

New hamamelid infructescences from the Paleocene of western Kamchatka, Russia

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Abstract

Hamamelid inflorescences and infructescences from Late Paleocene deposits of Kamchatka, Russian Far East, are assigned to a new genus *Evacarpa* N. Maslova et Krassilov, *gen. nov.* The inflorescences are similar to the respective extant and fossil platanoid structures (Platanaceae) in general form of pistillate heads and their arrangement on reproductive axes, unsealed carpels and their diachronous ripening, but differ in having fewer florets per head, paired carpels, intrafloral phyllomes, numerous ovules and the absence of a perianth. The latter characters are shared with *Liquidambar* and *Altingia*. These fossils contribute to knowledge of early hamamelid diversity but may also be relevant to current concepts of primitiveness in floral morphology.

Keywords: Angiosperms; Hamamelidaceae; Plant morphology; Phylogeny; Paleocene

1. Introduction

Small capitulate inflorescences and infructescences, found in a number of the Northern Hemisphere Cretaceous and Paleocene localities, are perhaps the most widespread structurally preserved reproductive organs of early angiosperms (Krassilov, 1973; Manchester, 1986; Crane, 1987; Crane et al., 1988; Friis et al., 1988; Pigg and Stockey, 1991; Krassilov and Shilin, 1995). Most of these fossils are described as “platanoid”, that is essentially similar to the staminate or pistillate heads of extant *Platanus* but differing from them in certain taxonomically less critical peculiarities of their floret (e.g. the more prominent perianths, fewer carpels per flower), pollen (tricolporate as well as tricolpate) or fruit (lacking dispersal hairs) morphology. Externally the infructescences

described in the present paper are quite similar to platanoid heads from other localities. However, under closer inspection they revealed features suggesting affinities with another group of primitive hamamelids—the altingioids (or liquidambroids: see below for controversial taxonomic position of this group). These fossils contribute to knowledge of early hamamelid diversity and also demonstrate the great antiquity of evolutionary significant floral characters in this group, such as the lack of perianth and intrafloral phyllomes. These features seem relevant to the discussions regarding the “true flower” and pseudanthial concepts as well as current notion of primitiveness in floral morphology.

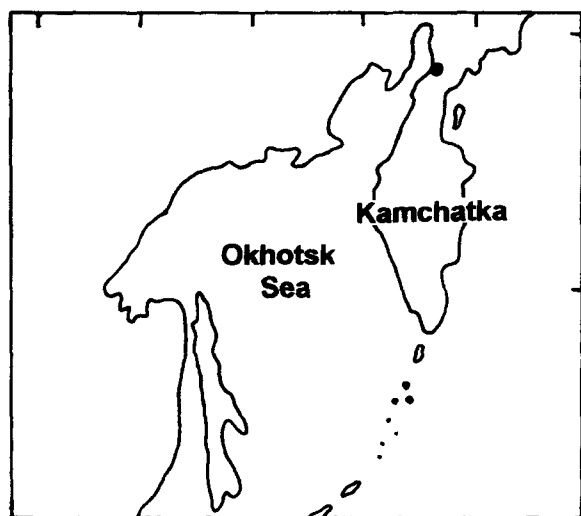


Fig. 1. Location of the Rebko Cape outcrop of Paleocene deposits.

2. Material and methods

The specimens were collected by Dr. L.I. Fotyanova in the coastal section of the Tkaprovayam Formation, a sandstone/siltstone sequence cropping out between the capes Rebko and Getkilnin, northwestern Kamchatka (Fig. 1). The locality is situated 0.6 km southeast of the Rebko Cape. It contains infructescences and a few leaf fragments. A richer locality downsection is well known due to the palm leaves and other thermophilic plant remains thought of as representing the terminal Paleocene–Early Eocene climatic optimum (Budantsev, 1979; Serova et al., 1989). The Tkaprovayam Formation is underlain by the marine Getkilninsk and marine to paralic Kamchiksk formations assigned to the Early and Late Paleocene, respectively, on the evidence of

benthic foraminifera and spore–pollen assemblages (Serova et al., 1989).

The material consists of part and counterpart of a fragmentary reproductive axis bearing three pedunculate heads and a few associated heads apparently belonging to the same compound infructescence but not actually attached. The heads are preserved as compressions on the bedding plane or partly imbedded in the siltstone matrix. The imbedded heads were uncovered with thin needles under a stereoscopic microscope. Photographs were taken with a Praktica BX20S camera attached to a Citoval 2 Stereomicroscope. A siltstone fragment containing three exposed heads covered with varnish film was dissolved in hydrofluoric acid. Compressions cleared from the rock matrix were mounted and examined with Cambridge Stereoscan electron microscope.

3. Systematics

EVACARPA N. Maslova et Krassilov, *gen. nov.*

Type: Evacarpa polysperma N. Maslova et Krassilov, *sp. nov.*

Diagnosis: Compound inflorescence (infructescence) of pistillate heads. The heads are pedunculate, globose, comprising about 16 closely packed florets. The florets are naked (lack a perianth) with staminodes and interfloral phyllomes, the latter adhering to the fruits at maturity. Carpels are paired, proximally connate for about one third to half their length, unsealed. Styles are deciduous leaving abscission scars. Ovules are numerous, marginal in the apocarpous part of the gynoecium, only one developing to seed.

