Systematics of Fossil Platanoids and Hamamelids

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Abstract—The data on fossil platanoids and hamamelids are generalized, their morphological diversity and probable patterns of the establishment of the extant families Platanaceae and Hamamelidaceae are analyzed. It is shown that morphological and epidermal characters of polymorphic leaves of typical platanoid appearance were formed in the Late Albian and remained essentially invariable to the present time, indicating the morphological stasis of these leaves combined with a wide variation range. In view of association with essentially different reproductive structures, it is proposed to classify these leaves by the morphological system irrespective of the natural system of angiosperms. A new system of extinct platanoids and hamamelids, which is based on reproductive structures and includes two orders, Hamamelidales and Sarbaicarpales ordo. nov., is proposed. Hamamelidales comprises two extant families, Platanaceae (with the subfamilies Platanoideae subfam. nov. and Gynoplatananthoideae subfam. nov.) and Hamamelidaceae, and the extinct family Bogutchanthaceae fam. nov.; the new extinct order Sarbaicarpales ordo. nov. consists of two new families, Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov. In a system of flowering plants that is based on molecular data, the families Platanaceae and Hamamelidaceae are assigned to remote orders, excluding close relationship (APG, 2003). At the same time, the system of APG II often contradicts morphological and paleontological data, while traditional ideas of morphologists concerning the common origin of these families have recently been supported by paleobotanic evidence. Probable origin of the families Platanaceae and Hamamelidaceae from a common polymorphic ancestral group is discussed.

Key words: Fossil platanoids, fossil hamamelids, Platanaceae, Hamamelidaceae, leaves, reproductive structures, systematics.

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CONTENTS

INTRODUCTION

Fossil platanoids and hamamelids have been studying for more than a century. The families Platanaceae and Hamamelidaceae attract attention of many paleo- and neobotanists because they first appeared in the fossil record at the initial stages of the establishment of angiosperms. In the systems of Takhtajan (1966, 1987) and Cronquist (1981), these families were combined in the order Hamamelidales, which occupies a central position in phylogenetic tree of dicotyledons, representing a link between flowering plant groups positioned close to the base of phylogenetic tree and a group of more advanced orders of "amentiferae" and combining a wide range of primitive and derived morphological and anatomical characters (Hallier, 1903, 1912; Takhtajan, 1966, 1970, 1987; Hutchinson, 1969; Cronquist, 1981; etc.).

In a recently proposed system of flowering plants based on molecular data (APG, 2003), the order Hamamelidales has been abandoned and the families Platanaceae and Hamamelidaceae are assigned to the orders Proteales and Saxifragales, respectively; this strongly contrasts with a close relationship between these groups. The representative paleobotanic data on these groups are almost completely disregarded in a modern variant of this system. The underestimation of paleobotanic data probably results from a superficial understanding of these data, which are artificially pushed into the systems of living flowering plants. In doing so, early angiosperms fall beyond the scope of phylogenetic analysis, although vary considerably and could have expanded the known range of morphological diversity of the group as a whole. Interrelation between groups at the initial stages of evolution also escaped analysis. Paleobotanic data are used at most for the confirmation of classifications and phylogenetic trees constructed based on extant plants; in the case of distinct disagreement, paleobotanic data are either considered to be unsuitable because of certain reasons or excluded without comment from the analysis.

The presently prevailing concept of the systematics and phylogeny of flowering plants is based on molecular data and omits alternative points of view, virtually excluding efficient development and resolution of the problem based on a wide range of data. In the last decades, paleobotanic studies have achieved a new level, which means the study of fossil objects in more detail with the aid of advanced electron and light microscopes to receive previously inaccessible data on their microstructure. Our knowledge of early plants increased considerably primarily with reference to the data on floral structures, the characters of which provide the foundation for taxonomic and phylogenetic constructions. Based on these data, it is possible to estimate the time of the formation, development, and (or) disappearance of particular characters, to recognize presumable transitional characters and phylogenetic trends. Comparison of paleobotanic specimens with extant taxa provides a means for the development of our knowledge of their relationships.

A new point of view concerning the taxonomic positions of the families Platanaceae and Hamamelidaceae, which is based on molecular data, is accepted by the majority of researchers, although it distinctly contrasts with the data of the fossil record. On the contrary, paleobotanic data suggest that the two families evolved from a single polymorphic group, which was widespread in the Cretaceous.

The first paleobotanic data on Hamamelidales were obtained more than a century ago and consisted of descriptions of leaves and inflorescences with distinctive morphological features, which were assigned to extant genera (Newberry, 1868; Lesquereux, 1892; etc.). As for leaf records, the assignment of dispersed Cretaceous leaves to extant genera remains a common practice. Although the earliest reproductive structures of the genus *Platanus* L. are known as late as the Santonian (Tschan et al., 2008), *Platanus*-like leaves from earlier deposits are also referred to the extant genus. In doing so, it is overlooked that the standard general leaf morphology is sometimes combined with cuticular–epidermal characters typical of other families (Rüffle, 1968; Krassilov and Shilin, 1995). In addition, the co-occurrence of these leaves and reproductive structures that are assigned to different families and display mosaic combinations of characters of more than one family (Krassilov and Shilin, 1995; Maslova and Herman, 2004, 2006; Maslova et al., 2005; Maslova, 2009) also cast doubt on the validity of the assignment of these dispersed leaves to one extant genus. Thus, reliable identification of dispersed fossil leaves of platanoid appearance requires new approaches and solutions. In the present study, the use of the genus *Ettingshausenia* Stiehler of the morphological system for designation of dispersed Cretaceous leaves which are identical in morphology to the leaves of the extant genus *Platanus* is substantiated. The same approach seems expedient for identification of entire leaves of the genus *Platimeliphyllum* N. Maslova, which display characters typical for Platanaceae and Hamamelidaceae.

To date, extensive morphological and anatomical data on leaves and reproductive structures of living representatives of the families Platanaceae and Hamamelidaceae have been accumulated. Because of relatively small sizes, it is sometimes impossible to homologize unambiguously the floral structures of Hamamelidales even with extant forms. As fossil material is analyzed, additional difficulties arise in the identification of certain structures. Therefore, paleobotanic studies were based for a long time exclusively on macromorphological characters of leaves and, to a lesser extent, on reproductive structures. As new materials were collected, it turned out that a large number of genera and species, which were mostly established based on leaves, were not provided with distinct diagnoses and, hence, they were difficult to classify. In this

connection, by the end of the 20th century, the systematics of fossil representatives of the families Platanaceae and Hamamelidaceae had mostly been based on the analysis of macromorphology (occasionally supplemented with cuticular–epidermal characters) of leaf remains, which are very polymorphic and, hence, they are of little significance for taxonomic and evolutionary studies. As scanning electron microscopy and, then, transmission electron microscopy were used in paleobotanic studies, it became possible to perform a detailed revision of fossil flowering plants based on all available data, including macromorphological and microstructural characters of vegetative and reproductive structures. Capitate inflorescences and infructescences of platanoids and hamamelids seem rather interesting for evolutionary studies, because their floral structures have undergone significant changes and deviated from the initial morphotypes. In living representatives of the families Platanaceae and Hamamelidaceae, reproductive structures differ considerably in appearance, whereas fossil forms are closely similar in macromorphology of capitate inflorescences and infructescences and show principal differences only at the micromorphological level.

Previous paleobotanic studies have shown that the presently monotypic family Platanaceae was represented in the geological past by an extensive group and played a significant role and often even dominated in the vegetative cover of the Northern Hemisphere in the Cretaceous and Cenozoic (Bůžek et al., 1967; Kvaček, 1970; Vakhrameev, 1976; Krassilov, 1976; Hickey and Doyle, 1977; Manchester, 1986; Crane et al., 1988; Friis et al., 1988; Pigg and Stockey, 1991; and others). Regarding the geological predecessors of the family Hamamelidaceae, which is more diverse in the modern flora, only poor data are available. This is particularly true for Cretaceous records, while Tertiary remains of leaves, wood, seeds, dispersed pollen grains, inflorescences, and infructescences are more abundant (Hu and Chaney, 1940; Brown, 1946; Mai, 1968; Wolfe, 1973; Knobloch and Kvaček, 1976; Mai and Walter, 1978; Tiffney, 1986; Ferguson, 1989; Wang, 1992). Only in the last decades, many new hamamelid taxa have been described, contributing to the hamamelid diversity in the geological past (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla et al., 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Benedict et al., 2008). It should be noted that researchers assigned all new records of leaves and reproductive structures that were similar in macromorphology and partly micromorphology to extant taxa of the extant families; as a result, their variation ranges excessively increased, while diagnoses of the families were not emended.

In addition, along with a considerable increase in the number of fossil reproductive structures and leaf remains referred to the families Platanaceae and Hamamelidaceae, the data on stable associations of platanoid leaves and reproductive structures displaying characters of platanoids (Krassilov and Shilin, 1995; Maslova, 2002a; Maslova and Kodrul, 2003; Maslova and Herman, 2006) and hamamelids (Maslova and Herman, 2004) and combining characters of the two families (Maslova et al., 2005, 2007; Maslova, 2009) have been obtained.

In the present work, available data on extinct and extant representatives of the families Platanaceae and Hamamelidaceae are generalized; a new system of early representatives of these groups is proposed based predominantly on paleobotanic data on reproductive structures. Available paleobotanic records provide a new insight into morphology, systematics, and phylogeny of the families Platanaceae and Hamamelidaceae. Based on these data, the taxonomic position of paleobotanic specimens of platanoids and hamamelids are revised, new extinct families are recognized, and the widely accepted idea of the widespread of extant families in the Cretaceous is put in doubt.

CHAPTER 1. POSITIONS OF THE FAMILIES PLATANACEAE AND HAMAMELIDACEAE IN THE PREVIOUSLY PROPOSED SYSTEMS OF ANGIOSPERMS

The creation and improvement of classifications is presently the basic challenge to the investigators of flowering plants. Approaches to the resolution of these tasks are rather diverse, developing throughout scientific study of botanical objects. It is possible to divide classifications of higher plants into two basic groups. **The first group** includes synthetic systems based on the analysis of heterogeneous morphological, anatomical, biochemical, karyological, and other characters. The greater number of various characters is involved in the development of these systems, the more reliable results of analysis seem to be. In this case, an important task is the establishment of taxonomic significance of particular characters and combination of diagnostic characters of taxa of various ranks. The systems of Takhtajan (1966, 1987, 1997, 2009) and Cronquist (1981) occupy a key place among these systems. They generalize results of the analysis of extensive botanical data obtained by many research teams during a long time. Certainly, the systems developed by Takhtajan and Cronquist remain some questionable points, some are a subject of long discussions; however, they are in general congruous with each other and open to further development based on new scientific data.

In the system of Cronquist and early systems of Takhtajan, the family Platanaceae and Hamamelidaceae were combined in the order Hamamelidales of the subclass Hamamelididae (Takhtajan, 1959) or Hamamelidae (Cronquist, 1968). The composition of this order was repeatedly reconsidered. In particular, Cronquist (1981) combined five families, Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamameli-

daceae, and Myrothamnaceae, in the order Hamamelidales.

In 1966, Takhtajan recognized four families (Hamamelidaceae, Altingiaceae, Platanaceae, and Myrothamnaceae) of Hamamelidales. Later (Takhtajan, 1970), Hamamelidales was considered to comprise three families, Hamamelidaceae (including Altingiaceae, Disanthaceae, and Rhodoleiaceae), Platanaceae, and Myrothamnaceae. In subsequent review (Takhtajan, 1987), Hamamelidales is divided into the families Hamamelidaceae, Rhodoleiaceae, Altingiaceae, and Platanaceae, while the family Myrothamnaceae is regarded following Nakai (1943) as the order Myrothamnales. In the last variant of the system of flowering plants, taking into account the results of genosystematics, Takhtajan (2009) removed the family Platanaceae from Hamamelidales and retained two families, Hamamelidaceae and Altingiaceae, in this order. According to the new concept of Takhtajan, the family Platanaceae is assigned to the monotypic order Platanales, which along with the orders Proteales and Nelumbonales is referred to the superorder Proteanae of the subclass Ranunculidae.

Note that Takhtajan (1966, 1987, 1997) and Cronquist (1981) believed that the order Hamamelidales comprises the families Platanaceae and Hamamelidaceae and provides a link between angiosperms that are close to the base of phylogenetic tree and more advanced orders of the Amentiferae, which combine both primitive and advanced morphological and anatomical characters. However, in the new system of Takhtajan (2009), Platanaceae and Hamamelidaceae are separated and included in different orders (Platanales and Hamamelidales), which belong to different subclasses, Ranunculidae and Hamamelidae, respectively.

The composition of Hamamelidales was also questionable in early systems. In particular, Hallier (1912) believed that Hamamelidales includes only two families, Hamamelidaceae (in which he assigned the genera *Trochodendron* Sieb. et Zucc., *Tetracentron* Oliv., *Euptelea* Sieb. et Zucc., *Cercidiphyllum* Sieb. et Zucc., and *Eucommia* Oliv.) and Coriariaceae. Hutchinson (1967) proposed that this order comprises the families Tetracentraceae, Platanaceae, Stachyuraceae, Buxaceae, Daphniphyllaceae, and Bruniaceae. In the system of Thorne (1973, 1992a, 1992b), Hamamelidales includes the families Trochodendraceae, Eupteleaceae, Cercidiphyllaceae, Platanaceae, and Hamamelidaceae. In the system of Dahlgren (1980), the order Hamamelidales comprises the families Hamamelidaceae (including Rhodoleaceae and Altingiaceae), Platanaceae, Myrothamnaceae, and Geissolomataceae.

Many researchers tested the system of Takhtajan (variants before 2009). In particular, the study of relationships between families of the subclass Hamamelidae based on 40 morphological and anatomical characters, using multifactor models, including principal component analysis (PCA) and the reciprocal averaging (RA), in general agreed with the system of Takhtajan (Barabé et al., 1981). Cladistic morphological analysis of a large set of heterogeneous characters also supported relatively close positions of the families Platanaceae and Hamamelidaceae (Barabé et al., 1982; Barabé, 1984). Hufford and Crane (1989) used cladistic analysis and showed that Platanaceae is a sister group of Hamamelidaceae. Another example is provided by the analysis of fine venation patterns, which involved 700 species of 140 families of dicotyledons, monocotyledons, and conifers (Gamalei, 1989). It was shown that the pattern of fine veins is species-specific, genus-specific, and family-specific. This study corroborated the assignment of the families Platanaceae and Hamamelidaceae to the same order. Zavada and Dilcher (1986) performed cladistic analysis of the subclass Hamamelidae based on palynological characters, such as the unit of dispersal (monads–tetrads), pollen grain shape (ellipsoidal–spheroidal–oblate), aperture type, exine sculpture, and ultrastructure (tectum, infratectum, foot layer, endexine). As a result, Platanaceae fell into the same group as Trochodendraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae (including Atingioideae), Eucommidaceae, and Myrothamnaceae.

The second group includes systems that were developed based on the study of individual characters of particular vegetative or reproductive structures. These "character" systems usually include a limited number of taxa of the same rank, for example, families, subfamilies, or tribes. Because of the narrow field of study, they often result in very narrow or unreasonably broad generalizations and, hence, contradictory conclusions. The systems involving the same taxa, but created based on different characters, may differ considerably from each other. For example, based on the number of ovules in the ovary, the family Hamamelidaceae was divided into two subfamilies, Hamamelidoideae (one ovule) and Bucklandioideae (many ovules) (Niedenzu, 1891), while, based on the seed coat structure, Zhang and Wen (1992) divided it into six subfamilies (Hamamelidoideae, Exbucklandioideae, Disanthoideae, Rhodoleioideae, Mytilarioideae, and Liquidambaroideae).

Different standpoints concerning classifications within the family Hamamelidaceae are illustrated by studies of the spermoderm (Melikyan, 1972, 1973a, 1973b), wood (Huang, 1986), epidermal structure of leaves (Pan et al., 1990), trichome type (Fang and Fan, 1993), etc. Based on the study of fruit and seed structure of the genus *Platanus*, Shevyreva and Doweld (2000) proposed to establish a separate order, Platanales, of the superorder Proteanae. Based on structural characters of the seed coat and pericarp, Doweld (1998) proposed to establish the order Altingiales, including the families Altingiaceae and Rhodoleaceae.

The systems based on molecular data, which have been developed during the last decades (APG, 2003 and others), deserve special consideration. Angiosperm systems that are based on molecular data are constructed anew at the level of orders, whereas the compositions of families remain mostly invariable. On the one hand, the systems of this kind are usually accepted without demur; on the other hand, the results of molecular analysis frequently conflict with the results of morphological studies (moreover, in some cases, the results based on different molecular markers distinctly conflict with each other), and the systems of flowering plants constructed based on these traits are in essence "character" systems. It should be noted that, at present, molecular studies play a role of monopolist in the systematics of plants, definitely rejecting (or completely ignoring) all alternative concepts without providing a means for discussions of results of different studies.

Phylogenetic tree of angiosperms was initially constructed based on one gene, *500rbcL* (Chase et al., 1993). This work was accompanied by 13 papers, which were devoted to the major angiosperm groups. These papers were combined in a special volume of *Annals of Missouri Botanical Garden* (1993, Vol. 80, No. 3). Subsequently, some other genes, for example, *18SrDNA*, were involved in the analysis and a phylogenetic tree of angiosperms with a new topology was obtained (Soltis et al., 1997). Then, three genes (*atpB*, *rbcL*, *18SrDNA*) of 560 angiosperm species were investigated and a summary phylogenetic scheme was constructed (Soltis et al., 1999, 2000).

The consideration of advantages or imperfections of the systems constructed based on molecular data is beyond the scope of the present study; this topic is discussed in detail by experts in genosystematics (see, e.g., bibliography provided by Antonov, 2007). Here we only note that a cladogram obtained by the analysis of DNA sequences (genes) is a tree reflecting phylogenetic changes in these sites, which are not the same as phylogeny of taxa possessing these genes. These trees reflect the process of molecular rather than organism evolution.

In contrast to the ideas developed by Cronquist (1981) and Takhtajan (variants of the system before 2009) and the assignment of the families Platanaceae and Hamamelidaceae to the order Hamamelidales, the system based on molecular data has abandoned this order (APG, 2003) and assigned the families Platanaceae and Hamamelidaceae to the orders Proteales and Saxifragales, respectively. Thus, the positions of these families in the system of flowering plants is one of the most prominent contradictions between molecular and traditional morphological concepts. It is evident that contradictions between molecular and morphological data result from distinctions in the principles of analysis and classification. If some conclusions of genosystematists disagree with the concept of botanists concerning phylogenetic relationships of taxa,

one should not change hastily the traditional systems, since this requires a comparison of the basic evolutionary mechanisms at the levels of DNA and organisms. In any event, each method for the reconstruction of systems and history of the organic world should be coordinated to a greater or lesser extent with the data of the fossil record.

When facing the geological history of Platanaceae and Hamamelidaceae, reconstructions based on molecular data strongly contrast with the fossil botanic record. New ideas based on molecular data concerning the taxonomic positions of the families Platanaceae and Hamamelidaceae have not yet been supported by the data of the fossil record; on the contrary, available paleobotanic data suggest that, in the geological past, Platanaceae and Hamamelidaceae had a common polymorphic ancestral group, which was subsequently split into several lineages. This idea is supported by both fossil leaves and remains of reproductive structures.

CHAPTER 2. TAXONOMIC COMPOSITION OF THE EXTANT FAMILIES PLATANACEAE AND HAMAMELIDACEAE

2.1. Family Platanaceae

The family Platanaceae includes the only extant genus *Platanus* (with the type species *P. orientalis* L.), consisting of the subgenera *Platanus* Leroy and *Castaneophyllum* Leroy (Leroy, 1982). The subgenus *Platanus* comprises species with typical lobate leaves and compound inflorescences, which consist of a short axis and from one to five heads set on the axis (species *P. occidentalis* L., *P. orientalis, P. mexicana* Moricaud, and *P. wrightii* S. Watson).

The subgenus *Castaneophyllum* includes the only species *P. kerri* Gagnepain, which has simple, elliptical leaves and compound inflorescences with an elongated axis and 12 or more heads.

The genus *Platanus* includes a number of allopatric species, which are frequently interfertile and occasionally hybridize. Thus, many plane species virtually lack isolation, and the ranges of their morphological variation frequently overlap because of well-pronounced polymorphism; therefore, different researchers accept different number of species and varieties and the composition of this genus is a subject of long discussion (Grant, 1981). Thus, the species composition of the extant genus *Platanus* is considered to include from 5 to 11 species (Ward, 1888; Berry, 1914; Oishi and Huzioka, 1943; Endo, 1963; *Life of Plants*, 1980). According to the latest data of Nixon and Poole (2003), the genus *Platanus* includes seven species and six varieties.

Species of the genus *Platanus* are traditionally established based on the geographical ranges. In North America, *P. occidentalis* is accompanied by morphologically different plane trees, i.e., *P. wrightii, P. race-*

mosa Nutt., *P. glabrata* Fernald, *P. mexicana, P. lindeniana* Mart. et Gal. (*Life of Plants*, 1980). These species usually have entire lobate leaves. Many authors believe that these species are similar and should be combined in one or two species with several varieties, which are determined by different growth conditions. In particular, MacGinitie (1937, 1941) marked that *P. racemosa* and *P. wrightii* are closely similar. The author cited believes that *P. glabrata* has a continuous series of transitional forms to *P. mexicana*, while *P. lindeniana* differs to the greatest extent from these species and similar in a number of characters to *P. occidentalis*. He believes that *P. lindeniana* is closer to Eocene species than any other extant form.

Nixon and Poole (2003) developed a new concept of the nature of taxonomic relationships of North American representatives of this genus. They have shown that there is one natural contact zone of plane species in that area. Specimens combining characters of *P. mexicana* and *P. rzedowskii* Nixon et Poole occur in the region of San Luis Potosi, Mexico. It is supposed that these trees are a result of hybridization and (or) reciprocal hybridization between two species. The zone of intergradation between these two morphologically different species is relatively narrow and possibly restricted to only one river valley. A wide introgression zone in North America has not been revealed. As a result, the intrageneric system of *Platanus* in North America, which was developed by Nixon and Poole, is based not only on morphological characters, but also takes into account probable interfertility of species with different morphology. These researchers recognized species based on the principle of pronounced differentiation in morphological characters, without introgression, and varieties were established based on the presence of transitional morphological forms with many shared characters. According to the data of Nixon and Poole, North America is inhabited by *P. gentrii* Nixon et Poole, *P. racemosa* var. *wrightii* (S. Wats.) Benson, *P. racemosa* var. *racemosa* Nutt., *P. mexicana* var. *mexicana* Moricaud, *P. mexicana* var. *interior* Nixon et Poole, *P. rzedowski, P. rzedowski × P. mexicana* var. *interior* Nixon et Poole, *P. occidentalis* var. *occidentalis* L., and *P. occidentalis* var. *palmeri* (Kuntze) Nixon et Poole.

The third subgenus of the genus *Platanus, Glandulosa*, was established based on fossil material (Kvaček et al., 2001); at present, it comprises *Platanus bella* (Heer) Kvaček, Manchester et Guo, *P. fraxinifolia* (Johnson et Gilmore) Walther, and *P. neptuni* (Ettingshausen) Bůžek, Holy et Kvaček. Distinctive features of the subgenus *Glandulosa* include the presence of both simple and compound (three- and five-leaflet) leaves with alternative heptacraspedodromous or camptodromous venation, large peltate trichomes, and a well-pronounced scar on the stalk of solitary infructescence. Kvaček and Manchester (2004) believe

that the subgenus *Glandulosa* represents a completely extinct lineage of Platanaceae.

2.2. Family Hamamelidaceae

The family Hamamelidaceae is very diverse and, according to the recent data (Endress et al., 1985; Deng et al., 1992), comprises 30 living genera (144 species), which differ considerably in macromorphological and microstructural features of vegetative and reproductive organs (Bogle, 1970; Skvortsova, 1975; Endress, 1989a; Zhang and Lu, 1995). The majority of genera include two or three species, the most diverse genus *Corylopsis* Sieb. et Zucc. includes 33 species (Morley and Chao, 1977), and the other 14 genera are monotypic.

Relationships between subfamilies and tribes of the Hamamelidaceae are a subject of long discussion (Reinsch, 1890; Harms, 1930; Nakai, 1943; Cronquist, 1968; Endress, 1989b; Shi et al., 1998; Li et al., 1999; etc.).

The classification of the family proposed by Endress (1989b) seems most plausible. Of six subfamilies known at that time, the subfamily Hamamelidoideae was most diverse, including 22 genera. The subfamily Altingioideae comprised three genera, Mytilarioideae included two, and each of Disanthoideae, Rhodoleioideae, and Exbucklandioideae included one. Endress concluded that the variation ranges of characters of genera of the monotypic subfamilies Exbucklandioideae, Mytilarioideae, and Disanthoideae do not exceed those of the subfamily Hamamelidoideae. Therefore, Endress combined these genera in the subfamily Exbucklandioideae (Endress, 1989b) based on morphological similarity in leaves and reproductive organs and identity in chromosome number. Thus, in the classification of Endress (1989b), the family Hamamelidaceae includes four subfamilies: Hamamelidoideae (with the tribes Hamamelideae, Fothergilleae, Eustigmateae, and Corylopsideae), Rhodoleioideae, Exbucklandioideae, and Altingioideae.

Recent molecular studies (Shi et al., 1998; Li et al., 1999) have not supported assignment of the genera *Disanthus* Maxim., *Mytilaria* Lecomte, and *Exbucklandia* R. Brown to one subfamily and ranked *Disanthus* as a separate subfamily. According to these data, Hamamelidaceae includes the following subfamilies: Altingioideae (sensu Endress 1989a), Exbucklandioideae (sensu Harms, 1930), Mytilarioideae (sensu Chang, 1973), Rhodoleioideae (sensu Harms, 1930), Disanthoideae (sensu Harms, 1930), and Hamamelidoideae (sensu Endress, 1989c).

The compositions of tribes and subtribes of the subfamily Hamamelidoideae, which includes the greatest number of genera, are also a subject of discussion; the other subfamilies include one or several genera (Harms, 1930; Endress, 1989c; Qiu et al., 1998; Shi et al., 1998; Li et al., 1999).

In the system proposed by Endress, the genera *Altingia* Noronha, *Liquidambar* L., and *Semiliquidambar* H.T. Chang compose the subfamily Altingioideae of the family Hamamelidaceae. The taxonomic positions of these genera have been discussed by botanists for more than a century, since this is one of the most debatable questions in the systematics of the Hamamelidaceae.

Lindley (1853) indicated that these genera are quite similar and proposed to assign them to a separate family, Altingiaceae; De Candolle (1864) assigned *Altingia* and *Liquidambar* to Platanaceae.

Supporters of the assignment of these genera to Altingiaceae (Lindley, 1853; Andersen and Sax, 1935; Skvortsova, 1960; Chang, 1964; Takhtajan, 1966, 1987, 2009; Melikyan, 1971, 1973a; Rao, 1974; Rao and Bhupal, 1974; Dahlgren, 1975; Chase et al., 1993; Li et al., 1999; APG, 2003; Ickert-Bond et al., 2005, 2007) indicate that this conclusion is based on both morphological (anatomy of seeds and conducting system, morphology of pollen grains) and molecular data. The results of molecular studies are ambiguous with reference to the positions of the genera *Altingia* and *Liquidambar* in the system. In particular, some researchers believe that these genera belong to the family Hamamelidaceae (Shi et al., 1998); however, the study of some other markers suggests that they should be assigned to the family Altingiaceae within the order Saxifragales (Chase et al., 1993; Magallón et al., 1999; Soltis et al., 2000; etc.).

Based on the study of morphology, anatomy, and ontogenetic features, other research teams placed the genera *Altingia* and *Liquidambar* in 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; Fang and Fan, 1993; Zhang and Lu, 1995; Endress and Igersheim, 1999). Relatively close relationships of *Altingia* and *Liquidambar* with the Hamamelidaceae is supported by some data of cladistic analysis (Hufford and Crane, 1989).

In an alternative classification based on structural characters of the spermoderm and pericarp, Doweld (1998) established the order Altingiales, including the families Altingiaceae and Rhodoleioceae.

Taxonomic independence of the genera *Altingia, Liquidambar*, and *Semiliquidambar* is also a subject of discussion. Some researchers combined *Altingia* and *Liquidambar* in one genus (*Liquidambar*), based only on morphological characters of leaves and infructescences (Lindley, 1836; Oken, 1841; De Candolle, 1864; Bentham and Hooker, 1865; Blume, 1928; Leroy, 1982). However, superficial morphological similarity of infructescences is not supported by anatomical characters, since distinct similarity in the basic structures is combined with considerable distinc-

tions, which confirm the independent status of each genus (Bogle, 1986). The assignment of *Altingia, Liquidambar*, and *Semiliquidambar* to one genus is strongly supported by molecular data (Shi et al., 2001; Ickert-Bond and Wen, 2006). In earlier studies, Reichinger (1943) and Meikle (1977) proposed to assign species of the genus *Liquidambar* to one species.

The genera *Altingia* and *Liquidambar* share the following distinctive features: the resin canals associated with vascular bundles in the stem, leaves, and inflorescences; compound bisexual inflorescences; capitate infructescences; naked functionally unisexual flowers; the presence of sterile structures (phyllomes and staminodia), surrounding the ovary in pistillate flowers; numerous anatropous ovules, most of which are underdeveloped; small winged seeds; and periporate pollen grains. The characters listed oppose these genera to other hamamelids. However, resin canals, compound inflorescences, sterile structures in pistillate flowers, and periporate pollen grains occur in other subfamilies of the Hamamelidaceae. These are not distinctive characters of the genera *Altingia* and *Liquidambar*. Based on the above stated and taking into account available paleobotanic data, I believe that it is better to assign these genera and related *Semiliquidambar* to the subfamily Altingioideae of the family Hamamelidaceae.

CHAPTER 3. FOSSIL RECORDS OF PLATANOIDS AND HAMAMELIDS AND PROBLEMS OF THEIR SYSTEMATICS

Fossil platanoids and hamamelids are known from the Cretaceous–Cenozoic of North America, Europe, and Asia. To date, all fossil leaves and reproductive organs that are similar in macromorphology to living representatives of the families Platanaceae and Hamamelidaceae have been assigned to these families or positioned close to them. In this chapter, available fossil specimens of platanoids and hamamelids are reviewed, with taxonomic affiliation provided by the authors of taxa.

3.1. Platanoid Fossils

Recent paleobotanic studies have shown that platanoids are represented in the modern flora by the only living genus *Platanus*, which is a relict representative of a large polymorphic group that played a significant role and sometimes dominated forest communities in a vast area of the Northern Hemisphere (Vakhrameev, 1976; Krassilov, 1976; Herman, 1994; etc.). To date, microstructural studies of fossil platanoids have displayed significant morphological diversity of reproductive organs and a wide variation range of leaf morphotypes. The family Platanaceae is probably one of the most thoroughly investigated group of early angiosperms with reference to its geological history. In addition, many new fossil forms combine macro- and

micromorphological characters of platanoids and hamamelids; therefore, it is topical to reconsider their taxonomic positions.

Fossil leaves referred to platanoids are extremely diverse in morphology. Along with variously lobate leaves of the genera *Ettingshausenia, Platanus* (subgenus *Platanus*), *Macginitiea* Wolfe et Wehr in Manchester, 1986, and *Tasymia* Golovneva, entire leaves of *Platanus* with the pinnate venation (subgenera *Castaneophyllum* and *Glandulosa*) and *Platimeliphyllum*, compound leaves of the genera *Erlingdorfia* Johnson (Johnson, 1996), *Platanites* Forbes (Crane et al., 1988), and *Platanus* (*P. bella*: Kvaček et al., 2001, and *P. neptuni*: Kvaček and Manchester, 2004) as well as compound and pinnatifid leaves of the genus *Sapindopsis* Fontaine have been described (Fontaine, 1889; Hickey and Doyle, 1977; Upchurch, 1984; Crane et al., 1993; Krassilov and Bacchia, 2000; Golovneva, 2007). The present study pays special attention to the terminology of dispersed variously lobate leaves that are typical in appearance to the extant plane tree and entire leaves with well-developed basal veins, the identification of the taxonomic position of which is particularly important.

3.1.1. Lobate Platanus-like Leaves and Rules for Their Denomination

Cretaceous floras of the Northern Hemisphere frequently contain abundant simple, variously lobate leaves, with more or less developed mostly suprabasally deviating basal veins and a dentate margin, which are similar in appearance to leaves of the living plane tree. This morphotype is characteristic of the subgenus *Platanus* of the genus *Platanus*. According to the tradition of the first paleobotanic descriptions by L. Lesquereux, J.S. Newberry, I. Velenovský, and O. Heer and other European and American paleobotanists of the 19th century, these leaves were for a long time assigned to the genus *Platanus* based on superficial similarity. This gave the impression that this genus appeared early in the fossil record.

The earliest known leaf morphotypes of *Platanus* are dated Late Albian. For a long time, these specimens were assigned to the extant genus, implying that *Platanus* emerged in the Cretaceous and existed along with various other platanoid genera. However, the identification of an extant genus in the Cretaceous based on leaves along seems questionable (Wolfe, 1973; Krassilov, 1976; Maslova, 2001, 2002b).

Recent studies have shown that the only extant genus *Platanus*, comprising a few species, is a small part of the once diverse platanoid group, which is known since the Early Cretaceous (Crane et al., 1988, 1993; Friis et al., 1988; Pigg and Stockey, 1991; Manchester, 1994; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 1997, 2002b; Maslova and Krassilov, 2002; etc.). Com-

prehensive morphological data on leaves and reproductive structures of fossil platanoids indicate the existence in the geological past of plants that combined lobate leaves typical of the plane tree with reproductive structures completely different from those of the plane tree (Krassilov and Shilin, 1995; Maslova and Herman, 2004, 2006; Maslova et al., 2005). This confirms that the assignment of these leaves to an extant genus is incorrect.

Note that both simple and compound leaves are assigned to platanoids. In *Platanites*, some morphotypes of *Erlingdorfia,* and some species of *Sapindopsis*, apical leaflets are similar to leaves of the plane tree, whereas lateral leaflets differ in morphology. It is not inconceivable that at least some of the so-called Cretaceous "plane trees" are apical leaflets of compound leaves, while the lateral leaflets may be determined as *Viburnum* L., *Grewiopsis* De Wild. et T. Durand, etc. (possibly, *Grewiopsis amurensis* Krysht. et Baik. or *Viburnum antiquum* (Newb.) Hollick: Kryshtofovich and Baikovskaya, 1966). It is evident that the determination of these specimens should be based on detailed studies of variation of macromorphological and microstructural characters in large monotopic samples.

As was mentioned above, extensive data on co-occurrence of leaves of morphotypes typical for *Platanus* and reproductive structures essentially differing from those of the living plane tree have recently been accumulated. Reproductive organs determined as *Platanus* are recorded since the Santonian (Tschan et al., 2008); however, this identification seems questionable because of ambiguous treatment of some morphological structures that are important for the generic identification. All presently known reproductive structures of Cretaceous platanoids differ considerably in micromorphology from those of the living plane tree (Crane et al., 1988, 1993; Friis et al., 1988; Pigg and Stockey, 1991; Manchester, 1994; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002a; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006). The earliest reproductive structures assigned with certainty to the plane tree are recorded in the Paleocene (Maslova, 1997; Kvaček et al., 2001).

3.1.1.1. Morphology and cuticular–epidermal structure of leaves in extant *Platanus acerifolia*: significance for paleobotanic identification. The identification of fossil leaves is complicated because researchers frequently have limited material or, in the case that representative samples with wide variation ranges of macromorphological characters are available, possible polymorphism of leaf laminas is usually not taken into account and, hence, every distinction is regarded as a species-specific character. This is in general true of Cretaceous leaves resembling leaves of the living plane tree. It is evident that a detailed study of morphological variation of leaf laminas in the living plane tree could have been useful for this task. The majority of previous morphological studies of plane-tree leaves

dealt with two species, *P. occidentalis* and *P. orientalis*; however, only a few studies of this kind have been performed (Shkarlet, 1979), and published data on the variation of leaf characters in living plane-tree species are contradictory (Henry and Flood, 1919; MacGinitie, 1937; Suzuki, 1958). This stimulated a detailed study of morphological characters and cuticular—epidermal features of leaves of the living species *P. acerifolia* Willd. (Maslova et al., 2008a, 2008b; Maslova and Gordenko, 2008), which is an interspecific hybrid (*P. occidentalis* × *P. orientalis*), displaying the highest polymorphism of the leaf lamina in this genus, and the variation ranges of particular leaf characters in order to obtain reference data for identification of Cretaceous *Platanus*-like leaves.

3.1.1.1.1. Leaf lamina morphology in extant *P. acerifolia*. The herbarium used in this study was collected in the city of Anapa, Krasnodar Region, in the summer seasons from 2004 to 2006. Scaled photographs of the tree crown were taken to test the occurrence of different leaf morphotypes in different sites of shoots. The herbarium was collected from a certain tree and shoot and labeled. The analysis of morphological variation of leaves was performed for each shoot separately to provide repeatability of results; then, the data were generalized.

The study has shown that the leaves located at the periphery and inside the crown differ considerably in texture. The leaves located at the periphery of the crown have thicker laminas and better developed veins and pubescence, forming a dense cover on leaves from the shoot apex. The leaves from inside of the crown show a thin, papery texture and a thin network of venation.

The variation series of laminae of *P. acerifolia* includes the entire variation range of the genus *Platanus*, i.e., from entire laminas to lobate leaves with variously developed lobes (Pl. 1, figs. 1—8; Fig. 1). Three basic morphological patterns of the lamina of *P. acerifolia* are distinctly outlined (Fig. 2).

(1) Entire laminas with pinnate craspedodromous (in the case of the dentate margin of laminas) or camptodromous (in the case of the entire margin) venation (Pl. 1, figs. 4, 7, 8; Figs. 1a—1g). This morphotype occurs only deep in the tree crown, usually at the base of shoots (Fig. 2). This morphotype is divided into two groups. The first includes oblong or elongated elliptical leaf laminas with secondary veins of equal thickness (Pl. 1, fig. 8; Figs. 1a, 1b, 1e—1g). The length-to-width ratio of the lamina is 2.4—3.5. The second group includes elliptical or ovoid laminas, with one or two pairs of secondary veins with many basiscopic branches (Pl. 1, fig. 4; Figs. 1c, 1d, 1i). In these leaves, the secondary veins of the second, third, or fourth pair are usually most developed, in contrast to lobate leaves, in which the basal pair of secondary veins is usually most developed. These leaves are at most 15 cm long and 8 cm wide. The length-to-width ratio in this leaf group is 1.6—1.9.

Leaves of this group include morphotypes with asymmetrical laminas (Fig. 1g).

(2) Asymmetrical laminas with a lobe formed only on one side. The development of lobes vary (Pl. 1, figs. 5, 6; Fig. 1h). This leaf morphotype is characteristic of the leaves located deep in the tree crown, in the middle part of the shoot (Fig. 2). These leaves are at most 9 cm long and 6 cm wide; the length-to-width ratio is 1.1—1.5.

(3) Lobate laminas with varying depth of the sinus between lobes and entire or dentate leaf margin (Pl. 1, figs. 1—3; Figs. 1j—1p). This morphotype prevails in *P. acerifolia*. They are located mostly at the periphery and in the middle part of the crown (Fig. 2). Two groups are established based on the lamina shape and the position in the crown. The first includes leaves from the middle part of the crown, which are longer than wide (Pl. 1, fig. 3; Figs. 1j—1l). The length-to-width ratio in this leaf group is 1.1—1.6. The second group includes leaves from the outer part of the crown, the lamina of which is wider than long to a greater or lesser extent (Pl. 1, figs. 1, 2; Figs. 1n—1p); the length-to-width ratio is 0.7—0.8. These leaves are up to 17 cm long and 22 cm wide.

The shape of the lamina base of *P. acerifolia* varies considerably (Pl. 2, figs. 1—3). The leaves of the first group of morphotype 1 (entire leaves with oblong laminas and the secondary veins equal in thickness) are characterized by a relatively stable shape of the base (slightly cuneate or rounded, see Pl. 2, figs. 7, 8). Lobate forms, along with typical plane-tree leaf bases, such as cuneate (Pl. 1, figs. 4, 5) and truncate (Pl. 1, fig. 3), show the following variations: cordate (Fig. 1m), inequilateral (asymmetrical) (Pl. 2, fig. 3; Fig. 1k), and peltate as well as bases with naked veins (in case of the basal type of deviation of the basal veins, see Pl. 2, fig. 1). The lamina base often has small basal lobes.

In the leaves of the first group of morphotype 1, the lamina apex is usually rounded (Figs. 1a, 1b). In all other morphotypes, the lamina apex is pointed.

The lamina margin of *P. acerifolia* varies widely. In the three morphotypes recognized, both entire (Pl. 2, fig. 8) and dentate margins occur. The teeth of the lamina margin vary in shape and size. The majority of teeth are concavo-convex, with the apical side much longer than the basal side (Pl. 2, fig. 4). The apices of these teeth are pointed to a greater or lesser extent and often contain the vein tip. Some leaves have low rounded teeth (Pl. 2, fig. 5), sometimes terminating in papillate thickenings resembling glands. Along with concavo-convex teeth, biconcave teeth also occur (Pl. 2, fig. 7). In the majority of leaves, the teeth develop at the ends of the secondary veins or their basiscopic branches; however, in some cases, several small teeth are located between large teeth. In some cases, the margin is double-toothed, i.e., one side of a larger tooth has a small tooth.

The density of teeth vary significantly. In some leaves, irregular distribution of teeth along the margin

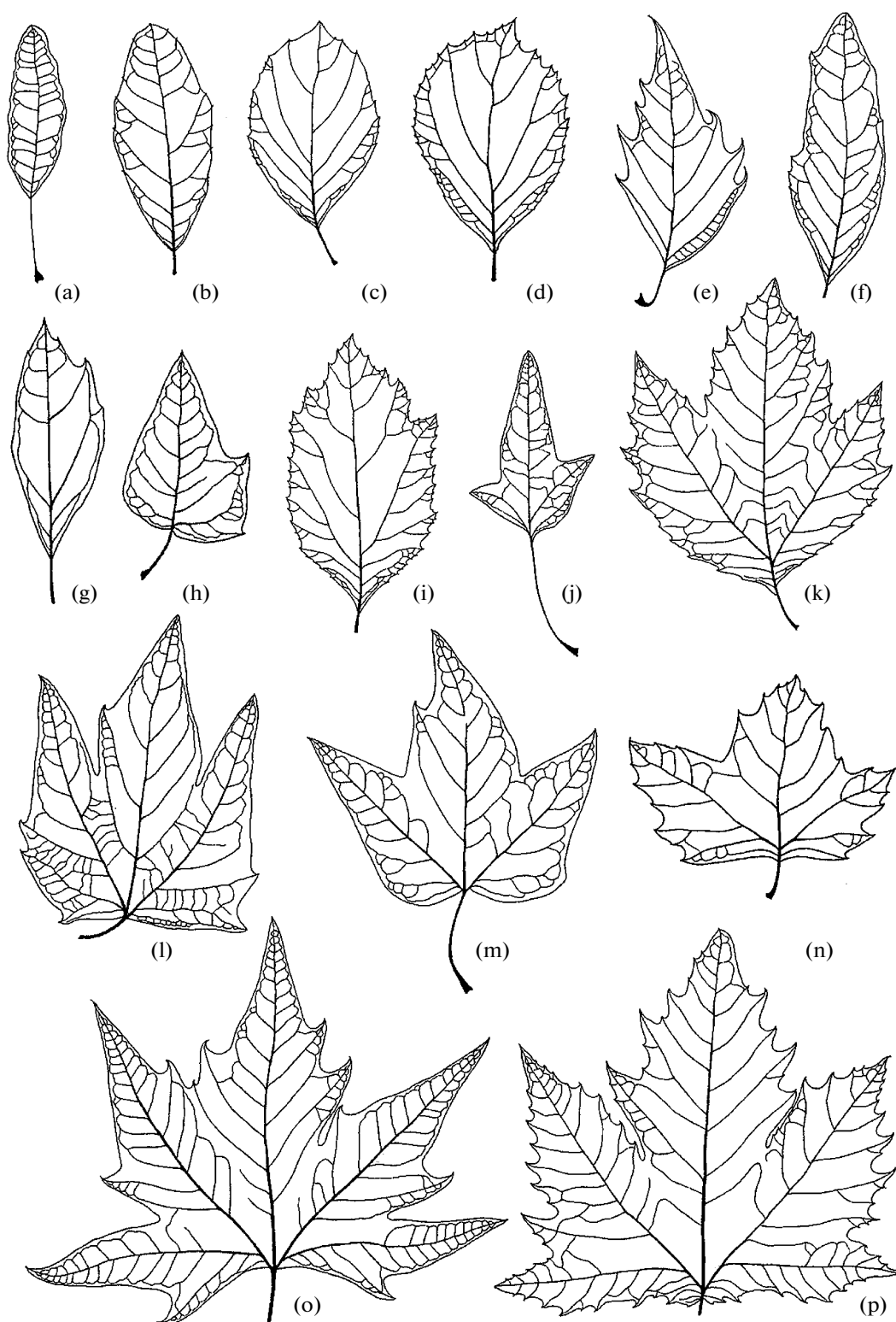**Fig. 1.** Variation series of the leaf lamina shape in extant *Platanus acerifolia* Willd.

is observed. Some entire leaves have one or two teeth (Fig. 1g); occasionally, teeth are observed only in the upper part of the lamina, while the lower part remains entire. Relatively regularly distributed teeth vary in density of arrangement, from one to four teeth per 1 cm of the margin extent.

