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Source: Acta Palaeontologica Polonica, 60(1) : 245-256

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0132

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Xenoxylon synecology and palaeoclimatic implications for the Mesozoic of Eurasia

CHANGHWAN OH, MARC PHILIPPE, and KYUNGSIK KIM



Oh, C., Philippe, M., and Kim, K. 2015. *Xenoxylon* synecology and palaeoclimatic implications for the Mesozoic of Eurasia. *Acta Palaeontologica Polonica* 60 (1): 245–256.

The distribution of fossil wood genera has been demonstrated to be an effective proxy for Mesozoic terrestrial climates. In this study, we investigated the phytocoenoses, which were associated with *Xenoxylon* confirmed to be a marker for a cool and/or wet climate in a boreal hemisphere (i.e., *Xenoxylon*-phytocoenoses) during the Mesozoic, using specimens of fossil wood. It was confirmed that *Xenoxylon* co-occurs more often with some wood genera than with others. For example, *Protocedroxylon*, a wood that is most likely related to the Pinaceae, is the genus most often associated with *Xenoxylon*-phytocoenoses. Although *Taxodioxylon* is also found in *Xenoxylon*-phytocoenoses, it is not found, however, as consistently as *Protocedroxylon*. The distribution and diversity of *Xenoxylon*-phytocoenoses changed throughout the Mesozoic. During the Late Triassic and Late Cretaceous, *Xenoxylon*-phytocoenoses had low diversity and were restricted to higher palaeolatitudes during the Late Cretaceous. However, during the Early to Middle Jurassic, *Xenoxylon*-phytocoenoses were distributed much farther south, while their diversity concomitantly increased sharply. From the Late Jurassic to the Early Cretaceous, the distribution of *Xenoxylon*-phytocoenoses moved northward in Europe and even more so in East Asia. The changes in the distribution of *Xenoxylon*-phytocoenoses are in agreement with changes in both global and regional climates. Our results also demonstrated that, within the *Xenoxylon* distribution range, the corresponding phytocoenoses were differentiated along a latitudinal gradient and according to the global climate change patterns during the Mesozoic.

Key words: Fossil wood, *Xenoxylon*-phytocoenoses, palaeoecology, palaeoclimate, Mesozoic, Eurasia.

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Received 11 December 2012, accepted 3 July 2013, available online 17 July 2013.

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Introduction

As the need to understand the long term evolution of climate has become a major scientific challenge, Mesozoic palaeoclimates have been revealed to be of great interest. With a distribution of continental masses different from the current one, during a globally warm climatic mode, and during a now well-documented and important shift in pCO^2, Mesozoic conditions are an interesting point of comparison for understanding the relative roles of major climate determinants. Several recent papers (e.g., Gröcke et al. 2003; Galli et al. 2005; Joral et al. 2011) focused on specific events, such as the Toarcian Oceanic Anoxic Event (OAE) (Mailliot et al. 2009; Gomez and Goy 2011), in order to decipher the determinism of major Mesozoic climate shifts. Most studies, if not all, have focused on the marine realm, as data from terrestrial environments are relatively scarce.

As trees are long-lived sessile organisms, they are of interest for documenting terrestrial environments, and in particular, climate changes at various scales. Using Quaternary trees, growth-rings are often used as a climate proxy. However, such an approach is difficult to transpose to the Mesozoic (Brison et al. 2001). In the fossil record, trees are represented by avatars, such as fossilised leaves, pollen, and wood. Fossilised wood is of interest for palaeoecological syntheses, as it is not very mobile and is more resistant than other plant megafossils. However, due to their rather chaotic systematics and nomenclature, fossilised wood samples have not frequently been used for palaeoecological purposes (Philippe 1993). Recently, nomenclatural (Philippe and

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Bamford 2008) and taxonomic (Philippe 1994; Philippe and Hayes 2010; Philippe et al. 2013) reappraisals of fossilised wood genera have been carried out. These reappraisals now allow for a reconsideration of the fossil record for wood, in search of global distribution patterns.

The distribution of fossil wood genera has been demonstrated to be an efficient proxy for Mesozoic terrestrial climates (Tsunada and Yamazaki 1984; Philippe et al. 2004; Oh et al. 2011). Specifically, the distribution of the wood of the extinct (Late Triassic to Late Cretaceous) conifer genus *Xenoxylon* Gothan, 1905 was confirmed as being a potential marker of a cool and/or wet climate in the boreal hemisphere (Philippe and Thévenard 1996; Philippe et al. 2009). Inferences from the *Xenoxylon* distribution data recently received support when they found agreement with the results obtained from analysing oxygen isotopes in vertebrate tooth enamel from the Cretaceous in Far-East Asia (Amiot et al. 2011).

In our current study, we investigated fossilised wood specimens associated with *Xenoxylon*, i.e., *Xenoxylon*-phytocoenoses. During preliminary research, we had noticed that *Xenoxylon* often co-occurs with two other wood genera, *Protocedroxylon* Gothan, 1910 and *Taxodioxylon* Hartig, 1848, in Far-East Asia. The frequent association of these genera in assemblages of fossilised wood was first noted by Gothan (1910). Since then, several researchers have noticed that *Protocedroxylon* and *Xenoxylon* often co-occurred (Shilkina 1967; Shilkina and Khudayberdyev 1971; Yamazaki and Tsunada 1981). Yamazaki and Tsunada (1982: 605) hypothesised that the corresponding trees may have inhabited similar ecologies. The co-occurrence of these genera was later hypothesised as being characteristic of cool and wet temperate climates (Philippe and Hayes 2010: 61). However, no study has yet investigated the association of *Xenoxylon* with other wood genera.

Therefore, this study addresses the synecology of *Xenoxylon*, a fossil wood genus that is restricted to the Mesozoic of Eurasia, and asks the following questions: Was *Xenoxylon* a part of diversified vegetation? When and where did this (these) phytocoenosi(e)s appear, spread, and disappear? Does the geographic distribution of this (these) phytocoenosi(e)s provide a climatic signal?

Institutional abbreviations.—BMNH, Natural History Museum in London; BIN, Komarov Botanical Institute of the Russian Academy of Sciences in Saint Petersburg; CBNU, Chonbuk National University, South Korea; HMB, Humboldt Museum in Berlin; NCU, Prof. Nishida's collection at Chuo University in Tokyo; NHMD, Natural History Museum of Denmark in Copenhagen; SMNH, Swedish Museum of Natural History in Stockholm; TUMS, Tohoku University Museum in Sendai.

Other abbreviations.—DI, diversity index; EMJ, Early to Middle Jurassic; FAD, First Appearance Date; GD, the number of genera; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous; LT, Late Triassic; N, the number of occurence; OAE, Oceanic Anoxic Event.



Fig. 1. **A**. In situ erect stump of Mesozoic *Xenoxylon* from Bayakodan, near Kuwajima in Shiraminemura, Japan. Used with the permission of Kazuo Terada (specimen no. 53901 in Suzuki and Terada 1992). **B**. Typical xenoxylean radial pitting and window-like cross-field pits in radial section of *Xenoxylon* (slide CBNU 73112).

Historical background

Xenoxylon is one among the approximately fifty Mesozoic fossil wood genera (Philippe and Bamford 2008). Its secondary xylem has distinctive anatomical features, which have no equivalents among extant wood, i.e., radial bordered pits that are exclusively, or at least partly, flattened and contiguous (xenoxylean radial pitting) and one or rarely two window-like simple cross-field pits in the early wood (Fig. 1).

There have been several arguments related to *Xenoxylon*'s systematic affinity. For example, *Podozamites* Braun, 1843, *Baiera* Braun, 1843, *Sciadopitys* Siebold and Zucc, 1842, or some extant Podocarpaceae have been suggested as its allied taxa (Nathorst 1897; Jarmolenko 1933; Arnold 1953; Bailey 1953; Shilkina and Khudayberdyev 1971). More recently, based on geochemical analysis, it appeared that *Xenoxylon* was closer to the Podocarpaceae, Cupressaceae sensu lato, and to a lesser extent, to the Cheirolepidiaceae than to the Pinaceae and Araucariaceae (Marynowski et al. 2008). The latter authors also suggested that *Xenoxylon* could be related to the Miroviaceae, which is an extinct Mesozoic conifer family. However, because *Xenoxylon* has never been found connected with foliage or any reproductive structures, it is difficult to make a decision about its systematic position.

Although the systematic position of this morphogenus is unclear, it is considered to be a monophyletic taxon (Marynowski et al. 2008). In addition, it is a bioindicator for a cool and/or wet climate (Philippe and Thévenard 1996; Philippe et al. 2009).

Material and methods

Time intervals and geographic subdivisions.—The *Xenoxylon* time range covers the Late Triassic–Late Cretaceous interval. As significant palaeobiogeographic changes occurred

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in the Northern Hemisphere during this time interval, we subsequently subdivided the interval into four more palaeoecologically uniform time slices: the Late Triassic (LT); the Early to Middle Jurassic (EMJ); the Late Jurassic to Early Cretaceous (LJEK); and the Late Cretaceous (LK). None of these are perfectly homogeneous, but separating the data onto more time slices would affect the significance.

Asia is here defined as the continental area east of a line running from the Ural Mountains southward to the Caucasus and then westwards to the Bosporus. Greenland is here included in Europe, as it was a part of that continent during that time. We investigated the palaeogeographic distribution of fossilised wood assemblages containing *Xenoxylon* specimens. For this purpose, we merged data, on the basis of geographic origin, into twenty-two super-localities (Table 1).

