lobed blades). The only living species with entire-margined leaves is *P. kerrii* Gagnep. Leaves of this plane tree are fundamentally different from leaf blades of all other species of the genus. Leaf blades of *P. kerrii* are elliptical or, rarely, elongate. The apex of the leaf blade is pointed, the base is wedge-shaped, teeth are small, and the venation is camptodromous. Intraspecific leaf variability is nearly absent.

Lobate leaves with a wedge-shaped base and distinct basal veins are most typical of the genus. Leaf lobes may be developed to a greater or lesser extent not only within a genus or a species, but also within one tree or even one shoot. Against a background of dominating trilobate or pentalobate leaves, entire-margined or incipiently lobate leaf blades occur quite often. The variability of leaf blades is different in different species of *Platanus*. Henry and Flood (1919) analyzed the leaf morphology of *Platanus* and revealed the high variability of many characters (base, apex, leaf blade margin, and teeth). The most stable character they determined is the depth of the sinuses between lobes. However, MacGinitie (1937) showed that the depth of sinuses

between lobes depends on lighting and temperature regimes; plane trees with deeply lobed leaves grow in well-illuminated and relatively dry sites, whereas species with weaker developed lobes more often occur in moist and overshadowed sites. Moreover, leaf size variability may be related to leaf mosaic, variability between leaves of one year's shoots and leaves of perennial shoots, leaves of ordinary or root shoots.

The analysis of numerous leaves of *P. acerifolia* (hybrid *P. occidentalis* × *P. orientalis*) has shown the high variability of leaf blades of this species (Fig. 1). Leaves collected from a single tree vary remarkably in macromorphology, including entire leaves with a variously toothed margin of the leaf blade, incipiently lobed leaves, asymmetrical, with a solitary developed lobe, and typical lobed leaf blades with uneven depths of sinuses between the lobes and different degree of dentation.

Other leaf characters of plane trees are also very variable. Thus, the base shape of the leaf blade varies widely within one species and one organism. It may be emarginate, wedge-shaped, attenuate, slightly more rarely cordate, truncated, and scalene.

The apices of lobes or entire leaf blades of *Platanus* are variously pointed.

Leaf blade margin. Modern plane trees include species that are characterized by predominantly entire-
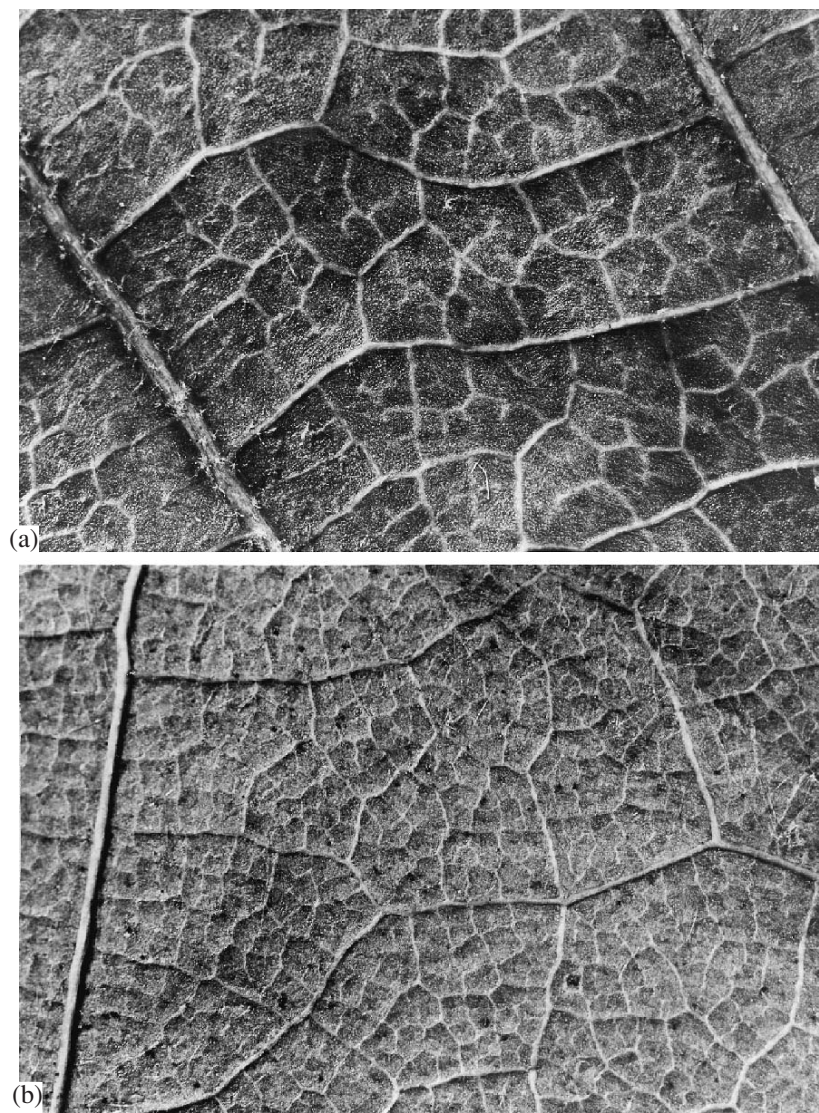
Fig. 2. Venation patterns of higher orders in (a) *Platanus acerifolia* Willd., ×10; and (b) *Liquidambar formosana* Hance, ×10.

margined leaf blades (e.g., *P. mexicana*), with dominating toothed morphotypes (*P. orientalis*), and species with both entire-margined and toothed morphotypes (*P. acerifolia*). Some species of plane trees differ in the density of teeth of the leaf blade margin, their sizes, height, etc. Leaves with one or several teeth often occur in species with predominantly entire-margined leaf blades. In lobed entire-margined leaves, small teeth are occasionally present in upper areas of lobes. In this case, the teeth are usually small and represent naked endings of veins. The study of a representative herbarium of modern species of *Platanus* shows that the dentation patterns change depending on the leaf's ontogenetic stage. Juvenile leaves bear low teeth and often have characteristic papilla-like thickenings. Mature leaves of plane trees have typically concave–concave teeth. In addition, a double dentation develops in leaves of plane trees, i.e., the longer part of a large tooth bears a smaller toothlet.

Venation. As a rule, entire leaves of *Platanus* have a camptodromous venation, and lobate leaves are actinodromous (palynactinodromous). The camptodromous venation is typical of leaves of *P. kerrii* as well as entire-leaved morphotypes of *P. acerifolia*. Lobed leaves, which are most frequently observed in the genus, vary in the extent to which the basal veins are developed. The basal veins may be as thick as the midrib, repeatedly acroscopically and basiscopically branching, or identical in thickness to the secondary veins. Basiscopic branches of basal veins may end craspedodromously or brochidodromously. It is customary to believe that suprabasal deviation of the basal veins is one of the main diagnostic features of the leaves of plane trees. However, more detailed morphological study shows that deviation of the basal veins from the base of the leaf blade is far from uncommon, in fact being usual for *Platanus*.
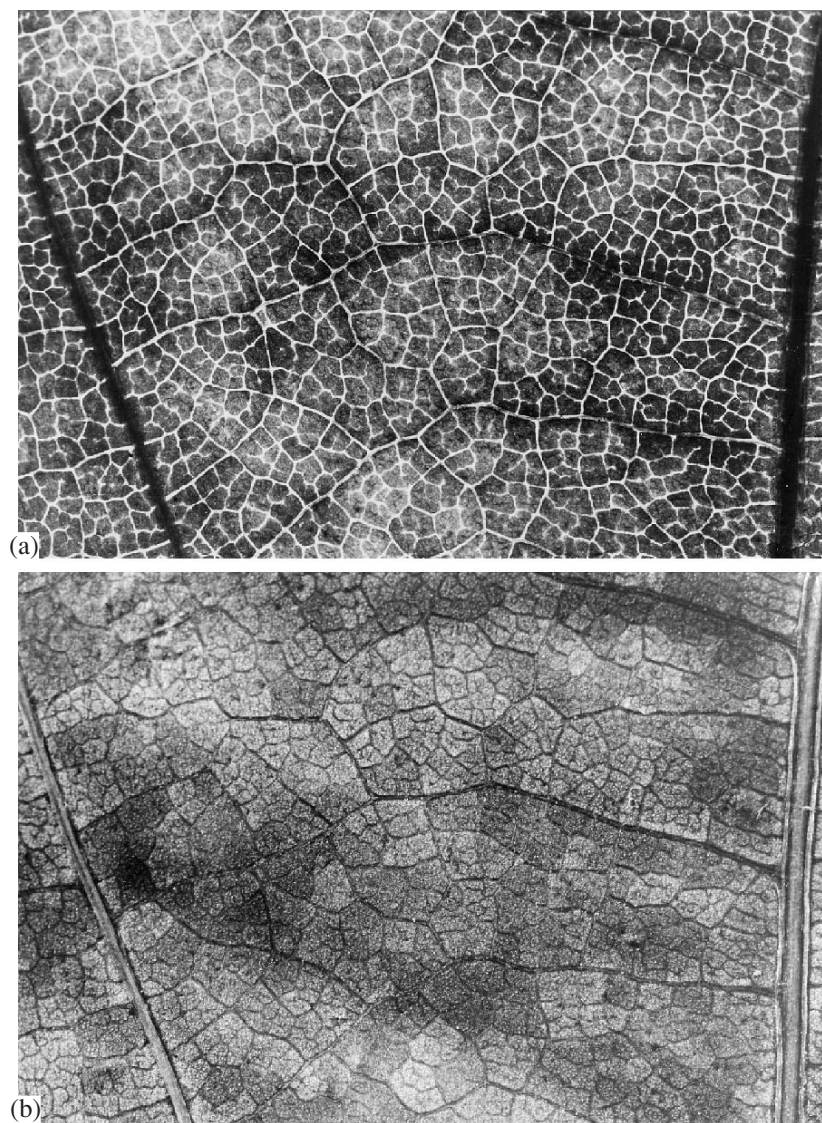
Fig. 3. Venation patterns of higher orders in (a) *Platanus acerifolia* Willd., ×10; and (b) *Liquidambar formosana*, ×10.

