



# Structure and diversity of the Mesozoic wood genus *Xenoxylon* in Far East Asia: implications for terrestrial palaeoclimates

MARC PHILIPPE, HONG-EN JIANG, KYUNGSIK KIM, CHANGHWAN OH, DMITRY GROMYKO, MELISE HARLAND, IN-SUNG PAIK AND FREDERIC THÉVENARD

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Although the faunal elements of Far East Asian Mesozoic terrestrial biota have attracted much attention in recent years, their palaeoecology remains poorly known. In particular, features of the palaeoclimate are highly controversial. To address this point we used the Mesozoic fossil wood *Xenoxylon*, a genus recognized as an indicator of wet temperate biotopes and which is common in the area during the Carnian–Maastrichtian interval. We re-appraised bibliographic data and gathered new data for *Xenoxylon* in the Mesozoic of Far East Asia. This demonstrated that previous taxonomic approaches to the genus have been so far idiosyncratic. We examined the anatomical diversity of morphogenus *Xenoxylon* in Far East Asia and compared it to that of samples from Europe. This indicates that in an area centred on north-eastern China, *Xenoxylon* reached a level of anatomical diversity unmatched elsewhere in the world. We hypothesize that this diversity witnesses the persistence of palaeoecological conditions particularly suitable for *Xenoxylon* and that a wet temperate climate prevailed over most of the area throughout the Carnian–Maastrichtian interval. It is in this setting that the famous Jehol Biota probably evolved. □ *Xenoxylon*, Mesozoic, Far East Asia, palaeoclimate, palaeobiogeography.

Marc Philippe [philippe@univ-lyon1.fr], UMR5125 (PEPS) of the CNRS, France; Université de Lyon; Université Lyon 1 (Campus de la Doua, Darwin A) F69622 Villeurbanne cedex, France; Hong-En Jiang [jianghongen4731@vip.sina.com], State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, P.R.China; Kyungsik Kim [kksik@chonbuk.ac.kr], Faculty of Biological Sciences, Chonbuk National University, Jeonju 561-756, Korea; Changhwan Ho [bluegaia@chonbuk.ac.kr], Faculty of Biological Sciences, Chonbuk National University, Jeonju 561-756, Korea; Dmitry Gromyko [dvgromyko@gmail.com], Komarov Botanical Institute, 2 Prof. Popova Street, 197376 Russia; Melise Harland [melise\_harland@yahoo.co.uk], School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK (now at CASP, University of Cambridge, West Building, 181A Huntingdon Road, Cambridge, CB3 0DH); In-Sung Paik [paikis@pknu.ac.kr], Department of Environmental Geosciences, Pukyong National University, Pusan, 608-737, Korea; Frédéric Thévenard [thevenar@univ-lyon1.fr], UMR5125 (PEPS) of the CNRS, France; Université de Lyon; Université Lyon 1 (Campus de la Doua, Darwin A) F69622 Villeurbanne cedex, France; manuscript received on 03/01/2008; manuscript accepted on 29/09/2008.

The Mesozoic terrestrial biota of Far East Asia has received much attention recently, following the discovery of many astonishing vertebrate and angiosperm fossils, especially in Liaoning and Hebei provinces, China. However, the terrestrial palaeoecology of Far East Asia at this time is still poorly known (Zhou *et al.* 2003). Data about terrestrial climates are especially needed (Barrett & Hilton 2006) and could help in the interpretation of features like the occurrence of feathers and furs, or flowers and carpels, but also in the general reconstruction of palaeoecology and Far East Asian Mesozoic biogeography.

Mesozoic terrestrial climates are generally poorly known. As for northeastern China during the Early

Cretaceous interval, very different climates have been hypothesized, based on differing approaches (Table 1). Wu (1999), described a hot and arid climate on the basis of fossil plant features, whereas Li (2003) assumes a relatively humid climate, on palynological studies. Fürsich *et al.* (2007), after a detailed palaeoecological and taphonomical analysis of a lake biota suggest that the climate was semi-arid and that a dry period with little air movement alternated with a stormier wet season. However, Yang *et al.* (2007) infer from miospore assemblages a wet subtropical climate, which was only seasonally dry.

Differences between interpreted data sets, which are not all from exactly the same environment and

Table 1. Mesozoic palaeoclimate inferred for northern Far East Asia by various authors.

Reference	Period	Temperature	Humidity	Evidence type
Wang <i>et al.</i> 2005	Early to Middle Jurassic	Temperate to subtropical	Semi-humid to humid (with warmer/drier snaps)	Leaf flora
Wang <i>et al.</i> 2006	Middle Jurassic	Subtropical to warm temperate	Humid	Plant mega and micro-fossils
Wang <i>et al.</i> 2000	Late Jurassic	Mild	Seasonally arid	Fossil wood
Wang <i>et al.</i> 2002	Late Jurassic	Mild	Seasonally arid	Fossil wood
Duan 1986	Late Jurassic	Subtropical	High rainfall	Fossil wood
Matsukawa <i>et al.</i> 2006; Haggart <i>et al.</i> 2006	Late Jurassic to early-Early Cretaceous	Temperate	Moderately humid	Miscellaneous
Wang <i>et al.</i> 2004	Late Jurassic to Early Cretaceous	Tropical to sub-tropical	Arid	Plant mega- and micro-fossils
Wu 1999	Early Cretaceous	Hot	Dry	Jehol Flora
Ding 2000	Early Cretaceous	Subtropical to warm temperate	Humid	Fossil wood
Saiki & Wang 2003	Early Cretaceous	Warm temperate	Humid	Leaf flora
Zhou <i>et al.</i> 2003	Early Cretaceous	–	Mesic to semi-arid	Miscellaneous
Li 2003	Early Cretaceous	–	Humid	Palynomorphs
Yang & Zheng 2003	Early Cretaceous	Mild	Humid (seasonal)	Fossil wood
Wang <i>et al.</i> 2004	Early Cretaceous	Subtropical to temperate	Seasonal, semi-arid to semi-humid	Plant mega- and micro-fossils
Fürsich <i>et al.</i> 2007	Early Cretaceous	–	Semi-arid, tropophilous	Sedimentology and others
Li & Batten 2007	Early Cretaceous	Warm	Short wet phases and longer arid periods	Palynology
Yang <i>et al.</i> 2007	Early Cretaceous	Subtropical	Seasonally dry	Miospores
Duck 1985	Late Early Cretaceous	Warm	Arid	Palynomorphs
Zhang <i>et al.</i> 2000a	Late Early Cretaceous (Jiufotang Fm)	Seasonal	Arid or seasonally arid	Red-variegated sandstones
Herman & Spicer 1996	Late Cretaceous	Temperate	Humid	Leaf flora

stratigraphical interval, may result in different palaeoclimate interpretations but could hardly account for almost opposite conclusions. As can be seen, palaeoclimatological interpretation of palaeobotanical data for the Mesozoic of Asia (based either on pollen or leaf fossils) is difficult, and results have not been unanimously approved (Umetsu & Sato 2007). Phytogeography could help, but this is still one of the most controversial topics among East Asian palaeobotanists (Golozoubov *et al.* 1999; Saiki & Wang 2003), with much disagreement about limits, degree of differentiation, assignment of some species to one or another zone, and the existence of oscillations of the palaeobiogeographical limits during the Mesozoic etc.

