

# Early Jurassic Climate Warming in Eastern Siberia: First Macrofloristic Evidence from Irkutsk Basin, Russia



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**Abstract:** Numerous new records of *Ferganiella*, *Podozamites*, and *Schidolepium*, including a new species, *Ferganiella ivantsovii* sp. nov., are described from the Early Jurassic (Toarcian) Middle Subformation of the Prisayan Formation from the Euro-Sinian paleofloristic region in the Irkutsk Basin, Eastern Siberia, Russia. An analysis of the paleogeographic distribution of *Ferganiella* and *Podozamites* shows that both genera were the most diverse and numerous in the East Asian province of the Euro-Sinian region and in the Northern Chinese province of the Siberian region during the Early and Middle Jurassic. These phytochoria were located in the subtropical and temperate subtropical climate zones, which allows us to consider *Ferganiella* and *Podozamites* as thermophilic plants, which are important indicators of the Early Toarcian climatic optimum. Their abundance in the Irkutsk Basin thus may indicate Early Toarcian warming; further abundant *Schidolepium* cones, which produced *Araucariacites* pollen, typical for Euro-Sinian flora complement the scenario. Thus, the new finds are the first macrofloristic indicators of the Toarcian climatic optimum in the Irkutsk Basin.

**Key words:** paleobotany, *Ferganiella*, *Podozamites*, *Schidolepium*, Toarcian climatic optimum, paleobiogeography, Siberian paleofloristic region, Irkutsk

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## 1 Introduction

The Jurassic period was a time of greenhouse climate. At that time, heat was more evenly distributed over the Earth, and there was no stable ice cover, even in the polar regions; nevertheless, climatic zonation did exist. Paleobotanical data from the Northern Hemisphere indicate the presence of two climatic zones in the Early and Middle Jurassic of Laurasia: moderately warm and subtropical. The flora of the Siberian paleofloristic region developed in the zone of moderately warm climate; this area covered the territories of present-day Siberia, Kazakhstan, Mongolia, and northern China. For example, forests of deciduous gymnosperms prevailed in this region with Ginkgoales, Leptostrobales, and ancient Pinaceae (*Pityophyllum* Nathorst, *Schizolepidopsis* Doweld and *Pityospermum* Nathorst). This contrasts with the Euro-Sinian paleofloristic region, which was located in the subtropical climate zone and extended from East Greenland through Central Asia to Japan. In this region, conifers of the Bennettiales, Cycadales, Caytoniales, and Cheirolepidiaceae prevailed (Vakhrameev, 1991).

However, the climate was not constant. Global climate warming began at the end of the Late Pliensbachian and reached an optimum in the Early Toarcian (ETO). This process was accompanied by a significant marine transgression and oxygen deficiency in the ocean, termed the Toarcian anoxic event (around 183–182 Ma) (Hallam, 2001; Lu et al., 2010; Gill et al., 2011; Dickson, 2017;

Them et al., 2018). This is evidenced by a wide distribution of marine black shales in Europe, Japan, Alaska and Canada (Jenkyns, 1988), as well as in Siberia (Shurygin et al., 2000), a biotic crisis for the marine fauna (Tremolada et al., 2005; Caswell et al., 2009; Mattioli et al., 2009), and a changover of floras in Europe, Asia, and Siberia (Slater et al., 2019; Vakhrameev, 1991).

In West Siberia, the climatic ETO is marked by palynological data: Palynozone 6 was established, reflecting changes in the floral composition during this warming; this zone comprises spores and pollen of Euro-Sinian thermophilic plants that migrated to Siberia and reached a maximum diversity and abundance: Dipteridaceae, *Duplexisporites* Deak, *Klukisporites* Couper, *Marattisporites* Couper, *Matonisporites* Couper, *Classopollis* Pflug, *Eucommiidites* Erdtman (Ilyina, 1985; Skoblo et al., 2001; Smokotina, 2006). The appearance of ferns *Clathropteris* Brongniart, *Klukia* Raciborski, *Phlebopteris* Brongniart, *Thaumatopteris* Göppert emend. Nathorst and bennettites *Pterophyllum* Brongniart, *Ptilophyllum* Morris emend. Bose and Kasat, *Otozamites* Braun in the West Siberian macroflora is also associated with the ETO warming (Vakhrameev, 1991; Kirichkova et al., 1992; Mogutcheva, 2014). These changes in the palynoflora and macroflora indicate that a moderately warm humid climate in the Early Toarcian in Siberia was replaced by a moderately subtropical climate, which was intermediate between the full subtropical in the Euro-Sinian paleofloristic region and the moderately warm Siberian paleofloristic region (Vakhrameev, 1991). Despite the influx of thermophilic plants from the Euro-

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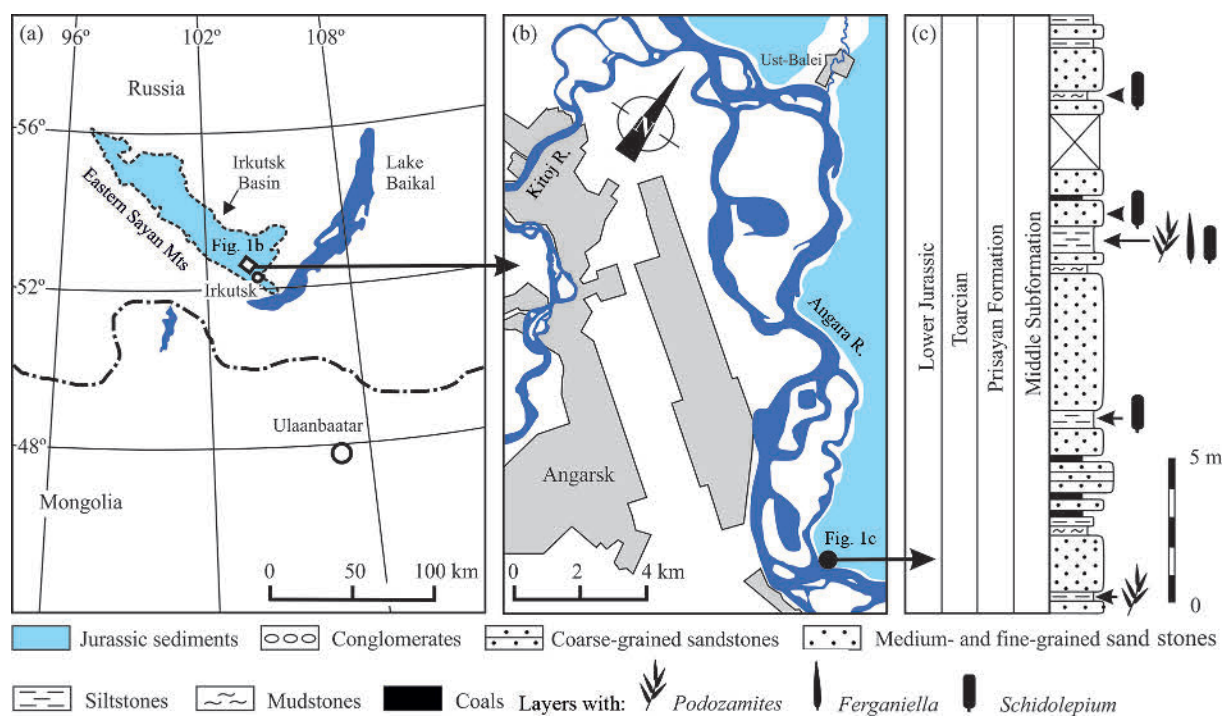


Fig. 1. Geographical position of the Irkutsk Coal Basin, eastern Russia (a) and the Sukhov Cape locality on the right bank of the Angara River (b) and its lithological structure (c); in (c) the distribution of *Schidolepium* strobiles and *Ferganiella* and *Podozamites* leaves is shown.

Sinian region, the broader of Siberian vegetation remained the same (Golbert, 1987; Ilyina, 1985; Vakhrameev, 1991). Thermophilic plants seem to have penetrated Siberia mainly along the sea coasts, while floral change in inland areas was insignificant (Vakhrameev, 1987). Until now this observation appears to have been valid for the Irkutsk Basin, where warming apparently did not manifest itself either in the composition of the macrofloras nor the palynofloras. Due to the position of this region inside the continent, far from the sea, and the presence of mountain systems around it, even significant global warming did not contribute to climate softening here (Frolov et al., 2022).

Despite recent paleobotanical and palynological studies (Frolov et al., 2022), the problem of how the Irkutsk Basin responded to the ETO warming still needs to be resolved. Previously (Skoblo et al., 2001), another palynoassemblage, Assemblage V, similar to Palynozone 6, which marks the moment of the ETO, has been recognized from the lower part of the Middle Prisyayan Subformation (Subfm.). The samples come from reference boreholes in the Ishideyi and Karantsayi coal deposits of the Irkutsk Basin, but there is no detailed description of this palynology. Also, we have not found Palynozone 6 in the natural outcrops of the Middle Prisyayan Subfm. studied by us. This can be explained by the fact that, in outcrops, the base of the subformation is composed of gravelites, which do not preserve spores and pollen (Frolov et al., 2022). The presence of single thermophilic ferns *Clathropteris* sp. and *Phlebopteris polypodioides* in the Prisyayan Formation (Fm.) has been indicated only by Prinada (1962) but the subformation of the Prisyayan Fm. where these ferns were found was not given and, these

plants have not been discovered again since. Nevertheless, geochemical indexes in sandstones of the Lower Prisyayan Subfm. suggest a change from a warm, humid to a hot, arid climate at this time (Mikheeva et al., 2021). Thus, the absence of ETO warming in the Irkutsk Basin could not be completely excluded and, therefore, we began searching for new evidence of the warming in outcrops of the Middle Prisyayan Subfm., where previous researchers found such evidence.

