

New Platanaceous Inflorescence *Archaranthus* gen. nov. from the Maastrichtian–Paleocene of the Amur Region

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Abstract—A new monotypic genus, *Archaranthus* gen. nov. (Platanaceae) with *A. krassilovii* sp. nov. as its type species, is erected for staminate inflorescences from the Maastrichtian–Paleocene deposits of the Amur Region on the basis of their microstructure. Leaves associated with the inflorescences are typical of *Platanus*. The existence of *Platanus* in the Cretaceous is discussed.

INTRODUCTION

Although the family Platanaceae is presently monotypic, it was a vast group in the past; its considerable and even dominant role in the formation of vegetation in the northern hemisphere during the Cretaceous and Cenozoic has attracted the constant attention of scientists to this family (Bůžek *et al.*, 1967; Kvaček, 1970; Krassilov, 1973; Vakhrameev, 1976; Krassilov, 1976; Hickey and Doyle, 1977; Knobloch and May, 1986; Manchester, 1986, 1994; Crane *et al.*, 1988, 1993; Friis *et al.*, 1988; Pigg and Stockey, 1991; Pedersen *et al.*, 1994; Krassilov and Shilin, 1995; Maslova, 1997, 2002a; Magallón-Puebla *et al.*, 1997; Maslova and Krassilov, 2002). To date, microstructural investigations of platanaceous fructifications have revealed their significant morphological diversity. The ancient Platanaceae also show a considerable range of leaf morphotypes. The geological history of the Platanaceae seems to be one of the best studied among the lower hamamelids. However, new finds of fossil platanaceous reproductive structures show that the morphological diversity of fossil Platanaceae is not restricted to the presently known genera.

Associations of leaves and reproductive structures that supposedly belong to the same plant are of special interest (Bůžek *et al.*, 1967; Kvaček, 1970; Manchester, 1986; Crane *et al.*, 1988, 1993; Pigg and Stockey, 1991; Maslova, 1997, 2002a). The staminate inflorescences described and assigned below to a new platanaceous genus, *Archaranthus*, on the basis of microstructural data associate with leaves macromorphologically typical of *Platanus* (subgenus *Platanus*). Notwithstanding the fact that such leaves, which are widespread and abundant in Late Cretaceous floras, are mostly assigned to the modern genus *Platanus*, thus giving the impression of the early appearance of this genus in the geological record, no reproductive structures of the

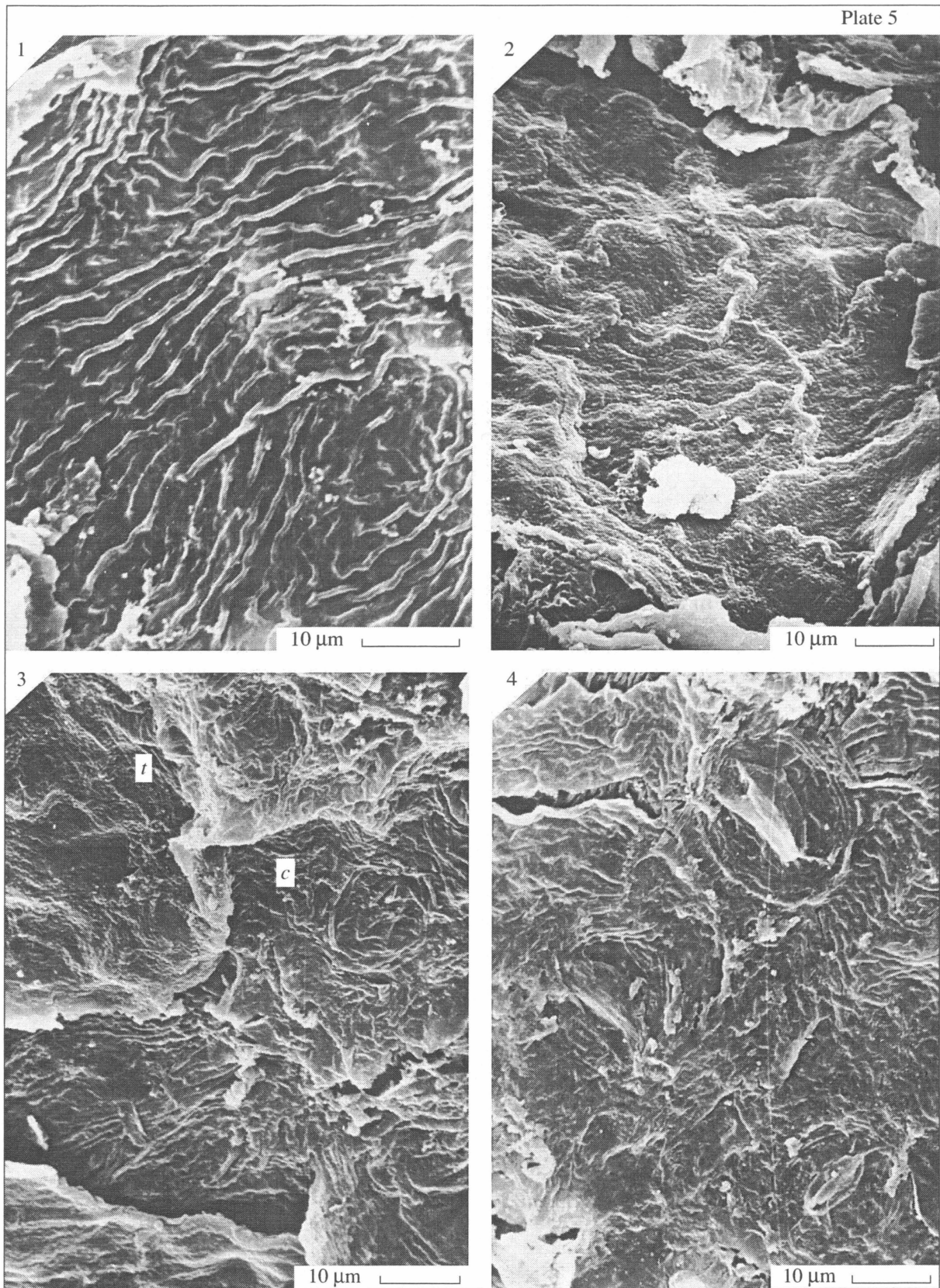
genus are known before the Paleocene (Maslova, 1997; Kvaček *et al.*, 2001).

