

AN UNUSUAL MIDDLE PERMIAN FLORA FROM THE BLAINE FORMATION (PEASE RIVER GROUP: LEONARDIAN-GUADALUPIAN SERIES) OF KING COUNTY, WEST TEXAS

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ABSTRACT—A new Middle Permian plant assemblage from South Ash Pasture in King County, Texas, may be the youngest and is certainly the most unusual flora known from the Permian of either West Texas or adjoining north-central Texas. Found serendipitously in the evaporite-rich upper Blaine Formation (Pease River Group, Guadalupian Series), the flora is of very low diversity despite intensive collecting efforts, and the affinities of nearly all taxa are enigmatic. The most common elements are parallel-veined leaves that resemble cordaites but that could be isolated pinnules of a pinnate leaf. Gigantopterid foliage is present but not assignable to any known taxon. A single foliar conifer specimen is too incomplete for assignment. Numerous reproductive organs, however, and an abundance of axes may represent conifers. Conchostracans, palaeoniscoid fish scales, and small heteropolar coprolites also occur in the deposit, which originated as a small, claystone-dominated channel fill in a coastal plain setting.

INTRODUCTION

THE RECORD of Permian floras in Texas has been augmented recently by the chance discovery of a remarkable, seemingly unique channel deposit in the upper part of the Blaine Formation in southern King County (Fig. 1). During previous field work in the lower part of this formation and the underlying San Angelo Formation, we recognized that surface concentrations of copper minerals and fusain-bearing permineralized logs usually indicated the occurrence of significant plant remains (DiMichele et al., 2001). When we shared this information with the manager of one of the ranches we were visiting, he led us to a pasture some 25 km west of our nearest collecting locality to show us a comparable occurrence in the upper part of the Blaine Formation. The new deposit, which is approximately 164 m above the youngest previously reported Blaine plant assemblage of the region, is known as South Ash Pasture.

The new flora is of low diversity and peculiar composition and gives no hint of affiliation with any previously known floras from the region. As such, it adds further to the regional floristic heterogeneity identified previously (Mamay et al., 1988; DiMichele et al., 2000, 2001; Hotton et al., 2002). The upper Blaine Formation of this region consists of red mudstones, bedded evaporites, and dolomites typical of Early Permian coastal plain and shallow-shelf settings. Several weeks of prospecting Blaine exposures in King, Stonewall, Foard, and Hardeman counties failed to locate analogous deposits and suggest that South Ash Pasture represents a rarely occurring paleoenvironment and minor part of the Blaine landscape.

GEOLOGY

South Ash Pasture is located in southern King County, West Texas (Fig. 1), situated on the Eastern Shelf of the Midland Basin, an intracratonic basin that formed as a result of fault reactivation and deformation during the Carboniferous and Early Permian (Ewing, 1991). Through time, the basin shrank as it filled with sediment that prograded inward along the margins, most rapidly along the Eastern Shelf. At the time Blaine sediments were deposited in King County, the basin itself occupied little more than parts of three West Texas counties. South Ash Pasture thus appears to have been deposited during the final stages of the Midland Basin, shortly before the entire region became a complex of salt lakes, evaporite pans, and mud flats.

In Texas, the Blaine and San Angelo formations comprise the Pease River Group, which is underlain by the Clear Fork Group

(Fig. 2). The Blaine Formation of King County is approximately 175 m thick where exposed in the eastern part of the county. On outcrop, it is underlain conformably by the San Angelo Formation and overlain by the Childress Dolomite of the overlying Whitehorse Sandstone. As in the type area of the Blaine Formation in northwestern Oklahoma (Fay, 1964), dominant rock types are red mudstones and laterally continuous beds of evaporites and dolomites. The intervals between the dolomite beds, as well as the dolomites themselves, are remarkably consistent in thickness and composition. Several of the carbonate members extend from the southern limit of Blaine outcrops in Stonewall County into southwestern Oklahoma, a distance of more than 150 km (Eifler et al., 1992, 1993). One of these members, the Guthrie Dolomite, occurs at the bottom of the South Ash Pasture section. The fossil deposit itself occupies the position of the Aspermont Dolomite Member, which is absent in the immediate area of the deposit but exposed nearby.

Because of their paleoenvironmental significance, we evaluated geophysical and sample logs within the general area of South Ash Pasture for evidence of bedded salt deposits in the subsurface. Density logs from oil test wells in King and Stonewall counties indicate that bedded salt deposits exceeding 2 m in thickness occur in the upper part of the Blaine Formation. The absence of these units at the surface reflects ground-water dissolution, which is common in the region (Hovorka and Granger, 1986).

In plan view, South Ash Pasture is a linear, north-south-oriented exposure of gray mudstone approximately 76 m long by 18 m wide. The margins of the deposit are formed in part by nonfossiliferous, buff-colored lithographic dolomite up to 5 cm thick that weathers into fractured aggregates at the surface. Red gypsiferous mudstones surround the deposit. In a backhoe-excavated trench near the northern end of the deposit, the maximum thickness of the fossiliferous gray mudstone was approximately 2 m, and the cross section was an asymmetrical U-shape (Fig. 3). Thin (≤ 5 cm) stringers and nodules of dolomite within the deposit form a series of concave-up beds, and the entire deposit incises subjacent flat-lying beds of red mudstone and gypsum that are nonfossiliferous. Most of the deposit consists of dark gray, massive claystones that break with a hackly-to-conchoidal fracture. Evidence of bioturbation and current transport are absent. On the west side of the trench, the gray claystone is underlain by two thin beds of barren siltstone that dip towards the axis of the deposit. Plant remains, including fragmentary limonite-bearing and fusinized

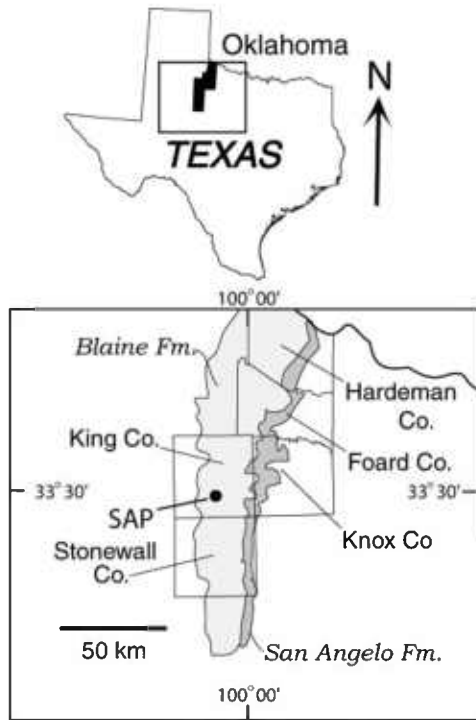


FIGURE 1—Location of South Ash Pasture. Top, location within Texas, black area corresponds to counties shown on map below. Bottom, regional map, heavy dot in southern King County is South Ash Pasture.

logs, are dispersed horizontally and vertically in the gray claystone. Rare conchostracans, palaeoniscoid fish scales, a single labyrinthine tooth, and small heteropolar coprolites also are preserved in the gray claystone. These data indicate that South Ash Pasture represents a mudstone-filled channel. A paleokarst origin was considered initially as an alternative hypothesis, but the geometry and sedimentology of the deposit, combined with a complete lack of collapse features, exclude this possibility. Whereas the more steeply inclined east side of the channel appears to represent a cutbank, the more gently sloping west side contains basal siltstone beds that suggest a lateral bar deposit. The absence of bioturbation, predominance of dark claystones, presence of copper minerals and carbonates, and general lack of bedding features indicative of current transport indicate that sediments were deposited under standing water that may have been anoxic at times. Although there is no direct evidence of a tidal-channel origin for the deposit, a tidal channel is consistent with other attributes of the upper Blaine Formation in this region, which is devoid of fluvial channels.

AGE OF THE ASPERMONT DOLOMITE

Based upon a meager record of marine invertebrates from the Blaine Formation, the Aspermont Dolomite and the plant locality in its position at South Ash Pasture are most likely early Guadalupian, and thus Middle Permian, in age. Here we adopt the tripartite division of the Permian into Early, Middle, and Late (Glenister et al., 1992). Age determinations for the Blaine Formation are of low resolution because index fossils are scarce, considerable distances separate the Oklahoma type area from collection sites in Texas, and even greater distances exist between Blaine exposures and stratotype sections. The following notes review biostratigraphic data from the upper Blaine of West Texas and the Aspermont Dolomite Member in particular.

The ammonoid *Perrinites hilli* (Smith, 1903) was described

Formation	Group	Time
Dockum		Trias.
***** Dickens Ash		
Quartermaster		Middle & Late Permian
Cloud Chief		
Whitehorse		
Blaine		
Aspermont Dolomite	Pease River	Middle Permian
Acme Dolomite		
San Angelo		Early Permian
undivided	Clear Fork	
Lueders	Wichita	Early Permian
Waggoner Ranch		
Petrolia		
Nocona		
Archer City	Bowie	Penn.
Markley		

FIGURE 2—Lithostratigraphic and chronostratigraphic relationships of rocks in the study area. The heavy dot labeled SAP shows the position of South Ash Pasture. Boundaries between time units are shown as dotted lines to reflect uncertainties about their placement; these approximations are based on the extension of data from distant marine sections into the King County area. The Lueders Formation is the uppermost division of the Albany Group, the marine equivalent of the predominantly continental Wichita Group.

originally from the Aspermont Dolomite at Salt Croton Falls, 15 km southwest of South Ash Pasture in northwestern Stonewall County and was regarded by early workers (Plummer and Scott, 1937; Miller and Furnish, 1940; King, 1942) as an index fossil for the Leonardian Series of the Lower Permian. In the Glass Mountains of Texas, however, Clifton (1945) identified this species in the lower limestone member of the type section of the Word Formation, which is regarded now as the Road Canyon Formation and which serves as the stratotype for the Roadian Stage, the oldest of the three stages of the Guadalupian Series of the Middle Permian. Because the Glass Mountains material was subsequently assigned to a different species, *P. hilli* is known presently only from the Eastern Shelf, where it extends downward into the Clear Fork Group, and no correlations between the two regions can be based upon this species (Tharalson, 1984).

Clifton (1942, 1945, 1946) reported five cephalopod species, in addition to *Perrinites hilli*, from the Blaine and Dog Creek formations of Texas and Oklahoma (the Dog Creek of Oklahoma corresponds to the upper part of the Blaine in Texas). These are the nautiloid *Pseudorthoceras splendens* Clifton (1942) and the ammonoids *Medlicottia burkhardti* Böse (1919), *Medlicottia whitneyi* Böse, 1919, *Pseudogastriceras roadense* (Böse, 1919), and *Pseudogastriceras texanum* Clifton (1942). According to Clifton, all five of these species occur also in rocks of the type Guadalupian Series, including the Road Canyon and Word formations in the Glass Mountains, the Cherry Canyon Formation in the Guadalupe Mountains, and the Delaware Mountain Group in the Delaware Mountains.

