

A New Conifer Species, *Mesocyparis rosanovii* sp. nov. (Cupressaceae, Coniferales), and Transberingian Floristic Connections

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Abstract—A new species, *Mesocyparis rosanovii* sp. nov. from the Lower Paleocene of the Amur Region, Russia, is characterized by a combination of advanced and primitive features: mixed opposite-alternate branching of vegetative shoots, leafy microsporophylls, as well as a relatively high number of sporangia per microsporophyll and seeds per cone scale. The Late Cretaceous–Early Paleogene genus *Mesocyparis* McIver et Basinger, which obviously embraces a natural group of closely related species, was a significant component of the vegetation in the middle and high latitudes of eastern Asia and western North America. The range of the genus testifies to terrestrial Transberingian connections between the continents during the Cretaceous warming phases.

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INTRODUCTION

The problem of floristic exchanges between eastern Asia and western regions of North America has long attracted the attention of phytogeographers. If in the geological past such exchanges occurred through Beringia (land mass that repeatedly appeared on the Beringian shelf), they show that a land bridge for migration of terrestrial organisms existed during this geological epoch, and, therefore, should be taken into account in tectonic reconstructions. The floristic connections via Beringia are also important in the context of paleoclimatology, since even during the period of existence of the land bridge the climate at high latitudes impeded the migration of thermophilic species. The exception to this rule were periods of warm polar climate, during which plants of temperate and even subtropical zones might have reached Beringia. Along with other characteristics, mass Transberingian migrations that included thermophiles can serve as indicators of such periods.

One of the warm polar periods took place during the Campanian of the Late Cretaceous (Jenkyns et al., 2004), when the floras of Alaska and northeastern Russia had many elements in common (Krassilov, 1975, 1976a, 1976b, 1979). After the cooling at the Cretaceous/Paleogene boundary, the global Late Paleocene warming also might have favored Transberingian migrations. However, some tectonic reconstructions claim that in the Late Cretaceous and Early Paleogene Asian and American parts of Beringia were still remote

from each other, which would have virtually excluded the possibility of migration.

In this context, phytogeographic relations between Asia and North America should be revised using modern paleobotanical methods. The similarity between the Paleocene floras of the western United States and Canada, on the one hand, and the Chukchi Peninsula, Sakhalin Island, and the Amur Region, on the other hand, was noted by many researchers. The Paleocene flora of Tsagayan (Amur Region) shares more than a half of its species with the floras of North America (Krishtofovich, 1939; Krassilov, 1976a). However, a significant proportion of these species are artificial taxa that remain unstudied in morphological detail. Therefore, taxonomic revision of this major East Asiatic fossil flora and the analysis of the resulting phytogeographic concepts are highly necessary.

To accomplish such a revision, we are going to study, in the first place, the well-preserved plant remains from the newly found localities of the Amur Region, the richest of which are outcropped in the Arkhara-Boguchan open-pit coal mine. Among fossil plants collected from this locality, coniferous shoots and cones that belong to the family Cupressaceae and were previously included in the morphological group *Cupressinocladus interruptus* (Newberry) Schweitzer stand out because of their good preservation. The application of light and electron microscopy allows these remains to be classified in terms of the natural system and to be compared with recently described closely related species of North America and northeastern Russia.

MATERIAL AND METHODS

The material comes from the coal-bearing deposits of Early Paleocene age that are exposed in the open-pit coal mines of the Arkhara-Boguchan brown coal field, 15 km southeast of Arkhara in the Amur Region (49°18'52.3" N, 130°12'42.7" E). Plant remains occur in bluish gray clays that overlie the coal layer "Nizhnii" (Akhmetiev et al., 2002; Markevich et al., 2004). The cupressaceous shoots and cones are preserved as impressions with coaly compressions. Pollen cones are either attached to the shoots or preserved detached, associating with the vegetative shoots. Isolated microsporophylls of disintegrated pollen cones frequently occur scattered on the bedding plane. Seed cones are partly preserved as casts of inner cavities between the scales. The compressions were macerated with concentrated nitric acid. We also succeeded in extracting pollen grains from sporangia.

The remains of shoots and cones were studied morphologically using a Leica MZ6 stereomicroscope. The macerated cuticles were studied in transmitted light under an Axioplan 2 compound microscope. Leaf cuticles, microsporophylls, and inner casts of seed scales were mounted on SEM stubs and covered with gold for study under a CAMSCAN SEM. Photographs were made using Leica DFC 320 and Nikon Coolpix 8700 digital cameras.

Pollen grains were prepared for transmission electron microscopy after Meyer-Melikian and Tel'nova (1990). Ultrathin sections were made with a ultramicrotome (LKB-3). Some of the sections obtained were additionally stained with lead citrate. Ultramicrographs were obtained using a TEM (Jeol 100 B).

The collection of several hundred vegetative shoots, pollen and seed cones, and microsporophylls with sporangia is housed in the Geological Institute of the Russian Academy of Sciences (GIN), no. 4867.

SYSTEMATIC PALEOBOTANY

Family Cupressaceae Richard ex Bartling, 1830

Genus *Mesocyparis* McIver et Basinger, 1987

Mesocyparis rosanovii Kodrul, Tekleva et Krassilov, sp. nov.

Plate 11, figs. 1–6, Plate 12, figs. 1–8

Etymology. In honor of Prof. A.Yu. Rozanov, acknowledging his contribution to the development of paleobotanical research at the Paleontological Institute of the Russian Academy of Sciences.

Holotype. GIN, no. AB1-233; a shoot bearing seed cones; Amur Region, Arkhara-Boguchan brown coal field, 15 km southeast of Arkhara; Tsagayan Formation, above the coal seam "Nizhnii"; Early Paleocene (Pl. 11, fig. 1).

