AN EARLY PERMIAN FLORA WITH LATE PERMIAN AND MESOZOIC AFFINITIES FROM NORTH-CENTRAL TEXAS

WILLIAM A. DiMICHELE,[1] SERGIUS H. MAMAY,[1] DAN S. CHANEY,[1] ROBERT W. HOOK,[2] AND W. JOHN NELSON[3]

[1]Department of Paleobiology, Smithsonian Institution, Washington, D.C., 20560, <dimichele.bill@nmnh.si.edu>,
[2]Texas Memorial Museum, The University of Texas at Austin, Austin 78758, and
[3]Illinois State Geological Survey, Champaign, IL 61820

ABSTRACT—Early Permian (late Leonardian Series) plant assemblages from King, Knox, and Stonewall Counties of North-Central Texas are dominated by seed plants, some apparently congeneric with taxa heretofore known only from the Late Permian or the Mesozoic. Conifers are the dominant elements, including one or more species of *Ullmannia, Pseudovoltzia liebeana,* both known from the Late Permian Zechstein flora of Germany and England, *Podozamites* sp., characteristic of the Mesozoic, and *Walchia* sp., abundant in Early Permian floras. Locally common are *Taeniopteris* cf. *eckardtii,* a Zechstein species, an unidentified plant represented by pinnule-like laminae with fine parallel veins, similar to pinnules of some Mesozoic cycads, and calamite stems. Rarely encountered are leaf fragments of the Paleozoic ginkgophyte *Dicranophyllum,* flabellate ginkgophyte leaves, leaves with a broad midvein and narrow, fimbriate lamina, and *Wattia,* typical of the Early Permian. Associated with these foliar remains are ovulate reproductive structures including the presumed cycad megasporophyll *Dioonitocarpidium,* known only from the Mesozoic, a voltzialean cone scale similar to *Swedenborgia,* and a variety of seeds, some remarkably similar to *Agathis,* of Cretaceous age. The assemblage includes only rare scraps of foliage and seeds possibly attributable to the pteridophyllous elements (gigantopterids, callipterids, and ferns) that dominate the Permian. The fossil plants occur in multistorey, fining-upwards, tidal-channel deposits that also include pelecypods and fragmentary palaeoniscoid fish. The occurrence of derived lineages in xeric habitats during the Early Permian indicates that some supposed Mesozoic groups actually preceded and survived the end-Permian extinction, reappearing in basinal lowlands during the mid-Mesozoic.

INTRODUCTION

R ECENT FIELD work in the Early Permian of North-Central Texas has produced plant assemblages that differ significantly from any Paleozoic floras known from Euramerica. Continental sediments of this area have long been recognized as a source of gymnosperm groups that would come to dominate most Mesozoic landscapes (Read and Mamay, 1964). However, previously reported Early Permian representatives of seasonally dry, gymnosperm-dominated floras appear to be primitive, and the emergence of the tropical seasonally dry flora is poorly understood. The new Early Permian material, which includes taxa heretofore known only from Late Permian and Mesozoic rocks, provides an enhanced understanding of late Paleozoic vegetational change and challenges existing hypotheses of plant evolution and paleoecology during the Permian and early Mesozoic.

The newly discovered flora was found at seven localities in the lower portion of the Pease River Group in King, Knox, and Stonewall counties, Texas (Fig. 1). Plants occur in association with locally abundant pelecypods and poorly preserved palaeoniscoid fish in copper-bearing, multistorey, fining-upward, tidal-channel deposits at or near the contact between the San Angelo Formation and the overlying Blaine Formation; the sedimentology and stratigraphy of these deposits have been described by Stroud et al. (1970) and Smith (1974). Although amphibian and reptile remains from the San Angelo Formation of this region have been attributed to the Guadalupian Series (Olson, 1962), biostratigraphic correlations based upon marine invertebrates (fusulinids and ammonoids) between our study area and the Delaware and Midland Basins indicate that the San Angelo Formation and lower part of the Blaine Formation are late Leonardian in age (Böse, 1917; Plummer and Scott, 1937; Clifton, 1945, 1946; Skinner, 1946; Mear, 1984).

GEOLOGIC SETTING

The fossiliferous deposits reported here occur at or near the contact between the San Angelo Formation and the overlying Blaine Formation, both within the Pease River Group in King, Knox, and Stonewall Counties, Texas (Fig. 2). The San Angelo Formation, 20–40 m thick, is divisible into two members of roughly equal thickness. The lower is the Duncan Sandstone Member, which consists of light-colored crossbedded and ripple-laminated sandstone, and the upper is the Flowerpot Shale Member, which is largely red mudstone, containing thin bodies of channel-form sandstone and nodules and stringers of gypsum. The Blaine Formation is over 200 m thick, composed of interbedded mudstone, gypsum in beds up to 10 m thick, and has regionally traceable members of limestone and dolomite. The San Angelo-Blaine contact is gradational, but customarily is mapped at the base of the lowest bed of gypsum thicker than 30 cm. The lithostratigraphic interval of the fossiliferous deposits spans approximately 12 m in the transitional interval between the two formations. The Clear Fork Group lies immediately below the Pease River Group in the study area. The upper part of the Clear Fork Group on outcrop is dominantly red mudstone, which contains nodules, stringers, veins, and thin (a few centimeters thick) beds of gypsum, along with thin (a few centimeters thick) but laterally continuous beds of micritic dolomite.

All plant-bearing deposits occur in channel facies that originated as tidal channels within a coastal plain setting on the Eastern Shelf of the Midland Basin. In overall aspect, the upper San Angelo is dominated by gypsum-bearing red mudstones that have been attributed to tidal-flat depositional settings (Smith, 1974, 1976). The occurrence of numerous thick (>3 m) bedded gypsum deposits in the Blaine Formation has been interpreted to indicate origin in sabkha-dominated coastal plain environments (Jones, 1971; Jones and Hentz, 1988). Paleosols in this interval range from immature protosols to well-developed vertisols that lack pedogenic carbonates, contain finely disseminated pedogenic sulfates within their matrix and along vertisol slickensides, and have poorly developed root structures. Preliminary analysis indicates that these paleosols developed under strongly seasonal climates (Neil Tabor, personal commun., 1998).

