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The Role of Transberingian Plant Migrations
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Abstract—For the first time, the Late Sagwon Flora is described from the upper beds of the Prince Creek Formation (Upper Paleocene) at the Sagavanirktok River (northern Alaska Peninsula). The flora is dominated by the angiosperm *Tiliaephyllum brooksense* Moiseeva et Herman sp. nov. and conifer *Metasequoia occidentalis* (Newb.) Chaney. The Late Sagwon Flora is most similar to the Danian or Danian-Selandian flora from the middle part of the Upper Tsagayan Subformation (Amur Region) and lower part of the Wuyun Formation (Heilongjiang Province, China). This similarity allows us to hypothesize that the genus *Tiliaephyllum*, which dominated in the Late Tsagayan Flora, migrated via the Bering Land Bridge from southern paleolatitudes of the Far East to high latitudes of the Arctic Pacific, due to the progressively warming climate of the Paleocene. Additional new angiosperm species are described from the Late Sagwon Flora: *Archeampelos mullii* Moiseeva et Herman sp. nov., *Tiliaephyllum brooksense* Moiseeva et Herman sp. nov., and *Dicotylodrya sagwonicum* Moiseeva et Herman sp. nov.

Key words: fossil flora, angiosperms, paleoclimate, plant migrations, Paleocene, northern Alaska Peninsula.

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INTRODUCTION

In summer 2005, the authors and A. Ahlberg (Lund University, Sweden) and D. W. Jolley (University of Aberdeen, UK) collected a fossil flora in the upper part of the Prince Creek Formation in the Sagavanirktok River basin, North Slope of Alaska. The flora is dominated by leaves of *Tiliaephyllum brooksense* Moiseeva et Herman sp. nov., a species that is very similar to *T. tsagajanicum* (Krysht. et Baik.) Krassil., known only from the Danian or Danian-Selandian of the Amur Region of the Russian Far East and northern China. This paper considers the taxonomic composition of the flora, its possible origin, and describes new angiosperm taxa found in the flora.

In the Sagavanirktok River basin (Fig. 1), Upper Cretaceous deposits of the Schrader Bluff and Seabee formations of the Colville Group are exposed. They are overlain and, in part, laterally substituted by terrigenous and coal-bearing deposits of the Prince Creek Formation of the Colville Group (Late Cretaceous–Paleocene). These in turn are overlain by sandstones and conglomerates belonging to the basal Sagwon Member of the Sagavanirktok Formation, dated to the Late Paleocene–Miocene (Mull and Harris, 1989; Mull et al., 2003). In the region under study, the upper part of the Prince Creek Formation is best exposed in the Sagwon Bluffs section, an outcrop on the left bank of the Sagavanirktok River (Fig. 1), and is composed of intercalating conglomerates, weakly cemented sandstones, siltstones, coaly shales, and coals (in total up to six or seven more or less continuous seams) reportedly up to 7 m (Mull et al., 2003). These deposits are interpreted as having accumulated in a coastal fluvial and lacustrine-dominated alluvial lowland. The plant remains considered in the present paper were collected from poorly exposed sandstones and siltstones in the middle part of the section, between coal beds nos. 3 and 4 (numeration from the bottom) in the northern part of the outcrop (Fig. 1). This fossil flora was named Late Sagwon Flora. The Early Sagwon Flora is known from the lower part of the section, below coal bed no. 3 (Fig. 1), which was named Sagwon Flora before the younger floristic assemblage was found (Spicer et al., 1994; Herman et al., 2004; Herman and Moiseeva, 2006). The total thickness of the plant-bearing member in the Sagwon Bluffs section reaches 100–115 m. It is dated to the Late Paleocene on the basis of palynological data (Frederiksen et al., 1996; Jolley et al., 2006).
The Late Sagwon Flora is characterized by a low taxonomic diversity, which is, at least in part, related to limited outcropping of its plant-bearing layers and distinct domination of angiosperm leaves of *Tiliaephyllum brooksiense* sp. nov. (Figs. 2a–2c, Pl. 22, figs. 1–7). Leafy shoots of *Metasequoia occidentalis* (Newb.) Chaney are also abundant (Fig. 2d, Pl. 23, figs. 9, 11). Male cones of the *Taxodiaceae* occur (Pl. 23, fig. 15) as well as shoots of *Taxodium* (?) and the cupressaceous *Mesocyparis* (?) (Pl. 23, figs. 12–14). Apart from *Tiliaephyllum brooksiense* sp. nov., angiosperms are represented by solitary leaf imprints of *Trochodendroides ex gr. arctica* (Heer) Berry (Pl. 22, fig. 8), *Archeampelos multii* Moiseeva et Herman, sp. nov. (Figs. 2e, 2f, Pl. 23, figs. 1, 2), and *Dicotylophyllum sagwonicum* Moiseeva et Herman, sp. nov. (Figs. 4a, 4b, Pl. 23, figs. 3–8). The collection also contains fructifications and scales of uncertain systematic position (Pl. 22, figs. 9, 10). The taxonomic composition of the Late Sagwon Flora and the presence in the section of thick coal beds testify to the existence of a temperate humid climate.

