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Article

Early Cretaceous *Keteleerioxylon* Wood in Songliao Basin, Northeast China, and Its Geographic and Environmental Implications

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Simple Summary: *Keteleeria* is a small group of Pinaceae, now only distributed in East and Southeast Asia, but it was widely distributed in Asia, Europe, and North America in the northern hemisphere during the late Mesozoic and Cenozoic. A new wood fossil of *Keteleeria*, *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov., has been described in the Early Cretaceous strata about 110 million years ago in Changchun, Jilin Province, Northeast China. The growth rings of wood contain rich paleoecological and paleoclimatic information. Quantitative analysis of growth rings revealed that the new species is evergreen with leaf longevity of 1-3 years. The growth rings of *Keteleerioxylon changchunense* indicate the climate seasonality was pronounced in the Songliao Basin during the Early Cretaceous. Reviewing *Keteleeria* and closely related fossil taxa, we depict the origin and migration route of *Keteleeria*. The group of *Keteleeria* might have originated in Northeast China no later than the Late Jurassic. They migrated to the middle and high latitudes, as a result of global warming during the Cretaceous. While during the Paleogene and Neogene cooling time, the thermophilic *Keteleeria* became scarce, especially in the Quaternary Glaciation, and till now, they have been strictly restricted to the subtropical and tropical regions of East and Southeast Asia.

Abstract: The extant *Keteleeria* is endemic to East and Southeast Asia, while it is widely distributed in the northern hemisphere in Earth's history. In this paper, we reported a novel wood fossil of *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov. collected from the middle member of Yingcheng Formation, Yingcheng Coal Mine, Changchun City, Jilin Province, Northeast China. The quantitative growth-ring analyses of *K. changchunense* indicate that it was evergreen and its leaf longevity was 1-3 years, which is consistent with the foliar retention of extant *Keteleeria*. Its high ring markedness index (RMI) indicates that the climate seasonality was pronounced during the early Albian in Songliao Basin, Northeast China. The fossil records of *Keteleeria* and closely related taxa indicate that this group might originate in Northeast China, spread and migrated northward during the Cretaceous, gradually decreased in the Cenozoic, and so far only survives in East and Southeast Asia.

Keywords: *Keteleerioxylon changchunense* sp. nov.; *Keteleeria*; geography; environment; Cretaceous

1. Introduction

Keteleeria is firstly described as a genus in 1866, named by Carrière after a French nurseryman [1]. The extant *Keteleeria* Carrière includes ten species and two variants, which are endemic to East and Southeast Asia and only found in southern China (from Qinling Mountain to Hainan Island), northern Laos, and southern Vietnam (Figure 1). *Keteleeria* is confined to humid, moderately warm (subtropical) areas with relatively low mountains (200–3000 m above sea level) [2-5].

Fossil woods with similar anatomy to extant *Keteleeria* were first described in the Lower Cretaceous of Franz Josef Land after the name *Keteleerioxylon* [6]. The oldest representatives of *Keteleeria*-type (including *Keteleeria*, *Keteleerioxylon* and *Protopiceoxylon*) woods might be in the Late Jurassic [7], most fossils related to the *Keteleeria* were discovered from the Cretaceous and Cenozoic strata of Asia, Europe, and North America in the northern hemisphere (e. g. [8-10]).

In this study, we described two new silicified wood specimens belonging to the genus *Keteleerioxylon* from the Early Cretaceous sediments of Songliao Basin, Northeast China, and named *Keteleerioxylon changchunense* sp. nov. Quantitative growth-ring analyses were made to understand its ecological and climatic indications. Meanwhile, the geological and geographical distributions of *Keteleeria*-type fossils were summarized in order to depict the relationship between its migration and paleoclimate changes during the Cretaceous and Cenozoic times.