Plate 1
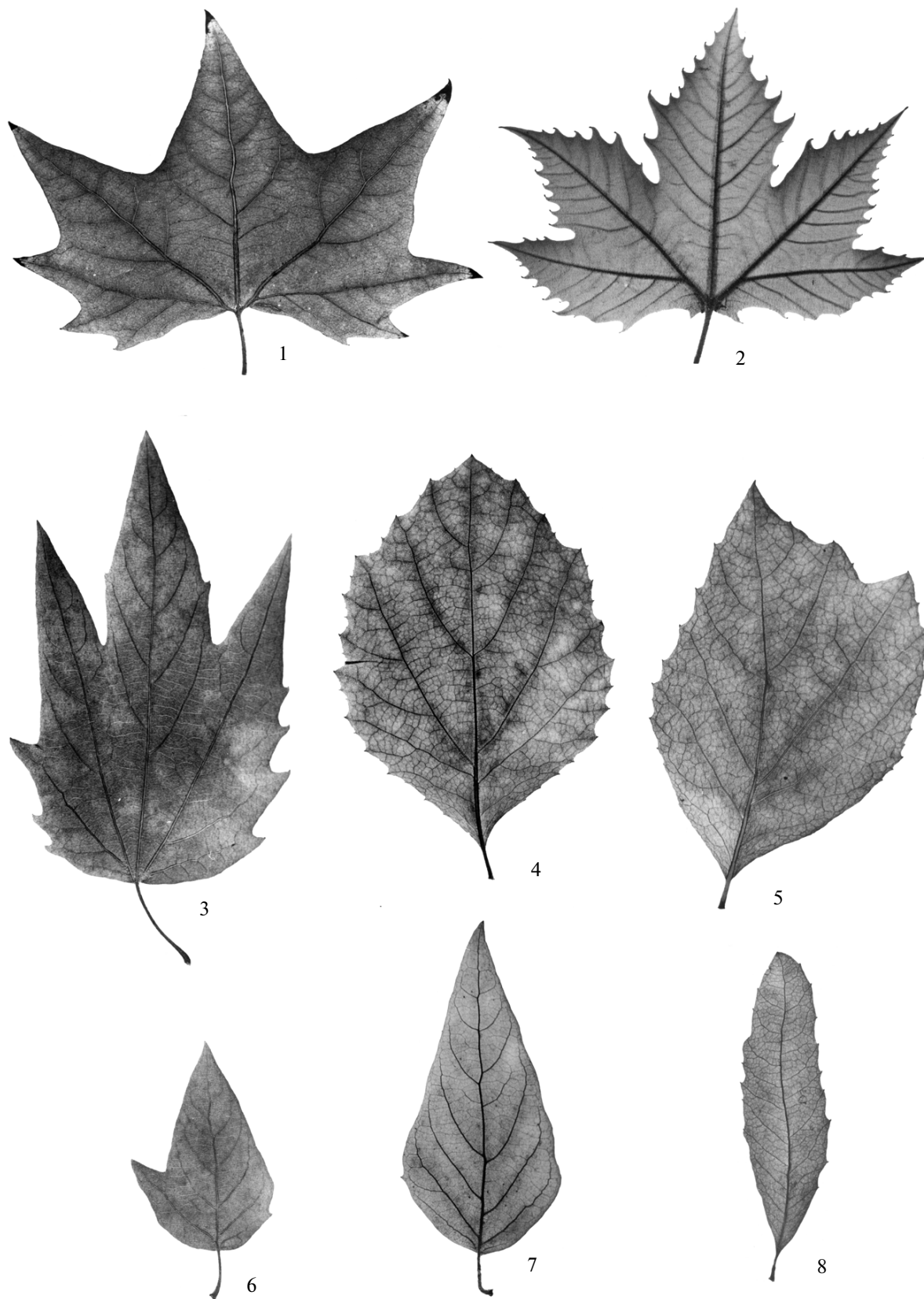
Entire leaves of *P. acerifolia* have pinnate camptodromous (in the case of entire leaves, Fig. 1a) or pinnate craspedodromous (in the case of dentate margin of leaves, Fig. 1e) venations. Some entire laminas show a mixed type of venation, since they often have ununiformly developed marginal teeth (Fig. 1b, 1f) or teeth are only present in the upper part of the lamina. Lobate leaves usually have actinodromous (palynactinodromous) venation.

In all leaves irrespective of the lamina shape, the main vein is usually well developed. It is more or less straight for about two-thirds of the extent; however, in the upper part of the lamina, the main vein is usually sinuous. The main vein gradually decreases in width by the thickness of the secondary vein deviating from it.

The leaves of *P. acerifolia* vary in the pattern of deviation of the basal veins and extent to which they are developed. About 60% of lobate leaves with well-developed basal veins have a suprabasal venation (Figs. 1k, 1l, 1n, 1p) and 40% have basally deviating basal veins (Figs. 1m, 1o). The basal veins are sometimes equal in thickness to the main vein, repeatedly basiscopically and acroscopically branching or equal in thickness to the secondary veins with a few branches. The basal veins deviate at an angle ranging from 30° to 80°. Basiscopic branches of the basal veins terminate craspedodromously or brochidodromously. The pomes (sites of the lamina located below the basal vein) vary in size depending on the shape of the lamina and the angle of deviation of the basal veins. If pomes are relatively large, they get basiscopic branches of basal veins and infrabasal veins (Figs. 1k, 1p). Infrabasal veins develop in leaves with suprabasal type of deviation of basal veins and cuneate base of the lamina.

The secondary veins are alternative, arcuate, from three to nine pairs in number. Tertiary venation varies considerably. In some leaves, the tertiary veins are relatively massive, scalariform or branching scalariform (Pl. 2, figs. 6, 8); in others, they are less developed and almost as thick as veins of the higher orders, which form a reticulate venation (Pl. 2, fig. 7). The veins of higher orders form a dense network of closed polygonal meshes.

3.1.1.1.2. Cuticular—epidermal structure of leaves in extant *P. acerifolia*.

The cuticular—epidermal characters of *P. acerifolia* were studied in leaves collected inside the tree crown and at the periphery. The following objects were examined: (1) small lobate leaves, with a dense, rough texture, located at the apex of shoots in the upper part of the tree crown; (2) large lobate leaves, with a gentle papery texture, located inside the crown; (3) lobate medium-sized leaves, with an intermediate texture, located in the middle of

inner crown part

intermediate crown part

peripheral crown part
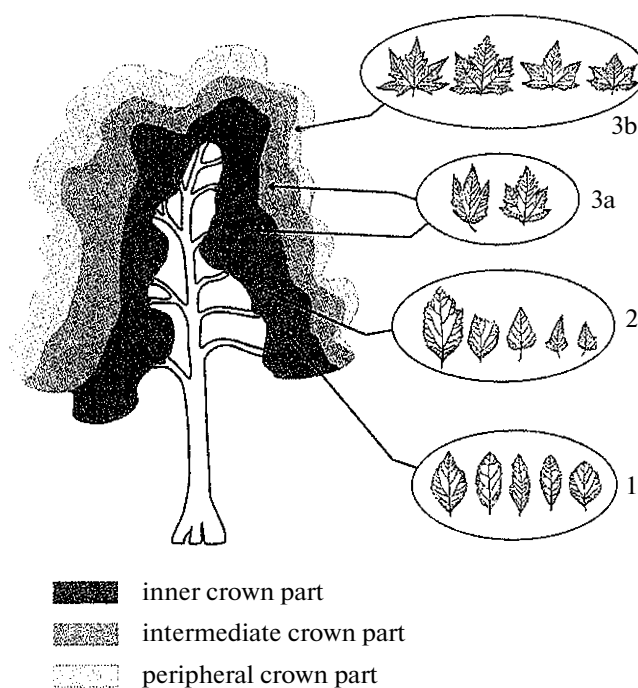
Fig. 2. Occurrence of various morphological types of leaves in particular sites of the tree crown of *Platanus acerifolia* Willd.: (1) entire; (2) with incipient lobes; (3) lobate: (a) length-to-width ratio of laminas is 1.1—1.6, (b) length-to-width ratio of laminas is 0.7—0.8.

shoots in the central part of the crown; and (4) entire leaves, with a gentle texture, located deep in the tree crown.

Group 1 (Pl. 3, figs. 1—4). Small lobate leaves, with a dense, rough texture, located at the apices of shoots in the upper part of the crown (under conditions of intense illumination, drying by the wind, and relatively poor water supply).

These leaves differ from others in the thicker, rough laminas, with a well-developed network of relatively thick veins and pronounced pubescence. The leaves are hypostomous.

Upper surface of the leaf lamina. The cuticle is relatively thick, its outer surface is relatively smooth, with widely spaced poorly pronounced folds oriented mostly along the long axis of the ordinary epidermal cells.

The ordinary epidermal cells on the upper surface of the lamina are irregularly tetragonal or polygonal, $10-20 \times 20-40$ μm, with almost straight, thickened anticlinal walls and poorly pronounced longitudinally folded periclinal walls. In the costal zone, the cells are tetragonal, extending along the vein axis. Trichomes are abundant, 20—30 per mm^2 of the leaf surface,

Explanation of Plate 1

Figs. 1—8. Morphological variations in leaves of extant *Platanus acerifolia* Willd., original herbarium: (1—3) lobate; (4, 7, 8) entire, and (5, 6) unilobate morphotypes. Scale bar, 10 mm.

Plate 2
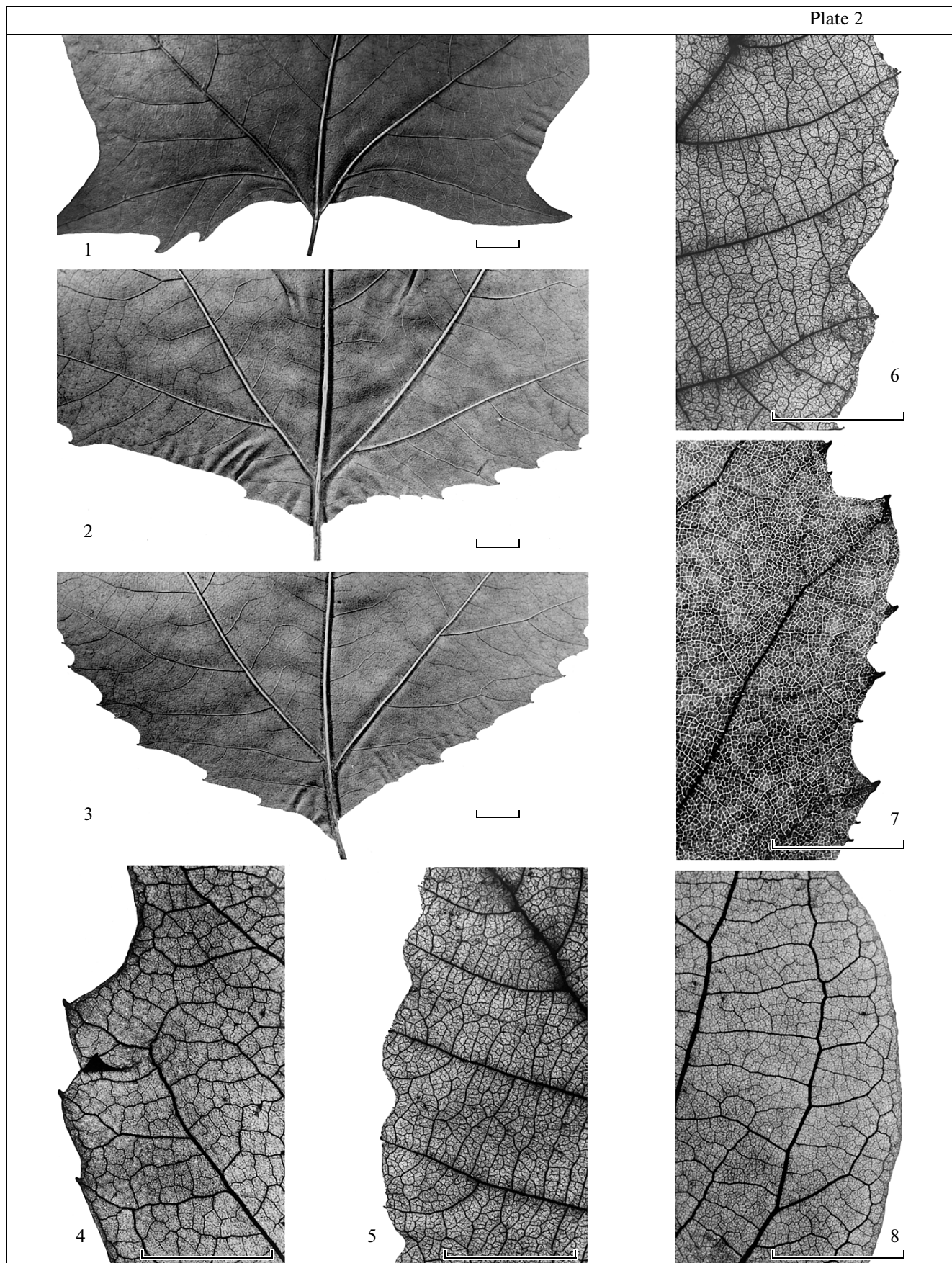
located on both veins and, more or less regularly, within the areolas. Two types of trichomes are recognized, i.e., candelabrum-like (as they shed, rounded bases are retained) and rounded glandular trichomes. The bases of candelabrum-like and capitate glandular trichomes are 12–18 and 27–30 μm in diameter, respectively.

Lower surface of the leaf lamina. The cuticle is relatively thick, with a finely folded external surface, the folds are oriented mostly in parallel to the long axis of cells.

The ordinary epidermal cells of the lower surface of the lamina are polygonal or irregularly tetragonal, $10–20 \times 20–30$ μm; the anticlinal walls are straight, the outer periclinal walls are finely longitudinally folded. In the costal zone, extended tetragonal cells prevail. The stomata are irregularly oriented, usually widely ovate or, less often, almost circular; dimensions range from 15×30 to 30×35 μm. The stomata are anomocytic, with the density about 50 per mm^2 of the leaf surface. Five or six subsidiary cells are present. The guard cells of the stomata are raised above the surface of the epidermis to form a ring-shaped eminence. This eminence is frequently encircled by concentric folds. The external apertures of the stomata are elliptical. The internal stomatal slit is spindle-shaped. Some large stomata have many fine radiating cuticular folds, positioned perpendicular to their long axis. Trichomes are numerous, located mostly at the veins; the trichome density is 10–20 per mm^2 of the leaf surface. There are bases of candelabrum-like trichomes, 15–20 μm in diameter, and capitate glandular trichomes, at most 30 μm in diameter.

Group 2 (Pl. 3, figs. 5–8). Large lobate leaves with a gentle papery texture, located inside the tree crown (under conditions of relatively low illumination, drying by the wind, and relatively poor water supply).

The leaves show fine papery texture, the venation network is relatively loose, pubescence is indiscernible. The leaves are hypostomous.

Upper surface of the leaf lamina. The cuticle is relatively thin, with distinct folds on the external surface, which are oriented mostly along the long axis of the ordinary epidermal cells. The bases of trichomes are surrounded by radiating cuticular folds.

The ordinary epidermal cells on the upper surface of the lamina are mostly tetragonal, $15–30 \times 25–40$ μm; the anticlinal walls are thickened, straight or slightly undulate; the external periclinal walls are finely longitudinally folded. Cells of the costal zone are tetragonal, extending along the vein axis. The trichome density is about 20 per mm^2 of the leaf surface, positioned mostly close to the leaf veins. The bases of candelabrum-like trichomes are 15–20 μm in diameter.

Lower surface of the leaf lamina. The cuticle is thin, with a finely folded external surface; the folds are mostly positioned in parallel to the long axis of cells.

The ordinary epidermal cells on the lower surface of the lamina are irregularly tetragonal, $15–20 \times 40–45$ μm; the anticlinal walls are straight or slightly undulate, the external periclinal walls are finely longitudinally folded. The costal zone contains longitudinally extended tetragonal cells. The stomata are irregularly oriented, range from widely ovate to rounded; their dimensions range from 25×40 to 20×20 μm. The stomata are anomocytic, with the density 20–30 per mm^2 of the leaf surface. Five or six subsidiary cells are present. The guard cells of the stomata are raised above the surface of the epidermis, forming a more or less prominent ring-shaped eminence. The external apertures of the stomata are elliptical. The internal stomatal slit is spindle-shaped. In relatively large stomata, this eminence is encircled by several distal ring-shaped, frequently sinuous folds. They also have many fine radiating folds of the cuticle, positioned perpendicular to their long axis. Trichomes are relatively small, positioned mostly near the leaf veins; the trichome density is 5–6 per mm^2 of the leaf surface. The bases of candelabrum-like trichomes are mostly less than 20 μm in diameter; rounded glandular trichomes of 20–30 μm in diameter are infrequent.

Group 3 (Pl. 4, figs. 1–4). Medium-sized lobate leaves located at the middle of shoots in the central part of the tree crown (under conditions of moderate illumination, drying by the wind, and restricted water supply).

The leaves of this group display an intermediate texture type, and intermediately developed venation. The leaves are hypostomous.

Upper surface of the leaf lamina. The external surface of the cuticle is smooth, with sparse longitudinal folds, oriented along the long axis of the ordinary epidermal cells.

The ordinary epidermal cells on the upper surface of the lamina are tetragonal or polygonal, $20–30 \times 25–40$ μm, with more or less straight anticlinal walls and widely spaced longitudinal folds on the periclinal walls. In the costal zone, cells are tetragonal, extending along the vein axis. Trichomes are located on veins and more or less regularly arranged within the areolas; the trichome density is about 10 per mm^2 of the leaf surface. The rounded bases of candelabrum-like trichomes are 10–15 μm in diameter, located mostly at the veins. The capitate glandular trichomes are less

Plate 3

1

2
100 μm

4
10 μm

3
100 μm

5

6
100 μm

8
30 μm

7
100 μm
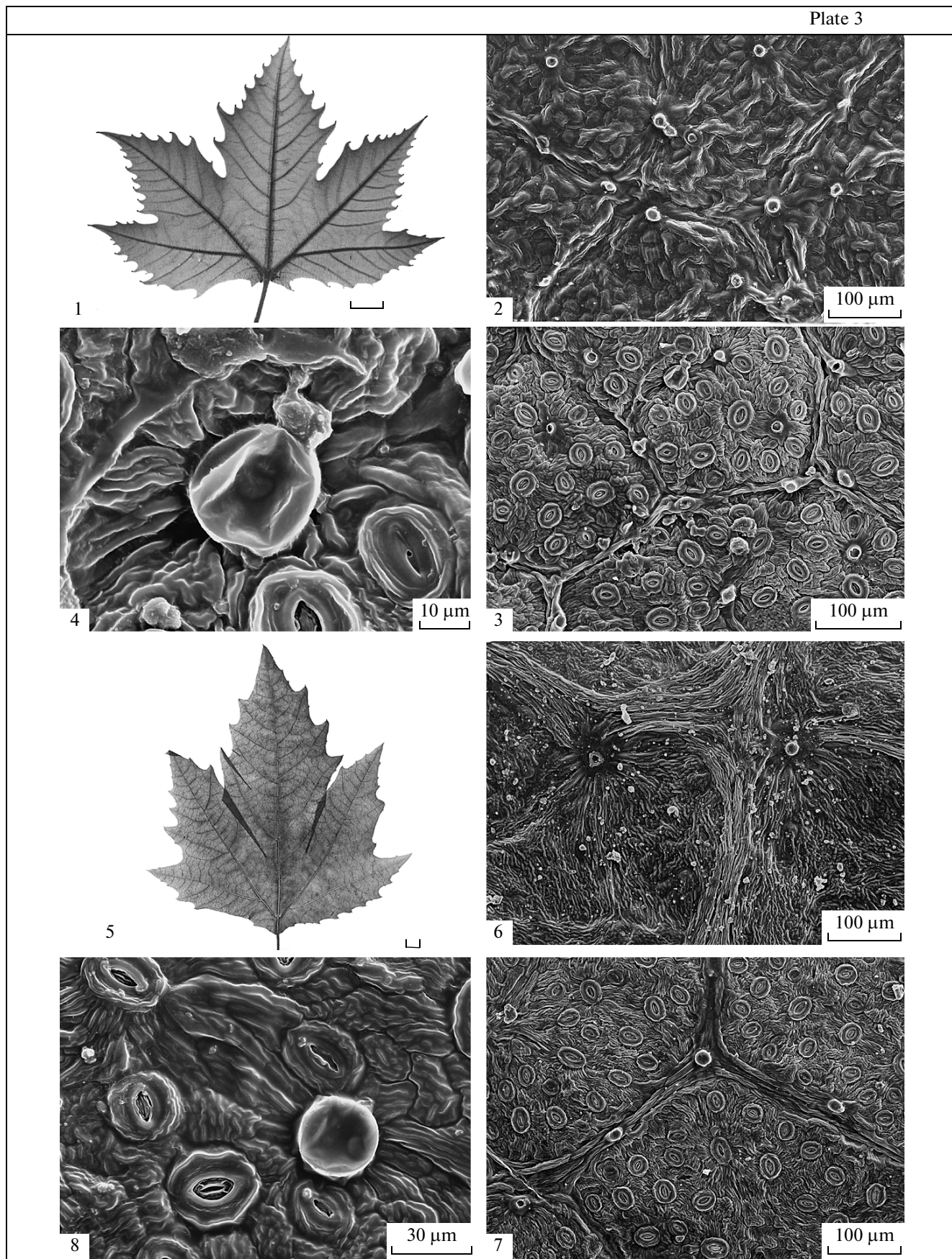
frequent, at most 28 μm in diameter, located beyond the veins within the areola.

Lower surface of the leaf lamina. The external surface of the cuticle is finely longitudinally folded.

The ordinary epidermal cells on the lower surface of the lamina are polygonal or tetragonal, $10-20 \times 15-35$ μm in dimensions; the anticlinal walls are straight, the periclinal walls are finely longitudinally folded. Cells of the costal zone are tetragonal, longitudinally extended. The stomata are irregularly oriented, widely ovate or circular, from 35×30 to 20×20 μm. The stomata are anomocytic, with the density $30-40$ per mm^2 of the leaf surface. Five or six subsidiary cells are present. The guard cells of the stomata are raised above the surface of the epidermis, forming a prominent ring-shaped eminence. In some stomata, the ring-shaped eminence is encircled by sinuous distal ring-shaped folds. Many stomata have numerous fine radiating cuticular folds, positioned perpendicular to their long axis. The external apertures of the stomata are elliptical. The internal stomatal slit is spindle-shaped. Trichomes are located mostly near the veins; the trichome density is 10 (8) per mm^2 of the leaf surface. Both bases of candelabrum-like trichomes (up to 20 μm in diameter) and glandular trichomes ($30-35$ μm in diameter) are present.

Group 4 (Pl. 4, figs. 5−8). Entire leaves located deep in the tree crown (under conditions of low illumination, drying by the wind, and relatively abundant water supply).

Distinctive features of this leaf group are the gentle texture of the lamina and very fine venation network. The leaves are epistomatal (the stomata are arranged in groups, mostly near the veins).

Upper surface of the leaf lamina. The cuticle is thin, covered with fine, densely spaced folds, which vary in orientation within the periclinal cell walls; there are also cuticular folds radiating from the stomata and bases of trichomes.

The ordinary epidermal cells on the upper surface of the lamina are amebiform, $30-35 \times 40-50$ μm in dimensions; the anticlinal walls are sinuous, with the sinuosity amplitude of $10-15$ μm. The external periclinal walls are ornamented with fine, variously directed folds. The shape of cells in the costal zone is almost invariable. The anomocytic stomata are widely spaced, located mostly near the veins or arranged in small groups within the areola. Trichomes are few in number, the trichome density is $2-4$ per mm^2 of the leaf surface; the bases of candelabrum-like trichomes

are $15-30$ μm in diameter, located mostly on the veins.

Lower surface of the leaf lamina. The cuticle is thin; the ordinary epidermal cells almost lack folds. Fine folds are present mostly on subsidiary cells and cells of the costal zones.

The ordinary epidermal cells on the lower surface of the lamina vary in shape from tetragonal or polygonal to amebiform, $8-10 \times 20-25$ μm in size; the anticlinal walls are variously sinuous. In the costal zone, cells are similar to the ordinary epidermal cells, sometimes extended longitudinally to a greater or lesser extent. The stomata are irregularly oriented, ranging from ovate to circular in shape and from 20×35 to 12×12 μm in size. The stomata are mostly anomocytic, with the density $60-70$ per mm^2 of the leaf surface. In addition to the anomocytic stomata, rare paracytic stomata are present. From four to seven subsidiary cells are present. The external apertures of the stomata are elliptical. In addition to the stomata elevated above the surface of the ordinary epidermal cells, there are more poorly cutinized stomata encircled by fine ring-shaped cuticular folds. Some small stomata are apparently abortive, with undeveloped apertures, which make them similar to the bases of trichomes. There are closely positioned stomata with the guard cells coming in contact. The internal stomatal slit is spindle-shaped. Some stomata are considerably larger than others, strongly raised above the subsidiary cells; cuticular folds radiating from them are positioned perpendicular to the long axis of the stomata and ornamented with shallower parallel folds. Only a few trichomes located mostly near the veins are present; the trichome density is $2-3$ per mm^2 of the leaf surface. The bases of candelabrum-like trichomes are $10-15$ μm in diameter, capitate glandular trichomes are at most 25 μm in diameter.

3.1.1.1.3. Analysis of morphological and cuticular−epidermal characters of extant *P. acerifolia*. M o r p h o l o g i c a l   c h a r a c t e r s. *Lamina shape and texture.* Morphological variability of leaves in living species of the genus *Platanus* was discussed in a number of works (Henry and Flood, 1919; MacGinitie, 1937; Suzuki, 1958; Santamour, 1972; Shkarlet, 1979; Nixon and Poole, 2003). It was shown that living plane trees include species that have only entire leaves (*P. kerrii*) and species with mostly lobate laminas. According to our studies, *P. acerifolia* displays the greatest leaf variability among species of this genus, including the entire range of morphological characters of the genus as a whole. Santamour (1972) has shown

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E x p l a n a t i o n   o f   P l a t e   3

Figs. 1−8. Cuticular−epidermal features of leaves of extant *Platanus acerifolia* Willd., original herbarium: (1−4) lobate leaves with dense and rough texture at the apex of shoots in the upper part of the tree crown, group 1: (1) leaf, (2) upper surface of leaf, (3) lower surface of leaf, (4) glandular trichomes on the lower surface of leaf; (5−8) lobate leaves with gentle papery texture, which occur inside the tree crown, group 2: (5) leaf, (6) upper surface of leaf; (7) lower surface of leaf; and (8) glandular trichomes on the lower surface of leaf. Scale bar in figs. 1 and 5, 10 mm.

Plate 4

1

2 100 μm

4 100 μm

3 100 μm

5

6 100 μm

8 30 μm

7 100 μm
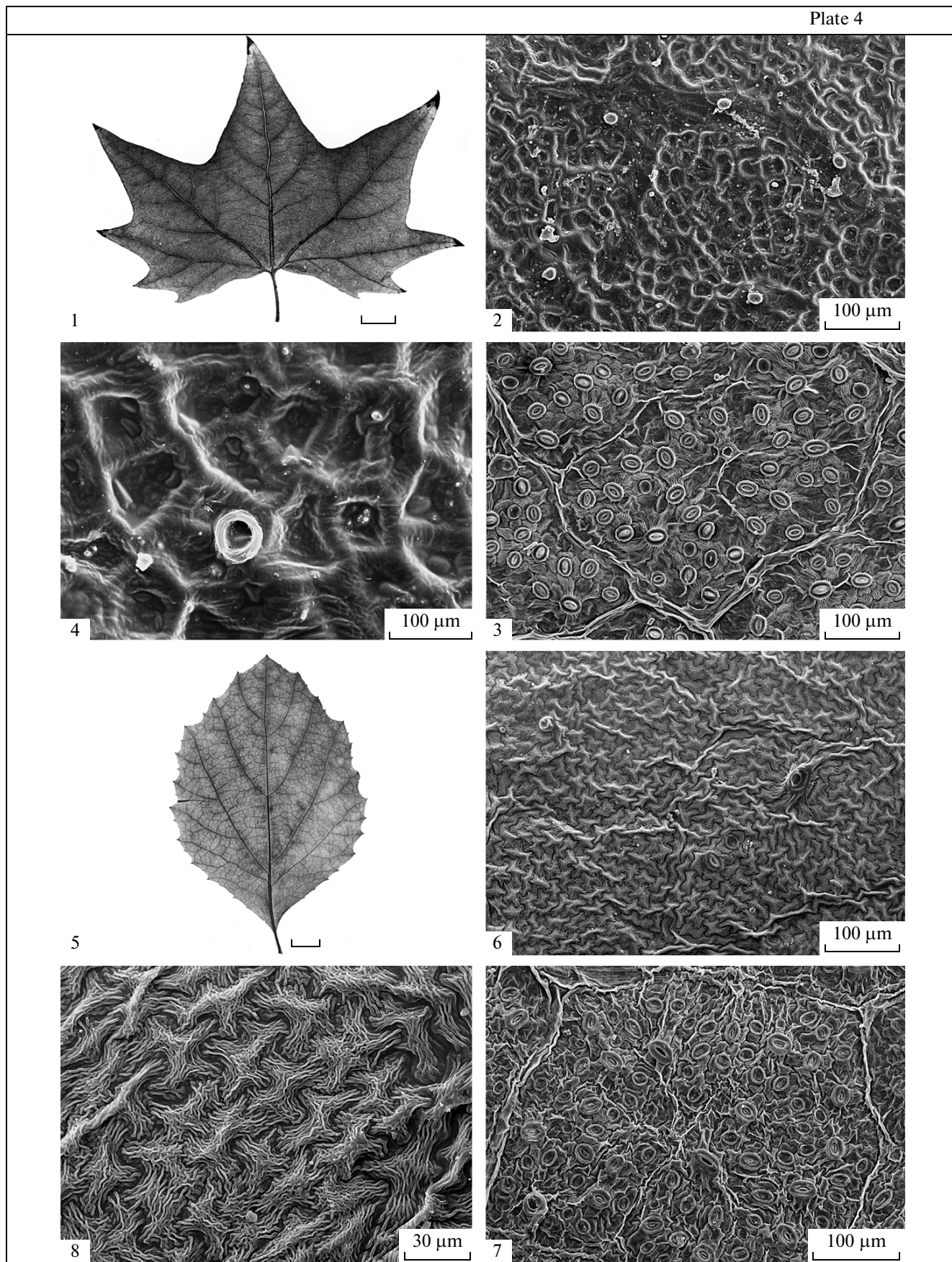
that some plane tree species are capable of producing more or less viable interspecific hybrids. There is no reason to exclude hybridization from the factors of speciation in fossil platanoids; therefore, it is possible to take the polymorphic species *P. acerifolia* for a model for reliable identification of paleobotanic material.

The diversity revealed by us of leaf morphotypes of *P. acerifolia* is shown in Figs. 2. In the tree crown, lobate leaves prevail (about 60%); asymmetrical (with one lobe) and entire leaves are recorded in 25 and 15%, respectively. Previously, it was believed that entire leaves occur in only one species, *P. kerrii*, which inhabits Vietnam and Laos, while, in other species of the genus, these leaves are teratomorphic deviations, which occasionally develop only on suckers. However, we have recorded entire leaves on ordinary shoots of *P. acerifolia*, although they occur inside the tree crown, mostly at the base of shoots, that is, these leaves develop in the crown under conditions of increased shading. A large proportion of entire leaves have asymmetrical laminas. The asymmetry is manifested in unequal development of halves of the lamina. On the one hand, these leaves are similar in shape to leaves of the genus *Hamamelis* L. (Hamamelidaceae), on the other hand, resemble lateral leaflets of the compound leaf of the Paleocene genus *Platanites*, which is referred to the family Platanaceae. Moreover, inside the tree crown, there are annual shoots resembling the leaf of the genus *Platanites*, i.e., the terminal leaf of a shoot has a typical lobate shape and two lateral leaves, positioned close to each other, are asymmetrical.

Lobate laminas vary in length-to-width ratio (1.1—1.6 and 0.7—0.8), the depth of the sinus, and in the extent to which marginal teeth are developed. When analyzing the morphology of lobate leaves of *Platanus*, Henry and Flood (1919) indicated that many characters (base, apex, and margin of the lamina and the type of dentation) vary widely and assumed that the depth of sinus is the most stable character. Suzuki (1958) also marked that the depth of the sinus is a stable character of the plane tree. However, MacGinitie (1937) proposed that the depth of sinuses depends on illumination and temperature, since plane trees with deeply lobate leaves (*P. orientalis, P. racemosa, P. wrightii*) grow in open river valleys, under conditions of intense illumination in relatively dry places, while *P. occidentalis*, the lobes of which are less pronounced, usually grow in damp, overshadow biotopes. The following arrangement of different morphotypes of lobate leaves in the crown of *P. acerifolia* was established in our study: deeply dissected leaves mostly occur close to the periphery of the tree crown, i.e., in more lighted sites, while the morphotypes with less pronounced or poorly developed lobes are located deep in the crown.

Leaf laminas of an individual tree vary in shape in both juvenile and several-year-old shoots and in ordinary shoots and suckers. The set of lamina morphotypes is generally similar in various shoot types and vary somewhat depending on the position of the shoot in the tree crown. Annual shoots located inside the crown have entire leaves at the base of shoots and asymmetrical and lobate leaves at the shoot apex, while the same shoots from the periphery of the crown almost lack entire morphotypes. Thus, *P. acerifolia* tends to form entire laminas under shading conditions and, hence, weaker heating, weaker drying, and weaker influence of winds. Considerable fluctuations of ecological factors that influence leaves in different positions in the crown of large trees and, as a result, variability of morphological characteristics of plant organs were described in extant taxa (Shennikov, 1950; Serebryakov, 1952; Goryshina, 1979; Lotova, 2000). The influence of conditions on the development of leaves in the crown of large trees is also manifested in different texture of leaves and features of the epidermal structure.

Leaves that grow in different parts of the tree crown (central and peripheral parts) undergo the influence of different illumination, heating, and air flows. In addition, leaves at different layers differ in water supply, since the upper layers are difficult to supply because of the necessity to overcome the gravity effect. Thus, the horizontal and vertical gradients of ecological factors determine the diversity of macromorphological and microstructural characters of leaves in the plant crown. This trend was in general form formulated in the rule of Zalensky (1904), which reads that the apical leaves of large plants are in general more xeromorphic than intermediate and, particularly, basal leaves. The dimensions of mature leaves of one tree follow the same rule, i.e., leaves located at the base and middle of shoots have larger laminas, while apical leaves are smaller.

With reference to paleobotanic studies, these data are useful for the analysis of samples of fossil leaves from the point of view of morphological variability. For example, various fossil leaves of the same morphotypes as in one individual of *P. acerifolia* could have been assigned to different genera or even different families of flowering plants; only the reconstruction of a complete variation series of morphological leaf characters provides the assignment of these specimens to

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Explanation of Plate 4

Figs. 1—8. Cuticular—epidermal features of leaves of extant *Platanus acerifolia* Willd., original herbarium: (1—4) medium-sized lobate leaves from the middle of shoots in the central part of tree crown, group 3: (1) leaf, (2) upper leaf surface, (3) lower leaf surface, and (4) base of candelabrum-like trichome on the upper leaf surface; (5—8) entire leaves from inner part of tree crown, group 4: (5) leaf; (6) upper leaf surface, with rare stomata; (7) lower leaf surface; and (8) fine folds of the cuticle on the leaf upper surface. Scale bar for figs. 1 and 5, 10 mm.

one species. In addition, Mamaev (1969) has shown that variations in morphological characters of one organism are in general similar to their population variations.

Base and apex of the leaf lamina. The shape of bases in lobate and asymmetrical (with one lobe) leaves of *P. acerifolia* vary widely, including cuneate, truncate, cordate, and inequilateral morphotypes. Leaves with naked bases of the basal veins and peltate morphotypes are frequent. Cuneate and truncate leaf bases are the most frequent morphotypes of plane trees. An inequilateral base is also relatively frequent in both lobate and entire leaves of *P. acerifolia*. This shape is characteristic of the leaf base of some genera of the family Hamamelidaceae, in particular, *Hamamelis, Parrotia* C.A. Mey, *Parrotiopsis* Schneider, etc. In leaves of *P. acerifolia* with inequilateral bases, venation is usually intermediate between craspedodromous and brochidodromous, which is also characteristic of the Hamamelidaceae. Peltate lamina bases are much rarer; the extent to which the pelta is developed varies widely from relatively small (only slightly changing the cuneate base) to relatively massive, with a well-developed venation and dentate margin. The presence or absence of a pelta is a varying character in other living plane species. In the diagnoses of Cretaceous formal genera of the Platanaceae, the presence of a pelta is a diagnostic character. In particular, nonpeltate leaves are usually referred to the genera *Credneria* Zenker or *Platanus*, and peltate leaves, to the genera *Protophyllum* Lesq. or *Pseudoprotophyllum* Hollick. When determining the genus of these leaves, it seems better to take into account the frequency rather than the presence or absence of this character.

Margin of the leaf lamina. Some extant plane tree species are characterized by mostly entire laminas, predominantly with a dentate margin; some other species have both entire and dentate morphotypes. The last variant is typical for *P. acerifolia.*

Variations in the marginal dentation of leaves of *P. acerifolia* is manifested in the shape, size, height, and density of arrangement of the teeth. In the classification of marginal teeth of leaves proposed by Hickey (1973), the teeth typical for plane trees are referred to the concavo-convex type. In addition to concavo-convex marginal teeth, *P. acerifolia* displays low rounded teeth, which are characteristic of some Hamamelidaceae, such as *Hamamelis, Parrotia*, and *Shaniodendron* (Chang) Deng, Wei et Wang, and small teeth representing the ends of veins. Biconcave marginal teeth also occur in the leaves of *P. acerifolia*. Note that the teeth change somewhat depending on the age stage of leaves. In young leaves, the teeth are relatively low and frequently have distinctive papillate thickenings. In addition, plane tree leaves occasionally have a "double" dentation, i.e., a side of a large tooth has a smaller tooth.

Venation. Entire leaves of *Platanus* usually show pinnate camptodromous (brochidodromous) venation; lobate leaves have actinodromous (palynactinodromous) venation. Lobate leaves of this genus most frequently have more or less developed basal veins. In some leaves, they are as thick as the main vein, with repeated acroscopic and basiscopic branching, or as thick as the secondary veins. According to our data, the angle of deviation of the basal veins of *P. acerifolia* varies considerably, which contrasts with the data of Shkarlet (1979), who reported that variation range of this character is very narrow and, hence, it is of considerable taxonomic significance.

Basiscopic branches of the basal veins terminate craspedodromously or brochidodromously. It is traditionally accepted that one of the main diagnostic characters of leaves of *Platanus* is suprabasal deviation of the basal veins. However, a more detailed study of the morphology of leaves of this genus shows that the basal veins frequently deviate from the base of the lamina. Morphotypes with naked basal veins, which are characteristic of the genera *Parrotia* and *Parrotiopsis* (Hamamelidaceae), are common in plane trees.

Some morphotypes of *P. acerifolia* display a special venation which was described by Skvortsova (1975) for leaves of the Hamamelidaceae. Skvortsova named it the pinnate—brochidodromous—craspedodromous venation and indicated that it is intermediate between the craspedodromous and brochidodromous variants. In this venation type, several pairs of veins in the lower part of the leaf lamina typically loop, while the secondary veins in the upper part terminate in marginal teeth. The proportions of the brochidodromous and craspedodromous veins differ in different genera. Thus, in *Fothergilla*, only one lower pair of veins forms loop contact with the next pair, while other secondary veins terminate in teeth. In *Sycopsis* Oliv., *Distylium* Sieb. et Zucc., and *Eustigma* Gardn. et Champ., only one to three pairs of secondary veins in the upper leaf region are directed to the teeth, whereas the majority of the secondary veins are looping. According to Skvortsova, only the Hamamelidaceae display this venation type; however, our study shows that it is characteristic of *P. acerifolia*. This venation pattern has been recorded in the Paleocene genus *Ushia* Kolak., which is closely similar to the Tertiary and Recent *Nothofagus* Blume (Krassilov et al., 1996).

The tertiary venation of platanoid leaves is often characterized by the terms *scalariform* or *branching scalariform*. In *Platanus*, the tertiary venation is usually well pronounced. However, it is known that the development of tertiary veins distinctly depends on ecological factors (Shennikov, 1950; Goryshina, 1979; Lotova, 2000). The tertiary venation is particularly prominent in leaves with a rough texture and well-developed pubescence. Leaves with a thinner papery texture have a poorly pronounced network of the tertiary venation. In these morphotypes, the tertiary veins are occasionally as thick as veins of the higher orders.

Cuticular—epidermal characters. All groups of leaves of *P. acerifolia* display a uniform struc-

tural plan of the epidermis. Certain differences are observed in the extent of sinuosity and thickness of the anticlinal walls of the ordinary epidermal cells, the type and diameter of the trichome bases, and the intensity and type of cuticular folds on the lower and upper surfaces of the lamina. Some epidermal structures vary in size and quantitative characteristics. Table 1 shows features of the cuticular–epidermal structure of leaves of the morphotypes of *P. acerifolia*.

Features of the cuticular cover. Leaf morphotypes of *P. acerifolia* vary in cuticular thickness. Small lobate leaves, with a dense rough texture, which frequently occur at the apex of shoots in the upper part of the tree crown (Group 1) display the most developed cuticle; on the upper surface of leaves, it is thicker than on the lower surface. In this case, the outlines of cell walls are barely discernible. In addition, the leaf surface is covered more or less regularly with parallel striate folds radiating from the trichome bases. The thinnest cuticle is on the lower surface of entire leaves located deep in the crown (Group 4). Radial folds are only observed in these leaves around relatively large stomata or trichome bases. This leaf group displays very fine sinuous cuticular folds on the upper leaf surface, which vary in orientation within the periclinal cell walls.

According to Carpenter et al. (2005), the cuticle of all species of *Platanus* (including evergreen *P. kerrii*) is thin, particularly on the lower side of the leaf; in *P. orientalis* and, to a lesser extent, *P. acerifolia*, the folds are more pronounced on the lower surface than on the upper surface. As follows from our study, in entire leaves located deep in the crown (Group 4), the cuticle of the upper leaf surface has distinct folds, radiating from the trichome bases and widely spaced stomata, and distinctive fine folds, which vary in orientation within the periclinal cell walls. These characters essentially differ this leaf morphotype from the others.

Ordinary epidermal cells of leaves. Leaf morphotypes differ somewhat in shape and size of the ordinary epidermal cells on both upper and lower leaf surfaces. The prevalence of tetragonal cells with thickened straight or slightly undulate walls is marked in the epidermis of large lobate leaves, with a gentle papery texture, located inside the crown (Group 2). In lobate leaves of Groups 1 and 3, which are distinguished by the position in the crown, the shape of the ordinary epidermal cells varies from tetragonal to polygonal; the anticlinal walls are mostly straight or, less often, slightly sinuous. Group 4 stands apart with reference to the shape of the ordinary epidermal cells. Amebiform epidermal cells on the upper leaf surface show a significant amplitude of sinuosity (10–15 μm); cells on the lower leaf surface range from tetragonal and polygonal with sinuous anticlinal walls to amebiform. Thus, within an individual tree, the ordinary epidermal cells vary significantly in shape and the anticlinal walls range widely from straight to strongly sinuous.

Variations in the shape of the ordinary epidermal cells on the lower leaf surface depending on the posi-

tion on the shoot of an individual tree were investigated using *Quercus pedunculata* Ehrh. as an example (Zalensky, 1904). Cells with strongly sinuous walls (up to amebiform) were recorded in the epidermis of leaves from a third-order branch of the lower part of the crown, while apical leaves display straight anticlinal walls of the ordinary epidermal cells. Zalensky proposed that these differences in cell walls are associated with different vertical positions of leaves in the tree crown and, hence, different water supply. Shennikov (1950) described variations in sinuosity of cell walls of shade and sun leaves. Our study of leaves from an individual tree of *P. acerifolia* has shown that the shape of the ordinary epidermal cells and sinuosity of their walls change considerably depending on the position in the tree crown.

The study of *P. acerifolia* shows that sinuosity of cell walls in leaves of one individual is mostly independent of illumination and water supply, i.e., sinuous cell walls are present in both shade (collected in the crown center) and sun (growing on radical and stump shoots) leaves of Group 4. Thus, manifestation of the sinuosity of cell walls in *P. acerifolia* positively correlates with the shape of the leaf lamina, i.e., strongly sinuous anticlinal cell walls are only observed in entire leaf morphotypes.

Note that, in Group 4, the upper and lower leaf surfaces differ somewhat in the shape of the ordinary epidermal cells; on the upper surface, the epidermis is formed exclusively of amebiform cells, while the lower epidermis is composed mostly of polygonal (tetragonal) cells or, less often, amebiform cells. This contrasts with the point of view of Baas (1969) that epidermal cells of both leaf surfaces of *Platanus* are identical.

Stomata. The majority of leaves of *P. acerifolia* are hypostomous; however, entire leaves that are located deep in the tree crown (Group 4) are epistomatal, have widely spaced stomata, usually located near the veins or arranged in small groups within the areola.

Variations in the stomatal complexes of *P. acerifolia* are manifested in the stomatal pattern, the development of the cuticular cover of guard cells, the shape and size of stomata, and the number of stomata per unit of the leaf surface. The anomocytic type of the stoma prevails in *P. acerifolia*; although the paracytic stomata are also present. In general, the stomata of the genus *Platanus* are usually referred to the anomocytic type (Metcalfe and Chalk, 1950). Krassilov (1973b) also assigned the stomata of platanoids to the anomocytic type, but indicated that *Platanus* often has a pair of narrow paracytic auxiliary cells. Fryns-Claessens and Van Cottem (1973) assigned the stomata of *Platanus* kerrii, which were described by Baas (1969), to the cyclocytic type. Brett (1979) assigned the stomatal apparatus of living *P. orientalis* to the pleioparacytic type. Carpenter et al. (2005) have shown that extant species of *Platanus* have anomocytic, laterocytic, and, sometimes, paracytic types of the stomatal apparatus.

Table 1. Features of the cuticular–epidermal structure of leaves in various morphotypes of *Platanus acerifolia* Willd.

