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Late Cretaceous Kholokhovchan Flora of Northeastern Asia: Composition, age and fossil plant descriptions

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ABSTRACT

The Kholokhovchan Flora comes from tuffaceous – terrigenous deposits of the Vetvinskaya Member (Chalbugchan Group) in the Penzhina and Oklan rivers interfluve, Northeastern Russia. The depositional environment of the plant-bearing deposits is interpreted to have been a freshwater lake. The Kholokhovchan Flora hosts 42 fossil plant species belonging to Marchantiopsida, Polypodiopsida, Ginkgoales, Leptostrobales, Bennettitales, Pinales and Magnoliopsida. It is characterised by diverse angiosperms, less diverse conifers and ferns, by the presence of relatively ancient *Sphenobaiera*, *Phoenicopsis* and *Pterophyllum* together with advanced Late Cretaceous *Taxodium*, *Glyptostrobus* and angiosperms, among which platanoids are quite diverse. The Kholokhovchan Flora is most similar to Penzhina and Kaivayam floras of the Anadyr-Koryak Subregion and Arman Flora of the Okhotsk-Chukotka volcanogenic belt (Northeastern Russia) and should be dated as Turonian–Coniacian. The Kholokhovchan Flora, that populated volcanic plateaus and intermontane valleys, are characterised by a mixture of ancient "Mesophytic" plants with typical Late Cretaceous "Cenophytic" taxa. This peculiar composition probably reflects a gradual penetration of new angiosperm-dominated plant assemblages into older floras: during the Late Cretaceous, "Cenophytic" assemblages migrated along river valleys and other disturbed habitats into the interior of Asia, eventually occupying volcanogenic uplands, and in places replacing the "Mesophytic" fern-gymnospermous communities that existed there. Two new angiosperm species, as well as four the most characteristic conifers of the Kholokhovchan Flora, are described: Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp., *Taxodium* cf. *olrikii*, *Taxodium* sp., *Glyptostrobus* sp., *Ettingshausenia vetviensis* sp. nov. and *Parvileguminophyllum penzhinense* sp. nov.

1. Introduction

In the Cretaceous, Asia was a large land mass surrounded by oceans. During the late Albian and Late Cretaceous time, Northeastern Asia was made up of a mosaic of sedimentary basins. A volcanic upland, the Okhotsk–Chukotka volcanogenic belt, extended along the northeastern margin of the continent (Fig. 1A); coastal plains and shallow shelf existed to the east of the volcanogenic belt, while isolated non-flooded lowlands were situated to the west. Herman (1999, 2011a, 2013) distinguished here three palaeofloristic–palaeogeographic subregions spanning late Albian–Paleocene time with different types of landscapes and sedimentation (Fig. 1A).

The Anadyr–Koryak Subregion (AKSR) comprised a system of palaeobasins with mixed continental-marine sedimentation. Coastal alluvial lowlands and plains of the AKSR were covered with meandering rivers, lakes and swamps. Abundant plant remains were buried in terrigenous coal-bearing alluvial, lacustrine, and palustrine deposits of the subregion. Subsequent marine transgression resulted in a shallow shelf basin with numerous islands, and shallow-water marine sedimentation covered the continental deposits. Well dated marine sediments containing stratigraphically important molluscan (ammonites and inoceramids) fauna interfinger with continental plant-bearing deposits allowing the construction of a well-constrained temporal framework throughout the subregion. Due to this, the AKSR undoubtedly represents the key area for substantiating Cretaceous stratigraphic schemes and for correlation of phytostratigraphic subdivisions with high-resolution marine biostratigraphy. Seven securely dated late Albian–Paleocene phases of floral evolution are distinguished in

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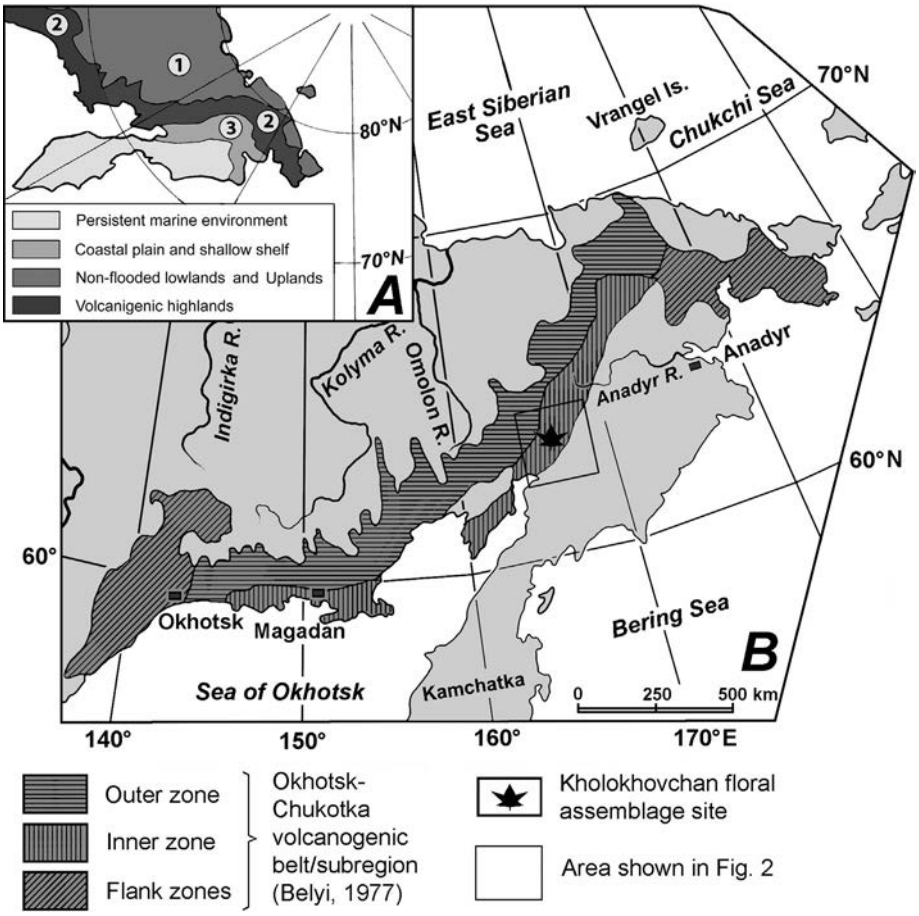


Fig. 1. Latest Albian–Late Cretaceous palaeobotanical–palaeogeographical subregions of the North Pacific Region (A); modern outline of North-Eastern Asia is shown for the Coniacian (after Smith et al., 1981): 1 – the Verkhoyansk–Chukotka Subregion, 2 – the Okhotsk–Chukotka Subregion, 3 – the Anadyr–Koryak Subregion (modified from: Herman, 2013); and geographical and geological position of the Kholokhovchan Flora site (B) (modified from: Shczepetov and Herman, 2013).

the AKSR: the Early Ginter (late Albian), Grebenka (late Albian–Cenomanian–early Turonian), Penzhina (late Turonian), Kaivayam (Coniacian), Barykov (Santonian–early to ?middle Campanian), Gornorechenian (?late Campanian–early Maastrichtian), and Koryak (early to late Maastrichtian–?Danian) (Herman, 2011a, 2013).

The Okhotsk–Chukotka Subregion (OCSR) included volcanic uplands with variably differentiated relief, which were formed in the middle–late Albian. Volcanogenic and terrigenous deposits of the OCSR reflect depositional environments of intermontane valleys and volcanic plateaus. These deposits are exclusively of continental origin, containing frequent plant fossils. The biostratigraphy of these deposits are based mainly on plant megafossils as well as on palaeomagnetic data and isotopic dating. It is obvious that the age determination of purely continental deposits in the OCSR depends on palaeobotanical correlation with securely dated floras of the adjacent AKSR.

The Verkhoyansk–Chukotka Subregion corresponded to a low-lying or slightly hilly plain situated to the west of the volcanogenic belt. This plain was not flooded by the sea, and sedimentation and synsedimentary coal accumulation took place here in isolated depressions.

The Late Cretaceous Kholokhovchan Flora from the volcanogenic-terrigenous deposits of the OCSR (Fig. 1B) was named by Lebedev (1987) after the Kholokhovchan River. The plant fossils were collected by him in 1978. Until recently this floristic assemblage was known only as a list of Lebedev's preliminary identifications (Lebedev, 1987). He concluded that the Kholokhovchan assemblage is correlative to the latest Albian–early Turonian Grebenka Flora from the middle reaches of the Anadyr River. Later Shczepetov and Herman (2013) re-examined this collection and suggested that the Kholokhovchan assemblage is most similar to the Turonian–Coniacian Arman Flora of the Okhotsk-Chukotka volcanogenic belt and, therefore, Turonian–Coniacian or Turonian in age. The present paper focuses on the composition, correlation and age of the Kholokhovchan Flora but we also describe here two new angiosperm species as well as four the most abundant, characteristic and well-documented conifers of this flora. However, we could not visit this flora locality in order to collect more plant fossils and measure the section because the field work is logistically extremely difficult and very expensive in this remote area.

In this paper we use a stratigraphic terminology employed by Belyi (1977) and Herman (2013), the system of suprageneric plant taxa devised by Meyen (1987), the conifer system proposed by Farjon (2005), the angiosperm leaf architectural terminology published in (Herman and Lebedev, 1991), and Krassilov's classification of dispersed angiosperm leaves.

Recent studies (primarily those of the reproductive structures) of Cretaceous angiosperms have shown that a morphological classification of their leaves proposed by Krassilov (1979) seems to be the most effective way of organising of fossil (Cretaceous and

Tertiary) dispersed leaves of these plants (Krassilov, 1979; Meyen, 1987; Maslova et al., 2005). The essence of this classification is using only the observed leaf morphological features to group together fossil leaves with certain morphological features into form genera, rather than using weak and often erroneous hypotheses about the morphology and anatomy of the whole plant. Krassilov (1979, p. 43) noticed, that "only an inductive system with clear diagnoses of the taxa (each taxon includes leaves of a definite morphological type rather than those resembling leaves of a particular extant genus) and consistent application of the principle of priority to names can provide a common language and reduce the loss of information". This approach allows a palaeobotanist to trace the appearance of a particular leaf morphotype, its geological history, and changes in the proportions of particular leaf morphotypes within certain time intervals and certain fossil floras. It therefore accommodates mosaic evolution arising from heterobathmy (Krassilov, 1989). Such a classification is independent from the supposed natural system applicable to modern angiosperms. This means that the taxa of the dispersed leaves morphological classification do not necessarily match those established for entire plants. To put it differently, a genus of the morphological system may occur in more than one genus or even family of whole plants and vice versa. Whole plants may be represented by leaves belonging to more than one genus of the morphological system. Hence we avoid attributing the dispersed angiosperm leaves described below to suprageneric taxa within the more natural system used for modern angiosperms (eutaxa). Instead they are ascribed to suprageneric taxa within Krassilov's morphological scheme (parataxa), which are named "groups" by Krassilov, with morphologically similar genera being included in a single group.

2. Geological setting of the Kholokhovchan Flora locality

The Kholokhovchan Flora comes from volcanogenic – terrigenous deposits in the interfluve of the Penzhina and Oklan rivers, Northeastern Russia (Figs. 1 and 2). The only locality yielding this flora (no. 17 in: Lebedev, 1987) is situated in the upper reaches of Vetvistyi Stream, which is tributary on the right bank of the Kholokhovchan River, which in turn is a right tributary of the Penzhina River (Fig. 2). The regional geological structure and lithostratigraphy has been documented by Belyi (1977), Filatova et al. (1977) and Lebedev (1987).

The plant-bearing deposits belong to the Vetvinskaya Member of the Chalbugchan Group. The Vetvinskaya Member, 1800–2000 m thick, consists of pyroxene andesites, olivine basalts and andesite basalts, andesites, tuff breccias, tuffs and tuffaceous-terrigenous deposits. The member conformably overlays basalt lavas, 1200–1600 m thick, ascribed to the Grebnev Member of the Chalbugchan Group; no palaeontological remains were found in this member. The Vetvinskaya Member is overlain by basalts, andesite basalts, ignimbrites and acidic tuffs of the Kubaveem Member with rare plant fossils provisionally dated as Senonian (Samylina, 1988; Herman, 2011a).

Plant fossils were collected from tuffaceous–terrigenous deposits in the lower part of the Vetvinskaya Member. The depositional environment of the plant-bearing deposits is interpreted to have been a freshwater lake of unknown size. However, a complete lack of aquatic plant remains in the assemblage should be emphasised. The plant-bearing deposits are fine- to medium-grained and possess a pronounced lamination; the absence of coarse-grained material shows that the surface topography was likely subdued. Relatively good preservation of plant fossils and finds of intact leaflets of compound leaves *Parvileguminophyllum* evidence a relatively short distance transport prior to burial.

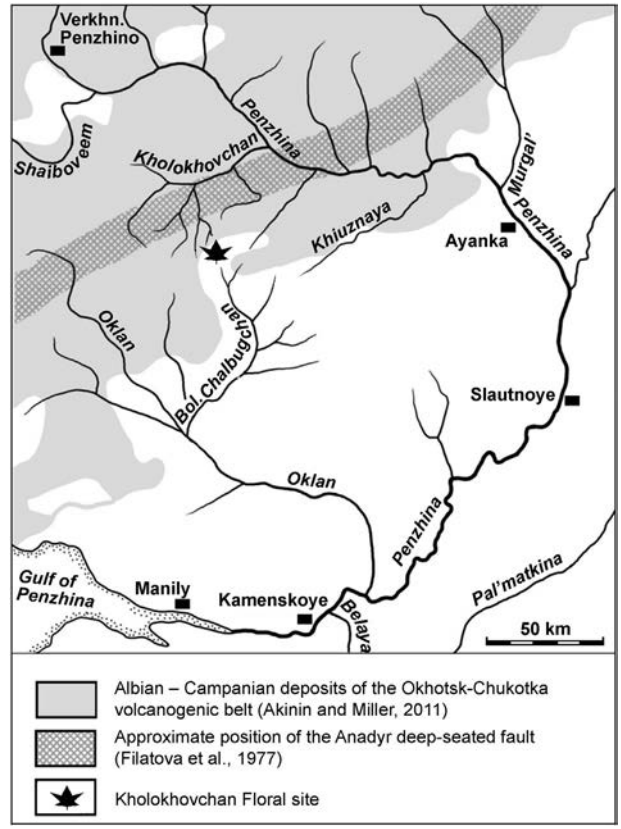


Fig. 2. Plant fossil site of the Kholokhovchan Flora (modified from: Shczepetov and Herman, 2013).

3. Material and methods

The available Lebedev's collection (195 samples and over 370 individual plant fossils) have been examined for this study. The collection is permanently stored at the Geological Institute, Russian Academy of Sciences (GIN RAS) in Moscow, Russia, collection no. 3384.

Plant remains are represented by thalli, leaves, leafy shoots, male and female cones, seeds and cone scales impressions. Fine details of venation and morphology are preserved in the fossil leaves and they show little evidence of long distance transport or decay prior to burial. Apart from plant fossils, rare conchostracan and insect remains (not studied yet) were found in the plant-bearing deposits.

All descriptions of the leaf and cone morphology are based on direct observations made using dissecting microscopes Carl Zeiss SM-XX and Leica M165C with Leica DFC420 digital camera. To highlight the venation of fossil leaves we used oblique lighting. After cleaning, the specimens were photographed under low angle incident light using a Panasonic GX7 digital camera with Leica DG Macro-Elmarit 1:2.8/45 mm macro lens. To enhance a contrast some specimens were photographed under water.

Some material yields fragments of compressed plant tissues. However, as the material was highly metamorphosed, we could not obtain any cuticles and could not study microstructural features. Observation of the plant imprints directly in the scanning electron microscope also failed to produce results.

4. Composition of the Kholokhovchan Flora

The Kholokhovchan Flora hosts 42 fossil plant species belonging to liverworts (Marchantiopsida), ferns (Polypodiopsida),

ginkgoaleans (Ginkgoales), leptostrobaleans (Leptostrobales), bennettitaleans (Bennettitales), conifers (Pinales) and dicotyledons (Magnoliopsida). All taxa listed below are illustrated in Figs. 3–13.

