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*Geology* 2009;37:923-926
doi: 10.1130/G30117A.1

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ABSTRACT

The idea that the Pennsylvanian tropical lowlands were temporally dominated by rainforest (i.e., the Coal Forest) is deeply ingrained in the literature. Here we challenge two centuries of research by suggesting that this concept is based on a taphonomic artifact, and that seasonally dry vegetation dominated instead. This controversial finding arises from the discovery of a new middle Pennsylvanian (Moscovian) fossil plant assemblage in southeast Illinois, United States. The assemblage, which contains xerophytic walchian conifers, occurs in channels incised into a calcic Vertisol below the Baker Coal. These plants grew on seasonally dry tropical lowlands inferred to have developed during a glacial phase. This xerophytic flora differs markedly from that of the typical clubmoss-dominated Coal Forest developed during deglaciation events. Although preserved very rarely, we argue that such xerophytic floras were temporally as dominant, and perhaps more dominant, than the iconic Coal Forests, which are overrepresented in the fossil record due to taphonomic megabias. These findings require the iconography of Pennsylvanian tropical lowlands to be redrawn.

INTRODUCTION

The Pennsylvanian Coal Forests are one of the most iconic terrestrial ecosystems in the entire history of life, depicted in numerous museum dioramas (DiMichele et al., 2001). These early rainforests were dominated by bizarre tree-sized clubmosses, horsetails, and ferns, and covered much of paleotropical North America, Europe, and Asia at their zenith (Hilton and Cleal, 2007). Fossil remains were preserved in spectacular detail at every scale from individual plant cells to entire forested landscapes (Gastaldo et al., 2004; DiMichele et al., 2007) and have been extensively studied for two centuries. Consequently, we know more about the biology and ecology of these ancient rainforests than almost any other fossil ecosystem.

Preserved alongside the remains of the Coal Forests are cryptic assemblages containing xerophytic conifers, generally interpreted as upland floras transported down into lowland basins (Lyons and Darrah, 1989). While this explanation may account for some of these fossils (Falcon-Lang and Bashforth, 2004), an alternative possibility is that the xerophytic assemblages record continent-wide changes in lowland vegetation driven by the onset of tropical aridity during glacial phases (Falcon-Lang, 2004). Given that glacial cycles may additionally cause altitudinal shifts in rainforest species (Colinvaux et al., 1996), it has proved difficult to test between these upland and dryland hypotheses.

In this paper we describe a new plant assemblage containing xerophytic conifers from Pennsylvanian channel-fill deposits in Illinois, United States, that resolves this enigma. Analyses of sedimentology, sequence stratigraphy, and plant taphonomy demonstrate that xerophytic conifers grew on seasonally dry soils within the lowland basin during glacial phases. Moreover, paleosol studies imply that these xerophytic communities may have been temporally dominant and that the better-preserved remains of the Coal Forests are overrepresented in the fossil record as a result of taphonomic megabias. These findings challenge the long-held belief that the Pennsylvanian tropics were temporally dominated by wetland rainforests.

GEOLOGICAL SETTING

Our work focuses on newly discovered fossil plants preserved within channels incised into a prominent paleosol beneath the middle Pennsylvanian (Moscovian; Asturian) Baker Coal of Illinois, Indiana, and Kentucky. Two large paleovalleys have been formerly documented at this level, the Winslow paleovalley in Indiana (Eggert, 1994) and the Henderson paleovalley in Kentucky (Beard and Williamson, 1979). Both attain a maximum depth of ≤43 m and incise through the underlying Herrin and Springfield Coals. Their similar size and trend, together with new borehole data, demonstrate that they are part of the same north-south valley system (Fig. 1).

Figure 1. Distribution and thickness of middle Pennsylvanian Baker Coal showing position of incised paleovalleys and location of Cottage Grove. Dark shading indicates coal thickness ≥1.5 m. Inset: above, index map of USA; below, middle Pennsylvanian stratigraphy of major coal seams mentioned in text and paleovalleys discussed in this paper. IVF—incised valley fill.

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Geology, October 2009; v. 37; no. 10; p. 923–926; doi: 10.1130/G30117A.1; 4 figures.
In this paper we describe smaller incised channels below the Baker Coal at the Cottage Grove surface mine in Saline and Gallatin Counties, southeast Illinois (37°46′N, 88°25′W). We interpret these features as forming a tributary to the larger Winslow-Henderson valley to the east. Extensive core data show that the Baker Coal pinches out 55 km to the north and west of Cottage Grove (Fig. 1) and its paleosol merges with the paleosol beneath the overlying Danville Coal such that ~8 m of strata are missing. From this we infer deposition on a gently sloping (<0.05°) landscape, which drained southward.

