

A New Taxon of Staminate Inflorescences *Bogutchanthus* gen. nov. (Hamamelidales) from the Paleocene of the Amur Region

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Abstract—Staminate inflorescences from the Paleocene deposits of the Amur Region (Russia) are described as a new genus, *Bogutchanthus* N. Maslova, Kodrul et Tekleva, on the basis of micromorphological characters. The inflorescences under description combine characters of the families Platanaceae and Hamamelidaceae (order Hamamelidales). Along with capitate inflorescences, tetramerous flowers with a differentiated perianth, and the presence of staminodes—typical characters of Cretaceous platanaceous plants—the new genus also shows some features that are known in extant and fossil members of the Hamamelidaceae: a loosely packed inflorescence, free stamens, secondarily bisporangiate stamens, crescent pollen sacs, and pantocolpate pollen grains. The inflorescences are associated with entire-margined leaves of the platanoid type.

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Key words: Paleocene, Platanaceae, Hamamelidaceae, inflorescences, micromorphology.

INTRODUCTION

Micromorphological study of superficially similar fossil capitate inflorescences and infructescences allows one to differentiate them at the generic and familial levels. Recent investigations have shown that such fossil reproductive structures identical at the level of macromorphology may either belong to the Platanaceae (Manchester, 1986; Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006), or the Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004), or combine characters of the both families (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005).

In the present paper we use the system proposed by Takhtajan (1966, 1987) and Cronquist (1981), where the Platanaceae and Hamamelidaceae are placed within the order Hamamelidales. A recently proposed system of angiosperms based on molecular data (Angiosperm..., 2003), discarded the order Hamamelidales and included the Platanaceae and Hamamelidaceae within the orders Proteales and Saxifragales, respectively, thereby destroying the previous concept that these families may be related to one another. Since an evaluation of angiosperm systematics is beyond the scope of the present paper, we will follow the system of Takhtajan and Cronquist, which is in better agreement with paleobotanical evidence concerning the families Platanaceae and Hamamelidaceae.

To date, paleobotany has achieved considerable success in the understanding of the geological history of the Platanaceae, some members of which played a significant role in the Cretaceous and Early Cenozoic floras of the Northern Hemisphere. The modern family is monotypic; however, having appeared in the Early Cretaceous (the earliest records are dated to the Albion, Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994), it showed a considerable generic diversity as early as the Late Cretaceous–Paleogene. Fossil Platanaceae are known from remains of both leaves and reproductive organs.

Abundant leaf remains from the Upper Cretaceous deposits that resemble leaves of the modern plane tree in macromorphology, are traditionally assigned to the genus *Platanus* L. Since the presence of this modern genus in Cretaceous deposits has not been confirmed by records of reproductive remains, Maslova et al. (2005) accomplished an analysis and proposed that the Cretaceous and Early Paleogene leaf remains showing a morphology that is typical of the modern plane tree should be placed under the generic name *Ettingshausenia* Stiehler of the morphological system of leaf remains, with the type species *E. cuneifolia* (Bronn) Stiehler. Apart from the typical lobate morphotype, which is characteristic of leaves of modern *Platanus* (subgenus *Platanus*), entire pinnate (Bůžek et al., 1967) and compound leaves (Crane et al., 1988, 1993; Johnson, 1996) are known among Cretaceous platanaceous leaf remains. The assignment of such leaves to the family is proved by their typically platanaceous epidermal morphology, as well as by the association with relevant reproductive

structures. It is important to note that although the lobate leaf typical of *Platanus* is very variable, in general, it has not changed from its appearance in the Early Cretaceous to the present day, and has been associated with reproductive structures that are assigned both to the Platanaceae (Krassilov and Shilin, 1995; Maslova and Kodrul, 2003; Maslova and Herman, 2006) and Hamamelidaceae (Maslova and Herman, 2004), or combining characters of these two families (Maslova et al., 2005). Therefore, the diversity of leaf morphotypes of the Platanaceae was very high in the Cretaceous and Early Paleogene.

The situation with reproductive structures of the Platanaceae is much the same. Sixteen platanaceous genera have been described to date on the basis of staminate and pistillate inflorescences (Krassilov, 1973, 1976; Manchester, 1986, 1994; Crane et al., 1988, 1993; Friis et al., 1988; Pedersen et al., 1994; Krassilov and Shilin, 1995; Magallón-Puebla et al., 1997; Maslova, 2002; Maslova and Krassilov, 2002; Maslova and Kodrul, 2003; Mindell et al., 2006). Although virtually identical in macromorphology, these reproductive structures are reliably differentiated by their micro-morphology. The rich diversity of fossil reproductive structures was analyzed and trends in the evolution of their elements were revealed (Maslova, 2003a, 2003b).

The geological history of the Hamamelidaceae is much less understood; however, nine extinct genera have been recently described on the basis of remains of reproductive organs (Endress and Friis, 1991; Manchester, 1994; Magallón-Puebla et al., 1996, 2001; Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004), five of which are capitate inflorescences and infructescences morphologically similar to those of the Platanaceae. Of particular interest are reproductive structures combining hamamelidaceous and platanaceous characters (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova et al., 2005). Earlier, possible phylogenetic relationships of these families were discussed (Crepet et al., 1992; Crepet and Nixon, 1996; Maslova, 2003; Maslova et al., 2005).

The present description of a new genus, *Bogutchanthus* gen. nov., contributes to our knowledge of the diversity in capitate reproductive structures, showing an eclectic combination of platanaceous and hamamelidaceous characters. Of interest is the association between these staminate inflorescences and leaf remains the prevailing morphotype of which is characteristic of leaves that accompany reproductive structures of some Platanaceae and Hamamelidaceae that are essentially different from those of *Bogutchanthus* gen. nov.

MATERIAL AND METHODS

Fragments of compound staminate inflorescences with coaly compressions come from the Tsagayan For-

mation of temporary open-pit coal mines of the Arkhara-Boguchan brown coal field, 15 km southeast of Arkhara of the Amur Region (49°18'45.1" N, 130°12'45.4" E; 49°18'52.3" N, 130°12'42.7" E; and 49°18'59.2" N, 130°12'44.5" E). Plant remains occur in a member of gray clays 6–8 m thick, between the coal beds "Nizhnii" and "Dvoynoi," in the upper part of the Middle Tsagayan Subformation (Akhmetiev et al., 2002). Paleobotanical and palynological studies dated these deposits to the Early Paleocene (Kodrul, 2004; Markevich et al., 2004).

After preparation of the reproductive structures, they were photographed using a Nikon Coolpix 8700 digital camera. An individual head was transferred onto a varnish film by dissolving the rock in hydrofluoric acid, and then macerated with Schulze's solution and alkali. Rock was removed from detached flowers using hydrofluoric acid, after which the flowers were mounted on SEM stubs. Floral elements were macerated using concentrated nitric acid and alkali and studied under an SEM. Micrographs were made under a CamScan SEM.

Individual pollen grains and fragments of sporangia were prepared for transmission electron microscopy using a standard technique (Tel'nova and Meyer-Melikian, 2002). Pollen grains were stained with OsO₄. Ultrathin sections were treated using the Reynolds method (Geyer, 1973).

The collection is housed in the Geological Institute of the Russian Academy of Sciences (GIN), no. 4867.

SYSTEMATIC PALEOBOTANY

Order Hamamelidales Wettstein

Bogutchanthus N. Maslova, Kodrul et Tekleva, gen. nov.

E t y m o l o g y. From the Boguchan village and the Latinized Greek *anthos* (flower).

Type species. *Bogutchanthus laxus* N. Maslova, Kodrul et Tekleva, gen. et sp. nov.

D i a g n o s i s. Sessile staminate heads 4–5 mm in diameter. Up to 40 flowers per head. Flowers in loose arrangement. Perianth differentiated. Epidermal cells of outer perianth elements vary in outline, strongly cutinized, in longitudinal rows. Epidermal cells of inner elements isodiametric and polygonal, with rare stomata and numerous weakly cutinized rounded bases of hairs. Flower tetramerous. Stamen filaments lacking. Immature stamens tetrasporangiate, mature stamens secondarily bisporangiate, pollen sacs vary in size and outline even within one stamen. Connective narrow; extension of connective small, triangular, often asymmetrical. Epidermis of extension of connective without stomata. Staminodes 300 µm long, resemble stamens in shape, apically with triangular widening, and basally fused with perianth elements. Pollen grains pantocolpate, colpi vary in size and position. Distinct colpus margin is formed by sporopollenin rim. Polar axis of mature

pollen grains 15.0–17.0 μm , and equatorial diameter 11.0–15.0 μm . Sculpture reticulate. Meshes of reticulum near colpus margin and in mesocolpium are identical. Pollen grains tectate and columellate.

Species composition. Type species.

