

Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biome

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ABSTRACT

Pennsylvanian fossil forests are known from hundreds of sites across tropical Pangea, but nearly all comprise remains of humid Coal Forests. Here we report a unique occurrence of seasonally dry vegetation, preserved in growth position along >5 km of strike, in the Pennsylvanian (early Kasimovian, Missourian) of New Mexico (United States). Analyses of stump anatomy, diameter, and spatial density, coupled with observations of vascular traces and associated megafloora, show that this was a deciduous, mixed-age, coniferopsid woodland (~100 trees per hectare) with an open canopy. The coniferopsids colonized coastal sabkha facies and show tree rings, confirming growth under seasonally dry conditions. Such woodlands probably served as the source of coniferopsids that replaced Coal Forests farther east in central Pangea during drier climate phases. Thus, the newly discovered woodland helps unravel biome-scale vegetation dynamics and allows calibration of climate models.

INTRODUCTION

Pennsylvanian fossil forests, preserved in growth position, are common in Europe and North America. Generally, they comprise upright stumps of lycopsids and calamitaleans, together with rare tree ferns, pteridosperms, and cordaitaleans (DiMichele et al., 2007), and represent remains of humid tropical vegetation (Coal Forests). Such fossil forests shed light on tree density, canopy structure, spatial heterogeneity, and ecological gradients of ancient vegetation (DiMichele and Falcon-Lang, 2011), phenomena that cannot be assessed in any other way.

In contrast to the humid Coal Forests, vegetation of the seasonal tropics is poorly known, despite being inferred to cover vast areas of western Pangea (Tabor and Poulsen, 2008). Limited reports indicate that conifers, cordaitaleans, and pteridosperms dominated these regions while pteridophytes were rare (DiMichele et al., 2001). Here we report the first example of an extensive fossil forest from the Pennsylvanian seasonal tropics that sheds light on ecology and helps unravel biome-scale vegetation dynamics (Falcon-Lang et al., 2009).

GEOLOGICAL SETTING

The fossil forest is located ~10 km east-southeast of Socorro, New Mexico, United States (34°05'N, 106°48'W; Fig. 1A). It occurs in the lower part of the type section of the ~130-m-thick Tinajas Member of the Atrasado Formation, above the contact with the Amado Member (Lucas et al., 2009). Bracketing conodont assemblages indicate that the fossil forest is of early Missourian age (*Streptognathodus cancellosus* biozone), equivalent to the mid-Kasimovian stage (ca. 305 Ma; Heckel, 2008; Davydov et al., 2010; Fig. 1B), when Socorro was at a paleolatitude of ~2°S (Blakey, 2007).

Sedimentary Facies

We mapped the lowermost 15–20 m of the Tinajas Member across the study area and recognized two interdigitating facies associations (Fig. 2).

The first association comprises medium gray, laminated, skeletal wackestone, 0.1–0.3 m thick, containing productid brachiopods or cri-

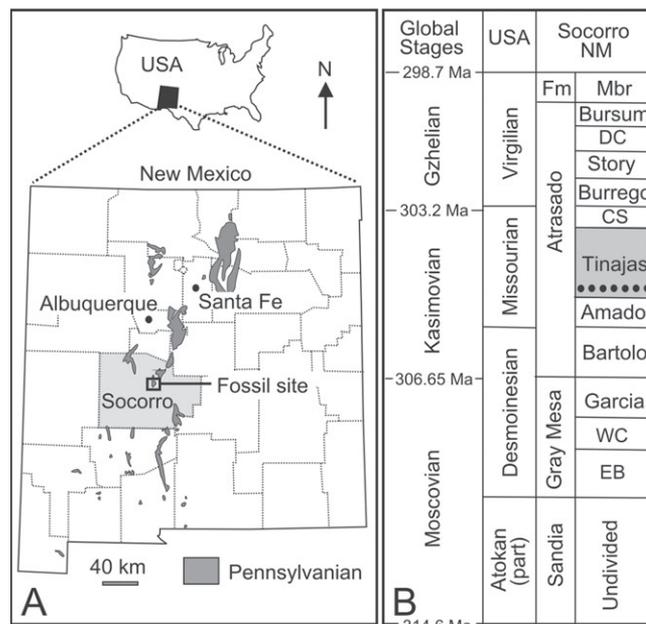


Figure 1. Location and stratigraphy. A: Location of fossil site in Socorro County, New Mexico (United States). B: Stratigraphic position of fossil site (black circles) in lowermost Tinajas Member (Lucas et al., 2009) calibrated against time scale of Davydov et al. (2010). Abbreviations: NM—New Mexico; Mbr—member; Fm—formation; EB—Elephant Butte; WC—Whiskey Canyon; CS—Council Spring; DC—Del Cuerto.

