

WHAT HAPPENED TO THE COAL FORESTS DURING PENNSYLVANIAN GLACIAL PHASES?

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ABSTRACT

Sequence stratigraphic analysis of Pennsylvanian coal-bearing strata suggests that glacial-interglacial fluctuations at high latitudes drove cyclic changes in tropical biomes. A literature review of plant assemblages in this paleoclimatic context suggests that coal forests dominated during humid interglacial phases, but were replaced by seasonally dry vegetation during glacial phases. After each glacial event, coal forests reassembled with largely the same species composition. This remarkable stasis implies that coal-forest refugia existed across the equatorial landscape during glacial phases, expanding to repopulate lowlands during and following deglaciation. One possibility is that refugia comprised small pockets of wetland forest strung out along valleys at some sites, but data are currently insufficient to test this hypothesis. The model presented here, if accepted, dramatically alters our understanding of the coal forests and helps explain aspects of their dynamics.

INTRODUCTION

Cyclic patterns of sedimentation in Pennsylvanian coal-bearing strata (cyclothem) have long been attributed to glacial-interglacial cycles (e.g., Wanless and Shepard, 1936). Although demonstrating a direct link with Gondwanan icecap dynamics (Fielding et al., 2008a, 2008b; Rygel et al., 2008) is beyond the resolution of present studies, the strongest evidence for glacioeustatic origin is the fact that cyclothem show evidence for coupled fluctuations in climate and sea level (Tandon and Gibling, 1994) within the Milankovitch band (Maynard and Leeder, 1992). These glacial-interglacial cycles profoundly affected Pennsylvanian tropical landscapes and vegetation as shown by fossil floras (Falcon-Lang, 2004) and computer simulations of paleoclimate (Poulsen et al., 2007).

The best-known Pennsylvanian tropical ecosystems were the so-called coal-swamp forests that formed widespread peatlands (now coal). Dominated at different times by lepidodendrids, cordaitaleans, and marattialean tree ferns (e.g., Phillips et al., 1985), these communities are often referred to as coal forests. Sequence stratigraphic studies show that most coal forests were established during the glacial-to-interglacial transition and, to a more limited extent, during interglacial phases (Tandon and Gibling, 1994; Flint et al., 1995). Continent-wide peat (now coal) formation was triggered by a combination of climate change from seasonally dry (semiarid to subhumid) to ever-wet (humid to perhumid) and a coeval rise in sea level, which elevated the regional water table. Sea-level rise also created the initial accommodation space to preserve the resultant peats (Bohacs and Suter, 1997), which ultimately required the creation of tectonically generated accommodation space for long-term preservation. In marked contrast, successions that occur between coal-bearing intervals commonly include deeply developed paleosols with vertic and calcic characteristics, incised by paleovalleys. These are interpreted as the

deposits of intervening glacial phases during which tropical climate was seasonally dry, and locally semiarid (Tandon and Gibling, 1994; Cecil et al., 2003).

Thus, the Pennsylvanian cyclothem of North America define a generalized climate framework of glacial-interglacial cycles. On the one hand, vertic and calcic paleosols locally incised by paleovalleys (Falling Stage and Lowstand Systems Tracts, FSST and LST) demonstrate that climate was seasonally dry when sea level was falling during the progression to glacial maxima (Gibling and Wightman, 1994; Tandon and Gibling, 1994; Feldman et al., 2005). On the other hand, overlying economic coal seams suggest a shift to ever-wet climate (Cecil et al., 2003). In addition, brackish-marine sediments of the Transgressive and Highstand System Tracts (TST and HST) suggest sea-level rise during deglaciation (e.g., Hampson et al., 1999; Heckel, 2008; Fischbein et al., 2009; Falcon-Lang et al., 2009). This glacial-interglacial signature is, of course, complicated by local tectonics and sediment supply.

