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New insights on the stepwise collapse of the Carboniferous Coal Forests: Evidence from cyclothems and coniferopsid tree-stumps near the Desmoinesian–Missourian boundary in Peoria County, Illinois, USA

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ABSTRACT

The first phase in the stepwise collapse of the Carboniferous Coal Forests occurred near the Desmoinesian–Missourian boundary (early Kasimovian, ~307 Ma), and involved extirpation of *Lycospora*-producing lepidodendrids, and some other lycopsids, across most of tropical Euramerica. In this paper, we follow-up on historical reports of silicified tree-stumps in Peoria County, northwest-central Illinois, USA, which have significant implications for understanding Carboniferous Coal Forest collapse. Rooted near the paleoweathered top of the Lonsdale Limestone, and widespread across an area of ~250 km^2, the silicified tree-stumps belong to *Amyelon*-type coniferopsids. A key feature of the fossil wood is the occurrence of abundant axial parenchyma arranged along irregular growth interruptions, suggestive of climatic seasonality, an inference consistent with silicic preservation. The silicified fossil forest directly underlies the Exline Limestone and Athensville Coal, the horizons that mark the US-wide loss of *Lycospora*, and demonstrate that lowland areas were colonized by dryland coniferopsid forests following Coal Forest collapse. Placed in a cyclothem context, the silicified fossil forest horizon lies above the Maria Creek mudstone paleosol (top of Piasa cyclothem), in which earlier d^{18}O analyses have identified a major pulse of global warming, and coincides with the 'Hanna City' paleosol (top of Lonsdale cyclothem), which is correlative with the Seminole Sandstone, a Midcontinent incised valley-fill representative of one of the most profound glacioeustatic falls seen in the Pennsylvanian record. Our new findings therefore demonstrate that Coal Forest collapse was closely linked to intensification of glacial cycle amplitude near the Desmoinesian–Missourian boundary, involving both extreme episodes of global warming and cooling.

1. Introduction

The iconic Carboniferous Coal Forests, mostly dominated by arborescent *Lycospora*-producing lepidodendrids and other lycopsids, covered much of north-equatorial Euramerica throughout latest Mississippian to late Middle Pennsylvanian times (Phillips and DiMichele, 1992; DiMichele et al., 2007; Thomas, 2007; DiMichele and Falcon-Lang, 2011; Falcon-Lang, 2006; Falcon-Lang et al., 2006; DiMichele et al., 1996b, 2001; Cleal et al., 2012). The first phase of their step-wise collapse (Phillips et al., 1974, 1985), occurred at the 'traditional' plant-based Desmoinesian–Missourian boundary in the USA (sensu Falcon-Lang et al., 2011a) at a level within the early part of the current Kasimovian global stage (c. 307 Ma; Richards, 2013). This short-lived episode witnessed the abrupt extirpation of lepidodendrids across the whole of north-equatorial Euramerica, west of the Appalachians (Phillips et al., 1985; Peppers 1997), and coincided with a marked reduction to the east of the Appalachians as well (Bek, 2012). In total, 87% of peatland tree species went extinct (DiMichele and Phillips, 1996), and Coal Forest collapse profoundly impacted the evolution of associated cosmopolitan tetrapod faunas (Sahney et al., 2010).

The cause of the Desmoinesian–Missourian event has received considerable attention, and there is agreement that a short-term episode of tropical aridification was involved (Phillips and Peppers, 1984; Winston, 1990; Kosanke and Cecil, 1996; Falcon-Lang and DiMichele, 2010; Rosenau et al., 2013a, 2013b). The inference is that – stressed beyond an ecological tipping point – the hydrophilic lepidodendrid

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forests that had dominated for the previous 15 million years were unable to recover (Phillips and Peppers, 1984; Heckel, 1991; Falcon-Lang and DiMichele, 2010). This event is marked by the abrupt loss of *Lycospora*, the dominant miospore of lepidodendrids, west of the Appalachians, at a level prior to the Mason Coal in the Appalachian Basin, the Lake Creek and Athensville coals in the Illinois Basin, and the Tulsa and Hepler Coals in the Midcontinent Basin, i.e., immediately following the Lost Branch cyclothem (Peppers, 1996, 1997; Heckel, 2008, 2013; Falcon-Lang et al., 2011a). When Coal Forest communities became re-established, following a return to humid climates in earliest Missourian times, marattialean tree-ferns rose to dominance (Phillips et al., 1974; Willard and Phillips, 1993; Kosanke and Cecil, 1996; Falcon-Lang, 2006; DiMichele and Phillips, 2002). What triggered this short-term arid excursion continues to be debated, with climatic cooling and warming implicated as competing drivers of vegetation change.

One hypothesis is that global cooling linked to Gondwanan ice-dynamics was involved. Glacial-interglacial cycles are known to have driven coupled fluctuations in climate and sea level (Tandon and Gibling, 1994; Cecil et al., 2003; Heckel, 2008; Eros et al., 2012) and forced Coal Forests to repeatedly contract into isolated refugia during drier glacial episodes (Heckel, 1991; Falcon-Lang, 2004; Falcon-Lang and DiMichele, 2010). Following most Desmoinesian glacial cycles, lepidodendrid-dominated Coal Forests managed to rebound with their species composition largely intact (DiMichele et al., 1996a). However, the glacioeustatic event at the Desmoinesian–Missourian boundary is inferred to have been particularly intense (Heckel, 1991), judging by the unusual magnitude of sea level fall (Rygel et al., 2008) and marine regression (Falcon-Lang et al., 2011a; Heckel, 1991, 2013). In this scenario, the establishment of widespread dryland environments, as the seas retreated, fragmented lepidodendrid populations to such an extent that they could not recover from the Lost Branch event (Falcon-Lang and DiMichele, 2010).

A second hypothesis to explain Coal Forest collapse involves global warming (Montañez et al., 2016). Rosenau et al. (2013a, 2013b) noted that paleosol pedotypes, formed during times of glacio-eustatic fall, shifted to a drier mode (typified by calcic Vertisols), just below the Desmoinesian–Missourian boundary, and also following it. Furthermore, based on $d^{18}O$ analyses of paired samples of flint-clay kaolinite and sphaerosiderite in paleosols in the Illinois Basin, Rosenau et al. (2013a) identified an intense but short-lived episode of temperature rise of up to 6 °C near the Desmoinesian–Missourian boundary, and inferred that Coal Forest collapse was linked to global warming and associated aridification (Rosenau et al., 2013b). This is consistent with near-field records that suggest that the Gondwanan ice cover was subdued during the Desmoinesian–Missourian boundary interval (Isbell et al., 2003; Fielding et al., 2008), and the Earth was experiencing a greenhouse episode (Montañez and Poulsen, 2013). Although the poles were not completely ice-free, cyclothems suggest reduced amplitude (30–60 m) of glacio-eustatic fluctuations in Missourian times (Rygel et al., 2008), following the major eustatic events near Desmoinesian–Missourian boundary (Heckel, 1991, 2008, 2013).

In this current paper, we further address these paleoclimatic issues through a detailed study of Desmoinesian–Missourian boundary sections in Peoria County, northwest-central Illinois, USA. In particular, we document silicified tree-stump sites within a sedimentologic and cyclothemic context, which sheds light on the vegetation-dynamics that occurred near the boundary in tropical Euramerica. Our findings show how the two alternative paleoclimate hypotheses explaining this significant ecological event can be reconciled when placed in a high-resolution temporal context.

2. Pennsylvanian cyclothems and the *Lycospora* extirpation

Based on conodont biozonation and previous correlation of major coal seams, Heckel (2008, 2013) identified Desmoinesian–Missourian cyclothems that can be traced across central to eastern USA (Fig. 1). Each major marine cyclothem represents a predominantly aggradational transgressive phase mostly characterized by marine beds, including limestone and a conodont-rich shale that represents sediment starvation in the condensed interval. Transgressive flooding progressed in a northeasterly direction, from the low to mid shelf of the Midcontinent Basin, through the high mid shelf of the Illinois Basin, and into the high shelf of the Appalachian Basin (Heckel, 2008). Cyclothems are separated by unconformity surfaces formed during predominantly degradational regressive and lowstand phases, which are represented by paleosols and equivalent incised paleovalleys, with the magnitude of sedimentary hiatus similarly increasing in duration in a northeasterly direction (Falcon-Lang et al., 2011a).

2.1. Desmoinesian-Missourian boundary cyclothems

Heckel (2008, 2013) also recognized major cyclothem groupings, calibrated to be of ~400 kyr duration, and typically comprising up to several transgressive-regressive cycles of lesser magnitudes, centered around one major transgressive episode. In the Illinois Basin (Figs. 1, 2), the major transgressive phases of the latest two Desmoinesian cyclothem groupings (Altamont and Lost Branch groupings) are represented by the Piasa and Lonsdale limestones, respectively, and their immediately underlying conodont-rich shales. Below the Piasa cyclothem, the shelly, conodont-rich shale at the base of the Farmington Shale and the directly underlying Danville Coal represent an intermediate cyclothem within the Altamont grouping, which provides an important marker zone throughout our study area in Peoria County. The base of the earliest Missourian cyclothem grouping (Hertha grouping) in Illinois is represented by the Scottville/Exline Limestone, a cyclothem of intermediate scale below the major cyclothem represented in Illinois by the Cramer Limestone, Chapel Coal, associated shale, and the Trivoli Sandstone. Across the Desmoinesian–Missourian boundary on the Midcontinent low shelf in southern Kansas and northern Oklahoma are two minor marine cycles, the Glenpool above the Lost Branch, and Checkerboard-South Mound below the Exline, which have no equivalents higher on the shelf in Illinois (Fig. 1).

Throughout most of the Desmoinesian–early Missourian interval (Fig. 1), regressive phases were typically subdued, with the lowstand shoreline not extending much south of the Kansas-Oklahoma border in the Midcontinent Basin, typical of small to moderate glacial buildup at these times. This is in contrast to the two regressions both immediately preceding and following the Lost Branch cyclothem, when shoreline withdrew to south-central Oklahoma, some 200–250 km south of the Kansas-Oklahoma border into the basin (Falcon-Lang et al., 2011a; Fig. 1). In this paper, we informally name the major regression that divides the Midcontinent Altamont and Lost Branch groupings as the 'Upper Memorial regression' because the lithic unit of that name can be traced as a paleosol from upper mid-shelf Iowa to the low shelf of central Oklahoma (Heckel, 1991). The major regression that divides the Lost Branch and Hertha cyclothem groupings is termed the 'Seminole regression', after the sandstone of that name that fills the incised paleovalleys at this horizon from northern to central Oklahoma (Fig. 1).

2.2. Timing of *Lycospora* extirpation

Within this cyclothem context (Fig. 1), and at a coarse scale of resolution, final *Lycospora* extirpation occurred at a horizon prior to deposition of the Mason Coal in the Appalachian Basin, the Lake Creek and Athensville coals in the Illinois Basin, and the Tulsa and Hepler coals in the Midcontinent Basin in the earliest part of the Midcontinent Hertha cyclothem grouping (Peppers, 1996; Heckel, 2008, 2013; Falcon-Lang et al., 2011a), i.e., following the 'Seminole regression'. However, more detailed intra-cyclothem analysis shows that sharp decline actually commenced during the minor Glenpool cyclothem (Fig. 1), near the end of the Lost Branch cyclothem grouping (Peppers, 1997), with *Lycospora* persisting only in tiny quantities into the earliest

