

# New species of *Sapindopsis* Fontaine (Platanaceae) from the mid-Cretaceous of northeastern Asia and their paleogeographical and evolutionary implications

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## ABSTRACT

In this paper we present four new species of *Sapindopsis* from northeastern Asia which extend our understanding about the geographical and stratigraphic ranges of the genus and also its morphology. *Sapindopsis orientalis* sp. nov. and *Sapindopsis* sp. 1 from the Frentseвка Formation, Partizansk basin, Primorye, Russia are the earliest (lower Albian) occurrences of the genus *Sapindopsis*. *Sapindopsis asiatica* (G. Philippova) Golovneva et Zolina comb. nov. from the upper Albian–lower Turonian Krivorechenskaya Formation, Anadyr River basin, Chukotka, Russia constitute the northernmost species (paleolatitude 74°N). *Sapindopsis chinensis* sp. nov. from the upper Albian Dalazi Formation, Jilin Province, China and upper Albian Alchan Formation, Alchan basin, Primorye, Russia is distinguished from other species by alternate arrangement of the leaflets. Analysis of morphological diversity in *Sapindopsis* provides new information about evolutionary trends of early Platanaceae during mid-Cretaceous.

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## 1. Introduction

The genus *Sapindopsis* was proposed by Fontaine (1889) for pinnatifid and pinnately compound foliage with general affinities to extant Sapindaceae from the Lower Cretaceous of the Patapsco Formation, Potomac Group of North America. Leaves of this genus are characterized by great variability in leaf blades and variously decurrent leaflets. Originally, Fontaine (1889) described eight species of *Sapindopsis* mostly from the Bank near Brooke locality in northern Virginia: *S. cordata* Fontaine, *S. elliptica* Fontaine, *S. magnifolia* Fontaine, *S. variabilis* Fontaine, *S. parvifolia* Fontaine, *S. brevifolia* Fontaine, *S. tenuinervis* Fontaine, and *S. obtusifolia* Fontaine. Later, Berry (1911) partially revised the species of *Sapindopsis* from the Potomac deposits. He considered *S. parvifolia* as a synonym of *S. variabilis*, and *S. tenuinervis* as a synonym of *S. magnifolia*. *S. cordata* and *S. elliptica*, with simple leaves, were excluded from the genus. The four remaining species, *S. magnifolia*, *S. variabilis*, *S. brevifolia*, and *S. obtusifolia*, are considered by many

authors as morphological variations of a single taxon (Upchurch, 1984; Crane et al., 1993), although they were not cited as synonyms. A detailed study of the Fontaine's type material is needed in order to resolve this question. Unfortunately, Fontaine (1889) designated no type species of *Sapindopsis*, when he established the genus. Later *S. magnifolia* was chosen as the type species of the genus (Dilcher and Basson, 1990). But the lectotype of this species has not been designated. The generic diagnosis of *Sapindopsis* was emended firstly by Dilcher and Basson (1990) and later by Golovneva (2007) to include the Asian late Albian and Cenomanian leaves with toothed margin.

In the Patapsco Formation, leaves of *Sapindopsis* co-occur with capitate generative structures showing platanaceous characters. The pistillate and staminate inflorescences were described as *Platanocarpus brookensis* Crane, Friis, Pedersen et Drinnan (now *Friisicarpus brookensis* (Crane, Pedersen, Friis et Drinnan) Maslova and Herman, 2006) and *Aquia brookensis* Crane, Friis, Pedersen et Drinnan, respectively (Crane et al., 1993). The association of these inflorescences and leaves of *Sapindopsis* and the similarity in the cuticular morphology of the leaves and tepals support the platanaceous affinity of *Sapindopsis*, although an affinity with the Rosidae had previously been also supposed (Doyle and Hickey, 1976).

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The epidermal anatomy of *Sapindopsis* leaves was studied from the Albian deposits of the Potomac Group in North America and from the Cenomanian Sannine Formation, Lebanon (Upchurch, 1984; Krassilov and Bacchia, 2000). These investigations also confirm the assignment of *Sapindopsis* to the Platanaceae.

The genus *Sapindopsis* was widely distributed in the Albian and Cenomanian of the North America (Berry, 1922; Bell, 1956; Hickey and Doyle, 1977; Upchurch et al., 1994; Huang and Dilcher, 1994), Middle Asia and Siberia (Golovneva, 2007). It was reported also from Greenland (Seward and Conway, 1935; Boyd, 1998), Europe (Sender et al., 2016), the Middle East (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000), Primorye (Krassilov, 1967; Bugdaeva et al., 2006) and China (Tao and Zhang, 1990). Occurrences in northeastern Asia are rare and insufficiently studied.

In this paper, we describe four species of *Sapindopsis* from northeastern Asia based on previous collections and new materials. These data provide new information on stratigraphic and geographical distribution of genus *Sapindopsis* and evolutionary trends of early Platanaceae during mid-Cretaceous.

## 2. Material and methods

The remains of the genus *Sapindopsis*, studied in this paper, come from five localities. One of them is located in Jilin Province, China and four are situated in Primorye and Chukotka, Russia (Fig. 1, 2).

Chinese specimens come from the upper part of the Dalazi Formation and were collected by Sun Yuewu from outcrops along the Dalazi ditch, near Zhixin village, south of the city of Yanji. The first *Sapindopsis* from this locality was recorded by Tao and Zhang (1990) under the name *Sapindopsis magnifolia* Fontaine. In this paper these fossils are described as new species *S. chinensis* sp. nov. Specimens are housed at the Institute of Botany, Academia Sinica, Beijing. The new material which provides additional data about morphology and venation details of these leaves is stored at Research Center of Palaeontology and Stratigraphy, Jilin University in Chanchun (prefix before specimen numbers JYDF).

In Primorye, *Sapindopsis* leaves were found in the Cretaceous deposits of the Alchan and Partizansk basins. In the Alchan basin, fossils, similar with *S. chinensis*, were collected by Volynets in the upper reaches of the Krutoyariha River (left tributary of the Alchan River) in site 53, in the tuffaceous sandstones of the upper part of the Alchan Formation. Specimens are kept in Vladivostok, in the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences (prefix before specimen numbers IBBS).

In the Partizansk basin, leaves of *Sapindopsis* are known from deposits of the upper part of the Frentseva Formation in two localities: 3rd Kamenka River and Andreev Inlet. *Sapindopsis* leaves in Andreev Inlet near Palets Cape (vicinity of Bolshoy Kamen town) were collected by Krassilov (1965, 1967) and described under the name *Sapindopsis cf. angusta* (Heer) Seward et Conway.

The locality in the upper reaches of 3rd Kamenka River is situated on the outskirts of Partizansk city. This locality has been known for a long time (Likht, 1961). Several fragmentary specimens, collected by Kononov in site 40, were described by Krassilov (1967) under the names *Aralia lucifera* Kryshtofovich and *Cissites* sp. Larger collections were made later by Volynets in site 325. About 30 specimens were investigated. Our examination of all angiosperm specimens from 3rd Kamenka River showed that they belong to one species, which described here as new species *Sapindopsis orientalis* sp. nov. Collections from 3rd Kamenka River are stored in Vladivostok, in the Federal Scientific Center of the East Asia Terrestrial Biodiversity (prefix IBBS).

*Sapindopsis asiatica* (G. Philippova) Golovneva et Zolina comb. nov. comes from the Krivorechenskaya Formation, which is

distributed on the right bank of the Anadyr River, North-East of Russia (Fig. 2). Formerly this species was referred to the genus *Sorbites* G. Philippova affiliated with Rosaceae (Philippova, 1978). The type material was collected by Philippova in 1975 in the Chukotskaya River basin and is deposited in the Geological Museum of the Territorial Fund of Geological Information on the Far East Federal Region in Magadan (prefix of specimen numbers TFI). Additional specimens are stored in the Northeastern Integrated Research Institute in Magadan (prefix NEISRI) and in the Magadan regional museum of local lore (prefix MRM).

All specimens are preserved as impressions and yield no structurally preserved material. We 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, sometimes underwater in order to increase contrast of leaf venation.

## 3. Geological setting and stratigraphy

The Dalazi Formation is distributed in the Yanji basin, which is located in eastern Jilin Province, northeastern China, near the China–North Korea border (Fig. 1). It was described by Kunio Uwatoko (1933) in the Dalazi town, southeast of Longjing city. The Dalazi Formation is attributed to the Yanji Group, which is divided into four formations: the Toudao, the Tongfosi, the Dalazi and the Longjing Formation (Yang, 1959; Zhou et al., 1980; Zhang, 1986; Liu and An, 1991). The Dalazi Formation rests conformably on the Tongfosi Formation and is unconformably overlain by the Longjing Formation.

