

Association of Vegetative and Reproductive Organs of Platanoids (Angiospermae): Significance for Systematics and Phylogeny

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Abstract—Some examples of association between platanoid leaves and various reproductive structures are considered. The expediency of determining dispersed Cretaceous platanoid leaves using a morphological system that is independent of the system of modern plants is discussed. It is confirmed that leaf structures are more conservative than reproductive organs. It is proposed that, in the geological past, there was a polymorphic group that was probably represented by extinct families which gave rise to modern families (in particular, Platanaceae and Hamamelidaceae).

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INTRODUCTION

Among rather representative material of fossil platanoids, the cases of co-occurrence of different organs are of particular interest. These records are mostly associations of leaves and reproductive structures; less often, they are accompanied by remains of wood, bark, or shoots. For a long time, different plant organs buried together were usually examined separately because it was not evident that they belonged to the same plant, as these records were extremely scarce. As these data accumulated, the taphonomic patterns of co-occurrence of different plant organs were generalized. Although reproductive structures and leaves almost never occur in natural association, repeated co-occurrences in the same bed and the same rock sample suggest that these organs belong to one plant. In addition, examples of these associations of plant organs are presently known in the beds of different time ranges.

Platanoid leaves are usually polymorphic; therefore, it is difficult to identify them at the generic and even family level. The epidermal characters, which could have facilitated identification of leaf specimens, are frequently controversial and are not always accessible for examination. Taking into account the fact that the same leaf morphotypes occur in Cretaceous deposits along with different reproductive structures, it has been proposed to determine some of these records following the morphological (independent of natural) system (Maslova et al., 2005). In particular, it was proposed to use the generic name *Ettingshausenia* Stiehler to designate Cretaceous leaf remains that were previously assigned based on the general morphology to the extant genus *Platanus* L. In contrast to leaves, it is possible to distinguish with certainty platanoid reproductive struc-

tures similar in macromorphology based on microstructural characters. Capitulate inflorescences and infructescences that seem almost identical in general shape show characters typical not only for different genera but even different families. These specimens are assigned to the families 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, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006) or Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004); sometimes, they combine the characters of both families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005, 2007).

The leaf morphotype typical for the subgenus *Platanus* of the genus *Platanus* first appeared in the geological record in the Albian; therefore, it was originally thought that this extant genus emerged in the Early Cretaceous. Subsequently, it was shown that, judging from the reproductive structures, this genus appeared in the Paleocene (Maslova, 1997; Kvaček et al., 2001). In the fossil record, platanoid forms associated with reproductive structures include simple lobate leaves of the genera *Ettingshausenia* and *Macginitiea* Wolfe et Wehr, simple nonlobate leaves of the genera *Platimeliphyllum* N. Maslova and *Evaphyllum* N. Maslova, and compound leaf morphotypes assigned to the genera *Sapindopsis* Fontaine and *Platanites* Forbes and to *Platanus neptuni* (Ettings.) Bůžek, Holý et Kvaček.

It is possible to classify co-occurrences of platanoid leaves and reproductive structures into several groups (Table 1). The first comprises associations of leaves of

Table 1. Associations of platanoid leaves and reproductive structures















Leaves	Reproductive structures			
	genus	supergeneric taxa	geological age	references
Simple lobate				
<i>Ettingshausenia</i>				
	<i>Anadyricarpa</i>	Altingioideae, Hamamelidaceae	Late Albian–Early Cenomanian	Maslova and Herman, 2004
	<i>Friisicarpus</i>	Platanaceae	Cenomanian	Maslova and Herman, 2006
	<i>Kasicarpa</i>	Hamamelidales	Turonian	Maslova et al., 2005
	<i>Oreocarpa</i> , <i>Tricolpopollianthus</i> , <i>Carinalaspermum</i>	Platanaceae	Early Paleocene	Krassilov, 1976; Maslova and Krassilov, 2002
<i>Platanus bacicordata</i>				
	<i>Platanus stenocarpa</i>	Platanaceae	Late Paleocene–Early Eocene	Maslova, 1997
<i>Macginitiea</i>				
	<i>Macginicarpa</i> , <i>Platananthus</i>	Platanaceae	Middle Eocene	Manchester, 1986
<i>Platanus nobilis</i>				
	<i>Macginicarpa</i> , <i>Platananthus</i>	Platanaceae	Paleocene	Pigg and Stockey, 1991

Table 1. (Contd.)

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

Ettingshausenia (1) and capitate inflorescences and fructifications assigned to platanoids (Krassilov, 1976; Krassilov and Shilin, 1995; Maslova and Herman, 2006), hamamelids (Maslova and Herman, 2004), and combining characters of the two families (Maslova et al., 2005). The lobate leaves of *P. basicordata* Budants., Platanaceae, characteristic of the subgenus *Platanus* (2) are associated with reproductive structures typical for *Platanus stenocarpa* N. Maslova (Maslova, 1997). Among lobate forms, leaves of the genus *Macginitiea*, Platanaceae (3) are associated with reproductive structures that are also assigned to Platanaceae (Manchester, 1986). Lobate leaves of *Platanus nobilis* Newb. sensu stricto, which are similar in morphology to *Macginitiea* (4) are also met in association with inflorescences of the same genera (Pigg and Stockey, 1991).