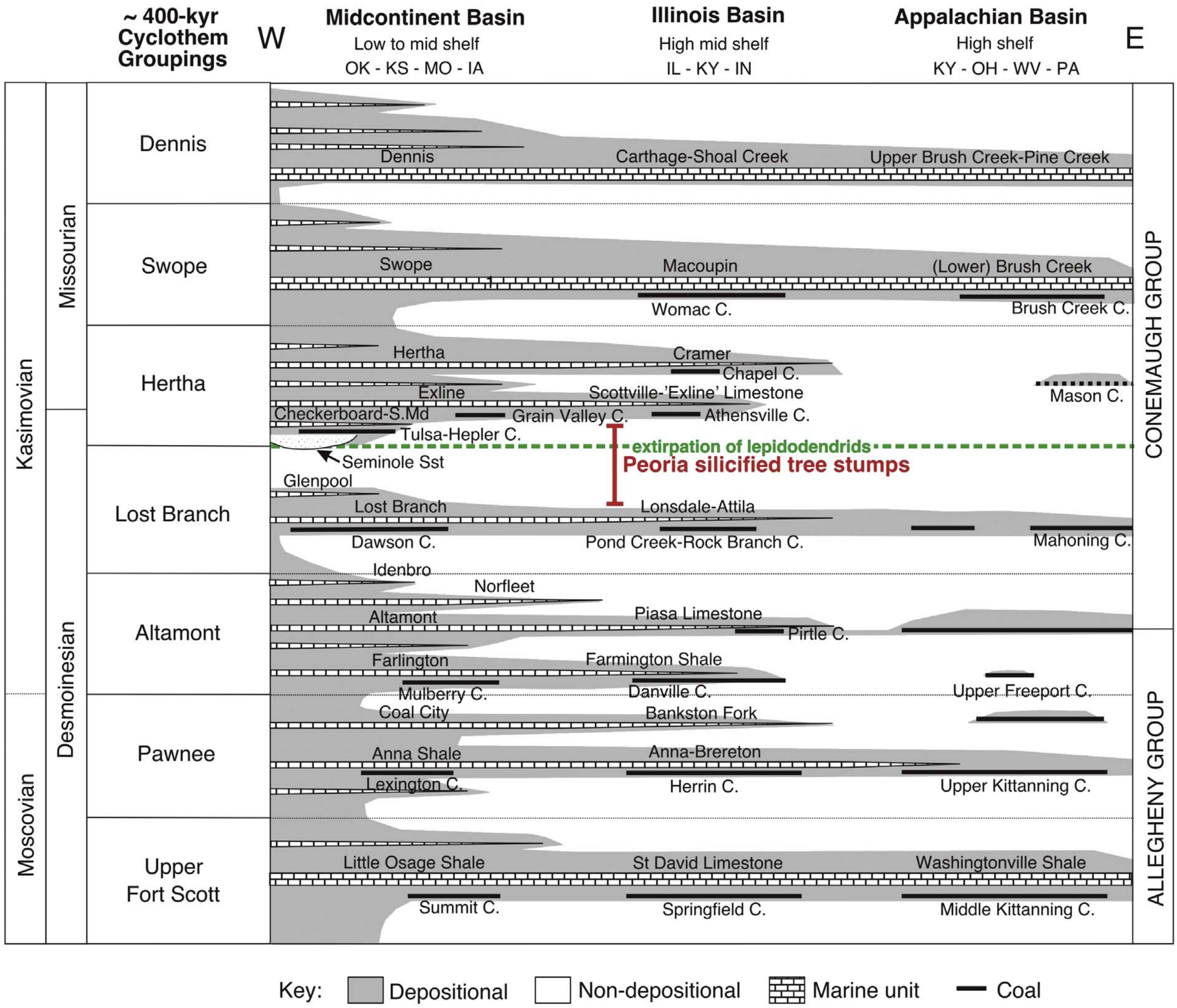

Fig. 1. Correlation of ~400-kyr marine cyclothem groupings across central and eastern USA, from complete succession in Midcontinent basin-margin region of Oklahoma through Kansas-Missouri low shelf, Illinois Basin mid-shelf, to Appalachian high shelf, showing up-shelf decrease in number of marine units and concomitant increase in time gaps between them (after Heckel et al., 2007; Falcon-Lang et al., 2011a; Heckel, 2013). Traditional Desmoinesian–Missourian boundary horizon marks US-wide loss of *Lycospora*, denoting lepidodendrid extirpation. Peoria Fossil Forest stump sites rest on Lonsdale Limestone and overlying complex paleosol that formed during a major stratigraphic gap within which a fossil tree trunk also is present in the Seminole Sandstone in Oklahoma. This forest developed following an intense transgression during the Lost Branch 400-kyr cyclothem grouping, when a short intense glacial episode took lowstand shoreline basinward into south-central Oklahoma both prior to and following the transgression; note that during three older Desmoinesian (Upper Fort Scott, Pawnee, Altamont) and two younger Missourian (Hertha, Swope) cyclothem groupings, lowstand shoreline did not extend much past Kansas-Oklahoma state border, during these longer-term generally more interglacial times.

coals in the Hertha grouping. Therefore, the extirpation event commenced towards the end of the Lost Branch grouping, during the medial stages of the 'Seminole regression' (Heckel, 1991) and was completed at an unrecorded point during that regressive phase when no sedimentary record was accumulating along accessible outcrop. It should be noted that the *Lycospora* is a proxy for a larger suite of spores, which also includes the lycopsid spore *Granisporites*, produced by members of the Diaphorodendraceae, another major wetland lycopsid element (DiMichele and Bateman, 1992).

3. Cyclothems and silicified trees in Peoria County

In this report, we describe Desmoinesian–Missourian boundary cyclothems, and associated silicified tree stumps, in Peoria County in northwest-central Illinois, USA (Fig. 3). This is an area of classic geology where Udden (1912) and Wanless and Weller (1932) first described and named cyclothems, and Wanless and Shepard (1936) interpreted them as the far-field expression of glacioeustatic cycles. The presence of silicified trees is noteworthy, because it is the only such confirmed occurrence in the entire Pennsylvanian succession of the Illinois Basin. (We note that at the time of writing, a second occurrence of silicified trees, but at the same stratigraphic level, has been reported from Vermilion County, east-central Illinois by one of us (SDE) – although we currently have insufficient data to fully integrate with the findings of this paper).

3.1. Previous work

The complex stratigraphy of the Desmoinesian–Missourian boundary succession for Peoria County is summarized in Fig. 4, which is based on our synthesis of various Illinois Geological Survey field reports (especially Udden, 1912; Cady et al., 1939; Dunbar and Henbest, 1942; Wanless, 1956, 1957, 1958) combined with our own general field observations. Four cyclothems of major to intermediate scale are recognized here, equivalent to the Altamont (2), Lost Branch, and Hertha groupings of the Midcontinent Basin (Heckel, 2008). The upper three cyclothems are separated by two prominent unconformities, representing significant erosional surfaces.

The first (lowermost) cyclothem is the Lower Farmington cyclothem, equivalent to the intermediate Farlington cyclothem at the

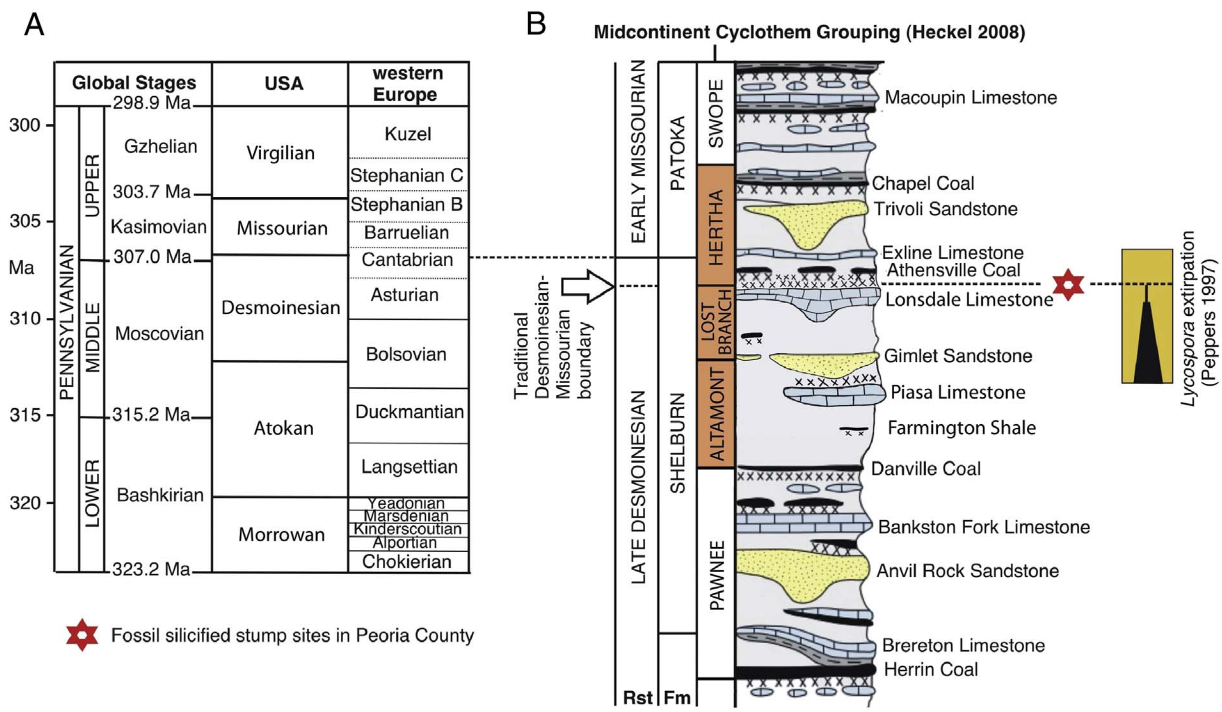

Fig. 2. Stratigraphic context. A., Pennsylvanian Timescale (after Richards, 2013). B., Generalized Late Desmoinesian-early Missourian stratigraphy of northwestern Illinois, showing key beds mentioned in text, horizon of silicified tree-stump sites, and timing of *Lycospora* demise (after Peppers, 1997). The three Midcontinent cyclothem groupings that are the focus of this study are highlighted in orange.

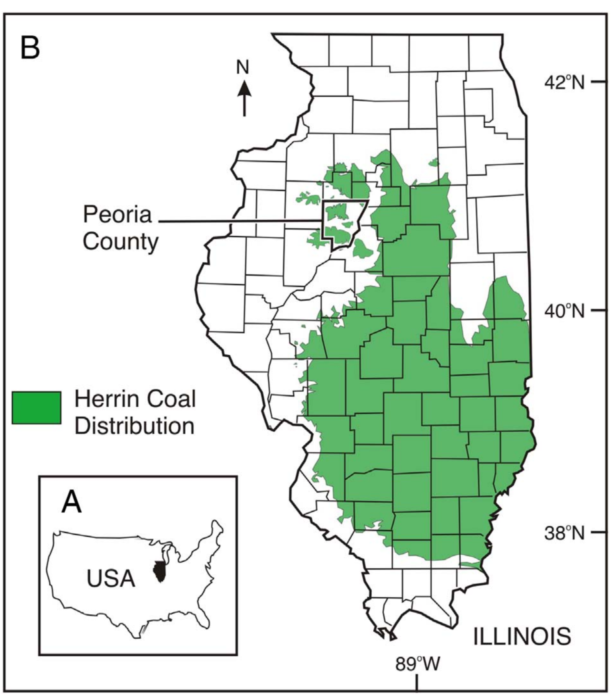

Fig. 3. General location and geology of study site in Illinois Basin. A., USA showing Illinois. B., County outline map of Illinois showing extent (green) of late Desmoinesian Herrin (No. 6) Coal, which everywhere underlies the fossil sites reported here. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Herrin Coal distribution data from Treworgy et al. (2000).

base of the Altamont grouping in the Midcontinent Basin (Fig. 1). It comprises the late Desmoinesian Danville Coal, sharply overlain by a thin, fossiliferous, conodont-rich marine shale to shaly limestone, followed by several metres of Farmington Shale. Conodont faunas (labeled [*1] on Figs. 4 and 6), collected above the Danville Coal at two localities west of Peoria are nearly exclusively dominated by *Swadelina neoshoensis* and lack *Idiognathodus* (Heckel, 2013). Above this zone, the lower part of the Farmington Shale coarsens upward into siltstone.

The second cyclothem upward is the major Piasa cyclothem, which commences with an unnamed coal followed upward by nonmarine to marine shale and the Piasa Limestone Member; it is equivalent to the middle part of the Altamont grouping in the Midcontinent Basin. The Piasa Limestone Member is a 1–2-m-thick skeletal wackestone with a rich marine fauna, and was previously unrecognized in Peoria County. In its type area in Jersey County, Illinois to the south, it overlies a dark shale that contains a conodont fauna (labeled [*2] on Figs. 4 and 6), which is dominated by *Idiognathodus* spp., contains *Neognathodus* spp., and includes *Swadelina neoshoensis* (Heckel, 2013). In Peoria County, and more widely across Illinois, the Piasa Limestone is overlain by a 1.5–3-m-thick, informally named Maria Creek mudstone, a prominent varicolored paleosol, and in places by its lateral equivalent, the Gimlet Sandstone Member, a paleovalley-fill that locally incises down ~45 m to just above the level of the Herrin Coal (Wanless, 1957), which is below the Danville Coal, thus representing a major phase of regression.

