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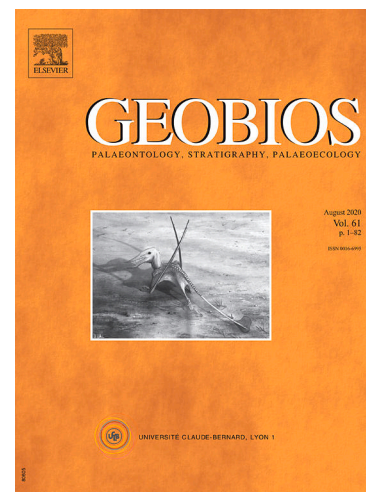
The environmental implications of upper Paleozoic plant-fossil assemblages with mixtures of wetland and drought-tolerant taxa in tropical Pangea ✡

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Abstract

We evaluate the influences of elevation and climate on the spatio-temporal distribution of wetland and dryland biomes during the Pennsylvanian and early Permian in tropical Pangea. The longstanding "upland model" places drought-tolerant vegetation in elevated habitats, where slope and drainage created moisture-limited substrates under a humid climate that simultaneously promoted peat accumulation in contemporaneous lowlands. Upland plants

were periodically transported to and buried in lowlands. Rare preservation of dryland vegetation thus reflects its general absence in basins, and taphonomic vagaries of long-distance transport. The alternative "climate model" proposes that drought-tolerant plants dominated tropical habitats when climate was seasonally dry, with wetland vegetation reduced to scattered refugia. Environmental changes attending glacial-interglacial cycles caused alternating wetter-drier conditions, and the relative abundance of wetland versus dryland biomes in basinal lowlands thus varied with climatic oscillations. The paucity of drought-tolerant plants reflects a preservational megabias against habitats with seasonal moisture deficits.

The environmental signal of "mixed" plant-fossil assemblages, comprising taxa characteristic of both wetland and dryland biomes, may help resolve these debates. We review key Pennsylvanian and lower Permian mixed assemblages from tropical Euramerican Pangea, and interpret their original habitats and climatic contexts based on multidisciplinary evidence, including sedimentology, taphonomy, physiology, and paleoecology. Evaluations also consider patterns of vegetational distribution and taphonomy in modern tropical environments. We suggest that even a cursory view of current tropical plant distribution exposes flaws in the upland model. Where tropical climate is sufficiently humid to support peat swamps, slopes and elevated habitats do not host drought-tolerant vegetation, but are occupied by plants similar to those in lowland settings. This occurs because equable, high precipitation strongly dampens water-table variation across entire landscapes. Furthermore, taphonomic studies indicate that most plant-fossil assemblages record vegetation living near the burial site. Fossil floras thus reflect environmental conditions near their growth site, excluding an upland origin for most occurrences of drought-tolerant taxa. Conversely, the climate model is consistent with modern tropical vegetational distribution and soundly explains upper Paleozoic floristic patterns. When Pangean tropical lowlands experienced seasonally dry conditions, plants tolerant of moisture deficits dominated most habitats, whereas wetland vegetation was restricted to wetter sites with greater preservation potential. This occurred because topographic variations are magnified under seasonal precipitation regimes, creating a complex habitat mosaic with wetland patches in a landscape subject to seasonal drought. Accordingly, we propose that a macrofloral assemblage with even rare drought-tolerant taxa indicates seasonality in the broader landscape.

At larger spatio-temporal scales, disagreement also persists about whether tectonic uplift or long-term climatic drying was the primary driver of changes in late Paleozoic floristic patterns and areal extent of tropical peat swamps. We argue that tectonic activity alone cannot

explain the drastic reduction in peat swamps or coincident changes in dominance-diversity of wetland vegetation. Rates of plant dispersal and evolution far outpace that of mountain building, and peat-forming wetlands persisted in elevated habitats well into the Late Pennsylvanian. Therefore, progressive late Paleozoic aridification was the most probable driver of changing floral patterns and the distribution of wetland and dryland biomes in tropical Pangea.

Keywords:

Pennsylvanian

Permian

Paleoclimate

Upland

Wetland biome

Dryland biome

1. Introduction

During part of the late Paleozoic (Late Mississippian to early Permian), Earth experienced icehouse conditions that were comparable to, but of much greater duration than, those of the Pleistocene and Holocene. Persisting for about 50 million years, this long interval of time encompassed a wide range of variation in the intensity and extent of polar and high altitude glaciation (Fielding et al., 2008), resulting in variable magnitudes of change in ice volume, global sea level, and the spectrum of regional climates (Cecil, 1990; Tandon and Gibling, 1994; Haq and Shutter, 2008; Heckel, 2008; Isbell et al., 2008; Rygel et al., 2008; Birgenheier et al., 2009; Fielding et al., 2010; Montañez and Poulsen, 2013; Archer et al., 2016). Fluctuations in the volume of polar glacial ice affected global atmospheric circulation and thus were manifested throughout the world, even in areas distant from ice centers (Falcon-Lang, 2004a; Driese and Ober, 2005; Peyser and Poulsen, 2007; Poulsen et al., 2007; Horton et al., 2012; Rosenau et al., 2013). Geological evidence shows that these climatic changes were imprinted on a complex and dynamic landmass, the Pangean supercontinent, and the effects thus were spatially heterogeneous (Roscher and Schneider, 2006; Tabor and Poulsen, 2008; Tabor et al., 2008). Furthermore, the pattern of change through time was complex, with variably intense glacial-interglacial cycles on 10^5-year time scales (Heckel, 2008) being superimposed on longer term, 10^6-year trends of warming and cooling (Roscher

and Schneider, 2006; Tabor and Poulsen, 2008; Montañez and Poulsen, 2013). Orbital forcing probably was the ultimate driver of these fluctuations (Davydov, 2014; Van den Belt et al., 2015), with atmospheric CO_2 content being the principal proximate variable (Montañez et al., 2007, 2016; Poulsen et al., 2007; Montañez and Poulsen, 2013). In addition, the icehouse world, within which these cyclic changes played out, may have been initiated during an interval of low volcanic activity, which could be a driver of long-term icehouse-greenhouse cycles (McKenzie et al., 2016).

Table 1 gives the parameters used to define the various climate modes discussed in this review. Table 1 also provides a simplified breakdown of the habitats, floral types, and dominant plant groups that existed under these different climatic regimes during the *Pennsylvanian* in tropical Euramerican Pangea. As noted in the table caption, the dominant plant groups that existed under any given environmental regime trended towards increasingly drought-tolerant taxa through the Late Pennsylvanian and Permian (DiMichele et al., 2008, 2020; Looy et al., 2014a). In this review, we use the term "xeromorphic" very broadly, to include those plants with physiological features that indicate a relatively high degree of drought tolerance (e.g., thick cuticles, shallow stomatal pits), and which enabled them to thrive in seasonally dry habitats. Representative taxa include the "dryland" cordaitaleans, callipterids, taeniopterids, and walchian conifers, plant groups that characterized the different late Paleozoic dryland biomes of Euramerica. We emphasize that none of these plants would qualify as true xerophytes, as defined by current botanical practice. We also apply the term "coniferopsid" in a general sense, to include diverse cordaitaleans, *Dicranophyllum*, and walchian and voltzian conifers. Furthermore, we use the terms "tropics", "tropical", and "equatorial" interchangeably and in a broad sense for the intertropical zone (i.e., between the Tropic of Cancer in the north and Tropic of Capricorn in the south), although our literature survey only involves studies from Euramerican localities, primarily being situated north of the equator. Such a general definition is justified, as the precise boundaries of the intertropical zone varied with the obliquity of Earth's rotational axis during the late Paleozoic, and because of the overall northward movement of Euramerica during the assembly of Pangea. We note that our definition of a "tropical climate" is equivalent to the "megathermal climate" used in modern climatological studies, and thus encompasses a wide range of possible climate modes, from (per)humid to arid.

Numerous studies, both empirical (e.g., Tandon and Gibling, 1994; Cecil et al., 2003a; Opluštil et al., 2013a; Rosenau et al., 2013; Davydov, 2014) and model-based (e.g., Horton et al., 2012), have focused on climatic oscillations that attended late Paleozoic glacial-

interglacial cycles, demonstrating that rhythmic fluctuations between (per)humid and subhumid to semiarid climates characterized the Pangean equatorial realm. However, the spatial and temporal positions of different climate states within a glacial-interglacial cycle remain highly contested (e.g., Tandon and Gibling, 1994; Heckel, 1995; West et al., 1997; Cecil et al., 2003a; Gibling et al., 2004; Feldman et al., 2005; Falcon-Lang and DiMichele, 2010; Eros et al., 2011; Jerrett et al., 2011; Dzenowski and Hembree, 2012; Rosenau et al., 2013; Cecil et al., 2014; Heavens et al., 2015). Nonetheless, despite differences in interpretation, all of the studies cited above, whether based on empirical evidence or modeling experiments, emphasize the strong linkages between ice volume, sea level, and climate. Likewise, multiple studies have demonstrated that vegetation in tropical Pangea responded rapidly and in concert with these swings in climate mode (e.g., Elias, 1936; Phillips and Peppers, 1984; DiMichele et al., 1996, 2001a, 2009, 2020; Gastaldo et al., 1996; Falcon-Lang, 2004a; Falcon-Lang et al., 2009; Falcon-Lang and DiMichele, 2010; Dolby et al., 2011; Opluštil et al., 2013a, 2015; Van Hoof et al., 2013; Cecil et al., 2014; DiMichele, 2014; Looy et al., 2014a, 2014b; Gulbranson et al., 2015; Bashforth et al., 2016a).

None of these postulations would surprise those who focus on late Cenozoic climate dynamics, as similar coupled fluctuations in polar ice volume, sea level, and climate also characterize our current icehouse world (Webb and Bartlein, 1992; Lisiecki and Raymo, 2007; Anderson et al., 2013). The manifestation of these climate changes varies greatly across the globe, depending on local continental configurations, physiography, and latitude. Furthermore, based on studies of the distribution of Pleistocene and Holocene vegetation, there is strong empirical evidence that plants reflect and track climatic conditions, with rainfall and temperature being the primary determinants (Köppen, 1936; Holdridge, 1947; Wittaker, 1970; Woodward, 1987; Colinvaux et al., 2000; Jackson and Overpeck, 2000; Martínez-Meyer and Peterson, 2006; Williams and Jackson, 2007; Ackerly et al., 2010; Bush et al., 2011; Clark et al., 2016; Guo et al., 2018; Zhang et al., 2018), although fire (Bond et al., 2005) and substrate (Gastaldo, 2010) also play a prominent role. Being cognizant that climate is the overriding control on the distribution of modern vegetation in space and time, it is logical to presume, and to posit, that climate acted as prominently in Deep Time as it does today in controlling the distribution of ancient vegetation.

Despite observations of modern and ancient climate dynamics, and the pronounced link between climate and plant distribution in the modern world, differences of opinion persist about the degree to which climate controlled the distribution of vegetation and floristic patterns in dominance and diversity during the late Paleozoic. The primary competing

argument is that elevation (with attendant differences in slope, aspect, and sediment output) was the main factor that determined the spatial and temporal distribution of late Paleozoic plants, especially those of the Pennsylvanian tropics, largely through its presumed effects on soil drainage (Cridland and Morris, 1963; Lyons and Darrah, 1989; Broutin et al., 1990; Cleal and Thomas, 1999, 2005; Dimitrova et al., 2011; Thomas and Cleal, 2017). In this "upland model" (Fig. 1), background climate either is not considered, or is implicitly assumed to have been constantly humid, ostensibly due to the presence of coal beds in the local stratigraphic section. Furthermore, siliciclastic intervals between coals have been interpreted as the product of short-term floods that inundated peat-forming habitats due a variety of mechanisms, including increased subsidence, eustasy, or violent cyclones (Cleal and Thomas, 2005; Dimitrova et al., 2010; Thomas and Cleal, 2015, 2017). At larger spatial and temporal scales, tectonic uplift and resulting drainage effects also have been implicated as the drivers of major changes in the areal extent of peat swamps and patterns of plant species origination and extinction, particularly near the Middle to Late Pennsylvanian boundary (Kerp, 1996; Cleal and Thomas, 2005; Cleal et al., 2009, 2011).

Differences of opinion about the role of elevation *vs*. climate as the primary mechanism controlling the distribution of late Paleozoic tropical vegetation come to a head when attempting to explain the occurrence of plant fossils with mesomorphic or xeromorphic characteristics, either as dominant components of an assemblage or when mixed with wetland taxa. Although the vast majority of Pennsylvanian macrofloral assemblages are typified by wetland elements, taphocoenoses that are coniferopsid-dominated or contain other derived taxa with physiological traits that point to periodic moisture deficits provide rare glimpses of tropical vegetation adapted to better-drained or seasonally dry conditions. Given the relative paucity of these occurrences in Pennsylvanian coal-bearing successions, such plant fossils have frequently been attributed to "upland" or "extrabasinal" source areas (Fig. 1). The main premise is that the plants were transported to basinal lowlands from elevated habitats, with arguments frequently centered on the tacit assumption of "elevation" being synonymous with "well-drained" (Chaloner, 1958; Havlena, 1961, 1971; Cridland and Morris, 1963; Leary and Pfefferkorn, 1977; Lyons and Darrah, 1989; Pfefferkorn, 1980; Broutin et al., 1990; Dimitrova et al., 2011; Thomas and Cleal, 2017). The rarity of these plant remains in the fossil record thus is interpreted to reflect their general absence in depositional basins, taphonomic vagaries associated with transport from upland habitats, and the fact that elevated regions generally are not preserved in the long-term geological record.

Nonetheless, macrofloral assemblages that contain the enigmatic, non-wetland plant fossils are invariably found *within* depocenters, rather than being confined to marginal settings or to the uplands themselves (DiMichele et al., 2010a). Accordingly, an alternative explanation for their presence is that the fossils represent "seasonally dry", "dryland", or "drought-tolerant" floras (terms used synonymously herein), with prior adaptation to moisture limitation enabling the plants to disperse into basinal lowlands during episodes of climatic drying (Elias, 1936; Moore et al., 1936; Mapes and Gastaldo, 1986; DiMichele and Aronson, 1992; Gastaldo, 1996; Falcon-Lang, 2004a; Tidwell and Ash, 2004; DiMichele et al., 2008, 2010a, 2016, 2020; Falcon-Lang et al., 2009, 2011a, 2012, 2014, 2016; Dolby et al., 2011; Van Hoof et al., 2013; Bashforth et al., 2014, 2016a; DiMichele, 2014; Ielpi et al., 2014; Looy and Hotton, 2014; Looy et al., 2014a, 2014b; Pfefferkorn et al., 2017; Blomenkemper et al., 2018). Under this "climate model" (Fig. 2), oscillations between relatively dry and wet edaphic conditions in basinal lowlands were an expression of climatic changes that occurred during glacial-interglacial cycles operating on 10^5-year time scales. These fluctuations determined the relative abundance of vegetation with dryland *vs*. wetland signatures in the lowlands. The paucity of plant fossils with mesomorphic or xeromorphic characters in basins is explained by a preservational megabias against habitats with seasonal moisture deficits, even if located in lowland settings (Behrensmeyer et al., 2000; DiMichele and Gastaldo, 2008; Gastaldo and Demko, 2011). This interpretation does not exclude the existence of resident populations of the dryland biome in permanently moisture-limited regions, from which that type of vegetation dispersed when equatorial lowlands experienced drier conditions (Read, 1947; DiMichele et al., 2010a, 2020; DiMichele, 2014). The dryland biome was permanently resident in western Pangea, for example, and other loci may have been in areas of rain shadow (Rowley et al., 1985; Van Hoof et al., 2013), or perhaps patches in elevated hinterlands (Broutin et al., 1990), such as exist in parts of the modern Andes due to regional effects on airflow patterns (Chavez and Takahashi, 2017).

We realize that inferring climate or habitat conditions solely from the morphological features of upper Paleozoic plant fossils is fraught with uncertainties, as the taxa have few modern homologues, and, even then, only at very high phylogenetic levels. Nonetheless, tested repeatedly through numerous studies, a general understanding has emerged of the link between the morphological and physiological characters of Pennsylvanian and Permian plant taxa and physical indicators of their environment (Elias, 1936; Havlena, 1971; Scott, 1978, 1979; Iwaniw, 1985a; Mapes and Gastaldo, 1986; Rothwell and Mapes, 1988; DiMichele and Aronson, 1992; DiMichele and Phillips, 1994; Calder et al., 1995, 2006; Gastaldo, 1996;

Falcon-Lang et al., 2004, 2009, 2011a, 2014, 2016; Falcon-Lang and Bashforth, 2005; Feldman et al., 2005; Opluštil and Cleal, 2007; Opluštil et al., 2007, 2016a, 2017a; Hernandez-Castillo et al., 2009; Libertín et al., 2009; Raymond et al., 2010, 2014; Bashforth et al., 2010, 2011, 2014, 2016a, 2016b; Wagner and Castro, 2011; Stull et al., 2012; Wilson et al., 2015, 2017; Simon et al., 2016; DiMichele et al., 2016, 2017a). Consequently, many taxa, at ranks from species to order, can now be used to estimate moisture availability on the landscape and the general climatic conditions under which they grew.

2. Objective of the review

The objective of this paper is to evaluate the relative influence of elevation and climate as controls on the spatial and temporal distribution of late Paleozoic vegetation in tropical Pangea. We believe that a means to resolving this longstanding debate rests in the environmental signal presented by "mixed" floral assemblages, namely those composed both of taxa indicative of humid climatic conditions with high soil moisture (wetland elements), and those indicative of subhumid to semiarid climatic conditions with permanently or seasonally low soil moisture (dryland elements). We provide a critical analysis of key mixed plant-fossil assemblages of Early Pennsylvanian to early Permian (Cisuralian) age from across the tropics of Euramerican Pangea, with interpretations of their original habitat and climatic conditions drawn from multidisciplinary lines of evidence, including sedimentology, taphonomy, plant physiology, and ecology. The dichotomy in hypotheses about the role played by climate *vs*. elevation in creating conditions of soil moisture deficit provides the framework of our evaluation. Although we do not present an exhaustive literature review of mixed Pennsylvanian and lower Permian floral assemblages from equatorial Pangea, the chosen studies touch on the broad themes of environmental variation in space and time.

3. Late Paleozoic tropical Pangea: paleogeographic and climatic setting

A key reason for the differences in opinion about the original habitat and ecological significance of drought-tolerant taxa in the upper Paleozoic plant-fossil record is that both climate and tectonics were dynamic factors in equatorial Pangea (Rowley et al., 1985; Opluštil, 2004; Torsvik and Cocks, 2004; Tabor and Poulsen, 2008; Hopper et al., 2017; Wagner, 2017). During the Pennsylvanian and Permian, Earth's landmasses were amalgamating into the supercontinent of Pangea (Fig. 3), which developed due to the oblique convergence of Euramerica, Gondwana, and associated terranes, and resulted in uplift of the Ancestral Rocky Mountain-Ouachita-Appalachian-Variscan Orogen (Central Pangean

Mountains) along a heterogeneous collision zone (Ziegler, 1989; Matte, 2001; Hatcher, 2010). The mountain belt probably comprised a spatially and temporally discontinuous chain of tectonically active centers (Roscher and Schneider, 2006; Wagner, 2017). This chain rose, and eroded down, earlier in the east than in the west, in zipper-like fashion (Hatcher, 2002), rather than being a continuous belt of high elevation that spanned the entire equatorial region. Nonetheless, relief in some parts of the belt may have been comparable to the present-day Himalayan Chain, based on the similarity of tectonic regimes and the metamorphic grade of exhumed roots (Dewey and Burke, 1973; Maierová et al., 2016), as well as inferences from climate-modeling studies (Fluteau et al., 2011).

The vast size of Pangea and the heterogeneous and diachronous nature of the collision between Euramerica and northern Gondwana resulted in pronounced regional differences in tectonic regime, physiography, and basin development in equatorial regions during the late Paleozoic (Fig. 3). Westernmost Pangea comprised the island-dotted coastal seaboard of the Panthalassan Ocean (Blakey, 2007; Nelson and Lucas, 2011), preserved today in the southwestern USA as predominantly shallow marine carbonates. West-central Pangea consisted of a low-gradient continental platform in the USA Midcontinent (Leighton et al., 1991) that passed eastward into the foreland basins of the Appalachian region (Hatcher, 2010), with the degree of marine influence also diminishing eastward. Small intramontane (mainly paralic) basins of central Pangea are found today in Atlantic Canada (Gibling et al., 2019), whereas east-central Pangea consisted of a variety of paralic and intramontane (mainly limnic) basins in the Variscan Deformation Zone of northern and central Europe (Roscher and Schneider, 2006; Schulmann et al., 2014; Wagner, 2017). Eastern Pangea primarily was a shallow marine zone that extended eastward from the Donets Basin of Ukraine and Russia into the Paleo-Tethyan realm (Sachsenhofer et al., 2010). Note that we use the term "intramontane basin" in its literal sense ("basin within mountains"), but differentiate those that were influenced by marine incursions (paralic) from those presumed to be the loci of entirely freshwater systems (limnic).

There also was a distinct spatial trend in moisture distribution from west to east across equatorial Pangea. For example, Cecil et al. (2003a) traced a single glacial-interglacial cycle of Desmoinesian (late Moscovian) age through a spectrum of climatic conditions, from arid in western Pangea, through seasonally moisture-limited in the Midcontinent and Illinois basins, to more humid in the Appalachian Basin. That widespread aridity prevailed almost continuously in western Pangea is confirmed by numerous proxies (Mack, 2003; Tabor and Montañez, 2004; Tabor et al., 2008; Jordan and Mountney, 2012), and the occurrence of

loessites in Permian cyclothem deposits in Kansas points to strongly seasonal climatic conditions during parts of glacial-interglacial cycles in the Midcontinent regions of the USA (Dubois et al., 2012). However, the (per)humid climatic conditions necessary for peat accumulation appear to have been widespread when and where they occurred. For example, the fact that a siliciclastic parting or layer of volcanic ash can persist at the same level within a coal bed over vast areas (Nelson, 1983; Greb et al., 1999, 2003) provides evidence for the widespread contemporaneity of many upper Desmoinesian (Asturian and Cantabrian) coal beds in paralic settings of west-central Pangea (Midcontinent through the Appalachians). Likewise, the wetland biome from clastic substrates was remarkably homogeneous over great distances during the early phases of deglaciation and sea-level rise (Moore et al., 2014; Bashforth et al., 2016b).

Superimposed on this west-to-east moisture gradient was a long-term (10^7-year) temporal trend of increasing temperature and aridity in equatorial Pangea through the late Paleozoic (Cecil et al., 1985; Schutter and Heckel, 1985; DiMichele et al., 2006, 2009, 2010a; Roscher and Schneider, 2006; Peyser and Poulsen, 2008; Tabor and Poulsen, 2008; Tabor et al., 2008, 2013b; Opluštil et al., 2013b, 2017a; Van Hoof et al., 2013; Michel et al., 2015; Tanner and Lucas, 2018). As a consequence of long-term aridification, wet-dry climatic oscillations that resulted from glacial-interglacial cycles on 10^5- to 10^6-year scales both trended towards the drier end of the spectrum in a stepwise fashion (Montañez et al., 2016). The duration and spatial extent of (per)humid conditions, necessary for widespread peat accumulation, diminished in the wet phases, whereas climatic seasonality became increasingly intense during the dry phases (Wagner, 2004; DiMichele et al., 2009, 2020; Falcon-Lang et al., 2009; Opluštil et al., 2013b; DiMichele, 2014). This progressive trend towards drier conditions is expressed by changes in the aerial extent and volume of coal in upper Paleozoic basins (Phillips and Peppers, 1984; Schutter and Heckel, 1985; Cleal and Thomas, 2005). Peat accumulation peaked in the late Bashkirian and Moscovian (late Early to Middle Pennsylvanian) throughout the tropics of Euramerica, but by the Kasimovian (early Late Pennsylvanian) was largely restricted to basins west of the Appalachian Mountains (west-central Pangea), isolated limnic intramontane basins in central Europe (east-central Pangea), and the Donets Basin (eastern Pangea).

4. Late Paleozoic Ice Age dynamics in tropical Pangea

Establishing the linkage between ice volume, sea level, and climate is crucial to the argument at hand. That there was abundant grounded ice in the south polar regions of Pangea

is firmly established by empirical evidence. Studies of Southern Hemisphere geology point to multiple ice centers (Isbell et al., 2012; Fig. 3), rather than a single large ice sheet, and to dynamic changes in ice volume (Isbell et al., 2003; Rygel et al., 2008; Birgenheier et al., 2009; Fielding et al., 2010). Modeling studies suggest that fluctuations in atmospheric CO_2 content were the proximate driver of ice volume (Horton et al., 2007, 2012; Montañez et al., 2007, 2016; Peyser and Poulsen, 2007; Poulsen et al., 2007; Chen et al., 2018). In the tropics, repeated fluctuations in ice volume were accompanied by changes in sea level, atmospheric circulation, and climate. The record of these oscillations varied greatly, even within the tropics of Pangea, depending on regional conditions: proximity to an ocean, physiognomy, tectonic setting, and position on the continent (Soreghan and Dickinson, 1994; Van den Belt et al., 2015). From the Midcontinent through to the eastern USA, and in the Donets Basin of Ukraine and Russia, cyclicity led to the deposition of so-called cyclothems (Wanless and Shepard, 1936; Langenheim and Nelson, 1992; Heckel et al., 2007; Gastaldo et al., 2009; Davydov et al., 2010; Eros et al., 2012; Cecil et al. 2014; Jirásek et al., 2018), within which terrestrial strata, frequently including coal beds, alternated with marine deposits. However, elsewhere in the tropics of Euramerican Pangea, such cyclicity is recorded in primarily marine strata (Goldhammer et al., 1991; Elrick and Scott, 2010), in mainly terrestrial successions (Gibling et al., 2004; Dubois et al., 2012; Cecil, 2013; Martino, 2016), or in limnic intramontane basins removed from marine influence (Opluštil et al., 2013a, 2015, 2019; Lojka et al., 2009, 2010, 2016).

The origin of these cyclic successions has long been attributed to the interplay of tectonics and eustasy (Langenheim and Nelson, 1992). However, it has become clear, particularly as modeling studies have advanced, that there were strong, systemic linkages between ice volume, sea level, and climate. In particular, as originally envisioned by Wanless and Shepard (1936), the role of climate in determining the lithological and depositional succession in cyclothems is now known to have been far more significant than previously understood (West et al., 1997; Cecil et al., 2003a; Horton et al., 2012; Heavens, 2015).

To interpret these patterns, observations of the Pleistocene and Holocene ice-house world provide some guidance about the conditions under which key lithological indicators of climate formed. For example, climate plays the primary role in peat accumulation in modern tropical environments, in which humid to perhumid conditions are requisite (Lottes and Ziegler, 1994; Hirano et al., 2009); the number of "wet months" (months during which rainfall exceeds evapotranspiration; Table 1) is more important than mean annual rainfall in predicting peat accumulation. Climate also exerts strong controls on erosion and sediment

transport by influencing vegetation density, rooting intensity, and canopy cover (Gyssels et al., 2005; Reubens et al., 2007). In fact, almost counter-intuitively, in humid to perhumid parts of the tropics, sediment supply to drainage networks is minimized because chemical weathering predominates and soils are bound by a dense cover of vegetation and roots (Ohmori, 1983; Cecil et al., 1993). Rather, maximum sediment production and transport occur under a subhumid climate, which is characterized by seasonal and frequently intense rainfall (Table 1), reduced plant cover, and decreased root density; less cover and soil binding promote physical weathering through erosion and result in increased sediment load in fluvial systems (Schumm, 1968; Hooke, 2000; Cecil and Dulong, 2003; Cecil et al., 2003b; Latrubesse et al., 2005). Thus, intervals of high, evenly distributed rainfall: (*i*) favor plant growth and soil saturation, fostering peat accumulation and dense vegetation cover on mineral soils, and (*ii*) suppress the movement of sediment that, if introduced into peat-forming environments, dilutes organic accumulations to such a degree that carbonaceous shales (rather than coal) will result. In contrast, in seasonally dry environments, large amounts of sediment are eroded and transported, leading to the development of complex, dynamic alluvial and coastal plains.

Although climatic cyclicity occurred throughout the Pennsylvanian and early Permian, regardless of geographic location, nowhere was the climate continuously humid to perhumid. Where such a climate state periodically existed, there also were intercalated and generally very long intervals (20,000 years or more) of seasonal climate (Tandon and Gibling, 1994; Falcon-Lang et al., 2009; Horton et al., 2012; Rosenau et al., 2013; Cecil et al., 2014). Glacial-interglacial cycles on the scale of 10^5-year left an indelible signature in the rock record, with resulting lithological patterns recording environmental variations in climate and sediment transport (Cecil et al., 1985, 2014; Cecil, 1990; Langenheim and Nelson, 1992), even in areas remote from eustatic effects (Roscher and Schneider, 2006; Opluštil et al., 2013a, 2015; Lojka et al., 2016). Evidence of these climatic fluctuations comes from several abiotic sources, most notably paleosols, sedimentological patterns, the extent and widespread correlation of stratigraphic sequences, and modeling studies. For example, many paleosols beneath coal beds record a dynamic and polygenetic history, with initial formation under seasonally distributed rainfall, progressing to aseasonal rainfall in late stages, prior to the onset of peat formation (Driese and Ober, 2005; Rosenau et al., 2013; Opluštil et al., 2019). Sedimentological studies have demonstrated a clear relationship between channel architecture, drainage-basin extent, and prevailing rainfall regime in tropical settings, both in paralic and limnic basins (Feldman et al., 2005; Fielding et al., 2009, 2018; Allen et al., 2011;

Lojka et al., 2016), with evidence of seasonally dry climates falling between peat-forming intervals. In strata between coal beds, shallow fluvial channels, largely filled with intraformational and locally derived sediment, have been identified as lateral facies of paleosols that record seasonal rainfall regimes (Feldman et al., 2005; Falcon-Lang et al., 2009; DiMichele et al., 2016).

Furthermore, coal beds that can be correlated over large areas apparently formed contemporaneously throughout their extent, based on the presence of siliciclastic partings, datable ash beds, petrographic characteristics of distinct and widespread benches, or the microfossil content of overlying marine beds (Gresley, 1894; Fisher, 1925; Nelson, 1983; White et al., 1994; Greb et al., 1999, 2003; Cecil et al., 2003a; Jerrett et al., 2011). As such, widespread, economic coal beds generally are not the lateral facies of siliciclastic paleosols, or of floodplain deposits, and cannot be traced laterally into such paleosols. At larger scales, the repetitive cycles of marine and nonmarine strata, including coal beds, have been widely correlated, effectively across the Euramerican continent (Heckel et al., 2007; Eros et al., 2012), demonstrating that regional allocyclic mechanisms were responsible for the architecture of sequences where tectonic overprinting was minimal. Finally, climate-modeling studies at scales larger than single glacial-interglacial cycles have shown strong associations between the extent of Pennsylvanian ice sheets and tropical climate (Crowley and Baum, 1992; Otto-Bliesner, 1992; Poulsen et al., 2007; Peyser and Poulsen, 2008; Montañez et al., 2016). Where such dynamics have been investigated at the scale of individual cycles (Horton et al., 2012; Montañez et al., 2016), there is conformance between the patterns of climate change and the physical evidence from the rock record.

5. Taphonomic processes of plant-fossil preservation

The preservation of identifiable plant fossils in the geological record requires the coincidence of a unique set of conditions (DiMichele and Gastaldo, 2008; Gastaldo and Demko, 2011; Looy et al., 2014a; DiMichele et al., 2016, 2020). The most important factor is burial of plant remains in a depositional environment where the effects of bacterial and fungal degradation are negligible, i.e., *short-term preservation*. In a terrestrial setting, this can be accomplished if material is buried below the fluctuating part of the water table, particularly in a setting where dysoxic to anoxic conditions prevail (Ferguson, 1985; Burnham, 1989; Gastaldo et al., 1989; Spicer, 1989). Burial must be rapid because microorganisms and macrodetritivores, mainly arthropods, will quickly destroy organic matter, especially in warm, tropical settings (Gastaldo, 1994; Falcon-Lang et al., 2015a). For *intermediate-term*

preservation (10^3- to 10^4-year), burial of the plant-bearing sediment beneath a flooded surface is an essential next step (Gastaldo and Demko, 2011). If this ensues, *long-term preservation* (10^6-year) can occur where tectonism or subsidence create sufficient accommodation space for further burial. The fact that identifiable plant remains are relatively uncommon in the fossil record testifies to how rarely all of these conditions are met.

Subsiding depositional basins are the most probable places for all three burial phases to coincide due to the possibility for long-term burial, removing the fossil-bearing deposits from the effects of erosion. This explains why so-called "uplands" rarely are directly represented in the Paleozoic rock record, although they may still survive in intramontane Cenozoic settings where erosion has yet to remove them (Frisch et al., 1998; Vincent, 2001; Rodríguez-Fernández and Sanz de Galdeano, 2006; Cather et al., 2012: table 4). Nonetheless, the preservation of elevated late Paleozoic areas has been postulated in the Variscan realm (Tenchov, 1976; Opluštil, 2005a), rare examples that may reflect unusual tectonic circumstances within a mountain belt.

Plant fossils occur in a variety of depositional environments in basins, including peat-forming habitats where plants were preserved largely *in situ*, on mudflats in coastal regions during marine transgressions, in lakes into which plants mainly were transported from the surrounding shoreline or from riparian habitats of streams debouching into the lake, or in fluvial channels that were abandoned and rapidly filled (Scheihing and Pfefferkorn, 1984; Ferguson, 1985, 2005; Burnham, 1989; Gastaldo, 1989; Gastaldo et al., 1989; Spicer, 1989). Of critical importance, empirical studies demonstrate that the source of most canopy litter in modern (para)tropical riparian forests is from local plants growing within an ~0.1 ha area (Burnham, 1989, 1993); such taphocoenoses were termed "parautochthonous" by Bateman (1991). Accordingly, most macrofloral assemblages afford "ecological snapshots" of plant communities that lived in the vicinity, and provide a rough estimate of relative abundances in the source vegetation (Wing and DiMichele, 1995; DiMichele and Gastaldo, 2008). However, in basins subjected to strongly seasonal climates, including the western regions of Pangea during the Pennsylvanian, and nearly everywhere in tropical Pangea outside of Cathaysia during the Permian (Hilton and Cleal, 2007; Wang et al., 2012), plant fossils are relatively rare because the conditions for both short- and intermediate-term preservation were seldom met.

Falcon-Lang et al. (2009) suggested that the seasonally dry phases of glacial-interglacial cycles were of significantly longer duration than the (per)humid intervals, but that the likelihood of plant-fossil preservation was low during those drier times due to a strong

taphonomic megabias (Behrensmeyer et al., 2000). If correct, vegetation adapted to seasonally dry conditions may have been the predominant tropical vegetation of the "Coal Age", rather than the oft-reconstructed Pennsylvanian peat swamps. However, the preservational potential of plant matter in seasonally dry landscapes is vanishingly small, resulting in an extremely poor record of these floras. When preserved, such assemblages commonly contain both "Lazarus" (Jablonski, 1986) and "Methuselah" (Looy et al., 2014a) taxa, being those that appear well after or well in advance (respectively) of stratigraphic intervals in which they are more commonly known. Examples include characteristically Mississippian taxa in Pennsylvanian assemblages (Read, 1934; Leary and Pfefferkorn, 1977; Wagner, 2001; Mamay and Bateman, 1991; Bashforth et al., 2014), or plants typical of the late Permian or Mesozoic being found in Upper Pennsylvanian and lower Permian assemblages (Looy, 2007; DiMichele et al., 2001b; Wagner and Álvarez-Vázquez, 2010; Looy et al., 2014a; Looy and Duijnstee, 2020). In nearly all instances, these temporally disjunct occurrences are from seasonally dry environments. Such assemblages also may contain plants of uncertain affinity (Mamay, 1990; Mamay and Mapes, 1992; Bashforth et al., 2016a; DiMichele et al., 2016), and fossil-taxa with large biogeographic range gaps or extensions (Read, 1947; DiMichele et al., 2001b; Falcon-Lang et al., 2015b; Blomenkemper et al., 2018). Such anomalies reflect the rarity with which seasonally dry vegetation was preserved, rather than the rarity with which it occurred, on Pennsylvanian and early Permian landscapes.

6. Selected examples of "mixed floras" in environmental context

In this section, the body of the review, summaries are given for a selection of studies that integrate sedimentologic, paleoclimatic, and paleofloristic evidence, the kind of investigations on which arguments in this review rest. The chosen papers represent only a subset of those that have examined upper Paleozoic plant-fossil assemblages that contain a mixture of wetland and drought-tolerant elements, but should suffice as an introduction to the sizeable body of literature that exists for such mixed floras. The examples (Table 2; Figs. 4, 5) are arranged chronologically within three time slices (Pennsylvanian, Pennsylvanian-Permian transition, and early Permian), and within these time bins, based on their paleogeographic position in equatorial Pangea, from west to east: western Pangea (western USA; Fig. 6), west-central Pangea (Midcontinent to Appalachian regions of the USA; Fig. 6), central Pangea (Atlantic Canada; Fig. 7), and east-central Pangea (Europe; Fig. 8). Organized in this manner, broad patterns in regional climatic conditions and temporal trends emerge.

6.1. Stratigraphic terminology and boundaries

The relative chronostratigraphic positions of localities or lithostratigraphic units reviewed herein are given in Figs. 4 and 5 and Table 2. Fig. 4 encompasses all localities outside of the Czech Republic (Fig. 5), and shows correlations between the global and regional divisions of the Pennsylvanian Subsystem (after Davydov et al., 2012; Richards, 2013) and the Cisuralian Series (lower Permian) (after Henderson et al., 2012; Lucas and Shen, 2017). The significant number of dashed lines at chronostratigraphic boundaries reflects ongoing uncertainties in the placement and correlation between global stages, North American regional stages, and Western European regional (sub)stages. Likewise, the position of many localities and the range of lithostratigraphic units are only approximated, particularly in the uppermost Pennsylvanian and lower Permian, due to a lack of biostratigraphic control and radioisotopic dates. The following adjustments were made to the base chart of Richards (2013) for increased precision: (*i*) the Bolsovian-Asturian Substage boundary was lowered to just below the Atokan-Desmoinesian Stage boundary, based on biostratigraphic correlations of macrofloral assemblages from the Illinois Basin (Bashforth and Nelson, 2015; Bashforth et al., 2016b); (*ii*) the Missourian-Virgilian Stage boundary, which is identified by the first appearance of the conodont *Streptognathodus zethus* (Heckel, 1999), was placed slightly below the Kasimovian-Gzhelian Stage boundary, which is marked by the first appearance of the conodont *Idiognathodus simulator* (Heckel et al., 2007, 2008); and (*iii*) the Virgilian-Wolfcampian Stage boundary was situated within the Gzhelian Stage (at the "Bursumian"-Nealian boundary; Davydov et al., 2010; Lucas et al., 2013a; Lucas and Shen, 2016), based on placement of the Pennsylvanian-Permian boundary at the first appearance of the conodont *Streptognathodus isolatus* (Davydov et al., 1998).