The finds of associations of leaves with characteristic *Platanus* morphotype and reproductive structures drastically different from those of *Platanus* necessitate the revision of the traditional idea that plane trees were common in the Cretaceous. The only exact point is the appearance during the Cretaceous of leaf morphotypes similar to those of modern plane trees, although none of the diverse reproductive structures correspond to those of the modern genus.

MATERIAL AND METHODS

In the Amur River Region the Tsagayan flora of the Cretaceous/Paleogene boundary has been known for more than a century. Recently, new data on the composition of the Tsagayan plant assemblages have been obtained from numerous localities of the southeastern Zeya and Bureya Basin (Akhmetiev *et al.*, 2002). A detailed paleobotanical study was accomplished for the first time in the large locality of Tsagayan plant fossils situated approximately 15 km southeast of the village of Arkhara, where a series of open pits of the Arkhara-Boguchanskoe brown coal mine exposed continental deposits of the middle and upper subformations of the Tsagayan Formation.

The age of the subformations is a matter of discussion. Krishtofovich and Baikovskaya (1966) believed that their characteristic plant assemblages are of Danian age. Krassilov (1976) correlated the middle Tsagayan flora with the flora of the lower part of the Fort Union Series (the United States) and, thus, dated the middle Tsagayan flora to the early Danian and the upper Tsagayan flora to the late Danian. On the basis of palynological and macrophyte fossil assemblages, Markevich and Bugdaeva dated the middle and upper Tsagayan to the late Maastrichtian and Danian, respec-



Explanation of Plate 5

Figs. 1–4. *Archaranthus krassilovii* sp. nov., SEM: (1) epidermis of the upper tepals; (2) epidermis of the inner tepals; (3) epidermis of the (*t*) inner tepals and (*c*) connective; and (4) connective epidermis showing stomata varying in size.