The third is the latest Desmoinesian Lonsdale cyclothem, equivalent to the Lost Branch cyclothem of the Midcontinent Basin (Figs. 1, 2). It consists of the Lonsdale Limestone (Worthen, 1873), a typically 1.8–2.5-m-thick bioclastic wackestone (Wanless, 1957), with a rich marine fauna (Waldo, 1928) and a brecciated top, overlain by an olive-grey mudstone paleosol, ~0.7 m thick, informally named here as the ‘Hanna City’ paleosol. Near its base in Peoria County, 15 km west-southwest of Hanna City (Wanless, 1957, locality 11), the typical Lonsdale Limestone facies contains a conodont-rich shale, with a fauna (labeled [*3] on Fig. 4) that is dominated by *Swadelina nodocarinata*, and contains *Neognathodus* spp., *Idiognathodus* sp. and *Gondolella magna*, the latter in its only stratigraphic appearance in the Illinois or Midcontinent basins (Swade, 1973; see Swade, 1985; Lambert et al., 2003; Barrick et al., 2013 for evolution of taxonomic names). Its components, particularly *Gondolella magna*, allow correlation of the Lonsdale Limestone with the Attila Shale of southern Illinois, and with the Nuyaka

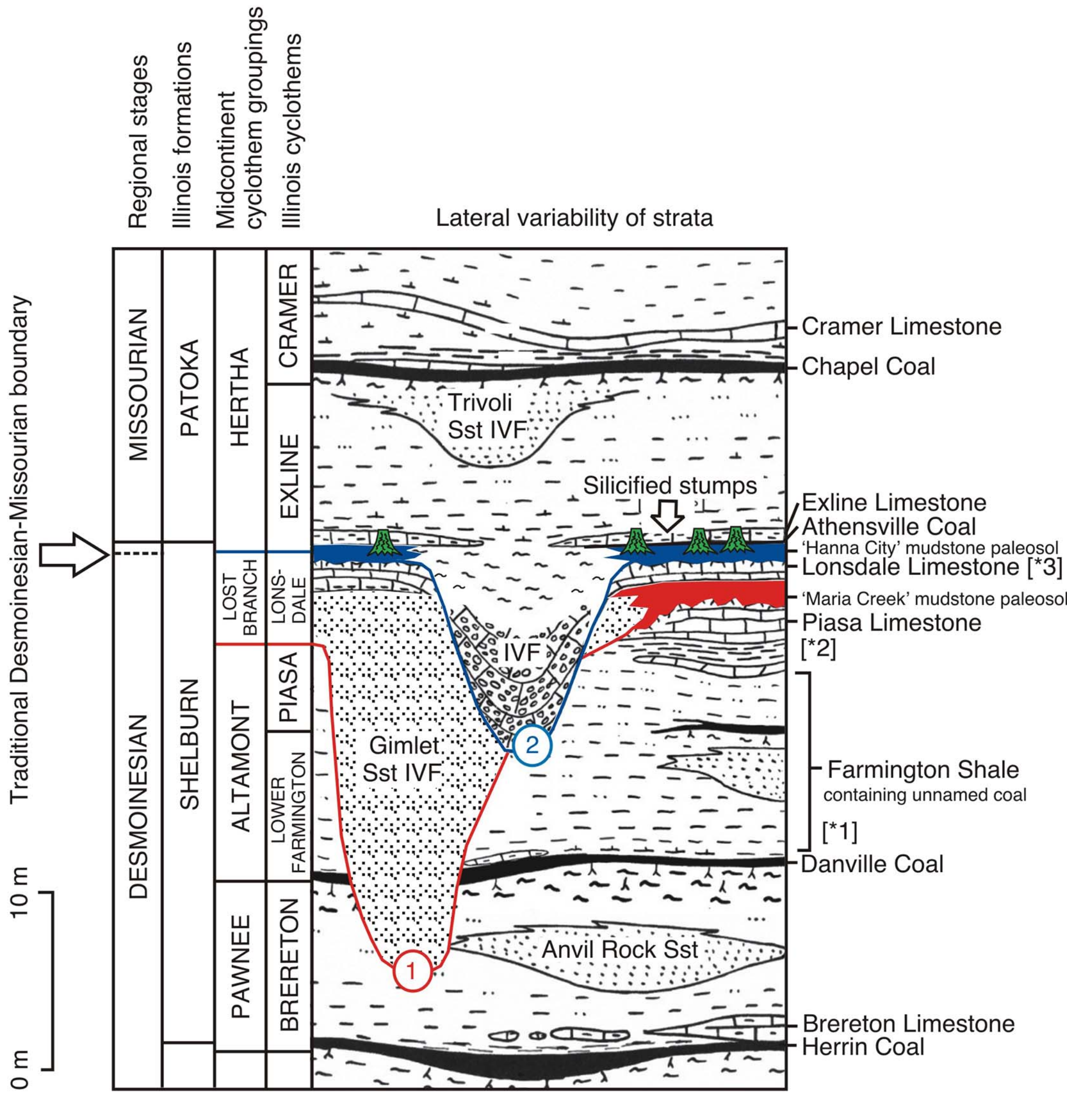

Fig. 4. Late Desmoinesian-early Missourian stratigraphy in Peoria area of Illinois, showing key beds named in text, cyclothems recognized in Illinois, correlation with Midcontinent cyclothem groupings (Heckel, 2008, 2013), and the horizon of silicified tree-stump sites (based on mapping of Wanless, 1957, 1958). Bracketed asterisks numbered 1, 2, and 3 mark positions of the conodont-rich zones characterizing the Lower Farmington, Piasa, and Lonsdale cyclothems, respectively, as described in the text. The red surface comprising an incised valley and paleosol labeled 1 represents the Upper Memorial regression. The blue surface comprising an incised valley and paleosol labeled 2 represents the Seminole regression. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Creek Shale in the Lost Branch cyclothem along the entire Midcontinent outcrop from Iowa to Oklahoma (Heckel, 1991, 2013). Lateral to the 'Hanna City' paleosol, in places, a conglomeratic limestone facies of the Lonsdale represents a paleovalley-fill that reworked fragments of the typical Lonsdale facies. This channel incises down ~15–20 m, close to the level of the Danville Coal (Fig. 4), and locally near the valley center, to only 6 m above the Herrin Coal (Wanless, 1957). Reworked limestone conglomerate is locally 9-m thick in parts of the paleovalley-fill. Together, this incised paleovalley and paleosol surface represents another major regressive phase. The silicified tree stumps, reported here, occur above the Lonsdale Limestone horizon (Wanless, 1958), at the level of the 'Hanna City' paleosol, as elaborated below.

The fourth (uppermost) cyclothem is equivalent to the Exline cyclothem in the lower part of the Hertha grouping in the Midcontinent Basin (Figs. 1–2, 4). It commences with the very thin Athensville Coal, whose base marks the 'traditional' Desmoinesian–Missourian boundary that is based on plant fossils (Fig. 4). This is overlain by the Scottville/Exline Limestone, whose base marks the 'revised' Desmoinesian–Missourian boundary, which is based on conodonts in the Midcontinent (see Falcon-Lang et al., 2011a, Fig. 2). In Peoria County, the Exline Limestone is a black, platy carbonaceous limestone, 0.1–0.8 m thick, with abundant plant fossils, worm tubes and some bivalves, and is typically overlain by black shale with plant fossils (Wanless, 1957).

3.2. ISGS borehole description of boundary section

To improve knowledge of these four boundary-section cyclothems, we drilled a borehole (Illinois State Geological Survey borehole: ISGS#1 Eric Miller) to a depth of 500 ft (~152 m) in the Hanna City 7.5′ Quadrangle at a location (Section 2, T8N, R6E, Peoria County, ISGS county number 35491) that is fairly central to the silicified tree-stump sites (Fig. 5A, B). The relevant portion of the borehole is presented on the accompanying graphic log (Fig. 6A), from the late Desmoinesian Danville Coal to the base of the shales and sandstone above the probable horizon of the earliest Missourian Exline Limestone. Depth is given in feet (with equivalent metres denoted below) to allow easy correlation with ISGS drill core records, which use imperial measurements. Logs and core descriptions are on file at Geologic Records of the ISGS and available via the ISGS website. Core is archived at the ISGS Samples Library in Champaign. To aid biostratigraphic correlation, the borehole

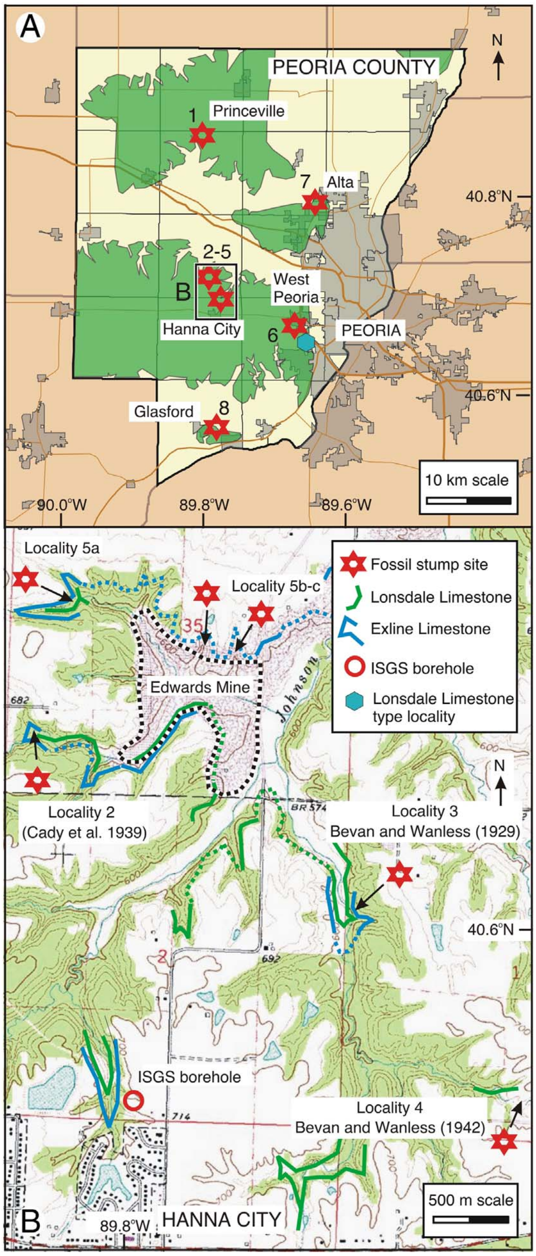

Fig. 5. Map of localities in Peoria County. A., Peoria County showing distribution (green) of Herrin Coal (after Treworgy et al., 2000), the eight sites where silicified tree-stumps have been located (see text for details), and type area of Lonsdale Limestone (Worthen, 1873; Wanless, 1957). B., Detailed geological map of region north of Hanna City, where the greatest abundance of silicified wood is present (based on our field mapping; Bevan and Wanless, 1929, 1942; Cady et al., 1939), showing locations of Illinois State Geological Survey borehole (ISGS#1 Eric Miller; Latitude 40°41′51″N; Longitude 89°47′15″W; Fig. 6) and northern highwall exposure of Edwards strip mine (Latitude 40°43′00″N; Longitude 89°46′59″W; Fig. 7). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was sampled for conodonts using standard procedures, and specimens were identified using Lambert et al. (2003) and Barrick et al. (2013).

The first (lowest) cyclothem, the Lower Farmington cyclothem, comprises the ~0.5-m-thick Danville coal (base at 118.9 ft/~39 m), overlain by black fossiliferous shale that contains abundant conodonts strongly dominated by *Swadelina neoshoensis* (fauna [*1] on Fig. 6A), followed upward by ~6.3 m of dark grey shale that grades upward to lighter grey siltstone at the top beneath the base of the unnamed coal at 97.1 ft (~29 m). This cyclothem is equivalent to the Midcontinent intermediate Farlington cyclothem at the base of the Altamont cyclothem grouping there (Fig. 1).

The second cyclothem, the Piasa cyclothem (depth interval of 61.2–97.1 ft/~29–18.4 m in the borehole core), comprises a ~10.6-m interval consisting of, from base to top, 0.3 m of coal, ~2.9 m of mostly non-marine grey shale, a thin 0.3-m bed of slightly dolomitic fossiliferous limestone, ~2 m of pyritic black shale, mottled at the top, ~2.7 m of nodular limestone in transition to grey shale with limestone nodules, gradationally overlain by ~2.7 m of dark olive grey, mostly massive mudstone with a brecciated zone in the upper part. The pyritic black shale produces a high gamma-ray spike on the wire-line log (Fig. 6A). Both it and the underlying thin dolomitic limestone bed contain an abundant conodont fauna ([*2] on Fig. 6A) dominated by *Idiognathodus* spp., containing *Neognathodus* spp., and including *Swadelina neoshoensis*, confirming the first recognition of the typically erosionally degraded Piasa unit in this area. Based on this fauna, the nodular carbonate unit that forms the upper marine part of this cyclothem is recognized as the Piasa Limestone, and is in its expected position above the Danville Coal and below the Lonsdale Limestone. Above the Piasa Limestone, the 2.7-m-thick unit of mostly massive to brecciated dark olive grey mudstone is recognized as the Maria Creek mudstone, a regionally extensive, mature, polygenetic paleosol. Based on all this information, we correlate this cyclothem with the major Altamont cyclothem in the Midcontinent Altamont grouping.

The third cyclothem, the Lonsdale cyclothem (depth of 56.4–61.2 ft/~16.9–18.4 m in the borehole core) is much thinner and less completely developed in the borehole. The only definitely recognizable element is the Lonsdale Limestone Member, here only 1.44 m thick, with brecciated fabric in the top. Above this unit, the core has poor recovery in the stratigraphic position of the 'Hanna City' paleosol, which is best exposed in the nearby Edwards strip mine (see Section 3.3). No conodonts were recovered from the shale below the Lonsdale. Their absence is probably a result of pervasive paleoweathering and erosional excavation of the shale below this limestone, during karstification associated with early development of the 'Hanna City' paleosol.

