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THE WHOLE PLANT OF *ARAUCARIA DELEVORYASII* AND *AGATHOXYLON HOODII*—GIANT TREES WITH SILICIFIED WOOD, GENTLY TAPERING TRUNKS, ARAUCARIAN SEED AND POLLEN CONES, AND *BRACHYPHYLLUM*-TYPE LEAVES WITH CUTICLE FROM THE UPPER JURASSIC MORRISON FORMATION OF THE HOWE-STEPHENS QUARRY, WYOMING, USA

Carole T. Gee, Aowei Xie, and Mariah M. Howell

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Cover

Photograph of the first tree trunk discovered in the Howe-Stephens Quarry in 1998 with Hans-Jakob Siber for scale. Image modified from Ayer (2000). Inset consists of photomicrographs of *Agathoxylon hoodii*. All images were taken of radial and tangential sections of thin sections of specimen number SMA 0424-021. See Figure 7 for detailed descriptions.

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The Whole Plant of *Araucaria delevoryasii* and *Agathoxylon hoodii*—Giant Trees with Silicified Wood, Gently Tapering Trunks, Araucarian Seed and Pollen Cones, and *Brachyphyllum*-Type Leaves with Cuticle from the Upper Jurassic Morrison Formation of the Howe-Stephens Quarry, Wyoming, USA

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ABSTRACT

Reconstructing whole plants based on their detached parts in an assemblage is a major goal in modern paleobotany. Plant parts pertaining to an ancient species of conifer, for example, can be found as separate organ fossils such as seed cones, pollen cones, twigs with leaves, pieces of wood, and tree trunks. Although fossil conifer remains are widely known from the Upper Jurassic Morrison Formation in the Western USA, until now, conifer cone compressions and silicified wood have not yet been linked with one another to form a whole plant. Here we identify silicified wood as *Agathoxylon hoodii*, based on a detailed description of its anatomy, from a dinosaur bonebed in the Howe-Stephens Quarry in north-central Wyoming. In addition to numerous pieces of wood, the fossil flora in the bonebed consists of hundreds of coalified compressions of conifer seed and pollen cones, detached seed scales, abscised seeds, and branches with *Brachyphyllum*-type leaves previously assigned to a single species, *Araucaria delevoryasii*. Two giant coalified tree trunks in the quarry also pertain to this Upper Jurassic conifer, and their preserved diameters reconstruct trees with minimum heights of 74 to 78 m and 64 to 65 m, respectively. The gross morphology of the trunks, especially their taper, is also described and found to be similar to that of living *Araucaria* trees. Collectively, the separate fossil plant organs are recognized here as a whole plant called the *Araucaria delevoryasii* tree. This species of tree likely grew directly on the riverbanks of a meandering river. The paleobiogeography of *Agathoxylon hoodii* wood at four localities in the central Morrison Formation documents the widest extent of all Morrison wood species thus far. The compression fossils and silicified wood from the Howe-Stephens Quarry in north-central Wyoming, as well as silicified logs in Utah, represent an *Araucaria* tree that helped to form the old-growth Upper Jurassic conifer forests in the central Morrison Formation.

Citation for this article.
Gee, C.T., Xie, A., and Howell, M.M., 2025, The whole plant of *Araucaria delevoryasii* and *Agathoxylon hoodii*—giant trees with silicified wood, gently tapering trunks, araucarian seed and pollen cones, and *Brachyphyllum*-type leaves with cuticle from the Upper Jurassic Morrison Formation of the Howe-Stephens Quarry, Wyoming, USA: Geology of the Intermountain West, v. 12, p. 293–314, https://doi.org/10.31711/giw.v12.pp293-314.

INTRODUCTION

A major goal in modern paleobotany is reconstructing whole plants based on their separate parts found in an assemblage. In regard to a Mesozoic conifer, for example, this would mean the linking of detached reproductive organs, such as seed and pollen cones, with non-reproductive parts, such as the trunk, wood, branches, and leaves, which are commonly not found in organic connection to one another. However, they can be found in abundance co-occurring in close physical association with one another in a deposit. Especially if the plant organs are morphologically and anatomically consistent with one another, as well as found in a fossil flora with few or no other species, they are likely to represent the various parts of a single species.

In the Upper Jurassic flora of the Howe-Stephens Quarry in north-central Wyoming, hundreds of fossils consisting of conifer seed cones, detached seed scales, isolated seeds, pollen cones, and branches with *Brachyphyllum*-type leaves (Gee and Tidwell, 2010) have been found intermixed in intimate association with numerous pieces of wood in a productive dinosaur bonebed (Ayer, 2000; Gee and Tidwell, 2010), with little evidence of other fossil plant species. The reproductive material, leaves, and branches pertain to a single species of araucarian conifer, *Araucaria delevoryasii* Gee (Gee and Tidwell, 2010), but until now, the abundant pieces of silicified wood and two giant tree trunks in the quarry had remained undescribed.

In recent years, renewed interest in the paleobotany of the Upper Jurassic Morrison Formation has encouraged a number of studies on fossil wood and logs (Gee, 2023). New occurrences of silicified wood have been correctly described and photographically documented from the State of Utah, i.e., *Agathoxylon hoodii* Tidwell et Medlyn (Gee et al., 2019) and *Xenoxylon utahense* Xie et Gee (Xie et al., 2021), and Montana[1], namely *Xenoxylon meisteri* Palibin et Jarmolendo (Richmond et al., 2019) and *Circoporoxylon bighornense* (Hoff, 2022; Hoff et al., 2025). The species of *Xenoxylon morrisonense* Medlyn et Tidwell (1975) has recently been transferred to a newly established genus, *Morrisonoxylon* Philippe, Richmond, Lupia et McLemore (2023), as the species *M. morrisonense*.

The four wood studies published in the last six years supplement the taxonomic list of species already known of the Morrison paleoxyloflora: *Cupressinoxylon jurassicum* Lutz (1930), *Mesembrioxylon carterii* Tidwell, Britt et Ash (1998), *M. obscurum* (Knowlton) Medlyn et Tidwell (2002), *Protocupressionoxylon medlynii* Tidwell, Britt et Ash (1998), *Protopiceoxylon resiniferous* Medlyn et Tidwell (1979), and *Xenoxylon moorei* Tidwell, Britt et Ash (1998)[2].

Silicified logs at several localities in northeastern Utah have been studied in regard to their taxonomic determination, wood anatomy, and estimated ancient living-tree height, such as with the logs of *Agathoxylon hoodii* and *Xenoxylon utahense* (Gee et al., 2019; Xie et al., 2021), as well as in regard to ecological interactions of Upper Jurassic insects and fungi found within the fossil woods (Gee et al., 2022; Xie et al., 2023). The petrified forest log assemblage in the Morrison Formation near the town of Escalante in south-central Utah (Morgan et al., 2024) is also currently under intense study (Gee et al., 2023). It should be noted that in general, intact fossil logs offer more biological information than isolated chunks of silicified wood, because ancient tree heights and trunk taper can be calculated using log diameter, which can lead to a deeper understanding of ancient tree sizes, appearance, and the structure of the forest canopy.

Here we describe the assemblage of silicified wood and coalified tree trunks that occurs in a dinosaur bonebed in the Howe-Stephens Quarry in the Morrison Formation of north-central Wyoming. The wood in this flora is identified here as *Agathoxylon hoodii* of the conifer family Araucariaceae, and the two giant fossil trunks co-occurring in the assemblage offer data on ancient tree height and trunk taper. The association of *Agathoxylon*

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[1] Other occurrences of fossil wood from Montana have been reported in meeting abstracts, but because these reports are not illustrated and/or peer-reviewed, these taxa are not included here.

[2] It has been suggested that *Xenoxylon moorei* be excluded from the genus *Xenoxylon* based on anatomy (Richmond et al., 2019), but a new taxonomic determination has not yet been made.

hoodii with the seed cones, seed cone scales, seeds, pollen cones, and leaved twigs of *Araucaria delevoryasii* allows for the first whole-plant reconstruction of a conifer species in the Morrison consisting of the tree trunk, wood, and reproductive material. It also provides evidence for a widespread distribution of the *Araucaria delevoryasii* tree species some 150 million years ago across what is today Wyoming and Utah.

GEOLOGICAL SETTING

The fossil wood specimens and log data under study here were collected from the Howe-Stephens Quarry on Howe Ranch located near the towns of Greybull and Shell in the Big Horn Basin in north-central Wyoming, USA (Figure 1). The Howe-Stephens Quarry is a prolific fossiliferous site that has produced numerous skeletons and isolated bones of dinosaurs (e.g., Ayer, 2000; Wiersma-Weyand et al., 2021) as well as fossil plant remains (Gee and Tidwell, 2010) that were excavated by Hans-Jakob Siber and his field team from the Sauriermuseum Aathal (Aathal Dinosaur Museum), in Aathal (near Zurich), Switzerland. Excavations in this particular quarry were initiated in 1992 and continued annually until 2002. During this decade, the Siber field team collected numerous pieces of silicified wood from this quarry.

In the Howe-Stephens Quarry, the dinosaur and plant fossils occur in the Morrison Formation, a geological unit that is widely distributed in the Western United States (Foster, 2020, and references therein). On Howe Ranch, the Morrison crops out in a southwest–northeast direction, and consists primarily of sandstone and mudstone with rare layers of limestone having a thickness of ca. 55 m. The fossiliferous layer in the quarry has not been attributed to a specific stratigraphic member by other paleontologists working on this deposit (e.g., Michelis, 2004; Tschopp and Mateus, 2017) because the Morrison is considered undifferentiated in northern Wyoming (Turner and Peterson, 1999; Foster, 2020).