AGE OF THE PLANT-BEARING ROCKS

Skinner (1946) dated the San Angelo Formation as latest Leonardian on the basis of the fusulinid *Schubertella melonica* in limestones interbedded with San Angelo sandstones in drill holes; this fusulinid is known only from the upper half of the Leonardian. Skinner (1946) did not specify a location, but it is probably along
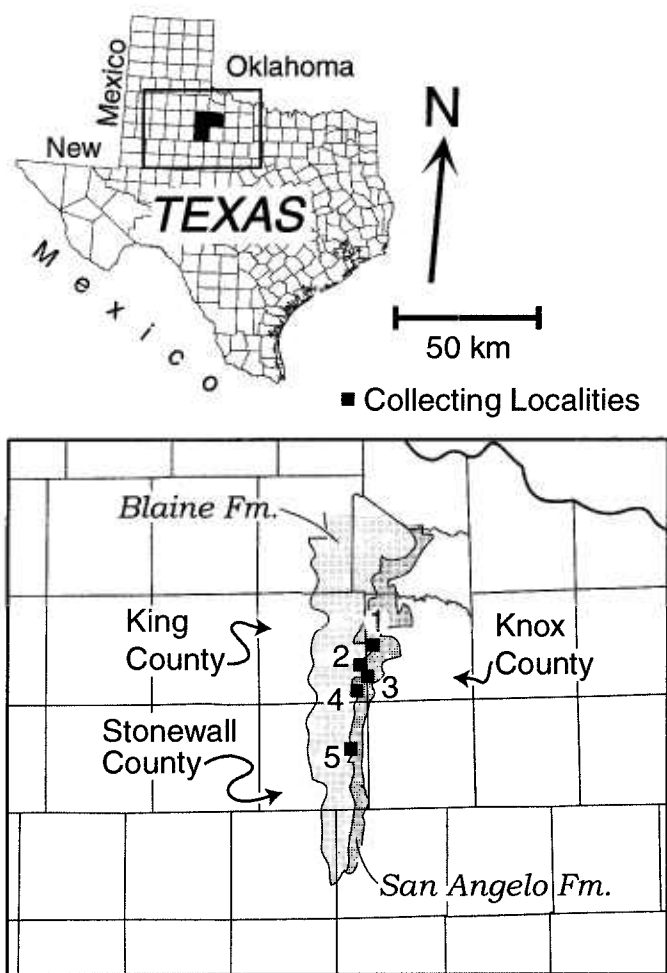
FIGURE *1*—Location of lower Pease River Group study area and collecting sites in North-Central Texas. Numbers refer to the following collecting sites: (1) Pyron Prospect, (2) Snake Den Tank, two sites, (3) Buzzard Peak, (4) East Taylor Pasture, two sites, (5) Devil's Canyon.

the margin of the Midland Basin, given that the San Angelo Formation does not extend into the deep Midland Basin or the Delaware Basin. A limestone above the San Angelo in Ector County in the western Midland Basin also contains a fusulinid known only from the uppermost Leonardian, *Parafusulina fountaini* (Skinner, 1946). Skinner's interpretations are supported by Mear (1984), who argued that the San Angelo is Leonardian in age and may be equivalent to the Glorieta Sandstone of West Texas and New Mexico.