While we generally agree on this paleoclimate framework (Fig. 1), we disagree about the exact sequence stratigraphic position of economic coals. WAD's view is that Pennsylvanian coals with well-developed underclay paleosols dominantly comprise late LST deposits. They most often lie below the ravinement surface of a major transgressive marine unit (usually a marine black shale in the midcontinent United States) that marks the TST (Demko and Gastaldo, 1992; Archer et al., 1994). In this model, peat formation occurs as a consequence of base-level rise driven by non-seasonal rainfall, originating from confinement of the Intertropical Convergence Zone close to the equator or its intensification due to increased Hadley Cell turnover during the late LST (Cecil et al., 2003; Poulsen et al., 2007; Elrick and Nelson, 2010).

In contrast, HFL's position is that coals dominantly comprise mid- to late-TST deposits (Flint et al., 1995) because brackish fauna and estuarine facies locally occur below coal seams within expanded valley-fill successions (e.g. Gibling and Wightman, 1994; Feldman et al., 1995), indicating that sea level had risen significantly prior to the onset of peat (coal) formation. In this latter model, peats kept pace with rising sea level and may represent, in part, time-transgressive units, albeit rapidly transgressive. Marine roof shales above coals demonstrate that the rate of sea level then accelerated, outpacing peat formation and resulting in marine flooding, as full interglacial conditions were approached.

TROPICAL VEGETATION DURING GLACIAL PHASES

Compared to our knowledge of coal forests, relatively little is known of the vegetation that covered Pennsylvanian tropical landscapes during seasonally dry glacial phases between the times of coal formation. To date only eight well-documented sites in North America have yielded fossil assemblages representative of this part of the climate cycle (Fig. 2). Most of these assemblages come from valley fills incised into lowstand seasonally dry paleosols (Cridland and Morris, 1963; McComas, 1988; Cunningham et al., 1993; Falcon-Lang, 2003, 2004; Feldman et al., 2005; Falcon-Lang et al., 2009). Where they are

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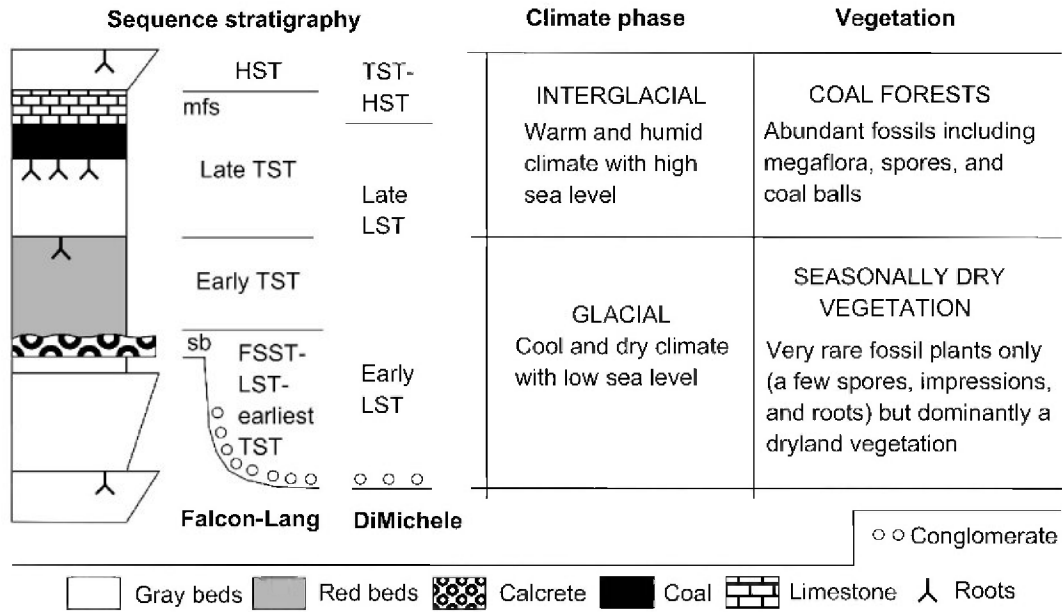


