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Original Publication Citation
Conifer wood from the Upper Jurassic of Utah I, Xenoxylon morrisonense sp. nov. David A. Medlyn and William D. Tidwell American Journal of Botany (February 1975), 62(2):23-28

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Tidwell, William D. and Medlyn, David A., "Conifer wood from the Upper Jurassic of Utah; I, Xenoxylon morrisonense sp. nov." (1975). All Faculty Publications. 1452.
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CONIFER WOOD FROM THE UPPER JURASSIC OF UTAH
PART I: XENOXYLON MORRISONENSE SP. NOV.¹

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ABSTRACT
A new species of conifer wood, Xenoxylon morrisonense, is described from the Morrison Formation on the Colorado Plateau. It is compared with other species of Xenoxylon, with X. latiporosum being the closest. Xenoxylon morrisonense differs from X. latiporosum in its marked indentations, simple pits on the horizontal and tangential walls of ray cells, absence of crassulae, presence of wood parenchyma, and thin borders on podocarpoid type crossfield pits. The origin of the septa in the tracheids is summarized, and the possible affinity of Xenoxylon with the Podocarpaceae is considered.

The petrified wood considered in this report was collected from the Upper Jurassic Morrison Formation on the Colorado Plateau in southcentral Utah. The locality, near Clay Point, Garfield Co., Utah², was shown to us by Mr. and Mrs. Thomas Hopkins of Hanksville, Utah. The site is relatively undisturbed and contains several well-preserved specimens. Petrified woods are locally abundant in the Morrison Formation. Many of these woods are highly siliceous and variously colored and are often poorly preserved. However, some specimens are well preserved and are generically comparable to previously reported fossil woods of similar age.

The specimen, a trunk measuring approximately twenty-two in. at its widest diam, was embedded in a pebble conglomerate (Fig. 1). The axis is partly silicified and contains areas of structurally preserved cells favorable for study. However, the pith, primary xylem, and phloem are not preserved.

DIAGNOSIS: Xenoxylon morrisonense sp. n.—
Transverse section—Growth rings narrow, sometimes indistinct (Fig. 2), 2–3 cells wide, late wood tracheids tangentially flattened, angular to rounded, 20 \( \mu m \) in diam, lumens round to elliptic; early wood tracheid size varies from 25–50 \( \mu m \) in diam, tracheids more or less regularly aligned, occasionally with smaller tracheids interspersed among the larger; cell walls 5–6 \( \mu m \) thick in both early and late wood; wood parenchyma present but not readily observable in cross section; rays uniseriate, occasionally biseriate, separated by one to five rows of tracheids, commonly four; horizontal walls of ray parenchyma pitted with 1–2 simple pits.

²Received for publication 16 January 1974.
traversely elongated pits on the radial walls of tracheids; (2) the absence of pitting on the horizontal and tangential walls of rays; and (3) large oval pits on the radial walls of the ray cells. *Xenoxylon* spans a comparatively narrow geological range (Middle Triassic to Lower Cretaceous). However, geographically it is widely distributed in northern latitudes. Since 1905, an increasing number of occurrences have been cited. In 1906, Gothan reported *Xenoxylon* from the Jurassic of Poland, and Holden (1913) described it from the Jurassic of Yorkshire, England. The oldest occurrence was cited by Fliche (1910) from Middle Triassic strata of France. *Xenoxylon* has been reported from the Jurassic of China (Chang, 1929; Gothan and Sze, 1933), Korea (Ogura, 1931), Japan and Manchuria (Shimakura, 1936; Watari, 1960), Jurassic of France (Grambast, 1953), and also the Cretaceous of Alaska (Arnold, 1952).

Five previously described species of *Xenoxylon* are *X. latiporosum* (Cramer) Gothan, *X. phylocladoides* Gothan, *X. conchylikuanum* Fliche, *X. hopeiense* Chang, and *X. barberi* (Seward) Kräusel. *Xenoxylon* *morissonense* shows a close affinity to *X. latiporosum* on the basis of the diagnostic tracheid septation which is lacking in the other four species. These thin, transverse septations were figured by Gothan (1905), Ogura (1944), Arnold (1952), and Watari (1960) in their reports of *X. latiporosum*. *Xenoxylon morissonense* differs from *X. latiporosum* in the absence of crassulae, and in having marked indentations and simple pits on both the horizontal and tangential walls of the rays (Fig. 5). The latter condition is not compatible with the generic designation, but it is not inconsistent with the admixture of characters associated with transitional conifers. Shimakura (1936) and Watari (1960) has stated that true crassulae, as seen in abietinean wood, are never present in *X. latiporosum*, although the contact between the borders of two adjacent pits are often dark brown. However, Arnold (1952) pointed out distinct crassulae that had apparently been overlooked by authors who previously described this species. He described these crassulae as being narrow because of the crowded condition of the pits. The tracheal pitting of *X. morissonense* is always contiguous (Fig. 9), but the pits are not always vertically flattened and horizontally elongated as in *X. latiporosum*. The conspicuous presence of a thin border on some of the crossfield pits of our specimen is also a notable difference.

