# Infructescences of *Cathiaria* gen. n. from the late Cretaceous of North Kazakhstan and Siberia (Russia)

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ABSTRACT. We used infructescences from the late Cretaceous deposits of northern Kazakhstan and Siberia to establish *Cathiaria* gen. n. These infructescences are compound, consisting of two orders of axes: a main axis that is irregularly finely ribbed, and alternate to subopposite secondary lateral axes. Immature lateral axes are short, flattened, and bract-like; they bear sessile fruits on the adaxial side. During maturation the lateral axes become elongated, more or less cylindrical, bearing nutlet-like, single-seeded fruits. The systematic position of *Cathiaria* is uncertain. Among the recent plant taxa this genus shares most features with the family Moraceae. The infructescences of *Cathiaria* have been found in association with the leaves of *Liriodendropsis simplex* (Newb.) Newb. in six localities and in association with the male inflorescences of *Freyantha sibirica* Krassilov & Golovneva at one locality. Here we present evidence to support the hypothesis that these organs may have been produced by the same plant, presenting an unusual combination of characters suggestive of an extinct angiosperm family.

KEY WORDS: infructescences, angiosperms, Cretaceous, Kazakhstan, Siberia, Russia

# INTRODUCTION

Studies of fossil reproductive structures are essential for understanding the evolutionary relationships within early angiosperms. Most of the information on fossil flowers, seeds and fruits of these plants has been gained from the rich localities of the Cretaceous strata of Laurasia, especially from western Europe and North America (Dilcher 1979, Friis 1983, 1985, 1999, 2000, Crane & Dilcher 1984, Dilcher & Crane 1984, Knobloch & Mai 1984, 1986, Drinnan et al. 1990, Kvaček 1992, Friis et al. 1994, Crane et al. 1994, 1995, Pedersen et al. 1994, Eklund et al. 1997, Crepet & Nixon 1998, Herendeen et al. 1999, Eklund & Kvaček 1998, Kvaček & Eklund 2003). Remains of the early angiosperm reproductive structures are considerably scarcer in the other palaeocontinents (Archangelsky & Taylor 1993, Douglas 1994, Taylor & Hickey 1990, Mohr & Friis 2000, Eklund et al. 2004). Such fossils are

also rarely reported in eastern parts of Laurasia. The majority of the known Cretaceous records from this region are represented by impressions or compressions, which usually yield incomplete anatomical information. Barremian-Aptian reproductive structures were described from Transbaikalia, Mongolia, and Northern China (Krassilov 1982, 1997, Sun et al. 1998, 2002, Sun & Dilcher 2002, Leng & Friis 2003). Samvlina (1959, 1960) investigated several flowers, fruits and seeds from the early Albian of the Buor-Kemyus Formation of the Kolyma River. Some fossils related to Platanaceae and Ranunculales have been described from the late Albian and Cenomanian deposits of Middle Asia and Kazakhstan (Vakhrameev & Krassilov 1979, Krassilov et al. 1983, Krassilov & Shilin 1995). Moreover, some lignitized heads of Hamamelidaceae and Platanaceae as well as other reproductive

structures have been recently documented from the Cenomanian-Turonian deposits of Siberia (Maslova & Golovneva 2000a, b, Krassilov & Golovneva 2001, 2004, Maslova et al. 2005).

In eastern Laurasia three-dimensional mesofossils with well preserved anatomical details were found only in Japan (Takahashi et al. 1999, 2001, 2002) and in northern Kazakhstan. In Japan, the mesofossil assemblages come from the Kamikitaba locality (Ashizawa Formation) of early Turonian age. This flora contains dozens of taxa including ferns, conifers and diverse angiosperms: Lauraceae, Hamamelidaceae, Magnoliaceae, Nymphaeaceae, Combretaceae, Fagaceae, and Cornaceae (Takahashi et al. 1999). Also several petrified reproductive structures were recorded from Hokkaido, Japan (Nishida 1994).

In northern Kazakhstan, numerous remains of charcoalified and lignitized fruits and seeds have been found in the Sarbay and Kachar magnetite quarries (Fig. 1) in the deposits of the Cenomanian-early Turonian Novokozyrevsky and Shet-Irgiz Formations (Zhilin et al. 1997, Gabrielyan & Zhilin 1997). The mesofossil assemblage of these localities contains more than a hundred different taxa, most of which remain to be studied in detail. Overall, the identified part of the Sarbay assemblage includes megaspores of Isoëtaceae, leaf fragments and sporangia of ferns, as well as twigs, cones and seeds of conifers, including one extinct taxodiaceous genus Alapaja Dorofeev (Frumina et al. 1995) and abundant angiosperms. These fossils were used to describe 8 taxa: four species of the extinct magnoliaceous genus *Liriodendroidea* Knobloch & Mai (Frumin & Friis 1996, 1999), two species of the extinct illiciaceous genus *Illiciospermum* Frumin & Friis (Frumin & Friis 1999), one species of the extinct lauraceous genus *Mauldinia* Drinnan, Crane, Friis & Pedersen (Frumin et al. 2004) and platanoid staminate inflorescences of *Sarbaya radiata* Krassilov & Shilin (Krassilov & Shilin 1995).

The mesofossil assemblage from the Kachar quarry, from which the genus Cathiaria is now described, is also very rich and diverse (Khval' 2001), but the exploration of this interesting and important flora is only in its initial phase. The Cathiaria material is represented by numerous fragments of fruits and infructescences at different stages of maturity, but with well-preserved structural details of reproductive organs. Similar complete mature infructescences were found in the Cenomanian deposits of East and West Siberia, where they are represented by lignitized compressions. Details of the anatomical structures are not preserved in these remains, but the remnants yield important information on the overall habit of the infructescences.



Fig. 1. Localization of the sites with fossil plant remains: 1 - Kachar quarry; northern Kazakhstan, 2 - Kem River, Western Siberia, 3 - Tyung River, Eastern Siberia

# MATERIAL AND METHODS

In northern Kazakhstan the Cretaceous deposits are located in the south-eastern foothills of the Ural Mountains. They are exposed in the rare natural outcrops that are mostly confined to the bank of the Ayat River and also in the several magnetite and bauxite quarries, from which the deposits of the Kachar and Sarbay quarries are the most completely studied ones (Papulov 1990). These deposits are continental and marine lagoon sediments from the late early Cretaceous to Campanian. The presence of plant macro- and mesofossils is documented only within the facially interrelated Shet-Irgiz and Novokozyrevsky formations. The widespread Shet-Irgiz Formation consists of grey sandy clays, occasionally with high content of kaolin. It is thought to be of lacustrine to alluvial origin and is assigned to the Cenomanian or Cenomanian-early Turonian age based mainly on the evidence of palynomorphs and leaf remains. These deposits are superposed by marine sands of the Santonian-Campanian Ayat Formation containing the stratigraphically relevant mollusc, Inoceramus cardissoides Goldfuss and I. pachti Arck. (Papulov 1990). Plant macrofossils from the Shet-Irgiz Formation are not diverse, and comprise mostly platanoid foliage. This assemblage, known as the Ayat flora, was partially studied by Kryshtofovich (1936), Vakhrameev (1952), and Shilin (1986). The three-dimensionally preserved mesofossils from the sediments of the Shet-Irgiz Formation were found in the Sarbay Quarry, Kustanay region (Frumina et al. 1995, Krassilov & Shilin 1995, Frumin & Friis 1996, 1999, Frumin et al. 2004).

The beds of the more local Novokozyrevsky Formation are distinguished by their apparently deluvial to proluvial origin. This formation consists of kaolinitic clays of different colours, and of bauxites with bands of grey clays which include plant remains. Palynological evidence indicates a Cenomanian to early Turonian age for this formation with the basal part perhaps extending into the late Albian (Papulov 1990). Age determination for the Shet-Irgiz and the Novokozyrevsky formations was supported by their correlation with the Cretaceous deposits on the eastern slope of the Ural Mountains. In that region the deposits of the Mysy Formation, containing the same Cenomanian-early Turonian palynocomplex, are overlain by the marine Kuznetsovo Formation which contains early Turonian molluscs Inoceramus labiatus Schloth. In the Kachar Quarry the deposits of the Novokozyrevsky Formation are overlain by 6-8 m thick layers of grev sand and clav containing rare foraminifera and cysts of dinoflagellates. They indicate that these sediments originated in the near-shore environment during sea transgression, which began in the Ural Mountains region in the early Turonian (Papulov 1990). Overall, the age of the fossil remains from the Shet-Irgiz and the Novokozyrevsky formations is considered as Cenomanian or possibly Cenomanian-early Turonian.