There is considerable complexity in the placement and terminology of chronostratigraphic boundaries and biostratigraphic events through the Middle to Upper Pennsylvanian transition, particularly as used in the American literature (see Falcon-Lang et al., 2011b, 2018). We attempt to clarify the various terms used here:

- The traditional Desmoinesian-Missourian Stage boundary in the central and eastern USA coincides with the abrupt disappearance of *Lycospora*-producing lycopsids and the concomitant influx of tree ferns in peat-forming habitats (Phillips et al., 1974, 1985; Phillips and Peppers, 1984; DiMichele and Phillips, 1996; Kosanke and Cecil, 1996; Peppers, 1996, 1997). The level of this floristic turnover is indicated with asterisks on Fig. 4. As employed in much of the American literature, including the aforementioned papers, this major floristic reorganization event is considered equivalent to the

traditional Westphalian-Stephanian Stage boundary of Western Europe, as that boundary was defined prior to introduction of the Cantabrian Substage, now the lowest substage of the Stephanian (Wagner and Winkler Prins, 1985). With establishment of the Cantabrian, the revised Westphalian-Stephanian boundary is now positioned in the upper Desmoinesian. Furthermore, we emphaize that many American workers continue to refer to the Desmoinesian-Missourian boundary as the "Middle-Upper Pennsylvanian boundary" (but see below). Others have disregarded the Cantabrian due to justifiable difficulties in correlating the unit into the USA, and continue to use a "pre-Cantabrian" framework, in which the traditional Desmoinesian-Missourian and traditional Westphalian-Stephanian boundaries are considered coincident;

- The revised Desmoinesian-Missourian Stage boundary in the USA is defined by the first appearance of the conodont *Idiognathodus eccentricus* (Heckel et al., 2002). The boundary now occurs at a slightly higher stratigraphic level than the traditional, palynology-based Desmoinesian-Missourian boundary and accompanying floral step-change (Fig. 4);

- The Middle to Upper Pennsylvanian Series boundary equates to, and is coupled with, the Moscovian-Kasimovian Stage boundary (Fig. 4), as presently defined in the Moscow Basin. In its current iteration, the boundary is situated below both the traditional and revised Desmoinesian-Missourian boundaries of the USA, and is within the lower Cantabrian Substage of Western Europe. As a Global boundary Stratotype Section and Point (GSSP) for the Moscovian-Kasimovian boundary has yet to be formally ratified, efforts are afoot that may see it adjusted to a higher level that coincides with the revised Desmoinesian-Missourian boundary (Villa and Task Group, 2008; Heckel, 2013).

The chart in Fig. 5 shows the relative chronostratigraphic positions of reviewed lithostratigraphic units from the Czech Republic. Correlations between the global and Western European divisions of the Pennsylvanian and lower Permian have recently been constrained by high-precision radioisotopic dating in numerous basins in the Czech Republic (Opluštil et al., 2016b, 2016c, 2017b) and in the Autun Basin of the French Massif Central (Pellenard et al., 2017). Refinements to the chronostratigraphic framework based on these data have resulted in marked upward shifts in the absolute ages of all Western European (sub)stages as they correlate to the global stages. As a consequence, we emphasize that the range of lithostratigraphic units shown for the Czech Republic (Fig. 5; Table 2) cannot be directly compared with those from elsewhere (Fig. 4). Although the refinements proposed by

Opluštil and colleagues may ultimately be accepted by the International Commission on Stratigraphy (ICS), the lack of biostratigraphically useful marine microfossils in the largely terrestrial fill of intramontane basins in the Variscan Mountains, and the paucity of radioisotopic data from the American successions, continues to hamper correlations between Western European (sub)stages and American stages. For this reason, we retained the chronostratigraphic framework for the Pennsylvanian and lower Permian, as currently recognized by the ICS (Davydov et al., 2012; Henderson et al., 2012; Richards, 2013; Lucas and Shen, 2017), for all localities outside of the Czech Republic.

6.2. Pennsylvanian

6.2.1. Western Pangea (western USA) (Fig. 6)

6.2.1.1. Atrasado Formation, Socorro County, New Mexico

The uppermost Desmoinesian to middle Virgilian Atrasado Fm. in Socorro County, New Mexico (Barrick et al., 2013) has yielded mixed floras from tens of stratigraphic levels and a variety of depositional environments, including prodeltaic mudstones, dysoxic lagoons, and floodplain channels (Lerner et al., 2009; Lucas et al., 2013b; DiMichele et al., 2017b). Almost all macrofloral assemblages have a mixed character. Typical wetland elements include the medullosalean pteridosperm *Neuropteris ovata*, marattialean tree fern foliage, calamitalean stems and foliage, and rare sigillarian lycopsids. Mesomorphic taxa, which are interpreted as having been tolerant of some seasonal drought, include several fossil-species of *Odontopteris*, *Neurodontopteris auriculata*, and *Sphenopteris germanica*, whereas the xeromorphic component includes cordaitaleans, conifers, and the noeggerathialean *Charliea*. Two locally widespread autochthonous plant-fossil accumulations in the Atrasado Formation record extreme environmental endpoints: (*i*) A Desmoinesian assemblage dominated by *Neuropteris ovata* with lesser calamitalean remains, interpreted as a coastal swamp community; and (*ii*) a Missourian assemblage of coniferopsid tree stumps rooted in a calcareous mudstone and buried in dunes of carbonate and gypsum (Falcon-Lang et al., 2011a, 2016), interpreted as having inhabited an arid coastal setting (Elrick et al., 2017). The autochthonous coniferopsid assemblage clearly demonstrates the existence of a Pennsylvanian drought-tolerant flora within a basin (and in a coastal setting no less), rather than being transported from an upland. Of equal significance, this coastal deposit is intercalated within fossiliferous strata that contained mixed macrofloral assemblages. The autochthonous *N. ovata*- and coniferopsid-dominated floras thus record the effects of vastly different moisture regimes on a coastal region, manifested in the vegetation.

These assemblages permit direct assessment of the ongoing conflict between elevational *vs*. climatic causations of floristic change. Both factors were active in this area during deposition of the Atrasado Fm., with eustatic sea-level fluctuations (Elrick and Scott, 2010) being superimposed on tectonically driven accommodation space and regional uplift (Lucas et al., 2013b). However, across the traditional Desmoinesian-Missourian boundary (see Section 6.1; Fig. 4), where significant floral changes have been documented in coal basins throughout west-central Pangea (Phillips et al., 1974; Kosanke and Cecil, 1996; Peppers, 1997), there is little change in the seasonally dry floras. Most of the Desmoinesian flora, mainly composed of drought-tolerant taxa, crosses the boundary nearly intact. Thus, in an area where there was active tectonism and regional uplift, there is significantly less floristic change than in the basins farther east, where tectonic influence was more passive and long-term subsidence mainly occurred through sediment loading.

6.2.1.2. Kinney Brick Company Quarry, New Mexico

The Kinney Brick Company Quarry locality near Albuquerque, New Mexico, provides some of the best known mixed macrofloral assemblages from the western, seasonally dry climate zone of western Pangea (Mamay and Mapes, 1992; DiMichele et al., 2013a). The plant-fossil-bearing strata (Tinajas Mb., Atrasado Fm.) are middle Missourian in age (Lucas et al., 2011), and are interpreted as having been deposited in a fluvial delta front that prograded over a coastal estuary (Feldman et al., 1992; Lorenz et al., 1992). The relatively diverse flora consists of approximately 35 "whole plant" species, with cordaitalean leaves (*Cordaites*) lumped at the genus level. Based on occurrence frequency, walchian conifers dominate, complemented by abundant and diverse pteridosperms, many of which have been considered typical of somewhat drier substrates. Marattialean tree ferns and calamitaleans, characteristic wetland plants, also are prominent. However, assemblages also include a number of unusual fossil-taxa, including noeggerathialeans and plants of uncertain affinity, a typical feature of seasonally dry settings. Situated far out in western Pangea, where permanently seasonally dry conditions prevailed and no contemporary coal beds are known, the assemblages still contain many elements characteristic of wetland floras found in clastic rocks of coal-bearing successions. Furthermore, there is no geological evidence of upland habitats in the immediate area. Instead, the combination of lithofacies and floral composition points to a low-gradient coastal setting dominated by conifers, but with pockets of wetland vegetation on more poorly drained landforms.

6.2.1.3. Cañon del Cobre, Rio Arriba County, New Mexico

DiMichele et al. (2010b) summarized the composition, age, and paleoenvironmental context of macrofloral assemblages in the uppermost Virgilian El Cobre Canyon Fm. (Cutler Group) in Cañon del Cobre, northern New Mexico. The lithostratigraphic unit is dominated by brownish siltstones with abundant rhizoliths and multistoried, trough cross-bedded sandstone bodies, and has been interpreted to record deposition on a braided-river plain with shallow, ephemeral, low-sinuosity channels that traversed vegetated floodplains (Eberth and Miall, 1991; Lucas and Krainer, 2005; Lucas et al., 2005). The pervasive sparry calcite cement, variably developed calcisols, ferric paleosols, calcareous rhizoconcretions, and sedimentologic indicators for flashy discharge all point to generally seasonal and oxidizing conditions throughout development of the formation (Tanner and Lucas, 2018). Nonetheless, most plant fossils recovered from Cañon del Cobre are characteristic of Late Pennsylvanian wetland communities (Hunt and Lucas, 1992; DiMichele and Chaney, 2005; DiMichele et al. 2010b). Macrofloral assemblages from facies interpreted as seasonally active channel bodies, abandoned-channels, and crevasse splays are dominated by diverse ferns and sphenopsids (frequently preserved *in situ* or as dense, tangled mats), with pteridosperms and lycopsids (*Sigillaria*) also being common at localities where there is evidence for generally wetter substrate conditions. DiMichele et al. (2010b) suggested that these taphocoenoses mainly represent riparian plants that were derived from local channel margins or in-channel bars and were rapidly buried during flood events. Plant fossils recovered from standing-water deposits contain very low diversity assemblages in which one or two species of medullosalean pteridosperm predominate (e.g., *Alethopteris zeilleri*, *Macroneuropteris scheuchzeri*), with lesser sphenopsids at some localities.

Although usually very rare, the remains of taxa that are more characteristic of periodically moisture-limited habitats also are present in Cañon del Cobre. For example, isolated walchian conifer fragments occur in a few taphocoenoses that otherwise only preserve typical wetland floras, whereas mesomorphic (*Odontopteris* sp. cf. *O. lingulata*) and xeromorphic (walchian conifers, *Taeniopteris*) taxa are more commonly mixed with hygromorphic ferns and other wetland plants in assemblages in the upper part of the succession. These observations are consistent with an overarching preservational megabias towards vegetation that occupies the wettest parts of a landscape. Given the seasonally dry climatic conditions that prevailed during deposition of the El Cobre Canyon Fm., we infer that plants adapted to seasonal moisture deficit not only were present, but probably occurred in much greater abundance than indicated by the macrofloral assemblages. Such drought-tolerant

taxa may actually have dominated most landforms on the braided-river plains. Nonetheless, riparian vegetation from the most poorly drained habitats predominates in most of the macrofloral assemblages, being derived from plants that lived adjacent to sites of deposition and thus more frequently affected by flooding, disturbance, and burial.

6.2.2. West-central Pangea (Midcontinent to Appalachian regions of USA) (Fig. 6)
6.2.2.1. "Basin margin" assemblages, northwestern Illinois Basin

The Late Mississippian exposure, erosion, and karstification of Paleozoic carbonates that floor much of the Illinois Basin resulted in a relatively flat landscape that was dissected by major paleovalleys, narrow ravines, sinkholes, and caves (Bristol and Howard, 1971; Leary, 1981; Greb, 1989). Scattered localities near the present-day northwestern erosional margin of the basin expose discontinuous and variable strata of the lowermost Caseyville Fm., which represent the earliest stages of infill along this irregular unconformity surface during the Morrowan (early? to late Namurian, early Bashkirian). Several of these deposits have yielded unusual mixed floras characterized by cordaitaleans and fossil-taxa that are very rare or absent in coeval assemblages in coal-bearing successions, particularly the putative pteridosperms *Megalopteris* and *Lesleya* and various noeggerathialean progymnosperms. White (1931) was the first to propose that these unique assemblages may preserve the vegetation that occupied thin calcareous soils that mantled the vast carbonate plains of west-central Pangea during the Early Pennsylvanian. White (1931) also suggested that the coriaceous and xeromorphic aspect of some elements in the floras could signify growth under more seasonal climatic conditions.

One of the best-documented sites hosts the "Spencer Farm Flora" in Brown County, west-central Illinois, along the erosional margin of an outlier of the Illinois Basin (Leary 1974a, 1974b; Leary and Pfefferkorn, 1977). The age of the locality is poorly constrained, but a Namurian B age was proposed (Leary and Pfefferkorn, 1977; Peppers, 1996), equivalent to the Kinderscoutian or Marsdenian (early Bashkirian). The macrofloral assemblage was recovered from irregularly interbedded siltstones, sandstones, and shales at the bottom of a steep-sided, ca. 12 m-deep paleo-ravine that downcuts through Middle Mississippian (Viséan) carbonates of the St. Louis and Salem formations. Plant fossils are preferentially preserved in coarser-grained units, such as lenses that comprise coarse sand grains floating in a matrix of siltstone and claystone, and crudely stratified sandstones that have irregular to wavy bedding and pebble-sized claystone intraclasts at their bases. Plant remains frequently cross-cut bedding planes and are twisted or distorted, indicative of rapid deposition and burial in

sediment slurries during flash flood events. As quantified by Leary and Pfefferkorn (1977), the flora is dominated by diverse pteridosperms, particularly *Sphenopteris*, *Eusphenopteris*, and *Alethopteris*, all of which are typical of roof-shale assemblages. However, foliage of *Megalopteris*, *Lesleya*, and *Rhodeopteridium*, fossil-genera that are very rare in wetland deposits, also are well represented. The foliage (*Palaeopteridium*, *Gulpenia*) and cones (*Lacoea*) of noeggerathialeans also are common; these taxa are not found in roof-shales in contemporaneous coal-bearing successions. Cordaitaleans are an important element of the flora, whereas sphenopsids and ferns are less common, and lycopsids are very rare.

The Spencer Farm Flora was interpreted to represent the vegetation that occupied seasonally dry, calcareous soils on the karstified "uplands", and which were washed into the ravine during episodic flood events (Leary 1974a, 1974b; Leary and Pfefferkorn, 1977). Although we largely agree with this evaluation, we suggest that undue emphasis has been placed on the inference that the carbonate bedrock in the vicinity of the paleo-ravine comprised well-drained "extrabasinal" or "upland" habitats, simply because it was at slightly higher elevations. Rather, we suggest that the better-drained edaphic conditions, and thus the mixed composition of the vegetation, resulted from growth under a seasonal climate mode, clear evidence for which is preserved in the irregularly interbedded deposits that entomb the distorted plant fossils. Furthermore, vegetational heterogeneity may have been accentuated by the fact that precipitation in karstified landscapes frequently has short retention times, as soils may be thin and free water rapidly lost to the subsurface through sinkholes and fractures (Bonacci, 2015).

Additional examples of these unusual mixed macrofloral assemblages were documented in the fills of karst topography farther north in Rock Island County, Illinois, along the northwestern erosional margin of the Illinois Basin (Leary, 1974a, 1975, 1981). The age of these localities is uncertain, although deposition may have begun as early as the Namurian A (Leary, 1981), perhaps equivalent to the Alportian (early Bashkirian) in current usage. The best-documented locality is at the Allied Stone Company Quarry, where the pre-Pennsylvanian unconformity consists of a nearly horizontal surface of limestone (Middle Devonian Cedar Valley Fm.) dissected by steep-sided, flat-bottomed channels that are approximately 4 to 6 m deep and 8 to 20 m wide. The channel-fills mainly comprise horizontally bedded successions of gray mudstone and shale, with irregular lenses and thin beds of clean, quartz-rich sandstone scattered throughout. However, pebble to cobble conglomerates and sandstones line the bases of some channels, and channel-fills frequently are capped by a black, pyrite-bearing, fissile shale. Plant-fossils from the mudstones and

shales generally are well-preserved, large and unfragmented, and occasionally include foliage attached to branches, indicative of minimal transport.

Based on the quantification of Leary (1981), two separate floras occur in the channel-fills at the Allied Stone Company Quarry. The lower gray mudstone and shale successions yield diverse mixed assemblages that are dominated by leaves of *Megalopteris*, *Lesleya*, and *Cordaites*; other common elements include lycopsids (*Lepidodendron sensu lato*), sphenopsids (mainly calamitaleans), diverse pteridosperms (especially *Sphenopteris*), and the cones of noeggerathialeans (*Lacoea*). Accordingly, the lower flora comprises a mixture of typical wetland taxa, together with plants that are rare or absent in such settings. In marked contrast, fossils in the distinct upper black shale units are restricted to abundant calamitalean axes and lycopsids, together with rare *Cordaites* and axes of marattialean tree ferns (see DiMichele and Phillips, 1977), all of which are characteristic of wetland habitats.

Leary (1974a, 1975, 1981) concluded that the channels on the limestone paleoplain were gradually encroached and filled by lacustrine or estuarine deposits under quiet water conditions. During initial stages of infilling, some plant remains (*Megalopteris*, *Lesleya*, cordaitaleans, noeggerathialeans) were introduced to the channels from local "uplands", which consisted of carbonate plains covered by thin, well-drained, terra rossa-type soils, whereas the "lowland" elements (calamitaleans, lycopsids) occupied wetter habitats directly adjacent to the channels. As the sea advanced, the channels were filled and the water table rose, resulting in a black, fissile shale that only preserved "lowland" plants, particularly lycopsids and calamitaleans with lesser cordaitaleans and ferns. Crucially, Leary (1981) postulated that a warm, humid climate existed throughout infilling of the channels.

As with the Spencer Farm Flora described above, we agree with the interpretation of where the different plant communities were situated in this Early Pennsylvanian landscape. However, again, we believe that the reconstruction relies too heavily on the idea that well-drained "uplands" hosted one flora and that poorly drained "lowlands" hosted another, all existing in immediate proximity under a humid climate mode, their distribution simply being controlled by slight differences in elevation. Rather, we would argue that such compartmentalization of the vegetation in the landscape was made possible due to a seasonal climate, under which slight elevational differences are accentuated, enabling wetland and drought-tolerant taxa to coexist with a patchy distribution. Furthermore, as noted for the Spencer Farm Flora, the rapid loss of most precipitation in the karstified landscape to the subsurface may have amplified the vegetational heterogeneity, with the carbonate plains being

quickly drained of free water and thus ideal for taxa adapted to seasonal drought (i.e., the cordaitaleans, *Megalopteris*, *Lesleya*, and noeggerathialeans).

The final point to make is that the unusual macrofloral assemblages described above, being characterized by *Megalopteris*, *Lesleya*, noeggerathialeans, and abundant cordaitaleans, have frequently been misattributed to being "basin margin", "upland", or "extrabasinal" floras in the literature. These terms are misnomers, and, even if inadvertent, their use has exacerbated the misconception that xeromorphic, rare, and/or enigmatic plant taxa were confined to such positions on late Paleozoic landscapes, whereas the more common wetland taxa occupied "lowland" settings. As predicted by White (1931), these drought-adapted plants would have occurred wherever the appropriate edaphic and climatic conditions existed, and probably were widespread on the thin calcareous soils that covered carbonate bedrock surfaces throughout west-central Pangea during the earliest Pennsylvanian. Accordingly, similar assemblages with *Megalopteris* and *Lesleya* almost certainly are widespread in the lowermost Caseyville Fm. (Morrowan, lower Bashkirian) at the base of the sedimentary fill of the Illinois Basin, but now are deeply buried and remain inaccessible without a serendipitous borehole. Thus, even though these floras have been exposed by erosion along the *present-day* basin margin, they were not restricted to "basin margin", "extrabasinal" or "upland" habitats. Furthermore, as described below in Section 6.2.2.3, deposits of a flashy discharge channel containing leaves of *Lesleya* have been identified in younger strata in the eastern Illinois Basin, at a locality that was not situated at the basin margin (Bashforth et al., 2016a).

6.2.2.2. Central Limestone Quarry, Illinois

At the Central Limestone Quarry in northeastern Illinois, on the northern margins of the Illinois Basin, unique macrofloral and microfloral assemblages are preserved in a Pennsylvanian-aged, heterolithic fill of cave and karst features developed in Ordovician limestone (Plotnick et al., 2009; Scott et al., 2010). Included in the Tradewater Fm., the Atokan strata probably correlate with the Duckmantian and/or Bolsovian of Western Europe (upper Bashkirian and/or lower Moscovian). The macrofloral assemblage is dominated by the fragmentary remains of cordaitaleans and walchian conifers. Many fragments are preserved as charcoal, particularly higher in the fill succession, suggesting that the climate may have been, at least periodically, seasonally dry. Although the microfloral assemblage also contains considerable cordaitalean and conifer pollen, spores derived from herbaceous lycopsids are abundant (together with rare arborescent lycopsid spores), particularly low in the fill succession. This unique environment of deposition and preservation captures a broad floristic

change, interpreted as corresponding to a shift from generally wetter to drier climatic conditions as the karst topography filled. Distinctly seasonal cycles of deposition recorded at the top of the succession may evidence annual flooding events (Plotnick et al., 2009; Scott et al., 2010).

6.2.2.3. Mixed assemblages below the Minshall Coal, Indiana

Bashforth et al. (2016a, 2016b) reported a juxtaposition of highly divergent floral signatures over a short stratigraphic interval at a single locality, based on collections from the Ashboro Pit in Clay County, west-central Indiana. The macrofloral and microfloral assemblage from roof shales (lowermost Staunton Fm., upper Atokan, lower Asturian) of the Minshall Coal are entirely composed of wetland plants (Bashforth et al., 2016b), consistent with the climate signature. However, directly below the paleosol of the coal, a heterolithic unit (uppermost Brazil Fm.) with sedimentological indicators of seasonal deposition yielded a distinctly different macrofloral assemblage. Characterized by interbedded shale, siltstone, and sandstone with local intraclasts, the fossiliferous heterolithic unit probably represents a shallow channel filled by flashy discharge. The assemblage is strongly dominated by drought-tolerant taxa, including cordaitaleans, *Lesleya*, and *Taeniopteris*, with rare sphenopsids and ferns typical of wetland habitats (Bashforth et al., 2016a). Wholly incongruent with the macroflora, the palynoflora from the heterolithic unit is dominated by tree ferns and lycopsids, with a significant component of cordaitalean pollen. Similarly, DiMichele et al. (2016) documented dryland-dominated macrofloral assemblages and wetland-dominated microfloral assemblages at numerous localities in Indiana at the same stratigraphic level (just below the paleosol of the Minshall Coal).

The floristic and sedimentologic findings from the mixed assemblages below the Minshall Coal demonstrate the cyclic nature of floral changeovers that occurred in basinal lowland settings of tropical Pangea in response to glacial-interglacial oscillations. A key observation is that the wetland- and dryland-dominated macrofloral assemblages are not intermixed, but interdigitate in the succession. However, as expected, the flora in which drought-tolerant taxa are predominant also contains a minor component of wetland species, as occurs in many western Pangean assemblages. Being situated on an extremely low-gradient landscape, at least 250 km from any elevated terrain and with no evidence of tectonic activity (Bashforth et al., 2016a), the most tenable explanation for this floristic pattern is a response to climatic change.

6.2.2.4. Cottage Grove Mine, Illinois

At the Cottage Grove Mine in southeastern Illinois, Falcon-Lang et al. (2009) described a mixed macrofloral assemblage from upper Desmoinesian (Cantabrian, uppermost Moscovian) channel-fill deposits situated beneath the Baker Coal (Shelburn Fm.) in the Illinois Basin. The channel is laterally equivalent to a Vertisol directly below the Baker Coal, indicating that a seasonally wet climate prevailed during channel incision and filling, preceding peat accumulation, which occurred under humid conditions. Collected from thin siltstones between conglomerates at the base of the channel fill, cordaitaleans are the dominant plant fossils, whereas walchian conifers are rare. Wetland elements are uncommon to rare, and include medullosalean pteridosperms, tree ferns, and calamitaleans. Similar to the mixed assemblages below the Minshall Coal (Section 6.2.2.3), the presence of a dryland-dominated assemblage a few meters below a coal seam, the precursor of which (peat) unequivocally developed under a (per)humid climate, is significant in demonstrating how, at a single locale, floristic patterns changed in concert with a climate shift.

Looy et al. (2014b) subsequently investigated the palynological content of two samples of siltstone from a fossiliferous slab collected for the Falcon-Lang et al. (2009) study. Despite being separated vertically by just millimeters on the same slab, one sample was dominated by lycopsid and tree fern spores with a significant admixture of cordaitalean pollen, and the other was dominated by cordaitalean pollen with a significant admixture of lycopsid and tree fern spores. No conifer pollen was identified in either. Looy et al. (2014b) suggested that the assemblages dominated by wetland palynofloral elements, particularly lycopsids and marattialean tree ferns, at a site situated hundreds of kilometers from any known upland source, recorded the existence of local wetland refugia in an otherwise seasonally dry basinal landscape.

6.2.2.5. 7–11 Mine, Ohio

McComas (1988) described two mixed macrofloral assemblages from the 7–11 Mine in northeastern Ohio (Central Appalachian Basin). This locality has been the focal point of considerable controversy regarding the age of the deposit based on plant fossils, with implications for the presence of a significant stratigraphic gap in the Appalachian Basin (Wagner and Lyons, 1997; Falcon-Lang et al., 2011b). Applying updated stratigraphic interpretations (Easterday, 2004; Belt et al., 2011; Falcon-Lang et al., 2011b), the two floras are situated within an incised paleovalley filled with lower Conemaugh Group strata that span both the traditional and revised Desmoinesian-Missourian boundaries (Kosanke and Cecil,

1996), being no older than middle to late Cantabrian. In the lower flora at the base of the paleovalley fill, McComas (1988) identified a diverse macrofloral assemblage in ironstone nodules dominated by typical wetland plants, particularly pteridosperms and ferns, but with scarce lycopsids. However, the lower flora also includes *Taeniopteris*, *Plagiozamites*, and walchian conifers (Wagner and Lyons, 1997), precocious elements generally considered to be typical of stratigraphically younger, seasonally dry habitats. The upper flora, found higher in the paleovalley fill, is compositionally distinct from, and less diverse than, the lower flora. The upper assemblage, which is found in a lacustrine organic shale above a thin, ash-rich coal and below a marine limestone, contains walchian conifers (Rothwell et al., 1997; Hernandez-Castillo et al., 2001), common cordaitaleans and sigillarian lycopsids, and rare marattialean tree ferns, pteridosperms, and sphenopsids.

The composition and high-quality preservation of the upper macrofloral assemblage described by McComas (1988) suggest that walchian conifers and cordaitaleans occupied the margins of a water body, with lycopsids colonizing areas of standing water. The paucity of other wetland plants indicates that the overall landscape was relatively dry. Nonetheless, the mixed nature and diversity of the lower flora led McComas (1988) and Wagner and Lyons (1997) to infer that the source vegetation was distributed in a gradational series of edaphic zones, from poorly drained floodplain and swamp soils, to mesic floodplain soils, to "better-drained" soils, with the conifers and other xeromorphic elements being allochthonous rather than drawn from the species pool immediately surrounding the site of deposition. Studies of plant taphonomy, however, do not support such an interpretation.

Actualistic studies of the origin, transport, and burial of plant remains in modern settings indicate generally low transport distances in fluvial systems (Ferguson, 1985, 2005; Spicer, 1989), and demonstrate that most vegetative remains are parautochthonous and drawn from local sources (Burnham, 1993). Accordingly, given the absence of elevated habitats near the 7–11 Mine locality during the Pennsylvanian, and considering the size and quality of preservation of conifer fossils in the upper flora, there is no doubt that these remains were drawn from the area surrounding the burial site, rather than having been transported from unsubstantiated "uplands". Although arguments persist that the conifers occupied slopes surrounding the paleovalley (e.g., Martino, 2017), observations of modern tropical vegetation in humid climates suggest otherwise. For example, in equatorial areas of South America, Africa, and southeast Asia with high and equable rainfall, local elevational variations of hundreds of meters have limited influence on the content of the local species pool (Foster, 1990; Collinvaux et al., 2000; Anshari et al., 2001; Wittmann et al., 2006; Bush et al., 2011;

Kenfack et al., 2014). Only under strongly seasonal rainfall regimes are elevational effects of sufficient magnitude to cause significant changes in species composition with small differences in topography. Studies in the Amazon and Andean regions indicate that moisture exerts the greatest control on vegetation at lower elevations, whereas temperature becomes most important at higher elevations (Marchant et al., 2004).

Drawing on these observations of the modern world, if the vegetation at the 7–11 Mine locality were distributed in a series of edaphic zones, the climate almost certainly would have been subhumid to semiarid, the conditions needed to exacerbate the effects of relatively small differences in elevation on soil moisture. However, the excellent quality of preservation of the conifer remains, those elements that presumably would have lived farthest from the site of deposition under the "upland model", conflicts with taphonomic expectations. On the other hand, if the plant fossils were not derived from zoned vegetation, but rather record local vegetation that all lived near the burial site, the distribution of which was controlled by habitat differentiation, the floristic composition again points to subhumid to semiarid climatic conditions.

6.2.2.6. Rock Lake Shale, Garnett, Kansas

The famous locality at Garnett, Kansas, yields upper Missourian assemblages that are overwhelmingly dominated by gymnosperms, but include very rare wetland elements (Elias, 1936; Moore et al., 1936; Cridland and Morris, 1963; Winston, 1983). This site and its flora are highly significant because they played a foundational role in early debate about the matter of climate *vs*. elevation and drainage as the primary controls of plant distribution on late Paleozoic landscapes (see discussion in Section 7.1). The fossiliferous stratum (Rock Lake Shale) comprises ca. 1.5 m of thinly bedded, calcareous shales with intercalated argillaceous limestones, and represents the uppermost part of a shallow, incised-valley-fill succession. The sedimentology and array of terrestrial vertebrates and marine to brackish invertebrates that accompany the plant fossils reflect deposition on tidally influenced estuarine mudflats (Moore et al., 1936; Reisz et al., 1982; Feldmann et al., 2005). Lateral equivalence to a widespread calcic Vertisol points to strong climatic seasonality during channel incision and filling (Winston, 1983; Joeckel, 1989; Feldman et al., 2005). The macroflora is dominated by walchian conifers, with cordaitaleans, callipterids, and taeniopterids being subdominant. Although wetland taxa are present, Winston (1983) reported only a few fragments of calamitalean, marattialean tree fern, and medullosalean pteridosperm foliage among the 700 specimens he sampled. The microfloral assemblage similarly is dominated by the pollen of

walchian conifers, cordaitaleans, and possibly callipterids, whereas pteridosperm pollen is uncommon, and tree fern spores are rare (Winston, 1983).

Elias (1936) and Moore et al. (1936) suggested that the dominance of xeromorphic to mesomorphic elements in the assemblage recorded an interval during which rarely preserved drought-tolerant vegetation prevailed in basinal lowlands under seasonally dry conditions. The deposit is intercalated among strata that contain typical wetland floras that flourished during climatically humid intervals throughout the Pangean tropics, and thus under conditions more conducive to preservation. In contrast, Cridland and Morris (1963) concluded that the presence of rare wetland taxa in the assemblage pointed to a humid tropical landscape, with the predominant dryland elements being transported from better-drained hummocks or upland habitats in the vicinity of the swampy lowlands. In effect, the Cridland and Morris (1963) model calls for the vast bulk of the plant remains – the drought-tolerant elements – to have been transported into the depositional setting, while the wetland vegetation that lived adjacent to the burial site was scarcely included in the taphocoenosis, supposedly by some quirk of filtering. The problems with that model are obvious, both from the perspective of taphonomy and with regard to the idea that drought-tolerant vegetation could live on low-elevation hummocks in the middle of a vast, wetland landscape.

6.2.2.7. Hamilton Quarry, Kansas

To the west of the Garnett locality, the Hamilton Quarry complex in eastern Kansas, on the western fringes of west-central Pangea, also yields gymnosperm-dominated macrofloral assemblages with a rare admixture of wetland taxa, together with a rich biota of marine and nonmarine invertebrates and vertebrates (Mapes and Mapes, 1988; Cunningham et al., 1993; Schultze et al., 1993). The age of the channel-fill deposit is controversial, with estimates ranging from Virgilian based on fusulinids, conodonts, and stratigraphic position (Mapes and Mapes, 1988) to early Permian based on palynology (Taggart and Ghavidel-Syooki, 1988). The fossiliferous deposits are 4 to 5 m thick, and consist of a basal limestone conglomerate overlain by thinly interbedded limestones and calcareous shales that fill a channel eroded into the lower half of the middle Virgilian Topeka Limestone and underlying Calhoun Shale (Shawnee Group) (Selley et al., 2005). Deposition clearly occurred close to the coast, with the incised channel becoming a tidally influenced estuary or lagoon during one or more episodes of sea-level rise (French et al., 1988; Busch et al., 1988; Cunningham et al., 1993). Sedimentological indicators for seasonal conditions during channel infilling include abundant charcoal and reworked caliche nodules in the basal conglomerate (Cunningham et al., 1993),

and alternations in limestone-mudstone couplets between dry (carbonate) and wet (mudstone) seasons in tidally influenced laminated limestones (Cunningham and Dickson, 1996). A diverse array of walchian conifers dominates the flora (Rothwell and Mapes, 1988; Mapes and Rothwell, 1991; Hernandez-Castillo et al., 2001, 2009; Rothwell et al., 2005), although other taxa include common cordaitalean foliage, diverse callipterids, and rare wetland elements, particularly calamitaleans and sigillarian lycopsids (Leisman et al., 1988).

The Hamilton Quarry preserves an extreme end-member of mixed floras, being overwhelmingly dominated by taxa characteristic of seasonally dry habitats, with a small admixture of wetland elements. In accord with the floristic signature, sedimentological indicators and the depositional setting evidently point to accumulation under a seasonally dry climatic regime. As with other, similar deposits that are dominated by dryland taxa, but that contain a wetland component, the "upland" model would call for the limited wetland elements to be indigenous and the principal drought-tolerant elements to have been transported into the site of deposition. Occam's razor might be employed to good effect in such situations.

We note that the early Permian age determined from palynomorphs (Taggart and Ghavidel-Syooki, 1988) is difficult to reconcile with the macrofloral content, a reflection of the fact that Carboniferous and lower Permian plant biostratigraphy is mainly based on the stratigraphic distribution of wetland plants. This interpretation is one of several examples in which a microfloral or macrofloral assemblage that consists of xeromorphic plants typical of seasonal, drought-prone habitats has been considered "Permian" in age, rather than recognizing the assemblage as a climatically influenced biofacies. Such interpretations have caused considerable confusion, as documented in debates about the age of specific localities or successions (e.g., 7–11 Mine, Ohio, Section 6.2.2.5; Garnet, Kansas, Section 6.2.2.6; DeLutte-6 borehole, The Netherlands, Section 6.2.4.1).

6.2.3. Central Pangea (Atlantic Canada) (Fig. 7)
6.2.3.1. Boss Point Formation, Cumberland Basin, Nova Scotia

A dryland ecosystem dominated by forests of gigantic cordaitaleans was inferred from the composition and facies context of log-jam deposits and *in situ* plant fossils in braided-fluvial strata of the Lower Pennsylvanian (Yeadonian to lower? Langsettian, middle Bashkirian) Boss Point Fm. of Nova Scotia (Cumberland Basin) (Ielpi et al., 2014; Rygel et al., 2015). Based on a detailed sedimentological analysis, the braided-river system accrued under a regime of highly seasonal precipitation, which resulted in variable flow energies and volumes. Log accumulations are overwhelmingly dominated by the remains of large

cordaitalean trees, which were interpreted to have occupied most available habitats, particularly well-drained floodplains, but including raised channel margins and stable in-channel barforms (mature vegetated islands). Calamitalean groves probably existed in highly disturbed habitats, including channel margins, crevasse splays, and incipient vegetated islands. Despite the overall seasonally dry climate, rare trunks of arborescent lycopsids also occur in the log jams, and the presence of autochthonous stigmarian rhizomorphs in thin carbonaceous shales indicates that these archetypal wetland plants occupied small patches of poorly drained floodplain. Surprisingly, the arborescent lycopsids identified (*Lepidodendron sensu stricto* and *Lepidophloios*) involve fossil-genera that existed on the wettest end of the ecological spectrum of Pennsylvanian wetlands (Phillips and DiMichele, 1992), pointing to the high degree of habitat partitioning and vegetational heterogeneity that characterizes seasonally dry environments.

6.2.3.2. *Joggins Formation, Cumberland Basin, Nova Scotia*

Based on studies of the Lower Pennsylvanian (middle? Langsettian, middle Bashkirian) Joggins Fm. of Nova Scotia (Cumberland Basin), Falcon-Lang (2003a, 2003b) and Falcon-Lang et al. (2006) demonstrated that Pennsylvanian wetland and dryland biomes alternated in tropical basinal lowlands in concert with glacial-interglacial cycles. Oscillating floristic patterns were interpreted in the framework of transgressive-regressive rhythms, with drainage conditions linked to base-level changes during eustasy, and climatic fluctuations tied to the proximity of open-marine waters. Although the authors of this review do not agree on all aspects of this sequence-stratigraphic model, the results of these studies are nonetheless transformative.

To precise, gray, coal-bearing strata in the Joggins Fm. contain wetland floral assemblages dominated by arborescent lycopsids (Calder et al., 2006), whereas all depositional environments represented in redbed intervals contain low-diversity floral assemblages dominated by large cordaitalean trees. However, wetland elements also existed within the dryland biome, including calamitaleans, a small number of pteridosperms, and rare lycopsids (possibly *Sigillaria*). The calamitaleans and lycopsids apparently were most prevalent alongside seasonally active anastomosing channels (Ielpi et al, 2015), which may have acted as "waterholes" on an otherwise moisture-stressed landscape (Falcon-Lang et al., 2004). Pteridosperms were interpreted as an understory element in cordaitalean forests that occupied the floodplains, and as a major component of communities on crevasse splays

adjacent to channel systems. These studies again demonstrate that wetland floras persisted in localized depositional settings within the background of seasonally dry tropical landscapes.

6.2.3.3. Tynemouth Creek Formation, Cumberland Basin, New Brunswick

In a follow-up to Falcon-Lang's (2006) study of the Tynemouth Creek Fm. of New Brunswick (Cumberland Basin), Bashforth et al. (2014) described the distribution of Early Pennsylvanian (middle to late? Langsettian) vegetation on an environmentally complex, seasonally dry landscape by combining evidence from sedimentology, paleosols, taphonomy, and the composition of macrofloral assemblages in facies context. The predominance of Vertisols in the succession implies that rainfall was highly seasonal. Although the entire dryland ecosystem was blanketed by a forest of gigantic cordaitaleans, some trees being preserved in growth position, pteridosperm-dominated communities existed around small "waterholes" on moisture-deficient distal interfluves. More diverse assemblages of cordaitaleans, pteridosperms, sphenopsids, lycopsids, and rare enigmatic fossil-taxa (e.g., *Megalopteris*, *Pseudadiantites*, and *Palaeopteridium*) occupied landforms within and adjacent to fluvial channels. No conifer remains were recorded, although their prepollen is relatively abundant in the succession (Dolby, 1997). This detailed analysis demonstrates the spatial heterogeneity that existed on tropical Pangean landscapes under regimes of highly seasonal precipitation, including the presence of local wet microhabitats supporting the sort of clastic-wetland vegetation that characterizes most of the Pennsylvanian plant-fossil record. Although Wagner (2001) interpreted the presence of so-called "extrabasinal" elements in the succession as having been transported from adjacent hinterland habitats, we argue that this stance was based more on tradition than evidence. By contrast, Bashforth et al. (2014) suggested that these enigmatic plants existed as scattered elements within the matrix of both wetland- and dryland-dominated communities in the basinal lowlands, which is in accord with modern taphonomic studies.

