

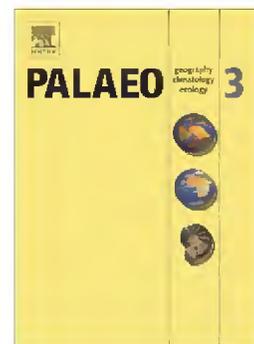
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The so-called “Paleophytic-Mesophytic” transition in equatorial Pangea – multiple biomes and vegetational tracking of climate change through geological time

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Abstract

The Paleophytic, Mesophytic and Cenophytic were originally conceptualized as chronostratigraphic intervals (not specific floras) and were used principally in that way for about 100 years. They supposedly reflected massive, irreversible biotic changes on land that were thought to have happened about half a geological period prior to the changes in marine faunas that mark the more traditional geological era boundaries. The terms were applied initially only to terrestrial rocks from the Euramerican portions of equatorial Pangea, especially parts of central Europe, where the boundary between the Paleophytic and Mesophytic, the “eras” of interest here, was placed at the top of the German Rotliegendes. More recently, the terms have been coopted to describe vegetation types (not chronostratigraphic units), even to the point where specific Linnean ordinal or class level clades (evolutionary lineages) of plants have been attributed solely to one vegetation type or the other at a global level. Furthermore, the “Paleophytic-Mesophytic” transition has been recognized in the largely taxonomically distinct vegetation types of temperate as well as the equatorial paleolatitudes. The result of this conceptual coopting of terms that already were of questionable value, is a blurring of the concepts almost to

the point of meaninglessness. A reading of the literature indicates confusion in terms of what represents the “Paleophytic” flora vs. the “Mesophytic” flora, the botanical basis for the floras and the taxonomic scale at which they can be recognized, the geographic pattern and temporal correlation of the supposed transition, and the evolutionary and ecological significance of the vegetational changes these terms supposedly capture. We propose that these terms be completely and utterly abandoned as confusing and, worse yet, misleading. Evidence suggests that Paleozoic vegetation tracked climate, which should not come as a surprise in light of what is known of plant dynamics in the Holocene and Recent. Furthermore, the evidence for a global “Paleophytic” vs. “Mesophytic” “vegetation” is simply unsubstantiated by the fossil record. Rather, there appear to have been a complex of global species pools reflecting climate at many spatio-temporal scales. The vegetational changes occurring in the late Paleozoic thus can be understood best when examined as spatial-temporal changes in biome-scale species pools responding to major global climate changes, locally and regionally manifested.

Keywords: Paleophytic, Mesophytic, paleobotany, paleoecology, extinction, evolution

1. Introduction

Paleobotanists have long accepted that the sweeping marine biotic changes characteristic of the major geological Era boundaries of the Phanerozoic were presaged by biotic changes on land by nearly a geological Period. Major changes in terrestrial plant groups, especially those of the ancient equatorial lowland regions, are marked by shifts in dominance from spore-producing and primitive seed plants to advanced seed plants during the Permian Period, which were replaced subsequently by the flowering plants during the later Early Cretaceous. Potonié (1899) makes what is perhaps the earliest reference to these changes, describing a “Period of the Zooidogamous Plants”, ranging up to the end of the Rotliegend (Early Permian), and a “Period of the Dicots”, which begins in the Early Cretaceous, and something in between that remained unnamed. This concept was refined by Gothan (1912), who defined a Paleophytic, Mesophytic, and Cenophytic (Paläozoikum der Pflanzenwelt, Mesozoikum der Pflanzenwelt, Känozoikum

der Pflanzenwelt) (Figure 1). Gothan and others also used different terms to subdivide the plant world, but these followed the same basic scheme for plants of the post-Middle Devonian. Initially these terms were meant to describe the succession of dominance changes among the major plant groups, not-so-much wholesale, catastrophic changes but rather changes in the relative proportions of major groups through time. In effect, these terms were meant to reflect major, irreversible changes in terrestrial dominance-diversity patterns that were perceived as chronostratigraphic units.

The change from the so-called Paleophytic to the Mesophytic “era” was defined in the German stratigraphic section, principally as occurring between the fossiliferous part of the Rotliegend (which is now believed to end, more or less, in the middle part of the Early Permian) and the Zechstein (beginning in the early part of the Late Permian) (e.g., R. Potonié, 1952; Gothan and Weyland, 1954; Kerp and Fichter, 1985). In his original, chronostratigraphic formulation, Gothan (1912) characterized the Paleophytic as composed mainly of lycopsids, ferns, sphenopsids, and primitive gymnosperms, the latter of a type typical of the Carboniferous. He acknowledged the rise of advanced gymnosperms near the end of the Paleophytic but placed the beginning of the Mesophytic at the time when conifers rose to vegetational dominance and the Carboniferous elements disappeared. The large temporal gap between the Rotliegend and Zechstein was not recognized at this time and ecological dominance was implicitly equated with apparent commonness of occurrence of particular plant groups. The more detailed spatio-temporal ecological patterns of plant co-occurrences were not considered, however, such as recognition that the period of “overlap” was not one of a mixed flora but rather the temporal intercalation or interdigitation of two distinct floras.

Differentiation of a Paleophytic “flora” and a Mesophytic “flora”, as opposed to time stratigraphic units of the same name, began with the recognition that the dominant elements of these two stratigraphic units in fact rarely occurred together in space. The discovery of what seemed to be typically Permian plants or pollen grains occurring rarely in Pennsylvanian lithological sequences, otherwise dominated by typically Pennsylvanian wetland “swamp” plants suggested a hinterland vegetation coexistent with that of the wetlands (e.g., Gothan and Gimm, 1930; Moore et al, 1936; Schopf, et al., 1944; Read, 1947; Potonié, 1952; Cridland and Morris, 1963; Havlena, 1971; Remy, 1975). These

developments were summarized by Fredericksen (1972) who formally separated the “Paleophytic” and “Mesophytic” floras from the stratigraphic units of the same name. Knoll (1984) later differentiated the two floras, identified a “transitional” flora, and argued for a time transgressive, west-to-east, change in landscape dominance from one flora to the other during the Permian.

Kerp (1996, 2000) recognized the confounding of time stratigraphic with vegetational terms and the confusion thus caused, and recommended abandonment of the terms altogether. He elaborated the interplay of different terminological approaches to this vegetational turnover, each set of terms reflective of different viewpoints of the problem (basinal vs. extrabasinal floras; time and place of evolutionary innovations; biogeographic overprints; regional timing differences).