Marchantiopsida: *Thallites* ex gr. *jimboi* (Kryshtofovich) Harris (Fig. 3B), *Thallites* sp. (Fig. 3A);

Polypodiopsida (Filicopsida): *Gleichenites* sp. (Fig. 3G), *Birisia ochotica* Samylina (Fig. 3E), *Asplenium dicksonianum* Heer (Fig. 3D), *Asplenium rigidum* Vassilevskaya (Fig. 3H), *Sphenopteris* sp. cf. *Birisia* (?) *oerstedtii* (Heer) E. Lebedev (Fig. 3C, F);

Bennettitales: *Pterophyllum validum* Hollick (Fig. 4D, E);

Ginkgoales: *Ginkgo* ex gr. *adiantoides* (Unger) Heer (Fig. 4A), *Sphenobaiera* ex gr. *czekanowskiana* (Heer) Florin (Fig. 4B);

Leptostrobales: *Phoenicopsis* ex gr. *angustifolia* Heer (Fig. 4C);

Pinales: *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nathorst (Fig. 4H), *Pityophyllum* ex gr. *staratschinii* (Heer) Nathorst (Fig. 4I), *Pityospermum* sp. (Fig. 4G), *Pityolepis* sp. (Fig. 4F), *Taxodium* cf. *olrikii* (Heer) Brown (Fig. 7A–K; Fig. 8Ab, c, d; Bb, c; Db), *Taxodium* sp. (Fig. 8Aa; Ba; C; Da), *Parataxodium* sp. (Fig. 5D), *Glyptostrobus* sp. (Fig. 9A–L), *Sequoites* sp. (Fig. 5F), Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp. (Fig. 6A–I), *Elatocladus* cf. *intermedius* (Hollick) Bell (Fig. 5A, B, C), *Elatocladus* cf. *smittiana* (Heer) Seward (Fig. 5E);

Magnoliopsida: *Araliaephyllum medium* (Philippova) Herman (Fig. 10C), *Araliaephyllum* sp. (Fig. 10F), *Cocculophyllum* sp. (Fig. 10A), *Cissites* cf. *cordatus* Philippova (Fig. 10G), *Cissites* cf. *pekulneensis* (Philippova) Moiseeva (Fig. 10D, E), *Cissites* sp. (Fig. 11B), *Menispermites marcovoensis* Philippova (Fig. 10H), *Menispermites* cf. *sibiricus* (Heer) Golovneva (Fig. 10B), *Terechovia* cf. *philippovae* Herman (Fig. 11A), *Arthollia* cf. *pacifica* Herman (Fig. 11E), *Ettingshausenia louravetlanica* (Herman et Shczepetov) Herman et Moiseeva (Fig. 11C, Fig. 12F), *Ettingshausenia vetviensis* Herman, sp. nov. (Fig. 12G–I), *Pseudoprotophyllum boreale* (Dawson) Hollick (Fig. 11F), *Celastrophyllum* (?) sp., *Dalembia pergamentii* Herman et Lebedev (Fig. 12A, B, C), *Parvileguminophyllum penzhinense* Herman, sp. nov. (Fig. 13A–J), *Chachlovia dombeyopsoida* (Herman) Herman (Fig. 12L), *Dicotylophyllum* sp. cf. *Schefflerаephyllum venustum* (Philippova) Philippova (Fig. 10I), *Dicotylophyllum* sp. (Fig. 12E).

Liverworts (Fig. 3A, B) are represented by rare impressions of thalli referable to two species: *Thallites* ex gr. *jimboi* and *Thallites* sp. Ferns (Fig. 3C–H) are quite numerous and diverse. They belong to four genera: *Gleichenites*, *Birisia*, *Asplenium* and *Sphenopteris* (only sterile leaves were found), with *Birisia* and *Asplenium* being the most abundant. Plant fossils representing the genus *Gleichenites* are rather scarce.

Ginkgoaleans are represented by the genera *Ginkgo* (Fig. 4A) and *Sphenobaiera* (Fig. 4B), *Sphenobaiera* being the most common. Leptostrobaleans and bennettitaleans are neither numerous nor diverse. Bennettitaleans are represented by a few leaves of *Pterophyllum validum* (Fig. 4D, E), and leptostrobaleans by three incompletely preserved elongate leaves with parallel venation, tentatively identified as *Phoenicopsis* ex gr. *angustifolia* (Fig. 4C); these leaves were probably attached to a single leafy short shoot (brachyblast) which is not preserved.

Conifers (Fig. 4F–I; Figs. 5–9) are represented by 12 species belonging to 9 genera. As a result of preservation of the fossil material, we are only dealing with morphological features of the fossil conifers. These features are known to be highly polymorphic and are often similar for genera of one or even several families. We should take into account that the number of the identified species may not reflect the natural diversity. This number includes formal taxa, which in combination may represent the same plant. Or, on the contrary, the fossil plants included in one species may belong to different natural taxa.

Among conifers, the most diverse are the representatives of the family Cupressaceae *sensu lato*: polymorphic shoots with pollen cones identified as *Glyptostrobus* sp. (Fig. 9), numerous shoots of *Taxodium* cf. *olrikii* (Fig. 7, Fig. 8A b, c, d; B b, c; D b), specialised generative twig with pollen cones *Taxodium* sp. (Fig. 8), a single shoot of *Parataxodium* sp. (Fig. 5D) with characteristic alternate or almost opposite leaf arrangement, and a *Sequoia*-like female cone attributed to *Sequoites* sp. (Fig. 5F). The only representative of the family Cupressaceae *sensu stricto* is a shoot of uncommon morphology, identified as Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp. (Fig. 6).

The family Pinaceae is represented by seeds *Pityospermum* sp. (Fig. 4G) and cone scales *Pityolepis* sp. (Fig. 4F). The collection also contains numerous dispersed linear leaves, due to their morphology related to *Pityophyllum* ex gr. *staratschinii* (Fig. 4I) and *P.* ex gr. *nordenskioldii* (Fig. 4H). In the absence of epidermal data, we conventionally assume the latter two belong to the Pinaceae.

The conifers *incertae sedis* are represented by shoots with long linear leaves formally attributed to *Elatocladus* cf. *intermedius* (Fig. 5A–C) and a single shoot *Elatocladus* cf. *smittiana* (Fig. 5E) with characteristic morphology. We have chosen the generic name *Elatocladus* Halle, instead of *Cephalotaxopsis* (Fontaine) Berry, identified for these shoots in Shczepetov and Herman (2013) because genus *Elatocladus* was proposed by Halle (1913) for sterile shoots of conifers, including shoots with linear-lanceolate leaves, spread in one plane and attached to the axis with petioles. Offering a generic name, Halle implied that it is independent from any kind of modern genera. Later Harris (1979) emended the diagnosis of this genus: "Fossil conifer shoot bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from stem." Kholokhovchan shoots show the same morphological characters and it seems appropriate to use the name *Elatocladus* in the case when we do not have epidermal data, are dealing with morphological features only and can not confidently identify even the family affinity.

Dicot leaves (Figs. 10–13) are represented by 19 species belonging to 13 genera. Among them, the most diverse are *Cissites* (three species: Fig. 10D, E, G; Fig. 11B), *Menispermites* (two species: Fig. 10B, H), *Araliaephyllum* (two species: Fig. 10C, F) and platanoids (group Platanofolia). The latter are represented by two *Ettingshausenia* species (Fig. 11C; Fig. 12G–I), one *Arthollia* species (Fig. 11E) and one *Pseudoprotophyllum* species (Fig. 11F). Often the most numerous impressions are leaflets of compound leaves *Dalembia pergamentii* (Fig. 12A–C) and *Parvileguminophyllum penzhinense* sp. nov. (Fig. 13A–J).

In general, the Kholokhovchan Flora is characterised by (1) abundant and diverse angiosperms, less numerous conifers and ferns and rare other plants, (2) a presence of relatively more modern taxa (*Sphenobaiera*, *Phoenicopsis*, and *Pterophyllum*) together with advanced plants, characteristic of Late Cretaceous and early Paleogene, such as *Taxodium* and *Glyptostrobus* and the large group of angiosperms, (3) quite diverse platanoid dicots referable to three genera: *Ettingshausenia*, *Arthollia* and *Pseudoprotophyllum*.

5. Systematic palaeobotany

Most species in the flora have been well documented in other studies and these taxa are not re-described here. Below we describe two new angiosperm species as well as four the most numerous and characteristic conifers of this flora.

Class PINOPSIDA (CONIFEROPSIDA)
Order PINALES (CONIFERALES)
Family CUPRESSACEAE Gray

Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp.
Fig. 6A–I

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

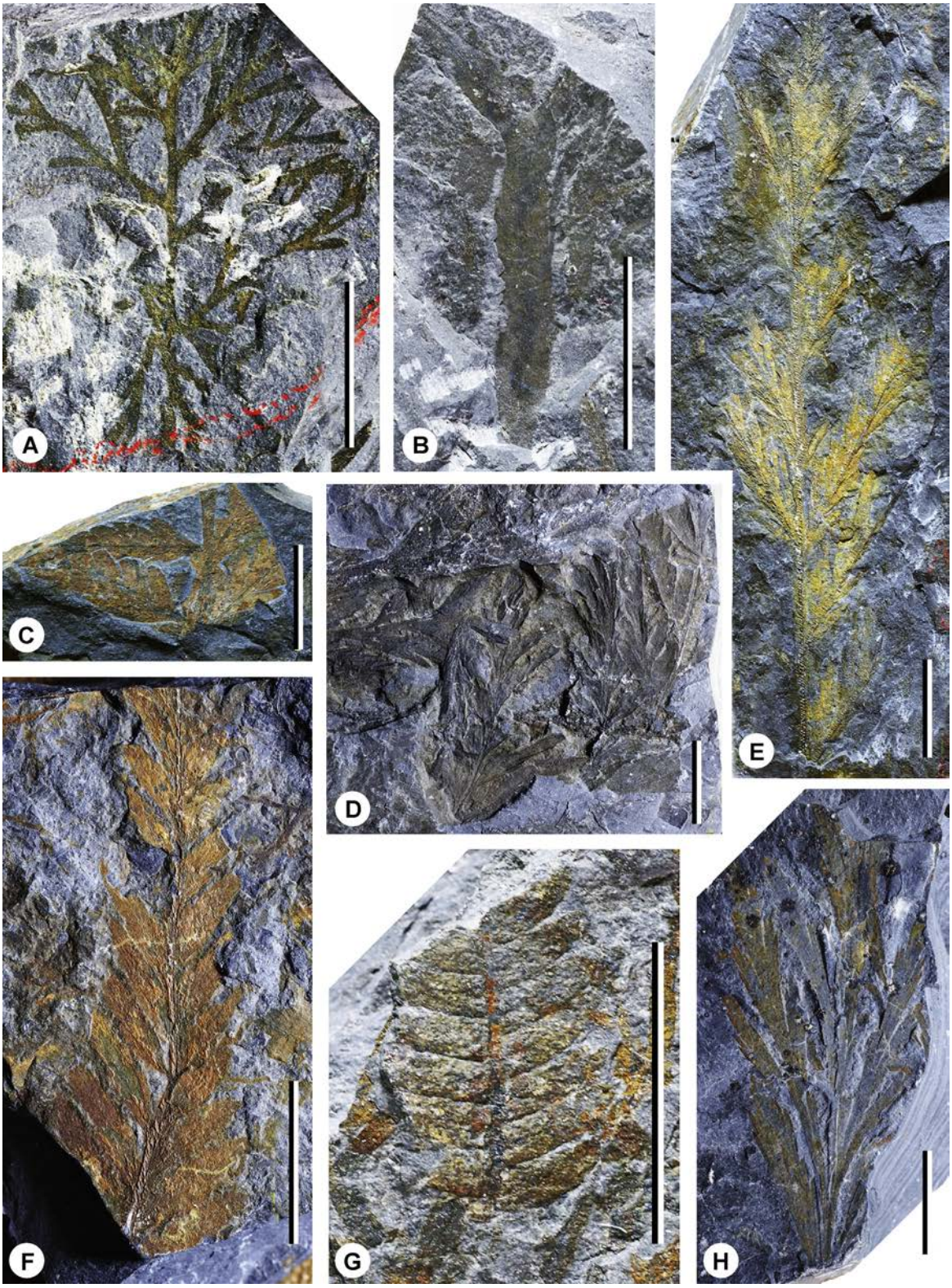


Fig. 3. Fossil liverworts and ferns of the Kholokhovchan Flora: A, *Thallites* sp., specimen no. 166; B, *Thallites* ex gr. *jimboi* (Kryshtofovich) Kryshtofovich, specimen no. 164; C, F, *Birisia (?) oerstedtii* (Heer) E. Lebedev: C, specimen no. 142; F, specimen no. 141; D, *Asplenium dicksonianum* Heer, specimen no. 132b; E, *Birisia ochotica* Samylina, specimen no. 131a; G, *Gleichenites* sp., specimen no. 156; H, *Asplenium rigidum* Vassilevskaya, specimen no. 67a. Scale bar 1 cm.

Type locality. Upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Material studied. Specimens no. 88a, 88b (counterpart).

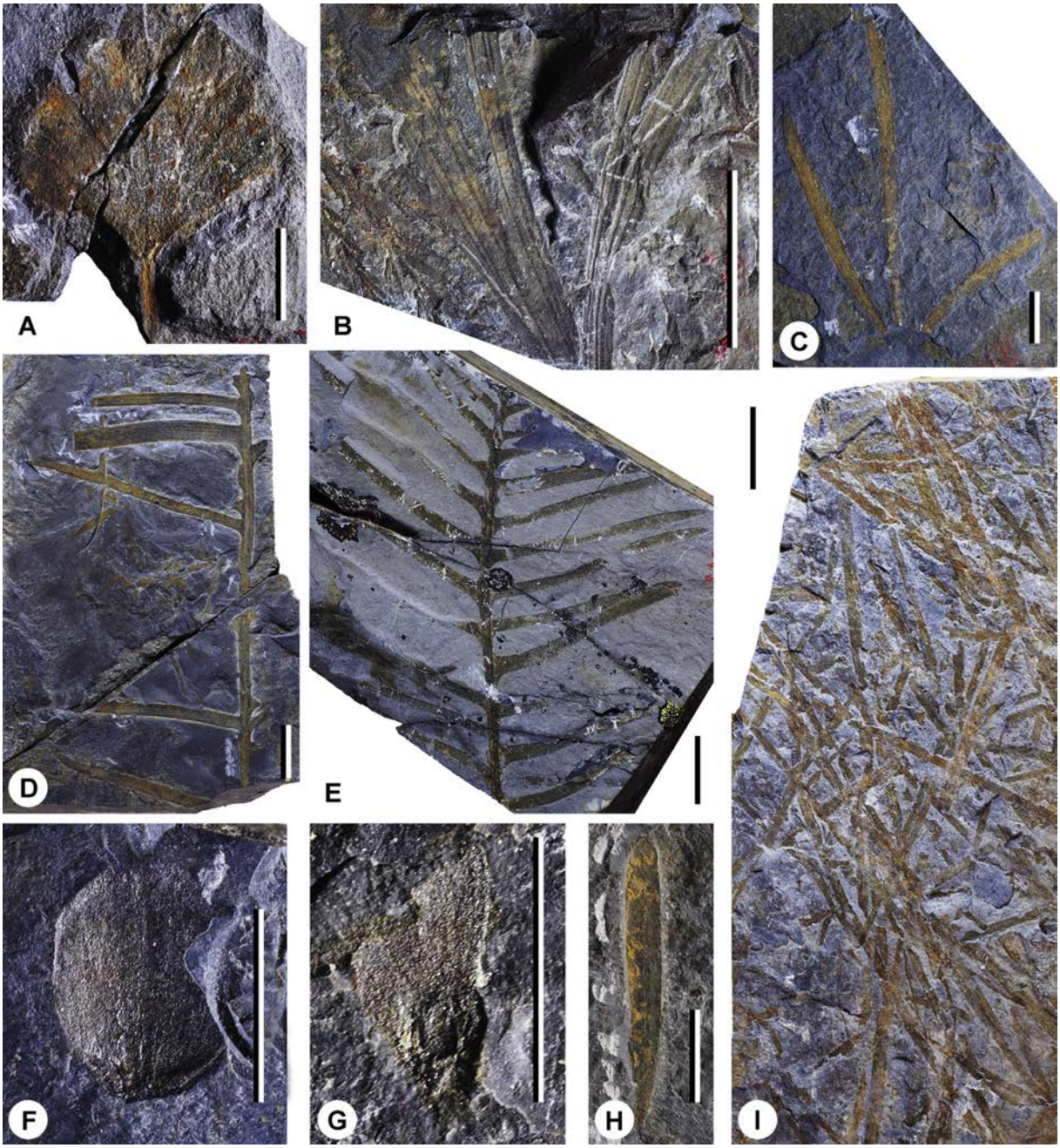


Fig. 4. Fossil ginkgoaleans, leptostrobaleans, bennettitaleans and conifers of the Kholokhovchan Flora: A, *Ginkgo* ex gr. *adiantoides* (Unger) Heer, specimen no. 182; B, *Sphenobaiera* ex gr. *czekanowskiana* (Heer) Florin, specimen no. 120; C, *Phoenicopsis* ex gr. *angustifolia* Heer, specimen no. 184; D, E, *Pterophyllum validum* Hollick: D, specimen no. 150a; E, specimen no. 151; F, *Pityolepis* sp., specimen no. 172; G, *Pityospermum* sp., specimen no. 173b; H, *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nathorst, specimen no. 125b; I, *Pityophyllum* ex gr. *staratschinii* (Heer) Nathorst, specimen no. 127. Scale bar 1 cm.

