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AGATHOXYLON LEMONII SP. NOV., FROM THE DAKOTA FORMATION, UTAH

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ABSTRACT.—Petrified wood specimens from the Dakota Formation of Utah are here described as *Agathoxylon lemonii*. This new species is characterized by having distinct growth rings, araucarian tracheary pitting, resin plates or plugs in its tracheids, abundant axial parenchyma, low uniseriate rays and 1–4 small, slightly bordered pits with circular to oval included apertures per crossfield. This is the first report of petrified wood from the Dakota Formation of the western United States and the first record of *Agathoxylon* from North America.

Although fossil plant remains are abundant in the Dakota Formation, reports of petrified plant material from this formation are rare. The study of fossil plants in the Dakota Formation began in the midwestern United States. Initial collections of fossil plants from this formation were obtained during western territorial surveys for a proposed route for a transcontinental railroad in the 1850s and 1860s (Dilcher et al. 1978). Hayden, in 1853, was the first to obtain leaves from the Dakota Group of Nebraska. He and Meek in 1856–57 collected additional plant materials from these sediments that were subsequently sent to Professor Oswald Heer in Switzerland for study. Heer (1859) published descriptions of these materials. This publication represents the first authentic record of North American Cretaceous plant fossils.

Well-preserved leaves were later collected in large numbers in Kansas during the 1860s and 1880s by various workers. These collections formed the basis for the first major publications on this flora by Lesquereux (1874, 1883, 1892).

Subsequent to Lesquereux's publications, very little work had been done on the flora of the Dakota Formation until recently, when considerable research on the reproductive structures and leaves of early angiosperms from this formation in Kansas was published (Dilcher et al. 1976, Dilcher et al. 1978, Dilcher 1979, Retallack and Dilcher 1981).

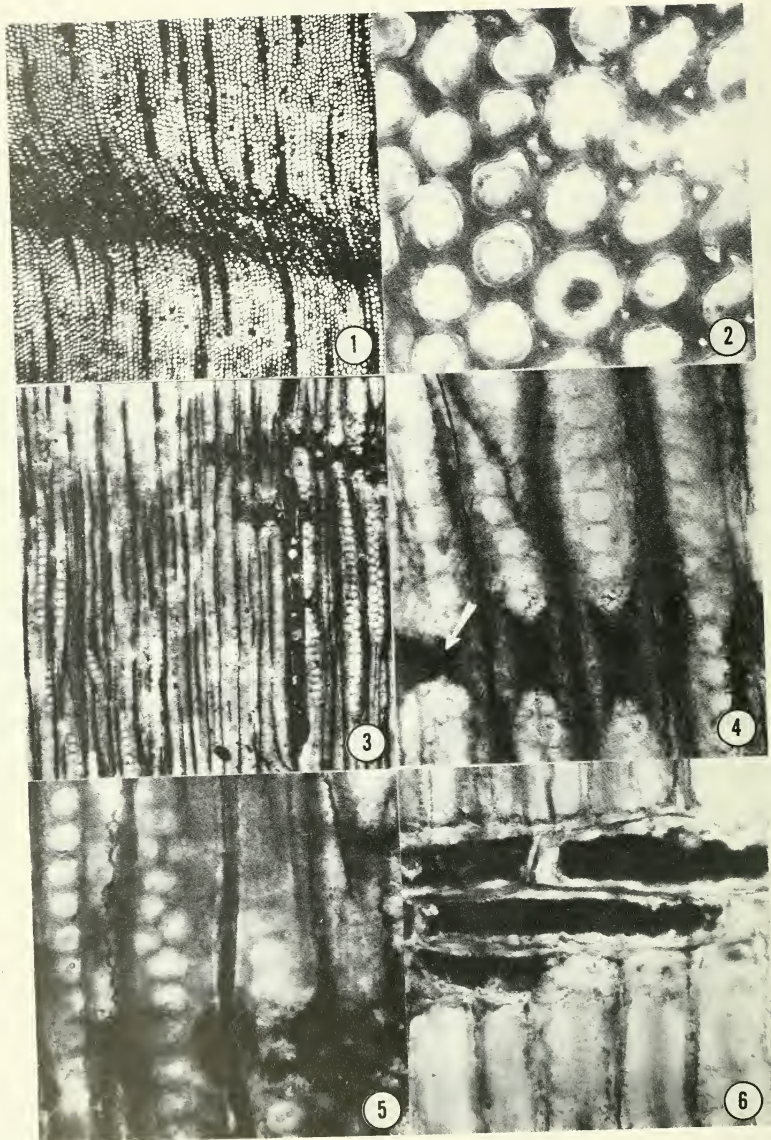
The Dakota Formation extends throughout much of the southwestern and midwestern