Entire leaves of the genera *Platimeliphyllum* (5) and *Evaphyllum* (6) are characterized by a set of 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, 2002; Maslova and Kodrul, 2003) or only determined to the order Hamamelidales (Kodrul and Maslova, 2007; Maslova et al., 2007). Leaves of the genus *Evaphyllum* co-occur with fructifications assigned to hamamelids (Maslova and Krassilov, 1997).

The polymorphic extinct species *Platanus neptuni* has both simple entire and compound leaves. Only extinct representatives of the genus *Platanus* have compound leaves. In some localities, leaves of *P. neptuni* (7) is associated with the unique inflorescences and fructifications of *P. neptuni* (Kvaček and Manchester, 2004). Compound leaves are also recorded in the genera *Sapindopsis* (8) and *Platanites* (9), which co-occur with various reproductive structures (Crane et al., 1988, 1993).

REVIEW OF ASSOCIATIONS OF PLATANOID LEAVES AND REPRODUCTIVE STRUCTURES

1. Associations of Leaves of *Ettingshausenia* and Capitate Inflorescences and Infructescences

Ettingshausenia is characterized by variable leaf blades (from entire triangular, pentagonal and hexagonal rhombic or ovate rhombic, with undeveloped or rudimentary blades to lobate, with two to six lateral lobes), frequently asymmetrical. The leaf base is usually more or less wedge-shaped, sometimes peltate; the tip is often pointed; the margin of the leaf blade is dentate-incised, occasionally, entire. The nervation is actinodromous (palinactinodromous) craspedodromous, with well-developed basal veins; the tertiary veins are scalariform or branchy scalariform.

As was marked above, the leaves of typical platanoid morphotype assigned to the genus *Ettingshausenia* occur in association with different reproductive

structures showing the characters of platanoids (Krassilov, 1976; Krassilov and Shilin, 1995; Maslova and Herman, 2006), hamamelids (Maslova and Herman, 2004), or combining the characters of both families (Maslova et al., 2005).

1.1. Leaves of *Ettingshausenia*—Infructescences of *Anadyricarpa* N. Maslova et Herman, Bark Fragments (Late Albian–Early Cenomanian, Northeastern Russia; Maslova and Herman, 2004). Infructescences of *Anadyricarpa* occur in association with leaves that were originally described as “*Platanus*” *louravetlanica* Herman et Shczepetov (Herman, 1994) and later assigned to the genus *Ettingshausenia* (Maslova et al., 2005) and with bark fragments resembling bark of the extant plane tree. These leaves are in general similar to the leaves of the extant plane tree; however, a number of characters show affinity to some hamamelids. This statement is supported by the asymmetry of the base and leaf blade, asymmetrical deviation of basal veins varying in length and thickness, and certain features of tertiary nervation (mostly orthogonal reticulate). These leaves are most similar to mature leaves of the genus *Shaniodendron* (Chang) Deng, Wei et Wang, Hamamelidaceae (Wang and Li, 2000, text-figs. c, d). Essential differences from hamamelids are the suprabasal deviation of the basal veins and the well-pronounced infrabasal veins. Unfortunately, the poor preservation of specimens prevents epidermal examination.

Capitate infructescences of *Anadyricarpa* consist of many fruits radiating from the center and varying in the extent of maturity. *Anadyricarpa* has a well-developed perianth, which forms the floral tube completely embracing the sole carpel. Note that, in fructifications of *Anadyricarpa*, hamamelid characters undoubtedly predominate, but some platanoid characters (such as the shape of fructifications and well-developed perianth) are also observed, whereas accompanying leaves display more pronounced platanoid characters are some features typical for hamamelids.

Platanoid leaves and infructescences of *Anadyricarpa* were accompanied by bark fragments, which were almost identical in shape and external sculpture to bark of extant *Platanus*. A characteristic feature of trunks and branches of the extant plane tree is the shedding of bark fragments in rather large pieces; therefore, the trunk shows a marble pattern. The shedding of bark, which often occurs in extant angiosperms, has not been described in fossil specimens. Our material gives evidence of the existence of this phenomenon at early stages of evolutionary development of angiosperms.

