THE LYCOPSID *SIGILLARIA BRARDII* BRONGNIART FROM THE LATE PENNSYLVANIAN TINAJAS MEMBER, ATRASADO FORMATION, SOCORRO COUNTY, NEW MEXICO

WILLIAM A. DIMICHELE[1], SPENCER G. LUCAS[2], and SUSAN K. HARRIS[2]

[1]Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, email: dimichel@si.edu; [2]New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104

Abstract—Excellent specimens of *Sigillaria brardii* were found in place on the surface of shale in Upper Pennsylvanian (Missourian) strata of Socorro County, New Mexico. Poor quality specimens have been reported from the Upper Pennsylvanian of New Mexico earlier, on at least two occasions. The current specimens, preserved in ironstone, reveal fine details of the stem surface. Given the large plant-fossil collections that have been made from the Pennsylvanian strata of Socorro County, the rarity of this plant is unusual and may reflect a scarcity of wetland habitat conditions in the region. *Sigillaria brardii* is the only arboreous lycopsid reported from Upper Pennsylvanian strata in equatorial latitudes of Euramerican Pangea, from the Appalachian coal basin to areas lacking coal in the western parts of the paleocontinent following the disappearance of other kinds of lycopsid trees at the Desmoinesian-Missourian stage boundary.

INTRODUCTION

The arborescent lycopsids were an important part of wetland ecosystems throughout the Late Mississippian to the Middle Pennsylvanian in most areas of equatorial Euramerica, from the Donets Basin of the Ukraine in the east to the western parts of the paleocontinent (Thomas, 2007; Thomas et al., 2019; DiMichele and Phillips, 1985; Phillips and DiMichele, 1992; Lucas et al., 2009). Most species of these plants disappeared from the Appalachian basin westward at the Middle-to-Late Pennsylvanian boundary (Phillips et al., 1974; Kosanke and Cecil, 1996; DiMichele and Phillps, 1996; Peppers, 1997); a few species have been reported from Central Europe (Opluštil et al., 2022), but their occurrences are uncommon. Although other causes for this dramatic event have been proposed, it is almost certainly due to climate change (Phillips and Peppers, 1984; Cecil, 1990), which is the only mechanism with a broad enough coverage to account for the widespread simultaneity of the loss of so many wetland species, not simply the arboreous lycopsids.

One lycopsid taxon that survived this event is *Sigillaria* Brongniart, and of the many species of that genus described in the paleobotanical literature, only *Sigillaria brardii* Brongniart is known from Euramerica. Other species have been reported from China (D'Antonio et al., 2021). *S. brardii*'s survival may be attributable to unique modifications of its rooting system, *Stigmaria*, which, in addition to having the broad, shallowly penetrating axial system characteristic of this organ system (Thomas and Seyfullah, 2015; Hetherington et al., 2016; DiMichele et al., 2022; D'Antonio et al., 2024), also had specialized descending rhizomorphic axes that appear to have allowed plants to access water sources located more deeply in the soil than those accessible to the usual array of shallow roots (Pfefferkorn and Wang, 2009; Chen et al., 2022).

We report some exceptionally well preserved impressions of the surface bark of *Sigillaria brardii* from Late Pennsylvanian age strata in central New Mexico. Although not the first report of this plant in far western Pangea (e.g., Schachat et al., 2023; DiMichele et al., 2024), it is, to our knowledge, the first unambiguous report of the plant and documents its occurrence at a time and place when regional climatic conditions were semi-arid to dry subhumid (terminology of Cecil, 2003).

GEOLOGY

The specimens under consideration were collected in Socorro County, central New Mexico on March 22, 2024. The site is designated New Mexico Museum of Natural History and Science Locality 9096 (Fig. 1). Exact coordinates of the locality are on file and will be supplied to qualified researchers upon request.

The plant remains were found in an organic shale. The shale also contains abundant siderite nodules of various sizes, although plant remains were not found in the nodules. Also found were other types of plant axes and coprolites. The organic shale likely originated as a lake or embayment. The fossiliferous deposit is 3 m thick and coarsens upward from a dark, non-silty shale at the base to a silty olive shale at the top.

