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The most ancient member of the Sequoioideae – the new genus *Krassilovidendron* Sokolova, Gordenko et Zavialova (Cupressaceae *s.l.*) from the Albian–Cenomanian of Western Siberia (Russia)

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ABSTRACT

The new genus *Krassilovidendron* Sokolova, Gordenko et Zavialova with the type species *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova is described on the basis of numerous compressions of polymorphic shoots in organic connection with seed and pollen cones from the Albian–Cenomanian of the Kubaevo locality (Russian Federation, Kemerovo region, Western Siberia). The new taxon is characterized by an assemblage of features that distinguishes it from all known extant and fossil conifer genera: shoots with helically arranged leaves varying from amphistomatic small scale-like leaves to strictly epistomatic linear-lanceolate leaves; terminal, ellipsoidal to obovate seed cones, bearing 14–26 helically arranged peltate bract-scale complexes (bract and ovuliferous scale are completely fused) with a cylindrical vascular bundle, bifurcating into abaxial and adaxial dichotomizing bundles; up to 22 inverted seeds of various shapes with a protruding micropyle and inconspicuous lateral wings, which are arranged in two to five arcuate rows; solitary terminal pollen cones with helically arranged microsporophylls, each bearing four abaxial microsporangia; and small pollen grains with a relatively short papilla, numerous orbicules on the surface, and a three-layered ectexine with a tectum of strongly fused granules, an infratectum of smaller and more loosely arranged granules, and a thin footlayer. The new taxon possesses a combination of characters indicating it belongs to the subfamily Sequoioideae. *Krassilovidendron* shares the greatest number of features with *Sequoia* Endlicher and *Sequoiadendron* Buchholz, and fewer characters with *Metasequoia* Miki ex Hu et W.C. Cheng.

1. Introduction

Sequoia–like conifer remains are widespread in the Cretaceous of Northern Asia and represented by shoots, leaves, and seed and pollen cones. Although they rarely occur in organic connection, dispersed fragments of these conifers are often identified within modern genus *Sequoia*, based on their external morphology (e.g., Kryshtofovich, 1958; Sveshnikova, 1967; Samylina, 1976, 1988; Filippova, 1984; Filippova and Abramova, 1993; Shczepetov and Golovneva, 2010). Essentially, such fragmentary remains should be considered as fossil-taxa for isolated organs of plants; the similarity of isolated fossil organs with those of extant conifers is not always a proof of taxonomic identity, but can be explained by evolutionary parallelism. Natural taxa can be distinguished by a combination of diagnostic characters of different morphological categories of organs, the most conservative of which are vegetative organs (Krassilov, 1971). The most promising for taxonomic and systematic purposes are ovulate reproductive organs (Bobrov, 2004; Stockey et al., 2005; Rothwell and Ohana, 2016). The common practice has been to refer fossil material assignable to the Sequoioideae from the Cretaceous, and sometimes the Cenozoic of both hemispheres, to new fossil genera. Such new genera show significant differences in the combination of features, but often share some morphological characters of individual organs with those of modern representatives of the subfamily (e.g., Miki, 1969; Peters and Christophel, 1978; Srinivasan and Friis, 1989; Serbet and Stockey, 1991). For example, *Protosequoia* Miki from the Cenozoic of Japan (Miki, 1969), *Quasisequoia* Srinivasan et Friis from the Upper Cretaceous of Sweden (Srinivasan and Friis, 1989), and *Austrosequoia* Peters et Christophel from the Cenomanian of Australia (Peters and Christophel, 1978) combine features of *Sequoia* and *Sequoiadendron*; *Drumhellera* Serbet et Stockey from

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the Upper Cretaceous of Alberta, Canada (Serbet and Stockey, 1991; Stockey et al., 2005; Serbet and Rothwell, 2016), and *Nephrostrobus* Miller et LaPasha from the Upper Cretaceous of New Jersey, United States (LaPasha and Miller, 1981), share characters of *Metasequoia*, *Sequoia* and *Sequoiadendron*. The conifer described here from the Albian–Cenomanian of Western Siberia is the oldest known representative of the subfamily Sequoioideae, combining features of three extant genera of the subfamily: *Sequoia*, *Sequoiadendron*, and *Metasequoia*, but exhibiting greatest similarity with *Sequoia* and *Sequoiadendron*.

2. Material and methods

The material comes from continental Cretaceous (Albian–Cenomanian) deposits of the Kubaevo locality, which is situated on the left bank of the Kiya River, 7 km north of the village of Dmitrievka (near the village of Kubaevo, Mariinsk district, Kemerovo Region; 56°04′30″ N, 87°52′21″ E; Fig. 1). Cretaceous deposits (up to 6 m thick) are exposed for approximately 400 m along the riverbank and are represented by an alluvial complex composed of gray-colored terrigenous sediments. The fossil plant remains studied come from the lower part of the section, composed of grey to nearly white sandy clays with root traces and signs of pedogenic alteration. The clays contain numerous sandy channel fills, often with accumulations of coarse plant debris. Both sandy clays and sandy channel fills contain the remains of the plant under study. Fragments of twigs with attached cones where found in the sandy clays, and numerous dehisced cones come predominantly from sandy channel fills. The remains from sandy clays are probably subautochthonous, whereas those in high energy sandy channel fills are allochthonous. Detailed description of the section and justification of the age of plant-bearing deposits is given in Maslova et al. (2011).

The material was studied as follows: after preparation of the samples (specimens were uncovered on bedding planes, prepared using fine needles to reveal details, and measured), photographs were taken using a Nikon D60 digital camera. Details of the morphology of the shoots, seed and pollen cones, and seeds were studied using a Leica M165C stereomicroscope equipped with a Leica DFC420 digital camera at A.A. Borissiak Paleontological Institute (PIN RAS). Hydrofluoric acid was used to dissolve the rock. Plant remains were macerated according to the standard technique using Schulze solution and alkali: cuticles of leaves, microsporophylls and bract-scale complexes, as well as sporangia and megaspore membranes were obtained this way.

Details of the anatomy of bract-scale complexes were observed using a SkyScan 1172 Micro Computer Tomography System (PIN RAS) and scanning electron microscope (SEM) Tescan Vega (PIN RAS). The morphology and epidermal structure of the shoots, pollen and seed cones, and seeds were studied under SEM in the low vacuum mode (Univac) without gold coating (accelerating voltage 20–30 kV). We used an Axioplan 2 (Zeiss) light microscope (LM) equipped with a Leica DFC420 and the same SEM, but in the high vacuum mode for a detailed study of epidermal features of the leaves and microsporophylls, the anatomical structure of the seed cones, seed structure and morphology of pollen grains. For observations in the high vacuum mode, the fossils were mounted on SEM stubs and coated with Au–Pd for 6 min.

The general morphology of pollen grains was also observed and documented at the Department of Higher Plants, Biological Faculty of Lomonosov Moscow State University (MSU) using a Nikon eclipse Ci, equipped with a Nikon DS–Vi1 digital camera and a 100 × oil immersion lens. Microphotographs of the pollen grains taken in different focal planes were stacked using Helicon Focus 6.6.1 software. Differential interference contrast (DIC) images of the

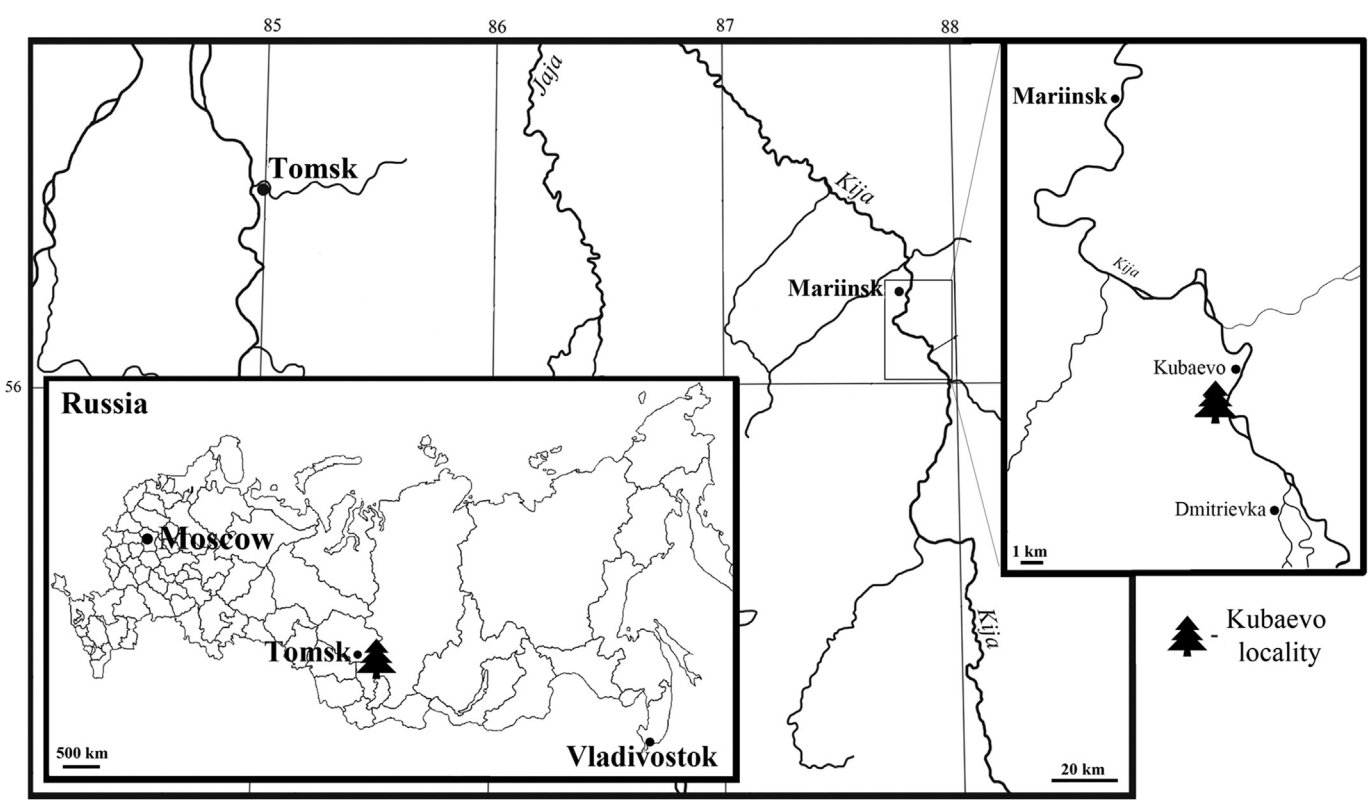

Fig. 1. Geographic position of the Kubaevo locality (modified from Maslova et al., 2011).

pollen grains were taken at MSU, using a Karl Zeiss Axioplan 2 transmitted light microscope, with an Axiocam MR digital camera and a DIC–Prisma III/0.9 Plan/Epiplan NEOFLUAR 100×/1.30 oil immersion lens.

For TEM, groups of pollen grains were removed from the SEM stubs and embedded in a mixture of epoxy resins [Epon–812, dodecenyl succinic anhydride (DDSA), methyl nadic anhydride (MNA), and an accelerator as 17:15:8:1 volume ratios] for 48 h at 62 °C. Some groups were embedded unstained and some were stained with 1% OsO_4 for 30 min at room temperature. Sections 70 nm thick were prepared using a Leica EMUC6 ultramicrotome at PIN RAS. They were viewed and photographed on Jeol JEM–100 B and Jeol JEM–1011 (accelerating voltage 80 kV) TEMs at the Electron Microscope Laboratory, MSU. Ultramicrographs were made on films on the Jeol JEM–100 B and digitized using an Epson Perfection V700 Photo Scanner. Digital images were taken using the Jeol JEM–1011, which is equipped with a side mounted digital camera Orius SC1000W (11 Megapixels, effective 8.5 Megapixels); Digital Micrograph v. 2.0 (Gatan) software was used.

Composite images were made from individual ultramicrographs using Photoshop 7.0.

Pollen terminology follows Punt et al. (2007) and Hesse et al. (2009).

The fossil plants were collected during summer field trips 2006–2009 by researchers of the laboratory of palaeobotany, PIN RAS (A.V. Broushkin, N.V. Gordenko, E.V. Karasev, V.A. Krassilov, and A.B. Sokolova), laboratory of arthropods, PIN RAS (A.S. Shmakov and E.V. Yan), laboratory of palaeobotany, Institute of Biology and Soil Sciences, Far East Branch of Russian Academy of Sciences (A.S. Avramenko), and Geological Faculty of MSU (D.A. Mamontov). Collection no. 5167 is housed at PIN RAS.

3. Systematics

Division Coniferophyta
Class Coniferopsida
Order Coniferales
Family Cupressaceae Gray
Subfamily Sequoioideae Saxton

Krassilovidendron Sokolova, Gordenko et Zavialova gen. nov.
Etymology. The name *Krassilovidendron* is given in honor of our teacher, the great palaeobotanist – Professor Valentin Krassilov, who devoted his life to palaeobotany.
Type species: *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov.

Generic diagnosis. Branching of shoots alternate, in one plane or three-dimensional. Leaves helically arranged and polymorphic: from scale-like to linear-lanceolate. Leaves with variously developed abaxial keel. Leaf margins dentate near apex at all types of leaves. Leaves epistomatic to amphistomatic. Stomatal bands on adaxial surface narrow, converging at leaf apex. Seed cones terminal, solitary, woody, not disintegrating, with helically arranged peltate bract-scale complexes; bract and ovuliferous scale completely fused. Escutcheons rhomboid to hexagonal, typically broader than long. Bract-scale complexes vascularized by cylindrical bundle, bifurcating into abaxial and adaxial dichotomizing branches. Seeds inverted, numerous (13–22), located on adaxial surface of bract-scale complex, forming two-five rows. Seeds varying in outlines; seed axis straight or curved. Lateral wings inconspicuous. Seed coat differentiated into exotesta, mesotesta and endotesta: exotesta consists of epidermis and hypodermis; mesotesta (sclerotesta) consists of one layer or few layers of cylindrical sclereids; endotesta consists of at least two layers of rectangular thin-walled cells. Nucellus free from integument. Pollen cones solitary and terminal. Microsporophylls bear abaxially (3) 4 ellipsoidal microsporangia. Pollen grains small, distally with broad leptoma crowned by relatively short papilla. Ectexine consisting of three sublayers: tectum of strongly fused granules, infratectum of smaller and more loosely arranged granules, and thin footlayer.

Comparison. The new genus possesses a suite of features that are characteristic of the subfamily Sequoioideae (Table 1): woody cones; peltate bract-scale complexes, formed by fusion of an ovuliferous scale and bract; rhomboid to hexagonal outlines of escutcheons, the vascularization of a bract-scale complex by a cylindrical bundle, bifurcating into abaxial and adaxial dichotomizing branches; inverted seeds with wings; pollen grains are small to medium in size, with a papilla on a distal leptoma, the surface is usually covered with orbicules, the ectexine includes a tectum of fused granules, an infratectum of smaller and loosely arranged granules, and a thin footlayer (comparable in thickness with one or two lamellae of the endexine), the endexine with 6–15 lamellae; and monocyclic to amphicyclic stomata, which are variously oriented (see description below). Because the presence of this combination of characters allows us to assign the fossil remains to the subfamily Sequoioideae, we restrict our comparison to the members of this subfamily. Together with extant *Sequoia*, *Sequoiadendron*, and *Metasequoia*, the following fossil genera are classified within the subfamily Sequoioideae: *Quasisequoia*, *Austrosequoia*, *Drumhellera*, *Nephrostrobus* LaPasha et Miller, *Rhombostrobus* LaPasha et Miller, *Yezosequoia* M. Nishida, H. Nishida et Ohsawa, *Yubaristrobus* Ohsawa, M. Nishida et H. Nishida (after Stockey et al., 2005), and also *Protosequoia*, *Parasequoia* Krassilov, *Stockeystrobus* Rothwell et Ohana, and *Haborosequoia* Ohsawa, M. Nishida et H. Nishida.

The new genus is most similar to *Sequoia* and *Sequoiadendron*, combining a number of characters of both genera.

Krassilovidendron shares several features with *Sequoia* (Table 1), such as polymorphic shoots with helically arranged leaves, which are scale-like to linear-lanceolate, with pointed apices and decurrent bases; rounded, ellipsoidal, or ovoid terminal seed cones with helically arranged peltate bract-scale complexes, having a central tooth on the escutcheon; and terminal pollen cones with 10–15 helically arranged microsporophylls, each bearing three or four microsporangia. Similar to the new genus, the seed cones of *Sequoia* are annual, without growth rings (Sveshnikova, 1963; Farjon, 2010). In both *Krassilovidendron* and *Sequoia* (Radais, 1894; observations by AS and NG), the vascular bundle departing from the cone axis is cylindrical, divided into abaxial and adaxial branches; the latter are frequently branching into numerous small vascular bundles, forming a rhomboid and then triangular pattern in the transverse section. The epidermal structure of the dorsal surface of the escutcheon in the new genus is similar to that in *Sequoia* in its rarely occurring stomata. *Krassilovidendron* also exhibits similarity to *Sequoia* in the stratification of the seed testa, which consists of a two-layered exotesta, a sclerified mesotesta, and an endotesta, composed of several layers of longitudinally extended thin-walled cells. The position, size and morphology of pollen cones of the new genus are very similar to those of *Sequoia.* Pollen grains of the new taxon and *Sequoia* (Buchholz and Kaeiser, 1940; Yamazaki and Takeoka, 1956; Gullvåg, 1966; Roscher, 1975; Meyer, 1977; Kvavadze, 1988; Xi and Wang, 1989; Serbet and Stockey, 1991) are similar in general morphology and the ectexine ultrastructure. In particular, pollen grains of both genera bear a papilla on the leptoma, their papilla length/pollen grain diameters are similar, and an infratectum is present in the ectexine of pollen grains of both genera.

Nonetheless, we cannot assign the new conifer to the genus *Sequoia* because of several significant differences. *Krassilovidendron* leaves are less polymorphic in shapes, not including, in particular, long

Table 1
Comparison of fossil and extant representatives of the subfamily Sequoioideae. References used: a) AS (unpublished data); b) Basinger, 1981, 1984; c) Buchholz, 1939; d) Farjon, 2010; e) Gullvåg, 1966; f) Krassilov, 1967; g) Kunzmann, 1999; h) Kvavadze, 1988; i) LaPasha and Miller, 1981; j) Meyer, 1977; k) Miki, 1969; l) Nishida et al., 1991; m) Ohsawa et al., 1992; n) Ohsawa et al., 1993; o) Peters and Christophel, 1978; p) Roscher, 1975; q) Rothwell and Basinger, 1979; r) Rothwell and Ohana, 2016; s) Serbet and Rothwell, 2016; t) Serbet and Stockey, 1991; u) Sokolova and Moiseeva, 2016; v) Srinivasan and Friis, 1989; w) Stockey et al., 2001; x) Watson and Eckenwalder, 1993; y) Xi, 1988; z) Xi and Wang, 1989; ab) Yamazaki and Takeoka, 1956.