The matrix of the bonebed consists of a light brown, very fine grained, cross-bedded sandstone. Carbonaceous plant remains are usually concentrated in lenses in the cross-bedded sandstone, ranging from a few centimeters to several decimeters in thickness (Ayer, 2000). The numerous pieces of silicified wood from the Howe-Stephens Quarry were found in close association with the dinosaur bones and skeletons, as well as alongside coalified compressions, which represent the conifer seed cones, detached seed cone scales and seeds, pollen cones, and twigs with leaves of *Araucaria delevoryasii* (Gee and Tidwell, 2010). Unlike the faunal remains, the exact provenance of the specimens of silicified wood and plant compressions gathered from the quarry was not noted, although the quarry map shows the exact location of two fossil tree trunks unearthed in the bonebed (Figure 2).

Geological mapping of the Howe-Stephens Quarry by Jacques Ayer (University of Neuchâtel, Switzerland) produced a schematic cross section of the bonebed (Figure 3), which shows diagrammatically the co-occurrence of dinosaur bones and fossil plants in the same lens of brownish sandstone. This sandstone lens was interpreted as channel-fill deposits of a point bar sequence in a meandering river depositional system (Jacques Ayer, University of Neuchâtel, Switzerland, written communication to CTG, 2006).

MATERIALS AND METHODS

Taxonomy and Wood Anatomy

Twenty-three specimens of silicified wood, grouped under the specimen number SMA 0424, were selected for study from the collections of the Sauriermuseum Aathal. To track the wood specimens through the thin section-making process at the University of Bonn, Germany, they were each given an additional specimen number, from 001 to 023. Paleoxyological study was initiated by CTG in 2005, concurrent with the study of the compression flora. However, the study of the fossil wood was soon set aside and later offered to two graduate students who, independently of one another, prepared some thin sections but were not able to continue successfully with the next stages of research. Conception and design of the fossil wood project (CTG), selection of wood specimens for study on multiple trips to the Sau-

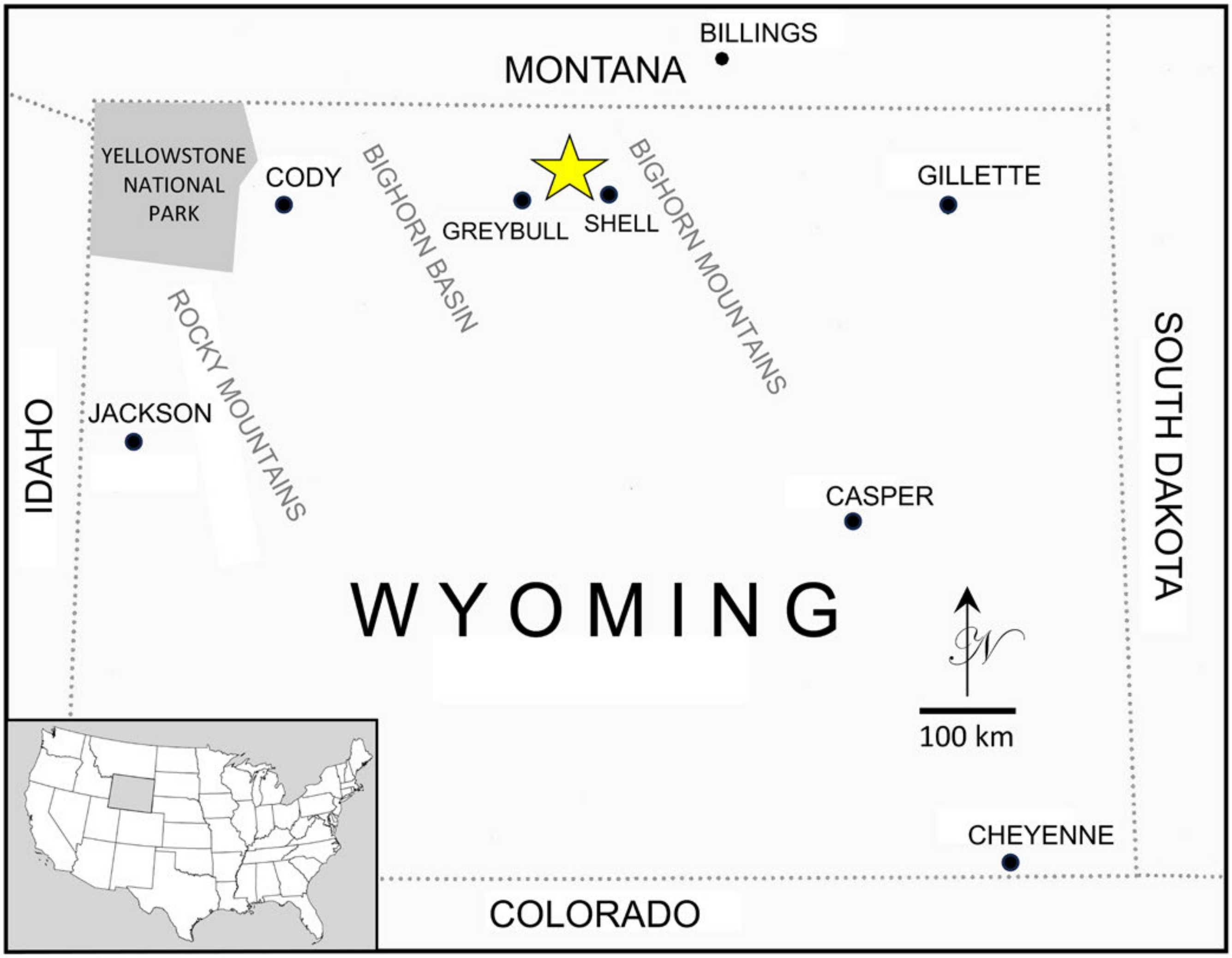

Figure 1. Locality map of the Howe-Stephens Quarry on Howe Ranch (star), located between Greybull and Shell in the Bighorn Basin in north-central Wyoming, USA. Modified from Ayer (2000). Inset: the location of the state of Wyoming (gray) within the contiguous USA.

riermuseum Aathal paleobotanical collection (CTG), identification of the wood to the genus and species level (CTG, Aowei Xie [AX]), description and interpretation of wood (AX, CTG) and cuticle (CTG), photography of the wood (AX) and cuticle (CTG), calculation and interpretation of trunk taper (CTG, AX, Mariah M. Howell [MMH]), cuticle preparation (MMH), preparation of line drawings (CTG, AX), writing of the manuscript (CTG, AX, MMH), and submission were performed by this core team.

For taxonomic identification and anatomical work, standard petrographic thin sections were made using conventional methods. All specimens of silicified wood were cut in the three planes of section necessary for study, namely, transversely, radially, and tangentially. The thin sections were investigated with a Leica DM2500 compound photomicroscope. Images and measurements were taken with software ImageAccess easyLab 7 integrated with the photomicroscope. In the wood description, we follow the anatomical terms defined by the IAWA Committee (IAWA Committee, 2004), with additional reference to Philippe and Bamford (2008) and Boura et al. (2021).