6.2.3.4. Sydney Mines Formation, Sydney Basin, Nova Scotia

In a further examination of the response of Pennsylvanian biomes to climatic changes that resulted from glacial-interglacial cyclicity, Falcon-Lang (2004a) provided a qualitative study of the distribution of plant fossils in sequence-stratigraphic context in the upper Middle Pennsylvanian (middle Asturian to lower Cantabrian) Sydney Mines Fm. of Nova Scotia (Sydney Basin). As in the Joggins Fm. (Section 6.2.3.2), climatically wetter intervals resulted in lycopsid-dominated coals and associated gray clastic mudrocks that contain abundant plant

fossils typical of the wetland tropical biome (Calder et al., 1996). In contrast, intervals of climatic drying were recorded in the fill of incised paleovalleys and overlying redbed deposits, with calcretes and calcic Vertisols on paleovalley interfluves providing evidence of seasonal precipitation (Gibling and Bird, 1994; Tandon and Gibling, 1994). Large logs and charcoal fragments derived from cordaitaleans in paleovalley fills again attest to the predominance of coniferopsid forests on moisture-stressed tropical landscapes, although the presence of lycopsid stumps rooted in thin coals between fluvial-channel bodies suggests that wetland refugia persisted in riparian habitats. Redbed successions overlying the paleovalleys include rare mixed macrofloral assemblages of cordaitaleans, medullosalean pteridosperms, sphenopsids, and marattialean tree ferns, whereas the only plant groups represented in palynological assemblages are tree ferns, cordaitaleans, and rare lycopsids. As interpreted by Falcon-Lang (2004a), these data indicate that a mixture of dryland and wetland plants coexisted on seasonally dry landscapes, with the most moisture-dependent groups being restricted to habitats where water was more readily available.

6.2.4. East-central Pangea (Europe) (Fig. 8)

6.2.4.1. De Lutte-6 borehole, The Netherlands

Van Hoof et al. (2013) described three palynofloras and associated macrofloras from three disparate lithofacies in the De Lutte-6 borehole of the east-central Netherlands, encompassing upper Bolsovian to middle Asturian strata (middle Middle Pennsylvanian) of the Tubbergen and De Lutte formations. The lower palynofloral assemblage was from gray mudstones situated between thick, multistory channel-sandstone bodies, interpreted to represent the poorly drained floodplains and interfluves of a braided fluvial system. Although fragmentary wetland macrofloral elements are present in the mudstones, the palynoflora is dominated by the pollen of coniferopsids, particularly that attributed to walchian conifers and enigmatic "ruflorioid" cordaitaleans, together with other cordaitalean pollen and spores of non-arborescent lycopsids, calamitaleans, and ferns.

The upper palynofloral assemblage was collected from laminated shales situated above a thick channel-sandstone body and below a caliche-bearing paleosol, interpreted to record a shallow but extensive floodplain lake that developed after a regional avulsion event on a seasonally dry braidplain. Wetland macrofloral remains are abundant and well preserved in the lacustrine strata, yet the palynofloral assemblage again is dominated by the pollen of drought-tolerant plants, especially conifers, cordaitaleans, and enigmatic pteridosperms, with less common spores of non-arborescent lycopsids and calamitaleans. These findings

emphasize the incongruity between the composition and proportion of different plant groups in macrofloral *vs*. microfloral assemblages collected from the same rocks, and, more importantly, again demonstrate the proximity of wetland and dryland floras on seasonally dry landscapes.

In marked contrast, the middle palynoflora studied by van Hoof et al. (2013) was derived from a coaly shale situated within a thick succession of gray mudstones, interpreted to record clastic swamp development under humid conditions. The palynological assemblage is overwhelmingly dominated by miospores typical of tropical wetland vegetation, particularly calamitaleans, arborescent and non-arborescent lycopsids, and various ferns, whereas pollen of the drought-tolerant plants seen in the lower and upper assemblages is exceedingly rare. These data suggest that, during climate modes on the wet end of the spectrum, dryland vegetation was situated too far from the main depositional sites to be represented in the macrofloral assemblages via "transport" in fluvial channels.

6.2.4.2. Intramontane (mainly limnic) basins

The absence or rarity of xeromorphic plant remains in plant-fossil assemblages also can be instructive, especially when evaluating floristic patterns in areas adjacent to uplands. For example, examination of numerous floras in intramontane basins in Germany (Uhl and Cleal, 2010), the Czech Republic (Opluštil and Cleal, 2007; Bashforth et al., 2011), the Iberian Peninsula (Wagner and Álvarez-Vázquez, 2010; Correia et al., 2016), and Sardinia (Cleal et al., 2016) has revealed a conspicuous paucity of conifers or other taxa considered typical of moisture-stressed substrates, despite the presence of significant topographic relief in the immediate vicinity. These observations suggest that slope and elevation alone did not create conditions favorable for the growth of such drought-adapted plants. In fact, even though seasonal conditions prevailed during the deposition of several of the successions discussed below, only rare pollen grains or extremely rare macrofloral remains herald the existence of xeromorphic vegetation, suggesting that these plants may have occupied hinterland habitats that were far beyond the depositional catchment.

The assumption that elevated habitats always hosted drought-tolerant, so-called "upland" vegetation, regardless of background climate conditions, remains entrenched in the literature. This paradigm was perhaps best summed up by Wagner and Álvarez-Vázquez (2010: p. 305): "[…] *it seems surprising that the presence of upstanding relief with alluvial fan deposits in the Peñarroya Basin (Westphalian) has not led to any conifer finds. There are also very few conifer records in the Stephanian B of NW Spain, despite the evidence for*

palaeovalleys associated with a rugged landscape in the near vicinity of the basin." We would argue that such absences reflect the fact that xeromorphic taxa were only present in significant numbers if climatic conditions, particularly rainfall patterns, were sufficiently seasonal, both in the depositional basins and adjacent uplands. Here, we detail four examples of successions deposited within intramontane basins and in the immediate vicinity of elevated settings, which support our interpretation.

Lower Radnice Member, Central and Western Bohemian Basin, Czech Republic. In a comparative analysis of paleofloristic patterns in basins within and north of the Variscan Mountains, Opluštil and Cleal (2007) noted that diversity in the Lower Radnice Mb. (LRM), Kladno Fm., of the Czech Republic (Central and Western Bohemian Basin) encompasses 139 species, thus being one of the most species-rich units known in the Pennsylvanian tropics. Long held to be Bolsovian in age, the LRM has been radioisotopically constrained to the uppermost Duckmantian (Opluštil et al., 2016b), based on the revised geochronology proposed by these authors. The unit was deposited in a series of narrow, steep-walled valleys in the heart of a mountain belt, at a proposed altitude of up to 1000 m (Opluštil, 2005a, 2005b), although revised estimates are closer to 500 m (S. Opluštil, pers. comm., Oct. 2020). As such, the exceptional diversity has been interpreted to reflect the inclusion of species adapted to growth on elevated valley slopes (Opluštil and Cleal, 2007; Opluštil et al., 2016a). However, the floral diversity also was amplified by the complex development of the LRM, as multiple volcanic ash falls briefly interrupted peat accumulation, resulting in unique depositional and preservational facies. To provide environmental context to the floras discussed below, we first provide a summary of the succession (Fig. 9), distilled from various sources (e.g., Mašek, 1973; Pešek, 2004; Opluštil, 2005a, 2005b; Opluštil et al., 1999, 2007, 2009a).

The lower part of the LRM comprises siliciclastic strata with thin coals of the Plzeň group. The overlying high-ash Lower Radnice Coal generally is 1 to 2 m thick and contains numerous siliciclastic partings. A high-energy volcanic eruption resulted in burial of the precursor Lower Radnice peat swamp by a volcaniclastic unit ("Whetstone Horizon"), which ranges from a few tens of cm to over 10 m thick and consists of two distinct components. The lower part comprises ca. 50 cm of tuff ("Bělka" in the Czech literature) that entombs peat-forming vegetation in growth position (Opluštil et al., 2007, 2009a, 2009b, 2014; Libertín et al., 2009). In contrast, the upper part of the Whetstone Horizon is a thicker unit of laminated tuffites ("Brousek"). This facies records the post-eruptive, rapid redeposition of

unconsolidated tephra in lakes that developed under conditions of abundant rainfall, combined with the subsidence and dewatering of peat beneath the heavy load of ash. Most plant fossils in these lacustrine tuffites are allochthonous and generally comprise vegetation typical of Duckmantian wetlands, although a number of enigmatic taxa also are present locally (e.g., Ettingshausen, 1852; Němejc, 1928, 1930, 1949; Opluštil et al., 2007, 2016a; Šimůnek and Cleal, 2011, 2016). In particular, these unusual elements are relatively common in laminated tuffites at the Strádonice locality in the relict Lísek outlier, where the Lower Radnice Coal is absent, and the Whetstone Horizon rests directly atop bedrock or conglomerates and sandstones in a number of steep-sided paleoravines (Ettingshausen, 1852; Němejc, 1930; Stárková et al., 2016). Based on these environmental and taphonomic indicators, many authors have inferred that such enigmatic taxa were washed in with the unconsolidated volcaniclastics that blanketed adjacent valley slopes and uplands, habitats that are not commonly sampled in the fossil record.

Despite the substantial thickness of the Whetstone Horizon, no roots or other evidence of soil development are present, except at the very top, where the unit is immediately overlain by the Upper Radnice Coal. This critical observation indicates that the lakes that formed after burial and dewatering of the underlying Lower Radnice swamp filled rapidly and were short-lived, and that peat accumulation immediately resumed once the lakes were sufficiently shallow. Thus, the Whetstone Horizon represents a temporary cessation of peat accumulation, in essence being a "coal split" (S. Opluštil, pers. comm., Aug. 2018). More importantly, the humid conditions that were necessary for development of the precursor Lower and Upper Radnice peat swamps almost certainly persisted during the brief interval when the intervening Whetstone Horizon was deposited. Therefore, we emphasize the point that all plant fossils found in the laminated tuffites (Brousek), regardless of their taxonomic affinity, original site of growth, or inferred habitat preferences, also lived and died under a humid climate mode.

The overlying Upper Radnice Coal ranges from ca. 3 to 14 m thick and consists of higher quality (lower ash) coal than the Lower Radnice Coal. Several thin, but regionally correlative, volcanic tuff partings ("opuky") occur in the coal. As in the underlying Whetstone Horizon, the bases of these volcaniclastic units preserve peat-forming vegetation in growth position, whereas a sparse and compositionally distinct suite of allochthonous elements is present in the upper laminated tuffite component of individual ash falls (Opluštil et al., 2007, 2016a). The Upper Radnice Coal is sharply overlain by a laminated lacustrine mudstone ("Mydlák") that records rapid drowning of the peat swamp, above which is an upward-coarsening lacustrine delta complex. Plant fossils in the Mydlák roof-shale are mainly

allochthonous and compositionally distinct from *in situ* remains in the volcanic tuffs (opuky). Nonetheless, the adpression assemblages in the roof-shale almost exclusively comprise taxa typical of Duckmantian wetland habitats, and were interpreted as having been transported from clastic substrates on the lake margins (Opluštil et al., 2016a).

Among the diverse fossil-taxa recorded in the LRM, the largest number of rare species are sphenopteroid ferns (many being singletons) and pteridosperms (Pešek, 2004; Opluštil and Cleal, 2007), and thus belong to clades that were characteristic of tropical floras from humid tropical regimes. However, statistical analyses demonstrate that the limnic intramontane basins of the Bohemian Massif contained several endemic medullosalean pteridosperms (Cleal, 2008). This hypothesis was confirmed by subsequent taxonomic studies (Šimůnek and Cleal, 2011, 2016), which showed that the fossil-genus *Havlenaea* and several fossil-species of *Laveineopteris*, among others, were unique to the Variscan intramontane basins. For the LRM, a critical point is that all of the medullosaleans that are endemic to this unit (*Havlenaea praeovata* = *Havlenaea coriacea*, *Havlenaea stradonitzensis*, and "*Mixoneura*" *muensterifolia*) are almost exclusively allochthonous elements from laminated lacustrine tuffites, with nearly all from the Brousek part of the Whetstone Horizon at the Strádonice locality (Ettingshausen, 1852; Němejc, 1930, 1949; Havlena, 1953; Stárková et al., 2016). As such, these endemic pteridosperms may have occupied (and been transported from) shallow, clastic soils on the steep slopes of local ravines. Nonetheless, we reiterate the point that these plants existed under a humid climatic regime, which is consistent with physiological evidence for high humidity conditions in their foliar cuticles (Šimůnek and Cleal, 2011). Furthermore, the macrofloral assemblages that contain these endemic pteridosperms are dominated by diverse taxa (including ferns, pteridosperms, and cordaitaleans, with rare lycopsids and sphenopsids) typical of clastic-wetland habitats (Ettingshausen, 1852; Němejc, 1930; Stárková et al., 2016).

The LRM has also yielded a diverse (albeit generally very rare) suite of enigmatic plant fossil-taxa, some of which have a "Mississippian" aspect, that traditionally have been considered more typical of seasonally dry habitats. For example, two families of noeggerathialeans of progymnospermous affinity, the Noeggerathiaceae and Discinitaceae, are represented, although their preservational mode and interpreted habitat preferences are markedly different. Members of the Discinitaceae include the fossil-genera *Rhacopteris* and *Palaeopteridium* (*sensu* Němejc, 1928, 1937, 1941; Bek and Šimůnek, 2005), which, together with specimens of the presumed progymnosperm "*Triphyllopteris*" (= *Pseudadiantites* according to Wagner, 2001), are best known from the laminated lacustrine tuffite (Brousek) at

the Strádonice locality. Although allochthonous, many specimens are relatively large and well-preserved (Ettingshausen, 1852; Němejc, 1928; Stárková et al., 2016), suggesting limited transport from local ravine slopes. We highlight the fact that these enigmatic taxa are found at the same localities and in the same tuffites as the endemic medullosaleans noted above (*Havlenaea coriacea*, *Havlenaea stradonitzensis*, "*Mixoneura*" *muensterifolia*), which probably also drifted in from adjacent slopes, yet show physiological adaptions to high humidity.

In the Kladno Coalfield, other rare and poorly preserved examples of *Rhacopteris* and *Palaeopteridium* have been found in the upper laminated (redeposited) tuffite component of the "Velká opuka", a prominent volcanic intercalation in the Upper Radnice Coal, whereas *Palaeopteridium* has also been recorded in the roof-shale (Mydlák) of the coal (Opluštil et al., 2016a). In all of these instances, the plants apparently lived under high rainfall conditions, and taphonomic and sedimentologic indicators imply that they were derived from clastic-substrate habitats that existed outside of the peat-forming environment. Furthermore, according to Opluštil et al. (2007), tuffs immediately above the Lower Radnice Coal (Bělka) have also yielded rare but large specimens of *Palaeopteridium* (Doubrava locality, Plzeň Basin) and *Rhacopteris* (Prago Mine, Kladno Coalfield), indicating that some of these enigmatic taxa occasionally occupied peat swamps.

The other group of noeggerathialeans (Noeggerathiaceae) comprises two whole-plant species (*Noeggerathia foliosa* and *Noeggerathia intermedia*) that are surprisingly abundant at some levels in the LRM. The vast majority of specimens have been recovered from the Velká opuka and other volcanic intercalations in the Upper Radnice Coal (Němejc, 1928; Šetlík, 1956; Šimůnek and Bek, 2003; Opluštil et al., 2016a), especially from localities in the Kladno-Rakovník Basin. A taphonomic observation that is difficult to tease from the existing literature is that most examples of *Noeggerathia* (including foliage, cones, axes) are found in the lower tuff component of volcanic intercalations (S. Opluštil, pers. comm., Aug. 2018). In other words, many of these plants were not transported, but were part of the peat-forming vegetation that was buried *in situ* by falling ash (Opluštil et al., 2016a). This interpretation is consistent with the co-occurrence of *Noeggerathia* and lycopsids that, based on their prevalence at the bases of tuffs that directly overlie coal, had a strong preference for peat substrates, particularly *Omphalophloios feistmantelii* and *Lepidodendron ophiurus* (*sensu* Němejc, 1947) (Šimůnek and Bek, 2003; Opluštil et al., 2007, 2009a, 2016a; Bek et al., 2015). That some noeggerathialeans occupied peat substrates is not without precedent, as other fossil-genera of these progymnosperms have been reported from lower Permian coals in

Inner Mongolia, China, also having been buried *in situ* by volcanic ash (Wang et al., 2004, 2009, 2012).

Finally, we draw attention to the extremely rare examples of *Dicranophyllum dominii*, the only coniferopsid recorded in the LRM (Pešek, 2004). Being an early conifer-like plant (Hernandez-Castillo et al., 2003; Rothwell et al., 2005) with physiological attributes that point to moisture-stressed conditions (Barthel 1977), the fossil-genus *Dicranophyllum* has traditionally been considered an archetypal "extrabasinal" plant that occupied well-drained, elevated habitats (e.g., Wagner and Lemos de Sousa, 1983; Wagner, 2005; Wagner and Álvarez-Vázquez, 2010). However, nearly complete specimens, essentially entombed in growth position in volcanic tuffs, have been documented from lowland habitats in the Saar-Nahe Basin (Donnersberg Fm., lowermost Upper Rotliegend, lower Permian; Barthel et al., 1998; Barthel and Noll, 1999). Remarkably, the examples of *D. dominii* described by Němejc (1929) from the Kladno-Rakovník Basin were found in tuffs in the Velká opuka in the Upper Radnice Coal, indicating that the plants grew on a peat substrate and were buried in place by volcanic ash. Similarly, Opluštil et al. (2016a) recorded rare, *in situ* examples of *D. dominii* in the Velká opuka in the Kladno Coalfield, and a few unpublished specimens have been found elsewhere in the LRM, always in a tuff horizon within a coal (S. Opluštil, pers. comm., Mar. 2019). Thus, there is strong evidence that at least one species of *Dicranophyllum* occupied late Duckmantian peat swamps.

This summary of the floristics of the LRM has yielded important insights into the complexities of late Paleozoic vegetational distribution in the context of this review:

- The noeggerathialeans and coniferophytes have customarily been considered as classic indicators of drought-stressed habitats in late Paleozoic ecosystems. However, the environmental and taphonomic contexts of occurrences of these plants in the LRM present a cautionary tale against making overarching assumptions about the ecological preferences of these (or any other) plant groups. In particular, at least during the late Duckmantian, two species of *Noeggerathia* and one species of *Dicranophyllum* apparently occupied peat substrates, and co-existed with more typical vegetation in swamps that could only have formed under high, weakly seasonal to aseasonal rainfall conditions;

- A unique suite of taxa, including several progymnosperms (e.g., *Rhacopteris*, *Palaeopteridium*, *Pseudadiantites*) and a few endemic medullosalean pteridosperms (e.g., *Havlenaea*, "*Mixoneura*"), are almost exclusively preserved as allochthonous elements, especially in laminated lacustrine tuffites. Crucially, these taxa, although

always rare, consistently are far more common close to pre-existing topographic highs, especially in the steep-sided ravines at the Strádonice locality and adjacent to paleovalley slopes elsewhere. These observations leave little doubt that topographic relief and elevation played a role in the distribution of these enigmatic plants, and a reasonable conclusion is that they generally inhabited the shallow, clastic soils of local ravine and valley slopes. Nonetheless, we consider this suite of taxa to simply represent a subset of the wetland vegetation in the LRM, as they existed under a humid climate mode and occur as rare elements in macrofloral assemblages that are otherwise dominated by Duckmantian plants typical of clastic-substrate habitats. Furthermore, most of these plants are derived from lineages that are ecologically centered in wetland habitats;

- Despite being deposited in narrow paleovalleys bounded by pronounced topographic relief, to date no macrofloral remains of xeromorphic conifers or similarly drought-tolerant taxa have been recovered from the LRM. We note that rare conifer pollen (*Potonieisporites*) has been recorded in gray claystones and carbonaceous mudstones at the Strádonice locality (Stárková et al., 2016), although the source-plant of this pollen is unknown. Regardless, to interpret the rare examples of *Rhacopteris*, *Palaeopteridium*, and *Pseudadiantites* as xerophytes, while interpreting all of the other, dominant taxa with which they are found as hygrophytes or mesophytes, would be incompatible with how vegetation is distributed in the modern tropics under (per)humid conditions. Accordingly, the plant-fossil record of the LRM indicates that, during intervals of humid climate, slope and elevation alone did not cause significant vegetational differentiation into a wetland flora in poorly drained lowlands and a seasonally dry flora on adjacent "well-drained" uplands.

Nýřany Member, Central and Western Bohemian Basin, Czech Republic. Bashforth et al. (2011) reconstructed plant communities on a late Asturian to middle Cantabrian (late Middle Pennsylvanian to early Late Pennsylvanian; *sensu* Opluštil et al., 2016b) braided-river plain, recorded in the Nýřany Mb. (Kladno Fm.), which disconformably overlies the Radnice Mb. in the Czech Republic (Opluštil et al., 2005; Lojka et al., 2016). Although clusters of coal seams occur at intervals within the Nýřany Mb., coarse-grained, fluvial strata predominate at the four main localities studied, with plant fossils quantified from facies interpreted as mainstem and minor abandoned channels, ponds on variably drained floodplains, and shallow lakes. Sedimentological indicators point to conditions of weakly to moderately seasonal

precipitation during deposition of all beds sampled. Although the dendritic, steep-sided paleovalleys that characterized Duckmantian to Bolsovian times were largely filled by the Radnice Mb., numerous emergent topographic highs still existed during accumulation of the Nýřany Mb., indicating that the braidplain frequently abutted elevated habitats.

Despite the proximity of upland environments, all of the nearly 12,500 identifiable plant fossils quantified by Bashforth et al. (2011) represent typical wetland taxa (lycopsids, sphenopsids, ferns, and pteridosperms) that dominated all landforms on the braided-river plain. The only exception is the large-statured cordaitaleans, interpreted as having occupied stable and better-drained channel margins, an interpretation complemented by palynological analyses from nine beds, which corroborate the common presence of cordaitaleans on the braidplain (2–20%). However, rare pollen of walchian conifers (1–2%) and peltasperms (0–7%) also were recorded in some beds, indicating that such drought-tolerant taxa existed somewhere on the landscape, either as scattered elements on the braidplain or in more distant hinterland habitats. That such plants were present is reinforced by previously documented, extremely rare finds of macrofloral remains in the Nýřany Mb., including taeniopterid-like foliage that Obrhel (1965) identified as *Pterophyllum* and *Ilfeldia lobecensis* (= *Ovulepteris lobecensis* of Pšenička et al., 2017), fragments of *Lesleya* leaves (Šimůnek, 1996), and poorly preserved conifer twigs (Šetlik, 1975). Nonetheless, given the juxtaposition of elevated habitats with the braided-river plain, the numbers of pollen and macrofloral remains of drought-tolerant taxa are conspicuously lower than would be predicted by the "upland model". If slope and aspect, and implied drainage effects, controlled the distribution of such plants, these taxa should be far more common in the Nýřany Mb.

San Giorgio Basin, Sardinia. Cleal et al. (2016) provided a taxonomic, biostratigraphic, and paleoecologic analysis of upper Asturian or Cantabrian (upper Moscovian) macrofloral remains from the limnic intramontane San Giorgio Basin, southwestern Sardinia. A product of late Variscan extension, the small (ca. 3 km^2) San Giorgio Basin was filled by about 45 m of primarily coarse-grained strata (San Giorgio Fm.), including fluvial conglomerates and sandstones and debris-flow breccias derived from rapid erosion of lower Paleozoic bedrock in the immediate vicinity (Del Rio et al., 2002; Barca and Costamagna, 2003). However, beds of dolostone, dolomitic siltstone, and plant-fossil-bearing carbonaceous mudstone occur more frequently in the middle of the succession, interpreted to record an interval of reduced subsidence characterized by lacustrine and lagoonal(?) environments with limited sediment input (Barca and Costamagna, 2003: Marchetti et al., 2018).

The plant fossils studied by Cleal et al. (2016) were collected over a period of 20 years from six different lithofacies, five from lacustrine mudstones and one from fluvial sandstone. All plant remains represent typical wetland plants, except for a single putative noeggerathialean cone (although, as noted in Section 6.2.4.2, some members of this group also occupied wetland habitats). The lacustrine deposits are overwhelmingly dominated by calamitaleans, with subordinate ferns and pteridosperms, although the latter groups are more common in a bed immediately below the thick fluvial conglomerate that caps the basin-fill succession. The fluvial sandstone lithofacies is represented by single occurrences of fern and pteridosperm(?) foliage and a cordaitalean pith cast. Based on the proportions of plant groups in the different lithofacies, Cleal et al. (2016) proposed that habitat partitioning existed on the landscape: calamitaleans dominated the wettest substrates around lake margins, ferns and pteridosperms preferred slightly better-drained wetland habitats, and even more distal (inferred to be well-drained) riparian settings were occupied by cordaitaleans and pteridosperms. Although largely in agreement with this paleoecological interpretation, we reiterate that the idea that substrate conditions necessarily became increasingly better-drained in concentric rings away from the basin floor is at odds with vegetational distribution in modern humid tropical regions.

Of particular relevance in the context of this review, prior paleobotanical studies in the San Giorgio Basin emphasized the presence of walchian conifer remains in macrofloral assemblages (e.g., Novarese, 1917; Novarese and Taricco, 1923; Cocozza, 1967). Unfortunately, none of these specimens were illustrated (C.J. Cleal, pers. comm., Aug. 2017), but we assume that they were correctly identified because conifer pollen is present in some palynological assemblages in the basin (Del Rio, 1973; Del Rio and Pittau, 1999; Pittau and Del Rio, 2002; Pittau et al., 2008). Cleal et al. (2016: p. 11) wrote: "*We have seen no macrofloral evidence of conifers from this basin, either in our collection or in the published literature* [...] *Given that the San Giorgio Basin was so small it would not be surprising to find the occasional conifer fragment from extra-basinal vegetation that had found its way into the depositional system here; this would have neither stratigraphical nor palaeoclimatic significance.*" Indeed, given the exceptionally small size of the depocenter (ca. 3 km^2), and conclusive evidence that exposed bedrock slopes existed in the immediate vicinity during much of its development, the San Giorgio Basin presents an ideal natural laboratory to test the validity of the "upland model". If late Paleozoic vegetation were simply organized along a gradient controlled by elevation and implied drainage effects, and if the presence of xeromorphic taxa in lowland deposits could be explained by transport from extrabasinal

habitats, then conifers and other drought-tolerant elements should have been well-represented in the floras examined by Cleal et al. (2016). The fact that they are not present suggests that other factors, especially climate, influenced the spatial and temporal distribution of vegetation types. Furthermore, the paucity of drought-tolerant taxa in the San Giorgio Basin stands in direct contrast with their occurrences at several localities in North America described above, where there was no upstanding relief within hundreds of kilometers. These situations are essentially the reverse of what would be expected when viewed through the lens of the "upland model": the deposits of flatlands should not contain drought-tolerant plants, but do, whereas intramontane paleovalleys should, but do not.

The middle part of the San Giorgio Fm. comprises relatively fine-grained strata, and lithological changes through this middle section may record a shift in climatic conditions. The thin, buff-colored, ichnofossil-bearing beds of (marginal) lacustrine dolostone and dolomitic siltstone that characterize the lower part of the formation bear the hallmarks of climatic seasonality, namely changes in the distribution of terrestrial ichnofacies due to rapid fluctuations in lake level and periodic subaerial exposure (Marchetti et al., 2018). In contrast, the upper part of the middle section of the formation is characterized by gray, plant-fossil-bearing carbonaceous mudstones, probably the product of sustained lacustrine development under more humid conditions. The thick package of fluvial conglomerates and sandstones at the top of the San Giorgio Fm. may represent a return to more seasonal conditions as the basin filled.

That the macrofloral assemblages documented by Cleal et al. (2016) comprise typical wetland taxa is not unexpected, as they were almost exclusively collected from the gray, lacustrine mudstones that presumably accumulated under relatively humid conditions. Under this climate mode, wetland vegetation probably also extended up the basin slopes, which would explain the absence of conifers and other drought-tolerant taxa in their macrofloral assemblages, despite the proximity to elevated habitats. In contrast, the conifer remains recorded by previous authors may have been collected from strata that were deposited during intervals of increased seasonality, when the dryland biome dominated both the basinal lowlands and basin-margin settings, with scattered pockets of wetland vegetation in low-lying areas. Although we suspect that biome distribution in the San Giorgio Basin was primarily controlled by climate, the validity of this hypothesis awaits the discovery of additional conifer remains in facies context.

<u>São Pedro da Cova region, Douro Basin, Portugal.</u> Correia et al. (2016) documented the depositional and environmental context of wetland-dominated macrofloral assemblages from Upper Pennsylvanian (lower Gzhelian, lower Stephanian C) fluvio-lacustrine strata in the São Pedro da Cova region of the limnic intramontane Douro Basin, northwestern Portugal. Recovered from seven distinct beds of micaceous shale in a 4 m-thick succession, the taphocoenoses mainly comprise ferns, pteridosperms, and cordaitaleans, whereas sphenopsids are less common. However, rare leaves of *Lesleya*, a fossil-genus typically associated with Early Pennsylvanian seasonally dry settings, were found at two discrete horizons. An important observation that is difficult to extract from the study is that two distinct types of macrofloral assemblage occur in the thin interbeds that make up a single fossiliferous shale unit (P. Correia, pers. comm., July 2018). Most interbeds preserve typical wetland plants (ferns, pteridosperms, sphenopsids), whereas others are overwhelmingly dominated by poorly preserved *Cordaites* leaves. The specimens of *Lesleya* were collected from two of the *Cordaites*-dominated horizons, suggesting that the cordaitalean foliage may have been derived from the type of high-statured trees that were adapted to periodically moisture-stressed habitats. That compositionally distinct taphocoenoses, one comprising a wetland flora and the other a dryland flora, are interbedded at such a fine scale points to a strongly compartmentalized vegetational mosaic, which is typical of riparian habitats under seasonal conditions. Although both wetland- and dryland-dominated communities coexisted on the same landscape, wetland vegetation was more frequently sampled during individual storm/flood events, a consequence of the taphonomic and preservational bias against landforms with seasonal moisture deficits. A similar example of bed-to-bed differences in species pools at the outcrop scale was documented in the Gzhelian (Virgilian) Markley Fm. of north-central Texas (see Section 6.3.1.1).

In an earlier paleobotanical summary of the Douro Basin, Wagner and Lemos de Sousa (1983) noted the presence of rare walchian conifers, taeniopterids (Pšenička et al., 2017), and dicranophylls among wetland-dominated assemblages, and considered these taxa to have been transported from elevated (i.e., "well-drained") habitats that flanked the narrow basin. In keeping with the earlier interpretations of Wagner and Lemos de Sousa (1983), Correia et al. (2016) acknowledged that the *Lesleya* leaves at their locality could record the vegetation from localized well-drained habitats in a landscape that was otherwise subjected to humid climatic conditions. However, they proposed (correctly, in our opinion) that the presence of these drought-tolerant elements was more likely a consequence of seasonal conditions having prevailed at intervals in the intramontane basin. Furthermore, if predictions from the "upland

model" were to hold, these xeromorphic elements should be far more common, given the proximity of rugged slopes in the catchment area of the narrow basin.

6.3. Pennsylvanian-Permian transition

Across equatorial regions of Euramerican Pangea, the Pennsylvanian-Permian transition generally is expressed in a similar manner. A trend toward increasing aridity, which can be determined on the basis of physical indicators such as paleosols and depositional facies, coincides with broad floristic changes through the interval. Overall drying was superimposed on a pattern of continuing cyclicity, although wetter phases of the cycles generally were drier than those that occurred during the peak peat-accumulating intervals of the Middle and Late Pennsylvanian. Likewise, drier phases shifted from being moist subhumid to variably dry subhumid to semiarid, and, in westernmost Pangea, even arid (Table 1). As the landscape became drier, an increase in mixed floras ensued, even in the wettest phases of cycles in some parts of the tropics (DiMichele et al., 2020). However, there remained considerable variability in edaphic conditions in different regions, depending on the particular circumstances of location, elevation, physiography, and proximity to the ocean (Roscher and Schneider, 2006).

6.3.1. Western Pangea (western USA) (Fig. 6)

The spatio-temporal relationship between dryland and wetland vegetation of tropical Pangea was explored at various scales in the uppermost Pennsylvanian to lowermost Permian Markley Fm. on the eastern shelf of the Midland Basin in north-central Texas (Tabor et al., 2013a, 2013b; Looy and Hotton, 2014; Xu et al., 2018). The formation is wholly terrestrial and accumulated on a fluvially dominated coastal plain (Tabor et al., 2013a). Plant-fossil-bearing exposures consistently comprise the following sequence (from base to top): (*i*) a paleosol (Ultisol) that developed on low-relief interfluves under predominantly humid conditions with limited seasonal dryness; (*ii*) a unit of kaolinite-dominated siltstones that fill scours on the paleosol surface, the product of local erosion of the paleosols themselves; (*iii*) a unit of carbonaceous shales (locally grading into high-ash coals) that contain thin, lensoid claystone partings, representing the accumulation of organics in a swamp that was occasionally traversed by small channels; (*iv*) an upward coarsening unit of interbedded mudstones and sandstones, with increasing paleosol content upwards, recording the transition from aggradation on distal floodplains to sites adjacent to meandering-river channels; and (*v*) a sandstone channel-body with an erosive base, representing an active-channel belt on the coastal plain.

Despite the fact that collections were made at 18 localities in a transect across four counties, each of these distinct lithofacies consistently yielded a compositionally unique suite of macrofloral and microfloral remains. The kaolinitic siltstones preserve dryland-dominated assemblages characterized by *Sphenopteris germanica* and walchian conifers, together with a rare admixture of wetland taxa (especially pteridosperms and calamitaleans). In contrast, the immediately overlying organic-rich lithofacies with claystone partings is overwhelmingly dominated by wetland taxa, particularly *Macroneuropteris scheuchzeri*, but including other pteridosperms, sphenopsids, marattialean ferns, and lycopsids. Upward coarsening packages of mudstone and sandstone also are dominated by wetland assemblages, although *S. germanica* occurs locally near the top of some floodplain units. The uppermost channel sandstones contain rare identifiable plant fossils, of which *Cordaites* leaves are characteristic.

These bed-by-bed macrofloral analyses demonstrate sharp contrasts between the composition, areal extent, and habitat preferences of the wetland and dryland biomes at outcrop scales in tropical Pangea. That ecotonal boundaries generally were pronounced is supported by palynological analyses, with the kaolinitic siltstones being dominated by drought-tolerant taxa and the overlying organic-rich units dominated by wetland elements. However, a detailed palynological analysis through a single cycle in the Markley Fm. found a transitional zone on the landscape, occurring between a changeover from the dryland- to wetland-dominated floras, interpreted as recording fragmentation of the prevailing drought-tolerant vegetation as edaphic conditions became wetter (Looy and Hotton, 2014).

The evidence for sharp ecotonal boundaries between wetland and dryland communities in the Markley Fm. contrasts with the greater mixing of elements seen in successions that span the Pennsylvanian-Permian boundary in the Variscan Mountains of the Czech Republic and Germany, or on the Iberian Peninsula (see Section 6.3.2). Such differences may be related to the fact that the eastern shelf of the Midland Basin in north-central Texas was a much greater distance from elevated terrain than were basinal areas in the limnic intramontane basins of Europe. Under a climatic regime that witnessed oscillations between wetter and drier (and overall increasingly drier) conditions, areas with more topographic variability may have harbored periodically drought-stressed dryland communities in closer proximity to wetland habitats, the effects of seasonal moisture limitation being magnified in such mountainous terrain.

6.3.2. East-central Pangea (Europe) (Fig. 8)

6.3.2.1 Iberian Peninsula survey

Wagner and Álvarez-Vázquez (2010) presented a comprehensive summary of floristic changes on the Iberian Peninsula, including during the Pennsylvanian-Permian transition, and provided an evaluation of the floral response to temporal changes in climate and topographic relief due to ongoing orogenesis. The Pennsylvanian-Permian interval is characterized by mixed floras that include hygromorphic (particularly calamitaleans, marattialean and filicalean ferns), mesomorphic (especially medullosalean pteridosperms) and even more drought-tolerant, xeromorphic (walchian conifers, callipterids, taeniopterids) taxa. The authors attributed floral compositions to a combination of climate and elevational heterogeneity. More xeromorphic elements (particularly the conifers) were interpreted as having been transported to depositional sites from "hinterlands", whereas the overall trend towards the seasonal aridity that characterized the Permian promoted the juxtaposition of taxa that required wet edaphic conditions and those tolerant of periodically low soil moisture.

Based on the taphonomic analysis of modern floral assemblages (see Section 5), the quality of preservation and relative abundances of the xeromorphic taxa in the Iberian plant-fossil assemblages imply shorter transport distances than those proposed by Wagner and Álvarez-Vázquez (2010). A more probable explanation is that these elements lived in close proximity to wetland communities in the depositional basins. In addition, given the relatively small geographic area under consideration, the entire region probably would have been subjected to whatever climatic regime existed at any given time. Although microclimatic differences certainly may have existed, such edaphic heterogeneity would have become accentuated as the regional climate became more arid. We also repeat the observation made by Wagner and Álvarez-Vázquez (2010) that, despite marked elevational heterogeneity in the region during the late Middle Pennsylvanian and early Late Pennsylvanian, conifers are conspicuously absent in the basinal floras. This implies that, during intervals of widespread humid climate, elevation alone did not cause the soil-moisture deficits necessary to support a distinct dryland biome/species pool.

6.3.2.2. Boskovice, Intra-Sudetic and other basins, Czech Republic

Šimůnek and Martínek (2009) summarized compositional changes in macrofloral assemblages through Upper Pennsylvanian to lower Permian strata in the Boskovice Basin of the southeastern Czech Republic; Opluštil et al. (2017b) provided a radioisotopically constrained analysis of the same succession. Upper Pennsylvanian rocks deposited under relatively wet conditions are dominated by typical Late Pennsylvanian wetland taxa, especially marattialean tree ferns, sphenopsids, and filicalean ferns, with rare medullosalean

pteridosperms and cordaitaleans. Aside from the cordaitaleans and perhaps some medullosaleans, none of the plant fossils are characteristic of seasonally dry floras. However, xeromorphic taxa, including walchian conifers, callipterids, and a greater proportion of cordaitaleans, begin to appear in lower Permian rocks, in concert with sedimentological indicators of climatic seasonality. Although the early Permian landscape was overall drier, localized habitats with sufficiently high water tables supported wetland floras dominated by calamitaleans and marattialean tree ferns.

