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## New Data on Composition and Age of Malomikhailovka Flora from the Upper Cretaceous of the Amur River Lower Courses

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**Abstract**—The described flora is studied near the village of Malomikhailovka, where it is confined to synonymous formation of an intermontane depression at the northern end of the Sikhote Alin volcanic belt. In its dominant taxa and in the composition of plant groupings, the studied flora notably differs from the coeval Tsagayan flora of the Zeya–Bureya depression and from floras occurring in western Sakhalin and eastern Sikhote Alin. It includes a new genus, *Amurocypris*, with type species *A. sokoloviae*, as well as *Larix puerensis* sp. nov., *Cryptomerites tutshkovii* sp. nov., *Corylites amurensis* sp. nov., and *Palaeocarpinus pacifica* sp. nov., which are described here. The latter taxon was discovered for the first time in Russia.

**Key words:** flora, Danian, Amur River, tuffaceous–sedimentary deposits, ferns, horsetails, conifers, pollen assemblage, *Amurocypris*.

The Malomikhailovka flora was found in a tuffaceous-sedimentary rock member about 25 m thick, which is exposed at the base of a 6- to 8-m-high terrace on the right-hand side of the Amur River. This locality is situated between the abandoned villages of Malomikhailovka and Pat, where the northeastern spur of the Chayatyn Ridge approaches to the river on the other side of its valley (Fig. 1). Sokolova (1940) was the first to collect fossil plants here in 1934. Later, the geological structure of this locality and its flora were examined by I.I. Tuchkov, Z.P. Potapova, V.I. Sukhov, L.P. Botyleva, T.N. Baikovskaya, M.M. Koshman, V.A. Vakhrameev, M.A. Akhmet'ev, and G.M. Brattseva (Vakhrameev, 1960; Tuchkov, 1960; Vereshchagin and Potapova, 1966; Sukhov, 1967; Akhmet'ev *et al.*, 1976; Akhmet'ev, 1993). However, the taxonomic composition of this flora is still insufficiently studied, and the stratigraphic position of the host beds remains disputable. In contrast to other transitional Cretaceous–Paleogene floras buried either in perioceanic coastal lowlands, or in spacious intercontinental depressions of the Amur–Zeya type, this one is deposited in a small intermontane trough at the western periphery of the Sikhote Alin volcanic belt far from the ocean. It exemplifies an unusual type of vegetation, because the trough bottom has been located higher than in other areas. Moreover, the flora in question is perfectly preserved, unlike the other floras, and this situation proved favorable for detecting a series of new plants characteristic of the region in the past.

The detailed study of flora-bearing deposits and bed-by-bed sampling of plant remains were performed by Akhmet'ev *et al.* (1976). To the south of Malo-

mikhailovka, the flora-bearing beds are exposed over a distance of several kilometers. They form a gentle synclinal fold striking northeastward and having dip angles of 10°–12° at its limbs (Fig. 2). The sequence consists of alternating volcanosedimentary and sedimentary rocks. It discordantly overlies the basement composed of variable extrusive and pyroclastic rocks represented by andesites in the north and by rhyolite to dacite varieties in the south. The fine-grained rocks of the tuffaceous–

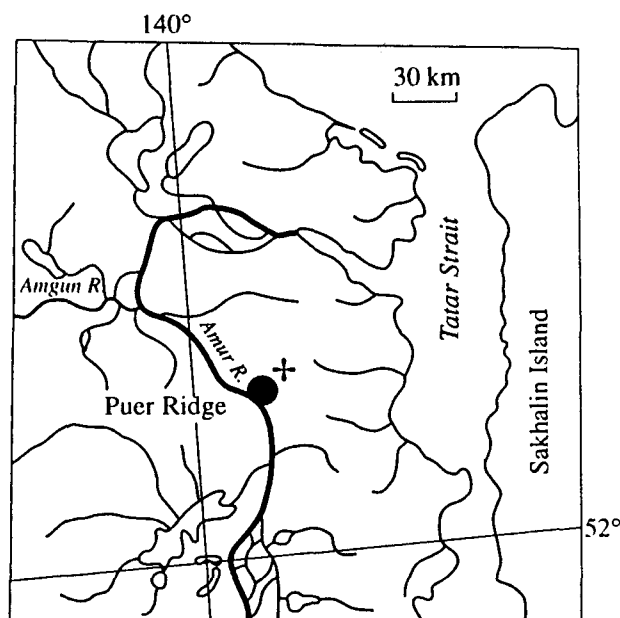


Fig. 1. Geographic locality of the Malomikhailovka flora.