noids, nautiloids, bivalves, and gastropods (facies A1); medium gray lime mudstone, typically 0.1 m thick, silty, containing paraparchitacean ostracodes and small (<2 mm) cerithiid gastropods (A2); medium gray calcareous siltstone, ≤2.2 m thick, laminated, showing scours, symmetrical ripple marks, intraclasts, and rare *Planolites* burrows (A3); and channel fills, ≤3.5 m thick (width indeterminate), of dark gray shale containing nautiloids, pectenoids, conchostracans, ostracodes, insects, and plants (A4).

The second facies association comprises reddish-gray dolomite and limestone, <0.1 m thick, showing vuggy texture and a microbial fabric (facies B1); medium-gray lime mudstone, ≤1.7 m thick, but typically ~0.1 m thick, unfossiliferous, showing wavy lamination, prominent intraclasts with curled margins, desiccation cracks, nodular chert and, in thin section, a microbial fabric and calcitized gypsum pseudomorphs in discrete layers (B2); and beds of white and/or brown crystalline gypsum, locally >3 m thick, showing weak horizontal bedding, undulating lamination, or contorted bedding crosscut by veins (B3).

Paleoenvironmental Interpretation

The lowermost Tinajas Member is interpreted as a coastal sabkha deposit because of the co-occurrence of thinly bedded marine limestone, microbial limestone, and evaporites. Climate was, at times, sufficiently hot and seasonally arid to accumulate gypsum (Warren, 2006), and

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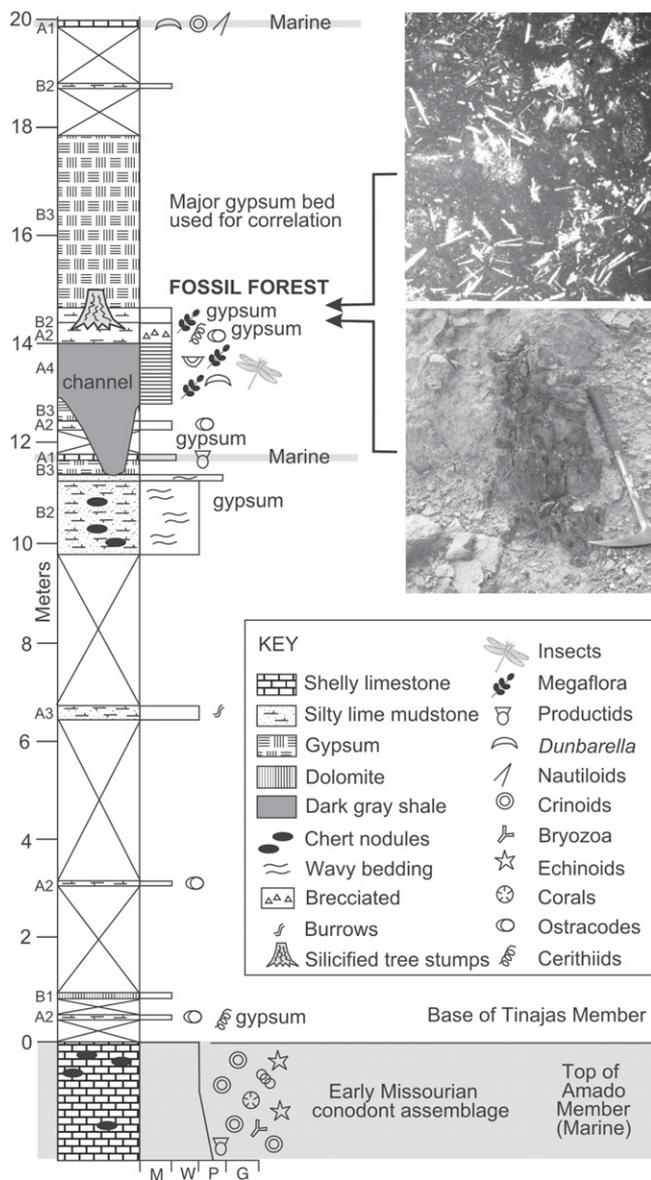


