

Lower Permian Flora of the Sanzenbacher Ranch, Clay County, Texas

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1. INTRODUCTION

Since 1989, field parties supported by the U.S. National Museum of Natural History have obtained large collections of mainly Permian plant fossils from north central Texas. This work was undertaken to study known localities and to find new fossiliferous deposits that would contribute to a better understanding of floral and paleoenvironmental changes within the region during the early Permian. From the outset, the effort was interdisciplinary and grew, through the contributions of nearly 20 paleobotanists, palynologists, invertebrate and vertebrate paleontologists, and sedimentary geologists of several subdisciplines, to be quite comprehensive. Our reporting of results, however, has been influenced by unexpected developments, including the discovery of new plant-fossil assemblages in areas once regarded as barren, opportunities to evaluate floras known only from core samples made available by oil and gas operators in West Texas, and the arrival of workers whose expertise provided novel stratigraphic and depositional interpretations. As a result, some of our earliest findings have not been presented in detail. This report is a remediation effort of sorts in which we document the fossil plants, palynology, and depositional context of the lower Permian Sanzenbacher Ranch locality of Clay County, Texas. Because the deposit occurs in what is regarded as the lower Wolfcamp part of the Texas section (Fig. 6.1) (DiMichele et al., 2006), this assemblage bears comparisons to coeval floras in North America (DiMichele et al., 2004, 2005; Glasspool et al., 2013) and equivalent lower Cisuralian, particularly Asselian, floras of Europe (e.g., Wagner and Martínez García, 1982; Wagner, 1983; Kerp and Fichter,

1985; Broutin, 1986; Popa, 1999; Steyer et al., 2000; Wagner and Mayoral, 2007; Bercovici and Broutin, 2008; Barthel, 2009; Wagner and Álvarez-Vázquez, 2010; Barthel and Brauner, 2015). Furthermore, because this locality was collected on three occasions over a time period of 50 years and by different parties, comparative analysis of the Sanzenbacher collections provides a basis for assessing sites that have comparable histories.

2. GEOLOGY

Clay County is the only county in the Permo-Carboniferous outcrop belt of north central Texas that lacks marine rocks. These alluvial sediments accumulated east of a broad coastal plain that bordered the Eastern Shelf of the Midland Basin. Early work outlined a regional relationship between terrestrial deposits in the northeast and coeval marine beds in the southwest (Cummins, 1890, 1891, 1897). Subsequent studies focused on either elaborating or reconciling stratigraphic nomenclature of the transition and rarely, if ever, mentioned Clay County. Sellards (1933) was the first to project formation-scale lithostratigraphic divisions from the marine-dominated southwest across Clay County based on unpublished oil company surveys and regional mapping conducted by the Texas Bureau of Economic Geology. After many years of field work related to vertebrate fossil collecting in the region, Romer (1974) produced a comprehensive geological map of north central Texas that included Clay County. This posthumously published map has numerous shortcomings that were addressed by Hentz and Brown (1987), whose 1:250,000-scale geologic map established new group and formation names for the

