

New Finds of Fossil Hamamelids and Data on the Phylogenetic Relationships between the Platanaceae and Hamamelidaceae

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Abstract—Pistillate heads of *Anadyricarpa altingiosimila* gen. et sp. nov. from the Late Albian–Early Cenomanian of northeastern Russia are assigned to the Hamamelidaceae (Altingioideae) on the basis of their microstructure. The heads were found in association with leaves of "*Platanus*" *louravetlanica* Herman et Shczepetov and bark impressions. The phylogenetic relationships between the Platanaceae and Hamamelidaceae are discussed.

Key words: reproductive structures, leaf and bark remains, Hamamelidaceae, Platanaceae, phylogeny, early angiosperms.

INTRODUCTION

To date, a considerable body of data has been accumulated on fossil members of two families of the order Hamamelidales, Platanaceae and Hamamelidaceae, which have different geological histories.

Having appeared in the Early Cretaceous, by the Late Cretaceous Platanaceae had become a significant, polymorphic, and taxonomically diverse group, with large numbers of impressions often dominating plant assemblages (Bůžek *et al.*, 1967; Kvaček, 1970; Krassilov, 1976; Vakhrameev, 1976; Hickey and Doyle, 1977; Crane *et al.*, 1988; Friis *et al.*, 1988; Herman, 1994; etc.). Since the Oligocene the family has been monotypic.

Until recently, information on the extinct members of the more diverse family Hamamelidaceae, which includes about 30 extant genera, was less comprehensive. This was especially true for Cretaceous finds, whereas Tertiary remains of leaves, wood, seeds, pollen grains, inflorescences, and infructescences are better represented (Hu and Chaney, 1940; Brown, 1946; Tanai, 1967; Mai, 1968; Wolfe, 1973; Knobloch and Kvaček, 1976; Mai and Walter, 1978; Ferguson, 1989; Wang, 1992). It is only in the last decade that newly published hamamelidaceous taxa have contributed to our knowledge of the past diversity of this family (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).

Recent paleobotanical research has clarified the phylogenetic relationships between the families Platanaceae and Hamamelidaceae and their intrafamilial hierarchy. A significant body of data supports a close rela-

tionship between these families, and their evolution from a common ancestor. Several taxa that share characters of both families have been discovered. Works describing the remains of reproductive organs of such taxa are of particular interest (Crepet *et al.*, 1992; Magallón-Puebla *et al.*, 1997; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, etc.). Unlike the reproductive structures of extant platanoids and hamamelids, which are reliably macromorphologically distinguishable, these fossils are very similar in macromorphology and are undeterminable on this basis at the generic and even familial level. Examination of the floral anatomy is necessary to differentiate these families.

Some hamamelid leaf remains share platanaceous and hamamelidaceous characters (Golovneva, 1994; Maslova, 2002a).

Of particular importance for the reconstruction of platanaceous plants are finds of leaves associated with reproductive structures (Bůžek *et al.*, 1967; Kvaček, 1970; Manchester, 1986; Crane *et al.*, 1988, 1993; Pigg and Stockey, 1991; Maslova, 1997, 2002a; Maslova and Kodrul, 2003). This is especially the case with the fossil material under study. The pistillate heads of *Anadyricarpa altingiosimila* gen. et sp. nov. show hamamelidaceous and, in particular, altingioid microstructures. However, these heads are also similar to platanoids in a number of characters. The leaves that were found in association with *Anadyricarpa altingiosimila* gen. et sp. nov. were previously described as *Platanus louravetlanica* Herman et Shczepetov (Herman, 1994). These entire or weakly lobed leaves of the typical *Platanus* morphotype also resemble the Hamamelidaceae in some characters. The cooccurrence of these leaves with reproductive structures that are different from

those of extant plane tree *Platanus* casts doubt on the generic and, possibly, familial assignment of the leaf remains. For the present, we will put the generic name *Platanus* in quotation marks. In addition to the reproductive structures and leaf remains, fragments of bark resembling that of the extant plane tree were found in the same plant assemblage. The shedding of bark is typical of the extant *Platanus* but has as yet not been recorded in fossil material. Thus, reproductive structures typical of the Hamamelidaceae and leaves and fragments of shed bark characteristic of the Platanaceae have been found in association and, therefore, supposedly belong to the same plant. Although the heads of *Anadyricarpa altingiosimila* gen. et sp. nov. and leaves of "*Platanus*" *louravetlanica* predominantly show characters typical of the Hamamelidaceae and Platanaceae, respectively, they each also have many morphological characters of the other family.

The data obtained are interesting in the context of the taxonomy and phylogeny of early angiosperms.

MATERIAL AND METHODS

The plant fossils under description were collected by S.V. Shczepetov and A.B. Herman in 1988 and by Spicer and Herman in 1997. The fossils came from the middle Krivorechenskaya Subformation, which outcrops on the right bank of the Grebenka River (a right-bank tributary of the middle Anadyr' River) 4 km downstream of the mouth of the Malaya Grebenka River. The locality of Eliseevskoe, which was named for its discoverer B.N. Eliseev, is the richest and best studied locality of the Grebenka flora (Filippova, 1979, 1989, 1998; Shczepetov *et al.*, 1992; Herman, 1999a, 1999b; Spicer *et al.*, 2002). The plant-bearing beds are interlayering conglomerates, gritstones, sandstones, and siltstones. Nearly all fine-grained and middle-grained components contain plant impressions or plant debris. The total thickness of the section of the middle Krivorechenskaya Subformation on the right bank of the Grebenka River is 105–115 m. The subformation has been dated to the Late Albian–Early Cenomanian on the basis of the correlation between the plant-bearing beds and marine beds on the Gornaya River, palynological analysis (Shczepetov *et al.*, 1992), and ⁴⁰Ar/³⁹Ar dating (Spicer *et al.*, 2002).