The Early Sagwon Flora, which preceded the flora under consideration, comes from the bottom of the same plant-bearing member in the Sagwon Bluffs section (Fig. 1). It is dated to the Danian–Selandian by palynological and macrofloristic data (Herman and Moiseeva, 2006; Jolley et al., 2006). This flora includes about 30 species of fossil plants (Spicer et al., 1994; Herman et al., 2004; Herman and Moiseeva, 2006). *Tiliaephyllum brooksiense* sp. nov., prevailing in the Late Sagwon Flora, was not found in the earlier flora, which is dominated by polymorphous large leaves of *Corylitites beringianus* (Krysh.) Moiseeva. The two floras are similar in exhibiting abundant *Metasequoia occidentalis* and the presence of *Trochodendroides ex gr. arctica* (Heer) Berry, genera *Archeampelos* McIver et Basinger and probably, *Mesocyparis* McIver and Basinger. The listed common taxa have wide geographic and stratigraphic ranges. In general, the floras differ both in the systematic composition and main dominants.

A fossil flora that is close in age to the flora under consideration is known in the southwest of the Saskatchewan Province in Canada, Ravenscrag Formation (McIver and Basinger, 1993). It is dated to the early half of the Paleocene by palynological and macroinvertebrate and vertebrate data. The Late Sagwon and Ravenscrag floras are similar in the presence of species of wide geographic range *Metasequoia occidentalis* (the species is rare in the Canadian flora by contrast to the Alaska flora) and the genera *Mesocyparis, Trochodendroides* Berry, and *Archeampelos* (two latter genera are represented in the Ravenscrag flora by different species). Other members of the floras do not coincide. The Late Sagwon Flora also has little in common with the Paleocene flora of the Paskapoo Formation in the Alberta Province of Canada (Bell, 1949): the similarities consist of a few common plant taxa of wide stratigraphic and geographic ranges, such as *Metasequoia occidentalis, Mesocyparis* (?) and *Trochodendroides arctica*.

In spite of its poor taxonomic composition, the Late Sagwon Flora of the northern Alaska Peninsula shows the most similarity to the Danian or Danian–Selandian flora of the Amur Region and northern China. This plant assemblage was found in the middle part of the Upper Tsagayan Subformation in the Amur River Region and the lower part of the Wuyun Subformation of the Heilongjiang Province of China (Kryshtofovich et al., 2001), or Danian–Selandian (Kezina, 2005). It has a low taxonomic diversity: three species, *Zizyphoides flabella* (Newb.) Crane, Manchester et Dilcher, *Trochodendroides arctica*, and *Tiliaephyllum tsagajanicum* dominate in the localities, reaching 50–75% of the total number of specimens within individual assemblages. *Metasequoia occidentalis, Ettingshausenia raynoldsii* (Newb.) Moiseeva, and *Archeampelos acerifolia* (Newb.) McIver et Basinger are also prominent in most of these assemblages. *Ginkgo ex gr. adiantoides* (Ung.) Heer, *Nyssa bureica* Krassilov, *Nordensiokidia borealis* Heer, and *Nyssidium arcticum* (Heer) Iljinsk. are prominent in some assemblages. Ferns of *Osmunda* sp. are solitary. Among conifers, rare *Picea* sp., *Pseudolarix* sp., *Glyptostrobus* sp., *Sequoia* sp., *Taxodium* sp., and cupressaceous *Ditaxocladius* sp. have been recovered. The angiosperms *Cornus* sp., *Juglandiphyllites* sp., and a species of *Dipteronia* Oliver were also found.

