PALAEONTOLOGY

Type material of *Trochodendroides richardsonii* (Heer) Krysht. (Cercidiphyllaceae) from the Atanikerdluk (Paleocene, Greenland)

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Abstract

Type material of *Trochodendroides richardsonii* (Heer) Krysht. from the Paleocene Atanikerdluk locality, Greenland, was restudied based on the original collection stored in the National Museum of Ireland, Dublin. This work allowed us to reveal the main diagnostic features of this species facilitating an emended diagnosis. Photos of the lectotype and syntypes are presented for the first time. The restudy of the collections stored in Dublin, Saint Petersburg and Stockholm shows that *T. richardsonii* was distributed in the early Paleocene in Greenland and Svalbard. The revision of *T. richardsonii* type material allows us to distinguish this species from the other species of the genus *Trochodendroides* Berry with similar morphology.

Keywords: *Trochodendroides*, Cercidiphyllaceae, Paleocene, O. Heer, Atanikerdluk, Greenland, Svalbard

Introduction

Family Cercidiphyllaceae is currently regarded as belonging to the order Saxifragales (Angiosperm Phylogeny Group, 2016). It includes only one extant genus *Cercidiphyllum* Siebold et Zucc. and two species: *C. japonicum* Sieb. et Zucc. and *C. magnificum* (Nakai) Nakai (Fu and Endress, 2001), that are distributed in Japan and China. Extinct representatives of Cercidiphyllaceae are significantly more diverse, represented by several genera.

The dispersed fossil leaves from the Cretaceous and Paleogene are assigned to the genus *Trochodedroides* Berry (1922). The type species, *T. rhomboidea* (Lesq.) Berry, was described from the Cenomanian deposits of Dakota Formation, USA (Lesquereux, 1874; Berry, 1922). Recently more than fifty species of this genus have been described (Golovneva and Alekseev, 2010). Members of *Trochodedroides* have simple leaves with actinodromous venation and a crenate or dentate margin. Many species are characterized by significant morphological variability (Golovneva and Alekseev, 2010; Golovneva, Alekseev, Gnilovskaya, and Yudova, 2017).

The earliest occurrences of *Trochodendroides* come from the early-middle Albian in North America and Northeastern Asia (Golovneva and Alekseev, 2010; Golovneva et al., 2021). Different species of *Trochodendroides* were an important component of the Late Cretaceous and Paleogene floras from middle and high latitudes of Northern Hemisphere (Budantsev, 1983; Crane, 1984; Philippova and Abramova, 1993; Golovneva, 1994; Golovneva and Alekseev, 2010; Golovneva, Alekseev, Gnilovskaya, and Yudova, 2017). The latest *Trochodendroides* are known from the late Eocene (Budantsev and Golovneva, 2009). Fossil leaves from the Oligocene associated with *Cercidiphyllum* infructescences usually are included in the extant genus *Cercidiphyllum* (Jähnichen, Mai, and Walther, 1980; Manchester and Meyer, 1987; Kovar-Eder, Meller, and Zetter, 1998). But this name has

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also been used for dispersed leaves from more ancient deposits from the Paleocene (Brown, 1932; Iljinskaja, 1974a; Chandrasekharam, 1974; Budantsev, 1983).

Leaves of *Trochodendroides* are associated with dispersed follicular fruits and infructescences, assigned to the genus *Jenkinsella* Reid et Chandler (Golovneva and Alekseev, 2017). Earlier these fructifications were also described under a wide range of extinct and extant generic names: *Nyssidium* Heer, *Leguminosites* Lesq., *Berrya* Knowlton, *Trochodendrocarpus* Krysht., *Kenella* Samylina, and *Joffrea* Crane et Stockey (Heer, 1870; Lesquereux, 1873, 1878; Schmalhausen, 1890; Hollick, 1936; Knowlton, 1930; Kryshtofovich, 1958; Iljinskaja, 1974b; Samylina, 1976; Crane, 1984; Crane and Stockey, 1986). Staminate inflorescences associated with *Trochodendroides* leaves were referred to the genus *Alasia* (Golovneva, 2006).

The investigation of associated reproductive structures as well as the cuticular features of *Trochodendroides* leaves reveals their similarity to living representatives of Cercidiphyllaceae (Golovneva and Alekseev, 2010) despite the presence of oblique fiber bundles in the Cretaceous and Paleogene fruits that are lacking in extant *Cercidiphyllum*.

Earlier the *Trochodendroides* leaves were usually assigned to the modern genus *Populus* L. In particular, O. Heer (1868, 1870) described several species of *Trochodendroides* under the name *Populus* in his classic works on the Paleogene flora of Greenland. Subsequently, Heer's names were widely used for the description of other Arctic floras. However, other paleobotanists interpreted Heer's species in various ways because they were only known from drawings. The original material from Greenland has never been revised.

The present study is devoted to a revision of *Trochodendroides richardsonii* (Heer) Krysht. type material. Initially it was described from the Paleocene deposits of Atanikerdluk, West Greenland (Fig. 1), under the name *Populus richardsonii* Heer (1868). Later Kryshtofovich (1958) transferred this species to the genus *Trochodendroides.* The lectotype was chosen by I. Iljinskaja (1971) based on the drawing in Heer's monograph. A detailed diagnosis of this species is absent and no photos of original material have ever been published.

Material and methods

Type material of *Trochodendroides richardsonii* comes from the locality Atanikerdluk along the southern coast of the Nuussuaq peninsula, West Greenland (Fig. 1). Fossil leaves were collected by Lieutenant Philip Howard Colomb, who served as a mate of the HMS "Phoenix" during the Arctic Expedition of 1854. This ship supplied the search for the Franklin expedition that had been lost in 1847.

