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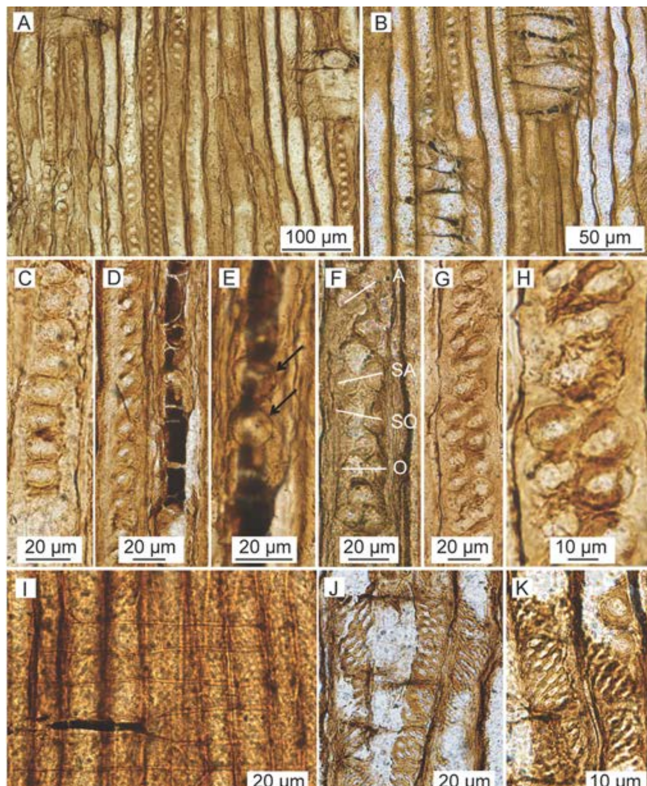
SILICIFIED LOGS OF *AGATHOXYLON HOODII* (TIDWELL ET MEDLYN) COMB. NOV. FROM RAINBOW DRAW, NEAR DINOSAUR NATIONAL MONUMENT, UINTAH COUNTY, UTAH, USA, AND THEIR IMPLICATIONS FOR ARAUCARIACEOUS CONIFER FORESTS IN THE UPPER JURASSIC MORRISON FORMATION

Carole T. Gee, Douglas A. Sprinkel, Mary Beth Bennis, and Dale E. Gray



Theme Issue
An Ecosystem We Thought We Knew—
The Emerging Complexities of the Morrison Formation
SOCIETY OF VERTEBRATE PALEONTOLOGY
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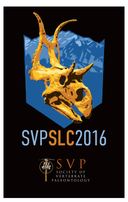

Cover

Fossil wood thin sections of ***Agathoxylon hoodii*** *showing fine anatomical details. All micrographs were taken of radial sections of thin section RDW-004. Two photographs of the fossil logs found in Rainbow Draw, Uintah County, Utah.*

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Silicified Logs of *Agathoxylon hoodii* (Tidwell et Medlyn) comb. nov. from Rainbow Draw, near Dinosaur National Monument, Uintah County, Utah, USA, and Their Implications for Araucariaceous Conifer Forests in the Upper Jurassic Morrison Formation

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ABSTRACT

A new local flora of silicified logs and wood has been discovered in the Upper Jurassic Morrison Formation in the Rainbow Draw area near Dinosaur National Monument, northeastern Utah, USA. Fossil logs and wood were found in the Salt Wash Member at nine sites at Rainbow Draw and at one site near Miners Draw, south of Blue Mountain. The fossil logs are large and relatively intact, the longest measuring 11 m. The wood is well preserved, coniferous, and can be identified to the species level. Diagnostic anatomical features include resin plugs in the ray cells and axial tracheids, araucarioid tracheary pitting and crossfield pitting, and the lack of resin canals and true, regularly occurring growth rings. This taxon of fossil wood, originally described as *Araucarioxylon hoodii* Tidwell et Medlyn, is recognized here as a new combination, *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray, which pertains to the conifer family Araucariaceae. Based on the preserved girth of the logs, the minimum height of the trees could be reconstructed. The largest fossil logs measured at least 127 cm in diameter and hence reached a minimum height of 28 m. Judging from the growth habit of all naturally occurring araucariaceous trees today, the fossil plants likely formed forests of moderately tall trees and were well over 100 years old. The lack of true growth rings shows that there was no seasonality in the local paleoclimate, neither variations in summer–winter temperatures, nor wet–dry cycles. Thus, during the Late Jurassic, tall conifer forests with *Agathoxylon hoodii* grew in at least two areas in what is now Utah: east of the city of Vernal and near Mt. Ellen in the Henry Mountains. Coupled with the fossil evidence of conifer seed cones and pollen found in the Morrison Formation throughout eastern Utah, the newly discovered fossil logs and wood argue for the reconstruction of Upper Jurassic habitats in this region as mesic and wooded, and the climate as equable, not seasonal, nor semi-arid or arid.

Citation for this article.
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INTRODUCTION

As in many ancient terrestrial ecosystems, fossil logs and wood are locally abundant in the Upper Jurassic Morrison Formation. In the older reports on the Morrison fossil flora, fossil logs and larger pieces of fossil wood were described from 11 localities (Tidwell, 1990; Ash and Tidwell, 1998; Peterson, undated). These localities are sites at Castle Dale, Ferron, Fremont Junction, Caineville Wash, Mount Ellen, Hansen Creek, and Clay Point in Utah; at Mygatt-Moore Quarry and East McElmo Creek in Colorado; in the Freezeout Hills in Wyoming; and in the Black Hills in South Dakota. If the narrow, woody axes of the enigmatic *Hermatophyton* and the short shoots of *Behuninia* spp. and *Steinerocaulis* spp. are included, the number of localities increases by seven to include Dinosaur National Monument, another two sites at Clay Point, Mussentuchit Wash, and Montezuma Creek in Utah; and Scott's site and Steiner's site in Wyoming (Ash and Tidwell, 1998; Peterson, undated). More recently, silicified wood floras have been reported from the Howe-Stephens Quarry near Greybull in north-central Wyoming (Gee and Tidwell, 2010), the Escalante Petrified Forest State Park in southern Utah (Morgan and others, 2010; Gee, unpublished data), and a new site west of Blanding in southern Utah (Kirkland, Utah Geological Survey, verbal communication to Gee, 2018), as well as a single piece of fossil wood from Dinosaur Ridge in Morrison, Colorado (Gee, unpublished data), making a total of at least 22 localities with fossil wood remains.

