

The Renardodden flora of Spitsbergen

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Abstract

The Renardodden flora combines fossil plants from the Skilvika and Renardodden formations of the Renardodden and Scottbreen areas south of Bellsund, the Sesshøgda Formation (Prins Karls Forland) and the Sarstangen conglomerate (Sarsbukta area). We considered them as representing a single fossil flora, because floristic assemblages from these four stratigraphic units contain a large number of common species. The Renardodden flora includes approximately 30 species of conifers and angiosperms. Angiosperms predominate and are represented by the families Platanaceae, Cercidiphyllaceae, Trochodendraceae, Hamamelidaceae, Betulaceae, Cornaceae, Tiliaceae, Aceraceae, and several taxa of an uncertain taxonomic position. Monocots are represented by two aquatic plants: *Haemanthophyllum nordenskioldii* and *Acorus spitsbergensis*. A new combination *Zizyphoides retusa* (Heer) Golovn. et Zolina, comb. nov. is proposed. The Renardodden flora is characterized by a high endemism and has no distinct floristic connections with other arctic and boreal floras. The age of the Renardodden flora is estimated as the late Eocene.

Keywords: paleoclimate, plant fossils, Eocene, the Renardodden flora, Spitsbergen

Introduction

The early Paleogene is characterized by a globally warm and humid climate (Corfield, 1994; Zachos et al., 2001; Zachos, Dickens, and Zeebe, 2008; Willard et al., 2019; Westerhold et al., 2020). Data based on oxygen isotope records derived from marine foraminifera showed that the most pronounced warming trend occurred from the mid-Paleocene to early Eocene, and peaked with the early Eocene Climatic Optimum at 52 to 50 Ma.

Quantitative estimates of the early Paleogene terrestrial climate have been obtained mostly from the midlatitude North American floras (Hickey, 1980; Wilf, 2000; Peppe, 2010). Data about the early Paleogene climate from the high latitudes are more scarce (Budantsev and Golovneva, 2009; Moiseeva, Herman, and Spicer, 2009; West, Greenwood, and Basinger, 2015, 2019).

The sequence of the early Paleogene floras of Spitsbergen is an excellent object for studying the ancient climates of the Arctic, since the fossil plants are among the best proxies for terrestrial paleoclimates. In the Paleogene, Spitsbergen was situated further south and closer to the northern part of Greenland and Ellesmere Island, Canada, than at present (Blythe and Kleinspehn, 1998). Paleomagnetic data indicate the paleolatitude of Spitsbergen in the early Paleogene was about 71°–72°N (about 6° south of its present position) according to Dalland (1977).

The great contribution to our knowledge of the Paleogene floras of Spitsbergen was made by the remarkable Swiss paleobotanist Oswald Heer (1868, 1870, 1876). Many of the species that he first established in Spitsbergen remain valid and continue to be used by researchers working on fossil floras throughout the Arctic.

In 1882 and 1898 A. Nathorst, who was in charge of the paleobotanical department of the Swedish Museum of Natural History, visited a number of areas

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on Spitsbergen to collect plant fossils. Nathorst prepared 36 plates of pencil drawings for his unfinished monograph “Zur Tertiären Flora Spitzbergens”, beautifully executed by the artist Carl Hedelin. These plates were published later by Z. Kvaček and S. Manum with short comments on the systematics (Kvaček and Manum, 1993, 1997; Kvaček, Manum, and Boulter, 1994).

In 1958, A. Schloemer-Jäger (1958) published a paper on the ‘Tertiary’ flora of the Brögger Peninsula collected in the area of the Norwegian mine at Ny-Ålesund. The work was accompanied for the first time by excellent quality photographs of plant fossils from Svalbard.

In 1963–1964, an expedition from the University of Bonn worked on Svalbard. One participant, H.-J. Schweitzer, studied the ‘Tertiary’ conifers using the collections of the Swedish Museum of Natural History, as well as his own material (Schweitzer, 1974).

Some plants from Spitsbergen were described by Budantsev (1983), Sveshnikova (1975) and Golovneva (1994a, 1994b, 1997, 2000a, 2000b, 2002). The most recent monographic description of the Paleogene flora of Svalbard is based on the studies of all Swedish, Russian and German collections (Budantsev and Golovneva, 2009). Currently, the Paleogene flora of Svalbard overall contains about 90 species of ferns, gymnosperms and angiosperms, combined into three paleofloras: the Barentsburg (early Paleocene), Storvola (early Eocene) and Renardodden (late Eocene).

The aim of this work is to revise the late Eocene Renardodden flora for further paleoclimatic study.

Material

Plant-bearing deposits with remains of the Renardodden flora come from two isolated sedimentary basins assigned to the West Spitsbergen fold-thrust belt: in the Renardodden area south of Bellsund, southwestern Spitsbergen and in the Forlandsundet Graben on western Spitsbergen and Prins Karls Forland (Fig. 1).

The Renardodden flora combines floristic assemblages from the Skilvika and Renardodden formations of the Renardodden area, the Sesshøgda Formation and the Sarstangen conglomerate of the Forlandsundet Graben.

The position of the most important localities is shown on the map (Fig. 1). In most cases, Norwegian names from Orvin’s (1958) work on the history of place names in Svalbard were used.

The Skilvika and Renardodden formations are exposed in the basement of a 10–25 m marine terrace and in the stream valleys on the coastal area adjacent to the Skilvika Bay, about 3 km long and 1.5 km wide. Small outcrops in stream valleys are referred to the Scottbreen (Scott Glacier) locality. Outcrops along the seashore in the area of Cape Renardodden are designated as the Re-

nardodden locality (Kapp Lyel or Cap Lyell in old literature). Plant fossils from both formations are identical in their systematic composition.

The plant fossils in this area were found by A. Nordenskiöld in 1872–1873 and described by O. Heer (1876). Subsequently, large collections were gathered by the Swedish geological expedition in 1882. These collections are stored in the Swedish Museum of Natural History, Stockholm (prefix before specimen numbers S). Data about these collections were published in the catalogue by Denk, Wanntrop, and Manum (1999).

Abundant collections were also gathered by Russian paleobotanists L. Budantsev and I. Sveshnikova (Komarov Botanical Institute) and by geologist J. Livshits (Arctic Geology Research Institute) during a stratigraphic research of the Paleogene deposits of Spitsbergen in 1959–1967. These collections are stored in the Komarov Botanical Institute, Saint Petersburg, Russia. Specimens have prefix BIN before numbers.

In 1964, Livshits collected numerous plant fossils in the deposits of the Sesshøgda Formation on the northern coast of Selvågen Bay, along the slope of Mount Sesshøgda and west of Cape Reinhardpynten. Some more localities were discovered on the opposite bank of the Forlandsundet in the area of Sarsbukta (Cape Grorud), in the Sarstangen conglomerate (Sesshøgda Formation in Livshits, 1967). Previously, very few plant remains with poor preservation were known from this area (Zastawniak, 1981). For a long time, it was impossible to compare them with the other floristic assemblages of Spitsbergen. Livshits found in this area diverse fossil plants, characteristic for the assemblage from Cape Renardodden (*Metasequoia disticha*, *Trochodendroides crenulata*, *Alnus inaequale*, *Acer arcticum*). This made it possible to combine floristic assemblages of the Forlandsundet area and the Renardodden area into a single Renardodden flora.

Stratigraphy

The Paleogene deposits of the Renardodden area were divided into two parts: the Skilvika Formation and the Renardodden Formation, which are joined under the name Calypsostranda Group (Dallmann, 1999). It unconformably overlies the Precambrian basement. The Calypsostranda Group comprises sandstones, siltstones, shales, coal seams and subordinate conglomerates.

The Skilvika Formation represents mainly fluvio-deltaic facies (Dallmann, 1999). It is about 100 m thick and consists of interbedded grey, fine-grained sandstones and dark claystones, with calcareous horizons in the middle part and abundant thin coal seams in the upper part (Atkinson, 1962; Livshits, 1967, 1974; Thiedig et al., 1979).

The Skilvika Formation is erosively overlain by conglomerates (2,6 m thick) of the Renardodden Formation.