Etymology: alluding to the locality, the Rebko

PLATE 1

Evacarpa polysperma N. Maslova et Krassilov, *gen. et sp. nov.*

1, 3. Detached pistillate heads.

1. $\times 7$.

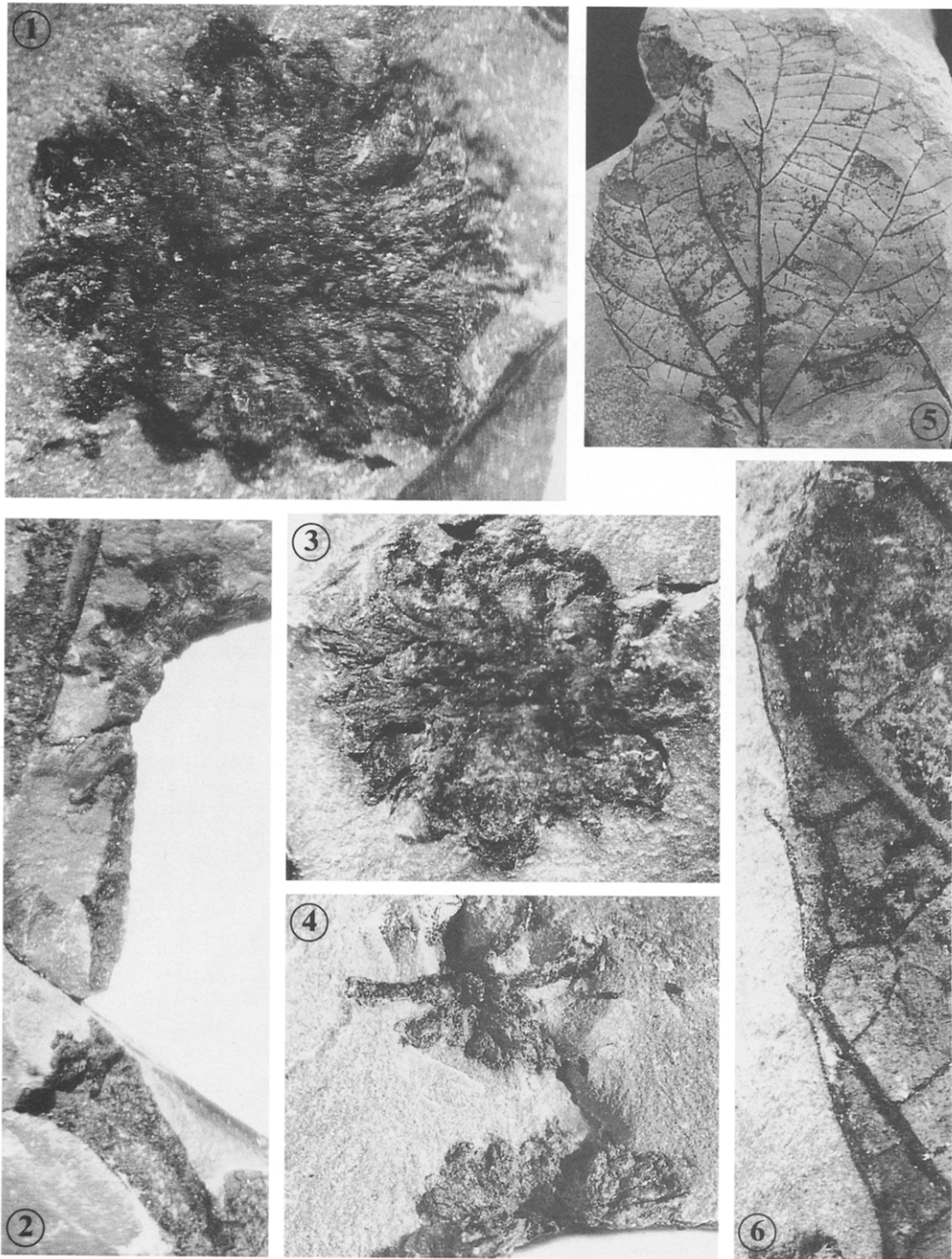
3. $\times 15$.

2, 4. Reproductive axis bearing pedunculate pistillate heads. $\times 7$.

5. Leaf associated with *Evacarpa polysperma*. $\times 1$.

6. Proximal part of the same leaf showing marginal teeth and venation. $\times 6$.

PLATE I



Cape (“rebro” is the Russian for “rib”, hence Eva made of a rib).

Evacarpa polysperma N. Maslova et Krassilov, *sp. nov.* (Plates I–V)

Holotype: N4257-16/16 (Plate I, 1).

Repository: Palaeontological Institute, Moscow.

Type locality: Western Kamchatka, southeast of the Rebro Cape.

Stratigraphy: Tkaprovayam Formation, uppermost Paleocene–Early Eocene.

Etymology: Greek, many seeded.

Diagnosis: As for the genus.

Description: All the heads studied are pistillate, showing neither stamens nor any adhering dispersed pollen which would suggest proximity of a pollen source. A fragment of the main axis is 1.5 mm thick, with a broad longitudinal ridge and is slightly expanded at the nodes. The heads are opposite or subopposite, on peduncles 5–7 mm long, 0.5 mm thick, arising at 30–60° to the main axis (Plate I, 2). There is an indication of a small subtending bract at the node (Plate I, 2) but the presence of this feature cannot be established unequivocally.