The base of the Whitehorse Formation is approximately 40 m

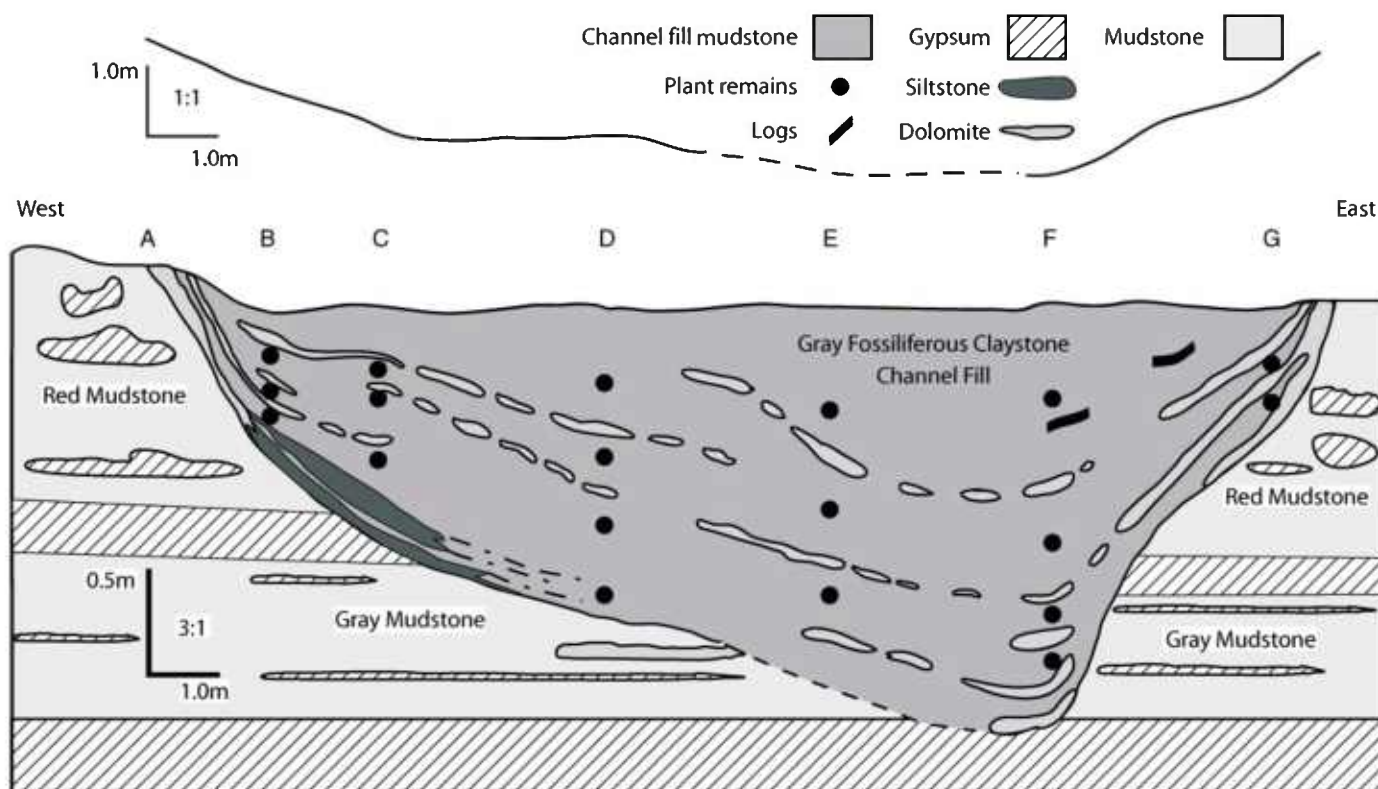


FIGURE 3—Cross section of South Ash Pasture based upon backhoe trench. Top, profile of channel bottom with no vertical exaggeration. Below, cross section based upon sections measured at stations A through G indicated at top of figure; 3:1 vertical exaggeration.

above the Aspermont Dolomite near South Ash Pasture. The Whitehorse is regarded as Capitanian, and thus Middle Permian, on the basis of fusulinids (Skinner, 1946) and mollusks and brachiopods (Newell, 1940).

In an effort to obtain isotopic age data, we collected samples of a prominent Blaine mudstone unit from three localities in King County that was reported previously as an ash bed (Roth, 1945). This bed is readily identified in the field based on Roth's measured sections and is widespread in northern King County. Six thin sections were prepared for microscopic study, and three samples were submitted for X-ray diffraction analysis. Unfortunately, neither the thin-section nor the X-ray diffraction analyses indicated volcanic components. The rock is a friable calcareous siltstone to a very fine-grained sandstone composed chiefly of detrital quartz, calcite, and dolomite, along with minor muscovite, plagioclase, potassium feldspar, illite, expandable clays, and possibly kaolinite but more likely chlorite. As exposed, this light greenish-gray unit is 1.5 m thick and generally exhibits fine planar laminations, although a few bioturbated zones occur. Its widespread occurrence along Blaine outcrops in much of eastern King County suggests that it may represent wind-blown silt that collected in a shallow body of quiet water, not an ash as reported previously.

An unequivocal ash bed was sampled in a road-cut on US Highway 82 just east of Dickens, Texas, approximately 52 km west-northwest of the South Ash Pasture deposit, near the top of the Quartermaster Formation. This ash has been radiometrically dated at 250.3 million years b.p., and thus is clearly of Late Permian age. Given that the South Ash Pasture deposit is approximately 490 m below this ash bed (Fig. 1), the Permian age of the deposit is assured.

LOCALITY, COLLECTING, AND REPOSITORY INFORMATION

South Ash Pasture is located in southern King County on the Bob Creek 7.5' topographic map. The present property owner does not wish us to disclose the location of the fossil deposit. This information, however, accompanies the South Ash Pasture specimens in the Paleobotanical Collections of the U.S. National Museum of Natural History, Smithsonian Institution.

Plants were collected by excavation of 12 approximately 1 m² pits to a maximum depth of 0.5 m. No a priori sampling design was used. Initial excavations were made to sample the length and breadth of the deposit. Later excavations concentrated on the west side of the deposit, where plant fossils appeared to be most numerous. Approximately 600 specimens were collected. Because the flora did not differ significantly among sites, all samples were combined for the purpose of this analysis. There are too few specimens per excavation pit to permit adequate statistical characterization of distribution patterns within the deposit. The most common elements were found in every excavation. In the trench exposure (Fig. 3), which was excavated mainly for sedimentologic data, sparse plant remains were noted at various levels but no concentrations were found, nor were scientifically useful specimens observed.

THE FLORA

Fossils are preserved as carbonaceous compressions, and include leaves, reproductive organs, and small axes. Cuticle was not preserved on the surfaces of the compressions, although surface features could be observed in parts of some fossils preserved as limonite petrifications. Palynomorphs could not be isolated from the mudstone matrix (Cindy Looy, personal commun., 2002).

Parallel-veined leaves.—Small leaves with parallel veins are the most common elements (Figs. 4, 5). Leaves are narrow at the base and widen to a broad lamina. Maximum length observed is 11 cm; maximum width is 3.1 cm. Most leaves appear to be smaller, and there is wide variation in length and width. The base of moderate-sized leaves is about 5 mm in width, expanding upward gradually to the broader lamina over a length of 3 to 5 cm (Fig. 4.1–4.4). In some leaves, the zone of expansion is minimal, the full lamina appearing a short distance above the base. There is an abscission zone at the base of the leaf (Fig. 4.1–4.4). Leaf tips are bluntly tapered (Figs. 4.9, 5.1).

Leaves have parallel venation (Fig. 5.2, 5.3), with veins converging at the tip of the leaf. Vein bifurcations are rare. There is no evidence of differentiation between veins and sclerenchyma bands.

Leaves have stomata on both upper and lower surfaces (amphistomatic). On one surface, stomata occur most commonly in pairs or in two irregular rows between the veins, but not between each pair of veins. On the other surface, the stomata are arrayed in a single longitudinal row between a pair of veins. The stomata are sunken in pits. Cells are arrayed around the apertures of the pits in two rings, with 10–12 cells in the outer ring and five to eight cells in the inner ring; cells in the outer ring are of larger diameter than those in the inner ring. Cells are permineralized in some specimens and thus are measurable. Scanning microscope images could be obtained of the permineralized epidermal surfaces. Specimens of the upper and lower surface were taken from the leaf illustrated in Figure 5.1 (at arrows), and are illustrated in Figure 6; although the upper and lower surfaces cannot be determined, the two surfaces differ quantitatively. Epidermal cells are approximately isodiametric and polygonal; measurements were taken of 100 cells in two areas on each of the illustrated specimens. Nonstomatal cells from the surface illustrated in Figure 6.1 average 0.04 mm long by 0.05 mm wide in one area, and 0.05 mm long by 0.04 mm wide in the other. Nonstomatal cells from the surface illustrated in Figure 5.2 average 0.05 mm long by 0.03 mm wide in one area, and 0.04 mm long by 0.03 mm wide in the other. On the specimen illustrated in Figure 6.2 there are five veins per mm of leaf width. The surface illustrated in Figure 6.1 has 33 stomata per mm²; the surface illustrated in Figure 6.2 has 44 stomata per mm².

Stomatal indices (I) (Salisbury, 1927) were calculated based on the specimens illustrated in Figure 5, according to the method described in Simunek (2000).

$$I = [S/(E + S)]$$

Where S is the number of stomata per unit area and E is the number of cells per unit area.

Based on the surface illustrated in Figure 6.1, the stomatal index (I) is 3.64 in one measured area and 3.82 in another. The stomatal index of the surface illustrated in Figure 6.2 is 4.98.

The affinity of these leaves is problematic. They may be cordaites. Unlike leaves of Euramerican cordaites, they do not appear to have sclerenchyma bands between the veins, though these will be admittedly difficult to distinguish from veins in compression preservation. Unlike Angaran rufflorians, stomata occur on both the upper and lower surfaces and do not occur in grooves between veins. It also cannot be ruled out that these elements are actually pinnules of a pinnate leaf, perhaps a noeggerathialean, akin to *Russelites* Mamay (1968), *Tingia* Halle (1925) (Gao and Thomas, 1987), *Plagiozamites* Zeiller (1894) (Wang and Shen, 2000), or even a cycadophyte.

Conifer foliage.—A single specimen has the external morphology of a conifer (Fig. 7). The specimen is 2.5 cm long. Leaves are narrow, about 1.8 mm wide, and up to 10 mm in length. The

central axis is 2 mm in diameter. The specimen has no characteristics that permit a more refined taxonomic identification.

Gigantopterid foliage.—Over a dozen partial specimens represent a broad, reticulate-veined leaf most similar to foliage of gigantopterids (Figs. 8–12). The leaves vary greatly in size. Maximum widths at the estimated midpoint of the lamina vary from 0.8 cm to between 3.8 and 4 cm. Maximum length of fragments is 7 cm, and these occur in some of the more narrow specimens. Although the leaves are distinctly tapered near the base (Fig. 8.5, 8.6), the very base has not been recovered. Apical parts of the leaves are known only from narrow specimens (Fig. 8.1–8.4). In several examples, the lamina tapers gradually to a rounded, but acute tip; one leaf, for example, tapers from 1.2 to 0.2 cm in width over a length of 5.5 cm. Overall, the leaves appear to be much smaller than those of other described gigantopterid species (Halle, 1927; Mamay, 1989; Li and Taylor, 1998, 1999).

Leaf margins are generally smooth (Figs. 8, 9.1). Two, possibly three, specimens, however, have what appear to be blunt, obliquely, apically oriented “teeth,” separated by broad shallow sinuses (Fig. 9.2–9.4). It is possible that these “teeth” represent insect damage along otherwise smooth leaf margins.

Leaves have three orders of venation (Figs. 9, 10). The midvein, or first order vein, may be as much as 5 mm wide in the midsection of the lamina. It is a vein bundle, composed of many separate veins that diverge successively and form the secondary veins. Secondary veins end at the leaf margin and in the “teeth” if present. As with the midvein, secondary veins are composed of several veins that form a vein bundle. The secondary veins thus may become progressively more indistinct as they approach the margin and “break up” near their terminus. Secondary veins are of different weight, with some marked very strongly throughout their length; between these stronger veins, there may be secondary veins that are less well defined, although this pattern is not consistent between specimens. Tertiary veins are herringbone in form, show limited lateral reticulation, and fuse with tertiary veins from adjacent secondary veins. Although a distinct suture vein is not formed, a zone of fusion occurs between some secondary veins. All tertiary veins are directed at a strong angle toward the margin and form an acute angle with the secondary vein.

A marginal vein is distinct in some specimens, and appears to be formed by a vascular bundle that arches between secondary veins, just below the leaf margin.

Stomata are arrayed irregularly over the surface of the lamina (Figs. 11, 12). They are sparse to absent above the veins (Figs. 11.1, 12.2), and in somewhat more ordered rows along the margins of the veins. They are surrounded by a ring of five to six subsidiary cells. Epidermal cells are isodiametric in the laminar portions of the leaf and distinctly elongate above the veins. Figure 12 illustrates the adaxial and abaxial surfaces of the same leaf, although we are unable to determine orientation.