Within this research framework, in 2020–2022, paleontological studies of the Middle Subfm. of the Prisyayan Fm., located on the right bank of the Angara River, in the Irkutsk Basin (Fig. 1), were carried out to ascertain new evidence. As a result, unusual assemblages for the Jurassic flora were found, which are described here. This work is also devoted to interpreting this combination of plants, which includes a new species of the genus *Ferganiella*.

## 2 Geological and Paleobotanical Background

The Irkutsk Coal Basin is located in the south of the Siberian Platform and extends along the Eastern Sayan Mountains (Fig. 1). The Early–Middle Jurassic sediments of the basin are subdivided into the Cheremkhovo, Prisyayan, and Kuda formations (fms) (Saks et al., 1981; Skoblo et al., 2001; Frolov and Mashchuk, 2018). Only the Cheremkhovo Fm. contains coal seams of industrial significance. An ash interlayer (tonstein) was found in the coal seam in the Azeisk coal deposit northwest of the basin (Arbuzov et al., 2016). According to U–Pb dates for accessory zircons from this layer, the age of the Upper

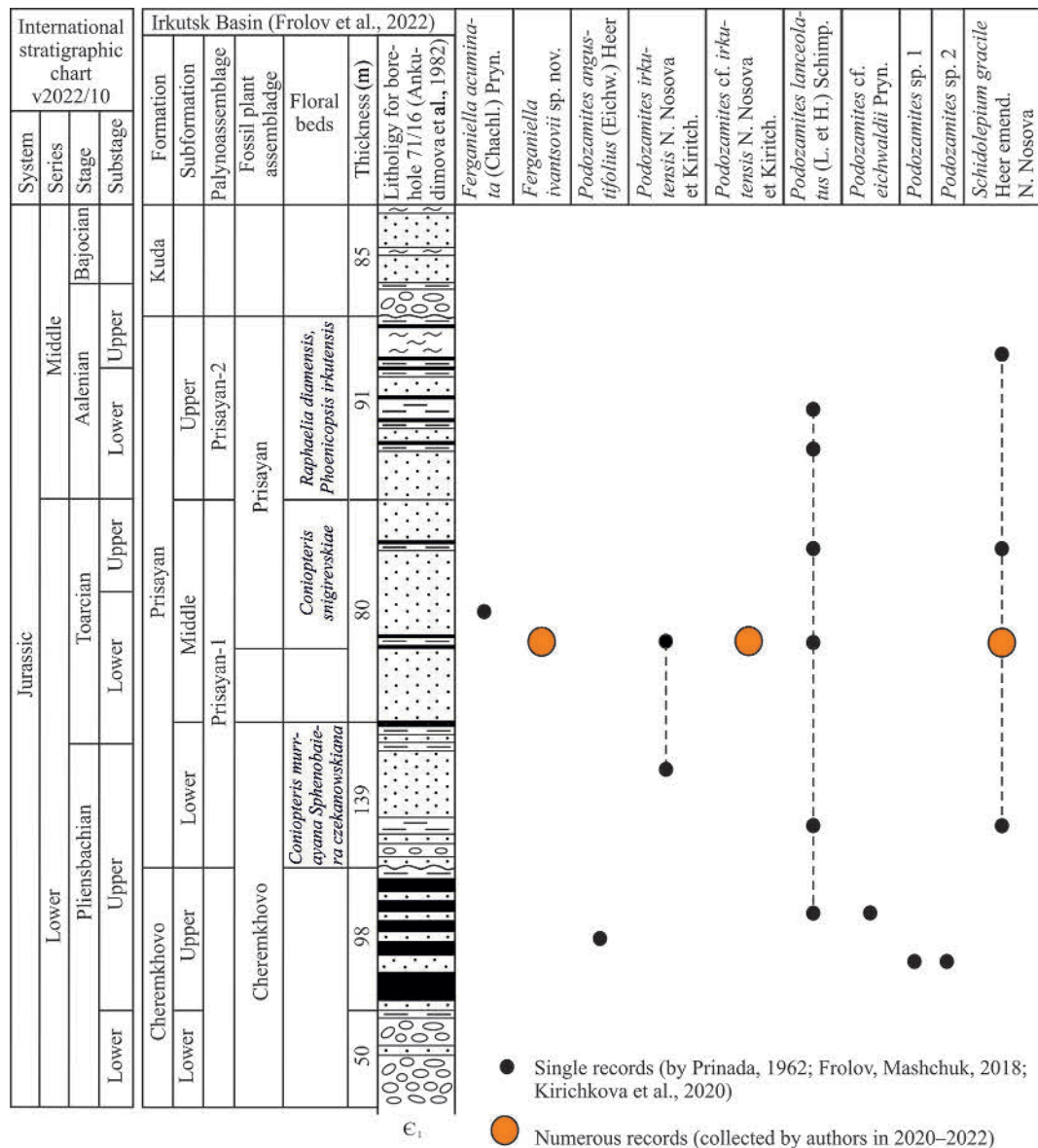


Fig. 2. Occurrence of *Ferganiella* Prynada, *Podozamites* Braun and *Schidolepium* Heer emend. N. Nosova in the Early and Middle Jurassic of the Irkutsk Basin.

(coal-bearing) Subfm. of the Cheremkhovo Fm. is 187.44 + 0.45 to 1.60 Ma (Pliensbachian) (Mikheeva et al., 2020). According to palynological data, the Upper Subfm. is dated as the Late Pliensbachian (Frolov et al., 2022). The overlying Prisayan Fm. is an alluvial megacycle, which begins with channel sediments (Lower Subfm.), passes into predominantly floodplain (Middle Subfm.), and ends with lacustrine-marsh beds (Upper Subfm.). From our point of view, based on the palaeobotanical and palynological data, the age of the Prisayan Lower Subfm. is determined by the end of the Late Pliensbachian, the Middle Subfm. one is Toarcian, and the Upper Subfm. is Aalenian (Frolov et al., 2022).

The Jurassic flora of the Irkutsk Basin is typical for the Siberian paleofloristic region. Its composition is dominated by ferns (Dipteridaceae, Cyatheaceae, Osmundaceae, and form-genus *Cladophlebis* Brongniart),

Ginkgoales, and Leptostrobales with a subordinate value of Cycadales, Bennettitales, Gnetales, and Cheirolepidiaceae conifers. Lycopsids, sphenopsids, and conifers of the Pinaceae family are not distinguished by high species diversity but can predominate in the assemblages. The most significant number of species is observed in Ginkgoales, Leptostrobales, and ferns (Prinada, 1962; Frolov and Mashchuk, 2018; Kirichkova et al., 2020).

Representatives of the genera *Podozamites*, *Ferganiella*, and *Schidolepium* are rare. However, taxa of *Podozamites* are the most diverse and represented by *P. angustifolius* (Eichwald) Heer, *P. irkutensis* N. Nosova et Kiritchkova, *P. lanceolatus* (Lindley et Hutton) Schimper, *P. cf. eichwaldii* Schimper, *Podozamites* sp. 1 and *Podozamites* sp. 2 (Prinada, 1962; Frolov and Mashchuk, 2018; Kirichkova et al., 2020). Most of these species are



represented by rare or single specimens in a few localities. Only *P. lanceolatus* can be traced from the Lower to Middle Jurassic (Fig. 2). *Ferganiella* is represented by two imprints of *F. acuminata* (Chachlov) Prynada, known from the Middle Prisayan Subfm. (Prynada, 1962) (Fig. 2). Rare pollen cones of *Schidolepium gracile* Heer emend. N. Nosova are found in three natural outcrops that expose the Lower, Middle, and Upper subfms. of the Prisayan Fm. (Prynada, 1962; Kirichkova et al., 2020) (Fig. 2).

In 2020–2022, we collected plant remains from the Middle Prisayan Subfm., exposed in natural outcrop at Sukhov Cape (52°30'18.3"N, 103°59'00.6"E), located on the right bank of the Angara River (Fig. 1b). The deposits are represented here by a sequence of fine-grained, gently undulating and horizontally laminated sandstones up to 20 m thick. Relatively thin layers of siltstones, mudstones, and coals occur among the sandstones. According to paleobotanical data, we determine that the age of the Middle Prisayan Subfm. is limited to the Toarcian (Frolov et al., 2022). Numerous records of *Podozamites* cf. *irkutensis*, *Ferganiella ivantsovii* sp. nov., and *Schidolepium gracile* have been found in some layers of the Sukhov Cape locality (Fig. 1). The abundance of these fossils contrasts strongly with the generally rare remains of *Podozamites*, *Ferganiella*, and *Schidolepium* in the Irkutsk Basin (Fig. 2).

### 3 Materials and Methods

The fossil material of *Ferganiella ivantsovii* sp. nov. is represented by 23 samples of leaf impressions and *P.* cf. *irkutensis* is represented by 13 samples. Cuticular analysis of the fossil leaves was not applied since the preserved organic matter is generally thin and strongly degraded. *Schidolepium gracile* is represented by 16 pollen cone impressions. On some specimens, compressions suitable for maceration were preserved.