Opluštil et al. (2013b) expanded the scope of analysis of floristic patterns across the Pennsylvanian-Permian transition in the Czech Republic by examining the plant-fossil record at various sites, most recently in the Intra-Sudetic Basin (Opluštil et al., 2017a). The same general pattern seems to hold: wetland and dryland macrofloral assemblages and corresponding depositional environments oscillate and intercalate through time, with a general trend towards aridization. Importantly, although wetland habitats that existed on the Late Pennsylvanian landscapes supported largely unmixed and typical wetland floras, small numbers of walchian conifers, cordaitaleans, callipterids, and various pteridosperms began to appear in early Permian wetland environments, a consequence of increased seasonality of moisture distribution. We emphasize that the compartmentalization of the landscape and increased frequency of occurrence of drought-tolerant elements across the Pennsylvanian-Permian boundary did not coincide with changes in tectonic regime or the proximity of elevated terrain, but rather reflects an overall shift to relatively drier climatic conditions across the Bohemian Massif.

6.3.2.3. Rotliegend Group, Saar-Nahe Basin, Germany

In compiling the distribution and composition of floral assemblages in the Rotliegend Group in the Saar-Nahe region of southwestern Germany, Kerp and Fichter (1985) provided comprehensive lists of fossil-taxa found at specific sites and summaries for major lithostratigraphic units. Nearly all of the floras comprise a mix of xeromorphic (conifers, callipterids) and hygromorphic (calamitaleans, marattialean ferns) elements, whereas mesomorphic pteridosperms (e.g., *Odontopteris*) and small ferns are less common, and the arborescent lycopsid *Sigillaria* is rare. Walchian conifers and callipterids have an effectively universal presence throughout the succession, and both groups are represented by a number of fossil-taxa at most localities; the degree of diversity is particularly evident after Kerp and Haubold (1988) segregated a number of new callipterid genera from the former *Callipteris*. The presence of calamitaleans and, to a lesser extent, marattialean tree ferns, is consistent

with their occurrence in most mixed assemblages in the Pangean tropics, and both groups occasionally are very diverse, particularly in the Lower Rotliegend Group. Although Kerp and Fichter (1985) did not provide sedimentological details for each locality, the Saar-Nahe region was situated on the northern flanks of the Variscan Mountains, and Kerp (1996) suggested that the composition and distribution of the vegetation may have been strongly influenced by the elevational heterogeneity of the landscape.

Supplementing the paleobotanical record of the Saar-Nahe Basin, Uhl and Jasper (2016) provided details of macrofloral assemblages from the Remigiusberg Fm., the lowest lithostratigraphic unit in the Lower Rotliegend Group. Plant fossils were collected from fluvio-lacustrine strata at two localities in the upper part of the formation, and either are late Gzhelian (latest Pennsylvanian) or early Asselian (earliest Permian) in age (Boy and Schindler, 2000; Roscher and Schneider, 2005). At one site, calamitaleans and marattialean tree ferns, typical wetland elements, are overwhelmingly dominant in gray lacustrine claystones, whereas callipterids and *Sphenopteris germanica*, taxa characteristic of seasonally dry habitats, are rare. Calamitaleans and tree ferns also are present at the second locality in interbedded gray and red siltstones and claystones (fluvial overbank deposits?), although the fact that sphenophytes predominate in gray beds and are nearly absent in the fern-dominated red beds points to habitat partitioning among the wetland communities.

Despite the prevalence of wetland plants in the macrofloral assemblages, palynological data from the Remigiusberg Fm. record abundant pollen derived from mesomorphic and xeromorphic taxa (including walchian conifers). Boy and Schindler (2000) suggested that this influx resulted from the dispersal of drought-tolerant plant communities from "hinterland" habitats into basinal lowland settings, where they predominated over and/or replaced wetland vegetation. In contrast, Uhl and Jasper (2016) explained the incongruence between the macrofloral and microfloral records in a taphonomic context. They hypothesized that wetland-dominated riparian environments in the lowlands acted as a barrier that prevented most mesomorphic (e.g., callipterids and *Sphenopteris germanica*) and all xeromorphic (e.g., walchian conifers) macroplant remains from reaching sites of potential preservation, whereas this buffer was ineffective against their highly transportable palynomorphs. We agree with their interpretation, and note that a similar pattern was recorded in an actualistic study of plant preservation in the Orinoco Delta of Venezuela (Scheihing and Pfefferkorn, 1984).

Although we acknowledge that densely vegetated riparian corridors may have blockaded plant remains from non-wetland habitats, we would modify the interpretation of Uhl and Jasper (2016) that wetland communities in the basinal lowlands existed under a

"humid" climate state, while dryland communities from farther afield prevailed simultaneously under "seasonal" conditions. We suggest that, during any given time slice, the entire Saar-Nahe Basin would have experienced the same climate. However, if the climate were seasonally dry, differences in drainage conditions across the landscape would have been magnified, depending on substrate characteristics in various habitats. By contrast, we reiterate that a humid climate would have masked most of these elevational differences. The occurrence (albeit rare) of callipterids and *Sphenopteris germanica*, and the abundance of pollen derived from mesomorphic and xeromorphic plants, imply that the Remigiusberg Fm. largely accumulated under seasonally dry conditions. As proposed by Uhl and Jasper (2016), sphenophytes and tree ferns were restricted to poorly drained riparian wetlands, where preservational potential was highest. However, the dryland biome probably dominated most habitats in the basin, with the distribution of various plant groups tracking local edaphic conditions.

6.4. Early Permian

6.4.1. Western Pangea (western USA) (Fig. 6)

6.4.1.1. Paradox Basin, Utah

DiMichele et al. (2014) described lower Permian (Wolfcampian) mixed floras from the Paradox Basin in southeastern Utah, situated in far western Pangea. The Halgaito Fm. was sampled in the Valley of the Gods and Lime Ridge areas, and the Cedar Mesa Fm. near Indian Creek. The assemblages were interpreted as representing vegetation that existed during pluvial intervals within an otherwise strongly xeric climate regime. The redbed-dominated successions primarily consist of sandstones deposited as eolian dunes, siltstone loessites, gypsum, and interspersed paleosols indicative of overall arid conditions (Tabor et al., 2008; Jordan and Mountney, 2012). However, poorly preserved plant remains occur in thin depositional facies that record relatively wetter riparian habitats, including small, shallow, sandstone channel bodies and interbedded siltstones and sandstones that accumulated on floodplains. A spectrum of macrofloral assemblages exists, ranging from those dominated by walchian conifers with subordinate calamitaleans, to those dominated by wetland plants (especially calamitaleans and tree ferns, with rare sigillarian lycopsids and pteridosperms) with scattered walchian conifers, to those almost exclusively comprising tree ferns. These macrofloral assemblages exemplify the high degree of patchiness that existed on tropical landscapes in strongly seasonally dry climate regimes. Wetland plants were common to dominant in riparian settings where moisture availability was greatest, and drought-tolerant

vegetation prevailed in interfluve environments, as well as flanking and encroaching on shallow fluvial channels.

6.4.1.2. Carrizo Arroyo, New Mexico

The Carrizo Arroyo flora from central New Mexico (Tidwell and Ash, 2004) is similar in preservational quality to the more widely known assemblages from the Upper Pennsylvanian Kinney Brick Company Quarry, Garnett, and Hamilton Quarry localities described above (Sections 6.2.1.2, 6.2.2.6, and 6.2.2.7, respectively). Collected from the Red Tanks Mb. of the Bursum Fm., the age of the plant-fossil-bearing strata is close to the Pennsylvanian-Permian boundary (DiMichele et al., 2004a), with Lucas et al. (2013a) settling on an earliest Permian (lower middle Asselian) age for the bed described by Tidwell and Ash (2004). The flora is accompanied by diverse invertebrate and vertebrate remains (Lucas et al., 2013a), and laterally adjacent, contemporaneous paleosols with pedogenic carbonate (calcrete) nodules demonstrate accumulation under a strongly seasonally dry climate (Krainer and Lucas, 2004). The frequent occurrence of shallow marine limestones in the Red Tanks Mb. points to the proximity of open marine conditions on the coastal plain. The mixed macrofloral assemblage includes diverse and abundant plant-fossil taxa typical of seasonally dry habitats, including walchian conifers, callipterids, cordaitaleans, taeniopterids, *Sphenopteris germanica*, and noeggerathialeans. However, rare and fragmentary remains of medullosalean pteridosperms, calamitaleans, and sigillarian lycopsids also are present, although marattialean tree ferns, a common representative of wetland elements in most mixed assemblages, are conspicuously absent (Tidwell and Ash, 2004). The Carrizo Arroyo flora is compositionally similar to that found in the lower Abo Fm. of early Permian age, described below (Section 6.4.1.3). Although the coastal plain was dominated by plants typical of seasonally dry environments, a small, persistent admixture of wetland plants that required higher soil-moisture conditions also existed on the same landscape.

6.4.1.3. Spanish Queen Mine, Abo Formation, New Mexico

Lucas et al. (2012) described a macrofloral assemblage of Wolfcampian (middle Asselian) age from the lower part of the Abo Fm. in the Jemez River Canyon, north-central New Mexico. The fossiliferous deposit, once exposed in the long-closed Spanish Queen (copper) Mine, comprises a 4 m thick sandstone body that contains numerous scours filled by finely laminated, micaceous siltstone, some of which bear dense accumulations of plant remains and abundant comminuted plant debris. The depositional environment was

interpreted as a braided stream, with organic-rich siltstones recording the burial of plant remains during waning phases of flooding. Thus, stream discharge was variable and generally carried a high sediment load, suggestive of seasonality of rainfall. The gymnosperm-rich flora is dominated by several species of conifers and callipterids, the medullosalean pteridosperm *Neurodontopteris auriculata*, and various taeniopterids. However, the collection also contains rare and fragmentary remains of marattialean ferns and calamitaleans, demonstrating the persistence of these plant groups on western Pangean landscapes far from widespread wetlands.

This lower Permian example repeats a floristic pattern found elsewhere in the tropical realm, including at several of the Pennsylvanian-aged sites described above, such as the Garnett and Hamilton Quarry localities in Kansas (Sections 6.2.2.6 and 6.2.2.7), and from below the Minshall Coal in Indiana (Section 6.2.2.3). The dominant elements in these macrofloral assemblages are xeromorphic, drought-tolerant taxa, among which are small (but persistent) admixtures of plants typical of wetlands, particularly marattialean ferns and calamitaleans. It seems untenable to argue that the dryland elements were transported into the midst of a wetland flora, and then came to represent both the overwhelmingly dominant and best-preserved specimens in the macrofloral assemblages. An alternative interpretation, which we argue is equally unsupportable, is that the rarer wetland elements were transported from extrabasinal wetlands into seasonally dry lowlands, and that elevation, in this instance, created wetter conditions than were found in basinal settings.

6.4.1.4. Other localities in the Abo Formation, New Mexico

Many other macrofloral assemblages have been collected from the lower Wolfcampian to lower Leonardian (middle Asselian to upper Artinskian) Abo Fm. over a wide area of central New Mexico. Most localities involve redbed-dominated successions that mainly comprise mudstones and sheet sandstones with splay-like architectures (Lucas et al. 2013c). Many mudstones exhibit a pedogenic overprint and contain carbonate nodules, indicative of well-drained and seasonally dry conditions (Mack et al., 2010). Most floras from the Abo redbeds are consistently dominated by isolated branches of walchian conifers and, locally, the peltasperm *Supaia* (Hunt, 1983; DiMichele et al., 2007, 2012, 2013b). However, over 30 assemblages have been collected from gray siltstones and shales at several localities, mainly in lower parts of the Abo Fm. Although macrofloral assemblages in these gray rocks also are dominated by conifers, they contain far fewer supaiaoids and greater numbers of cordaitaleans. In addition, the proportion of callipterids is similar to that of the medullosalean

pteridosperms, which are relatively diverse and generally include taxa that are typical of mesic rather than hydric habitats. Calamitaleans and marattialean foliage also are much more abundant in the gray beds. The relative rarity of supaiaoids and increased abundance of wetland elements in the gray beds suggest that compositional differences between the gray and red lithofacies are not the result of some overarching taphonomic bias. Rather, the contrast probably reflects different degrees of habitat and vegetational heterogeneity on the original landscape, with plants that required high soil moisture living in close proximity to those capable of surviving periodic drought.

6.4.1.5. Localities of David White in the western USA

White (1912) described a number of small, mixed floras from various areas in western Pangea. These Upper Pennsylvanian to lower Permian macrofloral assemblages have been underappreciated because the fossils were not illustrated; only taxonomic lists were provided. In addition, little sedimentological information was given to help interpret the depositional environments, and the stratigraphic provenance and stated geological ages of many sites are suspect. Nonetheless, the collections, some of which are stored at the National Museum of Natural History (NMNH) and are available for examination, provide rare examples of mixed floras from western Pangea, at localities situated various distances north of the paleoequator.

Some of the authors have re-collected one of White's localities, in the Waggoner Ranch Fm. at the Castle Hollow site in north-central Texas, which is of Leonardian (late Artinskian) age and was deposited in an equatorial setting. Plant fossils are preserved in sandstones that fill a small channel, and given the large size and excellent preservation of the foliage, appear to have been only locally transported. Marattialean fern foliage predominates, and other elements typical of higher water tables include calamitaleans, neuropterids, odontopterids, *Sigillaria,* and *Sphenophyllum*. However, well-preserved foliated branches of conifers and large taeniopterid leaves also are abundant and thoroughly intermixed with the wetland-dominated assemblage. That the remains of these drought-tolerant plants were transported from mountainous regions, situated hundreds of kilometers away, is an unrealistic interpretation.

To the paleo-north of Texas, and probably at the margin of tropical latitudes during the Pennsylvanian to early Permian, White (1912) recorded two other floras that deserve mention. The first is from a locality near Fairplay, Park County, central Colorado, where plant fossils were collected in a redbed-dominated succession from "[…] *buff and dark Carbonaceous shales nearly 4 miles southwest of Fairplay* […]" (emphasis added; White, 1912: p. 509). The

macrofloral assemblage includes xeromorphic elements typical of seasonally dry environments (conifers and callipterids), mesomorphic pteridosperms (*Odontopteris subcrenulata* and *Neurodontopteris auriculata*), and wetland taxa (the lycopsid *Sigillaria*, marattialean and sphenopterid fern foliage, *Sphenophyllum*, and calamitaleans). We believe that the "southwest" in White's description may be a slip of the pen, as this would situate the locality in the Middle Pennsylvanian (mainly Desmoinesian) Minturn Fm. (Widmann et al., 2007). Such an early age seems incompatible with the plant fossils found. Nonetheless, Arnold (1941) documented several Middle Pennsylvanian localities in central Colorado that may record precocious appearances of conifers and other plant-taxa typical of the Late Pennsylvanian to early Permian, which he interpreted to be a consequence of the climatic aridity of the region. Alternatively, 4 miles southeast of Fairplay would be at, or very close to, a locality that has yielded plant fossils (Lesquereux, 1882), but is best-known for its insect fossils (Scudder, 1890; Handlirsch, 1906; Durden, 1984a). These lower Permian (lower middle Asselian) strata belong to the Pony Spring Mb., Maroon Fm. (Kirkham et al., 2006; Schneider and Werneburg, 2006), and, based on insect biostratigraphy, correlate with the Red Tanks Mb. (Bursum Fm.) at the Carrizo Arroyo locality in New Mexico (Section 6.4.1.2; Durden 1984b; Schneider and Werneburg, 2006; Lucas et al., 2013a). We tentatively accept this correlation, although, given the age discrepancies and uncertainty of the whereabouts of the Fairplay locality of White (1912), further exploration of this site is warranted.

White (1912) also collected a small flora from a redbed-dominated succession at the south portal of the Swissvale railroad tunnel on the north side of the Arkansas River, Fremont County, central Colorado. The Swissvale assemblage includes a mixture of conifers, callipterids, *Odontopteris subcrenulata*, calamitaleans, and sigillarians, but no marattialean fern foliage. This locality is in the Sangre de Cristo Fm., a very thick and long-ranging lithostratigraphic unit with poor age constraints, and that has been subdivided in various schemes. For example, based on comparisons with illustrations in De Voto et al. (1971: figs. 3, 14), the locality is situated in "Unit V" of Pierce (1969), near the midpoint of the "Lower Member" of De Voto et al. (1971), and probably near the base of "Member 3" of Wallace et al. (2000). White (1912) confidently placed a Permian age on the flora, which was followed by De Voto et al. (1971), although Wallace et al. (2000) suggested a Late Pennsylvanian (Virgilian) age for this stratigraphic level. We have tentatively assigned an early Asselian age to the locality.

These mixed floras demonstrate that the wetland biome persisted well into the early Permian in western Pangea, and, despite the overall strongly seasonal conditions, may even

have predominated in local pockets on the landscape (DiMichele et al., 2006). Furthermore, these assemblages once again demonstrate that calamitaleans and marattialean ferns were the most common and widespread of the wetland elements on otherwise seasonally dry landscapes. The calamitaleans were adapted to repeated burial (Gastaldo, 1992), allowing them to withstand the recurring floods that characterize stream corridors in seasonal precipitation regimes, and the marattialeans were capable of extremely wide spore dispersal and probably also tolerated periodic moisture stress and disturbance (Lesnikowska, 1989).

6.4.1.6. Clear Fork Formation, Texas

Chaney and DiMichele (2007) summarized the composition of floras from redbeds of the lower Permian (middle to upper Leonardian, middle Kungurian) Clear Fork Fm. (Group) of north-central Texas. The flora that characterizes redbeds in the middle part of the formation was studied in detail during an analysis of arthropod damage (Schachat et al., 2014), and also provided evidence of branch abscission in walchian conifers (Looy, 2013). Studies involving the paleosols (Tabor and Montañez, 2004; DiMichele et al., 2006), sedimentology (Simon et al., 2016, 2018; Simon and Gibling, 2017), and climate (Montañez et al., 2007) of the unit all point to prevailing dry subhumid to arid conditions. Plant fossils are uniformly preserved in small channel bodies. Some channels contained standing water after abandonment, whereas others were filled during intermittent (seasonal?) flow, thereby facilitating short-term preservation of plant remains in a dry landscape. Plant fossils mainly are preserved as iron-rich permineralizations (Chaney et al., 2009), probably reflecting the presence of bacterial microfilms during early stages of diagenesis (Dunn et al., 1997; Locatelli et al., 2017). The dominant plant fossils are walchian conifers, taeniopterids, callipterids, gigantopterids, and comoioids. However, these gymnosperms are consistently associated with marattialean tree fern foliage, calamitalean stems and foliage, rare *Sphenophyllum*, and exceptionally rare *Sigillaria*, all of which are indicative of localized areas with high water tables in an otherwise strongly seasonally dry landscape.

Again, it is unreasonable to expect that the large number of drought-adapted floras preserved in various environments in the Clear Fork Fm., extending through several million years of deposition, largely represent plant remains that were transported into the basinal lowlands from elevated habitats. This skepticism is supported by the fact that the Clear Fork Fm. accumulated on the eastern shelf of the Midland Basin, which was a tectonically stable platform of extremely low relief (Nelson et al., 2013). Furthermore, the nearest upland areas during the Permian, the Red River Arch and the Wichita-Arbuckle Mountains, were at least

200 km away from any of the fossiliferous localities documented by Chaney and DiMichele (2007).

7. Discussion

7.1. Evaluating the upland vs. climate models: lessons from Garnett, Kansas

The Upper Pennsylvanian (Missourian) conifer-dominated macrofloral assemblages in the Rock Lake Shale at Garnett, Kansas (see Section 6.2.2.6; Fig. 6), played a formative role in the development of the hypothesis of Elias (1936) and Moore et al. (1936) that two compositionally distinct floras, one with wetland and the other with dryland signatures, occupied lowland habitats of tropical Pangea. They argued that the alternation of hygromorphic assemblages (predominantly pteridophytes) and mesomorphic to xeromorphic assemblages (predominantly gymnosperms) through the late Paleozoic was best explained by cyclic fluctuations in climate and attendant soil-moisture conditions. Elias (1936) and Moore et al. (1936) recognized that, although wetland vegetation was far more frequently preserved in Pennsylvanian strata, the Garnett locality presented a window into rarely preserved seasonally dry ecosystems that became increasingly apparent through the Permian due to the long-term aridification of Pangea. Crucially, they considered the gymnosperm-dominated floras at Garnett and elsewhere to record the local vegetation during seasonally dry phases, rather than having been transported from a distant source.

Reassessing the Garnett flora, but in the context of the more encompassing Pennsylvanian-aged coal measures in Kansas, Cridland and Morris (1963) agreed that two compositionally and ecologically distinct plant communities existed during the Pennsylvanian. However, based in large part on the absence of roots associated with the conifer-dominated assemblage, they argued that the xeromorphic plant fossils that dominate the Garnett flora must have been transported from better-drained "upland" habitats (Fig. 1(A)). Furthermore, Cridland and Morris (1963) rejected the speculations of Elias (1936) and Moore et al. (1936) about climatic cyclicity during the Pennsylvanian, and instead embraced the idea that the Pangean tropics always were humid enough to support typical peat-swamp vegetation. Their rejection primarily hinged on the discovery of a macrofloral assemblage in the Lawrence Fm. (Virgilian) at Baldwin, Kansas (Cridland and Morris, 1960), where abundant taeniopterids, rare conifers, and a single callipterid were mixed with the usual array of wetland elements found at other localities throughout the Lawrence Shale. Given that an admixture of xeromorphic, mesomorphic, and hygromorphic taxa occurred at the Baldwin and Garnett sites, and the observation that all other macrofloral assemblages from the Lawrence

Fm. only comprised wetland taxa, Cridland and Morris (1963) argued for the spatially intermixed coexistence of these two compositionally distinct communities under a persistently humid tropical climate during the Pennsylvanian.

In the scenario envisioned by Cridland and Morris (1963), wetland and drought-tolerant plant communities lived side-by-side, in immediate proximity, on the same landscape, being differentiated only by slight elevational differences (Fig. 1(A)). Plants with mesomorphic to xeromorphic traits were proposed to have lived on, and to have been transported from, hummocks within or directly adjacent to peat swamps, which were situated in low-lying areas and occupied by wetland taxa. These bumps (their so-called "uplands") on the landscape were considered sufficiently elevated, and by inference sufficiently well-drained, to produce local areas of soil-moisture deficit, even though the background climate was humid. Cridland and Morris (1963: p. 79) offered modern Kansas as an environmental parallel for what they envisioned for the heterogeneity of plant distribution in the Pennsylvanian, with swampy riparian settings being surrounded by drier interfluves: "*The relief of the regions in question need only have been of the order of 20-30 feet, i.e., the order of magnitude which is responsible for the profound differences of the floras of river bottoms and adjacent prairies in present-day Kansas.*" The minimal elevational differences posited by Cridland and Morris (1963) reflect the fact that they were constrained by the position of the fossiliferous deposit, far out in west-central Pangea and thus hundreds of kilometers from anything that might qualify as a true upland.

The reasoning presented by Cridland and Morris (1963) is a paragon of the confusion that surrounds the matter of mixed floral assemblages in upper Paleozoic strata and, by extension, for the persisting debate about whether mesomorphic and xeromorphic taxa characterized "upland" or "dryland" habitats. In comparing to modern Kansas, Cridland and Morris (1963) confounded several factors. First, modern Kansas does not have a climate in which vast peat-forming wetlands could exist. Second, the plant-fossil-bearing strata at the Garnett locality are not laterally adjacent to coal deposits. Rather, the conifer-dominated flora occurs in a channel-fill that is situated between coal beds, and thus was not contemporaneous with peat-forming habitats. Indeed, the Garnett flora may record habitat heterogeneity on a complex, seasonally dry landscape; taxa adapted to seasonal drought probably formed the matrix vegetation, whereas rare wetland communities were confined to low-lying and relatively poorly drained riparian habitats. However, what Cridland and Morris (1963) either failed to acknowledge or to recognize is that the observed heterogeneity in modern-day eastern Kansas is a product of its moist subhumid and distinctly seasonal climate, with peak

rainfall in the summer months and precipitation exceeding evapotranspiration for 8 months of the year (Thornthwaite, 1948: fig. 4k, table I). The close spatial proximity of Late Pennsylvanian plant communities proposed by Cridland and Morris (1963) does not account for the fact that the "dry" hummocks and the "wet" swamps thought to have surrounded them must have been subjected to the same background climate. Such a scenario does not account for the fact that habitat heterogeneity is fundamentally different under humid to perhumid conditions (9–12 wet months per year) than it is under subhumid to semiarid conditions (1–8 wet months per year) (Table 1). Patches of wetland are far more probable in seasonally dry climatic zones than are patches of dryland in a region with aseasonal and high rainfall, the type of environment necessary for widespread peat accumulation in the tropics.

We believe that the Cridland and Morris (1963) model presents a highly improbable scenario, and even cursory observations of plant ecology in the modern humid tropics support our misgivings. For example, in the extensive wetlands of Amazonia, vast areas are covered by wetland forests, known as Várzea (seasonally flooded whitewater; Wittmann et al., 2006; Luize et al., 2015) and Igapó (seasonally flooded blackwater; Montero et al., 2014). Plants in these forests are part of the same basic species pool common to surrounding, better-drained, terra firma habitats, which are subject to the same humid climate. Furthermore, raised hummocks in the Várzea forests (Borokotóh) are not occupied by a radically different suite of species than those in the flooded wetlands or surrounding terra firma, but also comprise plants from the same species pool (Barnett et al., 2015). Likewise, plant communities drawn from a common pool occupy the Andean slopes as far upslope as adequate rainfall persists and temperature extremes do not become the overriding factor (Colinvaux et al., 2000).

This pattern holds in even more extreme ecosystems, such as the ombrotrophic peat swamps of Sumatra. Posa et al. (2011) reported that, of the 1524 species present in the swamps, only 174 (11.4%) are restricted to peat substrates, whereas the vast majority are drawn from a species pool that also occupies surrounding areas of variable elevation, all under the same perhumid climate. Similarly, in a study of a Cameroonian rainforest with a three-month dry period, Kenfack et al. (2014) found that many species have habitat centroids that range from swamps to ridge tops (with elevation differences of up to 90 m). Importantly, however, all species reported are part of the same species pool, and are largely distributed throughout all or most of the five habitat types identified in the study area; areas of higher elevation do not harbor an assemblage of species entirely different from those in the low-lying swamps.

Returning to the late Paleozoic, many mixed floral assemblages are dominated by plants that preferred seasonally dry substrates, including conifers, gigantic cordaitaleans, callipterids, cycads, and taeniopterids, depending on the region and age involved. Nonetheless, such assemblages usually contain admixtures of plants typical of wetland habitats, albeit frequently being rare and fragmentary. The paucity and poor preservation of these wetland elements are important indicators of the climatic signature deduced from the dominant dryland taxa. Where the remains of drought-tolerant plants are well preserved as large specimens, but wetland elements are not, the explanation that the fragmentation of wetland taxa occurred during long-distance transport from poorly drained habitats seems improbable. More plausibly, wetland communities existed within a background of seasonally dry landscapes, but only in scattered patches or ephemeral habitats within riparian corridors or on the margins of lakes and ponds (Falcon-Lang et al., 2004; DiMichele et al., 2006; Opluštil et al., 2013b; Bashforth et al., 2014). Such depositional settings were favored by plants capable of recovering from repeated burial by flood-borne sediments (such as calamitaleans), groups that dispersed widely and rapidly to find stable, wet microhabitats (such as marattialean tree ferns), or taxa that could tolerate a degree of seasonal drought (including some medullosalean pteridosperms). Thus, we suggest that the rarity and fragmentary preservation of any type of plant remains in macrofloral assemblages should not immediately connote long-distance transport from remote sites, and the presence of wetland plants intermixed in taphocoenoses dominated by dryland taxa provides clear support for that argument.

7.2. True upland vegetation

Is it possible to assess unequivocally the composition of true upland vegetation in the Pennsylvanian and Permian tropics? This question has vexed scientists since the 19th century, and Ball (1879: pp. 578–579) did not conceal his pessimism: "*Among the many new and old truths which we owe to Darwin, must be reckoned the lively sense of the imperfection of the geological record now possessed by most naturalists, but not generally recognised before the appearance of the 'Origin of Species'. As regards fossil records of the vegetation of mountain regions, however, the case is very much stronger than he has put it; and with few and trifling exceptions, to one of which I shall refer, the documents from which we might have gained any direct knowledge of the mountain vegetation of the past are irrevocably lost. Fossil plants are, under favourable conditions, preserved in shallow lakes or estuaries; but only by the rarest of chances can a plant from the upper mountain region be preserved in such deposits.*

In attempting to reason about the ancient vegetation of the mountain regions of the earth, we are thus left unaided by direct evidence, and it is unavoidable that our conclusions should be to a great extent speculative."

Although such pessimism may be warranted, we are cautiously optimistic that the remains of true upland vegetation could be preserved in the geological record in at least two ways. The first involves the preservation of high-elevation landscapes that, through unusually rapid subsidence linked to orogen collapse, were drawn downward into the evolving accommodation space and buried before they could be obliterated by erosion. The premise for this assumption is intuitive; upland plants should have greater preservation potential in mountainous terrain, given the higher altitudes and pronounced topographic relief that places erosional and depositional settings in proximity. The second mechanism involves the transport of upland plants from basinal slopes or more distant hinterlands into lowland settings, where their preservation potential was greatly enhanced. Log-jam deposits, in particular, may hold some promise for determining the composition of true upland plant communities. Nonetheless, we emphasize that, depending on the prevailing climate mode, such upland vegetation could be homotaxial with coeval lowland communities, and thus indistinguishable in a plant-fossil assemblage.

7.2.1. Intramontane basins

Regarding the preservation of intramontane landscapes, some alpine basins of Cenozoic age still survive, particularly within the Alpide mountain belt of Europe and Asia, although the probability of them entering the longer-term geological record is exceedingly low because elevated regions are subject to net erosion. It follows that there are very few examples of upper Paleozoic successions that could potentially represent the fill of true limnic intramontane basins. Indeed, many basins that were formerly identified as limnic (ostensibly because they developed in the midst of mountainous terrain) contain evidence of marine incursions, including the Maritimes Basin of Atlantic Canada (Archer et al., 1995; Calder, 1998; Grey et al., 2011; Carpenter et al., 2015; Falcon-Lang et al., 2015c; Fig. 7). Likewise, in the post-Asturian Basin of northwestern Spain (Fig. 8), where deposition occurred in a broad foreland flanked by substantial topography, faunal evidence for brackish or marine influence has been found tens to hundreds of kilometers inland from the presumed Paleo-Tethys coastline (Eager and Weir, 1971; Eager, 1985; Knight, 1983; Wagner and Álvarez-Vázquez, 2010; Fig. 3). As such, sediment accumulation in these paralic intramontane basins must have occurred close to sea-level highstand and, even during lowstands at glacial

maxima, elevations would only have been ca. 100–120 m above sea level (Rygel et al., 2008), despite the coastline having retreated by many hundreds of kilometers.

The best candidates for late Paleozoic intramontane basins that could record true limnic successions deposited at elevation, and thus preserved through extraordinarily rapid subsidence, are the small, disconnected basin networks of Europe situated in the heart of the Variscan Orogen (reviewed by Opluštil, 2004; Opluštil and Cleal, 2007; Cleal et al., 2009; Fig. 8). Based on the presence of putative periglacial sedimentary features, Becq-Giraudon et al. (1996) proposed that basin-fill successions in the French Massif Central record accumulation at altitudes up to 4.5–5 km. However, this hypothesis is wholly incompatible with the timing and rates of denudation for the orogen (Schneider et al., 2005; Roscher and Schneider, 2006), and with the composition of associated macrofloral assemblages, which contain predominantly wetland taxa that are typical of Upper Pennsylvanian floras found elsewhere (Doubinger et al., 1995; Wagner, 1997; Wagner and Álvarez-Vázquez, 2010). Similarly, Tenchov (1976) suggested a paleoaltitude of 2 km for the Svoge Basin in Bulgaria based on floristic and biogeographic comparisons.

One of the best documented and most credible candidates for a late Paleozoic upland environment is the Kladno-Rakovník Basin and associated depocenters of the Bohemian Massif in the Czech Republic, where strata (including thick peats) were deposited in narrow, steep-sided paleovalleys and subsequently buried below the plane of erosion (Opluštil, 2005a, 2005b). Based on extrapolations of paleovalley gradients and estimated downstream distance to the North Variscan coastline (corrected by palinspastic reconstruction), Opluštil (2005a) suggested a maximum paleoaltitude of 900–1200 m for the basin during the Early to Middle Pennsylvanian. However, this value may be an overestimate, and a paleoaltitude of 500 m for the Kladno-Rakovník Basin is now considered more probable (S. Opluštil, pers. comm., Oct. 2020).

A significant hurdle to interpreting the late Paleozoic intramontane basins of the French Massif Central and Bohemian Massif as recording wholly terrestrial deposition at high elevations is the presence of intercalations that contain faunas suggestive of marine to brackish influence (reviewed by Schultze and Soler-Gijón, 2004; Schultze, 2009, 2013). Based on detailed critiques of the environmental constraints of these biotas, which include acritarchs, microconchids, bivalves, ostracodes, syncarids, xiphosurans, and fish, these authors concluded that the Variscan basins could not have formed at high altitudes because a marine connection was necessary, even if only intermittently. Again, this implies that low-lying areas within these basins were at the upper limits of the reach of marine highstands, at

elevations of ca. 100–120 m above sea level (Rygel et al., 2008). In keeping with this scenario, Bashforth et al. (2011) suggested that these intramontane basins may have had very steep margins that descended to relatively low-elevation floors. However, a more nuanced interpretation is that the marine to brackish faunas may have been euryhaline invaders linked to the "mid-Carboniferous diversification event" of continental ecosystems (Falcon-Lang et al., 2015d). Although some of these organisms may have been obligated to return to marine habitats to reproduce (Schultze and Soler-Gijón, 2004; Schultze, 2009), their occurrences in the intramontane Variscan basins may imply proximity to the coast rather than proximity to sea level (Ó Gogáin et al., 2016).

Although novel approaches to determining the paleoaltitude of late Paleozoic intramontane basins present an exciting research domain, to date only estimates of minimum elevation can be made with certainty, being based on the preserved magnitude of basement topography. In numerous basins situated within elevated terrain (e.g., Kladno-Rakovník Basin, Opluštil, 2005a; Dobrudzha Basin, Bulgaria, Tenchov, 1993; northern part of Bay St. George Basin, Newfoundland, Falcon-Lang and Bashforth, 2004), the maximum observed paleorelief is ca. 200 m. In northwestern Spain, greater incised-paleovalley depths were recorded in the Sabero and Ciñera-Matallana coalfields (200–300 m; Knight, 1971; Wagner, 1971) and the post-Leonian Basin near Ocejo de la Peña (up to 450 m; Iwaniw, 1985b), although these magnitudes may be exaggerated due to syn- and post-depositional tectonism (Alonso, 1989). As such, conservative estimates of basin paleo-altitudes are in the range of up to a few hundred meters, and probably well below 1000 m, above sea level (Falcon-Lang, 2004b).

Whereas many of the aforementioned intramontane basins clearly were deposited above sea level, their altitudes were probably not sufficient to affect overall floral composition. For example, as detailed in Section 6.2.4.2 (and references therein), several fossil-taxa that are rarely preserved in Pennsylvanian macrofloral assemblages have been recorded among the diverse record of the uppermost Duckmantian Lower Radnice Mb. in the Central and Western Bohemian Basin, Czech Republic (Opluštil and Cleal, 2007). Having been deposited in valleys and narrow ravines that were surrounded by rugged topography, these taxa, such as endemic medullosalean pteridosperms (e.g., *Havlenaea*), noeggerathialean progymnosperms (e.g., *Rhacopteris*, *Palaeopteridium*, *Noeggerathia*), and the coniferopsid *Dicranophyllum*, have frequently been cited as examples of "extrabasinal" or "upland" plants that washed into basinal areas from adjacent slopes (i.e., putative "well-drained" habitats). However, careful analysis of the distribution of these fossils in sedimentologic, taphonomic, and environmental

context indicates that *Noeggerathia* and *Dicranophyllum* actually preferred the peat swamps, whereas *Havlenaea*, *Rhacopteris*, and *Palaeopteridium* were a subset of the wetland vegetation that mainly occupied clastic-substrate habitats, perhaps preferentially occupying thin soils on local slopes. Importantly, all of these fossil-taxa lived and died under a humid climatic regime. Aside from rare conifer pollen (*Potonieisporites*) and unidentified (cordaitalean?) wood fragments at the Strádonice locality (Stárková et al., 2016), there is no unequivocal evidence of genuinely xeromorphic plants that grew under moisture-stressed conditions. As such, regardless of the original altitude of the basin and the existence of significant topographic relief during deposition of the Lower Radnice Mb., it is clear that elevation alone did not create conditions leading to dominance by a distinct dryland biome.

In modern tropical settings, vegetation zones along altitudinal transects reveal a shift between lowland rainforest and montane rainforest at elevations ranging from 700–1500 m, the exact level dependent on environmental characteristics and climate mode of the region (Richards, 1952; Grubb and Whitmore, 1966; Grubb, 1971, 1977; Nakashizuka et al., 1991). Gradational changes in lowland rainforest composition do occur at lower elevations, but these transitions comprise more subtle shifts in the vegetational mosaic, rather than recording a change to a distinct forest type (Lieberman et al., 1985; Nakashizuka et al., 1991; Lieberman et al., 1996). We consider it reasonable to assume that vegetation was organized along similar altitudinal gradients in Deep Time. Accordingly, it may be that none of the preserved basins of equatorial Pangea developed at sufficiently high elevations (i.e., above 700–1500 m) to support the late Paleozoic equivalent of the taxonomically distinct montane forests of the modern tropics. This assertion is supported by the fact that the Variscan Mountains resulted from continent-continent collision, and thus may have comprised a series of major (albeit disjunct) ranges, where the altitudinal threshold between lowland and montane forests would have been at higher elevations (ca. 1200–1500 m), rather than the lower limit (ca. 700–900 m) found on isolated mountains (i.e., the "Massenerhebung" effect; Grubb, 1971).

Although the composition of true upland vegetation in tropical Pangea remains an enigma, some clues can be drawn from biogeographical studies that demonstrate a close relationship between altitude and latitude in the distribution of modern plant biomes (e.g., the "life zones" of Holdridge, 1947). Under this bioclimatic framework, equatorial montane floras resemble those of lowland temperate zones, although diversity remains markedly higher in the tropical forests (Richards, 1952; Gentry, 1988). Applying this concept to the late Paleozoic, upland vegetation of equatorial Pangea may have had parallels with temperate lowland vegetation of the Angaran and/or Gondwanan paleokingdoms. There is support for this model

in the fossil record, as rare palynomorphs (typically pollen) attributable to taxa of Angaran and Gondwanan affinity occasionally occur in microfloral assemblages from clastic lowland deposits of Euramerica (Kirkland and Frederiksen, 1971; Bless et al., 1977; Winston, 1983; Dimitrova et al., 2011; Dolby et al., 2011; Van Hoof et al., 2013). We emphasize the fact that these exotic elements have not been recovered from coals, which record peat accumulation under a (per)humid climate mode. Rather, they have been found in clastic strata, which were deposited under seasonally dry conditions of varying amplitudes (Cecil, 2003; Cecil and Dulong, 2003; Table 1), under a climate mode that resulted in a landscape with heterogeneous drainage conditions and habitats.

