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Research paper

Systematics of a palaeoecologically significant boreal Mesozoic fossil wood genus, *Xenoxylon* Gothan

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ABSTRACT

The genus *Xenoxylon* was established for gymnosperm-like fossil wood with xenoxylean radial pitting and large oopores in its cross-fields. It is restricted to the Mesozoic and to the Northern Hemisphere, where it is commonly found. As an indicator of cool-wet boreal climates, as suggested by its distribution, *Xenoxylon* is of special interest to palaeoclimatology. Its systematics, however, is poorly known with several species needing re-evaluation. *Xenoxylon* nomenclature is also still unresolved, with various synonyms used for the same taxa even in recent literature. Having reviewed several types and a large number of specimens we performed a taxonomical and nomenclatural reappraisal of all species known to date. The results of this review are presented here, together with a taxonomical key. For most taxa stratigraphical and geographical distributions have also been re-evaluated.

1. Introduction

When, in 1905, Gothan coined the name *Xenoxylon* for a fossil wood from Svalbard which puzzled him, he probably did not imagine that this name had a prolific future. At this time *Xenoxylon* was known only by some poorly dated specimens from the Arctic. At present this genus is known to occur from the late Triassic through to the latest Cretaceous, throughout the Northern Hemisphere (Laurasia), with the noticeable exception of most of North America (Philippe et al., 2009). No less than 31 *Xenoxylon* species have been proposed (Table 1), and the genus is of palaeobiogeographical and palaeoecological interest (Philippe and Thévenard, 1996; Ding et al., 2000; Philippe et al., 2009). Indeed its distribution is restricted to Laurasia, mostly at high palaeolatitudes, and expanded southwards during cool intervals only, suggesting that *Xenoxylon* favoured cooler/wetter climates. Reliable indicators of terrestrial climates are greatly required for the understanding of Mesozoic climatic evolution. Mineralogical, sedimentological and geochemical evidence confirm that *Xenoxylon* was restricted to cool-wet temperate climates (Tchoumatchenco et al., 2008; Amiot et al., 2011; Selmeier and Grosser, 2011).

The taxonomy, systematics and nomenclature of the genus are, however, largely unsorted. From a taxonomic view point, some of the anatomical features of the genus that were originally considered to be of little significance have been re-evaluated (Philippe et al., 2009). As for the systematics, unexpected synonymies were recently discovered (Philippe and Hayes, 2010), whereas some names published by Chinese colleagues have been overlooked. Few types have been reviewed. Finally the nomenclature of *Xenoxylon* needs reappraisal as a putative earlier synonym (*Sciadopityoxylon* Schmalhausen; Philippe and Bamford, 2008) and several species names are still controversial (e.g. *Xenoxylon barberi* Seward).

Here we present a review of the genus, with full systematic treatment, taxonomical key and distribution data.

2. Material and methods

The material for *Xenoxylon* was studied at several institutional repositories listed with their respective abbreviations below and between parentheses the number of *Xenoxylon* samples studied there:

BIN	Komarov Botanical Institute of the Russian Academy of Sciences (RAS), St. Petersburg, Russia (30)
BMNH	Natural History Museum, London, UK (17)
BUPM	Berkeley University Palaeontological Museum, USA (1)
CNU	Chonbuk National University, South Korea (70)
CU	Chuo University, Tokyo, Japan (2)
HMB	Humboldt Museum, Berlin, Germany (9)
LPUL	Laboratoire de Paléobotanique de l'Université de Lyon, France (30)
MNHN	Muséum national d'Histoire naturelle, Paris, France (2)
NHMD	Natural History Museum of Denmark (38)

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Table 1
The thirty-one species names proposed within the genus *Xenoxylon*; those of which type was studied are underlined.