The heads are globose, 4–5 mm in diameter, showing, under stereomicroscope, a central core about 1 mm thick surrounded by the radially disposed overlapping appendages. Individual florets cannot be distinguished in the split compressions imbedded in the rock matrix. Heads isolated from the matrix are either entirely ripe infructescences (Plate II, 1–4) or comprise a mixture of mature fruits and ripening carpels (Plate III, 3). The constituent florets are either fairly conspicuous, divided by shallow grooves, or appressed and indistinct. A hemispheric surface of a complete

head comprises about eight florets; their total number should be about sixteen.

Each floret consists of a relatively massive gynoecium of paired carpels and surrounding scales some or all of which may be missing (Fig. 2; Plate II, 1). Of the most scales only stumps are preserved, but some of them show intact distal parts that are lingulate, about 0.4 mm long, 0.2 mm broad, with membranous, slightly involuted margins. These structures are abaxially striated and adaxially have an indistinct median groove. Outside these scales on the rim of the floret there are few peripheral structures that are shortly stalked, with an expanded part about 0.6 mm long, 0.3 mm broad, apiculate, showing a thick central core and abaxially convex lobes (Plate IV, 2). These structures resemble staminodes of extant *Liquidambar* (Bogle, 1986). The scales on the inside of them positionally correspond to intrafloral phyllomes of *Liquidambar* and *Altingia*, and morphologically resemble most closely the inconspicuous phyllomes of the latter genus. In the mature inflorescences the abaxially striated membranous scales adhere to the base of the fruits, their apices alone spreading from the fruit wall (Plate II, 4).

The gynoecium typically consists of two carpels (the possibility of a third carpel could not be decisively ruled out in a few cases of appressed florets), which seem fused proximally for about one third to half their length. A detached carpel in Plate IV, 4 shows a broad fusion scar with a partly preserved septum. At about anthesis the carpels are narrowly elliptical, longitudinally ridged, distally unsealed and show numerous ovules in rows along the involute margins. Ovules are apparently pendulous on the marginal placentae (Plate III, 1–4). The ovules are rounded ellipti-

PLATE II

Evacarpa polysperma N. Maslova et Krassilov, *gen. et sp. nov.*

1. Ripe head freed from the rock matrix, SEM. $\times 28$.
- 2, 3. Parts of the same head showing paired carpels surrounded by the remnants of intrafloral phyllomes; one phyllome is seen attached to the base of the fruit (arrow), SEM.
2. $\times 30$.
3. $\times 45$.
4. Phyllome marked by arrow in 3, SEM. $\times 140$.