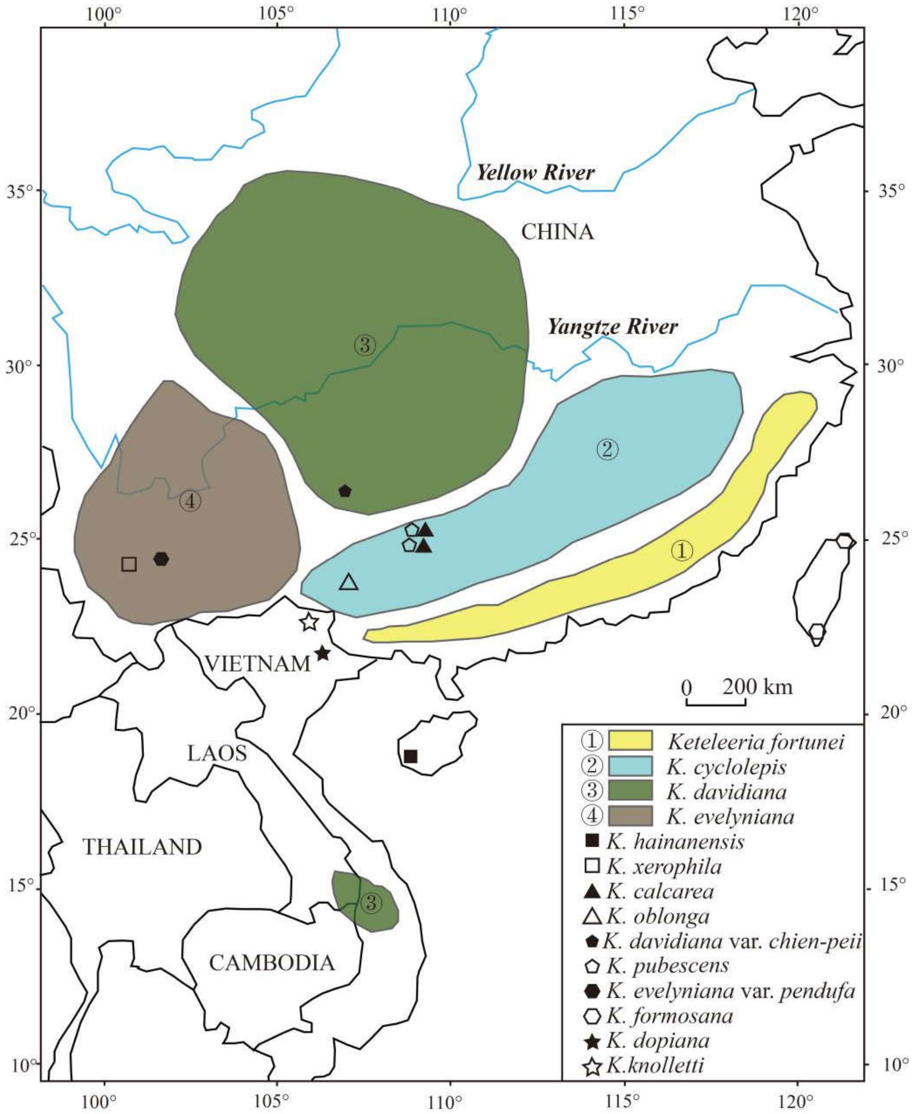

Figure 1. Distribution of the extant *Keteleeria* species and variants in the world (modified after [11])

2. Materials and Methods

2.1. Materials

Two silicified woods (registered nos. JLJY-01 and JLJY-02) were collected from the middle member of Yingcheng Formation, Yingcheng Coal Mine (44°9'47.53"N, 125°54'53.92"E), Changchun City, Jilin Province, Northeast China (Figure 2). The location is situated at the southeast margin of the Songliao Basin, the largest Mesozoic-Cenozoic terrestrial oil-bearing basin in Northeast Asia. The Lower Cretaceous succession in the Songliao Basin is composed of the Huoshiling, Shahezi, Yingcheng, and Denglouku formations in ascending order. The Yingcheng Formation dominated by medium-acid volcanic, volcaniclastic rocks and coal-bearing deposits can be divided into three members. The middle member is a set of sedimentary rocks with coal layers yielding spores and pollen, leaves, woods, and insects.

Detailed isotopic dating of volcanic rocks indicates that the middle member is late Aptian—early Albian in age, between 115.2±0.4 Ma and 110.0±2.0 Ma [12-14]. Based on palynological data, the Yingcheng Formation is Barremian—Albian in age [15-16]. Since the presence of *Tricolpites* sp. in the middle member of the Yingcheng Formation where the present silicified wood specimens were collected, the member is considered the earliest Albian in age [17].

The specimen JLJY-01 is 45.5 cm long with a maximum diameter of 13.5 cm. The specimen JLJY-02 is 29.4 cm long and 11.0—21.6 cm in diameter. They are gray to black in color with well-preserved secondary xylem. However, no pith and primary xylem are preserved.

All the specimens and slides are housed in the Research Center of Paleontology and Stratigraphy, Jilin University, Changchun.

Figure 2. Location of *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov. in the Yingcheng Coal Mine (red star), Changchun City, Jilin Province, Northeast China.

2.2. Methods

To investigate the anatomical characteristics of the silicified woods, microscopic slides of the transverse, radial and tangential sections were made in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan). The slides were observed using a microscope (Nikon AZ100M) with a digital camera

(Nikon DS-Ri2) in the International Center of Future Science, Dinosaur Evolution Research Center, Jilin University. Images are processed by the software Adobe Photoshop CC.

For the quantitative growth ring analysis, the radial diameters of tracheids were measured, and the percentage of diminution, percentage of latewood, ring markedness index (RMI), and the percentage of skews of CSDM (Cumulative Sum of the Deviation from Mean diameter) curves were calculated following the method of Falcon-Lang [18].

3. Results

ORDER Coniferales

FAMILY Pinaceae

GENUS *Keteleerioxylon* Shilkina, 1960

Type species: *Keteleerioxylon arcticum* Shilk., 1960

Keteleerioxylon changchunense Shi, Sun, Meng et Yu sp. nov.

Holotype: Specimen JLJY-02 (Figure 3A); Slides JLJY-02 a1, JLJY-02 a2, JLJY-02 b1, JLJY-02 b2, JLJY-02 c1, JLJY-02 c2.

Repository: Research Center of Paleontology and Stratigraphy, Jilin University, Changchun, China.

Type locality: Yingcheng Coal Mine, Changchun City, Jilin Province, China.

Stratigraphic horizon and age: The middle member of the Yingcheng Formation, earliest Albian (Early Cretaceous).

Etymology: The specific name is derived from Changchun, the locality specimens were collected.

Diagnosis: Growth rings distinct. Pits on radial walls of tracheids uniseriate to triseriate. Pits circular; Uniseriate pits scattered, rarely contiguous slightly; biseriate pits opposite, triseriate in a row. Crassulae present. Pits on tangential walls of tracheids absent. Transverse walls of axial parenchyma cells smooth. Rays, (1)6–11(37) cells high, uniseriate, sometimes with one to eight layers of biseriate cells. Horizontal and end walls of ray cells nodular. Ray marginal cells, resembling ray tracheids, with scattered uniseriate pits. Pits, of taxodioid-cupressoid type, 1–3(6) per cross-field, 5-10 μm in diameter. Resin canals, vertical, normal, surrounded by six to eleven thick-walled epithelial cells in a ring. Horizontal resin canals absent.