Data sources.—For this study, we performed a literature survey for Mesozoic fossilised wood, limiting ourselves to the assemblages that included *Xenoxylon*. We considered only fossilised wood data that were based on isolated secondary xylem (tracheidoxyls). Some unpublished data were also used, either established by samples sent by colleagues (see acknowledgments section), or obtained while revising collections at HMB, NHMD, BMNH, BIN, TUMS, SMNH, and NCU.

The process of extracting the data set considered in this paper was not an easy task. In order to decrease taxonomic biases, which are, unfortunately, all too common in the palaeoxylological literature, we decided to perform our analysis on the generic level. We also decided not to consider any fossilised wood assemblages that included *Protocedroxylon* and/or *Taxodioxylon* (two genera commonly associated with *Xenoxylon*) but not *Xenoxylon*, or those fossilised wood floras that were limited to *Xenoxylon* alone (like e.g., in Terada et al. 2011). Not considering *Xenoxylon*-free assemblages is a problem, as it limits the validity of co-occurrence results to the *Xenoxylon* distribution area. However, considering *Xenoxylon*-free assemblages would force us to incorporate a huge number of wood floras (a number estimated at over 300) into the data set that were far from being taxonomically and nomenclaturally uniform. Moreover, incorporating the *Xenoxylon*-free assemblages would be the equivalent of using negative data, which is always a perilous task in palaeontology. Finally, it must be kept in mind that fossilised wood taxa are fossil taxa; thus, two specimens belonging to the same fossil taxon did not necessarily originate from the same biological taxon. This is a strong limitation, but taking into account only those assemblages including both *Xenoxylon* and other genera, i.e., using a palaeoecological restriction, narrows the bias induced by form taxonomy.

Another limitation results from the incompleteness of the fossil record. Indeed, some *Xenoxylon* data might have been published for locations that have not been extensively sampled, or for which all wood specimens have not been determined. Little can be done about this limitation, as it is impossible to decipher a priori which assemblages may have been under-sampled.

Table 1. List of *Xenoxylon* super-localities.

No.	Super-localities	Continent
1	Sakhalin	Asia
2	Primorye	Asia
3	Japan	Asia
4	Korea (South and North Korea)	Asia
5	Northeastern China (Beijing, Liaoning, Jilin, Heilongjiang, and Inner Mongolia)	Asia
6	Central China (Henan)	Asia
7	Southern China (Guangdong)	Asia
8	Western China (Xinjiang)	Asia
9	Vietnam	Asia
10	Iran	Asia
11	Georgia	Asia
12	Uzbekistan	Asia
13	Southeastern Mongolia	Asia
14	Arctic (Franz Josef Land, Svalbard)	Europe
15	Poland	Europe
16	Germany	Europe
17	Lithuania	Europe
18	UK	Europe
19	Greenland	Europe
20	Alaska (Central North Slope)	North America
21	Canadian Arctic Archipelago (CAA)	North America
22	Canada (Alberta)	North America

To avoid redundancy, data in the database are understood to represent the occurrence of a fossil genus in a geological formation, not taking into account if this genus (or a synonym) had been reported several times from that formation, in one or several localities. Stratigraphically uncertain data were not considered for our study, specifically, the reworked fossilised wood assemblages from the Mekong River terraces (Vozenin-Serra and Privé-Gill 1991), or the loose wood assemblage from the Choshi area (Nishida et al. 1993). Several Mesozoic fossilised wood data points, particularly from China, are poorly age constrained. Geological formations were sometimes renamed after the original publication, or their age was reappraised. For Chinese data, we generally followed the recent review of Zheng et al. (2008).

A wood assemblage was reported from Korea by Kim et al. (2005) as being Late Triassic in age. However, the age of the corresponding Jogyeri Formation was subsequently revised to be Middle Jurassic by Egawa and Lee (2011).

Oh (2010), in his thesis, reported some fossilised wood assemblages, which included *Xenoxylon* from the Chengzihe and/or the Muling formations of the Jixi Group from the Early Cretaceous in Heilongjiang Province, China. Some of these fossilised wood specimens clearly originated from the Muling Formation, but the origin of some of the others was less clear; therefore, we grouped the two formations into one.

Parrish and Spicer (1988) reported two unidentified fossil wood taxa, taxon A and taxon B, with *Xenoxylon latiporosum* from the Nanushuk Group, Central North Slope, Alaska. The Nanushuk Group was then considered to be from the mid-Cretaceous (Albian to Cenomanian), based on Foramin-

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ifera (Sliter 1979) and palaeobotanical evidence (Spicer and Parrish 1986). Recently, the Nanushuk Group was renamed as the Nanushuk Formation, and its age was revised to be middle Albian to Cenomanian (Mull et al. 2003). According to Mull et al. (2003: 14), most of the formation is Albian; therefore, we assigned these fossilised wood assemblages to the Albian.

Nomenclature and taxonomy.—The nomenclature here follows Philippe (1993, 1995), Philippe and Bamford (2008), and Philippe and Hayes (2010).

In 2008, Philippe and Bamford suggested that the genera with Abietineentüpfelung (i.e., rounded pits occurring on the transverse wall of ray cells) *Metacedroxylon* Holden, 1913, *Protocedroxylon* and pro parte *Cedroxylon* Kraus in Schimper, 1870, might be synonyms of *Araucariopitys* Hollick and Jeffrey, 1909. However, examination by Philippe and Hayes (2010: 59–60) of a topotype for *Araucariopitys* revealed that this latter name should be used only for short shoots with preserved pith and araucarioid cross-fields, while *Protocedroxylon* should be used for tracheidoxyls with a clearly mixed type of radial pitting and few spaced taxodioid oculipores in the cross-fields. Some *Araucariopitys* species have been mentioned in our database, but all can be reassigned to *Protocedroxylon*. Consequently, we used *Protocedroxylon* here as the correct name for the data originally published for the study area and interval as *Cedroxylon*, *Metacedroxylon*, *Protocedroxylon*, and *Araucariopitys*.

In the case of araucaria-like fossilised woods (i.e., tracheidoxyls with araucarian radial pitting and araucarioid cross-field pitting, lacking Abietineentüpfelung and resin canals), many different names have been used until now (e.g., *Araucarioxylon* Kraus, 1870, *Dadoxylon* Endlicher, 1847, *Agathoxylon* Hartig, 1848, *Dammaroxylon* Schultze-Motel, 1966). Recently, the wood anatomist community was polled to clarify which name should be retained for araucaria-like fossilised wood (Rößler et al. 2014). In accordance with the conclusions from this poll, we used *Agathoxylon* here.

Despite these preliminary taxonomic reappraisals, the discrepancies between the systematic approaches of the various authors still obscured our database. Indeed, the same wood specimen can be assigned to different genera by different authors according to their taxonomic choices, e.g., a typical *Podocarpoxylon* Gothan, 1906, could be assigned to *Taxodioxylon* or to *Circoporoxylon* Kräusel, 1949 (see e.g., Müller-Stoll and Schultze-Motel 1989). It was considered to be too risky to revise all of the systematic attributions in the database only on the basis of the publications, without checking the types. Thus, to limit the taxonomical bias, during a second stage of data management, we chose to merge the data into seven informal taxonomical groups (Table 2), uniting similar-appearing genera. Group A (or the *Protocedroxylon* group) was for wood with Abietineentüpfelung, most likely related to the Pinaceae. Wood that resembled the extant Cupressaceae sensu lato was assigned here to group B (or the *Taxodioxylon* group). Group C (or the *Phyllocladoxylon* group) was for wood specimens with unbordered (or slightly bordered) oopores, which have unclear systematic affinities. Group D (the *Podocarpoxylon* group) contains wood specimens with taxodioid to podocarpoid oopores in the early wood cross-fields, and these mostly also have unclear systematic positions. All of the wood specimens having araucarian radial pitting and araucarioid cross-fields, group E, limited to *Agathoxylon*, appear more uniform, but certainly do not accommodate only the Araucariaceae and their relatives. Group F (*Brachyoxylon* group) is perhaps the most heteroclite, with wood specimens featuring a mixed type of radial pitting and araucarioid cross-fields. Group G is for all of the data that are not assigned to any of the previous groups. This partitioning does not mean that we consider that the various genera within each group are taxonomical synonyms or that they originate from the same botanical group, but only that the different genera in each group were often substituted one for the other in the literature, inconsistently, for the time interval we studied. The few wood specimen data that were nomenclaturally reassigned are listed in Table 3.

Table 2. Informal taxonomical groups of Mesozoic woods discussed in this study.