FIGURE 1—Diagram of a generalized cyclothem interpreted in terms of glacial-interglacial cycles (modified after Falcon-Lang, 2004), highlighting fossil plant data and showing the competing sequence stratigraphic interpretations. Abbreviations for systems tracts: FSST = Falling Stage Systems Tract; LST = Lowstand Systems Tract; TST = Transgressive Systems Tract; HST = Highstand Systems Tract; mfs = maximum flooding surface; sb = sequence boundary.

valley-confined, assemblages occur in the lowermost valley fill (late FSST and early LST deposits). They occur below the level of the first brackish-marine incursion, which is reflective of the early phases of base-level rise, triggered by a combination of increased rainfall and eustatic sea-level rise. These rare discoveries show that tropical landscapes were dominated by cordaites, conifers, and pteridosperms during glacial phases—a seasonally dry vegetation quite different from the interglacial coal forests.

Although this dataset is highly limited compared to the abundant fossil records from the interglacial parts of the climate cycle, there is good reason to suppose that these floras were generally characteristic of Euramerican tropical landscapes during glacial phases. As noted above,

the few key megafloras are associated with well-drained calcic and vertic paleosols, which developed during falling stages and comprise widespread lowstand surfaces (Cecil et al., 1985, 2003; Tandon and Gibling, 1994; Feldman et al., 2005; Korus et al., 2008; Berthier et al., 2008; Fischbein et al., 2009). As a strong linkage exists between vegetation and soil type today at the biome scale (Walter, 1973), the widespread occurrence of these paleosols (traceable over 100 km; Cecil et al., 2003) suggests a similarly widespread vegetation type.

Furthermore, these low-stand paleosols commonly contain roots. Although these remains are not identifiable at a precise taxonomic level, they have consistent morphological features; they may penetrate vertically to a depth of several meters and comprise a network of

