Cretaceous Research 50 (2014) 110–119

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Fossil woods from the Lower Cretaceous (Albian) of Kamchatka Peninsula, Russian Far East

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ARTICLE INFO

Article history:
Received 14 February 2014
Accepted in revised form 4 April 2014
Available online 16 May 2014

Keywords:
Protocedroxylon
Taxaceoxylon
Xenoxylon
Kedrovka Formation
Albian
Russian Far East

ABSTRACT

Three coniferous fossil wood taxa are described from the Kedrovka Formation (Albian) of Kamchatka Peninsula, Russian Far East: *Protocedroxylon gregussii* (Shilkina) Shilkina & Chudajberdyev, *Taxaceoxylon* sp. and *Xenoxylon phyllocladoides* Gothan. This wood flora is quite peculiar when compared to coeval wood floras from the same area. It yields the first safe report of *Taxaceoxylon* fossil wood from the Lower Cretaceous of Asia. The record of *Xenoxylon phyllocladoides* represents the latest stratigraphic occurrence of this species and the first from Russia. Taxaceae-like fossil wood record is reappraised and shown to be consistent with recent cladistic results, suggesting a boreal origin and a link to the Pinaceae. The palaeoecology of the Kedrovka Formation wood flora is investigated. The peculiarities of the flora might be explained by an oceanic palaeoclimate.

1. Introduction

Many palaeobotanical studies of the Lower Cretaceous of Russian Far East have been performed on macrofossils such as leaves, cones and seeds (e.g. Krasilov, 1967; Samylina, 1976; Lebedev, 1974; Herman and Lebedev, 1991; Bugdaeva et al., 2006; Herman, 2011). However, there is less information about the Early Cretaceous fossil woods from Russian Far-East, for which five species were previously reported: *Keteleerioxylon kamtschatkiense* Blokhina & M. Afonin (Blokhina et al., 2006), *Cedrus penzhinaensis* Blokhina & M. Afonin (Blokhina and Afonin, 2007), *Xenoxylon hopeiense* Chang, *X. latiporosum* (Cramer) Gothan (Afonin, 2008) and *Protocedroxylon primoryense* M. Afonin (Afonin, 2012).

This paper describes three coniferous fossil wood taxa, all new to the Early Cretaceous fossil wood record of the Russian Far East, from the Albian of the Kamchatka Peninsula: *Protocedroxylon gregussii* (Shilkina) Shilkina & Chudajberdyev, *Taxaceoxylon* sp. and *Xenoxylon phyllocladoides* Gothan.

The *Taxaceoxylon* sp. is an early data for wood possibly related to the Taxaceae. Since the fossil record of the woods of the Taxaceae is controversial it is discussed further here with new data from the reappraisal of three *Taxaceoxylon* species types.

This new Albian fossil wood flora is also relevant to the discussion of the palaeobiogeographic relationships of Russian Far-East during the Early Cretaceous and to the question of the climatic gradient which occurred at mid-latitudes at that time.

2. Material and methods

The fossil woods described here were collected by Dr. Alexander Popov (Far Eastern Geological Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok) on the left bank of the Melkaya River, Talovka River Basin, eastern coast of Penzhina Bay, Kamchatka Peninsula, during an expedition in 1999 (Fig. 1). The fossil woods are hard, permineralized with calcium carbonate, grey to almost black, and they represent the remains of trunks or large branches. They were studied using the conventional petrographic technique for preparing thin sections of permineralized wood. Three mutually perpendicular sections were prepared (transverse, longitudinal radial and longitudinal tangential) in order to fully demonstrate the anatomical features. The thin sections were examined under an Axioskop-40 light binocular microscope (Carl Zeiss) and the images were captured using an AxioCamHR camera (Carl Zeiss). The anatomical terms used in this paper follow the recommendations of the IAWA Committee (2004) and Philippe and Bamford (2008). The fossil woods were identified using published wood identification keys and fossil wood descriptions (e.g. Shilkina and Khudaiberdyev, 1971; Philippe and Bamford, 2008; Philippe et al., 2013).

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http://dx.doi.org/10.1016/j.cretres.2014.04.002
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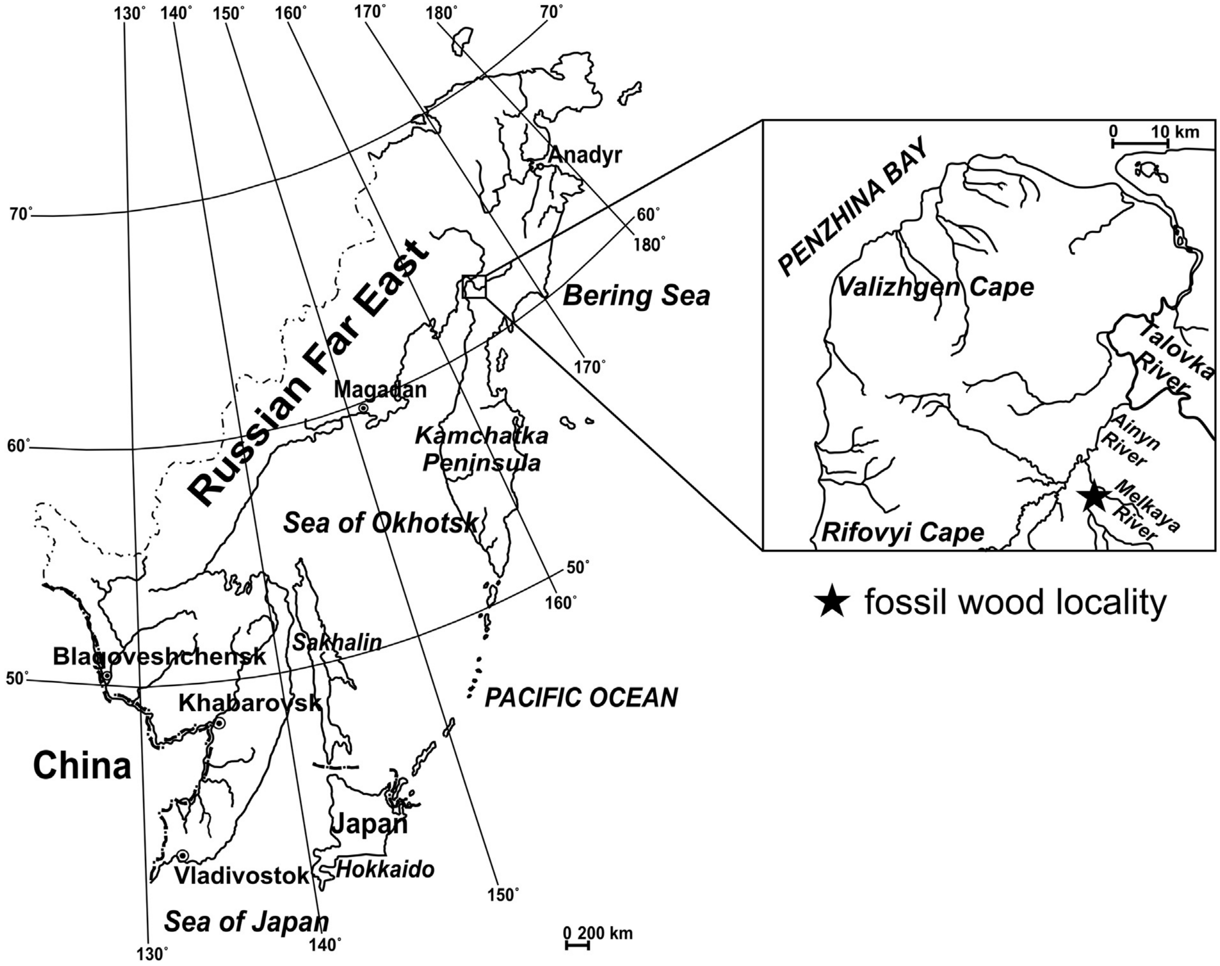