Epidermis of upper leaf surface

Characters / Leaf morphotypes	Cuticular folds	shape of ordinary cells	size of ordinary cells	anticlinal walls	trichomes			stomata
					number	candelabrum-like, diameter	glandular, diameter	
1	2	3	4	5	6	7	8	9
Group 1	Radial from the trichome base (++)	irregularly tetragonal or polygonal	10–20 × 20–40 μm	straight	20–30 per mm²	12–18 μm	27–30 μm	–
Group 2	" (++)	irregularly tetragonal	15–30 × 25–40 μm	straight or slightly curved	20 per mm²	15–20 μm	–	–
Group 3	" (+)	polygonal or tetragonal	20–30 × 25–40 μm	straight	10 per mm²	10–15 μm	up to 28 μm	–
Group 4	" (+), and fine folds of cuticle parallel to long axis of cells	amebiform	30–35 × 40–50 μm	sinuous	2–4 per mm²	15–30 μm	–	+

Epidermis of lower leaf surface

Characters / Leaf morphotypes	shape of ordinary cells	size of ordinary cells	anticlinal walls	trichomes			stomata		
				number	candelabrum-like, diameter	glandular, diameter	number	shape	size
1	10	11	12	13	14	15	16	17	18
Group 1	polygonal or irregularly tetragonal	10–20 × 20–30 μm	straight	10–20 per mm²	15–20 μm	up to 30 μm	50 per mm²	widely ovate or almost circular	15 × 30 (30 × 35) μm
Group 2	irregularly tetragonal	15–20 × 40–45 μm	straight or slightly curved	5–6 per mm²	20 μm	20–30 μm	20–30 per mm²	"	25 × 40 (20 × 20) μm
Group 3	polygonal or tetragonal	10–20 × 15–35 μm	straight	up to 10 (8) per mm²	20 μm	30–35 μm	30–40 per mm²	"	30 × 35 (20 × 20) μm
Group 4	from tetragonal and polygonal to amebiform	8–10 × 20–25 μm	sinuous	2–3 per mm²	10–15 μm	up to 25 μm	60–70 per mm²	from ovate to circular	20 × 35 (12 × 12) μm

Note: (–) character is absent, (+) character is present, (++) character is well pronounced.

Van Horn and Dilcher (1975) noted that guard cells of *Platanus* are slightly elevated above subsidiary cells. The study of the epidermis of living *P. occidentalis* has shown that guard cells of its stomata are considerably elevated above the surface of the ordinary epidermal cells, forming cylindrical (ring-shaped in projection) eminences (Maslova, 1997). Most of the stomata of *P. acerifolia* display the same features; however, along with the stomata with well-developed cylindrical eminence, leaves of Groups 2 and 4 have stomata with more poorly cutinized guard cells, which are encircled by distal ring cuticular folds and do not project above the epidermis.

The stomata of *P. acerifolia* are mostly widely ovate; however, in Leaf Group 4, the stomata vary from ovate (20×35 μm) to rounded (12×12 μm). This group differs from the others investigated by us in the wider variation range of dimensions of the stomata; the greatest number of stomata per mm^2, 60—70 against the least number (20—30), which is observed in Group 2; and in the rare paracytic stomata. Leaves of Group 4 are usually located inside the tree crown, that is, under conditions of relatively low illumination and weaker drying by air flows. The much greater number of stomata per unit of leaf surface in Group 4 compared with other leaf morphotypes contrasts with the generally accepted idea that the epidermis of shade leaves shows a relatively low density of stomata (Zalensky, 1904; Goryshina, 1979; Lotova, 2000).

Trichomes. All plane tree species have candelabrum-like trichomes, which vary in density and shedding intensity (Baas, 1969; Nixon and Poole, 2003). Sometimes, they form pubescence, which completely hides the stomata and, hence, contributes to the control of transpiration. Baas (1969) has shown that, in addition, *Platanus* has glandular trichomes, which, however, shed at very early stages of leaf development and, hence, are absent from mature leaves. At the same time, Metcalfe and Chalk (1979) have shown that glandular trichomes are present in *Platanus* at later morphogenetic stages of leaves. The large peltate glandular type of trichomes was described in fossil platanoid leaves. This is a distinctive character of the extinct subgenus *Glandulosa* (Kvaček et al., 2001; Kvaček and Manchester, 2004).

The epidermis of leaves of *P. acerifolia* has both candelabrum-like and glandular trichomes. As compound trichomes (developing at contact of two or more cells) shed, a thickened rounded base is usually retained, while, in the case of simple trichomes (developing on one cell), shedding results in cylindrical papillate stalks. Glandular trichomes are cutinized to a varying extent; therefore, they are either almost cylindrical (if relatively strongly cutinized) or circular, more or less flattened (if slightly cutinized). Young glandular trichomes are usually dome-shaped, gradually becoming capitate; at later morphogenetic stages, short stalks sometimes develop. Group 1 stands apart in regard to the greatest number of trichomes per unit of leaf surface; this agrees with the general trend, that is, a greater pubescence is characteristic of leaves that are exposed to increased illumination (Zalensky, 1904; Goryshina, 1979; Lotova, 2000). It should be noted that glandular trichomes have not been recorded in the epidermis of the upper surface of leaves of Groups 2 and 4 (shade leaves). The candelabrum-like trichomes on the upper surface of the epidermis of leaves of Groups 1—3 are approximately equal in diameter, while, in Group 4, they differ in the diameter of the base, ranging from 15 to 30 μm. In the epidermis on the lower surface of leaves of Group 4, the bases of candelabrum-like trichomes are considerably smaller in diameter than those of other groups.

3.1.1.1.4. Significance of morphological and cuticular—epidermal characters for taxonomic identification of Cretaceous *Platanus*-like leaves. The problem of differentiation and identification of Cretaceous *Platanus*-like leaves is topical because these leaves vary widely in morphology and, at the same time, leaf morphotype that is most typical for species of the subgenus *Platanus* of the genus *Platanus* first appeared in the Early Cretaceous and remained almost the same up to the present time. This situation has previously been considered in more detail (Maslova et al., 2005, 2008a; Maslova, 2007). Therefore, the identification of dispersed Cretaceous leaves of platanoid appearance based on morphological characters alone (mostly combinations of the same characters) does not provide an understanding of taxonomic diversity of ancient Platanaceae.

Fossil platanoid leaves often show obvious similarity to some representatives of the Hamamelidaceae. The two families share certain leaf characters, which are manifested in the genera *Platimelis* Golovneva (Golovneva, 1994a) and *Platimeliphyllum* (Maslova, 2002a) and some Cretaceous leaves usually assigned to the genus *Platanus*. It is possible that some of these specimens belong to extinct hamamelid genera, the geological history of which is poorly documented.

In particular, in the description of *Platanus prisca* Herman from the Coniacian of northwestern Kamchatka, Herman (1989) indicated that this species is characterized by a symmetrical leaf lamina, although the figures presented show a distinctly asymmetrical leaf, with the basal veins unequal in length and ascending to different levels. The lamina base is incompletely preserved; however, the figure presented allows the reconstruction of the asymmetrical shape; the teeth are large, widely spaced, with slightly convex sides; the basal veins are as thick as the main vein and succeeding pair of secondary veins; the tertiary veins form a fine network. *Platanus prisca* is extremely similar in these characters to the leaves of the extant genus *Hamamelis* (Hamamelidaceae) and differs from it in the presence of marginal glands on the teeth. This character is not typical of *Hamamelis* but usually occurs in some other hamamelid genera. In addition, the leaves of *Platanus*

prisca are similar to young leaves of the extant genus *Shaniodendron* (Hamamelidaceae).

The Late Albian–Early Cenomanian species *Ettingshausenia louravetlanica* (Herman et Shczepetov) Herman et Moiseeva is similar to some hamamelid genera (Herman, 1994; Moiseeva, 2010). They shared certain leaf characters, such as the asymmetrical base and leaf lamina as a whole; asymmetrical deviation of the basal veins, which differ in length and thickness; and features of the tertiary venation (which is mostly orthogonally reticulate). The characters listed show the similarity of *E. louravetlanica* to mature leaves of *Shaniodendron* (Wang and Li, 2000, text-figs. c, d). A significant distinction from the Hamamelidaceae is the suprabasal deviation of the basal veins and well-pronounced infrabasal veins.

Thus, based on the macromorphology of *Platanus*-like leaves, it is difficult to determine leaves to genus or even to family. Therefore, cuticular–epidermal data are often involved in the identification of fossil leaves. In particular, based on these data, the genus *Platimeliphyllum* was originally referred to the family Platanaceae (Maslova, 2002a). The genus *Arthollia* Golovneva et Herman from the platanoid group shows epidermal characters typical of platanoids (Maslova, 2003). Based on identical epidermal characters, Krassilov (1976) assigned the considerably differing leaf morphotypes from the Tsagayan Formation of the Amur Region to one species, "*Platanus*" *raynoldsii* Newb.

Until recently, the data on the cuticular–epidermal structure of fossil platanoid leaves have been fragmentary and contradictory. In a number of cases, seemingly reliable determination of leaves based on macromorphological characters was not supported by cuticular studies. For example, leaves of typical platanoid morphology often display epidermal features atypical of platanoids. In particular, the epidermal characters of Cenomanian *Platanus cuneifolia* (Bronn) Jarmolenko show that it is close to the family Menispermaceae (Rüffle, 1968). The leaves similar in morphology to *Platanus* and associated with Cretaceous staminate inflorescences of the genus *Sarbaya* are similar in epidermal characters to living *Quercus ilex* L. and some fossil Fagaceae (Alekseenko and Krassilov, 1980; Krassilov and Shilin, 1995). Late Cretaceous *Protophyllum ignatianum* Krysht. et Baik. is similar in leaf morphology to platanoids and, partially, to hamamelids; however, based on the epidermal structure, Krassilov (1973b) concluded that it is close to the genus *Liquidambar* of the family Hamamelidaceae.

Golovneva (2003, 2004, 2008) used cuticular analysis for the determination of genera of dispersed Cretaceous *Platanus*-like leaves. Unfortunately, to date, only one genus, *Tasymia*, referred to the family Platanaceae has been established (Golovneva 2008); however, in her previous study, Golovneva (2004) recognized two new genera, nine new species, and 16 new combinations based on cuticular–epidermal features of platanoid leaves from the Lena–Vilyui and Chulym–Yenisei depressions. The author concluded that cuticular–epidermal structures of Cretaceous platanoids were much more diverse than in the genus *Platanus*.

Previously, we were in doubt about the taxonomic rank of *Tasymia* (Maslova et al., 2008a, 2008b). Macromorphological characters of these leaves fit in the variation range of the extant genus *Platanus*; however, as the author of the genus indicated, its epidermal distinctions include the greater number of glandular trichomes, which are more cutinized, the presence of a cutinized ring at the base of trichomes, and the formation of a stalk of trichomes. Quantitative and dimensional characteristics of epidermal structures usually depend on ecological factors and, hence, are of little significance as the taxonomic affiliation of leaves is determined. At the same time, other characters occur in the leaves of some extant species of *Platanus* (see, e.g., Carpenter et al., 2005). As Golovneva (2005, 2008) correctly marked, the epidermis of all Platanaceae shows a uniform structural pattern, and particular species only slightly differ in cuticular–epidermal characters. Therefore, it seems ill-founded to establish new genera of extinct platanoids based on combinations of known characters (including cuticular–epidermal). This approach only increases the number of genera, diagnostic characters of which overlap. Such a "taxonomic inflation" does not provide a better understanding of a true taxonomic diversity of extinct platanoids.

As follows from the study of leaves of *P. acerifolia* collected within one tree, cuticular–epidermal characters vary widely depending on the position of leaves in the tree crown. Cuticular–epidermal characteristics (both quantitative and qualitative) of different leaf morphotypes of *P. acerifolia* also vary. For example, the ordinary epidermal cells of entire leaves of Group 4, which are located deep in the tree crowns, at the base of shoots (and, hence, relatively weakly lighted), have strongly sinuous (up to amebiform) anticlinal walls in contrast to the ordinary epidermal cells of lobate leaves of Group 1, which are located at the periphery of the crown (better lighted); this agrees with the previously obtained data (Zalensky, 1904; Goryshina, 1979; Lotova, 2000). However, entire leaves of *P. acerifolia* that are located at the base of suckers and stump sprouts (increased illumination) also have strongly sinuous walls of the ordinary cells of the upper and lower epidermis and differ from leaves of this morphotype growing on ordinary shoots (reduced illumination) in the thicker anticlinal walls, the greater number of trichomes, the denser leaf texture, and the thicker secondary and tertiary veins. Consequently, epidermal characters are determined by a complex set of factors rather than ecological conditions alone. *P. acerifolia* shows distinct correlation between the leaf lamina shape and sinuosity of the anticlinal walls of the ordinary epidermal cells.

Kvaček et al. (2001) has shown that the ordinary epidermal cells of living plane tree species have straight or slightly sinuous anticlinal walls; however, the extinct species *P. neptuni, P. fraxinifolia*, and *P. bella*, with entire laminas have sinuous (up to deeply sinuous, amebiform) cell walls. Kvaček and Manchester (2004) believe that, in Late Eocene—Late Miocene *P. neptuni*, small leaves (presumably sun leaves, in opinion of the authors) have less sinuous anticlinal walls, while, in large (presumably shade) leaves, the cell walls are more sinuous. Entire leaves of Early Paleocene *Platimeliphyllum valentinii* Kodrul et N. Maslova, with strongly sinuous anticlinal walls of the ordinary epidermal cells of the upper leaf surface, show a pattern resembling leaves of *P. acerifolia* (Group 4) (Kodrul and Maslova, 2007); the two species are also similar in the variation range (from tetragonal or polygonal to amebiform) of the ordinary cells of the lower epidermis. Leaves of *Platimeliphyllum valentinii* show a number of characters typical of representatives of both Platanaceae and Hamamelidaceae and are associated with various reproductive structures, displaying characters of both families (Maslova and Kodrul, 2003; Maslova et al., 2007).

Different leaf morphotypes collected from one tree of *P. acerifolia* vary not only in the shape and sinuosity of the anticlinal walls of the ordinary epidermal cells but also in the number, size, and cutinization of trichomes and in the number and structural features of the stomata. Thus, if leaves of different morphotypes of one *P. acerifolia* tree were found in fossil condition, they could have been referred to different angiosperm taxa based on both macromorphological (Maslova et al., 2008a) and cuticular—epidermal characters.

Upchurch (1984) has shown that cuticular—epidermal characters typical of the family Platanaceae were formed as early as the Albian. The cuticles examined by this researcher of Cretaceous *Platanus*-like leaves and leaves of *Sapindopsis* displayed features characteristic of the Platanaceae, i.e., mostly anomocytic stomata, character of trichomes, cuticular folds radiating from the stomata and bases of trichomes, and glandular trichomes. Upchurch (1984) and Kvaček et al. (2001) described the bases of trichomes of *Platanus* with a circular scar, located at contact between two or more underlying epidermal cells, which were also recorded in some other fossil platanoids (Kvaček and Manchester, 2004). Epidermal structures in a number of extant plane tree species were described in detail and compared with representatives of the family Proteaceae in a thorough study of Carpenter et al. (2005).

Thus, the analysis of published data and our studies have shown that the complex of cuticular—epidermal characters, which developed in the Early Cretaceous (mostly anomocytic stomata, character of trichomes, cuticular folds radiating from the stomata and bases of trichomes, glandular trichomes) and were characteris-

tic of the family Platanaceae, remained stable up to the present time. In living species of *Platanus*, distinctions in structural characters of the epidermis are poorly pronounced, while fossil members of *Platanus* contribute considerably to the diversity of epidermal characters of this genus (based on fossil records, the subgenus *Glandulosa* has been recognized in the composition of the genus *Platanus* (Kvaček et al., 2001); its epidermal characters display an unusual combination of relatively large peltate glandular trichomes and strongly sinuous anticlinal walls of the ordinary epidermal cells). Note that the authors of the subgenus *Glandulosa* were quite correct in the estimation of the taxonomic significance of epidermal distinctions of fossil specimens, retaining this taxon in the genus *Platanus*. In any event, all presently known "platanoid" cuticular—epidermal characters and their combinations in fossil *Platanus*-like leaves fit in the variation range of the genus *Platanus* and, hence, should not be taken for reliable criterion for the identification of genera and species; they only indicate a close relationship to the family Platanaceae.

3.1.1.2. Rules for denomination of dispersed Cretaceous *Platanus*-like leaves. Thus, the identification of fossil Cretaceous *Platanus*-like leaves is rather complex. The high polymorphism of these leaves, with a large proportion of macromorphological characters of other families (in particular, Hamamelidaceae), epidermal features that are atypical for *Platanus*, and even the family Platanaceae, combined with macromorphological features characteristic of this genus, and the fact of association of these leaves with different reproductive structures conflict with the assignment of these Cretaceous specimens to one genus, the more so, an extant genus. Based on this, it was initially proposed to use the generic name *Platanus* in quotes, as it concerns fossil Cretaceous leaves (Krassilov, 1976, 1979).

Since the assignment of Cretaceous angiosperm leaves to extant taxa had become customary in paleobotany, it was generally accepted that, in the Cretaceous, angiosperms did include some extant genera. Recent studies, primarily the investigation of reproductive structures of Cretaceous angiosperms, have shown that they differ considerably from living plants and, hence, cast doubt on the assignment of Cretaceous leaf fossils to extant generic and suprageneric taxa. In other words, despite complete macromorphological similarity between Cretaceous and Recent leaves, they should not be referred to a certain genus (or family) of living plants; this is only evidence of the occurrence in the Cretaceous of certain leaf morphotypes and the preservation of their standard morphology for a long time up to the present time.

Thus, from the point of view of the modern paleobotanic knowledge, it is incorrect to use the name of an extant genus for the designation of dispersed Cretaceous *Platanus*-like leaves. The use of quotes with the

extant generic name marks the problem rather than resolves it. Moreover, this kind of designation falls beyond the scope of the International Code of Botanical Nomenclature.

A way to distinguish between extant leaves and fossil records of similar morphology was the use of generic names with the suffix *ites* for the extinct members resembling a certain Recent taxon. For example, the genus *Hamamelites* Saporta (Saporta, 1868) comprised fossil leaves similar to those of extant *Hamamelis*. The name *Platanites* (Forbes, 1851) meant "leaves of extinct plane trees." Subsequently, it was shown that the leaves of *Platanites* are compound, consisting of a terminal leaflet of typical plane tree shape and two more or less asymmetrical lateral leaflets (Crane et al., 1988; Boulter and Kvaček, 1989; McIver and Basinger, 1993; Johnson, 1996).

In fact, works of Krassilov (1973a, 1976, 1979) gave rise to a new approach to the identification of Cretaceous capitate inflorescences and posed the question of designation of dispersed leaves of Cretaceous angiosperms, which is connected with the development of the morphological classification independent of the system for living plants. The classification of dispersed leaves of extinct dicotyledons was initially proposed by Krassilov (1979); subsequently, the use of this approach to the identification of dispersed fossil leaves of angiosperms similar in external morphology to extant genera was discussed by Meyen (1987, etc.) and Krassilov (1979, 1989, etc.).

Krassilov (1979, p. 43) remarked that "... only an inductive system, with clear diagnoses of taxa (including leaves of certain morphotypes rather than leaves similar to a particular extant genus) and strict adherence to the principle of priority in the use of names provide a ground for suitable language and reduce the loss of information." The use of this leaf classification, which is independent of the systematics of extant plants, means that there is no univocal correspondence between taxa of morphological classification and taxa established for complete plants. A genus of morphological classification of leaves may occur in more than one genus (or even family) of the system of complete living plants; and vice versa, the latter may have leaves of more than one genus on morphological classification of leaves.

Maslova et al. (2005) considered in detail the use of names of morphological classification for Cretaceous leaves previously assigned to the genus *Platanus*. When analyzing the present situation, it seems that the only way to solve the problem of designation of dispersed fossil leaves of angiosperms that are identical in macromorphology to living taxa is the use of the terminology of morphological classification of leaves, which is based on observable features of leaf morphology and independent of the system of living plants. For some reason (well-pronounced polymorphism of leaf characters; fundamental differences in epidermal charac-

ters of leaves which are uniform and resembling in macromorphology living plane trees; association of these leaves with different reproductive structures), we proposed to determine these leaves based on classification of leaves that is independent of the modern natural system and to assign these leaves to the genus *Ettingshausenia*.

Cretaceous representatives of *Ettingshausenia* vary widely in leaf morphology, corresponding in variability to extant *Platanus*. The lamina of *Ettingshausenia* ranges from entire triangular to penta- or hexagonal, rhombic or ovate−rhombic, with undeveloped or rudimentary lobes to lobate with 2−6 lateral lobes. The lamina is frequently asymmetrical. The leaf base is usually cuneate, descending along the petiole. In the case of truncate or cordate leaf base, its part adjoining the petiole forms a small proximally directed wedge. Vakhrameev (1976) believes that a distinctive feature of the lamina base of Cretaceous "plane trees" is a more or less pronounced extension of this wedge passing onto the petiole; in his opinion, this character distinguishes these leaves from morphologically similar leaves of other Cretaceous representatives of the family. The base is sometimes peltate. The leaf apex is pointed or, less often, obtuse. The leaf margin is toothed−emarginated or, less often, entire. The venation is actinodromous (palynactinodromous) craspedodromous or brochidodromous, with well-developed basal veins. The tertiary venation is scalariform or branching scalariform. The type series of the genus *Ettingshausenia* does not provide information on the cuticular−epidermal structure of these leaves.

The grouping of fossil leaves of a certain morphotype in one genus, which provides the foundation of the morphological classification, is presently most correct and inevitable principle for identification of Cretaceous *Platanus*-like leaves. In so doing, it is assumed that this genus possibly includes plants of the Platanaceae and other families (for example, Hamamelidaceae and others). A number of researchers have already started the taxonomic revision of known Cretaceous species of "plane trees" (Kvaček and Váchová, 2006; Moiseeva, 2007, 2008, 2010; Shilin, 2008); however, the majority of taxa have not yet been reexamined.

Tschan et al. (2008) have recently criticized this approach to the designation of dispersed fossil *Platanus*-like leaves as the genus *Ettingshausenia* (Maslova et al., 2005) of the morphological system. Perhaps, Tschan and coauthors incompletely understood the essence of the morphological system (Krassilov, 1979, 1989; Meyen, 1987; etc.) for classification of dispersed leaves that are identical in morphology to certain morphotypes of extant taxa. In their opinion, the diagnosis of the genus *Ettingshausenia* is questionable, since it lacks data on the cuticular−epidermal characters (Tschan et al., 2008). Note that the diagnoses of genera established based on fossil leaves not always

include information of this sort. Paleobotanists frequently deal with leaf imprints alone and have to identify these specimens based on available facts. In addition, when identifying dispersed leaves that are closely similar in macromorphology to living analogues, we followed the principles of the morphological system and consciously excluded cuticular–epidermal characters from consideration and chose the genus resembling *Platanus* in morphology and lacking data on the epidermal structure. Regarding *Platanus*-like leaves, note that there are data on quite nonplatanoid epidermal structure of some leaves of the "platanoid" morphotype (see, for example, Krassilov and Shilin, 1995). This raises the question as to which genus and family these leaves should be assigned to. Which genus and family it is possible to appoint for Cretaceous leaves that are identical in morphology to extant plane trees, lack phytoleims, and unsuitable for cuticular–epidermal analysis. However, leaves of this kind represent a large proportion of specimens, for example, in Cretaceous floras of northeastern Russia and other regions.

In addition, as remarked above, the set of cuticular–epidermal characters of platanoid leaves was in general formed as early as the Albian and gave evidence of the presence or absence of the family Platanaceae in particular fossil material. I agree with Tschan et al. (2008) that the family Platanaceae is characterized by distinct structural characters of the epidermis and cuticle (as has been shown a long time ago, see, e.g., Metcalfe and Chalk, 1950; Baas, 1969; Upchurch, 1984; Carpenter et al., 2005; etc.). However, it remains uncertain whether or not these characters can be used for reliable differentiation of platanoid genera and species. Paleobotansts often take into account quantitative and dimensional characteristics of epidermal structures, which are strongly influenced by ecological and microclimatic factors. Moreover, the choice of phytoleims for analysis is usually limited because of preservation of fossil specimens. A researcher has to use available material often lacking complete data, for example, about the topographic position of leaf fragments under study. However, the study of extant material has shown (Zalensky, 1904; unpublished original data) that these information is of great importance, since the epidermal structure in the central and marginal parts of the leaf lamina often differ in quantitative and dimensional characteristics. The variability of epidermal characters of fossil leaves is poorly understood. Following the principle of the attachment of generic or species rank to diagnostic sets of epidermal characters that have already been known and insignificantly differ quantitatively or in the extent of manifestation but, nevertheless, falling in the variation range of the extant genus *Platanus*, it is possible to increase excessively the number of new genera and species based on leaves, which do not reflect true taxonomic diversity of this group. As mentioned above, based on cuticular–epidermal distinc-

tions of this kind, Golovneva (2004) established two new genera, nine new species, and 16 new combinations among platanoids from a limited area of the Lena–Vilyui and Chulym–Yenisei basins, the taxonomic status of some of which is questionable.

In particular, the genus *Natalpa* Golovneva nom. nud. (Golovneva, 2004) is similar in a number of macromorphological leaf characters to the genera *Platimelis* and *Platimeliphyllum* and entire morphotypes of some living plane tree species, although it is almost identical in epidermal characters to the extant plane tree and, in Golovneva's opinion, to the extinct genus *Platanophyllum* Fontaine. According to Golovneva (2004), the genus *Platanophyllum* comprises morphotypes with variously lobate leaves, in some of which epidermal structures were examined and suggested the assignment to the family Platanaceae. Previously, Maslova et al. (2005) have put in doubt the expediency of the use of the generic name *Platanophyllum*.

A prominent example is provided by the genus *Tasymia* (Golovneva, 2008), which is almost identical to the living plane tree in both leaf macromorphology and epidermal characters. Moreover, these leaves were found in association with unique infructescences that are identical in macromorphology to those of the living plane tree, but have monocarpellate fruits with a solitary orthotropic seed and a well-developed perianth (Maslova et al., 2005). To date, a number of analogous examples of co-occurrence of *Platanus*-like leaves with various reproductive structures distinguished from those of the genus *Platanus* have been reported (Krassilov and Shilin, 1995; Maslova and Herman, 2004, 2006; Maslova et al., 2005; Maslova, 2009). Based on microstructural features, it is impossible to refer these reproductive structures to the Recent family Platanaceae. Certainly, leaves and reproductive structures from one burial do not necessarily belong to one individual, unless they occur in organic connection. However, these cases are probably frequent, taking into account available data and statistics of co-occurrence of different plant organs in the same burial. It is probable that different plant organs belong to one individual if they come from the same bed, the same sample of host rock, and the flora under study lacks remains of other morphologically similar forms. In any event, a paleobotanist always endeavors to study the history of complete plants rather than separate organs (leaves, inflorescences, infructescences, etc.). In the case of the genus *Tasymia*, it is evident that its leaves have morphological and epidermal characters typical for Platanaceae and are associated with infructescences that essentially differ from all known Platanaceae. Thus, this plant hardly belongs to a certain extant family.

Tschan et al. (2008) noted that the genus *Ettingshausenia* sensu Maslova et al. (2005) "would become a "garbage can" genus for possibly unrelated taxa." I agree with these researchers that *Ettingshausenia* probably includes leaves of different genera and even differ-

ent families of the natural plant system. This genus comprises leaves of typical *Platanus*-like morphology, with typical plane-tree epidermal characters and similar leaves without information on the epidermal structure or with contradictory epidermal characteristics. The introduction of such an artificial composite genus is forced rather than purposeful creation of "a garbage can." It would be wonderful to have exclusively complete fossil shoots (or plants), with intact, morphologically informative leaves, well-preserved phytoleims and attached reproductive structures. In this case, we would have had more complete information about ancient plants and more objective judgement of their taxonomic positions. However, these records are extremely scarce, while most of the paleobotanic objects are incompletely preserved, and paleobotanists have to deal with available features. In practice, the establishment of new genera based on individual leaf imprints with different combinations of known epidermal characters (quantitative and dimensional) would result in the formation of "a garbage can" at the family level, which would be reduced to several genera (or may be only one) as a more thorough analysis of cuticular—epidermal features in large monotopic samples was performed.

The lobate leaf morphotype, which is typical of the living plane tree, appeared in the Early Cretaceous; it is assigned to the genus *Ettingshausenia* of the morphological classification of dispersed Cretaceous leaves (Maslova et al., 2005); varying within a wide range, it remains stable to the present time, that is, leaves of this morphotype accompany the entire geological history of platanoids from the origin (late Early Cretaceous) through the developmental peak (Late Cretaceous) to the present time, when only one representative of the family is remained. Along with typical platanoid structural features of the leaf, *Ettingshausenia* displays a number of characters of hamamelids, including altingioids (see, e.g., Maslova and Herman, 2004). The high polymorphism of these leaves is a diagnostic character. In addition to well-known leaf polymorphism of the living plane tree, significant variability was shown in large monotopic samples of Cretaceous leaves of platanoid appearance (Moiseeva, 2003; Moiseeva et al., 2004). This situation is a prominent illustration of the statement of Krassilov (1976) about high variability combined with evolutionary conservatism of leaves. It seems possible to disclose the reasons for the preservation of stable morphology (morphological stasis) for a long time based on paleontological studies, in which the concept of the morphological species occupies a key position and morphological stasis is considered to be the same as evolutionary stasis.

3.1.2. Entire Leaves of the Genus *Platimeliphyllum*

The identification of leaves of the genus *Platimeliphyllum* is also complicated. The genus *Platimeliphyllum* (Maslova, 2002a) was established for entire leaves with the craspedodromous venation, variously developed basal veins, and dentate margin from the Upper Paleocene—Lower Eocene of the Kamchatka Peninsula and Sakhalin. Species of this genus show an unusual combination of characters typical of both Platanaceae and Hamamelidaceae. *Platimeliphyllum* has symmetrical and asymmetrical leaf lamina morphotypes with convexo-concave and concavo-concave teeth characteristic of platanoids or low triangular or rounded teeth characteristic of hamamelids. Along with macromorphological characters typical of the two families, leaves of *P. palanense* N. Maslova show epidermal characters typical of Platanaceae (Maslova, 2002a).

Of three originally described species of the genus *Platimeliphyllum*, two (*P. palanense* and *P. snatolense* N. Maslova) are associated with staminate inflorescences of the genus *Chemurnautia* N. Maslova. Co-occurrence of inflorescences of *Chemurnautia* and leaves of *Platimeliphyllum* in several localities of approximately equal age of the Kamchatka Peninsula (Snatol River; Napana Formation, Upper Paleocene; Chemurnaut Bay, upper part of the Kamchik—lower part of the Tkaprovayam Formation, Upper Paleocene—Lower Eocene; a section between the Rebro and Getkilnin capes, Tkaprovayam Formation, Upper Paleocene—Lower Eocene; and Evravavayam River, Tkaprovayam Formation, Lower Eocene) suggests that they could have belonged to one plant. Inflorescences of the genus *Chemurnautia* show a number of features resembling the living plane tree (Maslova, 2002a). Based on this fact and epidermal characteristics, leaves of the genus *Platimeliphyllum* were originally referred to the family Platanaceae.

Subsequently, Kodrul and Maslova (2007) found leaves of the genus *Platimeliphyllum* in the Paleocene beds of the Amur Region. Leaves of the Amur species *P. valentinii* were initially found in the Arkhara—Boguchansk lignite deposits near the village of Arkhara (Amur Region) in the middle part of the section of a clayey member between the "Nizhnii" and "Dvoinoi" coal beds, accompanied by staminate inflorescences of *Archaranthus* Maslova et Kodrul (Maslova and Kodrul, 2003). Because of a lack of material, it was impossible at that time to determine these leaves to genus; we only indicated co-occurrence of these leaves and inflorescences of *Archaranthus*, which were referred to the family Platanaceae based on micromorphological characters. Subsequently, newly collected plant remains and the study of distribution of plant fossils in other sections of several mines of the Arkhara—Boguchansk deposits provided additional leaf material and showed a stable association of these leaves with staminate inflorescences of the genus *Bogutchanthus* N. Maslova, Kodrul et Tekleva, which combine characters of platanoids and hamamelids (Maslova et al., 2007). *P. valentinii* Kodrul et N. Maslova has polymorphic entire leaves, which

combine morphological characters of platanoids and hamamelids. Epidermal characters (strongly sinuous anticlinal walls of the ordinary epidermal cells on the upper leaf surface, sinuous anticlinal walls of the ordinary epidermal cells on the lower leaf surface, and the ordinary cells of the lower epidermis ranging in shape from tetragonal or polygonal to amebiform) of this species resemble *P. neptuni* and entire morphotypes of the living species *P. acerifolia* and some hamamelid genera.

Thus, the genus *Platimeliphyllum*, which occurs in the fossil record from the Early Paleocene to the Middle Eocene and is associated with reproductive structures that are similar in macromorphology and essentially vary in micromorphology (*Archaranthus, Bogutchanthus, Chemurnautia*), as the Cretaceous genus *Ettingshausenia*, illustrates the statement of Krassilov (1976) about a greater evolutionary conservatism of leaves compared with reproductive structures. At the same time, this situation suggests to revise family affiliation of these leaves and systematize this genus based on the morphological (independent of natural) system.

3.1.3. Reproductive Structures

Like Cretaceous leaves resembling in morphology the living plane tree were for a long time referred to the genus *Platanus*, many capitate reproductive structures from the Cretaceous beds were also determined as this extant genus based only on superficial similarity to the living plane tree.

During the last two decades, the use of electron scanning and transmission microscopy has allowed the development of paleobotanic studies at an essentially new level, mostly by detailed examination of reproductive structures, which play a key role in the reconstruction of phylogenetic relationships of early angiosperms. These methods provided the establishment of the fact that fossil capitate inflorescences and infructescences are similar in macromorphological characters and vary widely at the micromorphological level. The reproductive structures characteristic of the genus *Platanus* were recorded with certainty beginning from the Paleocene (Maslova, 1997; Kvaček et al., 2001), whereas Cretaceous heads superficially identical to those of platanoids belong to different genera essentially differing from *Platanus*. The data on diversity in microstructures of superficially identical platanoid capitate inflorescences have been accumulated with time; thus, it has become evident that the assignment of these structures to the genus *Platanus* based on the appearance alone (without using microstructural data) is incorrect.

Reproductive organs of the genus *Platanus* are compound inflorescences consisting of the central axis and sessile or stalked unisexual heads, which often have rudimentary structures of the opposite sex (staminodia in pistillate flowers and rudimentary pistils in staminate flowers).

The head is a more or less massive core with many densely packed flowers radiating from the core. Because of the absence of a well-developed perianth, it is impossible to determine by eye the number of flowers in the head. A distinctive character of the flower of the living plane tree is the changeable number of elements. The pistillate flowers include from five to nine apocarpous carpels, the staminate flowers have from three to five stamens consisting of short filaments and elongated anthers.

The question of the presence of the perianth in flowers of *Platanus* has long been discussed. Following the results of Clark (1858), the perianth of the plane tree was initially considered to be double, consisting of separate calyx and corolla. Griggs (1909) indicated the absence of a corolla in pistillate flowers of *P. occidentalis*. Bretzler (1924) believed that the perianth of *Platanus* is strongly reduced and the flower is almost naked. Boothroyd (1930) recognized the calyx and corolla in the flower of the plane tree and indicated that corolla is frequently absent. The characters distinguishing these structures have not been designated and conducting elements have not been recognized. Manchester (1986) marked that the perianth of *Platanus* is small and did not divide it into a calyx and corolla. Ernst (1963) and Nixon and Poole (2003) supported the point of view that the staminate flower of all North American species has a perianth, whereas the pistillate flower of the plane tree lack a perianth. Douglas and Stevenson (1998) marked that, at early ontogenetic stages, the perianth develops in the staminate flowers; however, it is reduced just after the formation of the anlage.

Using *P. hispanica* Münchh. as an example, von Balthazar and Schönenberger (2009) have shown that the staminate and pistillate flowers have two circles of sterile structures encircling the androecium and gynoecium. The staminate flowers of *P. hispanica* have two circles of morphologically distinct elements, encircling the stamens. The external circle consists of narrow (of two or three layers of cells), subequal in length (up to 3 mm without hairs) elements, which are frequently fused at the base and have long multicellular hairs in the apical part. These elements are not vascularized. The elements of the second circle are short (about 500 μm long), thicker than the elements of the first circle, have a pronounced adaxial crest, nonvascularized. In the basal part, they are fused with the stamens to form a staminal tube. In the pistillate flowers of *P. hispanica*, the external circle of elements is morphologically the same as in the staminate flowers; however, they are considerably smaller (at most 500 μm long). The elements of the internal circle are less pronounced; they are also smaller in size and frequently reduced to one or two. Elements of both circles framing the gynoecium of pistillate flowers are not vascularized, as in the staminate flowers. Von Balth-

azar and Schönenberger (2009) believe that the two circles of structures framing the androecium and gynoecium are of different nature. The elements of the external circle belong to the perianth, while the elements of the internal circle represent the staminodia. The last statement is supported by the fact that the elements of the internal circle (with the adaxial crest) resemble in shape the stamens and are fused at the base with the stamens, forming a staminal tube. The presence of staminodia in pistillate flowers of the living plane tree and the presence of appendages of the stamens, which are treated as the staminodia, in the staminate flowers has been shown previously (Magallón-Puebla et al., 1997).

Comprehensive analysis of pollen grains of different species of *Platanus* with the aid of a light microscope and a scanning electron microscope has shown that their characters are very uniform. This primarily concerns the pollen grain characters, such as the size, ornamentation of exine, shape and size of colpi, etc. (Denk and Tekleva, 2006). The apocarpous gynoecium of *Platanus* consists of 5–8 (or, less often, 3–9) carpels with stylodia varying in length and arranged in two or three circles. In the plane tree, a mature fruit shows incompletely fused margins of the carpel (Sporne, 1974). One orthotropic ovule (rarely two) is present. The presence of a tuft of hairs at the base of the pistillate flower is a generic character of *Platanus*.

To date, the following genera have been referred to the family Platanaceae based on fossil staminate and pistillate inflorescences: *Aquia* Crane, Pedersen, Friis et Drinnan (Crane et al., 1993); *Archaranthus* (Maslova and Kodrul, 2003); *Carinalaspermum* Krassilov (Krassilov, 1976); *Chemurnautia* (Maslova, 2002a); *Friisicarpus* (Friis, Crane et Pedersen) N. Maslova et Herman (the generic name *Friisicarpus* was proposed for the previously established *Platanocarpus* Friis, Crane et Pedersen (Friis et al., 1988), which is an invalid late homonym of the genus *Platanocarpus* Jarmolenko; Maslova and Herman, 2006); *Gynoplatananthus* Mindell, Stockey et Beard (Mindell et al., 2006); *Hamatia* Pedersen, Friis, Crane et Drinnan (Pedersen et al., 1994); *Macginicarpa* Manchester (Manchester, 1986); *Macginistemon* (MacGinitie) Manchester (Manchester, 1986); *Oreocarpa* N. Maslova et Krassilov (Maslova and Krassilov, 2002); *Platananthus* Manchester (Manchester, 1986); *Plataninium* Unger (Manchester, 1986); *Platanites* (Crane et al., 1988); *Platanus* (Maslova, 1997; Kvaček et al., 2001); *Quadriplatanus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 1997); *Sarbaya* Krassilov et Shilin (Krassilov and Shilin, 1995); *Tanyoplatanus* Manchester (Manchester, 1994); and *Tricolpopollianthus* Krassilov (Krassilov, 1973a).

Reproductive organs of ancient platanoids examined with reference to microstructure are known from the Cretaceous (Krassilov, 1973a, 1976; Knobloch and May, 1986; Friis et al., 1988; Crane et al., 1993; Ped-

ersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Mindell et al., 2006; Wang, 2008), Paleocene (Crane et al., 1988; Pigg and Stockey, 1991; Maslova, 1997, 2002a; Kvaček et al., 2001; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003), Eocene (Manchester, 1986, 1994), and Oligocene–Miocene (Bůžek et al., 1967; Kvaček, 1970). The analysis of structural features of reproductive organs of ancient platanoids has displayed that they vary widely in morphology.

The majority of inflorescences of fossil platanoids are spherical capitate and usually lack stalks. External differences are mostly manifested in the size of heads. In particular, the smallest heads (3–4 mm) are recorded in *Friisicarpus marylandensis* (Friis, Crane et Pedersen) N. Maslova et Herman and *F. carolinensis* (Friis, Crane et Pedersen) N. Maslova et Herman (4.3–6.1 mm); larger heads are observed in *Platanites hybridicus* (10–17 mm), *Macginicarpa manchesteri* Pigg et Stockey (10–16 mm), and infructescences associated with *Gynoplatananthus oysterbayensis* Mindell, Stockey et Beard (20 mm).

In ancient platanoids, the spherical shape of infructescences and staminate inflorescences prevails. In this character, the genera *Tanyoplatanus* and *Oreocarpa* stand apart. *Tanyoplatanus* has an elongated cylindrical inflorescence about 30 mm long and up to 11 mm wide and consisting of a straight central axis, surrounded by many densely packed flowers. The genus *Oreocarpa* has very small heads, consisting of several underdeveloped carpellodia and a single well-developed fruit.

Mature infructescences of the living plane tree are retained in the tree during winter. In spring, the infructescences disintegrate into separate fruits. The Paleocene genus *Archaranthus* (Maslova and Kodrul, 2003) is of particular interest; its staminate inflorescence is broken into individual flowers and stamens after maturation.

The heads of the living plane tree are unisexual, flowers sometimes have rudimentary structures of the opposite sex (staminodia in pistillate flowers and rudimentary pistils in staminate flowers). All known fossil platanoid flowers are unisexual, except for the genus *Gynoplatananthus* (Mindell et al., 2006), the staminate flowers of which contain five (or, less often, four) rudimentary carpels.

An important distinction of extinct platanoid genera from the extant genus *Platanus* is the pronounced, frequently well-differentiated perianth (for example, in the genera *Friisicarpus, Macginicarpa, Platananthus, Quadriplatanus, Aquia, Hamatia, Gynoplatananthus, Tanyoplatanus, Archaranthus*). The extremely reduced perianth is observed in the Paleocene platanoids *Platanites hybridicus* Forbes (Crane et al., 1988; Boulter and Kvaček, 1989), *Platanus stenocarpa* N. Maslova (Maslova, 1997), and *Chemurnautia staminosa* N. Maslova (Maslova, 2002a). *Sarbaya radiata*

Krassilov et Shilin from the Cenomanian—Turonian of Kazakhstan, which was referred to platanoids by the authors of the genus, has a poorly developed perianth at most one-third as long as the stamen (Krassilov and Shilin, 1995). Middle Eocene *Platanus hirticarpa* Manchester (Manchester, 1994) differs from congeners in the poorly developed and nondifferentiated perianth.

The majority of extinct platanoid genera have a stable number of stamens per flower, which is constant within an inflorescence. The basic differences concern the structure of stamens and some characters of pollen grains. The massive anthers, which are positioned on short filaments, are characteristic of extinct platanoids with pentamerous [*Platananthus synandrus* Manchester (Manchester, 1986); *P. hueberi* Friis, Crane et Pedersen (Friis et al., 1988); *P. scanicus* Friis, Crane et Pedersen (Friis et al., 1988); *P. speirsae* Pigg et Stockey (Pigg and Stockey, 1991); and *Hamatia elkneckensis* Pedersen, Friis, Crane et Drinnan (Pedersen et al., 1994)] and tetramerous androecium [*Sarbaya radiata* (Krassilov and Shilin, 1995); *Quadriplatanus georgianus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 1997); and *Archaranthus krassilovii* Maslova et Kodrul (Maslova and Kodrul, 2003)]. The Early Cretaceous genus *Aquia* (Crane et al., 1993) differs in the structure of stamens, which have well-developed filaments twice as long as anthers.

The connectives of ancient platanoids vary in development, the apical part is occasionally poorly pronounced (*Aquia brookensis* Crane, Pedersen, Friis et Drinnan), conical (*Platananthus synandrus, P. speirsae*), triangular (*P. scanicus*), flattened (*P. hueberi*), or peltate (*Platanus richteri* Knobloch et Mai, *Platananthus potomacensis* Friis, Crane et Pedersen). The epidermis of connectives is pubescent (*Platananthus hueberi, P. synandrus, Platanus neptuni, Aquia brookensis*, staminal complexes of *Macginistemon mikaneides* (MacGinitie) Manchester, *Archaranthus krassilovii*) or lacks hairs (*Platananthus potomacensis, P. scanicus, P. speirsae, Platanus richteri*). The epidermis of the connective of *Aquia brookensis* is equipped with many stomata or stoma-like secretory pores; in *Archaranthus krassilovii*, it has anomocytic stomata.

The functionally unisexual flowers of the living plane tree and some fossil platanoids have rudimentary structures of the opposite sex (underdeveloped stamens (staminodia) in pistillate flowers and rudimentary pistils in staminate flowers). Among the genera referred to platanoids, *Quadriplatanus* stands apart (Magallón-Puebla et al., 1997). It has well-developed stamens fused with staminodia to form a staminal tube; the authors of the genus compared this character to the presence of a similar relatively massive ring, which is formed of the basally fused stamens and staminodia in the living plane tree. In the formation of the staminal tube by the fusion of the bases of stamens and staminodia, the inflorescences of *Quadriplatanus* are similar to Turonian inflorescences showing a set of characters typical of both Platanaceae and Hamamelidaceae (Crepet et al., 1992; Crepet and Nixon, 1996). The stamens and staminodia fused for a long extent and forming a staminal tube is a distinctive character of some extant representatives of the family Hamamelidaceae (Endress, 1977). The Paleocene genus *Bogutchanthus* (Maslova et al., 2007), showing a mosaic combination of characters of reproductive organs of platanoids and hamamelids, has staminodia located between mature stamens and elements of the perianth, which are partially fused at the base. They resemble mature stamens in shape.

