



ANGIOSPERM DIVERSIFICATION IN THE EARLY CRETACEOUS OF PRIMORYE, FAR EAST OF RUSSIA

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Abstract: The Partizansk and Razdolnaya coal basins of Primorye, Far East of Russia, contain diverse early angiosperm fossils (pollen, leaves, and fruits). In this paper, we revise the previous data on early angiosperms of this region and summarize the results of our latest research. Age of the plant-bearing deposits was clarified using isotopic U-Th-Pb LA-ICP-MS and U-Pb ID-TIMS methods. Age of the upper part of the Lipovtsy Formation is 118 ± 1.4 Ma, which corresponds to the late Aptian. The early Albian age (109 ± 1 Ma) is assigned to the upper part of the Frentsevka Formation. The diversification of angiosperms in the Early Cretaceous of Primorye region and their systematic affinity are analyzed. Early representatives of Laurales, Ranunculales, Platanaceae, and probable Cercidiphyllaceae are revealed. New combination *Pandanites ahnertii* (KRYSH.T.) GOLOVN., comb. nov. is created, and new species *Araliaephyllum vittenburgii* GOLOVN. et VOLYNETS, sp. nov. is described. Reconstructions of herbaceous angiosperms from autochthonous locality Bolshoy Kuvshin are proposed.

Key words: early angiosperms, Early Cretaceous, Far East, Primorye, Russia

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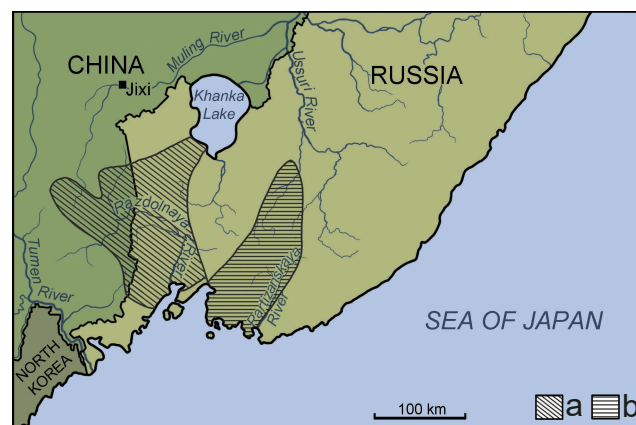
Introduction

Investigation of early angiosperms provides important data for our understanding of the early radiation of this group. In the Asian part of Russia, there are several Lower Cretaceous coal basins containing early angiosperm fossils: Zyryanka coal basin, Omsukchan coal basin, Bureya coal basin, Partizansk coal basin, Razdolnaya coal basin, Torom Trough, Lena-Vilyuy coal basin (Kiritchkova and Budantsev 1967, Krassilov 1967, Samylina 1968, 1976, Koshman 1973, Lebedev 1974). Among them, the most interesting are the Partizansk and Razdolnaya coal basins of Primorye, since there the greatest number of angiosperm remains was found.

The Razdolnaya (former Suifun) coal basin is located in the south-western part of southern Primorye (Text-fig. 1), where it occupies a spacious region from the Amur Bay coast to the middle reaches of the Razdolnaya River (Bugdaeva and Markevich 2009). The Partizansk (former Suchan) coal basin is located in the eastern part of southern Primorye, extending for more than 120 km from the Sea of Japan to the headwaters of the Bolshaya Ussurka River (Bugdaeva et al. 2014). The main industrial deposits are located near city of Partizansk.

The first researchers of the Cretaceous flora of Primorye are Kryshtofovich (1921, 1928, 1929), Prynada

(Kryshtofovich and Prynada 1932), Vakhrameev (1959) and Shtempel (1959, 1960). Kryshtofovich (1921) united plant fossils from the Cretaceous coal-bearing deposits under the name “Nikan flora”. Initially, this flora was considered to be Jurassic in age. The first finds of angiosperms *Aralia lucifera* KRYSH.T. and *Pandanophyllum ahnertii* KRYSH.T. reveal the Early Cretaceous (Aptian) age of the host



Text-fig. 1. Map of Primorye region, Russia. a – Razdolnaya coal basin; b – Partizansk coal basin.

Table 1. Repositories of plant fossils described in present paper (all in Russia).

Abbreviation	Institute	City
BIN	Komarov Botanical Institute, Russian Academy of Sciences	St. Petersburg
IBSS	Federal Scientific Center of the East Asia Terrestrial Biodiversity, FEB RAS (previously Institute of Botany and Soil Science)	Vladivostok
TSNIGRM	F. N. Chernyshev Central Geological Research Museum	St. Petersburg

deposits (Kryshstofovich and Pavlov 1928, Kryshstofovich 1929). Kryshstofovich (1928) studied the Cretaceous plants of the Lipovtsy coal mines for many years, and recognized a special type of resinite-rich coal composed of small resin rodlets, named rhabdopissite (from Greece $\rho\acute{\alpha}\beta\delta\omicron\zeta$ – rod and $\pi\acute{\iota}\sigma\sigma\alpha$ – resin). In the monograph on the Early Cretaceous flora, Krassilov (1967) elaborated the detailed stratigraphy of the Lower Cretaceous of the Razdolnaya basin, which is still relevant.

The history of biostratigraphic investigation of the Partizansk and Razdolnaya coal basins is also associated with Vereshchagin (1977), Konovalov (1964), Markevich et al. (2000), Oleynikov et al. (1990), Likht (1961, 1994), Perepechina et al. (1958) and many others. Pollen and spores from the Lower Cretaceous deposits of Primorye were studied by Verbitskaya (1962), Verbitskaya et al. (1965), Shugaevskaya and Markevich (1964), Markevich (1994, 1995), Bugdaeva and Markevich (2008), Bugdaeva et al. (2014), Kovaleva et al. (2016), Markevich et al. (2016).

Angiosperm megafossils were first recorded in Primorye by Kryshstofovich (1929). Later, many fossils were found by Krassilov (1965, 1967). In recent years, investigations of early angiosperms in Primorye were carried out in the Federal Scientific Center of the East Asia Terrestrial

Biodiversity, FEB RAS, Vladivostok, and in the Komarov Botanical Institute RAS, St. Petersburg (Kovaleva et al. 2016, Volynets and Bugdaeva 2017, Golovneva 2018, Golovneva and Zolina 2018, Golovneva et al. 2018).

In this paper, we revise the previous data about early angiosperms in Primorye and summarize the results of the latest research.

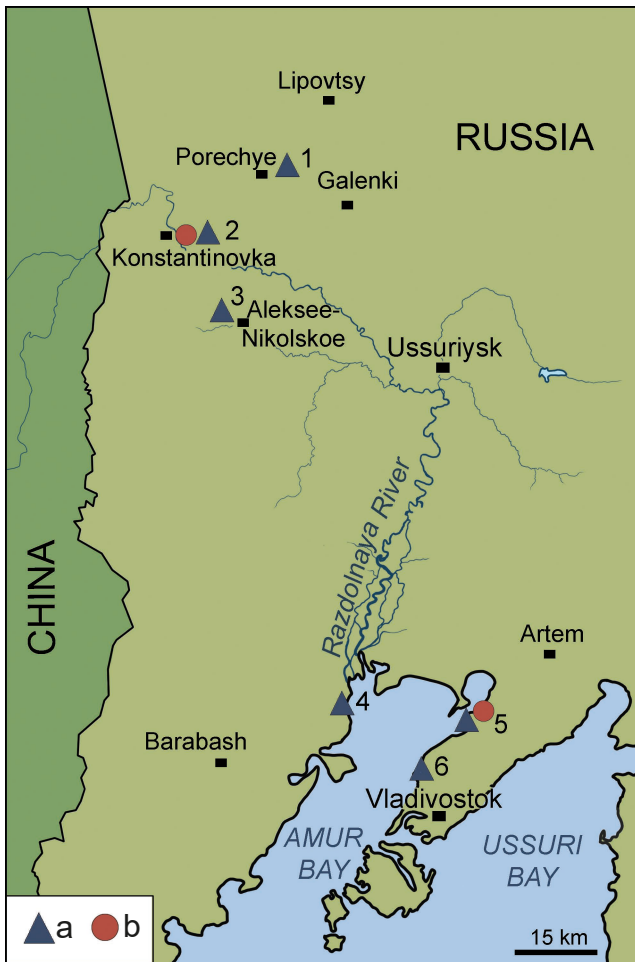
Material and methods

The remains of *Nyssidium orientale* SAMYLINA are stored at the Komarov Botanical Institute RAS, St. Petersburg, the collection BIN 506. Specimens of early angiosperms, described by Kryshstofovich, are stored in the F. N. Chernyshev Central Geological Research Museum, St. Petersburg (collection 3031). Specimens, described by Krassilov and discovered during further research, are kept in the Federal Scientific Center of the East Asia Terrestrial Biodiversity, FEB RAS, Vladivostok. Data about repositories of plant fossils are summarized in Table 1. The localities of plant fossils are shown in Text-figs 2, 3.

The majority of leaves and fruits are preserved as impressions. They yield no structurally preserved material, and details of leaf anatomy were impossible to study. We



Text-fig. 2. Map of Partizansk coal basin with early angiosperm localities. a: Severosuchan Formation, Aptian; b: Frentsevka Formation, early-middle Albian. 1 – Novoveselaya village; 2 – 3rd Kamenka River; 3 – Bolshoy Kuvshin; 4 – Andreev Inlet.



Text-fig. 3. Map of Razdolnaya coal basin with early angiosperm localities. a: Lipovtsy Formation, Aptian; b: Galenki Formation, early-middle Albian. 1 – Porechye coal mine; 2 – Konstantinovka; 3 – Aleksee-Nikolskoe coal mine; 4 – Fedorovsky Rudnik; 5 – Podgorodenka coalfield; 6 – Firsov Cape.

used Manual of Leaf Architecture (Ellis et al. 2009) for terminology of leaf morphology. The specimens were studied using a Carl Zeiss Jena SM-XX binocular microscope and photographed using a Nikon D5300 digital camera with macro-lens objective and a Nikon Coolpix P7700, sometimes underwater in order to increase contrast of leaf venation.

The samples for palynological analysis were subjected to treatment with standard maceration technique. The microscopic investigation of pollen and spores was conducted under an AxioScop-40 light microscope with a digital video camera AxioCam MRc and software CombineZM. The permanent preparations are stored in the laboratory of Paleobotany of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok.

Reconstructions of fossil plants were created using programs Xfrog, Adobe Photoshop CS5.1. and Terragen 4.

Volcanic rocks for isotopic dating were sampled in two sites: 1) in the upper part of the Lipovtsy Formation in the Porechye open-pit coal mine (Text-fig. 4, sample 160/4), 2) and in the upper part of the Frentsevka Formation below the conglomerates at the Palets Cape (Text-fig. 5c, d, sample 1).

In the Porechye open-pit coal mine, the main coal seam “Rabochy” yields three layers of tuffaceous silty mudstones

locally grading into tuffs. The sample was taken from the top tuff layer (Text-fig. 5a, b). Tuffs are composed of poorly sorted angular (frequently acute-angled) clasts of acid plagioclase (elongated laths) and more isometric quartz. Some clasts are represented by basic – intermediate volcanics and biotite flakes. The volcanic glass is brown, frequently highly altered. The rock is characterized by thin horizontal and horizontal-wavy bedding, and is slightly silicified (Kovaleva et al. 2016).

Zircons of the sample 160/4 were extracted by using the standard magnetic and heavy liquid technique in the Laboratory of Langfang Regional Geological Survey, Langfang, Hebei Province, China. Around 200 zircon grains were hand-picked and mounted in epoxy and polished to expose the crystal centers. Cathodoluminescence (CL) images were obtained using a Mono CL3 + microprobe.

U-Th-Pb isotopic measurements were performed on a Laser ablation inductively coupled plasma-mass spectrometer (LA-ICP-MS) at the Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China. The laser ablation spots were 44 µm in diameter. $^{207}\text{Pb}/^{206}\text{Pb}$ and $^{206}\text{Pb}/^{238}\text{U}$ ratios were calculated by Glitter 4.0 (Jackson et al. 2004, Griffin et al. 2008), using the Harvard zircon 91500 as an external standard. The relative standard deviations of reference values for zircon 91500 were set at 2 %. Common Pb was corrected using the Andersen method (Andersen 2002). The weighted mean U-Pb ages and concordia plot were processed using ISOPLOT (Ludwig 2003).