Lieutenant Colomb and the captain of "Phoenix" Sir Edward Augustus Inglefield visited the Atanikerdluk site on July 7, 1854. On return to England Captain Inglefield donated his collection to the Geological Survey in London. The plant fossils from Colomb's collection were transferred to the Royal Dublin Society on November 24, 1854. Now these fossils are stored in the National Museum of Ireland in Dublin (NMING).

The material is preserved as leaf impressions in sideritic shales. Most of the leaves are represented only by fragments (Fig. 2). According to modern data, plant fossils from Colomb's collection come from the Quikavsak Formation (Zolina, Manchester, and Golovneva, 2021) that consists of fluviatile conglomerates, sandstones and shales (Dam et al., 2009). Its thickness is 70–180 m. The age of these deposits was considered as the Danian (Dam et al., 2009).

Leaf architectural terminology follows that of "Manual of Leaf Architecture" (Ellis et al., 2009). Photographs of the specimens were made using Sony RX100II camera at low angle illumination. The plant drawings were completed using a graphics tablet Wacom Intuos Pro. The geographic place names in Greenland used in this paper are in modern Greenlandic orthography (after Dam et al., 2009).

Systematics

Class Magnoliopsida
Family Cercidiphyllaceae
Genus *Trochodendroides*, Berry, 1922
Trochodendroides richardsonii (Heer) Krysht.
(Figs. 3–6)

Trochodendroides richardsonii (Heer) Kryshtofovich, 1958, p. 97, *pro parte quoad* combination. — Budantsev, 1983, pl. 14, fig. 6, 8. — Budantsev and Golovneva, 2009, p. 105, text-fig. 10, pl. 16, fig. 1–4.

Populus richardsonii Heer, 1868, S. 98, *pro parte quoad* Taf. 4, Fig. 3–5. — Heer, 1869, S. 468, pro parte quoad Taf. 44, Fig. 8a,b. — Heer, 1870, S. 54, *pro parte quoad* Taf. 10, Fig. 9–11.

Cercidiphyllum richardsonii (Heer) Seward et Edwards, 1941, *pro parte quoad* combination. — Iljinskaja, 1971, p. 1632. — Iljinskaja, 1974a, p. 124, *pro parte quoad* text-fig. 77, 1, 2.

Cercidiphyllum arcticum auct. non (Heer) R. W. Brown, in Koch, 1963, p. 47, *pro parte quoad* pl. 17, fig. 1–3.

Original diagnosis (Heer, 1868): *foliis suboriculatis, basi leviter emarginatis, margine profunde crenatis, 5–7 nervis, asnervis primariss lateralibus erectis, valde flexuosis ramosis*.

Diagnosis emended: Leaves ovate, widely ovate or widely elliptical with acute or slightly attenuate apex and slightly cordate or truncate base; margin crenate; teeth

