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From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras

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ABSTRACT

Diverse wetland vegetation flourished at the margins of the Midland Basin in north-central Texas during the Pennsylvanian Period. Extensive coastal swamps and an ever-wet, tropical climate supported lush growth of pteridosperm, marattialean fern, lycopsid, and calamite trees, and a wide array of ground cover and vines. As the Pennsylvanian passed into the Permian, the climate of the area became drier and more seasonal, the great swamps disappeared regionally, and aridity spread. The climatic inferences are based on changes in sedimentary patterns and paleosols as well as the general paleobotanical trends. The lithological patterns include a change from a diverse array of paleosols, including Histosols (ever-wet waterlogged soils), in the late Pennsylvanian to greatly diminished paleosol diversity with poorly developed Vertisols by the Early–Middle Permian transition. In addition, coal seams were present with wide areal distribution in the late Pennsylvanian whereas beds of evaporates were common by the end of the Early Permian. During this climatic transition, wetland plants were confined to shrinking "wet spots" found along permanent streams where the vegetation they constituted remained distinct if increasingly depauperate in terms of species richness. By Leonardian (late Early Permian) time, most of the landscape was dominated by plants adapted to seasonal drought and a deep water table. Wetland elements were reduced to scattered pockets, dominated primarily by weedy forms and riparian specialists tolerant of flooding and burial. By the Middle Permian, even these small wetland pockets had disappeared from the region.

Keywords: climate change, paleosols, Permian, tropics, wetlands.

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INTRODUCTION

The fossil plant record of the Late Paleozoic tropics suggests a climate change from ever-wet during the Pennsylvanian to seasonally dry during the Early Permian. The floras characteristic of these different climatic conditions share few species and represent different biomes or species pools (Broutin et al., 1990; DiMichele and Aronson, 1992; Falcon-Lang, 2003): wetland, seasonally dry, or arid with a wet season. The wetland flora was dominated by lycopsids, ferns, and primitive seed plants, and first assembled in the tropics during the late Mississippian (Namurian) (Pfefferkorn et al., 2000), drawing on earlier wetlands of generally similar structure but composition that differed to varying degrees (e.g., Scheckler, 1986; Falcon-Lang, 2004a). It became progressively more areally restricted in most of the tropical belt particularly during the Permian, but in Cathaysia, present-day China representing the eastern-most parts of the tropical belt, climates remained ever-wet (Rees et al., 2002) and wetland floras very similar to those of the middle Late Carboniferous continued to survive well into the Permian (Guo, 1990; Tian et al., 1996; Hilton et al., 2001).

Floras characteristic of habitats inferred from independent sources (such as sedimentology or paleosols) to be seasonally dry existed prior to the Pennsylvanian (see for example, Scott et al., 1984) but were composed of a different flora than the one that appears in tropical seasonally dry habitats of Pennsylvanian age. This latter flora was dominated by evolutionarily derived seed plants and appears in Euramerica beginning in the early part of the Pennsylvanian (Lyons and Darrah, 1989; Falcon-Lang et al., 2004). Evidence of this derived flora occurs initially as rare and isolated deposits in red bed sequences or as fragmentary material transported into basins from nearby upland environments, and occurs only much later as well-preserved macrofossils (Cridland and Morris, 1963; Broutin et al., 1990; DiMichele and Aronson, 1992). This pattern suggests that seasonally dry floras evolved in tropical upland areas or paratropical regions (Zhou, 1994) and migrated into tropical basinal lowlands during times when these lowland basins began to experience seasonal moisture limitation. During the early and middle Pennsylvanian, such times of seasonality may have been largely during the drier periods of glacial-interglacial cycles (Cecil, 1990; Falcon-Lang, 2003, 2004b). Initially, this flora was not as highly divergent as it would ultimately be when seasonal drought became more widespread and presumably more severe in the late Pennsylvanian and Permian. The third biome, that of very dry environments with only a short wet season or seasons, was also present in the tropics and makes its first appearance near the end of the Early Permian, again in what is now western North America, which in the Permian was at the western end of the tropical landmass (DiMichele et al., 2001).

The objective of this paper is to document the final phases of this widespread vegetational change and to interpret it dynamically within an ecological context. We find that opportunistic wetland plants, because of their architecture and reproductive biology, are those most likely to survive in the fragmented wetter parts of dry landscapes. Dynamically direct resource competition among plants from wetland and seasonally dry habitats seems to play a minor part, if any at all, in the overall pattern of floristic change. Rather, environmental tracking of climatic conditions dominates the stratigraphic and spatial patterns of floristic distribution.

The pattern of change is revealed especially well in north-central Texas (Fig. 1), which preserves an excellent record of plants from the Virgilian (late Pennsylvanian/Stephanian) through the end of the Early Permian. The following synopsis is based upon surface and subsurface studies that began in the early 1990s and that now encompass ~41,000 km^2 and 15 counties in north-central Texas. This effort started as a reconnaissance of plant localities worked previously by field parties of the 1940–1941 Clay County Unit of the State-Wide Paleontologic-Mineralogic Survey (Works Projects Administration [WPA] collections, Texas Memorial Museum) and by our colleague S.H. Mamay, as well as other plant sites found by Chaney, R.W. Hook, and the late Nicholas Hotton III in the course of fossil vertebrate prospecting. From the outset, this work was interdisciplinary in nature with particular regard for the depositional context and stratigraphic position of fossil plant occurrences.

GEOLOGIC SETTING AND STRATIGRAPHY

Most of our study area lies on the Eastern Shelf of the Midland Basin. During Permian time, this region lay near the southern margin of the North American craton, inland from the Ouachita Mountains, which had arisen during Late Carboniferous time. Except for minor, intermittent fault movements along the Red River-Matador uplift (Brister et al., 2002), the Eastern Shelf was tectonically stable during the Permian. Primary sources of clastic sediment to the Eastern Shelf were the Ouachita Mountains to the east and the Arbuckle and Wichita Mountains to the northeast (Smith 1974; Hentz 1988). Gradient of the Eastern Shelf was extremely gentle, as shown by great lateral continuity of thin carbonate and gypsum beds.

Facies on the Eastern Shelf grade from terrestrial red beds on the northeast, near the source terranes, to shallow marine on the southwest approaching the Midland Basin. The outcrop belt crosses this facies trend obliquely, so that southern outcrops are generally more marine than northern. Thus, red beds of the Bowie and Wichita Groups of north-central Texas intergrade southward with marine shale and carbonate rocks of the Cisco and Albany Groups, respectively (Hentz 1988). In similar fashion, the Clear Fork Group of north-central Texas is entirely continental, yielding terrestrial plant and vertebrate fossils. Southward, interbeds of marine limestone and dolomite increase in number and thickness (Olson 1958, 1989; Olson and Mead 1982). The Pease River Group comprises two units: the San Angelo Formation of sandstone and conglomerate and the overlying Blaine Formation of interbedded mudstone, carbonate rock, and gypsum representing shallow marine and coastal sabkha settings. The San Angelo comprises an upward-fining clastic wedge derived from the Llano Uplift, which merges with a similar but smaller wedge

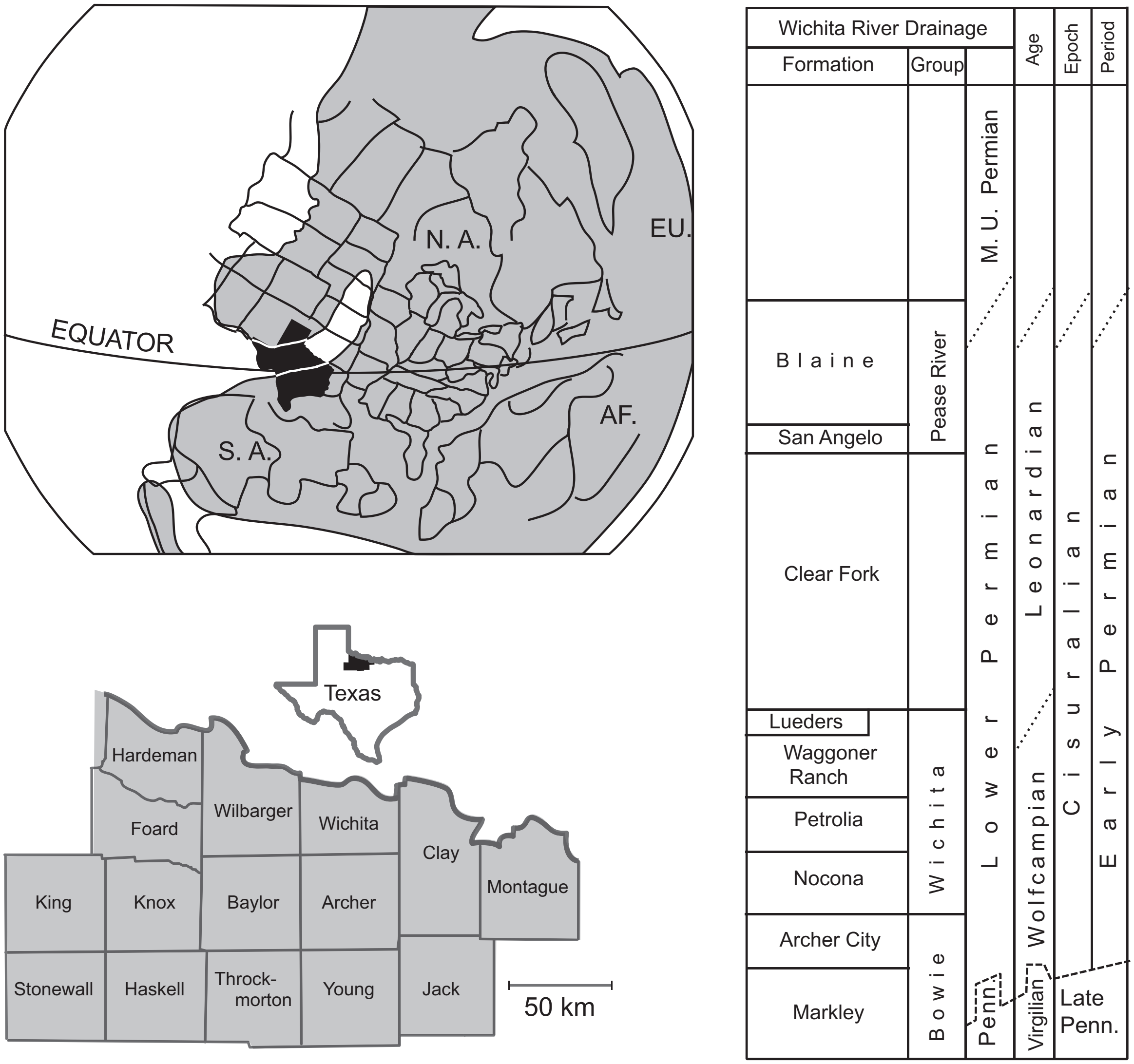

Figure 1. Study area in paleogeographic, modern geographic, and stratigraphic context. Top left: Paleogeographic map projection of Early Permian (from Christopher Scotese, Paleomap Project): N.A.—North America, EU.—Europe, S.A.—South America, AF.—Africa. Land areas shown in shading; oceanic areas in white. Texas is shown in black. Bottom left: Texas with study area in north-central region shown in black; counties shown below. Right: Stratigraphic nomenclature as used in this paper (refer to text).

from the Wichita Mountains. The upper San Angelo intergrades with the Blaine; sandstones pinch out in subsurface a short distance west of the outcrop (Franklin 1951; Mear 1963 and 1984; Smith 1974).

Age determinations on the Eastern Shelf are based on marine fossils, principally fusulinids, ammonoids, and nautiloids. Most authors place the Carboniferous-Permian boundary within the Harpersville Formation of the Cisco Group, correlating with the Markley Formation of the Bowie Group (Roth, 1931; Dunbar and Skinner, 1937; Plummer and Scott, 1937; Henbest, 1938; Miller and Youngquist, 1947). The Wolfcampian-Leonardian boundary apparently lies close to the Elm Creek Limestone in the Albany Group, which equates to the basal Petrolia Formation in the Wichita Group (Bose, 1917; Sellards, 1932; Plummer and Scott, 1937; Miller and Youngquist, 1947; Hentz and Brown, 1987). This horizon corresponds to the first appearance of gigantopterid plants in north-central Texas (Read and Mamay, 1964). The Leonardian-Guadalupian boundary on the Eastern Shelf is rather controversial, being based on scattered ammonoid finds in the Blaine. The weight of evidence favors placing this boundary within the Blaine (DiMichele et al. 2004).

PALEOCLIMATIC TRENDS

Paleoclimatic conditions in the study area have been inferred from four lines of evidence: (1) the nature of the primary sedimentary deposits, (2) the character of the paleosols, (3) the taxonomy and physiognomy of fossil plants, and (4) animal fossils, including trace fossils such as burrows and aestivation assemblages. Sedimentary patterns integrate climate and regional patterns of drainage with tectonics. Paleosols reflect local topographic and drainage signatures overprinted by regional climatic conditions. Plant fossils, especially those that were transported only short distances prior to burial and fossilization, reflect the local conditions proximal to the site of deposition.

Based on all these lines of evidence, we infer a trend toward generally drier conditions from the late Pennsylvanian through the end of the Early Permian in the north-central Texas study area. These changes were neither gradual nor continuous. There are some clear, relatively abrupt, directional changes in the succession and some intervals during which climate appears to have fluctuated repeatedly and, on average, non-directionally.

Lithologic Patterns

Bowie Group

The Bowie Group encompasses the Markley and Archer City Formations. The Markley Formation (Figs. 2A and 2B) is composed mainly of mudstone and sandstone, along with minor deposits of conglomerate, limestone, coal, and underclay. Fluvial sandstones are a prominent part of the Markley Formation, both at the surface and in the shallow subsurface. Braided fluvial channels are a common part of these deposits with a change to meandering fluvial systems up-section and westward (Galloway

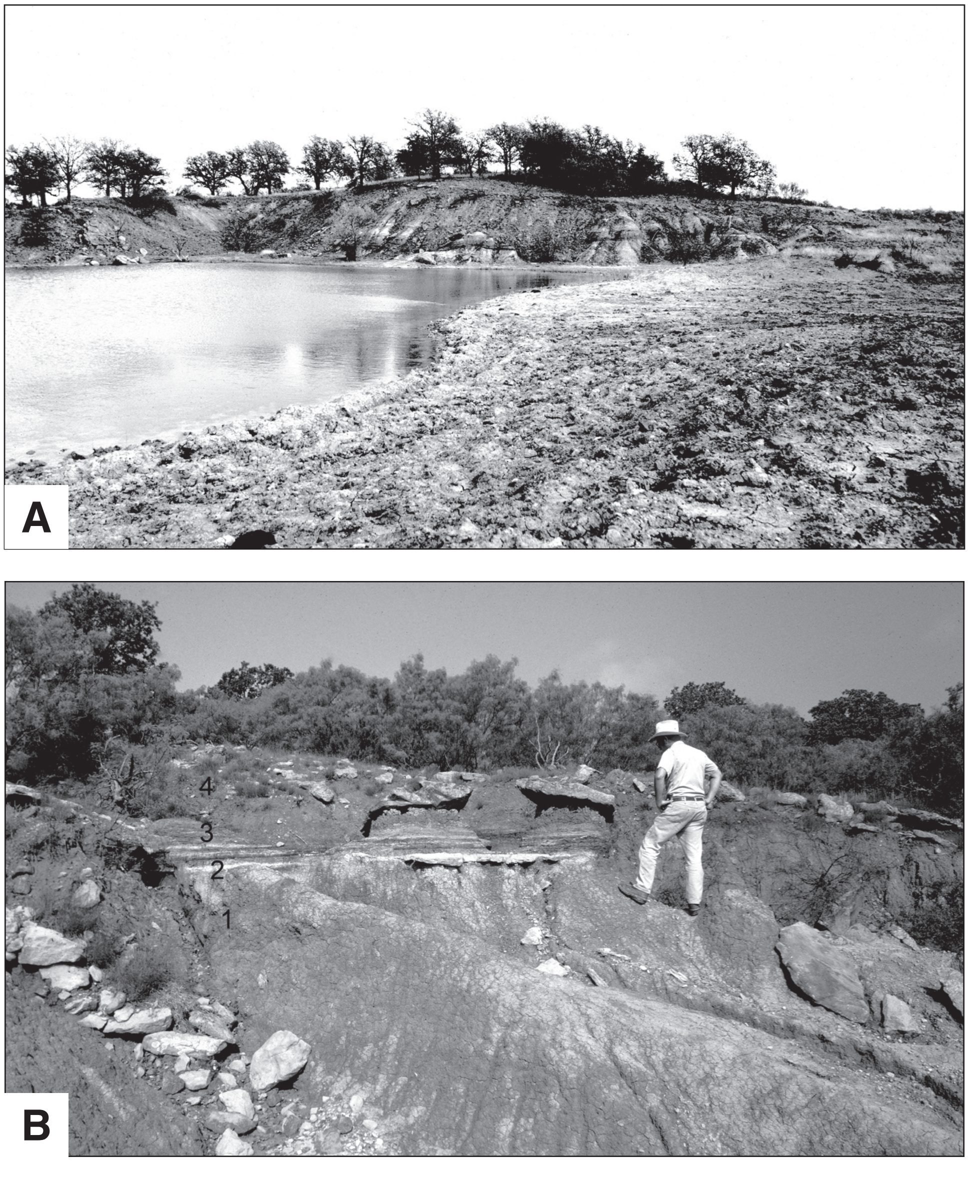

Figure 2. Upper Pennsylvanian outcrops showing basic sedimentological features. (A) "Walker" locality (NMNH 40007), Markley Formation, Pennsylvanian-Permian transition. Note shallow U shape of the deposit; paleosol at base. (B) "Maxey Ranch" locality (NMNH 40602), Markley Formation, Pennsylvanian-Permian transition. Details of typical lithological succession outcrops of this age and type. 1—Basal paleosol of Pedotype B. 2—Kaolinite layer at top of Pedotype B typical of lithologies enclosing a seasonally dry plant assemblage. 3—Organic shale layer, Pedotype A, containing a plant assemblage typical of swampy, ever-wet conditions. 4—Mudstones and sandstones deposited in a flood basin setting enclosing a plant assemblage of ever-wet conditions.

and Brown, 1972; Hentz and Brown, 1987; Hentz, 1988; Brown et al., 1987, 1990; McGowen et al., 1967 [1991]).

