On the Stratigraphic Setting and Composition of the Ayanka Flora from the Upper Cretaceous of Okhotsk-Chukotka Volcanogenic Belt, Northeastern Russia

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Abstract—Three floristic assemblages from the Upper Cretaceous volcanogenic deposits of the Bolshaya Ayanka River basin (Okhotsk-Chukotka volcanogenic belt (OChVB), Northeastern Russia) are described for the first time. The flora includes about 60 species of fossil plants. Conifers and angiosperms dominate; ferns are less diverse; horsetails, liverworts, ginkgoaleans, and cycads occur as single specimens. The Ayanka flora is similar to the Santonian–Campanian floras of Northeastern Russia and Northern Alaska (with Barykov, Late Bystraya, Ust-Emuneret, and, to a lesser extent, with the Ola and Early Kogosukruk floras), which allows to conclude the most probable Santonian–Campanian age of the studied flora. Floristic assemblages of the Ayanka flora reflect both slope vegetation dominated by conifers and vegetation of lowlands—river or lake banks—dominated by angiosperms. These assemblages demonstrate the penetration of plant communities dominated by advanced angiosperms from the coastal lowlands of the Anadyr–Koryak subregion to the territory of the volcanic highlands, where ferns and conifers are often found in the Late Cretaceous, and the relict plants of the Early and beginning of the Late Cretaceous are still preserved.

INTRODUCTION

Along with radioisotopic and paleomagnetic data, the information on the age of fossil plants is widely used for stratigraphic subdivision of subaerial deposits of the Okhotsk-Chukotka volcanogenic belt (OChVB) and geological mapping of this region. In particular, phytostratigraphic investigations played a crucial role in the discussion about the time of formation of the OChVB—whether it was an area of active volcanism only in the first half of the Cenomanian (Belyi, 1977), or whether volcanic activity continued in it until the middle Campanian inclusive (Filatova and Lebedev, 1982; Lebedev, 1992). Santonian–Campanian floras of this region are the least studied. Until recently, only lists of preliminary determinations of these floras have been presented in publications.

Fossil plant remains found by M.Yu. Khotin and V.A. Faradzhev in the Obryvistaya River basin of Chukotka, a tributary of the Bol'shaya Ayanka River (Filatova and Lebedev, 1982), were collected by Khotin in 1969, N.I. Filatova in 1970, E.L. Lebedev in 1977, and Lebedev, A.B. Herman, and E.I. Kostina in 1985. This plant assemblage was first described briefly by Filatova and Lebedev (1982). Later, Lebedev (1987) identified

this assemblage as the Ayanka flora (floristic assemblage) of Senonian age. The most complete list of Ayanka plants, including 26 species, is given in (Lebedev, 1987, p. 72). Lebedev assumed that the age of this flora approximately corresponds to the early Campanian (Lebedev, 1992). Note that this list is undoubtedly not complete since it was compiled on the basis of the results of preliminary determinations. In addition, the issue of the position of plant-bearing beds in the Obryvistaya River basin in the existing schemes of local stratigraphic subdivisions was not resolved.

It should be noted that Lebedev (1987) called fossil flora from the Obryvistaya River basin "Ayanka flora" or "Ayanka floristic assemblage." In the present paper, the terms "taphoflora" or "assemblage" ("floristic assemblage") cover the totality of fossil plants from one or a few geographically and stratigraphically close localities, reflecting the vegetation of a certain area at a certain period of time; plants of the taphoflora existed together in a limited area during a short interval of geological history. We use the term "fossil flora" (or simply "flora") as a loose term. Since, as will be shown below, fossil plants found in the Obryvistaya River basin derive from locations far enough apart from each
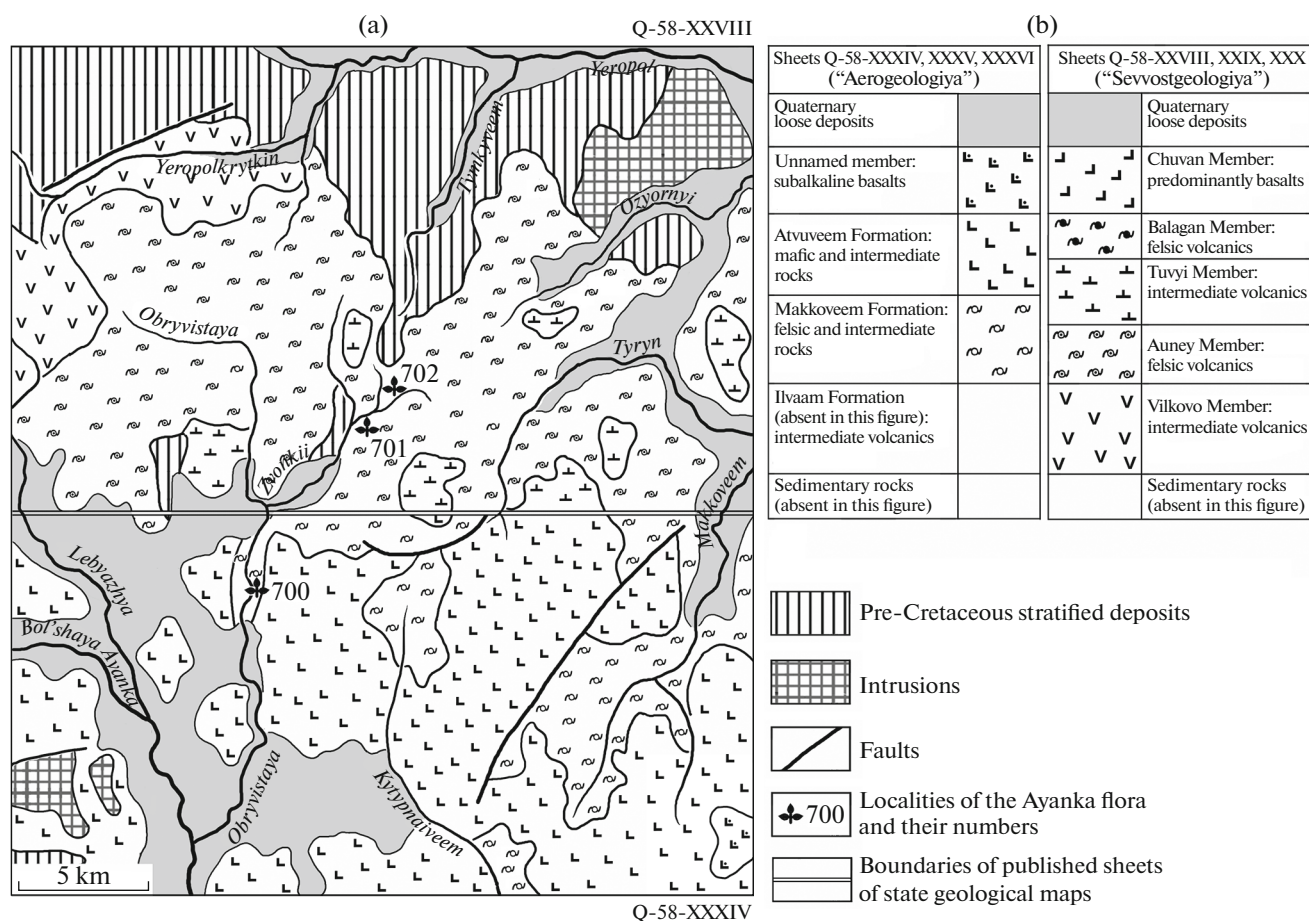
Fig. 1. Schematic geological map and the position of three localities of the Ayanka flora (a) and stratigraphic subdivisions distinguished by geologists of Federal State Unitary Scientific and Production Enterprise Aerogeologiya and JSC North-East Production and Geological Association Sevvostgeologiya (b) in the upper reaches of the Obryvistaya River, complied on the basis of the 1 : 200000 state geological maps of the Russian Federation.

other, we call their assemblage "Ayanka flora" and plants from each of these localities taphoflora or a floristic assemblage.

Later, Moiseeva et al. (2014) conducted a taxonomic revision of the Ayanka flora. As a result, 42 fossil plant species were identified. However, the authors did not sufficiently substantiate the conclusion about the age of plant-bearing beds, and the fossil plants were not characterized and depicted. This means that they are of little use for the purposes of phytostratigraphy and paleofloristics. In the present paper, we have tried to fill this gap and provide a detailed description of floristic assemblages from three localities of the Obryvistaya River basin, images of all major fossil plants of the Ayanka flora, and substantiation of the age of the studied flora.

MATERIALS AND METHODS

The studied fossil plants were collected by E.L. Lebedev, A.B. Herman, and E.I. Kostina in 1985 from three localities (700, 701, and 702), in the upper

reaches of the Obryvistaya River, a left tributary of the Bol'shaya Ayanka River, Chukotka (Fig. 1a).

The locality 700 includes plant-bearing beds of two closely located outcrops in the Obryvistaya River basin (Fig. 1a), about 20 km from its mouth. The largest outcrop (Fig. 2) is located on the left bank of the Obryvistaya River, about 1700 m southwest of a mountain height of 692 m. Here, gray and yellowish gray tuffs, tuff sandstones, and tuff siltstones crop out in a coastal cliff with exposed thickness of about 20—25 m. In the southern part of this outcrop, well-preserved plant remains are reported in several interbeds of fine-grained tuff sandstones and tuff siltstones; imprints of fossil conifers *Parataxodium* Arnold et Lowther and *Taxites* Brongniart dominate and angiosperms including single leaves of "*Macclintockia*" and *Barykovia tchucotica* (Abramova) Moiseeva are less abundant. In the northern part of the outcrop, composed of coarse- to very-coarse-grained tuff sandstones, plant remains are fragmentary and represented by angiosperms and conifers, fragments of which occur as isolated accumulations ("pockets"). In the

Fig. 2. The locality 700 on the Obryvistaya River left bank. Sampling sites of fossil plants in 1985 are shown with a trefoil icon.

middle, the highest part of the outcrop, remains of conifers and angiosperms were found in fine-grained tuff siltstones.

The second, smaller in thickness and extent, outcrop is located on the right bank of the Obryvistaya River, about 200 m upstream from the first one, about 300−350 m to the east of a mountain height of 658.9 m. Fossil plants are reported from the upper part of the outcrop in the interbed of fine-grained tuff sandstone, lying among coarser grained tuff sandstones. Both outcrops of the locality 700 are located close to the top of the plant-bearing unit of felsic rocks under mafic-intermediate lavas (Fig. 1), which allows one to consider these deposits coeval.