Sample 1 from the upper part of the Frentsevka Formation near the Palets Cape was processed at the Institute of Precambrian Geology and Geochronology in St. Petersburg, using U-Pb ID-TIMS single grain zircon method (Golovneva et al. in press).

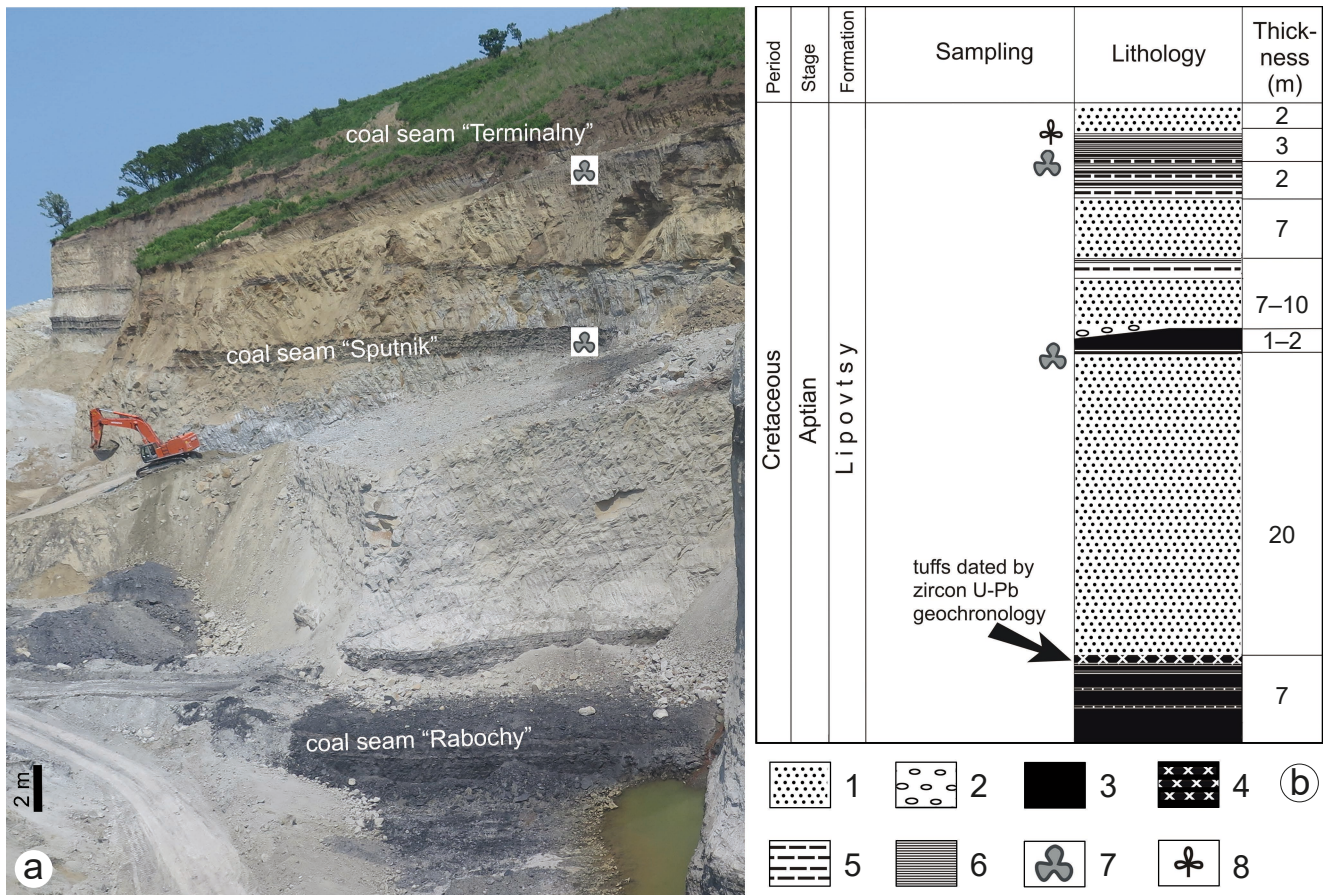
The new nomenclatural acts are registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP).

Stratigraphy and age

The Cretaceous deposits of the Razdolnaya coal basin consists of the Nikan (Barremian-early-middle Albian) and the Korkino (late Albian?-Cenomanian) Groups. The Lower Cretaceous deposits rest on Ordovician and Upper Permian granitoids, overlain by Neogene and Quaternary sediments (Golozubov 2006).

Krassilov (1967) divided coaliferous freshwater deposits of the Nikan Group into the Ussuriysk (Barremian), Lipovtsy (Aptian), and Galenki (Albian) formations, based on palaeobotanical and lithological data. The Galenki Formation is overlain unconformably by the Korkino Group (Tab. 2).

The Ussuriysk Formation includes conglomerates, sand-stones, siltstones, and thin coal layers. The Lipovtsy Formation is subdivided into two subformations. The lower unproductive subformation (up to 440 m thick) is composed of coarse-grained sandstones and conglomerates. The upper coaliferous subformation (up to 200 m thick), composed of fine-grained sandstones and siltstones, contains two productive coal seams (Rabochy and Verkhny), which are represented by humic and rhabdopissite coals. Recently



Text-fig. 4. Porechye open pit coal mine. a: photograph of the Lipovtsy Formation section; b: stratigraphic column, 1 – sandstone, 2 – conglomerate, 3 – coal, 4 – tuff dated by U-Th-Pb geochronology, 5 – siltstone, 6 – mudstone, 7 – palynological samples with angiosperm pollen, 8 – dispersed angiosperm cuticles.

Bugdaeva and Markevich (2009) revealed that plants which produced resinous coals of the Lipovtsy coalfield belong to Miroviaceae (*Mirovia orientalis* (NOSOVA) NOSOVA).

The Galenki Formation conformably overlies the Lipovtsy Formation. It consists mainly of polymictic fine- to medium-grained sandstones, lesser siltstones, tuffites, conglomerates, coaly mudstones, and andesites. A specific feature of sediments of this formation is the admixture of tuffaceous material along the whole sequences. Its thickness is 250–380 m (Golozubov 2006).

In the Partizansk coal basin, the Lower Cretaceous deposits were combined in the Suchan Group, which lies on the Lower Paleozoic complex of gabbroid and granitoid rocks, as well as on the marine and nonmarine Valanginian deposits (Golozubov 2006, Bugdaeva et al. 2014). The Valanginian deposits were mapped in a small area in the upper reaches of the Partizanskaya River and are divided into the Kapreevskaya and Klyuchi formations. The coal-bearing Kapreevskaya Formation is 280 m thick and consists of conglomerates, sandstones, siltstones, and coal (Oleynikov

Table 2. The stratigraphy of the Lower Cretaceous deposits in the southern Primorye, Russia.

Stage		Group	Partizansk coal basin	Group	Razdolnaya coal basin
Cenomanian	lower	Korkino	Romanovka Fm	Korkino	Korkino Group
	upper		Kangauz Fm		
Albian	middle	Suchan	Frentsevka Fm	Nikan	Galenki Fm
	lower		Severosuchan Fm		Lipovtsy Fm
Aptian	upper		Starosuchan Fm		Ussuriysk Fm
	lower				
Barremian					
Hauterivian					
Valanginian			Klyuchi Fm		



Text-fig. 5. a: coal seam “Rabochy” with three tuff layers in upper part of Lipovtsy Formation in Porechye open pit coal mine; b: same section, enlarged view, upper tuff layer, sample 160/4 site; c: tuff layer in upper part of Frentsevka Formation below conglomerate at Palets Cape; d: same section, enlarged view, sample 1 site.

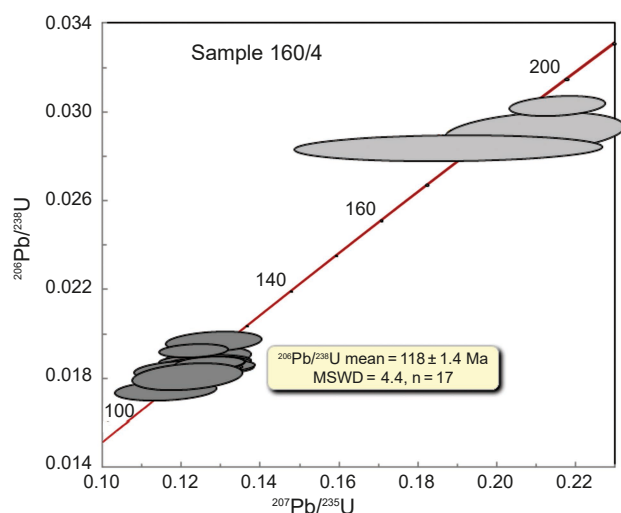
et al. 1990). The Klyuchi Formation is 1,000 m thick and records shallow-marine to nonmarine environments with buchiid bivalves and plants (Markevich et al. 2000).

According to Likht (1961, 1994) and Krassilov (1967), the Suchan Group consists of the Starosuchan, the Severosuchan and the Frentsevka formations. The Starosuchan Formation is composed of heterogranular coarse-grained sandstones, gravelstones, conglomerates, rare siltstones, claystones, and coal beds. Its thickness varies from 280 m at the northeast to 800 m in the central areas of the basin.

The Severosuchan Formation is subdivided into the lower coal-free and upper coal-bearing subformations. The first one is 80–220 m thick and is composed of fine-grained sandstones with rare interlayers of medium- to coarse-grained sandstones. The second subformation is 120–280 m thick and consists of sandstones, siltstones, claystones, coal beds, and rare conglomerates. The main industrial deposits are located in the eastern part of the basin, near Partizansk city, where they have been mined almost from the beginning of the last century. The upper boundary of the Severosuchan



Text-fig. 6. Cathodoluminescence (CL) images of selected zircons from sample 160/4.



Text-fig. 7. U-Pb concordia diagram for zircons from tuff sample 160/4.

Formation is marked by the last thick coal layer, known as the Velikan. The Frentsevka Formation includes marine *Trigonia* beds, nonmarine black shales and a measure of greenish-gray plant-bearing sandstones and siltstones.

The Suchan Group is conformably overlain by variegated or red-colored volcanoclastic deposits of the Korkino Group (up to 1,500 m), which is divided into the Kangauz (mostly sandstones) and the Romanovka (mostly siltstones) formations.

Based on plant megafossils and palynological data, the age of the Starosuchan Formation was estimated as Hauterivian-early Aptian or the Barremian-early Aptian (Krassilov 1967, Turbin 1994, Markevich et al. 2000, Volynets 2005), and the age of the Severosuchan Formation as the late Aptian or late Aptian-early Albian. The marine *Trigonia* beds in the bottom of the Frentsevka Formation were dated as middle Albian (Markevich et al. 2000). The sediments of the Korkino Group contain few fossil plants (Volynets 2005), and its age is inferred as the late Albian-early Cenomanian.

Isotopic data (U-Th-Pb LA-ICP-MS and U-Pb ID-TIMS dating) allow us to clarify the age of the plant-bearing deposits. Zircons from the Lipovtsy Formation (sample 160/4) are mostly transparent, colorless, prismatic, euhedral with oscillatory zoning (Text-fig. 6). Th/U ratios of these zircons are 0.30–0.91. Zircon morphology indicates their magmatic origin. Twenty U-Th-Pb zircon analyses were carried out on the tuff sample 160/4 (see Appendix). The seventeen most concordant analyses form a uniform cluster and yield a $^{206}\text{Pb}/^{238}\text{U}$ weighted mean age of 118 ± 1.4 Ma (MSWD = 4.4) (Text-fig. 7). Three zircon grains (# 11, 61 and 76; see Appendix) show a somewhat older age at about 190 Ma, and reflect the age of inherited zircons (Text-fig. 7). Despite the extra data dispersion (MSWD > 1), new U-Pb zircon ages suggest that the age of the tuff might be late Aptian, according to Geologic Time Scale 2020 (Gradstein et al. 2020).