Yet, the number of fossil conifer woods formally described from the Morrison Formation is limited to only eight: *Araucarioxylon hoodii* Tidwell et Medlyn (1993), *Cupressinoxylon jurassicum* Lutz (1930), *Mesembrioxylon carterii* Tidwell and others (1998), *Mesembrioxylon obscurum* (Knowlton) Medlyn et Tidwell (2002), *Protocupressinoxylon medlynii* Tidwell and others (1998), *Protopiceoxylon resiniferous* Medlyn et Tidwell (1979), *Xenoxylon moorei* Tidwell and others (1998), and *X. morrisonense* Medlyn et Tidwell (1975) (but see Philippe and others, 2013, regarding *X. moorei* and *X. morrisonense*). This relatively low number of taxa compared to the number of localities where fossil wood has been found does not necessarily reflect low species diversity in the Morrison conifer flora, but is more likely due to the poor preservation of most fossil wood specimens in the Morrison Formation. For example, the fossil wood at the Caineville Wash locality, called "black and white wood" by local collectors, is aesthetically pleasing and plentiful, but not worth paleobotanical study owing to the lack of the fine anatomical detail necessary for taxonomic determination (Gee, personal observation). However, because of the widespread terrestrial facies and locally abundant occurrence of fossil wood, the potential for finding fossil wood in the Morrison Formation that is suitable for paleobotanical investigation is high.

The discovery of a new local fossil flora with relatively intact logs and good wood preservation in the Morrison Formation near Dinosaur National Monument, northeastern Utah, has led to this paleobotanical investigation, as well as a concurrent in-depth stratigraphical and sedimentological study of the geological setting (Sprinkel and others, 2019). In the paleobotanical study here, we determine the taxonomic affinity of the fossil logs, interpret the paleoenvironmental signals inherent in the wood structure, and reconstruct the minimum heights of the trees based on the measurement of preserved log girth. The results of our study have implications for the floral composition and ecological structure of the Late Jurassic forests, and hence for dinosaur habitats in the Morrison Formation.

GEOLOGICAL SETTING

The fossil logs and wood were discovered by Mary Beth Bennis and Dale Gray in Utah (figure 1), on the southeastern flank of the Uinta Mountains, east of the city of Vernal, in two general areas: Rainbow Draw to the north and Miners Draw to the south (figure 2). Rainbow Draw is located about 36 km (22.4 highway miles) northeast of Vernal, and about 30 km northwest of the Miners Draw site.

Nine sites with fossil logs and wood have been found at the Rainbow Draw locality (table 1). All logs occur in the same stratigraphic interval in the Salt Wash Member of the Morrison Formation (figure 3; Sprinkel and others, 2019). The unit containing the logs is 11

Figure 1. Location of Utah (solid gray) and the city of Vernal (star) in the Western Interior of the United States. Map modified from http://www.nationsonline.org/oneworld/usa__blank_map.htm.

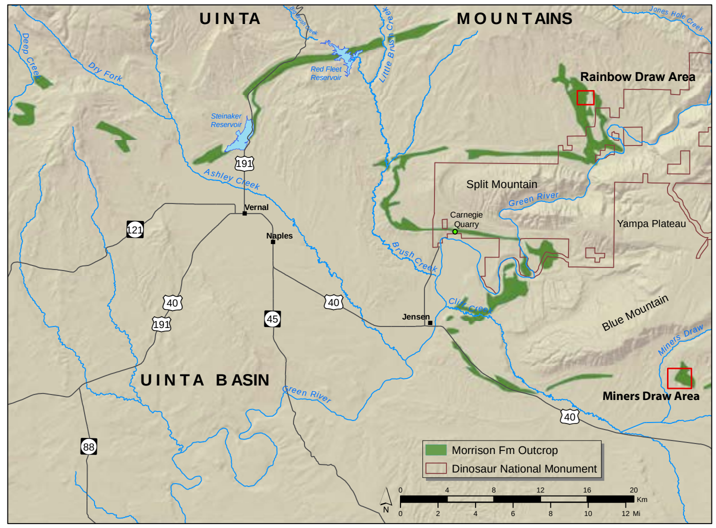

Figure 2. Map showing the Morrison Formation outcrop belt in and around Dinosaur National Monument and the location of the renowned Carnegie Quarry. The Miners Draw area is south of the Blue Mountain Plateau and Rainbow Draw is due north of Dinosaur National Monument. Both areas are east of the city of Vernal, Utah. Morrison outcrop locations from Hintze and others (2000).

m thick and is composed of fine- to very fine grained sandstone and siltstone. The sandstone is well sorted and friable with indistinct bedding and sedimentary features. The logs are mostly silicified, although some may have a coaly exterior. The exposed length of the fossil logs varies from 1 to 11 m.

At the Miners Draw locality, only one site yielding a fossil log has been found so far (table 1). The log at this site in the Miners Draw area occurs in a silty sandstone unit which is 4 m thick. Although this log is stratigraphically higher in the lower Salt Wash Member than those at Rainbow Draw, the unit is lithologically similar and correlates to the log-bearing unit at Rainbow Draw (figure 3; Sprinkel and others, 2019). Like the fossil logs at Rainbow Draw, this log is silicified and measures 6 m in exposed length.

The Morrison Formation is a laterally widespread formation in the Western Interior of North America (Dodson and others, 1980). At its greatest extent, the Morrison Formation covered an area from New Mexico in the south to Alberta and British Columbia, Canada, in the north. Most strata represent terrestrial environments, but some marginal marine beds also occur at the base of the formation in northern Utah and Colorado northwards (Turner and Peterson, 2004).

In regard to age, the chronostratigraphic age of the Morrison Formation is accepted to be Late Jurassic (Litwin and others, 1998; Schudack and others, 1998; Turner and Peterson, 2004). Recent studies based on single-crystal $^{40}Ar/^{39}Ar$ laser fusion methods have yielded recalibrated ages that suggest the lower Morrison Formation may begin at the end of the Oxfordian, but the majority of the formation is Kimmeridgian and the upper parts of the formation can reach into the lower Tithonian (Trujillo and Kowallis, 2015).

The stratigraphy of the Morrison Formation is best known on the Colorado Plateau, where it has been divided into several formally described members (Turner and Peterson, 2004). At Rainbow Draw, the members that crop out are the Windy Hill and Tidwell Members at the base of the section, which are overlain by the Salt Wash and Brushy Basin Members. The fossil log and wood horizons are ca. 17 to 27 m above the Tidwell Member/Salt Wash Member contact and ca. 20 to 50 m below the Salt Wash Member/Brushy Basin contact (figure 3). Recalibrated $^{40}Ar/^{39}Ar$ laser fusion dating of single crystals on samples from Rainbow Draw has yielded a Kimmeridgian age bracketed between 152 and 156 Ma (Trujillo and Kowallis, 2015) for the fossil log and wood horizons in the Salt Wash Member at Rainbow Draw and Blue Mountain.

Table 1. Data collected on Morrison Formation logs and wood in the field. Abbreviations: RD = Rainbow Draw, MD = Miners Draw.