Most of leaf impressions of "*Platanus*" *louravetlanica* and bark remains were collected from a 1-m-thick greenish gray solid fine-grained sandstone member, in the upper part of the section of the subformation, in the southern portion of the outcrop (burial no. 35, Shczepetov *et al.*, 1992). In addition to the leaf impressions of "*P.*" *louravetlanica*, which prevail in the locality and form a leaf mat, the following plant remains have been found: *Sagenopteris variabilis* (Velen.) Velen., *Nilssonsonia serotina* Heer, *Nilssonsonia* sp., *Nilssonniocladus* sp., *Ginkgo* ex gr. *adiantoides* (Unger) Heer, *Sphenobaiera vera* Samyl. et Shczep., *Phoenicopsis* ex gr. *angustifolia* Heer, *Pseudotorellia* (?) sp., *Taxites* ex

gr. *intermedius* (Hollick) Samyl., *Pityospermum semi-ovale* Samyl., *Sequoia* sp. (cone), *Magnoliaephyllum alternans* (Heer) Seward, *Menispermites* ex gr. *septentrionalis* Hollick, *Scheffleraephyllum* (= *Debeya*?) *venustum* (Phillipp.) Phillipp., *Clissites* sp., *Dalembia vachrameevii* E. Lebed. et Herman, *Grebenkia anadyrensis* (Krysht.) E. Lebed., *Dicotylophyllum* sp. cf. *Palaeonuphar nordenskioldii* (Heer) Bell. Apart from burial 35, leaf remains of "*Platanus*" *louravetlanica* occur in other plant-bearing beds of the outcrop (Shczepetov *et al.*, 1992; Spicer *et al.*, 2002). The generative structures of *Anadyricarpa altingiosimila* gen. et sp. nov. that are described in the present article and the leaves of "*Platanus*" *louravetlanica* were collected in the same plant-bearing beds as burial no. 35, approximately 30 m north of this burial.

Numerous heads of *Anadyricarpa altingiosimila* gen. et sp. nov. are structurally preserved. However, phytoleims are virtually lacking. The rock matrix was dissolved with hydrofluoric acid, a particular head was transmitted to a film of varnish and macerated with Schultz reagent and alkali. Microphotographs were made with a scanning electron microscope (CamScan).

Some of the specimens studied are housed at the Northeastern Integrated Research Institute of the Far Eastern Division of the Russian Academy of Sciences (NEIRI), Magadan, collection no. PF-1. The holotype of *Anadyricarpa altingiosimila* sp. nov. (specimen no. 4875/3-1) is housed at the Geological Institute of the Russian Academy of Sciences, Moscow (GIN).

SYSTEMATIC PALEOBOTANY

Order Hamamelidales

Family Hamamelidaceae R. Brown, 1818

Genus *Anadyricarpa* N. Maslova et Herman, gen. nov.

Etymology. From the Anadyr' River and the Latin *carpus* (fruit).

Type species. *Anadyricarpa altingiosimila* sp. nov.

Diagnosis. Pistillate heads globose, about 8 mm in diameter, gregarious, about 9 heads per axis. Basal heads pedicellate, distal sessile. Head consisting of spheroid receptacle bearing up to 35 radial florets at different developmental stages. Each floret with solitary carpel enclosed in perianth tube. Ripe fruit narrowly elliptical, stylode lacking.

Species composition. Type species.

Comparison. *Anadyricarpa altingiosimila* gen. et sp. nov. is most similar to the extant members of the Altingioideae (Hamamelidaceae) and related extinct genera. The similarity to the extant altingioids includes the general architecture of the compound inflorescence, number of flowers per head, diachronous maturation of carpels within the head, and the presence of a single carpel in the gynoecium. Although the bicarpellate gynoecium prevails in altingioids, monocarpellate forms also occur. The main character that differentiates

Anadyricarpa gen. nov. from extant members of the Altingioideae is the development of a perianth tube. The fossil genus *Lindacarpa* from the Coniacian of eastern Siberia (Maslova and Golovneva, 2000a) resembles *Anadyricarpa* gen. nov. in capitate inflorescences and a well-developed perianth that forms a tube. Both genera have a similar number of flowers per head (about 30). *Lindacarpa* differs by the constant presence of two carpels per gynoeceum, whereas *Anadyricarpa* gen. nov. has one carpel per gynoeceum.

R e m a r k s. *Anadyricarpa* gen. nov. has been found in association with leaves that were previously described as "*Platanus*" *louravetlanica* (Herman, 1994) and pieces of bark resembling those of extant *Platanus*. The generative structures and leaves were not found in organic connection. However, their repeated cooccurrence in the same beds and in the same pieces of rock suggests that they (as well as the bark fragments) belong to the same plant. Although hamamelidaceous characters prevail in the infructescences under description, they show some similarities to the Platanaceae (see below). Among the better expressed platanaceous characters, the leaves of "*Platanus*" *louravetlanica* also have certain hamamelidaceous features.

Anadyricarpa altingiosimila N. Maslova et Herman, sp. nov.

Plate 8, figs. 2–4; Plate 9, figs. 1–6

E t y m o l o g y. From the subfamily Altingioideae and the Latin *similis* (similar).

H o l o t y p e. GIN, no. 4875/3-1; fragment of a compound infructescence, middle course of the Grebenka River (Anadyr' River basin); middle Kri-vorechenskaya Subformation, Upper Albian–Lower Cenomanian.

D i a g n o s i s. As for the genus.

D e s c r i p t i o n (Fig. 1). The infructescence includes a relatively massive axis, with longitudinal ribs and a maximal diameter equal to 2.5 mm and several alternatively attached capitate infructescences with a diameter of about 8 mm (Fig. 1). The maximal observed number of heads per axis is nine. Closer to the axis base, the heads are attached with a pedicel (up to 4 mm long). Toward the apex of the axis, the pedicels become shorter, and apical heads are sessile.

The head consists of a central core (3 mm in diameter); radially attached, tightly adpressed flowers of various maturity; and fruits. Rounded or oval scars of slightly different diameter are scars of shed fruits and carpels: larger scars are obviously remains of mature fruits. The mean number of flowers per head is fewer than 35.

The microstructure of particular flowers was studied with SEM. The length of a separate flower is 1900–2100 μm ; the width varies from 230 to 750 μm depending on the maturity of the carpel. Each individual flower consists of a well-developed perianth and a solitary carpel. The members of the perianth form a tube, which embraces the carpel along nearly its entire length. In underdeveloped narrow carpels only apices of short sty-