The fourth (uppermost) cyclothem (depth of 36.2–56.4 ft/~10.9–16.9 m in the borehole core) is poorly represented at its base in the core profile because of the poor recovery in the interval directly above the Lonsdale Limestone (i.e., in the 'Hanna City' paleosol); however, an overlying sharp-based calcareous shale, 0.43 m thick, with thin-shelled brachiopods may represent a facies of the earliest Missourian Exline Limestone. Based on this information, we correlate this cyclothem with the intermediate Exline cyclothem in the lower part of the Midcontinent Hertha grouping, and place the Desmoinesian–Missourian boundary at a depth of 56.4 ft (~16.9 m) in the borehole core.

3.3. Edwards strip mine exposure of boundary section

The only known place in Peoria County where this Desmoinesian–Missourian boundary succession is accessible to more detailed study is in the abandoned Edwards strip mine, north of Hanna City and about 2 km north of the borehole core location (Fig. 5B). The floor of the Edwards strip mine is flooded but the upper ~10–12 m part of the northern highwall shows good exposure along a 500-m transect, principally through the interval from the late Desmoinesian Farmington Shale through the Piasa and Lonsdale limestones to the earliest Missourian Exline Limestone. Outcrop studies allow further insights into the paleoweathering profiles developed between each major cyclothem (Fig. 7).

The major Piasa cyclothem at this locality has thickened considerably from the borehole location. Here the Piasa Limestone is up to ~6 m thick, and its upper surface comprises a series of irregular pinnacles of carbonate, up to 2.5 m high and spaced 5–10 m apart (Fig. 7A). In the lower part of the Piasa Limestone, 2–4 m diameter blocks of bedded carbonate are randomly tilted at angles of up to 25°

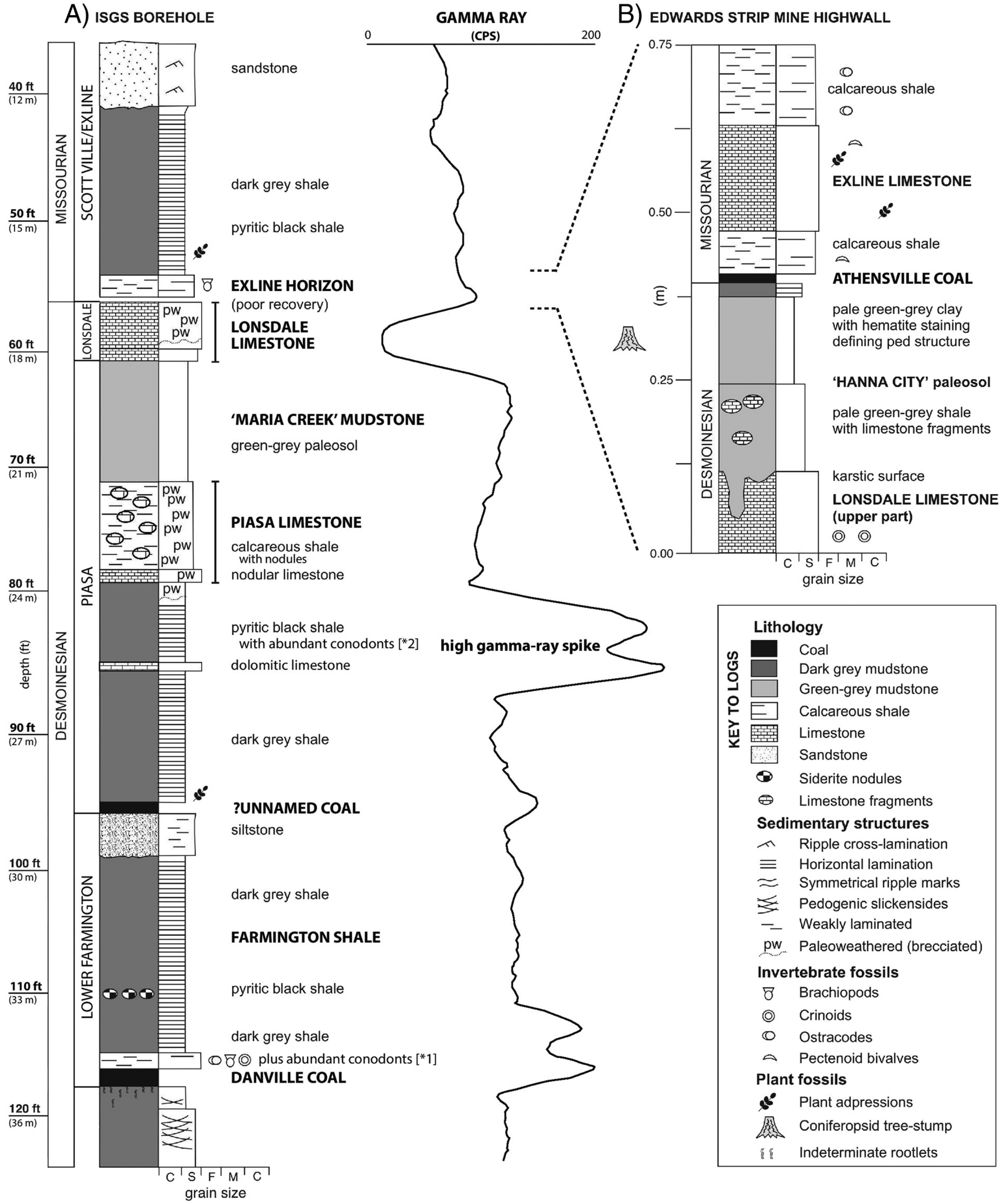

Fig. 6. Local stratigraphy. A, Graphic log of relevant part of Illinois State Geological Survey borehole (ISGS#1 Eric Miller; Latitude 40°41′51″N; Longitude 89°47′15″W; Section 2, T8N, R6E, Peoria County, ISGS county number 35491; see Fig. 5B for location), from late Desmoinesian Danville Coal to just above earliest Missourian Exline horizon, showing Illinois cyclothems and the trace of the accompanying gamma ray log that illustrates spikes at horizons of abundant conodonts; although conodont zones [*1] and [*2] are present in the core, zone [*3] typically present at the base of the Lonsdale Limestone was likely eroded out during karstification accompanying the major Seminole regression. B, Graphic log of exposure from top of Lonsdale Limestone to just above Exline Limestone observed in northern highwall of Edwards strip mine, with stump symbol showing probable position of fossil stumps within complex 'Hanna City' paleosol.

(Fig. 7C). We interpret these features as limestone dissolution phenomena developed in a karstic terrain; the large-scale pinnacles represent subdued tower-karst topography, and the tilted limestone blocks record sub-surface dissolution and bedrock foundering into caverns (Ford and Williams, 1989). The Maria Creek mudstone paleosol infills and overlies this karst topography, and comprises olive-grey mudstone beds that contain brecciated clasts of carbonate ranging in size from pebbles to boulders.

The major Lonsdale cyclothem is thin at this locality (< 1.75 m), and the upper surface of the Lonsdale Limestone similarly shows a karstified top with small-scale pot-hollows (Fig. 7B), interpreted as solution-widened grykes. It is overlain by a second olive-grey mudstone

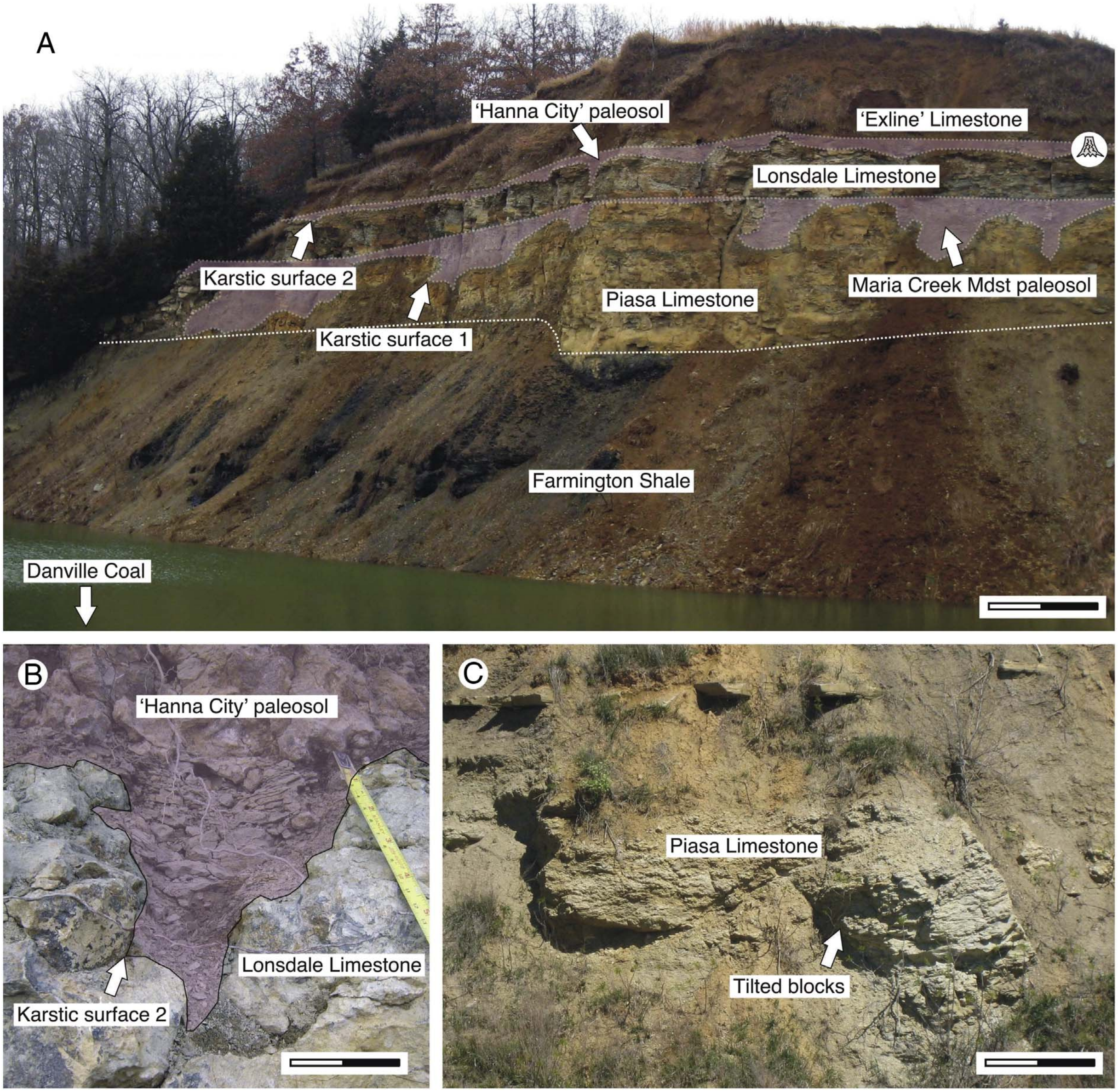

Fig. 7. Paleoweathering (karstification) features and paleosols, seen in Piasa and Lonsdale limestones exposed in northern highwall of Edwards strip mine. A., Carbonate pinnacles, up to 2.5 m high, interpreted as subdued tower karst, developed on top of Piasa Limestone, scale: ~2 m. B., Pot hollows, infilled by onlapping layers of green-grey clay, developed on top of Lonsdale Limestone, and interpreted as grykes, scale: 0.1 m. C., Large, randomly tilted blocks in Piasa Limestone, suggestive of foundering into solution caverns, scale: ~1 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

bed with brecciated clasts of carbonate, capped by a 12-cm thick claystone with a structure of hematite-skinned peds (Fig. 6B). Although representing a complex history of paleosol formation during the Desmoinesian transition, both are assigned to the 'Hanna City' paleosol based on its stratigraphic position (Fig. 7A). Silicified tree stumps are seen in several places around the Edwards mine highwall at the approximate level of the 'Hanna City' paleosol, although their precise stratigraphic position cannot be accurately determined due to cover, with approximately 0.5 m of vertical uncertainty in placement.

The base of the Exline cyclothem is marked by a 5-cm thick layer of dark grey shale, coaly shale and coal, which overlies the olive-grey paleosol of the underlying cyclothem with a sharp contact, and represents a younger poorly drained paleosol related to the Exline transgression. The thin coal smut is interpreted as the Athensville Coal (Fig. 6B), representing brief establishment of mire vegetation, and also recording final *Lycospora* extirpation. This is, in turn, overlain by a 10-cm thick calcareous shale with pectenoid bivalves, followed by the 15-cm-thick dark grey Exline Limestone with pectenoid bivalves (Fig. 8A), spirorbids (Fig. 8B), abundant plant assemblages (especially *Cordaites* leaves: Fig. 8), and insect wings. This facies of the Exline Limestone formed in a dysaerobic brackish-marine embayment. A further 12-cm-thick calcareous shale containing ostracods caps the highwall succession.

