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NEW HAMAMELID FRUTIFICATION FROM THE PALEOGENE OF KAMCHATKA, WITH COMMENTS ON *Trochodendrocarpus* AND *Nordenskioldia*

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Abstract. *Itelantha*, a new genus of spicate inflorescence-bearing flowers with bicarpellate gynoecia and small distinct sepals is described from the uppermost Paleocene-Lower Eocene of northwestern Kamchatka. It enlarges the diversity of Paleocene hamamelidaceans represented by the dominant *Nyssidium-Trochodendrocarpus* group. *Nordenskioldia*, another widespread genus, may represent a separate family related to magnoliids or hamamelids.

Новый род *Itelantha* описан по соплодием отношений верхнего палеоцена – нижнего эоцена Камчатки. Плоды развивались из бикарпеллятного гинецея с остающимися листочками околоцветника. Этот род дополняет разнообразие палеогеновых гамамелид, представленных также доминируюшей группой *Nyssidium – Trochodendrocarpus*. Другой широко распространенный род *Nordenskioldia* представляет самостоятельное семейство, близкое к магнолиевым и гамамелиевым.

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Introduction

Hamamelidaceae is phylogenetically important as a core family of Hamamelidales, a major order of angiosperms. Until recently, next to nothing was known of the early history of this family, although Platanaceae, a related family, has an extensive fossil record. Presently, the geological history of hamamelidaceans is traced to the Early Cretaceous [5, 7]. It appears, however, that the Paleocene was the acme for the lower hamamelids. Major Eurasian and North American plant localities of this age contain abundant fructifications that have been compared to *Nyssa* or *Cercidiphyllum* [1, 8]. Krassilov [10, 11] has described some of them as paniculate infructescences with paired proximally fused follicles, thus assignable to Hamamelidaceae and for the first time emerging as a dominant plant group. We will comment on some controversial opinions about this and related groups of Paleocene plants.

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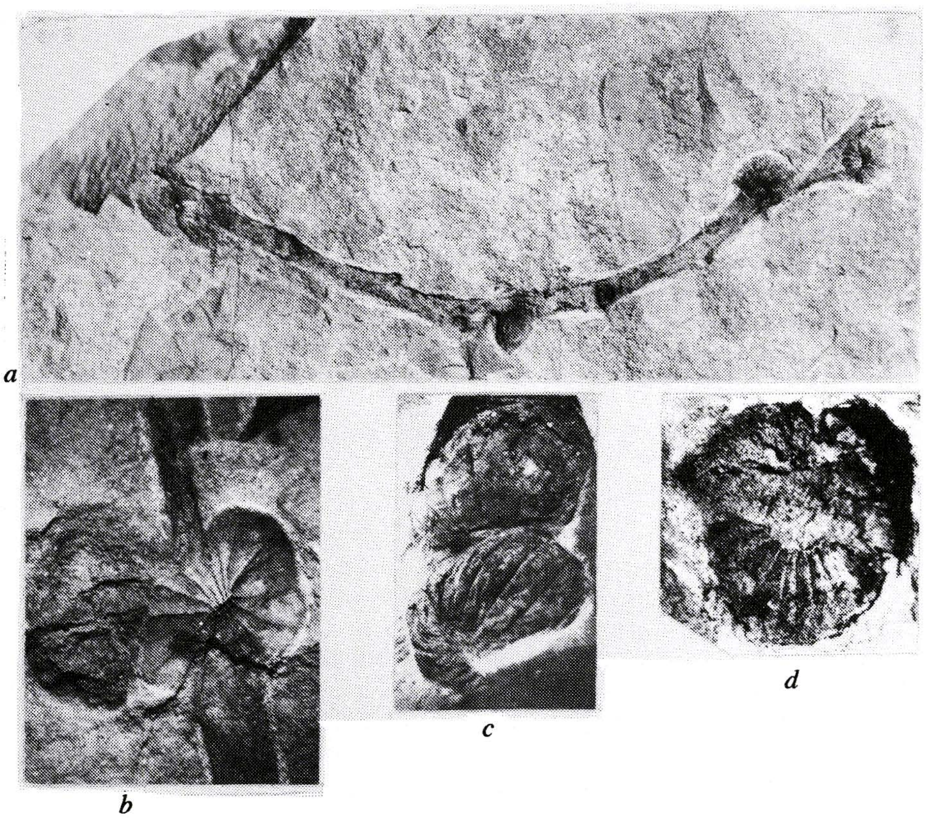