To address the problem of palaeoclimate in Far East Asia during the Jurassic and Cretaceous, we used the fossil wood genus *Xenoxylon* Gothan, which is known to be one of the few bio-indicators of Mesozoic terrestrial ecosystems. Indeed, because of Boreal circum-polar distribution of *Xenoxylon*, and as its distribution range increases southward during cooler periods, it was proposed in a previous review to be an indicator of cooler and/or wetter climates (Philippe & Thévenard 1996). This seminal work has received confirmation from various independent

sources, including geochemistry (Dromart *et al.* 2003; Hautevelle 2006), micropalaeontology (Tremolada *et al.* 2006), and sedimentology (Hesselbo *et al.* 2007). On the basis of growth ring characteristics, Harland (2005) came to the conclusion that *Xenoxylon* was an evergreen tree, with leaf retention time in excess of 5 years, a value typical of cold to temperate climates (Wright *et al.* 2004; Harland *et al.* 2007). Growth-ring width of *Xenoxylon* wood, even for large logs with a diameter exceeding 50 cm, is usually large (Duan 1986; He 1995; Ding *et al.* 2000), and log diameter above stump basal flaring can reach as much as 150 cm (Duan *et al.* 1995; our observations) or even 250 cm (Duan 1986), two features that do not fit with growth in a dry environment. He (1995) considered *Xenoxylon* as a xerophytic genus, on the basis of the lack of intercellular spaces in between tracheids, but the well-named swamp-cypress (*Taxodium distichum*) is also devoid of such spaces in secondary xylem. In Far East Asia *Xenoxylon* is often associated with thick coal seams (He 1995; Zhang *et al.* 2000a; our observations in Heilongjiang and Inner Mongolia autonomous region), for which it is difficult to suppose an arid environment.

Since Philippe & Thévenard's (1996) review, much new data have been published for this genus,

especially in Far East Asia. Several new species of the genus *Xenoxylon* have been described, sometimes in papers that are not easily accessible to Western scientists. Moreover, we recently identified several new samples from that region as *Xenoxylon*. All these data suggest that northern Far East Asia was an important place for *Xenoxylon* differentiation during the Mesozoic.

In this paper we analyse *Xenoxylon* data from Far East Asia, in order to: (1) update Philippe & Thévenard's (1996) review; (2) better circumscribe the spatial and temporal distribution of the genus in the studied area; and (3) analyse the species diversity from a palaeoecological perspective, because Far East Asia appears to have been a centre of differentiation.

## Material and biogeographical framework

Data were obtained from both literature survey and new identifications. Special attention was paid to Chinese, Japanese, and Russian literature on *Xenoxylon*, as it has often been overlooked by Western scientists. This bibliographical review was supplemented by new field collections from north-eastern China (Heilongjiang, Jilin and Liaoning provinces and Inner Mongolia autonomous region) in addition to identifications made from museum collections (Palaeontological Museum of Berkeley University, Natur Historiska Riksmuseet in Stockholm, Museum für Naturkunde of the Humboldt-University in Berlin, Geologisk Museum in Copenhagen, Komarov Institute in Saint-Petersburg, Muséum national d'Histoire naturelle in Paris).

### *Taxonomy and systematic relationships of the wood genus Xenoxylon*

The genus *Xenoxylon* is one of the most homogeneous of all genera of Mesozoic fossil woods, and is well characterized by the occurrence, at least locally, of xenoxylean pitting (Müller-Stoll 1951; Philippe & Bamford 2008) on tracheid radial walls. This type of pitting is considered by Philippe (1995) as an apomorphic feature (a derived character that arose relatively late among Conifers) and the genus is very probably monophyletic. The cross-field pitting is also typical, normally consisting of a single large window-like oopore (Ogura 1954), occupying the whole field, at least in the early wood. Attention should be paid to the fact that in other genera, like *Phyllocladoxylon* Gothan or *Protosciadopityoxylon* Zhang *et al.*, large window-like oopores can also occur in the early wood. Whilst revising Gothan's material stored in

Stockholm Natur Historiska Riksmuseet we noticed that the material from Svalbard that Gothan attributed to *Xenoxylon phyllocladooides* Gothan tends to have well-bordered oopores in the latewood (Fig. 1). It is the combination of xenoxylean radial pitting and the window-like oopores in the early wood that is characteristic of this genus.

The wood *Xenoxylon* has not been found connected to foliage or reproductive organs, and is thus of uncertain systematic position. Recent geochemical analysis has dismissed Pinaceae and Araucariaceae from any systematic relationship to *Xenoxylon* (Marynowski *et al.* 2007). Parichiev (1968) joined *Xenoxylon* and the extant Taxodiaceae *Sciadopitys* (the umbrella-pine, today endemic to Japan) on the basis of their palaeogeographic distribution and on the fact that *Xenoxylon* and *Sciadopitys*-like foliage are often found associated in Early Cretaceous sedimentary rocks all around the Arctic. It was demonstrated subsequently (Bose & Manum 1990, 1991) that this *Sciadopitys*-like foliage was not related to the modern genus *Sciadopitys* but to various different genera (*Mirovia*, *Oswaldheeria*, *Tritaenia*, etc.), which belong to the extinct family named Miroviaceae.

To whichever taxonomic group *Xenoxylon* is related, it is clear that this morphogenus does not necessarily fit with a single biological genus, and that the morphospecies that are described do not necessarily fit with biological species (Yamazaki *et al.* 1984).

### *Mesozoic Far East Asia in a terrestrial biogeographical perspective*

For this review we considered all of continental Asia east of 90° East plus the Japanese islands, therefore covering part of Siberia, Mongolia (*aru monggol*), China (including Inner Mongolia autonomous region or *Öbür Monggol*), South and North Korea, Japan, Vietnam, Laos, Cambodia, and Thailand.