The mesofossil remains described in this paper were collected from the Kachar magnetite quarry, located 40 km west of Kustanay city, near the town of Rudny. A detailed survey of Cretaceous sediments exposed within the Kachar Quarry was provided by

Zhelezko et al. (1990). Plant mesofossils were collected in 1988 by A.P. Levina and in 1995-1996 by the field team of S.G. Zhilin (Gabrielyan & Zhilin 1997). The material was taken in the north-eastern bank of the quarry from several sites belonging to the beds of the Novokozyrevsky Formation. These samples yielded a variety of well-preserved charcoalified or lignitized remains of conifers, angiosperms, ferns, and bryophytes (Khval' 2001). Twigs, seeds and isolated cone scales of conifers are among the most conspicuous components of the Kachar floral assemblage. The majority of identified conifer seeds belong to Taxodiastrum cretaceum Dorofeev, Seletya kryshtofovichii Dorofeev, Alapaja uralensis Dorofeev, Kozykorpeshia kokchetavica Dorofeev (Khval' 2001). The fruits, seeds, and also flowers of angiosperms are much more diverse, although their abundance is approximately the same as that of conifer remnants. Most of the angiosperm remains belong to new genera that have not yet been established. Some kinds of angiosperms, however, can be assigned to taxa previously described from other late Cretaceous localities. These include seeds of two or three species of Liriodendroidea (Magnoliaceae), Illiciospermum, Spirellea Knobloch & Mai, two species of Klikovispermum Knobloch & Mai (Hamamelidaceae?), Saccospermum Knobloch & Mai (probably Nymphaeales), and Platanocarpus (auct. non Jarmolenko) Friis, Crane & Pedersen (Khval' 2001). The presence of the Cathiaria remains has been documented in only two samples (collections 1702, 1707) collected from a seam of grey silty clays, presumably corresponding to the layer 4 sensu Zhelezko et al. (1990), lying approximately 5 m below a conspicuous seam of lignite (Gabrielyan & Zhilin 1997). These sediment samples also contain numerous plant macrofossils preserved as impressions or thin compressions.

The samples containing *Cathiaria* remains were washed through a 0.4 mm sieve without any chemical treatment. Specimens for scanning electron microscope (JEOL JSM-35C) were mounted on the stubs and coated by palladium. All collections are stored at the Komarov Botanical Institute (BIN), St. Petersburg, Nos. 1702 and 1707.

In Western Siberia, compressions of complete infructescences of Cathiaria occur in the Upper Cretaceous deposits of the Chulym-Enisey Basin (Krasnoyarsk region). The locality is an outcrop of the Kem River, which falls into the Enisey River slightly downstream of the town of Eniseysk. The Cathiaria infructescences were found in a clay lense in alluvial deposits of the lower part of the Simonovo Formation. 16 km upstream of Podgornaya village. This formation consists of loosely cemented light-grey kaolinitic alluvial sandstones with bands and lenses of clays. The lower part of the formation is dated to the Cenomanian mostly based on macrofossils (Golovneva 2005). The specimens were collected by Golovneva, Khval', and Oskolski in 1995 and 2001, and are housed at the Komarov Botanical Institute (BIN), collection No. 1198. Previously floristic assemblages from the lower part of the Simonovo Formation were studied by Ananyev (1948) and Lebedev (1962). The remains of Cathiaria were first described by Ananyev (1948) from the Kem River as *Carpolithes tyensis*. Overall, the Chulymian macrofossil assemblage from the lower

part of the Simonovo Formation includes 38 plant species. The main dominants are *Ginkgo* L., *Cedrus* L., *Sequoia* Endl., and the angiosperms *Platanus simonovskiensis* Lebed., *Sapindopsis kryshtofovichii* (Lebed.) Golovneva, *Liriodendropsis simplex* (Newb.) Newb., *Magnoliaephyllum baerianum* (Heer) Golovneva, and *Menispermites sibirica* (Heer) Golovneva (Golovneva 2005).

In Eastern Siberia, the remains of Cathiaria were collected by Lavrov (All-Union Oil Institute, St. Petersburg) from the deposits of the Lena-Vilyuy Basin, in the lower part of the Timmerdyakh Formation dated to the Cenomanian (Golovneva 2005). This locality is situated in the middle reaches of the Tyung River, which flows into the Vulyuy River near the town Vilyuisk, approximately 180 km upstream from the mouth of the Tyung River. This collection is housed at Komarov Botanical Institute, No. 1181. The Boskhian Cenomanian flora from the lower part of the Timmerdyakh Formation comprises Asplenium L., Coniopteris Brongn., Ginkgo L., Sequoia Endl., Cupressinocladus Seward, Magnoliaephyllum Seward, Scheffleraephyllum Philippova, Cinnamomophyllum Kräusel & Weyland, Celastrophyllum Goepp., Araliaephyllum Font., Trochodendroides Berry, Liriodendropsis simplex (Newb.) Newb., and Menispermites sibirica (Heer) Golovneva (Golovneva 2005).

# SYSTEMATIC DESCRIPTION

#### Cathiaria gen. n.

Type: *Cathiaria zhilinii* sp. n., northern Kazakhstan, Kustanay region, Kachar quarry, the Novokozyrevsky Formation, Cenomanianearly Turonian.

Etymology. From the latinized name of the Kachar quarry.

Diagnosis. Infructescences compound, consisting of two orders of axes. Main axis straight, irregularly finely ribbed, with alternate or almost opposite lateral axes. Lateral axes in immature condition short, flattened, bract-like, bearing sessile fruits on the adaxial side; in maturity lateral axes elongated, more or less cylindrical, straight or curved. Flower consisting of a single unilocular pistil with a more or less distinct style and occasional remnants of a bract or perianth at the base. Fruits nutlet-like, single-seeded, in immature condition ovoid, in maturity flattened in crosssection and D-shaped or ovate in outline. Pericarp comprising a thin outer layer, a middle mechanical layer, and a subtending layer of fibers.

Genus composition: 1) Cathiaria zhilinii sp. n.

2) Cathiaria tyensis (Ananjev) comb. n., Western Siberia, the Chulym-Enisey Basin, Kem River, lower part of the Simonovo Formation, Cenomanian, and Eastern Siberia, the Lena-Vilyuy Basin, Tyung River, lower part of the Timmerdyakh Formation, Cenomanian.

#### Cathiaria zhilinii sp. n.

Pl. 1, figs 1–8, Pl. 2, figs 1–8, Pl. 3, figs 1–6, Pl. 4, figs 1–4, Pl. 5, figs 1–8, Pl. 6, figs 1–8, Pl. 7, fig. 6.

Holotype (designated here): Coll. BIN 1707, specimen 162 (Pl. 1, fig. 4), fragment of compound infructescence; northern Kazakhstan, Kustanay region, Kachar quarry, Novokozyrevsky Formation, Cenomanian-early Turonian.

Material and locality. Northern Kazakhstan, Kustanay region, Kachar quarry (53°15'N; 63°00'E), Novokozyrevsky Formation, Cenomanian-early Turonian. Numerous fragments of three-dimensionally preserved charcoalified or lignitized juvenile and mature infructescences. Coll. BIN 1702, specimens 100, 110, coll. BIN 1707, specimens 101, 105– 152, 156–179, 180–190, 194–211.

Etymology. In honour of Dr. Sergey Zhilin who has re-initiated the Cretaceous carpological studies in Russia.

Diagnosis. Lateral axes of the mature infructescences bearing 5–12 sessile fruits, situated in 1–3 rows on the abaxial and lateral sides of the axis.

Description. All the specimens from the Kachar quarry are fragmentary. The mature infructescences are represented only by the lateral axes with fruits. The juvenile infructescences are represented also by secondary lateral axes with fruits and by several fragments of primary axes bearing one or two lateral axes. The most complete specimen was chosen as the holotype.

# IMMATURE INFRUCTESCENCES

Only few fragments of juvenile main axes were found in the Kachar material, the most complete of them bearing one pair of almost oppositely arranged lateral axes attached at angles of about  $40-50^{\circ}$  to the main axis.

The main axis of infructescence is straight and irregularly finely ribbed. The lateral axes are 2-4 mm long, flattened, bract-like, fleshy, straight or somewhat valvate, irregularly ovate in outline, with wide decurrent base and developed abaxial keel (Pl. 1, figs 1-8). The distal parts of the axes from the adaxial side is usually flat, wide triangular or rounded, with prominent cylindrical apex (Pl. 1, figs 1, 5); or sometimes longitudinally folded (Pl. 3, fig. 3). In the proximal part of the lateral axis there is an adaxial median ridge which gradually decreases to the apex (Pl. 1, fig. 7, Pl. 2, fig. 4). In transverse section the shape of the lateral axes is rather complicated and varies within individual specimens depending on the distance from the main axis. Usually this shape is cruciform in the proximal and middle part (Pl. 3, figs 1, 2), and becomes flat or Vshaped near the apex (Pl. 3, fig. 3). An adaxial ridge, an abaxial keel and two lateral extensions can be distinguished at the cruciform portions of lateral axes. Lateral extensions are somewhat asymmetric, about 0.5 mm in width. The radial extensions (adaxial ridges and abaxial keel) are generally less prominent. The abaxial keel ordinarily reaches the apical area (Pl. 1, fig. 6), and the adaxial one is commonly shorter, tapering distally (Pl. 1, fig. 1). The edges of all these lateral and radial extensions are commonly entire and rounded in cross-section or sometimes fork lengthwise to form more or less pronounced secondary lobes. The surface of the lateral axes is smooth but uneven, showing various small local thickenings (Pl. 1, figs 3, 6).

The adaxial side of the lateral axis bears up to 12 sessile fruits attached mostly in the proximal part of the axis along the adaxial ridges, and arranged in 3–5 dense, staggered rows (Pl. 1, figs 1–8). As a rule, the fruits are slightly sunken into the tissue of the axis (Pl. 2, fig. 1). The lateral extensions and the arrangement of fruits show some asymmetry: usually the right extension (from abaxial view) is wider and more concave than the left one (Pl. 1, fig. 3).