Figure 2. Sedimentary log through lowermost Tinajas Member showing sabkha facies associated with fossil trees in growth position at 14.5 m (center right; 40-cm-long hammer for scale). Trees are entombed in microbial laminites locally containing gypsum crystals (upper right, thin section; field of view is 4 mm wide). Abbreviations: M—mudstone, W—wackestone, P—packstone, G—grainstone, X pattern in column—covered interval. See text for explanation of facies codes (A1–4, B1–3).

such conditions prevailed throughout the southwestern United States, as inferred by the widespread occurrence of Pennsylvanian evaporites (Rueger, 1996), and climate model results (Tabor and Poulsen, 2008).

The first facies association is interpreted as representing the seaward side of the sabkha complex. Limestone with stenohaline fauna represents short-lived marine incursions. Limestone with paraparchitacean ostracode and cerithiid gastropod meiofauna is interpreted as the deposits of very shallow hypersaline embayments (Bennett, 2008), where grazing molluscs inhibited build-up of microbial mats. Calcareous siltstone with intraclasts and burrows represents very shallow to emergent coastal flats. Channels filled with dark shale containing euryhaline fauna represent dysoxic creeks that dissected the lower sabkha.

The second facies association is interpreted as representing the landward side of the sabkha complex. Vuggy dolomite and limestone with a

microbial fabric formed in peritidal embayments, where microbial mats developed in shallows too saline for grazing molluscs. Laminites with curled intraclasts and desiccation cracks formed as supratidal microbial mats, whereas local disruption by gypsum crystals indicates periodic hypersalinity. Thick beds of crystalline gypsum with microbial partings represent cycles of saline recharge and evaporation in ponds in the upper sabkha, where substantial evaporitic deposits precipitated (Warren, 2006).

FOSSIL FOREST

We identified fossil forests at 6 sites along >5 km of strike in the lowermost Tinajas Member (United States National Museum [USNM] localities 43466, 43468, 43473, 43476, 43490, 43491), one of which was previously noted in Tidwell et al. (2000; New Mexico Museum of Natural History [NMMNH] locality 4184; Fig. 3A). We infer this to be a single forest horizon because it is consistently underlain by the marine Amado Limestone (8–14 m below the fossil forest) and directly overlain by a 3-m-thick gypsum bed (by far the thickest in the section), which is a prominent marker bed used for correlation across the study area. However, continuity cannot be proven beyond a doubt because adjacent outcrop belts are disjunct.

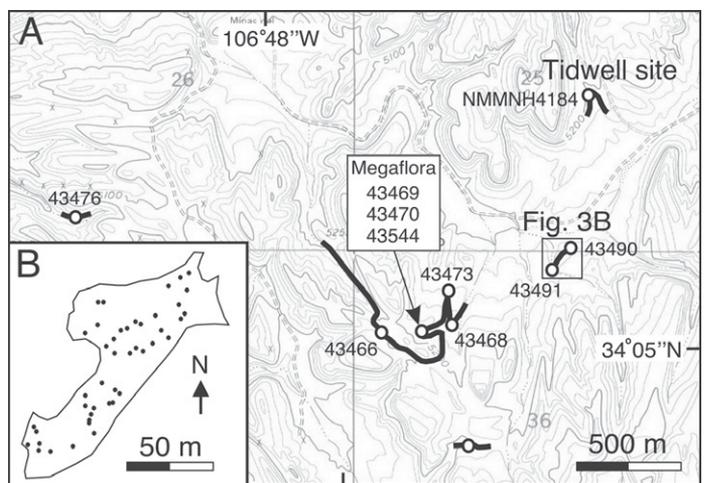


Figure 3. A: Map of fossil forest sites (United States Geological Survey topographic map, Loma de las Cañas 7.5 minute quadrangle). Dark lines indicate five areas with fossil trees (including site noted in Tidwell et al., 2000), whereas sixth is 2 km due west. B: Distribution of 39 fossil tree stumps on 0.38 ha dip-slope exposure.