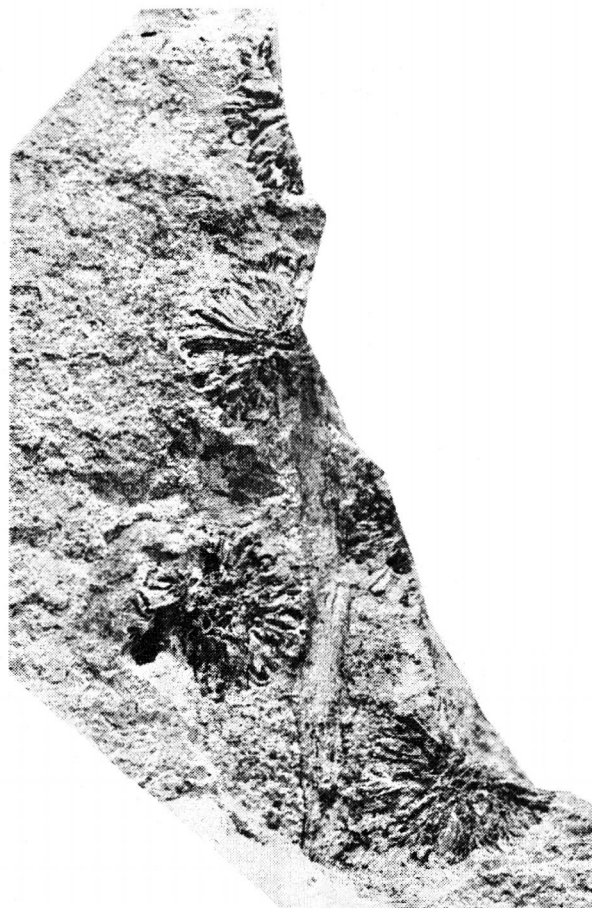


Fig. 1. *Anadyricarpa altingiosimila* sp. nov., NEIRI, no. 4875/1-1, $\times 3$.

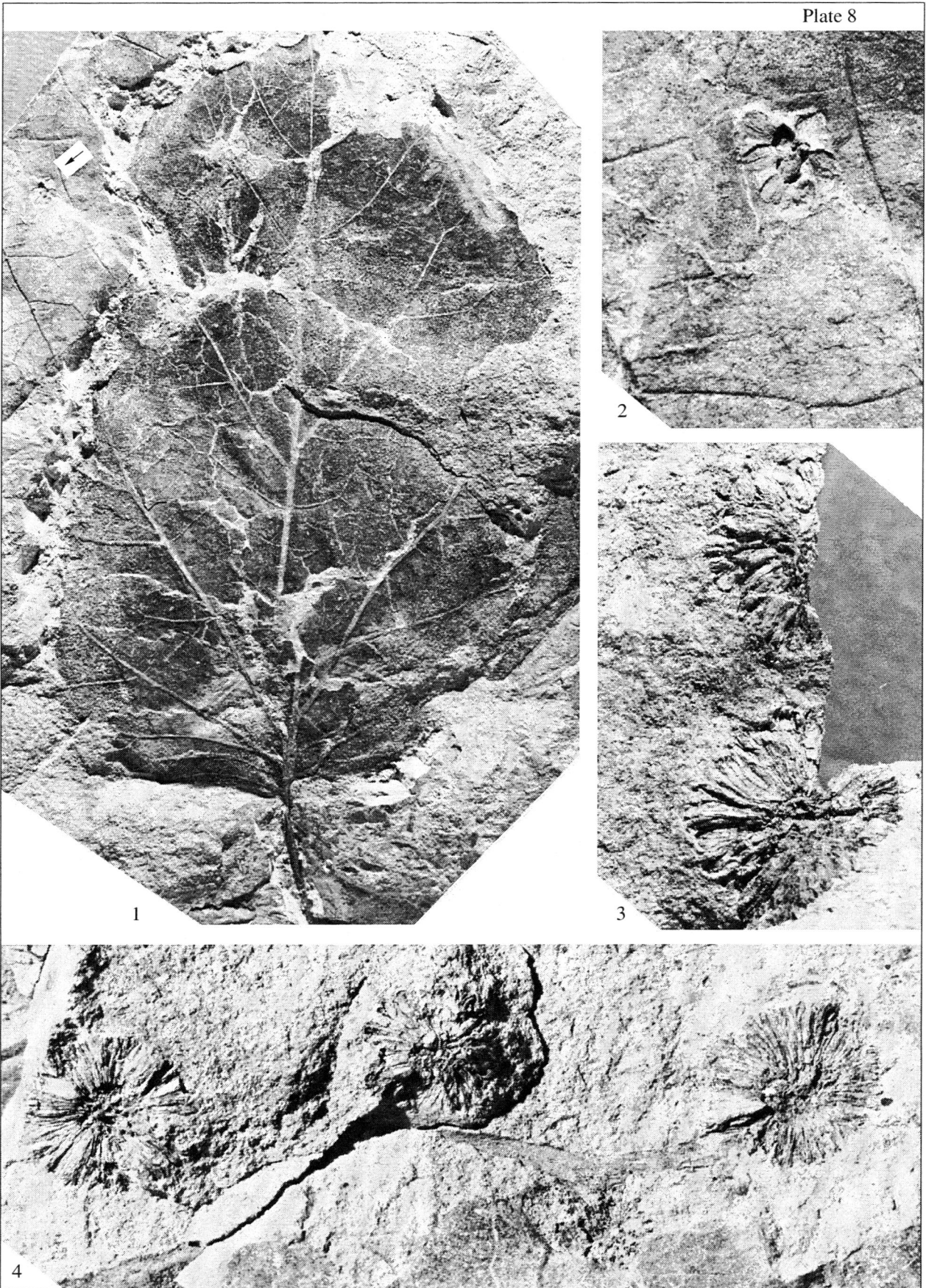
lodes remain free. The perianth tube persists in mature fruits as well. The number of perianth members and degree of perianth differentiation were not revealed because of the insufficient preservation. The upper surface of the flower is folded. In transverse section, a relatively thick layer is visible that consists of perianth members, which envelop the gynoeceum along its entire length. The upper cuticle of the perianth is formed by elongate cells with greater cutinized longitudinal walls (Pl. 9, fig. 6).

The mature fruit is narrowly elliptical, about 1700 μm long and up to 700 μm wide, with a distinct longitudinal suture (Pl. 9, fig. 4). The fruit base is conical. All visible fruits are devoid of stylodes. However, it is still uncertain whether this is taphonomic or whether the stylodes were shed after fruit became mature. The cuticle of the fruit wall is formed by tetragonal cells, often with equal sides (Pl. 9, fig. 5).

R e m a r k s. The heads of *Anadyricarpa altingiosimila* sp. nov. were found in association with the leaves of "*Platanus*" *louravetlanica* (Pl. 9, fig. 1, Fig. 3) and bark fragments (Fig. 2a). Bark fragments vary in outline and size. Their longitudinal relief is virtually identical to that of extant *Platanus*.

M a t e r i a l. Two fragmentary axes of compound infructescences with several heads and several isolated heads and fragments of heads from the type locality.