The Archer City and Markley Formations are very similar lithologically (Hentz and Brown, 1987). In general, fluvial sandstones of the Archer City Formation represent multistoried, high-sinuosity meandering channels (Sander, 1989). As detailed below, most of the Archer City mudstones exhibit paleosol characteristics typical of younger formations. Pedogenic carbonates first occur in this formation, and only a few exposures include organic shales rich in plant fossils, indicative of swamp conditions.

The widespread occurrence of bituminous coal in the Bowie Group is critical to an understanding of paleoclimatic conditions that prevailed during the latest Carboniferous and earliest Permian of this region. Coals within the Markley Formation have been mapped on outcrop from near the Red River in the Colorado River Valley, a distance of ~300 km, and from well data nearly 140 km westward in the subsurface (Mapel, 1967), indicating long periods of time during which climate was wet enough for peat formation to occur over large areas.

The distribution of Bowie/Cisco sandstones in the subsurface, as shown by well-log analysis, is a second point of paleoenvironmental importance. Sandstones exposed on outcrop have little basinward persistence. Sands appear to have become impounded in the vast, low-energy coastal plain that existed along the margin of the Eastern Shelf, which corresponds to sediment-starved conditions in the Midland Basin. This pattern continued through the Wolfcampian and Leonardian, even during periods of elevated clastic influx in the lower Clear Fork and basal Pease River Groups, and presaged the development of coastal evaporite pans in the Leonardian.

Wichita Group and Lueders Formation

The Wichita Group and Lueders Formation, in gross sedimentological character, comprise a large-scale fining-upward sequence that records a shift from alluvial upper coastal plain environments to lower coastal plain settings (Hentz 1988). That is to say, the coastline advanced landward transgressively over time.

Relatively few plant-bearing localities have been found in the Nocona Formation. This impoverished record contrasts with the abundance of vertebrate localities known from these same strata (Hook, 1989) and may be a taphonomic effect, the lack of plant preservation obscuring the true pattern of plant occurrences at that time.

Numerous plant deposits have been found in the overlying Petrolia Formation (Fig. 3B), dating back to some of the earliest collectors in the area (e.g., White, 1911). Additional plant localities occur in equivalent formations of the northern Albany Group in southern Baylor County; foremost among these is the Emily Irish locality (Mamay, 1968). The Petrolia Formation is mudstone dominated, and most sandstones in the southwestern portion of the outcrop represent single storey, suspended-load deposits of high-sinuosity fluvial channels. Local beds of carbonate-pebble and mudstone-clast conglomerate that contain mixed assemblages of fragmentary marine invertebrates and freshwater to terrestrial vertebrates are thought to represent supratidal storm deposits (Parrish, 1978; Hentz, 1988). Channel-fill deposits may contain a variety of animal fossils, some suggestive of brackish-water, especially in the lower and upper parts of the formation, and thus possibly tidal channels. Included are the following seen by us and reported by Hentz (1988): sharks and bony fishes of both freshwater and marine types; spirorbid and serpulid worms, various pelecypods including *Pinna*, and pecenoids; nautiloids and ammonoids; scraps of tetrapod bones—thus, a mixture of nonmarine, brackish, and fully marine life forms, although most of the latter might have been washed or driven ashore during storms. Unequivocal evidence of tidal sedimentation is lacking.

In the subsurface, the middle to upper part of the Petrolia Formation and equivalent rocks of the Albany Group include extensive deposits of dolomite and bedded anhydrite, or, at shallow depths, gypsum (Moore, 1949), which split and thin eastward into mudstones and pinch out in western Throckmorton and central Baylor Counties (Abilene Geological Society, 1949, 1953) and coincide with increased pedogenic carbonates and decreased fluvial sedimentation. This represents the first occurrence of widespread evaporites in the lower coastal plain, a facies pattern that recurs throughout Leonardian time in the region.

The Waggoner Ranch Formation includes brackish to possibly marine invertebrates and vertebrates in restricted channel-form lenses that may represent tidal deposits similar to those of the underlying Petrolia Formation (Read, 1943; Johnson, 1980).

Although it is a thin unit (15–25 m), the Lueders Formation of north-central Baylor County has attracted considerable paleontological interest (Berman, 1970; Dalquest and Kocurko, 1986, 1989). Plant, invertebrate, and vertebrate remains occur in small channel deposits. We tentatively interpret these as tidal channels, although they lack a clear lithological signature of tidal deposition, on the basis of the following evidence: brackish-water invertebrates together with terrestrial plants and tetrapods; channels laterally correlative to or intercalated with carbonate rocks containing marine invertebrates such as cephalopods.

At least two failed vertebrate aestivation assemblages, i.e., colonies of dozens to hundreds of calcified burrows containing skeletal remains of their inhabitants, occur in the Lueders Formation; "failed" aestivation ends in death for the animal, suggesting, especially when found in large numbers, that conditions suitable for reemergence did not reappear in a timely manner. More specifically, prolonged drought probably killed these animals in their burrows. In north-central Texas, such concentrations of lungfish and lysorophoid amphibian skeletons were generally thought to be limited to the Clear Fork Formation, but we verified in the field that the aestivation assemblages reported by Romer and Olson (1954) and Dalquest and Carpenter (1975) occur, respectively, in the uppermost and lowermost Lueders Formation. These older Leonardian aestivation assemblages reiterate the development of seasonal-moisture stress in coastal plain environments as indicated by paleosol data.

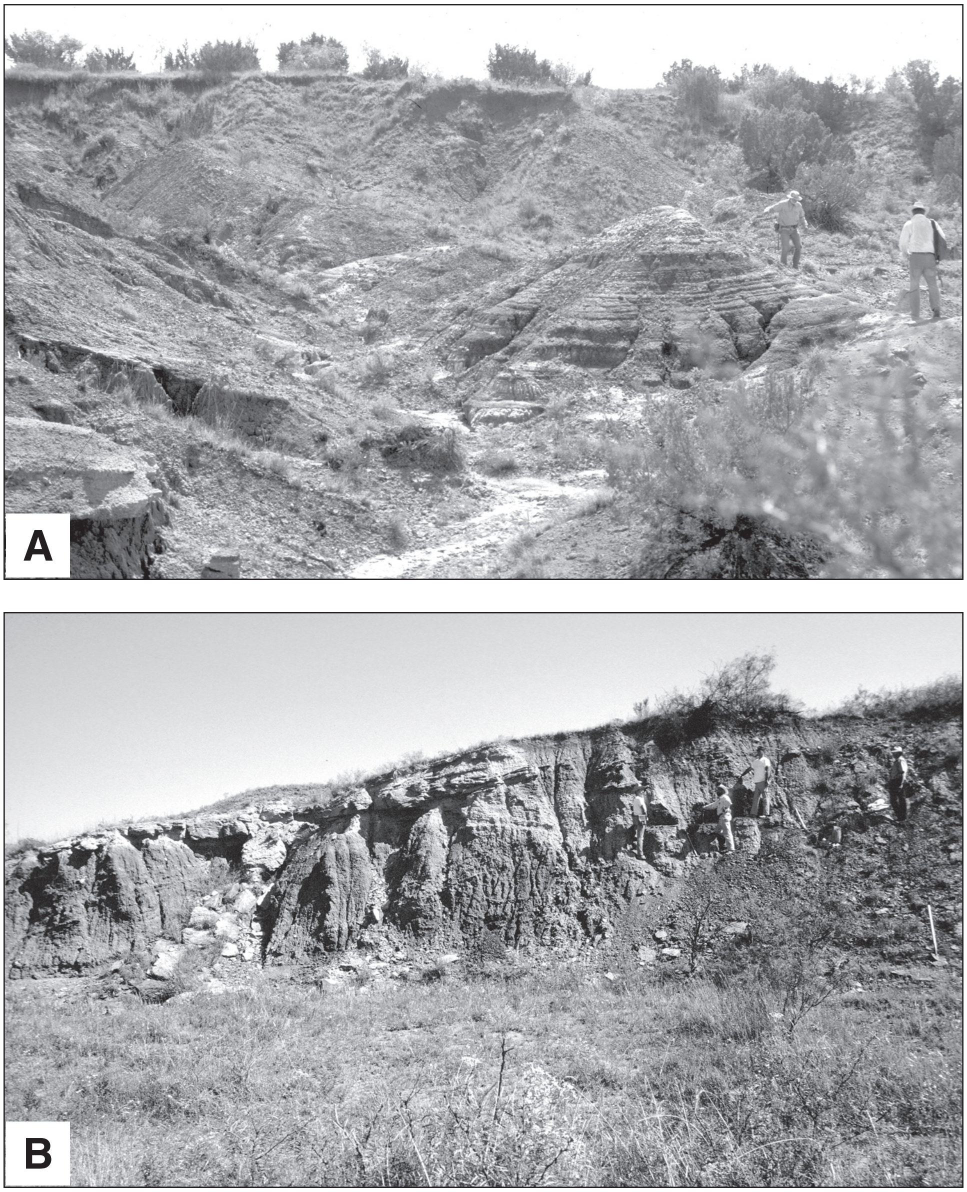

Figure 3. Lower Permian outcrops showing basic sedimentological features. (A) “North of Cedar Top” locality (NMNH 40972), middle Clear Fork Formation, Lower Permian. Note U shape of deposit and laminated, claystone fill. (B) “Red Hollow” locality (NMNH 40032), Petrolia Formation, Lower Permian. Paleosol at base truncated by active channel with features include trough cross beds, erosional contacts and multistory architecture. Plant fossils occur in swales of cross beds.

Clear Fork Formation

In this paper we classify the Clear Fork in north-central Texas as a formation that is informally divided into three parts, as outlined by Nelson et al. (2001). The lower 55–70 m in the general area of Lake Kemp includes a thin but widespread (<0.5 m) dolomite bed and two widespread fluvial channel belts. The dolomite resembles intertidal to supratidal dolomites of the underlying Wichita/Albany Groups. The lower sandstone belt consists of multistory, suspended-load deposits of a high-sinuosity, meandering system. Numerous, claystone-rich channel fills (Fig. 3A) within this lithofacies have yielded the majority of lower Clear Fork plant and vertebrate remains. In contrast, the upper sandstone belt is coarser grained, contains no significant fossiliferous channel fills, and is distinguished by large-scale bedforms characteristic of high-energy braided fluvial channels. Lower Clear Fork mudstones generally are reddish-brown and exhibit well-developed paleosol features described below. Other than failed aestivation assemblages (Olson and Bolles, 1975), fossil remains are exceedingly sparse in these well-drained flood-plain facies.

The middle 125–160-m-thick portion of the Clear Fork includes three mappable fluvial channel belts, all of which are similar sedimentologically and paleontologically to the high-sinuosity, suspended-load fluvial channel belt of the lower Clear Fork (Edwards et al. 1983) (Fig. 4). Upward in the middle Clear Fork, pedogenic carbonates gradually diminish and gypsum nodules, veins, and stringers increase in both vertical distribution and lateral persistence. Failed vertebrate aestivation assemblages occur intermittently through the middle Clear Fork section.

Figure 4. Lower Permian outcrop showing basic sedimentological features. "North Fork Pens" locality, middle Clear Fork Formation, Lower Permian, illustrating large scale accretion beds deposited in active channel and containing fossil plants.

The upper 165–180 m of the Clear Fork Group is a monotonous succession of reddish-brown, gypsum-rich mudstones that is nearly devoid of significant sandstone deposits. A few fossil localities are represented by channel-fills and an aestivation assemblage in the lowermost part of the upper section, but the remainder is nonfossiliferous (Olson, 1958; Murry and Johnson, 1987). The combination of dolomite and bedded anhydrite is common in the subsurface and indicates primary evaporites in the lower coastal plain.

Pease River Group

The Pease River Group consists of two formations in north-central Texas, the San Angelo and Blaine. In its lower portions the San Angelo consists of sandstones that Smith (1974) reported to be of a deltaic origin. Examination of these and other exposures indicate that sandstones of the San Angelo Formation are fluvial and have bedding characteristics of broad, shallow, multi-channel systems in some outcrops, and of incised, suspended-load, meandering streams in others. The upper half of the San Angelo Formation is composed mainly of red mudstones, small, discontinuous tabular and channel sandstones, and gypsum nodules. The contact with the overlying Blaine Formation is gradational and placed by convention at the lowest occurrence of bedded gypsum (Hentz and Brown, 1987). The Blaine Formation is composed chiefly of reddish-brown and gray-green siltstones, gypsum beds up to ~10 m thick, and regionally persistent dolomite beds. Local concentrations of marine invertebrates (gastropods, pelecypods, and cephalopods) preserved in some dolomite beds may represent storm-washed deposits (Clifton, 1944; Jones and Hentz, 1988). Rhythmically interbedded mudstones, dolomites, and gypsum in the lower to middle Blaine Formation have been interpreted as a combination of tidal flat and sabkha deposits (Smith, 1974). Bedded salt deposits in excess of 2 m thick occur in the upper part of the Blaine Formation in the subsurface of western King and Stonewall Counties.

An impoverished and generally fragmentary record of almost exclusively terrestrial vertebrates is known from the San Angelo of our study area (Olson, 1962); large herbivores are a significant part of this record. No terrestrial vertebrates have been reported from the Blaine Formation of Texas. As noted below, fossil plants also are rare in the Pease River Group. A series of presumed tidal-channel deposits near the San Angelo-Blaine contact contains a precocious flora that is distinct from all other Permian records in the region (DiMichele et al., 2001). Some 164 m higher in the section, a single upper Blaine deposit that also originated as a coastal plain channel has produced a flora that, again, is unique, though of low diversity (DiMichele et al., 2004). Nearly all the Pease River plant occurrences are accompanied by local concentrations of copper minerals in partially pyritized fossil wood.

Paleosol and Geochemical Evidence and Patterns

The characteristics and stratigraphic distribution of soil types, which we refer to here as "pedotypes" (sensu Retallack 1994), are perhaps the most direct indicator of moisture availability in terrestrial paleoenvironments. Virgilian through Leonardian rocks of north-central Texas include eight major pedotypes (soil types), designated A through H, and defined by paleosol (ancient soil) structure (horizonation, structure, fabric, and color), mineralogy, and chemical characteristics (Figs. 5–7). The following descriptions and interpretations are summarized from the detailed treatment of Tabor and Montañez (2004).