Description. In the collection there is an imprint and its counterpart of the small-leaved twig of the cupressoid morphology (Fig. 6A, B, I). It is about 5.5 cm long with 4–5 branching orders (Fig. 6A, B). The shoots are often "bifurcately" branched, flattened, and asymmetrical (Fig. 6C, E). The distance between the branching nodes of the terminal shoots is 1–3 mm; that of the axial shoots – up to 10 mm. The shoots are alternating or almost opposite. The axis is thin, broadening in the nodes, flattened in cross-section, and striated. Axial shoots are up to 1.5 mm thick. Terminal shoots are about 1 mm thick and 2–6 mm long, deviating from the axis at an angle of 20–50°. There are two types of leaf arrangement: the first one is helical (Fig. 6G) and the second one seems to be almost decussate (due to the preservation? Fig. 6D, F). The helical type occurs on the shoots of all branching orders. The "decussate" type is less common and appears on thick perennial shoots with densely arranged leaves (Fig. 6D, F); it also occurs at the bases of deviating shoots. The leaves on the both shoot types (including facial and lateral leaves on shoots with probably decussate leaf arrangement) are adpressed, sessile, boat-shaped, slightly falcate, with pointed apices, which are recurved towards the axis, and with wide decurrent bases (Fig. 6F, G). The sizes of leaves are 0.8–1.3 mm long and 0.3–0.6 mm wide. On the high-order shoots the leaves are less densely arranged, being more elongated. We also note the presence of single subulate leaves

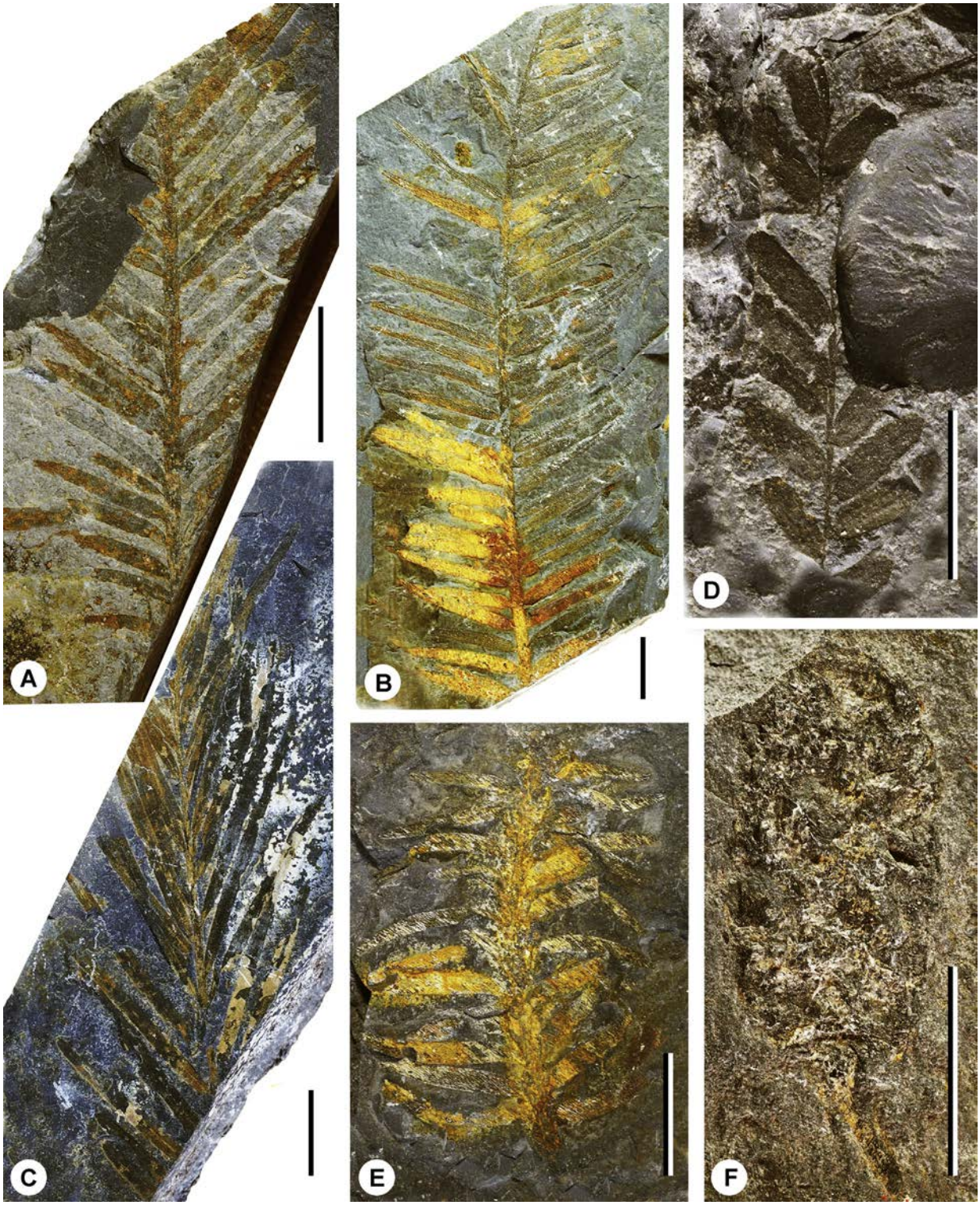


Fig. 5. Fossil conifers of the Kholokhovchan Flora: A, B, C, *Elatocladus intermedius* (Hollick) Bell: A, specimen no. 78; B, specimen no. 73; C, specimen no. 1; D, *Parataxodium* sp., specimen no. 183a; E, *Elatocladus* cf. *smittiana* (Heer) Seward, specimen no. 146b; F, *Sequoites* sp. (cone), specimen no. 174. Scale bar 1 cm.

deviating from the axis at an angle of about 45°, broad at the base and tapering to a pointed tip; they are 1.2–1.8 mm long and 0.8 mm wide at the base (Fig. 6H). There is probably a terminal pollen cone (or a bud?) being almost round in shape, and about 1.2 mm wide and 0.9 mm long on the shoot with decussate phyllotaxis (Fig. 6D, F).

Comparison and discussion. The combination of helical and decussate leaf arrangement is found in some modern Cupressaceae genera. For example, scale-like leaves of *Widdringtonia* Endlicher are decussately arranged on small terminal shoots, while leaves on the axial shoots are bigger in size, long-decurrent and more or less spirally arranged (Farjon, 2010). However, this

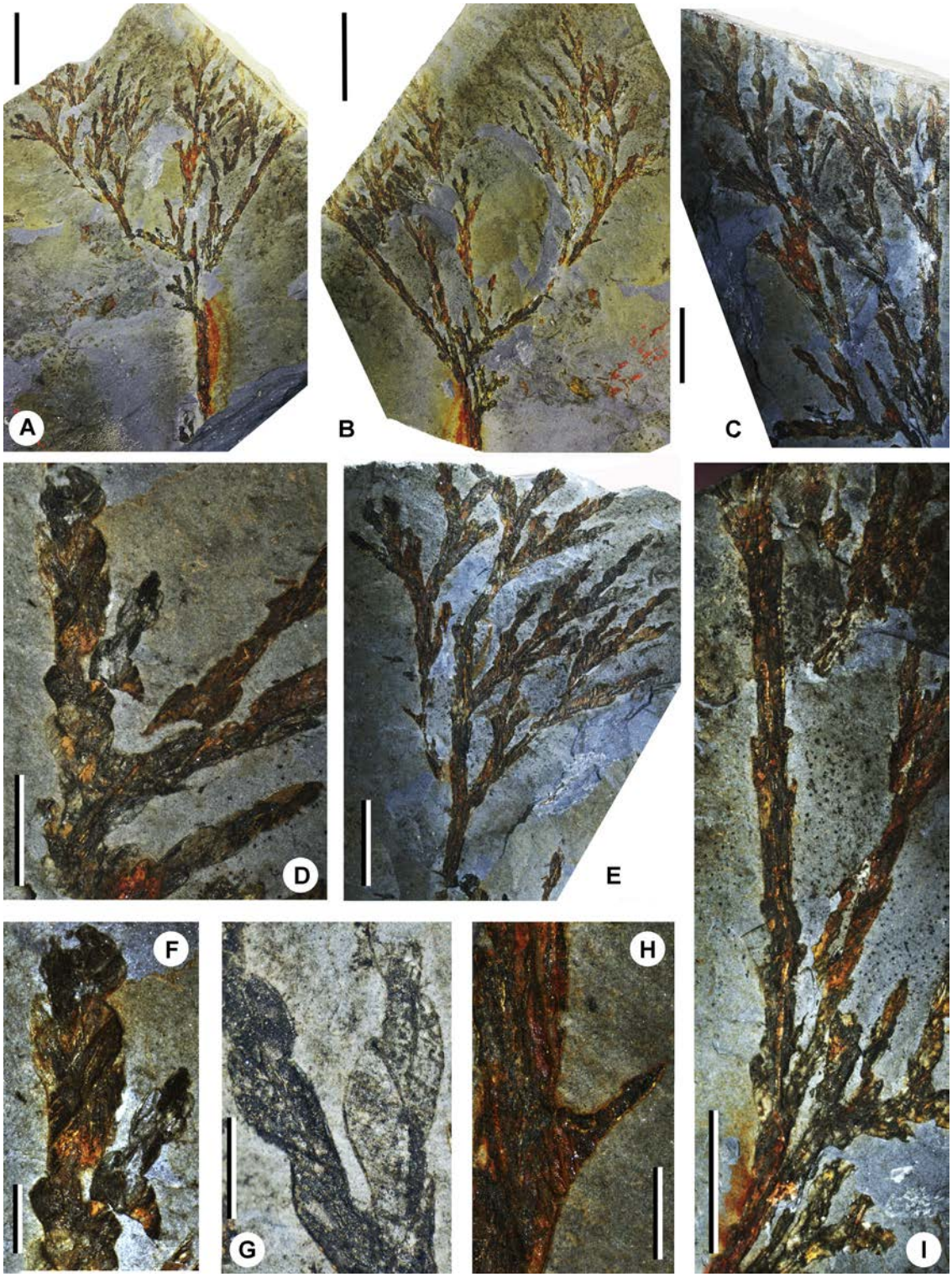


Fig. 6. Cupressaceae gen. et sp. indet. cf. *Widdringtonites* sp. of the Kholokhovchan Flora: A, C–G, specimen no. 88a: A, general view of the leafy shoot; C, E, enlarged fragments of the shoot; D, F, shoot with almost decussate scale-like leaves; G, shoot with alternate boat-shaped leaves; B, H, I, specimen no. 88b: B, general view of the shoot; H, single subulate leaf; I, enlarged fragment of the shoot. Scale bar A, B — 1 cm; C, E, I — 5 mm; D — 2 mm; F, G, H — 1 mm.

morphology does not correspond with that of the fossil shoots described here. As indicated by McIver (2001), the phyllotaxis of the genus *Widdringtonia* was also dimorphic in the geological past.

Velenovský (1885) attributed shoots with a spiral leaf arrangement passing to almost decussate on the shoots bearing pollen cones (very similar to the fossil shoots described here) to *Widdringtonia reichii* (Ettinsghausen) Velenovský, describing the new

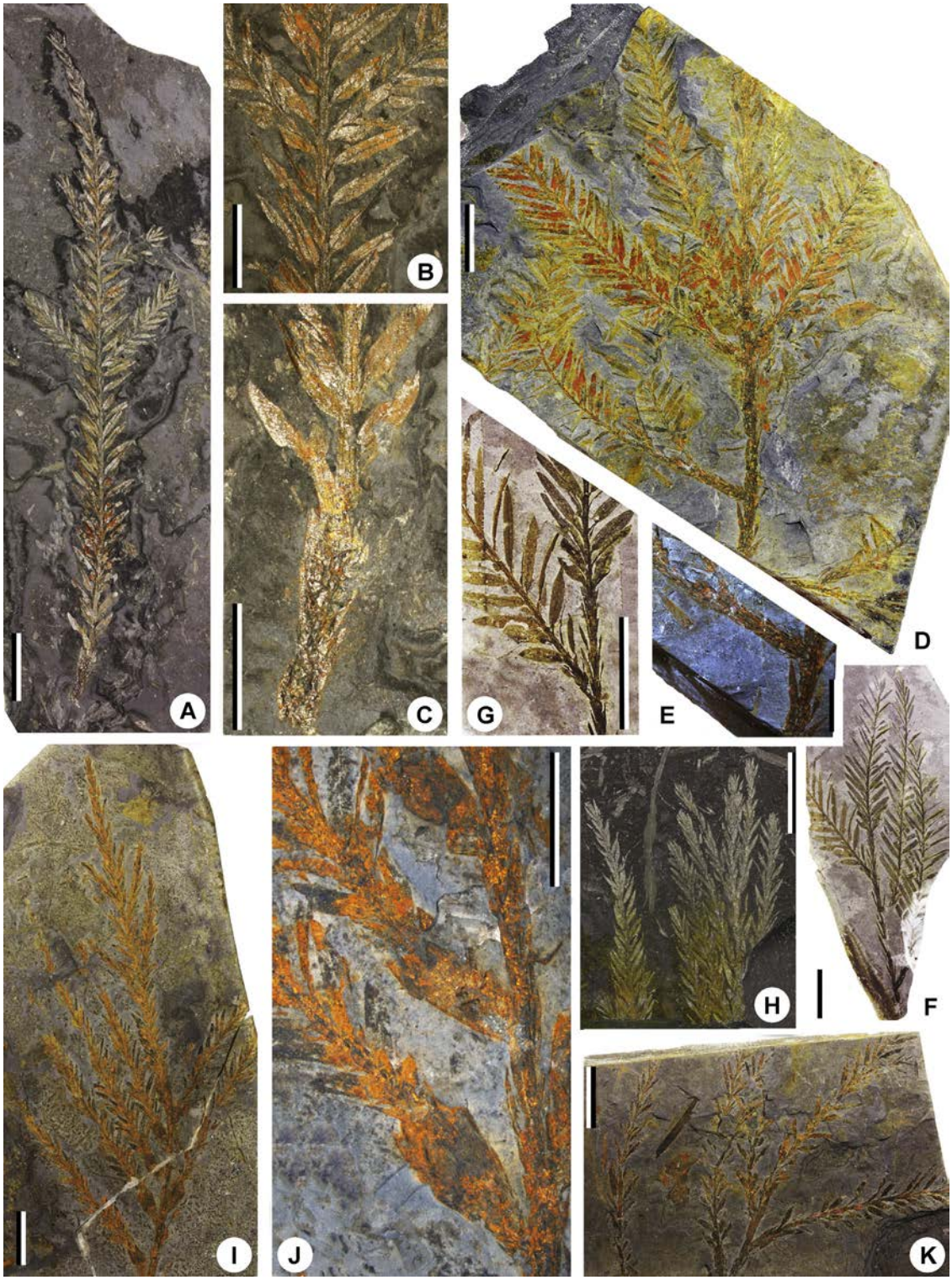


Fig. 7. *Taxodium* cf. *olrikii* (Heer) Brown of the Kholokhovchan Flora: A–C, specimen no. 52: A, general view of the shoot with dimorphous leaves; B, enlarged fragment of the shoot with oppositely disposed shoots of the last order; C, the base of the shoot of the last order with small scale-like leaves; D, E, specimen no. 45: D, general view of the shoot with dimorphous leaves; E, bases of the shoots with small scale-like leaves; F, G, specimen no. 60: F, general view of the shoot with dimorphous leaves; G, enlarged fragment of the shoot; I, J, specimen no. 112: I, general view of the shoot with dimorphous leaves; J, bases of the shoots with small scale-like leaves; H, specimen no. 119, general view of the shoot. K, specimen no. 62, general view of the shoot with dimorphous leaves. Scale bar A, D, F, G, H, I, K— 1 cm; B, C, E, J — 5 mm.