The locality 701 crops out on the slope of the left bank of the Zvonkii Stream (Fig. 1a), a left tributary of the Obryvistaya River, about 12 km from the locality 700. Here, the fossil plant remains were collected mainly from talus deposits represented by tuff siltstones and fine-grained tuff sandstones. The fossil plants in this locality show a low diversity. Conifers are most abundant (remains of "*Sequoia*" sp. polymorphic shoots), and there are rare angiosperm leaves of "*Macclintockia*" and *Quereuxia*.

The locality 702 is located on the slope of the right channel bank of the Zvonkii Stream (Fig. 1a). Fossil plants were collected from a small lens (1.5 × 0.5 m) of massive fine-grained tuff sandstones, which lie among coarser grained tuff sandstones approximately 10 m above the base of the slope. Leaf imprints of diverse angiosperms predominate here.

As follows from our field observations, plant-bearing beds of the localities 701 and 702 are located at approximately the same stratigraphic level. It is impossible to correlate them with the deposits of the locality 700 in the field since the latter is covered by taiga and tundra vegetation. There are no faults between these localities on geological maps.

A little north of the locality 700 is the boundary between two sheets of the 1 : 200000 State Geological Map (SGM-200), prepared by different organizations that used different stratigraphic schemes and nomenclature of mapped strata (Fig. 1). Along the sheet boundary, the outcrops of the Auney Member, enclosing plant-bearing beds of localities 701 and 702, are adjacent to the outcrops of the Makkoveem Formation (locality 700). Since there are no faults marked on the geological maps in this area, we can confidently assume that these are formations of one stratum, named on the southern and northern sheets of the map in different ways. On the basis of the above, we consider all three localities of fossil plants to be approximately of the same age.

The studied material is represented by impression of fossil leaves, leafy shoots, and reproductive organs (seed and pollen cones of conifers and fruits of angiosperms); cuticles are not preserved (Plates I–VI). Collection no. 3395, which includes 390 specimens with well-preserved fossil plant imprints, is stored at the Geological Institute of the Russian Academy of Sciences (GIN RAS, Moscow).

Fossil plants were studied after cleaning and preparation using a head-mounted binocular lens and a Zeiss Stemi 2000 C stereomicroscope equipped with a Canon G10 Power Shot digital camera and a Leica M165C stereomicroscope with a Leica DFC 420C

digital camera. The plant remains were photographed with a Canon EOS 7D digital camera with a Canon EF 1:2.5/50 mm macro lens. The fossil plant drawings were made using a Wacom Intuos3 drawing tablet.

SYSTEMATIC COMPOSITION OF THE AYANKA FLORA

As mentioned above, the Ayanka flora has never been studied in detail. Lebedev (1987) provided only a list of preliminary definitions of fossil plants (without images), which included 26 species: *Thallites* sp., *Equisetites* sp., *Cladophlebis* cf. *arctica* (Heer) Seward, *Cladophlebis* sp., *Sphenopteris* sp., *Ginkgo* ex gr. *adiantoides* (Unger) Heer, *G.* ex gr. *sibirica* Heer, *Phoenicopsis* sp., *Sphenobaiera* sp., *Cephalotaxopsis heterophylla* Hollick, *C. intermedia* Hollick, *C. magnifolia* Fontaine, *Sequoia minuta* Sveshnikova, *Sequoia* sp., *Metasequoia cuneata* (Knowlton) Chaney, *Pityolepis* sp., *Pityospermum* sp., *Libocedrus catenulata* (Bell) Kryshtofovich, *Macclintockia ochotica* Vachrameev et Herman, *Quercus tchucotica* Abramova, "*Acer*" aff. *arcticum* Heer, *Viburnum* sp., *Pseudoprotophyllum* sp., *Trochodendroides* ex gr. *arctica* (Heer) Berry, *Cissites* (?) sp., and *Dicotyledones* spp.

As a result of our studies, the composition of the Ayanka flora has been significantly expanded and now it includes about 60 species (Table 1), which is more than two times higher than previous estimates of this flora diversity. In general, conifers and angiosperms prevail in its composition; ferns are less diverse. In addition to them, single horsetails, liverworts, ginkgoaleans, and cycads were found. Conifers of the Ayanka flora are rather diverse and numerous. There are 24 species represented by different plant organs: leafy shoots (12 species), single leaves (1 species), seeds (1 species), seed scales (1 species), and also micro- (3 species) and macrostrobili (6 species), some of which are in a organic connection with shoots. Note that abundance of distinguished taxa does not reflect natural diversity of conifers since it includes taxa distinguished by the morphological classification of different organs, which together could belong to the same maternal plant. The detailed investigation of conifers with computed tomography and scanning electron microscopy shows volumetric preservation of some forms promising for detailed anatomical studies. Among angiosperms in the Ayanka flora, 22 species represented mainly by leaf (20 species) and fruit (2 species) imprints have been identified. New taxa have also been identified in their composition, a detailed description of which is being prepared for publication. Since the composition of the plant assemblages in different localities varies significantly, we consider them separately (Table 1).

The greatest diversity of fossil plant species is reported in the **locality 700** (Table 1). It should be noted that plant remains were collected here from several plant-bearing beds (Fig. 2) in two outcrops separated from each other. Two species of liverworts characterized by rather large branching thalli were identified from this locality. *Thallites* sp. 1 (Plate I, figs. 1, 2) is characterized by monopodial branching of thallom; lateral branches are more than 7 cm long, with an uneven lobate (?) edge, up to 15 mm wide. Thalli in *Thallites* sp. 2 branch dichotomously; the margin of thallus is unlobed, undulate or finely toothed; the width of fragments is about 1 cm (Plate I, fig. 3).

Ferns are represented by sterile and fertile pinnae of *Coniopteris tschuktschorum* (Kryshtofovich) Samylina (Plate I, fig. 8), as well as several small fragments of sterile pinnae of *Arctopteris* sp. 1 with rather large pinnules (Plate I, fig. 4), which are similar to those of species *A. ilirnensis* Golovneva, described from the Chaun and Ulya floras of the OChVB (Akinin et al., 2019; Golovneva, 2018). Similar ferns were also found in the Ust-Emuneret flora of Central Chukotka and previously attributed to *Arctopteris* aff. *rarytkensis* Vassilevskaja (Moiseeva and Sokolova, 2014). Fragments of sterile leaves with smaller pinnules (Plate I, fig. 5) were attributed to another species *Arctopteris* sp. 2. In addition, single fragments of sterile bipinnate leaves *Cladophlebis* sp. 1 were found in the locality 700 (Plate I, fig. 9).

Because of the lack of cuticles, the few ginkgoaleans are assigned to two formal species, *Ginkgo* ex gr. *adiantoides* Heer (weakly dissected leaves) (Plate I, fig. 10) and *Ginkgo* ex gr. *digitata* Brongniart (strongly dissected leaves) (Plate I, fig. 13), and also to *Ginkgodium* (?) sp. (Plate I, fig. 7).

Among conifers, representatives of the family Cupressaceae sensu lato dominate in the locality 700. Numerous leafy shoots of *Parataxodium* cf. *wigginsii* Arnold et Lowther (Plate II, figs. 1, 2, 8), which are similar to those of the type species of the genus *Parataxodium* from Santonian (?)—Maastrichtian taphofloras of the Early and Late Kogosukruk of Northern Alaska (Arnold and Lowther, 1955), dominate. The volume of this species has recently been revised (Rothwell et al., 2020). Shoots of *Parataxodium* sp. (Plate II, fig. 3) are assigned to the same genus. They are characterized by a combination of two types of leaf arrangement (alternate and opposite), being different from *Parataxodium* cf. *wigginsii* in leaf morphology and frequency of their arrangement on a shoot. In the locality 700, terminal shoots of the genus *Metasequoia* Miki ex Hu et Cheng with strictly opposite leaf arrangement of two types, *Metasequoia* sp. 1 (Plate II, fig. 7) and *Metasequoia* sp. 2 (Plate II, fig. 10), are common. They differ in leaf morphology (lanceolate with pointed apex in the former and ellipsoidal with wide, rounded apex in the latter) and the angle of attachment to shoot (25°—45° and 70°—90° in the first and second species, respectively). It should be noted that some of the first-type shoots may belong probably to *Parataxodium* cf. *wigginsii*.

Table 1. Distribution of fossil plants in the localities

No.	Names of fossil plants	Locality 700	Locality 701	Locality 702
1	*Thallites* sp. 1	+		
2	*Thallites* sp. 2	+		
3	*Equisetites* sp.		+	
4	*Coniopteris tschuktschorum* (Krysht.) Samyl.	+	+	
5	*Sphenopteris* sp.		+	
6	*Cladophlebis* sp. 1	+		+
7	*Cladophlebis* sp. 2		+	
8	*Arctopteris* sp. 1	+		
9	*Arctopteris* sp. 2	+	+	
10	*Raphaelia* (?) sp.			+
11	*Ginkgo* ex gr. *adiantoides* Heer	+	+	
12	*Ginkgo* ex gr. *digitata* Brong.	+	+	
13	*Ginkgodium* (?) sp.	+		
14	*Heilungia* (?) sp.			+
15	*Ditaxocladus* sp.	+		
16	*Cupressinocladus* sp.		+	
17	*Parataxodium* sp.	+		+
18	*Parataxodium* cf. *wigginsii* Arnold et Lowther	+		+
19	*Metasequoia* sp. 1	+	+	+
20	*Metasequoia* sp. 2	+		+
21	"*Sequoia*" sp.		+	
22	Cupressaceae seed cones, type 1 (subfamily Sequoioideae)	+		
23	Cupressaceae seed cones, type 2 (subfamily Taxodioideae ?)	+		
24	Cupressaceae (?) seed cones, type 3	+		
25	Cupressaceae seed cones, type 4 (subfamily Sequoioideae?)		+	
26	Cupressaceae pollen cones, type 1	+		
27	Cupressaceae pollen cones, type 2	+	+	
28	Cupressaceae pollen cones, type 3	+		
29	*Pityophyllum* sp.	+	+	
30	*Pityospermum* sp.	+		
31	*Pityostrobus* sp. 1	+		
32	*Pityostrobus* sp. 2	+		
33	*Pityocladus* sp.	+	+	
34	*Pityolepis* sp.	+		
35	*Taxites* sp.	+		
36	*Pagiophyllum* sp.		+	
37	*Elatocladus* sp. 1	+		
38	*Elatocladus* sp. 2		+	
39	*Monocotylophyllum* sp.	+		
40	"*Vitis*" *penzhinica* Herman	+		
41	*Trochodendroides notabilis* Herman	+		
42	*Trochodendroides* sp. 1	+		+

Table 1. (Contd.)