Pollen grains of fossil platanoids are rather uniform and differ from extant *Platanus* in the smaller size (for example, 8.5—12 μm in *Platananthus potomacensis*, 13—15 μm in *P. hueberi*, 16—20 μm in *Platanites hybridicus*). The most significant structural differences are observed in exine ornamentation. Pollen grains of *Aquia brookensis* have a foveolate—reticulate exine (Crane et al., 1993), in contrast to the reticulate exine of other fossil platanoids. Late Cretaceous *Platananthus hueberi* shows a peculiar coarsely reticulate sculpture, which essentially differs from that of living species of *Platanus*. Fossil platanoids differ from extant *Platanus* in the reticulum pattern at the transition from nonapertural to apertural regions. In contrast to the living plane tree, with a uniform reticulum throughout the pollen surface, the coarsely reticulate pollen grains of *Platananthus hueberi* form a narrow row of smaller cells along the apertural region (Friis et al., 1988; Friis and Pedersen, 1996); in pollen grains of *Hamatia*, the cell size gradually decreases towards the boundary between the apertural and nonapertural regions (Pedersen et al., 1994). In Late Cretaceous *Platananthus scanicus* (Friis et al., 1988; Friis and Pedersen, 1996) and *P. speirsae* (Pigg and Stockey, 1991) and Cenozoic *P. synandrus* (Manchester, 1986) and *Archranthus krassilovii*, the reticulum forms a distinct sporopollenin rim along the apertural regions. Note that some pollen grains of *Archaranthus krassilovii* have additional colpi, a characteristic feature of some genera of Hamamelidaceae.

A distinctive character of the majority of known fossil platanoids is the constant number of carpels per flower. Among the genera referred to the family Platanaceae, five carpels per flower are observed in *Friisicarpus brookensis, F. marylandensis, F. elkneckensis* (Pedersen, Friis, Crane et Drinnan) N. Maslova et Herman, *F. carolinensis, Macginicarpa manchesteri, M. glabra* Manchester, and infructescences associated with *Gynoplatananthus oysterbayensis*. The flower of *Quadriplatanus georgianus* is constantly tetramerous, four (or more) carpels are probably characteristic of *Platanus hirticarpa*, *Tanyoplatanus cranei* Manchester has three or four.

Carpels of ancient platanoids vary in shape from narrowly triangular in *Friisicarpus marylandensis, F. brookensis*, and *F. carolinensis* to narrowly elliptical in *Friisicarpus* sp. (Friis et al., 1988), from widely

elliptical in *Platanus richteri* to narrowly elliptical in *Platanus stenocarpa*, elliptical ovoid in *Macginicarpa glabra*, obovoid (to triangular) in *P. hirticarpa*, ovate (to obovoid) in *Tanyoplatanus cranei*. The genus *Oreocarpa*, which was originally referred to platanoids, differs considerably in fruit morphology; its fruit is elongated, larger than the head, with a short stylodium, consists of the basal locule and distal part with three longitudinal ribs.

A distinctive feature of fossil platanoids is the absence of dispersed hairs in pistillate flowers. An exception is Eocene *Tanyoplatanus*, which has abundant relatively large hairs at the fruit base. The presence of dispersed hairs in pistillate flowers is a generic character of *Platanus*. Extinct species of this genus had hairs on the surface of carpels (*Platanus laevis* Velen., *P. richteri, P. stenocarpa, P. neptuni*), but they lack a tuft of hairs at the fruit base. Fossil platanoids examined have one ovule per carpel. All known ancient platanoids have orthotropic ovules, the sole exception is *Quadriplatanus*, which has nonorthotropic ovules.

3.2. Hamamelid Fossils

In comparison with fossils associated with Platanaceae, paleobotanic data on reproductive organs and leaves tentatively assigned to Hamamelidaceae are scarce. In any event, they are insufficient for complete reconstruction of the origin of all basic lineages within this family. As mentioned above, the family includes up to 30 extant genera, which differ considerably in morphology; and only a few extinct taxa have been recorded. Fossil hamamelids are represented by leaves and reproductive structures.

3.2.1. Foliage Remains

Fossil hamamelid leaves include a group of forms assigned to extant taxa. The morphology of these leaves corresponds to generic criteria (e.g., the genera *Disanthus*: Matsuo, 1967; *Corylopsis*: Budantsev, 1983; Radtke et al., 2005; *Liquidambar*: Maslova, 1995a; *Parrotiopsis*: Maslova, 1995b; *Hamamelis*: Tanai and Suzuki, 1965; Fot'yanova et al., 1996, *Fortunearia* Rehd. et Wils.: Ozaki, 1991; *Distylium*: Huzioka and Takahasi, 1970; *Parrotia*: Maslova, 2003; *Matudaea* Lundell: Knobloch et al., 1996; *Sycopsis*: Ishida, 1970; *Eustigma* Gardn. et Champ.: Onoe, 1974; *Fothergilla*: Radtke et al., 2005; *Exbucklandia*: Wu et al., 2009); however, only a small part of known specimens enables the study of the epidermal structure of leaves, which could have provided more reliable identifications. General morphological similarity to extant representatives of the family is also observed in leaves, the names of which are formed of the generic name of respective extant genus and the endings "-phyllum" or "-ites" (e.g., *Dizanthophyllum* Golovneva: Golovneva, 1994b; *Hamamelites*: Saporta, 1868; *Corylopsiphyllum* Budants.: Budantsev, 1983; *Sycopsiphyllum*

N. Maslova: Maslova, 2003), which mark differences from extant analogues, unusual combination of characters, or poor preservation of fossil specimens, which prevents reliable assignment to a certain extant genus.

Among fossil specimens of extant genera, a prominent position is occupied by the genus *Liquidambar* (Altingioideae), which is easy to identify based on distinctive leaf characters and widespread in Cenozoic floras of the Northern Hemisphere (MacGinitie, 1941; Makarova, 1957; Uemura, 1983; Maslova, 1995a).

The earliest finds of leaves that are tentatively referred to Altingioideae are dated Cenomanian (Krassilov and Bacchia, 2000). These are simple leaves with a pinnate venation and relatively large teeth with characteristic glandular endings, which are assigned to the genus *Nammourophyllum* N. Maslova et Krassilov, resembling in general appearance the leaves of extant *Altingia*. Reliable finds of leaves comparable to *Liquidambar* are apparently absent from the Cretaceous beds. The known identifications of *Liquidambar* from the Upper Albian–Cenomanian of North America (Lesquereux, 1874) seem questionable, because they differ considerably in general morphology, while epidermal data and accompanying reproductive structures have not been reported. The leaf morphotype typical for *Liquidambar* appeared in the fossil record as late as the Eocene, reproductive structures of this genus occur beginning from the same time.

The situation with fossil leaves of *Liquidambar* in general resembles that with the genus *Platanus*; researchers often disregard probable polymorphism of leaf lamina characters in fossil specimens and, consequently, assign every slightly distinguished specimen to a separate species. As a result, the number of ancient species of *Liquidambar,* based on leaves, is probably considerably overestimated. Taking into account the high leaf polymorphism in extant *Liquidambar*, the establishment of a great number of extinct species of this genus seems groundless.

Although fossil leaves of *Liquidambar* are widespread in the Neogene of the Northern Hemisphere, they are almost unknown in pre-Tertiary floras. At the same time, reproductive structures that are thought to be related to Altingioideae are known, at least, from the Late Turonian (Zhou et al., 2001). The question of leaves that could have been produced by plants with such reproductive structures remains open. Of particular interest is the co-occurrence in the same burial of leaves of *Ettingshausenia*, which were previously determined as *Platanus louravetlanica* Herman et Shczepetov (Herman, 1994), and infructescences of *Anadyricarpa* N. Maslova et Herman, which were originally referred based on microstructural characters to the subfamily Altingioideae (Maslova and Herman, 2004).

A number of fossil leaves referred to hamamelids were described as extinct genera (Golovneva, 1994a, 1994b; Budantsev, 1997; Krassilov and Bacchia, 2000;

Maslova, 2003; etc.). Data on epidermal structures of extinct hamamelid genera have not been reported.

In the case of hamamelids, it is impossible to exclude the same situation as in the identification of fossil platanoids, which were initially identified exclusively as extant taxa. The geological history of Hamamelidaceae remains uncertain, we are at the beginning of the study of the development of particular subfamilies and genera and, hence, it is possible that the hypothesis concerning the first appearance of extant genera of this family in the fossil record will be changed in the future.

3.2.2. Reproductive Structures

Until recently, the data on morphological diversity of fossil reproductive structures assigned to Hamamelidaceae, were almost absent. The studies devoted to new hamamelid taxa established based on reproductive structures and expanding the knowledge of their diversity in the past first appeared in the 1990s (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla et al., 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004; Pigg et al., 2004; Ickert-Bond et al., 2005; Benedict et al., 2008; Zhao and Li, 2008). The capitate reproductive structures, which are differentiated with certainty by macromorphological features in living representatives of the families Platanaceae and Hamamelidaceae, are often very similar in macromorphology in fossil forms (Crepet et al., 1992; Magallón-Puebla et al., 1997; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a; Maslova and Herman, 2004; etc.). It became possible to identify them only with the use of a scanning electron microscope.

Of four hamamelid subfamilies established by Endress (1989b), the subfamilies Hamamelidoideae (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla et al., 1996, 2001; Benedict et al., 2008; Zhao and Li, 2008) and Altingioideae (Kirchheimer, 1943; Mai, 1968; Krassilov, 1976; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a; Zhou et al., 2001; Maslova and Herman, 2004; Pigg et al., 2004; Ickert-Bond et al., 2005, 2007) are most abundant in the fossil record. The genus *Viltyungia* N. Maslova from the Cenomanian of Eastern Siberia displays characters typical of three hamamelid subfamilies, Exbucklandioideae, Altingioideae, and Hamamelidoideae (Maslova and Golovneva, 2000b).

All Cretaceous reproductive structures of the Hamamelidaceae belong to extinct genera, while Recent taxa appear as late as the Paleogene. The exception is provided by isolated Cretaceous seeds, which, despite significant morphological distinctions, were determined as, for example, the genera *Hamamelis, Disanthus*, and *Rhodoleia* Champ. et Hook (Knobloch and Mai, 1986). These Cretaceous specimens are very important as evidence of the appearance of

evolutionary lineages leading to extant taxa; however, they are tentatively assigned to these taxa and a more thorough study of the systematics of extinct Platanaceae and Hamamelidaceae is needed to test these results.

The identification of extant hamamelid taxa among Late Cenozoic seeds is probably more reliable. In particular, *Fortunearia* cf. *sinensis* Rehd. et Wils. and *Corylopsis* cf. *pauciflora* Sieb. et Zucc. recorded in the Oligocene of Siberia (Dorofeev, 1963) are similar in macromorphology to living species of these genera, differing mostly in the smaller size.

The basic inflorescence type of the living hamamelids is the simple or compound spike; some genera have a more or less compressed, simple or compound raceme; and a rare variant is the head (Endress, 1977). Three genera, *Altingia, Liquidambar*, and *Semiliquidambar* (subfamily Altigioideae), have heads resembling somewhat that of platanoids. Microstructural features of their reproductive organs have been relatively thoroughly examined (Flint, 1959; Schmitt, 1965; Wisniewski and Bogle, 1982; Bogle, 1986; Ickert-Bond et al., 2005; Ickert-Bond et al., 2007). In some representatives of the subfamilies Hamamelidoideae and Exbucklandioideae, the inflorescence is strongly compressed, so that it looks like a head; however, they differ in flowers, which are unisexual or bisexual, with a well-developed perianth or without it.

Most of the fossil reproductive structures referred to the Hamamelidaceae are capitate inflorescences and infructescences, solitary flowers are less often. Fossil capitate reproductive structures of hamamelids are almost identical in macromorphology to those of platanoids. The family and generic affiliation of these specimens is determined exclusively by microstructural characters.

Among fossil specimens assigned by the authors of taxa to the Hamamelidaceae, the capitate type of inflorescences is known in *Evacarpa* N. Maslova et Krassilov (Maslova and Krassilov, 1997), *Lindacarpa* N. Maslova (Maslova and Golovneva, 2000a), and *Microaltingia* Zhou, Crepet et Nixon (Zhou et al., 2001) of the subfamily Altingioideae and the genus *Viltyungia* (Maslova and Golovneva, 2000b), which shows microstructural characters typical of the subfamilies Exbucklandioideae, Altingioideae, and Hamamelidoideae. The infructescences and seeds referred to the extant genus *Liquidambar* are known from the Eocene–Pliocene of western North America, Europe, and Asia (Uemura, 1983; Friis, 1985; Ferguson, 1989; Manchester, 1999; Maslova, 2003; Pigg et al., 2004). The heads morphologically similar to the genus *Liquidambar* are observed in the genus *Steinhauera* Presl. (Kirchheimer, 1943, 1957; Tiffney, 1986; Krassilov, 1989, 1997; Ferguson, 1989).

Manchester (1994) described the capitate staminate inflorescences with pollen grains in situ, which are associated with raceme infructescences of *Fortunearites endressii* Manchester. The researcher pro-

posed that these reproductive structures belonged to different plants, since the infructescences are similar to the extant genera *Fortunearia* and *Sinowilsonia* Hemsl., while the staminate inflorescences share certain characters with *Hamamelis* and *Corylopsis.*

The fossil hamamelids *Archamamelis* Endress et Friis (Endress and Friis, 1991), *Allonia* Magallón-Puebla, Herendeen et Endress (Magallón-Puebla et al., 1996), and *Androdecidua* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 2001) are solitary flowers; the data on their position in inflorescences have not been reported.

The genus *Archamamelis* is apparently characterized by bisexual (probably functionally unisexual) flowers; the flower of *Androdecidua* is probably bisexual (although the gynoecium was not preserved, the authors (Magallón-Puebla, 2000) proposed that it was present based on the comparison with previously known specimens), pentamerous, actinomorphic, with a well-developed androecium. The genus *Allonia* was established for the flowers at an early developmental stage, with incompletely formed fertile organs; thus, it is difficult to judge whether or not they had female structures, whereas male structures are identified with certainty. The elements of the perianth of these flowers are completely formed and open. The flowers of *Viltyungia* are bisexual, and the genera *Lindacarpa* and *Microaltingia* have unisexual flowers. The pistillate flower of the genus *Evacarpa* contains sterile structures resembling staminodia and intrafloral structures.

Most of the extant genera of Hamamelidaceae have a double tetra- or pentamerous perianth, which is differentiated into the calyx and corolla developed to a varying extent; less often, hamamelid flowers are naked (Endress, 1989a; Drinnan et al., 1994). Elements of the perianth are free or fused to a greater or lesser extent to form a tube; sometimes, they are partially fused with the ovary. The subfamily Hamamelidoideae includes living representatives, the leaflets of the perianth of which are fused basally with the stamens to form a hypanthium (*Parrotia, Fothergilla*), which was probably accompanied by a decrease in the number of stamens (*Parrotiopsis, Molinadendron, Sycopsis sinensis*) or partial fusion between the hypanthium and ovary (*Parrotiopsis, Fothergilla*) (Bogle, 1970). Representatives of the subfamily Altingioideae have naked flowers. Many fossil hamamelids have well-developed and often differentiated perianths. Bogle (1986) proposed that, in the geological past, there were ancestors of hamamelids with well-developed perianths. In the flowers of *Allonia*, the perianth is differentiated, has a well-developed corolla of narrow petals, with parallel margins and irregularly arranged elements of the calyx. In the flowers of *Androdecidua*, elements of the calyx have not been recorded, the petals of the corolla are spindle-shaped, with tapering bases and apices, partially fused with the stamens of the external circle of the androecium. The

genus *Archamamelis* probably has a differentiated hexamerous or heptamerous perianth, with triangular, basally widened petals similar to those of extant *Disanthus.* The well-developed perianth in flowers of *Viltyungia* is differentiated into morphologically different elements, the narrower internal elements and wider external elements with hairs. The pubescence on the elements of the perianth has been recorded, for example, in extant *Parrotia* (Bogle, 1970). A well-developed perianth, which is attached somewhat above the base of the gynoecium and covers the flower for almost the whole of its length, has been described in *Lindacarpa.* In *Anadyricarpa*, which was considered in the original description to be close to the subfamily Altingioideae (Maslova and Herman, 2004), petals of the perianth form the flower tube, which covers the solitary carpel for almost the whole of its length and is retained in mature fruit. The flowers of *Evacarpa, Microaltingia*, and *Liquidambar* are naked.

It has been shown that almost all extant Hamamelidaceae have tetrasporangiate anthers; the theca with a solitary locule is only present in the genera *Hamamelis* and *Exbucklandia* (Shoemaker, 1905; Kaul and Kapil, 1974; Endress, 1989a; Hufford and Endress, 1989). Some hamamelid genera are characterized by the basally attached anthers and expanded apex of the connective; many representatives of this family have a well-developed connective extension, which is longer than the theca. Among fossil hamamelids, the genus *Allonia* has anthers with a distinct horny connective extension, which is a distinctive character of the extant subtribe Loropetalinae. The androecium of *Androdecidua* consists of ten stamens arranged in two circles. Massive, wide anther filaments with parallel margins are fused at the base. The staminal bases of the external circle are also fused with the bases of the petals of the corolla. Connective extensions are well-developed, directed towards the center of the flower, where they closely adjoin each other to form a conical peak. A distinctive feature of *Androdecidua* is different morphology of the stamens in the external and internal circles. The stamens of the external circle have bisporangiate anthers, which consist of two thecae. Each theca lacks an adaxial pollen sac, anthers burst open through a solitary valve. The stamens of the internal circle have tetrasporangiate anthers, which consist of two thecae and open into two valves.

Flowers with valved anthers have been recorded in the genera *Archamamelis* and *Allonia.* The anther of *Viltyungia* opens by a longitudinal slit. It is noteworthy that the anther shape in this Cretaceous genus (which has a strongly convex dorsal face) is identical to that of Recent *Disanthus* (Endress, 1989a, 1989b; Hufford and Endress, 1989). *Viltyungia* is the sole currently known extinct hamamelid whose anthers open by a longitudinal slit.

Hamamelid flowers include two different types of sterile structures, staminodium and intrafloral phyllomes. Taking into account disagreements in interpre-

tation of the nature of these structures even in Recent hamamelids, difficulties in the description of fossil forms are quite clear.

Sterile structures of flowers are extremely scarcely described in the fossil record. Among genera that are considered to be close to the Altingioideae, both types of sterile structures, differing in size and shape, are recorded in the genus *Evacarpa*. The smaller and narrower elements are interpreted as phyllomes, the more massive and wider elements are staminodia, which probably did not produce pollen grains. Flowers of *Microaltingia* have two or three circles of rounded phyllomes located at the hypanthium margin.

The synthetic genus *Viltyungia*, which combines characters of three subfamilies (Altingioideae, Hamamelidoideae, and Exbucklandioideae), probably had staminodia, which produced abundant pollen grains. Pollen masses, composed of underdeveloped and conglutinated pollen grains, which are considerably smaller than fertile pollen, were found attached to the surface of the gynoecium.

In the subfamily Hamamelidoideae, the staminodia have been recorded in the Santonian–Campanian genus *Archamamelis* and Eocene staminate capitate inflorescences that are considered to be similar in some characters to *Hamamelis* and *Corylopsis* (Manchester, 1994).

The tricolpate pollen grains of extant representatives of Hamamelidaceae vary in the configuration of colpi (in *Rhodoleia, Exbucklandia, Eustigma, Loropetalum* R. Brown ex Reich., and *Fothergilla*, the colpi closely approach the poles, while the colpi of *Forthunearia, Chunia* H.T. Chang, and *Molinadendron* Endress are short); the width of the apocolpia; and in the size, shape, and number of reticular meshes. Hamamelids include a group of genera with peculiar pollen grains bearing various additional apertures (pantocolpate pollen grains). Fossil hamamelids include genera characterized by tricolpate pollen grains with fine reticulate exine, i.e., *Archamamelis, Allonia*, staminate inflorescences associated with *Fortunearites endressii*. The pollen grains of *Androdecidua* are also tricolpate, distinguished by a coarser extinal reticulum. Pollen grains of the pantocolpate type, with three meridional and three additional colpi are characteristic of the genus *Viltyungia*. The Late Turonian genus *Microaltingia* is of interest, since it was assigned in the original description to the subfamily Altingioideae based on inflorescence morphology. However, this genus differs from Altingioideae in the tricolpate (instead of periporate, as is typical of this subfamily) pollen grains, the coarser extinal reticulum, and in the somewhat different seed structure.

The syncarpous semi-inferior ovary composed of two carpels is a key character of all hamamelids. Although this character prevails in living hamamelids, in some genera, the number of carpels per flower is variable. For instance, *Exbucklandia* has one to five carpels, with the prevalence of the bicarpellate gyno-

ecium (Kaul and Kapil, 1974); *Parrotiopsis* has from one to three carpels (Kapil and Kaul, 1972). The majority of fossil specimens referred to the family Hamamelidaceae have a bicarpellate gynoecium. However, based on the fact that some extant hamamelid genera vary in the number of carpels per flower, the Late Albian–Early Cenomanian genus *Anadyricarpa*, which has a monocarpellate gynoecium, was originally referred to hamamelids.

The genus *Hamawilsonia* Benedict, Pigg et De Vore from the Late Paleocene of central North Dakota (Benedict et al., 2008) is of particular interest. This anatomically complete infructescence is a spike with 20 ovoid sessile fruits. The fruits are bilocular, with well-developed curved persistent stylodia and a solitary seed in the locule. The genus *Hamawilsonia* combines characters of several extant hamamelid genera. In particular, in infructescence morphology and characters of pollen grains, which were established in staminate inflorescences associated with *Hamawilsonia*, it is similar to *Sinowilsonia*, whereas in seed morphology it is similar to *Hamamelis*. Anatomical seed characters show a mosaic combination of features characteristic of several extant genera of Hamamelidaceae.

CHAPTER 4. SYSTEMATICS OF PLATANOIDS AND HAMAMELIDS IN VIEW OF PALEOBOTANIC DATA

To date, all fossil capitate inflorescences and infructescences, macromorphology similar to those of living representatives of the families Platanaceae and Hamamelidaceae, have been assigned to these families or positioned close to them. As new specimens were accumulated and the knowledge of their morphological diversity expanded, the variation ranges of these families increased unreasonably and extended beyond the generally accepted family diagnoses. This mostly concerns the family Platanaceae, which includes the only extant genus, *Platanus*. The family Hamamelidaceae includes a greater number of extant genera and is more diverse in morphology of vegetative and generative organs; however, its geological history is much more poorly understood, and the knowledge of probable geological predecessors of the morphologically different extant hamamelid subfamilies is scarce.

The determination of taxonomic affiliation of some fossil specimens is complicated by numerous facts of co-occurrence of leaves and reproductive structures referred to different families (see, for example, Maslova and Herman, 2004; Maslova et al., 2005, 2007). The association of plant organs assigned to different families or showing a mosaic combination of characters of Platanaceae and Hamamelidaceae has already been analyzed as a basis for the revision of systematics of early platanoids and hamamelids (Maslova and Kodrul, 2007; Maslova, 2008c).

In the present study, a new concept of the taxonomic position of extinct platanoid and hamamelid genera is proposed based on the analysis of reproductive organs, which are particularly important for the development of the modern classical morphological systematics. Note that the inflorescence (in particular, flower) is the most complex system of plants. In contrast to the relatively simple leaves, roots, and stalks, flowers are complex structures, consisting of several organs united into an integrated system. In fact, floral organs are differentiated and function as individual objects, and in the case of fusion of individual elements into complex structures (sympetaly, synandry, etc.), they play a role of new floral elements, providing a new evolutionary status of these flowers. It is possible to trace the establishment of complex structures in capitate inflorescences using paleobotanic material (see, for example, Crepet et al., 1992; Magallón-Puebla et al., 1997). Thus, the system of extinct plants constructed based on available characters of reproductive organs most completely reflects relationships between taxa.

Since reproductive structures are much rarer and new taxa are frequently established based on few unique specimens, the data on variation in floral characters of capitate inflorescences at the generic and species levels are very poor and available data suggest that they are relatively stable (Maslova, 2003). In contrast to fossil specimens, extant reproductive structures of platanoids and hamamelids are quite remote in macromorphology. Consequently, reproductive structures provide an example of strategy opposite to that of leaves, in which stability (rather than changes) of characters in one chronological plane is combined with high evolutionary rates.

As mentioned above, fossil leaves are much more difficult to diagnose because of their high polymorphism and relative stability of morphological types through geological time. Some of them are assigned with confidence to a certain family of the natural angiosperm system, while others are only determined within the framework of the morphological system.

4.1. Reproductive Structures Previously Assigned to the Family Platanaceae

To date, the following extinct genera have been included in the family Platanaceae, based on reproductive structures: staminate inflorescences: *Tricolpopollianthus, Chemurnautia, Platananthus, Aquia, Hamatia, Gynoplatananthus, Sarbaya*, and *Archaranthus*; infructescences: *Macginicarpa, Oreocarpa, Tanyoplatanus*, and *Friisicarpus*; staminate inflorescences and infructescences: *Platanites* and *Quadriplatanus*; dispersed staminate complexes: *Macginistemon*; seeds: *Carinalaspermum*. Each genus differs to a greater or lesser extent from *Platanus*, the earliest reliable record of which is dated Late Paleocene (Maslova, 1997; Kvaček et al., 2001). Taking into account the recent finds of capitate reproductive structures identical in appearance to platanoid specimens which, however, combine diagnostic structural characters of various platanoid genera and even hamamelids, it is urgent to revise family affiliation of all known fossil specimens.

In the previous studies, I have marked that, in the Cretaceous, two lineages, with tetramerous and pentamerous flowers, emerged (Maslova, 2001, 2003); in the Cretaceous, they developed in parallel and, subsequently, followed different pathways. The lineage with tetramerous flowers, which differentiated at the initial stage of the establishment of platanoids, became extinct in the Paleocene. At the same time, the lineage with pentamerous flowers, which appeared in the Early Cretaceous and persisted to the Eocene, probably gave rise to the extant genus *Platanus*. New data concerning the lineage with tetramerous flowers (genus *Bogutchanthus*) and a more thorough comparison of reproductive organs of these genera with platanoids and hamamelids resulted in the establishment of an independent family, Bogutchantaceae fam. nov., which combines characters of both extant families and provides a link between them in the geological past.

The family Bogutchantaceae fam. nov. includes the genera *Sarbaya, Quadriplatanus, Archaranthus, Bogutchanthus*, and staminate inflorescences and infructescences described by Crepet et al. (1992). The genera *Sarbaya, Quadriplatanus*, and *Archaranthus* were originally referred by the authors to the family Platanaceae; the Turonian capitate staminate inflorescences and infructescences were positioned close to the family Hamamelidaceae (Crepet et al., 1992); and the genus *Bogutchanthus* was only determined to the order Hamamelidales because of mosaic combination of characters of staminate inflorescences, combining features of both families. The genera listed are assigned to the new family based on certain characters, such as distinctly tetramerous flowers, the nonorthotropic type of the solitary seed in the fruit, and varying types of pollen grains (tricolpate, tricolporate, and pantocolpate).

Representatives of the family Bogutchantaceae fam. nov. are similar to the Platanaceae in the presence of capitate inflorescences and infructescences and staminodia, some Bogutchantaceae fam. nov. resemble extinct Platanaceae in the presence of well-developed perianth (*Quadriplatanus, Archaranthus, Bogutchanthus*) and some (in particular, *Sarbaya*) have flowers without a distinct perianth, as the living plane tree.

The new family Bogutchantaceae fam. nov. is similar to the family Hamamelidaceae (in particular, the subfamilies Exbucklandioideae, Hamamelidoideae, and Altingioideae) in the general morphology of capitate inflorescences and infructescences (Altingioideae and Exbucklandioideae), the presence of bisporangiate stamens (genera *Hamamelis* and *Exbucklandia*), basally fused pollen sacs forming a staminal tube, and fused elements of the perianth and staminodia (genera *Parrotia* and *Fothergilla*) or elements of the perianth

and stamens (genera *Embolanthera* Merr. and *Dicoryphe* Du Petit-Thouars), pantocolpate pollen grains (genera *Distylium*, *Matudaea*, *Sycopsis*, and *Chunia*), nonorthotropic (anatropous) seeds (all Hamamelidaceae).

As genera with tetramerous flowers (family Bogutchantaceae fam. nov.) are removed from extinct platanoids, the family Platanaceae becomes a group of genera, which are represented in the geological past by two subfamilies, Platanoideae subfam. nov. and Gynoplatananthoideae subfam. nov., distinguished by the flower structure. The subfamily Platanoideae subfam. nov., along with the extant genus *Platanus*, includes the extinct genera *Tricolpopollianthus*, *Platanites*, *Chemurnautia*, and *Tanyoplatanus*. Distinctive characters of this subfamily are the naked flowers or flowers with an underdeveloped perianth and unstable number of elements in the flower. Extinct genera of this subfamily are similar to *Platanus* in the flowers without a distinct perianth (all genera, except for *Tanyoplatanus*), flowers with unstable number of elements, poorly developed connective extension in the stamens, and a tuft of hairs for dispersal at the fruit base (genus *Tanyoplatanus*).

The subfamily Gynoplatananthoideae subfam. nov. comprises the extinct genera *Platananthus*, *Friisicarpus*, *Aquia*, *Hamatia*, *Macginicarpa*, *Macginistemon*, and *Gynoplatananthus*. In addition to the strictly pentamerous flowers with well-developed perianths, which distinctly differ this subfamily from other platanoids, representatives of these genera are rather diverse in other characters of the generative system. In particular, the genus *Gynoplatananthus* is distinguished by the presence of rudimentary carpels in the staminate flowers. Sporadic participation of rudimentary carpels in the flower has been shown in living *Platanus occidentalis*, *P. acerifolia*, *P. racemosa*, and *P. orientalis*; however, constant participation of rudimentary carpels in flowers with a constant number (five) of stamens has not been recorded in extant taxa (Mindell et al., 2006). The genus *Aquia* is characterized by flowers with the stamens, the anther filaments of which are twice as long as the anthers, and pollen grains with a foveolate-reticulate exine. The genus *Hamatia* has tricolporate pollen grains. It is probable that, in the future, as new data on extinct platanoids with pentamerous flowers and well-developed perianths are available, the subfamily Gynoplatananthoideae subfam. nov. will be ranked family of the order Hamamelidales.

4.2. Reproductive Structures Previously Assigned to the Family Hamamelidaceae

The following extinct genera established based on reproductive structures are referred to the family Hamamelidaceae: infructescences: *Anadyricarpa*, *Viltyungia*, *Evacarpa*, *Lindacarpa*, *Liquidambar*, *Fortunearites*, and *Microaltingia*; solitary flowers: *Allonia*, *Androdecidua*, and *Archamamelis*. Fossil reproductive structures of extant taxa are only known for the genus *Liquidambar*. As was shown in the previous studies (Maslova, 2001, 2003), hamamelids probably descend from the synthetic genus *Viltyungia*, which combines characters of three subfamilies (Exbucklandioideae, Hamamelidoideae, and Altingioideae). The characters of these basic hamamelid subfamilies appeared as early as the Cenomanian; however, evolutionary history of the family remains mostly an open question. This is partially caused by a limited number of fossil specimens that contribute to the understanding of the establishment of this diverse family.

The majority of fossil hamamelid specimens were referred by the authors to a certain extant subfamily; these conclusions seem mostly correct. In addition to *Viltyungia*, which combines characters of three subfamilies, the genus *Microaltingia* is particularly interesting; although the authors of this genus assigned it to the subfamily Altingioideae (Zhou et al., 2001), it also combines characters of different subfamilies. Zhou et al. (2001) indicated that *Microaltingia* displays a combination of characters (capitate unisexual inflorescences, tricolpate pollen grains with a reticulate exine, sterile phyllomes encircling the gynoecium, lower ovary, abundant nonwinged seeds) that has not been recorded in any extant genus or subfamily of Hamamelidaceae. Most of these characters are observed in the subfamily Altingioideae (except for the type of pollen grains, ornamentation of exine, and ovary type), some are characteristic of the subfamilies Exbucklandioideae (morphology of pollen grains and presence of sterile phyllomes) and Hamamelidoideae (pollen morphology). Thus, by analogy with the genus *Viltyungia*, it seems plausible to assign the genus *Microaltingia* to the family Hamamelidaceae, without placing it in any extant subfamily. Apparently, as new data are available, this genus will be placed in a separate hamamelid subfamily or an extinct family related to Hamamelidaceae.

The taxonomic position of the genus *Anadyricarpa* should also be improved. This genus was referred to Altingioideae (Maslova and Herman, 2004) based on the similarity in general arrangement of the compound inflorescence, the number of flowers per head, nonsimultaneous maturation of carpels, and the presence of the monocarpellate gynoecium. In living representatives of this subfamily, the bicarpellate gynoecium prevails, although monocarpellate forms are also recorded (Bogle, 1986). The genus *Anadyricarpa* differs from living representatives of Altingioideae in the development of the flower tube. In addition, because of poor preservation, the number of seeds in a fruit and the seed type of *Anadyricarpa* remain uncertain.

The group characterized by the monomeric gynoecium was expanded due to the finds of the Cretaceous genera *Kasicarpa* N. Maslova, Golovneva et Tekleva (Maslova et al., 2005) and *Sarbaicarpa* N. Maslova (Maslova, 2009). The unique preservation of these
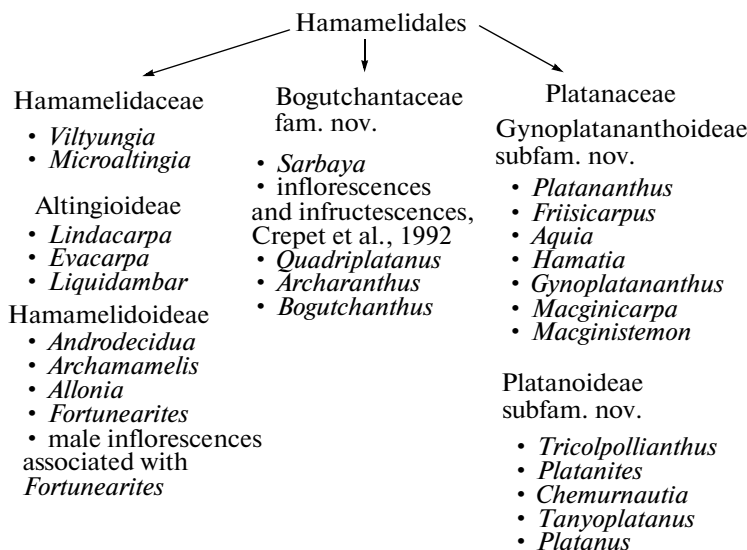
Hamamelidales

Hamamelidaceae

- *Viltyungia*
- *Microaltingia*

Altingioideae
- *Lindacarpa*
- *Evacarpa*
- *Liquidambar*

Hamamelidoideae
- *Androdecidua*
- *Archamamelis*
- *Allonia*
- *Fortunearites*
- male inflorescences associated with *Fortunearites*

Bogutchantaceae fam. nov.

- *Sarbaya*
- inflorescences and infructescences, Crepet et al., 1992
- *Quadriplatanus*
- *Archaranthus*
- *Bogutchanthus*

Platanaceae

Gynoplatananthoideae subfam. nov.

- *Platananthus*
- *Friisicarpus*
- *Aquia*
- *Hamatia*
- *Gynoplatananthus*
- *Macginicarpa*
- *Macginistemon*

Platanoideae subfam. nov.

- *Tricolpollianthus*
- *Platanites*
- *Chemurnautia*
- *Tanyoplatanus*
- *Platanus*

Fig. 3. Taxonomic composition of the order Hamamelidales.

Sarbaicarpales ordo nov.

Kasicarpaceae fam. nov.   Sarbaicarpaceae fam. nov.

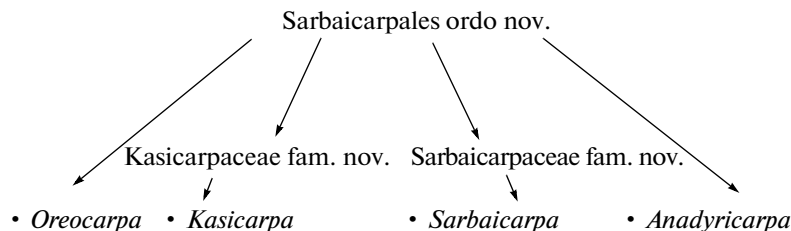- *Oreocarpa*   - *Kasicarpa*   - *Sarbaicarpa*   - *Anadyricarpa*

Fig. 4. Taxonomic composition of the order Sarbaicarpales ordo nov.

specimens allowed a thorough study of structural features and, based on comparative analysis with reproductive structures of hamamelids and platanoids, the establishment of new extinct order Sarbaicarpales ordo nov. with two families, Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov. The genus *Anadyricarpa* is also assigned to the order Sarbaicarpales ordo nov.; however, because of the absence of information on the number and type of seeds, this genus is not referred to any family of Sarbaicarpales ordo nov. It is also proposed to include the genus *Oreocarpa* in Sarbaicarpales ordo nov. This genus was originally referred to platanoids (Maslova and Krassilov, 2002); it is distinguished by the only fruit per inflorescence, which essentially differs in structure from that of platanoids. These distinctions prevent the assignment of the genus *Oreocarpa* to any presently established family.

4.3. Systematics of Extinct Platanoids and Hamamelids

Based on the foregoing, the following system of extinct platanoids and hamamelids is proposed (Maslova, 2008b; Figs. 3, 4).

Order Hamamelidales C. Martius, 1835

Family Platanaceae Lestiboudois, 1826

Subfamily Platanoideae N. Maslova, subfam. nov.

Type genus. *Platanus* L.

Diagnosis. Plants with compound staminate and pistillate inflorescences, composed of axis and attached heads. Capitate inflorescence including central core and many radiating flowers. Perianth variously developed or absent. Number of floral elements unstable. Pollen grains tricolpate. Seed solitary and orthotropic.

Generic composition. *Tricolpopollianthus, Platanites, Chemurnautia, Tanyoplatanus*, and *Platanus*.

Comparison. The subfamily Platanoideae subfam. nov. differs from the subfamily Gynoplatananthoideae subfam. nov. in the presence of flowers without a perianth and in the unstable number of elements in the flower.

Subfamily Gynoplatananthoideae N. Maslova, subfam. nov.

Type genus. *Gynoplatananthus* Mindell, Stockey et Beard, Canada, islands of Vancouver; Oys-

ter Bay Formation, Middle Eocene (Mindell et al., 2006).

Diagnosis. Plants with compound staminate and pistillate inflorescences, composed of axis and attached heads. Capitate inflorescence including central core and many radiating flowers. Flowers unisexual or bisexual. Perianth well developed. Floral elements five in number. Pollen grains tricolpate. Seed solitary and orthotropic.

Generic composition. *Platananthus, Friisicarpus, Aquia, Hamatia, Macginicarpa, Macginistemon*, and *Gynoplatananthus*.

Comparison. The subfamily Gynoplatananthoideae subfam. nov. differs from the subfamily Platanoideae subfam. nov. in the presence of flowers with a well-developed perianth and stable (five) number of elements in the flower (carpels in pistillate flowers and stamens in staminate flowers).

Family Bogutchantaceae N. Maslova, fam. nov.

Type genus. *Bogutchanthus* N. Maslova, Kodrul et Tekleva, Amur Region, Arkhara—Boguchansk lignite deposits; Tsagayan Formation, Lower Paleocene (Maslova et al., 2007).

Diagnosis. Plants with compound staminate and pistillate inflorescences, composed of axis and attached heads. Capitate inflorescence including central core and many radiating flowers. Perianth variously developed or absent. Flower with four stamens (or number of stamens divisible by four). Pollen grains tri- or pantocolpate. Seed solitary and nonorthotropic.

Generic composition. *Sarbaya, Quadriplatanus, Archaranthus*, and *Bogutchanthus*.

Comparison and remarks. The family Bogutchantaceae fam. nov. combines characters of reproductive organs characteristic of the families Platanaceae and Hamamelidaceae.

The family Bogutchantaceae fam. nov. is similar to extant and extinct Platanaceae in the capitate shape of the inflorescence, the presence of staminodia, and tricolpate type of pollen grains in some representatives. Flowers with a well-developed perianth are only characteristic of extinct Platanaceae. Although the pollen grains described in the genus *Bogutchanthus* (of the pantocolpate type) differ in morphology from other Bogutchantaceae fam. nov. and Platanaceae, they are similar in ultrastructure of the sporoderm of these pollen grains to both Platanaceae and Hamamelidaceae (Tekleva, 2007).

The family Bogutchantaceae fam. nov. is similar to extant and extinct Hamamelidaceae in characters of general morphology of the inflorescence, the number of flowers per head, and in the presence of secondarily bisporangiate stamens (*Bogutchanthus*), staminodia (*Bogutchanthus* and infructescence from the Turonian beds of the Raritan Formation, New Jersey: Crepet et al., 1992), pantocolpate pollen grains (*Bogutchan-*

thus, Archaranthus), and nonorthotropic type of seeds (*Quadriplatanus*). In the ability of forming capitate inflorescences, the presence of bisporangiate anthers and pantocolpate pollen grains, representatives of the family Bogutchantaceae fam. nov. (in particular, the genus *Bogutchanthus*) are most similar to the extant genus *Chunia* (subfamily Exbucklandioideae). Of fossil hamamelids, the Cenomanian genus *Viltyungia* is most similar to the new family in the inflorescence shape, the presence of staminodia, and the type of pollen grains.

The staminate inflorescences and infructescences from the Turonian beds of the Raritan Formation, New Jersey (Crepet et al., 1992), which were described without a generic name, probably also belong to the family Bogutchantaceae fam. nov.

Order Sarbaicarpales N. Maslova, ordo nov.

Etymology. From the type family Sarbaicarpaceae fam. nov.

Diagnosis. Plants with compound staminate and pistillate inflorescences, composed of axis and attached heads. Capitate inflorescence including central core and many radiating flowers. Fruit monocarpellate. Seed solitary.

Composition. The families Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov., genera *Anadyricarpa* and *Oreocarpa*.

Comparison and remarks. The new order differs from all known orders of flowering plants in the unique combination of characters, such as the capitate infructescence, monocarpellate fruits, and solitary seed in the fruit. Taking into account the great diversity of orders of flowering plants (more than one hundred), it is expedient to confine the list of taxa involved in comparisons to orders that show certain relationships with the new order. They primarily include the group of orders of the subclass Hamamelididae, which are close to the base of phylogenetic tree (after Takhtajan, 1966) and show certain similarity to Hamamelidales.

The order Trochodendrales is similar to the new order in the presence of naked flowers and anatropous ovules with a well-developed endosperm (Sarbaicarpaceae fam. nov.) and differs in the bisexual flowers, the greater number of carpels (4(5)−11, sometimes up to 17 in Trochodendraceae and 4 in Tetracentraceae), which are fused laterally, and the greater number of ovules per fruit (25−30 in Trochodendraceae and 5−6 in Tetracentraceae).

The order Cercidiphyllales is similar to Sarbaicarpales ordo nov. in the naked flowers, monocarpellate gynoecium, and anatropous ovules (Sarbaicarpaceae fam. nov.) and differs in the well-developed stylodium, many winged seeds in a fruit, and poorly developed endosperm.

The order Eupteleales is similar to the new order in the presence of naked flowers and anatropous ovules,

with a well-developed endosperm (Sarbaicarpaceae fam. nov.) and differs considerably in the bisexual flowers, the gynoecium consisting of 6–18 carpels, and many ovules.

The order Didymelales is similar to the new order in the monocarpellate gynoecium and single ovule in a fruit (Sarbaicarpaceae fam. nov.) and differs in the carpel structure, epitropous ovules with considerably extended apices, and the absence of endosperm.

In addition, Sarbaicarpales ordo nov. differs from all the orders listed in the capitate inflorescences, the presence of sterile structures in the inflorescence (family Sarbaicarpaceae fam. nov.), the well-developed perianth, and in the orthotropic seed type (Kasicarpaceae fam. nov.).

For comparisons, it is expedient to consider the order Ranunculales of the subclass Ranunculidae. This order includes a number of families, some of which are distinctly similar to Sarbaicarpales ordo nov. These families are Nandinaceae, Berberidaceae, and Podophyllaceae (after Takhtajan, 1966; in Takhtajan, 1987, the family Podophyllaceae is regarded as a subfamily of the family Berberidaceae). The major shared characters are the monomeric (pseudo-monomeric in opinion of some researchers) gynoecium, anatropous ovules, and the well-developed endosperm. Distinctive features are the bisexual flowers and many ovules in the carpel. In addition, representatives of these families have racemose or paniculate inflorescences.

The family Ranunculaceae of the order Ranunculales (Takhtajan, 1966, 1987) is characterized by flowers with a well-developed and differentiated perianth, which shows relationship with the family Kasicarpaceae fam. nov. Representatives of Ranunculaceae are compared to the family Sarbaicarpaceae fam. nov. in the presence of monomeric gynoecium (although the gynoecium with many carpels prevails, some forms are monomeric, e.g., the genus *Delphinium* L.); single ovule in the ovary (although multiple ovules prevail); anatropous ovule type; and well-developed endosperm.

The genera *Anadyricarpa* and *Oreocarpa* have monocarpellate fruits, based on which they are assigned to the order Sarbaicarpales ordo nov.; however, it is impossible to refer these genera to any previously established families. In the case of *Anadyricarpa*, the data on the type and number of seeds in the fruit are absent. The genus *Oreocarpa* is distinguished by the domination of the sole well-developed fruit in the head, with a single winged seed; based on this, it is considered to be close to the family Sarbaicarpaceae fam. nov. However, the fruit of this genus is extraordinary in structure (elongated, longer than the head, crowned by a short stylodium, consisting of the basal locule of the seed, and winged distal part with three longitudinal ribs), considerably differs from other representatives of Sarbaicarpales ordo nov. In addition, it remains uncertain whether the underdevelopment of

some carpellodia is a stable diagnostic character or, by analogy with, for example, *Macginicarpa glabra* (Manchester, 1986), it occurs sporadically and depends on certain external factors. Until new data are available, it seems plausible to refer the genus *Oreocarpa* to the order Sarbaicarpales ordo nov. without designation of family affiliation.