Stratigraphically, the shale bed is located in the middle Tinajas Member of the Atrasado Formation. It is stratigraphically above the much more extensive black shale lake deposit of the Tinajas Member (Lerner et al., 2009) and represents a similar, but much more localized depositional system. Conodont studies of the carbonate beds exposed in this area indicate that the deposit is middle Missourian (Kasimovian) in age (Barrick et al., 2013).

DESCRIPTION

Three of the *Sigillaria* specimens are illustrated in Figures 2-4. The specimen illustrated in its entirety in Figure 2, in particular, shows nearly undistorted fine details of the stem surface. The details can be seen more fully in Figure 3. Details are somewhat distorted in the specimen illustrated in Figure 4A; the specimen in Figure 4C was photographed in the field. Several other specimens also were found at this site and a nearby location, but do not preserve the level of detail seen here.

Specimen NMMNHS P-98270 (Figs. 2 and 3) demonstrates that the leaf bases of *Sigillaria brardii* are quadrilateral with rounded corners and reflection symmetry across the median vertical axis. This is a shape typical of many arboreous lycopsids. Phylogenetic studies have shown this shape to be a plesiomorphic/primitive characteristic of the broader group, which includes the Sigillariaceae (Bateman et al., 1992; Bateman, 1994). The stigmarian lycopsids are distinguished from the cormose based Isoetales, which may be their sister group, both originating in the Devonian (e.g., Chitaley and Pigg, 1996; Stein et al., 2020). As part of this typical leaf base shape, the cushions also display a clearly marked lower keel (Fig. 3, LK) with horizontal wrinkles. This keel is somewhat protuberant and has been made prominent by flattening. Above the leaf scar there also is a short keel. This upper keel is rounded, rather than sharply ridge-like, and forms a slight hood over the top of the leaf scar.

Characters that distinguish *Sigillaria* from other lycopsids

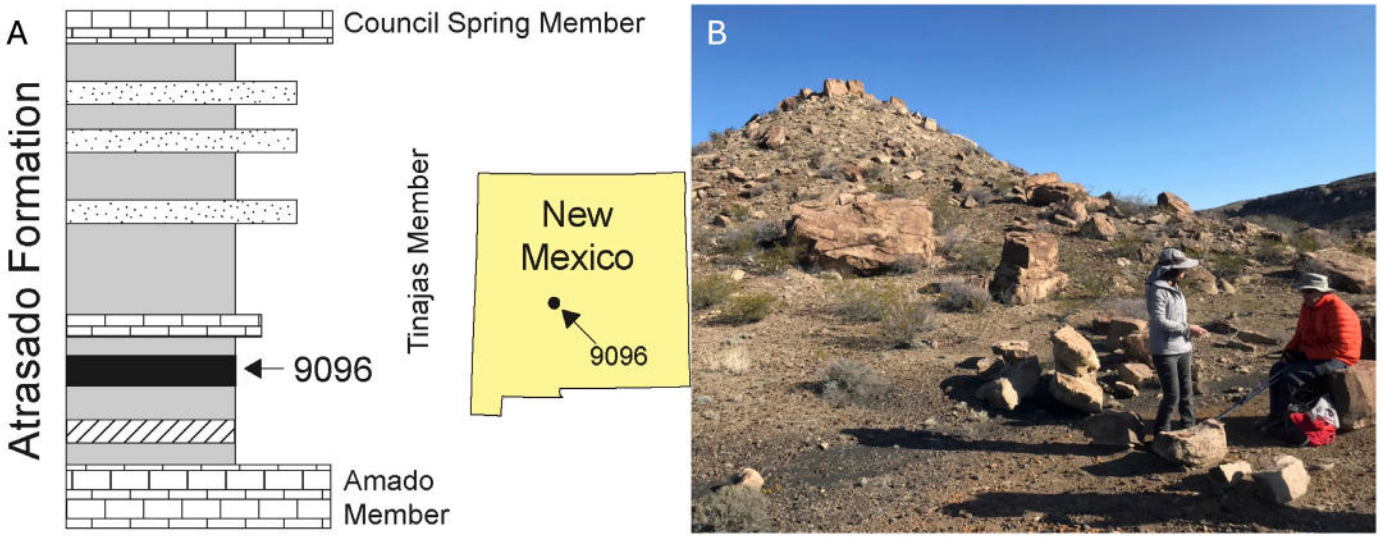

FIGURE 1. New Mexico Museum of Natural History and Science Locality 9096. **A,** Location map and stratigraphic position of locality 9096 in Missourian interval of Atrasado Formation in central New Mexico. Lithology schematic/generalized; total Tinajas Member thickness is about 80 m. **B,** Outcrop of the Tinajas Member of the Atrasado Formation, Missourian, Upper Pennsylvanian.

