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New Representative of *Pinus* L. from Jurassic Deposits of Belgorod Region, Russia

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Abstract—A new species of fossil pines, *P. bukatkinii* sp. nov., was found in the Middle Jurassic of Stoilensk open mine (the vicinity of Stary Oskol town, Belgorod Region). Seed cones of the new species possess four key diagnostic characters of representatives of the genus *Pinus* L.: thickened scale apices with apophyses and umbo; trace to the seed scale and bract represents a single unit; resin canals enter the seed scale base abaxially; adaxially convex vascular bundles in the seed scale. The distinctive feature of the new species is a strong sclerification of the seed scale ground tissue. Galleries, made by herbivores, were found in seed cones of *P. bukatkinii* sp. nov., that represents the oldest documented evidence of parasitism on pinaceous seed cones.

Keywords: Jurassic, Pinaceae, morphology, anatomy, systematics, plant damages

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INTRODUCTION

Number of occurrences of anatomically preserved seed cones assigned to the genus *Pinus* is extremely small. One of the earliest representatives of the genus, *Pinus yorkshirensis* Ryberg, Stockey, Hilton, Mapes, Riding et Rothwell, comes from the Lower Cretaceous (Hauterivian-Barremian deposits of Yorkshire, England (Ryberg et al., 2012), other, *P. belgica* Alvin, from the Wealden of Belgium (Alvin, 1960). Only two species are known from the Upper Cretaceous: *P. mutoi* Saiki from the Coniacian of Hokkaido, Japan (Saiki, 1996) and *P. driftwoodensis* Miller et Malinky from the Santonian of New Jersey, USA (Miller and Malinky, 1986). In addition to these four species assigned to the extant genus, in the Cretaceous there were taxa, which exhibited a number of morphological and anatomical features characteristic of *Pinus* seed cones, but distinguished from them to various extent (Miller, 1976; Falder et al., 1998; Taylor et al., 2009). Such cones are assigned to the genera *Pityostrobus* Dutt, *Pseudoaraucaria* Fliche and *Obirastrobus* T. Ohsawa, M. Nishida, H. Nishida (Alvin, 1957; Miller, 1976; Ohsawa et al., 1992). Some researchers argue against the independence of the genus *Obirastrobus* and propose to attribute its representatives to the genus *Pityostrobus* (Smith and Stockey, 2001, 2002). The new species under description is at present only second Jurassic member of the family Pinaceae, for which the anatomical structure is studied. The anatomical structure of the first one, *Eathiestrobus mackenziei* Rothwell, Mapes, Stockey et Hilton from the Kimmeridgian deposits of Black Island, Northeastern Scotland (Rothwell et al., 2012), is primitive, and it differs significantly from the representatives of the genus *Pinus*.

According to some researchers, the genus *Schizolepidopsis* Doweld, appeared in the Triassic and widespread in the Jurassic–Early Cretaceous, should also be attributed to Pinaceae (Harris, 1979; Leslie et al., 2013; Matsunaga et al., 2021; etc.). Anatomical evidence is so far available only for one of the Early Cretaceous representatives of this genus (Matsunaga et al., 2021), relationships of which with the more ancient representatives is not entirely clear.

Pinus bukatkinii sp. nov. is the earliest occurrence of seed cones exhibiting all key anatomical features characteristic of cones of the genus *Pinus*, according to Ch.N. Miller (1976), as well as the earliest occurrence of anatomically preserved reproductive organs of the family Pinaceae.

MATERIAL AND METHOD

The material studied comes from Stoilensk open mine, Belgorod region (the vicinity of Stary Oskol town), where it was collected by Vladimir Vladimirovich Bukatkin (Stoilensky Mining and Beneficiation Plant) in 2001–2002, from a small sandy lens with plant detritus, dated by the Middle Jurassic, supposedly, Bathonian (Bazhenova and Bazhenov, 2022). Fragments of seed cones were preserved predominantly as lignite, but some of them underwent partial

pyritization; in several specimens tissues were partly replaced by white clay matter. Some of coalified cones have excellent anatomical preservation. After cones were collected, their surface was coated with epoxy adhesive to prevent destruction. When the coaly matter of cones is wetted it begins disintegrate, that prevents preparation of thin sections. Cone morphology has been studied using a Leica M165C stereomicroscope with Leica DFC 420C digital camera. The anatomical structure of the cones was studied on transverse and longitudinal fractured surfaces in Tescan SEM, as well as using SkyScan 1172 and Neoscan 80 X-ray Micro Computer Tomography System. Large coalified fragments poorly endure coating with gold and destroyed when a high vacuum mode used, so the low vacuum mode without coating was predominantly applied (BSE detector, 20 kV). Fragments of seed cones and seeds were studied in the high vacuum mode (SE detector, 30 kV) with gold and palladium coating. Seed coat preparations were made using the standard method, by successive immersion in hydrofluoric and nitric acids, and then in KOH solution. Obtained preparations were studied using SEM Tescan and Axioplan-2 light microscope. Pollen grains were studied under SEM Tescan in the high vacuum mode (SE detector, 30 kV).

The material is housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, collection no. 5851.

SYSTEMATIC PALEOBOTANY

Order Pinales

Family Pinaceae Lindley, 1836

Genus *Pinus* L., 1753

Pinus bukatkinii* Bazhenova et Bazhenov, *sp. nov.

Pl. 9, figs. 1–16; Pl. 10, figs. 1–6

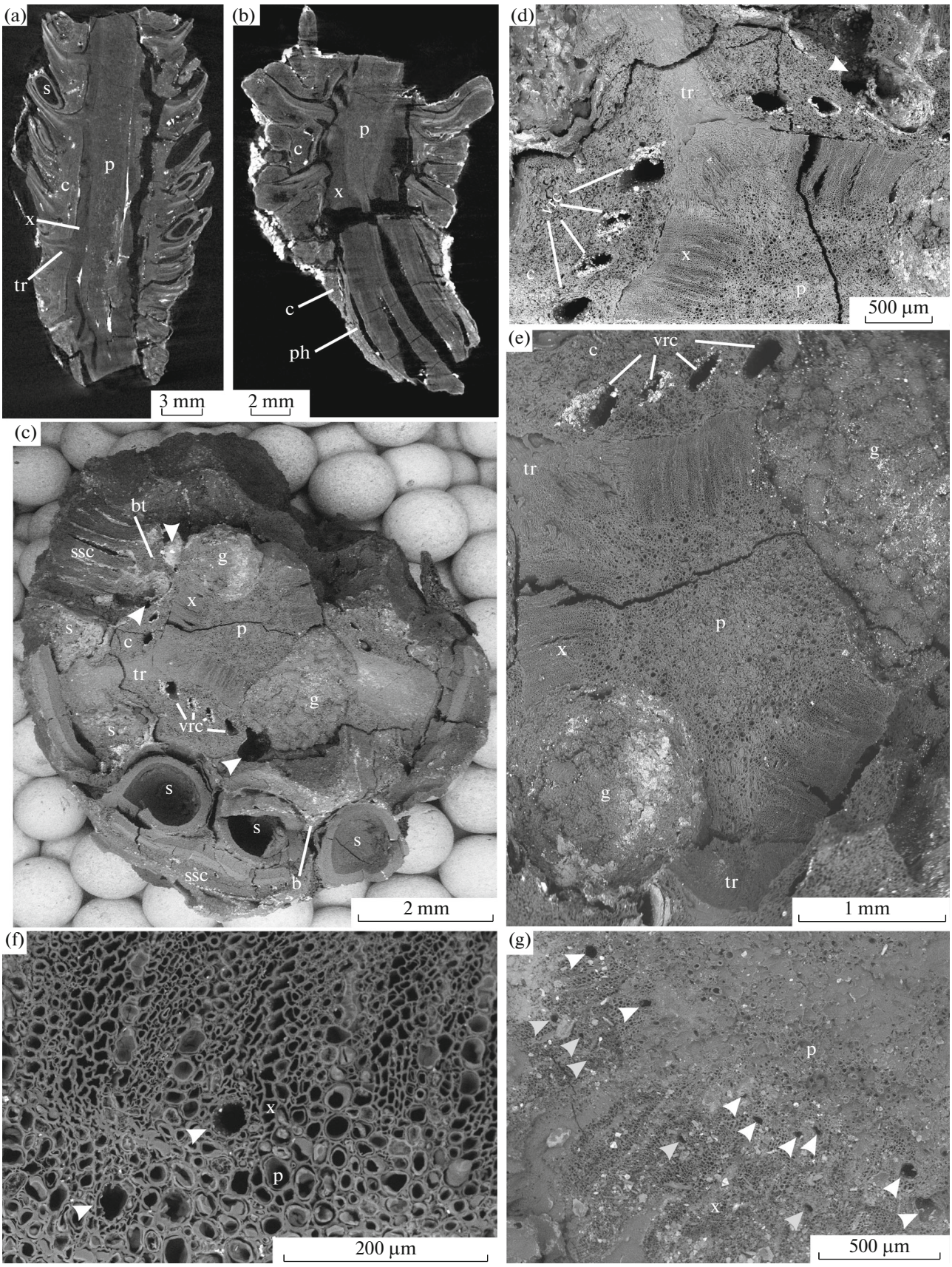
E t y m o l o g y. In honor of V.V. Bukatkin, founder of the museum "Art and Paleontological Center" at Stoilensky Mining and Beneficiation Plant.

H o l o t y p e. PIN no. 5851/9, lignified cone fragment, Stoilensk open mine, the vicinity of Stary Oskol town, European Russia, Middle Jurassic, Bathonian? (Pl. 9, figs. 3, 4); designated here.

