Leaf and Fruit remains of *Davidia* (Cornales) from the Nezhino Flora (Miocene of Primorye)

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Abstract—The geology of beds containing the Nezhino flora is outlined. The taxonomic composition of the flora is discussed. The flora is dated to the second half of the Early Miocene on the basis of geological, paleobotanical, and radioisotope information. Leaf and fruit imprints are described as new species of *Davidia* Baillon.

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INTRODUCTION

The Nezhino flora was found in 2006, in southern Primorye, in the lower course of the Razdol'naya River, 3 km north of the village of Nezhino (Fig. 1). The locality (site 9180) is situated at 43°29' N and 131°47' E. Geologically, the flora is related to Nezhino beds of the Pushkinskaya Depression. The type section of the beds is situated at the southern margin of the depression. Fossil plants were collected in an open-pit lignite mine. Below, a bed-by-bed description of the plant-bearing beds is given. The following beds overlay (with washouts) the Verkhnii coal seam of the Pavlovka Formation (Upper Oligocene).

1. Light gray sandstone is loosely cemented, medium-grained, coarse-grained at the base of the bed, with thin (up to 5 cm) siltstone bands enriched with lignitified plant debris4.0

2. Yellowish-white laminated tuff-siltstone is firmly cemented (by ferruginous and siliceous material), with lenses of lapilli tuff and bands of finely laminated yellowish-gray siltstone (up to 0.2 m). Numerous imprints of leaves and fruits occur throughout the layer.....1.0

3. Siltstone is dark olive-green, with finely fractured cleavage......0.2

4. Coal is lignitic, strongly decomposed, and relatively friable.....0.2

The total thickness is 5.4 m.

The section is overlain (with a stratigraphic gap) by pebbles of the Upper Miocene Ust'-Suifun Formation. The beds, which are slightly thicker than 5 m in the open-pit mine, become thicker northwards, up to some dozens of meters in the center of the depression. Tuff also becomes more prominent in this direction: lenses of psammitic tuffs appear, which are almost completely composed of rhyodacitic volcanic glass; bands of lignitified plant remains transforming into lignites are also characteristic.

Plant-bearing rocks feature thin-slabcleavage and extraordinary firm siliceous cementation. Often, they are intensely limonitized along microcracks coinciding with the bedding surfaces. The limonitization colors the

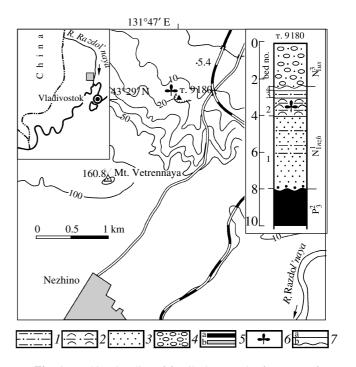
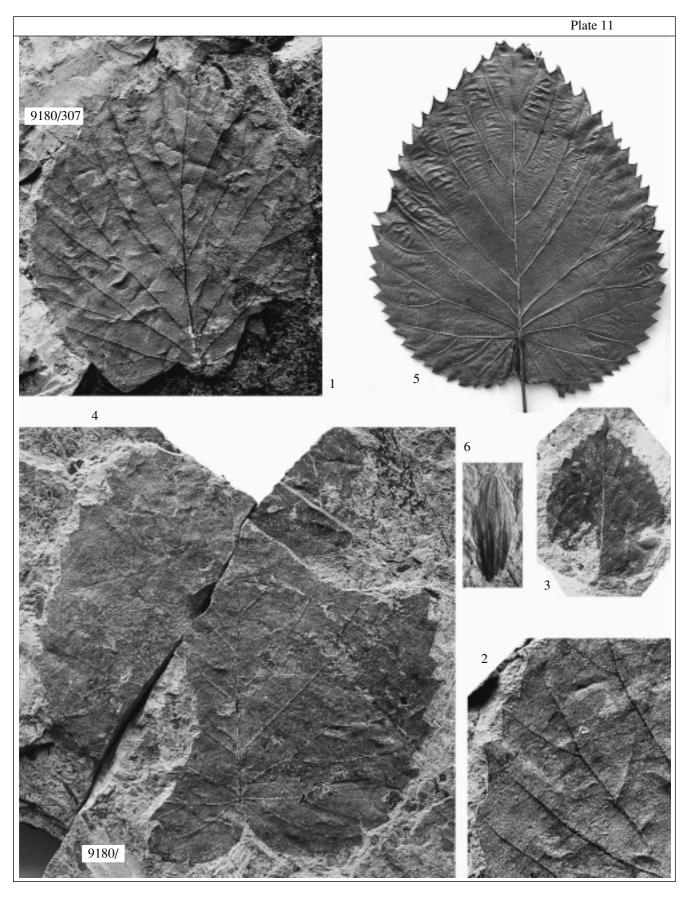