Comparison. The new genus is characterized by a peculiar combination of platanaceous and hamamelidaceous reproductive characters.

This genus resembles the Platanaceae in the general morphology of the compound capitate inflorescence, strictly tetramerous flowers with a differentiated perianth, and the presence of staminodes. *Bogutchanthus* gen. nov. differs from the Platanaceae in having free flowers in the inflorescence, free stamens in the flowers, secondarily bisporangiate anthers, and pantocolpate pollen grains. Flowers with four stamens are known in the following Cretaceous members of the Platanaceae: *Sarbaya* Krassilov et Shilin (Krassilov and Shilin, 1995), *Quadriplatanus* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 1997), and *Archaranthus* N. Maslova et Kodrul (Maslova and Kodrul, 2003). The new genus differs from *Sarbaya* in having a differentiated perianth, staminodes, pollen sacs varying in size and shape, and pollen grains with finer sculpture. *Bogutchanthus* gen. nov. differs from *Quadriplatanus* in the size and shape of pollen sacs, less developed epiconnective without stomata in the epidermis, and pollen grains with finer sculpture. The new genus differs from *Archaranthus* in its sessile heads, better developed perianth, less developed connective lacking stomata, less developed epiconnective, presence of staminodes, and pollen grains with finer sculpture.

The similarity between the new genus and members of the Hamamelidaceae is expressed in the general aspect of the heads, presence of staminodes, bisporangiate anthers, and pantocolpate pollen grains. Among modern members of the Hamamelidaceae, macromorphologically similar capitate inflorescences are characteristic of the subfamily Altingioideae and the genus *Exbucklandia* R. Brown of the Exbucklandioideae (Kaul and Kapil, 1974; Bogle, 1986). Fossil heads that are assigned to the Hamamelidaceae (Maslova and Krassilov, 1997; Maslova and Golovneva, 2000a, 2000b; Zhou et al., 2001; Maslova and Herman, 2004) or referable to this family (Maslova et al., 2005) are also known.

Staminodes are recorded in extant members of the Altingioideae, Exbucklandioideae, and Rhodoleioideae, in the Paleocene genus *Evacarpa* N. Maslova et Krassilov (Maslova and Krassilov, 1997), Cenomanian

Viltyungia N. Maslova (Maslova and Golovneva, 2000), and Santonian–Campanian *Archamamelis* Endress et Friis (Endress and Friis, 1991).

Among modern members of the Hamamelidaceae, the genera *Hamamelis* L. from the subfamily Hamamelidoideae (Schoemaker, 1905; Mione and Bogle, 1990) and *Exbucklandia* from the subfamily Exbucklandioideae (Kaul and Kapil, 1974) have bisporangiate anthers. In fossil members of this family, bisporangiate anthers are known in the subfamily Hamamelidoideae. Thus, flowers of the Late Santonian genus *Androdecidua* Magallón-Puebla, Herendeen et Crane (Magallón-Puebla et al., 2001) have bisporangiate stamens of the outer circle and tetrasporangiate stamens of the inner circle. Bisporangiate stamens are described in flowers of *Archamamelis* from the Santonian–Campanian of Sweden (Endress and Friis, 1991).

The presence of pantocolpate pollen grains makes *Bogutchanthus* gen. nov. comparable to members of the Hamamelidaceae. Among modern Hamamelidaceae, such pollen grains occur in members of the Hamamelidoideae, such as *Distylium* Sieb. et Zucc., *Matudaea* Lundell, and *Sycopsis* Oliv., and Exbucklandioideae, such as *Chunia* Chang (Bogle and Philbrick, 1980). Pantocolpate pollen grains are described in the Cenomanian *Viltyungia* (Maslova and Golovneva, 2000) and are known as aberrant forms in the modern *Platanus occidentalis* L. (Zavada and Dilcher, 1986) and Paleocene *Archaranthus krassilovii* N. Maslova et Kodrul (Maslova and Kodrul, 2003).

Tetramerous flowers and presence of staminodes characterize staminate heads from the Raritan Formation of New Jersey (Turonian), which combine platanaceous and hamamelidaceous characters (Crepet et al., 1992; Crepet and Nixon, 1996). Unlike *Bogutchanthus* gen. nov., they have a distinct undifferentiated perianth, stamens fused in a tube, and tricolpate pollen grains.

Bogutchanthus laxus N. Maslova, Kodrul et Tekleva, sp. nov.

Plate 8, figs. 1–8; Plate 9, figs. 1–8

Etymology. From the Latin *laxus* (loosely arranged).

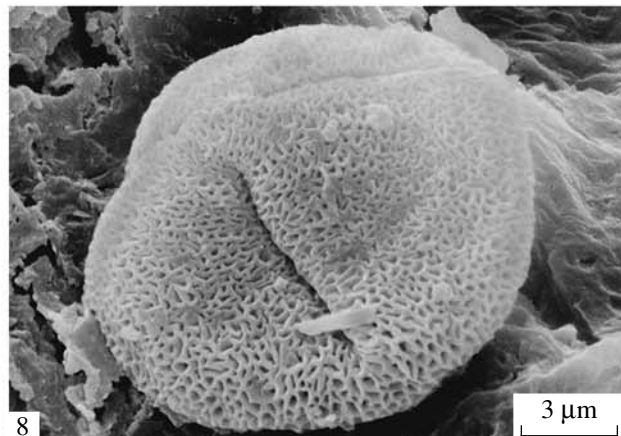
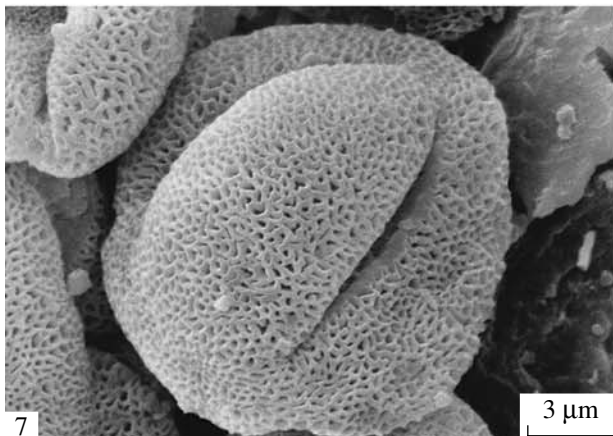
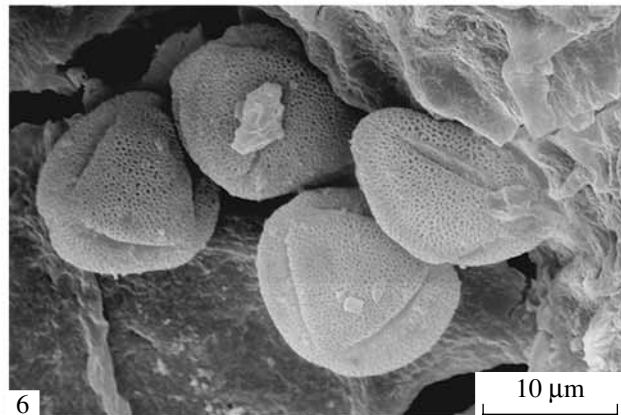
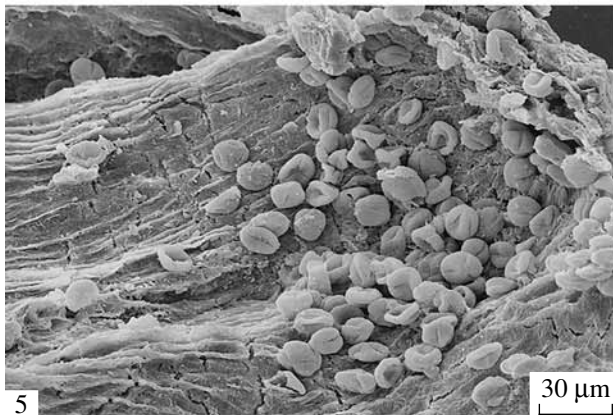
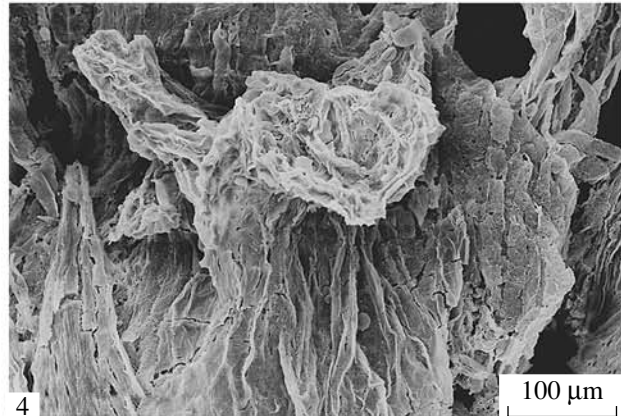
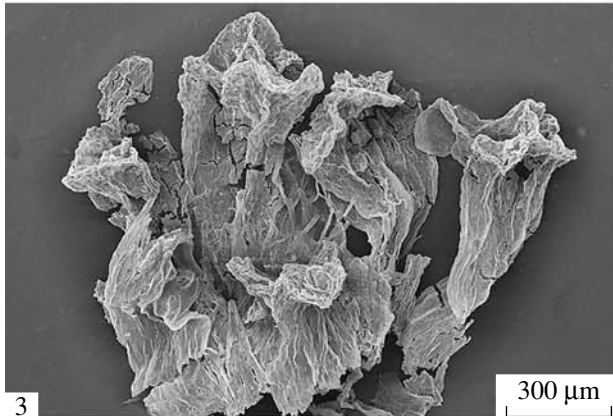
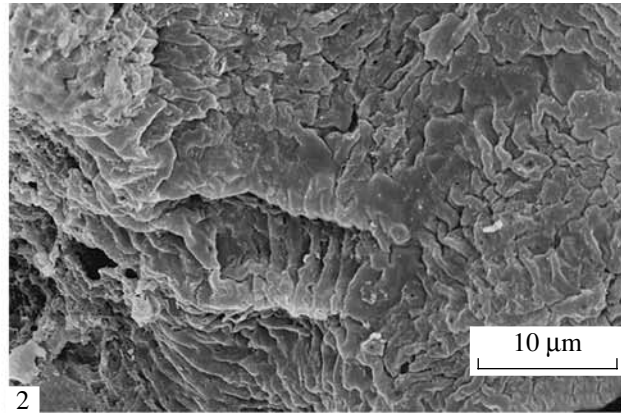
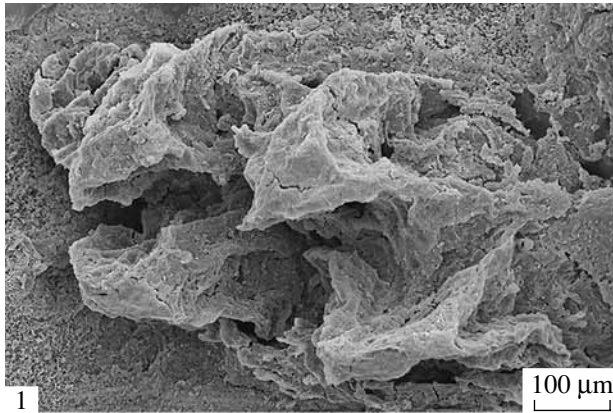
Holotype. GIN, no. AB1-136, capitate inflorescence with a preserved axis; Amur Region, Arkhara-Buguchan coal field, 15 km southeast of the village of Arkhara; Tsagayan Formation, between the coal beds “Nizhnii” and “Dvoynoi”; Lower Paleocene.