During the Late Triassic Indochina and the North and South China blocks (Fig. 2), previously rifted from northeastern Gondwana, accreted to Mongolia and the Siberian platform (Metcalf 1998; Zhou *et al.* 2004; Metcalfe 2006). By the end of the Triassic period, Qiantang and Sibumasu in turn collided with the South China block (Metcalf 1998), which allowed exchanges of terrestrial biota during the Liassic (Philippe *et al.* 2004), and noticeably the spread of *Xenoxylon* towards lower latitudes. From the Late Triassic to the Late Cretaceous the eastern margin of the Asian continent, including north-eastern China (Liaoning, Jilin and Heilongjiang), the Korean Peninsula, and Japan, was under an Andean-type tectonic setting (Choi 1986). Accretionary complex belts were formed along the eastern margin of the Asian



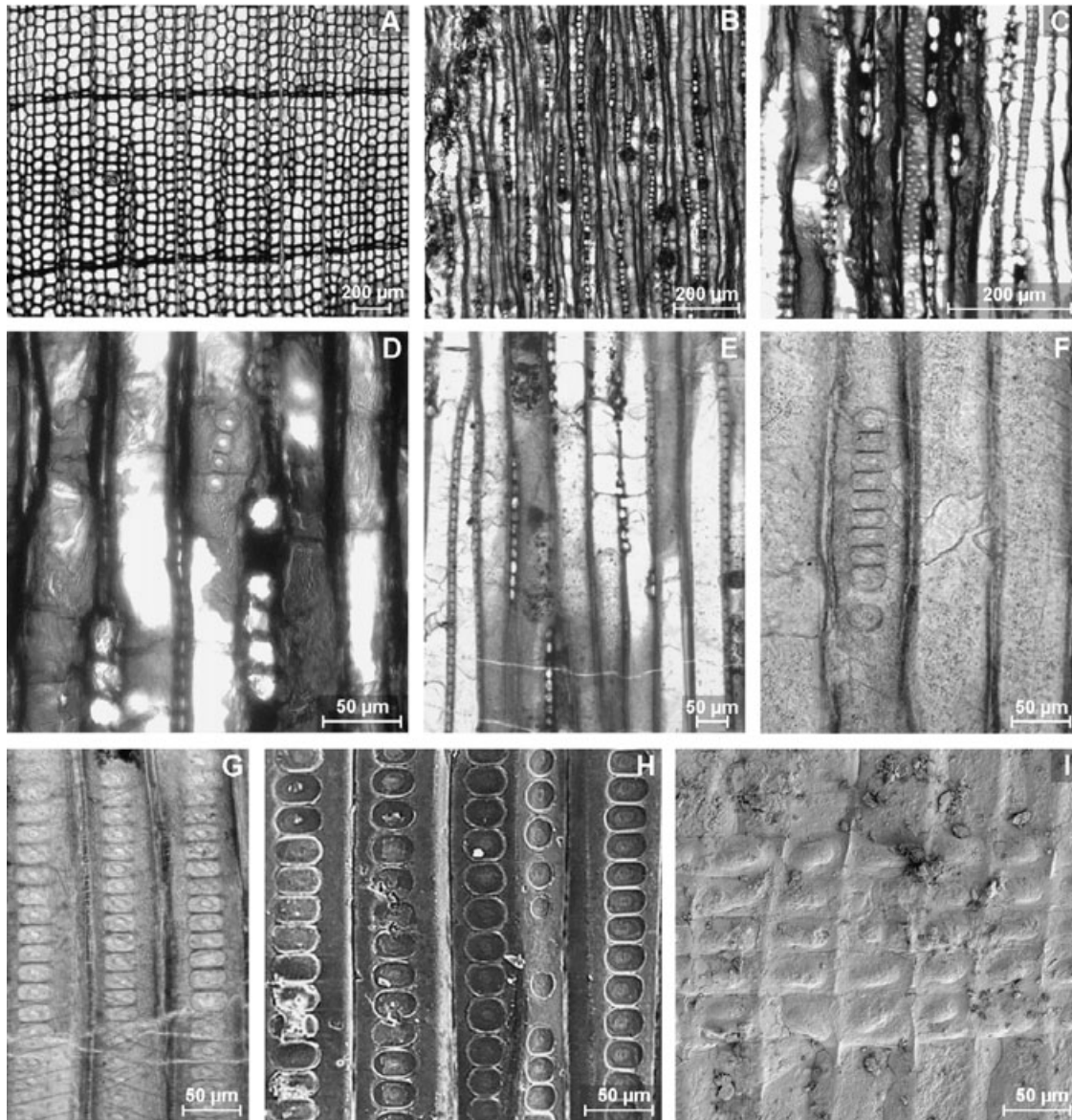


Fig. 1. *Xenoxylon* wood features. A, cross view, growth-rings with typical narrow late-wood (*Xenoxylon phyllocladoides*, sample 117 in Stockholm, Koenig's Karl Land). B, tangential view, high rays, one exceeding 40 cells in height (sample 73111 in Chonbuk, Inner Mongolia). C, tangential view, prominent pitting on tangential wall of a tracheid (sample 73100 in Chonbuk, Inner Mongolia). D, tangential view, small cluster of contiguous pits (sample 73100 in Chonbuk, Inner Mongolia). E, tangential view, low rays, long rows of sectioned radial pits and fungal hyphae (*Xenoxylon latiporosum* lectotype in Stockholm, Svalbard). F, radial view, small isolated cluster of contiguous pits (same specimen as for E); G, radial view, typical xenoxylean radial pitting (same specimen as for E). H, radial view, unique observation of an alternate tracheid with pitting on both sub-radial walls, pits getting locally round and spaced at the narrowest level, whereas other pits are typically of the 'latiporosum' type (*Xenoxylon latiporosum*, sample 1991/38 in Berlin, Poland). I, radial view, cross-field pitting in SEM (*Xenoxylon phyllocladoides*, sample S2983 in Stockholm, Greenland).

continent. A high (3500–4000 m) cordillera, the East Asian Coastal Range, spread along the eastern rim of the continent (Okada 2000) and had a strong rain-shadow effect on its western side (Philippe *et al.* in press). In the same time, further to the north-west, the Tan-Lu fault zone evolved (Vergely *et al.* 2007) from an oblique subduction zone (in the Late Triassic) to a

sinistral transform fault (during the Jurassic) and eventually a transcurrent fault (Early Cretaceous).

By the Mid-Jurassic, Indochina's terrestrial biota became biogeographically isolated, probably by a sea sound connecting the Tethys to the Arctic Ocean, at least until the end of the Early Cretaceous (Buffetaut & Suteethorn 1998; Zhou *et al.* 2003).

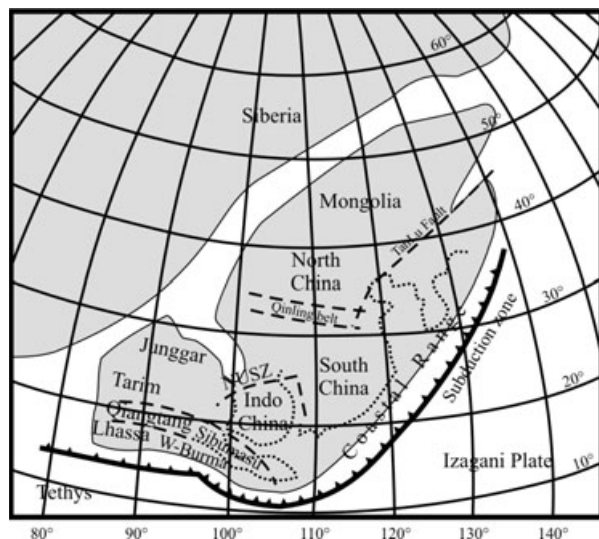


Fig. 2. Palaeogeographic map of Far East Asia for the Early Cretaceous, with main tectonic elements indicated. Adapted from Okada (2000), Carter & Bristow (2003), Zhou *et al.* (2003) and ODSN (<http://www.odsn.de/odsn/services/paleomap/paleomap.html>), accessed 2 November 2007.