Fig. 1. Nezhino locality of fossil plants and a fragment of the lithological-stratigraphic column (site 9180): (1) silt-stone; (2) tuff-siltstone; (3) medium-grained sandstones, basally coarse-grained sandstones; (4) pebbles; (5a) brown coal; (5b) lignites; (6) fossil plants; (7a) lithological bound-aries; (7b) stratigraphic unconformities.



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Explanation of Plate 11

Figs. 1–4. *Davidia palaeoinvolucrata* sp. nov.: (1) holotype FEGI, no. 9180/307, \times 1; (2) specimen FEGI, no. 9180/307, leaf fragment \times 2; (3) specimen FEGI, no. 9180/414, \times 1; and (4) specimen FEGI, no. 9180/303, \times 1.

Fig. 5. Modern species Davidia involucrata Baillon, leaf, ×1, China, Yunnan Province, collected by the author.

Fig. 6. Davidia nezhinoensis sp. nov., holotype FEGI, no. 9180/36, ×1.5, endocarp.

surface of the beds brownish-red. Along the cleavage surfaces these rocks are overfilled with coalified plant debris. Leaf imprints are visible against the background of these debris. The tissue of the leaves is coalified, and patterns of venation and leaf margin are indistinct. Such leaf remains virtually defy preparation because the enclosing rock is both strong and brittle. The specimens confined to the bands of yellowish gray siltstones are more easily prepared: these siltstones do not contain plant debris and are not so firmly cemented. Similarly to the rocks of the first type, leaf remains occur separately, not overlapping each other, but they are much rarer and nearly identical to the enclosing rock in color. This flora is represented by fairly large leaves. Thus, leaves of some members of the Betulaceae reach 15 cm in length, and this feature is also characteristic of the Fagaceae and Salicaceae.

The collection comprises slightly more than 500 specimens of mostly leaf remains and rarer fruits. The assemblage is overwhelmingly dominated by angiosperms. There are only isolated conifer specimens: needles of Pinus miocenica Tanai, deciduous shoots of Taxodium and Glyptostrobus, and winged seeds of Keteleeria and Larix. Of interest is the presence of the ferns Osmunda and Dryopteris, which are quite untypical of the Miocene floras known in Primorye. In particular, Osmunda greatly resembles Osmunda cf. japonica Thunb. from the Miocene of Honshu Island (Japan) and differs from the widely known Paleocene O. sachalinensis Krysht.

Small coalified leaf fragments of monocots form aggregations on contacts between beds. These fragments are often undeterminable even at the generic level. The larger fragments are uncommon and belong to Phragmites and Typha. Dicots are characterized by the maximal taxonomic diversity. The preliminary examination of this collection has allowed the identification of about 90 species belonging to 57 genera and 31 families. Several morphotypes remain undetermined even at the familial level. The flora is mixed and polydominant, although members of valley associations are most prominent: Populus (five species), Salix (six species), Ulmus (three species), Zelkova, Pterocarya (four species, leaflets and fruits), Cyclocarya, Carya, and Juglans. Plants growing exclusively or mostly on slopes are also very diverse. These are members of the Betulaceae (Betula, Carpinus, Ostrya, and Corylus), Aceraceae (five species of Acer, including those with compound leaves), Rosaceae (Sorbus, Pyrus, and Rubus), Actinidiaceae, Vitaceae, Tiliaceae, Araliaceae, and Celastraceae. The flora is characterized by thermo-

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philic elements, which are nowadays related to subtropics and the south of the warm temperate area. Arborescent members of the Fabaceae (four distinct morphotypes) are clear evidence that the flora was thermophilic. Moreover, the presence of *Liquidambar*, *Celtis, Theaceae, Idesia, Meliosma, Nyssa, Alangium, Paliurus, Grewia, Parthenocissus*, and *Cissus* was established. Currently, I am not sure about the presence of Lauraceae, since its members *Lindera* and *Litsea* are difficult to diagnose by examining leaf remains. Of particular interest is the record of leaves and fruits of *Davidia*, an endemic of mountainous subtropical forests of southwestern China. The collection contains 17 variously preserved leaf imprints and 5 endocarps.