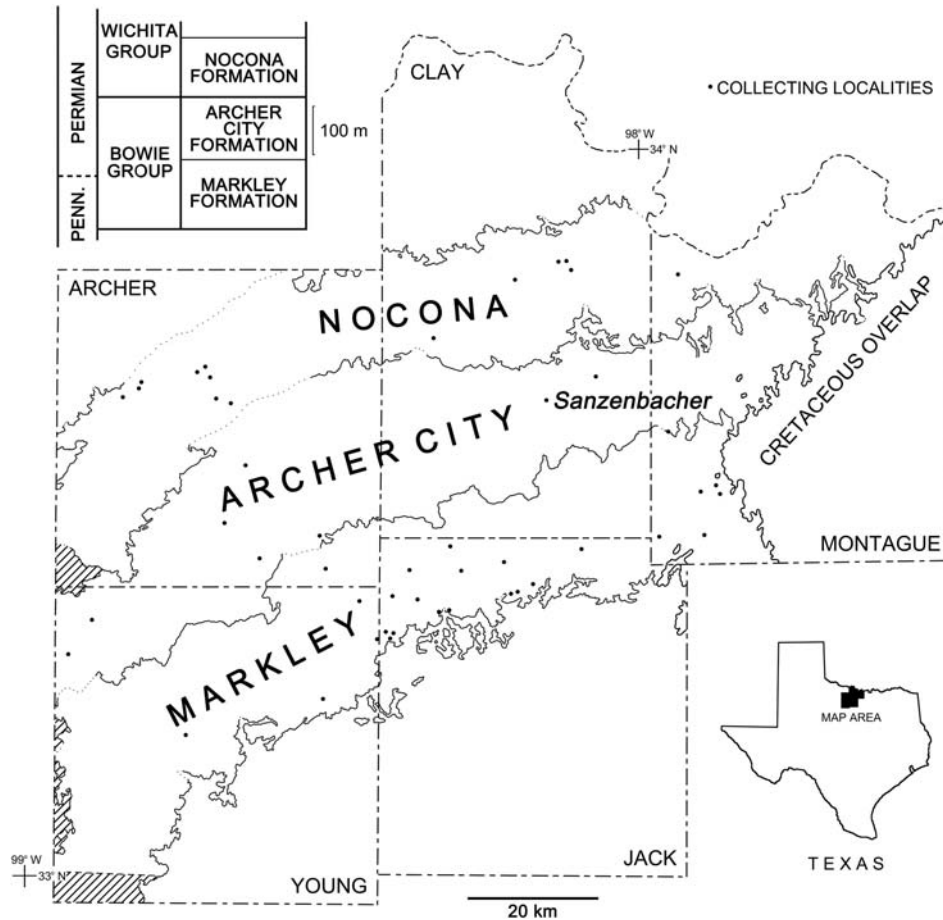


FIGURE 6.1 Generalized bedrock geology of Clay County and adjacent counties, north central Texas. Average formation thicknesses shown in stratigraphic column from ranges estimated by Hentz and Brown (1987). Formation contacts dotted in areas of surficial cover. Large dots indicate plant-collecting localities represented by USGS, USNM, or NPL collections, including Sanzenbacher (south central Clay County). Areas in southwestern Archer and Young counties marked by diagonal lines represent marine-influenced rocks of the Albany and Cisco groups, respectively, which are coeval with continental rocks of the Wichita and Bowie groups, respectively. Inset shows map location within Texas. *Geological mapping adapted from Hentz, T.F., and L.F. Brown, Jr. 1987. Wichita Falls-Lawton Sheet. The University of Texas at Austin Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250,000, with explanatory pamphlet; McGowen, J.H., T.R. Hentz, D.E. Owen, and M.K. Pieper. 1991. Sherman Sheet. The University of Texas Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250,000, with explanatory pamphlet; and Brown, L.F., Jr., and J.L. Goodson. 1972. Abilene Sheet. The University of Texas at Austin Bureau of Economic Geology, Geologic Atlas of Texas, scale 1:250,000, with explanatory pamphlet.*

continental rocks of the region (Hentz, 1988). Applying this most recent stratigraphic framework, the Sanzenbacher plant deposit occurs in the middle part of the Archer City Formation, the lower of two formations that compose the Bowie Group (Fig. 6.1).

Surface exposures of the Archer City Formation and other rocks are generally poor in Clay County. They consist mainly of gently sloping uplands with a few modest escarpments, and total relief within the county is less than 100 m. Based on interpretation of stereoscopic aerial photographs, Hentz (1988, 1989) estimated the thickness of the Archer City Formation to be from 107 to 122 m and mapped nine informal sandstone members that occur most commonly as resistant caprocks of low ridges. Observed in

the field, these sandstone bodies measure up to approximately 15 m in thickness, are erosive with basal conglomerates, and exhibit an overall fining-upward character indicative of fluvial deposition. Mud rocks form the greater portion of the formation and commonly contain calcareous and ferruginous nodules that mantle gently sloping surfaces and retard erosion. Field descriptions and laboratory analyses of these predominantly reddish brown mudstones in neighboring Archer County indicate a range of paleosol types and hydrologic conditions (Tabor et al., 2002; Tabor and Montañez, 2004).

The Sanzenbacher deposit occurs in a partially exposed mudstone interval below an outlier of informal sandstone member 8, on a bench supported by underlying informal

sandstone member 5 of [Hentz and Brown \(1987\)](#). Where we collected, fossil plants were dispersed through an interval of approximately 1 m in a coarsening-upward deposit that consists of blue-gray and light green–gray, slightly silty claystones to buff-colored siltstones. Subtle color banding in the claystones indicates thickly laminated (0.3–1 cm) to very thinly bedded (1–3 cm) muds, but the rock lacks fissility and has a conchoidal to starchy fracture, as shown in the specimen illustrations. Increased silt content coincides with drab gray-buff to light buff colors and an increase in organic remains. Massive siltstone beds are up to 8 cm thick and blocky, breaking with a hackly fracture. Thinly bedded siltstones also are blocky and nonfissile. Small-scale slickensides occur rarely and appear to represent compaction structures, in the absence of unequivocal paleosol features. Fossil charcoal is present in trace amounts. No burrows occur in the plant-bearing beds. As noted in the following section, the original Sanzenbacher collection includes a distinct fossiliferous lithology that was not sampled by later workers. This matrix is coarser grained, up to a very fine-grained sand, with mm-scale silt streaks. Yet, the rocks contain considerable clay – the margins of some specimens appear to have been whittled to reduce their dimensions. A few samples of this coarser matrix include irregular concentrations of calcareous, fine-grained sands that are ovoid to elliptical in cross section and less than 2 cm in greatest dimension. Whereas these may be pedogenic, their origin cannot be determined from hand samples alone.

3. COLLECTIONS

Fossils were first collected on the Henry Sanzenbacher Ranch by the Clay County Unit of the State-Wide Paleontological-Mineralogical Survey of the Work Projects Administration (WPA), a federal works agency of the Roosevelt New Deal era. From September 13, 1940, to October 1, 1941, the unit was led by Adolph H. Witte

(1895–1983) ([Plate I, 1](#)), a local resident who prospected Clay County and adjacent counties and supervised a collecting crew of up to 12 men. Initial objectives were to collect fossil vertebrates and archaeological objects. Witte’s discovery of plant-bearing deposits, however, resulted in sizeable paleobotanical collections that, a half-century later, became the starting point for much of our work in Texas ([DiMichele et al., 2005](#)).

Field operations of the WPA Texas Paleontological-Mineralogical Survey were the charge of Glen L. Evans (1911–2010), a native of Henrietta, the county seat of Clay County, Texas. Evans first tapped Witte to work for the WPA in Bee County, where a large quarry was opened in 1939 that produced a wealth of Miocene vertebrates ([Sellards, 1940](#)). The most senior scientist involved with the Texas WPA paleontological project was Elias H. Sellards (1875–1961), who was director of both the Texas Bureau of Economic Geology and the Texas Memorial Museum at the time. Sellards had studied lower Permian plants and insects from Kansas ([Morey and Lesnikowska, 1995](#)) and understood the potential that fossil plants held for refining the vague division between Carboniferous and Permian terrestrial rocks in north central Texas.