Fig. 1. *Nordenskioldia borealis* Heer: *a* - fruiting twig, ×1; *b* - fruit emerging from its calyptra which remains attached to axis, ×5; *c* - fruit (top) preserved alongside the open calyptra, ×5; *d* - open calyptra still containing fruit, ×5.

Trochodendrocarpus Kryshtofovich

Type species. *Trochodendrocarpus arcticus* Kryshtofovich, 1958 [13].

Neotype. No. 563-221, Krassilov [1], p. 60, pl. XXI, fig. 1, Tsagajan locality near mouth of Bureya River, Lower Paleocene.

Comments. Kryshtofovich [13] has identified this species as "*Nyssa*" *arctica* Heer [8]. While it has been shown that *Nyssidium arcticum* is generically, or at least specifically distinct from *Trochodendrocarpus* [2], the latter must be assigned to a different species for which the name *Trochodendrocarpus arcticus* can be validated by retypification. Since Kryshtofovich's collection is lost, a neotype has been selected from the Tsagajan collection described in [11]. Crane [2] has interpreted *Trochodendrocarpus* as a leafy twig bearing racemose fructifications rather than panicles. However, all the specimens from the Tsagajan locality, and there are several dozens of them, are branched infructescences which obviously have been shed as a unit. There are no definite leaf scars and the side branches diverge at regular intervals and angles. Therefore, the original interpretation of *Trochodendrocarpus* as a large (about 50 cm long) panicle

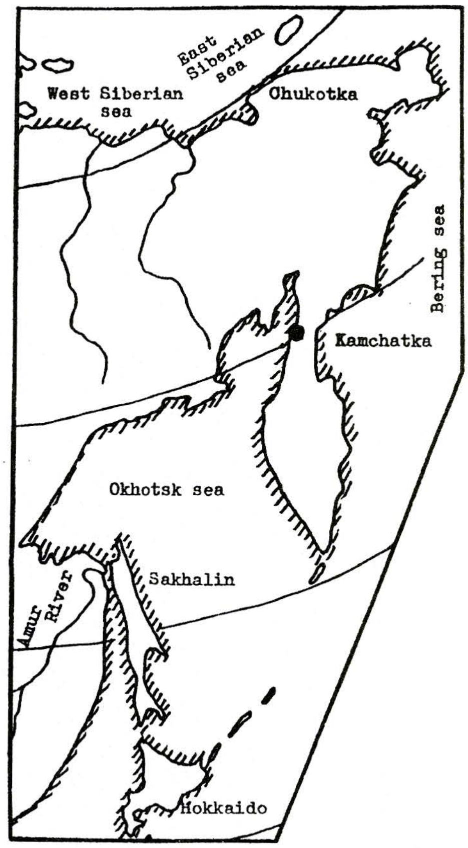


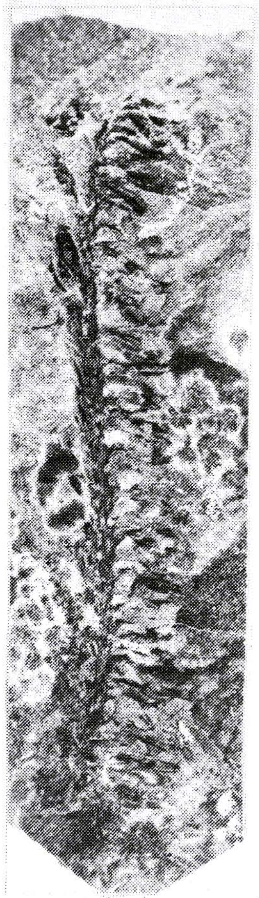
Fig. 2. Locality of *Itelantha densiflora* gen. et sp. nov.

is retained here. The plant might have been a small tree producing a few such panicles high in the crown, like extant aralias.