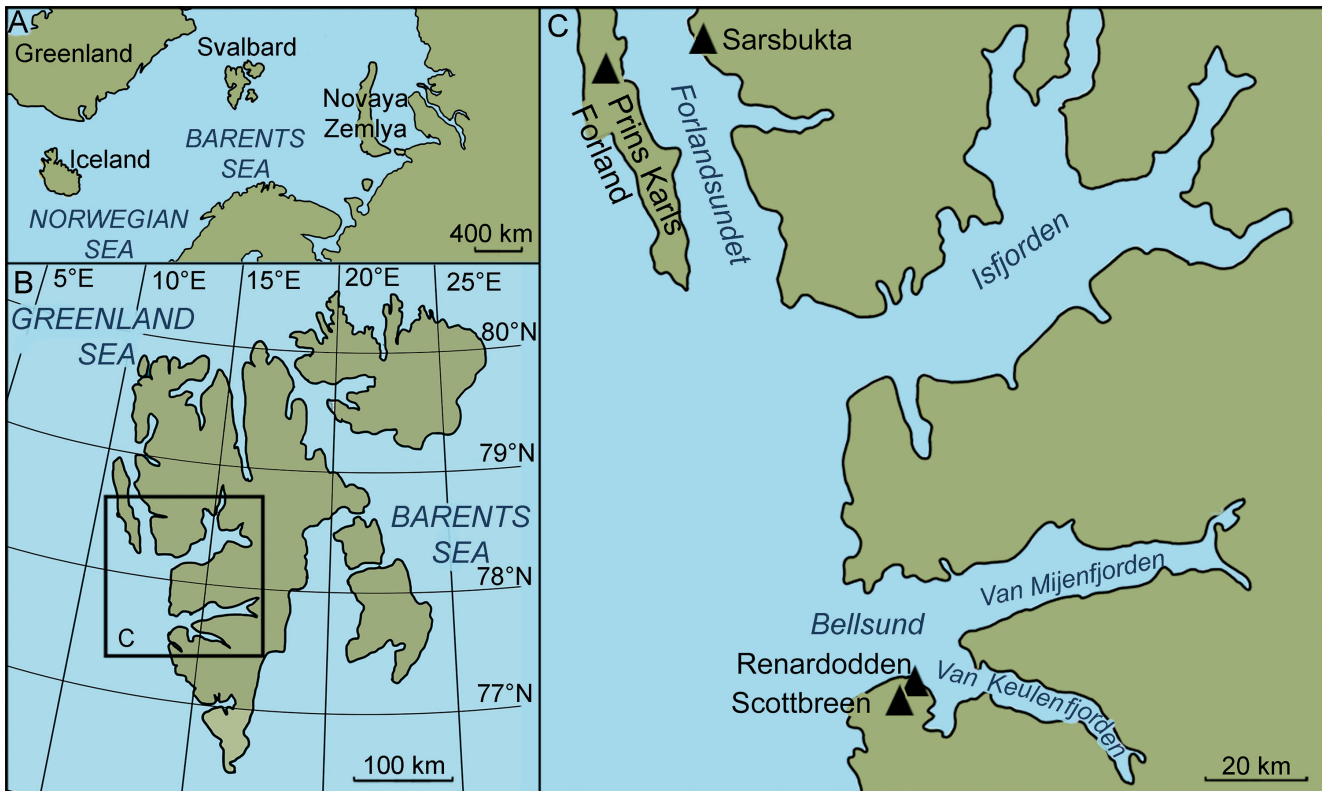


Fig. 1. A — location of the Svalbard archipelago; B — map of Spitsbergen with the position of the study area; C — main localities of the Renardodden flora.

This formation represents mostly shallow marine facies (Dallmann, 1999). It is 160–300 m thick and comprises monotonous, grey, loosely cemented fine-grained sandstones, with some interbeds of dark grey siltstones and claystones and also thin coal seams (Lehmann, Thiedig, and Harland, 1978; Thiedig et al., 1979; Livshits, 1992). The sandstones contain numerous siderite concretions. Both formations contain abundant plant fossils.

Within the Forlandsundet Graben, Paleogene strata are exposed on the western coast of Spitsbergen and, particularly, on the northeastern coast of Prins Karls Forland. They are divided into seven stratigraphic units (Selvågen, Sesshøgda, Reinhardpynten, Krokodillen, Marchaislaguna, Aberdeenflya formations and Balanuspynten conglomerate), and being joined under the name Buchananisen Group, unconformably overlies Precambrian basement (Dallmann, 1999). The Buchananisen Group consists of conglomerates, sandstones, siltstones and shales. The individual formations are local and sometimes laterally replacing each other.

The most extensive collections of plant fossils come from the Sesshøgda Formation. The Reinhardpynten Formation contains a scattered marine bivalve fauna. The Balanuspynten conglomerate is also distributed on the eastern side of Forlandsundet, near Sarsbukta, where this unit is divided into Sarsbukta and Sarstangen conglomerates (Dallmann, 1999). Relations between these two subunits are unknown. The Sarsbukta conglomerate

contains scattered plant remains. Foraminifera, dinoflagellates, and palynological remains were found in the Sarstangen conglomerate (Manum, 1960, 1962; Feyling-Hanssen and Ulleberg, 1984; Manum and Throndsen, 1986; Livshits, 1992).

The composition of the Renardodden flora

The Renardodden flora combines floristic assemblages from four stratigraphic units. The distribution of species in localities and units is given in Table. The most common species are shown in Figs. 2–7.

All localities are dominated by the same set of plant fossils including *Metasequoia disticha* (Fig. 2A, E), *Sequoia brevifolia* (Fig. 2B, I), *Trochodendroides crenulata* (Fig. 2A–C, E, G), *Zizyphoides retusa* (Fig. 4A–D, F–L), *Carpinus gracilis* (Fig. 5B, I), *Alnus inaequale* (Fig. 6A), *Corylites* sp. (Fig. 6D), *Acer arcticum* (Fig. 7B, C, E–J), although the assemblages from the Forlandsundet Graben are somewhat poorer. Since the floristic assemblages from these four units have a large number of common species, we consider them as representing a single fossil flora.

The taxonomic composition of the Renardodden flora is given according to the list in the monograph by Budantsev and Golovneva (2009) with minor changes. After revision of the type material of the genus *Zizyphoides* Seward et Conway (Zolina, Manchester, and