Some morphotypes of *P. acerifolia* are distinguished by a particular type of venation that was described by Skvortsova (1960) in leaves of Hamamelidaceae. She named this type pinnate-brochidodromous-craspedodromous and considered it to be transitional between craspedodromous and brochidodromous types. In this type, several lower pairs of veins are looping with each other, and secondary veins of the upper portion of the leaf end in teeth. The ratio between brochidodromous and craspedodromous veins in different species may be different. Thus, in *Fothergilla* only one lower pair of veins is looping with the subsequent pair of veins; other secondary veins end in teeth. In the genera *Sycopsis, Distylium*, and *Eustigma* only one to three pairs of secondary veins in the upper portion of the leaf extend into the teeth, whereas the majority of the secondary veins are looping. According to Skvorts-

ova, this venation type is only characteristic of hamamelidaceous leaves and may serve as a reliable diagnostic character. However, the study of representative leaf material of modern *P. acerifolia* shows that this morphotype is also characteristic of platanaceous leaves. Such patterns of venation are found in the Paleocene genus *Ushia* Kolak., which demonstrates a close similarity to Tertiary and modern *Nothofagus* (Krassilov et al., 1996).

While characterizing tertiary venation, the terms opposite percurrent and alternate percurrent are often used. As a rule, leaves of the plane tree have a well-developed tertiary venation. However, the distinctness of tertiary veins greatly depends on ecological factors. Leaves with a coarser texture and distinct pubescence have the most distinct tertiary venation (Fig. 2a). Leaves with a finer paper-like texture show a weakly developed net of tertiary veins (Fig. 3a). In these mor-

photypes, the tertiary veins may be virtually identical in thickness to veins of subsequent orders. Veins of higher orders form a dense net of closed polygonal meshes.

LEAF BLADE MORPHOLOGY IN MODERN MEMBERS OF THE ALTINGIOIDEAE, HAMAMELIDACEAE

Leaf blade outline. *Altingia* has evergreen narrowly or broadly elliptical, elongate, or ovate leaves with a camptodromous venation. The apex of the leaf blade is usually slightly attenuated and often lacking teeth. The base of the leaf blade is wedge-shaped, rounded, or slightly emarginate. The leaf margin has small, regularly arranged teeth.

Liquidambar is characterized by deciduous, predominantly lobate leaves. The morphological variability in leaves of *Liquidambar* is sufficiently well studied (Holm, 1930; Dunkan, 1959; Smith, 1967; Makarova, 1957; Ferguson, 1989).

Ferguson (1989) analyzed leaf morphotypes of different species of *Liquidambar*. It was shown that leaf blades vary within this genus from entire with pinnate venation to lobate (with three or five lobes) with variously developed lobes. For instance, *L. acalycina* H.-T. Chang has mostly trilobate leaves, but entire leaf blades and leaves with one lobe occur quite often. Among leaves of *L. formosana* Hanse, trilobate leaves prevail, while entire, one-lobed, and pentalobate morphotypes are rarer. *L. macrophylla* Oersted is equally characterized by trilobate and pentalobate leaves; leaves with four lobes (asymmetric) also occur.

The genus *Semiliquidambar* is characterized by polymorphic foliage; the same shoot bears entire, one-lobed, and typically lobate leaves. Originally, plants with such leaf morphotypes characteristic of both *Altingia* and *Liquidambar* were described as *Altingia changii* Metcalf (Metcalf, 1931), but later referred to as the new genus *Semiliquidambar* (Chang, 1962).

Leaf morphotypes of the genus *Semiliquidambar* that resemble *Altingia* are virtually identical in macromorphology to leaves of *Altingia*, but for trilobate leaves, typical of *Liquidambar*, Ferguson (1989) determined distinguishing characters. In particular, it was shown using *L. acalycina* as an example, that the length-to-width ratio in leaf blades of trilobate leaves and the ratio between lengths of petiole and leaf blade differ significantly from those of similar leaves of *Semiliquidambar cathaensis* H.-T. Chang.

Makarova (1957) emphasized the high variability of the leaf outline in modern *Liquidambar formosana* Hense and concluded that leaves of extinct members of this genus might have been equally variable. Along with the trilobate leaves typical for this species, forms transitional to *Altingia* were found, i.e., entire leaves with incipient lobes, with one lobe, or typical *Altingia*-like entire leaves (Makarova, 1957). Such diversity was

discovered in the herbarium of *Liquidambar formosana* that was collected in Kwangtung Province of China. It is possible that the leaf blade polymorphism attributed to *Liquidambar formosana* by Makarova (1957) was in fact attributable to the genus *Semiliquidambar*, which was described later (Chang, 1962). It is pertinent that the specimens attributed to *Liquidambar formosana* that were described by Makarova as polymorphic were Chinese.

Leaf blade margin. A leaf blade margin with regularly distributed small teeth is typical of the Altingioideae. Possible variations of this character that are worthy of mention include double dentation (each larger tooth has a smaller tooth on its longer side) in *Liquidambar formosana*, entire-margined leaf blades in Chinese *Liquidambar edentata* Merrill (Merrill, 1927), and the absence of teeth on the attenuated apices of leaf blades in *Altingia chinensis* (Champ.) Oliv. Small glandular teeth of leaves of the Altingioideae are also characteristic (Li and Hickey, 1988).

Venation. The main venation types of the Altingioideae are camptodromous (*Altingia* and entire morphotypes of *Liquidambar* and *Semiliquidambar*) and actinodromous (rarely palynactinodromous in lobed leaves of *Liquidambar* and *Semiliquidambar*).

Ferguson (1989) showed that the venation near the leaf blade margin is almost identical in all three altingioid genera and, therefore, cannot be used as a diagnostic feature. Ferguson also studied venation of higher orders in *Altingia excelsa* Noronha and concluded that this feature is highly variable, depending on climatic conditions. These variations concern the size of areoles and the number of free endings of veins within one areole.

GENERAL MORPHOLOGY AND MICROSTRUCTURAL FEATURES OF REPRODUCTIVE ORGANS OF MODERN *PLATANUS*

The reproductive sphere of the genus *Platanus* is represented by compound inflorescences and infructescences (Fig. 4a). The inflorescences consist of a central axis and sessile or petiolate unisexual heads, occasionally with rudimentary structures of the opposite sex, i.e., staminodes in pistillate flowers and rudimentary pistils in staminate flowers.

Heads of *Platanus* consist of a relatively large receptacle and numerous radiating densely packed flowers with a varying number of flower elements. Staminate flowers of extant plane trees have from three to five stamens, with a short filament and elongate tetrasporangiate anthers. Underdeveloped carpels are occasionally present in staminate flowers. The number of stamens varies even within an individual head (Boothroyd, 1930). The stamen filament is sometimes so short that the anthers appear sessile. Each anther consists of two thecae with two pollen sacs. The thecae are
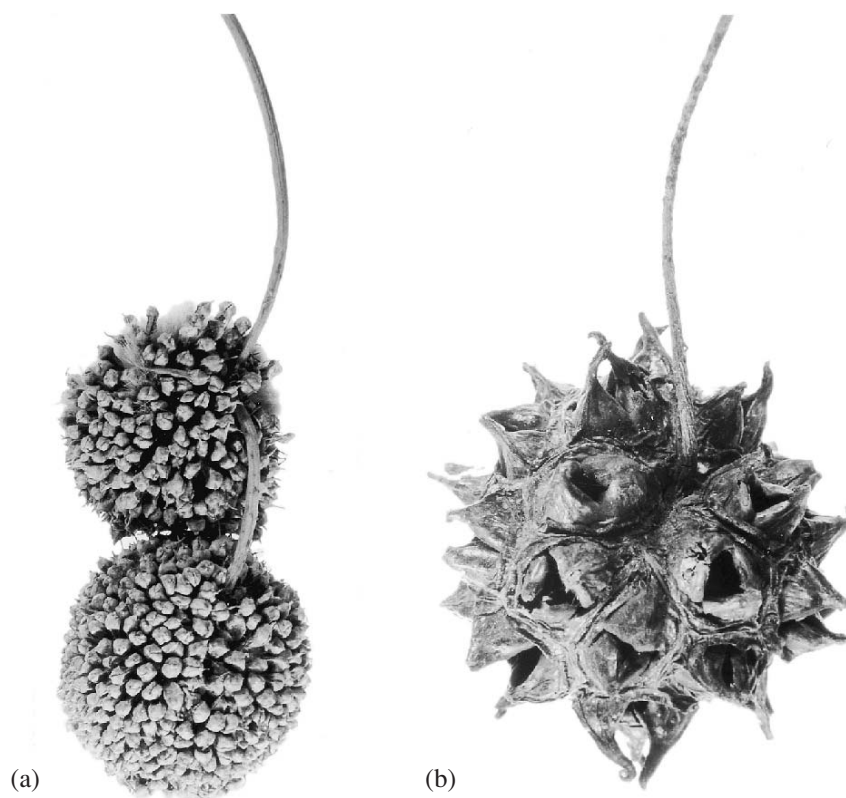
Fig. 4. Infructescences of modern members of *Platanus* and *Liquidambar*: (a) *Platanus occidentalis* L., ×1; (b) *Liquidambar formosana* Hance, ×2.

connected in a peltate way by the apically widened connective. Pollen sacs are asymmetrical, as the thecae develop unequally and differ in size within one stamen (Hufford and Endress, 1989). There is evidence that, in staminate inflorescences, well-developed stamens are accompanied by relatively small staminodes, which basally fuse with stamens to form a relatively large tissue ring (Magallón-Puebla et al., 1997). Stamens of *Platanus* produce tricolpate reticulate pollen grains, spherical or slightly elongate in the equatorial position and angular in the polar position. Aberrant pantocolpate pollen grains were recorded in both the modern plane tree (Zavada and Dilcher, 1986) and the fossil genus *Archaranthus* N. Maslova et Kodrul of the Platanaceae (Maslova and Kodrul, 2003).

Pistillate flowers of *Platanus* are characterized by apocarpous gynecium of five–eight (rarely, three–nine) carpels in two or three circles, with long stylodes. A distinguishing feature of *Platanus* is the incomplete fusion of the carpel margin even in the mature state (Sporne, 1974). The stigma is decurrent along the ventral suture of the style. The ovule is usually solitary and orthotropic. The presence of dispersed hairs in pistillate flowers and bunches of hairs at the base of the fruit are generic characters of *Platanus*.

GENERAL MORPHOLOGY AND MICROSTRUCTURAL FEATURES OF REPRODUCTIVE ORGANS OF MODERN MEMBERS OF THE ALTINGIOIDEAE, HAMAMELIDACEAE

The Altingioideae have capitate inflorescences and infructescences (Fig. 4b). Their compound inflorescences consist of an axis with several staminate heads and a solitary basal pistillate head. A head in the inflorescence of *Altingia* contains 6–25 flowers, and in *Liquidambar* up to 40 flowers. Infructescences of the Altingioideae vary in density. For example, *L. styraciflua, L. orientalis*, and *L. formosana* have basally coalescent fruits forming a conjunct infructescence, whereas in *L. acalycina*, as in *Altingia*, the fruits are loosely attached and the infructescence parts under mechanical pressure (Ickert-Bond et al., 2005).