Area, Site, Log	Fossil Type	Length of Log (m)	Max. Long Diameter (cm)	Max. Short Diameter (cm)	Comments
RD, Site 1, Log 1	Log	11.0	127.0	22.9	
RD, Site 2, Log 1	Log	2.29	71.1	38.1	
RD, Site 2, Log 2	Log	1.27	91.4	30.5	
RD, Site 3a	Wood pieces				Not sampled
RD, Site 3b	Wood piece				Not sampled
RD, Site 3c	Wood pieces				
RD, Site 4, Log 1	Log	1.74	101.6	63.5	
RD, Site 4, Log 2	Log	1.27	105.4	110.5	Continuation of Log 1 at Site 4
RD, Site 5	Wood pieces				
RD, Site 6	Log				Buried, eroding out of hillside
RD, Site 7	Wood piece				Wood convoluted
RD, Site 8	Wood pieces				
RD, Site 9	Log				Fragmented
MD, Site 10, Log 1	Log	6.1			Buried; full size could not be measured

MATERIALS AND METHODS

Fieldwork

The location of the fossil logs and wood was mapped in the field (figure 4). Exact locality information on all collecting sites is on file at the Utah Field House of Natural History State Park Museum (FHNHM) in Vernal, Utah. Altogether, there were 10 fossil sites—nine at Rainbow Draw and one at Miners Draw, south of Blue Mountain. A fist-size sample of fossil wood was collected for identification from each log or piece of wood. Six fossil logs were found at four of the 10 sites (sites 1, 2, 4, 10). The preserved or exposed length of each fossil log (figure 5A), as well as the maximum diameters at both ends of each log, were measured. If the cross section of the log was not symmetrical, the longest diameter and the so-called short diameter oriented 90˚ to the long diameter was measured. Inventory numbers for the specimens were assigned by the FHNHM.

Laboratory Work

The ten fossil wood specimens were logged into the inventory system for fossil woods at the University of Bonn with the prefix RDW in consecutive order of receipt from RDW-001 to RDW-013. Thin sections of all specimens were made at the University of Bonn using conventional techniques for petrographic sections. Five specimens (RDW-001 to RDW-005) were made in the standard three planes of section—cross, radial, and tangential. Thin sections of the other five specimens were cut in only radial section (RDW-006 to RDW-013). All thin sections were studied with a Leica DM2500 compound photomicroscope. Digital images were taken and processed using the integrated measurement software ImageAccess easyLab 7.

Fossil wood thin sections are archived at the Division of Paleontology, University of Bonn, Germany, whereas fossil wood samples and duplicate thin sections are deposited at the FHNHM.

Log Length and Tree Height

Following the methodology of Mosbrugger and others (1994), the minimum height of the trees was reconstructed based on the preserved girth of the logs. The equation

$$L = 0.32\ (E/w)^{1/3}\ r^{2/3}$$

was applied, where L is the estimated minimum height of the tree, E is Young's modulus of the wood, w is the specific weight of the wood, and r is the preserved radius

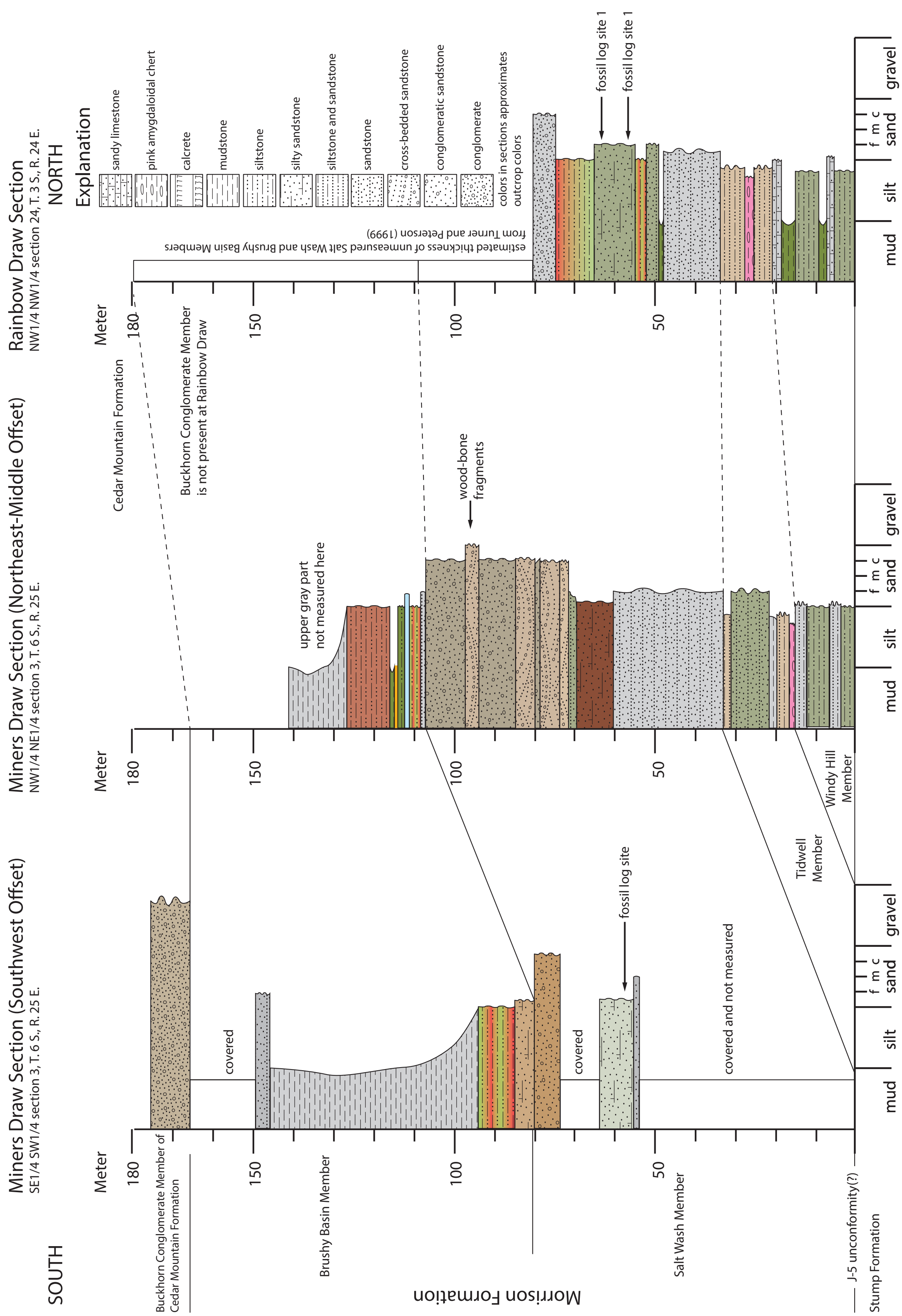

Figure 3. Stratigraphic sections measured in the Miners Draw and Rainbow Draw areas showing the fossil log-bearing intervals.