Description: The only preserved secondary xylem consists of tracheids, rays, axial parenchyma cells and epithelial cells of resin canals. The growth rings are distinct, 0.79—2.85 mm wide, with distinct and relatively straight boundaries (Figure 3B, D). The early-late wood transition is abrupt. In the transverse section, the early wood tracheids are large, thin-walled, and mainly rectangular (sometimes polygonal or circular). The latewood tracheids are thick-walled, radially compressed, and lumens almost disappeared near the growth-ring margin. The radial tracheid lumens are 0—89 μm in diameter. Intercellular space is absent. Xylem rays consist of uniseriate cells, 1—10 seriates of tracheids in between.

Figure 3. *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov. A. General view of the specimen JLJY-02. B. Transverse section showing the resin canals (red arrows) and growth ring boundaries. C. Close-up of the resin canals. D. Close-up of the growth ring boundary. E Radial section showing the vertical resin canal. F. Radial section showing the biseriate pits on the radial walls of tracheids and the crassulae. G. Radial section showing the triseriate pits on the radial walls of tracheids. H. Radial section showing the nodular horizontal and end walls of the ray parenchyma cells. Scale bar: A: the longer scale mark in the card is 1 cm; B = 1 mm; C, D, E = 200 μm; F, G, H =50 μm.

Pits on the radial walls are borded, circular in shape, (11)12–17(20) μm in diameter. In the late woods, they are uniseriate, partly biseriate, and scattered, rarely slightly contiguous, with an included aperture (circular or elliptical). In the early woods, they are mostly biseriate or triseriate, occasionally uniseriate (Figure 3F, G). When biseriate, the pits are opposite; when triseriate, the pits arrange in a row. The pits are (16)18–22(25) μm in diameter, with circular or elliptical apertures. Crassulae are present (Figure 3F). Axial parenchyma cells are rare, and their transverse walls are smooth (Figure 4D).

Rays are (1)6–11(37) cells in height, uniseriate, occasionally with one to eight layers of biseriate cells (Figure 4E, F). In the radial section, ray cells are brick-shaped, 19–25 μm in height, and 50-129 μm in length. The horizontal and end walls of the ray parenchyma cells are nodular. In the tangential section, ray cells are 10–28 μm in width, elliptical, circular, or rectangular, but rounded-triangular in marginal ray cells. Marginal ray cells resemble those ray tracheids with scattered uniseriate pits (Figure 4C).

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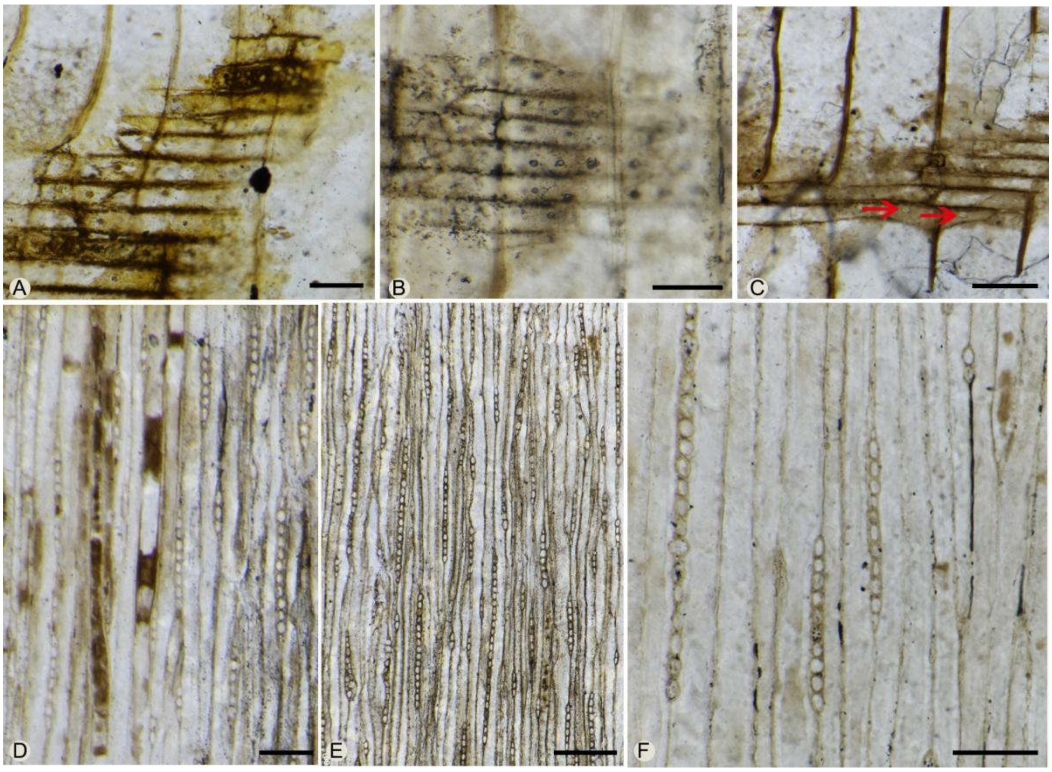

Figure 4. *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov. A,B. Radial section showing taxodioid-cupressoid type cross-field pits. C. Radial section showing the marginal ray cells resembling ray tracheids with scattered uniseriate pits (red arrows). D. Tangential section showing the axial parenchyma cell. E. Tangential section showing uniseriate, partly biseriate rays. F. Close-up of the rays showing uniseriate rays. Scale bar: A, B, C = 50 μm; D, F = 100 μm; E = 200 μm.

