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Lindacarpa gen. nov., a New Hamamelid Fructification from the Upper Cretaceous of Eastern Siberia

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Abstract—Structurally preserved pistillate heads from the Upper Cretaceous of Eastern Siberia are described and assigned to a new genus *Lindacarpa* N. Maslova gen. nov. (Hamamelidaceae). The question of the morphological divergence of platanoid and hamamelioid pistillate structures is addressed. The implications of the new discovery for the evolutionary morphology of hamamelids are explored.

INTRODUCTION

The order Hamamelidales Wettstein maintains a key position in modern phylogenetic systems (Takhtajan, 1966, 1987; Cronquist, 1981). As a link between ancestral lineages and the relatively advanced amentiferous orders, the hamamelids show a combination of primitive and supposedly advanced morphological characters. Palaeobotanical data on hamamelids, in particular on their reproductive structures, are important in this context.

The most representative of the Hamamelidales is the family Hamamelidaceae R. Br. that includes, according to various authors, from 24 to 30 genera (Skvortsova, 1975; Bogle, 1970; Endress, 1989). The genera Altingia Nor., Liquidambar L. and Semiliquidambar Chang are sometimes placed in a separate family the Altingiaceae Lindl. (Skvortsova, 1960; Melikian, 1973; Rao, 1974: Takhtajan, 1966, 1989). However, some recent studies are in favor of demoting this group to a subfamily of the Hamamelidaceae (Cronquist, 1981; Wisniewski and Bogle, 1982; Bogle, 1986; Endress, 1987). Traditionally this subfamily has been named Liquidambaroideaea as proposed by Harms (1930). However, the name Altingioideae is valid under the principle of priority (Reinsch, 1890). This subfamily differs from the rest of the Hamamelidaceae principally by the typically capitate inflorescences.

Representatives of the Altingioideae are similar to *Platanus* L. (Platanaceae Dumortier, Hamamelidales) in the gross morphology of the leaves and fructifications. The geological history of Platanaceae is relatively well studied. The earliest records come from the Early Cretaceous (Hickey and Doyle, 1977). The Platanaceae were an abundant and highly polymorphic group of angiosperms over the Late Cretaceous and Paleogene, but declined in the Neogene, with a single extant genus *Platanaceae* are perhaps the most thoroughly studied group of angiosperms. In addition to the

numerous records of dispersed leaves and fruiting heads there are a few whole plant reconstructions based on various organs (Bužek *et al.*, 1967; Kvaček, 1970; Manchester, 1986; Crane *et al.*, 1988; Pigg and Stockey, 1991; Maslova, 1997).

Much less is known of the fossil Hamamelidaceae, in particular of the Altingioideae. Only Liquidambar with its easily recognizable leaves has a representative Cenozoic record, though its species content is controversial (Harms, 1930; Makarova, 1957; Uemura, 1983; Bogle, 1986; Maslova, 1995). Most fossil species of this genus are based on leaf remains alone. A few records of reproductive structures are based on macromorphological descriptions. We noted already (Maslova, 1997; Maslova and Krassilov, 1997) that macromorphology is not enough for precise generic assignment of fossil Platanaceae and Altingioideae. Though similar in their general aspect, the capitate fructifications of these groups differ markedly in microstructural characters which are, therefore, critical for their taxonomical assignments.

Most micromorphologically studied fructifications of fossil hamamelids resemble those of the extant Hamamelidoideae (Endress and Friis, 1991; Manchester, 1994; Magallon-Puebla et al., 1996), while next to nothing is known of the progenitorial Altingioideae. The fructifications Steinhauera Presl. from the Maastrichtian to Palaeocene deposits (Mai, 1968; Krassilov, 1976; Friis and Crane, 1989) are related to Liquidambar or Altingia (Tiffney, 1986; Krassilov, 1989; Fergusson, 1989; Krassilov, 1997). Typically altingioid characters are found in Evacarpa polysperma Maslova et Krassilov from the Late Paleocene of Western Kamchatka (Maslova and Krassilov, 1997). A new genus Lindacarpa from the Late Cretaceous of Eastern Siberia, described later in this paper, adds to the known diversity of reproductive structures in early hamamelids and is of certain interest for their phylogeny and systematics.