PLATE II

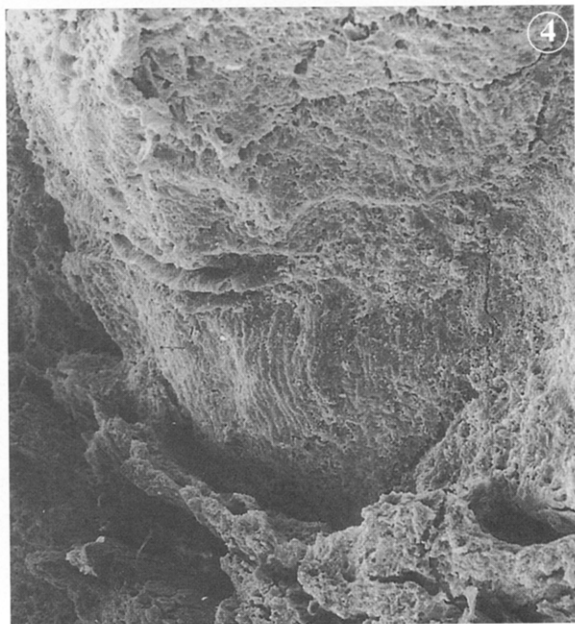
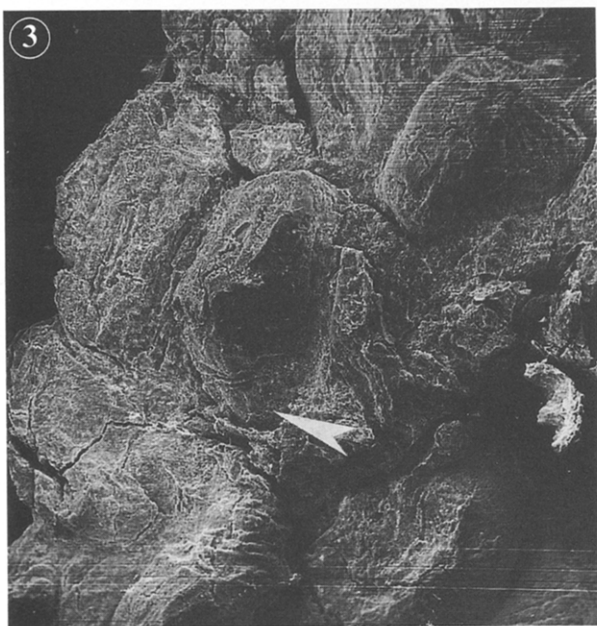
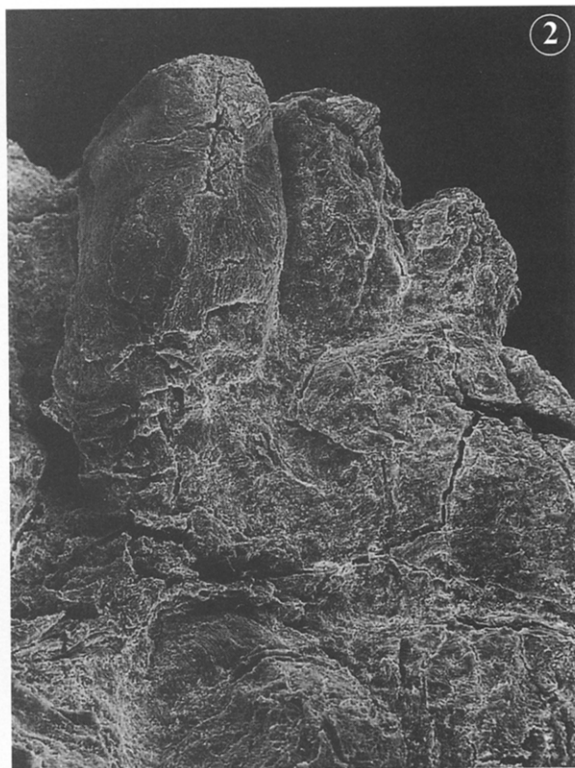
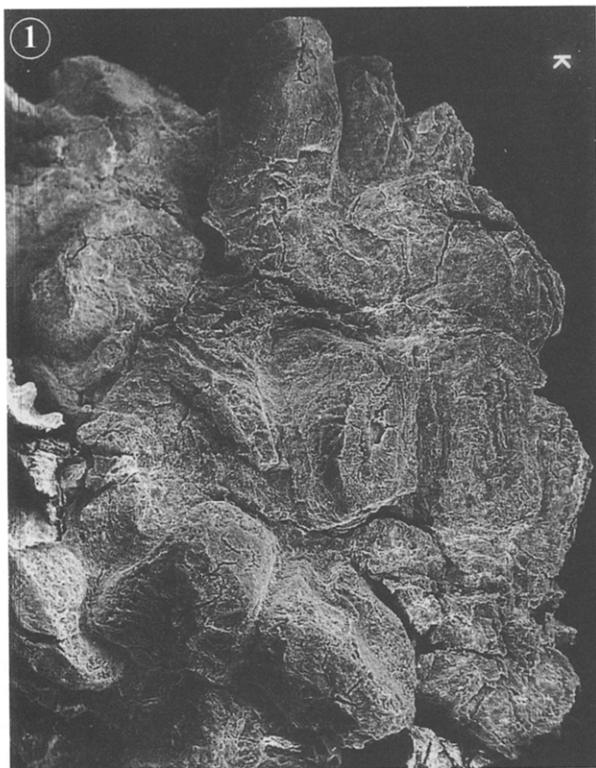


PLATE III

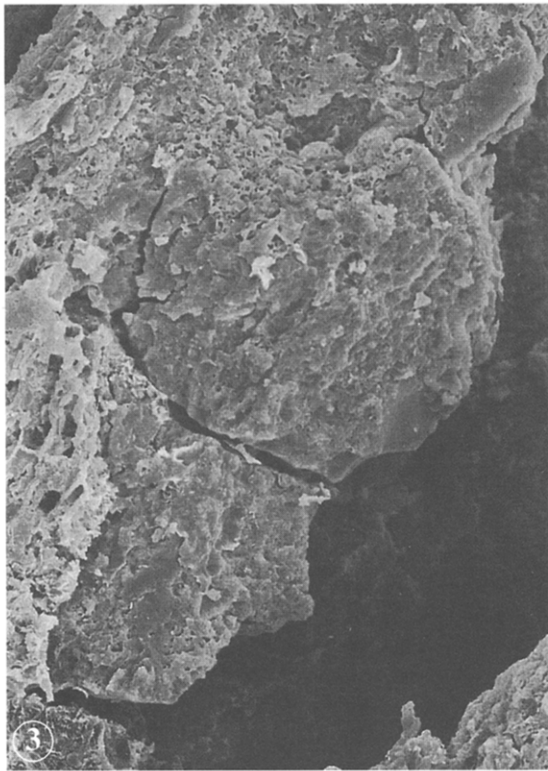
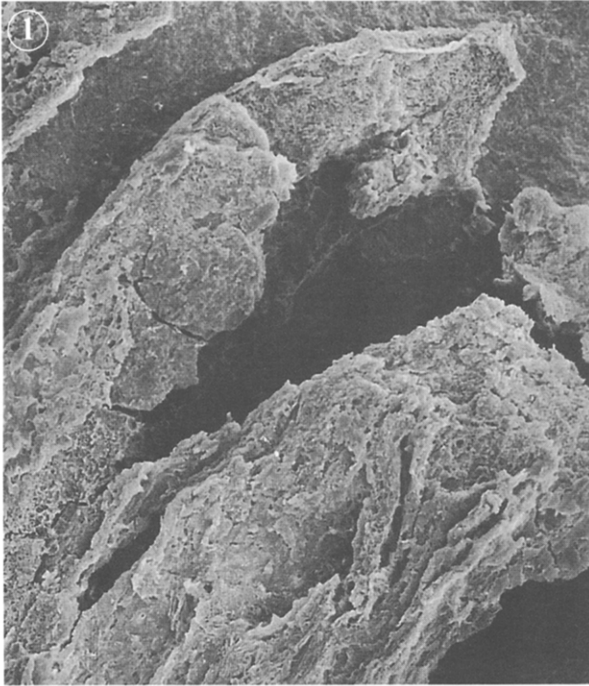