Field Observations of Tree Stumps

Nearly all the large fossil wood specimens observed are tree stumps in growth position (≤ 0.84 m diameter, ≤ 0.67 m high). Most large fragments, no longer in place, also bear features consistent with tree stumps (i.e., basal flare, anastomosed tracheids, attached roots). Only a few specimens demonstrably represent horizontal (prone) tree trunks that lay on the forest floor; among these, the largest is ~ 0.3 m in diameter and 2.8 m long.

The relationship of the tree stumps to bedding is best seen in vertical profile at five of the sites. Here, stumps are rooted in, and entombed by, a ≤ 0.67 -m-thick succession of cherty microbial laminites containing gypsum pseudomorphs with bedded gypsum below and above. The stumps are typically subvertical to bedding ($\sim 70^\circ$ – 85°) with large subhorizontal primary roots (≤ 0.22 m diameter), which may be traced laterally between beds of microbial laminite, in one example for 1.1 m. Secondary roots, where seen, are 10–15 mm in diameter, and root traces weakly disrupt microbial laminae to a depth of 0.1–0.3 m below the stump base. Where exposed in plan view, roots compose horizontal bifurcating systems. Apart from root traces, microbial laminites show no discernible alteration.

Stumps are 0.08–0.84 m (mean 0.34 m, $n = 58$) in diameter; 52% are in the 0.15–0.30 m range, the remainder being evenly distributed through the other size classes. Most stumps are preserved to a height of 0.21–0.35 m, projecting just above the level of the enclosing microbial laminites. Others, visible at the edge of gypsum outcrops, attain heights of ≤ 0.67 m, terminating within the overlying gypsum bed, which suggests that those terminating at the top of the laminites also likely projected into the gypsum prior to its modern erosional removal. One stump bifurcates at its base and may represent a forked trunk, or two closely adjacent trees.

On a single dip-slope exposure, 39 stumps were counted on an ~ 0.38 ha surface (Fig. 3B), together with 6 prone logs, and positioned using a global positioning system (NAD83 datum). Discarding prone material, this equates to a density of ~ 102 trees per hectare. Spatial analysis (method of Hayek and Buzas, 1997) indicates that trees are randomly distributed. For the five vertical profiles, stump spacing was measured along crop lines. Mean tree spacing for the two longest transects was 10.68 ($n = 7$) and 11.81 m ($n = 10$), which approximates a density of 101 and 83 trees per hectare, respectively.

Stump Anatomy

The anatomy of 6 well-preserved stumps, silicified by length-slow chalcedony, was studied in detail (NMMNH P-29433, P-60590–P-60594). Features include a septate pith, 11–19 mm in diameter (Fig. 4A), bordered by < 7 rows of rectangular parenchyma cells, and a nonsymptodial vasculature comprising mesarch cauline bundles (Figs. 4B and 4D). Vascular

traces, ~ 350 μm in diameter, are helically arranged (phyllotaxis could not be determined), and abruptly occluded by parenchyma at the first tree-ring boundary (Fig. 4E).

The juvenile secondary xylem (< 10 mm from pith) comprises tracheids 24–33 μm (mean 27.11 μm) in diameter showing dominantly contiguous (81%), alternately arranged circular pits, which are either uniseriate (79%) or 2–3 seriate (21%). Rays are uniseriate, 1–10 cells high (mean 3.92) with 8–12 cross-field pits. The mature secondary xylem (> 100 mm from pith) comprises tracheids, 32–51 μm in diameter (mean 39.12 μm), showing contiguous (57%) or spaced (43%), circular pits, which are uniseriate (98%) or rarely 2–3 seriate (2%), and alternately arranged (Fig. 4F). Rays are uniseriate, 1–18 cells high (mean 5.43), with 3–9 cross-field pits (Fig. 4C). Tree rings, 1–14 mm wide (mean 8.1 mm, $n = 67$), show a sharp, asymmetric boundary defined by 3–6 thick-walled latewood tracheids, < 20 μm in diameter (Fig. 4G).