Available samples were studied in reflected light using an MBS-10 stereo microscope and photographed using a digital camera Canon EOS 650D. The samples were processed using equipment at the Centre of Geodynamics and Geochronology, Institute of the Earth's Crust, SB RAS (Irkutsk, Russia). Pollen cone cuticles were macerated using a standard method in a Schulze mixture, then treated with an ammonia solution (10%), and enclosed in a medium for preparing histological sections of Bio Mount. Nine microslides with an agglomeration of pollen grains were made in total. The microslides were studied in transmitted light using a Micromed 3 Led M light microscope equipped with a TouPCam 8.0 MP digital video camera.

The samples and slides are deposited at the Institute of the Earth's Crust SB RAS (Irkutsk, Russia), coll. No. SM-20 and SM-22.

### 4 Systematic Palaeontology

Phylum Pinophyta Cronquist, Takhtajan et W. Zimmerman, 1966

Classis Pinopsida Burnett, 1835

Family Podozamitaceae Nemejc, 1950

### Genus *Ferganiella* Prynada in Neuburg, 1936

**Type species:** *Ferganiella urjanchaica* Neuburg, 1936  
*Ferganiella ivantsovii* A. Frolov et Mashchuk sp. nov.

Figs. 3–5

**Diagnosis:** Leaves oblong-lanceolate with narrow, acute apex and wedge-shaped base and short petiole. Maximum width of leaf is in lower quarter of its length. Venation dense, thin. Veins branch dichotomously in petiole upper part and leaf base. There are 6–8 veins per 5 mm of leaf width. They run parallel to each other and extend to leaf margin as leaf blade narrows.

**Etymology:** In honor of the Russian paleontologist Stepan Valerievich Ivantsov (Tomsk State University), who took an active part in the fieldwork and discovered of the type specimen.

**Holotype:** No. SM-22/20-7a (Figs. 3a; 4a; 5a, f).

**Other material:** Specimen no. SM-22/20-1a (Figs. 3b, 4b), SM-20/18-6 (Figs. 3c, 4d), SM-22/15-2 (Figs. 3d, 4c, 5b), SM-22/20-2 (Figs. 3e, 4g, 5c), SM-22/20-3 (Figs. 3f, 4f), SM-22/15-4 (Fig. 4e), SM-22/20-6 (Fig. 5d, e), SM-22/20-1b (Fig. 5g), SM-22/20-7b (Fig. 5h).

**Type locality:** Irkutsk Coal Basin, right bank of the Angara River, Sukhov Cape locality, 52°30'12.6"N, 103°59'07.4"E (Fig. 1b), Eastern Siberia, Russia.

**Horizon:** Middle Prisayan Subformation, Prisayan Fm.

**Age:** Early Jurassic (Toarcian).

**Description:** The fossil material is represented by 23 imprints of leaf fragments (Figs. 3, 4). The leaves are elongate-lanceolate, margins entire, with a wedge-shaped base, turning into a short and thick petiole (4 mm long, 1.5–2 mm wide) (Figs. 3a, e, f; 4a, f, g; 5a, c, h). The maximum width of the leaf blade (14–16 mm) falls on the lower quarter of its length, then the leaf gradually narrows to an acute (Figs. 3b, 4b, 5d), less often blunt apex (Figs. 3c, 4d). The most complete leaf reaches 116 mm in length (Figs. 3a, 4a). The length of other fragments visible on the imprints varies from 20 to 84 mm. Almost complete leaves imprints with bases and apices make it possible to estimate their initial size at 120–130 mm.

The venation is dense (6–8 veins per 5 mm of leaf width) and very thin, visible only in oblique light. The base of the petiole includes 3–4 veins, which begin to branch dichotomously in its upper part (Figs. 3a, e, f; 5a, c, h). Thus, up to 8–12 veins may be present at the base of the leaf blade. They continue to branch in the lower quarter of the leaf (Figs. 3a, d, e; 4c; 5b) and become 20–24 in the widest part of the leaf. Further, the veins run parallel to each other and extend to the leaf margin as the leaf blade narrows (Figs. 3a–f; 5d–f). As the leaf apex is approached, the veins gradually converge and there are 9–11 veins per 5 mm of the apex width.

**Comparison and remarks.** The studied material is represented by large fragments of isolated leaves. This fragmentation is not because of leaf transportation to the burial site but the tendency of the host rock to break into small tiles. Thus, the original plant lived near the burial place. The absence of leafy stems in our collection most likely indicates that the original plant shed leaves rather than stems.

Comparison of *Ferganiella ivantsovii* sp. nov. with

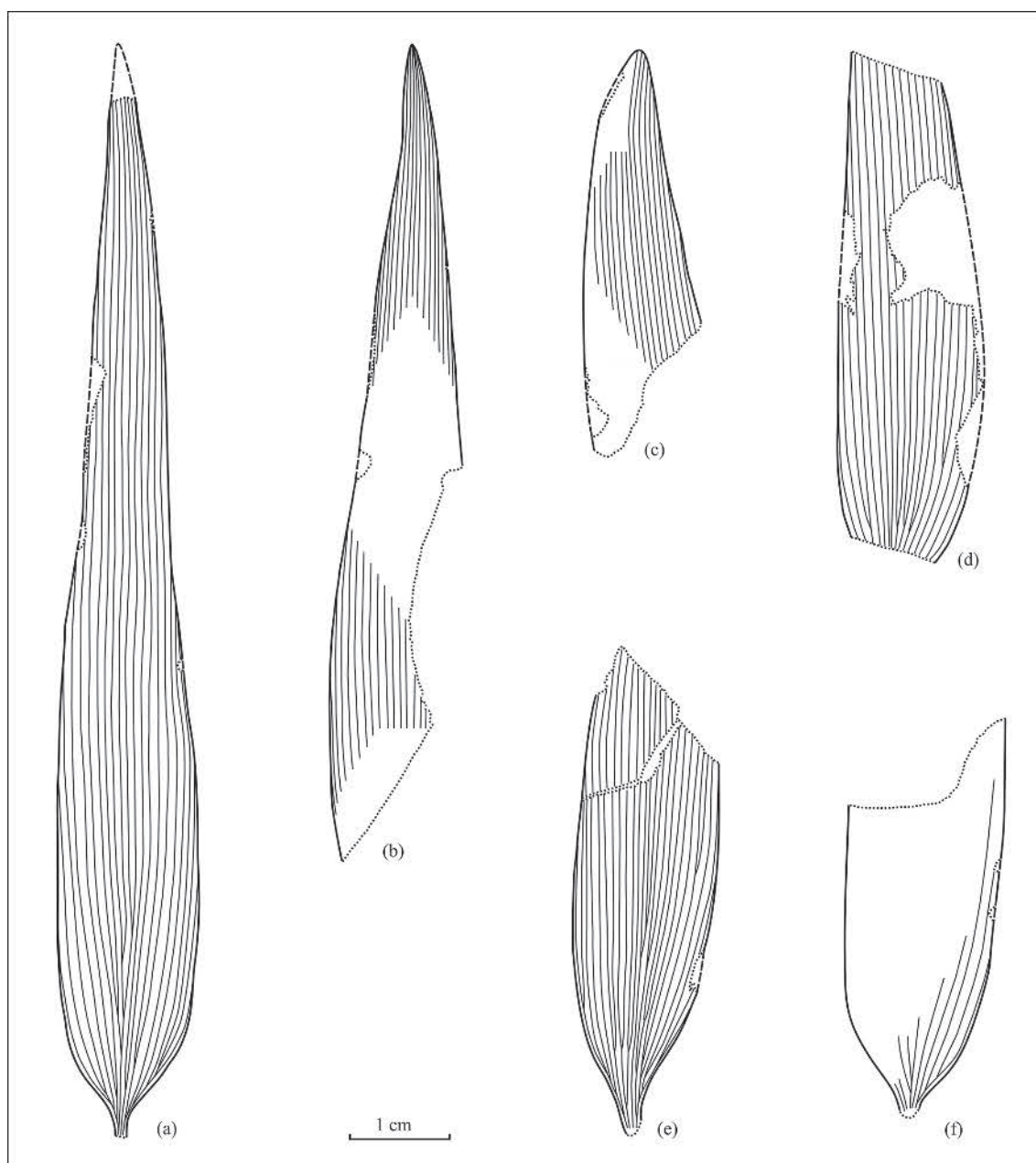


Fig. 3. *Ferganiella ivantsovii* sp. nov. leaf morphology.

(a) The most completely preserved leaf (with missing apex), specimen no. SM-22/20-7a (holotype); (b) the most fully preserved leaf (only base missing), specimen no. SM-22/20-1a; (c) leaf apex, specimen no. SM-20/18-6; (d) middle part of the leaf, specimen no. SM-22/15-2; (e, f) leaf bases, (e) specimen no. SM-22/20-2, (f) specimen no. SM-22/20-3.

other *Ferganiella* species is given in Table 1. *Ferganiella acuminata* (Chachl.) Pryn. from the Lower Jurassic of Irkutsk Basin (Prinada, 1962) is characterized by the presence of leafy stems with lanceolate leaves, the length of which is 70–80 mm with a width of 10–14 mm (Table 1). *F. ivantsovii* sp. nov. has other features: its leaves are elongate-lanceolate, larger [116 mm × (14–16) mm], and isolated from stems.

*Ferganiella elongata* Turutanova-Ketova, found in the Lower Jurassic of Kyrgyzstan (Turutanova-Ketova, 1960), differs from *F. ivantsovii* sp. nov. by smaller leaves [(20–40) mm × (9–13.5) mm], the presence of a blunt apex,

and denser venation (7–10 veins per 5 mm wide) (Table 1). *F. ivantsovii* sp. nov. shows a different picture: leaves are large [116 mm × (14–16) mm] with an acute apex and more widely spaced veins (6–8 by 5 mm wide).