No.	Names of fossil plants	Locality 700	Locality 701	Locality 702
43	*Trochodendroides* sp. 2			+
44	"*Macclintockia*" *ochotica* Vachr. et Herman	+	+	+
45	*Cissites* sp.	+		
46	*Menispermites* sp.	+		+
47	*Celastrinites* sp.	+		
48	*Celastrophyllum* sp.			+
49	*Viburniphyllum* sp.	+		
50	Leaf fragments of platanoids (?)	+		
51	*Dicotylophyllum* sp. 1	+		
52	*Dicotylophyllum* sp. 2	+		
53	*Dicotylophyllum* sp. 3	+		
54	*Dicotylophyllum* sp. 4		+	
55	*Dicotylophyllum* sp. 5			+
56	*Dicotylophyllum* sp. 6			+
57	*Quereuxia angulata* (Newb.) Krysht.		+	
58	*Phragmites* sp.		+	
59	*Nyssidium* sp.		+	+
60	*Carpolites* sp.		+	

The reproductive organs of conifers collected at this locality are of particular interest. From Cypressaceae, we can note single seed cones of three types, the first of which (Plate II, fig. 5) definitely belongs to the subfamily Sequoioideae, the second (cryptomeroid) type (Plate I, fig. 6) probably belongs to subfamily Taxodioideae, and the third one (Plate I, fig. 14) has an uncertain taxonomic affinity within the family Cupressaceae sensu lato at the given stage of research. We also consider three varieties of fertile shoots with pollen cones, conventionally called type 1 (Plate II, fig. 13), type 2 (Plate II, fig. 9), and type 3 (Plate I, fig. 15), as belonging to the family Cupressaceae s.l. They differ in the size of pollen cones, the pattern of attachment to shoots, and the morphology of leaves on shoots. In the locality 700, shoots of the Cupressaceae s.s. family attributed to *Ditaxocladus* sp. are common (Plate I, figs. 11, 12).

Of the conifers of the family Pinaceae, large seed cones of two species (*Pityostrobus* sp. 1 (Plate II, fig. 15) and *Pityostrobus* sp. 2 (Plate II, fig. 11)) varying in shape, as well as single cone scales of *Pityolepis* sp. (Plate II, fig. 16), seeds of *Pityospermum* sp. (Plate II, fig. 14), and shoots of *Pityocladus* sp. (Plate II, fig. 4) were identified.

Another characteristic component of the taphoflora of the locality 700 is large shoots with long linear-lanceolate leaves, formally defined as *Taxites* sp. (Plate II, fig. 12). These shoots are common components of Cretaceous floras of the Northern Hemisphere, which are identified in various works within

the fossil genera *Cephalotaxopsis* Fontaine (Efimova, 1966; Filippova and Abramova, 1993), *Elatocladus* Halle (Bell, 1949), and *Taxites* (Samylina, 1988) or within the modern genus *Taxodium* Richard (Golovneva, 2018; Golovneva and Shczepetov, 2011; Herman et al., 2016; Shczepetov et al., 2019). We refrain from attributing the above-listed fossil plants to modern genera, since there is insufficient evidence for this: there are no data on the structure of the epiderm and/or fertile organs found in a organic connection with shoots. The morphology of these shoots, apart from Cupressaceae sensu lato, is quite typical of representatives of other families of conifers, for example Taxaceae. Therefore, we consider that it would be more appropriate to consider the remains of such preservation within the fossil genera without reference to the families of modern conifers (for example, genus *Taxites*). The study of the epidermal structure of the type species of the genus *Cephalotaxopsis* indicates its belonging to the family Taxaceae (Berry, 1911; Florin, 1958). Therefore, this generic name is not appropriate for the fossil shoots studied.

Of conifers of uncertain taxonomic affinity, the assemblage includes abundant long and narrow poorly preserved leaves of *Pityophyllum* sp., which form leaf accumulations on bedding planes. These leaves are common components of Late Cretaceous floras of Northeast Asia. In addition, there are single shoots with linear leaves *Elatocladus* sp. 1 (Plate II, fig. 6).

Along with conifers, the locality 700 is dominated by angiosperms, represented by 13 species. Fossil leaves of

"*Vitis*" *penzhinica* Herman (Plate III, figs. 1, 2, 4; Figs. 3h and 3i)—a typical species of the Santonian–Campanian floras of Northwestern Kamchatka and Ugolnaya Bay (Chukotka)—are the most abundant in this floristic assemblage (Herman and Lebedev, 1991; Moiseeva and Sokolova, 2011). Similar fossil leaves are also reported from the Late Cretaceous (Santonian?–Maastrichtian) flora of Northern Alaska as *Archeampelos* sp. (Rothwell et al., 2020).

The locality 700 is dominated by imprints of lobate leaves *Cissites* sp. (Plate III, fig. 5; Figs. 3a–3c), which are likely to be assigned to a new species. "*Macclintockia*" *ochotica* Vachrameev et Herman (Plate III, fig. 7; Fig. 3e) is also a typical component of the Santonian–Campanian floras of northeastern Russia. Recently, Golovneva et al. (2017) transferred this species to the genus *Trochodendroides* Berry. However, from our point of view, the morphology of this species is not consistent in full volume with the diagnosis of the genus (Berry, 1922; Crane, 1984). The generic belonging of this species needs further clarification. At this stage of research, we leave its original name in quotation marks for the time being. The genus *Trochodendroides* from the locality 700 is represented by two species. Fossil leaves with double crenate margin are assigned to *T. notabilis* Herman (Plate III, figs. 8, 13). Apart from them, there are small leaves with rare rounded teeth or with an undulate margin, which were identified as *Trochodendroides* sp. 1 (Plate III, fig. 3). The species *T. notabilis* was originally described from the Turonian–Coniacian deposits of Northwestern Kamchatka (Herman and Lebedev, 1991), but it is also reported from the Early Campanian Barykov flora of the Ugolnaya Bay, Chukotka (Moiseeva and Sokolova, 2011). In addition to the above species, fragments of *Menispermites* sp. peltate leaves with an undulate margin (Plate III, figs. 14, 15), untoothed leaves with prominent brochidodromous venation of *Celastrinites* sp. (Plate III, fig. 6), and leaf fragments with a double-toothed margin and pinnate semicraspedodromous venation of *Viburniphyllum* sp. (Plate III, figs. 11, 12) were found at the locality 700.

In the locality 700, a few fragments of large platanoid leaves (Plate III, fig. 16), as well as fossil leaves of Dicotyledoneae of uncertain taxonomic affinity (*Dicotylophyllum* sp. 1–3 (Plate III, figs. 9, 10)), were found. Narrow linear leaves with rounded apex, a rather thick median vein of the first order, and numerous thin parallel veins of the second order were attributed to

monocotyledon *Monocotylophyllum* sp. (Plate I, figs. 15, 16). It should be noted that, as evidenced from the description of the Ayanka floristic assemblage in the works of Lebedev (1987, 1992) and notes in the field book by A.B. Herman, individual leaves of *Barykovia tchucotica* (Abramova) Moiseeva, originally described as *Quercus tchucotica* Abramova (Abramova, 1979), were found in the locality 700. Unfortunately, these samples were lost.

The fossil plant diversity in the **locality 701** is small (24 species), with conifers predominating in a number of specimens and diversity. Among the horsetails, there are single *Equisetites* sp. (Plate IV, Fig. 4). As in the locality 700, ferns are represented here by *Coniopteris tschuktschorum* (Plate IV, fig. 6) and *Arctopteris* sp. 2 (Plate IV, figs. 5, 13, 15). The latter is represented here by fertile and sterile leaves. Single fragments of terminal sterile leaves are attributed to *Sphenopteris* sp. (Plate IV, fig. 3) and *Cladophlebis* sp. 2 (Plate IV, fig. 7). The latter differs from *Cladophlebis* sp. 1 reported from the locality 700 in larger falcate pinnules, as well as the pattern of their venation: straight median vein and branching lateral veins. As in the locality 700, ginkgoaleans are represented by *Ginkgo* ex gr. *adiantoides* leaves with weakly dissected lamina and *Ginkgo* ex gr. *digitata* with strongly dissected lamina (Plate IV, fig. 14).

Among conifers, leafy polymorphic shoots, defined as "*Sequoia*" sp., are the absolute dominants, found only at the locality 701 (Plate IV, fig. 1; Plate V, figs. 1, 2). In this case, a generic name in quotation marks means that we do not ascribe fossil plant remains to the modern genus *Sequoia* Endlicher since the existence of this taxon in the Cretaceous period has been repeatedly questioned (Rothwell and Ohana, 2016; Sokolova et al., 2017). It is probable that a shoot with pollen cones (Table V, fig. 3) and, possibly, seed cones of *Sequoia*-like (?) type (Plate IV, figs. 11, 12) belong to the same plant. In addition, shoots of *Metasequoia* sp. 1 are reported from the locality 701 (Plate V, fig. 6). Only a single shoot of *Cupressinocladus* sp. is ascribed to Cupressaceae s.s. (Plate IV, fig. 9). As in the locality 700, single linear leaves of *Pityophyllum* sp. (Plate IV, fig. 10) and shoots of *Pityocladus* sp. were found in the locality 701 (Plate V, fig. 7). Of the characteristic taxa of the locality 701, we must note a conifer of uncertain taxonomic affinity *Pagiophyllum* sp. (Plate IV, figs. 2, 8). There occur single shoots with linear leaves belonging to *Elatocladus* sp. 2 (Plate V, fig. 4), which differ from

Plate I. Fossil plants of the Ayanka flora from the locality 700, Obryvistaya River. Scale bar is 1 cm for all images, except for figs. 2, 6, 15, and 17; for figs. 2 and 15, 0.5 cm; for fig. 6, 0.2 cm; for fig. 17, 0.1 cm. (1, 2) *Thallites* sp. 1, specimen 3395/328: (1) thallus, general view, (2) enlarged details; (3) *Thallites* sp. 2, specimen 3395/329a; (4) *Arctopteris* sp. 1, specimen 3395/323b-1; (5) *Arctopteris* sp. 2, specimen 3395/326; (6) Cupressaceae seed cone type 3, specimen 3395/13; (7) *Ginkgodium* (?) sp., specimen 3395/383; (8) *Coniopteris tschuktschorum* (Krysht.) Samyl., fragment of fertile pinnae, specimen 3395/357; (9) *Cladophlebis* sp. 1, specimen 3395/295-5; (10) *Ginkgo* ex gr. *adiantoides* Heer, specimen 3395/381-3; (11, 12) *Ditaxocladus* sp.: (11) specimen 3395/79, (12) specimen 3395/85; (13) *Ginkgo* ex gr. *digitata* Brong., specimen 3395/387; (14) Cupressaceae seed cone type 3, specimen 3395/301; (15) Shoot with Cupressaceae pollen cones type 3, specimen 3395/116; (16, 17) *Monocotylophyllum* sp., specimen 3395/286-8: (16) leaf, general view; (17) enlarged, details of leaf apex and venation.