1.2. Leaves of *Ettingshausenia*—Staminate Inflorescences of *Sarbaya* Krassilov et Shilin (Cenomanian–Turonian, Kazakhstan, Krassilov and Shilin, 1995). Lobate leaves, varying in the development of blades, from the Cenomanian–Turonian of Kazakhstan were originally assigned to *Platanus pseudoquillelmae* Krass. and *P. cuneiformis* Krass. (Shilin, 1986). Along with characters typical for *Platanus*, they show some

structural features resembling representatives of Altingioideae, in particular, frequent veins intermediate between the secondary veins and reaching approximately half the distance to the edge of the leaf blade, and well-developed marginal glandules. The epidermal structure of these leaves shows characters typical for representatives of Fagaceae (Krassilov and Shilin, 1995).

Staminate inflorescences of the genus *Sarbaya* display a considerably reduced perianth, which is at most one-third as long as the stamens, strictly tetramerous organization of flowers, and tricolpate pollen grains.

1.3. Leaves of *Ettingshausenia*—Infructescences of *Friisicarpus* (Friis, Crane et Pedersen) N. Maslova et Herman (Cenomanian–Turonian, Western Siberia, Russia; Maslova and Herman, 2006). In the majority of cases, the records of reproductive structures of the genus *Friisicarpus* (*F. marylandensis* (Friis, Crane et Pedersen) N. Maslova et Herman, *F. carolinensis* (Friis, Crane et Pedersen) N. Maslova et Herman, *F. elkneckensis* (Pedersen, Friis, Crane et Drinnan) N. Maslova et Herman) are not accompanied by leaves. The only species, *F. brookensis* (Crane, Pedersen, Friis et Drinnan) N. Maslova et Herman (Crane et al., 1993), has been recorded in association with staminate inflorescences of *Aquia brookensis* Crane, Pedersen, Friis et Drinnan and leaves of cf. *Sapindopsis variabilis* Fontaine.

We have described an association of infructescences of *Friisicarpus* sp. and leaves of *Ettingshausenia* from the Cenomanian of Western Siberia. Fructifications of *Friisicarpus* consist of many strictly pentamerous flowers included in a well-developed perianth, the carpels of which lack styloids.

The find of infructescences of *Friisicarpus* sp. in the Cenomanian of Western Siberia not only expanded the geographical range of this genus but also provided evidence of significant conservatism of female reproductive organs of early platanoids. Apparently, similar fructifications are associated with different leaf morphotypes, i.e., compound pinnate or pinnatifid leaves of the genus *Sapindopsis* (Crane et al., 1993) and lobate leaves of *Ettingshausenia* (Maslova and Herman, 2006).

1.4. Leaves of *Ettingshausenia*—Infructescences of *Kasicarpa* N. Maslova and Golovneva et Tekleva (Turonian, Western Siberia, Russia, Maslova et al., 2005). Infructescences of *Kasicarpa* have been recorded in association with platanoid-like leaves, originally described as *Populites pseudoplatanoides* Lebedev (1955). Subsequently, Golovneva (2007) examined the epidermal structure of these leaves and established a new genus, *Tasymia* Golovneva, assigning it to the family Platanaceae. We have already questioned the statement that *Tasymia* is a separate genus (Maslova et al., 2008). It should be noted here that macromorphological characters of these leaves fit in the range of the extant genus *Platanus*, whereas, as indicated by the author of the genus, epidermal distinctions include a greater number of glandular trichomes, which are more cutinized, the presence of a cutinized ring at the base of

the trichomes, and the formation of pedicles in trichomes. However, the quantitative and dimensional characteristics of the epidermal structures depend mostly on certain ecological factors and, hence, should not be taken into account as the taxonomic status is established. At the same time, other characters are not unique and occur in the leaves of extant species of *Platanus* (see, for example, Carpenter et al., 2005). Therefore, I assign the leaves associated with fructifications of *Kasicarpa* to the genus *Ettingshausenia*.

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

As compared with Hamamelidaceae, *Kasicarpa* is most similar to genera of the subfamilies Altingioideae and Hamamelidoideae. *Kasicarpa* is similar to extant Altingioideae in the general pattern of the complex unisexual inflorescence in the shape of an axis with heads, in the number of flowers per head, and in the nonsimultaneous maturation of carpels. The major differences are the bicarpellate gynoecium with a half-inferior ovary and several seeds in a fruit in Altingioideae and the monomeric gynoecium with a superior ovary and the only seed in *Kasicarpa*. However, as was previously shown (Bogle, 1986), although the bicarpellate gynoecium dominated in Altingioideae, monocarpellate forms also occurred. In addition, extant Altingioideae lack a perianth. On the contrary, extinct genera related to Altingioideae usually had a well-developed perianth. Of extinct Altingioideae, *Anadyricarpa* from the Late Albian–Early Cenomanian of northeastern Russia is most similar in infructescences to *Kasicarpa* (Maslova and Herman, 2004). The similarity is manifested primarily in the presence of a single carpel per flower, in the capitate infructescences, the number of flowers per head, and in the well-developed perianth. Extant representatives of the subfamily Hamamelidoideae are distinguished by the wider variation range of floral structures. *Kasicarpa* is similar to some genera of Hamamelidoideae (for example, *Sycopsis* Oliv. and *Parrotia* C.A. Mey) in the presence of a well-pronounced perianth and a single seed in the carpel (in almost all Hamamelidoideae). In addition, some extant Hamamelidoideae (e.g., *Parrotiopsis* Schneider) have a monomeric gynoecium (Kapil and Kaul, 1972). Significant distinctions of Hamamelidoideae from *Kasicarpa* are the bicarpellate gynoecium with a half-inferior ovary and dense capitate inflorescences composed of a larger number of non synchronously ripening fruits.