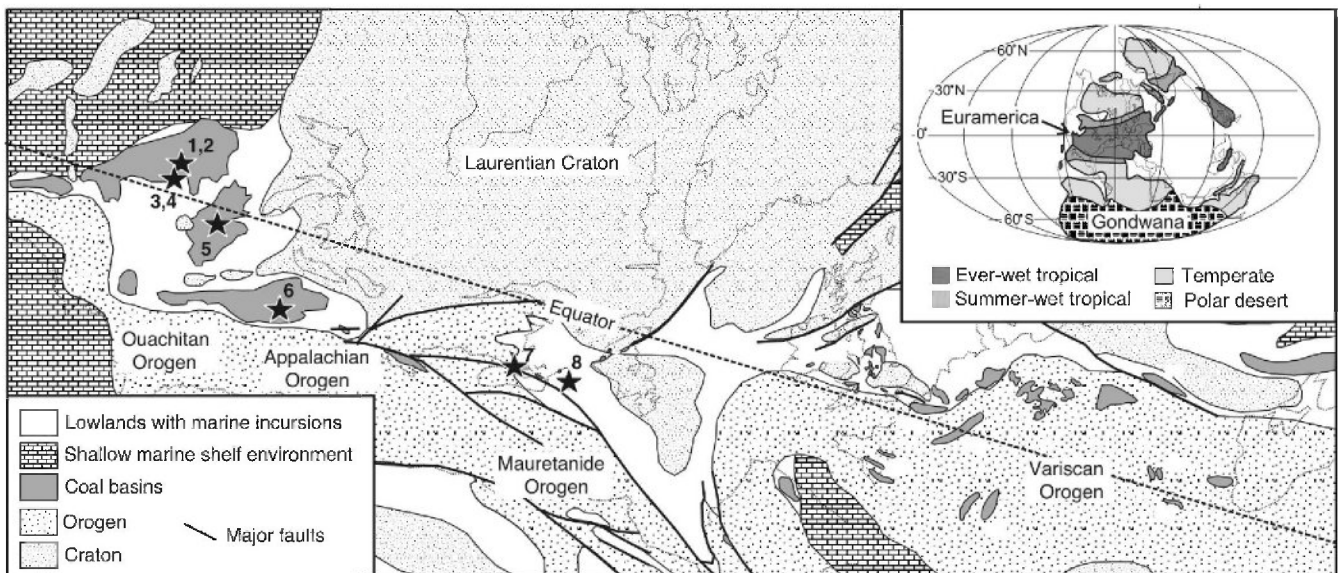


FIGURE 2—The Pennsylvanian tropical zone (with inset of paleoglobe for context) showing the distribution of coal-bearing strata (after Falcon-Lang et al., 2006) and the occurrence of megafloras preserved in lowstand valley fills (Cridland and Morris, 1963; McComas, 1988; Cunningham et al., 1993; Falcon-Lang, 2003, 2004; Feldman et al., 2005; Falcon-Lang et al., 2009). Sites: (1–2) Hamilton and Garnett, Kansas; (3–4) Feldman et al. sites, Kansas; (5) Cottage Grove, Illinois; (6) 7–11 Mine, Iowa; (7) Joggins, Nova Scotia; (8) Sydney, Nova Scotia.