Plate I
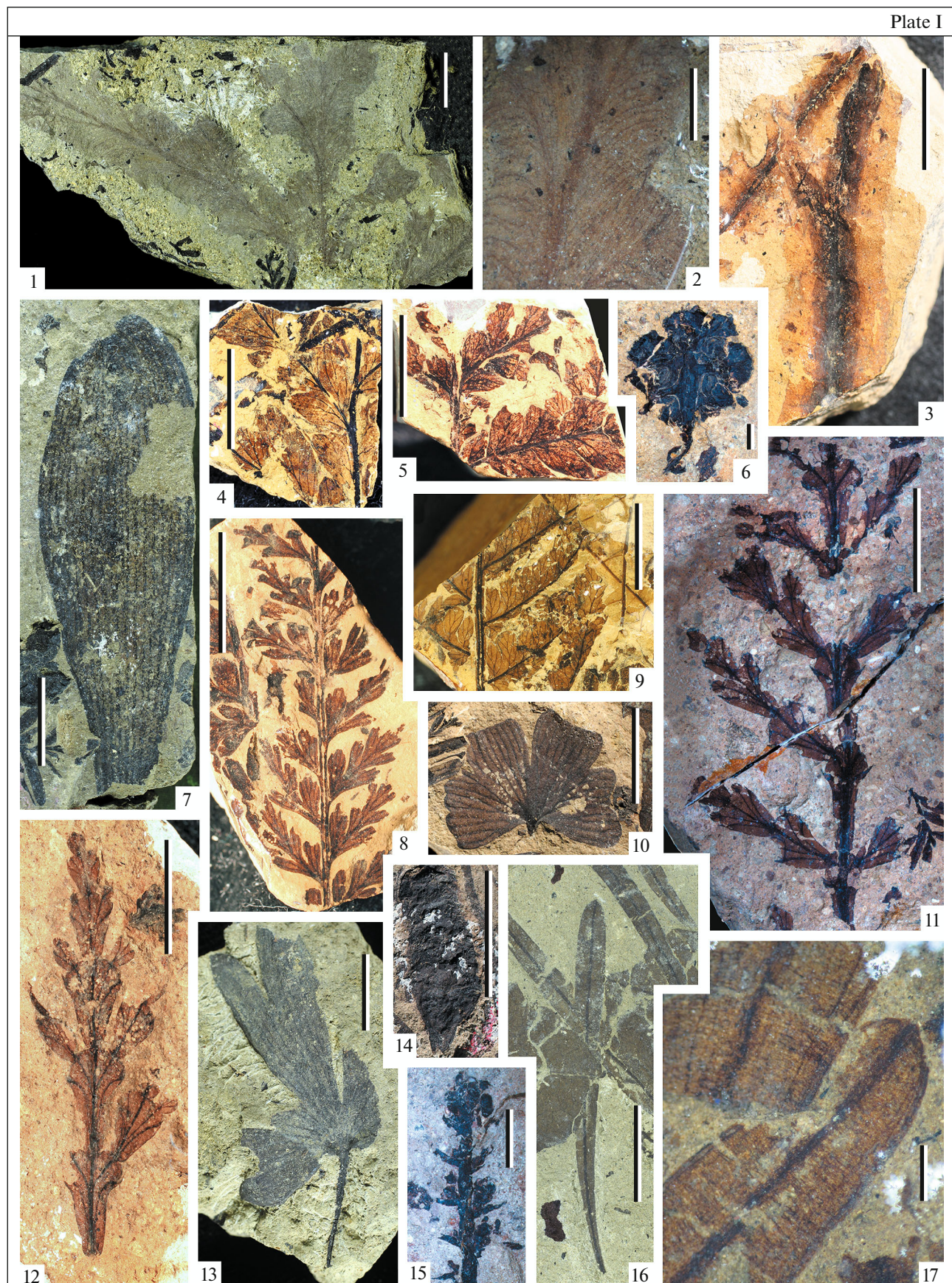
shoots of *Elatocladus* sp. 1 from the locality 700 in straight, but not curved, linear leaves with a long-pointed triangular apex, differing from the short-pointed apex of *Elatocladus* sp. 1.

The remains of angiosperms in the locality 701 are rare and fragmentary. They are represented by fossil leaves of aquatic plant *Quereuxia angulata* (Newberry) Kryshtofovich (Plate V, figs. 9, 10) and poorly preserved leaf fragments of "*Macclintockia*" *ochotica* (Plate V, fig. 13), *Dicotylophyllum* sp. 4 with finely serrate leaf margin (Plate V, figs. 5, 12), and *Phragmites* sp., as well as small fruits of *Nyssidium* (?) sp. (Plate V, fig. 8) and *Carpolithes* sp. (Plate V, fig. 11).

The floristic assemblage of **locality 702** is also characterized by a low diversity but in contrast to the taphoflora from the locality 701, it is dominated by angiosperms. In addition, there are only single fragments of ferns such as *Cladophlebis* sp. 1 (Plate VI, fig. 1) and *Raphaelia* (?) sp. (Plate VI, fig. 9), cycad leaves of *Heilungia* (?) sp. (Plate VI, fig. 2), and single shoots of conifers *Metasequoia* sp. 1 (Plate VI, fig. 11), *Metasequoia* sp. 2 (Plate VI, fig. 3), *Parataxodium* cf. *wigginsii* (Plate VI, fig. 4), and *Parataxodium* sp. Polymorphic leaves of *Trochodendroides* dominate among the angiosperms. *Trochodendroides* sp. 1 is represented by small leaves with variable lamina shape and leaf margin, which varies from untoothed undulate or irregularly dentate to crenate, with few relatively large teeth (Plate VI, figs. 14, 15, 18; Figs. 3g, 3j, 3k). Fossil Leaves of *Trochodendroides* sp. 2 have finely serrate margin with numerous glandular teeth of two–three orders (Plate VI, figs. 6–8; Fig. 3l). Also, fossil leaves of "*Macclintockia*" *ochotica* (Plate VI, fig. 20; Figs. 3d and 3f) are predominant in this locality. Small fossil leaves of *Menispermites* sp. (Plate VI, fig. 16) and *Celastrophyllum* sp. (Plate VI, figs. 5, 13) are less common. There are single fruits *Nyssidium* (?) sp. (Plate VI, fig. 10), as well as leaves of angiosperms of unclear systematic position *Dicotylophyllum* sp. 5 (Plate VI, figs. 12, 17) and *Dicotylophyllum* sp. 6 (Plate VI, figs. 19).

CORRELATION WITH OTHER LATE CRETACEOUS FLORAS AND THE AGE OF THE AYANKA FLORA

In its taxonomy, the Ayanka flora is the most similar to the early Campanian Barykov flora from the Ugolnaya Bay, Chukotka (Moiseeva and Sokolova, 2011). The Barykov flora is reliably dated based on

correlation of of plant-bearing deposits with marine ones bearing remains of marine mollusk (Herman, 2011; Pergament, 1974). Similarity of conifers of these floras is manifested in the presence of numerous shoots with long linear–lanceolate leaves, formally identified as *Taxites* sp. in the present paper and as *Elatocladus gracillimus* (Hollick) Sveshnikova in the Barykov flora. In addition, both floras include a few morphologically similar species with shoots of *Metasequoia*-like and *Sequoia*-like types and seed cones of the subfamily Sequoioideae. Also, seed cones of conifers of the genus *Pityostrobus* Nathorst and shoots of the genus *Cupressinocladus* Seward were identified in the Ayanka and Barykov floras. Angiosperms from both assemblages are represented by the following taxa: "*Vitis*" *penzhinica*, "*Macclintockia*" *ochotica*, *Trochodendroides notabilis*, and also representatives of the genera *Barykovia* Moiseeva, *Cissites* Debey in Capellini et Heer, *Menispermites* Lesquereux, and *Celastrinites* Saporta. Note the presence of large platanoid leaves, aquatic angiosperms *Quereuxia angulata*, cycads (represented by various genera), ginkgoaleans, and ferns *Arctopteris* in the Ayanka and Barykov floristic assemblages.

In general, the Ayanka flora differs from the Barykov flora in a lower diversity, including ferns and cycads, and different dominants in the composition of conifers (*Parataxodium* and "*Sequoia*" sp.) and angiosperms. Among the latter, the Barykov flora is dominated by large-leaved platanoides, *Barykovia tchucotica*, and a rather large number of untoothed and large-leaved taxa, while the Ayanka flora is dominated by small-leaved forms *Trochodendroides*, "*Vitis*" *penzhinica*, and *Cissites*.

In terms of taxonomy, angiosperms show the similarity of the Ayanka flora to the Late Bystraya flora of Northwestern Kamchatka (Herman, 2011; Herman and Lebedev, 1991). The age of plant-bearing beds of the Upper Bystraya Subformation was established as early Campanian (possibly including late Santonian and middle Campanian) based on correlation with underlying and overlying marine deposits (Herman, 2011; Herman and Lebedev, 1991). "*Vitis*" *penzhinica*, "*Macclintockia*" *ochotica* and *Quereuxia angulata*, as well as representatives of the genera of *Barykovia*, *Trochodendroides*, *Cissites*, *Celastrinites*, and *Viburniphyllum* Nathorst, are found in both floras, with minor participation of platanoids. Ferns are rather rare in the Late Bystraya flora, but, as well as the Ayanka flora,

Plate II. Fossil plants of the Ayanka flora from the locality 700, Obryvistaya River. Scale bar is 1 cm for all images, except for fig. 2 (2 mm). (1, 2, 8) *Parataxodium* cf. *wigginsii* Arnold et Lowther, leafy shoots: (1) specimen 3395/26a, shoot with pollen cones; (2, 8) specimen 3395/11, shoot with two types of leaf arrangement: both alternate and opposite; (3) *Parataxodium* sp., specimen 3395/30-1, leafy shoot; (4) *Pityocladus* sp., shoot with brachyblasts, specimen 3395/114; (5) Cupressaceae seed cone type 1, specimen 3395/93a; (6) *Elatocladus* sp. 1, leafy shoot, specimen 3395/16a; (7) *Metasequoia* sp. 1, leafy shoot with opposite leaf arrangement, specimen 3395/19; (9) shoot with Cupressaceae pollen cones type 2, specimen 3395/113; (10) *Metasequoia* sp. 2, shoot with opposite leaf arrangement, specimen 3395/1-3; (11) *Pityostrobus* sp. 2, seed cone, specimen 3395/96; (12) *Taxites* sp., leafy shoot, specimen 3395/75; (13) Cupressaceae pollen cone type 1, specimen 3395/96; (14) *Pityospermum* sp., winged seed, specimen 3395/109a; (15) *Pityostrobus* sp. 1, seed cone, specimen 3395/97; (16) *Pityolepis* sp., single cone scale, specimen 3395/47.