Diagnosis. Branching shoots plagiotropic, opposite and alternate, branches and branchlets arising in axils of lateral leaves, obliquely spreading. Leaves persistent, decussate, scaly, dimorphic, on penultimate

branches at least twice as long as on ultimate branches. Facial and lateral leaves approximately equal in length; facial leaves flatly adpressed, thickened along midline, typically keeled, apices acute to acuminate, thickened; lateral leaves folded, decurrent, free portion narrowly spreading, acute, clasping facial leaves or subtending branches of higher order. Leaves of axes bearing seed cones of one type, decurrent, distally free, falcate. Leaves amphistomatic, stomata in irregular bands on abaxial side of facial leaves, mostly oblique to midline. Stomata mono- or (rarely) amphicyclic, with typically five subsidiary cells, which are indistinctly differentiated into polar and lateral cells, often contiguous. Trichomes as irregularly developed small pits on subsidiary and ordinary cells.

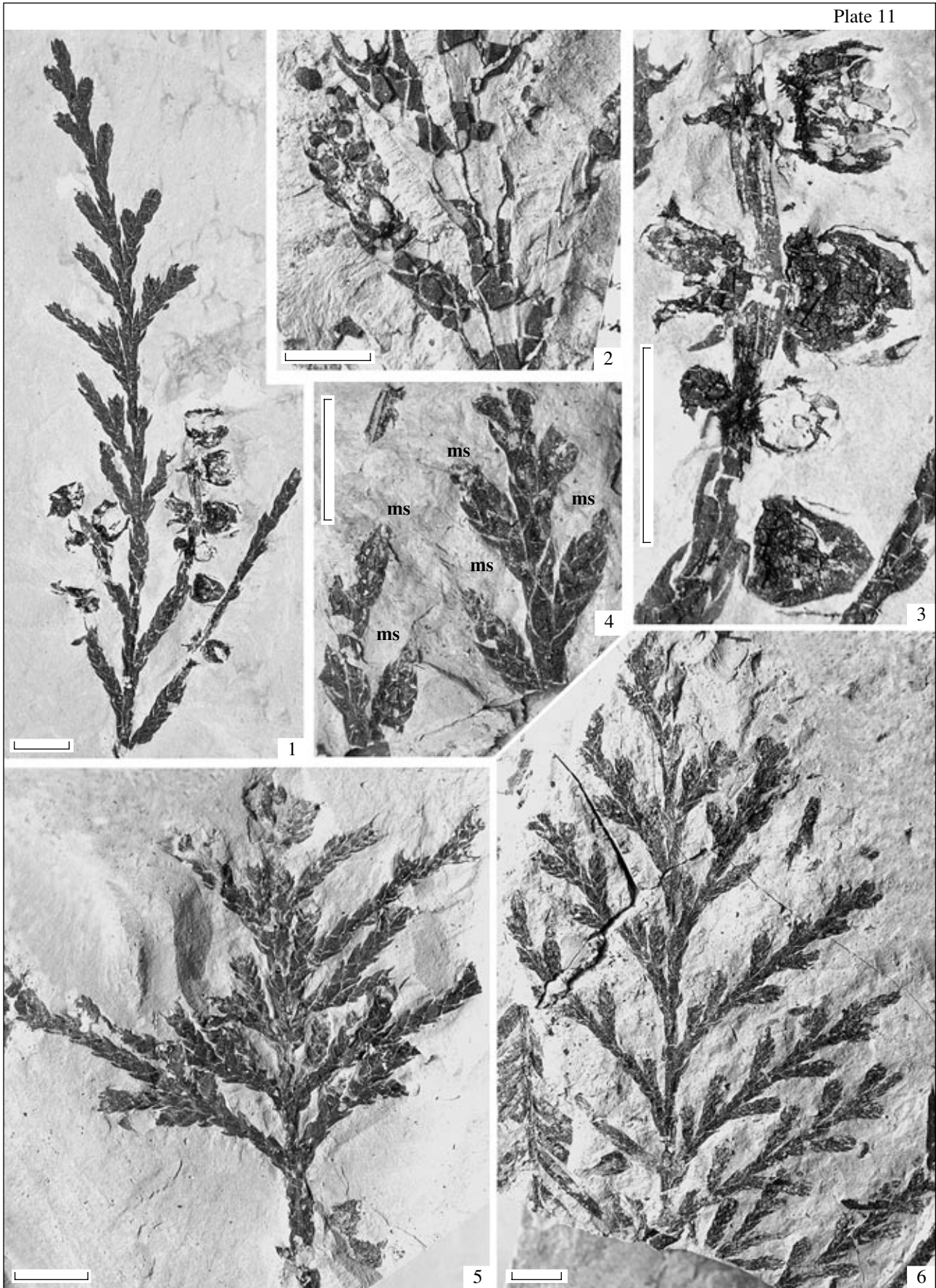
Pollen cones up to 7 mm long, 1–4 mm in diameter, terminal on ultimate branchlets, consisting of three to five decussate pairs of peltate microsporophylls. Peltae of microsporophylls leafy, 1–2.2 mm long, 0.5–2 mm wide; larger (proximal) pelta with stomata. Sporangia abaxial, two to five at base of peltae, globose to obovate, 0.4–0.5 mm long, 0.35–0.45 mm in diameter. Pollen about 20 µm in diameter, spherical to slightly elliptical, irregularly gemmate, with leptomatic germinal area of reduced ectexine discernible under TEM.

Seed cones erect, globose to oblong, 3.5–5 mm long, 3–4 mm in diameter, borne on short stalks in one to six opposite pairs in two side rows or decussate over fertile zones of penultimate axes, which is leafy above. Fertile cone scales four in two decussate pairs, approximately equal in size, woody, subpeltate, umbo subapical with prominent, erect point. Seeds three to five per scale, inverted on short funiculus, bilaterally winged.

Description (Figs. 1–3). Vegetative shoots are plagiotropic; ultimate branchlets are prostrate in one plane, leafy, mostly opposite or, more rarely, alternate. Most shoot remains bear branches of two or three orders. The branches may be attached oppositely or alternately. Ultimate branchlets are often present only on the acroscopic side facing the shoot apex (Fig. 1a). Leaves of vegetative shoots are scaly, decussate, and dimorphic: facial and lateral.