All reproductive structures referred to the order Sarbaicarpales ordo nov., are found in association with leaves of a uniform morphotype that was previously assigned to the extant genus *Platanus*. Since these leaves vary in epidermal structure (Krassilov, 1976; Krassilov and Shilin, 1995; Golovneva, 2008) and the reproductive structures associated with them belong to different extinct genera of different families of the new order, it is proposed to determine these leaves as the genus *Ettingshausenia* of the morphological system, which is independent of the natural angiosperm system (Maslova et al., 2005).

Family Sarbaicarpaceae N. Maslova, fam. nov.

Type genus. *Sarbaicarpa* N. Maslova; western Kazakhstan, Sarbai locality near the town of Rudnyi; Zhirkindekskaya Formation, Cenomanian–Turonian (Maslova, 2009).

Diagnosis. Plants with compound infructescences, composed of axis and attached heads. Capitate infructescence, including central core and many loosely arranged radiating fruits. Perianth absent. Fruit monocarpellate. Seed solitary and anatropous.

Generic composition. Type genus.

Comparison. The new family differs from the family Kasicarpaceae fam. nov. in the loose arrangement of heads, flowers without a perianth, and the anatropous seed type.

Family Kasicarpaceae N. Maslova, fam. nov.

Type genus. *Kasicarpa* N. Maslova, Golovneva et Tekleva, Chulym–Yenisei Depression, Kas River, left tributary of the Yenisei River; roof of the Simonovskaya Formation, Turonian (Maslova et al., 2005).

Diagnosis. Plants with compound infructescences, composed of axis with attached heads. Capitate infructescence consisting of central core and many radiating densely packed fruits. Perianth present. Fruit monocarpellate. Seed solitary and orthotropic.

Composition. Type genus.

Comparison. The new family differs from the family Sarbaicarpaceae fam. nov. in the densely packed heads, the presence of a well-developed perianth, and the orthotropic seed type.

Thus, based on the reproductive structures, the systematics of extinct platanoids and hamamelids is as follows:

Order Hamamelidales C. Martius, 1835

Family Platanaceae Lestiboudois, 1826

Subfamily Platanoideae N. Maslova, subfam. nov.

Genus *Chemurnautia* N. Maslova

Genus *Platanites* Forbes

Genus *Platanus* L.

Genus *Tanyoplatanus* Manchester

Genus *Tricolpopollianthus* Krassilov

Subfamily Gynoplatananthoideae N. Maslova, subfam. nov.

Genus *Aquia* Crane, Pedersen, Friis et Drinnan

Genus *Friisicarpus* (Friis, Crane et Pedersen) N. Maslova et Herman

Genus *Hamatia* Pedersen, Friis, Crane et Drinnan

Genus *Macginicarpa* Manchester

Genus *Macginistemon* Manchester

Genus *Platananthus* Manchester

Genus *Gynoplatananthus* Mindell, Stockey et Beard

Family Hamamelidaceae R. Brown

Genus *Microaltingia* Zhou, Crepet et Nixon

Genus *Viltyungia* N. Maslova

Subfamily Altingioideae Reinsch

Genus *Evacarpa* N. Maslova et Krassilov

Genus *Lindacarpa* N. Maslova

Genus *Liquidambar* L.

Subfamily Hamamelidoideae Reinsch

Genus *Allonia* Magallón-Puebla, Herendeen et Endress

Genus *Androdecidua* Magallón-Puebla, Herendeen et Crane

Genus *Archamamelis* Endress et Friis

Genus *Fortunearites* Manchester

Genus *Hamawilsonia* Benedict, Pigg et Devore

Family Bogutchantaceae N. Maslova, fam. nov.

Genus *Archaranthus* N. Maslova et Kodrul

Genus *Bogutchanthus* N. Maslova, Kodrul et Tekleva

Genus *Quadriplatanus* Magallón-Puebla, Herendeen et Crane

Genus *Sarbaya* Krassilov et Shilin

Order Sarbaicarpales N. Maslova, ordo nov.

Genus *Anadyricarpa* N. Maslova et Herman

Genus *Oreocarpa* N. Maslova et Krassilov

Family Sarbaicarpaceae N. Maslova, fam. nov.

Genus *Sarbaicarpa* N. Maslova

Family Kasicarpaceae N. Maslova, fam. nov.

Genus *Kasicarpa* N. Maslova, Golovneva et Tekleva

CHAPTER 5. SOME CONTROVERSIAL QUESTIONS OF SYSTEMATICS AND PHYLOGENY OF THE FAMILIES PLATANACEAE AND HAMAMELIDACEAE

The knowledge of historical development of particular plant groups may be of great importance for the improvement of the taxonomic system. In this respect, the geological history of the families Platanaceae and Hamamelidaceae is of particular interest, since their taxonomic positions changed essentially in connection with the results of molecular studies (APG, 2003 and others), which, however, contradict the results of morphological analysis and have not yet been supported by paleobotanic records. In this connection, a key problem is reconstruction of the major evolutionary trends in the development of particular characters of reproductive and vegetative systems within the families and reconstruction of their phylogenetic relationships.

In the previous studies (Maslova, 2001, 2003), two stages of adaptive radiation, in the Albian–Cenomanian and Early Paleocene, have been recognized in the evolution of the family Platanaceae. At the first stage, staminate organs and pollen morphology underwent differentiation, while the structure of female organs remained stable. A number of forms that appeared at this stage were short-lived. The lineage with the staminate morphotype *Platananthus* passed into the Paleocene, where there was adaptive radiation that changed pistillate organs.

The functionally bisexual flowers characteristic of the genus *Gynoplatananthus* (Gynoplatananthoideae subfam. nov.) and occurring in some living species of *Platanus* and the extinct species *P. neptuni* (Platanoideae subfam. nov.) are only recorded in Platanaceae beginning from the Paleocene and, hence, should not be regarded as the primary condition in the family as a whole. At the same time, staminate flowers with a tissue expansion in the center of the flower between the stamens, which is treated as rudimentary carpels, are described in the Cretaceous genus *Quadriplatanus* (Bogutchanthaceae fam. nov.); in the family Hamamelidaceae, bisexual flowers are recorded in the basal genus *Viltyungia* and some living forms.

The family Hamamelidaceae followed an alternative pathway of evolutionary changes (Maslova, 2003). The characters of three major subfamilies (Hamamelidoideae, Exbucklandioideae, and Altingioideae) emerged as early as the Cenomanian–Turonian. The evolutionary lineage of Altingioideae is relatively completely represented in the fossil record, with the transitional forms *Lindacarpa* and *Evacarpa* and the extant genus *Liquidambar*, the reproductive structures of which are known from the Eocene. It is possible that all Cretaceous members of evolutionary lineages leading to extant genera were characterized by significant heterobathmy of morphological characters. At the same time, a few hamamelid genera previously

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described based on leaves will be supplemented in the future by some morphotypes that are presently assigned to platanoids or other families or determined within the morphological classification.

Phylogenetic relationships between taxa within the families Platanaceae and Hamamelidaceae and relationships between these families are a subject of long discussion. The first hypotheses concerning relationships between genera within these families were based on combinations of morphological (Wolfe, 1973; Skvortsova, 1975; Endress, 1989a, 1989b; Fang and Fan, 1993; etc.), cytological (Goldblatt and Endress, 1977), and palynological (Bogle and Philbrick, 1980) characters and other data on extant taxa. During the last decades, cladistic analysis has widely been used with reference to morphological characters to produce phylogenetic schemes of particular taxa (see, for example, Schwarzwalder and Dilcher, 1991; Radtke et al., 2005). Based on the newest molecular data treated by the cladistic method, a new angiosperm system was developed and phylogenetic relationships between groups reconstructed; these reconstructions in regard to the families Platanaceae and Hamamelidaceae turned out to be essentially different from the previous traditional systems (Chase et al., 1993; Hoot et al., 1999; Hilu et al., 2003; etc.).

Note that all the approaches listed to the creation of phylogenetic schemes ignored or insignificantly involved extinct taxa. Moreover, available paleobotanic data often conflict with the schemes proposed. However, the study of evolution is tightly connected with the factor of time and, hence, efficient reconstruction of relationships between taxa requires the use of paleobotanic data. An alternative approach implies the analysis of transitional conditions of characters in view of geological age of particular specimens (Maslova, 2001, 2004, 2007). Tentative schemes for the Platanaceae and Hamamelidaceae were developed based on fossil reproductive structures (which were determined most reliably with the use of the microstructural method) and published in the previous studies (Maslova, 2001, 2003).

In practice, phylogenetic schemes based on extant material alone, without taking into account time relationships (Skvortsova, 1975; Fang and Fan, 1993; etc.), are mostly conditional, proceeding from a priori ideas about evolutionary trends in particular characters, and attempts to find ancestral forms among living taxa are doomed to failure. The problem of relative primitiveness (least specialized condition) and advantage (most specialized condition) is solved in morphology of extant plants based on correlations between characters and general hypotheses about trends in the evolution of a group. A priori hypotheses of complication or reduction of morphological structures are frequently proposed without sufficient factual support.

As Rasnitsyn (2002, 2006b, etc.) has shown, modern taxonomy combines three major approaches: cladistics, phenetics, and phyletics, which essentially differ in the evolutionary basis and relation to the phylogenetic aspects of systematics.

Supporters of the cladistic approach believe that the system must reflect relationships irrespective of similarity in characters. Adherents of the phenetic systematics believe that the system should be based on quantitative criteria of similarities and dissimilarities irrespective of presumable relationships. The evolutionary systematics (or phyletics, as it was termed by Ponomarenko and Rasnitsyn, 1971) takes into account historical development of characters, not only relationships but also nonuniformity of the rate of divergence of characters (Krassilov, 1975; Rasnitsyn, 1983).

The systems constructed based on the traditional comparative morphological method and cladistic analysis may differ considerably, as has been shown using both botanical and zoological material. Comprehensive analysis of this discrepancy in taxonomic and phylogenetic constructions was performed by Rasnitsyn (1983, 1987, 1988, 1992, 1996, 2002, 2006a, 2006b, etc.). He has shown that the basic contradiction between cladistics and traditional systematics is underlain by the essential difference between two competitive paradigms, synthetic and epigenetic evolutionary theories. As the evolutionary process and its results are analyzed, it is necessary to make sense of differences between the paradigms used. Simultaneous use of incompatible principles and approaches would have resulted in erroneous conclusions.

From the point of view of the synthetic theory, the evolutionary process is stable reproduction of phenotypic features determined by genes and controlled by natural selection. Phenotypic features are considered to appear and change as a result of mutations and recombinations of genes. The epigenetic theory treats the evolutionary process as evolutionary changes in ontogeny (Shishkin, 1987, 1988, etc.). The foundation of this concept is inheritance of normal ontogeny rather than isolated characters. Various deviations from the norm (aberrations) result from latent heterogeneity of populations and are exposed to natural selection. Thus, an organism has a certain spectrum of probable developmental pathways, which Waddington (1942) called *creods*, and their aberrations.

In the last decades, the traditional comparative morphological approach to the study of phylogenetic relationships between taxa was almost completely replaced by the rapidly developing cladistic analysis (including the analysis of molecular data), which has become in essence a monopolist in taxonomic and phylogenetic studies. The cladistic method produces cladograms—the schemes reflecting the sequence of branching, which determines the rank of taxa. The system is strictly dichotomous; the analysis involves exclusively derived (synapomorphic) characters; sister groups are considered to be of equal rank (and, hence, equal extent of divergence); and, as two sister groups are formed, ancestral taxon disappears. Thus, cladis-

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tics is based on the synthetic evolutionary theory, regarding divergence as the major process and relationships as the only basis of the system.

Many examples provided by the practice of paleontological studies show that evolution is a much more complex and multifactor process, its laws are considerably more complex than simple dichotomous branching. The basic postulates of cladistics (divergence and evenness of evolution) are not supported by paleontological data, which, on the contrary, give evidence that ancestral taxa coexist with direct descendants and the evolutionary rates vary considerably. The minimization of the number of parallels in neighboring branches of a cladogram is a principle of cladistic analysis; however, there are many examples of parallel development in related branches of many groups of organisms, which are reliably supported by the fossil record (see, for example, Tatarinov, 1976; Ponomarenko, 2005; and others).

Molecular studies, which prevail in the modern systematics, follow the cladistic paradigm and the paradigm of the synthetic evolutionary theory; in essence, they ignore the achievements of traditional taxonomists—morphologists and pay very little attention to paleontological data; certainly, this impedes the construction of the most adequate system of living organisms. Results that do not fit into accepted ideas are merely ignored. Here, it is expedient to recollect the parable of a detachment of soldiers which march in step, such that break down a bridge due to resonance and, hence, cannot cross it; thus, the way out is a nonuniform rhythm of walking. With reference to the analysis of relationships between organisms, such a way out is probably correlation of the results obtained with the fossil record, which is taken for a criterion of soundness of these results and efficiency of particular methods.

As for cladistic ideas concerning relationships of platanoids and hamamelids, available phylogenetic schemes are contradictory and disagree with paleobotanic data. In particular, in the scheme for lower hamamelids, with the families Tetracentraceae and Trochodendraceae as outer groups, Schwarzwalder and Dilcher (1991) placed the family Platanaceae inside the Hamamelidaceae sensu lato, which was a sister group of the subfamily Altingioideae. According to these data, the family Platanaceae was one of the latest to deviate from the ancestral stem, which was preceded by a series of branches that gave rise to hamamelid subfamilies; however, fossil platanoids, dated Albian, conflict with this statement. The hamamelid subfamilies differentiated in the following sequence: Disanthoideae, Rhodoleioideae, Exbucklandioideae, Hamamelidoideae, and Altingioideae (the researchers cited ranked Disanthoideae and Exbucklandioideae as separate subfamilies); however, paleobotanic data suggest that characters of the subfamily Altingioideae appeared earlier. An alternative scheme, with the family Platanaceae as outer group,

has shown a different sequence of deviation of hamamelid subfamilies: Altingioideae and Exbucklandioideae, Hamamelidoideae, Disanthoideae, and Rhodoleioideae. This variant agrees with paleobotanic data with reference to the early appearance of Platanaceae; however, the position of Disanthoideae and Rhodoleioideae as relatively recently differentiated groups conflicts with paleobotanic data and generally accepted idea of the primitiveness of these subfamilies.

A number of cladistic schemes (see, e.g., Igersheim and Endress, 1998; Endress and Igersheim, 1999) confirms the establishment of the sister group Platanaceae—Proteaceae, while other cladistic studies (Doyle and Endress, 2000) place Platanaceae and Proteaceae, along with *Nelumbo* L., *Euptelea, Buxaceae*, and Trochodendraceae, at the base of eudicots.

It turned out that conclusions of cladistic analysis concerning relationships of the families Platanaceae and Hamamelidaceae change considerably depending on the set of taxa involved in the study. In particular, a number of schemes based on morphological characters confirm affinity of these families (Barabé et al., 1982; Barabé, 1984; Hufford and Crane, 1989; Schwarzwalder and Dilcher, 1991), while others reject this conclusion (Hufford, 1992).

Cladistic analysis is also applied to construct phylogenetic schemes based on molecular data. Although this field of research is relatively young, its results have been generalized and used as a basis for a new system of higher plants (APG, 2003), which is treated from the evolutionary point of view and differs considerably from traditional systems (Takhtajan, 1966, 1987; Cronquist, 1981; etc.). It is evident that comparative analysis of biopolymer sequences (proteins and nucleic acids) introduces a unique heuristic aspect in the knowledge of evolutionary history of plants. At different stages of the development of taxonomic and evolutionary studies, characters of different nature were used, the choice of which was determined among other things by contemporaneous technique and methodological level. The modern technique, which allows the study in detail of the mechanisms of the formation and functioning of molecules and their fragments, provide new important information. However, the presently dominating taxonomic and phylogenetic interpretation of molecular data, which is obtained at the analytical stage of investigation, is in conflict with creative discussions and gaining natural reconstructions. In addition, data processing generally accepted in molecular studies is based on a great number of a priori assumptions, the nonobvious character of which should be taken into account in the analysis of results. Advantages and shortages of the presently used molecular methods have been analyzed in detail in a number of works (Antonov and Troitsky, 1986; Goremykin et al., 1997; Antonov, 1999, 2000, 2007; Rokas et al., 2003; etc.). There is no need to provide here a complete list of these problems; however, it is noteworthy to indicate some points that suggest to treat with cau-

tion taxonomic and phylogenetic conclusions of molecular studies (in particular, those concerning the families Platanaceae and Hamamelidaceae, which are particularly contradictory).

The evolutionary treatment of molecular data, which is accepted in modern studies, in which phylogenetic changes in one or a few genes are considered to be the same as evolutionary history of organisms bearing these genes, remains questionable. A phylogenetic scheme constructed based on isolated DNA sequences shows evolutionary changes in this molecule in the group analyzed rather than evolution of this group.

There are a number of methodological aspects that should be taken into account in the treatment of taxonomic and phylogenetic results of molecular studies. First, special studies (for example, Bobrova et al., 1987) have shown that evolutionary rates differ in different phylogenetic lineages of individual genes, gene products of plants, and DNA from the nucleus, chloroplasts, and mitochondria; this casts doubt on the hypothesis of molecular clock, which forms the basis for the cluster analysis. Second, selection of homologous gene fragments in different groups of plants is complicated by the nature of genetic matter. It is known that genes may duplicate, with the formation of multigenic families, some of which change their function compared to ancestral genes and, hence, complicate considerably the recognition of proper homologous sites. The widespread introgressive hybridization between taxa of various rank and probable genetic polymorphism of ancestral forms make this task even more complex. The preparation of primary data, alignment of the nucleotide sequences analyzed, is particularly difficult in the case of plant groups that diverged long ago (Antonov, 2000) and fraught with unpredictable results (Sokolov, 2007). Moreover, genes show different (and sometimes insufficient) resolution to provide stable cladograms with many taxa (Kellog and Juliano, 1997; Duvall and Ervin, 2004), and the tree topology varies depending on the sample size of species (Rydin et al., 2002) and genes involved in analysis (Goremykin et al., 2003; Rokas et al., 2003). Taking into account the fact that all phylogenetic reconstructions of gene taxonomists are based on the comparison of neutral replacements (i.e., DNA sequences without adaptive phenotypic manifestation), it seems plausible to regard phylogenetic trees obtained in molecular studies as schemes of molecular rather than organism evolution. It is also noteworthy that gene taxonomists use taxonomic categories within the framework outlined by taxonomists—morphologists, i.e., the classification based on molecular data (APG, 2003) is in essence constructed based on taxa established by morphologists; this seems inconsistent from the methodological point of view.

In any event, the question of application and extension of results of particular studies always remains open. As the outstanding geneticist Prof. Antonov (2006, p. 173) indicated, "Actual significance

of these works [*based on molecular analysis*, remark of N.M.] consists merely in the description of the evolution of a certain DNA sequence, which is important for an understanding of general patterns of molecular evolution. We live in the epoch of the analysis and tentative (frequently, insufficiently substantiated) hypotheses; the time of final synthesis has not yet come." Certainly, this does not mean disregarding the results obtained by the molecular method, especially as they fit into the traditional concept. Apparently, the task of researchers is improvement of the technique, critical analysis of results, and correct use of these results in the resolution of taxonomic and phylogenetic questions. In general, the judgement of systematics concerning the data obtained based on molecular studies is determined primarily by the opinion concerning the ideology of cladistics rather than by the recognition or nonrecognition of the data analyzed (or particular techniques of molecular studies).

As for molecular concepts of the taxonomy and phylogeny of Platanaceae and Hamamelidaceae, as mentioned above, they are probably the most controversial groups in these studies because of considerable disagreements with morphological and paleontological data. The fossil record shows that molecular and paleobotanic data on the Platanaceae and Hamamelidaceae contrast considerably.

The study of the plastid *rbcL* gene has shown relationship between *Platanus* and *Nelumbo* (Nelumbonaceae), the geological history of which is known beginning from the Late Albian (Upchurch et al., 1994). In the analysis of the plastid *aptB* gene, *Platanus* is a sister group of the family Proteaceae (Savolainen et al., 1996). Subsequently, these results were repeatedly tested using various genetic markers and summary cladistic analysis of morphological and molecular traits; however, the results obtained remain controversial.

The family Platanaceae, along with the families Proteaceae and Nelumbonaceae (Proteales), is positioned at the base of eudicots, while Hamamelidaceae falls in the order Saxifragales, at the base of core eudicots (Soltis and Soltis, 1997; APG, 2003; Judd and Olmstead, 2004; Soltis et al., 2003, 2005; Qiu et al. 2005; etc.). A recent study of molecular and morphological characters of the order Saxifragales involved a number of extinct taxa (Hermsen et al., 2006). The schemes obtained were also controversial with reference to the position of some taxa. For example, according to Hermsen et al. (2006), the Late Turonian genus *Microaltingia* is related to Altingiaceae and *Cercidiphyllum*, while in the study of Zhou et al. (2001), who analyzed the matrix of morphological characters provided by Hufford (1992), the clade *Microaltingia*–Altingiaceae stands far apart from *Cercidiphyllum*. The study of the flower structure of the extant genus *Cercidiphyllum* has shown that it lacks morphological evidence of relationship with Saxifragales (Krassilov and Loven, 2007).

The data on the position of the Campanian genus *Allonia* in the phylogenetic schemes are also controversial (Magallón-Puebla et al., 1996; Hermsen et al., 2006). Hermsen et al. (2006) proposed that the disagreement probably results from the fact that molecular data are poorly informative.

Morphological data do not support with certainty close relationships of the families Nelumbonaceae, Proteaceae, and Platanaceae (Proteales) nor the assignment of the family Hamamelidaceae to the order Saxifragales. It was proposed that these groups were connected long ago and morphological distinctions are caused by extinction of transitional forms (Magallón and Sanderson, 2001, 2005; Judd and Olmstead, 2004). However, paleobotanic evidence of relationships between these taxa has not been obtained. On the contrary, the data on extinct predecessors of Platanaceae and Hamamelidaceae, which support the idea of their relationship, have been accumulated. When analyzing these data, it seems plausible to reconstruct phylogenetic relationships of these groups based on available paleobotanic studies.

Paleobotanic data provide information not only on the time of appearance of particular characters and their evolutionary trends, but also probable phylogenetic relationships between taxa. Nevertheless, it should be noted that phylogenetic schemes that are based on the geochronological sequence of extinct forms strongly depend on the completeness of the fossil record, reliability of geological dating of remains, and interpretation of morphological structures.

CHAPTER 6. PROBLEMS OF RELATIONSHIPS OF THE FAMILIES PLATANACEAE AND HAMAMELIDACEAE

The above phylogenetic schemes of the families Platanaceae and Hamamelidaceae, which are based on the chronological sequence of the appearance of taxa and transitional forms of characters of reproductive organs, have shown that, in general, their topology differs essentially and illustrates two alternative pathways of the evolution of ancient angiosperm families. Recent finds of fossil reproductive organs of platanoids, on the one hand, supplemented the previously proposed schemes (Maslova, 2003) and, on the other hand, provided new data that do not fit into these schemes. The last statement primarily concerns synthetic taxa, with mosaic sets of characters, which are typical for both Platanaceae and Hamamelidaceae and, hence, have not been assigned to any extant family. In addition, the recently established associations between leaves of the same morphotype and different reproductive structures referred to either platanoids or hamamelids also support affinity of the families considered and suggest to revise family affiliation of some fossil specimens. At present, it is evident that extinct platanoids and hamamelids are a polymorphic group of related forms that belong to extant and extinct families.

Phylogenetic relationships of Platanaceae and Hamamelidaceae have long been discussed. As mentioned above, based on the synthesis of extensive data provided by various fields of biology, these families have been combined in the order Hamamelidales, which occupies the central position in phylogenetic tree of dicotyledons (Takhtajan, 1966, 1987; Cronquist, 1981). Molecular studies placed Platanaceae and Hamamelidaceae in different orders (Proteales and Saxifragales, respectively), which are rather remote and, hence, exclude relationship between these families (Chase et al., 1993; APG, 2003; etc.). Although the system and relationships between particular taxa of angiosperms that are based on molecular data are widely accepted in modern studies, they remain vulnerable with reference to the confirmation by morphological and, particularly, paleobotanic data, which provide evidence in favor of the previous point of view (Takhtajan, 1966, 1987; Cronquist, 1981). In his last system of flowering plants, Takhtajan (2009), following molecular taxonomists, separated Platanaceae and Hamamelidaceae and placed them in different orders and subclasses.

The relationship between Platanaceae and Hamamelidaceae was initially established in the studies devoted to living representatives of these families, using morphological, anatomical, and biochemical characteristics (Tippo, 1938; Takhtajan, 1966; Jay, 1968; Cronquist, 1981; Zavada and Dilcher, 1986; Krassilov, 1989; Schwarzwalder and Dilcher, 1991; etc.). These studies mostly discussed whether these families are primitive or advanced and the extent to which platanoids are related to representatives of individual hamamelid subfamilies. In particular, Bretzler (1924) believed that Platanaceae is a more advanced family and, hence, placed it in the system after Hamamelidaceae. Brouwer (1924) proposed that Platanaceae occupy an isolated position among angiosperms. Based on anatomical studies, including wood, Tippo (1938) believed that Platanaceae is an advanced family in relation to Hamamelidaceae as well as Myrothamnaceae and Buxaceae. Hickey and Wolfe (1975) noted that platanoid leaf morphotypes appeared early in the fossil record and proposed that they were the first representatives of the lower hamamelid lineage. Cronquist (1981) indicated that platanoids and hamamelids were undoubtedly closely related and diverged from a common ancestral stem; the family Platanaceae was more primitive and differentiated earlier than the Hamamelidaceae. Wisniewski and Bogle (1982) believed that platanoids are most similar to the subfamily Altingioideae, although this is a convergent similarity.

The study of macro- and micromorphology of living representatives of the families Platanaceae and Hamamelidaceae corroborated the hypothesis of the closest affinity of platanoids to altingioids in a number

of characters of vegetative and reproductive organs (Wisniewski and Bogle, 1982) and provided an example of isomorphic polymorphism (Maslova, 1998). Moreover, as fossil material was involved in the analysis, it was shown that these groups have similar variation ranges of some characters, transitional forms of characters, and similar phylogenetic trends in the development of certain characters of floral structures (Maslova, 2007). In the previous studies, it was marked that living Platanaceae are similar in many morphological leaf characters to the subfamily Hamamelidoideae (Maslova, 2003). A number of similar structural characters are also observed in reproductive organs; however, characters of the flower structure, such as the apocarpous gynoecium composed of three to five carpels and single orthotropic ovule in *Platanus*, on the one hand, and the paired syncarpous carpels with many (or single) anatropous ovules in hamamelids, on the other hand, strongly suggest that living representatives of the two groups are independent and rather remote. The hypothesis of the common origin of the families Platanaceae and Hamamelidaceae is supported by the data of the fossil record, which has already provided representative material, isolated facts of which should be generalized.

6.1. Isomorphic Polymorphism, Exemplified by Platanaceae and Representatives of the Subfamily Altingioideae, Hamamelidaceae

The study of taxonomic diversity of fossil platanoid leaves and capitate reproductive structures and the analysis of the appearance and evolutionary pathways of changes in particular morphological structures (Maslova, 2001, 2003) have shown that it is necessary to perform a detailed comparative examination of living representatives of the families Platanaceae and Hamamelidaceae, in particular, the subfamily Altingioideae, and fossil remains of platanoid appearance. This study extended considerably the knowledge of variability of morphological characters of vegetative and reproductive organs of Platanaceae and Altingioideae and allowed us to compare variation series of individual characters to illustrate the phenomenon of isomorphic polymorphism, which is characteristic of platanoids and altingioids. The first examples of isomorphic polymorphism in the living plane tree and the genera *Liquidambar* and *Altingia* were provided by Krassilov (1976); subsequently, they were discussed in more detail, using the data on extinct taxa (Bogle, 1986; Maslova, 1998, 2003, 2007). The phenomenon of isomorphic polymorphism in the characters of leaves and heads of species of the genus *Platanus* and genera of Altingioideae are considered here as evidence of structural parallelism in the development of Platanaceae and Altingioideae, which suggests their probable relationship.

6.1.1. Leaves

The phenomenon of isomorphic polymorphism in Platanaceae and Altingioideae is well-pronounced, as their leaf morphology is considered. The study of morphological variability of leaves in these taxa has shown many characters, the variation ranges of which are surprisingly similar and the variation series constructed on this basis are almost identical. Isomorphism in leaf characters is observed at the levels of both species and genera (Fig. 5).

Lobate leaves, which are typical of the subgenus *Platanus* (Figs. 5e–5j), are similar in macromorphology to lobate leaves of *Liquidambar* (Figs. 5q, 5r, 5t–5w, 5y, 5z). The similarity is manifested 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), identical depth of the sinuses between lobes (Figs. 5e, 5r), similar shape of lobes (Figs. 5g, 5z), the presence of both simple and double dentation, and the presence of forms with well-pronounced scalariform or mostly reticulate tertiary venation.

The morphotypes of entire leaves with the pinnate venation, which are characteristic of *Platanus kerrii*, subgenus *Castaneophyllum* (Fig. 5k), and occur in *P. acerifolia* (Fig. 5a) and *P. racemosa* (Nixon and Poole, 2003), are comparable to laminas of the genus *Altingia* (Fig. 5l) and some morphotypes of *Liquidambar formosana* Hanse and *L. styraciflua* L. (Figs. 5m, 5s). Note that both leaves of *Platanus kerrii* and leaves of species of *Altingia* show a stable morphological pattern, with insignificant variations in macromorphological features. The morphological similarity of *Platanus kerrii* and species of *Altingia* is observed in the lamina shape, venation type, and the shape of marginal teeth. It is noteworthy that leaves of *Altingia*, along with glandular marginal teeth (for example, in *A. excelsa* Noronha) characteristic of Altingioideae, have concavo-convex teeth (*Altingia tachtadjanii* Trung.) characteristic of *Platanus*. Entire laminae are also observed in the Paleocene species *Platanus neptuni*.

Both variation groups (lobate leaves of *Platanus–Liquidambar* and entire leaves of *Platanus kerrii–Altingia*) occur in the genus *Semiliquidambar* and the species *Platanus acerifolia* (Fig. 1). Note that the two taxa are hybrids, intergeneric (*Semiliquidambar = Liquidambar × Altingia*) and interspecific (*Platanus acerifolia = P. orientalis × P. occidentalis*).

Along with macromorphological characters of leaves, these taxa show similar variations in anatomical characters. In particular, Ferguson (1989) has shown that, despite generally accepted idea that the stomata of *Liquidambar* are only positioned on the lower side of the lamina (Sharma and Tyree, 1973), they also occur on the upper side, where they are located mostly near the veins. The same picture is observed in *Platanus acerifolia*, some leaf morphotypes of which have stomata on the upper surface,
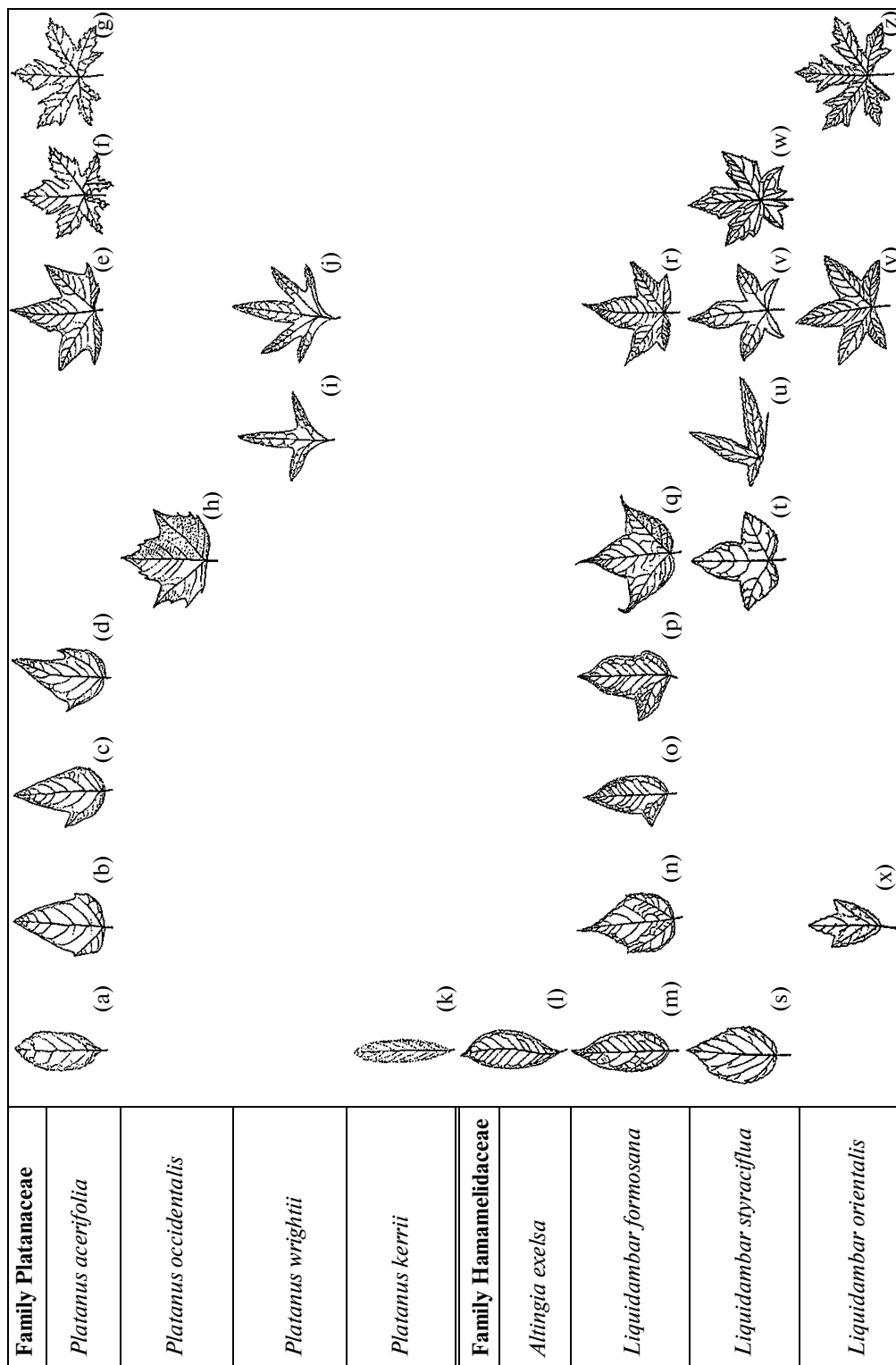
Fig. 5. Variations of the leaf lamina shape in representatives of the family Platanaceae and subfamily Altingioideae, Hamamelidaceae: (a–l, v) original herbarium; (m–r, u, w–z) Makarova, 1957: (m) pl. 11, fig. 2; (n) pl. 11, fig. 8; (o) pl. 11, fig. 3; (p) pl. 11, fig. 9; (q) pl. 11, fig. 1; (r) pl. 11, fig. 10; (u) pl. 1, fig. 5; (w) pl. 1, fig. 4; (x) pl. 11, fig. 13; (y) pl. 11, fig. 14; and (z) pl. 11, fig. 12; (s, t) Holm, 1930: (s) pl. 201, fig. 10; and (t) pl. 200, fig. 5; out of scale.

where they are also positioned close to the veins (Pl. 4, fig. 6). In addition, it should be noted that the Altingioideae have a paracytic type of the stomatal apparatus (Pan et al., 1990), while the stomata of *Platanus* are frequently classified as anomocytic (Metcalfe and Chalk, 1950). However, describing the platanoid stomata as anomocytic, Krassilov (1973b) indicated that, in *Platanus*, a pair of narrow paracytic subsidiary cells are occasionally present; Brett (1979) described the stomata of living *P. orientalis* as pleioparacytic. Carpenter et al. (2005) indicated that, along with the anomocytic stomata, *Platanus* has paracytic stomata. At

the same time, some representatives of the subfamily Hamamelidoideae are characterized by the anomocytic stomata (Pan et al., 1990), in contrast to the paracytic type, which is characteristic of hamamelids.

It has been shown that the adaxial leaf surface of extant *Platanus* have circular trichome bases, which have apertures strengthened by supplementary cuticular layers on the interior side of the cuticle (Carpenter et al., 2005). Similar cuticular structures occur around the stomatal apertures on the internal side of the leaf cuticle of *Liquidambar formosana*.

6.1.2. Reproductive Structures

The pistillate inflorescences and infructescences of living Platanaceae and Altingioideae differ considerably in external morphology, whereas the staminate heads retain similar exterior. As for their geological predecessors, modern paleobotanic studies show that, up to a certain stage of their historical development, the reproductive structures had been almost identical in appearance, and the range of their morphological variation was established based only on anatomical data.

The following morphological variants shared by extinct and extant Platanaceae and Altingioideae have been recognized based on generative organs: (1) flowers with a well-developed perianth (almost all fossil platanoids and many fossil altingioids)—naked flowers or flowers with an underdeveloped perianth (genus *Platanus*, extant altingioids, and the genus *Evacarpa*); (2) structurally unisexual flowers (some fossil platanoids, for example, *Platananthus* and *Friisicarpus*, and the extinct genus *Lindacarpa*)—structurally bisexual flowers (fossil flowers of the genus *Gynoplatananthus* and some infructescences of the extant genus *Liquidambar*, with well-developed stamens producing mature pollen grains: Ickert-Bond et al., 2005); (3) structurally unisexual heads (some extinct platanoids, for example, *Platananthus* and *Friisicarpus*, and the extinct genus *Lindacarpa*)—functionally unisexual heads, with rudimentary structures of the opposite sex (extant *Platanus* and extant genera of Altingioideae); (4) stable number of floral elements (most of the fossil Platanaceae, for example, pentastaminate flowers of the genus *Platananthus* and pentacarpellate flowers of the genus *Friisicarpus* and some living altingioids)—unstable number of floral elements (genus *Platanus* and some living altingioids); and (5) long anther filaments (fossil genus *Aquia* and extant genus *Liquidambar*)—short anther filaments (many extinct platanoids and extant *Platanus* and *Altingia*). Evolutionary trends in the development of reproductive structures of platanoids and hamamelids have been considered in detail in the previous study (Maslova, 2003). Platanoids and genera of Altingioideae share the following evolutionary trends in the development of reproductive structures: an increase in the diameter of inflorescences and infructescences, increase in the

size of fruits, reduction of the perianth, and an increase in size of pollen grains.

6.1.3. Isomorphic Polymorphism and Vavilov's Law of Homologous Series

The phenomenon of isomorphic polymorphism considered above is characteristic of Platanaceae and Altingioideae and provides an illustration of the law of homologous series developed by Vavilov (1921), which is possible to regard as a display of evolutionary parallelism and indirect evidence of affinity of platanoids and hamamelids.

The characters involved in the construction of homologous series are unequal, differ in taxonomic significance. The basic criteria for the estimation of morphological characters are the range of variation and boundary conditions, variation amplitude depending on the type of character, environment, and ontogenetic stage. Vavilov's law allows the arrangement of deviations from the norm in relatively regular series. Related plant groups show similar patterns of variation and similar trends of variability. The phenomenon of parallel variability allows one to predict the existence of certain ranges of variation of characters in poorly understood (or unknown) species by comparison with thoroughly investigated taxa. For example, based on the knowledge of variability of characters, such as the extent of development of the marginal dentation of the leaf lamina and the leaf size in *Betula verrucosa* Ehrh., the existence of variants with coarse teeth and forms varying in lamina size in some Siberian and Far East birches was predicted (Mamaev, 1969).

Thus, according to Vavilov's law, based on the knowledge of morphological variability in one species (genus), it is possible to predict the presence of similar series of morphotypes in another closely related species (genus). Vavilov arranged his data in tables, where each line corresponded to particular character and each column corresponded to a species. Vavilov used these tables for prediction of the existence of certain variants unknown at that time in certain living plant species. In addition, it was shown that the law is applicable not only to species of the same genus, but also to genera of different families. Tables 2 and 3 contain morphological characters of reproductive structures of extinct platanoids and hamamelids and genera combining characters of the families Platanaceae and Hamamelidaceae, which suggest that they share common morphogenetic basis.

The study of variability in morphological characters has displayed the entire set of conditions. The variation series obtained are particularly interesting as they are compared with each other (Fig. 5). These series should be compared not only with reference to the presence of identical elements, but also the presence of similar variations and trends in the transformation of characters (refrains). The variation range of

Table 2. Major diagnostic characters of pistillate inflorescences of fossil platanoids and hamamelids

Taxonomic grouping of the columns:

- **Hamamelidales**
  - **Platanaceae**
    - Gynoplatanoideae subfam. nov.: *Friisicarpus*, *Macginicarpa*, Infructescences associated with *Gynoplatananthus*
    - Platanoideae subfam. nov.: *Platanites*, *Tanyoplatanus*, *Platanus*
  - **Hamamelidaceae**
    - Insert subfam.: *Microaltingia*, *Viltyungia*
    - Altingioideae: *Evacarpa*, *Lindacarpa*, *Liquidambar*
    - Hamamelidoideae: *Acrhamamelis*
  - **Bogutchanhaceae fam. nov.**: *Quadriplatanus*
- **Sarbaicarpales ordo nov.**
  - Incert. fam.: *Anadyricarpa*, *Oreocarpa*
  - Sarbaicarpaceae fam. nov.: *Sarbaicarpa*
  - Kasicarpaceae fam. nov.: *Kasicarpa*

Characters of pistillate inflorescences / infructescences	*Friisicarpus*	*Macginicarpa*	Infructescences assoc. with *Gynoplatananthus*	*Platanites*	*Tanyoplatanus*	*Platanus*	*Microaltingia*	*Viltyungia*	*Evacarpa*	*Lindacarpa*	*Liquidambar*	*Acrhamamelis*	*Quadriplatanus*	*Anadyricarpa*	*Oreocarpa*	*Sarbaicarpa*	*Kasicarpa*
Capitate infructescence	+	+	+	+		+	+	+	+	+	+		+	+	+	+	+
5-merous gynoecium	+	+	+				+										
4-merous gynoecium					+								+				
3-merous gynoecium												+					
2-merous gynoecium									+	+	+						
Monomerous gynoecium														+	+	+	+
Unstable number of carpels in fruit																	
Perianth well developed	+	+	+		+		+	+		+		+	+	+			+
Perianth absent						+									+	+	
Tuft of hairs at the fruit base						+			+		+				+	+	
Stylodium present	+	+	+	+	+	+	+	+	+	+	+			+			
Stylodium absent													+			+	+
Sterile structures							+	+	+				+			+	
Single seed in carpel	+	+														+	+
Many seed in carpel							+	+	+		+						
Orthotropic seed	+	+															+
Anatropous seed							+				+					+	

Table 3. Major diagnostic characters of staminate inflorescences of fossil platanoids and hamamelids

Characters of staminate inflorescences	Hamamelidales																		Sarbaicarpales ordo nov.	
	Platanaceae								Insert subfam.		Hamamelidaceae				Bogutchanthaceae fam. nov.					Kasicarpaceae fam. nov.
	Gynoplatanoideae subfam. nov.				Platanoideae subfam. nov.						Hamamelidoideae								Pollen grains associated with *Oreocarpa*	Pollen grains associated with *Kasicarpa*
	Aquia	*Hamatia*	*Platananthus*	*Gynoplatananthus*	*Chemurnautia*	*Platanites*	*Platanus*	*Tricolpopollianthus*	*Microaltingia*	*Villyungia*	*Allonia*	*Androdecidua*	*Archamamelis*	Inflorescences associated with *Fortunearites*	*Archaranthus*	*Bogutchanthus*	*Quadriplatanus*	*Sarbaya*		
Capitate inflorescence	+	+	+	+	+	+	+	+	+	+				+	+	+	+	+		
5-merous flower	+	+	+	+							+	+		+						
4-merous flower	+						+								+	+	+	+		
Unstable number of elements in flower																				
Perianth well developed	+	+	+	+						+	+	+	+	+	+	+	+			
Perianth is tiny or absent																		+		
Long filament	+				+	+		+										+		
Short filament															+	+	+	+		
Tetrasporangiate stamens		+	+	+	+	+	+	+		+	+	+				+		+		
Bisporangiate stamens	+											+	+			+				
Well-developed connective extension		+	+	+			+	+			+	+	+		+	+	+			
Connective extension undeveloped					+					+			+	+		+				
Staminodia	+			+					+											
Rudimentary pistils			+																	
Tricolpate pollen grains		+	+	+	+	+	+	+	+		+	+	+	+	+		+	+	+	+
Pantocolpate pollen grains																+				
Tricolporate pollen grains		+								+						+		+		
Sporopollenin rim at colpi margin			+							+					+	+				
Reticulate exine		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Foveolate–reticulate exine	+																			

a character in closely related taxa may be closely similar, while dominant forms may differ, as follows from the law of Krenke.

According to Vavilov's law, the more closely related taxa are studied, the more complete concordance of their variations is observed. Opinions differ on the mechanism determining this similarity. In the above example of isomorphic polymorphism in platanoids and altingioids, it is important to emphasize the presence of similar variations in leaf and reproductive characters, which are manifested in both extant and extinct forms, while the identification whether these variations are provided by genetic or partially epigenetic mechanisms is the task of a special study.

The realization of different conditions of a character is determined by various factors, although the number of variants is restricted by the morphogenetic foundation. The presence of similar sets of variants suggests that they are controlled by similar morphogenetic foundation. It is probable that the more uniform morphogenetic foundation is retained, the greater number of identical characters and spectra of their conditions are provided and, hence, the establishment of parallel series of variation is indirect evidence of relationships between the forms examined. The conclusion about probable affinity of taxa depends directly on the completeness of homologous series and the number of characters with similar variation series. The more remote taxa are compared, the less pronounced parallelism in variation and the fewer number of shared characters are observed. The similarity in variation series of characters in different taxa is a prerequisite for similar evolutionary pathways in the development of characters, that is, for similar evolutionary trends.