During the Cretaceous, in the western part Lhasa and West Burma blocks accreted to the Qiantang and Sibumasu terranes. Farther to the east, East Asian tectonics were controlled by combined stresses of both plate movement of the palaeo-Pacific (Izanaki) and Tethys plates and superplume activity (Okada 1999). Diverse types of sedimentary basins were present (Okada 2000), including flexural, rift, and pull-apart basins. Because of the oblique, northward subduction of the Izanagi Plate located in the ocean side of Asia during the Early Cretaceous, sinistral strike-slip movement occurred on the continental margin (Okada & Sakai 1993), which resulted in the formation of a number of pull-apart basins in Far East Asia.

Such an active tectonic setting during the Mesozoic resulted in the development of topography with a steep coast along the continental margin, cordilleras with intra-montane basins, and back-arc flexural continental basins. In several basins, post-depositional tectonic displacement occurred, which resulted in uncertain biogeographical relationships (Kimura 1987; Carter & Bristow 2003; Matsukawa *et al.* 2006). To the north, the Siberian plate remained relatively stable all through the Jurassic–Cretaceous interval, with marine sedimentation on its margins.

In Far East Asia several classical floristic studies based on leaf assemblages have shown a clear partition between two different types of flora (Kimura 1987; Cao 1994; Ohana & Kimura 1995; Saiki & Wang 2003). In the northern part the so-called Tetori-type

flora or North-type flora is found, which has Siberian affinities, whereas the southern part is home to the Ryoseki-type flora or South-type flora, with Euro-Sinian affinities (Fig. 3). Between them a narrow, slightly oblique latitudinal band stretches from Xianqiang to the Korean Peninsula, characterized by a mixed flora. Albeit the general lines of this palaeo-phytogeographical plan are known, much controversy remains about the exact position of the boundaries and about their possible variation during the Mesozoic (Saiki & Wang 2003; Umetsu & Sato 2007).

## Results

### Data from literature

We located 99 data from literature (see Fig. 3 captions for corresponding references and locations), corresponding to following taxa (names used in original publications): *Araucarioxylon koreanum* Felix, *Xenoxylon barberi* (Seward) Kräusel, *X. conchyliatum* Fliche, *X. ellipticum* Schultz-Motel *ex* Vogelhehner, *X. fuxinense* Ding in Ding *et al.*, *X. hopeiense* Chang, *X. huolinense* Ding in Ding *et al.*, *X. jakutiense* Shilkina, *X. japonicum* Vogelhehner *ex* Suzuki & Terada, *X. latiporosum* (Cramer) Gothan, *X. liaoningense* Duan & Wang in Duan *et al.*, *X. meisterii* Palibin & Jarmolenko, *X. nariwaense* Yamazaki *et al.*, *X. peideense* Zheng & Zhang, *X. phyllocladoides* Gothan, *X. pseudoellipticum* Yamazaki & Tsunada, *X. shimakurai* Yamazaki & Tsunada, *X. tsuruokae* Nishida, Nishida & Suzuki, *X. watarianum* Nishida & Nishida, *X. yixianense* Zhang & Shang, *X. sp.* Stratigraphy and age of north-eastern Chinese and Korean formations were updated using Chang & Park (2003) and Jiang & Sha (2006).

### New data on Xenoxylon from Far East Asia

In the palaeontological collections of Berkeley University, California, we located a sample numbered 576.7/26:5 and labeled 'Mongolia', with typical *X. latiporosum* anatomy. Unfortunately the field locality and age are unknown. In the Komarov Institute (Saint-Petersburg, Russia) we located several *Xenoxyla* specimens in the palaeobotanical collection [no. 6, 8, 630 & 627 (Baikal region, Early Cretaceous); no. 9 (Baikal region, Early Cretaceous); no. 243 (Sikhote Aline Mountains, unknown age); no. 507 & 508, unnumbered specimen leg. Preskianov (Baikal region, Cretaceous); no. N706 (Olenek river area, Early Cretaceous)]. Eventually, S4846 (Jinxi, Liaoning Province, unknown age) in Naturhistoriska Riksmuseet (Stockholm), is also referred to *Xenoxylon*.