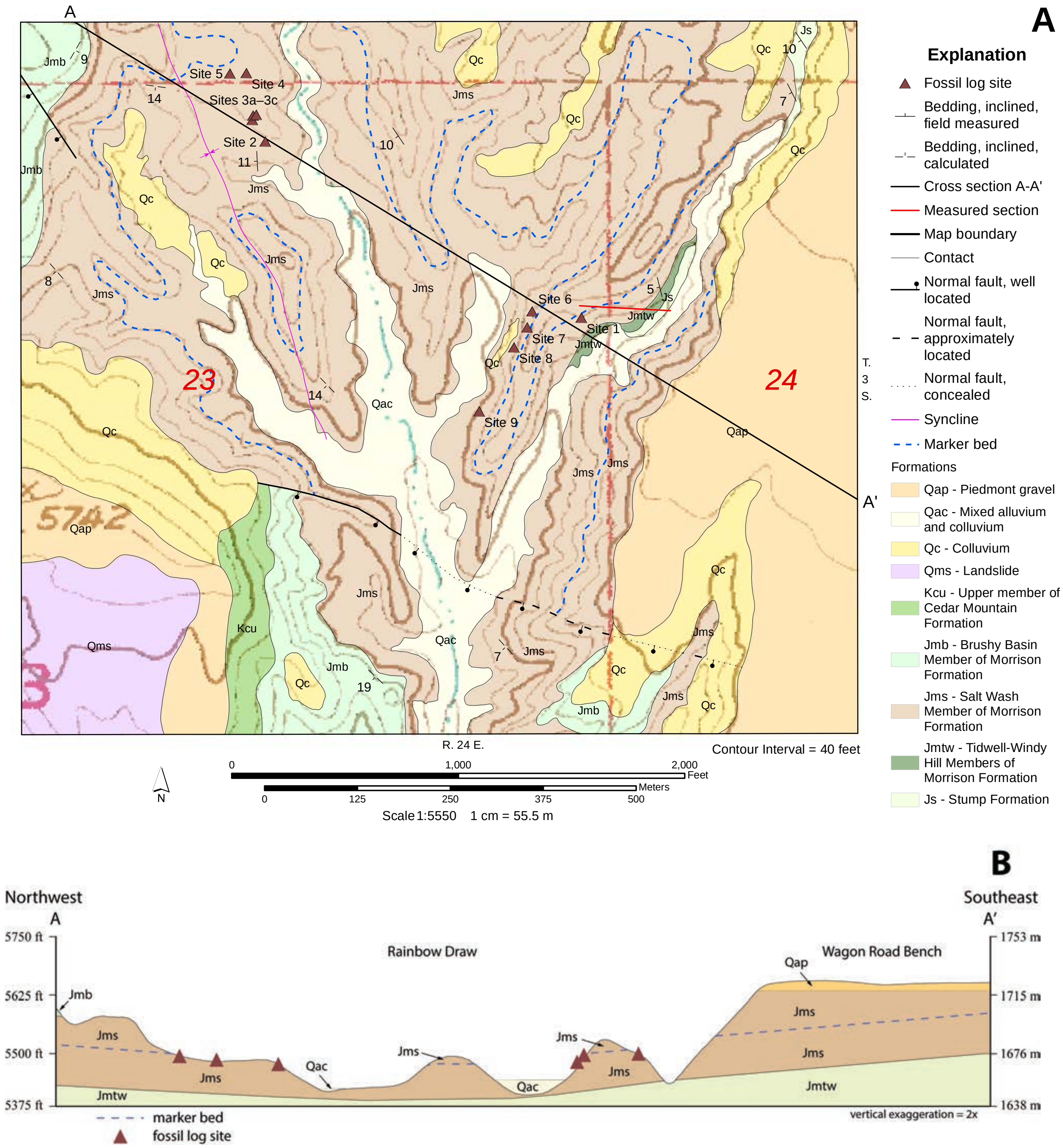

Figure 4. (A) Geologic map and (B) cross section of the Rainbow Draw area wood sites. The Morrison Formation overlies the Stump Formation and underlies the Cedar Mountain Formation in Rainbow Draw. In the mapped area, the Morrison includes the Windy Hill, Tidwell, Salt Wash, and Brushy Basin Members. The fossil log sites are concentrated in two groups on separate ridges. Both groups of logs occur in light-colored, fine-grained sandstone and siltstone below a mostly reddish-colored siltstone that was used as a marker bed (blue dashed line).