Diagnosis. As for the genus.

Explanation of Plate 8

Figs. 1–8. *Bogutchanthus laxus* sp. nov., SEM: (1) holotype GIN, no. AB1-136, tetramerous flower; (2) holotype GIN, no. AB1-136, surface of an epiconnective; (3) GIN, no. AB1-316, macerated tetramerous flower showing fragments of the perianth, four stamens, and staminodes; (4) GIN, no. AB1-316, staminode; (5) GIN, no. AB1-316, pollen mass in a pollen sac; (6) GIN, no. AB1-316, pantocolpate pollen grains; (7) GIN, AB1-316, pollen grain in equatorial position; (8) GIN, no. AB1-316, pollen grain in polar position; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene.

Plate 8



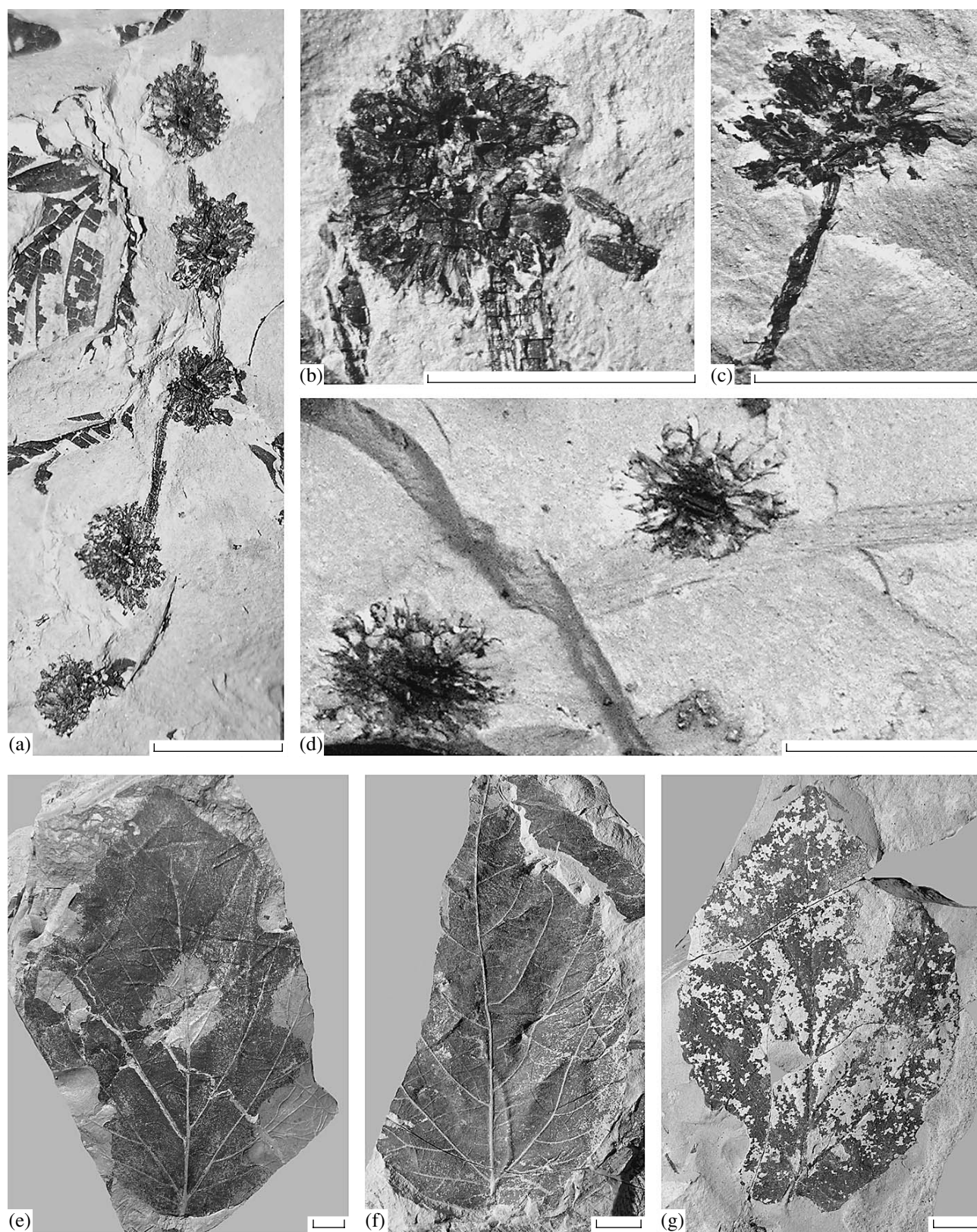


Fig. 1. General view of inflorescences of *Bogutchanthus laxis* sp. nov. and associating leaves of the *Platanus* type: (a) GIN, no. AB1-214, axis with five sessile heads; (b) holotype GIN, no. AB1-136; (c) GIN, no. AB1-239; (d) GIN, no. AB1-429; (e) GIN, no. AB1-92; (f) GIN, no. AB3-44; (g) GIN, no. AB3-115; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene. Scale bar (a–d) 5 mm and (e–g) 10 mm.