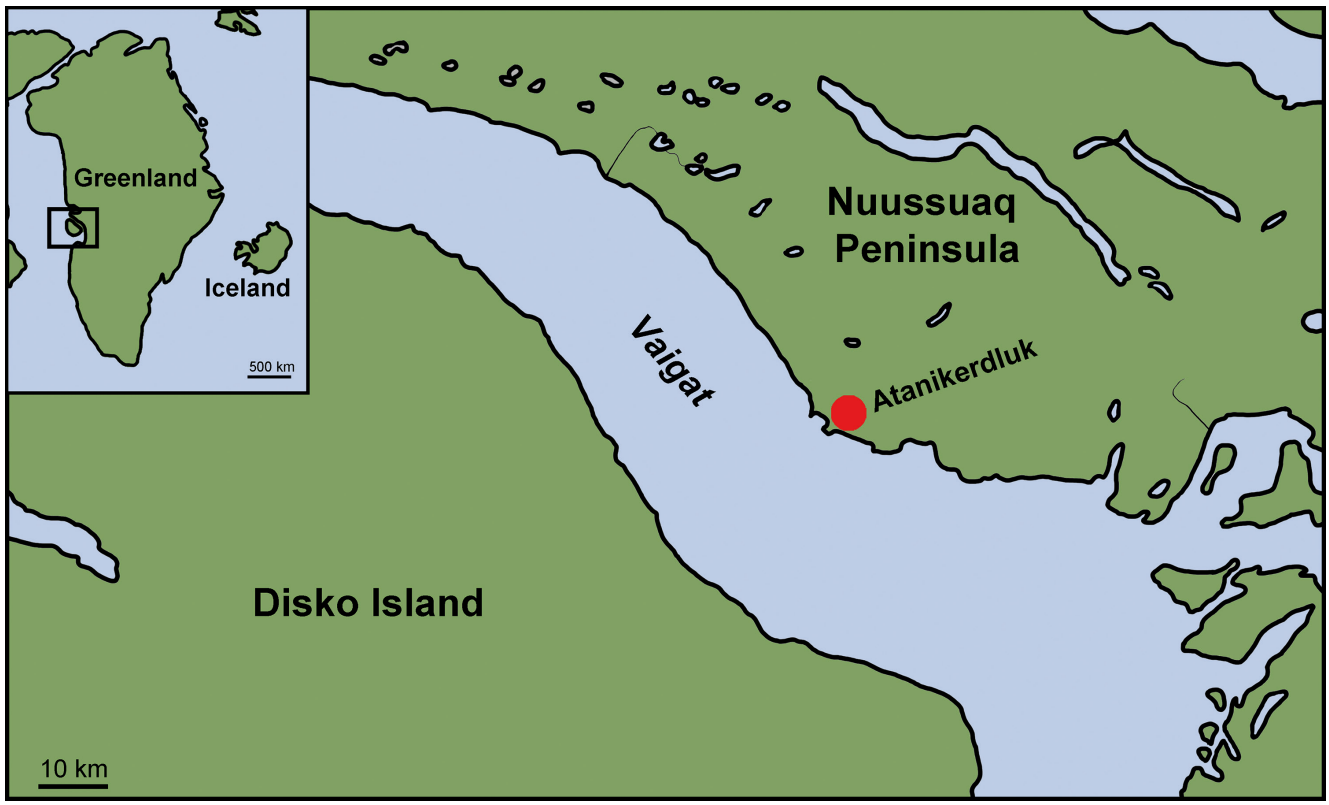


Fig. 1. Type locality of *Trochodendroides richardsonii* (Heer) Krysht. in West Greenland.

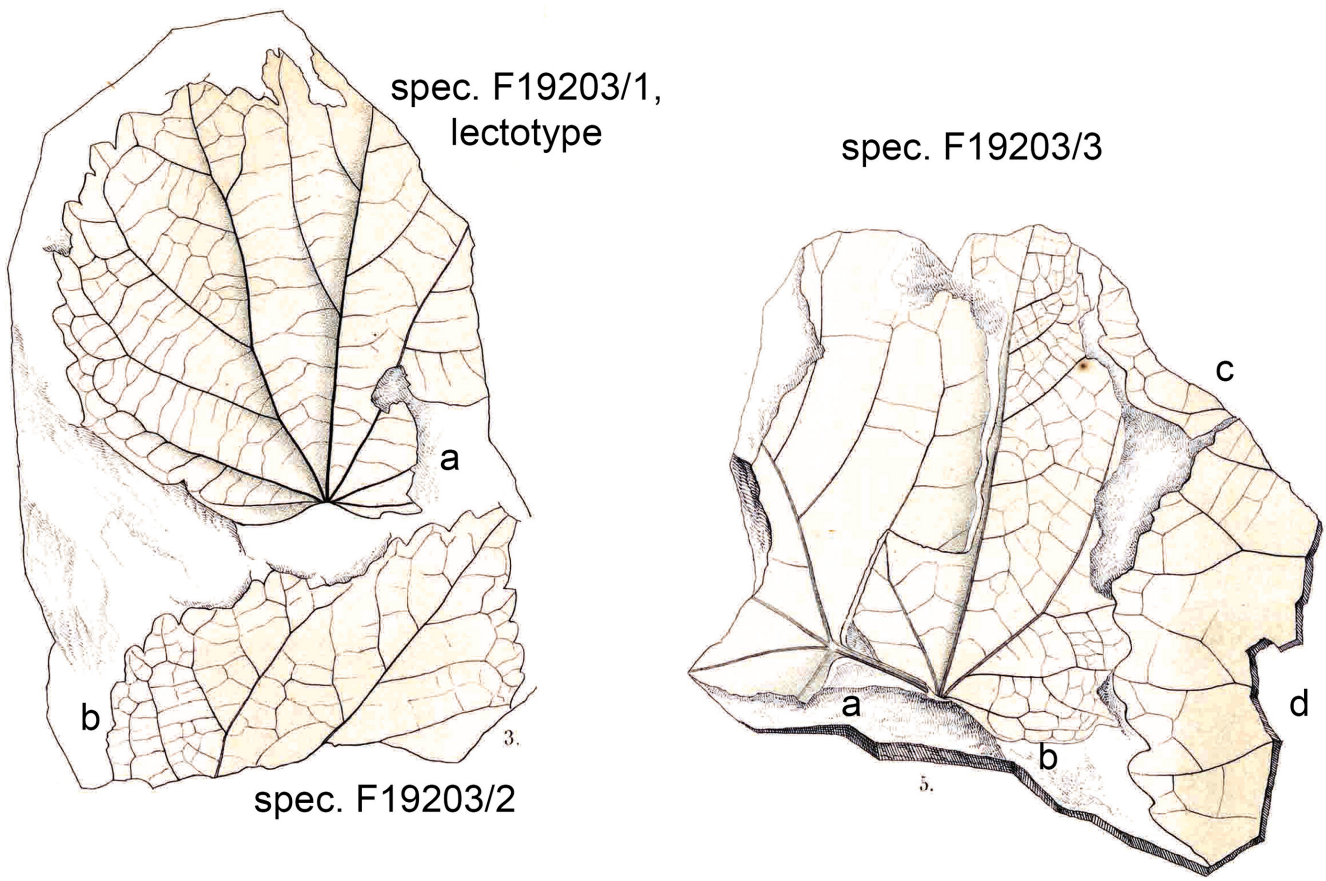


Fig. 2. Original illustration of leaves described by Heer (1868, Taf. IV) under the name *Populus richardsonii* Heer and the corresponding specimen numbers in the National Museum of Ireland collection.