Pistillate inflorescences have naked flowers with paired carpels, which are basally fused, variously apocarpous in their apical parts, and form a semiinferior syncarpous ovary with numerous ovules. The syncarpous semiinferior ovary of two carpels is a key character of all Hamamelidaceae. However, an inconstant number of carpels in flowers of one genus was recorded; monocarpellate gynecia among prevailing bicarpellate gynecia were found in *Altingia* and *Liquidambar* (Wisniewski and Bogle, 1982; Bogle, 1986).

Plate 12
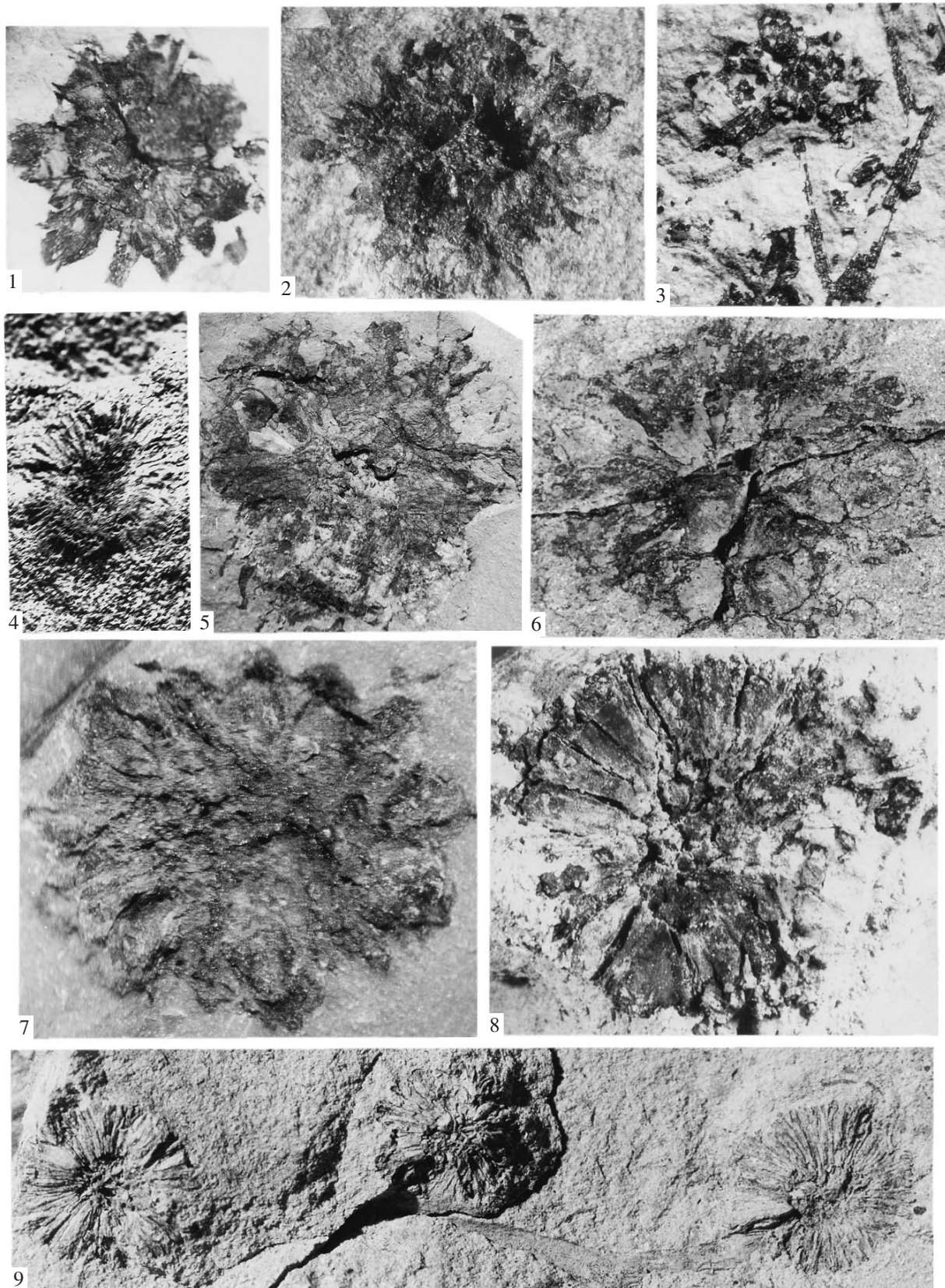
A distinctive feature of pistillate flowers in the Altingioideae is the presence of sterile elements, staminodes and intrafloral phyllomes (Bogle, 1986). These flowers are also characterized by asynchronous maturation of fruits; one head contains mature fruits and carpels at early stages of maturation.

Staminate inflorescences of the Altingioideae are smaller heads. The staminate flower has a simple circle of five–nine stamens and usually two central abortive pistils. The anthers are tetrasporangiate and almost sessile. The pollen grains are polyporate; however, polyporate pollen grains with distinctly elongated pores were observed in *L. orientalis*; this is comparable to pantocolpate pollen grains of *Chunia* (Exbucklandioideae, Hamamelidaceae; Chang, 1964).

ON THE GEOLOGICAL HISTORY OF THE PRINCIPAL LEAF AND REPRODUCTIVE MORPHOTYPES OF PLATANOIDS AND ALTINGIOIDS

The lobate leaf morphotype typical of modern *Platanus* appeared in the Early Cretaceous and was assigned to the genus *Ettingshausenia* Stiehler of the morphological system of dispersed Cretaceous leaves (Maslova et al., 2005). In spite of its significant variability, this morphotype has remained generally unchanged, i.e., leaves of this type accompany platanoids throughout the evolution, from their origin (late Early Cretaceous), through their peak (Late Cretaceous), to the present day, when only one genus of the once large family survives. Along with typical *Platanus* characters of leaf morphology, *Ettingshausenia* shows several hamamelidaceous (in particular, Altingioideae) characters (see, e.g., Maslova and Herman, 2004). The high degree of leaf polymorphism is itself a diagnostic character. Complementing the generally recognized

knowledge about the polymorphism of leaves of the modern plane tree, studies of representative monotopic samples show the high variability of leaf characters in Cretaceous leaves of the *Platanus* appearance (Moiseeva, 2003; Moiseeva et al., 2004). This situation is a perfect illustration of the hypothesis earlier expressed by Krassilov (1976) that high leaf variability is combined with evolutionary conservatism. The reasons for the preservation of a standard morphology over a long period (morphological stasis) may be hypothesized on a paleontological basis, where the concept of morphological species is generally adopted, and morphological stasis is in fact equivalent to evolutionary stasis.

The formation of leaf morphotypes in the Altingioideae differs from those in the Platanaceae. The oldest finds of Altingioideae-like leaves are dated Cenomanian (Krassilov and Bacchia, 1998). These simple leaves with pinnate venation and relatively large teeth with characteristic glandular endings were described as the genus *Nammourophyllum* N. Maslova et Krassilov and resemble leaves of modern *Altingia*. Reliable leaf remains that are assignable or comparable to the genus *Liquidambar* are probably absent from the Cretaceous. The determinations of *Liquidambar* in the Upper Albian–Cenomanian of North America (Lesquereux, 1874) are unconvincing, since these fossils differ significantly from the modern genus in general morphology, and data on the epidermal structure and reproductive remains are absent. The leaf morphotype that is typical of *Liquidambar* appears in the geological record as late as the Eocene; since then reproductive remains of this genus are also known. It should be pointed out that a leaf imprint found in the Upper Paleocene of the Chemurnaut Bay of the Kamchatka Peninsula (Maslova, 2003) shows a morphology that is very close to *Liquidambar*, but also has some features that are not characteristic of this genus; the midvein is straight

Explanation of Plate 12

Fig. 1. Staminate inflorescence of *Tricolpopollianthus burejensis* Krassilov (Platanaceae), BPI, no. 575-149, Amur Region, Tsagayan Formation, Paleocene, ×7.

Fig. 2. Staminate inflorescence of *Chemurnautia staminosa* N. Maslova (Platanaceae), specimen PIN, no. 3736/45, northwestern Kamchatka Peninsula, Chemurnaut Bay, upper part of the Kamchik Formation–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene, ×12.

Fig. 3. Staminate inflorescence of *Archaranthus krassilovii* N. Maslova et Kodrul (Platanaceae), specimen PIN, no. AB-3/81, Amur Region, Tsagayan Formation, upper part of the middle subformation, Maastrichtian–Danian, ×7.

Fig. 4. Infructescence of *Platanus stenocarpa* N. Maslova (Platanaceae), specimen PIN, no. 3736/57, northwestern Kamchatka Peninsula, Chemurnaut Bay, upper part of the Kamchik Formation–lower part of the Tkaprovayam Formation, Upper Paleocene–Lower Eocene, ×2.

Fig. 5. Infructescence of *Viltyungia eclecta* N. Maslova (Hamamelidaceae), specimen PIN, no. 1181-3-585, Eastern Siberia, Lena–Vilyui Depression, Tyung River, Timerdyakhskaya Formation, Cenomanian, ×7.

Fig. 6. Infructescence of *Liquidambar* sp. (Hamamelidaceae), specimen PIN, no. 4855/4, eastern Sakhalin Island, Shakhtnaya River Basin, tributary of the Gornaya River, Verkheduiskaya Formation, Lower Miocene, ×2.5.

Fig. 7. Infructescence of *Evacarpa polysperma* N. Maslova et Krassilov (Hamamelidaceae), specimen PIN, no. 4257/44, northwestern Kamchatka Peninsula, section between Rebro and Getkilnin capes, Tkaprovayam Formation, Upper Paleocene–Lower Eocene, ×15.

Fig. 8. Infructescence of *Lindacarpa pubescens* N. Maslova (Hamamelidaceae), specimen PIN, no. 1196-20-62, Eastern Siberia, Lena-Vilyui Depression, Linda River, Chirimyiskaya Formation, Coniacian, ×4.

Fig. 9. Infructescence of *Anadyricarpa altingiosimila* N. Maslova et Herman (Hamamelidaceae), specimen PIN, no. 4875/3-1, northeastern Russia, Anadyr River Basin, middle reach of the Grebenka River, Srednekrivorechenskaya Subformation, Upper Albian–Lower Cenomanian, ×4.5.

along the whole length of the leaf, and loops of secondary veins are angular.