The U-Pb age of single zircon (ID-TIMS method) from the upper part of the Frentsevka Formation is 109 ± 1 Ma (Golovneva et al. in press). Thus, early Albian age (most likely the end of the early Albian) is assigned to the plant-bearing deposits of the Frentsevka Formation. Isotopic data generally confirmed previous age estimates based on palaeobotanical, palynological and mollusk data.

Pollen

The Early Cretaceous palynoflora of Primorye is dominated by diverse fern spores and gymnosperm pollen grains. The angiosperm pollen is usually scarce in the late Aptian and Albian palynospectra. Markevich (1994, 1995) established seven palynological zones for the Lower Cretaceous deposits of the Razdolnaya and Partizansk coal

Period	Epoch	Stage	Sub-stage	Palynozones	Formations	Appearance of angiosperm pollen in geological record
Cretaceous	Late	Cenomanian	early	VII <i>Selaginella kemensis</i> - <i>Tricolpites micromunus</i>	Romanovka Kangauz	<i>Tricolpites micromunus</i> , <i>Fraxinopollenites variabilis</i> , <i>Rousea delicipollis</i>
			late			
	Early	Albian	middle	VI <i>Rouseisporites reticulatus</i> - <i>Asteropollis asteroides</i>	Frentsevka Galenki	<i>Asteropollis asteroides</i> , <i>Clavatipollenites hughesii</i> , <i>Tricolpites</i> spp., <i>Retitricolpites vulgaris</i>
			early	V <i>Coptospora paradoxa</i> - <i>Tricolpites</i>		<i>Clavatipollenites incisus</i> , <i>Tricolpites</i> spp., <i>Retitricolpites</i> sp.
		Aptian		IV <i>Rouseisporites laevigatus</i> - <i>Gleicheniidites</i>	Severosuchan, Lipovtsy	<i>Asteropollis asteroides</i> , <i>Clavatipollenites hughesii</i> , <i>Tricolpites micromunus</i> , <i>T. vulgaris</i> , <i>T. spp.</i> , <i>Quercites sparsus</i> , <i>Retitricolpites georgiensis</i>
		Barremian		III <i>Appendicisporites macrorhizus</i> - <i>Trilobosporites mirabilis</i>	Starosuchan, Ussuriysk	
		Hauterivian				
		Valanginian		II <i>Gleicheniidites carinatus</i> - <i>Pilosporites echinaceus</i>	Klyuchi	
Berriasian		I <i>Classopollis</i> - <i>Concavissimisporites asper</i>	Tauhe, Tetyuhe, Gorbushinka			

Text-fig. 8. Appearance of angiosperm pollen in the Lower Cretaceous deposits of southern Primorye.



Text-fig. 9. a–d: *Nyssidium orientale* SAMYLINA, Partizansk, Starosuchan Formation, Barremian, a – spec. BIN 506/3749, general view of four fruits, b1 – spec. BIN 506/3749-1, holotype, b2 – spec. BIN 506/3749-2, c – spec. BIN 506/3749-6, d – spec. BIN 506/3749-5; e–f: *Cercidiphyllum suffunense* KRASSILOV, Konstantinovka, Galenki Formation, early-middle Albian, e – spec. IBSS 11-135, fruit, f – spec. IBSS 11-134, leaf, holotype. Scale bar 5 mm in a, e, f and 2 mm in b–d.

basins (Text-fig. 8). Previously, angiosperm pollen was known only since the early Albian (Markevich 1994). Subsequently, some extremely rare angiosperm grains were discovered in the late Aptian pollen spectra from the Lipovtsy Formation, which corresponds to the fourth palynozone, named *Rouseisporites laevigatus-Gleicheniidites*. Angiosperm pollen was found in two localities in the Razdolnaya River basin: Porechye and Aleksee-Nikolskoe quarries (Kovaleva et al. 2016, Markevich et al. 2016).

In the Porechye coal mine, rare monosulcate and tricolpate grains were revealed in the thin coal seams and overlying clastic deposits, exposed above the main productive coal seam (Text-fig. 4). These are *Tricolpites micromunus* (J.J.GROOT et J.S.PENNY) D.BURGER, *Tricolpites vulgaris* (R.L.PIERCE) SAT.K.SRIVAST., *Tricolpites* spp., *Clavatipollenites hughesii* COUPER, *Quercites sparsus* (MARTYNOVA) SAMOIL., *Retitricolpites georgiensis* G.J.BRENNER (Kovaleva et al. 2016).

In the Aleksee-Nikolskoe quarry, angiosperm pollen was found in the siltstone layer overlying the productive coal seam. The angiosperms are represented by *Tricolpites* spp. and *Clavatipollenites hughesii* (Markevich et al. 2016).

The fifth palynozone, named *Coptospora paradoxa-Tricolpites*, comes from the lower part of the Galenki Formation and lower part of the Frentsevka Formation. It is early Albian in age (Markevich 1994). Angiosperms occur rarely, but constantly. They are represented by *Tricolpites* spp., *Retitricolpites* sp., and *Clavatipollenites incisus* CHLON.

The sixth palynozone, named *Rouseisporites reticulatus-Asteropollis asteroides*, includes the deposits from the upper part of the Galenki Formation and the upper part of the Frentsevka Formation. It was dated as middle Albian (Markevich 1994). Pollen of flowering plants becomes more numerous in palynospectra. Angiosperms are represented by *Asteropollis asteroides* R.W.HEDL. et G.NORRIS, *Tricolpites* spp., *Retitricolpites vulgaris* R.L.PIERCE, and *Clavatipollenites hughesii*.

The seventh palynozone is named *Selaginella kemensis-Tricolpites micromunus* (late Albian-early Cenomanian age). The type assemblage comes from the deposits of the Korkino Group in the Razdolnaya River Basin. The amount and diversity of angiosperm pollen increase. In addition to existing taxa, new ones appeared. They are represented by *Fraxinopollenites variabilis* E.A.STANLEY and *Rousea delicipollis* SAT.K.SRIVAST.

Thus, according to palynological data, the first appearance of early angiosperm pollen was recorded in the upper Aptian Lipovtsy Formation of the Razdolnaya coal basin.

Putative angiosperm megafossils

Barremian, Partizansk coal basin, Starosuchan Formation

The putative remains of *Nyssidium orientale* SAMYLINA were discovered in the well No. 1847 drilled in the city Partizansk (Samylina 1961). These putative fruits are flattened, wide elliptical in outline; about 10 mm in length and 6 mm in width, with 6–7 narrow ridges running longitudinally over the surface. There is a rounded protrusion about 1.5 mm in diameter at one pole of the fruits and

a smooth, without ridges, circle at the other one (Text-fig. 9a–d). Samylina (1961) believed that the external morphology and overall shape of these fruits resemble endocarps of *Nyssa* L. (Cornales) and assigned them to form-genus *Nyssidium*, established by Heer (1870) for *Nyssa*-like fossils from the Paleogene of Spitsbergen. In fact, *N. orientale* from the Starosuchan Formation corresponds fairly well to the diagnosis of the genus *Nyssidium* in the sense of Heer (small size, elliptical shape and ribbed surfaces), but its affinity to angiosperms is doubtful. They have no follicular characters, such as stalk, terminal style and suture grooves. These fossils can be also the seeds of conifers or other gymnosperms.

Angiosperm megafossils

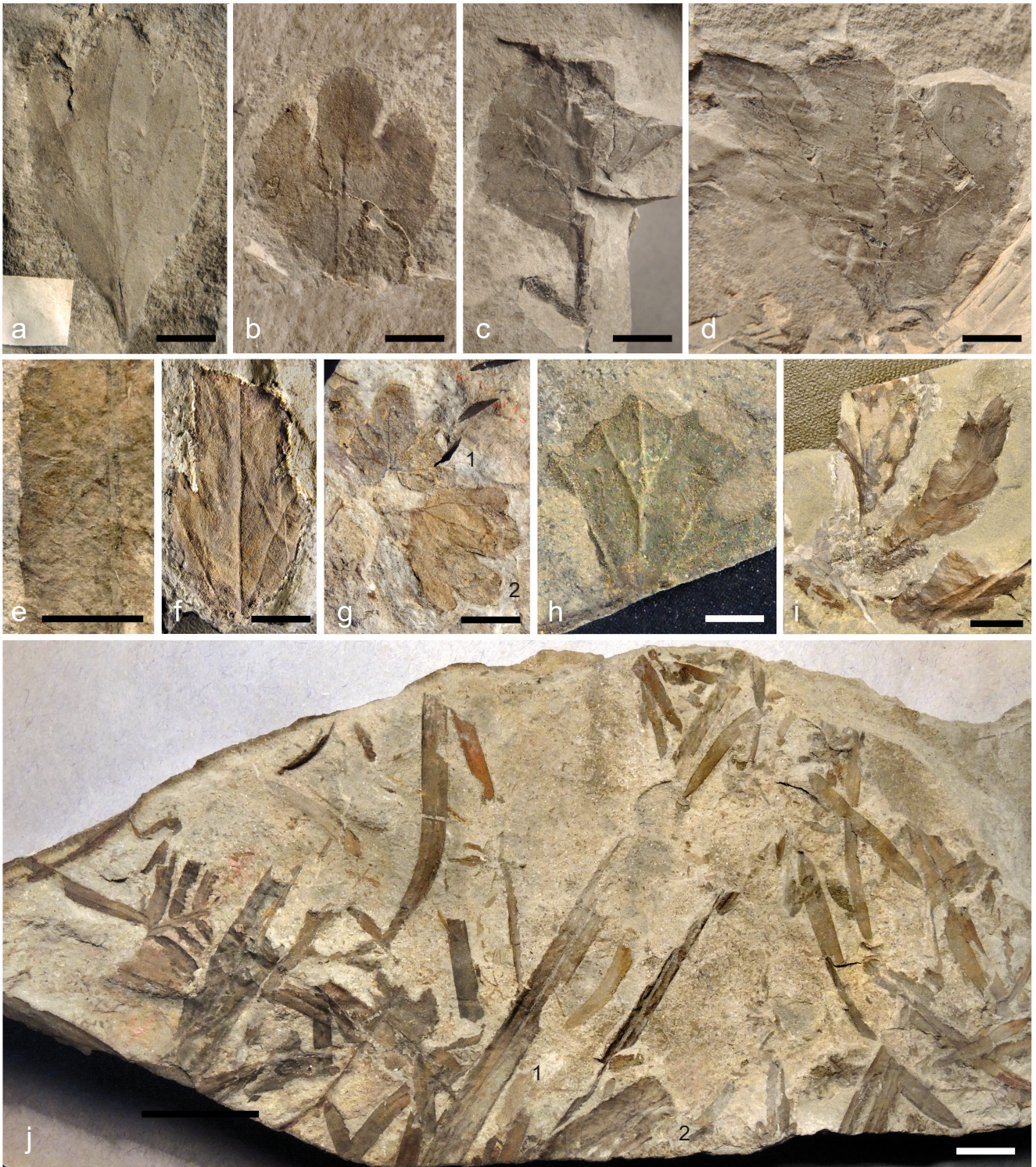
Late Aptian, Partizansk coal basin, Severosuchan Formation

Only one early angiosperm species is known from the Aptian deposits of the Partizansk basin. Leaves of *Aralia lucifera* KRYSHT. were discovered by geologist M. A. Pavlov in 1927 (Kryshtofovich and Pavlov 1928) on the left bank of the Postyshevka River (previously Malaya Sitza River) near Novoveselaya village (now the territory of Partizansk city). There are four leaf impressions from 1.5 to 3.4 cm in length on one piece of rock, which was found in the Velikan (Giant) coal layer in the top of the Severosuchan Formation (Text-fig. 10a–d). This species was initially assigned by Kryshtofovich (1929) to the modern genus *Aralia*, and later it was transferred to the fossil genus *Araliaephyllum* FONTAINE (Golovneva 2018). The type material has been restudied in detail, and the lectotype has been selected (Golovneva 2018). Leaves of *A. luciferum* (KRYSHT.) GOLOVNEV. are trilobate, up to 3.5 cm long, with cuneate, decurrent near the petiole, base, serrate margin, and small, adpressed teeth.