Group	Included morphotaxa
A (*Protocedroxylon*-group)	*Keteleerioxylon*, *Laricioxylon*, *Palaeopiceoxylon*, *Piceoxylon*, *Pinoxylon*, *Protocedroxylon*, *Protopiceoxylon*, *Protojuniperoxylon*
B (*Taxodioxylon*-group)	*Cupressinoxylon*, *Juniperoxylon*, *Taxodioxylon*
C (*Phyllocladoxylon*-group)	*Paraphyllocladoxylon*, *Phyllocladoxylon*, *Protophyllocladoxylon*, *Protosciadopityoxylon*, *Sciadopityoxylon*
D (*Podocarpoxylon*-group)	*Podocarpoxylon*, *Protopodocarpoxylon*, *Prototaxodioxylon*, *Protaxodioxylon*
E (*Agathoxylon*)	*Agathoxylon*
F (*Brachyoxylon*-group)	*Brachyoxylon*, *Protobrachyoxylon*, *Protocupressinoxylon*
G (others)	all the data which are not in groups A to F

Results

Our bibliographical review and unpublished observations allowed to assemble 148 data of co-occurrence (Supplementary Online Material, SOM available at http://app.pan.pl/app60-Oh_etal_SOM.pdf). On this basis, we prepared a table and a graph of the fossilised wood genera associated with *Xenoxylon* (Table 4 and Fig. 2), summarising the raw information for the entire time range for *Xenoxylon*, i.e., from the Late Triassic to the Late Cretaceous. Because the different nomenclatural approaches had induced an artificial scattering of data, the graphs of Fig. 2, were then redrawn to Fig. 3, using the taxonomic grouping (Table 5). The circle charts were drawn on the corresponding palaeomaps, illustrating the shares of the seven

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Table 3. The data of nomenclatural and taxonomically modified taxa in this study.

Original taxon name	Modifed taxon name or group	Reasons of modification	Reference
Prototaxoxylon persicum	*Prototelicoxylon*	invalidly published name	Nadjafi (1982)
Metataxodioxylon iranicum	*Protaxodioxylon*	invalidly published name	
Protopinoxylon fakhri	*Protocedroxylon*	invalidly published name	
taxon A	*Xenoxylon*	similar anatomical features	Parrish and Spicer (1988)
taxon B	*Protocedroxylon*-group	presence of pitted rays	
taxa C, D	*Protocedroxylon*-group	presence of fusiform rays	Spicer and Parrish (1990)
taxa B, E	*Protocedroxylon*-group	presence of ray tracheids	
Scotoxylon yanqingense	*Protojuniperoxylon*	*Scotoxylon* was named for a fossil wood having the secondary xylem of *Protojuniperoxylon* with primarily xylem and pith by Vogellehner (1968)	Zhang et al. (2000)
Planoxylon sp.	*Protocedroxylon*	*Planoxylon* is limited to the Cretaceous of southernmost Gondwana	Oh (2010)
Dacrydioxylon sp.	*Xenoxylon*	very similar anatomical features between both taxa and for logical explanation of *Dacrydioxylon*'s occurrence in Canadian Arctic	Selmeier and Groser (2011)

recognised taxonomic groups (A–G) in the geographically merged data (Figs. 5A, B, 6A, B). All of them have the same diameters, although they do not represent the same quantities of data. They merely reflect the relative frequencies of each taxonomic wood group at a specific super-locality.

Co-occurrence of *Xenoxylon* with other genera.—Fig. 2 shows that *Protocedroxylon* is the fossil genus most commonly associated with *Xenoxylon*. The co-occurrence of *Xenoxylon* with other genera is much more infrequent (at least 50% less common). Interestingly, *Agathoxylon* is more commonly associated with *Xenoxylon* than we expected based on previous results from Asia (Oh et al. 2011).

The association of the *Protocedroxylon* group with *Xenoxylon* in the fossil strata is reported for the entire time range of the latter, from the Late Triassic to the Late Cretaceous, shortly before *Xenoxylon* disappeared (Yamazaki et al. 1980; Yamazaki and Tsunada 1981; Nishida and Nishida 1986; Spicer and Parrish 1990). The *Protocedroxylon* group is usually dominant in the *Xenoxylon* wood assemblages, more markedly so during the Late Triassic and Late Cretaceous. The oldest *Xenoxylon–Protocedroxylon* co-occurrence is reported from the Late Triassic (Carnian to Norian) of the Nariwa and Mine groups in Japan (Yamazaki et al. 1980; Yamazaki and Tsunada 1981). In the Russian Arctic, Shilkina (1967) reported *Xenoxylon* with *Araucariopitys* (in this case, a taxonomic synonym of *Protocedroxylon*) in the Late Triassic of the Heiss Island formation in Franz Josef Land. The youngest *Xenoxylon* wood assemblage with the *Protocedroxylon* group is

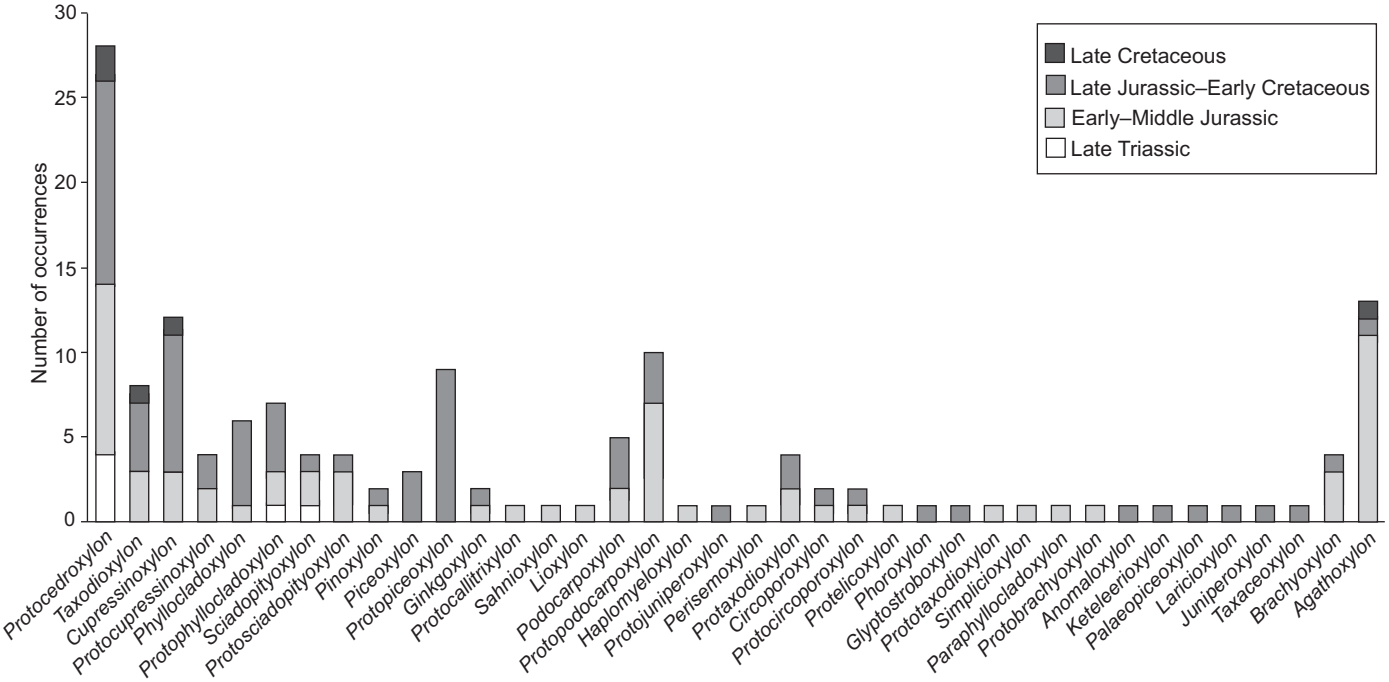


Fig. 2. Fossil wood genera co-occurring with *Xenoxylon* from the Late Triassic to the Late Cretaceous in Northern Hemisphere.

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Table 4. Number of fossil wood genera co-occurring with *Xenoxylon* from the Late Triassic to the Late Cretaceous in Northern Hemisphere. Abbreviations: LT, Late Triassic; EMJ, Early to Middle Jurassic; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous; A, Asia; E, Europe; NA, North America.

Genus	LT		EMJ		LJEK			LK		Total
	A	E	A	E	A	E	NA	A	NA	
Protocedroxylon	3	1	4	6	6	4	2	1	1	28
Taxodioxylon			2	1	3	1		1		8
Cupressinoxylon			1	2	4	3	1	1		12
Protocupressinoxylon			2		2					4
Phyllocladoxylon			1		4	1				6
Protophyllocladoxylon	1		2		4					7
Sciadopityoxylon	1		2		1					4
Protosciadopityoxylon			3		1					4
Pinoxylon			1			1				2
Piceoxylon					1	2				3
Protopiceoxylon					5	3	1			9
Ginkgoxylon			1		1					2
Protocallitrixylon			1							1
Sahnioxylon			1							1
Lioxylon			1							1
Podocarpoxylon			1	1	2	1				5
Protopodocarpoxylon			3	4	3					10
Haplomyeloxylon			1							1
Protojuniperoxylon					1					1
Perisemoxylon			1							1
Protaxodioxylon			1	1	2					4
Circoporoxylon			1		1					2
Protocircoporoxylon				1	1					2
Protelicoxylon			1							1
Phoroxylon					1					1
Glyptostroboxylon					1					1
Prototaxodioxylon				1						1
Simplicioxylon				1						1
Paraphyllocladoxylon				1						1
Protobrachyoxylon				1						1
Anomaloxylon						1				1
Keteleerioxylon						1				1
Palaeopiceoxylon						1				1
Laricioxylon						1				1
Juniperoxylon						1				1
Taxaceoxylon						1				1
Brachyoxylon				3		1				4
Agathoxylon			2	9	1			1		13

dated as Campanian to Maastrichtian, from the Central North Slope, Alaska (Spicer and Parrish 1990).