Associated Megafloral Assemblages

Megafloral compressions occur at three sites associated with the fossil forest (USNM localities 43469, 43473, 43544). Two were obtained from a dark gray channel fill, 1–2 m below the fossil forest horizon. Both these allochthonous assemblages (130 plant fragments) contain abundant remains of the cycadophyte *Charliea manzanitana* (Fig. 5A), common walchian conifers (three species, including *Walchia piniformis* [Fig. 5B], cone scales, and platyspermic seeds), pteridosperms (cf. *Sphenopteris germanica*; Fig. 5C), and rare *Dicranophyllum*, *Taeniopteris*, and medullosan pteridosperms. A third site produced an allochthonous assemblage from a thinly bedded, silty micrite lateral to the stump beds (Fig. 2). This assemblage (24 plant fragments) is composed of walchian conifers with single specimens of *Dicranophyllum* and a putative medullosan.

Identity of Tree Stumps

Based on primary anatomy (septate pith and mesarch cauline bundles arranged in a nonsymptodial vasculature), our stumps are classified as *Mesoxylon* and would be normally assigned to cordaitaleans. However, three observations raise the possibility that they may be conifers: (1) the dominance of uniseriate tracheid pits and short rays in mature

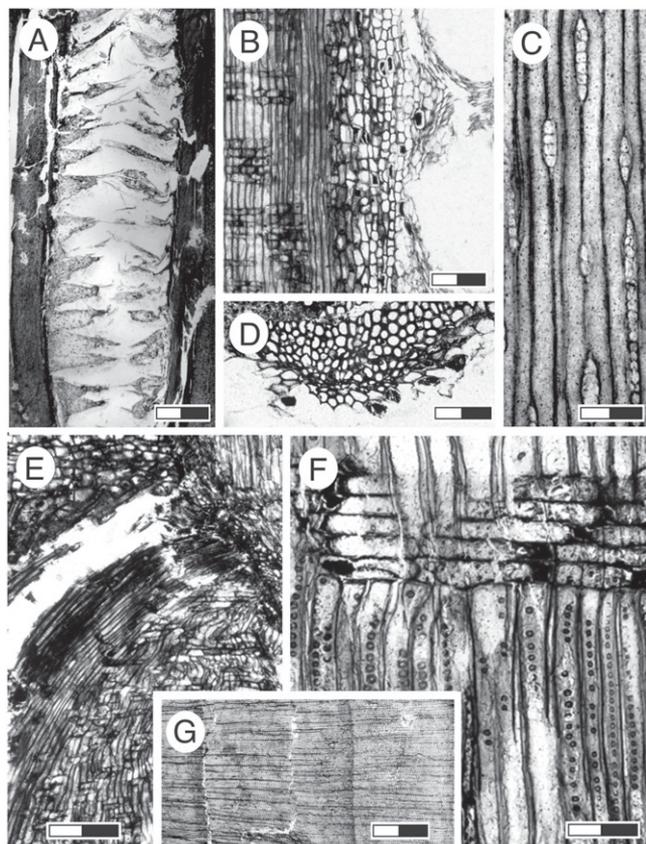


Figure 4. Anatomy of fossil trees, all NMMNH (New Mexico Museum of Natural History) P-60590. A: Septate pith, radial longitudinal section (RLS), scale 5 mm. B: Pith to xylem transition, RLS, scale 150 μm . C: Short rays in mature wood, tangential longitudinal section, scale 100 μm . D: Mesarch cauline bundle, transverse section (TS), scale 200 μm . E: Leaf trace occluded by parenchyma, RLS, scale 250 μm . F: Tracheids with mostly uniseriate pits in mature wood, RLS, scale 100 μm . G: Wide tree rings, TS, scale: 1 mm.