United States. Stanton (1905) in working with Jurassic and Cretaceous formations and the Dakota in southern Colorado, New Mexico, and Oklahoma, demonstrated that the Dakota Formation of this region, as originally defined, contains both Lower and Upper Cretaceous strata. In Utah the Dakota Formation occurs between the Lower Cretaceous Cedar Mountain Formation and the Upper Cretaceous Mancos Shale and is considered to be mid-Cretaceous in age. Fossil plants in the Dakota Formation of western Colorado and eastern Utah were first reported by Brown (1950) and later by Tidwell et al. (1967), Rushforth and Tidwell (1968), and Rushforth (1970, 1971).

Brown (1950) described a flora from the Burro Canyon Formation that is more or less equivalent to at least a portion of the Cedar Mountain Formation (Young 1960, Tschudy et al. 1984) and a flora from the Dakota Formation near Naturita, Colorado. This flora, like the Dakota flora from Westwater, Utah, is atypical in that the percentage of ferns is high as compared with the number of angiosperms. The Dakota flora near Westwater is dominated by the ferns *Astralopteris* Tidwell, Rushforth, and Reveal, *Matonidium* Schenk, *Gleichenia* Smith, *Hausmania* Dunker, *Asplenium* L., *Cladophlebis* Brong., and *Coniopteris* Brong. (Rushforth 1970, 1971). No coniferous foliage has been reported from this flora in Utah. However, Retallack and Dilcher (1981) noted that *Sequoia*-like foliage, cones, and cone scales were common conifer megafossil material in the Dakota Formation

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Figs. 1-6. *Agathoxylon lemonii*: 1, Transverse section illustrating a growth ring and dark axial parenchyma. (33X) (Holotype). 2, Transverse section illustrating an axial parenchyma cell with dark contents and overlapping tracheids (495X) (Holotype). 3, Radial section illustrating axial parenchyma, radial intertracheary pitting and resin plates (123X) (Holotype). 4, Radial section illustrating uniseriate and biseriate pitting. Note resin plates in lower portion of photograph (495X) (Holotype). 5, Radial section showing a close up of radial pits. Note both elliptic and circular apertures (495X) (Holotype). 6, Radial section illustrating the nature of the ray cell walls and contents. Note crossfield pitting in the right portion of the photograph and showing through ray cell contents in upper right side ray cell (495X) (Holotype).

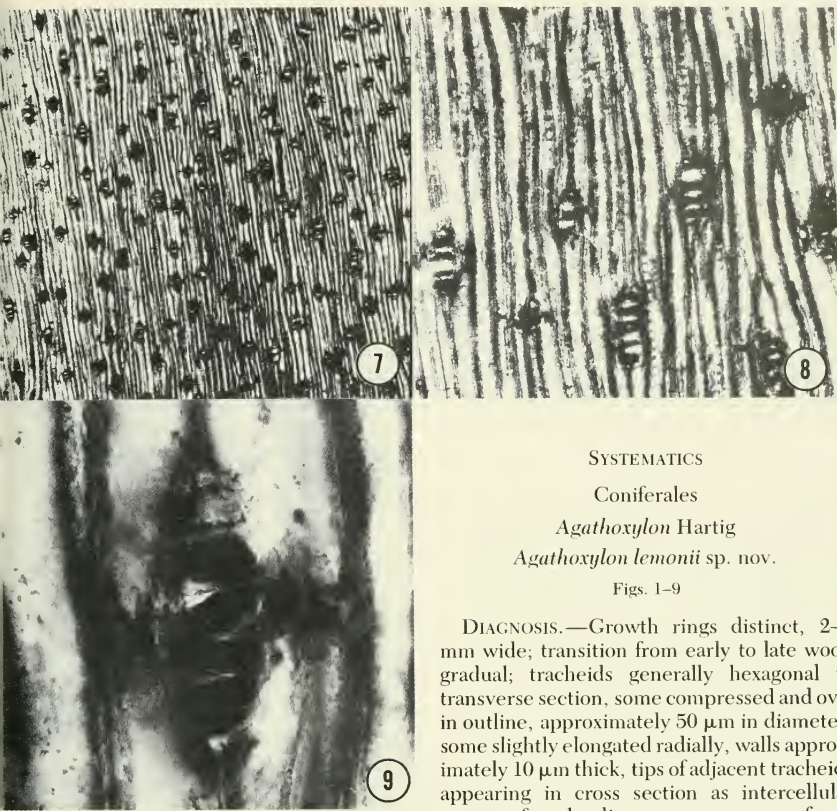


Fig. 7–9. *Agathoxylon lemonii*: 7, Tangential section showing general size, shape, and arrangement of the rays (33X) (Holotype). 8, Tangential section illustrating ray size and shape. Note tangential tracheid pitting. (123X) (Holotype). 9, Tangential section showing outline of ray and ray cells (495X) (Holotype).