The first association of *Xenoxylon* with *Taxodioxylon* is mentioned from the Liassic (Lower Jurassic) of the Toyama Prefecture, Japan (Suzuki et al. 1982). This time frame is also the First Appearance Date (FAD) for the latter genus. Group B (*Taxodioxylon* group) is found associated with *Xenoxylon* during the entire Jurassic–Cretaceous interval. This group is one of the few groups that remained associated with *Xenoxylon* during the Late Cretaceous (Fig. 3).

Xenoxylon is also associated at several stages during the Late Triassic–Early Cretaceous interval with the *Phyllocladoxylon* group (group C) (Fig. 3). It must be emphasised, however, that some of the wood specimens included in the group C appear to be poorly preserved and/or taphonomically biased *Xenoxylon* specimens.

In contrast, *Xenoxylon* is rarely associated with the *Agathoxylon* or *Brachyoxylon* groups (groups E and F) (Fig. 3). Such associations are commonly reported only from the Middle Jurassic, mostly in Europe and sometimes in the Middle East and East Asia (e.g., Gothan 1906; Holden 1913; Kim et al. 2005; Poole and Ataabadi 2005; Marynowski et al. 2008). However, the Middle Jurassic fossilised wood record in East Asia, is rather limited (Oh et al. 2011). Neither of the two genus groups (E and F) co-occurred with *Xenoxylon* during the Late Triassic. After the Middle Jurassic, the genera *Agathoxylon* and *Brachyoxylon* became almost exclusively disassociated from *Xenoxylon* in Far-East Asia and in Europe as well (Fig. 3). During the Late Cretaceous, *Agathoxylon* was only found associated with *Xenoxylon* once, in Sakhalin (Nishida and Nishida 1986).

Several other genera of wood specimens are only occasionally associated with *Xenoxylon*. The small number of data, as well as the broad spectrum of possible biological affinities for these fossilised wood genera (specifically, *Podocarpoxylon* Gothan, 1906) make interpretations difficult and risky.

Evolution of the diversity of *Xenoxylon*-taphocoenoses.—For the Late Triassic, the fossilised wood assemblages containing *Xenoxylon* have a low diversity globally (3 genera) (Fig. 4). After the Triassic, the global generic diversity of *Xenoxylon*-taphocoenoses increased to 27 genera for the Early to Middle Jurassic interval, as shown in Fig. 4, with a well distributed share for the different genera, although the *Protocedroxylon* group (A), the *Podocarpoxylon* group (D), and *Agathoxylon* (E) are co-dominant (Fig. 3). The diversity remained high (28 genera) during the Late Jurassic to Early Cretaceous interval, but the contributions from groups D, E, and F decreased, in favour of those from groups B (*Taxodioxylon* group) and C (*Phyllocladoxylon* group) (Figs. 3, 4). For the Late Cretaceous, the number of associations reported in the database is low (Fig. 4), and their generic diversity is

Table 5. Number of data for the seven taxonomical groups and for four intervals. Abbreviations: LT, Late Triassic; EMJ, Early to Middle Jurassic; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous (for the composition of each taxonomical group see Table 2).

Group	LT	EMJ	LJEK	LK	Total number
A	4	10	21	2	37
B		5	11	1	17
C	2	5	9		16
D		11	7		18
E		11	1	1	13
F		6	3		9
G		8	5		13

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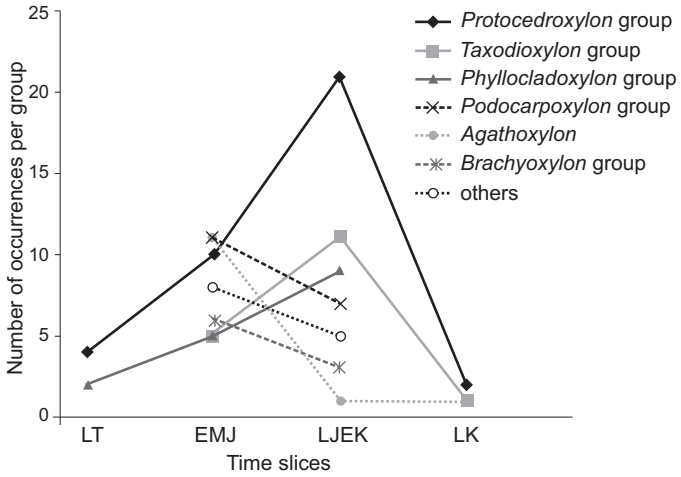


Fig. 3. Number of data for each taxonomical wood group (for the composition of each taxonomical group see Table 2); LT, Late Triassic; EMJ, Early to Middle Jurassic; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous.

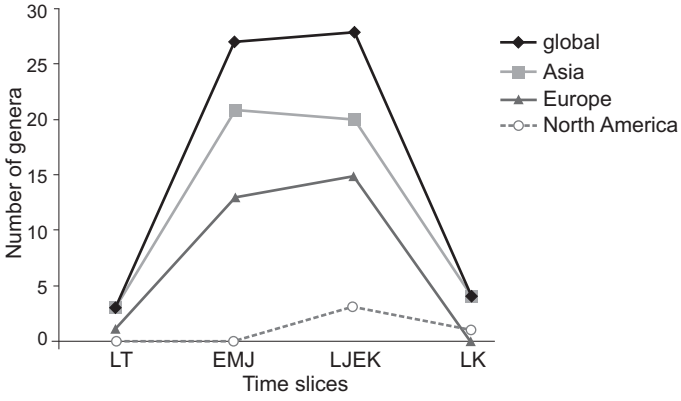


Fig. 4. Generic diversity of *Xenoxylon* wood-assemblages during the Mesozoic times—global curve and curve for specific geographic areas. Note that the real diversity was probably much lower, because of taxonomical bias. Abbreviations: LT, Late Triassic; EMJ, Early to Middle Jurassic; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous.

low as well (4 genera). The *Protocedroxylon* group remained dominant (Fig. 3). The evolution of the generic diversity in the *Xenoxylon* wood assemblages from the various geographic areas is relatively similar, while Asia hosts more diversity for every stage. North America only had a *Xenoxylon* wood flora in its northernmost regions (Canada) and only during a short period (late Early Cretaceous) (Gordon 1932; Arnold 1953; Parrish and Spicer 1988; Selmeier and Grosser 2011).

The palaeobiogeographic distribution of *Xenoxylon*-taphocoenoses.—From the Late Triassic, only four fossilised wood assemblages containing *Xenoxylon* are documented, all from eastern Asia and the Arctic region (Fig. 5A). The *Protocedroxylon* group and the *Phyllocladoxylon* group are associated with *Xenoxylon* only in the three northernmost super-localities. The southernmost one only has wood specimens from the *Phyllocladoxylon* group associated with *Xenoxylon*. According to our data, in the Early to Middle Jurassic, the global distribution of *Xenoxylon*-containing fossilised wood floras expanded widely, while their diversity also increased sharply (Fig. 5B). It is worth mentioning, however, that the southernmost *Xenoxylon* flora in Vietnam was isolated from the main range of the genus as this region belongs to the Indochina block, which most likely shifted significantly southwards during the Cretaceous (Carter and Bristow 2003).

During the Late Jurassic and Early Cretaceous, the global distribution of *Xenoxylon*-containing fossilised wood floras was somewhat reduced globally and shifted slightly northward (Fig. 6A). This pattern is particularly clear in Europe, but not so marked in Asia, while, curiously, *Xenoxylon* extended its range in North America. For the Late Cretaceous (Fig. 6B), there are, unfortunately, few assemblages containing *Xenoxylon* reported in the Arctic or in Asia, all at relatively high palaeolatitudes (Nishida and Nishida 1986; Spicer and Parrish 1990). The Late Triassic and Late Cretaceous figures are strikingly similar for both the distribution and the composition of fossilised wood assemblages containing *Xenoxylon.*

Discussion

Limits to the interpretation of the results.—In most cases the fossil wood taxa do not represent true biological entities, what introduces some degree of uncertainty in integrating the Mesozoic fossilised wood taxa in the plant systematics. Distribution data (Figs. 5A, B, 6A, B) show that *Xenoxylon* had a narrower latitudinal distribution than most coeval fossilised wood genera and therefore most likely had a more restricted ecology. Limiting the area being studied to the area of *Xenoxylon* distribution (i.e., taking into account, for the purpose of this discussion, only the floras containing *Xenoxylon*) limits the systematic bias somewhat by focusing on an ecologically more coherent unit. By the Late Triassic, all significant conifer clades were present (Renner 2009), although wood from the B, C, D, and F groups are only documented with certainty from the Early Jurassic onwards. All wood groups studied are represented from the Early Jurassic to the Late Cretaceous. Other limits encountered are the geological megabiases (Benson et al. 2009), in particular the fact that the various geological units do not outcrop on equivalent surfaces, and have not been subjected to the same investigation pressures. A global approach decreases this type of bias.