PALAEON-TOLOGY

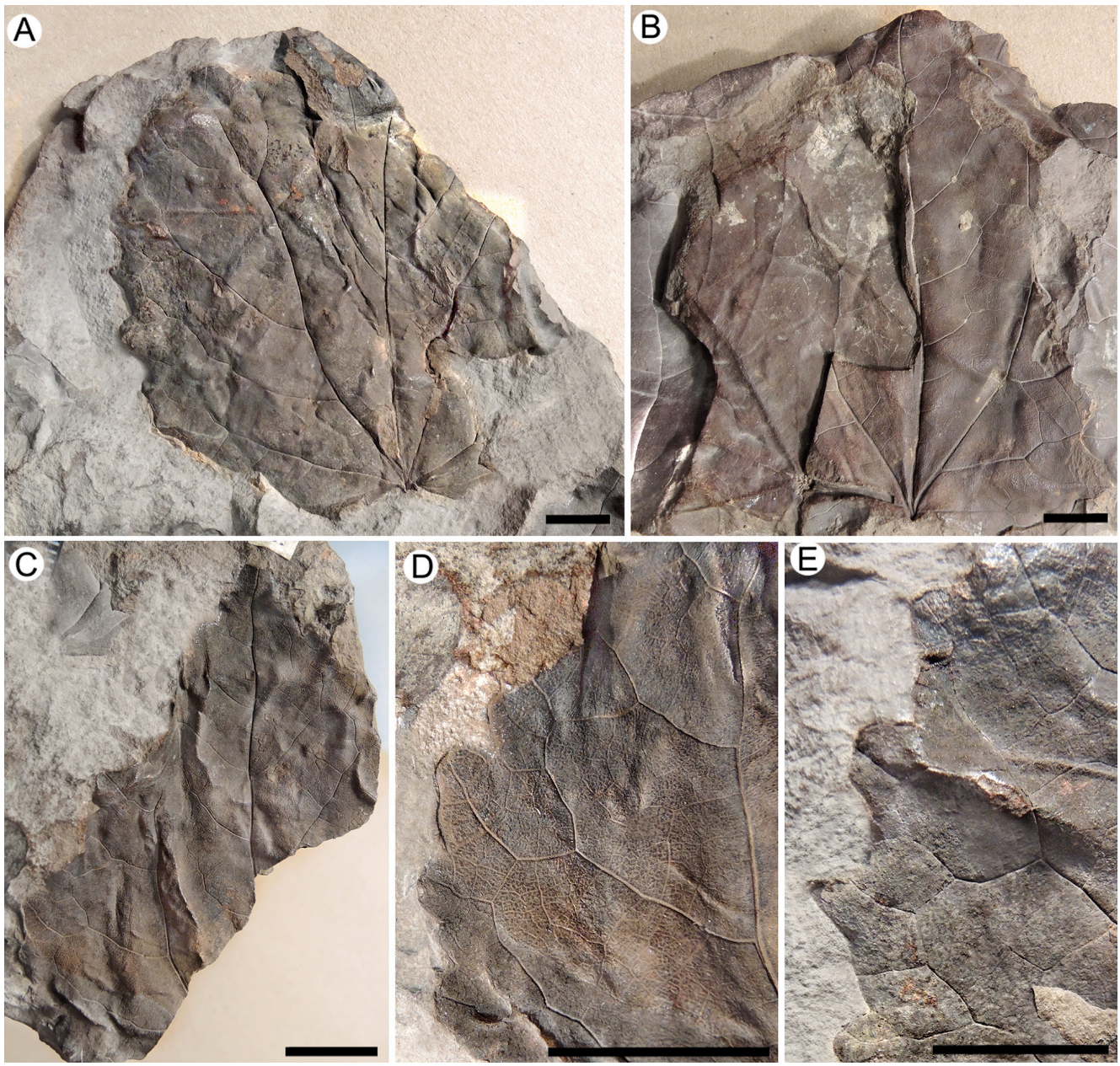


Fig. 3. *Trochodendroides richardsonii* (Heer) Krysht., the Quikavsak Formation, West Greenland: A — spec. F19203/1, lectotype, figured by Heer, 1868, Taf. IV, Fig. 3a, general view; B — spec. F19203/3, syntype, figured by Heer, 1868, Taf. IV, Fig. 5b; C, D — spec. F19203/2, syntype, figured by Heer, 1868, Taf. IV, Fig. 3b: C — leaf apex, D — margin details; E — lectotype margin details, enlarged from A. Scale bar is 1 cm.

simple, regular, large, 3–5 mm in height and 3–6 mm in width, with obtuse or rounded apices and biconvex sides, innervated by thin central vein; venation 3–5 nervous, arena between inner lateral veins usually triangular in shape.

Lectotype (Fig. 3A, E; Fig. 4a): Spec. F19203/1, National Museum of Ireland, Greenland, locality Atanikerdluk, the Quikavsak Formation, the lower Paleocene. Iljinskaja (1971) designated the drawing in Heer's monograph (Heer, 1868, Taf. 4, Fig. 3a) as the lectotype of the species. The place of storage of type material and specimen number of lectotype were first indicated by Budantsev and Golovneva (2009).

Syntypes: National Museum of Ireland, Dublin, Colomb collection, specimens F19203/2, F19203/3.

Heer (1868) depicted ten leaves of *Populus richardsonii* from Atanikerdluk. Eight of them have survived in the collection of National Museum of Ireland. Two specimens, figured in Taf. 4, Fig. 4 and Taf. 15, Fig. 1c, are missing. Some leaves from Collomb collection (Heer, 1868, Taf. 4, Fig. 5a, c, d, Taf. 6, Fig. 7, 8) are fragments without clear diagnostic features. Since there are other species of *Trochodendroides* in the Atanikerdluk flora (Budantsev, 1983; Budantsev and Golovneva, 2009), we do not include these dubious fragments in the type material of *Populus richardsonii.* As syntypes, we consider