Remnants and thin sections of the fossil wood spec-

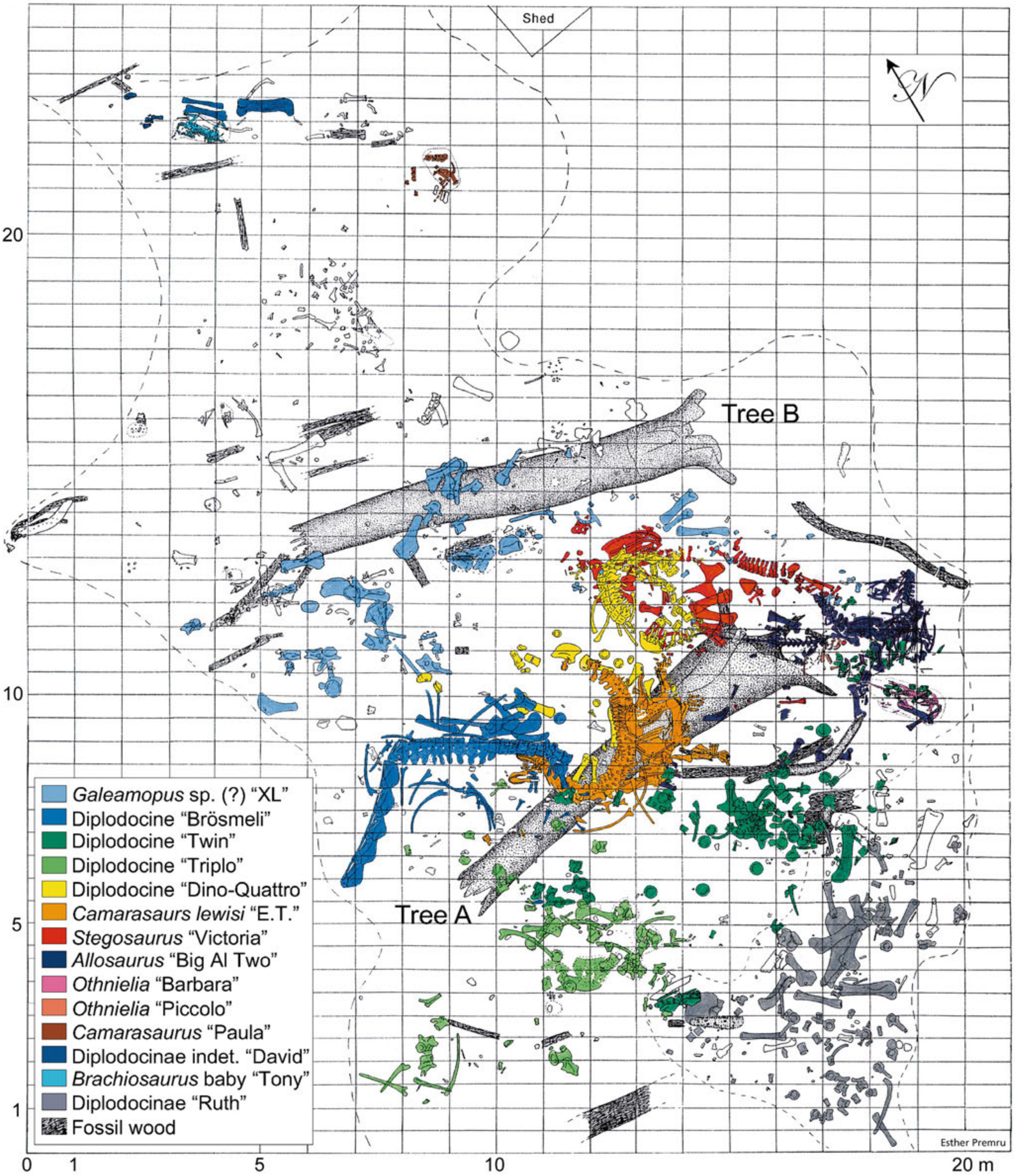

Figure 2. Detailed, 21 x 30 m quarry map of the Howe-Stephens Quarry, showing dinosaur skeletons, bones, and two giant coalified trunks (labeled here as Tree A and Tree B), plotted to scale by Esther Premru, Sauriermuseum Aathal. Colors represent the bones of 14 individual dinosaurs, following color scheme of Ayer (2000) and Wiersma-Weyand et al. (2021). Dashed lines show associated bones grouped together on the same horizon.

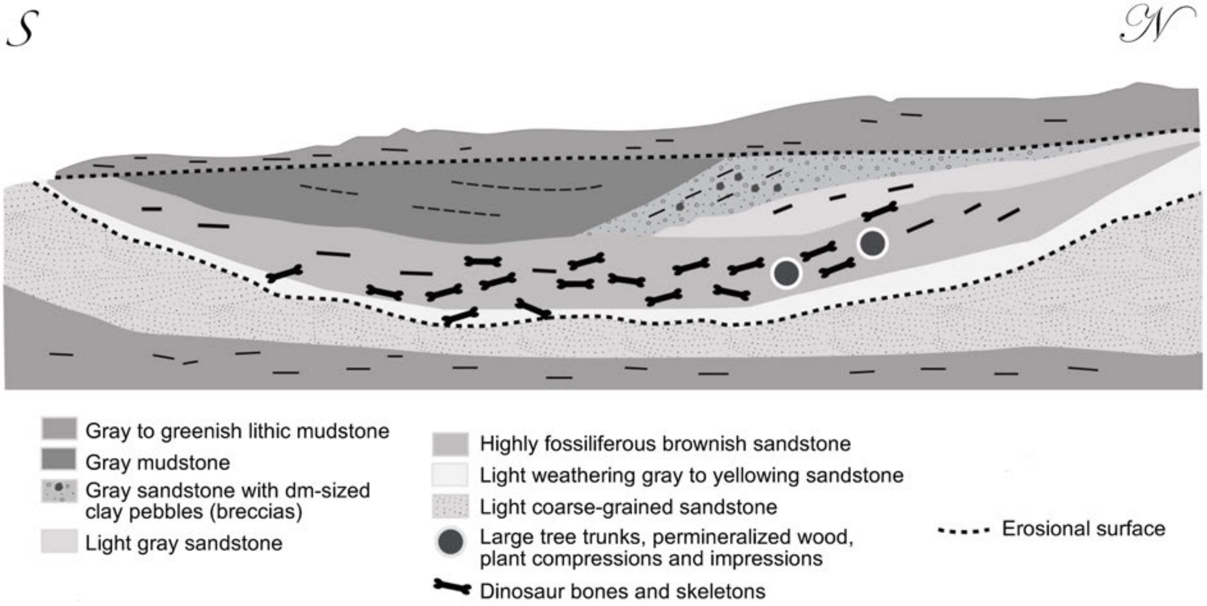

Figure 3. Schematic cross section through the Howe-Stephens Quarry interpreted as containing the channel-fill facies of a meandering river. The dinosaur bones and fossil plants (coalified tree trunks, silicified wood, cone and twig compressions and impressions) occur jumbled in the same bonebed. Redrawn and modified from a stratigraphic section mapped by Jacques Ayer (University of Neuchâtel, Switzerland).

imens are stored at the Sauriermuseum Aathal, grouped under specimen number SMA 0424.

Gross Morphology of Tree Trunks

Two large, coalified tree trunks were found in the Howe-Stephens Quarry bonebed through the original excavation activity by the Siber team. The fossil tree to the south, designated here as Tree A, was discovered in 1998 (Figure 4), and the fossil tree to the north, called here Tree B, was uncovered in 2002 (Esther Premru, Sauriermuseum Aathal, verbal communication to CTG, 2004). Description of the gross morphology of these tree trunks here is based on the drawing of the trunks in the quarry map made by E. Premru during the multi-year excavation of the bonebed by the Siber team. Given the division of the quarry map into 1 x 0.5 m squares as well as the precise and detailed illustration of the skeletal remains, it is assumed that the fossil trunks, designated here as Trees A and B, were also drawn in a similarly accurate manner.

Estimation of Tree Height

The two fossil tree trunks sketched on the quarry map offered good approximations for trunk diameter. While exact measurements of the tree trunks' girth were not made during the excavation process, we extrapolated from the quarry map approximate diameter values, such as diameter at breast height (DBH), a standard forestry measurement defined as 130 cm from the tree trunk–soil interface, for the purpose of estimating the height of the ancient trees.

Based on the height–diameter relationship of living trees of *Araucaria* spp., three height–diameter growth models have been recognized as the most appropriate models for reconstructing the minimum heights of the ancient araucarian trees (Xie et al., 2024). They are the median modified Mosbrugger model (Equation 1), the median 2pPower model (Equation 2), and the median Curtis model (Equation 3), respectively, and can be given as:

Figure 4. Photograph of the first tree trunk discovered in the Howe-Stephens Quarry in 1998, called here Tree A, with Hans-Jakob Siber for scale. Image modified from Ayer (2000).

Equation 1

$$H = 57.22 \times D^{0.67}$$

Equation 2

$$H = 58.03 \times D^{0.72}$$

Equation 3

$$H = 101.78 \times D \mathbin{/} (1+D)^{0.80}$$

where:

H = estimated tree height in m, and
D = maximum preserved diameter of the fossil log in m.

We apply all three equations to the two fossil tree trunks in the Howe-Stephens Quarry to obtain a minimum estimated height of the trees when living.

Calculation of Trunk Taper

In addition to ancient tree height, trunk taper was also reconstructed based on the drawing of the two fossil trunks on the quarry map. In living trees, there is a relationship between diameter and taper that characterize individual taxa (Larsen, 2017). Any one trunk will exhibit at least two rates of taper: the first rate of taper is trunk diameter from the soil–trunk interface to DBH, and the second rate is from DBH to the diameter at base of the tree crown. The “simple taper” equation developed by Larsen (2017) was based on the stem analysis of 11,610 angiosperm and conifer trees encompassing 34 species, including 14 species of *Pinus*, *Taxodium,* and *Tsuga*.

The simple taper equation of Larsen (2017) is given here as Equation 4:

Equation 4

$$d_h = dbh + p \times (h - bh)$$

where:

d_h = trunk diameter d at height h of the tree,
dbh = trunk diameter at breast height,
p = tree taper rate,
h = a second height of the tree serving as starting point or an endpoint for taper, and
bh = breast height of the tree.

Mathematically, this equation can be rearranged to determine trunk taper (Equation 5) and expressed as:

Equation 5

$$p = (d_h - dbh) / (h - bh)$$

Equation 5 was then used to determine three rates of taper in the fossil trees: in the stump from trunk base to breast height, in the mid trunk from breast height to 4-m height mark, and in the upper trunk from the 4-m height mark to the top of the tree.

Calculating the taper rates for the fossil trees was based on eight trunk parameters observed in the Howe-Stephens Quarry map (Figure 5). These measurements included: stump diameter (dark blue), breast height (130 cm, light green), DBH (light blue), stem length between DBH and 4-m height mark (orange), diameter at 4-m height mark (green), stem length between 4-m height mark and top of tree (yellow), diameter at top of trunk (purple), and stem length of entire trunk (white).

For comparison, size data from five living trees of *Araucaria araucana* were measured at the Botanical Garden of the University of Bonn in October 2022, using the same trunk parameters to calculate their stump and mid-trunk stem taper rates. In these cases, measurements were taken of their trunk circumference with a flexible tape measure and later mathematically converted to diameter data.