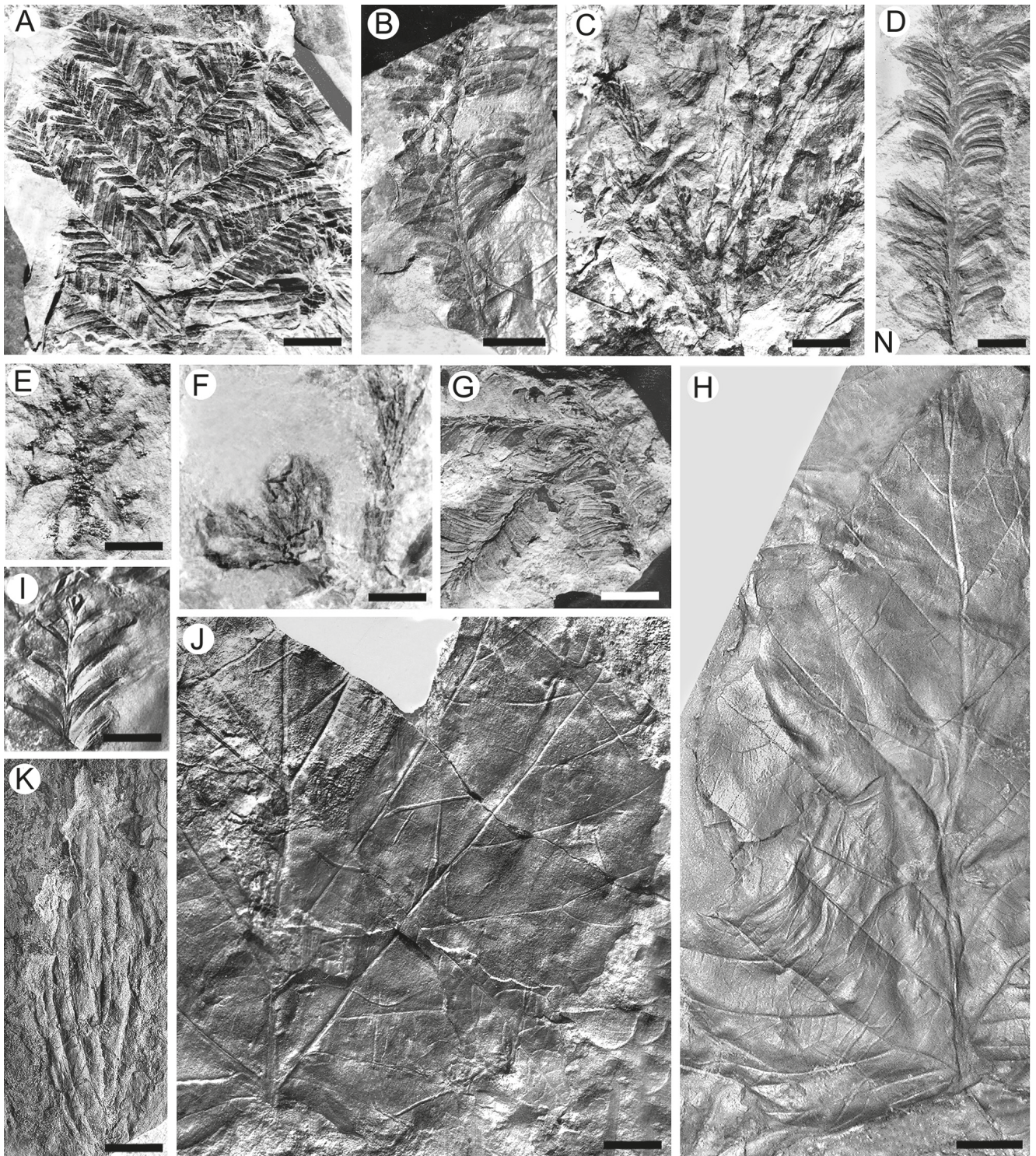


Fig. 2. A, E — *Metasequoia disticha* (Heer) Miki, Renardodden: A — spec. S051180, E — spec. S051232; B, I — *Sequoia brevifolia* Heer: B — Renardodden, spec. S050897-2, I — Prins Karls Forland, spec. BIN 955-2/24; C, F — *Glyptostrobus nordenskiöldii* (Heer) R. W. Brown, Renardodden: C — spec. S050830-2, F — spec. S050939; D, G — *Elatocladus scottii* Golovn. et Budants., Renardodden: D — spec. S050890, G — spec. S051076, holotype; H, J — *Platanus selvogensis* Golovn. et Budants., Prins Karls Forland: H — spec. BIN 955-2/3a, J — spec. BIN 955-2/18a; K — *Cornus* sp., Sarsbukta, spec. BIN 955-4/3. Scale bars represent 1 cm.

Golovneva, 2021), we showed the presence of this genus in the Renardodden flora. Previously, these leaves were assigned to *Trochodendroides retusa* (Heer) Golovn. Female infructescences with follicular fruits, previously described as *Nyssidium arcticum* (Heer) Iljinsk., now

are considered as *Jenkinsella arctica* (Heer) Bell (Fig. 3D, E), because the name *Jenkinsella* Reid et Chandler is the earliest appropriate generic name designated for these fruits (Golovneva and Alekseev, 2017). A taxonomic list of the Renardodden flora is presented in Table.

Table. The composition of the Renardodden flora

Species	Localities and formations			
	Renardodden, Skilvika and Renardodden formations	Scottbreen, Skilvika and Renardodden formations	Prins Karls Forland, Sessshøgda Formation	Sarsbukta, Sarstangen conglomerate
<i>Equisetum arcticum</i> Heer			+	
<i>Metasequoia disticha</i> Heer	+	+	+	+
<i>Glyptostrobus</i> sp.	+	+		
<i>Sequoia brevifolia</i> Heer	+		+	
<i>Elatocladus scottii</i> Golovn. et Budants.	+			
<i>Platanus selvogensis</i> Golovn. et Budants.			+	
<i>Platanus</i> sp.	+	+		
<i>Trochodendroides crenulata</i> (Heer) Kvaček, Manum et Boulter	+		+	
<i>T. curvidens</i> (Heer) Golovn. et Budants.	+	+		
<i>Zizyphoides retusa</i> (Heer) Golovn. et Zolina, comb. nov.	+	+		
<i>Jenkinsella arctica</i> (Heer) Bell	+	+		
<i>Nordenskioldia borealis</i> Heer	+			
<i>Alasia</i> sp.	+			
<i>Carpinus gracilis</i> Budants	+	+		
<i>Alnus inaequale</i> (Heer) Golovn. et Budants.	+	+		+
<i>Corylites</i> sp.	+	+		+
<i>Acer arcticum</i> Heer	+	+		
<i>Acer thulense</i> Heer	+			
<i>Acer</i> sp.		+		
<i>Hamamelites skilvikensis</i> Golovn.	+		+	
" <i>Koelreuteria</i> " <i>borealis</i> Heer	+			
<i>Craigia bronni</i> (Unger) Kvaček, Bůžek et Manchester	+			
<i>Haemanthophyllum nordenskioldii</i> (Heer) Boulter et Kvaček		+		
<i>Magnoliaephyllum</i> sp.	+			
<i>Cornus</i> sp.	+			
<i>Acorus spitsbergensis</i> Golovn. et Budants.	+			
<i>Dicotylophyllum</i> sp. 1	+			
<i>Dicotylophyllum</i> sp. 2	+			

The Renardodden flora consists of 28 species. Of these, conifers are represented by four species, aquatic monocot flowering plants — by two species, and dicotyledonous woody plants — by 22 species.

The remains of horsetails, represented by underground roots, are rare. Ferns and ginkgos are not present. Conifers are represented by taxa from the family Cupressaceae. Among them, remains of *Metasequoia disticha* (shoots and cones) predominate (Fig. 2A, E).

Shoots of *Sequoia brevifolia* (Fig. 2B, I), *Glyptostrobus* sp. and *Elatocladus scottii* (Fig. 2D) are less common.

Monocots are represented by two aquatic plants: *Haemanthophyllum nordenskioldii* (Fig. 5A) and *Acorus spitsbergensis* (Fig. 7A). The first species had a rosette of petiolate submerged leaves. The genus *Haemanthophyllum* was widespread in the Paleogene floras of the Northern Hemisphere and, most likely, related to the modern family Aponogetonaceae (Golovneva, 1997).