Plate II

representatives of the genus *Arctopteris* are found among them. Since conifers from the Late Bystraya flora, unfortunately, have not yet been studied in detail, they were not correlated with the Ayanka plants. According to preliminary determinations by Herman (2011), the Late Bystraya flora is characterized by the presence of such species as *Cephalotaxopsis heterophylla* Hollick, *Sequoia* sp., *Metasequoia cuneata* (Newberry) Chaney, and *Cupressinocladus cretaceus* (Heer) Seward.

In general, the Ayanka flora is similar to the Ust-Emuneret flora from volcanogenic formations of Central Chukotka (Moiseeva and Sokolova, 2014; Moiseeva, 2015; Sokolova and Moiseeva, 2016; Nosova et al., 2020). The age of the Ust-Emuneret flora was determined as Santonian−early Campanian according to the recent isotope dating (Tikhomirov et al., 2012). The following common taxa are distinguished: liverworts *Thallites* sp. 1 (our unpublished data), ferns *Arctopteris* and *Coniopteris tschuktschorum*, and ginkgoaleans *Ginkgo* ex gr. *adiantoides* and *Ginkgodium*. The coniferous species are quite diverse in both assemblages, including seeds of *Pityospermum* Nathorst, cone scales of *Pityolepis* Nathorst, leaves of *Pityophyllum* Nathorst, shoots of *Cupressinocladus*, and shoots of "*Sequoia*" sp. The presence in both floras of a shoot with pollen cones which is identified as "*Sequoia*" sp. in the Ayanka flora and determined as *Glyptostrobus comoxensis* Bell in the Ust-Emuneret flora is of interest. Shoots with pollen cones of such type are common components of Late Cretaceous floras of North Asia and North America (Bell, 1956; Krassilov, 1979).

Representatives of the genus *Parataxodium* are also established in both floras, being the main dominant for the Ayanka flora and a single specimen for the Ust-Emuneret flora. In terms of taxonomy of angiosperms, the similarity is manifested in the predominance of small-leaved species *Trochodendroides*. "*Macclintockia*" *ochotica*, *Barykovia tchucotica*, and representatives of the genera *Cissites*, *Menispermites*, and *Viburniphyllum* are a characteristic component of both floras; platanoids are absent in the Ust-Emuneret flora and only occasionally occur in the Ayanka flora. In general, small-leaved taxa prevail among angiosperms of both floras.

Ayanka flora differs from the Ust-Emuneret flora in the almost complete absence of relict forms among ginkgoaleans and czekanowskiales (such as *Sphenobaiera* ex gr. *pulchella* (Heer) Florin, *S.* ex gr. *longifolia*

(Pomel) Florin, *Ginkgo insperata* E. Lebedev, *Phoenicopsis chukotkensis* Nosova) and the predominance of conifers with linear-lanceolate leaves: *Taxites*, *Parataxodium*, *Metasequoia*, and *Elatocladus*. In contrast, the Ust-Emuneret flora is dominated by coniferous shoots of *Sequoiadendron tchucoticum* A. Sokolova with various, scalelike to falcate leaves (Sokolova and Moiseeva, 2016), which are not found in the Ayanka flora. Also, no characteristic species of angiosperms from the Ust-Emuneret flora have been established in the Ayanka flora: *Cissites reticulatus* Moiseeva, *Viburniphyllum emuneretum* Moiseeva, and *Dicotylophyllum stipulare* Moiseeva (Moiseeva, 2014).

The Ayanka flora shows a certain similarity to the Early Kogosukruk flora from the Prince Creek Formation of Northern Alaska especially in the composition of conifers and angiosperms from the locality 700 (Arnold and Lowther, 1955; Herman, 2013; Rothwell et al., 2020; http://arcticfossils.nsii.org.cn/). Santonian?−Campanian age of this flora was determined on the basis of the relationship of plant-bearing deposits to beds of marine deposits replacing the former laterally (Detterman and Bickel, 1963; Frederiksen and McIntyre, 2000; http://arcticfossils.nsii.org.cn/). In addition to the main component among conifers—*Parataxodium wigginsii* shoots—both floras have similar fertile remains of conifers, including several types of seed cones of sequoioid and cryptomeroid appearance and pollen cones of the family Cupressaceae, as well as single *Pityophyllum* leaves. Angiosperms in the Early Kogosukruk flora are extremely rare and mostly represented fragmentarily. It should be noted, however, that taxa similar to Ayanka plants were identified among them. In particular, they include the leaves we defined in the Ayanka flora as "*Vitis*" *penzhinica* and in the flora of Northern Alaska as *Archeampelos* sp. (Rothwell et al., 2020). The small leaf of dicotyledon plant morphotype 2 (Rothwell et al., 2020, fig. 6.5) with large glandular teeth and actinodromous (probably, acrodromous) venation is similar to the Ayanka *Trochodendroides* sp. 1. A leaf fragment of the dicotyledonous morphotype 3 (Rothwell et al., 2020, figs. 7.3−7.5) is very similar to a leaf apex of *Barykovia tchucotica*. In addition, in the Early Kogosukruk flora, as in the Ayanka flora, *Quereuxia angulata* and remains of platanoid leaves assigned to the genus *Paraprotophyllum* Herman of the Alaska flora (Herman, 2011) are established.

Plate III. Fossil plants of the Ayanka flora from the locality 700, Obryvistaya River. Scale bar is 1 cm for all images, except for figs. 4 and 11; for fig. 4, 0.5 cm; for fig. 11, 0.1 cm. (1, 2, 4) "*Vitis*" *penzhinica* Herman: (1) specimen 3395/383b, (2) specimen 3395/382a, (4) specimen 3395/383b, details of marginal teeth; (3) *Trochodendroides* sp. 1, specimen 3395/297a; (5) *Cissites* sp., specimen 3395/381-1; (6) *Celastrinites* sp., specimen 3395/259; (7) "*Macclintockia*" *ochotica* Vachrameev et Herman, specimen 3395/286a; (8, 13) *Trochodendroides notabilis* Herman: (8) specimen 3395/249a, details of marginal teeth; (13) specimen 3395/249b, leaf, general view; (9) *Dicotylophyllum* sp. 1, specimen 3395/285a; (10) *Dicotylophyllum* sp. 2, specimen 3395/295-1a; (11, 12) *Viburniphyllum* sp., specimen 3395/299-1: (11) details of marginal teeth; (12) leaf, general view; (14, 15) *Menispermites* sp.: (14) specimen 3395/247a, fragment of leaf margin, (15) specimen 3395/250, the lower part of peltate leaf; (16) fragment of platanoid leaf, specimen 3395/281.

Plate III
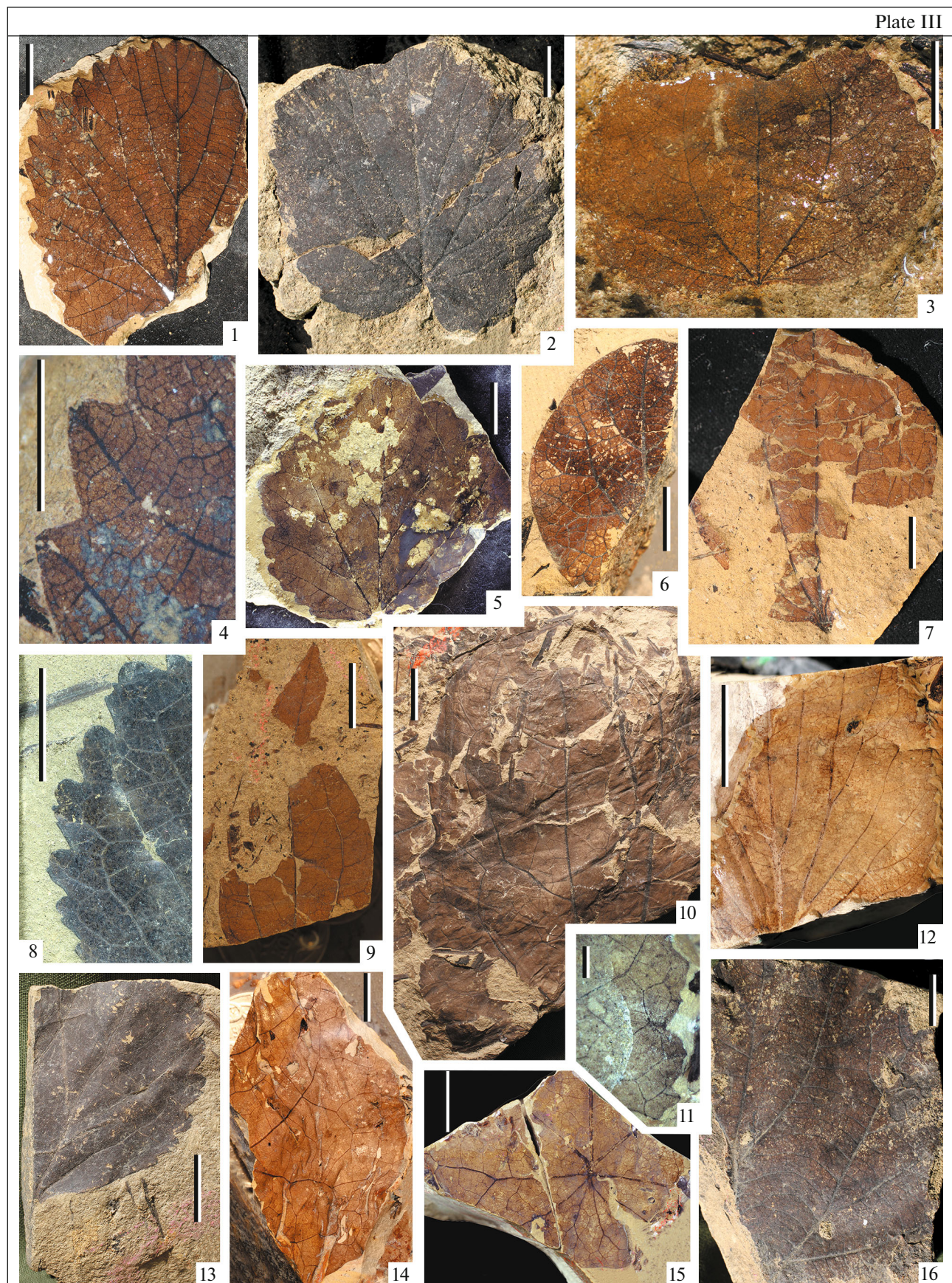
It was also of interest to compare the Ayanka and Ola floras (Filippova and Abramova, 1993; Samylina, 1988; Herman, 2011; Shczepetov et al., 2019). On the basis of the isotope data, the age of the latter is estimated as Campanian (80−83 Ma; Akinin and Miller, 2011). The composition of the Ola flora, in contrast to the Ayanka flora, is dominated by a variety of conifers. Comparison of these assemblages shows a certain similarity in morphological types of conifers. Thus, in both floras, similar representatives of the Pinaceae family are found: cone scales of the genus *Pityolepis*, single seeds of *Pityospermum*, seed cones of *Pityostrobus*, and shoots with brachyblasts of *Pityocladus* (Nathorst) Seward. Also, single leaves of *Pityophyllum* were established in these floras.