	Locality	Age	Leaf arrangement	Leaf shape	Leaf size, mm	Stomatal distribution	Orientation of stomata	Cone shape	Cone size, mm	Cone scale taxis
Krassilovidendron gen. nov. (present study)	Western Siberia, Russia	Early-Late Cretaceous (Albian –Cenomanian)	Helical or almost distichous and alternate	Scale-like and falcate to linear-lanceolate	1.5–3 × 0.8	Epistomatic to amphistomatic	Mostly transverse; rarely oblique; parallel in single cases	Ellipsoidal to ovate and obovate	14–20 × 9–12	Helical
Sequoia (a, b, c, d, e, g, h, j, p, x, y, z, ab)	Extant	Cretaceous? – recent	Helical or distichous and alternate	Scale-like, subulate, falcate to long linear	1–35 × 1–3	Hypostomatic to amphistomatic	Irregular	Ellipsoidal, ovate and obovate	13–35 × 13 –18	Helical
Sequoiadendron (a, b, c, d, g, p, u, x, z)	Extant	Late Cretaceous? – recent	Helical	Scale-like to subulate	1–20 × 0.6–5	Amphistomatic	Irregular	Ellipsoidal, subglobose, ovate and obovate	30–95 × 25 –65	Helical
Metasequoia (a, b, d, h, p, q, y, z, ab)	Extant	Paleocene (?) – recent	Decussate or distichous and opposite	Ovate to long linear	2–50 × 0.5–4.5	Hypostomatic	Parallel, rarely oblique	Ellipsoidal, cylindrical to globose	15–30 × 10 –23	Helical to decussate
Protosequoia (k)	Honshu, Japan	Oligocene – Miocene	Helical	Scale-like to subulate	1–4 × 1	Epistomatic	Irregular	Ellipsoidal or globose	10–15 × 10 –12	Helical
Drumhellera (r, s, t)	Alberta, Canada	Late Cretaceous (Campanian –Maastrichtian)	Helical	Needle-like, linear	?	Hypostomatic	?	Ellipsoidal	20–30 × 17 –23	Helical
Quasisequoia (g, v)	Europe	Late Cretaceous – Late Miocene	Helical	Subulate to lanceolate or scale-like	0.7–3.75 × 0.4 –1.15	Amphistomatic	Irregular	Ellipsoidal, oblong-ellipsoidal or globose	8–25 × 8–20	Helical
Austrosequoia (o)	Queensland, Australia	Late Cretaceous	Helical	Scale-like	1–1.2 × 2–2.2	?	?	Ellipsoidal (ovoid)	9–16 × 6–11	Helical
Yezosequoia (l)	Hokkaido, Japan	Late Cretaceous (Turonian-Santonian)	?	?	?	?	?	Conical	25–29 × 22 –25	Helical
Stockeystrobus (r)	Hokkaido, Japan	Late Cretaceous (Coniacian –Santonian)	?	?	?	?	?	Cylindrical	>47 × 27	Helical
Nephrostrobus (i)	New Jersey, USA	Late Cretaceous	?	?	?	?	?	Ellipsoidal (oblong)	15–50 × 14 –15	Helical
Rhombostrobus (i)	New Jersey, USA	Late Cretaceous	?	?	?	?	?	Ellipsoidal (oblong)	35 × 12	Helical
Yubaristrobus (n)	Hokkaido, Japan	Late Cretaceous (Coniacian –Santonian)	?	?	?	?	?	Ellipsoidal	45 × 26	Helical
Haborosequoia (m)	Hokkaido, Japan	Late Cretaceous (Santonian)	?	?	?	?	?	Ovoid	16–17 × 14 –15	Helical
Parasequoia (f)	Primorie, Russia	Early Cretaceous (Aptian)	Distichous, alternate	Linear	8–9 × 1–1.2	Hypostomatic	Parallel	?	?	?

disti-
chous
linear-

	Number of cone scales	Seed orientation	Seed wing	Seeds per scale	Rows of seeds	Seeds, mm	Pollen cone size, mm	Microsporophyll taxis	Pollen sacs	Pollen diameter, μm	Papilla, μm	Endexine lamellae
Krassilovidendron gen. nov. (present study)	14–26	Inverted	Very narrow and inconspicuous	13–22	2–5	1.2–2.5 × 0.65–1.5	3–4 × 3.2	Helical	(3) 4	15.2–27.52	3.4	6–7
Sequoia (a, b, c, d, e, g, h, j, p, x, y, z, ab)	15–30	Inverted	Narrow–wide	2–8	1	5–6 × 3–4	3–5 × 3–4	Helical	2–6 (usually 3)	30.5–40.6	3.5–4.5	7–12
Sequoiadendron (a, b, c, d, g, p, u, x, z)	25–45	Inverted	Wide	3–9 (12)	2	5–7 × 3–5	4–6 × 3–5	Helical	2–5 (usually 3)	25.4–30.5	3.3–6.9	9–10
Metasequoia (a, b, d, h, p, q, y, z, ab)	16–30	Inverted	Narrow–wide	4–8	1	3.5–9 × 2.75–7	1–10 × 1.2–8	Decussate, helical or irregular	2–3	17.2–32.3	2–5.2	7–15
Protosequoia (k)	~16–20	Inverted?	Inconspicuous	?	?	4–5 × 3	3 × 2	Helical	?	?	?	?
Drumhellera (r, s, t)	≤27	Inverted	Wide	≤13	2	≤5 × 4	1–1.2 × 1.5–2	Helical	2–3	12–16	2	6
Quasisequoia (g, v)	20–51	Inverted	Inconspicuous	3–10	1	1.6–3 × 1–2.6	?	?	?	?	?	?
Austrosequoia (o)	29–49	Inverted	?	4–7	1	0.6 × 0.2	?	?	?	?	?	?
Yezosequoia (l)	~20 (~35)	Inverted	Narrow	4	1	2.4 × 1.2	?	?	?	?	?	?
Stockeystrobus (r)	>40	Inverted	Wide	6–8	1	5.5 × 5.5	?	?	?	?	?	?
Nephrostrobus (i)	>20–40	Inverted?	Narrow/absent	≥2 (5–7?)	?	3 × 1.3	?	?	?	?	?	?
Rhombostrobus (i)	≥50	Inverted	Present	2	?	2 × 1.2	?	?	?	?	?	?
Yubaristrobus (n)	>25	Erect	Very narrow	3–4	1	3.9–4.1 × 2.3–3.5	?	?	?	?	?	?
Haborosequoia (m)	>15	Inverted?	?	?	?	?	?	?	?	?	?	?
Parasequoia (f)	?	?	?	?	?	?	?	?	?	?	?	?

lanceolate hypostomatic to amphistomatic types, which are characteristic of *Sequoia* (Florin, 1931; Sveshnikova, 1963; observations by AS), whereas linear-lanceolate leaves in the new genus are epistomatic. Bract-scale complexes in the new genus possess well-developed adaxial resin canals, whereas they are about twice smaller and rarely occurring in *Sequoia* (Radais, 1894). In *Krassilovidendron*, each complex bears a smaller central tooth on its dorsal surface and possesses many seeds that are arranged in two to five rows instead of one row in *Sequoia.* The variability of seed shape in the new genus is also much higher than in *Sequoia.* The seed wings in the new genus are very narrow, often inconspicuous, whereas they are wide and well-developed in *Sequoia.* Moreover, the sclerotesta in *Krassilovidendron* consists of one layer of longitudinally extended cylindrical sclereids, whereas the sclerotesta in *Sequoia* consists of several layers of sclereids, showing more or less isodiametric outlines (Bobrov and Melikian, 2006). Pollen grains of the new taxon differ from those of *Sequoia* (Buchholz and Kaeiser, 1940; Yamazaki and Takeoka, 1956; Gullvåg, 1966; Roscher, 1975; Meyer, 1977; Kvavadze, 1988; Xi and Wang, 1989; Serbet and Stockey, 1991) in being slightly smaller (17.6–(22.6)–27.5 μm and 29.0–(32.85)–40.6 μm, respectively), having an erect papilla, obtuse sculptural elements of orbicules, and a thinner endexine due to a smaller number of endexine lamellae. Pollen grains of the new taxon have six to seven endexine lamellae; and from seven to twelve lamellae have been observed in the endexine of *Sequoia* pollen by different authors (Gullvåg, 1966; Roscher, 1975; Meyer, 1977; Xi and Wang, 1989). Endexine lamellae continue to be deposited at the free-spore stage in taxodiaceous pollen (Kurmann, 1990); therefore, the smaller number of endexine lamellae were probably counted at early free-spore stage in somewhat immature pollen grains of *Sequoia*; the slightly immature state is also supported by the equal electron density of the ectexine and endexine and loosely packed endexine lamellae (e.g., Meyer, 1977). The pollen grains described here were most likely preserved in fully mature state, since the endexine lamellae are tightly packed and the endexine is more electron-dense than the ectexine. Therefore, the new taxon differs from *Sequoia* by the number of endexine lamellae in fully mature pollen (six to seven and twelve, respectively).

Krassilovidendron resembles *Sequoiadendron* in shoot morphology, its scale-like leaves, the seed cones, and pollen cones (Table 1). The anatomical structure of the bract-scale complexes in the new genus is also similar to that in *Sequoiadendron* by the presence of a cylindrical vascular bundle at the base of the bract-scale complex, initially branching to five bundles, which later give rhomboidal to triangular outlines. Resin canals in the new genus are well developed adaxially and abaxially, like in *Sequoiadendron.* Additionally, in the new genus the seed wings are formed by the exotesta and the mesotesta, similarly to the seeds of *Sequoiadendron* (Bobrov and Melikian, 2006; observations by AS and NG). The most frequent diameter of *Sequoiadendron* pollen grains is very close to that of *Krassilovidendron*; pollen grains of both genera bear a papilla on the leptoma, and an infratectum is developed in the ectexine of both genera (Buchholz and Kaeiser, 1940; Roscher, 1975; Kvavadze, 1988). The new genus differs from *Sequoiadendron* in a higher leaf polymorphism, the occurrence of epistomatic leaves distinct from the exclusively amphistomatic leaves of *Sequoiadendron* (Florin, 1931; observations by AS), smaller seed cones (14–20 × 9–12 mm instead of 30–95 × 25–65 mm in *Sequoiadendron*), less numerous bract-scale complexes (14–26 instead of 25–45 in *Sequoiadendron*), a higher number of seeds per scale (13–22 instead of 3–9 (12) in *Sequoiadendron*), and two to five seed rows, as opposed to only two seed rows in *Sequoiadendron* (Table 1; Buchholz, 1939; Farjon, 2010; observations by AS). The tooth in the central part of the dorsal surface of an escutcheon in the new genus

is half the size of that in *Sequoiadendron*, or smaller. Moreover, stomata on the dorsal surface of the escutcheon in the new genus are scanty, whereas they are numerous in *Sequoiadendron* (Miki, 1969; observations by AS and NG). In addition, cones in *Sequoiadendron* become mature in two years (Buchholz, 1939), whereas they probably were annual in the new genus, judging by the presence of only one annual ring in mature seed cones. The exotesta of the seeds in *Sequoiadendron* is single-layered and lacks the hypodermis (Bobrov and Melikian, 2006), in contrast to the new genus. The pollen cones in the new genus differ from those of *Sequoiadendron*: pollen sacs in the latter are adpressed to the sporophyll stalk and their longitudinal axes are orientated nearly perpendicularly to the pollen cone axis; they are not adpressed to the stalk in *Krassilovidendron*. Pollen grains of *Sequoiadendron* differ from those of the new taxon in their higher papilla length/pollen diameter ratio, a longer papilla (that can be curved), acute, more widely spaced, and more numerous sculptural elements of orbicules (about 15–20 sculptural elements are visible on an orbicule according to unpublished SEM data of AS, as compared to 8–10 sculptural elements in the new taxon), a better-developed infratectum of loosely arranged granules, and more numerous (nine or ten) endexine lamellae (Buchholz and Kaeiser, 1940; Roscher, 1975; Kvavadze, 1988).

Among extant members of the Sequoioideae, *Metasequoia* is the most different from *Krassilovidendron*. Nevertheless, some common features are present in both genera: the terminal position of seed cones, the number of bract-scale complexes (14–26 in *Krassilovidendron* and 16–30 in *Metasequoia*), the morphology of the pollen cones, and a number of characters of the morphology and ultrastructure of pollen grains. Pollen grains of the new taxon coincide with those of *Metasequoia* in the size range. They are also similar to pollen grains of *Metasequoia* in their papilla/pollen diameter ratio (Yamazaki and Takeoka, 1956; Rothwell and Basinger, 1979; Kvavadze, 1988; Surova and Kvavadze, 1988; Xi, 1988; Liu et al., 1999; Stockey et al., 2001). For *Metasequoia*, Kvavadze (1988) reported a papilla of 2–3.5 μm, and Xi (1988) described a papilla of 3.5–5.2 μm. Although pollen grains of *Metasequoia* are apparently more variable in papilla length (we measured a papilla of about 3.4 μm in pollen grains of the new taxon), the pollen grains of both genera appear very similar in their outlines in lateral view, which is the view used for identification of fossil dispersed pollen at the generic level (e.g., Yamazaki and Takeoka, 1956; Grímsson and Zetter, 2011). The two genera are very similar in the ultrastructure of the exine, which is a palynological character that is most valuable for differentiation between genera: three sublayers are present in the ectexine, the relative thicknesses of sublayers are similar in both genera, and the constituting elements of the ectexine sublayers are packed with a similar density (Roscher, 1975; Kvavadze, 1988; Xi, 1988; Xi and Wang, 1989).

Unlike *Krassilovidendron*, *Metasequoia* is characterized by seasonally deciduous twigs with distichous monomorphic linear-lanceolate hypostomatic leaves and seed cones with decussate bract-scale complexes. Stomata in *Metasequoia* are monocyclic (Sveshnikova, 1963). Pollen cones are predominantly lateral, opposite, and arranged on specialized shoots (Farjon, 2010). Each microsporophyll bears three abaxial sporangia (Miki, 1969; Serbet and Stockey, 1991; Kunzmann, 1999), whereas in the new genus there are (3) 4. Differences include a substantially greater number of seeds per scale in the new genus (13–22 in *Krassilovidendron* vs 4–8 in *Metasequoia*), their arrangement in two to five rows and less developed inconspicuous wings. Moreover, the vascularization of the bract-scale complexes in *Metasequoia* differs by exhibiting in cross sections an abaxially concave reniform pattern, formed by small bundles as a result of ramification of abaxial and adaxial branches of the vascular bundle (Rothwell and Ohana, 2016). The pollen of the new taxon differs from *Metasequoia* in the orbicule surface (the information is available only for modern *M. glyptostroboides*, but this character has not been documented in fossil *M. milleri*). The new taxon also differs from *Metasequoia* in a thinner endexine with much less numerous lamellae: six to seven lamellae as compared to 10–15 lamellae (Roscher, 1975; Kvavadze, 1988; Xi, 1988; Xi and Wang, 1989). Although we have information on the number of lamellae only in modern *M. glyptostroboides* and do not have it for fossil *M. milleri*, one can see a considerably thick endexine in a pollen section published for *M. milleri* (Rothwell and Basinger, 1979). This means that the two genera are most probably differ in the number of endexine lamellae. The number of endexine lamellae seems to be a taxonomic character that is useful at the generic level. However, we believe that it is less important for differentiation between taxodiaceous genera than details of the ectexine. The new genus and *Metasequoia* are far from a close match in palynological characters. However, we consider that the features they share are among the most important for generic differentiation.

Among the known fossil conifers, the same type of preservation of sterile and fertile organs in natural connection occurs in *Protosequoia* from the Oligocene–Miocene of Central Honshu of Japan (Miki, 1969). *Protosequoia* is represented by abundantly branched twigs with helically arranged scale-like to subulate leaves and seed and pollen cones in organic connection. *Protosequoia* shows characters in common with the new genus (Table 1), such as the presence of epistomatic leaves of similar size, terminal position of seed and pollen cones, similar number of peltate bract-scale complexes, bearing inverted seeds on the adaxial side and a small central dorsal tooth on the escutcheon. However, seed cones in *Krassilovidendron* are longer, having the same width (14–20 × 9–12 mm vs 10–15 × 10–12 mm in *Protosequoia*); bract-scale complexes bear rare stomata, scattered mainly around the central tooth; seeds with substantially less developed wings, and larger pollen cones (3–4 × 3.2 mm vs 3 × 2 mm in *Protosequoia*). Moreover, stomata of the new genus are more regularly arranged on the leaves. The seed cone anatomy in *Protosequoia*, the number of seeds and their arrangement, the structure of pollen cones and pollen morphology were not elucidated, and the epidermal structure of leaves was not described in detail, preventing further comparison between the genera.

A similarity of the new genus to *Drumhellera* from the Campanian–Maastrichtian of Alberta, Canada (Table 1; Serbet and Stockey, 1991; Rothwell and Ohana, 2016; Serbet and Rothwell, 2016), appears in the helical arrangement of leaves, microsporophylls and bract-scale complexes. Seed cones of both genera have terminal position, similar number of bract-scale complexes (up to 26–27), and a cylindrical vascular bundle, departing from the cone axis into the bract-scale complex and diverging into abundantly branched abaxial and adaxial bundles. As to shared pollen morphological features, a papilla is present in pollen grains of both genera, surface patterns of pollen grains of the new taxon and *Drumhellera* appear similar (although we cannot evaluate the surface of orbicules of the latter because of insufficient magnification of the published photographs), an infratectum is present in both genera, and six endexine lamellae are counted in *Drumhellera* (Serbet and Stockey, 1991), similar to the six to seven lamellae present in *Krassilovidendron*. *Krassilovidendron* differs from *Drumhellera* in possessing epistomatic or amphistomatic leaves (unlike the hypostomatic leaves in the Canadian genus), and terminal pollen cones half the size of those of *Drumhellera*, bearing fewer microsporophylls; each microsporophyll bears three to four microsporangia (instead of two to three in *Drumhellera*). Prior to the discovery of *Krassilovidendron*, *Drumhellera* had the greatest

number of seeds per bract-scale complex – up to 13, but the Siberian genus has almost twice as many (up to 22 per scale). The seeds of the Canadian genus, more than twice as large as those of *Krassilovidendron*, have wide and well-developed wings and are arranged in two rows, in contrast to the weakly winged seeds of the new genus, arranged in two to five rows. *Drumhellera* has smaller pollen grains (about 14 μm) than those of the new taxon and a shorter papilla. The tectum in pollen grains of *Drumhellera* grades into an infratectum, whereas the ectexine in the new taxon shows more densely packed structural elements (Serbet and Stockey, 1991).