As was said above, leaves of *Ettingshausenia* were associated with reproductive structures assigned to different genera of the Platanaceae, Altingioideae (Hamamelidaceae), or combining characters of both families. Generic and familial diagnostics of such fossil reproductive structures can only be accomplished at the level of microstructure, as their general morphology, with rare exceptions, is identical (Pl. 12). These are capitate inflorescences and infructescences, with elements packed at different densities, consisting of a rounded receptacle and radiating flowers. In terms of morphology, the inflorescences and flowers are the most compound parts of the plant. In comparison with leaves, roots, and stems, flowers are more complicated structures constituted of several elements forming a whole. Floral organs effectively differentiate and function as if they were individual objects; as particular elements are connected in compound structures (sympetalia, synandria, etc.), they may play a role of new floral elements, providing such flowers with a new evolutionary status. The formation of such structures in capitate inflorescences may be traced on paleobotanical material (see, e.g., Crepet et al., 1992; Magallón-Puebla et al., 1997).

Such heads first appear in the geological record in the Late Albian (Friis et al., 1988; Crane et al., 1993). They are characterized by the Platanaceae-like morphology and are assigned to that family. Later, an association of these structures with the foliage of *Ettingshausenia* was shown (Krassilov and Shilin, 1995; Maslova and Kodrul, 2003; Maslova and Herman, 2006). However, there are other data that suggest that such heads are affiliated with the Altingioideae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a; Zhou et al., 2001; Maslova and Herman, 2004), including one case of their co-occurrence with leaves of *Ettingshausenia*. A similar association is also known for heads combining characters of the Platanaceae and Hamamelidaceae (Maslova et al., 2005, 2007). Consequently, during a certain period (from the Late Albian–Cenomanian until at least the Early Paleocene), leaves of *Ettingshausenia* were associated with both platanaceous and hamamelidaceous heads.

Leaves of *Platimeliphyllum* N. Maslova show a similar situation. Leaf remains of this polymorphous genus were first described in association with staminate inflorescences of *Chemurnautia* N. Maslova, which were assigned to the Platanaceae (Maslova, 2002). Later, it was revealed that these leaves are related to inflorescences of *Archaranthus*, which also show platanaceous morphology (Maslova and Kodrul, 2003), and *Bogutchanthus* N. Maslova, Kodrul et Tekleva (Maslova et al., 2007; Kodrul and Maslova, 2007).

The association of a particular leaf morphotype with different reproductive structures confirms the validity of the morphological system of Cretaceous dispersed leaves independent of the system of modern plants (Krassilov, 1979). On the other hand, the fact that leaves of *Ettingshausenia* and *Platimeliphyllum* are most probably remnants of both platanaceous and hamamelidaceous plants leads one to believe that the associated heads fit outside the framework of modern families. This concept is supported by recent finds of reproductive structures showing typical characters of both modern Platanaceae and Hamamelidaceae as well as features that are typical of neither of these families (Maslova et al., 2005; 2007). However, further paleobotanical evidence is required.

As reproductive structures are found much more rarely than leaf remains, and new taxa are often erected based on unique material of a few specimens, data on specific and generic variability of floral characteristics in capitate inflorescences are virtually lacking, and available data count in favor of their stability (Maslova, 2003). Unlike fossil finds, the reproductive structures of modern members of the Platanaceae and Altingioideae are remarkably different in macromorphology. Therefore, the reproductive structures show a strategy opposite to that of the leaves: stability of characters at a given chronological plane (in contrast to variability) is combined with high evolutionary rates.

Thus, the leaves of modern Platanaceae and Altingioideae, being elements of a single temporal section, mostly allow one to compare variation series of leaf characters, whereas paleontological data may serve for the comparison of reproductive characters in genera of different ages and for the reconstruction of their evolutionary trends.

ISOMORPHIC POLYMORPHISM IN MEMBERS OF THE PLATANACEAE AND ALTINGIOIDEAE, HAMAMELIDACEAE

Leaves. Isomorphic polymorphism in the Platanaceae and Altingioideae (Hamamelidaceae) is most pronounced in the leaf morphology of their members. The study of the leaf morphological variability in these taxa has revealed a number of features with surprisingly similar variation ranges and substantiated the construction of almost identical variation series. Isomorphism in leaf characters is expressed at the specific and generic levels (Fig. 5).

Lobed leaves typical of the subgenus *Platanus* (Figs. 5e–5j) are comparable in macromorphology with lobed leaves of *Liquidambar* (Figs. 5q, 5r, 5t–5w, 5y, 5z). The similarity is expressed in the presence of morphotypes with identical number of lobes (trilobate leaves: Figs. 5h, 5q, 5t; pentalobate leaves: Figs. 5e–5g, 5j, 5r, 5v, 5w, 5y, 5z), equal depth of sinuses between lobes (Figs. 5e, 5r), similar outline of lobes (Figs. 5g, 5z), presence of both double and ordinary dentations, and the presence of forms with distinct opposite percurrent (Fig. 2) or predominantly reticulate tertiary venation (Fig. 3).
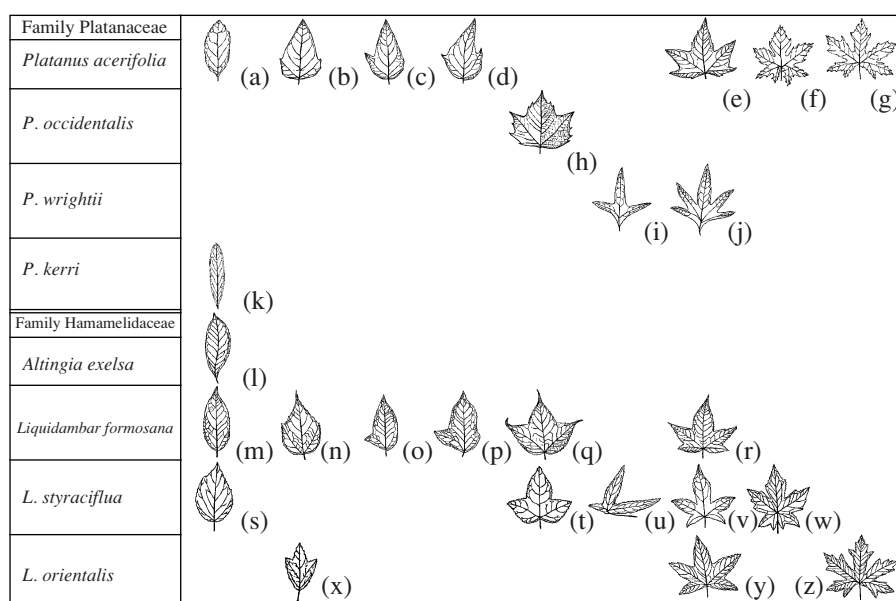
Fig. 5. Leaf blade variability in members of the family Platanaceae and subfamily Altingioideae, Hamamelidaceae: (a–l, v) original herbarium; (m) Makarova, 1957, pl. 11, fig. 2; (n) Makarova, 1957, pl. 11, fig. 8; (o) Makarova, 1957, pl. 11. fig. 3; (p) Makarova, 1957, pl. 11, fig. 9; (q) Makarova, 1957, pl. 11, fig. 1; (r) Makarova, 1957, pl. 11, fig. 10; (s) Holm, 1930, pl. 201, fig. 10; (t) Holm, 1930, pl. 200, fig. 5; (u) Makarova, 1957, pl. 1, fig. 5; (w) Makarova, 1957, pl. 1, fig. 4; (x) Makarova, 1957, pl. 11, fig. 13; (y) Makarova, 1957, pl. 11, fig. 14; and (z) Makarova, 1957, pl. 11, fig. 12; not to scale.

Along with macromorphological characters, anatomical characters also exhibit similar variation. It was a generally accepted opinion that, in *Liquidambar*, stomata were situated exclusively on the lower side of the leaf blade (Sharma and Tyree, 1973), but Ferguson (1989) found that they were also present on the upper side, near veins. Similarly, some leaf morphotypes of *Platanus acerifolia* bear on their upper surface isolated stomata mostly restricted to leaf veins. Genera of the Altingioideae are characterized by paracytic stomata (Pan et al., 1990), and stomata of *Platanus* are described as anomocytic (Metcalfe and Chalk, 1950). However, describing stomata of the plane tree as anomocytic, Krassilov (1973b) pointed out that a pair of narrow paracytic subsidiary cells also occur in *Platanus*; Brett (1979) described stomata of modern *P. orientalis* as pleioparacytic. The presence of paracytic stomata in addition to anomocytic stomatal apparatuses were observed in *Platanus* (Carpenter et al., 2005).

Carpenter (et al., 2005) found on the adaxial surface of leaves of modern *Platanus* rounded bases of trichomes, which are supplied with cutin-armored apertures on the inner face of the cuticle. Similar cuticular structures around stomatal apertures occur on the inner face of the leaf cuticle in modern *Liquidambar formosana*.

Morphotypes of entire leaves with pinnate venation, which are characteristic of *Platanus kerrii* (subgenus *Castaneophyllum*; Fig. 5k) and occur in *P. acerifolia* (Fig. 5a) are comparable to leaf blades of the genus *Altingia* (Fig. 5l) and some morphotypes of *Liquidambar formosana* and *L. styraciflua* (Figs. 5m, 5s). It is necessary to emphasize that leaves of both *Platanus kerrii*

and species of *Altingia* are relatively constant in general morphology, with very low variability. The morphological similarity between *Platanus kerrii* and species of *Altingia* is expressed in the general outline of the leaf blade, venation type, and shape of marginal teeth. It is interesting that leaves of *Altingia*, along with typically altingioid glandular marginal teeth (for example, in *A. excelsa* Nor.), have the concave–concave teeth typical of *Platanus* (e.g., *Altingia tachtadjanii* Trung.).

Both variation groups of morphotypes (lobed leaves of *Platanus* and *Liquidambar* and entire leaves of *Platanus kerrii* and *Altingia*) occur in the genus *Semiliquidambar* (Fig. 6) and the species *Platanus acerifolia* (Fig. 1). Both taxa are of hybrid origin; *Semiliquidambar* is a hybrid between the genera *Liquidambar* and *Altingia*, and *Platanus acerifolia* is a hybrid between the species *P. orientalis* and *P. occidentalis*.

Reproductive structures. Pistillate inflorescences and infructescences of modern members of the Platanaceae and Altingioideae (Hamamelidaceae) differ remarkably in general morphology (Fig. 4), whereas staminate heads have a general similarity. As to their geological predecessors, recent paleobotanical studies have shown that, until a certain evolutionary stage, the female reproductive organs of these taxa were also nearly identical (Pl. 12). They varied exclusively in anatomical characteristics.