The axes of the first order 4–10 cm long bear up to 16 branches, which are borne in the axils of lateral leaves at an angle of 20°–45° and at intervals of 0.5–0.7 cm and are up to 2.5 cm long. Facial leaves on thick axes are 4–6 mm long and 0.8–1 mm wide, flatly adpressed, linear, slightly expanded in the upper portion, with an acute apex that reaches the leaf bases of the next whorl. Lateral leaves are 4–5 mm long and 0.5–0.8 mm wide, longitudinally folded, with a decurrent leaf cushion and a falcate free upper portion that ensheathes the bases of the axial second order shoots.

The penultimate shoots bear facial leaves 1.5–3 mm long and 0.8–2 mm wide, rounded-triangular, with an acute or pointed apex, flatly adpressed along the whole length of the leaf, with or without a weak keel. Lateral leaves are 1.5–3 mm long and 0.4–0.8 mm wide, longi-



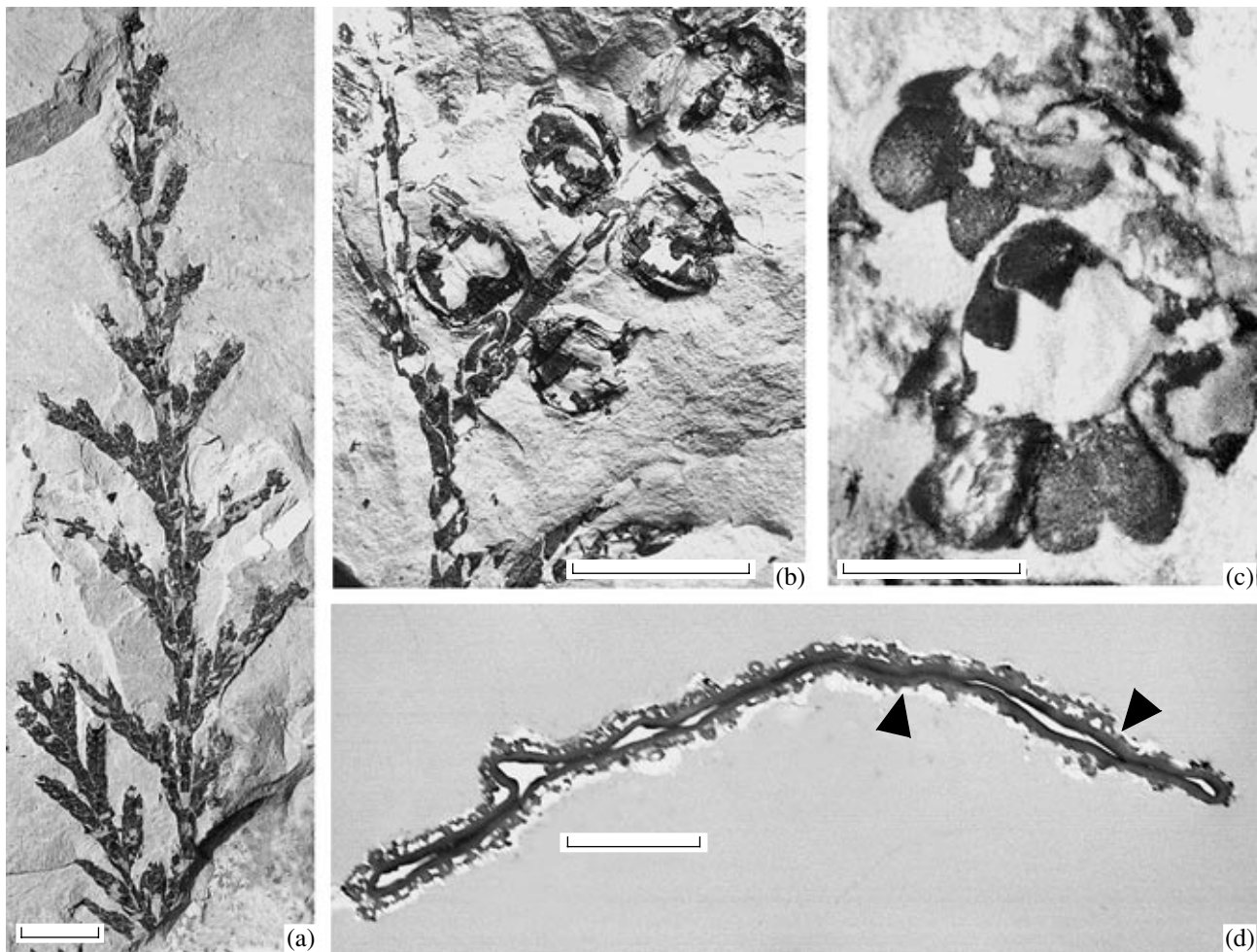


Fig. 1. *Mesocyparis rosanovii* sp. nov.: (a) paratype GIN, no. AB1-371, shoot branching; (b) paratype GIN, no. AB1-278, shoot with two-row and decussate seed cones and non-differentiated leaves below the fertile zones; (c) paratype GIN, no. AB1-101, microsporophyll with sporangia and a cluster of sporangia; (d) paratype GIN, no. AB1-101, section of the exine, leptomatic area is marked with arrows, TEM. Arkhara-Boguchan brown coal field, Amur Region, Tsagayan Formation, Lower Paleocene. Scale bar (a, b) 5 mm; (c) 1 mm; (d) 3 μ m.

tudinally folded, decurrent, basally fused, broadly turned out in the free portion, and subtending axial shoots of the last order. Their pointed apices clasp lower facial leaves of the ultimate branchlets.

