

**MUTOVIASPERMUM KRASSILOVII GEN. ET SP. NOV.: A PECULIAR COMPOUND
OVULIFEROUS CONIFER CONE FROM THE LOPINGIAN (LATE PERMIAN)
OF EUROPEAN RUSSIA (VOLOGDA REGION)**

Eugeniy Karasev,* Giuseppa Forte,† Mario Coiro,‡ and Evelyn Kustatscher¹†§

*A. A. Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia, and Kazan (Volga) Federal University, Kazan 420008, Russia; †Museum of Nature South Tyrol, Via Bottai, 1, Bolzano (BZ) 39100, Italy; ‡Department of Systematic and Evolutionary Botany, University of Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland; and §Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, München 80539, Germany, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 München, Germany

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Premise of research. Late Permian Voltziales are interpreted to have given rise to most extant conifer families, although their origin and evolutionary relationships are still poorly understood. The Poldarsa Formation (Kichuga Member) of Mutovino (= Isady) in European Russia yielded a diverse Lopingian (upper Permian) flora including some very peculiar compound ovuliferous cones.

Methodology. The micromorphologies of eight specimens of dispersed compound ovuliferous cones—some in organic connection with conifer shoot fragments—are described, and their relationships are tested in a phylogenetic analysis.

Pivotal results. *Mutoviaspermum krassilovii* gen. et sp. nov. is characterized by a stout main axis with helically arranged ovuliferous scales protected by coriaceous bracts. The polysperms have a peltate structure with an apical whorl of segments fused only in the basal part near the stalk and with a seed scar on each segment. The anatomical connection between *M. krassilovii* and *Quadrocladus*-like leaves provides the basis for reassessing the botanical affinities of these taxa.

Conclusions. A morphological phylogenetic analysis supports the placement of *Mutoviaspermum* as an early-diverging genus within Voltziales, although a precise relationship of this genus with other early conifers remains uncertain. Results of this analysis underline the ambiguous position of *Quadrocladus* and highlight its complex and poorly understood relationship within the Permian conifers.

Keywords: gymnosperms, conifers, Voltziales, Subangara, phylogenetic analysis.

Online enhancements: appendixes.

Introduction

The Lopingian (260–251 Ma) was a very important interval for the evolution of gymnosperms, including conifers. The earliest record of primitive conifers comes from the Middle Pennsylvanian of Euramerica (e.g., Plotnick et al. 2009), and they became a prominent constituent of dry to seasonally dry environments of Euramerica, western Gondwana (e.g., Archangelsky and Cuneo 1987; Jasper et al. 2005), and western Angara (e.g., Meyen 1997) during the Lopingian. After the end-Permian mass extinction, coniferous plants became the dominant elements of the recovery floras during the Early Triassic in Angara in the Northern Hemisphere (Meyen 1981; Mogutcheva and Krugovykh 2009), thus marking the beginning of their dominance through the Mesozoic.

The late Permian conifers are important since they are considered to have given rise to most modern families of conifers, although the timing of their origination and the detailed relationship with other conifer groups are still poorly understood (Rothwell et al. 2005; Taylor et al. 2009).

One of the most important plant groups during the Permian–Triassic transition was the Voltziales, since it is, besides the Podocarpaceae (Blumenkemper et al. 2018), one of only two conifer lineages that crossed the Permian–Triassic boundary. The Voltziales group is also considered a possible stem lineage of several modern conifer families (e.g., Miller 1999; Taylor et al. 2009). The waltchian Voltziales (sensu Rothwell et al. 2005) are among the earliest conifers to appear in the fossil record (Falcon-Lang et al. 2009; Plotnick et al. 2009). Waltchian Voltziales are considered a paraphyletic group (Rothwell et al. 2005). The group comprises small trees characterized by a plagiotropic branching system, triangular to needle-like leaves (e.g., Florin 1938–1945; Clement-Westerhof 1984; Kerp and Clement-Westerhof 1991; Mapes and Rothwell 1991, 2003; Hernandez-Castillo et al.

¹ Author for correspondence; email: evelyn.kustatscher@naturmuseum.it.

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2001, 2003; Rothwell et al. 2005), and ovuliferous scales with numerous sterile and few fertile segments, with some reminiscence of radial symmetry (Looy 2007). During the Cisuralian (299–273 Ma), walcchian conifers represent common elements of the basinal Euramerican lowland floras (e.g., DiMichele et al. 2008; Looy et al. 2014), gradually reducing in the late Cisuralian when the voltzian Voltziales became the dominant conifers (e.g., Clement-Westerhof 1984; Looy 2007). Voltzian Voltziales appear to be more derived conifers with typically irregular branching systems, bifacial to linear leaves, and ovuliferous scales characterized by bilateral symmetry, a well-defined stalk-like base, and a reduction of the number of sterile segments, with various degrees of fusion between the shoot and the fertile or sterile segments (e.g., Clement-Westerhof 1987; Rothwell et al. 2005). The voltzian Voltziales are well known from the late Permian of the Germanic Basin, northeast Italy (Clement-Westerhof 1987, 1988; Meyen 1997), and North America (DiMichele et al. 2004; Looy 2007). According to Rothwell and colleagues (2005), a paraphyletic group of walcchian Voltziales subtends the stem of the voltzian Voltziales. Nonetheless, the time of origination of the voltzian Voltziales has not yet been established, owing to the incomplete paleontological record (e.g., Looy et al. 2014).

Gondwanan Permian conifers have also been found in various fossiliferous sites of the Southern Hemisphere, such as India (e.g., Singh et al. 2000, 2003), South America (e.g., Cazzulio-Klepzig and Guerra-Sommer 1983; Archangelsky 1996; Jasper et al. 2005), Australia (White 1981), and Antarctica (e.g., Serbet et al. 2010). They were reproductively quite distinct from the paleoequatorial taxa (e.g., Taylor et al. 2009), especially regarding their female reproductive organs. The two most representative families are the Ferugliocladales and the poorly understood Buriadiaceae (e.g., Cuneo 1985; Archangelsky and Cuneo 1987; Archangelsky 1996). Distinct from the Voltziales of Euramerica and western Angaraland, these families are characterized by ovuliferous scales with stalked ovules in orthotropous subaxillary position (inverted in *Buriadia* Seward et Sahni) and the absence of sterile segments (Archangelsky and Cuneo 1987; Archangelsky 1996; Jasper et al. 2005; Serbet et al. 2010). Other conifer ovuliferous organs known from the Lopingian of Gondwana are *Walkomiella* Florin and *Voltziopsis* (Potonié) Townrow, associated with vegetative shoots of *Brachyphyllum* Brongniart. The phylogenetic relationships of these Gondwanan conifer groups are still poorly resolved, mainly because of the lack of information on the whole plants.

The Lopingian succession at Mutovino (fig. 1; Golubev 2000; Molostovskii and Minikh 2001; Arefiev et al. 2015; also called Isady by Gomankov and Meyen 1986; Aristov 2013; Aristov et al. 2013; Zavialova and Karasev 2015) has yielded one of the richest and most diverse plant assemblages from the late Permian of European Russia (Gomankov and Meyen 1986; Meyen 1997). The fossiliferous succession of the Kichuga Member of the Poldarsa Formation yielded not only plant fossils but also a rich fauna of bivalves, insects, ostracods, branchiopods, fishes, and tetrapods (Meyen and Gomankov 1971, 1980; Gomankov and Meyen 1979, 1986; Gomankov 2002, 2008). The plant assemblage is dominated by conifer shoots (e.g., *Quadrocladus* Mädlér), male cones (*Dvinostrobus* Gomankov et Meyen), and female cones (described in this article). Additional gymnosperm remains include peltasperm leaves (*Tatarina* Meyen, *Rhaphidopteris* Barale), ovuliferous organs (*Peltaspermopsis* Goman-

kov in Gomankov et Meyen), male reproductive organs (*Permotheca* Zalesky), seeds (*Salpingocarpus* Gomankov in Gomankov et Meyen), and the cardiolepid *Phylladoderma* (*Aequistomia* Meyen) Zalesky. Spore-producing plants are represented by microphylls of the lycopsid *Lepidophylloides* Snigirevskaya, the moss *Protosphagnum* Neuburg, and dispersed megaspores. Leaf fragments and dispersed cuticles of uncertain botanical affinity are assigned to the genera *Arisada* Meyen in Gomankov et Meyen and *Taeniopteris* Brongniart.

The vegetative conifer shoots of the Lopingian east European platform have been assigned to *Ullmannia* Göppert, *Geinitzia* Endlicher, *Pseudovoltzia* Florin, and *Steirophyllum* Eichwald (Meyen 1981, 1997; Gomankov and Meyen 1986; Gomankov 2008, 2010). The conifers of Subangara are dominated by the reproductive organs *Sashinia* Meyen and *Dvinostrobus*, with accessory shoot fragments of *Quadrocladus*. However, the floristic affinity and phylogenetic relationships among these taxa are still unresolved. Meyen (1997) associated the female cones of *Sashinia* and male cones of *Dvinostrobus* with the shoots of *Quadrocladus* and assigned them to the conifer family Lebachiaceae based on the primitive morphology of the ovuliferous organs. Gomankov and Meyen (1986) underlined the similarities between *Dvinostrobus* and the voltzian-type male cones *Darneya* Schaarschmidt et Maubeuge and *Sertostrobus* Grauvogel-Stamm from the Triassic of western Europe. Later, Gomankov (2010) created for *Sashinia* the new family Sashiniaceae.

The vegetative organs and female and male cones of most Permian conifers occur dispersed in the sediment. This makes the discovery of well-preserved plant fossils and whole-plant reconstructions essential for the understanding of the evolution of this important gymnosperm group. The discovery of female reproductive organs in organic connection with *Quadrocladus*-type leaves is one of the rare cases where vegetative shoots and ovuliferous organs are found in organic connection, and this may give us some insights into the botanical affinity of *Quadrocladus* (Meyen 1981, 1997) and into the phylogenetic position of the conifers of European Russia. Here, we describe the new female reproductive organ *Mutoviaspermum krassilovii* gen. et sp. nov. and discuss its phylogenetic and evolutionary position in the context of the late Permian conifers.

Material and Methods

Geological Setting

The material studied consists of eight specimens, most of which are preserved as compressions and impressions with part and counterpart and commonly with limonite permineralization, collected in 2006 from a clay lens of the middle part of the river-bank slope at the Sukhona River (Russia, Vologda region). The lenses are composed of gray siltstones and clays, horizontally laminated, and rich in fossil plant remains, bivalves, insects, ostracods, and conchostracans (Meyen and Gomankov 1971, 1980; Gomankov and Meyen 1979, 1986; Gomankov 2002, 2008). The plant remains include dispersed female cones, some in organic connection with conifer shoot fragments.