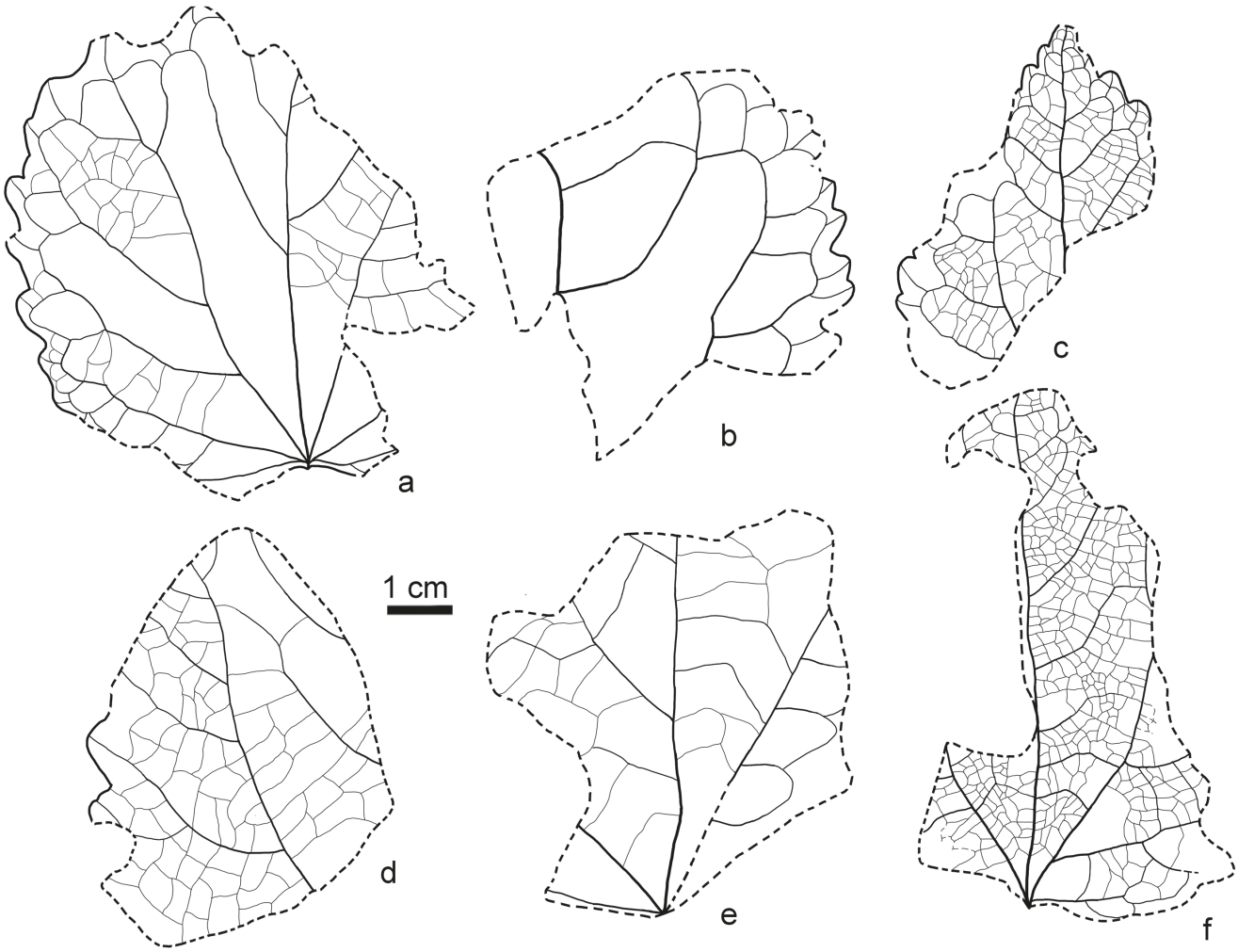


Fig. 4. Drawings of *Trochodendroides richardsonii* (Heer) Krysht., the Quikavsak Formation, West Greenland: a — spec. F19203/1, lectotype, figured by Heer, 1868, Taf. IV, Fig. 3a; b — spec. F19190/2; c — spec. F19203/2, syntype, figured by Heer, 1868, Taf. IV, Fig. 3b; d — spec. F19213A/1; e — spec. F19177/2; f — spec. F19203/3, syntype, figured by Heer, 1868, Taf. IV, Fig. 5b.

only the two almost complete leaves with clearly specific diagnostic characters (Fig. 2; Fig. 3B, C).

Other specimens: In addition to the published material, there are several leaves of *Populus richardsonii* in the Colomb collection that were not depicted in Heer (1868): spec. F19177/2, F19190/2, F19213A/1.