The confounding of the concepts of Paleophytic and Mesophytic eras vs. vegetation types can be seen as filling a need for a floristic/vegetational concept for what might be called “biomes” today. Landscapes of the time were actually composed of multiple, distinct floras, or “species pools”. The terminological difficulties and associated confusion have arisen because, indeed, despite sharp compositional differences, there is no sharp temporal break separating the occurrences of these many distinct floras, which appear to be characteristic of different environmental conditions, broadly climate (Ziegler, 1990; Rees et al., 1999), inclusive of such things as ground water availability (Cleal and Thomas, 2005), temperature, and in part of changing proximities to depositional basins (Gothan and Gimm, 1930; Havlena, 1971; Gastaldo, 1996). As generally envisioned for Euramerican parts of the equatorial regions of the later Carboniferous and earliest Permian, these floras interdigitate spatio-temporally, even at the outcrop-scale, but have few species in common (Kerp and Fichter, 1985; Mapes and Gastaldo, 1987; Broutin et al., 1990; DiMichele and Aronson, 1992; DiMichele et al., 2005b). These patterns indicate coexistence during the Pennsylvanian in the equatorial regions long before typically Permian elements rose to dominance in the lowlands.

Further confounding the way the “transition” has been envisioned was, first, Gothan’s (1912) original definition, in which he allowed for the stratigraphic overlap of the earliest conifers with the typical Carboniferous wetland flora (Fig. 1). The conifers of

the Early Permian (Rotliegend) are distinct from those of the Late Permian (Zechstein), and actually comprise two distinct species pools. The early conifers became evidence for a transition between the supposed “two” floras. The second confounding matter has been a persistent attempt to shoehorn elements from the several different species pools/biomes into two “floras”, the so-called Paleophytic and Mesophytic, with the concept even expanded to include floras from the northern and southern temperate zones (e.g. Rees, 2002).

Accumulated evidence unequivocally demonstrates the coexistence of several distinct vegetation types in the equatorial regions deep into the Carboniferous (Daber, 1959; Havlena, 1971; Leary and Pfefferkorn, 1977). These can be juxtaposed generally as floristic pairs, one typical of wetter, more humid conditions vs. one typical of somewhat-to-much drier conditions. The occurrence as “pairs” reflects proximity of the rarer, “outlier” flora to the more commonly encountered flora of the depositional basins. Yet more spatially remote vegetation types appear progressively later in time. Depending on the time and place of the floristic comparisons to be made, different pairs of distinct floras coexisted regionally as early as the Middle Mississippian (Daber, 1959; Chalot-Pratt and Galtier, 1989), during the Early and through the Middle Pennsylvanian (Leary and Pfefferkorn, 1977), or the early Middle Pennsylvanian through the Early Permian (Scott and Chaloner, 1983; Lyons and Darrah, 1989; DiMichele et al., 2006a). It is this last case, which involves the appearance of a flora rich in primitive conifers and other derived seed plants, that represents the classical Paleophytic-Mesophytic floral contrast (though not the vegetation types originally envisioned across the Paleophytic-Mesophytic stratigraphic boundary). These two floras appear to be environmentally distinct, effectively representing different biomes. Furthermore, recent findings have documented yet additional vegetation types/biomes within the Permian equatorial regions, some containing taxa previously known only from the Upper Permian or Mesozoic (e.g., Kerp, 2006; DiMichele et al., 2001; Looy, 2007).

Thus, as argued by Kerp (1996, 2000), the terms “Paleophytic” and “Mesophytic” should be abandoned and replaced by more detailed descriptions of the patterns, and of the possible processes underlying the patterns, during this important transitional time in Earth history. The terms have not proven robust as chronostratigraphic entities. Neither

do they summarize the reality of late Paleozoic global vegetational patterns, nor even the patterns in the equatorial region. Furthermore, the patterns of change in terrestrial flora and fauna should be tied to modern ecological concepts reflective of the way in which biota respond to environmental conditions and changes therein. Terminology must be modernized, as much as possible, and be reflective of plant responses to environmental change. There is ample evidence from modern plant biogeography, from burgeoning studies of plant distributional changes accompanying Holocene glacial advances and retreats (Delcourt and Delcourt, 1991), and from detailed studies of plant responses to ancient pulses of global warming (e.g., Wing et al., 2005; Tabor et al., submitted), that plants track climate. Furthermore, there is arguable evidence that plant and animal “individualistic” responses, while undeniable, must be viewed from the perspective of spatio-temporal scale. They largely occur within rather than between biomes, the variously sharp boundaries of which may reflect atmospheric boundaries and hence breaks or transitions in prevailing climatic conditions (Alroy, 1999; Ziegler et al., 2003; DiMichele et al., 2005a).

2. Context of the late Paleozoic vegetational transition

2.1 Sampling

The geological record of floral changes during the late Paleozoic varies greatly in quality among major floristic realms. The concept of Paleophytic and Mesophytic Eras was based on floras from equatorial Pangea (specifically central Europe), which encompasses both everwet and seasonally dry vegetation types. The data set compiled by Alister Rees (Rees, 2002), redrawn in our Figure 2, shows that the equatorial tropical regions of Europe and North America in fact lack plant fossils or contain few reported fossil assemblages at critical time intervals during the Permian. The Chinese record fills some of these gaps, but is thin at other important times. However, the physical evidence for this transition remains a composite with missing data from some significant times and areas.

The temperate realms of Angara and Gondwana, and the paratropical region of North China have good records, based on the number of known fossil deposits. Temporal

correlations and thus comparisons of patterns of vegetational change between the higher latitude areas and the equatorial regions are difficult. Furthermore, there are limited floristic overlaps among any of these floristic realms, so that the very concepts of “Paleophytic” and “Mesophytic” vegetation types must be called into question when extended to the higher latitudes (there undoubtedly are vegetational changes in these regions, possibly under the same large scale global climatic forcing factors that affect the tropics). On the largest spatial scales, peak occurrences of fossil deposits vary between floristic realms, meaning that “global trends” tend to be composites of disjoint regional patterns, potentially obscuring these broader global controls.