Species name	Authority	Reference	Notes
arcticum	Shilkina	Shilkina and Yatsenko-Khmelevsky (1980)	*Nomen nudum*
barberi	Seward (as *Cupressinoxylon*)	Kräusel (1949)	p.p. a synonym of *X. huttonianum*
canoasense	Rau (as *Cedroxylon*)	Kräusel (1949)	Not a *Xenoxylon*
conchylianum	Fliche	Fliche (1910)	Type lost
ellipticum	Müller-Stoll	Vogellehner (1968)	A synonym of *X. huttonianum*
fuxinense	Ding	Ding et al. (2000)	
hopeiense	Chang	Chang (1929)	
huolinhense	Ding	Ding et al. (2000)	
huttonianum	Witham (as *Peuce*)	Philippe and Hayes (2010)	
jakutiense	Shilkina	Shilkina (1986)	A *nomen nudum* in Shilkina & Yatsenko-Khmelevsky, 1980
japonicum	Vogellehner (not validly published in 1968)	Suzuki and Terada (1992)	A synonym of *X. meisteri*
jurassicum	Eckhold (as *Protopodocarpoxylon*)	Kräusel (1949)	Not a *Xenoxylon*; topotypes seen
[*kurumaense*]	Tsunada	Unpublished thesis (1980)	Not a validly published name
latiporosum	Cramer	Gothan (1905)	
[*liaoningense*]	Duan & Wang	Duan et al. (1995)	Not a validly published name
meisteri	Palibin & Jarmolenko	Palibin and Jarmolenko (1932)	
moorei	Tidwell	Tidwell et al. (1998)	Not a *Xenoxylon*
morrisonii	Medlyn & Tidwell	Medlyn and Tidwell (1975)	Not a *Xenoxylon*
nariwaense	Yamazaki, Tsunada & Koike	Yamazaki et al. (1980)	Type lost
parvipunctatum	Vogellehner	Vogellehner (1965)	
peideensis	Zheng & Zhang	Zheng and Zhang (1982)	As *peidense*
phyllocladoides	Gothan	Gothan (1906)	Type lost, topotypes seen
pseudoellipticum	Yamazaki & Tsunada	Yamazaki and Tsunada (1981)	Type lost
saadawii	Youssef	Youssef (2002)	Not a *Xenoxylon*
shimakurai	Yamazaki & Tsunada	Yamazaki and Tsunada in Yamazaki et al. (1984)	= *X. meisteri*; type lost
suljuctense	Shilkina & Khudayberdyev	Shilkina and Khudaiberdyev (1971)	Type lost
tomiense	Larichev	Larishchev (1948)	Probably not a *Xenoxylon*; type lost
tsuruokai	Nishida, Nishida, & Suzuki	Nishida et al. (1993)	Not a *Xenoxylon*
wattarianum	Nishida & Nishida	Nishida and Nishida (1986)	
yatsenkoi	Yunusov	Yunusov in Gomolitzky et al. (1981)	Not a *Xenoxylon*
yixianense	Zhang & Shang	Zhang and Shang (1996)	

SMNH Swedish Museum of Natural History, Stockholm, Sweden (29)
TUMS Tohoku University Museum in Sendai, Japan (32)
UTM University of Tokyo Museum (15).

Other abbreviations used:

ISBT Institut für spezielle Botanik der Universität Tübingen, Germany
NIGPAS Nanjing Institute of Geology and Palaeontology, Academia Sinica, China
SIGMR Shenyang Institute of Geology and Mineral Resources, Liaoning, China.

More than 285 samples of *Xenoxylon* were studied microscopically, either with scanning electronic microscopy, or light microscopy, using thin-sections or Collodion casts (Philippe et al., 2006). For all the taxa mentioned here protologues were accessed. An extensive bibliographical survey was performed, which to the best of our knowledge covers all published data for *Xenoxylon*.

3. Results

3.1. Circumscription of Xenoxylon

Since the seminal work by Gothan (1905) the circumscription of *Xenoxylon* has been little questioned. This genus is based on the occurrence of at least partially xenoxylean radial pitting in the tracheids (strongly flattened contiguous areolated pits; Müller-Stoll, 1951; Fig. 1) and a large fenestriform oopore in the early wood cross-fields (characteristically two when a ray cell terminal wall divides the cross-field; Fig. 2). Kräusel (1949) included in *Xenoxylon*, woods with a mixed type of radial pitting and with 2–4 rounded oopores per cross-field. As clearly demonstrated by Vogellehner (1967, 1968), such woods belong to distinct genera such as *Protocircoporoxylon* Vogellehner or *Protopolyporoxylon* Vogellehner. The term "xenoxylean" applies to a type of tracheid radial pitting where pits are contiguous and appear much flattened. In order to quantify this flattening from slide S1765 at the SMNH (holotype for *Xenoxylon latiporosum*; Philippe and Cantrill, 2007) we measured the longitudinal diameter/radial diameter ratio for 34 radial pits. The maximum was 0.69 and the minimum 0.45, whilst the mean-value was 0.57 and the standard-deviation 0.05. This ratio, also known as the "height/width" ratio, is rarely lower than 0.6 in the wood of most extant species with araucarian radial pitting (sensu IAWA, 2004). The 0.6 value is thus a limit below which a radial pit can be characterised as xenoxylean (see illustration in Figs. 1 and 3).

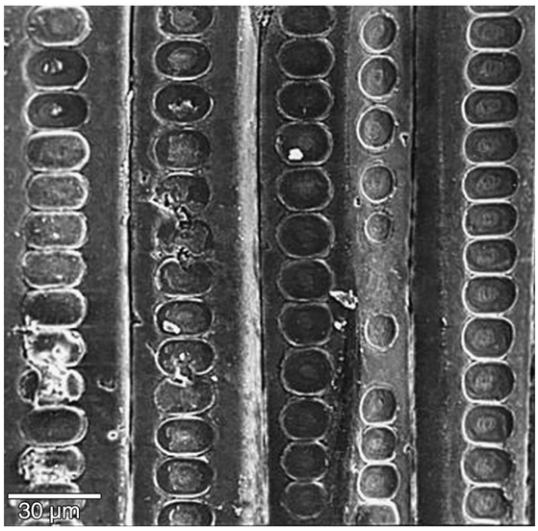

Fig. 1. *Xenoxylon latiporosum* (Cramer) Gothan; sample 1991/38 at the HMB, Jurassic, Poland; typical xenoxylean radial pitting on tracheids; note that on the narrow radial face of a tracheid, pits are locally round and distant (a very rare feature for this species and the *latiporosum* group).