Fig. 1. Map showing fossil wood collection site of Kamchatka Peninsula.

The fossil wood samples and thin sections are housed in the Institute of Biology and Soil Science, Far Eastern Branch, Russian Academy of Sciences, Vladivostok.

3. Geological setting

The fossil woods described in this report were collected from the marine terrigenous deposits of the Kedrovka Formation. According to Zakharov et al. (2002, 2006) on the left bank of the Melkaya River (Talovka River Basin) the Kedrovka Formation includes (from the base upward):

(1) Greenish-grey siltstones, with small calcareous concretions containing remains of brachiopods, gastropods and ammonoids *Anagaudryceras* sp., *Marshallites* sp., *Sciponoceras* sp. – thickness 2.3 m;
(2) Greenish-grey, fine-grained sandstones – thickness 0.12 m;
(3) Greenish-grey siltstones, with small (rarely large) calcareous concretions containing brachiopods *Penzhinothyris plana* Smirnova – thickness 15 m;
(4) Greenish-grey siltstones, with horizons of mudstones, numerous large calcareous concretions containing brachiopods *Penzhinothyris plana*, molluscs *Inoceramus* sp., ammonoids *Beudanticeras* sp., *Hulenites* sp., and plant macrofossils including fossil woods and solitary leaf imprints of conifers – thickness 5.5 m;
(5) Grey siltstones, with small calcareous concretions – thickness 12–14 m.

The age of the Kedrovka Formation is late Early Cretaceous (Albian), based on diagnostic marine fossils (Avdeiko, 1968; Paraketsov et al., 1974; Alabushev, 1995). A detailed overview of the marine fossils from the Kedrovka Formation in the Talovka River Basin is given in Avdeiko (1968) and Alabushev (1995).

Plant macrofossils (excluding woods), pollen and spores have not yet been described from the deposits of the Kedrovka Formation. Two fossil wood species, *Keteleerioxylon kamtschatkiense* (Blokhina et al., 2006) and *Cedrus penzhinaensis* (Blokhina and Afonin, 2007), however, were previously reported from this formation.

4. Systematics

Order: Coniferales
Morphogenus *Protocedroxylon* Gothan, 1910
Type species. *Protocedroxylon araucarioides* Gothan, 1910

Protocedroxylon gregussii (Shilkina) Shilkina & Chudajberdyev, 1971
Fig. 2A–H.

Material. Three samples: n°. IBSS 23/6-1, 4 cm in length, transverse section (tangential × radial) 2 × 4 cm, with three thin sections (transverse, radial, tangential); n°. IBSS 23/6-2, 6 cm in length, transverse section (tangential × radial) 4 × 7 cm, with three thin sections (transverse, radial, tangential); n°. IBSS 23/6-3, 8 cm in length, transverse section (tangential × radial) 3 × 5 cm, with eight thin sections (two transverse, four radial, two tangential).

Locality, stratigraphic horizon, stage. Melkaya River, Talovka River Basin, Kamchatka Peninsula, Russian Far East, Kedrovka Formation, upper Lower Cretaceous (Albian).

Description. Growth rings are distinct, 1–2 mm wide; the transition from the early wood to the late wood is gradual (Fig. 2A). Early wood tracheids are thin-walled, with broad lumen, rounded, rounded-square, rounded-rectangular or rounded-polygonal in transverse section. Late wood tracheids are thick-walled, rounded-rectangular, radially flattened in transverse section. Normal and traumatic resin canals are absent. Axial parenchyma is scanty, diffuse, sometimes with resin contents; transverse end walls of axial parenchyma cells are smooth or rarely irregularly thickened (Fig. 2G).

Pits on the radial walls of tracheids are uniseriate or, rarely, biseriate and in stellate clusters of three–four pits (Fig. 2B–D). The uniseriate pits are elliptic (18–19 × 20–25 μm in size), horizontally elongated, or rarely circular (17–22 μm in diameter), with elliptic and circular apertures, respectively; pits are contiguous, round or compressed, or more rarely spaced along the tracheid length and then round or elliptical. The biseriate pits are elliptic, penta- and hexagonal, 18–23 μm in diameter, with circular and elliptic apertures; biseriate pitting belongs to the mixed type (alternate or opposite). Crassulae are absent. Pits on the tangential walls of tracheids are uniseriate, circular, 7–8 μm in diameter and widely spaced (Fig. 2G, H). Tyloses are sometimes present in longitudinal tracheids.