# Anatomy of the axes in immature infructescences

The anatomical structure of the main axis has been examined in radial section. The cortex layers of ca. 400  $\mu$ m in width, xylem (ca. 300  $\mu$ m in width), and pith (more than 400  $\mu$ m in diameter) can be distinguished (Pl. 5, fig. 2). The boundaries of cortical cells are indistinct. Pith consists of the flattened oval to rounded parenchyma cells of 5–8  $\mu$ m in diameter (Pl. 5, fig. 8). The xylem of the main axis of the infructescences consists of elongated tracheid-like cells with bordered pits, tracheary elements with helical or scalariform secondary thickenings, and also of fusiform parenchyma cells of ca. 10  $\mu$ m in diameter (Pl. 5, fig. 4). Tracheid-like cells are small (3–4  $\mu$ m in diameter) with rounded bordered pits (ca. 2  $\mu$ m in diameter) on their lateral walls.

Tracheary elements with helical secondary thickenings situated near the pith in the central part of the main axes are  $6-7 \mu m$  in diameter (Pl. 5, fig. 3). Width of secondary thickenings is  $1.5-2.0 \mu m$  lead of their helices is  $6-7 \mu m$ . Conceivably, these cells are protoxylem elements.

In outer parts of the main axis the xylem consists of larger tracheary elements (10– 15 µm in diameter). On their cell walls these cells bear either helical secondary thickenings of 1.0–1.5 µm in width with the helix lead of 4-5 µm, or scalariform secondary thickenings, 2–3 µm in width, alternating with narrow slit-like hollows ca. 0.5–2 µm wide. No distinct perforation plates have been observed. Apparently, these tracheary elements are the tracheids of the metaxylem.

The outer epidermal layer of the lateral infructescence axis is thin, often crushed, consisting of small irregular to isodiametric tabular cells about 20 µm in diameter with thickened periclinal outer walls. These cells are arranged in few indistinct periclinal rows. The underlying tissue seemingly constitutes an outer framework of the axis, forming a moderately wide ring composed of 5-6 rows of densely packed, shallow cells about 40–70 µm long and 15–20 µm thick (Pl. 3, figs 1, 2, 4). A vascular bundle about 150 µm in diameter (Pl. 3, fig. 5) follows along the core of the axis adjacent to the adaxial ridge acting as its inner support (Pl. 1, fig. 7, Pl. 3, fig. 1). Its xylem consists mostly of small tracheid-like cells (Pl. 5, fig. 1) which resemble in size and shape those cells found in the main axis. A few tracheary elements (also 3–4 µm in diameter) with circular or helical thickenings on their cell walls are developed adjacent to the tracheid-like cells (Pl. 5, fig. 1). Length of these cells exceeds 150 µm.

The space around a vascular bundle is filled by loosely arranged parenchyma cells of various sizes and outlines, usually  $30-70 \mu m \log and 10-20 \mu m$  wide (Pl. 3, fig. 5). Inside the radial ridges and lateral extensions the parenchyma layer is very thin or may be almost completely absent (Pl. 3, fig. 4).

#### MATURE INFRUCTESCENCES

Lateral axes are 4 to 5 times longer than the immature ones and reach 10 mm in length and 0.8 mm in diameter. Mature axes are cylindrical with irregular longitudinal ribs (Pl. 6, figs 7, 8). The fruits are arranged mostly at the adaxial and lateral sides of the axes (Pl. 6, figs 2, 6) and are loosely aggregated in the distal part of the axes. Some fruits remain undeveloped and these small aborted fruits are often preserved among mature ones (Pl. 6, figs 6–8, Pl. 7, fig. 6), confirming the developmental succession between juvenile and mature infructescences.

#### Fruits

Juvenile fruits are of rather uniform shape, normally ovoid with a short gradually attenuate apex, 1-1.5 mm long (Pl. 1, figs 1-8, Pl. 2, figs 1, 3, 5). Mature fruits are distinctly asymmetric, obliquely ovate to D-shaped in outline and strongly flattened in cross-section, considerably larger than the juvenile ones, about 2.5–3 mm long, 1.5–2 mm wide, and about 1 mm thick (Pl. 6, figs 1–8). Besides shape and sizes, the mature fruits differ from the juvenile ones by a more elongated and attenuated apex. The attachment scar is sub-basal to median; it is less developed in juvenile forms, becoming more pronounced in mature ones extending in some fruits up to half of their length (Pl. 6, fig. 1). The juvenile fruits usually split into two equal valves, with a narrow dorsiventral fissure extending from the apex towards the base (Pl. 1, figs 1-8, Pl. 2, figs 3, 4). In contrast, the mature fruits are only rarely found in split condition. The sutures are inconspicuous in juvenile fruits, but both the ventral and especially the dorsal sutures are often quite distinct in mature forms: the former appearing as a shallow groove, and the latter as a more or less prominent narrow rib (Pl. 6, figs 4, 5). The apex of the style, preserved only in few mature fruits, is bifid, comprising two short lobes (Pl. 2, fig. 7). The fruit surface is smooth to weakly rugulate, in mature fruits

sometimes bearing small rounded knobs (Pl. 6, fig. 2), which are observable mainly along the dorsal suture.

In the juvenile infructescences some of the fruits are surrounded by a tightly adjacent vaguely cup-like structure that apparently is a remnant of the perianth or bracts (Pl. 1, fig. 5, Pl. 2, figs 3, 5, 6).

# Pericarp

In both juvenile and mature fruits, the pericarp is composed of three layers. The outer layer is thin, one or occasionally two cell rows high, consisting of tabular, isodiametric to irregularly-shaped cells with flat to convex outer periclinal walls. The underlying mechanical layer, constituting a major part of the pericarp, is made of isodiametric to longitudinally elongated cells, 20-30 µm in width and 7-12 µm in height, arranged in 3 to 5 more or less distinct periclinal rows (Pl. 4, fig. 4). In some of the juvenile fruits examined, these cells are hollow with moderately thickened walls and distinct intercellular spaces, while in most other cases they appear filled with homogeneous contents. The innermost layer is typically formed by one or two periclinal rows of large fibers, 6–8 µm in diameter, diverging from an area at the fruit base and lining the locule surface (Pl. 4, fig. 3). In cross-section, the fibers are rounded to rectangular with more or less thickened walls and wide lumina, often crushed, and sometimes of rather variable size and outline.

#### Seed

The locule cavity is occupied by a single seed (Pl. 4, figs 1, 2, Pl. 6, fig. 3) attached presumably sub-basally or basally, close to the attachment area of the fruit itself. The seed axis is straight in the juvenile fruits, but it becomes more or less bent during maturation. Many details of the seed morphology remain unknown as the seeds have never been found isolated from the enclosing pericarp.

#### Cathiaria tyensis (Ananjev) comb. n.

# Pl. 7, figs 1–5, 7, 8, Pl. 8, fig. 3.

1948 Carpolithes tyensis sp. n., Ananyev, p. 42. pl. 4, fig. 5

N e o t y p e (designated here): Coll. BIN 1198, specimen 105; mature infructescence, Chulym-Enisey basin, Kem River, lower part of the Simonovo Formation, Cenomanian, Pl. 7, fig. 1.

D i a g n o s i s. Lateral axes of the mature infructescences bear 10-20 sessile fruits, forming dense oblong or cylindrical aggregations.

The neotype is designated, because the holotype, described and figured by Ananyev in 1948 is lost. The surviving part of collection, decribed by Ananyev in this paper, is stored in the Tomsk Polytechnical University, Tomsk. The neotype is derived from the same locality at Kem River as the holotype.

M a t e r i a l a n d l o c a l i t i e s. Entire infructescences and their parts preserved as weakly mineralized compressions. 1) Coll. BIN 1198, Western Siberia, the Chulym-Enisey Basin, lower part of the Simonovo Formation, Cenomanian, Kem River, site 8, specimens 33, 34, 43–45, 47–49, 52–56, 60–61. 2) Coll. BIN 1181, Eastern Siberia, the Lena-Vilyuy Basin, lower part of the Timmerdyakh Formation, Cenomanian: Tyung River, site 1, specimens 146b, 560–576, 590–592; Lepiske River, site 1118, specimens 175, 176; Linde River, site 1000, specimens 211–216.

D e s c r i p t i o n. All specimens in the collections are broken at the base, so the full length is not yet known. The largest infructescences reach 6 cm in length and 2–3 cm in diameter (Pl. 7, fig. 1). Main axis straight, with irregular ribs and grooves, 2–3 mm in diameter, bearing up to 16 straight, alternate or almost opposite lateral axes at angles of 30–40°. Arrangement of the lateral axes irregular; they can be densely arranged or widely spaced. Distance between lateral axes varying from 3-4 up to 15 mm. Lateral axes up to 15-20 mm long, straight, more or less cylindrical with irregular ribs. Cross-section of immature specimens sometimes cruciform in shape (Pl. 7, fig. 3), but the arrangement of ribs is usually irregular. Lateral axes bearing 10–20 sessile fruits situated mostly on the adaxial and lateral sides (Pl. 7, figs 5, 8). Fruits nutlet-like, smooth, D-shaped in outline and flattened in cross-section, 2.5–3 mm long, 1.5–2 mm wide and about 1 mm thick (Pl. 7, figs 4, 5). Position of the attachment scar of fruits sub-basal to median; occupying from 1/10 up to 1/4 of their length. Fruits arranged in dense oblong or cylindrical aggregations 11–13 mm long and 4–6 mm in

diameter. At 3–5 mm distance the proximal part of the lateral axes is free from fruits (Pl. 7. figs 3, 7, 8).