D i a g n o s i s. Incomplete cones oblong cylindrical, 19–30 mm in diameter when closed, more than 55 mm long; cone base broadly cuneate, symmetrical, with massive peduncle more than 10 mm long, 5–7.3 mm in diameter. Bract-scale complexes helically arranged. Seed scales oblong to obovoid-oblong, up to 17 mm long, 7–10 mm wide; interseminal ridge well-developed. Apophyses widely rhomboidal to pentagonal with distinctly rounded upper margin, 5–8 mm long, 7–11.4 mm wide, transversely keeled, bearing dorsal transversely oval umbo. Apophyses in lower third of seed cone distinctly raised (up to 3–5 mm high) with protruding slightly recurved umbo; apophysis and umbo less prominent toward apex. Pith 2–2.7 mm in diameter. Secondary xylem forming complete cylinder up to 600 μm thick without grows rings; resin canals near pith area, occasionally forming additional incomplete ring in middle part of xylem. Cortex about 1–2 mm thick, parenchymatose; inner zone with 16–20 vertical resin canals dilated 2–6 times at places of branching. Trace of seed scale and bract single, with sclerified pith. Bract trace detaching from cone-scale complex trace downward then recurving to supply bract. Bract up to 2.5 mm long, parenchymatose. Seed scale vascular bundle branching in middle part of scale to form 12–15 vascular bundles. Vascular bundles initially arranged in one row, then in two rows in apical part of scale. Resin canals abaxial near seed scale base, then abaxial, adaxial, and interfascicular. Ground tissue below vascular bundles strongly sclerified in the proximal half of seed scale. Abaxial hypodermal layer thin, uneven, consisting of one–three rows of small sclerenchyma cells. Adaxial cortex in proximal part of seed scale non-sclerified; in its middle part, containing sclerenchyma nests and thin hypodermal layer of one–three cells; in distal part, non-sclerified. Seeds two per scale, inverted, winged, narrowly ellipsoidal, 2.5–4 mm long, 1.2–1.6 mm wide; wing semi-oval, thickened near seed body; seed including wing up to 9 mm long.

D e s c r i p t i o n (Figs. 1–7). The collection contains three fragments of cone bases 22 mm (no. 5851/4), 29 mm (no. 5851/8) and 44 mm (no. 5851/6) long, 20, 15 and 33 mm wide respectively, and also fragments of middle parts of cones 33–47 mm long, 27–32 mm wide, and one large fragment with preserved apex, but without base (Pl. 9, figs. 1–16; Fig. 1a), 55 mm long, 19 mm wide. Since some exemplars are slightly flattened, their width is somewhat larger than real diameter, which didn't exceed 30 mm. Both partially closed and opened seed cones fragments are presented. Based on sizes and proportions of the cones, they were oblong cylindrical, more than 55 mm long, 16–30 mm in the diameter. Cone bases are broadly cuneate (Pl. 9, figs. 1, 2, 9, 10), bract-scale complexes are spirally arranged.

The stalk (well preserved only in one exemplar) is straight, massive, more than 10 mm long, about 5–7.3 mm in the diameter (Pl. 9, figs. 9, 10; Figs. 1b; 6c). The stalk pith is about 1200 μm in the diameter, composed of thick-walled cells 8–40 μm in the diameter, 40–120 μm long, often filled with organic content (Pl. 10, figs. 1, 4; Figs. 6c, 6h). A protoxylem is endarch (Pl. 10, fig. 4). A secondary xylem forms continuous ring about 1700 μm thick; consists of tracheids up to 20 μm in the diameter. The pitting of radial tracheids walls is uniseriate, pits are usually contiguous, but occasionally the distance between neighboring pits is 2–6 μm; pits with alternate arrangement may occur on tracheids ends (Pl. 10, figs. 6, 7). The pits are circular, 9–11 μm in the diameter, their border is 3–6 μm wide, an aperture is rounded, 2.5–3 μm in the diame-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ter. The pitting of tangential walls is uniseriate. Xylem rays are 1–11 cells high, predominantly uniseriate, but biseriate areas are also found (Pl. 10, figs. 2, 5; Figs. 5j, 5k). Ray cells are 15–120 μm long, 15–20 μm high, with relatively thin even walls (Fig. 5k). Horizontal ray-cell walls with simple pits about 2 μm in the diameter, end walls are smooth, without pitting (Pl. 10, fig. 3). Cross-fields with one—three piceoid or cupressoid pits 4–5 μm in the diameter (Pl. 2, fig. 5; Fig. 5k). Ray tracheids were not found. Vertical non-traumatic resin canals are rare, up to 180 μm in the diameter, with large thin-walled epithelial cells; they are scattered across the entire width of the xylem ring (Pl. 10, figs. 1, 4). A phloem is about 150 μm wide (Figs. 6c, 6i). The phloem cells are 4–10 μm in the diameter, arranged in indistinct radial rows within small arrays, separated by radial rows of large idioblasts (about five in one row) up to 40 μm in the diameter. A cortex is up to 1250 μm wide, partially preserved, and consists of parenchymatose cells 30–50 μm in the diameter; resin canals are about 100 μm in the diameter, lined with thin-walled epithelial cells (Figs. 6c, 6j).

The cone axis in the middle part is about 6.5 mm in the diameter, with a well-developed pith 2–2.7 mm in the diameter, composed of thick-walled cells 5–60 μm in the diameter and surrounded by a xylem ring 0.6–1.10 mm thick (Figs. 1a–1e; Figs. 3a, 3c, 3f). The secondary xylem of the cone axis forms an entire cylinder. Tracheids in the cross-section are from rounded to rounded-polygonal, 5–20 μm in the diameter (Fig. 1a). Xylem rays are uniseriate. Ray cells are up to 20 μm long, 40 μm wide. Vertical non-traumatic resin canals, usually about 20 μm (up to 95 μm) in the diameter, are visible near the pith (Fig. 1f, 1g). Two specimens possess an additional incomplete ring of resin canals near the middle part of the xylem ring (Fig. 1g). Growth rings are not pronounced, but probably, this additional ring of resin canals marks a boundary between two grows rings. A phloem is not preserved. The pith is 1–2 mm thick, consists of predominantly thick-walled parenchyma cells 10–50 μm in the diameter, homogenous. Only a thin outer part of the cortex (up to four cells thick) consists of relatively small cells up to 25 μm in the diameter (Fig. 1d). In the cortex inner zone there is a ring of 16–20 vertical resin canals 90–300 μm in the diameter, which can dilate significantly at the point of branching (up to 800 μm).

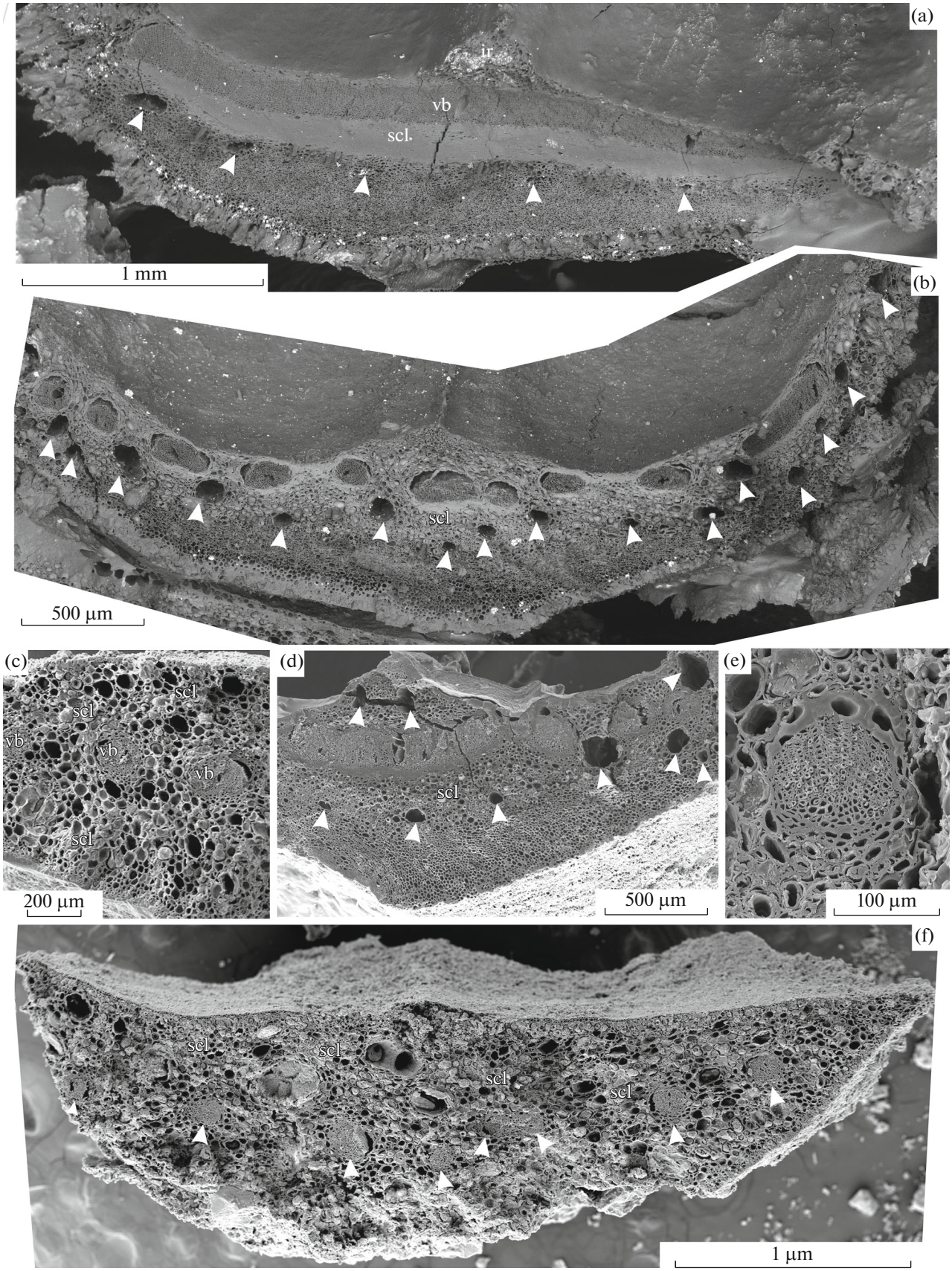
Vascular bundles, supplying bract-scale complexes, depart from the axis vascular cylinder under more or less straight angle; each of them is accompanied by two resin canals, which branch off from two vertical resin canals in the inner cortex (Figs. 1a–1d; 3a–3c, 3f; 7a, 7b). The vascular bundles are endarch, with sclerified pith. They are initially rounded, 0.7–1.2 mm in the diameter (Fig. 1e), but soon are divided on an adaxial arch-shaped bundle, supplying the seed scale, and small rounded abaxial bundle, vascularizing the bract (Figs. 1b, 1d; 3f; 6b, 6f, 6g). The bundle, vascularizing the bract, departs (in the part of the cortex between resin canals) primarily downwards at an angle close to 90°, then flattens out and follows parallel to the bundle, supplying the seed scale; at the place of bract separation from the seed scale this bundle sharply bents upwards and enters the bract base.