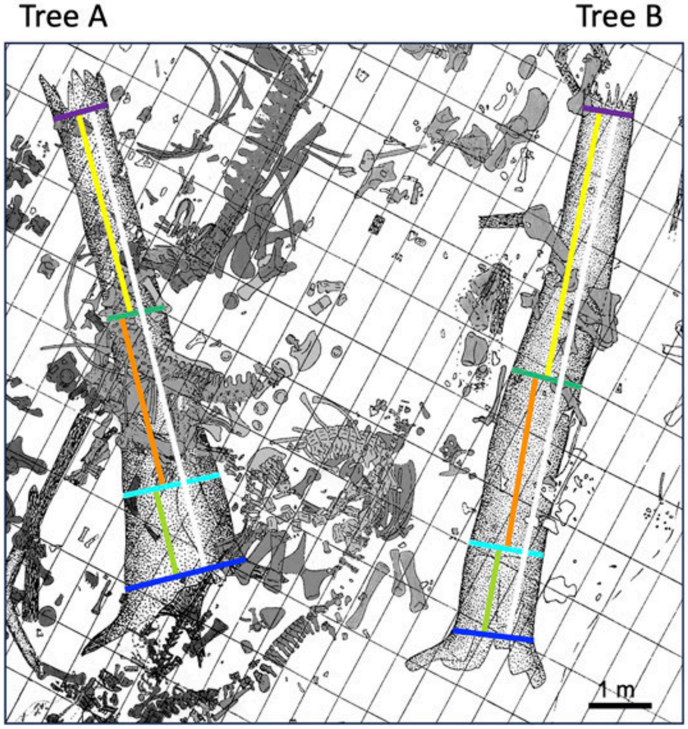

Figure 5. Trunk parameters of Trees A and B measured using the Howe-Stephens Quarry map to determine the stump taper rate and stem taper rates. Color key: dark blue = stump diameter, light green = breast height (130 cm), light blue = DBH (diameter at breast height), orange = stem length between DBH and 4-m height mark, green = diameter at 4-m height mark, yellow = stem length between 4-m height mark and top of tree, purple = diameter at top of trunk, white = stem length of entire trunk.

Leaf Cuticle

Cuticle was extracted from *Brachyphyllum*-type leaves on fossil twigs collected from the same bonebed and considered as pertaining to *Araucaria delevoryasii* (Gee and Tidwell, 2010). Samples from five specimens were prepared using either standard cuticle preparation with Schulze's Reagent (Kerp, 1990) or with gentle bleaching with sodium hypochlorite (Howell et al., 2022). The prepared cuticle samples were mounted on glass slides with Euparal mounting medium and studied using light microscopy, or examined using scanning electron microscopy.

RESULTS

Systematic Paleobotany of Silicified Wood

Division Coniferophyta
Class Coniferopsida
Order Coniferales
Family Araucariaceae
Genus *Agathoxylon* Hartig, 1848 sensu Philippe, 1995
***Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray, 2019;**
Figures 6 and 7

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; Plate 1, Figures 1 to 6; Plate 2, Figures 1 to 6; Text-Figure 2.

Fossil logs in Rainbow Draw – Sprinkel et al. (2019), Stratigraphic setting of the fossil log sites in the Morrison Formation (Upper Jurassic) near Dinosaur National Monument, Uintah County, Utah, USA: Geology of the Intermountain West, v. 6, p. 61–76; Figures 10, 11A, and 12.

Agathoxylon hoodii (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray – Gee et al. (2019), 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: Geology of the Intermountain West, v. 6, p. 77–92; Figures 5 and 6. Note: the fossil log in Miners Draw is excluded here in this synonymy (see instead *Xenoxylon utahense* described by Xie et al., 2021).

Type species: *Araucarioxylon hoodii* Tidwell et Medlyn, 1993, which was later recognized as a new combination, *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray, 2019.

Description of wood anatomy: Only secondary xylem is described here, because bark, pith, and primary xylem are lacking. In transverse section, true growth rings absent (Figures 6A through 6C); irregular, discontinuous concentric bands of tracheids with narrower lumina locally apparent (Figures 6B and 6C), ranging from one to four cells thick and developing asynchronously during the growth of the tree. Tracheids subround to elliptical to polygonal in transverse section (Figures 6B though 6F); lumen ranging from 25 to 66 μm in tangential diameter, those of normal-size cells about 46 μm (Figure 6E). Axial parenchyma and resin canals absent.

In radial section, tracheids on average 61 μm wide (52 to 75 μm). Radial tracheid pits usually uniseriate, but also locally biseriate. When uniseriate, arrangement of tracheary pits contiguous and compressed (Figures 6G and 6H), occasionally distant (Figure 6H); when biseriate, alternate (Figures 7A and 7B, arrows), occasionally opposite (Figure 7C, arrow). Bordered pits generally oblate in outline. Crassulae not observed. Resinous remains coalesced along the periphery in ray cells and the cell corners (Figure 7D, arrow). Rays consisting of parenchymatous cells with thin, smooth horizontal and end walls (Figure 7D). Cross-field pitting araucarioid type sensu IAWA Committee (2004). Each cross-field bearing numerous pits, 7 through 16 cupressoid pits with a circular or oval outline, contiguous, arranged in 3 through 5 alternate vertical rows (Figures 7E and 7F).

In tangential section, rays are homogenous, parenchymatous, uniseriate (Figures 7G through 7J). The rays are variable in height, ranging from very low to high, 2 to 25 cells high, mostly 3 to 8 cells tall. Bordered pits on the tangential tracheary walls circular, 15.8 μm in diameter, usually uniseriate distant, but also locally contiguous (Figures 7I, arrow, and 7J). Resin plugs also evident in tracheids of axial system (Figure 7J, arrow).

Locality: Howe-Stephens Quarry, Howe Ranch, near Greybull, Wyoming, USA.

Specimens studied: SMA 0424-001 to 023.

Horizon and age: Morrison Formation undifferentiated, Upper Jurassic (Kimmeridgian). This site is considered WY-62 in Dinosaur Zone 2 of Turner and Peterson (1999) and systems tract C5 of Maidment and Muxworthy (2019) and Maidment (2024).

Repository: Sauriermuseum Aathal, Switzerland.

Taxonomic Assignment of Wood

All pieces of silicified wood from the Howe-Stephens Quarry described here can be assigned to the genus *Agathoxylon* based on a shared suite of distinct characters: araucarian radial tracheid pitting and araucarioid cross-