The age of the Blaine Formation, which lies immediately above

the San Angelo in the study area, is problematic. The new flora occurs about 120 m stratigraphically below the Aspermont Dolomite Member of the upper part of the Blaine Formation. The ammonoid *Perrinites hilli* is common in the Blaine and occurs in the Aspermont Dolomite (Böse, 1917; Jones and Hentz, 1988). This taxon has a global range of middle Leonardian (Artinskian) through Wordian (the middle stage of the Guadalupian) (Clifton, 1946). On the basis of *P. hilli*, other ammonoids, and fusulinids, Clifton (1945) correlated limestones from the Glass Mountains of what is now known as the Road Canyon Formation (Guadalupian) with portions of the Blaine Formation on the eastern shelf of the Midland Basin. Plummer and Scott (1937) identified a *Eumedlicottia burckhardti* assemblage from the Acme Dolomite Member of the middle of the Blaine Formation in Hardeman County, Texas, immediately to the north of our study area. This ammonoid assemblage also occurs in the Word Formation of the Delaware and Permian Basins, where *E. burckhardti* occurs in close association with *Waagenoceras*, an ammonoid confined to the Guadalupian. Clifton (1942) identified six ammonite species in the Blaine that, when their age ranges (Zhou et al., 1996) are considered jointly, overlap only within the Guadalupian Series. Based on these various lines of evidence, it appears that the Blaine Formation is largely Guadalupian in age, but may include the latest Leonardian at its base (this cannot be ruled out; all fossiliferous carbonates lie above the plant-bearing interval). Therefore, the flora can be no older than Leonardian and no younger than Guadalupian and most likely is late Leonardian.
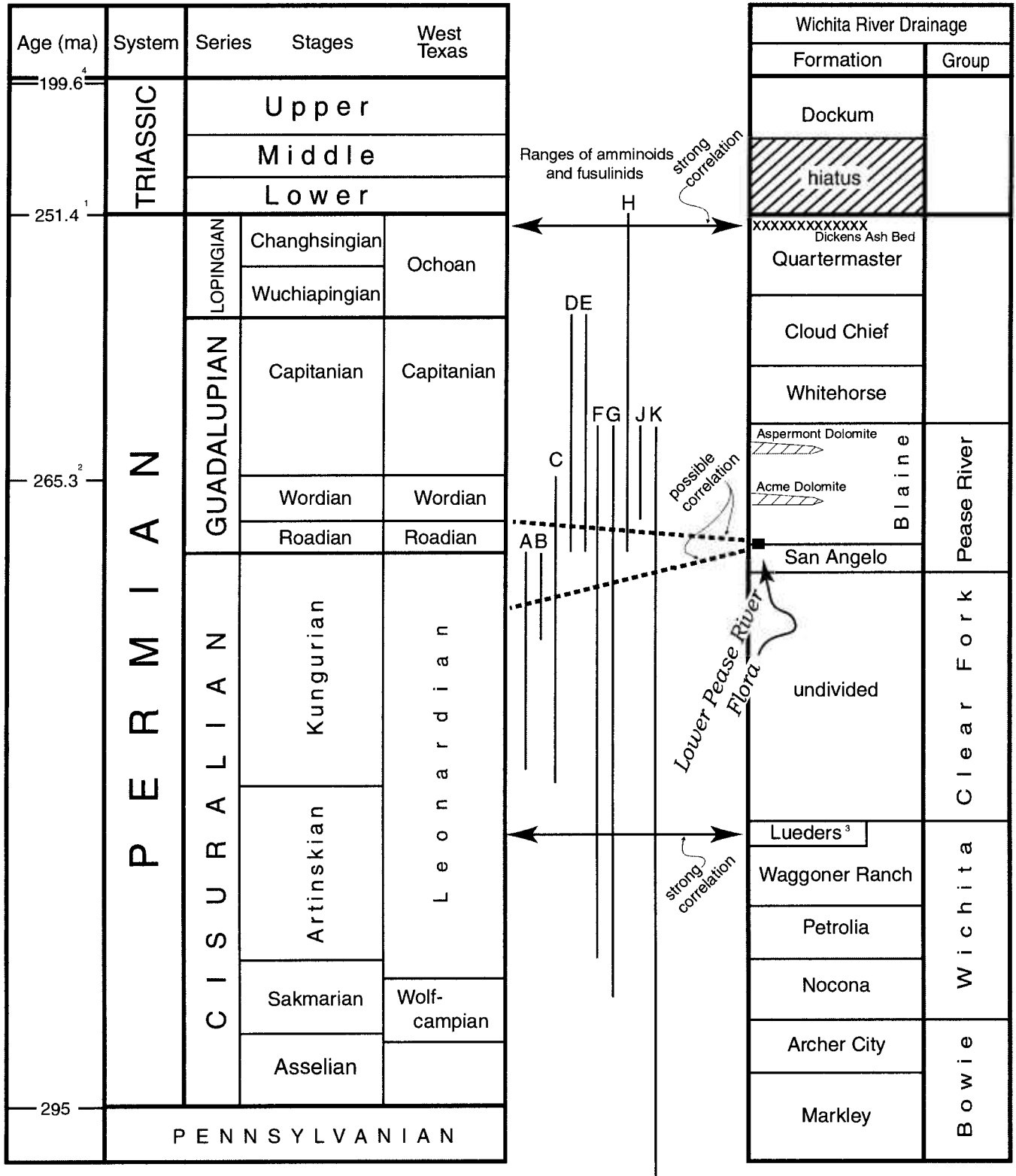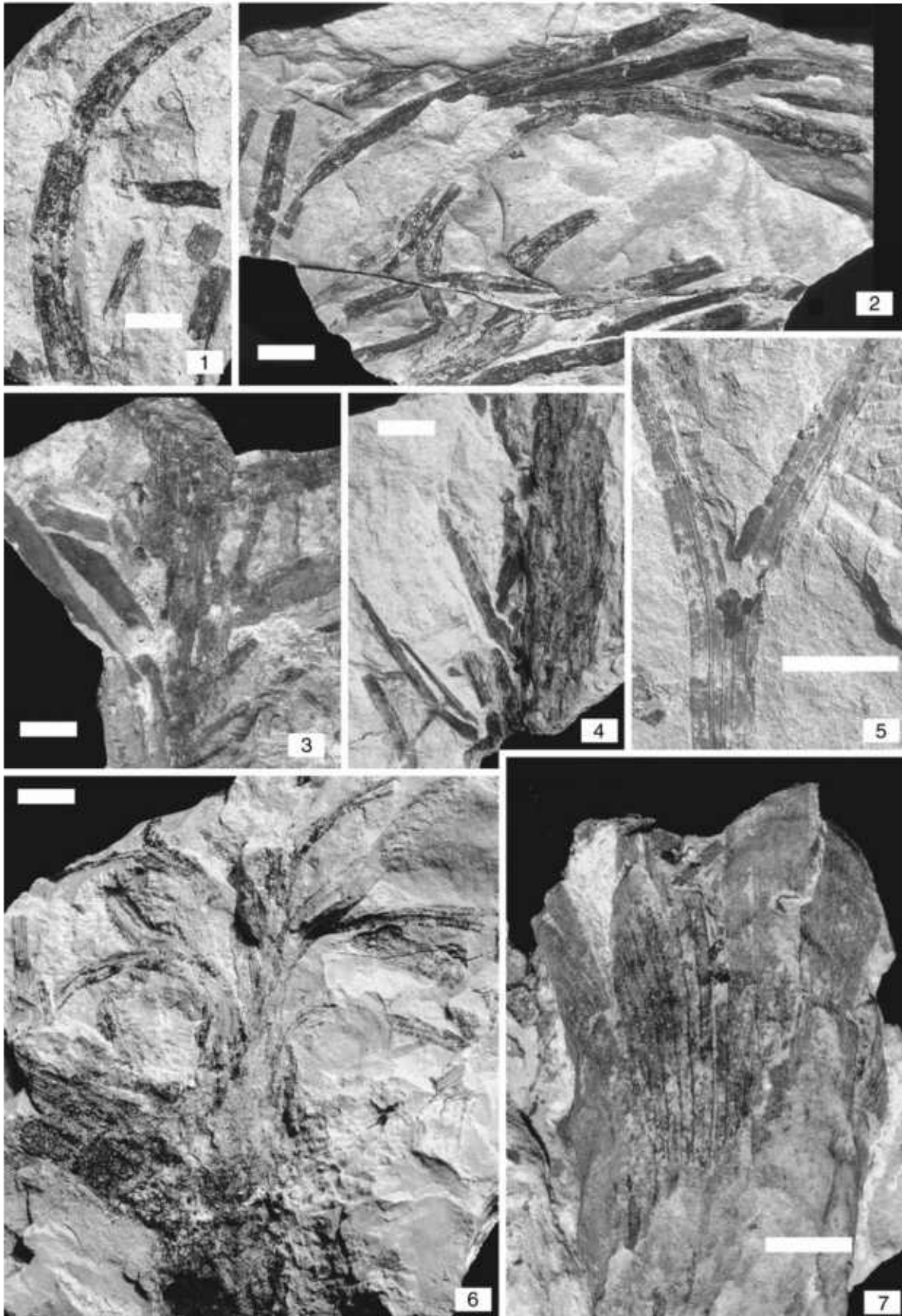
LOCALITY AND REPOSITORY INFORMATION

All specimens examined in this study are housed in the Paleobotanical Collections of the United States National Museum of Natural History, Smithsonian Institution. All illustrated specimens are housed in the Paleobotanical Type and Illustrated Collections under the USNM catalogue numbers cited in the figure captions.

At the request of property owners, locality information is to the general collecting areas rather than exact sites. Collections were made at seven sites. These sites are listed below according to their occurrence from north to south in the outcrop belt of the lower Pease River Group. (Longitude and Latitude are for the middle of the indicated 7.5″ USGS map quadrangle.)