in Kansas. They also noted the presence of *Brachyphyllum*, which, although not common, was evidently a minor constituent of the fossil angiospermous swamp woodland flora of this formation. Possible conifer dominance in the inland vegetation of the Dakota flora is supported by a number of palynological studies of this formation and rock units of equivalent age in North America (Pierce 1961, Agasie 1969, Romans 1975, Retallack and Dilcher 1981).

SYSTEMATICS

Coniferales

Agathoxylon Hartig

Agathoxylon lemonii sp. nov.

Figs. 1–9

DIAGNOSIS.—Growth rings distinct, 2–6 mm wide; transition from early to late wood gradual; tracheids generally hexagonal in transverse section, some compressed and oval in outline, approximately 50 μm in diameter, some slightly elongated radially, walls approximately 10 μm thick, tips of adjacent tracheids appearing in cross section as intercellular spaces often lending an appearance of collenchyma to the xylem; radial pitting generally uniseriate, frequently biseriate, pits slightly appressed, circular to horizontally elongate, 12–14 μm diameter with 2.4–7.8 μm apertures; tangential pitting uniseriate with pits same size as radial pitting, generally isolated; resin plates or plugs observed in many tracheids; axial parenchyma abundant, diffuse, with smooth thick walls and dark intercellular contents; rays uniseriate, homocellular, approximately six per millimeter, 20–70 μm wide, 10 (commonly 5 or 6) cells high, 30–150 μm high; ray cells vertically flattened and elongate horizontally, nearly twice as wide tangentially as high, often 50 μm wide tangentially by 30 μm in vertical dimension and 30–100 μm (average 70 μm) in radial dimension; ray cells filled with dark cell contents, ray cell walls approximately 3 μm thick

and unpitted except at crossfield; crossfield pits commonly obscured by cell contents, observable crossfields with 1–4, small (approximately 5 μ m), slightly bordered pits with circular to oval included apertures.

REPOSITORY: Brigham Young University, 5029 (Holotype).

LOCALITIES: 7 mi (11.2 km) east of Ferron, Utah; U.S. Geol. Surv. Map: Desert Lake Quadrangle, SE 1/4, Sec 26, T20S, R8E (Holotype). Other specimen: 2.5 mi (4.02 km) north of Westwater, Utah.

HORIZON: Dakota Formation.

AGE: Lower Upper Cretaceous (Cenomanian).

ETYMOLOGY: The specific epithet is for Mr. and Mrs. Frank Lemon of Moab, Utah, who donated specimens for this study.

DISCUSSION

The presence of araucarian tracheary pitting and of resin cysts, plugs, plates or spools in *Agathoxylon lemonii* indicate that it is allied to the Araucariaceae. The Araucariaceae consist of two extant genera, *Araucaria* De Jussieu with 18 species (De Laubenfels 1972) and *Agathis* Salisbury composed of 13 species (Whitmore 1980). Fossil woods with araucarian structure are abundant in the geologic record. They range in age from Carboniferous to Recent and have been assigned to many genera, including *Araucarites* Presl, *Pinites* Lindl. & Hutton sensu Presl, *Dadoxylon* Endlicher, *Araucarioxylon* Kraus, *Agathoxylon* Hartig, and *Araucariopitys* Jeffrey. These woods may also be related to *Cordaioxylon* Gr. Eury, *Cordaites* Unger, or early conifers such as *Lebachia* Florin or *Ernestodendron* Florin. Knowlton (1899), Penhallow (1907), Stopes (1914), Holden (1914), and Jeffrey (1926) assigned Paleozoic araucarian woods to *Dadoxylon* and reserved the name *Araucarioxylon* for Mesozoic and Tertiary materials. Further, Seward (1919) proposed adding qualifying terms such as *Araucarioxylon* or *Cordaioxylon* in parenthesis after *Dadoxylon* whenever evidence supports such designation. Torrey (1923) agreed somewhat with using *Araucarioxylon* for Mesozoic and Cenozoic woods and *Dadoxylon* for Late Paleozoic types. However, he also separated them by assigning *Dadoxylon* to fossil woods lacking