The basal part of the formation is composed of white and light gray pebbled conglomerates and sandstones. The upper part of the formation consists of dark gray shales, silty shales, black oilshales with yellow sandstones and siltstone, bearing abundant fossils. The biota from the Dalazi Formation in the Yanji Basin comprises abundant terrestrial and freshwater invertebrates (bivalves, ostracods, insects, and clam shrimp), along with vertebrates (fish, lizards), and diverse plant fossils (Chang et al., 1977; Zhou et al., 1980; Tao and Zhang, 1990; Yang and Deng, 2007; Deng et al., 2012; Xu and Yang, 2019; Choi et al., 2020).

The geologic age of the Dalazi Formation has been debated for a long time. It was regarded as Aptian (Tao and Zhang, 1990), Albian (Cao, 1994) or Cenomanian (Nichols et al., 2006). The isotopic age of the upper Dalazi Formation based on (SIMS) U–Pb zircon dating, was determined at  $105.1 \pm 0.4$  Ma (Zhong et al., 2021) or  $105.7 \pm 0.8$  Ma (Shen et al., 2021). The bottom of the Dalazi Formation was estimated at  $109.9 \pm 2.9$  Ma based on the LA-ICP-MS U–Pb dating of tuffs (Li et al., 2015). Thus, terrestrial sedimentary sequence of the Dalazi Formation is of middle-late Albian age.

The Alchan basin is located in the northwest Primorye, occupying the western slope of the Sikhote-Alin ridge, in the basins of Alchan and Bikin rivers (Fig. 1). The stratigraphy of the area has been studied by Amelchenko et al. (2001) and Markevich et al. (2000). The Cretaceous deposits of the Alchan basin rest on the Paleozoic rocks and are divided into Assikaevka, Alchan, Stolbovaya, Zalomnaja and Severjanka formations in ascending order. The two lower formations are assigned to the Lower Cretaceous, and three upper formations are assigned to the Upper Cretaceous.

The Assikaevka Formation consists of marine, coastal and terrestrial terrigenous sediments and yields diverse marine mollusks and plant fossils. The age of this formation is inferred to be Aptian–middle Albian (Markevich et al., 2000). The Alchan Formation lies conformably at the Assikaevka Formation and is overlain conformably by the Stolbovaya Formation. It is 1500 m thick and comprises volcanic rocks of intermediate composition and



**Fig. 1.** Localities of *Sapindopsis* in Far East: 1 – Zhixin village, Dalazi Formation, upper Albian, *S. chinensis* Golovn., Volynets et Sun Yuewu; 2 – Andreev Inlet, Frentsevk Formation, lower Albian, *Sapindopsis* sp. 1; 3 – 3rd Kamenka River, Frentsevk Formation, lower Albian, *S. orientalis* Volynets, Golovn. et Zolina; 4 – Krutoyarikha River, Alchan Formation, upper Albian, *S. chinensis*.

volcanogenic-sedimentary deposits, including abundant plant fossils, studied by Bugdaeva et al. (2006). Overlying formations also consist of volcanogenic deposits. Marine mollusks in this formation were found only in the northeast part of the Alchan basin.



**Fig. 2.** Locality of *S. asiatica* in North-East of Russia, Chukotskaya River, Krivorechenskaya Formation, upper Albian–lower Turonian.

According to Konovalov (Markevich et al., 2000) the age of the Alchan Formation is the middle-late Albian.

The Frensevk Formation is distributed in the Partizansk coal basin, which is located in southern Primorye (Fig. 1). This formation is assigned to the coal-bearing Suchan Group, which lie on the Lower Paleozoic complex of gabbroid and granitoid rocks or on the marine and nonmarine Valanginian deposits and is conformably overlain by variegated or red-colored volcanoclastic deposits of the Korkino Group. According to Krassilov (1967) the Suchan Group consists of the Starosuchan, the Severosuchan and the Frentsevk formations. The Frentsevk Formation includes marine *Trigonia* beds, nonmarine black shales and a measure of greenish gray plant-bearing sandstones and siltstones (Golozubov, 2006). The abundant plant fossils of the Suchan Group were studied by Krassilov (1967).

The age of the lower part of the Frentsevk Formation was estimated as early-middle Albian, based on the marine mollusks and plant fossils (Markevich et al., 2000; Golovneva et al., 2018). The U–Pb age of single zircon (ID-TIMS method) from the upper part of the Frentsevk Formation is  $109 \pm 1$  Ma (Golovneva et al., 2021). Thus, early Albian age (most likely the end of the early Albian) is assigned to the Frentsevk Formation.

The Krivorechenskaya Formation is widely exposed on the right bank of the Anadyr River, North-East of Russia and was deposited in a fore-arc basin under the influence of the nearby Okhotsk-Chukotka volcanogenic belt (Herman, 2011). This formation overlies Valanginian and Hauterivian rocks with an angular discordance, is disconformably overlain by deposits of Maastrichtian to Eocene age (Devyatilova et al., 1980). The lower part of the Krivorechenskaya Formation is 400–600 m thick, and composed of conglomerates with subordinate coarse-grained sandstones. The upper part of the Krivorechenskaya Formation is 700–900 m thick, and is represented mostly nonmarine sandstones and siltstones



yielding plant fossils, and marine beds containing molluscs. These deposits reflect depositional environments of alluvial to coastal plains and adjacent shallow marine basins. Based on marine molluscs and the results of the  $^{40}\text{Ar}/^{39}\text{Ar}$  dating the age of the plant-bearing beds was determined as late Albian–early Turonian (Spicer et al., 2002; Herman, 2011).

#### 4. Systematics

Division Magnoliophyta Cronq., Takht. et W. Zimm., 1966

Class Magnoliopsida Brong., 1843

Family Platanaceae T. Lestiboudois, 1826

Genus *Sapindopsis* Fontaine, 1889

***Sapindopsis orientalis*** Volynets, Golovneva et Zolina, sp. nov.

Fig. 3, A–N; Fig. 4, A–E

*Aralia lucifera* auct. non Krysht., in Krassilov, 1967, p. 235, pl. XCII, fig. 4, text-fig. 33.

*Cissites* sp., Krassilov, 1967, p. 236, pl. XCII, fig. 3.

*Derivation of specific epithet.* – Latin, *orientalis* = eastern.

*Holotype.* Spec. IBBS 325/16a, southern Primorye, Partizansk city, 3rd Kamenka River, Frenstevka Formation, lower-middle Albian, – Fig. 3, I, Fig. 4, A.

*Diagnosis.* Leaves pinnatifid to pinnately compound, with three to five pairs of lateral leaflets, 30–90 mm long and 20–60 mm wide; three (five) apical leaflets usually united in one trilobed (five-lobed) terminal lamina; margin dentate; dentation decreasing upwards both along leaf and along leaflets; teeth in the upper and middle parts of leaves widely spaced, up to 2–3 mm high, narrow triangular with acute or rounded apex and convex apical and basal sides; sinuses between teeth narrow with rounded apices; teeth in the upper part of leaves smaller, 0.5–1 mm high, and more frequent.

*Description.* Leaves are pinnatifid to pinnately compound, with one terminal leaflet and three to five pairs of lateral leaflets, widely elliptic or ovate in outline. Leaves are medium in size, 30–90 mm long and 20–60 mm wide. Petiole is not preserved. Leaf rachis is stout, up to 1.5 mm in diameter in its lower part.

The lateral leaflets are closely spaced, especially in the upper part of lamina, opposite or subopposite, sessile, linear-lanceolate, 20–40 mm long and 6–13 mm wide, with an acute or obtuse apex and narrow wedge-shaped, asymmetrical base, decurrent on the leaf rachis. Decurrent parts of the lateral and terminal leaflets form wings along leaf rachis, which are more developed in the apical part of the leaf. Three (sometimes five) apical leaflets are usually merging in their bases, forming a trilobed (five-lobed) terminal lamina. In the lower part of the leaf, rachis has no distinct wings and lower leaflets may have short petiolules. The length of the leaflets decreases upwards.

The margin is dentate. The size of the teeth decreases upwards both along the leaf and along the leaflets. Teeth in the upper and middle parts of leaves are rather widely spaced, large, up to 2–3 mm high, asymmetric, slightly adpressed, narrow triangular with acute or, more rarely, rounded apex and convex apical and basal sides. Sinuses between teeth are narrow with rounded apices. Teeth in the upper part of leaves are smaller, 0.5–1 mm high, and more frequent, with acute apices.

The venation of the leaflets is pinnate, brochidodromous. The midvein is prominent and straight. Secondary veins are thin, subopposite, diverging at moderate acute angles, subparallel, looping near the margin. Thin, short veins, which diverge from the external side of loops, enter the teeth. Intercoastal tertiary venation is thin, irregularly reticulate.

*Material.* Collection IBBS 325, specimens 1–16; collection IBBS 40, specimens 1–3.