WPA correspondence and reports archived at the Vertebrate Paleontology Laboratory (VPL), Jackson School of Geoscience, The University of Texas at Austin, indicate that the first Sanzenbacher collection consisted of a few fragmentary vertebrates and a large number of coprolites found on the surface in either late December 1940 or the first week of 1941. When fossil plants and a possible insect were discovered soon thereafter, Sellards urged Witte to make a larger collection. The Clay County crew opened a quarry, blocking out and plastering two “large fronds apparently somewhat like present-day cypress”, as well as collecting individual hand-sample–sized plant specimens (Witte report for period ending January 27, 1941). Work continued intermittently into mid-March 1941. By that time, Sellards had examined the initial Sanzenbacher plant



PLATE I Sanzenbacher collectors and exposure. (1) Adolph H. Witte, Supervisor of WPA Clay County Unit; 1939, WPA fossil vertebrate quarry, Bee County, Texas (courtesy of the Texas Archaeological Research Laboratory; photo No. 41-BE-2-51). (2) Sergius H. Mamay, 1991, North–Central Texas. (3) Sanzenbacher Ranch collecting area, May 2, 1991, Dan S. Chaney (left) and Sergius H. Mamay (right); X indicates area believed to have been excavated intermittently by WPA personnel from late December, 1940, to mid-March, 1941.

collections, determined the flora to be Permian in age, and directed Witte, through Evans, “to get material down to and into the definite Pennsylvanian” (Evans to Witte, March 15, 1941). This was the end of WPA collecting at Sanzenbacher but the start of Witte’s prolific work in the Permian–Carboniferous coal-bearing rocks of adjacent Jack and Montague counties. There, in the next 6 months, Witte found 14 significant plant localities. The resulting collections, now held by the Non-vertebrate Paleontology Laboratory (NPL), Jackson School of Geoscience, The University of Texas at Austin, total over 2600 catalogued specimens (Ann M. Molineux, 2017, personal communication). Concurrently with collecting plant deposits, Witte discovered numerous important lower Permian vertebrate localities, two of which developed into sizeable quarries (collections at the VPL, [Craddock and Hook, 1989](#)).

On April 10, 1961, Witte, still living in Henrietta, directed, but did not accompany, our colleague Sergius H. Mamay (1921–2008) ([Plate I, 2](#)), then with the USGS, to the Sanzenbacher site. At the ranch property, Mamay was taken to the site by the owner, Carl Sanzenbacher. Over the next 2 days, Mamay and Arthur D. Watt made a second Sanzenbacher collection, USGS 9999. A third collection, USNM 40600, was made in 1991 by Mamay, DiMichele, Chaney, and Hook ([Plate I, 3](#)). Before the creation of the NPL in 1999, most of the WPA Sanzenbacher collection was catalogued under Texas Memorial Museum locality number TX1161, and individual hand samples received unique numbers, TX1161.1 through TX1161.192. An additional 98 NPL catalogue numbers were assigned subsequently to samples that either lacked original numbers or contained multiple taxa of significance.

The fossiliferous matrix of the USGS and USNM collections is similar to most of the NPL specimens. However, the sandy plant-bearing beds mentioned earlier appear to have been collected from higher in the coarsening-upward section, an interval largely covered today by fallen sandstone blocks that mark the former WPA excavation. This interpretation is supported by the fact that the two plant blocks were removed in plaster during the earliest phase of the WPA work, that conifers (Witte’s “cypress-like” fossils) are common in the sandy matrix but rare in the claystone matrix, and that large blocks of the underlying, irregularly fractured, claystones would have been very difficult to remove in plaster jackets. There is no record of what happened to the blocks. We suspect they were partitioned into smaller specimens, as were many of the WPA vertebrate fossils collected in plaster jackets (R.W. Hook, personal observation).

The exact location of the WPA (TX1161) and USGS (USGS locality 9999) excavations in relation to USNM locality 40600 is uncertain. Mamay led the 1990 field party to what he believed was at or near the site of the USGS excavation ([Plate I, 3](#)), given in the USGS locality register

as “At foot of high bluff, 1 mile due east of ranch house, 10 miles due south of Henrietta.” Mamay’s 1961 field notes provide more detailed directions. USNM 40600 constitutes several small excavations made in close lateral proximity. The approximate location of this collection is 18 km south-southeast of Henrietta in the L.N. Sparks land survey (exact coordinates can be made available by contacting the NMNH Department of Paleobiology). There are no known field notes describing the outcrops associated with the WPA collection. The USGS collection site is described in Mamay’s field notes as consisting of 3 feet (~1 m) of light and dark gray shales, overlain by nodular tan shale and siltstone, the latter barren of plant fossils; the shales included evidence of small-scale scour and fill, and the plants were irregularly distributed throughout an interval of 2–3 ft (~0.5–1 m), concentrated mostly in the lower part of the excavations. The plant beds were described as extending laterally for only about 15 ft (~4.5 m).