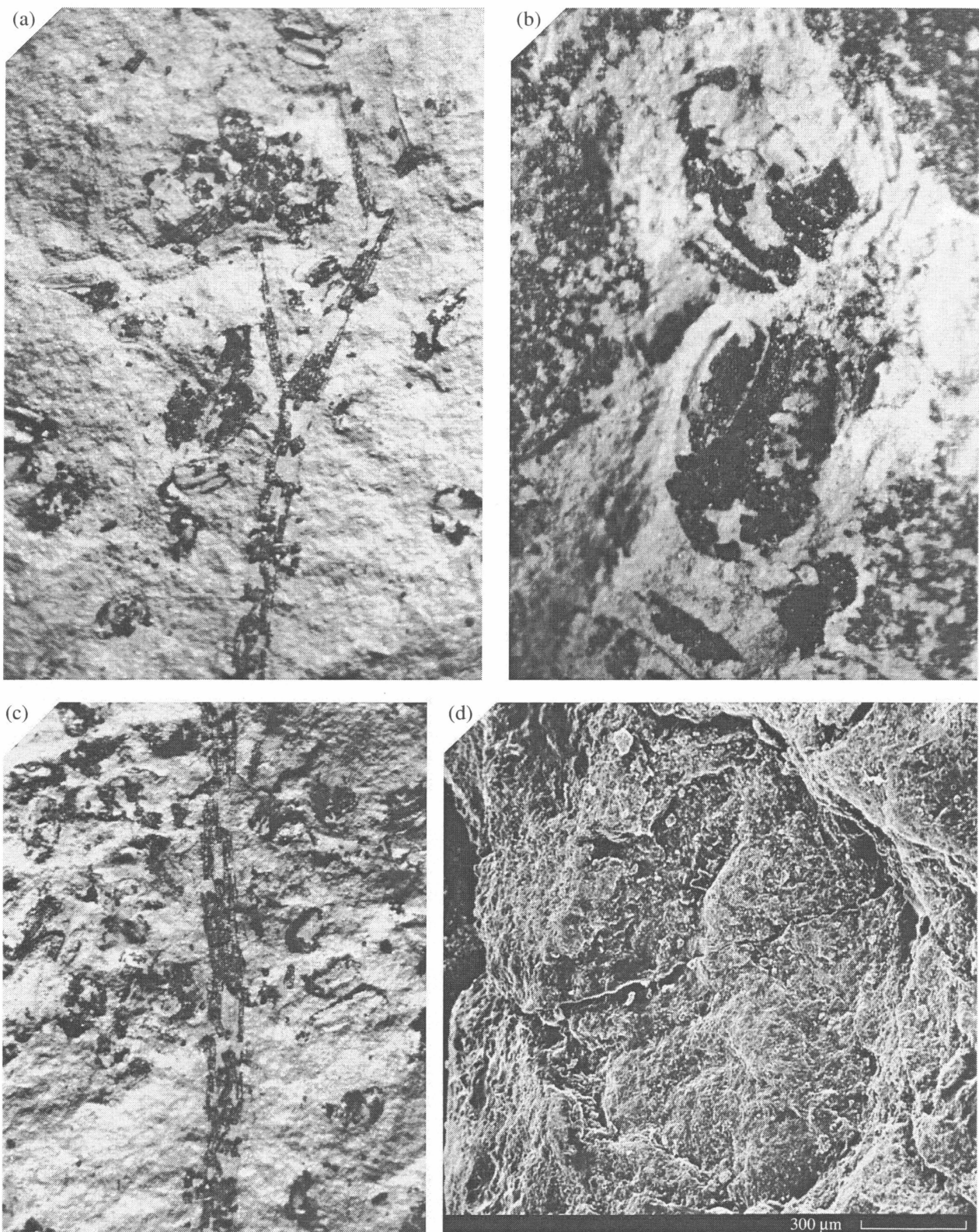
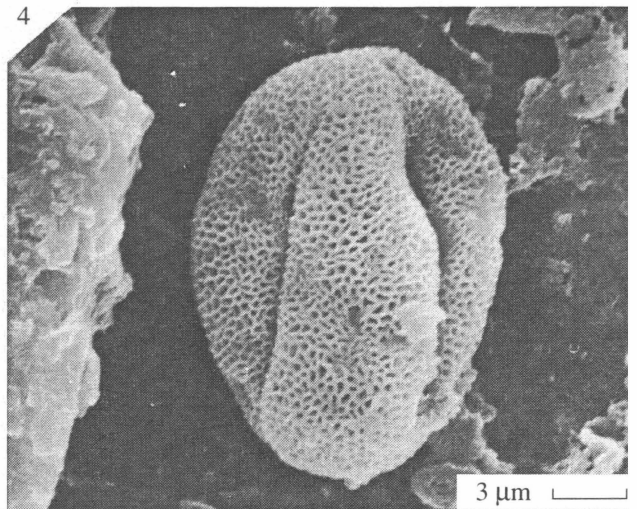
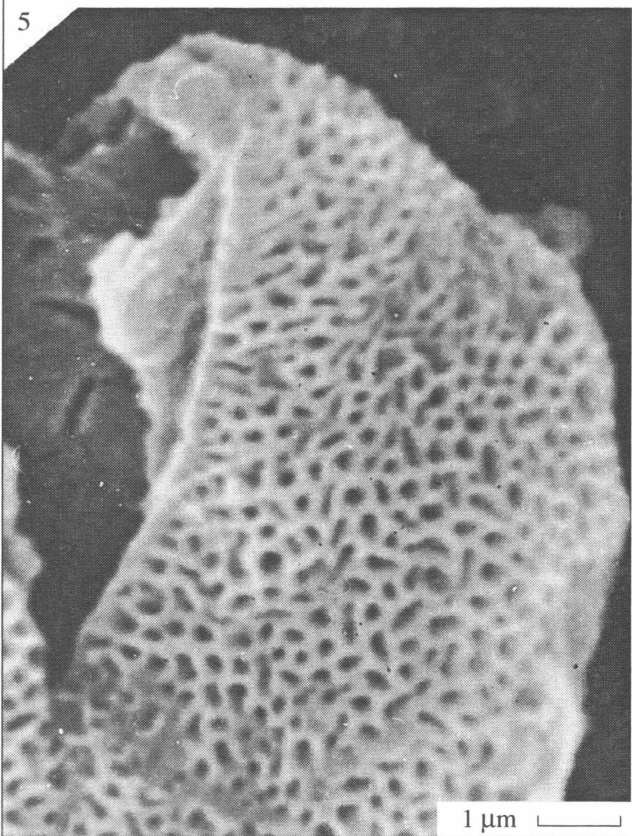
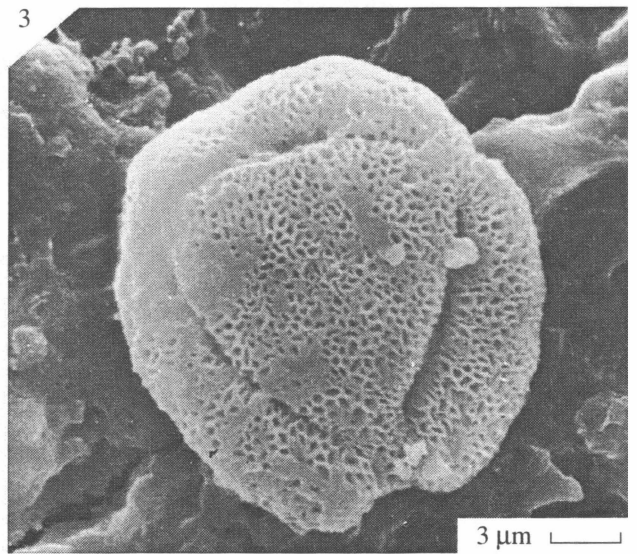
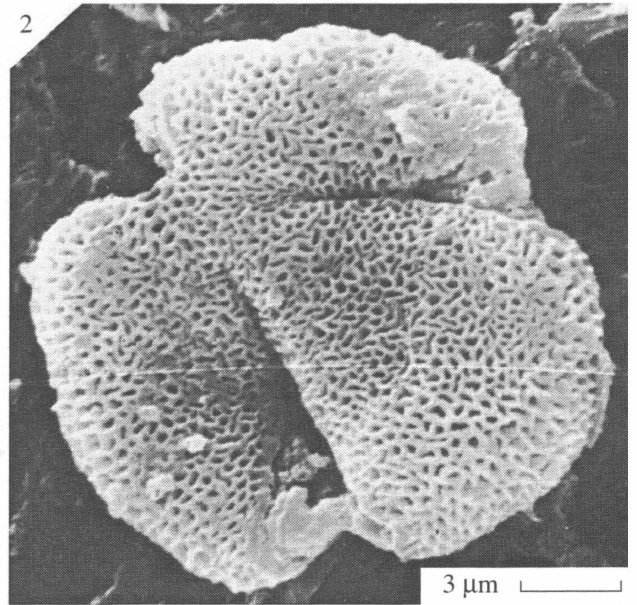
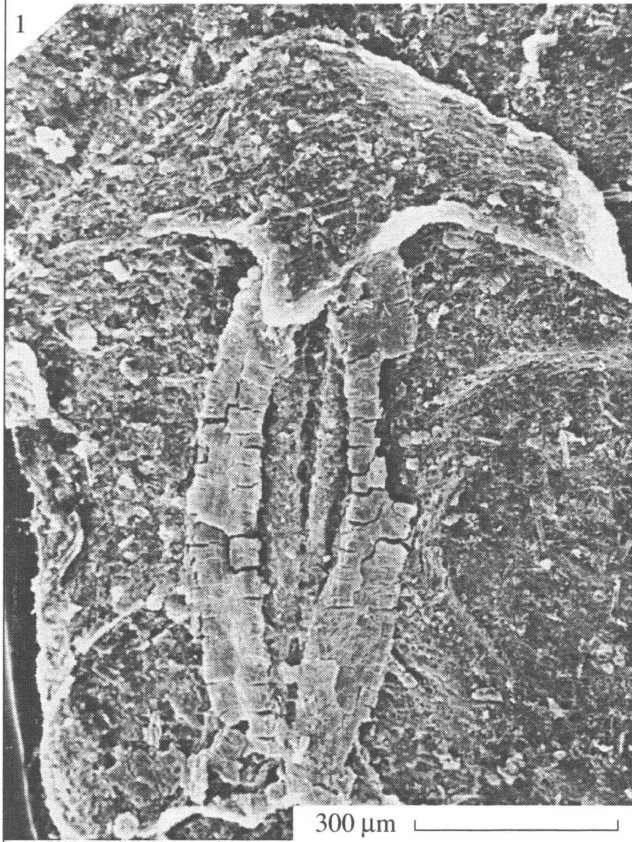