1.5. Leaves of *Ettingshausenia*—Infructescences of *Oreocarpa* N. Maslova et Krassilov, Staminate Inflorescences of *Tricolpopollianthus* Krassilov (Early Paleocene, Amur Region, Russia, Krassilov, 1976; Maslova and Krassilov, 2002). The platanoid-

like leaves determined as *Platanus raynoldsii* Newb. have been recorded in many Cretaceous localities. Using extensive material from Tsagayan beds of the Amur Region, Krassilov (1976) described many diverse morphotypes of these leaves, which are identical in epidermal structure. Since these leaves were associated with peculiar reproductive structures (seeds of *Carinalaspermum bureicum* Krassilov and staminate heads of *Tricolpopollianthus burejensis* Krassilov), showing characters of Platanaceae, but distinct from the extant plane tree, Krassilov put in doubt the existence in the Cretaceous of the genus *Platanus*. These leaves were tentatively assigned to the extant genus; in particular, the generic name was given in inverted commas. Tsagayan leaves of "*Platanus*" *raynoldsii* described by Krassilov show significant polymorphism; based on macromorphology, it is possible to assign extreme variants to different genera of other families. The most frequent morphotype is the same as in the genus *Platanus*; however, it is evident that the Tsagayan plant has typical platanoid leaves along with other morphotypes and its reproductive organs differ from those of *Platanus*. Subsequently, a new combination, *Ettingshausenia raynoldsii* (Newb) Moiseeva, was proposed (Moiseeva, 2008).

The original description of *Carinalaspermum bureicum* considers individual winged seeds and fruits with carpellodia preserved at their base (Krassilov, 1976, pl. 33, figs. 3, 4). Subsequently, in the material collected in the same locality, M.A. Akhmetiev and T.M. Kodrul (Geological Institute of the Russian Academy of Sciences) revealed and transferred to us for examination additional specimens with imprints of characteristic fructifications. They were determined by us as *Oreocarpa bureica* N. Maslova et Krassilov (Maslova and Krassilov, 2002). These infructescences differ from capitate fructifications of platanoids and other Hamamelidales in the very small size, small number of seed organs, only one of which reached maturity, becoming in this state larger than the head.

The surface of the carpellodium displays elliptical tricolpate pollen grains, with a reticulated exine. Individual pollen grains occurred on the cuticle of carpellodia of several heads, strongly suggesting that these pollen grains were preserved attached to the carpellodia after pollination and, hence, were produced by staminate organs of a plant that had pistillate inflorescences as in *Oreocarpa*. These pollen grains are similar in the key characters to those of *Tricolpopollianthus burejensis* (Krassilov, 1976).

Staminate inflorescences of the genus *Tricolpopollianthus* are similar to those of *Platanus* and differ in the less peltate connective and the longer colpi of pollen grains.

2. Association of Lobate Leaves of *Platanus basicordata* and Capitate Infructescences of *P. stenocarpa* (Late Paleocene–Early Eocene, Northwestern Kamchatka, Russia, Maslova, 1997)

Leaves of *P. basicordata* are trilobate, with a cordate base slightly descending onto the leafstalk, indented margin, suprabasal basal veins with many basiscopic branches, and several infrabasal veins. They occur in association with capitate fructifications, which show certain structural features typical of extant representatives of this genus. These specimens of the reproductive structures, along with *P. bella* (Heer) Kvaček and Manchester et Guo (Kvaček et al., 2001) and *P. neptuni* (Kvaček and Manchester, 2004), mark the first occurrence in the fossil record of the extant genus *Platanus*. Infructescences of *P. stenocarpa* are associated with leaves of *P. basicordata* and show absence of the perianth in flowers, carpels of more or less similar size (probably evidence of similar state of maturity), and pubescent carpels.