PLATE IV

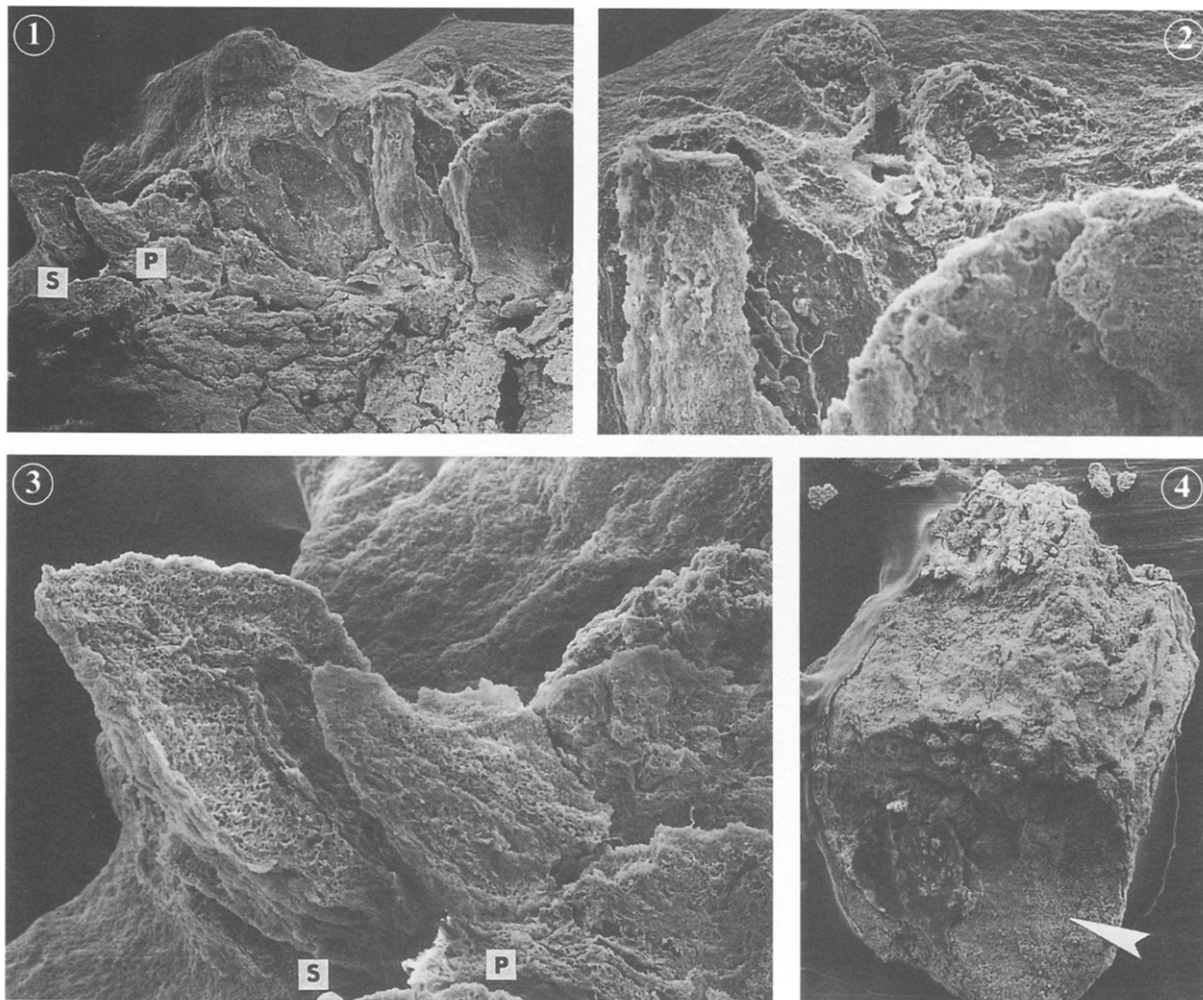


PLATE IV

Evacarpa polysperma N. Maslova et Krassilov, *gen. et sp. nov.*

1. Gynoecium surrounded by intrafloral phyllomes (*p*) and staminodes (*s*), SEM. $\times 30$.
2. Staminode and intrafloral phyllome magnified from 1, SEM. $\times 125$.
3. Carpels cut transversely at the base of styles, SEM. $\times 90$.
4. Detached carpel showing partly preserved septum (arrow), SEM. $\times 40$.

PLATE III

Evacarpa polysperma N. Maslova et Krassilov, *gen. et sp. nov.*

- 1, 2. Split carpel showing marginal ovules, SEM.
 1. $\times 110$.
 2. $\times 330$.
3. Two bicarpellate flowers, the carpels to the right are immature, at or about the anthesis while those to the left are in fruiting state, SEM. $\times 30$.
4. Unsealed carpel showing ovules, SEM. $\times 90$.