We evaluated the quality of the data set by calculating a diversity index (DI) for each time interval (LT, EMJ, LJEK, and LK). For this index, we calculated DI = GD / N, where GD is the number of genera found associated with *Xenoxylon* for a given interval, and N is the number of data for this interval (see Table 5). The results are given in Fig. 7. For the Late Triassic, the diversity index is low. This finding, however, is congruent with the fact that fossilised wood flora are poorly diversified globally at this time, including those that do not feature *Xenoxylon*. With the DI decreasing slightly from the LT to the EMJ, while the GD is nine times larger, it can legitimately be hypothesised that the sampling

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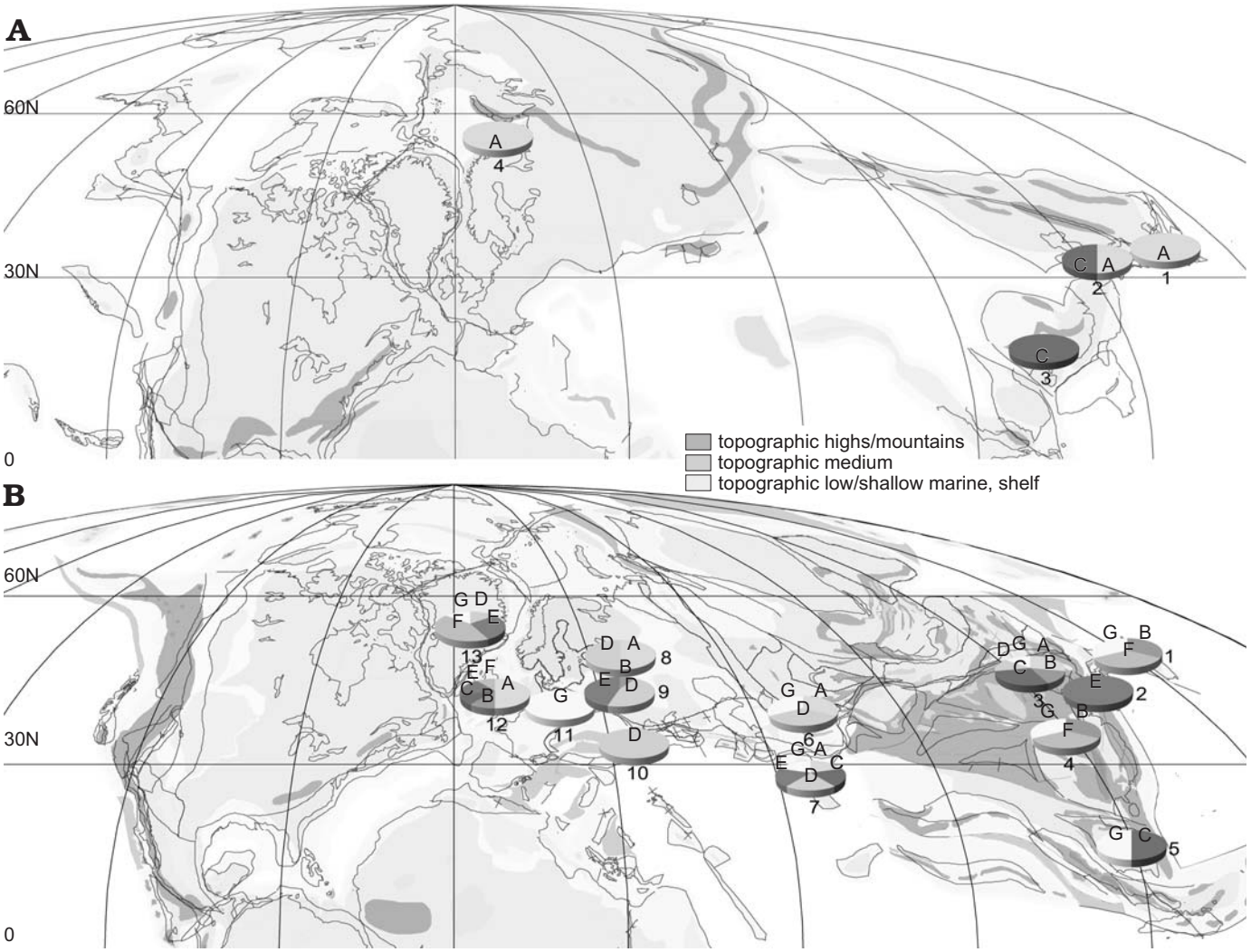


Fig. 5. Distribution and diversity of the fossil wood groups associated with *Xenoxylon*. **A**. Late Triassic (modified from the DINODATA; www.dinodata.org; accessed Oct. 11. 2011) (1, Japan; 2, Korea; 3, Southern China-Guangdong; 4, Arctic. **B**. Early to Middle Jurassic (1, Japan; 2, Korea; 3, Northeast China-Beijing, Liaoning, Jilin, Heilongjiang, and Inner Mongolia; 4, Central China-Henan; 5, Vietnam; 6, Uzbekistan; 7, Iran; 8, Lithuania; 9, Poland; 10, Georgia; 11, Germany; 12, UK; 13, Greenland). Abbreviations: A, *Protocedroxylon*-group; B, *Taxodioxylon*-group; C, *Phyllocladoxylon*-group; D, *Podocarpoxylon*-group; E, *Agathoxylon*; F, *Brachyoxylon*-group; G, others (for the composition of each taxonomical group see Table 2).

was good for this time period. Increasing the number of data would most likely not reveal new associated genera. The figure is similar for the LJEK. For the Late Cretaceous, the DI doubles. This result might be due to either a decrease in the number of data or to an increase in the GD. Because even in well-documented Late Cretaceous fossilised wood flora containing *Xenoxylon* the generic diversity is always low, we interpret the increase in DI as reflecting a strong reduction in *Xenoxylon* distribution and thus in the amount of data. Once this was considered, we assumed that the data set in Table 4 was not strongly biased.

Was *Xenoxylon* part of a diversified vegetation type?—From our data, *Xenoxylon* is typically associated with other genera in the outcrops. Our data originate from taphocoenoses, which represent the post-mortem gathering of fossilised wood pieces. There is a little evidence from in situ fossilised wood floras that include *Xenoxylon* (Shimakura 1936; Ogura et al. 1951; Wang et al. 2000), with *Protopiceoxylon* (a type of wood from the *Protocedroxylon* group) being reported in Wang et al. (2000). Nevertheless, the fact that, among fossilised wood assemblages, *Protocedroxylon* co-occurs with *Xenoxylon* more than eight times more than with any other fossilised wood genus from the Late Triassic to the Late Cretaceous demonstrates that *Protocedroxylon* was a component of the *Xenoxylon*-phytocoenoses. The results for the other genera are not as conclusive. From our data, it is impossible to assert that *Xenoxylon* was growing locally in exclusive stands. It seems, however, that when sufficient numbers of wood specimens are analysed from a locality, *Xenoxylon* is usually associated with other taxa.

As far as we know, *Xenoxylon* has never been reported as co-occurring with angiosperm wood. There have been reports of angiosperm wood specimens from Cretaceous deposits, mostly from the Upper Cretaceous, in North America,

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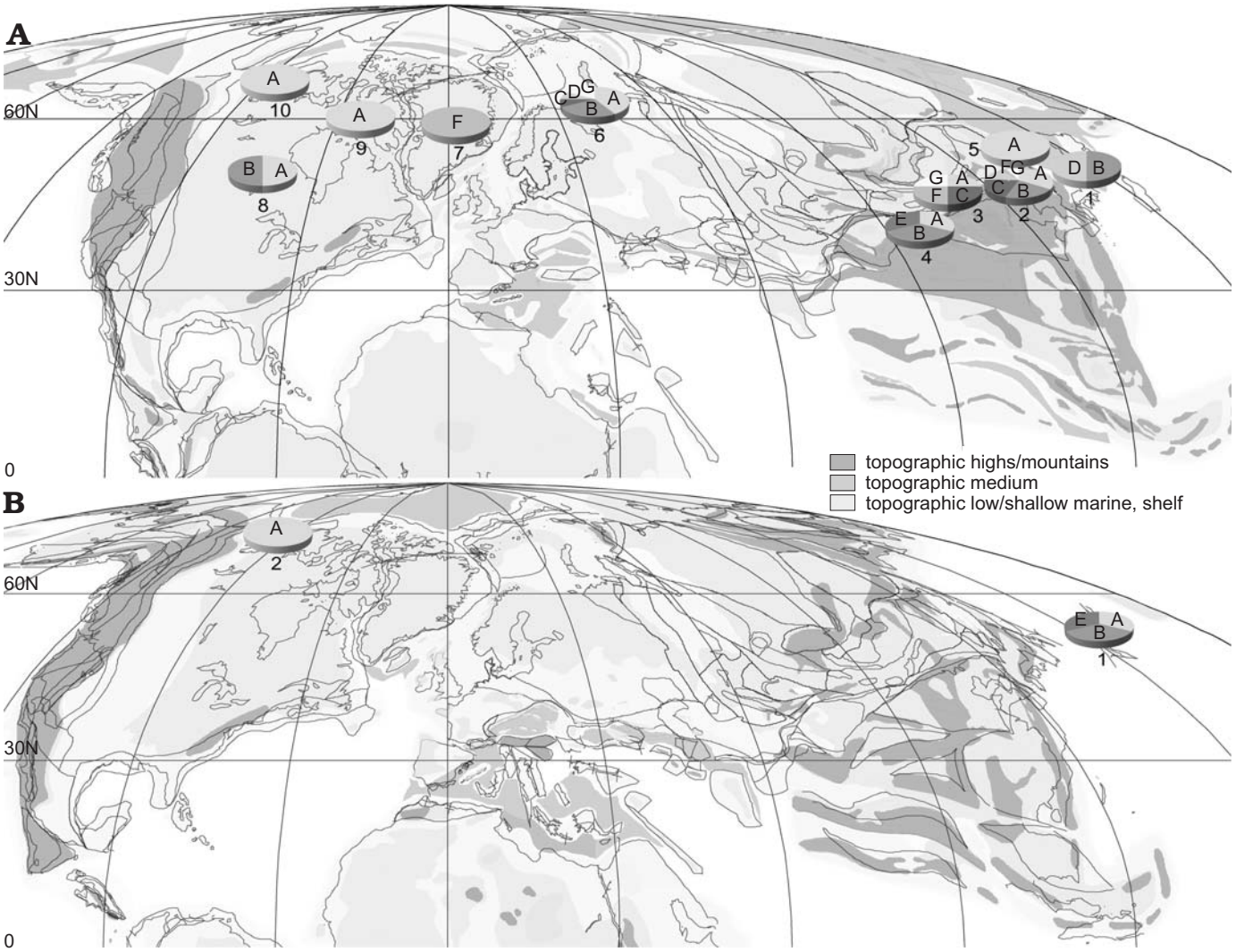