3. Association of Lobate Leaves of *Macginitiea*, Capitate Staminate Inflorescences of *Platananthus Manchester*, Infructescences of *Macginicarpa Manchester*, Dispersed Fruits, Stamen Groups of *Macginistemon Manchester*, and Wood of *Plataninium Unger* (Middle–Late Eocene, Western North America, Manchester, 1986)

Leaves of the genus *Macginitiea* have five–nine-lobate leaf blades with deep sinuses, palinactinodromous veins, and distinct chevrons distributed along the entire length of the leaf blade. Manchester (1986) described the association of these leaf morphotypes with reproductive structures (infructescences of *Macginicarpa glabra* Manchester, staminate inflorescences of *Platananthus synandrus* Manchester, dispersed staminate complexes of *Macginistemon mikanoides* Manchester) and fossil wood of *Plataninium haydenii* Felix emend. Wheeler, Scott et Barghoorn, and named it after the Clarno Plane Formation. Associations of leaves and other plant organs in various combinations have been 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 (often several fruits dominate in a fructification), the presence of a well-developed nondifferentiated perianth, and a well-developed persistent styloidium. The staminate inflorescences of *Platananthus* have many flowers with a well-developed perianth and a constant number of stamens (five), producing reticulate tricolpate pollen grains. The dispersed staminate complexes of *Macginistemon*, found at different developmental stages, are similar in stamen structure and some characters of pollen grains to *Platananthus*. However, because of unusual preservation of *Macginistemon*, the data on the presence of

the perianth are not available; therefore, it is impossible to determine these specimens as *Platananthus*. The wood fragments of *Plataninium* demonstrate anatomic characters typical for platanoids.

4. *Association of Lobate Leaves and Seedlings at Various Developmental Stages of Platanus nobilis sensu stricto, Capitulate Staminate Inflorescences of Platananthus, Infructescences of Macginicarpa, and Dispersed Staminate Complexes (Paleocene, Canada, Pigg and Stockey, 1991)*

The leaves of *Platanus nobilis sensu stricto* described by Pigg and Stockey (1991) display three-lobate leaf blades, with actinodromous primary veins deviating from the base and extending into the lobes by a few chevrons and with indented margins. The authors indicated distinct similarity of these leaves to the leaves of the genus *Macginitiea* and marked that they are transitional 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 designated as the “Joffre plane tree.” Note that, on the one hand, morphologically similar leaves of *Macginitiea* and *Platanus nobilis* (which include transitional forms) are associated with the same reproductive structures and, on the other hand, leaves of *P. nobilis*, which are assigned to the extant genus, co-occur with inflorescences and infructescences essentially distinguished from those of the plane tree. This probably supports the assignment of these leaf remains to the genus *Macginitiea*; however, this necessitates further detailed examination.

5. *Association of Entire Leaves of Platimeliphyllum and Capitulate Staminate Inflorescences of the Genera Chemurnautia N. Maslova, Archaranthus N. Maslova et Kodrul, and Bogutchanthus N. Maslova, Kodrul et Tekleva (Maastrichtian–Danian, Early Eocene, Northwestern Kamchatka, Amur Region, Russia, Maslova, 2002; Maslova and Kodrul, 2003; Kodrul and Maslova, 2007; Maslova et al., 2007)*

Leaves of the genus *Platimeliphyllum* show a combination of characters typical for the families Platanaceae and Hamamelidaceae (Maslova, 2002). The macromorphology of these leaves varies widely; in particular, some morphotypes within one species (from one locality and one layer) are comparable to hamamelids (asymmetrical leaf blade and its base, poorly developed basal veins, camptodromous connection of the basis-copic veins, low blunt teeth), while others resemble platanoids (typical suprabasal deviation of the well-developed basal veins, basis-copic branches of which show craspedodromous termination; well-developed infra-

basal veins, biconvex teeth, with a longer basal side). Particular leaf morphotypes of this genus show morphological similarity to various extant genera of Hamamelidaceae, such as *Corylopsis* Sieb. et Zucc. and *Hamamelis* L., and *Parrotia*.

The genus *Platimeliphyllum* includes four species, *P. palanense* (Budantsev) N. Maslova, *P. snatolense* N. Maslova, *P. denticulatum* N. Maslova (Maslova, 2002), and *P. valentini* Kodrul et N. Maslova (Kodrul and Maslova, 2007). Two (*P. palanense* and *P. snatolense*) co-occur with staminate inflorescences of the genus *Chemurnautia* in three localities of the north-western Kamchatka Peninsula (Chemurnaut Bay and Evravavayam and Snatol rivers) within the range from the Late Paleocene to the Early Eocene. Staminate inflorescences of the genus *Chemurnautia* display a number of characters shared with the extant plane tree, including capitulate inflorescences, short anther filaments, narrow spindle-shaped sporangia with parallel margins, well-developed endothecium, and reticulate tricolpate pollen. The genus *Chemurnautia* differs from extant *Platanus* in the considerably smaller diameter of the inflorescences, the anther structure lacking an extension of the connective, the absence of trichomes on the epidermis of the connective, and in the finer pollen grains with relatively wide colpi. Another unique feature of the genus *Chemurnautia* that distinguishes it from both Platanaceae and other Hamamelidales is the radial position of very narrow almost linear sporangia, which are nonfused or slightly fused, without forming distinct synangia (thecae).