PLATE V

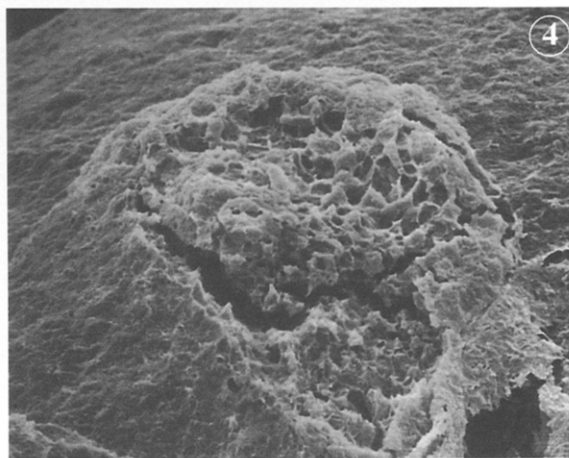
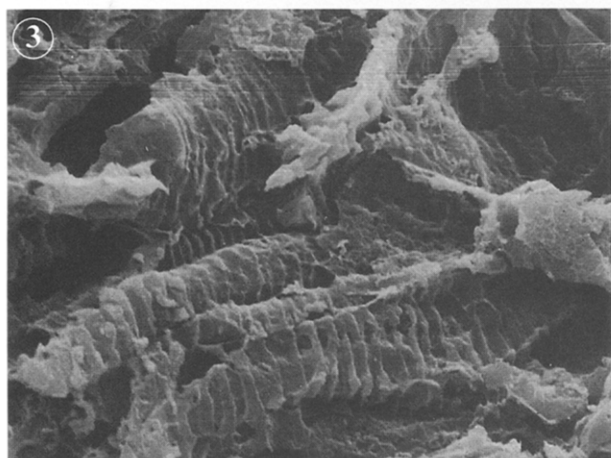
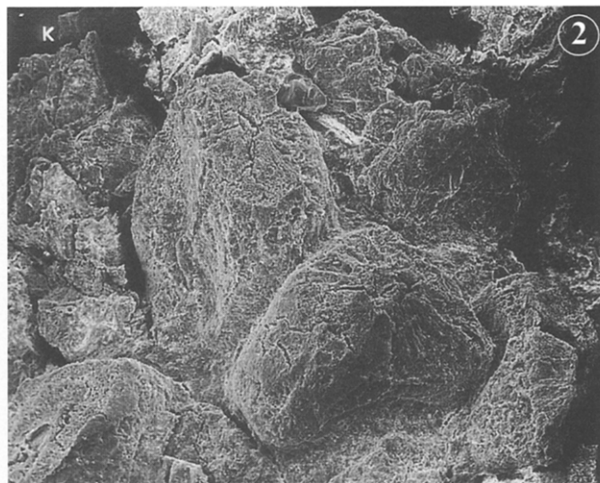
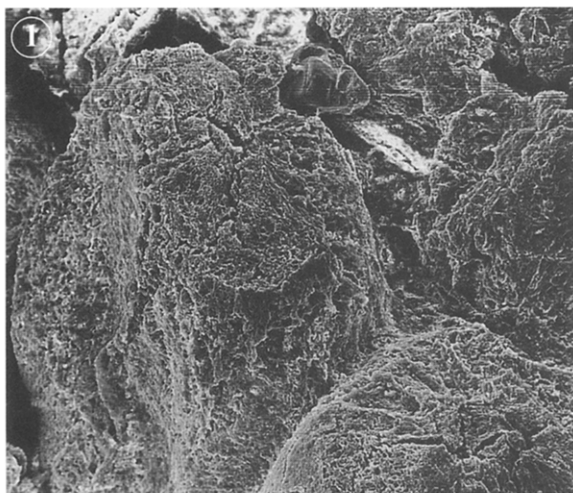


PLATE V

Evacarpa polysperma N. Maslova et Krassilov, gen. et sp. nov.

1, 2. Carpels showing abscission scars of stylodia, SEM.

1. $\times 90$.

2. $\times 50$.

3. Transverse cut through the style base showing vascular bundles, SEM. $\times 330$.

4. Helical tracheids from the vascular bundles in 3, SEM. $\times 2000$.

cal or slightly angular, about 0.1 mm long. The mature fruits (occasionally occurring adjacent to the ripening carpels, as in Plate III, 3) show outlines of a single inner body. They are ovate, 0.7–0.9 mm long, commonly one of a pair longer than the other, slightly laterally compressed, with a distinct adaxial suture. Their epidermal cells are rectangular and arranged in longitudinal files. They

lack either stomata or trichomes. The styles are shed leaving an elliptical abscission scar with thin ridges radiating from the central slit-like pore (Plate V, 1). Transverse cuts at the style base reveal vascular bundles with helical tracheids (Plate V, 2, 4).

Associated leaves: Only one kind of leaves associate with the fructification on the bedding plane.

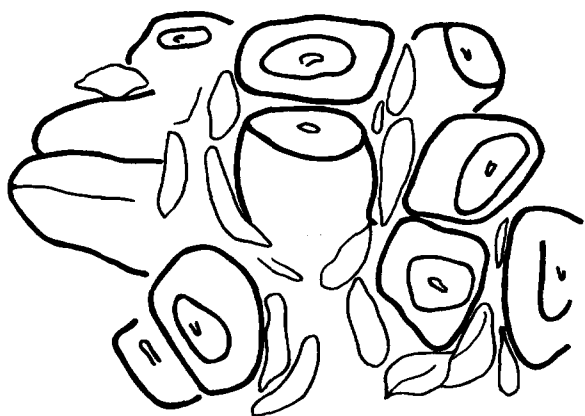


Fig. 2. Schematic drawing of the head, same as in Plate II, 1 showing several florets of paired carpels and their surrounding phyllomes.