Fig. 1. *Archaranthus krassilovii* sp. nov., holotype GIN, no. AB3-81: (a) head attached to the axis of compound inflorescence with a pedicel, detached stamens are seen, $\times 7$; (b) two stamens, $\times 20$; (c) accumulation of stamens around the inflorescence axis, $\times 7$; and (d) flower with four stamens, top view, SEM.



tively (*Flora ...*, 2001). On the basis of preliminary study of plant fossils, Akhmetiev *et al.* (2002) dated the upper Tsagayan to the Danian and did not exclude the possibility that the middle Tsagayan may be of Maastriichtian age.

The reproductive structures described below have been discovered in light gray clays of the upper part of the middle Tsagayan between the Nizhnii and Dvoinoi coal beds of the northern region of the Arkharo-Boruchanskoe coal field. Numerous remains of ferns, conifers of the families Taxodiaceae and Cupressaceae, and various angiosperms have been found in association.

The reproductive structures have preserved as imprints with fragments of phytolite. They include a nearly disintegrated staminate head attached to the axis of a compound inflorescence with a pedicel, detached flowers, and numerous dispersed stamens.

After preparation individual structures were photographed with a stereomicroscope CITOVAL. Isolated flowers were cleaned with hydrofluoric acid and mounted on standard stages for scanning electron microscopy (SEM). Elements of the flowers were macerated with concentrated nitric acid and alkali and studied with SEM. Microphotographs were made with a CamScan microscope.

Collection no. 4867 is housed at the Geological Institute of the Russian Academy of Sciences (GIN).

SYSTEMATIC PALEOBOTANY

Family Platanaceae Dumortier, 1829

Genus *Archaranthus* N. Maslova et Kodrul, gen. nov.

Ety m o l o g y. After the village of Arkhara and Latin *anthus* (anther).

T y p e s p e c i e s. *Archaranthus krassilovii* sp. nov.

D i a g n o s i s. Staminate heads 5 mm in diameter, pedicellate, composed of about 15 florets. Ripe inflorescence disintegrates into separate florets and stamens. Perianth well developed. Cuticle of the outer tepals with elongate cells in rows. Cuticle of the inner tepals with isodiametric cells showing undulate walls. Florets tetramerous. Stamens with very short filaments and elongate, massive anthers. Connective expanding into a distally forming triangular apical extension. Cuticle of the connective with isodiametric cells showing numerous stomata. Cuticle of the apical extension without stomata. Pollen grains 13.3–15.3 μm in equatorial diameter, 16.0–16.8 μm in polar diameter, tricolpate with reticulate exine and colpi extending nearly from pole to pole.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. Although pedicellate inflorescences are characteristic of many platanoids, *Archaranthus* gen. nov. differs from them in having a smaller number of flowers within the inflorescence and by the disintegration of the ripe head into individual flowers and stamens. Within the family Platanaceae the Cretaceous genera *Sarbaya* Krassilov et Shilin (Krassilov and Shilin, 1995) and *Quadriplatanus* Magallón-Puebla, Herendeen, et Crane (Magallón-Puebla *et al.*, 1997) also have flowers with four stamens. The new genus differs from *Sarbaya* by the well-developed and differentiated perianth, the presence of stomata in the epidermis of connective, and finer lumens of the exine. It also differs from the genus *Quadriplatanus* by the more poorly developed apical extension of the connective devoid of stomata and greater stability of the size and shape of pollen grains with finer exine lumens.

Archaranthus krassilovii N. Maslova et Kodrul, sp. nov.

Plate 5, figs. 1–4; Plate 6, figs. 1–5

E t y m o l o g y. In honor of the paleobotanist V.A. Krassilov, who accomplished a monographic study of the Tsagayan flora.

H o l o t y p e. Specimen GIN, no. AB3-81, southeast of the village of Arkhara, Amur Region; upper part of the middle Tsagayan, Maastriichtian–Danian.

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

D e s c r i p t i o n (Figs. 1a–1d). A fragment of the first order axis 1 mm thick with a staminate head attached by a pedicel 4 mm long (Fig. 1a). The inflorescence consists of a rounded receptacle 2 mm in diameter and radially arranged flowers. The diameter of the head is about 5 mm.

After maturation the inflorescence disintegrated into flowers and stamens (Fig. 1c). In a light microscope one may see rounded scars remained after shedding of flowers and partly preserved elements of perianth on the receptacle surface. There are seven or eight scars on the visible subspheroidal surface of the head; therefore, the total scar number within a head is about 15.