The bract near its base is more or less triangular in transverse section, 2.5–3 mm wide, up to 1.5 mm thick, separating from the seed scale base starting from margins (Figs. 3d, 3g); its free part is relatively short, up to 2.5 mm, the bract cortex is parenchymatose, resin canals are located on the sides of the vascular bundle (Fig. 3d).

Seed scales are woody, up to 17 mm long, 3–4 mm wide at their base, about 1.3–2 mm thick, 7–10 mm wide in their middle part, dilated near apophysis (Figs. 2a, 2b, 2d, 2f; Fig. 3c; Fig. 6e). Apophyses are mainly transversally-rhombic to pentagonal, with rounded upper margin, 7–11.4 mm wide, about 5–8 mm high. At the cone bases they are strongly raised (3–5 mm), pyramidal, with a distinct transverse keel, bearing convex transversally-rhombic dorsal umbo (Pl. 9, figs. 1, 2, 7, 9, 10, 13, 14) 2–2.5 mm wide, slightly bent downward. It is impossible to establish the presence/absence of mucro. Nearer to the apical part of the cone, the apophyses become sligtly convex; the configuration of an umbo is unclear (Pl. 9, figs. 3, 4).

Seed scales in the middle part of a cone depart from the cone axis under an angle 40–45º (Fig. 1a). The vascular bundle at the seed scale base is flattened, 2–2.5 mm wide, 200–270 μm height. The ground tissue below the vascular bundle represents for the most part a continuous massive of sclerenchyma up to 300 μm thick, composed of cells 20–30 μm in the diameter (Fig. 2a; Fig. 3a–3g). Between this tissue and the abaxial cortex, there is a row of resin canals up to 90 μm in the diameter. Large resin canals up to 90 μm in the diameter are also presented on the sides of the vascular bundle (Fig. 6a). The resin canals are lined by a single-layered epithelium (Fig. 6d). The epithelial

Fig. 1. *Pinus bukatkinii*, sp. nov.: (a) paratype PIN no. 5851/8, longitudinal tomogram of seed cone fragment; (b, g) paratype PIN, no. 5851/4: (b) longitudinal tomogram of the seed cone base; (g) vertical resin canals in xylem of the seed cone axis, forming two rings—the complete near pith (noted by white arrows) and the additional incomplete (marked by grey arrows), SEM; (c–f) paratype PIN no. 5851/2, SEM: (c) transverse fracture of the seed cone, vertical resin canals in the cortex of the cone axis, dilated at place of branching, are visible, marked by arrows; (d) detail of (c), normal vertical resin canals and the canal, extended at place of branching (marked by white arrow), are visible; (e) detail of (c), pith surrounded by the xylem ring; (f) vertical resin canals in the xylem of cone axis, located near the pith (marked by with arrows). Legend: (bt) bract trace, (c) cortex, (g) gallery, (p) pith, (ph) phloem, (ssc) seed scale, (tr) single trace to the bract and seed scale, (vrc) vertical resin canals, (x) xylem.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cells are thin-walled, longitudinally elongated, up to 20 μm wide. Cells directly adjacent to epithelial cells are not sclerified, 20–40 μm in the diameter in transverse section, up to 110 μm long.

The abaxial cortex below resin canals is parenchymatose (the cells diameter is 10–30 μm), the outer part of the abaxial cortex is formed by a single layer of large, columnar, relatively thin-walled cells up to 150 μm high, up to 50 μm wide; the cells are almost perpendicularly orientated to the surface of the seed scale and usually filled with contents, in the marginal zones being replaced by a thin (one–two cells thick) layer of hypodermal fibers (Fig. 2a; Fig. 6a). The adaxial cortex is thin, no more than 50 μm, parenchymatose, cells are 5–20 μm in the diameter. In the central part of a seed scale, there is a distinct interseminal ridge separating two seed cavities (Fig. 2a; Figs. 3a–3c). It is initially wide, connected with the cone axis, near the middle of seed cavities separates from the axis and becomes triangular in transverse section, about 400 μm high, approximately 500 μm wide near base, consists of thick-walled parenchyma cells 5–30 μm in the diameter., The ridge gradually becomes lower and narrower and completely disappears towards the upper third of the seed scale.

The flattened vascular bundle begins to split into separate bundles at the level of the middle of seed cavities, or immediately behind them. The resulting vascular bundles are arranged in one row; a wider central vascular bundle is usually recognized (Figs. 2b, 2d).

Behind seed cavities, approximately in the middle part, the seed scale is 7–10 mm wide, crescent-shaped in cross-section; the vascular bundles of the seed scale reach their maximum number of 12–15. The bundles are collateral, rounded or reniform, distinctly convex from the phloem side, with relatively well-definite tracheids rows and poorly distinguishable xylem rays, without resin canals (Figs. 2c, 2e). The vascular bundles in the middle part of a seed scale are up to 200 μm wide, 120–150 μm high. Tracheids are thick-walled, up to 10 μm in the diameter. Large sclerified arrays in the ground tissue accompany vascular bundles (Figs. 2b, 2e, 2f). The resin canals in the abaxial cortex are predominantly small, up to 50–100 μm in the diameter; the adaxial cortex of the seed scale gradually thickens up to 200–250 μm (Figs. 2b, 2c; Fig. 3c), adaxial resin canals of different sizes appear in it; also occasionally de novo resin canals are observed in the interseminal ridge (Fig. 2d). As the adaxial cortex of the seed scale thickens in distal direction, the boundary between the ground parenchyma and cortex is erased, numerous randomly arranged sclerenchyma nests appears in tissues of the seed scale; a thin layer of hypodermal fibers 2–3 cells thick is formed in the outer part of the abaxial and adaxial cortex; resin canals are evenly distributed in the scale tissues (Fig. 2c).

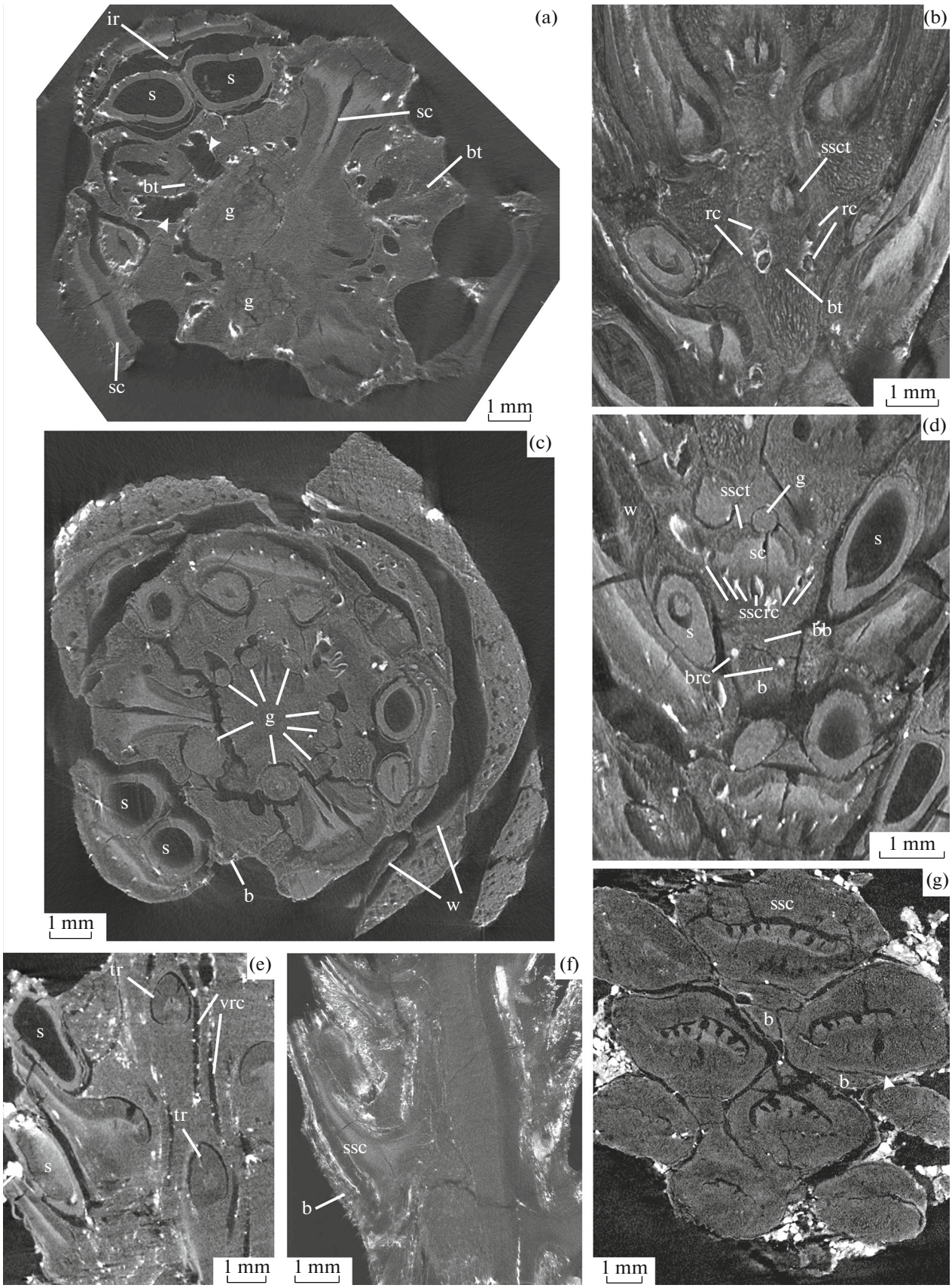
Closer to the apophysis base, the seed scale thickens on overage to 1450 μm and becomes subtriangular in cross-section. The adaxial cortex here is thickens up to 550 μm. The quantity of resin canals, which are arranged here randomly, increases. The resin canals are up to 100 μm in the diameter. The abaxial cortex is thickening to 900 μm. Small scattered abaxial resin canals are also presented. The vascular bundles start to loose their horizontal orientation and form small arquate groups (Fig. 2f).