Sedimentology and Stratigraphy

In addition to this regional analysis, we made a detailed study of the 10–12-m-thick interval between the Herrin and Baker Coals at Cottage Grove, where retreating highwalls were observed repeatedly over a period of two years (Fig. 2). Here, the Herrin Coal is sharply over lain by the Anna Shale, a fissile black phosphatic mudstone containing inarticulate brachiopods, which grades up into the Bre rerton Limestone, which contains productid brachiopods and crinoids. Above this is an upward-coarsening succession of rhythmically laminated mudstone (Lawson Shale), topped by a thin lens of coal. Next is the sharp-based Bankston Fork Limestone, containing productid brachiopods, with dolomitization and roots in its upper part. Overlying this is a prominent paleosol into which channels are incised. The Baker Coal completes our study interval and thickens into the axes of the underlying incised channels.

We conducted a detailed study of the paleosol containing the incised channels beneath the Baker Coal. The paleosol comprises three units. The lower unit, ≤1.3 m thick, is a green-gray claystone containing stage II pedogenic carbonate nodules, pervasive slickensides, pseudoanticlones, and a structure of wedge-shaped or blocky ped with clay skins. Trunc ated gilgai topography forms the upper surface of this unit. The middle unit, ≤0.2 m thick, is an olive-green, poorly laminated mudstone with a hackly fracture, showing occasional siderite nodules, coalified roots, and a sharp top. The upper unit, ≤0.1 m thick, which is in contact with the Baker Coal, comprises dark laminated shale containing plant adpressions and abundant spirobid s.

Observations in excellent highwall exposures show that the incised channels down-cut from precisely the level of this paleosol. We mapped two channels, ~3 km apart, using data from closely spaced test holes drilled prior to mining. In Pit 7, the channel has an east-west trend, curving north-south near the western end. The channel in Pit 1 extends north-east-southwest and deepens toward the southwest. The channels converge southward, but their inferred junction is south of the Baker outcrop. The incised channels are ~250 m wide with a maximum depth of 9–12 m and show gently sloping, nearly symmetrical sides. Paleoslumps occur on the channel margins in which blocks of Bankston Fork Limestone are rotated along glide planes in the Lawson Shale.

The channel fill comprises two main units. The lower channel fill, ≤1.6 m thick, is a conglomerate of rounded to subangular cobbles (≤22 cm diameter) of Bre reton and Bankston Fork Limestones, and sharply angular cobbles of Anna Shale. Siderite pebbles, derived from the Lawson Shale, fragments of coal, and pedogenic carbonate also occur. The matrix comprises sand-grade fragments of the same rocks that form the clasts (quartz sand is rare) and some mudstone. Conglomerates occur as decimeter-scale lenses, which may coarsen upward, show local matrix-support and flute clasts, or fine upward into plane-bedded sandstone. Mudstone laminae contain adpressed fossil plants (the focus of this paper). The upper channel fill, 3–4 m thick, sharply truncates these beds and comprises laminated gray shale and sandstone with abundant spirobids and plant adpressions dominated by Macroneuropteris scheuchzeri. This is overlain by the Baker Coal, which thickens from ≤0.3 m on the flanks of the channel to ≤1.8 m at the axis.

Paleoenvironment and Climate Cycles

This succession at Cottage Grove is correlatable at a regional scale and may be interpreted using sequence stratigraphic nomenclature (Fig. 2). The Herrin Coal, developed in a coastal mire forest, and the overlying Anna Shale, deposited in an anoxic sea, compose a transgressive systems tract (TST) formed under conditions of rapid sea-level rise. The Bre reton and Bankston Fork Limestones, interpreted as a shallow-marine deposits, and the Lawson Shale, interpreted as a tidally influenced coastal deposit, compose a highstand systems tract (HST) representing times of high but fluctuating sea level (Heckel et al., 1998). The overlying paleosol, interpreted as a calcic Vertisol, and the incised channels it contains, compose a lowstand systems tract (LST), which records falling sea level, exposure of the craton, and the onset of climatic aridity. The Baker Coal, underlain by shales containing brackish spirobids (TST), marks renewed sea-level rise and a shift to a more humid climate. Such coupled oscillations in climate and sea level probably represent coastal response to high-frequency glacial-interglacial cycles (Tandon and Gibling, 1994).