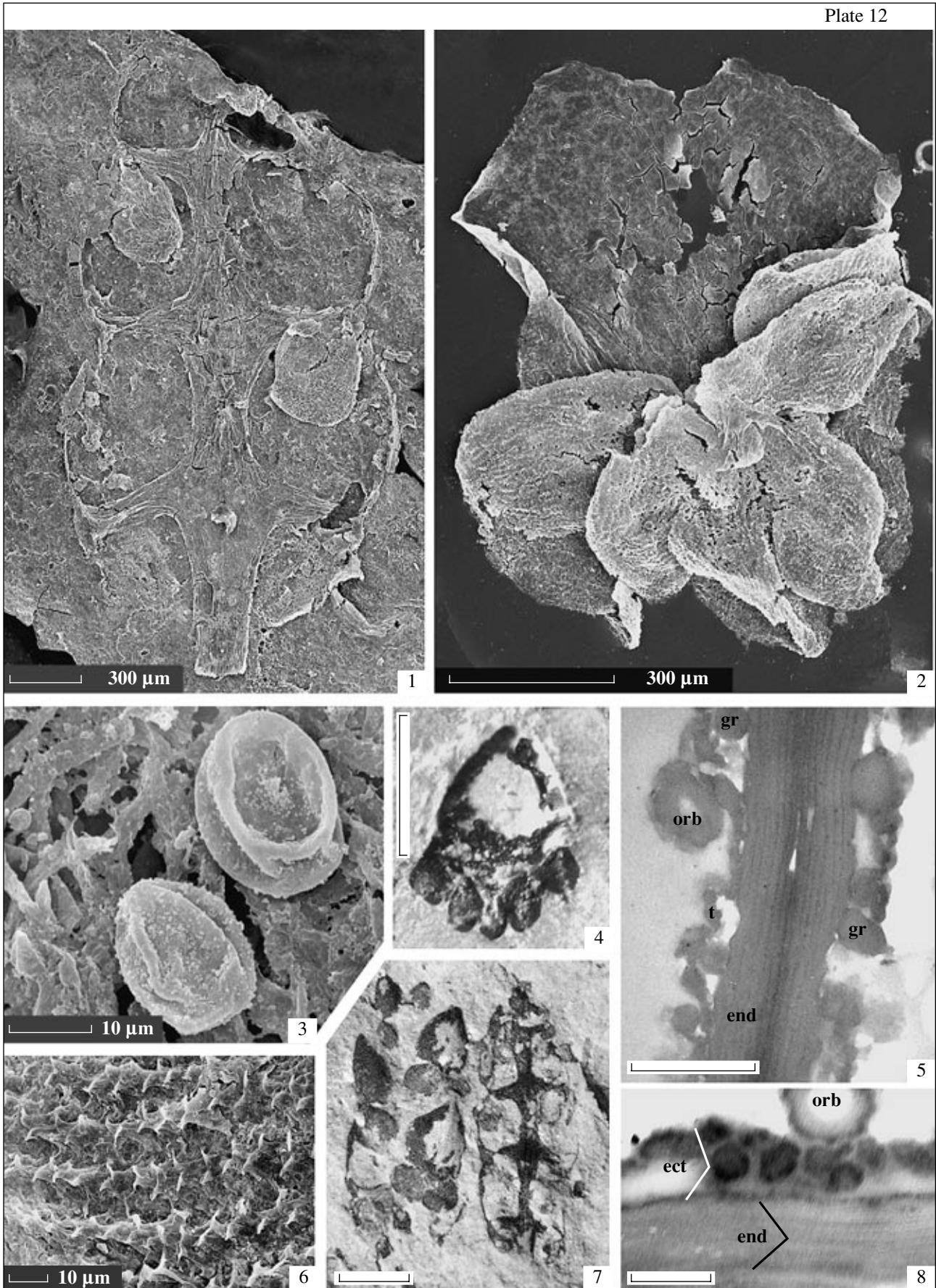
The ultimate branchlets are up to 8 mm long. They depart from axils of lateral leaves of the penultimate order at intervals of 3–6 mm and at an angle of 20°–30°. The lower facial leaves of these branchlets are approximately half as long as those of the bearing penultimate shoot (1.5 \times 1 mm). The bases of the rounded-triangular facial leaves are overlapped by the lateral leaves. The uncovered portion of the facial leaves is rhomboidal

and keeled; the apex is keeled and reaches the point of separation of the next pair of lateral leaves. The lateral leaves are longitudinally folded, decurrent, and connate at about two-thirds their length. Their free portion is pointed, falcate, and clasping the facial leaf.

In the epidermis of the abaxial region of facial leaves, there are narrow marginal non-stomatal zones, two indistinctly delineated stomatal zones that wedge out towards the apex, and a broad median non-stomatal zone between them. Stomata are orientated predominantly obliquely to the leaf keel. They are mono- or, more rarely, amphicyclic, usually with five subsidiary

Explanation of Plate 11

Figs. 1–6. *Mesocyparis rosanovii* sp. nov.: (1) holotype GIN, no. AB1-233, shoot with seed cones; (2) paratype GIN, no. AB1-276, shoot with a terminal microstrobilus; (3) holotype GIN, no. AB1-233, fertile zone of a shoot bearing seed cones; (4) paratype GIN, no. AB1-152, terminal microstrobili on ultimate shoots forming a fertile zone; (5) paratype GIN, no. AB1-169, shoot with opposite branching; (6) paratype GIN, no. AB1-152, shoot with alternate branching. Arkhara-Boguchan brown coal field, Amur Region, Tsagayan Formation, Lower Paleocene. Scale bar (1, 3–6) 5 mm, (2) 2 mm. Designations: (ms) microstrobilus.