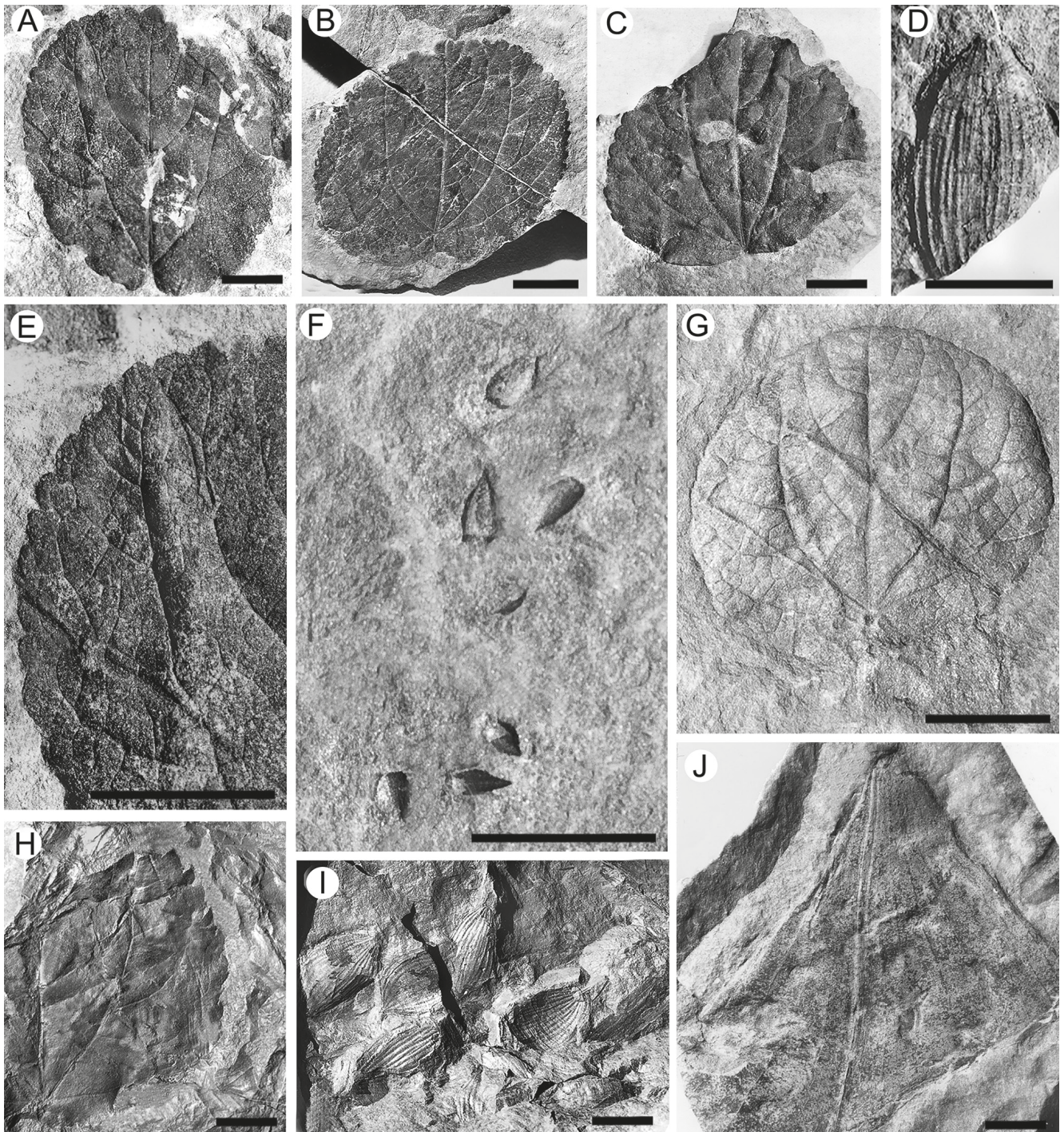


Fig. 3. A–C, E, G — *Trochodendroides crenulata* (Heer) Kvaček, Manum et Boulter, Renardodden: A, E — spec. BIN 956-1: A — general view, E — margin details; B — spec. S051054; C — spec. BIN 956-1/53; G — spec. S050849, lectotype; D, I — *Jenkinsula arctica* (Heer) Bell: D — Scottbreen, spec. BIN 956-2/8, I — Renardodden, spec. S050842-1; F — *Alasia* sp., Renardodden, spec. S050884; H — *Trochodendroides curvidens* (Heer) Golovn. et Budants., Renardodden, spec. S051247; J — *Haemanthophyllum nordenskiöldii* (Heer) Boulter et Kvaček, Scottbreen, spec. S051234. Scale bars represent 1 cm.

The second species is represented by leaves and stems with inflorescences. This is the oldest representative of the family Acoraceae.

Arboreal dicotyledons comprise families Platana-ceae, Cercidiphyllaceae, Trochodendraceae, Hamameli-daceae, Betulaceae, Cornaceae, Tiliaceae and Aceraceae.

Sycamores include two species: endemic *Platanus selvo-gensis* (Fig. 2H, J) with an entire blade and *Platanus* sp. with trilobite leaves. Leaves of *Trochodendroides crenulata* (Fig. 3A–C, E, G) and *T. curvidens* (Fig. 3H), fruits of *Jenkinsula arctica* (Fig. 3D, I) and bracts of male inflorescences *Alasia* sp. (Fig. 3F) are assigned to the fam-

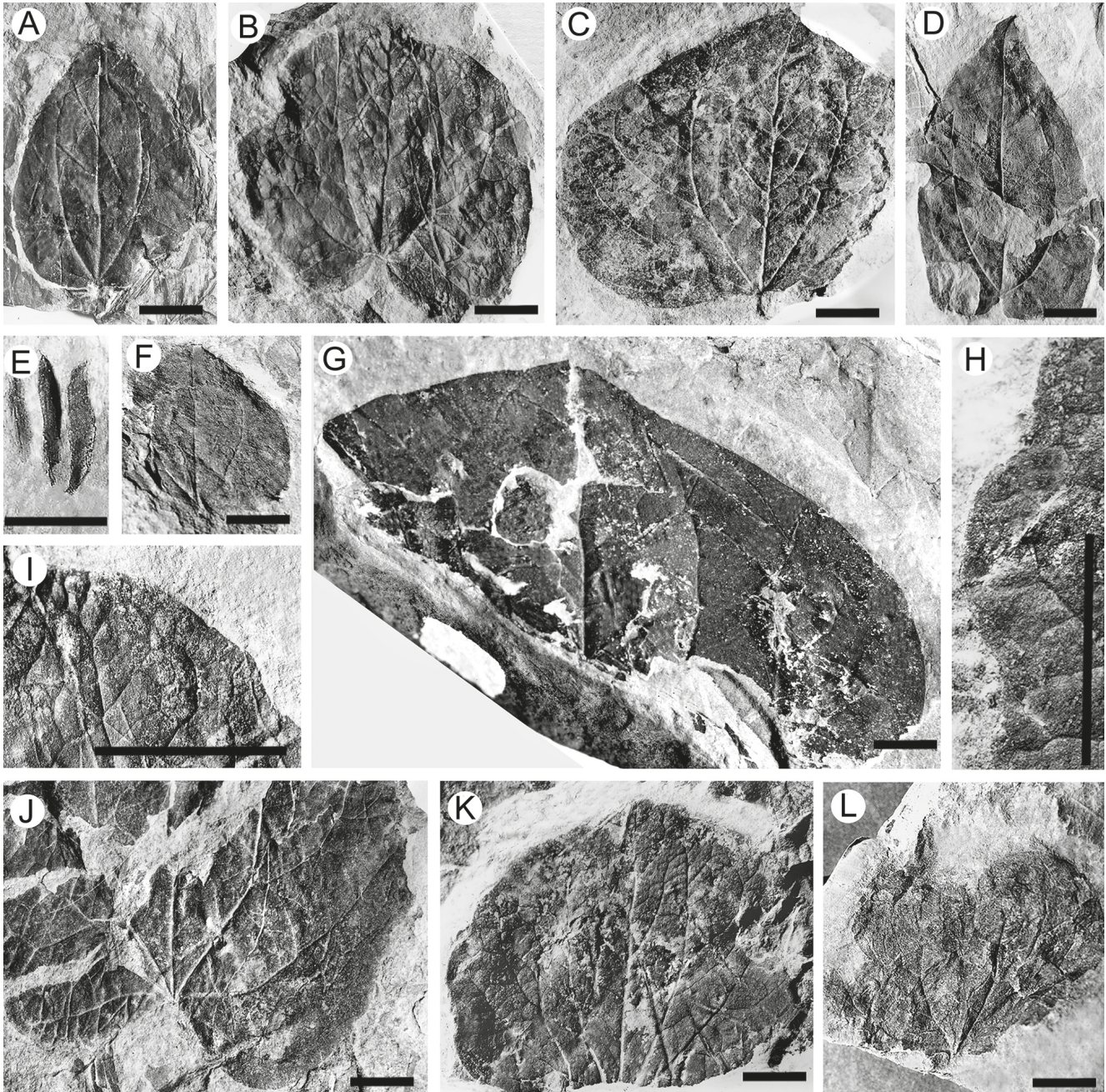


Fig. 4. A–D, F–L — *Zizyphoides retusa* (Heer) Golovn. et Zolina, comb. nov., Renardodden: A — spec. BIN 956-1/15, B — spec. BIN 956-1/52, C — spec. BIN 956-1/18, D — spec. S051167, F — spec. S050810, G — spec. BIN 956-1/19, H, K — spec. BIN 956-1/17: H — margin details, K — general view, J — spec. BIN 956-1/24, L — spec. S050811, lectotype; E — *Nordenskiöldia borealis* Heer, Renardodden, spec. BIN 956-1/65. Scale bars represent 1 cm.

ily Cercidiphyllaceae. The family Trochodendraceae is represented by leaves of *Zizyphoides retusa* and fruits of *Nordenskiöldia borealis* (Fig. 4E).

The family Betulaceae includes three genera: *Alnus*, *Carpinus* and *Corylites*. Since the genus *Alnus* is represented by only one species, *A. inaequale* (Fig. 6A), it is likely that the female alder fruits found in the sediments of Sarsbukta, belong to the same species.

The family Aceraceae contains two species of the genus *Acer*: *A. arcticum* (Fig. 7B, C, E–J) and *A. thulense*. Both species have leaf plates with short lobes and differ

in the dentation. *A. arcticum* is usually associated with samaras *Acer* sp. (Fig. 6C, E).