The age of the Nezhino flora is an important question, which should be solved based on the stratigraphic position of the plant-bearing beds and taxonomic composition of the flora. As previously noted, the plantbearing beds are overlain by pebbles, which correspond to the Ust'-Suifun horizon both in lithology and in the composition of the plant assemblage (Baikovskaya, 1974). The absolute age of its lower boundary was estimated to be 12.3 Ma by K-Ar method using the monofraction of volcanic glass (Pavlyutkin et al., 1999). The contact between the beds, which is exposed over a distance of at least 100 m, shows evidence of a deep washout.

The lower boundary of the plant-bearing beds is also quite remarkable. The loosely cemented sandstones at the base of the beds transform into solid and thicker sandstones toward the opposite (northern) pit wall and are underlain by fine-grained clastic rocks (siltstones and argillites with two lignite seams of workable thickness). This boundary also can be interpreted with confidence as a stratigraphic unconformity. The previously studied underlying beds fit the Upper Oligocene or a transitional Oligocene–Miocene interval (Pavlyutkin and Petrenko, 1994). Consequently, the beds containing the Nezhino flora are dated based on geological data within the second half of the Early Miocene.

This conclusion agrees well with data on the flora composition. On the one hand, no Paleogene elements have been recorded from the Nezhino assemblage, which is also true for both Eocene and Early Oligocene (so-called Engelhardtian) elements, not counting few transient conifers, such as *Taxodium* and *Glyptostrobus*. Therefore, the Nezhino flora cannot be considered as an Eocene–Early Oligocene flora. It does not share any common species with the underlying Oligocene Pavlovka flora. The latter flora is temperate and homogeneous in composition. *Nelumbo nipponica* Endo,

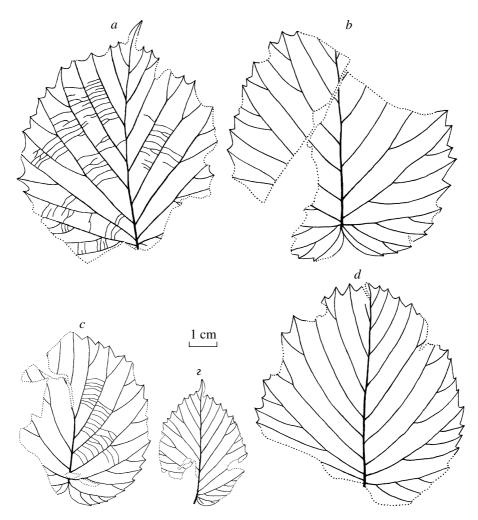


Fig. 2. Leaves of *Davidia palaeoinvolucrata* sp. nov.: (a) specimen FEGI, no. 9180/307; (b) specimen FEGI, no. 9180/303; (c) specimen FEGI, no. 9180/465; (d) specimen FEGI, no. 9180/414; (e) specimen FEGI, no. 9180/290. Nezhino locality of fossil plants: Early Miocene, Primorye.

Salvinia neurolaqueata Fotjan., and *Potamogeton* sp., which are aquatic or semiaquatic plants, are prominent in the Pavlovka flora. The assemblage is dominated by leaves of *Populus* cf. *marchenkoi* Cheleb.

On the other hand, the Nezhino assemblage is related to the Miocene assemblages of Primorye (Sinii Utes, Khanka, and Ust'-Suifun) and floras of the optimal Miocene of Japan (Utto flora) and China (Shanwang flora), with closest similarity with the Shanwang flora. The conifers have an extremely low proportion in both floras. These floras also share many common or closely related species: Betula mioluminifera Hu et Chaney, Carpinus miofangiana Hu et Chaney, Castanea miomollissima Hu et Chaney, Juglans miocathayensis Hu et Chaney, Kalopanax acerifolium Hu et Chaney, Euonymus protobungeana Hu et Chaney, and species of *Paliurus* and *Celastrus*. There are strong grounds for believing that further research of the Nezhino assemblage will show a still greater degree of similarity between these floras owing to new common

(or closely related) species shared by of the families Ulmaceae, Salicaceae, Fabaceae, Sabiaceae, Hippocastanaceae, and Aceraceae.