*Ferganiella mongugaica* Srebrodolskaya, found in the Upper Triassic of the Far East (Russia) (Srebrodolskaya, 1968), differs from *F. ivantsovii* sp. nov. by smaller leaf size [(60–80) mm × (10–13) mm], rounded base, and well-developed veins. In the new species, the leaves are large [116 mm × (14–16) mm] with wedge-shaped bases and thin veins visible only under oblique light.

*Ferganiella lanceolata* Brick ex Turutanova-Ketova,



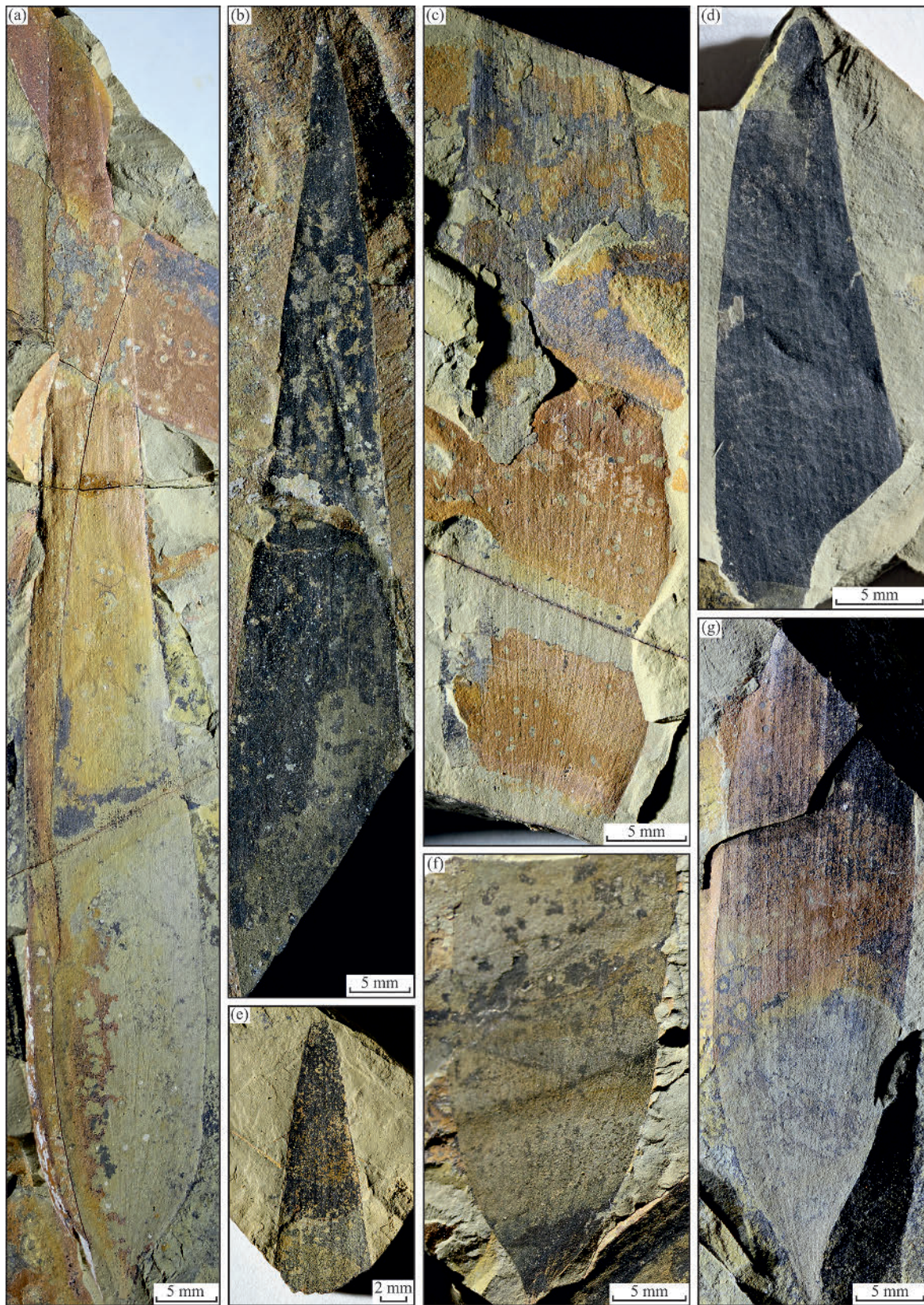


Fig. 4. *Ferganiella ivantsovii* sp. nov. leaf morphology.

(a) The most completely preserved leaf (only apex missing), specimen no. SM-22/20-7a (holotype); (b) the most fully preserved leaf (only base missing), specimen no. SM-22/20-1a; (c) middle part of the leaf with clearly visible veins, specimen no. SM-22/15-2; (d) leaf apex, specimen no. SM-20/18-6; (e) upper part of the leaf without the apex, specimen no. SM-22/15-4; (f, g) leaf bases, (f) specimen no. SM-22/20-3, (g) specimen no. SM-22/20-2.



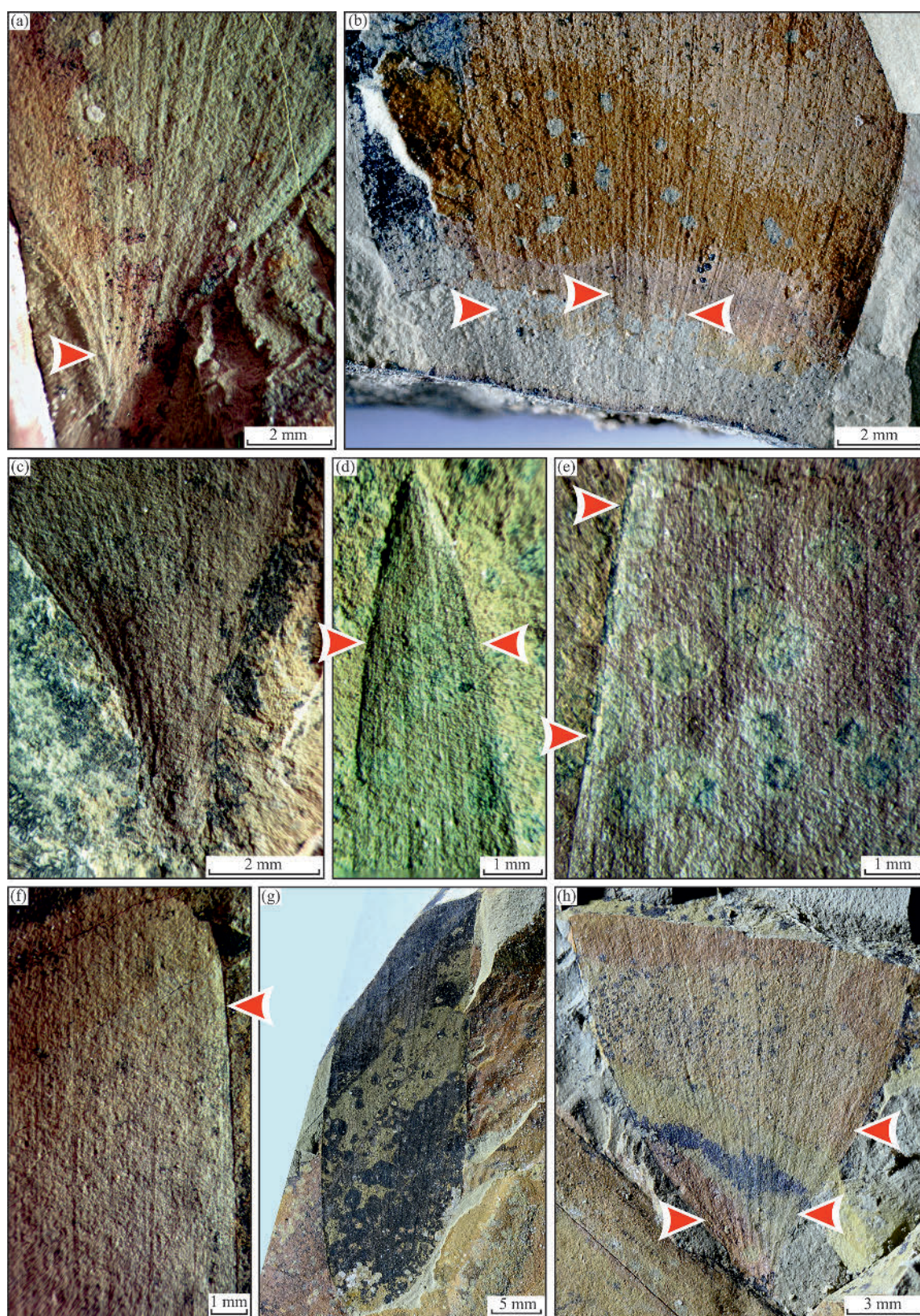


Fig. 5. Details of *Ferganiella ivantsovii* sp. nov. leaves venation.

(a, c, h) Leaf bases with petioles, (a) specimen no. SM-22/20-7a (holotype), (c) specimen no. SM-22/20-2, (h) specimen no. SM-22/20-7b; (b, g) leaf lower part is above the base, (b) specimen no. SM-22/15-2, (g) specimen no. SM-22/20-1b; (d) leaf apex, specimen no. SM-22/20-6; (e, f) close-up of the middle part of the leaf, (e) specimen no. SM-22/20-6, (f) specimen no. SM-22/20-7a (holotype). (a–b, h) arrows show branching sites of veins; (d–f) arrows show sites where the veins exit to the leaf edge.