***Sapindopsis chinensis*** Golovneva, Volynets et Sun Yuewu, sp. nov.

Fig. 5, A–D, F, G; Fig. 6, C

*Sapindopsis magnifolia* auct. non Fontaine in Tao, Zhang, 1990, p. 225, pl. II, fig. 1, 2, text-fig. 2; Tao et al., 2000, p. 173, pl. II, fig. 1, 2. *Sapindopsis variabilis* auct. non Fontaine, in Bugdaeva et al., 2006, pl. XXV, fig. 1.

*Holotype* (designated here). Spec. K1d43-20, China, Jilin, Dalazi Formation, upper Albian; Tao, Zhang, 1990, pl. 2, fig. 1, text-fig. 2. – Fig. 6, C.

*Diagnosis.* Leaves pinnatifid to pinnately compound, with one terminal leaflet and several alternate lateral leaflets; notophyll to mesophyll; margin entire.

*Description.* Leaves are pinnatifid to pinnately compound, widely elliptic or ovate in outline, with one terminal leaflet and several alternate lateral leaflets. Leaves are small and medium in size. They are usually 40–110 mm long and 20–90 mm wide. Leaf rachis is stout, slightly zigzag, up to 1–1.5 mm in diameter in its lower part. The margin is entire.

The lateral leaflets are sessile, 5–50 mm long and 3–14 mm wide, linear-lanceolate or lanceolate, with acute or obtuse apex and narrowed, asymmetrical base, decurrent on the leaf rachis. The length of the leaflets decreases toward the leaf apex. Leaf apex is asymmetrical, consisting from two leaflets (Fig. 6, C), or terminal lamina consists of three nearly symmetrical, basally confluent lobes (Fig. 5, C). Sometimes several short apical lateral leaflets are confluent basally (Fig. 5, F).

The leaflet bases in the middle and lower parts of the leaf are strongly asymmetric (Fig. 5, D, G), with acroscopic side narrowing abruptly toward base of the lobe and decurrent basiscopic side forming wide wings. Wings along leaf rachis are more developed in the apical part of the leaf, where they are comparable in width to the leaflets. In the lower part of the leaf wings are narrower and shorter. Leaf base is symmetrical (Fig. 5, D).

The venation of the leaflets is pinnate, brochidodromous. The midvein is prominent, straight. Secondary veins are very thin, irregular, diverging at acute angles, subparallel, looping near the margin. Intersecondary veins are poorly distinguishable from secondary veins, very thin, irregular, forming longitudinally elongated meshes.

*Material.* Institute of Botany, Academia Sinica, specimens K1d43-20 and K1d43-032; Research Center of Palaeontology and Stratigraphy, Jilin University, specimens JYDF008, JYDF015a, b, c, JYDF018, JYDF03-78; Federal Scientific Center of the East Asia Terrestrial Biodiversity, specimens IBBS 53-124a, IBBS 53-201, IBBS 53-220.

***Sapindopsis asiatica*** (G. Philippova) Golovneva et Zolina, comb. nov.

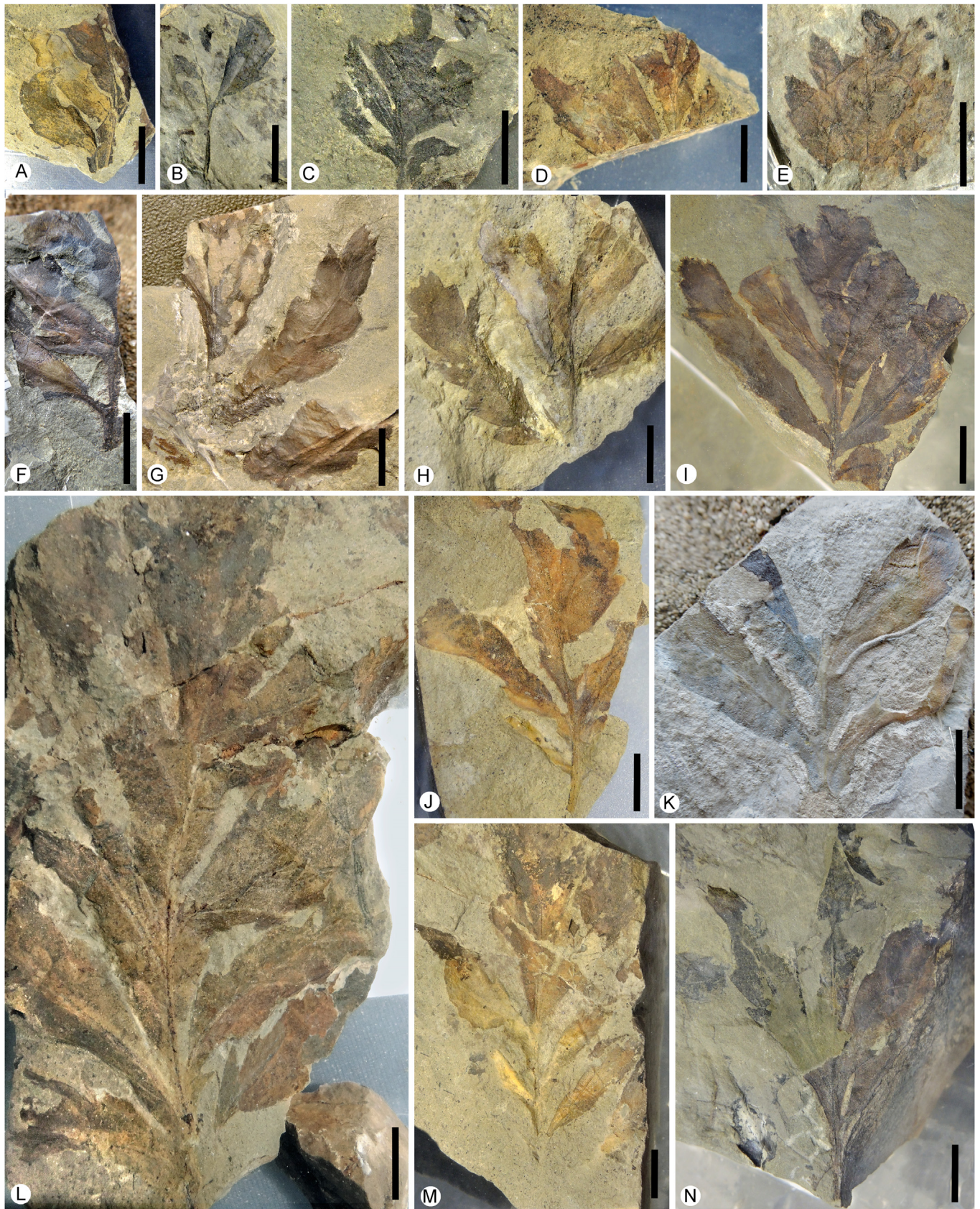
Fig. 6, A, B; Fig. 7, A–G

*Sorbites asiatica* G. Philippova, 1978, Novye melovye pokrytosemennyye is basseina r. Anadyr [New Cretaceous angiosperms from the Anadyr River basin], Paleontologicheskii zhurnal, 1978(1), p. 142, pl. X, fig. 3, 4. – Philippova, Abramova, 1993, p. 144, pl. XXXV, fig. 3, 4, pl. XXXVII, fig. 3.

*Holotype.* Spec. TFI 622/7, North-East of Russia, Anadyr River basin, Chukotskaya River, Krivorechenskaya Formation, upper Albian–lower Turonian; Philippova, 1978, pl. X, fig. 4.