C o m p a r i s o n. Fruit shape and overall structure of mature lateral axes of Cathiaria tyensis and C. zhilinii are very similar. These species differ by the number of fruits on the lateral axes and by their arrangment. The number of fruits on juvenile axes reaches 5-12 in C. zhilinii but the mature axes bear only 5-9 well-developed fruits and several small aborted ones whereas in C. tyensis the fruits are joined into dense oblong aggregations of 10–20 per mature axis. Adaxial arrangement of fruits is maintained in C. zhilinii but is indistinct in C. tyensis. The differences between types of preservation of the infructescences preclude more detailed comparison between these two species. The structure of fruits and axes is not known for C. tyensis whereas the architecture of complete infructescences cannot be examined for C. zhilinii.

# DISCUSSION

#### INTERPRETATION OF MORPHOLOGICAL AND ANATOMICAL FEATURES

The infructescences of *Cathiaria* have quite a complicated structure, so the morphological interpretation of some traits remains ambiguous. The pistils of *Cathiaria* can be interpreted as unicarpellate because of their ovoid shape and unilocular construction with an attenuate style as well as of the ventral and dorsal sutures which are distinctly marked in the mature fruits. However, some morphological traits, such as the inconspicuous sutures in juvenile fruits and their splitting into two valves with a narrow dorsiventral fissure extending from the apex towards the base, support an alternative interpretation, that the pistils are bicarpellate.

The interpretation of the *Cathiaria* infructescences as unisexual is based on the absence of any remains of stamens, staminodes or stamen scars. However, stamens can fall off at the end of flowering, and it cannot be ruled out that these infructescences were derived from bisexual inflorescences.

Some juvenile fruits of *Cathiaria* have incomplete remnants of cup-like structures near their bases. These remnants may be interpreted either as bracts or as reduced perianth with basally fused parts.

# Relationships

The characteristic features of Cathiaria are unisexual flowers with a single unilocular pistil and reduced perianth, nutlet-like indehiscent one-seeded fruits, and compound infructescences with dorsiventral arrangement of fruits on flattened lateral axes. Among recent plants, the infructescences of Cathiaria share most traits with the family Moraceae and partially with the Urticaceae. Previously these two families together with Ulmaceae and Cannabaceae were included in the order Urticales, which was placed in the subclass Hamamelidae, e.g. Cronquist (1981). According to recent molecular data, the Moraceae are considered as member of the Rosales (Sytsma et al. 2002, Soltis et al. 2005).

The basic structure of the inflorescence in former Urticales appears to be a compound dichasium (Berg 1977, 1989). The main variation which is observed in the inflorescences of Moraceae and Urticaceae are tendencies towards shortening of the axis, reduction in the number of axes, fusion of the axes, dorsiventral orientation (=adaxial orientation of the flowers), change from dichasial to monochasial growth, change from bisexual to unisexual. The inflorescences of Moraceae are unisexual and very variable in architecture including spikes, racemes, heads, solitary flowers and the more derived syconia or discoid-involucrate inflorescences (Corner 1962, Berg 1977). The pistillate and staminate inflorescences often differ in size and shape. Flowers of the Urticales are very small and consist basically of 4–5 tepals, 4–5 stamens and one pistil. In Moraceae and Urticaceae flowers are unisexual and reduction of the number of floral parts is the main trend, leading to flowers consisting of a single pistil as in *Treculia* Decne. ex Trec. or only a single stamen as in Brosimum Swartz. The gynoecium of the Urticales is formed by 2(3) carpels of which 1(2) is usually suppressed, and in some groups provides only a second style or stigma (Bechtel 1921). The pistil is pseudomonomerous, usually with one locule and with a single ovule. The tepals of the pistillate flowers in Moraceae and Urticaceae are often fused, forming a tubular perianth which in turn is often fused with the pistil or fruit. The perianth can be reduced

to complete absence and this is apparently preceded by irregularities in the number and shape of tepals.

The basic fruit type in the Moraceae seems to be a dehiscent one-seeded drupe (druplet) and is found in several genera belonging to different tribes. Other types are indehiscent drupes or achenes, often fleshy or enclosed in a fleshy receptacle (Berg 1989).

Cathiaria shares with the Urticales the following features: compound branched unisexual inflorescences, dorsiventral arrangement of flowers and fruits, flowers with a single unilocular pistil, reduced perianth, indehiscent one-seeded fruits. However, we could not find any extant taxon, which would really be closely similar with Cathiaria. Branched inflorescences with the adaxial orientation of unisexual pistillate flowers (stalked or sessile) with reduced perianth occur in Trophis Browne and Sorocea St.-Hil. (Moraceae), and in Boehmeria Jacq. & Urtica L. (Urticaceae). But all these genera have cylindrical axes of inflorescences, whereas in Cathiaria these axes are flattened. Flattened lateral axes of inflorescences with adaxial arrangement of flowers have been considered by Berg (1977) as a hypothetical stage in evolutionary transformation of branched inflorescences of Moraceae into discoid ones. Moreover, these genera of Moraceae and Urticaceae show other types of fruits than Cathiaria. Many Trophis species have rather big fleshy fruits, whereas the fruits in *Boehmeria* and *Urtica* are usually enclosed by an accrescent tubular perianth.

*Cathiaria* is somewhat similar to some other extant taxa. Branched unisexual inflorescences, flowers with single unilocular pistil and reduced perianth, and indehiscent oneseeded fruits occur in Chloranthaceae and *Didymeles* Thouars.

Didymeles is variously treated in the family Buxaceae, or as the only genus of the family Didymelaceae (Soltis et al. 2005). This genus is native to Madagascar and the Comoro Islands and consists of two species of evergreen trees. Female flowers are in axillary compound unisexual racemes or thyrses. In the axil of a bract on the main inflorescence axis, there is a pair of transverse bract-like organs on a stalk. A carpel is situated in the axil of each bract-like organ. Female flowers have 1–4 minute scale-like sepals and one carpel with widely decurrent stigma. Fruits are fleshy drupes with persistent stigma and style (Balthazar et al. 2003).

*Cathiaria* is distinguished from *Didymeles* by the structure of its female inflorescence consisting of two orders of axes with flattened secondary axes bearing up to 20 flowers. In contrast, *Didymeles* has three orders of axes (if the last unit of inflorescences can be interpreted as two unicarpellate flowers, rather than one bicarpellate flower), and the secondary axes bear paired flowers. In contrast to *Cathiaria*, the fruits of *Didymeles* are large and fleshy.

In Chloranthaceae, branched unisexual inflorescences and small flowers with single unilocular pistil are characteristic for several species of *Ascarina* Forst. & Forst. (Doyle et al. 2003). Its flower has no perianth, the pistil is borne in the bract axil. Fruits of *Ascarina* are one-seeded, drupaceous and fleshy. *Cathiaria* differs from *Ascarina* by the adaxial arrangement of flowers and fruits at flattened lateral axes of infructescences and by non-fleshy fruits.

Unfortunately, we do not have enough information about floral structure and seed anatomy of *Cathiaria* for a more detailed comparison of this fossil taxon with extant groups.

# Comparison with other fossil plants

Fossil infructescences similar to Cathiaria were found in Japan and in Czech Republic. In north-eastern Japan these remains were figured in the composition of the Kamikitaba assemblage from Ashizawa Formation, Lower Coniacian (Takahashi et al. 1999). They are represented by two specimens that consist of flattened axes bearing three sessile ovoid fruits (carpels) with a short bract near the base (Takahashi et al. 1999, figs 4 G, H, flower type 4). These specimens are very similar to fragments of juvenile lateral axes of Cathiaria. In contrast to *Cathiaria*, which has remnants of a cup-like structure around the fruit base, the remains from Japan have rather well-preserved bracts near the base of juvenile fruits.

Complete fossil infructescences, similar to the mature infructescences of *Cathiaria tyensis*, have been found by J. Kvaček (pers. comm.) in the collections of the National Museum in Prague, Czech Republic. These remains occur in the deposits of the Peruč Formation, Cenomanian. Like *Cathiaria*, these infructescences are compound with two orders of axes; flattened lateral axes bear sessile nutlet-like D-shaped fruits at their adaxial side. These infructescences are preserved as impressions, lacking anatomical details. In contrast to *Cathiaria*, the Peruč specimens are longer, with a larger number of lateral axes. Their lateral axes are usually curved and bear only few (5–6) fruits only at the adaxial side. In *C. tyensis* the lateral axes are straight and bear up to 20 fruits that are densely aggregated in the distal part of the axes. Probably, the Peruč fossils represent another species of *Cathiaria*.