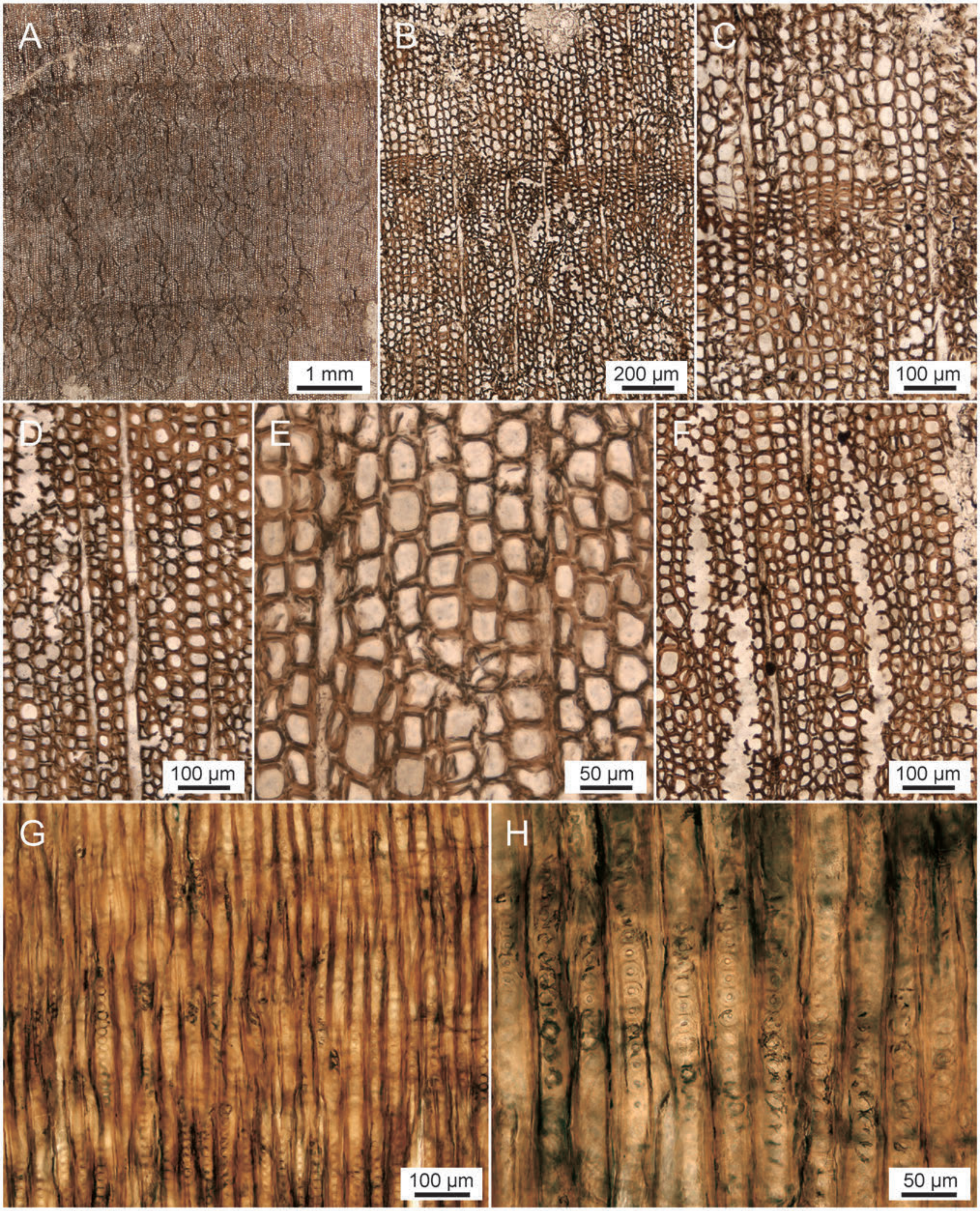

Figure 6 caption is on the following page

Figure 6 is on the previous page. *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis, et Gray from the Upper Jurassic Morrison Formation at the Howe-Stephens Quarry; all photographs were taken of transverse and radial sections of thin sections of specimen number SMA 0424-021. (A) Transverse section showing growth rings indistinct, true growth rings absent. (B) Transverse section showing irregular, discontinuous concentric bands of tracheids with narrower lumina apparent. (C) Close-up of B, transverse section showing details of tracheids with narrower lumina. (D) Transverse section showing ray cells. (E) Transverse section showing details of tracheids, subround to elliptical to polygonal. (F) Transverse section showing details of decayed tracheids. (G) Radial section showing tracheids with uniseriate, contiguous, and compressed bordered pits. (H) Close-up of G, radial section showing details of radial tracheid pits. Modified from Xie (2022).

field pitting; many radial tracheid pits uniseriate, contiguous, and compressed, but also uniseriate contiguous to distant, or biseriate alternate to opposite; cross-fields bearing 7 to 16 densely arranged cupressoid pits; resin plugs or resin remnants in the ray cells or in the axial parenchyma cells.

In particular, two specimens of wood (SMA 0424-021 and 022) are well-preserved enough to determine the wood to the species *Agathoxylon hoodii* and form the basis of the anatomical description of the wood here. The species-specific characters include the dominance of axial tracheids (Figures 6A through 6F), the absence of axial parenchyma (Figures 6A through 6F), and the lack of resin canals (Figures 6A through 6F); contiguous to distantly arranged, uniseriate circular bordered pits on the radial walls of the tracheids (Figures 6G, 6H, and 7A through 7C), the alternate (or occasionally opposite) arrangement of the circular bordered pits in the tracheids, when biseriate (Figures 7A through 7C, arrows); the smooth, unpitted sidewalls and endwalls of the ray cells (Figure 7D); and the numerous, small, crowded cupressoid pits in the cross-fields (Figures 7E and 7F); the presence of resinous remains and resin plugs, particularly in the radial system (Figures 7D, arrow, 7G, 7H, and 7J, arrow), but also in the axial system (Figure 6J, arrow). What appears in cross section to superficially resemble growth rings are not consistent across the trunk (Figures 6B and 6C), and thus represent irregular slow-downs in growth, not true growth rings. All of these features are found in *Agathoxylon hoodii* wood from Mt. Ellen in southeastern Utah (Tidwell and Medlyn, 1993) and from Rainbow Draw in northeastern Utah (Gee et al., 2019), and pinpoint the assignment of the Howe-Stephens wood species to this species that has only been described up to now from the Morrison Formation of Utah.

Remarks

Although numerous pieces of fossil wood were excavated and collected from the Howe-Stephens Quarry, 23 specimens were selected for thin sectioning and study. Of these, only seven wood specimens yielded anatomical characters sufficient for unequivocal identification, due to the generally poor preservation of the fossil wood flora from the Howe-Stephens Quarry. The two specimens (SMA 4024-021 and 022) that show moderately good preservation also show tangential tracheid pits that are usually uniseriate distant, but occasionally contiguous. Because this character was not mentioned in the original description of *Araucarioxylon hoodii* by Tidwell and Medlyn (1993), nor in the description of the new combination of *Agathoxylon hoodii* by Gee et al. (2019), we have added this minor detail here.

Gross Morphology of Tree Trunks

The gross morphology of both coalified trees found in the Howe-Stephens Quarry is similar (Figures 2 and 5). Both trees consist of long trunks with a very slight and uniform taper in the upper trunks for most of their respective lengths. Each tree has a sudden root flare at their trunk base. However, the root flare of Tree A is visually much greater than that of Tree B (Figure 5). There is no obvious evidence of branching, nor large branch scars, along either trunk.

In Tree A, ca. 7.24 m of the original length is preserved, whereas in Tree B, ca. 8.22 m of its length is still evident (Table 1). For each fossil trunk, the DBH, i.e., the diameter of the trunk 1.3 m above the base of each fossil tree, is estimated for Tree A as 152 cm and for Tree B as 117 cm (Table 1).

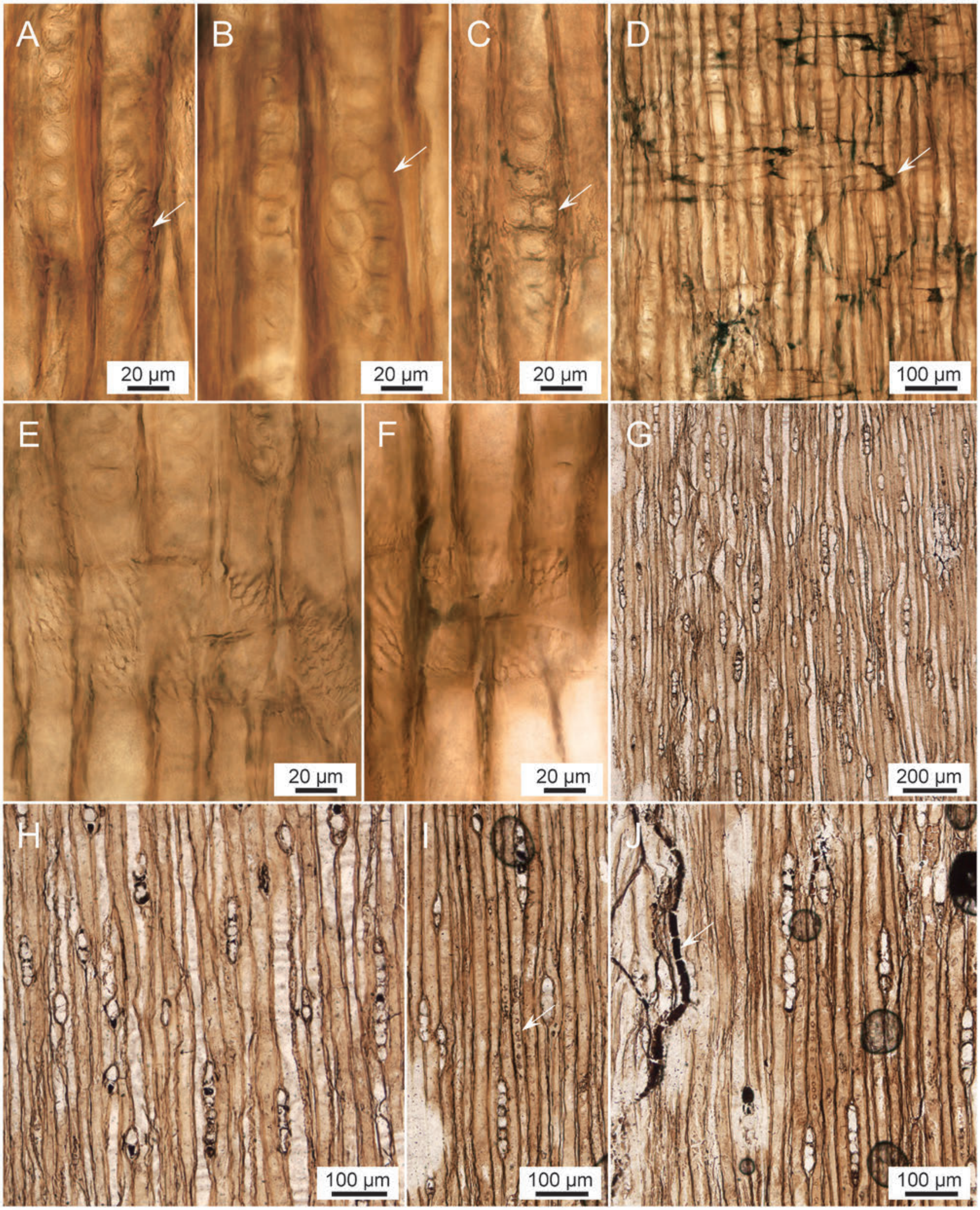

Figure 7 caption is on the following page

Figure 7 is on the previous page. *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis, et Gray from the Morrison Formation at the Howe-Stephens Quarry; all photographs were taken of radial and tangential sections of thin sections of specimen number SMA 0424-021. (A and B) Radial section showing tracheids with biseriate alternate bordered pits (arrow). (C) Radial section showing tracheids with biseriate opposite bordered pits (arrow). (D) Radial section showing resinous remains coalesced along the periphery in ray cells and the cell corners (arrow). (E and F) Radial section showing details of araucarioid cross-field pits in which each cross-field bears 7 to 16 cupressoid pits. (G) Tangential section showing uniseriate rays. (H) Close-up of G, tangential section showing details of uniseriate rays. (I) Tangential section showing uniseriate tangential tracheid pitting (arrow). (J) Tangential section showing resin plugs (arrow). Modified from Xie (2022).