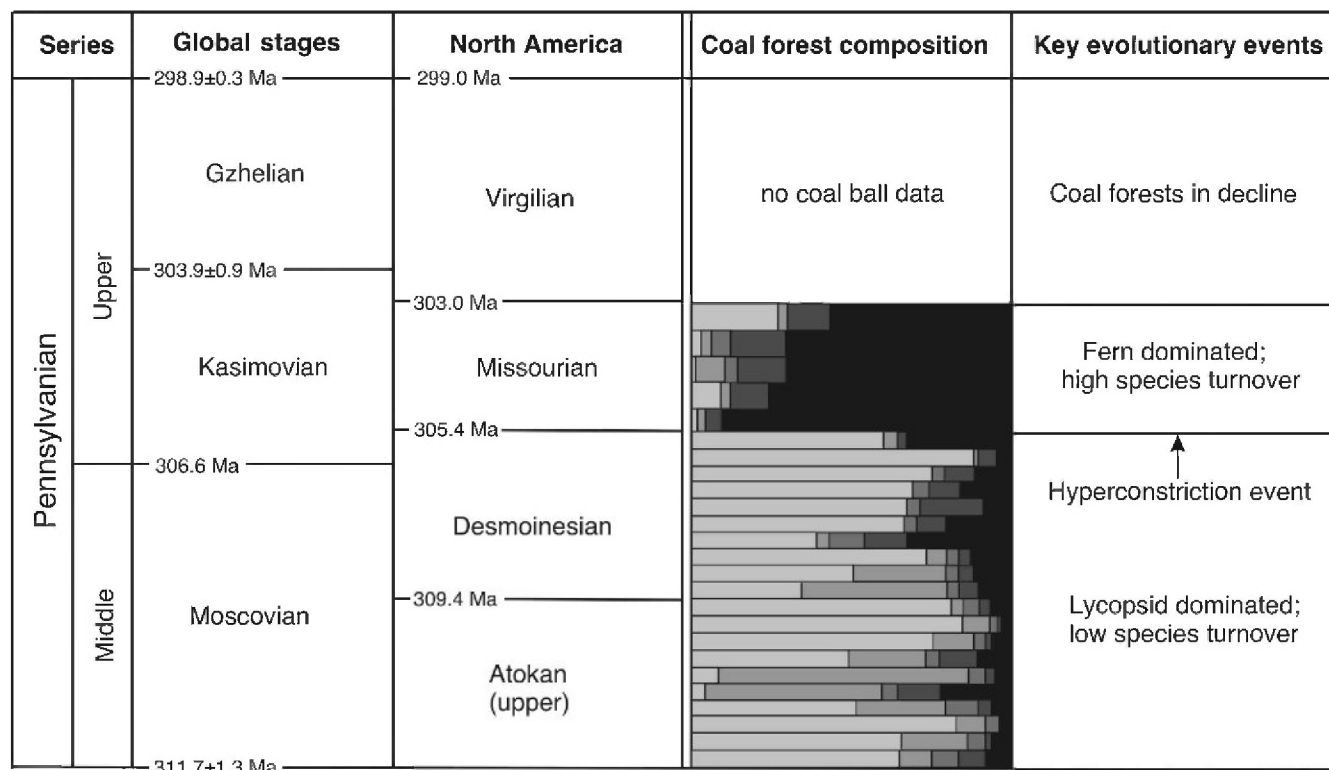


FIGURE 3—Compilation of coal-ball data showing high levels of persistence from one coal bed to the next (data from DiMichele and Phillips, 1994) and the abrupt vegetation step change that occurred at the Middle–Upper Pennsylvanian boundary (see text for discussion). Plant groups (pale gray to black), left to right: lycopsids, cordaites, sphenopsids, pteridosperms, and ferns. Global time scale (Gradstein et al., 2004) with cyclothem-calibrated dates for North American stratigraphy after Heckel (2008).

branching rootlets terminating in fine root masses (DiMichele et al., 2010). Root systems with these characteristics are not known for any coal-forest plants (DiMichele and Phillips, 1994), but occur in some cordate trees of probable upland ecology (Falcon-Lang and Bashforth, 2004) and are generally suggestive of gymnosperms (pteridosperms, cordaites, and conifers; DiMichele et al., 2010). Further, deep roots are characteristic of plants growing on well-drained soils. These findings support the idea that seasonally dry vegetation widely covered the Pennsylvanian tropics during glacial phases (Falcon-Lang et al., 2009).

COAL-FOREST REFUGIA

Summarizing this sequence stratigraphic analysis, abundant fossil assemblages suggest that coal-forest vegetation was confined to deglaciation and interglacial intervals whereas seasonally dry vegetation, represented by very rare assemblages, dominated lowstand, glacial phases (Fig. 1). This leaves us with a rather profound paradox. On the one hand, widespread coal forests repeatedly disappeared from the fossil record during glacial phases; however, abundant data (coal balls, megaflores, palynology) show that when coal forests reappeared at the start of the next interglacial, they typically experienced <10% species turnover compared to the previous interglacial (Fig. 3; DiMichele and Phillips, 1996b; Gastaldo et al., 2009).

There is only one credible solution to this paradox. Coal forests contracted into geographically restricted refugia during glacial phases and surviving taxa then repopulated tropical lowlands when climate became more humid at the start of the next interglacial. A similar hypothesis has been proposed to explain patterns of rainforest response to Quaternary glacial-interglacial cycles (Haffer, 1969; Meave and Kellman, 1994; Hooghiemstra and van der Hammen, 1998; Prentice and Jolly, 2000), although alternate models have been proposed for Amazonia, where rainforests appear to have been more resilient to climate change (Colinvaux et al., 1996).

Because plant remains (of any kind) are extremely rare in lowstand deposits, there are only a few sites where remains of these refugia can be positively identified. For example, based on palynological assemblages, which gives a coarse picture of regional vegetation makeup, as a result of the potential for long-distance transport of palynomorphs, coal-forest refugia can be identified in Middle Pennsylvanian successions in Nova Scotia (Dolby, 1988). Here, strata comprise prominent cyclothem with sequence boundaries defined by paleovalleys and their correlative equivalent, interfluvial calcretes (Tandon and Gibling, 1994). These lowstand interfluvial successions, interpreted as being deposited during glacial phases, are dominated by the pollen of conifers, cordaites, and pteridosperms, a typical dryland flora. They also, however, contain a few spores of *Lycospora pusilla* (the spore of *Lepidodendron hickii*) and *Lycospora pellucida* (= *Lepidophloios harcourtii*) (Dolby, 1988), both key coal-forest taxa seen in much greater abundance in bracketing coal beds (Phillips and DiMichele, 1992). Although much reduced in numbers, these data imply that coal-forest taxa were still present in the equatorial belt during glacial phases. As these lepidodendrid trees were obligate wetland plants, their occurrence implies they occupied wet areas within the dominantly tropical drylands.