As for the supposed relationship of the *Trochodendrocarpus-Nyssidium* group to *Cercidiphyllum*, a single genus of Cercidiphyllaceae currently in the order Trochodendrales, we could not find any reliable evidence of phylogenetic continuity. *Cercidiphyllum* have pseudanthia of four, perhaps originally decussate, flowers consisting of a single abaxially dehiscent follicle subtended by a bract. To produce such a structure from *Trochodendrocarpus* or *Nyssidium*, the panicle or raceme has to be reduced to a single flower, one carpel of the syncarpous pair has to be lost, and the dehiscent suture has to be reversed [2].

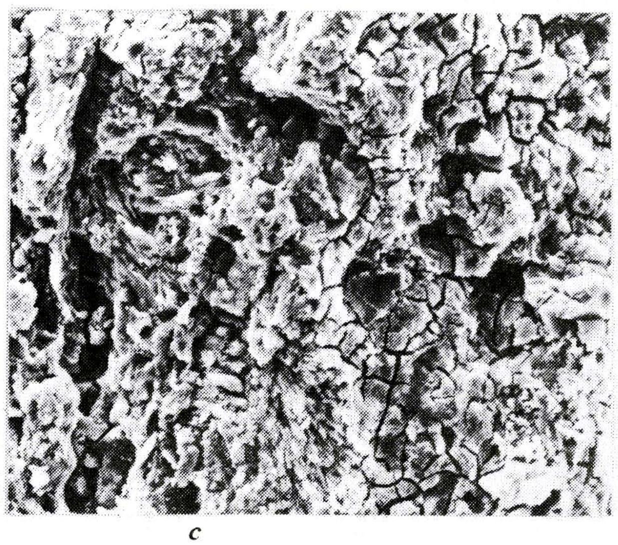
However, *Trochodendrocarpus*-type morphology has remained fairly constant for about 50 mln years, while the unmistakable *Cercidiphyllum* pseudanthia appeared in the Miocene some 40 mln years after the time of vigorous dispersion and diversification of the *Nyssidium-Trochodendrocarpus* group.

It seems more parsimonious to derive *Cercidiphyllum* from the early ranunculids, such



a

b



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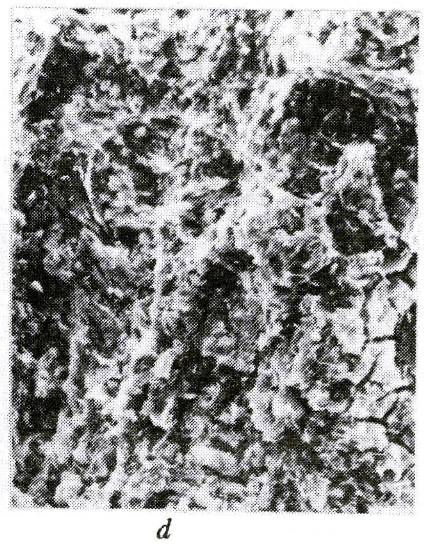

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as *Caspiocarpus* with apocarpous abaxially dehiscent follicles [12]. The Trochodendrales might then be conceived of as true "woody Ranales," that is, sister group of ranunculids in which the woody habit is derived. However, this remains an open question.

Nordenskioldia Heer

Type species. *Nordenskioldia borealis* Heer [9], p. 65, pl. 11, figs. 1-13, Paleocene of Spitsbergen, revised in [4], p. 1314, figs. 2-4.

Comments. *Nordenskioldia* includes the easily recognizable fruit remains known from each of the larger Paleocene plant localities in northern Eurasia and North America. The fruits consist of about 20 fruitlets arranged in a single circle on the apically protruding receptacle. The fruitlets are laterally connate at the ovary level, with the persistent free short reflexed styles, separable when ripe, with a single seed.