Table 1 Comparison of leaf morphology of *Ferganiella ivantsovii* sp. nov. with other *Ferganiella* species

Species	Characters				Veins number	Location	Age	Reference		
	Stems	Leaf Shape	Base shape	Apex shape					Petiole	Leaf size (mm × mm)
<i>F. ivantsovii</i> sp. nov.	Unknown	Oblong-lanceolate	Wedge	Narrow, acute	Flat, well developed	~(120–130) × (14–16)	6–8	Eastern Siberia, Russia	J <sub>1</sub>	This study
<i>F. acuminata</i> (Chachl.) Pryn.	Present	Lanceolate	Wedge	Narrow, acute	Well developed	(70–80) × (10–14)	6–7	Eastern Siberia, Russia	J <sub>1</sub>	Chachlov, 1924; Primada, 1962
<i>F. bilanashensis</i> Kiritch.	Unknown	Linear-lanceolate	Heart	Unknown	Short	50 × 13	1	Ural, Russia	T <sub>3</sub>	Kiritchkova, 1969
<i>F. elongata</i> Tur.-Ket.	Unknown	Oblong-lanceolate	Wedge	Obtuse	Flat, well developed	(20–40) × (9–13.5)	7–10	Kyrgyzstan	J <sub>1</sub>	Turutanova-Ketova, 1960
<i>F. kurunzulajensis</i> Pryn.	Unknown	Lanceolate	Rounded	Narrow, subacute	Short, wide	(30–80) × (10–18)	12–13	Transbaikalia, Russia	J <sub>1-2</sub>	Primada, 1962
<i>F. lanceolata</i> Brick ex Tur.-Ket.	Present	Oblong-lanceolate	Strongly narrow	Subacute	Short	(70–114) × (21–31)	9–10	Kazakhstan, Uzbekistan	J <sub>1-2</sub>	Turutanova-Ketova, 1960; Doludenko Orlovskaya, 1976
<i>F. latifolia</i> Brick ex Tur.-Ket.	Present	Broadly lanceolate	Strongly narrow	Acute	Thin, flat	(53–80) × (20–35)	13–15	Kazakhstan, Uzbekistan	J <sub>1-2</sub>	Turutanova-Ketova, 1960; Doludenko Orlovskaya, 1976
<i>F. mesonervis</i> Zhang	Present	Oblong-lanceolate	Narrow	Obtusely rounded	Short	12 × (1–2)	4–5 per leaf width	Longhai Basin, Southern China	J <sub>1</sub>	Zhang, 1982
<i>F. mongolica</i> Srebr.	Unknown	Oblong-lanceolate	Rounded	Acute	Wide	(60–80) × (10–13)	7	Amur Bay, Russia	T <sub>3</sub>	Srebrodolskaya, 1968
<i>F. otzamioides</i> Yang	Unknown	Lanceolate	Heart-shaped	Obtuse	Present	50 × 15	–	Sichuan, China	T <sub>3</sub>	Yang, 1982
<i>F. ovalis</i> Tur.-Ket.	Unknown	Elliptical or short-lanceolate	Sharply narrowed	Obtusely rounded	Short	(18–35) × (10–17)	8–10	Kazakhstan, Kyrgyzstan	J <sub>1-2</sub>	Turutanova-Ketova, 1960; Doludenko Orlovskaya, 1976
<i>F. paucinervis</i> Li	Present	Broadly lanceolate	Sharply narrow	Narrow, acute	Short	80 × (18–25)	7	Yunnan, China	T <sub>3</sub>	Li et al., 1976
<i>F. podozamioides</i> Lih	Present	Lanceolate	Narrow	Unknown	Short	(60–90) × (10–12)	10–12	Yunnan, Sichuan, Shaanxi, Hubei, China	T <sub>3</sub>	Li et al., 1976
<i>F. urfanchaica</i> Neub.	No data	Oblong-lanceolate	Narrow	Subacute	Short	72 × 13	–	Siberia, Russia	J <sub>1-2</sub>	Teslenko, 1970
<i>F. weiyuanensis</i> Yang	Unknown	Broadly lanceolate	Sharply narrowed	Obtuse	Present	(30–50) × (5–11)	–	Sichuan, China	T <sub>3</sub>	Yang, 1982



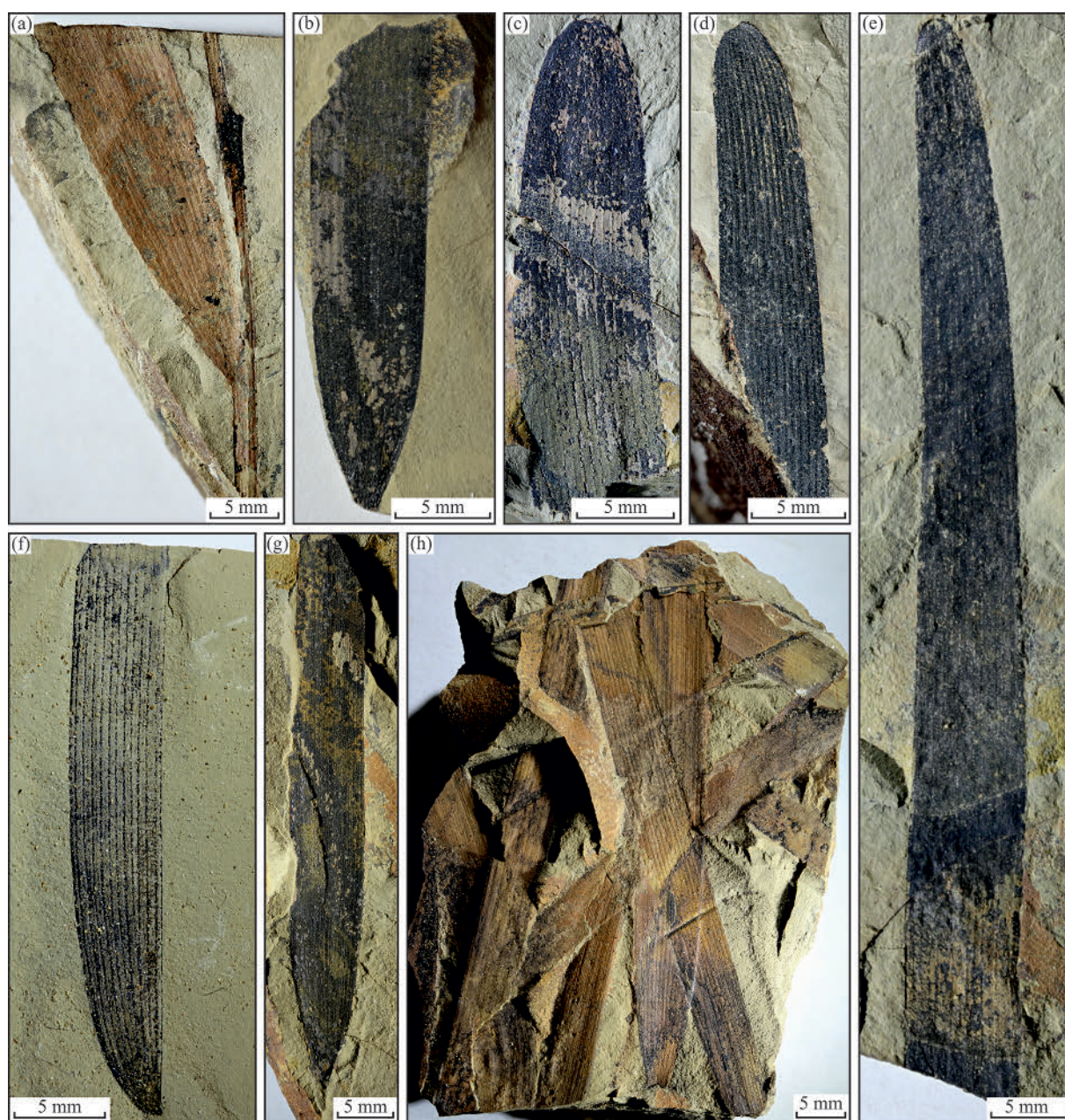


Fig. 6. *Podozamites* cf. *irkutensis* N. Nosova et Kiritchkova.

(a) Branch with leaf base attached, specimen no. SM-20/10-16; (b, f, g) lower parts of leaves with clearly visible veins, (b) specimen no. SM-20/10-17, (f) specimen no. SM-20/18-12, (g) specimen no. SM-22/20-42; (c, d) upper parts of the leaves, where veins converge without merging towards the apex. (c) specimen no. SM-22/15-8, (d) specimen no. SM-20/10-4; (e) the most completely preserved leaf, specimen no. SM-22/15-11; (h) accumulation of large leaf fragments, specimen no. SM-22/16-25.

known from the Lower and Middle Jurassic of Kazakhstan and Uzbekistan (Turutanova-Ketova, 1960; Doludenko and Orlovskaya, 1976), is characterized by wide (21–31 mm) leaves with a pointed apex, a short (1.5 mm) petiole, and dense venation (9–10 veins per 5 mm wide). These characteristics differentiate this species from *F. ivantsovii* sp. nov., the leaves of which are narrower (14–16 mm), with an acute apex, a long (4 mm) petiole, and a sparser venation (6–7 veins per 5 mm).