2.2 Climatic conditions

There is excellent support from physical environmental data for progressive drying in equatorial Pangea during the Permian, summarized in Figure 3, which would have had a major effect on the distribution of plants during this time period. The geology of the Permo-Carboniferous Pangean continental tropics, and its climate evolution, is understood best from basins in the southwestern and eastern U.S.A., the Maritimes of eastern Canada, western and central Europe, and the east-Asian tectonic blocks that include parts of southern Mongolia and China (e.g., Ziegler et al., 1997). Abundant coals, bauxites and laterites in Pennsylvanian strata among all these regions suggest warm, moist and equable climate across most of the Pangean tropical latitudes (e.g., Ziegler et al., 1997; 2002; Tabor and Montanez, 2002; 2004; Roscher and Schneider, 2006; Noe, 1930; Halle, 1935; Scott and Rex, 1985; Jia and Wu, 1996; Jia et al., 2001; Cleal and Wang, 2002). These climate sensitive lithologies suggest that these regions received mean annual precipitation in excess of ~1200mm/yr (Tabor, this volume). However, ecosystems characterized by seasonal variations in soil moisture availability, net soil moisture deficiency, and mean annual precipitation values <900 mm/yr (Royer, 1999; Tabor, this volume) were present, at least intermittently, in northwestern tropical Pangea during the Pennsylvanian (Joeckel, 1999; Tabor and Montanez, 2004; Falcon-Lang, 2003), indicated by vertisols, calcic vertisols and Calcisols in the basins between ~5 and 15° on the North American tectonic plate. The coal- and laterite-bearing Pennsylvanian strata of the North American and European plates are replaced in the

Lower Permian by paleosol morphologies such as Vertisols, calcic Vertisols and Calcisols (Tabor and Montanez, 2002; 2004; Ziegler et al., 2002; Roscher and Schneider, 2006; Schneider et al., 2006). This trend is suggestive of a rapid and great aridification of western tropical Pangea at or very near the Permo-Carboniferous boundary (Fig. 3). This aridification event might have included a significant drop in mean annual precipitation values from >1200 to $<\sim 900$ mm/yr. There was apparently a progressive trend toward generally drier climate that developed over the western Pangean tropics in the North American and European plates, with mean annual precipitation values becoming <300 mm/yr (Watson, 1992), based upon the presence of paleosol morphologies that include evaporite minerals in upper Lower Permian and Upper Permian strata of North America and Europe (Mack and Dinterman, 2002; Cassinis et al., 1988).

Several recent studies have demonstrated the potential for quantitative reconstructions of continental paleoclimate from authigenic minerals. These proxies primarily focus on the elemental composition of paleosols as estimates of paleoprecipitation (e.g., Sheldon et al., 2002; Sheldon and Retallack, 2004; Dreise et al., 2005; Prochnow et al., 2006) and light stable isotope composition of authigenic minerals (Yapp, 1983, 1987, 1993, 2001; Yapp and Poths, 1992; Delgado and Reyes, 1996; Vitali et al., 2002; Tabor and Montanez, 2002; 2005; Tabor et al., 2002; 2004; Tabor and Yapp, 2005) and fluid inclusions (Bennison and Goldstein, 1999) as estimates of paleotemperature. With the exception of western equatorial Pangea (Tabor and Montanez, 2002, 2005; Tabor et al., 2002, 2004), however, quantitative paleoclimate reconstructions of this sort have not been applied to Permo-Carboniferous terrestrial strata. Nevertheless, those studies provide light stable isotope evidence for (1) transition from nearly perennially wet soil moisture conditions in Pennsylvanian strata to distinct seasonal variations in soil moisture availability (possibly monsoonal) across the Permo-Carboniferous boundary. Furthermore, there is evidence for generally progressively greater soil moisture deficiency through Lower and Middle Permian strata (Fig. 3) and (2) significant change in mean annual temperature, from $\sim 22^{\circ}\pm 3^{\circ}\text{C}$ to $\sim 35^{\circ}\pm 3^{\circ}\text{C}$, across the Permo-Carboniferous boundary in the eastern Midland basin of north-central Texas. In this regard, the quantitative paleoclimate reconstructions appear to agree very well with lithologic-based paleoclimate reconstructions in this region. These indicators of

rapid climate change across the Permo-Carboniferous boundary would have undoubtedly impacted tropical ecosystems. In particular, decreased soil moisture availability, in conjunction with increased evapotranspiration associated with an $\sim 10^{\circ}$ - 13° C temperature increase, could have lowered local- to regional-scale water tables and should have favored floras with adaptations for drought tolerance and survival under conditions of seasonal moisture deficiency. Such a climatic change would have driven the shift in plant spatial distributions that is reflected in the tropics at this time.

3. Late Paleozoic tropical biomes and their spatio-temporal distribution

The manner in which the distribution of ancient plants has been described and the degree to which such patterns have been resolved both spatially and taphonomically provides a key framework within which vegetational change through time is, has been, and can be understood. Historically, the geographically distinct fossil floras from the Carboniferous and Permian were conceptualized as floristic provinces or realms (e.g., Chaloner and Lacey, 1973; Chaloner and Meyen, 1973; Raymond, 1988). This treatment captured major biogeographic patterns but did not provide a terminology that permitted clear resolution of patterns within the various floral realms or at relatively finely resolved time scales. Nor did it allow for a spatio-temporal understanding of the change from the wetland floras typical of the Carboniferous to the seasonally dry floras typical of the Permian. Reconceptualization of spatial patterns in terms of climatically sensitive biomes by Ziegler and his colleagues (Ziegler, 1990; Rees et al., 1999) changed the nature of the way these spatio-temporal vegetational changes could be visualized, tying plant distributions and sharp compositional breaks between floras to climatic patterns (Ziegler et al., 2003).

Paralleling these biogeographic studies were others that were attempting to explain the sporadic stratigraphic occurrences or incursions into basinal areas of unusual fossil plants, clearly indicative of non-wetland floras, which were rarely seen in basinal lowlands of the Pennsylvanian. Such floras were assumed to be growing in the equatorial regions but outside areas where preservation was likely, what might be considered a “taphonomic megabias” in the terminology of Behrensmeyer and Hook (1992) or

Behrensmeyer et al. (2000). These occurrences gave rise to terminological debates about “uplands”, “extrabasinal lowlands” and so forth (e.g., Gothan and Gimm, 1930; Chaloner, 1958; Cridland and Morris, 1962; Havlena, 1971; Pfefferkorn, 1980). Such conceptual considerations were not linked clearly to the biogeographic studies, although they led to natural linkages with the biome-thinking of Ziegler’s group. Ziegler and his colleagues were working with fairly coarsely resolved patterns (dividing the Permian world as a whole, for example, into a series of static biomes and averaging floral composition into bins of temporal durations far exceeding the scale of climatic fluctuations), and while the biome approach was a major conceptual advance, it did not incorporate the taphonomic component that would permit linkage to the spatio-temporal terminological struggles that accompanied attempts to explain the vegetational change in the latest Carboniferous-Early Permian equatorial regions.

More recent studies of late Paleozoic vegetational changes through time, including the early appearances of unexpected elements, such as conifers, have begun to address explicitly the relationship between climate, plant distribution, taphonomy, and preservational likelihood, initially implicitly adopting the biome-approach but more recently doing so explicitly (e.g., Mapes and Gastaldo, 1987; Broutin et al., 1990; DiMichele and Aronson, 1992; Kerp, 1996; DiMichele et al., 2002, 2005a; Kerp, 2006). From these studies, a more conceptually refined understanding of the so-called “Paleophytic-Mesophytic” transition is emerging.