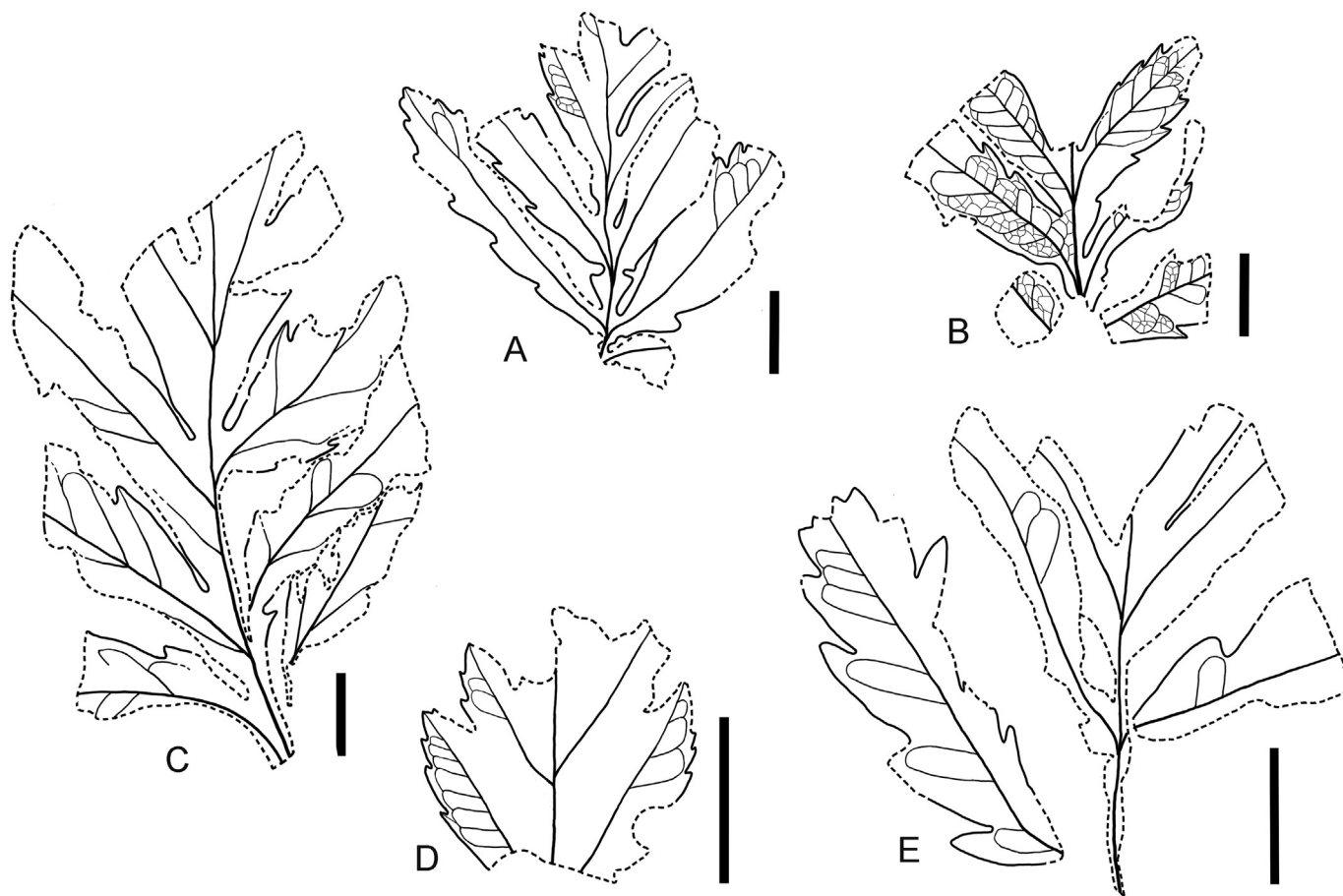
*Diagnosis emended.* Leaves pinnatifid to pinnately compound, large, with four pairs of subopposite linear-lanceolate or oblong lateral leaflets; margin dentate; teeth small, triangular, unequal in size, sometimes double, with acute apices, convex basiscopic side and straight or concave acroscopic side; secondary veins of leaflets well developed, diverging from the midvein at slightly different angles,





**Fig. 3.** *Sapindopsis orientalis* Volynets, Golovn. et Zolina, sp. nov., Frentsevka Formation, lower Albian: A – spec. IBBS 325/6; B – spec. IBBS 325/10; C – spec. IBBS 325/7; D – spec. IBBS 325/5a; E – spec. IBBS 40/1; F – spec. IBBS 325/3; G – spec. IBBS 40/2; H – spec. IBBS 325/8; I – spec. IBBS 325/16a; J – spec. IBBS 325/9; K – spec. IBBS 325/4; L – spec. IBBS 325/14; M – spec. IBBS 325/13; N – spec. IBBS 325/10. Scale bar 1 cm.





**Fig. 4.** *Sapindopsis orientalis* Volynets, Golovneva et Zolina, sp. nov., Frentsevka Formation, lower Albian: A – spec. IBBS 325/16a; B – spec. IBBS 325/4; C – spec. IBBS 325/14; D – spec. IBBS 40/1; E – spec. IBBS 325/8. Scale bar 1 cm.

often dichotomous in the upper third; intersecondary veins well developed.

**Description.** Leaves are pinnatifid to pinnately compound, oblong or obovate in outline, large, up to 20 cm in length and 18 cm in width, with one terminal leaflet and four pairs of lateral leaflets. The largest width is in the upper third of the lamina. Leaflets are opposite or subopposite, linear-lanceolate or oblong, with acute apex, up to 8.5 cm long and 2.1 cm wide. The degree of decurrence of leaflet base onto the rachis decreases downwards.

In the lower part of the leaf, the leaflets are sessile or petiolate with a rounded or wide-wedge-shaped base. In the upper part of the leaf, the leaflets are sessile, with base, decurrent to the rachis from their basiscopic and acroscopic sides, forming wings. The sinuses between the leaflets are widened at the bottom, rounded. The upper three leaflets usually merge at their bases, forming one trilobed terminal lamina. Sometimes it can be significantly asymmetrical if the lateral lobes extend from the rachis at different heights. The upper leaflets depart from the rachis at an acute angle, the middle and lower leaflets depart at an angle close to the right. Sometimes the lower pair of leaflets can deviate downward.

The margin is dentate, near the sinuses entire. The teeth are small (1–2.5 mm in height), triangular, unequal in size, sometimes double, with acute apices, convex basiscopic side and straight or concave acroscopic side.

The venation of the leaflets is pinnate, brochidodromous. The midvein is prominent, straight. Secondary veins are well developed, subopposite or alternate, numerous (up to 18 pairs), slightly curved, diverging from the midvein at slightly different angles, often dichotomous in the upper third, looping near the margin.

Intersecondary veins are well developed. Tertiary venation is thin, irregularly reticulate. The teeth include small veins extending from the outside of the loops.

**Material.** Collection NEISRI, specimen 176-1. Collection MRM, specimens 176-2–176-5. Collection TFI 622, specimens 1, 2, 7.

### *Sapindopsis* sp. 1

Fig. 5, E

*Sapindopsis* cf. *angusta* (Heer) Seward et V.M. Conway, in Krassilov, 1967, p. 235, pl. XCII, fig. 12, text-fig. 33.

**Description.** The specimen of *Sapindopsis* cf. *angusta* represents the lower part of a compound leaf of middle sizes with bases three linear-lanceolate opposite entire-margined leaflets. Upper part of leaflets have not preserved.

The venation of the leaflets is pinnate, brochidodromous. The midvein is prominent, straight. Secondary veins are well developed, slightly curved, diverging from the midvein at different angles, sometimes dichotomous. Intersecondary veins are well developed. Tertiary veins are not visible.

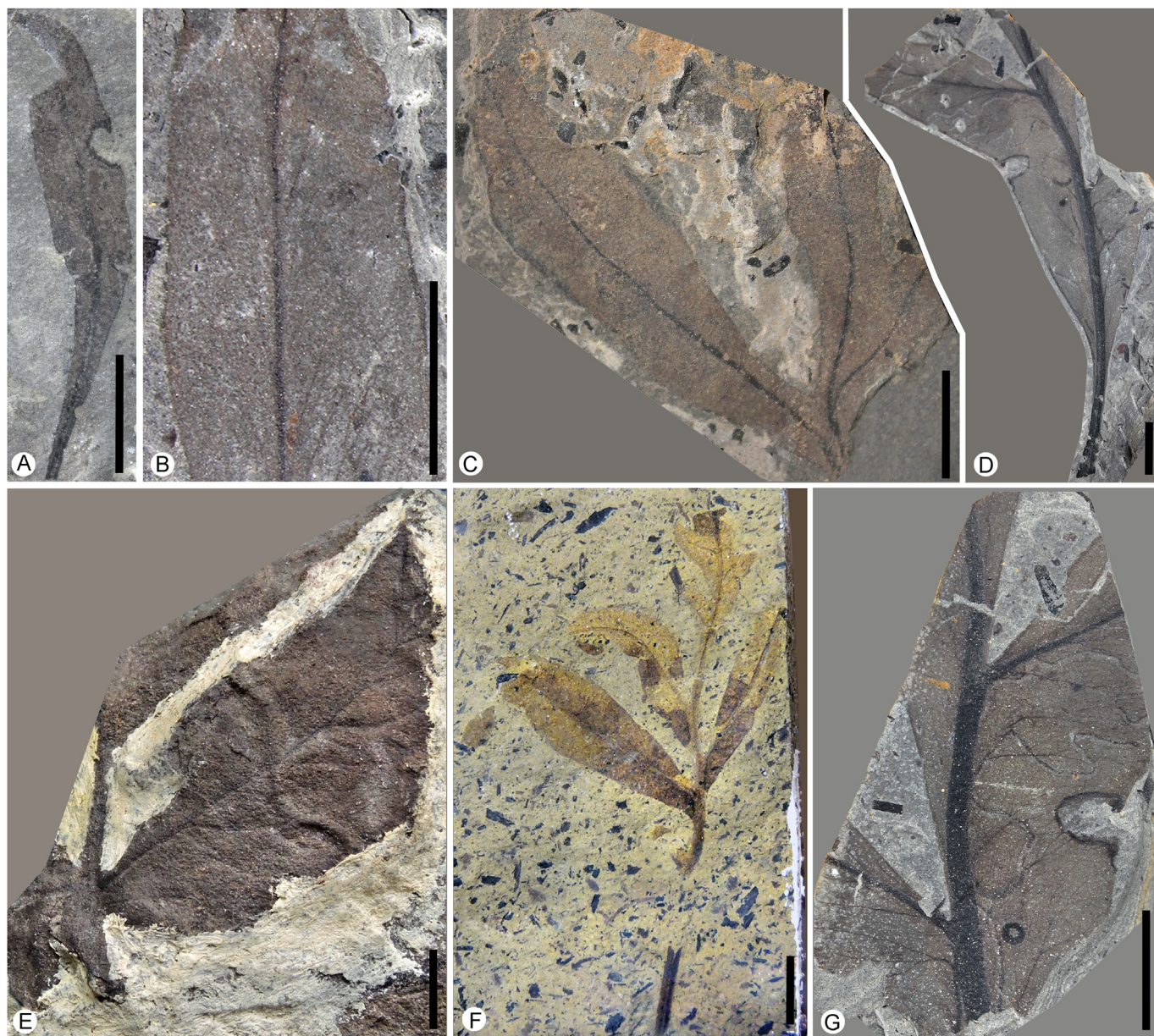
**Material.** Collection IBBS 28, specimens 104.