The most unusual characters of *Cathiaria* are its flattened axes and dorsivental arrangement of its fruits. These features are characteristic also for the Cretaceous angiosperm genus *Mauldinia* from the Cenomanian deposits of North America, Europe and Kazakhstan (Drinnan et al. 1990, Eklund & Kvaček 1998, Frumin et al. 2004). However, the flattened lateral axes of *Mauldinia* are two-lobed. Their adaxial surface bears several sessile bisexual flowers as is characteristic of Lauraceae. The fruits of *Cathiaria* show no lauraceous characters; hence, the flattened axes of infructescences have probably appeared convergently in these two genera.

Vegetative and reproductive structures of Urticales occur in the regions of Europe and northern Asia from the Cenomanian (Knobloch & Mai 1984, 1986, Shilin 1986, Collinson 1989). In the Cretaceous deposits Urticales are represented mostly by fruit and leaf remains of Ulmaceae and Urticaceae. All urticaceous fruits were reported by Knobloch and Mai (op.cit.) from Europe. They described the genera *Boehmeria* Jacquin, *Pouzolzia* Gaudich., and *Urticoidea* Knobloch & Mai. Among these fossil Urticales there are no fruits or infructescences, similar to *Cathiaria*.

# ASSOCIATED POLLEN, LEAVES AND FLOWERS

Tricolpate pollen was found on the surface of many juvenile fruits of *Cathiaria zhilinii* (Pl. 8, figs 5, 6). These pollen grains are nearly spherical, equatorial axis 13–16  $\mu$ m, polar axis 16–18  $\mu$ m, equatorial aspect wide-elliptical, and polar aspect trilobate. The grain surface is reticulate with slit-like colpi. Since all the pollen grains are of one kind, they probably belong to the same plant as *Cathiaria* infructescences, although most of the grains were found not near the stigma, but at different parts of the lateral surface of fruits.

These infructescences were found in association with leaves of *Liriodendropsis simplex* in all Siberian localities yielding Cathiaria tyensis (Tab. 1). In these localities clay lenses yield monodominant taphocoenoses of Liriodendropsis Newberry leaves. Remains of Cathiaria infructescences are also rather numerous in these localities (Pl. 8, fig. 3). In the Czech Republic Cathiaria was also found in a clay lense of the Mala Chuchla locality, which contains almost exclusively Liriodendropsis leaves (J. Kvaček, pers. comm.). Cathiaria zhilinii is known to date only from three mesofossil localities in Kachar guarry in North Kazakhstan. These sites do not contain dicotyledonous leaves, but Liriodendropsis remains were described from the Ayat macroflora (Vakhrameev 1952, Shilin 1986, as Dalbergites Berry), which derived from the same formation that include the mesofossil assemblage with Cathiaria.

The leaf remains of *Liriodendropsis* (widely known also under its former name *Dalbergites*) were widespread in the Cenomanian floras of Eurasia and North America (Golovneva et al. 2000, Golovneva 2003). These leaves were compound, biternate with articulate petiole. Leaflets were 3–10 cm long, ovate, oblong or lanceolate, with rounded base and emarginate apex. The margin was entire with finely pinnate venation, and secondary veins forming a series of arches. The leaflets of *Liriodendropsis* form almost monodominant taphocoenoses in lenses of lacustrine deposits in all the studied localities. Probably, these plants occurred in monospecific communities along lakes or oxbows where they were afterwards burried.

The infructescences of *Cathiaria* and the leaves of *Liriodendropsis* have not been found in direct connection, but they commonly occur together. Based on co-occurrence at six nearly monodominant localities from different Eurasian regions, we infer that these organs were produced by the same biological genus.

In addition, in the only locality in Western Siberia (the Kem River) *Cathiaria* infructescences and *Liriodendropsis* leaves were found together with numerous staminate flowers and one complete male inflorescences of *Freyantha sibirica* Krassilov & Golovneva (Krassilov & Golovneva 2001). Besides numerous *Cathiaria*, *Liriodendropsis*, and *Freyantha* remains only few fragments of other dicotyledonous leaves were found in this site.

The inflorescence of Freyantha Krassilov & Golovneva (Pl. 8, fig. 1) is unisexual, racemose, with a blossom of staminate flowers in two opposite rows. The flowers are pedicellate, slightly zygomorphous, with one large curved bract protecting the flower on the bottom and outside (Krassilov & Golovneva 2001). There are five stamens, three proximal stamens are basally fused, and two others are arranged on the receptacle more distally. Each stamen consists of a short filament and massive bithecate anther with a slightly protruding extension of the connective. The pollen grains in anthers are tricolpate with reticulate exine (Pl. 8, fig. 4). These pollen grains are very similar to pollen grains stuck to the juvenile fruits of Cathiaria zhilinii from Kazakhstan (Pl. 8, figs 5, 6).

The *Freyantha* inflorescences are considered to represent one entity with the *Liriodendropsis-Cathiaria* complex. This suggestion is confirmed by the co-occurrence of these organs

Table 1. Distribution of Cathiaria infructescences, showing co-occurrence with Liriodendropsis leaves

	Sites with Liriodendropsis leaves			Sites without <i>Lirio-</i> <i>dendropsis</i> leaves
Species	Western Siberia, lower part of the Simonovo Formation, Cenomanian	Eastern Siberia, lower part of the Timmerdyakh Formation, Cenomanian	Czech Republic, Peruč Formation, Cenomanian	Northern Kazakhstan, Cenomanian
Cathiaria tyensis	1) Kem River, site 8 2) Kiya River, site 16	<ol> <li>Tyung River, site 1</li> <li>Lepiske River, site 1118</li> <li>Linde River, site 1000</li> </ol>		
Cathiaria unknown species			Mala Chuchla	
Cathiaria zhilinii				Kachar quarry

in the almost monospecific assemblage from the Kem River site and by the presence of *Freyantha*-like pollen on the surface of juvenile fruits of *Cathiaria*.

All the associated organs do not confirm urticalean affinity of *Cathiaria*. Tricolpate pollen grains found in the stamens of *Freyantha* and on the surface of juvenile fruits of *Cathiaria* are characteristic of many taxa within the eudicot clade, whereas most Moraceae and Urticaceae have porate pollen (Berg 1977).

Liriodendropsis leaflets resemble in the emarginate shape and the numerous irregular brochidodromous secondary and intercalate veins some genera of the Fabaceae such as Pterocarpus Jacq., Sweetia Spreng, and Dalbergia L. (Golovneva 2003). However, venation of the leaflets in Fabaceae is more regular, and their petiolules are distinctly shorter (not exceeding one-fifth of the leaf blade length) than in *Liriodendropsis* whose petiolules are approximately as long as the leaf blades. The biternate leaf organization is not characteristic of Fabaceae. In extant plants, biternate leaves are common in the Ranunculales. Articulate petioles can also be found in Ranunculales (for example Akebia Decne.). Among the fossil plants, biternate leaves are described for Leguminosites karatscheensis Vachr. from the Albian deposits of the Kyzylshen Formation of western Kazakhstan, which are associated with Hyrcantha fruits Krassilov, Shilin & Vakhrameev (Krassilov et al. 1983). Among Urticales there are no taxa with leaves similar to Liriodendropsis. In the Cretaceous deposits of Siberia and Kazakhstan urticalean leaf taxa are represented by the genera Aryzkumia Shilin, Celtis L., and Celtidophyllum Krasser (Shilin 1986, Golovneva 2005) that are characterized by simple leaf blades with entire or toothed margin. All these taxa are usually considered as members of Ulmaceae or Celtidaceae.

The *Freyantha* inflorescences have also no clear similarities with Urticales. Urticaceae and many genera of Moraceae are characterized by inflexed stamens which bend outwards at anthesis suddenly and elastically, thus shedding their pollen simultaneously (Berg 1977). Flowers with such stamens normally have a well-developed perianth with 4–5 tepals, 4–5 stamens and a more or less conspicuous pistillode. In groups of the Urticales with straight stamens (many Moraceae) the number of

tepals and stamens is often reduced to 3 or 2. Futher reduction can result in disappearance of the perianth, leaving a single stamen. Diminished protection of young stamens due to the loss of perianth means that the stamens must be protected in some other ways. In Brosimum (Moraceae) the necessary protection is given by bracts which form a pseudoperianth or by firm peltate bracts which cover the young flowers. The Freyantha inflorescences are also characterized by reduced perianth and large bracts, protecting stamens, but they show no real similarity to any extant genus of the Moraceae. Similar inflorescence features can also be observed in the Menispermaceae, and previously Freyantha inflorescences were compared with Ranunculales (Krassilov & Golovneva 2001).

Overall, the relationships of *Cathiaria* are uncertain. This taxon reveals a mosaic of characters found today in different families along with some unique features. Furthermore, the *Cathiaria-Liriodendropsis-Freyantha* complex is not assignable to any of the modern families and perhaps represents an extinct family of ancient angiosperms.

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#### REFERENCES

- ANANYEV A.R. 1948. Ostatki verkhnemelovoy i tretichnoy flory s reki Kem, levovo pritoka reki Enisey. Trudy Tomskovo Universiteta. Ser. Geol., 99: 29–74.
- ARCHANGELSKY S. & TAYLOR T.N. 1993. The ultrastructure of *in situ Clavatipollenites* pollen from the Early Cretaceous of Patagonia. Amer. J. Bot. 80: 879–885.
- BALTHAZAR M., SCHATZ G.E. & ENDRESS P.K. 2003. Female flowers and inflorescences of Didymelaceae. Plant Syst. Evol., 237: 199–208
- BECHTEL A.R. 1921. The floral anatomy of the Urticales. Amer. J. Bot., 8: 386–410.