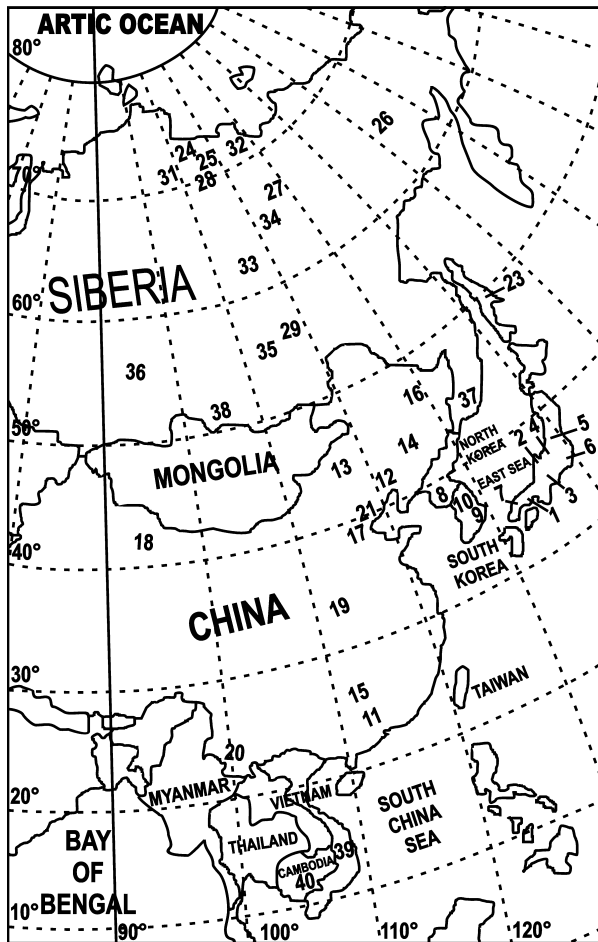


Fig. 3. Modern map with the localities mentioned in the text as source for *Xenoxylon*. **Japan:** 1, Okayama (Ogura 1950; Shimakura & Fujiyama 1962; Kimura 1987; Yamazaki *et al.* 1980; Yamazaki & Tsunada 1982b). 2, Ishikawa (Ogura *et al.* 1951; Yamazaki *et al.* 1984; Suzuki & Terada 1992; Terada *et al.* 2002). 3, Gifu (Ogura *et al.* 1951; Nozawa *et al.* 1975). 4, Toyama (Maeda 1954; Suzuki *et al.* 1982; Yamazaki & Tsunada 1981a, 1982a; Yamazaki *et al.* 1984; Terada *et al.* 2004). 5, Niigata (Watari 1960; Suzuki *et al.* 1982). 6, Chiba (Nishida *et al.* 1993). 7, Yamaguchi (Yamazaki & Tsunada, 1981b). **North-Korea:** 8, Phyongyang/Heizyo (Felix 1887; Shimakura 1936; Ogura 1944). **South-Korea:** 9, Gyongsangdo/Kyong-sang Dô/Hakruji (Ogura 1944; new data). 10, Cheongyang (Kim *et al.* 2005). **P.R. China:** 11, Northern Guangdong (Wang 1991). 12, Liaoning (Chang 1929; Gothan & Sze 1933; Shimakura 1936; Duan *et al.* 1995; Zhang & Shang 1996; Duan 2000; Ding *et al.* 2000; Ding 2000; Zhang *et al.* 2000a; Zheng *et al.* 2001; Zheng 2004; Wang *et al.* 2004; Wang *et al.* 2006). 13, Inner Mongolia autonomous region (Ding *et al.* 2000; He 1995; new data). 14, Jilin (Shimakura 1936; new data). 15, Southern Hunan (Hsü 1950a). 16, Heilongjiang (Sze 1951; Du 1982; Zheng & Zhang 1982; Terada & Nishida 2004; Sun *et al.* 2006; new data). 17, Beijing (Duan 1986; Zhang *et al.* 2000b). 18, Xinjiang (Hsü 1950b; Wang *et al.* 2000, 2002). 19, Henan (Miao *et al.* 1989). 20, Western Yunnan (Liu *et al.* 2001). 21, Hebei (Wang 1995). **Mongolia:** 22, Locality unknown (new data, Berkeley collection; UNESCO 1972). **Sakhalin:** 23, Nayba River (Nishida & Nishida 1986). **Siberia:** 24, Begichev River (74°5' N and 112°E) (Shilkina & Khudaiberdyev 1971). 25, Anabar River (Shilkina & Khudaiberdyev 1971). 26, Ziranika (Shilkina & Khudaiberdyev 1971). 27, Orulganski Mountains (Shilkina & Khudaiberdyev 1971). 28, Olenek River (Shilkina & Khudaiberdyev 1971; Shilkina 1986). 29, Dauria (Dorofejuk & Filin 1969). 30, N'ooloon River (Shilkina & Khudaiberdyev 1971). 31, Popigaj River (Shilkina & Khudaiberdyev 1971).

In South Korea at Hakruji, Gyoungsang Province, we found *Xenoxylon latiporosum* (sample JNU21100 in the Chonbuk National University collection) from the Nakdong Fm, which is dated as Hauterivian–Late Barremian.

In north-east China Jilin and Heilongjiang provinces, as well as in Inner Mongolia autonomous region of China, one of us (C.H.) collected several tens of samples from coal mine dumps related to *Xenoxylon* (see Table 2).

In Liaoning Province, during an excursion led by Professor Sun Ge, at Tianshifu Coal-Mine we collected in Middle Jurassic Dapu Formation a small charcoal piece which we investigated with Collodion cast. We assigned it to *Xenoxylon* sp.

## Discussion

### Stratigraphical and geographical distribution of the genus *Xenoxylon*

The genus *Xenoxylon* appeared during the Late Triassic. The first data are from the Carnian of Germany (Vogelheiner 1965; Rumpel 1979; but not Selmeier 1968, *vide* Philippe & Thévenard 1996), Japan (Yamazaki & Tsunada 1981b, 1982) and France (Fliche 1910; given as Middle Triassic Muschelkalk, but actually from the Carnian Schilfsandstein, see Philippe & Thévenard 1996). It is also present in the Norian of middle Asia (Khudaiberdyev 1993) and in several Asian localities within deposits, which cannot be dated more accurately than as late Triassic: e.g. Hongweikeng Fm. of the Gengkou Group, northern Guangdong (Wang 1991); Jogyeri Fm. of the Nampo Group, South Korea (Kim *et al.* 2005); or Hinahata Fm. of the Nariwa Group, Honshu (Yamazaki & Tsunada 1982).

The genus *Xenoxylon* lingered on until the latest Cretaceous, but data are scarce after the Cenomanian: late Turonian or Santonian of Sakhalin (Nishida & Nishida 1986); *cf.* Maastrichtian of northern Alaska (Spicer & Parrish 1990); Taipinlingchang Fm. (?Campanian–?Maastrichtian) of Amur (Heilongjiang) River (Terada & Nishida 2004). During revising a collection of fossil wood from Nuussuaq Peninsula

32, Beinchime River (Shilkina & Khudaiberdyev 1971). 33, Lensk (Shilkina & Khudaiberdyev 1971). 34, Lena River (Shilkina & Khudaiberdyev 1971). 35, Vitim plateau (Palibin & Jarmolenko 1932). 36, Krasnoyarsk (Natschokin 1961, 1962). 37, Sikhote Aline Mountains (Philippe & Thévenard 1996). 38, Djungarski Alatau (Philippe & Thévenard 1996). **Vietnam:** 39, Quangnam (Boureau 1950; Serra 1966, 1970). **Cambodia:** 40, Maekong River (Vozenin-Serra & Privé-Gill 1991).



Table 2. New data for *Xenoxylon* in Far East Asia. All data for P.R. China are based on samples collected by one of us (H.C.) from coal mine dumps. Abbreviations: B = Basin; J3 = Late Jurassic; K1 = Early Cretaceous; SG = Supergroup. All samples kept in Chonbuk National University collection.

Province and country	Locality	Geological Unit	Formation	Sample(s)	Age	Species name
Jilin Province, P.R. China	Yangcaogou	Songliao B	Yingcheng	71079, 71020, 71027, 71028	K1	<i>latiporosum</i>
	Pinggang	Liaoyuan B	Changan	71038	J3-K1	<i>sp.</i>
	Baiquan	Liaoyuan B	Changan	71047–71049, 71052	J3-K1	<i>latiporosum</i>
	Liaoyuan	Liaoyuan B	Changan	71065	J3-K1	<i>latiporosum</i>
Heilongjiang Province, P.R. China	Laotouju	Yanji B	Chancai	71095, 71096, 71098, 71099, 71104, 71105	K1	<i>latiporosum</i>
	Songxiaping	Yanji B	Chancai	71092	K1	<i>latiporosum</i>
	Chuangye	Bouqing B	Muling	71134–71136, 71140	Aptian-Albian	<i>latiporosum</i>
	Laoqijing	Bouqing B	Muling	71141	Aptian-Albian	<i>latiporosum</i>
Inner Mongolia autonomous region, P.R. China	Yaouu	Bouqing B	Muling	71142	Aptian-Albian	<i>latiporosum</i>
	Shujing	Bouqing B	Muling	71143–71145	Aptian-Albian	<i>phyllocladoides</i>
	Baofa	Huolinguole B	Damoguaihe	73001, 73002, 73005, 73006, 73008, 73009, 73011, 73012, 73014, 73016, 73017, 73021, 73023, 73026, 73032, 73037, 73040–73042, 73045, 73046, 73048, 73050–73055	upper Lower Cretaceous	<i>latiporosum aff. phyllocladoides</i>
	Zhenyuan	Huolinguole B	Damoguaihe	73062, 73065–73067, 73072, 73079	upper Lower Cretaceous	<i>latiporosum aff. phyllocladoides</i>
	Huolinhe	Huolinguole B	Damoguaihe	73098–73100, 73102, 73105, 73106, 73109, 73111, 73112	upper Lower Cretaceous	<i>latiporosum aff. phyllocladoides</i>
				21100	Hauterivian – Late Barremian	<i>latiporosum</i>
South-Korea	Hakruji	–	Nakdong			