Wood parenchyma is present in *Xenoxylon morissonense* but not in *X. latiporosum*. The latter species has small oval or circular pits on the tangential walls of the late wood tracheids (Shimakura, 1936), which are missing in the former. Seward (1919) stated there are no resin canals or xylem parenchyma in *Xenoxylon*. However, *X. hopeiense* Chang, recorded from China in 1929, is said to differ from other described species of *Xenoxylon* in having crassulae, wood parenchyma, occasional biseriate rays, and resinous cells in the rays.

Thus, on the basis of marked indentations, pitted horizontal and tangential walls of ray cells, absence of crassulae, thin borders on podocarpoid-type crossfield pits, and wood parenchyma, *X. morissonense* is proposed as a new species.

The origin of the septa in tracheids has been reviewed and postulated by several authors. Penhallow (1907) attributed similar structures to resin plates which divided the tracheids. Conrad (1910) and Record (1918) proposed that these septa are of parenchymatous origin. Thomson (1913) described septate tracheids from the xylem of the Araucarinea. Some of these are partial septations composed of secondary walls, whereas others are complete septations which Thomson described from *Agathis bornensis* and *A. alba*. In connection with the latter, Thomson (1913, p. 25) stated "... there are often parenchyma cells replacing some of the septated parts. This may go so far that the whole tracheid is replaced parenchyma, but usually there is some vestige of the origin of these vertical series of cells from the tracheary elements." He also mentioned that septate tracheids and parenchyma cells replace tracheids in vertical rows in the wood of *Abies* and also in association with the resin canals of pines. Jeffery (1925) considered septate tracheids to be intermediate stages between tracheids and wood parenchyma, as viewed in *Picea*, and that they represent a primitive form of axillary parenchyma. He further mentioned that tracheids in the roots and cones of pine are occluded by ingrowing parenchyma cells (Jeffery, 1917), although this condition is not normal to the vegetative axis of living pines. Jane (1956) discussed horizontal biconcave resin plates characteristic of the genera *Agathis* and *Araucaria*. He explained
that if these plates were cut medianly, the tracheid would appear to be full of resin; whereas if cut near the upper boundary, there would appear to be a resinous lining to the tracheid lumen.

Both Ogura (1944) and Watari (1960) discussed the origin of septate tracheids in *Xenoxyylon latiporosum* and concluded they were tylosoid. The septa were formed by the fusion of membranes of adjacent tyloses which originated by the projecting of the parenchymatous ray cells through the ray pit. Watari (1960) demonstrated the development of the tylose from its origin as a bladder until it formed the septum. In *Araucaroxylon mineense* and *A. huzinamiense* Ogura (1960) observed the projection of the contents of wood parenchyma into some tracheids. The presence of tylose formation in some species of living conifers (Batton and Boureau, 1965; Ogura, 1944) makes the presence of these structures in fossil woods entirely possible.

Arnold (1952), commenting on the tylosoid nature of the septa in his specimen of *Xenoxyylon latiporosum*, remarked, "... they are present in such great numbers that connection of all them with ray cells does not seem quite possible." This is also the case in *Xenoxyylon morrisonense*; although some septa definitely appear to have formed from tyloses, others appear as transverse walls (Fig. 7). Ogura (1944) postulates a similar condition as being due to the lateral mem-

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**Fig. 7-10. Xenoxyyon morrisonense. BYU 926 holotype.**

branes of the tyloses coming in close contact with
the tracheid walls and thereby obscuring the ty-
lose-like structure. The horizontal portion of the
membranes then appear as thin, flattened plates
crossing the tracheid lumen. Ogura (1960) con-
cluded that differences in tracheid septation may
be due to species variation and the age of the
wood.

Affinities—As is the case with many Mesozoic
conifers, placing *Xenoxyylon* in an extant family
or genus is rather problematical. In tracing coni-
fers through the geologic past, the Mesozoic,
especially Middle Mesozoic, would have to be
termed "The Age of Conifers." It was at this
time that conifers were undergoing rapid diver-
gence. The species of this Era had retained many
ancestral characteristics, but at the same time
many of the characteristics which denote modern
forms were evolving. Hence some authors have
called them "transitional conifers." If classifica-
tion of these species were based only on primitive
characters, which some authors have done, all
would be diagnosed as araucarian or, probably
more accurately, cordaitalean conifers.

Arnold (1952) reviewed the previous concepts
of araucarian affinities proposed for *Xenoxyylon*
by Holden (1913) and others. He pointed out
discrepancies in using some criteria, particularly
presence or absence of crassulae, as a fundamen-
tal difference between araucarian and the "more
advanced" conifers. As stated by Arnold (1952),
"Considerable confusion and misunderstanding
about the affinities of fossil conifers has resulted
from an 'either-or' attitude on the part of in-
vestigators who have endeavored to force mis-
fits into modern families where they do not be-
long." Perhaps by using a combination of ancestral
and living characters with special emphasis on the
"more advanced" features, a semiorderly system of
classification of these fossil conifers may yet be
established.