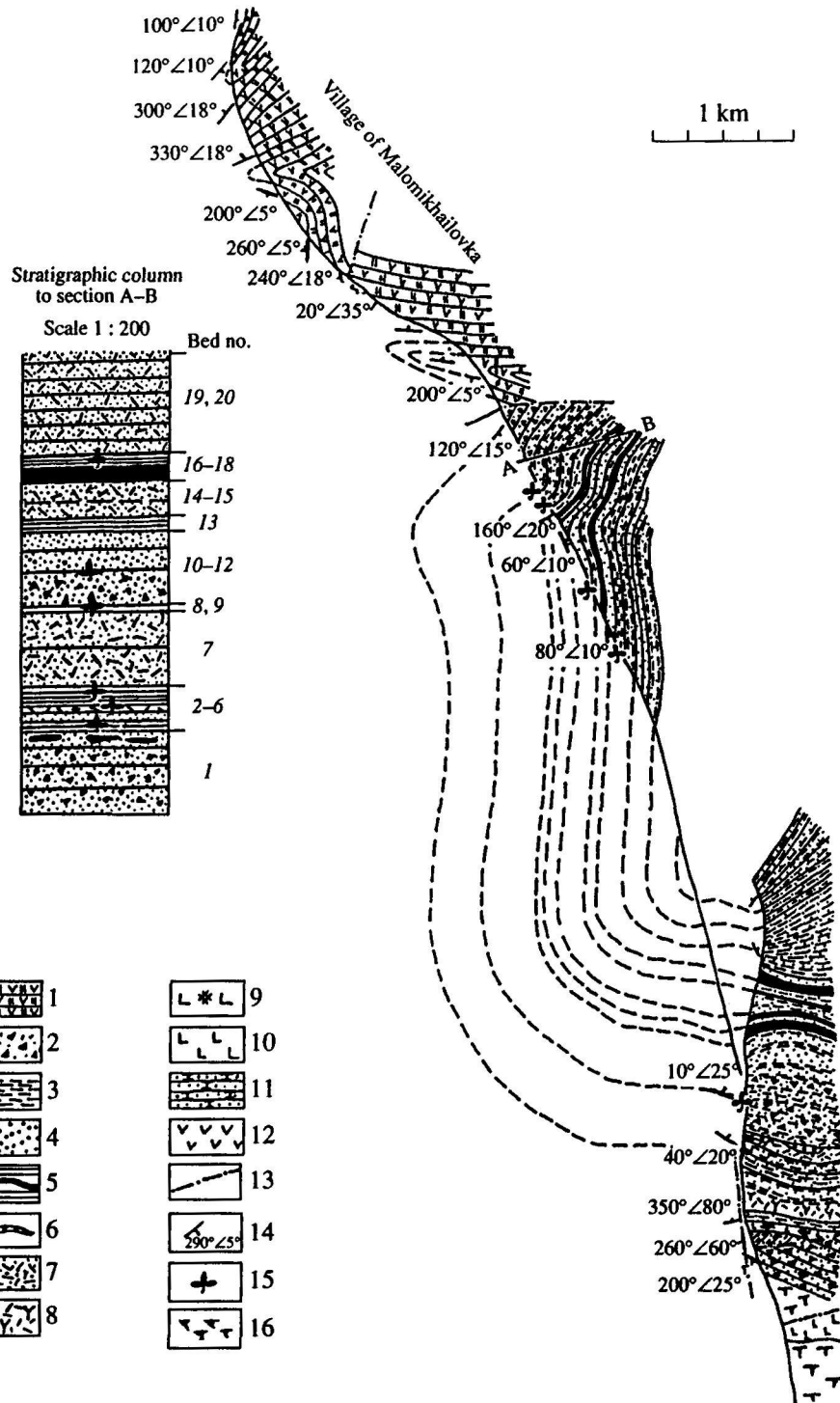


Fig. 2. Geological scheme of the Amur River bank, the Malomikhailovka-Pat area (compiled by M.A. Akhmet'ev and Yu.A. Ivanov): (1) andesite-dacite; (2) tuff and tuffaceous sandstone; (3) tuffite and tuffaceous siltstone; (4) fine- to medium-grained sandstone; (5) lignite and carbonaceous claystone; (6) lenses of tuffaceous conglomerate and gravel; (7) acidic tuff; (8) dacite; (9) amygdaloidal basaltic andesite; (10) basalt; (11) sandstone; (12) andesite; (13) fault; (14) bed attitude; (15) sampling points of fossil flora; (16) unconsolidated Quaternary deposits.

sedimentary member grade to the southeast into the coarse-grained beds of rhyolite tuffs. Andesites are estimated to be 74 Ma old (radiometric determination by T.G. Koval'chuk from the Far East State University,

oral presentation in 1969). Tuchkov (1960), who distinguished the Malomikhailovka Formation, considered the tuffaceous-sedimentary member as its upper unit overlying the lower part, composed of andesites.

Akhmet'ev *et al.* (1976), who established the tectonic nature of contact between this member and andesites and traced the lateral transition of the former into beds of rhyolite composition, argued against the idea of uniting the first two rock types into a single formation.

The flora-bearing sequence shown in Fig. 2 consists of the following beds:

(1) tuffaceous sandstone, coarse-grained, indistinctly laminated, enclosing in the middle part an interlayer with remains of fossil wood (4 m);

(2) tuffite, light brown, grading upward into cherty tuffaceous siltstone of dark gray color (0.8 m);

(3) tuffaceous siltstone, dark gray, carbonaceous (0.15 m);

(4) tuffite, dark gray, intercalated with interlayers of tuffaceous sandstones locally as thick as 0.5–0.6 m (2–2.5 m);

(5) tuffaceous siltstone, dark gray, carbonaceous (0.2 m);

(6) tuffite, dark gray (0.5 m);

(7) tuffaceous sandstone, rusty brown, medium- to coarse-grained, alternating with tuffite and tuffaceous siltstone interlayers (3.2 m);

(8) tuffaceous siltstone, dark gray, carbonaceous (0.05 m);

(9) tuffite, dark gray (0.6 m);

(10) tuffaceous sandstone, brown, coarse-grained (1.3 m);

(11) tuffaceous claystone, dark gray, carbonaceous (0.12 m);

(12) tuffaceous sandstone, coarse-grained, enclosing interlayers of tuffaceous siltstone (1.5 m);

(13) tuffaceous claystone, dark gray, carbonaceous (0.15 m);

(14) tuffaceous sandstone, coarse-grained, with spheroid and loaflike jointing (2.5 m);

(15) tuff, brownish gray, fine-grained, intercalated with tuffite interlayers (1 m);

(16) tuffaceous siltstone, dark gray, carbonaceous (0.2 m);

(17) tuff, fine-grained (0.5 m);

(18) lignite (0.5 m);

(19) tuff, light gray, fine-grained (1 m);

(20) tuffaceous sandstone, dark brown, fine-grained, enclosing thin interlayers of carbonaceous claystone (3 m).

Lignite interlayers in carbonaceous siltstone and sandstone, together with structural and textural features of rocks and the types of fossil plants characteristic of boggy landscapes, indicate that flora-bearing beds have accumulated in an intermontane basin surrounded by volcanic edifices supplying the basin with volcanic material. Hydrological environments in the basin were variable. Lignite and carbonaceous siltstone beds mark periods of swamping, whereas lenticular interlayers of

cross-bedded gravelstone and shingle point to alluvial environments of sedimentation.

Megafossils were encountered in beds 2, 6, 9, 11, 13, and 20. They were most abundant in Bed 2. The basal part of the bed yielded plentiful (more than 100 specimens) remains of horsetail species. Less abundant (dozens of specimens) are *Onoclea* fern fragments and Pinaceae megastrobiles. Interlayers of tuffaceous siltstone in the bed contain hundreds of *Metasequoia* shoot remains and are only somewhat less rich in specimens of *Fokieniopsis*, *Cryptomerites*, *Amurocypris*, and *Dennstaedtia*. These taxa coexist with considerably less abundant remains of *Onoclea*, mosses, micro- and megastrobiles of Taxodiaceae, and *Corylites* leaves.

Bed 6 is also saturated with fossil plants. *Metasequoia* shoots (hundreds of specimens) and *Corylites* leaves (dozens of specimens) are dominant at this level. Less abundant (10–15 specimens) are ferns *Onoclea* and *Dennstaedtia*, *Amurocypris* shoots, and remains of horsetails. We also detected two leaves of *Trochodendroides* ex gr. *arctica* (Heer) Berry.

Bed 9 yielded only 10–15 specimens of poorly preserved remains of *Corylites* and *Metasequoia*.

Bed 11, especially its basal portion, turned out to be rich in fossil flora. Above the contact with underlying coarse-grained sandstone, we found here remains of horsetails, several impressions of *Ginkgo* leaves, more than ten impressions of *Nyssidium* fruits, and abundant *Trochodendroides* leaves and *Metasequoia* shoots.

Bed 13 contains plentiful remains of *Onoclea*, and the tuffaceous sandstone of Bed 20 bears fragmented remains of horsetails.

The assemblage of *Corylites* and *Metasequoia* with accessory *Amurocypris*, *Fokieniopsis*, and *Dennstaedtia*, which is confined to carbonaceous tuffite beds, is most persistent. Accordingly, it may correspond to the most characteristic type of past vegetation around a small water basin. Fossil horsetails and *Onoclea* ferns mainly form the monodominant burials confined to coarse-grained rocks, in the first case, and to fine-grained sediments, in the second. In general, this is concordant with present-day habitat environments of these plants, as some horsetail species often populate the recently exsiccated shoals, and *Onoclea* overgrowths are typical of marshy lowlands. The discrete occurrence of *Corylites* and *Trochodendroides* leaves is particularly interesting. Both taxa were clearly dominant and coexisted with *Metasequoia*, although the abundant *Trochodendroides* remains are concentrated together with *Ginkgo* leaves in the coarse-grained rocks at the point of contact between beds 10 and 11. It is quite possible that these latter two species populated some elevated areas of embankment type with well-aerated soils. In other coeval flora localities of the same lithologic facies, no such an interrelation has been observed. Remains of *Cryptomerites*, *Larix* strobiles, and coniferous needles of other indeterminable Pinaceae are less abundant. These, especially *Larix*

specimens, are presumable elements of upland and slope vegetation formerly located at some distance from the water basin in question.