combination instead of *Widdringtonites reichii* (Ettinsghausen) Heer. The fossil genus *Widdringtonites* Endlicher was originally erected by Endlicher (1847) for shoots with small scale-like appressed leaves with spiral phyllotaxis only. Later the diagnosis was emended by Miller and Hickey (2010): "Shoots not in one plane, bearing helically arranged scale leaves. Free part of leaf narrowing gradually from a basal cushion, flattened, appressed to the stem, elongate; its length exceeding the width of the basal

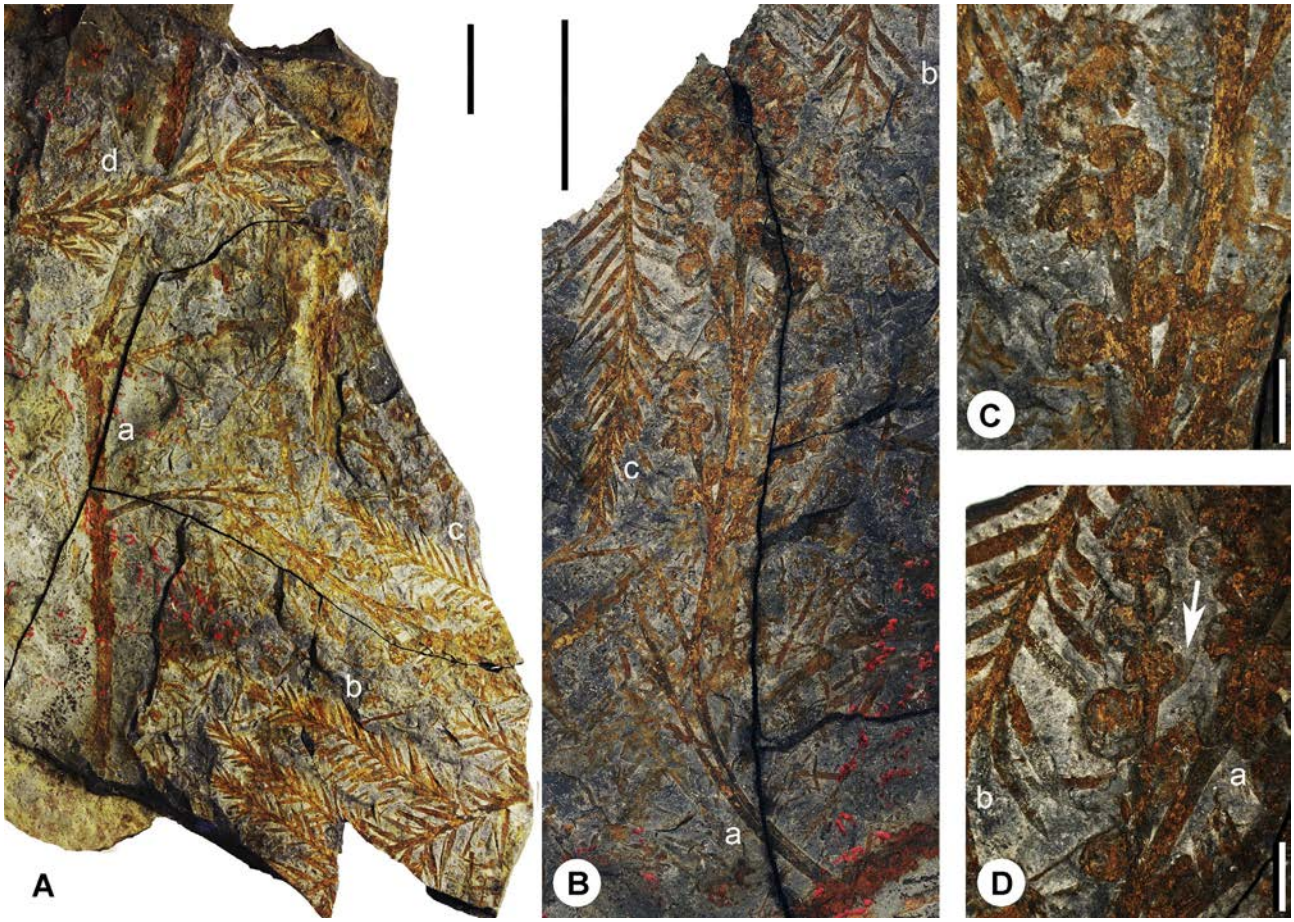


Fig. 8. Representatives of *Taxodium* of the Kholokhovchan Flora, specimen no. 50: Aa, Ba, C, Da, *Taxodium* sp.; specialised shoot bearing terminate and lateral pollen cones; Da, arrow indicates a probable falcate leaf bearing a pollen cone in its axil. Ab, Ac, Ad, Bb, Bc, Db, *Taxodium* cf. *olrikii* (Heer) Brown; leafy shoots. Scale bar A, B — 1 cm; C, D — 2 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cushion." The shoots described here are suitable for the emended diagnosis of the genus *Widdringtonites* in all of the features, besides being not only helically arranged. The presence of decussate leaves, being doubtful, however, makes the assignment of the shoots described here to the genus *Widdringtonites* impossible. Nevertheless we found the representatives of this genus the most similar to Kholokhovchan shoots.

Krassilov (1971) noted that all Cretaceous Cupressaceae representatives can be divided into two provisional groups: "*Widdringtonites*" and "*Thuja*". The first group is represented by very small-leaved conifers, and the second – by plant fossils, morphologically similar to the modern *Chaemacyparis*. Following this formal classification, the fossil shoots described here undoubtedly belong to the group "*Widdringtonites*".

Subfamily Taxodioideae Endlicher ex K. Koch

Genus *Taxodium* Richard, 1810

Taxodium* cf. *olrikii (Heer) Brown
Fig. 7A–K; Fig. 8Ab, c, d; Bb, c; Db

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

Type locality. Upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Material studied. Specimens nos. 45, 51, 52, 54, 60, 62, 112, 119, 121.

Description. In the collection there are numerous leafy vegetative shoots with up to three branching orders preserved. The shoots are up to 10 cm long. Their characteristic feature is a presence of scale-like leaves at the base of juvenile shoots with linear leaves (Fig. 7A, C, E, G, J). The shoots appear to be branching alternately or almost oppositely in one or several planes. The distances between the branching nodes of terminal shoots vary from 0.7 to 2.2 cm. Lateral branchlets depart at an angle of 25–60°. Terminal shoots vary in length from 1 to 6–7 cm. The axes are thick, rounded or slightly flattened in section; reaching up to 3 mm in diameter in shoots with three orders of branching preserved. Leaves are thin, not leathery, polymorphic within a single shoot: scale-like at the base of the shoot, linear-lanceolate on the terminal shoot (Fig. 7A, B, D, G, K; Fig. 8Ab; Bb, c; Db) and of transitional shapes: from needle-like to subulate (Fig. 7I, G, H; Fig. 8Ad). The largest leaves are situated in the middle part of the shoots; leaf size often decreases towards the shoot base and apex. Leaf arrangement is spiral, from dense to rather sparse. Scale-like leaves at the base of the shoots are sessile, overlapping, adpressed; shape of the free part of the leaf is triangular, with a pointed apex. Scale-like leaves are up to 5 mm long and up to 3 mm wide. Linear leaves vary in shape from linear-lanceolate and subulate to sabre-like. All linear leaves are sessile, with long-pointed apices and narrowed, petiolate, mostly decurrent at the base, leaving parallel longitudinal lines on the axis (Fig. 7B, C). The leaf margin is smooth. The maximum width of the leaf occurs in its middle part. The midrib is

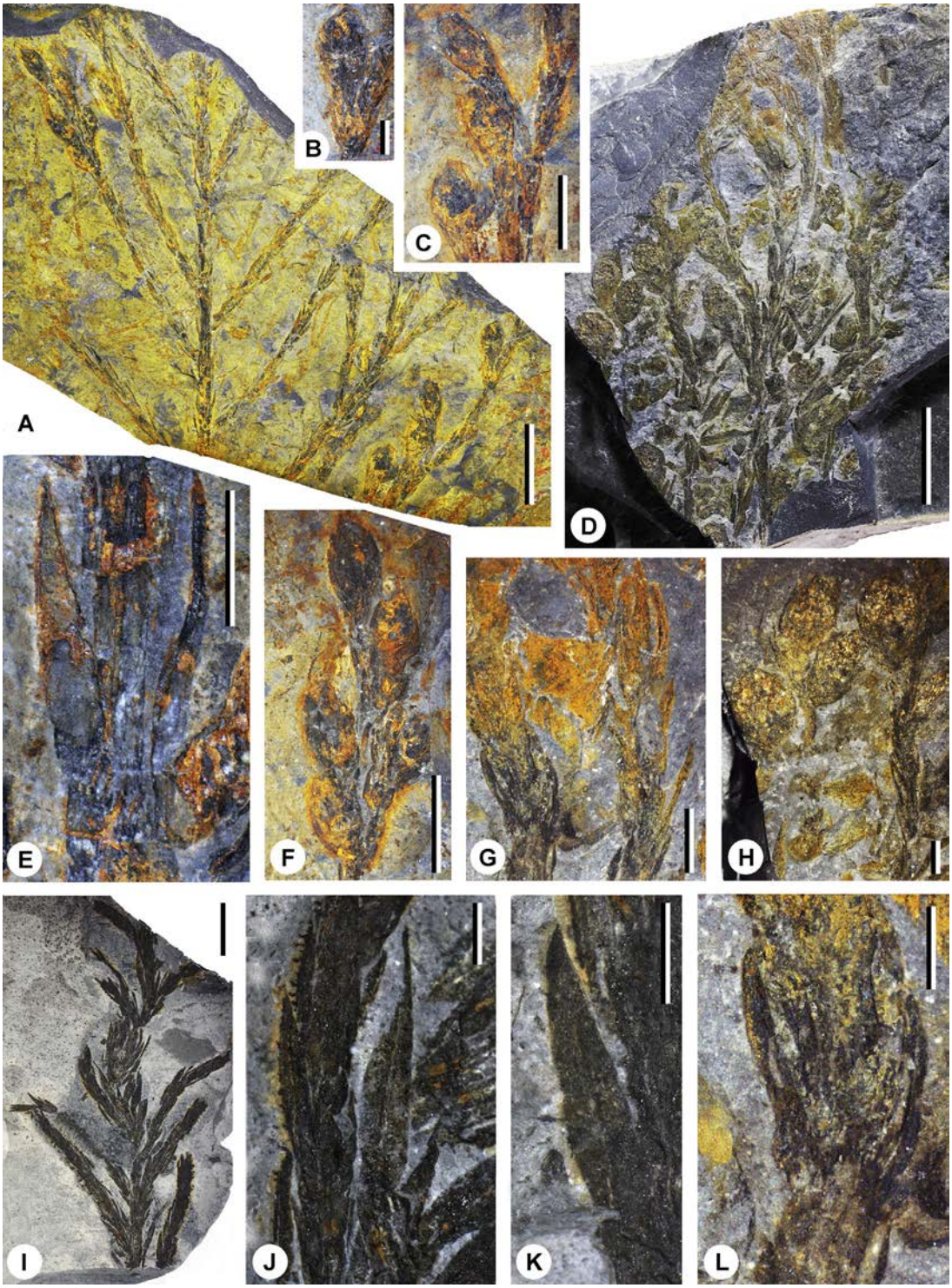


Fig. 9. *Glyptostrobus* sp. of the Kholokhovchan Flora: A–C, E, F, specimen no. 86: A, general view of the shoots bearing terminal pollen cones; B, C, F, enlarged fragments showing obovate pollen cones; E, enlarged fragment showing subulate leaves; D, G, H, L, specimen no. 85: D, general view of the shoot with pollen cones; G, L, enlarged fragment showing leaf arrangement and shape; H, obovate to globose pollen cones; I–K, specimen no. 87: I, general view of the shoot with subulate leaves; J, K, enlarged fragments showing leaves and their arrangement; Scale bar A, D — 1 cm; C, F, I — 5 mm; B, E, G, H — 2 mm; J–L — 1 mm.

clearly expressed on both sides of the leaves on well-preserved specimens; gradually thinning to the top of the leaf. The leaf surface is more or less flat and smooth. Linear leaves are 0.3–1.1 cm long and up to 1.3 mm wide at the widest part.