The Late Sagwon Flora is also similar to the Late Tsagayan assemblage, primarily by the domination of *Tiliaephyllum Newberry* and *Metasequoia occidentalis*. The Alaska species *Tiliaephyllum brooksiense* sp. nov. resembles very closely *T. tsagajanicum*, which is only known, apart from the Late Tsagayan assemblage, from the Paleocene floristic assemblage of the Kivda beds of the Tsagayan Formation of the Amur Region (Akmetiev et al., 2002). Because of the similarity between the northern Alaska and Amur species of *Tiliaephyllum*, we first assigned the former species to *T. tsagajanicum* (Herman and Moiseeva, 2006).
2006), but later thorough examination of the leaf imprints from the Late Sagwon Flora resulted in the description of a new species. The two floras are also linked by having common taxa: *Trochodendroides ex gr. arctica* and the genera *Taxodium* Richard and *Archeampelos*.

The similarity between the two floras allows us to hypothesize that the genus *Tiliaephyllum*, which dominated in the Late Tsagayan Flora, migrated via the Bering Land Bridge from southern paleolatitudes of the Far East to high latitudes of the Arctic Pacific, due to the progressively warming climate of the Paleocene (Moiseeva, 2005a; Herman and Moiseeva, 2006). This warming episode started near the end of the Maastrichtian or beginning of the Paleocene and reached the maximum at the Paleocene/Eocene boundary or in the Early Eocene. In the northern Alaska Peninsula, *Tiliaephyllum brooksense* sp. nov. substituted *Corylites beringianus* (Krysht.) Moiseeva, which dominated in the older Early Sagwon Flora. Consequently, the Late Paleocene Late Sagwon Flora of the northern Alaska Peninsula was formed at the expense of the evolution of the plants of the preceding flora and Transberingian migrations of plants from Eastern Asia, which became possible due to the climatic warming in northern Alaska.

**MATERIAL**

Collection GIN, no. 4886 is kept at the Geological Institute of the Russian Academy of Sciences. New angiosperm species are described below.

**SYSTEMATIC PALEOBOTANY**

Division Magnoliophyta  
Class Magnoliopsida  
**Genus Tiliaephyllum Newberry, 1895**

*Tiliaephyllum brooksense* Moiseeva et Herman, sp. nov.

Plate 22, figs. 1–7

**Etymology.** From Brooks Range, northern Alaska.

**Holotype.** GIN, no. 4886/21a-1, 4886/21b-1 (counterpart); leaf imprint; Sagavanirktok River, northern Alaska Peninsula; upper part of the Prince Creek Formation; Upper Paleocene (Pl. 22, fig. 2; Fig. 2a).

**Diagnosis.** Leaves simple, entire, medium-sized to large. Leaf lamina elliptic-ovate or broadly ovate. Leaf base asymmetric, typically deeply cordate or, more rarely, emarginate. Leaf apex acuminate to attenuate. Leaf margin unequally toothed or double-serrate. Teeth from small to large, acute, triangular, symmetric, or, more rarely, narrow asymmetric and oriented apically. Venation pinnate and craspedodromous. Secondary veins 10–13 pairs, opposite or, more rarely, alternate. The third basal pair of secondary veins the strongest and copiously branched.

**Description** (Figs. 2a–2c). The leaves are medium-sized or large, 5–12 cm long and 3.5–10 cm wide, simple, entire-margined, oval-ovate or broadly ovate, the maximum width is located in the middle of the leaf or below the middle. The leaf base is asymmetrical, deeply cordate or, more rarely, emarginate; the apex is acute and, as a rule, acuminate. The petiole is relatively thick, its length is about one third of the leaf lamina length. The leaf margin is unequally toothed or double-serrate. The teeth from small to large, up to 2.5 mm high and 3–4 mm wide). Usually, they are acute, triangular, with straight or slightly concave sides, symmetrical, or, more rarely, narrower, with a concave apical side, and orientated towards the leaf apex. The notches between the teeth are mostly acute or, more rarely, rounded.