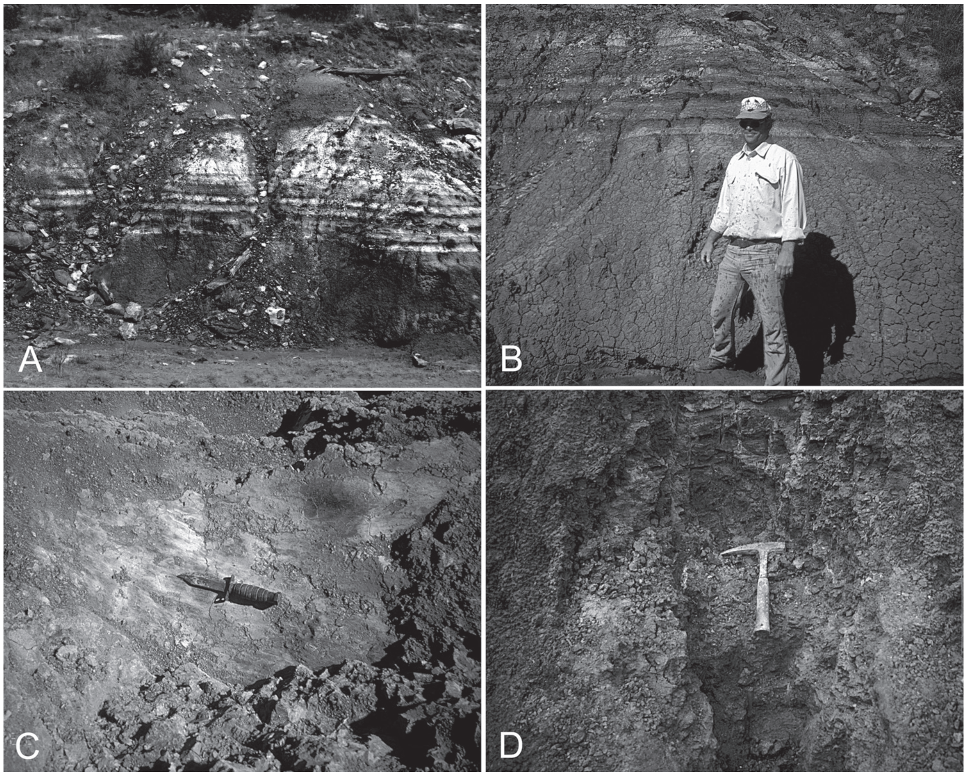

Figure 5. Paleosol types from study area. (A) Pedotype A above Pedotype B at "Cooper" locality (NMNH 39991), Markley Formation, upper Pennsylvanian. (B) Pedotype A above Pedotype B at "Cooper" locality (NMNH 39991), Markley Formation, upper Pennsylvanian. (C) Slickensides typical of Pedotype D and Pedotype G, Nocona Formation stratotype, Lower Permian. (D) Clastic dykes typical of Pedotype D and Pedotype G, Nocona Formation stratotype, Lower Permian.

Paleosols are an important component of Virgilian through Leonardian strata of the Eastern Shelf. Pedotypes A through D occur only in the Virgilian and lower Wolfcampian Bowie Group. These paleosols have morphological, mineralogical, and chemical characteristics indicative of ever-wet to seasonally dry conditions. In particular Pedotypes A–D preserve redoximorphic features, which are recognized by "redox depletions" and "redox concentrations." Specifically, redox depletions refer to drab gray, yellow, and green colors of the paleosol matrix and/or mottles, whereas redoximorphic concentrations are nodular or vermicular concentrations of red, orange, and bright yellow (e.g., hematite, goethite, jarosite; e.g., Vepraskas 1994). In modern soils, redoximorphic features form in seasonally saturated profiles through removal of Fe and Mn from areas of low Eh (redox depletions) and re-precipitation as Fe- and Mn-oxides (redox concentrations) in better-oxidized areas. Gley matrix colors indicate reduced conditions, which are typical of relatively prolonged saturation (25%–50% of the year), whereas yellow-brown to reddish mottles record seasonal soil drying (Daniels et al., 1971; Duchaufour, 1982). By analogy to modern soils, paleosol redoximorphic features are interpreted to have formed in seasonally saturated portions of the profile with sufficient organic content to yield reducing conditions (see Pipujol and Buurman 1994). Preservation of these features likely reflects alternating episodes of soil saturation and aeration (Soil Survey Staff, 1975, 1998).

Pedotypes F through H occur only in Permian (Wolfcampian and lower Leonardian) rocks within the study area. These paleosols have a range of morphological, mineralogical, and chemical characteristics indicative of seasonally dry to seasonally wet moisture budgets that reflect a seasonal climate regime. Both the morphological diversity and stratigraphic occurrence of paleosols are greatly diminished in the late Leonardian San Angelo and Blaine Formations. The vast majority of the floodplain facies in these formations exhibit little or no diagnostic evidence of pedogenesis. The most common profiles at this stratigraphic level are weakly developed, thin (<50 cm) type E paleosols, which have characteristics indicative of a shallow fluctuating water table leading to alternating oxidation and reduction of iron compounds and associated mottling. In addition, these paleosols are observed typically as weakly rooted horizons within channel sandstones that apparently developed along banks of fluvial and/or tidal channels.

Pedotype A (Histosols)

Pedotype A (Figs. 5A, 5B, 8, 9) is characterized by an upper organic layer of weakly degraded plant material and an underlying fine angular blocky kaolinitic claystone that contains abundant, thin root traces that are relatively shallow in the profile (~10 cm) and have a tabular orientation. Type A paleosols occur in the Markley Formation. They are developed within laminated to thin-bedded claystones and silty claystones that, on outcrop appear to be shallow depressions on poorly drained flood plains and coastal plains. Bituminous coal to highly carbonaceous shale forms the organic-rich portion of these paleosols, which may

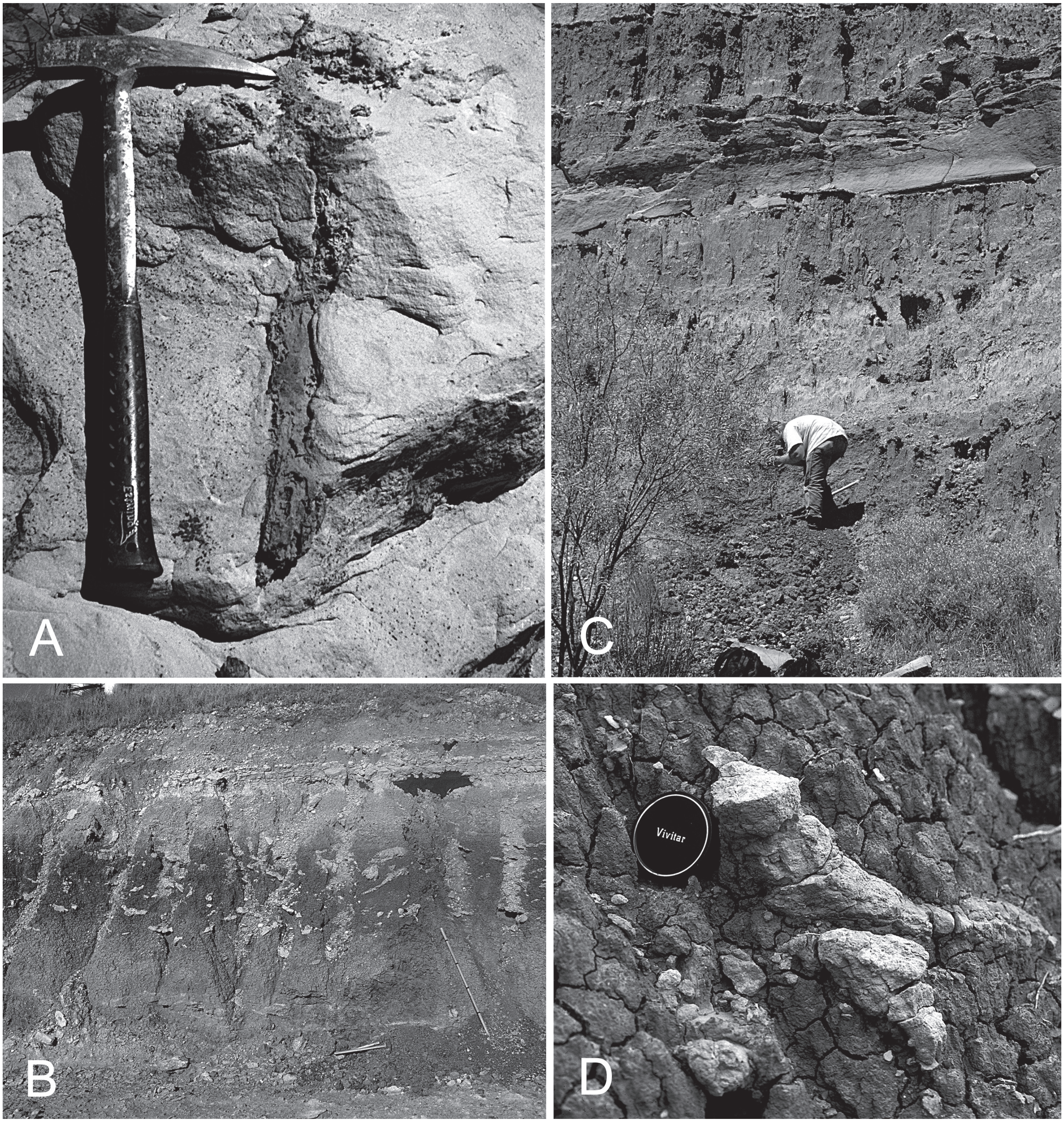

Figure 6. Paleosol types from study area. (A) Rhizolith in Pedotype E, Wellington Formation (Oklahoma), Lower Permian. (B) Pedotype G at "Grayback" locality (NMNH 40059), Lueders Formation, Lower Permian. (C) Pedotype H at "Wichita River Cutbank" locality, Waggoner Ranch Formation, Lower Permian. (D) Rhizolith in Pedotype H, near "FM 1919 Lungfish" locality, middle Clear Fork Formation, Lower Permian.

Figure 7. Paleosol from study area. Pedotype H with calcic horizon, near Little Moonshine Creek, upper Waggoner Ranch Formation, Lower Permian.

have been similar to modern, peat-bearing Histosols (Soil Survey Staff, 1998). Paleosols of this type are good indicators of regional climate when they are observed to extend over wide geographic areas. Small isolated pockets of this pedotype might indicate a micro-environment on a landscape.

Pedotype B (Ultisols)

Pedotype B (Figs. 5A, 5B, 8, 9) consists of two intergradational units, an upper highly differentiated kaolinitic claystone that has an angular blocky structure with clay coatings, and a lower massive claystone cemented by iron and manganese oxides with redoximorphic features. Type B paleosols are found in the Markley Formation, stratigraphically associated with Pedotypes A and C, and are developed within mudstone and claystone deposits of flood-plain facies. The upper portion of the claystone is interpreted as an argillic (clay-rich) horizon, whereas the lower, iron-cemented claystone is interpreted as a plinthite horizon. The redoximorphic features and plinthite horizon record fluctuation of a relatively shallow water table and saturation of soil horizons at depth (Duchaufour, 1982; Soil Survey Staff, 1998); moreover, the argillic (Bt) horizon of Type B paleosols requires periodically well-drained conditions.

As modern parallels of periodic soil drainage, consider the flood plains along the Mekong, Yellow, Missouri, Mississippi, Nile, Amazon, and every other pre-historical flood plain that did not have a natural dam. During the rainy season, or after large, individual rainfall events, rivers overtop their levees and flood extensive regions of their flood plains, saturating soils. Such flooding leads to soil anoxia with relatively little physical transport of solids within the soils. After flooding has waned and soils have drained, subsequent rainfall may pass through the soil profile by way of percolating, free drainage. Under these conditions, physical transport of solids and chemical leaching occurs and may lead to the formation of argillic horizons. This scenario is common in nature and is explicitly related to dynamics of the groundwater table.

Pedotype B is interpreted as an Ultisol that formed upon relatively better drained local topographic highs (or more permeable substrates) within Permo-Carboniferous flood plains and coastal plains, possibly pedogenesis upon stream levees or stream terraces (see Markewich and Pavich, 1991).

Pedotype C (Inceptisols)

Pedotype C (Figs. 8, 9) is a highly differentiated mudstone with weak, angular, blocky structure and a plinthite horizon at or very near the presumed upper surface of the paleosol. Redoximorphic features are present in the upper portions of these paleosols. Deeper portions are massive and grade downward to weakly laminated, green to brown mudstone. Type C paleosols occur primarily in the Markley Formation and into the basal most parts of the Archer City Formation. They are developed within mudstones and claystones of flood-plain facies and are generally stratigraphically associated with channel sandstones. The presence of redoximorphic features and plinthite horizons near the surface of the paleosol record a shallow, fluctuating paleogroundwater table and generally poorly drained conditions during soil formation (see Duchaufour, 1982). Pedotype C paleosols are interpreted to have been inceptisols that likely developed upon flood-plain deposits near fluvial channels, but intervals between floods were long enough to permit development of soil structure and horizonation (Kraus, 1987; Wright and Marriott, 1996). Although this pedotype is broadly distributed across the Pennsylvanian flood plains, its morphological characteristics are attributed to local, micro-environmental controls related to a shallow, fluctuating groundwater table.

Pedotype D (Vertisols)

Pedotype D (Figs. 5C, 5D, 8, 9) consists of red smectitic (expandable clays) mudstone that grades downward to gray smectitic mudstone with wedge-shape aggregate structure, slickensides, and sand-filled clastic dikes. Redoximorphic features are present throughout the profile. Type D paleosols occur in the Markley Formation in association with type E paleosols (above Sandstone (ss) 13 [Hentz, 1988] on Figs. 2, 5C, 5D).

Type D paleosols are developed within mudstone intercalated with cross-laminated sandstones of the braid-bar facies, reflecting their restricted distribution in the western portion of the study area (Hentz, 1988). The wedge-shaped structure, slickensides, and clastic dikes are all indicative of strongly contrasted seasonal wetting and drying, typical of Mediterranean or monsoon-type climates (Soil Survey Staff, 1998). However, the presence of redoximorphic features throughout these paleosols indicates moist, aquic (high water table) conditions for extended periods punctuated by only short intervals of soil-moisture deficit (drought, or drying). Type D paleosols are interpreted as aquerts that were strongly influenced by local factors such as a shallow water table. Nevertheless, this characteristic morphology is indicative of strongly contrasted, seasonal changes in moisture availability upon portions of the Pennsylvanian flood plains.

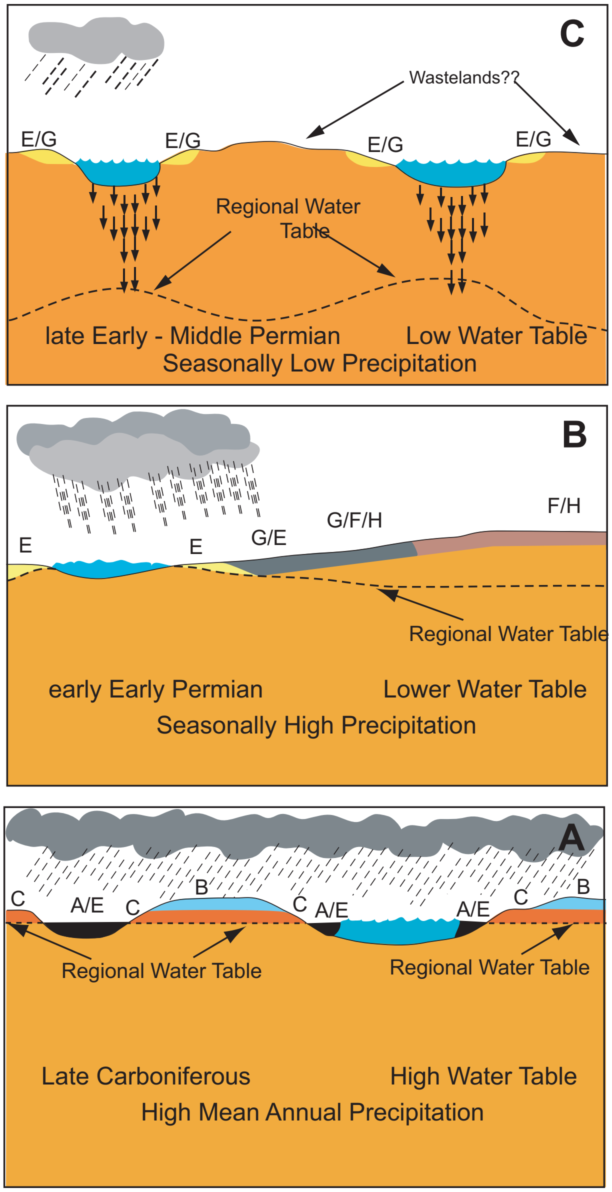

Figure 8. Diagrammatic representation of pedotype development on the landscape in relation to groundwater supply. Pedotypes marked by letters. (A) Late Pennsylvanian ever-wet conditions. (B) Early Permian seasonally dry conditions. (C) Middle Permian with short wet season.

Pedotype E (Entisols)

Pedotype E (Figs. 6A, 8, 9) is composed of poorly differentiated, massive sandstone with several superimposed horizons of vertical and laminar, iron-oxide-rich root traces and hematitic nodules. These paleosols are the most common and widely distributed of those found in the north-central Texas section, occurring throughout the upper Pennsylvanian and Lower Permian.

The most diagnostic evidence of soil formation typically found in these weakly developed paleosols is rooting structures and rhizoliths (e.g., Fig. 6A). They are developed in (1) finely laminated or bioturbated mudstones that cap cross-laminated, fine-grained sandstones of levee, crevasse splay, and proximal lacustrine deposits and (2) sandstones of levee and crevasse splay deposits. The great majority of type E paleosols in the Bowie Group exhibit redoximorphic features. In the Permian section, these paleosols are the only pedotype that may be gleyed, meaning soils that exhibit mottled drab yellow, gray, and green colors due to intermittent water saturation and the associated oxidation and reduction of iron compounds. These characteristics are indicative of generally very wet conditions likely associated with a shallow water table. The development of these paleosols is controlled by the availability of shallow groundwater, even in driest times. Such conditions reflect "humid" micro-environmental conditions upon the paleolandscape. Although this pedotype is observed throughout the Permo-Pennsylvanian strata of north-central Texas, it is particularly important to note that such paleosols are observed in strata with independent lithological and geochemical evidence that is indicative of regionally dry climate (Tabor et al., 2002; Tabor and Montañez, 2004). These humid micro-environments are most likely the paleosols of "wet spots" upon the paleolandscape and therefore may have provided the substrates upon which many of the fossil plants grew in the Lower–Middle Permian strata of north-central Texas.