The microstructure of flowers was studied with SEM. An individual flower consists of four stamens and a well-developed perianth. Due to the mature stage of the inflorescence, which is accompanied by disintegrating into separate flowers and stamens, the perianth elements are either preserved as fragments attached to the receptacle or occur in individual flowers. The epidermis of outer tepals is composed of longitudinal rows of elongated cells with weakly undulate well-cutinized

Explanation of Plate 6

Figs. 1–5. *Archaranthus krassilovii* sp. nov., SEM: (1) stamen with a triangular apical extension of the connective; (2) polar view of a pollen grain showing colpi nearly reaching the poles; (3) polar view of a pollen grain showing additional colpi; (4) equatorial view of a pollen grain; and (5) region of a pollen grain showing the reticulate exine structure and sporopollenin thread along the colpus margin.

longitudinal walls and nearly indistinct transverse walls (Pl. 5, fig. 1). The epidermis of inner tepals consists of nearly isodiametric cells with distinct undulate walls (Pl. 5, fig. 2). Abaxially the walls of the epidermal cells are more cutinized and their undulate outlines are more visible. On the perianth elements neither hair bases nor stomata have been found.

The androecium includes four stamens (Fig. 1d). The stamen filament is short, anthers are tetrasporangiate, and thecae are joined together by the connective that runs along the entire anther. The connective is thin at the base and slightly widened apically. The epidermis of the connective is formed by isodiametric cells, with anomocytic stomata slightly varying in size (Pl. 5, fig. 4) and rounded hair bases. The maximal length of stoma is 25 μm , the minimal length is 15 μm , the maximal width is 18 μm , and the minimal width is 14 μm . The apical extension of the connective is conical, triangular in plan (Pl. 6, fig. 1). Its epidermis consists of isodiametric cells, devoid of stomata, with occasional hair bases.

An individual mature stamen is approximately 1200 μm long and about 900 μm wide in its central region. Anthers are oval, slightly widened distally. The inner epidermis of the anthers consists of longitudinal rows of elongated cells.

Pollen grains are elliptical and tricolpate. The equatorial diameter of the mature pollen grain is 13.3–15.3 μm , the polar diameter is 16.0–16.8 μm . Colpi nearly reach the poles (Pl. 6, fig. 2). The maximal width of the apocolpium is 4.5–4.8 μm , that of mesocolpium is 7.5–11.0 μm . The exine is reticulate. The lumens of the reticulum vary in form (from circular to elongated) and in size. Two or three lumens occur per micrometer. The margin of the corpus is distinct and consists of a thin sporopollenin thread (Pl. 6, fig. 5). The lumens situated close to the colpus margin and those in the central part of the mesocolpium are identical.

Some pollen grains have additional colpi situated in the polar region (Pl. 6, fig. 3). The colpi are short, surficial, virtually devoid of apocolpium and distinct margins.

Material. Part and counterpart of the head attached to the axis and numerous separated stamens from the type locality (holotype and counterpart GIN, no. AB3-80-1).

DISCUSSION

The modern family Platanaceae consists of a single genus, *Platanus*, with a few species. This genus was paleobotanically proved to be only a small part of the formerly very diverse platanaceous group, known since the Early Cretaceous.

The early determinations of Platanaceae were based on leaves. Only recently have reproductive organs begun to be studied microstructurally.

In addition to the wide diversity of platanaceous leaf morphotypes, 14 fossil platanaceous genera have been

described on the basis of reproductive structures. These are pistillate inflorescences of *Macginicarpa* Manchester (Manchester, 1986), *Platanocarpus* Friis, Crane et Pedersen (Friis *et al.*, 1988), *Tanyoplatanus* (Manchester, 1994), and *Oreocarpa* N. Maslova et Krassilov (Maslova and Krassilov, 2002); staminate inflorescences of *Tricolpopollianthus* Krassilov (Krassilov, 1973), *Platananthus* Manchester (Manchester, 1986), *Aquia* Crane, Pedersen, Friis et Drinnan (Crane *et al.*, 1993), *Hamatia* Pedersen, Friis, Crane et Drinnan (Pedersen *et al.*, 1994), *Sarbaya* Krassilov et Shilin (Krassilov and Shilin, 1995), and *Chemurnautia* N. Maslova (Maslova, 2002a); staminate clusters of *Macginistemon* Manchester (Manchester, 1986); the genus *Carinalaspermum* Krassilov (Krassilov, 1976) described on the basis of seeds; the genus *Quadriplatanus* Magallón-Puebla, Herendeen, et Crane described on the basis of pistillate and staminate inflorescences (Magallón-Puebla *et al.*, 1997); and the genus *Platanites* Forbes that was primarily established on the basis of leaves and later included pistillate and staminate inflorescences (Crane *et al.*, 1988).

Platanaceae are characterized by capitate, mostly sessile, inflorescences and infructescences. The head of *Archaranthus* gen. nov. was attached with a pedicel. Among staminate inflorescences, only some species of *Platananthus* have well-developed pedicels.

The number of heads per compound inflorescence axis of *Archaranthus* gen. nov. is unknown. There were apparently at least two heads, since on the preserved region of the first order axis one may see, in addition to the solitary pedicellate head, a fragment of one more pedicel (Fig. 1a). The new genus stands apart within the family by the number of flowers per inflorescence (about 15). The staminate heads of the modern *Platanus* include up to 300 flowers, 50–100 flowers per head are known in the Cretaceous *Platananthus*. The degree of preservation of many fossil platanaceous inflorescences is insufficient for revealing the exact number of flowers per inflorescence. In addition, not all scientists report this quantitative character. However, judging from figures one can estimate considerably greater than 15 flowers per head.

The disintegration of mature inflorescence into flowers and stamens is reported only in the new genus. Describing Paleocene pistillate inflorescences associated with *Platanites hebridicus* Forbes, Crane *et al.* (1988, text-figs. 3b, 3c) showed a head with partly preserved perianth elements and stamens. Since detached flower or stamens were not reported near these heads, the question of whether such a separation is a result of maturation or fossilization remains unclear.