As noted earlier, the initial Sanzenbacher collection reported by Witte consisted of fragmentary vertebrates and a large number of coprolites, all found on the surface. Whereas the vertebrate scraps survive in the VPL (locality number 31238, catalogued as “Stone Mountain”), the coprolite collection does not. The VPL Sanzenbacher material includes a vial of several xenacanth shark teeth (VPL 31238-4) that are comparable to a specimen (USNM 612433) found by Mamay among the fossil plants. Invertebrate remains include blattoids, an incomplete myriapod, and conchostracans. [Durden \(1984a, 1984b\)](#) noted the blattoids. The myriapod (USNM 612363) was collected by Mamay and appears to be an archipolypod. As at many other plant localities we have worked, well-preserved conchostracans occur. They do not, however, occur in concentrations on bedding planes. Rather, they appear as singletons in the clay-rich part of the deposit that we regard as the bottom of the fossil-bearing interval.

4. METHODS

4.1 Macrofossils

The three macrofossil collections are of approximately the same size, each consisting of about 250 hand specimens ([Table 6.1](#)). The taxonomic composition of each collection was evaluated by using hand lens, a microscope where needed, and photography. Photography of most of the USGS specimens was done in black and white under flood lamps; the USNM and NPL collections were photographed in color and with natural light.

The collections were quantitatively assessed by using the quadrat method of [Pfefferkorn et al. \(1975\)](#), as modified by [Bashforth et al. \(2016\)](#). Each surface of a hand sample is treated as a “quadrat,” or sampling unit. The taxa, or other objects (roots, unidentifiable axes, charcoal, etc.) present on

TABLE 6.1 Categories of Plant Taxa, Organs, and Other Objects Recognized in Quantification of Sanzenbacher Macrofossil Collections

	USGS 9999	USNM 40600	NPL 1161
Quadrats-Informative	314	311	302
Quadrats barren	183	188	182
Quadrats total	497	499	484
Callipterids			
<i>Autunia conferta</i>	95	70	54
<i>Peltaspermum</i>	2	2	0
<i>Rhachiphyllum schenkii</i>	11	7	12
cf. <i>Lodevia</i> sp.	7	8	5
Unidentified callipterid (may be <i>A. conferta</i>)	4	2	0
Medullosan Pteridosperms			
<i>Odontopteris subcrenulata</i>	23	3	6
<i>Odontopteris</i> sp.	0	0	4
<i>Neurodopteris auriculata</i>	12	35	11
cf. <i>Eusphenopteris</i> (<i>trifoliolata</i> -like)	1	0	0
Neuropterid-like plant with possible reticulate venation	0	1	0
<i>Neuropteris</i> -like pinnules	0	1	0
Coniferophytes			
<i>Walchia</i> sp.	20	1	58
<i>Dicranophyllum</i> sp.	0	0	1
Conifer cones, scales, bracts	12	3	12
<i>Cordaites</i> sp.	4	15	3
<i>Cordaitanthus</i> sp.	2	2	1
Sphenopsids			
<i>Sphenophyllum oblongifolium</i>	1	0	0
<i>Sphenophyllum thonii/verticillatum</i>	7	3	4
<i>Sphenophyllum angustifolium</i>	2	8	0
<i>Asterophyllites equisetiformis</i>	2	6	1
<i>Annularia spicata</i>	0	0	33
<i>Annularia carinata</i>	0	1	0
<i>Calamites</i> stems	0	1	47
<i>Calamostachys</i> sp.	0	0	1
<i>Palaeostachya</i> sp.	0	0	1
Ferns			
<i>Pecopteris</i> sp.	7	47	6
<i>Pecopteris hemitelioides</i>	1	1	6
<i>Pecopteris monyei</i>	1	2	1
<i>Asterotheca</i> sp.	3	21	0
cf. <i>Danaeites</i> sp.	3	7	0
<i>Aphlebia</i>	0	1	0

Continued

TABLE 6.1 Categories of Plant Taxa, Organs, and Other Objects Recognized in Quantification of Sanzenbacher Macrofossil Collections—cont'd

	USGS 9999	USNM 40600	NPL 1161
<i>cf. Oligocarpia</i> sp.	5	7	0
<i>cf. Sphenopteris</i> pointy tiny pinnules	3	10	0
<i>Sphenopteris</i> tiny round pinnules	1	1	0
<i>Sphenopteris</i> (<i>Pecopteris</i>) tiny pinnules	0	0	2
<i>Sphenopteris</i> sp.	0	2	2
<i>cf. Nemejcopteris feminaeformis</i>	0	1	0
<i>cf. Senftenbergia plumosa</i>	1	0	0
Incertae Sedis			
<i>Sphenopteris germanica</i>	32	17	21
<i>Cf. Psymphyllum</i> sp.	0	0	1
<i>Taeniopteris</i> sp.	2	0	1
<i>Yuania</i> sp.	1	0	0
<i>Remia pinnatifida</i>	2	0	3
Unknown leaf	1	0	0
Miscellaneous			
Small seeds	70	60	14
<i>Trigonocarpus</i>	0	4	3
Stalked seed	0	1	0
“Floret” reproductive organs and “horned” seeds	6	6	3
Stalked reproductive structure	1	1	0
Striate axes	11	22	12
Woody axes	—	—	28
Roots	2	6	0
Unidentified plant remains	17	6	5
Nonplant Items			
Charcoal	11	35	4
Conchostracans	3	8	11
Coprolites	1	1	0
Insects	1	3	0
Counts reflect the number of quadrats on which each category was recognized.			

that surface, are identified and counted only once, regardless of the number of individual specimens. Part and counterpart surfaces are treated as the same quadrat. Barren surfaces are noted. The result is a distribution of frequencies recording the number of quadrats on which each taxon or object was identified. When percent occurrences are calculated, the barren quadrats are subtracted from the quadrat total. The rationale for use of this method can be found in various publications, including those cited here earlier.