The affinities of these specimens are unclear. The closest similarities are with *Delnortea* Mamay et al. (1988), *Gigantonoclea* Koidzumi (1936), and *Evolsonia* Mamay (1989), all known from the Permian of Texas. *Delnortea* has rounded marginal teeth, secondary veins that end in the sinuses between the teeth, and four orders of venation; the venation is strongly herringbone (Mamay et al., 1988). *Gigantonoclea* in Texas is known only from one small internal laminar fragment. Based on Chinese material, this genus has four orders of venation, strong secondary veins, and a variety of marginal morphologies, from smooth to acutely toothed; ultimate venation forms a fine, reticulate mesh (Li et al., 1994). *Evolsonia* has margins that vary from smooth to shallowly toothed, secondary veins that end in the teeth, if teeth are present, and four orders of venation, herringbone in form throughout (Mamay, 1989); vein angles are much less acute than those in the

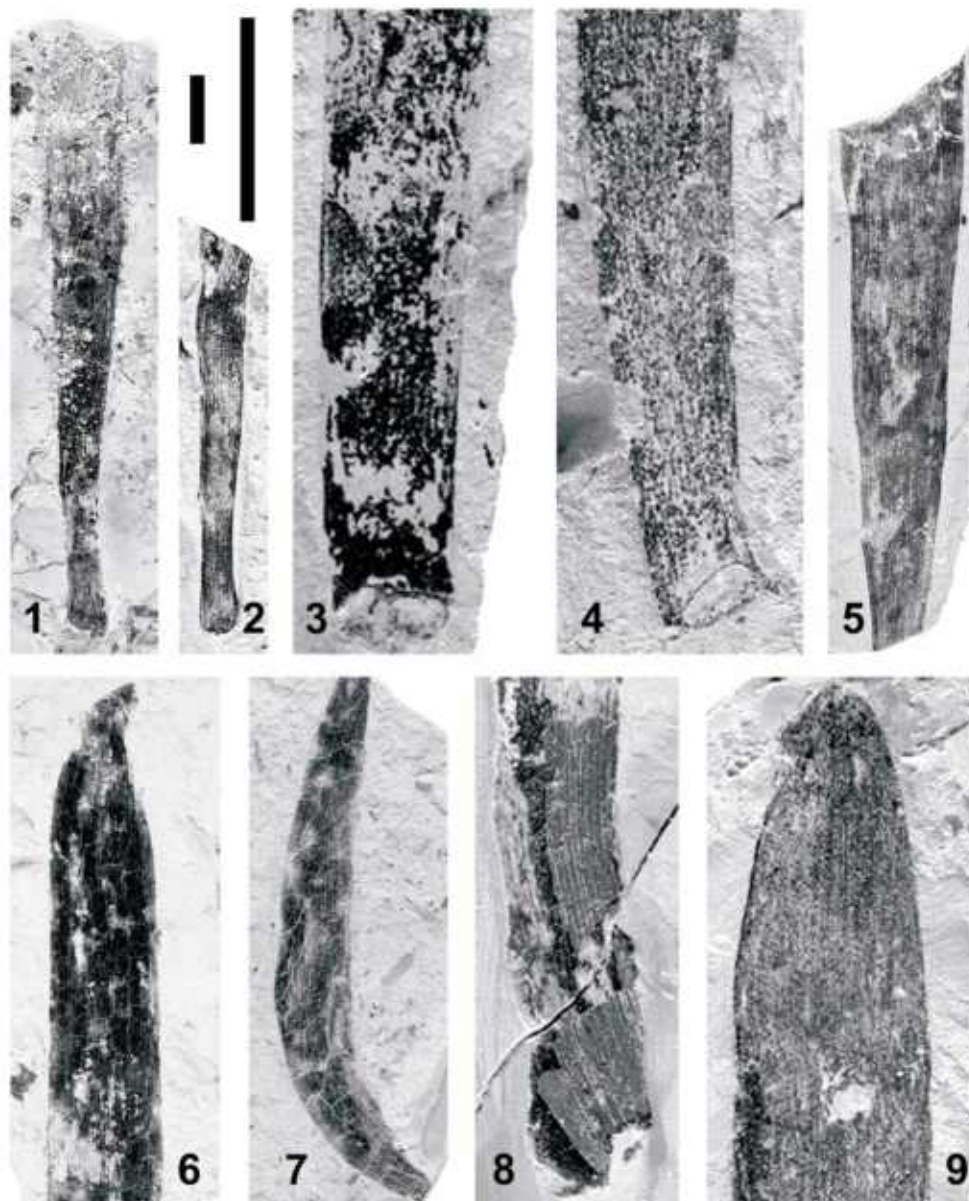


FIGURE 4—Parallel-veined, strap-shaped leaves of uncertain, possibly cordaitan affinity. Scale bars: small bar = 1 cm and applies to 1, 2, 5–8; large bar = 1 cm and applies to 3, 4, 9. 1, Base of leaf showing abscission scar and tapering, X1, USNM 520369; 2, base of leaf showing abscission scar and tapering, X1, USNM 520370; 3, base of leaf showing abscission scar, X3, USNM 520371; 4, base of leaf showing abscission scar and parallel venation, X3, USNM 520372; 5, leaf lamina immediately above proximal taper zone, X1, USNM 520373; 6, leaf lamina near tip, which appears to have been deformed prior to fossilization, X1, USNM 520374; 7, nearly complete small leaf showing taper at each end, X1, USNM 520375; 8, leaf lamina showing parallel venation, X1, USNM 520378; 9, leaf tip, bluntly tapered, X3, USNM 520377.

specimens described here. None of these genera, however, is a clear fit with the South Ash specimens.

Putative conifer cones.—Six specimens resemble coniferous ovulate cones (Fig. 13), similar to cones of *Pseudovoltzia* Florin (1927) (Clement-Westerhof, 1988). The cones are preserved as three-dimensional, bilaterally compacted compressions, permitting examination of both external and internal morphology; anatomical features are not preserved. Overall cone diameters are approximately 3.0 cm. The longest fragment is 11 cm, and is slightly tapered, though incomplete, at each end. The central axis of the cone is 10 mm in diameter.

Dwarf shoots are bilaterally compressed and scalelike. They consist of an elongate, horizontal, proximal portion about 1.5 mm

wide and 7 to 8 mm long. At the distal end, the axis is turned upward and lobate and is divided into five lobes (Fig. 13.1, 13.2, 13.5). The central lobe is the largest and is rounded at the tip. Lateral lobes are smaller, triangular in shape, and have tapered to acutely pointed ends. The lobed portion of the dwarf shoot is approximately 6 mm wide and 7 to 8 mm high. Below the dwarf shoot is a thin bract. Bracts are as much as 15 mm long and thus extend beyond the cone scales by as much as 6 mm (Fig. 13.1b, 13.2b). The bract appears to be fused with the base of the dwarf shoot and to separate just prior to the terminal lobed portion. Distances between dwarf shoots vary from 1.5 to 5 mm, measured along the central axis, the variability reflecting the helical arrangement of the dwarf shoots on the axis.

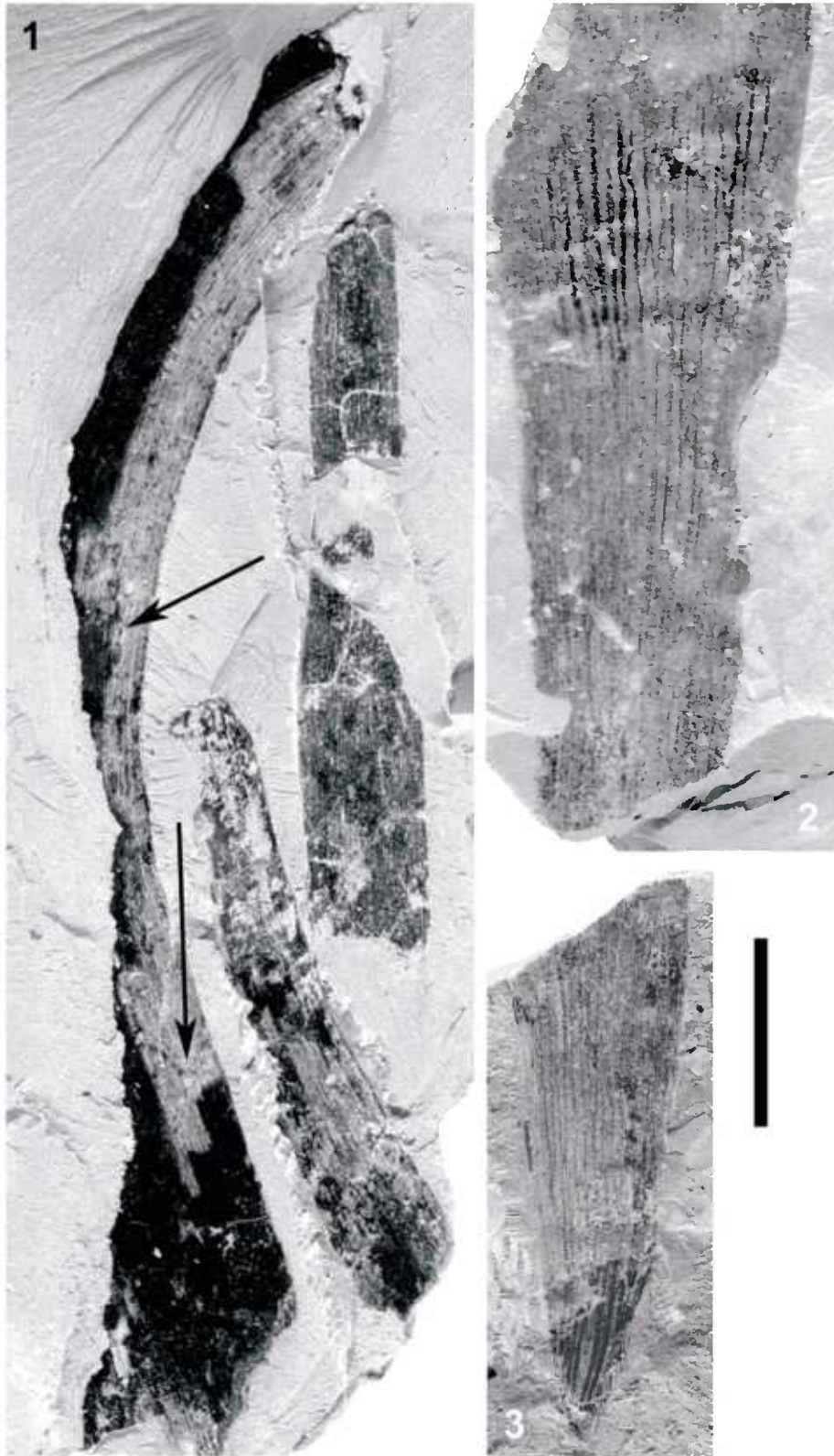


FIGURE 5—Parallel-veined, strap-shaped leaves of uncertain, possibly cordaitan affinity. All images are $3\times$, scale bar = 1 cm. 1, Partially iron-permineralized leaf. Arrows denote places where specimens were removed for scanning electron microscopic examination, illustrated in Figure 6, USNM 520378; 2, lamina illustrating parallel veins, USNM 520379; 3, lamina illustrating parallel veins, USNM 520380.