Plate 8



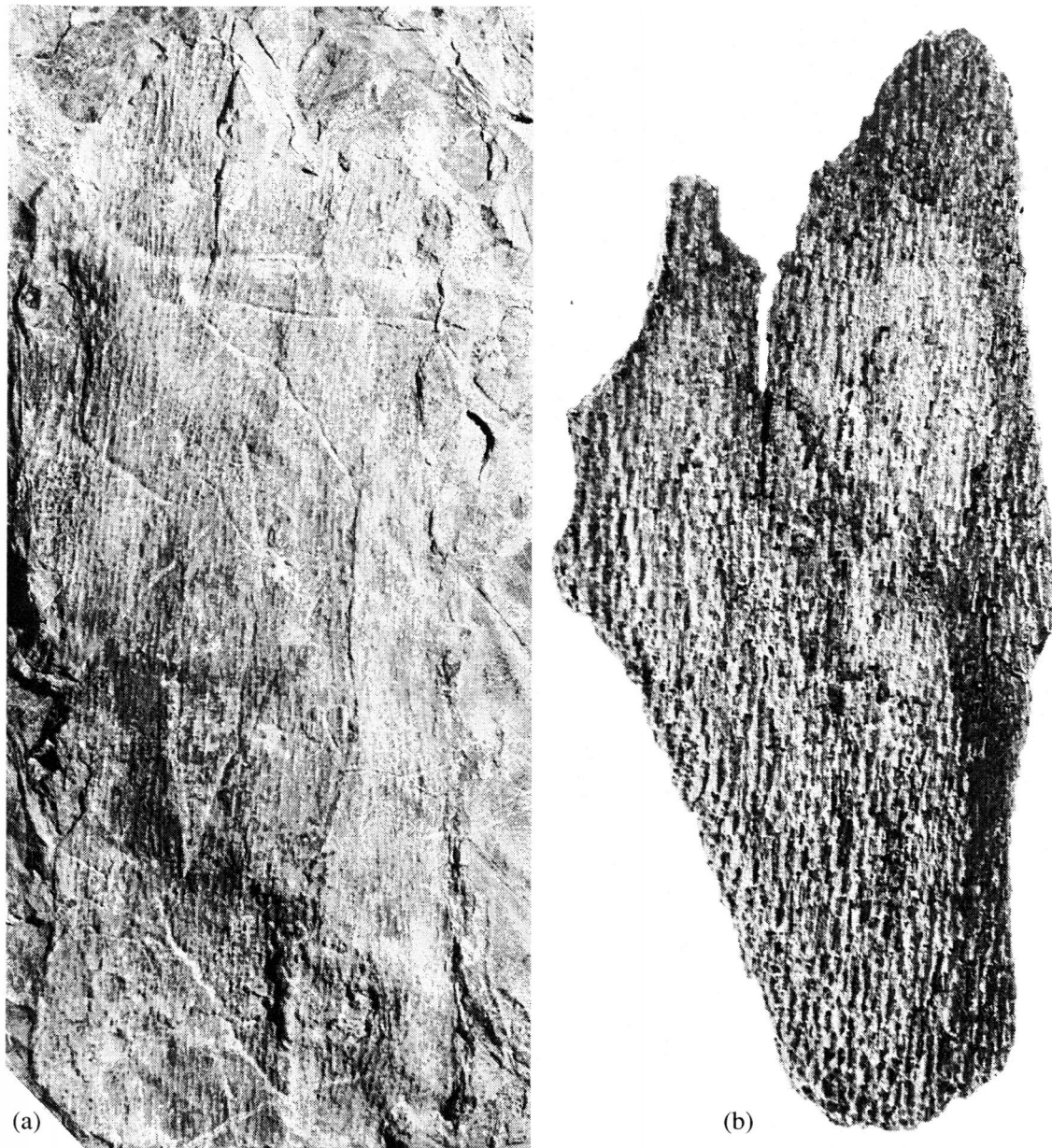


Fig. 2. Fossil and extant bark: (a) a fragment of bark that was found in association with the infructescences of *Anadyricarpa altingiosimila* sp. nov. and leaves of "*Platanus*" *louravetlanica* Herman et Shczepetov, NEIRI, no. 1007/35-646-2b, $\times 2$; (b) the bark of the extant *Platanus occidentalis* L. shown for comparison, $\times 2$.

DISCUSSION

Generative structures of *Anadyricarpa altingiosimila* gen. nov.