The hand specimens in each of the three Sanzenbacher collections fit within a narrow size range, with largest dimension between 5 and 15 cm. Variable quadrat size presents statistical challenges (Rhodes and Syverson, 2013) that are somewhat mitigated by greater uniformity. We generally subdivide large fossiliferous slabs to bring them into conformance with the average hand-sample size; in the Sanzenbacher collections, however, this was not necessary.

4.2 Microfossils

Samples of rock matrix were broken from the edges of fossiliferous hand-samples to be macerated for palynological analysis. Approximately 10 cm³ was used for each maceration. Chemical maceration and slide preparations were made by Global Geolab Ltd., Medicine Hat, Alberta, Canada (acid maceration in hydrochloric and hydrofluoric acid, heavy liquid separation, residue screened in 10- μ m mesh and strew-mounted in Elvacite, no coarser filter used). Recovery of palynomorphs from all three collections was excellent. Three hundred grains were counted to obtain an estimate of relative abundance of palynomorphs, using a

Nikon Eclipse 80i compound microscope. An additional approximately 1700 grains were scanned for additional rare taxa. High-resolution images were taken with the Nikon Eclipse 80i microscope, using differential interference contrast (DIC), a Plan Apo 63 \times oil objective, in combination with a Nikon DXM1200F camera, or with a Leica DM2500 microscope using DIC, a Plan Apo 63 \times oil objective, and a Nikon DS-Fi1 digital camera. Specimen locations were noted with an England Finder graticule. Extended depth-of-field (EDF) images were generated by using Photoshop CS 6 version 13.0. Results are presented as counts and as a proportion of the total sample (Table 6.2). Where known, palynomorphs were related to

TABLE 6.2 Taxa Recognized in a 300-Grain Count of Each of the Following Samples: USGS9999-1, NPL53178B-1, USNM40600-1

Taxon	Inferred Affinity
<i>Anapiculatisporites</i> sp. sensu Ravn 1986, p. 85	Polypodiidae
<i>Cadiospora magna</i> Kosanke 1950: p. 50, Plate 16, Fig. 1	<i>Sigillaria</i>
<i>Calamospora breviradiata</i> Kosanke 1950: p. 41, Plate 9, Fig. 4	Calamitaceae, Sphenophyllales
<i>Camptotriletes triangularis</i> Peppers 1970: p. 116, Plate 10, Figs. 1 and 2	Polypodiidae
<i>Columinisporites ovalis</i> Peppers 1964: p. 16, Plate 1, Figs. 11 and 12	Sphenophyllales
<i>Convolutispora</i> cf. <i>C. florida</i> Hoffmeister, Staplin and Malloy 1955: p. 384, Plate 38, Fig. 6	Polypodiidae
<i>Convolutispora mellita</i> Hoffmeister, Staplin and Malloy 1955: p. 384–385, Plate 38	Polypodiidae
<i>Crassispora kosankei</i> (Potonie and Kremp 1955) Bhardwaj 1957 emend. Smith and Butterworth, 1967: p. 234, Plate 19, Figs. 2–4	<i>Sigillaria</i>
<i>Cyclogranisporites minutus</i> Bhardwaj 1957: emend. Ravn 1986: p. 31, Plate 3, Figs. 3 and 4	Marattiales
<i>Cyclogranisporites obliquus</i> (Kosanke 1950) Upshaw and Hedlund 1967: p. 150, Plate 2, Fig. 5	Marattiales
<i>Deltoidospora sphaerotriangula</i> (Loose 1932) Ravn, 1986: p. 23, Plate 1, Fig. 4	Polypodiidae
<i>Dictyomonolites</i> sp. sensu Ravn 1986, pp. 114–115	? Marattiales
<i>Endosporites globiformis</i> (Ibrahim 1932) Schopf, Wilson and Bentall 1944: p. 45	Isoetales: <i>Polysporia</i>
<i>Fabasporites pallidus</i> Sullivan 1964: Plate 61, Fig. 11	Probably Marattiales
<i>Granulatisporites</i> sp. sensu Ravn 1986, p. 27	Probably Polypodiopsida
<i>Laevigatosporites medius</i> Kosanke 1950: p. 29, Plate 16, Fig. 12	Sphenophyllales
<i>Laevigatosporites minor</i> Loose 1934: p. 158, Plate 7, Fig. 12	Sphenophyllales
<i>Leioaletes circularis</i> Ravn and Fitzgerald 1982: p. 150, Plate 12, Figs. 1–5	? Marattiales, ? Sphenophyllales, ? Equisetales
<i>Lophotriletes microsaeosus</i> sensu (Loose 1955) Potonié and Kremp 1955 sensu Ravn 1986: p. 36, Plate 4, Figs. 5 and 6	Polypodiidae
<i>Punctatisporites glaber</i> (Naumova 1956) Playford 1962: p. 576, Plate 78, Figs. 15 and 16	Polypodiopsida, ? Marattiales
<i>Punctatisporites</i> cf. <i>P. nudus</i> Artuez 1957 sensu Ravn 1986: 27, Plate 1, Fig. 17	Polypodiopsida, ? Marattiales
<i>Punctatisporites obesus</i> (Loose 1932) Potonié and Kremp 1955 sensu Ravn 1986: p. 27, Plate 2, Fig. 17	Sphenophyllales
<i>Punctatosporites</i> cf. <i>P. granifer</i> Potonié and Kremp 1956, p. 142, Plate 19, Fig. 442	? Marattiales
<i>Punctatosporites minutus</i> Ibrahim 1933 sensu Smith and Butterworth 1967, Plate 24, Figs. 8 and 9	Marattiales
<i>Raistrickia</i> cf. <i>R. aculeata</i> Kosanke 1950: p. 46, Plate 10, Fig. 9	Polypodiidae