Rays are uniseriate, rarely with biseriate parts (one to nine cells high), 1–32 cells high, mostly 7–20 cells (Fig. 2G, H). Horizontal and end walls of ray cells are pitted (Fig. 2E, F). Median ray cells are

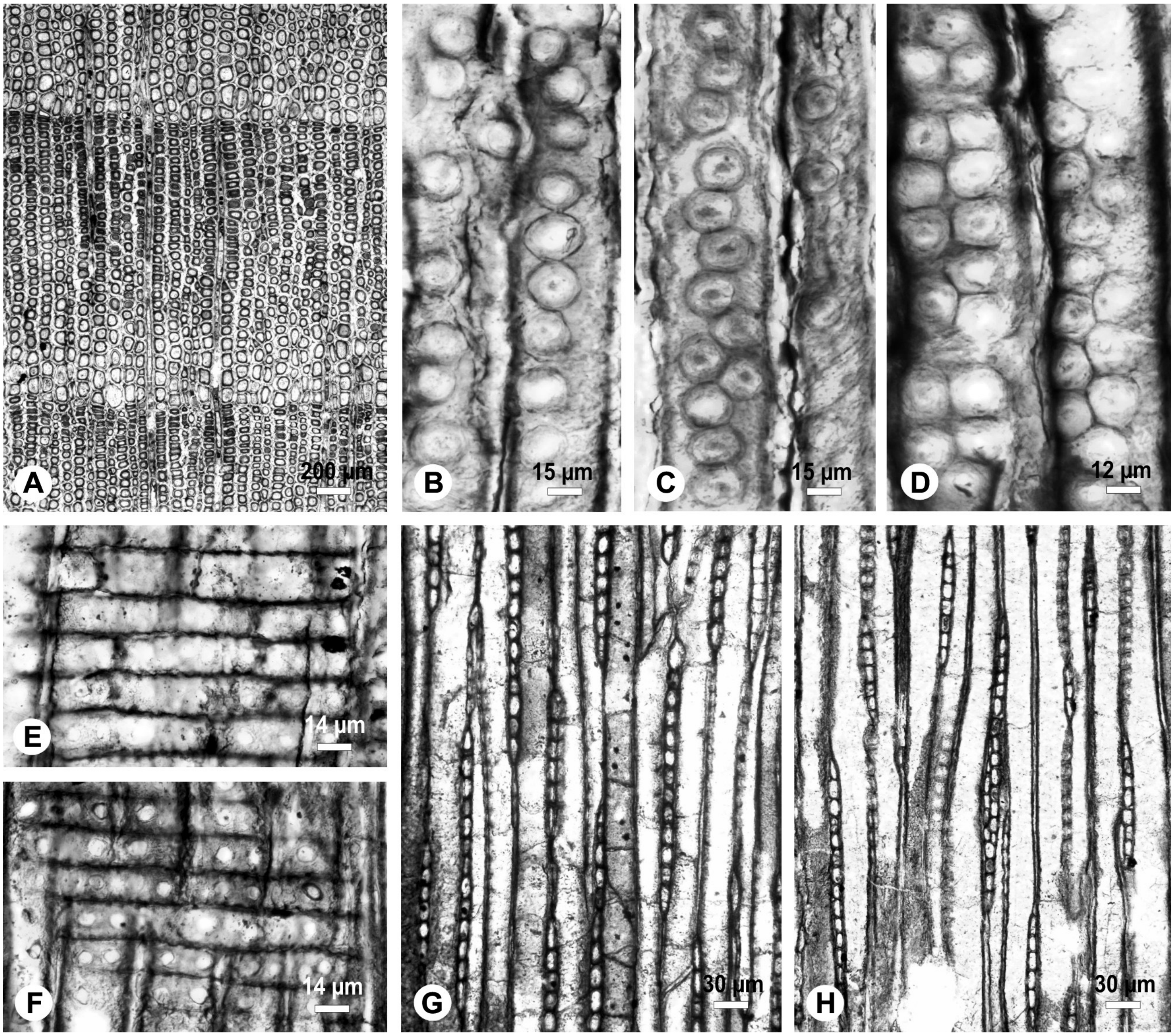

Fig. 2. Photomicrographs of *Protocedroxylon gregussii* (sample n°. IBSS 23/6-3). A. Transverse section showing distinct growth rings and gradual transition from the early wood to the late wood. B, C. Radial sections showing one row of radial tracheid bordered pits. D. Radial section showing two rows of radial tracheid bordered pits. E, F. Radial sections showing simple or bordered cross-field pits and pitted horizontal and end walls of ray cells. G. Tangential section showing uniseriate rays, tangential tracheid bordered pits, and smooth transverse end walls of axial parenchyma cells. H. Tangential section showing uniseriate rays, uniseriate ray with biseriate part and tangential tracheid bordered pits.

elliptical, rounded-rectangular, radially elongated or rarely rounded; marginal ray cells are rounded-triangular and approximately of the same size as the median cells (Fig. 2G, H). Ray tracheids are absent. Cross-field pits are circular, simple and bordered, possibly of the cupressoid type, 6–10 µm in diameter, one to three per cross-field (Fig. 2E, F). The pits are arranged in a single horizontal row in the case of two pits per cross-field, in two horizontal rows in case of three pits.

Identification. These samples are characterized by distinct growth rings, absence of normal resin canals, mixed pitting on the radial tracheid walls, and pitted ray cell walls. Therefore, the fossils can be assigned to the morphogenus *Protocedroxylon* Gothan.

Protocedroxylon was established by Gothan (1910) for material from the Mesozoic deposits of West Spitsbergen (Norway) and comprises fossil woods of Mesozoic conifers, which combine anatomical features of the pre-Mesozoic conifer woods, like *Agathoxylon* Hartig, with that of modern representatives of the Pinaceae as *Abies* Miller, *Tsuga* Carriére, *Pseudolarix* Gordon, and *Cedrus* Trew. Kräusel (1919) united *Protocedroxylon* and *Araucariopitys* Hollick & Jeffrey, and consequently, following the priority rule, he considered *Protocedroxylon* as a junior taxonomical synonym of *Araucariopitys*. However, Vogellehner (1967), Shilkina and Khudaiberdyev (1971) and later Philippe and Hayes (2010) proposed that *Protocedroxylon* and *Araucariopitys* are independent genera as the woods of their types differ in their radial tracheid wall pitting type and, moreover, their cross-fields. In addition, *Araucariopitys* was established on the basis six-year-old short shoots, while *Protocedroxylon* was described for mature trunk wood.