Pedotype F (Alfisols)

Pedotype F (Figs. 8, 9) is a highly differentiated angular blocky red mudstone with clay skins in the upper horizons and calcium carbonate nodules and vertically oriented calcareous rhizoliths (root casts or traces replaced by calcite) at depth. Type F paleosols are found throughout the Lower Permian strata of the study area. They occur most commonly in the mud-rich strata of the flood-plain facies.

Pedotype F compares most favorably to Modern Alfisols, which form on stable, well-drained portions of the landscape in subhumid to semiarid climates (Franzmeier et al., 1985; Retallack, 1990); Alfisols typically do not occur in climates characterized by exceedingly high rainfall (~1200 mm/yr) and extensive hydrolysis of base-rich parent material and soil (Buol et al., 1997; Soil Survey Staff, 1975). They are a typical component of tropical landscapes with limited rainfall (Wilson, 1999). The

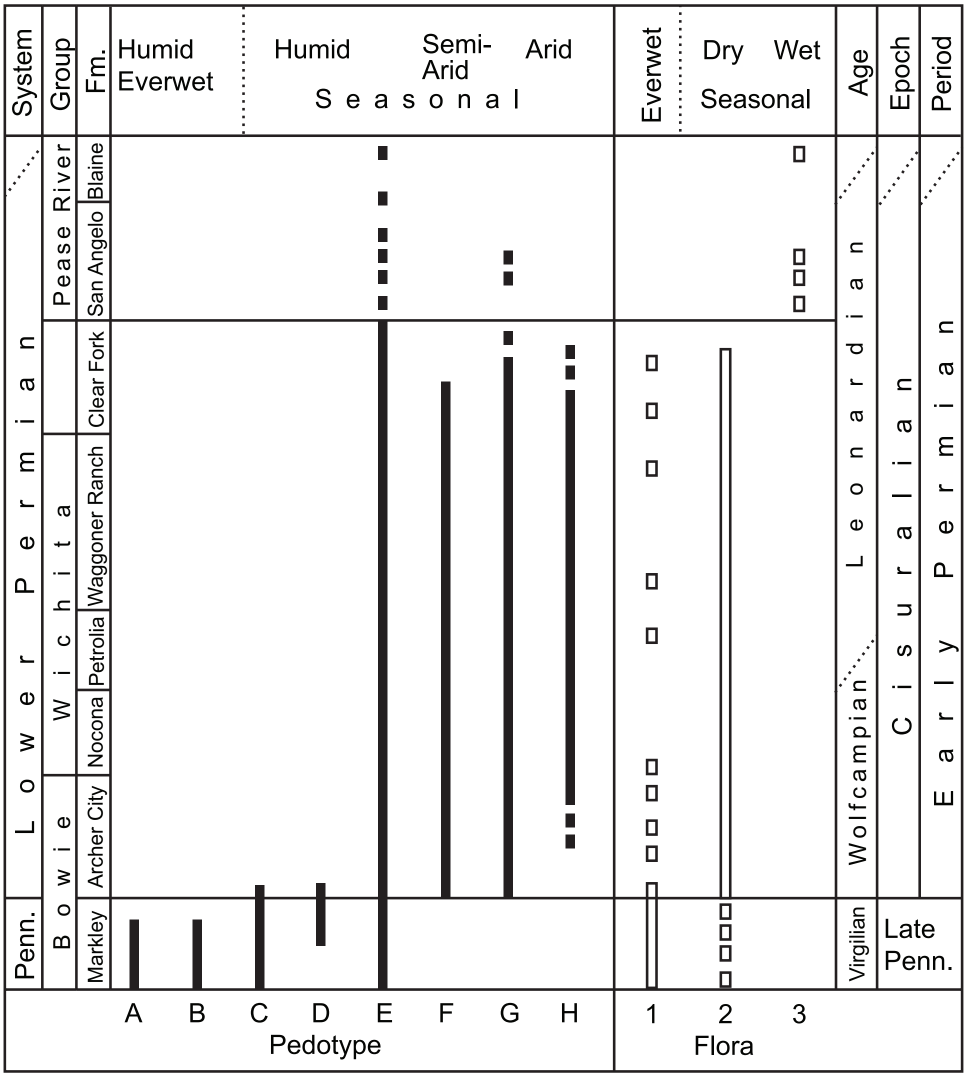

Figure 9. Stratigraphic distributions of pedotypes and paleofloras. Formational thicknesses not to scale.

dominant pedogenic process in the Alfisol order is translocation of expansible 2:1 phyllosilicates (e.g., smectite). Translocation of these clay-size particles is facilitated by leaching of Ca^{2+} from phyllosilicate interlayers. Type F (Alfisols) are typically leached of carbonate above and within the upper layers of argillic horizons, further indicating that these paleosols formed in a manner analogous to modern Alfisols. Pedogenic carbonate beneath noncalcareous argillic horizons in type F (Alfisols) likely indicates formation in a xeric, or semiarid, dry soil moisture regime, characterized by incomplete soil leaching due to seasonal drying (Buol et al., 1997; Soil Survey Staff, 1975).

We interpret type F (Alfisols) to have developed upon stable topographic highs of the interchannel flood-plain facies. This interpretation is based on the fine-grained nature of the sedimentary strata associated with the profiles, and features such as argillic horizons, that formed upon older, more stable portions of the landscape (Soil Survey Staff, 1975; Buol et al., 1997). Profiles were apparently well drained and formed well above the water table, judging from (1) the presence of argillic horizons and (2) oxidized paleosol matrix colors without redoximorphic features.

In contrast to Pedotype E, Pedotype F paleosols can be regionally extensive and are reasonably good indicators of regional climate. Although these paleosols do indicate an abundant flora (e.g., Retallack, 1990) during soil formation, they are also indicative of stable landscapes that are distal from major depocenters. In this regard, the floras associated with these paleosols are not likely preserved as part of the fossil record.

Type G (Vertisols)

Type G paleosols (Figs. 6B, 8, 9) have highly differentiated profiles with red to brown claystone, wedge-shaped aggregate structure, slickensides, and calcium carbonate nodules. Smectite is the dominant mineral in the <2 μm fraction of this profile, with trace amounts of kaolinite and weathered micas. Type G paleosols are found throughout the Lower Permian, from the Archer City through the Clear Fork Formations and sporadically in the San Angelo Formation. They developed in fine-grained muds of the flood-plain facies, reflecting their widespread distribution in the study area during Early Permian time.

Pedotype G is interpreted as a Vertisol, based on evidence of cracking in the form of clastic dikes and slickensides with wedge-shaped aggregates between 25 cm and 1 m depth (Soil Survey Staff 1975; 1998). Type G (Vertisols) exhibit two major differences from type D (Vertisols): (1) accumulation of pedogenic carbonate and (2) lack of redox features (Fig. 6B). Paleosol matrix colors in type G (Vertisols) indicate that these profiles formed under oxidized conditions well above the paleo–water table. The development of pedogenic slickensides records periods of soil saturation that allowed for periodic shrinking and swelling of expandable smectite clays. We interpret type G (Vertisols) to have developed on seasonally flooded, low-lying portions of the lower coastal plain province in positions proximal to stream channels or in internally drained, shallow depressions in the upper coastal plain and piedmont settings.

Type H (Inceptisols)

Type H paleosols (Figs. 6C, 6D, 7–9) are highly differentiated angular blocky red mudstones. They may exhibit an upper layer of massive carbonate and subsurface horizons with weakly expressed wedge-shaped aggregate structure and slickensides. However, all Type H paleosols have horizons of mudstone with common calcareous nodules and rhizoliths (Figs. 6C, 6D) that may cement entire layers with $CaCO_3$ (Fig. 7). Hydroxy-interlayered minerals and mica-like minerals dominate the <2 µm fraction in this pedotype, with trace amounts of kaolinite and chlorite. Type H paleosols are found in the Lower Permian Archer City through Clear Fork Formations in what we infer to be upper and lower coastal-plain environments.

Type H paleosols may have been Aridisols. However, such a classification requires specific knowledge of the soil moisture content and temperature during Permian time. These values are not known. In reality, Pedotype H paleosols may be classified only as Inceptisols, despite their apparent level of morphological maturity, which includes thick (≥15 cm) zones of carbonate accumulation (Soil survey Staff, 1998). Nevertheless, chlorite in the <2 µm fraction of Type H (Inceptisols) suggests arid conditions, given that this mineral is not stable in sub-humid and humid climates (Yemane, et al. 1996).

From estimates for development of modern calcic-horizons and their typical stratigraphic association with fine-grained sediments, we interpret Type H (Inceptisol) to have formed on stable regions of the flood-plain facies, removed from any frequently flooded fluvial systems. However, slickensides in layers coincident with, and beneath, calcic horizons suggest seasonal variations in soil moisture.

Similar to Pedotype F, Pedotype H developed upon stable portions of the landscape that were distal from active sedimentary environments. Its morphological characteristics likely represent regional climate, and it is unlikely that the floral elements associated with this pedotype would have been incorporated into the fossil record.

Summary of Permo-Pennsylvanian Paleosols

The paleo-landscape positions associated with the formation of different Permo-Pennsylvanian paleosols result in a representative suite of eight pedotypes. The morphology of pedotypes that record soil formation in stable, well-drained portions of the landscape, which were distal from major depocenters, likely record the effect of regional paleoclimate. These well-drained pedotypes are B, F, G, and H. Nevertheless, the regional continuity of pedotypes with morphologies that are indicative of poorly drained conditions (A, C, D, and E) through the upper Pennsylvanian strata of north-central Texas probably corresponds to a regionally humid paleoenvironment characterized by a very shallow groundwater table (Tabor and Montañez, 2004). However, pedotypes with morphologies indicative of poor drainage (most notably Pedotype E) are volumetrically very small through the Lower Permian strata and probably represent aberrant moisture availability upon a semiarid to arid regional landscape. In this regard, our most parsimonious explanation of "ever-wet" fossil floras preserved in the dry climate associated with the deposition of the Lower Permian strata is that these aberrant, poorly drained paleosols provided miniature "inliers" of ever-wet refuge, or "wet spots," for these plants.

PATTERNS OF PLANT PRESERVATION AND DISTRIBUTION

The plant fossil record, in general, is strongly biased toward floras from lowland basins, mainly representing plants that grew within a few meters of where their remains are found (Scheihing and Pfefferkorn, 1984; Burnham et al., 1992). There also are other, slightly smaller scale "megabiases" (Behrensmeyer and Hook, 1992). Most importantly, leaves have limited potential for long-distance transport (Spicer, 1981; Gastaldo, 1989). Leaf assemblages generally represent species growing in the wetter parts of the local landscape (pedotypes A, C, D, and E), close to standing bodies of water where burial and subsequent fossilization are most likely. Consequently, plant fossils can provide a significantly "wetter" climatic signature for a region than do paleosols or geochemical indicators. This is of importance when considering plants as indicators of climatic trends. At still smaller scales, it is necessary to consider the nature of the burial processes that preceded fossilization. Parautochthonous plant assemblages are transported but deposited within the habitat of growth (Bateman, 1991); these are most common. Autochthonous assemblages are not transported; they occur rarely, mainly as in situ tree stumps (e.g., Gastaldo, 1986), or where plants are buried in place by floods (Andrews et al., 1977) or volcanic ash (Wing et al., 1993). Allochthonous plant assemblages are transported and deposited in environments different from those in which the parent plants grew; although allochthonous plant debris is common in some lithological sequences, well-preserved allochthonous assemblages are rare. The overly "wet" bias notwithstanding, the north-central Texas section preserves a clear pattern of diminishment of Late Carboniferous dominants and their replacement by seed plants of more xeromorphic aspect.

Plant fossils in rocks of the upper Pennsylvanian and Lower Permian of north-central Texas are mostly parautochthonous and occur almost exclusively in small channel-form deposits composed of claystone, mudstone, and very fine grained sandstone. Such deposits rarely exceed 20 m in width or 2 m in thickness. The bases of these channel-form deposits are in erosional contact with underlying rocks, frequently paleosols, and may include sandstone accretion beds. Within these deposits, plant fossils are most often preserved in finely laminated claystones and mudstones deposited from suspension, probably during late stages of channel abandonment or as oxbow lakes. Less frequently, plant fossils may occur in sandstones or coarse siltstones deposited at the bases of accretion surfaces, probably on bars during slack-water intervals following floods in active channels. Some deposits are isolated stratigraphically and geographically; others recur in multiple, discrete deposits within a restricted stratigraphic interval that extends across several square kilometers. The most extensive plant-bearing deposits are those of the coal-bearing parts of the Virgilian to lower Wolfcampian Bowie Group (DiMichele et al., 1991), which are traceable for tens of kilometers along outcrop. Those parts of the Permian section that lack significant channel facies, such as the Leonardian upper Clear Fork (Nelson et al., 2001), have not yielded plant assemblages. In this respect, and at a somewhat coarse scale of resolution, the north-central Texas plant record can be regarded as "isotaphonomic," meaning that it formed under the same kind of conditions at the scale of analysis.

Physiognomic and Taxonomic Patterns

The most commonly preserved plants indicative of ever-wet conditions include tree ferns, sphenopsids, and lycopsids (Fig. 11), which have architectures and reproductive biologies that are closely tied to wet substrates (for a review, see DiMichele and Phillips, 1994). For example, lycopsids are heterosporous, which is a plant life history closely tied to water. The female reproductive organs of these plants appear to be water dispersed (Phillips, 1979). In addition, their root systems are broadly spreading yet shallow and have growth tips and lateral appendages that are structurally incapable of penetrating hard substrates (Phillips and DiMichele, 1992). They also have limited water-conducting systems that require high levels of moisture availability. Calamitean sphenopsids have underground rhizomes that permit them to recover from burial by sediment; they are generally found in disturbance-prone streamside, bayside, and lakeside deposits and may recover from repeated rapid, shallow burial (e.g., Gastaldo, 1992). In some instances they may form a succession to buried lycopsid forests in Pennsylvanian equatorial wetlands (Calder et al., this volume). Marattialean tree ferns are homosporous, with freely released spores that require moist, but not flooded, conditions to complete their life cycle. They also have highly divided, large fronds indicative of high water transpiration rates and thus high levels of soil moisture. Tree fern rooting systems have numerous air chambers, an anatomy found in extant plants that grow all or part of the year under submerged conditions, and appear to have been shallowly penetrating (DiMichele and Phillips, 2002).

In contrast, plants typical of seasonally dry conditions have small or reduced foliage, sunken stomatal pores, various kinds of water-retention attributes of the leaf surface or subsurface, reduced stature if broad-leaved, and deep, vertical patterns of rooting (Algeo and Scheckler, 1998). Conifers, gigantopterids, peltasperms, taeniopterids, and cordaites are examples of plants that bear some or all of these characteristics, depending on the extent to which they are known (Kerp, 1990).

Composite Floristic Patterns

The Upper Carboniferous "Wet" Flora

Upper Pennsylvanian wetland plant assemblages of north-central Texas (Flora 1, Figs. 9–11) can be divided into two groups, those from organic shales and those from flood-plain mudstones. Although they are compositionally similar, patterns of dominance differ and there are some species that apparently occur exclusively or nearly exclusively in one ecological setting or the other.

Organic shales and coals, deposits formed in forested wetlands (swamps and mires), represent the wettest habitats supporting plants on the landscape. As noted above, these deposits are associated with Pedotype A, as the organic upper horizon, and have a regional extent in parts of the Bowie and Cisco Groups. Organic-rich deposits commonly contain thick lenses of fusain (fossil charcoal), indicating recurring fires during the time of forest growth, and thus probable periods of short-term drying. The plant assemblages of these deposits are dominated by medullosan pteridosperms, particularly the species *Neuropteris scheuchzeri*. Associated elements that are locally abundant include the marattialean foliage *Pecopteris*, which is dominant in the youngest known deposit of this kind. *Sigillaria brardii*, a small arborescent lycopsid, is locally common to abundant, but is not everywhere a member of the flora. Calamitean stems and foliage attributable to *Asterophyllites equisetiformis* are the most common members of this group of plants in organic-rich deposits. Locally common are the reproductive organs *Macrostachya*, although no particular foliage has been found that can be attributed to this cone. In general, these floras contain few species, with the pteridosperm *Neuropteris scheuchzeri* dominating (as high as 90% of the biomass determined by quadrat analysis; see Pfefferkorn et al., 1975, for description of the techniques used).