Leaves of *Platimeliphyllum valentini* were initially found in the same burial as staminate inflorescences of *Archaranthus*, in a locality near the village of Arkhara of the Amur Region in the middle part of a clayey member between the “Lower” and “Double” coal beds (Maslova and Kodrul, 2003); however, insufficient material prevented the determination of the genus. We only indicated the association of these leaves with inflorescences of *Archaranthus* and assigned them to the family Platanaceae based on micromorphological characters. Distinctive features of the genus *Archaranthus* are the fine capitulate inflorescences on the pedicle, which are divided in mature condition into isolated flowers and stamens, consisting of approximately 15 tetramerous flowers. Capitulate inflorescences on pedicles are characteristic of many platanoids; however, *Archaranthus* is distinguished by the smaller number of flowers per inflorescence and by the division of the mature head into isolated flowers and stamens. In the family Platanaceae, four-stamen flowers are also observed in the Cretaceous genera *Sarbaya* (Krassilov and Shilin, 1995) and *Quadriplatanus* (Magallón-Puebla et al., 1997).

Subsequent collection of the fossil flora and the study of distribution of phytofossils in other sections of temporary quarries of the Arkhara–Bogutchan Brown Coal Field provided additional leaf material and

showed stable association between these leaves and inflorescences of the genus *Bogutchanthus* (Maslova et al., 2007). Staminate inflorescences of *Bogutchanthus* combine characters typical for both Platanaceae and Hamamelidaceae. This genus is similar to extant and extinct Platanaceae in the capitate shape of the inflorescences, the presence of staminodia, and the strictly tetramerous flowers with a well-developed perianth. Among representatives of Platanaceae, the 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 inflorescences and in the presence of secondarily bisporangiate stamens, staminodia, and the pantocolpate type of pollen grains. In the formation of the capitate inflorescences, the presence of bisporangial anthers and pantocolpate pollen grains, *Bogutchanthus* is most similar to the extant genus *Chunia* Chang (subfamily Exbucklandioideae). Among fossil hamamelids, *Bogutchanthus* is most similar in the shape of inflorescences, the presence of staminodia, and the type of pollen grains to the Cenomanian genus *Viltyungia* N. Maslova (Maslova and Golovneva, 2000).

Thus, within the Arkhara–Bogutchan Brown Coal Field, the leaves of *Platimeliphyllum valentinii* occur in association with various staminate inflorescences (genera *Archaranthus* and *Bogutchanthus*), differing in the pattern of attachment of heads to the axis; the development of the perianth, connective, and extension of the connective; the presence–absence of the staminodia; and the type and features of the sculpture of pollen grains.

6. Association of Entire Leaves of *Evaphyllum* N. Maslova and Capitate Infructescences of *Evacarpa* N. Maslova et Krassilov (Late Paleocene–Early Eocene, Northwestern Kamchatka, Russia, Maslova and Krassilov, 1997; Maslova, 2003)

The entire elliptic leaves of the genus *Evaphyllum* combine the characters typical of the genus *Platanus* with those of *Liquidambar* L. and *Altingia* Nor. (Hamamelidaceae, Altingioideae). They are similar to *Platanus* in the shape of the leaf blade (most of the Cretaceous and Early Paleogene platanoid leaves had entire or slightly lobate leaf blade); the deviation of basal veins above the leaf base; well-developed basisopic branches from the basal veins, which fork such that the basal vein looks weakly curved (“polygonal,” which is characteristic of ancient *Platanus*, while the basal veins of *Liquidambar* and extant *Platanus* are straight); and in the pattern of tertiary nervation. These leaves are similar to *Liquidambar* in the brochidodromous secondary veins and basisopic branches of the basal veins; short branchlets deviating from these loops and terminating in sinuses between the teeth or in the teeth; and in the shape of the teeth. Leaves of *Evaphyllum*

kamchaticum N. Maslova are associated with capitate infructescences of *Evacarpa polysperma* N. Maslova et Krassilov (Maslova and Krassilov, 1997), which are characterized by naked flowers with bicarpellate gynoecium, staminodia, and intrafloral phyllomes. Based on the characters, such as 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 assigned to the subfamily Altingioideae of the family Hamamelidaceae.