Among the Cupressaceae, shoots of the genus *Metasequoia* are common for both floras, and similar seed cones of Sequoioideae are found, identified in the Ola flora as *Pityostrobus* sp. (Shczepetov et al., 2019; Plate 14, figs. 13, 14). Some shoots of *Tollia* cf. *cunninghamoides* Sveshnikova et Budantsev (Shczepetov et al., 2019, Plate 16, figs. 1, 2) from the Ola flora resemble the Ayanka sequoia-like shoots from the locality 701 (Plate V, fig. 1).

One should also note the similarity of large shoots with long linear leaves, determined by us as *Taxites* sp., and in the Ola flora, as *Taxodium amguemensis* (Efimova) Golovneva and *Elatocladus kukenliveemsis* Philippova. In general, these floras differ in the main dominants: the Ayanka flora is dominated by *Parataxodium* cf. *wigginsii* and "*Sequoia*" sp., and the Ola flora is dominated by *Taiwania cretacea* Samylina, *Tollia* cf. *cunninghamoides*, and *Elatocladus communis* Philippova. In addition, the characteristic taxa of the Ola flora such as *Cunninghamia orientalis* (Philippova) Samylina and *Pagiophyllum* sp. were not found in the Ayanka flora (Shczepetov et al., 2019).

The main difference of correlated floras is also predominance of diverse angiosperms in the Ayanka flora, among which only *Quereuxia angulata*, small leaves of *Trochodendroides* and *Macclintockia beringiana* Herman, and rare fragments of dicotyledon plants of uncertain taxonomic affinity were reported from the Ola flora. Ferns are represented only by one common species—*Coniopteris tschuktschorum*.

To a much lesser extent, there is a similarity between the Ayanka flora and the Turonian−Coniacian Arman flora of Magadan oblast (Herman et al., 2016). Among the common conifer taxa, there are only *Taxites* sp., described in the Arman flora as *Taxodium amguemensis*, as well as shoots of "*Sequoia*" sp. (dominated in the locality 701), assigned to the species *Sequoia armanensis* Golovneva in the Arman flora (Herman et al., 2016). Moreover, both floras include morphologically similar seed cones of *Pityostrobus* sp., seeds of *Pityospermum* sp., and dispersed leaves of *Pityophyllum*. Among angiosperms, a distant resemblance can be traced only at the generic level: these are genera *Trochodendroides*, *Cissites*, *Menispermites*, and *Celastrophyllum*. The Ayanka flora differs significantly in the composition of ferns. The Arman relic ginkgoaleans (*Sphenobaiera* Florin), czekanowskiales (*Czekanowskia* Heer, *Phoenicopsis* Heer, *Leptostrobus* Heer), cycads (*Nilssonia* Brongniart), and Bennettitales (*Pterophyllum* Brongniart) are absent in the Ayanka flora. The Arman flora also includes relic conifer taxa, such as two species of the genus *Podozamites* F. Braun and *Elatocladus smittiana* (Heer) Seward, which are not reported from the Ayanka flora.

Only a slight similarity between the Ayanka flora and the Chaun flora was established. The latter comes from volcanogenic formations of the Chaun Group, exposed in the Pegtymel Trough of Central Chukotka (Shczepetov, 1991; Golovneva, 2018). The age of the Chaun flora was determined on the basis of the recent isotope data as Coniacian (~88 Ma; Kelley et al., 1999).

The Chaun flora is characterized by a high level of diversity of ferns, of which only *Coniopteris tschuktschorum* and *Arctopteris* are common with the Ayanka plants. The characteristic elements of the Chaun flora are ferns *Tchaunia tchaunensis* Samylina et Philippova, *T. lobifolia* Philippova, and *Kolymella raevskii* Samylina et Philippova, which were not established in the Ayanka flora. Cycads are also more diverse in the Chaun flora (several species of *Heilungia* Prynada and *Ctenis* Lindley et Hutton), while in the Ayanka flora only isolated fragments of *Heilungia* are found. When comparing conifers, the similarity of representatives of the family Pinaceae (*Pityostrobus*, *Pityolepis*, *Pityospermum*) at the generic level, as well as dispersed linear leaves of *Pityophyllum*, often forming accumulations at both localities, stands out. Note that Pinaceae in the Chaun flora is significantly more diverse in species composition compared to Ayanka plants. Shoots determined as *Taxites* sp. (*Taxodium amguemensis* in the Chaun flora), as well as shoots of *Metasequoia* and seed cones of sequoioid type (family Sequoioideae), attributed to *Sequoia ochotica* Yudova et Golovneva in

Plate IV. Fossil plants of the Ayanka flora from the locality 701, Zvonkii Stream. Scale bar is 1 cm for all images, except for figs. 2, 4, 9, 13; for fig. 2, (2) 0.2 cm, for figs. 4, 9, 13, 0.5 cm. (1) "*Sequoia*" sp., leafy shoot, specimen 3395/119; (2, 8) *Pagiophyllum* sp., specimen 3395/122: (2) enlarged fragment; (8) shoot, general view; (3) *Sphenopteris* sp., specimen 3395/344; (4) *Equisetites* sp., specimen 3395/379; (5, 13, 15) *Arctopteris* sp. 2: (5) fertile leaf, general view, specimen 3395/339-1b; (13) the same, enlarged fragment; (15) the upper part of sterile leaf, specimen 3395/335-1; (6) *Coniopteris tschuktschorum* (Krysht.) Samyl., specimen 3395/340; (7) *Cladophlebis* sp. 2, specimen 3395/349; (9) *Cupressinocladus* sp., fragment of shoot, specimen 3395/148-2; (10) *Pityophyllum* sp., accumulation of dispersed leaves, specimen 3395/138; (11, 12) Cupressaceae seed cones type 4: (11) specimen 3395/138-1, (12) specimen 3395/138-2; (14) *Ginkgo* ex gr. *digitata* Brong., specimen 3395/388-1.

Plate IV

the Chaun flora, are also common for both floristic assemblages (Golovneva, 2018).

Angiosperms, represented mainly by small leaves *Trochodendroides microphylla* Philippova and *Quereuxia angulata*, are very rare in the Chaun flora. In contrast to the Ayanka flora, the Chaun flora includes abundant relicts: *Phoenicopsis*, *Leptostrobus*, *Sphenobaiera*, *Podozamites*, as well as characteristic conifers of genera *Araucarites* Presl, *Elatocladus*, and *Pagiophyllum* Heer, determining a more ancient appearance of this flora.

The Auney floristic assemblage, which originated from volcanogenic deposits of the Auney Member in the middle reaches of the Yeropol River (Anadyr River basin) (Golovneva and Shczepetov, 2013), is similar to the composition of the Chaun flora and has little in common with the Ayanka flora. The latter significantly differs from the Auney flora in the absence of characteristic genera *Tchaunia* Samylina et Philippova and *Kolymella* Samylina et Philippova among ferns, as well as relic taxa of conifers *Podozamites*, *Elatocladus zheltovskii* Philippova, and *Araucarites subacutensis* Philippova; the predominance of *Parataxodium* cf. *wigginsii* among conifers and various fertile shoots of Sequoioideae; and the predominance of angiosperms. Among common taxa, both floras include similar representatives of Pinaceae and Sequoioideae, as well as angiosperms *Quereuxia angulata* and small leaves of *Trochodendroides*, one of which is similar to *Trochodendroides* sp. 1 from the Ayanka flora (Golovneva and Shczepetov, 2013; Plate I, fig. 5).

In addition, we have compared the Ayanka flora with the Ulya flora of the OChVB from the Amka Formation of the Ulya Trough, the age of which was determined as the terminal Coniacian on the basis of the recent isotope data (Akinin et al., 2019). Among ferns, only *Arctopteris* is a close taxon. Of the common conifer taxa, *Ditaxocladus* S.X. Guo et Z.H. Sun and *Cupressinocladus* and similar shoots of *Metasequoia*-like and *Sequoia*-like types, as well as seed cones of *Pityostrobus*, cone scales of *Pityolepis*, and dispersed leaves of *Pityophyllum*, were established. In addition, large shoots with long linear leaves of *Taxites* sp. (*Taxodium amguemensis* in the Ulya flora) are reported from these localities. The common angiosperm species are only *Quereuxia angulata* and different species of the genus *Trochodendroides*. As the Chaun, Auney, and Arman floras, the Ulya flora includes a number of relict taxa (*Hausmannia* Dunker, *Podozamites*, *Phoenicopsis*, *Baiera* Braun, *Sphenobaiera*). The typical species of the Ulya flora, such as *Tchaunia*, *Sagenopteris*

Presl, *Araucarites sheikashoviae* Golovneva, *Elatocladus amkensis* Golovneva, *Elatocladus gyrbykensis* Golovneva, and *Pagiophyllum umitbaevii* Golovneva, were not found in the Ayanka flora.

Thus, detailed comparison of the Ayanka flora revealed its undoubted similarity to the Santonian–Campanian floras of Northeastern Russia and Northern Alaska (with Barykov, Late Bystraya, Ust-Emuneret, and, to a lesser extent, with Ola and Early Kogosukruk), which allows us to conclude that the Ayanka flora is most likely of Santonian–Campanian age.

PLANT ASSEMBLAGES OF THE AYANKA FLORA

Plant-bearing deposits of the studied localities of the Ayanka flora are approximately of the same age. However, the compositions of fossil remains from them differ markedly (Table 1): only species *Metasequoia* sp. 1 and "*Macclintockia*" *ochotica* are reported from all three localities, and another 13 species were found only in two localities. The most significant differences are observed in the composition of plants from the localities 701 and 702. Four species are common. Conifers are the absolute dominant species in diversity and number of specimens at the locality 701; there are single findings of angiosperms. On the contrary, the floristic assemblage in the locality 702 is dominated by angiosperms. It is interesting to note that the proportion of relatively ancient plants, more typical of floras of the Early Cretaceous and early Late Cretaceous in the composition of the taphoflora of the locality 701, is higher than in the taphoflora composition of the locality 702. These are *Coniopteris tschuktschorum*, *Ginkgo* ex gr. *digitata*, and representatives of the genera *Arctopteris*, *Pagiophyllum*, and *Elatocladus*.