Mudstone-filled hollows with erosional basal contacts commonly directly overlie organic shales and are closely associated with Pedotype C. These deposits are a mixture of small-scale channels and scours with standing-water mud infillings,

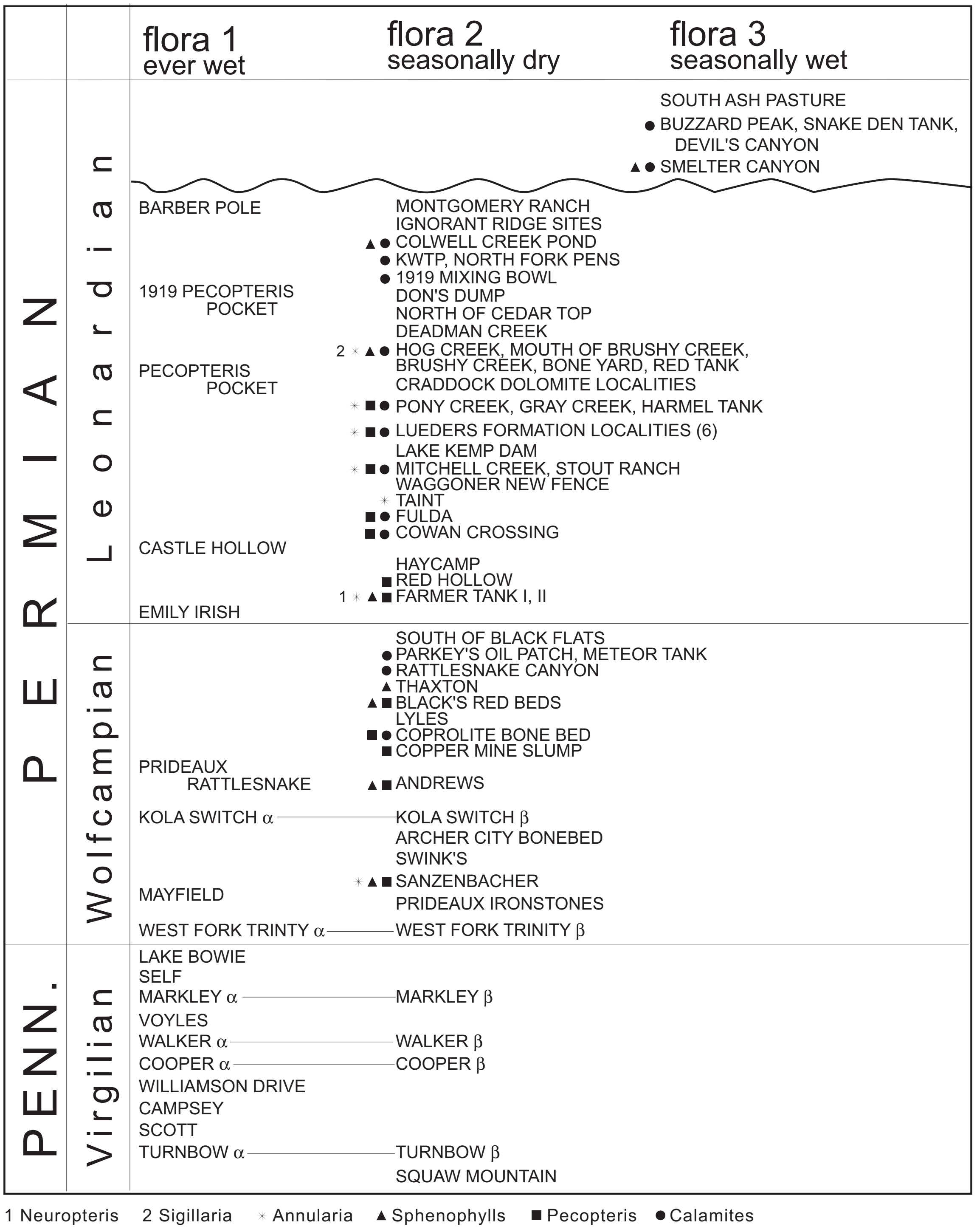

Figure 10. Stratigraphic distributions of the three major floras. Localities are noted by their informal names. Sites joined by a horizontal line and marked with α and β indicate occurrences in the same outcrop of the wet (α) flora and seasonally dry (β) flora (see Fig. 2B for an example). Symbols adjoining locality names in Flora 2 and Flora 3 represent occurrences of wet elements either as part of plant assemblages otherwise compositionally typical of seasonally dry conditions, or as dominant elements of an assemblage.

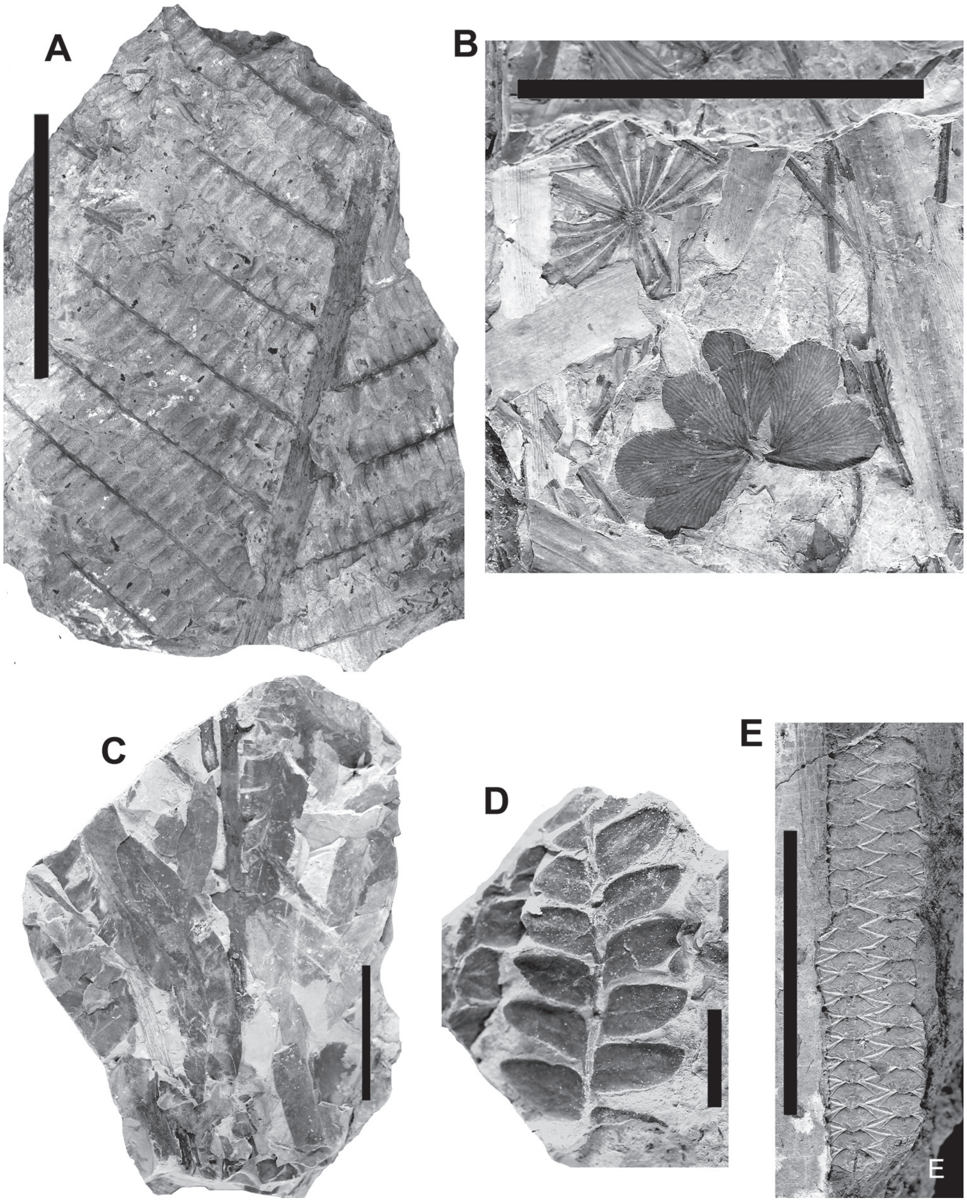

Figure 11. Common plant fossils of Flora 1. (A) *Pecopteris* sp. (USNM 526025), Castle Hollow locality (USGS 8960), Petrolia Formation, Lower Permian. (B) Sphenopsids: top, *Annularia carinata*; bottom, *Lilpopia raciborskii* (USNM 526026); both, Williamson Drive locality (NMNH 40013), Markley Formation, upper Pennsylvanian. (C) *Neuropteris scheuchzeri* (USNM 526027), Self School locality (USGS 10056), Markley Formation, upper Pennsylvanian. (D) *Pseudomariopteris cordata-ovata* (USNM 526028), Cooper locality (NMNH 39992), Markley Formation, upper Pennsylvanian. (E) *Sigillaria brardii* (USNM 526029), Maxey Ranch locality (NMNH 40602), Markley Formation, upper Pennsylvanian. Scale bars, 5 cm in A–C, E; 1 cm in D.

interbedded with thin, poorly developed, lightly rooted paleosols that represent flood-plain deposits (Fig. 2). The plant assemblages characteristic of these environments (Fig. 11) are typical of late Pennsylvanian clastic deposits in coal-bearing intervals from the midcontinent of the United States and from western Europe (see especially Wagner, 1983, Kerp and Fichter, 1985, and Laveine, 1989, for floristic comparisons). Dominant elements vary from location to location in north-central Texas, but common species include the pteridosperms *Neuropteris ovata*, *Neuropteris auriculata*, and *Alethopteris zeilleri*. Many species of marattialean tree fern foliage also are common, including the *Pecopteris cyathea*-group (sensu Zodrow, 1990), *Lobatopteris puertollanensis*, and *Polymorphopteris polymorpha* (Wagner, 1983). The most common calamitean remains are stems and foliage attributable to *Annularia carinata* (Kerp and Fichter, 1985). A wide variety of ground cover is associated with these arborescent taxa including the sphenopsids, *Sphenophyllum oblongifolium* and *Lilpopia raciborskii* (Kerp, 1984), and small fern foliage of the genus *Sphenopteris*. This assemblage is derived from a flora typical of humid atmospheric conditions and wet substrates environments.

The Permian "Seasonally Dry" Flora

During the Early Permian the most common elements of plant assemblages are seed plants (Fig. 12). The first distinctively Permian assemblages identified (Flora 2 of Fig. 10), occur in

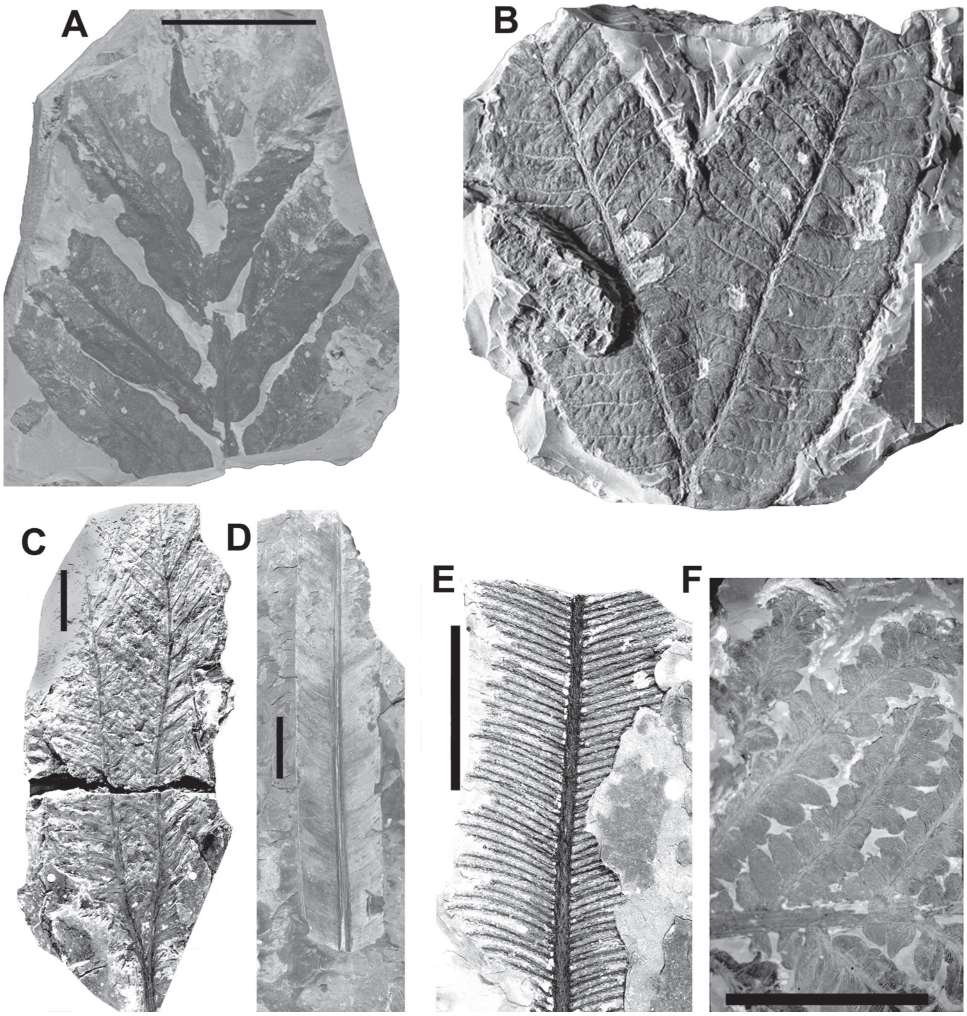

Figure 12. Common plant fossils of Flora 2. (A) Comioid peltasperm, undescribed (USNM 526030), 1919 Mixing Bowl locality (NMNH 40992), middle Clear Fork Formation, Lower Permian. (B) *Zeilleropteris wattii* (USNM 526031), Brushy Creek #2 locality (NMNH 40048), lower Clear Fork Formation, Lower Permian. (C) *Supaia* sp. (USNM526032), KWTP #1 locality (NMNH 40979), middle Clear Fork Formation, Lower Permian. (D) *Taeniopteris* sp. (USNM 526033), Mouth of Colwell Creek locality (NMNH 41005), middle Clear Fork Formation, Lower Permian. (E) Walchian conifer (USNM 526034), Mouth of Colwell Creek locality (NMNH 41006), middle Clear Fork Formation, Lower Permian. (F) Callipterid (USNM 526035), Brushy Creek #2 locality (NMNH 40048), lower Clear Fork Formation, Lower Permian. Scale bars, 5 cm.

association with physical indicators of seasonal dryness. The specific and generic composition of Flora 2 (Figs. 10, 12) changes gradually during the Early Permian. Most widespread and long-ranging are conifers of the genera *Walchia*, *Culmitzschia*, and *Ernestiodendron* (Clement-Westerhoff, 1988). Associated with these plants are a number of peltasperms (seed plants belonging to the order Peltaspermales), most commonly *Autunia* and related callipterids (Kerp, 1988). In the Wolfcampian, but not the Leonardian, part of the section, *Sphenopteridium* is common (Mamay, 1992). In the Leonardian part of the section, the probable peltasperms *Comia*, *Supaia*, *Brongniartites,* and, possibly, *Compsopteris* are prominent (Naugolnykh,1999; Read and Mamay, 1964). Also in the Leonardian, several genera of gigantopterids, which may be peltaspermous seed plants, also become prominent elements of the flora; included, in the approximate stratigraphic order of their appearance and relative abundance, are *Gigantopteridium*, *Cathaysiopteris*, *Zeilleropteris*, *Evolsonia*, and *Delnortea* (Mamay, 1986, 1989; Mamay et al., 1988). Other seed plants locally common include *Russelites* (Mamay, 1968), cordaitean foliage, and *Odontopteris* of the *Mixoneura* form. *Taeniopteris*, a form that may represent seed plants and ferns, is locally common to abundant.