One more specimen of *Aralia lucifera* was described by Krassilov (1967: pl. XCII, fig. 3, text-fig. 33). It was found by V. P. Konovalov in 1958 on the left bank of the 3rd Kamenka River, 3.5 km from its mouth (territory of Partizansk city). The deposits are attributed now to the upper part of the Frentsevka Formation. Reexamination of this specimen (IBSS, spec. 40-1) in Vladivostok shows that in fact it has five lobes and pinnate venation. The second (upper) pair of lobes is innervated by secondary veins, which diverge from midvein above basal veins (Text-fig. 11a). Therefore, the features of this leaf do not match the diagnosis of genus *Araliaephyllum*. This specimen is very similar to united apical leaflets of *Sapindopsis* FONTAINE, which is very abundant in this locality.

Late Aptian, Razdolnaya coal basin, Lipovtsy Formation

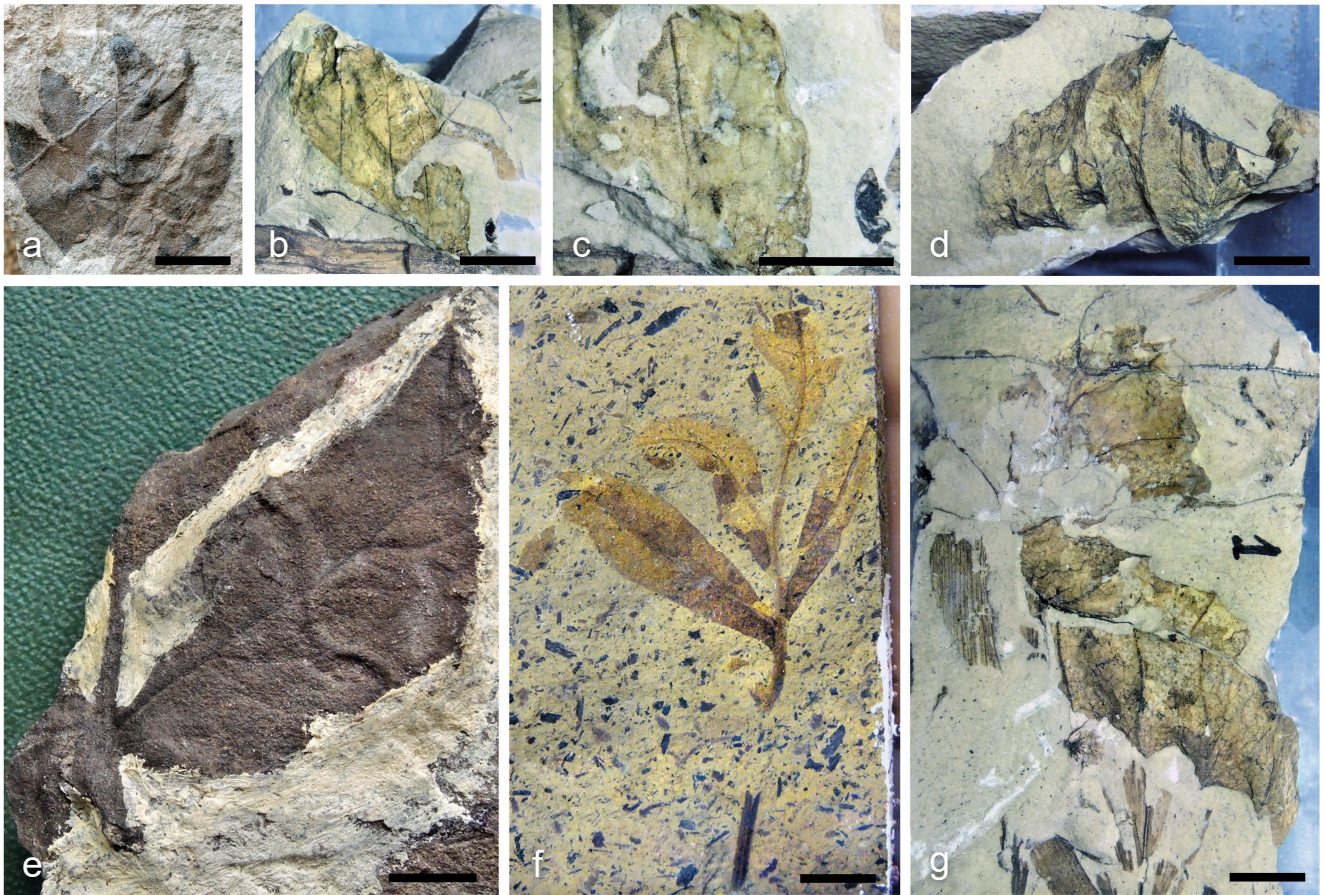
The most ancient angiosperm remains in the Razdolnaya basin were first discovered by Kryshtofovich (1929). In 1924, he found linear leaves of *Pandanophyllum ahnertii* KRYSHT. on the right bank of the Razdolnaya River near the Konstantinovka village. One specimen of the rock contains several fragments of leaves up to 0.4–1.0 cm wide and up to 9 cm long, with a thick central vein and usually with small marginal spines, but sometimes entire-margined (Text-fig. 10e, j). Spines are



Text-fig. 10. a–d: *Araliaephyllum luciferum* (KRYSHCHUK) GOLOVNEV., Partizansk, Severosuchan Formation, Aptian, a – spec. TSNIGRM 3013/1, lectotype, b – spec TSNIGRM 3013/2, c – spec. TSNIGRM 3013/4, d – spec. TSNIGRM 3013/3; e, j: *Pandanites ahnertii* (KRYSHCHUK) GOLOVNEV., Konstantinovka, Lipovtsy Formation, Aptian, TSNIGRM 3013/5, e – fragment of leaf margin, j – general view, j1 – lectotype, j2 – leaf, figured in (e); f: *Araliaephyllum ussuriense* (KRASSILOV) GOLOVNEV., Andreev Inlet, Frentsevka Formation, early-middle Albian, spec. IBBS 28/103; g: *Araliaephyllum vittenburgii* GOLOVNEV. et VOLYNETS, Podgorodenka coalfield, Galenki Formation, early-middle Albian, spec. IBBS 41/1, g1 – spec. IBBS 41/1a, holotype, g2 – spec. IBBS 41/1b; h: *Dicotylophyllum* sp. 1, Podgorodenka coalfield, Lipovtsy Formation, Aptian, spec. IBBS 28L-4; i: *Sapindopsis* sp., 3rd Kamenka, Frentsevka Formation, early-middle Albian, spec. IBBS 325/8. Scale bar 5 mm in a–h and 1 cm in i, j.

0.5–1.0 mm long and regularly distributed along margin at distance 1–2 mm. Leaves gradually taper towards the top, but apex is usually broken. Several very thin secondary veins run parallel to the midvein, but they are not always clearly visible, since the leaf lamina is rather thick.

Kryshchuk compared these leaves with leaves of modern genus *Pandanus* PARKINSON and with leaves from the Upper Cretaceous deposits of Austria, described by Ettingshausen (1852) under the names *Pandanus trinervis* ETTINGSH., *P. austriacus* ETTINGSH., and *P. pseudo-inermis*



Text-fig. 11. a: *Sapindopsis* sp., 3rd Kamenka, Frentsevka Formation, early-middle Albian, spec. IBSS 40-1; b, c: *Trochodendroides* sp., Konstantinovka, Galenki Formation, early-middle Albian, spec. IBBS 11/145, b – upper part of leaf, c – crenate margin; d: *Dicotylophyllum* sp. 2, Konstantinovka, Galenki Formation, early-middle Albian, spec. IBBS 11/133; e: *Sapindopsis* cf. *angusta* (HEER) SEWARD et V.M.CONWAY, Andreev Inlet, Frentsevka Formation, early-middle Albian, spec. IBSS 28/104; f: *Sapindopsis* *variabilis* FONTAINE, Bikin River, Alchan Formation, early-middle Albian, spec. IBSS 4561/124-1; g: *Laurophyllum* sp., Konstantinovka, Galenki Formation, early-middle Albian, spec. IBBS 11/131. Scale bar 1 cm in a, b, d, f, g and 5 mm in c, e.

ETTINGSH. Currently, these species are combined under the name *Pandanites trinervis* (ETTINGSH.) J.KVAČEK et A.B.HERMAN (Kvaček and Herman 2004). This species comes from the lower Campanian Grünbach Formation (Herman and Kvaček 2010).

According to Kvaček and Herman (2004), the genus *Pandanophyllum* KRYSHT. (Kryshtofovich 1929) is considered a junior synonym of the genus *Pandanites* TUZSON. Therefore, we transfer *Pandanophyllum ahnertii* to the genus *Pandanites*, with the formation of the combination *Pandanites ahnertii* (KRYSHT.) GOLOVN.

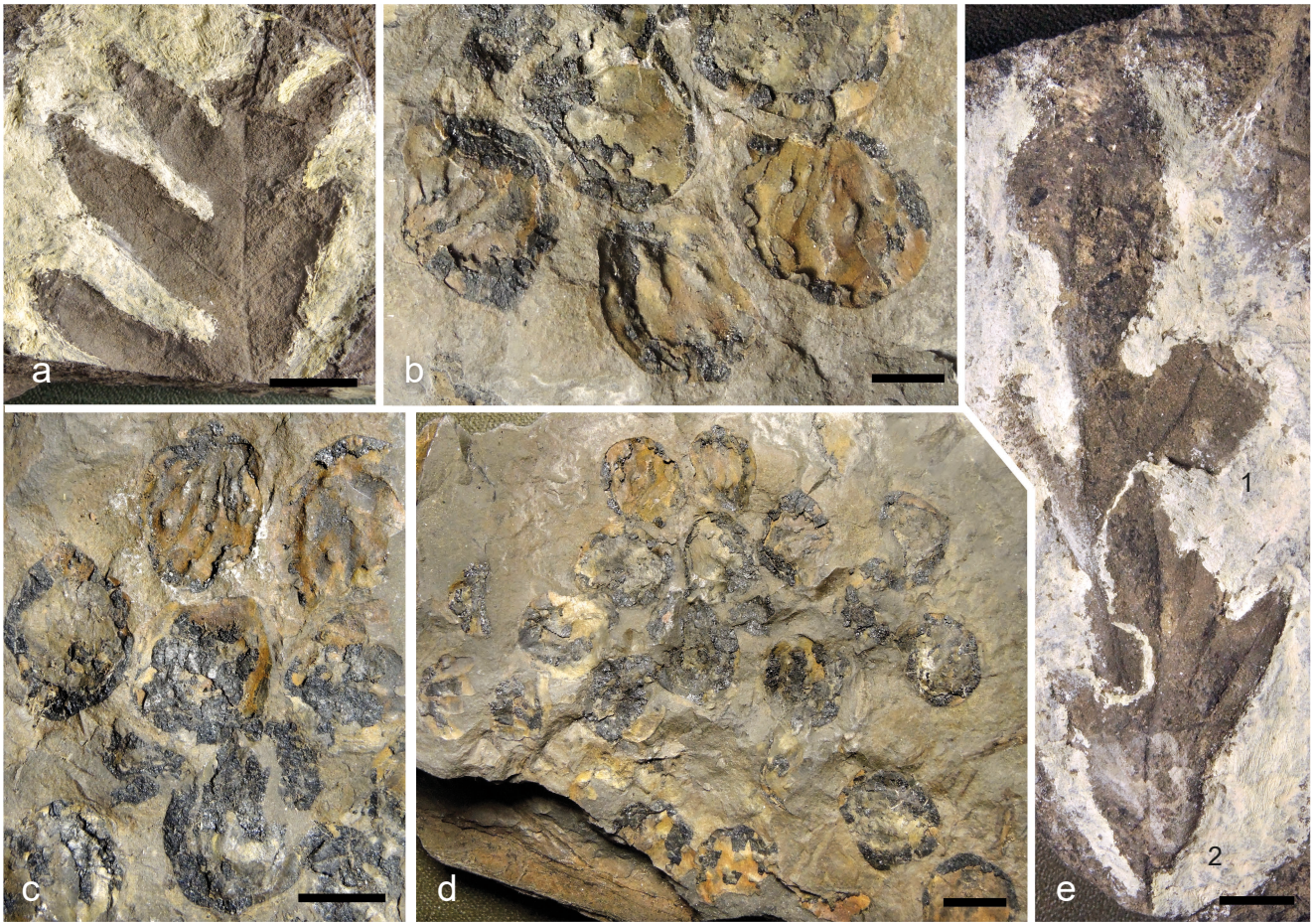
The leaves *P. ahnertii* are very similar to those of *P. trinervis* in leaf morphology and serration, but smaller, and differ by a more pronounced central vein. However, some leaves of *P. trinervis* also display similar structures. Herman and Kvaček (2010) assume that these structures actually represent fibers, which became more pronounced in certain stages of natural maceration in water. If the similarity between *P. ahnertii* and *P. trinervis* is not superficial, then *P. ahnertii* may represent one of the earliest occurrences of Pandanaceae in the fossil record. Unfortunately, its preservation is too poor for a reliable comparison.