The so-called Mutovino lens is located in the lower part of the Kalikino Member of the Poldarsa Formation and was formed by a side arm of the mouth of a river originating on the Baltic

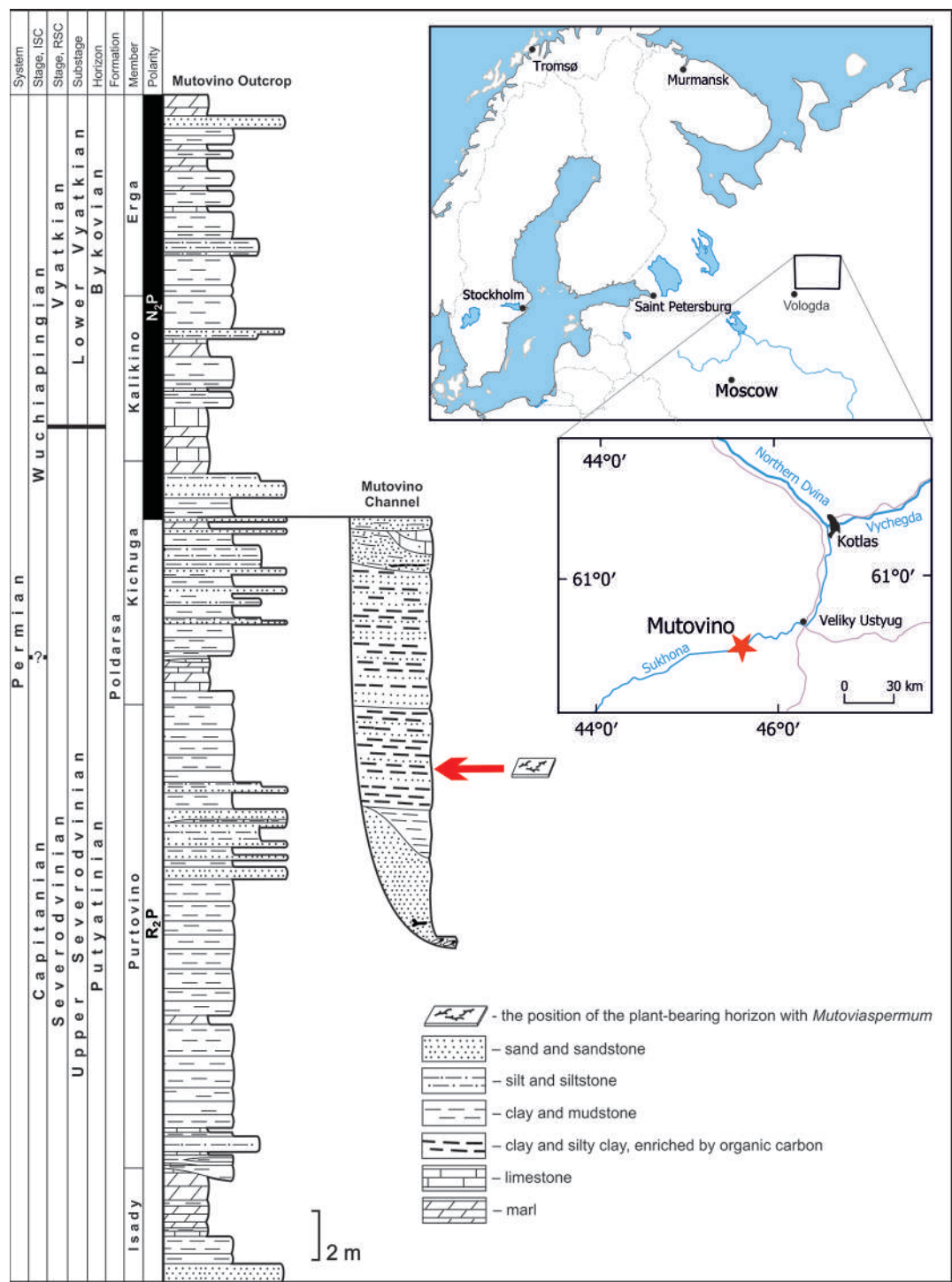


Fig. 1 Map showing location and stratigraphy of Mutovino section, Vologda region. Arrow pointing to the Mutovino channel (stratigraphy and lithological column after Arefiev et al. 2015).

Shield and debouching into a large lake located in the northeastern part of the Moscow Syncline (fig. 1; for more details see Aristov et al. 2013; Arefiev et al. 2015). The age of the section is the middle part of the Wuchiapingian, based on magnetostratigraphic and chemostratigraphic data (Arefiev et al. 2015).

Material Examined, Fossil Preparation, Imaging, and Repository

The plant macromaterial was photographed with a Nikon D5000 digital camera, digitally analyzed with the free software

ImageJ64, and studied using a dissecting Leica M165 stereo-microscope with attached Leica DFC420 camera and a VEGA Tescan scanning electron microscope. Attempts to prepare cuticles from axes and shoots and to extract in situ spores and pollen were unsuccessful. Discussions on cuticles are based on the cuticles prepared by Gomankov and Meyen (1986) from sterile shoots of *Quadrocladus schweitzeri* Meyen. Some of the seed-like structures were macerated in 30% HNO₃ and neutralized in water with 5%–10% KOH. They were mounted in glycerine jelly on microscope slides for light microscopic analysis, analyzed with a Zeiss Axioplan 2 microscope, and photographed with a Zeiss AxioCam 105 color digital camera.

All slabs yielding plant remains are stored at the A. A. Borisiak Paleontological Institute, Laboratory of Paleobotany, in Moscow. All specimens were inventoried with the code “PIN 5339” followed by a progressive number (151–212). The holotype of *Mutoviaspermum krassilovii* gen. et sp. nov. was labeled with the code PIN 5339/211.

Homologies and Terminology

The homologies of reproductive structures in the conifers have a long and contentious history. Florin (1949, 1951) established the idea that ovulate conifer cones are compound strobili (i.e., two order of branches with the ultimate order bearing megasporophylls). However, the compound nature of the cones of some fossil (Archangelsky and Cuneo 1987) and extant (Tomlinson and Takaso 2002) conifers is not immediately clear. If the origin of apparently simple cones in Cupressaceae is more clearly explained by the reduction of the ovuliferous scale, and fossil evidence supports such a view (Escapa et al. 2008; Spencer et al. 2015), the cones of the Gondwanan Ferugliocladales are harder to fit in this framework. Here, we follow the interpretation of Rothwell et al. (2005) in considering the Gondwanan conifers as having compound cones with a reduced ovuliferous scale.

For *Mutoviaspermum*, we interpret the whole cone as a compound ovuliferous cone, with the supra-axillary structure interpreted as an ovuliferous scale bearing basally fused megasporophylls in an apical whorl.

Given this interpretation, we use “compound ovuliferous cone” (“compound strobilus” sensu Florin 1949, 1951) for the “ultimate ovule bearing unit” sensu Rothwell et al. (2005). We use the term “ovuliferous scale” (“fertile scale/ovuliferous scale” sensu Mapes and Rothwell 1991; “(supra)axillary shoot/ovuliferous scale” sensu Rothwell et al. 2005) to refer to the shoot bearing the (mega)sporophylls and vegetative segments. This term is applicable both to a three-dimensionally arranged “polysperm” sensu Meyen (1987) and to a bilaterally symmetrical, flattened “dwarf shoot.”

Phylogenetic Analysis

Though a thorough test of the relationships of *Mutoviaspermum* would require an extensive matrix including all seed plant groups, we decided to test its placement assuming our interpretation of the fossil as a conifer using the morphological matrix of Rothwell et al. (2005), which includes 22 taxa and 57 morphological characters. *Mutoviaspermum krassilovii* has been added to the original matrix (apps. A, B, available online), which we analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). A separate matrix with vege-

tative characters coded as uncertain was used to test the sensitivity of our hypothesis to assumptions about these characters. MP analyses were conducted with PAUP* version 4.0a136 (Swofford 2003). We employed a heuristic search algorithm with random addition of taxa and 1000 replicates, setting the maximum number of trees to keep in memory to 1000. Bootstrap analyses were run with 10,000 replicates using the “asis” addition option and keeping a single tree for each replicate (Müller 2005). ML analyses were run on RaxML version 8.2.10 (Stamatakis 2014) using a matrix in which all ambiguities were recoded as missing data. We ran 1000 bootstrap replicates and modeled transitions with the Markov k-states (Mk) model (Lewis 2001) with a gamma-distributed rate variation. BI analyses were run on MrBayes version 3.2.3 (Ronquist et al. 2012) under the Mk model corrected for parsimony-informative characters with gamma-distributed rate variation. Two independent Markov chain Monte Carlo (MCMC) simulations were run for 1,000,000 generations using four chains (one cold chain and three heated chains), sampling every one-hundredth generation. The first 25% of the run was discarded as burn-in. The posterior parameter traces were inspected for convergence using Tracer (Rambaut and Drummond 2007). Consensus networks of the MP bootstrap, the ML bootstrap, and the combined post-burn-in MCMC trace were generated using SplitsTree 4 (Huson and Bryant 2006), with a cutoff of 0.20 for visualizing the splits.

Results

Systematics

Division—Coniferophyta

Class—Coniferopsida

Order—Incertae Sedis

Genus—*Mutoviaspermum*, Karasev, Forte, Coiro et Kustatscher gen. nov.

Type Species—*Mutoviaspermum krassilovii* Karasev, Forte, Coiro et Kustatscher sp. nov. (Figs. 2–10, Here Designated)

Generic diagnosis. Compound ovuliferous cone characterized by a stout axis with helically arranged bracts and ovuliferous scales. Ovuliferous scales peltate, arising from the axis in the axils of the bracts in supra-axillary position. Ovuliferous scales composed of a sturdy, central stalk with an apical whorl of elongated segments, fused only in the lowermost part. Seed attachment area on the adaxial side of each segment. Basally, axis covered by helically arranged linear to slightly falcate leaves with a single vein with an unrestricted base.

Etymology. The genus is named after the locality Mutovino, where the plant remains were found in a clay lens.

Mutoviaspermum krassilovii Karasev, Forte, Coiro et Kustatscher sp. nov.

Specific diagnosis. Bracts spatulate to lanceolate with rounded apex arising perpendicularly in a loose spiral from the axis,

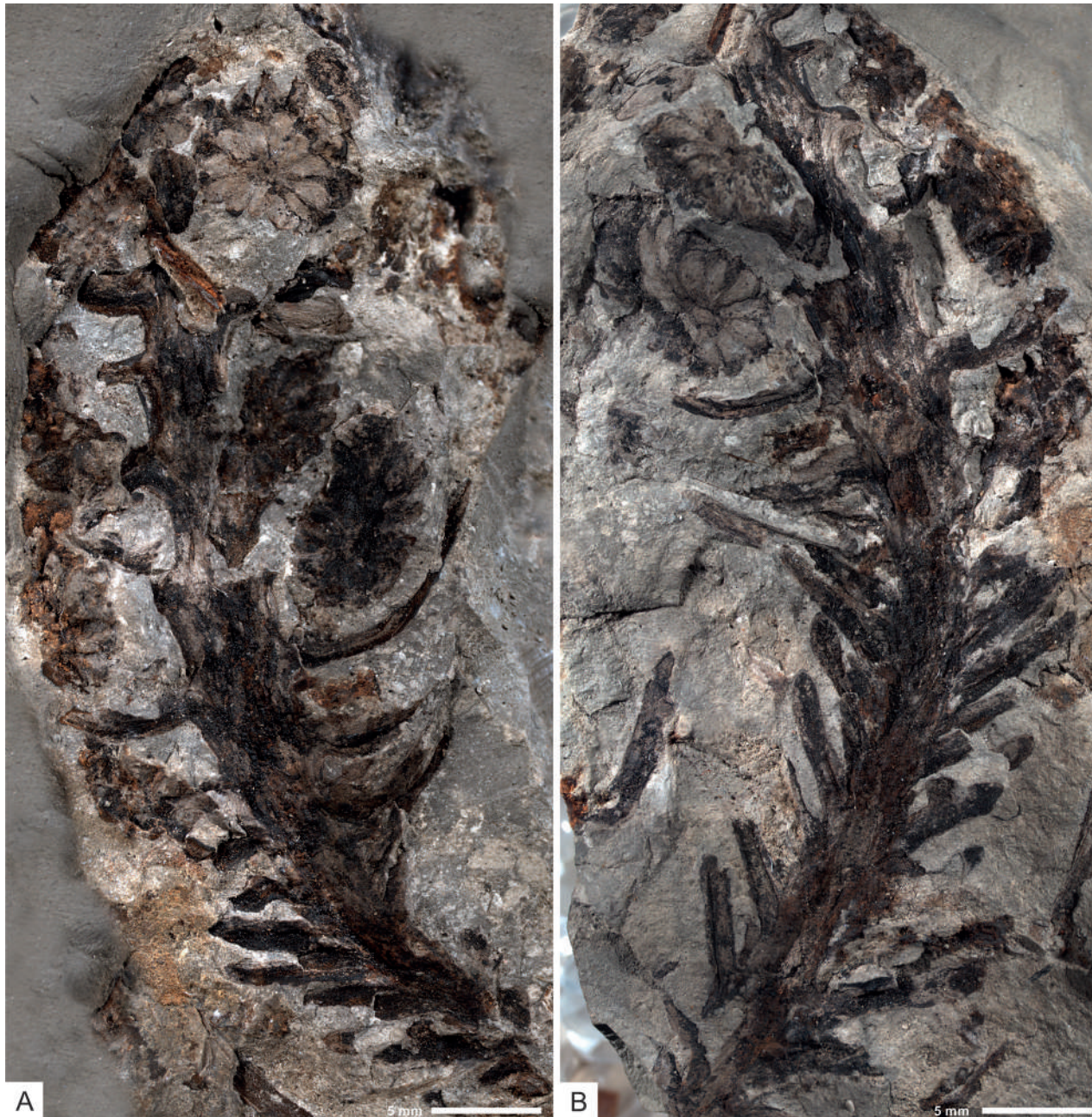


Fig. 2 *Mutoviaspermum krassilovii* gen. et sp. nov. seed cone (holotype, PIN 5339/211ab). A, Lateral view showing seven scale-bract complexes, PIN 5339/211a. B, Counterpart of the holotype, PIN 5339/211b.

curving toward the apex, and continuing almost parallel to the axis; bracts extending beyond the ovuliferous organs and several times as long as the vegetative leaves. Ovuliferous scales with an apical whorl of 9–13 elongated segments, apical part of the segments pointed, oriented parallel to the axis or directed outward (abaxially). Seed attachment areas on the adaxial side, in central position. Leaves of the ultimate shoots below the cones closely spaced, basally partially imbricated, much longer than wide, entire margin, and rounded apex.