It is worth noting that the Nezhino flora is very distinctive. It is much less thermophilic than the Japanese floras of the optimal Miocene, in which the Lauraceae and evergreen oaks (species of Cyclobalanopsis) are very prominent. As previously noted, this is explained by the difference in the paleoclimatic conditions under which Japanese (insular) and Primorye (continental) floras were formed (Pavlyutkin, 2005). The composition of the Nezhino flora also sharply differs from that of the younger Middle Miocene Khanka flora. The latter flora is totally dominated by beeches, constituting up to 50% of the total in some localities, and is characterized by the presence of diverse and abundant conifers (Pavlyutkin, 2005). The presence of two species of beech with a relatively narrow temporal range is most important for the age determination of the Nezhino flora. One of them, Fagus chankaica T. Alexeenko,

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characterizes the Middle Miocene of Primorye and Korea; and the other, F. evenensis Cheleb., is known from the Late Oligocene-Early Miocene of Primorye and Sakhalin Island and from the Late Oligocene-Middle Miocene of the Kamchatka Peninsula. In Primorye, this species was recorded from the Early Miocene Sinii Utes assemblage. This allows one to consider the Nezhino flora as a transient flora between the Khanka and Sinii Utes floras and to date it to the second half of the Early Miocene. Paleobotanical data support the absolute age of 17.1 ± 1.3 Ma obtained by the fissiontrack method for a band of volcanic ash from the beds under consideration, which earlier were correlated with the Ust'-Davydovskaya Formation (Pavlyutkin et al., 1984). It is worth noting that although this correlation is slightly unusual it is easily explainable, since the Ust'-Davydovskaya Formation with lignite sublayers was then dated to the Early–Middle Miocene.

New fossil species of *Davidia* from the Nezhino flora are described below.

SYSTEMATIC PALEOBOTANY

Family Davidiaceae Baillon, 1871 Genus Davidia Baillon, 1871 Davidia palaeoinvolucrata Pavlyutkin, sp. nov.

Plate 11, figs. 1-4

E t y m o l o g y. From the modern species *D. involucrata* Baillon.

Holotype. Far East Geological Institute, Far East Division, Russian Academy of Sciences, FEGI, no. 9180/307; leaf imprint, village of Nezhino`, lignite beds; Early Miocene (Pl. 11, fig. 1).

D i a g n o s i s. Leaf oval symmetrical, with broadly rounded cordate base and tapered apex abruptly transforming into long-pointed entire-margined tip. Leaf margin coarsely dentate. Teeth large, symmetrical, simple, low, and with sharp tip lacking glandules. Venation pinnate and craspedodromous. Midrib moderately thick and slightly sinuous. Secondaries (eight pairs) straight or slightly up-curved with one to four bifurcations; they arise regularly (except for three connivent lower pairs) at angle of 35°–45°. Veins of basal pair opposite, deviate from leaf base at angle of 70°. Tertiary veins subperpendicular to secondaries, percurrent, or occasionally forking in middle area.

D e s c r i p t i o n (Figs. 2a–2e). Leaves are symmetrical, mostly moderate in size or large (6.5–12.0 cm long and 5.4–10.5 cm wide), rounded, broadly oval, and up to ovate-oval with a broadly rounded or more or less cordate base and a rounded apex, sharply transforming into an entire-margined long-pointed tip. The leaf index varies from 1.2 to 1.4. The leaf margin is coarsely dentate, starting from the petiole. In the lower part of the leaf, the teeth are less distinct, more or less equal in size, 1.5–2.0 times as wide as the high; the inner side is straight or slightly concave, and the outer side is concave or convex-concave; the tip is pointed,

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slightly tapered, lacking a gland, and curved downward in some specimens. The inner side is shortened in comparison to the straight outer side in basal teeth. The sinuses are broadly angular or rounded. The venation is pinnate and craspedodromous. The midrib is relatively thin and slightly broken-undulate. There are eight or nine pairs of secondary veins, which are straight or slightly curved upward, alternating, connivent in pairs in the lower part of the lamina (three lower pairs), or nearly opposite (basal pair). The angle of deviation diminishes from 70° in the lower pair to 30° in the upper pairs. Toward the leaf margin, most of secondary veins bifurcate once or twice. Lower pairs have up to four deviations. The angle between the secondary veins and their deviations is 30°-40°. The deviations are nearly as thick as the secondary veins. The deviations also end craspedodromously, but the corresponding teeth are slightly smaller than the main teeth. Tertiary veins are perpendicular to the secondary veins. Usually, they do not branch; only few of them bifurcate in the middle. In some specimens, secondary veins are slightly convex toward the leaf periphery. Veins of the fourth order are virtually indistinct. No petiole is preserved.