Other evidence for coal-forest refugia can be found in lowstand valley-fill deposits at sites scattered across the Appalachian, Illinois, and Midcontinent basins of the United States. One such example is the Late Pennsylvanian assemblage from the 7–11 Mine, Ohio (McComas, 1988), which occurs near the base of an incised valley fill (Easterday, 2004) and comprises a few coal-forest plants (e.g., *Sigillaria*, *Calamites*, *Pecopteris*, and *Alethopteris*) in addition to the dryland elements more usually seen during glacial phases (*Walchia* and *Taeniopteris*). A second example is in Cottage Grove, Illinois, where lycopsid megaspores (*C. Looy*, personal communication, 2009) are associated with a dryland megaflores (*Walchia* and *Cordaites*) within an incised channel (Falcon-Lang et al., 2009). A third comprises the famous Hamilton Quarry, in

Kansas, which contains a range of coal-forest lycopsids and ferns mixed with dryland plants (diverse conifers) within the lowstand strata of a Late Pennsylvanian tidally influenced valley fill (Cunningham et al., 1993; Hernández-Castillo et al., 2009, and references therein). Finally, there are the classic Late Pennsylvanian exposures near Garnett, Kansas (Cridland and Morris, 1963; Winston, 1983; Feldman et al., 2005), which preserve a flora dominated by conifers and other seed plants, along with tetrapods, in an incised valley fill.

WHAT KIND OF REFUGIA?

It is also important to assess the nature of the refugia in which coal-forest plants survived during glacial phases, i.e., their location, size, and degree of interconnection. We hypothesize the existence of three possible types of refugia: block, migrant, and dispersed refugia. We define block refugia as the existence of a few very large tracts of coal forest (each $>10^6$ ha) that may have persisted in humid equatorial areas during glacial maxima. Migrant refugia refer to large tracts of tropical forest (each $>10^6$ ha) that might have developed outside the tropics, assuming that ecosystems tracked shifts in climate patterns. Dispersed refugia refer to tiny pockets of coal forest (each $<10^3$ ha) that might have occurred in the tens of thousands, dispersed across the tropical zone.

If coal forests contracted into large tropical blocks, one would expect to find very thick coal seams that accumulated through multiple glacial-interglacial cycles. One notable coal that seems to fit this description on first appearance is the 8.5-m-thick Warwickshire Thick Coal, UK (Fulton, 1987), which, if deposited continuously, might represent ~ 100 kyr, i.e., spanning one or more glacial cycles. Flint et al. (1995), however, argued that this coal comprises several amalgamated parasequences and records successive deglaciation events on a stable interfluvium rather than a persistent peatland. While this interpretation may be questioned, we know of no coals where an unequivocal case can be made for continuous accumulation through multiple climate cycles. Consequently the block refugia model is rejected, as is the migrant refugia hypothesis for similar reasons. If coal forests had migrated into the extratropical belt tracking climate change, we would expect to encounter mid-latitude coals; however, no such deposits occur. In addition, climate models do not predict the presence of large wetlands either within or outside of the tropical belts during interglacial periods (Poulsen et al., 2007).

Concerning the dispersed refugia model, unfortunately data are insufficient to falsify or confirm this hypothesis. As noted above, however, the limited sites where coal-forest refugia have been found are geographically widespread and always associated with valley-fill deposits, consistent at least with this model. In fact incised valleys, formed by the downcutting of trunk drainages, were widespread across Pennsylvanian tropical landscapes during glacial phases. They have a mean depth of ~ 31 m and a mean width of ~ 10 km ($n = 29$) and contain lenticular coals at some sites (data repository in Gibling, 2006). It is possible that some of these coal seams represent small pockets of coal forest that became established in localized wetlands on the valley floor. It is difficult to determine, however, whether these discontinuous seams represent true lowstand (glacial) accumulations or formed as the valley fill aggraded following a climate change to humid conditions (Gibling, 2006).