There is no sclerification at the apophysis base (Fig. 6e). The vascular bundles become slightly smaller, 75–200 μm in the diameter, arranged in two rows in the central part. Resin canals are mainly small, 50–100 μm in the diameter, randomly distributed, but clustered predominantly around vascular bundles. The resin canals in the apophysis can occasionally dilate up to 250 μm.

Seeds are narrowly-ellipsoidal, 2.5–4 mm long, 1.2–1.6 mm wide, with a pointed micropylar end, rounded chalaza, and well-developed semi-oval persisting wing (Figs. 4a–4c). The seed length including the wing is up to 9 mm. The seed wing is strongly thickened near the chalaza (Fig. 3b; Fig. 4b). The testa consists of sarcotesta, sclerotesta, and endotesta (Fig. 4g). The sarcotesta is thin, about 100 μm. Sclerotesta is unevenly developed, ribbed, with maximal thickness 280 μm, in thinner areas—100 μm. Vascular bundles in the testa are absent. The nucellus is free from the integument in its upper part, thinly cutinized, 2.3 mm long, 1.2 mm wide (Figs. 4d–4f). The nucellus cells are longitudinally elongated, rectangular, up to 40 μm long, up to 20 μm wide (Fig. 4i). The megaspore membrane is about 3 μm thick, possessing alveolar structure (Fig. 4j).

Comparison and remarks. The new species demonstrates all the features characteristic of the genus *Pinus* L. cones, according Ch.N. Miller (1976):

Fig. 2. *Pinus bukatkinii*, sp. nov., SEM: (a) paratype PIN, no. 5851/2, transverse fracture of seed scale on the level of seed cavities, single flattened vascular bundle and row of resin canals below it (marked by white arrows) are visible; (b, f) paratype PIN, no. 5851/9: (b) transverse fracture of the seed scale in the middle part, numerous vascular bundles and resin canals that have lost their single row arrangement (marked by white arrows) are visible; (f) transverse fracture of the seed scale below apophysis, vascular bundles (marked by white arrows) began to lose their single-row arrangement, abaxial and adaxial resin canals are visible; (c–e) paratype PIN, no. 5851/1: (c) fragment of the transverse fracture of seed scale in the middle part, thin abaxial and adaxial hypoderm, small sclereid nests in the abaxial and adaxial cortex, as well as in the ground parenchyma, are visible; (d) fracture of the seed scale fragment behind seed cavities, sclerified ground tissue and resin canals moving to the adaxial position (marked by white arrows) are visible; (e) vascular bundle, surrounded by sclerified tissues. Legend: (ir) interseminal ridge, (scl) sclerification, (vb) vascular bundle.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dilated apices of seed scales; the single rounded trace to the bract and seed scale; resin canals, entering the base of a seed scale only abaxially; adaxially convex vascular bundles of a seed scale. Also, representatives of this genus have vertical resin canals in the cone axis xylem and small subtriangular bract separating starting from margins.

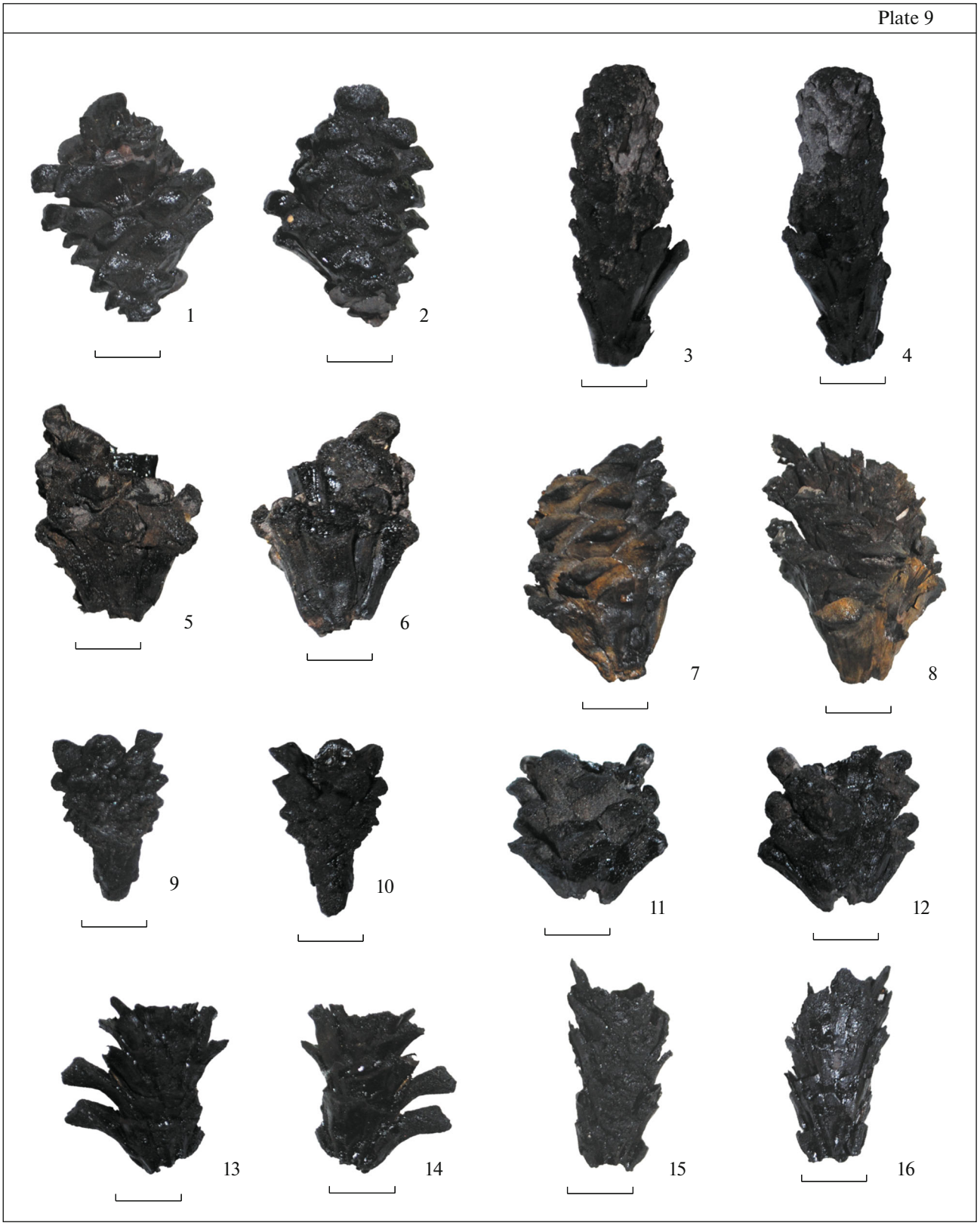
Morphological features of *P. bukatkinii* sp. nov. do not allow attributing it to any of two modern subgenera of the genus *Pinus* (*Pinus* or *Strobus*). Strongly raised apophyses with prominent dorsal umbo are known in representatives of both subgenera, for example, in *Pinus gerardiana* Wallich ex D. Don (subgenus *Strobus*) and *Pinus sabiniana* Douglas ex D. Don (subgenus *Pinus*), so this character is not significant. Oblong cylindrical seed cones are also known in representatives of both subgenera (Farjon, 2010).