7.2.2. Log-jam deposits

The second way to assess the composition of upland communities is by analyzing log-jam deposits preserved in basinal lowlands situated adjacent to erosional settings. Numerous examples of log jams dominated by the trunks and stumps of gigantic cordaitalean trees have been documented from Lower and Middle Pennsylvanian fluvial successions in the Maritimes Basin of Atlantic Canada (Calder, 1998; Falcon-Lang and Scott, 2000; Falcon-Lang and Bashforth, 2004, 2005; Bashforth, 2005; Falcon-Lang, 2006; Gibling et al., 2010; Bashforth et al., 2014; Ielpi et al., 2014; Fig. 7). In all of these instances, strata were laid down in basinal lowlands that were closely flanked by elevated hinterlands (Calder, 1994, 1998; Gibling et al., 2019), although deposition generally occurred at elevations within the limits of sea-level highstands. Given the setting, the predominance of cordaitalean logs may reflect the proximity to, and transport from, adjacent hinterland habitats. For example, in a survey of log jams in Middle Pennsylvanian fluvial deposits in the Sydney Basin, Gibling et al. (2010) recorded an increase in the proportion and size of cordaitalean remains, as well as changes in their preservational mode, at occurrences closest to the basin margin. However, none of the log jams documented in Atlantic Canada exclusively comprise suspected upland elements, as axial remains (trunks, branches, large petioles) of plants typical of low-lying wetland habitats (lycopsids, calamitaleans, tree ferns, pteridosperms) also are present (and sometimes predominant). As such, most of these plants probably were entrained from lowland riparian habitats, including from peat swamps that were crosscut and eroded by fluvial systems that developed after peat accumulation had ceased, possibly due to a shift to seasonal conditions.

A similar scenario was envisioned for a Lower Pennsylvanian log-jam deposit in the Black Warrior Basin of Alabama (Fig. 6), where lycopsid, calamitalean, and large cordaitalean trunks occur in a fluvial conglomerate situated between two benches of the Mary

Lee Coal (Liu and Gastaldo, 1992; Gastaldo and Degges, 2007). Clast lithotypes, including pebbles that fill interior hollows of many axes, indicate derivation from highlands of the Appalachian Mountains, suggesting that the logs and outsized clasts rafted into the basinal lowlands from extrabasinal sources up to 100 km upstream. Based on the presence of upright lycopsids and calamitaleans in the lower bench of the Mary Lee Coal (Gastaldo, 1990), and the composition of palynological assemblages in the coal itself (Eble, 1990; Eble et al., 1994), Gastaldo and Degges (2007) suggested that most of these axes were eroded from the local peat swamps and lowland riparian habitats. In contrast, the large-statured cordaitalean logs were interpreted to have been transported from more distant, elevated sources near the Appalachian Mountains.

   We emphasize the point that such log-jam deposits may indeed include plant remains transported from true upland settings, but only those organs with the most strongly lignified and thus resistant tissues, particularly woody stems and some seeds, would represent upland vegetation. These deposits probably will not contain the foliage or other delicate organs reported from macrofloral assemblages that, as discussed in many of the above papers (Section 6), we interpret as being composed entirely of plants derived from intrabasinal, lowland settings. Furthermore, even if stems derived from upland habitats are present, they invariably are mixed with logs from lowland settings. In light of these observations on the composition of log-jam deposits, we consider it highly improbable that the foliage or delicate branch systems of "extrabasinal" or "upland" plants could survive extended transport into basinal lowlands, let alone be preserved with the same quality as the wetland taxa with which they frequently are mixed. Are there "exotic" upland plants represented in some log-jam deposits? There almost certainly are. However, in the absence of more readily identifiable foliar remains, and the difficulty of differentiating plant groups based on decorticated and flattened logs, we would argue that the composition of vegetation from true elevated habitats remains ambiguous.

7.3. Inferences from palynological assemblages

   Palynology, frequently exhorted as providing a window on upland vegetation, may be a significantly less reliable indicator for determining upland *vs*. lowland plant sources than promoted. The literature is replete with instances of palynomorphs, especially those from enigmatic or rare plant groups that are not represented in the regional macrofossil record, being attributed an upland origin (Chaloner, 1958; Kirkland and Frederiksen, 1971; Bless et al., 1977; Dimitrova et al., 2011). However, such occurrences could just as easily be

explained as having been derived from vegetation that occupied a local basinal lowland environment during an interval of climatically induced moisture deficit. A particularly interesting case study is a comparison of papers by Dolby et al. (2011) and Dimitrova et al. (2011), both of which examined the same palynological data from the uppermost Middle Pennsylvanian Sydney Mines Fm. in the Sydney Basin of Nova Scotia (Fig. 7), but came to entirely different interpretations about the composition and distribution of the source vegetation. Both studies involved roof-shales immediately above coal beds and other siliciclastic units in successions between coal beds, whereas Dolby et al. (2011) also examined palynological assemblages from the coal beds themselves. Although the two analyses converge in their tacit agreement that the plants and physical environment were closely linked, the geological context and resulting interpretations of plant distribution in time and space are widely divergent.

Dolby et al. (2011) interpreted the depositional context of the Sydney Mines Fm. under a high-precision framework of glacial-interglacial cyclicity developed for the unit (Gibling and Bird, 1994; Gibling et al., 2004), with evidence of climatic fluctuations determined in part from sedimentology, sequence stratigraphy, and paleosols between coal beds, including calcic Vertisols indicative of strongly seasonal rainfall (Tandon and Gibling, 1994). The composition of palynofloral assemblages was linked directly to environmental conditions at the site of deposition. Temporal changes in palynological spectra were interpreted as recording attendant changes in climate, highlighted by the strong contrast between dryland assemblages dominated by conifers and other gymnosperms, and wetland assemblages dominated by lycopsids, ferns, and cordaitaleans. In marked contrast, Dimitrova et al. (2011) interpreted the climate as uniform throughout the succession, with the coals, limestones, siliciclastic deposits, and paleosols recording gradational shifts in depositional environments and topography through time and space. According to this framework, expanded on by Thomas and Cleal (2017), the region was interpreted as consisting of a series of vegetational zones that extended inland from coastal peat swamps to increasingly elevated areas; the composition of plant communities simply changed upslope due to increasing moisture stress resulting from drainage effects (Fig. 1(B)). These floristic patterns were largely inferred from *a priori* interpretations about the tolerance of different plant groups to drought stress, rather than directly linking the palynological assemblages to the lithofacies from which they were collected.

We would be remiss not to point out that the model undergirding the interpretations of Dimitrova et al. (2011) and Thomas and Cleal (2017) would be described as entirely

"autocyclic" in the terminology introduced by Beerbower (1964; discussed by Cecil, 2013). Applying this paradigm, climate is held constant, and facies changes are considered to result entirely from the shifting of depositional conditions across the landscape. Dimitrova et al. (2011) and Thomas and Cleal (2017) offered no mechanism to explain the great variety of depositional environments, all assumed to have occurred contemporaneously and in close proximity, on the landscape they envisioned – the heterogeneity is simply asserted. Importantly, many of the stratigraphic facies implied to have been concurrent are, in fact, indicators of markedly different and entirely incompatible environmental conditions. The sustained accumulation of tropical peat, for example, requires a (per)humid climate, and is intolerant of sediment influx. Furthermore, under such climatic conditions, tropical rivers, even those with high flow volumes, carry low sediment loads (Cecil et al., 2003b; Latrubesse et al., 2005) due to soil shielding by high-density canopies, and binding by roots, mycorrhizal fungi, and their exudates. In contrast, rivers with high siliciclastic loads and active floodplains are most common under seasonally dry climates (Cecil and Dulong, 2003; Latrubesse et al., 2005).

In the context of this discussion, we are reminded of one entirely autocyclic model, dubbed the "Allegheny Duck", in which the dynamics of modern coastal deltas were applied to account for changes in the spatial position of various depositional environments represented in coal-bearing strata in the Appalachian Basin (Ferm, 1970; Horne et al., 1978). Unfortunately, the Allegheny Duck model was not in conformance with the sedimentary patterns and the nature of peat formation in modern deltas. Not having the predictive power hoped for, the model ultimately was abandoned by its originators (Ferm and Staub, 1984).

As Beerbower (1964) presented so eloquently, one must consider both autocyclic and allocyclic factors when attempting to interpret and reconstruct ancient landscapes. Given the overwhelming evidence in the Pennsylvanian geological record for rhythmic climate change, and for its imposition on longer-term climate trends, we favor interpretations that acknowledge the strong role that climate must have played in determining the distribution of vegetation in time and space. However, because of the high potential for palynomorph transport, palynofloras of "mixed" floral composition must be used in combination with geological evidence that considers such matters as depositional setting, the potential for reworking of some grains, position of the study assemblages relative to sea-level fluctuation and sequence architecture, and non-biological indicators of climatic conditions, such as paleosols and sedimentary features.

7.4. Floristic patterns near the Middle to Late Pennsylvanian boundary: tectonics vs. *climate*

Considering the literature reviews and discussions presented herein, we return to the matter of climate *vs.* tectonics as the main driver of plant distribution, including extinctions and originations, during the late Paleozoic. The areal extent of peat swamps in Euramerican parts of Pangea underwent a significant reduction just after the Middle to Late Pennsylvanian (Moscovian-Kasimovian) boundary (Phillips and Peppers, 1984; Kerp, 1996; Cleal and Thomas, 1999, 2005), an event that coincided with a prominent shift from lycopsid to tree-fern dominance in the peat swamps (Phillips et al., 1974, 1985; Phillips and Peppers, 1984). In the central and eastern USA, this extinction event equates to the traditional Desmoinesian-Missourian boundary (see Section 6.1; Fig. 4), and has been attributed to a threshold-type ecosystem response (DiMichele and Phillips, 1996; DiMichele et al., 2001a, 2009; Falcon-Lang et al., 2018) to the overall warming and drying trend that affected tropical Pangea through the Pennsylvanian (Cecil et al., 1985; Roscher and Schneider, 2006; Tabor and Poulsen, 2008; Tabor et al., 2013b; Montañez et al., 2016). However, Kerp (1996) and Cleal and Thomas (1999, 2005) invoked tectonism, namely the rise of the Variscan mountain belt and attendant changes in elevation and sediment output, as the primary mechanism for the drastic reduction of peat-forming habitats and concomitant extinction near the Middle to Late Pennsylvanian boundary.

Kerp (1996) presented a comprehensive model for the influence that mountain building would have had on a large, flat, low-elevation alluvial plain, the type of setting favorable to peat accumulation. In effect, he envisioned that increased elevation and topographic relief in the Variscan region due to orogenesis would have fragmented those landscapes where high water tables were formerly able to persist. In this model, the rise of the Variscan mountains promoted spatial heterogeneity, with a strong reduction in the areal extent of landscapes that had a sufficiently high water table to support peat swamps and other wetlands. The creation of mountainous areas may also have had a strong effect on the heterogeneity of microclimates, sediment types and accumulation rates, and substrate conditions, thus potentially bringing vegetation adapted to very different conditions into closer proximity than might occur on a low-gradient, homogenous landscape. Such a varied vegetational mosaic could have enhanced the possibility for the assembly of mixed plant taphocoenoses.

We acknowledge that landscape partitioning during orogenesis would have played a role in fragmenting and redistributing the dryland and wetland biomes on large-scale time frames. However, the rate of mountain building is significantly slower than the rate of plant dispersal and establishment. For example, studies of orogenic activity indicate that maximum

rates of sustained tectonic uplift are ca. 1 km per million years (Abbott et al., 1997). Expressed more tangibly, at a maximum rise of 1 m per thousand years, rates of vegetation dispersal would far outpace such increases in elevation. Furthermore, using modern Amazonian vegetational patterns as an analog, an increase of at least 1 km would be necessary to influence equatorial climate and to cause major disruptions in plant distribution and composition (Colinvaux et al., 1996). Finally, regional climatic conditions do not become more seasonal simply due to elevation. As discussed in Section 7.1, there are many locations in the modern world where wetlands, including peat swamps, occur at various elevations, including within mountainous areas, so long as a favorable climate exists. Take the British moorlands in the northern temperate zone, for example, where peat covers steep terrain, the effects of drainage being overcome by persistently high rainfall and low evapotranspiration. In tropical areas, swamps, some extensive, also are known in central Congo (Lawson et al., 2015; Dargie et al., 2017, 2018), and in the interiors of Western Malaysia (Wüst and Bustin, 2001, 2004) and Sumatra (Flenley and Butler, 2001); even elevated terrain in the vicinity of these peat swamps is covered by dense rainforest.

Based on these records from the modern world, we consider that a very slow increase in topographic heterogeneity is a highly improbable mechanism to explain the "drying out" of wetland habitats, or to cause the extinction of plant populations during the late Paleozoic (Falcon-Lang et al., 2018). So long as there remained elevated areas where the climate was suitable for wetland plants to live and reproduce, the wetland biome would have persisted in tropical Pangea. Indeed, thick peats (now mineable coals) accumulated within the Variscan and other mountainous regions of Pangea during the Late Pennsylvanian (see reviews of Opluštil and Cleal, 2007; Cleal et al., 2009; Wagner and Álvarez-Vázquez, 2010; Opluštil et al., 2013b, 2016b, 2017a), well after the major extinction event, indicating that there were elevated areas where the climate was compatible with the development of organic deposits of considerable extent and thickness. Furthermore, numerous Upper Pennsylvanian wetland floral assemblages have been documented from areas of Europe within the broadly defined Variscan realm, and it is noteworthy that drought-tolerant taxa are absent in many of these taphocoenoses, despite being deposited directly adjacent to upland settings. Accordingly, we argue that simple increases in slope, aspect, and elevation would not, on their own, have created uniform "drought" over an area as vast as the Variscan mountain belt.

If orogenesis were responsible for the extinction of a large component of the Middle Pennsylvanian wetland flora in east-central Pangea (present-day Europe), what caused the extinction of the same wetland taxa in western parts of Pangea (present-day USA), where

similar mountain building did not occur? Cleal et al. (2011: p. 9) suggested that the floristic reorganization event at the traditional Desmoinesian-Missourian boundary in the USA "[...] *is merely the culmination of an extended process that gradually rolled-out across Euramerica between Duckmantian and Cantabrian times.*" This is not, however, a mechanistic, biologically meaningful explanation. Furthermore, palynological evidence suggests that the extinction was time transgressive, beginning in western Pangea and progressing eastward into the European parts of Pangea (Peppers, 1996), consistent with a general shift to drier conditions from west to east across tropical latitudes (Schutter and Heckel, 1985; Cecil et al., 2003a; Tabor and Poulsen, 2008; DiMichele et al., 2011). Such congruence of climatic and biologic patterns would be unexpected if Variscan tectonism initiated widespread extinctions that, by some unidentified mechanism, spread westward across the remainder of the Pangean continent, all the way to the Panthalassan coast, but not eastward to Cathaysia, where broadly comparable wetland floras persisted well into the Permian (Hilton and Cleal, 2007; Wang et al., 2012).

7.5. Distribution of late Paleozoic biomes in time and space: an updated "climate model"

Drawing on the body of evidence and discussions provided in this review, we present a schematic illustration (Fig. 10, legend on Fig. 11) that demonstrates how the wetland and dryland biomes tracked the various climate zones that existed in tropical Pangea during the late Paleozoic. Due to the figure's complexity – a reflection of the dynamism of plant distribution in time and space – we provide fuller explanations here, rather than in an extended figure caption.

The horizontal axis shows the lateral distribution of different climate zones and their corresponding vegetational biomes. Basinal lowlands are situated on the left, and increasingly distant extrabasinal regions are shown towards the right; we emphasize that the distance between these landscape positions could be 100s to 1000s of kilometers. Climatic conditions are wettest on the left, and become increasingly moisture-stressed towards the right. The large climate icons on the left side represent the climate mode in the basinal lowlands for each panel, whereas smaller climate icons in the upper part of each panel demonstrate the change to more moisture-stressed conditions towards the right. The long-term (10^6-year) burial and preservation of identifiable plant fossils is most likely to occur in subsiding depositional basins, indicated as the "preservation window" (pink rectangle) in basinal lowland positions on the left side of each panel. Although other biomes and climate zones existed contemporaneously in increasingly distant extrabasinal habitats, their landscape position

outside of the "preservation window" negated long-term preservation potential. We reiterate the point that the lateral shifts between various climate states and plant biomes occurred over regional- to continent-scale gradients, similar to the progressive drying that existed from east to west between west-central and western Pangea (present-day USA) during the late Paleozoic.

On the vertical axis, the distribution of vegetation under different climate states is given for three broad time slices: Early/Middle Pennsylvanian, Late Pennsylvanian, and early Permian. To demonstrate the stepwise aridification of the Euramerican tropics during the late Paleozoic, the spectrum of climate zones in basinal lowland positions (large climate icons) in each time slice trends towards progressively drier conditions through time: Early/Middle Pennsylvanian (three panels: perhumid, humid, and subhumid modes), Late Pennsylvanian (three panels: humid, subhumid, and semiarid modes), and early Permian (two panels: subhumid and semiarid modes) (see Table 1 for definitions of each climate mode). Thus, for each broad time slice, the panels record different potential scenarios for how the climate zones and corresponding biomes were distributed across a hypothetical regional- or continent-scale landscape. The panel that was "relevant" at any point in time depended on the prevailing climate mode in the basinal lowlands, and recurred cyclically as the climate oscillated in tandem with glacial-interglacial phases that operated at various time scales.

The landscape surface only shows minimal topographical differences and intentionally has been maintained at the same elevation. Displaying the landscape in this manner stresses the crucial point that the lateral distribution of plant biomes was controlled by the climatic conditions of a region, rather than having been determined by slope aspect and the drainage effects called for in the "upland model". Although mountainous and other elevated regions obviously existed over continent-scale distances in tropical Pangea, such upland settings hosted whatever vegetational biomes were adapted to the local climatic conditions. As in the modern tropics, elevated habitats were just as likely to be occupied by the wetland biome, to the exclusion of the dryland biome, under a (per)humid climate mode.

We recognize four vegetational biomes (one wetland and three dryland) in tropical Euramerica during the Pennsylvanian and early Permian. The diverse wetland biome (Biome 1) is here divided into three subbiomes, all of which drew from a common taxonomic pool, but which contained different proportions of the same families, genera, and/or species. Ombrotrophic (domed) peat swamps (Subbiome 1a) formed under a perhumid climate, were characterized by sub-arborescent lycopsids and diverse ferns, and were most common in the Early to Middle Pennsylvanian. Rheotrophic (planar) peat swamps (Subbiome 1b) mostly

accumulated under humid climates. These swamps were dominated by arborescent lycopsids (Early to Middle Pennsylvanian) or tree ferns (Upper Pennsylvanian), but also included sub-arborescent lycopsids, sphenopsids, diverse ferns, pteridosperms, and low-statured "wetland" cordaitaleans. Clastic swamps and associated clastic wetlands (Subbiome 1c) were most prevalent under subhumid to humid climate modes, and, being characterized by varying degrees of seasonality, acted as a floristic transition between the wetland and dryland biomes. This very diverse biome included various lycopsids, sphenopsids, ferns, pteridosperms, and cordaitaleans, and is represented in the vast majority of upper Paleozoic macrofloral assemblages that are preserved as adpressions.

Of the three dryland biomes, forests dominated by gigantic "dryland" cordaitaleans (Biome 2) were on the wettest end of the spectrum. These forests thrived under conditions of strongly seasonal precipitation in subhumid to semiarid climates, particularly during the Early to Middle Pennsylvanian. Associated understorey plants included pteridosperms and several taxa of enigmatic affinity (e.g., *Megalopteris*, *Lesleya*, *Taeniopteris*, and diverse putative progymnosperms), depending on the time interval involved. Forests dominated by walchian conifers (Biome 3) also existed under strongly seasonal conditions in subhumid to semiarid climates, and appeared in basinal lowland settings with increasing frequency in the Late Pennsylvanian and Permian. This biome also was characterized by medullosalean pteridosperms, several peltasperms (e.g., *Autunia*, *Supaia*), taeniopterids, and unusual progymnospermous plants. On the driest end of the spectrum, forests dominated by voltzian conifers (Biome 4) may have existed in semiarid to arid climate zones during the latest Pennsylvanian and Permian. Associated taxa included diverse peltasperms, gigantopterids, and cycadophytes, many of which had a "late Permian to Mesozoic" aspect. Although this biome may have existed somewhere "out there" in extrabasinal habitats since the Late Pennsylvanian, only under the most moisture-stressed conditions did these derived taxa make very rare appearances in basinal lowlands in the early to middle Permian (DiMichele et al., 2001b, 2004b; Looy, 2007; Looy and Stevenson, 2014; Falcon-Lang et al., 2015b; Forte et al., 2017).

With regard to "mixed" assemblages, the subject of this review, the illustration demonstrates how wetland vegetation existed in localized patches within the matrix of drought-tolerant taxa in each of the dryland biomes. The most frequently encountered wetland plants in the dryland biomes included calamitaleans and tree ferns, although a subset of medullosalean pteridosperms may also have been present, together with rare lycopsids (especially *Sigillaria*) and sphenophylls. The scattered wetland habitats, such as riparian

corridors and the margins of lakes and estuaries, provided substrates that ranged from permanently waterlogged to intermittently damp, depending on the background climate mode, and acted as restricted "waterholes" in landscapes that experienced seasonal moisture deficit. Due to the taphonomic megabias towards vegetation from more poorly drained landforms, where deposition, burial, and short-term preservation were possible, these wetland elements frequently are over-represented in "mixed" assemblages, despite being relatively rare components of the dryland biomes.

Integrating these concepts, the "climate model" in Fig. 10 demonstrates how the various late Paleozoic plant biomes tracked climate through space and time. When conditions were on the wet end of the climate spectrum in each time slice, one or more of the wettest available (sub)biomes may have been situated in the "preservation window" in the basinal lowlands, whereas increasingly more dryland biomes were pushed far out into extrabasinal habitats, where there was no preservation potential. As the basinal lowlands experienced increasingly drier conditions, biomes on the drier end of the climate spectrum expanded basinward into the "preservation window", with wetland vegetation becoming increasingly restricted to scattered patches on an otherwise seasonally dry landscape, resulting in "mixed" assemblages. The rhythmic expansion and contraction of these wetland and dryland biomes recorded the dynamism of climatic oscillations in tropical Pangea, which were intricately linked to glacial-interglacial cycles that occurred at variable frequencies during the late Paleozoic.

8. Concluding remarks

The integration of data from the plant-fossil record and observations of Pleistocene and Holocene plant distribution indicate that floristic composition is a reliable indicator of climate at a variety of spatial and temporal scales. For late Paleozoic plant taxa, the correlation of species, genera and even higher order lineages with particular climatic centroids has been established over almost two centuries of investigation, and has involved repeated observations of linkages between independent environmental indicators, the composition of floral assemblages, and physiological attributes of the plant fossils themselves. Given the restrictions that climate places on plant distribution, we conclude that the presence of fossil-taxa typical of moisture-stressed habitats within a macrofloral assemblage dictates that some degree of climatic seasonality characterized the broader regional landscape. This is the case even if a macrofloral assemblage is dominated by wetland elements, but includes at least some drought-tolerant taxa. Furthermore, the notion that long-distant transport is the default mechanism to explain the presence of mesomorphic and xeromorphic plant taxa in floral

assemblages is patently incorrect. Many fossil assemblages that contain such drought-tolerant plants, whether rare or dominant elements, are located many hundreds of kilometers from any elevated habitat that would qualify as an upland. Our opinion does not exclude the possibility that many of these plants also occupied elevated habitats during the late Paleozoic; they had to have lived somewhere when basinal lowlands were dominated by vast peat-accumulating swamps and other wetland habitats during climatically wet intervals. However, rather than being exclusive to upland habitats, we assert that the dryland biome repeatedly dispersed into basinal lowlands, in concert with glacial-interglacial rhythms, where its members thrived equally well when climatic and edaphic conditions were suitable.

Finally, we consider it untenable that tectonism and associated changes in elevation and sediment output were the main factors responsible for the marked reduction in the areal extent of peat swamps near the Middle to Late Pennsylvanian boundary, or for the coincident changes in dominance and diversity patterns observed in the peat-forming floras. Given that the rate of mountain building is significantly slower than the rate of plant dispersal and establishment, and that wetlands existed in elevated habitats well into the Late Pennsylvanian, just as they do today where suitable climates prevail, a very slow increase in altitude and topographic heterogeneity would not have created uniformly dry conditions over an area as vast as the Variscan Mountains. To quote Pausas and Austin (2001: p. 153): "*To advance in understanding species richness patterns along environmental gradients, we emphasise the importance of* […] *using variables that are related to the growth of plants (latitudinal and altitudinal gradients have no direct process impact on plant growth).*" This observation should have been as true in the late Paleozoic as it is today, notwithstanding the possibility that plant physiologies differed radically from those of modern plants, for which there is neither morphological nor geochemical evidence.

References

Abbott, L.D., Silver, E.A., Anderson, R.S., Haig, D., Small, E., Galewsky, J., Sliter, W., 1997. Measurement of tectonic surface uplift rate in a young collisional mountain belt. Nature 385, 501–507.

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Diversity and Distributions 16, 476–487.

Allen, J.P., Fielding, C.R., Gibling, M.R., Rygel, M.C., 2011. Fluvial response to paleoequatorial climate fluctuations during the late Paleozoic ice age. Geological Society of America Bulletin 123, 1524–1538.

Alonso, J.L., 1989. Fold reactivation involving angular unconformable sequences: theoretical analysis and natural examples from the Cantabrian Zone (Northwest Spain). Tectonophysics 170, 57–77.

Anderson, D., Goudie, A., Parker, A., 2013. Global Environments Through the Quaternary: Exploring Environmental Change (Second Edition). Oxford University Press, Oxford.

Anshari, G., Kershaw, A.P., Van der Kaars, S., 2001. A Late Pleistocene and Holocene pollen and charcoal record from peat swamp forest, Lake Sentarum Wildlife Reserve, West Kalimantan, Indonesia. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 213–228.

Archer, A.W., Calder, J.H., Gibling, M.R., Naylor, R.D., Reid, D.R., Wightman, W.G., 1995. Invertebrate trace fossils and agglutinated foraminifera as indicators of marine influences within the classic Carboniferous section at Joggins, Nova Scotia, Canada. Canadian Journal of Earth Sciences 32, 2027–2039.

Archer, A.W., Elrick, S., Nelson, W.J., DiMichele, W.A., 2016. Cataclysmic burial of Pennsylvanian Period coal swamps in the Illinois Basin: Hypertidal sedimentation during Gondwanan glacial melt-water pulses. In: Tessier, B., Reynaud, J.-Y. (Eds.), Contributions to Modern and Ancient Tidal Sedimentology: Proceedings of the Tidalites 2012 Conference. International Association of Sedimentologists Special Publication 47, pp. 217–231.

Arnold, C.A., 1941. Some Paleozoic plants from central Colorado and their stratigraphic significance. Contributions from the Museum of Paleontology, University of Michigan 6, 59–70.

Ball, J., 1879. On the origin of the flora of the European Alps. Proceedings of the Royal Geographical Society and Monthly Record of Geography 1, 564–589.

Barca, S., Costamagna, L.G., 2003. The Upper Carboniferous S. Giorgio succession (Iglesiente, SW Sardinia): stratigraphy, depositional setting and evolution of the late to post-Variscan molassic basin. Bollettino della Società Geologica Italiana, Volume Speciale 2, 89–98.

Barnett, A.A., Silva, W.S., Shaw, P.J., Ramsay, P.M., 2015. Inundation duration and vertical vegetation zonation: a preliminary description of the vegetation and structuring factors in borokotóh (hummock igapó), an overlooked, high-diversity, Amazonian vegetation association. Nordic Journal of Botany 33, 601–614.

Barrick, J.E., Lucas, S.G., Krainer, K., 2013. Conodonts of the Atrasado Formation (uppermost Middle to Upper Pennsylvanian), Cerros de Amado region, central New Mexico, U.S.A. In: Lucas, S.G., Nelson, W.J., DiMichele, W.A., Speilmann, J.A., Krainer, K., Barrick, J.E., Elrick, S., Voigt, S. (Eds.), The Carboniferous-Permian Transition in Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, pp. 239–252.

Barthel, M., 1977. Die Gattung *Dicranophyllum* Gr. Eury in den varistischen Innensenken der DDR. Hallesches Jahrbuch für Geowissenschaften 2, 73–86.

Barthel, M., Bettag, E., Noll, R., 1998. *Dicranophyllum hallei* Remy & Remy im obern Rotliegend. Veröffentlichungen des Museums für Naturkunde Chemnitz 21, 5–20.

Barthel, M., Noll, R., 1999. On the growth habit of *Dicranophyllum hallei* Remy et Remy. Veröffentlichungen Naturhistorisches Museum Schleusingen 14, 59–64.

Bashforth, A.R., 2005. Late Carboniferous (Bolsovian) macroflora from the Barachois Group, Bay St. George Basin, southwestern Newfoundland, Canada. Palaeontographica Canadiana 24, 1–123.

Bashforth, A.R., Cleal, C.J., Gibling, M.R., Falcon-Lang, H.R., Miller, R.F., 2014. Paleoecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada). Review of Palaeobotany and Palynology 200, 229–263.

Bashforth, A.R., DiMichele, W.A., Eble, C.F., Nelson, W.J., 2016a. Dryland vegetation from the Middle Pennsylvanian of Indiana (Illinois Basin): the dryland biome in glacioeustatic, paleobiogeographic, and paleoecologic context. Journal of Paleontology 80, 785–814.

Bashforth, A.R., DiMichele, W.A., Eble, C.F., Nelson, W.J., 2016b. A Middle Pennsylvanian macrofloral assemblage from wetland deposits in Indiana (Illinois Basin): a taxonomic contribution with biostratigraphic, paleobiogeographic, and paleoecologic implications. Journal of Paleontology 80, 589–631.

Bashforth, A.R., Drábková, J., Opluštil, S., Gibling, M.R., Falcon-Lang, H.J., 2011. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic). Review of Palaeobotany and Palynology 163, 153–189.

Bashforth, A.R., Falcon-Lang, H.J., Gibling, M.R., 2010. Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 292, 367–390.

Bashforth, A.R., Nelson, W.J., 2015. A Middle Pennsylvanian macrofloral assemblage from below the Rock Island (No. 1) Coal Member, Illinois: Resolving the Bolsovian–Asturian boundary in the Illinois Basin. Review of Palaeobotany and Palynology 222, 67–83.

Bateman, R.M., 1991. Palaeoecology. In: Cleal, C.J. (Ed.), Plant Fossils in Geological Investigation: The Palaeozoic. Ellis-Horwood, Chichester, pp. 34–116.

Becq-Giraudon, J.-F., Montenat, C., Van den Driessche, J., 1996. Hercynian high-altitude phenomena in the French Massif Central: tectonic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 122, 227–241.

Beerbower, J.R., 1964. Cyclothems and cyclic depositional mechanisms in alluvial plain sedimentation. Kansas Geological Survey Bulletin 169, 31–42.

Behrensmeyer, A.K., Kidwell, S.M., Gastaldo, R.A., 2000. Taphonomy and paleobiology. Paleobiology 46 (No. 4, Suppl.), 103–147.

Bek, J., Opluštil, S., Drábková, J., Pšenička, J., 2015. The sub-arborescent lycopsid *Omphalophloios feistmantelii* (O. Feistmantel) comb. nov. emend. from the Middle Pennsylvanian of the Czech Republic. Bulletin of Geosciences 90, 227–279.

Bek, J., Šimůnek, Z., 2005. Revision of the cone genus *Discinites* from the Carboniferous continental basins of Bohemia. Palaeontology 48, 1377–1397.

Belt, E.S., Heckel, P.H., Lentz, L.J., Bragonier, W.A., Lyons, T.W., 2011. Record of glacial–eustatic sea-level fluctuations in complex middle to late Pennsylvanian facies in the Northern Appalachian Basin and relation to similar events in the Midcontinent basin. Sedimentary Geology 238, 79–100.

Birgenheier, L.P., Fielding, C.R., Rygel, M.C., Frank, T.D., Roberts, J., 2009. Evidence for dynamic climate change on sub-10^6-year scales from the late Paleozoic glacial record, Tamworth Belt, New South Wales, Australia. Journal of Sedimentary Research 79, 56–82.

Blakey, R.C., 2007. Carboniferous–Permian paleogeography of the assembly of Pangaea. In: Wong, Th.E. (Ed.), Proceedings of the 15th International Congress on Carboniferous and Permian Stratigraphy, Utrecht 2003, pp. 443–456.

Bless, M.J.M., Loboziak, S., Streel, M., 1977. An upper Westphalian C 'hinterland' microflora from the Haaksbergen-1 Borehole (Netherlands). Mededelingen Rijks Geologische Dienst 28, 135–147.

Blomenkemper, P., Kerp, H., Abu Hamad, A., DiMichele, W.A., Bomfleur, B., 2018. A hidden cradle of plant evolution in Permian tropical lowlands. Science 362, 1414–1416.

Bonacci, O., 2015. Surface waters and groundwater in karst. In: Stevanović, Z. (Ed.), Karst Aquifers – Characterization and Engineering. Professional Practice in Earth Sciences, Springer, Switzerland, pp. 149–169.

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. New Phytologist 165, 525–538.

Boy, J.A., Schindler, T., 2000. Ökostratigraphische Bioevents im Grenzbereich Stephanium/Autunium (höchstes Karbon) des Saar-Nahe-Beckens (SW-Deutschland) und benachbarter Gebiete. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 216, 89–152.

Bristol, H.M., Howard, R.H., 1971. Paleogeographic map of the sub-Pennsylvanian Chesterian (Upper Mississippian) surface in the Illinois Basin. Illinois State Geological Survey Circular 458, 1–14.

Broutin, J., Doubinger, J., Farjanel, G., Freytet, F., Kerp, H., Langiaux, J., Lebreton, M.-L., Sebban, S., Satta, S., 1990. Le renouvellement des flores au passage Carbonifère Permien : approches stratigraphique, biologique, sédimentologique. Comptes Rendus de l'Académie des Sciences, Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre 311, 1563–1569.

Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. Review of Palaeobotany and Palynology 58, 5–32.

Burnham, R.J., 1993. Reconstructing richness in the plant fossil record. Palaios 8, 376–384.

Busch, R.M., Bogina, M.A., Clark, M.H., 1988. Genetic stratigraphy of fossil localities. In: Mapes, G., Mapes, R. (Eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6, pp. 59–65.

Bush, M., Flenley, M., Gosling, W., 2011. Tropical Rainforest Responses to Climate Change. Springer-Verlag, Berlin.

Calder, J.H., 1994. The impact of climate change, tectonism and hydrology on the formation of Carboniferous tropical intermontane mires: the Springhill coalfield, Cumberland Basin, Nova Scotia. Palaeogeography, Palaeoclimatology, Palaeoecology 106, 323–351.

Calder, J.H., 1998. The Carboniferous evolution of Nova Scotia. In: Blundell, D., Scott, A.C. (Eds.), Lyell: The Past is the Key to the Present. Geological Society Special Publications 143, pp. 296–331.

Calder, J.H., Gibling, M.R., Eble, C.F., Scott, A.C., MacNeil, D.J., 1996. The Westphalian D fossil lepidodendrid forest at Table Head, Sydney Basin, Nova Scotia: Sedimentology, paleoecology and floral response to changing edaphic conditions. International Journal of Coal Geology 31, 277–313.

Calder, J.H., Gibling, M.R., Scott, A.C., Davies, S.J., Hebert, B.L., 2006. A fossil lycopsid forest succession in the classic Joggins section of Nova Scotia: Paleoecology of a disturbance-prone Pennsylvanian wetland. In: Greb, S.F., DiMichele, W.A. (Eds.), Wetlands through Time. Geological Society of America Special Paper 399, pp. 169–195.

Carpenter, D., Falcon-Lang, H.J., Benton, M.J., Grey, M., 2015. Early Pennsylvanian (Langsettian) fish assemblages from the Joggins Formation, Canada, and their implications for palaeoecology and palaeogeography. Palaeontology 68, 661–690.

Cather, S.M., Chapin, C.E., Kelley, S.A., 2012. Diachronous episodes of Cenozoic erosion in

southwestern North America and their relationship to surface uplift, paleoclimate, paleodrainage, and paleoaltimetry. Geosphere 8, 1177–1206.

Cecil, C.B., 1990. Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks. Geology 18, 533–536.

Cecil, C.B., 2003. The concept of autocyclic and allocyclic controls on sedimentation and stratigraphy, emphasizing the climatic variable. In: Cecil, C.B., Edgar, N.T. (Eds.), Climate Controls on Stratigraphy. SEPM (Society for Sedimentary Geology) Special Publication 77, pp. 13–20.

Cecil, C.B., 2013. An overview and interpretation of autocyclic and allocyclic processes and the accumulation of strata during the Pennsylvanian–Permian transition in the central Appalachian Basin, USA. International Journal of Coal Geology 119, 21–31.

Cecil, C.B., DiMichele, W.A., Elrick, S.D., 2014. Middle and Late Pennsylvanian cyclothems, American Midcontinent: Ice-age environmental changes and terrestrial biotic dynamics. Comptes Rendus Geoscience 346, 159–168.

Cecil, C.B., Dulong, F.T., 2003. Precipitation models for sediment supply in warm climates. In: Cecil, C.B., Edgar, N.T. (Eds.), Climate Controls on Stratigraphy. SEPM (Society for Sedimentary Geology) Special Publication 77, pp. 21–28.

Cecil, C.B., Dulong, F.T., Cobb, J.C., Supardi, 1993. Allogenic and autogenic controls on sedimentation in the central Sumatra basins as an analogue for Pennsylvanian coal-bearing strata in the Appalachian basin. In: Cobb, J.C., Cecil, C.B. (Eds.), Modern and Ancient Coal-Forming Environments. Geological Society of America Special Paper 286, pp. 3–22.

Cecil, C.B., Dulong, F.T., Harris, R.A., Cobb, J.C., Gluskoter, H.G., Nugroho, H., 2003b. Observations on climate and sediment discharge in selected tropical rivers, Indonesia. In: Cecil, C.B., Edgar, N.T. (Eds.), Climate Controls on Stratigraphy. SEPM (Society for Sedimentary Geology) Special Publication 77, pp. 29–50.

Cecil, C.B., Dulong, F.T., West, R.R., Stamm, R., Wardlaw, B.A., Edgar, N.T., 2003a. Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothem in North America. In: Cecil, C.B., Edgar, N.T. (Eds.), Climate Controls on Stratigraphy. SEPM (Society for Sedimentary Geology) Special Publication 77, pp. 151–182.

Cecil, C.B., Stanton, R.W., Neuzeil, S.G., Dulong, F.T., Ruppert, L.F., Pierce, B.S., 1985. Paleoclimate controls on late Paleozoic sedimentation and peat formation in the central Appalachian basin (U.S.A.). International Journal of Coal Geology 5, 195–230.

Chaloner, W.G., 1958. The Carboniferous upland flora. Geological Magazine 95, 261–262.

Chaney, D.S., DiMichele, W.A., 2007. Paleobotany of the classic redbeds (Clear Fork Group – Early Permian) of north central Texas. In: Wong, Th.E. (Ed.), Proceedings of the 15th International Congress on Carboniferous and Permian Stratigraphy, Utrecht 2003), pp. 357–366.

Chaney, D.S., Mamay, S.H., DiMichele, W.A., Kerp, H., 2009. *Auritifolia* gen. nov., probable seed plant foliage with comioid affinities from the Early Permian of Texas, U.S.A. International Journal of Plant Sciences 170, 247–266.