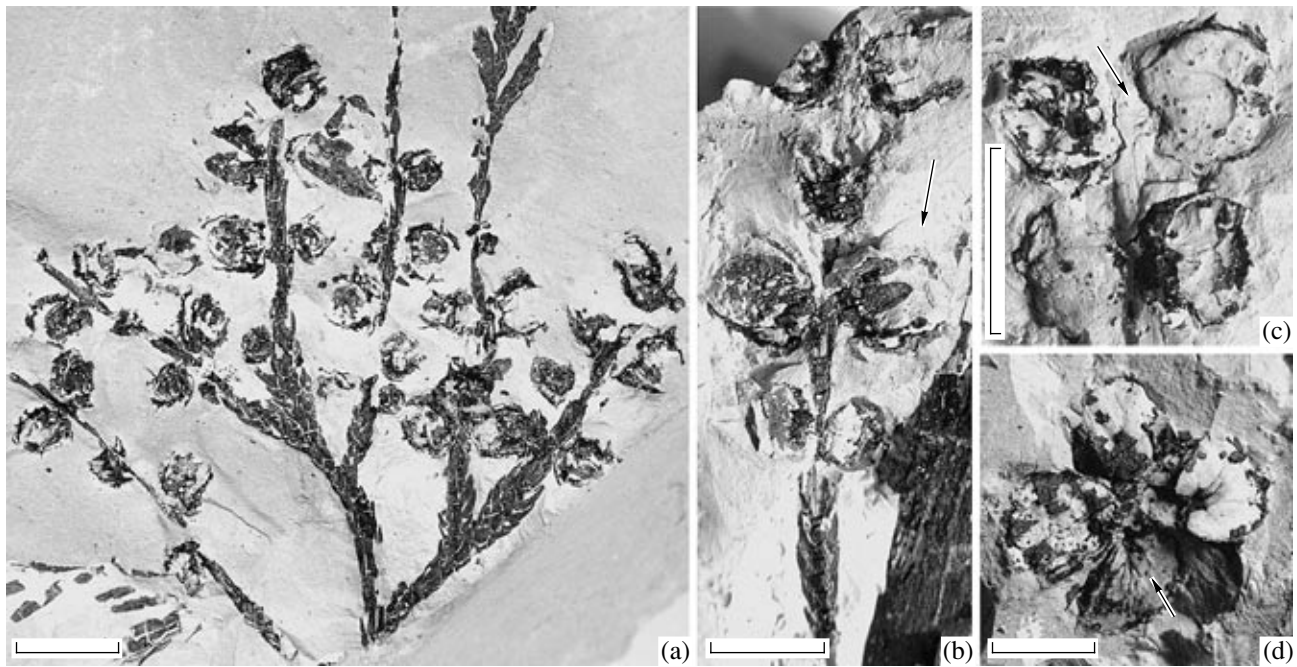


Fig. 2. Seed cones of *Mesocyparis rosanovii* sp. nov.: (a) paratype GIN, no. AB1-141; (b) paratype GIN, no. AB1-370, arrow indicates a cone with weakly developed lower scales; (c) paratype GIN, no. AB1-151, arrow indicates a short stalk of the cone; (d) paratype GIN, no. AB1-246, decussate arrangement of a pair of cones, arrow indicates a sterile scale. Arkhara-Boguchan brown coal field, Amur Region, Tsagayan Formation, Lower Paleocene. Scale bar (a–c) 5 mm; (d) 3 mm.

cells, which are indistinctly differentiated into polar and lateral (slightly more elongated) cells. The lateral cells of adjacent stomatal apparatuses are often contiguous or are shared by neighboring stomatal apparatuses. The bases of trichomes are shallow, rounded, variously developed pits on guard cells and ordinary cells.

Pollen cones (microstrobili) terminate ultimate branchlets, which are solitary or aggregated in fertile zones of the penultimate shoots (Pl. 11, figs. 2, 4, 6). The cones are cylindrical, narrowing and more rounded toward the apex, 1–7 mm long, and with a basal diameter of 4 mm. The microstrobilus axis is thin, straight, thickened at the nodes, and longitudinally striate (Pl. 12, figs. 1, 7). The cones consist of three to five pairs of decussate microsporophylls. The microsporophylls are attached to the axis at an angle of about 90°. They are peltate, consisting of a short stalk and leafy pelta (apophysis), which is curved upwards and overlaps the base of a sporophyll of the next node so that the sporangia are completely enclosed (oblique section shows that sporangia are situated within a cavity that is

formed by overlapping microsporophylls). Sporangia of lower sporophylls are underdeveloped. The microsporophylls diminish greatly towards the apex: the proximal microsporophylls are nearly twice as large as the distal. Larger basal microsporophylls show stomata that form indistinct digitate rows at the base of the pelta. Sporangia are attached near the base of leafy peltae in clusters of two to five. They are rounded-elliptical, dehiscent by a longitudinal slit (Pl. 12, figs. 2, 4, 7; Fig. 1c). There is no correlation between the dimensions of sporangia and those of microsporophylls: each microsporophyll in any region of the pollen cone is about 0.5 mm long. Two layers are discernible within the sporangial wall: the outer layer consists of longitudinal rows of narrow fusiform cells appearing as longitudinal striation of the sporangial surface and the inner layer is composed of relatively short rectangular cells with spiny appendages on anticlinal walls. Appendages of adjacent cells intertwine (Pl. 12, fig. 6). We failed to count the exact number of pollen grains per sporangium, but it is no less than 32. Pollen grains are spheroidal or prolate spheroidal

Explanation of Plate 12

Figs. 1–8. *Mesocyparis rosanovii* sp. nov.: (1) paratype GIN, no. AB1-101, longitudinal section of a microstrobilus, the position of sporangia is discernible, SEM; (2) paratype GIN, no. AB1-101, microsporophyll with sporangia, adaxial view, SEM; (3) paratype GIN, no. AB1-101, pollen grains on the inner sporangial wall, SEM; (4) paratype GIN, no. AB1-374, microsporophyll with sporangia, abaxial view; (5) paratype GIN, AB1-101, region of the exine that was not stained with lead citrate, TEM; (6) paratype GIN, no. AB1-101, sporangial wall, SEM; (7) paratype GIN, no. AB1-101, microstrobili; (8) paratype GIN, no. AB1-101, region of the exine that was stained with lead citrate, note the difference in electron density between the ectexine and endexine, TEM. Arkhara-Boguchan brown coal field, Amur Region, Tsagayan Formation, Lower Paleocene. Scale bar (4, 7) 1 mm, (5) 0.5 μ m, (8) 0.3 μ m. Designations: (gr) infratectal granules; (orb) orbicule; (t) tectum; (end) endexine; (ect) ectexine.