(western Greenland) in the Copenhagen Geological Museum, we located two specimens we assigned to *Xenoxylon* sp. (no.165 and 36802). According to attached labels, they were found loose on the ground and could thus originate from either the upper part of Attane Fm., the Itilli Fm., or the lowermost Kangilia Fm., their age being thus sandwiched between the Coniacian and the Maastrichtian (see Dam *et al.* 2000).

Surprisingly, there are no published data from North America for *Xenoxylon*, the occurrences reported by Medlyn & Tidwell (1975), Tidwell (1990), Murphy (2005) and Parrish & Falcon-Lang (2007) being based either on an uncritical application of Kräusel's taxonomical choices (according to which *Xenoxylon* might include wood with several small oopores per cross-field in the early wood) or on poorly preserved material. However, Roy (1972) reported an unpublished mention by Gordon (1932) from the Early Cretaceous of Alberta, which we have not yet been able to check. In the American continent the genus is known only from the North Slope of Alaska, a displaced terrain of unclear palaeobiogeographical affinities. The genus *Xenoxylon* did not reach

Gondwana, the only data from there (Youssef 2002) being based on the misinterpretation of a wood related to *Metapodocarpoxylon libanoticum* (Philippe *et al.* 2003).

In southern and Western Europe as well as in middle Asia the genus *Xenoxylon* appeared in the fossil record by the Late Triassic, was well represented throughout the Early and Middle Jurassic, but then disappeared after the Oxfordian. These observations fit with the hypothesis of a large extension of *Xenoxylon*-unfriendly strongly tropophilous climates over most of the northern rim of Tethys Ocean from the Late Jurassic to the end of the Cretaceous. The setting of an at least seasonally dry climate would have exterminated the water-demanding *Xenoxylon* out from Western Europe. Meanwhile, the genus lingered on until the end of the Late Cretaceous in northern Far East Asia.

Northern Far East Asia is the only area in the world where *Xenoxylon* persisted from the Late Triassic to the Late Cretaceous. It is well represented in every stage of this interval, even though local hiatuses exist, for example the mid-Late Jurassic in Japan and the Korean Peninsula. These hiatuses are

probably resulting from the lack of suitable sedimentation regimes to allow preservation as those areas were tectonically highly active during these intervals.

The persistence of *Xenoxylon* in northern Far East Asia, together with the large number of species described, demonstrates that ecological conditions remained favourable to *Xenoxylon*-inhabited biocenoses all through the Carnian–Maastrichtian interval. Moreover, this area stretching roughly from Japan to Lake Baikal and from Beijing to Sikhote Alin Mountains, is home to amazing anatomical diversity for the wood *Xenoxylon*, opening the question of whether northern Far East Asia was a centre of differentiation for this genus.

### *Northern Far East Asia as a centre of differentiation for Xenoxylon*

Out of the 19 species of *Xenoxylon* described so far, 16 occur in Far East Asia, versus only 6 for all the rest of the world (Table 3). The two species of *Xenoxylon* that are not yet known in Far East Asia are *X. parvipunctatum* Vogellehner and *X. suljuctense* Shilkina & Khudaiberdyev: the former name could well be a synonym of *X. conchylianum* Fliche, which is described from Far East Asia, and the later was tentatively mentioned from Japan (Yamazaki & Tsunada 1981a). For every stage but two (out of six) there are at least twice as many species east of longitude 90° East as compared to west of this meridian. The figures reach an extreme for the Early Cretaceous when ten species are described in Far East Asia versus only two outside.

This diversity could be the result of a taxonomical bias. In other words, Asian wood anatomists could be more prone to describe wood species, based on anatomical features that elsewhere would be considered to fall within the natural variability of classical morphospecies such as *X. latiporosum* or *X. phyllocladoides*. The taxonomic key given by Ding *et al.* (2000) enhances this suspicion as several entries in the key use features that are known for their variability, sometimes even within a single specimen. Another point that suggests taxonomic bias is our observation, from Gothan & Sze's (1933) material from China identified as *X. latiporosum* (kept in Stockholm), of features otherwise known from *Xenoxylon nariwaense* Yamazaki *et al.* and *X. peideense* Zheng & Zhang. A superficial approach to the genus could lead to the conclusion that only two species, *X. latiporosum* and *X. phyllocladoides* are worth recognition within *Xenoxylon*. The taxonomic approach to fossil wood is still too idiosyncratic and is not yet standardized sufficiently to be pertinently used to estimate diversity. Without time-consuming examination of all

published material, it is impossible to draw inferences based only on a taxonomic approach.

To avoid a possible taxonomic bias, and as most types from Far East Asia were not easily accessible to us, we tried another approach to analyse *Xenoxylon* diversity. We analysed 113 specimens from Europe and the western Arctic (Greenland, Svalbard, King Karl's Land, Russian Arctic west of 70° East) and from a time interval ranging from the Early Liassic to the Late Cretaceous (list in Table 4; this is more than two-thirds of the total number of *Xenoxylon* specimens yet described from this area). Slides of all these specimens have been carefully screened for the xylological peculiarities, which are documented in the literature on Far East Asian *Xenoxylon*: partly biseriate radial pitting (as in *X. japonicum*); dense and locally biseriate tangential pitting on tracheids (as in *X. nariwaense*); locally biseriate rays; scalariform pits on the radial wall of tracheids (see e.g. *X. nariwaense*); rays higher than 30 cells; very elongated oopores in early wood (as in *X. peideense*); isolated radial clusters (as in *X. huolinhense*). Among this set of samples, however, only those from Franz-Josef Land (Russian Arctic) occasionally have some tangential pitting or biseriate rays. Tangential pits sometimes occur in specimens from the Arctic (Greenland, Svalbard), but are always small and isolated, never showing strong 'pitting'. Only two samples, both from Spitzbergen, display isolated radial clusters (Philippe & Cantrill 2007, pl. 8 fig. F). Very elongated oopores in early wood cross fields were observed only in one specimen (but they have been reported twice in Germany, see Philippe 1995). The other xylological features mentioned above have not been observed in this set of samples from Europe and Western Arctic.