Flora 3 (Figs. 10, 13) contains elements that are precocious, appearing much earlier than previously known from the fossil record. This flora occurs in the San Angelo and Blaine Formations of the Pease River Group. These rocks are upper Lower Permian to lower Middle Permian and are characterized by abundant gypsum and weakly developed paleosols, characteristic of deposition under conditions with a short wet season and long hot, dry intervals. The flora contains elements that previously were known only from the Mesozoic, including such taxa as the putative cycad *Dioonitocarpidium* and some conifers such as *Podozamites*, and others known only from the Late Permian, such as *Ulmannia* and *Pseudovoltzia* (DiMichele et al., 2001, 2004). Flora 3 has been identified at several stratigraphic horizons in the San Angelo Formation at a single locality in the Blaine Formation. However, the composition of the plant assemblages from these two formations is different, indicating much drier conditions in

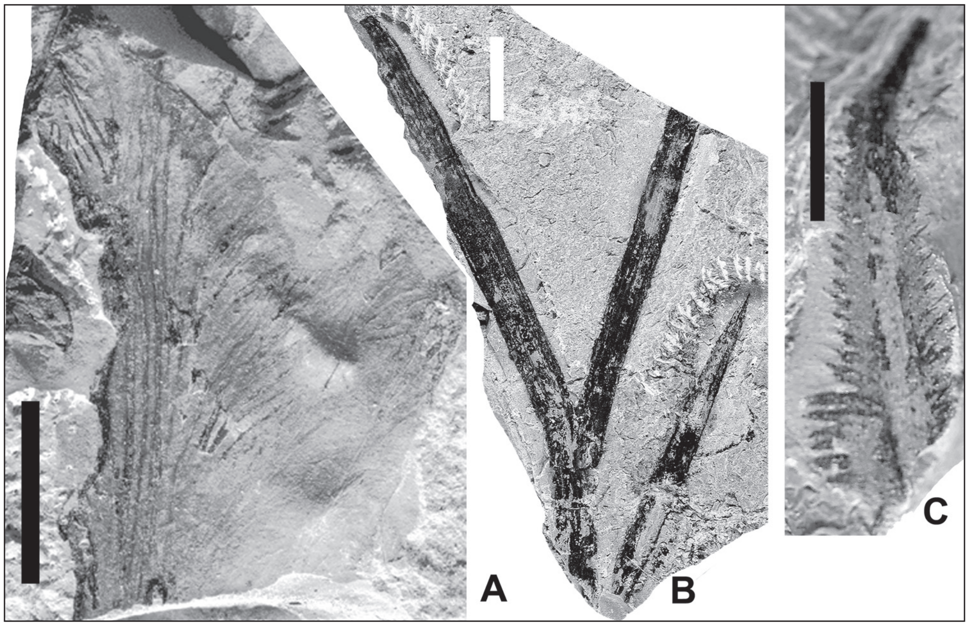

Figure 13. Selected elements of Flora 3. (A) Gigantopterid (USNM 520384), South Ash Pasture locality (NMNH 40968), Blaine Formation, Middle Permian. (B) *Dicranophyllum* sp. (USNM 526036), Buzzard Peak locality (NMNH 41394), contact of San Angelo and Blaine Formations, Lower Permian. (C) *Dioonitocarpidium* sp. (USNM 526037), Buzzard Peak locality (NMNH 41384), contact of San Angelo and Blaine Formations, Lower Permian. Scale bars, 1 cm.

the younger Blaine deposit. In the precociousness of their taxonomic composition, these floras parallel the early appearance of Flora 2 in isolated deposits or as thin beds intercalated within typical wetland deposits containing Flora 1 during the Virgilian in the Late Carboniferous.

Patterns of Change in the Distribution of Wetland Plants

The distribution of deposits bearing wetland plants is illustrated in Figures 9 and 10. In general, plants of the wetland biome (Flora 1) clearly predominate during the latest Carboniferous and earliest Permian. However, there is a shift to dominance by plants of the seasonally dry biome (Flora 2) in the early Early Permian (Wolfcampian), and this pattern persists through the later parts of the Early Permian (Leonardian). In the latest Early Permian or Middle Permian, a third biome appears, characterized by yet more evolutionarily derived seed plants (Flora 3); some of these taxa appear elsewhere in the world in rocks of Late Permian and early Mesozoic age (DiMichele et al., 2001).

Outcrop-Scale Alternation of Wetland and Seasonally Dry Biomes in the Upper Carboniferous and Lower Permian

In the Late Carboniferous deposits of the study area, wetland floras are diverse and found in a variety of lithologies typical of the environmentally heterogeneous, wet tropics. Habitat specialization can be documented, however, by the restriction of species occurrence or of dominance to particular lithologies. For example, there is a distinct pattern of differentiation between the most common forms of calamite foliage: *Annularia carinata* is abundant in flood-plain mudstones, whereas *Asterophyllities equisetiformis* is most common in swamp deposits represented by organic shales. The only macro-trend visible in these deposits is the disappearance of pteridosperm dominance in organic shales/coals and its replacement by tree fern dominance in the youngest organic-shale deposit. Otherwise, the same basic plant taxa are found in all wetland deposits with the same general patterns of lithological distribution. These deposits are typically associated with Pedotypes A and C.

Occurring with these wetland floras in the same Upper Carboniferous and lowermost Permian outcrops is a distinct flora composed of seed plants typical of the seasonally dry biome that is dominant through most of the Lower Permian. Conifers, callipterid peltasperms, *Neuropteris*, and *Sphenopteridium* form the dominant elements, with rare scraps of foliage similar to *Russelites* or *Charliea* (Mamay, 1968, 1990). This flora occurs in distinct, kaolinite-rich beds associated with Pedotype B (Figs. 5A, 5B, 8, 9), which may have formed on topographic highs, during periods of lowered water table. Some of these kaolinite deposits appear to mark the base of channel fills and may have contributed to ponding of water and initial development of subsequently deposited organic-rich mucks that contain plant assemblages representative of the wetland biome (see Gardner et al., 1988).

These two floras are spatially and temporally distinct, inferred from the positions and extents of their host sediments on outcrop. Typically, deposits of this type occur in coal/organic-shale-bearing portions of the Markley Formation but continue into the Lower Permian where such heterogeneous deposits become progressively less common. One of the youngest examples (Kola Switch) occurs ~8 m below the base of informal sandstone member 8 of the Archer City Formation (Hentz and Brown, 1987). These deposits have significant depositional relief and are lithologically heterogeneous. Where well exposed, they are shallow, broadly U-shaped, channel-form deposits, ~6–10 m deep and 50–100 m in width. Some have erosive sandstones and intraformational conglomerates at the base, indicative of proximal crevasse-splay channels. Others lack coarser-grained clastics and may have originated as more distal overbank channels, minor tributaries, or interior flood-plain channels. Floristically, the distinct plant assemblages are preserved in several different lithologies. Flood-plain paleosols commonly contain tree fern roots, generally preserved as casts and molds but occasionally with the distinctive anatomy characteristic of these organs. Rarely occurring kaolinitic lenses associated with the upper boundary of Pedotype C paleosols contain allochthonous floras typical of seasonally dry conditions. Autochthonous to parautochthonous swamp deposits of organic shale to shaly coal occur above the kaolinites and may be up to 1 m in thickness, and preserve a densely packed, low-diversity flora characteristic of the ever-wet biome. Overlying flood-plain sediments typically include small, mud-filled scours intermixed with weakly developed paleosols. These small channels contain a diverse, parautochthonous assemblage also typical of the ever-wet biome.

Patterns in the Lower Permian Wichita, Clear Fork, and Pease River Groups

Typically Carboniferous plants occur in association with the seasonally dry floras of the Lower and Middle Permian in two ways (Fig. 10): Either the Carboniferous wetland elements occur intermixed as rare elements within assemblages heavily dominated by the seasonally dry biome, or the wetland plants dominate (often nearly monospecifically) in assemblages that contain few or no species typical of seasonally dry habitats. There are a few rare and notable exceptions to this pattern, where a strong wetland component dominates with minor occurrences of plants from the seasonally dry biome (see below).

The wetland species most commonly encountered are the marattialean tree fern foliage *Pecopteris* and calamite stems (Fig. 14). Other wet indicators, such as *Sphenopteris,* a true fern, occur in the earliest Permian but are rare to absent in younger rocks. The lycopsid tree *Sigillaria* (Fig. 14), the ground cover sphenopsid *Sphenophyllum* (Fig. 14), and medullosan foliage scraps have been found quite rarely in the Leonardian as components of otherwise seasonally dry floras. Such unusual and unexpected occurrences suggest the existence of unsampled wet areas from which these plants were transported into the seasonally dry assemblages. The Late Carboniferous wetland plants that occur most commonly as holdovers in Permian deposits are largely "weedy," opportunistic forms also tolerant of wet substrates (see also Calder and Falcon-Lang, this volume, for similar ecological interpretations of these same plants in the early Pennsylvanian Joggins section). Tree ferns are most notable in this respect. They are cheaply constructed, with root mantles and, often, stems filled with air spaces, suggesting rapid growth and minimal resource allocation to the vegetative tissues used to attain tree heights. Quantitative analyses of the "cost" of tree fern tissues per unit volume show them to have the lowest biomass among all groups of Late Carboniferous swamp plants (Baker and DiMichele, 1997). In addition, their large fronds produce very large numbers of tiny, highly dispersible spores, permitting them to locate and colonize disturbed open sites rapidly. Similarly, sphenopsids appear to have strongly favored streamside and aggradational flood-basin habitats where their rhizomes allowed rapid recovery from catastrophic burial. Other groups, such as the lycopsid tree *Sigillaria* or ground cover plants such as the sphenopsid *Sphenophyllum*, are much rarer and may have existed only in isolated populations.

Monospecific assemblages of wetland plants in Lower Permian rocks are dominated by tree ferns exclusively. Their range of dispersal, due to their small, wind-dispersed spores, probably gave them access to short-lived and areally limited wet spots that could not be reached by other plants restricted to wet habitats. The youngest Clear Fork locality known is dominated by tree ferns. Calamitean sphenopsids are very common to abundant in rare instances. For example, at the North Fork Pens site, of the Middle Clear Fork Group, large numbers of calamite stems were encountered lying three-dimensionally within red siltstones, crossing bedding planes and flattened unidirectionally, indicating rapid burial by sediment-laden flood waters. Such calamite-dominated deposits are of very limited areal extent.

The Emily Irish locality in the basal Petrolia Formation was collected intensively by Sergius Mamay and colleagues in the 1960s and is perhaps the best sampled Early Permian flora from the United States. It is overwhelmingly dominated by tree fern foliage but contains a diversity of other kinds of plants, many of which are typical of the seasonally dry biome. Emily Irish was sampled in bulk; no effort was made to collect specimens layer by layer. Thus, we do not know if the tree-fern-rich assemblages occurred in the same rock layers as those enriched in evolutionarily derived seed plants. If they did co-occur, then this assemblage would represent one of the only examples in the study area where plants of the seasonally dry biome occurred as minor elements in a wetland-dominated assemblage. The occurrence of rare elements, either wetland or seasonally dry, in assemblages dominated by plants of the other biome, suggests strongly that these two vegetation types coexisted in close proximity on Early Permian landscapes, their distributions controlled by water table level rather than regional climate.

The seasonally wet biome of the Pease River Group is characteristic of environments with a relatively short wet season within a generally xeric climatic background. It is known from small channel fills that bear entirely distinct floras of unique composition compared with other Lower Permian floras of the paleotropical belt (DiMichele et al., 2001, 2004). There are virtually no known wetland plants associated with these floras, which, in fact, also lack species common in the earlier seasonally dry biome.

DISCUSSION

The loss of wetland assemblages during the Pennsylvanian-Permian transition in north-central Texas is mirrored by the increase of seasonally dry assemblages during the later

Figure 14. Ever-wet elements persisting as components of Early Permian seasonally dry landscapes presumably in “wet spots.” (A) *Calamites* sp. stem (USNM 526038), Deadman Creek locality (NMNH 40670), lower Clear Fork Formation, Lower Permian. (B) *Pecopteris* sp. (USNM 526039), Pecopteris pocket locality (NMNH 40645), lower Clear Fork Formation, Lower Permian. (C) *Sigillaria brardii* (USNM 526040), Mouth of Brushy Creek locality (NMNH 38907), lower Clear Fork Formation, Lower Permian. (D) *Annularia spicata* (USNM 526041), Brushy Creek West locality (NMNH 38908), lower Clear Fork Formation, Lower Permian. Scale bars, 1 cm for A, C, D; 5 cm for B.

Pennsylvanian and earliest Permian on a global basis. When sampled on a bed-by-bed basis, it appears that few species cross over between assemblages drawn from these two floras (Kerp and Fichter, 1985; Broutin et al., 1990; DiMichele and Aronson, 1992). The flora typical of seasonally dry conditions begins to appear sporadically during the Stephanian (late Pennsylvanian) intercalated within geological sequences otherwise dominated by assemblages of plants typical of ever-wet conditions (McComas, 1988; Cridland and Morris, 1963; Doubinger et al., 1995; Mamay and Mapes, 1992; Rothwell and Mapes, 1988). In some cases plant assemblages have been collected from single, well-documented beds and often these are quite distinct in dominance and diversity patterns from wetland assemblages. In the latest Pennsylvanian of north-central Texas, for example, the seasonally dry and ever-wet floras occur within the same outcrops but in different beds. In some of the other studies the plants are binned by stratigraphic intervals or units, such as formations, and thus the two floras are analytically combined and treated as part of a single flora, rather than being broken down into specific time-space assemblages. This approach limits understanding to broad trends only. Using either approach, ultimately the seasonally dry flora becomes dominant in the early Lower Permian.

The conditions and patterns surrounding the origin of the seasonally dry flora are not quite as clear as its rise to prominence in the Pennsylvanian-Permian transition. Elements such as conifers make their initial appearances as scrappy plant remains, sometimes preserved as charcoal, evidently washed or blown into the depositional lowlands from adjacent “upland” areas (Lyons and Darrah, 1989) beginning in the middle Westphalian (middle Pennsylvanian) (Scott and Chaloner, 1983; Galtier et al., 1992). However, there is considerable evidence of “upland” vegetation prior to or concurrent with the first appearances of the conifer-rich “Permian” flora, which raises questions about the degree to which vegetation was differentiated in extrabasinal areas (sensu Pfefferkorn, 1980). For example, Leary (1975) and Leary and Pfefferkorn (1977) described early Pennsylvanian–aged plant assemblages from the margin of the Illinois basin that are distinct from contemporaneous basinal assemblages associated with coal beds; however, the marginal floras do not contain conifers or any plants that could be seen as precursors to the plants that come to dominate Permian seasonally dry habitats. Similarly, Falcon-Lang and Bashforth (2004) describe early Pennsylvanian forested uplands dominated by cordaitalean trees, but not intermixed with conifers and other elements that might have been parts of the seasonally dry vegetation that subsequently dominates the lowland tropics. Interestingly, some plants characteristic of late Mississippian seasonal climates, such as *Sphenopteridium*, reappear in late Pennsylvanian and Early Permian conifer-rich floras (Mamay, 1992), but not in these other kinds of Pennsylvanian extrabasinal assemblages, suggesting the possibility of biogeographic differentiation controlled largely by climatic factors—the conifer-rich flora may have been primarily subtropical or true upland in evolutionary origin and primary distribution.

Paleosols from the late Pennsylvanian and Early Permian in north-central Texas closely mirror the changes in the patterns of plant distribution. The most striking characteristic of the late Pennsylvanian paleosols is redox features. The combination of (1) redox features in Pedotypes B, C, and D (Ultisols, Inceptisols, and Aquerts) and (2) organic matter accumulation and tabular rooting systems in Pedotype A (Histosols) indicates that poorly drained conditions varied between continuous and episodic, suggesting a regionally shallow water table. In addition, the dominance of kaolinite in late Pennsylvanian profiles is consistent with an environment characterized by high rates of chemical weathering, conditions expected in humid tropical environments (Yemane et al., 1996).

In contrast, Permian paleosols typically do not exhibit redoximorphic features indicative of a regionally extensive shallow groundwater table. Oxidized paleosol matrix colors, vertically extensive rooting structures, and pedogenic carbonate accumulation in Pedotypes F, G, and H (Alfisols, Vertisols, and Inceptisols) indicate that large portions of the Lower Permian landscape were well drained and remained above the water table for extended periods. In addition, the presence of smectite, hydroxy-interlayered phyllosilicate minerals, and chlorite clay minerals suggests well-drained and dry conditions (Tabor and Montañez, 2004).

Another indicator of changing hydrologic conditions is the paucity of pedogenic carbonate in late Pennsylvanian paleosols and its abundance in Early Permian paleosols. Pedogenic carbonate accumulation is a response to net moisture deficit in which annual evaporation exceeds precipitation (Birkeland 1999; Retallack 1990). In most cases carbonate will not be retained in the soil if mean annual precipitation exceeds 760 mm (Royer 1999). This suggests that carbonate-bearing Early Permian paleosols developed under conditions of low precipitation and net moisture deficiency, whereas Late Carboniferous paleosols, which do not contain pedogenic carbonate, probably received higher mean annual precipitation without extended episodes of moisture deficiency. Early Permian paleosol morphologies in the Archer City, Nocona, Petrolia, Waggoner Ranch, and lower half of the Clear Fork Formations suggest development under warm and relatively dry, subhumid to semiarid climate.

Finally, the paucity of soil profiles across the lower coastal plain facies of the San Angelo and Blaine Formations may indicate generally unfavorable conditions for soil formation. The fact that the only diagnostic morphologies (i.e., root traces and soil structure) indicative of soil formation occur along channel sandstones may indicate either (1) regional water table levels generally were very low except along stream galleries, where the regional water table intersects surface topography, or (2) these stream corridors provided the only regional sources of fresh water for plant-growth and soil formation.

Lithological features of the Pease River Group support the second option above. These include thick deposits of bedded gypsum interbedded with marine-invertebrate-bearing limestone and dolomite beds, which record repeated incursions of salt water from the Midland Basin into the study area, suggesting a landscape of hot, arid coastal mudflats and salt pans largely devoid of vegetation. Between marine incursions, it is likely that nothing grew except along the margins of little brackish creeks, such as the one sampled at South Ash Pasture in the Blaine Formation (DiMichele et al., 2004). The water table may have been high (the region frequently was under water), yet the alkali-laden soil and extreme drought conditions precluded most plant growth or development of soil horizons.