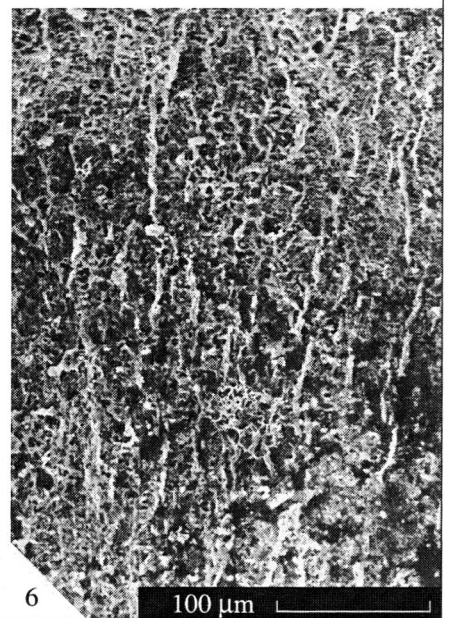
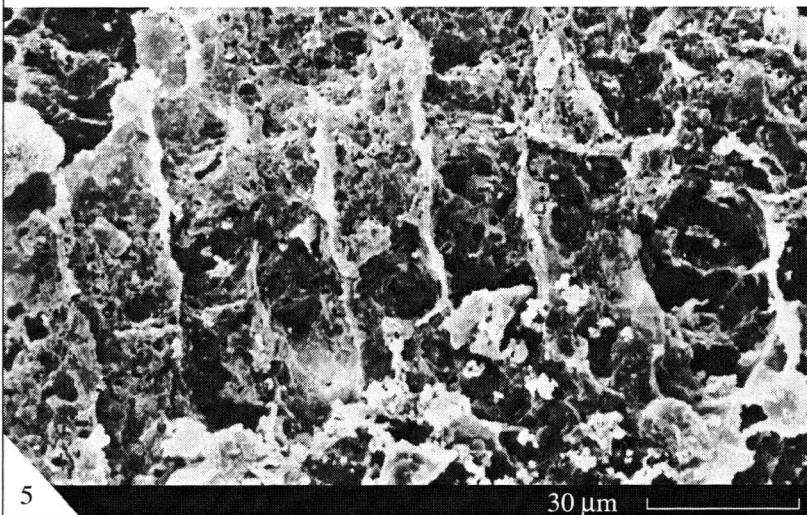
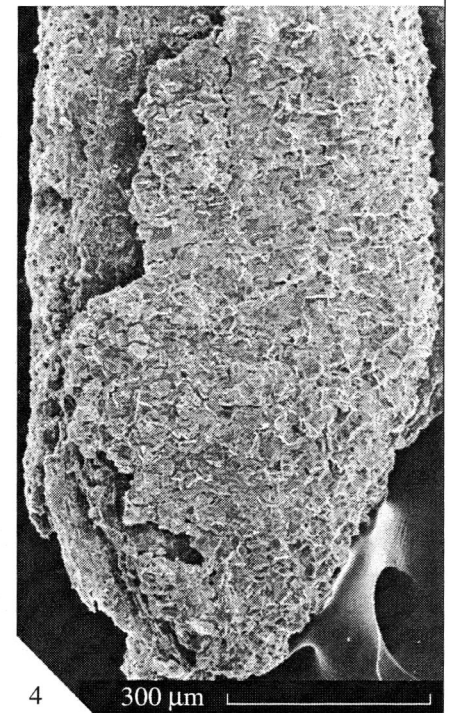
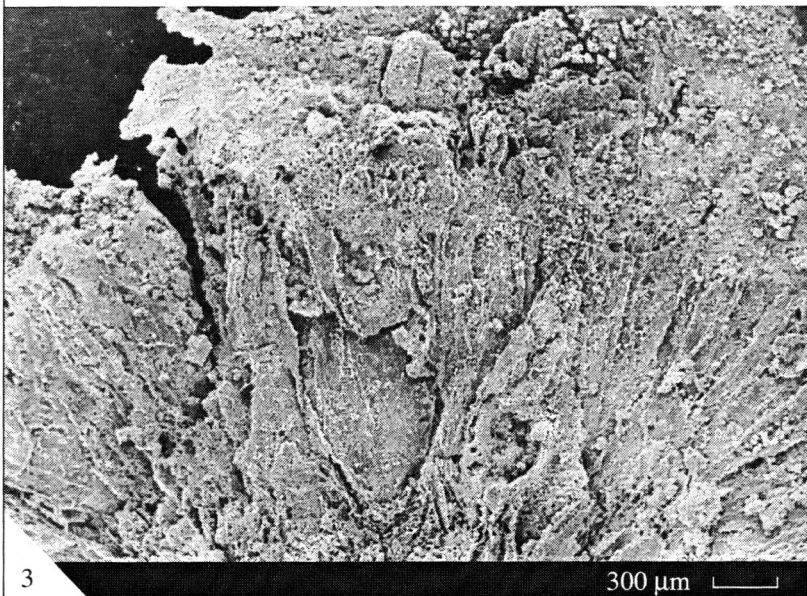
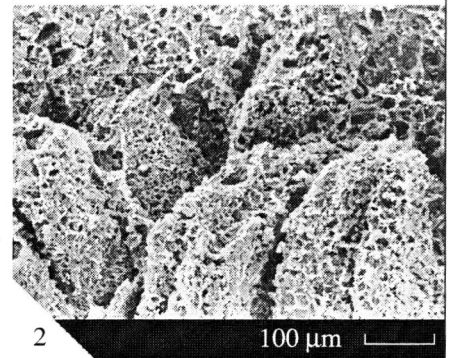
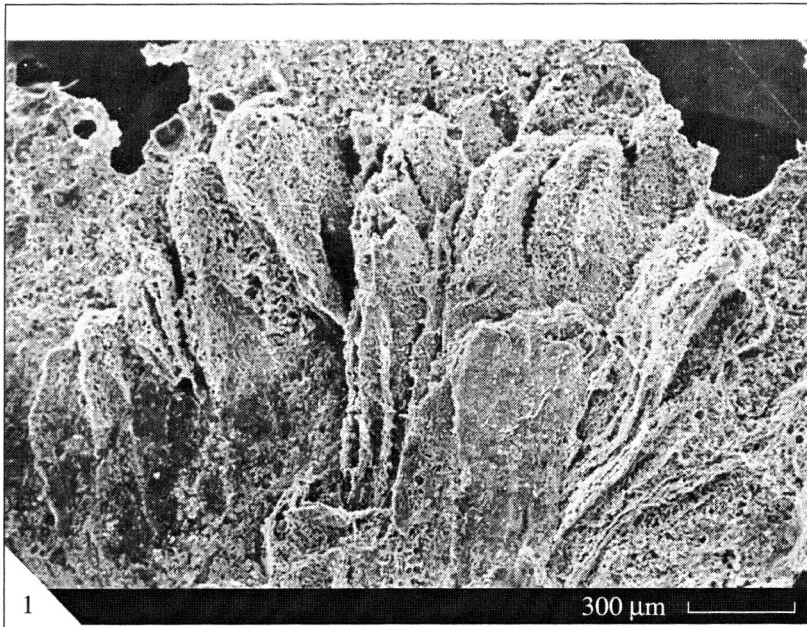
Capitate inflorescences and infructescences, which are known from many Cretaceous and Early Cenozoic deposits of the Northern Hemisphere, are the most

common structurally preserved generative remains of early angiosperms. To date, 14 platanaceous genera and 8 hamamedaceous genera have been described on the basis of fossil generative remains. The heads of *Anadyricarpa altingiosimila* gen. nov., which are described here, are assigned to the Hamamelidaceae (subfamily Altingioideae). Some characters of the new

Explanation of Plate 8

Fig. 1. "*Platanus*" *louravetlanica* Herman et Shczepetov, NEIRI, no. 4875/2-1, a leaf, the arrow indicates a fragment of the infructescences of *Anadyricarpa altingiosimila* sp. nov., NEIRI, no. 4875/2-2, $\times 1.5$.

Figs. 2–4. *Anadyricarpa altingiosimila* sp. nov.: (2) NEIRI, no. 4875/2-2, a fragment of capitate infructescence shown in Fig. 1, $\times 5.5$; (3) NEIRI, no. 4875/1-1, a fragment of axis bearing two heads, $\times 5.5$; (4) GIN, no. 4875/3-1, holotype, a fragment of an axis bearing four heads, $\times 4.5$.



genus are similar to those of some ancient members of the Platanaceae.