Holotype. PIN 5339/211ab, shoot fragment with a terminal ovuliferous cone, figures 2–4, here designated.

Other studied specimens. PIN 5339/151ab, PIN 5339/162, PIN 5339/163ab, PIN 5339/209ab, PIN 5339/212-2ab, PIN 5339/223ab, PIN 5339/227ab.

Repository. A. A. Borissiak Paleontological Institute, Laboratory of Paleobotany, Moscow.

Type locality. Mutovino, Vologda region, European Russia.

Type unit and age. Kichuga Member, Poldarsa Formation, Severodvinian regional stage, Wuchiapingian stage, Lopingian series.

Etymology. The specific epithet honors the late Professor V. A. Krassilov.

Description

Strobili. The plant assemblage includes eight compound ovuliferous cones and cone fragments. The individual compound ovuliferous cones closely resemble each other in general organization but differ subtly in appearance: the best-preserved cone is the holotype (PIN 5339/211; figs. 2–4). Most specimens differ in the spacing and orientation of the ovuliferous scales. The ovuliferous scales are relatively closely spaced and more protected by the bracts in PIN 5339/151, whereas they are somewhat more loosely organized and extend from the axis at an angle of 90° in specimen PIN 5339/211 (figs. 2, 3). Specimens PIN 5339/153 and PIN 5339/209 (fig. 5A–5F) are partially disarticulated spec-

imens, with partially broken bracts, well-extended ovuliferous scales, and mature seeds. In PIN 5339/151, PIN 5339/212-2, and PIN 5339/211 (figs. 2, 3), portions of the main axis are preserved and covered by helically arranged linear to slightly falcate leaves.

The compound ovuliferous cones are 40–60 mm long and 19–30 mm wide. The axis is generally sturdy, about 2–3 mm thick where it is covered by leaves and generally thicker in the fertile part (3.5–5 mm) of the shoot (figs. 2, 3). Specimen PIN 5339/212-2 (fig. 6) is composed basally of a thicker axis with leaves and/or ovuliferous scales, which is succeeded by a vegetative shoot segment and apically a disassociated cone. In specimens PIN 5339/211 and PIN 5339/151 (figs. 7, 8), the cones

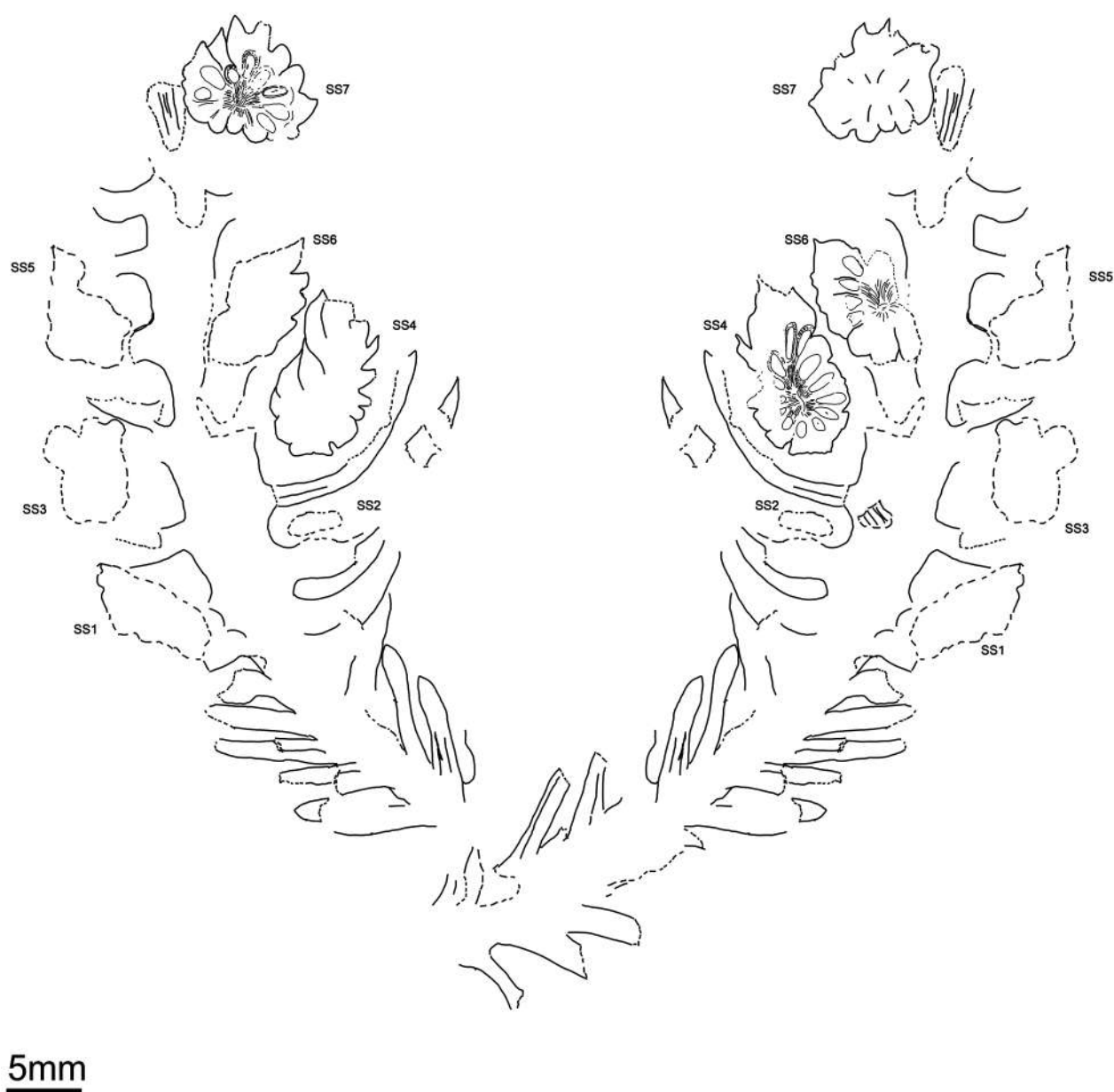


Fig. 3 *Mutoviaspermum krassilovii* gen. et sp. nov., line drawing of seed cone (holotype, PIN 5339/211ab) with seven seed scales (ss).

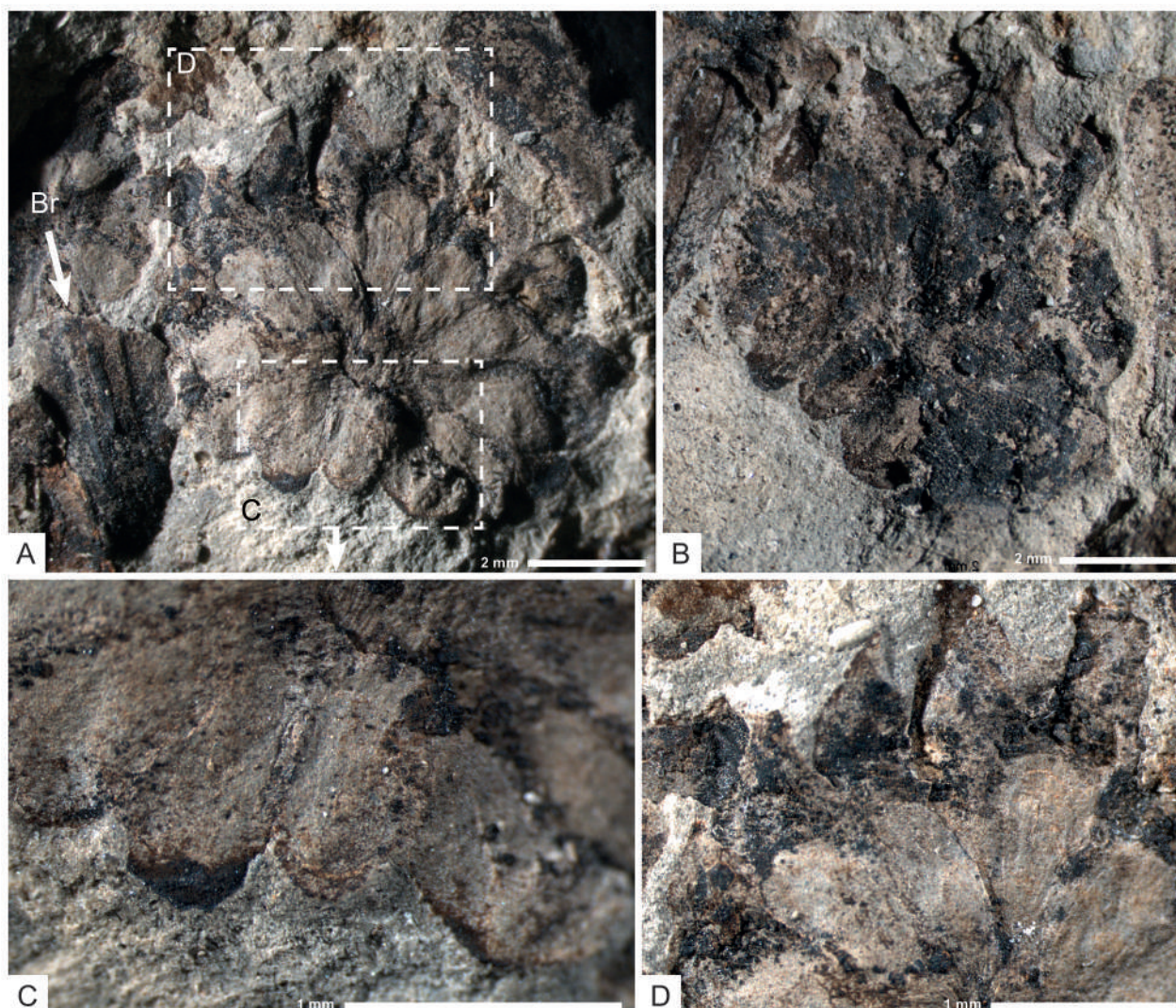


Fig. 4 *Mutoviaspermum krassilovii* gen. et sp. nov., details of holotype. A, Ovuliferous organs preserved in adaxial view and fragment of bract (Br) with two stripe-like longitudinal zones, PIN 5339/211a. B, Ovuliferous organs preserved in abaxial view, PIN 5339/211b. C, Magnification of A showing sterile(?) proximal lobes. D, Magnification of A showing distal lobes with seed scars and apical, triangular tips that are curved outward.

are apparently in terminal position, with leaves in the proximal part of the shoot fragments. The ovuliferous scales and bracts are arranged along the axis in a loose spiral without imbrication, although the bracts appear to surround the ovuliferous scales almost completely in the slightly immature stage (PIN 5339/151; figs. 7B, 9A, 9B).