Craigia bronni, represented by winged fruits, is assigned to the family Tiliaceae. This modern genus was often reported in fossil floras of Eurasia from the Eocene up to Miocene (Kvaček et al., 1991). The family Cornaceae includes only *Cornus* sp. Species *Hamamelites skilvikensis* (Fig. 5A) and is probably related to the family Hamamelidaceae. Taxa of uncertain affinity are represented by *Magnoliaephyllum* sp. (Fig. 6F) and “*Koelreuteria*” *borealis* (Fig. 6G).

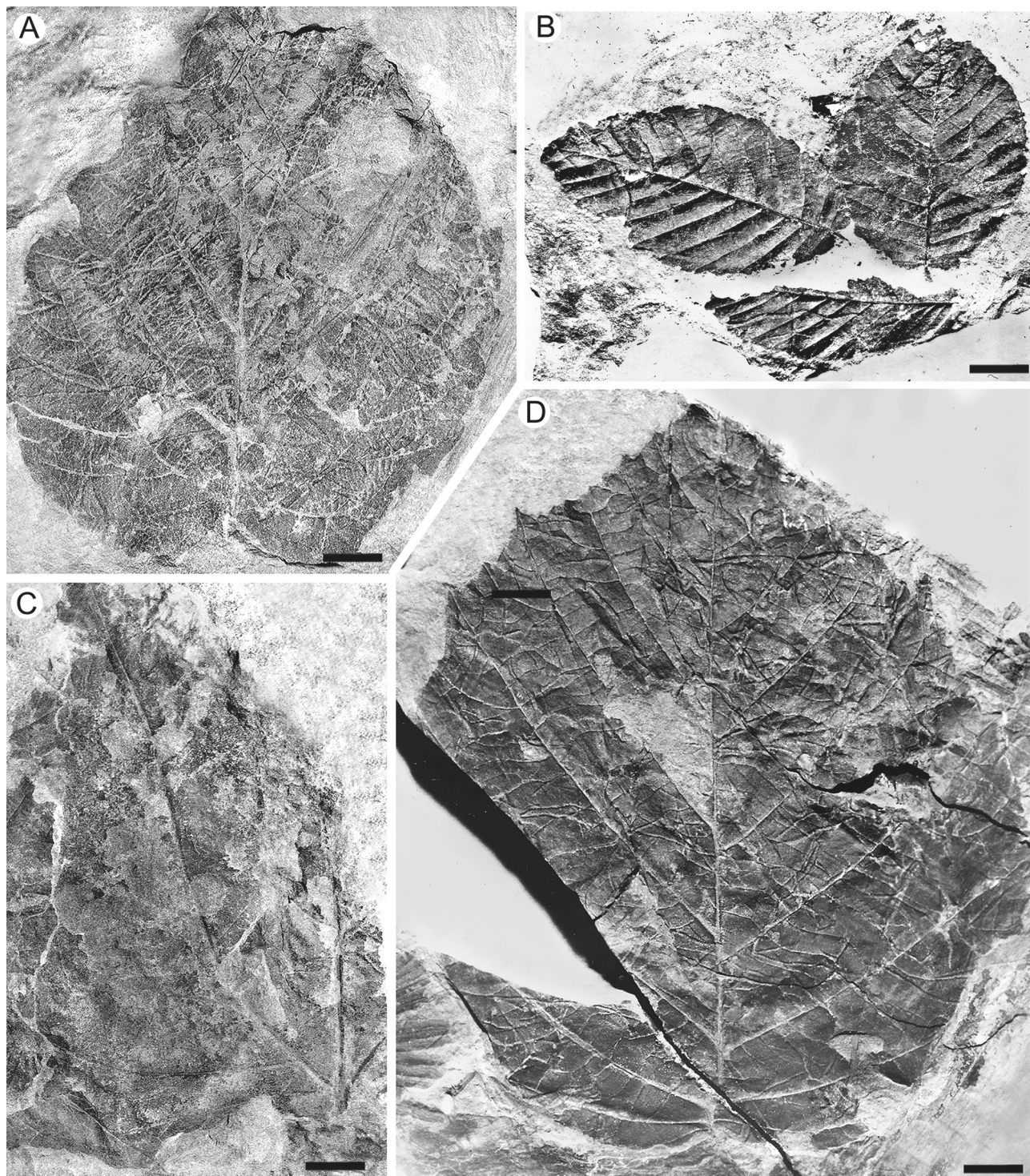


Fig. 5. A — *Hamamelites skilvikensis* Golovn. et Budants., Renardodden spec. S050896, holotype; B — *Carpinus gracilis* Budants., Renardodden, spec. BIN 956-1/6; C — *Platanus* sp., Scottbreen, spec. S051288; D — *Alnus inaequale* (Heer) Golovn. et Budants., Renardodden, spec. S051044. Scale bars represent 1 cm.

Systematics

Class Magnoliopsida

Family Trochodendraceae

Genus *Zizyphoides* Seward et Conway, emend. Zolina et al., 2021

Zizyphoides retusa (Heer) Golovn. et Zolina, comb. nov.
Fig. 4A–D, F–L

Populus retusa Heer, 1876, S. 69, Taf. 14, Fig. 6.

Trochodendroides retusa (Heer) Golovn. et Budants., in Budantsev and Golovneva, 2009, p. 112, pl. 87, fig. 1–4, 6–12, text-fig. 13.

Trochodendroides spitsbergiana Budants., 1983, p. 133, pl. 16, fig. 7–10.

Populus hookeri auct. non Heer, 1868, in Heer, 1876, S. 69, Taf. 14, Fig. 5.