A combination of large podocarpoid pits in the
crossfields, smooth horizontal and tangential walls
on the ray cells, and the absence of resin canals
suggests a possible phyletic affinity of *Xenoxyylon*
with the modern family Podocarpaceae. Some
*Xenoxyylon* species are said to be indistinguish-
able from *Sciadopitys* and *Podocarpus* (Arnold,
1952). The occurrence of pitted horizontal and
tangential walls of the rays of *X. morrisonense*
also suggests a possible ancestral tie to some
members of the Pinaceae.

There are three established fossil genera, *Mes-
embrioxylon*, *Protophyllocladoxylon*, and *Xen-
oxyylon*, for petrified woods which show possible
affinities to the Podocarpaceae. In addition, *Em-
bergerixylon* is similar but has not yet been
allied with woods related to this family.

*Mesembrioxylon* is an artificial genus estab-
lished by Seward (1919) to include those extinct
genera which show affinity to the modern family
Podocarpaceae. It was primarily intended to re-
place Gothan's two genera *Podocarpoxylon* and
*Phyllocladoxylon*. Earlier Stopes' (1915), recog-
nizing the inconsistencies between these two
genera, lumped them into the single genus *Podo-
carpoxylon*. Seward in his original diagnosis de-
fined *Mesembrioxylon* as a coniferous wood in
which the features are similar to those associated
with *Cupressinoxylon*, although the xylem paren-
chyma may or may not be present. Another
feature that Seward described for the former
genus is the presence of one or two large simple
pits, or in some species two or more smaller bor-
dered pits, in the crossfields. In either case, the
apertures are more vertical than horizontal.

When Gothan established *Xenoxyylon* he did
not mention its affinities with the Podocarpaceae
but alluded to some relationship by naming one
species *X. phyllocladoideae*. Seward (1919) also
recognized a relationship when he said that *Xen-
oxyylon* showed a close resemblance to Gothan's
species *Phyllocladoxylon (=Mesembrioxylon)*.

Kräusel (1939) proposed *Protophyllocladox-
ylon* for woods similar to that of the Podocarpaceae
but which differ by having araucaria-type pitting
on the radial walls of the tracheids. The previ-
ously described species of this genus range strat-
igraphically from the Upper Carboniferous (?) to
the Tertiary. All species are characterized by the
presence of araucaria-type crossfield pitting. Sep-
tate tracheids are present in some species. Spe-
cies of *Protophyllocladoxylon* show many striking
similarities to *Xenoxyylon morrisonense*, especially
those having septate tracheids. However, the
araucarian pitting on the radial walls of the tra-
cheids of *Protophyllocladoxylon* excludes our
specimen.

Lemoigne (1966) and Demarcq and Lemoigne
(1967) placed two new species in *Dadoxylon*,
but Lemoigne (1968) later removed them by as-
signing them to a new genus, *Embergerixylon*,
which features septate trachyids with uniseriate
and, more rarely, biseriate (araucarian) trachey-
ary pitting on the radial walls. The crossfield pitting
is also of the araucarian type, although poorly pre-
served, which is probably why any possible af-
finity of this genus with the Podocarpaceae was
not mentioned. *Xenoxyylon morrisonense* and *Em-
bergerixylon alpinum* are very similar but differ
in their crossfield pitting.

All of the above genera tend to merge into one
another, part of the problem of affinities being the
great range of structural variability in both living
and extinct conifers. The rest of the enigma lies in
the lack of precise generic delineation.

The foliage of *Xenoxyylon* is unknown although
Nathorst (1897) suggested a possible relationship
between this genus and *Elatides*. Arnold (1952)
noted the association of his specimen with *Podo-
Podozamites and Baiera. Watari (1960) mentioned that Podozamites occurs in the same strata as his specimens of Xenoxyylon latiporosum. No fossil foliage has yet been collected in the area where Xenoxyylon morrisonense was found. However, Brown (1972) reported Podozamites with the conifers Pagiophyllum and Pityophyllum from the Morrison Formation in Montana. If an organic foliage has yet been collected in the area where specimens of Xenoxyylon, which appears to be unlikely, the evidence would be against the placement of Xenoxyylon in the Podocarpaceae.

Xenoxyylon has a wide geographical distribution in the Northern Hemisphere. It has been reported from western Canada, and northern Alaska (Arnold, 1952). The occurrence of Xenoxyylon morrisonense in Utah is the southernmost extension of the genus in North America.

Xenoxyylon is not known from the Southern Hemisphere. In contrast, the Podocarpaceae is the most important family of Coniferales in the Southern Hemisphere today. Species of this family grown mainly in mountain tropical forests, although some occur in lowland forests (Florin, 1958).

Xenoxyylon and other allied genera seem to be widespread in the Mesozoic. Of the described species of Xenoxyylon, Protophyllocladoxylon, Mesembrioxylon, and Embergerixylon, approximately 75% are found in the Mesozoic, thus showing that these possible representatives of the Podocarpaceae were an important aspect of the Mesozoic flora.

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