Thus, the study of paleosols shows that the climate became drier through time and the regional water table dropped. Late Pennsylvanian paleosol morphologies suggest formation in a warm and moist climate with a generally shallow and seasonally fluctuating groundwater table. Groundwater table levels were more variable during Permian time and apparently followed the regional physiography of the eastern Midland Basin. Morphologies indicative of generally wet soil conditions apparently formed proximal to streams and oxbow ponds, whereas morphologies indicative of drier soil-moisture budgets formed upon the open coastal flood plains, distant from major streams. Finally, beginning in the upper Clear Fork Formation (middle Lower Permian) and continuing through the San Angelo and Blaine Formations (upper Lower Permian/lower Middle Permian), paleosol distribution and diversity of morphologies progressively diminish until the only evident soils formed along stream galleries. These stream galleries may have comprised the only plant-accessible source of fresh water at this time, and indicate either that the regional groundwater was deep or that despite a high water table the coastal sabkhas were hostile to plant life.

Thus, vegetation tolerant of periodic drought became more common and ultimately dominated the landscape (diagrammatically represented in Fig. 15). Floras of ever-wet habitats retreated to isolated wet areas along permanent streams. Initially, these "wet spots" were numerous and hosted a fairly diverse selection of wetland plants persisting from the latest Carboniferous. Ultimately, these little wetlands diminished, both in area and species diversity, until only *Pecopteris* and calamites were common. The

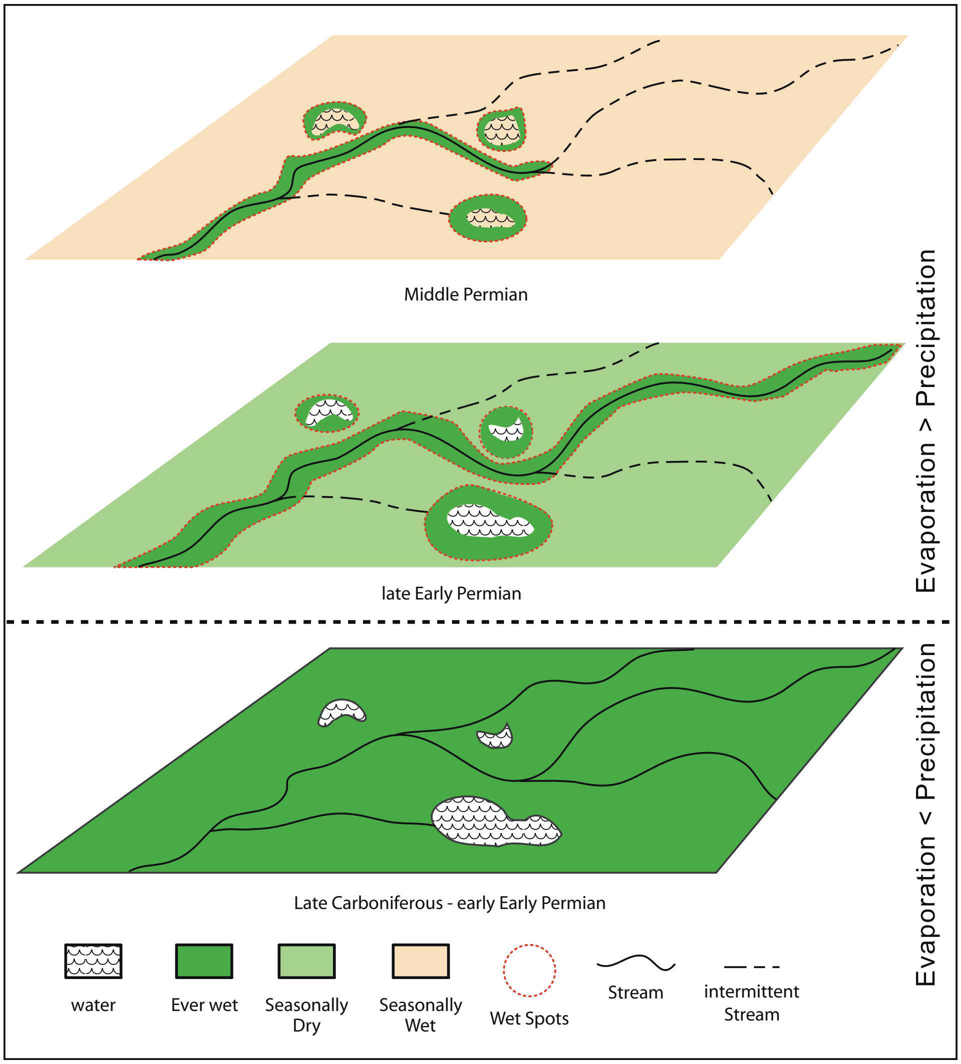

Figure 15. From wetlands to wet spots. Landscape progression and restriction of available habitat area for wetland plants under progressive moisture limitation.

plants that survived in the areally diminished wetlands represent two major ecological strategies. One is that of the sphenopsids, particularly the calamites. Calamites are the only tree group of the late Paleozoic with clonal growth, permitting them to recover from burial by sediment and thus to occupy aggradational, disturbed environments. Calamites occurred and locally flourished throughout the Early Permian and into the early Middle Permian. Some specimens record evidence of burial and recovery from disturbance, in the form of streamside flooding. Calamite foliage is very rare; stems routinely are the only fossil encountered. However, these plants may have resembled modern *Equisetum*, which has highly reduced foliage and photosynthetic stems.

The second "survivor" group is the marattialean tree ferns. These trees were "cheaply constructed." Anatomical studies demonstrate that their root mantles, and sometimes their stems and petioles, were filled with air spaces. In addition, they produced massive numbers of spores on large fronds, the wide broadcast of which permitted them to colonize any suitable landscape patch. Cheap construction and massive reproduction typify opportunistic, "weedy" species. It is likely that this life history permitted these plants to survive in a wide array of habitats, those where sufficient moisture for reproduction was available during part of the year, and where substrates stayed wet enough for the year-round maintenance of large fronds. Opportunism may have encouraged an evolutionary response to changing environments as well, permitting the formation of many populational isolates, some of which may have evolved greater tolerance to limited periods of drought.

More problematic is the very rare occurrence, isolated both stratigraphically and spatially, of such plants as *Sigillaria* and *Sphenophyllum*. These taxa were abundant in the Late Carboniferous in widespread wetlands, although *Sigillaria brardii*, the likely species in question, is heir to a legacy of complex ecologies, including some species that may have been tolerant of disturbance and moisture stress (DiMichele and Phillips, 1994; Calder and Falcon-Lang, this volume). The discovery of these taxa as transported singletons in rocks of the Clear Fork Group, well above previously known occurrences, indicates that they persisted in isolated refuges, unlikely to be sampled. Nonetheless, the low dispersibility of these plants, relative to tree ferns or calamites, requires that wetlands have enough connectivity for populations to survive as wet spaces fluctuated in space and time. These rare occurrences thus may be taken as a barometer of the inadequacy of the fossil record itself (Darwin, 1859). The fossils are much rarer than the weedy wetland forms, but the overall sample size of fossil-bearing deposits themselves is very small compared with the vast size of the landscape being sampled. We thus can infer that small, almost completely unseen, populations must have existed continuously, and that the populations of the more commonly encountered, if still rare, forms were of significant size. That these plants were most typical of the wettest parts of landscapes, but are so rarely found, indicates that suitable habitat patches also were uncommon.

The fossil record of wetlands is relevant to larger questions of ecosystem organization that are central to debates in modern ecology. This is of particular interest when wetlands are examined in the context of a large-scale environmental shift, such as that at the transition from the Pennsylvanian to the Permian. The patterns described here indicate that environmental tracking by plants is a major factor in their spatial distribution. Why should this be surprising? Much of the debate in ecology has centered on the "individualism" of species, suggesting that plant associations or "communities" at any given place and time are simply happenstance, reflecting the momentary co-occurrence of plants with similar resource requirements under currently ambient climatic conditions. As visualized, such communities have no spatio-temporal bounds and, hypothetically at least, any combination of species is possible under this kind of lottery. The alternative is a system with some kind of identifiable limits to possible species combinations, and perhaps even identifiable rules governing species combinations (Weiher and Keddy, 1999). "Individualistic" responses of species to local changes in habitat conditions have been documented in studies of Holocene and Quaternary floras, particularly of North America and Europe (Delcourt and Delcourt, 1991; Bennett, 1997), including "non-analogue" floras (Overpeck et al., 1992). However, spatial patterns indicate that there may be limits to such dynamics, perhaps at the scale of biomes. Individualism in postglacial floras, such as it is, appears to be restricted largely to mixing within particular vegetation types/biomes. The deep fossil record, such as that of the Permian described here, suggests that there are environmental limits, or bounds, to the extent of these responses. The very concept of the biome has embedded within it the recognition that species are not randomly distributed across vast physical spaces in a gradient-like fashion. Rather, species tend to cluster around certain environmental norms, and to track those norms in a haphazard but nonetheless identifiable manner. The fossil record, despite its flaws, may be the best place to search for general patterns of this nature.

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REFERENCES CITED

Abilene Geological Society, 1949, Cross section, Stonewall County to Hood County, Texas: Abilene Geological Society, one sheet.

Abilene Geological Society, 1953, Cross section, Schleicher County to Childress County, Texas: Abilene Geological Society, one sheet.

Algeo, T.J., and Scheckler, S.E., 1998, Terrestrial-marine teleconnections in the Devonian: Links between the evolution of land plants, weathering processes, and marine anoxic events: Royal Society of London Philosophical Transactions, ser. B, v. 353, p. 113–130.

Andrews, H.N., Kasper, A.E., Forbes, W.H., Gensel, P.G., and Chaloner, W.G., 1977, Early Devonian Flora of the Trout Valley Formation of northern Maine: Review of Palaeobotany and Palynology, v. 23, p. 255–285, doi: 10.1016/0034-6667(77)90052-5.

Baker, R., and DiMichele, W.A., 1997, Resource allocation in Late Pennsylvanian coal-swamp plants: Palaios, v. 12, p. 127–132.

Bateman, R.M., 1991, Palaeoecology, *in* C.J. Cleal, ed., Plant fossils in geological investigation: The Palaeozoic: Chichester, UK, Ellis-Horwood, p. 34–116.

Behrensmeyer, A.K., and Hook, R.W., rapporteurs, 1992, Paleoenvironmental contexts and Taphonomic Modes, *in* Behrensmeyer, A. K. et al., eds., Terrestrial ecosystems through time: Chicago, University of Chicago Press, p. 14–136.

Bennett, K.D., 1997, Evolution and ecology, the pace of life: Cambridge, UK, Cambridge University Press, 241 p.

Berman, D.S., 1970, Vertebrate fossils from the Lueders Formation, Lower Permian of north-central Texas: University of California Publications in Geological Sciences, v. 86, p. 1–61.

Birkeland, P.W., 1999, Soils and geomorphology (third edition): New York, Oxford University Press, 430 p.

Bose, E., 1917, The Permo-Carboniferous ammonoids of the Glass Mountains, West Texas, and their stratigraphical significance: University of Texas Bulletin, no. 1762, 241 p.

Brister, B.S., Stephens, W.C., and Norman, G.A., 2002, Structure, stratigraphy, and hydrocarbon system of a Pennsylvanian pull-apart basin in north-central Texas: American Association of Petroleum Geologists Bulletin, v. 86, p. 1–20.

Broutin, J., Doubinger, J., Farjanel, G., Freytet, F., Kerp, H., Langiaux, J., Leberton, L., Sebban, S., and Satta, S., 1990, Le renouvellement des flores au passage Carbonifère Permien: Approaches stratigraphique, biologique, sédimentologique: Comptes Rendus de l'Académie des Sciences, Paris, v. 311, p. 1563–1569.

Brown, L.F., Jr., Solis-Iriarte, R.F., and Johns, D.A., 1987, Regional stratigraphic cross sections, Upper Pennsylvanian and Lower Permian strata (Virgilian and Wolfcampian Series), north-central Texas: University of Texas at Austin Bureau of Economic Geology Cross Sections, 27 p.

Brown, L.F., Jr., Solis-Iriarte, R.F., and Johns, D.A., 1990, Regional depositional systems tracts, paleogeography, and sequence stratigraphy, Upper Pennsylvanian and Lower Permian strata, north- and west-central Texas: University of Texas at Austin Bureau of Economic Geology Report of Investigations, v. 197, p. 1–116.

Buol, S.W., Hole, F.D., McCracken, R.J., and Southard, R.J., 1997, Soil genesis and classification: Ames, Iowa, Iowa State University Press, 527 p.

Burnham, R.J., Wing, S.L., and Parker, G.G., 1992, The reflection of deciduous forest communities in leaf litter: Implications for autochthonous litter assemblages from the fossil record: Paleobiology, v. 18, p. 30–49.

Cecil, C.B., 1990, Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks: Geology, v. 18, p. 533–536, doi: 10.1130/0091-7613(1990)018<0533:PCOSRO>2.3.CO;2.

Clement-Westerhoff, J.A., 1988, Morphology and phylogeny of Paleozoic Conifers *in* Beck, C. B., ed., Origin and evolution of gymnosperms: New York, Columbia University Press, p. 298–337.

Clifton, R.L., 1944, Paleoecology and environments inferred from some marginal middle Permian marine strata: American Association of Petroleum Geologists Bulletin, v. 28, p. 1021–1031.

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

Dalquest, W.W., and Carpenter, R.M., 1975, A new discovery of fossil lungfish burrows: Texas Journal of Science, v. 26, p. 611.

Dalquest, W.W., and Kocurko, M.J., 1986, Geology and vertebrate paleontology of a Lower Permian delta margin in Baylor County, Texas: Southwestern Naturalist, v. 31, p. 477–492.

Dalquest, W.W., and Kocurko, M.J., 1989, Notes on Permian fishes from Lake Kemp, Baylor County, Texas, with a synopsis of Texas palaeonisciform fishes: Southwestern Naturalist, v. 33, p. 263–274.

Daniels, R.B., Gamble, E.E., and Nelson, L.A., 1971, Relations between soil morphology and water table levels on a dissected North-central Carolina coastal plain surface: Soil Science Society of America Proceedings, v. 35, p. 157–175.

Darwin, C., 1859, The origin of species by means of natural selection: London, John Murray, 513 p.

Delcourt, H.R., and Delcourt, P.A., 1991, Quaternary ecology, a paleoecological perspective: New York, Chapman and Hall, 242 p.

DiMichele, W.A., and Aronson, R.B., 1992, The Pennsylvanian-Permian vegetational transition: A terrestrial analogue to the onshore-offshore hypothesis: Evolution—International Journal of Organic Evolution, v. 46, p. 807–824.

DiMichele, W.A., and Phillips, T.L., 1994, Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 106, p. 39–90, doi: 10.1016/0031-0182(94)90004-3.

DiMichele, W.A., and Phillips, T.L., 2002, The ecology of Paleozoic ferns: Review of Palaeobotany and Palynology, v. 119, p. 143–159, doi: 10.1016/S0034-6667(01)00134-8.

DiMichele, W.A., Hook, R.W., Mamay, S.H., and Willard, D.A., 1991, Paleoecology of Carboniferous-Permian transitional vegetation in north-central Texas: American Journal of Botany, Abstracts Supplement, v. 78, no. 6, p. 111–112.

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

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

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

Duchaufour, P., 1982, Pedology: Pedogenesis and classification: London, Allen and Unwin, 448 p.

Dunbar, C.O., and Skinner, J.W., 1937, Permian Fusulinidae of Texas: University of Texas Bulletin, no. 3701, The geology of Texas, v. 3, part 1, p. 516–732.

Edwards, M.B., Eriksson, K.A., and Kier, R.S., 1983, Paleochannel geometry and flow patterns determined from exhumed Permian point bars in north-central Texas: Journal of Sedimentary Petrology, v. 53, p. 1261–1270.

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

Falcon-Lang, H.J., 2004a, Early Mississippian lycopsid forests in a delta-plain setting at Norton, near Sussex, New Brunswick, Canada: Journal of the Geological Society [London], v. 161, p. 964–981.

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

Falcon-Lang, H.J., and Bashforth, A., 2004, Pennsylvanian uplands were forested by giant cordaitalean trees: Geology, v. 32, p. 417–420, doi: 10.1130/G20371.1.

Falcon-Lang, H.J., Rygel, M.C., Calder, J.H., and Gibling, M.R., 2004, An early Pennsylvanian waterhole deposit and its fossil biota in a dryland alluvial plain setting, Joggins, Nova Scotia: Journal of the Geological Society [London], v. 161, p. 209–224.

Franklin, D.W., Chairman, 1951, Fall field excursion: Abilene Geological Society, 24 p.

Franzmeier, F.P., Bryant, R.B., and Steinhardt, G.C., 1985, Characteristics of Wisconsinan glacial tills in Indiana and their influence on Argillic horizon development: Soil Science Society of America Journal, v. 49, p. 1481–1486.

Galloway, W.E., and Brown, L.F., Jr., 1972, Depositional systems and shelf-slope relationships in Upper Pennsylvanian rocks, north-central Texas: University of Texas at Austin Bureau of Economic Geology Report of Investigations, v. 75, p. 1–62.