Comparison and discussion. According to the observed characteristics, such as the shape and thickness of the polymorphous leaves, the nature of their attachment to the axis, branching of the shoots etc., three genera of the family Cupressaceae *sensu lato* (former

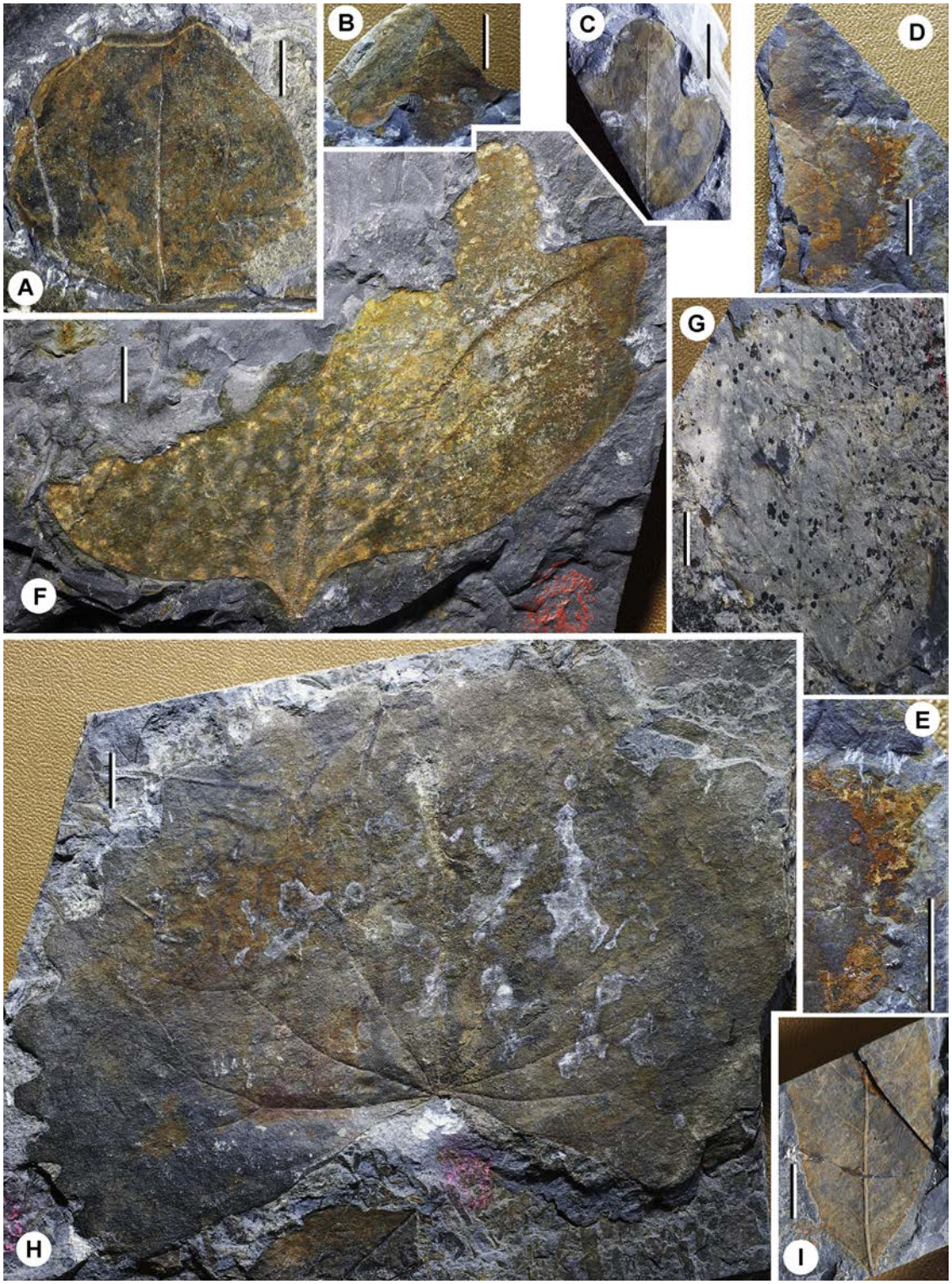


Fig. 10. Fossil angiosperms of the Kholokhovchan Flora: A, *Cocculophyllum* sp., entire-margined leaf, specimen no. 147. B, *Menispermites* cf. *sibiricus* (Heer) Golovneva, fragment of the peltate lobed leaf base, specimen no. 175. C, *Araliaephyllum medium* (Philippova) Herman, trilobed leaf, specimen no. 169. D, E, *Cissites* cf. *pekulneensis* (Philippova) Moiseeva, specimen no. 171: D, leaf fragment; E, detail of marginal teeth and venation. F, *Araliaephyllum* sp., lobed leaf fragment, specimen no. 43. G, *Cissites* cf. *cordatus* Philippova, asymmetric leaf, specimen no. 44. H, *Menispermites marcovoensis* Philippova, large almost complete leaf, specimen no. 195a. I, *Dicotylophyllum* sp. cf. *Schefflerаephyllum venustum* (Philippova) Philippova, leaf (leaflet ?) fragment, specimen no. 145. Scale bar 1 cm.

Taxodiaceae) are comparable with the fossils studied: *Sequoia* Endlicher, *Glyptostrobus* Endlicher and *Taxodium* Richard. While having the annual shoots among the fossil plant studied, we leave only two genera for further comparison: *Taxodium* and *Glyptostrobus*, which drop their annual shoots seasonally. It is very difficult to distinguish these two genera in the absence of generative organs in organic connection with shoots (Brown, 1936; Kryshtofovich and Baikovskaya, 1960). Stefanoff and Jordanoff

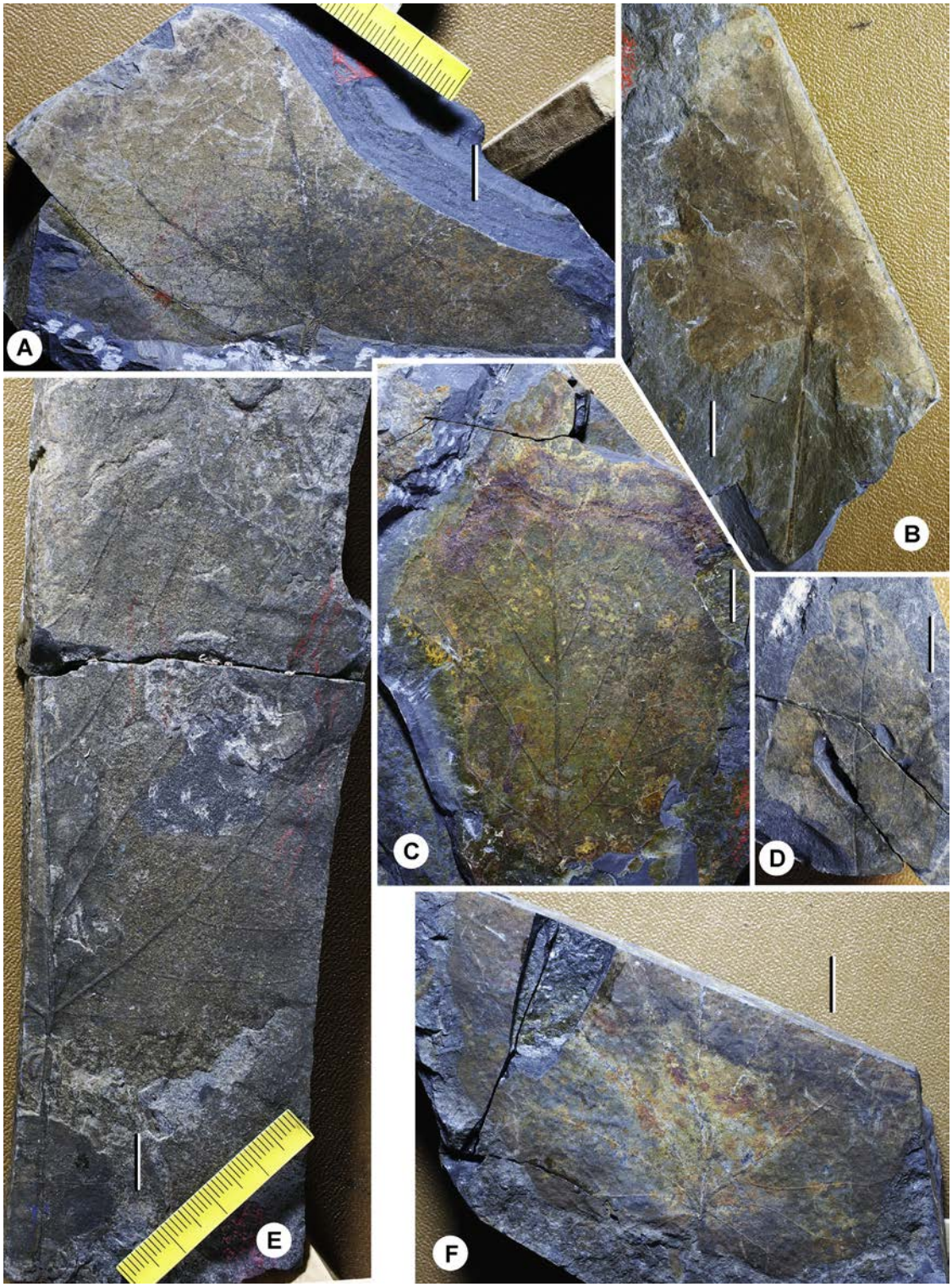


Fig. 11. Fossil angiosperms of the Kholokhovchan Flora: A, *Terechovia* cf. *philippovae* Herman, fragment of leaf base, specimen no. 66. B, *Cissites* sp., lobed leaf with long petiole, specimen no. 64b. C, *Ettingshausenia louravetlanica* (Herman et Shczepetov) Herman et Moiseeva, almost complete leaf, specimen no. 108. D, *Celastrophyllum* (?) sp., leaf fragment, specimen no. 168b. E, *Arthollia* cf. *pacifica* Herman, large leaf fragment, specimen no. 105. F, *Pseudoprotophyllum boreale* (Dawson) Hollick, fragment of peltate leaf base, specimen no. 109a. Scale bar 1 cm.

(1935) believed that the inclusion of fossil conifers in these genera has been rather random. However, *Taxodium* leaves can display a distichous arrangement and are narrowed at the base, whereas *Glyptostrobus* leaves do not form a distichous arrangement and are thickened at the base (Ablaev, 1974; LePage, 2011). This allows us to attribute the fossil polymorphous shoots described here to *Taxodium*.

The fossil shoots studied resemble *T. wallissii* Aulenback et LePage from the Upper Cretaceous of Alberta (Canada) (Aulenback

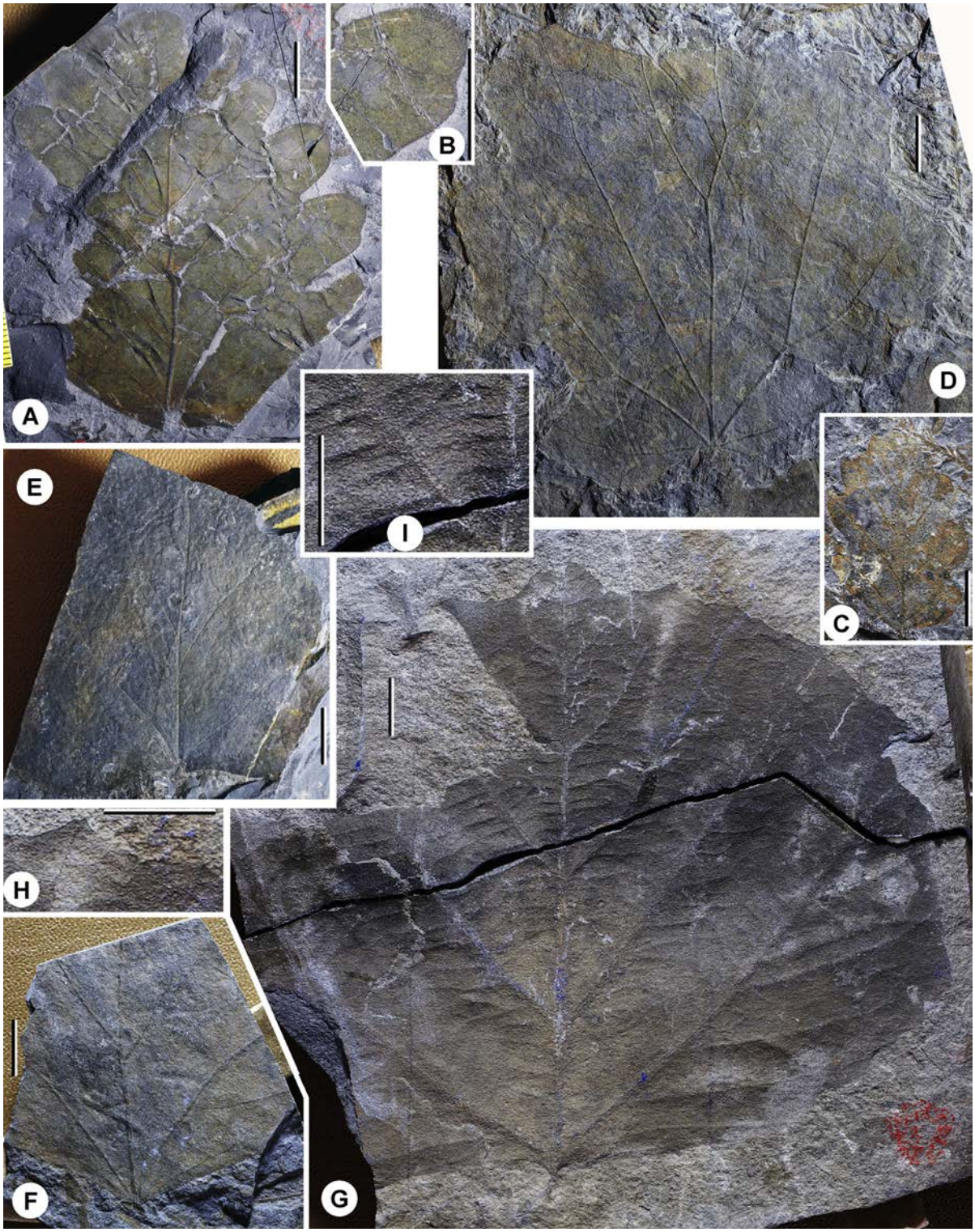


Fig. 12. Fossil angiosperms of the Kholokhovchan Flora: A, B, C, *Dalembia pergamentii* Herman et Lebedev: A, large lobed leaflet, specimen no. 89a; B, detail of Fig. 12A, lateral lobe, specimen no. 89a; C, small leaflet, specimen no. 97. D, *Chachlovia dombeyopsoida* (Herman) Herman, lobed leaf, specimen no. 179-1. E, *Dicotylophyllum* sp., leaf fragment, specimen no. 148. F, *Ettingshausenia louravetlanica* (Herman et Shczepetov) Herman et Moiseeva, fragment of leaf base, specimen no. 106. G, H, I, *Ettingshausenia vetviensis* Herman, sp. nov., holotype no. 107: G, leaf; H, marginal teeeth and detail of venation; I, detail of tertiary venation. Scale bar 1 cm.

and LePage, 1998). The similarities are the presence of several types of foliage, including linear (taxodioid) and scale-like (cupressoid) leaves, with the scale-like leaves being basal to the taxodioid leaf form when present; in leaf arrangement, and in the shape of leaf bases. The Canadian shoots differ in having a swelling at the base of free portion of linear-falcate leaves and in having apices of the leaves, sharply recurved towards the shoot axis; they also differ in having smaller sized cupressoid leaves. The fossil shoots described

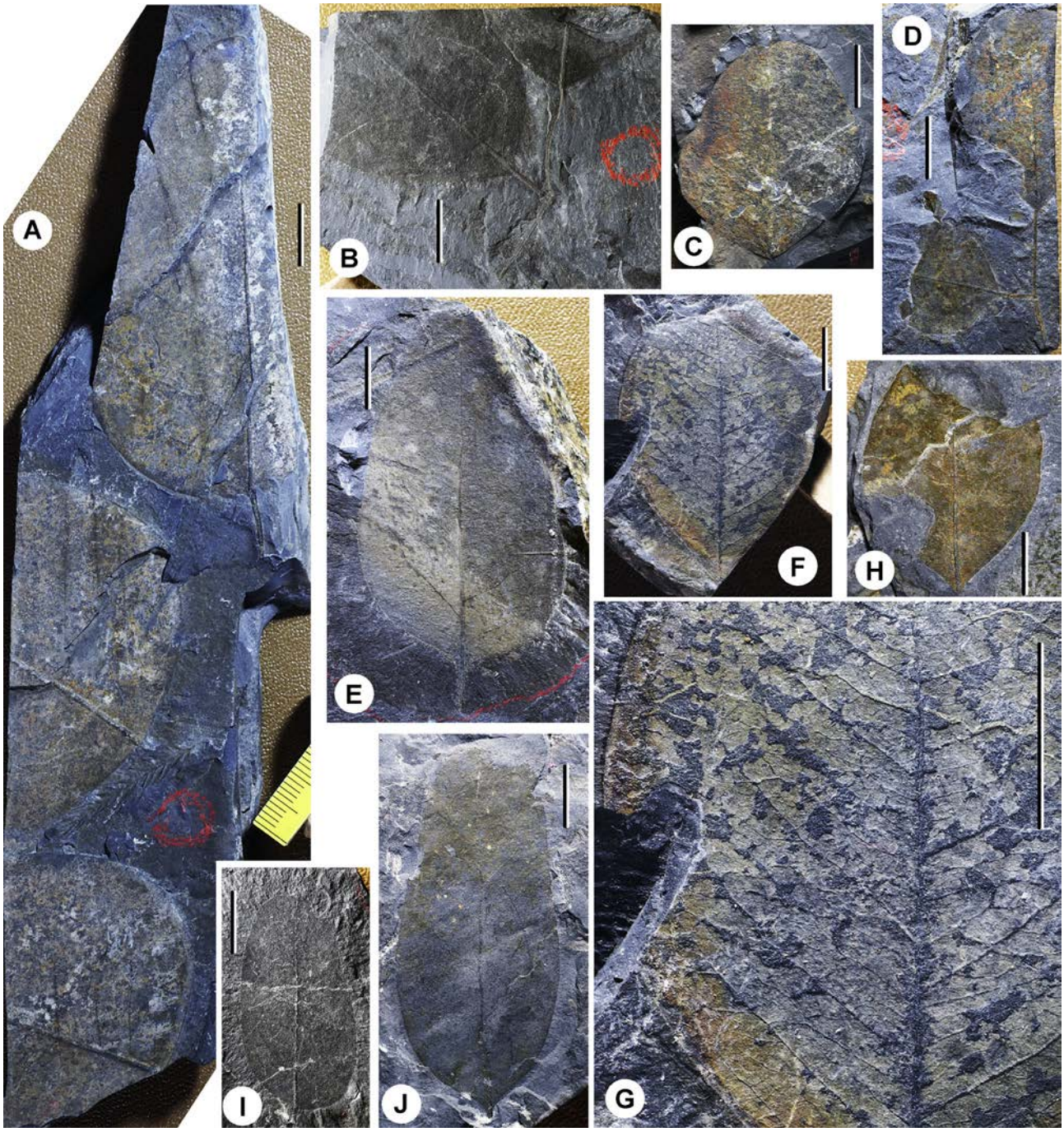


Fig. 13. *Parvileguminophyllum penzhinense* Herman, sp. nov. of the Kholokhovchan Flora. A, three leaflets of the compound leaf fragment, specimen no. 2. B, compound leaf fragment with two leaflets attached, specimen no. 9a. C, subtrilobed leaflet, specimen no. 20a. D, compound leaf fragment with two leaflets attached, holotype no. 10. E, leaflet, specimen no. 8. F, leaflet, specimen no. 15. G, detail of Fig. 13F, specimen no. 15. H, leaflet, specimen no. 63-1. I, leaflet, specimen no. 3. J, leaflet, specimen no. 12-4. Scale bar 1 cm.

have more polymorphic foliage, including linear-lanceolate, sabre-shaped and single subulate leaves.