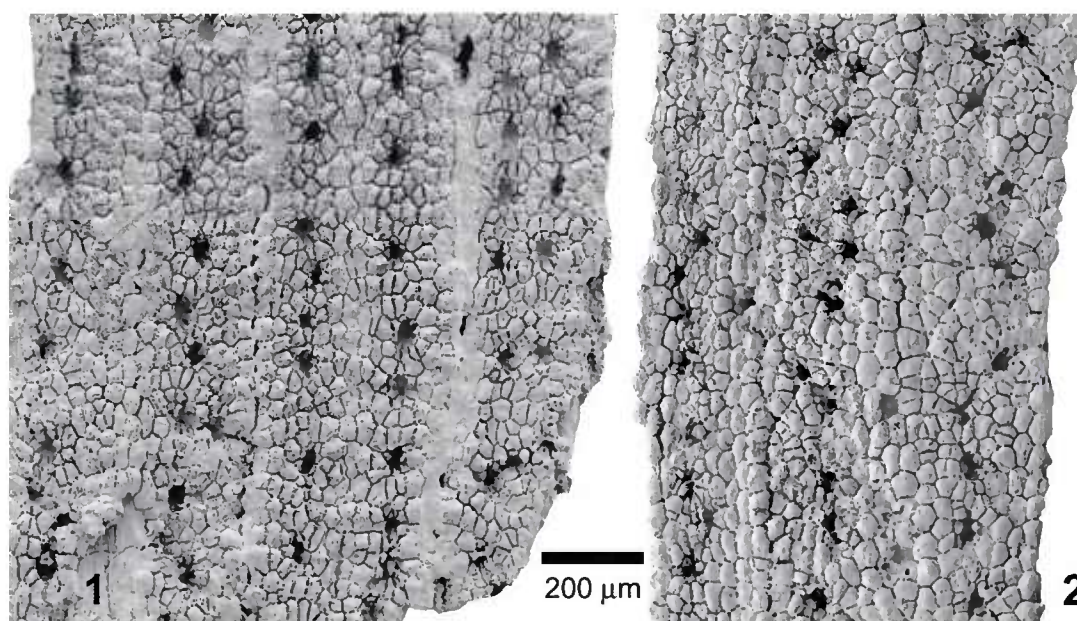


FIGURE 6—Epidermal features of the two surfaces of leaf illustrated in Figure 5.1. Scanning electron microscopic images. Scale bar = 200 μm . 1, Stomatal apertures in rows parallel with long axis of the leaf; 2, stomatal apertures in irregular longitudinal rows and occasional pairs. SEM stub USNM 520381.

Strobili of indeterminate, possibly noeggerathialean, affinity.—Two specimens appear to be microsporangiata strobili. In overall aspect, these strobili have some similarities to those of the Noeggerathiales, a long-ranging problematic group, possibly related to the Progymnosperms (Leary and Pfefferkorn, 1977; Leary, 1980; Beck, 1981), occurring through much of the Carboniferous and Permian. The lunate microsporophylls and densely packed sporangia are consistent with the morphology of other noeggerathialean cones, such as *Discinites* Feistmantel (1864) (Mamay, 1954). However, they lack some of the crucial features

of sporangial arrangement that would permit certain assignment to that group of plants (Wang and Shen, 2000).

A three-dimensionally preserved strobilius consists of arcs or partial rings of clustered sporangia, possibly fused to a sporophyll (Fig. 14.1). As many as 16 sporangia are visible in any one cluster. The clusters are 7 to 8 mm across. Individual sporangia are approximately 2 mm long and 0.5 to 0.6 mm wide. The cone axis is not visible, but the sporangial clusters appear to be arranged spirally. Counting along the margin of the specimen, 14 clusters can be identified in a preserved length of 8 cm. The specimen is incomplete: neither base nor apex is visible and the fragmentary width is only 1.8 cm. The proper orientation of the specimen cannot be determined.

A second strobilus may be identical to the first but is preserved somewhat differently. It is 9 cm long and 3 cm in total diameter, with a central axis 7 mm wide. Scattered around the central axis and along its entire length, but not definitively attached to it, are scales of the type described below. No sporangia are identifiable. The disposition of the scales suggests that they and the central axis are part of the same organ.

Microsporophylls of the type described from these two cones also occur in isolation (Figs. 14.2, 14.3, 15). These are almost square in outline, 9 to 10 mm long and approximately 8 mm wide. They taper to a narrow base or attachment point, which, in some specimens, has a short pedicel. The outer edge of the sporophylls is fringed by 15 to 20 short, rounded teeth that turn outward slightly near the edges of some specimens. Numerous veins spread from the base, run to the margin, and end in the sinuses between the teeth. The specimen illustrated in Figure 14.2 is drawn in Figure 15. This specimen was composed of two carbonized layers separated by a thin layer of clastic sediment. The top layer was fragmentary and lies slightly to the left center of the specimen. It appeared to have independent venation that is more dense than that of the underlying surface.

Coniferous cone scales.—Three kinds of cone scales occur in the deposit. The first is an apparently woody scale, represented by four specimens (Fig. 14.5–14.7). Scales are approximately 20



FIGURE 7—Fragmentary shoot of possible coniferous affinity, $\times 3$, scale bar = 1 cm, USNM 520398.

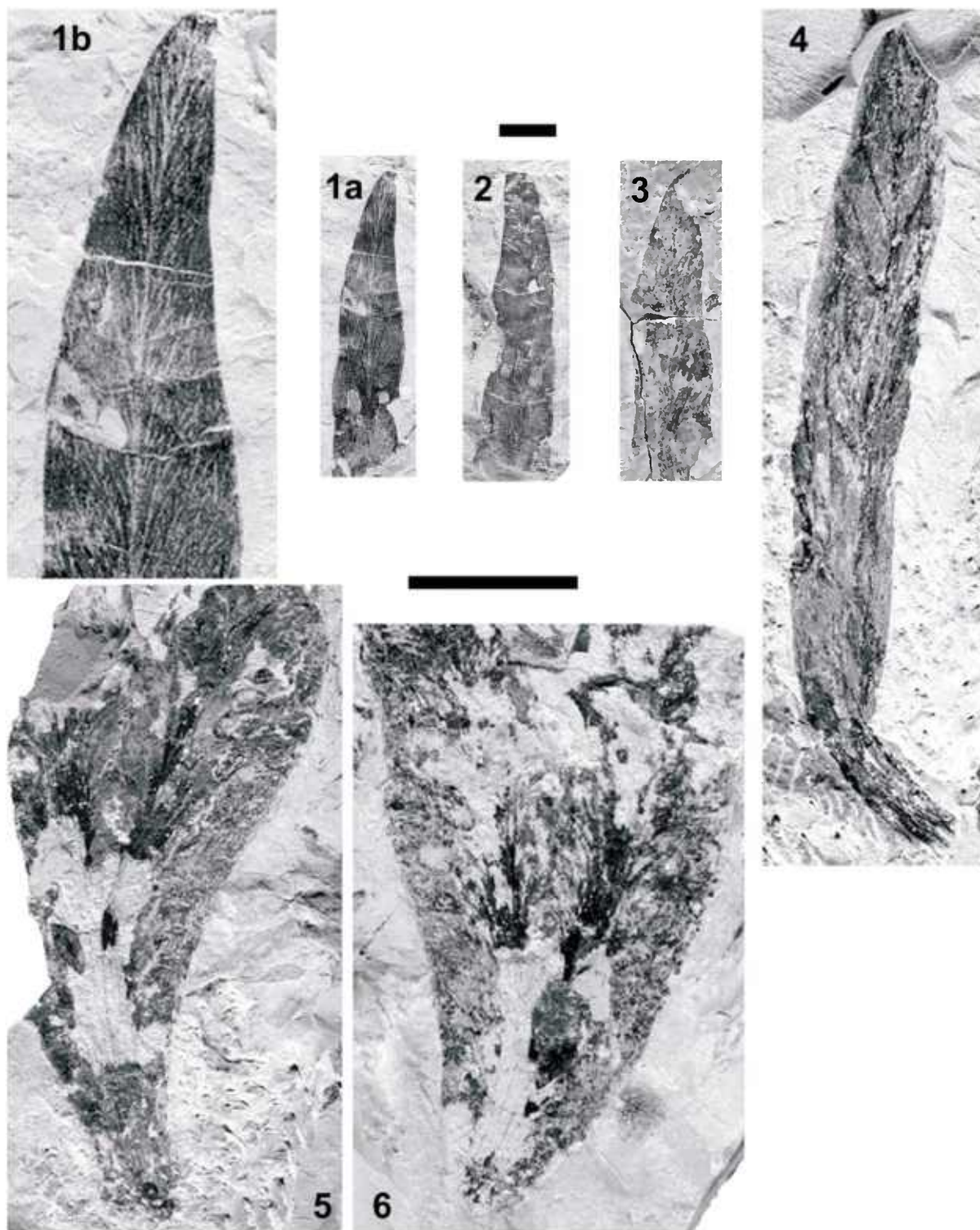


FIGURE 8—Gigantopterid. Scale bars = 1 cm. Small scale bar applies to *1a*, *2*, *3*. Large scale bar applies to *1b*, *4–6*. *1*, Tip of small narrow leaf, *1a*, X1, *1b*, X3, USNM 520387; *2*, leaf tip counterpart, X1, USNM 520387; *3*, tip of small narrow leaf, X1, USNM 520389; *4*, narrow lamina with well-marked primary and secondary veins and blunt tip, X3, USNM 520390; *5*, leaf base with tapering and venation, X3, USNM 520391; *6*, leaf base counterpart, X3, USNM 520391.

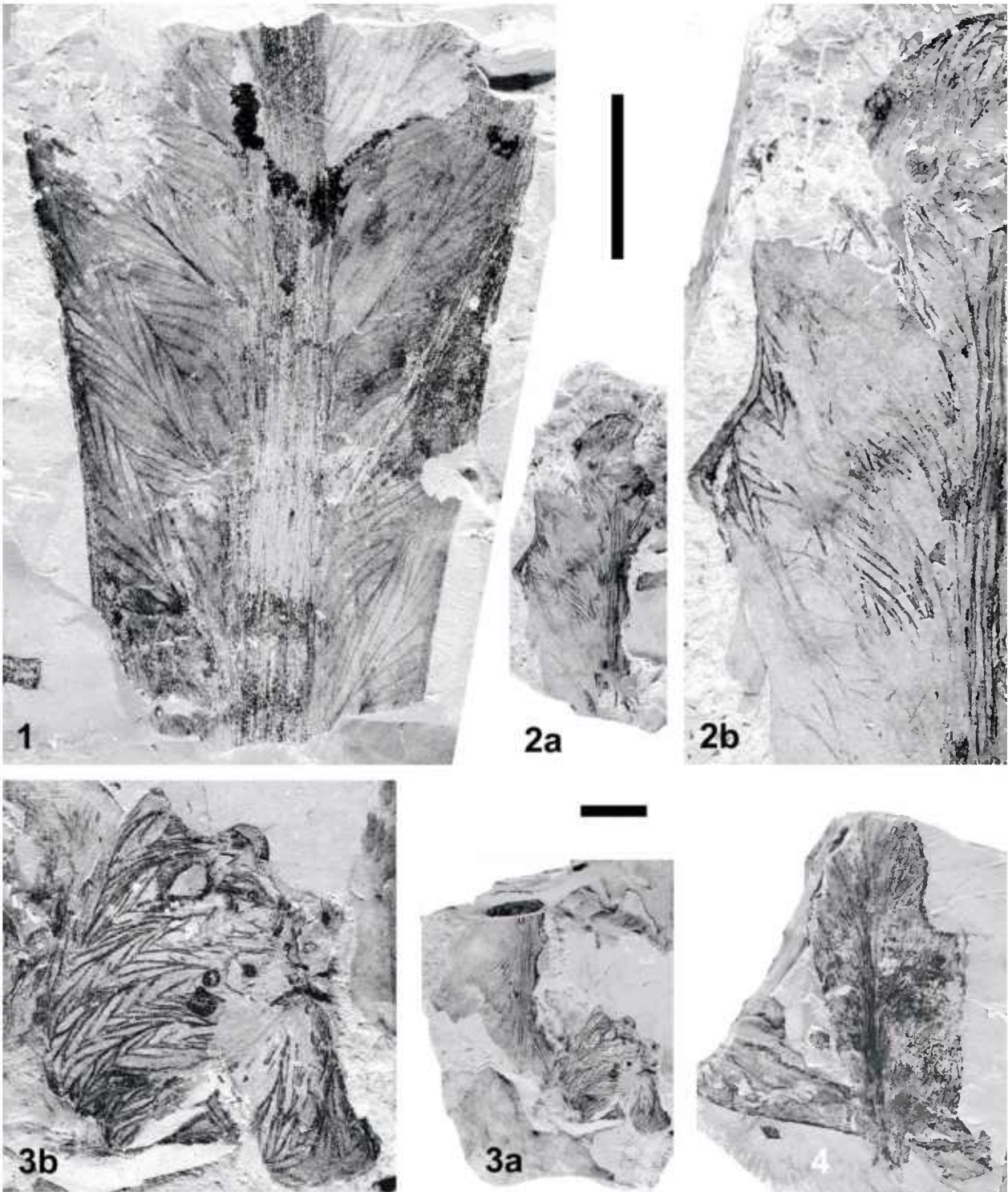


FIGURE 9—Gigantopterid. Scale bars = 1 cm. Small scale bar applies to 2a, 3a, 4. Large scale bar applies to 1, 2b, 3b. 1, Basal portion of lamina with massive primary vein and herringbone venation. Suture vein is weakly developed where tertiary veins fuse and the margin lacks “teeth.” Specimen is also illustrated as line drawing in Figure 10, X3, USNM 520383; 2, partial lamina near apex. Possibly toothed margin. Note sub-marginal vein, which suggests that scalloped edge is not a result of damage, 2a, X1, 2b, X3, USNM 520384; 3, lamina fragment with well-marked secondary and tertiary veins. Note suture vein where tertiary veins fuse, 3a, X1, 3b, X3, USNM 520384; 4, Lamina fragment, near apex. Margin appears to have been damaged, possibly by insect herbivory, no marginal vein comparable to that in Figure 2a and 2b is visible in this specimen, X1, USNM 520386.