Data on the generative morphology and anatomy of the extant genera of the Altingioideae (Flint, 1959; Schmitt, 1965; Wisniewski and Bogle, 1982; Bogle, 1986) and the genus *Platanus* (Boothroyd, 1930; Baas, 1969) are fairly complete. Generative organs of the extant genera *Liquidambar*, *Altingia*, and *Semiliquidambar* (Altingioideae) are compound capitate inflorescences (infructescences). For example, the inflorescence of *Altingia* contains 6–25 flowers, and that of *Liquidambar* contains up to 40 flowers. The inflorescences are characterized by flowers with paired carpels, which are basally connate and variously apocarpous in the upper region, diachronous maturation of fruits (mature fruits and carpels at early developmental stages are present in one and the same head), absence of a developed perianth, presence in pistillate flowers of sterile structures (staminodes) and intrafloral phyllomes, and inferior ovary with numerous ovules.

Extant members of the genus *Platanus* have a significantly greater number of flowers per inflorescence (up to 300), simultaneous maturation of fruits in the head, absence of a distinct perianth, varying number of floral elements within one head (five to nine apocarpous carpels), superior ovary, solitary ovule, and hairy achenes.

Among known fossil members of the Hamamelidaceae, *Microaltingia*, *Lindacarpa*, and *Evacarpa* show certain similarities to the Altingioideae. The Late Turonian genus *Microaltingia* (Zhou *et al.*, 2001) has unisexual flowers with a bicarpellate gynoecium, developed hypanthium, phyllomes that are arranged in circles, and numerous ovules. These are characters of the Altingioideae. However, *Microaltingia* has pollen grains which are not typical of the subfamily, being small, elongate, tricolpate and with reticulate exines. The genus *Lindacarpa* is characterized by the diachronous maturation of fruits in the head, the bicarpellate gynoecium, and the semiinferior ovary (Maslova and Golovneva, 2000a). It differs from typical altingioids in having a well-developed perianth and lacking sterile floral structures (staminodes and phyllomes). The Early Paleogene genus *Evacarpa* has naked flowers with a bicarpellate gynoecium, staminodes, and infrafloral phyllomes (Maslova and Krassilov, 1997).

The genus *Viltyungia* from the Cenomanian of eastern Siberia exhibits a distinctive assemblage of floral characteristics that occurs in extant genera of the subfamilies Altingioideae, Exbucklandioideae, and Hamamelidoideae (Maslova and Golovneva, 2000b). The shape of the inflorescence, number of flowers per head, type of hairs on the surface of the ovary, presence of

staminodes, numerous ovaries of *Viltyungia* are reminiscent of the Altingioideae. However, *Viltyungia* differs from the latter subfamily by the bisexual flowers, anthers with a strongly convex dorsal side and opening with a longitudinal slit, and diffuse-colpate pollen grains.

Anadyricarpa altingiosimila gen. et sp. nov. resembles fossil members of the Platanaceae in the inflorescence shape and well-developed perianth. The main characters that differentiate ancient members of the Platanaceae from *Anadyricarpa* gen. nov. are the obligate pentamerous (*Platanocarpus*, Friis *et al.*, 1988; *Macginicarpa*, Manchester, 1986) or tetra-octomerous (*Quadriplatanus*, Magallón-Puebla *et al.*, 1997) flowers and a greater number of flowers per head.

The infructescence of *Anadyricarpa* gen. nov. consists of a relatively robust axis and several (up to nine) alternating heads attached to the axis. The heads that are situated near the axis base are pedicellate; the pedicels are more or less prominent. The apical heads are sessile and are situated more tightly close to each other than the basal heads are. Such an attachment is also characteristic of extant altingioids (Bogle, 1986). However, the inflorescences of *Altingia* and *Liquidambar* consist of an axis bearing several staminate heads and a solitary basal pistillate head, whereas the compound inflorescence of *Anadyricarpa* gen. nov. includes exclusively pistillate heads. The occurrence of only pistillate heads on the axis of a compound inflorescence is also known in the Early Paleogene genus *Evacarpa* (Maslova and Krassilov, 1997).

Anadyricarpa gen. nov. is similar to the extant altingioids in the number of flowers per inflorescence (up to 35). The extant genus *Platanus* and extinct members of the Platanaceae are characterized by a significantly greater number of flowers in pistillate inflorescences (about 300 in the extant plane tree instead of 60–100 in *Platanocarpus* and *Macginicarpa*).

Usually, the flowers of the extant Hamamelidaceae have a double tetra-pentamerous perianth with variously developed calyx and corolla. The perianth members are free, coalesced in a tube in a different degree, or occasionally partially fused to the ovary (Bogle, 1970). In some members of the Hamamelidaceae, the calyx is separated only at early ontogenetic stages. Flowers of members of the Altingioideae are devoid of sepals. Naked flowers also occur in several genera of other subfamilies of the Hamamelidaceae.

Bogle (1986) was the first to hypothesize that flowers with a well-developed perianth existed in the Hamamelidaceae in the geological past. Later, this assumption was confirmed: most of known extinct hamameli-

Explanation of Plate 9

Figs. 1–6. *Anadyricarpa altingiosimila* sp. nov., SEM, NEIRI, no. 4875/1-1; (1) head fragment showing tops of the carpels; (2) stylodes of underdeveloped carpels; (3) head fragment showing the base of a mature fruits and perianth members; (4) a fragment of a mature fruit with a lateral suture; (5) an imprint of the upper cuticle of the perianth; (6) an imprint of the cuticle of the fruit wall.

daceous flowers have well-developed perianths. For example, *Lindacarpa* (Altingioideae) has a perianth that is attached slightly above the gynoecium base and envelops the flower virtually along its entire length; *Evacarpa* has naked flowers. A different degree of perianth development is described in ancient members of the Hamamelidoideae. In the flowers of *Androdecidua* petals are fusiform, with narrowing bases and apices that are partially fused to the stamens of the upper circle (Magallón-Puebla *et al.*, 2001). *Archamamelis* has a supposedly differentiated perianth with the number of members divisible by six or seven and with triangular and basally broad petals (Endress and Friis, 1991). The genus *Allonia* has a developed corolla of narrow and parallel-margined petals and calyx with irregularly developed sepals (Magallón-Puebla *et al.*, 1996). Exhibiting the characters of the three subfamilies of the Hamamelidaceae (Altingioideae, Exbucklandioideae, and Hamamelidoideae), the genus *Viltyungia* has a developed perianth with dissimilar elements: the inner ones are narrower and the upper ones are broad and hairy.

Perianth members in *Anadyricarpa* gen. nov. form a perianth tube that persists even on mature fruits. We failed to reveal the number of perianth members. Nonetheless, the observed folding of the external surface of the flower suggests that the perianth members were relatively well developed and significantly exceeded the carpel diameter in the total width.