On their anatomy, the cones studied are more similar to the representatives of subgenus *Pinus*. For example, vascular bundles in the middle part of the seed scale in *P. bukatkinii* sp. nov. are arranged in one row, whereas for subgenus *Strobus* their two-rowed arrangement is indicated (Yamada and Yamada, 2017). The absence of sclerification of the resin canal epithelial cells and adjacent ring of cells in the seed scale is characteristic of representatives of both subgenera (Yamada and Yamada, 2017). The non-sclerified cortex of the cone axis in combination with a sclerified cortex of the seed scale is the feature characteristic for cones of subsection *Ponderosae*, subgenus *Pinus*, as well as for some representatives of *Contortae* and *Australes*, whereas in representatives of subgenus *Strobus*, the sclerification of the cone axis and scale is absent (Radais, 1894; Shaw, 1914; Miller, 1976). The thickened base of a seed wing is also characteristic of some representatives of the subgenus *Pinus* (Shaw, 1914; Miller, 1978).

From all fossil and modern pines, for which the anatomical structure has been studied, the new species differs by highly developed sclerification of the ground tissue in seed scales directly under vascular bundles; moreover, the feature can be traced from the very base of the seed scale (pith cells of the brat-scale complex single bundle are sclerified). The strong sclerification of the ground tissue is characteristic of some representatives of the genus *Pityostrobus* and the modern *Pseudolarix* Gordon (Miller, 1976). For example, in *Pityostrobus hokodzensis* Ratzel, Rothwell, G. Mapes, R.H. Mapes et Doguzhaeva from the Lower Cretaceous deposits of North Caucasus, Russia, sclerification is also observed in the seed scale trace and distributed in a similar way in its tissues (Ratzel et al., 2001). In *Pityostrobus hallii* Miller from the Upper Cretaceous of Maryland, USA, the sclerenchyma forms a continuous array in the ground parenchyma and moves distally to the adaxial side, forming an adaxial hypoderm (Miller, 1974). According to Miller, among the modern pines, the sclerification of a ground parenchyma can occur only in the dilated apex of the seed scale of representatives of the subgenus *Pinus* (Miller, 1976). Among fossil pines, the presence in the parenchymatose outer cortex of the cone axis and in the ground parenchyma of the seed scale base of of sclereids nests, which are further transformed into separate strands to form adaxial hypoderm in the distal part, was indicated only for *Pinus cliffwoodensis* from the Santonian of New-Jersey, USA (Miller and Malinky, 1986). Unfortunately, the sclereid nests themselves were not illustrated in this work, but, judging by the description, the character of sclerification in *Pinus cliffwoodensis* sufficiently differs from such in *P. bukatkinii* sp. nov. Unlike the new species, *P. cliffwoodensis* has ovoid-conical cones with a pith and xylem which are about twice as large in diameter, with distinct grows rings and resin canals just distal to the grows ring; an interseminal ridge is absent, the presence/absence of a wing in the seed is not established.

The Lower Cretaceous *Pinus yorkshirensis* from the Hauterivian-Barremian deposits of Yorkshire, UK (Ryberg et al., 2012) and *P. belgica* from the Wealden of Belgium (Alvin, 1960) are closest in age to the new species. Of these, *P. yorkshirensis* is most similar to *P. bukatkinii* sp. nov. But in *P. yorkshirensis* cones are conical, whereas in the new species they are cylindrical, with more raised apophyses. Moreover, resin channels in the cone axis xylem of *P. bukatkinii* sp. nov. are more frequent, sometimes located not only near the pith, but also in the middle part of the growth ring. Resin canals in *P. yorkshirensis* ran in the middle part of the cone axis cortex; the outer cortex is sclerified, in contrast to the cortex of *P. bukatkinii* sp. nov. The bract in *P. yorkshirensis* supposedly is very short; resin canals are poorly preserved. The authors point to

Fig. 3. *Pinus bukatkinii*, sp. nov., X-ray tomograms: (a, f) paratype PIN, no. 5851/2, (a) transverse section demonstrating the main details of the seed cone anatomy and two large galleries; (f) radial section demonstrating separation of the bract trace from the single trace; (b–d) holotype PIN, no. 5851/9: (b) tangential section, separation of the bract trace from the single trace and branching of pair of resin canals (upper branches enter the seed scale, lower branches enter the bract); (c) transverse section demonstrating the main details of the seed cone anatomy and galleries of various diameters; (d) tangential section, the bract separating from the seed scale may be observed; (e) paratype PIN, no. 5851/8, tangential section, single traces of a seed scale and bract are visible; (g) paratype PIN, no. 5851/4, tangential section, sterile scales with bracts separating from them are visible at the cone base. Legend: (b) bract, (bb) vascular bundle of the bract, (brc) resin canals of the bract, (bt) bract trace, (g) gallery, (ir) interseminal ridge, (ph) phloem, (s) seed, (sc) sclerification, (ssc) seed scale, (ssct) trace to the seed scale, (sscrc) resin canals of the seed scale, (tr) single trace to the bract and seed scale, (vrc) vertical resin canals, (w) wing.



Explanation of plate 9

Figs. 1–16. *Pinus bukatkinii*, sp. nov., fragments of cones, LM; (1, 2) paratype PIN no. 5851/6; (3, 4) holotype PIN no. 5851/9; (5, 6) paratype PIN no. 5851/7; (7, 8) paratype PIN no. 5851/3; (9, 10) paratype PIN no. 5851/4; (11, 12) paratype PIN no. 5851/5; (13, 14) paratype PIN no. 5851/1; (15, 16) paratype PIN no. 5851/2; scale bar length 1 cm; the vicinity of Stary Oskol town, Middle Jurassic.

their marginal position, while in the new species they are located close to the vascular bundle. Adaxial resin canals are absent in *P. yorkshirensis* seed scale. The nature of the seed scale sclerification is also different: a strong sclerification is observed below the resin canals, as well as in the marginal zones of the seed scale, where all tissues are sclerified. The type of the bract/seed scale trace divergence is unknown for *P. yorkshirensis*.

In *Pinus belgica* from the Wealden of Belgium (Alvin, 1960), cones are oval-conical, the pith and wood are somewhat more massive than in *P. bukatkinii* sp. nov. In addition, the outer cortex of the cone axis in *P. belgica* is sclerified; sclereids were found also in the inner cortex. The hypoderm of the seed scale in this species was strongly sclerified, and interseminal ridge was supposedly absent. Moreover, seeds in *P. belgica* mach larger, than in the new species (the seed body length reaches 9 mm).

In *Pinus mutoi* from the Coniacian of Hokkaido, Japan (Saiki, 1996), cones are cylindrical, with raised apophyses, but they mach larger than in the new species, up to 20 cm long and 6 cm in the diameter. In addition, the outer cortex of the cone axis in *P. mutoi* is sclerified, seed scales are without the interseminal ridge, seeds are almost spherical in plane, and the length of seed wing is only half of length of the seed scale. Unfortunately, some anatomical characters have not been preserved, which makes comparison difficult.

Among Cenozoic species, the following ones have parenchymatose outer cortex of the cone axis in combination with sclerified cortex of the seed scale: *P. driftwoodensis* Stockey from the Eocene of British Columbia and *P. escalantensis* Banks, Ortiz-Sotomayor et Hartman from the Oligocene of British Columbia, Canada (Banks et al., 1981; Stockey, 1983), *P. avonensis* Miller from the Oligocene of Montana, (Miller, 1969), *P. buchananii* Underwood et Miller from the Oligocene of Washington (Underwood, Miller, 1980), and *P. matthewsii* McCown, Stockey et Schweger from Pliocene of Yukon, Canada (McKown et al., 2002). Of these, *P. driftwoodensis* and *P. escalantensis*, possessing cylindrical cones with protruding apophyses, are the most similar to P. *bukatkinii* sp. nov. (Banks et al., 1981; Stockey, 1983).

The difference between the new species and *Pinus escalantensis* is that in the latter cones are significantly longer and narrower, the bract is sclerified, vertical resin canals in the xylem are located not near the boundary with a pith, but about on one third of the distance between the inner and outer borders of the xylem; they supposedly mark the boundary between growth rings. Moreover, the pith and vascular cylinder in *P. escalantensis* are three times wider than in the new species, and vertical resin canals are presented in the xylem of trace to the bract-scale complex. Cortical resin canals show no significant dilation at the point of branching. Seeds in *Pinus escalantensis* were not preserved.

In *Pinus driftwoodensis* the cones are somewhat smaller, resin canals in the cone axis xylem mach larger and more frequent than in the new species. The resin canals in the cortex of the cone axis do not dilate as much as in the new species, the interseminal ridge is absent, and resin canals are observed in the entire trace of bract-scale complex. In addition, the resin canals throughout almost the entire length of the seed scale are abaxial in contrast to the new species. The presence/absence of wing in seeds is unknown.

Other species with parenchymatose outer cortex of the cone axis significantly differ from the new species on the morphology, because they have conical cones with non-protruding apophyses.

Other Cenozoic species: *Pinus prinstonensis* Stockey and *P. arnoldii* Miller from the Eocene of British Columbia (Stockey, 1983; Klymiuk et al., 2011), *P. wolfei* Miller from the Eocene of Washington, USA (Miller, 1974) and *P. burtii* Miller from the Miocene of Massachusets, USA (Miller, 1978) have a strongly sclerified outer cortex of the cone axis and in the whole significantly differ from the new species on their morphology and anatomy. Of them, only *P. prinstonensis* has cylindrical cones.

M a t e r i a l. 9 ex., preserved as lignified fragments of seed cones.