Fig. 6. Distribution and diversity of the fossil wood groups associated with *Xenoxylon*. **A**. Late Jurassic to Early Cretaceous (1, Japan; 2, Northeast China-Beijing, Liaoning, Jilin, Heilongjiang, and Inner Mongolia; 3, Southeast Mongolia; 4, Western China-Xinjiang; 5, Primorye; 6, Arctic; 7, Greenland; 8, Canada-Alberta; 9, Canadian Arctic Archipelago; 10, Alaska-Central North Slope). **B**. Late Cretaceous (1, Sakhalin; 2, Alaska-Central North Slope). Abbreviations: A, *Protocedroxylon*-group; B, *Taxodioxylon*-group; C, *Phyllocladoxylon*-group; D, *Podocarpoxylon*-group; E, *Agathoxylon*; F, *Brachyoxylon*-group; G, others (for the composition of each taxonomical group see Table 2).

Japan, Europe, and Antarctica (e.g., Wheeler et al. 1987, 1994; Meijer 2000; Poole and Francis 2000; Takahashi and Suzuki 2003). These are, however, mostly from low- to mid-latitudes, while during this time span, the *Xenoxylon* range shifted towards high latitudes.

The global diversity of *Xenoxylon* floras, as judged from wood assemblages, was low during the Late Triassic but increased sharply at the Triassic–Jurassic boundary. This is in accordance with a global southward expansion of *Xenoxylon* during the Early Jurassic (Philippe and Thévenard 1996), as well as with a simultaneous strong diversification of wood types (Philippe and Harland 2007). During the Late Jurassic to Early Cretaceous interval, the diversity of the *Xenoxylon* flora is similar to that during the Early to Middle Jurassic, although it decreased slightly in the southern part of the range. By the Late Cretaceous, the diversity of *Xenoxylon*-floras decreased and their distribution was reduced.

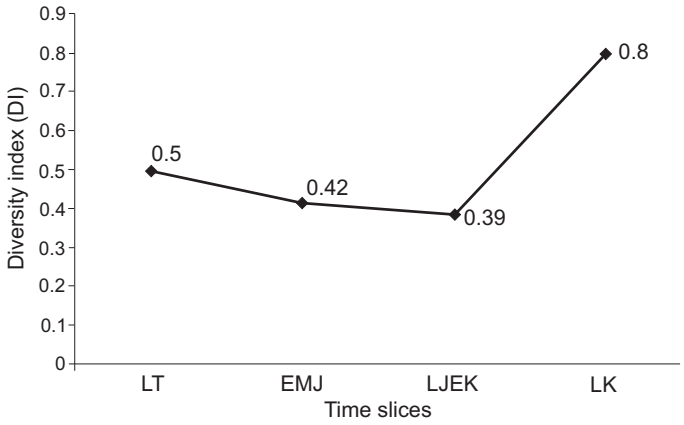


Fig. 7. Diversity index (DI = GD/N, where GD is the number of genera associated with *Xenoxylon*, and N the number of occurrences) for each time period. Abbreviations: LT, Late Triassic; EMJ, Early to Middle Jurassic; LJEK, Late Jurassic to Early Cretaceous; LK, Late Cretaceous.

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***Xenoxylon*-phytocoenoses and palaeoclimates**.—The Pangaean supercontinent became fragmented during the Triassic, while the climate remained warm and dry globally. It is noteworthy that *Xenoxylon*-phytocoenoses appeared worldwide during the Carnian, with *Protocedroxylon* as an associated element, during a time that might correspond to a cooling and pluvial event (Simms and Ruffell 1989). Continents became increasingly separated during the Early Jurassic, while concomitantly, the world climate became more equable and more humid than during the Triassic (Chandler et al. 1992; Golonka and Ford 2000; Ruckwied and Götz 2009). Such a globally more humid climatic environment was most likely the primary cause of the spread and the increase in the diversity of the *Xenoxylon*-phytocoenoses.

This diversity increased slightly during the Late Jurassic to Early Cretaceous interval, except in northern East Asia. The Cretaceous is regarded as having been globally warmer than the Jurassic (Spicer et al. 1993; Ziegler et al. 1993), although significant cooling events most likely occurred during the Early Cretaceous (Pucéat et al. 2003; Maurer et al. 2012). In Europe, specifically after the Middle Oxfordian, the climate became more arid (Dromart et al. 2003), while the range of *Xenoxylon* decreased northward (Philippe and Thévenard 1996). However, in Far-East Asia, this distribution restriction did not occur for *Xenoxylon*, and the associated phytocoenoses remained rich and diverse, especially in northeast China (Liaoning, Jilin, Heilongjiang, and Inner Mongolia provinces). Recent geochemical results (Amiot et al. 2011) evidenced that cool climates prevailed in northern Far-East Asia, at least during the Early Cretaceous (Barremian–early Albian). The prevalence of a cool environment during the Early Cretaceous most likely determined the persistence of diverse *Xenoxylon*-phytocoenoses in northern Far-East Asia.

The globally warm Late Cretaceous saw a concomitant severe decrease in the distribution of *Xenoxylon* and a sharp decrease in the diversity of *Xenoxylon*-phytocoenoses, confirming a relationship, for this genus, between its distribution and associated diversity. The most recent data for *Xenoxylon*-phytocoenoses, and for the genus, are from northern Far-East Asia and Alaska, supporting the idea that this area remained cool and/or humid throughout the Cretaceous, although Maastrichtian data from fossilised leaves indicate a significant local warming slightly to the south (Hermann and Spicer 1996).

Two genera (*Brachyoxylon* and *Agathoxylon*), found episodically associated with *Xenoxylon,* have special palaeoclimatic significance. *Brachyoxylon* was found in southwestern Europe, during the Middle to Late Jurassic interval, to be bound mostly to the tropophilous climates of tropical lowlands and perireefal systems (Garcia et al. 1998), while during the Early Jurassic, it had a more diverse palaeoecology (Philippe 1995). *Brachyoxylon* is only rarely associated with *Xenoxylon* after the Early Jurassic, except in Greenland, an exception that might be due to a taxonomic bias. Indeed, *Brachyoxylon* is related to diverse types of plants, and the Greenland associations might be caused by the local persistence of the more hygrophilous Early Jurassic *Brachyoxylon* plants. *Agathoxylon*, most likely a "bin" taxon for several botanical groups (pteridosperms, caytoniales, possibly also some cycads and Bennettitales) does not present a clear palaeoecological pattern. In Eurasia, it was, however, distributed mostly in the south throughout the Middle Jurassic–Late Cretaceous interval. After the Middle Jurassic, in Asia, *Agathoxylon* and *Xenoxylon* appear to be exclusive (Oh et al. 2011), whereas this is not the case in Europe. However, *Agathoxylon* might include taxa there that were not represented in Asia and that inhabit a different ecology.

The results and discussions confirm that *Xenoxylon* was bound to "northern climates", i.e., cooler and/or humid ones, and that it was associated with a more diverse flora in the southernmost (i.e., warmest) parts of its distribution. This result suggests that the occurrence of *Xenoxylon* at lower latitudes is bound to more humid climatic episodes, which were not necessarily cooler.

Conclusion

From its appearance in the Late Triassic to its disappearance at the K–T boundary, *Xenoxylon* most likely lived in association with other genera. During the globally most arid/warmest intervals (Late Triassic and Late Cretaceous), *Xenoxylon*-phytocoenoses had a limited diversity, with *Protocedroxylon* being the primary associated genus, and a northern distribution. During the globally more humid/cooler times, and especially during the Early Jurassic, *Xenoxylon*-phytocoenoses are encountered in significantly more southern regions and are more diverse, often including *Taxodioxylon*, particularly during the Early Cretaceous. The distribution patterns for *Xenoxylon*-phytocoenoses in Europe, North America and Asia differ sharply. Our results suggest that within *Xenoxylon*'s range, corresponding phytocoenoses were differentiated on a latitudinal gradient according to the climate change patterns during the Mesozoic, and the occurrence of diverse *Xenoxylon*-phytocoenoses at mid- to low palaeolatitudes characterise more humid episodes.