The genus *Quasisequoia* from the Upper Cretaceous of Sweden is described based on coalified fragments of twigs in organic connection with seed cones (Srinivasan and Friis, 1989) and exhibits similarity with *Krassilovidendron* in the general morphology of seed cones, and in the helical arrangement of bract-scale complexes and leaves of similar types. Differences are seen in the presence of predominantly epistomatic leaves and morphologically variable seed cones and escutcheons of the bract-scale complexes in *Krassilovidendron*, whereas the leaves in *Quasisequoia* are amphistomatic, and the escutcheons are rhomboid. Moreover, the new genus has numerous seeds arranged in two to five rows and with less developed wings, whereas 3–10 seeds arranged in one row were noted for *Quasisequoia* (Table 1; Kunzmann, 1999). Seed wings in *Quasisequoia* are inconspicuous (Srinivasan and Friis, 1989), but distinctly larger than in the new genus; that is why *Quasisequoia* seeds are twice as wide as those of *Krassilovidendron*, even though the length of seeds of the two genera is similar.

The genus *Austrosequoia* was described from the Upper Cretaceous deposits of Queensland (Australia) from permineralized fragments of seed cones found in organic connection with leafy shoots (Peters and Christophel, 1978). *Austrosequoia* also shares some characters with the new genus (Table 1): helical arrangement of leaves and bract-scale complexes, general morphology and sizes of seed cones and bract-scale complexes, and the presence of adpressed scale-like leaves. Both *Austrosequoia* and *Krassilovidendron* bract-scale complexes are vascularized by a cylindrical bundle departing from a cone axis that produces abundantly diverging abaxial and adaxial bundles (Peters and Christophel, 1978). Aside from these shared characters, significant differences exist between *Austrosequoia* and *Krassilovidendron*: the presence of several leaf morphologies in *Krassilovidendron*; a larger number of seeds and their arrangement in two to five rows (4–7 seeds in one row in *Austrosequoia*); and twice as many bract-scale complexes per seed cone in *Austrosequoia* (29–49). The epidermal structure was not documented in the type species of *Austrosequoia*, but it is known for the second species of the genus, described from the Oligocene of Tasmania (Hill et al., 1993). However, the generic diagnosis of *Austrosequoia* was not emended after description of the new species (Hill et al., 1993). Furthermore, the second species was attributed to the genus, probably based on the morphological similarity of shoots and fragment of the seed cone, while the most important features that distinguish this genus from other Sequoioideae, are in the anatomy of seed cones, number of bract scale complexes and the arrangement and size of seeds – all unknown for the Tasmanian species. This makes questionable the attribution of the latter to *Austrosequoia* and this Tasmanian plant was not included in our comparisons.

Yezosequoia, represented by permineralized remains of seed cones from the Turonian–Santonian of Hokkaido (Japan), has peltate bract-scale complexes with completely fused ovuliferous scale and bract, and with bracts larger than the ovuliferous scales (Nishida et al., 1991). Similarly to the new genus, bract-scale complexes of *Yezosequoia* are helically arranged and bear inverted narrowly winged seeds (Table 1). However, *Yezosequoia* shows a different anatomical structure of the bract-scale complexes compared to *Krassilovidendron*. In *Yezosequoia*, the vascular bundle entering the bract-scale complex is positioned abaxially and C-shaped; distally, it branches into numerous abaxial bundles that supply the bract and fewer bundles that supply the ovuliferous scale (Nishida et al., 1991); following subsequent branching of these bundles, their overall arrangement within the bract-scale complex becomes similar to that of *Krassilovidendron* and forms a rhomboid outline in transverse sections. Additionally, vascular bundles are more loosely spaced and relatively less numerous in *Yezosequoia* compared to *Krassilovidendron*. *Yezosequoia* also has only four seeds per scale, arranged in one row (Table 1). All these characters make *Yezosequoia* substantially different from the new genus.

The new genus shares some common features (e.g. helically arranged peltate bract-scale complexes and completely fused bract and ovuliferous scales, Table 1) with the recently described *Stockeystrobus* from the Upper Cretaceous (Santonian–Coniacian) of Hokkaido, Japan (Rothwell and Ohana, 2016). However, *Krassilovidendron* differs from *Stockeystrobus* in the shape of the seed cones and their smaller size (half as small, compared to the 4.7 cm long cones of *Stockeystrobus*, which are cylindrical) as well as in the number of bract-scale complexes (again, twice as small as in *Stockeystrobus*). Six to eight seeds arranged in one row on each bract-scale complex characterize *Stockeystrobus*, whereas up to 22 seeds forming up to five rows occur in the new genus (Table 1). Similarly to the new genus, the bract-scale complexes of *Stockeystrobus* are vascularized by one cylindrical vascular bundle basally, but, in contrast to *Krassilovidendron*, the vascular bundle gives rise distally to a line of adaxial bundles and a single abaxial bundle. The latter branches more distally to form a ring of collateral vascular bundles. The line of abaxial bundles in the distal part of bract-scale complexes is uneven, with obliquely oriented bundles. Moreover, *Stockeystrobus* possesses long papillae on the escutcheons margins that are not observed in *Krassilovidendron*.

Permineralized remains of seed cones of the genus *Nephrostrobus* from the Upper Cretaceous of New Jersey, United States (Table 1; LaPasha and Miller, 1981) show the vascular bundles in the bract-scale complex forming a reniform pattern with an adaxial concavity in cross sections, which is very different from that seen in *Krassilovidendron*. Moreover, a cylindrical vascular bundle diverging from the seed cone axis possesses wide pith, whereas in the new genus the pith of the basal bract-scale complex bundle is poorly developed. The number of seeds in *Nephrostrobus* is unknown.

Permineralized seed cones of *Rhombostrobus* from the Upper Cretaceous of New Jersey (Table 1; LaPasha and Miller, 1981) are similar to the seed cones of the new genus in the arrangement of their bract-scale complexes and the position of seeds, which have almost the same size, but differ in the number of bract-scale complexes, which reaching 50, each bearing only two seeds (instead of 14–26 bract-scale complexes each bearing up to 22 seeds in *Krassilovidendron*). *Rhombostrobus* demonstrates a uniseriate arrangement of the resin canals, which is characteristic for *Cunninghamia* (LaPasha and Miller, 1981). Vascular bundles were not preserved in *Rhombostrobus*.

In *Yubaristrobus* (Table 1; Ohsawa et al., 1993), based on a permineralized seed cone from the Upper Cretaceous of Hokkaido (Japan), the vascularization of bract-scale complexes differs from that of the new genus in the presence of several additional medullary vascular bundles within an ellipsoidal outline formed by small vascular bundles. Unlike the new genus, seeds in *Yubaristrobus* are erect. The number of seeds in this Japanese genus is much lower (3–4 per bract-scale complex) and the seeds are almost twice as large as in *Krassilovidendron*, though the seed wings are similarly developed (Table 1).

The seed cones of the new genus are similar to petrified seed cones of *Haborosequoia* from the Upper Cretaceous (Santonian) of Hokkaido, Japan (Table 1; Ohsawa et al., 1992) in size and outlines, helical arrangement of peltate bract-scale complexes and their number per a cone, but the vascular system forms a reniform pattern in the escutcheons of *Haborosequoia*. Moreover, resin canals in this genus are poorly developed. The absence of data on the arrangement and number of seeds, as well as on shoot and pollen cone morphology, complicates the comparison of this genus with *Krassilovidendron*.

The genus *Parasequoia* Krassilov from the Lower Cretaceous of the Suifun Basin, South Primorye, Russia (Table 1; Krassilov, 1967) is the only genus assigned to the Sequoioideae on the basis of vegetative organs. It is represented by coalified branched twigs with distichous linear leaves. The comparison between this genus and *Krassilovidendron* is difficult due to the lack of information on the reproductive structures of *Parasequoia*. The new genus shares few features with *Parasequoia*, such as the presence of linear leaves, two stomatal bands, amphicyclic stomata, and tetragonal epidermal cells. Other characters of *Parasequoia* strongly differ from *Krassilovidendron*. For instance, the new genus has epistomatic to amphistomatic polymorphic leaves with rather transversely orientated stomatal complexes, which are arranged within a stomatal band in one or two indistinct rows and have four to six subsidiary cells, whereas *Parasequoia* has hypostomatic leaves exhibiting stomatal bands with three to four rows of loosely spaced and longitudinally orientated amphicyclic stomata with six to eight strongly cutinized subsidiary cells (Table 1; Krassilov, 1967).

Remarks. A new species of the genus *Sequoia* – *S. lebedevii* N. Nosova et Golovn. was described by Golovneva and Nosova (2012) on the basis of a detailed study of the morphology and epidermal structure of coalified compressions of vegetative shoots and external morphology of seed and pollen cones from the same deposits at the Kubaevo locality and also from Simonovo, Kem, Kas and Seversk floristic assemblages of the Chulym–Yenisei area in the southwestern part of Western Siberia. While there is no doubt that the vegetative shoots with linear leaves of *S. lebedevii* represent a plant distinct from *Krassilovidendron*, some of the specimens and types of leaves assigned to *S. lebedevii* could belong to the new genus. For example, shoots shown on Plate 31, figs. 8–9 of Golovneva and Nosova (2012), look very similar to those of *Krassilovidendron.* No epidermal structure was documented by Golovneva and Nosova (2012) for those shoots, nor for any shoots with scale-like and falcate leaves from Kubaevo. However, the epidermal structure of these two Siberian plants (comparing epidermal characters of linear leaves of *Sequoia lebedevii* and *Krassilovidendron fecundum*) differs significantly. Leaves of *Krassilovidendron* are epistomatic and stomatal bands are one or two (rarely three) stomata wide, with stomata arranged densely and mainly transversely to the leaf length, whereas leaves of *Sequoia lebedevii* are hypostomatic, stomatal bands are three-five stomata wide, and the stomata are oriented longitudinally, obliquely or irregularly.

In terms of seed cones, the *Sequoia lebedevii* cones figured on plate 31 fig. 2 by Golovneva and Nosova (2012) belong most probably to *Krassilovidendron*, but studies of the epidermal structure of cone-bearing shoots and of the structure and anatomy of these seed cones and seeds (if present) are needed to confirm this hypothesis.

Krassilovidendron fecundum Sokolova, Gordenko et Zavialova sp. nov.

Figs. 2–17

Holotype. Designated here, specimen PIN RAS no. 5167/278 (Fig. 6A, D),

Paratypes. Specimens PIN RAS nos. 5167/328a (Figs. 2A, B, 3J, 4A, B, H, I, M, 5A–E), 5167/334 (Figs. 13–16); 5167/513 (Fig. 6C); 5167/705 (Figs. 6M, P, 8M, N), 5167/710 (Figs. 6E, 7B, 10–12), 5167/711 (Fig. 7A, C, D, F, G).

Repository. PIN RAS, Moscow, Russia, collection no. 5167.

Type locality. Kubaevo locality, left bank of the Kiya River, 7 km north of the village of Dmitrievka, near the village of Kubaevo, Mariinsk district, Kemerovo Region, Russia, 56°04′30″ N, 87°52′21″ E (Fig. 1).

Type stratum. Kiya Formation, Cretaceous, Albian–Cenomanian.

Etymology. The specific epithet *fecundum* (from the Latin *fecundum* – fruitful) refers to abundant number of seeds in the seed cones.

Material studied. Specimens PIN RAS nos. 5167/23, 5167/89, 5167/107, 5167/278 (holotype), 5167/310, 5167/326, 5167/328a (paratype), 5167/328b, 5167/334 (paratype), 5167/453a, 5167/513 (paratype), 5167/564, 5167/701-704, 5167/705 (paratype), 5167/706, 5167/707-709, 5167/710 (paratype), 5167/711 (paratype), 5167/712-726, 5167/800-817.

Specific diagnosis. Branching of shoots alternate, in one plane or three-dimensional. Main axis straight; shoots arising at acute angle about 25°–60°. Leaves helically arranged, polymorphic: from small scale-like to linear-lanceolate, with transitional falcate type. Scale-like and falcate leaves with variously developed abaxial keel. Lanceolate leaf margins dentate near apex in all types of leaves. Cuticle thin; leaves epistomatic to amphistomatic. Stomatal bands on adaxial surface narrow, distinct, and converging at leaf apex. Stomata on abaxial surface form two short zones near leaf base in scale-like leaves, a single zone in falcate leaves, and lacking in lanceolate leaves. Stomata incompletely amphicyclic, rarely monocyclic and amphicyclic, oriented transversely, obliquely, or, rarely, longitudinally to leaf margins; guard cells sunken. Seed cones solitary, woody, not disintegrating, borne terminally on shoots with scale-like leaves. Cones ellipsoidal, rarely obovate, and with 14–26 helically arranged peltate bract-scale complexes; bract and ovuliferous scale completely fused, almost equally developed. Cone axis exhibits cortex and cylinder of secondary xylem with well-developed pith; xylem rays uniseriate; growth rings absent. Escutcheons rhomboid to (rarely) hexagonal. Dorsal surface of escutcheons slightly convex or with small cross depression and small central triangular tooth, from which thin lateral keels diverge to the lateral angles. Dorsal surface of escutcheons bearing stomata, concentrated in central part. Bract-scale complex vascularized by basally cylindrical vascular bundle, bifurcating into abaxial and adaxial dichotomizing branches, forming in cross section rhomboid outline of more than 40 vascular bundles; distally from this, bract-scale bundles form triangular outline in cross section, with abaxial base and up to 40 adaxial bundles. Abaxial and adaxial resin canals present. Seeds inverted, numerous (up to 22 seeds per scale), 1.2–2.5 mm long and 0.65–1.5 mm wide, located on adaxial surface of bract-scale complex in two to five arcuate rows. Seeds elongated-rectangular and ellipsoidal to rounded–triangular and obovate; seed axis straight or curved, with protruding terminal micropyle and flattened to convex chalaza. Lateral wings, reaching micropyle and chalaza, very narrow and inconspicuous. Seed coat differentiated into exotesta, mesotesta and endotesta: exotesta consists of epidermis and hypodermis; mesotesta (sclerotesta) consists of single layer of cylindrical sclereids; endotesta consists of at least two layers of rectangular thin-walled cells. Wings formed by exotesta and mesotesta. Nucellus delicate, free from integument. Megaspore membrane thick. Pollen cones solitary, terminal on shoots with scale-like leaves. Two rows of large rhomboid sterile microsporophylls, covering fertile part, situated at base of cones. Microsporophylls consist of thin peduncle, extending into lamina, which bears abaxially (3) 4 ellipsoidal microsporangia, oriented more or less parallel to cone axis. Pollen grains small, distally with

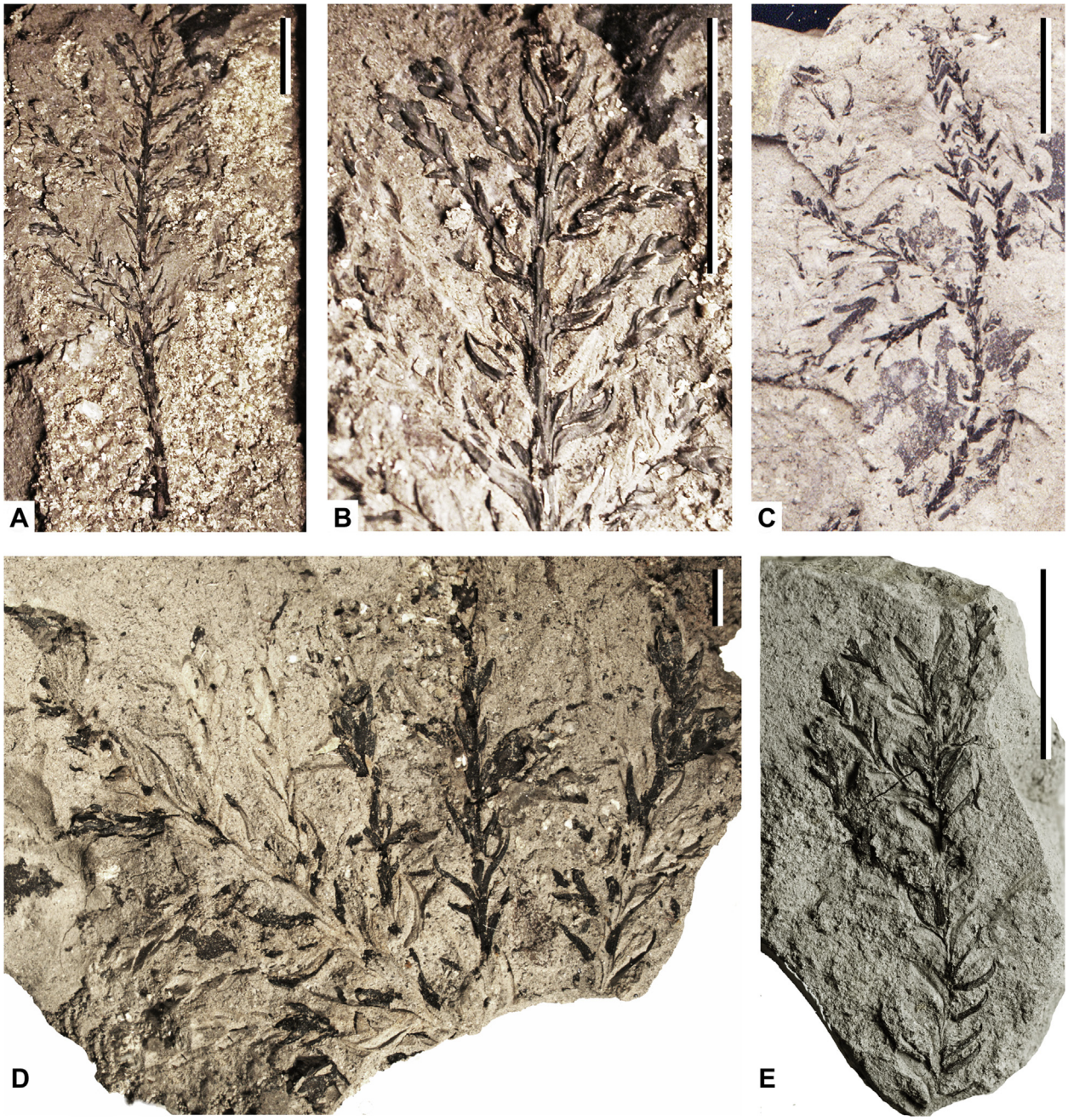

Fig. 2. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., general view of the shoots: A, B, specimen PIN RAS no. 5167/328a (paratype); C, specimen PIN RAS no. 5167/89; D, specimen PIN RAS no.5167/328b; E, specimen PIN RAS no. 5167/326. Scale bars: A–C, E = 1 cm, D = 2 mm.

broad leptoma crowned by relatively short papilla. Numerous orbicules covered with densely packed granules. Ectexine consisting of three sublayers: tectum of strongly fused granules, much thinner infratectum of smaller and more loosely arranged granules, and thin footlayer. Endexine with six to seven lamellae.