Certainly, the uniform morphogenetic foundation promotes the manifestation of parallel variations. However, similar phenotypes may be inherited from a common ancestor or appear independently. Phenotypic similarity does not necessarily mean genotypic similarity and, vice versa, identical genotypes do not necessarily mean identical phenotypes. Taking into account the fact that, at present, molecular data are insufficient for comprehensive comparison of genotypes of taxa under study and a certain character is controlled by a gene network, which may have a changeable configuration (see a review in Kolchanov and Suslov, 2006), rather than encoded by a single gene (i.e., there is no univocal correspondence between a gene and a character), it is difficult to recognize whether morphological similarity of taxa results from common origin or homoplasy.

Vavilov formulated the law of homologous series based on the study of variability in morphological characters of living plants, i.e., contemporaneous plants. Subsequently, it turned out that the law is applicable to various biological objects and various chronological ranges. In particular, using Cambrian archaeocyaths as an example, Rozanov (1973) has shown that the establishment of homologous variation is of great importance for the systematics of organisms (construction of Vavilov's tables made possible to predict the existence in the geological past of many previously unknown archaeocyath forms) and allows one to estimate the completeness of the fossil record and validity of data on particular groups. Parallel variability has also been studied based on other paleontological objects (see, e.g., Tatarinov, 1976; Ponomarenko, 2005; Rozhnov, 2005).

In platanoids and hamamelids, variation series of particular characters were considered using extant and all known fossil taxa; as a result, uniform trends in the development of characters were recognized, although they remained uncertain as living forms alone were investigated. The phenomenon of isomorphic polymorphism in Platanaceae and Altingioideae is considered here as evidence of structural parallelism in the development of these plant groups, which is caused by the morphogenetic basis inherited by these groups. This is confirmed by (1) many identical characters of vegetative and generative organs of these plants, which are recorded over a long geological time (it is possible to regard these characters as either new formations or manifestation of latent opportunities); (2) fusion of floral structures (for example, the formation of staminate and floral tubes) in both groups; and (3) uniform phylogenetic trends in the development of a number of characters of reproductive organs. It is important that the similar variations in the development of characters of Platanaceae and Altingioideae concern not only individual macromorphological characters, but also a number of anatomical characters as well as leaves (which are relatively simple in organization) and complex structures, such as inflorescences (infructescences) and flowers.

6.2. Paleobotanic Evidence of Relationships between Platanaceae and Hamamelidaceae

To date, extensive paleobotanic data have been accumulated in favor of the existence in the geological past of a common polymorphic ancestral group of Platanaceae and Hamamelidaceae, which was subsequently divided into a number of separate lineages. They include fossil remains of leaves and reproductive structures combining diagnostic characters of both families. In addition, the common origin of the extant families is supported by the co-occurrence of particular plant organs, which were tentatively assigned to the same individual combining diagnostic characters of different families.

6.2.1. Extinct Taxa Combining Characters of the Families Platanaceae and Hamamelidaceae

6.2.1.1. Leaves. As for leaf remains that display more or less pronounced characters of Platanaceae and Hamamelidaceae, they are assigned to one of

these families, to a group of platanoid genera (Vakhrameev, 1976), or determined to order. New data have recently been reported on the association of some of these leaves with the reproductive structures varying considerably in micromorphology (Krassilov and Shilin, 1995; Maslova, 2002a; Maslova and Kodrul, 2003; Maslova and Herman, 2004, 2006; Maslova et al., 2005, 2007); this, along with other data, suggests to identify these leaf remains within the framework of the morphological system, which is independent of the natural system of angiosperms (Maslova et al., 2005; Kodrul and Maslova, 2007). This primarily concerns the genera *Ettingshausenia* and *Platimeliphyllum*, which combine characters of both platanoids and hamamelids and show wide polymorphism of the major leaf characters. Leaves of these morphological genera could have belonged to Platanaceae, Hamamelidaceae, or plants of certain extinct families. Note that mosaic combinations of leaf characters of Platanaceae and Hamamelidaceae are observed at both macro- and micromorphological levels.

The overwhelming majority of representatives of the genus *Ettingshausenia* show mostly macromorphological characters of the living plane tree; therefore, they were usually referred to the extant genus *Platanus*. At the same time, these leaves show a significant proportion of macromorphological characters of hamamelids. In particular, Late Albian–Early Cenomanian *Ettingshausenia louravetlanica* has an asymmetrical lamina, with an asymmetrical base, asymmetrical deviation of the basal veins, which differ in length and thickness, and mostly orthogonally reticulate tertiary venation (Moiseeva, 2010). The characters listed are characteristic of some hamamelid genera. The suprabasal deviation of the basal veins and well-pronounced infrabasal veins suggest that *E. louravetlanica* is related to platanoids.

Lobate leaves that Shilin (1986) described as *Platanus pseudoquillelmae* Krass. and *P. cuneiformis* Krass. are in general characterized by macromorphological features typical of leaves of *Platanus*. At the same time, a number of features (relatively densely spaced veins positioned between the secondary veins and reaching approximately the middle of the distance to the lamina margin and well-developed marginal glands) show that they are related to Altingioideae. In addition, the epidermal structure of these leaves shows characters typical of Fagaceae (Krassilov and Shilin, 1995).

Another genus which is better to identify based on the morphological classification is *Platimeliphyllum* (Maslova, 2002a; Kodrul and Maslova, 2007). Leaves of the genus *Platimeliphyllum* are highly polymorphic with reference to macromorphological characters and combine characters typical of the families Platanaceae and Hamamelidaceae. The Hamamelidaceae included in comparative analysis belong mostly to extant genera of the subfamily Hamamelidoideae (*Hamamelis, Parrotia*, etc.). Leaves of *Platimeliphyllum* are similar to Platanaceae in the presence of typical suprabasal deviation of well-developed basal veins, basiscopic branches of which terminate craspedodromously, well-developed infrabasal veins, and concavoconvex teeth, the basal side of which is longer. The following characters are shared with Hamamelidaceae: asymmetry of the lamina and its base, poorly developed basal veins, camptodromous basiscopic veins, and low obtuse teeth.

The combination in a number of taxa of macromorphological characters of the two families is supplemented by epidermal characters. In particular, Early Paleocene *Platimeliphyllum valentinii* (Kodrul and Maslova, 2007) combine the anomocytic stomata, which are typical of platanoids, with strongly sinuous anticlinal walls of the ordinary epidermal cells, which are recorded in entire leaf morphotypes of living *P. acerifolia* (Maslova et al., 2008b). This character is also observed in Paleocene–Eocene *Platanus neptuni* (Bůžek et al., 1967; Kvaček and Manchester, 2004). On the one hand, the sinuosity of cell walls depends on a number of microclimatic factors (Zalensky, 1904; Shennikov, 1950; etc.), on the other hand, this character is correlated with the entire leaf lamina (Maslova et al., 2008b). This shape of ordinary epidermal cells (with strongly sinuous, up to amebiform, walls) is a diagnostic character of some species of extant hamamelid genera, for example, *Altingia, Liquidambar, Sinowilsonia, Distylium*, etc. (Pan et al., 1990). The main difference in epidermal characteristics of living representatives of the families Platanaceae and Hamamelidaceae is the stomatal type, which is usually anomocytic in the plane tree and paracytic in the majority of hamamelids (less often, cyclocytic or anomocytic). Among extant Hamamelidaceae, the anomocytic stomatal apparatus is recorded in a number of species of the subfamily Hamamelidoideae (Pan et al., 1990). Pan et al. (1990) have shown that the stomatal type correlates with other epidermal characters (for example, the extent of sinuosity of the anticlinal walls of ordinary epidermal cells). In addition, in both extinct and extant platanoid stomata, the guard cells are markedly raised above the surface of the ordinary epidermal cells to form a cylindrical (ring-shaped in projection) elevation (Van Horn and Dilcher, 1975; Maslova, 1997; Maslova et al., 2008b). The same features of the stomatal apparatus are observed in some hamamelids (Pan et al., 1990). The similarity is also manifested in the type of cuticular ornamentation (ring-shaped, striate) of the guard cells.

Among leaves combining macromorphological characters of the families Platanaceae and Hamamelidaceae, the genera *Platimelis* (Golovneva, 1994) and *Evaphyllum* N. Maslova (Maslova, 2003) are of particular interest. The same combination of characters is observed in some platanoids (Vakhrameev, 1976). For example, *Credneria grewiopsioides* Hollick from the Cretaceous of Sakhalin (Kryshtofovich and Baikovskaya, 1960) differs from the type material in the pronounced asymmetry of the leaf lamina and the

lower deviation of the basal veins, which differ in length. These characters combined with the low, wide, and widely spaced marginal teeth, the sinuous secondary veins, and weak tertiary veins are characteristic of hamamelids. Unfortunately, cuticular—epidermal data have not been obtained for the majority of platanoid genera, which could have contributed to the identification of the family of these forms. Note that the species *Protophyllum ignatianum* Krysht. et Baik. combines macromorphological characters resembling platanoids with the epidermal characters typical for hamamelids (genus *Liquidambar*) (Krassilov, 1973b).

6.2.1.2. Reproductive structures. In the light of the problem discussed, fossil reproductive structures combining the characters of Platanaceae and Hamamelidaceae are particularly interesting. This primarily concerns the general structural pattern of capitate inflorescences and infructescences. However, along with the uniform pattern of external morphology, there are combinations of the major diagnostic characters of compound inflorescences and infructescences of the two families, based on which it is impossible to assign particular specimens to a certain family. These finds combining characters of both families were considered to belong to the order Hamamelidales. They comprise capitate inflorescences and infructescences from the Turonian beds of the Raritan Formation, New Jersey (Crepet et al., 1992; Crepet and Nixon, 1996), infructescence of *Kasicarpa* from the Turonian of the Chulym—Yenisei Depression (Maslova et al., 2005), staminate inflorescences of Early Paleocene *Bogutchanthus* from the Amur Region (Maslova et al., 2007), and infructescence of Cenomanian—Turonian *Sarbaicarpa* from northern Kazakhstan (Maslova, 2008c). In the present study, these specimens are considered within the framework of new extinct families and order.

Order Hamamelidales, Family Bogutchanthaceae fam. nov.

(1) Genus *Bogutchanthus*. The genus *Bogutchanthus* (Maslova et al., 2007) from the Early Paleocene of the Amur Region is also characterized by an unusual combination of characters of reproductive organs typical of platanoids and to an even greater extent to hamamelids, in particular, the subfamilies Hamamelidoideae and Exbucklandioideae as well as Altingioideae (Table 4). In the present study, the genus *Bogutchanthus* is assigned to a new family, Bogutchanthaceae fam. nov., of the order Hamamelidales, which comprises fossil reproductive structures with tetramerous flowers.

The similarity to platanoids is manifested in the general morphology of the compound capitate inflorescence, the differentiated perianth (as in fossil platanoids), irregular development of pollen sacs within a single theca, and in the presence of intrafloral staminodia. In the living plane tree, the heads are very dense, consisting of a relatively massive core and radially

Table 4. Characters of the reproductive system of the families Platanaceae and Hamamelidaceae, observed in the genus *Bogutchanthus* (Bogutchantaceae fam. nov.)

Platanaceae		Bogutchanthaceae	Hamamelidaceae	
extinct	extant	*Bogutchanthus*	extinct	extant
+	+	capitate inflorescence	+	+
		loose inflorescence		+
+		well-developed perianth	+	+
	+	staminodia	+	+
+	+	tetrasporangiate stamens	+	+
		bisporangiate stamens	+	+
	+	varying size of pollen sacs		
		pantocolpate pollen grains	+	+

attached flowers; the flowers are densely packed, so that outlines of individual flowers are almost indiscernible. In fossil platanoids with relatively well-developed perianths (e.g., the genus *Platananthus*), flowers are distinctly outlined; although the heads are very dense. In the inflorescence of *Bogutchanthus*, flowers are arranged freely, loosely; the boundaries of individual flowers are more or less distinct; in addition, *Bogutchanthus* displays a free arrangement of stamens in the flower, which has not been recorded in extinct and extant representatives of the family Platanaceae.

The perianth of *Bogutchanthus* is half as long as the flower. It is differentiated into external and internal elements. In the first, the epidermis consists of cells arranged in longitudinal rows and varying in shape from square or trapezoid to extended rectangular, with strongly cutinized walls. In the internal elements, the epidermis is poorly cutinized, formed of more or less isodiametric polygonal cells and many hairs and scarce stomata. The majority of researchers believe that flowers of the living plane tree lack a well-developed perianth (a diagnostic character of this genus); however, in the overwhelming majority of fossil platanoids, the perianth is well developed, frequently differentiated. Among platanoid genera established based on staminate inflorescences, a more or less developed perianth is observed in the genera *Aquia* (Albian: Crane et al., 1993), *Platananthus* (Albian—Eocene: Manchester, 1986; Friis et al., 1988; Pigg and Stockey, 1991), and *Hamatia* (Albian: Pedersen et al., 1994). The extremely reduced perianth is recorded in the genus *Chemurnautia* (Late Paleocene: Maslova, 2002a).

Bogutchanthus differs from all known platanoid genera in the free arrangement of stamens in the flower. In living *Platanus* and Cretaceous representatives of Platanaceae, floral elements are usually

densely packed. An exception is the genus *Chemurnautia*, the pollen sacs of which are relatively freely arranged and fused at the base. This flower structure prevented the determination of the number of flowers in an inflorescence and the number of stamens in the flower of *Chemurnautia*.

The pollen sacs of *Bogutchanthus* from one stamen occasionally differ in size and shape (ranging from narrow, elongated, with almost parallel margins to asymmetrical crescentic); as a result, the stamen is often asymmetrical. Unequal development of pollen sacs from one theca and, hence, asymmetrical thecae occur in the living plane tree (Hufford and Endress, 1989); however, in *Platanus*, this character is less pronounced and the sac shape is relatively stable. In the elongated pollen sacs with parallel margins, *Bogutchanthus* is similar to extant *Platanus* and extinct *Chemurnautia*; however, along with this shape, *Bogutchanthus* also has crescent sporangia. In addition, in the presence of basally fused pollen sacs, *Bogutchanthus* resembles *Chemurnautia*, the narrow linear pollen sacs of which are partially fused at the base, diverging in the middle part, and do not form distinct thecae.

Stamens of the genus *Bogutchanthus* have a narrow connective and poorly developed connective extension, which lack hairs and stomata. The majority of fossil platanoids have more or less developed connectives, which pass into triangular conical connective extensions. The connective extensions range widely from poorly developed in *Aquia brookensis* (Crane et al., 1993) to more or less massive, varying in shape: conical in *Platananthus synandrus* (Manchester, 1986) and *P. speirsae* (Pigg and Stockey, 1991); triangular in *P. scanicus* (Friis et al., 1988); flattened in *P. hueberi* (Friis et al., 1988); or peltate in *P. potomacensis* (Friis et al. 1988). Nonpubescent connectives are also observed in *P. potomacensis, P. scanicus*, and *P. speirsae*.

The staminodia of *Bogutchanthus* are positioned between mature stamens and elements of the perianth, which were probably partially fused at the base. Thus, they resemble in shape mature stamens. The functionally unisexual flowers of some platanoids and hamamelids occasionally have rudimentary structures of the opposite sex (underdeveloped stamens (staminodia) in pistillate flowers and rudimentary pistils in staminate flowers). Pistillate flowers of the living plane tree contain rare staminodia; the presence of staminal appendages interpreted as staminodia is also observed in staminate flowers of *Platanus* (Magallón-Puebla et al., 1997).

Pantocolpate pollen grains, which are characteristic of the genus *Bogutchanthus*, occur in living *Platanus occidentalis* as an aberration (Zavada and Dilcher, 1986). In ultrastructural features of the exine, *Bogutchanthus* is similar to both platanoids and hamamelids (Tekleva, 2007).

Bogutchanthus is similar to extant and extinct Hamamelidaceae in characters of general morphology of the inflorescence and in the presence of the flower tube, secondarily bisporangiate stamens, staminodia, and pantocolpate pollen grains. In the ability of forming capitate inflorescences, the presence of bisporangiate anthers and pantocolpate pollen grains, *Bogutchanthus* is most similar to the extant genus *Chunia* (subfamily Exbucklandioideae). Among fossil Hamamelidaceae, the Cenomanian genus *Viltyungia* (which shows characters of three hamamelids subfamilies: Exbucklandioideae, Altingioideae, and Hamamelidoideae) is most similar to *Bogutchanthus* in the shape of inflorescences, the presence of staminodia, and in the type of pollen grains; however, *Viltyungia*, shows a much greater proportion of characters of Exbucklandioideae.

A distinctive feature of *Bogutchanthus* is the loose arrangement of flowers in the inflorescence and stamens in the flower; these characters are atypical for platanoids, but usually occur in hamamelids and are recorded in *Liquidambar acalycina* H.-T. Chang, Altingioideae (Ickert-Bond et al., 2005).

In the basal part of the flower of *Bogutchanthus*, elements of the perianth tightly adjoin each other and the flower tube is possibly formed, which becomes broken as it moves towards the apex of the mature flower. Flowers of extant Hamamelidaceae usually have a double 4—5-merous perianth, with the calyx and corolla developed to varying extent. Elements of the perianth are free or fused to a greater or lesser extent to form a tube; sometimes, they are partially fused with the stamens and ovary (Bogle, 1970). In the genera *Parrotia* and *Fothergilla* (subfamily Hamamelidoideae), elements of the perianth are basally fused with the stamens, forming the hypanthium; in *Dicoryphe* (subfamily Hamamelidoideae), the androecium and petals are fused in a circle (Bogle, 1970). Living hamamelids with capitate reproductive structures lack well-developed perianths. Only in the genus *Exbucklandia*, the calyx is detached at early ontogenetic stages; flowers of Altingioideae are apetalous (Bogle, 1986). Fossil capitate inflorescences and infructescences assigned or positioned close to Altingioideae usually have a well-developed perianth. In particular, the perianth of *Lindacarpa* was attached somewhat above the base of the gynoecium and covered the flower over almost the entire length (Maslova and Golovneva, 2000a). In the genus *Viltyungia*, which displays the characters of three subfamilies (Altingioideae, Exbucklandioideae, and Hamamelidoideae), the perianth is well developed, consists of different elements: the internal elements are narrower and the external elements are wide, supplied with hairs (Maslova and Golovneva, 2000b). Ancient Hamamelidoideae vary in the extent of development of the perianth. For example, the genus *Allonia* (Magallón-Puebla et al., 1996) is distinguished by the well-developed corolla, which consists of narrow petals with parallel margins, with irregularly developed elements of the calyx. In flowers of *Androdecidua*, petals of the corolla are spindle-shaped, with narrowed bases and

apices, partially fused with the stamens of the external circle of the androecium (Magallón-Puebla et al., 2001). In *Archamamelis*, a differentiated 6—7-merous perianth with triangular, basally wide petals was described (Endress and Friis, 1991). Note that elements of the perianth and staminodia of *Bogutchanthus* are fused at the base, resembling partial fusion of petals with the stamens of the external circle of the androecium, which was described in the extinct genus *Androdecidua* and some extant Hamamelidaceae, for example, *Parrotia* and *Fothergilla* (Bogle, 1970). Magallón-Puebla et al. (1997) indicated that the staminal tubes were formed with the participation of elements of the perianth in living representatives of Hamamelidaceae, the genera *Embolanthera* and *Dicoryphe*.

The androecium of *Bogutchanthus* is formed of four free stamens, with a poorly pronounced filament and almost sessile anther. The stamens are primarily tetrasporangiate; however, as becoming mature, they look bisporangiate because the septa between locules of anthers disappear. The presence within one head of both tetrasporangiate and bisporangiate stamens is considered to be a result of nonsimultaneous maturation. In almost all living Hamamelidaceae, the stamens are tetrasporangiate; the theca with one locule is only observed in the genera *Hamamelis* (Shoemaker, 1905) and *Exbucklandia* (Kaul and Kapil, 1974). A distinctive feature of the androecium of the extinct genus *Androdecidua* (subfamily Hamamelidoideae) is different morphology of stamens in the external and internal circles. The stamens of the external circle have bisporangiate anthers, while the stamens of the internal circle have tetrasporangiate anthers. Bisporangiate stamens have been described in the Santonian—Campanian genus *Archamamelis*, subfamily Hamamelidoideae (Endress and Friis, 1991). The genus *Bogutchanthus* has both pollen sacs with parallel margins and asymmetrical pollen sacs in the shape of a crescent. This shape of pollen sacs is known in the extant genus *Disanthus* (Exbucklandioideae, Hamamelidaceae) and the Turonian genus *Viltyungia*, which combines characters of the subfamilies Exbucklandioideae, Altingioideae, and Hamamelidoideae and has pantocolpate pollen grains, identical to those of *Bogutchanthus*.

The staminodia of *Bogutchanthus*, which resemble in shape mature stamens, are positioned between the stamens and elements of the perianth and probably partially fused with them at the base. The staminodia are present in pistillate flowers of the genera *Altingia* and *Liquidambar* of the subfamily Altingioideae (Bogle, 1986) and *Rhodoleia* of the subfamily Rhodoleioideae (Bogle, 1987). Bisexual flowers of some living hamamelids, for example, the genus *Maingaya* (Bogle, 1984), have both normally developed stamens and staminodia. It was also indicated that two functionally different circles of the androecium (with normally developed stamens in the external circle and sta-

minodia in the internal circle) are present in tetramerous flowers of *Dicoryphe* and *Hamamelis* and pentamerous flowers of *Ostrearia* Baill. (Magallón-Puebla et al., 1996).

In fossil hamamelids, the staminodia have been described in the genera assigned or positioned close to the subfamilies Altingioideae, Hamamelidoideae, and Exbucklandioideae. The synthetic genus *Viltyungia*, which combines characters of these three subfamilies, has bisexual flowers with the staminodia producing abundant small pollen grains, smaller than pollen grains produced by normally developed stamens. Among Altingioideae, the staminodia have been described in the genus *Evacarpa*. In the subfamily Hamamelidoideae, the staminodia are known in the Santonian—Campanian genus *Archamamelis* and Eocene staminate capitate inflorescences, which are considered to be related to *Hamamelis* and *Corylopsis* based on a number of characters (Manchester, 1994).

The genus *Bogutchanthus* is characterized by small pollen grains mostly of pantocolpate type, with a reticulate sculpture. Grains with six colpi prevail, although small proportions of grains with 7, 4, and 3 colpi are also present. The majority of genera of extant Hamamelidaceae and Platanaceae have tricolpate pollen grains, similar in external morphology. However, some hamamelid genera are distinguished by pantocolpate pollen grains. In particular, among living hamamelids of the subfamily Hamamelidoideae, *Distylium*, along with short colpi with rounded ends, has up to ten rugae or pores; *Matudaea* displays diverse pollen grains, ranging from tetracolpate to 12-rugate; *Sycopsis* is characterized by the apertures varying from more or less elongated rugae to rounded pores (Bogle and Philbrick, 1980). The genus *Parrotia* also shows morphological variations in pollen grains; tricolpate pollen grains prevail, but bicolpate, tetracolpate, and periporate pollen grains are also present. This variability in the number of colpi is observed in both living and extinct species of *Parrotia* (Binka et al., 2003). In the subfamily Exbucklandioideae, the genus *Chunia* displays both tricolpate and tetra- and hexarugate pollen grains. The pantocolpate type of pollen grains was described in the Cenomanian genus *Viltyungia* (Maslova and Golovneva, 2000b).

Pollen grains of *Bogutchanthus* are fine reticulate, as in the majority of Cretaceous—Paleogene and Recent platanoids and some extinct and extant hamamelids; the reticulum is in general uniform within a pollen grain; the margin of colpi is formed by a continuous sporopollenin rim. This character is also observed in *Archaranthus krassilovii* (Bogutchanthaceae fam. nov.), *Platananthus scanicus, P. speirsae, P. synandrus* (Platanaceae), and a number of living hamamelids (Bogle and Philbrick, 1980).

(2) Staminate inflorescences and infructescences (after Crepet et al., 1992). A mosaic combination of characters is observed in capitate inflorescences and infructescences from the Turonian beds of the Raritan

Table 5. Characters of the reproductive system of the families Platanaceae and Hamamelidaceae, observed in the genus *Sarbaicarpa* (Sarbaicarpaceae fam. nov.)

Platanaceae		Sarbaicarpaceae fam. nov.	Hamamelidaceae	
extinct	extant	*Sarbaicarpa*	extinct	extant
+	+	capitate inflorescence	+	+
	+	simultaneous maturation of fruits		
	+	perianth is tiny or absent	+	+
+	+	tuft of hairs at the fruit base		
+	+	monocarpellate gynoecium	+	+
	+	sterile structures	+	+
		anatropous seed	+	+
+	+	solitary seed in carpel	+	+
		well-developed endosperm		+

Formation, New Jersey (Crepet et al., 1992). Pistillate inflorescences displaying the characters typical for hamamelids (bicarpellate syncarpous ovary, well-developed perianth, and presence of staminodia, which probably perform nectariferous function) are associated with staminate heads, which mostly display characters of platanoids (capitate shape and unisexual nature of inflorescences, densely packed stamens in the flower, widely triangular apical expansion of the connective, and reticulate tricolpate pollen grains); however, the formation of the staminal tube suggests that they are similar to some hamamelids.

(3) Genus *Quadriplatanus*. In the original description, the genus *Quadriplatanus* was referred to the family Platanaceae, since, in opinion of the authors of this genus (Magallón-Puebla et al., 1997), most of the characters of its inflorescences and infructescences corresponded to Platanaceae. Because *Quadriplatanus* combines diagnostic characters of platanoids and hamamelids, I assign it to the new family Bogutchanthaceae fam. nov. The genus *Quadriplatanus* is similar to the subfamily Gynoplatananthoideae subfam. nov. of the family Platanaceae in the regularity of the floral elements (four in *Quadriplatanus* in contrast to five in Gynoplatananthoideae subfam. nov.), a well-developed perianth, and tricolpate pollen grains. In *Quadriplatanus*, well-developed stamens are fused with staminodia to form the staminal tube, which is compared by the authors with the presence of a similar relatively massive tissue ring, which is formed by the basal fusion of the stamens and staminodia in the living plane tree. In the formation of the staminal tube by the basal fusion of stamens and staminodia, inflorescences of *Quadriplatanus* are also similar to Turonian inflores-

cences displaying characters typical for both Platanaceae and Hamamelidaceae (Crepet et al., 1992; Crepet and Nixon, 1996). The fusion of stamens and staminodia over a long extent, which results in the formation of the staminal tube, is a distinctive character of some living representatives of the family Hamamelidaceae (Endress, 1977). Magallón-Puebla et al. (1997) marked that, in this character, the genus *Quadriplatanus* is similar to the genera *Embolanthera, Dicoryphe*, and *Mytilaria* (Hamamelidaceae). The non-orthotropic seed type also distinguishes the genus *Quadriplatanus* from platanoids with orthotropic seeds.

Order Sarbaicarpales ordo nov.

(1) Family Sarbaicarpaceae fam. nov., genus *Sarbaicarpa*. Infructescences of *Sarbaicarpa* are characterized by a mosaic combination of characters, which are diagnostic to both *Platanus* and some Hamamelidaceae (Table 5). The genus *Sarbaicarpa* is similar to the living plane tree in the capitate infructescence, the absence of a well-developed perianth, the presence of a tuft of hairs at the fruit bases, more or less simultaneous maturation of fruits in the infructescence, single seed in the fruit, and the presence of sterile structures in the infructescence. Living representatives of the genus *Platanus* differ from *Sarbaicarpa* in the much greater number of flowers per inflorescence (up to 300), the greater number of apocarpous carpels per flower (5—9), the presence of hairs on the fruit surface of the majority of species, the smaller size and different shape of sterile structures, and the orthotropic seed type. The main difference of ancient platanoid genera from *Sarbaicarpa* is also the greater number of carpels per flower, five in *Friisicarpus* (Friis et al., 1988) and *Macginicarpa* (Manchester, 1986). The genus *Friisicarpus* is characterized by the orthotropic seed type, whereas seeds of *Sarbaicarpa* are anatropous.

Among Hamamelidaceae, *Sarbaicarpa* is most similar to extant genera of the subfamily Altingioideae and related extinct genera as well as representatives of Hamamelidoideae. The similarity to extant Altingioideae is observed in the number of flowers per head, the absence of a perianth, the presence of the monocarpellate gynoecium, the anatropous seed type, the structure of the spermoderm, and the presence of sterile structures in the infructescence.

In the number of fruits per infructescence (up to 30), the genus *Sarbaicarpa* resembles the extant genera *Altingia* (up to 25 flowers) and *Liquidambar* (from 26 to 40). Miocene *L. changii* has approximately 25—30 fruits. The majority of capitate inflorescences and infructescences have a very dense structure, so that it is often difficult (or impossible) to determine with certainty the number of flowers in the head. For example, heads of the living plane tree are very dense, flowers are densely packed, the boundaries of individual flowers are almost indiscernible. In fossil platanoids with a well-

developed perianth (e.g., the genera *Platananthus* and *Friisicarpus*), the boundaries of flowers are distinct, although the heads are also very dense. It has been indicated that infructescences of extant *Liquidambar* vary in density depending on the extent to which the carpels are fused (Ickert-Bond et al., 2005). In the majority of species, bilocular fruits are cuneate or spindle-shaped, fused basally to a greater or lesser extent and free distally; however, in *L. acalycina* (and the related genus *Altingia*), fruits are relatively free, unfused, and, when compressed mechanically, come apart (Ickert-Bond et al., 2005, 2007). In the external arrangement of the infructescence, its density, and the fruit shape, the genus *Sarbaicarpa* is similar to *Liquidambar acalycina.*

In the presence of flowers without a perianth, the genus *Sarbaicarpa* is comparable to living representatives of the subfamily Altingioideae, which is also characterized by naked flowers, lacking perianth elements even at early ontogenetic stages (Wisniewski and Bogle, 1982). In this subfamily, the bicarpellate gynoecium predominates, although monocarpellate forms, which are usual in *Sarbaicarpa*, have also been recorded (Wisniewski and Bogle, 1982; Bogle, 1986). The similarity between *Sarbaicarpa* and extant and extinct Altingioideae is also manifested in the fruit shape. The fruit of *Sarbaicarpa* is widely cuneate, with a conical base. A similar fruit base has been described in the Coniacian genus *Lindacarpa* and Miocene *Liquidambar changii* Pigg, Ickert-Bond et Wen (Pigg et al., 2004). The genus *Sarbaicarpa* is also similar to extant *Liquidambar acalycina* in the general outline of fruits.

The major difference of *Sarbaicarpa* from living Altingioideae is the development of one seed in the fruit, while the anatropous seed type is a shared character. Anatropous seeds of extant Altingioideae have more or less developed rounded or distal wings, while the majority of genera of Hamamelidaceae have ballistic seeds without a wing (Tiffney, 1986). The wing of Altingioideae varies from large distal in *Liquidambar formosana* and *L. styraciflua* to shorter in *L. orientalis*. Seeds of *L. acalycina* have a small rounded or triangular wing, which is similar to that of *Altingia* and *Semiliquidambar*; a rounded wing is characteristic of Miocene *Liquidambar changii* (Pigg et al., 2004). The seed of *Sarbaicarpa* lacks similar structures.

The genus *Sarbaicarpa* is also similar to extant Altingioideae in spermoderm structure. The seed coat of *Sarbaicarpa* is relatively thin, nonmultilayer, well differentiated. The micromorphology of the seed surface of *Sarbaicarpa* is in general similar to that of living *Liquidambar acalycina* (Ickert-Bond et al., 2005). Ickert-Bond et al. indicated that cells of the seed surface of *Liquidambar* are mostly isometric; however, in *Sarbaicarpa*, epidermal cells gradually decrease in size from the center to periphery of the seed. The genus *Sarbaicarpa* is similar to Altingioideae and Platanaceae in the structure of the mechanical layer, which consists of relatively small thick-walled cylindrical

sclereids, almost lacking cellular contents. The number of layers of these cells in *Sarbaicarpa* and Altingioideae and Platanaceae ranges from one to three. The subfamily Hamamelidoideae is distinguished by the more massive structure of the mechanical layer, manifested in the greater number of cellular layers and varying structure of sclereids (*Comparative Anatomy ...,* 1991).

In the presence of sterile structures in the infructescence, the genus *Sarbaicarpa* is similar to both Platanaceae and Hamamelidaceae. The extrafloral phyllomes have been described in extant genera of different Hamamelidaceae subfamilies (Altingioideae: *Altingia, Liquidambar*; Exbucklandioideae: *Exbucklandia*; Rhodoleioideae: *Rhodoleia*) and in *Platanus*. They vary in size and, particularly, in shape; in some cases, these distinctions are species-specific. For example, needle-shaped phyllomes are characteristic of *Liquidambar formosana* and *L. acalycina*, wider cone-shaped phyllomes occur in *L. styraciflua*, and wide, slightly elevated phyllomes are observed in *L. orientalis*. In *Altingia*, these structures are found in the same positions, but they are smaller, in the shape of tubercles (Ickert-Bond et al., 2005, 2007).

The genus *Sarbaicarpa* is characterized by the presence of two morphologically different types of sterile extrafloral structures. The first are relatively large, almost as large as fruits, consist of a small stalk and massive slightly flattened hemispherical part. The arrangement of these structures in the infructescence is also irregular. They are less frequent than needle-shaped sterile structures, at most eight per infructescence. From eight to twelve extrafloral phyllomes occur in living species of *Liquidambar* (Ickert-Bond et al., 2005); however, they are uniform within a species and differ in shape and size. These large sterile structures have not been recorded in extant and extinct platanoids and hamamelids. The surface of hemispherical sterile structures of *Sarbaicarpa* is covered with many rounded trichomes; as they shed, distinct rounded bases are left. On the internal cuticular surface of these structures, massive cuticular thickenings encircling the aperture of the trichome are visible. The same pattern is observed in leaves of extant *Platanus*: the adaxial leaf surface has circular trichome bases, the interior side of the cuticle of which has apertures reinforced by additional cuticular layers (Carpenter et al., 2005). We also recorded cuticular formations around the stomatal apertures on the internal side of the leaf cuticle of extant *Liquidambar*. It is likely that, in *Sarbaicarpa*, the function of sterile extrafloral structures of the first type was attraction of insects for pollination. These structures possibly produced nectar, and abundant glandular trichomes could have played a secretory role. Production of nectar has not been established in living *Platanus* or fossil platanoids. In some genera of Hamamelidaceae, the nectariferous function is performed by several fused scales located between the androecium and gynoecium (*Loropetalum, Tetrathir-*

Table 6. Characters of the reproductive system of the families Platanaceae and Hamamelidaceae, shown in the genus *Kasicarpa* (Kasicarpaceae fam. nov.)

Platanaceae		Kasicarpaceae	Hamamelidaceae	
extinct	extant	*Kasicarpa*	extinct	extant
+	+	capitate infructescences	+	+
		nonsimultaneous maturation of fruits	+	+
+		well-developed perianth	+	+
		monocarpellate gynoecium		+
+	+	orthotropic seed	+	+
+	+	solitary seed in carpel		+
	+	spermoderm structure		+

ium Benth., *Maingaya, Corylopsis, Fortunearia, Rhodoleia*: Endress, 1970). In *Hamamelis*, the nectariferous function is performed by staminodia (Endress, 1970). In *Disanthus*, nectaries are positioned at the base of petals (Mizushima, 1968; Endress, 1989a). The nectariferous disks of *Exbucklandia* are sometimes incorrectly interpreted as the calyx (Endress, 1989a). It is sometimes proposed that, judging from the morphology and time of appearance in ontogeny, the sterile structures of *Liquidambar styraciflua* could have been glands or nectaries; however, the data on their secretory activity and histology are absent (Wisniewski and Bogle, 1982).

The second type of sterile extrafloral structures of *Sarbaicarpa* is narrow needle-shaped structures with parallel margins, which reach at least the midlength of the fruit. In the infructescence of *Sarbaicarpa*, fruits are relatively loosely arranged and the needle-shaped structures are very friable; therefore, the apical regions of these structures are usually broken off during fossilization. It is difficult to judge, whether or not the apical regions of these structures differed from the basal regions, whether or not they were complex, possessing supplementary structures. Apparently, these structures are irregularly arranged between fruits, sometimes grouped in pairs; each infructescence usually has about 15 structures of this kind. In the extent of cutinization they are similar to fruit, both are strongly cutinized, which is manifested in the presence of cuticular ribbing; however, the cuticle of fruit shows transverse ribbing, while the cuticle of needle-shaped sterile structures has a longitudinal ribbing. It is difficult to reconstruct the function of these structures, the more so as they lack apical regions. It is hardly probable that they were staminodia, since pollen grains have

not been recorded on these structures or other structures of the infructescence. The idea that these structures could have been elements of the perianth contrasts with their irregular arrangement between fruits. They are similar in shape to the needle-shaped extrafloral phyllomes of *Liquidambar formosana* and *L. acalycina*; however, they are considerably longer than phyllomes of living species of *Liquidambar* and differ in the strongly cutinized surface ribbing. They could have been compared to bracts, which support inflorescences of some hamamelids, with bright color attracting insects, for example, in the genus *Parrotiopsis* (Kapil and Kaul, 1972); however, the irregular arrangement in the infructescence conflicts with this conclusion.

Sterile fossil structures have been recorded in the genus *Evacarpa*, Altingioideae (Maslova and Krassilov, 1997). The smaller and narrower structures are interpreted as phyllomes and more massive and wide structures, as staminodia, which probably did not produce pollen grains. The genus *Viltyungia*, which combines characters of three hamamelid subfamilies (Exbucklandioideae, Hamamelidoideae, and Altingioideae) (Maslova and Golovneva, 2000b), probably had staminodia, which produced abundant pollen grains. Accumulations of underdeveloped adhering pollen grains, which are much smaller than fertile grains, were found on the surface of the gynoecium.

The genus *Sarbaicarpa* is similar to the subfamily Hamamelidoideae mostly in the presence of one anatropous seed per fruit and in the well-developed endosperm. Living representatives of the subfamily Hamamelidoideae are distinguished by the uniform number of anatropous ovules (one). The seed of *Sarbaicarpa* has a relatively thick endosperm, which is also characteristic of Hamamelidoideae. In contrast to genera of Hamamelidoideae, the endosperm of altingioids is very poorly developed and, in living species of *Platanus*, the endosperm is almost completely consumed by the growing embryo, so that, in mature seeds, it is represented by a thin layer preserved at the periphery (Poddubnaya-Arnoldi, 1982). In addition, the genus *Sarbaicarpa* is similar to Hamamelidoideae in the presence of sterile structures in flowers and inflorescences. In the subfamily Hamamelidoideae, the staminodia have been recorded in the Santonian–Campanian genus *Archamamelis* (Endress and Friis, 1991) and Eocene staminate capitate inflorescences that are considered to be close to *Hamamelis* and *Corylopsis* in a number characters (Manchester, 1994).

(2) Family Kasicarpaceae fam. nov., genus *Kasicarpa*. The genus *Kasicarpa*, which was described from the Turonian of the Chulym–Yenisei Depression (Maslova et al., 2005), is also similar in a set of characters to extant and extinct representatives of the families Platanaceae and Hamamelidaceae (Table 6). The characters shared with Platanaceae are the capitate inflorescences, well-developed perianths (in extinct genera), single orthotropic ovule, and the spermod-

erm structure. However, platanoids usually have more flowers within a head (up to 100 in the Late Cretaceous genus *Friisicarpus* and up to 300 in the living plane tree) and are additionally distinguished by simultaneous maturation of flowers.

The fruit of *Kasicarpa* contains only one orthotropic seed, which tightly adjoins the walls and occupies almost the whole volume. The only orthotropic seed is also observed in fruits of extant *Platanus* and fossil *Friisicarpus* and *Macginicarpa*. The similarity to platanoids is also observed in the spermoderm structure, particularly, in the external layer. In *Kasicarpa*, this layer consists of dome-shaped cells with a small pore at the apex. The same structure of the external spermoderm layer is characteristic of the living plane tree, in which it plays a mucinous role, contributing to the retention of moisture (*Comparative Anatomy ...*, 1991). External morphology and ultrastructure of the exine of pollen grains adhering to fruits of *Kasicarpa* resemble those of both Platanaceae and Hamamelidaceae (Maslova et al., 2005; Tekleva, 2007).

As compared with the Hamamelidaceae, *Kasicarpa* is most similar to the subfamilies Altingioideae and Hamamelidoideae. The similarity to extant Altingioideae is manifested in the general pattern of the compound unisexual inflorescence, which consists of an axis with heads; the number of flowers per head; and nonsimultaneous maturation of carpels. Within one head, *Kasicarpa* has fruits at different stages of maturation, from those only beginning their development to more or less mature fruits. Nonsimultaneous maturation of carpels within one head is also observed in extant *Altingia* and *Liquidambar*. Heads with carpels at different maturation stages are known in the extinct genera *Anadyricarpa, Lindacarpa*, and *Evacarpa*.

The major differences of *Kasicarpa* from the subfamily Altingioideae are the monomeric gynoecium with the upper ovary and single seed, while the Altingioideae have a bicarpellate gynoecium with half-inferior ovary and several seeds in the fruit. However, as Bogle (1986) has shown, although the bicarpellate gynoecium prevails among Altingioideae, monocarpellate forms also occur; however, the monomeric gynoecium is infrequent among hamamelids. In addition, extant Altingioideae lack a perianth, although extinct genera that are considered to be closely related to altingioids frequently have a well-developed perianth. In the spermoderm structure of seeds, *Kasicarpa* is similar to extant *Liquidambar* and *Altingia* (Melikyan, 1973a, 1973b); however, its fruits have up to several dozen ovules, which are anatropous. The infructescence of *Kasicarpa* is most similar to that of *Anadyricarpa*, which was originally referred to Altingioideae (Maslova and Herman, 2004). The major shared characters are the single carpel per flower, the capitate infructescence, the number of flowers per head, nonsimultaneous maturation of fruits in the

infructescence, and the presence of a well-developed perianth.

The genus *Kasicarpa* is similar to the subfamily Hamamelidoideae mostly in the number of carpels per flower (from one to three carpels are observed in flowers of *Parrotiopsis*, Hamamelidoideae: Kapil and Kaul, 1972) and the number of ovules in the ovary (all members of the subfamily Hamamelidoideae are uniform in having one ovule). However, ovules of Hamamelidoideae are anatropous, whereas *Kasicarpa* has orthotropic ovules. Differences are also observed in spermoderm structure.

6.2.2. Association of Different Plant Organs with Characters of the Families Platanaceae and Hamamelidaceae

Among fossil platanoids, which are already represented by rather extensive materials, co-occurrence of different plant organs are of particular interest. These cases are mostly associations of leaves and reproductive structures, which are sometimes accompanied by remains of wood, bark, and shoots. Different plant organs buried together were examined separately for a long time, because researchers were not sure that they belonged to the same plant, since these finds were scarce. As these data were accumulated, the patterns of these occurrences were analyzed (Maslova, 2008a, 2008c; Maslova and Kodrul, 2008). Although reproductive structures and leaves are rarely found in organic connection, repeated co-occurrences within one bed, in the same piece of rock suggest that these organs belonged to one plant. In addition, cases of these associations of plant organs are presently known from different stratigraphic ranges (Fig. 6).

Platanoid leaves are usually very polymorphic, complicating considerably their generic and even family identification. The epidermal characters, which could have simplified the identification of leaf specimens, are frequently contradictory and are not always accessible for investigation. Taking into account the fact that the same leaf morphotypes co-occur in Cretaceous deposits with essentially different reproductive structures, it was proposed to determine some of these specimens following the morphological (independent of natural) system (Maslova et al., 2005). In particular, the generic name *Ettingshausenia* was proposed for Cretaceous leaf remains that were previously assigned to the extant genus *Platanus*. In contrast to leaves, platanoid reproductive structures that are similar in macromorphology are distinguished with certainty by microstructural characters. Capitate inflorescences and infructescences that are almost identical in appearance display characters typical of different genera and even different families. These specimens were referred to the family 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, 1997,

Examples of association of platanoid leaves and reproductive structures				
Leaves	Reproductive structures			
	genus	suprageneric systematics	age	reference
Simple lobate *Ettingshausenia*	*Anadyricarpa*	Altingioideae, Hamamelidaceae	Late Albian– Early Cenomanian	Maslova and Herman, 2004
	Friisicarpus	Platanaceae	Cenomanian	Maslova and Herman, 2006
	Kasicarpa	Hamamelidales	Turonian	Maslova et. al., 2005
	Oreocarpa, Tricolpopollianthus, Carinalaspermum	Platanaceae	Early Paleocene	Krassilov, 1976 Maslova and Krassilov, 2002
Platanus basicordata	*Platanus stenocarpa*	Platanaceae	Late Paleocene– Early Eocene	Maslova, 1997
Macginitiea	*Macginicarpa, Platananthus*	Platanaceae	Middle Eocene	Manchester, 1986
Platanus nobilis	*Macginicarpa, Platananthus*	Platanaceae	Paleocene	Pigg and Stockey, 1991

Fig. 6. Association of platanoid leaves and various reproductive structures.

2002a; Maslova and Kodrul, 2003; Mindell et al., 2006) or the family Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004, 2006); sometimes, they combine characters of both families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005, 2007; Maslova, 2009).