Acknowledgements

Thanks are owed to Marion Bamford (University of the Witwatersrand, Johannesburg, South Africa), Fabrice Malartre (Ecole Nationale Supérieure de Géologie, Nancy, France), Kazuo Terada (Fukui Prefectural Dinosaur Museum, Fukui, Japan), Wu Zhang (Shenyang Institute of Geology and Mineral Resources, Ministry of Land and Resources, Shenyang, PR China), Shaolin Zheng (Shenyang Institute of Geology and Mineral Resources, Ministry of Land and Resources, Shenyang, PR China), and an anonymous reviewer for constructive discussions. Our thanks also go to Maria Doludenko (Geology Institute, Moscow, Russia), Leszek Marynowski (University of Silesia, Sosnowiec, Poland), Frank Wittler (Karlsruhe University, Germany), and Michał Zatoń (University of Silesia, Sosnowiec, Poland), who donated specimens; and to Peta Hayes (Natural History Museum, London, UK), David Cantrill (Royal Botanic Gardens Melbourne, Melbourne, Australia), Gilles Cuny (Natural History Museum of Denmark, Copenhagen,

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Denmark), Dario de Franceschi (Muséum national d'Histoire naturelle, Paris, France), Paul Kenrick (Natural History Museum, London, UK), Harufumi Nishida (Chuo University, Tokyo, Japan), and Mitsuo Suzuki (Tohoku University, Sendai, Japan) for their help while reviewing collections. Kazuo Terada is thanked for kind permission to use his in situ *Xenoxylon* photo.

References

Amiot, R., Wang, X., Zhou, Z., Wang, X., Buffetaut, E., Lécuyer, C., Ding, Z., Fluteau, F., Hibino, T., Kusuhashi, N., Mo, J., Suteethorn, V., Wang, Y., Xu, X., and Zhang, F. 2011. Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climates. *Proceedings of the National Academy of Sciences USA* 108: 5179–5183.

Arnold, C.A. 1953. Silicified plant remains from the Mesozoic and Tertiary of Western North America. II. Some fossil woods from Alaska. *Papers of the Michigan Academy of Sciences, Arts and Letters* 38: 8–20.

Bailey, I.W. 1953. Evolution of the tracheary tissue of land plants. *American Journal of Botany* 40: 4–8.

Benson, R.B.J., Butler, R.J., Lindgren, J., and Smith, A.S. 2009. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceedings of the Royal Society B* 277: 829–834.

Brison, A.-L., Philippe, M., and Thévenard, F. 2001. Are Mesozoic wood growth rings climate-induced? *Paleobiology* 27: 531–538.

Carter, A. and Bristow, C. 2003. Linking hinterland evolution and continental basin sedimentation using detrital zircon themochronology: a study of the Khorat Plateau Basin, Eastern Thailand. *Basin Research* 15: 1–15.

Chandler, M.A., Rind, D., and Ruedy, R. 1992. Pangaean climate during the Early Jurassic: GCM simulations and the sedimentary record of paleoclimate. *Geological Society of America Bulletin* 104: 543–559.

Dromart, G., Garcia, J.-P., Picard, S., Atrops, F., Lécuyer, C., and Sheppard, S. 2003. Ice age at the Middle–Late Jurassic transition? *Earth and Planetary Science Letters* 213: 205–220.

Egawa, K. and Lee, Y.I. 2011. K-Ar dating of illites for time constraint on tectonic burial metamorphism of the Jurassic Nampo Group (West Korea). *Geosciences Journal* 15: 131–135.

Galli, M.T., Jadoul, F., Bernasconi, S.M., and Weissert, H. 2005. Anomalies in global carbon cycling and extinction at the Triassic/Jurassic boundary: evidence from a marine C-isotope record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 216: 203–214.

Garcia, J.-P., Philippe, M., and Gaumet, F. 1998. Fossil wood in Middle–Upper Jurassic marine sedimentary cycles of France: relations with climate, sea-level dynamics, and carbonate-platform environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141: 199–214.

Golonka, J. and Ford, D. 2000. Pangean (Late Carboniferous–Middle Jurassic) paleoenvironment and lithofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 161: 1–34.

Gomez, J.J. and Goy, A. 2011. Warming driven mass extinction in the Early Toarcian (Early Jurassic) of northern and central Spain. Correlation with other time-equivalent European sections. *Palaeogeography, Palaeoclimatology, Palaeoecology* 306: 176–195.

Gordon, A.G. 1932. *The Anatomical Structure of Mesozoic Plants from the Bituminous Sands of the McMurray Formation*. 116 pp. Unpubliehed M.Sc. Thesis, University of Alberta, Edmonton.

Gothan, W. 1905. Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. *Abhandlungen preußische geologische Landesanstalt* 44: 1–108.

Gothan, W. 1910. Die fossilen Holzreste von Spitzbergen. *Kungliga Svenska Vetenskapsakademiens Handlingar* 45: 1–56.

Gröcke, D.R., Price, G.D., Ruffell, A.H., Mutterlose, J., and Baraboshkin, E. 2003. Isotopic evidence for Late Jurassic–Early Cretaceous climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology* 202: 97–118.

Herman, A.B. and Spicer, R.A. 1996. Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. *Nature* 380: 330–333.

Holden, R. 1913. Contributions to the anatomy of Mesozoic conifers. No. I. Jurassic coniferous woods from Yorkshire. *Annals of Botany* 27: 533–545.

Jarmolenko, A.V. 1933. The experimental application of stem secondary wood anatomy to investigation of conifer phylogeny. *Soviet Botany* 6: 46–63.

Joral, F.G., Gómez, J.J., and Goy, A. 2011. Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in Northern and Central Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 302: 367–380.

Kim, K., Jeong, E.K., Kim, J.H., Paek, S.D., Suzuki, M., and Philippe, M. 2005. Coniferous fossil woods from the Jogyeri Formation (Upper Triassic) of the Nampo Group, Korea. *International Association of Wood Anatomists Journal* 26: 253–265.

Mailliot, S., Mattioli, E., Bartolini, A., Baudin, F., Pittet, B., and Guex, J. 2009. Late Pliensbachian–Early Toarcian (Early Jurassic) environmental changes in an epicontinental basin of NW Europe (Causses area, central France): a micropaleontological and geochemical approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 273: 346–364.

Marynowski, L., Philippe, M., Zatoń, M., and Hautevelle, Y. 2008. Systematic relationships of the Mesozoic wood genus *Xenoxylon*: an integrative biomolecular and palaeobotanical approach. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 247: 177–189.

Maurer, F., van Buchem, F.S.P., Eberli, G.P., Pierson, B.J., Raven, M.J., Larsen, P.-H., Al-Husseini, M.I., and Vincent, B. 2012. Late Aptian long-lived glacio-eustatic lowstand recorded on the Arabian Plate. *Terra Nova* 25: 87–94.

Meijer, J.J.F. 2000. Fossil woods from the Late Cretaceous Aachen Formation. *Review of Palaeobotany and Palynology* 112: 297–336.

Mull, C.G., Houseknecht, D.W., and Bird, K.J. 2003. Revised Cretaceous and Tertiary stratigraphic nomenclature in the Colville Basin, Northern Alaska. *U.S. Geological Survey Professional Paper* 1673: 1–51.

Müller-Stoll, W.R. and Schultze-Motel, J. 1989. Gymnospermen-Hölzer des deutschen Jura. teil 2: die protopinoiden Hölzer. *Zeitschrift der deutschen geologischen Gesellschaft* 140: 53–71.

Nadjafi, A. 1982. *Contribution à la connaissance de la flore ligneuse du Jurassique d'Iran* [in French]. 111 pp. Unpublished Ph.D. Thesis. Paris VI University, Paris.

Nathorst, A.G. 1897. Zur mesozoischen Flora Spitzbergens. *Kungliga Svenska Vetenskapsakademiens Handligar* 30: 1–77.

Nishida, M. and Nishida, H. 1986. Structure and affinities of the petrified plants from the Cretaceous of northern Japan and Saghalien III. Petrified plants from the Upper Cretaceous of Saghalien (1). *Botanical Magazine, Tokyo* 99: 191–204.

Nishida, M., Nishida, H., and Suzuki, Y. 1993. On some petrified plants from the Cretaceous of Choshi, Chiba Prefecture VIII. *Journal of Japanese Botany* 68: 289–299.

Ogura, Y., Kobayashi, T., and Maeda, S. 1951. Discovery of erect stumps of *Xenoxylon latiporosum* in the Jurassic Tetori series in Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* 4: 113–119.

Oh, C. 2010. *Conifer Fossil Woods of the Cretaceous in Northeast Asia: Occurrences and Paleobiological Implications*. 183 pp. Partly published Ph.D. Thesis. Chonbuk National University, Korea.

Oh, C., Legrand, J., Kim, K., Philippe, M., and Paik, I.S. 2011. Fossil wood diversity gradient and Far-East Asia palaeoclimatology during the Late Triassic–Cretaceous interval. *Journal of Asian Earth Sciences* 40: 710–721.

Parrish, J.T. and Spicer, R.A. 1988. Middle Cretaceous wood from the Nanushuk Group, Central North Slope, Alaska. *Palaeontology* 31: 19–34.

Philippe, M. 1993. Nomenclature générique des trachéidoxyles mésozoïques à champs araucarioïdes. *Taxon* 42: 74–80.

Philippe, M. 1994. Radiation précoce des conifères Taxodiaceae et bois affines du Jurassique de France. *Lethaia* 27: 67–75.