Many studies have contributed to the gradual development of this understanding, fitting together much like pieces of a puzzle. Some of these are described briefly below. They can be categorized roughly into three kinds of studies, with high degrees of overlap among them. Taken together, they present both a historical developmental sequence and a basis for emergence of our current understanding. (1) The oldest focus was on the recognition and description of contemporaneous but compositionally distinct vegetation types in the general equatorial region. (2) The coexistence of different kinds of vegetation led to explanation by way of spatial distribution within the tropical landscape, particularly as related to drainage, elevation, or preservational potential. (3) Finally, attempts have emerged to tie vegetational patterns to distinct environmental conditions, including climates.

3.1 Vegetational distinctiveness – proof of more than one kind of coexistent vegetation

Leary and Pfefferkorn (1977) and Leary (1981) described distinctive Early Pennsylvanian floras from the northwestern margin of the Illinois basin. These floras are dominated by plants with uncertain distributions subsequently, such as *Megalopteris* and *Lesleya*. *Lesleya*-rich floras occur sporadically (personal observations of the authors) into the Middle Pennsylvanian (late Moscovian: Westphalian C-D: Duckmantian-Asturian) of the Illinois basin, within otherwise typical coal-roof shale floristic sequences, suggesting a long period of coexistence of these kinds of floras in the American mid-continent, where conifer-rich floras are rare but present (Andrew Scott and Roy Plotnik, personal communication, 2006).

Gothan and Gimm (1930) early recognized distinct floras from the coal basins of the German Rotliegend, dividing them into basinal (coal facies) floras and extrabasinal or hinterland floras. Havlena (1961), summarized succinctly in English by Gastaldo (1996), recognized distinct differences between floras from the roof shales of coal beds and from the rocks between the immediate coal-roof shale packages in latest Mississippian/Serpukhovian age intermontane basins of central Europe (at the time, these rocks were considered to be Namurian A of the Late Carboniferous). He proposed that the wetland floras, which he termed “flöznah” were growing close to coastal wetland habitats. The interbed floras, termed “flözfern” were envisioned as growing in habitats that were more inland, growing in alluvial plain settings. These two kinds of floras are not substantially different in generic composition, differing rather in common species, reflecting gradational differences perhaps within one similar climatic belt.

The coexistence of “upland” or “extrabasinal” tropical floras rich in cordaitalean gymnosperms with lowland wetland floras has been hypothesized on the basis of a variety of lines of evidence. Chaloner (1958) first suggested such an association based on palynological studies of coals and marine shales. Gastaldo and Degges (2007) reported “log jams” composed of cordaitalean trunks, evidently transported from extrabasinal areas and trapped within typically wet, lowland depositional settings. Falcon-Lang and Scott (2000) found in situ cordaitalean floras in red bed deposits from

the Early Pennsylvanian Joggins section in Nova Scotia, in close association, but not intermixed with, more typically wetland floras. The cordaitaleans clearly were a diverse and widely distributed group, with some taxa seemingly specialized for wetland swamp settings (Cridland, 1964; Raymond and Phillips, 1983; Costanza, 1985; Trivett and Rothwell, 1991), and other, generally larger forest-tree-sized forms growing along streams in better-drained parts of the tropical wetlands. This contrast may parallel, to a large extent, the patterns described by Havlena (1971).

During their study of floras from the Kansas coal measures, Cridland and Morris (1963) encountered and described in detail the flora from Garnett, Kansas of Late Pennsylvanian age, first recognized by Moore et al. (1936). Sandwiched in the midst of otherwise typical coal roof-shale floras, dominated by tree ferns and pteridosperms, the Garnett flora is dominated by the conifer *Walchia* and associated derived seed plants. Cridland and Morris (1963) hypothesized that two floras existed contemporaneously in the tropics. One of these floras was characteristic of swampy lowlands, with the other envisioned as growing in better-drained upland habitats, a juxtaposition represented in a widely reproduced and influential figure (reproduced here as Fig. 4). Similar kinds of floristic discontinuities have since been described in detail from sporadic occurrences in Upper Pennsylvanian sequences in many parts of the United States, from the Appalachian basin, through the mid-continent, to the inter-mountain west. The best described of these include the 7-11 flora from Ohio (McComas et al. 1988), the Kinney Quarry from New Mexico (Mamay and Mapes, 1992) and the Hamilton Quarry from Kansas (Rothwell and Mapes, 1988). These are all examples of classic “Paleophytic” vs. “Mesophytic” floras.

3.2 Spatial distinctiveness

Implicit in the concept of distinct floras/vegetation types is spatial distinctiveness. This concept was clearly elaborated by Chaloner (1958) to explain the abundance of cordaite pollen in nearshore marine sediments, overlying coal beds. He imagined the cordaites to be “upland” plants, shedding pollen into river courses that passed through peat-rich areas, supposedly lacking in cordaites. Cordaitean abundance in peat-forming vegetation of the early Middle Pennsylvanian has since been established unequivocally

(e.g., Phillips and Peppers, 1984), however, Chaloner's original idea of cordaitan trees in the drier or better drained parts of the humid climate belts has also been documented by macrofossil evidence (e.g., Falcon-Lang, 2003; Gastaldo and Degges, 2007).

Cridland and Morris (1963), upon discovery of the distinctive, conifer-rich Garnett flora in Kansas, proposed spatial and environmental separation within the equatorial regions to explain the compositional distinctiveness of this unusual flora from that typical of wetlands. In their original figure (Fig. 4), they show the conifer flora positioned in areas of higher elevation and presumed better drainage than the flora of peat mires and wet floodbasins. As with Chaloner's original concept of "upland" vegetation, this reconstruction was not supported by direct evidence of such higher elevation areas.

A more direct inference of spatial position was made by Havlena (1971), with regard to subfloras within the general wet climate belts of the equatorial regions. Based on adpression assemblages, he made note of two distinct kinds of vegetation. These corresponding broadly to the same overall species pool, or at least were drawn from the same basic generic and family level clades. One type of flora occurred principally in the roof shales of coal beds, presumably growing under wet climatic conditions similar to those under which the peats had been deposited. He also inferred that such floras most likely were drawn from species pools acclimated to growth in wet areas, much as had been inferred for the peat deposits. Consequently he named these flöz nah – close to the peat. Floras drawn from between the coal beds, however, were different from those of the roof shales, which led Havlena to presume an origin in areas somewhat more distant from the coastal regions, deposited in what might be thought of as alluvial plains. He referred to these as the flöz fern – distant from the peat. Havlena's (1971) ideas address the question of what may have been growing in coastal areas between times of peat formation and parallel the inferences of Gothan and Gimm (1930).