These fruits are borne singly or in pairs on very long axes that have been found in the Amur Province, Mongolian and North American localities [3, 4, 14, 15]. Some infructescences are bearing umbrella-like structures from which the fruits have fallen.

Crane et al. [3, 4] and Manchester et al. [15] have supported an earlier suggestion of trochodendracean affinity [13], although the inflorescence morphology (loosely spicate in *Nordenskioldia* vs. cymose in *Trochodendron*), fruit type (follicetum vs. septicidal capsule), and seeds are entirely different. The interpretation of umbrella-like structures as exocarps [4] is rather questionable, the more so that in the Tsagajan (Amur Province) material these structures are bivalvate and calyptrate, spreading umbrella-like after the fruits are shed (fig. 2).

Moreover, there is some evidence from buds and incompletely preserved flowers that *Nordenskioldia* had heterochlamydeous perianths (fig. 1). In the latter case the caliptrate umbrellas could be formed of connate tepals, as in Magnoliaceae and some Hamamelidaceae.

Other families with similar gynoecial structures are Illiciaceae, with apically protruding receptacles and radially spreading one-seeded follicles, and Menispermaceae, with whorled apocarpous carpels and closely comparable leaf morphology, but distinct in the seed characters. We feel that *Nordenskioldia* represents a separate extinct family (Nordenskioldiaceae), perhaps related to magnoliids or hamamelids.

Itelantha Krassilov et Fotyanova, gen. nov.

Name. After Itelmen, indigenous people of Kamchatka, and *anthos* - flower.

Fig. 3. *Itelantha densiflora* gen. et sp. nov.: *a* - fruiting axis, holotype No. 487-23, ×1.3; *b* - part of same, showing bracts and tepals at base of three distal flowers, ×8; *c, d* - stomata on impression of follicle, SEM, ×500 and ×700.