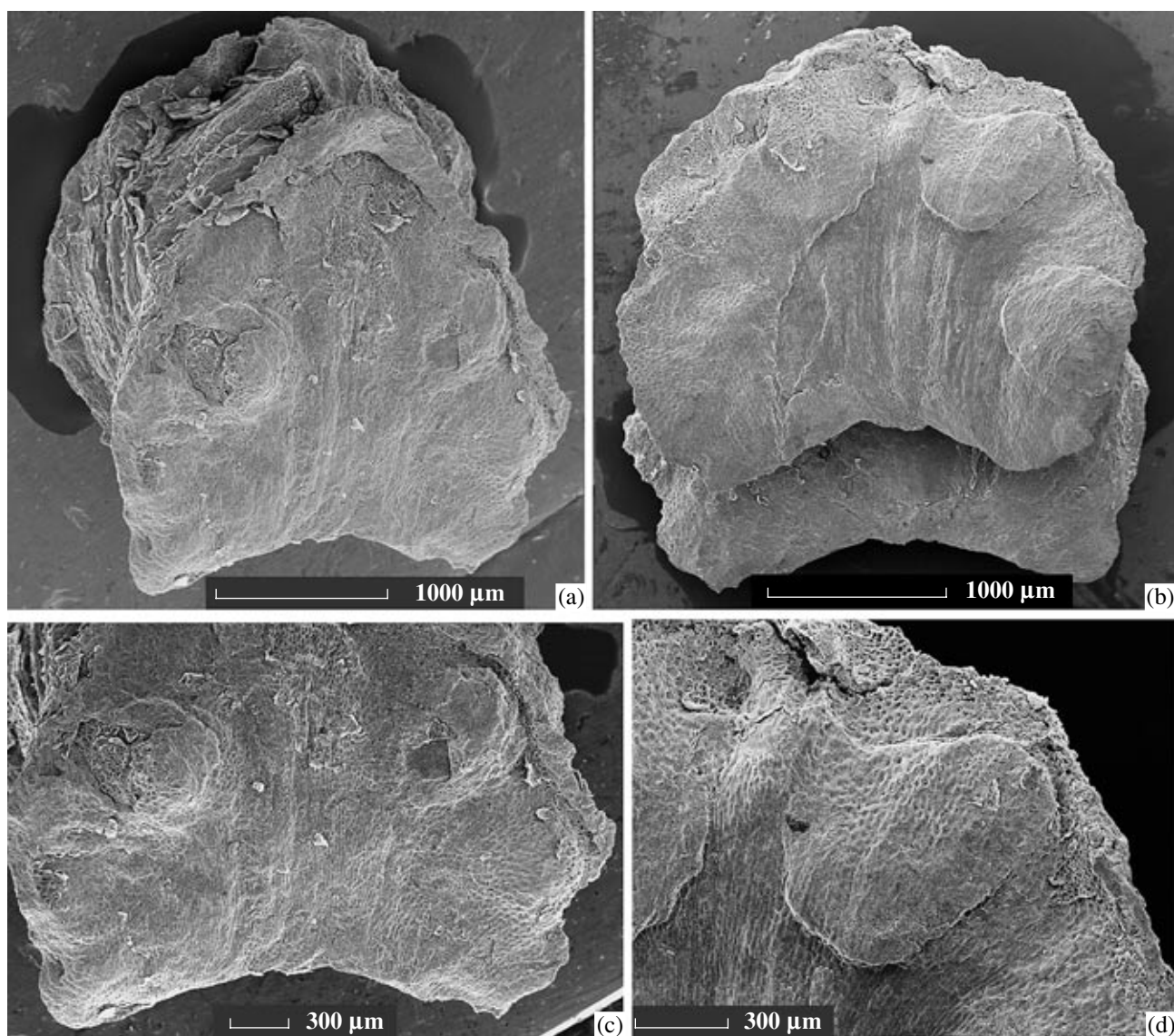


Fig. 3. Cast of inner cavities between scales of the seed cone of *Mesocyparis rosanovii* sp. nov., paratype GIN, no. AB1-246, SEM: (a, c) inner surface of the seed scale showing scars of five ovules; (b, d) inner surface of the seed scale with two immature ovules. Arkhara-Boguchan brown coal field, Amur Region, Tsagayan Formation, Lower Paleocene.

dal, about 20 μm in diameter, occasionally split into two valves. Small granules are scattered over the surface of pollen grains (Pl. 12, fig. 3). The outer layer of the exine is loose and fits only loosely the inner layer, which is more rigid (its outlines are seen in thick sections). The outer layer is folded; the folds are often circular. No apertures have been detected.

The exine consists of ectexine and endexine, the boundary between which is clearly seen in stained sections because of the difference in electron density; in unstained sections, the structure of particular layers of the exine is better distinguishable. The thickness of the exine varies from 0.3 to 0.9 μm . The ectexine consists of three layers: the tectum is 0.02–0.05 μm thick and undulate; the infratectum is composed of large loosely

packed granules 0.09–0.2 μm in diameter; and the foot layer is thin, with an average thickness of 0.009 μm , closely addressed to the outer lamella of the endexine (Pl. 12, figs. 5, 8). The endexine is about 0.22 μm thick, lamellate, consists of six (occasionally five) distinct, parallel, closely adjacent lamellae of nearly equal thickness.

In some sections, a region with a normally developed endexine and reduced ectexine, which is restrict to the foot layer and rare granules, may be seen. This region may represent a leptomatic germinal area (Fig. 1d). Hollow orbicules occur on the pollen surface.

Seed cones are arranged in opposite pairs, most of them in decussate order and some in rows, one to six pairs over a fertile zone. Below the fertile zone, the

shoot is covered with crowded differentiated leaves, which are similar in size and morphology to the leaves of penultimate shoots. Rarely, the leaves are non-differentiated (Fig. 1b). The axes bearing seed cones are covered with uniform decurrent leaves, which are free and falcate in their upper portion (Pl. 11, fig. 3; Figs. 1b, 2a, 2b). Above the fertile zone, the shoot continues to grow and branches repeatedly; leaves on such axes do not differ from leaves of vegetative shoots of respective orders. Seed cones are globose to oblong, 3.5–5 mm long, 3–4 mm in diameter, attached to the shoot by a short stalk of 0.3–0.8 mm long (Fig. 2c). Large woody fertile scales in two decussate pairs are approximately equal in size. Occasionally, the lower pair is poorly developed compared with the upper pair, or nearly reduced (Fig. 2b). Small thin sterile scales with a short point are sometimes preserved at the base (Fig. 2d). In juvenile cones, scales are closely adpressed to each other. With maturation, they separate to open narrow slitlike cavities. The seed scales are subpeltate, with the umbo near the apex, their points spreading at a right angle, and with digitate ribs on the inner side. The interior epidermis of the scale consists of narrow tetragonal cells arranged in rows that are parallel to the ribs. Under an SEM, scars of five seeds are discernible on the inner cast (Figs. 3a, 3c). The opposite scale of the same pair shows two scars and one underdeveloped inverted ovule near the apex (Figs. 3b, 3d). This ovule is reniform, 0.9 mm wide, on a short pedicel, with two incipient slightly asymmetric lateral wings. The seed coat is formed by isodiametric convex smooth-walled cells.