1. Pyron Prospect (USNM 41399) Cedar Mountain 7.5′ quad. Knox Co. TX; 33 33 45N 99 56 15W
2. Snake Den Tank
   A. Shooting Range (USNM 41386) Buzzard Peak 7.5′ quad. King Co. TX; 33 33 45N 100 03 45W
   B. Log Jam (USNM 41426, 41644, 41645, 41646, 41647, 41648, 41658, 41659, 41660) Buzzard Peak 7.5′ quad. King Co. TX; 33 33 45N 100 03 45W
3. Buzzard Peak (USNM 41384, 41391, 41393, 41394, 41395, 41396, 41397, 41398) Cedar Mountain 7.5′ quad. Knox Co. TX; 33 33 45N 99 56 15W
4. East Taylor Pasture

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FIGURE 2—Generalized stratigraphic column for the San Angelo and Blaine Formations and the lower Pease River floras, north central Texas. Chronostratigraphic sequence is shown on the left; lithostratigraphic sequence is shown on the right. Ranges of fusilinids (A and B) ammonoids (C through K) used in bracketing the age of the lower Pease River flora are shown in the center: A = *Schubertella melonica*, B = *Parafusulina fountani*, C = *Perrinites hilli*, D = *Waagenoceras*, E = *Eumedlicottia burckhardti*, F = *Propinacoceras knighti*, G = *Medlicottia whitneyi*, H = *Pseudogastroceras texanum*, J = *Adrianites newelli*, K = *Agathiceras girtyi*. Ammonoids C and F–K occur in the Blaine Formation, according to Clifton (1942). Their ranges are taken from Zhou et al. (1996), except for H, which has been identified in Roadian and Wordian rocks of West Texas by Clifton (1946, p. 558). ¹Date of Permo-Triassic boundary event, 251 +/− 0.3 ma at Meishan, China (Bowring et al., 1998). ²Date at base of Capitanian, 265.3 +/− 0.2 ma in West Texas (Bowring et al., 1998). ³Leuders Formation is part of the marine Albany Group, which is the upper unit in the southern lateral equivalent of the Wichita Group. ⁴Date at Tr/J boundary 199.6 +/− 0.3 mybp, Kunga Island, Canada (Pálfy et al., 2000).

Age (ma)	System	Series	Stages		West Texas
199.6 [4]	TRIASSIC		Upper		
			Middle		
251.4 [1]			Lower		
	PERMIAN	LOPINGIAN	Changhsingian		Ochoan
			Wuchiapingian		
		GUADALUPIAN	Capitanian		Capitanian
265.3 [2]			Wordian		Wordian
			Roadian		Roadian
		CISURALIAN	Kungurian	Leonardian	
			Artinskian		
			Sakmarian		Wolf-campian
			Asselian		
295			PENNSYLVANIAN		

Ranges of amminoids and fusulinids

strong correlation

H

DE

FG JK

C

AB

possible correlation

Lower Pease River Flora

strong correlation

Wichita River Drainage

Formation	Group
Dockum	
hiatus	
xxxxxxxxxxxx Dickens Ash Bed Quartermaster	
Cloud Chief	Pease River
Whitehorse	
Aspermont Dolomite / Acme Dolomite / San Angelo	Blaine
undivided	Clear Fork
Lueders [3]	
Waggoner Ranch	Wichita
Petrolia	
Nocona	
Archer City	Bowie
Markley	

A. Brazos–Wichita Mine (USNM 41385) Kiowa Peak NE 7.5′ quad. King Co. TX; 33 26 15N 100 03 45W

B. Main site (USNM 41383) Kiowa Peak NE 7.5′ quad. King Co. TX; 33 26 15N 100 03 45W

5. Devil's Canyon (USNM 41653, 41654, 41655, 41656, 41657) Frog Mountain 7.5′ quad. Stonewall Co. TX; 33 03 45N 100 03 45W

THE FLORA

Plant fossils of the lower Pease River Flora are preserved mainly as compressions and coalifications. Included are partial remains of large trunks up to 33 cm wide and over 8 m long, variously disarticulated foliage, cones, and seeds. Cuticles are present on a few specimens; many without cuticles yield carbonaceous films that contain anatomical detail, such as placement of stomata. Despite incomplete preservation, we have recognized several taxa on the basis of gross morphology. Our taxonomic appraisal of the flora is detailed in Table 1.

Ribbon-like foliar organs.—The most prominent element in the lower Pease River flora is strap- or ribbon-like foliar organs. In several instances, these remains occur in abundance on single bedding planes and show distinct current-lineation patterns. Dimensions vary, but two forms can be identified based on gross morphology. We interpret these two forms to be taxonomically distinct.

One form may reach lengths of about 6.0 cm and widths of 0.5 cm. Some specimens are considerably wider, approaching 1 cm in width; others are much narrower and shorter. All have parallel sides with acute, tapered distal ends, and basal ends that terminate squarely, with no diminution of width. When visible, veins are fine, parallel and closely spaced. Many of the specimens are strongly falcate and appear to be pinnules rather than leaves (Fig. 3.1); they often have longitudinal wrinkles that appear to result from compression of a thick lamina. These falcate ribbon-like organs may be pinnae of a pinnately compound cycad-like frond. If pinnae, the square base suggests that the pinnae were inserted perpendicularly, rather than obliquely, and broke away by abscission, as seen in some modern cycads. Among the known fossil cycad-like foliar forms, is the genus *Pseudoctenis,* reported from the Zechstein flora of the Late Permian and commonly from the Jurassic (Schweitzer, 1986). *Ctenophyllum,* which occurs in the Early Mesozoic of Europe and North America, also has similar morphological features.

The other form of ribbon-like lamina is narrower and appears to have been thicker or more fleshy in life (Fig. 3.2). Laminae are straight and narrow, 0.3–0.5 cm wide, and veins are generally obscure. Presumed proximal ends terminate squarely and tips are bluntly rounded.

The conifer Podozamites.—Wide, ribbon-like leaves with fine, parallel venation have been found in attachment to stems of various diameters (Fig. 3.3). The tips of such leaves are not preserved and, thus, they cannot be equated with certainty to larger ribbon-like forms described above. They appear most similar to *Podozamites,* known from early Mesozoic floras (Harris, 1926; Halle, 1927). The affinities of *Podozamites* are disputed, although it is generally interpreted as most closely aligned with the conifers (Harris, 1926).

Voltzialean conifers.—Numerous specimens have been found

TABLE 1. Flora of the lower Pease River Group

Equisetales
  Calamitaceae
    cf. *Neocalamites* sp.
Cordaitales
  Cordaitaceae
    Cordaites sp.
Coniferales
  Ullmanniaceae
    Ullmannia sp.
  Majonicaceae
    Pseudovoltzia liebeana
  Majonicaceae or Araucariaceae
    cf. *Agathis*-like seeds
  Walchiaceae
    Culmitzschia sp.
  Coniferales Incertae sedis
    Podozamites sp.
Ginkgoales
  Dicranophyllaceae
    Dicranophyllum sp.
  Ginkgoales incertae sedis
    Undetermined foliage
Cycadales
  Cycadaceae
    Dioonitocarpidium sp.
Incertae Sedis
    Taeniopteris eckardtii
    Taeniopters sp.
    Wattia texana
    Undetermined pteridophyll foliage of ferns or pteridosperms
    Undetermined seeds and cones

in which ribbon-like leaves, similar to the more narrow class of dispersed laminae, are attached in a spiral manner to an axis and show clasping bases. In these instances they can be interpreted unambiguously as leaves (Fig. 3.4). Such specimens bear a strong similarity to *Pseudovoltzia liebeana,* a conifer common in the Upper Permian and the dominant element of the Late Permian Zechstein flora (Schweitzer, 1986).