There are 1–3(6) pits per cross-field, of taxodioid-cupressoid type, 5–10 μm in diameter. (Figure 4A, B). Two or three pits arrange in a row, while, four to six pits are in a diffuse.

Vertical resin canals are present only (Figure 3E). Resin canals are circular or oval, radially elongated, 47–206 μm in diameter, single or in pairs (Figure 3B, C). They are lined with six to eleven thick-walled epithelial cells in a ring and situated in both early and latewood. Horizontal resin canals are absent.

Comparison: The fossil woods described here are characterized by (1) the cross-fields with mostly taxodioid pits, (2) the presence of axial resin canals, and (3) the nodular horizontal and end walls of the ray parenchyma cells. They closely resemble *Keteleeria*, *Keteleerioxylon* and *Protopiceoxylon*.

The present fossil woods differ from the extant species of *Keteleeria* in having uniseriate to triseriate pits on the radial walls of tracheids, in lacking pits on tangential walls of tracheids, and in possessing taxodioid and cupressoid cross-field pits (Table 1).

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Table 1. Comparison of wood anatomical characteristics of *Keteleerioxylon changchunense* sp. nov. and woods of extant *Keteleeria* [19].

Anatomical characters	*Keteleeria davidiana* (Bertr.) Beissner [20-23]	*Keteleeria evelyniana* Masters [21]	*Keteleeria fortunei* (Andr. Murray) Carr.[21,22,24]	***Keteleerioxylon changchunense* sp. nov.**
Pits on radial walls of tracheids	Uniseriate to tetraseriate	Uniseriate to biseriate	Uniseriate to biseriate	**Uniseriate to triseriate**
diameter of pits, m	(10)12–15(16)	15–21	12–15(16)	**(11)12–17(20)**
Pits on tangential walls of tracheids	Present	Present	Present	**Absent**
Crassulae	Present	Present	No data	**Present**
Uniseriate rays:				
height (in cells)	1–30(34)	1–30	1-40	**(1)6–11(37)**
number of biseriate layers	1–8	Uncommon	Present	**1–8**
marginal ray cells of the ray tracheid type	Present	Present	Present	**Present**
Transverse walls of axial parenchyma	Knotty	?	Knotty	**Smooth**
Number of epithelial cells in vertical resin canals	6–7(8–11)	6	6-8	**6-11**
Pitting on cross-fields: number of pits	1–3(6)	1-4	1–4(6)	**1–3(6)**
diameter of pits, m	(4)5–8(12)	No data	4-6	**5-10**
type of pitting	Taxodioid, piceoid and pinoid	taxodioid	taxodioid	**Taxodioid and cupressoid**

The fossil wood genus *Keteleerioxylon* was established on the materials collected from the Early Cretaceous Franz Josef Land, Russia by Shilkina [6] Until now, four species of *Keteleerioxylon* have been described. *K. arcticum* Shikkina, 1960 differs from *K. changchunense* in having uniseriate to biseriate pits on the radial walls of tracheids, in possessing pits on tangential walls of tracheids, in lacking marginal ray cells of the ray tracheid type, and in having fewer pits per cross-field [6]. *K. fokinii* Shilkina, 1986 was found in the Early Cretaceous Kirovsk Region of Russia [25]. *K. fokinii* differs from the present woods in having uniseriate to biseriate pits on the radial walls of tracheids, in the absence of crassula, and in the taxodioid cross-field pits. *K. primoryense* Blokhina, 2000 from the Oligocene–Miocene of Primorye differs from *K. changchunense* in having uniseriate to biseriate pits on the radial walls of tracheids, in possessing pits on tangential walls of tracheids, and in the cupressoid cross-field pits [26]. *K. kamtshatkiense* Blokh. et Afonin, 2006, from the Lower Cretaceous of the Kamchatka Peninsula, Russia, are different from the woods under the description, in having uniseriate to biseriate pits on the radial walls of tracheids, in possessing pits on tangential walls of tracheids, and in the absence of crassula [19].

There are many woods that were identified as *Keteleeria*. *Keteleeria mabetiensis* Watari, 1941 were collected from the Lower Miocene of Japan [27,28]. *Keteleeria mabetiensis* differs from *Keteleerioxylon changchunense* in possessing pits on tangential walls of tracheids, in knotty transverse walls of axial parenchyma, and taxodioid and piceooid cross-field pits. *Keteleeria zhilinii* Blokhina et Bondarenko, 2005 was first discovered in the Pliocene of Primorye, Russia [8]. *K. zhilinii* differs from the woods under study in having uniseriate to biseriate pits on the radial walls of tracheids, in having pits on tangential walls of tracheids, and in the taxodioid cross-field pits. Yang et al. discovered a silicified wood belonging to the genus *Keteleeria* in the Late Cretaceous of Henan, China [29]. They named these woods after the extant species "*Keteleeria fortunei*". "*Keteleeria fortunei*" is different from *Keteleerioxylon changchunense* in having uniseriate to biseriate pits on the radial walls of tracheids and in the absence of axial parenchyma. *Keteleeria* sp. from the early Holocene of Hubei, China, differs from *Keteleerioxylon changchunense* in having uniseriate to biseriate pits on the radial walls of tracheids and in the taxodioid cross-field pits [30]. *Keteleeria* sp.

from Guangdong, China differs from the woods under study in having uniseriate to biseriate pits on the radial walls of tracheids, in lower rays, and in having fewer pits per cross-field [31].