wood (axillary) parenchyma and assigning woods with parenchyma to *Araucarioxylon*. Edwards (1921) proposed using *Dadoxylon* for araucariaceous wood that could not be related to either *Agathis* or *Araucaria*. Some authors, such as Krausel and Jain (1963), Sah and Jain (1963), and Vogelhehner (1964) followed Gothan's (1905) recommendation that all woods having an anatomical similarity to Araucariaceae or Cordaiteae should be placed into *Dadoxylon* as a single nomenclatural unit. Krausel (1949) designated *Araucarioxylon* as the genus for all woods related to *Agathis* or *Araucaria*. Hartig (1848) instituted the genus *Agathoxylon* for fossil having "zellfasern" or axial parenchyma woods similar to the living genus *Agathis*. The presence of axial or wood parenchyma is the only character absent or rarely found in *Araucaria*. Krausel and Jain (1963), in discussing *Agathoxylon* remarked that Hartig had not given any details of his specimen. Sah and Jain (1963) went further and suggested that the "zellfasern" of the Hartig specimen were perhaps resinous tracheids. According to Seward (1919), resin plates in tracheids are often interpreted as end walls of axial parenchyma, thus leading to erroneous reports of *Agathoxylon*. Greguss (1955), Jane (1970), and Stockey (1982) considered the anatomical separation between *Agathis* and *Araucaria* on the basis of wood anatomy to be not only difficult but nearly impossible. Greguss (1967) later reversed himself by pointing out that, of the living species in the Araucariaceae, only those in the genus *Agathis* contain true axial parenchyma, and subsequently he assigned two species to *Agathoxylon*. The fact that the Dakota wood under study bears axial parenchyma places it in *Agathoxylon*.

Members of the genus *Araucariopitys* bear short shoots, have resin ducts and abietinuous crossfield pitting, and are, therefore, not related to this wood from the Dakota Formation.

COMPARISON

Of the living species of *Agathis*, *Agathoxylon lemonii* bears striking resemblance to the wood of *Agathis hypoleuca*. It differs from *A. hypoleuca* in having higher rays (1–10 cells high as opposed to 1–4 cells in *A. hypoleuca*)

fewer pits per crossfield (1–4 in *A. lemonii*, 4–8 in *A. hypoleuca*), and more abundant axial parenchyma.

Dadoxylon septentrionale Gothan (1905) differs from *A. lemonii* in having typically 2–4 elliptical to oblique crossfield pits and lacking tangential pitting. *Dadoxylon eocenum* Chitaley (1949) and *Dadoxylon (Araucarioxylon) japonicum* Shimakura (1936) have tangential pitting, but both lack the xylem parenchyma of *A. lemonii*. *Dadoxylon agathoides* Krausel & Jain from the Jurassic of India is similar to the Dakota specimen. However, it lacks axial parenchyma, has higher, narrower rays and has crossfield pits that are arranged in clusters.

Araucarioxylon texense Torrey has axial parenchyma and pitting similar to the specimen from the Dakota Formation, although *A. texense* has narrower rays and short shoots, which *A. lemonii* lacks. *Araucarioxylon hopertoniae* Knowlton from the Cretaceous of the Black Hills is similar to *A. lemonii* in having few pits per crossfield and low rays, but it lacks the characteristic axial parenchyma. Holden (1914) mentioned an araucarian type wood from the Cretaceous of New Jersey (Raritan Formation) whose pith contains large masses of stone cells similar to those in living *Agathis* but lacks wood parenchyma. *Dadoxylon noveboracense* (Holl. & Jeff.) from the mid-Cretaceous beds of Staten Island lacks definite growth rings and has uniseriate tracheary pitting. These characters are similar to *A. wyomingense* Andrews and Pannell (1942) from Cretaceous strata of Gros Ventre Canyon in Wyoming. *Araucarioxylon wyomingense* lacks the wood parenchyma and tangential pitting that separates this species from *A. lemonii*.

Among the species belonging to this genus described from the Mesozoic of Africa, the following four possess wood parenchyma (Gazeau 1969): *D. (A.) aegyptiacum* Unger (1859), *D. (A.) paumieri* Loubiere (1935), *D. (A.) septatum* Boureau (1951) from the Sahara Soudanais, and *D. (A.) koufraense* Batton (1965) from the continental series of Libya. They differ from *A. lemonii*, in general, by having different ray height, different tracheary pitting, and, with some, having septations in their tracheids.

Dadoxylon alpinum Lemoigne (1966) from the Jurassic of the Bassin de la Durance has

wood parenchyma, but it differs from *A. lemonii* in possessing septate tracheids, having large crossfield pits with large lumens, and lacking tangential pitting. *Dadoxylon (Araucarioxylon) breveradiatum* (Lignier) Seward from the Cenomanian of Normandy has abundant resiniferous parenchyma, but it differs from *A. lemonii* by having higher rays (4–80, usually 10–40, cells high) and septate tracheids.