In addition, Kryshtofovich (1929) described two *Proteaephyllum* species from Cape Firsov, Muravyov-Amursky Peninsula north of the Vtoraya Rechka River

mouth, territory of Vladivostok (Text-fig. 3): *P. reniforme* FONTAINE and *P. cordatum* KRYSHT. et PRYNADA. The first specimen was found by A. G. Kuznetsov in 1918 and is now lost. The second one was found by V. V. Nosikov-Nevsky and is currently kept at the TSNIGRM. Leaves of *P. reniforme* are reniform up to 6 cm long, with truncate base and wide rounded apex. Leaves of *P. cordatum* are distinguished by a cordate base. The venation of both species is reticulate, forming elongated alveoles. The central vein is not pronounced. Later, Krassilov (1967) established that these leaves are in fact segments of cycadophytes, and transferred the species *P. cordatum* to the genus *Dictyozamites* OLDHAM ex FEISTM.

The fruits of *Onoana nicanica* KRASSILOV were found by Krassilov (1967) on the west coast of Amur Bay near the abandoned village Fedorovsky Rudnik (Text-fig. 3). They are oval-rounded endocarps up to 15 mm in diameter (Text-fig. 12b–d). The endocarp wall is pierced by rounded conically tapering canals 1.0–2.5 mm in diameter. Krassilov compared these fruits with the fruits of *O. californica* M.CHANDLER et AXELROD from the Early Cretaceous of California.

New finds of early angiosperms in the upper part of the Lipovtsy Formation have been discovered on the territory of the Podgorodenka coalfield and Porechye coal mine (Volynets and Bugdaeva 2017). In the Podgorodenka



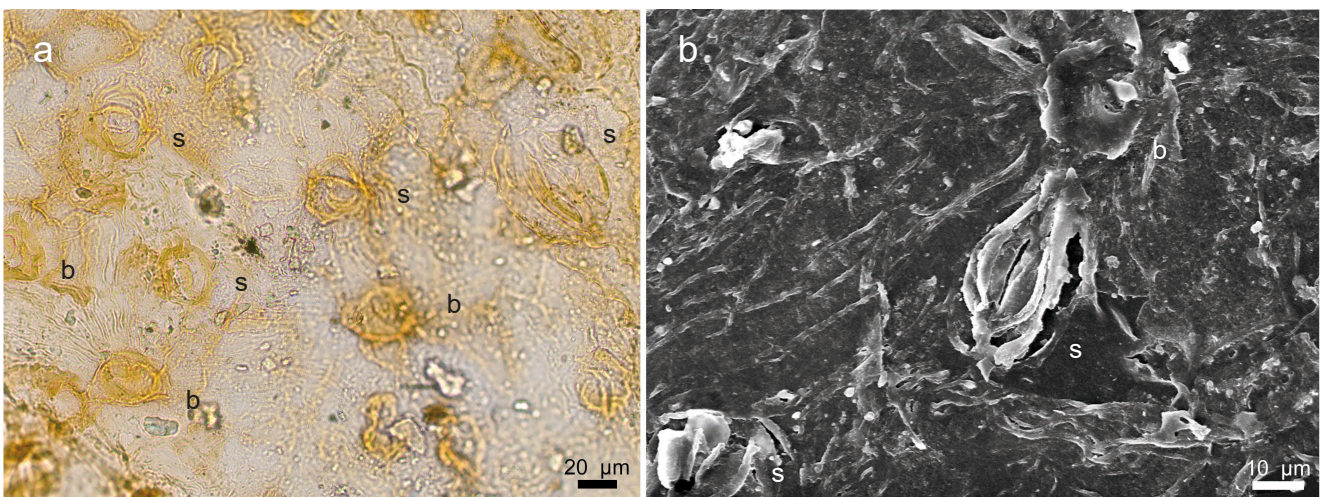
Text-fig. 12. a: *Artocarpidium* sp., Andreev Inlet, Frentsevska Formation, early-middle Albian, spec. IBSS 28-105; b–d: *Onoana nicanica* KRASSILOV, Fedorovsky Rudnik, Lipovtsy Formation, Aptian, spec. IBSS 63-83; e: *Araliaephyllum ussuriense* (KRASSILOV) GOLOVN., Andreev Inlet, Frentsevska Formation, early-middle Albian, e1 – spec. IBSS 28-102/1, lectotype, e2 – spec. IBSS 28-102/2. Scale bar 1 cm in a, d, e and 5 mm in b, c.

coalfield, early angiosperms were found in the Sokol Inlet. They are represented by several leaf fragments of unknown taxonomic affinity, identified as *Dicotylophyllum* spp.

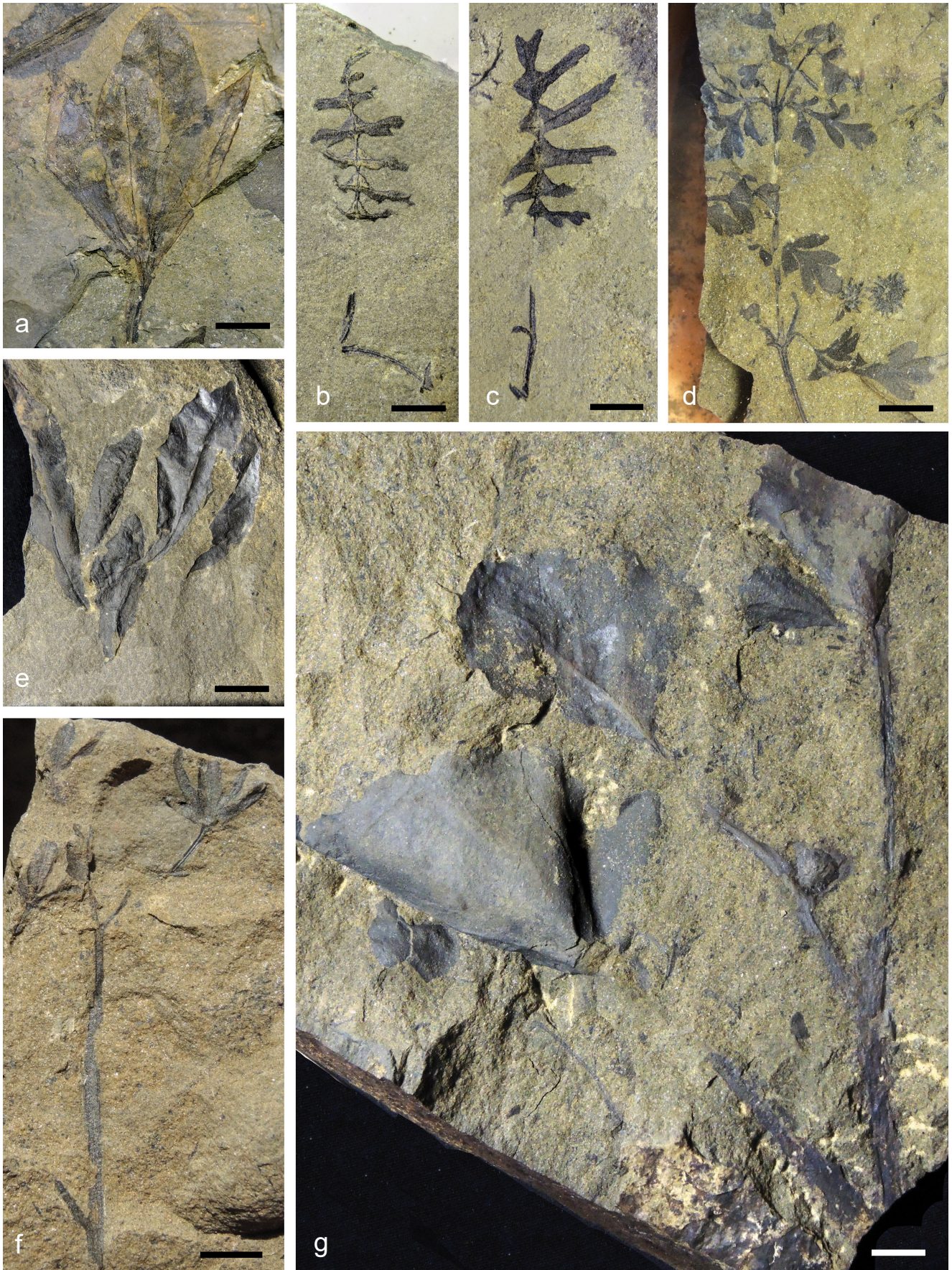
Dicotylophyllum sp. 1 is the apex of a rather large wide leaf, the length of which was probably about 5 cm (Text-fig. 10h). It is characterized by dentate margin and pinnate craspedodromous venation. The morphology of

the secondary venation and the dentate-emarginate margin resemble those of plane trees.

A dispersed angiosperm cuticle was found during maceration of coal from the Terminalny coal seam of the Porechye coal mine (Text-fig. 13a, b). The cuticle is very thin, possibly from lower leaf surface. The boundaries between cells are almost indistinguishable. Numerous



Text-fig. 13. Dispersed platanoid cuticle. a: LM; b: SEM, upper surface. s – stoma; b – hair base.



Text-fig. 14. Bolshoy Kuvshin, Frentsevka Formation, early-middle Albian. a, e: *Asiatifolium elegans* G.SUN, SHUANG X.GUO et SHAO L.ZHENG, a – spec. IBSS 320-8, e – spec. IBSS 320-75; b, c: *Jixia pinnatipartita* SHUANG X.GUO et G.SUN, b – spec. IBSS 320-359, c – spec. IBSS 320-367; d: *Achaenocarpites capitellatus* KRASSILOV et VOLYNETS, spec. IBSS 320-120; f: *Ternaricarpites floribundus* KRASSILOV et VOLYNETS, spec. IBSS 320-10; g: undescribed species, spec. IBSS 320-137. Scale bar 1 cm in a, e-g and 5 mm in b-d.

stomata and bases of broken hairs were present on the lower epidermis. The abscission scars appear as thickened rings about 20–50 µm across, surrounded by radial striation of the outer surface. Stomata are numerous, broadly oval in outline, varied in size, anomocytic, with elliptical aperture and thickened stomatal ledges. Similar epidermal structures are characteristic of Platanaceae (Upchurch 1984, Pedersen et al. 1994, Golovneva 2008).

Early Albian, Partizansk coal basin, Frentsevka Formation

Three localities of early angiosperms are known in the deposits of the Frentsevka Formation: 3rd Kamenka River, Andreev Inlet, and Bolshoy Kuvshin Cape (Text-fig. 2).

The locality in Andreev Inlet near Palets Cape was discovered by Krassilov (1965, 1967). Three species were described from there: *Sassafras ussuriensis* KRASSILOV, *Artocarpidium* sp., and *Sapindopsis* cf. *angusta* (HEER) SEWARD et V.M.CONWAY.

Species *Sassafras ussuriensis* was later transferred to the genus *Araliaephyllum* (Golovneva 2018). Krassilov designated hand-specimen IBSS 28-102 (Text-fig. 12e) as the holotype of this species, but this hand-specimen includes two leaves of *A. ussuriense*. One of them was chosen by Golovneva (2018) as the lectotype. Leaves of *A. ussuriense* (KRASSILOV) GOLOVNEV. are trilobate, rhomboid in outline, sometimes asymmetric, 5.5–7.0 cm long, 3–4 cm wide, with cuneate base, decurrent near the petiole, and entire margin (Text-figs 10f, 12e). The central lobe is significantly larger than the lateral ones, elliptic, slightly narrowing basally, its length is equal to about 1/2 of the blade length. Lateral lobes are small, triangular, 0.6–1.0 cm long. Sinuses are shallow, rather wide, with rounded apices.