(Plate I, 5, 6). The leaves are simple, elliptical, with pinnate venation and serrate margin. In the available fragments of the lower part of the blade, the midrib is straight and as thick as the secondaries. The basal veins rise to the middle of the blade departing at 25–30° to the midrib and giving off 6–7 basicopic branches. They change their course at the points of branching. The branches form a series of loops along the margin. Weak branches on the outer side of the loops enter the marginal teeth or end in the sinuses. The five proximal pairs of secondaries are brochidodromous, arising at 20–30° to the midrib. The lower 2 pairs give off 1–2 basicopic branches, which are also looped. The tertiaries are percurrent, typically unbranched, occasionally forked. There are 4–5 tertiaries per 1 cm secondary vein length. The margin is serrate. The teeth are minute, non-glandular, thin, falcate and widely spaced with about 2–3 per 1 cm of the margin.

4. Remarks

Closely comparable compound inflorescences with pedunculate female heads occur in extant *Platanus*, *Liquidambar* and *Altingia*, as well as in the fossil genera *Platanocarpus* and *Macginicarpa* assigned to the Platanaceae. In *Liquidambar* and *Altingia* the compound inflorescences are typically

bisexual bearing pistillate heads at the basal node alone. However, all-female inflorescences sporadically occur in both genera (Bogle, 1986). In the number of flowers the above described pistillate heads are closer to *Altingia* than to *Liquidambar*, *Platanus* and platanoid fossil genera all of which typically have many more (typically 40–100) flowers per head. The presence of staminodes in pistillate flowers is a common feature of the three extant genera. Perianths are lacking in *Liquidambar*, *Altingia* and apparently also *Macginicarpa manchesteri* (Pigg and Stockey, 1991), while in other platanoids their development is variable, the fossil species tending to produce much more conspicuous perianths than the extant species. In the Early Cretaceous *Platanocarpus marylandensis* the perianth consists of 3–4 whorls of membranous scales, the outer of which are short and broad while the inner ones are spatulate to linear and extend almost to the top of the carpels. Some of the spatulate scales bearing large clumps of pollen (e.g. Friis et al., 1988, pl. 9, fig. 7) may be staminodes (which commonly produce a considerable amount of viable pollen in *Liquidambar* and other extant genera) while the longer linear ones resemble the intrafloral phyllomes of extant *Liquidambar formosana*. Insofar as intrafloral phyllomes of even the extant *Liquidambar* and *Altingia* are sometimes described as tepals (as discussed in Bogle, 1986), the situation in the fossil flowers perhaps deserves further study.

The paired, proximally fused, distally free carpels that are unsealed before maturity, with numerous ovules is a definitely liquidambroid (altingioid) feature, although in the extant representatives the carpels separate above the locules. In contrast, in *Platanus* the gynoecia consist of a highly variable (3–9, more commonly 5–8) number of free carpels with solitary (or sometimes two) ovules. In fossil platanoids there are typically five carpels although in *Platanocarpus* the number can be variable. The styles are persistent in mature heads of *Liquidambar* and the majority of platanoids but are occasionally deciduous in *Altingia* and Cretaceous *Platanocarpus*, the latter differing from *Platanus* mainly in the lack of dispersal hairs on the achenes. Furthermore, the actual number of ovules is difficult to ascertain in the fossil material

showing mature stages alone, although in *Macginicarpa*, like in our fossil, some heads contain fully mature fruits alongside with ripening carpels (Manchester, 1986; Pigg and Stockey, 1991). At least in *M. glabra* both the developing and mature carpels contain solitary seeds (Manchester, 1986).

The leaves associated with the inflorescences and infructescences have several features in common both with *Platanus* and extinct platanoids, as well as with *Liquidambar* and *Altingia*. They resemble platanoid leaves in the shape of lamina (the majority of Cretaceous and early Palaeogene platanoid plants had entire or slightly lobed leaves), suprabasal venation, well developed basiscopic veins, which are slightly sinuous and change their course at the points of branching, and tertiary venation. This character is present in all the fossil platanoids, while the basal veins of *Liquidambar* and extant *Platanus* are typically straight. These leaves are closely similar to *Liquidambar* and *Altingia* in having brochidodromous secondaries with weak veins rising from the marginal loops to the teeth or sinuses and the distant falcate teeth.

In summary, the fossil inflorescence is similar to the extant and fossil platanoid inflorescences in general form of pistillate heads and their arrangement on reproductive axes, unsealed carpels and their diachronous ripening, but differs in fewer florets per head, paired carpels and, less definitely, in features that are more difficult to recognize, such as the lack of perianths, intrafloral phyllomes and numerous ovules. However, the latter characters are shared with *Liquidambar* and *Altingia* which differ primarily in the extent of carpel fusion and also in such less constant features as the typically bisexual compound inflorescences, larger (especially in *Liquidambar*) number of flowers in florets and persistent styles. The fossil genus *Steinhauera* comprises superficially similar heads of possible liquidambroid affinities (Kirchheimer, 1957), but their floret structure remains unknown.