- BERG C.C. 1977. Urticales, their differentiation and systematic position. Plant Syst. Evol., Suppl., 1: 349–374.
- BERG C.C. 1989. Systematics and phylogeny of the Urticales: 193–220. In: Crane P.R. & Blackmore S. (eds) Evolution, Systematics and fossil history of the Hamamelidae. Vol. 2. "Higher" Hamamelidae. Systematics Association Special Volume N 40B. Clarendon Press. Oxford.
- COLLINSON M.E. 1989. The fossil history of the Moraceae, Urticaceae (including Cecropiaceae), and Cannabaceae: 319–339. In: Crane P.R. & Blackmore S. (eds) Evolution, Systematics and fossil history of the Hamamelidae. Vol. 2. "Higher" Hamamelidae. Systematics Association Special Volume N 40B. Clarendon Press, Oxford.
- CORNER E.J.H. 1962. The classification of Moraceae. Gard. Bull. Singapore, 19: 187–252.
- CRANE P.R. & DILCHER D.L. 1984. *Lesqueria*: an early angiosperm fruiting axis from the mid-Cretaceous. Ann. Missouri Bot. Gard., 71: 384–402.
- CRANE P.R., FRIIS E.M. & PEDERSEN K.R. 1994. Paleobotanical evidence on the early radiation of magnoliid angiosperms. Plant Syst. Evol., Suppl., 8: 51-72.
- CRANE P.R., FRIIS E.M. & PEDERSEN K.R. 1995. The origin and early diversification of angiosperms. Nature. 374: 27–33.
- CREPET W.L. & NIXON K.C. 1998. Two new fossil flowers of magnoliid affinity from the Late Cretaceous of New Jersey. Am. J. Bot., 85: 1273–1288.
- CRONQUIST A. 1981. An integrated system of classification of flowering plants. Houghton Mifflin, Boston.
- DILCHER D.L. 1979. Early angiosperm reproduction: an introductory report. Rev. Palaebot. Palynol., 27: 291–328.
- DILCHER D.L. & CRANE P.R. 1984. Archaeanthus: an early angiosperm from the Cenomanian of the Western Interior of North America. Ann. Missouri Bot. Gard. 71: 315–383.
- DOUGLAS J.G. 1994. Cretaceous vegetation: the macrofossil record: 171–188. In: Hills R.S. (ed.) History of the Australian vegetation: Cretaceous to recent. Cambridge University Press, Cambridge.
- DOYLE J.A., EKLUND H. & HERENDEEN P.S. 2003. Floral evolution in Chloranthaceae: Implications of a morphological phylogenetic analysis. Int. J. Plant Sci., 164: 365–382.
- DRINNAN A.N., CRANE P.R., FRIIS E.M. & PED-ERSEN K.R. 1990. Lauraceous flowers from the Potomac group (mid-Cretaceous) of eastern North America. Bot. Gaz., 151(3): 370–384.
- EKLUND H. & KVAČEK J. 1998 Lauraceous inflorescences and flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). Int. J. Plant Sci., 159(4): 668–686.
- EKLUND H., CANTRILL D.J. & FRANCIS J.E. 2004. A Late Cretaceous mesofossil assemblage from

Table Nunatak Antarctica: lycopods, ferns and vegetative structures of conifers and angiosperms. Cret. Reseach, 25: 211–228.

- EKLUND H., FRIIS E.M. & PEDERSEN K.R. 1997. Late Cretaceous reproductive organs of chloranthaceous affinity from Scania, southern Sweden. Plant Syst. Evol., 207: 13–42.
- FRIIS E.M. 1983. Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing Normapolles pollen. Rev. Palaeobot. Palynol., 39: 161–188.
- FRIIS E.M. 1985. Preliminary report on Upper Cretaceous angiosperm reproductive organs from Sweden and their level of organization. Ann. Missouri Bot. Gard., 71: 403–418.
- FRIIS E.M. 1999. Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous from Portugal. Ann. Missouri Bot. Gard., 86: 259–296.
- FRIIS E.M. 2000. Reproductive structure and organization of basal angiosperms from the Early Cretaceous (Barremiam or Aptian) of western Portugal. Int. J. Plant Sci., 161 (Suppl): S169–S182.
- FRIIS E.M., PEDERSEN K.R. & CRANE P.R. 1994. Angiosperm floral structures from the Early Cretaceous of Portygal. Plant Syst. Evol. Suppl., 8: 31–49.
- FRUMIN S. & FRIIS E.M. 1996. Liriodendroid seeds from the Late Cretaceous of Kazakhstan and North Carolina, USA. Rev. Palaeobot. Palynol., 94: 39–55.
- FRUMIN S. & FRIIS E.M. 1999. Magnoliid reproductive organs from the Cenomanian-Turonian of north-western Kazakhstan: Magnoliaceae and Illiciaceae. Plant Syst. Evol., 216: 265–288.
- FRUMIN S., EKLUND H. & FRIIS E.M. 2004. Mauldinia hirsuta sp. nov., a new member of the extinct genus Mauldinia (Lauraceae) from the Late Cretaceous (Cenomanian-Turonian) of Kazakhstan. Int. J. Plant Sci., 165(5): 883–895.
- FRUMINA S., ZHILIN S.G. & KORCHAGINA I.A. 1995. Alapaja (Taxodiaceae) seeds from the Cenomanian-Turonian of Northern Kazakhstan. Paleont. J., 29(1A): 194–202.
- GABRIELYAN I.G. & ZHILIN S.G. 1997. Novye nakhodki ostatkov pozdnemelovykh rasteny v kariere Kachar (Severny Kazakhstan) (New findings of the Late Cretaceous plant remains in the Kachar Quarry (Northern Kazakhstan). Toporkovskie chteniya, 3: 200–202. (in Russian).
- GOLOVNEVA L.B. 2003. Leaves of Liriodendropsis simplex (Newb.) Newb. from the Cretaceous of Siberia. Paleont. J., 2003(5): C. 1–9.
- GOLOVNEVA L.B. 2005. Fitostratigrafiya i evolutsiya alb-kampanskoi flory na territorii Sibiri (Phytostratigraphy and evolution of the Albian-Campanian flora in the Siberian region): 177–197. In: Arkadiev V.V. & Prozorovskii V.A. (eds) Melovaya sistema Rossii: problemy stratigrafii i paleogeo-

grafii. St. Petersburg State University Press, St. Petersburg. (in Russian with English abstract

- GOLOVNEVA L.B., KHVAL' A.V., KRASSILOV V.A. 2000. Leaves of *Liriodendropsis* and associated reproductive structure from the Cretaceous of Siberia and Kazakhstan: 41. In: The 6<sup>th</sup> Conference of International Organization of Palaeobotany. Abstracts. Qinhuangdao, China.
- HERENDEEN P.S., MAGALLON-PUEBLA S., LUPIA R., CRANE P.R. & KOBYLINSKA J. 1999. A preliminary conspectus of the Allon Flora from the Late Cretaceous (Late Santonian) of Central Georgia, USA. Ann. Missouri Bot. Gard., 86: 407–471.
- KHVAL' A.V. 2001. (unpubl). Karpologia srednemelovyh khvoinykh i zvetkovykh Kachara (yugovostochnoe Zauralie). St. Petersburg. Ph.D. Thesis Komarov Botanical Institute. (in Russian).
- KNOBLOCH E. & MAI D.H. 1984. Neue Gattungen nach Früchten and Samen aus dem Cenoman bis Maastricht (Kreide) von Mitteleuropa. Feddes Repert., 95: 1–341.
- KNOBLOCH E. & MAI D.H. 1986. Monographie der Früchte and Samen in der Kreide von Mitteleuropa. Rozpr. Ústr. Ústavu Geol., 47: 1–219.
- KRASSILOV V.A. 1982. Early Cretaceous flora of Mongolia. Palaeontographica, B, 181: 1–43.
- KRASSILOV V.A. 1997. Angiosperm origins: Morphological and ecological aspects. PENSOFT, Sofia, Bulgaria.
- KRASSILOV V.A. & GOLOVNEVA L.B. 2001. Inflorescence with tricolpate pollen grains from the Cenomanian of Tschulymo-Yenisey Basin, West Siberia. Rev. Palaeobot. Palynol., 115: 99–106.
- KRASSILOV V.A. & GOLOVNEVA L.B. 2004. A minute mid-Cretaceous flower from Siberia and implications for the problem of basal angiosperms. Geodiversitas, 26: 5–15.
- KRASSILOV V.A. & SHILIN P.V. 1995. New platanoid staminate heads from the mid-Cretaceous of Kazakhstan. Rev. Palaeobot. Palynol., 85: 207–211.
- KRASSILOV V.A., SHILIN P.V. & VAKHRAMEEV V.A. 1983. Cretaceous flowers from Kazakhstan. Rev. Palaeobot. Palynol., 40: 91–113.
- KRYSHTOFOVICH A.N. 1936. O melovoi flore vostochnovo sklona Urala i otnoshenii eyo k zalezham boksitov. Materialy TSNIGRI. Obshchaya seriya. 1936(1): 42–49.
- KVAČEK J. & EKLUND H. 2003. A report on newly recovered reproductive structures from the Cenomanian of Bohemia (Central Europe). Int. J. Plant Sci., 164(6): 1021–1039.
- KVAČEK Z. 1992. Lauralean angiosperms in the Cretaceous. Cour. Forschungsinst. Senckenberg, 147: 345–367.
- LEBEDEV I.V. 1962. Verkhnemelovye rasteniya. Biostratigrafiya mezozoyskikh i tretichnykh otlozheny Zapadnoy Sibiri. SNIIGGMS Transaction, 22: 237–282.