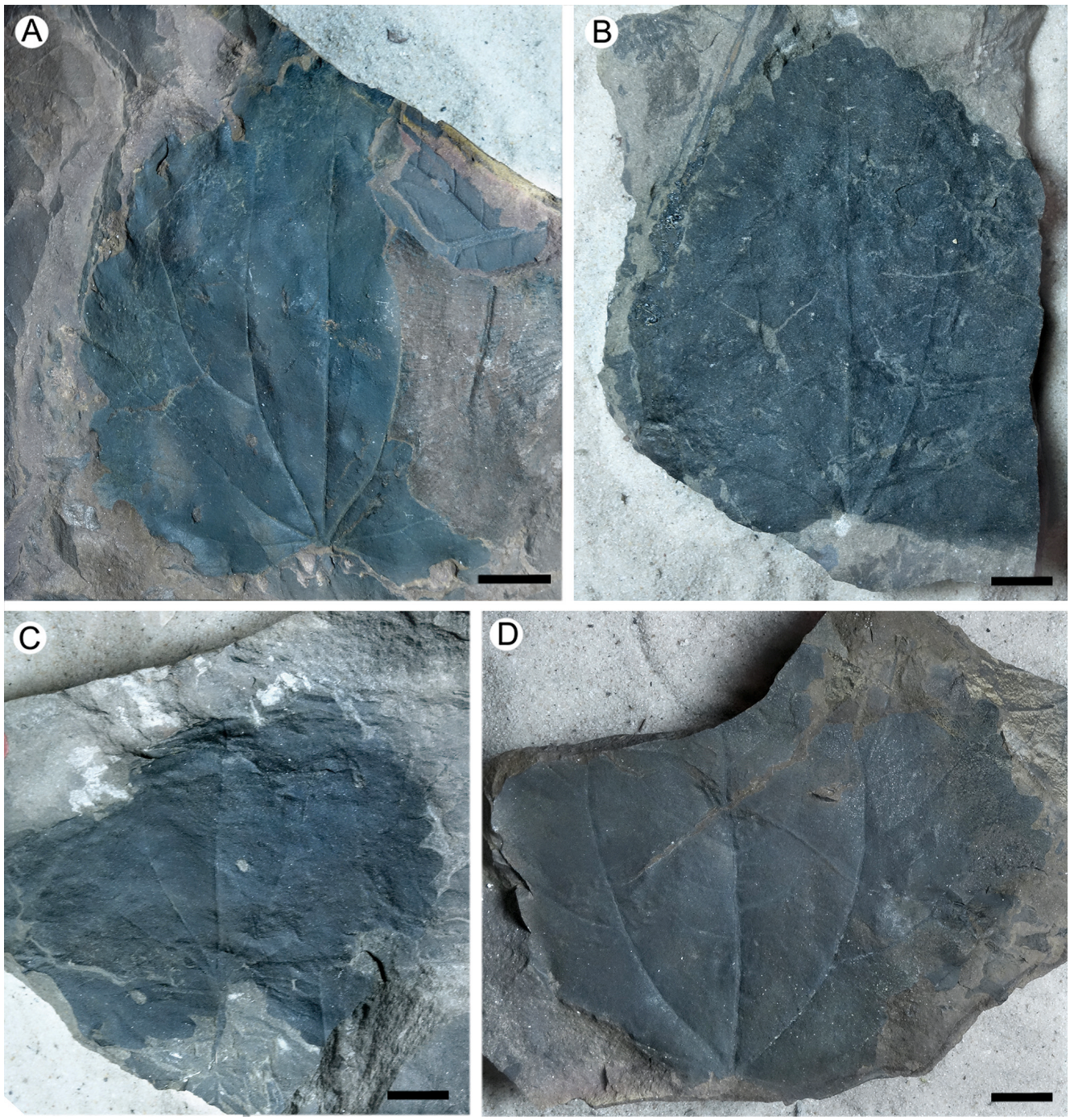
Besides, we attribute to *Trochodendroides richardsonii* the following specimens that were revealed during the re-examination of the original materials from Spitsbergen.

Spitsbergen, the Firkanten Formation, the Danian, collection of the Komarov Botanical Institute of the Russian Academy of Sciences, Saint Petersburg: spec. BIN 952–1–4/14, BIN 951–1–6: spec. 1, 20, 46, 52, 54, 56, 62; Swedish Museum of Natural History, spec. S051864

Description: Leaves are simple, petiolate. Lamina is ovate, widely ovate or widely elliptical, 5–11 cm in length and 5–10 cm in wide, with acute or slightly attenuate apex and slightly cordate or truncate base. Margin is crenate. Teeth are simple or rarely compound, regularly spaced, large (3–5 mm in height and 3–6 mm in width), with convex apical and basal sides. Tooth apex is obtuse or rounded. Sinuses between teeth are acute or rounded, triangular.

Venation is actinodromous, with 3–5 primary veins. Midvein is straight, running to the leaf apex, producing 2–5 alternately arranged secondary veins in the upper one-third of the lamina. Inner lateral veins are thin, curving, connecting with lower secondary veins extending from the midvein. Sometimes inner lateral veins terminate in large teeth. The area between inner lateral veins is usually triangular in shape, sometimes elliptical.

Outer lateral primary veins (if present) are thinner than inner primaries and diverging from the midvein at a wider angle. Secondary veins arising from the midvein and basiscopic branches of inner and outer lateral primaries form series of brochidodromous loops near the margin. Teeth are innervated by thin veins that diverge from loops near the margin. Tertiary veins form irregular connections between the primaries and secondary



Fig, 5. Leaves of *Trochodendroides richardsonii* (Heer) Krysht. from the Firkanten Formation, Spitsbergen: A— spec. BIN 952-1-6/56; B — spec. BIN 952-1-4/19; C — spec. BIN 952-1-6/55; D — spec. BIN 952-1-6/52. Scale bar is 1 cm.

branches. Quaternary veins are very thin, forming an orthogonal network.

Discussion

The species *Populus richardsonii* was described by O. Heer (1868) from the Paleocene Atanikerdluk locality in West Greenland. In the same monograph Heer also referred a leaf from Spitsbergen (locality Kohleberg) to this species. A study of plant fossils in the Swedish Museum of Natural History showed that the leaf from Spitsbergen (Svalbard) actually belongs to the species of *Zizyphoides colombii* (Budantsev and Golovneva, 2009; Zolina, Manchester, and Golovneva, 2021). Thus, the type material of *P. richardsonii* comes from a single locality (Atanikerdluk, Greenland) and from a single collection (Colomb collection, 1854).