7. Association of Simple and Compound Leaves of *Platanus neptuni* with 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 the records from the Oligocene and Miocene deposits of northern Bohemia (Bůžek et al., 1967); then, the knowledge of morphological variations of this species expanded considerably due to Tertiary records from western and central Europe of compound leaves with three or five leaflets, which were similar in epidermal characters to *P. neptuni* (Walter, 1985). Subsequently, it was shown that simple, tricomponent, and pentacomponent leaves of fossil plane trees co-occur in many localities, include transitional forms, display identical epidermal structure, and co-occur with the same reproductive structures (Kvaček and Manchester, 2004). Based on this, Kvaček and Manchester proposed to designate the entire set of elements as *P. neptuni*. The complex of records of *P. neptuni* is a part of the extinct subgenus *Glandulosa* of the genus *Platanus*. Fructifications of this subgenus display a capitate structure characteristic of platanoids, differing in the presence of a well-pronounced scar on the axis at the base of the head. The maturation of fruits in the head is nonsimultaneous. The pistillate flowers include from three to eight carpels enclosed in a well-developed perianth; in the lower third, the surface of the carpel has abundant glandular trichomes; the stylodia are distinct, slightly curved; the seed is single. The staminate inflorescences consist of flowers, with a poorly developed perianth and several stamens with elongated pollen sacs. Pollen grains of *P. neptuni* are typical for platanoids, i.e., tricolpate, with a reticulate exine. In addition to the variation in leaves (simple along with compound three- and five-leaflets), with alternate semicraspedodromous or camptodromous nervation, and epidermal characters (strongly sinuous anticlinal walls of the main epidermal cells), distinctive features of this subgenus are the presence of large peltate trichomes on the surface of fruits and a well-pronounced scar on the pedicle of the single infructescence. Note that, apparently, some leaf morphotypes assigned to the subgenus *Glandulosa* do not belong to Platanaceae. The genera *Debeya* and *Dewalquea*, with a peculiar combination of morphological

and epidermal characters, are questionable. This problem is discussed in detail in the monograph devoted to the Turonian Flora of the Negev Desert (Krassilov et al., 2005).

8. *Association of Compound Leaves of Sapindopsis and Capitulate 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 the morphology of leaf blades and margins (Fontaine, 1889; Hickey and Doyle, 1977). Some morphotypes (compound pinnate leaves) have trilobate 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 indicated above, infructescences of *Friisicarpus brookensis* consist exclusively of five-carpel fruits enclosed in a well-developed differentiated perianth. Staminate inflorescences of *Aquia brookensis* are characterized by five-staminate flowers, the main distinctions of which are the long anther filaments, which are twice as long as the anther, and the pollen grains with a cellular–reticulate exine, in contrast to the typical reticulate exine of other extinct platanoids. The assignment of these specimens to the same plant is supported by the identical cuticle of leaves and perianth elements and similar cuticles of the carpels and connectives. In addition, pollen grains identical to those in the anther of *Aquia* were recorded on the leaves of *Sapindopsis* (Crane et al., 1993).

9. *Association of Compound Leaves of Platanites and Capitulate Inflorescences and Infructescences (Paleocene, Isle of Mull, Northwestern Scotland, Crane et al., 1988)*

Compound leaves of *Platanites hybridicus* Forbes consist of a terminal leaflet, which resembles the lobate leaf of *Platanus* of the subgenus *Platanus*, and two lateral leaflets differing in the extent of asymmetry. They are associated with infructescences and staminate inflorescences of the platanoid type. The name *Platanites* was originally introduced for leaves (Forbes, 1851) in the description of association between these leaves and reproductive structures (Crane et al., 1988) and was used subsequently to designate both leaves and reproductive organs (see, for example, Magallón-Puebla et al., 1997).

The pistillate inflorescences associated with *Platanites* have naked flowers with uncertain number of elements and carpels having a well-developed curved styloidium and lacking trichomes. The number of stamens in the flower of staminate inflorescences is not known; at the base of the flower, there are short perianth ele-

ments; the extension of the connectives are peltate; the pollen grains are tricolpate, reticulate, comparable in size (16–22 µm) to those of the extant plane tree.

DISCUSSION

The examples considered above show that fossil platanoid leaves occur in the geological record in combination with essentially different reproductive structures of different angiosperm families. The association of capitulate reproductive structures and leaves of the genera *Ettingshausenia* and *Platimeliphyllum* is of special interest. In different periods of geological history, these leaves were associated with capitulate inflorescences and infructescences which were similar but differed considerably in micromorphology.

In particular, the first co-occurrence of leaves of *Ettingshausenia* and capitulate reproductive structures (infructescences of *Anadyricarpa*) is dated Late Albian–Early Cenomanian (Maslova and Herman, 2004); the Cenomanian–Turonian deposits have yielded these leaves along with staminate inflorescences of *Sarbaya* (Krassilov and Shilin, 1995) 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). From the Late Albian–Cenomanian to, at least, Early Paleocene, leaves of *Ettingshausenia* were associated with reproductive structures assigned to both Platanaceae and Hamamelidaceae and displaying characters of both families (Table 1). These data, on the one hand, contradict the assignment of all similar Cretaceous leaves to only one extant genus (*Platanus*), which has until recently been a usual practice in paleobotanical studies, and, on the other hand, illustrate the statement of a greater evolutionary conservatism of leaf structures compared to reproductive organs. In addition, these data suggest that, in the Cretaceous, there was a polymorphic group, probably including extinct families, which gave rise to the extant families Platanaceae and Hamamelidaceae.