The venation is pinnate and craspedodromous. The midrib is thick, straight, or slightly sinuous. There are ten to thirteen pairs of secondary veins. Most secondary veins are opposite, some are alternating. Three lower pairs of veins are connivent with their bases. The longest and most branched pair of veins is the third (from the bottom) pair: up to six basiscopic branchlets depart from this pair of veins. Below this pair, the first two pairs of secondary veins are situated; they are also quite frequently branched (with four or five branchlets), but much shorter. They depart from the midrib at a right angle; the lowest are slightly curved downwards, the angle of deviation of other secondary veins is 40–50°. The tertiary venation is scalariform or, more rarely, branched-scalariform.
Comparison. The new species differs from *Tiliaephyllum tsagajanicum* from the Upper Tsagayan Flora of the Amur Region (Krassilov, 1976) by the pattern of secondary venation in the lower part of the leaf. The third (from the bottom) pair of secondary veins is longest and most branched in *T. brooksense* sp. nov. Unlike this species, *T. tsagajanicum* has the longest lower pair of secondary veins departing immediately from the leaf base.

Remarks. The morphologically close species *Tiliaephyllum tsagajanicum* was first described by Kryshtofovich and Baikovskaya (1966) from the Tsagayan Flora of the Amur Region as *Tilia* L. The holotype of this species is shown in Fig. 3 (no photograph was published by Kryshtofovich and Baikovskaya). This specimen has smaller and more steeply apically oriented teeth than the majority of other specimens of *T. tsagajanicum*, that, in our opinion, accords with intraspecific variability.

The new species has something in common with leaves of *Corylites*, which were wide-spread in many temperate floras of Asia, Europe, and North America (Boulter and Kvaløk, 1989; Manchester and Guo, 1996; Akhmetiev and Golovneva, 1998; Moiseeva, 2005a; and others). *Tiliaephyllum brooksense* sp. nov. differs from most species of *Corylites* by wider and more rounded outlines of the leaf lamina and larger and usually symmetrical marginal triangular teeth. In addition, the new species is characterized by highly branched third (from the bottom) pair of secondary veins, whereas most species of *Corylites* usually have the lower or the second (from the bottom) pair of secondary veins most strongly developed. One of the distinguishing features of *Tiliaephyllum* is an acuminate leaf apex, which occurs much more rarely in *Corylites*.

Material. Twenty-two specimens from the type locality.

**Genus Archeampelos McIver et Basinger, 1993**

*Archeampelos mullii* Moiseeva et Herman, sp. nov.

Plate 23, figs. 1, 2

Etymology. In honor of the eminent geologist C.G. Mull.

Holotype. GIN, no. 4886/24c (part) and 4886/24a-3 (counterpart); leaf imprint, Sagavanirktok River, northern Alaska; upper part of the Prince Creek Formation, Upper Paleocene; Pl. 23, fig. 2, Fig. 2F (part) and Pl. 23, fig. 1, Fig. 2e (counterpart).

Diagnosis. Leaves simple, entire, medium-sized, length/width ratio about 1 : 1. Leaf lamina rounded and symmetric. Leaf base truncate or broadly rounded. Leaf apex obtuse or mucronate. Leaf margin irregularly undulate-crenate, entire at leaf base. Teeth rounded asymmetric, of variable prominence and spacing. Venation pinnate-palmate and craspedodromous. Midrib sinuous. Secondary veins three or four pairs, of which two basal pairs nearly as strong as midrib, ascending to upper third of leaf lamina, forking and ending in marginal teeth.

Description (Figs. 2e, 2f). The only specimen (part and counterpart) is moderate in size, about 6–7 cm long and 7–8 cm wide. The leaf is simple, entire, symmetrical, and rounded. The maximal width occurs in the middle of the leaf lamina. The length/width ratio is about 1 : 1. The leaf base is truncated or broadly rounded. The apex is broadly rounded or shortly acuminate. The leaf margin is basally entire and irregularly undulate-dentate in other regions. The teeth are low, rounded, variable in size, up to 3 mm long and 6 mm wide, asymmetrical. The notches between the teeth are usually rounded or, occasionally, acute. The venation is palmate-pinnate and craspedodromous. The midrib is sinuous. Three or four pairs of secondary veins are alternating from the midrib at an angle of about 40°. Each secondary vein also produces several branchlets. Two lower pairs of secondary veins are nearly as thick as the midrib. They depart from the leaf base, fork in the middle area of the leaf lamina, and end in marginal teeth. The tertiary venation is relatively loose, branched-scalariform, and orthogonal-reticulate in places. The tertiary veins are sinuous and loop near the margin.