Description.

Shoots and Leaves. There are more than 30 shoots in the collection. Some of them are in organic connection with seed and pollen cones. Shoots are mainly represented by isolated terminal shoots, but a few display two or three orders of branching. Branching is alternate, three-dimensional, or in one plane (Fig. 2A–E). The distance between the branching nodes is 3–7 mm. Angle formed by lateral branches with the main shoots is acute – 45° (25°–60°). The main axis is straight and does not change direction at branching points; it is round in cross section and relatively thin: up to 2 mm in diameter at the base (for shoots with three orders of branching). The axes of terminal shoots are up to 0.7 mm in diameter. Leaves are polymorphic: they vary from small scale-like (Figs. 3A–E, 4C, F, G, K, L, 5H, 6F–I, 13E, F) to linear-lanceolate (Figs. 3I, K, L, 4D, E, J, 5F), with transitional falcate types (Figs. 3F–H, J, 4A, B, H, I, M, 5A–E). The distinction between these three types of leaves is conventional. Changes in leaf size are sometimes seen in shoots with linear leaves, where leaf size decreases from the base of the shoot toward the tip (Fig. 3K–L). Leaves of all types are helically arranged.

Scale-like leaves (Figs. 3A–E, 4C, F, G, K, L, 5H, 6F–I, 13E, F) are present mostly on shoots bearing seed or pollen cones, at the bases of the cones; they are rhomboid, densely arranged, adpressed to the

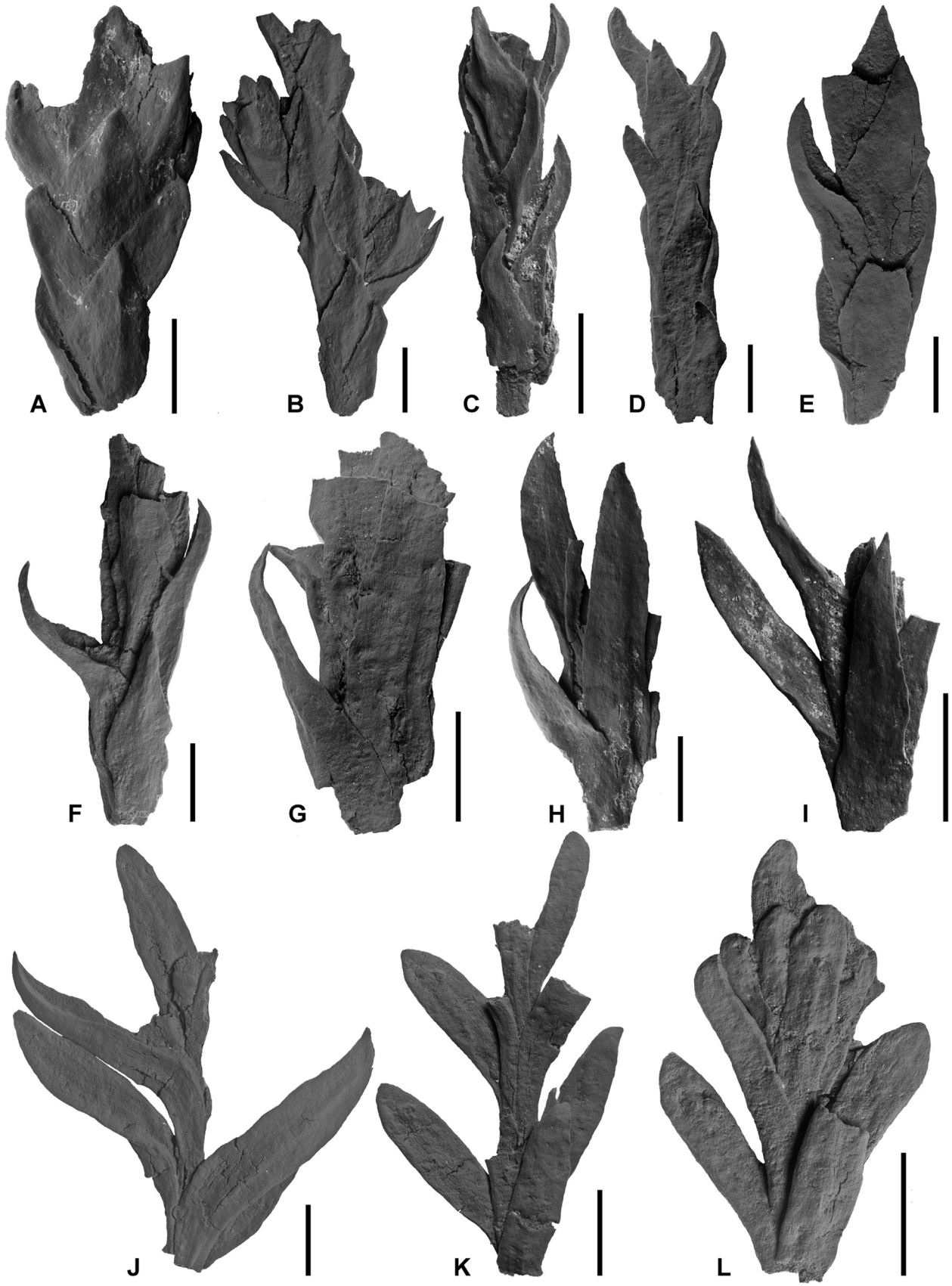

Fig. 3. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., dispersed fragments of shoots with different types of leaves: A, specimen PIN RAS no. 5167/800; B, specimen PIN RAS no. 5167/801; C, specimen PIN RAS no. 5167/802; D, specimen PIN RAS no. 5167/803; E, specimen PIN RAS no. 5167/804; F, specimen PIN RAS no. 5167/805; G, specimen PIN RAS no. 5167/806; H, specimen PIN RAS no. 5167/807; I, specimen PIN RAS no. 5167/808; J, specimen PIN RAS no. 5167/328a (paratype); K, specimen PIN RAS no. 5167/810; L, specimen PIN RAS no. 5167/811. Scale bars = 1 mm.

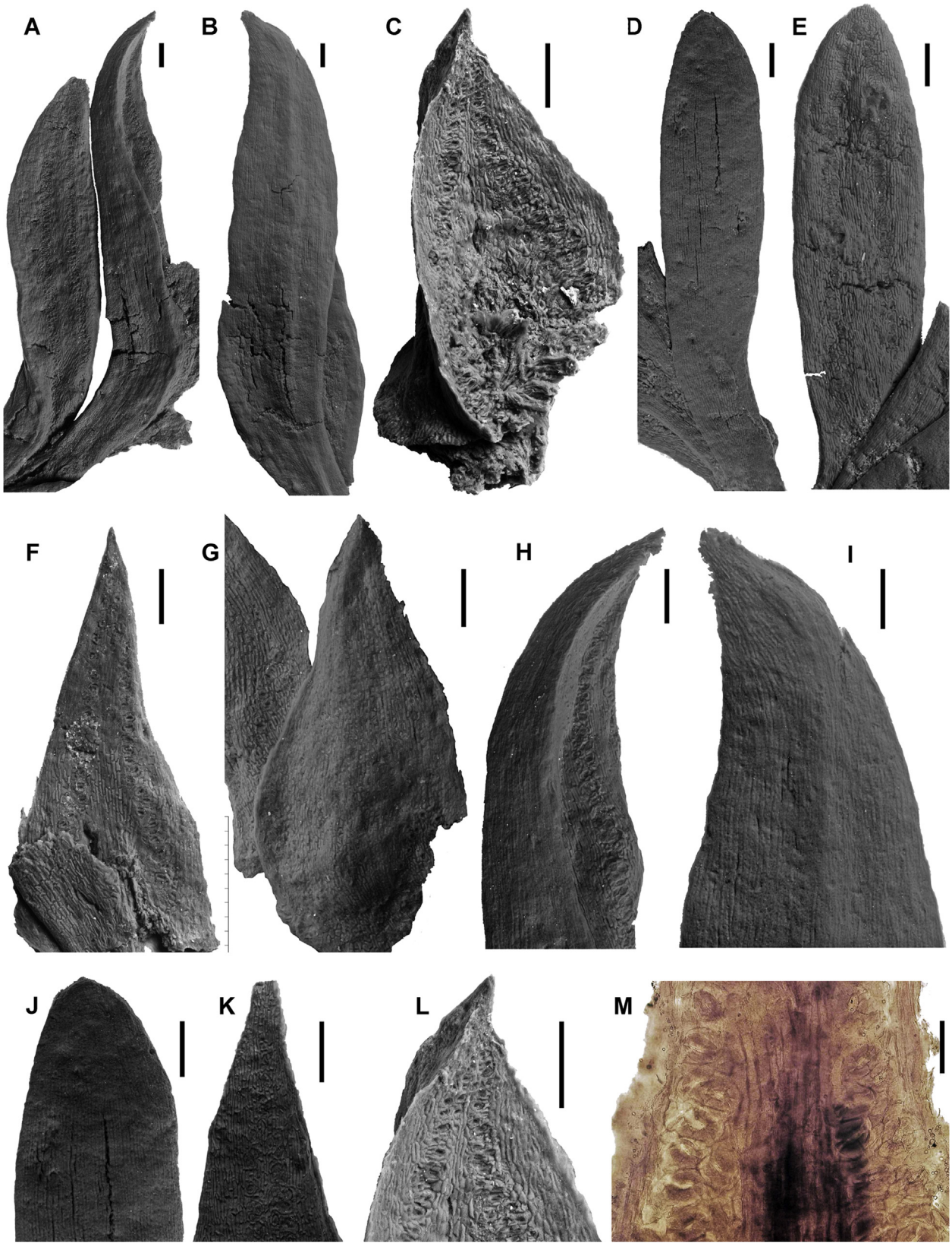

Fig. 4. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., different types of leaves with visible epidermal structure: A, B, H, I, M, specimen PIN RAS no. 5167/328 a (paratype); C, L, specimen PIN RAS no. 5167/812; D, E, J, specimen PIN RAS no. 5167/810; F, specimen PIN RAS no. 5167/813; G, specimen PIN RAS no. 5167/814; K, specimen PIN RAS no. 5167/815. Scale bars: A–L = 200 μm; M = 50 μm.

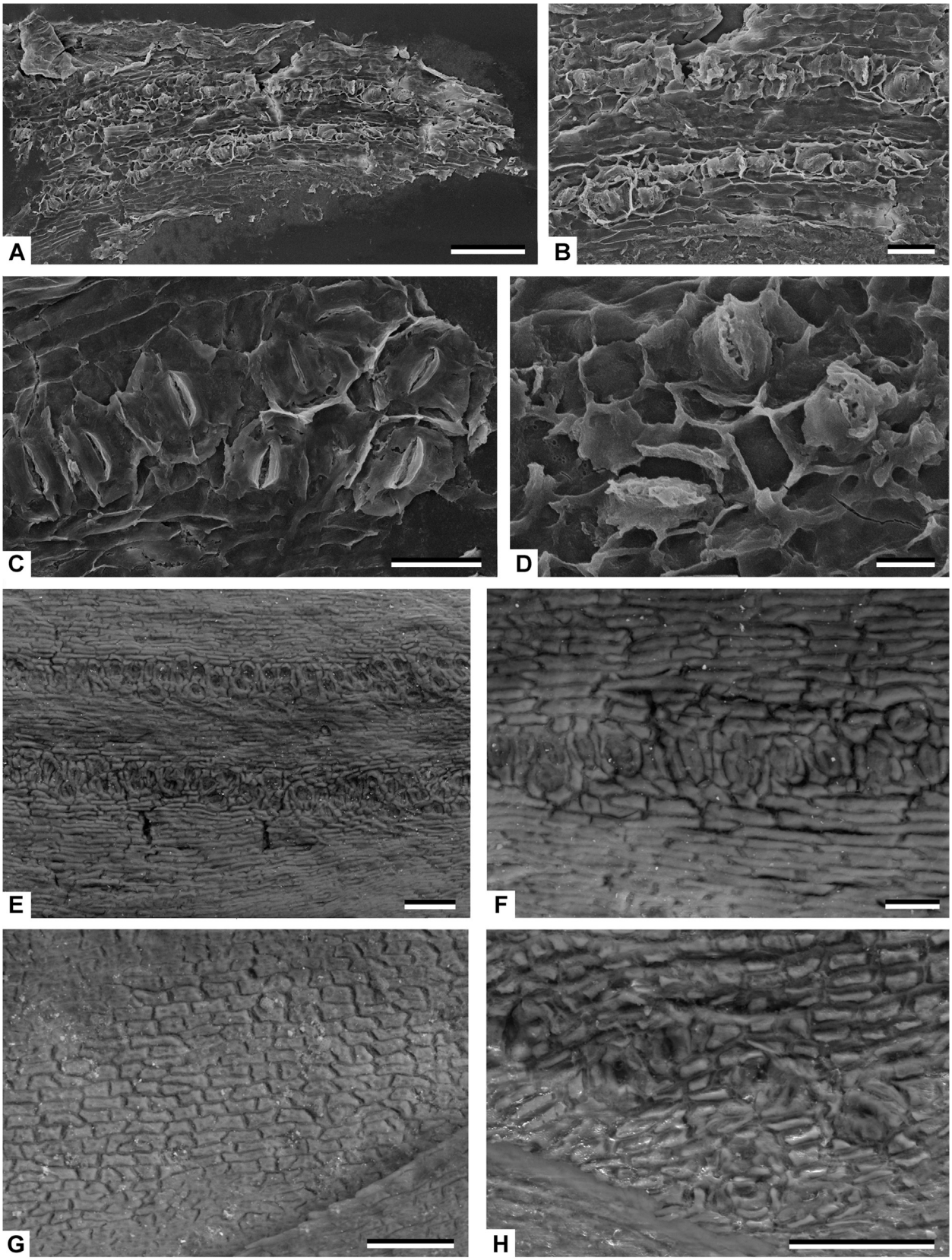

Fig. 5. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., epidermal characters of leaves: A–F, adaxial surface of leaves with stomatal bands; G, H, abaxial surface of scale leaves: G, epidermal cells; H, area with irregularly oriented stomata. A–E, specimen PIN RAS no. 5167/328a (paratype); F, specimen PIN RAS no. 5167/810; G, specimen PIN RAS no. 5167/817; H, specimen PIN RAS no. 5167/801. Scale bars: A, E, G, H = 100 μm; B, C = 30 μm; D = 10 μm; F = 50 μm.

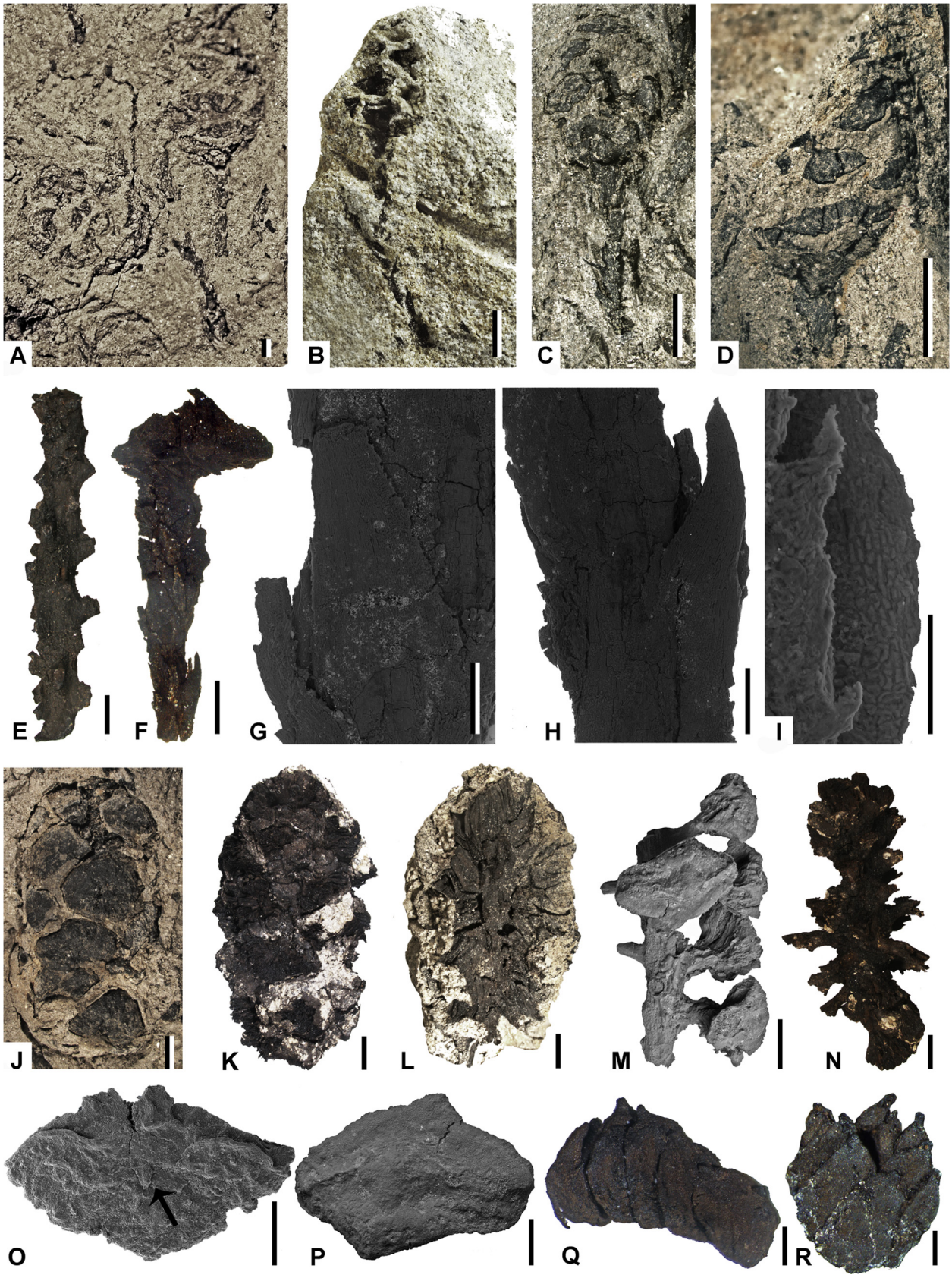

Fig. 6. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov.: A–D, seed cones in organic connection with shoots; E, M, N, cone axes; F–I, shoot with scale-like amphistomatic leaves, bearing seed cone; J–L, dispersed seed cones with *in situ* seeds; O, P, bract-scale complexes; Q, R, seeds extracted from seed cones; A, D, holotype PIN RAS no. 5167/278; B, specimen PIN RAS no. 5167/453 a; C, specimen PIN RAS no. 5167/513 (paratype); E, specimen PIN RAS no. 5167/710 (paratype); F–I, specimen PIN RAS no. 5167/701; J, specimen PIN RAS no. 5167/702; K, specimen PIN RAS no. 5167/703; L, specimen PIN RAS no. 5167/704; M, P, specimen PIN RAS no. 5167/705 (paratype); N, Q, R, specimen PIN RAS no. 5167/706; O, specimen PIN RAS no. 5167/712. Scale bars: A–D = 5 mm; E, F, J–N = 2 mm; G, H, Q, R = 500 μm; I = 200 μm.