The leaves of *Ferganiella ovalis* Turutanova-Ketova, present in the Lower and Middle Jurassic of Kazakhstan

and Kyrgyzstan (Turutanova-Ketova, 1960; Doludenko and Orlovskaya, 1976), are elliptical or short-lanceolate with obtusely rounded apex. On the contrary, *F. ivantsovii* sp. nov. leaves are elongate-lanceolate, with an acute apex. These features distinguish *F. ovalis* from *F. ivantsovii* sp. nov.

*Ferganiella paucinervis* Li, from the Upper Triassic of Yunnan Province (China) (Li et al., 1976), differs from *F. ivantsovii* sp. nov. by the presence of leafy stems with broadly lanceolate leaves 80 mm long and 18–25 mm wide. The leaves of the new species are isolated, oblong-



lanceolate, narrower (14–16 mm), and longer (116 mm) than those of *F. paucinervis*.

Thus the new species differs from other *Ferganiella* species in its large leaves and very thin venation, visible only under oblique lighting.

Genus *Podozamites* Braun, 1843

**Type species:** *Podozamites distans* (Presl, 1838) Braun, 1843

*Podozamites* cf. *irkutensis* Nosova et Kiritchkova, 2017 in Nosova et al., 2017a

Fig. 6

**Material:** Specimen no. SM-20/10-16 (Fig. 6a), SM-20/10-17 (Fig. 6b), SM-22/15-8 (Fig. 6c), SM-20/10-4 (Fig. 6d), SM-22/15-11 (Fig. 6e), SM-20/18-12 (Fig. 6f), SM-22/20-42 (Fig. 6g), SM-22/16-25 (Fig. 6h).

**Description:** The fossil material is represented by isolated large fragments of lanceolate leaves with a rapidly narrowed wedge-shaped base (Fig. 6b, f–h) and a rounded apex (Fig. 6c–e). Fig. 6a shows a single specimen that preserved a thin (1 mm) stem with an attached leaf base. The leaf fragments are 15–70 mm long (usually 30–40 mm) and 4–8.5 mm wide (usually 5–7 mm). Fragmentation of the material is caused by cracking of the host rock. The veins dichotomize at the base of the leaf, then run parallel to its margin (Fig. 6a, f, h) and converge at the apex (Figs. 6c, d). There are 12–14 simple parallel veins in the middle part of the leaf.

**Remarks:** The leaf size and apex and base shape, as well as the nature of venation observed on the studied samples, allow us to attribute them to *Podozamites irkutensis* Nosova et Kiritchkova., which are already known from this locality (Nosova et al., 2017a). However, the structure of leaf cuticles is known in *P. irkutensis*, while in our specimens, the cuticle was not preserved. In this regard, we define our samples in open nomenclature as *Podozamites* cf. *irkutensis*.

Pinopsida incertae sedis

Genus *Schidolepium* Heer, 1880, emend. N. Nosova in Nosova et al., 2017b

**Type species:** *Schidolepium gracile* Heer, 1880, emend. N. Nosova in Nosova et al., 2017b

*Schidolepium gracile* Heer, 1880, emend. N. Nosova in Nosova et al., 2017b

Fig. 7

**Synonyms:**

1880. *Schidolepium gracile*, Heer, s. 27, pro parte, taf. VIII, figs. 6–12 (non fig. 5).

1951. *Schizolepidium gracile* Heer, nom. illeg.; Prinada, plate 18, figs. 13, 14.

1962. *Schizolepidium gracile* Heer, nom. illeg.; Prinada, p. 279, plate XVIII, figs. 13, 14.

2017b. *Schidolepium gracile* Heer; Nosova et al., p. 10, plate IV, figs. 1b–14; plate V, figs. 1–18.

2020. *Schidolepium gracile* Heer emend. N. Nosova; Kirichkova et al., p. 135, plate CXXXII, figs. 1a–10; plate CXXXIII, figs. 1–14.

**Material:** Specimen no. SM-20/14-28 (Fig. 7a, g–k), SM-20/14-25 (Fig. 7b), SM-22/19-55 (Fig. 7c), SM-20/14-26 (Fig. 7d), SM-22/10-4 (Fig. 7e).

**Description:** The fossil material is represented by whole pollen cones (Fig. 7a–c) and their large fragments (Fig. 7d, e). Fragmentation of the material is caused by cracking of the host rock. Cones are elongated, cylindrical, 25–29 mm long, 7–8 mm wide, and have a thin (1 mm) axis, where microsporophylls are densely arranged in a spiral order, 4 mm long in the middle part, 2–3 mm wide, and overlap each other with their pointed apices (Fig. 7a–e).

The cuticle of the pollen sacs was destroyed during maceration. Only one whole microsporangium, which was slightly bent, was obtained (Fig. 7f). It is elongated, fusiform, 2200 µm long, 400 µm wide. The content of the pollen sac is represented by an agglomeration (Fig. 7g) of rounded, asaccate, inaperturate pollen grains 50 µm in diameter (Fig. 7h–j). The pollen has a subequatorial annular area (Fig. 7j–l) and granular exine with thin leptomic creases (Fig. 7h).

**Remarks:** *Schidolepium gracile* cones from the Irkutsk Basin were studied in detail by Nosova et al., 2017b; they compared this species with the pollen cones of *Elatides curvifolia* (Dunker) Nath. from the Early Cretaceous of Montana, United States (Miller and LaPasha, 1984), *E. sandaolingensis* Z.X. Wang et B.N. Sun from the Middle Jurassic of Xinjiang, China (Wang et al., 2016), *E. harrisii* Zhou from the Early Cretaceous of Liaoning, China (Zhou, 1987; Shi et al., 2014), and *Sewardiodendron laxum* (Phillips) Florin from the Middle Jurassic of Henan province (Yao et al., 1998). Some similarity of *Schidolepium gracile* with pollen cones of some extant species of *Araucaria* Jussieu was also noted (Nosova et al., 2017b). The pollen grains we found in the cones of *Schidolepium gracile* are very similar to the pollen of modern Araucariaceae: they are round, inaperturate, asaccate, and have a granular exine, and subequatorial annular area. Isolated pollen of this structure is assigned to the genus *Araucariacites* Cookson (Cookson, 1947). This association may also indicate that *Schidolepium* is related to the Araucariaceae family.

## 5 Discussion

### 5.1 Taxonomic position

*Podozamites* and *Ferganiella* are used as morpho-genera of conifers, combining stems with lanceolate leaves and dense parallel venation. In *Podozamites*, the veins run parallel to the leaf margin and converge at the leaf apex. In *Ferganiella*, the veins extend to the leaf margin. Such large multi-veined leaves among modern conifers are found only in the Araucariaceae (*Agathis* Salisbury) and Podocarpaceae (*Nageia* Gaertner). However, in *P. cf. irkutensis* and *F. ivantsovii* sp. nov., there are no data on the structure of the leaf cuticles, which makes it impossible at this stage to compare in detail with modern genera.

In the Mesozoic of the Northern Hemisphere, a series of reproductive structures associated with the leaves of *Podozamites* have been identified. In the Late Triassic to Late Jurassic, *Podozamites* leaves are regularly associated with the reproductive structures of *Cycadocarpidium* Nathorst and *Swedenborgia* Nathorst (Oishi and Takahasi,