Chavez, S.P., Takahashi, K., 2017. Orographic rainfall hot spots in the Andes-Amazon transition according to the TRMM precipitation radar and in situ data. Journal of Geophysical Research - Atmospheres 122, 5870–5882.

Chen, J., Montañez, I.P., Qi, Y., Shen, S., Wang, X., 2018. Strontium and carbon isotopic evidence for decoupling of pCO$_2$ from continental weathering at the apex of the late Paleozoic glaciation. Geology 46, 395–398.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A.W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology 22, 2329–2352.

Cleal, C.J., 2008. Palaeofloristics of Middle Pennsylvanian medullosaleans in Variscan Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 164–180.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., 2011. Pennsylvanian vegetation and climate in tropical Variscan Euramerica. Episodes 34, 3–12.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., Abbink, O.A., Bek, J., Dimitrova, T., Drábková, J., Hartkopf-Fröder, C., Van Hoof, T., Kędzior, A., Jarzembowski, E., Jasper, K., Libertín, M., McLean, D., Oliwkiewicz-Miklasinska, M., Pšenička, J., Ptak, B., Schneider, J.W., Schultka, S., Šimůnek, Z., Uhl, D., Waksmundzka, M.I., Van Waveren, I., Zodrow, E.L., 2009. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. Netherlands Journal of Geosciences 88, 181–278.

Cleal, C.J., Scanu, G.G., Buosi, C., Pittau, P., Kustatscher, E., 2016. Middle Pennsylvanian vegetation of the San Giorgio Basin, southern Sardinia (Italy). Geological Magazine 154, 1155–1170.

Cleal, C.J., Thomas, B.A., 1999. Tectonics, tropical forest destruction and global warming in the Late Palaeozoic. Acta Palaeobotanica, Suppl. 2, 17–19.

Cleal, C.J., Thomas, B.A., 2005. Palaeozoic tropical rainforests and their effect on global climates: is the past the key to the present? Geobiology 3, 13–31.

Cocozza, T., 1967. Il Permo-Carbonifero del bacino di San Giorgio (Iglesiente, Sardegna sud-occidentale). Memorie della Società Geologica Italiana 6, 607–642.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. Quaternary Science Reviews 19, 141–169.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: forests and cooling in glacial times. Science 274, 85–88.

Correia, P., Sá, A.A., Murphy, J.B., Šimůnek, Z., Flores, D., 2016. *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a dryland megaflora from the Variscan orogen, northwestern Portugal. Canadian Journal of Earth Sciences 53, 883–895.

Cridland, A.A., Morris, J.E., 1960. *Spermopteris*, a new genus of pteridosperms from the Upper Pennsylvanian Series of Kansas. American Journal of Botany 47, 855–859.

Cridland, A.A., Morris, J.E., 1963. *Taeniopteris*, *Walchia* and *Dichophyllum* in the Pennsylvanian System of Kansas. University of Kansas Science Bulletin 44, 71–85.

Crowley, T.J., Baum, S.K., 1992. Modeling late Paleozoic glaciation. Geology 20, 507–510.

Cunningham, C.R., Dickson, E.D., III, 1996. Distributions of Kansas Permo-Carboniferous vertebrate assemblages as a function of wet and dry seasons. Transactions of the Kansas Academy of Science 99, 16–28.

Cunningham, C.R., Feldman, H.R., Franseen, E.K., Gastaldo, R.A., Mapes, G., Maples, C.G., Schultze, H.-P., 1993. The Upper Carboniferous Hamilton Fossil-Lagerstätte in Kansas: a valley-fill, tidally influenced deposit. Lethaia 26, 225–236.

Dargie, G.C., Lawson, I.T., Rayden, T.J., Miles, L., Mitchard, E.T.A, Page, S.E., Bocko, Y.E., Ifo, S.A., Lewis, S.L., 2018. Congo Basin peatlands: threats and conservation priorities. Mitigation and Adaptation Strategies for Global Change 24, 669–686.

Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T.A., Page, S.E., Bocko, Y.E., Ifo, S.A., 2017. Age, extent and carbon storage of the central Congo Basin peatland complex. Nature 542, 86–90.

Davydov, V., 2014. Warm water benthic foraminifera document the Pennsylvanian–Permian warming and cooling events – The record from the Western Pangea tropical shelves. Palaeogeography, Palaeoclimatology, Palaeoecology 414, 284–295.

Davydov, V.I., Crowley, J.L., Schmitz, M.D., Poletaev, V.I., 2010. High-precision U-Pb zircon age calibration of the global Carboniferous time scale and Milankovitch band cyclicity in the Donets Basin, eastern Ukraine. Geochemistry Geophysics Geosystems 11, Q0AA04.

Davydov, V.I., Glenister, B.F., Spinosa, C., Ritter, S.M., Chernykh, V.V., Wardlaw, B.R., Snyder, W.S., 1998. Proposal of Aidaralash as Global Stratotype Section and Point (GSSP) for base of the Permian System. Episodes 21, 11–18.

Davydov, V.I., Korn, D., Schmitz, M.D., Gradstein, F.M., Hammer, Ø., 2012. The Carboniferous Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), The Geologic Time Scale 2012. Elsevier, Amsterdam, pp. 603–651.

Del Rio, M., 1973. Palinologia di un livello "permocarbonifero" do San Giorgio (Iglesiente, Sardegna sudoccidentale). Bollettino della Società Geologica Italiana 93, 113–124.

Del Rio, M., Pillola, G.L., Muntoni, F., 2002. The Upper Carboniferous of the San Giorgio basin. In: Cherchi, A., Corradini, C., Putzu, T. (Eds.), Sardinia Field Trip – Palaeontology and Stratigraphy. Rendiconti della Società Paleontologica Italiana 1, pp. 223–229.

Del Rio, M., Pittau, P., 1999. The Upper Carboniferous of the San Giorgio Basin. In: Cassinis, G., Cortesogno, L., Gaggero, L., Pittau, P., Ronchi, A., Sarria, E. (Eds.), Late Palaeozoic Continental Basins of Sardinia. Field Trip Guidebook 15–18 September 1999, Earth Science Department, University of Pavia, Pavia, pp. 37–39.

De Voto, R.H., Peel, F.A., Pierce, W.H., 1971. Pennsylvanian and Permian stratigraphy, tectonism, and history, northern Sangre de Cristo Range, Colorado. In: James, H.L. (Ed.), San Luis Basin (Colorado). New Mexico Geological Society Guidebook, 22nd Annual Fall Field Conference, pp. 141–163.

Dewey, J.F., Burke, K.C.A., 1973. Tibetan, Variscan, and Precambrian basement reactivation: products of continental collision. The Journal of Geology 81, 683–692.

DiMichele, W.A., 2014. Wetland-dryland vegetational dynamics in the Pennsylvanian ice age tropics. International Journal of Plant Sciences 175, 123–164.

DiMichele, W.A., Aronson, R.B., 1992. The Pennsylvanian–Permian vegetational transition: a terrestrial analog to the onshore–offshore hypothesis. Evolution 46, 807–824.

DiMichele, W.A., Bashforth, A.R., Eble, C.F., Nelson, W.J., 2016. A Middle Pennsylvanian (early Asturian) tropical dry forest, Atokan-Desmoinesian boundary, Illinois Basin, USA. Spanish Journal of Palaeontology 31, 41–84.

DiMichele, W.A., Bashforth, A.R., Falcon-Lang, H.J., Lucas, S.G., 2020. Uplands, lowlands, and climate: Taphonomic megabiases and the apparent rise of a xeromorphic, drought-tolerant flora during the Pennsylvanian-Permian transition. Palaeogeography, Palaeoclimatology, Palaeoecology 559, 109965.

DiMichele, W.A., Cecil, C.B., Chaney, D.S., Elrick, S.D., Lucas, S.G., Lupia, R., Nelson, W.J., Tabor, N.J., 2011. Pennsylvanian-Permian vegetational changes in tropical Euramerica. In: Harper, J.A. (Ed.), Geology of the Pennsylvanian–Permian in the Dunkard Basin. Guidebook, 76th Annual Field Conference of Pennsylvania Geologists, pp. 60–102.

DiMichele, W.A., Cecil, C.B., Chaney, D.S., Elrick, S.D., Nelson, W.J., 2014. Fossil floras from the Pennsylvanian-Permian Cutler Group of southeastern Utah. In: MacLean, J.S., Biek, R.F., Huntoon, J.E. (Eds.), Geology of Utah's Far South. Utah Geological Association Publication 43, pp. 491–504.

DiMichele, W.A., Cecil, C.B., Montañez, I.P., Falcon-Lang, H.J., 2010a. Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. International Journal of Coal Geology 83, 329–344.

DiMichele, W.A., Chaney, D.S., 2005. Pennsylvanian-Permian fossil floras from the Cutler Group, Cañon del Cobre and Arroyo del Agua areas, in northern New Mexico. In: Lucas, S.G., Zeigler, K.E., Spielmann, J.A. (Eds.), The Permian of Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 31, pp. 26–33.

DiMichele, W.A., Chaney, D.S., Kerp, H., Lucas, S.G., 2010b. Late Pennsylvanian floras in western equatorial Pangea, Cañon del Cobre, New Mexico. In: Lucas, S.G., Schneider, J.W., Speilmann, J.A. (Eds.), Carboniferous-Permian Transition in Cañon del Cobre, northern New Mexico. New Mexico Museum of Natural History and Science Bulletin 49, pp. 75–113.

DiMichele, W.A., Chaney, D.S., Lucas, S.G., Kerp, H., Voigt, S., 2013b. Flora of the Lower Permian Abo Formation redbeds, western equatorial Pangea, New Mexico. In: Lucas, S.G., Nelson, W.J., DiMichele, W.A., Speilmann, J.A., Krainer, K., Barrick, J.E., Elrick, S., Voigt, S. (Eds.), The Carboniferous-Permian Transition in Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, pp. 265–287.

DiMichele, W.A., Chaney, D.S., Nelson, W.J., Lucas, S.G., Looy, C.V., Quick, K., Jun, W., 2007. A low diversity, seasonal tropical landscape dominated by conifers and

peltasperms: Early Permian Abo Formation, New Mexico. Review of Palaeobotany and Palynology 145, 249–273.

DiMichele, W.A., Elrick, S.D., Nelson, W.J., 2017a. Vegetational zonation in a swamp forest, Middle Pennsylvanian, Illinois Basin, U.S.A., indicates niche differentiation in a wetland plant community. Palaeogeography, Palaeoclimatology, Palaeoecology 487, 71–92.

DiMichele, W.A., Gastaldo, R.A., 2008. Plant paleoecology in deep time. Annals of the Missouri Botanical Garden 95, 144–198.

DiMichele, W.A., Hook, R.W., Nelson, W.J., Chaney, D.S., 2004b. An unusual Middle Permian flora from the Blaine Formation (Pease River Group: Leonardian-Guadalupian Series) of King County, West Texas. Journal of Paleontology 78, 765–782.

DiMichele, W.A., Kerp, H., Chaney, D.S., 2004a. Tropical floras of the Late Pennsylvanian– Early Permian transition: Carrizo Arroyo in context. In: Lucas, S.G., Zeigler, K.E. (Eds.), Carboniferous-Permian Transition at Carrizo Arroyo, Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 25, pp. 105–109.

DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called "Paleophytic– Mesophytic" transition in equatorial Pangea – Multiple biomes and vegetational tracking of climate through geological time. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 152–163.

DiMichele, W.A., Lucas, S.G., Krainer, K., 2012. Vertebrate trackways among a stand of *Supaia* White plants on an Early Permian floodplain, New Mexico. Journal of Paleontology 86, 584–594.

DiMichele, W.A., Lucas, S.G., Looy, C.V., Kerp, H., Chaney, D.S., 2017b. Plant fossils from the Pennsylvanian–Permian transition in western Pangea, Abo Pass, New Mexico. Smithsonian Contributions to Paleobiology 99, 1–40.

DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., Nelson, W.J., 2001b. An Early Permian flora with Late Permian and Mesozoic affinities from North-Central Texas. Journal of Paleontology 75, 449–460.

DiMichele, W.A., Montañez, I.P., Poulsen, C.J., Tabor, N.J., 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. Geobiology 7, 200–226.

DiMichele, W.A., Pfefferkorn, H.W., Gastaldo, R.A., 2001a. Response of Late Carboniferous and Early Permian plant communities to climate change. Annual Review of Earth and Planetary Sciences 29, 461–487.

DiMichele, W.A., Phillips, T.L., 1977. Monocyclic *Psaronius* from the lower Pennsylvanian of the Illinois Basin. Canadian Journal of Botany 55, 2514–2524.

DiMichele, W.A., Phillips, T.L., 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 106, 39–90.

DiMichele, W.A., Phillips, T.L., 1996. Climate change, plant extinctions, and vegetational recovery during the Middle-Late Pennsylvanian transition: the case of tropical peat-forming environments in North America. In: Hart, M.L. (Ed.), Biotic Recovery from Mass Extinction Events. Geological Society Special Publications 102, pp. 201–221.

DiMichele, W.A., Phillips, T.L., Pfefferkorn, H.W., 1996. Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. Palaeogeography, Palaeoclimatology, Palaeoecology 125, 105–128.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. In: Greb, S.F., DiMichele, W.A. (Eds.), Wetlands through Time. Geological Society of America Special Paper 399, pp. 223–248.

DiMichele, W.A., Wagner, R.H., Bashforth, A.R., Álvarez-Vázquez, C., 2013a. An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. In: Lucas, S.G., Nelson, W.J., DiMichele, W.A., Speilmann, J.A., Krainer, K., Barrick, J.E., Elrick, S., Voigt, S. (Eds.), The Carboniferous-Permian Transition in Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, pp. 289–325.

Dimitrova, T.K., Cleal, C.J., Thomas, B.A., 2011. Palynological evidence for Pennsylvanian extra-basinal vegetation in Atlantic Canada. Journal of the Geological Society 168, 559–569.

Dimitrova, T.K., Zodrow, E.L., Cleal, C.J., Thomas, B.A., 2010. Palynological evidence for Pennsylvanian (Late Carboniferous) vegetation change in the Sydney Coalfield, eastern Canada. Geological Journal 45, 388–396.

Dolby, G., 1997. Palynological analysis of Carboniferous outcrop and corehole samples from the NATMAP Program, 1996 Field Season (Section 5-C. St. Peter). Geological Survey of Canada Report 96-21, 27–36.

Dolby, G., Falcon-Lang, H.J., Gibling, M.R., 2011. A conifer-dominated palynological assemblage from Pennsylvanian (late Moscovian) alluvial drylands in Atlantic Canada:

implications for the vegetation of tropical lowlands during glacial phases. Journal of the Geological Society 168, 571–584.

Doubinger, J., Vetter, P., Langiaux, J., Galtier, J., Broutin, J., 1995. La flore fossile du basin houiller de Saint-Étienne. Mémoires du Muséum National d'Histoire Naturelle 164, 1–355.

Driese, S.G., Ober, E.G., 2005. Paleopedologic and paleohydrologic records of precipitation seasonality from Early Pennsylvanian "underclay" paleosols, USA. Journal of Sedimentary Research 75, 997–1010.

Dubois, M.K., Goldstein, R.H., Hasiotis, S.T., 2012. Climate-controlled aggradation and cyclicity of continental loessic siliciclastic sediments in Asselian–Sakmarian cyclothems, Permian, Hugoton embayment, USA. Sedimentology 59, 1782–1816.

Dunn, K.A., McLean, R.J.C., Upchurch, G.R., Folk, R.L., 1997. Enhancement of leaf fossilization potential by bacterial biofilms. Geology 25, 1119–1122.

Durden, C.J., 1984a. Carboniferous and Permian entomology of western North America. Compte Rendu Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère, Washington and Champaign-Urbana 1979, 2, 81–89.

Durden, C.J., 1984b. North American provincial insect ages for the continental last half of the Carboniferous and first half of the Permian. Compte Rendu Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère, Washington and Champaign-Urbana 1979, 2, 606–612.

Dzenowski, N.B., Hembree, D.I., 2012. Examining local climate variability in the Late Pennsylvanian through paleosols: an example from the lower Conemaugh Group of southeastern Ohio, USA. Geosciences 2, 260–276.

Eagar, R.M.C., 1985. The stratigraphical and palaeoecological distribution of non-marine bivalves in the coalfields of northwest Spain. Compte Rendu Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 2, 455–476.

Eagar, R.M.C., Weir, J., 1971. Some Spanish Upper Carboniferous non-marine bivalve faunas: a preliminary statement with emphasis on facies in north-west Spain and in Britain. Trabajos de Geología 3, 87–99.

Easterday, C.R., 2004. Stratigraphy and Paleontology of Cemetery Hill (Desmoinesian–Missourian: Upper Carboniferous), Columbiana County, Eastern Ohio. M.Sc. thesis, Ohio State University (unpubl.).

Eberth, D.A., Miall, A.D., 1991. Stratigraphy, sedimentology and evolution of a vertebrate-bearing, braided to anastomosed fluvial system, Cutler Formation (Permian-Pennsylvanian), north-central New Mexico. Sedimentary Geology 72, 225–252.

Eble, C.F., 1990. A palynological transect, swamp interior to swamp margin, in the Mary Lee coal bed, Warrior Basin, Alabama. In: Gastaldo, R.A., Demko, T.M., Liu, Y. (Eds.), Carboniferous Coastal Environments and Paleocommunities of the Mary Lee Coal Zone, Marion and Walker Counties, Alabama. Geological Survey of Alabama, Tuscaloosa, pp. 65–81.

Eble, C.F., Gastaldo, R.A., Demko, T.M., Liu, Y., 1994. Coal compositional changes along a swamp interior to swamp margin transect in the Mary Lee Coal bed, Warrior Basin, Alabama, U.S.A. International Journal of Coal Geology 26, 43–62.

Elias, M.K., 1936. Late Paleozoic plants of the Midcontinent region as indicators of time and environment. Report of the 16th International Geological Congress, Washington 1933, pp. 691–700.

Elrick, M., Scott, L.A., 2010. Carbon and oxygen isotope evidence for high-frequency (10^4–10^5 yr) and My-scale glacio-eustasy in Middle Pennsylvanian cyclic carbonates (Gray Mesa Formation), central New Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology 285, 307–320.

Elrick, S.D., Nelson, W.J., Lucas, S.G., 2017. Fossil wood from Late Pennsylvanian sabkas in Socorro County, New Mexico. In: Lucas, S.G., DiMichele, W.A., Krainer, K. (Eds.), Carboniferous-Permian Transition in Socorro County, New Mexico. New Mexico Museum of Natural History and Science Bulletin 77, pp. 101–108.

Eros, J.M., Montañez, I.P., Osleger, D.A., Davydov, V.I., Nemyrovska, T.I., Poletaev, V.I., Zhykalyak, M.V., 2012. Sequence stratigraphy and onlap history of the Donets Basin, Ukraine: Insight into Carboniferous icehouse dynamics. Palaeogeography, Palaeoclimatology, Palaeoecology 313, 1–25.

Ettingshausen, C. von, 1852. Steinkohlenflora von Stradonitz in Böhmen. Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt I, 3(4), 1–18.

Falcon-Lang, H.J., 2003a. Late Carboniferous tropical dryland vegetation in an alluvial-plain setting, Joggins, Nova Scotia, Canada. Palaios 18, 197–211.

Falcon-Lang, H.J., 2003b. Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia. Journal of the Geological Society 160, 643–648.

Falcon-Lang, H.J., 2004a. Pennsylvanian tropical rain forests responded to glacial-interglacial rhythms. Geology 32, 689–692.

Falcon-Lang, H.J., 2004b. Pennsylvanian upland vegetation and its implications for the demise of the peat-forming tropical biome. Geologica Balcanica 34, 39–45.

Falcon-Lang, H.J., 2006. Vegetation ecology of Early Pennsylvanian alluvial fan and piedmont environments in southern New Brunswick, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 233, 34–50.

Falcon-Lang, H.J., Bashforth, A.R., 2004. Pennsylvanian uplands were forested by giant cordaitalean trees. Geology 32, 417–420.

Falcon-Lang, H.J., Bashforth, A.R., 2005. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. Review of Palaeobotany and Palynology 135, 223–243.

Falcon-Lang, H.J., Benton, M.J., Braddy, S.J., Davies, S.J., 2006. The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. Journal of the Geological Society 163, 561–576.

Falcon-Lang, H.J., Cleal, C.J., Pendleton, J.L., Wellman, C.H., 2012. Pennsylvanian (mid/late Bolsovian-Asturian) permineralised plant assemblages of the Pennant Sandstone Formation of southern Britain: Systematics and palaeoecology. Review of Palaeobotany and Palynology 173, 23–45.

Falcon-Lang, H.J., DiMichele, W.A., 2010. What happened to the coal forests during Pennsylvanian glacial phases? Palaios 25, 611–617.

Falcon-Lang, H.J., Heckel, P.H., DiMichele, W.A., Blake, B.M., Easterday, C.R., Eble, C.F., Elrick, S., Gastaldo, R.A., Greb, S.F., Martino, R.L., Nelson, W.J., 2011b. No major stratigraphic gap exists near the Middle–Upper Pennsylvanian (Desmoinesian–Missourian) boundary in North America. Palaios 26, 125–139.

Falcon-Lang, H.J., Jud, N.A., Nelson, W.J., DiMichele, W.A., Chaney, D.S., Lucas, S.G., 2011a. Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biomes. Geology 39, 371–374.

Falcon-Lang, H.J., Kurzawe, F., Lucas, S.G., 2014. Coniferopsid tree-trunks preserved in sabkha facies in the Permian (Sakmarian) Community Pit Formation in south-central New Mexico, U.S.A. Review of Palaeobotany and Palynology 200, 138–160.

Falcon-Lang, H.J., Kurzawe, F., Lucas, S.G., 2016. A Late Pennsylvanian coniferopsid forest in growth position, near Socorro, New Mexico, USA: Tree systematics and palaeoclimatic significance. Review of Palaeobotany and Palynology 225, 67–83.

Falcon-Lang, H.J., Labandeira, C., Kirk, R., 2015a. Herbivorous and detritivorous arthropod trace-fossils associated with sub-humid vegetation in the Middle Pennsylvanian of southern Britain. Palaios 30, 192–206.

Falcon-Lang, H.J., Lucas, S.G., Kerp, H., Krainer, K., Montañez, I.P., Vachard, D., Chaney, D.S., Elrick, S.D., Contreras, D.L., Kurzawe, F., DiMichele, W.A., Looy, C.V., 2015b. Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangea: Paleoecology and evolutionary significance. Palaeogeography, Palaeoclimatology, Palaeoecology 433, 158–173.

Falcon-Lang, H.J., Minter, N., Bashforth, A.R., Gibling, M.R., Miller, R.F., 2015d. The mid-Carboniferous diversification of continental ecosystems inferred from trace fossil suites in the Tynemouth Creek Formation of New Brunswick, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 440, 142–160.

Falcon-Lang, H.J., Nelson, W.J., Heckel, P.H., DiMichele, W.A., Elrick, S.D., 2018. 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. Palaeogeography, Palaeoclimatology, Palaeoecology 490, 375–392.

Falcon-Lang, H.J., Nelson, J., Looy, C., Ames, P., Elrick, S., DiMichele, W.A., 2009. Incised channel-fills containing conifers imply that seasonally-dry vegetation dominated Pennsylvanian tropical lowlands. Geology 37, 923–926.

Falcon-Lang, H.J., Pufahl, P., Bashforth, A.R., Gibling, M.R., Miller, R.F., Minter, N., 2015c. A marine incursion and its biota in the Lower Pennsylvanian Tynemouth Creek Formation, southern New Brunswick: implications for paleogeography, stratigraphy and paleoecology. Palaios 30, 779–791.

Falcon-Lang, H.J., Rygel, M.C., Gibling, M.R., Calder, J.H., 2004. An early Pennsylvanian waterhole deposit and its fossil biota in dryland alluvial plain setting, Joggins, Nova Scotia. Journal of the Geological Society 161, 209–222.

Falcon-Lang, H.J., Scott, A.C., 2000. Upland ecology of some Late Carboniferous cordaitalean trees from Nova Scotia and England. Palaeogeography, Palaeoclimatology, Palaeoecology 156, 225–242.

Feldman, H.R., Archer, A.W., West, R.R., Maples, C.G., 1992. The Kinney Brick Company Quarry: Preliminary analysis using an estuarine depositional model. In: Zidek, J. (Ed.), Geology and Paleontology of the Kinney Brick Quarry, Late Pennsylvanian, Central

New Mexico. New Mexico Bureau Mines & Mineral Resources Bulletin 138, pp. 21–26.

Feldman, H.R., Franseen, E.K., Joeckel, R.M., Heckel, P.H., 2005. Impact of longer-term modest climate shifts on architecture of high-frequency sequences (cyclothems), Pennsylvanian of Midcontinent USA. Journal of Sedimentary Research 75, 350–368.

Ferguson, D.K., 1985. The origin of leaf assemblages – new light on an old problem. Review of Palaeobotany and Palynology 46, 117–188.

Ferguson, D.K., 2005. Plant taphonomy: ruminations on the past, the present, and the future. Palaios 20, 418–428.

Ferm, J.C., 1970. Allegheny deltaic deposits. In: Morgan, J.P. (Ed.), Deltaic Sedimentation, Modern and Ancient. Society of Economic Paleontologists and Mineralogists Special Publication 15, 246–255.

Ferm, J.C., Staub, J.R., 1984. Depositional controls of mineable coal bodies. In: Rahmani, R.A., Flores, R.M. (Eds.), Sedimentology of Coal and Coal-bearing Sequences. International Association of Sedimentologists Special Publication 7, pp. 275–289.

Fielding, C.R., Alexander, J., Allen, J.P., 2018. The role of discharge variability in the formation and preservation of alluvial sediment bodies. Sedimentary Geology 365, 1–20.

Fielding, C.R., Allen, J.P., Alexander, J., Gibling, M.R., 2009. Facies model for fluvial systems in the seasonal tropics and subtropics. Geology 37, 623–626.

Fielding, C.R., Frank, T.D., Isbell, J.L., 2008. The late Paleozoic ice age – A review of current understanding and synthesis of global climate patterns. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, pp. 343–354.

Fielding, C.R., Frank, T.D., Isbell, J.L., Henry, L.C., Domack, E.W., 2010. Stratigraphic signature of the late Palaeozoic Ice Age in the Parmeener Supergroup of Tasmania, SE Australia, and inter-regional comparisons. Palaeogeography, Palaeoclimatology, Palaeoecology 298, 70–90.

Fisher, D.J., 1925. Structure of Herrin (No. 6) coal seam near Duquoin. Illinois State Geological Survey Report of Investigations 5, 1–34.

Flenley, J.R., Butler, K., 2001. Evidence for continued disturbance of upland rain forest in Sumatra for the last 7000 years of an 11,000-year record. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 289–305.

Fluteau, F., Besse, J., Broutin, J., Ramstein, G., 2001. The Late Permian climate. What can be inferred from climate modelling concerning Pangea scenarios and Hercynian range altitude? Palaeogeography, Palaeoclimatology, Palaeoecology 167, 39–71.

Forte, G., Kustatscher, E., van Konijnenburg-van Cittert, J.H.A., Looy, C.V., Kerp, H., 2017. Conifer diversity in the Kungurian of Europe –Evidence from dwarf-shoot morphology. Review of Palaeobotany and Palynology 244, 308–315.

Foster, R.B., 1990. The floristic composition of the Rio Manu floodplain forest. In: Gentry, A.H. (Ed.), Four Neotropical Rainforests. Yale University Press, New Haven, pp. 99–111.

French, J.A., Watney, W.L., Anderson, J.E., 1988. Stratigraphic and sedimentologic considerations relating to the fossiliferous limestones (Upper Pennsylvanian?) at Hamilton Quarry, Greenwood County, Kansas. In: Mapes, G., Mapes, R. (Eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6, pp. 37–58.

Frisch, W., Kuhlemann, J., Dunkl, I., Brügel, A., 2008. Palinspastic reconstruction and topographic evolution of the Eastern Alps during late Tertiary tectonic extrusion. Tectonophysics 297, 1–15.

Gastaldo, R.A., 1989. Preliminary observations on phytotaphonomic assemblages in a subtropical/temperate Holocene bayhead delta: Mobile Delta, Gulf Coastal Plain, Alabama. Review of Palaeobotany and Palynology 58, 61–83.

Gastaldo, R.A., 1990. Early Pennsylvanian swamp forests in the Mary Lee coal zone, Warrior Basin, Alabama. In: Gastaldo, R.A., Demko, T.M., Liu, Y. (Eds.), Carboniferous Coastal Environments and Paleocommunities of the Mary Lee Coal Zone, Marion and Walker Counties, Alabama. Geological Survey of Alabama, Tuscaloosa, pp. 45–65.

Gastaldo, R.A., 1992. Regenerative growth in fossil horsetails following burial by alluvium. Historical Biology 6, 203–219.

Gastaldo, R.A., 1994. The genesis and sedimentation of phytoclasts with examples from coastal environments. In: Traverse, A. (Ed.), Sedimentation of Organic Particles. Cambridge University Press, Cambridge, pp. 103–127.

Gastaldo, R.A., 1996. Flöznah and flözfern assemblages: potential predictors of Late Carboniferous biome replacement? In: Leary, R.L. (Ed.), Patterns in Paleobotany: Proceedings of a Czech–U.S. Carboniferous Paleobotany Workshop. Illinois State Museum Scientific Papers 26, pp. 19–27.

Gastaldo, R.A., 2010. Peat or no peat: Why do the Rajang and Mahakam Deltas differ? International Journal of Coal Geology 83, 162–172.

Gastaldo, R.A., Bearce, S.C., Degges, C.W., Hunt, R.J., Peebles, M.W., Violette, D.L., 1989. Biostratinomy of a Holocene oxbow lake: a backswamp to mid-channel transect. Review of Palaeobotany and Palynology 58, 47–59.

Gastaldo, R.A., Degges, C.W., 2007. Sedimentology and paleontology of a Carboniferous log jam. International Journal of Coal Geology 69, 103–118.

Gastaldo, R.A., Demko, T.M., 2011. Long term hydrology controls the plant fossil record. In: Allison, P.A., Bottjer, D.J. (Eds.), Taphonomy: Processes and Bias Through Time (Second Edition). Topics in Geobiology 32, pp. 249–286.

Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1996. Out of the icehouse into the greenhouse: a late Paleozoic analog for modern global vegetational change. GSA Today 6, 1–7.

Gastaldo, R.A., Purkyňová, E., Šimůnek, Z, Schmitz, M.D., 2009. Ecological persistence in the Late Mississippian (Serpukhovian, Namurian A) megafloral record of the Upper Silesian Basin, Czech Republic. Palaios 24, 336–350.Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75, 1–34.

Gibling, M.R., Bashforth, A.R., Falcon-Lang, H.J., Allen, J.P., Fielding, C.R., 2010. Log jams and flood sediment buildup caused channel avulsion in the Pennsylvanian of Atlantic Canada. Journal of Sedimentary Research 80, 268–287.

Gibling, M.R., Bird, D.J., 1994. Late Carboniferous cyclothems and alluvial paleovalleys in the Sydney Basin, Nova Scotia. Geological Society of America Bulletin 106, 105–117.

Gibling, M.R., Culshaw, N., Rygel, M.C., Pascucci, V., 2019. Chapter 6 - The Maritimes Basin of Atlantic Canada: basin creation and destruction during the Paleozoic assembly of Pangea. In: Miall, A.D. (Ed.), The Sedimentary Basins of the United States and Canada (Second Edition). Elsevier, Amsterdam, pp. 267–314.

Gibling, M.R., Saunders, K.I., Tibert, N.E., White, J.A., 2004. Sequence sets, high-accommodation events, and the coal window in the Carboniferous Sydney coalfield, Atlantic Canada. In: Pashin, J.C., Gastaldo, R.A. (Eds.), Sequence Stratigraphy, Paleoclimate, and Tectonics of Coal-bearing Strata. American Association of Petroleum Geologists Studies in Geology 51, pp. 169–197.

Goldhammer, R.K., Oswald, E.J., Dunn, P.A., 1991. Hierarchy of stratigraphic forcing: Example from Middle Pennsylvanian shelf carbonates of the Paradox basin. Kansas Geological Survey Bulletin 233, 361–413.

Greb, S.F., 1989. A sub-rectangular paleovalley system, Caseyville Formation, Eastern Interior Basin, western Kentucky. Southeastern Geology 30, 59–75.

Greb, S.F., Andrews, W.M., Eble, C.F., DiMichele, W.A., Cecil, C.B., Hower, J.C., 2003. Desmoinesian coal beds of the Eastern Interior and surrounding basins: The largest tropical peat mires in Earth history. In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time. Geological Society of America Special Paper 370, pp. 127–150.

Greb, S.F., Eble, C.F., Hower, J.C., 1999. Depositional history of the Fire Clay coal bed (Late Duckmantian), eastern Kentucky, USA. International Journal of Coal Geology 40, 255–280.

Gresley, W.S., 1894. The "slate binders" of the "Pittsburg" coal bed. American Geologist 14, 356–365.

Grey, M., Pufahl, P.K., Aziz, A.A., 2011. Using multiple environmental proxies to determine degree of marine influence and paleogeographical position of the Joggins Fossil Cliffs UNESCO World Heritage Site. Palaios 26, 256–263.

Grubb, P.J., 1971. Interpretation of the 'Massenerhebung' effect on tropical mountains. Nature 229, 44–45.

Grubb, P.J., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Annual Review of Ecology and Systematics 8, 83–107.

Grubb, P.J., Whitmore, T.C., 1966. A comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the forests. Journal of Ecology 54, 303–333.

Gulbranson, E.L., Montañez, I.P., Tabor, N.J., Limarino, C.O., 2015. Late Pennsylvanian aridification on the southwestern margin of Gondwana (Paganzo Basin, NW Argentina): A regional expression of a global climate perturbation. Palaeogeography, Palaeoclimatology, Palaeoecology 417, 220–235.

Guo, F., Lenoir, J., Bonebrake, T.C., 2018. Land-use change interacts with climate to determine elevational species redistribution. Nature Communications 9, 1315.

Gyssels, G., Poesen, J., Bochet, E., Li, Y., 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. Progress in Physical Geography 29, 189–217.

Handlirsch, A., 1906. Revision of American Paleozoic insects. Proceedings of the United States National Museum 29, 661–820.

Haq, B.U., Shutter, S.R., 2008. A chronology of Paleozoic sea-level changes. Science 322, 64–68.

Hatcher, R.D., 2002. Alleghanian (Appalachian) orogeny, a product of zipper tectonics: Rotational transpressive continent-continent collision and closing of ancient oceans along irregular margins. In: Martinez Catalán, J.R., Hatcher, Jr., R.D., Arenas, R., Díaz García, F. (Eds.), Variscan-Appalachian Dynamics: The Building of the Late Paleozoic Basement. Geological Society of America Special Paper 364, pp. 199–208.

Hatcher, R.D., 2010. The Appalachian orogen: A brief summary. In: Tollo, R.P. (Ed.), From Rodinia to Pangea, the Lithotectonic Record of the Appalachian Region. Geological Society of America Memoir 206, pp. 1–19.

Havlena, V., 1953. Neuropteridy českého karbonu a permu. Neuropterides excl. Mixoneurae div. auct. Rozpravy Ústředního Ústavu Geologického 16, 1–168.

Havlena, V., 1961. Die flöznahe und flözfremde Flora des oberschlesischen Namurs A und B. Palaeontographica Abteilung B (Palaeophytologie) 108, 22–38.

Havlena, V., 1971. Die zeitgleichen Floren des europäischen Oberkarbons und die mesophile Floras des Ostrau-Karwiner Steinkohlenreviers. Review of Palaeobotany and Palynology 12, 245–270.

Heavens, N.G., 2015. Injecting climate modeling into deep time studies: ideas for nearly every project. The Sedimentary Record 13, 4–10.

Heavens, N.G., Mahowald, N.M., Soreghan, G.S., Soreghan, M.J., Shields, C.A., 2015. A model-based evaluation of tropical climate in Pangaea during the late Palaeozoic icehouse. Palaeogeography, Palaeoclimatology, Palaeoecology 425, 109–127.

Heckel, P.H., 1995. Glacial-eustatic base-level--climatic model for late Middle to Late Pennsylvanian coal-bed formation in the Appalachian basin. Journal of Sedimentary Research 65, 348–356.

Heckel, P.H., 1999. Overview of Pennsylvanian (Upper Carboniferous) stratigraphy in Midcontinent region of North America. In: Heckel, P.H. (Ed.), Guidebook, Fieldtrip #8, 16th International Congress on the Carboniferous-Permian. Kansas Geological Survey Open File Report 99-27, pp. 68–102.

Heckel, P.H., 2008. Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D.,

Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, pp. 275–289.

Heckel, P.H., 2013. Pennsylvanian stratigraphy of Northern Midcontinent Shelf and biostratigraphic correlation of cyclothems. Stratigraphy 10, 3–39.

Heckel, P.H., Alekseev, A.S., Barrick, J.E., Boardman, D.R., Goreva, N.V., Isakova, T.N., Nemyrovska, T.I., Ueno, K., Villa, E., Work, D.M., 2008. Choice of conodont *Idiognathodus simulator* (sensu stricto) as the event marker for the base of the global Gzhelian Stage (Upper Pennsylvanian Series, Carboniferous System). Episodes 31, 319–325.

Heckel, P.H., Alekseev, A.S., Barrick, J.E., Boardman, D.R., Goreva, N.V., Nemyrovska, T.I., Ueno, K., Villa, E., Work, D.M., 2007. Cyclothem ["digital"] correlation and biostratigraphy across the global Moscovian-Kasimovian-Gzhelian stage boundary interval (Middle-Upper Pennsylvanian) in North America and eastern Europe. Geology 35, 607–610.

Heckel, P.H., Boardman, D.R., Barrick, J.E., 2002. Desmoinesian-Missourian regional stage boundary reference position for North American. In: Hills, L.V., Henderson, C.M, Bamber, E.W. (Eds.), The Carboniferous and Permian of the World. Canadian Society of Petroleum Geologists Memoir 19, pp. 710–724.

Henderson, C.M., Davydov, V.I., Wardlaw, B.R., Gradstein, F.M., Hammer, Ø., 2012. The Permian Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), The Geologic Time Scale 2012. Elsevier, Amsterdam, pp. 653–679.

Hernandez-Castillo, G.R., Rothwell, G.W., Mapes, G., 2001. Thucydiaceae fam. nov., with a review and reevaluation of Paleozoic walchian conifers. International Journal of Plant Sciences 162, 1155–1185.

Hernandez-Castillo, G.R., Rothwell, G.W., Stockey, R.A., Mapes, G., 2003. Growth architecture of *Thycydia mahoningensis*, a model for primitive walchian conifer plants. International Journal of Plant Sciences 164, 443–452.

Hernandez-Castillo, G.R., Stockey, R.A., Rothwell, G.W., Mapes, G., 2009. Reconstructing *Emporia lockardii* (Voltziales: Emporiaceae) and initial thoughts on Paleozoic conifer ecology. International Journal of Plant Sciences 170, 1056–1074.

Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: Palaeobiogeographical and palaeogeographical implications. Earth-Science Reviews 85, 85–116.