Protocedroxylon was recorded from the Upper Triassic (Shilkina, 1967; Yamazaki et al., 1980; Yamazaki and Tsunada, 1981; Nishida and Oishi, 1982; Yamazaki and Tsunada, 1982) to the Upper Cretaceous (Nishida and Nishida, 1984) of the Northern Hemisphere. In Russia, the following species of this morphogenus were described: *Protocedroxylon haraulachica* (Shilkina) Vogellehner from the Lower Jurassic of Eastern Siberia (Shilkina, 1958; Vogellehner, 1968), *P. dibneri* (Shilkina) Shilkina & Chudajberdyev from the Upper Triassic of Franz Josef Land, *P. gregussii* from the Upper Triassic–Lower Cretaceous of Franz Josef Land, *P. polyporosum* (Shilkina) Shilkina & Chudajberdyev from the Lower Cretaceous of Franz Josef Land (Shilkina, 1967; Shilkina and Khudaiberdyev, 1971), *P. bojarense* Shilkina & Blokhina (Blokhina, 1975) and *P. ronkinii* Shilkina (Shilkina, 1986) from the Upper Jurassic of Eastern Siberia, *P. kryshtofovichii* Shilkina and *P. magnoradiatum* Shilkina from the Lower Cretaceous of European Russia (Shilkina, 1989) and *P. primoryense* from the Lower Cretaceous of Russian Far East (Afonin, 2012).

A comparison of the studied material with known species of *Protocedroxylon* indicates that it has most similarities with *P. gregussii*, described from the Upper Triassic–Lower Cretaceous of Franz Josef Land (Shilkina, 1967; Shilkina and Khudaiberdyev, 1971). The main characteristics of *P. gregussii* are the presence of uniseriate and biseriate pits on the radial walls of tracheids, pits on the tracheid tangential walls, smooth (rarely irregularly thickened) transverse end walls of axial parenchyma cells, and absence of traumatic resin canals. Except for the ray height there is a very close agreement in all features between the Kamchatka fossils and *P. gregussii*. The rays in *P. gregussii* are commonly 5 to 12 cells high but reach a maximum height of 19 cells. In the studied fossils the rays are mostly 7 to 20 cells; some attain a maximum height of 32 cells. However, ray height only should not be regarded as diagnostic at species level. Therefore, the fossils are identified as *P. gregussii*.

Morphogenus *Taxaceoxylon* Kräusel & Jain, 1964
Type species. *Taxaceoxylon torreyanum* (Shimakura) Kräusel & Jain, 1964

Taxaceoxylon sp.
Fig. 3A–H.

Material. One sample, n°. IBSS 23/10, 28 cm in length, transverse section (tangential × radial) 8 × 11 cm; 13 thin sections (eight transverse, three radial, two tangential).

Locality, stratigraphic horizon, stage. Melkaya River, Talovka River Basin, Kamchatka Peninsula, Russian Far East, Kedrovka Formation, upper Lower Cretaceous (Albian).

Description. Growth rings are distinct, 0.5–1.5 mm wide; the transition from the early wood to the late wood is usually gradual, but sometimes abrupt in some growth rings (Fig. 3A). Early wood tracheids are thin-walled, with broad lumen, and rounded or rounded-polygonal transverse sections. Late wood tracheids are thick-walled, rounded-rectangular, radially flattened in transverse section. The late wood occupies about 1/5–1/3 of the growth ring width. Resin canals and axial parenchyma are absent.

Pits on the radial walls of tracheids are uniseriate, but sometimes biseriate pairs of pits occur (Fig. 3B, C). The pits are circular (10–13 µm in diameter) or elliptical (12 × 15 µm in size), horizontally elongated, with circular and elliptical apertures, respectively; pits are scattered or more rarely contiguous, distributed all along the tracheid length. Crassulae are absent. Pits on the tangential walls of tracheids were not observed.

Helical thickenings are present on longitudinal tracheid walls. The helical thickenings are well developed on the radial and tangential walls of tracheids, sometimes single but mostly grouped in pairs, running parallel and widely spaced (Fig. 3C–E). The helical thickening angles on the wall of the tracheid range from 30° to 50°.

Rays are not numerous, uniseriate, rarely with short biseriate parts (one-two layers), 1–10 cells high (Fig. 3H). Horizontal and end walls of ray cells are smooth, unpitted (Fig. 3F). Median ray cells are rounded or elliptical, radially elongated; marginal ray cells are elliptical, rounded-triangular and approximately of the same size as the median cells (Fig. 3H). Ray tracheids are absent. Cross-field pits are poorly preserved, possibly cupressoid or taxodioid type, 4–5 µm in diameter, about one-three pits per cross-field (Fig. 3G).

Identification. The combination of helical thickenings in tracheids, smooth unpitted walls of ray cells, and absence of resin canals and ray tracheids is characteristic of modern Taxaceae (Phillips, 1948; Yatsenko-Khmelevsky, 1954; Greguss, 1955; Chavchavadze, 1979), which includes six genera: *Amentotaxus* Pilger, *Austrotaxus* R.H. Compton, *Cephalotaxus* Siebold & Zuccarini *ex* Endlicher, *Pseudotaxus* W.C. Cheng, *Taxus* L. and *Torreya* Arnott *nom. cons.* (Ghimire and Heo, 2014).

The presence of distinct growth rings, helical thickenings in tracheids (single or grouped in pairs), and the absence of axial parenchyma suggest that the studied fossil has affinities with modern *Pseudotaxus*, *Taxus* and *Torreya*.

Kräusel and Jain (1964) proposed the morphogenus *Taxaceoxylon* for fossil woods that show definitive affinity with the modern representatives of Taxaceae. We assigned the fossil wood described here to this morphogenus. The names *Taxoxylon* Unger and *Taxoxylon* Houlbert should definitively be avoided for this purpose (Philippe and Bamford, 2009). *Taxaceoxylon* has mainly been reported from the Lower Cretaceous (Bhardwaj, 1952; Kräusel and Jain, 1964; Sharma, 1970) to the Pleistocene (Shimakura, 1936; Kräusel and Jain, 1964) of the Northern Hemisphere, however this record needs reappraisal. Only two records of *Taxaceoxylon* were reported from Russia. One is *T. saghalienense* H. Nishida & M. Nishida from the Turonian–Coniacian (Upper Cretaceous) of Sakhalin Island, Russian Far East (H. Nishida and Nishida, 1986b) and the other is *T. jarmolenkoi* Shilkina from the Valanginian (Lower Cretaceous) of the Kirov Region, European Russia (Shilkina, 1989).

Among the species of *Taxaceoxylon* previously described, the studied fossil shows most similarity to the above-mentioned species of *Taxaceoxylon* from the Cretaceous of Russia. However, it differs from both *T. saghalienense* and *T. jarmolenkoi* in the inclination angle of its spirals, the presence of some biseriate pits on the radial walls of tracheids and in its partially biseriate rays. From *T. saghalienense* it differs in the absence of pits on the tangential walls of tracheids. Nevertheless, the preservation of the studied specimen is insufficient for a clear identification. Therefore, this material will be referred to as *Taxaceoxylon* sp.