The specimen of *Sapindopsis* cf. *angusta* is a lower part of a compound leaf, with three linear-lanceolate opposite entire-margined leaflets (Text-fig. 11e). In size and morphology, this leaf has significant similarity to leaves of *Sapindopsis angusta* from the Early Cretaceous of Canada (Bell 1956) and *S. magnifolia* FONTAINE from the Potomac Group, USA (Fontaine 1889, Crane et al. 1993). However, the poor preservation of this specimen does not allow a detailed comparison with other species. A similar leaf (Text-fig. 11f) with an entire margin was described from the Alchan basin (Primorye) under the name *Sapindopsis variabilis* FONTAINE (Bugdaeva et al. 2006).

The specimen of *Artocarpidium* sp. is the upper part of a pinnate-lobed leaf with several entire-margined linear lobes up to 10 mm wide with very deep sinuses (Text-fig. 12a). It is very possible that this specimen is the upper part of a *Sapindopsis* leaf.

The locality of early angiosperms in the upper reaches of the 3rd Kamenka River has been known for a long time (Likht 1961). However, the fossils from there were never formally described and figured. Only Krassilov (1967) described two leaves under the names *Aralia lucifera* and *Cissites* sp. Our examination of these specimens showed that they both belong to the genus *Sapindopsis*. These leaves differ from *Sapindopsis* leaves from the Palets Cape by a dentate margin (Text-figs 10i, 11a), and are similar to *S. belviderensis* E.W.BERRY from the late Albian Cheyenne Formation of

Kansas (Berry 1922) and *S. minutifolia* UPCHURCH from the late Albian Quantico Group of the Potomac (Upchurch et al. 1994). They probably represent a new species.

The locality Bolshoy Kuvshin is situated on the coast of the Ussuri Bay on the Bolshoy Kuvshin Cape near the town of Bolshoy Kamen. It was discovered by geologist A. Oleynikov, then studied by Krassilov and Volynets (2008), who described two species of tiny herbaceous angiosperms from there: *Achaenocarpites capitellatus* KRASSILOV et VOLYNETS and *Ternaricarpites floribundus* KRASSILOV et VOLYNETS (Text-fig. 14d, f). The angiosperm assemblage also includes *Jixia pinnatipartita* SHUANG X.GUO et G.SUN, *Asiatifolium elegans* G.SUN, SHUANG X.GUO et SHAO L.ZHENG and several undescribed species (Text-fig. 14g). The last two named species are also found in the angiosperm assemblage from the Chengzihe Formation (Sun and Dilcher 2002), exposed near the city of Jixi in northeastern China (Text-fig. 1).

The majority of specimens are fragments of branching stems with attached leaves or fruits, or almost complete plants. The most complete specimen of *Achaenocarpites* KRASSILOV et VOLYNETS is a whole plant about 15 cm high with a straight thin branching stem, several whorls of leaves and terminal heads, consisting of numerous achenes (Text-fig. 14d). The leaves are stipulate, ternate, and pinnatisect. Krassilov compared this species with different representatives of Ranunculales.

Asiatifolium elegans (Text-fig. 14a, e) is represented by the upper parts of stems with several helically attached and closely spaced leaves. The leaves are entire-margined, very diverse both in shape and size. Usually they are oblong, lanceolate or obovate, with an obtuse to rounded apex and decurrent base. Venation is pinnate, brochidodromous, with 5–8 secondary veins.

Ternaricarpites floribundus is represented by a slender branching axis with several fruits, consisting of two to five follicles, most commonly three (Text-fig. 14f). Based on morphological characters and comparisons with other fossils, it appears that *Ternaricarpites* may also be related to Ranunculales, such as *Achaenocarpites* (Krassilov and Volynets 2008).

Jixia pinnatipartita has simple deeply pinnately lobed entire-margined leaves (Text-fig. 14b, c). The lobes are thin, sublinear, usually with additional small lobes and widened bases, decurrent up and down along the midvein. The leaf base is truncate or with triangular incision. Venation is pinnate, craspedodromous.

The angiosperm remains are accompanied by the ferns *Onychiopsis psilotoides* (C.STOKES et WEBB) WARD and *Birisia mandshurica* GOLOVNEV., GRABOVSKIY et ZOLINA, which are represented by almost entire young plants (Golovneva et al. 2020). According to environmental reconstruction, *Onychiopsis* M.YOKOY. probably grew along meander belt systems and on the backbarrier flats at the margin of a brackish bay (Friis and Pedersen 1990). The plant fossils in Bolshoy Kuvshin locality were buried during a single flooding event, and remained very close to their original location. They formed a pioneer open herbaceous community (Text-figs 15, 16), consisting of ferns and angiosperms with a predominance of the latter and adapted to colonize fresh sediments in periodically flooded areas (Golovneva et al. 2018).



Text-fig. 15. Reconstruction of herbaceous angiosperms from Bolshoy Kuvshin locality, Frentsevka Formation, early-middle Albian. a: *Asiatifolium elegans* G.SUN, SHUANG X.GUO et SHAO L.ZHENG; b: *Jixia pinnatipartita* SHUANG X.GUO et G.SUN.



Text-fig. 16. Reconstruction of herbaceous angiosperms from Bolshoy Kuvshin locality, Frentsevka Formation, early-middle Albian. a: undescribed species, spec. IBSS 320-137; b: *Achaenocarpites capitellatus* KRASSILOV et VOLYNETS.

Early-middle Albian, Razdolnaya coal basin, Galenki Formation

Two localities of early angiosperms are known in the tuffaceous deposits of the Galenki Formation: Konstantinovka village in the upper reaches of the Razdolnaya river and Dachny Creek in the territory of the Podgorodenka coalfield (Text-fig. 3).

In Konstantinovka, several angiosperms were found by Krassilov (1967). Under the name *Cercidiphyllum suffunense* KRASSILOV (Krassilov 1967), both leaf and fruit were described, although they were not found in organic connection. The leaf is elliptic, with cuneate base and entire margin (Text-fig. 9f). The venation is pinnate, brochidodromous; secondary lateral veins are decurrent near the middle vein. This leaf is completely different from other leaves of *Cercidiphyllum* SIEBOLD et ZUCC. or *Trochodendroides* E.W.BERRY, which have palmate venation and dentate or crenate margin. The leaf from the Galenki Formation is comparable with those of *Asiatifolium elegans*, which were recorded from the Frentsevka Formation of the Partizansk coal basin. The fruit of *C. suffunense* (Text-fig. 9e) is similar with *Jenkinsella* E.REID et M.CHANDLER fruits in short stalk and attenuate apex, but it has no suture grooves, longitudinal ridges or transverse striae. We believe that this fruit cannot be assigned to Cercidiphyllaceae.

However, Krassilov's collection contains one undescribed specimen, which morphologically corresponds to the diagnosis of genus *Trochodendroides* (Text-fig. 11b, c). This is the upper part of an elliptic leaf, about 3 cm long, with acute apex. The margin is crenate. Teeth are short, with wide base, rounded, obtuse apex, convex sides and acute sinuses. Primary venation is actinodromous, with three primary basal veins, which rise to the apex and join with the middle vein. Basisopic branches of upper basal veins form a series of loops along the margin. Short thin veins go from the outer part of the loops to the tooth apices. Tertiary venation is percurrent-reticulate, very thin. This leaf is very similar to leaves of *Trochodendroides sittensis* GOLOVN. from early-middle Albian Khatyryk Formation of the Lena River basin, Yakutia, Russia (Golovneva and Zolina 2018).

In addition to *C. suffunense*, Krassilov (1967) described *Laurophyllum* sp. (Text-fig. 11g) and *Dicotylophyllum* sp. also from Konstantinovka. Both these additional species are indeterminate fragments.

One more undescribed leaf with dentate margin and pinnate craspedodromous venation, figured here under the name *Dicotylophyllum* sp. 2 (Text-fig. 11d), is similar with Aptian *Dicotylophyllum* sp. 1 from the Sokol Inlet, and resembles Platanaceae leaves.

In Dachny Creek, two small reniform, 5–7-lobed leaves were found (Text-fig. 10g). They are very small, up to 2 cm long, with cordate base and entire margin. The central lobe is equal in length to the upper lateral lobes, or slightly shorter. These leaves are described below as a new species *Araliaephyllum vittenburgii*, sp. nov.

Systematic palaeobotany

Division Magnoliophyta CRONQ., TAKHT. et W.ZIMM.,
1966

Class Liliopsida BATSCH, 1802

Family Pandanaceae R.BR., 1810 nom. cons.

Genus *Pandanites* TUZSON, 1913 emend. by Kvaček and
Herman (2004)

Pandanites ahnertii (KRYSH.T.) GOLOVN. comb. nov.
Text-fig. 10e, j

Basionym. *Pandanophyllum ahnertii* KRYSH.T.,
Otkrytie drevneishikh dvudolnykh pokrytosemennykh
i ekvivalentov potomakskikh sloev na Suchane
v Ussuriyskom krae [The discovery of the oldest dico-
tyledons angiosperms and equivalents of the Potomac beds
on Suchan in the Ussuri region.], Izv. Geol. Komit. 49: 1364,
pl. LIX, figs 1–3. 1929.

Plant Fossil Names Registry Number.
PFN002698 (for new combination).

Lectotype. Designated here. No. 3013/5a, coll.
TSNIGR Museum, southern Primorye, Razdolnaya coal
basin, Konstantinovka, Lipovtsy Formation, Aptian
(Kryshstofovich 1929: pl. LIX, fig. 1). Among several leaf
fragments at the surface of Kryshstofovich specimen, the
longest leaf with preserved serration was chosen as the
lectotype (Text-fig. 10j1).

Plant Fossil Names Registry Number.
PFN002700 (for lectotype designation).

Diagnosis. *Pandanophyllum* foliis tenerrimis,
linearibus, satis angustis, 0.4–1.0 cm, latis, margine
spinuloso-ciliato-serratis, partim duplicato serratis, nervo
mediano satis valido, nervis longitudinalibus lateralibus
obsoletis, tenuissimis, circa 14–16 (Kryshstofovich 1929).

Class Magnoliopsida BRONGN., 1843
Magnoliopsida incertae sedis

Genus *Araliaephyllum* FONTAINE, 1889

Araliaephyllum vittenburgii GOLOVN. et VOLYNETS,
sp. nov.
Text-fig. 10g1–2

Holotype. No. IBSS 41/1a (Text-fig. 10g1).

Plant Fossil Names Registry Number:
PFN002696 (for new species).

Repository. Federal Scientific Center of the East
Asia Terrestrial Biodiversity (previously Institute of Botany
and Soil Science), Far Eastern Branch, Russian Academy of
Sciences, Vladivostok, Russia.

Etymology. After geologist P. V. Vittenburg.

Type locality and age. Dachny Creek,
Podgorodenka coalfield, Razdolnaya coal basin, Southern
Primorye, Russia; Galenki Formation, early-middle Albian.

Diagnosis. Leaves very small, 5–7-lobed, rounded
or widely ovate in outline, with cordate base; margin entire;
lobes linear-elliptic, with wide rounded apices; central lobe
equal in length to upper lateral lobes or slightly shorter;
lateral lobes gradually decrease in size towards leaf base;
lobe length equal to 1/2 of blade length; sinuses between
lobes narrow with rounded apices; basal veins end before
lobe apex; lowest basisopic branches of lateral basal veins
strong and innervate 1–2 additional pairs of lateral lobes.

Additional material. Specimens IBSS 17/1a and IBSS 17/1b.

Description. Leaves are simple, 5–7-lobed, rounded or widely ovate in outline, with cordate base, 1.4–2.0 cm long, 2.0–3.6 cm wide. Margin is entire. Lobes are wide, linear-elliptic, with wide rounded apices. The central lobe is equal in length to the upper lateral lobes, or slightly shorter.

The upper lateral lobes are usually the longest and widest. Lateral lobes gradually decrease in size towards the leaf base. The lobe length is equal to 1/2 of the blade length. Sinuses between lobes are narrow, triangular, with rounded apices. The primary venation is palmate, the secondary venation is brochidodromous. Lateral basal veins diverge from the midvein at an angle of 65–75°, strong, slightly curved, ending before the lobe apex. They bear several curved acroscopic and basispic branches, which form loops near the margin. The lowest basispic branches are stronger, and innervate 1–2 additional pairs of lateral lobes. Tertiary venation is very thin, usually irregular. Higher-order venation is not well preserved.