In total, the Malomikhailovka flora includes the following taxa: *Equisetum* sp., *Muscites* sp., *Ginkgo* ex gr. *adiantoides* (Unger) Heer, *Asplenium* sp., *Onoclea hebridica* (Forbes) Johnson, *Dennstaedtia tschuktschorum* Krysht., *Metasequoia occidentalis* (Newb.) Chaney, *Fokieniopsis catenulata* (Bell) McIver et Basinger, *Cryptomerites tutshkovii* sp. nov., *Amurocyparis sokoloviae* gen. et sp. nov., *Pityospermum* sp., *Pityostrobus* sp., *Larix puerensis* sp. nov., *Corylites amurensis* sp. nov., *Palaeocarpinus pacifica* sp. nov., *Trochodendroides* ex gr. *arctica* (Heer) Berry, *Trochodendroides* sp., and *Nyssidium arcticum* (Krysht.) Iljinsk. Plants dominant flora of limited diversity include *Corylites*, *Metasequoia*, *Trochodendroides*, *Nyssidium*, *Onoclea*, *Dennstaedtia*, *Fokieniopsis*, and *Ginkgo* genera, all very characteristic of floral assemblages of the terminal Cretaceous–initial Paleogene period. Many of them display wide geographic ranges and a high degree of individual variability. Apart from *Trochodendroides* ex gr. *arctica*, the Malomikhailovka Formation yielded several other leaf specimens of this genus, which are elongated and rimmed by frequent sharp dens (Fig. 3, no. 8). Impressions of *Corylites amurensis* leaves occur together with fruits of *Palaeocarpinus pacifica*, discovered for the first time in Russia. Shoots of *Amurocyparis* and *Larix* bearing female strobiles are of particular scientific significance. Remains of *Larix puerensis* represent the oldest known species of this genus at present. The discovered generative organs of Cupressaceae are extremely rare in Cretaceous–Paleogene deposits and highly important for understanding the evolution of this family.

In its composition, the Malomikhailovka flora most closely resembles the Danian Boshnyakovo flora of Sakhalin (Krasilov, 1979), the late Maastrichtian–Danian Rarytkin flora of Koryak Upland (Golovneva, 1994), and the Maastrichtian Samarga flora of Sikhote Alin (Oleinikov and Nevolina, 1985). All these floras display a predominance of *Metasequoia* and different *Corylus* species, in association with *Trochodendroides* remains. The second taxon is represented by *Corylus beringiana* (Krysht.) Golovn. in the Rarytkin flora, by *Corylus* (*Corylites*) *protoinsignis* Krasilov in the Boshnyakovo assemblage, and by *Corylus* sp. in the Samarga flora. The latter, which represents former vegetation of the Sikhote Alin volcanic belt, is most similar to the Malomikhailovka flora. Characteristic conifers of the Samarga flora are *Metasequoia* and typical Cretaceous taxa *Sequoia* sp. and *Thuja cretacea* Newb. At the same time, this flora is rich in a different taxon of Betulaceae and includes some old taxa of angiosperms. The Samarga flora, similar in composition of megafossils to Danian floras, is attributed to the Maastrichtian on the basis of palynological spectra and radiological dates. According to the latter, the Samarga Horizon could be as old as 50 to 75 Ma (Oleinikov,

1978; Filimonova, 1983; Mikhailov and Gracheva, 1987; Matyunin, 1988). This interval corresponds to both the late Campanian–Maastrichtian and the Danian, if the Cretaceous–Paleogene boundary is 65 Ma old (Harland *et al.*, 1990). However, pollen assemblages from the Samarga Formation show a preponderance of *Aquilapollenites*, *Mancicorpus*, *Wodehouseia*, *Orbiculapollis*, and *Ulmoidepites* genera, which is typical of the Maastrichtian (Markevich, 1987). In addition to the Malomikhailovka flora from the Amur River lower courses, the *Corylites amurensis*–*Metasequoia* plant assemblage is detected in the upper part of the Levaya Sobolevka Formation, occupying a higher stratigraphic level as compared to the Samarga Formation. Palynological spectra from the Levaya Sobolevka Formation are considerably depleted in Maastrichtian taxa and display a predominance of pollen of Betulaceae and a Miricaceae affinity. Diverse pollen of flowering plants is replaced here by dominant Taxodiaceae in association with rather abundant fern spores. These pollen spectra are dated back to the early Danian or late Maastrichtian–early Danian. Pollen assemblages from flora-bearing beds of the Malomikhailovka Formation, which are similar to the above spectra in composition, are also the early Paleocene in age (Akhmet'ev *et al.*, 1976).

Thus, the data suggest that the age interval of the Malomikhailovka flora spans the Danian and probably the uppermost Maastrichtian. In palynological aspect, this flora is most similar to the upper Tsagayan, Boshnyakovo, and upper Rarytkin floras. It should be mentioned that the Danian age has been suggested for the Malomikhailovka flora from the very beginning (Sokolova, 1940), when it was correlated with the Tsagayan flora of the Amur region, though the latter represents a somewhat different type of Danian floras and demonstrates a predominance of the *Trochodendroides*–*Taxodium* assemblage, instead of the *Corylites*–*Metasequoia* group. At present, the indicated age interval of the Malomikhailovka flora is substantiated by results of stratigraphic and paleobotanical data obtained by various researchers.

A description of several new taxa distinguished in the Malomikhailovka flora is presented below. They all are from the fossil plant collection no. 3808, assembled by V.A. Vakhrameev and M.A. Akhmet'ev in 1973 and stored at the Laboratory of Paleobotany of the Geological Institute, Russian Academy of Sciences.