Somewhat more difficult to reconcile are the occurrences of the *Megalopteris* flora (mentioned above – Leary and Pfefferkorn, 1977) within the basinal lowlands well into the middle part of the Westphalian, as late as the Bolsovian-Asturian boundary (Westphalian C-D). Such floras have been found in fortuitously preserved slump blocks between coal beds in the eastern parts of the Illinois Basin (DiMichele, unpublished data). This is not a typical "flöz fern" flora, nor does it contain any elements of the

conifer-rich floras typical of the Permian that make their first appearances in the basinal lowlands around this same time (Lyons and Darrah, 1989). The plants that make up this flora clearly preferred habitats that were better drained/drier than those of the wetland vegetation most commonly encountered in the Pennsylvanian coal belts of the paleoequatorial regions. The elements of these flözfern floras also appear to have been long persistent temporally, deduced from their stratigraphic record, indicating landscape complexities that presently are not understood (reflecting the assertions of Kerp, 1996, that much of the confusion surrounding these matters devolves from the incompleteness of the terrestrial fossil record).

The traditional “Mesophytic” flora, mainly the conifers, have long been assumed to have originated outside of the wet regions of the tropical equatorial lowlands. Lyons and Darrah (1989) summarized the known evidence of early conifers – more has appeared since then, but the patterns remain the same – and noted that virtually all early appearances are of fragmentary, allochthonous, remains. The basins in which such remains appear, initially in the Duckmantian (Westphalian B) (Scott and Chaloner, 1983), were virtually all proximate to contemporaneous elevated regions that were likely better drained and, thus, not conducive to the growth and flourishing of the typical Pennsylvanian wetland flora (Read, 1947; Frederiksen, 1972; Lyons and Darrah, 1989). Broutin et al. (1990) summarized an even broader range of literature that suggested spatial distinctiveness of these distinct, but spatially proximate, vegetation types.

Pfefferkorn (1980), in an attempt to bring some terminological stabilization to the matter of spatial position, noted that the real essence of this concept was taphonomic. For the most part, especially in the Paleozoic, fossil-plant deposits are preserved in depositional basins, places where at least some portion of the record of sedimentation could be preserved by the creation of accommodation space and subsequent deep subaqueous burial. Areas outside of basins need not have constituted “uplands” per se, and need not have been particularly better drained. After all, basins preserve a wide variety of paleosol evidence suggesting low water tables, excellent drainage, and deep rooting (e.g. Tabor and Montañez, 2004). The matter seems to be that we can differentiate those floras that populated basins during any given interval from those that were most common in the “extrabasinal” areas, to use Pfefferkorn’s term. Appearing

through incursions into the basins during periods of widespread climate change, such floras parallel what Brett and Baird (1995) termed “epibole faunas” for Paleozoic marine assemblages that appear in basins in rare but widespread beds, suggesting incursions into the basinal areas under exceptional conditions. It is unclear just where the dominant basinal floras or faunas went during the times when these exceptional biotas were dominant. The Hamilton Quarry flora of Kansas (Mamay and Mapes, 1992), for example, has been reconstructed in a diorama on display at the Denver Museum of Nature and Science, which suggests that the wet flora was restricted to in-place, swamp and stream-side refugial areas during the times when drier climate prevailed across the basins. The other possibility is range shift along watercourses into areas where higher moisture availability may have continued, or survival in areas where geographic configurations may have permitted wet conditions to remain stable (e.g. the eastern equatorial regions of Pangea, now China – see Rees et al., 1999).

3.3 *Environmental distinctiveness*

Closely tied to the matter of spatial separation is that of environmental distinctiveness of otherwise taxonomically distinct floras. This is somewhat more easily established than spatial distinctiveness by tying fossil-plant deposits to associated indicators of paleoclimatic conditions, such as paleosols, geochemical evidence, or sedimentological indicators. For example, White (1929) argued strongly that Early Permian Hermit Shale flora of Arizona, rich in conifers, callipterids and *Supaia*, grew originally under strong seasonal moisture limitation. He linked the morphology of the plants (narrow, leathery leaves; leaf spines and hairs) with sedimentological features such as salt crystal molds within the plant-bearing beds. DiMichele et al. (2007) also were able to link climatic seasonality to conifer- and *Supaia*-rich vegetation, documenting their occurrence in sheet flood deposits consisting of silty mud layers separated by clay drapes with mudcracks and animal tracks, evidencing periods of exposure following periods of flood. From the geochemical and paleosol perspectives, Tabor and Montañez (2004) linked geochemical proxies for temperature and paleosol evidence of rainfall patterns to

major changes in plant composition near the Carboniferous-Permian boundary in western Pangea.

All approaches to the fossil-plant by climate problems have their difficulties and making linkages between fossil floras and paleosols is no exception. Beds bearing macrofossils generally occur between paleosols, which tend to lack fossils other than roots, perhaps not the roots of the plants preserved as macrofossils. Similarly, geochemical proxies for terrestrial temperature and rainfall are often based on minerals found in paleosols. Sedimentologically distinct beds, indicative of high levels of evapotranspiration and seasonal water availability, may surround fossiliferous beds, but the plant fossils are rarely found within these demonstrable indicators of strong evapotranspiration.

A deposit from the lower Middle Permian of Texas (DiMichele et al., 2004) serves as an example; it was found in a small channel between calic, red vertisols, themselves sandwiched between gypsum beds and oolitic limestones. It is clear from such a deposit that there was a very dry end to the climatic spectrum. The fossil bearing bed, however, seems to have been deposited during a “pluvial” period of somewhat higher regional moisture availability.

Summaries of data and published papers linking various aspects of the “Paleophytic” and “Mesophytic” floras and the transition between them to distinctive climatic conditions have appeared in numerous papers. These papers explicitly tie vegetation types to indicators of physical environment and/or climate. Examples include Mapes and Gastaldo (1987), Broutin et al. (1990), DiMichele and Aronson (1992), Kerp (1996), DiMichele et al. (2002, 2004), DiMichele et al. (2005b).