The following morphological variations are discernable, from characters of the reproductive sphere, in fossil and modern Platanaceae and Altingioideae: (1) flowers with well-developed perianths (almost all fossil

Fig. 6. Leaf blade polymorphism in *Semiliquidambar cathayensis* H.T. Chang (after *Flora of China,* 2003, pp. 22, 23, text-fig. 10).

members of the Platanaceae and many fossil altingioids) or naked flowers (*Platanus* and modern altingioids, as well as the fossil genus *Evacarpa* N. Maslova et Krassilov); (2) structurally unisexual flowers (some fossil members of the Platanaceae, e.g., *Platananthus* and *Friisicarpus*, and the fossil genus *Anadyricarpa*) or structurally bisexual flowers (flowers of the fossil genus *Gynoplatananthus* Mindell, Stockey et Beard; Mindell et al., 2006, and some infructescences of the modern genus *Liquidambar* with well-developed stamens producing mature pollen grains; Ickert-Bond et al., 2005); (3) structurally unisexual heads (some fossil members of the Platanaceae, e.g., *Platananthus* and *Friisicarpus*, and the fossil genus *Anadyricarpa*) or functionally unisexual heads with rudiments of the opposite sex (modern *Platanus* and modern genera of the Altingioideae); (4) constant number of floral elements (the majority of fossil members of the Platanaceae, e.g., penta- and tetrastaminate flowers of *Platananthus* and *Archaranthus*, respectively, or penta- and tetrapistillate flowers of *Friisicarpus* and *Quadriplatanus*, respectively, and modern Altingioideae) or an inconsistent number of floral elements (*Platanus* and modern Altingioideae); (5) long stamen filaments (the fossil genus *Aquia* and modern *Liquidambar*) or short stamen filaments (many fossil members of the Platanaceae and modern *Platanus* and *Altingia*). Trends in the evolution of reproductive organs of the Platanaceae and

Hamamelidaceae were previously discussed in detail (Maslova, 2003). The following trends in the evolution of reproductive structures are recognized in both Planataceae and Altingioideae: increasing diameter of inflorescences and infructescences, increasing size of fruits, reduction of the perianth, and increasing size of the pollen grains.

RELATIONSHIPS BETWEEN THE PLATANACEAE AND MEMBERS OF THE ALTINGIOIDEAE, HAMAMELIDACEAE

The phylogenetic relationships between the Platanaceae and Hamamelidaceae have long been a matter of discussion. Similarities between these families were suggested by many scientists on the basis of morphological, anatomical, and biochemical characteristics (Tippo, 1938; Takhtajan, 1966; Jay, 1968; Cronquist, 1981; Zavada and Dilcher, 1986; Krassilov, 1989; Schwarzwalder and Dilcher, 1991; etc.). The synthesis of data accumulated by many branches of biology led to the combining of these families into the order Hamamelidales, which occupied a key position in the phylogenetic tree of dicots (Takhtajan, 1966, 1987; Cronquist, 1981). Molecular research (Chase et al., 1993; APG, 2003; and others) did not support the concept of a relationship between these families, and placed the Platanaceae and Hamamelidaceae in remote orders (Proteales and Saxifragales, respectively). The contradictions between molecular and morphological conclusions are predetermined not only by the type and specificity of data and analytical methods, but, more importantly, by different principles of classification. When the conclusions of molecular systematists about phylogenetic relationships between taxa do not fit those of botanists, the existing system should not be hurriedly revised, at least, until the main mechanisms of evolution are compared at the levels of DNA and organisms. In any event, any method that claims to be able to construct the system and reconstruct the history of the organic world needs to be more or less compatible with the fossil record. Referring to the geological record, a considerable discrepancy is obvious between concepts based on molecular and paleobotanical data about members of the Platanaceae and Hamamelidaceae.

There is already considerable paleobotanical evidence supporting the existence in the geological past of a polymorphous ancestral group that was common for the Platanaceae and Hamamelidaceae, and later split into several individual lineages. This evidence comes from both leaf and reproductive remains.

Finds of fossil leaves allowed Golovneva (1994) and Maslova (2002) to describe several genera combining platanaceous and hamamelidaceous characters. All these Cretaceous genera of fossil leaves show both platanaceous and hamamelidaceous characters, the latters are mostly of the subfamily Hamamelidoideae (*Hamamelis, Parrotia*, and others). Cretaceous leaf remains of the Altingioideae are virtually unknown. The genus

Evacarpa described from the Paleocene deposits is close to the Altingioideae in the micromorphology of floral structures, and similar to *Platanus* in the presence of staminodes in pistillate flowers. The foliage of *Evaphyllum kamchaticum* N. Maslova associated with *Evacarpa* combines characters of the genera *Platanus* and *Altingia* (Maslova, 2003). Lobed leaf morphotypes of the Altingioideae (*Liquidambar*) appear in the fossil record as late as the Eocene.

As was shown above, leaves of *Ettingshausenia*, which morphotypes resemble those of the modern plane tree, but often exhibiting hamamelidaceous characters, were associated in the Cretaceous with members of the Platanaceae, Hamamelidaceae (including Altingioideae), and reproductive structures combining characters of both families. Such co-occurrences of reproductive structures assigned by paleobotanists to different modern families and leaves of the same morphotype suggest the existence in the Cretaceous of an ancestral group that gave rise to both modern Platanaceae and Hamamelidaceae.

The fossil reproductive structures combining characters of the Platanaceae and Hamamelidaceae (in particular, Altingioideae) are of great interest in relation to the problem under discussion. This primarily concerns the general morphological pattern of capitate inflorescences and infructescences (genera *Lindacarpa, Evacarpa*, and *Anadyricarpa*). However, in spite of the common general morphological pattern, there are variations combining important diagnostic characters of compound inflorescences and infructescences of these two families that prevent the assignment of such finds to either of the families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005, 2007).

Capitate inflorescences and infructescences from the Raritan Formation (Turonian) of New Jersey demonstrate an eclectic combination of characters (Crepet et al., 1992). Pistillate inflorescences showing hamamelidaceous characters (bicarpellate syncarpous ovary, well-developed perianth, and supposed nectar-producing staminodes in flowers) are associated with staminate heads of predominantly platanaceous characteristics (capitate shape, unisexual inflorescence, densely packed stamens in the flower, broadly triangular apex of the connective, and reticulate tricolpate pollen); however, the pollen tube formation makes them closer to some members of the Hamamelidaceae.

The genus *Kasicarpa* N. Maslova, Golovneva et Tekleva, described from the Turonian of the Chulym–Yenisei Depression, is also similar to modern and fossil members of the Platanaceae and Hamamelidaceae in the totality of its characters (Maslova et al., 2005). It shares with the Platanaceae the capitate shape of inflorescences, developed perianths (predominantly in fossil genera), solitary orthotropic ovule, and spermoderm morphology.

Among members of the Hamamelidaceae, *Kasicarpa* is most similar to genera of the subfamilies Alt-

ingioideae and Hamamelidoideae. The similarity to modern Altingioideae includes the general morphological pattern of the compound unisexual inflorescence (axis with heads), the number of flowers within a head, and the asynchronous maturation of carpels. The main distinctions are the bicarpellate gynecium with a semiinferior ovary and several seeds in a fruit in the Altingioideae contrasting to the monomeric gynecium with an inferior ovary and solitary seed in *Kasicarpa.* However, Bogle (1986) showed that, although bicarpellate gynecium dominates in members of the Altingioideae, monocarpellate forms are also present. In addition, modern Altingioideae lack a perianth. However, well-developed perianths are typical of fossil genera related to altingioids. The infructescences of *Kasicarpa* are particularly similar to those of *Anadyricarpa*, a genus described from the Late Albian–Early Cenomanian of northeastern Russia (Maslova and Herman, 2004). This is primarily expressed in the solitary carpel in the flower, the capitate shape of infructescences, the number of flowers within a head, and the well-developed perianth.

The genus *Bogutchanthus* (Maslova et al., 2007) from the Early Paleocene of the Amur Region also peculiarly combines platanaceous and hamamelidaceous reproductive characters, mostly the characters of the subfamilies Hamamelidoideae and Exbucklandioideae, but also of the Altingioideae. The similarity to the Platanaceae concerns the general morphological pattern of the compound capitate inflorescence, strictly tetramerous flowers with a differentiated perianth, and the presence of intrafloral staminodes.

The similarity between *Bogutchanthus* and members of the Hamamelidaceae is expressed in the general appearance of capitate inflorescences, presence of staminodes in flowers, bisporangiate anthers, and pantocolpate pollen grains. The subfamily Altingioideae and *Bogutchanthus* are similar in the presence of capitate inflorescences and staminodes. A characteristic feature of *Bogutchanthus* is free arrangement of flowers in the inflorescence and free arrangement of stamens in flowers; this is not characteristic of the Platanaceae, but is usual in the Hamamelidaceae and occurs in *Liquidambar acalycina* of the Altingioideae (Ickert-Bond et al., 2005).

Among fossil specimens that are determined to the family level, characters of a different family were also detected. In particular, Late Turonian *Microaltingia,* assigned to the Altingioideae (Zhou et al., 2001), has unisexual flowers with a bicarpellate gynecium, well-developed hypanthium, phyllomes arranged in cycles, and numerous ovules. However, *Microaltingia* has small elongate tricolpate pollen grains with reticulate exine, which are characteristic of the Platanaceae and representatives of other subfamilies of the Hamamelidaceae.

The discoveries of fossil genera uniting characters of both families under consideration, and co-occurrence of different organs that supposedly belong to the same plant, but by their morphology and anatomy are assignable to different modern families, suggest that

Table 1. Prognosis of finding fossil capitate reproductive structures on the basis of combination of the perianth and gynecium characters

Perianth / Gynoecium	Perianth absent	Perianth present	Floral tube
Monomeric			*Kasicarpa* *Anadyricarpa*
Dimeric	*Liquidambar* *Evacarpa* *Microaltingia*	*Viltyungia*	*Lindacarpa*
Tetramerous		*Quadriplatanus*	
Pentamerous		*Friisicarpus* *Gynoplatananthus* *Macginicarpa*	
Varying number of elements	*Platanus*		

Table 2. Prognosis of finding fossil capitate reproductive structures on the basis of combination of the perianth and seed characters

Perianth / Seed	Perianth absent	Perianth present	Floral tube
One		*Quadriplatanus* *Macginicarpa*	
One, orthotropic	*Platanus*	*Friisicarpus*	*Kasicarpa*
One, anatropic			
More than one	*Evacarpa*	*Viltyungia*	
More than one, orthotropic			
More than one, anatropic	*Liquidambar* *Microaltingia*		

the Platanaceae and Hamamelidaceae are related. Therefore, at the dawn of both families, more finds of fossil genera combining platanaceous and hamamelidaceous morphological features are expected.