While we cannot demonstrate unequivocally that dispersed refugia survived in equatorial valleys during glacial phases, it remains a viable hypothesis that is amenable to additional testing. It is worth emphasizing that incised valley systems acted as long-term refugia for wetland plant taxa during periods of dry climate at other times in geological history (Demko et al., 1998). Perhaps the most remarkable example is the survival of the araucarian conifer, *Wollemia nobilis*, for probably tens of millions of years, in bedrock valleys in Australia following climatic drying (Hill and Brodribb, 1999). Furthermore,

valley drainages have been proposed as refugia for tropical rainforest species during Pleistocene glacial phases (Meave and Kellman, 1994) and the Pennsylvanian megafloora preserved in the Hamilton paleovalley in Kansas, United States (Cunningham et al., 1993) has been reconstructed as a valley-confined refugium of pteridophytes (Fig. 4).

EXPLANATORY POWER OF REFUGIA

The success of the coal-forest refugia hypothesis will be judged on its explanatory power. One key event that is explained more fully by our findings is the vegetation step change that occurred around the Middle–Late Pennsylvanian boundary (DiMichele and Phillips, 1996a; DiMichele et al., 2009). At this boundary species turnover briefly exceeded 85% from one coal bed (interglacial) to the next (compared to background levels of $<10\%$ change) and lycopsid dominance abruptly gave way to tree-fern dominance (DiMichele and Phillips, 1996a). In the two million years preceding this step change, tree-fern abundance gradually increased in non-peat-forming wetlands (Pfefferkorn and Thomson, 1982) and peat mires (Phillips and Peppers, 1984). Immediately following the turnover, dominance-diversity patterns were highly variable from one coal bed to the next (Peppers, 1996), before tree ferns ultimately rose to dominance. Yet even following their ascendancy, tree-fern composition was variable, with the dominant species changing through successive coal beds (Willard and Phillips, 1993).

How does the coal-forest refugia hypothesis fit with these data? During much of the Early–early Middle Pennsylvanian, glacial phases were of relatively moderate intensity, as indicated by the morphology and geochemistry of lowstand far-field paleosols, which suggest subhumid climates (Cecil et al., 1985; Driese and Ober, 2005). During this interval ecological stasis characterized the equatorial coal forests. We see similar communities comprising similar species and exhibiting similar ecological partitioning reoccurring from one coal bed to the next—an interval of several million years encompassing many glacial-interglacial cycles (DiMichele et al., 1996, 2002; Pfefferkorn et al., 2000, 2008). If we assume that these Early–Middle Pennsylvanian coal forests were confined to refugia during glacial phases, then the ecological structure of tropical communities must have been conserved during this fragmentation. This, in turn, implies that refugial areas were either sufficiently large or well connected by dispersal corridors to permit ecological resuscitation (e.g., Meave and Kellman, 1994). In either case, the overall refugial population must have been relatively large to allow species survival.

What environmental changes accompanied the progressive rise in abundance of ferns during the later Middle Pennsylvanian followed by the abrupt step change at the Middle–Late Pennsylvanian boundary? The distribution and character of paleosols, which shed light of the extent of marine regression and coeval climate change, indicate that glacial phases became more intense through this interval, resulting in increasing seasonality (Tandon and Gibling, 1994; Cecil et al., 2003; Feldman et al., 2005; Korus et al., 2008; Berthier et al., 2008; Fischbein et al., 2009). This trend culminated in maximum intensity at the Middle–Late Pennsylvanian boundary, marked by an extreme marine regression (Heckel, 1991), the formation of deep calcic paleosols (based on our field observations in Peoria, Illinois, 2010) under highly seasonal conditions in far-field sites, and valley incision (Easterday, 2004).