## 5. Discussion

### 5.1. Comparison with other species

To date, more than 20 species of the genus *Sapindopsis* are known. Several of them have a dentate margin: *S. belviderensis*





**Fig. 5.** A–D, F, G – *Sapindopsis chinensis* Golovn., Volynets et Sun Yuewu, sp. nov., from Dalazi Formation, upper Albian (A–D, G) and Alchan Formation, upper Albian (F): A – spec. JYDF008; B – spec. JYDF015C; C – spec. JYDF03-78; D – spec. JYDF015A; F – spec. IBBS 53-124a; G – spec. JYDF015B. E – *Sapindopsis* sp. 1, Frentsevka Formation, lower Albian, spec. IBBS 28/104. Scale bar 1 cm.

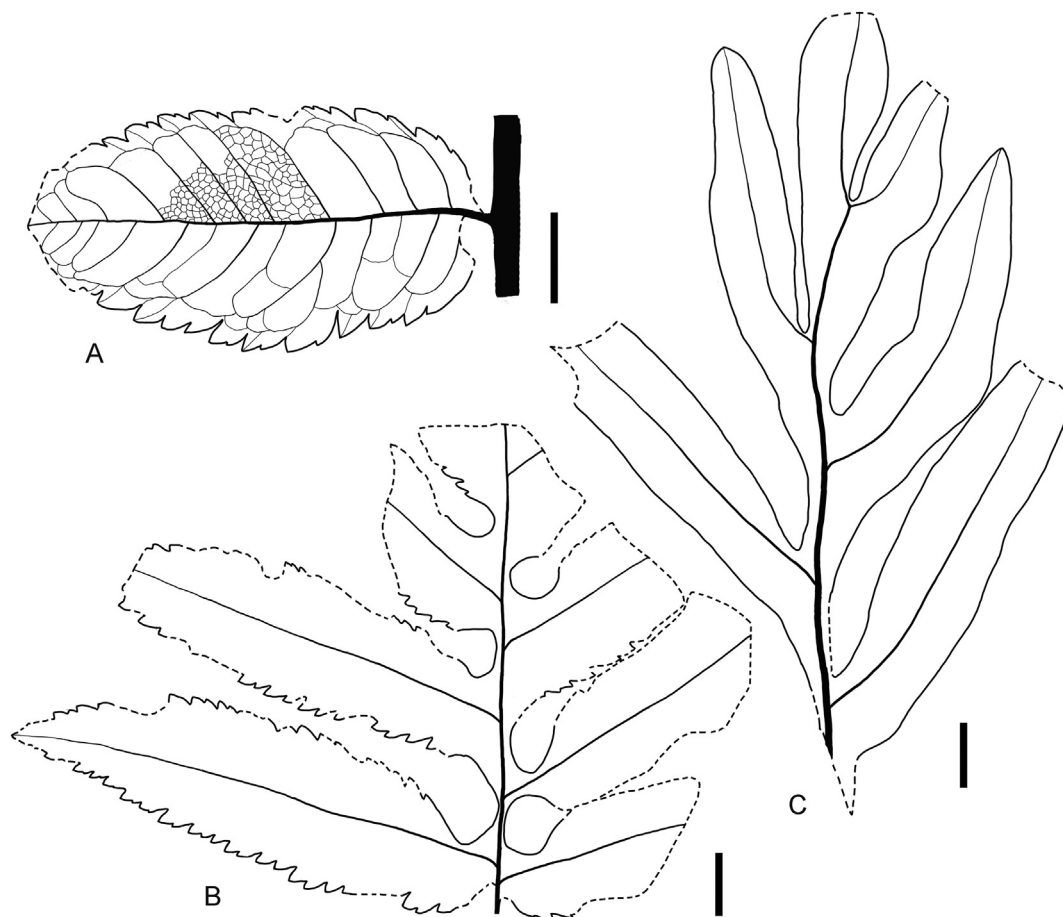
Berry from the upper Albian Cheyenne Sandstone of Kansas, USA (Berry, 1922); *S. minutifolia* Upchurch, Crane et Drinnan from the upper Albian Quantico locality, Potomac Group, USA (Upchurch et al., 1994); *S. neuburgae* (Vachrameev) Golovneva from the Cenomanian Upper Altykuduk subformation, western Kazakhstan, *S. janschinii* (Vachrameev) Golovneva from the upper Albian Lower Altykuduk subformation, western Kazakhstan and the Cenomanian Simonovo Formation, Western Siberia, *S. kryshstofvichii* (I. Lebedev) Golovneva from the Cenomanian Simonovo Formation, Western Siberia (Golovneva, 2007).

The new species *Sapindopsis orientalis* (3–9 cm long and 2–6 cm wide) is significantly smaller than *S. belviderensis* (8–19 cm long and 4.5–14 cm wide), *S. neuburgae* (20–30 cm long and 10–15 cm wide), *S. janschinii* (up to 25 cm long and 14 cm wide) and *S. kryshstofvichii* (15–35 cm long) and larger than *S. minutifolia* (2.8 cm long and 2.5 cm wide).

*Sapindopsis belviderensis* and *S. minutifolia* have only three pairs of lateral leaflets and they increase in size towards the apex, while *S. orientalis* has three to five pairs of leaflets, which increase towards the base. Leaflets in *S. belviderensis* are narrowly spatulate to broadly ovate or obovate with obtuse apex, and they are linear-lanceolate in *S. orientalis*. *Sapindopsis janschinii* and *S. kryshstofvichii* also differ from *S. orientalis* in leaflets shape. The leaflets in *S. janschinii* are widely lanceolate or ovate, and in *S. kryshstofvichii* range from narrowly lanceolate, nearly linear, to widely lanceolate with a shortly acuminate apex. *S. neuburgae* has several pairs or linear-lanceolate leaflets as *S. orientalis*, but its leaflets are practically not decurrent to the rachis. Besides that, the teeth of *S. orientalis* are more prominent and less regular while the teeth of *S. neuburgae* are small, serrate and frequent.

Krassilov (1967) has described two leaves from 3rd Kamenka River under the names *Aralia lucifera* and *Cissites* sp. Reexamination





**Fig. 6.** A, B — *Sapindopsis asiatica* (G. Philippova) Golovn. et Zolina, comb. nov., Krivorechenskaya Formation, upper Albian–lower Turonian: A — spec. TFI 622/2; B — spec. TFI 622/7; holotype. C — *Sapindopsis chinensis* Golovn., Volynets et Sun Yuewu, Dalazi Formation, lower Albian, spec. K1d43-20, holotype (after Tao, Zhang, 1990, pl. 2, fig. 1). Scale bar 1 cm.

of these specimens (Fig. 3 E, G) showed that they both belong to *S. orientalis*.

The main distinguishing feature of *S. chinensis* is the alternate arrangement of the leaflets. Most other species are usually characterized by an opposite or subopposite leaflet arrangement, although some species may have alternate leaflets in the upper part of the leaf. In *S. anhouryi*, *S. lebanensis* and *S. powelliana* leaflets may be either alternate or opposite. Another characteristic feature of *S. chinensis* is the wide wings along the rachis. Similar wide wings are observed in *S. turolensis* Sender, J.A. Doyle, Villanueva-Amadoz, Pons, Diez et Ferrer from the late Albian of Spain (Sender et al., 2016).