Reconstruction of Ancient Tree Heights

Applying the median modified Mosbrugger model, the median 2pPower model, and the median Curtis model, which were given earlier as equations 1, 2, and 3, respectively, results in the reconstruction of a minimum height of the fossil trees at Howe-Stephens Quarry (Table 2). For Tree A, the minimum height of the living tree would have ranged between 73.9 and 78.5 m, averaging 76.0 m. For Tree B, the minimum height of the living tree would have varied between 63.6 and 65.0 m, averaging 64.2 m.

Stump and Stem Taper Rates of Fossil and Living Trees

The measurements given in Table 3 were used to calculate stump taper rate and stem taper rates of the fossil trees in the Howe-Stephens Quarry, as well as the living *Araucaria* trees measured in Bonn University Botanic Garden. These data yielded a stump taper rate (p_b), a stem taper rate for the mid trunk ($p_{mid\ trunk}$), and a stem taper rate ($p_{upper\ trunk}$) for each of the eight trees studied (Table 3).

The results reveal that fossil Tree A has a stump taper rate (p_b = -0.28) and a mid-trunk stem taper rate ($p_{mid\ trunk}$ = -0.23) that is much greater than those of the second fossil tree (Tree B), which has a stump taper rate (p_b = -0.08) and a mid-trunk stem taper rate ($p_{mid\ trunk}$ = -0.03). Interestingly, the stump and the two stem taper rates of Tree B are much closer to those of the living *Araucaria araucana* trees. Among living *A. araucana* trees, stump taper ranges from -0.03 to -0.18, with an average of -0.09. In the upper trunk of the two fossil trees, stem taper rate is relatively low (Tree A: $p_{upper\ trunk}$ = -0.01; Tree B: $p_{upper\ trunk}$ = -0.05). These values are comparable to the variation in stem taper rates found in living *A. araucana* trees, which range from -0.02 to -0.05, with an average of -0.03.

Fossil Leaf Cuticle

The leaf cuticle is moderately well-preserved (Figure 8A). Stomata are arranged in longitudinal files along the length of the leaf, commonly represented by holes in the leaf tissue where the guard cells are not found preserved (Figure 8B). The paired guard cells appear lightly sunken. The ring of subsidiary cells adjacent to the guard cells is monocyclic and consists of wide cells (Figure 8C); the number of subsidiary cells in each ring was not observable. The oval area occupied by one set of guard cells and the stoma measures roughly between 16 to 19 µm, whereas the stomatal complex has a diameter of approximately 37 µm. On the basis of the long axis of the stomatal apparatuses aligning with longitudinal axis of the leaf, it appears that they are oriented parallel to leaf axis (Figure 8B).

In the non-stomatal zones, epidermal cells are elongate and rectangular, with their long axis parallel to leaf long axis (Figure 8B). Average epidermal cell measures roughly 16 x 11 µm. Anticlinal walls and periclinal are straight, not sinuous. There are about 10 files of epidermal cells between the stomatal zones.

No papillae, protrusions, or trichomes were observed, neither on the guard cells nor on the epidermal cells.

Table 1. Preserved length and diameter at breast height (DBH) for Trees A and B, estimated from the Howe-Stephens Quarry map (Figure 5).

Tree	Preserved length (m)	Preserved diameter at DBH (cm)
A	7.24	152
B	8.22	117

Table 2. Minimum estimated heights for the two coalified tree trunks at the Howe-Stephens Quarry, based on their respective DBH and calculated using the three most appropriate growth models for ancient araucarian trees, as tested by Xie et al. (2024).

Tree	Median modified Mosbrugger model (m)	Median Power model (m)	Median Curtis model (m)	Averaged minimum height of living tree (m)
A	75.8	78.5	73.9	76
B	63.6	65	64.1	64.2

DISCUSSION

Comparison to Other Morrison Woods

All silicified woods from the Howe-Stephens Quarry studied here can be assigned to *Agathoxylon hoodii*, based on a shared suite of characters. As described in detail above, these characters include araucarian radial tracheid pitting and araucarioid cross-field pitting; most radial tracheid pits uniseriate, contiguous, and compressed, but also uniseriate contiguous to distant, or biseriate alternate to opposite; cross-fields each bearing 7 to 16 densely arranged cupressoid pits. Previously, this species had only been described from Utah (Tidwell and Medlyn, 1993; Gee et al., 2019).

Prior to our study, only two species of fossil araucariaceous woods from the Morrison Formation had been reported from Wyoming, namely, *Araucarioxylon*? *obscurum* Knowlton from the Freezeout Hills, south-central Wyoming (Knowlton, 1900) and *Araucarioxylon wyomingense* Andrews et Pannell from the Gros Ventre Canyon in western Wyoming (Andrews and Pannell, 1942). When the Freezeout Hills wood was described in 1900, Knowlton was uncertain of its generic position and tentatively assigned the wood to *Araucarioxylon*, because it had obscure growth rings and a relatively low ray height (Knowlton, 1900; Medlyn and Tidwell, 2002). Although the Freezeout Hills wood was transferred to *Mesembrioxylon obscurum* on the basis of its podocarpaceaous anatomy (Medlyn and Tidwell, 2002), the genus *Mesembrioxylon* Seward (1919) is considered invalidly published because this genus name was proposed to replace Gothan's two valid genera *Podocarpoxylon* and *Phyllocladoxylon* (see arguments made by Bamford and Philippe, 2001; Philippe and Bamford, 2008). The Freezeout Hills wood differs from the Howe-Stephens Quarry wood by having mostly uniseriate, distant radial tracheid pits and one to three thin-bordered podocarpaceous pits per cross-field (Medlyn and Tidwell, 2002), whereas our wood show mostly uniseriate, contiguous, compressed radial tracheid pits, and araucarioid cross-field pitting.

The second araucariaceous species from Wyoming, *Araucarioxylon wyomingense*, differs from the Howe-Stephens Quarry wood in its very low rays (one to three cells high), locally strongly flattened radial tracheid pits, and a lack of tangential tracheid pits (Andrews and Pannell, 1942). Our wood has mostly uniseriate, distant tangential tracheid pits, higher rays (one to nine cells high), and a lack of strongly flattened radial tracheid pits.

Beyond Wyoming, with the exception of *Agathoxylon hoodii* in Utah, the Howe-Stephens Quarry wood differs from all other Upper Jurassic wood taxa in the Morrison Formation. Major differences are most evident in the cross-field pitting between the ray cells and axial tracheids, as well as in the abundance of resin in *A. hoodii*. This includes fossil woods previously described from Utah, such as *Mesembrioxylon carterii* (Tidwell et al., 1998), *Mesembrioxylon obscurum* (Medlyn and Tidwell, 2002), *Protocupressinoxylon medlynii* (Tidwell et al., 1998), *Protopiceoxylon resiniferous (*Medlyn and Tidwell, 1979), *Xenoxylon utahense* (Xie et al., 2021), and *Morrisonoxylon morrisonense* (Philippe et al., 2023); from Montana, such as *Xenoxylon meisteri*

Table 3. Trunk data collected from the Upper Jurassic logs in the Howe-Stephens Quarry and living trees of *Araucaria araucana* cultivated at the Bonn University Botanic Garden and calculated stump taper rate (p_b), mid-trunk stem taper rate ($p_{mid\ trunk}$), and upper-trunk stem taper rate ($p_{upper\ trunk}$).

Tree	Location, accession number	Stump diameter (cm)	Height from trunk base to breast height (cm)	Diameter at breast height, DBH (cm)	Stem length from DBH to 400 (cm), $h_{mid\ trunk}$	Diameter at 4-m height mark (cm)	Stem length from 4-m height mark to top of tree (cm), $h_{upper\ trunk}$	Diameter at top of tree (cm)	Maximum preserved length (fossil tree) or total estimated height (living tree) (m)	Stump taper rate, p_b	Stem taper rate from DBH to 3 or 4 m, $p_{mid\ trunk}$	Stem taper from 4 m to top of tree, $p_{upper\ trunk}$
Tree A	Howe-Stephens Quarry	189	130	152	270	89	324	85	7.24	-0.28	-0.23	-0.01
Tree B	Howe-Stephens Quarry	128	130	117	270	109	422	80	8.22	-0.08	-0.03	-0.05
Araucaria araucana	*Magnolia* Garden, 3980-00-1979/2	43	130	34	270	24	Not measured	Not measured	14.6	-0.07	-0.04	Incalculable
Araucaria araucana	*Magnolia* Garden, 09735	56	130	32.5	270	21	Not measured	Not measured	12	-0.18	-0.04	Incalculable
Araucaria araucana	*Magnolia* Garden, 07163	35.7	130	31.2	270	25	Not measured	Not measured	9.2	-0.03	-0.02	Incalculable
Araucaria araucana	Mesozoic Forest, 11995-9-1920	60.5	130	48.4	270	41	Not measured	Not measured	17.1	-0.09	-0.03	Incalculable
Araucaria araucana	Nees Institute parking lot, shorter tree	30.2	130	19.4	270	10.5 (at base of crown)	Not measured	Not measured	5.05	-0.08	-0.05	Incalculable
Araucaria araucana (tree since cut down)	Nees Institute parking lot, taller tree	38.2	130	23.9	270	19 (at base of crown)	Not measured	Not measured	8	-0.11	-0.02	Incalculable

(Richmond et al., 2019) and *Circoporoxylon bighornense* (Hoff, 2022; Hoff et al., 2025); and from South Dakota, *Cupressinoxylon jurassicum* (Lutz, 1930). Other wood genera (Richmond, 2023) reported as occurring in Montana, such as *Cupressinoxylon*, *Piceoxylon*, *Protocedroxylon*, and in western Oklahoma, such as *Xenoxylon*, *Cupressionoxylon*, and *Agathoxylon*, are not accepted here, but are still pending acceptance, as they have not yet been identified, fully described, and adequately figured in peer-reviewed publications.