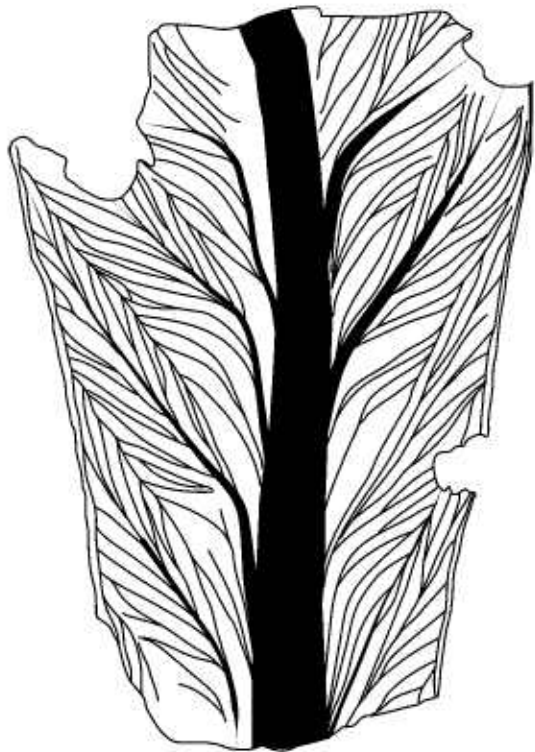


FIGURE 10—Gigantopterid. Line drawing of specimen USNM 520383, illustrated in Figure 9.1. Note marginal vein.

mm from base to apex and about 15 mm wide. The terminal portion is five-lobed and the scale tapers to a constricted base. A single vein enters the base of the scale and, in a sequence of dichotomies, lateral veins diverge, each ending in a sinus between the lobes, the central vein ending near the apex of the central lobe. One scale may have had either two or three ovules attached to its surface (Fig. 14.5). Ovulelike bodies are 5.7 mm long and 4 mm wide.

The second type of cone scale is represented by a single specimen that is 14 mm in both width and length (Fig. 14.4). It terminates in small teeth along the distal margin. Teeth at the edges of the distal margin are elongate and bend outward irregularly. The surface is longitudinally striate, the striations possibly representing fine veins.

Thirdly, there are several examples of apparent conifer dwarf shoots (Fig. 13.5), similar to those on the intact cone described above and similar to scales found in plant deposits of the San Angelo Formation (DiMichele et al., 2001). The scales are composed of a distal peltate portion borne on a narrow pedicel. The peltate portion is five-lobed distally and about 10 mm wide by 7 mm from the point of pedicel attachment to the central distal lobe. The pedicel is up to 9 mm long, 3 mm wide at the point of expansion into the peltate portion, and 2.5 mm wide at the base.

Seeds.—Up to three types of seeds are represented, all by few specimens. Most common is *Samaropsis* Göppert (1864), 13–15 mm in diameter with a central body, 7 to 7.5 mm in diameter, and a wing up to 4 mm in width (Fig. 16.3). Two other specimens attached to the distal ends of stalklike sporophylls suggest cordaitan affinity (Fig. 16.6, 16.7). A final category is known from several ovoid seeds that are tapered acutely at the presumed micropylar end (Fig. 16.4, 16.5) and of different size ranges (the largest was 13 mm long and 6.5 mm wide; the smallest were

approximately 9 mm long and 5 mm wide). Because of small sample size it is unclear if these size differences are significant.

Incertae sedis.—Scraps of unidentifiable but distinctive foliage are worthy of mention because they are clearly different from other elements of the flora. The first are small laminae 8 mm long by 6 mm wide, with open dichotomous venation and no distinct midvein (Fig. 16.1, 16.2). Veins are high-angled and arch slightly to the margins. The lamina appears to be folded or divided into two to three lobes that can overlap in compression.

On one hand sample, two specimens were encountered with several attached leaves. Leaves are parallel veined and appear to be helically arranged. Surface features were not visible. These may represent conifer shoots.

Fossil wood.—Fusinized woody stems occur throughout the deposit. Fire altered some of the fine detail, but the basic characteristics are still observable in scanning electron microscopic investigation (Fig. 17). The wood from these axes is of the basic araucarioxylon-type. Tracheids are of uniform diameter (Fig. 17.1). They bear pits on their radial walls; the pits occur in single rows (Fig. 17.2). Rays are composed of radially elongate cells that share pits with adjacent tracheids; multicellular rays up to 15 cells high were observed (Fig. 17.3). This type of wood is widely distributed in the Permian and is characteristic of both cordaites and conifers. Given the composition of the assemblage, we suspect that it most likely comes from the plants that produced the cordaitelike leaves.

DISCUSSION

Although fossil-bearing abandoned channels occur through most of the Lower Permian in north-central Texas, the example of South Ash Pasture is uncommon in the context of the upper Blaine Formation, and the flora itself is highly unusual. Only two other channel-like deposits were found in this part of the Blaine, and these yielded only problematic algal impressions and unidentifiable scraps that may not even be of organic origin. Isolated stratigraphically and geographically, and yielding a small, low-diversity sample of mainly enigmatic taxa, South Ash Pasture gives a tantalizing glimpse of a Middle Permian flora that is otherwise almost entirely unknown.

The recurrence of channel fills as a nearly exclusive depositional setting for plant assemblages in the Lower Permian of north-central and West Texas has an understated influence on floral records and paleoclimatic interpretations derived from these records. In some parts of the section, channel deposits are abundant and plant assemblages, therefore, numerous. During early Leonardian time, subsidence in the Midland Basin and source-area input diminished. As a result, laterally extensive carbonates and evaporites encroached upon the landward margins of the Eastern Shelf (Abilene Geological Society, 1949, 1953). By the end of the Leonardian or the earliest Guadalupian, channel settings conducive to the preservation of organics were nearly nonexistent, leaving the false impression of a barren, uninhabited landscape. A similar pattern is apparent in the vertebrate record, though floodplain aestivation assemblages are known (DiMichele and Hook, 1992).

Thus, there are several scales of paleoenvironmental comparisons. At the scale of the abandoned channel, South Ash Pasture is no different from many other deposits throughout the Lower Permian. At the scale of the depositional landscape, South Ash Pasture also is very similar to certain parts of the lower part of the Clear Fork Group, which has yielded numerous fossil assemblages on outcrop and includes evaporites and carbonates in the shallow subsurface. Finally, at the scale of depositional systems, which would encompass physiographic and climatic variations, the northern Blaine Formation appears to have been deposited as part of a continuation of the same conditions and controls that can be recognized

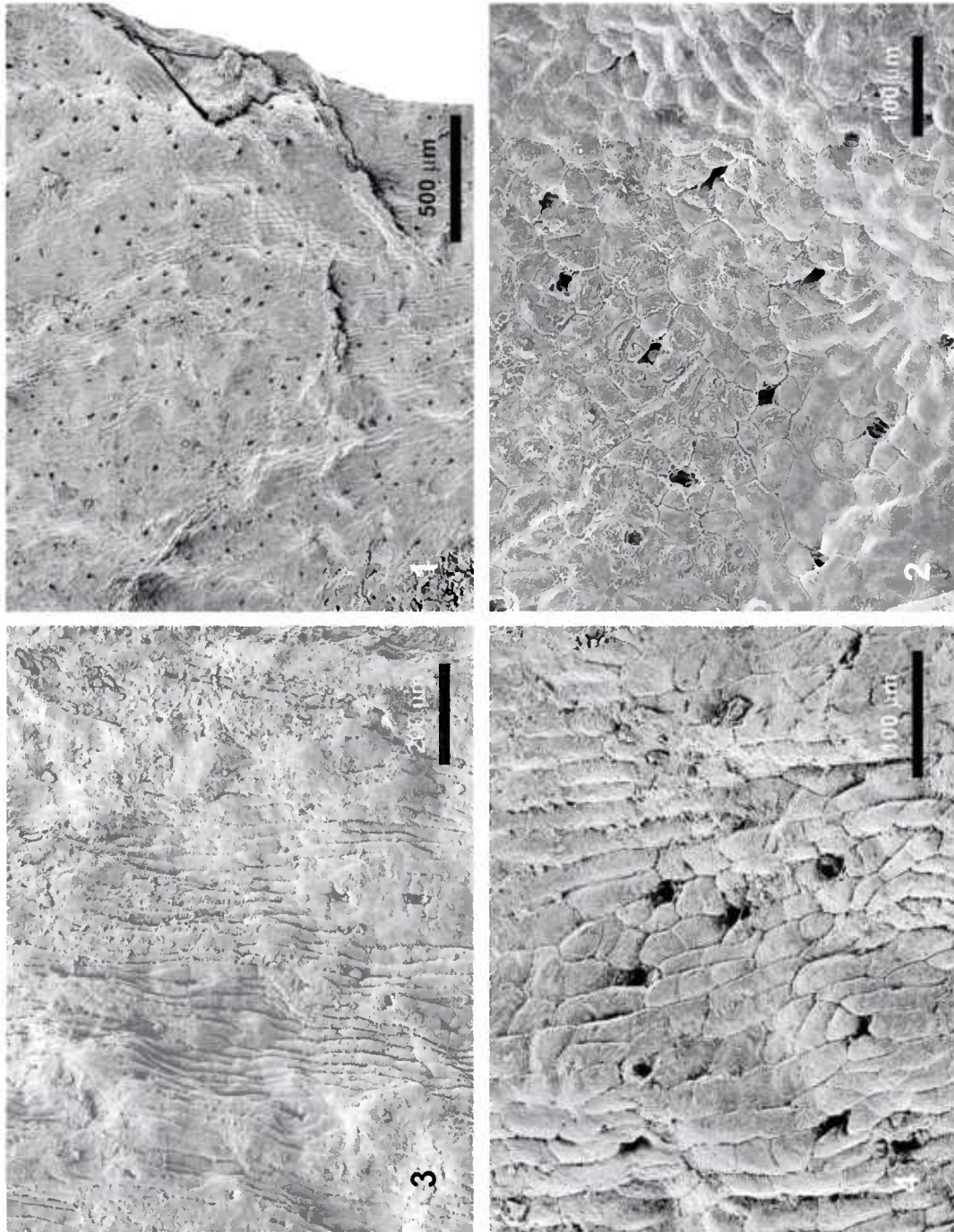


FIGURE 11—Gigantopterid. Epidermal features. USNM 520376. Scanning electron microscope images. Scale bars as shown. Adaxial and abaxial surfaces cannot be positively identified. 1, Elongate cells grade to more isodiametric cells near the margin; 2, surface area between veins. Stomata surrounded by four to six subsidiary cells; 3, surface area above a vein with elongate cells and few stomata; 4, surface in transitional area between vein and intervein parts of lamina.

in the subsurface as far down as the top of the Wolfcampian in the same geographic area.