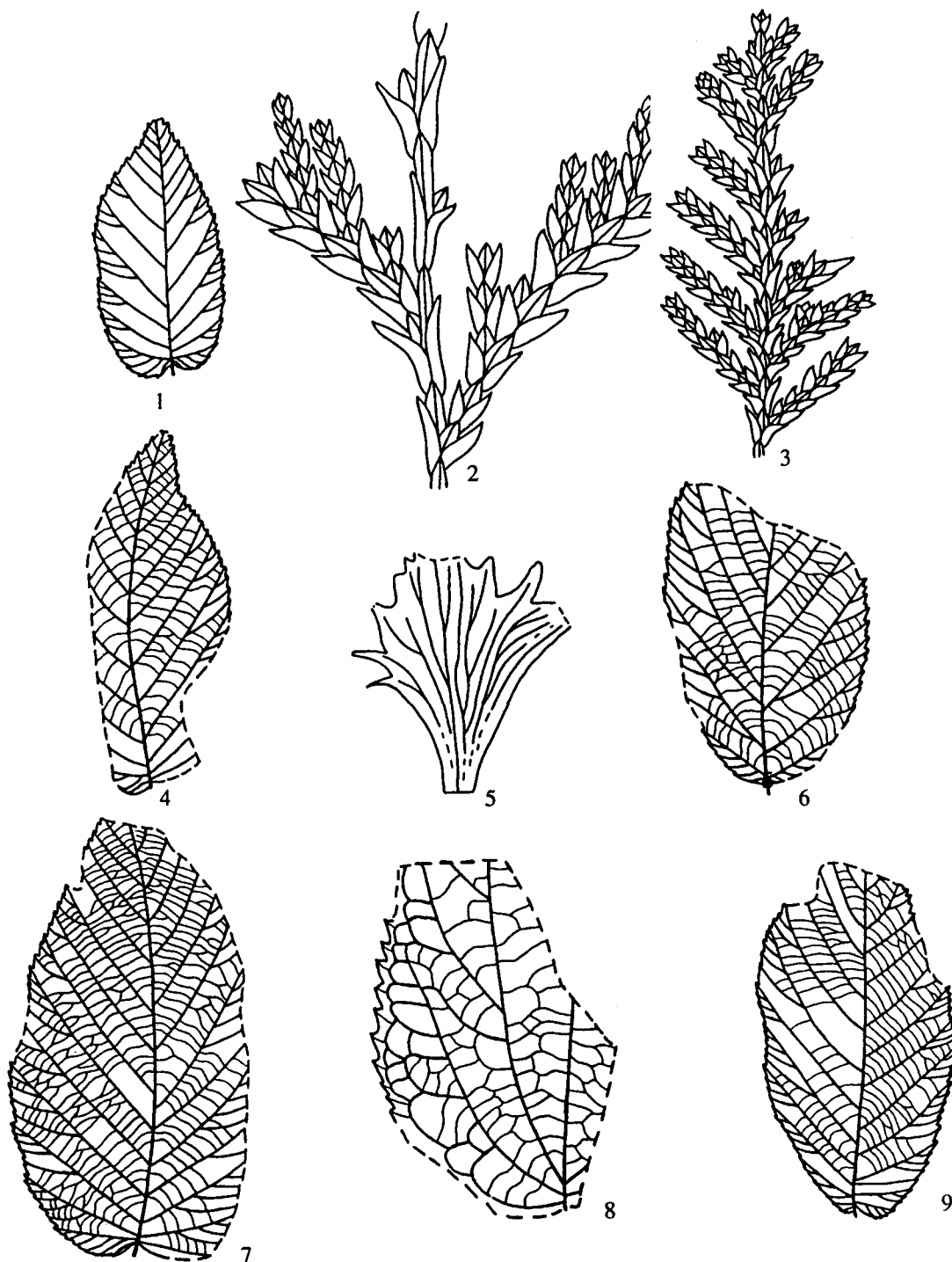
#### Family Cupressaceae

Genus *Amurocyparis* Golovn. et Akhmetiev, gen. nov.

Genus name is after the Amur River.

Type species: *Amurocyparis sokoloviae* sp. nov.; Danian, Malomikhailovka Formation, Amur River (lower courses).

Diagnosis. Shoots are branching in a single plane, mainly in an alternate, and sometimes in a decussate, arrangement. Leaves are lepidoid. Facial leaves are flat



**Fig. 3.** Fossil Danian plants from the Malomikhailovka Formation and the Amur River lower courses: (1) leaf of *Corylites amurensis* Golovn. et Akhmetiev, specimen no. 3808/121,  $\times 1$ ; (2, 3) *Amurocyparis sokoloviae*, paratype, specimen no. 110,  $\times 2$  (2), and specimen no. 389,  $\times 2$  (3); (4) leaf of *Corylites amurensis* Golovn. et Akhmetiev, specimen no. 3808/603,  $\times 1$ ; (5) *Palaeocarpinus pacifica*, holotype, specimen no. 3c,  $\times 7$ ; (6, 7) leaves of *Corylites amurensis* Golovn. et Akhmetiev, specimen no. 3808/116,  $\times 1$  (6) and specimen no. 3808/295a,  $\times 1$  (7); (8) *Trochodendroides* sp., specimen no. 3808/394,  $\times 1$ ; (9) leaf of *Corylites amurensis* Golovn. et Akhmetiev, specimen no. 3808/370,  $\times 1$ .

and pressed against the stem; their upper ends overlap the bases of higher lateral leaves, which are falcate in shape and have a wide base and acuminate free apex.

Semeniferous strobiles are rounded and small (2.5–3 mm in diameter); they occupy terminal positions at

short foliaceous lateral shoots set alternately or at one side of the branch in the base of lateral leaves. After dissemination, strobiles remain to be fixed at the branch. They consist of four ligneous squamae of obtriangular or rounded-rhomboid form. Microstrobiles of about

1 mm in diameter consist of several squama pairs and rest at the ends of short acroscopic sprays.

*Species composition:* *A. sokoloviae* (type species); *A. corpulenta* (Bell) Golovn. [= *Thuites corpulentus* Bell, 1957, p. 35, Plate 18, no. 8; = *Chamaecyparis corpulenta* (Bell) McIver, 1994]; Santonian, Comox Formation, Vancouver Island.

*Comparison.* In morphology of leaves, *Amurocyparis* shoots are most similar to those of Cupressaceae tribes Thujopsidae and Cupresseae. The leafing of *A. corpulenta* branches resembles that typical of the genus *Thuja*. In both cases, lateral leaves are falcate and pressed against shoots, leaving only the acuminate apex free. Lateral leaves of *A. sokoloviae* have long free ends. Similar shoots are characteristic of genus *Chamaecyparis*, for instance, *C. nootkatensis* (D. Don) Spach.; however, the decussate ramification is nontypical of the tribes Thujopsidae and Cupresseae. This type of branching is characteristic of representatives of the Libocedreae tribe from the southern hemisphere and of the fossil genus *Mesocyparis* from the Maastriechian and Paleocene deposits of northeastern Russia, Canada, and Spitsbergen (McIver and Basinger, 1987; Golovneva, 1988, 1994; McIver and Aulenback, 1994). Some representatives of Libocedreae and Maastriechian *Mesocyparis umbonata* McIver et Aulenback display a combination of decussate and alternate ramification (McIver, 1994). Fragments of decussate shoots of *A. sokoloviae* are almost identical to those of *Mesocyparis*. At the same time, if decussate ramification is the rule for *M. umbonata* and the alternate shoot arrangement is the exception, the last type of branching is, in contrast, typical of *Amurocyparis* species, and the number of their shoots with decussate ramification is below 5%.

Seminiferous strobiles of *Amurocyparis* closely resemble those of *Mesocyparis*. They are equally small and consist of four ligneous squamae, each presumably bearing two seeds. However, assidenous strobiles of *Mesocyparis* are arranged as series of decussate pairs at special aphyllous twigs, whereas the terminal strobiles of *Amurocyparis* are situated at short lateral leaf-bearing twigs branching either in the alternate manner, or from one side of a shoot. Strobile arrangements of this kind are typical of many Cupressaceae. Among present-day species of this family, only *Microbiota decussata* Komarov, from the Thujopsidae tribe and growing in the Sikhote Alin Ridge, has small four-squama strobiles; however, their squamae are coriaceous but not ligneous, and each strobile bears only one seed.