Continued

TABLE 6.2 Taxa Recognized in a 300-Grain Count of Each of the Following Samples: USGS9999-1, NPL53178B-1, USNM40600-1—cont'd

Taxon	Inferred Affinity
<i>Raistrickia</i> cf. <i>R. protensa</i> Kosanke 1950: p. 46, Plate 11, Figs. 1–3	Polypodiidae
<i>Savitrisporites nux</i> (Butterworth and Williams 1958) Sullivan 1964 emend. Smith and Butterworth 1967: 223–225, Plate 15, Figs. 1–3	? Polypodiidae
<i>Triquirites</i> cf. <i>T. sculptilis</i> Balme 1952 <i>sensu</i> Smith and Butterworth 1967, Plate 12, Figs. 10–15	Polypodiidae: Gleicheniaceae
<i>Verrucosporites microtuberosus</i> (Loose 1932) Smith and Butterworth 1967: pp. 149–150, Plate 5, Figs. 9–11	Marattiales
<i>Verrucosporites verrucosus</i> (Ibrahim 1932) Ibrahim 1933 <i>sensu</i> Smith and Butterworth 1967: p. 154, Plate 5, Fig. 7 and 8	Polypodiidae: Zygotpteridales
Pollen/Prepollen	
<i>Alisporites</i> cf. <i>A. plicatus</i> Jizba 1962: p. 884, Plate 124, Figs. 51–53	? Seed fern
<i>Anguisporites intonsus</i> Wilson 1962: p. 12, Plate 1, Fig. 3	Unknown but probably a seed plant
<i>Cannanoropollis</i> cf. <i>C. janakii</i> Potonié and Sah: pp. 127–128, Plate 2, Figs. 15 and 16	Ferugliocladaeae (see text)
<i>Falcisporites</i> cf. <i>F. zapfei</i> (Potonié and Klaus 1954) Leschik 1956: p. 17, Plate 22, Fig. 7	? Seed fern
<i>Florinites mediapudens</i> (Loose 1936) Potonié and Kremp, 1956: p. 169, Plate 21, Figs. 468–471	Cordaitales
<i>Florinites millottii</i> Smith and Butterworth 1954, p. 760, Plate 26, Fig. 9	Cordaitales
<i>Florinites occultus</i> Habib 1966, p. 649, Plate 108, Figs. 4 and 5(A,B)	Cordaitales
<i>Illinites elegans</i> Kosanke 1950: p. 52, Plate 1, Figs. 1 and 2	? Voltziales
<i>Illinites unicus</i> Kosanke 1950: 51–52, Plate 1, Figs. 3 and 4; also Jizba 1962: 879, Plate 121, Figs. 1–14, as <i>Complexisporites polymorphus</i>	? Voltziales
<i>Illinites</i> cf. <i>I. talchirensis</i> (Lele and Makada 1972) Azcuy et al. 2002 in Cesari, Loinaze and Limirano 2013, p. 78, Fig. 4I–J	? Voltziales
<i>Klausipollenites</i> cf. <i>K. staplinii</i> Jansonius 1962: p. 56, Plate 12, Figs. 21–27	? Seed fern or conifer
<i>Paravesicaspora splendens</i> (Leschik 1955) Klaus 1963: pp. 330–331, Plate 18, Figs. 90 and 91	? Peltaspermales
<i>Platysaccus</i> cf. <i>P. papilionis</i> Potonié and Klaus 1959: p. 539, Plate 10, Fig. 12	Seed fern or conifer
<i>Platysaccus</i> cf. <i>P. saarensis</i> (Bhardwaj 1957) Jizba 1962: p. 885, Plate 124, Fig. 59–61	Seed fern or conifer
<i>Protohaploxylinus</i> sp. A	? Peltaspermales or ? Voltziales
<i>Potonieisporites novicus</i> Bhardwaj 1954 emend. Poort and Veld 1997: Fig. 1a–f	Voltziales
<i>Potonieisporites simplex</i> Wilson 1962: pp. 14–15, Plate 3, Figs. 1–3	Voltziales
<i>Schopfipollenites ellipsoides</i> (Ibrahim 1932) Potonié and Kremp 1954: pp. 180, Plate 19, Figs. 89–92, Plate 20, Fig. 107	Medullosaceae
<i>Striatoabietites richteri</i> (Klaus 1955) Hart 1964 <i>sensu</i> Jizba 1962: p. 880, Plate 122, Figs. 16–21, 25–30, as <i>Striatites richteri</i> (Klaus 1955) Jizba 1962	? Peltaspermales or ? Voltziales
<i>Strotersporites communis</i> Wilson 1962: pp. 18–19, Plate 2, Figs. 1–3	? Voltziales
<i>Tinnulisporites</i> cf. <i>T. microsaccus</i> Dempsey 1967: p. 115, Plate 1 Figs. F–N	Unknown, but seed plant
<i>Vesicaspora wilsonii</i> Schemel 1951: pp. 749–750, Figs. 1 and 3	Peltaspermales (? Autunia)
<i>Scheuringipollenites ovata</i> (Balme and Hennelly 1955) Hart 1964; in Balme and Hennelly 1955: p. 96, Plate 5, Figs. 49–52	? Peltaspermales
<i>Vesicaspora</i> sp. 'globose'	? Peltaspermales
<i>Vittatina costabilis</i> Wilson 1962: pp. 25–26, Plate 3, Fig. 12	Unknown, but seed plant
<i>Vittatina lata</i> Wilson 1962, p. 25, Plate 3, Fig. 11	Unknown, but seed plant
<i>Wilsonites</i> cf. <i>W. delicatus</i> (Kosanke 1950) Kosanke 1959; in Kosanke 1950: p. 54, Plate 14, Fig. 4, as 'Wilsonia'	? Peltaspermales