Bracts. Bracts are free, lanceolate, and loosely arranged (fig. 8C). In lateral (section) view, they are about 10–13 mm long and 0.3 mm wide, increasing distally in width (e.g., PIN 5339/151, PIN 5339/211; fig. 8D). They arise at an angle of ca. 90° from the axis, bend after a third of their length toward the apex, and proceed almost parallel to the axis (e.g., PIN 5339/151, PIN 5339/211; figs. 3, 8A). In abaxial view, they broaden into a shield and reach up to 2.5 mm in width with three longitudinal lines that include two stripe-like longitudinal zones (e.g., PIN 5339/151; fig. 8C). Apically, the bract decreases in width and terminates with a pointed apex (e.g., PIN 5339/209; fig. 5B).

Ovuliferous scales. The eight strobili contain 30 identified peltate ovuliferous scales, preserved in most cases in adaxial/abaxial view (e.g., PIN 5339/211, PIN 5339/209, PIN 5339/151; figs. 4, 5E, 9A) with a few specimens in lateral view (e.g., PIN 5339/209, PIN 5339/151; figs. 5F, 9B). The ovuliferous scales arise from the axes in a supra-axillary position (sensu Meyen 1997) with an angle of ca. 90° (e.g., PIN 5339/151ab, part and counterpart; fig. 8). The stalk of the peltate ovuliferous scales is 2.5–3 mm long and 0.5–1 mm wide, with the basal part of the stalk being broader than the central part. The surface of the stalk appears covered by irregular furrows (e.g., PIN 5339/151b; fig. 9B). Apically, a whorl of 9–13 lobes arises from the stalk, constituting a peltate structure with a diameter of 5–8 mm (e.g., PIN 5339/151, PIN 539/211; figs. 4A, 4B, 6A, 6D).

The segments are fused only in the lowermost third in a funnel-shape structure characterized in the central part by radial wrinkles, similar to the surface of the stalk (e.g., PIN 5339/211; figs. 4C, 6B).

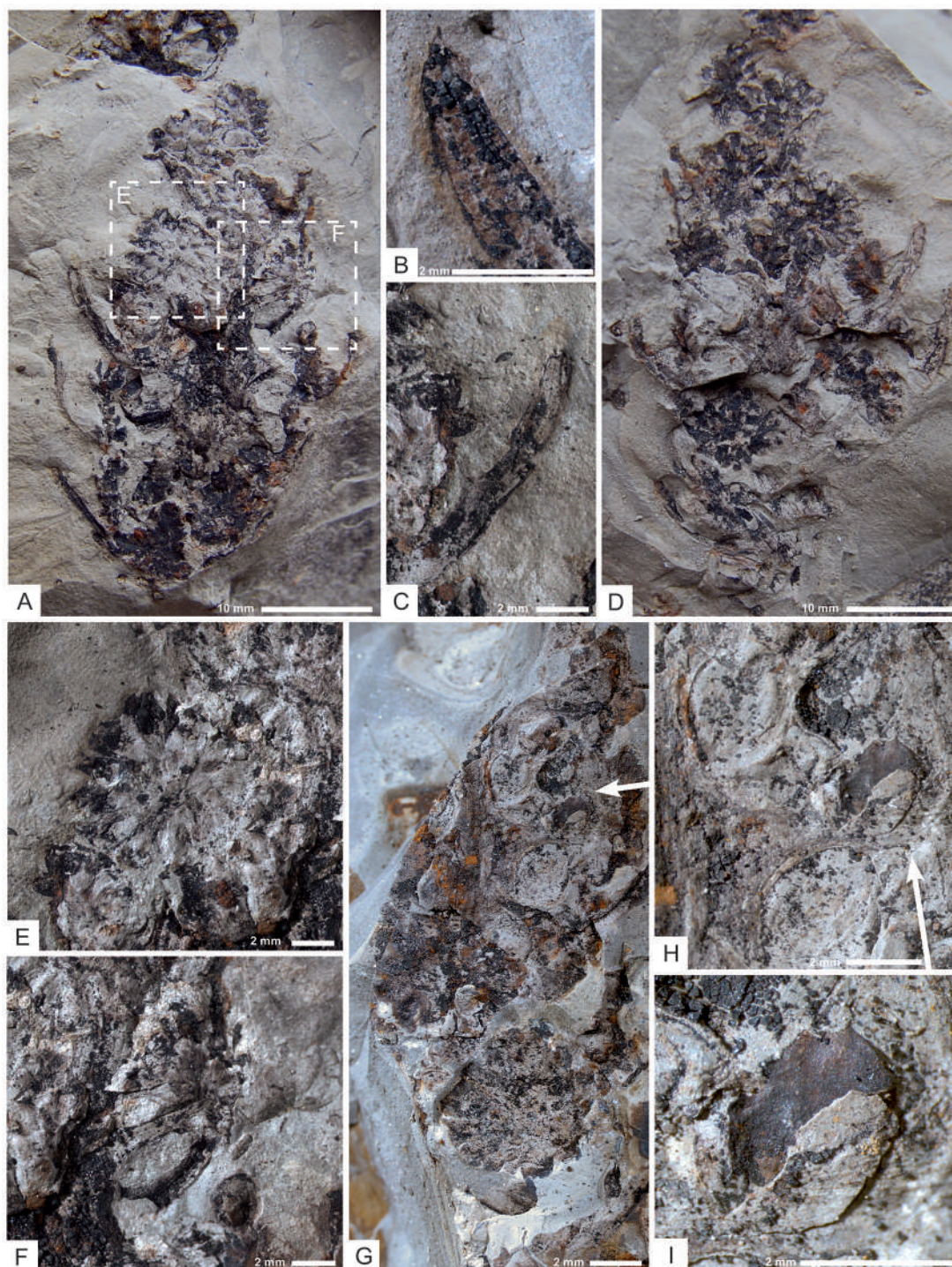


Fig. 5 *Mutoviaspermum krassilovii* gen. et sp. nov., partially disarticulated specimens with well-extended ovuliferous organs and mature seeds. A–F, PIN 5339/209a. A, General view of parts of strobili preserved in adaxial/abaxial view, PIN 5339/209a. B, C, Magnification of the bracts that terminate with a pointed apex. D, Counterpart of the specimen in A, PIN 5339/209b. E, Ovuliferous organ preserved in adaxial view, PIN 5339/209a. F, Ovuliferous organ in lateral view, PIN 5339/209a. G–I, PIN 5339/162. G, General view. H, I, Magnification of mature seeds in G.

Each lobe is 2.5–4.5 mm long (from the apex to the center of the pel-tate structure) and 1–1.5 mm wide. The apex of each segment is rounded, but in some cases (e.g., PIN 5339/211, PIN 5339/212-2; fig. 4D), the segments appear to have an apical, triangular tip of

coalified tissues that curves outward (abaxially) or extends parallel to the axis. On the adaxial side of each segment, an ovate depression, 0.7–1.2 mm in length and 0.40.5 mm in width, surrounds a small, central, circular to elliptical field of ca. 1 mm in length and

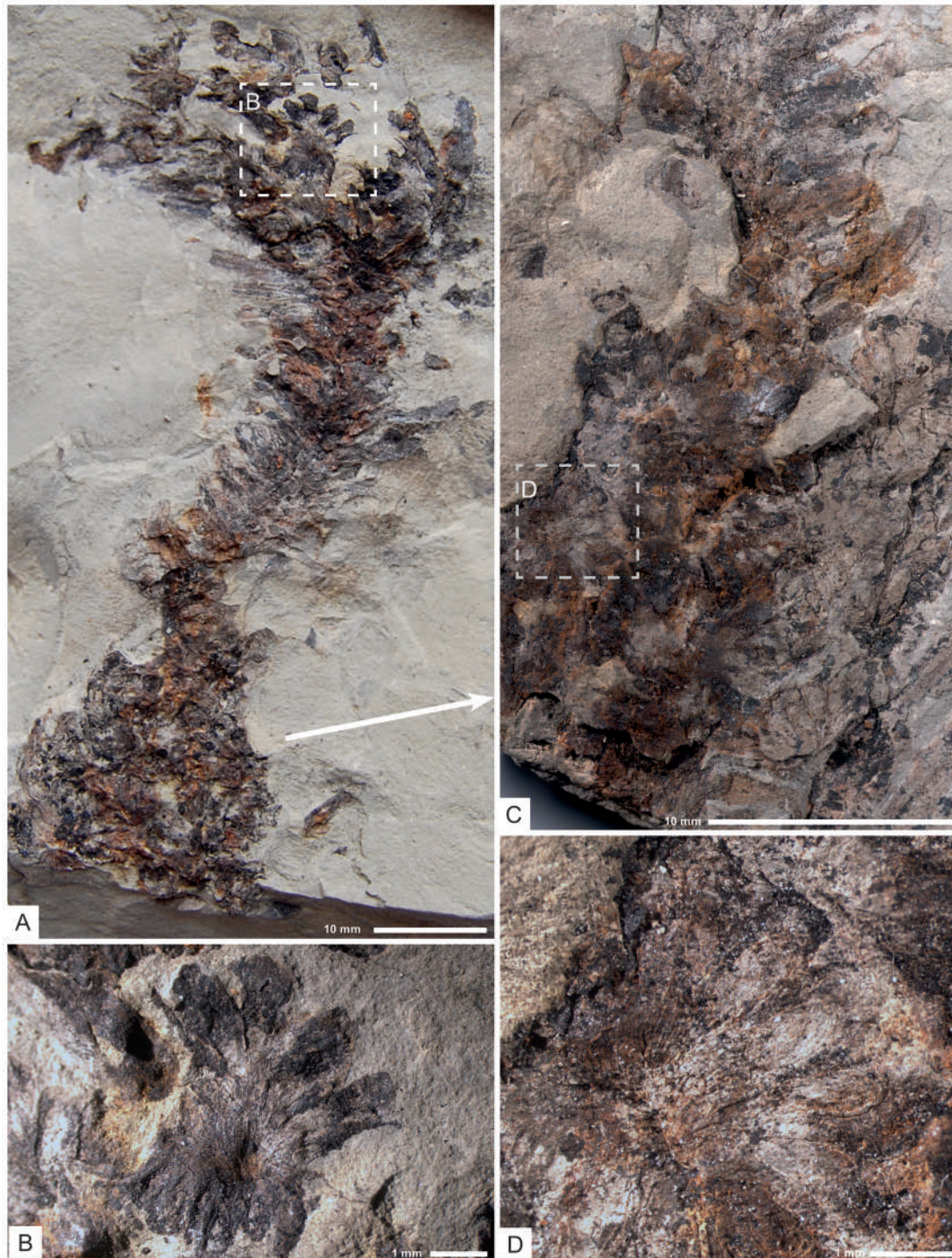


Fig. 6 *Mutoviaspermum krassilovii* gen. et sp. nov., PIN 5339/212-2ab. Strobilus followed by a vegetative shoot and apically a disassociated cone. A, General view, PIN 5339-212-2a. B, Detail from A showing ovuliferous organ at fertile area. C, Detail of counterpart, PIN 5339-212-2b. D, Detail from C showing ovuliferous organ preserved in adaxial view with evident ovate depressions.

0.1 mm in width (e.g., PIN 5339/151, PIN 5339/211; figs. 6D, 9C–9E). This oval depression is oriented longitudinally.