4. Summary of what we know

The fossil record of the late Paleozoic equatorial regions, as presently understood, indicates the existence of several largely distinct vegetation types that share few species in common and are dominated in some instances by completely different clades/evolutionary lineages. At the coarsest level of resolution, at any one time only two such distinct vegetation types appear to coexist in close enough spatial proximity to be

temporally intercalated within the basinal lowlands, reflective of the tracking of regional environmental (principally climatic) changes. Throughout the later Carboniferous (Pennsylvanian) and earliest Permian, one of these biome pairs, dominated by primitive seed plants and free-sporing lower vascular plants, is consistently present and associated with indicators of wet soil conditions. There is evidence of three or four other distinct kinds of vegetation from moisture-limited environments, each dominated by documented or presumed seed plants, more derived evolutionarily than those from the wetland habitats (these are: cordaitalean-flora from the drier margins of the wet basinal lowlands; *Megalopteris*-flora from outside the basinal lowlands; walchian conifer-flora from outside the basinal lowlands; voltzian conifer-flora from outside the basinal lowlands). Thus, the concept of a clear spatio-temporal delineation of two, and only two, biomes clearly is not accurate. The temporal ranges of the several different vegetation types, especially those from drier habitats, suggest that there was not a simple side-by-side distribution of a “Paleophytic” biome 1 and a “Mesophytic” biome 2. Rather, the spatio-temporal distribution can be understood only in light of evolutionary as well as biogeographic dynamics. The main wet-dry vegetation contrasts are summarized below.

The earliest examples of spatial proximity of distinct, edaphically-climatically distinct vegetation types are from the later Mississippian (Lower Carboniferous). During the early phases of establishment of a typically Pennsylvanian wetland flora in the equatorial regions, floras composed of seed ferns that had been dominant in seasonally dry habitats from the earlier Mississippian continued to persist regionally, appearing as rare, allochthonous elements (Chalot-Prat and Galtier, 1989). Some taxa from these floras, such as *Sphenopteridium* or *Archaocalamites*, disappeared and returned during the latest Pennsylvanian as part of floras associated with returning drier climates, dominated by advanced seed plants (Mamay and Bateman, 1991; Mamay, 1992).

The oldest example in the Pennsylvanian of coexistence of “wet” and “dry” floras involves typical Early Pennsylvanian coal swamp vegetation and the *Megalopteris-Lesleya* floras in the western parts of the equatorial belt (Leary, 1981; Leary and Pfefferkorn 1977). There is little species overlap between these two floras, even though they may succeed one another within a single deposit. For example, in channel fills within a limestone landscape, an allochthonous *Megalopteris-Lesleya* flora is found in

gray siltstones in the lower 2/3 of a fill sequence, probably derived from plants growing on the limestone-based soils surrounding the channels, succeeded by a lycopsid-sphenopsid-pteridosperm flora in the upper part of the channel fill in organic shales, representing development of a parautochthonous standing-water swamp deposit (Leary, 1981; DiMichele and Phillips, 1977). This peculiar flora reappears sporadically into the Middle Pennsylvanian within siltstones between coal beds, not associated with coal roof-shale floras. Thus, these taxa persisted in the equatorial lowlands for millions of years, generally outside the window of preservation. This flora is completely distinct from the later, conifer and callipterid flora

Within the broad construct of the Pennsylvanian coal-age wetland or humid climate vegetation, there are several distinct kinds of assemblages. These are composed of variably overlapping species and generic composition, effectively representing the same broad species pool. The centroids of the dominant plant lineages (lycopsids, pteridosperms, calamitaleans, marattialean ferns, and cordaitaleans), however, appear to be different (DiMichele and Phillips, 1996b; DiMichele, Stein and Bateman, 2000), with substantial degrees of overlap among them (Gastaldo et al., 2004). The end points of this humid-wetland equatorial species pool arguably are the peat-forming floras, dominated by free-sporing plants and primitive pteridosperms and some cordaitaleans vs. a cordaitalean-dominated vegetation growing in better drained, but still wet, “upland/extrabasinal” habitats. This distinction is most clearly expressed in the Early and Middle Pennsylvanian (Falcon-Lang and Scott, 2000; Falcon-Lang, 2003; Gastaldo and Deggas, 2007). It is probable that these were endpoints in a vegetational continuum within the generally wet biome/species pool. The cordaitaleans themselves are a complex group taxonomically and are not completely understood. The best taxonomy is for the wetland taxa preserved as coal-ball petrifications (Costanza 1985; Trivett and Rothwell, 1991). Taxonomy of those forms from extra-mire habitats, preserved as adpressions, seemed much less well resolved (Šimůnek, 2000), but the most recent study demonstrates a considerable taxonomic diversity (Šimůnek, 2007). Thus, the extrabasinal areas may have been populated by different cordaitalean species than the swampy wetlands. Indirect evidence from the studies cited above, suggests that the extrabasinal species were of much larger stature, forming gallery forests.

The best documented and environmentally understood equatorial floristic dichotomy is that between the spore-producing-plant rich vegetation of everwet habitats and a flora rich in primitive walchian conifers, peltasperms, and other kinds of seed plants of varyingly understood evolutionary affinity. This pairing of floras is the classic “Paleophytic” vs. “Mesophytic” split as described by Frederiksen (1972) and later authors (but not as defined chronostratigraphically by Gothan, 1912). The vegetation types are almost entirely distinct compositionally but appear to have been spatially proximate within the equatorial belt (e.g., Cridland and Morris, 1963; Lyons and Darrah, 1989). Conifer-peltasperm floras appear sporadically in equatorial basinal lowlands during the Late Pennsylvanian (Stephanian), both in Europe (Broutin et al., 1990) and in North America (Lyons and Darrah, 1989; DiMichele and Aronson, 1992). They become dominant in these same equatorial basinal areas during the Permian. The position in the basinal lowlands of conifer-peltasperm floras appears to reflect climatic changes within the coastal, equatorial regions in the latest Carboniferous and Early Permian.

Taxa from the “Carboniferous-type” wetland biome that appear in landscapes otherwise dominated by the “Permian-type” seasonally dry biomes are mainly stream-side elements (DiMichele et al., 2006a), such as calamitaleans, or weedy opportunists that also favored wetter parts of the landscape, such as tree ferns. Some cordaites also may reflect the persistence of elements from the wetland species pool, although the taxonomic relationships of these to earlier occurring cordaitaleans is uncertain. The diversity of these cross-over taxa is much less than that known from the time of the full development and widespread geographic dominance of the wetland biome, suggesting much reduced resources to support a diverse assemblage. This pattern-reversal in the lowlands (during the Pennsylvanian the dry biota appears sporadically; during the Permian, the wet biota appears sporadically) strongly supports the model of environmental tracking by these species pools, given that the physical gradients between them appear to be sharp. Hygromorphic elements from the wet biome penetrated the drier landscapes along water courses and survived in much reduced wetlands areas or “wetspots” (DiMichele et al., 2006a). It is significant that the long term aridification trends through Permian time at equatorial latitudes in the southwestern U.S.A. and Europe (Fig. 2) appear to be interrupted several times by short-lived “pluvial” intervals of increased moisture,

suggested by stratigraphically short intervals of paleosol morphologies that are indicative of greater soil moisture availability (Miller et al., 1996; Tabor and Montanez, 2004; Roscher and Schneider, 2006). During these wetter intervals the holdover elements from the wet biome may have expanded in aerial coverage and reentered the fossil record in detectable numbers.