Comparison. *Araliaephyllum luciferum* from the Partizansk differs from *A. vittenburgii* in having a dentate margin and three lobes. *A. ussuriense* from the Palets Cape also has only three narrow lobes, with the central lobe the largest. Specimens of *A. vittenburgii* are the most similar to leaves of *Araliaephyllum arenarium* (G.G.FILIPPOVA) G.G.FILIPPOVA from the Cenomanian Krivorechenskaya Formation of the Anadyr River (Filippova and Abramova, 1993) in number and arrangement of the lobes, but the lobes of *A. arenarium* are narrower and longer. In addition, the base of *A. arenarium* is cuneate, while the base of *A. vittenburgii* is cordate. The leaves of *A. vittenburgii* are much smaller.

Stratigraphic horizon and occurrence. Galenki Formation, early-middle Albian.

Araliaephyllum luciferum (KRYSH.T.) GOLOVN.

Text-fig. 10a–d

- 1929 *Aralia lucifera* KRYSH.T., p. 1360, pl. LVIII, figs 1, 2.
2018 *Araliaephyllum luciferum* (KRYSH.T.) GOLOVN., p. 23, fig. 6C, E, F, H.

Lectotype. No. 3013/1, coll. TSNIGR Museum (designated by Golovneva 2018), Southern Primorye, Suchan (Partizansk) coal basin, left bank of the Malaya Sitza (Postyshevka) River near Novoveselaya village, Severosuchan Formation, lower-middle Albian (Kryshstofovich 1929: pl. LVIII, fig. 2).

Description. Leaves of *Araliaephyllum luciferum* (KRYSH.T.) GOLOVN. are simple, trilobate, fan-shaped, ovate and rounded in outline, 1.5–3.5 cm long, 1.3–2.6 cm wide, cuneate base, decurrent near the petiole, and serrate margin. Teeth are small, adpressed. Apices of lobes are acute or rounded. The central lobe is the largest; its length is equal to 1/4–1/2 of the blade length. Lateral lobes are shorter and narrower, usually directed to the leaf apex. Sinuses between lobes are shallow and narrow, with rounded apices. Venation is palmate, 3-nerved, brochidodromous. Midvein is straight. Lateral basal veins are slightly curved, diverging from the midvein at an angle of 20–35° in 3–5 mm above leaf margin,

ending in the lobe apices. Basal veins bear several curved basispic branches, which form a series of loops near the margin. Three to five pairs of secondary veins diverge from the midvein at an angle of 35–55°, also forming loops. Tertiary venation is very thin and poorly preserved.

Comparison and remarks. *Araliaephyllum luciferum* differs from other species of this genus from eastern Russia in having a serrate margin. This character was reported for several species of *Araliaephyllum* or “*Aralia*” from Cenomanian Peruc flora of the Czech Republic, but all of them have deeper dissected leaf blades and longer lobes (Velenovský 1882, 1884, Greguš and Kvaček 2015). Besides that, lobes of *Araliaephyllum formosum* (HEER) GREGUŠ et J.KVAČEK from the Maletín are serrate only in the apical parts. “*Aralia*” *decurrens* VELEN. from Vyšehořovice (Velenovský 1884) has very narrow lobes; lateral lobes of “*Aralia*” *minor* VELEN. are significantly smaller than the medial ones, and the leaf base is not cuneate (Velenovský 1884).

“*Aralia*” *calomorpha* SAPORTA from the Albian of Buarcos in Portugal (Saporta 1894) also has a serrate margin, but differs from *Araliaephyllum luciferum* in having narrow lobes separated by deep incisions. This species was considered as a presumable report of lauraceous leaves (Friis et al. 2011). Toothed leaves of “*Aralia*” *wellingtoniana* LESQ. from the Raritan Formation (USA) differ in larger size (up to 20 cm), and in deeply trilobate blades, with long, lanceolate lobes (Lesquereux 1892).

Discussion

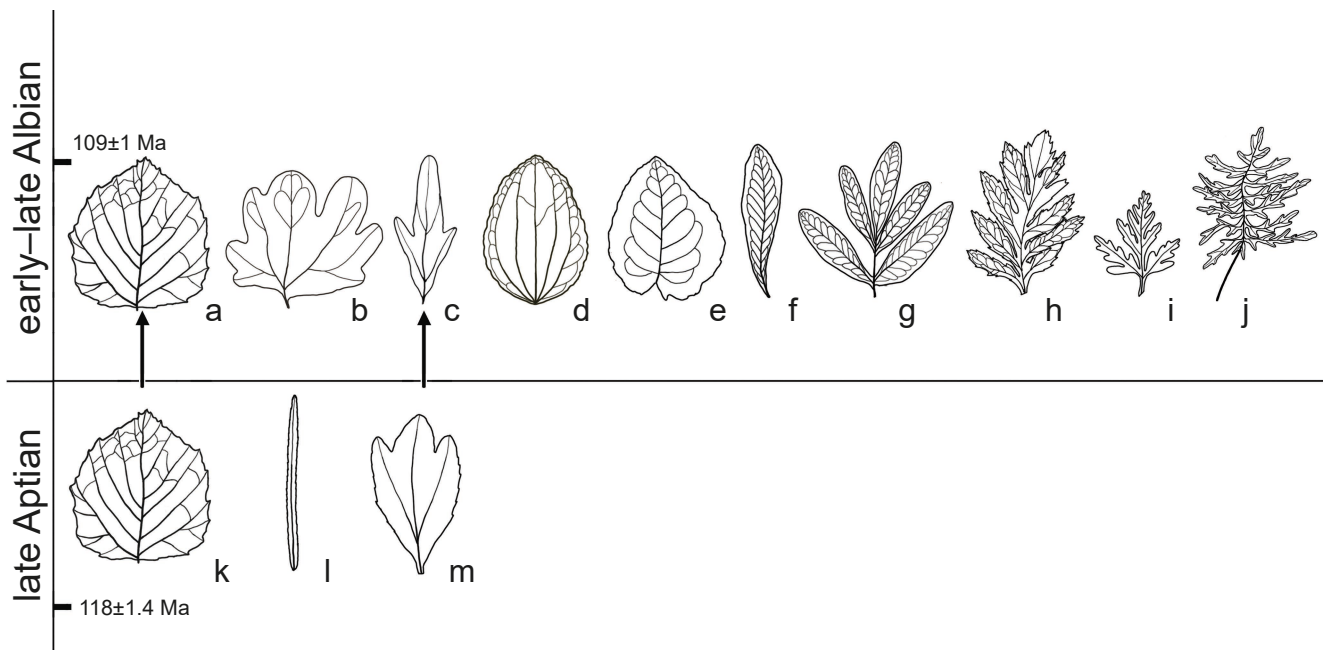
Evolution of early angiosperms

The evolution of angiosperms in the Early Cretaceous of Primorye is divided into two phases, based on pollen and megafossil remains: late Aptian and early Albian (or early-middle Albian). The age of these stages is determined based on isotopic data (118 ± 1.4 Ma and 109 ± 1 Ma correspondingly). During the Early Cretaceous, this region was located in the lower middle palaeolatitudes, about 30–35° (Golozubov 2006).

During the late Aptian, monosulcate, tricolpate, and pentachotomocolpate angiosperm pollen appeared in the geological record of Primorye simultaneously. In most other regions, the successive appearance of reticulate-columellar monosulcate, tricolpate, tricolporate, and triporate pollen types was recorded.

The classical Lower Cretaceous succession of the Potomac Group of the eastern United States demonstrates the gradual morphological changes of angiosperm pollen and leaves (Hickey and Doyle 1977, Muller 1981, Doyle 1992). The pollen of *Clavatipollenites* COUPER appears first, then *Liliacidites* COUPER, and towards the end of the early Albian, the presence of tricolpate pollen was recorded. In the late Potomac (middle to late Albian), the rise of tricolpate pollen and local dominance of angiosperm leaves mark the influx of near-basal eudicot clades (Doyle and Upchurch 2014).

In Argentina, first monosulcate pollen appeared in the late Barremian–Aptian, and the presence of the first definitive eudicots was recorded in the latest Aptian–earliest Albian (Archangelsky et al. 2009). A similar picture is observed



Text-fig. 17. Angiosperm leaf morphotypes in late Aptian and early-middle Albian of Primorye. a, k: *Dicotylophyllum* sp. 1, 2; b: *Araliaephyllum vittenburgii* GOLOVN. et VOLYNETS; c: *Araliaephyllum ussuriense* (KRASSILOV) GOLOVN.; d: *Trochodendroides* sp., e: undescribed species, spec. IBSS 320-137; f: *Asiatifolium elegans* G.SUN, SHUANG X.GUO et SHAO L.ZHENG; g: *Sapindopsis* cf. *angusta* (HEER) SEWARD et V.M.CONWAY; h: *Sapindopsis* sp.; i: *Achaenocarpites capitellatus* KRASSILOV et VOLYNETS; j: *Jixia pinnatipartita* SHUANG X.GUO et G.SUN; l: *Pandanites ahnertii* (KRYSHI.) GOLOVN.; m: *Araliaephyllum luciferum* (KRYSHI.) GOLOVN.

in the Barremian-Aptian sequence in southern England (Hughes and McDougall 1990).

In the Western Portuguese and Algarve basins, the late Barremian interval contains only a few taxa attributed to the *Clavatipollenites* group (Heimhoffer et al. 2005). The Aptian is characterized by the increasing diversification of basal angiosperm pollen. The appearance of tricolpate pollen grains was recorded from the early Albian. The Portuguese record reveals that the onset of the radiation of monocots-magnoliids preceded the radiation of eudicots by at least 10 Ma (Hochuli et al. 2006). This record was used for recalibration of the continental succession of the Potomac Group (Hochuli et al. 2006, Doyle and Upchurch 2014). But the time of appearance of different types of pollen may be different in different regions. Palynofloras of the Serrania de Cuenca region (Eastern Iberia, Spain) differ from other floras of Europe and North America in the occurrence of tricolpate pollen in the Aptian (Buono-Cebollada et al. 2021).

We hope that earlier phase of angiosperm evolution will be revealed in Primorye in the future with a more thorough study of the Barremian and lower Aptian parts of the sections. Moreover, in adjacent regions, angiosperm pollen was recorded in sediments of this age. *Clavatipollenites hughesii*, *C. incisus*, *Asteropollis* R.W.HEDL. et G.NORRIS and *Tricolpites* sp. were discovered in the Barremian-Aptian of Transbaikalia (Vakhrameev and Kotova 1977). *C. hughesii* was found in the Barremian-Aptian Longpan Formation, Anchow Basin, North Korea (Jiang and Yang 1996). *Clavatipollenites* sp. and *Tricolpopollenites* sp. were recorded in the Barremian-Aptian Yimin Formation, north-eastern Heilongjiang Province, China (Pu and Wu 1985). Recently, *C. hughesii* was discovered in the Huolinhe Formation, eastern Inner Mongolia, China (Shi et al. 2021). U-Pb zircon geochronology constrains the depositional age

of the lower part of this formation to be 125.6 ± 1.0 Ma (the beginning of the Barremian, according to the Geologic Time Scale 2020 (Gradstein et al. 2020)). In addition to *Clavatipollenites*, previous researchers also found *Asteropollis* and *Tricolpites* COOKSON ex COUPER here (Guo 1995). It should be noted that some Asian Barremian-Aptian palynofloras contain tricolpate pollen, like the late Aptian flora of Primorye, which indicates an early development of eudicots in Asia. Pollen of this type is also known from the late Barremian – early Aptian of southern England (Hughes and McDougall 1990), Egypt (Penny 1991) and Israel (Brenner 1996).