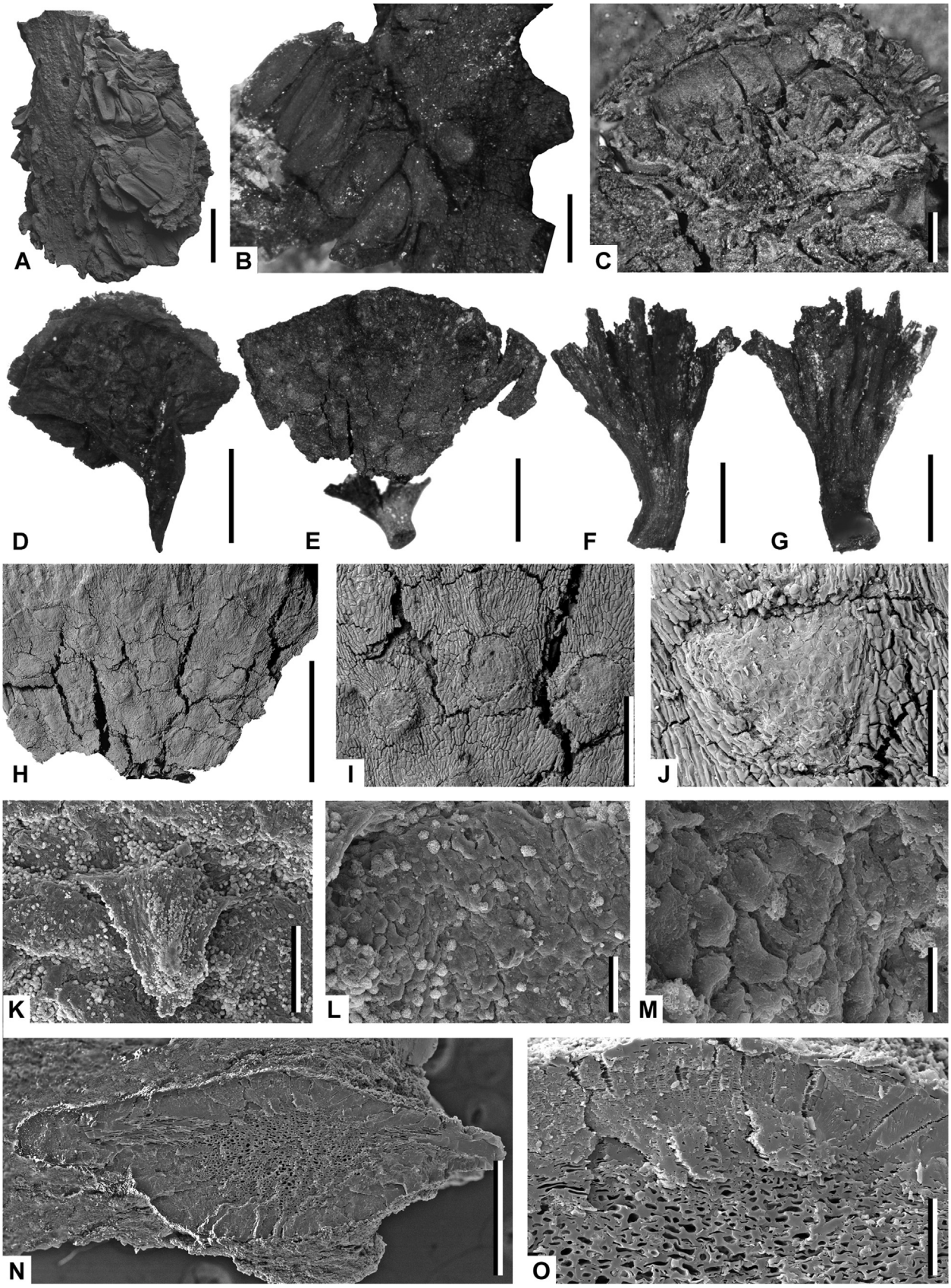

Fig. 7. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., A–C, *in situ* seeds attached to the bract-scale complexes; D, E, H–J, seed scars on the bract-scale complexes; F, G, naturally macerated conductive bundles in the bract-scale complex; K–M, dorsal surface of the bract-scale complex: K, median tooth; L, M, stomata in the central area; N, transverse section of the seed cone axis; O, detail of Fig. 7N; A, C, D, F, G, specimen PIN RAS no. 5167/711 (paratype); B, specimen PIN RAS no. 5167/710 (paratype); E, H–J, specimen PIN RAS no. 5167/707; K–O, specimen PIN RAS no. 5167/712. Scale bars: A, D, E, H = 2 mm; B, C, F, G = 1 mm; I, N = 500 μm; J, K = 200 μm; L = 50 μm; M = 20 μm; O = 100 μm.

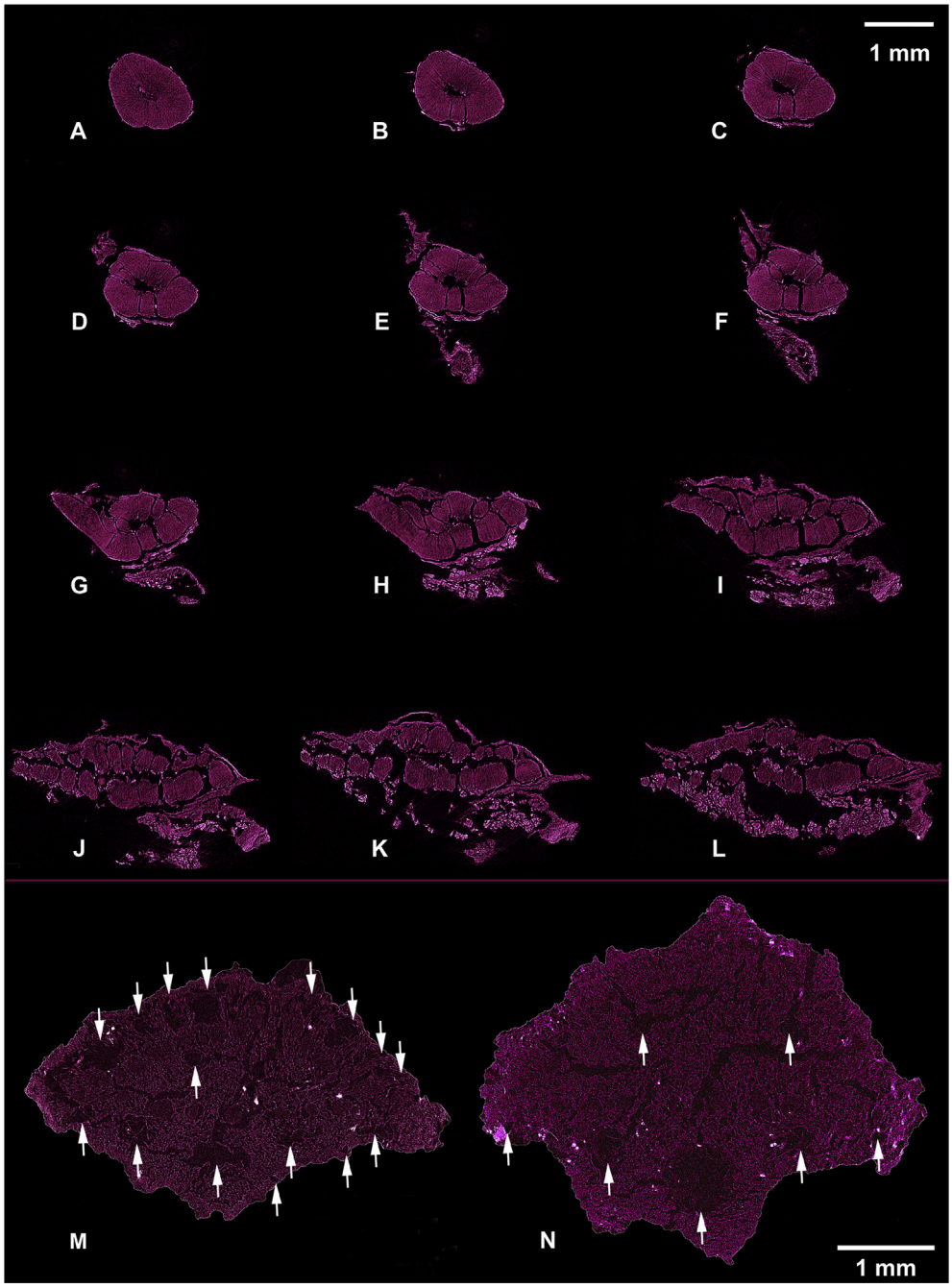

Fig. 8. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., serial cross sections of the bract-scale complex from the base of peduncle to the escutcheon: A–L: differentiation of the vascular system is visible; M, cross section near the escutcheon base: position of resin canals (arrows) and configuration of vascular system are visible; N, cross section of the same bract-scale complex in the middle of escutcheon: position of resin canals (arrows) and triangular configuration of vascular system with numerous adaxial bundles are visible; computer tomography (CT). A–L, specimen PIN RAS no. 5167/707; M, N, specimen PIN RAS no. 5167/705 (paratype).

axis or slightly diverging from it; the outline of leaf scars is triangular; the free portion of the leaves also has a triangular outline; the apex is acuminate (Fig. 4F, K), straight or slightly curved towards the stem (Fig. 4L); occasionally a variously developed keel is present, running from the base to the tip of the leaf (Fig. 3A–E). Scale-like leaves are about 1.5–2.5 mm long and 0.8–1.3 mm wide. The length of the free portion of leaves is 0.8–1.3 mm.

Falcate leaves (Figs. 3F–H, J, 4A, B, H, I, M, 5A–E) are keeled, often boat-shaped (with a depression on the adaxial surface); the free portion reaches up to 2/3 of the leaf length and the angle of divergence from the stem is up to 70°; the apex is acute, curved towards the stem or parallel to it (Fig. 4H, I); the base is long decurrent; leaves are 1.5–3.5 mm long (free part is 0.8–2 mm long) and up to 1.2 mm wide.

Linear-lanceolate leaves (Figs. 3I, K, L, 4D, E, J, 5F) are sessile with a long decurrent base (Fig. 4D) and a round (Figs. 3K, L, 4D, E, J) or pointed apex (Fig. 3I), straight or slightly curved towards the stem; the free portion of the leaf diverges from the stem at an angle of 25–45°; leaves are 1.5–3 mm long (free portion is up to 2 mm long); the margins are parallel over most of the leaf length; the maximum width occurs in the central part of the leaf and reaches 0.8 mm; the midrib is inconspicuous.

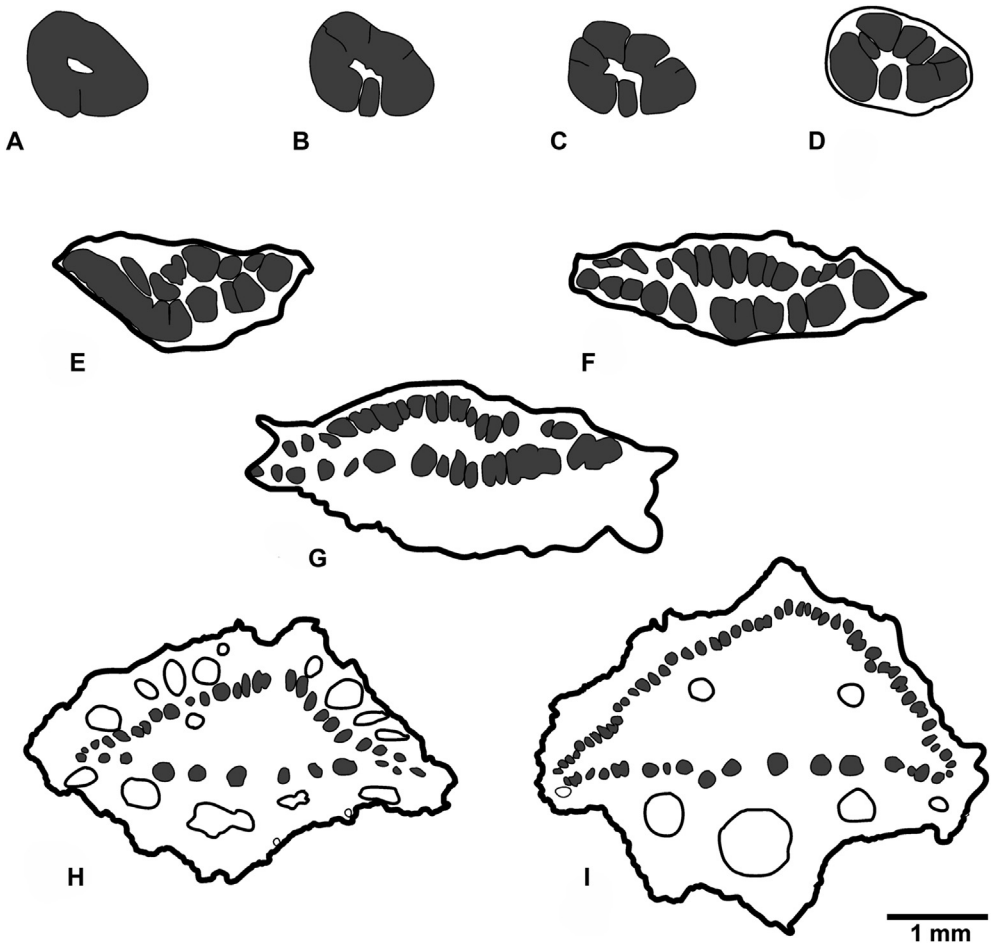

Fig. 9. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., drawings of the cross sections of bract-scale complexes represented on Fig. 8: A, Fig. 8A; B, Fig. 8B; C, Fig. 8C; D, Fig. 8F; E, Fig. 8H; F, Fig. 8J; G, Fig. 8L; H, Fig. 8M; I, Fig. 8N; specimen PIN RAS no. 5167/707; H, I, specimen PIN RAS no. 5167/705 (paratype); vascular bundles are dark grey; resin canals, outlined by a thin black line, are white.

A characteristic feature of all leaf types is the microdentate margin in apical areas (Figs. 4G, I, L, M, 13F); the leaf surface is with fine longitudinal striations on the abaxial side (Fig. 4E, I, J).

Leaf epidermis. The cuticle of all types of leaves is very thin. Linear-lanceolate leaves are strictly epistomatic (Figs. 3K, L, 4D, E); falcate leaves are epistomatic (Figs. 3J, 4A, B, H, I, M) with rare stomata on the abaxial surface at the base (Fig. 4B); and scale-like leaves are mainly amphistomatic (Figs. 4G, 5H). The adaxial surface of leaves of all types shows two distinct, not sunken stomatal bands, converging at the leaf apex (Figs. 4A, C, E, F, H, K–M, 5A, B, E, F). Each stomatal band is 30–100 μm wide, with one or two (rarely three at the base of leaves) stomata on its width. The width of the midrib zone of the linear-lanceolate leaves is up to 200 μm; and the width of marginal zones – 150–300 μm. The stomatal band consists of irregular rows of densely arranged stomata (Figs. 4M, 5A, B, E, F). The orientation of stomata is mostly transverse, rarely oblique, and, in rare cases, parallel to the length of the leaf. Stomata are incompletely amphicyclic or, rarely, monocyclic and completely amphicyclic, with four to six subsidiary cells, radially surrounding the stoma; differentiation of subsidiary cells into polar and lateral cells is occasionally observed; subsidiary or encircling cells are sometimes shared by neighboring stomata (Fig. 5C, D). The anticlinal cell walls are more strongly cutinized than those of ordinary epidermal cells. Guard cells are reniform, 15–30 μm long and 14–20 μm wide; the stomatal aperture is 15–20 μm long (Fig. 5A–D). Ordinary epidermal cells of non-stomatal zones (Fig. 5A, E, F, G) form regular rows parallel to the margins of linear leaves; cell outlines vary from elongated rectangular to almost isodiametric, mostly tetragonal, with straight or oblique, rounded end walls. The anticlinal cell walls are straight or slightly undulate, in the shape of thin ribs on the inner surface of the cuticles; periclinal walls are slightly convex. Epidermal cells vary within 10–100 μm in length and 5–15 μm in width; the length/width ratio is ca. 10/1. Ordinary epidermal cells of the abaxial surface of all leaf types (Figs. 4B, D, I, J, 5G) are generally less elongated than those in the marginal and midrib zones of the adaxial surface; they are 15–30 μm long and 5–15 μm wide; their length/width ratio does not exceed 5/1 (Fig. 5G). Few stomata, occurring on the abaxial surface of scale-like leaves, form a stomatal area that begins at the leaf base and reaches the widest part of the leaf (Figs. 4G, 5H); the structure of stomata is identical on both sides of the leaves.

Seed cones vary in maturity: immature ones contain *in situ* seeds, whereas mature ones are dehisced, lacking seeds. The seed cones are terminal, solitary, woody, non-disintegrating. Some cones are borne on shoots with scale-like leaves (Fig. 6A–D, F), others are found detached. Their outlines vary from ellipsoidal to ovate and obovate (Fig. 6A–D, G–L). Cones are 14–20 mm long and 9–12 mm wide. The cone axis is woody, straight, maintaining an even diameter from base to apex, or slightly tapering towards the apex; the diameter of the axis is 1.2–1.8 mm (Fig. 6E, M, N). The cone axis exhibits a cortex and a cylinder of secondary xylem with distinct pith; xylem rays are uniseriate; growth rings are absent (Fig. 7N, O).