Ovules/seeds. Ovules/seeds are generally found dispersed in the sediment, partly covering the strobili (e.g., PIN 5339/153; figs. 7A, 9F, 9G) but without any anatomical connection. They

are ovate to elliptical in shape, 1.5–3 mm long, 0.5–2 mm wide, and strongly coalified. The macerated seeds have a slight half-moon shape with a strongly convex distal part and an almost straight proximal part and are split open in the macerated specimen (e.g., PIN 5339/153; fig. 9F–9G).

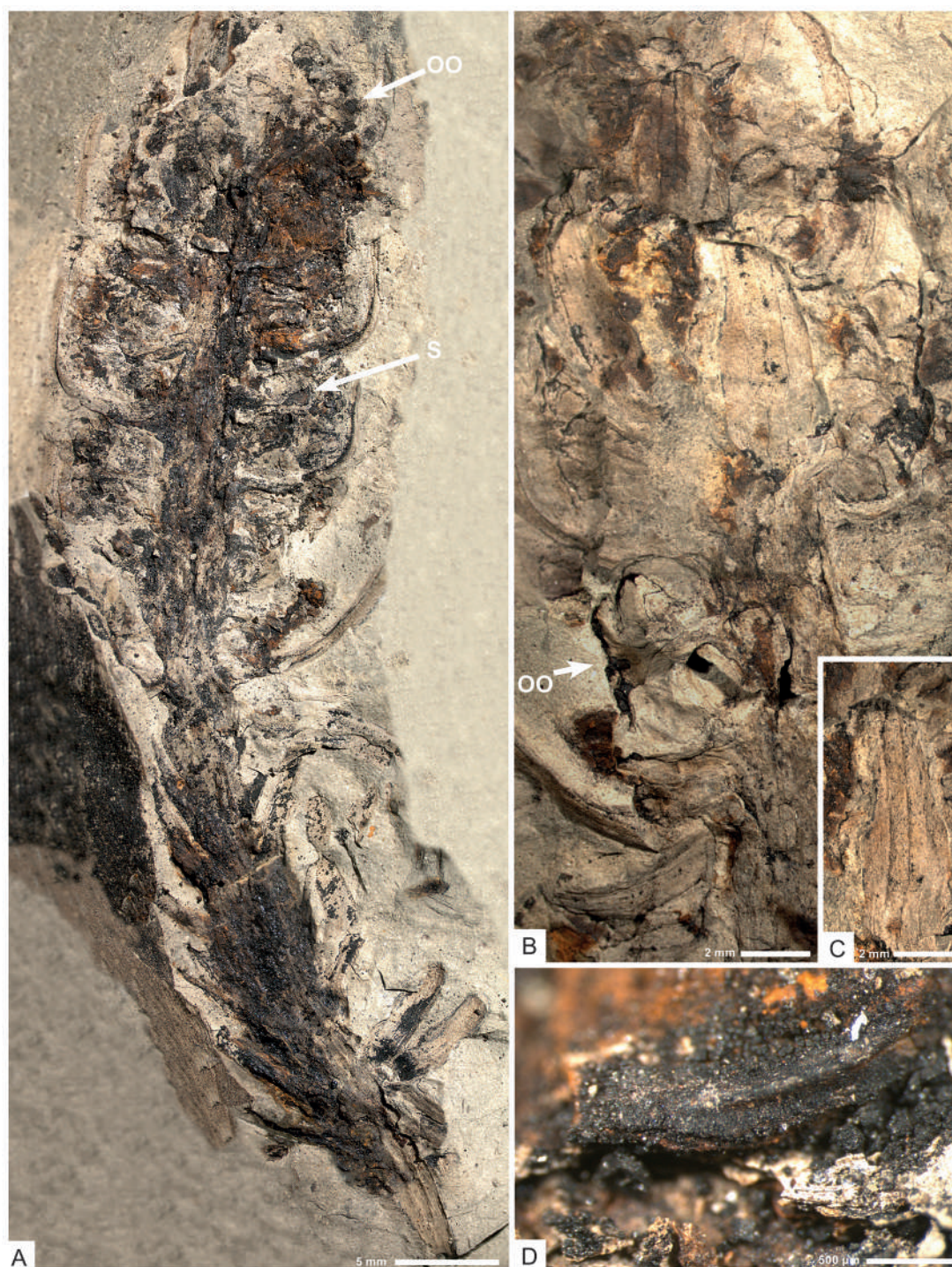


Fig. 7 *Mutoviaspermum krassilovii* gen. et sp. nov. A, Lateral view of well-preserved seed cone with seven scale-bract complexes and ovules (S), PIN 5339/151ab. B, Counterpart of specimen in A showing bracts outline, PIN 5339/151b. C, Detail of B showing bract in abaxial view with three longitudinal lines that include two stripe-like longitudinal zones and ovuliferous organ (OO). D, Base of bract in lateral view, PIN 5339/151b.

Vegetative shoots. Vegetative shoot fragments occur in organic connection with some of the compound ovuliferous cones and cone fragments (e.g., PIN 5339/151, PIN 5339/211; figs. 2, 6, 7). The leaves are linear to slightly falcate with an obtuse to

slightly pointed apex; the base is slightly decurrent. The leaves arise from the axis in a close spiral at an angle of 25°–50° but bend outward 60°–90° after a third of its length. The apexes of the leaves turn slightly apically. The bases cover each other partly

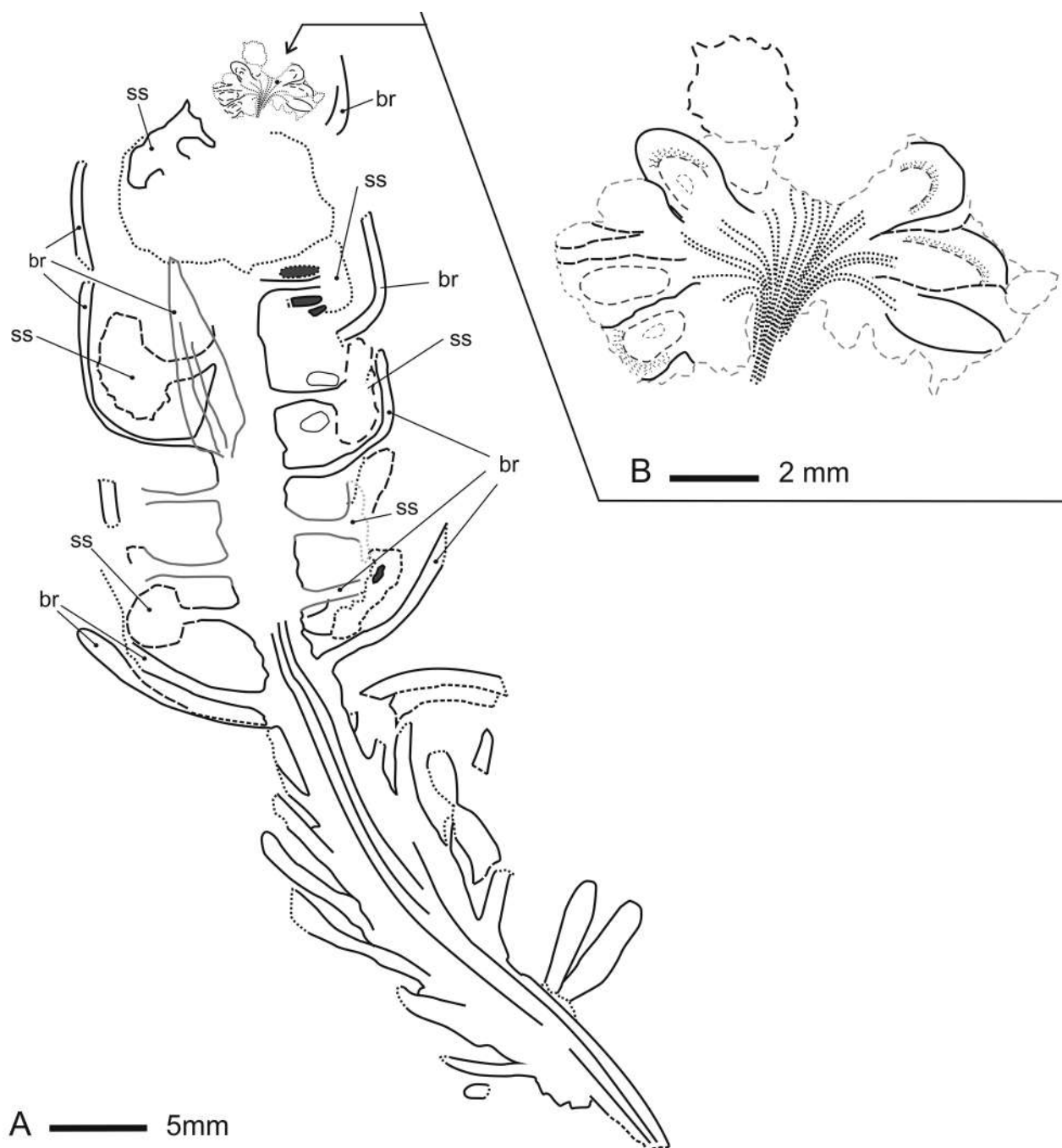


Fig. 8 *Mutoviaspermum krassilovii* gen. et sp. nov., line drawing of specimen PIN 5339/151ab. A, General view showing bracts (br), seed scales (ss), and position of ovules (blackened). B, Detail of seed scale.

(slightly imbricating). The leaves are 5.5–10 mm long (average, 8 mm) and 1–1.7 mm wide (average, 1.4 mm). In cross section, they appear to be oval or slightly rhombic. The margin is entire without any denticulation. In some specimens, a distinct vein can be observed that arises slightly sinuously from the axis and reaches the apex (PIN 5339/211; figs. 2, 3). Because of the small shoot length, no clear heterophylly can be observed, although in

one specimen (PIN 5339/211; figs. 2, 3), the leaves seem to become longer toward the base of the cone.

Discussion

The compound ovuliferous cones are preserved at various stages of maturity and preservation from PIN 5339/211 (fig. 3),