In the following year Heer (1869) assigned to *Populus richardsonii* several additional leaves from the same locality (Atanikerdluk), collected by E. Whymper in

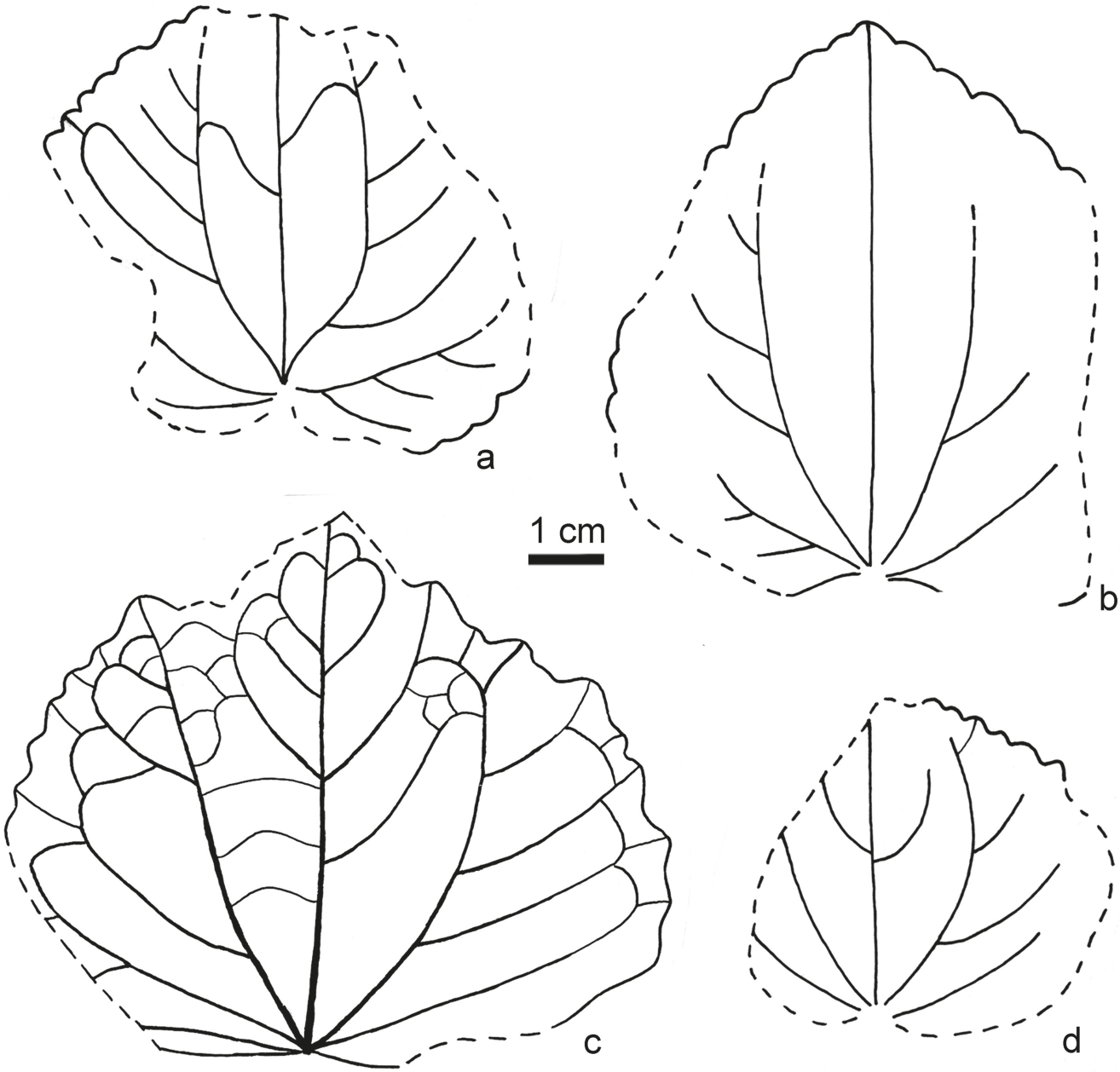


Fig. 6. Drawings of *Trochodendroides richardsonii* (Heer) Krysht. from the Firkanten Formation, Spitzbergen: a — spec. BIN 952-1-6/69; b — spec. BIN 952-1-4/19; c — spec. F19203/2; d — spec. 952-1-6/54. Scale bar is 1 cm.

1867. Three of them (Heer, 1869, Taf. 44, Fig. 7, 9; Taf. 55, Fig. 3) are represented by fragments without clearly diagnostic features. So, we attribute to *Populus richardsonii* only two of those leaves (Heer, 1869, Taf. 44, Fig. 7, 9).

In 1870 Heer again described *Populus richardsonii* from Spitsbergen, locality Cap Staratschin (Heer, 1870). We also considered this material as belonged to *Populus richardsonii,* although not all specimens have clearly diagnostic features (see Systematics).

We also attribute to *T. richardsonii* several specimens from the localities Festningsodden (synonym of Cap Staratschin), Kolfjellet, and Barentsburg, based on the examination of Spitsbergen collections from the Komarov Botanical Institute of the Russian Academy of Sciences and the Swedish Museum of Natural History (Fig. 5, 6). All of these localities now are referred to the Paleocene Firkanten Formation (Budantsev and Golovneva, 2009).

A. Seward and W. Edwards (1941) transferred the species *P. richardsonii* to extant *Cercidiphyllum* based on the material from East Greenland. We doubt that these leaves really belong to this species, although we have not been able to re-examine the original material. Since the modern genus *Cercidiphyllum* appears in the fossil records with condensed rather than racemose infructescences only from the Oligocene (Jähnichen, Mai, and Walther, 1980; Manchester and Meyer, 1987; Kovar-Eder, Meller, and Zetter, 1998), we consider the application

of the generic name *Cercidiphyllum* to the Paleocene species to be questionable without additional evidence.