There is only one minor difference between the *Agathoxylon hoodii* specimens from the 13 logs in Rainbow Draw and the 23 wood specimens of *A. hoodii* from the Howe-Stephens Quarry. The Rainbow Draw wood appears to contain a greater number of resin plugs or resinous remains, especially in the ray cells. Differences in resin abundance were also already noted by Gee et al. (2019) when comparing the Rainbow Draw wood flora with the holotype specimen from Mt. Ellen (cf. Tidwell and Medlyn, 1993). However, because a scantiness or absence of organic deposits such as resin plugs is not diagnostic for systematic identification (IAWA Committee, 2004), all fossil wood specimens from the Howe-Stephens Quarry should be considered as pertaining to *A. hoodii.*

PALEOBIOGEOGRAPHIC EXTENT OF *AGATHOXYLON HOODII*

The identification of *Agathoxylon hoodii* wood in the Howe-Stephens Quarry flora expands the paleobiogeographic range of the species to north-central Wyoming (Figure 9, yellow star). This new occurrence is ca.

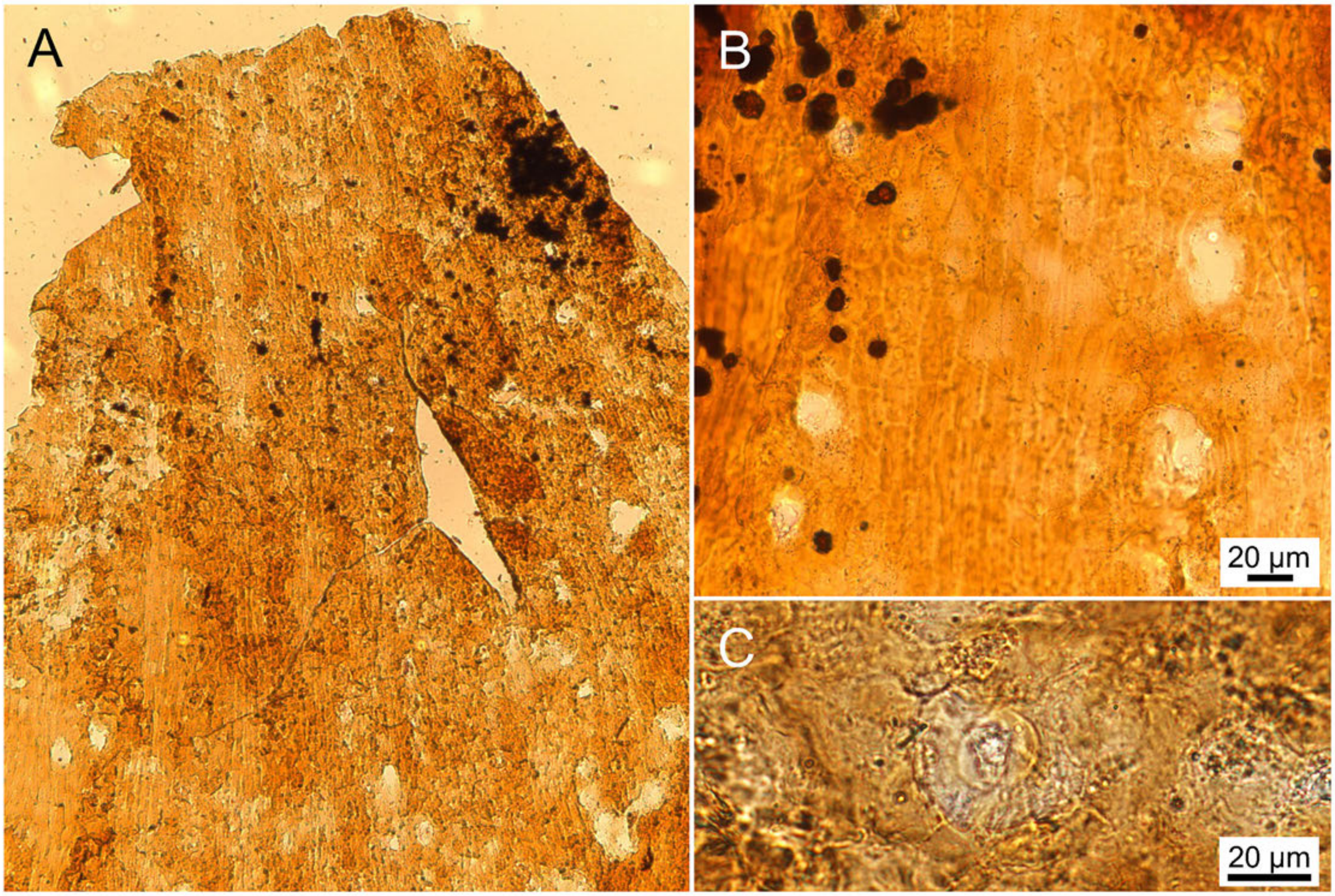

Figure 8. In situ cuticle from a twig bearing *Brachyphyllum*-type leaves from the Howe-Stephens Quarry. (A) Cuticle from near the leaf apex, showing the general pattern of longitudinal files of stomata. (B) Close-up of A, showing the arrangement of stomata in longitudinal files. The actual stomatal apparatuses are not preserved, but are represented by holes in the tissue. Note the rectangular epidermal cells between the lines of stomata. (C) One stomatal apparatus complete with a central stoma, a pair of guard cells, and a single ring of subsidiary cells.

1000 km northeast from where it was last described at Rainbow Draw in northeastern Utah (Figure 9, orange star) and ca. 1600 km away from its type locality on Mt. Ellen (Figure 9, green star). Recently, another well-preserved specimen of *Agathoxylon hoodii* has been identified (Gee, unpublished data) from a new fossil log and dinosaur locality called the Tal Site log assemblage (Figure 9, blue star) in southern Utah (John R. Foster, Utah Field House of Natural History State Park Museum, written communication to CTG, 2024). This makes for a current total of four occurrences in the Morrison Formation, from what is today north-central Wyoming to the north, to southeastern Utah to the south.

Among all fossil wood species described from the Morrison Formation so far, *A. hoodii* appears to have the widest paleobiogeographic extent known to date and thus may have comprised a sizeable part of the conifer forests in the central Morrison Formation during the Late Jurassic. Hence, it would not be surprising if the fossil wood species *Agathoxylon hoodii* or the fossil seed cones *Araucaria delevoryasii* were to show up in deposits of the Morrison in western Colorado sometime in the future.

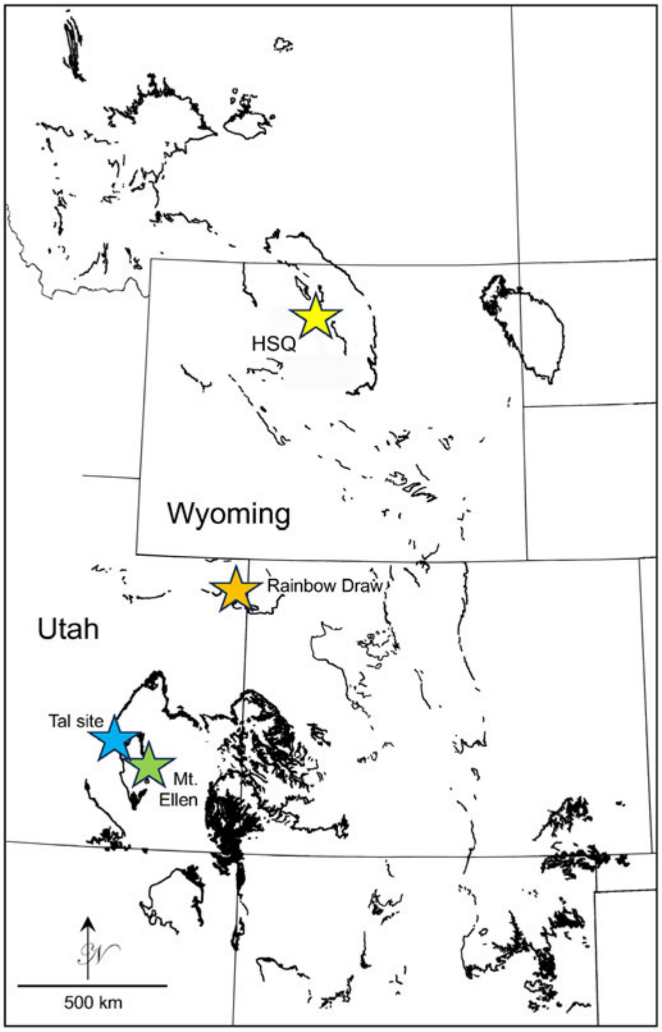

Figure 9. Occurrences of *Agathoxylon hoodii* (stars) in the Upper Jurassic Morrison Formation. Color key: yellow = Howe-Stephens Quarry (HSQ, this study), orange = Rainbow Draw (Gee et al., 2019), blue = Tal Site (Gee, unpublished data), and green = Mt. Ellen (Tidwell and Medlyn, 1993). Map of Morrison Formation outcrops (black) courtesy of Kenneth Carpenter, Museum of Natural History, University of Colorado.