Among the fossil woods assigned to *Protopiceoxylon*, Gothan *P. amurense* Du, 1982 [32–34], *P. yizhouense* Duan et Cui, 1995 [35], and *P. chaoyangensis* Duan, 2000 [36] show the greatest similarity with the genus *Keteleerioxylon*. *P. amurense* was found in the Upper Cretaceous and Paleocene of Heilongjiang, Northeast China [32–34]. *P. amurense* differs from the present woods in having uniseriate to biseriate pits on the radial walls of tracheids, in higher rays, and in fewer cross-field pits. *e P. yizhouense* from the Early Cretaceous Liaoning, China is different from *K. changchunens* in having uniseriate pits on the radial walls of tracheids, in lower rays, and in abietoid cross-field pits [35]. *P. chaoyangensis* from the Early Cretaceous Liaoning, Northeast China are different from the fossil wood under study in having uniseriate to biseriate pits on the radial walls of tracheids, in lower rays, and in abietoid cross-field pits [36].

For the details of each fossil record, please see Table S1.

4. Discussion

4.1. Paleoecological and paleoclimatic implications

Quantitative analysis of growth rings can be used to see whether the conifer species is evergreen or deciduous, and how long the leaf longevity is [18, 37]. Through the measuring of radial diameters of five adjacent files of tracheid cells, four parameters are calculated, including (1) percentage of latewood, (2) percentage of cell diminution in a ring increment, (3) RMI, and (4) percentage of skews of CSDM curves (Table 2, supplementary data).

Table 2. Results of the quantitative growth ring analysis of *Keteleerioxylon changchunense* sp. nov.

Ring number	Percentage latewood	Percentage diminution	Ring Markedness Index (RMI)	Percentage skews
Ring A	48.00%	97.06%	46.42%	+4.35%
Ring B	50.00%	97.50%	48.75%	0%
Ring C	48.00%	89.39%	42.76%	+4.35%
Ring D	40.00%	97.30%	38.92%	+20.00%
Ring E	42.00%	96.00%	40.72%	+15.15%
Averages	45.60%	95.45%	43.51%	+8.77%

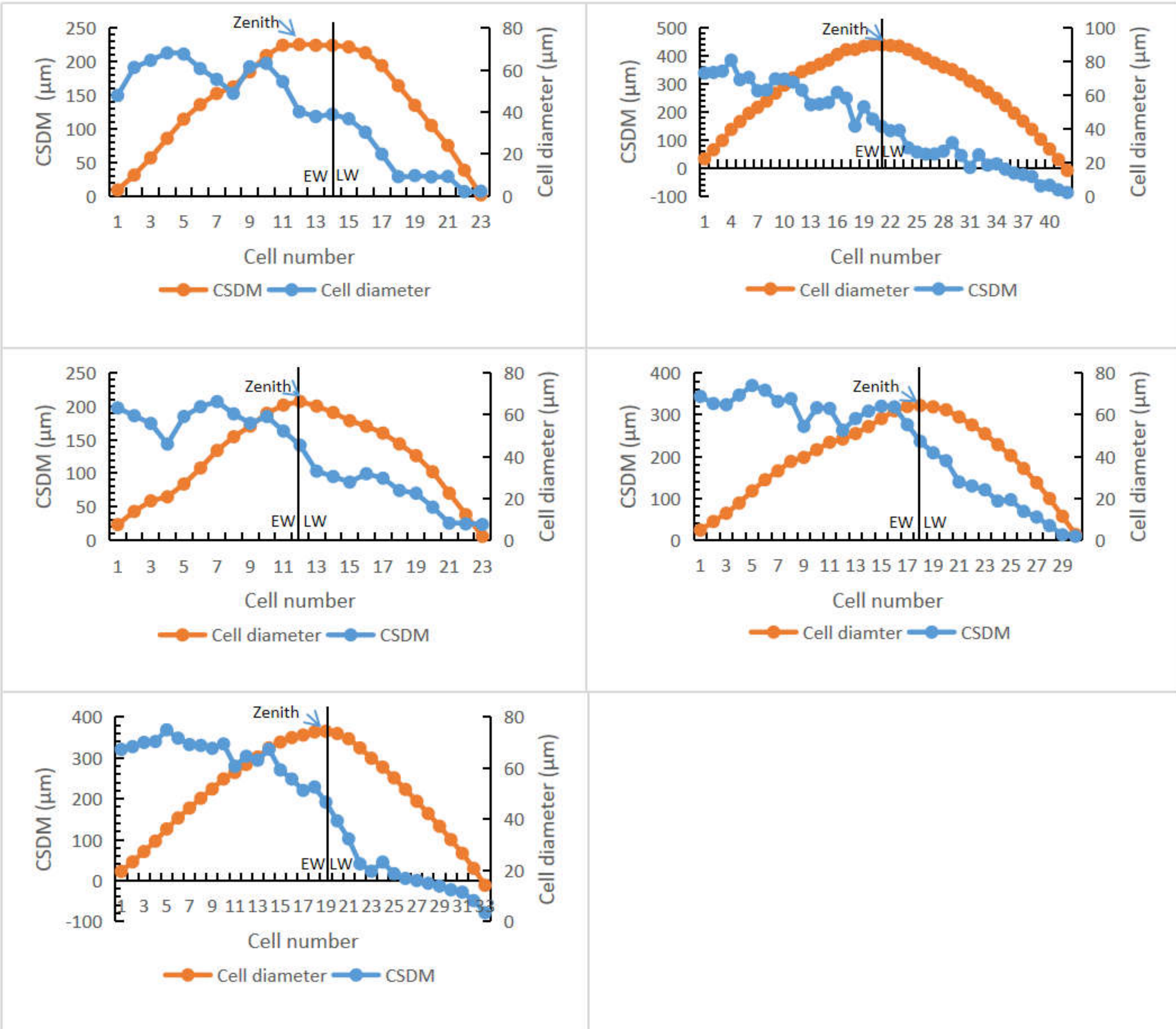

Figure 5. the CSDM curves of five growth rings and cell diameters of growth ring increment. EW: Earlywood, LW: Latewood.