In comparison, during studying samples from Far East Asia (94 specimens studied) we observed tangential pitting on the tracheid walls in more than 30% of the specimens, as well as occasional biseriate tangential pitting. In the Stockholm Natur Historika Riksmuseet we checked three slides described by Gothan and Sze (1933), under accession number S4846 (the corresponding sample is stored in Humboldt Museum, Berlin, Germany, no. 357). This specimen originates from Liaoning and was assigned to *Xenoxylon latiporosum* by Gothan and Sze. Interestingly, those slides feature a radial pitting typical for that species, but also, very locally, opposite and alternate pairs, as those illustrated for *Xenoxylon nariwaense* Yamazaki *et al.*, as well as almost scalariform pits, such as those illustrated for *X. peideense* Zheng & Zhang.

From our literature survey and examination of thin sections we established Table 5, comparing *Xenoxylon* wood diversity in and outside of Far East



Table 3. Distribution of *Xenoxylon* species in Far East Asia, east of 90° East and the rest of the world from west of 90° East. The species *X. pseudoellipticum* is not plotted as its age is unknown. Data are from Philippe & Thévenard (1996) and references already cited, with only limited taxonomic reappraisal (thus some synonymy is probable).

	West of 90° East	East of 90° East			
		Southern China and Indochina	Japan and Korea	North-eastern China	Eastern Siberia and Mongolia
<b>Late Triassic</b>	<i>conchylianum</i>	<i>ellipticum</i>	<i>latiporosum</i>		
	<i>parvipunctatum</i>		<i>nariwaense</i>		
<b>Early Jurassic</b>	<i>ellipticum</i> <i>latiporosum</i> <i>phyllocladoides</i>	<i>latiporosum</i>	<i>phyllocladoides</i> <i>latiporosum</i> <i>shimakurai</i>	<i>hopeiense</i> <i>japonicum</i> <i>latiporosum</i> <i>peideense</i>	<i>latiporosum</i> <i>phyllocladoides</i>
<b>Middle Jurassic</b>	<i>latiporosum</i> <i>phyllocladoides</i> <i>suljuctense</i>	sp. (Miao <i>et al.</i> 1989)		<i>conchylianum?</i> <i>hopeiense</i> <i>latiporosum</i> <i>peideense</i> <i>ellipticum</i>	<i>latiporosum</i> <i>phyllocladoides</i>
<b>Late Jurassic</b>	<i>latiporosum</i> <i>phyllocladoides</i>			<i>latiporosum</i> <i>peideense</i> <i>fuixinense</i> <i>hopeiense</i> <i>huolinhense</i> <i>latiporosum</i> <i>liaoningense</i> <i>peideense yixianense</i> <i>latiporosum</i>	
<b>Early Cretaceous</b>	<i>latiporosum</i> <i>phyllocladoides</i>		<i>latiporosum</i> <i>tsuruokae</i>		<i>hopeiense</i> <i>jakutiense</i> <i>latiporosum</i> <i>phyllocladoides</i>
<b>Late Cretaceous</b>	<i>latiporosum</i>				<i>latiporosum</i> <i>watarianum</i>

Table 4. *Xenoxylon* samples examined from Europe and Western Arctic (West of 70° East)

Collection	Accession number (Locality, Age)
Humboldt Museum (Berlin)	n°391 (Seichamp, Germany, Toarcian); n°1984/1059, n°1986/7 (Salzgitter, Germany, Toarcian); n°1986/8 (Wolfenbüttel, Germany, Hettangian); n°370 (Green Harbour, Spitzberg, unknown age); n°371 (König Karl's Land, unknown age)
Geological and Palaeontological Museum (Copenhagen), Mathiesen's collection	n°47, 48, 62, 64, 65, 66, 68, 70 (Jamesonland, Greenland, Early Pliensbachian); n°82, 83, 92, 95, 104 (Jamesonland, Early Toarcian); n°92, 95 (Jamesonland, Late Aalenian Early Bajocian); M5 (Jamesonland, Bathonian); n°119, 135, 136, 139, 145, 146, 147, 148, 149, 154, 155, 157, 158, 159, 163, 168, M11, M16, M18, M19, M21 (Jamesonland, Callovian); n°173 (Jamesonland, Kimmeridgian); M21 (Western Greenland, Coniacian ?)
University of Leeds Research Collection	n°LD130 (Lundstromdalen, Svalbard, Aptian-Albian)
Natural History Museum, London	n°20471 (Kilsby Northands, UK, Toarcian)
Laboratoire de Paléobotanique de l'Université de Lyon (Villeurbanne), Philippe's collection	n°MP5 (Chemaudin, France, Late Pliensbachian); MP407 (bei Ringelheim, Germany, Early Toarcian); MP184 (Belmont (69), France, Late Toarcian); MP411 (Harzburg, Germany, Toarcian); MP323 (Chemaudin, France, Toarcian); MP391 (Tchakpak, Kazakhstan, Late Liassic, leg. M. Doludenko); MP413 (Lehbin, Poland, Aalenian); MP907 (Osnabruck, Germany, Mid-Bajocian, leg. F. Wittler); MP1539, MP1550, MP1554, MP1569, MP1571, MP1572, MP1746 (Czestochowa, Poland, Late Bajocian, leg. M. Zaton); MP1553, MP1558, MP1588, MP1605 (Czentoschaw, Bathonian, leg. M. Zaton); MP1713, MP1714, MP1724, MP1735 (Luckow, Poland, Callovian, leg. M. Zaton & L. Marynovski); MP307, MP309 (Crouzet, France, Early Oxfordian); MP1593 (Talant, France, Oxfordian); MP1544 (Spitzberg, Latest Jurassic, leg. E. Buffetaut)
Muséum national d'Histoire Naturelle (Paris), Unger's collection	n°201, 202 (Whitby, UK, Toarcian).
Komarov Institute collection (Saint-Petersburg)	n°688 (Mangichlak, Caspian Sea, Toarcian); n°N65 (Chalimov, Crimea, Bathonian?); n°458 (Tkvarcheli, Georgia, Bathonian); n°1181, n°1181 (Russian Western Arctic, age unknown); n°17 (Arctic ocean 78°N80°E, unknown age); n°660, n°673, n°741, n°744, n°747, n°753, n°761, n°767, n°773 (Franz-Josef Land, unknown age); n°N17-539 (Lavrov, Komi, Russia, unknown age)
Naturhistoriska Riksmuseet (Stockholm), Nathorst's collection	n°3, 4, 84, 86, 93, 100, 101, 105, 106, 117, 120, 121, 92, A (König Karl's Land, unknown age); n°4, 6, 9a, 16, I, II (Green Harbour, Spitzberg, latest Jurassic); n°S4947 and 4971 (Franz-Josef Land, Early Cretaceous).

Table 5. Comparison on xylogenetic diversity in two geographical sets of samples of *Xenoxylon*. The two sets have comparable numbers of specimens, ca. 100. Frequency classes given as very rare (less than 2% of examined samples), rare (less than 5%), present (less than 10%), common (more than 10%).