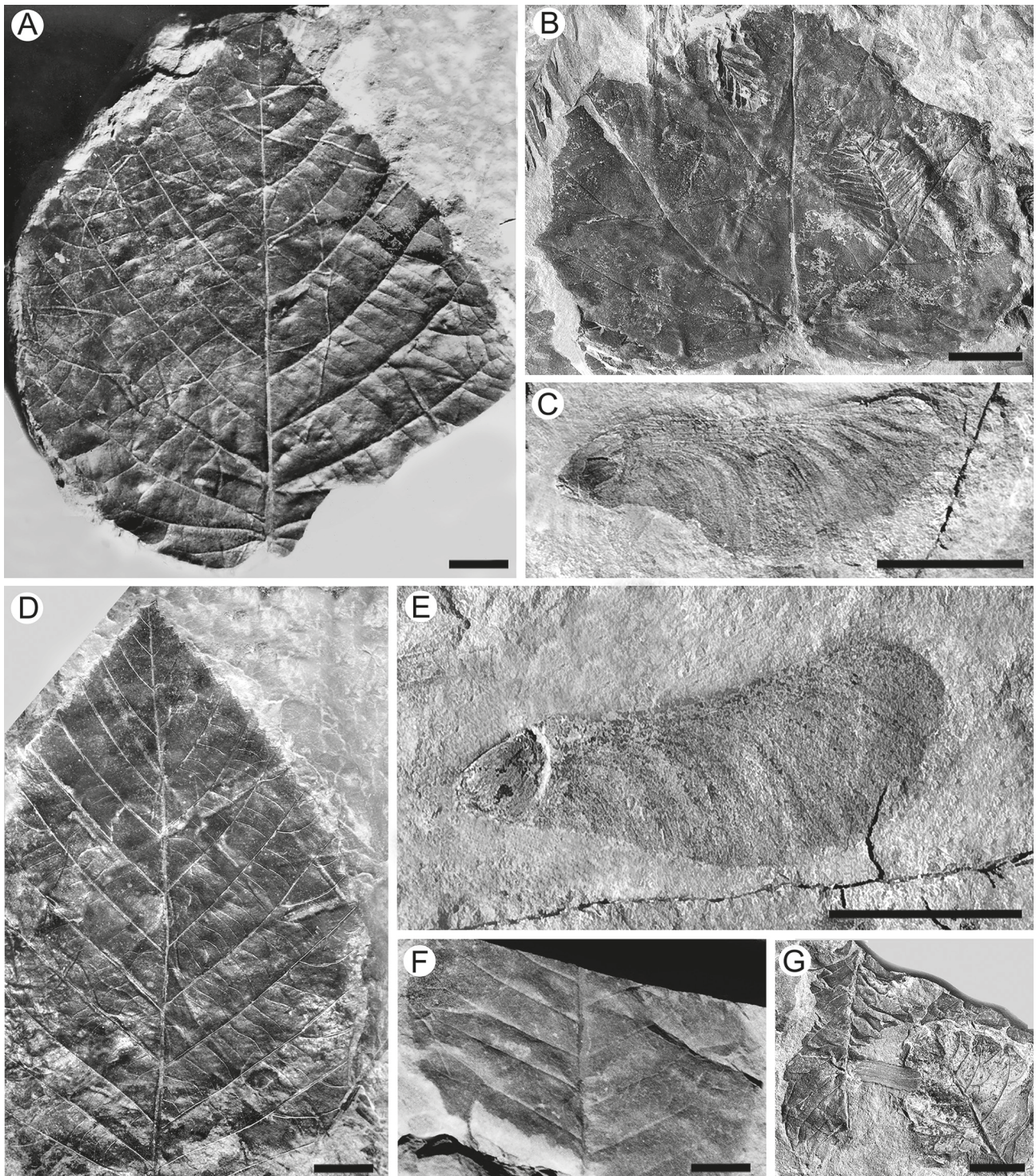


Fig. 6. A — *Alnus inaequale* (Heer) Golovn. et Budants., Renardodden, spec. S051043/1; B — *Acer thulense* Heer, Renardodden, spec. S050872, lectotype; C, E — *Acer* sp., Renardodden: C — spec. S056858a, E — spec. S056858b; D — *Corylites* sp., Renardodden, spec. S050895a; F — *Magnoliaephyllum* sp., Renardodden, spec. S050823; G — “*Koelreuteria*” *borealis* Heer, Renardodden, spec. S050879. Scale bars represent 1 cm.

P. richardsonii auct. non Heer, 1868, in Heer, 1876, S. 69, Taf. 14, Fig. 4.

P. zaddachii auct. non Heer, 1869, in Heer, 1876, S. 68, Taf. 28, Fig. 3.

T. arctica auct. non (Heer) Berry, in Zastawniak, 1981, p. 40, text-fig. 2b.

Menispermites septentrionalis auct. non Holl., in Zastawniak, 1981, p. 40, text-fig. 2c.

Dicotylophyllum sp., Kvaček, Manum, 1997, pl. 3, fig. 6.

Original diagnosis (Heer, 1876): *P. foliis rotundatis, longitudine latioribus, integerrimis, apice emarginatis, quinquenerviis, nervis ramosis, deinde in rete dissolutis.*

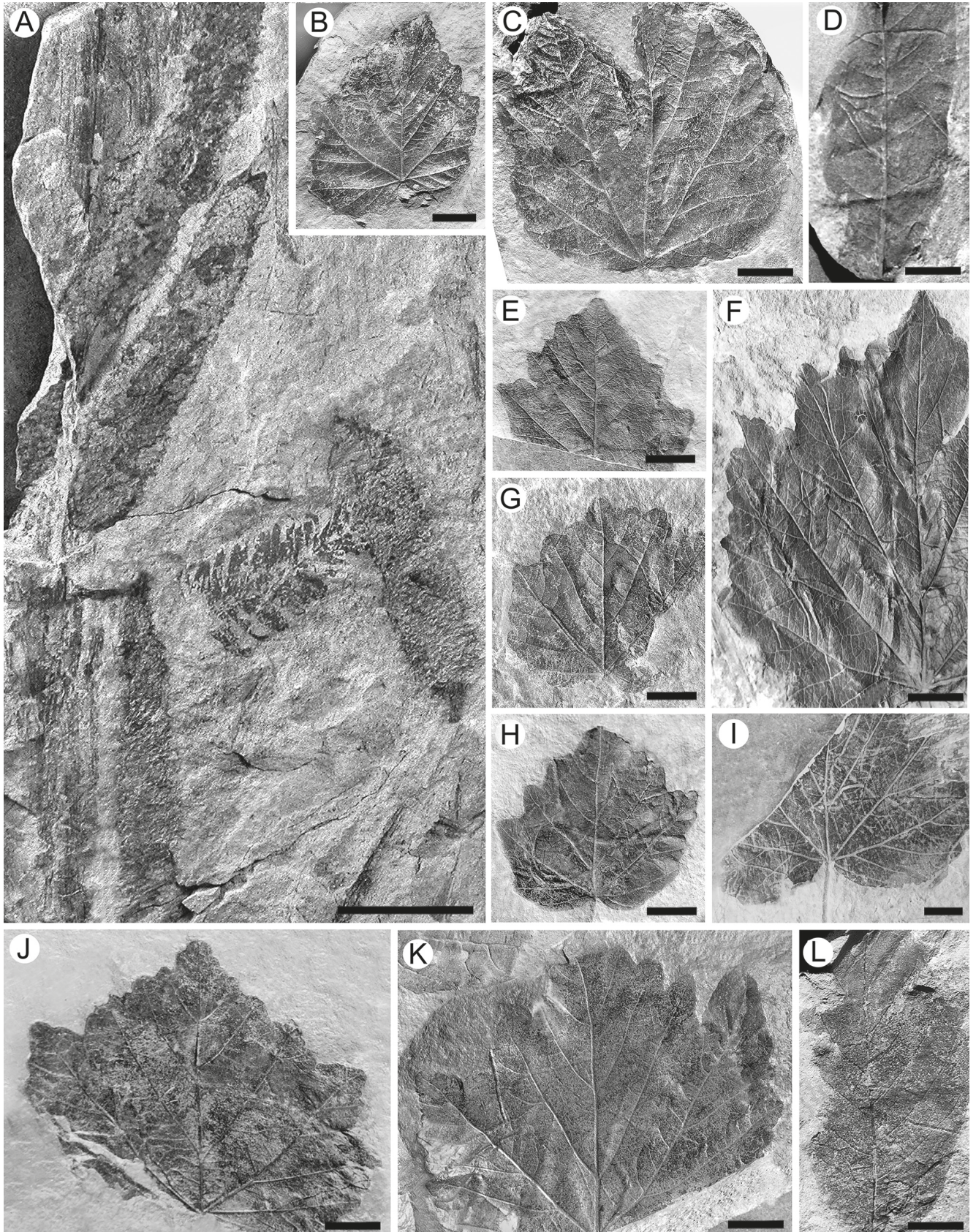


Fig. 7. A — *Acorus spitsbergensis* Golovn. et Budants., Renardodden, spec. BIN 956-1/43a; B, C, E–J — *Acer arcticum* Heer, Renardodden: B — spec. S050861, C — spec. S050870, E — spec. S051197, F — spec. S051149, G — spec. S051145-1, H — spec. S051151, I — spec. S050998, K — spec. S050865-1, J — spec. S050862, lectotype; D — *Dicotylophyllum* sp. 1, Renardodden, spec. S050822; L — *Dicotylophyllum* sp. 2, Renardodden, spec. S050878. Scale bars represent 1 cm.

Diagnosis emended. Leaves rounded, ovate, or transversely widely elliptical; apex acute; base broadly cuneate, truncate or cordate; margin entire or undulate.

Lectotype (Fig. 4L). Spec. S050811, Swedish Museum of Natural History, Spitsbergen, Renardodden; Heer, 1876, Taf. 14, Fig. 6 sub. nom. *Populus retusa* Heer.

Material. Spitsbergen, Renardodden, collection of the Swedish Museum of Natural History, specimens S050810, S050811, S051167; collection BIN 956–1, specimens 15, 17–21, 24, 25, 52, 55, 56.

Description. Leaves are simple, petiolate. Lamina is ovate, rounded or transversely widely elliptical in shape, 2.5–8 cm long and 2.5–10 cm wide. The leaf apex is acute. The leaf base is broadly cuneate, truncate or cordate. Margin is entire or undulate.

Venation is actinodromous, 3–5 nervous. Midvein is straight, running to the leaf apex, producing 2–5 alternately arranged short secondary veins in the upper part of the lamina. Inner lateral veins are curving, connecting with lower secondary veins extending from the midvein, forming an elliptical arena. The inner lateral veins produce 5–6 secondary basisopic thin veins. Outer lateral primary veins (if present) are thinner than inner lateral veins, form loops in the lower half of the lamina. Veins arising from inner and outer lateral veins form series of brochidodromous loops near the margin. Tertiary veins are very thin, percurrent.

Discussion. The type species of the genus *Zizyphoides*, *Z. colombii* (Heer) Seward et Conway, comes from the early Paleocene of the Atanikerdluk locality (the Quikavsak Formation), West Greenland (Zolina, Manchester, and Golovneva, 2021). This species has entire, undulate, crenate or irregularly dentate margin. Leaves of *Zizyphoides retusa* are very similar to morphotype of *Z. colombii* with entire margin. But crenate or dentate margin never occurred in *Z. retusa*.