ASSOCIATED POLLEN

Nine pollen grains found on the surface of holotype seeds. (Figs. 5a–5g). Pollen grains are bisaccate, bilaterally symmetrical, heteropolar. The corpus is elliptical or circular in polar view, plano-convex in lateral view, 57 (49–67.7) × 42.6 (41.2–58) μm (width x length). The sacci are elliptical in polar view, biconvex in lateral view, both sacci are of the similar size and shape, they are considered here as left and right sacci for convenience, the left saccus is 55.9 (48.9–66.4) × 20.6 (13.6–37.3) μm, right saccus is 55.2 (51.5–57.8) × 22.2 (10.8–38.1) μm. A thinned area on the distal side of the corpus represents a leptoma. One pollen grain from the distal view shows a leptoma of 5 μm wide with a smooth folded membrane (Fig. 5f). The cappa is granulate or microverrucate, the sculpture elements are from 0.3 to 0.5 μm (Figs. 5a–5d, 5g). The sacci are foveolate (Figs. 5e, 5f).

Three pollen grains found on the adaxial surface of the holotype seed scale. (Figs. 5h, 5i). One pollen grain from the proximal view (Fig. 5h). The overall description is similar; the corpus is 60.3 μm wide and 47.5 μm long, the left saccus is 65.1 × 18.3 μm, right saccus is 59 × 17 μm. This pollen grain differs consid-

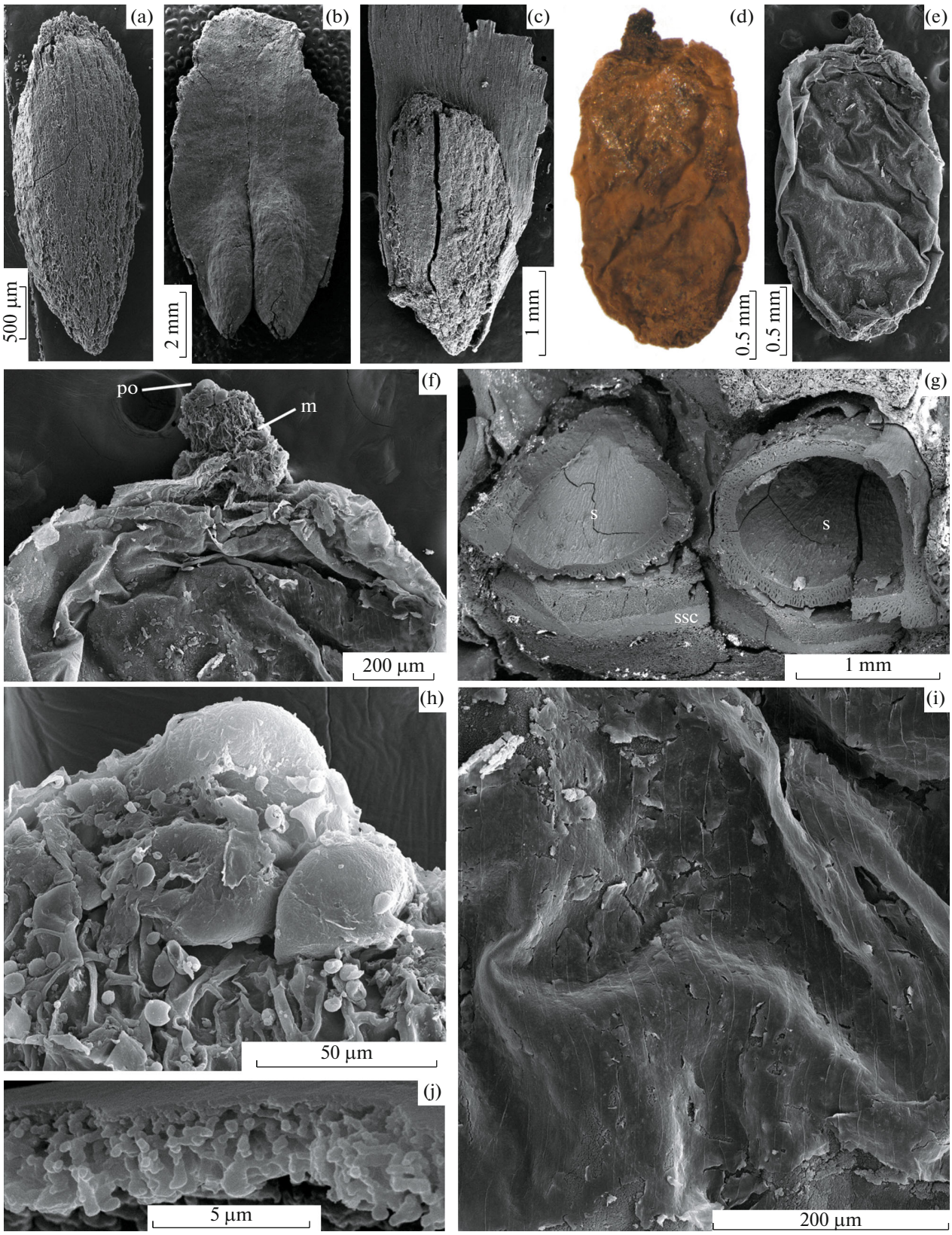


Fig. 4. *Pinus bukatkinii*, sp. nov.: (a–c) holotype PIN, no. 5851/9, SEM: (a) seed with removed sarcotesta, the ribbed surface of sclerotesta is visible; (b) two winged seeds in dorsal view, (c) seed in ventral view; (d, e, h–j) paratype PIN, no. 5851/5, (d) nucellus with the megaspore membrane, LM; (e) nucellus with the megaspore membrane, SEM; (f) detail of (e), the nucellus apex with micropyle; (h) detail of (f), the micropyle with bisaccate pollen grain; (i) cuticle of the nucellus; (j) megaspore membrane on the transverse fracture; (g) paratype PIN, no. 5851/2, transverse fracture of the seed scale with seeds, SEM. Legend: (m) micropyle, (po) pollen grain, (s) seed, (ssc) seed scale.

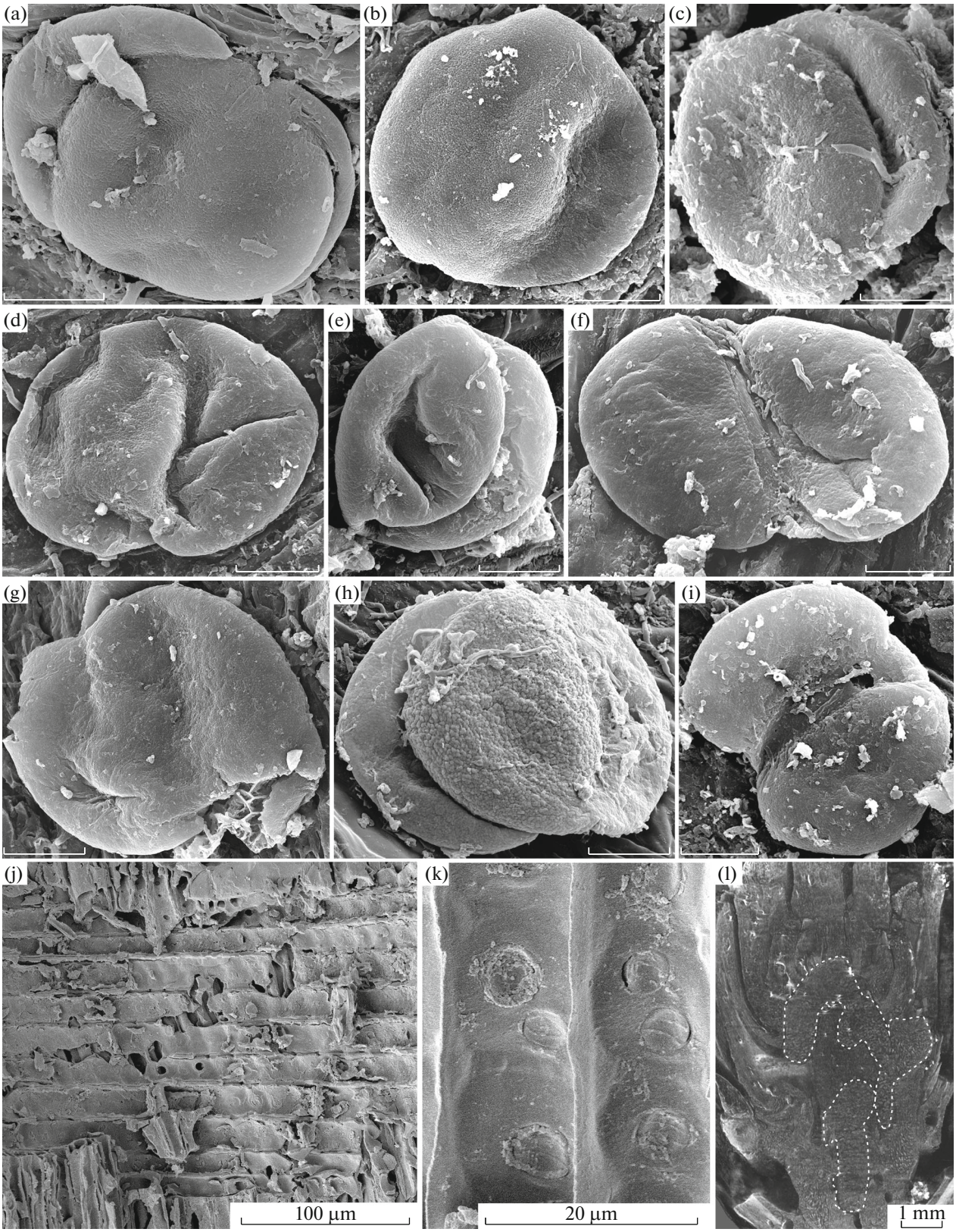


Fig. 5. *Pinus bukatkinii*, sp. nov.: (a–i) pollen grains from surfaces inside the holotype PIN, no. 5851/9, SEM: (a–g) pollen grains, found on the surfaces of seeds; (h, i) pollen grains, found on the adaxial surface of seed scale; (a–d, g, h) pollen grains in proximal view, on (g) inner structure (endoreticulations) of the saccus at the break is seen; (e) pollen grain in the lateral view; (f, i) pollen grains in the distal view, leptoma is seen. Scale bar length 20 μm; (j–k) paratype PIN, no. 5851/4, SEM: (j) xylem ray on the radial fracture of the seed cone peduncle xylem; (k) detail of (j), cross-fields with piceoid pitting are visible; (l) holotype PIN, no. 5851/9, longitudinal tomogram shows large gallery giving branches (circled with dotted line) and turning backward near the cone apex.

erably in the greater granule size of the exine sculpturing, the granules are about 1–1.4 μm (Fig. 5h).