Voltzialean conifers also are represented by numerous cone-scale complexes (Fig. 5.8). These are bilaterally symmetrical fan-like structures characterized by a group of five to seven pointed scale-like units reaching 5.0 mm in length and attached to the end of a naked stalk up to 1.2 cm in length. The stalk is sharply truncated at the base, as though abscissed. Many examples also bear a single, somewhat rounded central lobe. Similar lobate cone scales from the Zechstein flora of England have been attributed to *Pseudovoltzia* (Stoneley, 1958; Clement-Westerhof, 1988). The overall aspects of the specimens also strongly resemble the form-genus *Swedenborgia,* originally described from the Lower Jurassic of Sweden (Nathorst, 1876), with occurrences elsewhere in Europe, Greenland, and Asia all of Early Mesozoic age. *Swedenborgia* consists of a loosely constructed ovulate cone that bears long stalks terminated in a deeply dentate, five-lobed cone-scale aggregate, each lobe of which bore one seed.

Possible araucarian conifers.—Winged seeds are a conspicuous element of some of the collections (Fig. 4.1–4.3). The specimens are flattened, ovoid to pyriform or narrowly triangular bodies measuring about 1.2 cm in length and 0.2 cm wide. The bottom (presumably micropylar) end may be pointed but more often

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FIGURE 3—Plant fossils from the Early Permian lower Pease River Group, Texas. Scale bars in all photographs equal 1 cm. *1,* Broad ribbon-like foliar organ with falcate shape and acute, tapered apical end, USNM 508139. *2,* Narrow ribbon-like foliar organs; wrinkling on surfaces suggests originally thick texture, USNM 508140. *3, Podozamites* sp., axis with wide, ribbon-like leaves in attachment arranged helically, USNM 508141. *4, Pseudovoltzia liebeana,* axis with attached narrow, ribbon-like leaves, USNM 508142. *5, Dicranophyllum* sp., fragment of a leaf showing the major fork and prominent, sparse, parallel veins, USNM 508143. *6, Dicranophyllum* sp., axis with forked leaves attached helically, USNM 508144. *7,* Ginkgophyte leaf, flabellate with parallel veins, dividing into terminal lobes, USNM 508145.

is bluntly rounded. The opposite (chalazal) end bears a pair of thin, wing-like appendages, positioned oppositely on the seed "shoulders" in the plane of the seed, which creates a V-shaped configuration. The wings are irregularly ovoid or orbiculoid in outline, usually with a slightly constricted base and outward flare, with a slightly curved upper edge and a more deeply rounded lower edge. The largest wing has dimensions of 1.2 by 1.0 cm. Beyond the basal, slightly thickened area of attachment, the wing tissue is thin with a faint indication of a venation pattern, approximately parallel to the long axis of the wing. The two wings of a given seed may be essentially equal in size, but more often are unequal. Several stages in size differential are present, with the most reduced individual wing represented only by a short, stubby outgrowth about 2.0 mm long.

Many modern conifers have winged seeds, but aside from the living araucarian genus *Agathis*, none produce paired, unequal wings similar to those of the material from the lower Pease River flora. The smaller wing of *Agathis* seeds (Fig. 4.4) varies among species from a slight hump in the seed outline to a well-defined outgrowth of the integument in most specimens (*A. labillardieri*); sometimes it forms a rigid point. The large wings on *Agathis* seeds are extremely thin and delicate and are proportionately nearly twice as large as those of the Permian fossils. Nonetheless, the similarities between *Agathis* seeds and lower Pease River fossils set them apart from all other conifers. In a recent review of the Araucariaceae, Stockey (1994), noted that *Agathis* is not known from strata older than Cretaceous. Thus, if further study of the lower Pease River seeds and associated remains prove to have an affinity with *Agathis,* the age of *Agathis* would be extended by roughly 100 m.y. to about 260 m.y.

At present, however, the affinities of the lower Pease River fossils are unclear. A single specimen was found in which a bi-winged seed was superimposed, perhaps accidentally, on a lobed cone scale similar to those typical of *Pseudovoltzia* (Fig. 4.2), suggesting possible affinities with that group of conifers. A similar type of seed was described by Clement-Westerhof (1987, 1988) from the cone *Majonica alpina,* a European species of Late Permian age. Such seeds are of approximately the same size as those reported here. They bear a single wing on one shoulder of the triangular seed body, opposite the tapered, micropylar end, which renders them bilaterally asymmetrical in the plane of compression. Although such seeds are attached to lobed cone scales, they differ from any found in the lower Pease River flora. Clement-Westerhof (1988) classified these seeds and their attendant cone-scale complexes in the Majonicaceae, a family in which she also placed *Pseudovoltzia* on the basis of distinct organization of the cone-scales and ovules.

Conifers of the Ullmanniaceae.—The conifer *Ullmannia* is predominantly an Upper Permian, European genus, with occurrences in the Triassic of Manchuria and Africa (Seward, 1926; Zalessky, 1928). A plant identified as cf. *Ullmannia bronnii* is prominent in the lower Pease River flora, where it appears as leafy shoot fragments. The axes are stout and clothed with close, helically arranged leaves that reach a maximum length of about 1.2 cm and are relatively thick (Fig. 4.5). The leaves are strongly decurrent and apparently did not become detached readily (Fig. 4.6).

Other specimens resemble *Ullmannia frumentaria* in having longer leaves with stomata in the distinct rows typical of this species. Overall, it is possible that this entire complex represents a single species, given the broad range of variation found among the specimens collected.

Although no fertile structures can be attributed definitely to *Ullmannia* from the lower Pease River flora, abundant dispersed oval seeds, mostly about 3.0 by 5.0 mm in dimensions, actually may be examples of the highly reduced cone-scale complexes characteristic of *Ullmannia.* As interpreted by Florin (1951), each cone-scale complex in *Ullmannia* is a uniovulate strobilus, closely invested by a reduced ovuliferous scale with its five adnate component scales; the whole then rests on the adaxial face of its subtending bract. Nearly all lower Pease River seeds in this size class show a carbon-filled seam or crevice along their length suggestive of the junction between the inverted ovule and its stalk.