Page and figure citations refer to diagnosis and illustrations of basionym or combining author(s), except in cases of emendations or where another authority concept is followed '*sensu*' author. Inferred affinity for each taxon follows [Looy and Hotton 2014](#) and literature cited therein. Higher classification of pteridophytes follows that of the Pteridophyte Phylogeny Group I ([PPG I, 2016](#)). ? indicates uncertain but presumed affinity.

their parent plants or plant groups (per [Looy and Hotton, 2014](#), Table 1). Preservation of palynomorphs was excellent, so skewing of abundance due to differential preservation quality is likely not significant. The assemblages were relatively uniform in color, and relatively little damage from mechanical abrasion or chemical dissolution was observed, suggesting that most of the grains in the assemblage had not undergone major reworking or transport.

5. RESULTS

5.1 Taxonomic Composition of the Flora

The macrofossil taxonomic elements of the Sanzenbacher flora are reported in [Tabor et al. \(2013a, Table 1\)](#) and referred to briefly in [DiMichele et al. \(2006, Fig. 10\)](#) and [Montañez et al. \(2007, Supplementary Material, Table S6\)](#). These are, to our knowledge, the only reports of this flora or any element of it, in the literature. None of these were accompanied by illustrations of the plants. Next, we describe the macroflora and microflora.

5.1.1 Macroflora

The elements of the flora identified in the three collections are listed in [Table 6.1](#). Many of these taxonomic entities are represented by one or only a few specimens that, in many instances, are fragmentary. Consequently, identifications must be considered tentative in light of the preservational state of the material.

No lycopsids were identified in the macroflora. This is noteworthy given the sample size and that multiple samples were collected from the Sanzenbacher locality. Our observations and collections indicate that *Sigillaria brardii* is present, but uncommon, in Wolfcampian strata from the region. In addition, the presence of rare lycopsid spores suggests that populations were present locally.

Sphenopsids are represented by both calamitaleans ([Plate II](#)) and sphenophylls ([Plate III](#)). Calamitalean stems are rare to absent in the USNM and USGS collections but abundant in the WPA/NPL collection. In the latter, the specimens occur primarily in a poorly bedded siltstone layer in which they were abundant and overlapping ([Plate II, 1](#)); these axes may be rhizomes rather than aerial stems. Nodes were rarely observed, and no branch scars were noted ([Plate II, 2](#)). Three kinds of calamitalean foliage are present: *Annularia spicata* ([Plate II, 3](#)), *Annularia* cf. *carinata* ([Plate II, 5](#)), and *Asterophyllites equisetiformis* ([Plate II, 4](#)). Only *A. spicata* is abundant; it occurs only in the WPA/NPL collections in what we interpret to have been a single layer a few centimeters in thickness. Witte reported to Sellards (letter of March 19, 1941) that it “was found only near the base of the fossiliferous horizon...and is very plentiful.” Calamitalean reproductive remains occur only in

the WPA/NPL collection, as single specimens of relatively poorly preserved *Calamostachys* sp. ([Plate II, 6](#)) and *Palaeostachya* sp. ([Plate II, 7](#)). Three species of *Sphenophyllum*, all rare, are present in the collections. The most common, found in all three collections, are specimens, usually isolated leaves, attributable to either *Sphenophyllum verticillatum* ([Plate III, 1](#)) or *Sphenophyllum thonii* ([Plate III, 4](#)). These could be differentiated if preservation were good, particularly of leaf terminal margins; *S. thonii* is indicated unambiguously by the terminal fringe. *Sphenophyllum angustifolium* is found in the USGS and USNM collections, typified by its narrow, generally laterally projecting leaves and toothed terminal leaf margins ([Plate III, 2, 3](#)). A single fragmentary specimen of *Sphenophyllum oblongifolium* was identified in the USNM collection.

Ferns in the collection include both the remains of marattialean tree ferns ([Plate IV](#)) and groundcover ferns of likely filicalean affinities ([Plate V](#)). The taxonomy of marattialean tree-fern foliage is complex and all identifications here are provisional, based as they are on fragmentary material. [Cleal \(2015\)](#) suggested abandoning the commonly used name *Pecopteris* for sterile foliage (the type species is not a marattialean) and adopting instead the nomenclature applied to fertile foliage. Unfortunately, we cannot link most of the fragmentary sterile specimens confidently to reproductive forms; thus, while agreeing with Cleal’s proposal, we are constrained to continue using *Pecopteris*, although we use the term “marattialean foliage” wherever possible.