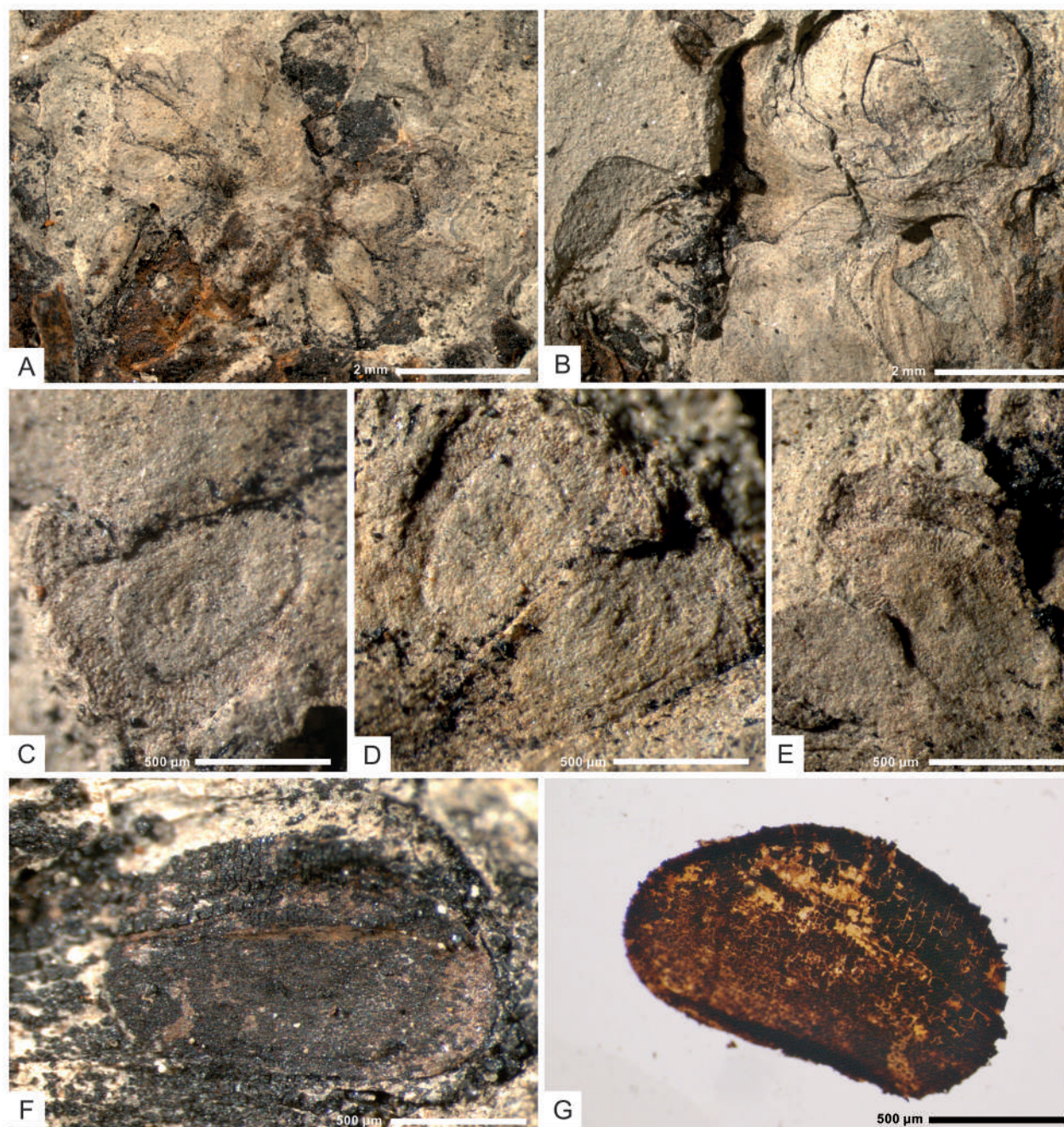


Fig. 9 *Mutoviaspermum krassilovii* gen. et sp. nov., scale-bract complexes and seeds. *A*, Detail of PIN 5339/151a (fig. 8A) showing ovuliferous organ in abaxial view. *B*, Lateral view of ovuliferous organ, detail of PIN 5339/151b (fig. 8B). *C–E*, Details of *A* showing ovate depressions on the lobes. *F*, Ovule. *G*, Macerated ovule from *F*.

which probably represents a slightly immature specimen to the older, disaggregated cones (e.g., PIN 5339/153, PIN 5339/209; fig. 5A, 5D) with partially broken bracts, well-extended ovuliferous scales, and dispersed mature seeds. The axis is generally sturdier and thicker in the fertile parts than in the vegetative parts. This could have allowed the axis to elongate once the strobilus was completely mature and/or the ovuliferous organs detached. Unfortunately, it is very difficult to determine whether the strobilus

grew in terminal or in intercalary position along the shoots, although one specimen (PIN 5339/212-2; fig. 6) would suggest that an intercalary growth cannot be completely excluded.

The long and wide bracts almost completely surrounding the ovuliferous scales in the immature specimens and the supra-axillary position of the ovuliferous scales suggest that the bracts had a protective function. Moreover, the thickness and stoutness of the bracts with strongly coalified lobes suggest that they were

woody and lignified or at least leathery. The peltate ovuliferous scales are covered on the stalk by irregular furrows, giving the impression of a pleated surface. The concentric arrangement of radial striae on the abaxial side of the peltate head corresponds to a funnel-shaped structure (e.g., fig. 6B, 6D), suggesting that the segments are only basally fused.

Although the seeds were found dispersed only in the sediment, the attachment areas on the adaxial side of the segments support an abaxial attachment of the seed on the ovuliferous scale. No organic connection was found between the ovuliferous organs and the dispersed seeds, but the comparable dimensions and shape between the seeds and the adaxial ovate depressions at the base of the lobes of the ovuliferous organs and the close association on the same specimens would support this theory. The difference in size among the seeds (1.5–3 mm × 0.5–2 mm) may relate to a range of ontogenetic stages and/or different ways the seeds are compressed.

A pollen grain of *Protohaploxylinus* type was found adhering to the apical part of one of the macerated ovules/seeds (PIN 5339/151). Pollen assigned to the genus *Protohaploxylinus* Samoilovitch has so far been found in situ in Glossopteridales (e.g., in situ in *Arberiella* Pant et Nautiyal, *Pterygospermum* Pant et Nautiyal; Zavada 1991; Balme 1995; Lindström et al. 1997) and Peltaspermales (e.g., in situ in *Permothea*, *Salpingocarpus*, *Tatarina*; Gomankov and Meyen 1986; Balme 1995; Meyen 1997). The same locality as *Mutoviaspermum* also yielded the peltaspermalean male reproductive organ *Permothea striatifer* Meyen et Gomankov. *Protohaploxylinus*-type pollen grains were extracted from its pollen sacs (Zavialova and Karasev 2015). This suggests that the pollen grain found attached to *Mutoviaspermum* is a contamination rather than a genuine in situ finding.

The leaves in organic connection with the cones of *M. krasilovii* are linear, with a rounded to slightly pointed apex, a decurrent base, and entire margins. Unfortunately, no cuticle is preserved. A comparison with other species is thus possible based only on macromorphological characters. Among the Permian Subangaran conifers, our leaves closely resemble the dispersed vegetative shoots of *Quadrocladus schweitzeri* Meyen in Gomankov et Meyen, which were found dispersed in the same fossiliferous layer at Mutovino (table 1). In both cases, the leaves are linear with a rounded apex, and our specimens probably also share an oval leaf cross section. The size of the leaves is similar as well, 5–10 mm × 1–1.7 mm for the leaves in organic connection with *Mutoviaspermum* and 5–11 mm × 1–2 mm for *Q. schweitzeri*. The only potential difference is the occasional denticulation of the margin found in *Q. schweitzeri*, which was never observed in *M. krasilovii*. *Quadrocladus dvinensis* Meyen differs from the leaves of *M. krasilovii* because of the constantly denticulate margin of the leaves and the strongly decurrent leaves with a circular cross section. In *Quadrocladus borealis* Meyen the leaves are attached both on long and on short shoots, whereas in *Mutoviaspermum* no short shoots are observed. The leaves are also much smaller (up to 5 mm × 0.6–1.3 mm) than in *Q. borealis*. Some resemblance also exists between the leaves of *Mutoviaspermum* and *Quadrocladus sibiricus* (Neuburg) Meyen. Macro-morphologically, the latter differs because of its narrower leaves (12 mm × 0.8–1.5 mm) and the more circular to rhombohedric cross section of the leaves. Moreover, *Q. sibiricus* may have lateral dwarf shoots with shorter leaves that were not observed in

Mutoviaspermum. Leaf dimensions of *Mutoviaspermum* are not comparable with the two European species of *Quadrocladus*—that is, *Quadrocladus orobiformis* (Gothan and Nagalhard) Schweitzer and *Quadrocladus solmsii* (Gothan and Nagalhard) Schweitzer. *Quadrocladus orobiformis* is characterized by non-decurrent linear leaves (20–35 mm × 2–3 mm) arising from the axis at about 90°, with a diamond-shaped cross section and an obtuse apex, whereas *Q. solmsii* has shorter linear leaves (10–20 mm × 2–3 mm) arising at 45° from the axis, with a circular cross section and an obtuse apex. The leaves of both species have a smooth margin.

Comparisons

The general morphology of *Mutoviaspermum* (fig. 10) has some peculiar aspects in common with compound ovuliferous cones of various typically Subangaran plant groups and some taxa from other regions. Ovuliferous scales with terminal ovules arranged helically on a central unbranched stalk also occur in some cordaitaleans (= Cordaitaceae in Meyen 1997); the conifer families Vojnovskyaceae, Ruffiaceae, and some Subangaran Voltziales (e.g., Lebachiaceae in Meyen 1997); and the Peltaspermales (e.g., Harris 1937; Gomankov and Meyen 1986; Naugolnykh and Kerp 1996; Rothwell et al. 1996; Kerp et al. 2001; Anderson et al. 2007). The relationships between these groups remain unclear (e.g., Taylor et al. 2009), and their reproductive organs have been interpreted in different ways by various authors (e.g., Meyen 1987, 1997; Ignatiev and Meyen 1989; Naugolnykh 2001). We compared *Mutoviaspermum* with the compound ovuliferous cones of different gymnosperm families and orders, taking into account the following list of morphological characters: (i) helical arrangement of the ovuliferous scales around an unbranched axis, (ii) presence/absence of free or basally fused ovuliferous segments (sporophylls), (iii) peltate structure of the ovuliferous scales, (iv) presence/absence of sterile segments, (v) presence/absence of bracts, (vi) axillary or supra-axillary position of the ovuliferous scales, (vii) attachment position of the ovules/seeds, and (viii) aggregation or not of the ovuliferous scales into a compound ovuliferous cone. A short description of the compared taxa and the interpretations of the various authors about the relationships among these groups are provided.

The Vojnovskyaceae incorporate several of the abovementioned characters, most importantly with ovuliferous scales sitting in a supra-axillary position with respect to the bracts, but they differ in the organization of the ovuliferous scales forming a so-called polysperm or “compound polysperm” (i.e., a loose spiral of bract-like leaves and supra-axillary polysperms; Meyen 1987; Rothwell et al. 1996). *Scirostrobis* Doweld et Naugolnykh (= *Pholidophyllum* Zalesky) from the lower Permian closely resembles *Mutoviaspermum* because of the peltate shape of the ovuliferous scale. It differs from *Mutoviaspermum* because of the asymmetrical shape of its polysperm, where the sterile segments and longitudinally striated fertile seed stalks (sporophylls?) are fused asymmetrical to the stalk (Ignatiev and Meyen 1989; Naugolnykh 1998, 2001). The ovules/seeds of *Scirostrobis pterocerum* (Naugolnykh) Doweld et Naugolnykh are attached marginally on the sporophylls, and wing-shaped structures occur at the margin of the umbrella. Moreover, no sterile bract is known, since *Scirostrobis* has so far never been found attached to an axis (e.g., Naugolnykh 1998).

Table 1

Comparison Chart of the Different *Quadrocladus* Species

Species/characters	Ultimate branching arrangements	Angle of insertion of ultimate shoots	Lateral dwarf shoots	Leaf shape	Leaf in cross section	Leaf apex	Leaf margins	Leaf base	Leaf attachment angle	Leaf length (mm)	Leaf width (mm)	Heterophylly	Veins	Additional characters
<i>Quadrocladus</i> -type leaves of	Linear to slightly falcate	Oval to slightly rhombic	Obtuse or slightly sharpened	Smooth	Slightly decurrent	Spirally, base slightly imbricating, angle basally 25°-50°	5.5-10 (average, 8)	1-1.7 (average, 1.4)	Not observed	1 distinct vein	Attached to compound ovuliferous cones
<i>Mutoviaspermum brassilovii</i> sp. nov.	...	90°	Absent	Linear	Diamond to triangular	Obtuse	Smooth	Broad, non-decurrent	Spirally	20-35	1.2-3	...	Not distinct	...
<i>Q. orobifomis</i>	...	45°	Absent	Linear to slightly club shaped	Round	Obtuse	Smooth	Slightly contracted	Spirally	10-20	2-3	...	Not visible	...
<i>Q. solmsii</i>	...	Acute	Present	Tongue shaped to obovate	Nearly circular	Obtuse or acuminate	Minutely denticulate	...	Spirally, strongly imbricating, angle very acute	Up to 6	1-2	Yes
<i>Q. diuensis</i>	Present	Linear to spatulate	Round	Obtuse or slightly sharpened	Smooth or (very rare) minutely denticulate	Nondecurrent	Spirally, acute	Up to 5	.6-1.3	Yes
<i>Q. borealis</i>	Present	Linear	Oval, flattened	Acuminate	Smooth only solitary leaves (very rare) may be denticulate	Decurrent	Spirally, imbricated, attached with acute angles	5-11	.9-2	Not observed
<i>Q. schweitzeri</i>	Spirally?	70°-90°	Present	Linear	Round or rhombic	Obtuse, evenu-ally with distinct "micro"	Smooth	Decurrent	Spirally, crowded on penultimate shoots, pinnate on ultimate shoots	l.o. 6-10, p.o. 10-12	l.o. 8-1.3, p.o. 1.2-1.5	Yes
<i>Q. sibiricus</i>	Pinnately	Acute, 40°-60°	Alternation of long and short shoots?	Linear	...	Rounded or slightly pointed	Smooth	Occasionally decurrent	...	Up to 6	Up to 2	...	Not visible	Junior synonym of <i>Q. solmsii</i>
<i>Q. florinii</i>	Linear

Note. l.o. = branches of last order, p.o. = branches of penultimate order.