MATERIALS AND METHODS

The material was collected by L.B. Golovneva on the Linda River, a left tributary of the Lena River (Eastern Siberia), about 35 km from the mouth (Fig. 1). The locality is an outcrop of lenticular clayey deposits interbedding with alluvial sandstones. In the basin of the Linda River the Upper Cretaceous deposits are subdivided into the Agrafenovskaya and Chirimyjskaya formations (Vakhrameev, 1958; Reshenia ..., 1981). They mostly consist of light-gray, locally ferruginous soft sandstones and clays of alluvial origin, containing abundant plant remains. The infructescence is preserved as a compression in the Chirimyjskaya Formation, which also yields diverse remains of ferns, conifers and angiosperms. This assemblage is preliminarily dated as Coniacian.

The inflorescence was cleared from the rock matrix under Cytoval disecting microscope and photographed. A few fruits were removed from the heads, cleared in fluoric acid and mounted for SEM. For cuticular studies fragments of compressed fruits were macerated in Shultze's solution and alkali. Microphotographs are obtained with Camscan SEM.

The collection is deposited in the Botanical Institute, Russian Academy of Sciences (BIN RAN) St. Petersburg, no. 1196.

SYSTEMATIC PALEONTOLOGY

Family Hamamelidaceae R. Brown, 1818

Genus Lindacarpa N. Maslova, gen. nov.

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

Type species. Lindacarpa pubescens, sp. nov.

D i a g n o s i s. Pistillate heads of many radial florets of different developmental stages. Florets cuneate, with protruding conical ovary base. Perianth attached above the ovary base. Outer tepals thick, connate, with tabloid epidermal cells. Inner tepals thin, with larger irregular epidermal cells. Gynoecium pubescent, encased in perianth tube, consisting of two carpels, proximally syncarpous, distally diverging.

Composition. Type species.

C o m p a r i s o n. This genus differs from the macromorphologically similar capitate inflorescences of *Platanus* and fossil platanoids in the gynoecial structure of the two carpels that form a syncarpous semiinferior ovary. It differs from altingioid fructifications in having a better developed perianth. In particular, in the recently described more typically altingioid *Evacarpa* (Maslova and Krassilov, 1997) the perianth is lacking, while the interfloral phyllomes and staminodia are relatively well preserved. The capitate inflorescences from the Turonian (Raritan Formation) of New Jersey (Crepet *et al.*, 1992) are much smaller (male heads 1–2 mm, female heads up to 2.7 mm) and the perianth is relatively poorly developed.



Fig. 1. Locality of *Lindacarpa pubescens* sp. nov. (no. 20) on the river Linda in the Lena River Basin.

Lindacarpa pubescens N. Maslova, sp. nov.

Plate 12, figs. 1-6

Etymology. From Latin *pubescent* (hairy).

Holotype. BIN RAN, no. 1196-20-62; Linda River, Eastern Siberia; Chirimyjskaya Formation, the Coniacian, Upper Cretaceous.

Diagnosis. As for the genus.

Description (Fig. 2). A pistillate head is preserved as an impression with fragmentary compression. The head is 19 mm in diameter, with a massive receptacle 5.5 mm in diameter bearing crowded, radially disposed floral units at different developmental stages, some perhaps at the fruiting stage, with persistent perianths (Pl. 12, fig. 1). Boundaries between individual flowers were only occasionally distinct under the dissecting microscope. The total number of flowers was approximately thirty. Shed flowers leave rounded scars on the receptacle. The microstructure was studied using SEM.