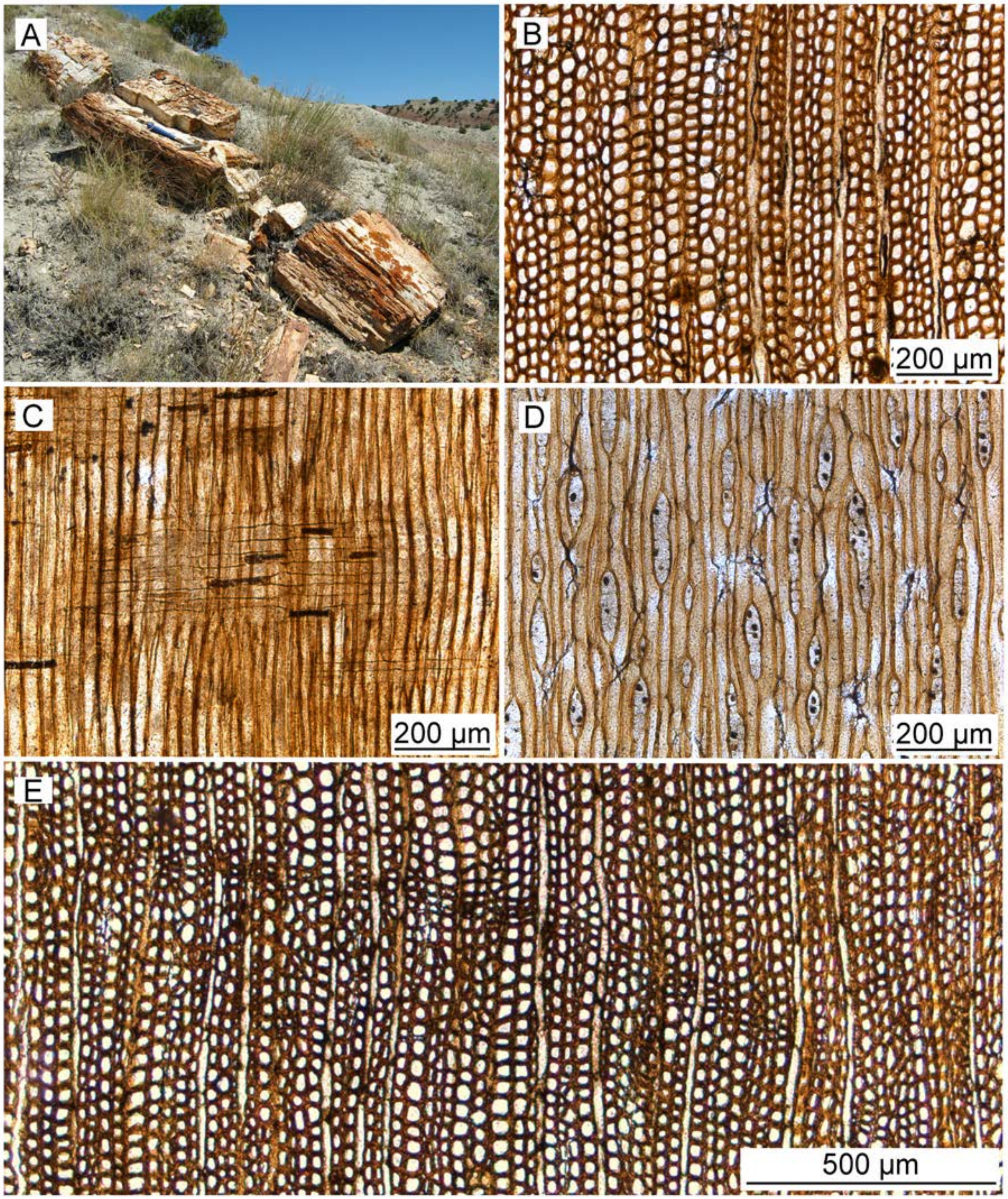

Figure 5. Outcrop photo (A) and micrographs of fossil wood thin sections (B–E) of *Agathoxylon hoodii* comb. nov. Gee, Sprinkel, Bennis et Gray. (A) Fossil log at Rainbow Draw (Site 2, Log 2) that has broken up naturally into pieces. The anatomical structure of this log's wood is featured in figures 5B, 5C, and 5D. (B) Cross section showing an abundance of axial tracheids, but no axial parenchyma nor resin canals. Thin section number RDW-002. (C) Radial section showing axial tracheids and rays with ray parenchyma cells, some of which bear resin plugs (dark-colored bars). Thin section RDW-002. (D) Tangential section showing low, uniseriate rays. In this plane, the plugs in the ray cells appear circular in cross section. Thin section RDW-002. (E) Cross section showing an irregular, discontinuous, partial zone of tracheids with lumina smaller than those of their neighbors. In this case, development of these narrower tracheids was clearly asynchronous relative to tracheids in the same concentric position around the tree trunk. Thin section RDW-004.

of the tree trunk. The exact values for E and w are unknown for these ancient trees, but the ratio E/w is fairly constant (McMahon and Kronauer, 1976; Mosbrugger, 1990). In this case, E/w = 1.7 x 10^6 m was used, which corresponds to a typical conifer such as *Taxodium* or *Sequoia* (Wagenführ and Schreiber, 1985; cf. Mosbrugger and others, 1994).

RESULTS

Systematic Paleobotany

Division Coniferophyta
Class Coniferospida
Order Coniferales
Family Araucariaceae
Genus *Agathoxylon* Hartig 1848, sensu Philippe 1995
Agathoxylon hoodii (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray comb. nov.
Figures 5 and 6

Synonymy

Araucarioxylon hoodii Tidwell et Medlyn — Tidwell and Medlyn (1993), Conifer wood from the Upper Jurassic of Utah, USA—Part II: *Araucarioxylon hoodii* sp. nov.: The Palaeobotanist, v. 42, p. 70–77; diagnosis on p. 71; plate 1, figures 1 to 6; plate 2, figures 1 to 6; text figure 2.

Description: Secondary xylem of a fossil trunk (figure 5A); true growth rings absent (figures 5B, 5C, and 5D). In cross section, there are some areas of slower growth that appear as irregular, discontinuous concentric bands of tracheids with narrower lumina (figure 5E). These irregular bands range from 1 to 4 cells thick and did not develop synchronously during the growth of the tree. Tracheids subround to elliptical to subangular in cross section; lumen diameters ranging from 11 to 45 µm, those of normal-size cells about 25 µm (figure 5B). Tracheid cell walls more uniform in thickness, from 4 to 7 µm thick.

Radial tracheary pitting consisting of circular bordered pits, most commonly uniseriate (figures 6A, 6B, 6C, and 6D left), or occasionally mixed biseriate and uniseriate (figures 6F, 6G, and 6H). Spacing between circular bordered pits along the same tracheid usually contiguous (figures 6A, 6B, and 6D), but also found distant from one another, or so tightly packed that the circular bordered pits begin to take on an angular appearance (figure 6C). When biseriate, pits irregularly arranged (not always in straight lines), varying from alternate to subalternate to subopposite to opposite (figures 6F, 6G, and 6H), even within a single tracheid (figure 6F). Pits 10 to 14 µm in diameter, apertures circular, ca. 5 µm in diameter. Axial parenchyma not observed. Resin plugs common and distinctive in ray cells (figures 5C and 6I), but also clearly observable in cross, radial, and tangential sections (figures 5B, 5C, and 5D). Resin plugs also occur in tracheids in the axial system (figure 6D), but less frequently; the tracheids can be identified by the circular bordered pits on their radial walls (figure 6E, arrows). Resinous remains also coalesce along the periphery in ray cells, as well as in the cell corners (figures 6A and 6B).

Rays uniseriate, from 1 to 18 cells high, homocellular, parenchymatous, 20 to 30 µm wide at widest point in tangential section (figures 5C and 6I). Horizontal and end walls of ray cells smooth, 1.5 to 3 µm thick, unpitted (figure 6I). Crossfield pits numerous and crowded, up to 24 pits per crossfield, contiguous but unordered, with little or no border, bearing a slanted, narrowed aperture (figures 6J and 6K).

Material studied: The set of fossil wood specimens logged into the University of Bonn as RDW-001 to RDW-013 were studied in thin section.

Repositories: Figured thin sections: Institute of Geosciences, Division of Paleontology, University of Bonn, Bonn, Germany. FHNM-inventoried specimens of fossil wood and duplicate thin sections: Utah Field House of Natural History State Park Museum in Vernal, Utah.

Collecting sites: Sites 1 to 9 in the Rainbow Draw area (figures 2, 4) and site 10 in the Blue Mountain area (figure 2), Uintah County, Utah. The geographic coordinates for all localities are on file at the FHNHM.