Maslova and Golovneva (2000a) noticed that the finds of fossil members of the Hamamelidaceae with developed perianths suggest that the evolution of this character was directed towards reduction and, therefore, the naked flowers of some extant members of the family are a secondary character. An analogous trend developed in parallel in the Platanaceae: relatively prominent and differentiated perianths are characteristic of extinct platanaceous genera, whereas the extant plane tree has naked flowers.

Diachronous maturation of carpels within the head is a characteristic feature of the Altingioideae. Similar to *Anadyricarpa* gen. nov., the infructescences of *Altingia* and *Liquidambar* contain underdeveloped carpels among mature fruits. This character is also known in fossil members of the subfamily. Heads with carpels at different stages of maturity are described in Cretaceous *Lindacarpa* and Early Paleogene *Evacarpa*.

Syncarpous semiinferior ovary with two carpels is among the key characters of the Hamamelidaceae. This feature is described in flowers of all genera of four hamamelidaceous subfamilies. However, variations in the number of carpels in flowers of the same genus are known. Thus, *Exbucklandia* (Exbucklandioideae) has one to five carpels with domination of the bicarpellate gynoecium (Kaul and Kapil, 1974); the flowers of *Parrotiopsis* (Hamamelidoideae) have one to three carpels (Kapil and Kaul, 1972). Although a bicarpellate gynoecium dominates in *Altingia* and *Liquidambar*, gynoecia with one carpel also occur in these genera (Wis-

niewski and Bogle, 1982; Bogle, 1986). However, among extant members of the Hamamelidaceae a monocarpellate gynoecium occurs in a few genera and never dominates. The heads of *Anadyricarpa* gen. nov. have exclusively monocarpellate flowers, which set them apart from other members of the Hamamelidaceae. Previously, fossil hamamelidaceous flowers with a monocarpellate gynoecium have not been described. It should be noted that flowers of all fossil platanaceous genera have pentamerous or tetramerous flowers.

Leaves and bark fragments associated with *Anadyricarpa* gen. nov.

Leaves that were previously described as "*Platanus*" *louravetlanica* (Herman, 1994) were found in association with the heads of *Anadyricarpa* gen. nov. The leaves of "*Platanus*" *louravetlanica* are simple, with small lateral lobes, asymmetrical, of moderate or large size, 7–16 cm long and 6–14 cm wide (Fig. 3). The petiole is long, at least 6–7 cm (although it may be longer, since the preservation is fragmentary). The outline of the leaf blade is rounded, oval, broadly rhomboidal, broadly obovate, or rounded-obovate. The leaf base is broadly or narrowly wedge-shaped and decurrent. The apices of the central and two lateral lobes are acute or obtuse. The pomes are relatively narrow, their width is usually 1.2–1.5 times the distance between the basal and lower suprabasal veins. The lateral lobes are small and triangular. The left and right lobes are often situated at different heights and may differ in size. The leaf margin is toothed sinuate nearly up to the leaf base. The teeth are acute, triangular, with small glands on their apices. The teeth vary in size both in different specimens and within one leaf. Areas between the teeth are rounded.

The venation is palmate-pinnate and craspedodromous. As a rule, basal veins deviate asymmetrically from the midvein. They are alternate or, occasionally, opposite, are elevated over the leaf base at 5–25 mm, weakly distinguishable from the secondary veins by the thickness and degree of branching. Basal veins may vary in thickness and length even in one specimen. They are straight or slightly curved. Each basal vein has one or two nonbranching acroscopic deviations and five to seven basicopic deviations, the lower of these also branch one to three times. There are up to four pairs of infrabasal veins, which are short and nonbranching or are well developed and branch two to three times. The secondary veins are in four to five pairs, the lower of them are branching, the upper ones nonbranching. Tertiary venation is orthogonal-reticulate to branching-scalariform. Veins of the third and fourth orders may be hardly differentiable. The venation of the fourth order is orthogonal-reticulate.

It should be noted that a range of characters makes "*P.*" *louravetlanica* closer to some members of the Hamamelidaceae. These are the asymmetry of the leaf