*Sapindopsis asiatica* is similar to other species with large leaves and dentate margin: *S. belviderensis*, *S. kryshfovichii*, and *S. janschinii*, from which it differs in the number of lateral leaflets, in the shape of the leaflets and in the shape of the teeth. *Sapindopsis belviderensis* has three pairs of lateral leaflets, while *S. asiatica* has four pairs. The leaflets in *S. janschinii* are widely lanceolate or ovate, in *S. kryshfovichii* range from narrowly lanceolate, nearly linear, to widely lanceolate with a shortly acuminate apex, and in *S. asiatica* they are linear-lanceolate or oblong. The teeth in *S. janschinii* are large, 2.0–3.5 mm high, with acute or obtuse apices and rounded sinuses, in *S. kryshfovichii* they are small (up to 1–2 mm high), adpressed, with an acute apex, while in *S. asiatica* teeth are triangular, unequal in size, sometimes double.

Leaves of *Sapindopsis* sp. 1 from the Frentsevka Formation differ from *S. orientalis* by entire margin and from *S. chinensis* by opposite leaflet arrangement. In size and morphology, this leaf has

significant similarity to leaves of *S. magnifolia* Fontaine from the Potomac Group, USA. Insufficient preservation of a single specimen does not allow for a more detailed comparison. This is most likely a new species.

## 5.2. Geographical and stratigraphic distribution

*Sapindopsis* is among the most ancient members of the Platanaceae. The earliest occurrences are two species from the Frentsevka Formation, Primorye, Russia: *Sapindopsis orientalis* and *Sapindopsis* sp. 1 (Table 1, Fig. 8). U–Pb zircon geochronology constrains the depositional age of the upper part of this formation to be  $109 \pm 1$  Ma (Golovneva et al., 2021), which corresponds to the late early Albian according to Geologic Time Scale 2020 (Gradstein et al., 2020). Isotopic data generally confirmed previous age estimates (early-middle Albian) based on paleobotanical, palynological and mollusk data (Golovneva et al., 2018).

In North America, *Sapindopsis magnifolia* appears in the deposits of lower Subzone II-B (the Patapsco Formation, the Potomac group), which are considered to be the middle Albian in age (Doyle and Upchurch, 2014). However, there was a significant hiatus between Zones I and II (Hochuli et al., 2006) and possibly, that Potomac Group *Sapindopsis* could have arisen at an earlier time, like *S. orientalis* and *Sapindopsis* sp. 1 in Primorye. The second middle-late Albian species (*S. turolensis*) was recorded in the upper member of the Escucha Formation, Spain (Sender et al., 2016). Thus, already at the beginning of its appearance in the geological record, *Sapindopsis* was widely distributed in the territory of the





**Fig. 7.** *Sapindopsis asiatica* (G. Philippova) Golovna. et Zolina, comb. nov., Krivorechenskaya Formation, upper Albian–lower Turonian: A, F – spec. TFI 622/2, margin details and lower part of the leaf; B – spec. MRM 176/2; C – spec. MRM 176/3; D – spec. MRM 176/4; E – spec. MRM 176/5; G – spec. NEISRI 176-1. Scale bar 1 cm.



**Table 1**  
Occurrences of *Sapindopsis* in the Cretaceous of Northern Hemisphere.

Age		North America	Greenland	Europe Middle East	Western Siberia, Middle Asia	North-East of Russia Primorye, northeastern China
Cenomanian			<i>S. angusta</i>	<i>S. anhouryi</i> <i>S. lebanensis</i> <i>S. cf. heterophylla</i> <i>Sapindopsis</i> sp. 2	<i>S. kryshstofovichii</i> <i>S. neuburgae</i> <i>S. janshinii</i>	<i>S. asiatica</i>
Albian	Late	<i>S. powelliana</i> <i>S. retallackii</i> <i>S. belviderensis</i> <i>S. minutifolia</i> <i>S. magnifolia</i> <i>Sapindopsis</i> sp. A <i>Sapindopsis</i> sp. B	<i>S. ravnkloeftensis</i>			<i>S. chinensis</i>
	Middle Early	<i>S. magnifolia</i>		<i>S. turolensis</i>		<i>S. orientalis</i> <i>Sapindopsis</i> sp. 1

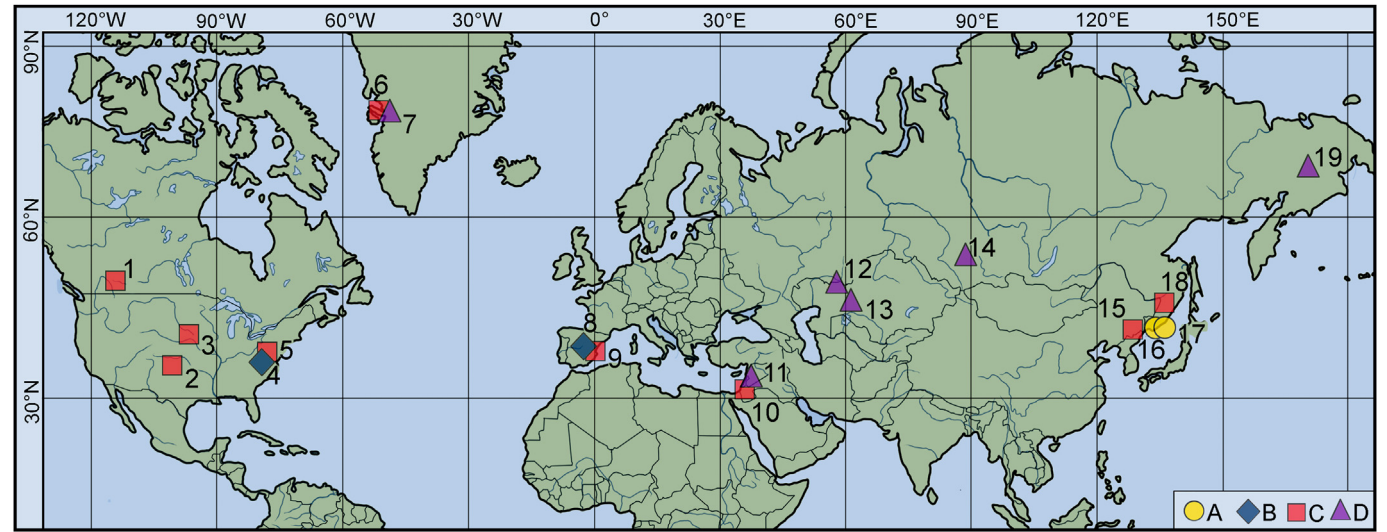
Siberian–Canadian and Euro-Sinian paleofloristic regions (Vakhrameev, 1988; Golovneva, 2007, 2014). Its range covered North America, Europe and northeastern Asia. Such wide distribution suggests a rather long preliminary history of this taxon and Platanaceae family in general. This assumption is confirmed by the finds of a dispersed cuticle of Platanaceae in the upper Aptian Lipovtsy Formation in Primorye (Volynets et al., 2016; Volynets and Bugdaeva, 2017; Golovneva et al., 2021)

Species diversity of the genus *Sapindopsis* increases considerably in the late Albian, especially in North America (Table 1). *Sapindopsis magnifolia* occurs in the late Albian upper Subzone II-B of the Potomac group and in the early late Albian Cheyenne Sandstone of Kansas (Berry, 1922; Doyle and Upchurch, 2014). Several other species were recorded additionally to *S. magnifolia*. They are *S. minutifolia* from the Potomac Group (Upchurch et al., 1994), *S. belviderensis*, *Sapindopsis* sp. A and *Sapindopsis* sp. B from the Cheyenne Sandstone (Berry, 1922; Huang and Dilcher, 1994), and *S. powelliana* (Lesquereux) H. Wang et Dilcher and *S. retallackii* H. Wang et Dilcher from the lower part of the Dakota

Formation. Of these leaves, *Sapindopsis* sp. B is very similar to the trifoliate leaf of *S. powelliana* and, perhaps, conspecific with it.

In Canada, leaf fragments of *Sapindopsis*, named *S. angusta* (Heer) Seward et V.M. Conway, were found in the Lower Blairmore floristic assemblage (the middle Albian (?) of the Beaver Formation and Geits beds of the Commotion Formation). These leaves become more common in the Upper Blairmore floristic assemblage, in the upper Albian Mill Creek Formation and Boulder Creek beds of the Commotion Formation (Bell, 1956). Since the leaf fragments are small, their true species identity cannot be established. Their assignment to the Cenomanian *S. angusta* from Greenland is unlikely.