Deciduous conifers have dominantly left-skewed CSDM or symmetrical curves, whereas evergreen conifers have dominantly right-skewed CSDM curves. The CSDM curves of *Keteleerioxylon changchunense* are from 0 to +20.00% (mean percentage of skew +8.77%), right-skewed, suggesting that this species was evergreen (Figure 5, Table 3).

The percentage of latewood in *Keteleerioxylon changchunense* is 40.00%–50.00%, with a mean of 45.62%; and the percentages of skews of CSDM curves range from 0–20.00% (mean 8.77%). These two parameters are quite close to those of *Pinus sylvestris* and *Picea abies*. While, the percentage of cell diminution (89.39%–97.50%, mean 95.45%) and the RMI (38.92%–48.75%, mean 43.51%) are higher than those of *Larix decidua* (Table 2). Therefore, the leaf retention time of *Keteleerioxylon changchunense* is considered to be 1–3 years, the most likely approach to the extent of *Keteleeria* [38].

Table 3. Comparison of the quantification of ring markedness parameters for *Keteleerioxylon changchunense* sp. nov. with the five extant taxa [18].

Tree habits	Species	Leaf retention time (in years)	Percentage of latewood (%)	Percentage diminution (%)	Ring Markedness Index (RMI) (%)	Range of percentage skews (mean value) (%)
Deciduous	*Larix decidua*	< 1 year	50.00–54.83	71.55–85.91	35.77–44.36	-40.0 to +7.7 (-6.8)
Evergreen	***K. changchunense***	**1-3years**	**40.00-50.00**	**89.39-97.50**	**38.92-48.75**	**0.0 to +20.0 (+8.8)**
	Pinus sylvestris	1–3 years	41.03-50.00	70.53-77.28	31.56-35.26	-9.1 to +17.9 (+5.2)
	Picea abies	3–5 years	25.93-44.19	74.02-84.03	19.90-35.42	0.0 to +38.2 (+12.0)
	Cedrus libani	3–6 years	30.77-39.58	62.33-72.06	20.22-24.68	+35.7 to +42.9 (+39.0)
	Araucaria araucana	3–15 years	10.00-22.50	28.67-51.79	3.17-10.35	+55.0 to +80.0 (66.7)

The CSDM curves are widely used for identifying evergreen or deciduous habits (cankaowe). However, an exception came from the Late Pleistocene *Keteleeria* sp. of Guangdong, China. and its CSDM curves showed both left and right skews [31]. But the radial cells in three growth rings of *Keteleeria* sp. are less than 15, this might result from false rings triggered by the East Asian monsoon. Therefore, we still think the right skew of CSDM curves is reliable in recognizing evergreen trees like *K. changchunense*.

The earliest Albian climate is regarded as a greenhouse with high atmospheric carbon dioxide concentration [17]. The global temperature in the Aptian and Albian would be much higher than today [39], and the Arctic area was covered by evergreen broadleaf mixed with deciduous conifer forests in the Late Cretaceous [40]. The growth ring RMI is considered as an indicator of the intensity of climatic seasonality [18]. *Keteleerioxylon changchunense* shows very marked growth rings (high RMI) (Table 3). This might indicate that the climate seasonality was strong in the earliest Albian in the Songliao Basin, Northeast China.

4.2. Phytogeographical distributions

Although extant *Keteleeria* is endemic to East and Southeast Asia, the genus had been widely distributed in Europe, North America, and Asia in the northern hemisphere since the Late Cretaceous. Some of the Cretaceous fossils, especially the Early Cretaceous woods with similar characteristics were named under the genera *Keteleerioxylon* and *Protopiceoxylon*. They are included in the *Keteleeria*-type group (Table 4).

Table 4. Geological distribution of Keteleeria-type fossils.