Walchian conifers.—Conifers attributable to *Walchia* or possibly *Culmitzschia* (Clement-Westerhof, 1984) occur at several sites in abundance, although they are generally rare. Typically, these plants consist of axes clothed in short, sinusoidally curved, decurrent leaves up to 1 cm in length and 0.5 cm wide (Fig. 5.1). Stripped of leaves, stems are covered with elongate, diamond-shaped leaf scars. It is probable that some of the unattributed winged seeds were produced by these plants.

Dicranophyllum and possible ginkgophyte foliage.—Several specimens consist of an elongate, narrow lamina that is forked, the lobes terminating either bluntly or in tapered acute ends (Fig. 3.5). All specimens are incomplete, although fragments vary from stems with attached leaves (Fig. 3.6) to terminal portions of forked leaves. Affinities of these specimens lie clearly with *Dicranophyllum* (Grand 'Eury, 1877), which is known from the Late Carboniferous of Euramerica, generally in association with xeromorphic vegetation. Leaves fork at least once and have sparse, strong veins that diminish in number with each dichotomy. It seems possible that some of the narrow, ribbon-like organs may be fragments of *Dicranophyllum* leaves, although they lack the prominent veins.

Rare fragments of foliage possibly attributable to ginkgophytes, also were found. These have broad, but terminally lobate laminae and open, dichotomous venation (Fig. 3.7).

Cycads.—Prior to this report, the cycadaceous megasporophyll *Dioonitocarpidium* was known only from the upper Triassic of Bavaria. It is characterized as a simple megasporophyll with a pinnate apex and a broad, undissected basal portion to which paired ovules are attached. It was first reported in 1928 by Lilienstern (1928). Kräusel (1949, 1953) subsequently described two additional species from the same area. The lower Pease River collection contains dozens of detached sporophyllar fragments (Fig. 6.6–6.8), two of which have a single seed attached near their bases. They have a dense covering of short, stiff hairs, reminiscent of the megasporophylls of modern cycads (Fig. 6.8). The Texas specimens present no major morphological differences from the European material.

The present material does not permit certain identification of the sterile foliage of *Dioonitocarpidium.* However, laminae with parallel veins and a dense covering of short hairs (possibly linking

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FIGURE 4—Plant fossils from the Early Permian lower Pease River Group, Texas. Scale bar in *4* applies to all elements and represents 1 cm. *1–3,* Seeds of Araucarian aspect, similar to modern *Agathis; 3* is a reversed image to allow easier comparison with *4,* both at the same magnification. Seed body bears unequally developed wings. In *2,* the seed is superimposed on a cone scale of *Pseudovoltzia* (see Fig. 5.8), USNM 508146, 508147, 508148. *4,* Seed of modern *Agathis* for comparison. *5. Ullmannia* sp., possibly *U. bronnii.* Axis with broad leaves attached helically. Leaf surfaces have stomata arranged conspicuously in rows paralleling the long axis of the leaf, USNM 508149. *6, Ullmannia* sp., bases of attached leaves on stem surface showing stomatal bands, USNM 508150.
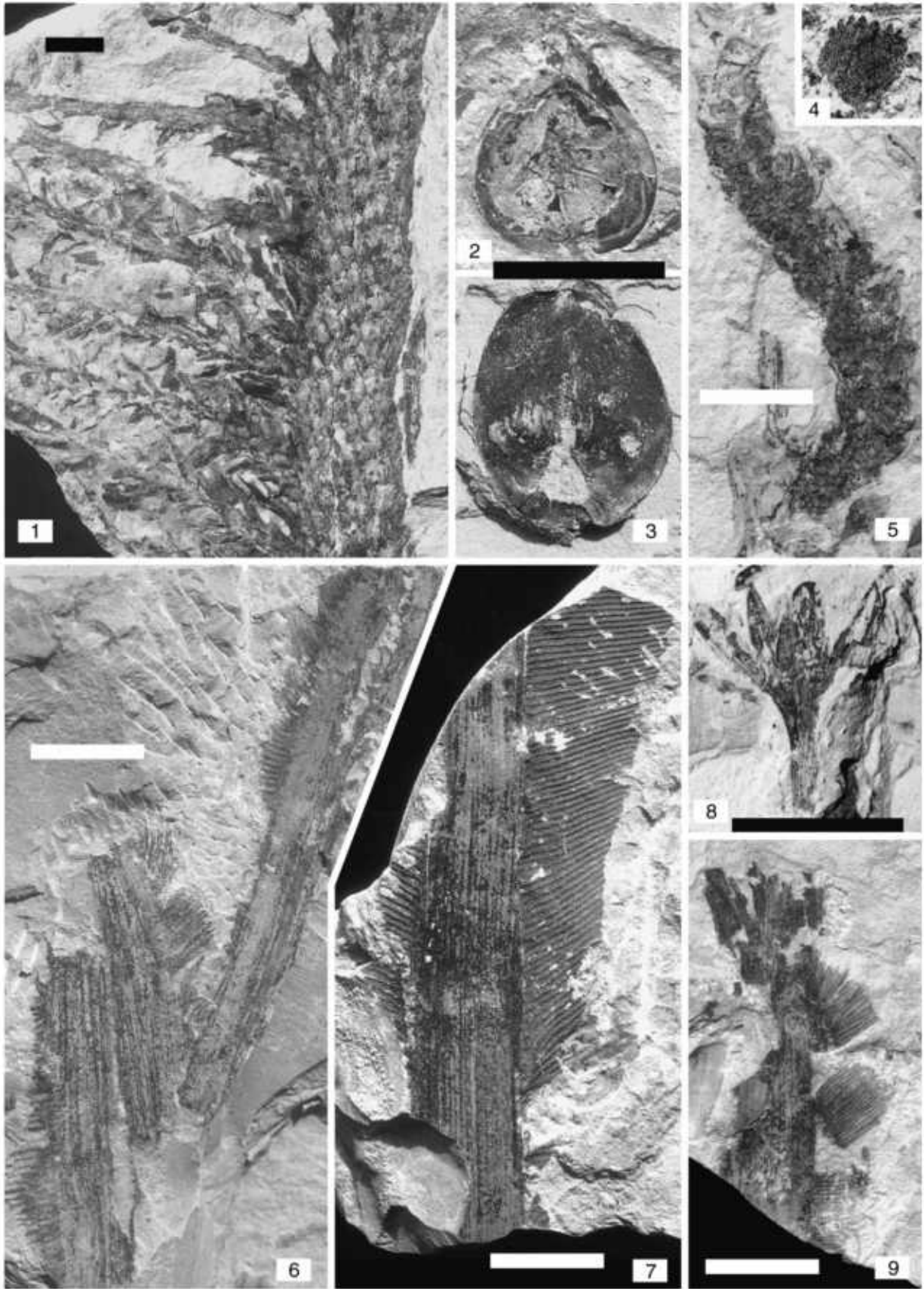
them to *Dioonitocarpidium*) also occur rarely. These vary in width and length and cannot be assigned unambiguously to any taxon; they resemble most closely fragments of wide *Taeniopteris,* but this seems unlikely given the lack of any specimens with a recognizable midrib.