In West Greenland *S. ravnkloeftensis* Boyd appears in the upper Albian Ravn Kløft locality of the Come Formation (Boyd, 1998). In Spain, *Sapindopsis* sp. B was found in the latest Albian Boundary Marls Unit of Teruel Province (Sender et al., 2016). In Israel, leaves of *Sapindopsis* were described under the name *S. cf. heterophylla* Fontaine from the middle-upper Albian Upper Hatira Formation, distributed in the northern Negev, Makhtesh Qatan (Krassilov and Schrank, 2011). However, Fontaine did not describe such a species



**Fig. 8.** Distribution of *Sapindopsis* in the Northern Hemisphere: A – lower Albian; B – middle Albian; C – upper Albian; D – Cenomanian. Localities: 1 – Mill Creek Formation, upper Albian; 2 – Cheyenne Formation, upper Albian (Berry, 1922; Huang and Dilcher, 1994); 3 – Hoisington III, Dakota Formation, upper Albian (Wang and Dilcher, 2018); 4 – Quantico locality, Potomac Group, upper Albian (Upchurch et al., 1994); 5 – Patapsco Formation, middle-upper Albian (Doyle and Upchurch, 2014); 6 – Come Formation, upper Albian (Boyd, 1998); 7 – Atane Formation, Cenomanian (Boyd, 1998); 8 – Escucha Formation, middle Albian (Sender et al., 2016); 9 – Boundary Marls Unit, upper Albian (Sender et al., 2016); 10 – Upper Hatira Formation, middle-upper Albian (Krassilov and Schrank, 2011); 11 – Sannine Formation, Cenomanian (Krassilov and Bacchia, 2000); 12, 13 – Altykuduk Formation, upper Albian–Cenomanian (Golovneva, 2007); 14 – Simonovo Formation, Cenomanian (Golovneva, 2007); 15 – Dalazi Formation, upper Albian (present paper); 16, 17 – Frensevkka Formation, lower Albian (present paper); 18 – Alchan Formation, upper Albian (present paper); 19 – Krivorechenskaya Formation, upper Albian–lower Turonian (present paper).



from the Potomac Group. And finally, *S. chinensis*, described in this paper, was recorded in the upper Albian deposits of the Dalazi Formation (Jilin, China) and in the Alchan Formation (Primorye, Russia).

In the Cenomanian of North America, the genus *Sapindopsis* disappear. New late Albian–Cenomanian species appear in West Greenland, Middle East, Middle Asia and the North-East of Russia. *Sapindopsis angusta* was found in the Cenomanian Atane Formation, Atanikerdruk, West Greenland (Seward and Conway, 1935; Boyd, 1998). Both Middle Eastern species, *Sapindopsis anhouryi* Dilcher et Basson and *S. lebanensis* Krassilov et Maslova, come from the same locality Nammoura, the Sannine Formation, Lebanon (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000). These Lebanese species are characterized by similar narrow, coriaceous xeromorphic leaf blades, and, probably, are conspecific. Three species have been recognized from Middle Asia and Western Siberia (Golovneva, 2007). *Sapindopsis janschinii* comes from the lower part of the Altykuduk Formation (upper Albian) in Kazakhstan and *S. neuburgae* comes from the upper (Cenomanian) part of this formation. The first species was also found in the Cenomanian Simonovo Formation, Western Siberia. The third species, *S. kryshstofovichii* is common in the upper Albian Kiya Formation and also in the overlying Cenomanian Simonovo Formation, Western Siberia. In the North-East of Russia, *S. asiatica* was found in the Anadyr River basin, in the deposits of the Krivorechenskaya Formation, which was deposited from upper Albian up to lower Turonian (Spicer et al., 2002). Unfortunately, the exact age of the locality at the Chukotskaya River is unknown. Until late Albian–Cenomanian, the genus *Sapindopsis* was not recorded in Middle Asia and North-East of Russia.

Thus, the genus *Sapindopsis* is known from the early Albian up to the Cenomanian (or possibly up to early Turonian). It appears at the end of the early Albian in Far East, from where two species are known. In the middle Albian, the range of the genus expands and covers the North of America and Europe. In the late Albian, the diversity is the greatest and the range of the genus is the largest. Fourteen species have been described at this time and *Sapindopsis* is very common in North America and is among dominants of the late Albian floras of the Potomac Group, lower part of the Dakota Formation and Cheyenne Sandstone. In addition to North America and Europe, the genus appears in Greenland, Middle East, Western Siberia, and Middle Asia. In the Cenomanian, the number of species is reduced to seven; the genus disappears in North America and Europe. Most species are known from Middle Asia and Western Siberia.

All species of the genus had narrow geographical and stratigraphic distribution and are known from one or two localities. Only *S. magnifolia* s.l. was recorded from several localities.

The predominant number of species was distributed in the middle latitudes of the North Hemisphere (Fig. 8). The northernmost locality is the Chukotskaya River in the Anadyr River basin, Chukotka, Russia. In the Cenomanian, it was located at 74°N (Torsvik et al., 2012). The southernmost localities are situated in Lebanon (paleolatitude 11°N) and Israel (paleolatitude 8°N).

Most *Sapindopsis* species have mesomorphic appearance and occur in channel-margin deposits (Doyle and Hickey 1976; Hickey and Doyle 1977). Probably they were a part of the riparian plant communities. Only leaves of the equatorial species (*S. anhouryi* and *S. lebanensis*) have a more xeromorphic character (Dilcher and Basson, 1990).

### 5.3. Evolutionary trends in morphology of the genus *Sapindopsis*

Comparison of different species of *Sapindopsis* demonstrates great diversity in margin structure, secondary and tertiary venation

of leaflets, size and dissecting of leaf blade, number, shape and arrangement of leaflets, winging of the rachis and petiolule development (Fig. 9).

The size of leaf blade varies considerably from 2.8 cm in *Sapindopsis minutifolia* up to 35 cm in *S. kryshstofovichii*. The Cenomanian species are usually larger than early and middle Albian ones, but this trend is not an absolute rule. The late Albian species are characterized by very different sizes.

*Sapindopsis* includes pinnately divided leaves that range from deeply pinnatifid, with lobes connected by a decurrent wing of laminar tissue, to pinnately compound, with sessile or petiolate leaflets. The dissecting of leaf blade significantly varies both within and between species, and even inside the leaf blade. It depends on winging of the rachis and petiolule development. Usually leaflets in the upper part of the leaf lamina are decurrent on the rachis and extending downward to the point of insertion of the next lower pair. Sometimes the three upper leaflets may be fused to form a three-lobed terminal leaflet. Leaflets in the lower part of the leaf are usually more independent, attached to the rachis by distinct petiolules or sessile.

Doyle and Hickey (1976) proposed that compound leaves arose from pinnatifid ones. This idea was based on the study of the leaves in stratigraphic succession in the Potomac Group. Pinnatifid leaves occur mostly in lower Subzone II-B locality near Brooke, Virginia, while truly compound leaves dominate at upper Subzone II-B localities, such as West Brothers and Red Point in Maryland. Berry (1911) described both these leaf types as *S. magnifolia*, but some authors believe that leaves upper Subzone II-B represent a distinct unnamed species.