Hirano, T., Jauhiainen, J., Inoue, T., Takahashi, H., 2009. Controls on the carbon balance of tropical peatlands. Ecosystems 12, 873–887.

Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. Science 105, 367–368.

Hooke, R.LeB., 2000. Toward a uniform theory of clastic sediment yield in fluvial systems. Geological Society of America Bulletin 112, 1778–1786.

Hopper, E., Fischer, K.M., Wagner, L.S., Hawman, R.B., 2017. Reconstructing the end of the Appalachian orogeny. Geology 45, 15–18.

Horne, J.C., Ferm, J.C., Caruccio, F.T., Baganz, B.P., 1978. Depositional models in coal exploration and mine planning in Appalachian region. American Association of Petroleum Geologists Bulletin 62, 2379–2411.

Horton, D.E., Poulsen, C.J., Montañez, I.P., DiMichele, W.A., 2012. Eccentricity-paced late Paleozoic climate change. Palaeogeography, Palaeoclimatology, Palaeoecology 331, 150–161.

Horton, D.E., Poulsen, C.J., Pollard, D., 2007. Orbital and CO_2 forcing of late Paleozoic continental ice sheets. Geophysical Research Letters 34, L19708.

Hunt, A., 1983. Plant fossils and lithostratigraphy of the Abo Formation (Lower Permian) in the Socorro area and plant biostratigraphy of Abo red beds in New Mexico. In: Chapin, C.E., Callender, J.F. (Eds.), Socorro Region II. New Mexico Geological Society Guidebook, 34th Annual Fall Field Conference, pp. 157–163.

Hunt, A.P., Lucas, S.G., 1992. The paleoflora of the lower Cutler Formation (Pennsylvanian, Desmoinesian?) in El Cobre Canyon, New Mexico, and its biochronological significance. In: Lucas, S.G., Kues, B.S., Williamson, T.E., Hunt, A.P. (Eds.), San Juan Basin IV. New Mexico Geological Society Guidebook, 43rd Field Conference, pp. 145–150.

Ielpi, A., Gibling, M.R., Bashforth, A.R., Dennar, C.I., 2015. Impact of vegetation on early Pennsylvanian fluvial channels: insight from the Joggins Formation of Atlantic Canada. Journal of Sedimentary Research 85, 999–1018.

Ielpi, A., Gibling, M.R., Bashforth, A.R., Lally, C., Rygel, M.C., Al-Silwadi, S., 2014. Role of vegetation in shaping Early Pennsylvanian braided rivers: Architecture of the Boss Point Formation, Atlantic Canada. Sedimentology 61, 1659–1700.

Isbell, J.L., Cole, D.I., Catuneanu, O., 2008. Carboniferous-Permian glaciation in the main Karoo Basin, South Africa: Stratigraphy, depositional controls, and glacial dynamics.

In: Fielding, C.R., Frank, T.D. Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, pp. 71–82.

Isbell, J.L., Henry, L.C., Gulbranson, E.L., Limarino, C.O., Fraiser, M.L., Koch, Z.J., Ciccioli, P.L., Dineen, A.A., 2012. Glacial paradoxes during the late Paleozoic ice age: Evaluating the equilibrium line altitude as a control on glaciation. Gondwana Research 22, 1–19.

Isbell, J.L., Miller, M.F., Wolfe, K.L., Lenaker, P.A., 2003. Timing of late Paleozoic glaciation in Gondwana: Was glaciation responsible for the development of Northern Hemisphere cyclothems? In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time. Geological Society of America Special Paper 370, pp. 5–24.

Iwaniw, E., 1985a. Floral palaeoecology of debris flow dominated valley-fill in the lower Cantabrian of NE León, NW Spain. In: Lemos de Sousa, M.J., Wagner, R.H. (Eds.), Papers on the Carboniferous of the Iberian Peninsula (Sedimentology, Stratigraphy, Palaeontology, Tectonics and Geochronology). Anais da Faculdade de Ciências, Universidade do Porto, Porto, Supplement to volume 64 (1983), pp. 283–357.

Iwaniw, E., 1985b. The sedimentology of lower Cantabrian basin margin deposits in NE León, Spain. In: Lemos de Sousa, M.J., Wagner, R.H. (Eds.), Papers on the Carboniferous of the Iberian Peninsula (Sedimentology, Stratigraphy, Palaeontology, Tectonics and Geochronology). Anais da Faculdade de Ciências, Universidade do Porto, Porto, Supplement to volume 64 (1983), pp. 49–115.

Jablonksi, D., 1986. Causes and consequences of mass extinctions: a comparative approach. In: Elliott, D.K. (Ed.), Dynamics of Extinction. Wiley, New York, pp. 183–229.

Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26, 194–220.

Jerrett, R.M., Flint, S.S., Davies, R.C., Hodgson, D.M., 2011. Sequence stratigraphic interpretation of a Pennsylvanian (Upper Carboniferous) coal from the central Appalachian Basin, USA. Sedimentology 58, 1180–1207.

Jirásek, J., Opluštil, S., Sivek, M., Schmitz, D.M., Abels, H.A., 2018. Astronomical forcing of Carboniferous paralic sedimentary cycles in the Upper Silesian Basin, Czech Republic (Serpukhovian, latest Mississippian): New radiometric ages afford an astronomical age model for European biozonations and substages. Earth-Science Reviews 177, 715–741.

Joeckel, R.M., 1989. Geomorphology of a Pennsylvanian land surface: pedogenesis in the Rock Lake Shale Member, southeastern Nebraska. Journal of Sedimentary Petrology 59, 469–481.

Jordan, O.D., Mountney, N.P., 2012. Sequence stratigraphic evolution and cyclicity of an ancient coastal desert system: the Pennsylvanian–Permian Lower Cutler Beds, Paradox Basin, Utah, USA. Journal of Sedimentary Research 82, 755–780.

Kenfack, D., Chuyong, G.B., Condit, R., Russo, S.E., Thomas, D.W., 2014. Demographic variation and habitat specialization of tree species in a diverse tropical forest of Cameroon. Forest Ecosystems 1, 22.

Kerp, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. Review of Palaeobotany and Palynology 90, 263–285.

Kerp, H., Fichter, J., 1985. Die Makrofloren des saarpfälzischen Rotliegenden (? Ober-Karbon-Unter-Perm; SW-Deutschland). Mainzer Geowissenschaftliche Mitteilungen 14, 159–286.

Kerp, J.H.F., Haubold, H., 1988. Aspects of Permian palaeobotany and palynology. VIII. On the reclassification of the West- and Central European species of the form-genus *Callipteris* Brongniart 1849. Review of Palaeobotany and Palynology 54, 135–150.

Kirkham, R.M., Keller, J.W., Houck, K.J., Lindsay, N.R., 2006. Geologic map of the Fairplay East Quadrangle, Park County, Colorado. Geologic map 1:24,000, Open-file Report 06-9. Colorado Geological Survey, Denver.

Kirkland, D.W., Frederiksen, N.O., 1970. *Cordaitina* pollen from Pennsylvanian strata of Oklahoma and Texas. Review of Palaeobotany and Palynology 10, 221–231.

Knight, J.A., 1971. The sequence and stratigraphy of the eastern end of the Sabero Coalfield (León, N. W. Spain). Trabajos de Geología 3, 193–229.

Knight, J.A., 1983. The stratigraphy of the Stephanian rocks of the Sabero Coalfield, León (NW. Spain) and an investigation of the fossil flora. Part I – the stratigraphy and general geology of the Sabero Coalfield. Palaeontographica Abteilung B (Palaeophytologie) 187, 1–88.

Köppen, W., 1936. Das geographische System der Klimate. In: Köppen, W., Geiger, R. (Eds.), Handbuch der Klimatologie, Vol. 1, Part C. Gebrüder Borntraeger, Berlin, pp. 1–46.

Kosanke, R.M., Cecil, C.B., 1996. Late Pennsylvanian climate changes and palynomorph extinctions. Review of Palaeobotany and Palynology 90, 113–140.

Krainer, K., Lucas, S.G., 2004. The Upper Pennsylvanian Red Tanks Member of the Bursum

Formation at Carrizo Arroyo, central New Mexico: transition from shallow marine to nonmarine facies. In: Lucas, S.G., Zeigler, K.E. (Eds.), Carboniferous-Permian Transition at Carrizo Arroyo, Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 25, pp. 53–69.

Langenheim, R.L., Nelson, W.J., 1992. The cyclothemic concept in the Illinois Basin: A review. In: Dott, R.H. (Ed.), Eustasy: The Historical Ups and Downs of a Major Geological Concept. Geological Society of America Memoir 180, pp. 55–72.

Latrubesse, E.M., Stevaux, J.C., Sinha, R., 2005. Tropical rivers. Geomorphology 70, 187–206.

Lawson, I.T., Kelly, T.J., Aplin, P., Boom, A., Dargie, G., Draper, F.C.H., Hassan, P.N.Z.B.P., Hoyos-Santillan, J., Kaduk, J., Large, D., Murphy, W., 2015. Improving estimates of tropical peatland area, carbon storage, and greenhouse gas fluxes. Wetlands Ecology and Management 23, 327–346.

Leary, R.L., 1974a. Two early Pennsylvanian floras of western Illinois. Transactions of the Illinois State Academy of Science 67, 430–440.

Leary, R.L., 1974b. Stratigraphy and floral characteristics of the basal Pennsylvanian strata in west central Illinois. Compte Rendu Septième Congrès International de Stratigraphie et de Géologie du Carbonifère, Krefeld 1971, 3, 341–350.

Leary, R.L., 1975. Early Pennsylvanian paleogeography of an upland area western Illinois USA. Bulletin de la Société Belge de Géologie 84, 19–31.

Leary, R.L., 1981. Early Pennsylvanian geology and paleobotany of the Rock Island County, Illinois, area. Part 1: Geology. Illinois State Museum Reports of Investigations 37, 1–88.

Leary, R.L., Pfefferkorn, H.W., 1977. An early Pennsylvanian flora with *Megalopteris* and Noeggerathiales from west-central Illinois. Illinois State Geological Survey Circular 500, 1–77.

Leighton, M.W., Kolata, D.R., Oltz, D.F., Eidel, J.J., Eds., 1991. Interior Cratonic Basins. American Association of Petroleum Geologists Memoir 51. American Association of Petroleum Geologists, Tulsa.

Leisman, G.A., Gillespie, W.H., Mapes, G., 1988. Plant megafossils from the Hartford Limestone (Virgilian–Upper Pennsylvanian) near Hamilton, Kansas. In: Mapes, G., Mapes, R. (Eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6, pp. 203–212.

Lerner, A.J., Lucas, S.G., Spielmann, J.A., Krainer, K., DiMichele, W.A., Chaney, D.S., Schneider, J.W., Nelson, W.J., Ivanov, A.B., 2009. The biota and paleoecology of the Upper Pennsylvanian (Missourian) Tinajas locality, Socorro County, New Mexico. In: Lueth, V.W., Lucas, S.G., Chamberlin, R.M. (Eds.), Geology of the Chupadera Mesa Region. New Mexico Geological Society Guidebook, 60th Field Conference, pp. 267–280.

Lesnikowska, A.D., 1989. Anatomically Preserved Marattiales from Coal Swamps of the Desmoinesian and Missourian of the Midcontinent United States: Systematics, Ecology, and Evolution. Ph.D. Thesis, University of Illinois at Urbana-Champaign (unpubl.).

Lesquereux, L., 1882. On some specimens of Permian fossil plants from Colorado. Bulletin of the Museum of Comparative Zoology 7, 243–247.

Libertín, M., Opluštil, S., Pšenička, J., Bek, J., Sýkorová, I., Dašková, J., 2009. Middle Pennsylvanian pioneer plant assemblage buried in situ by volcanic ash-fall, central Bohemia, Czech Republic. Review of Palaeobotany and Palynology 155, 204–233.

Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. Journal of Ecology 84, 137–152.

Lieberman, M., Lieberman, D., Hartshorn, G.S., Peralta, R., 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73, 505–516.

Lisiecki, L.E., Raymo, M.E., 2007. Plio–Pleistocene climate evolution: trends and transitions in glacial cycle dynamics. Quaternary Science Reviews 26, 56–69.

Liu, Y., Gastaldo, R.A., 1992. Characteristics and provenance of log-transported gravels in a Carboniferous channel deposit. Journal of Sedimentary Petrology 62, 1072–1083.

Locatelli, E.R., McMahon, S., Bilger, H., 2017. Biofilms mediate the preservation of leaf adpression fossils by clays. Palaios 32, 708–724.

Lojka, R., Drábková, J., Zajíc, J., Sýkorová, I., Franců, J., Bláhová, A., Grygar, T., 2009. Climate variability in the Stephanian B based on environmental record of the Mšec Lake deposits (Kladno–Rakovník Basin, Czech Republic). Palaeogeography, Palaeoclimatology, Palaeoecology 280, 78–93.

Lojka, R., Rosenau, N.A., Sidorinova, T., Strnad, L., 2016. Architecture, paleosols and cyclicity of the Middle-Late Pennsylvanian proximal fluvial system (Nýřany Member, Pilsen Basin, Czech Republic). Bulletin of Geosciences 91, 111–140.

Lojka, R., Sýkorová, I., Laurin, J., Matysova, P., Grygar, T.M., 2010. Lacustrine coupletlamination: evidence for Late Pennsylvanian seasonality in central equatorial Pangaea

(Stephanian B, Mšec Member, Central and Western Bohemian basins). Bulletin of Geosciences 85, 709–734.

Looy, C.V., 2007. Extending the range of derived Late Paleozoic conifers: *Lebowskia* gen. nov. (Majonicaceae). International Journal of Plant Sciences 168, 957–972.

Looy C.V., 2013. Natural history of a plant trait: branch-system abscission in Paleozoic conifers and its environmental, autecological, and ecosystem implications in a fire-prone world. Paleobiology 39, 235–252.

Looy, C.V., Duijnstee I.A.P., 2020. Voltzian conifers of the South Ash Pasture Flora (Guadalupian, Texas): *Johniphyllum multinerve* gen. et sp. nov., *Pseudovoltzia sapflorensis* sp. nov., and *Wantus acaulis* gen. et sp. nov. International Journal of Plant Sciences 181, 363–385.

Looy, C.V., Hotton, C.L., 2014. Spatiotemporal relationships among Late Pennsylvanian plant assemblages: Palynological evidence from the Markley Formation, West Texas, USA. Review of Palaeobotany and Palynology 211, 10–27.

Looy, C.V., Kerp, H., Duijnstee, I.A.P, DiMichele, W.A., 2014a. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. The Sedimentary Record 12, 4–18.

Looy C.V., Stevenson R.A., 2014. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian-Roadian) *Manifera talaris* gen. et sp. nov. International Journal of Plant Sciences 75, 841–854.

Looy, C.V., Stevenson, R.A., Van Hoof, T.B., Mander, L., 2014b. Evidence for coal forest refugia in the seasonally dry Pennsylvanian tropical lowlands of the Illinois Basin, USA. PeerJ 2, e630.

Lorenz, J.C., Smith, G.S., Lucas, S.G., 1992. Sedimentation patterns in Pennsylvanian strata at the Kinney Brick Quarry, Bernallilo County, New Mexico. In: Zidek, J. (Ed.), Geology and Paleontology of the Kinney Brick Quarry, Late Pennsylvanian, Central New Mexico. New Mexico Bureau of Mines & Mineral Resources Bulletin 138, pp. 13–19.

Lottes, A.L, Ziegler, A.M., 1994. World peat occurrence and the seasonality of climate and vegetation. Palaeogeography, Palaeoclimatology, Palaeoecology 106, 23–37.

Lucas, S.G., Allen, B.D., Krainer, K., Barrick, J., Vachard, D., Schneider, J.W., DiMichele, W.A., Bashforth, A.R., 2011. Precise age and biostratigraphic significance of the Kinney Brick Quarry Lagerstätte, Pennsylvanian of New Mexico, USA. Stratigraphy 8, 7–27.

Lucas, S.G., Barrick, J.E., Krainer, K., Schneider, J.W., 2013a. The Carboniferous-Permian boundary at Carrizo Arroyo, central New Mexico, USA. Stratigraphy 10, 153–170.

Lucas, S.G., Harris, S.K., Spielmann, J.A., Berman, D.S., Henrici, A.C., 2005. Vertebrate biostratigraphy and biochronology of the Pennsylvanian-Permian Cutler Group, El Cobre Canyon, northern New Mexico. In: Lucas, S.G., Zeigler, K.E., Spielmann, J.A. (Eds.), The Permian of Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 31, pp. 128–139.

Lucas, S.G., Harris, S.K., Spielmann, J.A., Berman, D.S., Henrici, A.C., Krainer, K., Rinehart, L.F., DiMichele, W.A., Chaney, D.S., Kerp, H., 2012. Lithostratigraphy, paleontology, biostratigraphy, and age of the upper Paleozoic Abo Formation near Jemez Springs, northern New Mexico, USA. Annals of Carnegie Museum 80, 323–350.

Lucas, S.G., Krainer, K., 2004. The Red Tanks Member of the Bursum Formation in the Lucero uplift and regional stratigraphy of the Bursum Formation in New Mexico. In: Lucas, S.G., Zeigler, K.E. (Eds.), Carboniferous-Permian Transition at Carrizo Arroyo, Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 25, pp. 43–52.

Lucas, S.G., Krainer, K., 2005. Cutler Group (Permo-Carboniferous) stratigraphy, Chama Basin, New Mexico. In: Lucas, S.G., Zeigler, K.E., Spielmann, J.A. (Eds.), The Permian of Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 31, pp. 90–100.

Lucas, S.G., Krainer, K., Chaney, D.S., DiMichele, W.A., Voigt, S., Berman, D.S., Henrici, A.C., 2013c. The Lower Permian Abo Formation in central New Mexico. In: Lucas, S.G., Nelson, W.J., DiMichele, W.A., Speilmann, J.A., Krainer, K., Barrick, J.E., Elrick, S., Voigt, S. (Eds.), The Carboniferous-Permian Transition in Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, pp. 161–179.

Lucas, S.G., Nelson, W.J., DiMichele, W.A., Krainer, K., Barrick, J.E., Voigt, S., Chaney, D.S., Elrick, S., Spielmann, J.A., 2013b. Field guide to the Carboniferous-Permian transition in the Cerros de Amado and vicinity, Socorro County, central New Mexico. In: Lucas, S.G., Nelson, W.J., DiMichele, W.A., Speilmann, J.A., Krainer, K., Barrick, J.E., Elrick, S., Voigt, S. (Eds.), The Carboniferous-Permian Transition in Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, pp. 39–76.

Lucas, S.G., Shen, S.Z., 2016. The Permian chronostratigraphic scale: history, status and prospectus. In: Lucas, S.G., Shen, S.Z. (Eds.), The Permian Timescale. Geological Society Special Publications 450, pp. 21–50.

Lucas, S.G., Shen, S.Z., 2017. The Permian timescale: an introduction. In: Lucas, S.G., Shen, S.Z. (Eds.), The Permian Timescale. Geological Society Special Publications 450, pp. 1–19.

Luize, B.G., Silva, T.S., Wittmann, F., Assis, R.L., Venticinque, E.M., 2015. Effects of the flooding gradient on tree community diversity in várzea forests of the Purus River, central Amazon, Brazil. Biotropica 47, 137–142.

Lyons, P.C., Darrah, W.C., 1989. Earliest conifers in North America: upland and/or paleoecological indicators? Palaios 4, 480–486.

Mack, G.H., 2003. Lower Permian terrestrial palaeoclimate indicators in New Mexico and their comparison to palaeoclimate models. In: Lucas, S.G., Semken, S.C., Berglof, W., Ulmer-Scholle, D. (Eds.), Geology of the Zuni Plateau. New Mexico Geological Society Guidebook, 54th Annual Fall Field Conference, pp. 231–240.

Mack, G.H., Tabor, N.J., Zollinger, H.J., 2010. Palaeosols and sequence stratigraphy of the Lower Permian Abo Member, south-central New Mexico, USA. Sedimentology 57, 1566–1583.

Maierová, P., Schulmann, K., Lexa, O., Guillot, S., Štípská, P., Janoušek, V., Čadek, O., 2016. European Variscan orogenic evolution as an analogue of Tibetan-Himalayan orogen: Insights from petrology and numerical modeling. Tectonics 35, 1760-1780.

Mamay, S.H., 1990. *Charliea manzanitana*, n. gen., n. sp., and other enigmatic parallel-veined foliar forms from the Upper Pennsylvanian of New Mexico and Texas. American Journal of Botany 77, 858–866.

Mamay, S.H., Bateman, R.M., 1991. *Archaeocalamites lazarii*, sp. nov.: the range of Archaeocalamitaceae extended from the lowermost Pennsylvanian to the mid-Lower Permian. American Journal of Botany 78, 489–496.

Mamay, S.H., Mapes, G., 1992. Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico. In: Zidek, J. (Ed.), Geology and Paleontology of the Kinney Brick Quarry, Late Pennsylvanian, Central New Mexico. New Mexico Bureau of Mines & Mineral Resources Bulletin 138, pp. 61–86.

Mapes, G., Gastaldo, R.A., 1986. Late Paleozoic non-peat accumulating floras. In: Gastaldo, R.A. (Ed.), Land Plants. Notes for a Short Course. University of Tennessee, Department of Geological Sciences, Studies in Geology 15, pp. 115–127.

Mapes, R.H., Mapes, G., Eds., 1988. Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6. Kansas Geological Survey, Lawrence.

Mapes, G., Rothwell, G.W., 1991. Structure and relationships of primitive conifers. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 183, 269–287.

Marchant, R., Boom, A., Behling, H., Hooghiemstra, H., Melief, B., Van Geel, B., Van der Hammen, T., Wille, M., 2004. Colombian vegetation at the Last Glacial Maximum: a comparison of model- and pollen-based biome reconstructions. Journal of Quaternary Science 19, 721–732.

Marchetti, L., Petti, F.M., Zoboli, D., Pillola, G.L., 2018. Vertebrate and invertebrate trace fossils in the Late Pennsylvanian (Carboniferous) fluvio-lacustrine San Giorgio Basin (south-west Sardinia): remarks on the oldest continental ichnoassociation of Italy. Ichnos 25, 94–105.

Martínez-Meyer, E., Peterson, A.T., 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. Journal of Biogeography 33, 1779–1789.

Martino, R.L., 2016. Sequence stratigraphy of fluvially-dominated strata of the Mid-Late Pennsylvanian Conemaugh Formation, Central Appalachian Basin. International Journal of Coal Geology 154, 136-154.

Martino, R.L., 2017. Walchian conifers from the Mid-Late Pennsylvanian Conemaugh Group in the Appalachian Basin: Stratigraphic and depositional context, and paleoclimatic significance. International Journal of Coal Geology 171, 153–168.

Mašek, J., 1973. Vulkanické produkty středočeského karbonu. Sborník Geologických Věd, Geologie 24, 73–104.

Matte, P., 2001. The Variscan collage and orogeny (480–290 Ma) and the tectonic definition of the Armorica microplate: a review. Terra Nova 13, 122–128.

McComas, M.A., 1988. Upper Pennsylvanian compression floras of the 7-11 mine, Columbiana County, northeastern Ohio. Ohio Journal of Science 88, 48–52.

McKenzie, N.R., Horton, B.K., Loomis, S.E., Stockli, D.F., Planavsky, N.J., Lee, C.T.A., 2016. Continental arc volcanism as the principal driver of icehouse-greenhouse variability. Science 352, 444–447.

Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: Evidence for a

pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 430, 118–131.

Montañez, I.P., McElwain, J.C., Poulsen, C.J., White, J.D., DiMichele, W.A., Wilson, J.P., Griggs, G., Hren, M.T., 2016. Climate, pCO$_2$ and terrestrial carbon cycle linkages during late Palaeozoic glacial-interglacial cycles. Nature Geoscience 9, 824–828.

Montañez, I.P., Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annual Review of Earth and Planetary Sciences 41, 629–656.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.P., Rygel, M.C, 2007. CO$_2$-forced climate and vegetation instability during late Paleozoic deglaciation. Science 315, 87–91.

Montero, J.C., Piedade, M.T.F., Wittmann, F., 2014. Floristic variation across 600 km of inundation forests (Igapó) along the Negro River, Central Amazonia. Hydrobiologia 729, 229–246.

Moore, L.C., Wittry, J., DiMichele, W.A., 2014. The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: Spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km. Review of Palaeobotany and Palynology 200, 24–52.

Moore, R.C., Elias, M.K., Newell, N.D., 1936. A "Permian" flora from the Pennsylvanian rocks of Kansas. The Journal of Geology 44, 1–31.

Nakashizuka, T., Yusop, Z., Nik, A.R., 1991. Altitudinal zonation of forest communities in Selangor, Peninsular Malaysia. Journal of Tropical Forest Science 4, 233–244.

Nelson, W.J., 1983. Geologic disturbances in Illinois coal seams. Illinois State Geological Survey Circular 530, 1–47.

Nelson, W.J., Hook, R.W., Chaney, D.S., 2013. Lithostratigraphy of the Lower Permian (Leonardian) Clear Fork Formation of north-central Texas. In: Lucas, S.G., DiMichele, W.A., Barrick, J.E., Schneider, J.W., Spielmann, J.A. (Eds.), The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science Bulletin 60, pp. 286–311.

Nelson, W.J., Lucas, S.G., 2011. Carboniferous geologic history of the Rocky Mountain region. In: Sullivan, R.M, Lucas, S.G., Spielmann, J.A. (Eds.), Fossil Record 3. New Mexico Museum of Natural History and Science Bulletin 53, pp. 115–142.

Němejc, F., 1928. A revision of the carboniferous and permian flora of the coal-districts in Central Bohemia. I. The *Noeggerathiae* and *Archaeopterides* in the coal-basins of Central Bohemia. Palaeontographica Bohemiæ 12, 47–82.

Němejc, F., 1929. On some discoveries of fossil plantremains in the carboniferous districts of Central Bohemia. (II.). Bulletin International de l'Académie des Sciences de Bohême 30, 131–138.

Němejc, F., 1930. Floristic remarks to the stratigraphy of several small coal basins between Rokycany and Beroun in Central Bohemia. Věstník Státního Geologického Ústavu Československé Republiky 6, 13–19.

Němejc, F., 1937. On *Discinites* K. Feistmantel. Bulletin International de l'Académie des Sciences de Bohême 2, 1–7.

Němejc, F., 1941. Further indications of the type *Discinites* in addition to some remarks on the Archaeopteriden of the Middle Bohemian coal basins. Mitteilungen der Tschechischen Akademie der Wissenschaften 19, 1–13.

Němejc, F., 1947. The Lepidodendraceae of the coaldistricts of Central Bohemia (A preliminary study). Sborník Národního Muzea v Praze, Rada B, Přírodní vědy 3, 45–87.

Němejc, F., 1949. Odontopterides and Mixoneurae of the Permocarboniferous of Bohemia. (A preliminary study.). Sborník Národního Muzea v Praze, Rada B, Přírodní vědy 5, 3–32.

Novarese, V., 1917. L'Autuniano in Sardegna. Bollettino della Società Geologica Italiana 36, 58–91.

Novarese, V., Taricco, M., 1923. Cenni sommari sul Paleozoico dell'Iglesiente. Bollettino della Società Geologica Italiana 41, 316–325.

Obrhel, J., 1965. *Ilfeldia* und *Pterophyllum* aus dem Oberstephan Böhmens. Věstník Ústředního Ústavu Geologického 40, 211–213.

Ó Gogáin, A., Falcon-Lang, H.J., Carpenter, D.K., Miller, R.F., Benton, M.J., Pufahl, P.K., Ruta, M., Davies, T.G., Hinds, S.J., Stimson, M.R., 2016. Fish and tetrapod communities across a marine to brackish salinity gradient in the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and their palaeoecological and palaeogeographical implications. Palaeontology 59, 689–724.

Ohmori, H., 1983. Erosion rates and their relation to vegetation from the view point of world-wide distribution. Bulletin of the Department of Geography, University of Tokyo 15, 77–91.

Opluštil, S., 2004. Late Carboniferous tectono-sedimentary evolution and related terrestrial biotic changes on the North Variscan and Appalachian forelands, and adjacent paralic and continental basins. Geologica Balcanica 34, 51–67.

Opluštil, S., 2005a. Evolution of the Middle Westphalian river valley drainage system in central Bohemia (Czech Republic) and its palaeogeographic implication. Palaeogeography, Palaeoclimatology, Palaeoecology 222, 223–258.

Opluštil, S., 2005b. The effect of paleotopography, tectonics and sediment supply on quality of coal seams in continental basins of central and western Bohemia (Westphalian), Czech Republic. International Journal of Coal Geology 64, 173–203.

Opluštil, S., Cleal, C.J., 2007. A comparative analysis of some Late Carboniferous basins of Variscan Europe. Geological Magazine 144, 417–448.

Opluštil, S., Edress, N.A., Sýkorová, I., 2013a. Climatic vs. tectonic controls on peat accretion in non-marine setting; an example from the Žacléř Formation (Yeadonian–Bolsovian) in the Intra-Sudetic Basin (Czech Republic). International Journal of Coal Geology 116, 135–157.

Opluštil, S., Jirásek, J., Schmitz, M., Matýsek, D., 2017b. Biotic changes around the radioisotopically constrained Carboniferous-Permian boundary in the Boskovice Basin (Czech Republic). Bulletin of Geosciences 92, 95–122.

Opluštil, S., Lojka, R., Rosenau, N., Strnad, L., Kędzior, A., 2019. Climatically-driven cyclicity and peat formation in fluvial setting of the Moscovian – Early Kasimovian Cracow Sandstone Series, Upper Silesia (Poland). International Journal of Coal Geology, 212, 103234.

Opluštil, S., Lojka, R., Rosenau, N.A., Strnad, L., Sýkorová, I., 2015. Middle Moscovian climate of eastern equatorial Pangea recorded in paleosols and fluvial architecture. Palaeogeography, Palaeoclimatology, Palaeoecology 440, 328–352.

Opluštil, S., Martínek, K., Tasáryová, Z., 2005. Facies and architectural analysis of fluvial deposits of the Nýřany Member and the Týnec Formation (Westphalian D – Barruelian) in the Kladno-Rakovník and Pilsen basins. Bulletin of Geosciences 80, 45–66.

Opluštil, S., Pšenička, J., Bek., J., Wang, J., Feng, Z., Libertín, M., Šimůnek, Z., Bureš, J., Drábková, J., 2014. T^0 peat-forming plant assemblage preserved in growth position by volcanic ash: A case study from the Middle Pennsylvanian of the Czech Republic. Bulletin of Geosciences 89, 773–818.

Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimůnek, Z., Drábková, J., Dašková, J, 2009a. A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved *in situ* in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. Review of Palaeobotany and Palynology 155, 234–274.

Opluštil, S., Pšenička, J., Libertín, M., Bek, J., Dašková, J, Šimůnek, Z., Drábková, J., 2009b. Composition and structure of an *in situ* Middle Pennsylvanian peat-forming plant assemblage buried in volcanic ash, Radnice Basin (Czech Republic). Palaios 24, 726–746.

Opluštil, S., Pšenička, J., Libertín, M., Šimůnek, Z., 2007. Vegetation patterns of Westphalian and Lower Stephanian mire assemblages preserved in tuff beds of the continental basins of Czech Republic. Review of Palaeobotany and Palynology 143, 107–154.

Opluštil, S., Pšenička, J., Šimůnek, Z., Libertín, M., 2016a. Floras of clastic and peat-forming Pennsylvanian wetlands: are they different? A case study from the Upper Radnice Coal (late Duckmantian), Kladno Coalfield, Czech Republic. Spanish Journal of Palaeontology 31, 145–180.

Opluštil, S., Schmitz, M., Cleal, C.J., Martínek, K., 2016b. A review of the Middle–Late Pennsylvanian west European regional substages and floral biozones, and their correlation to the Geological Time Scale based on new U–Pb ages. Earth-Science Reviews 154, 301–335.

Opluštil, S., Schmitz, M., Kachlík, V., Štamberg, S., 2016c. Re-assessment of lithostratigraphy, biostratigraphy, and volcanic activity of the Late Paleozoic Intra-Sudetic, Krkonose-Piedmont and Mnichovo Hradiště basins (Czech Republic) based on new U-Pb CA-ID-TIMS ages. Bulletin of Geosciences 91, 399–432.

Opluštil, S., Šimůnek, Z., Pšenička, J., Bek, J., Libertín, M., 2017a. A 25 million year macrofloral record (Carboniferous–Permian) in the Czech part of the Intra-Sudetic Basin; biostratigraphy, plant biodiversity and vegetation patterns. Review of Palaeobotany and Palynology 244, 241–307.

Opluštil, S., Šimůnek, Z., Zajíc, J., Mencl, V., 2013b. Climatic and biotic changes around the Carboniferous/Permian boundary recorded in the continental basins of the Czech Republic. International Journal of Coal Geology 119, 114–151.

Opluštil, S., Sýkorová, I., Bek, J., 1999. Sedimentology, coal petrology and palynology of the Radnice Member in the S-E part of the Kladno-Rakovník Basin, Central Bohemia (Bolsovian). Acta Universitatis Carolinae, Geologica 43, 599–623.

Otto-Bliesner, B.L., 1993. Tropical mountains and coal formation: A climate model study of the Westphalian (306 Ma). Geophysical Research Letters 20, 1947–1950.

Pausas, J.G., Austin, M.P., 2001. Patterns of plant species richness in relation to different environments: An appraisal. Journal of Vegetation Science 12, 153–166.

Pellenard, P., Gand, G., Schmitz, M., Galtier, J., Broutin, J., Stéyer, J-S., 2017. High-precision U-Pb zircon ages for explosive volcanism calibrating the NW European continental Autunian stratotype. Gondwana Research 51, 118–136.

Peppers, R.A., 1996. Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. Geological Society of America Memoir 188, 1–112.

Peppers, R.A., 1997. Palynology of the Lost Branch Formation of Kansas – new insights on the major floral transition at the Middle-Upper Pennsylvanian boundary. Review of Palaeobotany and Palynology 98, 223–246.

Pešek, J., 2004. Late Paleozoic limnic basins and coal deposits of the Czech Republic. Folia Musei Rerum Naturalium Bohemiae Occidentalis, Geologica, Editio Specialis 1, 1–188.

Peyser, C.E., Poulsen, C.J., 2008. Controls on Permo-Carboniferous precipitation over tropical Pangaea: A GCM sensitivity study. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 181–192.

Pfefferkorn, H.W., 1980. A note on the term "upland" flora. Review of Palaeobotany and Palynology 30, 157–158.

Pfefferkorn, H.W., Gastaldo, R.A., DiMichele, W.A., 2017. Impact of an icehouse climate interval on tropical vegetation and plant evolution. Stratigraphy 14, 365–376.

Phillips, T.L., DiMichele, W.A., 1992. Comparative ecology and life-history biology of arborescent lycopsids in Late Carboniferous swamps of Euramerica. Annals of the Missouri Botanical Garden 79, 560–588.

Phillips, T.L., Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. International Journal of Coal Geology 3, 205–255.

Phillips, T.L., Peppers, R.A., Avcin, M.J., Laughnan, P.F., 1974. Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. Science 184, 1367–1369.

Phillips, T.L., Peppers, R.A., DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: Environmental inferences. International Journal of Coal Geology 5, 43–109.

Pierce, W.H., 1969. Geology and Pennsylvanian-Permian Stratigraphy of the Howard Area, Fremont County, Colorado. M.Sc. Thesis, Colorado School of Mines (unpubl.).

Pittau, P., Del Rio, M., 2002. Palynofloral biostratigraphy of the Permian and Triassic sequences of Sardinia. In: Cherchi, A., Corradini, C., Putzu, T. (Eds.), Sardinia Field

Trip – Palaeontology and Stratigraphy. Rendiconti della Società Paleontologica Italiana 1, pp. 93–109.

Pittau, P., Del Rio, M., Funedda, A., 2008. Relationships between plant communities characterization and basin formation in the Carboniferous-Permian of Sardinia. Bollettino della Società Geologica Italiana 127, 637–653.

Posa, M.R.C., Wijedasa, L.S., Corlett, R.T., 2011. Biodiversity and conservation of tropical peat swamp forests. BioScience 61, 49–57.

Poulsen, C.J., Pollard, D., Montañez, I.P., Rowley, D., 2007. Late Paleozoic tropical climate response to Gondwanan deglaciation. Geology 35, 771–774.

Pšenička, J., Correia, P., Šimůnek, Z., Sá, A., Murphy, J.B., Flores, D., 2017. Revision of *Ilfeldia* and establishment of *Ovulepteris* gen. nov. from the Pennsylvanian of Europe, with a discussion of their concepts. Review of Palaeobotany and Palynology 236, 59–73.

Raymond, A., Lambert, L., Costanza, S., Slone, E.J., Cutlip, P.C., 2010. Cordaiteans in paleotropical wetlands: An ecological re-evaluation. International Journal of Coal Geology 83, 248–265.

Raymond, A., Wehner, M., Costanza, S.H., 2014. Permineralized *Alethopteris ambigua* (Lesquereux) White: A medullosan with relatively long-lived leaves, adapted for sunny habitats in mires and floodplains. Review of Palaeobotany and Palynology 200, 82–96.

Read, C.B., 1934. A Flora of Pottsville age from the Mosquito Range, Colorado. United States Geological Survey Professional Paper 185-D, 79–96.

Read, C.B., 1947. Pennsylvanian floral zones and floral provinces. The Journal of Geology 55, 271–279.

Reisz, R.R., Heaton, M.J., Pynn, B.R., 1982. Vertebrate fauna of Late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. Journal of Paleontology 56, 741–750.

Reubens, B., Poesen, J., Danjon, F., Geudens, G., Muys, B., 2007. The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. Trees 21, 385–402.

Richards, B.C., 2013. Current status of the international Carboniferous time scale. In: Lucas, S.G., DiMichele, W.A., Barrick, J.E., Schneider, J.W., Spielmann, J.A. (Eds.), The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science Bulletin 60, pp. 348–353.

Richards, P.W., 1952. The Tropical Rain Forest. Cambridge University Press, Cambridge.

Rodríguez-Fernández, J., Sanz de Galdeano, C., 2006. Late orogenic intramontane basin development: the Granada basin, Betics (southern Spain). Basin Research 18, 85–102.

Roscher, M., Schneider, J.W., 2005. An annotated correlation chart for continental Late Pennsylvanian and Permian basins and the marine scale. In: Lucas, S.G., Zeigler, K.E. (Eds.), The Nonmarine Permian. New Mexico Museum of Natural History and Science Bulletin 30, pp. 282–291.

Roscher, M., Schneider, J.W., 2006. Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. In: Lucas, S.G., Cassinis, G., Schneider, J.W. (Eds.), Non-Marine Permian Biostratigraphy and Biochronology. Geological Society Special Publications 265, pp. 95–136.

Rosenau, N.A., Tabor, N.J., Elrick, S.D., Nelson, W.J., 2013. Polygenetic history of paleosols in middle–upper Pennsylvanian cyclothems of the Illinois basin, USA: Part II. Integrating geomorphology, climate, and glacioeustasy. Journal of Sedimentary Research 83, 637–668.

Rothwell, G.W., Mapes, G., 1988. Vegetation of a Paleozoic conifer community. In: Mapes, G., Mapes, R. (Eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6, pp. 213–223.

Rothwell, G.W., Mapes, G., Hernandez-Castillo, G.R., 2005. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). Taxon 54, 733–750.