Krassilov (1976) described similar shoots from Lower Paleogene (Danian) of the Amur River region (Russian Far East) as *Taxodium olrikii* (Heer) Brown. The Amur and Kholokhovchan shoots possess several features in common: leaf polymorphism, the presence of a "wrapper" of scale-like leaves at the base of shoots with linear leaves, the angle of deviation of branching shoots and leaves from the axis, the presence of subulate leaves, as well as the appearance of the narrowed bases of the leaves. The differences occur in the presence of longer terminal shoots, carrying leaves almost twice as long as those from the Amur region, in Kholokhovchan specimens. These differences are quantitative, but being present, do not allow us to identify fossil shoots as *Taxodium olrikii* (Heer) Brown. However, among the known fossil and modern species, *T. olrikii* seems to be the most similar to the shoots described.

The fossil shoots studied also show common features with *Taxodium dubium* (Sternberg) Heer emend. Kunzmann et al. from the Paleogene and Neogene of Central Europe (Kunzmann et al., 2009). Those features are: the characteristic shape of the terminal

shoots with linear leaves reaching their greatest length in the middle of the shoot, and the arrangement and shape of the leaves – needle-like, subulate, and linear-lanceolate. The differences occur in the smaller variability of sizes of the leaves and shoots in the plant studied (this is possibly associated with a markedly smaller collection), as well as in the presence of characteristic scale-like leaves at the base of shoots with linear leaves.

Taxodium sp.
Fig. 8Aa; Ba; C; Da

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

Type locality. Upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Material studied. Specimen no. 50 a-1.

Description. In the collection there is one incomplete impression of a specialised generative branching shoot about 10 cm long, bearing laterally and terminally disposed pollen cones, forming a "cluster". The shoot axis bears no visible leaves (perhaps due to preservation of the material). There is only one place where we can assume the presence of the long falcate leaf, bearing a pollen cone in its axil; the leaf is about 2 mm long (Fig. 8Da, arrow). The main axis is up to 3 mm in diameter, changing its direction. Shoots of the next branching order are much thinner, 0.8–1 mm in diameter. Terminal shoots, about 0.5–0.8 mm in diameter, bear up to seven pollen cones; they are spirally arranged or almost opposite. There is one terminal cone at the tip of the axis. Pollen cones are spherical, 1.5–2 mm in diameter. The shape, number, arrangement and size of microsporophylls are unclear due to preservation.

Comparison and discussion. Specialised taxodiaceous shoots bearing terminally and laterally arranged pollen cones are known in modern genera *Taxodium* and *Metasequoia* Hu et Cheng, as well as in the fossil genera *Parataxodium* Arnold et Lowther and *Drumhellera* Serbet et Stockey (Serbet and Stockey, 1991).

The comparison of generative shoots from the Kholokhovchan Flora with the only species of the genus *Drumhellera* – *D. kurmanniae* Serbet et Stockey from the Upper Cretaceous of Alberta (Canada) (Serbet and Stockey, 1991) is difficult due to the type of preservation of the Canadian material, which is permineralised. There are however two common characters: the spiral arrangement of pollen cones and their diameter. The differences appear in the presence of the leaves on the axes bearing pollen cones and the larger thickness of the axes in the Canadian specimens. Unfortunately, other features for comparison of these shoots are lacking.

The specimen studied differs from the only extant and all known fossil representatives of the genus *Metasequoia* in having a helical arrangement of the pollen cones.

The fossil shoot studied here is also similar to *Parataxodium wigginsii* Arnold et Lowther from the Upper Cretaceous of North Alaska (Arnold and Lowther, 1955) in size and the arrangement of pollen cones. Differences occur in the absence of long (more than twice as long as the cones) scale-like leaves, bearing pollen cones in their axils; more spherical, rather than oval shape of the cones, and much thinner cone-bearing axes in the plant of the Kholokhovchan Flora.

The fossil shoot studied here is most similar, both in the arrangement of pollen cones and in the cones-bearing axis morphology, to representatives of the genus *Taxodium*, especially to extant *T. distichum* and to *T. dubium* from the Paleogene and Neogene of Europe (Kunzmann et al., 2009). However, the lack of preserved features doesn't allow us a detailed comparison. For this reason, we name the fossil shoots as *Taxodium* sp.

Krassilov (1976) described pollen cone-bearing shoots with similar morphology from the early Paleogene Tsagayan Flora of the Amur Region as *T. olrikii*. The shoot from the Kholokhovchan Flora differs from the Amur plant in lack of leaves on the shoot, as well as having pollen cones half the diameter, which are predominantly spherical and not obovate.

With high probability we can assume that the Kholokhovchan material represents female fertile shoots of *T.* cf. *olrikii* vegetative shoots described above. However, the fertile shoot is not connected organically to leafy shoots, despite the fact that they occur on the same bedding planes. Due to poor preservation, we do not have an opportunity to study the epidermal characteristics of the leaves, axes and microsporophylls so we do not have sufficient basis to assign this fertile shoot to *T.* cf. *olrikii*.

Genus *Glyptostrobus* Endlicher, 1847

Glyptostrobus sp.
Fig. 9A–L

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

Type locality. upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Material studied. Specimens nos. 85–87.

Description. The collection contains leafy shoots, some of which bear terminal pollen cones. Shoots branch alternately, three-dimensionally; the distance between the branching nodes varies from 5 to 15 mm; the angle of deviation of lateral branches is 30–45°. The axis is relatively thick, mostly straight. Leaves are polymorphous: mainly subulate and rarely linear to thin needle-like and also scale-like at the base of the shoots. Leaves are sessile, with free portions or rarely adpressed to the axis; they are densely spirally arranged. The shape of the free portion of the leaf is triangular and acute; its maximum length is 4–5 mm. The leaf base is slightly broadened and long-decurrent. The apices of the leaves are gradually acuminate. The leaf margin is smooth; the maximum width is at the base of the leaf.

Pollen cones are terminal, obovate or oblong-oval. They are arranged on the unspecialised shoots, directly on the main axis or on the lateral branches of different lengths varying from 3 to 15 mm. Cones are 5–7 mm long and 3–4 mm wide. Microsporophylls are spirally arranged.

Comparison and discussion. In our previous discussion on the affinity of our shoots of *Taxodium* cf. *olrikii*, we highlighted some morphological features that allowed to distinguish *Taxodium* and *Glyptostrobus* (see above). The more significant feature is the terminal position of the pollen cones on the unspecialised shoots, typical for the genus *Glyptostrobus*. This feature is also present in representatives of the genera *Sequoia* and *Sequoiadendron* Buchholz (Serbet and Stockey, 1991). However, in combination with the leaf morphology, we assign these shoots to the genus *Glyptostrobus*.

A recent review of the genus *Glyptostrobus* showed that more than 30 species of this genus have been mentioned in the literature (LePage, 2007). Apart from fossils, this genus is represented by only one extant species *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch. It is quite probable that most of the fossil specific names are just synonyms. This suggests the need for a revision of the genus for the understanding of its natural evolutionary history. An attempt to classify the shoots of the Kholokhovchan Flora, which are characterised only morphologically, would enhance the nomenclatural problem. Therefore, it seems logical to leave the name as *Glyptostrobus* sp.

We also can compare our shoots with morphologically similar shoots of the representatives of few extinct genera lacking of information on pollen cones. They are *Elatidopsis* Srinivasan et Friis emend. Van der Ham, *Quasisequoia* Srinivasan et Friis, and *Cryptomeriopsis* Stopes et Fujii emend. Van der Ham. However, the comparison is difficult due to different preservation of the fossil material: the epidermal features are known for the above-mentioned fossil genera, while our material is lacking microstructural data.

The most similar to Kholokhovchan shoots are the representatives of the genus *Elatidopsis*, especially shoots of *E. nykvistii* Srinivasan et Friis from the Upper Cretaceous of Sweden (Srinivasan and Friis, 1989). The differences occur in less variety of leaf-shapes in Sweden species. Shoots of *E. cryptomerioides* (Miquel) Van der Ham from the Maastrichtian of Belgium (Van der Ham et al., 2001) have much longer leaves, than Kholokhovchan shoots does.

Shoots of all species of the genus *Quasisequoia* (Srinivasan and Friis, 1989; Kvaček, 1999) differ from the described shoots in lacking needle-like leaves and being less polymorphous.

The differences between Kholokhovchan shoots and those of the *Cryptomeriopsis eluvialis* Van der Ham from the Maastrichtian of Belgium (Van der Ham et al., 2001) occur in smaller length of the leaves of the described specimens.

As far as our fossil shoots show organic connection with pollen cones, we find it possible to assign them to the modern genus *Glyptostrobus* with similar morphology, rather then to fossil genera with unknown male organs.

Division MAGNOLIOPHYTA (ANGIOSPERMAE)
Class MAGNOLIOPSIDA (DICOTYLEDONS)
Group PLATANOFOLIA KRASSILOV, 1979

Genus *Ettingshausenia* Stiehler, 1857

Remarks. The genus *Ettingshausenia* with the type *E. cuneifolia* (Bronn) Stiehler was proposed by Stiehler (1857, p. 66). The type was initially described by Bronn (1837, p. 583, pl. 28, fig. 11) as *Credneria cuneifolia* Bronn from the Cenomanian of Niederschöna in Germany. Here we use the generic name *Ettingshausenia* for dispersed fossil *Platanus*-like leaves that cannot be assigned to the modern genus *Platanus* L. due to the lack of associated reproductive organs (Maslova et al., 2005). The emended diagnosis of this genus published by Maslova et al. (2005) is as follows: Leaf blades vary from entire triangular and pentagonal hexangular, rhomboidal or oval rhomboidal, without lobes or with vestigial lobes, to leaf blades with two to six lateral lobes. Leaf lamina often asymmetric. Leaf base usually cuneate and decurrent on the petiole. If the leaf base is truncate or cordate, the region of the leaf base adjacent to the petiole forms a small wedge. A peltate base is occasionally present. Leaf apex acute or, more rarely, obtuse. Leaf margin dentate; more rarely entire-margined. Leaf venation craspedodromous or palinactinodromous, with developed lateral basal veins. Tertiary venation percurrent or ramified-percurrent.

Zenker (1833) erected the genus *Credneria* Zenker with the type *C. integerrima* Zenker on the basis of leaf impressions from the Senonian of Hartz. Several *Credneria* species were described from these deposits, most likely all of them are variations of a single polymorphic species (Nemejc and Kvaček, 1975; Maslova et al., 2005). Their leaves are obovate, with round, truncate, or slightly cordate base; leaf margin is entire or with some teeth in the upper pat of the leaf lamina; venation is palmate-pinnate camptodromous or partially craspedodromous; there are two to five pairs of well-developed infrabasal veins derivating from the midvein at nearly a right angle. Platanoid leaves attributed to the genus *Ettingshausenia*, including the type *E. cuneifolia*, differ from *Credneria* species in having triangular, pentagonal and rhomboidal leaf lamina, cuneate and decurrent leaf base and fewer less developed infrabasal secondary veins (Maslova et al., 2005).

Ettingshausenia vetviensis Herman, sp. nov.
Fig. 12G–I

2013 *Ettingshausenia* sp. 1: Shczepetov and Herman, Plate IX, fig. 7.

Holotype. Designated here, specimen no. 107 (Fig. 12G–I).

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

Type locality. Upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Etymology. After the Vetvistyi Stream.

Material studied. Holotype no. 107.

Diagnosis. Leaves large, simple, probably trilobate, symmetric or slightly asymmetric, with dentate margin. Leaf lamina transversely-elliptic, base broadly cuneate and slightly decurrent, apex obtuse. Leaf margin dentate, teeth simple, rare, medium in size, triangular, with acute apices, sinuses between them round. Venation palmately-pinnate craspedodromous. Midvein stout and straight. Two lateral basal veins straight and slightly curving upwards, terminating at the lateral lobe apices. Six or seven abaxial and one or two adaxial secondaries emerge from each lateral basal vein. Three pairs of simple opposite craspedodromous suprabasal secondary veins and one pair of thin and short infrabasal secondary vein emerge from a midvein. Tertiary veins prominent, slightly curved, percurrent or ramified-percurrent, almost perpendicular to the midvein and emerging from the secondary veins at an acute angle.

Description. This species is represented by a single fossil leaf in the collection. Leaf is large in size, simple, probably trilobate, symmetric or slightly asymmetric at the leaf base, with a dentate margin (Fig. 12G). Leaf length is 112 mm, leaf width is approximately 145 mm. Leaf lamina is transversely-elliptic in shape (length to width ratio is less than 1:1, the maximum width being in the middle part of the leaf or slightly above the middle part). Leaf base is broadly cuneate and slightly decurrent, slightly asymmetric; apex is obtuse. To judge by the leaf outline, there was a single small lateral lobe on each side of the leaf lamina, situated in its middle part; however, the lobes are not completely preserved. Leaf margin is dentate, poorly preserved. Marginal teeth are simple, rare, medium in size, up to 2 mm in height, triangular, with acute apices (Fig. 12H). Sinuses between the teeth are round. Petiole is poorly preserved, approximately 1 mm thick.

Venation is palmately-pinnate craspedodromous. Midvein is stout, straight, terminating at the leaf apex, approximately 1–1.2 mm thick in its basal part, narrowing towards the leaf apex. Two stout lateral basal veins, of approximately the same width as the midvein or slightly thinner, are straight and slightly curving upwards, emerging from the midvein 1.5–2 mm above the leaf base at an angle of 45–50° and terminating at the lateral lobe apices. Six or seven abaxial and one or two adaxial secondaries emerge from each lateral basal vein. Three pairs of simple suprabasal secondary veins emerge from a midvein. They are opposite, craspedodromous, emerging from the midvein at an angle of 35–40° and going into the apices of the marginal teeth. One pair of thin and short camptodromous or craspedodromous infrabasal secondary veins emerges from the midvein. Tertiary veins are prominent, slightly curved, percurrent or ramified-percurrent, almost perpendicular to the midvein and emerging from the secondary veins at an acute angle (Fig. 12I). Quaternary venation and venation near leaf margins poorly preserved.