Isolated flowers are broadly obcuniate, 7 mm long, distally up to 2 mm broad, with a conspicuous obconical base. They are enveloped by perianth members that are attached about 0.8 mm above the base (Pl. 12, figs. 2–4). The outer perianth members are connate almost over their entire length forming a distally lobed floral tube. The inner tepals can be seen inside the tube (Pl. 12, fig. 6). They differ from the outer ones in their epidermal structure (see below). The ovary is seen in gaps of split perianths and in transversely cut flowers. In lateral view (Pl. 12, fig. 2) the carpels diverge about 1.7 mm above the base. The ovary is thus syncarpus over 1/4 of its length. Free parts of carpels are adnate for some distance and are spread funnel-shaped near the apex. An ovary transversely cut near the base (Pl. 12, fig. 5) shows two locules that are elongate-rhomboid or elliptical, and of unequal width. Stylodes are lacking, perhaps having been shed before fossilization.



LINDACARPA GEN. NOV., A NEW HAMAMELID FRUCTIFICATION

Explanation of Plate 12

Figs. 1–6. *Lindacarpa pubescens* sp. nov., holotype no. 1196-20-62: (1) general aspect, \times 4; (2) flower with a longitudinally split floral tube exposing the ovary (arrow), SEM, \times 22; (3) several flowers with ovaries basally protruding from floral tubes (arrow), SEM, \times 33; (4) ovary base with tepals attached, proximal view, SEM, \times 143; (5) transversly cut gynoecium of two carpels (arrow) surrounded by tepals, SEM, \times 75; (6) part of perianth showing inner tepals (arrow), SEM, \times 33.

The external cuticle of the carpels shows irregularly arranged isodiametric cells of irregular shapes, about $10-15 \ \mu\text{m}$ wide. At the contact point of the carpels the epidermal cell walls are folded. The hair bases are irregularly scattered all over the surface, occasionally forming fascicles of three hairs (Fig. 2a).

The abaxial cuticle of the outer perianth members shows the squarish tabloid cells $10-15 \,\mu\text{m}$ wide, with pitted periclinal wall, disposed in distinct longitudinal rows (Fig. 2b). The abaxial cuticle of the inner tepals shows irregular-polygonal cells $20-30 \,\mu\text{m}$ long, $10-15 \,\mu\text{m}$ wide, not forming distinct rows (Fig. 2d). Their



Fig. 2. *Lindacarpa pubescens* sp. nov., holotype no. 1196-20-62, epidermal structures, SEM: (a) ovary, external cuticle with hairs, ×210; (b) floral tube, external cuticle, ×300; (c) inner tepal, adaxial cuticle, ×470; (d) inner tepal, abaxial cuticle, ×330.

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abaxial epidermis consists of larger polygonal cells of variable dimensions, $40-80 \ \mu m \ \text{long}$, $5-30 \ \mu m \ \text{wide}$. Occasional small rounded-elliptical cells might have been hair bases (Fig. 2c).

Material. Holotype.

DISCUSSION

Capitate fructifications, found in many Cretaceous and Paleogene localities of the Northern Hemisphere, are the most common structurally preserved reproductive structures of early angiosperms. Most of them are similar to either staminate or pistillate heads of extant *Platanus* and are thereby assigned to the Platanaceae (Krassilov, 1973; Manchester, 1986; Crane, 1987; Crane *et al.*, 1988; Friis *et al.*, 1988; Pigg and Stockey, 1991; Manchester, 1994; Krassilov and Shilin, 1995; Magallon-Puebla *et al.*, 1997; Maslova, 1997). They are also similar to some hamamelidaceous heads, in particular those of the Altingioideae. Such similarities might sometimes result in ambiguous taxonomic situations that can be resolved on the basis of microstructural studies alone.

The reproductive structures of both the extant *Planus* (Boothroyd, 1930; Baas, 1969) and altingioid genera (Flint, 1959; Schmitt, 1965; Wisniewski and Bogle, 1982; Bogle, 1986) are thoroughly studied. The large number of flowers per head (up to 300) and their simultaneous development, is similar to modern *Platanus*. The perianth is either lacking or strongly reduced. The number of floral parts is variable (5–9), even in a single head. The ovary is inferior, apocarpous, with a solitary ovule, developing into a pubescent achene. The fossil platanoids (*Platanocarpus* Friis, Crane et Pedersen, *Macginicarpa* Manchester) have smaller heads, with fewer flowers (60–100), a constant number of floral parts (commonly five), well developed perianth and glabrous fruits.