The other species, *Z. flabella* (Newberry) Crane, Manchester et Dilcher, was described from the Paleocene to Eocene Puget Group of Chuckanut near Bellingham Bay, Washington, USA (Newberry, 1863, 1898) based on one poor preserved leaf with an entire margin. Later numerous leaves with entire, slightly undulate, crenate or scalloped margin from different localities of North America were assigned to *Z. flabella* (Crane, Manchester, and Dilcher, 1991). This species typically is characterized by obovate leaf blades with a scalloped margin that was not found in *Z. retusa*. However, to understand the distinctive features of this species, it is necessary to study additional material from a type locality.

The Miocene *Zizyphoides auriculata* (Heer) Manchester, Crane et Dilcher from North America and Japan (Tanai, 1961; Manchester, Crane, and Dilcher, 1991) differs from *Z. retusa* in large scalloped teeth along the margin.

Discussion

The Renardodden flora is characterized by a high degree of endemism. Overall, 65% of the Renardodden flora are endemic species, and 20–25% are species that were widespread in northern temperate floras throughout the Paleogene. Other species were common with the early Paleocene Barentsburg or the late Paleocene-early Eocene Storvola flora of Spitsbergen.

Widespread species are *Equisetum arcticum*, *Sequoia brevifolia*, *Acer arcticum*, *Nordenskioldia borealis*, *Jenkinsella arctica*, *Craigia bronni*, *Alasia* sp. Aquatic plant *Haemanthophyllum nordenskioldii*, in addition to the Renardodden flora, is present in the Barentsburg flora, but absent in the Storvola flora. Leaves of *Corylites* sp. are very similar to leaves of *Craspedodromophyllum malmgrenii* from the Storvola flora, but since this species is represented mainly by fragmentary material, a reliable comparison with other Betulaceae cannot be made.

Thus, at the species level, the Renardodden flora has no distinct floristic connections with other arctic and boreal floras. In the Tulean Province of Boreal floristic region, floras of this age are not known. In the Beringian Province, the early Eocene Napan flora from Anadyrka River, Kamchatka (Budantsev, 2006), is the closest in composition to the Renardodden flora. Common or similar species in these two floras are *Acer arcticum*, *Alnus beringiana* Budants., *Carpinus oblongifolia* Budants., *Platanus relictus* O. Lavrenko, *Hamamelites palanensis* Budants., *Craigia bronni*, *Cornophyllum swidiiformis* Budants., *Haemanthophyllum kamtschaticum* Budants., various *Trochodendroides* species and conifers.

The age of the Renardodden flora is less accurately determined than the ages of other Paleogene Spitsbergen floras, since this flora is characterized by significant endemism at the species level, and the Paleogene deposits within the West Spitsbergen fold-and-thrust belt contain a small number of marine organisms.

Reliable fossil age determinations have been reported only from the Sarstangen conglomerate, which is not stratigraphically correlated with the other formations with certainty. The age of the Sarstangen conglomerate was determined as the Eocene-Oligocene, based on dinoflagellates (Manum, 1960, 1962; Manum and Thronsen, 1986), although the foraminifera from the same deposits indicate the middle-late Oligocene age (Feyling-Hanssen and Ulleberg, 1984). Livshits (1974) refers the deposits of Sarsbukta to the upper Eocene. Budantsev (1983) dated the Renardodden flora as the Eocene. Head (1988) indicated the late Eocene-early Oligocene age for the Calypsostranda Group based on dinoflagellates.

However, the Renardodden flora corresponds mostly to the Eocene floras of the Arctic zone based on the generic and species composition. The Oligocene floras of the boreal regions are characterized by a wider pres-

ence of modern genera from the families Betulaceae, Fagaceae, Juglandaceae and others, as well as a greater diversity of Pinaceae. In our opinion, the age of the Renardodden flora is, most likely, the late Eocene.

Conclusion

1. We join fossil plants from the Skilvika, Renardodden and Sesshøgda formations and the Sarstangen conglomerate in the single Renardodden flora.
2. The Renardodden flora contains about 30 species of conifers and angiosperms.
3. The Renardodden flora is peculiar by a high level of endemism.
4. A new combination *Zizyphoides retusa* (Heer) Golovnev et Zolina, comb. nov. is proposed.
5. The age of the Renardodden flora is determined as the late Eocene.

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References

- Atkinson, D.J. 1962. Tectonic control of sedimentation and the interpretation of sediment alternation in the Tertiary of Prins Karls Forland, Spitsbergen. *Geological Society of America, Bulletin* 73:343–364. [https://doi.org/10.1130/0016-7606\(1962\)73\[343:TCOSAT\]2.0.CO;2](https://doi.org/10.1130/0016-7606(1962)73[343:TCOSAT]2.0.CO;2)
- Blythe, A. E. and Kleinspehn, K. L. 1998. Tectonically versus climatically driven Cenozoic exhumation of the Eurasian plate margin, Svalbard: Fission track analyses. *Tectonics* 17:621–639. <https://doi.org/10.1029/98TC01890>
- Budantsev, L. Yu. 1983. History of the Arctic flora of the Early Cenozoic epoch. 156 pp. Nauka Publ., Leningrad. (In Russian)
- Budantsev, L. Yu. 2006. The Early Paleogene flora of Kamchatka. 160 pp. BIN, Saint Petersburg. (In Russian)
- Budantsev, L. Yu. and Golovneva, L. B. 2009. Fossil Flora of Arctic II. Palaeogene Flora of Spitsbergen. 400 pp. Marafon Publ., Saint Petersburg. (In Russian)
- Corfield, R. M. 1994. Palaeocene oceans and climate: an isotopic perspective. *Earth-Science Reviews* 37(3–4):225–252. [https://doi.org/10.1016/0012-8252\(94\)90030-2](https://doi.org/10.1016/0012-8252(94)90030-2)
- Crane, P. R., Manchester, S. R., and Dilcher, D. L. 1991. Reproductive and vegetative structure of *Nordenskiöldia* (Trochodendraceae), a vesselless dicotyledon from the Early Tertiary of the Northern hemisphere. *American Journal of Botany* 78:1311–1344. <https://doi.org/10.1002/j.1537-2197.1991.tb12599.x>
- Dalland, A. 1977. Erratic clasts in the Lower Tertiary deposits of Svalbard — evidence of transport by winter ice. *Norsk Polarinst. Årbok* 1976: 151–165.
- Dallmann, W. K. 1999. Lithostratigraphic Lexicon of Svalbard. 360 pp. Norsk Polarinstitutt, Tromsø.
- Denk, T., Wannrop, I., and Manum, S. B. 1999. Catalogue of the Tertiary plant fossils from Spitsbergen housed in the Swedish Museum of Natural History, Stockholm. 184 pp. The Swedish Museum of Natural History, Stockholm.
- Feyling-Hanssen, R. W. and Ulleberg, K. 1984. A Tertiary-Quaternary section at Sarsbukta, Spitsbergen, Svalbard, and its foraminifera. *Polar Research* 2:77–106. <https://doi.org/10.1111/j.1751-8369.1984.tb00487.x>
- Golovneva, L. B. 1994a. Maastrichtian-Danian floras of the Koryak Upland. *Proceedings of the Komarov Botanical Institute, Russian Academy of Science* 13:1–146. (In Russian)
- Golovneva, L. B. 1994b. A new genus *Platimelis* in the Late Cretaceous–Early Paleogene Arctic floras. *Botanicheskii Zhurnal* 79(1):98–107. (In Russian)
- Golovneva, L. B. 1997. Morphology, systematics and distribution of the genus *Haemanthophyllum* in the Paleogene floras of the Northern Hemisphere. *Paleontological Journal* 31(2):197–207.
- Golovneva, L. B. 2000a. Early Palaeogene floras of Spitsbergen and North Atlantic floristic exchange. *Acta Universitatis Carolinae — Geologica* 44(1):39–50.
- Golovneva, L. B. 2000b. Palaeogene climates of Spitsbergen. *GFF, The Geological Society of Sweden* 122:62–63. <https://doi.org/10.1080/11035890001221062>
- Golovneva, L. B. 2002. *Palaeocarpinus* (Betulaceae) from Paleogene of Spitsbergen and transatlantic floristic migrations. *Paleontological Journal* 36(4):422–428.
- Golovneva, L. B. and Alekseev, P. I. 2017. Taxonomy and morphological diversity of infructescences *Jenkinsella* co-occurred with *Trochodendroides* leaves in the Cretaceous and Paleogene. *Palaeobotany* 8:92–121. <https://doi.org/10.31111/palaeobotany/2017.8.92>
- Head, M. J. 1988. Palynostratigraphy of the Central basin (Paleocene — lower Eocene?), Spitsbergen. *Palynology* 13:283.
- Heer, O. 1868. Die fossile Flora der Polarländer enthaltend die in Nordgrönland, auf der Melville-Insel, im Banksland, am Mackenzie, in Island und in Spitzbergen entdeckten fossilen Pflanzen. In: *Flora fossilis arctica*. Bd 1. 192 S. Druck und Verlag von Friedrich Schulthess, Zürich. <https://doi.org/10.5962/bhl.title.52346>
- Heer, O. 1869. Contributions to the fossil flora of North Greenland, being a description of the plants collected by Mr. Edward Whymper during the summer of 1867. *Philosophical Transactions of the Royal Society of London* 159:445–488. <https://doi.org/10.1098/rstl.1869.0016>
- Heer, O. 1870. Die Miocene Flora und Fauna Spitzbergens. *Kongl. Svenska Vetensk. Akad. Handl.* 8(7):1–98.
- Heer, O. 1876. Beiträge zur fossilen Flora Spitzbergens. *Kongl. Svenska Vetensk. Akad. Handl.* 14:1–141.
- Hickey, L. J. 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin; pp. 33–49 in P. O. Gingerich (ed.). *Early Cenozoic paleontology and stratigraphy of the Big-horn Basin*. Wyoming. University of Michigan Papers on Paleontology 24.
- Kvaček, Z. and Manum, S. B. 1993. Ferns in the Spitsbergen Palaeogene. *Palaeontographica Abteilung B* 230:143–155.
- Kvaček, Z. and Manum, S. 1997. A. G. Nathorst's (1850–1921) unpublished plates of Tertiary plants from Spitsbergen. 8 pp. SMNH, Stockholm.
- Kvaček, Z., Manum, S. B., and Boulter, M. C. 1994. Angiosperms from the Palaeogene of Spitsbergen, including an unfinished work by A. G. Nathorst. *Palaeontographica Abteilung B* 232:103–128.
- Lehmann, U., Thiedig, F., and Harland, W. B. 1978. Spitzbergen im Tertiär. *Polaforschung* 48. Jahrgang (1/2):120–138.
- Livshits, J. J. 1967. Tertiary deposits of the western part of the Svalbard archipelago. 36 pp. Nedra Publ., Leningrad. (In Russian)
- Livshits, J. J. 1974. Palaeogene deposits and the platform structure of Svalbard. *Norsk Polarinstitutt Skrifter* 159:1–55.
- Livshits, J. J. 1992. Tectonic history of Tertiary sedimentation of Svalbard. Discussion; pp. 121–127 in W. K. Dallmann,