THE WHOLE PLANT OF *AGATHOXYLON HOODII*/*ARAUCARIA DELEVORYASII*

Virtually all specimens in the coalified compression flora from the Howe-Stephens Quarry were previously recognized as the associated plant organs of a whole-plant *Araucaria* (Gee and Tidwell, 2010). These organs consisted of the mature and immature seed and pollen cones, detached seed scales, isolated seeds, as well as branches and twigs with *Brachyphyllum*-type scale leaves. Whereas hundreds of individual compression specimens were excavated from the Howe-Stephens Quarry, the biodiversity of the compression flora is extremely low, because nearly all of these specimens represent just a single species, *Araucaria delevoryasii*.

In 2010, most of the fossil plant material from the Howe-Stephens Quarry that was not considered as belonging to this whole-plant species were the many pieces of silicified wood and the coalified tree trunks because they had not yet been studied. However, now that our current investigation has identified the silicified wood as pertaining to the Araucariaceae and that the morphology and taper of the two coalified trunks in the quarry are consistent with living *Araucaria* trunks, the likelihood of the fossil reproductive material, foliage, wood, and tree trunks representing the different parts of the same Upper Jurassic plant species is high.

Given the intimate association of the abundance of silicified wood and huge numbers of seed cones, seed cone scales, seeds, pollen cones, and twigs with leaves bearing cuticle, and the two giant tree trunks, as well as the extremely low paleobotanical diversity known from the Howe-Stephens Quarry, it is extremely likely that the compression fossils and silicified wood all represent various parts of the whole plant consisting of *Araucaria delevoryasii* and *Agathoxylon hoodii*, which should be known hereafter as the *Araucaria delevoryasii* tree.

HABITAT OF THE *ARAUCARIA DELEVORYASII* TREE

Because the fossiliferous sandstone lens at the Howe-Stephens Quarry was interpreted as channel-fill deposits of a point bar sequence (Ayer, 2000), the abundance of conifer compression and wood fossils in this horizon suggests that *Araucaria delevoryasii* trees grew alongside this meandering river. That they were rooted directly on the riverbanks is suggested by the abundance of intermixed conifer cones and twigs all through the sandstone layer, which likely dropped directly into the river from overhanging branches, then were transported by water. The occurrence of two large fossil tree trunks replete with their respective rootstocks in the Howe-Stephens Quarry also offers more evidence that *Araucaria delevoryasii* trees were likely rooted directly at the edge of the river, since these trees must have grown close enough to the river channel that they could slide into the river as entire trees once the riverbank substrate where they grew was eroded away.

OLD-GROWTH *ARAUCARIA* FORESTS IN THE MORRISON FORMATION

The preserved diameters of 152 cm and 117 cm at DBH of the two tree trunks in the Howe-Stephens Quarry and their minimum reconstructed heights of 74 to 78 m and 64 to 65 m, respectively, confirm the presence of old-growth forest trees in the Morrison Formation of what is today Wyoming. Based on their sizes, these two *Araucaria delevoryasii* trees were likely some of the largest trees in the Morrison forest. In the neighboring state of Utah, the five silicified logs of *A. hoodii* with preserved diameters ranging from 71 to 127 cm (Gee et al., 2019) were estimated to have reached minimum heights between 45 to 69 m (Xie et al., 2024).

In the present-day world, old-growth forest trees of *Araucaria* have been found to possess a DBH ranging from 150 to 300 cm and to attain heights from 50 to 90 m (Eckenwalder, 2009). These include the species *A. hunsteinii*, *A. cunninghamii*, and *A. heterophylla* in Australasia and *A. angustifolia* and *A. araucana* in South America. In Australia and Papua New Guinea, large trees of *A. cunninghamii* D. Don range from 120 to 174 cm at DBH and reach heights up to 71 m, whereas those of *A. hunsteinii* K. Schumann measured 120 to 136 cm at DBH and attained even greater heights up to 89 m (Gray, 1975).

Of the living species of *Araucaria*, the *A. angustifolia* trees in the Brazilian Atlantic forests have probably received the most attention, due to its critically endangered species status, the number of giant trees now being limited to 21 individuals (Scipioni et al., 2019). Here, the giant trees of *A. angustifolia* have very wide trunks with a DBH extending from 160 to 325 cm; many of these trees reached a total height of 40 m (Scipioni et al., 2022), with an average of 38.4 m. It should be noted, however, that *A. angustifolia* trees tend to be relatively stout morphologically (Table 4), compared to other species of *Araucaria*.

Old-growth *Araucaria* trees in living forests have specific structural characteristics associated with their trunks, such as basal cavities, regenerated branches, and new trunk growth (Scipioni et al., 2022). Basal cavities, for example, are usually found in giant trees of *Araucaria angustifolia* that have a DBH exceeding 150 cm. These cavities can measure between 1 to 2 m wide and can extend over 4 m into the height of the inner tree trunk. Trunk cavities in such large, old trees offer forest inhabitants shelter and are thus of high ecological value for wildlife. The decay of wood tissue is most commonly carried out by fungi (e.g., Schwarze et al., 2000; Zabel and Morrell, 2020), although considerable damage can also be caused by wood-boring insects. All three genera of living Araucariaceae trees are prey to a wide array of diseases and pathogens (Balocchi et al., 2022).

Large trunk cavities were not observed in the Howe-Stephens Quarry trees, nor in the fossil logs at Rainbow Draw, although silicified wood in the Morrison Formation in both Utah and Wyoming show evidence of ancient fungal degradation and insect activity. In Utah, a fossil log of *Agathoxylon hoodii* in Rainbow Draw, which likely attained heights of 68 to 72 m, shows evidence of wood-boring beetles and parasitic white-rot wood-decay fungus (Gee et al., 2022). A fossil log of *Xenoxylon utahense* in nearby Miners Draw, Blue Mountain, which has a diameter of 90 cm, contains the fossil hyphae of saprophytic white-rot fungi (Xie et al., 2023). The more poorly preserved wood of *A. hoodii* from the Howe-Stephens Quarry exhibits considerable cellular damage from what was likely ancient white-rot fungi (Gee, unpublished data).

The fossil trunks of *Agathoxylon hoodii* at the Howe-Stephens Quarry in Wyoming and Rainbow Draw in Utah clearly represent the remains of 150-million-year-old giant trees, but the araucarian forests of the Morrison Formation were certainly comprised of younger trees as well. The Morrison forests likely con-

Table 4. Size comparison of fossil *Agathoxylon hoodii* and living *Araucaria* trees in regard to DBH and height.

Fossil *Agathoxylon hoodii* or living *Araucaria* spp.	DBH or maximum preserved diameter (cm)	Reconstructed height of fossil trees or measured height of living trees (m)	References
HSQ trees A, B	152, 117	Up to 78, 65	This study
Rainbow Draw, 5 logs	71–127	45–69	Gee et al., 2019; Xie et al., 2024
A. cunninghamii	120–174	Up to 71	Gray, 1975
A. hunsteinii	120–136	Up to 89	Gray, 1975
A. angustifolia	160–325	Up to 45	Scipioni et al., 2022

sisted of a healthy, multi-generational population of trees that included several large and venerable trees, as it has been suggested for the Escalante Petrified Forest State Park in southern Utah (Gee et al., 2023; Morgan et al., 2024).

CONCLUSIONS

We describe here a new whole plant of *Agathoxylon hoodii* (Tidwell et Medlyn) Gee, Sprinkel, Bennis et Gray and *Araucaria delevoryasii* Gee from the Upper Jurassic Morrison Formation of the Howe-Stephens Quarry on Howe Ranch in north-central Wyoming. The whole plant should be referred to as the *Araucaria delevoryasii* tree. It is the first whole plant from the Morrison and is known through anatomically preserved wood, coalified compressions of seed cones, detached seed scales and abscised seeds, pollen cones, branches with *Brachyphyllum*-type leaves, and giant coalified tree trunks. The silicified wood of *Agathoxylon hoodii* occurring in the Howe-Stephens Quarry is identified and described in detail, which occurs intermixed with araucarian fossil compressions in a prolific dinosaur bonebed.

The fossil plant assemblage also includes two enormous coalified tree trunks, which provide data on the gross morphology, size, and taper of the Upper Jurassic *Araucaria* trees. According to height–diameter models, these two ancient trees reached heights between 64 to 78 m, comparable to those of living *Araucaria* trees, and had a stem taper that is also similar to that of present-day araucarian species. The *Araucaria delevoryasii* tree was likely rooted directly on the riverbanks of a meandering river. Paleobiogeography of *Agathoxylon hoodii* wood in what is today north-central Wyoming and southern Utah documents the widest extent of all wood species in the Morrison Formation. Based on its size and paleobiogeographic range, the *Araucaria delevoryasii* tree was likely the largest tree that flourished in widespread, old-growth conifer forests in the central Morrison Formation.

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