C o m p a r i s o n. Based on the morphology of plagiotropic shoots, type of branching, leaf outline, and general characteristics of pollen and seed cones, the species under description fits well to the diagnosis of the genus *Mesocyparis*, which was described from the Paleocene (Ravenscrag Formation) of the Saskatchewan Province, western Canada (McIver and Basinger, 1987). This genus was erected from the formal group *Cupressinocladus interruptus* and characterized in its diagnosis as follows: “Branches spreading, pinnate, opposite, forming flat frondlike sprays. Leaves decussate, scalelike, acute-tipped, overlapping; lateral and facial leaves approximately equal in length; lateral leaves folded, facial leaves obovate to linear, adpressed. Seed cones erect, globose to oblong, borne in opposite pairs. Cone scales woody, obovate. Seeds with two broad, bilaterally symmetrical wings” (McIver and Basinger, 1987, p. 2340).

Apart from the type species *M. borealis* McIver et Basinger from the Paleocene of Saskatchewan, western Canada, and of Wyoming, the United States, the genus also includes *M. umbonata* McIver et Aulenback from the Maastrichtian of Alberta, western Canada (McIver and Aulenback, 1994), and *M. beringiana* (Golovneva) McIver et Aulenback from the Maastrichtian–Danian of the Chukchi Peninsula, which was originally described as *Microconium beringianum* Golovneva (Golovneva, 1988; McIver and Aulenback, 1994).

These species differ from each other in details of branching of vegetative shoots, leaf dimensions, arrangement of seed cones in fertile zones, and morphology of cone scales. The Cretaceous species *M. umbonata* shows not only an opposite, but also an alternate arrangement of ultimate branchlets; the leaves are relatively small, the seed cones are decussate, the umbo is central on the scale and its point is not spreading, the microsporophylls are deltoid. In the Paleocene species *M. borealis* the arrangement of ultimate branchlets as well as seed cones in fertile zones is constantly opposite, the microsporophylls are leafy, the points of apophysis are closer to the apex and turned downwards. *M. beringiana* from the Chukchi Peninsula resembles the Paleocene species *M. borealis* in the opposite branching and in the umbo of cone seed-cone scales situated near the apex (Golovneva, 1988; McIver and Aulenback, 1994). An initial phase of differentiation into small basal scales (supposedly sterile) and larger distal scales may be seen in this latter species.

All three species are characterized by the aggregation of seed cones into fertile zones on the penultimate axes. The information about the arrangement of microstrobili is somewhat controversial, since only shed microstrobili are known for the type species. In Cretaceous *M. umbonata* microstrobili terminate ultimate shoots. However, the reconstruction by McIver and Aulenback (1994, text-fig. 4) suggests that microstrobili might have been grouped within the fertile zone. Typically, each microstrobilus bears two sporangia. The diagnosis of *M. borealis* mentions two or three sporangia, but only bisporangiate microsporophylls are illustrated. Later, McIver and Aulenback (1994) spoke of only two sporangia. It is conceivable that the occurrence of three sporangia is a rare anomaly in this species. The pollen grains are virtually identical, only slightly differing in dimensions.

The new species from the Paleocene of the Amur Region most closely resembles *M. umbonata* from the Maastrichtian of Canada, differing insignificantly in leaf size, cone scale morphology, and, mainly, in the number of sporangia per microsporophyll and the number of seeds per seed scale. Although two latter characteristics are quantitative, they make this species distinguishable from the other species of *Mesocyparis*, which have a lesser and virtually constant number of sporangia and seeds. In the morphology of seed cones *M. rosanovii* sp. nov. is similar to *M. beringiana* from the Chukchi Peninsula, but these species are distinct otherwise.

M a t e r i a l. Several hundreds specimens from the type locality.

DISCUSSION

Until recently, the Cupressaceae was considered as a relatively ancient family, appearing in the Triassic. However, previously, cheirolepidiaceae shoots with

decussate branching and/or leaf arrangement have been commonly assigned to the Cupressaceae (Watson, 1988). Triassic and Jurassic records of the family seem to be unreliable. Indisputable members of the family appeared only in the mid-Cretaceous, to the end of the period they reached a significant morphological diversity and even included forms with phylloclades that resembled pinnate fronds of the ferns. Evidently, we deal with a relatively young group of conifers that is chronologically close to angiosperms.

The modern flora enumerates 20 genera of the Cupressaceae, which occur in both the Northern and Southern hemispheres (Page, 1990), greatly varying in ecology and growing from the mid-latitude uplands to the dry subtropics. Consequently, the growth forms vary from high canopy trees to subalpine dwarf shrubs. The arrangement of genera within the family mostly reflects ecological preferences and are hardly related to the phylogeny (Page, 1990; McIver and Aulenback, 1994). The phylogenetic polarization of the characters is unclear. Considering the branching pattern, different groups might have shown opposite trends. The number of metameric organs (microsporophylls, sporangia, cone scale, and seeds) might also have undergone polymerization/oligomerization cycles. Fossil members are still insufficiently studied in this context.

The genus *Mesocyparis* was erected from the formal morphological group *Cupressinocladus interruptus* as a natural one or approaching the status of a natural taxon. However, its generic diagnosis (above) includes characters that are present in many genera of the Cupressaceae. On the other hand, the aggregation of cones in fertile zones is not indicated; the number of scales in a seed cone, a diagnostic character of cupressaceous genera, and the number of seeds are not included in the diagnosis, the characters of pollen cones and pollen grains are not mentioned at all. In fact, if the original diagnosis were strictly followed, the genus should have been treated as an artificial one. Taking into consideration the characters of the type species and the related species, the main characters of *Mesocyparis* are the plagiotropic shoot morphology, the development of ultimate branchlets in the axils of each lateral leaf pair of penultimate axis, scaly decussate leaves, dimorphic lateral and facial leaves, aggregation of both male and female cones in fertile zones of penultimate axes, microsporophylls with leafy overlapping apophyses, two to five sporangia per microsporophyll, leptomatic pollen grains, seed cones of four fertile scales, and seeds with two lateral wings. Considering these characters, it is possible to compare the genus with some natural genera of the Cupressaceae.