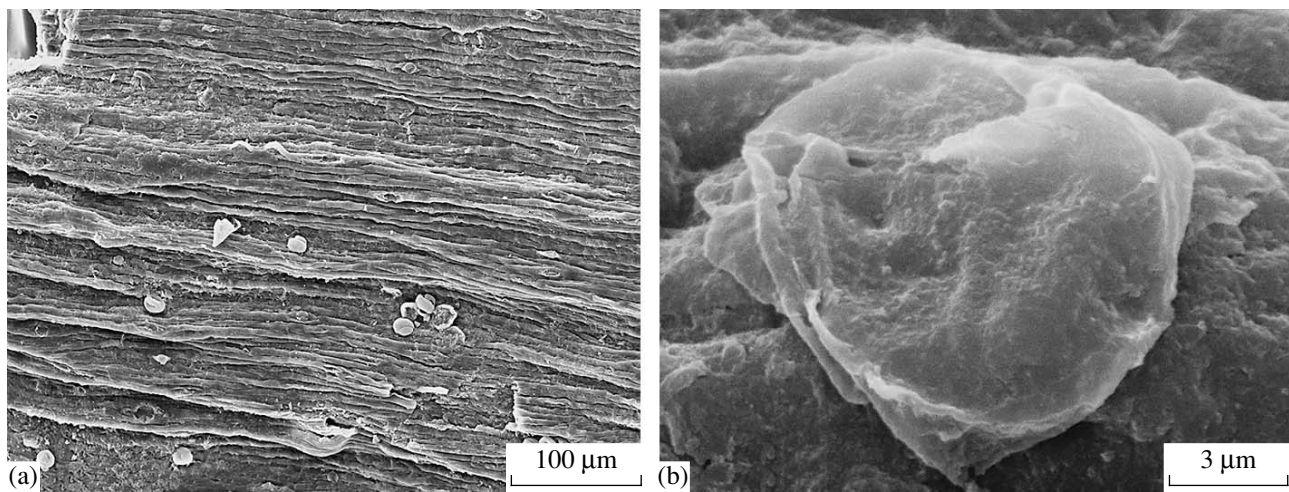


Fig. 2. *Bogutchanthus laxus* sp. nov., GIN, no. AB1-316, SEM: (a) surface of the inflorescence axis; (b) rounded trichome on the surface of the inflorescence axis; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene.

Description (Figs. 1–4). The staminate inflorescence consists of a relatively massive longitudinally striate axis up to 2 mm in diameter and several (at least nine) alternating sessile heads 4–5 mm in diameter (Figs. 1a–1d). The longitudinal striation is formed by distinct cuticular ridges. The surface of the axis is uniformly covered with rounded trichomes 10 µm in diameter (Fig. 2).

Loose arrangement of the head is visible in reflected light. Individual flowers are not in contact, but relatively loosely arranged. The central core of the inflorescence is about 1 mm in diameter. There are up to 40 flowers per head.

The flowers are 500–700 µm long and 450–750 µm wide, strictly tetramerous (SEM data; Pl. 8, fig. 1). The perianth reaches half of the stamen length, perianth elements tightly embrace the basal part of the flower. Two types of the perianth elements are distinct. The epidermis of outer elements consists of cells that are arranged in longitudinal rows and vary in outline from nearly square (10 × 10 µm) or trapezoid to elongated rectangular (10 × 45 µm). The walls of epidermal cells of the outer perianth elements are strongly cutinized (Figs. 3b, 3c). Inner perianth elements differ in the very thin cuticle, which is folded after maceration (Fig. 3d). Cellular walls are weakly cutinized, and the outlines of cells of the inner perianth elements are not always traceable. In some regions of the cuticle, we were able to reveal that outlines of ordinary epidermal cells are isodiametric and polygonal, stomata 20–22 × 12–15 µm are occasionally present (Fig. 3e), as well as weakly cutinized rounded bases of hairs about 10 µm in diameter (Fig. 3f).

Staminodes are situated between stamens and perianth resembling mature stamens in shape (Pl. 8, figs. 3, 4). Basally, they are partially adnate with perianth elements, which is evidenced by the absence of distinct histological boundaries of cuticles of individual

floral elements in the base of the flower. We cannot judge the number of staminodes per flower, since (because of the loose arrangement of flowers) the full number of small staminodes might not have been preserved during fossilization. An individual staminode is up to 500 µm long and bears a triangular apical extension (Pl. 8, fig. 4).

Androecium consists of four stamens (Pl. 8, fig. 1). The stamens are free over most of their length and widely spaced. The stamen filament is not developed. Within a head, immature anthers are tetrasporangiate (Fig. 4f); during maturation up to dehiscence, the septum between the anther lobe is destroyed, and the initially tetrasporangiate anther becomes bisporangiate (Fig. 4e). Connective and epiconnective of stamens in some flowers are observable after the transfer of the inflorescence on a varnish film by dissolving the rock in hydrofluoric acid. The connective is thin. The epiconnective is small, triangular, often asymmetrical (because pollen sacs are uneven in length), and bears no stomata (Pl. 8, fig. 2).

As a rule, during maceration, flowers are separated into individual stamens, and the connective and epiconnective do not sustain maceration. Pollen sacs are significantly flattened and are connected basally in the theca (Fig. 4b). They vary in shape and size even within one theca (Fig. 4). Along with narrow, elongate, and nearly parallel-margined pollen sacs of 500–700 µm long and 90–150 µm wide (Fig. 4d), there are crescent pollen sacs about 500 µm long and with a maximum width about 150 µm in their central part (Fig. 4c).

Pollen grains vary from nearly spheroidal to elliptical. They are pantocolpate, with four to six (occasionally more) colpi (Pl. 8, figs. 5–8; Pl. 9, figs. 1–3), or, very rarely, tricolpate (Pl. 9, fig. 4). The polar axis of is 15.0–17.0 µm, and the equatorial diameter is 11.0–15.0 µm. The distribution of colpi varies depending on their number. In tetracolpate pollen, three colpi are

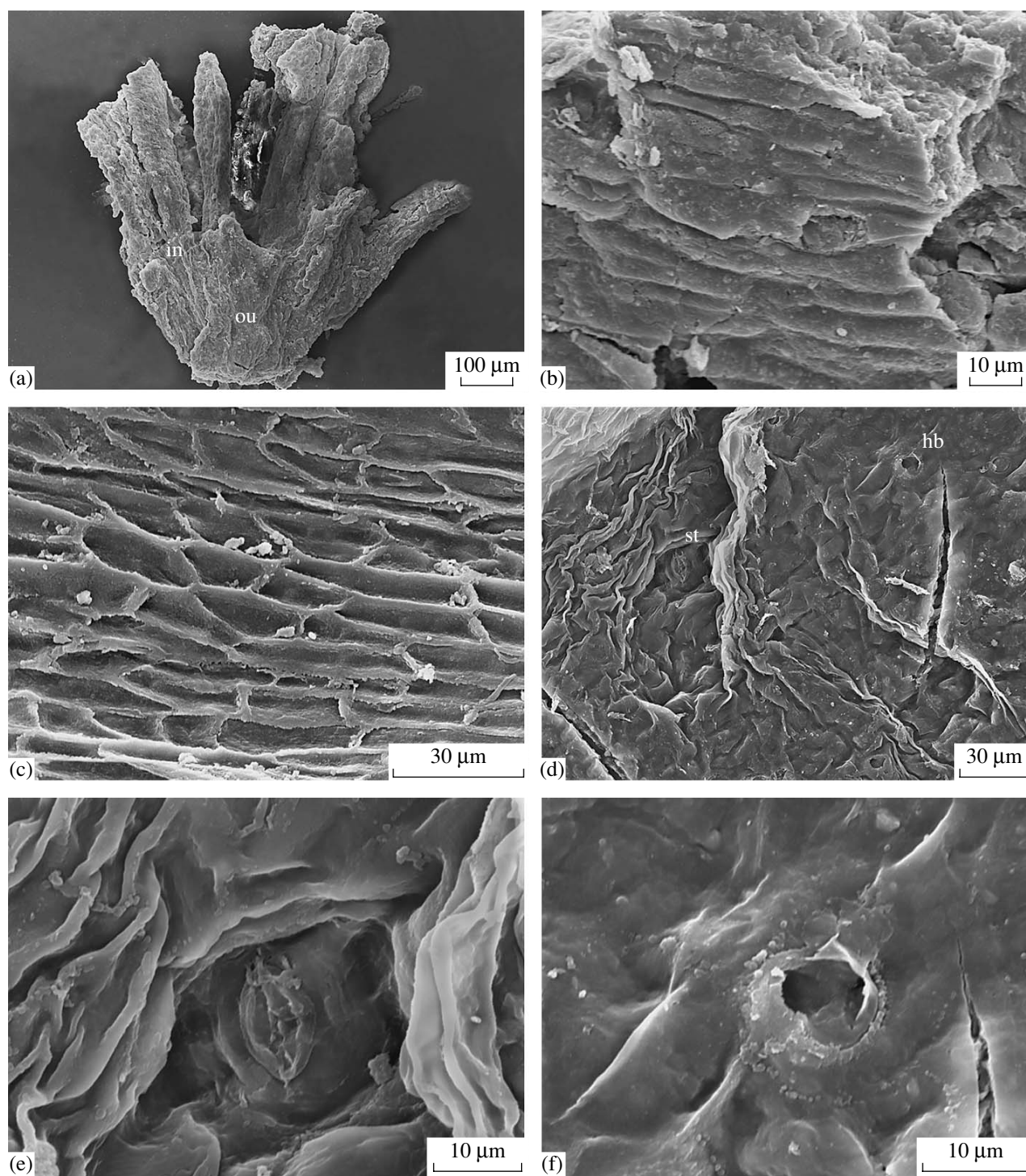


Fig. 3. *Bogutchanthus laxus* sp. nov., holotype GIN, no. AB1-136, SEM: (a) individual flower with partially broken stamens, note the loose arrangement of stamens, fragments of outer (ou) and inner (in) perianth elements; (b) cuticle of outer perianth elements, outside view; (c) cuticle of outer perianth elements, inside view; (d) cuticle of inner perianth elements, note a stoma (st) and hair bases (hb); (e) cuticle of an inner perianth element, a stoma; (f) cuticle of an inner perianth element, note a hair base; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene.