A similar pattern of clade-level vegetational distribution in Early Permian landscapes has been reported from the Paraná Basin of Brazil (Ricardi-Branco and Rösler, 2004). In this case, lycopsids (*Brazilodendron*) dominate swamp wetlands, broad-leaved seed plants (*Glossopteris*) dominate wet floodplains, and conifers (*Paranocladus* and *Buriadia*) dominate basin margin better drained habitats. Although the flora is entirely distinct from that at the tropics at the generic and probably familial levels, the basic ordinal level distribution of groups is the same as that in the tropics, reflecting the strong clade-by-environment partitioning that is characteristic of Phanerozoic land plants (DiMichele et al., 2000)

A yet more distinct vegetation composed of taxa with Late Permian and Mesozoic affinities follows on, but is not known to be intercalated with or share any species with, the earlier primitive conifer-peltasperm equatorial biome (DiMichele et al., 2002; Looy, in press). Like the early allochthonous appearances of elements of the conifer-peltasperm vegetation in the tropics, there are rare early appearances, during the Early Permian, of elements of this Late Permian-Mesozoic vegetation within the basinal vegetation that precedes it spatially (Looy and DiMichele, unpublished data). It has been described from the latest Early Permian only in the western portions of equatorial Pangea (DiMichele et al., 2002; Looy, 2007). Closely related elements, the same genera but apparently differing at the species level, appear again in the equatorial lowlands either in the Late Permian or in the Late Triassic. The appearance of this new species pool in the basinal lowlands can be correlated directly with the appearance of cooler and drier conditions, perhaps related to a synchronous, south-polar glaciation (Montañez et al., 2007), again demonstrating strong ties of vegetation to climatic conditions.

A fourth distinct Permian-aged biome occurs in widely divergent parts of equatorial Pangea. It is associated with very dry conditions, possibly even restricted to channel margins in otherwise arid climates and appears without clear precursors or prior

indicators of its existence (DiMichele et al., 2004). This flora is dominated by probable broad-leaved conifers, presently of uncertain affinity, and contains a gigantopterid species known from the lower Middle Permian in both the western (SW USA) and eastern (China) equatorial regions (DiMichele et al., 2004; Yao and Liu, 2004). Its subsequent history is not known. It occurs in association with indicators of severe aridity, such as bedded gypsum, oolitic limestones, and poorly developed soils (Tabor and Montañez 2002; 2004; DiMichele et al., 2006a).

Recently, the characteristically high-latitude, southern hemisphere, Mesozoic plant *Dicroidium* (Boucher et al., 1995) has been reported from the Upper Permian of Jordan (Kerp et al., 2006), which at the time was positioned in the equatorial region. This finding adds to the occurrence of Mesozoic lineages, even to generic level, now known from the Paleozoic. Whereas the flora associated with this plant has yet to be described completely, it suggests that earlier in time than expected, the equatorial regions harbored many lineages and floras considered typical of later times and even of very different latitudinal regions.

5. Conclusions

The terrestrial plant record, especially that of the Paleozoic, is primarily basinal. This record has been subjected to extensive, post-depositional erosion of “upland”/“extrabasinal” areas, resulting in a heavily biased spatial representation of the distribution of vegetation on the landscape at any given point in time. Our ability to infer landscape complexity comes mainly from studies of the appearance of different vegetation types within stratigraphic sequences where plant-bearing beds can be correlated with independent physical indicators of environmental change.

The supposed “Paleophytic” and “Mesophytic” stratigraphic intervals, identified by their distinct constituent floras, do not exist as such. The floras that supposedly define these time periods interfinger beginning as early as the Middle Pennsylvanian (Lyons and Darrah, 1989), with a general switch in dominance in basinal lowlands taking place during the Permian in equatorial regions (Kerp, 1996). More extensive sampling since this concept was initially developed indicates that significantly more than two

compositionally distinct vegetation types coexisted in equatorial Pangea during the Permo-Carboniferous, and even more when the north- and south-temperate regions are considered. Prior attempts to clarify the spatio-temporal nature of the “Paleophytic-Mesophytic” transition (Frederiksen, 1972; Knoll, 1984; Rees, 2002) have generally placed plants from these different floras into one or the other of these two vegetational categories. In fact, ambiguities in which plants belong to which group reflect the fact that there are a number of distinct coexistent vegetation types, not just two. These vegetation types reflect different norms of response to environmental conditions and represent distinct biomes or species pools – assemblages of plants tied to different kinds and ranges of environmental conditions, and strongly reflective of the naturally sharp environmental discontinuities that characterize terrestrial Earth (Fig. 5). This pattern is unremarkable, and to be expected given the relationships of modern vegetation to climate.

“Species individuality” is the concept that biotic “communities” or species assemblages reflect the fortuitous coincidence of species with similar resource requirements under momentarily prevailing local climatic and edaphic conditions. There is strong evidence for such individual species spatial dynamics on modern ecological scales, based on changes in species distributional/range patterns following the last glacial maximum. There also is clear indication, however, of limited species crossover between biomes, either in the modern or in these Paleozoic biomes, excepting plants that penetrate drier environments along swamp, stream and lakeside microhabitats. When examined at the spatio-temporal scales available in paleoecology, the plant fossil record suggests that such individual species behavior is confined largely to the biome/species pool level of hierarchical organization, just as can be seen today if one analyzes such patterns on larger spatial scales (DiMichele et al., 2005a). The sharp environmental discontinuities that are the primary foundation of the biomic boundaries (e.g. Ziegler et al., 2003) form the basis for biogeographic subdivision of the modern world (e.g. Walter, 1985). In the geological past, of course, these distributions varied from those of today based on the extent to which the emergent terrestrial realm was naturally subdivided by mountain and oceanic barriers.

Climatic changes affecting the land surface are strongly reflected by changes in biomic spatial distributions. In effect, the biomes “track” climate effectively

instantaneously, in terms of the time resolution possible in the geological record. This is essentially what has been found for north temperate species and migrations within biomes following the retreat of glaciers after the last glacial maximum (Webb, 1987; Overpeck et al., 1992). Lags in vegetational response can be detected occasionally, by very fine sampling. In Quaternary settings these have been attributed to “vegetational inertia” (Cole, 1985), reflecting recruitment dynamics. Each of the vegetational or biome spatial pairs and/or temporal replacements discussed in this paper appear to reflect such distinct climatic and edaphic differences as the major controlling factors.