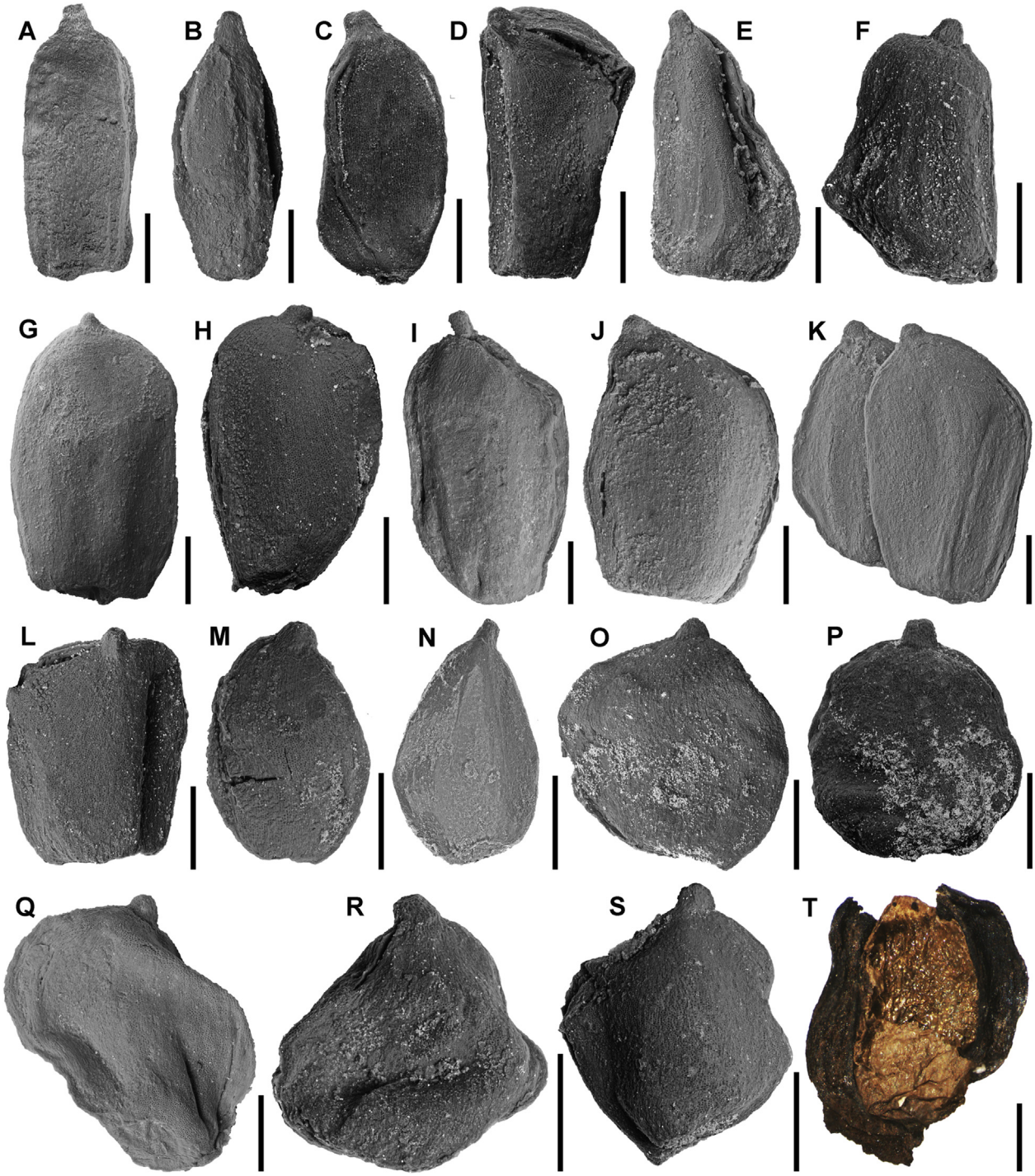

Fig. 10. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., A–S, variability in seed morphology; T, longitudinal split of the seed with remains of the nucellus with megaspore membrane. A–T, specimen PIN RAS no. 5167/710 (paratype). Scale bars = 500 μm.

Bract and ovuliferous scale are completely fused and almost equally developed; there are 14–26 bract-scale complexes per cone; they are helically arranged, five to seven per parastichy. Bract-scale complexes are peltate; the peduncle of the bract-scale complex is perpendicular to the cone axis (Fig. 6M, N), expanding to the escutcheon. The dorsal surface of escutcheons is rhomboid, flattened-rhomboid to hexagonal, with sharp or slightly rounded corners, convex, or having a small depression (Fig. 6M, O, P). A small triangular tooth is sometimes observed in the center of the escutcheons (Figs. 6O, 7K); thin lateral ridges depart from the tooth into the lateral corners. Escutcheons are 4.5–7 mm long and 2.8–4 mm wide. The epidermis of the bract-scale complexes is composed of rectangular cells varying in outline from isodiametric to longitudinally elongate (20–100 μm long, 15–30 μm wide); aggregations of stomata are observed in the central part of the dorsal surface of escutcheons (Fig. 7K–M). The bract-scale complexes are 3–4.1 mm long (from the base of the peduncle to the escutcheons). The peduncle of the scale is round or ellipsoidal in cross section; its

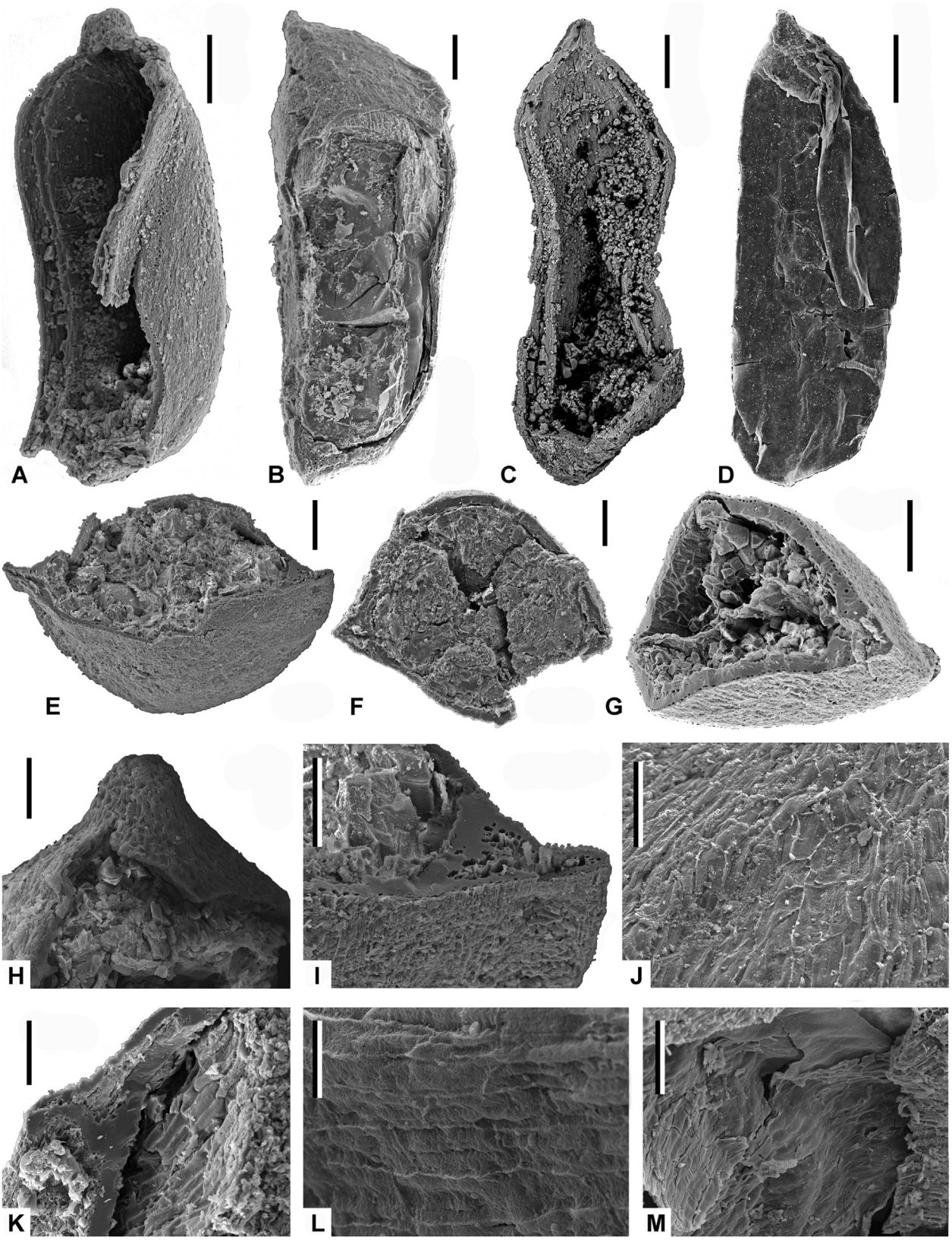

Fig. 11. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova gen. et sp. nov., structure of seeds: A–C, longitudinal splits; D, megaspore membrane; E–G, transverse section of seeds; H, micropylar part of the seed; I, K, narrow wings; J, outlines of epidermal cells with underlying hypodermal layer; L, cells of the endotesta; M, fragments of nucellus on the megaspore membrane. A–M, specimen PIN RAS no. 5167/710 (paratype). Scale bars: A–G = 200 μm; H, I, K, M = 100 μm; J = 50 μm; L = 20 μm.

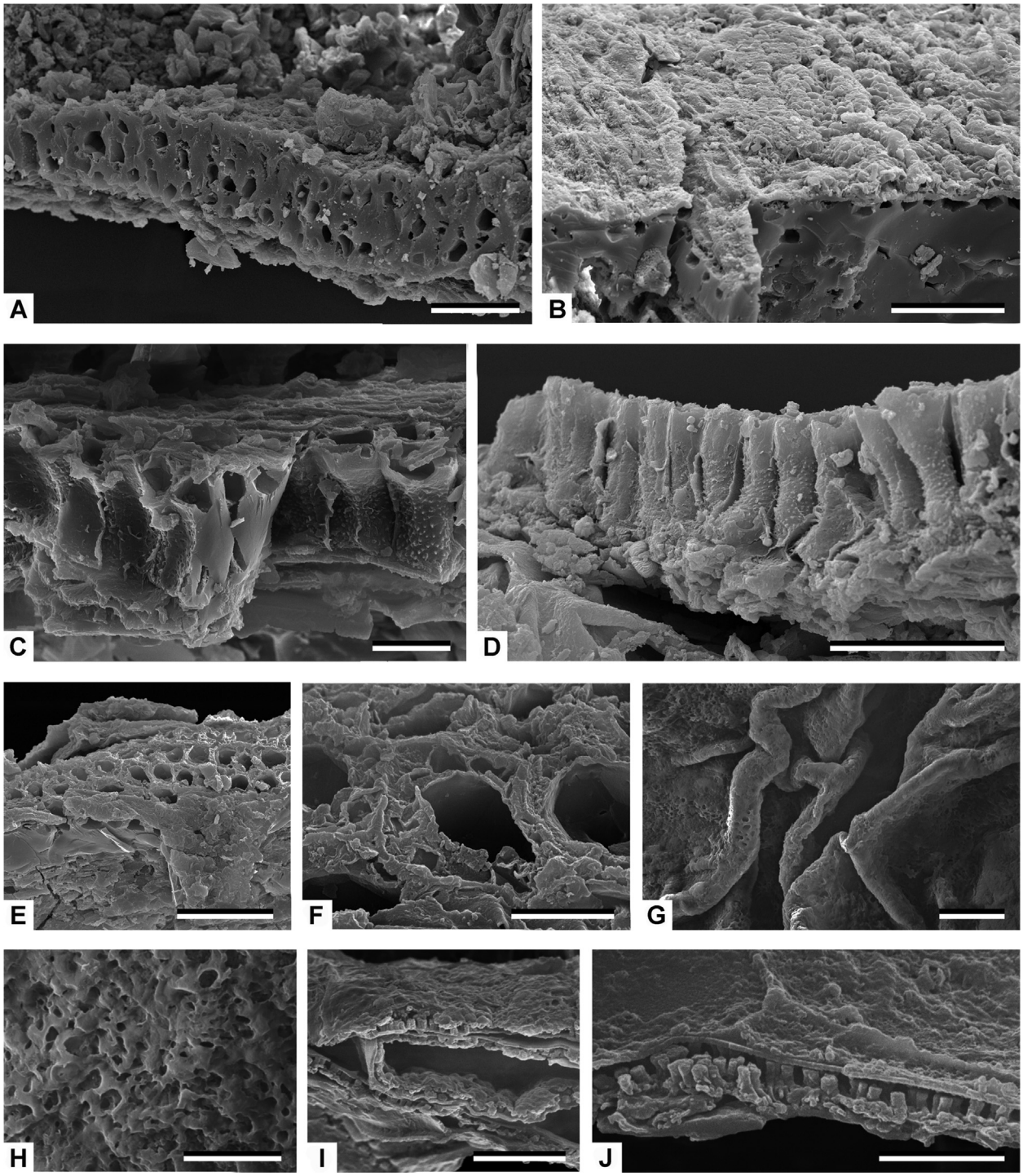

Fig. 12. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova: A, structure of the mesotesta in the chalazal zone; B, epidermal and hypodermal cells, above the sclerotesta; C–F, structure of the sclerotesta: C, D, sclereids, lateral view; E, F, sclereids, outer view; G–J, structure of the megaspore membrane. A–J, specimen PIN RAS no. 5167/710 (paratype). Scale bars: A, B, D, E = 50 μm; C, G = 20 μm; F, H, I = 10 μm; J = 5 μm.

diameter at the base is 0.5–1 mm. Seed scars (places of attachment of the seeds to the bract-scale complex) are rounded (Fig. 7H, I), rounded triangular (Fig. 7H, J) or ellipsoidal (Fig. 7H); their sizes are 0.21–0.7 mm × 0.2–0.4 mm.

The bract-scale complex is vascularized by a single cylindrical vascular bundle (0.5–1 mm in diameter) at the base; then the first abaxial bundle starts diverging (Figs. 8A, 9A); then two more abaxial and two adaxial bundles diverge from the first bundle (Figs. 8B, 9B): the total number of bundles at this level is five. Distally, abaxial and adaxial branches continue to dichotomize, forming a rhomboid shape of more than 40 vascular bundles, in cross sections of the bract-scale complex (Figs. 7F, G, 8C–L, 9C–G); in even more distal sections, the rhomboid shape becomes triangular with an abaxial base, and the number of adaxial bundles increases up to about 40. Resin canals are well developed in the bract-scale complex (Figs. 8M, N, 9H, I). They are present adaxially and

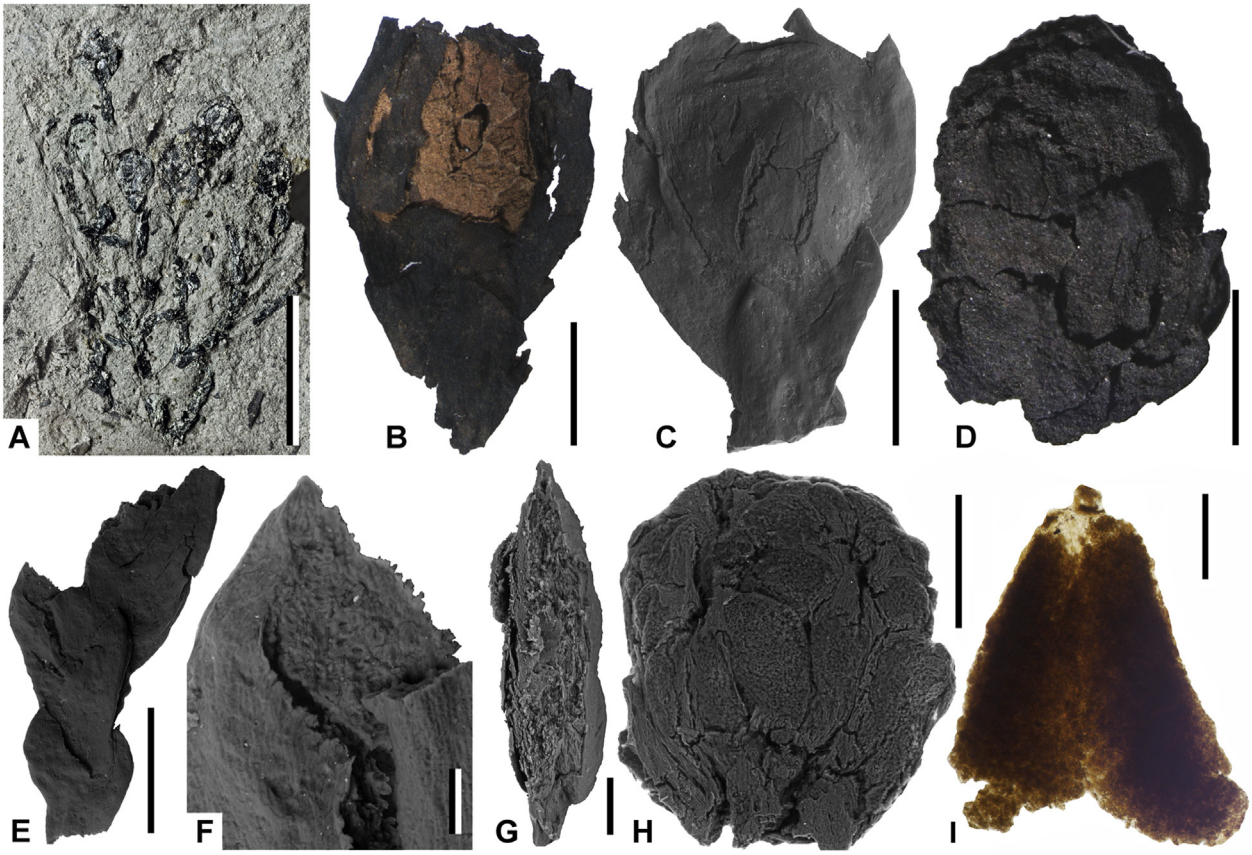

Fig. 13. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova, pollen cones in organic connection with leafy shoots: A, general view; B–D, morphology of pollen cones; E, shoot with scale-like leaves, bearing pollen cones; F, scale-like leaf with stomata on the adaxial surface; G, cross section of the pollen cone; I, macerated pollen cone: position and the number of sporangia is visible; I, two sporangia fused at the base. A–I, specimen PIN RAS no. 5167/334 (paratype). Scale bars: A = 1 cm; B–E = 1 mm; F = 100 μm; G, I = 200 μm; H = 500 μm.