long, and one is conspicuously shorter. In hexacolpate pollen grains, the colpi are arranged in groups of three forming a more or less distinct triangle on the pollen surface (Pl. 8, fig. 6; Pl. 9, fig. 2); often three colpi are

situated very close to each other or nearly fused, imitating a ring colpous (Pl. 9, fig. 3). Colpi vary from long (stretching from one pole to the other) to short (as long as half or one-third of the longest colpi). The

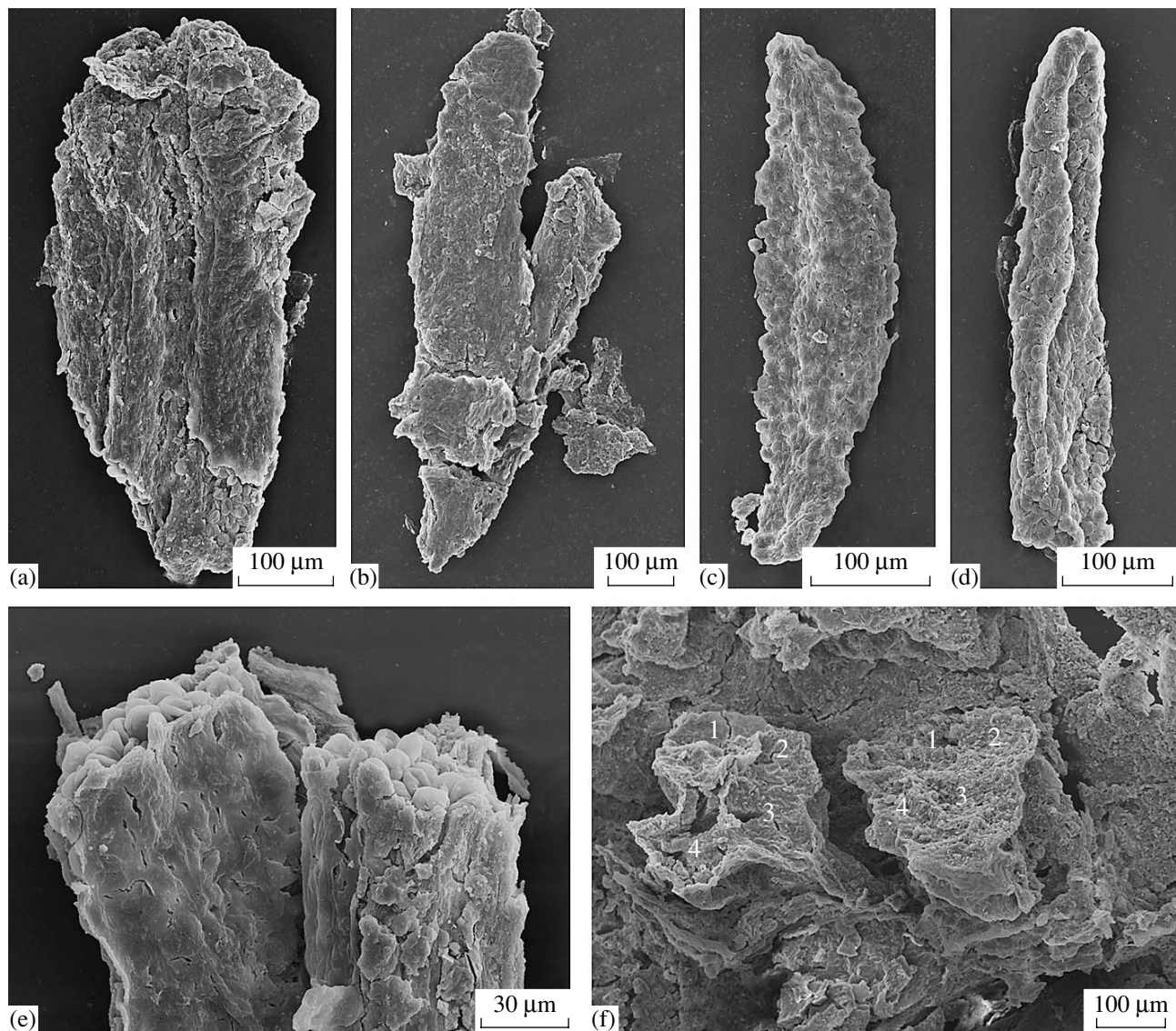


Fig. 4. *Bogutchanthus laxus* sp. nov., holotype GIN, no. AB1-136, SEM: (a) individual stamen; (b) two basally fused pollen sacs of unequal sizes; (c) crescent pollen sac; (d) elongate parallel-margined pollen sac; (e) bisporangiate stamen with mature pollen grains; (f) transverse section through two tetrasporangiate stamens, numbers indicate pollen sacs; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene.

colpus margin is distinct and formed by a sporopollenin rim (Pl. 9, fig. 5). The maximum width of the mesocolpium is $12.0\ \mu\text{m}$. The sculpture is reticulate. The meshes of the reticulum vary from rounded to elongate (Pl. 9, fig. 5). The meshes near the colpus margin are identical to those of the mesocolpium. There are three or four meshes per $1\ \mu\text{m}$.

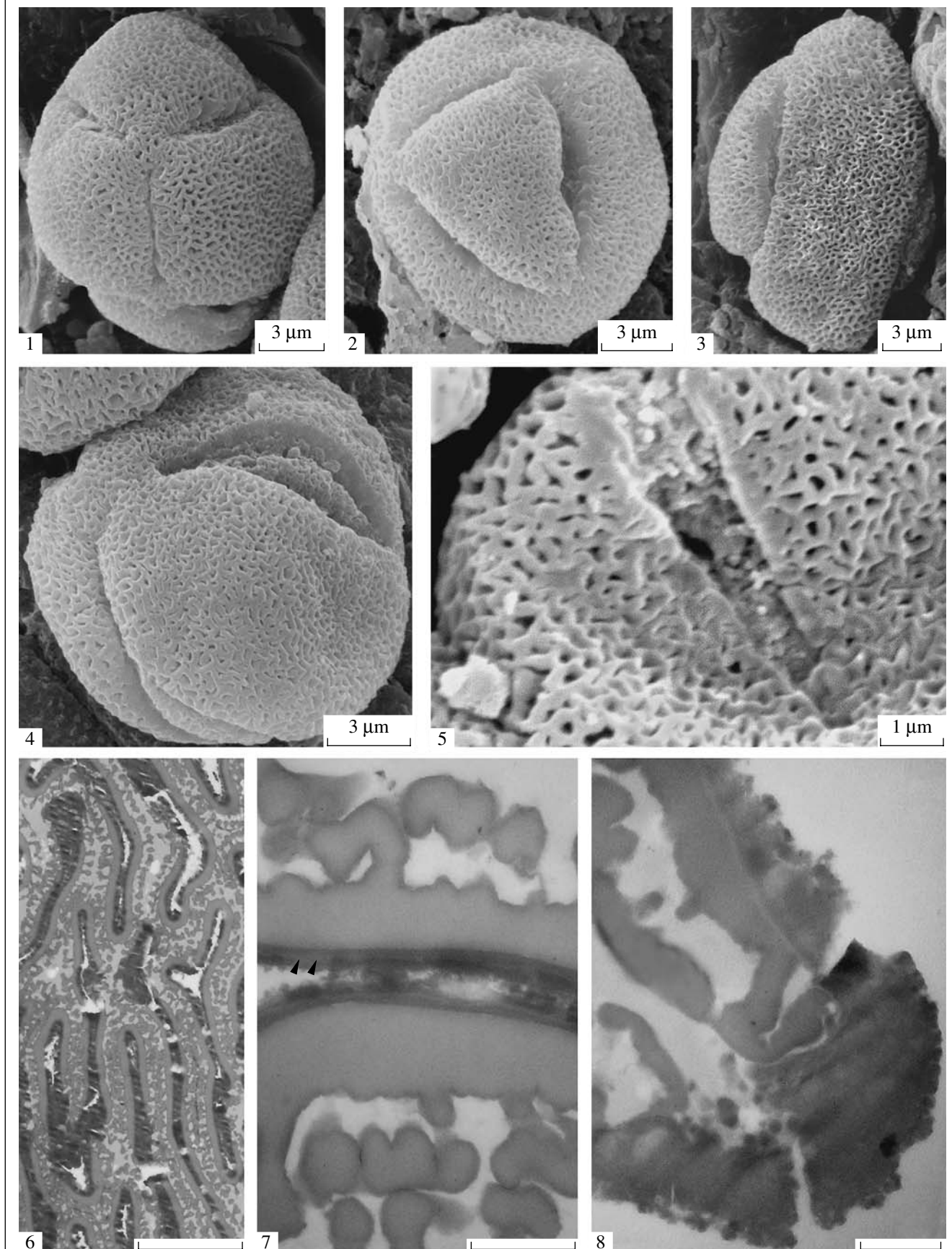
The non-apertural exine is about $0.98\ \mu\text{m}$ thick (Pl. 9, figs. 6–8). The exine is semitectate, the tectum is formed by the heads of columellae, about $0.38\ \mu\text{m}$ high. The columellae are $0.24\ \mu\text{m}$ high and $0.14\ \mu\text{m}$ wide (basally). They are relatively closely spaced. The foot layer is about $0.36\ \mu\text{m}$ thick (Pl. 9, fig. 7).