Comparison. The new species resembles by the leaf lamina outline, its base, and primary and secondary venation the type species of *Archeampelos, A. _cerifolia* from the Ravenscrag Formation (Paleocene) in
western Canada (McIver and Basinger, 1993). The new species differs by having an irregularly undulate-crenate margin, sinuous forking veins of the first order, and rare and less regular tertiary venation.

Remarks. Similar leaves were described from the Paleocene of western Canada as *Acer arcticum* Heer (Bell, 1949). *Archeampelos mullii* differs from this species by a sinuous midrib and the leaf margin, which has less distinct teeth in places transforming into an undulate margin.

Morphologically similar leaves from the Late Maastrichtian Koryak Flora of the Amaam Lagoon in northeastern Russia were assigned to *Cissites* Heer (Moiseeva, 2005b). *Archeampelos mullii* sp. nov. most resembles leaves of *Cissites hermani* Moiseeva, which also has forking lateral primary veins. Unlike these leaves, the leaves of the new species are characterized by a rounded outlines, absence of lobes, smaller marginal teeth, and rarer tertiary venation.

Material. Holotype.

**Genus Dicotylophyllum Saporta, 1894**

**Dicotylophyllum sagwonicum** Moiseeva et Herman, sp. nov.

Plate 23, figs. 3–8

Etymology. From the Sagwon Region, northern Alaska.

Holotype. GIN, nos. 4886/24a-1 (part) and 4886/24b-1 (counterpart); leaf imprint; Sagavanirktok River, northern Alaska; upper part of the Prince Creek Formation, Upper Paleocene; Pl. 23, figs. 4, 6, Fig. 4A (part); Pl. 23, figs. 5, 7, Fig. 4b (counterpart).


Description (Figs. 4a, 4b). The leaves are medium-sized, about 8–9 cm long and 4-4.5 cm wide, simple, entire-margined, elliptical or ovate. The maximum width is situated at the middle of the leaf lamina. The length/width ratio is about 2 : 1. The leaf base is narrowly or broadly cuneate and decurrent. The leaf apex is missing. The leaf margin is finely crenate, and at the base it is entire. The teeth are very small, about 0.5 mm long, rounded, slightly asymmetric, directed towards the leaf apex, without glands. The notches between the teeth are acute.

The venation is craspedodromous. There are six or seven pairs of secondary veins, which are slightly curved, deviating from the midrib at an angle of 25º–35º. Two lower pairs are basally connivent, the next pair of veins is situated at a greater distance, and the distance between veins gradually becomes smaller above. The second pair of the secondary veins from the base is longest and most branched (with five or six branchlets). The secondary veins are forked. Tertiary venation is scalariform or branched-scalariform. The tertiary veins are curved or, more rarely, straight, situated nearly perpendicular to the secondary veins. The venation of the forth order is in form of fine polygonal net.

Comparison and remarks. Leaves of the new genus are characterized by a combination of characters that do not occur in known angiosperm genera and are, therefore, assigned here to the artificial genus *Dicotylophyllum* of unknown taxonomic position.

In terms of the leaf lamina outline, venation pattern, and, in particular, the forked secondary veins, the new species resembles fossil members of *Viburnum* L. and *Viburniphyllum* Nathorst, described from several Cretaceous and Paleocene floras of the Northern Hemisphere (Ward, 1887; Brown, 1962; Herman and Lebedev, 1991; Golovneva, 1994). The new species differs from the majority of these species by having a considerably reduced number of secondary veins and finely crenate leaf margin.
Bell (1949) reported leaves of *Viburnum simile* Knowlton from Upper Cretaceous of western Alberta in Canada, which resemble leaves of the new species in terms of the secondary venation and the morphology of the lower part of the leaf. *Dicotylophyllum sagwonicum* differs from *V. simile* primarily in terms of the leaf margin. Additional species of *Viburnum* were also described from the deposits, including *V. asperum* Newberry, which resembles the new species by having the same finely dentate leaf margin (Bell, 1949). Our specimens differ from leaves of this species by exhibiting a more sparse secondary venation, narrowly cuneate base, and rounded teeth.