- A. Andresen, and A. Krill (eds.). Post-Caledonian tectonic evolution of Svalbard. *Norsk Geologisk Tidsskrift* 72/1.
- Manchester, S. R., Crane, P. R., and Dilcher, D. L. 1991. *Nordenskiöldia* and *Trochodendron* (Trochodendraceae) from the Miocene of northwestern North America. *Botanical Gazette* 152(3):357–368. <https://doi.org/10.1086/337898>
- Manum, S. B. 1960. Some dinoflagellates and hystrichosphaerids from the lower Tertiary of Spitsbergen. *Nytt Magasin for Botanik* 8:17–26.
- Manum, S. B. 1962. Studies in the Tertiary flora of Spitsbergen, with notes on Tertiary floras of Ellsmere Island, Greenland and Iceland. A palynological investigation. *Norsk Polarinstitutt Skrifter* 125:1–127.
- Manum, S. B. and Thronsen, T. 1986. Age of Tertiary formations on Spitsbergen. *Polar Research* 4:103–131. <https://doi.org/10.1111/j.1751-8369.1986.tb00526.x>
- Moiseeva, M. G., Herman, A. B., and Spicer, R. A. 2009. Late Paleocene flora of the Northern Alaska Peninsula: the role of transberingian plant migrations and climatic change. *Paleontological Journal* 43(10):1298–1308. <https://doi.org/10.1134/S0031030109100116>
- Newberry, J. S. 1863. Descriptions of fossil plants collected by Mr. George Gibbs. *Boston Natural History Journal* 7:506–524.
- Newberry, J. S. 1898. The later extinct floras of North America. *Monographs of the United States Geological Survey* 35:1–295.
- Orvin, A. K. 1958. Supplement to the place-names of Svalbard. *Norsk Polarinstitutt Skrifter* 112:1–133.
- Peppe, D. J. 2010. Megafloral change in the early and middle Paleocene in the Williston Basin, North Dakota, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 298:224–234. <https://doi.org/10.1016/j.palaeo.2010.09.027>
- Schloemer-Jäger, A. 1958. Alttertiäre Pflanzen aus Floren der Brögger-Halbinsel Spitsbergens. *Palaeontographica Abteilung B* 119:54–75.
- Schweitzer, H. J. 1974. Die “Tertiären” Koniferen Spitzbergen. *Palaeontographica Abteilung B* 149:1–89.
- Sveshnikova, I. N. 1975. On the paleobotanical history of the genus *Metasequoia* Miki. *Botanicheskii Zhurnal* 60(4):465–475. (In Russian)
- Tanai, T. 1961. Neogene floral change in Japan. *Journal of the Faculty of Science, Hokkaido University. Series 4, Geology and mineralogy* 11(2):119–398.
- Thiedig, E., Pickton, C. A. G., Lehmann, U., Harkand, W. B., and Anderson, H. J. 1979. Das Tertitir von Renardodden. *Mitteilungen des Geologisch Palaontologischen Instituts der Universität Hamburg* 49:135–146.
- West, C. K., Greenwood, D. R., and Basinger, J. F. 2015. Was the Arctic Eocene ‘rainforest’ monsoonal? Estimates of seasonal precipitation from early Eocene megaflores from Ellesmere Island Nunavut. *Earth and Planetary Science Letters* 427:18–30. <https://doi.org/10.1016/j.epsl.2015.06.036>
- West, C. K., Greenwood, D. R., and Basinger, J. F. 2019. The late Paleocene and early Eocene Arctic megaflores of Ellesmere and Axel Heiberg islands, Nunavut, Canada. *Palaeontographica Abteilung B* 300:47–163. <https://doi.org/10.1127/palb/2019/0066>
- Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Laurentino, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A., and Zachos, J. C. 2020. An astronomically dated record of Earth’s climate and its predictability over the last 66 million years. *Science* 369(6509):1383–1387. <https://doi.org/10.1126/science.aba6853>
- Wilf, P. 2000. Late Paleocene-early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. *Geological Society of America Bulletin* 112:292–307. [https://doi.org/10.1130/0016-7606\(2000\)112%3C292:LPECCI%3E2.0.CO;2](https://doi.org/10.1130/0016-7606(2000)112%3C292:LPECCI%3E2.0.CO;2)
- Willard, D. A., Donders, T. H., Reichgelt, T., Greenwood, D. R., Sangiorgi, F., Peterse, F., Nierop, K. G. J., Frieling, J., Schouten, S., and Sluijs, A. 2019. Arctic vegetation, temperature, and hydrology during Early Eocene transient global warming events. *Global and Planetary Change* 178:139–152. <https://doi.org/10.1016/j.gloplacha.2019.04.012>
- Zachos, J. C., Dickens, G. R., and Zeebe, R. E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451:279–283. <https://doi.org/10.1038/nature06588>
- Zachos, J. C., Pagani, M., Sloan, L., Thomas, E., and Billups, K., 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. *Science* 292:686693. <https://doi.org/10.1126/science.1059412>
- Zastawniak, E. 1981. Tertiary plant remains from Kaffioryra and Sarsøyra, Forlandsundet, Spitsbergen. *Studia Geologia Polonica* 73:37–42.
- Zolina, A. A., Manchester, S. R., and Golovneva, L. B. 2021. Typification of the genus *Zizyphoides* Seward et Conway (Magnoliophyta, Trochodendraceae). *Acta Palaeobotanica* 61(2):123–135. <https://doi.org/10.35535/acpa-2021-0007>