The reproductive structures of extant *Liquidambar*, *Altingia* and the interfertile and probably hybridogenic *Semiliquidambar* are coaxial capitate inflorescences (infructescences), several per axis, with 6–25 (*Altingia*) to 40 (*Liquidambar*) flowers per head. Typical of altingioid flowers are gynoecia with paired carpels, proximally syncarpous, but to a different extent apocarpous above. Fruit maturation is diachronous, with flowers and ripe fruits occurring in the same head. Perianths are lacking. The ovary is semi-inferior, with staminodes and sterile interfloral phyllomes surrounding the apocarpous distal part and, in *Altingia*, with deciduous stylodes. The ovules are numerous.

The genus *Lindacarpa*, gen. nov. is similar to *Altingia* and *Liquidambar* in the number of flowers per head (which are much more numerous in the Platanaceae) and their variable dimensions indicating diachronous maturation. The gynoecium consists of two carpels forming a semi-inferior ovule, with perianth members attached above the base. These characters are typical of hamamelids.

At the same time, Lindacarpa resembles extant Platanus in having pubescent gynoecia and is similar to the fossil Platanaceae in the well developed perianth. Notably, the gynoecia are glabrous in the Cretaceous Platanaceae as distinct from *Platanus* in which pubescent fruits had already appeared in the Paleocene (Maslova, 1997) and are retained by all extant species. In contrast, the Altingioideae (with the sole exception of Altingia excelsa Norr.), lack gynoecial hairs (Bogle, 1986). However, the hairy gynoecia of *Lindocarpa* indicate that this character appeared in early altingioids but was lost by their descendants. The paired carpels of Linda*carpa* are fully enveloped by a tube of connate tepals of a possible bracteate origin. The inner tepals are different from the outer ones. Their epidermal characters are consistent with both petaloid and bracteate origin. More material is needed to elucidate their morphology. The presence of interfloral phyllomes also remains uncertain. However, even in the extant genera their interpretation is the subject of debate (see Schmitt, 1965; Chang, 1962; 1973; Endress, 1977; Wisniewski and Bogle, 1982; Bogle, 1986).

Flowers of extant Liquidambar are interpreted as naked. Even developmental studies in L. styraciflua L. failed to reveal a primordial perianth (Wisniewski and Bogle, 1982). However Bogle (1986) has admitted the possibility of chlamideous flowers in some extinct members of the family, with a later transformation of the perianth into a sclerotic tissue between the flowers. Dichlamideous flowers, as well as flowers with variously reduced perianths, occur in other hamamelid subfamilies. For example, Mytilaria Leconte, in the Exbucklandioideae has well developed sepals, while in Exbucklandia R.W. Br. the sepals are distinct only in the early developmental stages. In Chunia Chang the flowers are naked, while in *Rhodolea* Champ, ex Hook, the Rhodoleioideae, they are dichlamideous with strongly reduced sepals (Bogle, 1986). Among the Hamamelidoideae the perianths are sometimes reduced or lost completely (Bogle, 1970). Our material shows well developed perianths in an early hamamelids, with a tendency toward reduction mirrored in several other lineages of the family. Therefore, naked flowers of extant Liquidambar and Altingia can be interpreted as derived rather than primitive.

CONCLUSIONS

(1) The key reproductive characters of the Altingioideae (the diachronous fruit maturation, paired carpels, semi-inferior ovary) had already appeared by the Late Cretaceous.

(2) The pistillate flowers of early altingioides had well developed perianths forming floral tubes, as well as densely pubescent ovaries and fruits. Lack of these

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characters in extant representatives of these lineages is therefore a derived condition.

(3) The morphological similarity of the modern Platanaceae and Hamamelidaceae appears to be convergent. The disparities in their reproductive morphologies were already been apparent in the Late Cretaceous (Coniacian).

ACKNOWLEDGMENTS

We are grateful to professor V.A. Krassilov for his advice in microstructural studies and interpretations. This work is partly supported by the Russian Foundation for Basic Research, grant no. 98-04-49010.

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