Two pollen grains from the distal view (Fig. 5i). The overall description is similar; the corpus is 46.8 and 49 μm wide and 51.6 μm long, the left saccus is 52.9 × 23.7 μm and ? × 29.7 μm, right saccus is 50.8 × 32.5 μm.

A pollen grain from the micropyle. Only sacci are visible in this pollen grain (Fig. 4h), they are similar to those of the pollen grains from seed surfaces.

GALLERIES

In the cone axes of two cone fragments of *Pinus bukatkinii* sp. nov., an evidence of damage by phytophages was found, represented predominantly by longitudinal galleries of various diameters (400–1000 μm), affecting manly the outer part of xylem and phloem of the cone axis and traces vascularizing cone scales; at the same tame, seeds and scales are not damaged. The galleries are filled with a dense accumulation of pellets mixed with a frass. In both cone fragments, two relatively large galleries about 1000 μm in the diameter are observed, following more or less along the cone axis (Figs. 1c, 1e; 3a, 3c). The cone no. 5851/2 exhibits only supposed imago boring. In the cone no. 5851/9 it can be traced that the gallery follows from its base towards the apex where it makes U-turn and goes to the cone base. Much narrower sinuous galleries depart from a large one; they are orientated both transversally and longitudinally (Fig. 3c). Some of them enter the seed scales affecting xylem (Fig. 3d). The sizes of pellets are related to the diameter of galleries. In the large galleries (1000 μm in diameter), the maximal pellet length is 200 μm, whereas in the smallest galleries (up to 400 μm in the diameter), the maximum pellet length is 80 μm. The large gallery extending from the axis base and turning towards its base, most probably, is an uterine passage, since smaller ones (supposedly larval) galleries diverge from it. The difference lies in the fact that the female of *Conophtorus* Hopkins leaves a cone near the apex, whereas in the fossil cones, the large gallery changes direction at the apex and again goes to the base (Fig. 5l).

In the fossil record, similar galleries are known in pinaceous cones *Pityostrobus milleri* Falder, Rothwell, G. Mapes, R.H Mapes et Doguzhaeva from the Early Cretaceous of Caucasus, Russia, compared with borings of the modern North American species *Conophthorus resinosae* Hopkins (Falder et al., 1998). Galleries were also found In *Pityostrobus hokodzensis* from the same locality, but, apparently, they were abandoned by another phytophage (Ratzel et al., 2001). Two large longitudinal galleries in the cone of *Pinus escalantensis* from Oligocene of British Columbia, Kanada (Banks et al., 1981) are also known. In all these cases there is no direct evidence that the cones were damaged by bark beetles, since the phytophages themselves have not been preserved. At the same time, the oldest reliable find of a bark beetle is known from the Early Cretaceous of Sudan (Kirejtshuk et al., 2009). Based on the type of damages in cones of the new species, we believe that bark beetles were the most probable pests of this ancient pine.