Rothwell, G.W., Mapes, G., Mapes, R.H., 1997. Late Paleozoic conifers of North America: structure, diversity and occurrences. Review of Palaeobotany and Palynology 95, 95–113.

Rowley, D.B., Raymond, A., Parrish, J.T., Lottes, A.L., Scotese, C.R., Ziegler, A.M., 1985. Carboniferous paleogeographic, phytogeographic, and paleoclimatic reconstructions. International Journal of Coal Geology 5, 7–42.

Rygel, M.C., Fielding, C.R., Frank, T.D., Birgenheier, L.P., 2008. The magnitude of late Paleozoic glacioeustatic fluctuations: a synthesis. Journal of Sedimentary Research 78, 500–511.

Rygel, M.C., Lally, C., Gibling, M.R., Ielpi, A., Calder, J.H., Bashforth, A.R., 2015. Sedimentology and stratigraphy of the type section of the Pennsylvanian Boss Point Formation, Joggins Fossil Cliffs, Nova Scotia, Canada. Atlantic Geology 51, 1–43.

Sachsenhofer, R.F., Privalov, V.A., Panova, E.A., 2010. Basin evolution and coal geology of the Donets Basin (Ukraine, Russia): An overview. International Journal of Coal Geology 89, 26–40.

Schachat, S.R., Labandeira, C.C., Gordon, J., Chaney, D.S., Levi, S., Halthore, M.N, Alvarez, J., 2014. Plant-insect interactions from Early Permian (Kungurian) Colwell Creek Pond, north-central Texas: The early spread of herbivory in riparian environments. International Journal of Plant Sciences 175, 855–890.

Scheihing, M.H., Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta: a model for the incorporation of plant parts in clastic sediments of Late Carboniferous age of Euramerica. Review of Palaeobotany and Palynology 41, 205–240.

Schneider, J.W., Hoth, K., Gaitzsch, B.G., Berger, H.J., Steinborn, H., Walter, H., Zeidler, M.K., 1995. Carboniferous stratigraphy and development of the Erzgebirge Basin, East Germany. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 156, 431–466.

Schneider, J.W., Werneburg, R., 2006. Insect biostratigraphy of the Euramerican continental Late Pennsylvanian and Early Permian. In: Lucas, S.G., Cassinis, G., Schneider, J.W. (Eds.), Non-Marine Permian Biostratigraphy and Biochronology. Geological Society Special Publications 265, pp. 325–336.

Schulmann, J.R., Martínez Catalán, J.R., Lardeaux, J.M., Janoušek, V., Oggiana, G., Eds, 2014. The Variscan Orogeny: Extent, Timescale and the Formation of the European Crust. Geological Society Special Publications 405. The Geological Society, London.

Schultze, H.-P., 2009. Interpretation of marine and freshwater paleoenvironments in Permo–Carboniferous deposits. Palaeogeography, Palaeoclimatology, Palaeoecology 281, 126–136.

Schultze, H.-P., 2013. The paleoenvironment at the transition from piscine to tetrapod sarcopterygians. In: Lucas, S.G., DiMichele, W.A., Barrick, J.E., Schneider, J.W., Spielmann, J.A. (Eds.), The Carboniferous-Permian Transition. New Mexico Museum of Natural History and Science Bulletin 60, pp. 373–397.

Schultze, H.-P., Maples, C.G., Cunningham, C.R., 1993. The Hamilton Konservat-Lagerstätte: Stephanian terrestrial biota in a marginal-marine setting. Transactions of the Royal Society of Edinburgh: Earth Sciences 84, 443–451.

Schultze, H.-P., Soler-Gijón, R., 2004. A xenacanth clasper from the uppermost Carboniferous–Lower Permian of Buxières-les-Mines (Massif Central, France) and the palaeoecology of the European Permo–Carboniferous basins. Neues Jahrbuch für

Geologie und Paläontologie, Abhandlungen 232, 325–363.

Schumm, S.A., 1968. Speculations concerning paleohydrologic controls of terrestrial sedimentation. Geological Society of America Bulletin 79, 1573–1588.

Schutter, S.R., Heckel, P.H., 1985. Missourian (early Late Pennsylvanian) climate in Midcontinent North America. International Journal of Coal Geology 5, 111–140.

Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire. Proceedings of the Yorkshire Geological Society 41, 461–508.

Scott, A.C., 1979. The ecology of coal measure floras from northern Britain. Proceedings of the Geologists' Association 90, 97–116.

Scott, A.C., Kenig, F., Plotnick, R.E., Glasspool, I.J., Chaloner, W.G., Eble, C.F., 2010. Evidence of multiple late Bashkirian to early Moscovian (Pennsylvanian) fire events preserved in contemporaneous cave fills. Palaeogeography, Palaeoclimatology, Palaeoecology 291, 72–84.

Scudder, S.H., 1890. The insects of the Triassic beds at Fairplay, Colorado. Memoirs Read Before the Boston Society of Natural History 4, 457–472.

Selley, S., Morales, M., Sleezer, R.O., 2005. Surficial geology of the Hamilton Quarry area, Greenwood County, Kansas. Kansas Geological Survey Open-file Report 2005-13. http://www.kgs.ku.edu/Publications/OFR/2005/OFR05_13/index.html (accessed 8 October 2017)

Šetlík, J., 1956. Příspěvek k poznání druhu *Noeggerathia foliosa* Sternberg. Rozpravy Ústředního Ústavu Geologického 21, 1–106.

Šetlík, J., 1975. Étapes de l'évolution de la flore carbonifère dans la Bohême occidentale, centrale et nord-orientale. Compte Rendu du Septième Congrès International de Stratigraphie et de Géologie du Carbonifère, Krefeld, 1971 4, 227–238.

Simon, S.S.T., Gibling, M.R., 2017. Pedogenic mud aggregates preserved in a fine-grained meandering channel in the Lower Permian Clear Fork Formation, North-Central Texas, USA. Journal of Sedimentary Research 87, 230–252.

Simon, S.S.T., Gibling, M.R., DiMichele, W.A., Chaney, D.S., Koll, R., 2018. An exhumed fine-grained meandering channel in the lower Permian Clear Fork Formation, north-central Texas: Processes of mud accumulation and the role of vegetation in channel dynamics. In: Ghinassi, M., Colombera, L., Mountney, N.P., Reesink, A.J.H., Bateman, M. (Eds.), Fluvial Meanders and Their Sedimentary Products in the Rock Record. International Association of Sedimentologists Special Publication 48, pp. 149–172.

Simon, S.S.T., Gibling, M.R., DiMichele, W.A., Chaney, D.S., Looy, C.V., Tabor, N.J., 2016. An abandoned-channel fill with exquisitely preserved plants in redbeds of the Clear Fork Formation, Texas, USA: An Early Permian water-dependent habitat on the arid plains of Pangea. Journal of Sedimentary Research 86, 944–964.

Šimůnek, Z., 1996. Leaves and cuticles of the genus *Lesleya* Lesquereux from the Czech Republic and from Illinois (U.S.A.). In: Leary, R.L. (Ed.), Patterns in Paleobotany: Proceedings of a Czech–U.S. Carboniferous Paleobotany Workshop. Illinois State Museum Scientific Papers 26, pp. 43–56.

Šimůnek, Z., Bek. J., 2003. Noeggerathiaceae from the Carboniferous basins of the Bohemian Massif. Review of Palaeobotany and Palynology 125, 249–284.

Šimůnek, Z., Cleal, C.J., 2011. Imparipinnate neuropteroid foliage (Medullosales) from the middle Westphalian of the west and central Bohemia Coal Basin, Czech Republic. Review of Palaeobotany and Palynology 166, 163–201.

Šimůnek, Z., Cleal, C.J., 2016. The Carboniferous medullosalean pteridosperm *Havlenaea praeovata* (Němejc) Šimůnek & Cleal (Stradonice, Central Bohemia) is conspecific with *Neuropteris coriacea* Ettingshausen. Acta Palaeobotanica 56, 115–119.

Šimůnek, Z., Martínek, K., 2009. A study of Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. Review of Palaeobotany and Palynology 155, 275–307.

Soreghan, G.S., Dickinson, W.R., 1994. Generic types of stratigraphic cycles controlled by eustasy. Geology 22, 759–761.

Spicer, R.A., 1989. The formation and interpretation of plant fossil assemblages. Advances in Botanical Research 16, 95–191.

Stárková, M., Šimůnek, Z., Drábková, J., 2016. Geology of the Carboniferous outlier between Lísek and Hýskov in paleobotanical and palynological context (Westphalian, Duckmantian). Czech Geological Survey, Geoscience Research Reports 49, 215–224.

Stull, G.W., DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S., 2012. Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of 'xeromorphic' plants in Pennsylvanian wetlands. Palaeogeography, Palaeoclimatology, Palaeoecology 331, 162–176.

Tabor, N.J., DiMichele, W.A., Montañez, I.P., Chaney, D.S., 2013b. Late Paleozoic continental warming of a cold tropical basin and floristic change in western Pangea. International Journal of Coal Geology 119, 177–186.

Tabor, N.J., Montañez, I.P., 2004. Permo-Pennsylvanian alluvial paleosols (north-central Texas): High-resolution proxy records of the evolution of early Pangean paleoclimate. Sedimentology 51, 851–884.

Tabor, N.J., Montañez, I.P., Scotese, C.R., Poulsen, C.J., Mack, G.H., 2008. Paleosol archives of environmental and climatic history in paleotropical western Pangea during the latest Pennsylvanian through Early Permian. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the Late Paleozoic Ice Age in Time and Space. Geological Society of America Special Paper 441, pp. 291–303.

Tabor, N.J., Poulsen, C.J., 2008. Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: A review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 293–310.

Tabor, N.J., Romanchock, C.M., Looy, C.V., Hotton, C.L., DiMichele, W.A., Chaney, D.S., 2013a. Conservatism of Late Pennsylvanian vegetational patterns during short-term cyclic and long-term directional environmental change, western equatorial Pangea. In: Gąsiewicz, A., Słowakiewicz, M. (Eds.), Palaeozoic Climate Cycles: Their Evolutionary and Sedimentological Impact. Geological Society Special Publications 376, pp. 201–234.

Taggart, R.E., Ghavidel-Syooki, M., 1988. Palynology of the conifer macrofossil horizon. In: Mapes, G., Mapes, R. (Eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook Series 6, pp. 245–252.

Tandon, S.K., Gibling, M.R., 1994. Calcrete and coal in late Carboniferous cyclothems of Nova Scotia, Canada: Climate and sea-level changes linked. Geology 22, 755–758.

Tanner, L.H., Lucas, S.G., 2018. Pedogenic record of climate change across the Pennsylvanian-Permian boundary in red-bed strata of the Cutler Group, northern New Mexico, USA. Sedimentary Geology 373, 98–110.

Tenchov, Y.G., 1976. Composition peculiarities of the Carboniferous flora of the Svoge Basin, west Bulgaria. Geologica Balcanica 6, 3–11.

Tenchov, Y.G., 1993. Sedimentation and erosion during the Late Carboniferous in the Dobrudzha Coal Field (north-east Bulgaria). Geologica Balcanica 23, 3–18.

Thomas, B.A., Cleal, C.J., 2015. Cyclones and the formation of plant beds in late Carboniferous tropical swamps. Palaeobiodiversity and Palaeoenvironments 95, 531–536.

Thomas, B.A., Cleal, C.J., 2017. Distinguishing Pennsylvanian-age lowland, extra-basinal and upland vegetation. Palaeobiodiversity and Palaeoenvironments 97, 273–293.

Tidwell, W.D., Ash, S.R., 2004. Synopsis of the flora in the Red Tanks Formation, Carrizo Arroyo, New Mexico. In: Lucas, S.G., Zeigler, K.E. (Eds.), Carboniferous-Permian Transition at Carrizo Arroyo, Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 25, pp. 97–103.

Torsvik, T.H., Cocks, L.M., 2004. Earth geography from 400 to 250 Ma: a palaeomagnetic, faunal and facies review. Journal of the Geological Society 161, 555–572.

Uhl, D., Cleal, C.J., 2010. Late Carboniferous vegetation change in lowland and intramontane basins in Germany. International Journal of Coal Geology 83, 318–328.

Uhl, D., Jasper, A., 2016. New data on the macroflora of the basal Rotliegend group (Remigiusberg Formation; Gzhelian) in the Saar-Nahe Basin (SW-Germany). Fossil Imprint 72, 239–250.

Van den Belt, F.J., Van Hoof, T.B., Pagnier, H.J., 2015. Revealing the hidden Milankovitch record from Pennsylvanian cyclothem successions and implications regarding late Paleozoic chronology and terrestrial-carbon (coal) storage. Geosphere 11, 1062–1076.

Van Hoof, T.B., Falcon-Lang, H.J., Hartkopf-Fröder, C., Kerp, H., 2013. Conifer-dominated palynofloras in the Middle Pennsylvanian strata of the De Lutte-6 borehole, The Netherlands: Implications for evolution, palaeoecology and biostratigraphy. Review of Palaeobotany and Palynology 188, 18–37.

Villa, E. and Task Group, 2008. Progress report of the Task Group to establish the Moscovian–Kasimovian and Kasimovian–Gzhelian boundaries. Newsletter on Carboniferous Stratigraphy 26, 12–13.

Vincent, S.J., 2001. The Sis palaeovalley: a record of proximal fluvial sedimentation and drainage basin development in response to Pyrenean mountain building. Sedimentology 48, 1235–1276.

Wagner, R.H., 1971. The stratigraphy and structure of the Ciñera-Matallana Coalfield (Prov. León, N. W. Spain). Trabajos de Geología 4, 385–429.

Wagner, R.H., 1997. Floral palaeoecology of the Carboniferous/Permian. In: Aguirre, E., Morales, J., Soria, D. (Eds.), Registros Fósiles e Historia de la Tierra. Cursos de Verano de El Escorial. Editorial Complutense, Madrid, pp. 143–172.

Wagner, R.H., 2001 The extrabasinal elements in lower Pennsylvanian floras of the Maritimes Provinces, Canada: description of *Adiantites, Pseudadiantites* and *Rhacopteridium*. Revista Española de Paleontología 16, 187–207.

Wagner, R.H., 2004. Climatic changes as mirrored by Carboniferous and Permian floral distribution. Monografías del Jardín Botánico de Córdoba 11, 29–39.

Wagner, R.H., 2005. *Dicranophyllum glabrum* (Dawson) Stopes, an unusual element of lower Westphalian floras in Atlantic Canada. Revista Española de Paleontología 20, 7–13.

Wagner, R.H., 2017. The "global" scheme of Pennsylvanian chronostratigraphic units contrasted with the West European and North American regional classifications. Discussion of paleogeographic zones/regions and problems of correlation. Stratigraphy 14, 405–423.

Wagner, R.H., Álvarez-Vázquez, C., 2010. The Carboniferous floras of the Iberian Peninsula: A synthesis with geological connotations. Review of Palaeobotany and Palynology 162, 239–324.

Wagner, R.H., Castro, M.P., 2011. Compositional changes in a mid-Stephanian (Kasimovian) flora in relation to alluvial plain deposits derived from westward-receding mountains and bordered by the Paleotethys: La Magdalena Coalfield, northwestern Spain. Palaios 26, 33–54.

Wagner, R.H., Lemos de Sousa, M.J., 1983. The Carboniferous megafloras of Portugal – A revision of identifications and discussion of stratigraphic ages. In: Lemos de Sousa, M.J., Oliveira, J.T. (Eds.), The Carboniferous of Portugal. Memórias dos Serviços Geológicos de Portugal 29, pp. 127–152.

Wagner, R.H., Lyons, P.C., 1997. A critical analysis of the higher Pennsylvanian megafloras of the Appalachian region. Review of Palaeobotany and Palynology 95, 255–283.

Wagner, R. H., Winkler Prins, C.F., 1985. Stratotypes of the two lower Stephanian stages, Cantabrian and Barruelian. Compte Rendu Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 4, 473–483.

Wallace, C.A., Apeland, A.D., Cappa, J.A., 2000. Geologic map of the Jack Hall Mountain Quadrangle, Fremont County, Colorado. Geologic map 1:24,000, Open-file Rep. 00-1. Colorado Geological Survey, Denver.

Wang, J., Pfefferkorn, H.W., Bek, J., 2009. *Paratingia wudensis* sp. nov., a whole noeggerathialean plant preserved in an earliest Permian air fall tuff in Inner Mongolia, China. American Journal of Botany 96, 1676-1689.

Wang, J., Pfefferkorn, H.W., Feng, Z., Shen, G., 2004. A new species of *Discinites* (Noeggerathiales) associated with a new species of *Yuania* from the Lower Permian of Inner Mongolia, China. International Journal of Plant Sciences 165, 1107–1119.

Wang, J., Pfefferkorn, H.W., Zhang, Y., Feng, Z., 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proceedings of the National Academy of Sciences of the United States of America 109, 4927–4932.

Wanless, H.R., Shepard, F.P., 1936. Sea level and climatic changes related to late Paleozoic cycles. Geological Society of America Bulletin 47, 1177–1206.

Webb, T., III, Bartlein, P.J., 1992. Global changes during the last 3 million years: climatic controls and biotic responses. Annual Review of Ecology and Systematics 23, 141–173.

West, R.R., Archer, A.W., Miller, K.B., 1997. The role of climate in stratigraphic patterns exhibited by late Palaeozoic rocks exposed in Kansas. Palaeogeography, Palaeoclimatology, Palaeoecology 128, 1–16.

White, D., 1912. The characters of the fossil plant *Gigantopteris* Schenk and its occurrence in North America. Proceedings of the United States National Museum 41, 493–516.

White, D. 1931. Climatic implications of Pennsylvanian flora. Illinois State Geological Survey Bulletin 60, 271–281.

White, J.C., Gibling, M.R., Kalkreuth, W.D., 1994. The Backpit seam, Sydney Mines Formation, Nova Scotia: A record of peat accumulation and drowning in a Westphalian coastal mire. Palaeogeography, Palaeoclimatology, Palaeoecology 106, 223–239.

Widmann, B.L., Kirkham, R.M., Houck, K.J., Lindsay, N.R., 2007. Geologic map of the Fairplay West Quadrangle, Park County, Colorado. Geologic map 1:24,000, Open-file Rep. 06-07. Colorado Geological Survey, Denver.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5, 475–482.

Wilson, J.P., Montañez, I.P., White, J.D., DiMichele, W.A., McElwain, J.C., Poulsen, C.J., Hren, M.T., 2017. Dynamic Carboniferous tropical forests: new views of plant function and potential for physiological forcing of climate. New Phytologist 215, 1333–1353.

Wilson, J.P., White, J.D., DiMichele, W.A., Hren, M.T., Poulsen, C.J., McElwain, J.C., Montañez, I.P., 2015. Reconstructing extinct plant water use for understanding vegetation–climate feedbacks: methods, synthesis, and a case study using the Paleozoic-Era medullosan seed ferns. The Paleontological Society Papers 21, 167–195.

Wing, S.L., DiMichele, W.A., 1995. Conflict between local and global changes in plant diversity through geological time. Palaios 10, 551–564.

Wittaker, R.H., 1970. Communities and Ecosystems. Collier-Macmillan, London.

Wittmann, F., Schöngart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T., Queiroz, H.L., Worbes, M., 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. Journal of Biogeography 33, 1334–1347.

Woodward, F.I., 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge.

Wüst, R.A.J., Bustin, R.M., 2001. Low-ash peat deposits from a dendritic, intermontane basin in the tropics: a new model for good quality coal. International Journal of Coal Geology 46, 179–206.

Wüst, R.A.J., Bustin, R.M., 2004. Late Pleistocene and Holocene development of the interior peat-accumulating basin of tropical Tasek Bera, Peninsular Malaysia. Palaeogeography, Palaeoclimatology, Palaeoecology 211, 241–270.

Xu, Q., Jin, J., Labandeira, C.C., 2018. Williamson Drive: Herbivory from a north-central Texas flora of latest Pennsylvanian age shows discrete component community structure, expansion of piercing and sucking, and plant counterdefenses. Review of Palaeobotany and Palynology 251, 28–72.

Zhang, T., Niinemets, Ü., Sheffield, J., Lichstein, J.W., 2018. Shifts in tree functional composition amplify the response of forest biomass to climate. Nature 556, 99–102.

Ziegler, P.A., 1989. Evolution of Laurussia: A Study in Late Palaeozoic Plate Tectonics. Kluwer Academic Publishers, Dordrecht.

Table and Figure captions

Table 1. Segregation of habitats, floral types, and main plant groups that existed in tropics of Euramerican Pangea during the Pennsylvanian, depending on seasonality of precipitation and climate. "Wet months" are months when rainfall exceeds evapotranspiration. Vegetation present under a particular environmental regime shifted towards increasingly drought-tolerant taxa during the Late Pennsylvanian and Permian (DiMichele et al., 2008: fig. 5; Looy et al., 2014a: fig. 2; Fig. 10). Ecotone boundaries between wetland and dryland settings varied with climate mode. Note that patches of clastic wetland also existed under dry subhumid conditions, as discussed in the text. "Wet months", precipitation regime, and seasonality adapted from Cecil (2003: table 1). Floral types adapted and modified from DiMichele et al. (2010a: table 1).

Table 2. Localities and lithostratigraphic units reviewed in Section 6, listed in stratigraphic order (youngest to oldest) for each regional area (western Pangea, west-central Pangea, central Pangea, and east-central Pangea) within three time-bins (early Permian, Pennsylvanian-Permian transition, and Pennsylvanian). Designation of regional stages or substages (i.e., North American or Western European) based on system applied in source publication(s).

Figure 1. Two schematic illustrations of "upland model", which invokes elevational differences to explain the distribution of wetland and dryland vegetation in late Paleozoic landscapes of equatorial Pangea. Drought-tolerant plants become progressively more xeromorphic in tandem with increasing elevation, due to combination of slope and soil drainage that results in moisture-limited substrates, despite humid background climate that supports wetland vegetation and peat accumulation in contemporaneous lowlands. Presence of dryland taxa in lowland fossil assemblages attributed to transport from local elevated habitats. **A**. Cridland and Morris (1963: fig. 2, p. 83), based on upper Missourian (upper Kasimovian) macrofloral assemblages in Rock Lake Shale, Garnett, Kansas, USA (see Sections 6.2.2.6 and 7.1). Original figure caption: "Idealized profile of an Upper Pennsylvanian landscape in Kansas. To the right of the figure there is a lowland coal swamp community composed of *Cordaites* (C), *Calamites* (Ca), *Lepidodendron* (L), ferns and pteridosperms (F) and *Sigillaria* (S). To the left of the figure there is a community of plants

growing on slightly higher, hence better drained and drier, soil. This community contains *Dichophyllum* (D), *Taeniopteris* (T) and *Walchia* (W)." Copyright © 1963, University of Kansas, Museum of Natural History. Used with permission. **B**. Dimitrova et al. (2011: fig. 6, p. 566), based on palynological assemblages in upper Asturian to lower Cantabrian (uppermost Moscovian) part of Sydney Mines Formation, Sydney Basin, Nova Scotia, Canada (see Section 7.3). Original figure caption: "Reconstruction of the succession of late Middle Pennsylvanian lowland vegetation of the Canadian Maritimes, between the peat-substrates swamps (left) and the more xeric clastic substrates (right)." Some text enlarged from original for legibility. Copyright © 2011, The Geological Society, London. Used with permission of the artist (Christopher J. Cleal, National Museum Wales, Cardiff).

Figure 2. Distribution of wetland and dryland biomes in late Paleozoic landscapes of equatorial Pangea explained by the "climate model". Four reconstructions of basinal lowland vegetation *at a single hypothetical locality*, with differences in plant composition dependent on time interval involved and prevailing climate mode. **A**. Middle Pennsylvanian peat swamp under humid climate mode. Lycopsids (*Lepidophloios*) predominate above patchy understory of tree ferns and pteridosperms. **B**. Same locality after shift to (dry) subhumid climate mode during the Middle Pennsylvanian. Landscape (undergoing seasonal flooding) blanketed by forest of large, "dryland" cordaitalean trees, with understory and groundcover of pteridosperms and tree ferns mainly restricted to flanks of swollen fluvial channel, where preservation potential was amplified. **C**. Same locality during the Late Pennsylvanian under humid climate mode. Peat swamp dominated by tree ferns, with emergent lycopsids (*Sigillaria*) and pteridosperms in understory. **D**. Same locality after shift to semiarid climate mode during the Late Pennsylvanian. Open woodland dominated by walchian conifers, with groundcover of small pteridosperms and ferns, and calamitaleans lining ephemeral stream in seasonal flood. All illustrations used with permission of the artist (Mary Parrish, National Museum of Natural History, Smithsonian Institution).

Figure 3. Paleogeographic reconstruction of Earth during the latest Pennsylvanian (300 Ma), showing major features of assembling Pangean supercontinent and surrounding oceans. From Global Paleogeography and Tectonics in Deep Time Series (https://deeptimemaps.com/), © 2016 Colorado Plateau Geosystems, Inc. Used with license.

Figure 4. Stratigraphic positions of reviewed localities and lithostratigraphic units, excluding those from the Czech Republic (Fig. 5). Chronostratigraphic chart shows correlations between global and regional (North American and Western European) divisions of Pennsylvanian Subsystem (after Davydov et al., 2012: fig. 23.1; Richards, 2013: fig. 2) and Cisuralian Series (lower Permian; after Henderson et al., 2010: fig. 23.1; Lucas and Shen, 2017: fig. 4). Incomplete chronostratigraphic units marked with asterisk. See Section 6.1 for discussions on modified placement of Bolsovian-Asturian Substage, Missourian-Virgilian Stage, and Virgilian-Wolfcampian Stage boundaries. Position of traditional Desmoinesian-Missourian Stage boundary, which coincides with a major floristic reorganization event in peat-swamp floras in the USA, marked with row of asterisks, slightly below revised Desmoinesian-Missourian boundary. Localities and lithostratigraphic units listed in approximate order (numbered 1 to 30) presented in Section 6 and Table 2; those from western Pangea (western USA) in pink circles, west-central Pangea (Midcontinent to Appalachian regions of USA) in yellow hexagons, central Pangea (Atlantic Canada) in green squares with inverted corners, and east-central Pangea (Europe) in blue squares.

Figure 5. Stratigraphic positions of reviewed lithostratigraphic units from the Czech Republic. Chronostratigraphic chart shows global divisions for upper portion of Pennsylvanian Subsystem (after Davydov et al., 2012: fig. 23.1; Richards, 2013: fig. 2) and lower portion of Cisuralian Series (lowermost Permian; after Henderson et al., 2010: fig. 23.1; Lucas and Shen, 2017: fig. 4), correlated to radioisotopically constrained Western European divisions, based on high-precision dates from the Czech Republic (Opluštil et al., 2016b, 2016c, 2017b) and Autun Basin of the French Massif Central (Pellenard et al., 2017). Incomplete chronostratigraphic units marked with asterisk; "L. P.": Lower Pennsylvanian; Artinskian Stage begins at 290.1 Ma.

Figure 6. Map of contiguous USA, with current distribution of basins that contain coal-bearing strata of Pennsylvanian age. Position of reviewed localities and study areas of lithostratigraphic units shown: Pennsylvanian (blue squares), Pennsylvanian-Permian transition (green triangle), and Permian (red circles and hatching). Thick hatched line separates western Pangea (western USA) and west-central Pangea (Midcontinent to Appalachian regions of USA), as used herein. North arrow applies to center of map.

Figure 7. Map of Atlantic Canada (central Pangea, as used herein), showing current onshore distribution of (sub)basins that comprise Maritimes Basin (mainly upper Devonian to lower Permian strata). Position of study areas of reviewed Pennsylvanian lithostratigraphic units noted with blue squares.

Figure 8. Map of Europe, with current distribution of (sub)basins that generally contain coal-bearing strata of Pennsylvanian to Permian age (coal may be negligible or absent in some depocenters). Position of reviewed localities or study areas of lithostratigraphic units noted as blue squares (Pennsylvanian) and green triangles (Pennsylvanian-Permian transition; regional Iberian Peninsula survey denoted as green hatching). Other basins mentioned in text identified. Thick hatched line separates east-central Pangea (majority of Europe) and eastern Pangea (easternmost Europe), as used herein. North arrow applies to center of map.

Figure 9. Schematic stratigraphic log for uppermost Duckmantian Lower and Upper Radnice coals (Lower Radnice Member, Kladno Formation) in Kladno-Rakovník Basin, Czech Republic (modified from Opluštil et al., 2016a: fig. 1b). Almost all plant fossils in tuff at base of the Whetstone Horizon (Bělka, directly overlying Lower Radnice Coal) and tuffs intercalated within the Upper Radnice Coal (e.g., Velká opuka) represent peat-swamp vegetation buried in place. In contrast, almost all plant fossils in laminated, lacustrine tuffite in upper part of Whetstone Horizon (Brousek) and (where present) Velká opuka represent vegetation transported from outside of the peat-forming environment. See Section 6.2.4.2 for detailed discussions on sedimentology, taphonomy, and paleoecologic context of plant remains in Lower Radnice Member.

Figure 10. Schematic illustration of an updated "climate model", demonstrating how wetland and dryland biomes tracked climate in equatorial Pangea during the late Paleozoic. Each panel in three broad time slices (Early/Middle Pennsylvanian, Late Pennsylvanian, and early Permian) represents potential scenario for how climate zones and corresponding vegetation were distributed across a hypothetical continent-scale landscape, depending on climate mode present in basinal lowlands. Note distance between adjacent climate zones at scales of 100s to 1000s of kilometers (see variable scale bar in upper panel). Only (sub)biomes in basinal lowlands fall within "preservation window", where potential exists for long-term preservation (10^6-year) of identifiable plant fossils; vegetated extrabasinal regions provide no long-term preservation potential. Rhythmic expansion and contraction of wetland and dryland biomes

intricately linked to glacial-interglacial cycles operating on various temporal scales. See Fig. 11 for legend, and Section 7.5 for detailed explanation.

Figure 11. Legend to Fig. 10, showing key to symbols used for climate modes, (sub)biomes, and plant taxa.

CLIMATE MODE IN BASINAL LOWLANDS | CLIMATE MODES IN EXTRABASINAL REGIONS

EARLY PERMIAN

Semiarid

Subhumid

100 to 1000 km
scale variable

?

?

LATE PENNSYLVANIAN

Semiarid

Subhumid

Humid

EARLY/MIDDLE PENNSYLVANIAN

Subhumid

Humid

Perhumid

PRESERVATION WINDOW | NO PRESERVATION POTENTIAL

Distance between adjacent climate zones at scales of 100s to 1000s of kilometers

CLIMATE MODES

Perhumid   Humid   Subhumid   Semiarid   Arid

WETLAND SUBBIOMES
1a Ombrotrophic (domed) peat swamps
1b Rheotrophic (planar) peat swamps
1c Clastic swamps and associated wetlands

DRYLAND BIOMES
2 "Dryland" cordaitalean-dominated forests
3 Walchian conifer-dominated forests
4 Voltzian conifer-dominated forests

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

LYCOPSIDS
Arborescent
  1 - *Paralycopodites*
  2 - *Diaphorodendron*
  3 - *Lepidophloios*
  4 - *Lepidodendron*
  5 - *Sigillaria*
Sub-arborescent
  6 - *Polysporia*
  7 - *Omphalophloios*

SPHENOPSIDS
  8 - *Calamites*
  9 - *Sphenophyllum*

TREE FERNS
  10 - *Pecopteris s.l.*
  11 - *Acitheca*

PTERIDOSPERMS
Medullosaleans
  12 - *Neuropteris/Macroneuropteris*
  13 - *Paripteris/Linopteris*
  14 - *Alethopteris*
Peltasperms
  15 - *Autunia/Rhachiphyllum*
  16 - *Supaia/Comia*
Gigantopterids
  17 - *Delnortea/Gigantopteridium*

CONIFEROPSIDS
  18 - "Wetland" cordaitaleans
  19 - "Dryland" cordaitaleans
  20 - Walchian conifers
  21 - Voltzian conifers

OTHER PLANTS
  22 - Progymnosperms
  23 - *Lesleya/Megalopteris*
  24 - *Taeniopteris*
  25 - Cycadophytes

Legend box:

RANGE OF LITHOSTRATIGRAPHIC UNIT
solid line: well-defined
dashed line: approximated

POSITION OF LOCALITY
well-defined
approximated

EARLY PERMIAN

Western Pangea
30 Clear Fork Formation, Texas
29 Castle Hollow, Texas
28 Indian Creek, Utah
27 Abo Formation, New Mexico
26 Spanish Queen Mine, New Mexico
25 Fairplay, Colorado
24 Carrizo Arroyo, New Mexico
23 Valley of the Gods/Lime Ridge, Utah
22 Swissvale Tunnel, Colorado

PENNSYLVANIAN-PERMIAN TRANSITION

Western Pangea
18 Markley Formation, Texas

East-Central Pangea
21 Rotliegend Group, Saar-Nahe Basin, Germany
20 Remigiusberg Formation, Germany
19 Post "Asturian Phase", Iberian Peninsula

PENNSYLVANIAN

Western Pangea
3 Cañon del Cobre, New Mexico
2 Kinney Brick Company Quarry, New Mexico
1 Atrasado Formation, New Mexico

West-Central Pangea
10 Hamilton Quarry, Kansas
9 Garnett, Kansas
8 7–11 Mine, Ohio
7 Cottage Grove Mine, Illinois
6 Assemblages below Minshall Coal, Indiana
5 Central Limestone Quarry, Illinois
4 "Basin margin" assemblages, Illinois Basin

Central Pangea
14 Sydney Mines Formation, Nova Scotia
13 Tynemouth Creek Formation, New Brunswick
12 Joggins Formation, Nova Scotia
11 Boss Point Formation, Nova Scotia

East-Central Pangea
17 Douro Basin, Portugal
16 San Giorgio Formation, Sardinia, Italy
15 De Lutte-6 borehole, The Netherlands

AGE (Ma)	GLOBAL (SUB)SYSTEM	GLOBAL SERIES	GLOBAL STAGE	REGIONAL STAGE (W EUR)	REGIONAL SUBSTAGE (WESTERN EUROPE)	
290	PERMIAN*	CISURALIAN*	290.1 Ma **Sakmarian** 293.5 Ma	Autunian	upper Autunian	Boskovice Basin (study interval)
295			**Asselian** 298.9 Ma		lower Autunian (Stephanian C?)	
300	PENNSYLVANIAN*	UPPER PENNSYLVANIAN	**Gzhelian** 303.7 Ma	Stephanian	Stephanian B	Intra-Sudetic Basin
305			**Kasimovian** 307.0 Ma		Saberian	
					Barruelian	Nýřany Member
					Cantabrian	
310		MIDDLE PENNSYLVANIAN	**Moscovian**	Westphalian*	Asturian	
					Bolsovian	Lower Radnice Member
315			315.2 Ma		Duckmantian	
		L. P.*	**Bashkirian***			

Michigan
Basin

Northern
Appalachian
Basin

WESTERN
PANGEA

WEST-
CENTRAL
PANGEA

Illinois
Basin

Central
Limestone
Quarry

7–11
Mine

Western
Interior
Basin

Indian
Creek

Fairplay

Garnett

below
Minshall
Coal

Valley of the Gods
& Lime Ridge

Swissvale
Tunnel

Cañon
del Cobre

Hamilton
Quarry

"Basin
margin"
assemblages

Cottage
Grove
Mine

Spanish Queen Mine

Kinney Brick
Quarry

Carrizo Arroyo

Clear Fork
Formation

Castle Hollow

Central
Appalachian
Basin

Abo Formation

Atrasado
Formation
(Socorro
County)

Midland
Basin

Markley
Formation

Black
Warrior
Basin

N

500 km

● ///// Permian locality or study area of unit
▲ Pennsylvanian-Permian transition
  study area of unit
■ Pennsylvanian locality

OTHER COMPONENT (SUB)BASINS OF MARITIMES BASIN

NC Northern Central   DL Deer Lake
CN Central   WB White Bay
MV Marysville
MO Moncton
ST Stellarton
MI Minas
MA Mabou

N

QUÉBEC

WB

NEW
BRUNSWICK

DL

Maritimes Basin

NEWFOUNDLAND

MAINE
(USA)

NC

PRINCE
EDWARD
ISLAND

Bay St. George
Basin

CN

MV

MO

Sydney Mines
Formation

TCF

BPF

JF

MA

Sydney Basin

Cumberland
Basin

ST

NOVA
SCOTIA

MI

■ Onshore Maritimes Basin
▨ Elevated terrain (upland) within basin
■ Study area of Pennsylvanian unit

JF   Joggins Formation
TCF   Tynemouth Creek Formation
BPF   Boss Point Formation

200 km

erosively overlain by
Upper Radnice Member

Mydlák (most plant remains transported)
Stropní opuka

Modrá opuka I

Modrá opuka II

Modrá opuka III

Upper Radnice Coal

Malá opuka

Velká opuka
(swamp vegetation buried in place at base,
may contain transported plant remains
in upper part)

Whetstone Horizon

Brousek (most plant remains transported)

Bělka (swamp vegetation buried in place)

Lower Radnice Coal

1 m
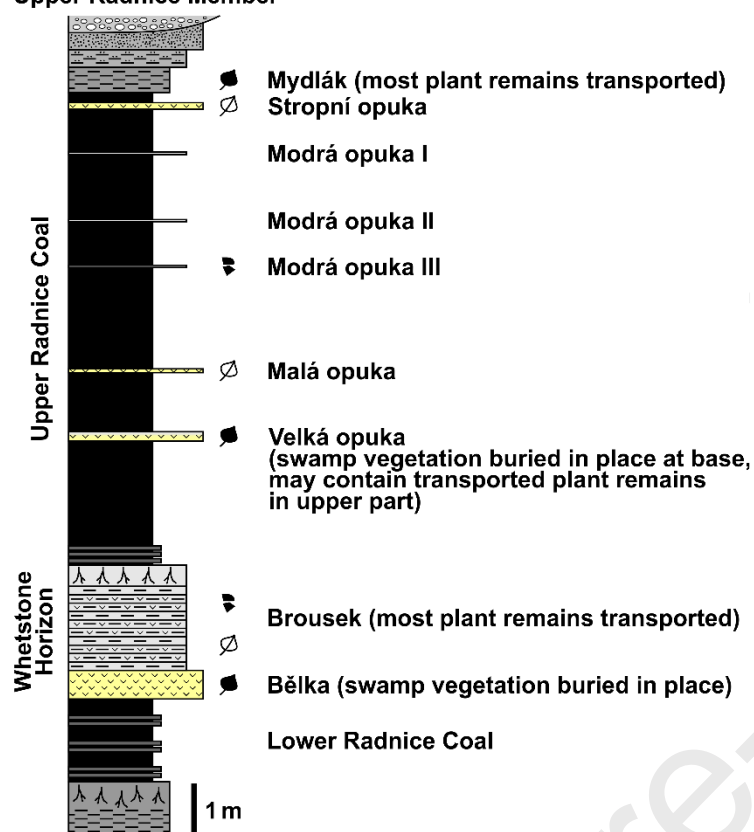
underlain by siliciclastic succession
with thin coals of Plzeň group

conglomerate		tuff	
sandstone		laminated tuffite	
siltstone		roots	
laminated mudstone		identifiable plant remains (abundant to common)	
coal with siliciclastic partings		identifiable plant remains (uncommon to rare)	
coal		comminuted plant remains	