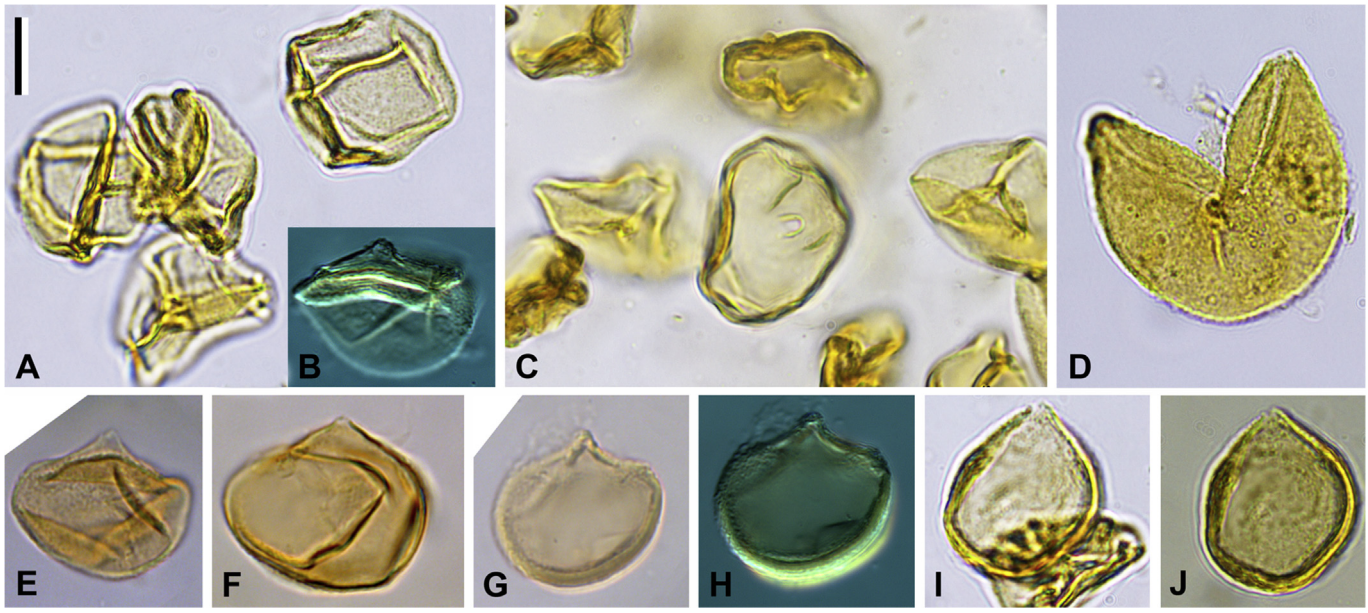

Fig. 14. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova, general morphology of pollen grains: A, folded pollen grains, no papillae are visible; B, E–H, pollen grains in lateral view showing an unequivocal papilla; C, several pollen grains, a pollen grain in the center seen in polar view shows a papilla (compare with Fig. 15K); D, clamshell-like pollen grain, which is most probably not conspecific; H, the presence of orbicules is evident on the pollen and near it; I, J, pollen grains in lateral view showing exine becoming thinner toward the papilla. A, C, D, I, J, photos were made with a Nikon eclipse Ci, equipped with a Nikon DS–Vi1 digital camera. E–G. Photos were made with a Karl Zeiss Axioplan 2, equipped with a Leica DFC–420 digital camera. B, H. Photos were made with a Karl Zeiss Axioplan 2, Axiocam MR digital camera, DIS. A, C, J. Helicon Focus 6.6.1 was used. A–J, specimen PIN RAS no. 5167/334 (paratype). Scale bar = 20 μm.

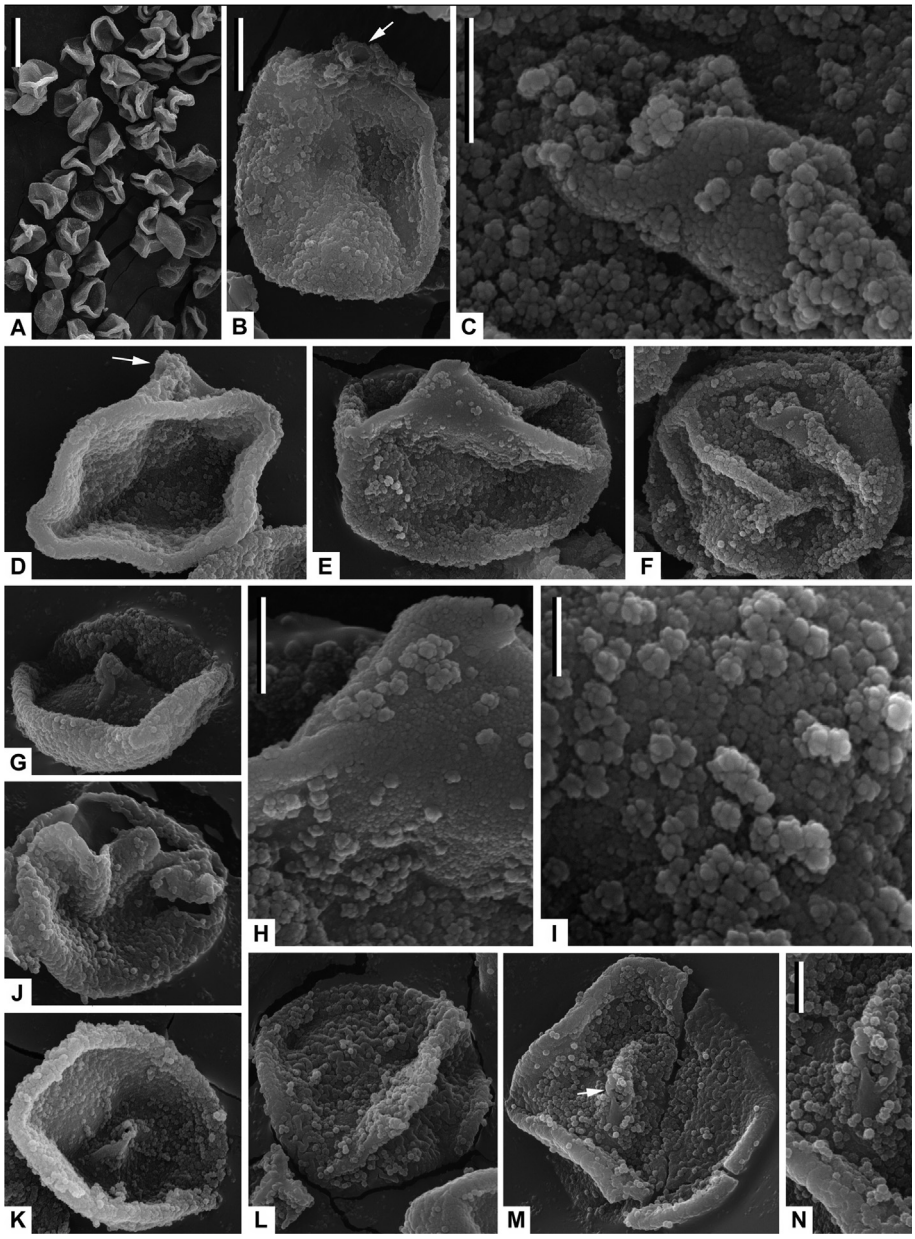

Fig. 15. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova, general morphology and surface pattern of pollen grains. A, variously folded pollen grains; B, pollen grain in lateral view with open papilla visible at distal pole; C, enlargement of Fig. 15F, granulate proximal surface is powdered with orbicules; D, E, variously folded pollen grains in lateral view; F, folded pollen grain showing the proximal surface; G, K, pollen grains show the distal pole with a papilla; H, enlargement of Fig. 15E, showing finely granulate surface of the leptoma area bearing orbicules; I, orbicules on the granulate surface of the exine; the orbicules are covered with densely situated granules; J, broken pollen grain; inner surface of the endexine is visible; L, pollen grain in polar view; a papilla is visible on the distal pole, on a flexure of the exine; fossulae are visible outside the apertural area; M, pollen grain in polar view; an open papilla is visible on the distal pole; fossulae are visible outside the apertural area; N, enlargement of Fig. 15M, numerous orbicules cover the surface of the pollen and enter the open papilla. A–N, specimen PIN RAS no. 5167/334 (paratype). Scale bars: A = 20 μm; B, D–G, J–M = 5 μm (photos are made at the same magnification, scale bar is inserted in Fig. 15B); C, H, N = 2 μm; I = 1 μm.

abaxially in relation to the vascular cylinder, as well as inside this cylinder. One broadened median and four lateral canals, arranged in one row, are presented in the abaxial part. Some small resin canals may occur below this row. Adaxial resin canals are numerous (about 14) and relatively large; they are arranged in one row.

Seeds are sessile and inverted: the micropyle of the seed is facing toward the cone axis (Fig. 7A–C); seeds are numerous, up to 22 per bract-scale complex, arranged in two to five arcuate rows (Figs. 6Q, R, 7D, E, H). Seed outlines vary from elongated rectangular (Fig. 10A), rectangular (Fig. 10L), rhomboid (Fig. 10S) and ellipsoidal (Fig. 10B, C, G, I), to rounded–triangular (Fig. 10R), rounded (Fig. 10O, P), ovate (Fig. 10M, N) and obovate (Fig. 10H); seeds can be nearly bilaterally symmetrical (Fig. 10A, B, G) or somewhat asymmetrical (Figs. 10D, E, F, Q, R, 11A–C), broadened in the micropylar (Fig. 10D, H) or chalazal area (Fig. 10E, F, R). Seeds are 1.2–2.5 mm long and 0.65–1.5 mm wide. The cross section of the seed is lenticular. The seed axis is straight (Figs. 10A, B, E, L, P, S, 11A, C) or curved (Figs. 10N, 11B). The micropyle is apical, in the shape of a convex protuberance (Fig. 10A–S), and 50–190 μm long. The chalaza is rounded (Fig. 10I, N, Q) or flattened (Fig. 10A, D, E, J, L). All seeds are winged, but the wings are very narrow and inconspicuous (Fig. 11E–G). Wings are 100–200 μm wide and triangular in cross section (Fig. 11I, K). The wings are formed by the exotesta and mesotesta. The seed coat is composed of three layers: an exotesta, a

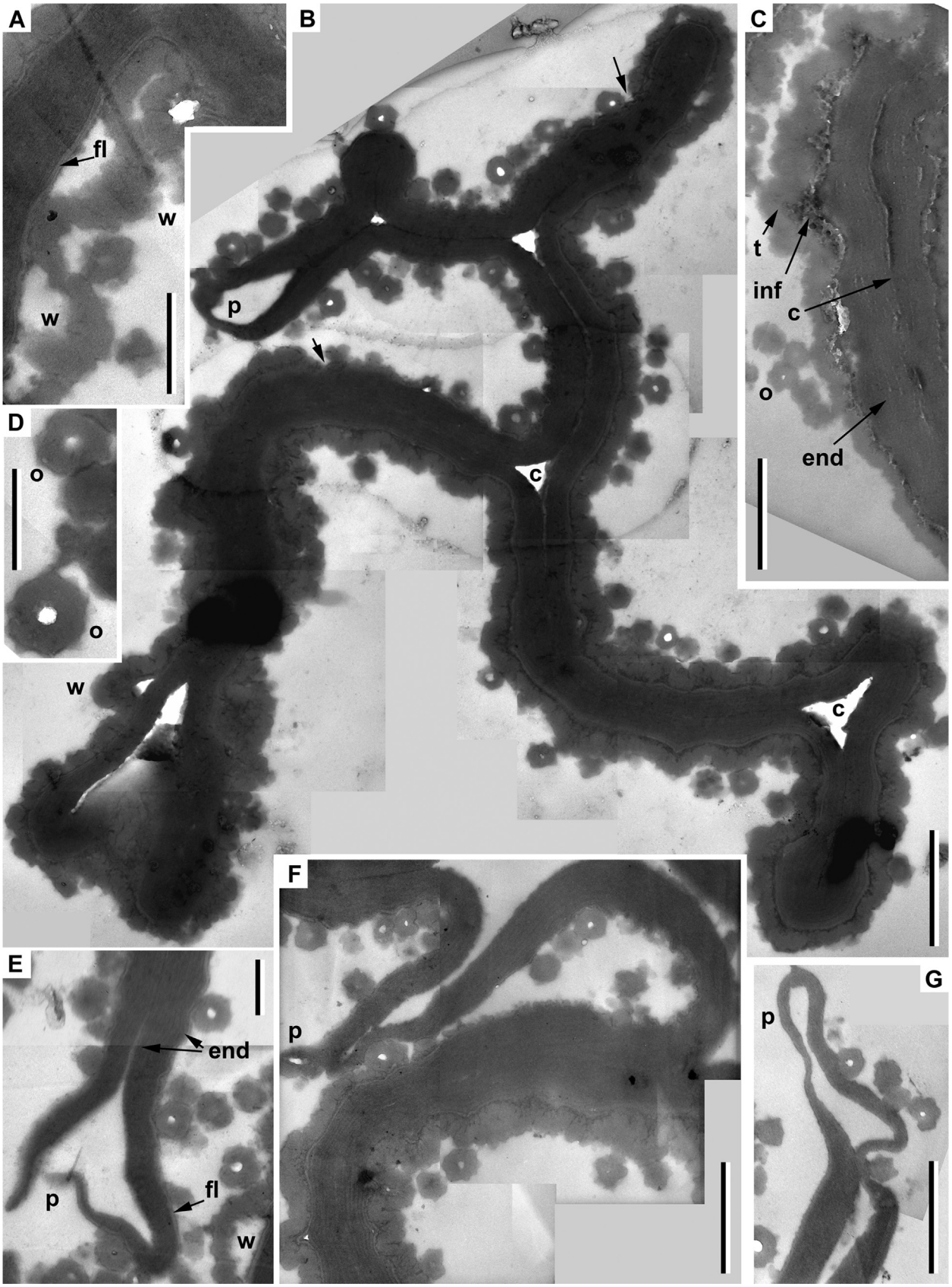

Fig. 16. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova, exine ultrastructure of pollen grains. A, upper portion of the ectexine deviates from the footlayer; B, composite image of a pollen exine with several flexures; leptoma is between arrows; C, the presence of an infratectum is evident; the endexine is lamellate; D, enlargement of Fig. 16B in the area of the papilla, several orbicules are cut; E, area of an opened papilla, wavy footlayer is visible; F, area of a papilla and leptoma; endexine lamellae are clearly distinguishable at the bottom of the figure; G, thinning endexine is the only layer that is present over a protruding papilla. A–G, specimen PIN RAS no. 5167/334 (paratype). Scale bars: A = 0.5 μm; B, C, F, G = 1 μm; D = 0.5 μm; E = 0.4 μm p – papilla; o – orbicule; inf – infratectum; fl – footlayer; end – endexine; w – wave; c – compressed cavity of the pollen grain.

mesotesta, and an endotesta. The exotesta consists of epidermal and hypodermal cells, which are infrequently preserved (Figs. 11J, 12B). Epidermal cells are thin-walled, irregularly tetragonal to elongate rectangular; they are 40–50 μm long and 15–30 μm wide (Figs. 11J, 12B). The hypodermis consists of thick-walled elongated cells, rounded in cross section (diameter is 5–8 μm; Figs. 11J, 12B). The mesotesta (sclerotesta) consists of a single layer of cylindrical sclereids; they are 10–15 μm in diameter and 40–50 μm long (Fig. 12C–F). The sclerotesta becomes thicker in the chalazal area, reaching 50–60 μm; here it consists of three or four layers of isodiametric sclereids (Fig. 12A). The endotesta is composed of at least two layers of cells (Fig. 11K, L). A layer located directly under the sclerotesta consists of thick-walled elongated cells with oblique end walls; cells are more than 100 μm long and 5–8 μm wide. The underlying layer is composed of larger thin-walled rectangular cells with undulate anticlinal walls; they are 30–65 μm long and 10–15 μm wide. In the area of wings, below the layer of sclereids, the testa is filled with fibrous tissue; the diameter of fibers is 5–7 μm (Fig. 11I). The nucellus is free from the integument (Fig. 10T) and finely cutinized; cells of the nucellus are more or less rectangular, with straight or oblique end walls; they are longitudinal, 30–130 μm long and 10–15 μm wide (Fig. 11M). The megaspore membrane is well developed (Fig. 11D), up to 2.5 μm thick; the foot layer is about 0.25 μm thick; the middle layer consists of columns of 0.5 μm high and up to 0.3 μm in diameter; the outer layer is composed of irregularly dichotomizing rods, forming an alveolar pattern (Fig. 12G–J).

The pollen cones are solitary, terminal (Fig. 13A), 3–4 mm long and 3.2 mm wide; located on regular shoots with scale-like leaves (Fig. 13A–C, E). Large rounded–rhomboid sterile scales (which form the first two helical rows) are located at the base of the cone, covering fertile microsporophylls; they are about 1.3–1.5 mm in both dimensions. The pollen cone axis is about 200 μm in diameter (Fig. 13G). The microsporophylls are helically arranged (Fig. 13C, D), consisting of a thin peduncle, extending to a thin lamina. There are (3) 4 abaxial pollen sacs, oriented more or less parallel to the cone axis and attached to the base of the sporophyll (Fig. 13H). There are about 11–13 microsporophylls in a pollen cone. Sporangia are ellipsoidal, slightly tapering towards the bottom, 700–800 μm long and 300–350 μm wide (Fig.13I).

Pollen. Pollen grains are small and strongly folded (Figs. 14A, 15F). Although they bear a papilla, it is clearly visible only in a few pollen grains by contrast to hundreds of pollen grains, where the papilla is hidden by numerous folds of the exine (Fig. 15A). Because of the folds, the most common outline of the pollen grain is an irregular polygon; many pollen grains are irregularly oval (Figs. 14A, 15A); those specimens that show a papilla are usually observed in lateral view (Figs. 14E–J, 15B, D). We did not observe boat-shaped pollen grains. Clamshell-like torn pollen grains occur rarely, and they are most probably not conspecific with the pollen cone: they are larger than other pollen grains and have a denser exine (Fig. 14D). We have also observed a fossil bisaccate pollen grain in our preparations, clearly indicating that alien pollen grains can be present. We measured 20 pollen grains in transmitted light: the average dimensions are 22.6 × 18.9 μm, the range is 17.6–27.5 × 15.2–25.0 μm.

An unequivocal papilla is visible in laterally preserved specimens with fewer folds (Figs. 14B, E–H, 15D). It protrudes over the oval outlines of the pollen as an isosceles triangle, which is about 3.4 μm high and with a broad base of about 7.4 μm (Fig. 14E). It is less obvious in some other laterally preserved specimens (Fig. 14I, J), but these specimens show that the exine becomes thinner towards the papilla. We also observed a papilla in a few pollen grains preserved in polar view (Figs. 14C, 15G, K, M).