Comparison and discussion. The most characteristic features of the new species are a broad leaf lamina, small lateral lobes, rare opposite suprabasal secondary veins and prominent tertiary veins, slightly curved and perpendicular to the midvein.

The new species differs from the type of the genus *E. cuneifolia* (Bronn) Stiehler (Bronn, 1837, 1838; Stiehler, 1857; see also: Maslova et al., 2005) from the Cenomanian of Niederschöna in Germany in having a broad transversely-elliptical leaf lamina with a broadly cuneate leaf base. *Ettingshausenia vetviensis* sp. nov., unlike *E. louravetlanica* (Herman et Shczepetov) Herman et Moiseeva from the uppermost Albian–lower Turonian of the Anadyr River basin (Herman, 1994; Maslova and Herman, 2004), has broader leaves with broadly cuneate base, smaller lateral lobes and fewer secondary veins. These features also allow to distinguish the new species from *E. raynoldsii* (Newberry) Moiseeva from the Maastrichtian of the Amaam Lagoon in Northeastern Russia (Moiseeva, 2008, 2012) and *E. laevis* (Velenovský) J. Kvaček et Váchová from the Cenomanian of Czech Republic (Kvaček and Váchová, 2006) and early Campanian Grünbach Flora in Austria (Herman and Kvaček, 2010). A leaf fragment described as *Ettingshausenia* sp. from the early Campanian Grünbach Flora (Herman and Kvaček, 2010) resembles the new species in having a broad leaf lamina and a few suprabasal opposite secondary veins, but, unlike *E. vetviensis* sp. nov., possesses better developed lateral lobes and curved tertiary veins oriented at an acute angle to the midvein.

Several fossil leaves resembling the new species were ascribed to the modern genus *Platanus* L. Among them, *P. primaeva* Lesquereux from the Upper Cretaceous of North America, Northeastern Russia, Western Siberia and Kazakhstan (Lesquereux, 1874; Vakhrameev, 1952; Herman and Lebedev, 1991) and *P. embicola* Vakhrameev from the Cenomanian of Western Kazakhstan (Vakhrameev, 1952) are the most similar to *Ettingshausenia vetviensis* sp. nov. in having broad leaf laminae and rare secondary veins. *E. vetviensis* sp. nov., however, differs from *Platanus primaeva* in its transversely-elliptic, not broadly triangular, shape and generally smaller size and from *P. embicola* in having less pronounced lateral lobes and fewer secondary veins. Moreover, these *Platanus* species, unlike *Ettingshausenia vetviensis* sp. nov., possess curved tertiary veins oriented at an acute angle to the midvein.

Group LEGUMINOFOLIA KRASSILOV, 1979

Genus *Parvileguminophyllum* Herendeen et Dilcher, 1990

Remarks. The genus *Parvileguminophyllum* with the type species *P. georgianum* (Berry) Herendeen et Dilcher was erected by Herendeen and Dilcher (1990) for dispersed leaves and leaflets lacking morphological and cuticular characters. This genus was proposed to encompass small entire-margined leaflets isolated or attached to short petioles having pulvini; the leaflet bases are usually asymmetric, apices are symmetric, with a pinnately brochidodromous secondary venation (Herendeen and Dilcher, 1990). It was assumed that this genus is related to the family Leguminosae. Here we ascribe the genus *Parvileguminophyllum* to the group Leguminifolia Krassilov of the classification of dispersed angiosperm leaves (Krassilov, 1979). The new species fits well the diagnosis of the genus *Parvileguminophyllum* to which it has been assigned.

Parvileguminophyllum penzhinense Herman, sp. nov.
Fig. 13A–J

2013 *Parvileguminophyllum* aff. *samylinae* Herman: Shczepetov and Herman, Plate IX, figs 1–3, Plate X, figs 1–6.

Holotype. Designated here, specimen no. 10 (Fig. 13D).

Repository. GIN RAS, Moscow, Russia, collection no. 3384.

Type locality. Upper reaches of the Vetvistyi Stream, locality no. 17 (Lebedev, 1987), Penzhina and Oklan rivers interfluve, Northeastern Russia.

Type stratum. Chalbugchan Group, Vetvinskaya Member, lower part, Upper Cretaceous, Turonian–Coniacian.

Etymology. After the Penzhina River.

Material studied. Specimens nos 2, 3, 4, 6, 7, 8, 9a, 9b, 10 (holotype), 11, 12-4, 13, 14, 15, 18, 19, 20a, 20b, 21, 24, 25, 26, 27, 29, 30, 31, 32, 33, 34, 35, 36, 37, 39, 40-1, 40-2, 41, 42, 63-1.

Diagnosis. Leaves pinnately compound. Leaflets simple, very small to large in size, entire-margined, symmetric or slightly asymmetric, ovate, broadly ovate, elliptic and broadly elliptic. Leaflet base round, broadly round, acute and broadly acute, slightly decurrent, apex broadly round, often emarginate. Venation pinnate festooned-brochidodromous, with 5–10 pairs of thin secondary veins. Secondary veins going towards the leaflet margin, bifurcating, straight or curving upward and forming brochidodromous loops decreasing towards the leaflet margin. Tertiary venation ramified-reticulate.

Description. In the collection there are three fragments of compound leaves (Fig. 13A, B, D) and numerous isolated leaflets (Fig. 13C, E–J). Leaves are pinnately compound, incompletely preserved and hence of unknown size and appearance. Leaflets are simple, very small to large in size, entire-margined, symmetric (Fig. 13A, B, D, H, J) or with a slightly asymmetric (Fig. 13E, I) base, variable in size. In the collection there is a single leaflet (apical leaflet ?) possessing a subtrilobed shape, with a pair of small round lateral lobes (Fig. 13C). Leaflets are 18–100 mm in length and 15–56 mm in width. Leaflet shape is ovate, broadly ovate, elliptic and broadly elliptic, with the maximal width situating in the middle or lower part of leaflet. Leaflet base is symmetric or slightly asymmetric, round, broadly round, acute and broadly acute, often slightly decurrent at the petiole. Leaflet apex is broadly round, often emarginate (with a shallow notch: Fig. 13C, D, E, I), while the margin is entire and rarely slightly undulate. Leaflet petiolule is thin and short, 5–12 mm in length and 0.5–0.8 mm in width (Fig. 13A, B, D). Common petiole is incompletely preserved, approximately 1 mm in width (Fig. 13B, D).

Venation is pinnate festooned-brochidodromous. Midvein is straight, terminating at the leaflet apex. There are five to approximately ten pairs of thin secondary veins. The most

developed are those of the second, third or fourth pair from the base. Secondary veins emerge from the midvein at an angle of 40–75° and go towards the leaflet margin, often bifurcating, straight or curving upward and forming brochidodromous loops decreasing towards the leaflet margin (Fig. 13F, G). Usually there are one to three thin intersecondary veins (Fig. 13G). Tertiary venation is ramified-reticulate (Fig. 13G), poorly preserved. Thinner veins are missing.

Comparison and discussion. Originally, this species was named *Parvileguminophyllum* aff. *samylinae* Herman (Shczepetov and Herman, 2013). The new species resembles *P. samylinae* from the Turonian–Coniacian Arman Flora of the Magadan District (Herman et al., 2012) in having compound leaves with asymmetrical entire-margined leaflets and pinnate festooned-brochidodromous venation, but, unlike *P. samylinae*, possesses relatively longer leaflets, round and emarginate non-mucronate apex, a larger number of secondary veins and ramified-reticulate, rather than ramified-percurrent, tertiary venation. A number of species from the Eocene of the southeastern United States (Herendeen and Dilcher, 1990) and Utah and Colorado (Call and Dilcher, 1994) that were earlier placed in the genus *Mimosites* Bowerbank have been assigned to *Parvileguminophyllum*. *P. penzhinense* sp. nov. differs from these species in having a less elongate leaf lamina, being round and emarginate non-mucronate apex and festooned-brochidodromous venation.

Several fossil entire-margined leaves or leaflets have been attributed to the genus *Leguminosites* Bowerbank. It should be emphasised that such an attribution is erroneous since this genus was erected to accommodate fossil seeds (Vakhrameev, 1952; Andrews, 1970), and hence this generic name is not applicable for leaf remains (Krassilov, 1979). The new species is similar to *Leguminosites mucronatus* Herman et J. Kvaček from the early Campanian Grünbach Flora in Austria (Herman and Kvaček, 2010) in the shape of the entire-margined lamina, asymmetric round decurrent base and pinnate venation. However, *Parvileguminophyllum penzhinense* sp. nov. differs in the round and emarginate, but not mucronate, apex and festooned-brochidodromous venation. An additional species similar to the new one is *Leguminosites schachshachensis* Shilin from the Senonian of Kazakhstan (Shilin and Romanova, 1978). However, unlike *Parvileguminophyllum penzhinense* sp. nov., it possesses an almost round leaf lamina with a long petiole, brochidodromous loops located closer to the leaf margin and ramified-percurrent, rather than ramified-reticulate, tertiary venation. The new species differs from *Leguminosites ovalifolius* Heer from the upper Albian of Kazakhstan (Vakhrameev, 1952) in possessing brochidodromous, not craspedodromous, venation. *Parvileguminophyllum penzhinense* sp. nov. differs from *L. karatscheensis* Vakhrameev from the middle Albian of Kazakhstan (Vakhrameev, 1952) in having a larger number of secondary veins and brochidodromous venation.

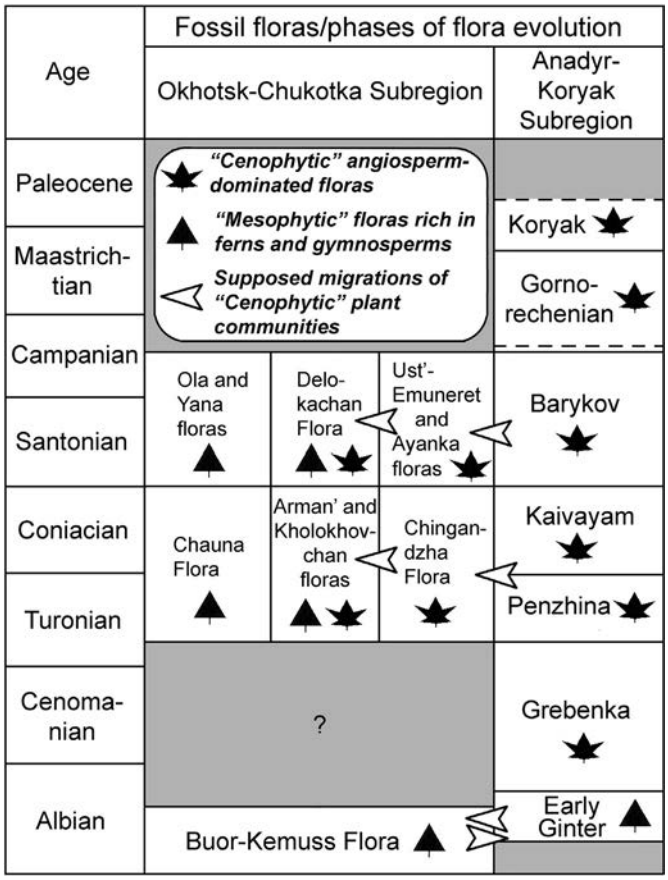
Golovneva and Nosova (2012) described pinnately compound leaves with entire-margined leaflets possessing festooned-brochidodromous venation as *Liriodendropsis simplex* (Newberry) Newberry from the upper Albian–Cenomanian of Western Siberia. However, this species differs from *Parvileguminophyllum penzhinense* sp. nov. in having lobed (deeply notched) leaflet apices and longer petiolules.

6. Correlation and age of the Kholokhovchan Flora

The Kholokhovchan Flora is obviously of a "Cenophytic" aspect due to the predominance of angiosperms together with some ferns and conifers typical of the Late Cretaceous floras of Northeastern Asia. In order to determine the age of the Kholokhovchan Flora, which comes from the purely non-marine volcanogenic-terrigenous deposits, it needs to be compared with the securely dated Cretaceous floras of the AKSR. The most similar to the Kholokhovchan Flora are the Grebenka, Penzhina and Kaivayam floras.

The **Grebenka Flora** (Table 1) comes from the Krivorechenskaya Formation (Shczepetov et al., 1992). Deposits of this formation are widespread in the middle reaches of the Anadyr' River. The upper plant-bearing part of this formation, which conformably overlies a lower, predominantly conglomerate, part is composed of conglomerates, gravelites, sandstones, tuffstones, siltstones, and tuffaceous siltstones representing continental plant-rich deposits and marine beds, in which fossil mollusks have been found (Shczepetov et al., 1992). Based on these fossils, the age of the plant-bearing beds was determined as latest Albian–early Turonian. The $^{40}Ar/^{39}Ar$ dating of two samples of tuff from the Yelisseev outcrop gave an age of 98.6 Ma (Spicer et al., 2002). Since the detailed study of the sedimentology suggested high deposition rates, most of the plant-bearing deposits were likely to be of early Cenomanian age (Spicer et al., 2002). The Grebenka Flora is very diverse, consisting of at least 180–200 taxa (Shczepetov et al., 1992; Filippova and Abramova, 1993; Herman, 2011a, 2013; Alekseev et al., 2014), a considerable part of which has not been studied in detail from a systematic point of view. The Grebenka Flora is dominated by angiosperms. Ferns and conifers are of approximately equal diversity, although fern impressions prevail in many local assemblages. Common among ferns are the genera *Gleichenites*, *Birisia*, *Coniopteris*, *Hausmannia*, *Cladophlebis* etc.; *Birisia* and *Coniopteris* remains are frequently very abundant in local assemblages. Caytonialeans (*Sagenopteris*) are relatively rare. Cycadophytes represented by leaves of *Cycadites*, *Nilssonia* (often forming accumulations of remains or "leaf mats"), *Taeniopteris* and by short leafy shoots of *Nilssoniocladus* (Spicer and Herman, 1996) are common components. Ginkgoaleans include the genera *Ginkgo*, *Baiera*, and *Sphenobaiera*, the czekanowskialeans are represented by the genus *Phoenicopsis*, finds of which are extremely scarce. Conifers are represented both by the relatively ancient, typically Early Cretaceous, genera (*Podozamites*, "*Athrotaxopsis*", *Pagiophyllum*, *Pityophyllum*) and more advanced plants (*Sequoia*, *Cupressinocladus*, *Cryptomeria*); the most common and frequently occurring species are "*Cephalotaxopsis*" *intermedia (=Elatocladus intermedius)*, *Araucarites anadyrensis* Kryshtofovich, *Elatocladus smittiana* and, in some localities, *Sequoia* ex gr. *reichenbachii* (Geinitz) Heer and *Pagiophyllum triangulare* Prynada (Shczepetov et al., 1992). A characteristic element among angiosperms in the Grebenka Flora is the genus *Menispermites*, which is represented by at least several species (Golovneva et al., 2015). Platanoids constitute a significant, although not dominant, component of the Grebenka Flora. Their diversity is not very high: the majority of them belong to the genus *Ettingshausenia*, associated with fertile organs of *Anadyricarpa* (Maslova and Herman, 2004), while the remains of peltate leaves of *Pseudoprotophyllum* are sporadic. The presence of the genera *Protophyllum* and *Credneria* is doubtful. Records of the genus *Trochodendroides* are extremely uncommon. It is noteworthy that the angiosperms of the Grebenka Flora are represented by a considerable number of entire-margined (*Magnoliaephyllum*, *Myrtophyllum*, *Scheffleraephyllum*, *Dalbergites*, *Soninia*, etc.), lobed (*Ettingshausenia*, *Cissites*, *Menispermites*, *Araliaephyllum*, leaflets of *Dalembia*), and compound (*Scheffleraephyllum*, *Dalembia*, *Sorbites*) leaves. A large number of the entire-margined angiosperms in the Grebenka Flora probably reflects a relatively warm palaeoclimate experienced by its plants (Spicer et al., 2002; Spicer and Herman, 2010).