Morphogenus *Xenoxylon* Gothan, 1905
Type species. *Xenoxylon latiporosum* (Cramer) Gothan, 1905

Xenoxylon phyllocladoides Gothan, 1906
Fig. 4A–F.

Material. One sample, n°. IBSS 23/1-2, 8 cm in length, transverse section (tangential × radial) 2 × 6.5 cm; three thin sections (transverse, radial, tangential).

Locality, stratigraphic horizon, stage. Melkaya River, Talovka River Basin, Kamchatka Peninsula, Russian Far East, Kedrovka Formation, upper Lower Cretaceous (Albian).

Description. Growth rings are distinct, 1.2–1.8 mm wide; the transition from the early wood to the late wood is abrupt (Fig. 4A). Early wood tracheids are thin-walled, with broad lumen, rounded, rounded-square, rounded-rectangular and rounded-polygonal in

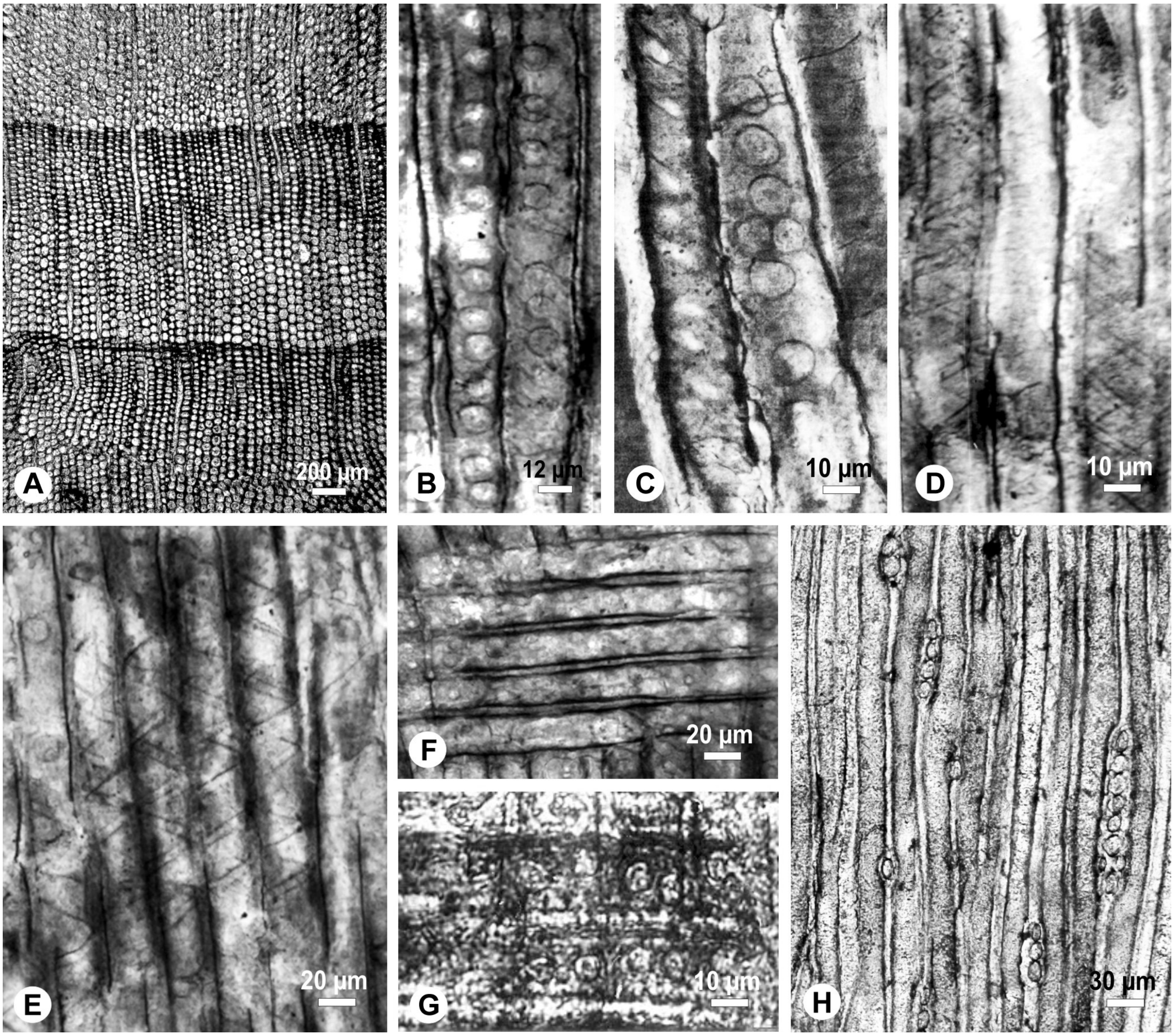

Fig. 3. Photomicrographs of *Taxaceoxylon* sp. (sample n°. IBSS 23/10). A. Transverse section showing distinct growth rings and gradual transition from the early wood to the late wood. B. Radial section showing one row of radial tracheid bordered pits. C. Radial section showing one and two rows of radial tracheid bordered pits and helical thickenings on longitudinal tracheid walls. D, E. Radial sections showing helical thickenings on longitudinal tracheid walls. F. Radial section showing smooth transverse end walls of ray cells. G. Radial section showing cupressoid or taxodioid cross-field pits. H. Tangential section showing uniseriate rays and uniseriate ray with biseriate part.

transverse section. Late wood tracheids are thick-walled, rounded-rectangular, radially flattened in transverse section. Resin canals and axial parenchyma are absent.

Pits on the radial walls of tracheids are uniseriate or rarely biseriate (Fig. 4B–D). The uniseriate pits are circular (17–19 μm in diameter) and elliptic (15–18 × 21–24 μm in size), horizontally elongated, with circular and elliptic apertures, respectively; pits are contiguous or separated, rarely compressed. The biseriate pits are circular, 15–17 μm in diameter, with circular apertures, opposite. Crassulae are absent. Pits on the tangential walls of tracheids are rare, uniseriate, circular, 10–12 μm in diameter, with circular apertures; tangential pits are distant along the tracheid length (Fig. 4F).