Of special interest to this study is the calcic Vertisol and associated incised channels. Formed as sea level dropped and climate became drier, these lowstand deposits are best interpreted as having developed during the onset of glaciation. Deep Vertic soils like this may take 103–106 years to form and the presence of truncated gilgai topography further implies surface deflation and a time gap (Tandon and Gibling, 1994). Middle and upper parts of the paleosol mark renewed aggradation under a progressively more humid climate, eventually culminating in the formation of peat (coal) in permanently waterlogged soils. Vertisols with this kind of gley overprint may represent a transition from...
glacial to interglacial conditions in a highly condensed interfluvial suc-
cession (Driese and Ober, 2005).

Sediments infilling channels incised into this Vertisol are interpreted
as a much-expanded succession through this glacial-interglacial trans-
formation. The cogenetic of the lower channel fill and the Vertisol is confirmed
by the occurrence of pedogenic carbonate clasts in the conglomerate,
reworked from well-drained interfluvial soils. The conglomerate accumu-
lated throughout channel incision. Clasts were locally derived (cf. Feld-
man et al., 2005) and probably introduced by landslides and rockfalls,
as indicated by paleoslopes of the channel sides. Conglomerate facies imply
that sediments were emplaced as slurry-like flows, or deposited by brief
floods, perhaps driven by seasonal rainfall. The conglomerate was finally
preserved when brackish waters flooded the channel floor, probably as
deglaciation triggered sea-level rise. This, in turn, implies that the con-
glomerate and the fossils it contains date from the interval around glacial
maximum (Feldman et al., 2005).

FOSSIL PLANT ASSEMBLAGE

Fossils were examined and collected, and a semiquantitative census
of taxa undertaken, from large excavated blocks of conglomerate in Pit 7.
As conglomerate only occurs in the base of the incised channels, the prov-
enance of this material is certain. To ensure that fossils from other parts
of the succession were excluded from the census, only plants attached to
conglomerate blocks were recorded.

Adpression Fossils

Counts of the number of plant fragments in 1 m² quadrats (mean
62.11, n = 5) scaled to the area of the spoil pile (~400 m²) suggest ~25,000
fossils were visible at our site. However, although common, most were
very poorly preserved. An intensive survey revealed only 41 fragments
that could be identified to generic level (±0.2%). Of these, most common
(68%) were remains of cordaitaleans, represented by Cordaites leaves (n
= 17), Cordaicarpus seeds (n = 7), trunks with Artisia-type pith (n = 3),
and a Cordaichladae branch (n = 1). Less common were medullosan pteri-
dosperms (12%) represented by Linopteris pinnules (n = 4) and a neuro-
teroid pinnule (n = 1), tree ferns (10%) represented by Pecopteris pinnules
(n = 4), walchian conifers (7%; n = 3), and horsetails (3%) represented by
Calamites (n = 1).

Much more abundant were fossils that preserved sufficient char-
acteristics to be assigned to major groups, but insufficient for generic
determination (~10% of the total material). These included axes showing
downward recurved branches indicative of medullosan pteridosperms,
and punctate axes suggestive of tree ferns or medullosan pteridosperms (e.g.,
Linopteris). Also present were vitrinous trunks, ≤0.4 m diameter, with
circular pith, and abundant clasts of charcoal, ≤30 mm diameter, showing
a pyncnoxylic Dadoxylon structure, both suggestive of cordaitaleans and/
or conifers. However, the vast majority of the plant material (~90%) could
not be identified.

Conifer Shoots and Wood

Conifers are the most unusual element in our assemblage. This group
is extremely rare in strata of Moscovian age and older (Lyons and Darrah,
1989; Plotnick et al., 2008). Consequently, to ensure accurate identifica-
tion we studied this material in detail. Walchian shoots were macerated
with Schulze’s reagents and imaged with a Leica DM2500-LB2 micro-
scope while charcoal was imaged with a Hitachi S-3500N scanning elec-
tron microscope.

Vegetative ultimate shoots of our walchian specimens show helically
arranged bifacial leaves, 0.7–1.2 mm wide and 4–5 mm long, arising at
≤40° (Fig. 3). Leaves are linear to narrowly triangular with a mucronate
apex, show an S-shaped profile, and dentate margins. The thick adxal
surface shows rectangular epidermal cells with rounded papillae. Stomata
on the thin abaxial surface are indistinct and arranged within short rows
(possibly within two bands). Abundant trichome bases occur on both sur-
faces. This combination of characters is diagnostic of walchian conifers
(or walchian Voltziales) but not indicative of any particular taxon (Her-
nandez-Castillo et al., 2001).