4. Geological context of silicified tree-stumps

Sites with silicified tree-stumps (Fig. 5) were first reported in Peoria County in the course of late nineteenth to mid-twentieth century field mapping by Illinois State Geological Survey field geologists (Worthen, 1873; Lesquereux, 1879; Udden, 1912; Bevan and Wanless, 1929, 1942; Cady et al., 1939; Dunbar and Henbest, 1942; Wanless, 1957, 1958). In this study, we were able to re-locate most of the historic sites, find new ones, and place them in a precise sedimentologic, stratigraphic and cyclothemic context within the Desmoinesian-Missourian boundary section.

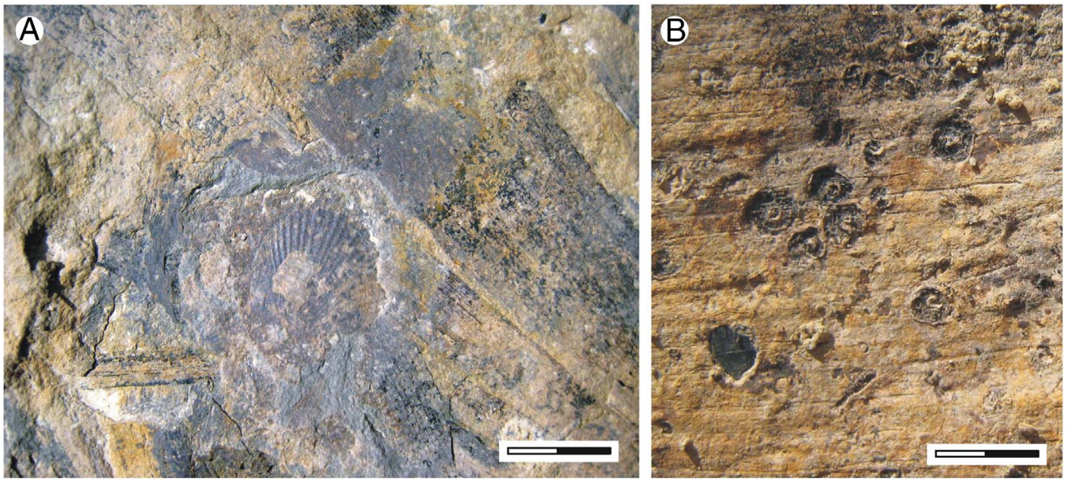

Fig. 8. *Cordaites* leaves in earliest Missourian Exline Limestone at Edwards strip mine. A., Randomly orientated *Cordaites* leaves with pectinoid bivalves, scale: 2.5 cm. B., Close-up of a *Cordaites* leaf enrusted with spirorbids, scale: 5 mm.

4.1. Oak Hill 7.5′ Quadrangle

The earliest report was by Worthen (1873), who noted highly abundant "fossil wood, all of it completely silicified" along a branch of the north fork of Kickapoo Creek (Oak Hill 7.5′ Quadrangle; Section 4, T10N R6E; no spot in section; Locality 1 on Fig. 5A). Worthen (1873) commented that pieces are "two to three feet in length" and represent remains of "what were once large trees" (p. 245). All the material that Worthen (1873) observed was in float, but he had "no doubt" that it derived from an interval of yellow/green shale developed on top of the Lonsdale Limestone (Worthen's "limestone conglomerate") and below the 'Exline' Limestone, i.e., the interval of the 'Hanna City' paleosol. Worthen (1873) made no comment about whether the fossil wood specimens were rooted tree stumps, specifically, and we were unable to re-locate this site to confirm details.

4.2. Hanna City 7.5′ Quadrangle

A further cluster of six occurrences was documented in the Hanna City 7.5′ Quadrangle (Fig. 5A). In this region, Cady et al. (1939) recorded "an exposure of black limestone" (the Exline Limestone based on our own field mapping) close to "an upright tree stump" exposed in a ravine (Locality 2 of Fig. 5B), 400 m west of the Edwards strip mine. We managed to re-locate this site and confirm that fossil material did, in fact, comprise silicified tree-stumps rather than more general trunk fragments. However, material was exclusively in float, and whereas stumps were below the level of the Exline Limestone, and close to outcrops of the Lonsdale Limestone, their precise stratigraphic position could not be determined accurately. At other nearby localities southeast of the Edwards strip mine, Bevan and Wanless (1929) reported "large pieces of petrified wood, source not seen" (Section 1; T8N R6N; NW-SW-NW; Locality 3 on Fig. 5B), and Bevan and Wanless (1942) noted "many blocks of silicified wood" in a clay overlying the Lonsdale Limestone (Section 1; T8N R6E; NE-SW-SE; Locality 4 on Fig. 5B). We documented three additional occurrences of silicified tree stumps (grouped together as Locality 5a–c), north and west of the Edwards strip mine (Fig. 5B), and our own mapping confirmed that these occurrences were near the level of the Lonsdale Limestone, although exact field relationships were obscured by cover. We also met several local people in the area who had silicified wood specimens in their yards, and Kent Snowdon, the owner of the Edwards strip mine site, reported that, "all the local kids have collections of fossil wood", suggesting that this material is widely scattered across the Hanna City area. It is difficult to determine, with precision, the stratigraphic horizon of these occurrences, but most likely they derive from the 'Hanna City' paleosol.

4.3. Peoria West 7.5′ Quadrangle

Udden (1912) described "large pieces of silicified trunks of trees" associated with a "dirt bed" (p. 38) developed 1.5 m above the Lonsdale Limestone from a locality in the Peoria West 7.5′ Quadrangle (Section 11 of Limestone Township; T8N R7E; Locality 6 on Fig. 5A). The historically obsolete quarryman term "dirt bed" was used to refer to paleosols associated with the Purbeck Fossil Forest in the Jurassic of Dorset, UK (Francis, 1984), and its usage was popularized in geological textbooks (e.g., Lyell, 1871) that would have been familiar to Udden. It is certain that Udden (1912) was using "dirt bed" in this sense, to signify a paleosol, because he described the layer with the silicified wood as an "old soil, indurated, dark, micaceous, with fragments of vegetation, impressions of stems" (p. 39). We could not re-locate this site to confirm details but the stratigraphic description closely fits with the 'Hanna City' paleosol.

4.4. Dunlap 7.5′ Quadrangle

Lesquereux (1879) described a silicified tree-fern trunk, referred to *Caulopteris* (*Psaronius*) *giffordi* (Lendemer, 2002), from Alta, northwest of Peoria (Dunlap 7.5′ Quadrangle; T10N R7E, no spot in section; Locality 7 on Fig. 5A). No details of the geological context were given, but this location comprises a small outlier above the Danville Coal, near the level of the Lonsdale Limestone. It remains uncertain if this fossil is from exactly the same horizon as the other tree-stumps although it clearly came from near the 'traditional' Desmoinesian-Missourian boundary.

4.5. Glasford 7.5′ Quadrangle

In the most explicit documentation of silicified tree stumps in their geological context, Wanless (1958, p. 23) reported the following observations: "In one locality in the Glasford Quadrangle, erect silicified stumps were observed rooted in the top of the Lonsdale Limestone, and fragments of silicified wood are common at the top of the Lonsdale Limestone at several places. This is interpreted as showing that the sea drained away shortly after the Lonsdale limestone was formed and the emerged limestone provided a "soil" that supported forest vegetation". No specific localities were identified, but the geologic maps show that this area comprises a small outlier of Middle Pennsylvanian strata capped near the level of the Lonsdale Limestone (Locality 8 on Fig. 5A). We visited the site, and identified outcrops of Lonsdale Limestone in stream sections but did not find evidence of the in situ stumps reported by Wanless (1958). However, Steve Thomson, the landowner, showed

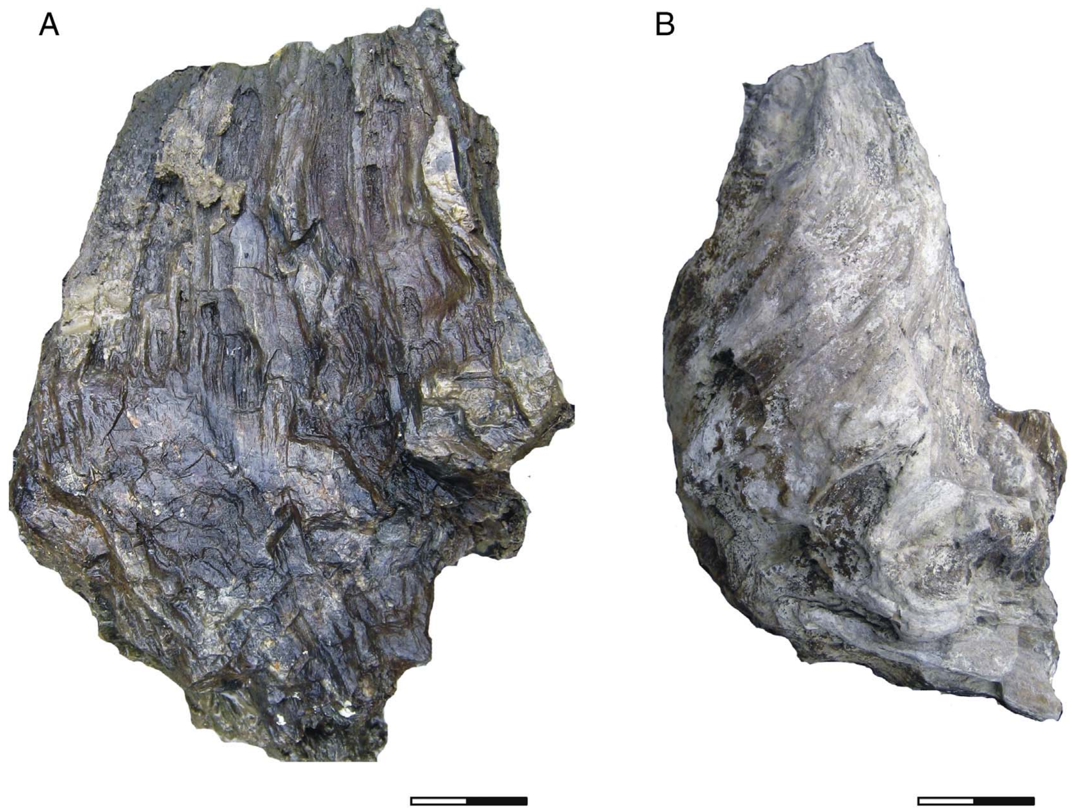

Fig. 9. Silicified tree-stump morphology. A., The larger stump morphotype showing a gently tapering trunk, robust taproot, and symmetrically distributed lateral roots, scale: 10 cm. B., The smaller stump morphotype showing a sharply tapering trunk, twisted wood grain, and asymmetrical roots, scale: 6.5 cm.

us eight large specimens of silicified wood, including at least one tree-stump, in his yard, which he had collected in float, lending credence to the historical observations. This is a clear record of silicified tree-stumps rooted in the 'Hanna City' paleosol.

4.6. Stratigraphic context of silicified tree-stumps

Despite our own field survey, we were unable to observe silicified tree-stumps in growth position, in a sedimentologic context, with the level of geological detail given by earlier workers. Examination of late nineteenth to mid-twentieth century field photographs (ISGS archives) show that rock exposure was more widespread in the ravines of Peoria County than it is today. This is almost certainly because, at that time, much of the land had been cleared for farming. With improved soil conservation today, many formerly bare areas have become re-vegetated, concealing rock exposures. And, as mentioned above, local collectors have hauled away many of the most accessible specimens over the past 150 years. Consequently, we have had to be more reliant on historical sources that we would have liked in order to glean an understanding of the silicified tree-stumps.

4.6.1. Critical stratigraphic placement

Only Wanless (1958) reported to have observed field relationships clearly, and he was certain that "erect silicified stumps" were rooted within what we now know as the 'Hanna City' paleosol developed on the paleoweathered top of the Lonsdale Limestone. Udden (1912) is also noteworthy for stating that the silicified trees were associated with a paleosol. While his stratigraphic section points to an association with the 'Hanna City' paleosol, he does not specifically state that silicified trees were rooted in the paleosol. Other reports (Worthen, 1873; Cady et al., 1939; Bevan and Wanless, 1942) infer a similar relationship, with greater uncertainty. Least certain is if the material described by Lesquereux (1879) is from the same horizon as the rest of the material, although it is clearly from that approximate interval. Our own field observations confirm that silicified fossil wood is abundant near the level of the Lonsdale Limestone, and within 0.5 m of the 'Hanna City' paleosol level, at many localities, and comprises, specifically, mostly tree-stumps with lateral roots as described below. Overall, it is highly probable that this material derives from an autochthonous silicified 'fossil forest' (sensu DiMichele and Falcon-Lang, 2011), rooted in growth position in the 'Hanna City' paleosol developed on top of the Lonsdale Limestone. The area over which silicified tree stumps are found amounts to ~250 km^2, making it one of the most widespread fossil forests ever described. Outside of Peoria County, silicified wood is extremely rare in Pennsylvanian rocks of the Illinois Basin. To find such uncommon fossils at more than one stratigraphic horizon in the same geographic area would be most remarkable.