The isomorphic polymorphism in the Platanaceae and Altingioideae, which is considered in the present paper, is an additional illustration of Vavilov's law of homologous series (1921). It may be considered as an expression of evolutionary parallelism, indirectly confirming the close relationship of the Platanaceae and Hamamelidaceae.

It is evident that characters differ in taxonomic value. The main criteria estimating a morphological feature include the degree of its variability, marginal states, and the range of variation dependent on the type of feature, environment, and the ontogenetic phases of the plant. Vavilov's law allows the existing deviations of characters from their normal state to be systemized into more or less distinct series. This process reveals that allied plant groups show similar variation patterns and similar general trends of variability. Parallel variability foresees a certain range of variation in a given character of a poorly studied (or unknown) species by comparison with a well-studied closely related species. For example, the variation range in the development of

the marginal teeth and the leaf blade size in *Betula verrucosa* Ehrh. allowed Mamaev (1969) to predict the presence of large teeth and leaf blades varying in size in some Siberian and Far Eastern birches.

According to Vavilov's law, the study of the morphological variability of characters in one species (genus) allows one to predict an analogous series of morphological forms in a related species (genus). Vavilov arranged his data in tables where each character occupied a separate row, and each species, a separate column. This way, he predicted the existence of some species of modern plants which were unknown at time he was working. Later, it was shown that the law is applicable to both related species of one genus and to genera of different families. Tables 1–4 show an attempt to predict the existence of so far unknown fossil forms on the basis of morphological variations in capitate inflorescences.

The study of morphological variability reveals the entire range of possible states. The variation series obtained are more important for comparative purposes rather than per se (Fig. 5). Such series should be compared both by the presence of analogous elements and similar variation ranges. The limits of variation of a given character will apparently be constricted by its

genetic potential. Realization of different states of a character is determined by many factors, but the number of possibilities is limited by the available morphogenetic basis. If similar combinations of variational states of characters are present, then similar morphogenetic grounds are conceivable. It is probable that the closer are these grounds, the greater number of identical characters and ranges of their states appear from these grounds, and, therefore, such parallel series indirectly testify to the possible relationships between the taxa under study. The conclusion concerning possible genetic closeness of the taxa under comparison is directly dependent on the completeness of the homologous series as well as on the number of characters which variation series may be similar. The farther apart the taxa are, the less distinct is the parallelism in the variability of characters. The number of characters that determine the possible alliance of these taxa also decreases. Similar variations in different taxa are a basis for similar evolutionary trends (in the development of characters) to be expressed, i.e., they predetermine the similarity in the evolutionary trends.

A common morphological basis very greatly increases the likelihood of parallelism in variability being expressed. Admittedly, a similarity between phenotypes may be inherited from a common ancestor or acquired independently. Phenotypical similarity does not necessarily imply genotypical similarity, and *vice versa* identical genotypes do not guarantee identical phenotypes. Taking into account that the data of molecular genetics are so far insufficient for adequate comparison between the genotypes of taxa under study, and, as geneticists have shown, expression of a character is not coded by a separate gene (i.e., there is no direct identity between a gene and a character), but by gene net, which may be variably configured, it is difficult, if not impossible, to answer whether this morphological similarity is a result of the common origin or it should be treated as an example of homoplasy. The consideration of homologies of morphological structures in terms of homologies at other (cellular, genetic, etc.) levels, or, worse, subordination of some concepts to others, seems unjustified. As early as 1935, Vavilov wrote, "Although not always, but, nevertheless, very often a change in different genera is expressed by the same, i.e., homologous genes. Identical changes in phenotypes may be caused by different genes as well. As far as systematics deals with characters, and, reviewing plant and animal kingdoms, we mostly do not deal with genes, about which little information is so far available, but with characters expressing under certain environmental conditions, it is more correct to discuss homologous characters." I believe that the only available criterion for revealing the nature of parallelisms is the fossil record confirming (or denying) possible phylogenetic relationships between taxa under consideration.

Vavilov established his law of homologous series on the basis of variability of morphological characters in modern plants, i.e., in one temporal interval. Later, this

Table 3. Prognosis of finding fossil capitate reproductive structures on the basis of combination of the perianth and androecium characters

Androecium / Perianth	Perianth almost or completely absent	Well-developed perianth
Tetramerous	*Sarbaya*	*Archaranthus* *Quadriplatanus* *Bogutchanthus*
Pentamerous		*Platananthus* *Hamatia* *Aquia* *Gynoplatananthus*
Varying number of elements	*Platanus* *Chemurnautia*	

Table 4. Prognosis of finding fossil capitate reproductive structures on the basis of combination of the perianth and palynological characters

Pollen grains / Perianth	Perianth almost or completely absent	Well-developed perianth
Tricolpate	*Platanus* *Chemurnautia* *Microaltingia*	*Platananthus* *Quadriplatanus* *Archaranthus* *Aquia* *Gynoplatananthus*
Tricolporate	*Sarbaya*	*Hamatia*
Pantocolpate		*Bogutchanthus* *Viltyungia*
Periporate	*Liquidambar*	

law was revealed to be applicable to other biological objects and different chronological ranges. Thus, Rozanov (1973) showed that, in Cambrian Archaeocyatha, the study of homologous variability is important for systematics (the existence of many previously unknown forms of Archaeocyatha was predicted by means of Vavilov's tables) and allows the completeness of the geological record and validity of information about a particular fossil group to be estimated. Parallel variability was studied on other paleontological objects (see, e.g., Tatarinov, 1976; Rozhnov, 2002; Ponomarenko, 2005). I consider the isomorphic polymorphism in the Platanaceae and Altingioideae as evidence of structural parallelism in the development of these plant groups, predetermined by a common inherited morphogenetic base. This may be confirmed by: (1) the identity of many vegetative and generative characters during a considerable interval of geological time (characters may be considered either as innovations or reactivation of latent possibilities); (2) fusion of floral structures in both groups (staminate and floral tubes); and (3) common phyloge-

netic trends in several reproductive characters. Of importance is the fact that similar variations in the development of characters in the Platanaceae and Altingioideae include both macromorphological and anatomical characters and, moreover, apart from such relatively simple structures as leaves, concern such compound structures as inflorescences (infructescences) and flowers.

ACKNOWLEDGMENTS

REFERENCES

1. E. Anderson and K. Sax, "Chromosome Numbers in the Hamamelidaceae and Their Phylogenetic Significance," J. Arnold Arbor. **16** (2), 210–215 (1935).

2. APG: Angiosperm Phylogeny Group, "An Update of the Angiosperm Phylogeny Group Classification for the Orders and Families of Flowering Plants: APG II," Bot. J. Linn. Soc. **141**, 399-436 (2003).

3. G. Bentham and J. D. Hooker, *Genera plantarum* (Reeve, London, 1865), Vol. 1.

4. C. L. Blume, *Flora Javae nec non insularum adjacentium* (J. Frank, Brussels, 1928).

5. A. L. Bogle, "The Floral Morphology and Vascular Anatomy of the Hamamelidaceae: Subfamily Liquidambaroideae," Ann. Miss. Bot. Garden. **73** (2), 325–347 (1986).

6. D. W. Brett, "Ontogeny and Classification of the Stomatal Complex of *Platanus* L.," Ann. Bot. Cr. Brit. **44**, 249–251 (1979).

7. R. J. Carpenter, R. S. Hill, and G. J. Jordan, "Leaf Cuticular Morphology Links Platanaceae and Proteaceae," Int. J. Plant Sci. **166** (5), 843–855 (2005).

8. H. T. Chang, "*Semiliquidambar*, Novum Hamamelidacearum Genus Sinicum," Bull. Sunyatsen Univ. **1**, 34–44 (1962).

9. H. T. Chang, "A Revision of the Hamamelidaceous Flora of China," Bull. Sunyatsen Univ. **1**, 54–71 (1973).

10. H. T. Chang, "Hamamelidaceae," Flora Rep. Pop. Sin. **35**, 36–116 (1979) [in Chinese].

11. Ts.-T. Chang, "Pollen Morphology in the Families Hamamelidaceae and Altingiaceae," Tr. Botan. Inst. Akad. Nauk SSSR, Ser. 1 **13**, 173–232 (1964).

12. M. K. Chase, D. E. Soltis, R. G. Olmstead, et al., "Phylogenetics of Seed Plants: An Analysis of Nucleotide Sequences from the Plastid Gene *rbc*L," Ann. Miss. Bot. Gard. **80**, 528–580 (1993).

13. P. R. Crane, S. R. Manchester, and D. L. Dilcher, "Morphology and Phylogenetic Significance of the Angiosperm *Platanites hybridicus* from the Palaeocene of Scotland," Palaeontology **31**, 503–517 (1988).

14. P. R. Crane, K. R. Pedersen, E. M. Friis, and A. N. Drinnan, "Early Cretaceous (Early to Middle Albian) Platanoid Inflorescences Assotiated with *Sapindopsis* Leaves from the Potomac Group of Eastern North America," Syst. Bot. **18** (2), 328–324 (1993).

15. W. L. Crepet and K. Nixon, "The Fossil History of Stamens," in *The Anther: Form, Function and Phylogeny*, Ed. by G. D'Arcy and R. C. Keating (Cambridge Univ. Press, Cambridge, 1996), pp. 25–57.

16. W. L. Crepet, K. C. Nixon, E. M. Friis, and J. V. Freudenstein, "Oldest Fossil Flowers of Hamamelidaceous Affinity, from the Late Cretaceous of New Jersey," Proc. Nat. Acad. Sci. USA **89**, 8986–8989 (1992).

17. A. Cronquist, *An Integrated System of Classification of Flowering Plants* (Columbia Univ. Press, New York, 1981).

18. R. Dahlgren, "A System of Classification of the Angiosperms to Be Used to Demonstrate the Distribution of Characters," Bot. Not. **128**, 119–147 (1975).

19. G. Depape, "Remarques sur quelques arbres monotypes actuels et leur histoire geologique," Bull. Soc. bot. Frauce., No. 113, 204–211 (1966).

20. W. H. Dunkan, "Leaf Variation of *Liquidambar styraciflua* L.," Castanea **24**, 99–111 (1959).

21. P. K. Endress, "A Suprageneric Taxonomic Classification of the Hamamelidaceae," Taxon **38**, 371–376 (1989a).

22. P. K. Endress, "Aspects of Evolutionary Differentiation of the Hamamelidaceae and the Lower Hamamelididae," Pl. Syst. Evol. **162**, 193–211 (1989b).