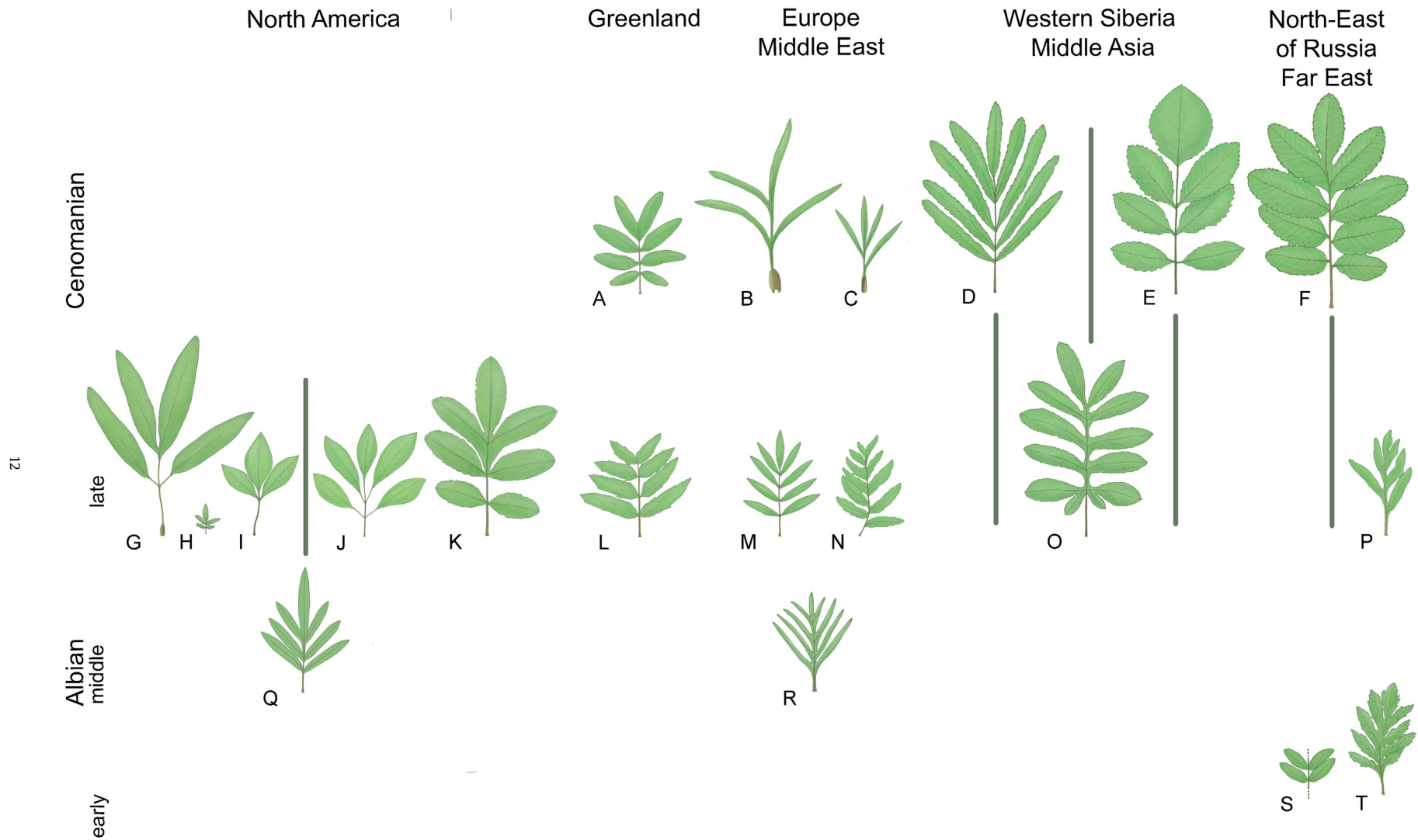
If we consider all species of *Sapindopsis*, then the tendency to more dissected leaves is also not an absolute rule. The early Albian *S. orientalis* has fused terminal leaflets and decurrent lamina tissue on the rachis, but early Albian *Sapindopsis* sp. 1 has compound leaves. Late species (late Albian–Cenomanian) also show significant diversity in this character. Leaflets of *S. janshinii* have short petiolules, leaves of *S. neuburgae* has sessile leaflets and lack any decurrent lamina tissue on the rachis, leaves of *S. kryshstofovichii* have decurrent leaflets that are basally connected by a wide wing of laminar tissue along the whole rachis. The late Albian *S. powelliana* has the longest petiolules up to 3.5 cm long.

Leaflets are linear-lanceolate or oblong in most species, but sometimes they are broadly lanceolate, broadly ovate or obovate. The apical leaflet and some upper lateral leaflets may be bilobed in some species (often in *Sapindopsis magnifolia* and *S. powelliana*). In *S. kryshstofovichii* the lower leaflets often bear additional long lobes on the basiscopic side. In many species three (rarely five) upper leaflets may be fused in their bases to form a three(five)-lobed terminal leaflet.

Margin of leaflets is entire or toothed. Of the 21 species, seven have a toothed margin. This feature occurs both in early (*Sapindopsis orientalis*) and late species (*S. asiatica*, *S. neuburgae*, *S. janschinii*). There is great variation in the amount and degree to which the teeth are developed. In *S. kryshstofovichii* the margin may be either entire or dentate. In *S. ravnkloeftensis* the margin is only occasionally toothed with widely and irregularly spaced teeth.

Leaves of most *Sapindopsis* species are imparipinnate. Only *S. powelliana* and both Greenland species (*S. angusta* and *S. ravnkloeftensis*) may have paripinnate leaves. Leaflets arrangement in *Sapindopsis* is usually opposite or subopposite. However, leaflets arrangement in *S. chinensis* is alternate. In *S. anhouryi*, *S. lebanensis* and *S. powelliana* leaflets may be either alternate or opposite.

The number of leaflets varies from three up to nine. Three leaflets were recorded in *Sapindopsis* sp. A and some specimens *S. powelliana* from the late Albian of North America. The leaflets of



**Fig. 9.** Morphological diversity of *Sapindopsis* leaves: A – *S. angusta* (Boyd, 1998); B – *S. anhouryi* (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000); C – *S. lebanensis* (Krassilov and Bacchia, 2000); D – *S. neuburgae* (Golovneva, 2007); E – *S. janshinii* (Golovneva, 2007); F – *S. asiatica* (present paper); G – *S. powelliana* (Wang and Dilcher, 2018); H – *S. minutifolia* (Upchurch et al., 1994); I – *Sapindopsis* sp. A (Berry, 1922; Huang and Dilcher, 1994); J – *Sapindopsis* sp. B (Berry, 1922; Huang and Dilcher, 1994); K – *S. belviderensis* (Berry, 1922); L – *S. ravnkloeftensis* (Boyd, 1998); M – *Sapindopsis* sp. 2 (Sender et al., 2016); N – *S. cf. heterophylla* (Krassilov and Schrank, 2011); O – *S. kryshfovichii* (Golovneva, 2007); P – *S. chinensis* (present paper); Q – *S. magnifolia* (Upchurch, 1984; Crane et al., 1993); R – *S. turoensis* (Sender et al., 2016); S – *Sapindopsis* sp. 1 (present paper); T – *S. orientalis* (present paper).

these species have long petiolules and mesomorphic appearance. Lebanese species *S. anhouryi* and *S. lebanensis* also have a small number of narrow coriaceous decurrent leaflets (3–4), which is probably related to xeromorphism. Most species from eastern Asia and Middle Asia have nine leaflets, while most American species have seven.

The study of the leaf succession in the Potomac Group shows that middle Albian specimens of *S. magnifolia* have less-organized venation, then late Albian ones (Doyle and Hickey, 1976). This tendency expresses in poor differentiation between secondary and intersecondary veins and between the tertiary and higher vein orders. A similar trend is observed in the venation analysis of other species. Probably the most primitive venation can be seen in late Albian *S. chinensis* (Fig. 5, A–D, F, G). In this species secondary veins are weak, numerous, irregularly and closely spaced. Tertiaries connect secondaries, commonly running parallel to them. Tertiary and higher order veins are practically indistinguishable. The most advanced venation can be seen in *S. powelliana*. Secondary and intersecondary veins are well differentiated. Tertiary veins are predominately percurrent. Quaternary veins are orthogonal, forming quadrangular or pentagonal imperfect areoles; veinlets simple, curved or straight (Wang and Dilcher, 2018).

In the Late Cretaceous *Sapindopsis* was apparently replaced by simple-leaved platanoids. Pinnately compound platanaceous leaves reappear only in the end of the Cretaceous and are represented by the genera *Platanites* Forbes and *Erlingdorfia* Johnson. *Platanites* is characterized by a large trilobate terminal leaflet and two smaller entire asymmetrical lateral leaflets (Forbes, 1851; Crane et al., 1988). The earliest members of the genus (*Platanites marginata* (Lesq.) Johnson) appeared in the Maastrichtian (Johnson, 1996). However, in general, this genus is more typical for the Paleogene (Crane et al., 1988; McIver and Basinger, 1993; Manchester, 2014). *Erlingdorfia* is characterized by a trilobate terminal leaflet and two bilobate lateral leaflets and is known only from the Maastrichtian of North America (Johnson, 1996). It is supposed that the pinnately compound leaf in these genera is a reversion to the primitive state, characteristic of *Sapindopsis*, and not a result of specialization (Crane et al., 1988).

## 6. Conclusion

The genus *Sapindopsis* is recorded from the lower Albian up to the Cenomanian (or possibly lower Turonian). It appears in the lower Albian in the territory of Far East of Russia. Newly described species from the Frentzevka Formation (*S. orientalis* and *Sapindopsis* sp. 1) are the lowermost (lower Albian) occurrences of the genus *Sapindopsis*. In the middle Albian, the range of the genus expands and covers the North of America and Europe. The diversity of *Sapindopsis* is the greatest in the late Albian (14 species). In addition to North America and Europe, the genus appears in Greenland, Middle East, Western Siberia, and Middle Asia and North-East of Russia. *S. asiatica* is the northernmost species of the genus (paleolatitude 74°N). In the Cenomanian, the number of species is reduced to seven and *Sapindopsis* disappears in North America and Europe.

The genus *Sapindopsis* is characterized by rapid adaptive radiation and a large number of short-lived, endemic species. This diversity was formed due to changes of the following features: size of leaf blade, number and shape of leaflets, dissecting the leaf blade, petiolules development, leaflets arrangement, margin structure, winging of the rachis, structure of the secondary and tertiary venation. Main trends in the morphological evolution of the genus include an increase of leaf dissection, an increase in size, and differentiation of leaf venation.

## Data availability

Data will be made available on request.

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