Dadoxylon (Araucarioxylon) novaezeelandii (Stopes) Seward from the Cretaceous of New Zealand has well-marked growth rings, resin plates, and araucarian pitting. However, it differs from the Dakota Formation species in its lack of wood parenchyma and having thick-walled tracheids on each side of the rays.

There are a few reported species of *Dadoxylon* or *Araucarioxylon* from Japan that are similar to *Agathoxylon lemonii*. *Dadoxylon (Araucarioxylon) sidugawaense* Shimakura (1936) from the Jurassic of Miyagi Prefecture is similar in possessing distinct growth rings, similar radial pitting, tangential pitting, and, in the presence of xylem, parenchyma. But *D. (A.) sidugawaense* differs from the former species in having circular, alternate tangential pits and simple crossfield pits, whereas the tangential pits of *A. lemonii* are the same size as the pits on the radial walls. These tangential pits are isolated rather than contiguous, and the crossfield pits of the latter species are slightly bordered rather than simple. Two Lower Cretaceous species from Japan, *Araucarioxylon hujinamiense* Ogura (1960) from Wakayama and Chiba and *A. pseudo-hujinamiense* Nishida and Oishi (1982) from the Kwanto Mountain, both differ from *A. lemonii* in possessing tylosislike structures in their tracheids and in lacking wood parenchyma. *Araucarioxylon nihongii* Nishida and Nishida (1984) is quite similar to this Dakota Formation species. The Japanese species, however, has 3–5 rows of pits on its tracheid walls, has shorter parenchyma cells, and lacks tangential pitting.

Agathoxylon species similar to *Agathoxylon lemonii* include *A. australe* Evans, *A. hungaricum* (Andreanszky) Greguss, and *A. meckense* Greguss. *Agathoxylon australe* is a Pliocene fossil from New Zealand that has vested pits and lacks axial parenchyma.

Evans (1934) originally assigned this species to *Agathis* and later renamed it *Agathoxylon australe* (Evans 1937). Krausel and Jain (1963) noted that *Agathoxylon australe* is very similar to living *Agathis australis*. *Agathoxylon mecsekense* from the Jurassic of Hungary has high, narrow rays and commonly has triseriate pitting. Although the description given for *A. hungaricum* is incomplete, it appears to have higher rays and more pits per crossfield than our specimen.

PALEOECOLOGY

The extant genus *Agathis* may be found growing in association with the fern *Matonia* in the tropical uplands of the Malay Peninsula and the island of Borneo (Seward 1899). Morphologically, the fossil genus *Matonidium* is similar to the extant *Matonia* (Berry 1919). *Matonidium* occurs in abundance in the Dakota Formation near Westwater, Utah, a locality quite close to a collecting site for *Agathoxylon lemonii*. Mahabale (1954) considered matoniaceous ferns to be among a select group of ferns that served as reliable indicators of subtropical to tropical paleoclimate; the presence of abundant *Matonidium* is, therefore, suggestive of a similarly warm, climatic regime during the deposition of this formation in this area. This reconstruction is supported by Roman's (1972) study of the schizeaceous spores of the Dakota Formation and other reconstructions that have emphasized the subtropical to tropical nature of the regional fossil assemblage (Rushforth 1971).

The precise community assignment for *A. lemonii* is more elusive. Agasie (1969), Rushforth (1971), and May and Traverse (1973) all suggested that the Dakota Formation was deposited on a wet, low-lying landscape in close proximity to drier uplands. The *Matonidium* leaf material occurs in an ash layer associated with a coal bed at the Westwater site. The swamps of the Dakota Formation, which produced the peat that is the original source of the coals of the region, apparently supported a diverse tree and shrub flora in which ferns were probable understory elements (Retallack and Dilcher 1981). In such situations, however, microtopographic variability can result in a complex vegetation mosaic with somewhat drier sites, possibly dominated by

angiosperms, in close spatial association with the actual swamp vegetation. The coarser clastics of modern distributary channels and coastal lagoons usually include a mixed assemblage derived primarily from the lower coastal plain but also including wood that may have been transported for greater distances than is typically the case with the angiosperm leaves or conifer needles in such deposits. The coarser sandstone in which the specimens of *Agathoxylon lemonii* were collected suggests the possibility that they were transported from a well-drained habitat occurring somewhere along the lower delta plain associated with the deposition of the Dakota Formation.

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