FIGURE 2. Iron permineralized surface of a *Sigillaria* stem, likely *S. brardii*. NMMNHS Specimen P-98270. Scale bar = 1 cm.

FIGURE 3. Enlargement of a portion of specimen P-98270 showing details of the leaf bases/cushions, particularly emphasizing their quadrilateral shape, typical of most arborescent lycopsids, and features such as the Lower Keel (LK) which has transverse wrinkles. The leaf scar is typically sigillarian in shape. Note lunate parichnos strands (PR) lateral to the leaf trace (LT), and the ligule pit aperture (LP) at the top of the scar. Scale bar = 1 cm.

can be seen most clearly in the leaf scars. These scars also have a more or less distorted quadrilateral shape, like the leaf cushions, but with rounded angles. They are approximately 25% greater width (horizontal axis) than length (vertical axis). The base of a scar is placed approximately at the vertical center of the leaf base. Scars are notched at the top, which presumably indicates the opening of a ligule pit (Fig. 3, LP). Also, as is typical of *Sigillaria*, the leaf trace (Fig. 3, LT) is a distinct, horizontally elongate mark on the center vertical axis of the scar above the midpoint. *Sigillaria* leaves are double veined, and the traces are V-shaped when viewed in anatomical transverse section, which may be consistent with the width of the vascular trace. Also typical is the shape and placement of the parichnos strands (Fig. 3, PR). These are arcuate, concave toward the leaf trace, and flank the trace at its horizontal level and slightly above. The scars clearly illustrate the low helix of the leaf-base distribution.

DISCUSSION

Sigillaria brardii is a common plant in wetland deposits of Late Pennsylvanian and early Permian age in central Pangea. It