Species	Location	Age	Type of fossil	References
Keteleerioxylon fokinii Shilk	Kirovsk Region, Russia	Valanginian (Early Cretaceous)	Wood	Shilkina, 1986 [25]
Protopiceoxylon amurense Du	Heilongjiang Province, China	Aptian-Albian (Early Cretaceous); Coniacian-Maastrichtian (Late Cretaceous); Paleocene	Wood	Du, 1982 [32]; Wang et al., 1997 [33]; Terada et al., [34]
Protopiceoxylon chaoyangensis Duan	Liaoning Province, China	Aptian-Albian (Early Cretaceous)	Wood	Duan, 2000 [36]
Protopiceoxylon yizhouensis Duan et Cui	Liaoning Province, China	Aptian-Albian (Early Cretaceous)	Wood	Duan et al., 1995 [35]
Keteleerioxylon arcticum Shilk	Franz Josef Land, Russia	Aptian-Albian (Early Cretaceous)	Wood	Shilkina, 1960 [6]
Keteleerioxylon kamtschatkiense Blokhina et Afonin	Kamchatka Peninsula, Russia	Aptian-Albian (Early Cretaceous); Turonian-Coniacian (Late Cretaceous)	Wood	Blokhina et al., 2006 [19]
Keteleerioxylon changchunense Shi, Sun, Meng et Yu	Jilin Province, China	Albian (Early Cretaceous)	Wood	This paper
Keteleeria fortunei (Andr. Murray) Carr.	Henan Province, China	Late Cretaceous	Wood	Yang et al., 1990 [29]
Keteleeria cretacea Miki et Maeda	Awaji, Japan	Late Cretaceous	Cone	Miki and Maeda, 1966 [41]
Keteleeria sp.	British Columbia, Canada	Early Eocene	Seed	Mathewes et al., 2016 [10]
Keteleeria sp.	Liaoning Province, China	Eocene	Cone	The Writing Group of Cenozoic Plants of China, 1978 [42]
Keteleeria mabetiensis Watari	Ishikawa Prefecture and Akita Prefecture, Japan	Oligocene and Miocene	Wood	Watari, 1941, 1956 [27,28]; Terada, 1998 [43]; Choi et al., 2010 [44]
Keteleeria sp.	Primorye, Russia	Oligocene to Early Miocene	Leaves, cones, and seeds	Rybalko et al., 1980 [45]
Keteleerioxylon primoryense Blokh.	Primorye, Russia	Oligocene to Miocene	Wood	Blokhina and Klimova, 2000 [26]
Keteleeria rujadana Lakhanpal	Oregon, USA	Oligocene	Cone	Lakhanpal, 1958 [46]
Keteleeria ptesimosperma Meyer et Manchester	Oregon, USA	Oligocene	Winged seeds	Meyer and Manchester, 1997 [47]
Keteleeria prambachensis (Hofmann) Klaus	Prambachkirchen, Austria	Oligocene	Cone	Hofmann, 1944 [48]; Klaus, 1977 [49]
Keteleeria rhenana Kräusel	Mainz, Germany	Early Miocene	Seed	Kräusel, 1938 [50]
Keteleeria davidiana Miki	Honshu, Japan	Miocene	Cones and seeds	Miki 1941, 1957, 1958 [51-53]
Keteleeria ezoana Tanai	Niigata and Hokkaido Prefecture, Japan	Miocene	Seed scales, seeds, and leaves	Tanai, 1961 [54]; Tanai & Suzuki, 1963 [55]; Kamoi et al., 1978 [56]; Ozaki, 1979 [57]
Keteleeria shanwangensis Wang et al.	Shandong Province, China	Miocene	Cone, winged seeds,	Wang et al., 2006 [58]
Keteleeria hoehnei Kirchheimer	Saxony, Germany	Miocene	Cones, seeds, and needles	Kirchheimer, 1942 [59]; Kunzmann and Mai, 2005 [60]
Keteleeria bergeri Kirchheimer	Saxony, Germany	Miocene	Cones, seeds, and needles	Kirchheimer, 1942 [59]

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Keteleeria bergeri Kirchheimer	Turowo, Poland	Miocene	Cone	Zalewska, 1961 [61]
Keteleeria hoehnei Kirchheimer	Kanton Schwyz, Switzerland	Miocene	Cone	Hantke, 1973 [62]
Keteleeria microreticulata Ananova	Taganrog peninsula, Russia	Middle Miocene	Pollen	Ananova, 1974 [63]
Keteleeria caucasica Ramischvili	Zugdidi municipalitet, Georgia	Late Miocene	Pollen	Ramischvili, 1969 [64]
Keteleeria heterophylloides (Berry) Brown	Idaho, USA	Miocene	Vegetative shoots	Brown, 1935 [65]
Keteleeria zhilinii Blokh. et Bondarenko	Primorye, Russia	Pliocene	Wood	Blokhina and Bondarenko, 2005 [8]
Keteleeria sp.	Maoming, China	Late Pleistocene	Wood	Huang et al., 2019 [31]
Keteleeria sp.	Wuhan, China	Early Holocene	Wood	Yang et al., 2003 [30]

The Early Cretaceous *Keteleeria*-type trees are widely distributed from western Liaoning, China [32,33] to the Arctic areas [6] (Figure 6). Their paleolatitudes range from 45°N to 85°N (Figure 7). This indicates that the Early Cretaceous climate might be warm and suitable for these subtropical thermophilic *Keteleeria*-type trees. In the Late Cretaceous, *Keteleeria*-type trees were still persistently distributed in the middle and high latitudes of the Russian Far East and Northeast China. After the K-Pg mass extinction, records of *Keteleeria* fossils were rare in the Paleocene [36]. In the Eocene, *Keteleeria* migrated from the Jiayin of Heilongjiang, Northeast China to North America [10]. This migration was contemporary with the Paleocene–Eocene thermal maximum [66,67]. During Oligocene and Miocene, *Keteleeria* was widely distributed in the mid-latitudes of North America, Europe, and East Asia in the northern hemisphere. From Pliocene on, *Keteleeria* started to retreat southward from Primorye, Russia to the subtropical and tropical monsoon climate regions of South China and Southeast Asia in the middle and low latitudes (~13.8°N-35.5°N) in the Quaternary. Therefore, the paleogeographical distribution of *Keteleeria*-type was closely related to the paleoclimate changes (Figure 6,7).