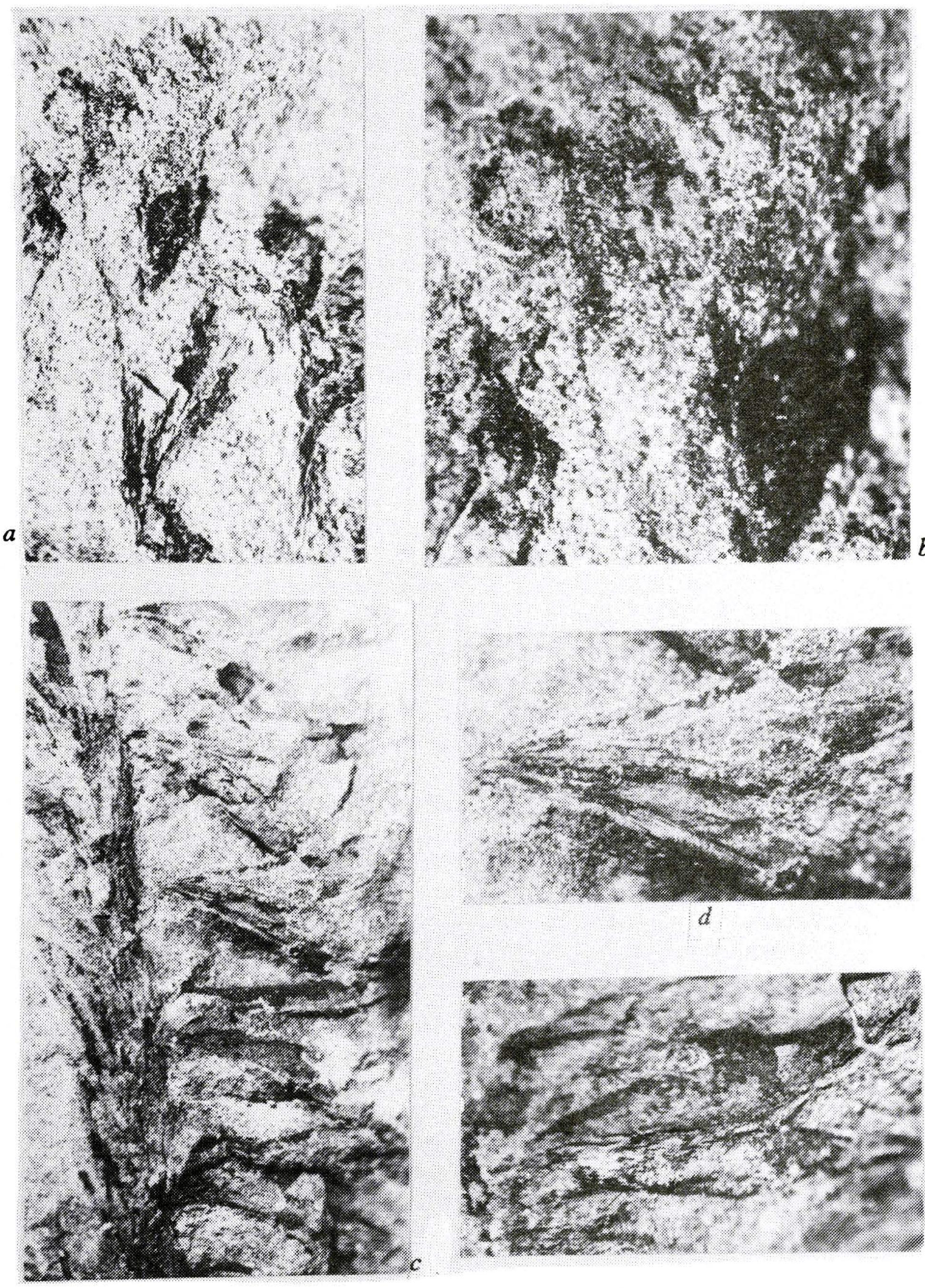

Fig. 4. ***Itelantha densiflora*** gen. et sp. nov.: *a* - paired follicles with seed at distal end of left follicle, ×9; *b* - seed magnified, ×20; *c* - part of fruiting axis, ×5; *d* - paired follicles, ×9; *e* - split follicle, ×9.

Type species. *Itelantha densiflora* Krassilov et Fotyanova, sp. nov., northwestern Kamchatka, Late Paleocene-Early Eocene.

Diagnosis. Dense spike of unisexual flowers in axils of small bracts. Perianth of small tepals adnate to base of ovary, persistent at fruit. Gynoecium of two proximally fused, distally diverging carpels developing into adaxially dehiscent follicles. Seeds several to many per locule, narrowly winged in median plane, slightly notched at micropylar end.

Itelantha densiflora Krassilov et Fotyanova sp. nov.

Figs. 3-5

Name. From *densus* (L.) - dense, and *floris* (L.) - flower.

Holotype. Coll. 3736, No. 4/87-23, Paleontological Institute, Moscow, Evrava-veyem River, northwestern Kamchatka, Upper Paleocene - Lower Eocene.

Locality. The fruiting axis came from the Upper Paleocene Tkaprovayam Formation of conglomerates and sandstones with shale interbeds, cropping out along the Evrava-veyem River, northwestern Kamchatka. This locality occurs 1.5 km upstream of the mouth of its tributary, Kupol Creek. It was found in 1987 by Fotyanova who preliminarily identified leaf remains of *Magnolia* sp., *Trochodendroides arctica* (Heer) Berry, *Platanus* sp., *Alnus beringiana* Budants., *Populus* sp., *Nyssa budantsevii* Fotyanova, *Ambroma* sp., *Cornophyllum svidiiformis* Budants., *Aesculus magnificum* (Newb.) Iljinsk., *Rhus* sp., *Leguminosites* sp. (pod), "*Cordia*" *kamchatica* Cheleb., *Ceanothus* sp. and *Peculnea* sp.

