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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

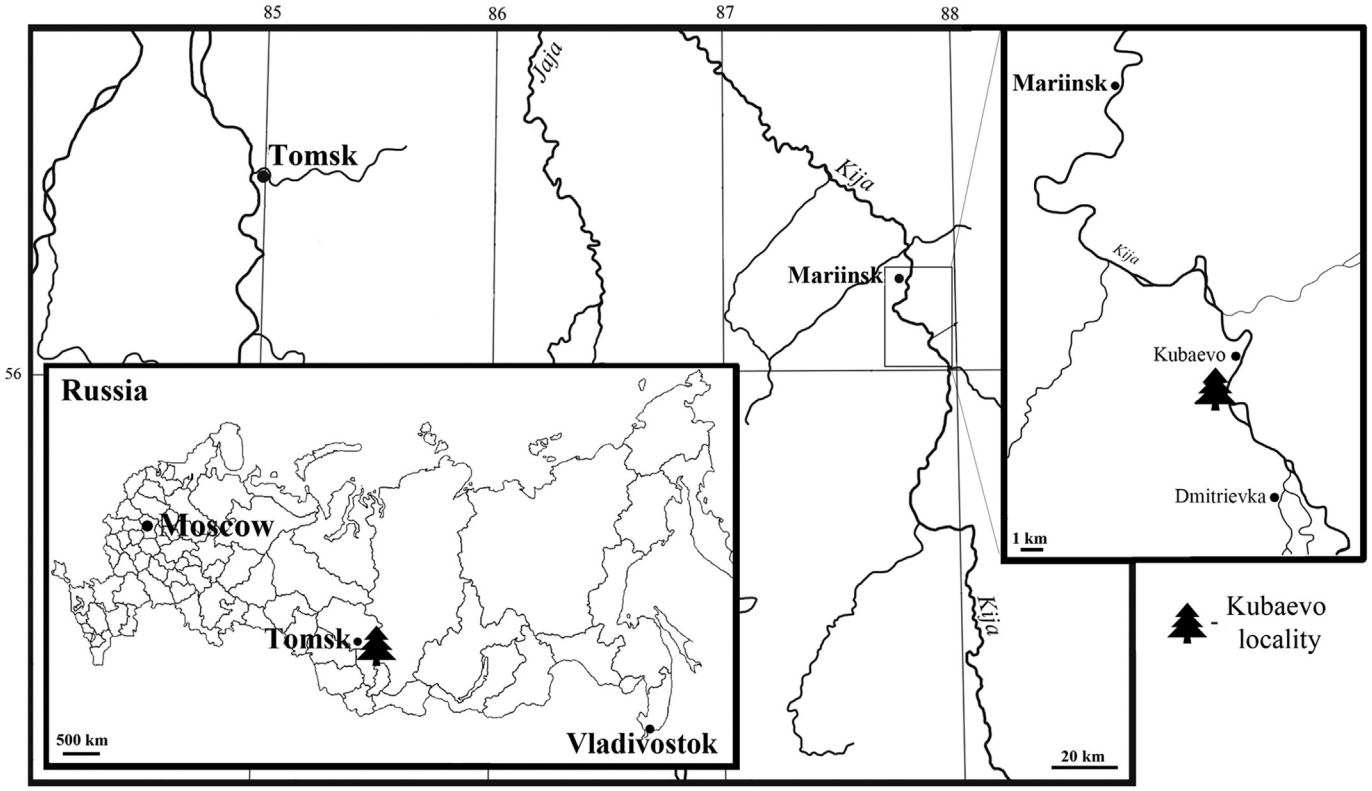

Fig. 1. Geographic position of the Kubaevo locality (modified from Maslova et al., 2011).