The composition of the South Ash Pasture flora is by far the most peculiar yet described from the late Paleozoic North American tropical zone. The affinities of the flora are obscure, with suggestions of linkages to both the Angaran and Cathaysian floral realms (Rees et al., 2002). Most suggestive are the parallel-veined

leaves that may be rufflorian-like cordaites, a dominant group in Angaraland (Meyen, 1982), and a gigantopterid without clear similarities to any described taxa. Gigantopterids are prominent members of Permian floras only in western Euramerica and Cathaysia. Large, apparently female, conifer cones are suggestive of the conifer family Majonicaceae (Clement-Westerhoff, 1987). The lack of conifer foliage, however, confounds this interpretation, unless

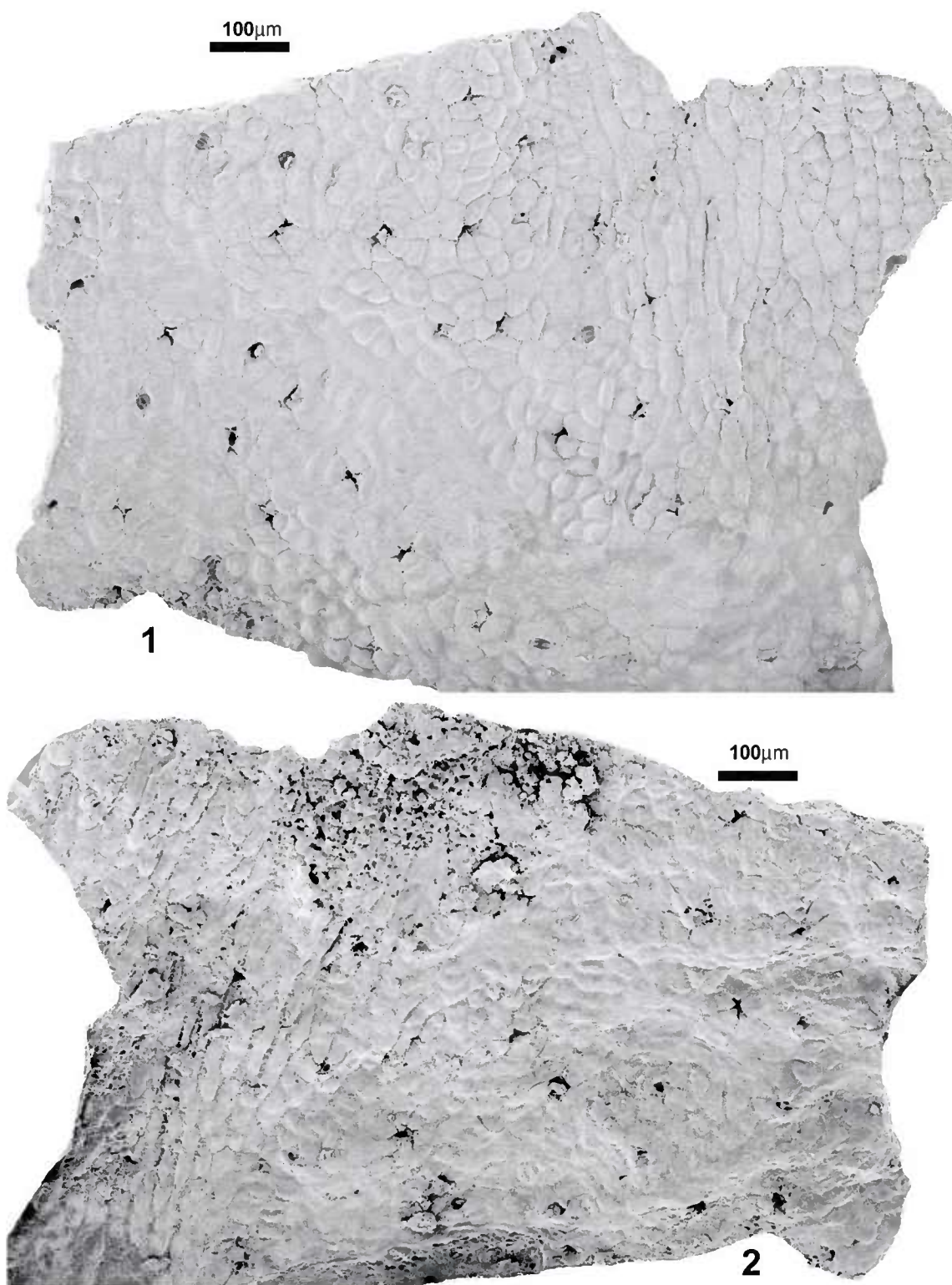


FIGURE 12—Gigantopterid. Epidermal features. USNM 520382. Adaxial and abaxial surfaces of the same specimen (which is which cannot be determined). Surface area above a vein is on the right of 1 and on the left of 2. Same magnification.

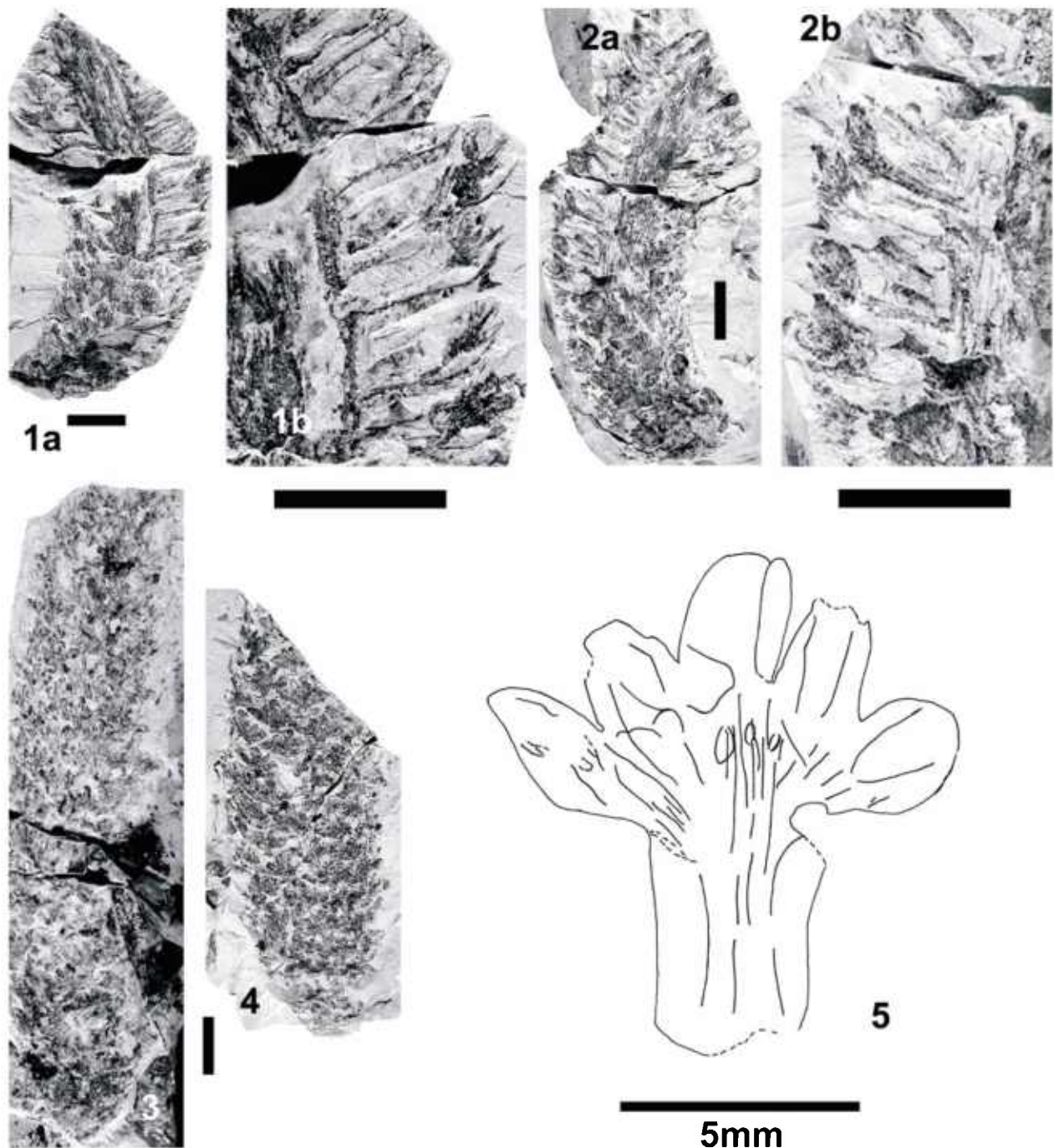


FIGURE 13—Cones of presumed coniferous affinity. Bar scales in 1–4 = 1 cm. 1, Cone axis in surface and median longitudinal section, plus median longitudinal section through sporophylls. Terminal portions of sporophylls five-lobed. Thin bracts subtend and extend beyond sporophylls at margin of cone, 1a, X1, 1b, X2, USNM 520393; 2, cone median longitudinal section, counterpart, 2a, X1, 2b, X2, USNM 520393; 3, surface view of cone, lobed terminal portions of cone scales visible, X1, USNM 520396; 4, surface view of cone, lobed terminal portions of cone scales visible, X1, USNM 520397; 5, line drawing of isolated cone scale, USNM 520388.

the cordaitan-like leaves are actually coniferous in affinity. A cycadophyte or noeggeratialean affinity for the dominant foliage also cannot be ruled out (Wang and Shen, 2000).

Parallel-veined foliage is the overwhelmingly dominant element of the assemblage, which is probably autochthonous at the scale of the channel and its immediate surroundings. Taphonomic studies indicate that plants preserved in channel fills are drawn

almost exclusively from within 20 m of the channel margin and actually from within the confines of elevated stream banks (Scheiing and Pfefferkorn, 1984; Burnham, 1989). Fossil wood is common at South Ash Pasture and is consistent with woody vegetation at the channel margins. Furthermore, the low diversity of the assemblage and associated primary dolomites and evaporites suggest a flora adapted to periodic water stress.