Stratigraphic occurrence: Salt Wash Member of the

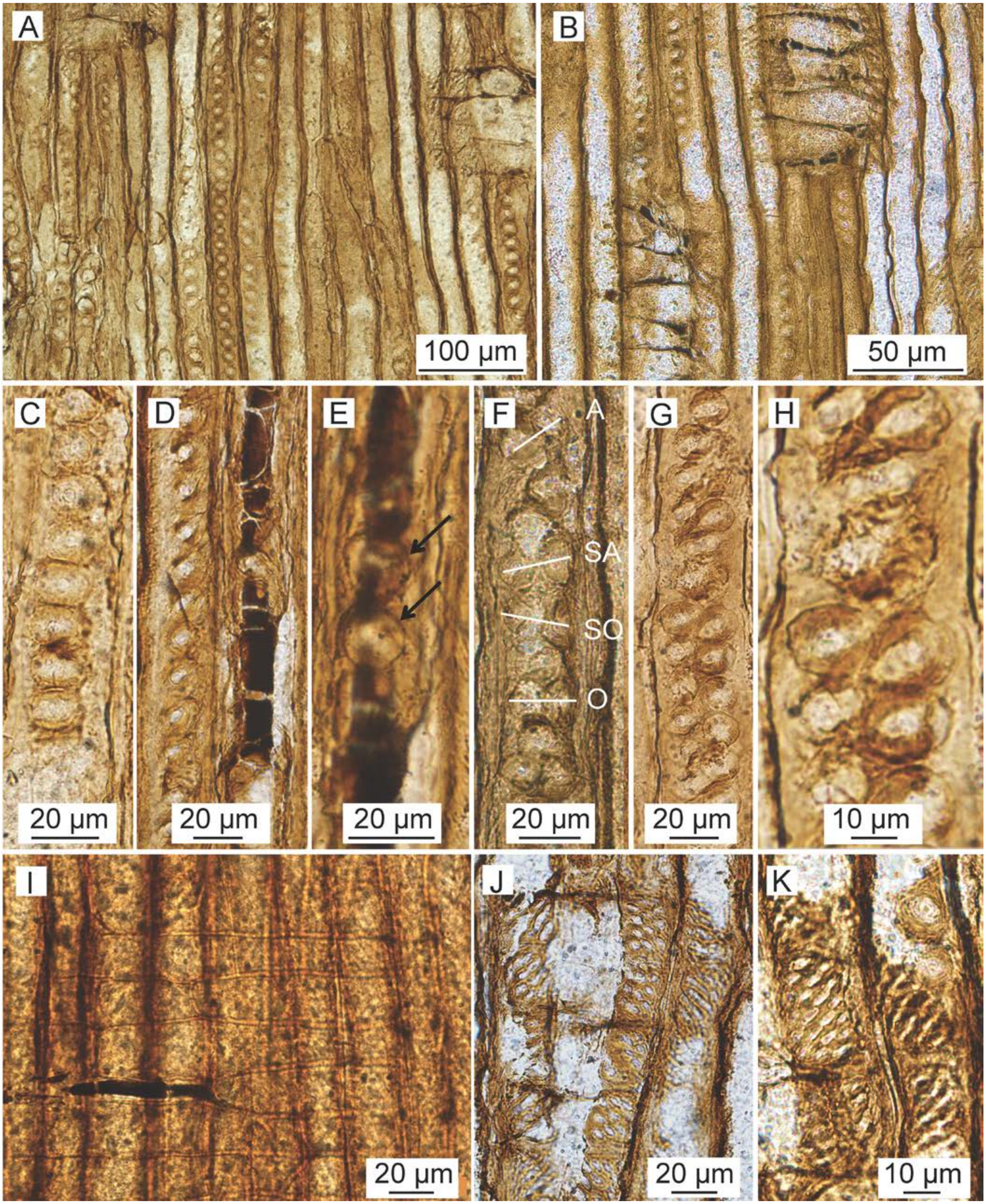

Figure 6. Caption on the following page.

Figure 6 is on the previous page. Fossil wood thin sections of *Agathoxylon hoodii* showing fine anatomical details. All micrographs were taken of radial sections of thin section RDW-004. (A) Axial tracheids with uniseriate, contiguous circular bordered pits. Top right, resin remains in the corners of some ray cells. (B) Detail of ray cells with resin concentrated along the periphery of the cell walls. (C) Radial tracheary pitting so closely spaced that the normally round tracheary pits begin to take on a more angular appearance. (D) Two neighboring tracheids: left, one with uniseriate pitting and right, one containing a thick resin plug. (E) Close-up of the tracheid with the resin plug in 6D. The focal plane has been shifted to show the outlines of circular bordered pits (arrows), which signify that this is indeed a tracheid and not an axial parenchyma cell. (F) Radial tracheary pitting of a single tracheid, showing mixed biseriate and uniseriate pitting. When biseriate, pit arrangement varies from alternate (A), subalternate (SA), subopposite (SO), to opposite (O). White lines connect the pit centers of adjacent cells to illustrate the variation in pit arrangement. (G) Another example of mixed biseriate and uniseriate tracheary pitting, here in a subalternate arrangement. (H) Close-up of the tracheid in 6G to more clearly show the subalternate pit arrangement when biseriate. (I) Several cells of a ray showing its homocellular nature and the smooth walls of the ray cells. Note the thick, dark-colored resin plug. (J) Araucarioid crossfield pitting in ray cells, numerous and crowded, contiguous but unordered, with little or no border, and a slanted, narrowed aperture. (K) Another example of araucarioid crossfield pitting in ray cells, showing more clearly the slanted, narrow apertures of the pits.

Morrison Formation, Late Jurassic (figure 3; Sprinkel and others, 2019).

Basionym and type locality: *Araucarioxylon hoodii* Tidwell et Medlyn from the Brushy Basin Member of the Upper Jurassic Morrison Formation on the eastern flank of Mt. Ellen, Henry Mountains, Utah (Tidwell and Medlyn, 1993). The holotype was not examined directly during the course of this study.

Preservation of Logs and Wood

The thin sections made from the wood samples show only secondary xylem. No pith or primary xylem of phloem is present. In the field, the fossil logs are not preserved with bark, and their outer surface appears abraded (figure 5A). Even the fossil logs that are relatively intact have weathered surfaces and are worn off unevenly in regard to girth, resulting in logs with different long and short diameters (table 1). These differential girth measurements cannot be attributed to lateral compression of the tree trunks, for the anatomy of the wood cells do not show compression. Thus, along with the lack of bark, it can be concluded that the tree trunks are not preserved in their full, original size.

Taxonomic Considerations

After over a century of confusion concerning the application of generic names to araucariaceous woods in the fossil record, attempts are being made now to bring the paleoxylological community into agreement regarding the taxonomic priority and validity of *Agathoxylon*, *Araucarioxylon*, *Dadoxylon*, *Dammaroxylon*, and other fossil genera (e.g., Philippe and Bamford, 2008; Philippe, 2011; Rößler and others, 2014). Most recently, it has been suggested that *Araucarioxylon* be synonymized into *Agathoxylon* (Philippe, 2011; Rößler and others, 2014), as emended by Philippe (1995). Thus, following the general consensus of the paleobotanical community for this synonymy (e.g., Pujama and others, 2014; Rößler and others, 2014), a new nomenclatural combination of *Agathoxylon hoodii* is formally carried out here in our study. Until now, this species of fossil wood has only been reported from the Upper Jurassic Morrison Formation.

Comparisons

The anatomy of the fossil wood (figures 5B, 5C, 5D, and 5E) shows that all wood studied thus far represents conifer trees and pertains to the same taxon, *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray comb. nov. Characteristic of this species are the dominance of axial tracheids (figures 5B, 5C, 5D, and 5E) and the absence of axial parenchyma (figures 5B and 5E) or of any resin canals (figures 5B, 5C, 5D, and 5E); the presence of abundant resin plugs (figures 5B, 5C, 5D, 6D, 6E, and 6I) and other resinous remains (figures 6A and 6B); the alternate arrangement of the circular bordered pits in the tracheids, when biseriate (figures 6F, 6G, and 6H); the smooth, unpitted sidewalls and endwalls of the ray cells (figure 6I); and the numerous, small, crowded pits in the crossfields (figures 6J and 6K).

True growth rings are absent (figure 5B). However, some wood samples show irregularly occurring, short-term, slowdowns in growth (figure 5E). These bands or zones of smaller cells with thicker cell walls do not necessarily reach around the entire trunk (figure 5E). Furthermore, the cells in the same band of slower growth were not synchronous in their development.

Reconstruction of Minimum Tree Height

The preserved maximum diameters of the four logs at the Rainbow Draw area vary between 71.1 cm and 127.0 cm (table 1), which results in a minimum reconstructed height of the trees between 19.3 and 28.4 m (table 2), respectively.