A similar picture is true of the leaves of the genus *Platimeliphyllum*, which from the Maastrichtian–Danian to the Early Eocene, were associated with staminate inflorescences of three genera, two of Platanaceae (*Chemurnautia*, see Maslova, 2002, and *Archaranthus*, see Maslova and Kodrul, 2003) and one combining characters of Platanaceae and Hamamelidaceae (*Bogutchanthus*, Maslova et al., 2007). Inflorescences of essentially different micromorphology (*Chemurnautia*, *Archaranthus*, and *Bogutchanthus*), associated with a uniform leaf morphotype (*Platimeliphyllum*), also illustrate the statement of the morphological stasis of platanoid leaves and, consequently, a greater evolution-

ary conservatism of leaves compared to the more labile reproductive structures.

Infructescences of the genus *Friisicarpus*, which co-occur in the Lower–Middle Albian of eastern North America (Crane et al., 1993) with compound leaves of the genus *Sapindopsis*, and, in the Cenomanian–Turonian of Western Siberia (Maslova and Herman, 2006) co-occur with typical platanoid leaves of the genus *Ettingshausenia*, are of special interest. It is possible that, in the Cretaceous, there were plants with similar reproductive structure (genus *Friisicarpus*) and different leaf morphology (genera *Sapindopsis* and *Ettingshausenia*). In general, as was indicated earlier (Maslova, 2003), early platanoids showed distinct conservatism of female reproductive organs, i.e., the same infructescences are associated with different staminate inflorescences. It is also possible that one of the two associations is not evidence that the specimens in question belong to the same plant. The genus *Sapindopsis* is characterized by compound pinnate or pinnatifid leaves, which are unusual for the extant plane tree and, for a long time, were thought to be close to the subclass Rosidae. Nevertheless, the study of epidermal leaf characteristics of *Sapindopsis* (Upchurch, 1984) and microstructure of pistillate and staminate capitate inflorescences associated with them (Crane et al., 1993) corroborated the assignment of this genus to the family Platanaceae, as had been previously proposed (Hickey and Doyle, 1977; Crane, 1989). A recent detailed study of epidermal characters of extant species of *Platanus* revealed certain distinctive features and put in doubt the assignment of *Sapindopsis* to Platanaceae based on epidermal characters (Carpenter et al., 2005). It is evident that the solution of this question requires additional examination.

An example of association between the same reproductive structures and different leaves is 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, the co-occurrence of the same reproductive structures and leaves similar in morphology probably supports the assignment of these leaves to one genus. The more so as the leaves of *P. nobilis* sensu stricto are very similar to the leaves of *Macginitiea*, as indicated by Pigg and Stockey (1991). In fact, the two genera show similar variations of the leaf characters and should be combined in one genus based on the presence of transitional forms. In addition, inflorescences of *Platananthus* and infructescences of *Macginicarpa* differ considerably from those of the genus *Platanus*; consequently, it is hardly probable that the leaves of a plant with such reproductive structures belong to the extant genus *Platanus* (*P. nobilis* sensu stricto). However, the resolution of this question necessitates additional studies.

The extensive material accumulated of various organs of fossil platanoids, in particular, co-occur-

ences of leaves and reproductive structures, allows the conclusion that Platanaceae should be regarded as one of the best documented families of early angiosperms. On the other hand, representative data showing that, in a number of localities, different plant organs combine characters of more than one extant family (and associations of different organs suggesting the assignment to different families), lead to the conclusion that it is necessary to develop an essentially different approach to the determination of the taxonomic position of these records.

A recently proposed system of flowering plants, which is based on molecular data (Angiosperm Phylogeny..., 2003), has abolished the order Hamamelidales and placed the families Platanaceae and Hamamelidaceae in the orders Proteales and Saxifragales, respectively, in contrast to the generally accepted concept suggesting a relationship between these families (Takhtajan, 1966, 1987; Cronquist, 1981). The new molecular-based hypothesis of the taxonomic position of the families Platanaceae and Hamamelidaceae has been accepted without reservations by many researchers; however, it is not supported by the data of the paleontological record.

On the contrary, paleobotanical data strongly suggest that the two families evolved from the same polymorphic group, which was widespread in the Cretaceous. In a number of cases, the characters typical for Platanaceae and Hamamelidaceae are superposed (Golovneva, 1994; Maslova, 2002; etc.). The co-occurrences of transitional leaf morphotypes and reproductive structures assigned to both Platanaceae and Hamamelidaceae have been recorded (for example, Maslova, 2002; Maslova and Herman, 2004). The records of reproductive structures combining the characters of Hamamelidaceae and Platanaceae are of particular interest (Crepet et al., 1992; Maslova et al., 2005, 2007). Thus, paleobotanical studies have shown significant heterogeneity of Cretaceous platanoids, which probably comprised more than one family. The determination of the taxonomic position of these forms probably requires an essentially different approach, i.e., assignment to extinct families differing in the extent to which they are related to living Platanaceae, in contrast to the generally accepted concept of the wide distribution in the Cretaceous of the extant families Platanaceae and Hamamelidaceae.

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