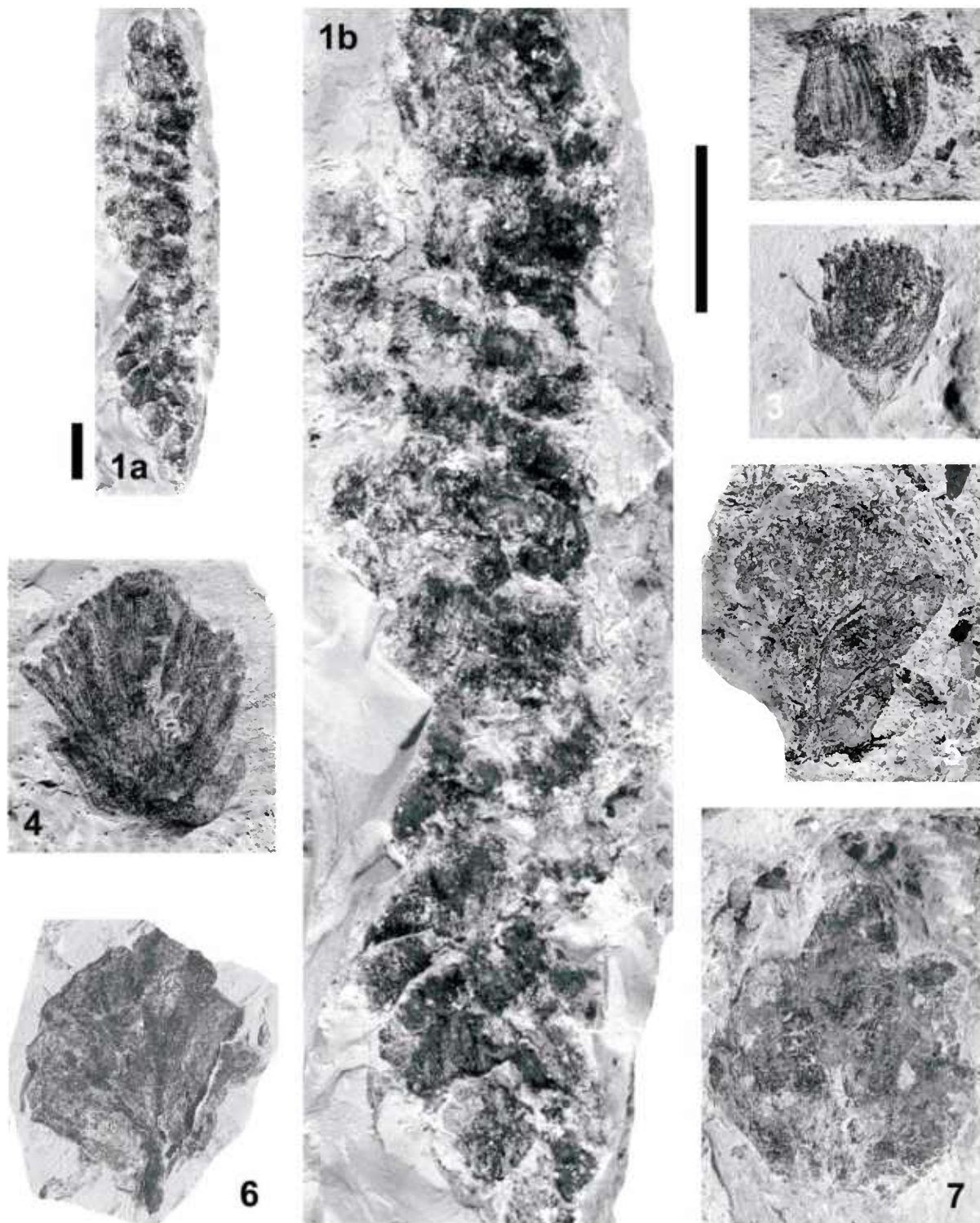


FIGURE 14—1–3, Cone and cone scales of indeterminate, possible noeggerathialean, affinity; 4–7, cone scales of coniferous affinity. Small scale bar = 1 cm, applies to 1a; large scale bar = 1 cm, applies to 1b, 2–7. 1, Sporophylls each end in many small lobes or teeth and are spirally arranged 1a, X1, 1b, X3, USNM 520399; 2, isolated cone scale similar to those of specimen illustrated in 1; a vein terminates in each marginal tooth, X3, USNM 520400; 3, isolated cone scale similar to those of specimen illustrated in 1, X3, USNM 520401; 4, conifer (?) cone scale, numerous veins terminate in terminal teeth, X3, USNM 520402; 5, conifer cone scale with five terminal lobes and possible ovules on scale surface, X3, USNM 520403; 6, conifer cone scale with reduced lobing. A single vein enters the base of the scale and divides so that lateral divisions terminate in sinuses of lobes, X3, USNM 520404; 7, conifer cone scale with five terminal lobes. A single vein at base of scale divides and divisions terminate in sinuses of lobes, X3, USNM 520405.



FIGURE 15—Line drawing of specimen illustrated in Figure 14.2. USNM 520400.

The extreme taxonomic isolation of this flora from others of the late Paleozoic tropics is part of a pattern that begins in the later part of the Leonardian. Channel fills in the basal Blaine Formation and the underlying San Angelo Formation contain a flora that includes several genera or species with Late Permian to Mesozoic affinities and a few relatively weak links to the older Euramerican tropics (DiMichele et al., 2001). Similarly, a flora from a coastal island setting in the upper Clear Fork Group of the Central Basin Platform, West Texas, includes a mixture of

environmentally restricted and environmentally widespread taxa and is distinct from older coastal plain floras (DiMichele et al., 2000).

A rise in seed-plant dominance, drop in overall taxonomic diversity, and general reduction in abundance in spore-producing plants are trends throughout western North America during the Early Permian and a pattern found through the Euramerican tropics. By and large, there is little overlap between the floras typical of the wetter parts and times in the tropics and those of the seasonally dry to seasonally wet parts (Kerp and Fichter, 1985; Broutin et al., 1990; DiMichele and Aronson, 1992). These vegetational patterns probably reflect changes in regional climates related to climatic zonation (Ziegler, 1990), possibly brought on by changing continental positions or by changes in the dynamics of the intertropical convergence zone with the waning and disappearance of South Polar glaciation. All the vegetation types may have coexisted in different climatic zones, even in close proximity if extrabasinal areas had significant elevation, and may have represented distinct species pools.

In effect, Lower to Middle Permian stratigraphic floral changes do not necessarily demonstrate temporally progressive vegetational evolution. The record in north-central and West Texas is heavily biased toward assemblages that accumulated with minimal transport in standing-water deposits. Thus, we cannot say with confidence when or where the plants that comprise South Ash Pasture and other peculiar vegetation types first evolved and were assembled in the equatorial regions. The ecological overprint on this terrestrial record completely confounds our ability to read the stratigraphic progression of taxa as a record of temporal evolution, at least at our current level of resolution.

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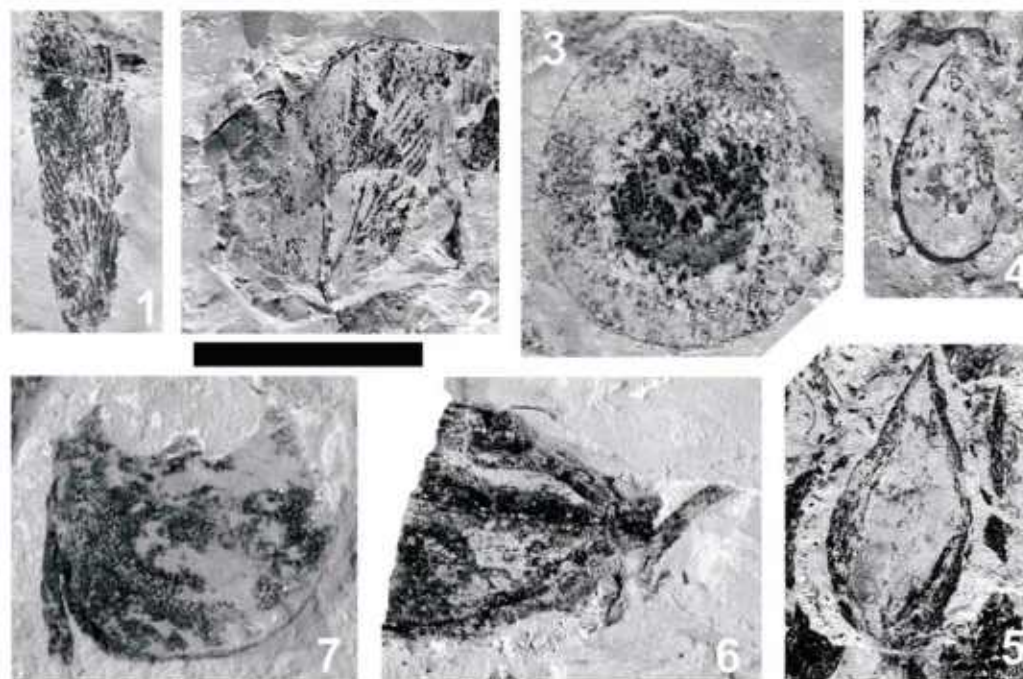


FIGURE 16—1, 2, Unidentified fragments of foliage with high-angle, open dichotomous venation and no clear midvein, X3. 1, USNM 520406; 2, counterpart, USNM 520406. 3, *Samaropsis* seed, nucule surrounded by broad wing of oval shape, X3, USNM 520408. 4, 5, Ovoid seeds without wings, X3; 4, USNM 520409, 5, USNM 520412. 6, 7, Seeds of apparent *Samaropsis* Göppert, 1864 affinity attached to sporophylls, X3; 6, USNM 520411, 7, USNM 520410.

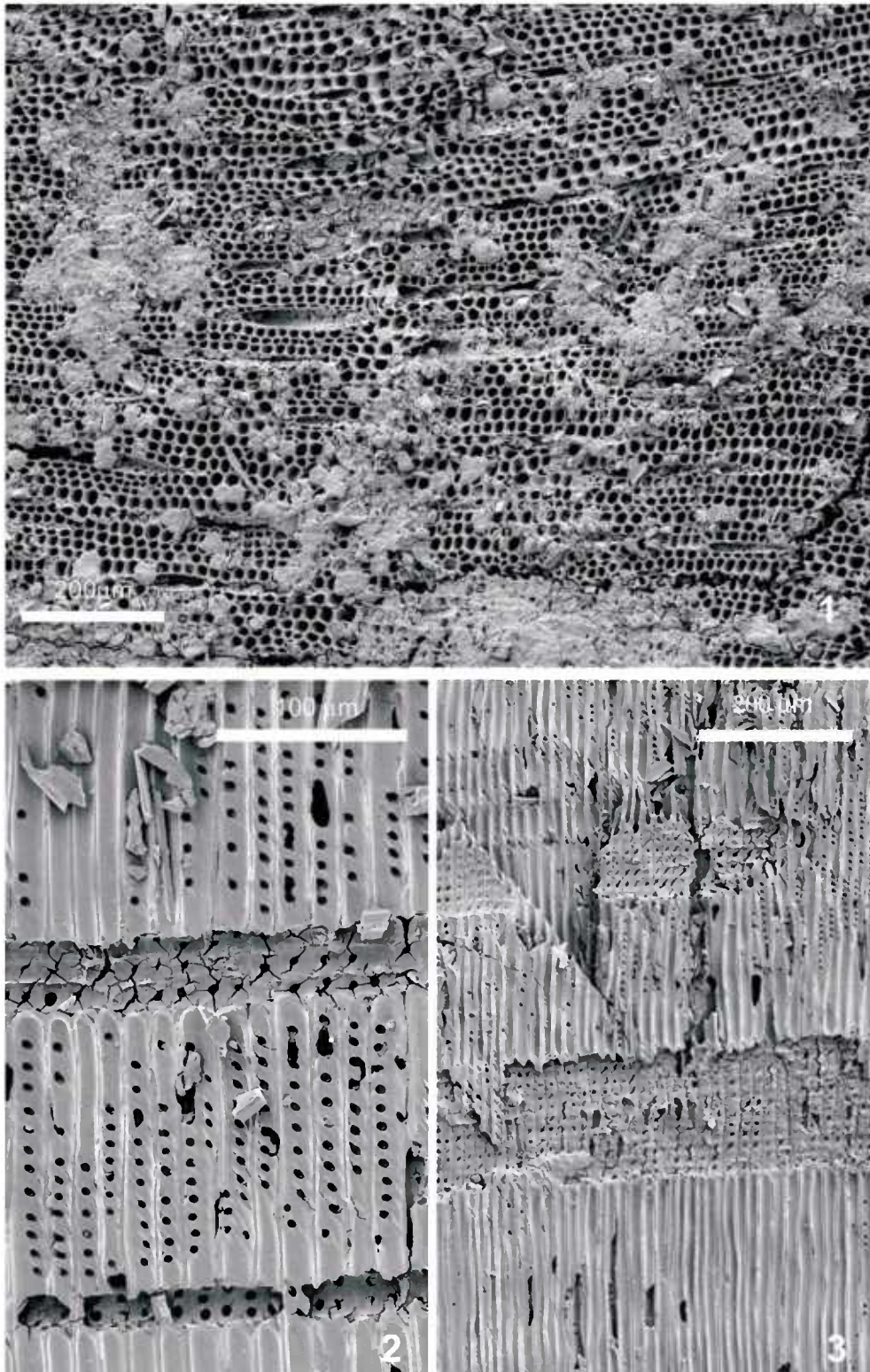


FIGURE 17—Scanning electron microscope images of wood fragments preserved as charcoal (fusain), USNM 520385. 1, Transverse section. Tracheids are of uniform diameter, rays are thin and obscure, no growth rings are visible, scale bar = 200 μm . 2, Radial longitudinal section. Pits on tracheids are in a single longitudinal row, rays are one to two cells high with crossfield pits, scale bar = 100 μm . 3, Radial longitudinal section illustrating rays up to 15 cells high, pitting is scattered on tracheid radial walls, scale bar = 200 μm .