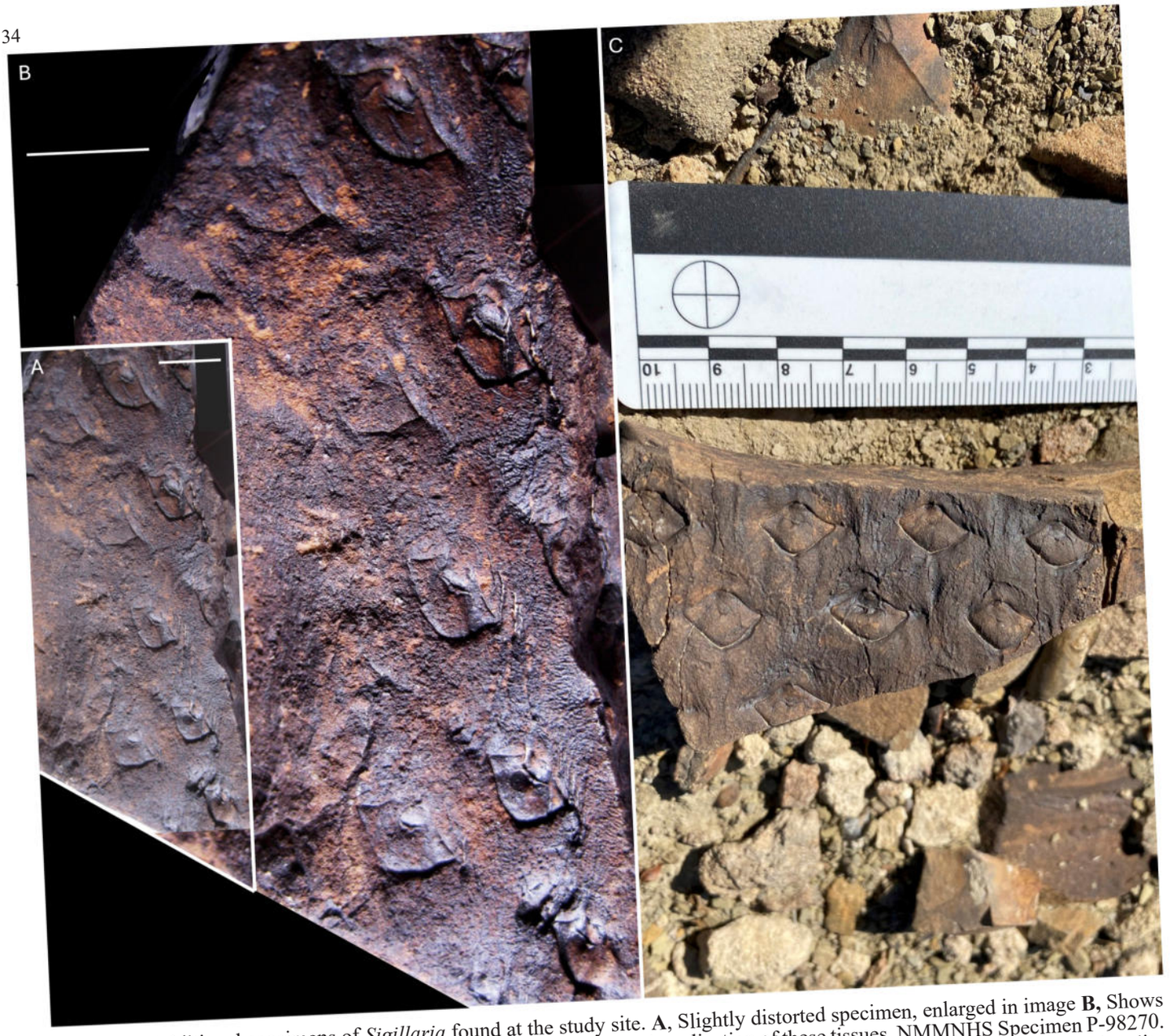

FIGURE 4. Additional specimens of *Sigillaria* found at the study site. **A**, Slightly distorted specimen, enlarged in image **B,** Shows the thickness and protrusion of the leaf bases. This indicates early permineralization of these tissues. NMMNHS Specimen P-98270. **C,** Counterpart of specimen P-98270 preserved as an impression. The resulting stem surface lacks the degree of three dimensionality of the part, deemphasizing the larger shape of the leaf base/cushion and its details, such as the prominent wrinkled keel. Scale bars = 1 cm.

occurs commonly in western Pangea as far west as Texas and Oklahoma, particularly in organic shales (DiMichele et al., 2005; Looy and Hotton, 2014). It is not common farther to the west in areas we have studied in New Mexico, Arizona, and Utah, although it has been reported there in macrofloras (DiMichele and Chaney, 2006; DiMichele et al., 2013, 2017, 2024) and palynofloras (Willard, 1992), where it is most common in allochthonous assemblages, often in strata interpreted as lakes or lagoons.

Our intention in this paper has been to document particularly well preserved impressions of *Sigillaria*, in this case found in an organic-rich shale, but one formed as a lake or coastal embayment, and in which all the plant remains are allochthonous. The detail of these specimens leaves no doubt as to their identification as *Sigillaria*, and most likely *S. brardii,* a member of the Subsigillaria subgroup. They reveal, however, that the leaf scars are borne on leaf bases not unlike those found on other kinds of arboreous, rhizomorphic lycopsids. This gross morphology is very different from that found in many *Sigillaria* specimens, particularly those of the Eusigillaria group, where the helices of leaf scars lead to the distribution of those scars in longitudinal columns, with the leaf scars often tightly packed with only very limited, surrounding "cushion" tissues.

Sigillaria occurs in far western Pangea as part of wetland plant associations that, based on geological context, appear to have occupied the marginal areas of streams and lakes where soil moisture may have been high. These floras often are mixed with more xeromorphic plants inferred to have occupied areas with soil moisture fluctuations (Bashforth et al., 2021). The floras from Promontory Butte, Arizona (DiMichele et al., 2024) and Valley of the Gods, Utah (DiMichele et al. 2014) may be the best examples, and appear to be confined to narrow portions

of the landscape, bordering streams, lakes, lagoons, and other such bodies of water, where local water tables might have been elevated. The often "mixed" character (sensu Bashforth et al., 2021) of these floras, containing well preserved remains of drought-tolerant, xeromorphic plants, such as conifers, indicates the derivation of all the plant remains from the local vegetation. The xeromorphic forms did not arrive via long distance transport from far-off uplands. A further interpretation, based on these patterns, is that the regional climate was seasonally dry and that the xeromorphic elements occupied most of the landscape.