A well-developed perianth differentiates all known members of the Cretaceous Platanaceae from the modern plane trees that have naked flowers. After the flowers shed during the head maturation, perianth elements are partly retained on the receptacle and partly in the bases of flowers. The number of perianth elements in

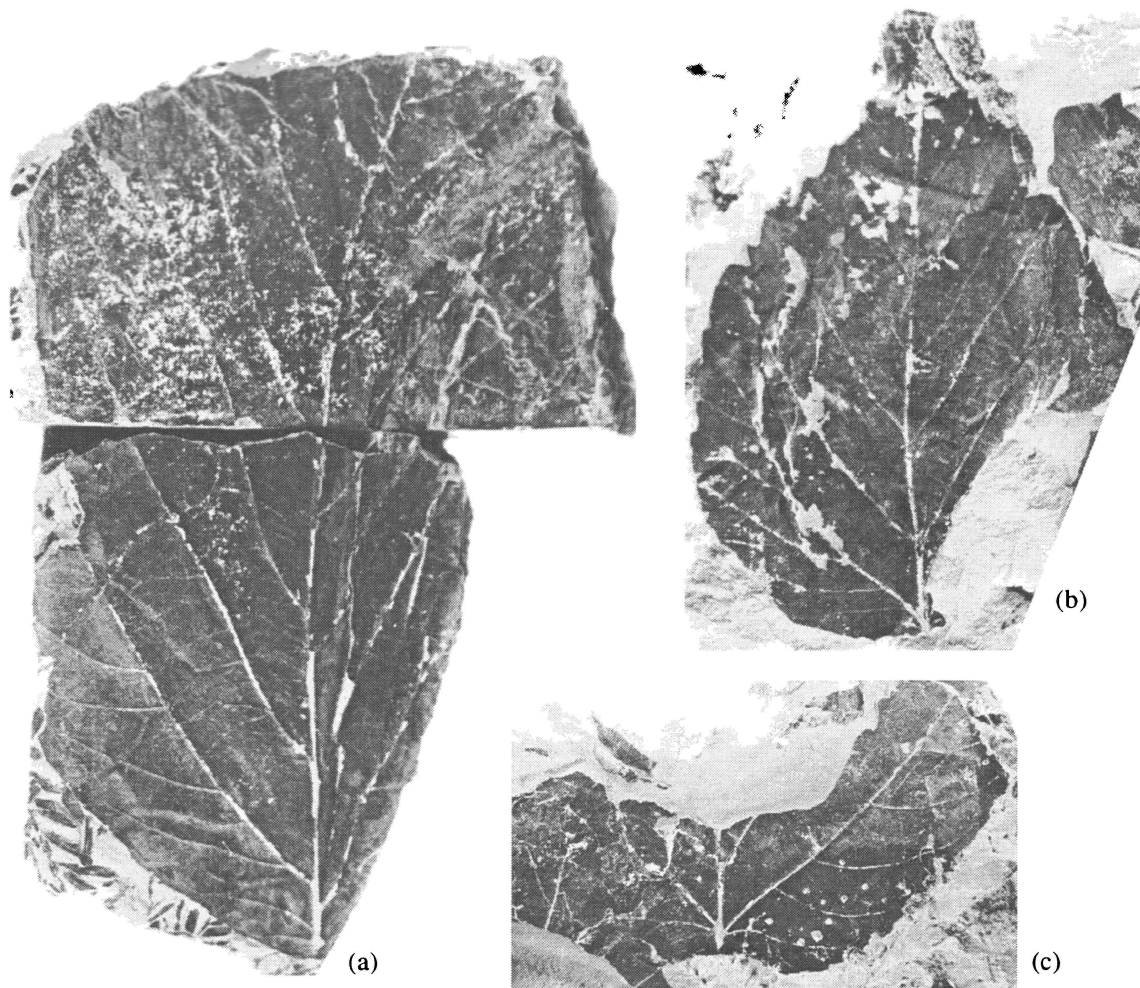


Fig. 2. Leaves associated with the inflorescences *Archaranthus krassilovii* sp. nov.: (a) specimen GIN, no. AB2-2, $\times 1$; (b) specimen GIN, no. AB2-29, $\times 1$; and (c) specimen GIN, no. AB3-80, $\times 0.8$.

the flowers of *Archaranthus* gen. nov. is unknown. However, two types of perianth tepals having different epidermal morphologies are clearly distinguishable (Pl. 5, figs. 1, 2).

The flowers of *A. krassilovii* sp. nov. are tetramerous. The flowers of *Sarbaya* and *Quadriplatanus* also have four stamens. The representatives of the genus *Platananthus* and, possibly, *Hamatia* invariably have five stamens in each flower. The modern *Platanus* has a variable number of flower elements within a head (Boothroyd, 1930).

The stamens of the new genus are morphologically typical of the Platanaceae. The anthers are tetrasporangiate, theca are joined together by a connective that runs along the entire length of the anthers and widens apically to form a conical apical extension. There are differences in the epidermal morphology of both connective and extension. In *Archaranthus krassilovii* sp. nov. the connective epidermis is composed of isodiametric cells with numerous anomocytic stomata and widely spaced rounded hair bases. The extension epidermis bears rare hair bases and is devoid of stomata.

Among fossil Platanaceae pubescent connectives occur in *Platananthus hueberi* Friis, Crane, et Pedersen; *P. synandrus* Manchester; *Platanus neptuni* (Ettings.) Bůžek, Holý, et Kvaček; *Aquia brookensis* Crane, Pedersen, Friis, et Drinnan; and in staminate clusters of *Macginistemon mikaneides* (MacGinitie) Manchester. Stomata only occur on the extensions of *Aquia brookensis*, *Quadriplatanus georgianus* Magallón-Puebla, Herendeen, et Crane and dispersed platanaceous stamens from the Santonian–Campanian of Sweden (Friis *et al.*, 1988).