4.6.2. Biostratigraphic age of 'Hanna City' paleosol and fossil forest

The typical Lonsdale Limestone facies contains a conodont-rich shale near its base dominated by *Swadelina nodocarinata*, and including *Neognathodus*, *Idiognathodus* and *Gondolella magna*. This fauna ([*3]), particularly *Gondolella magna*, allows correlation of the Lonsdale Limestone with the Attila Shale of southern Illinois, and with the Nuyaka Creek Shale in the Lost Branch cyclothem along the entire Midcontinent outcrop from Iowa to Oklahoma (Heckel, 1991, 2013). In this cyclothem context, the silicified forest correlates with the major marine drawdown event related to part of the 'Seminole' regression (Fig. 1).

5. Anatomy of silicified tree stumps

In the course of our field investigations, ~45 specimens of silicified fossil wood were observed, all in float, near the top of the Lonsdale Limestone of Peoria County. The morphology and anatomy of the four most completely preserved silicified tree-stumps are described.

5.1. Stump gross morphology

The four specimens represent two tree-stump morphotypes. The larger morphotype (n = 3) comprises buttressed stumps, 0.51–0.67 m diameter, that slowly taper upwards, show a single, robust, vertical taproot, up to 0.21 m diameter, and a broadly symmetrical pattern of robust lateral roots that curve towards the horizontal plane (Fig. 9A). The smaller morphotype (n = 1), 0.19 m diameter, comprises a much more sharply tapering stump, showing a distinctively corkscrew twisted grain, and a complex array of lateral roots, of various sizes, which are strongly asymmetric in distribution (Fig. 9B).

5.2. Wood anatomy

Standard petrographic thin sections were prepared for each of the four stump specimens in transverse, radial longitudinal and tangential longitudinal sections (TS, RLS, and TLS, respectively). Thin sections were described and imaged using an Olympus binocular BH-5 and a Nikon digital camera system. Only secondary xylem was preserved, and anatomy was identical for both stump morphotypes.

In RLS, tracheids show 1–5 (mostly 2–3) seriate, alternate, circular bordered pits (Fig. 10A, B), 8–12 μm diameter, with oblique, oppositely oriented apertures (Fig. 10C). Cross-field pitting comprises 2–6 araucarioid pits per field (Fig. 10B). In TLS, rays are dominantly uniseriate, 1–17 cells high, with short biseriate portions (Fig. 10D–F). Very common are strands of axial parenchyma, typically up to 5–10 cells high (Fig. 10D, E). In TS, tracheids, 35–50 μm diameter are arranged in radial files (Fig. 10G), and show irregular growth interruptions, 1–4 mm wide, comprising zones of smaller, thin-walled tracheids, 20–25 μm diameter, interspersed with abundant axial parenchyma (Fig. 10H) with profusely pitted transverse walls (Fig. 10I).

5.3. Stump identification

Secondary xylem of this type is characteristic of late Palaeozoic coniferopsids (Falcon-Lang et al., 2014). Where found without details of pith and vasculature, such material would normally be placed in *Dadoxylon* (Noll et al., 2005); however, the presence of growth interruptions with abundant axial parenchyma is uncommon for this genus. Identical, but more completely preserved material, assigned to *Amyelon* (Barnard, 1962) and inferred to represent the root/stump wood of cordaitaleans (Cridland, 1964), has recently been described from Middle Pennsylvanian dryland alluvial facies in Staplehill, Bristol, UK (Falcon-Lang et al., 2011b). Therefore, we assign the Peoria material to *Amyelon*, an inference that is consistent with its known origin as root/stump tissue.

In the Staplehill assemblage, *Amyelon* is closely associated with specimens of *Mesoxylon*, which Falcon-Lang et al. (2011b), similarly, interpreted as a dryland cordaitalean. However, those Staplehill axes, also, closely resemble axes more-recently described as *Giblingodendron* (Falcon-Lang et al., 2014), an enigmatic dryland coniferopsid, which has been compared with cordaitaleans, conifers and dicranophylls (see Falcon-Lang et al., 2016, for an in-depth discussion of affinity). Nonetheless, three considerations favour a cordaitalean affinity for the Peoria specimens: (1) *Cordaites* leaves are co-dominant, together with pecopterid ferns, in the adpression assemblage in the earliest Missourian 'Exline' Limestone that directly overlies the silicified fossil forest (Fig. 8); (2) walchian conifers are extremely rare in latest Desmoinesian time, with only four records known (Arnold, 1941; Rothwell, 1982; Falcon-Lang et al., 2009; Plotnick et al., 2009; Scott et al., 2010); and (3) dicranophylls generally do not occur west of the Appalachians until mid-to-late Missourian times (Fig. 10A; Mamay, 1981; Falcon-Lang et al., 2016). However, given the uncertainties surrounding wood identification, we remain cautious about assigning the Peoria stumps to any particular clade, and refer to them here as indeterminate coniferopsids.

5.4. Paleoecologic and paleoclimatic interpretation

Based on anatomical observations, there is no evidence that the two stump morphotypes are of systematic significance, and we interpret them here as either ontogenetic variants or, more likely, reflecting local growing conditions. For example, the larger stump morphotype is characteristic of trees growing on thick, well-drained soils, where the taproot is able to penetrate deeply and the lateral roots spread symmetrically (Gasson and Cutler, 1990). In contrast, the smaller morphotype, though more adaptable with regard to soil depth, has features that are consistent with growth on thin rocky soils, where the root bole develops asymmetrically due to obstacles, and the grain of the wood becomes twisted as the tree compensates to maintain an erect trunk (Gasson and Cutler, 1990). Another significant feature is the presence of growth interruptions, marked by small, thin-walled tracheids and an abundance of axial parenchyma. Weakly developed growth rings are typical of stump wood, and correlate with more marked rings higher in the trunk of some cordaitalean taxa (Falcon-Lang et al., 2011b). The presence of such features suggests growth under intermittent periods of edaphic water stress, the most likely cause of which would be tropical seasonality (Jacoby, 1989).

6. Silicified tree stumps in cyclothem context

Here we discuss the significance of the silicified tree-stumps in Peoria County, and their implications for the stepwise collapse of the Carboniferous Coal Forests. This discussion is based on a critical synthesis of the new findings with earlier analyses of the contemporaneous Lost Branch cyclothem in the Midcontinent (Heckel, 1991), the continent-wide sea-level curve and correlation of cyclothems (Heckel, 2008, 2013), and the extraordinarily high paleotemperature inferred from a late Desmoinesian Maria Creek mudstone paleosol (Rosenau et al., 2013b).

6.1. Intensification of end-Desmoinesian glacial cycles

Although near-field records suggest that Gondwanan ice cover was fairly low during the Desmoinesian–Missourian interval (Isbell et al., 2003; Fielding et al., 2008), and the Earth was experiencing a greenhouse episode (Montañez and Poulsen, 2013; Montañez et al., 2016), near-field records are generally coarse compared to the far-field record of lateral extent of correlatable cyclothemic marine transgression (glacial melting) alternating with sea-level fall (glacial buildup) that resulted in formation of paleosols and incised valleys.

The far-field sea-level curve for the Midcontinent (Heckel, 2008, 2013) shows that lowstand shorelines between most late Desmoinesian and early Missourian cyclothems (Fig. 1) did not extend basinward very far south of the Kansas-Oklahoma border (long interglacials I and II of Heckel, 2008, 2013; see also Rygel et al., 2008). However, after the minor Idenbro transgression into southeastern Kansas, there was a marked intensification of the amplitude of glacial cycles. The shoreline regressed some 250 km farther, to the vicinity of Ada, about 100 km southeast of Oklahoma City in south-central Oklahoma (Fig. 1). The evidence is the development of a paleosol in the Upper member of the Memorial Shale across the Midcontinent, which we informally name the 'Upper Memorial' regression. This major regression was in response to a short, but much greater, buildup of Gondwanan ice than for, perhaps, the previous two million years of the late Desmoinesian (Fig. 1; Heckel, 2013, p. 15). It is noteworthy that the North American record conforms closely to the sea-level curve developed for the Donets Basin (Eros et al., 2012; Montañez et al., 2016), which is also the time during which the latter authors inferred the greatest fluctuations in the amplitude of CO_2 fluctuations.

During this time of significant regression, all cyclothemic sediments of the major Altamont grouping were subject to subaerial exposure, soil formation, erosion, and paleovalley incision. This was particularly true

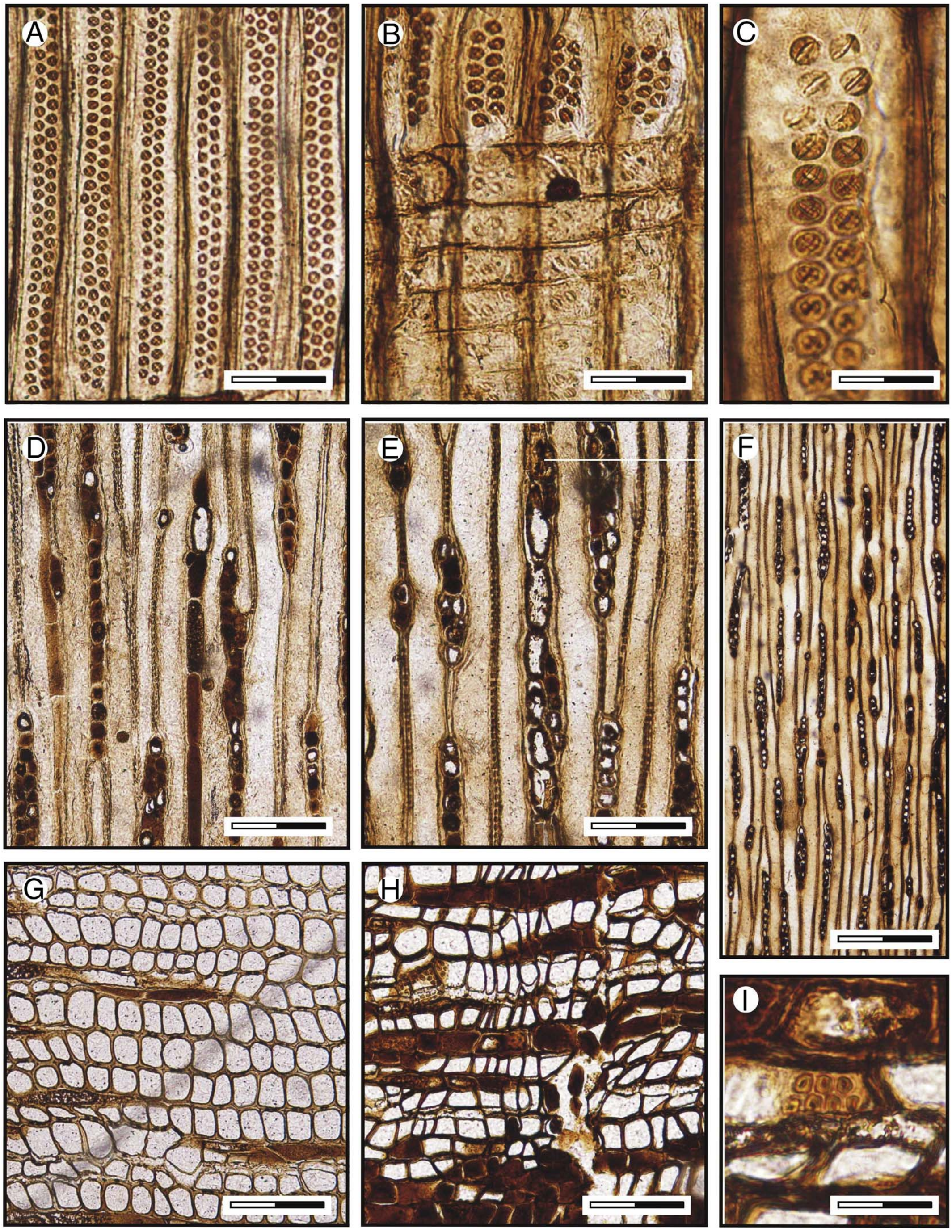

Fig. 10. Silicified stump anatomy. A., Tracheid showing 2–3-seriate, alternate, circular bordered pits, RLS, scale: 100 µm. B., Cross-field pitting with 2–6 araucarioid pits per field, RLS, scale: 50 µm. C., Close-up of tracheid pitting showing distinctly circular shape (not hexagonal) and opposite, oblique apertures, RLS, scale: 25 µm. D., Axial parenchyma strands, TLS, scale: 100 µm. E., Axial parenchyma strand > 8 cells high, TLS, scale: 80 µm. F., Uniseriate rays, 1–17 cells high, with short biseriate portions, TLS, scale: 300 µm. G., Tracheids, 35–50 µm diameter, arranged in radial files, TS, scale: 150 µm. H., Close-up of growth interruption zone showing smaller, thin-walled trachieds, 20–25 µm diameter, interspersed with abundant axial parenchyma, TS, scale: 150 µm. I., Axial parenchyma cells show profusely pitted transverse walls, TS, scale: 25 µm.

for the major Altamont and equivalent Piasa cyclothems, which were exposed for the longest times on the higher mid-shelf of their respective basins. It must have been during the initial part of the 'Upper Memorial' regression that the top of the Piasa Limestone became strongly karstified, under humid climate conditions, as seen in the Edwards mine north of Hanna City in Peoria County (Fig. 7). After exposure, this dissolution surface became overlain by the cumulative paleosols of the Maria Creek mudstone observed across the northwest part of Illinois Basin, including the study area in Peoria County.