The presence in these semi-arid to arid, western Pangean landscapes of wetland plants typical of central Pangean coal basins is consistent with the low diversity of late Paleozoic tropical wetland floras compared to what is seen today or even in the Late Cretaceous and Cenozoic (e.g., Wing and DiMichele, 1995; King et al., 2011; Cleal et al., 2012). The wetland species pools of the time were small and regionally homogeneous. The occurrence of the same species of marattialeans, calamitaleans, sigillarian lycopsids, and pteridosperms in central and western Panegean wetlands may be due to several factors, keeping in mind that the Pangean tropics were subjected to the climatic variations accompanying glacial-interglacial cycles (e.g., Heckel, 2008; Eros et al., 2012; Cecil et al., 2014; Laurin et al., 2024; Opluštil et al., 2024) and that in western Pangea all parts of cycles were drier than in the more central regions, indicated by the lack of coal and the presence of evaporites and eolian deposits.

The most important factor in floristic homogeneity across vast geographic extent may be the phenomenon of "few players in the game", so to speak, that is the relatively low diversity of the wetland floras on all spatial scales. Secondly is the connectivity created by the Pangean supercontinent. Although there were mountainous areas in the central and western parts of the continent, there still was a continuous land surface that permitted a great deal of species exchange. Such barriers as there were had effects on species migration patterns and stratigraphic ranges in different regions (e.g., Laveine et al., 1993; Blake and Gillespie, 2011; Bashforth et al., 2016), but floras nonetheless maintained continuity across broad areas.

Given climate cyclicity in the equatorial latitudes, and the more extreme climate conditions in western than in central Pangea, how did the wetland elements remain important in the more western regions of the continent? There are several possibilities. The wetland species may have persisted as isolated populations in refugial areas during the most unfavorable periods, reemerging as wetter conditions returned. They also may have disappeared completely from the west, a not unlikely scenario given how arid some areas became (e.g., Cecil et al., 2003; Jordan and Mountney, 2012), returning via dispersal along corridors that reappeared during the wettest parts of the glacial-interglacial cycles. A third possibility, particularly in the case of marattialean tree ferns and calamitaleans, is long-distance dispersal, made possible by their homosporous reproduction; these plants may have been able to reach widely separated sites with high soil moisture from which further rapid colonization occurred in a series of step-like founder events. Perhaps the closest comparison to this phenomenon is the recovery of ecosystems following the retreat of glaciers, a subject of intensive current study (e.g., Ficetoia et al., 2021 for a review), although the patterns resulting from tropical wet-dry and warm-cold cycles might be expected to differ in the importance of the variables at play from recolonization of an entirely denuded landscape.

Sigillaria brardii may have been among the species of the genus with rooting systems, as noted above, that permitted it to survive under conditions of periodic drought. As such, it represents one of the few arboreous lycopsids capable of escaping the constraints, likely imposed by the stigmarian rooting system, requiring soft, wet substrates. Of all the plants found in later Pennsylvanian and Permian western Pangean landscapes, this may be, as an arboreous lycopsid, one of the most exceptional, an ecological outlier among the clade as a whole.

If small, isolated populations of the above mentioned wetland plants did colonize small parts of western Pangea or persist in such areas while surrounded by large areas of unfavorable conditions, why do the species (recognizing that they are strictly "morphospecies") persist with such low rates of turnover? There seems to have been little evolutionary innovation despite temporal changes in the sizes and distributions of their basic habitat. One reason to consider is that, with the exception of the pteridosperms, the other major groups were either wind pollinated, wind dispersed, or both. This would apply, as well, to those taxa that had water-dispersed propagules, a portion of their life cycle nonetheless involving wind. This reproductive biology may have proven key to maintaining connectivity between otherwise physically isolated populations, keeping gene flow and heterozygosity high enough to swamp out the establishment of variation and thus suppress the appearance of morphological novelties (new species).

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