Tricolpate reticulate pollen grains are typical of the Platanaceae. It is interesting to note that in anthers of *Archaranthus krassilovii* sp. nov. there are several pollen grains with additional polar colpi (Pl. 6, fig. 3). Such a pollen type is characteristic of the Hamamelidaceae (genera *Distylium* Sieb. et Zucc., *Matudaea* Lundell, *Sycopsis* Oliv. of the subfamily Hamamelidoideae and genus *Chunia* Chang of the subfamily Exbucklandioideae, Bogle and Philbrick, 1980). An aberrant additional colpus was recorded by Zavada and

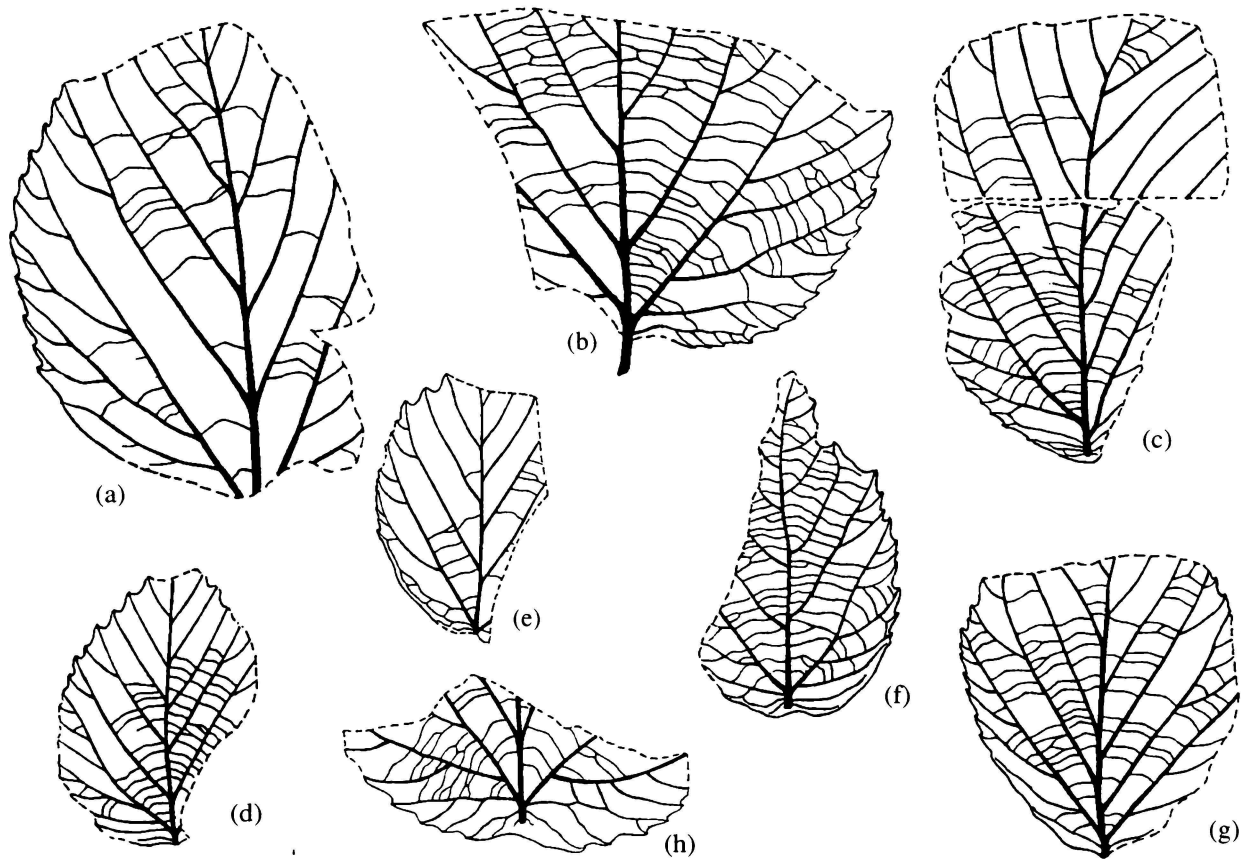


Fig. 3. Morphological variability of the leaves associated with the inflorescences of *Archaranthus krassilovii* sp. nov., $\times 0.5$: (a) specimen GIN, no. AB3-69; (b) specimen GIN, no. AB3-91; (c) specimen GIN, no. AB2-2; (d) specimen GIN, no. AB2-29; (e) specimen GIN, no. AB3-64; (f) specimen GIN, no. AB3-44; (g) specimen GIN, no. AB3-7; and (h) specimen GIN, no. AB3-66.

Dilcher (1986, p. 352, fig. 9) in the modern *Platanus occidentalis* L.

The inflorescences assigned to *Archaranthus* gen. nov. associate with leaves the morphotype of which is typical of the *Platanus* (Figs. 2, 3). Although the leaves and inflorescences were not found in organic connection, they obviously belonged to the same plant. They were found within the same layer, even within the same lump of rock. Any other leaves assignable to the Platanaceae are absent in the plant assemblage. Moreover, pollen grains identical to those extracted from the anthers of *Archaranthus* gen. nov. were found on the leaf surface (Fig. 4).

Leaves associated with the inflorescences have entire or weakly lobed plates with peltate bases, digitate-pinnate craspedodromous venation, well-developed infrabasal veins, and frequently branching basal veins. Figure 3 shows the variability of the leaves.

Simple variously lobed leaves had been assigned to the modern genus *Platanus* for a long time. Such leaf morphotypes are known from the Cretaceous. However, the presence of the genus *Platanus* in the Cretaceous has not been confirmed by corresponding reproductive organs. Numerous reproductive structures of the Cretaceous Platanaceae differ greatly from those of

the modern *Platanus*. The first finds of *Platanus* reproductive organs are dated to the late Paleocene (Maslova, 1997; Kvaček *et al.*, 2001). Therefore, the assignment of the modern genus to as early as the Cretaceous based solely on finds of leaves has raised reasonable doubts (Wolfe, 1973; Krassilov, 1976; Maslova, 1997, 2001, 2002a, 2002b).