Rays are uniseriate, rarely with short biseriate parts (one to two layers), and 1–10(17) cells high (Fig. 4F). Horizontal and end walls of ray cells are smooth (unpitted). Median ray cells are rounded and elliptical, radially elongated; marginal ray cells are elliptical, rarely rounded-triangular (Fig. 4F). Ray tracheids are absent. Cross-field pits are large, simple or slightly bordered, window-like type, one or rarely two per cross-field (Fig. 4D, E). Their size is 12–17 × 19–33 in vertical × horizontal diameter.

Identification. The present fossil is assigned to *Xenoxylon* Gothan based on the following features: distinct growth rings, smooth (unpitted) ray cell walls, single large window-like pit in the cross-field, and absence of resin canals and ray tracheids.

The morphogenus *Xenoxylon* was proposed by Gothan (1905) for fossil woods previously described by Cramer (1868) as *Pinites latiporosus* from the Mesozoic of West Spitsbergen. *Xenoxylon* is a common wood from the Mesozoic of the Northern Hemisphere. Unfortunately, despite the large amount of data for *Xenoxylon*, its systematic position among conifers is still unclear (Marynowski et al., 2008). *Xenoxylon* species were reported from the Carnian (Upper Triassic) to the Maastrichtian (Upper Cretaceous) of the Northern Hemisphere (see e.g. Philippe et al., 2013). The following species of this morphogenus were documented from Russia: *X. meisteri* Palibin & Jarmolenko from the Cretaceous of Eastern

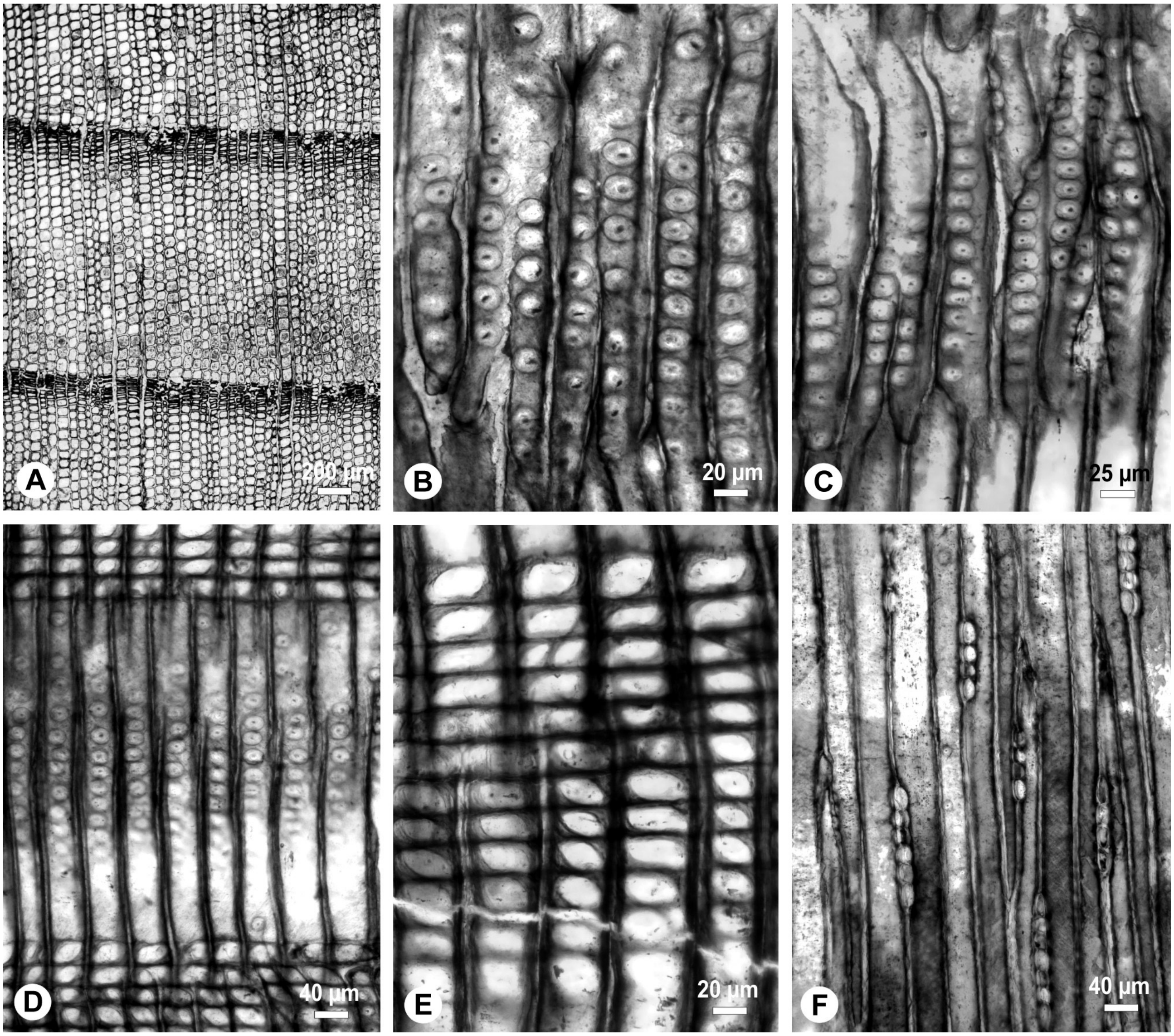

Fig. 4. Photomicrographs of *Xenoxylon phyllocladoides* (sample n°. IBSS 23/1-2). A. Transverse section showing distinct growth rings and abrupt transition from the early wood to the late wood. B. Radial section showing one row of radial tracheid bordered pits. C. Radial section showing one and two rows of radial tracheid bordered pits. D. Radial section showing one row of radial tracheid bordered pits and window-like cross-field pits. E. Radial section showing window-like cross-field pits. F. Tangential section showing uniseriate rays and tangential tracheid bordered pits.

Table 1
Mesozoic record of *Taxoxylon* Unger and *Taxaceoxylon* Kräusel & Jain. *Taxoxylon anglicum* Stopes is considered as doubtful (Kräusel, 1919).