Table 1
Correlation of the Albian–Paleocene floras and florogenesis in the Okhotsk-Chukotka and Anadyr-Koryak subregions, Northeastern Russia (modified from: Herman, 2013).



Lebedev (1987) pointed out that the Kholokhovchan Flora is similar to the Grebenka Flora. Indeed, these floras are characterised by a significant, although not dominant, role of platanoid plants and by a high diversity of *Menispermites*. Common plants of these floras are *Thallites* ex gr. *jimboi*, *Birisia ochotica*, *Asplenium dicksonianum*, *A. rigidum*, *Ginkgo* ex gr. *adiantoides*, *Phoenicopsis* ex gr. *angustifolia*, "*Cephalotaxopsis*" *intermedia (=Elatocladus intermedius)*, *Pityophyllum* ex gr. *nordenskioldii*, *P.* ex gr. *staratschinii*, *Elatocladus smittiana*, *Araliaephyllum medium*, *Menispermites marcovoensis*, *M.* cf. *sibiricus*, *Arthollia* cf. *pacifica*, *Ettingshausenia louravetlanica*, possibly *Birisia* (?) *oerstedtii* and *Schefflerаephyllum* (?) *venustum*, as well as the genera *Gleichenites*, *Sphenobaiera*, *Sequoia*, *Parataxodium*, *Pityospermum*, *Cocculophyllum*, *Cissites*, *Pseudoprotophyllum*, *Dalembia* and possibly *Celastrophyllum*. Among these plants, *Araliaephyllum medium* and *Menispermites marcovoensis* are known only from the Grebenka and Kholokhovchan floras.

However, a large number of fossil plants typical for the Grebenka Flora have not been found in the Kholokhovchan Flora. The Grebenka Flora differs in possessing more abundant and diverse ferns, cycadophytes, ginkgoaleans and conifers as well as the presence of rare caytonialeans *Sagenopteris*, numerous ferns *Birisia jelisejevii* (Kryshtofovich) Philippova, *Coniopteris anadyrensis* Philippova, *Coniopteris (Birisia ?) grebencaensis* Philippova, *Arctopteris penzhinensis* E. Lebedev, *Hausmannia bipartita* Samylina et Shczepetov, and several representatives of *Cladophlebis*, the conifers *Araucarites anadyrensis* Kryshtofovich, *Pagiophyllum triangulare* Prynada, *Sequoia fastigiata* (Sternberg) Heer, *S.* cf. *minuta* Sveshnikova, and *S.* ex gr. *reichenbachii* (Geinitz) Heer and angiosperms *Anadyricarpa altingiosimila* N. Maslova et Herman, *Sorbites asiatica* Philippova, *Myrtophyllum acuminata* (Philippova) Herman, *Cissites orbiculatus* Philippova, *Dalembia vachrameevii* E. Lebedev et Herman, *Grebenkia anadyrensis* (Kryshtofovich) E. Lebedev, and *Soninia integerrima* Herman et Shczepetov.

The **Penzhina Flora** (Table 1) comes from the lower part of the Valizhgen Formation in northwest Kamchatka and from the lower plant-bearing layer of the same formation on the Yelistratov Peninsula (Herman and Lebedev, 1991; Herman, 2011a, 2013). The plant-bearing beds are securely dated as late Turonian due to their correlation with marine biostratigraphy (Pergament, 1961): they are replaced laterally by beds of the upper Turonian part of the Pel-El Formation of marine origin containing stratigraphically important inoceramid remains and conformably overlain by continental deposits containing the Coniacian Kaivayam Flora (see below). In the Penzhina Flora angiosperms make up a little more than a half of all plant species. Dominant among them are species of the large-leaved platanoid genera *Ettingshausenia*, *Arthollia* and *Paraprotophyllum*. The abundance of *Menispermites* leaves is somewhat lower in the Penzhina Flora than in Grebenka Flora, although they are still common components. A representative of the genus *Compositiphyllum* is a characteristic component of the Penzhina floral assemblages. Plants with leaves belonging to the genus *Trochodendroides* make up significant part of the angiosperm flora. Ferns are not very abundant nor are they diverse. Ginkgoaleans are represented solely by *Ginkgo* ex gr. *adiantoides*. The ginkgoalean genus *Sphenobaiera*, caytonialeans, leptostrobaleans (*Phoenicopsis*), and cycadophytes are unknown in the Penzhina

Flora. "*Cephalotaxopsis*" and *Sequoia tenuifolia* (Schmalhausen) Sveshnikova et Budantsev are the most frequent conifer taxa. The prevalence of large-leaved platanoids, the appearance of *Protophyllocladus*, *Metasequoia*, *Paraprotophyllum*, *Viburniphyllum whymperi* (Heer) Herman, *Trochodendroides budantsevii* Golovneva, and a considerably higher abundance of *Trochodendroides* are the main features distinguishing the Penzhina Flora from the older Grebenka Flora.

The plant fossils found in the upper part of the Valizhgen Formation in northwest Kamchatka constitute the **Kaivayam Flora** (Herman and Lebedev, 1991; Herman, 2011a, 2013; Table 1). This flora is also known from the upper plant-bearing layer of the same formation on the Yelistratov Peninsula. The Coniacian age of the terrestrial plant-bearing deposits is substantiated by their relations with marine facies: the terrestrial units are replaced laterally by beds of the upper (Coniacian) part of the marine Pel-El Formation and conformably overlain by Santonian layers of the Bystrinskaya Formation. Both formations contain stratigraphically important inoceramid remains (Pergament, 1961). The early Coniacian Tylpegyrgynai Flora from the Poperechnaya and Tylpegyrgynai formations of the Pekulnei Ridge also belongs to the Kaivayam phase of floral evolution. Plant-bearing beds of this flora are securely dated due to their correlation with formations containing stratigraphically important inoceramid remains (Terekhova and Filippova, 1983, 1984; Craggs, 2005; Filippova, 2010). The Kaivayam Flora (Herman and Lebedev, 1991; Herman, 2011a, 2013) is characterised by a high diversity of fossil plants (approximately 45 species). The diversity of ferns, which are dominated by the *Ruffordia* and *Arctopteris* species, is generally low, and cycadophytes are missing. The genus *Ginkgo* is represented only by the species *Ginkgo* ex gr. *adiantoides*, the remains of which are abundant in some assemblages. Conifers are mostly represented by *Sequoia* and "*Cephalotaxopsis*", which are usually accompanied by *Elatocladus*, *Metasequoia*, *Glyptostrobus* and *Cupressinocladus* species. Angiosperms constitute at least half of the total species diversity. The remains of large-leaved platanoids, in particular the genera *Paraprotophyllum* and *Arthollia*, play the dominant role, although species of the genus *Ettingshausenia* are relatively rare. The genera *Trochodendroides* and *Araliaephyllum* are abundant and diverse, while *Dalembia* is represented by two species: *D. pergamentii* and *D. krassilovii* Herman et E. Lebedev (Lebedev and Herman, 1989). The share of *Menispermites* and *Celastrophyllum* is insignificant and representatives of the genera *Ternstroemites*, *Celastrinites*, and *Grewiopsis* are also rare. In addition, the flora includes entire-margined leaves of *Magnoliaephyllum*. The characteristic element of the Kaivayam flora is *Chachlovia dombeyopsoida*.

The Kholokhovchan Flora exhibits a marked similarity to the Penzhina and Kaivayam floras. The most characteristic feature of these floras is a predominance of angiosperms, with platanoids (*Arthollia*, *Ettingshausenia*, *Pseudoprotophyllum*, etc.) being numerous and diverse. Kholokhovchan, Penzhina and Kaivayam floras have the following plant species in common: *Thallites* ex gr. *jimboi*, *Sphenopteris* sp. cf. *Birisia* (?) *oerstedtii*, *Ginkgo* ex gr. *adiantoides*, "*Cephalotaxopsis*" *intermedia*, *Pityophyllum* ex gr. *nordenskioldii*, *Elatocladus* cf. *smittiana*, *Menispermites* cf. *sibiricus*, *Arthollia* cf. *pacifica*, *Pseudoprotophyllum boreale*, *Dalembia pergamentii* and *Chachlovia dombeyopsoida*. *C. dombeyopsoida* was described in the Kaivayam Flora (Herman and Lebedev, 1991; Alekseev et al., 2014) and is now known only in this flora and the Kholokhovchan Flora. A fragment of a lobed leaf assigned to *Cissites* cf. *pekulneensis* posseses a close similarity to this species known from the early Coniacian Tylpegyrgynai Flora (Filippova, 1991) as well as from the Maastrichtian Koryak Formation (Moiseeva, 2005, 2012) and Maastrichtian–Danian Rarytkin Formation (Golovneva and Herman, 1992) of Northeastern Asia.

Among the Cretaceous floras of the OCSR (and the Okhoksk-Chukotka volcanogenic belt), the Kholokhovchan Flora is most similar to the **Arman Flora** (Table 1). The Arman Flora comes from volcanic–sedimentary deposits of the Arman Formation in the Arman River basin and from volcanic and volcanic–sedimentary rocks of the Nel'kandzha–Khasyn interfluve. It includes 73 fossil plant species comprising liverworts, horsetails, ferns, caytonealeans, cycadaleans, ginkgoaleans, czekanowskialeans, conifers, gymnosperms *incertae sedis*, and angiosperms (Samylina, 1974, 1976, 1988; Filippova and Abramova, 1993; Herman, 2011a, 2011b, 2013; Herman et al., 2012). The Arman Flora appears to be of Turonian–Coniacian age, as it is close to the Turonian Penzhina and Coniacian Kaivayam floras from the northwest Kamchatka and to the early Coniacian Tylpegyrgynai Flora of the Pekulnei Ridge, AKSR. Importantly, these three floras are reliably dated by correlation of plant-bearing deposits with marine beds (see above). This dating is corroborated by isotopic ($^{40}Ar/^{39}Ar$ and U–Pb SHRIMP) age determination for the plant-bearing layers (Akinin and Miller, 2011). As Samylina (1974, 1976, 1988) pointed out, a peculiar combination of Early and Late Cretaceous taxa is characteristic of the Arman Flora. Plant remains most frequently occurring in the fossil assemblages are *Birisia ochotica* Samylina and conifers of genera *Podozamites*, *Elatocladus*, and *Sequoia*. It is also remarkable that dominants of the Arman Flora include typical Early Cretaceous forms (several *Podozamites* species and *Birisia ochotica* which is close to the Early Cretaceous *B. alata* (Prynada) Samylina) associated with plant remains widespread in the Late Cretaceous floras (*Elatocladus* and *Sequoia*). Among the other Arman taxa there are a number of relict Early Cretaceous forms known from Albian deposits of Northeastern Asia and North America. These are *Ginkgo* ex gr. *sibirica* Heer, *Phoenicopsis* ex gr. *angustifolia*, *Sagenopteris variabilis* (Velenovský) Velenovský, *Hausmannia*, *Onychiopsis*, *Pterophyllum*, *Baiera*, *Sphenobaiera*, *Pagiophyllum*, and others. However, the Arman Flora is dominated by plant fossils typical of Late Cretaceous floras. In addition to conifers *Elatocladus* and *Sequoia* mentioned above, there are *Taxodium* and *Libocedrus* species and a large group of angiosperms. Especially remarkable among the angiosperms are lobed leaves *Araliaephyllum*, platanoids *Arthollia*, *Paraprotophyllum*, *Ettingshausenia* and *Pseudoprotophyllum*, two or three *Trochodendroides* species, compound leaves *Schefferaephyllum*, *Parvileguminosites* and *Dalembia*, and remains of presumably aquatic plants *Brasenites*.

Both the Kholokhovchan Flora and Arman Flora possess numerous and diverse angiosperms, and particularly the platanoids *Arthollia*, *Ettingshausenia* and *Pseudoprotophyllum*. These floras share a large number of common plant species: *Thallites* sp., *Birisia ochotica*, *Asplenium dicksonianum*, *Ginkgo* ex gr. *adiantoides*, *Phoenicopsis* ex gr. *angustifolia*, *Elatocladus intermedius*, *Elatocladus* cf. *smittiana*, *Cissites* cf. *cordatus*, *Menispermites marcovoensis*, *M.* cf. *sibiricus*, *Terechovia* cf. *philippovae*, *Arthollia* cf. *pacifica*, *Ettingshausenia louravetlanica*, *Pseudoprotophyllum boreale*, *Dalembia pergamentii*, possible *Schefferaephyllum* (?) *venustum* and genera: *Sphenobaiera*, *Pterophyllum*, *Pityophyllum*, *Pityospermum*, *Araliaephyllum*, *Parvileguminophyllum*, and possible *Celastrophyllum*. Among these taxa, *Birisia ochotica* predominates in Kholokhovchan and Arman floras and *Cissites* cf. *cordatus* and *Terechovia* cf. *philippovae* are not known in any other floras of Northeastern Asia.

The Kholokhovchan Flora is less similar with the younger Santonian–Campanian Barykov, Ust'-Emuneret, Ayanka and Delokachan floras of the AKSR and OCSR (Table 1).

Therefore, our study shows that the Kholokhovchan Flora is most similar to the Arman Flora of the Okhotsk-Chukotka volcanogenic belt; it also exhibits a certain similarity with the Grebenka, Penzhina and Kaivayam floras of the AKSR. Hence the Kholokhovchan Flora should be dated as the Turonian–Coniacian.

Both the Kholokhovchan Flora and Arman Flora, that populated the volcanic uplands, plateaux and intermontane valleys of the Okhotsk-Chukotka volcanogenic belt, are characterised by a peculiar mixture of the relatively ancient "Mesophytic" plants with the typical Late Cretaceous "Cenophytic" taxa, in particular diverse angiosperms and advanced conifers. Moreover, several definitely Late Cretaceous floras of the OCSR (Ola, Yana and Chauna floras – Table 1) are of a purely "Mesophytic" aspect and dominated by ferns and gymnosperms, but contain extremely rare advanced angiosperm taxa. In contrast, such a peculiarity is not observed among the Late Cretaceous floras of the AKSR which existed within the coastal plains and lowlands: all of these habitats were typically dominated by the "Cenophytic" angiosperms-rich plant communities (Table 1).

The observed phenomenon can be explained by the early angiosperm ability to colonise disturbed coastal plain environments (Retallack and Dilcher, 1981, 1986). Probably the new plant communities dominated by the advanced angiosperms and conifers initially populated unstable habitats in coastal plains and lowlands of Northeastern Asia and Alaska. During the Late Cretaceous, the "Cenophytic" plant communities migrated along river valleys and other disturbed habitats into the interior of Asia, eventually occupying volcanogenic uplands and intracontinental basins, in places replacing the "Mesophytic" communities dominated by ferns and gymnosperms that existed there (Herman, 2002, 2013). Perhaps the scenario of a gradual penetration of new plant communities dominated by angiosperms into older floras is reflected in the taxonomic composition of the Kholokhovchan and Arman floras.

7. Concluding remarks

The Kholokhovchan Flora (42 fossil plant species) from the volcanogenic – terrigenous deposits in the interfluve of the Penzhina and Oklan rivers is one of the oldest Late Cretaceous floras of the Okhotsk–Chukotka volcanogenic belt. This flora is of Turonian–Coniacian age based on its close similarity to the securely dated Penzhina and the Kaivayam floras of the AKSR as well as to the Arman Flora of the OCSR. Until now, no analogue of the late Albian–early Turonian Grebenka Flora of the AKSR has been found within the Okhotsk–Chukotka volcanogenic belt (Table 1).

The Kholokhovchan Flora, as well as the Arman Flora, is characterised by a peculiar mixture of relatively ancient plants and typical Late Cretaceous taxa. These floras populated the volcanic uplands, plateaux and intermontane valleys of the Okhotsk-Chukotka volcanogenic belt. The composition of the Kholokhovchan and Arman floras probably reflects invasion of angiosperm-rich "Cenophytic" plant communities into the interior of Asia and gradual replacement of the pre-existing fern and gymnosperm dominated "Mesophytic" communities.

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