Cupressinocladus interruptus was compared with *Thuja* L., and, with more support, with *Chamaecyparis* Spach, a forest-forming element of moist coniferous forests of the Pacific coast (Krassilov, 1976). Affinities with this genus were also supposed for *Mesocyparis* (McIver and Basinger, 1987; McIver and Aulenback,

1994). However, *Chamaecyparis* has solitary pollen cones and seed cones of eight fertile scales. Among the temperate genera, *Microbiota* Komarov, a subalpine shrub of Far-Eastern mountain ranges, is comparable on account of seed cones of four scales. On the other hand, clustered pollen cones in combination with four-scale seed cones are more characteristic of the xerophilous southern genera *Callitris* Vent., *Widdringtonia* Endl., and *Actinostrobus* Miq. ex Lehm., and the Mediterranean *Tetraclinis* Masters (Page, 1990).

These morphological comparisons do not testify to similar ecology. The abundance of remains and the association of vegetative shoots, cones, isolated microsporophylls, and cone scales indicate that *Mesocyparis* grew in peat bogs. Among modern cupressaceous plants of such ecology, the monotypic genus *Pilgerodendron* Florin from South America is of particular interest. Morphologically, it resembles *Mesocyparis* in having leafy microsporophylls with relatively numerous sporangia, four-scaled seed cones with better-developed lower scales, and in the shape of subpeltate spoon-shaped concave scales with umbo near the apex. Unlike *Mesocyparis*, the leaves of *Pilgerodendron* are not differentiated into the facial and lateral, supposedly a primitive character. It is not inconceivable that *Pilgerodendron* originated from the same ancestral group as *Mesocyparis* did.

The pollen grains of *Cupressaceae* are rather uniform both at the level of light and electron (scanning and transmission) microscopy, varying insignificantly in quantitative characteristics: the thickness of the tectum, diameter of infratectal granules, and the thickness and number of endexinal lamellae. The similar morphology and ultrastructure of pollen grains occur in both the Taxodiaceae and Taxaceae (Gullvåg, 1966; Meyer, 1977; Surova and Gumbatov, 1986; Surova and Kvavadze, 1988; Kurmann, 1990). Pollen grains are spheroidal or flattened spheroidal, rarely prolate, with granular ectexine and lamellate endexine, numerous orbicules that are retained even after acetolysis (Kurmann, 1994), and with porelike leptome (Ueno, 1959), although often appearing inaperturate because the aperture is small and is masked by the folds of the exine. The surface sculpture is mostly granulate or finely verrucose. The leptome is situated at the distal pole. Usually, there are certain differences in sculpture between the area surrounding the aperture (germinal area) and the rest of the exine surface (body area). In sections, the germinal area includes the endexine and foot layer, which occasionally is reduced (Lugardon, 1995; Kurmann and Zavada, 1994). In the apertural region, the exine is usually reduced to a single lamella of the endexine (Kurmann, 1994). The germinal area is leptomatic, with a reduced ectexine.

The comparison between the Cretaceous–Paleogene and extant members of the Cupressaceae has revealed several trends in the early evolution of the group that disappeared with time. Thus, shoot flattening and leaf

fusion were already distinct in the cupressaceous species as early as the Late Cretaceous and sometimes led to formation of cladodia (*Androvettia* Hollick et Jeffrey and *Protophyllocladus* Berry); however, this trend was even more strongly expressed at this evolutionary stage than in modern members of the Cupressaceae. The aggregation of seed cones in fertile zones is characteristic of ancient members of the group. The analogous aggregation of microstrobili, which is observed in *Mesocyparis rosanovii* sp. nov. and, to a greater or lesser degree, is developed in the other species of the genus, is known in only one modern member of the Cupressaceae, *Callitris*. The fact that subpelate cone scales occur in small numbers in modern genera is conventionally considered to be a result of oligomerization; however, it is typical of the Cretaceous and Paleocene species of *Mesocyparis*.

The diagnostic differences between the species of the genus *Mesocyparis* mostly pertain to the branching pattern and the number of metameric organs. The transition from the mixed, alternate and opposite, branching in the Cretaceous species to the consistently opposite branching in the Paleocene species apparently represents a progressive trend. *Mesocyparis rosanovii* sp. nov. outnumbers the other species of the genus in sporangia and ovules. However, the large number of sporangia in this species, which approaches the maximum number for the family (six), correlates with leafy microsporophylls, the lower of which have stomata. It is possible that the similarity of fertile and sterile parts is secondary; however, since we are dealing with an early evolutionary stage, initially weak differentiation is also conceivable. If so, a relatively large number of sporangia per microsporophyll is hardly related to polymerization, but is rather a persistent ancestral state.

These hypotheses need further verification and their pertinence to the phylogeny of Transberingian species is not as yet fully understood. The genus *Mesocyparis*, which was distributed in Asia from the Amur Region to the Chukchi Peninsula and in North America from Alberta to Wyoming, apparently was a natural group of closely related species, the degree of morphological differentiation being to certain extent related to geographical distance. The range of this genus at the end of the Cretaceous and in the Paleocene unequivocally testifies to terrestrial connections between the continents via Beringia that was accessible for invasion of temperate species during the Late Cretaceous warming. The Early Paleocene species from the intracontinental depression of the Amur Region still retain such characters of Cretaceous ancestors as the mixed opposite-alternate branching of vegetative shoots, decussate arrangement of seed cones, numerous sporangia and seeds, and the other archaic features of reproductive organs, but show trends toward the double-row arrangement of cones and the cone morphology characteristic of the relatively more advanced Paleocene species of the Chukchi Peninsula and North America. We believe that ancestral species migrated from an inland Asiatic

center via Beringia, acquiring on the way the more advanced morphologies of the Chukotkan and North American species.

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