It is likely that, under the conditions of the dissected relief of the OChVB, plant assemblages that varied considerably in the taxonomic composition and inhabited different habitat areas existed simultaneously. As in many present-day habitats of vegetation (Fig. 4), angiosperms dominated in river valleys and on lake banks, and conifers dominated on mountains and their slopes. The floristic assemblage from the locality 701 most likely represents slope vegetation, whereas plant remains found in the locality 702 probably inhabited local lowlands—river or lake banks.

A high proportion of relatively ancient plants in the taphoflora of the locality 701 can be explained in the following way. A crucial role in the Late Cretaceous florogenesis of the North Pacific belongs to new Ceno-

Plate V. Fossil plants of the Ayanka flora from the locality 701, Zvonkii Stream. Scale bar is 1 cm for all images, except for figs. 8, 10, 11; for figs. 8, 10, 0.5 cm, for fig. 11, 0.1 cm. (1, 2, 3) "*Sequoia*" sp., leafy shoots: (1) specimen 3395/118, (2) specimen 3395/134, (3) specimen 3395/135, shoot with pollen cones; (4) *Elatocladus* sp. 2, shoot with linear leaves, specimen 3395/140; (5, 12) *Dicotylophyllum* sp. 4, specimen 3395/260: (5) details of leaf margin, (12) leaf, general view; (6) *Metasequoia* sp. 1, fragment of leafy shoot, specimen 3395/143; (7) *Pityocladus* sp., shoot with brachyblasts, specimen 3395/147; (8) *Nyssidium* (?) sp., specimen 3395/196; (9, 10) *Quereuxia angulata* (Newb.) Krysht.: (9) specimen 3395/237-1b, (10) specimen 3395/238; (11) *Carpolithes* sp., specimen 3395/335-2; (13) "*Macclintockia*" *ochotica* Vachrameev et Herman, specimen 3395/241a.

Plate V

phytic communities with predominance of angio-sperms, which gradually penetrated the Mesophytic communities (Herman, 2002, 2011; Shczepetov et al., 2019). During the Albian, these assemblages appar-ently occupied disturbed near-channel coastal low-lands of Northeastern Asia and Alaska, within which the vegetation cover was periodically destroyed by marine transgressions, migrations of channels of meandering rivers, and lateral erosion. During the Late Cretaceous, Cenophytic communities penetrated along river valleys and other unstable habitats into the Asian continent—the volcanic highlands of the OChVB and internal regions of Asia—and gradually displaced the predominantly conifer-fern vegetation that existed there.

Most fossil floras from Cretaceous deposits of the OChVB differ significantly in their systematic compo-sition from the coeval floras of coastal lowlands. It is likely that the vegetation cover of this vast volcanic area became restored after active volcanic eruptions mainly at the expense of the pool of local species, and the lack of competition with angiosperms contributed to the long-term preservation of relatively ancient plant groups in such floras and the appearance of some new taxa on their basis (Shczepetov et al., 2019). The Ayanka flora is a clear evidence of the introduc-tion of plant communities dominated by advanced angiosperms from the adjacent coastal lowlands to the volcanic highlands inhabited in the Late Cretaceous by communities dominated by ferns and conifers at the subordinate proportion of plant species transitional from the Early and early Late Cretaceous floras.

In contrast to the localities 701 and 702, in which plant fossils were collected from outcrops, small in thickness and extent, plant fossils from the locality 700 were collected from several plant-bearing beds in two outcrops separated from each other. This explains both the more diverse composition of the fossil plants of the locality 700 and the lack of a distinct dominant group. It can be assumed with a high degree of confi-dence that the plant assemblage of this locality includes remains of plants from different (two or more) plant communities.

STRATIGRAPHIC POSITION OF PLANT-BEARING DEPOSITS

As noted above, the issue of stratigraphic position of plant-bearing deposits of the Ayanka floristic

assemblage arose owing to the fact that localities of fossil plants lie on two adjacent sheets of the 1 : 200 000 state geological maps (SGM-200): Q-58-XXXIV in the south and Q-58-XXVIII in the north, compiled by different geological organizations using different stratigraphic schemes and nomenclature of the mapped units (Belyi, 1977; Filatova et al., 1977).

When characterizing the Ayanka floristic assem-blage, Lebedev (1987) indicated that it derives from the Obryvistaya River basin (a left tributary of the Bol'shaya Ayanka River), about 20 km from the mouth, as well as the Zvonkii Stream. On sheet Q-58-XXXIV (SGM-200), compiled by geologists of Federal State Unitary Scien-tific and Production Enterprise "Aerogeologiya" in 1987, the Zvonkii Stream is not shown, and the only locality of fossil plant remains is marked in the Obryvistaya River valley (Alekseev, 1987; http://www.geolkarta.ru/list_200.php?idlist=Q-58-XXXIV). It is confined to the **Makkoveem** Formation near the northern boundary of the sheet (Fig. 1a). Judging by the distance from the river mouth and the volume of the stratigraphic column to sheet Q-58-XXXIV, this is the locality 700, which is described in (Lebedev, 1987). In (Herman, 2011, p. 237), it was erroneously indicated that Ayanka flora originates from the overly-ing deposits of the Atvuveem Formation.

The southern boundary of sheet Q-58-XXVIII (SGM-200), compiled by geologists of JSC North-East Production and Geological Association "Sev-vostgeologiya" in 1987 is about 3 km to the north of the locality 700 (Evstafiev, 1987; http://www.geolkarta.ru/list_200.php?idlist=Q-58-XXVIII). Along the boundary of the sheets, the field of felsic rocks of the **Auney** Member (Fig. 1a), including localities 701 and 702, is confined to outcrops of felsic volcanics of the Makkoveem Formation. No faults are marked on maps. These are certainly formations belonging to one stratigraphic unit, but named differently. The same is observed for deposits of the Atvuveem Formation (in the south) and the Tuvyi Member (in the north) over-lying the plant-bearing unit. At the boundary of the SGM-200 sheets, distribution fields of these forma-tions are adjacent to each other, and their lower boundaries coincide (Fig. 1a).

However, according to the stratigraphic column for sheets Q-58-XXVIII, XXIX, XXX (SGM-200), the Auney Member should be considered the first (lower) volcanogenic member in the contrast succession of volcanism in the OChVB outer zone (Akinin and