Also occurring rarely are foliar fragments similar to cycad foliage. These leaves have wide midribs and narrow laminae that have parallel veins perpendicular to the midvein; the margins of these leaves are very difficult to uncover from the matrix and appear to be dissected into narrow lobes, each containing a single vein, again similar to the toothed margins of *Dioonitocarpidium* megasporphylls (Fig. 5.6, 5.9).

Other elements.—The remaining identifiable elements in the flora include *Taeniopteris* cf. *eckardtii,* a form known from the Late Permian Zechstein flora, characterized by a narrow lamina, 1.0 to 1.5 cm wide, bluntly rounded apices, strong midvein, lateral veins that branch close to the midrib or are unbranched, and form an angle of about 60 degrees with the midrib (Stoneley, 1958; Schweitzer, 1986) (Fig. 6.1–6.3). Calamites are rare at all but one site; they have weakly developed nodes and no foliage has been positively identified (Fig. 6.4). Also in the flora is *Wattia* sp. (Fig. 6.9), a plant of uncertain affinities characteristic of the Early Permian (Mamay, 1967). Small fragments of strap-like foliage with parallel veins suggest the presence of cordaites, but this identification is tentative. Pteridophyllous elements in the flora are represented only by small scraps of foliage: a single pinnule was found reminiscent of fern foliage and several small fragments were recovered of laminar foliage with parallel, open dichotomous venation, not assignable to any taxa. A variety of unattributable seeds were recovered (Figs. 5.2, 5.3, 6.5, 6.10, 6.11). Strobili of likely conifer affinity also were found (Fig. 5.5), as were some organs similar to cone scales (Fig. 5.4). Rare, fragmentary specimens similar to *Taeniopteris* sp. also were encountered at several sites (Fig. 5.7); these often occur in association with the fragmentary frimbriate laminae associated with *Dioonitocarpidium,* and, thus, we reserve our taxonomic assessment.

DISCUSSION

Continental sediments of the Permian tropics record the change from ever-wet, pteridophyte-rich, coal-age rainforests to vegetation from seasonally dry environments, rich in the more advanced groups of gymnosperms that would dominate most Mesozoic landscapes (Read and Mamay, 1964; Frederiksen, 1972). The replacement of everwet lowland-wetland forests by gymnosperm dominated xeromorphic vegetation was globally asynchronous, proceeding eastward from its first appearance in western North America (Knoll, 1984). Although Early Permian representatives of the seasonally dry flora include members of derived gymnospermous groups such as conifers, cycads, and peltasperms, these were still quite primitive when compared with their Mesozoic descendants. The evolutionary modernization of the tropical, seasonally dry flora, however, is poorly understood for several reasons. Late Permian fossil floras from the Eurasian tropics are few and paleogeographic coverage is limited (none are known from North America, for example); in China and eastern Russia, Late Permian floras share many genera with those from the Early

Permian of North America, or, if preserved in coal beds, are similar to middle Carboniferous floras of Europe and North America (Guo, 1990). Similarly, Early Triassic tropical floras are few and are notably distinct from those of both the Permian and those of the later Triassic. The end-Permian extinction appears to have had a major, devastating effect on the ecological organization of lowland vegetation, leaving Early Triassic floras species-poor and dominated largely by opportunists (Retallack, 1995, 1997). More complex floras began to reappear in the Middle Triassic (Ash, 1994; Looy et al., 1999).

The lower Pease River flora is one of the youngest Permian floras yet discovered in North America. Still younger floras occur in the upper Pease River Group (Chaney et al., 1997) and the Del Norte Mountains of west Texas (Mamay et al., 1988). Compared to these younger floras, the Lower Pease River flora is quite diverse, including at least six orders, predominantly gymnosperms. The as-yet-undescribed Upper Pease River flora is quite limited in composition, with cordaitean material most conspicuous and minor representatives of calamites, gigantopterids, and pteridophylls. The flora of the Del Norte mountains is species poor and dominated by the gigantopterid genus *Delnortea,* a flora possibly characteristic of coastal regions (DiMichele et al., 2000). The lower Pease River flora indicates that the radiation of major Mesozoic seed-plant-lineages was well advanced by the Early Permian. The transition from earlier Paleozoic vegetation, composed of lower vascular and primitive seed plants, to a seed-plant and fern flora typical of the Mesozoic was a multistage process that involved successive replacement of lowland forms by groups of species from progressively more remote, physically drier regions. In the tropics, this transition involved at least three distinct species pools. The first was the incumbent wetland flora with origins in the early Carboniferous. The second was an extrabasinal flora, the earliest evidence of which comes from reports of scrappy conifers in the Middle Pennsylvanian (Scott, 1974; Lyons and Darrah, 1989). The replacement of flora 1 by flora 2 began during the Late Pennsylvanian, when a few strikingly anomalous "Permian"-like assemblages appeared in lowland depositional environments, apparently during pulses of seasonal dryness (Cridland and Morris, 1963; Rothwell and Mapes, 1988; Winston, 1983; Broutin et al., 1990; DiMichele and Aronson, 1992; Mamay, 1992). Such floras became increasingly common in the depositional lowlands during the Permian and eventually replaced the wetland vegetation, except in parts of China (Ziegler, 1990).

The lower Pease River flora is evidence of yet a third, more typically Late Permian and "Mesozoic" flora in low latitudes during the Early Permian. The occurrence of highly derived cycads and conifers is an indication that major centers of plant evolution, favoring the survival of the most novel morphologies, existed significantly earlier than previously known, likely in the more environmentally peripheral, stressful environments. Extreme drying of the basinal lowlands caused the constriction and possible migration of the incumbent lowland vegetation of flora 2 and permitted plants of flora 3, from environmentally peripheral areas, to move in. Rare Mesozoic elements have been described elsewhere in the Paleozoic, as part of the Late Permian Zechstein flora (Schweitzer, 1986) and from palynomorph records of