The combination *Cercidiphyllum richardsonii* (Heer) Seward et Edwards was used also by I. Iljinskaja (1971, 1974a), who designated the lectotype of *Populus richardsonii* based on Heer's drawings.

B. Koch (1963) described leaves of *Populus richardsonii* from the Paleocene Agatdalen Formation of Greenland as *Cercidiphyllum arcticum* (Heer) R. W. Brown. Under this name Brown (1939) united different species from the Cretaceous and Paleogene. The basionym of *Cercidiphyllum arcticum* is *Populus arctica* Heer, which now is considered as a junior synonym of type species of the genus *Zizyphoides* Seward at Conway — *Z. colombii* (Heer) Seward et Conway (Zolina, Manchester, and Golovneva, 2021). Therefore, the use of the name *Cercidiphyllum arcticum* is currently invalid (Golovneva and Alekseev, 2017; Zolina, Manchester, and Golovneva, 2021).

A. Kryshtofovich (1958) transferred *Populus richardsonii* to the genus *Trochodendroides,* because these leaves were significantly different from those of extant *Populus* (Salicaceae). The genus *Trochodendroides* united extinct species, with leaves similar to those of Trochodendreceae and Cercidiphyllaceae (Berry, 1922). We consider *Trochodendroides richardsonii* to be the most appropriate name for the species that was initially described as *Populus richardsonii*. However, the specimens attributed by Kryshtofovich to *Trochodendroides richardsonii* from the territory of Northeastern Russia are currently assigned to another species of *Trochodendroides*: *T. deminii* Yudova et Golovn. (Golovneva, Alekseev, Gnilovskaya, and Yudova, 2017).

Thus, it is confirmed that *Trochodendroides richardsonii* was distributed in the early Paleocene at Greenland and Spitsbergen.

The name *Trochodendroides richardsonii* was also used later by many authors for different leaves from the Cretaceous and Paleogene floras (Herman and Lebedev, 1991; Philippova, 2001; Shczepetov et al., 2020). The revision of all these numerous findings is beyond the scope of this paper, since in many cases this requires a re-examination of the original materials.

Trochodendroides richardsonii has the greatest resemblance to *T. amurensis* (Krysht. ex Iljinsk.) Iljinsk., *T. deminii*, and *T. bidentata* Vassilevsk. et Golovn. All of these species are characterized by ovate shape and crenate margin with large teeth that have rounded apex and biconvex sides.

Trochodendroides amurensis comes from the Paleocene Tsagayan Formation, Amur Region, Russia (Kryshtofovich and Baikovskaya, 1966; Iljinskaja, 1974c). It differs from *T. richardsonii* by smaller and more frequent teeth and by narrower laminas. Leaves of *T. amurensis* are characterized by an elliptical area between inner lateral veins, while those of *T. richardsonii* have a triangular area in this position.

The species *T. deminii* was described from the Turonian-Coniacian Chingandzha Formation, North-East of Russia (Yudova and Golovneva, 2014). Later, Golovneva, Alekseev, Gnilovskaya, and Yudova (2017) recorded it in the late Albian–early Turonian Krivorechenskaya Formation (Anadyr River basin), the Coniacian Tylpegyrgynay and Poporechnaya formations (Pekulney Ridge), the Coniacian Valizhgen Formation (Cape Konglomeratovy), the Coniacian Amka Formation (Ulya River basin), the lower Campanian Upper Bystrinskaya Formation (Cape Valizhgen, Northwestern Kamchatka), and in the Maastrichtian Kakanaut Formation (Koryak Upland). This species is distinguished from *T. richardsonii* by smaller and narrower leaf blades and by smaller and narrower teeth. *T. deminii* also has an elliptical area between inner lateral veins.

Leaves of *T. bidentata* from the Maastrichitian-Danian part of the Rarytkin Formation are similar with leaves of *T. richardsonii* by large leaf blades with truncate to cordate base and acute or attenuate apex, and also in the triangular area between inner lateral veins. But *T. bidentata* differs by large double teeth.

Besides *Populus richardsonii,* Heer (1868) described two other species of the genus *Populus* from Atanikerdluk*: P. zaddashii* Heer and *P. arctica*. The first species differs by a dentate margin with small frequent acute teeth. *P. arctica* is distinguished from *P. richardsonii* by an entire, undulate, crenate or irregularly dentate margin. In addition, teeth of *P. arctica* are innervated by thin loops, while those of *T. richardsonii* are innervated by a vein that terminates in the tooth apex.

Berry's (1926) transfer of *P. arctica* to the genus *Trochodendroides* and species *Trochodendroides arctica* (Heer) Berry was followed in many Cretaceous and Paleogene floras (Seward and Conway, 1935; Kryshtofovich and Baikovskaya, 1966; Krassilov, 1976; Budantsev, 1983; Budantsev and Mokhov, 1986; Golovneva, 1994; Manchester, Chen, Geng, and Tao, 2005; Budantsev and Golovneva, 2009). However, the type material of *T. arctica* should be assigned to the genus *Zizyphoides* of the family Trochodendraceae (Crane, Manchester, and Dilcher, 1991; Zolina, Manchester, and Golovneva, 2021).

Conclusion

In result of the re-examination of the *Trochodendroides richardsonii* type material, the emended diagnosis of this species was provided and the photos of lectotype and syntypes were presented for the first time. The analysis of findings of this species in Arctic floras showed that *T. richardsonii* was best documented only in the early Paleocene in Greenland and Spitsbergen. Other records of this species in the Cretaceous and Paleogene floras need careful reconsideration in light of a more detailed comparison with the type material.

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