McIver (1994) believes that strobiles of the *Amurocyparis* type are characteristic of the genus *Chamaecyparis*, and he refers their fossil remains to this taxon. This is not entirely correct, because strobiles of *Chamaecyparis* are notably larger and covered with numerous peltate squamae.

In our opinion, the structure and arrangement of *Amurocyparis* microstrobiles are almost identical to these morphological elements of *Mesocyparis*.

Thus, the fossil genus *Amurocyparis* is most similar to *Mesocyparis* in the ramification style and structure of seminiferous strobiles. In morphology of shoots and leaves, as well as in strobile arrangement, it shows an affinity with the taxa of Thujopsidae and Cupresseae tribes. Morphological features of *Mesocyparis* can be found in both Thujopsidae and Libocedreae forms. In contrast to this genus, *Amurocyparis* is much closer to Thujopsidae and other Cupressaceae from the northern hemisphere.

*Amurocyparis sokoloviae* Golovn. et Akhmetiev, sp. nov.  
Plate I, nos. 1–4, 7–10, and 12; Plate II, no. 1; Fig. 3, nos. 2 and 3

*Androvettia catenulata* Bell (Akhmet'ev, 1993;  
Plate III, nos. 4, 5, 7, and 13; Plate IX, no. 1)

*Species name* given in honor of geologist E.I. Sokolova, who discovered the Malomikhailovka flora locality.

*Holotype:* specimen no. 3808/600 in collection of Geological Institute, Russian Academy of Sciences; seminiferous strobiles, Malomikhailovka Formation, Danian, Plate I, no. 2.

*Paratype:* specimen no. 3808/110 in collection of Geological Institute, Russian Academy of Sciences; leaf-bearing shoots, Malomikhailovka Formation, Danian; Plate I, no. 10; Fig. 3, no. 2.

*Description.* Our collection includes small shoots with ramifications of three orders and less. Ramification, which is predominantly alternate and rarely decussate, takes place in a single plane. Offshoots of penultimate order in larger shoots are often asymmetrically branching: 5–6 terminal twigs are situated at the acroscopic side, whereas basiscopic side has either 1–2 or no terminal twigs. Leaf arrangement is decussate. Facial leaves are long, narrow, and pressed against the stem; their carina is weakly pronounced, and the acute apex either gradually narrowing, or rhomboid in shape, overlapping the base of the higher lateral leaf. The lateral leaves have a wide base and narrowing acute apex; they are either straight or slightly falcate in form. Free parts of lateral leaves deviate from the stem approximately for a half of their length. Terminal twigs 0.6–1.5 cm long consist of 3–7 pairs of lateral leaves. Penultimate offshoots are 1.5–5 cm long and unite 7 to 20 pairs of lateral leaves. Lateral and facial leaves of large axial shoots with extended internodes are more elongated and narrow; they can be 2–3 times longer than leaves of the terminal and penultimate offshoots. The leaf length varies from 1.5–2.5 mm at the terminal twigs to 3–4 and 5–8 mm at the penultimate and long axial shoots respectively.

About 5% of all shoots display decussate ramification. In this case, the final lateral offshoots have their origin in each base of lateral leaves and usually consist of 2–4 pairs of new lateral leaves. One of the specimens has rounded microstrobiles (0.8–0.9 mm in diameter), which rest in the base of lateral leaves at the acroscopic

side of decussate lateral offshoots and consist of several squama pairs. Large, normally evolved shoots with decussate ramification are absent.

Rounded and small female strobiles (2.5–3 mm in diameter) are situated at the ends of short lateral twigs bearing 3 to 4 pairs of dimorphic decussate leaves either alternating or located at one side of the twig. Squamae are oval-obtriangular or oval-rhomboid in shape; they have the brachyacut apex sometimes ornamented with small dens. There are two seed impressions in inner sides of squamae.

*Comparison.* New species differs from *Amurocyparis corpulenta* (Bell) comb. nov. chiefly in morphology of leaves. Lateral leaves of *A. corpulenta* are short and tightly envelope facial leaves mainly without free ends. Lateral leaves of *A. sokoloviae* are longer and diverge out of shoots approximately beginning from their middle part.

*Distribution:* Malomikhailovka Formation, Amur River lower courses, Danian.

*Material:* seminiferous strobiles (specimens 3a, 62, 257, 308a, 387, and 600); microstrobiles (specimen 257); vegetative shoots (specimens 30, 47, 64, 71, 77, 110, 131, 143c, 246, 309, 312, 369, 371, 382a, 389, 390, 400, and others).

#### Family Taxodiaceae (?)

*Cryptomerites tutshkovii* Golovn. et Akhmetiev, sp. nov.  
Plate II, no. 4

*Sequoia* sp. (Akhmet'ev, 1993, Plate IV,  
nos. 11, 13, and 14)

*Species name* is given in honor of geologist I.I. Tuchkov.

*Holotype:* specimen no. 3808/519 in collection of Geological Institute, Russian Academy of Sciences; Malomikhailovka Formation, Danian; Plate II, no. 4.

*Description.* Ramification of shoots is alternate, and arrangement of leaves is spiral. In their cross sections, leaves are approximately tetrahedral, laterally flattened. They are straight or slightly falcate in shape and acute at the apex; the leaf base is decurrent toward the shoot axis. Leaf is 3–8 mm long and about 1.5 mm wide.

*Comparison.* Shoots of new species differ from those of *C. ancistrophyllus* Golovn. from Maastrichtian deposits of the Koryak Upland (Golovneva, 1994) in having wider and longer leaves, which are almost straight, but not hamiform, and sparsely arranged at the shoot. The present-day genus *Cryptomeria* has similar tetrahedral decurrent leaves, but, in contrast to ancient species, its leaves are longer and thinner. In addition, they are more densely arranged at the shoot. The oldest forms of *Cryptomeria*, whose affinity to this genus is established on the basis of epidermis, are known to occur since the Cenomanian in northeastern Asia (Samylna, 1988).

*Distribution:* Malomikhailovka Formation, Amur River lower courses, Danian.

*Material:* specimens 519 and 215.

#### Family Pinaceae

*Larix puerensis* Golovn. et Akhmetiev, sp. nov.

Plate I, no. 11; Plate II, nos. 2 and 6

*Species name* is after the Puer Ridge in the Amur River lower courses.

*Holotype:* specimen no. 3808/601 in collection of Geological Institute, Russian Academy of Sciences; long shoot with short offshoots and strobile; Plate I, no. 11.