Taxon	Reference	Origin	
Taxaceoxylon japonomesozoicum	Nishida, 1973	Cretaceous, Japan	**type seen**; mixed type of radial pitting, Sanio's Rim but no spiral thickenings
Taxaceoxylon jarmolenkoi	Shilkina, 1989	Valanginian, Kirov area, Russia	from its protologue this wood has distant paired transversal thickenings of tracheid wall, most of them subhorizontal, sometimes oblique, never building convincing spirals
Taxaceoxylon mcmurrayensis	Roy, 1972	Lower Cretaceous, Alberta, Canada	from the protologue "spirals" are alteration cracks within the S2 layer (fig. 4) and preservation artefacts (fig. 7)
Taxaceoxylon rajmahalense	Bhardwaj, 1952 (as *Taxoxylon*)	Lower Cretaceous, India	this wood is illustrated in its protologue as having a peculiar dense network of transversal almost horizontal thickenings; it apparently has mixed type of radial pitting, but is not well preserved
Taxaceoxylon saghalinense	H. Nishida & M. Nishida, 1986b	Turonian–Coniacian, Sakhalin, Russia	from its protologue this wood has distant paired transversal thickenings of tracheid wall, most of them subhorizontal, sometimes oblique, rarely building convincing spirals
Taxaceoxylon sp.	Kahlert et al., 1999	cf. Aptian, Tanzania	not convincingly illustrated in its protologue
Taxoxylon anglicum	Stopes, 1915	?	type seen; no convincing spirals
Taxoxylon antiquum	Boeshore and Gray, 1936 (as *Torreya antiqua*) assigned to *Taxoxylon* by Kräusel (1919: 151)	Black Creek Formation (Campanian – to Santonian?), North Carolina, USA	Well illustrated in its protologue and completely convincing as a wood related to the Taxaceae.
Taxoxylon cretaceum	Unger, 1859	Cretaceous, Germany	**type seen**; poorly preserved
Taxoxylon indicum	*nomen nudum* in Lakhanpal et al., 1976	Lower Cretaceous, India	?
Taxoxylon liaoxiense	Duan, 2000	Shahai Formation (?Aptian), Liaoning, China	the original illustration is poor, the occurrence of spirals is not safe and the radial pittings is obscure
Taxoxylon philpii	Shirley, 1902	Triassic, Queensland, Australia	**type seen**; poorly preserved, araucarian radial pitting
Taxoxylon pulchrum	He Dechang, 1995	Yimin Formation, Lower Cretaceous, Inner Mongolia, China	from its protologue this wood has distant paired transversal thickenings of tracheid wall, most of them almost horizontal, sometimes oblique, never building convincing spirals

Siberia (Palibin and Yarmolenko, 1932); *X. latiporosum* from the Upper Triassic and Lower Cretaceous of Franz Josef Land (Shilkina, 1967), the Lower Jurassic – Lower Cretaceous of Western and Eastern Siberia (Nashchokin, 1968; Shilkina and Khudaiberdyev, 1971) and the Lower Cretaceous of Russian Far East (Afonin, 2008); *X. barberi* (Seward) Kräusel (this name is however p.p. a synonym of *X. huttonianum*, see Philippe and Hayes, 2010) from the Lower Cretaceous of Franz Josef Land (Shilkina, 1967) and the Lower Jurassic – Lower Cretaceous of Eastern Siberia (Shilkina and Khudaiberdyev, 1971); *X. hopeiense* from the Lower Cretaceous of Eastern Siberia (Shilkina and Khudaiberdyev, 1971) and the Russian Far East (Afonin, 2008); [*X. jakutiense*] from the Lower Cretaceous of Eastern Siberia (Shilkina, 1986, a *nomen nudum*) and eventually *X. watarianum* M. Nishida & H. Nishida from the Upper Cretaceous of the Russian Far East (M. Nishida and Nishida, 1986a). Recent taxonomical and nomenclatural reappraisal of the genus *Xenoxylon* (Philippe et al., 2013) evidenced that the Russian record should be revised.

Among *Xenoxylon* species, the studied fossil is most similar to *X. phyllocladoides*, which was first described by Gothan (1906) from the Middle Jurassic of Poland. It fits well with the recently designated topotype (Philippe et al., 2013). The main diagnostic characteristics of this species are the presence of round uniseriate spaced sometimes biseriate opposite pits together with round contiguous and more rarely xenoxylean pits on the radial walls of tracheids, rare pits on the tangential walls of tracheids, cross-field oopores 1–2(3) times as wide as high, and absence of axial parenchyma and crassulae between pits on the radial walls of tracheids.

The discovery of *X. phyllocladoides* from the Lower Cretaceous of Kamchatka Peninsula extends the stratigraphic range of this taxon to the Albian age. Moreover, this is the first univocal record of *X. phyllocladoides* from Russia.

5. Discussion

5.1. Contribution to the fossil wood record of the Taxaceae

Countless artefacts have been interpreted as spiral thickenings in fossil woods: S2 layer alteration streaks, compression wood spiral splits, permineralizing crystal striations, diagenetic cracks, etc. Moreover, tertiary thickenings usually described as callitroid thickenings were also used to assign some wood to *Taxaceoxylon* (see e.g. *Taxoxylon pulchrum* from the Lower Cretaceous of Mongolia in He Dechang, 1995). Nomenclaturally, authors have used either *Taxoxylon* Unger or *Taxaceoxylon* for woods with features similar to those of modern Taxaceae. Eventually, woods with different types of radial pitting were assigned to these genera. As a result the Mesozoic record of Taxaceae-like wood is most confusing.

Table 1 synthesizes the Mesozoic record of *Taxaceoxylon* and *Taxoxylon*, two names which were widely used as taxonomical synonyms for *Taxus*-like fossil woods with spiral tertiary thickenings and abietinean radial pitting. Table 1 does not consider woods which, like *Protocallitrixylon* Yamazaki & Tsunada, were described as having both tertiary spirals and a mixed type of radial pitting, as their affinities are dubious. As a matter of fact, species in Table 1 mostly do not build convincing spiral tertiary thickenings. *Taxoxylon rajmahalense* is poorly preserved and apparently has quite peculiar thickenings. Three species only display clearly unequivocal tertiary thickenings, *Taxaceoxylon jarmolenkoi, T. saghalinense* and *Taxoxylon pulchrum.* Interestingly within these three species

Table 2
Far-East Asia fossil wood record for the Aptian–Cenomanian interval.