These various observations come together to suggest that much evolution was going on in areas outside of basinal preservational windows (Frederiksen, 1972; DiMichele and Aronson, 1992; Kerp, 1996; DiMichele et al., 2002; Kerp et al., 2006; Looy, 2007). Based on the temporal pattern of appearance of these vegetation types (and their associated climatic conditions) in the fossil record, progressively more positionally and environmentally remote areas supported ever more derived taxa. This perhaps reflects greater opportunities for survival of highly derived forms under the reduced resource competition that might be expected in physical habitats that were underexploited and undersaturated. The results of the evolutionary changes in these remote areas are revealed to us only sporadically, by environmental changes that affect the basins, especially making them much drier, allowing marginal vegetation types to migrate in.

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Fig. 1. Figure and caption from Gothan (1912). "Graphische Darstellung des Auftretens der wichtigsten Pflanzengruppen ", translated as: Graphic reconstruction of the occurrences of major plant groups. Plant groups include algae (Algen), fungi (Pilze), mosses (Moose), and ferns (Farne). Reproduced with permission of Elsevier Scientific Publishers from Gothan, W. 1912. Paläobotanik. In: Korschelt, E., Linck, G, Schaum, K., Simon, H. Th., Verworn, M., and Teichmann, E. (eds.), Handwörterbuch der Naturwissenschaften. Jena: Gustav Fischer Verlag. Pp. 408-460.

Figure 2. Proportional diversity per stage (bin) within geographic regions of genera grouped into the categories Paleophytic, Unassigned, Sphenopsids, and Mesophytic. Bar width represents total number of localities within any one stage (bin), also indicated beneath bar. Stage indicated above bar. Data from Rees, 2002 (Data Repository Table 2).

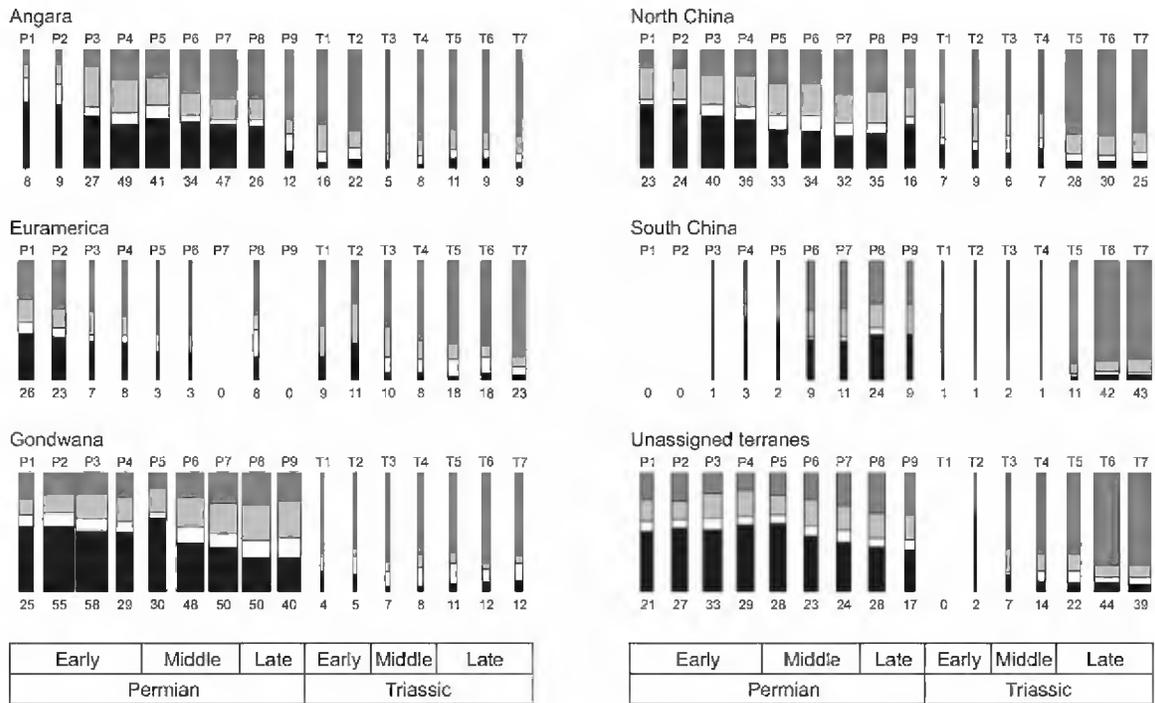
Figure 3. Inferred temporal trends in climate based on stratigraphic changes in climate-sensitive lithologies across tropical Pangea. "Humid" indicates the presence of climate-sensitive lithologies corresponding to humid conditions (>1000 mm/yr) and most months (~9) with precipitation in excess of evapotranspiration, including coal, laterite and bauxite. "Arid" indicates the presence of lithologies corresponding to dry conditions with precipitation less than ~300 mm/yr, and less than 5 months/yr with precipitation in excess of evapotranspiration, including paleosol profiles with evaporite minerals (e.g., gypsum) and carbonate. The shaded gray areas indicate stratigraphy with evidence of distinct seasonality, such as vertic paleosol morphology (e.g., Tabor and Montanez, 2004) and fusain (Falcon-Lang, 2000). The schematic climate curves are developed from Tabor and Montanez (2002, 2004), Mack (2003), and DiMichele and others (2006) for the western Pangean basins, from Ziegler et al. (2002) for the Maritimes Basin, from Roscher and

Schneider (2006) for the Lodève Basin, from Yang et al. (in press) for the Junggar basin, and from Rees et al. (2002) for the North Chinese Block.

Fig 4. Cridland and Morris (1963), figure 2 and caption. "Idealized profile of an Upper Pennsylvanian landscape in Kansas. To the right is a lowland coal swamp community composed of *Cordaites* (C), *Calamites* (Ca), *Lepidodendron* (L), ferns and pteridosperms (F), and *Sigillaria*. To the left is a community of plants growing on slightly drier, hence better drained and drier, soil. This community contains *Dichophyllum* (D), *Taeniopteris* (T), and *Walchia* (W)." Reproduced with permission of the University of Kansas, Natural History Museum.

Fig. 5. Schematic representation of the time-space relationship of different biomes (species pools) during the late Paleozoic in western equatorial Pangea. Shaded areas on left represent basinal areas where fossil preservation potential is high. White areas on left represent extrabasinal areas where fossil preservation potential is low to absent. A wet-to-less wet spatial pattern in space is duplicated through time in this region. Few species cross between biomes. Biome replacement in time reflects tracking of climatic changes rather than competitive displacement. See text for details.

Fig 2



= MESOPHYTIC (cycadophytes, ferns, ginkgophytes, peltasperms, pinales)
 = sphenopsids
 = unassigned
 = PALEOPHYTIC (cordaites, gigantopterids, glossopterids, lycopsids, pteridosperms)

Fig 4



Fig 5