- LENG Q. & FRIIS E.M. 2003. *Sinocarpus decussatus* gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. Plant. Syst. Evol., 241: 77–88.
- MASLOVA N.P. & GOLOVNEVA L.B. 2000a. Lindacarpa gen. et sp.nov. – Novoe sotsvetie gamamelidovykh iz verkhnevo mela Vostochnoi Sibir'i. (A new hamamelid infructescence from the Upper Cretaceaous of eastern Siberia). Paleont. Jour. 34(4): 100–106.
- MASLOVA N.P. & GOLOVNEVA L.B. 2000b. A hamamelid inflorescence with *in situ* pollen grains from the Cenomanian of Eastern Siberia. Paleont.. J.. 34(Suppl.): 40–49.
- MASLOVA N.P., GOLOVNEVA L.B. & TEKLEVA M.V. 2005. Infructescences of *Kasicarpa* gen. nov. (Hamamelidales) from the Late Cretaceous (Turonian) of the Chulym-Enisey depression, western Siberia, Russia. Acta Palaeobot., 45(2): 121–137.
- MOHR B.A.R. & FRIIS E.M. 2000. Early angiosperms from the Lower Cretaceous Crato Formation (Brazil), a preliminary report. Int. J. Plant Sci., 161(6 Suppl.): 155–167.
- NISHIDA H. 1994. *Elsemaria*, a late Cretaceous angiosperm fructification from Hokkaido, Japan. Plant Syst. Evol., 8 (Suppl.): 123–135.
- PAPULOV G.N. 1990. Biostratigrafiya verkhnemelovykh otlozheny rayona: 154–173. In: Papulov G.N., Zhelezko V.I. & Levina A.P. (eds) Verkhnemelovye otlozheniya Yuzhnogo Zaural'ya. Akad Nauk SSSR, Sverdlovsk.
- PEDERSEN K.R., FRIIS E.M., CRANE P.R. & DRIN-NAN A.N. 1994. Reproductive structures of an extinct platanoid from the Early Cretaceous (latest Albian) of eastern North America. Rev. Palaeobot. Palynol., 80: 291–303.
- SAMYLINA V.A. 1959. Novye nakhodki pokrytosemennykh rasteny v nizhnemelovykh otlozheniyakh Kolymy. Bot. Zhur., 44: 483–491.
- SAMYLINA V.A. 1960. Pokrytosemennye rasteniya is nizhnemelovykh otlozheny Kolymy. Bot. Zhur., 45: 335–352.
- SHILIN P.V. 1986. Verchnemelovye flory Kazakhstana. Systematika, istoriya i stratigrafiya. Nauka, Alma-Ata.
- SOLTIS D.E., SOLTIS P.S., ENDRESS P.R. & CHASE M.W. 2005. Phylogeny and evolution of angiosperms. Smithsonian Books, Washington.
- SUN G. & DILCHER D.L. 2002. Early angiosperms from the Lower Cretaceous of Jixi, eastern Heilongjiang, China. Rev. Palaeobot. Palynol., 121: 91–112.
- SUN G., DILCHER D.L., ZHENG S. & ZHOU Z. 1998. In search of the first flower: a Jurassic angiosperm, *Archaefructus* from N.E. China. Science, 282: 1692–1695.

- SUN G., JI Q., DILCHER D.L., ZHENG S., NIXON K.C. & WANG X. 2002. Archaefructaceae, a new basal angiosperm family. Science, 296: 899–904.
- SYTSMA K.J., MORAWETZ J., PIRES J.C., NEPOK-ROEFF M., CONTI E., ZJHRA M., HALL J.C. & CHASE M.W. 2002 Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbcL*, *trnL-F*, and *ndhF* sequences. Amer. J. Bot., 89: 1531–1546.
- TAKAHASHI M., CRANE P.R. & ANDO H. 1999. Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, Futuba Group, lower Coniacian, Upper Cretaceous) of northeast Japan. J. Plant Res., 112: 187–206.
- TAKAHASHI M., HERENDEEN P.S. & CRANE P.R. 2001. Lauraceous fossil flowers from the Kamikitaba locality (Lower Coniacian; Upper Cretaceous) in Northeastern Japan. J. Plant Res., 114: 429–434.
- TAKAHASHI M., CRANE P.R. & MANCHESTER S.R. 2002. *Hironia fusiformis* gen. et sp. nov.; a cornalean fruit from the Kamikitaba locality (Upper Cretaceous, Lower Coniacian) in northeastern Japan. J. Plant Res., 115: 463–473.

- TAYLOR D.W. & HICKEY L.J. 1990. An Aptian plant with attached leaves and flowers: implication for angiosperm origin. Science, 247: 702–704.
- VAKHRAMEEV V.A. 1952. Stratigrafiya i iskopaemaya flora melovykh otlozheny Zapadnovo Kazakhstana. Izdatelstvo Akad. Nauk SSSR, Moskva.
- VAKHRAMEEV V.A. & KRASSILOV V.A. 1979. Reproductivnye organy tsvetkovykh iz alba Kazakhstana. Paleont. J., 1979(1): 121–128.
- ZHELEZKO V.I., LEVINA A.P., PAPULOV G.N., AMON E.O., ZOTEEVA E.A., NAIDIN D.P., PAS-KAR' Z.C. & PONOMARENKO Z.K. 1990. Kacharsky zhelezorudny karier: 9–26 In: Papulov G.N., Zhelezko V.I. & Levina A.P. (eds) Verkhnemelovye otlozheniya Yuzhnovo Zaural'ya. Akad. Nauk SSSR, Sverdlovsk.
- ZHILIN S.G., KORCHAGINA I.A., POTAPOVA Ya.Yu., TARASEVICH V.F., FRIIS E.M. & FRUMINA S.I. 1997. O nakhodke bogatovo paleokarpologicheskovo kompleksa na urovne senomana-turona v Sarbaiskom kariere – Severny Kazakhstan (Discovery of the rich palaeocarpological assemblages at the Cenomanian-Turonian level in Sarbay Quarry (Northern Kazakhstan). Toporkovskie chteniya, 3: 190–200. (in Russian).

# PLATES

Juvenile infructescences of *Cathiaria zhilinii* sp. n., Kazakhstan, Cenomanian, SEM, showing different shape of flattened lateral axes and arrangement of fruits

- 1. Rounded flattened lateral axis (LA) with prominent apex (A) and 6 sessile fruits, adaxial view. Abaxial median ridge is indistinct in the apex area. Specimen BIN 1707-152. Scale bar  $-1000 \mu m$
- 2. Widely triangular flattened lateral axis (LA) showing staggered rows of sessile fruits, adaxial view. Specimen BIN 1707-164. Scale bar 1000  $\mu$ m
- 3. Widely triangular flattened lateral axis (LA), apical view, showing apex (A), abaxial keel (AB), fruits and uneven surface with various small local thickenings. Note some asymmetry of the lateral extensions and the arrangement of fruits: usually the right extension (from abaxial view) is wider and more concave than the left one. Specimen BIN 1707-133. Scale bar 100 µm
- Fragment of main axis (MA) with two flattened lateral axes (LA), lateral view. Right lateral axis showing a widely decurrent base (B) and young fruits, holotype. Specimen BIN 1707-162, holotype. Scale bar 1000 μm
- 5. Oblong flattened lateral axis (LA) with prominent cylindrical apex (A) and fruits, adaxial view; uppermost fruit showing a cup-like structure (C) at the base. Specimen BIN 1707-142. Scale bar 1000  $\mu$ m
- 6. Widely triangular flattened lateral axis (LA) with young fruits, abaxial view, showing abaxial keel (AB) reaching the apical area, and the uneven surface with various small local thickenings. Specimen BIN 1707-133. Scale bar 100  $\mu$ m
- 7. Upper part of an lateral axis with 2 fruits showing abaxial keel (**AB**), attenuate apex (**A**), and conductive tissue (**CT**) in crushed adaxial ridge gradually decreasing towards the apex; lateral view. Specimen BIN 1707-163. Scale bar 100  $\mu$ m
- 8. Flattened lateral axis showing abaxial keel (**AB**) and the fruits situated on the upper surface of the lateral extensions (**LE**) and adaxial ridge (**AD**), lateral view. Specimen BIN 1707-160. Scale bar 1000 μm



Juvenile infructescences of Cathiaria zhilinii sp. n., Kazakhstan, Cenomanian, SEM