The endexine is more electron-dense than the ectexine, at average $0.1\ \mu\text{m}$ thick, bilayered, both layers are

of approximately equal thickness in non-apertural regions. The upper layer of the endexine is homogeneous, less electron-dense than the outer layer, of uniform thickness along the entire perimeter of the pollen grain, except the apertural area. The inner layer of the endexine is homogeneous, at places, in the inner area of this layer, grained particles form larger granules and are relatively loosely disposed (Pl. 9, fig. 7).

Toward the apertural area, the ectexine abruptly reduces and disappears. In the apertural area, the exine is represented only by a bilayered endexine $1.8\ \mu\text{m}$ thick (Pl. 9, fig. 8). The endexine becomes thicker in the apertural area predominantly at the expense of its inner layer.

Plate 9



Material. Twelve fragmentary inflorescences from localities within the Arkhara-Boguchan coal field.

DISCUSSION

The genus under description is characterized by the combination of platanaceous and hamamelidaceous characters. It is similar to modern and fossil members of the Platanaceae in having capitate inflorescences, strictly tetramerous flowers with a developed perianth, and the presence of staminodes. Among the Platanaceae, the new genus bears the closest resemblance to the group of fossil genera with tetramerous flowers (*Sarbaya*, *Quadriplatanus*, and *Archaranthus*).

Modern and fossil members of the Hamamelidaceae are close to the new genus in characters of the general morphology of inflorescence, secondarily bisporangiate stamens, and pantocolpate pollen grains. The ability to form capitate inflorescences and the presence of bisporangiate anthers and pantocolpate pollen grains make *Bogutchanthus* gen. nov. most similar to the modern genus *Chunia* (subfamily Exbucklandioideae). The Cenomanian genus *Viltyungia* is the closest fossil member of the Hamamelidaceae because of the inflorescence shape, presence of staminodes, and pollen type.

Inflorescence architecture. The genus *Bogutchanthus* gen. nov. is characterized by a relatively massive axis with numerous sessile heads. The axis of the compound inflorescence is covered with a longitudinal striation, which is distinguishable in reflected light and formed by cutin rims, and numerous unicellular trichomes. Similar trichomes are described in some modern members of the Platanaceae and Proteaceae (Carpenter et al., 2005).

Most members of the Platanaceae are characterized by sessile heads. Among staminate inflorescences, only *Archaranthus* and some species of *Platananthus* Manchester have heads that are attached to the axis by a pedicel.

Heads of the modern plane tree, as well as those of the majority of fossil platanaceous genera, consist of a relatively massive receptacle and radiating flowers. The modern plane tree has very dense heads with tightly packed flowers. Margins between individual flowers are virtually indistinct. In fossil Platanaceae with a relatively developed perianth (e.g., *Platananthus*), the margins between flowers are distinct; however, the heads are very dense. The main inflorescence type in the Hamamelidaceae is spike or compound spike

(Endress, 1977). Some genera have variously compact racemes or compound racemes. Some members of the Hamamelidoideae and Exbucklandioideae have inflorescences that are extremely compact and superficially resemble heads. Thus, the genus *Exbucklandia* has distinct capitate inflorescences (Kaul and Kapil, 1974). Three extant members of the Altingioideae, *Altingia* Nor., *Liquidambar* L., and *Semiliquidambar* Chang, have heads that are similar in morphology to those of the Platanaceae (Bogle, 1986). It should be noted that infructescences of the modern *Liquidambar* show a various degree of density. Most species have biloculate wedge-shaped or fusiform fruits, more or less basally fused, and distally free. However, *L. acalycina* Chang (and the close genus *Altingia*) has relatively loosely spaced fruits that disintegrate under mechanical compression (Ickert-Bond et al., 2005). *Bogutchanthus* gen. nov. is characterized by a peculiar morphology of the head. The flowers are relatively loosely spaced with more or less distinct boundaries between individual flowers. In addition, stamens in flowers of the new genus are also free, which is unknown in fossil and modern members of the Platanaceae.

The number of flowers per inflorescence varies among the genera of the Platanaceae. *Bogutchanthus* gen. nov. is comparable with *Quadriplatanus* in this character (40 flowers). Staminate inflorescences of some species of *Platananthus* contain a slightly higher number of pentamerous flowers (50). The genera *Sarbaya* and *Archaranthus* differ in having a smaller number of flowers per inflorescence (about 24 and 15, respectively). As a rule, the number of flowers per inflorescence in heads of the Platanaceae is high (about 100 in some species of the Late Cretaceous *Platananthus* and up to 300 in the modern plane tree). Among members of the Hamamelidaceae with capitate inflorescences, *Exbucklandia* has 8–13 flowers (Kaul and Kapil, 1974), *Altingia* has 6–25 flowers, and *Liquidambar* has up to 40 flowers (Bogle, 1986).

Perianth. The perianth of *Bogutchanthus* gen. nov. reaches half of the flower length. It includes outer and inner elements. The epidermis of the outer elements is composed of longitudinal rows of cells of various outlines: from square or trapezoid to elongate rectangular, with strongly cutinized walls. The inner elements have a weakly cutinized epidermis, constituted of more or less isodiametric polygonal cells, with numerous hairs and rare stomata.

Explanation of Plate 9

Figs. 1–8. *Bogutchanthus laxus* sp. nov., GIN, no. AB1-316: (1) pantocolpate pollen grain showing two annular colpi, each is formed by merging three closely spaced colpi, and an additional (seventh) small colpus, SEM; (2) pollen grain with three visible colpi forming a triangle (the total number of colpi is probably six), SEM; (3) pollen grain with two annular colpi, SEM; (4) tricolpate pollen grain, SEM; (5) colpus margin formed by a continuous sporopollenin rim, SEM; (6) agglomeration of pollen grains, scale bar 5 µm, TEM; (7) non-apertural area of the pollen grain, double arrowheads indicate the boundary between the endexine layers, scale bar 0.5 µm, TEM; (8) apertural area of the pollen grain, scale bar 0.5 µm, TEM; Amur Region, Arkhara-Buguchan coal field, Tsagayan Formation, Lower Paleocene.

Most scientists believe that flowers of the modern plane tree are devoid of perianth, which is considered among the diagnostic features of this genus. The overwhelming majority of extinct members of the Platanaceae had a well-developed and often differentiated perianth. Among platanaceous genera with staminate inflorescences, more or less developed perianths are present in *Aquia* Crane, Pedersen, Friis et Drinnan (Albian, Crane et al., 1993), *Platananthus* (Albian–Eocene, Manchester, 1986, Friis et al., 1988, Pigg and Stockey, 1991), *Hamatia* Pedersen, Crane et Drinnan (Albian, Pedersen et al., 1994), *Quadriplatanus* (Coniacian–Santonian, Magallón-Puebla et al., 1997), and *Archaranthus* (Danian, Maslova and Kodrul, 2003). An extremely reduced perianth or no perianth is described in *Sarbaya* (Cenomanian–Turonian, Krassilov and Shilin, 1995) and *Chemurnautia* N. Maslova (Late Paleocene, Maslova, 2002).

Archaranthus, a platanaceous genus with tetramerous flowers, as well as *Bogutchanthus* gen. nov., clearly shows two types of perianth elements with different epidermal features. The new genus differs in the presence of hairs and stomata in the epidermis of inner elements. The perianth of staminate flowers of *Quadriplatanus* nearly completely embraces the stamens. It is undifferentiated, tetramerous, and the abaxial and adaxial epidermides of its elements show some differences from each other. An undifferentiated perianth with basally adnate elements characterizes flowers of staminate heads from the Raritan Formation, Turonian of New Jersey (Crepet et al., 1992).