The angiosperm leaf morphotype evolution in the Early Cretaceous of Primorye region is shown in Text-fig. 17. Only three leaf morphotypes were recorded in the late Aptian: trilobate leaves with serrate margin, ovate leaves with pinnate secondary venation and dentate margin, and narrow linear serrate leaves. Similar morphotypes are absent in the Aptian of the Potomac Group and Aptian of Argentina. In the Potomac succession (Zone I), lanceolate leaves with pinnate brochidodromous venation and entire or serrate margin predominate (Doyle and Upchurch 2014). Leaves from the Aptian of South America correspond to the nymphaeaphyll, pinnately-lobate serrate and crenate lobate morphotypes (Archangelsky et al. 2009). The diversity of leaf morphology in the early Albian increases significantly. More than 10 different morphotypes were recognized. Various ternate, pinnatifid and pinnately compound leaves appeared, also nymphaeaphylls and trochodendrophylls.

Systematic affinity

The assignment of fossil leaves, especially from the Early Cretaceous, to modern groups has always been questionable. However, the vegetative organs of some groups are

characterized by certain conservatism in comparison with the rapid evolution of the generative organs. This makes it possible to trace the early evolution of some lines in the Early Cretaceous. In Primorye, the representatives of Laurales, Ranunculales, Platanaceae, and probable Cercidiphyllaceae were identified.

Many Cretaceous *Araliaephyllum* are now considered as having Laurales affinity (Upchurch et al. 1994, Golovneva 2018). The fossil record of *Araliaephyllum* is rich and diverse, especially in mid-Cretaceous floras of the Northern Hemisphere (Lesquereux 1892, Crabtree 1987, Herman and Lebedev 1991, Upchurch et al. 1994, Golovneva and Nosova 2012, Herman 2013, Herman et al. 2016). In the extensively studied sequence of the Potomac Group, the first trilobate morphotypes appeared in the early-middle Albian, in the Zone II-B (Doyle and Upchurch 2014). In Primorye, the first *Araliaephyllum* (*A. luciferum*) appears in the late Aptian. From the early-middle Albian, two species were recorded (*A. ussuriense* and *A. vittenburgii*).

Many palmately lobed leaves from the Potomac Group were previously assigned to the “platanoid” complex (Hickey and Doyle 1977, Upchurch 1984). *Araliaephyllum obtusilobum* (type species of the genus) from the Brooke locality (early Albian) was considered an early member of this group. It is characterized by palinactinodromous primary venation, occasionally the presence of small accessory lobes at the base of each of the large lateral lobes, and weak and irregular tertiaries. More recent research shows that *Araliaephyllum* leaves from Potomac Group were misassigned to the platanoid complex, and are better interpreted as Laurales. Lauralean features of *Araliaephyllum* include: (1) curved lateral primary veins decurrent into the petiole, (2) thin secondary and tertiary venation, (3) fimbrial veins along margin of leaf base, and (4) the basal-most branches of the lateral primaries run at a more acute angle than others, and terminate at the margin or at the apex of small additional lobes (Upchurch et al. 1994). The true platanoids, which dominate at level zones IIC and III in Potomac, differ in more regular secondary and tertiary venation. They have perpendicularly percurrent, closely spaced tertiaries (Doyle and Hickey 1976, Hickey and Doyle 1977).

The Platanaceae family is represented in Primorye by two species of genus *Sapindopsis*, which appeared in the early-middle Albian, like in the Potomac Group. However, cuticle of the platanoid type was discovered in the Porechye coal mine from the late Aptian. It is possible that leaves with pinnate craspedodromous venation and dentate-emarginate margin from the late Aptian and lower-middle Albian can also be interpreted as Platanaceae (Text-figs 10h, 11d, 17a–k).

Trochodendroides sp. from the lower-middle Albian Galenki Formation is very similar with *T. sittensis* GOLOVNEVA from the lower-middle Albian Khatyryk Formation, Lena River basin, Eastern Siberia, Russia (Golovneva and Zolina 2018). Leaves of *Trochodendroides* are associated with fruits *Jenkinsella* (*Nyssidium*) and inflorescences *Alasia* GOLOVNEVA. (Golovneva 2006, Golovneva and Alekseev 2017). Pollen grains, extracted from the *Alasia* anthers, are small tricolpate with long colpi and a variably microreticulate to verrucate-scabrate ornamentation (Krassilov and Kodrul

2008). Investigation of cuticular features of the Cretaceous *Trochodendroides* E.W.BERRY leaves reveals the similarity with those of living *Cercidiphyllum* SIEBOLD et ZUCC. (Golovneva and Alekseev 2010). *Trochodendroides-Jenkinsella* (*Nyssidium*)-*Alasia* plants and the most completely preserved plant from this group, *Joffrea speirsii* P.R.CRANE et STOCKEY, were interpreted as extinct representatives of Cercidiphyllaceae (Crane and Stockey 1985, 1986, Golovneva and Alekseev 2017). In the majority of overviews, this family is not considered among the ancient groups of eudicots, and the timing of its appearance is estimated as the latest Cretaceous (Friis et al. 2011). However, during the Late Cretaceous, *Trochodendroides-Jenkinsella-Alasia* fossils were widespread in middle and high latitudes of the Northern Hemisphere. In the lower-middle Albian deposits of Northeastern Asia, they are represented by one species of *Jenkinsella* fruits and five species of *Trochodendroides* leaves from different localities (Golovneva and Zolina 2018). These fossils reflect the early history of Cercidiphyllaceae or its ancestors.

Fruits of “*Nyssidium*” *orientale* SAMYLINA from the Barremian Starosuchan Formation, and leaves and fruits of “*Cercidiphyllum*” *sujfunense* KRASSILOV from the lower-middle Albian Galenki Formation cannot be assigned to Cercidiphyllaceae.

Herbaceous angiosperms from the Bolshoy Kuvshin locality were compared by Krassilov (Krassilov and Volynets 2008) with Ranunculales. However, many early angiosperms have similar features in fruit structure and leaf venation. Additional research is needed to establish the systematic position of these taxa.

Palynological data indicate the presence of the chloranthaceous line, which is represented by genera *Clavatipollenites* and *Asteropollis* (Eklund et al. 2004). *Asteropollis* pollen is monoaperturate and reticulate, with beaded or spiny supracteal ornamentation on the muri. Its aperture is irregularly star-shaped. Its relationship is confirmed by the discovery of *Asteropollis* pollen in situ in stamens and adhering to pistillate flowers that are closely similar to staminate and pistillate flowers of *Hedyosmum* Sw. (Friis et al. 2011). Dispersed *Asteropollis* pollen was widely distributed in the Early and mid-Cretaceous palynofloras from both the Northern and the Southern Hemisphere. The oldest records are known from the probable Hauterivian-Barremian Anda-Khuduk Formation of Mongolia (Vakhrameev 1991). In addition, *Asteropollis* was found in the Barremian-Aptian of Lake Baikal area (Vakhrameev 1991), China (Li 1995), Europe (Friis et al. 1999, 2011), and North Africa (Schrank 1987).

The opinion about chloranthaceous affinity of *Clavatipollenites* was expressed by Muller (1981). This view was confirmed by association of this pollen with fruit *Couperites* K.R.PEDERSEN, P.R.CRANE, DRINNAN et E.M.FRIIS (Pedersen et al. 1991). Pollen of “*Clavatipollenites*” type has been compared with pollen of modern *Ascarina* J.R.FORST. et G.FORST., but not directly linked with the latter. Doyle (2015) concluded that *Clavatipollenites* is systematically heterogeneous and is not yet convincingly related to Chloranthaceae. Thus, this pollen may provide evidence for the chloranthaceous lineage as a whole (Eklund et al. 2004).

Monocolpate angiosperm grains resembling *Clavati-pollenites* first appeared in the Valanginian–Hauterivian of the palaeoequatorial regions (Friis et al. 2011). In middle and high latitude regions of the northern hemisphere, however, the earliest appearance of *Clavati-pollenites* is later, commonly in the Barremian. It has been reported from the Barremian through Albian of Europe, North America, Asia, South America, Israel, Australia, and the Albian of New Zealand and Antarctica (Eklund et al. 2004).

Tricolpate pollen is considered to have eudicotyledonous affinity. Pollen of early eudicot is rather similar in morphology, and its systematic position is usually unclear.

Age

The Bolshoy Kuvshin assemblage includes two species, in common with the flora of the Chengzihe Formation, including in Jixi Group: *Jixia pinnatipartita* and *Asiatifolium elegans*. The angiosperms from the Chengzihe Formation were initially considered to be Hauterivian to early Barremian in age (Sun and Dilcher 2002). More recently, reinvestigation of *Aucellina* bivalves from the Jixi Group indicated a younger age, from the Barremian to Albian (Gu et al. 1997). In the result, the Chengzihe Formation is considered to be mainly Aptian (Sha et al. 2003).

New isotopic data indicate late Aptian-early Albian age for the Chengzihe Formation (Chen et al. 2018). This corresponds to our isotopic age of the upper part of the Frentsevka Formation (109 ± 1 Ma). This means that the Bolshoy Kuvshin assemblage of herbaceous angiosperms and the Chengzihe flora existed at the same time.

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Appendix

Results of U-Th-Pb zircon analyses for sample 160/4 (Lipovtsy Formation).

Spots	Isotopic ratios and errors (1 σ)						Ages (Ma) and errors (1 σ)									
	207Pb/206Pb	1 σ	207Pb/235U	1 σ	206Pb/238U	1 σ	208Pb/232Th	1 σ	207Pb/206Pb	1 σ	207Pb/235U	1 σ	206Pb/238U	1 σ	208Pb/232Th	1 σ
160/4-03	0.0497	0.0031	0.1265	0.0078	0.0185	0.0002	0.0058	0.0001	180	143	121	7	118	1	118	1
160/4-11	0.052	0.0046	0.2093	0.0151	0.0291	0.0006	0.0082	0.0004	285	128	193	13	185	4	165	9
160/4-20	0.0488	0.0029	0.1248	0.0067	0.0186	0.0002	0.0057	0.0002	139	99	119	6	119	1	115	4
160/4-21	0.0489	0.0031	0.1267	0.0072	0.019	0.0003	0.0055	0.0002	141	101	121	7	121	2	110	5
160/4-27	0.0479	0.0034	0.128	0.0081	0.0197	0.0003	0.0066	0.0003	93	111	122	7	126	2	134	6
160/4-32	0.0485	0.003	0.1258	0.0077	0.0188	0.0002	0.006	0.0001	123	141	120	7	120	2	120	2
160/4-35	0.0493	0.0028	0.127	0.007	0.0187	0.0002	0.0059	0.0001	162	128	121	6	119	1	119	1
160/4-36	0.0494	0.0031	0.1269	0.0077	0.0186	0.0002	0.0059	0.0001	168	142	121	7	119	1	119	1
160/4-37	0.0486	0.003	0.1239	0.0075	0.0185	0.0002	0.0059	0.0002	129	139	119	7	118	2	118	3
160/4-42	0.0493	0.0043	0.1213	0.0089	0.0184	0.0003	0.0062	0.0004	161	132	116	8	117	2	126	7
160/4-47	0.0461	0.0022	0.1228	0.0058	0.0193	0.0002	0.0062	0.0002	314	104	118	5	123	1	124	4
160/4-57	0.0484	0.0027	0.1207	0.0071	0.018	0.0003	0.0058	0.0002	120	99	116	6	115	2	116	4
160/4-58	0.0496	0.0023	0.1245	0.0053	0.0184	0.0002	0.0059	0.0002	177	79	119	5	117	1	118	3
160/4-59	0.05	0.0019	0.1289	0.0047	0.0187	0.0002	0.0057	0.0001	193	65	123	4	120	1	115	3
160/4-61	0.0515	0.002	0.2152	0.0081	0.0303	0.0003	0.0095	0.0001	261	92	198	7	193	2	192	3
160/4-71	0.0499	0.0025	0.127	0.0058	0.0187	0.0002	0.0059	0.0002	190	84	121	5	119	1	119	4
160/4-76	0.048	0.0066	0.1876	0.0258	0.0284	0.0004	0.009	0.0012	97	277	175	22	180	2	181	23
160/4-84	0.0491	0.0027	0.1214	0.0065	0.0179	0.0002	0.0057	0.0001	155	125	116	6	114	1	114	1
160/4-86	0.0489	0.0043	0.1158	0.0085	0.0175	0.0003	0.006	0.0002	143	132	111	8	112	2	122	5
160/4-88	0.0498	0.0044	0.1213	0.0093	0.0181	0.0004	0.0062	0.0003	184	135	116	8	115	2	126	6