C o m p a r i s o n. The comparison between the new species from the Nezhino flora and the modern Davidia involucrata Baill. growing in mountainous subtropical forests of southwestern China shows that the fossil and modern species are very similar (Pl. 11, fig. 5). There are only minor differences between the new species and Davidia antiqua (Newb.) Manchester from the Paleogene of North America and the Kamchatka Peninsular. The latter species has smaller teeth with convex outlines and markedly obtuse apices and a less distinctly cordate base, which is broadly emarginate in some specimens. Greater differences exist between the new species and Davidia sp. from the eastern Sikhote-Alin Range (Akhmetiev, 1993). The latter is characterized by an emarginate-dentate leaf margin with very small teeth and secondary veins distinctly connivent toward their distal part, a feature that is more typical of several members of the Hamamelidaceae, in particular, fossil Langeria magnifica Wolfe et Wehr from the Eocene Republic flora in North America (Wolfe and Wehr, 1987).

R e m a r k s. Until recently, leaves of *Davidia* were not reported from Tertiary floras of the Far East, with the exception of a leaf imprint of *Davidia* sp. from the Oligocene (Miocene?) Maksimovskaya flora, eastern Sikhote-Alin Range (Akhmetiev, 1993). Manchester (2002) revised fossil remains from the Lower Paleogene of the western territories of the United States, which were earlier described as *Viburnum antiquum* Newb. A new combination was proposed: *Davidia antiqua* (Newb.) Manchester. Similar leaves from the Lower Paleogene of the western Kamchatka Peninsula were later transferred into *D. antiqua* by Budantsev (2006); and leaves from the Eocene–Oligocene of the western Kamchatka Peninsula were described as the new species *D. arssanovii* Cheleb. (Gladenkov et al., 2005). Leaf remains from the Eocene of Washington (United States) that were included into the formal genus *Tsukada* Wolfe et Wehr are also close to the Davidiaceae (Wolfe and Wehr, 1987).

Manchester (2002), who summarized data on fossil finds of *Davidia* in East Asia and North America, pointed out that leaves of *Tiliaephyllum tsagajanicum* Krassilov from the Lower Paleocene (Tsagayan Formation) of the Bureya River (Amur River region) morphologically resemble leaves of *Davidia*. On the other hand, distinct differences between them exist: more densely deviating secondary veins, more numerous secondary veins, and bidentate leaf margin in Tsagayan specimens of *Tiliaephyllum*. Krassilov (1976) questioned the relationship between *T. tsagajanicum* and *Davidia*.

M at erial. Seventeen variously preserved leaves from the type locality.

Davidia nezhinoensis Pavlyutkin, sp. nov.

Plate 11, fig. 6

Et y molog y. From the village of Nezhino.

H o l o t y p e. Far East Geological Institute, Far East Division, Russian Academy of Sciences, FEGI, no. 9180/307, endocarp imprint, Primorye, village of Nezhino, lignite beds, Early Miocene (Pl. 11, fig. 6).

D i a g n o s i s. Endocarp fusiform, with apparently no more than eight distinct longitudinal ribs (five ribs imprinted on visible part of endocarp). Intercalary ribs between main ribs are less distinct.

D e s c r i p t i o n. Endocarps are ellipsoidal or fusiform, 2.0–2.6 cm long, and 0.8–1.5 cm wide in the equatorial diameter, and, apparently, with no more than eight distinct longitudinal ribs (five ribs were observed on the visible part of the imprint). Intercalary ribs are visible less distinctly between the main ribs.

C o m p a r i s o n. The endocarps from the village of Nezhino assigned to the genus *Davidia* do not significantly differ in shape from the endocarps described by Manchester (2002) in association with leaves of this genus. However, some of the endocarps from Nezhino are larger, particularly, larger than Tsagayan endocarps. In addition, no ovate specimens were found.

R e m a r k s. According to the International Code of Botanical Nomenclature, leaf and fruit remains from the Nezhino locality are described separately, since no data on their organic connection are available. Most probably, they belonged to the same plant. The situation is complicated by the fact that the presence of *Nyssa* is revealed on the basis of leaf remains, and endocarps of *Nyssa* and *Davidia* are similar. It is difficult to differentiate between endocarps of these genera, since it is impossible to study the inner structure in imprints. A similar situation exists in the Amur River region: in addition to fructifications assigned to *Davidia* (Akhmetiev et al., 2002), Tsagayan deposits contain leaf remains of *Nyssa* (Krassilov, 1976).

M a t e r i a l. Five endocarps from the type locality.

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