Fig. 10 Suggested reconstruction of the scale-bract complexes of *Mutoviaspermum krassilovii* gen. et sp. nov.

Vojnovskya Neuburg from the lower Permian of the Pechora Basin resembles *Mutoviaspermum* in the presence of bracts and the supra-axillary position of the ovuliferous scale but differs in the ovuliferous scale corresponding to a polysperm that consists of a thick axis with spirally attached, reflexed seed stalks (spo-

rophylls?) with widened apices. Naugolnykh (2001) considered the interpretation of *Vojnovskya* equivocal because it strictly depends on the preservation and on the compression plane of the fossil. The “polysperms” of *Vojnovskya*, if apically compressed, resemble an umbrella-like, flattened, radial structure that can

be misinterpreted as *Paravojnovskya* Doweld and thus erroneously attributed to the Rufloriaceae (e.g., Durante 1976; Naugolnykh 2001).

Paravojnovskya Doweld (= *Gaussia* Neuburg) more closely resembles *Mutoviaspermum* with its ovuliferous scales composed of a short central stalk with whorls of sporophylls arising from the distal part, forming a peltate structure (Naugolnykh 1998; Doweld 2004). *Paravojnovskya imbricata* (Naugolnykh) Doweld is characterized by its asymmetrical umbrella-like structure with numerous and well-developed segments but without a defined attachment area of the seeds (e.g., Naugolnykh 1998, 2001). *Mutoviaspermum* and *Paravojnovskya* are similar in the general peltate structure of the ovuliferous scale but differ in the number of different whorls arranged around each stalk; there is a single apical whorl in *Mutoviaspermum*, while in *Paravojnovskya*, each ovuliferous scale bears multiple whorls. Moreover, in *Paravojnovskya scutellata*, some sterile scales might occur beneath the sporophylls (Neuburg 1934; Meyen 1982b; Doweld 2004). Furthermore, no compound ovuliferous cones or bracts are known for Rufloriaceae (Meyen 1988), whereas the polysperms are axillary in *Sergeia* Rothwell et al. 1996 and supra-axillary in *Vojnovskya* (e.g., Meyen 1987) and *Mutoviaspermum*.

Suchoviella Ignatiev et Meyen consists of a racemose polysperm with an unbranched stalk bearing short, helically arranged seed stalks (sporophylls?) that are associated with *Samaropsis synensis* (Dombrovskaya) Ignatiev et Meyen seeds. *Suchoviella* differs from the other members of Rufloriaceae by the presence of an involucre of sterile scales at the base of the polysperm, with sparse trichomes on the outer surface (e.g., Meyen 1988; Ignatiev and Meyen 1989). The Carboniferous *Krylovia* Chachlov is represented by two forms: one in which the sporophylls are helically arranged on an elongate axis that is somewhat expanded toward the apex and the other in which the sporophylls are concentrated at the apex of a short, obconic axis that is recurved outward and downward (e.g., Meyen 1988; Ignatiev and Meyen 1989). These two forms are associated with some transitional forms and are considered to fall within the range of intrageneric variability (Meyen 1982a, 1982b, 1988). Unfortunately, neither the spatial arrangement of the ovuliferous scales on the axis nor the shape and arrangement of bracts are known for these two genera, hindering their comparison with *M. krassilovii*.

The organic connection between *M. krassilovii* and *Quadrocladus*-type leaves supports an affinity between the Subangaran and Euramerican voltzialean conifers. Among the western Angaran walthian Voltziales, *Timanostrobus* has a peculiar morphology, including some similarities with *Mutoviaspermum*. Its compound ovuliferous cones arise terminally from leafy shoots covered by *Brachyphyllum*/*Pagiophyllum*-type leaves and consist of helically arranged ovuliferous scales (polysperms sensu Meyen 1987, 1997). It differs, however, in that the ovuliferous scales are not subtended by bracts but arranged in a dense spiral on the axis. Moreover, the stalk is densely covered by numerous sporophylls (= monosperms in Meyen 1997) and sterile segments, both apically and likely in the basal part.

In other Subangaran (e.g., *Kungurodendron* Meyen) and Euramerican (e.g., *Pseudovoltzia liebeana* Florin, *Dolomitia cittertie* Clement-Westerhof, and *Lebowskia grandifolia* Looy) conifers, the ovuliferous scales are flattened. *Sashinia*, associated—although not in organic connection—with vegetative remains of *Quadrocladus* (e.g., Meyen 1997), corresponds to a compound ovulif-

erous cone with lax, spirally arranged ovuliferous scales (= simple polysperm in Meyen 1997) subtended by bracts. The ovuliferous scales are composed basally of helically arranged sterile scales and apical fertile scales that bear single inverted ovules on their abaxial surface. Bracts and scales resemble *Quadrocladus* leaves in morphology and epidermal anatomy (e.g., Clement-Westerhof 1988; Meyen 1997). The overall symmetry of the dwarf shoot is radial (umbrella-shape arrangement of the fertile scales) like in *Mutoviaspermum*, and the dwarf shoot is supra-axillary. However, the dwarf shoot also bears numerous sterile scales, and the fertile scales are not fused.

Kungurodendron from the lower Permian of the Subangara has been described as a female reproductive organ and was found associated with leafy shoots of *Cyprisissidium appressum* (Zalessky) Meyen. The cone axis bears long leaf-like bracts, which subtend shorter, flattened ovuliferous scales (dwarf shoots), in a spiral arrangement, with reduced sterile segments in the basal part and several recurved fertile segments in the apical part (e.g., Clement-Westerhof 1988; Meyen 1997). The axillary position of the ovuliferous scale and its helical arrangement on the cone axis are similar to *Mutoviaspermum*. The genus differs, however, in the numerous sterile and fertile segments on the dwarf shoot, which are not fused, and the bilateral symmetry of the ovuliferous organ.

Other comparable Voltziales, such as *Krassilovia* Herrera et al. from the Triassic of Mongolia, are characterized by imbricated and tightly interlocked ovuliferous scale-bract complexes. The shape of the ovuliferous scale, the fact that it is fused with the bract, and the imbricated attachment of the scales on the axis distinguish it noticeably from *Mutoviaspermum*. *Conewagia longiloba* Axsmith et al., a conifer from the Upper Triassic of North America, differs from *Mutoviaspermum* because of the *Pagiophyllum*-type sterile leaves (narrower and slenderer), the closely spaced scale-bract complexes, and the ovuliferous scales with a stalk-like base and an expanded apical portion terminating in several (11) apical segments. All modern Voltziales share a similar set of morphological traits that distinguishes them from *Mutoviaspermum*: (i) fused scales and bracts that form scale-bract complexes, (ii) scale-bract complexes that are closely spaced on the axis, and (iii) dorsiventrally flattened ovuliferous scales that have a proximal stalk and expanded distal part with several fused segments.

The typical peltate ovuliferous organ of *Mutoviaspermum* is superficially similar to the female reproductive organs of peltaspermalean seed ferns, such as *Peltaspermopsis*, *Peltaspermum* Harris, and *Germaropteris* Kustatscher et al. These female reproductive organs are simple cones with umbrella-like ovuliferous scales topped by a radial or elliptical disk with marginal lobes, on which seeds are attached abaxially (e.g., Gomankov and Meyen 1986; Kustatscher and van Konijnenburg-van Cittert 2010). The similarities between the female peltaspermalean reproductive organs and *Mutoviaspermum* are limited to the peltate shape of the ovuliferous organ (ovuliferous scales) and the proximal attachment area of the seeds. In *Mutoviaspermum*, the peltate structure is composed of lobes that are fused only in the basal part and free for about two-thirds of their length, whereas in *Peltaspermum* and *Permotheca*, lobes are very short and present only on the margin of the disk (e.g., Taylor et al. 2009; Kustatscher et al. 2014). Moreover, the helical arrangement of the ovuliferous organs on the cone axis is not certain

in peltasperms (see also Kustatscher and van Konijnenburg-van Cittert 2010), and there is no bract subtending the peltate appendages as far as we know.

Although certain structural details of *Mutoviaspermum* are reminiscent of features seen in other primitive conifers and Cordaitales (supra-axillary position of the ovuliferous organs, presence of bracts), including Vojnovskyaceae (organization of the ovuliferous scales on the axis, supra-axillary position of the ovuliferous scales, presence of bracts), Ruffiaceae (peltate structure of the ovuliferous scales, attachment position of the ovules/seeds), primitive Voltziales (axillary or supra-axillary position of the ovuliferous scales, helical arrangement of the ovuliferous scales in a compound ovuliferous cone, presence of bracts), and Peltaspermales (peltate structure of the ovuliferous organ/ovuliferous scales), it does not fit well into any of these gymnosperm groups.

Phylogenetic Analyses and Relationships of the Permian Conifers

The relationships between Paleozoic and Mesozoic coniferophyte taxa are still actively debated. Some of the earliest and most influential hypotheses were established on an ontogenetic and morphological basis (Florin 1927, 1951). More recent investigations have flourished after the adoption of formal phylogenetic methods. A pivotal study was conducted by Rothwell et al. (2005), who evaluated the relationships among waltchian and other ancient conifers. Their study made use of characters first identified by Hernandez-Castillo et al. (2001), who developed sound methodologies and reliable criteria for circumscribing species of waltchian conifers and for resolving the systematic relationships among fossil and extant conifers. However, these two studies used mainly Permian conifers from Europe and North America, with only a few examples from Subangara (coded on data from Meyen 1987) and Gondwana.

The pioneering work on the relationships among Angaran conifers was carried out by Meyen (1987), who established Vojnovskyaceae and Ruffiaceae and included them in the Cordaitales (= Cordaitanthales in Meyen 1987). However, since the reproductive biology of the Vojnovskyaceae is still poorly understood, Taylor et al. (2009) treated them as a group of enigmatic gymnosperms, whereas other authors (e.g., Meyen 1982b; Rothwell 1988; Anderson et al. 2007) attributed them to the Angaran cordaites because of their association with *Cordaites* leaves. Whether *Vojnovskya* Neuburg is interpreted as a lateral bisexual cone (Neuburg 1955; Zimina 1967, 1977) or as a unisexual cone, associated with seeds of *Samaropsis stricta* Neuburg (e.g., Meyen 1984, 1988), may depend on the preservation and compression plane of the “polyspermy” (Nagolnykh 2001).

Meyen (1987, 1997) highlighted similarities between *Timanostrobus* and *Vojnovskya*, suggesting a closer relationship of the former to Vojnovskyaceae than to conifers. Meyen (1987) noted also that some of the Subangaran taxa exhibit a very long retention of characteristics of fairly primitive plant types. *Sashinia* was interpreted as a primitive taxon (Lebachiaceae) because of the subapical attachment of the seeds and the bent seed axes (e.g., Clement-Westerhof 1988), whereas the flattening and bilateral symmetry of the dwarf shoot in *Kungurodendron* were considered derived characters, common to various Euramerican lower Permian genera, such as *Pseudovoltzia*, *Dolomitia* Clement-

Westerhof 1987, and *Lebowskia* Looy 2007 (e.g., Clement-Westerhof 1988; Looy 2007; Forte et al. 2017). However, cladistic analyses of voltzialean conifers placed both *Kungurodendron* and *Timanostrobus* outside the European voltzian and waltchian Voltziales and among the so-called Angara Voltziales (e.g., Hernandez-Castillo et al. 2003; Rothwell et al. 2005).