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FIGURE 5—Plant fossils from the Early Permian lower Pease River Group, Texas. Scale bars in all photographs equal 1 cm. *1,* Conifer branch system, attributable to the Walchiaceae, possibly *Culmitzschia,* USNM 508151. *2,* Platyspermic seed with narrow wing. Most commonly encountered seed morphotype in the deposits, USNM 508152. *3,* Ovoid seed, possibly with narrow wing, USNM 508153. Scale bar between the two seeds applies to *2, 3,* and *4. 4,* Small, possible cone scale with fringed margin, USNM 508154. *5,* Male cone of indeterminate affinity, probably coniferous, USNM 508155. *6, 9,* Wide rachis with narrow, possibly divided lamina, with fringed margin, USNM 508156, 508159. *7, Taeniopteris*-like axis of uncertain affinity, USNM 508157. *8,* Cone scale of *Pseudovoltzia,* similar in morphology to *Swedenborgia,* USNM 508158.
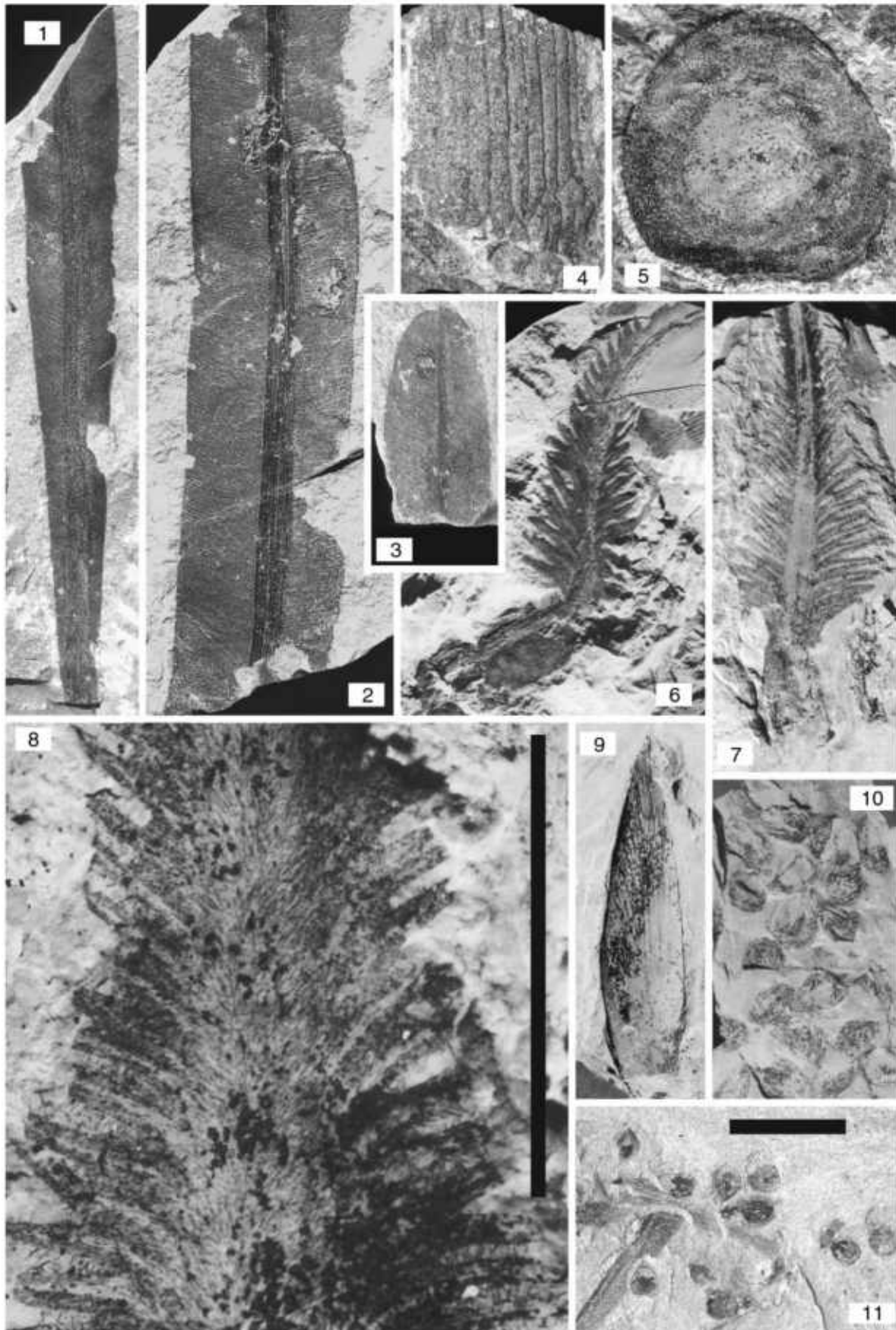
Oklahoma (Wilson, 1962). Scraps of such plants also have been seen in still older floras in the mid-Leonardian of Texas (Mamay, unpublished data). However, the lower Pease River flora includes more such forms and earlier than described previously.

The marine invertebrate record across the Permo-Triassic boundary is one of rapid, <1 m.y., extinction during which over 85 percent of known species did not survive (Bowring et al., 1998). This was followed by radiation of surviving forms into available ecospace. Even though terrestrial sequences thus far lack the temporal control and resolution found in the marine strata across the Permo-Triassic boundary, the lower Pease River flora makes it clear that the mechanics of the end-Permian event for terrestrial plants were very different from those of the marine invertebrates. If, as proposed by Retallack (1995, 1997), the Early Triassic lowlands were an ecological wasteland, elements of the Permian "Mesozoic" flora must have survived in peripheral areas until basinal conditions began to ameliorate in the Middle Triassic (Ash, 1994; Looy et al., 1999). This emphasizes the elusiveness of major evolutionary transitions in continental biotas, due to the poor representation of extrabasinal areas prior to the late Neogene (Pfefferkorn, 1980). It should discourage a direct, stratigraphic reading of evolutionary and biogeographic patterns from the continental stratigraphic record without strong consideration of paleoecology.

ACKNOWLEDGMENTS

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FIGURE 6—Plant fossils from the Early Permian lower Pease River Group, Texas. Scale bar in *11* applies to all elements of this figure except *8.* Scale bars in both *8* and *11* equal 1 cm. *1–3, Taeniopteris eckardtii,* base, mid-section, and tip of leaf, USNM 508160, 508161, 508170. *4,* Calamite stem, USNM 508162. *5,* Platyspermic seed with wide wing, USNM 508163. *6–8, Dioonitocarpidium* sp. megasporophylls. Area of seed attachment at base proximal to fimbriate, tapering terminal segment. Hairs covering surface are visible on *8,* USNM 508164, 508165, 508166. *9, Wattia texana,* organ of indeterminate affinity, USNM 508167. *10,* Small, unwinged seeds possibly attributable to *Ullmannia.* Seeds have a small groove running their length, USNM 508168. *11,* Small, cordate seeds, USNM 508169.

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