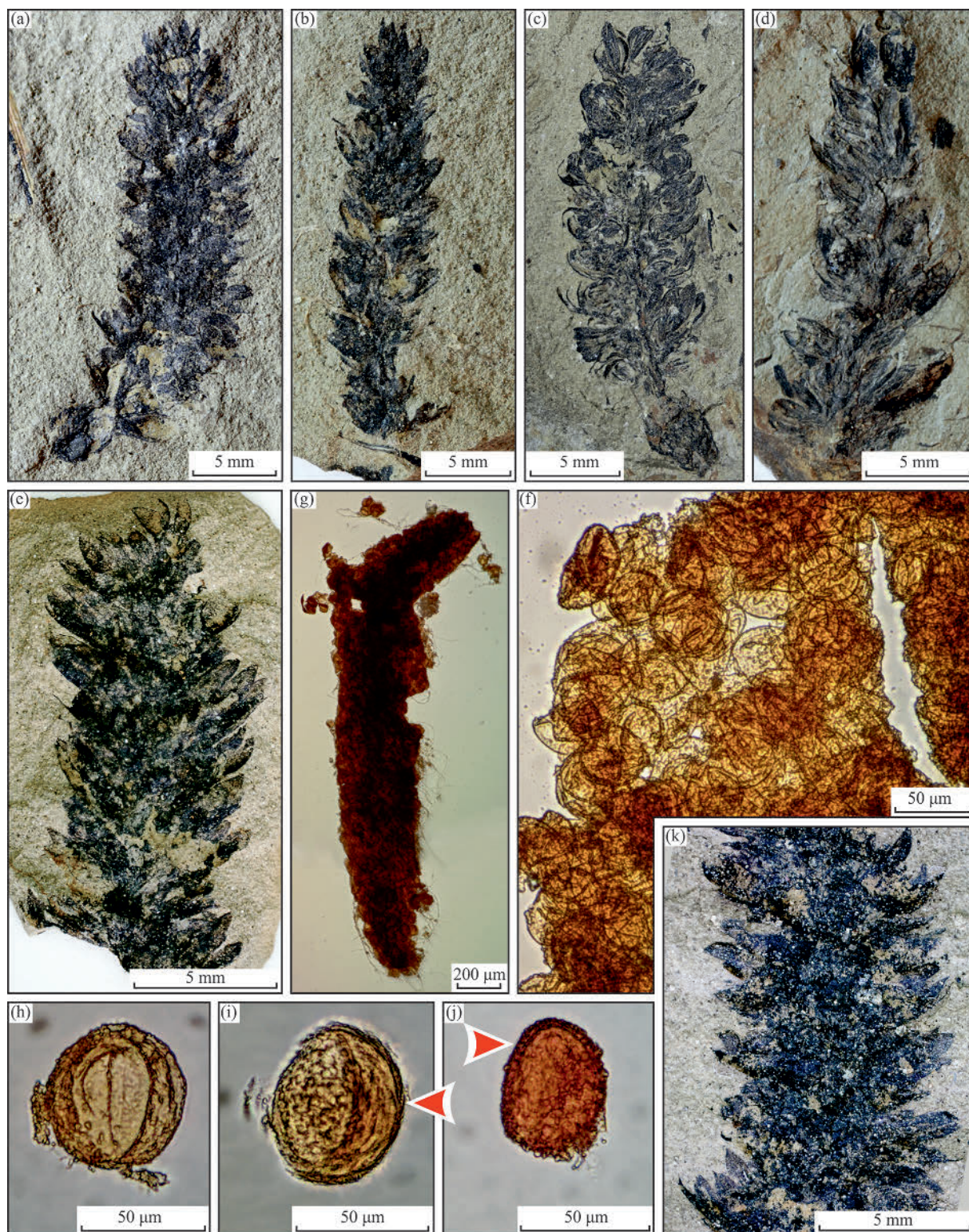


Fig. 7. *Schidolepium gracile* Heer emend. N. Nosova.

(a–c) Pollen cones, (a) specimen no. SM-20/14-28, (b) specimen no. SM-20/14-25, (c) specimen no. SM-22/19-55; (d, e) large fragments of pollen cones, (d) specimen no. SM-20/14-26, (e) specimen no. SM-22/10-4; (f–l) specimen no. SM-20/14-28 from which microsporangia have been macerated, (f) microsporangium, (g) middle part of the microsporangium with pollen grains, (h–l) pollen grains. (i, j) arrows show the subequatorial annular area.



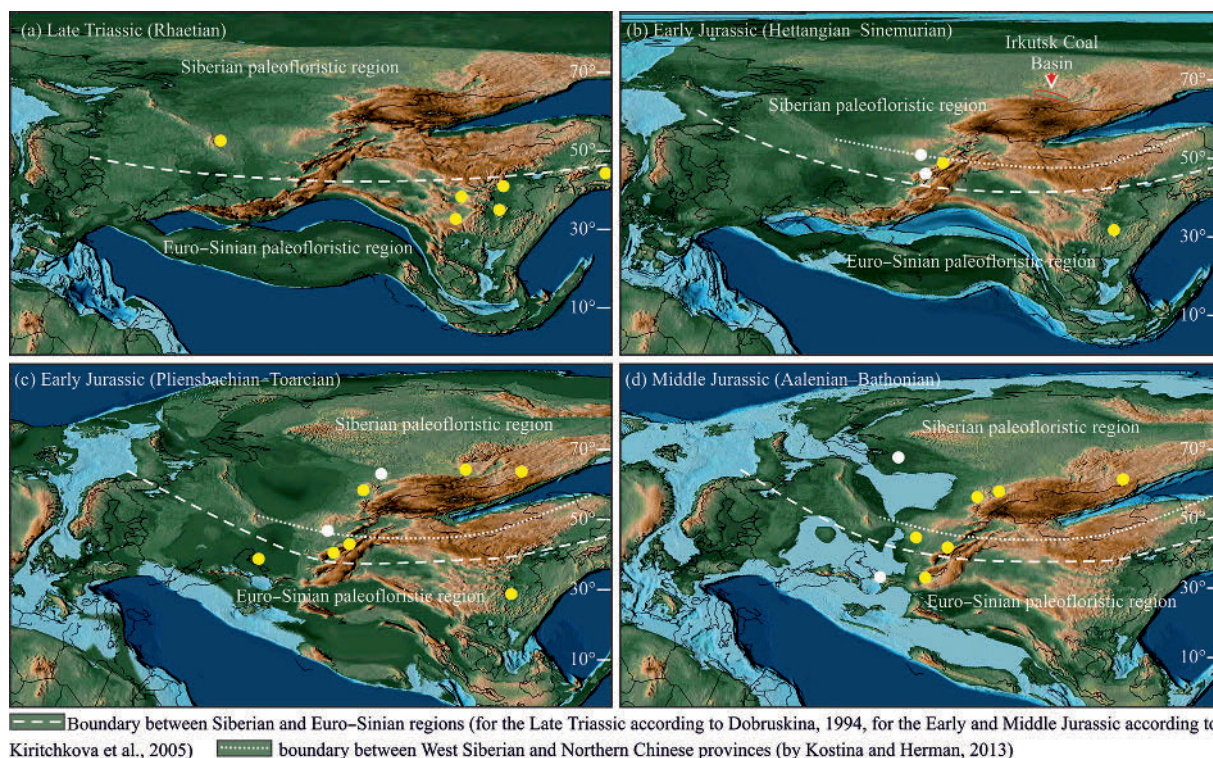


Fig. 8. Paleogeographic maps (based on Scotese, 2016) to show fossil occurrences of *Ferganiella* species from the Late Triassic to the Middle Jurassic.

Yellow dots represent the fossils defined to species, and white dots represent the fossils identified only to genus.

1936; Harris, 1937; Anderson, 1978). The Lower Cretaceous *Podozamites* from Siberia are associated with *Swedenborgia* seed cones (Bugdaeva, 1995), and from the Lower Cretaceous of Mongolia, with seed cones of *Krassilovia* Herrera, Shi, Leslie, Knopf, Ichinnorov, Takahashi, Crane et Herendeen (Herrera et al., 2020). The *Cycadocarpidium* and *Swedenborgia* reproductive structures belong to the Voltziaceae family (Anderson et al., 2007), and *Krassilovia* belong to the Krassiloviaceae family (Herrera et al., 2020). However, no such reproductive structures are associated with the *Podozamites* leaves in the Jurassic of the Irkutsk Basin, and so, the latter probably did not belong to the Krassiloviaceae and/or Voltziaceae.

Harris (1951) formulated a general rule of thumb which states that if any reproductive structures (usually rarer than vegetative remains) are present in a fossil site, then among the vegetative parts present in the burial there must be those with which these reproductive structures were associated: “Association between fossils proves only one thing: that they were more or less associated during life, occurring at the same time and in the same district. It is chiefly when such association is repeated that it becomes impressive. A second general point is that leaves are nearly always commoner than reproductive organs, except in floras sorted by floating great distances in water, and none of the present floras is of that type. It follows that where several unassigned specimens of a reproductive organ are found, its foliage is most probably present in some abundance” (Harris, 1951, p. 65–66).

In the layers containing *Podozamites* cf. *irkutensis* and *Ferganiella ivantsovii* sp. nov. the following remains of gymnosperms have also been found: *Baiera* sp., *Eretmophyllum* sp., *Ginkgoites* ex gr. *sibirica* (Heer) Seward, *G. tapkensis* Doludenko et Rasskazova, *Sphenobaiera spectabilis* (Nathorst) Florin, *Pseudotorellia* cf. *angustifolia* Doludenko emend. N. Nosova, *Czekanowskia rigida* Heer, *Leptostrobus laxiflora* Heer, *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nathorst, *Carpolithes* sp., *Samaropsis rotundata* Heer, *Samaropsis* sp., *Schidolepium gracile*, *Sorosaccus sibiricus* Prynada emend. N. Nosova. Leaves of *Eretmophyllum* sp., *Ginkgoites* ex gr. *sibirica*, *G. tapkensis*, *Czekanowskia rigida*, *Ferganiella ivantsovii* sp. nov., *Podozamites* cf. *irkutensis* dominate in burials. All these plant remains are of hypoautochthonous origin since they are represented by whole and almost whole leaves, which do not have traces of transportation and orientation by water flow. Thus, following the Harris rule, the micro- and megastrobili found in the burials (*Leptostrobus laxiflora*, *Schidolepium gracile*, and *Sorosaccus sibiricus*) could most likely be associated with these leaves. *Leptostrobus laxiflora* megastrobili and *Czekanowskia rigida* leaves belong to the same parent plant (Krassilov, 1968). The microstrobili of *Sorosaccus sibiricus* are associated with the order Ginkgoales (Nosova et al., 2018), which includes the leaves of *Eretmophyllum* and *Ginkgoites*. In our collections, numerous records of *Schidolepium gracile* pollen cones occur together with leaves of *Podozamites* cf. *irkutensis* and *Ferganiella ivantsovii* sp. nov., which are



also numerous. This suggests that the *Schidolepium gracile* cones and leaves of one of the above species could belong to the same parent plant. The presence of *Ferganiella ivantsovii* sp. nov. and *Podozamites* cf. *irkutensis*, both with multi-veined leaves, in addition to the *Schidolepium gracile* pollen grains, and their similarity with *Araucariacites*, may indicate that the original plant belongs to the family Araucariaceae, which is known to have been common in the Euro–Sinian paleofloristic region (Vakhrameev, 1991). Additional study of the cuticle from the scales of *Schidolepium* cones and from *Podozamites* and *Ferganiella* leaves is required to verify such a relationship with Araucariaceae.