Xylogenetic features	Far East Asia, East of 90° east	Europe and Arctic, West of 90° east
Pitting on the tangential wall of the tracheids	Common, sometimes prominent, with biseriolate alternate pits (e.g. <i>X. japonicum</i> , <i>X. shimakurai</i> )	Rare, always small, uniseriate and spaced
Occurrence of scalariform pits on the radial wall of tracheids	Rare ( <i>X. peideense</i> )	Unknown
Occurrence of very high rays (> 30 cells)	Present (e.g. <i>X. japonicum</i> )	Very rare
Occurrence of much elongated oopores in early wood cross-field	Present ( <i>X. ellipticum</i> , <i>X. pseudoellipticum</i> , <i>X. peideense</i> )	Rare ( <i>X. ellipticum</i> )
Occurrence of isolated clusters of 4–10 xenoxylean radial pits	Present (e.g. <i>X. nariwaense</i> , <i>X. huolinhense</i> )	Very rare
Occurrence of traumatic resin canals	Very rare ( <i>X. yixianense</i> )	Unknown

Asia, independently of morphospecies framework. Table 4 clearly shows that xylogenetic diversity of *Xenoxylon* is much higher in Far East Asia, regardless of the number of morphospecies. Those features observed in Far East Asia, and not (or rarely) elsewhere, are not controlled by the environment, and the difference cannot be explained by palaeoecology. We thus make the hypothesis that high-specific diversity in *Xenoxylon* in Far East Asia is not the result of a taxonomic bias. In this case, the notes by Yamazaki *et al.* (1984) that *Xenoxylon* pith can be quite different in Triassic and Cretaceous specimens is of great interest as it implies that besides secondary xylem variability, the *Xenoxylon* plant could also have an ever greater variability in Far East Asia.

In conclusion, during the Mesozoic, *Xenoxylon* was widespread in Far East Asia and reached an anatomical diversity unmatched anywhere else. This seems to be particularly clear in an area comprising North Korea, northeastern China, eastern Mongolia, and southern Siberia, which can be considered as the centre of differentiation for the genus. The limits of this differentiation centre are not yet well known because of the limited amount of data, and also as they probably oscillated or moved during the Mesozoic.

### Palaeoclimatological implications

It is sometimes hypothesized for modern flora that the differentiation centre of a genus is also its cradle, the area where it originated (Briggs & Walters 1997). We do not yet have enough data to know if this is the case for *Xenoxylon*.

A genus can survive in a given area over a given time interval only if ecological conditions always remain compatible with the genus ecological requirements, at least locally. Moreover, intuitively the

probability is very low that the fossil record of a genus would register a high diversity if ecological conditions are extreme most of the time, at the edge of genus ecological spectrum.

From our results an outstanding anatomical diversity is observed for the morphogenus *Xenoxylon* in Far East Asia as compared to the rest of the world. Because *Xenoxylon* favours wet temperate climates (Philippe & Thévenard 1996), we assume that for most of the genus stratigraphical range, i.e. from the Carnian to the Maastrichtian, such a climate prevailed over the *Xenoxylon* differentiation centre.

During interpreting *Xenoxylon* Boreal circum-polar distribution (Philippe & Thévenard 1996), it was difficult to differentiate the respective roles of temperature and of 'humidity' in this distribution pattern. As stated in the previous discussion, we know now from geochemistry, micropalaeontology, sedimentology, and growth ring characteristics that *Xenoxylon* inhabited temperate to cool temperate climates (Dromart *et al.* 2003; Harland 2005; Hauteville 2006; Tremolada *et al.* 2006; Hesselbo *et al.* 2007). On the basis of large log size, wide growth rings, and frequent association with thick coal seams (Ogura *et al.* 1951; Duan 1986; Duan *et al.* 1995; He 1995; Ding *et al.* 2000; our observations on material from Spitsbergen and China), it is obvious that the *Xenoxylon* tree grew in wet environments. This water could, however, have been obtained through precipitation (meteoritic water) or from the water table (phreatic water). At this stage it is difficult to decipher if the *Xenoxylon* tree was bound to wetlands or rather to areas of high rainfall.

According to its distribution in Far East Asia the wood genus *Xenoxylon* is part of the 'Northern-type' leaf-flora (also call Tetori-type or Siberian-Canadian, Saiki & Wang 2003), albeit it occasionally spread as far south as Vietnam (during the Pliensbachian or

the Toarcian; Boureau 1950), Yunnan (Liu *et al.* 2001), and Henan (during the Early Bathonian, Yima Fm.; Miao *et al.* 1989). According to Philippe & Thévenard's (1996) hypothesis, these sporadic southern occurrences indicate colder/wetter climatic snaps. In southern Europe *Xenoxylon* also occurs sporadically (Philippe 1995; Philippe & Thévenard 1996; Philippe *et al.* 2006), especially during four time intervals: Late Pliensbachian–Early Toarcian; Middle Aalenian–Early Bajocian; Late Bajocian–Early Bathonian; Late Callovian–Early Oxfordian. Two periods correspond to when *Xenoxylon* is documented in southern Far East Asia, the two other phases having left no fossil wood record in southern Far East Asia. In the Qaidam Basin, northwest China, one of the most completely developed Early–Middle Jurassic plant-bearing sequences in northern China is recorded. Wang *et al.* (2005) demonstrated that there, in Qaidam Basin, these Late Pliensbachian–Early Toarcian and Middle Aalenian–Early Bajocian intervals are wetter and more temperate.

In the detailed study by Wang *et al.* (2004) of the type section for Tuchengzi Fm. (Oxfordian–Kimmeridgian), in western Liaoning, it is striking to note that *Xenoxylon* occurs within a bed with low *Classopollis* percentage (8.77%, 228 palynomorphs counted). Similarly, Wang *et al.* (2006) report 15.4% only of *Classopollis* among palynological assemblages from the Mid-Jurassic Tiaojishan Fm. (Bathonian to Callovian) of Western Liaoning, in which *Xenoxylon latiporosum* is frequent. Such *Classopollis* percentages are considered typical for high latitudes (Vakhrameev 1991). These low percentages, however, are only encountered in some levels of these formations, whereas the average percentage is around 80%, a much more typical value for palaeolatitudes like those of Liaoning by the Mid-Mesozoic (Vakhrameev 1991). This raises the question of the temporal continuity of the *Xenoxylon* inhabited phytocoenosis in western Liaoning. It must be remembered that Liaoning was at the southern limit of 'Northern-type' floristic province (Saiki & Wang 2003), in a situation particularly suitable to record even small-scale climatological oscillations. *Xenoxylon* confirms independently that, as deduced from the prevalence of North-type of leaf flora, the climate in northern Far East Asia during the Mesozoic was temperate. However, it also suggests that climate oscillations occurred. This fits well with the recent results of Yabe *et al.* (2003) and Umetsu & Sato (2007) who demonstrated that the differences between the types of flora (e.g. Tetori versus Ryoseki) weakened occasionally and those of Paik & Lee (1995) who evidenced short-term climatic changes in the Early Cretaceous of Korea.

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