23. D. K. Ferguson, "A Survey of the Liquidambaroideae (Hamamelidaceae) with a View to Elucidating Its Fossil Record," in *Evolution, Systematics and Fossil History of the Hamamelidae, 1: Introduction and "Lower" Hamamelidae*, Ed. by P. R. Crane and S. Blackmore (Clarendon Press, Oxford, 1989), pp. 249–272.

24. *Flora of China*, Vol. 9 *Pittosporaceae through Connaraceae* (Sci. Press and Missouri Botan. Garden, Beijing–St. Louis, 2003), pp. 22–23.

25. E. M. Friis, "Angiosperm Fruits and Seeds from the Middle Miocene of Jutland (Denmark)," Kong. Danske Vidensk. Selskab Biol. Skrifter. **24**, 1–165 (1985).

26. E. M. Friis, P. R. Crane, and K. R. Pedersen, "Reproductive Structures of Cretaceous Platanaceae," Kong. Danske Vidensk. Selskab Biol. Skrifter. **31**, 1–55 (1988).

27. A. Goldberg, "Classification, Evolution and Phylogeny of the Families of Dicotyledons," Smithsonian Contrib. Bot., No. 58, 1–314 (1986).

28. P. Goldblatt and P. K. Endress, "Cytology and Evolution in Hamamelidaceae," J. Arnold Arbor. **58** (1), 67–71 (1974).

29. L. B. Golovneva, "The New Genus *Platimelis* in the Late Cretaceous–Early Paleogene Floras of the Arctic Region," Botan. Zh. **79** (1), 98–107 (1994).

30. H. Harms, "Hamamelidaceae," in *Die Naturlichen Pflanzenfamilien*, Ed. by A. Engler and K. Prantl (Engelmann, Leipzig, 1930), pp. 303–345.

31. A. Henry and M. G. Flood, "The History of the London Plane," Proc. Roy. Arish. Acad. Sec. B. **35** (2), 9–18 (1919).

32. A. B. Herman, "Diversity of Cretaceous Platanaceae of Anadyr–Koryak Subregion in Connection with Climatic Changes," Stratigr. Geol. Korrelyatsia **2** (4), 62–77 (1994).

33. A. B. Herman and L. B. Golovneva, "A New Genus of Late Cretaceous Platanaceae from the Northeastern USSR," Botan. Zh. **73** (10), 1456–1467 (1988).

34. M. T. Hoey and C. R. Parks, "Isozyme Divergence between Eastern Asian, North American, and Turkish Species of *Liquidambar* (Hamamelidaceae)," Am. J. Bot. **78**, 938–947 (1991).

35. M. T. Hoey and C. R. Parks, "Genetic Divergence in *Liquidambar styraciflua, L. formasana* and *L. acalycina* (Hamamelidaceae)," Syst. Bot. **19**, 308–316 (1994).

36. A. Hollick, "The Upper Cretaceous Floras of Alaska," US Geol. Surv. Prof. Paper., No. 159, 1–123 (1930).

37. T. Holm, "Leaf-Variation in *Liquidambar styraciflua* L.," Rhodora. **32** (37), 95–100 (1930).

38. L. D. Hufford and P. K. Endress, "The Diversity of Anther Structures and Dehiscence Patterns among Hamamelididae," Bot. J. Linn. Soc. **99** (4), 301–346 (1989).

39. J. Hutchinson, *Evolution and Phylogeny of Flowering Plants* (Academic, London–New York, 1969).

40. S. M. Ickert-Bond, K. B. Pigg, and Wen Jun, "Comparative Infructescence Morphology in *Liquidambar* (Altingiaceae) and Its Evolutionary Significance," Am. J. Bot. **92** (8), 1234–1255 (2005).

41. K. R. Johnson, "Description of Seven Common Fossil Leaf Species from the Hell Creek Formation (Upper Cretaceous: Upper Maastrichtian), North Dakota, South Dakota, and Montana," Proc. Denver Mus. Nat. Hist., Ser. 3, No. 12, 1–47 (1996).

42. F. Kirchheimer, "Ueber *Steinhauera subglobosa* Presl. und die Reste von *Liquidambar*–Fruchstanden aus Tertiar Mitteleuropas," Neues Jahrb. Mineral. Abt. B, 216–225 (1943).

43. T. M. Kodrul and N. P. Maslova, "A New Species of the Genus *Platimeliphyllum* N. Maslova from the Paleocene of the Amur Region, Russia," Paleontol. J., No. 11, 402–411 (2007).

44. V. A. Krassilov, "Upper Cretaceous Staminate Heads with Pollen Grains," Palaeontology **16**, 41–44 (1973a).

45. V. A. Krassilov, "Cuticular Structure of Cretaceous Angiosperms from the Far East of the USSR," Palaeontogr. B **142**, 105–116 (1973b).

46. V. A. Krassilov, *Tsagayan Flora of the Amur Region* (Nauka, Moscow, 1976) [in Russian].

47. V. A. Krassilov, *Cretaceous Flora of Sakhalin* (Nauka, Moscow, 1979) [in Russian].

48. V. A. Krassilov, *The Origin and Early Evolution of Flowering Plants* (Nauka, Moscow, 1989) [in Russian].

49. V. A. Krassilov and F. Bacchia, "Cenomanian Florule of Nammoura, Lebanon," Cretac. Res. **21**, 785–799 (2000).

50. V. A. Krassilov, N. M. Makulbekov, and N. P. Maslova, "*Ushia*, a Palaeocene Angiosperm of Nothofagus Affinities from the Lower Volga and Western Kazakhstan," Palaeontographica **239B**, 137–145 (1996).

51. A. N. Krishtofovich and T. N. Baikovskaya, *Cretaceous Flora of Sakhalin* (Akad. Nauk SSSR, Moscow–Leningrad, 1960) [in Russian].

52. Z. Kvaček and S. R. Manchester, and Shuang-xing Guo, "Trifoliolate Leaves of *Platanus bella* (Heer) comb. n. from the Paleocene of North America, Greenland, and Asia and Their Relationships among Extinct and Extant Platanaceae," Int. J. Plant Sci. **162** (2), 441–458 (2001).

53. L. Lesquereux, "Contributions to the Fossil Flora of the Western Territories: Part 1. The Cretaceous Flora," Rep. US Geol. Surv. **6**, 1–136 (1874).

54. J. F. Leroy, "Origine et evolution du genre *Platanus* (Platanaceae)," CR Hebd. Seanc. Acad. Sci. **295**, 251–254 (1982).

55. J. Li, A. L. Bogle, and A. S. Klein, "Phylogenetic Relationships in the Hamamelidaceae: Evidence from the Nucleotide Sequences of the Plastid Gene *mat*K," Plant Syst. Evol. **218**, 205–219 (1999).

56. N. M. Li and L. J. Hickey, "Leaf Architecture and Systematics of the Hamamelidaceae sensu lato," Acta Phytotaxon. Sin. **26** (2), 96–110 (1988).

57. J. Lindley, *A Natural System of Botany* (Longman, London, 1836).

58. J. Lindley, *The Vegetable Kingdom*, 3rd ed. (Bradbury and Evans, London, 1853).

59. H. D. MacGinitie, "The Flora of the Weaverille Beds of Trinity County, California," Carnegie Inst. Washington Publ. **465**, 83–151 (1937).

60. H. D. MacGinitie, "A Middle Eocene Flora from the Central Sierra Nevada," Carnegie Inst. Washington Publ. **534**, 1–178 (1941).

61. S. Magallón-Puebla, P. S. Herendeen, and P. R. Crane, "*Quadriplatanus georgianus* gen. et sp. nov.: Staminate and Pistillate Platanaceous Flowers from the Late Cretaceous (Coniacian–Santonian) of Georgia, USA," Int. J. Plant Sci. **158** (3), 373–394 (1997).

62. S. Magallón-Puebla, P. R. Crane, and P. S. Herendeen, "Phylogenetic Pattern, Diversity and Diversification of Eudicots," Ann. Mis. Bot. Gard. **86**, 297–372 (1999).

63. D. H. Mai, "Zwei ausgestorbene Gattungen im Tertiar Europas und ihre florengeschichtliche Bedeutung," Palaeontographica Abt. B **123**, 184–199 (1968).

64. Z. I. Makarova, "On the History of the Genus *Liquidambar* L.," Botan. Zh. **42** (8), 1182–1195 (1957).

65. S. A. Mamaev, "On the Problems and Methods of Intraspecific Systematics of Trees: 2. Variation Range," in *The Patterns of the Formation and Differentiation of Species in Trees,* Tr. Inst. Ekol. Rast. Zhiv., No. 64, 3–38 (1969).

66. S. R. Manchester, "Vegetation and Reproductive Morphology of an Extinct Plane Tree (Platanaceae) from the Eocene of Western North America," Bot. Gaz. **147**, 200–226 (1986).

67. S. R. Manchester, "Fruits and Seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon," Palaeontogr. Am., No. 58, 1–205 (1994).

68. S. R. Manchester, "Biogeographical Relationships of North American Tertiary Floras," Ann. Mo. Bot. Gard. **86**, 472–522 (1999).

69. N. P. Maslova, "*Liquidambar* L. from the Cenozoic of Eastern Asia," Paleontol. J. **29** (1A), 145–158 (1995).

70. N. P. Maslova, "The Genus *Platanus* L. (Platanaceae Dumortier) in the Paleocene of the Kamchatka Penin-

sula," Paleontol. Zh., No. 2, 88–93 (1997) [Paleontol. J. **31** (2), 203–208 (1997)].

71. N. P. Maslova, "Ancient Platanoids and Hamamelids: A Case of Morphological Convergence?," in *Abstracts of the Fifth Paleobotanical and Palinological Conference, June 26–30, 1998, Kracow, Poland* (Kracow, 1998), p. 114.

72. N. P. Maslova, "A New Early Paleogene Plant of the Family Platanaceae (on the Basis of Leaves and Inflorescences)," Paleontol. Zh., No. 2, 89–101 (2002) [Paleontol. J. **36** (2), 201–213 (2002)].

73. N. P. Maslova, "Extinct and Extant Platanaceae and Hamamelidaceae: Morphology, Systematics, and Phylogeny," Paleontol. J. **37** (Suppl. 5), 467–589 (2003).

74. N. P. Maslova and L. B. Golovneva, "*Lindacarpa* gen. et sp. nov.—A New Hamamelid Infructescence from the Upper Cretaceous of Eastern Siberia," Paleontol. Zh., No. 4, 100–106 (2000a) [Paleontol. J. **34** (4), 445–451 (2000)].