The leaf morphotype typical of the subgenus *Platanus* appeared in the fossil record in the Albian; therefore, it was initially proposed that the extant

Leaves	Reproductive structures			
	genus	suprageneric systematics	age	reference
Simple entire *Platimeliphyllum*	*Archaranthus*	Platanaceae	Maastrichtian– Danian	Maslova and Kodrul, 2003
	Bogutchanthus	Hamamelidales	Early Paleocene	Maslova et al., 2007
	Chemurnautia	Platanaceae	Late Paleocene– Early Eocene	Maslova, 2002
Evaphyllum	*Evacarpa*	Altingioideae, Hamamelidaceae	Late Paleocene– Early Eocene	Maslova and Krassilov, 1997; Maslova, 2003
Simple and compound *Platanus neptuni*	*Platanus neptuni* (infructescences, staminate inflorescences)	Platanaceae	Late Eocene– Late Miocene	Kvaček and Manchester, 2004
Compound *Sapindopsis*	*Friisicarpus, Aquia*	Platanaceae	Early–Middle Albian	Crane et al., 1993
Platanites	Infructescences, staminate inflorescences	Platanaceae	Paleocene	Crane et al., 1988

Fig. 6. (Contd.)

genus *Platanus* appeared in the Early Cretaceous. Subsequently, it was shown with certainty that, judging from the reproductive structures, this genus appeared as late as the Paleocene (Maslova, 1997; Kvaček et al., 2001). Among fossil platanoid forms associated with reproductive structures, there are simple lobate leaves of the genera *Ettingshausenia* and *Macginitiea*, simple nonlobate leaves of the gen-

era *Platimeliphyllum* and *Evaphyllum*, and compound leaf morphotypes referred to the genera *Sapindopsis* and *Platanites* and the species *Platanus neptuni*.

The co-occurrences of platanoid leaves and reproductive structures are divisible into several groups. The first includes associations of leaves of *Ettingshausenia* (1) and capitate inflorescences and infructescences assigned to Platanaceae (Krassilov, 1976; Krassilov and Shilin, 1995; Maslova and Herman, 2006), Hamamelidaceae (Maslova and Herman, 2004), or combining characters of both families (Maslova et al., 2005). Lobate leaves of *P. basicordata* Budants., Platanaceae (2) (typical of the subgenus *Platanus* of the genus *Platanus*), are associated with reproductive structures typical of the living plane tree *P. stenocarpa* (Maslova, 1997). Among lobate morphotypes, leaves of the genus *Macginitiea*, Platanaceae (3), are associated with reproductive structures also assigned to Platanaceae (Manchester, 1986). Lobate leaves of *Platanus nobilis* Newb. sensu stricto (4), which are similar in morphology to *Macginitiea*, occur in association with inflorescences of the same genera (Pigg and Stockey, 1991).

Entire leaves of the genera *Platimeliphyllum* (5) and *Evaphyllum* (6) display characters typical of both Platanaceae and Hamamelidaceae. Leaves of different species of *Platimeliphyllum* are associated with essentially different reproductive structures, which are assigned to the family Platanaceae (Maslova, 2002a; Maslova and Kodrul, 2003) or referred to as the order Hamamelidales (Kodrul and Maslova, 2007; Maslova et al., 2007). Leaves of the genus *Evaphyllum* co-occur with infructescences referred to Hamamelidaceae (Maslova and Krassilov, 1997).

The polymorphic extinct species *Platanus neptuni* has both simple entire and compound leaf morphotypes. Compound leaves of the plane tree are only known in fossil state. Leaves of *P. neptuni* (7) are associated with unusual inflorescences and infructescences of *P. neptuni* in a number of localities (Kvaček and Manchester, 2004). Compound leaves are also recorded in the genera *Sapindopsis* (8) and *Platanites* (9), which also occur in association with different reproductive structures (Crane et al., 1988, 1993). Let us consider in detail cases of associations between platanoid leaves and reproductive structures.

(1) Association of leaves of Ettingshausenia and capitate inflorescences and infructescences. Leaves of *Ettingshausenia* are characterized by variable, frequently asymmetrical leaf laminas, ranging from entire triangular, penta-, and hexagon, rhombic or ovate–rhombic, with undeveloped or rudimentary lobes or lobate forms with 2–6 lateral lobes. The leaf base is usually more or less cuneate, sometimes peltate; the apex is often pointed; the lamina margin is serrated or, less frequently, entire. The venation is actinodromous (palynactinodromous) craspedodro-

mous, with well-developed basal veins; the tertiary veins are scalariform or branching scalariform.

As mentioned above, leaves of the typical platanoid morphotype, referred to the genus *Ettingshausenia*, occur in association with various reproductive structures displaying characters of Platanaceae (Krassilov, 1976; Krassilov and Shilin, 1995; Maslova and Herman, 2006), Hamamelidaceae (Maslova and Herman, 2004), or combining characters of both families (Maslova et al., 2005).

1.1. Leaves of *Ettingshausenia*–infructescences of *Anadyricarpa*, bark fragments (Fig. 7); Late Albian–Early Cenomanian, northeastern Russia (Maslova and Herman, 2004).

Infructescences of *Anadyricarpa* occur in association with the leaves initially described as *Platanus louravetlanica* (Herman, 1994) and later referred to the genus *Ettingshausenia* (Moiseeva, 2010) and with bark fragments resembling bark of the living plane tree. Although these leaves are undoubtedly similar to leaves of the living plane tree, certain characters show affinity to some Hamamelidaceae. This is manifested in the asymmetrical leaf lamina and asymmetrical base, asymmetrical deviation of the basal veins varying in length and thickness, and features of the tertiary venation (mostly orthogonal reticulate). These leaves are most similar to mature leaves of the genus *Shaniodendron*, Hamamelidaceae (Wang and Li, 2000, text-figs. c, d). They essentially differ from Hamamelidaceae in the suprabasal deviation of the basal veins and in the well-pronounced infrabasal veins. Unfortunately, the poor preservation of specimens prevented the study of epidermal features.

Capitate infructescences of *Anadyricarpa* consist of many fruits radiating from the central core and varying in maturity. *Anadyricarpa* has a well-developed perianth, which forms the flower tube enveloping completely the single carpel. Note that, in infructescences of *Anadyricarpa*, hamamelid characters undoubtedly predominate, but some platanoid characters are also observed (such as the shape of the infructescence and a well-developed perianth); at the same time, the leaves accompanying them show mostly platanoid characters, although some features characteristic of hamamelids are distinct.

Platanoid leaves and infructescences of *Anadyricarpa* were accompanied by bark fragments, which are almost identical in shape and external sculpture to that of extant *Platanus*. A distinctive feature of stems and branches of the living plane tree is scaling and shedding bark fragments in the shape of relatively large plates; as a result, the stem displays a marmoreal pattern. Bark shedding, which frequently occurs in living angiosperms, has also been described in fossils from the Santonian of Germany (Tschan et al., 2008). Our material (Maslova and Herman, 2004) shows that this phenomenon existed at early stages (Late Albian–Early Cenomanian) of historical development of angiosperms.
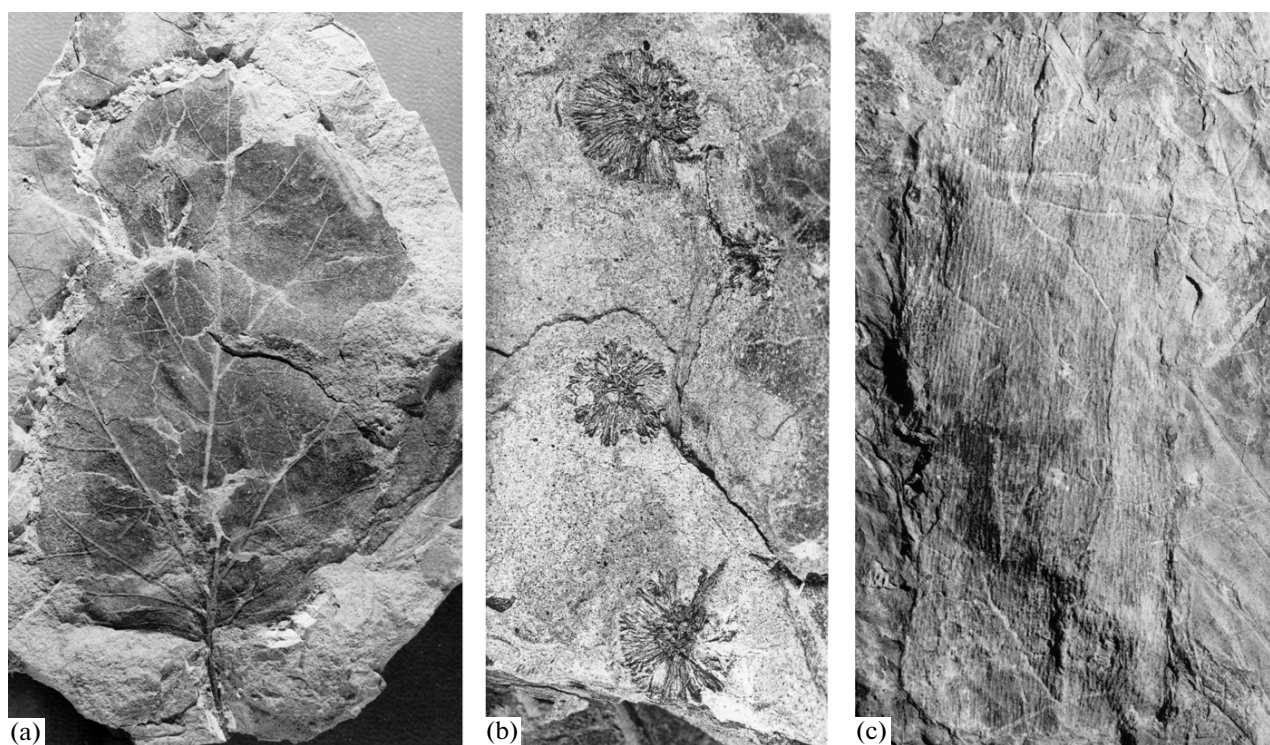
Fig. 7. Association of (a) leaves of *Ettingshausenia louravetlanica* (Herman et Shczepetov) Herman et Moiseeva, (b) infructescences of *Anadyricarpa altingiosimila* N. Maslova et Herman, and (c) bark fragments; Late Albian−Early Cenomanian, northeastern Russia: (a) specimen GIN, no. 4975/2-1, ×0.8; (b) specimen GIN, no. 4975/3-1, ×2; (c) specimen GIN, no. 1007/35-646-2b, ×1. All specimens are stored in the Laboratory of Paleofloristics of the Geological Institute of the Russian Academy of Sciences (GIN).

1.2. Leaves of *Ettingshausenia*−staminate inflorescences of *Sarbaya*, infructescence of *Sarbaicarpa*; Cenomanian−Turonian, Kazakhstan (Krassilov and Shilin, 1995; Maslova, 2009).

Lobate leaves with variously developed lobes from the Cenomanian−Turonian of Kazakhstan were referred to *Platanus pseudoquillelmae* and *P. cuneiformis* Krass. (Shilin, 1986). Along with typical leaf characters of *Platanus,* they demonstrate some features of the leaf structure, which resemble Altingioideae, in particular, relatively densely spaced veins positioned between the secondary veins and reaching approximately the middle of the distance to the blade margin and well-developed marginal glands. As Krassilov and Shilin (1995) indicated, the epidermal structure of these leaves shows characters typical of Fagaceae.

Staminate inflorescences of the genus *Sarbaya* show a strongly reduced perianth, which is at most one-third as long as the stamen; strictly tetramerous flowers; and tricolporate pollen grains.

Infructescences of *Sarbaicarpa* is distinguished by the mosaic combination of characters typical of both Platanaceae and Hamamelidaceae. The infructescence consists of approximately 30 loosely arranged, widely cuneate fruits. The fruit is monocarpellate, lacks a stylodium, and has a tuft of hairs at the fruit base. The seed is single, anatropous. Two types of sterile structures are present, i.e., hemispherical, similar

in size to fruits, covered with densely spaced rounded trichomes; and narrow linear trichomes, extending farther than the midlength of the fruit.

1.3. Leaves of *Ettingshausenia*−infructescences of *Friisicarpus* (Fig. 8); Cenomanian−Turonian, Western Siberia, Russia (Maslova and Herman, 2006).

Most of the presently known reproductive structures of the genus *Friisicarpus* (*F. marylandensis, F. carolinensis, F. elkneckensis*) have not been associated with leaves. The only species, *F. brookensis* (Crane et al., 1993), is known in association with staminate inflorescences of *Aquia brookensis* and leaves of cf. *Sapindopsis variabilis* Fontaine (see below).

In the Cenomanian of Western Siberia, infructescences of *Friisicarpus* sp. in association with leaves of *Ettingshausenia* have been recorded and described (Maslova and Herman, 2006). Infructescences of *Friisicarpus* consist of many pentamerous flowers arranged in a well-developed perianth; their carpels lack stylodia.

The find of infructescences of *Friisicarpus* sp. in the Cenomanian of Western Siberia not only expanded the knowledge of geographical distribution of this genus, but also showed well-pronounced stability of female reproductive organs of early platanoids. Apparently, the same infructescences are associated with leaves of different morphotypes, i.e., compound pinnate or pinnatifid leaves of the genus *Sapindopsis* (Crane et al.,
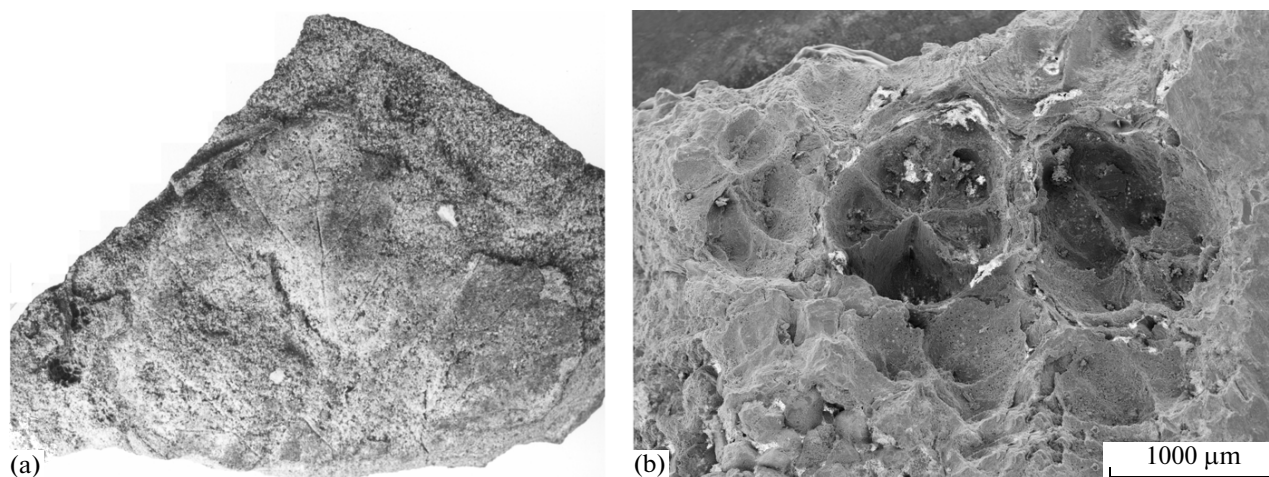
Fig. 8. Associations of (a) leaves of *Ettingshausenia* sp. and (b) infructescences of *Friisicarpus* sp.; Cenomanian–Turonian, Western Siberia, Russia: (a) specimen GIN, no. 4874/1a-1, ×0.8; (b) specimen GIN, no. 4874/1b-2, SEM. All specimens are stored in the Laboratory of Paleofloristics, GIN.

1993) and lobate leaves of *Ettingshausenia* (Maslova and Herman, 2006).

1.4. Leaves of *Ettingshausenia*–infructescences of *Kasicarpa* (Fig. 9); Turonian, Western Siberia, Russia (Maslova et al., 2005).

Infructescences of *Kasicarpa* occur in association with *Platanus*-like leaves that were originally described as *Populites pseudoplatanoides* I. Lebed. (Lebedev, 1962). Subsequently, Golovneva (2008) studied the epidermal structure of these leaves and established a new genus, *Tasymia*, assigning it to the family Platanaceae. Previously, Maslova et al. (2008b) have doubted that *Tasymia* is a separate genus. It should be noted here that macromorphological characters of these leaves mostly fall in the variation range of the extant genus *Platanus*, while epidermal differences, as the author of the genus indicated, consist of the greater number of glandular trichomes, greater cutinization, the presence of a cutinized ring at the base of trichomes, and the formation of a stalk in trichomes. However, quantitative and dimensional characteristics of epidermal structures mostly depend on certain ecological factors; therefore, they should not be taken for a key criterion for the establishment of the taxonomic position of leaves. At the same time, other characters are not unique, they have been recorded in leaves of living species of *Platanus* (see, e.g., Carpenter et al., 2005). Therefore, I assign the leaves associated with infructescences of *Kasicarpa* to the genus *Ettingshausenia*.

Infructescences of *Kasicarpa* are similar to extant and extinct representatives of the families Platanaceae and Hamamelidaceae in the complex of characters. The characters shared with Platanaceae are the capitate inflorescences, well-developed perianths (in extinct genera), single orthotropic ovule, and the spermoderm structure.

As compared with the Hamamelidaceae, *Kasicarpa* is most similar to the subfamilies Altingioideae and Hamamelidoideae. The characters shared with extant Altingioideae include the general pattern of the compound unisexual inflorescence (axis with heads), the number of flowers per head, and nonsimultaneous maturation of carpels. The major differences are the bicarpellate gynoecium with a half-inferior ovary and several seeds per fruit in Altingioideae and monomeric gynoecium with the upper ovary and single seed in *Kasicarpa*. However, as Bogle (1986) has shown, the bicarpellate gynoecium prevails in the Altingioideae, although monocarpellate forms also occur. In addition, the living Altingioideae lack a perianth. However, extinct genera that are considered to be close to altingioids usually have a well-developed perianth. Among extinct Altingioideae, *Anadyricarpa* from the Late Albian–Early Cenomanian of northeastern Russia (Maslova and Herman, 2004) is most similar in infructescence structure to *Kasicarpa*. The similarity is manifested primarily in the presence of single carpel per flower, and in the capitate infructescence, the number of flowers per head, and the presence of a well-developed perianth. Living representatives of the subfamily Hamamelidoideae are distinguished by the great diversity of floral structures. *Kasicarpa* is similar to representatives of Hamamelidoideae in the development in some genera (e.g., *Sycopsis* and *Parrotia*) of a well-pronounced perianth and single seed in the carpel (almost all Hamamelidoideae). In addition, in some living representatives of Hamamelidoideae (*Parrotiopsis*), the monomeric gynoecium has been recorded (Kapil and Kaul, 1972). Key differences of Hamamelidoideae from the genus *Kasicarpa* are the bicarpellate gynoecium with a half-inferior ovary and dense capitate inflorescences consisting of a greater number of nonsimultaneously ripening flowers.
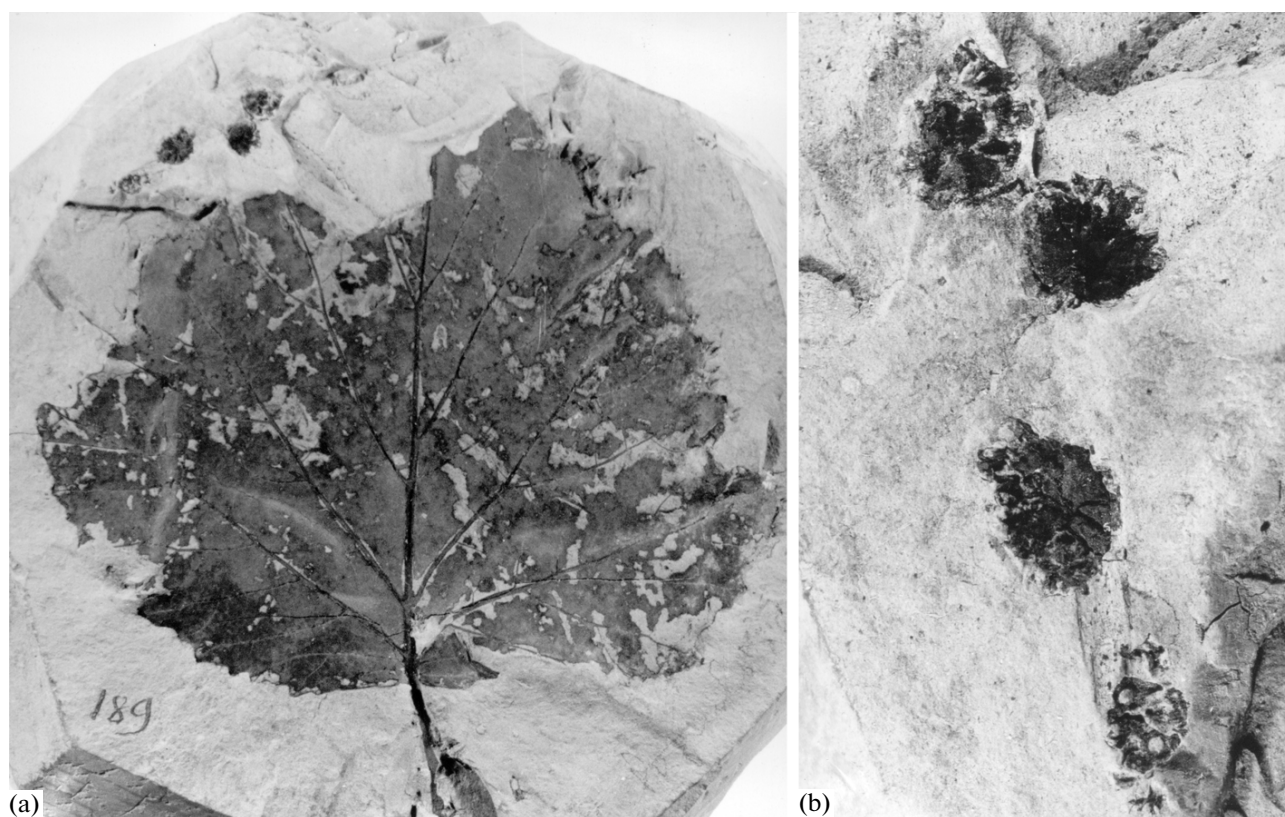
Fig. 9. Association of (a) leaves of *Ettingshausenia* sp. and (b) infructescences of *Kasicarpa melikianii* N. Maslova, Golovneva et Tekleva; Turonian, Western Siberia, Russia: (a) specimen TPI, no. 29/8a, ×1; (b) specimen TPI, no. 29/8b, ×3.2. All specimens are stored in the museum of Tomsk Polytechnic Institute (TPI).

1.5. Leaves of *Ettingshausenia*–infructescences of *Oreocarpa* N. Maslova et Krassilov, staminate inflorescences of *Tricolpopollianthus*; Early Paleocene; Amur Region, Russia (Krassilov, 1976; Maslova and Krassilov, 2002).

The *Platanus*-like leaves determined as *Platanus raynoldsii* Newb. are known from many Cretaceous localities. Based on extensive material from the Tsagayan Beds of the Amur Region, Krassilov (1976) described many diverse leaf morphotypes of this kind, which are identical in epidermal structure. Based on the association of these leaves with unusual reproductive structures (seeds of *Carinalaspermum bureicum* Krassilov and staminate heads of *Tricolpopollianthus burejensis* Krassilov), which show characters of Platanaceae, but are distinguished from the living plane tree, Krassilov cast doubt on the existence of the genus *Platanus* in the Cretaceous. These leaves were tentatively assigned to this extant genus, which was designated by putting the generic name in inverted commas. The leaves of *"Platanus" raynoldsii* described by Krassilov from Tsagayan show significant polymorphism, so that, based on macromorphology, it is possible to assign the extreme morphotypes to different genera of other families. The most typical morphotype is identical to that of the genus *Platanus*; however, it is evident that, along with typical platanoid morphotypes, the Tsagayan plant had other leaf morphotypes and reproductive organs other than in *Platanus*. Subsequently, a new combination, *Ettingshausenia raynoldsii* (Newb.) Moiseeva, was proposed (Moiseeva, 2008).

In the original description of *Carinalaspermum bureicum*, along with individual winged seeds, fruits with carpellodia preserved at their bases were recorded (Krassilov, 1976, pl. 33, figs. 3, 4). Subsequently, in the material collected by Akhmetiev and Kodrul (Geological Institute, Russian Academy of Sciences) in the same locality, additional specimens with imprints of specific infructescences were found and transferred to us for examination; they were determined as *Oreocarpa bureica* N. Maslova et Krassilov (Maslova and Krassilov, 2002). These infructescences differ from capitate infructescences of platanoids and other Hamamelidales in the very small size and a few seed organs, only one of which becomes mature, exceeding in size the head.

On the cuticular surface of carpellodia, there were elliptical tricolpate pollen grains, with a reticulate exine. Individual pollen grains occurred on the cuticle
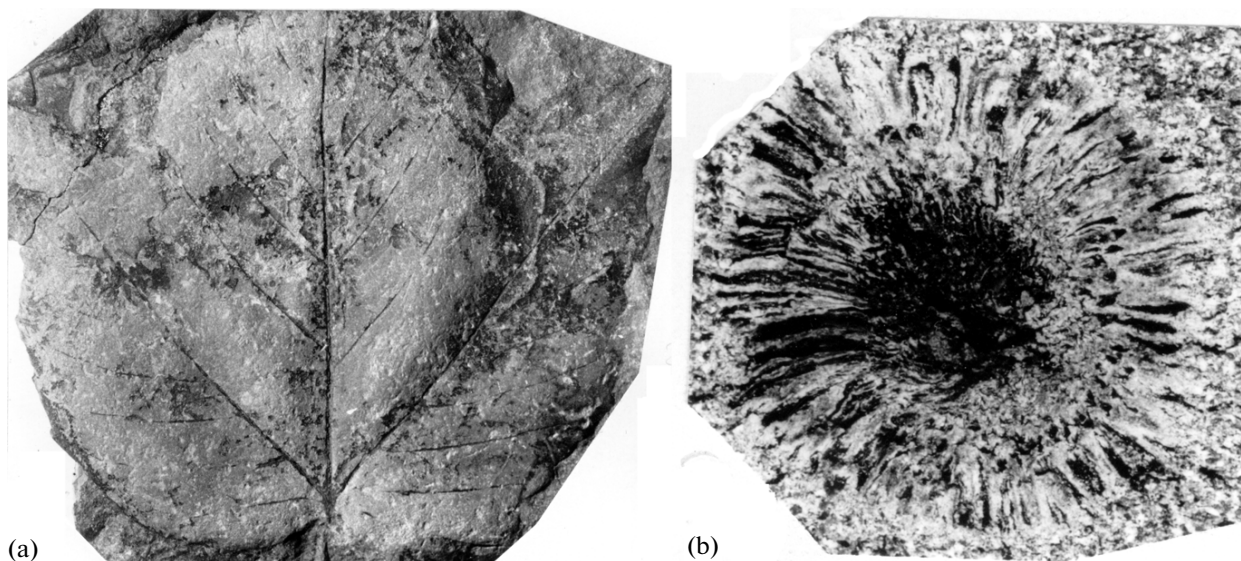
(a)

(b)

Fig. 10. Association of (a) leaves of *Platanus basicordata* Budantsev and (b) infructescences of *P. stenocarpa* N. Maslova; Late Paleocene−Early Eocene, northwestern Kamchatka, Russia: (a) specimen PIN, no. 3736/6, ×0.6; (b) specimen PIN, no. 3735/57, ×6. All specimens are stored in the Laboratory of Paleobotany of the Borissiak Paleontological Institute of the Russian Academy of Sciences.

of carpellodia of several heads; this suggests that these pollen grains remained attached to the carpellodia after pollination and, hence, were produced by staminate organs of a plant with pistillate inflorescences resembling *Oreocarpa*. In the basic characters, these pollen grains are similar to those of *Tricolpopollianthus burejensis* (Krassilov, 1976).

The staminate inflorescence of the genus *Tricolpopollianthus* is similar to that of *Platanus* and differs in the less pronounced peltate pattern of the connective and in the longer colpi of pollen grains.

(2) Association of lobate leaves of Platanus basicordata and capitate infructescences of P. stenocarpa (Fig. 10); Late Paleocene−Early Eocene, northwestern Kamchatka, Russia (Maslova, 1997).

Leaves of *P. basicordata* are trilobate, with a cordate base, slightly descending along the petiole, dentate margin, suprabasal basal veins with many basiscopic branches and several infrabasal veins. They were recorded in association with capitate infructescences, which show some structural features typical of living representatives of this genus. Along with *P. bella* (Kvaček et al., 2001) and *P. neptuni* (Kvaček and Manchester, 2004), these finds of reproductive structures mark the first occurrence in the fossil record of the extant genus *Platanus*. Infructescences of *P. stenocarpa* in association with leaves of *P. basicordata* are characterized by the absence of a perianth in flowers, pubescent carpels, more or less uniform size of carpels; the last character suggests that they are at the same stage of maturity.

(3) Association of lobate leaves of Platanus intermedia Knappe et Rüffle emend. Tschan, Denk et von Balthazar, capitate staminate inflorescences and infructescences of P. quedlingburgensis Pacltová emend. Tschan, Denk et von Balthazar, and bark fragments; Santonian, central Germany (Tschan et al., 2008).

Leaves of *P. intermedia* are represented by two morphotypes. Both are simple symmetrical lobate leaves, which differ in the length-to-width ratio of the lamina (1.36 : 1 in the first morphotype and 0.92 : 1 in the second) and arrangement of the marginal teeth (in the first morphotype, the teeth are in the apical two-thirds of the lamina length; in the second morphotype, the lamina is entire). Epidermal data confirm the assignment of these leaves to the family Platanaceae.

Staminate capitate inflorescences described as *P. quedlingburgensis* are 10 mm in diameter, consist of approximately 50 flowers. Each flower has six or seven stamens without a pronounced connective extension and two circles of well-developed perianth, the elements of which are as long as the stamen. External and internal elements of the perianth differ in epidermal structure. Pollen grains are similar in size and character of the tectum to *Platanus*.

Capitate infructescences of *P. quedlingburgensis* are about 10 mm in diameter. The number of fruits in the infructescence is uncertain. The fruit has a well-developed stylodium, elements of the perianth are undeveloped. A tuft of hairs at the fruit base, which is characteristic of *Platanus* and participates in dispersal, is indiscernible. The type and number of seeds in fruits are not known.

The bark fragments found with leaves and reproductive structures, are similar in appearance to the bark of the living plane tree.

Tschan et al. (2008) believe that this association of *Platanus*-like leaves, staminate and pistillate inflorescences, and bark remains is evidence that the extant genus *Platanus* appeared in the Santonian, in contrast to the previous concept about the Early Cenozoic appearance of this genus in the fossil record, which was based on the finds of reproductive structures. This conclusion seems premature, because available data are insufficient. Regarding the identification of these leaves as an extant genus, see Chapter 3. The staminate inflorescence of *P. quedlingburgensis* is characterized by the unstable number of stamens in the flower (a typical character of *Platanus*); however, the flower of *P. quedlingburgensis* has 6 or 7 stamens, while living species of the genus have from 3 to 5. Certain characteristic features of the plane tree stamens, such as the parallel-sided pollen sacs differing in length and well-developed endothecium have not been observed in *P. quedlingburgensis*. Pollen grains are in general similar in morphology to those of living plane tree species and fossil platanoids; however, the sporoderm structure shows some distinctions, which are shared by pollen grains of *P. quedlingburgensis* and extinct genera (M.V. Tekleva, personal communication).

The assignment of inflorescences with a well-developed perianth to the extant genus *Platanus* is particularly questionable. The discussion concerning the presence of a perianth in the flower of the plane tree is considered in Chapter 3. The development of a character, in this case, of the perianth (well-developed in *P. quedlingburgensis* and hardly discernible or undeveloped in the living plane tree) is a diagnostic character, which may distinguish extinct platanoid taxa from the extant genus *Platanus*. Note that, in the original description of the genus *Platanus*, Linnaeus (1754, p. 433) treated the elements of the perianth as tiny, hardly discernible. Subsequent studies of living species of *Platanus* confirmed that they lack a well-developed perianth (see, e.g., von Balthazar and Schönenberger, 2009); thus, there is no need to modify in this respect the generic diagnosis of Linnaeus. Thus, according to the diagnosis, the genus *Platanus* comprises inflorescences, the perianth of which is underdeveloped.

As to infructescences of *P. quedlingburgensis*, their characters are insufficient to assign with confidence these infructescences to the extant genus. The number and type of seeds, which are not known in the form in question, are the key diagnostic characters. As was shown previously, morphologically similar capitate infructescences occasionally contain several seeds instead of one, as in the extant plane tree (Maslova and Krassilov, 1997); the seed type also varies, it is orthotropic (Maslova et al., 2005), nonorthotropic (Magallón-Puebla et al., 1997), or anatropous (Maslova, 2009). For example, the Eocene infructescences described by Manchester (1994), which are much more similar to infructescences of the living plane tree in the presence of fruits with unstable number of carpels (three or four), well-developed stylodia, and well-developed tuft of hairs for dispersal at the fruit base, were correctly referred to the extinct genus *Tanyoplatanus*, because they have a well-developed perianth and unknown type and number of seeds. A tuft of hairs at the fruit base (a distinctive character of *Platanus*) is absent in infructescences of *P. quedlingburgensis*.

Bark fragments similar in morphology to the living plane tree were described previously (Maslova and Herman, 2004). They accompanied the capitate infructescences of *Anadyricarpa*, which differ essentially from that of the living plane tree. The ability of shedding bark fragments was probably characteristic of a number of angiosperms (which are closely related but other than the plane tree) as early as the Late Albian.

Thus, it seems unconvincing to assign the leaves, infructescences, and staminate inflorescences in question to the extant plane tree genus based mostly on superficial similarity and a number of questionable assumptions, which place these specimens beyond the limits of its generic criteria.

(4) Association of lobate leaves of Macginitiea, capitate staminate inflorescences of Platananthus, infructescences of Macginicarpa, dispersed fruits, groups of stamens of Macginistemon, and wood of Plataninium; Middle–Late Eocene, western North America (Manchester, 1986).

Leaves of the genus *Macginitiea* have to 5–9-lobate laminas with deep sinuses, palynactinodromous veins, distinct chevrons located along the entire extent of the lamina. Manchester (1986) described an association of these leaves with reproductive structures (infructescence of *Macginicarpa glabra*, staminate inflorescences of *Platananthus synandrus*, and dispersed staminate complexes of *Macginistemon mikanoides*) and wood remains (*Plataninium haydenii* Felix emend. Wheeler, Scott et Barghoorn) and named it "Clarno plane" after the Clarno Formation. Associations of leaves and various other plant organs were recorded in more than ten localities.

Infructescences of *Macginicarpa* are characterized by a constant number of carpels per flower (five), varying development of fruits in the head (several fruits often dominate in the infructescence), well-developed nondifferentiated perianth, and well-developed persistent stylodium. Staminate inflorescences of *Platananthus* have many flowers with a well-developed perianth and constant number of stamens (five), producing tricolpate reticulate pollen grains. The dispersed staminate complexes at various stages of maturity, referred to the genus *Macginistemon*, display the same staminal structure and character of pollen grains as *Platananthus*; however, because of unusual preservation of *Macginistemon*, the data on the presence of the perianth are absent; therefore, it was impossible to

determine these specimens as the genus *Platananthus*. Wood fragments of *Plataninium* demonstrate structural characters typical of platanoids.

(5) Association of lobate leaves and seedlings at various developmental stages of Platanus nobilis sensu stricto, capitate staminate inflorescences of Platananthus, and infructescences of Macginicarpa, dispersed staminate complexes; Paleocene, Canada (Pigg and Stockey, 1991).

The leaves of *Platanus nobilis* sensu stricto described by Pigg and Stockey (1991) are characterized by trilobate laminas with basally deviating actinodromous primary veins, which extend into the lobe, a few chevrons, and dentate margin. The authors marked distinct similarity of these leaves to leaves of the genus *Macginitiea* and proposed that they were a transitional form between ancient *Macginitiea* and extant *Platanus*. In addition to mature leaves, the locality has yielded many seedlings at various developmental stages from the first cotyledonous leaves to the appearance of the first, second, and subsequent true leaves. The association of these vegetative structures with infructescences of the genus *Macginicarpa* and staminate inflorescences of the genus *Platananthus* was named "Joffre plane tree." Note that, on the one hand, morphologically similar leaves of *Macginitiea* and *Platanus nobilis* (transitional forms are known) are associated with the same reproductive structures and, on the other hand, leaves of *P. nobilis*, which are referred to extant genus, co-occur with inflorescences and infructescences that differ essentially from those of the plane tree. These data suggest to assign these leaf specimens to the genus *Macginitiea*, although this requires further studies.

(6) Association of entire leaves of Platimeliphyllum and capitate staminate inflorescences of the genera Chemurnautia, Archaranthus, and Bogutchanthus (Figs. 11–13); Maastrichtian–Danian–Early Eocene, northwestern Kamchatka Peninsula, Amur Region, Russia (Maslova, 2002a; Maslova and Kodrul, 2003, 2008; Kodrul and Maslova, 2007; Maslova et al., 2007).

Leaves of the genus *Platimeliphyllum* show a combination of characters typical of the families Platanaceae and Hamamelidaceae (Maslova, 2002a). The macromorphology of these leaves is very diverse, so that some morphotypes of one species (from the same locality and the same bed) are comparable to Hamamelidaceae (general asymmetry of the lamina and its base, poorly developed basal veins, camptodromous basiscopic veins, low and obtuse teeth), while others, to Platanaceae (typical suprabasal deviation of well-developed basal veins, basiscopic branches of which terminate craspedodromously, well-developed infrabasal veins, concavo-convex teeth with the longer basal side). Individual leaf morphotypes of this genus show morphological similarity to different extant genera of Hamamelidaceae (e.g., *Corylopsis*, *Hamamelis*, *Parrotia*).

The genus *Platimeliphyllum* comprises four species: *P. palanense, P. snatolense, P. denticulatum* N. Maslova (Maslova, 2002a), and *P. valentinii* (Kodrul and Maslova, 2007). Two (*P. palanense* and *P. snatolense*) were recorded in association with staminate inflorescences of the genus *Chemurnautia* in three localities of the northwestern Kamchatka Peninsula (Chemurnaut Bay, Evravavayam River, and Snatol River) dated from the Late Paleocene to Early Eocene. Staminate inflorescences of the genus *Chemurnautia* have a number of features resembling the living plane tree. The shared characters are the capitate inflorescence, short anther filaments, narrow fusiform sporangia with parallel margins, well-developed endothecium, and tricolpate reticulate pollen grains. The genus *Chemurnautia* differs from extant *Platanus* in the considerably smaller inflorescences, the anther lacking a well-developed connective extension, the absence of trichomes on the epidermis of the connective, and in the smaller pollen grains with wide colpi. Another unique feature of the genus *Chemurnautia*, which distinguishes it from both platanoids and other Hamamelidales, is the radial arrangement of its very narrow, almost linear sporangia, unfused or slightly fused with each other, without the formation of distinct synangia (theca).

Leaves of *Platimeliphyllum valentinii* were initially recorded in association with staminate inflorescences of *Archaranthus* in a locality near the village of Arkhara, Amur Region, in the middle part of the section of a clayey member between the coal layers "Nizhnii" and "Dvoinoi" (Maslova and Kodrul, 2003). However, because of a lack of material, it was then impossible to determine these specimens to genus. We only indicated the association of these leaves with inflorescences of *Archaranthus*, which were assigned to the family Platanaceae based on micromorphological characters. Distinctive features of the genus *Archaranthus* are the small capitate inflorescences with a stalk, which are scattered at the mature state into isolated flowers and stamens, consisting of approximately 15 tetramerous flowers. The capitate stalked inflorescences are characteristic of many platanoids; however, *Archaranthus* is distinguished by the fewer flowers in the inflorescence and by the disintegration of mature heads into separate flowers and stamens. Tetrastaminate flowers are also recorded in the Cretaceous genera *Sarbaya* (Krassilov and Shilin, 1995) and *Quadriplatanus* (Magallón-Puebla et al., 1997), which the authors of these genera assigned to the family Platanaceae.

Subsequent collecting and studying plant fossils from other sections of temporary mines of the Arkhara–Boguchansk locality have provided supplementary leaf material and displayed a stable association of these leaves with inflorescences of the genus *Bogutchanthus* (Maslova et al., 2007). Staminate inflorescences of *Bogutchanthus* combine characters typical of both Platanaceae and Hamamelidaceae. This
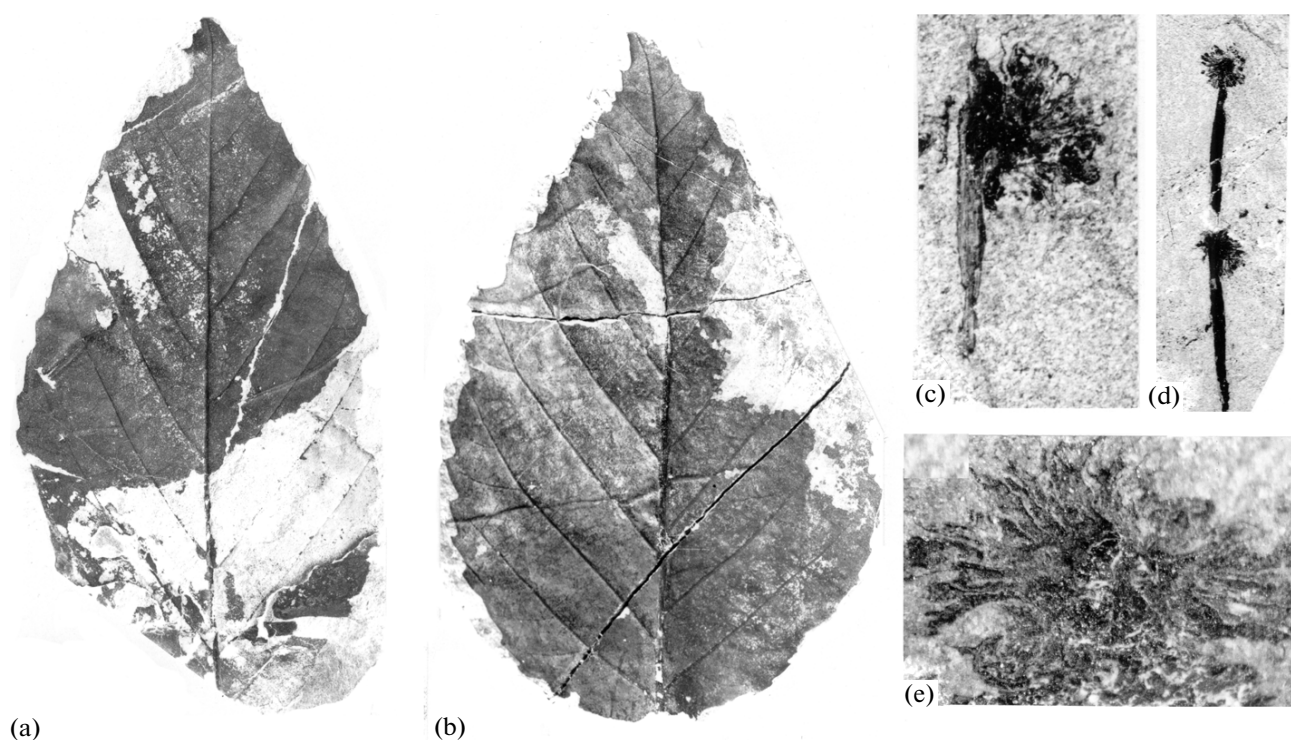
Fig. 11. Association of (a, b) leaves of *Platimeliphyllum snatolense* N. Maslova and (c–e) staminate inflorescences of *Chemurnautia stenocarpa* N. Maslova; Paleocene–Early Eocene, northwestern Kamchatka, Russia: (a) specimen PIN, no. 4256/49, × 0.85; (b) specimen PIN, no. 4256/55, ×1.1; (c) PIN, no. 4256/36, ×10; (d) PIN, no. 4256/14, ×2; (e) PIN, no. 4256/28, ×10. All specimens are stored in the Laboratory of Paleobotany of PIN.
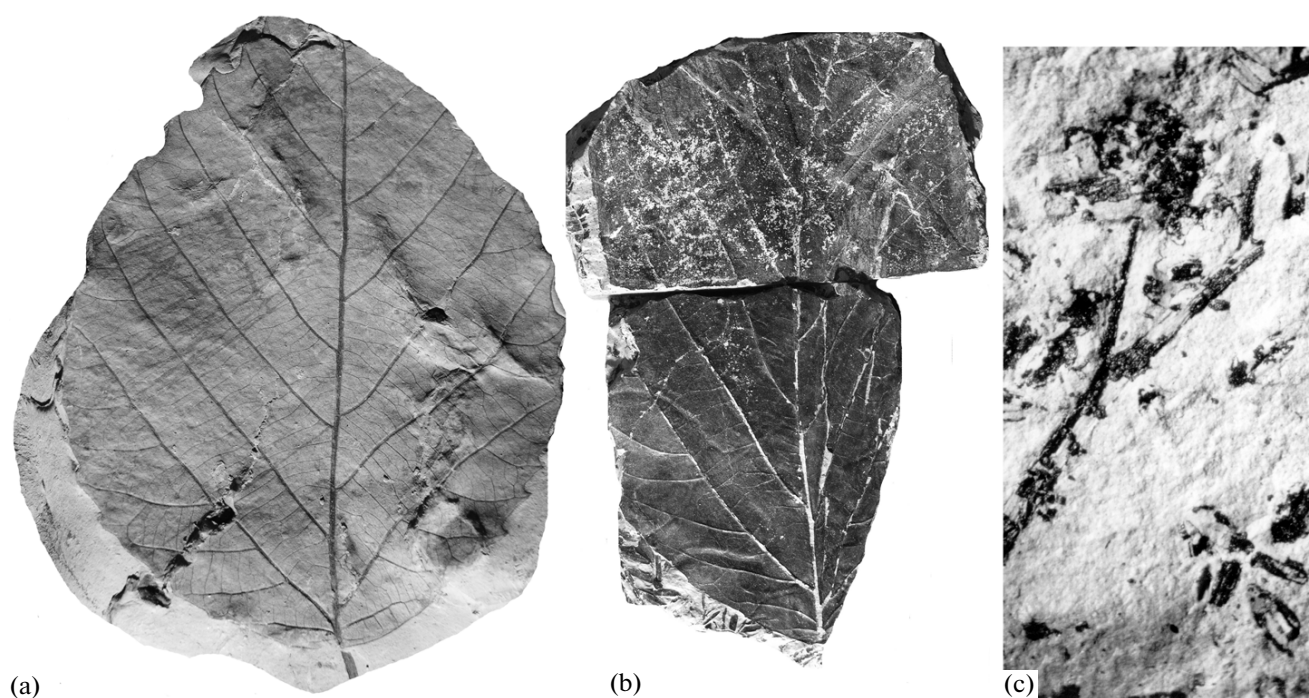

Fig. 12. Association of (a, b) leaves of *Platimeliphyllum valentinii* Kodrul et N. Maslova and (c) staminate inflorescences of *Archaranthus krassilovii* N. Maslova et Kodrul; Maastrichtian–Danian, Amur Region, Russia: (a) specimen GIN, no. BG-67, ×1.1; (b) GIN, no. AB2-2, ×0.75; (c) GIN, no. AB3-81, ×4. All specimens are stored in the Laboratory of Paleofloristics of GIN.
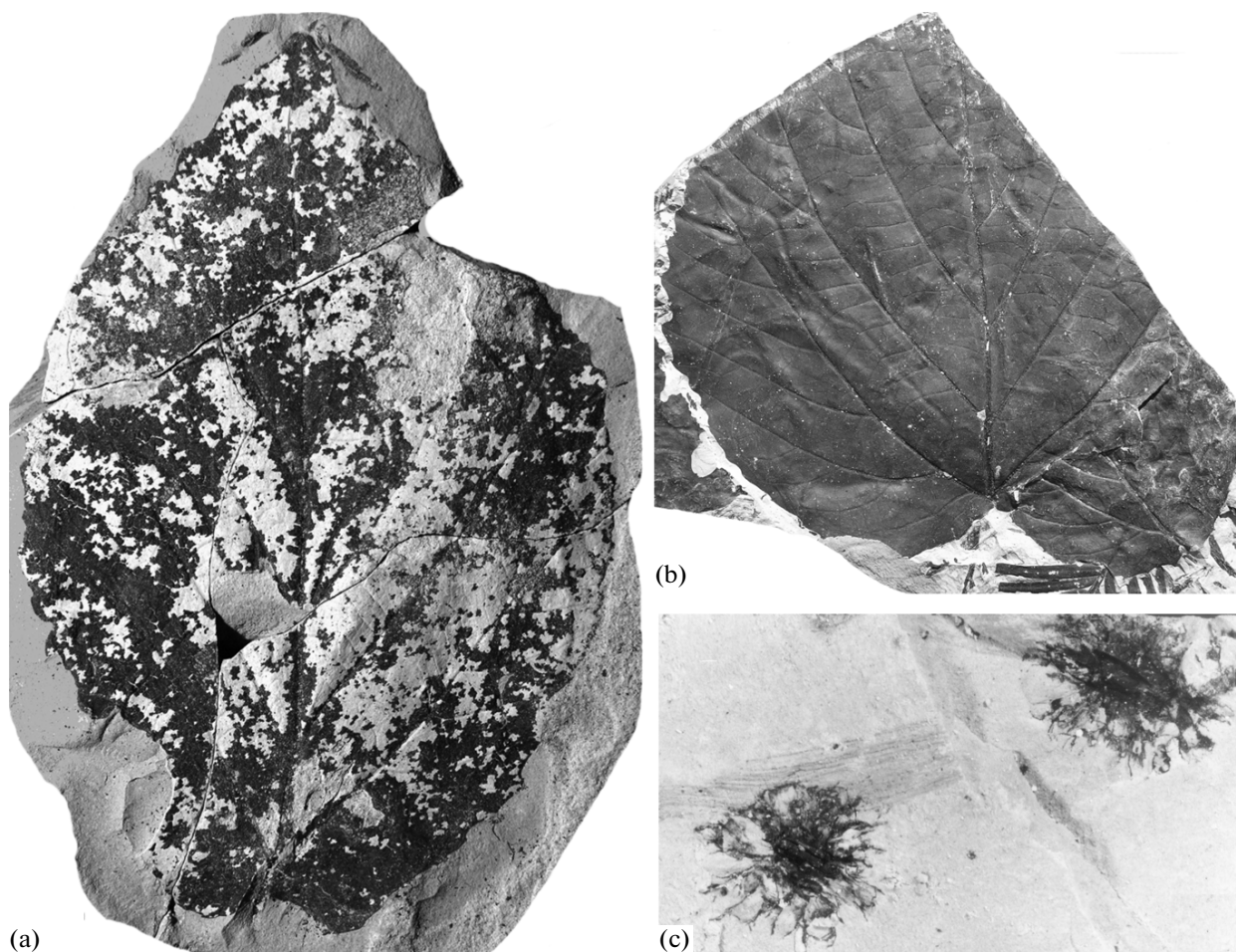
Fig. 13. Association of (a, b) leaves of *Platimeliphyllum valentinii* Kodrul et N. Maslova and (c) staminate inflorescences of *Bogutchanthus laxus* N. Maslova, Kodrul et Tekleva; Maastrichtian–Danian, Amur Region, Russia: (a) specimen GIN, no. AB3-115, ×1.3; (b) GIN, no. AB1-463, ×1; (c) GIN, no. AB1-429, ×6. All specimens are stored in the Laboratory of Paleofloristics of GIN.

genus is similar to extant and extinct platanoids in the capitate inflorescence, strictly tetramerous flowers with a well-developed perianth, and in the presence of staminodia. This genus is most similar to the group of extinct genera with tetramerous flowers (*Sarbaya, Quadriplatanus,* and *Archaranthus*).