It was from the Maria Creek mudstone paleosol that Rosenau et al. (2013b) obtained their significant temperature excursion showing up to 6 °C of global warming. These were sufficiently high temperatures and aridity, in the latter stage of paleosol formation, for the mudstone to become locally reddened to high-chroma color, unlike any older Desmoinesian paleosols or any younger early Missourian paleosols in the region. The paleotemperature estimate obtained by Rosenau et al. (2013b) from this paleosol characterizes an interglacial phase warm enough to melt the greater buildup of Gondwanan ice and trigger the Attila-Lonsdale transgression into the Illinois Basin. During the early part of this major transgression, peat mires (represented by the

Lycospora-rich Dawson Coal in northern Oklahoma and southern Kansas, and the Pond Creek and Rock Branch coals in southern Illinois) were populated by the last widespread lepidodendrid forests west of the Appalachians (Peppers, 1996). Palynological studies from overlying sections show a progressive decline in *Lycospora* through the medial interval of the Lost Branch cyclothem (Peppers, 1997).

The regression that followed deposition of the Lonsdale Limestone on the northern shelf of the Illinois Basin, again took the shoreline far southward and basinward into south-central Oklahoma with only a minor transgression (Glenpool) in the Kansas-Oklahoma border region (Fig. 1). No coals are known to be associated with this minor reversal of shoreline trend, but the abundance of palynomorphs associated with lycopsids decreased moderately upward through the Lost Branch-Glenpool interval and these kinds of spores nearly disappeared above the Glenpool, whereas those associated with ferns increased significantly above the Glenpool into the Hepler Coal (Peppers, 1997). In Oklahoma, the shoreline regressed far enough that a major incised paleovalley system formed and ultimately became filled with the Seminole Sandstone, hence we informally name this episode the 'Seminole' regression. This paleovalley-fill contains a silicified tree trunk near Ada, Oklahoma that shows seasonal growth rings (Wilson, 1963), indicating that the lowstand coincided with a seasonally dry climate.

This regression was in response to the second and final major Gondwanan glacial buildup of the relatively short-term glacial episode B of Heckel (2008, 2013), and may have been the most intense short-lived glacial phase of the Pennsylvanian. This event probably further stressed any remaining sparse lepidodendrid communities, by taking the shoreline into the steeper margins of the basins of central Oklahoma, where the swamps they required for reproduction were greatly reduced in areal extent (Heckel, 1991). *Lycospora* finally disappeared from Pennsylvanian sediments west of the Appalachians during an unrecorded interval of the non-depositional episode represented by the Seminole regression (Peppers, 1997).

After deposition of the Seminole Sandstone, initial melting of the Gondwanan ice cap resulted in the Checkerboard-South Mound transgression, which extended only into southeastern Kansas. This was preceded by mires that produced the Tulsa and Hepler coals of northern Oklahoma and southern Kansas, respectively, which lack *Lycospora* and are dominated by palynomorphs of tree-ferns and seed-ferns (Peppers, 1996, 1997). After the shoreline regressed back into northern Oklahoma, the next transgression deposited the open marine Exline Limestone onto the northern Midcontinent shelf into Iowa, and the open marine Scottville Limestone in the Illinois Basin, which extends into Peoria County as the black dysaerobic limestone and calcareous shale that have long been termed the Exline Limestone in this area.

6.2. 'Hanna City' paleosol and the silicified fossil forest

Prior to the Scottville-Exline transgression, the northern shelf of the Illinois Basin was subject to a long period of subaerial exposure (Fig. 1). During this Seminole regression, the Lonsdale Limestone initially became subject to intense meteoric diagenesis, resulting generally in a mottled semi-brecciated appearance with partially spar-filled fractures separating in-place irregular 'clasts'. In parts of Peoria County, however, meteoric diagenesis went much further, resulting in karstification that left grykes and pinnacles at the top of the Lonsdale, and erosion in some places that cut out large areas of the limestone and allowed cutting of deep channels into the underlying mudstone. Collapse of much of the remaining karstic brecciated carbonate into the channels and later reworking by running water rounded the clasts into pebbles and formed the limestone conglomerates that dominate the Lonsdale in these places. All this must have occurred under moist subhumid to humid climates (as circumscribed by Cecil, 2003, based on monthly rainfall vs. evapotranspiration patterns). As sea-level continued to fall, material was reworked into incised valleys, cutting down in places, up to 55 m, nearly to the level of the Herrin Coal (Wanless, 1957), and infilling with accumulations of carbonate conglomerate, up to 9 m thick.

It was during this long sedimentary hiatus, of perhaps ~300 kyr (Fig. 1), that the tree-stumps, reported here, grew on top of the Lonsdale Limestone in northwestern Illinois, and eventually became silicified. That hiatus includes two minor glacial-interglacial climate cycles, probably with coupled oscillations in wet-dry climates (Glenpool and Checkerboard-South Mound cyclothems: Fig.1). It is therefore of no surprise that historical reports of the geological context of this fossil forest are variable and uncertain because the forest must have been established on a complex paleoweathered surface that may have been further altered after the forest was fossilized. It is unfortunate that the complicated paleosol facies means that we cannot place the silicified stumps in a more definite paleoclimatic context based on independent sedimentary criteria; however, growth interruption features of the tree-stumps themselves do provide some inferences as to the climate context, suggesting that these trees flourished under seasonally dry climates.

This implies that the establishment of the Peoria silicified fossil forest did not coincide with early periods of karstification of the Lonsdale Limestone (which would have required mostly humid climatic conditions: Ford and Williams, 1989), but with subsequent drier subhumid climatic phases, marked by wet-dry seasonality. An origin during a drier climate is also supported by preservation of the wood in a silicified state; silicification mostly occurs in dryland soils with an elevated pH (Parrish and Falcon-Lang, 2007; Mencl et al., 2009), when not associated with volcanism (Scott, 1990). Those drier climatic phases probably occurred after sea level had withdrawn from the mid shelf (Heckel, 2013), when the upper surface of the Lonsdale Limestone was becoming incised by valley-systems (Wanless, 1957), and calcic Vertisols and Calcisols were forming elsewhere in the Illinois Basin (Rosenau et al., 2013a), although we have no direct evidence of well-drained paleosol development on the complex polygenetic Lonsdale karstified *catena* in Peoria County.

6.3. Reconciling competing hypotheses for Lycospora extirpation

In the introduction, we outlined two hypotheses to explain the stepwise collapse of the Carboniferous Coal Forests: Was this profound ecological event caused by global cooling (Falcon-Lang and DiMichele, 2010) or global warming (Rosenau et al., 2013a, 2013b)? Our new findings, presented here, allow these apparently competing hypotheses to be reconciled.

We show that in the interval leading up to Coal Forest collapse, there was an intensification of the amplitude of glacial cycles in end-Desmoinesian times. This conclusion also was reached by Montañez et al. (2016) with an independent data set. The penultimate Desmoinesian major Piasa (and Altamont) cyclothems were followed by a profound sea-level fall ('Upper Memorial' regression), signaling significant ice buildup on Gondwana, followed by a global temperature spike, signaling onset of sharp global warming (Rosenau et al., 2013b). The inferred temperature rise of up to 6 °C (Rosenau et al., 2013b) seen in the latest Desmoinesian Maria Creek mudstone paleosol above the Piasa Limestone is larger than the trough-to-peak temperature changes of 4 °C ± 0.8 °C inferred for the last Quaternary glacial cycle (Annan and Hargreaves, 2013), and would necessitate a shift to so-called 'super interglacial' conditions (Melles et al., 2012), consistent with the spike in atmospheric CO_2 inferred at this time (Montañez et al., 2016). This was then followed by the largest of all, marine regressions, the 'Seminole' regression that witnessed the sea retreat beyond the Midcontinent shelf edge.

Detailed analysis of palynological data in this context allows the following conclusions to be drawn: (1) Whereas the Maria Creek warming pulse must have stressed lepidodendrid Coal Forests, it failed to completely destabilize them. This is indicated by the continued development of *Lycospora*-rich mires as warming was reaching its peak, represented by the Dawson Coal in the subsequent Lost Branch cyclothem in the Midcontinent and by the Rock Branch and Pond Creek coals in southern Illinois (Peppers, 1996). (2) *Lycospora* began its final sharp decline after this global warming spike, during the peak of the minor Glenpool transgression (Peppers, 1997), which preceded the profound glacial phase represented by the 'Seminole' regression (Heckel, 1991, 2008, 2013). The lepidodendrids were then completely eradicated in western Euramerica at the 'traditional' Desmoinesian-Missourian boundary.

The commencement of *Lycospora* decline in the course of a transition between sharp warming and sharp cooling means that it is currently impossible to ascertain which was the more pivotal event. Rather than hot or cold temperature extremes being to blame, a further related possibility is that it was the rate of global climate change that was a key factor in *Lycospora* extirpation.

7. Discussion

In this paper, we report evidence for silicified coniferopsid tree-stumps (Figs. 9–10), possibly associated with localized tree-ferns (Lesquereux, 1879), which grew and were preserved during a 300-kyr hiatus in sedimentation within the study area, spanning the 'traditional' Desmoinesian–Missourian boundary. The forest is documented throughout an area of ~250 km^2 in Peoria County, northwest-central Illinois, USA, making it one of the largest fossil forests ever so documented. Should the other documented occurrence of silicified wood from Vermilion County, east-central Illinois, be confirmed from the same horizon, this fossil forest would be of even greater extent. Based on growth interruptions and silicic preservation, the coniferopsid (and marratialean?) trees flourished during a seasonally dry episode. The stratigraphic position of the forest coincides exactly (within the limits of stratigraphic resolution) with the initial stepwise collapse of the Carboniferous Coal Forests, characterized by the extirpation of *Lycospora*-producing lepidodendrids, west of the Appalachians (Phillips et al., 1974, 1985; DiMichele and Phillips, 1996; Kosanke and Cecil, 1996; Peppers, 1997; Falcon-Lang et al., 2011a). The collapse event was probably linked to an intensification of the amplitude of glacial cyclicity, and the spike of warming represented by isotopic records in the Maria Creek mudstone may have been the initial trigger. Here, we discuss the implications of the new fossil discoveries for the better understanding of this key event in the History of Life.

7.1. Biogeography of north-equatorial Euramerica, west of Appalachians

To appreciate the wider significance of the Peoria silicified fossil forest for understanding the biome-scale vegetation-dynamics that may have been involved in the Desmoinesian–Missourian lepidodendrid extirpation, it is important to clarify regional tectonics and vegetation biogeography (Fig. 11A). During Middle Pennsylvanian time, north-equatorial Euramerica contained a number of interconnected tectonic basins (Opluštil, 2004), which were effectively separated into two drainage networks by a continental divide, associated with a northern spur of the Appalachian Orogen (Gibling et al., 1992, 2008); one network, west of the orogenic spur (USA), drained towards Panthallassa, and the other, east of the spur (Atlantic Canada, Europe, Ukraine), drained towards the Paleo-Tethys.

West of the Appalachians, in the area that forms the focus of this study (Fig. 11B), at least two major vegetation biomes existed. In the area closest to the Orogen, including the Appalachian, Michigan, Illinois, Midcontinent, and Midland basins (Greb et al., 2003), wetland forests dominated by arborescent lycopsids, including the *Lycospora*-producing lepidodendrids prevailed during humid climate episodes (DiMichele et al., 2010). This vegetation was broadly similar on both peatland soils (DiMichele and Phillips, 1985, 1994; Phillips and DiMichele, 1992) and waterlogged clastic soils associated with fluvial drainages (Pfefferkorn and Thomson, 1982; DiMichele and DeMaris, 1987; Gastaldo, 1987; DiMichele and Philips, 1988; Willard et al., 1995; DiMichele et al., 2007; Thomas, 2007; Cleal et al., 2009, 2012).