DISCUSSION

The form genus, or now more correctly fossil-taxon (cf. Turland and others, 2018), of *Agathoxylon* was proposed 20 years ago to apply to fossil woods similar to that of the living Araucariaceae, following a review of the systematic history and type material of *Agathoxylon*, *Araucarioxylon*, and *Dadoxylon* (Philippe, 2011). In the case of the fossil wood taxon *Agathoxylon hoodii*, its affinity to the Araucariaceae is supported by the common occurrence of fossil araucariaceous remains from throughout the Morrison Formation. In fact, *Araucaria* is known from this formation in the form of seed cones, detached cone scales, seeds, pollen cones, and pollen (Litwin and others, 1998; Gee and Tidwell, 2010; Hotton and Baghai-Riding, 2010; Gee, 2013; Gee and others, 2014), as well as leaved twigs and branches (Gee and Tidwell, 2010). *Agathoxylon hoodii* was originally described as *Araucarioxylon hoodii* from the eastern flank of Mt. Ellen in the Henry Mountains, south of Hanksville in southern Utah, which is situated over 300 km southwest of Rainbow Draw. There are a few minor differences in anatomy between the fossil wood from Mt. Ellen and the many specimens from the Rainbow Draw and Blue Mountain sites. The first difference is that the type material from Mt. Ellen, a small block of fossil wood roughly 4 cm by 3 cm, appears to contain more resin plugs, especially in the axial tracheids. However, a wide variation in the abundance or scantiness of resin plugs

Table 2. Utah Field House of Natural History State Park Museum inventory numbers, calculated data, University of Bonn thin section numbers, and taxonomic identification of Morrison Formation logs and wood.

Area, Site, Log	FHNHM Inventory No.	Max. Radius (cm)	Reconstructed Min. Tree Height (m)	Univ. Bonn Thin Section No.	Taxonomic Identification
RD, Site 1, Log 1	FHPR 13360	63.5	28.4	RDW-001, RDW-004	*Agathoxylon hoodii* comb. nov.
RD, Site 2, Log 1	FHPR 11749	35.6	19.3	RDW-006	*Agathoxylon hoodii* comb. nov.
RD, Site 2, Log 2	FHPR 11361	45.7	22.8	RDW-002	*Agathoxylon hoodii* comb. nov.
RD, Site 3a	N.A.			N.A.	*Agathoxylon hoodii* comb. nov.
RD, Site 3b	N.A.			N.A.	*Agathoxylon hoodii* comb. nov.
RD, Site 3c	FHPR 11751			RDW-007	*Agathoxylon hoodii* comb. nov.
RD, Site 4, Log 1	FHPR 11753	50.8	22.4	RDW-008	*Agathoxylon hoodii* comb. nov.
RD, Site 4, Log 2	FHPR 13362	52.7	25.0	RDW-003	*Agathoxylon hoodii* comb. nov.
RD, Site 5	FHPR 11755			RDW-009	*Agathoxylon hoodii* comb. nov.
RD, Site 6	FHPR 11557			RDW-010	*Agathoxylon hoodii* comb. nov.
RD, Site 7	FHPR 13363			RDW-005	*Agathoxylon hoodii* comb. nov.
RD, Site 8	FHPR 11759			RDW-011	*Agathoxylon hoodii* comb. nov.
RD, Site 9	FHPR 11761			RDW-012	*Agathoxylon hoodii* comb. nov.
MD, Site 10, Log 1	FHPR 11747			RDW-013	*Agathoxylon hoodii* comb. nov.

is evident among the wood specimens from Rainbow Draw. In RDW-002, for example, the resin plugs are only moderately abundant and usually occur in the ray cells, not in the axial tracheids (figures 5B and 5C). In living Araucariaceae, the quantity of resin plugs in the wood of individual trees of *Araucaria bidwillii* Hook. and *A. cunninghamii* Ait. ex D. Don is widely variable, ranging from absent to present (Ilic, 1995).

In the single specimen of *Agathoxylon hoodii* wood from its type locality on Mt. Ellen (Tidwell and Medlyn, 1993), the resin plugs are so plentiful in the rays that it is difficult to observe the crossfield pitting in the ray cells; many axial tracheids in the holotype also contain resin plugs. The abundance and placement of resin plugs in individual wood samples are thus not reliable characters to be used in separating species because they may be subject to individual variations between trees, due to fluctuations in endogenous factors or differences in the paleoenvironment.

Other minor differences concern the shape of the circular bordered pits and the crossfield pitting. Most circular bordered pits on the radial walls of the tracheids are contiguous and round in outline (figures 6A, 6B, and 6D); when more closely arranged, the circular bordered pits take on the more angular appearance (figure 6C) that is characteristic of most other araucarioid wood (e.g., Richter and others, 2004). For example, circular bordered pits with a round outline can also be observed in other species of *Agathoxylon*, such as *A. desnoyersii* (Lemoigne) Philippe from the Middle Jurassic of France (Philippe, 2011), especially when the circular bordered pits are not crowded and pressing against one another.

In the Rainbow Draw wood specimens, the circular bordered pits are almost always uniseriate. In the rare examples in which the tracheary pitting is biseriate, the circular bordered pits are round in outline (figures 6F, 6G, and 6H), unlike the more angular or hexagonal pits in the single sample of *A. hoodii* from Mt. Ellen. In these cases, the round outline of the circular bordered pits in the Rainbow Draw wood may be attributed to the lack of crowding of the pits in the radial tracheary pitting. The outline of the circular bordered pits can, however, take on a more angular shape approaching hexagonal, for example, when the pits are more closely spaced (figure 6C).

In the Rainbow Draw wood, the pits in the crossfields are narrowly elliptical in shape, with no border or a very narrow border, whereas those in the Mt. Ellen wood are reported as round to subround and bordered (Tidwell and Medlyn, 1993). The lack of a round outline in the crossfield pitting of the Rainbow Draw wood specimens may be attributed to crowding of the pits in the crossfields. Similar, elliptical, unbordered crossfield pits can also be observed in *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana, Santillana et Marenssi from the Eocene of western Antarctica (Pujana and others, 2014).

The fossil wood from the Rainbow Draw and Blue Mountain sites does not have true growth rings with well-developed earlywood and latewood, but shows zones of slower and non-synchronous growth. As to be expected in individual trees living under slightly different environmental conditions, the wood specimens have differences regarding the extent and frequency of zones of slower growth. These slowdowns in growth show up as tracheid size in cross section; these tracheids have relatively smaller lumina and relatively thicker cell walls than neighboring, normal-size cells. However, these zones of slower growth are not seasonally induced growth rings, which normally occur in temperate trees, because there is no gradual deceleration in the growth of the secondary xylem (the latewood of one season) followed by a sharp acceleration in growth (the earlywood of the new growing season).