## 5.2 Paleobiogeography and climate

The abundance of *Podozamites*, *Ferganiella*, and *Schidolepium* in some assemblages, which is unusual for the Jurassic of the Irkutsk Basin, is not accidental and might be associated with climate change. The paleogeographic distribution of *Podozamites* and *Ferganiella* records in the Late Triassic to Middle Jurassic is discussed below to address this possibility. We ignore the distribution of *Schidolepium*, since it is known only in the Irkutsk Basin.

An analysis of the paleogeographic distribution of *Podozamites* in eastern Asia is given by Pole et al. (2016), who showed that *Podozamites* was distributed between 30° and 70° paleolatitudes in the Late Triassic–Early Jurassic. Moreover, in the middle latitudes (mainly in present-day China), *Podozamites* formed almost monospecific deciduous, broad-leaved forests. *Podozamites* species were part of deciduous and evergreen communities at high latitudes in Siberia (Pole et al., 2016) and considering this distribution by comparison with paleophytogeographic regions and provinces proposed by Vakhrameev (1991) and Kirichkova (in Kiritchkova et al., 2005), we get the following: 1, *Podozamites* dominated the East Asian province of the Euro–Sinian region and the Northern Chinese province south of the Siberian region; thus, *Podozamites* prevailed in the warm subtropical climate zone typical for the Euro–Sinian region and temperate subtropical climate typical for the Northern Chinese province; 2, in the West Siberian province, located in the northern Siberian region, *Podozamites* taxa were not the dominant components of the Early Jurassic floras (Prinada, 1962; Kirichkova et al., 2005; Kirichkova et al., 2020; Frolov and Mashchuk, 2018), which might have been associated with the moderately warm climate of this area (Vakhrameev, 1991; Kiritchkova et al., 2005).

The Irkutsk Coal Basin in the Early and Middle Jurassic was located to the north of the West Siberian province (Fig. 8b). Numerous records of *Podozamites* cf. *irkutensis* discovered in the basin are dated to the Toarcian (Frolov et al., 2022). Their abundance might be associated with climate warming in the early Toarcian and the formation of a moderately subtropical climate in Siberia, intermediate between the full subtropical in the Euro–Sinian region and the moderately warm Siberian region (Vakhrameev, 1991).

*Ferganiella* occurs from the Late Triassic to the Middle Jurassic. In the Late Triassic, the genus included six

species: *F. bulanaschensis* Kiritchkova, *F. mongugaica* Srebrodolskaya, *F. otozamioides* Yang, *F. paucinervis* Li, *F. podozamioides* Lih, *F. weiyuanensis* Yang (Srebrodolskaya, 1968; Kirichkova, 1969; Li et al., 1976; Yang, 1982). Only *F. bulanaschensis* existed south of the Siberian region (Chelyabinsk Basin, Russia); the other five species inhabited the East Asia Province of the Euro–Sinian region (Fig. 8a). All Triassic species of *Ferganiella* became extinct at the Triassic–Jurassic boundary. In the first half of the Early Jurassic (Hettangian–Sinemurian), the diversity dropped to two species, *F. elongata* and *F. mesonervis* Zhang (Turutanova-Ketova, 1960; Zhang, 1982). However, the distribution of *Ferganiella* at this time was almost the same as in the Late Triassic (Fig. 8b). *F. mesonervis* inhabited the East Asia Province, while *F. elongata* inhabited the west of the Northern Chinese Province (Issyk-Kul depression, Kyrgyzstan). Thus, *Ferganiella* in the Late Triassic and the first half of the Early Jurassic occupied an area between 30° and 60° paleolatitudes in a subtropical and temperate subtropical climate (Fig. 8a, b), which indicates the initial thermophilicity of this genus.

In the second half of the Early Jurassic (Pliensbachian–Toarcian), *Ferganiella* reached its maximum diversity (nine species) and distribution: *F. elongata* and *F. mesonervis*, appeared at the beginning of the Early Jurassic and continued their existence; new species included *F. acuminata* (Chachlov) Prynada, *F. ivantsovii* sp. nov., *F. kurunzulajensis* Prynada, *F. lanceolata*, *F. latifolia* Brick ex Turutanova-Ketova, *F. ovalis* and *F. urjanichaica* Neuburg (Turutanova-Ketova, 1960; Prinada, 1962; Teslenko, 1970; Doludenko and Orlovskaya, 1976; Zhang, 1982). The range of the genus expanded northward, into the West Siberian province of the Siberian region and reached the Kuznetsk, Ulugkhem, and Irkutsk basins and Transbaikalia (Russia) (Fig. 8c). The distribution of *Ferganiella* to the north of 60° paleolatitude could have been promoted by climate warming, which began at the end of the Pliensbachian and reached its maximum in the ETO. By that time, the moderately warm climate in northern Siberia was replaced by a moderately subtropical one (Vakhrameev, 1991). Thus, *Ferganiella acuminata*, *F. ivantsovii* sp. nov., *F. kurunzulajensis*, and *F. urjanichaica*, common in the north of the West Siberian province, could indicate climate warming. *Ferganiella acuminata*, *F. ivantsovii* sp. nov., *F. elongata*, and *F. mesonervis* are not yet found in the overlying Middle Jurassic strata, probably due to extinction at the Early–Middle Jurassic boundary. The observed extinction was probably due to climate cooling, which began in the second half of the Toarcian and reached its maximum in the Aalenian (Ilyina, 1985; Shurygin et al., 2000).

In the Middle Jurassic, *F. kurunzulajensis*, *F. lanceolata*, *F. latifolia*, *F. ovalis* and *F. urjanichaica* continued to exist. Most of these taxa (*F. lanceolata*, *F. latifolia*, *F. ovalis*, *F. urjanichaica*) inhabited the west of the Northern Chinese province (present-day Kazakhstan, Kyrgyzstan, and Uzbekistan) and the Central Asian province of the Euro–Sinian region in a subtropical and temperate subtropical climate (Fig. 8d). In the West

Siberian province, in a warm temperate climate, the genus was represented by *F. kurunzulajensis* (Transbaikalia) and *F. urjanchaica* (Kuznetsk and Ulugkhem basins) (Prinada, 1962; Kirichkova et al., 1992), species that were probably more resistant to climate cooling in the Aalenian.

Up until now, only geochemical indicators (CIA and PIA, Rb/Sr, and Sr/Cu ratios) have indicated climate change in the Irkutsk Basin (Mikheeva et al., 2021). They show the change in climate conditions from warm and humid in the Cheremkhovo Fm. (Late Pliensbachian), to hot and arid during the deposition of the Lower Prisayan Fm. (end of Late Pliensbachian—the beginning of warming). In this study, we propose that the numerous records of *Ferganiella ivantsovii* sp. nov., *Podozamites* cf. *irkutensis* and *Schidolepium gracile* from the Toarcian Middle Subfm. of the Prisayan Fm. may be indicators of warming. *Ferganiella* prevailed between 30° and 60° paleolatitudes in a subtropical and temperate subtropical climate (Fig. 8a, b). *Podozamites* also dominated in subtropical and temperate-subtropical climate zones, where they formed almost monospecific deciduous, broad-leaved forests (Pole et al., 2016). This distribution indicates the thermophilic nature of *Podozamites* and *Ferganiella*. *Schidolepium gracile* belongs to the Araucariaceae, common in the Euro-Sinian paleofloristic region (Vakhrameev, 1991). Thus, the unusually numerous records of *Ferganiella ivantsovii* sp. nov., *Podozamites* cf. *irkutensis* and *Schidolepium gracile* could be the first macrofloristic evidence of the ETO climate warming in the Irkutsk Basin.

## 6 Conclusions

Collecting in the Early Jurassic Middle Prisayan Subformation (Subfm.) deposits of the Irkutsk Basin, Russia, which are attributed to the Toarcian stage, has resulted in a new paleobotanical flora, in which the leaves of *Podozamites* and *Ferganiella* predominate. In the same beds, pollen cones of *Schidolepium* containing *Araucariacites* pollen grains are often found, which is unusual for the Irkutsk paleoflora. As a result of the study, a new species, *Ferganiella ivantsovii* sp. nov., has been described.

This paleoflora, notably indicators *Ferganiella ivantsovii* sp. nov., *Podozamites* cf. *irkutensis* and *Schidolepium gracile*, provides the first macrofloristic and palynological evidence of the Early Toarcian climatic optimum (ETO) up in the region. This has previously been explained by the paleogeographic position of the basin inside the continent, far from the seas and mountain systems around it, in which continental effects would have overruled the broader equable climate. On the other hand, the stratigraphic interval corresponding to the ETO in the Irkutsk Basin might have been short, and therefore, it may not have previously been identified.

There are unusually numerous records of *Ferganiella ivantsovii* sp. nov., *Podozamites* cf. *irkutensis* and *Schidolepium gracile* from the Toarcian Middle Prisayan Subfm. and in the Early and Middle Jurassic, taxa of the genera *Podozamites* and *Ferganiella* were most diverse and numerous in the East Asian province, Euro–Sinian

region, and the Northern Chinese province, Siberian region.

The phytochoria of these regions were located in the subtropical and temperate subtropical climate zones, which makes it possible to consider *Ferganiella* and *Podozamites* as thermophilic plants. In northern Siberia, including the Irkutsk Basin, the typical Early Jurassic vegetation was deciduous gymnosperm forest; however, the appearance within this of a large number of *Ferganiella* and *Podozamites* records in some assemblages is explained by the ETO, which briefly replaced a moderately warm climate by a moderately subtropical one. This scenario is complemented by the finding of numerous cones of *Schidolepium gracile*, which produced *Araucariacites* pollen, typical for the Euro-Sinian region.

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