Orbicules are numerous (Fig. 15C, I, N); they are irregularly distributed over the surface of pollen grains (Figs. 15E, F, K, 16B). Orbicules are 0.32–0.48 μm in diameter (as measured under SEM) and densely covered with granules. About eight to ten granules are visible on each orbicule; fully visible granules reach 0.13–0.18 μm in diameter (Fig. 15C, I). The orbicule sections appear as polygons, most of which have obtuse angles, though acute angles were also occasionally observed (Fig. 16D). The maximal diameter of orbicules on sections is about 0.3–0.45 μm. The diameter of their inner cavity varies from 0.05 μm to 0.1 μm.

The surface pattern of pollen grains is better understood on the basis of both SEM and TEM data, because it is otherwise largely hidden by orbicules and because it is often difficult to understand which area of the pollen grain is exposed to the observer. The surface is granulate. The granules are strongly fused into a tectum, and occasionally the outer portion of the ectexine separates from the footlayer forming a wavy pattern (Fig. 16A, B). Such areas with ridges and depressions between them are visible under SEM in non-apertural regions as a fossulate surface covered with granules (Fig. 15L, M). A leptoma occupies a considerable portion of the distal surface, which is more conspicuous in TEM images (Figs. 16B, F, 17), whereas orbicules and numerous exine folds hide the boundaries of the leptoma in SEM (Fig. 15M). The leptoma is composed of a footlayer and patchy remnants of the overlaying ectexine (Fig. 16B, F); the leptoma surface appears granulate because of these patches and because the exposed footlayer becomes wavy (Fig. 16E, F). The granulate surface of the leptoma is finer than the non-apertural surface. The endexine is the only layer that remains over the papilla, making its surface more or less smooth. We observed in some torn pollen grains that the inner surface of the endexine is also smooth (Fig. 15J).

The tectum is formed by densely fused granules and underlain by a thinner infratectum of smaller granules. The infratectal granules are more loosely arranged than those of the tectum (Fig. 16C). The

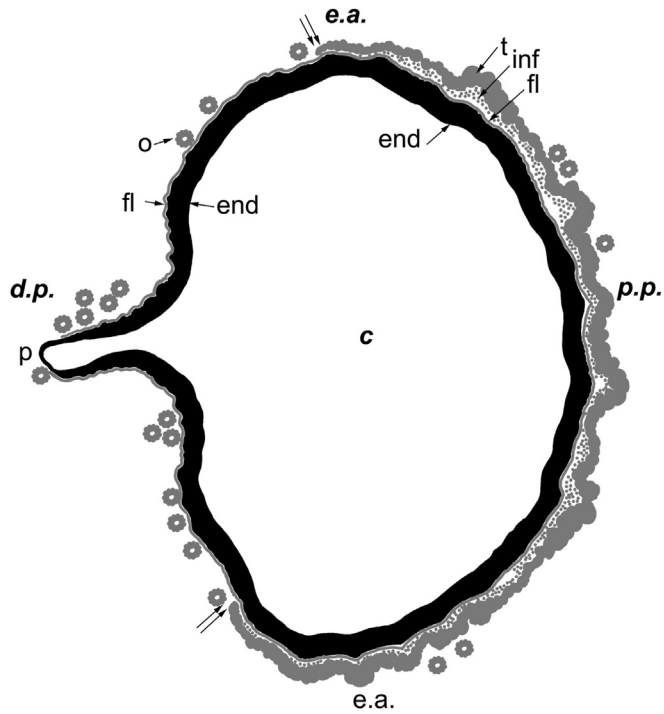

Fig. 17. *Krassilovidendron fecundum* Sokolova, Gordenko et Zavialova,: schematic section of a pollen grain: double arrows – leptoma/non-apertural area boundary; d.p. – distal pole; e.a. – equatorial area; p.p. – proximal pole; p – papilla; o – orbicule; t – tectum; inf – infratectum; fl – footlayer; end – endexine; c –cavity of the pollen grain.

tectum/infratectum boundary is not very sharp. The infratectum rests on a footlayer, which is represented by a single lamella (Fig. 16F) or double lamella (Fig. 16A) of the same electron density as the other ectexine layers and is slightly thicker than the outermost lamella of the endexine. The endexine is thick, more electron-dense than the ectexine, and comprises six or seven lamellae (Fig. 16A, F). In places, the outer portion of the exine is separated from the underlying exine with formation of one or several short waves. More often, the footlayer remains attached to the endexine, and the waves are composed by the tectum and infratectum (Fig. 16A). The exine is easily flexible. These folds, which affect the entire exine, are preservational. In transmitted light, they can look very similar to papillae, but the ultrastructure allows us to differentiate between apertural and non-apertural areas.

The aperture is represented by a wide distal leptoma with a papilla in the center (Figs. 15K, B, 17). The tectum becomes thinner and disappears over the leptoma. The infratectum transforms to patches scattered over the footlayer and also disappears further towards the distal pole (Figs. 16F, 17). Most portion of the surface of the leptoma consists of the footlayer alone (Fig. 17). Its external contour becomes wavy, and the granulate surface of the leptoma as observed under SEM is the footlayer surface (Fig. 15H). The outermost lamella of the endexine reproduces waves of the footlayer (Fig. 16E). The footlayer disappears only over the papilla (Figs. 16G, 17). The endexine is more or less constant in thickness in non-apertural areas and in the area of the leptoma, but gradually becomes much thinner in the papilla area (Figs. 16B, E, F, 17). Endexine lamellae are clearly discernible in non-apertural areas and in the area of the leptoma, but no individual lamellae are clearly recognizable over the papillae. Therefore, we were able to count lamellae only in non-apertural areas and in the area of the leptoma (there are six or seven lamellae). As to the papilla area, we merely compared the thickness of the endexine in this and other regions and concluded that a few lamellae or only one lamella most probably is present in the papilla (Fig. 16G).

Remarks. Characters of pollen morphology and ultrastructure can be differently expressed in mature vs. maturing pollen grains of the same plant; for example, the relative thicknesses of ectexine sublayers can be different as well as the number of endexine lamellae. Therefore, for meaningful comparisons it is important to evaluate correctly the degree of maturity of pollen grains of the fossil plant analyzed.

The *Krassilovidendron* pollen grains we observed are most probably mature. Although apertures were not detected in all pollen grains, this cannot be considered as an index of immaturity, as was sometimes erroneously done (e.g. Buczkowksi et al., 2016). Studies on modern plants show that apertures are formed very early during pollen ontogeny. They are always present as early as the tetrad stage (e.g., Meyer, 1977; Uehara and Sahashi, 2000). In general, if apertures are observed in some of the pollen grains, then they must be present in all the pollen grains, even though they may not be visible. Papillae or pores are difficult to detect in fossil taxodiaceous pollen because these structures are small and, therefore, easily hidden by folds. The presence of numerous folds is not an index of immaturity either. Comparable folding is absent in living pollen grains because the turgid cellular content allows the pollen grain to maintain its shape. However, as soon as the gametophyte is lost, a taxodiaceous pollen grain becomes folded, since it has a very thin and flexible exine.

Pollen grains of *Krassilovidendron* are preserved as monads, that means that their development had already passed the tetrad stage. The tetrads are unlikely to have come apart during fossilization, because apertures were detected. In addition, orbicules are abundant on the observed pollen grains, and Meyer (1977) showed that orbicules are deposited on taxodiaceous pollen grains only after the callose wall of the tetrad is dissolved and the tetrad stage is finished. The presence of numerous orbicules on the surface of mature pollen grains is common in taxodiaceous plants, as indicated by numerous studies of unequivocally mature pollen grains of modern members of the group (e.g., Roscher, 1975).

For the post-tetrad stages of ontogeny, Kurmann (1990) showed that in slightly immature taxodiaceous pollen grains the ectexine and endexine exhibit equal electron density, whereas in fully mature pollen grains the electron density of these layers conspicuous: the ectexine is less electron dense than the endexine. Additionally, endexine lamellae are quite loosely packed in slightly immature pollen grains, whereas in fully mature pollen they are tightly packed (because of the pressure of enlarging gametophyte). Since our material shows tightly packed endexine lamellae, which are more electron dense than the overlying ectexine, we can conclude that the pollen grains are mature.

4. Discussion

4.1. Evolutionary significance

To date, *Krassilovidendron* is the oldest and one of the most completely characterized fossil natural taxa of the Sequoioideae, sharing the greatest number of features with extant *Sequoia* and *Sequoiadendron*. The morphological and anatomical data from the fossil record show that the main characters typical of the genera *Sequoia* and *Sequoiadendron* had already evolved by the end of the Albian: 1) leaf polymorphism (however, less developed in the new genus and *Sequoiadendron* than in *Sequoia*) with at least three types of leaves ranging from scale-like to lanceolate; 2) epidermal characters, such as the presence of two stomatal bands on the adaxial surface of leaves, with variously oriented stomata; 3) general morphology of terminal seed cones showing nearly globose to ellipsoidal outlines; 4) helical arrangement of peltate bract-scale complexes, formed by fused bract and ovuliferous scales; 5) anatomy of bract-scale complexes, vascularized at the base by a cylindrical bundle that bifurcates to form abaxial and adaxial dichotomizing sets of bundles; 6) inverted position of winged seeds, located on the adaxial surface of bract-scale complexes; 7) stratification of the seed testa into exotesta, mesotesta and endotesta; 8) general morphology of terminal pollen cones, located on unspecialized, regular shoots; 9) helically arranged microsporophylls, consisting of a thin peduncle and thin lamina; 10) the abaxial ellipsoidal microsporangia (pollen sacs) attached basally to microsporophylls; 11) small pollen grains with a distal leptoma crowned by a papilla; 12) presence of numerous orbicules on the pollen surface; and 13) three-layered pollen ectexine with a tectum of strongly fused granules, an infratectum of smaller and more loosely arranged granules, and a thin footlayer.

However, along with features characteristic of *Sequoia* and *Sequoiadendron*, *Krassilovidendron* also combines features that may be plesiomorphic within the Sequoioideae, such as the presence of seeds with weakly developed wings, the high number of seeds, and their arrangement in many rows. Among extant and extinct members of the Sequoioideae, seeds arranged in two rows (the maximum number of rows previously known for the Sequoioideae) have been documented only in *Sequoiadendron* (Buchholz, 1939) and *Drumhellera* (Serbet and Rothwell, 2016; Rothwell and Ohana, 2016). Among modern taxa of the Cupressaceae, a distribution and number of seeds comparable to *Krassilovidendron* is known only in species of *Cupressus* L., which may also indicate that this feature, uncommon within the Cupressaceae, is plesiomorphic in this family (Farjon and Garcia, 2002). It is possible that this character of *Cupressus* was inherited from its Cretaceous ancestors, although

parallel evolution cannot be ruled out. As for the peltate shape of sequoioid bract-scale complexes, it is possible that it evolved in parallel with, and in order to accommodate, a large number of small seeds. Subsequently, the number of seeds per bract-scale complex could have been reduced and the seeds enlarged, but with the peltate shapes of bract-scale complexes being retained.

Poorly developed wings have been noted for other Cretaceous and Cenozoic Sequoioideae, such as *Quasisequoia* (Srinivasan and Friis, 1989), *Yezosequoia* (Nishida et al., 1991), *Nephrostrobus* (LaPasha and Miller, 1981), *Yubaristrobus* (Ohsawa et al., 1993) and *Protosequoia* (Miki, 1969). However, wings still seem to be much better developed in *Quasisequoia* and *Protosequoia* than in *Krassilovidendron*. It is possible that one of the main evolutionary trends in the Sequoioideae led to the reduction of the number of seeds and the enlargement of wings—this is consistent with the data published by Contreras et al. (2017).

Another character of *Krassilovidendron* that is potentially plesiomorphic is leaf polymorphism. The same types of leaves are known for another fossil representative of the Sequoioideae—*Protosequoia* (Miki, 1969). This feature is also present in modern *Sequoia sempervirens*, in which the number of leaf types is higher than in *Krassilovidendron fecundum*. Leaf polymorphism is also characteristic of some fossil shoots traditionally identified as *Sequoia* (Sveshnikova, 1967; Krassilov, 1979; Samylina, 1988), although the generic assignment of those specimens should be revised, based on the fact that they are too fragmentary and, as such, should be treated as fossil-taxa (Krassilov, 1971). Polymorphic leaves also occur in fossil and modern representatives of *Sequoiadendron* (Buchholz, 1939; Kunzmann, 1999; Sokolova and Moiseeva, 2016). Although the new genus is characterized by the same range of leaf types as *Sequoia* and *Sequoiadendron*, leaves of the new genus differ from these in a number of epidermal characters, as discussed above. These epidermal characters of the new genus are very similar to those of representatives of the fossil genus *Elatides* Heer emend. Harris, for example *E. williamsonii* (Lindley et Hutton) Nathorst from the Middle Jurassic of England (Harris, 1979), *E. bommeri* Harris from the Lower Cretaceous of Belgium (Harris, 1953), *E. harrisii* from the Lower Cretaceous of China (Zhou, 1987), and *E. zhoui* Shi et al. from the Lower Cretaceous of Mongolia (Shi et al., 2014). It is difficult to conclude whether the similarity in the epidermal structure points to the origin of Sequoioideae from a stem group including *Elatides* or is the result of convergent evolution.

In terms of pollen, all genera of the Cupressaceae have very similar pollen grains (Meyer, 1977; Kurmann, 1994; Kodrul et al., 2006). However, a number of differences in pollen morphology and exine ultrastructure are sufficient to differentiate between the genera. The new genus shares several important features of pollen morphology and exine ultrastructure with other members of the Sequoioideae; however, we have also revealed similarities between pollen grains of the new taxon and some members of other subfamilies. Thus, pollen grains of *Cryptomeria* (Roscher, 1975; Xi and Wang, 1989; Miki–Hiroshige et al., 1994; Uehara and Sahashi, 2000) are similar to those of *Krassilovidendron* in features that we consider as characteristic, i.e. papilla length/pollen diameter ratio and the presence of an infratectum (as well as some other details of the ectexine). Pollen grains of all members of the Sequoioideae have an extended leptoma with a papilla; their ectexine includes a tectum of large and densely packed granules and an infratectum of small and rather loosely packed granules. *Sequoia*, *Sequoiadendron*, and *Metasequoia* differ from *Krassilovidendron* by a high number of lamellae in the endexine. *Drumhellera* (Serbet and Stockey, 1991) has a similar number of endexine lamellae to *Krassilovidendron*, but those specimens may contain evidence that pollen grains of *Drumhellera* are slightly underdeveloped, thus, a higher number of endexine lamellae could have been by the time the pollen grains reached full maturity. In conclusion, we are unable to demonstrate complete similarity between the new taxon and any modern or fossil taxodiaceous plant in characters of pollen morphology and ultrastructure; nevertheless, pollen of *Sequoia* and *Metasequoia* is most similar to the new taxon, whereas *Sequoiadendron* and *Drumhellera* (among members of the Sequoioideae) are less similar.

More generally, the information available on fossil Sequoioideae is so scattered and incomplete in coverage, both morphologically and taxonomically, that phylogenetic relationships within this group, including the fossils, have remained unresolved. It has been hypothesized that the most probable ancestor of *Sequoia* and *Sequoiadendron* is *Yezosequoia* (Ohsawa, 1994). However, information now available on *Krassilovidendron* shows that in this genus the anatomical structure is more similar to the two modern genera than *Yezosequoia*. Genera combining characters of both *Sequoia* and *Sequoiadendron* (for example, *Quasisequoia*, *Austrosequoia*, and *Protosequoia*) existed during the Late Cretaceous and Paleogene. These plants may represent descendants of plants like *Krassilovidendron*. Obviously, *Sequoia* and *Sequoiadendron* are younger taxa.

4.2. Ecology

Based on the lithology and taphonomy at the Kubaevo locality (Maslova et al., 2011), where plant-bearing lenses with abundant remains of *Krassilovidendron* are closely associated with immature sandy and clayey paleosoils that contain coalified roots preserved *in situ*, we hypothesize that *Krassilovidendron* preferred riparian environments, similar to the habitats of modern *Sequoia*, *Sequoiadendron*, and *Metasequoia* (Farjon, 2010). If this is the case, then the ecological niche of the Sequoioideae may not have changed significantly since the Cretaceous. The *Krassilovidendron* material is found in association with other members of the Cupressaceae, various angiosperms (platanoids, Nymphaeales, and others), Pinaceae, ginkgos, and cycads (Maslova et al., 2011; Golovneva and Nosova, 2012). The seed cones of the new genus were probably reaching maturity within one year, similarly to *Sequoia*. This is suggested by the fact that the cone axis in mature opened cones of *Krassilovidendron* contains only one annual ring of wood. In contrast, in *Sequoiadendron* the seeds begin maturing only in the second year and seed cones persist for several years on the tree being green and closed (Hartesveldt et al., 1975). Additionally, we suggest that the peculiar wings of the *Krassilovidendron* seeds could have acted as floating devices and, thus, represented adaptation for riverine dispersal. Seeds of the modern Sequoioideae with significantly better developed wings possess relatively low capacity for wind dispersal (no more than 400 m away from the parent tree) (Hartesveldt et al., 1975). The viability of dispersed seeds is very low in modern Sequoioideae, and *Krassilovidendron* with its small and nearly wingless seeds may not have represented an exception.

5. Conclusions

The presence of *Sequoia* and *Sequoiadendron* in the mid-Cretaceous has yet to be confirmed based on reproductive organs. At the same time, numerous of morphological and anatomical characters of *Sequoia* and *Sequoiadendron* were present at that point in time. The oldest known representative of Sequoioideae possessed putatively plesiomorphic characters, such as conspicuous leaf polymorphism, large number of seeds, their arrangement in several rows, and rudimentary seed wings. The ecology of *Krassilovidendron* was similar to that of modern *Sequoia* and *Sequoiadendron* and that may indicate evolutionary stasis in some morphological and anatomical characters of these plants.

On the whole, fossil Sequoioideae demonstrate a high mosaicism in morphological and anatomical characters (Peters and Christophel, 1978; LaPasha and Miller, 1981; Serbet and Stockey, 1991; Stockey et al., 2005; Serbet and Rothwell, 2016), and *Krassilovidendron* is a new piece of this still incomplete morpho-anatomical puzzle. The patchiness of this mosaicism is often complicated by scanty information on fossil taxa, like those preserved as three-dimensional coalified remains. Data presented here shows that such a material is very promising in terms of anatomical studies. A reinvestigation of similarly preserved material by modern methods is strongly needed. Certainly, new data obtained by revisiting previously described material will contribute to a more complete understanding of the evolutionary processes that generated the modern Sequoioideae.

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