Basally, perianth elements are tightly packed in the flower of *Bogutchanthus* gen. nov., suggesting the formation of a floral tube that was torn as it progressed toward the apex of the mature flower. Flowers of modern members of the Hamamelidaceae usually have a tetra- or pentamerous perianth with a variously developed calyx and corolla. Perianth elements are free or fused (in varying degrees) into a tube, which may adnate to stamens and ovary (Bogle, 1970). *Parrotia* C. A. Mey and *Fothergilla* Murray of the Hamamelidoideae have perianth elements that basally fuse with stamens resulting in a subpistillate hypanthium, *Dicoryphe* Du Petit-Thouars of the same subfamily shows the fusion of the androecium and corolla in a circle (Bogle, 1970). Modern Hamamelidaceae with capitate reproductive structures lack well-developed perianths. Only in *Exbucklandia*, a calyx is separated at early ontogenetic stages; flowers of the Altingioideae are apetalous (Bogle, 1986). Fossil capitate inflorescences and infructescences that are assigned or assignable to the Altingioideae usually have well-developed perianths. Thus, *Lindacarpa* N. Maslova has a perianth that is attached slightly above the base of the gynoecium and embraces the flower virtually along its whole length (Maslova and Golovneva, 2000a); perianth elements in *Anadyricarpa* N. Maslova et Herman constitute a floral tube persisting even in mature fruits (Maslova and Herman, 2004). *Viltyungia*, which dem-

onstrates characters of three subfamilies, Altingioideae, Exbucklandioideae, and Hamamelidoideae, has a well-developed perianth with narrower inner elements and wide and hairy outer elements (Maslova and Golovneva, 2000b). Ancient members of the Hamamelidoideae show varying degrees of perianth development. Thus, *Allonia* Magallón-Puebla, Herendeen et Endress is characterized by a well-developed corolla with narrow parallel-margined petals and irregularly developed sepals (Magallón-Puebla et al., 1996). *Androdecidua* has fusiform petals with narrowing bases and apices, partially fused with stamens of the outer circle of the androecium (Magallón-Puebla et al., 2001). A differentiated hexa- or heptamerous perianth with triangular and basally wide petals is described in *Archamamelis* (Endress and Friis, 1991).

The Turonian genus *Kasicarpa* N. Maslova, Golovneva et Tekleva, combining platanaceous and hamamelidaceous characters, has a well-developed perianth that forms a floral tube (Maslova et al., 2005).

Bogutchanthus gen. nov. shows a basal fusion of perianth elements and staminodes, which is reminiscent of a partial fusion of petals with stamens of the outer androecium circle, known in the fossil genus *Androdecidua*, as well as in some modern Hamamelidaceae such as *Parrotia* and *Fothergilla* (Bogle, 1970).

Androecium. Flowers of *Bogutchanthus* gen. nov. are strictly tetramerous. Fossil Platanaceae are dominated by genera with a constant number of floral elements, whereas the modern genus *Platanus* is characterized by an unstable number of floral elements in flowers even within one head (Boothroyd, 1930). In addition to *Bogutchanthus* gen. nov., tetramerous flowers are also a character of *Archaranthus*, *Sarbaya*, *Quadriplatanus*, and staminate and pistillate heads from the Turonian of the Raritan Formation (New Jersey), which combine platanaceous and hamamelidaceous characters (Crepet et al., 1992; Crepet and Nixon, 1996). *Platananthus*, *Gynoplatananthus* Mindell, Stockey et Beard (Mindell et al., 2006), and, possibly, *Hamatia* have strictly pentamerous flowers.

Bogutchanthus gen. nov. differs from all platanaceous genera in having free stamens. As a rule, the modern *Platanus* and Cretaceous members of the Platanaceae have tightly adpressed elements of the flower. The exception is *Chemurnautia*, which is characterized by relatively loosely spaced pollen sacs, partially fused basally (Maslova, 2002). This peculiarity of flowers of *Chemurnautia* prevented the determination of the exact number of flowers per inflorescence, as well as the number of stamens per flower.

Staminate flowers of the modern plane tree have three to five stamens consisting of a short filament and elongate tetrasporangiate anthers. The androecium of *Bogutchanthus* gen. nov. is not typical of the Platanaceae. It is formed by four free stamens lacking a distinct filament and virtually sessile anthers. The stamens are primarily tetrasporangiate; however, they appear

bisporangiate at maturity because the septa between the anther lobes disappear. We consider the cooccurrence of tetrasporangiate and bisporangiate stamens in the same head as a result of their non-simultaneous maturation. Stamens of all members of the Platanaceae are tetrasporangiate; no bisporangiate stamens are found in the Platanaceae. Nearly all modern members of the Hamamelidaceae have tetrasporangiate stamens, thecae with one lobe are known only in species of *Hamamelis* (Schoemaker, 1905) and *Exbucklandia* (Kaul and Kapil, 1974). The androecium of the fossil genus *Androdecidua* (subfamily Hamamelidoideae) is characterized by the different morphology of stamens of the outer and inner circles. The stamens of the outer circle have bisporangiate anthers, whereas the stamens of the inner circle have tetrasporangiate anthers. Bisporangiate anthers are known in the Santonian–Campanian genus *Archamamelis* of the Hamamelidoideae (Endress and Friis, 1991).

Pollen sacs of *Bogutchanthus* gen. nov. constituting a single stamen vary in shape (from narrow, elongate, with nearly parallel margins, to crescent and asymmetrical) and size; hence its often asymmetrical appearance. Unequal development of pollen sacs within one theca and, as a result, asymmetrical thecae are also characteristic of the modern plane tree (Hufford and Endress, 1989). However, in *Platanus*, this feature is expressed to a much lesser degree, and the shape of sacs is relatively constant. The elongate and parallel-margined pollen sacs of *Bogutchanthus* gen. nov. resemble those of the modern *Platanus* and Early Eocene *Chemurnautia*. However, crescent sporangia are also present in the new genus. Asymmetric crescent pollen sacs are known in the modern *Chunia* (Exbucklandioideae, Hamamelidaceae) and Turonian *Viltyungia*, which combines characters of the subfamilies Exbucklandioideae, Altingioideae, and Hamamelidoideae and, among other things, is characterized by the same pantocolpate pollen type.

Pollen sacs of *Bogutchanthus* gen. nov. are basally fused. Narrow linear pollen sacs of *Chemurnautia* do not form distinct thecae and also are partially fused basally, but free in the middle area. *Quadriplatanus* is also characterized by basally adnate stamens forming a distinct ring. This peculiarity is comparable with a similar distinct tissular ring that is formed by a basal adnation of stamens and staminodes in the modern plane tree (Magallón-Puebla et al., 1997). Tetramerous flowers in staminate heads from the Turonian of the Raritan Formation of New Jersey, which share several characters with the Platanaceae and Hamamelidaceae, show a distinct continuous fusion of stamens and staminodes resulting in a stamen tube (Crepet et al., 1992; Crepet and Nixon, 1996). This feature is also known in some members of the Hamamelidaceae (Endress, 1977). Magallón-Puebla et al. (1997) discussed the similarity between the fusion of stamens and staminodes in *Quadriplatanus* and stamen tubes of modern members of the Hamamelidaceae *Embolanthera* Merr. and *Dicoryphe*.

As a differentiating feature, they mentioned the contribution of perianth elements to the formation of the pollen tube in the Hamamelidaceae. The similarly fused perianth elements and staminodes are described in *Bogutchanthus* gen. nov.

Stamens of *Bogutchanthus* gen. nov. have a thin connective and weakly developed epiconnective, both of those are devoid of hairs and stomata. Most fossil members of the Platanaceae have more or less developed connectives continuing into triangular conical epiconnectives. Epiconnectives may be developed in varying degrees: from weakly developed (*Aquia brookensis* Crane, Pedersen, Friis et Drinnan; Crane et al., 1993) to more or less massive of varying shapes: conical in *Platananthus synandrus* Manchester (Manchester, 1986) and *P. speirsae* Pigg et Stockey (Pigg and Stockey, 1991), triangular in *P. scanicus* Friis, Crane et Pedersen (Friis et al., 1988) and *Archaranthus krassilovii* (Maslova and Kodrul, 2003), flattened in *Platananthus hueberi* Friis, Crane et Pedersen (Friis et al., 1988), and peltate in *P. potomacensis* Friis, Crane et Pedersen (Friis et al., 1988). Naked connectives are known in *Sarbaya*, *Platananthus potomacensis*, *P. scanicus*, and *P. speirsae*. The connective epidermis in *Archaranthus krassilovii* has numerous anomocytic stomata and widely spaced rounded bases of hairs, the epidermis of its epiconnective bears widely spaced hairs and is devoid of stomata. The epiconnective in *Quadriplatanus* is massive and has anomocytic stomata. Many members of the Hamamelidaceae are characterized by an epiconnective that is longer than thecae. This peculiarity is particularly well expressed in the tribe Hamamelideae (*Loropetalum* R. Brown ex Reich., *Tetrathirium* Benth., *Maingaya* Oliv., and *Embolanthera*). Epiconnectives in these genera are horn-shaped. Among fossil members of the Hamamelidaceae, *Allonia* and *Androdecidua* have massive epiconnectives.