Not all fossil leaves assigned to the genus *Platanus* factually belong to the genus. For example, the leaves from the Tsagayan deposits of the Amur Region described by Krassilov (1976) as "*Platanus*" *raynoldsii* are associated with distinctive reproductive structures (pistillate heads of *Oreocarpa bureica* N. Maslova et Krassilov, seeds of *Carinalaspermum bureicum* Krassilov, and staminate heads of *Tricolpopollianthus burejensis* Krassilov) have a platanaceous morphology different from the morphology of the modern *Platanus* (Maslova and Krassilov, 2002). Leaves of "*Platanus*" *raynoldsii* are highly polymorphous; macromorphologically, the extreme members may be assigned to different genera of other families. Although the most typical morphotype is traditionally assigned to *Platanus*, such an assignment is apparently invalid for the Tsagayan finds. It is obvious that this Tsagayan plant had, in addition to typically platanaceous leaf morphotypes, not

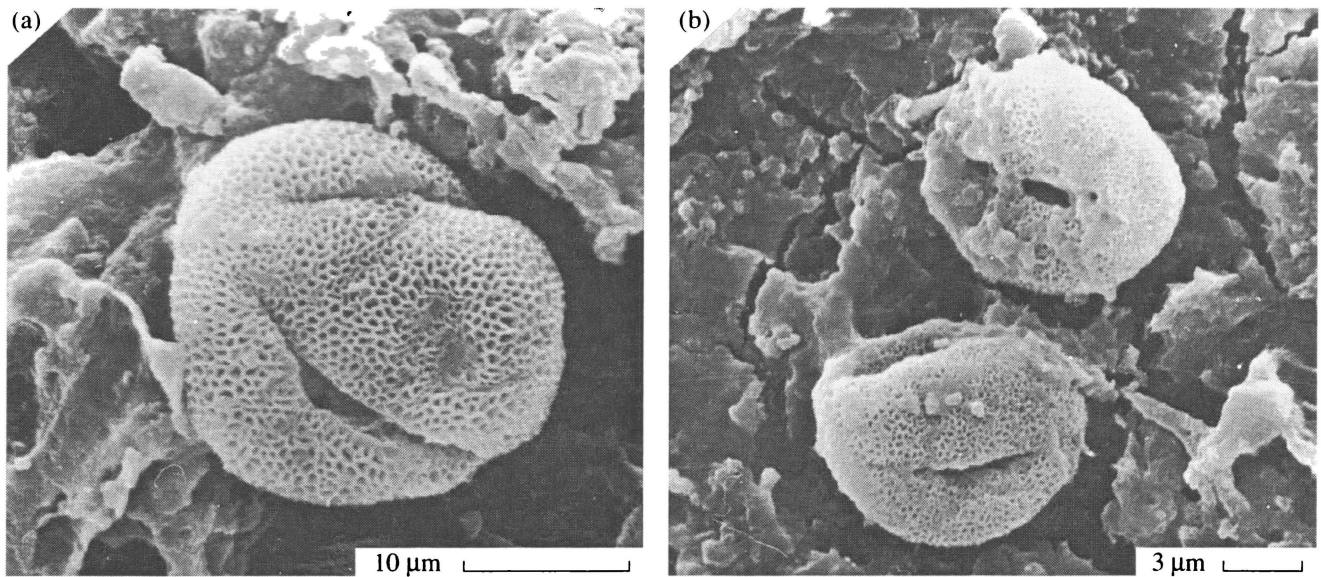


Fig. 4. Pollen grains found on the surface of the leaves associated with the inflorescences *Archaranthus krassilovii* sp. nov.: (a) polar view of the pollen grain and (b) two pollen grains in equatorial view.

only other leaf morphotypes but also reproductive organs different from those of *Platanus*.

To date, a significant body of data on leaf morphotypes of fossil Platanaceae have been gathered. In addition to the typical lobed leaves of the genera *Platanus* (subgenus *Platanus*) and *Macginitiea* Wolfe et Wehr, there existed entire pinnate leaves of *Platanus* (subgenus *Castaneophyllum*). Pinnately compound and pinnately dentate leaves of the Cretaceous *Sapindopsis* Fontaine and compound leaves of the Cretaceous–Paleocene *Platanites* and Late Cretaceous *Erlingdorfia* Johnson also occurred. The compound leaves of the genera *Platanites* and *Erlingdorfia* consist of a typically platanoid terminal leaflet resembling the leaf of *Platanus* (subgenus *Platanus*) and two simple and variously asymmetrical lateral leaflets. The apical leaflet of *Sapindopsis* also could have three lobes. Terminal leaflets found detached from a compound leaf evidently might be determined to be *Platanus* leaves. Leaves of the genera *Sapindopsis* and *Platanites* associating with reproductive organs are shown to be considerably different from those of *Platanus*.

Moreover, leaves of ancient Platanaceae often are strikingly similar to certain Hamamelidaceae. Common features of both families are present in the leaves of *Platimelis* Golovneva (Golovneva, 1994), *Platimeliophyllum* N. Maslova (Maslova, 2002a), and some Cretaceous leaves determined as members of *Platanus*. It should not be excluded that some of these leaves belong to fossil genera of Hamamelidaceae, a family with an insufficiently documented geological history, especially in leaf records. Some reproductive structures of the Hamamelidaceae also converged to the Platanaceae and could be differentiated only microstructurally (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b). It should be noted that epi-

dermal data do not always confirm macromorphological generic determinations. Thus, Ruffle (1968) grouped Cenomanian *Platanus* (*Credneria*) *cuneifolia* (Bronn) Jarmol. with the family Menispermaceae on the basis of epidermal morphology. Leaves morphologically similar to *Platanus* and associated with staminate inflorescences of the genus *Sarbaya* demonstrate epidermal features characteristic of the modern *Quercus ilex* L. and some fossil Fagaceae (Krassilov and Shilin, 1995).

Accordingly, the assignment of fossil leaves of this morphotype to other genera and even families cannot be excluded. The application of the generic name *Platanus* to Cretaceous leaf remains should be supported by microstructural studies and/or associations with reproductive organs.

The association of platanoid leaves and reproductive structures different from those of *Platanus* and assigned to the new genus *Archaranthus* gen. nov. on the basis of microstructure contributes to our knowledge of the morphological diversity of the fossil members of the family and confirms the necessity of the revision of the traditional concept that the genus *Platanus* existed in the Cretaceous.

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