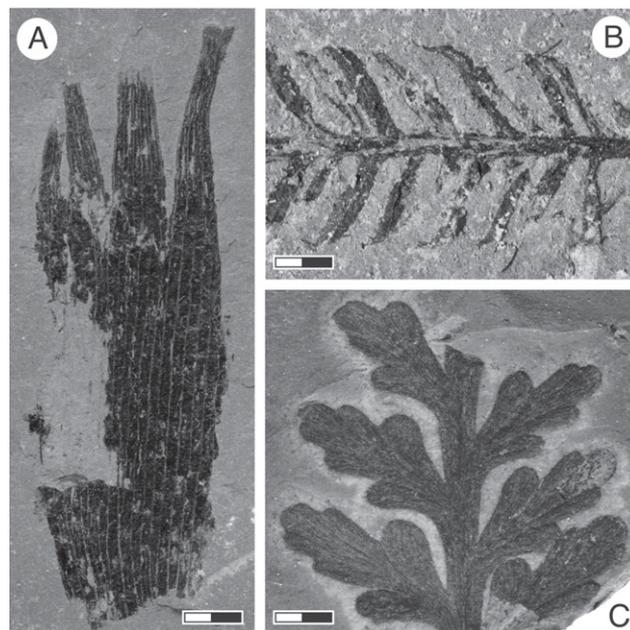


Figure 5. Key elements of megafloral assemblage, 1–2 m below fossil forest. A: *Charliea manzanitana*, USNM (United States National Museum) 508829, scale 3 mm. B: *Walchia piniformis*, USNM 508826, scale 1 mm. C: *Sphenopteris germanica*, USNM 508832, scale 2 mm.

wood are more suggestive of conifers than cordaitaleans (Doubling and Marguerier, 1975); (2) deciduous phenology is unknown in cordaitaleans (Rothwell, 1993), but several distantly related modern conifers seasonally drop shoots, and deciduous phenology is inferred for some Paleozoic conifers based on litter-layer assemblages bearing same-sized shoots; and (3) associated megafloreal assemblages lack cordaitaleans, but contain common to abundant conifers, especially in the micrite bed assemblage most intimately associated with the fossil forest.

Given these uncertainties, we employ the general term coniferopsid (which includes both cordaitaleans and conifers) to describe our stumps. If the stumps are conifers, they are unique among conifers in their mesarch and nonsympodial vasculature, and are noteworthy for their deciduous phenology. If they are cordaitaleans, they are the first documented seasonally deciduous cordaitaleans, and they are unusual in possessing predominantly uniseriate bordered pits and low rays in mature wood.

ECOLOGIC AND CLIMATIC SIGNIFICANCE

Our fossil forest represents the only known example of a widespread in situ coniferopsid forest preserved in the Pennsylvanian seasonal tropics. Assuming that all the in situ coniferopsid stumps lived and were preserved at the same time, this forest had a tree density of ~100 per hectare. Compared with the modern seasonal tropics, this implies open woodland with large canopy gaps (Duadze, 2004).

Biomechanical calculations that utilize stump diameter (Niklas, 1994) further suggest that trees were 9–36 m high (mean 23 m). The strongly right-skewed distribution of stump diameter data with a few large outliers (<0.84 m) and abundant small trees (0.15–0.30 m), together with their random distribution, also suggest that initial colonists seeded subsequent cohorts (a mixed-age community).

The fossil trees are rooted in a coastal sabkha succession and show tree rings, confirming growth under conditions of seasonal aridity. The very wide tree rings (mean 8.1 mm) probably reflect stump buttressing rather than high growth rate. Nonetheless, tree rings differ markedly from fossil and recent occurrences of sabkha vegetation, where rings are very narrow and erratic (Francis, 1984). One possibility is that the trees established during a short-term pluvial episode when aridity was minimized, or occupied a perched freshwater table partly buffered against aridity (Parrish and Falcon-Lang, 2007). This latter hypothesis is supported by the presence of horizontal rooting systems that imply growth in waterlogged soils.

Our seasonally dry woodlands differ markedly from the broadly contemporaneous Coal Forests in central Pangea. With this in mind, it is intriguing that early lowstand plant assemblages between coal beds (Falcon-Lang et al., 2009) show that Coal Forests were replaced by coniferopsids during drier climate phases (Falcon-Lang, 2004; Falcon-Lang and DiMichele, 2010). Presumably the cause of this changeover was an eastward shift of the ecotone dividing the seasonal and humid tropical biomes. Thus, the style of coniferopsid woodland that we report here may be an analogue for the poorly known ecosystems that existed between times of coal formation farther eastward (DiMichele et al., 2010). These data are essential to fine tune Paleozoic climate-vegetation models (Horton et al., 2010) and unravel biome-scale dynamics.

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