Staminodes of *Bogutchanthus* gen. nov. are situated between mature stamens and perianth elements and probably are partially adnate to them basally. They are similar to mature stamens in shape.

Functionally unisexual flowers of some members of the Platanaceae and Hamamelidaceae can retain rudimentary structures of the opposite sex (underdeveloped stamens (staminodes) in pistillate flowers and rudimentary pistils in staminate flowers). Rare staminodes are present in pistillate flowers of the modern plane tree; the presence of stamen processes that are interpreted as staminodes are recorded in staminate flowers of *Platanus* (Magallón-Puebla et al., 1997). Staminodes are found in pistillate flowers of *Altingia* and *Liquidambar* of the subfamily Altingioideae (Bogle, 1986) and *Rhodoleia* Champ. ex Hook of the Rhodoleioideae (Bogle, 1987). In some modern members of the Hamamelidaceae, bisexual flowers contain both normal stamens and staminodes (e.g., *Maingaya*; Bogle, 1984). There are some indications of the presence of two functionally different circles of androecium (outer circle

with normal stamens and inner circles of staminodes) in tetramerous flowers of *Dicoryphe* and *Hamamelis* and pentamerous flowers of *Ostrearia* Baill. (Magallón-Puebla et al., 1996).

Staminodes are also known in fossil members of the Platanaceae and Hamamelidaceae. The platanaceous *Quadriplatanus* is characterized by a stamen tube formed by adnate stamens and staminodes. This character makes inflorescences of this genus similar to the Turonian inflorescences combining platanaceous and hamamelidaceous characters (Crepet et al., 1992; Crepet and Nixon, 1996).

In fossil Hamamelidaceae, staminodes are known in species assigned or related to the Altingioideae, Hamamelidoideae, and Exbucklandioideae. The synthetic genus *Viltyungia*, which combines characters of these three subfamilies, had bisexual flowers with staminodes that produced numerous pollen grains, smaller in comparison with normally developed pollen grains. In members of the Altingioideae, staminodes are described in *Evacarpa*. In the Hamamelidoideae, they are known in the Santonian–Campanian genus *Archamamelis* and Eocene staminate capitate inflorescences that share several characters with *Hamamelis* and *Corylopsis* Sieb. et Zucc. (Manchester, 1994).

Pollen grains. *Bogutchanthus* gen. nov. is characterized by small reticulate mostly pantocolpate pollen grains. Hexacolpate pollen grains prevail; however, pollen grains with seven, four, and three colpi are present in small amount. All modern and fossil members of the Platanaceae have tricolpate reticulate pollen grains. Although pollen grains of different platanaceous genera are quite similar, some differentiating characters can be named: the apertural type (tricolporate pollen grains in some fossil forms, such as *Hamatia elknekenensis* Pedersen, Crane et Drinnan and *Sarbaya radiata* Krassilov et Shilin, and tricolporoid pollen grains in some species of the modern *Platanus*; unpublished data); the reticulum type; the patterns of meshes within one pollen grain; the peculiarities of the colpus margin; the thickness of the ectexine and its constituting layers, in particular, the share of the foot layer in the total thickness of the ectexine; and the endexine structure (Tekleva and Maslova, 2004; Denk and Tekleva, 2006).

The majority of modern hamamelidaceous genera possess tricolpate pollen grains, similar to those of the Platanaceae in general morphology. Among them, several genera with pantoaperturate pollen grains stand apart. Thus, among modern genera of the Hamamelidoideae, *Distylium* has up to ten rugae or pores in addition to short colpi with rounded extremities, pollen grains of *Matudaea* vary from tetracolpate to 12-rugate, and apertures of *Sycopsis* vary from more or less elongated rugae to pores (Bogle and Philbrick, 1980). In *Parrotia*, pollen morphology also varies: although tricolpate pollen grains prevail, bicolpate, tetracolpate, and porate pollen grains also occur. Both modern and

extinct species of *Parrotia* are known to vary in number of colpi (Binka et al., 2003).

Chunia (Exbucklandioideae) is characterized by tricolpate and tetra- and hexarugate pollen grains. Pantocolpate pollen grains are described in the Cenomanian *Viltyungia* (Maslova and Golovneva, 2000).

Pantocolpate pollen grains are known both in the Hamamelidaceae and in modern and fossil members of the Platanaceae. In the Hamamelidaceae, if pantocolpate pollen grains are known in a genus, they prevail over tricolpate pollen grains; by contrast, in the Platanaceae, tricolpate pollen grains constantly dominate, the appearance of the pantocolpate type is only recorded as an aberration (modern *Platanus occidentalis*, Zavada and Dilcher, 1986; Paleocene *Archaranthus krassilovii*, Maslova and Kodrul, 2003).

Pollen grains of *Bogutchanthus* gen. nov. are finely reticulate, similarly to most Cretaceous–Paleogene and modern members of the Platanaceae and some fossil and modern members of the Hamamelidaceae. Generally, the pattern of the reticulum is uniform over the entire surface of the pollen grain. The margin of the colpus is formed by a continuous sporopollenin rim. This character is also described in *Archaranthus krassilovii*, *Platananthus scanicus*, *P. speirsae*, *P. synandrus*, and some modern members of the Hamamelidaceae (Bogle and Philbrick, 1980).

Bogutchanthus gen. nov. shows no significant differences from fossil and modern Platanaceae and Hamamelidaceae in the structure of the ectexine. The share of the foot layer to the total ectexine thickness (0.37) answers the general trend observed in the Platanaceae: 0.4–0.5 in fossil members and 0.2–0.3 in modern members.

The endexine structure in *Bogutchanthus* gen. nov. is similar to that of the majority of studied fossil Platanaceae, as well as *Archamamelis*, a Cretaceous member of the Hamamelidaceae (Endress and Friis, 1991). The endexine is electron-dense, homogenous and/or granulate in its inner part, relatively thin in the non-apertural region, rather abruptly thickening toward the apertural region, where its inner part becomes more loosely arranged showing distinct granules. Like pollen grains of *Chemurnautia* and *Archaranthus*, *Bogutchanthus* gen. nov. has a bilayered endexine, the layers of which differ in electron density over the entire perimeter of the pollen grain.

The comparison between *Bogutchanthus* gen. nov. and known tetrastaminate members of the Platanaceae shows that *Archaranthus* most closely resembles *Bogutchanthus* in general pollen morphology and endexine ultrastructure. Both genera have a bilayered endexine over the entire pollen grain perimeter, with layers that differ in electron density. *Sarbaya* and *Quadriplatanus* are characterized by a similar finely reticulate sculpture of the pollen surface. However, unlike *Bogutchanthus* and *Archaranthus*, no continuous sporopollenin rim is present demarcating the non-

apertural area and colpi. Unfortunately, the pollen ultrastructures of *Sarbaya* and *Quadriplatanus* have so far been unstudied, thus preventing us from comparing them at the ultrastructural level.

Associated leaves. Remains of *Bogutchanthus* gen. nov. were found in association with leaves of the *Platanus* type (Figs. 1e–1g). The leaf plate is entire, oval or ovate, rarely asymmetrical. The base is cordate or rounded (up to narrowly rounded), occasionally peltate; asymmetrical, the apex is attenuated. The leaf plate margin is toothed, the teeth vary in size and outline from concave-concave to rounded.

Leaves of this morphotype were buried together with staminate inflorescences of *Archaranthus* in the type locality, in the middle part of clays between the “Nizhnii” and “Dvoynoi” coal beds (Maslova and Kodrul, 2003). The additional study of occurrence of plant fossils in other sections of temporary open-pit mines of the Arkhara-Boguchan coal field revealed a stable association between such leaves and inflorescences of *Bogutchanthus* gen. nov. Both these leaves and inflorescences of *Bogutchanthus* gen. nov. occur throughout the plant-bearing clays. Therefore, the inflorescences that are assigned to the genera *Archaranthus* and *Bogutchanthus* gen. nov. and have essentially different micromorphology are proved to associate with leaves of one and the same morphotype. This confirms the necessity of the application of morphological system for dispersed leaves of fossil angiosperms (Krassilov, 1979; Maslova et al., 2005).

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