- 1. Juvenile fruit in the pit on the edge of a lateral extension. Specimen BIN 1707-200. Scale bar 100 µm
- 2. Cells on the outer surface of a juvenile fruit with straight anticlinal walls and thickened periclinal ones. Specimen BIN 1707-133. Scale bar 10  $\mu m$
- 3. Juvenile fruit with well-preserved cup-like structure (C) near its base. Specimen BIN 1707-200. Scale bar 100  $\mu m$
- Fragment of flattened lateral axis (LA) with one fruit borne at the median adaxial ridge (AD). Specimen BIN 1707-115. Scale bar – 10 μm
- 5. Juvenile fruit with cup-like structure (C) near its base. Specimen BIN 1707-203. Scale bar  $-100 \mu m$
- 6. Cup-like structure (C) and conductive bundle (CB) near the base of a juvenile fruit (F). Specimen BIN 1707-171. Scale bar 10  $\mu m$
- 7. Style of mature fruit with bifid apex. Specimen BIN 1707-204. Scale bar 10  $\mu m$
- 8. Cross-section of a cup-like structure (C) near a fruit base; the cell boundaries are indiscernible. Specimen BIN 1707-200. Scale bar 10  $\mu m$



Juvenile infructescences of Cathiaria zhilinii sp. n., Kazakhstan, Cenomanian, SEM

- 1. Cruciform cross-section of a juvenile lateral axis, proximal view, showing abaxial keel (**AB**), lateral extensions (**LE**), adaxial median ridge with conductive bundle (**CB**) and fruits (**F**). Specimen BIN 1707-168. Scale bar  $-100 \mu m$
- Cruciform cross-section of juvenile lateral axis, distal view, showing abaxial keel (AB), lateral extensions (LE), and adaxial median ridge (AD) and also a conductive bundle (CB) in the middle of median ridge. Specimen BIN 1707-148. Scale bar – 100 μm
- 3. V-shape cross-section of the upper part of juvenile lateral axis viewing abaxial keel (**AB**), lateral extensions (**LE**), and juvenile fruits (**F**) situated along low adaxial median ridge (**AD**). Specimen BIN 1707-177,  $\times$  37, proximal view. Scale bar 100 µm
- 4. Cross-section of lateral extension (**LE**) bearing sessile juvenile fruits (**F**). The extension consists mostly of sclerenchyma. Specimen BIN 1707-147. Scale bar  $-100 \mu m$
- 5. Conductive tissue (**CT**) and adjacent parenchyma (**P**) inside a partially crushed lateral axis. Specimen BIN 1707-145, abaxial view. Scale bar 100 μm
- 6. Parenchyma cells near the conductive bundle in a lateral axis. Specimen BIN 1707-145. Scale bar 10 μm



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Structure of the juvenile fruits of Cathiaria zhilinii sp. n., Kazakhstan, Cenomanian, SEM

- 1. Longitudinal section of a juvenile fruit with a single seed inside. Specimen BIN 1707-140. Scale bar  $-\,100\,\,\mu\text{m}$
- 2. Seed base. Specimen BIN 1707-139. Scale bar 100  $\mu m$
- 3. Section of a juvenile fruit along its ventral and dorsal sutures viewing elongated cells of the inner pericarp layer. Specimen BIN 1707-130. Scale bar  $100 \mu m$
- 4. Pericarp of a juvenile fruit at cross-section viewing top-down thick sclerenchyma (S), layer of elongated thin-walled cells (EC), and layer of obliterated cells (OC) adjacent to the seed coat (on the bottom). Specimen BIN 1707-133. Scale bar 10  $\mu$ m



Conductive tissue of juvenile infructescences of Cathiaria zhilinii sp. n., Kazakhstan, Cenomanian, SEM

- 1. Tracheid-like cell (**TL**) with bordered pits on its lateral wall, and the cells (**CT**) with circular or helical thickenings in the xylem of a vascular bundle in the lateral axis. Specimen BIN 1707-145. Scale bar  $-1 \mu m$
- 2. Radial section of the main axis of an infructe scence; zones of cortex (CO), xylem (X), and pith (P) can be distinguished. Specimen BIN 1707-158. Scale bar – 100  $\mu$ m
- 3. Helical secondary thickenings on the cell wall of a tracheary element (probably a protoxylem cell) situated near the pith of the main axis. Specimen BIN 1707-158. Scale bar 10 μm
- 4–6. Supposed metaxylem cells in the outer region of xylem in the main axis of an infructescence: 4. Fusiform parenchyma cell (**FP**) and tracheary elements with helical (**HE**) and scalariform (**SC**) secondary thickenings on the cell walls. Specimen BIN 1707-158; 5. Tracheary element with scalariform secondary thickenings on the cell wall. Specimen BIN 1707-158; 6. Ending of tracheary element with helical secondary thickenings on the cell wall. Specimen BIN 1707-158; 5. Scale bar 10  $\mu$ m
- 7. Tracheary elements in the pericarp. Specimen BIN 1707-130. Scale bar  $\; 1 \; \mu m$
- 8. Parenchyma cells in the pith of the main axis of an infruct escence. Specimen BIN 1707-158. Scale bar  $-10\,\mu\mathrm{m}$



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Mature infructescences and fruits of Cathiaria zhilinii sp. n., Kazakhstan, Cenomanian, SEM

- 1. Lateral view on a mature fruit, note style and dorsal suture; the fruit is attached to the lateral axis by the most part of its ventral surface. Specimen BIN 1707-112. Scale bar  $-100 \mu m$
- 2. Unit of mature fruits, attached to the adaxial side of lateral axis. Specimen BIN 1707-199. Scale bar  $-1000 \mu$ m. The fruit surface is smooth, but sometimes with small rounded knobs along the dorsal suture (lower fruit in the centre)
- 3. Longitudinal section of a mature fruit with a single seed inside. Specimen BIN 1707-135. Scale bar  $-100\ \mu\text{m}$
- 4. Ventral suture in the upper part of mature fruits. Specimen BIN 1707-113. Scale bar 100  $\mu m$
- 5. Dorsal suture of a mature fruit showing lengthwise elongated epidermal cells. Specimen BIN 1707-111. Scale bar 100  $\mu m$
- 6. Cross-section of an elongated lateral axis (LA) bearing three well-developed fruits (F) on the adaxial side and an aborted one (A). Fruits are situated mainly on the adaxial side; abaxial keel in the lower part of the axis is distinct. Specimen BIN 1707-107, distal view. Scale bar – 1000  $\mu$ m
- 7. Part of an elongated lateral axis with irregular longitudinal ribs bearing two well-developed fruits (F) and three aborted ones (A). Specimen BIN 1707-198, lateral view. Scale bar  $-1000 \ \mu m$
- 8. Part of an elongated lateral axis with irregular longitudinal ribs bearing three well-developed fruits (**F**) and a small aborted one (**A**). Specimen BIN 1707-195, lateral view. Scale bar  $-1000 \mu m$



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Infructescences of *Cathiaria tyensis* (Ananjev) comb. n. from East (2,4,5,7) and West (1,3,8) Siberia, Cenomanian and *Cathiaria zhilinii* sp. n. (6), Kazakhstan, Cenomanian

- 1. Fragment of an infructescence of Cathiaria tyensis, ×1.5, specimen BIN 1198-105, neotype
- 2. Infructescence with decussate lateral axes in close aggregation, ×1.5, specimen BIN 1181-562
- 3. Lateral axis of an infructescence with fruits. Note finely ribbed surface of the main axis, and the cruciform (in cross-section) shape of the lateral axis (LA), ×6.5, specimen BIN 1198-45
- 4. Part of an lateral axis with sessile fruits,  $\times 10$ , specimen BIN 1181-564b
- 5. Part of an lateral axis bearing three sessile fruits on its adaxial and lateral sides, ×11, specimen BIN 1181-564a
- Lateral view on a part of the mature elongated lateral axis of *Cathiaria zhilinii* with a single well-developed fruit (F) and few aborted fruits (A). Note maintained cruciform shape (in cross-section) of the lateral axis (LA), ×13, specimen BIN 1707-196
- 7. Part of an infructescence with loosely arranged opposite lateral axes. Proximal part of the lateral axes bears no fruits, ×3, specimen BIN 1181-590
- 8. Main infructescence axis with lateral axis bearing fruits. Note asymmetric arrangement of the fruits situated mostly on the adaxial side of lateral axis, ×7.5, BIN 1198-61



Infructescences of Cathiaria and associated leaves, flowers and pollen

- 1. Staminate inflorescence of *Freyantha sibirica* Krassilov & Golovneva, general view, showing main axis (**AX**) with several staminate flowers (**SF**), ×4, specimen BIN 1198-42
- 2. United leaflets of *Liriodendropsis simplex* (Newb.) Newb. from the Western Siberia, Chulym River, × 1, specimen BIN 53-30
- 3. Leaflet *Liriodendropsis simplex* (Newb.) Newb. and infructescence of *Cathiaria tyensis* (Ananjev) comb. n. on the same piece of rock, Western Siberia, Kem River, ×1.3, specimen BIN 1531-6
- 4. Tricolpate reticulate pollen grain of *Freyantha sibirica* Krassilov & Golovneva. from stamen, ×2300, specimen BIN 1198-42
- 5. Pollen grains on the surface of a juvenile fruit of Cathiaria zhilinii. Specimen BIN 1707-141. Scale bar $-\,10~\mu{\rm m}$
- 6. Reticulate tricolpate pollen grain on the fruit surface of Cathiaria zhilinii. Specimen BIN 1707-135. Scale bar 1  $\mu m$



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