The MP analysis carried out on the matrix of Rothwell et al. (2005) resulted in eight trees of 186 steps, distributed in three islands. One island has *Mutoviaspermum* as sister to all other taxa except the outgroup, with the trees differing in the placement of *Timanostrobus* and *Concholepis* in relationship to the Gondwanan clade (fig. 11A). In another, *Mutoviaspermum* is placed as sister to all taxa except Cordaitales and the “Vojnovskialean plants,” with the trees differing in the placement of *Timanostrobus* and *Concholepis* in relationship to the Gondwanan clade, as well as the topology of the Cordaitales, which are retrieved either as monophyletic or as successive sisters to the other taxa (fig. 11B). The third island has *Mutoviaspermum* as sister to the Gondwanan clade, with *Timanostrobus* and *Concholepis* in an uncertain position either as sister to the *Mutoviaspermum* + Gondwana clade or as sister to this clade and the rest of the conifers (fig. 11C).

MP bootstrap shows that none of the placements receives substantial support (fig. 11D), with *Mutoviaspermum* as sister to the rest being retrieved in only 18% of the replicates, *Mutoviaspermum* as sister to all but the Cordaitales and the “Vojnovskialean plants” being retrieved in 31% of the replicates, and the *Mutoviaspermum* + Gondwanan clade being present in less than 5% of the replicates. ML and BI analyses mainly favor two placements of *Mutoviaspermum*, with the other relationships being coherent with the MP analyses. *Mutoviaspermum* is placed above the Cordaitales and the “Vojnovskialean plants,” although with relatively low support (55 ML bootstrap and 77 posterior probability). Both *Mutoviaspermum* and *Dicranophyllum* are retrieved as sister to the rest of the conifers with similar (low) support from all three methods (fig. 11E). Even if support is generally low, it seems that no major conflicting signal is present in this part of the tree.

Our analyses show that *Mutoviaspermum* is placed in a relatively basal, though uncertain, position in the tree, with different methods more strongly supporting a placement between Cordaitales and Vojnovskiales and the rest of the conifers (fig. 12). However, the many derived characters of *Mutoviaspermum*, such as the terminal arrangement of the sporophylls and the absence of sterile scales, indicate that this taxon already reached a high level of specialization and might represent a parallel experiment toward reduction of the ovuliferous shoot and protection of the seeds that converged with the more advanced voltzian Voltziales. Better sampling and understanding of the many Subangaran taxa are necessary to really solve the relationships between these peculiar forms.

Conclusions

The Lopingian succession at Mutovino yielded one of the richest and most diverse Tatarina floras of European Russia including several taxa of mosses, lycophytes, seed ferns, and conifers and some taxa of uncertain botanical affinity. The co-occurrence in the same assemblage of vegetative shoots belonging to *Quadrocladus schweitzeri*, male strobili of *Dvinostrobus sagittalis*,

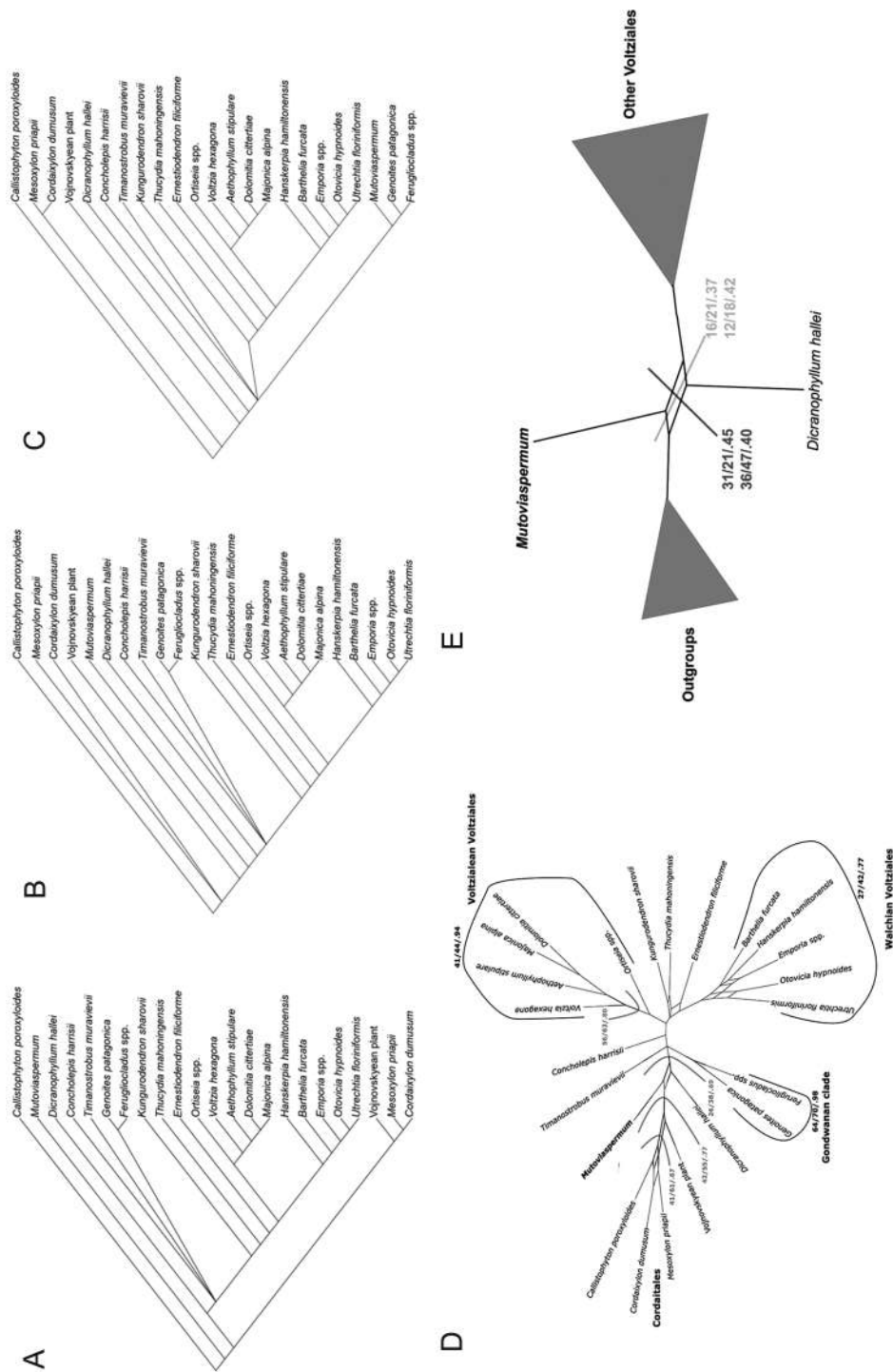


Fig. 11 Results of the phylogenetic analyses. A–C, Consensus trees from the three islands retrieved by the maximum parsimony (MP) analyses, showing the different placements of *Mutoviaspermum*. D, Consensus network with a 20% cutoff of the maximum likelihood (ML) bootstraps. Support for some of the major splits is shown as MP bootstrap/ML bootstrap/Bayesian inference (BI) posterior probability. E, Simplified version of D that details the two equally likely placements of *Mutoviaspermum* retrieved by ML and BI with the full matrix (top row) and a matrix with most vegetative characters inferred from *Quadrocladus schweizeri* removed (bottom row).

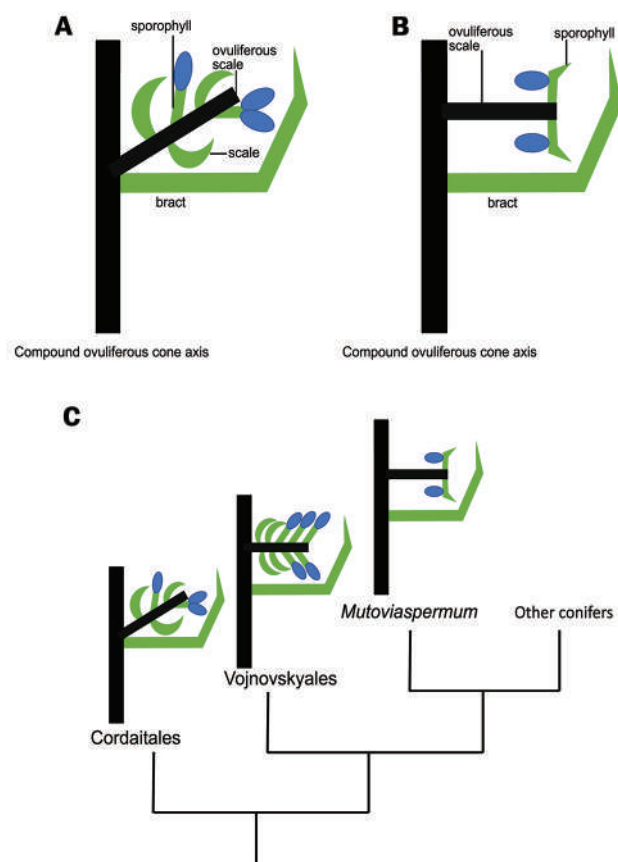


Fig. 12 Schematic interpretation of homologies and evolution of the *Mutoviaspermum* ovulate compound cone. Synthesis of the interpretation of the different organs in a cordaitalean plant (A) and in *Mutoviaspermum* (B), with stems colored in black, leaf homologues in green, and ovules in blue. C, Potential evolutionary series leading from a cordaitalean-like ovuliferous cone to a *Mutoviaspermum*-like ovuliferous cone via a vojnovskyalean-like intermediate.

and *Mutoviaspermum krassilovii* gen. et sp. nov. would suggest a relationship between these three taxa, although so far, an anatomical connection is known only for *Quadrocladus*-type leaves and *M. krassilovii*. The fact that the ovuliferous organs of *M. krassilovii* were always found attached to the axis but the seeds were often not attached or only partly overlying the compound ovuliferous cone could suggest that the seeds were shed before the ovuliferous scales. This differs from what appears to be the dissemination modus of Peltaspermales, where *Peltaspermum* or *Germaropteris* is always found dispersed in the sediment. This, to-

gether with the degree of fusion and attachment of the segments, might also help in the distinction between *Mutoviaspermum*-type and peltaspermalean-type reproductive organs.

No cones of *Mutoviaspermum* type have yet been found outside of Russia. Vegetative leaves of *Quadrocladus* type have been found in anatomical connection with *Mutoviaspermum* and associated with the female cone *Sashinia*, which has been assigned to Lebachiaeeae (Meyen 1997) or Sashiniaceae (Gomankov 2010). This opens the question whether the attributions to the other taxa were only coincidental (co-occurrence without any botanical affinity) or whether they could indicate that *Quadrocladus*-type vegetative shoots were produced by different conifer families, similar to *Brachyphyllum* Brongniart and *Pagiophyllum* Heer.

Mutoviaspermum shows a mixture of primitive and derived characters with at least one of its characters, the peltate structure of the ovuliferous organs, not having been described before from Permian conifers. This, as well as the missing botanical connection with any male cone, makes the placement in the phylogeny of Permian conifers difficult. It underlines how little of the phylogeny of Permian–Triassic conifers is understood. Moreover, it shows the high diversity of characters in early conifers, especially considering that the paleogeographic area of Subangara was previously neglected in phylogenetic analyses both because of linguistic barriers and because the history of paleobotanical studies in Russia is much shorter than in Europe or North America. In order to understand the evolutionary history of the early conifers, it will thus be important to also focus more on the peculiar taxa occurring in these geographic areas and include them in the phylogenetic analyses.

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