Galtier, J., Scott, A.C., Powell, J.H., Glover, B.W., and Waters, C.N., 1992, Anatomically preserved conifer-like stems from the Upper Carboniferous of England: Proceedings of the Royal Society of London, ser. B, v. 247, p. 211–214.

Gardner, T.W., Williams, E.G., and Holbrook, P.W., 1988, Pedogenesis of some Pennsylvanian underclays: Ground-water, topographic and tectonic controls, *in* Reinhardt, J. and Sigleo, W.R., eds., Paleosols and weathering through geological time: Principles and applications: Geological Society of America Special Paper 216, p. 81–102.

Gastaldo, R.A., 1986, Implications on the paleoecology of autochthonous lycopods in clastic sedimentary environments of the Early Pennsylvanian of Alabama: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 53, p. 191–212, doi: 10.1016/0031-0182(86)90044-1.

Gastaldo, R.A., 1989, Processes of incorporation of plant parts in deltaic coastal sedimentary environments: Implications for paleoecological restorations: International Carboniferous Congress of Stratigraphy and Geology, 11th, Beijing, China, Compte Rendu, v. 3, p. 109–120.

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

Guo, Y., 1990, Paleoecology of flora from coal measures of Upper Permian in western Guizhou: Journal China Coal Society, v. 15, p. 48–54.

Henbest, L.G., 1938, Notes on the ranges of Fusulinidae in the Cisco Group (restricted) of the Brazos River region, north-central Texas: The University of Texas, publication 3801, p. 237–247.

Hentz, T.F., 1988, Lithostratigraphy and paleoenvironments of upper Paleozoic continental red beds, north-central Texas: Bowie (new) and Wichita (revised) Groups: The University of Texas at Austin Bureau of Economic Geology Report of Investigations, v. 170, p. 1–55.

Hilton, J., Wang, S.-J., Galtier, J., and Li, C.-S., 2001, An Early Permian plant assemblage from the Taiyuan Formation of northern China with compression/impression and permineralized preservation: Review of Palaeobotany and Palynology, v. 114, p. 175–189, doi: 10.1016/S0034-6667(01)00045-8.

Hentz, T.F., and Brown, L.F., Jr., 1987, Wichita Falls-Lawton Sheet. University of Texas at Austin Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250 000.

Hook, R.W., 1989, Stratigraphic distribution of tetrapods in the Bowie and Wichita Groups, Permo-Carboniferous of north-central Texas, *in* Hook, R.W., ed., Permo-Carboniferous vertebrate paleontology, lithostratigraphy, and depositional environments of north-central Texas: Society of Vertebrate Paleontology, 49th Annual Meeting, Austin, Texas, Field Trip Guidebook 2, p. 47–53.

Johnson, G.D., 1980, Early Permian vertebrates from Texas: Actinopterygii (Schaefferichthys), Chondrichthyes (including Pennsylvanian and Triassic Xenacanthodii), and Acanthodii [Ph.D. Dissertation]: Dallas, Southern Methodist University, 653 p.

Jones, J.O., and Hentz, T.F., 1988, Permian strata of north-central Texas, *in* Hayward, O.T., ed., South-Central Section of the Geological Society of America: Boulder, Colorado, Geological Society of America Centennial Field Guide, v. 4, p. 309–316.

Kerp, J.H.F., 1984, Aspects of Permian palaeobotany and palynology. III. A new reconstruction of *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt (Sphenopsida): Review of Palaeobotany and Palynology, v. 40, p. 237–261, doi: 10.1016/0034-6667(84)90011-3.

Kerp, J.H.F., 1988, Aspects of Permian palaeobotany and palynology. X. The west- and central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaceae) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage): Review of Palaeobotany and Palynology, v. 54, p. 249–360, doi: 10.1016/0034-6667(88)90017-6.

Kerp, H., 1990, The study of fossil gymnosperms by means of cuticular analysis: Palaios, v. 5, p. 548–569.

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

Kraus, M.J., 1987, Integration of channel and flood-plain suites. II. Vertical relations of alluvial paleosols: Journal of Sedimentary Petrology, v. 57, p. 602–612.

Laveine, J.-P., 1989, Guide Paleobotanique dans le terrain Houiller Sarro-Lorrain: Documents des Houilleres du Bassin de Lorraine, Imprimerie de Houillères du Bassin de Lorraine, 154 p.

Leary, R.L., 1975, Early Pennsylvanian paleoecology of an upland area, western Illinois, USA: Bulletin de la Société Géologique Belgique, v. 84, p. 19–31.

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

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

Markewich, H.W., and Pavich, M.J., 1991, Soil chronosequence studies in temperate to subtropical, low-latitude, low relief terrain with data from the eastern United States: Geoderma, v. 51, p. 213–239, doi: 10.1016/0016-7061(91)90072-2.

Mamay, S.H., 1968, *Russellites*, new genus, a problematical plant from the Lower Permian of Texas: U.S. Geological Survey Professional Paper 593-I, 15 p.

Mamay, S.H., 1986, New species of Gigantopteridaceae from the Lower Permian of Texas: Phytologia, v. 61, p. 311–315.

Mamay, S.H., 1989, *Evolsonia*, a new genus of Gigantopteridaceae from the Lower Permian Vale Formation, north-central Texas: American Journal of Botany, v. 76, p. 1299–1311.

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

Mamay, S.H., 1992, *Sphenopteridium* and *Telangiopsis* in a *Diplopteridium*-like association from the Virgilian (Upper Pennsylvanian) of New Mexico: American Journal of Botany, v. 79, p. 1092–1101.

Mamay, S.H., and Mapes, G., 1992, Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources Bulletin, v. 138, p. 61–85.

Mamay, S.H., Miller, D.M., Rohr, D.M., and Stein, W.E., 1988, Foliar morphology and anatomy of the gigantopterid plant *Delnortea abbottiae*, from the Lower Permian of west Texas: American Journal of Botany, v. 75, p. 1409–1433.

Mapel, W.J., 1967, Bituminous coal resources of Texas: U.S. Geological Survey Bulletin, v. 1242-D, p. D1–D28.

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

McGowen, J.H., Hentz, T.F., Owen, D.E., Pieper, M.K., Shelby, C.A., and Barnes, V.E., 1967 [revised 1991], Sherman Sheet, University of Texas at Austin, Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250 000, 1 sheet.

Mear, C.E., 1963, Stratigraphy of Permian outcrops, Coke County, Texas: Bulletin of the American Association of Petroleum Geologists, v. 47, p. 1952–1962.

Mear, C.E., 1984, Stratigraphy of Upper Permian rocks, Midland Basin and Eastern Shelf, Texas: Society of Economic Paleontologists and Mineralogists, Permian Basin Section, Publication no. 84–23, p. 89–93.

Miller, A.K., and Youngquist, W., 1947, Lower Permian cephalopods from the Texas Colorado River Valley: University of Kansas Paleontological Contributions, no. 2, Mollusca, Article 1, p. 1–15.

Moore, R.C., 1949, Rocks of Permian(?) age in the Colorado River Valley, north-central Texas: U.S. Geological Survey Oil and Gas Investigation Preliminary Map 80, scale 1:62 500, 2 sheets.

Murry, P.A., and Johnson, G.D., 1987, Clear Fork vertebrates and environments from the Lower Permian of north-central Texas: Texas Journal of Science, v. 39, p. 254–266.

Naugolnykh, S.V., 1999, A new species of *Compsopteris* Zalessky from the Upper Permian of the Kama River Basin (Perm Region): Palaeontological Journal, v. 33, p. 686–697.

Nelson, W.J., Hook, R.W., and Tabor, N., 2001, Clear Fork Group (Leonardian, Lower Permian) of north-central Texas: Oklahoma Geological Survey Circular 104, p. 167–169.

Olson, E.C., 1958, Fauna of the Vale and Choza, 14: Summary, review, and integration of the geology and the faunas: Fieldiana, Geology, v. 10, p. 397–448.

Olson, E.C., 1962, Late Permian terrestrial vertebrates: USA and USSR: Transactions of the American Philosophical Society, v. 52, p. 3–224.

Olson, E.C., 1989, The Arroyo Formation (Leonardian: Lower Permian) and its vertebrate fossils: Texas Memorial Museum Bulletin, v. 35, 25 p.

Olson, E.C., and Bolles, K., 1975, Permo-Carboniferous fresh water burrows: Fieldiana, Geology, v. 33, p. 271–290.

Olson, E.C., and Mead, J.G., 1982, The Vale Formation (Lower Permian), its vertebrates and paleoecology: Texas Memorial Museum Bulletin, v. 29, 46 p.

Overpeck, J.T., Webb, R.S., and Webb, T., III, 1992, Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future: Geology, v. 20, p. 1071–1074, doi: 10.1130/0091-7613(1992)020<1071:MENAVC>2.3.CO;2.

Parrish, W.C., 1978, Paleoenvironmental analysis of Lower Permian bonebed and adjacent sediments, Wichita County, Texas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 24, p. 209–237, doi: 10.1016/0031-0182(78)90043-3.

Pfefferkorn, H.W., 1980, A note on the term "upland flora": Review of Palaeobotany and Palynology, v. 30, p. 157–158, doi: 10.1016/0034-6667(80)90011-1.

Pfefferkorn, H.W., Mustafa, H., and Hass, H., 1975, Quantitative Charakterisierung ober-karboner Abdruckfloren (Quantitative characterization of compression-impression floras of Upper Carboniferous age): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 150, p. 253–269.

Pfefferkorn, H.W., Gastaldo, R.A. and DiMichele, W.A. 2000. Ecological stability during the Late Paleozoic cold interval, *in* Gastaldo, R.A., and DiMichele, W.A., eds., Phanerozoic terrestrial ecosystems: Paleontological Society Special Papers v. 6, p. 63–78.

Phillips, T.L., 1979, Reproduction of heterosporous arborescent lycopods in the Mississippian-Pennsylvanian of Euramerica: Review of Palaeobotany and Palynology, v. 27, p. 239–289, doi: 10.1016/0034-6667(79)90014-9.

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

Pipujol, M.D., and Buurman, P., 1994, The distinction between groundwater gley and surface-water gley phenomena in Tertiary paleosols of the Ebro Basin, NE Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 110, p. 103–110.

Plummer, F.B., and Scott, G., 1937, Upper Paleozoic ammonites in Texas: University of Texas Bulletin, no. 3701, The geology of Texas, v. 3, part 1, p. 1–516.

Read, C.B., and Mamay, S.H., 1964, Upper Paleozoic floral zones and floral provinces of the United States: U.S. Geological Survey Professional Paper 454-K, p. 1–35.

Read, W.F., 1943, Environmental significance of a small deposit in the Texas Permian: Journal of Geology, v. 51, p. 473–487.

Rees, P.M., Ziegler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P.J., and Rowley, D.B., 2002, Permian phytogeographic patterns and climate data/model comparisons: Journal of Geology, v. 110, p. 1–31, doi: 10.1086/324203.

Retallack, G.J., 1990, Soils of the past: An introduction to paleopedology: Boston, Unwin-Hyman, 520 p.

Retallack, G.J., 1994, A pedotype approach to latest Cretaceous and earliest Tertiary paleosols in eastern Montana: Geological Society of America Bulletin, v. 106, p. 1377–1397, doi: 10.1130/0016-7606(1994)106<1377:APATLC>2.3.CO;2.

Romer, A.S., and Olson, E.C., 1954, Aestivation in a Permian lungfish: Breviora, v. 30, p. 1–8.

Roth, R., 1931, New information on the base of the Permian in north-central Texas: Journal of Paleontology, v. 5, p. 295.

Rothwell, G.W., and Mapes, G., 1988, Vegetation of a Paleozoic conifer community, *in* Mapes, G., and Mapes, R.H., eds., Regional geology and paleontology of upper Paleozoic Hamilton Quarry Area in southeastern Kansas: Geological Society of America, South-Central Section, 33rd Annual Meeting, Guidebook, p. 213–223.

Royer, D.L., 1999, Depth to pedogenic carbonate horizon as a paleoprecipitation indicator?: Geology, v. 27, p. 1123–1126, doi: 10.1130/0091-7613(1999)027<1123:DTPCHA>2.3.CO;2.

Sander, P.M., 1989, Early Permian depositional environments and pond bonebeds in central Archer County, Texas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 69, p. 1–21, doi: 10.1016/0031-0182(89)90153-3.

Scheckler, S.E., 1986, Floras of the Devonian-Mississippian transition, *in* Gastaldo, R.A., ed., Land plants: Notes for a short course: University of Tennessee, Studies in Geology, v. 15, p. 81–96.

Scheihing, M.H., and 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, v. 41, p. 205–280, doi: 10.1016/0034-6667(84)90047-2.

Scott, A.C., and Chaloner, W.G., 1983, The earliest fossil conifer from the Westphalian B of Yorkshire: Proceedings of the Royal Society of London, ser. B, v. 220, p. 163–182.

Scott, A.C., Galtier, J., and Clayton, G., 1984, Distribution of anatomically-preserved floras in the Lower Carboniferous in Western Europe: the Royal Society of Edinburgh, Earth Sciences, v. 75, p. 311–340.

Sellards, E.H., 1932, Pre-Paleozoic and Paleozoic systems in Texas, *in* Sellards, E.H., Adkins, W.S., and Plummer, F.B., eds., University of Texas Bulletin, no. 3232, The Geology of Texas, v. 1, p. 15–238.

Smith, G.E., 1974, Depositional systems, San Angelo Formation (Permian), North Texas—Facies control on red-bed copper mineralization: University of Texas at Austin Bureau of Economic Geology Report of Investigations, v. 80, p. 1–74.

Soil Survey Staff, 1975, Soil taxonomy: Washington, D.C., U.S. Department of Agriculture Handbook 436, 754 p.

Soil Survey Staff, 1998, Keys to soil taxonomy: Washington, D.C., U.S. Department of Agriculture, Natural Resources Conservation Service, 325 p.

Spicer, R.A., 1981, The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. U.S. Geological Survey Professional Paper 1143, p. 1–77.

Tabor, N.J., and Montañez, I.P., 2004, Morphology and distribution of fossil soils in the Permo-Pennsylvanian Wichita and Bowie Groups, north-central Texas, USA: Implications for western equatorial Pangean paleoclimate during icehouse-greenhouse transition: Sedimentology, v. 51, p. 851–884, doi: 10.1111/j.1365-3091.2004.00655.x.

Tabor, N.J., Montañez, I.P., and Southard, R.J., 2002, Paleoenvironmental reconstruction from chemical and isotopic compositions of Permo-Pennsylvanian pedogenic minerals: Geochimica et Cosmochimica Acta, v. 66, p. 3093–3107, doi: 10.1016/S0016-7037(02)00879-7.

Tian, B.L., Wang, S.J., Gao, Y.T., Chen, G.R., and Zhao, H., 1996, Flora of Palaeozoic coal balls in China: Palaeobotanist, v. 45, p. 247–254.

Wagner, R.H., 1983, Upper Stephanian stratigraphy and palaeontology of the Puertollano Basin, Ciudad Real, Spain, *in* Lemos de Sousa, M.J., and Wagner, R.H., eds., Papers on the Carboniferous of the Iberian Peninsula: Annals Facultad de Ciências, Porto, Supplement, v. 64, p. 171–231.

Weiher, E., and Keddy, P., 1999 (2001). Assembly rules as general constraints on community composition, *in* Weiher, E., and Keddy, P., eds., Ecological assembly rules: Cambridge, UK, Cambridge University Press, p. 251–271.

White, D.W., 1911, *in* Gordon, C. H., Geology and underground waters of northeastern Texas: U.S. Geological Survey Water-Supply Paper 276 p. 1–78.

Wilson, M.J., 1999, The origin and formation of clay minerals in soils; past, present and future perspectives: Clay Minerals, v. 34, p. 7–25.

Wing, S.L., Hickey, L.J., and Swisher, C.C., 1993, Implications of an exceptional fossil flora for Late Cretaceous vegetation: Nature, v. 363, p. 342–344, doi: 10.1038/363342a0.

Wright, V.P., and Marriott, S.B., 1996, A quantitative approach to soil occurrence in alluvial deposits and its application to the Old Red Sandstone of Britain: Journal of the Geological Society [London], v. 153, p. 907–913.

Yemane, K., Kahr, G., and Kelts, K., 1996, Imprints of post-glacial climates and paleogeography in the detrital clay mineral assemblages of an Upper Permian fluviolacustrine Gondwana deposit from north-central Malawi: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 125, p. 27–49, doi: 10.1016/S0031-0182(96)00023-5.

Zhou, Y.-X., 1994, Earliest pollen-dominated microfloras from the early Late Carboniferous of the Tian Shan, northwest China: Their significance for the origin of conifers and palaeophytogeography: Review of Palaeobotany and Palynology, v. 81, p. 193–211, doi: 10.1016/0034-6667(94)90108-2.

Zodrow, E.L., 1990, Revision and emendation of *Pecopteris arborescens* Group, Permo-Carboniferous: Palaeontographica, ser. B, v. 217, p. 1–49.

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