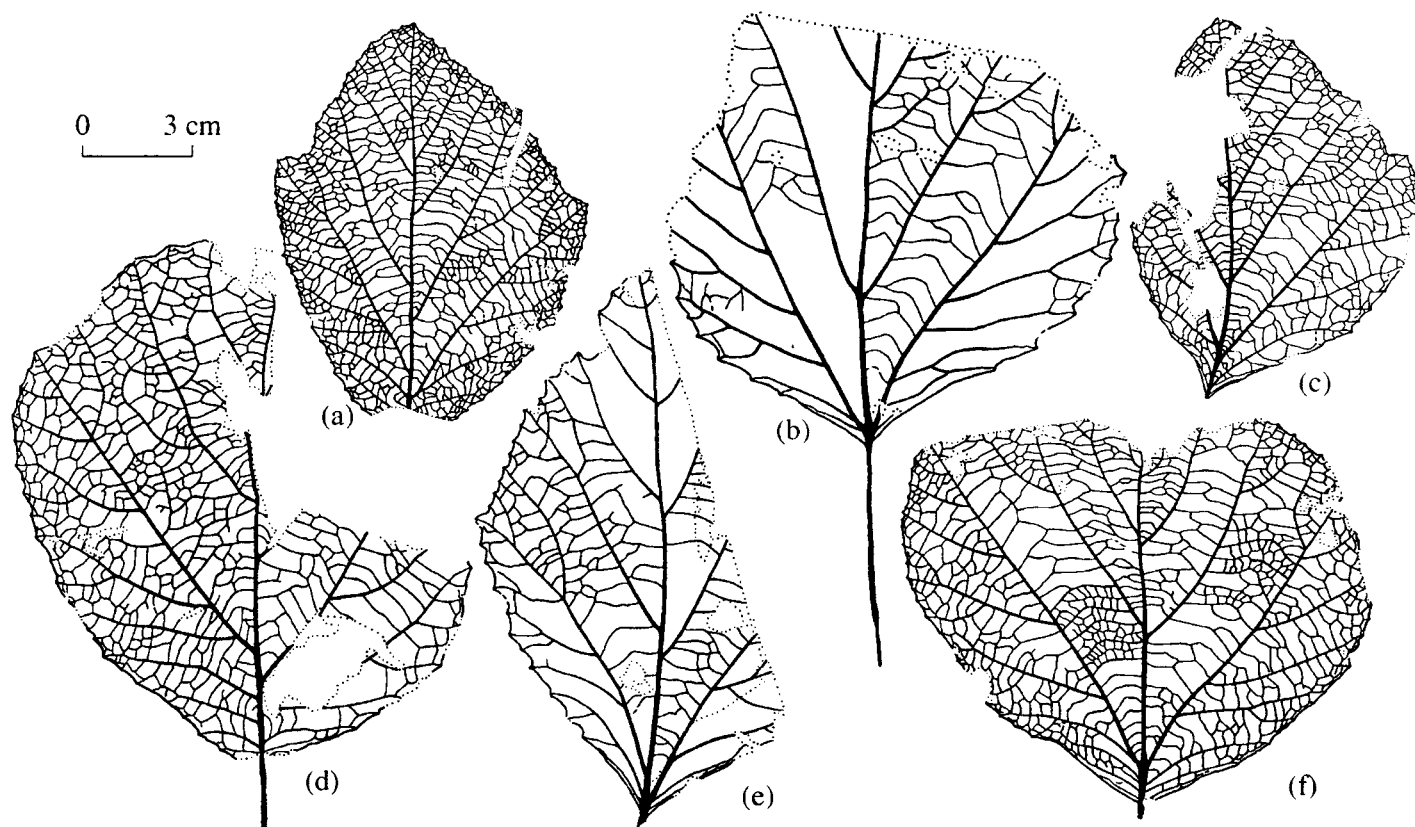


Fig. 3. "*Platanus*" *louravetlanica* Herman et Shczepetov: (a) holotype, NEIRI, no. 1007/35-632a; (b) NEIRI, no. 1007/35-629a; (c) NEIRI, no. 1007/35-649; (d) NEIRI, no. 1007/35-653; (e) NEIRI, no. 1007/35-651; (f) NEIRI, no. 1007/35-646-1b.

base, the leaf blade, and the deviation of the basal veins (uneven in length and thickness) as well as a peculiar tertiary venation (predominantly orthogonal-reticulate). "*P.*" *louravetlanica* most closely resembles the mature leaves of *Shaniodendron* (Wang and Li, 2000, text-figs. c, d). A significant difference between "*P.*" *louravetlanica* and the Hamamelidaceae is the suprabasal deviation of basal veins and well-developed infrabasal veins. Unfortunately, the insufficient preservation of the material under study prevented the familial assignment of these leaves from being clarified based on epidermal data.

The generic assignment of the leaves also needs a significant correction. Maslova (2002b) and Maslova and Kodrul (2003) remarked that the cooccurrence of leaves of the typically *Platanus* morphotype and reproductive structures different from those of this genus questions the traditional conception of the broad distribution of *Platanus* during the Cretaceous time. In the Cretaceous, leaf morphotypes appeared that are reminiscent of extant plane tree, but supposedly belonging to different genera or even families. However, the considerably diverse generative structures didn't correspond to those of the extant genus. In this connection, the determination of the genus *Platanus* in the Cretaceous on the basis of leaf remains has already caused doubts (Wolfe, 1973; Krassilov, 1976, 1979; Maslova, 2001, 2002a, 2002b). Before the detailed investigation that this problem merits, we believe that it is inadvis-

able to adjust the nomenclature, save by adding quotation marks to the genus *Platanus*.

In association with the leaves of "*Platanus*" *louravetlanica* and infructescences of *Anadyricarpa* gen. nov., fragments of bark were found that are virtually identical to the bark of the extant *Platanus* in shape and external sculpture. A characteristic feature of the extant plane tree is the peeling and shedding of the bark in relatively large patches, resulting in a mottled appearance of the trunk. Although not rare in extant angiosperms, bark shedding has not previously been reported in the fossil state. The material under description shows that this phenomenon was present even at early stages of angiosperm evolution.

Phylogenetic relationships between the Platanaceae and Hamamelidaceae

To date, the vegetative and generative morphology and anatomy of the extant members of the Platanaceae and Hamamelidaceae are studied in close detail. Paleobotanical data are significant to solve phylogenetic relationships between the orders of lower and higher hamamelids as well as between the taxa belonging to the Hamamelidales.

The similarities between the families Platanaceae and Hamamelidaceae in morphology, anatomy, and biochemistry are unquestioned (Tippe, 1938; Takhtajan, 1966; Jay, 1968; Cronquist, 1981; Zavada and

Among hamamelid genera that were established on the basis of leaf remains, several forms also combine platanaceous and hamamelidaceous characters. Thus, the genus *Platimelis*, which is well known in northern moderate floras of the Upper Cretaceous–Paleocene, was erected on the basis of macromorphological analysis of leaf remains (Golovneva, 1994). The author of the genus compares *Platimelis* with some Cretaceous platanoids (*Arthollia*, *Credneria*, etc.), but also points to a significant similarity to the Hamamelidaceae. Leaf blades of this genus have infrequent broadly triangular rounded teeth typical of many hamamelids. The epidermal data are lacking.

Although polymorphous Early Paleogene *Platimeliphylum* shows macromorphological characters of several hamamelidaceous genera, this genus was revealed to have the typically platanaceous epidermal structure (Maslova, 2002a). The reproductive structures of *Chemurnautia*, which associate with the *Platimeliphylum* foliage, also demonstrate a platanaceous affinity. The morphology of the leaves of *Platimeliphylum* varies to such an extent that some morphotypes are indistinguishable from hamamelidaceous leaves on the basis of macromorphology (asymmetric leaf blade and leaf base, weakly developed basal veins, camptodromous connection of basisopic veins, and low obtuse teeth), whereas macromorphological characteristic of other morphotypes (typically suprabasal deviation of well-developed basal veins, which basisopic deviations have craspedodromous endings, developed infrabasal veins, and concave-concave teeth with a longer basal side) allow one to describe them as members of the Platanaceae.

Maslova (2003) noticed that some Cretaceous leaf remains, described as *Credneria* (Platanaceae), should be assigned, on macromorphological grounds, to hamamelids rather than to platanoids.

Such examples make one aware of a potential misinterpretation of taxonomic affinities (Platanaceae/Hamamelidaceae) when based on leaf remains. The role of platanoids in ancient ecosystems is probably overestimated at the expense of the Hamamelidaceae.

To conclude, finds of fossil morphotypes showing a combination of platanoid and hamamelid characters support the close relation of these families. Cooccurrences of different organs that supposedly belonged to the same plant but have been assigned, on morphological and anatomical grounds, to different extant families, prove the previously suggested hypothesis on the existence in the geological past of a common polymorphic ancestral group. This group gave rise to diverging phylogenetic lineages leading to the extant families Platanaceae and Hamamelidaceae (Maslova and Krassilov, 1997; Maslova, 2002a, 2002b, 2003).

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