Although crushed, the Dadoxylon charcoal has a pyncnoxylic struc-
ture. Tracheids, ~30–40 µm diameter, show uniseriate bordered pits and
uniseriate rays 1–7 cells high. Pennsylvanian wood with these properties
is characteristic of juvenile cordaitaleans (Falcon-Lang and Bashforth,
2004) and mature wood of conifers. Given that our material comprises
large blocks of charcoal, it is more likely to be coniferous.

PALEOECOLOGICAL IMPLICATIONS

The association of the conifer-bearing plant assemblage with locally
derived conglomerate suggests that this vegetation was growing on adjac-
ent interfluves, or within the incised channels (Fielding et al., 2009). As
the conglomerates and interfluvial Vertisols are inferred to be cogenetic,
this further implies that vegetation grew under seasonally dry climate
at near-maximum glaciation (Fig. 4). This inference is supported by the
occurrence of papillae and trichomes on the conifer leaves, suggestive of
a degree of xerophyly. Plant remains are quickly oxidized in well-drained
soils, and preservation of our assemblage resulted from fortuitous and
rapid burial within channels. Although close to the eroded edge of the Illi-
nois Basin today, at the time of deposition Cottage Grove was positioned
at least 55 km from the basin margin, as defined by the outcrop area of the
Baker Coal (Fig. 1). In addition, the thickness and maturity of the calcic
Vertisol with which the plant assemblage is associated indicates develop-
ment over 10³–10⁴ a (Tandon and Gibling, 1994). Consequently, we argue

Figure 3. Ultimate shoot and cuticle of walchian conifer (U.S. National
Museum of Natural History, USNM 536629). A: Face and side view of
leaves, scale 5 mm. B: Cuticle seen from adaxial side, scale 500 µm.
C: Cuticle showing trichomes (t) and papillae (p), scale 100 µm.
that our xerophytic flora dominated much, if not all, of the lowland basinal areas for long periods of time.

Cryptic xerophytic plant assemblages like ours are known from several sites in the Pennsylvanian of North America, extending from the Appalachians to the Western Interior basin (Lyons and Darrah, 1989; DiMichele and Aronson, 1992; Feldman et al., 2005), where they are typically associated with incised paleovalleys. Although most assemblages have not been subject to the kind of detailed analysis presented in this paper, we hypothesize that they represent the remains of seasonally dry lowland vegetation that repeatedly alternated with Coal Forests during glacial-interglacial cycles (Falcon-Lang, 2004). The Coal Forests, which dominated during deglaciation and various times in the interglacial during glacial-interglacial cycles (Falcon-Lang, 2004). Our biased knowledge of the Coal Forests highlights the fact that xerophytic floras were at least as temporally dominant across Pennsylvanian tropical lowlands as the Coal Forests, and perhaps more so. Indeed, if the Quaternary is an appropriate analogue for tropical analogues and a compaction coefficient for Pennsylvanian coals of 0.5–1.0, coal seams represent ~2.5–20 ka of accumulation. Such calculations of the longevity of Coal Forests are highly uncertain, as are estimates of the duration of our xerophytic vegetation. Nevertheless, they serve to highlight the fact that xerophytic vegetation was at least as temporally dominant across Pennsylvanian tropical lowlands as the Coal Forests, and perhaps more so. Indeed, if the Quaternary is an appropriate analogue for the Pennsylvanian, then this supports dominance by seasonally dry vegetation, because glacial phases are usually much longer than interglacial phases (Falcon-Lang, 2004). Our biased knowledge of the Coal Forests reflects the fact that these plants grew in wetlands where they were readily preserved and today co-occur with economic coals where they are readily accessible to paleobotanists. We thus conclude that reconstructions of this time interval are hugely distorted by this double bias and the iconography of the Pennsylvanian tropical lowlands, depicted in countless museum dioramas, needs to be redrawn.

ACKNOWLEDGMENTS

We thank Peabody Energy for allowing access to the Cottage Grove Mine, and David Williams (Kentucky Geological Survey) for sharing data. Falcon-Lang acknowledges a Natural Environment Research Council Advanced Postdoctoral Fellowship (NE/F014120/2).

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Manuscript received 9 February 2009
Revised manuscript received 12 May 2009
Manuscript accepted 26 May 2009

Printed in USA