Farther to the west, in the tectonic basins associated with the Ancestral Rocky Mountains in Colorado and New Mexico and the Antler volcanic arc in Idaho, Oregon, and Nevada (Blakey, 2008), climate conditions were more uniformly arid with environments including evaporitic gulfs, sabkhas, aeolian ergs, and dryland alluvial plains (Blakey and Knepp, 1989; Blakey et al., 1988; Blakey, 2009; Soreghan et al., 2008; Sur et al., 2010; Jordan and Mountney, 2012). The vegetation of this western arid region included permanent populations of drought-adapted gymnosperms such as conifers, cordaitaleans and certain pteridosperms, with lepidodendrids, sigillarians, and sphenopsids restricted, mostly, to localized wetland settings (Fig. 11B; Arnold, 1941; Rothwell, 1982; Mamay and Mapes, 1992; Tidwell and Ash, 2004; Lerner et al., 2009; Lucas et al., 2009; DiMichele et al., 2010; Falcon-Lang et al., 2011c; DiMichele et al., 2017). This type of vegetational mosaic persisted during the glacial-interglacial cycles that were accompanied, in the more central region of Pangaea, by major swings between the wetland and seasonally dry adapted biomes (Falcon-Lang et al., 2009; Falcon-Lang and DiMichele, 2010).

7.2. Significance of Peoria silicified fossil forest

The silicified tree-stumps, reported here, are unusual and surprising because they represent evidence for the existence of a seasonally dry coniferopsid (and possibly marattialean) vegetation, similar to that known from the arid western part of Euramerica (Falcon-Lang et al., 2011c), but developed much farther east in the region, in an area (Illinois Basin) that lay near the center of the lepidodendrid Coal Forest belt in end-Desmoinesian times (Greb et al., 2003). The silicified stumps provide fossil evidence that stepwise Coal Forest collapse was associated with an arid climate phase and the temporary colonization by dryland coniferopsid vegetation of the regions occupied by lepidodendrid Coal Forests, prior to the rise of the tree-fern coal forests of the Missourian. This coniferopsid vegetation, probably, dispersed eastwards from the Ancestral Rocky Mountains region in response to climate change (Fig. 11C; DiMichele, 2014).

As summarized above, the cause of this short-term phase of extreme tropical aridification apparently involved an intensification of glacial cycles including a super interglacial phase (the initial trigger) and subsequent profound cooling, drying, and sea-level fall (which ultimately eradicated the lepidodendrids). This climatic excursion, in the area west of the Appalachians, evidentially pushed the hydrophilic lepidodendrids beyond an ecological tipping point from which they could not recover (Phillips et al., 1974; Falcon-Lang and DiMichele, 2010), leading to their extirpation across this region. The orogenic spur that formed the continental drainage divide (Gibling et al., 1992) must have been sufficiently elevated to prevent the subsequent re-introduction of lepidodendrids from the eastern Euramerican region, where they continued to persist, although in much reduced numbers, until, at least, until the end-Carboniferous (Bek and Opluštil, 2006; Opluštil et al., 2013). The Peoria silicified fossil forests therefore shed important light on the biome-scale vegetation-dynamics that accompanied Coal Forest collapse.

7.3. Was Coal Forest collapse pan-tropical?

If tropical aridification was to blame for Coal Forest collapse, a pertinent question is why did it affect the western side of north-equatorial Euramerica more profoundly than the eastern side? Although it is possible that climate change and its impact on vegetation was regionally variable, a more nuanced look at the fossil record suggests that the apparent partial collapse of lepidodendrid Coal Forests may actually be an artifact of an incomplete understanding of the fossil record, and that the collapse may, in fact, have been pan-tropical.

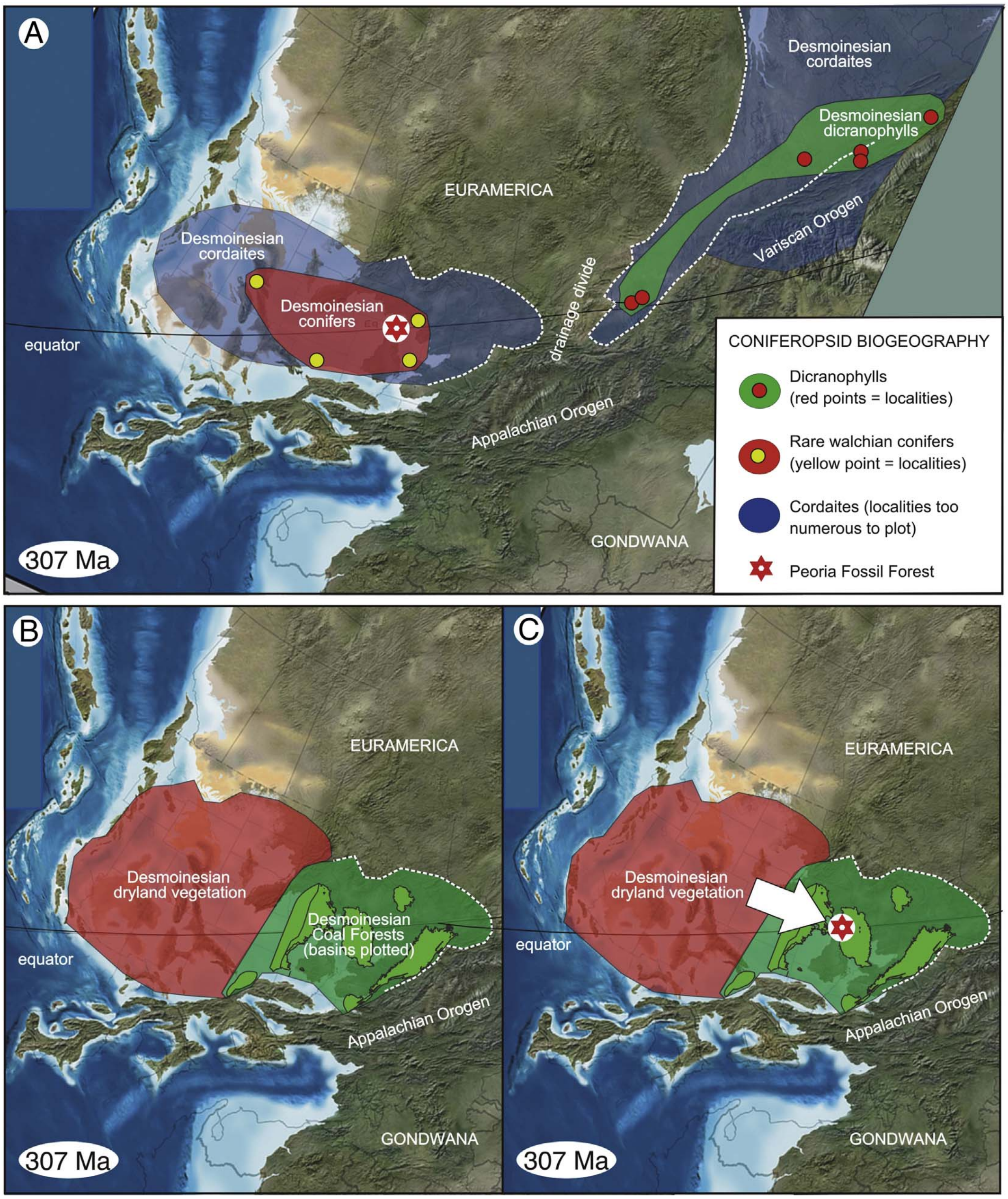

Fig. 11. Biome-scale vegetation-dynamics at the Desmoinesian–Missourian boundary (paleomaps courtesy of Ron Blakey, deeptimemaps.com). A., Desmoinesian biogeography of the three coniferopsid clades (cordaitaleans, dicranophylls, conifers), to constrain the identity of the Peoria tree stumps. B., Biogeography of tropical Euramerica, west of the Appalachians, showing the two major vegetation biomes (see text for discussion) including location of major US coal basins. C., Inferred eastward dispersal (arrow) of dryland vegetation displacing Coal Forests at Desmoinesian-Missourian boundary.

The *Lycospora*-producing lepidodendrids are mostly represented by three taxa of the Lepidodendraceae: *Lepidodendron* sensu stricto, *Lepidophloios*, and *Paralycopodites* (DiMichele and Phillips, 1985). In addition to their well-known extirpation, west of the Appalachians, the *Lycospora*-producing lepidodendrids appear to have undergone sharp decline at a level equivalent to the Desmoinesian–Missourian boundary, east of the Appalachians (Bek and Opluštil, 2006). Of the six *Lycospora* groups identified by Bek (2012), only two persisted, in small numbers, into the late Pennsylvanian of Europe (Bek, 2012): the *L. micropapillata* group found within *Lepidocarpon magnificum* strobili (Balbach, 1966) and produced by an unknown lepidodendrid, and the *L. brevijuga* group found within *Lepidostrobus stephanicus* strobili and believed to be produced by *Asolanus* (Bek and Opluštil, 2004, 2006). Therefore, not only was there a sharp loss of *Lycospora*-producing lepidodendrids in Europe based on palynology, there also seems to have been a total loss of the most iconic taxa: *Lepidodendron* s.s., *Lepidophloios*, and *Paralycopodites* (*Ulodendron* in adpression; Thomas, 1967), the core taxa of the Lepidodendraceae and the Ulodendraceae in the classification of DiMichele and Bateman (1996).

This is borne out by a review of the literature of adpression fossils. Although '*Lepidodendron*' is commonly described from the Stephanian of Europe (Pšenička et al., 2014; Opluštil et al., 2017), assignment may not always be strictly correct. The genus *Lepidodendron*, as traditionally recognized in adpression floras, has been subdivided into two families, Lepidodendraceae and Diaphorodendraceae, based on permineralised coal ball material (DiMichele and Bateman, 1992, 1996), but adpression remains are easily confused. Examination of the published images of the Stephanian records of various species attributed to '*Lepidodendron*' suggests that they actually are representatives of the Diaphorodendraceae (see comments in Bashforth, 2005; Wagner and Álvarez-

Vázquez, 2010; Pendleton et al., 2012; Álvarez-Vázquez and Wagner, 2014), a group that also disappeared along with the *Lycospora*-producers to the west of the Appalachian divide. It is beyond the scope of this paper, however, to undertake a comprehensive systematic review of this matter. Nevertheless, the findings presented here suggest that Coal Forest collapse at the Desmoinesian–Missourian boundary was, probably, pan-tropical, at least for the best-known members of the Lepidodendraceae and Ulodendraceae.

7.4. Excluding orogenesis as a significant confounding factor

One final point requiring discussion is the putative role of orogenesis in Carboniferous Coal Forest collapse. Cleal and Thomas (1999, 2005) have argued that the rise of the Variscan-Appalachian-Ouachita mountain chain may influenced the extirpation of *Lycospora*-producing lepidodendrids, through suppression of the regional water table, and development of palaeosols of drier character. This hypothesis can be excluded from various perspectives. First, orogenesis, in a very general sense, developed with an east to west diachrony (Leveridge and Hartley, 2006), and does not closely coincide with the near-synchronous pan-tropical extirpation (Falcon-Lang et al., 2011a) identified at the Desmoinesian-Missourian boundary. Indeed, the Coal Forest collapse event reported here, in detail, from Illinois occurred in a stable cratonic area, 750 km north of the nascent Orogen, and at least 10 million years before the first signs of regional uplift of the Laurentian craton. Second, the wet/dry climate-fluctuations reported here from Illinois occur with a 100–400 kyr periodicity (Heckel, 2008; Falcon-Lang et al., 2011a) whereas studies of orogenesis suggest that maximal rates of sustained surficial uplift of 1 km per million years (Abbott et al., 1997). Given that an increase in elevation of at least 1 km would be required to influence equatorial climate and vegetation based on Amazonian analogues (Colinvaux et al., 1996), the rate of orogenesis is at least an order of magnitude too slow to generate the palaeoclimate signatures observed. Further, the climate oscillations observed would necessitate repeated cycles of rapid uplift and subsidence for which no plate tectonic model exist. For these reasons, evidence marshaled here points to an amplification of glacial cyclicity as the driver of near-synchronous, pan-tropical Coal Forest collapse at the Desmoinesian-Missourian boundary.

8. Conclusions

1. We describe autochthonous silicified tree-stumps preserved at the Desmoinesian-Missourian boundary at seven localities spread over ~250 km^2 of Peoria County, Illinois, USA.
2. The stumps, referred to *Amyelon*, represent large coniferopsid trees, and parenchyma-rich growth interruptions and silicic preservation are consistent with growth under seasonally dry conditions
3. The new findings shed light on the biome-scale vegetation dynamics that led to the extirpation of lepidodendrid Coal Forests at the Desmoinesian-Missourian boundary. We infer that lepidodendrid extirpation was in response to an intensification of the amplitude of glacial cycles involving, first, a spike of global warming (which stressed forests), followed by, second, intense cooling and greater withdrawal of the sea. Coal Forest collapse commenced during the rapid transition from hot to cold climate states, with final extirpation occurring during the 'Seminole' regression.
4. The wetland areas occupied by lepidodendrids, and the vegetation for which they are iconic, were colonized by dryland coniferopsid populations present in western Euramerica, which temporarily dispersed eastwards in response to an unusual high amplitude climate oscillation, after which hydrophilic lepidodendrid communities were pushed beyond an ecological tipping point from which they were unable to recover.

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