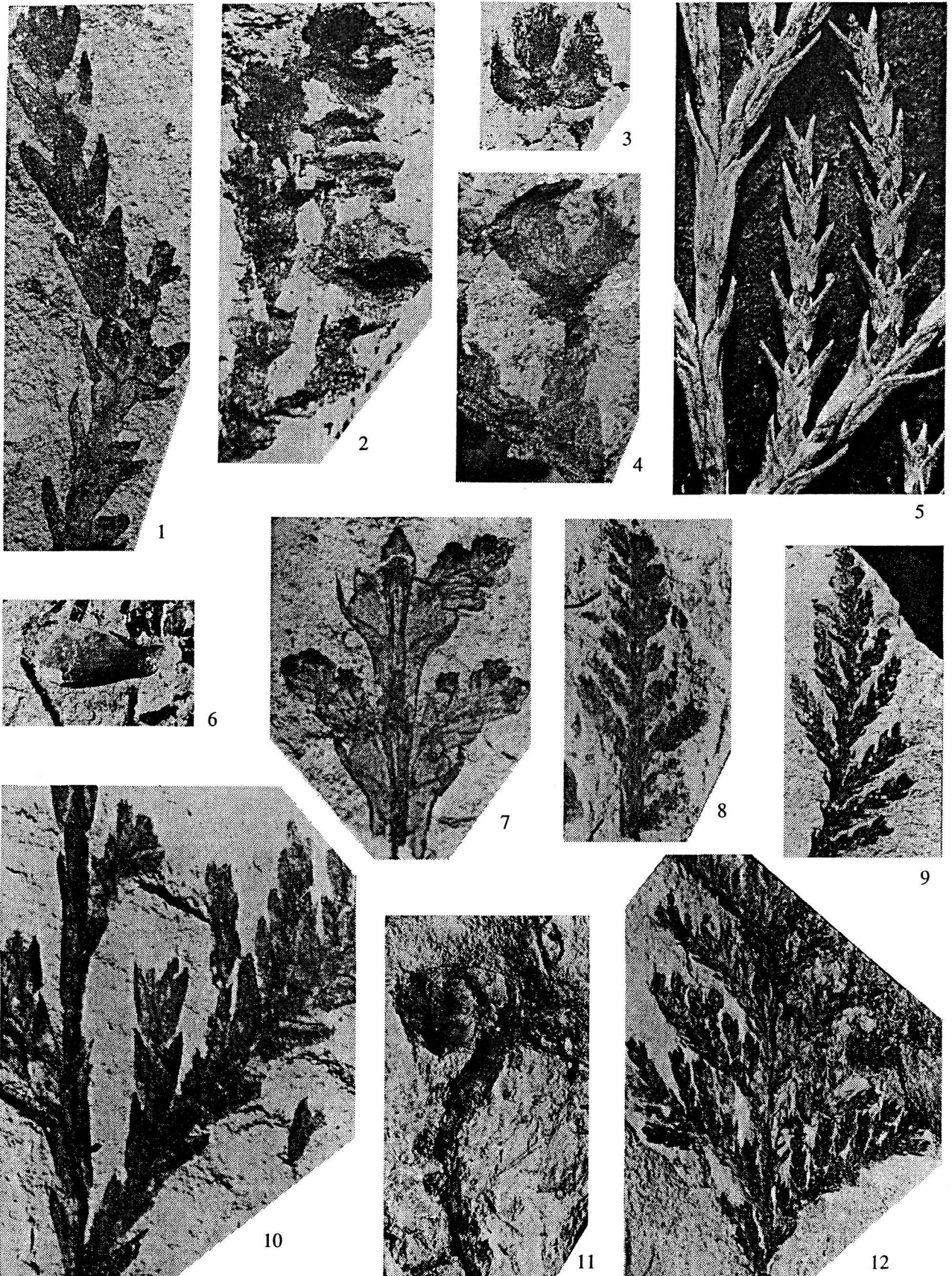
*Paratype:* specimen no. 3808/36 in collection of Geological Institute, Russian Academy of Sciences; leaves; Plate II, no. 6.

*Description.* Specimen represents a long shoot 3–4 mm in diameter with insertion points of solitary leaves and with short offshoots arranged in a spiral manner. The latter are elongated-oval or egg-shaped, 3–6 mm long, and 3–4 mm in diameter. In their apical parts, they are covered with small, tightly assembled scales. The egg-shaped or elliptical female strobiles are up to 2.5 cm long and 1.5 cm in diameter; they bear numerous coriaceous squamae and crown short offshoots. Seminiferous squamae are about 1 cm long, rounded at the base, and obtuse at the apex.

Deciduous leaves are flat and linear, up to 6 cm long, and 1–1.5 mm wide. They are gradually narrowing toward the base and rounded to brachyacut at the apex.

*Comparison and remarks.* Species from the Malomikhailovka Formation is the oldest representative of genus *Larix*, described on the basis of leaves and strobiles. *Larix* species usually occur in the temperate northern latitudes beginning from the Oligocene, and remains of *Larix altoborealis* Le Page et Basinger from the middle–upper Eocene deposits of Arctic Canada used to be considered as the most ancient specimens of the genus (Le Page and Basinger, 1991). The species in question differs from *L. altoborealis* in having longer and wider leaves, and also in the shape of seminiferous squamae. Squamae of *L. puerensis* are wider and truncated at the top, whereas these elements of *L. altoborealis* are oval, or almost circular in shape. Unfortunately, coating squamae, which are important in taxonomy of *Larix* genus, have not been preserved in impressions of *L. puerensis* strobiles. It is well known that the morphological similarity of leaves and strobiles is characteristic of *Larix* species that differ substantially in other aspects. Accordingly, our specimen is inappropriate for a detailed comparison with younger taxa. Despite its ancient features, the material we have is represented only by impressions, thus being inappropriate for elucidating the evolutionary history of *Larix* genus in contrast to *L. altoborealis*, whose remains include the mummified shoots, strobiles, and wood.





Rather long leaves (5–6 cm in average) represent one of characteristic features of *L. puerensis*. Among the present-day larches, *L. olgensis* Henry, widespread in northeastern China, has similar leaves, acute at the apex and gradually narrowing toward the base. Some researchers (Ostenfeld and Larsen, 1930) consider this form only as a subspecies of *L. gmelini*. Leaves of this species are generally shorter (3–4 cm), but they also can be as long as 5–6 cm. The leaves we refer to *L. puerensis* have been found separately from shoots, however they are very similar to leaves of recent larches growing not far from the locality under consideration, and this is a good opportunity to suggest that the studied leaves and shoots with strobiles originated from one plant. In their size and form, these leaves resemble those of *Pseudolarix*, although in the latter case they are usually larger (up to 10–13 cm long and 5 mm wide). Moreover, we did not detect any other type of *Pseudolarix* remains in the Malomikhailovka Formation. In addition to strobiles and leaves from this formation, there are impressions of alate seeds of the *Larix* genus affinity (Plate II, no. 3). However, their precise identification is nearly impossible, because the Malomikhailovka flora includes several representatives of Pinaceae (Akhmet'ev, 1993).

**Distribution:** Malomikhailovka Formation, Amur River lower courses, Danian.

**Material:** seminiferous strobiles (specimens 376, 463, and 601); vegetative shoots (specimens 36, 312, and 3826).

#### Family Betulaceae

*Corylites amurensis* Golovn. et Akhmetiev, sp. nov.  
Plate II, nos. 5 and 8–10; Fig. 3, nos. 1, 4, 6, 7, and 9

*Alnites* sp. (Akhmet'ev, 1993; Plate VII, nos. 4 and 7; Plate VIII, nos. 1 and 4; Plate IX, nos. 8 and 9).

**Holotype:** specimen no. 3808/385 in collection of Geological Institute, Russian Academy of Sciences; Malomikhailovka Formation, Danian; Plate II, no. 10.