	Northern China (Fuxin and Chengzihe formations, Aptian–Albian)	Korea (north & south) (Hayang Group)	Northeastern Japan (Iwate Prefecture)	Kamchatka (Kedrovka Formation, Albian)
Palaeolatitude	45°N	35°N	32°N	50°N
Palaeoclimate	Cool temperate continental	Temperate continental	Warm temperate oceanic	Cool temperate possibly oceanic
Wood flora	*Phoroxylon* *Protocedroxylon s.l.* *Xenoxylon*	*Agathoxylon Brachyoxylon* *Circoporoxylon* *Taxodioxylon*	*Agathoxylon* *Brachyoxylon* *Podocarpoxylon*	*Protocedroxylon s.l.* *Taxaceoxylon* *Xenoxylon*

thickenings are often paired and mostly almost horizontal. They are often spaced in a way which demonstrates they did not build spirals. In each of these woods, however, in some other parts, clear spirals are also formed. These are usually paired, as is also the case in the Kamchatka material. The latter do not seem to have sub-horizontal thickenings, nevertheless.

The woods *Taxaceoxylon jarmolenkoi, T. saghalinense, Taxoxylon pulchrum* and the Kamchatka material all come from the Cretaceous, from a narrow latitudinal interval, within the same palaeobiogeographical area (Northern Eurasia), and were all found associated with wood of the *Protocedroxylon* type (sensu lato). This is of interest because according to recent cladistic analyses (Ghimire and Heo, 2014) the Taxaceae are a monophyletic clade, related to the Pinaceae, and originating from the Northern Hemisphere. Our results completely corroborate these conclusions with the earliest Taxaceae-like fossil woods being found associated with *Protocedroxylon*, which was probably the wood of primitive Pinaceae (Philippe and Hayes, 2010), and associated with *Xenoxylon* which characterizes Mesozoic cool temperate northern biota (Philippe and Thévenard, 1996; Oh et al., 2013). As the Mongolian material is not well dated, the new material from Kamchatka is important as it attests that already by the Early Cretaceous Taxaceae-like woods were distributed over a large area, ranging from west of the Urals to the Russian Far-East.

5.2. *Early Cretaceous palaeobiogeography of Asian Far East*

Table 2, compiled from Oh et al. (2011, 2013) kindly edited by Dr. Kazuo Terada (pers. com.) and our new data, summarizes the Aptian–Cenomanian fossil wood record in Far-East Asia. At the generic level the Kedrovka Formation fossil wood flora has most similarities with those of northern China. It does not include any thermophilic elements like *Agathoxylon* or *Brachyoxylon* Hollick & Jeffrey. Table 2 confirms that a strong gradient existed for terrestrial climate over Far East Asia in the late Early Cretaceous (Amiot et al., 2011) and that Kamchatka had a cool temperate climate. The occurrence of *Taxaceoxylon*, yet unrecorded in coeval Asian strata (otherwise with a well documented fossil wood record; Oh et al., 2011) is of interest in so far as it suggests that Kamchatka Albian palaeobiogeography was somewhat peculiar. This could possibly be an oceanic influence as Kamchatka was located close to the Pacific at that time. Interestingly such oceanic influenced climate also existed during the Valanginian, west of the Urals in the Kirov area, from where *T. jarmolenkoi* is reported. In contrast it was absent from most of Siberia, Mongolia and northern China, where *Taxaceoxylon* has not yet been reported, despite the occurrence of numerous and well studied fossil wood floras (Zheng et al., 2008; Oh et al., 2011). The case of northeastern Japan is also of interest a possibly coeval late Early Cretaceous wood flora was recorded by Shimakura (1937) from the Iwate Prefecture, featuring *Agathoxylon*, *Brachyoxylon* and *Podocarpoxylon* Gothan (as taxonomically reappraised by us from Shimakura's original material). This flora was deposited and probably grew in a coastal setting, under influence of an oceanic climate. As compared to the South-Korea wood flora, roughly at the same latitude but much more continental, the Japanese flora is similar in displaying both *Agathoxylon* and *Brachyoxylon*, and differs in having *Podocarpoxylon* instead of *Circoporoxylon* Kräusel. Those two genera, however, are similar. Coastal and continental floras were seemingly less differentiated at these latitudes than northward. The Iwate flora lacks *Taxaceoxylon*, confirming it was bound to more temperate climate. Whatever the reason for the peculiar ecology of Kamchatka area during the Early Cretaceous, it might also explain why *Xenoxylon phyllocladoides* survived there whereas it had disappeared from elsewhere.

6. Conclusions

Three coniferous fossil wood taxa, *Protocedroxylon gregussii*, *Taxaceoxylon* sp. and *Xenoxylon phyllocladoides*, are described from the Kedrovka Formation (Albian) of Kamchatka Peninsula, Russian Far East.

The Kedrovka Formation wood flora is quite peculiar when compared to coeval wood floras from the same area. It yields the first safe report of *Taxaceoxylon* fossil wood from the Lower Cretaceous of Asia. The record of *Xenoxylon phyllocladoides* represents the latest stratigraphic occurrence of this species and the first from Russia.

Taxaceae-like fossil wood record is reappraised and shown to be consistent with recent cladistic results, suggesting a boreal origin and a link to the Pinaceae.

The occurrence of *Taxaceoxylon*, yet unrecorded in coeval Asian strata is of interest in so far as it suggests that Kamchatka Albian palaeobiogeography was somewhat peculiar.

The peculiarities of the Kedrovka Formation wood flora might be explained by an oceanic palaeoclimate.

Acknowledgements

The authors are grateful to Dr. Alexander Popov (Far Eastern Geological Institute FEB RAS, Vladivostok) for the provided fossil wood samples and to the staff of the grinding workshop (Far Eastern Geological Institute FEB RAS, Vladivostok) for preparing thin sections. Prof. Harufumi Nishida (Chuo University, Tokyo), Dr. Dario de Franceschi (Muséum national d'Histoire Naturelle, Paris), Dr. Dmitry Gromyko (Komarov Botanical Institute RAS, St. Petersburg) and Dr. Sue Parfrey (Queensland Geological Survey, Brisbane) kindly made it possible to review type materials. Dr. Christine Strullu-Derrien (Natural History Museum, London) is acknowledged for her help with literature.

A first version benefited much of editing by an anonymous reviewer, Dr. Kazuo Terada (Fukui Prefectural Dinosaur Museum, Japan) and editor Dr. Eduardo Koutsoukos.

This research was supported by the Presidium of the Russian Academy of Sciences (project no. 12-I-P-28-01 of the Program

«Problems of an Origin of Life and Biosphere Formation»), by the Presidium of Far Eastern Branch of the Russian Academy of Sciences (project no. 14-III-V-06-002) and Russian Foundation for Basic Research (project no. 14-04-31068 mol-a).

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