5. Discussion

Here we have the earliest record of structurally preserved liquidambroid inflorescences represent-

ing various stages of development from anthesis to fruiting heads and showing such salient features as intrafloral phyllomes and staminodes in pistillate flowers, paired carpels and numerous ovules. At the same time they appear more primitive (according to the widely accepted advancement criteria, see, e.g. Sporne, 1974) than extant representatives of the group in having less fused carpels that are unsealed at anthesis while placentation is marginal in the apocarpous part of the carpels. The intrafloral phyllomes represent the most enigmatic feature of liquidambroid flowers occurring also in a number of "primitive" living angiosperms, such as *Degeneria*, *Austrobaileya*, *Eupomatia* and *Exbucklandia*. In *Liquidambar* their vascular anatomy suggests association with stamens rather than carpels, although they are definitely distinct from the staminodes (Bogle, 1986).

It seems worth mentioning that in the Cyperaceae the pseudanthia formed of a perianthless pistillate flower and a number of one-stamen bracteate staminate flowers are conventionally recognized by having sterile bracts between stamens and carpels (Eiten, 1976). There is no a priori reason why this morphological criterion would not work for the flowering structures of "primitive" dicotyledons as well, though it would drastically alter the conventional ideas of "primitiveness". Actually a pseudanthial nature of the perianthless flowers of *Distylium* and some other hamamelidacean genera have been suggested by Bogle (1970) but the issue remains controversial (Endress, 1978). Our findings may add to the discussion that the intrafloral phyllomes are a conservative feature occurring already in Paleocene liquidambroid flowering structures. Thereby these features are perhaps primary for the group. Additionally, in the fossil flowers the intrafloral phyllomes are less conspicuous and less pistilloid than, for example, the corresponding structures of the extant *Liquidambar formosana* raising the possibility that the pistilloid appearance of these structure is secondary in the extant taxa.

The present findings suggest that platanoid and liquidambroid fructifications may be virtually indistinguishable as impressions. Even structurally preserved heads may prove not always readily assignable to one family or another. A revision of

previous assignments, allowing for variability in the number of carpels per flower and the extent of their proximal fusion as well as the often occurring, even in herbarium studies, confusion of interfloral phyllomes and perianth lobes, may prove worthwhile.

The closely similar and supposedly interfertile genera *Liquidambar* and *Altingia* (with *Semiliquidambar* as their probable hybrid form) are variously assigned to the Hamamelidaceae, subfamily Liquidambroideae or Altingioidae (e.g. Cronquist, 1981) or, more rarely, to a separate family Altingiaceae (see Takhtajan (1966) for morphological arguments and Kirchheimer (1957) for palaeobotanical standpoint). The major distinctions from the bulk of hamamelidaceous genera, cited by Takhtajan (1966), are resin ducts in the bark, wood and leaves, concentric midvein structure, clustered (rather than solitary) calcium oxalate crystals, multiporate (pantoporate) pollen and a higher chromosome number ($x=15$). We can add from other sources the petioles with 3–5 vascular bundles, parietal to marginal (rather than axile) placentation and orthotropous ovules. Several of these distinctions, notably those of anatomical structure and the type of ovule, are shared with Platanaceae which are obviously similar in the inflorescence and leaf characters but differ in their flowers having recognizable, though reduced, perianths (while lacking intrafloral phyllomes), tricolpate pollen grains, apocarpous gynoecea and solitary pendulous ovules. In the both families the inflorescences are typically condensed, capitulate, aggregated (less consistently in *Platanus*) in compound racemose inflorescences of second order. The leaves show a remarkable parallelism of variation of lobed and entire blades, with both leaf forms occurring in *Semiliquidambar*.

The fossil record supplies new evidence of the close links between the two families. Typical liquidambroid leaves appear not earlier than Late Paleocene (Maslova, 1995). However, some mid-Cretaceous "*Aralia*" and *Araliaephyllum*, notably *Aralia lucifera* Kryshstofovich from the Aptian of the Russian Far East, resemble *Liquidambar* in their leaf shape and venation (Krassilov, 1977, 1989). Among the leaf morphotypes of the diverse Cretaceous–Palaeogene platanoid complex, the

5- and 7-lobed *Macginitiea wyomingensis* and *M. angustiloba* (Manchester, 1986) resemble the 5- and 7-lobed forms of extant *Liquidambar styraciflua*, respectively, while the 3-lobed entire-margined *Credneria* (Richter, 1905) is similar to *rotundifolia* form of the latter species. On the other hand, "*Platanus*" *raynoldsii* from the Lower Paleocene of the Amur Province shows a platanoid cuticular structure associates with staminate heads yielding tricolpate pollen grains and with liquidambroid *Steinhauera*-type heads as well as winged seeds (Krassilov, 1976). Although transitional pollen types are yet unknown, the extinct Platanaceae show diverse pollen morphologies including tricolporate grains with well developed lalongate endoapertures (Krassilov and Shilin, 1995). Rather than confirming the often postulated origin of one family from another (reviewed in Takhtajan, 1966), these data seem suggestive of a common highly polymorphous ancestral group in the process of splitting into several lineages leading to the present-day families.

Acknowledgements

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