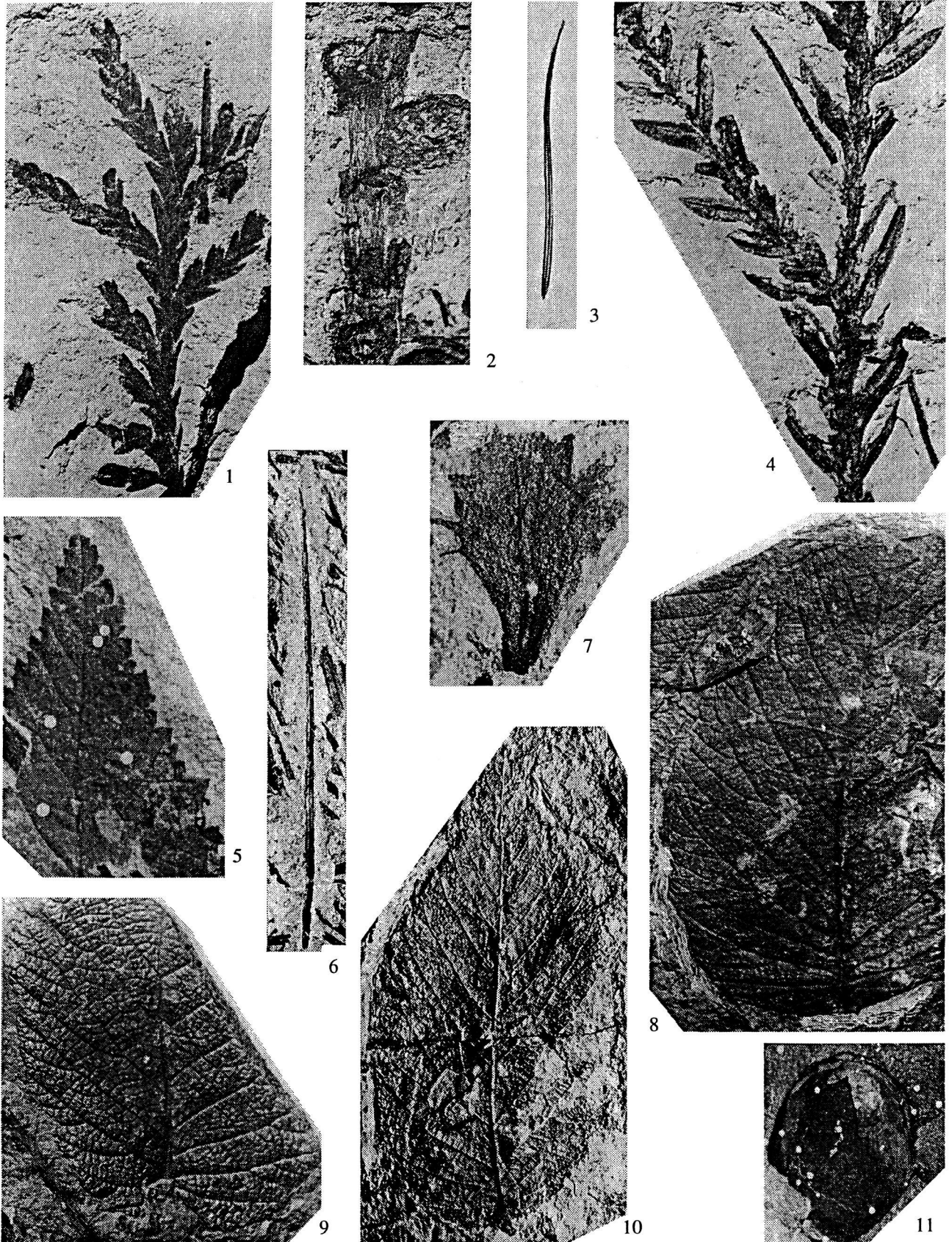
**Description.** Leaves are 5–10 cm long and 2.5–5.5 cm wide, elliptical to wide oval- or egg-shaped. They display various degrees of asymmetry and have an extended acute apex and rounded to slightly cordate base. The leaf edge is serrate. Serratures are small (1–2 mm high), frequent, and triangular to galeate in shape; their apex is somewhat extended. Venation is of the pinnate-craspedodromous type. Secondary veins consist-

ing of 14 to 19 pairs are straight to slightly curved. Three to four pairs of secondary veins usually are tightly arranged and almost perpendicular to the longitudinal vein. Upper secondary veins are more widely spaced and depart from the longitudinal vein with angles less than 30°–59°. In the middle part of a leaf, they are most long and have 4 to 6 basicopic offsets. Venation of the third order is represented by frequent and curved anastomosing scalas. Venation of higher orders is well developed in a form of reticulum.

**Comparison and remarks.** Genus *Corylites* was first identified in the Paleocene flora of the Mall Island in Scotland (Gardner, 1887). In the course of subsequent, more comprehensive investigations of this flora (Boulter and Kvaček, 1989; Seward and Holttum, 1924), diagnostic features of the genus have been revised. According to the results obtained, characteristic features of *Corylites* leaves include numerous secondary veins (up to 17 pairs), even serrulate edges, and shortened narrow-spaced veins in the leaf base. Similar leaf peculiarities are characteristic of present-day *Alnus*, *Carpinus*, and some *Corylus* species. All generative organs of Betulaceae affinity useful for elucidating the taxonomic position of *Corylites* genus are missing in the Mall Island flora.

Because the morphology of Betulaceae leaves from the Malomikhailovka flora fits the diagnosis of *Corylites* species, they have been included into this taxon. In contrast to type species *C. hebridicus* Seward et Holttum, widespread in Paleocene deposits of Scotland and Spitsbergen, leaves of *C. amurensis* are generally lesser in size (Boulter and Kvaček, 1989); their secondary veins are more distinctly curved, and marginal serratures are smaller. Other representatives of Betulaceae from the Maastrichtian and Paleocene floras of northeastern Asia display far fewer lateral veins in leaves, and the arrangement of these veins differs from that of *Corylites* forms. Nevertheless, many such species have been attributed to this genus (Krasilov, 1979; Herman and Spicer, 1995; Manchester and Guo, 1996). Such a situation illustrates a tendency of including ancient Betulaceae variable in morphology into the *Corylites* genus, when their taxonomic position relative to recent taxa is unclear. This approach can be hardly accepted as correct, because it blurs distinction between genera *Corylus* and *Corylites*, and the latter, thus being morphologically boundless, turns out to be transformed into the composite taxon. The practice of transposing species from genus *Corylus* to genus *Corylites* by no

**Plate I.** Danian plants from the Malomikhailovka locality (the Amur River lower courses). (1–4) *Amurocyparis sokoloviae*: (1) shoot, specimen no. 369, ×5; (2) shoot with strobiles, holotype, specimen no. 600, ×6; (3) strobile, specimen no. 62, ×6; (4) shoot with strobile, specimen no. 3a, ×6. (5) *Chamaecyparis nootkatensis*, shoot, ×3, specimen from herbarium of the Botanical Institute, Russian Academy of Sciences. (6) *Pityospermum* sp., specimen no. 254, ×2.5. (7–10) *Amurocyparis sokoloviae*: (7) shoot with microstrobiles, specimen no. 257, ×4.5; (8) shoot with decussate ramification, specimen no. 604, ×3; (9) shoot with alternate ramification, specimen no. 371, ×2; (10) shoot, paratype, specimen no. 110, ×3. (11) *Larix puerensis*, shoot with strobile, holotype, specimen no. 601, ×1. (12) *Amurocyparis sokoloviae*, shoot, specimen no. 30, ×2.



means helps to get insight into their taxonomic position, and that of creating the composite taxon is useless for understanding the diversity of ancient Betulaceae.