Plate VI. Fossil plants of the Ayanka flora from the locality 702, Zvonkii Stream. Scale bar is 1 cm for all images, except for fig. 12 (0.1 cm). (1) *Cladophlebis* sp. 1, specimen 3395/370; (2) *Heilungia* (?) sp., specimen 3395/373a; (3) *Metasequoia* sp. 2, leafy shoot, specimen 3395/152; (4) *Parataxodium* cf. *wigginsii* Arnold et Lowther, polymorphic shoot, specimen 3395/150-1; (5, 13) *Celastrophyllum* sp.: (5) specimen 3395/201a, (13) specimen 3395/200; (6–8) *Trochodendroides* sp. 2: (6) specimen 3395/156b; (7) specimen 3395/157, leaf, general view; (8) the same, enlarged fragment; (9) *Raphaelia* (?) sp., specimen 3395/164-2b; (10) *Nyssidium* (?) sp., specimen 3395/194; (11) *Metasequoia* sp. 1, leafy shoot, specimen 3395/153; (12, 17) *Dicotylophyllum* sp. 5, specimen 3395/208: (12) details of leaf margin; (17) leaf, general view; (14, 15, 18) *Trochodendroides* sp. 1: (14) specimen 3395/176, (15) specimen 3395/165b, (18) specimen 3395/171; (16) *Menispermites* sp., specimen 3395/246; (19) *Dicotylophyllum* sp. 6, spec-imen 3395/220-2; (20) "*Macclintockia*" *ochotica* Vachrameev et Herman, specimen 3395/220-1.
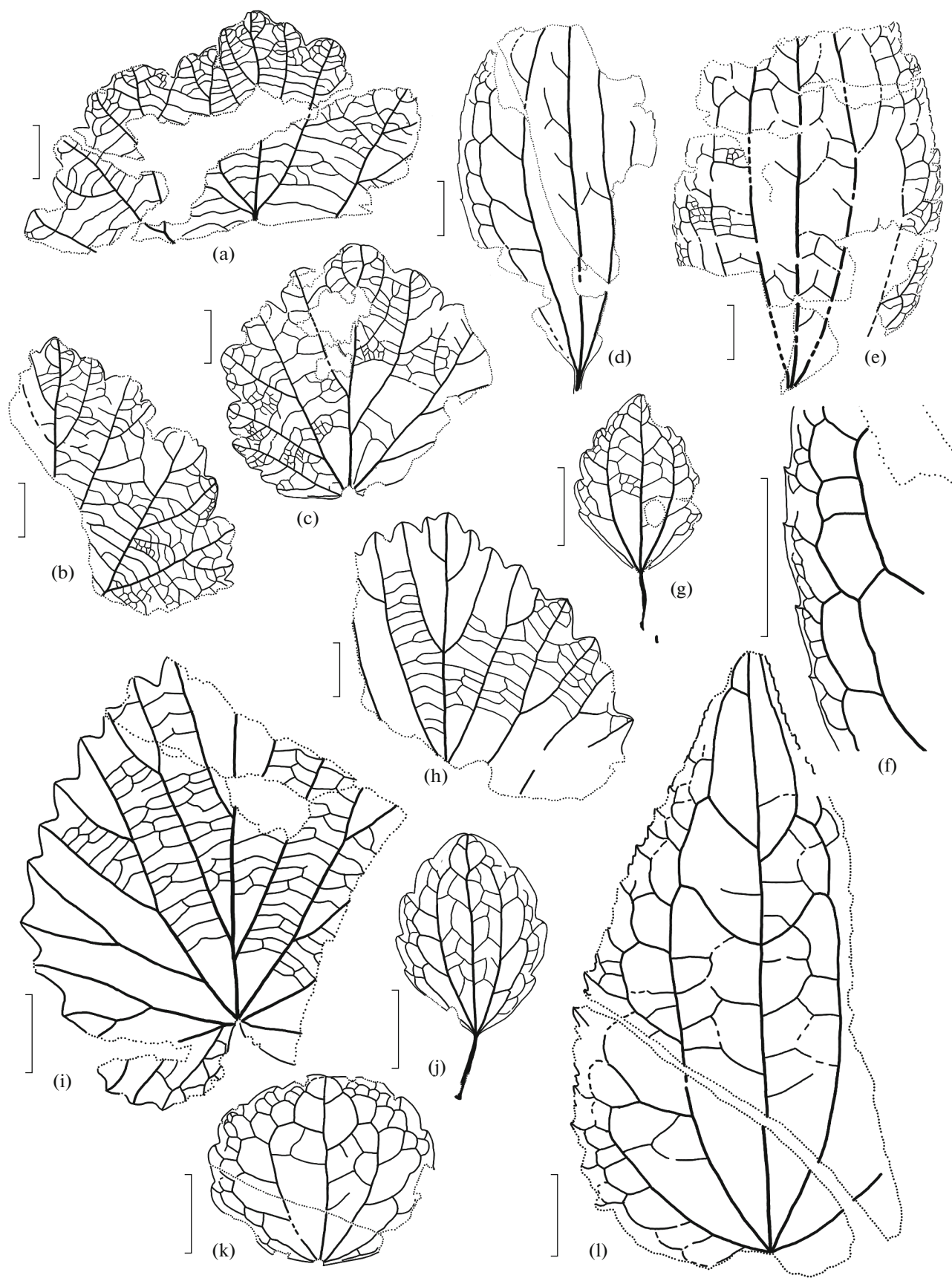
Plate VI
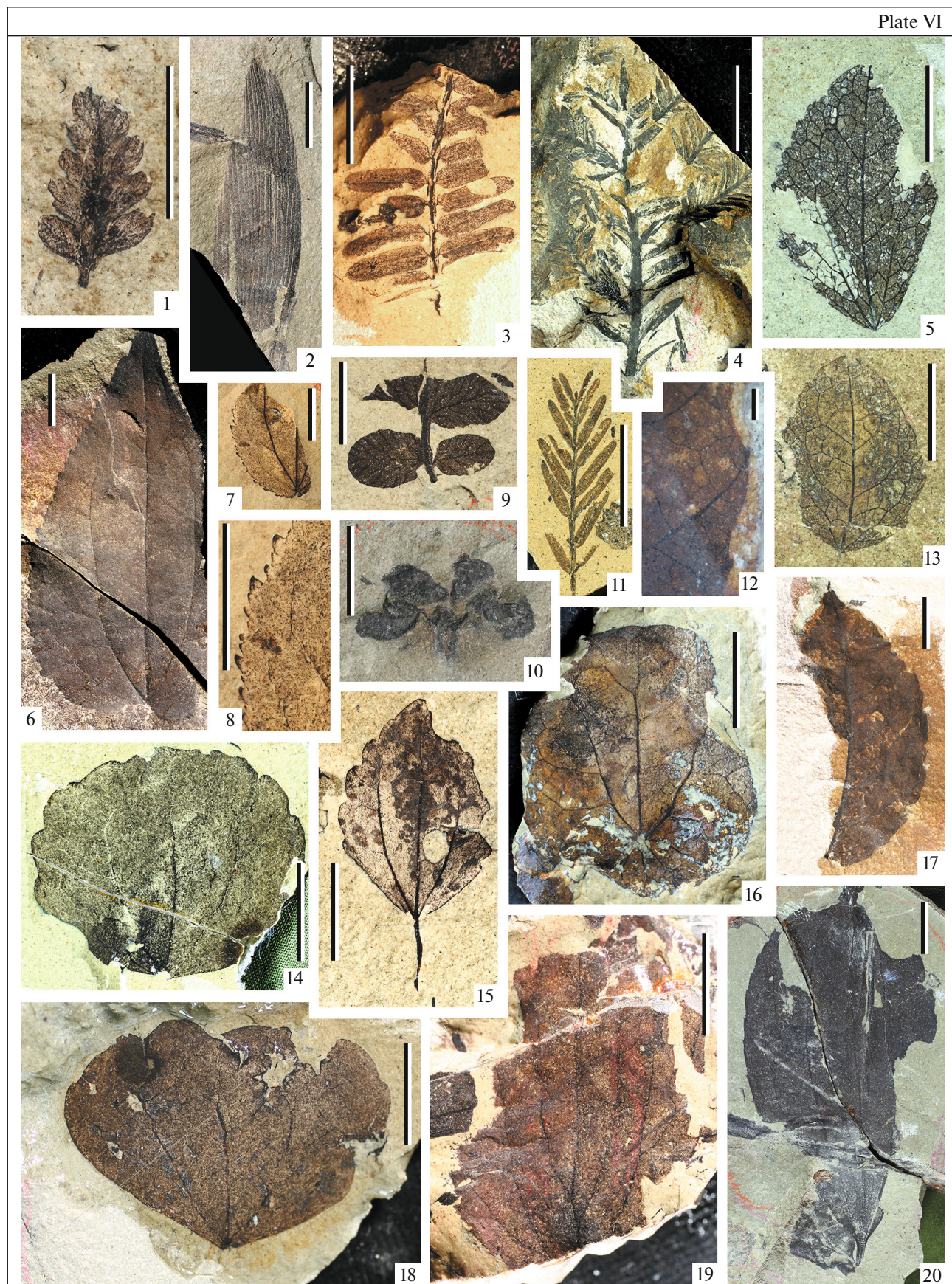
Fig. 3. Fossil angiosperms of the Ayanka flora from the Obryvistaya River basin (localities 700 and 702). Scale bar is 1 cm. (a−c) *Cissites* sp.: (a) specimen 3395/270a, (b) specimen 3395/380, (c) specimen 3395/381-1; (d−f) "*Macclintockia*" *ochotica* Vachrameev et Herman: (d) specimen 3395/220-1; (e) specimen 3395/286b; (f) specimen 3395/220-1, enlarged fragment; (g, j, k) *Trochodendroides* sp. 1: (g) specimen 3395/165b, (j) specimen 3395/166, (k) specimen 3395/167b; (h, i) "*Vitis*" *penzhinica* Herman: (h) specimen 3395/266, (i) specimen 3395/382b; (l) *Trochodendroides* sp. 2, specimen 3395/156b.

Miller, 2011). It is overlain by intermediate volcanics of the Tuvyi Member, then the Balagan Member; the succession is crowned by olivine-pyroxene basalts of the Chuvan Member (Fig. 1b).

At about 80 km to the east from the locality 700, the Auney plant assemblage was established in the Auney Member (Golovneva and Shczepetov, 2013). It is similar significantly to the *Tchaunia-Kolymella* flora from the Chaun Group of the Pegtymel Trough (Samylina, 1974; Belyi, 1977; Shczepetov, 1991, 2020; Shczepetov and Neshataeva, 2021): 14 of 21 species of the Auney floristic assemblage are common with the Chaun

flora, including several endemic species of this flora. According to relatively new results of the $^{40}Ar/^{39}Ar$ dating and new paleobotanical data (Kelley et al., 1999; Golovneva and Shczepetov, 2013), the age of the *Tchaunia-Kolymella* flora is estimated to be Turonian–Coniacian (Herman, 2011) or Coniacian (Golovneva and Shczepetov, 2013). According to this, Golovneva and Shczepetov (2013) determined the age of the Auney plant assemblage and the Auney Member as Coniacian. Later, however, Shczepetov changed his opinion about the age of the Chaun flora, assuming that "it has no distinct lateral and stratigraphic belong-

Fig. 4. Penetration of poplar trees along river bars into the area with dissected relief inhabited mainly by conifers. Tibet, upper reaches of the Mekong River (after Shczepetov et al., 2019, with amendments).

ing" (Shczepetov and Neshataeva, 2021, p. 55) and existed from the Turonian to Campanian. However, it is difficult to agree with this opinion. Anyway, the Ayanka flora (Santonian–Campanian) is younger than the Auney flora (Turonian–Coniacian or Coniacian) and most likely originates from the upper part of the plant-bearing unit, which was mapped as the Makkoveem Formation and the Auney Member (Fig. 1a).

Lebedev (1987, p. 72) notes: "Ayanka plant-bearing deposits in the Bol'shaya Ayanka River basin lies under 'upper' basaltoids of the OChVB...." However, on the geological map (Fig. 1), plant-bearing deposits overlie the Atvuveem Formation, composed of andesibasalts, basalts, and andesites, which can hardly be considered "upper basaltoids of the OChVB." These are probably the overlying unnamed member of subalkaline basalts, dated to the Paleogene (Fig. 1b). In any respect, both outcrops in the locality 700 are indeed located close to the top of the felsic member overlain by mafic–intermediate lavas.

One can suggest that the Atvuveem Formation and overlying subalkaline basalts are a stratigraphic analog of the Chuvan Member, distinguished on the northern sheets of SGM-200 by geologists of JSC North-East Production and Geological Association "Sevvostgeologiya". However, in that part where the Atvuveem Formation crosses the sheet boundary, it was identified as the Tuvyi Member (Fig. 1a); in the area located 50–60 km eastward (sheet Q-58-XXX: Kuklev, 1980; http://www.geolkarta.ru/list_200.php?idlist=Q-58-XXX), the Tuvyi Member is separated from the "upper basaltoids of the belt" (in this area, Chuvan Member) by another (Balagan) felsic member. The Balagan Member or its analogs, as well as the Chuvan Member, are absent on sheets within which fossil plant remains of the Ayanka flora were collected (Fig. 1a).

CONCLUSIONS

The first detailed study of the Ayanka flora, which contains about 60 fossil plant species from three localities, allows us to date this flora to the Santonian and Campanian (Late Cretaceous). The early Campanian age proposed in (Lebedev, 1987, 1992) seems to us insufficiently substantiated.

Floristic assemblages of the Ayanka flora represent slope vegetation dominated by conifers (taphoflora of the locality 701) and vegetation of lowland areas (river or lake banks), in which angiosperms dominated (taphoflora of the locality 702). Thus, the coexistence of these taphofloras apparently reflects the process of gradual invasion of Cenophytic plant communities to the territory of the volcanic highlands, which was still occupied by Mesophytic communities in the Late Cretaceous.

Regarding the stratigraphic position of plant-bearing deposits of the Ayanka flora, we can conclude that (1) the Ayanka flora originates from the upper part of the plant-bearing unit, which is mapped as the Makkoveem Formation and Auney Member on different sheets of the 1 : 200000 state geological maps (SGM-200); (2) the Auney floristic assemblage is older than the Ayanka one and most likely originates from the stratigraphically lower part of plant-bearing deposits; (3) we assume that the volcanics of the Balagan Member reflect a local stage of felsic volcanism that preceded the outpouring of the "upper" basalts of the OChVB (Chuvan Member and its analogs) and was not manifested in the adjacent areas to the west. The latter assumption can be confirmed or rejected only with additional field studies.

The Cretaceous florogenesis in Northeast Asia was not a simple "linear" process of replacement of some floras by others, more advanced. The given data on the composition and age of the Ayanka flora show that determining the age of the Upper Cretaceous plant-bearing deposits of the OChVB on the basis of fossil plant remains is not an easy or nontrivial task.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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