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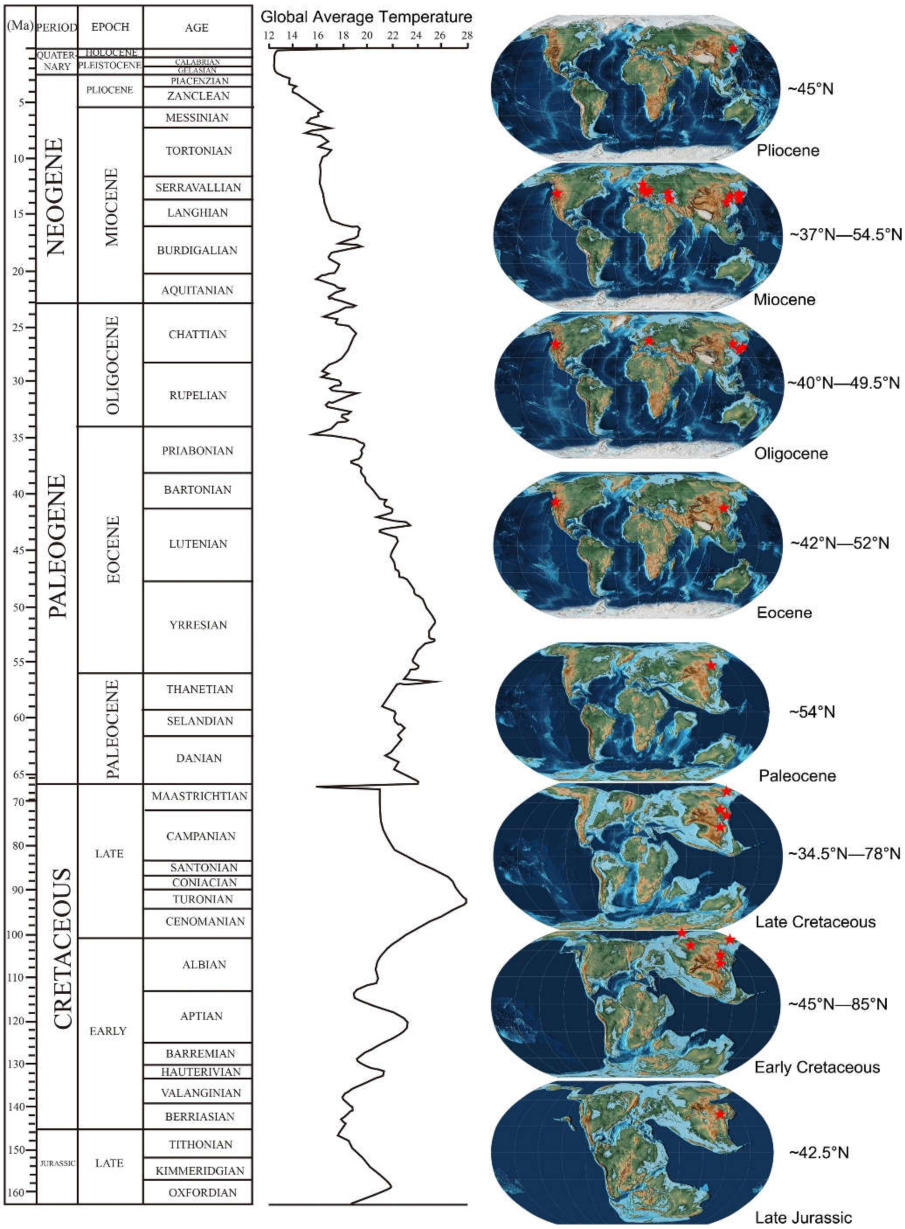

Figure 6. Geographical and geological distribution of *Keteleeria*-type fossils (red stars) in the world (global average temperature data from [68]).

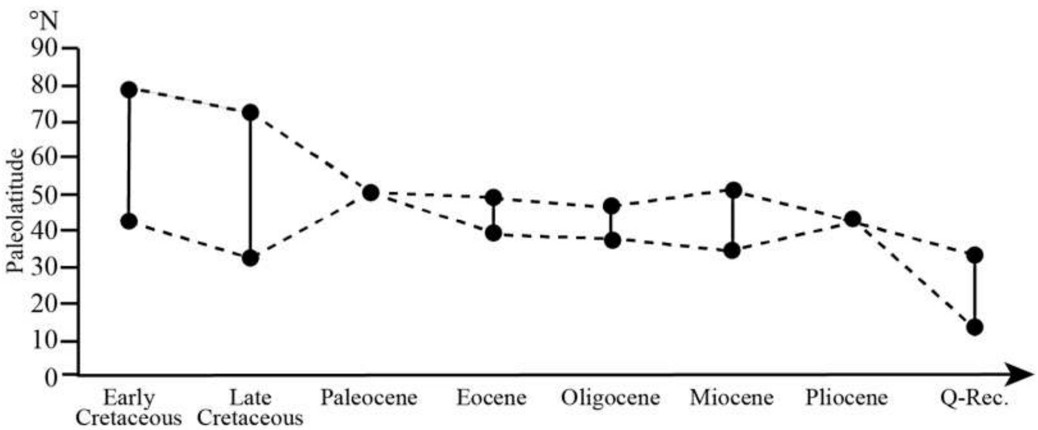

Figure 7. Paleolatitude range of the *Keteleeria*-type fossils in the geological time.

5. Conclusions

In this study, the species *Keteleerioxylon changchunense* Shi, Sun, Meng et Yu sp. nov. is described for the first time in the late Early Cretaceous deposits of Changchun, Northeast China. The quantitative growth ring analysis of the two specimens shows that the species is evergreen, with the foliar long around 1-3 years. This is quite consistent with the habits of extant *Keteleeria*. The presence of very marked growth rings indicates that it lived in an seasonal climate during the earliest Albian in the Songliao Basin, Northeast China. The paleogeographical distribution of *Keteleeria*-type fossils indicates that they were distributed in both the middle and the high latitudes during the Cretaceous global warming time. While, they retreated to the middle latitude in the Cenozoic due to global cooling, and after the Quaternary glaciations, they only survive in East and Southeast Asia now.

6. Patents

Supplementary Materials: Figure S1: Comparison of wood anatomical characters of *Keteleerioxylon changchunense* sp. nov. and closely related fossil species. Supplementary da ta:Cell diameter for CSDM curve.

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