Leaves of *Corylites protoinsignis* Krassilov from the Danian Boshnyakovo flora of Sakhalin have the digitipinnate venation, lobulate margin, and 6 to 7 pairs of bow-shaped secondary veins (Krasilov, 1979).

According to Herman and Spicer (1995), *Corylites beringianus* (Krysht.) Herman [= *Corylus beringianum* (Krysht.) Golovn.] from the Maastrichtian–Danian deposits of the Rarytkin and Koryak formations of the Koryak Upland shows a high variability of leaf morphology (Golovneva, 1994). Despite the even serrulate margin and rather numerous secondary veins (10–15 pairs), many leaves of this species also display the digitipinnate type of venation and have well-developed basal veins with abundant offspring. Some morphotypes of this species, such as *carpinifolia* and *viburnifolia*, have leaves with pinnate venation and short basal veins, but these leaves have no narrow-spaced veins at their base.

Leaves of *Corylites bellatula* (Guo et Li) Manchester et Guo (= *Corylus bellatula* Guo et Li) from the Paleocene flora of northeastern China (Manchester and Guo, 1995) also show the pinnate venation; however, their lateral veins are not numerous (only 6–9 pairs). Thus, the morphology of all three species is incompatible with diagnostic features of genus *Corylites*, and they should not be affiliated with this taxon.

Leaves of *C. amurensis* have been found together with bracteal involucre *Palaeocarpinus pacifica* sp. nov., and the absence of other leaves and generative organs of Betulaceae suggests that both kinds of remains represent the same plant. In addition, deposits of the Malomikhailovka Formation yielded rather numerous remains of coccuslike morphostructures 1–2 cm in diameter (Plate II, no. 11) most likely corresponding to *Ginkgo* seeds.

**Distribution:** Malomikhailovka Formation of the Amur River lower courses and Levaya Sobolevka Formation of the Sikhote Alin Ridge, Danian.

**Material:** more than 50 leaf impressions, e.g., specimens 143a, 258, 308b, 370, 385, 524, and others.

*Palaeocarpinus pacifica* Golovn. et Akhmetiev, sp. nov.  
Plate II, no. 7; Fig. 3, no. 5

**Holotype** no. 3808/3c in collection of Geological Institute, Russian Academy of Sciences; Malomikhailovka Formation, Danian, Plate II, no. 7; Fig. 3, no. 5.

**Description.** The semiflosculous bracteal involucre is about 6 mm long and 4 mm wide, narrow at the base and rounded at the top, where it is decorated with several acute denses 1–1.5 mm long. In its basal part, there are several veins ramifying and anastomosing upward, where venation is of the parallel-dictyodromous type. Nutlets are missing.

**Comparison and remarks.** Infructescences of *Palaeocarpinus* were first described from the upper Paleocene deposits of southern England (Crane, 1981). They consist of small nutlets set in an envelope, which is composed of two deeply divided bracts equal in size. Similar fruits were later found in several localities of North America, France, and China, and at present, there are known to be several species of *Palaeocarpinus*. Bracts of the type species *P. laciniata* Crane from the Reading Beds are up to 8–15 mm long and divided into five lobes having large denses of irregular shape. Bracts of *P. joffrensis* Sun et Stockey from the Paleocene deposits of Canada are 3–6 mm long and have two or three lobes with denses varying in shape and dimensions (Sun and Stockey, 1992). As compared to both species, the bract from the Malomikhailovka Formation is not as lacinate and intermediate in size (larger than that of *P. joffrensis* and is lesser than in the case of *P. laciniata*). It is not divided into lobes, just having denses up to 1.5 mm long, and thus better resembling the undivided bracts of *P. joffrensis*, although denses of the latter are longer. Bracts of sole Asiatic species *P. orientalis* so far known only from northeastern China (Manchester and Guo, 1996) are very similar in morphology to those of *P. joffrensis*. Bracts of *Palaeocarpinus* affinity from the Paleocene Menat Beds of France have been described long ago under names *Corylus lamottei* Saporta (Saporta and Marion, 1885) and "*Atriplex*" *borealis* (Heer) Laurent (Laurent, 1912). They are up to 9 mm long, almost orbicular, and have margins divided into numerous acute denses. Thus, all *Palaeocarpinus* forms are highly variable in size, morphology, and marginal structure of their bracts. Since *P. pacifica* from our collection is represented by sole specimen, the diversity degree of its bracts, as well as size and morphology of its nutlets are so far unknown.

It is remarkable that leaves of Betulaceae, which have been found together with different *Palaeocarpinus* species, are also variable in morphology. For instance, *P. laciniata* coexists with narrow elliptical leaves of *Craspedodromophyllum acutum* Crane, which have the acute base and apex, and displays 12 to 16 pairs of secondary veins. Fruits of *P. joffrensis*,

**Plate II.** Danian plants from the Malomikhailovka locality (the Amur River lower courses). (1) *Amurocyparis sokoloviae*, shoot, specimen no. 77,  $\times 1.5$ . (2) *Larix puerensis*, shortened shoots, specimen no. 382b,  $\times 4$ . (3) *Larix olgensis*, specimen from herbarium of the Botanical Institute, Russian Academy of Sciences,  $\times 1$ . (4) *Cryptomerites tutshkovii*, holotype, specimen no. 519,  $\times 3$ . (5) *Corylites amurensis*, leaf margin, specimen no. 360,  $\times 2$ . (6) *Larix puerensis*, leaf, paratype, specimen no. 3b,  $\times 1$ . (7) *Palaeocarpinus pacifica*, bract, holotype, specimen no. 3c,  $\times 7$ . (8–10) *Corylites amurensis*, specimens nos. 524 (8); 294 (9); and 385 (10), holotype. (11) *Ginkgo* sp. ?, seed, specimen no. 605,  $\times 2.5$ .

*P. orientalis*, and "*Atriplex*" *borealis* occur together with predominantly oval leaves, which are cordate at the base and acute at the top. These leaves, which have 6–9 pairs of secondary veins, are most similar to leaves of *Corylus insignis* Heer from Canada, *C. macquarrii* (Forbes) Heer from France, and *C. bellatula* Guo et Li from China. In the Malomikhailovka Formation, *C. pacifica* is associated with elliptical to egg-shaped leaves of *Corylites amurensis* showing 14–19 pairs of secondary veins. Fruits of various *Palaeocarpinus* species and coexisting leaves of Betulaceae display a combination of features most often characteristic of representatives of Coryleae tribe (Sun and Stockey, 1992), but, in one way or another, all of its recent genera differ from this taxon. Taking into account the wide geographic distribution (the moderately warm zone of the Boreal belt) and diversity of vegetative organs of *Palaeocarpinus* forms, we believe that this genus was important for the Paleocene evolution of early Betulaceae.

**Distribution:** Malomikhailovka Formation, Amur River lower courses, Danian.

**Material:** specimen 3c.

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