This floristic assemblage dominated by *Nyssa* and *Ambroma* is thought to be stratigraphic-

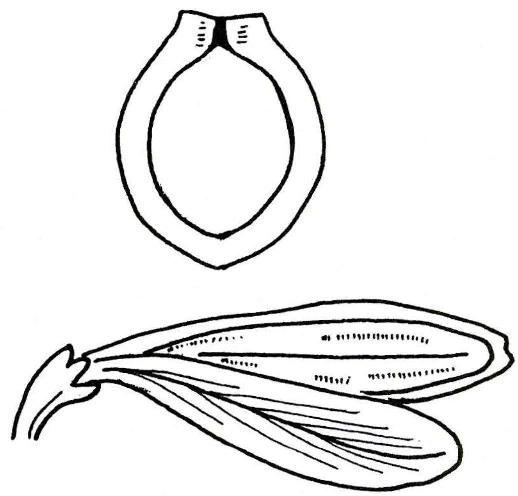

Fig. 5. *Itelantha densiflora* gen. et sp. nov., paired follicles and seed.

cally equivalent to the coastal Chemurnaut locality assigned to the Upper Paleocene-Lower Eocene by Sevora, Fotyanova and Fradkina [16].

Description. A single specimen is an impression of an incomplete fruiting axis preserved on a gray shale slab. The axis is 70 mm long, 1 mm thick, bearing ca. 38 flowers at fruiting stage. Most of the flowers are on one side of the axis (to the right in fig. 3) while those on the other side are buried in the rock, typically showing one of the follicles. This arrangement suggests that the flowers were originally borne in two rows in a one-sided spike or raceme. They are about 2 mm apart, practically sessile, although with a very short decurrent stalk. A small bract less than 1 mm long is discernible in most flowers, while the minute tepals at the base of the gynoecium are seen in a few flowers only.

No more than two sepals are seen on the impression, suggesting four as their most probable number. The sepals are free, rounded-triangular, adaxially slightly convex. No stamen scars are discernible.

The gynoecium consists of two carpels proximally fused about 1/3 of their length, then diverging at acute angle. The carpels are about 18 mm long, dehiscent along the adaxial suture (facing away from the subtending bract), abaxially showing a prominent keel from which thin but distinct striation spreads at acute angle, distally stretching almost parallel to the keel. The apices of the follicles are rounded or slightly notched, lacking any remains of stigmatic structures. Some follicles are variously bent or folded, their impressions appearing not to be woody structures.

Impression fragments mounted for SEM occasionally show outlines of sinuate cell walls, as well as rather dense stomata, some contiguous, variously oriented, with guard cells sunken in rounded stomatal pits surrounded by no less than six radially disposed subsidiary cells.

No seeds have been observed within the locules. However, three seeds are preserved at the tips of three different follicles. These seeds are ovate, slightly pointed at chalazal end, truncate and slightly notched at the micropylar end, 1.1 mm long with a central body about 2/3 of their length.

Comparison. This fruiting axis shows a typical hamamelidacean gynoecial structure of two proximally united, distally free carpels developing in follicular fruits. Spicate inflorescences and much reduced tepals are also common in the Hamamelidaceae. The seed size suggests many, or at least several, ovules per locule, which is less common in the latter family. The position of a few preserved seeds protruding from the follicles agrees with a dispersal mechanism by which the seeds are squirted out from the locule by the pressure of contracting fruit walls, as in *Hamamelis* [17]. The Kamchatkan fossil is obviously different form the recently described Cretaceous hamamelidacean flowers which are epigynous or semiepigynous with hypanthial perianths [5, 7]. These flowers are either longly stalked, perhaps solitary, or borne in compact heads.

The more readily comparable group is *Nyssidium-Joffrea-Trochodendrocarpus* from Paleocene and younger deposits of Eurasia and North America. At least in *Trochodendrocarpus*, but perhaps also in other genera of the group, the gynoecia consist of two proximally fused carpels which are externally similar to those of *Itelantha*. However, in the *Nyssidium* group, flowers are borne in loose racemes or panicles rather than dense spikes and they are distinctly stalked. Furthermore, they do not show persistent tepals and their seeds have a well-developed one-sided wing.

The dense spicate inflorescence of *Itelantha* suggests a pollination vector different from both *Archamamelis* (which could be beetle-pollinated like the majority of epigynous flowers) and the loosely racemose or paniculate and supposedly wind-pollinated *Nyssidium*-group.

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