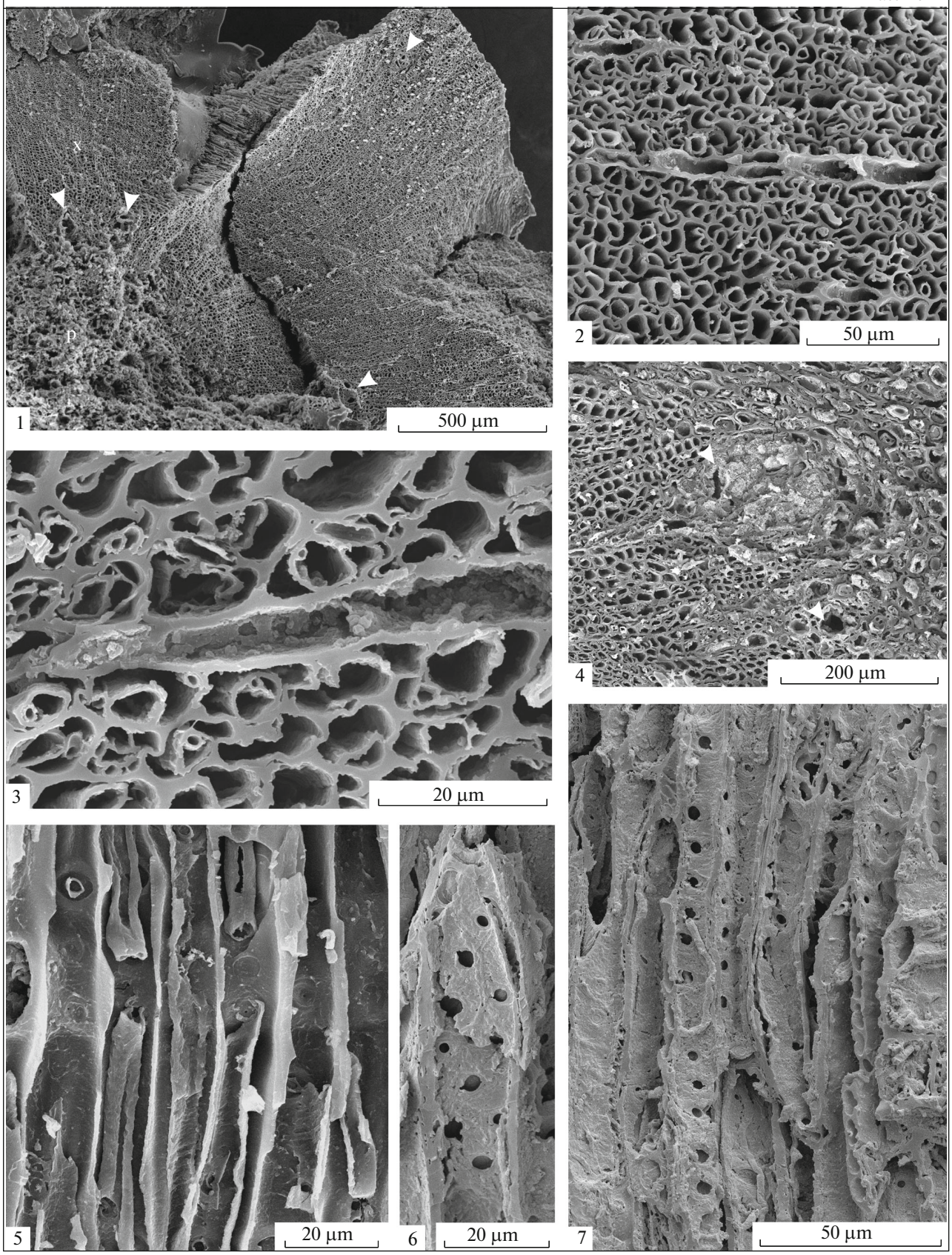
DISCUSSION

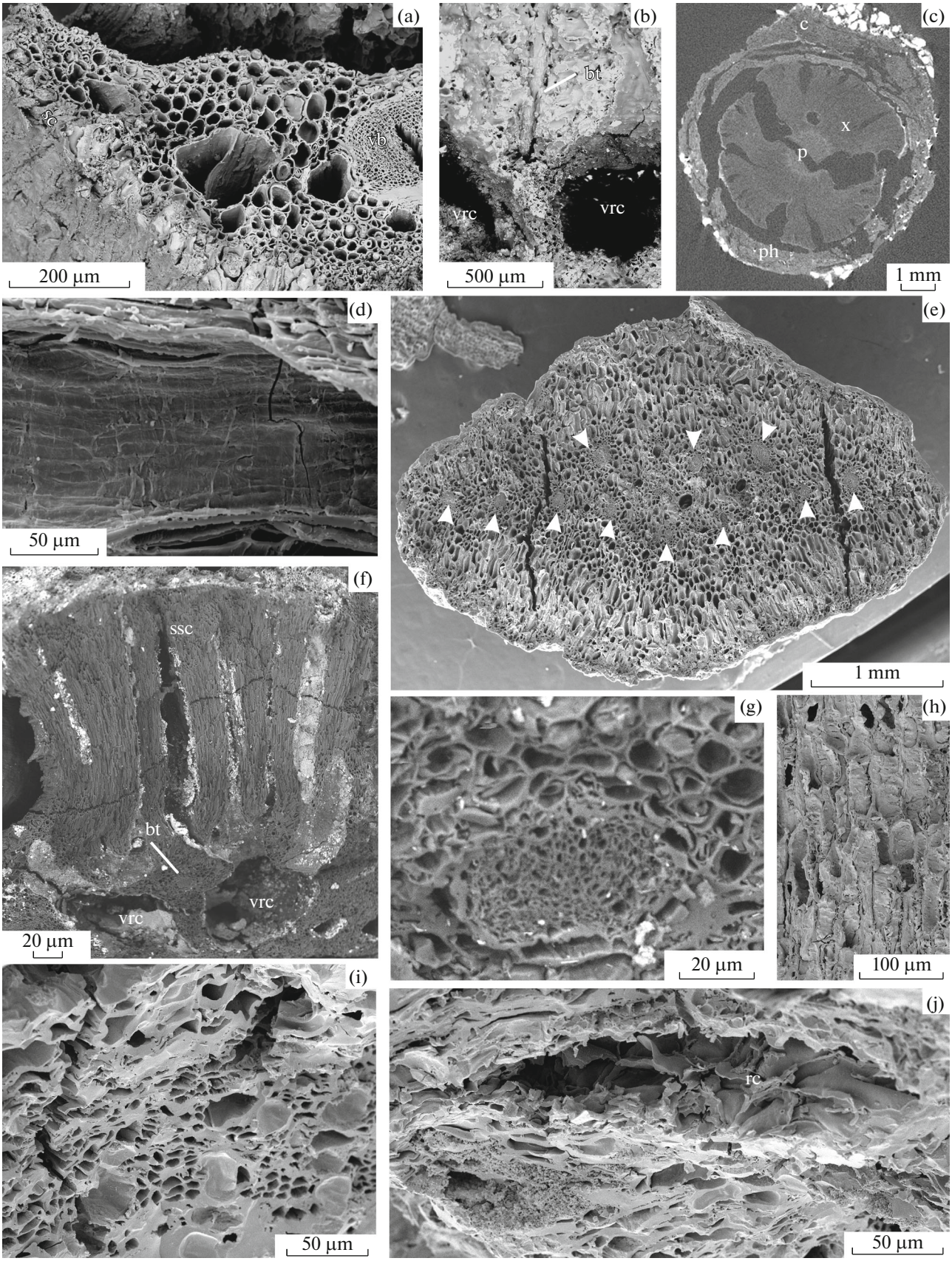
The assignment of fossil anatomically preserved *Pinus*-like seed cones to the genus *Pinus* is based on the concept of Miller, which has been proposed by him as a result of investigation of extensive material on extant species of the genus and its comparing with fossil representatives of Pinaceae; at present this concept is widely accepted (Miller, 1976; Miller, 1977; Banks et al., 1981; McKown et al., 2002; Ryberg et al., 2012; etc.). Nevertheless, it is important to understand the somewhat conditional nature of the assignment of fossil pinaceous seed cones to the genus *Pinus*, which is a particular case of the general problem of assignment of fossil anatomically preserved material, represented by isolated organs, even studied in details, to extant taxa (see Bazhenova, Bazhenov, 2019). The correlation between various organs of most fossil plants can be more or less reliably established merely in isolated cases. Only for a few structurally preserved fossil pine species there is evidence on leaves associated with cones (Banks et al., 1981; Ryberg et al., 2012), but yet data on the shoot structure and pollen cones are lacking. The only fossil species, for which the organismal concept was proposed, is the Eocene *P. arnoldii*. According the report, anatomy of seed cones of this species is characteristic for representatives of subgenus *Pinus*, whereas the structure of wood and brachyblasts with leaves suggests relationships to the subgenus *Strobus* (Klymiuk et al., 2011). This evidence points on the impossibility of assigning fossil pines, except youngest representatives, to a particular subgenus if correlation

Explanation of plate 10

Figs. 1–6. *Pinus bukatkinii*, sp. nov., paratype PIN no. 5851/4, SEM; (1) fragment of the cone peduncle on the transverse fracture, xylem array (x) with vertical resin canals (marked by white arrows) and pith (p) are visible; (2) ray with biseriate part; (3) simple pits on the horizontal wall of ray cell; (4) resin canals in the peduncle xylem (marked by white arrows); (5) cross-fields with one–two pits; (6) alternate pitting near the tracheid end; (7) pitting in the radial and tangential tracheids walls; the vicinity of Stary Oskol town, Middle Jurassic.

Plate 10

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20 μm
(g)
20 μm
(h)
100 μm
(i)
50 μm
(j)
rc
50 μm

Fig. 6. *Pinus bukatkinii*, sp. nov.: (a) holotype PIN, no. 5851/9, SEM, the marginal part of seed scale, perpendicularly orientated large cells and weakly sclerified abaxial hypoderm, and also non-sclerified ground tissue, resin canals and thin-walled cells surrounding them are visible; (b, f, g) paratype PIN, no. 5851/2, SEM: (b) bract trace and dilated vertical resin canals in the cone axis cortex; (f) bract trace which has just separated from united trace and is heading down, resin canals going to the seed scale are also visible; (g) detail of (f), ellipsoidal vascular bundle of the bract trace; (c, h–j) paratype PIN, no. 5851/4: (c) transverse tomogram of the seed cone peduncle shows pith, xylem ring, phloem, and cortex; (h) pith cells of the seed cone peduncle on the longitudinal fracture, SEM; (i) phloem of the seed cone peduncle on the transverse fracture, arrays of phloem cells, alternating with areas containing large idioblasts, are visible, SEM; (j) resin canal in the seed cone peduncle cortex; (d, e) paratype PIN, no. 5851/1, SEM: (d) resin canal on the longitudinal fracture of the seed scale; (e) vascular bundles arranged in two rows on the transverse fracture of the apophysis base (marked by white arrows). Legend: (bt) bract trace, (c) cortex, (p) pith, (ph) phloem, (rc) resin canal, (sc) sclerification, (ssc) seed scale, (tr) common trace of the bract and seed scale, (vb) vascular bundle, (vrc) vertical resin canals, (x) xylem.

between ovuliferous and vegetative organs is not established.

Central to Miller's concept, developed for identification of cones of the genus *Pinus*, is a set of four main diagnostic characters: dilated apices of seed scales, possessing apophyses and umbos; entire vascular trace supplying the seed scale and the bract; resin canals entering the base of seed scale abaxially; adaxially convex vascular bundles of the seed scale (Miller, 1976). In some reports, Miller didn't recognize these characters as the only sufficient for assignment of fossil seed cones to the genus *Pinus* (see, e.g., Miller and Robison, 1975; Miller, 1978). He added to them such characters as the presence of vertical resin canals in the xylem of cone axis, presence of a free bract, the type of its separation from seed scale (pines are characterized by separation starting from margins) and the degree of its vascularization (Miller and Robison, 1975; Miller, 1977). At the same time, presence of entire vascular trace supplying both seed scale and bract may be a facultative character, because it is not shared by several extant representatives of the genus (Miller, 1978; Gernandt et al., 2011; Ryberg et al., 2012). In *P. bukatkinii* sp. nov., in addition to four key characters, proposed by Miller, there are also supplementary features, namely the presence of vertical resin canals in the xylem of cone axis and presence of the free bract, separating from margins. In our opinion, such characters as the type of separation of bract and the degree of its vascularization are in fact not significant for identification of *Pinus* cones, because they vary within the genus. For example, the medial separation of the bract is peculiar for *P. matthewsii* (McKown et al., 2002), and the vascular bundle, not reaching the apical part of bract, – for *P. escalantensis* (Banks et al., 1981).

In connection with the discovery in the Middle Jurassic of seed cones, which demonstrate morphological and anatomical features of *Pinus*, it is necessary to mention Miller's hypothesis on archaism of the general structure of seed organs in this genus (Miller, 1976). The new find confirms the assumption that cones, exhibiting all main morphological and anatomical characters of *Pinus*, were ancestral to the whole diversity of the Cretaceous *Pityostrobus*, *sensu* Miller (Miller, 1976); the relationships of these two genera with other representatives of the family is not clear. The presence in the Middle Jurassic *P. bukatkinii* sp. nov. of the whole set of *Pinus* main features in the completely formed state indicates probable much earlier origin of each individual feature. At present, the available data on ovuliferous organs of the earliest Pinaceae and taxa supposedly referred to the family are so scarce that they can not provide any reliable basis even for preliminary phylogenetic hypotheses. The oldest supposed Pinaceae are *Compsostrobus neotericus* from the Upper Triassic of North Carolina (Delevoryas and Hope, 1973, 1987; Taylor et al., 2009) and *Schizolepidopsis liasokeuperianus* (C.F.W. Braun) Doweld, widespread in the Middle–Upper Triassic of Eurasia (the authenticity of Permian finds of *Schizolepidopsis* was not confirmed: Domogatskaya and Herman, 2019), but the anatomy of these cones is not known, thus they can not be used in reconstruction of phylogeny of the family Pinaceae with confidence. In the same time, available data suggest that immediate ancestors of the genus *Pinus* most likely to be found in the Early Jurassic.

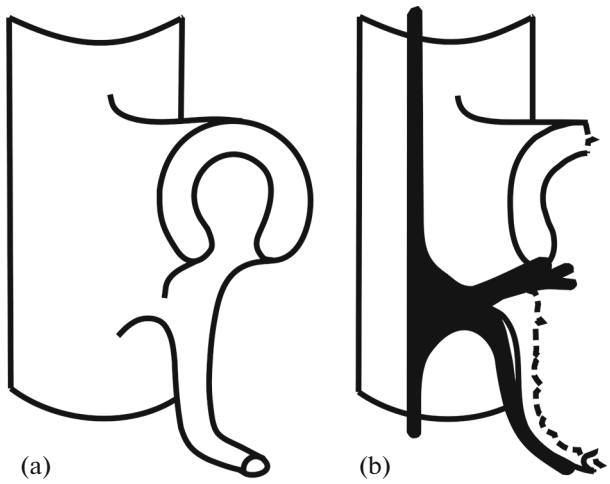

Fig. 7. *Pinus bukatkinii*, sp. nov.; (a) departure of a single trace to the bract and seed scale; (b) resin canals of the bract-scale complex and their connection with vertical resin canals of the cone axis cortex (resin canals only on one side of the trace following to the bract and seed scale are shown).

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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