The effect of increasing glacial intensity through the late Middle Pennsylvanian would have been to progressively reduce the size and connectivity of tropical refugia from one glacial phase to the next. Habitat shrinkage and isolation would have offered rare species, particularly those with opportunistic life histories, the opportunity to rise in importance in the smaller refugia, thus reducing abundances of dominant species. Through time, these combined factors would have created the potential for significant dominance-diversity changes of



FIGURE 4—A reconstruction of the Late Pennsylvanian ecosystems associated with the Hamilton paleovalley, Kansas. Note that pteridophytes, including arborescent sigillarian lycopsids and herbaceous sphenophytes, dominate the valley floor while conifers cover the interfluves (All rights reserved, image archives, Denver Museum of Nature and Science).

variable character among refugial areas at any given time, simply as a consequence of the dynamics of small populations and the increase in the degree of isolation of the refugia from one another. Hence, increased species turnover would be a clearly expected result of the inferred environmental trends.

In the case of the tree ferns, the key to their rise to dominance and the decline of the lycopsids may have been differential dispersal abilities, exacerbated by shrinking refugia. The arborescent lycopsids, dominant in Middle Pennsylvanian mires, produced large, water-born dispersal units (megasporeangium-sporophyll units; Phillips, 1979), whereas tree ferns, which dominated Late Pennsylvanian mires, produced wind-born isospores in massive quantities. Hence, during each deglaciation, tropical tree ferns would have been able to disperse faster and more effectively than the lycopsids—the colonization of the latter being restricted to flooded corridors. The result of this inequality would be a steady increase in tree-fern abundance from one interglacial (coal bed) to the next, a hypothesis supported by the fossil record (DiMichele and Phillips, 1996a). Even a relatively small differential in tree-fern dispersal and establishment rate would have permitted development of a positive feedback loop in tree-fern dominance during successive glacial-interglacial cycles.

In effect, the periodic changeover from lowstand to highstand created conditions for shifting ecological dynamics. During those periods when refugia were large and well connected, the dominant plants from the previous periods of widespread wetland development continued to rule in terms of numbers. As refugia became progressively more constricted and spatially isolated, however, the apparently opportunistic ferns progressively increased in numbers during periods of wetland rejuvenation, enhanced by their rapid dispersal and consequent resource-occupation abilities. Thus, the abrupt step change from coal forests dominated by lycopsids to those dominated by tree ferns around the Middle–Upper Pennsylvanian boundary ultimately resulted from hyperconstriction of equatorial refugia during an extreme glacial phase. These changes presumably reduced the already-diminished lycopsids to

unsustainably low numbers that eliminated some species and severely reduced the ability of survivors to recolonize environmentally favorable areas following deglaciation at the start of the Late Pennsylvanian. A similar hypothesis was proposed by Heckel (1991), who related the step change to a greater-than-normal withdrawal of the sea at glacial maximum. Instability in coal-forest dominance-diversity patterns in the early Late Pennsylvanian was probably linked to the continued climatic seasonality during glacial phases. This would have promoted highly patchy refugia, resulting in reduced population sizes and connectivity of populations among refugial areas, as well as changes in species abundances within refugia, leading to high species turnover. A result was high fluctuation in fern-species dominance from one coal bed to the next during this time (Peppers, 1996).

CONCLUSIONS

1. Based on literature surveys of plant assemblages in a sequence stratigraphic context, we infer that equatorial coal forests contracted into isolated refugia during Pennsylvanian glacial phases.
2. The best-supported hypothesis is that refugia comprised small and dispersed pockets of coal forest within paleovalleys downcut into glacial drylands.
3. This hypothesis explains many aspects of coal-forest dynamics, including the Middle–Late Pennsylvanian step change in vegetational composition in North American coal floras.

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