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REFERENCES

- ABILENE GEOLOGICAL SOCIETY. 1949. Cross Section, Stonewall Co. to Hood Co., Texas. One sheet.
- ABILENE GEOLOGICAL SOCIETY. 1953. Cross Section, Schleicher Co. to Childress Co., Texas. One sheet.
- BECK, C. B. 1981. *Archaeopteris* and its role in vascular plant evolution, v. 1, p. 193–230. In K. J. Niklas (ed.), *Paleobotany, Paleoecology, and Evolution*. Praeger Scientific Publishers, New York.
- BÖSE, E. 1919. The Permo-Carboniferous ammonoids of the Glass Mountains, West Texas, and their stratigraphical significance. *University of Texas Bulletin*, 1762:1–241.
- BROUTIN, J., J. DOUBINGER, G. FARJANEL, F. FREYTET, H. KERP, J. LANGIAUX, M. L. LEBRETON, S. SEBBAN, AND S. SATTI. 1990. Le renouvellement des flores au passage Carbonifère Permien: approches stratigraphique, biologique, sédimentologique. *Académie des Sciences Paris, Comptes Rendues*, 311:1563–1569.
- BURNHAM, R. J. 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. *Review of Palaeobotany and Palynology*, 58:5–32.
- CLEMENT-WESTERHOF, J. A. 1987. Aspects of Permian palaeobotany and palynology, 7: The Majonicaceae, a new family of Late Permian conifers. *Review of Palaeobotany and Palynology*, 41:51–166.
- CLEMENT-WESTERHOF, J. A. 1988. Morphology and phylogeny of Paleozoic conifers, p. 298–337. In C. B. Beck (ed.), *Origin and Evolution of Gymnosperms*. Columbia University Press, New York.
- CLIFTON, R. L. 1942. Invertebrate faunas from the Blaine and Dog Creek Formations of the Permian Leonard Series. *Journal of Paleontology*, 16:685–699.
- CLIFTON, R. L. 1945. Permian Word Formation: its faunal and stratigraphic correlatives. *American Association of Petroleum Geologists Bulletin*, 29:1766–1776.
- CLIFTON, R. L. 1946. Middle Permian Cephalopoda from Texas and New Mexico. *Journal of Paleontology*, 20:556–559.
- DiMICHELE, W. A., AND R. B. ARONSON. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. *Evolution*, 46:807–824.
- DiMICHELE, W. A., AND R. W. HOOK. 1992. Paleozoic terrestrial ecosystems, p. 204–325. In A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing (eds.), *Terrestrial Ecosystems Through Time*. University of Chicago Press, Chicago.
- DiMICHELE, W. A., D. S. CHANEY, W. H. DIXON, W. J. NELSON, AND R. W. HOOK. 2000. An Early Permian coastal flora from the Central Basin Platform of Gaines County, West Texas. *Palaio*, 15:524–534.
- DiMICHELE, W. A., S. H. MAMAY, D. S. CHANEY, R. W. HOOK, AND W. J. NELSON. 2001. An Early Permian flora with Late Permian and Mesozoic affinities from North-Central Texas. *Journal of Paleontology*, 75:449–460.
- EIFLER, G. K., J. C. FRYE, A. B. LEONARD, T. F. HENTZ, AND V. E. BARNES. 1992. *Geologic Atlas of Texas, Plainview Sheet* (revised). The University of Texas at Austin, Bureau of Economic Geology, scale 1:250,000.
- EIFLER, G. K., J. C. FRYE, A. B. LEONARD, T. F. HENTZ, AND V. E. BARNES. 1993. *Geologic Atlas of Texas, Lubbock Sheet* (revised). The University of Texas at Austin, Bureau of Economic Geology, scale 1:250,000.
- EWING, T. E. 1991. The tectonic framework of Texas. Text to accompany “The Tectonic Map of Texas,” The University of Texas at Austin, Bureau of Economic Geology, 36 p.
- FAY, R. O. 1964. Blaine Formation of northwestern Oklahoma. *Oklahoma Geological Survey Bulletin*, 98, 238 p.
- FEISTMANTEL, O. 1879. Bemerkungen über die Gattung *Nöggerathia* Stbg., sowie die neuen Gattungen *Nöggerathiopsis* Fstm. und *Rhiptomites* Schmalh. *Sitzungsberichte der Königl Böhmisches Gesellschaft der Wissenschaften* (Prague), 1879:444–454.
- FLORIN, R. 1927. Preliminary descriptions of some Paleozoic genera of Coniferae. *Arkiv Botanik*, 21A:1–7.
- GAO, Z., AND B. A. THOMAS. 1987. A re-evaluation of the plants *Tingia* and *Tingiostrubus* from the Permian of Taiyuan, China. *Palaeontology*, 30:815–828.
- GLENISTER, B. F., D. W. BOYD, W. M. FURNISH, R. E. GRANT, M. T. HARRIS, H. KOZUR, L. L. LAMBERT, W. W. NASSICHUK, N. D. NEWELL, L. C. PRAY, C. SPINOSA, B. R. WARDLAW, G. L. WILDE, AND T. E. YANCEY. 1992. The Guadalupian: proposed international standard for a Middle Permian Series. *International Geology Review*, 34:857–888.
- GÖPPERT, H. R. 1864. Die fossile Flora der Permischen Formation. *Paleontographica*, 12, 244 p.
- HALLE, T. G. 1925. *Tingia*, a new genus of fossil plants from the Permian of China. *China Geological Survey Bulletin*, 7:1–12.
- HALLE, T. G. 1927. Paleozoic plants from Central Shansi. *Paleontologica Sinica*, 2:1–316.
- HOTTON, N. III, R. M. FELDMANN, R. W. HOOK, AND W. A. DiMICHELE. 2002. Crustacean-bearing continental deposits in the Petrolia Formation (Leonardian Series, Lower Permian) of North-Central Texas. *Journal of Paleontology*, 76:486–494.
- HOVORKA, S. D., AND P. A. GRANGER. 1986. Subsurface to surface correlation of Permian evaporates: San Andres—Blaine—Flowerpot relationships, Texas Panhandle. *Midcontinent SEPM Special Paper*, 1:137–159.
- KERP, H., AND J. FICHTER. 1985. Die Makrofloren des saarpfälzischen Rotliegenden (?Ober-Karbon—Unter-Perm; SW-Deutschland). *Mainzer geowissenschaftliche Mitteilungen*, 14:159–286.
- KING, P. B. 1942. Permian of West Texas and southeastern New Mexico. *American Association of Petroleum Geologists Bulletin*, 26:535–763.
- KOIZUMI, G. 1936. Gigantopteris flora. *Acta Phytotaxonomica et Geobotanica*, 5:130–144.
- LEARY, R. L. 1980. *Lacoea* with sporangia and *Calamospora* spores from Rock Island, Illinois. *Review of Palaeobotany and Palynology*, 29:23–28.
- LEARY, R. L., AND H. W. PFEFFERKORN. 1977. An Early Pennsylvanian flora with *Megalopteris* and *Noeggerthiales* from west-central Illinois. *Illinois State Geological Survey Circular*, 500:1–77.
- LI, H., AND D. W. TAYLOR. 1998. *Aculeovinea yungiensis* gen. et sp. nov. (Gigantopteridales), a new taxon of gigantopterid stem from the Upper Permian of Guizhou Province, China. *International Journal of Plant Sciences*, 159:1023–1033.
- LI, H., AND D. W. TAYLOR. 1999. Vessel-bearing stems of *Vasovinea tianii* gen. et sp. nov. (Gigantopteridales) from the Upper Permian of Guizhou Province, China. *American Journal of Botany*, 86:1563–1575.
- LI, H., B. TIAN, E. L. TAYLOR, AND T. N. TAYLOR. 1994. Foliar anatomy of *Gigantonoclea guizhouensis* (Gigantopteridales) from the Upper Permian of Guizhou Province, China. *American Journal of Botany*, 81:678–689.
- MAMAY, S. H. 1954. A Permian *Discinites* cone. *Journal of the Washington Academy of Sciences*, 44:7–11.
- MAMAY, S. H. 1968. *Russellites*, new genus, a problematic plant from the Lower Permian of Texas. *United States Geological Survey Professional Paper*, 593-I:11–115.
- MAMAY, S. H. 1989. *Evolsonia*, a new genus of Gigantopteridaceae from the Lower Permian Vale Formation, North-Central Texas. *American Journal of Botany*, 76:1299–1311.
- MAMAY, S. H., J. M. MILLER, D. M. ROHR, AND W. E. STEIN JR. 1988. Foliar morphology and anatomy of the gigantopterid plant *Delnortea abbottiae*, from the Lower Permian of West Texas. *American Journal of Botany*, 75:1409–1433.
- MEYEN, S. V. 1982. The Carboniferous and Permian floras of Angaraland (a synthesis). *Biological Memoirs*, 7:1–110.
- MILLER, A. K., AND W. M. FURNISH. 1940. Permian ammonoids of the Guadalupe Mountains regions and adjacent areas. *Geological Society of America Special Paper*, 26, 242 p.

- NEWELL, N. D. 1940. Invertebrate fauna of the Late Permian Whitehorse Sandstone. *Geological Society of America Bulletin*, 51:261–336.
- PLUMMER, F. B., AND G. SCOTT. 1937. Upper Paleozoic ammonites in Texas. *The University of Texas Bulletin*, 3701, 516 p.
- REES, P. M., A. M. ZIEGLER, M. T. GIBBS, J. E. KUTZBACH, P. J. BEHLING, AND D. B. ROWLEY. 2002. Permian phytogeographic patterns and climate data/model comparisons. *Journal of Geology*, 110:1–31.
- ROTH, R. 1945. Permian Pease River Group of Texas. *Geological Society of America Bulletin*, 56:893–908.
- SALISBURY, E. J. 1927. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London, series B*, 216: 1–65.
- SCHEIHING, M. H., AND H. W. PFEFFERKORN. 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 Palaeobotany and Palynology*, 41:205–240.
- SIMUNEK, Z. 2000. Cuticles of *Cordaites* from the Westphalian, Stephanian and Autunian of the Bohemian Massif (Czech Republic). *Acta Palaeobotanica*, 40:25–34.
- SKINNER, J. W. 1946. Correlation of Permian of West Texas and southeast New Mexico. *American Association of Petroleum Geologists Bulletin*, 30:1857–1974.
- SMITH, J. P. 1903. Carboniferous ammonoids of America. *United States Geological Survey Monograph*, 42, 211 p.
- TAYLOR, T. N., AND E. L. TAYLOR. 1993. *The Biology and Evolution of Fossil Plants*. Prentice-Hall, Englewood Cliffs, New Jersey, 982 p.
- THARALSON, D. B. 1984. Revision of the Permian ammonoid family Perinitidae. *Journal of Paleontology*, 58:804–833.
- WANG, J., AND G. SHEN. 2000. A new species of *Discinites* (Noeggerathiales) from the Upper Permian of Weibei Coalfield, North China. *Review of Palaeobotany and Palynology*, 110:175–190.
- ZEILLER, R. 1894. Notes sur le flore des couches permienes de Trienbach (Alsace). *Bulletin Société Géologique de la France*, 3 ser., T 22:163–182.
- ZIEGLER, A. M. 1990. Phytogeographic patterns and continental configurations during the Permian Period. *Geological Society of London Memoir*, 12:363–379.

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