*Dicotylophyllum sagwonicum* has some characters in common with *Viburnum acutifolium* Golovn. from the Rarytkin Formation of the Koryak Upland (Golovneva, 1994). Both species have a small number of secondary veins and finely dentate leaf margin. The new species differs in terms of the form of the base, secondary veins departing at an acute angle, and much narrower teeth.

**Material.** Four specimens from the type locality.

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Fig. 1. Schematic geological map in the Sagwon area, Sagavanirktok River (after Mull and Harris, 1989, with changes): (A) occurrence of deposits; (B) stratigraphic column.

Fig. 2. Selected fossil plants of the Late Sagwon Flora: (a–c) *Tiliaephyllum brookense* Moiseeva et Herman, sp. nov.; (a) holotype GIN, no. 4886/21-a-1; (b) GIN, no. 4886/24a, b-2; (c) GIN, no. 4886/18; (d) *Metasequoia occidentalis* (Newberry) Chaney, GIN, no. 4886/14a-1; (e, f) *Archeampelos multii* Moiseeva et Herman, sp. nov.; (e) holotype GIN, no. 4886/24a-3 (counterpart); (f) holotype GIN, no. 4886/24c. Scale bar 1 cm.

Fig. 3. *Tiliaephyllum tsagajanicum* (Kryshtofovich et Baikovskaya) Krassilov, TsNIGR Museum (St. Petersburg), no. E 26-37, Bureya River, locality VI (Kryshotofich and Baikovskaya, 1966): (a) general view of a leaf without apex; (b) marginal teeth and venation. Scale bar 1 cm.

Fig. 4. *Dicotylophyllum sagwonicum* Moiseeva et Herman, sp. nov.: (a) holotype, GIN, no. 4886/24a-1; (b) holotype, GIN, no. 4886/24b-1 (counterpart). Scale bar 1 cm.
Figs. 1–7. *Tiliaephyllum brooksense* Moiseeva et Herman, sp. nov.: (1) GIN, no. 4886/21b-3, general view of the leaf, x1; (2) holotype GIN, no. 4886/21a-1, general view of the leaf, x1; (3) GIN, no. 4886/22, leaf margin details, x2; (4) GIN, no. 4886/24a, b-2, small petiolar leaf, x1; (5) GIN, no. 4886/16-1, rounded leaf, x1; (6) GIN, no. 4886/18, general view of the leaf, x1; (7) GIN, no. 4886/18, details of the leaf apex, x2.

Fig. 8. *Trochodendroides* sp., GIN, no. 4886/25, upper part of the leaf, x1.

Figs. 9, 10. Scales: (9) GIN, no. 4886/9, x2; (10) 4886/8b-2, x2.

All specimens come from Prince Creek Formation, Sagwon Bluffs outcrop, northern Alaska.

Explanation of Plate 23

Figs. 1 and 2. *Archeampelos mullii* Moiseeva et Herman, sp. nov.: (1) holotype GIN, no. 4886/24a-3 (counterpart), leaf apex, x1.5; (2) holotype, no. 4886/24c, general view of the leaf, x1.

Figs. 3–8. *Dicotylophyllum sagwonicum* Moiseeva et Herman, sp. nov.: (3) GIN, no. 4886/23b-1, leaf base, x1; (4) holotype GIN, no. 4886/24a-1, leaf margin details, x2.5; (5) holotype GIN, no. 4886/24b-1 (counterpart), details, x2.5; (6) holotype GIN, no. 4886/24a-1, general view of the leaf, x1; (7) holotype GIN, no. 4886/24b-1 (counterpart), general view of the leaf, x1; (8) GIN, no. 4886/23a-1, lower part of the leaf, x1.

Figs. 9–11. *Metasequoia occidentalis* (Newberry) Chaney: (9) GIN, no. 4886/14a-1, x1.5; (10) GIN, no. 4886/4, x1.5; (11) GIN, no. 4886/13-2, x1.5.

Figs. 12–14. *Mesocyparis* (?) sp.: (12) GIN, no. 4886/6, x1.5; (13) GIN, no. 4886/8a-1, x1.5; (14) GIN, no. 4886/7.

Fig. 15. Male cones of the Taxodiaceae, GIN, no. 4886/14b-2, x2.

All specimens come from Prince Creek Formation, Sagwon Bluffs outcrop, northern Alaska.
Figure 1.