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Philippe, M. 1995. Bois fossiles du Jurassique de Franche-Comté (nord-est de la France): systématique et biogeographie. *Palaeontographica B* 236: 45–103.

Philippe, M. and Bamford, M.K. 2008. A key to morphogenera used for Mesozoic conifer-like woods. *Review of Palaeobotany and Palynology* 148: 184–207.

Philippe, M. and Harland, M. 2007. The diversification of wood in Mesozoic terrestrial ecosystems. *In*: G. Sun (ed.), *Proceedings of the International Symposium on Paleontology and Stratigraphy in Benxi of China*, 71. Benxi, Liaoning Province.

Philippe, M. and Hayes, P. 2010. Reappraisal of two of Witham's species of fossil wood with taxonomical and nomenclatural notes on *Planoxylon* Stopes, *Protocedroxylon* Gothan and *Xenoxylon* Gothan. *Review of Palaeobotany and Palynology* 162: 54–62.

Philippe, M. and Thévenard, F. 1996. Distribution and palaeoecology of the Mesozoic wood genus *Xenoxylon*: palaeoclimatological implications for the Jurassic of Western Europe. *Review of Palaeobotany and Palynology* 9: 353–370.

Philippe, M., Bamford, M., McLoughlin, S., Alves, L.S.R., Falcon-Lang, H.J., Gnaedinger, S., Ottone, E.G., Pole, M., Rajanikanth, A., Shoemaker, R.E., Torres, T., and Zamuner, A. 2004. Biogeographic analysis of Jurassic–Early Cretaceous wood assemblages from Gondwana. *Review of Palaeobotany and Palynology* 129: 141–173.

Philippe, M., Jiang, H.-E., Kim, K., Oh, C., Gromyko, D., Harland, M., Paik, I.-S., and Thévenard, F. 2009. Structure and diversity of the Mesozoic wood genus *Xenoxylon* in Far East Asia: implications for terrestrial palaeoclimates. *Lethaia* 42: 393–406.

Philippe, M., Thévenard, F., Nosova, N., Kim, K., and Naugolnykh, S. 2013. Systematics of a palaeoecologically significant boreal Mesozoic fossil wood genus, *Xenoxylon* Gothan. *Review of Palaeobotany and Palynology* 193: 128–140.

Poole, I. and Ataabadi, M.M. 2005. Conifer woods of the Middle Jurassic Hojedk Formation (Kerman Basin) Central Iran. *International Association of Wood Anatomists Journal* 26: 489–505.

Poole, I. and Francis, J.E. 2000. The first record of fossil wood of Winteraceae from the Upper Cretaceous of Antarctica. *Annals of Botany* 85: 307–315.

Pucéat, E., Lécuyer, C., Sheppard, S.M.F., Dromart, G., Reboulet, S., and Grandjean, P. 2003. Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels. *Paleoceanography* 18: 7-1–7-12.

Renner, S. 2009. Gymnosperms. *In*: S.B. Hedges and S. Kumar (eds.), *The Time Tree of Life*, 157–160. Oxford University Press, New York.

Rößler, R., Philippe, M., van Konijnenburg-van Cittert, J.H.A., McLoughlin, S., Sakala, J., and Zijlstra, G. (coordinating authors), and 35 contributors. 2014. Which name(s) should be used for Araucaria-like fossil wood? Results of a poll. *Taxon* 63: 177–184.

Ruckwied, K. and Götz, A.E. 2009. Climate change at the Triassic/Jurassic boundary: palynological evidence from the Furkaska section (Tatra Mountains, Slovakia). *Geologica Carpathica* 60: 139–149.

Selmeier, A. and Grosser, D. 2011. Lower Cretaceous conifer drift wood from Sverdrup Basin, Canadian Arctic Archipelago. *Zitteliana A* 51: 19–35.

Shilkina, I.A. [Šilkina, I.A.] 1967. Fossil woods of Franz-Josef Land [in Russian]. *Acta Botanica Institut Komarov (Akademia nauk SSSR), ser. 8, Paleobotanika* 6: 29–50.

Shilkina, I.A. [Šilkina, I.A.] and Khudayberdyev, R. [Hudajberdyev, R.] 1971. Reappraisal of genera *Protocedroxylon* and *Xenoxylon* [in Russian]. *Paleobotanica Uzbekistana* 2: 117–133.

Shimakura, M. 1936. Studies on fossil woods from Japan and adjacent lands, contribution I. *Science Reports of the Tohoku Imperial University* 18: 267–298.

Simms, M.J. and Ruffell, A.H. 1989. Synchroneity of climatic change and extinctions in the Late Triassic. *Geology* 17: 165–268.

Sliter, W.V. 1979. Cretaceous foraminifers from the North Slope of Alaska. *In*: T.S. Ahlbrandt (ed.), Preliminary Geologic, Petrologic, and Paleontologic Results of the Study of Nanushuk Group Rocks North Slope, Alaska. *U.S. Geological Survey Circular* 794: 147–157.

Spicer, R.A. and Parrish, J.T. 1986. Paleobotanical evidence for cool North Polar climates in middle Cretaceous (Albian–Cenomanian) time. *Geology* 14: 703–706.

Spicer, R.A. and Parrish, J.T. 1990. Latest Cretaceous woods of the Central North Slope, Alaska. *Palaeontology* 33: 225–242.

Spicer, R.A., Rees, P.M., and Chapman, J.L. 1993. Cretaceous phytogeography and climate signals. *Philosophical Transactions of the Royal Society of London B* 341: 27–286.

Suzuki, M. and Terada, K. 1992. *Xenoxylon* fossil woods from the Lower Cretaceous Akaiwa Subgroup of Shiramine, Central Japan. *Journal of Phytogeography and Taxonomy* 40: 91–97.

Suzuki, M., Goto, M., and Akahane, H. 1982. Some fossil woods from the Kuruma Group of Toyama and Niigata Prefectures. *Annals of Science of the Kanazawa University* 19: 43–61.

Takahashi, K. and Suzuki, M. 2003. Dicotyledonous fossil wood flora and early evolution of wood characters in the Cretaceous of Hokkaido, Japan. *International Association of Wood Anatomists Journal* 24: 269–309.

Terada, K., Nishida, H., and Sun, G. 2011. Fossil woods from the Upper Cretaceous to Paleocene of Heilongjang (Amur) River area of China and Russia. *Global Geology* 14: 192–208.

Tsunada, K. and Yamazaki, S. 1984. Mesozoic coniferous woods and phytogeography. *Memoirs of the School of Science and Engineering, Waseda University* 48: 117–136.

Vozenin-Serra, C. and Privé-Gill, C. 1991. Les terrasses alluviales pléistocènes du Mékong (Cambodge). I Les bois silicifiés homoxylés récoltés entre Stung-Treng et Snoul. *Review of Palaeobotany and Palynology* 67: 115–132.

Vogellehner, D. 1968. Zur Anatomie und Phylogenie mesozoischer Gymnospermenhölzer, Beitrag 7: Prodromus zu einer Monographie der Protopinaceae. II: die protopinoiden Hölzer der Jura. *Palaeontographica B* 124: 125–162.

Wang, Y.-D., Zhang, W., and Saiki, K. 2000. Fossil woods from the Upper Jurassic of Qitai, Junggar Basin, Xinjiang, China. *Acta Palaeontologica Sinica* 39: 176–185.

Wheeler, E.A., Lee, M., and Matten, L.C. 1987. Dicotyledonous woods from the Upper Cretaceous of Southern Illinois. *Botanical Journal of the Linnean Society* 95: 77–100.

Wheeler, E.A., Lehman, T.M., and Gasson, P.E. 1994. *Javelinoxylon*, an Upper Cretaceous dicotyledonous tree from Big Bend National Park, Texas, with presumed malvalean affinities. *American Journal of Botany* 81: 703–710.

Yamazaki, S. and Tsunada, K. 1981. Fossil coniferous woods belonging to *Protocedroxylon* Gothan and *Xenoxylon* Gothan, obtained from the Upper Triassic Miné Group, Southwest Japan. *Bulletin of Science and Engineering Research Laboratory Waseda University* 97: 1–18.

Yamazaki, S. and Tsunada, K. 1982. Some fossil woods from the Upper Triassic Nariwa and Miné groups, the inner zone of southwest Japan. *Journal of the Geological Society of Japan* 88: 595–611.

Yamazaki, S., Tsunada, K., and Koike, N. 1980. Some fossil woods from the Upper Triassic Nariwa Group, Southwest Japan. *Memoirs of the School of Sciences and Engineering* 44: 91–131.

Zhang, W., Zheng, S.-L., and Ding, Q.-H. 2000. First discovery of a genus *Scotoxylon* from China. *Chinese Bulletin of Botany* 17: 202–205.

Zheng, S.L., Li, Y., Zhang, W., Li, L., Wang, Y.-D., Yang, X.J., Yi, T., Yang, J., and Fu, X.-P. 2008. *Fossil Wood of China*. 356 pp. China Forestry Publishing House, Beijing.

Ziegler, A.M., Parrish, J.M., Jiping, Y., Gyllenhaal, E.D., Rowley, D.B., Parrish, J.T., Shangyou, N., Bekker, A., and Hulver, M.L. 1993. Early Mesozoic phytogeography and climate. *Philosophical Transactions of the Royal Society of London B* 341: 297–305.

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