Bogutchanthus is similar to extant and extinct hamamelids in the general morphology of the inflorescence, the presence of secondarily bisporangiate stamens, staminodia, and pantocolpate pollen grains. In the ability of forming the capitate inflorescences, the presence of bisporangiate anthers, and pantocolpate pollen grains, *Bogutchanthus* is most similar to the extant genus *Chunia* Chang (subfamily Exbucklandioideae). Among extinct hamamelids, *Bogutchanthus* is most similar to the Cenomanian genus *Viltyungia* in the shape of the inflorescence, the presence of staminodia, and the type of pollen grains (Maslova and Golovneva, 2000b).

Thus, within the Arkhara–Boguchansk Lignite Field, leaves of *Platimeliphyllum valentinii* co-occur with various staminate inflorescences (genera *Archaranthus* and *Bogutchanthus*), which differ in the attachment of heads to the axis; the development of the perianth, connective, and connective extension; the presence–absence of the staminodia; and the type and features of the sculpture of pollen grains.

(7) Association of entire leaves of Evaphyllum and capitate infructescences of Evacarpa; Late Paleocene–Early Eocene, northwestern Kamchatka, Russia (Maslova and Krassilov, 1997; Maslova, 2003).

Entire elliptical leaves of the genus *Evaphyllum* combine characters typical of *Platanus* and the genera *Liquidambar* and *Altingia* (Hamamelidaceae, Altingioideae). They are similar to the extant genus *Platanus* in the shape of the lamina (most of the Cretaceous and Early Paleogene platanoid leaves have an entire or slightly lobate lamina); deviation of the basal veins above the leaf base; well-developed basiscopic branches of the basal veins, which deviate in the shape of a fork, so that the basal vein looks slightly arched (bent) (this is characteristic of ancient *Platanus*; in

Liquidambar and living *Platanus*, the basal veins are straight); and similar tertiary venation. The characters shared with *Liquidambar* include the brochidodromous secondary veins and basiscopic branches of the basal veins; deviation from these loops of short branchlets, which terminate in the tooth notches or teeth themselves; and the tooth shape. Leaves of *Evaphyllum kamchaticum* are associated with capitate infructescences of *Evacarpa polysperma* (Maslova and Krassilov, 1997), which have naked flowers with bicarpellate gynoecium, staminodia, and intrafloral phyllomes. Based on the number of flowers in the head (16), the absence of a perianth, the bicarpellate gynoecium, the presence of sterile structures (staminodia and intrafloral phyllomes), and many ovules, the genus *Evacarpa* is referred to the subfamily Altingioideae of the family Hamamelidaceae.

(8) Association of simple and compound leaves, capitate inflorescences and infructescences of Platanus neptuni; Late Eocene–Late Miocene, Europe (Kvaček and Manchester, 2004).

Simple leaves of *P. neptuni* were described based on specimens from the Oligocene and Miocene of northern Bohemia (Bůžek et al., 1967); subsequently, the knowledge of morphological variability of this species expanded considerably due to the finds in the Tertiary deposits of western and central Europe of compound leaves with three or five leaflets, which are similar in epidermal characters to *P. neptuni* (Walter, 1985). Later, it was shown that simple, trefoliolate, and pentafoliolate leaves of fossil plane trees co-occurred in many burials, demonstrated transitional forms between morphotypes, showed identical epidermal structure, and were accompanied by the same reproductive structures (Kvaček and Manchester, 2004).

Based on this, Kvaček and Manchester proposed the name *P. neptuni* for the entire complex. The complex *P. neptuni* belongs to the extinct subgenus *Glandulosa* of the genus *Platanus*. Infructescences of this subgenus have a capitate shape characteristic of platanoids and differ significantly in the presence of a well-pronounced scar on the axis at the head base. Fruits in one head become mature nonsimultaneously. Pistillate flowers consist of 3–8 carpels included in a well-developed perianth; the carpel surface has many glandular trichomes in the lower third, the stylodia are distinct, slightly curved, the seed is solitary. The staminate inflorescence consists of flowers with a poorly developed perianth and several stamens with elongated pollen sacs. Pollen grains of *P. neptuni* are typical of platanoids; they are tricolpate, with a reticulate exine. In addition to the presence of various leaf morphotypes (simple and compound with three and five leaflets), with alternative semicraspedodromous or camptodromous venation, the epidermal characters (strongly sinuous anticlinal walls of the ordinary epidermal cells) of this subgenus are distinguished by the presence of large peltate trichomes on the fruit surface and the well-pronounced scar on the stalk of the single infructescence.

(9) Association of compound leaves of Sapindopsis, capitate staminate inflorescences of Aquia brookensis and infructescences of Friisicarpus brookensis; Early–Middle Albian, eastern North America (Crane et al., 1993).

Leaves of the genus *Sapindopsis* vary in morphology of the lamina and margin (Fontaine, 1889; Hickey and Doyle, 1977). Some morphotypes (pinnate compound leaves) have three-lobate terminal leaflets, resembling typical leaves of *Platanus* (Hickey and Doyle, 1977).

Leaves of *Sapindopsis* co-occur with infructescences of *Friisicarpus brookensis* and staminate inflorescences of *Aquia brookensis* (Crane et al., 1993). As marked above, infructescences of *Friisicarpus brookensis* consist of pentacarpellate fruits enclosed in a well-developed differentiated perianth. Staminate inflorescences of *Aquia brookensis* have pentastaminate flowers, the main distinction of which is long anther filaments, twice as long as anthers, pollen grains with foveolate–reticulate exine, in contrast to typical reticulate exine of other fossil platanoids. The fact that these specimens belong to one plant is supported by the identical cuticle of leaves and elements of the perianth and similar cuticle of carpels and connectives. In addition, pollen grains identical to those from the anthers of *Aquia* were found on the leaves of *Sapindopsis* (Crane et al., 1993).

(10) Association of compound leaves of Platanites and capitate inflorescences and infructescences; Paleocene, Island Mal, northwestern Scotland (Crane et al., 1988).

Compound leaves of *Platanites hybridicus* consist of a terminal leaflet, resembling a lobate leaf of *Platanus* from the section *Platanus*, and two lateral leaflets varying in the extent of asymmetry. They are associated with infructescences and staminate inflorescences of platanoid appearance. The name *Platanites* was initially proposed for leaves (Forbes, 1851); subsequently, as they were described in association with reproductive structures (Crane et al., 1988); the same name was used to designate both leaves and generative plant organs (e.g., Magallón-Puebla et al., 1997).

The pistillate inflorescences associated with *Platanites* have naked flowers with unknown number of elements; carpels have a well-developed curved stylodium; carpels lack hairs. The number of stamens per flower of staminate inflorescences is also unknown; at the flower base, there are short elements of the perianth, connective extensions are peltate, pollen grains are tricolpate, reticulate, of approximately the same size (16–22 μm) as pollen grains of the living plane tree.

The above examples show that fossil platanoid leaves co-occur with essentially different reproductive structures belonging to different angiosperm families. Associations of capitate reproductive structures with leaves of the genera *Ettingshausenia* and *Platimeliphyl-*

lum are of particular interest. During different periods of geological time, leaves of these genera were associated with capitate inflorescences and infructescences, which were superficially similar but considerably differed in micromorphology.

In particular, the earliest co-occurrence of leaves of *Ettingshausenia* and capitate reproductive structures (infructescence of *Anadyricarpa*) is dated Late Albian−Early Cenomanian (Maslova and Herman, 2004); the Cenomanian−Turonian beds have yielded these leaves in association with staminate inflorescences of *Sarbaya* (Krassilov and Shilin, 1995), infructescences of *Sarbaicarpa* (Maslova, 2009), and infructescences of *Friisicarpus* (Maslova and Herman, 2006); in the Turonian, leaves of *Ettingshausenia* are associated with infructescences of *Kasicarpa* (Maslova et al., 2005); and in the Early Paleocene, with infructescences of *Oreocarpa*, seeds of *Carinalaspermum*, and staminate inflorescences of *Tricolpopollianthus* (Krassilov, 1976; Maslova and Krassilov, 2002). Figure 6 shows that, during certain period (from the Late Albian−Cenomanian to at least Early Paleocene), leaves of *Ettingshausenia* were associated with reproductive structures assigned to both Platanaceae and Hamamelidaceae or displaying characters of both families. These facts, on the one hand, confirm that it is incorrect to refer these Cretaceous leaves to one extant genus *Platanus* (until recently, this was the usual practice in paleobotanic studies) and corroborate the assumption that, in the Cretaceous, there was a polymorphic group of taxa (probably at the level of extinct families), which gave rise to the extant families Platanaceae and Hamamelidaceae; on the other hand, they illustrate the concept of a greater evolutionary conservatism of leaf structures as compared with reproductive organs.

A similar picture is probably true of leaves of the genus *Platimeliphyllum*; during the period from Maastrichtian−Danian to the Early Eocene, they were associated with staminate inflorescences of three genera belonging to both Platanaceae (*Chemurnautia*: Maslova, 2002) and the extinct family Bogutchanthaceae fam. nov. (*Archaranthus*: Maslova and Kodrul, 2003; *Bogutchanthus:* Maslova et al., 2007). Inflorescences with essentially heterogeneous micromorphology (*Chemurnautia, Archaranthus*, and *Bogutchanthus*), associated with leaves of one morphotype (*Platimeliphyllum*), also illustrate the idea of the morphological stasis of platanoid leaves and, hence, greater evolutionary conservatism of leaves compared with more labile reproductive structures.

Infructescences of the genus *Friisicarpus* deserve special attention; in the Early−Middle Albian of eastern North America, they co-occur with compound leaves of the genus *Sapindopsis* (Crane et al., 1993); in the Cenomanian−Turonian of western Siberia (Russia) they are recorded in association with typical *Platanus*-like leaves of the genus *Ettingshausenia* (Maslova and Herman, 2006). Apparently, in the Cretaceous, there were plants with similar reproductive structures (genus *Friisicarpus*) and different leaf morphology (genera *Sapindopsis* and *Ettingshausenia*). As was indicated previously (Maslova, 2003), early platanoids had conservative female reproductive organs, since the same infructescences are associated with different staminate inflorescences. It is also possible that one of the two associations should not be regarded as evidence for the assignment of the specimens to one plant. The genus *Sapindopsis* shows compound pinnate or pinnatifid leaves, which are unusual for the living plane tree; therefore, it was considered for a long time to be close to the subclass Rosidae. Nevertheless, the study of epidermal features of leaves of *Sapindopsis* (Upchurch, 1984) and microstructure of pistillate and staminate capitate inflorescences associated with these leaves (Crane et al., 1993) confirmed the idea of Hickey and Doyle (1977) and Crane (1989) that this genus belongs to the family Platanaceae. However, the assumption that cuticular−epidermal characters of *Sapindopsis* are typical for Platanaceae was put in doubt (Carpenter et al., 2005).

An example of association between the same reproductive structures and different leaves is also provided by the finds of inflorescences and infructescences of the genera *Platananthus* and *Macginicarpa* and leaves of *Macginitiea* (Manchester, 1986) and *Platanus nobilis* sensu stricto (Pigg and Stockey, 1991). In this case, co-occurrence of the same reproductive structures and morphologically similar leaves is evidence for the assignment of these leaves to one genus, the more so as Pigg and Stockey (1991) indicated that leaves of *P. nobilis* sensu stricto are extremely similar to the leaves of the genus *Macginitiea*. In fact, the two genera show similar variations of leaf characters and it is possible to combine them in one genus based on the existence of transitional forms. In addition, inflorescences of *Platananthus* and infructescences of *Macginicarpa* differ essentially from those of the genus *Platanus*. Hence, it is probably unjustified to use the name of an extant genus (*Platanus*) to designate leaves of a plant with these reproductive structures (*P. nobilis* sensu stricto). However, conclusive resolution of this question requires additional studies.

Abundant and representative fossil material of various platanoid organs, in particular, co-occurrence of leaves and reproductive structures suggest that Platanaceae is one of the best documented families of early angiosperms. At the same time, representative data showing that, in a number of records, different plant organs (and associations of different organs suggesting that they belong to different families) combine characters of more than one Recent family lead to the conclusion that taxonomic affiliation of these records requires an essentially new approach. Many examples of association of platanoid leaves with other plant organs, in particular, various inflorescences and infructescences, dispersed pollen organs, isolated fruits, bark and wood fragments are evidence of the

existence in the geological past of a polymorphic plant group, the taxonomic position of some members of which should be determined beyond the framework of extant angiosperm families.

6.2.3. Probable Phylogenetic Relationships of Early Platanoids and Hamamelids

I propose to assign fossil reproductive organs that display more or less pronounced characters of living representatives of the families Platanaceae and Hamamelidaceae to the order Hamamelidales, including the families Platanaceae (with two subfamilies, Platanoideae subfam. nov. and Gynoplatananthoideae subfam. nov.), Hamamelidaceae (with four subfamilies: Hamamelidoideae, Altingioideae, Exbucklandioideae, and Rhodoleioideae), and Bogutchanthaceae fam. nov., and the order Sarbaicarpales ordo nov., comprising the extinct families Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov. Both orders, Hamamelidales and Sarbaicarpales ordo nov., emerged in the Late Albian–Cenomanian (Fig. 14). The first representatives of the families Platanaceae (subfamily Gynoplatananthoideae subfam. nov.) and Hamamelidaceae (genera *Microaltingia* and *Viltyungia*) appeared in the Albian–Cenomanian; the family Bogutchanthaceae fam. nov. appeared for the first time in the Cenomanian–Turonian. The origin of the families Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov. is also dated Cenomanian–Turonian.

The previous studies (Maslova, 2001, 2003) have shown that the form-building processes in these families were characterized by particular evolutionary features. In particular, in the family Platanaceae, new taxa appeared mostly due to morphological innovations, while an increase in taxonomic diversity of Hamamelidaceae was provided during their geological history mostly by combination of characters, which appeared at an early evolutionary stage. Although information on representatives of the newly established extinct families and order is presently incomplete, it is possible to draw tentative conclusions concerning their early phylogenetic relationships and major evolutionary trends, which resulted in the modern state of the families Platanaceae and Hamamelidaceae. The analysis of the polymorphic group of fossil platanoids and hamamelids allows the recognition of transitional forms between morphologically different living representatives of the families Platanaceae and Hamamelidaceae.

Affinity between the orders Hamamelidales and Sarbaicarpales ordo nov. is supported by the presence of shared characters in the structure of generative organs, the combination of which is unique to these orders (Fig. 15). The shared characters include primarily the capitate inflorescences and stable number of elements in the flower of early representatives. Within the order Hamamelidales, the relationship of the families Platanaceae and Hamamelidaceae is supported by the finds of

representatives of the extinct family Bogutchanthaceae fam. nov., which shows characters typical of both families. In particular, the characters shared with early platanoids include the capitate inflorescences, stable number of elements in the flower (five in Platanaceae and four in Bogutchanthaceae fam. nov.), well-developed perianth (e.g., the genera *Archaranthus* and *Quadriplatanus*), tetrasporangiate anthers (e.g., the genera *Archaranthus* and *Sarbaya*), and tricolpate pollen grains (e.g., the genera *Archaranthus* and *Quadriplatanus*). At the same time, representatives of Bogutchanthaceae fam. nov. are similar to Hamamelidaceae in the fusion of elements of the perianth and fertile elements of the flower, androecium–gynoecium (e.g., the genera *Quadriplatanus* and *Bogutchanthus*), bisporangiate anthers (genus *Bogutchanthus*), the presence of staminodia (e.g., staminate inflorescences and infructescences described by Crepet et al. (1992) and the genus *Bogutchanthus*), tricolpate pollen grains (e.g., the genera *Archaranthus* and *Quadriplatanus*), pantocolpate pollen grains (genus *Bogutchanthus*), and the nonorthotropic seed type (genus *Quadriplatanus*).

At present, the time of appearance and developmental trends of the subfamily Rhodoleioideae, which is only represented in the fossil record by Late Cretaceous seeds, remain uncertain. It is only possible to note that representatives of the extant genus *Rhodoleia* have naked flowers (or a poorly developed perianth in some species) and sterile structures, as the genus *Sarbaicarpa* (Sarbaicarpaceae fam. nov., Sarbaicarpales ordo nov.). At the same time, it is possible to reconstruct tentatively the origin of the other three subfamilies of Hamamelidaceae based on fossil reproductive organs. The characters of the subfamily Exbucklandioideae (capitate inflorescence, many ovules, the presence of staminodia, anthers in the shape of crescents, pantocolpate pollen grains, with a continuous sporopollenin rim forming the margin of the grain colpi) are observed in two families: in the synthetic genus *Viltyungia* (Hamamelidaceae) and the genus *Bogutchanthus* (Bogutchanthaceae fam. nov.). The most representative and diverse subfamily Hamamelidoideae is connected with the genera *Allonia, Androdecidua, Archamamelis,* and *Fortunearites*. In addition, particular characters of some genera of this subfamily (such as the monocarpellate gynoecium, single seed in the fruit, well-developed endosperm, bisporangiate anthers) are recorded in the genera *Sarbaicarpa* (Sarbaicarpaceae fam. nov., Sarbaicarpales ordo nov.), *Kasicarpa* (Kasicarpaceae fam. nov., Sarbaicarpales ordo nov.), and *Bogutchanthus* (Bogutchanthaceae fam. nov.). The characters of the subfamily Altingioideae (capitate inflorescence, bicarpellate gynoecium, intrafloral sterile structures, many ovules) are observed in the genus *Microaltingia*, Hamamelidaceae. However, it seems incorrect to refer this genus to the subfamily Altingioideae, because it shows a different type of pollen grains (tricolpate with a reticulate exine, which are characteristic of Platanaceae and a
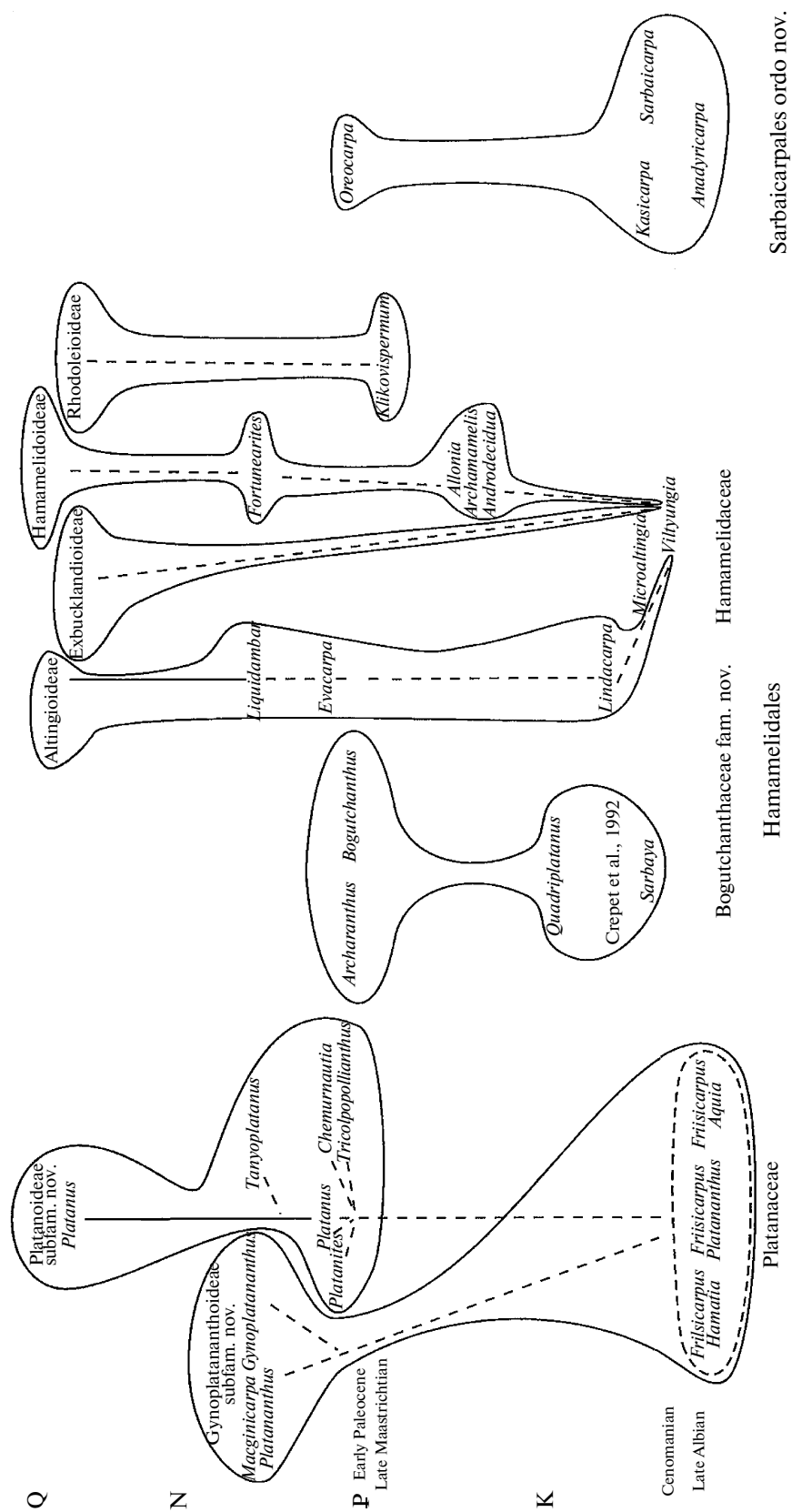
Fig. 14. Geochronology of appearance and development of the main groups of platanoids and hamamelids.
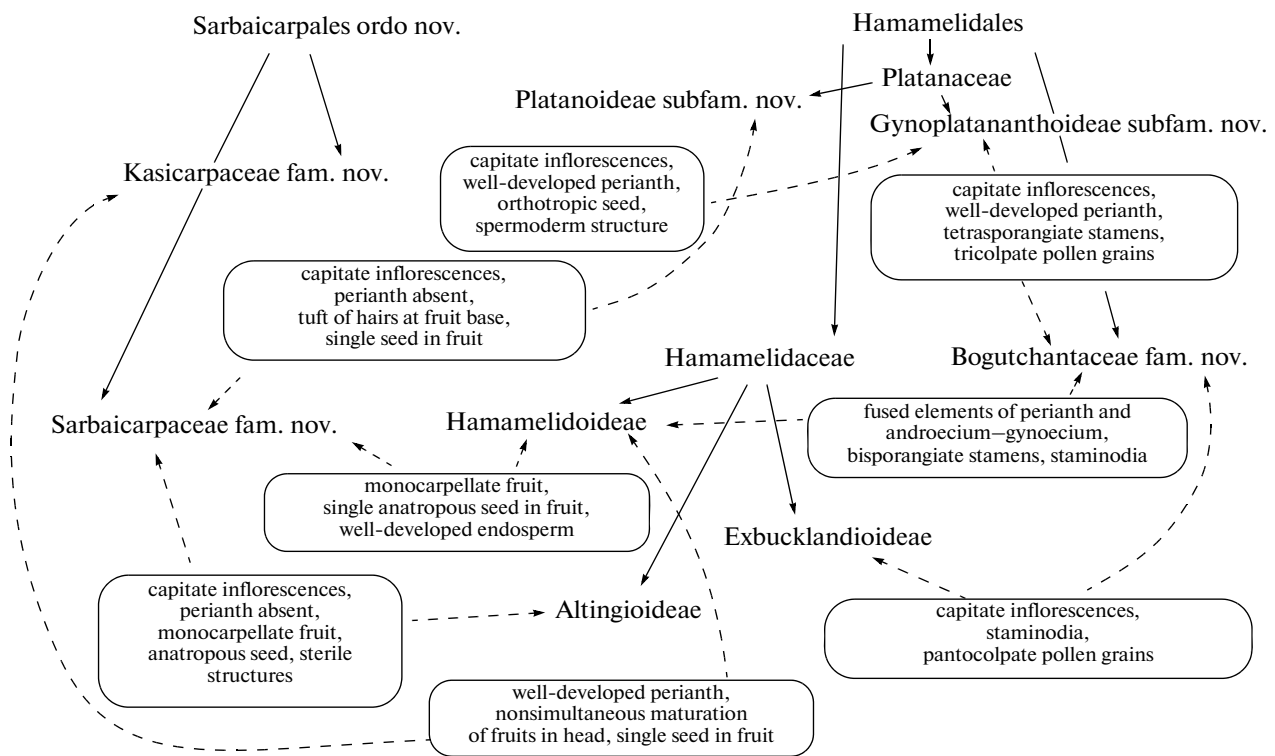
Fig. 15. Shared characters of the reproductive system in families and subfamilies of the orders Hamamelidales and Sarbaicarpales ordo. nov.: solid lines show taxonomic relationships, dotted lines show the presence of characters in particular taxa.

number of hamamelids of other subfamilies) and some distinctions in the seed structure. The characters of the subfamily Altingioideae are also recorded in the genera *Bogutchanthus*, Bogutchanthaceae fam. nov. and representatives of the order Sarbaicarpales ordo nov. In particular, the characters shared by *Bogutchanthus* and some representatives of Altingioideae are the loose capitate inflorescence, free arrangement of elements in the flower, and the presence of staminodia. Representatives of the order Sarbaicarpales ordo nov. are similar to some genera of Altingioideae in the following characters: the presence of capitate infructescences (all representatives of the order), nonsimultaneous maturation of fruits in the head (genera *Anadyricarpa*, Sarbaicarpales ordo nov., and *Kasicarpa*, Kasicarpaceae fam. nov.), naked flowers (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.), monocarpellate gynoecium (all representatives of the order), micromorphology of the seed surface (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.), spermoderm structure (*Sarbaicarpa*, Sarbaicarpaceae fam. nov.), and the presence of sterile extrafloral structures (*Sarbaicarpa*, Sarbaicarpaceae fam. nov.).

Relationships between the ancient order Sarbaicarpales ordo nov. and Hamamelidales are not limited to a number of shared characters of living representatives of Hamamelidaceae. In addition, genera of Sarbaicarpales ordo nov. display the characters typical of Platanaceae. The similarity with fossil platanoids and the

extinct family Kasicarpaceae fam. nov. is manifested in the following characters: capitate inflorescences, well-developed perianths (in all genera of Gynoplatananthoideae subfam. nov. and some genera of Platanoideae subfam. nov.), one orthotropic seed per fruit, and tricolpate pollen grains. The family Sarbaicarpaceae fam. nov. and fossil platanoids are similar in the presence of capitate inflorescences, one seed per fruit, the presence of sterile extrafloral structures in inflorescences, and in the absence or weak development of the perianth (the majority of genera of Platanoideae subfam. nov.). Note that, to date, there are only paleobotanic data on female reproductive structures referred to the order Sarbaicarpales ordo nov., while information on staminate inflorescences that could have been attributed to this order are virtually absent. The data on pollen grains are restricted to the grains adhering to the fruit surface of the genus *Kasicarpa* and regarded as those probably produced by staminate plant organs of the plant with these infructescences. These tricolpate pollen grains with a reticulate exine also combine morphological and ultrastructural characters of platanoids and some hamamelids.

Thus, paleobotanic data, namely, the discovery of extinct genera combining diagnostic characters of the families Platanaceae and Hamamelidaceae, and co-occurrence of different organs probably belonging to the same plant, but referred based on available mor-

phological and anatomical data to different extant families, suggest that they are closely related and descend from the same polymorphic group, which was represented in the geological past by extinct families and orders. Therefore, it is possible to expect new finds of extinct genera that combine morphological features of Platanaceae and Hamamelidaceae, which correspond to the beginning of the establishment of the families Platanaceae and Hamamelidaceae.

CONCLUSIONS

(1) The establishment of the taxonomic position of dispersed Cretaceous *Platanus*-like leaves has become an urgent problem. Available paleobotanic data strongly suggest that the commonly accepted assignment of these leaves to the extant genus *Platanus* is unacceptable. The high polymorphism of these leaves, with a significant proportion of macromorphological characters of other families (in particular, Hamamelidaceae); the epidermal structure, which is frequently atypical for *Platanus* and the family Platanaceae, combined with macromorphological features characteristic of *Platanus*; and the cases of association of these leaves with different reproductive structures prevent the assignment of these Cretaceous specimens to one genus, particularly, an extant genus.

The study of the variation range of morphological and cuticular–epidermal leaf characters of the polymorphic living species *Platanus acerifolia* provided a model useful for identification of dispersed fossil platanoid leaves. As a result, wide morphological variability, involving almost all macromorphological leaf characters, with three basic morphotypes of leaf lamina, was recognized; in addition, the distribution of morphotypes within the tree crown, depending on local conditions was established. It was shown that leaves of *P. acerifolia* combine morphological characters typical of both Platanaceae and Hamamelidaceae genera. The data on morphological variability of leaves of the living plane tree are useful for the determination of taxonomic affiliation of Cretaceous leaves of platanoid appearance; this could have prevented unreasonable establishment of new platanoid genera based on leaves combining certain macromorphological characters.

In my opinion, the recently developed approach to the establishment of new extinct platanoid genera based on cuticular–epidermal characters (Golovneva, 2003, 2004, 2007) does not reflect actual diversity of ancient platanoids. Based on ecological stipulation of a number of cuticular–epidermal characters (Zalensky, 1904; Shennikov, 1950; Goryshina, 1979; etc.), characteristics of the epidermis of different leaf morphotypes of extant *P. acerifolia* were investigated; as a result, variation of cuticular–epidermal characters depending on the position of leaves in the tree crown was shown. All leaf morphotypes of *P. acerifolia* display generally the same pattern of the epidermal struc-

ture. Differences are observed in the extent of sinuosity and thickness of the anticlinal walls of the ordinary epidermal cells, the type and basal diameter of trichomes, extent and type of cuticular folds on the lower and upper surfaces of the lamina. Significant variations are also observed in dimensional and quantitative characteristics of various epidermal structures, such as the number, size, and extent of cutinization of trichomes and the number of stomata. These characters are manifested in one individual of *P. acerifolia* and, at the same time, usually provide the basis for the establishment of new fossil platanoid taxa. Along with the confirmation of the well-known concept of differences in epidermal characters between sun and shade leaves (Zalensky's law), the study of *P. acerifolia* has shown a correlation between a number of epidermal characters and the lamina shape.

Thus, taking into account the fact that the complex of cuticular–epidermal characters of the family Platanaceae was formed as early as the Early Cretaceous, while species of the extant genus show little differences in structural epidermal characters, the majority of presently known cuticular–epidermal characters or their combinations in fossil *Platanus*-like leaves fall in the variation range of the genus *Platanus* and should not be taken for a reliable criterion for the identification of genera and species; they only show relationship to (or difference from) the family Platanaceae. Both morphological and epidermal characters of polymorphic leaves of typical platanoid appearance were formed in the Late Albian and remained almost constant to the present time, illustrating the statement of the morphological stasis of these leaves. It is important that fossil *Platanus*-like leaves include both morphotypes with variations of epidermal characters typical of Platanaceae and morphotypes with the cuticular–epidermal characters differing essentially from those of Platanaceae.

In contrast to the frequently used principle of the designation of dispersed Cretaceous leaves as extant genera, in a number of works (Maslova et al., 2005, 2008a, 2008b; Kodrul and Maslova, 2007; etc.) it proved necessary to name dispersed leaf remains of Cretaceous angiosperms according to the morphological leaf classification, which is not connected with the natural classification (Krassilov, 1979), which is based on the observable characters of leaf morphology. It is proposed to use the generic name *Ettingshausenia* for Cretaceous and Early Paleogene leaves showing the morphology typical of the living plane tree. The name *Platimeliphyllum* is proposed for Paleocene–Eocene entire leaves with craspedodromous venation, variously developed basal veins, and dentate margin.

(2) In contrast to the commonly accepted idea that the extant families Platanaceae and Hamamelidaceae were widespread in the Cretaceous, I propose a new system of fossil platanoids and hamamelids, which is based on reproductive structures.

The analysis of fossil capitate inflorescences and infructescences has shown that, despite external uniformity, they vary considerably in micromorphological characters, which display similarity to Platanaceae, Hamamelidaceae, or combine characters of the two families. Based on this fact and co-occurrences of leaves of one morphotype with different reproductive structures, it is proposed to assign fossil specimens with more or less pronounced characters of living representatives of the families Platanaceae and Hamamelidaceae to (I) the order Hamamelidales, including (1) the family Platanaceae with two subfamilies, Platanoideae subfam. nov. and Gynoplatananthoideae subfam. nov.; (2) the family Hamamelidaceae, with four subfamilies, Hamamelidoideae, Altingioideae, Exbucklandioideae, and Rhodoleioideae (after Endress, 1989a); and (3) the family Bogutchanthaceae fam. nov., and (II) the order Sarbaicarpales ordo nov., comprising the extinct families (1) Sarbaicarpaceae fam. nov. and (2) Kasicarpaceae fam. nov. Both orders, Hamamelidales and Sarbaicarpales ordo nov., emerged in the Late Albian–Cenomanian. In the Albian–Cenomanian, the first representatives of the families Platanaceae (subfamily Gynoplatananthoideae subfam. nov.) and Hamamelidaceae (genera *Microaltingia* and *Viltyungia*) appeared; in the Cenomanian–Turonian, the first record of the family Bogutchanthaceae fam. nov. is marked. The origin of the families Sarbaicarpaceae fam. nov. and Kasicarpaceae fam. nov. is also dated to the Cenomanian–Turonian.

It is evident that extinct platanoids and hamamelids compose a heterogeneous group of taxa, more or less related to the Recent families Platanaceae and Hamamelidaceae. The affinity between the orders Hamamelidales and Sarbaicarpales ordo nov. is supported by the presence of shared characters in the structure of reproductive organs (primarily capitate inflorescences and stable number of elements in the flower in early representatives). The extinct family Bogutchanthaceae fam. nov., which displays characters typical of both Platanaceae and Hamamelidaceae, provides transitional forms between these families. The characters shared with ancient platanoids include the capitate inflorescences, stable number of elements in the flower (five in Platanaceae and four in Bogutchanthaceae fam. nov.), well-developed perianths (e.g., the genera *Archaranthus* and *Quadriplatanus*), tetrasporangiate anthers (e.g., the genera *Archaranthus* and *Sarbaya*), and tricolpate pollen grains (e.g., the genera *Archaranthus* and *Quadriplatanus*). Bogutchanthaceae fam. nov. is similar to the Hamamelidaceae in the fusion of elements of the perianth and fertile parts of the flower, androecium–gynoecium (e.g., the genera *Quadriplatanus* and *Bogutchanthus*); bisporangiate anthers (genus *Bogutchanthus*); presence of staminodia (e.g., staminate inflorescences and infructescences described by Crepet et al. (1992) and the genus *Bogutchanthus*); tricolpate pollen grains (e.g., the gen-

era *Archaranthus* and *Quadriplatanus*); pantocolpate pollen grains (genus *Bogutchanthus*); and nonorthotropic seeds (genus *Quadriplatanus*).

Based on the study of fossil reproductive organs, the origins of three subfamilies of Hamamelidaceae have tentatively been established. The characters of the subfamily Exbucklandioideae (capitate inflorescence, many ovules, the presence of staminodia, crescentic anthers, pantocolpate pollen grains, and continuous sporopollenin rim forming the margin of the colpi of the pollen grain) are observed in two families: the Cenomanian synthetic genus *Viltyngia* (Hamamelidaceae) and the Paleocene genus *Bogutchanthus* (Bogutchanthaceae fam. nov.). The most representative and diverse subfamily Hamamelidoideae comprises the Late Cretaceous genera *Allonia, Androdecidua, Archamamelis*, and *Fortunearites*. Certain characters of some genera of this subfamily (monocarpellate gynoecium, single seed in the fruit, well-developed endosperm, bisporangiate anthers) are recorded in the genera *Sarbaicarpa* (Sarbaicarpaceae fam. nov., Sarbaicarpales ordo nov.), *Kasicarpa* (Kasicarpaceae fam. nov., Sarbaicarpales ordo nov.), and *Bogutchanthus* (Bogutchanthaceae fam. nov.). The first finds of the subfamily Altingioideae are dated Coniacian (genus *Lindacarpa*). Certain characters of this subfamily (capitate inflorescence, bicarpellate gynoecium, sterile intrafloral structures, many ovules) are recorded in the genera *Microaltingia* (Hamamelidaceae) and *Bogutchanthus* (Bogutchanthaceae fam. nov.) and representatives of the order Sarbaicarpales ordo nov. Representatives of the order Sarbaicarpales ordo nov. are similar to some genera of Altingioideae in the following characters: the presence of capitate infructescences (all representatives of the order), non-simultaneous maturation of fruits in the head (genera *Anadyricarpa*, Sarbaicarpales ordo nov. and *Kasicarpa*, Kasicarpaceae fam. nov.), naked flowers (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.), monocarpellate gynoecium (all representatives of the order), micromorphology of the seed surface (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.), spermoderm structure (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.), and the presence of sterile extrafloral structures (genus *Sarbaicarpa*, Sarbaicarpaceae fam. nov.).

The time of appearance and developmental pathways of the subfamily Rhodoleioideae, which is only represented in the fossil record by Late Cretaceous seeds, remain uncertain. It is only possible to mark that the extant genus *Rhodoleia* is similar to *Sarbaicarpa* (Sarbaicarpaceae fam. nov., Sarbaicarpales ordo nov.) in the presence of naked flowers (or a poorly developed perianth in some species of *Rhodoleia*) and sterile structures.

Relationships of the ancient order Sarbaicarpales ordo nov. and the order Hamamelidales are also manifested in the presence of characters typical of Platanaceae. The characters shared with extinct platanoids and the extinct family Kasicarpaceae fam. nov. are as

follows: capitate inflorescences, well-developed peri-anths (in all genera of Gynoplatananthoideae subfam. nov. and some genera of Platanoideae subfam. nov.), single orthotropic seed in the fruit, and tricolpate pollen grains. The family Sarbaicarpaceae fam. nov. and fossil platanoids are similar in the presence of capitate inflorescences, single seed in the fruit, the presence of sterile extrafloral structures in inflorescences, and in the absence of a perianth (most of the genera of Platanoideae subfam. nov.).

Phylogenetic affinity of the extant families Platanaceae and Hamamelidaceae is supported not only by fossil reproductive and leaf structures combining characters of these families but also by the isomorphic polymorphism, which is manifested in macro- and micromorphological characters. The phenomenon of isomorphic polymorphism, illustrated by the example of Platanaceae and Altingioideae, is considered to be evidence of structural parallelism in the development of these plant groups, which is determined by the morphogenetic basis inherited from a common ancestor. This statement is supported by (1) many uniform characters of vegetative and generative organs over a long geological time (it is possible to regard these characters as either new formations or reactivated latent potentialities); (2) the fusion of floral structures (e.g., the formation of staminal and floral tubes) in either group; and (3) uniform phylogenetic trends in the development of a number of characters of reproductive organs. It has been shown that leaves of living Platanaceae and Altingioideae, displaying a simple temporary section, allow primary comparisons of variation series of leaf characters, while paleontological data are more important for comparisons of reproductive organs in genera of different ages and for the reconstruction of their evolutionary trends.

Associations of fossil platanoid leaves with essentially different reproductive structures assigned to different angiosperm families have repeatedly been found during various time periods. In different periods of geological time, leaves of the genera *Ettingshausenia* and *Platimeliphyllum* co-occurred with externally uniform capitate inflorescences and infructescences, which, however, vary considerably in micromorphology and display characters of both Platanaceae and Hamamelidaceae and combine characters of both families; therefore, these genera should be considered within the framework of the morphological system. These associations illustrate the statement that leaf structures are evolutionarily more stable than reproductive organs. At the same time, reproductive structures show a strategy opposite to leaves, i.e., the stability of characters in one chronological aspect (in contrast to variability) is combined with high evolutionary rates.

Repeated co-occurrences of leaves and reproductive structures promote the solution of taxonomic questions. In particular, the same reproductive structures (inflorescence and infructescences of the genera *Platananthus* and *Macginicarpa*) are associated with leaves referred to different genera (*Macginitiea*: Manchester, 1986; *Platanus nobilis* sensu stricto: Pigg and Stockey, 1991); however, transitional morphotypes and co-occurrences of uniform reproductive structures and morphologically similar leaves are evidence for the assignment of these leaves to one genus.

(3) The disagreement between molecular and traditional morphological concepts of the taxonomic positions and phylogenetic relationships of Platanaceae and Hamamelidaceae is caused primarily by the difference in methodological principles and insufficient involvement in cladistic analysis of extinct taxa. At the same time, extinct platanoids and hamamelids are mostly artificially fit in the framework of extant families and, hence, introduce additional contradictions in the analysis. The new systematics proposed in this study refers fossil forms to new extinct families and is believed to contribute to the resolution of some contradictions. The synthesis of data obtained in various fields of biology (traditional morphology, molecular data, paleobotanic records) is probably the only correct approach to the reconstruction of true phylogenetic relationships between taxa.

ACKNOWLEDGMENTS

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