Furthermore, because the cells within the same zone do not appear to have developed synchronously during the growth of the tree, the slowdowns in growth were possibly induced by endogenous fluxes in growth hormones, such as auxins, in individual trees. Such irregular-occurring zones and bands, false rings, and generally uneven growth (e.g., Dunwiddie, 1979; Oliveira and others, 2010) are common in *Agathis* and *Araucaria*, two of the three living genera in the Araucariaceae. In the wood of *Agathis australia*, for example, there may be "areas of locally suppressed or accelerated growth [that] may 'migrate' around the tree as it grows," incomplete sets of growth rings that suddenly appear and 'wedge out' on one side of the tree, as well as irregular growth-ring thickness within the same ring (Dunwiddie, 1979). The wood of *Wollemia*, while very similar to that of *Agathis* and *Araucaria* in many characteristics, appears to be more regular in the pattern of its growth rings (cf. Heady and others, 2002).

Paleoclimatic Signal from the Lack of Growth Rings

The lack of true growth rings in *Agathoxylon hoodii* suggests that conditions were equable during the entire year and that seasonality was absent, either in temperature or in precipitation, or both. Specifically, this means a lack of summer–winter temperature cycles and the associated optimal–nonoptimal growing seasons in temperate woods, or the lack of the wet–dry cyclicity found in monsoonal climates.

The climatic equability evident in the wood of *Agathoxylon hoodii* was already pointed out in its original description by Tidwell and Medlyn (1993), who also remarked on the similarity of the wood to those of living araucarians growing in a warm, humid climate with little or no seasonal fluctuation. Other fossil woods from the Morrison Formation show more seasonality. *Xenoxylon morrisonense*, for example, has either indistinct growth rings, or growth rings with a very wide band of earlywood and a very narrow band of latewood, indicating a long growing season (Medlyn and Tidwell, 1975). On the other hand, *Protopiceoxylon resiniferous* has well-developed growth rings with a gradual transition from the earlywood to the latewood, which is the pattern commonly in trees undergoing seasonal cyclicity (Medlyn and Tidwell, 1979). For this reason, Tidwell and Medlyn (1993) suggested that these tree species grew in different environments; *A. hoodii* and *X. morrisonense* likely represent trees in the lowland flora that grew in more equable climates during the Late Jurassic, whereas the wood of *P. resiniferous* may have been transported longer distances to lowland facies from environments with more seasonal climate.

Paleoenvironmental Implications

The sedimentological occurrence of *Agathoxylon hoodii* in northeastern Utah (Sprinkel and others, 2019) also supports the hypothesis that *A. hoodii* was part of the lowland flora. The fossil logs and wood occur in a low-energy fluvial facies, such as found on a floodplain, and they were not transported far from the original growth site of the parent tree (Sprinkel and others, 2019).

In general, fossil logs and wood in the Salt Wash Member of the Morrison Formation in Utah are found in channel sandstone and conglomeratic sandstone beds. However, the fossil logs in Rainbow Draw and Miners Draw occur in very fine to fine-grained sandstone and siltstone beds lacking any sedimentary structures. These beds have been interpreted as overbank deposits on the floodplain (Sprinkel and others, 2019), not as a high-energy facies in the river channel. The parautochthonous nature of the logs is reflected in the fine-grained and structureless strata in which they are found. These Jurassic trees may have toppled and then been preserved near their original place of growth. Alternatively, they may have fallen and then were shifted slightly by low-energy currents during a period of flooding.

Height, Age of Morrison Trees, and Extent of Forests

The preserved lengths and diameters of the logs at Rainbow Draw indicate that they represent large trees. The longest fossil tree trunk is log 1 at site 1, which measured 11 m. When the fossil log's preserved diameter of 127.0 cm is used to reconstruct the height of the living tree (table 1), a minimum height of 28.4 m is attained (table 2); in this case, about 40% of the length of the fossil tree is still intact today. Height calculations for the rest of the fossil logs result in minimum reconstructed heights of 25, 22.4, and 19.3 m. These four logs thus yield a canopy height of at least 19 to 28 m for the Morrison trees.

A height of at least 25 m corresponds to the size of many conifer species native to North America today (Burns and Honkala, 1990). For example, mature trees of *Pinus contorta* (Lodgepole Pine), which is a very common species in the Rocky Mountain and Pacific coast regions of North America, reach an average height of 25 m at 140 years of age (Burns and Honkala, 1990).

In the subtropical forests of northern Queensland in northeastern Australia, the native species of *A. bidwillii* and the plantation trees of *A. cunninghamii*, *A. heterophylla*, and *A. hunsteinii* that were planted about a century ago generally attained heights of about 20 to 30 m (Gee, personal observation). In the case of *Araucaria angustifolia* in subtropical Brazil, the average height of trees out of 60 trees studied by Oliviera and others (2010) was 18 m at one site (average age of trees was 122 years) and 14 m (average age of trees was 90 years) at another site. The minimum tree heights between 19 and 28 m, as calculated for the Morrison trees, indicate that the fossil trees were likely as tall, if not taller, than the trees of many extant *Araucaria* species.

Thus, extrapolating from the height and ages of tall forest conifer trees, specifically those of living *Araucaria* and *Pinus* (Burns and Honkala, 1990; Oliviera and others, 2010), these trees of *Agathoxylon hoodii* most likely were well over 100 years old before they died.

Some extant species of *Araucaria*, such as *A. angustifolia*, form large, monospecific forests in Brazil, South America (Oliviera and others, 2010). Other species, such as *A. bidwillii* in northern Queensland, Australia, or *A. angustifolia* in Brazil, grow in dense, species-diverse forests and are often the oldest and tallest trees in the forest (Gee, personal observation), the so-called canopy emergents (Bittencourt, 2007). In any case, extant *Araucaria* spp. are trees that commonly form or grow in forests. If the Morrison trees with *Agathoxylon hoodii* wood were similar in habit to living *Araucaria* spp., they would have also formed forests, especially given the optimal growth conditions in the warm, humid, climatically equable, water-unlimited environment. The numerous finds of *Araucarioxylon hoodii* logs and wood in the same stratigraphic horizon at the Rainbow Draw and Miners Draw localities—all of which occur in the Salt Wash Member—suggest that the trees were part of a common forest biome in this area, although it is unknown if the individual trees actually lived at the same time. Considering the occurrence of *A. hoodii* in the overlying Brushy Basin Member on what is now Mt. Ellen in southern Utah, a strong case could be made for the widespread presence of *A. hoodii* conifer forests in northeastern and southeastern Utah during the Late Jurassic.

CONCLUSIONS

In summary, newly discovered fossil logs and wood in the Rainbow Draw and Miners Draw areas in northeastern Utah were found to pertain to *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray comb. nov., a new taxonomic combination proposed in this paper. They were trees that attained at least 127 cm in diameter and 28 m in height, and formed forests of large conifer trees that reached individual ages of over 100 years. Their growth rings indicate that the climate was equable; there was no seasonality in the local paleoclimate, neither annual summer–winter temperature cycles, nor wet–dry periods. During the Late Jurassic, tall conifer forests with *Agathoxylon hoodii* wood grew in at least two areas of what is now Utah: east of the city of Vernal and near Mt. Ellen in the Henry Mountains, south-central Utah.

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