75. N. P. Maslova and L. B. Golovneva, "A Hamamelid Inflorescence with in situ Pollen Grains from the Cenomanian of Eastern Siberia," Paleontol. J. **34** (Suppl. 1), 40–49 (2000b).

76. N. P. Maslova, L. B. Golovneva, and M. V. Tekleva, "Infructescences of *Kasicarpa* gen. nov. (Hamamelidales) from the Late Cretaceous (Turonian) of the Chulym–Enisey Depression, Western Siberia, Russia," Acta Paleobotan. **45** (2), 121–137 (2005).

77. N. P. Maslova and A. B. Herman, "New Finds of Fossil Hamamelids and Data on the Phylogenetic Relationships between the Platanaceae and Hamamelidaceae," Paleontol. Zh., No. 5, 94–105 (2004) [Paleontol. J. **38** (5), 563–575 (2004)].

78. N. P. Maslova and A. B. Herman, "Infructescences of *Friisicarpus* nom. nov. (Platanaceae) and Associated Foliage of the Platanoid Type from the Cenomanian of Western Siberia," Paleontol. Zh., No. 1, 103–106 (2006) [Paleontol. J. **40** (1), 109–113 (2006)].

79. N. P. Maslova and T. M. Kodrul, "New Platanaceae Infructescence *Archaranthus* gen. nov. from the Maastrichtian–Paleocene of the Amur Region," Paleontol. Zh., No. 1, 92–100 (2003) [Paleontol. J. **37** (1), 89–98 (2003)].

80. N. P. Maslova, T. M. Kodrul, and M. V. Tekleva, "New Staminate Inflorescence of *Bogutchanthus* gen. nov. (Hamamelidales) from the Paleocene Beds of the Amur Region, Russia," Paleontol. Zh., No. 5, 89–103 (2007) [Paleontol. J. **41** (5), 564–579 (2007)].

81. N. P. Maslova and V. A. Krassilov, "New Hamamelid Infructescences from the Palaeocene of Western Kamchatka, Russia," Rev. Palaeobotan. Palynol. **97**, 67–78 (1997).

82. N. P. Maslova, M. G. Moiseeva, A. B. Herman, and J. Kvaček, "Did Plane Trees Exist in the Cretaceous?," Paleontol. Zh., No. 4, 98–110 (2005) [Paleontol. J. **39** (4), 440–453 (2005)].

83. A. D. J. Meeuse, "Floral Evolution in the Hamamelideae: 3. Hamamelidales and Associated Groups Including Urticales, and Final Conclusions," Acta Bot. Neerl. **24** (2), 181–191 (1975).

84. A. P. Melikyan, "The Anatomical Structure of Testa in Representatives of the Genera *Liquidambar* L. and *Alt-*

ingia Nor. in the Context of Their Systematics," Biol. Zh. Arm. **24** (10), 17–24 (1971).

85. E. D. Merrill, "New Chinese Ligneous Plants," J. Arnold Arboret. **8**, 3–19 (1927).

86. F. P. Metcalf, "Botanical Notes on Fukien and Southeast China I," Lingnan Sci. J. **10** (4), 413–414 (1931).

87. C. R. Metcalfe and L. Chalk, *Anatomy of the Dicotyledons* (Oxford, 1950), Vol. 1.

88. H. W. Meyer and S. R. Manchester, *The Oligocene Bridge Creek Flora of the John Day Formation, Oregon* (Univ. California Press, Berkeley, 1997).

89. R. A. Mindell, R. A. Stockey, and G. Beardt, "Anatomically Preserved Staminate Inflorescences of *Gynoplatananthus oysterbayensis* gen. et sp. nov. (Platanaceae) and Assotiated Pistillate Fructifications from the Eocene of Vancouver Island, British Columbia," Int. J. Plant Sci. **167** (3), 591–600 (2006).

90. M. G. Moiseeva, "Morphological Variability of Leaves of *"Platanus" raynoldsii* Newberry from the Maastrichtian of the Koryak Highland," Paleontol. Zh., No. 3, 98–107 (2003) [Paleontol. J. **37** (3), 319–330 (2003)].

91. M. G. Moiseeva, T. M. Kodrul, and A. B. Herman, "Fossil Leaves of *"Platanus" raynoldsii* Newberry from Tsagayan Formation in Amur River Region," in *Proceedings of the 3rd Symposium on the Cretaceous Biota and the Cretaceous–Tertiary Boubary, Heilongjiang River Area, China* (China, 2004), pp. 27–31.

92. K. C. Nixon and J. M. Poole, "Revision of the Mexican and Guatemalan Species of *Platanus* (Platanaceae)," Lundellia, No. 6, 103–137 (2003).

93. L. Oken, *Allgemeine Naturgeschichte für alle Stünde* Hoffman'sche (Verlagsbuchhandlung, Stuttgart, 1841).

94. K. Y. Pan, A. M. Lu, and J. Wen, "Characters of Leaf Epidermis in Hamamelidaceae (s. l.)," Acta Phytotaxon. Sin. **28** (1), 10–26 (1990).

95. K. B. Pigg, S. M. Ickert-Bond, and Jun Wen, "Anatomically Preserved *Liquidambar* (Altingiaceae) from the Middle Miocene of Yakima Canyon, Washington State, USA, and Its Biogaographic Implications," Am. J. Botany **91** (3), 499–509 (2004).

96. A. G. Ponomarenko, "Paleontological Data on the Origin of Arthropods," in *Evolutionary Factors of the Formation of Faunal Diversity* (KMK, Moscow, 2005), pp. 146–155 [in Russian].

97. T. A. Rao and O. P. Bhupal, "Typology of Foliar Sclereids in Various Taxa of Hamamelidaceae," Proc. Ind. Acad. Sci., Sect. B **79**, 127–138 (1974).

98. A. Yu. Rozanov, *Patterns of Morphological Evolution of Archaeocyatha and Questions of Stage Zonation of the Lower Cambrian* (Nauka, Moscow, 1973) [in Russian].

99. S. V. Rozhnov, "Morphological Patterns of the Establishment and Evolution of Higher Taxa of Echinoderms," in *Evolutionary Factors of the Formation of Faunal Diversity* (KMK, Moscow, 2005), pp. 156–170 [in Russian].

100. F. S. Santamour, Jr., "Interspecific Hybridization in Liquidambar," Forest Sci. **18**, 23–26 (1972).

101. D. Schmitt, "The Pistillate Inflorescence of Sweetgum (*Liquidambar styraciflua* L.)," Sylvae Genet. **15** (2), 33–35 (1965).

102. G. K. Sharma and J. Tyree, "Geographic Leaf Cuticular and Gross Morphological Variations in *Liquidambar styraciflua* L. and Their Possible Relationship to Environmental Pollution," Botan. Gaz. **134**, 179–184 (1973).

103. S. Shi, Y. Huang, Y. Zhong, et al., "Phylogeny of the Altingiaceae Based on cpDNA matK, PY-IGS and nrDNA ITS Sequences," Plant Syst. Evol. **230**, 13–24 (2001).

104. N. T. Skvortsova, "The Structure of Epidermis in Representatives of the Family Hamamelidaceae," Botan. Zh. **45** (5), 712–717 (1960).

105. R. F. Smith, "The Leaf Dimorphism of *Liquidambar styraciflua* L.," Am. Midland Natur. **77** (1), 42–50 (1967).

106. D. E. Soltis, P. S. Soltis, M. W. Chase, et al., "Angiosperm Phylogeny Inferred from 18S rDNA, rbcL, and atpB Sequences," Bot. J. Linn. Soc. **133**, 381–461 (2000).

107. K. R. Sporne, *The Morphology of Angiosperms* (Hutchinson, London, 1974).

108. A. L. Takhtajan, *The System and Phylogeny of Flowering Plants* (Nauka, Moscow–Leningrad, 1966) [in Russian].

109. A. L. Takhtajan, *The System of Magnoliophyta* (Nauka, Leningrad, 1987) [in Russian].

110. L. P. Tatarinov, *Morphological Evolution of Theriodonts and General Questions of Phylogenetics* (Nauka, Moscow, 1976) [in Russian].

111. R. Thorne, "Synopsis of a Putatively Phylogenetic Classification of the Flowering Plants," Aliso **6**, 57–66 (1968).

112. B. H. Tiffney, "Fruit and Seed Dispersal and the Evolution of the Hamamelidae," Ann. Miss. Bot. Gard. **73** (2), 394–416 (1986).

113. K. Uemura, "Late Neogene *Liquidambar* (Hamamelidaceae) from the Southern Part of Northeast Honshu, Japan," Mem. Nat. Sci. Mus. **16**, 25–36 (1983).

114. G. R. Upchurch, "Cuticle Evolution in Early Cretaceous Angiosperms from the Potomac Group of Virginia and Maryland," Ann. Mo. Bot. Gard. **71**, 522–550 (1984).

115. V. A. Vakhrameev, "Late Cretaceous Platanaceae," in *Sketches of Geology and Paleontology of the Far East* (Dal'nevost. Nauchn. Tsentr Akad. Nauk SSSR, Vladivostok, 1976), pp. 66–78 [in Russian].

116. N. I. Vavilov, "The Law of Homologous Series in Hereditary Variation," Selisk. Lesn. Khoz-vo, No. 1–3, 84–89 (1921).

117. N. I. Vavilov, "The Law of Homologous Series in Hereditary Variation," in *Theoretical Foundation of Plant Selection* (Nauka, Leningrad–Moscow, 1935), Vol. 1 [in Russian].

118. M. Wisniewski and A. L. Bogle, "The Ontogeny of the Inflorescence and Flower of *Liquidambar styraciflua* L. (Hamamelidaceae)," Am. J. Bot. **69** (10), 1612–1624 (1982).

119. M. S. Zavada and D. L. Dilcher, "Comparative Pollen Morphology and Its Relationship to Phylogeny of Pollen in the Hamamelidae," Ann. Miss. Bot. Gard. **73**, 348–381 (1986).

120. Z. Y. Zhang and A. M. Lu, "Hamamelidaceae: Geographic Distribution, Fossil History and Origin," Acta Phytotaxon. Sin. **33**, 313–339 (1995).

121. Z. K. Zhou, W. L. Crepet, and K. C. Nixon, "The Earliest Fossil Evidence of the Hamamelidaceae: Late Cretaceous (Turonian) Inflorescences and Fruits of Altingioideae," Am. J. Bot. **88** (5), 753–766 (2001).