Marattialean foliage is far more abundant in the USNM collections than in the USGS or WPA/NPL collections. Most of the specimens could not be attributed to species due to inadequate preservation but were subdivided into groups based on pinnule shape and size and, where visible, venation patterns. We attribute a few of the specimens to the species *Pecopteris monyi* ([Plate IV, 1–3](#)) and *Pecopteris hemitelioides* ([Plate IV, 5](#)), with indeterminate forms that fall in between these two species in their characteristics ([Plate IV, 4](#)). A number of specimens had very small, closely spaced pinnules ([Plate IV, 6](#)); these are similar in some respects to *Pecopteris permica*. Charred remains of marattialean foliage ([Plate IV, 7](#)) also were identified in all the collections, suggestive of minimal transport, given the delicacy of the construction of marattialean foliage and the brittle nature of charcoal. The most common fertile remains bear round synangia, attributable to *Asterotheca* ([Plate IV, 8, 9](#)); these are most abundant in the USNM collections and have an elongate, narrow, pinnule shape, similar to *P. hemitelioides*. A few poorly preserved specimens have what appear to be ovoid synangia; we attribute these to cf. *Danaeites*.

Small fern remains are generally uncommon in all three collections, occurring most abundantly in the USNM suite. This may reflect the small size and adherent leaves of these

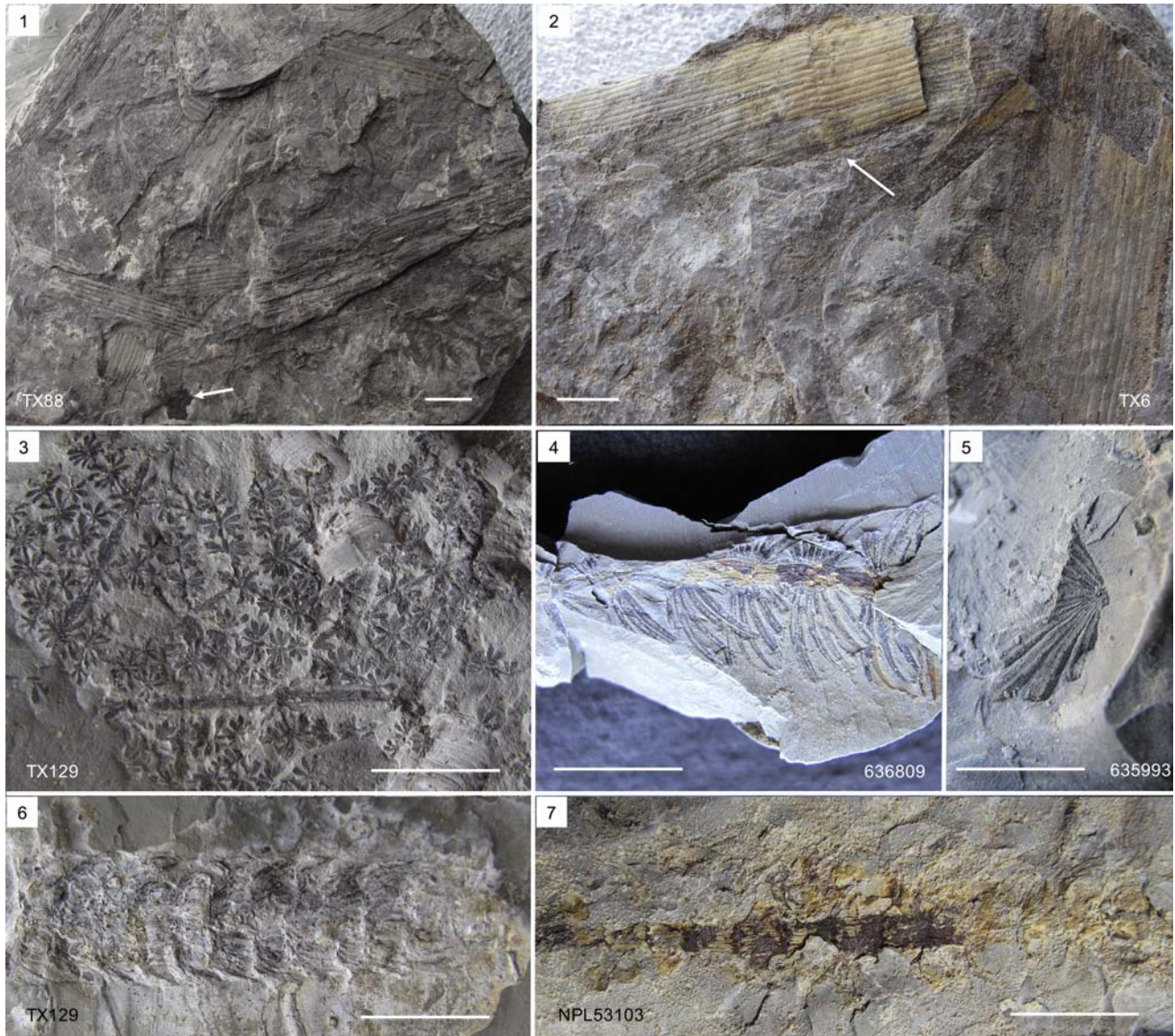


PLATE II Calamitaleans. (1) Overlapping calamitalean axes in hackley textured siltstone; arrow points to piece of charcoal, NPL TX88. (2) Calamitalean axes, one with node (arrow), NPL TX6. (3) *Annularia spicata*, NPL TX129. (4) *Asterophyllites equisetiformis*, USNM 636809. (5) *Annularia* cf. *carinata*, USNM 635993. (6) *Calamostachys* sp., NPL TX129. (7) *Palaeostachya* sp., NPL 53103. Scale bars = 1 cm.

small plants (Scheihing, 1980). Specimens we believe to be identifiable include *Oligocarpia gutbieri* (Plate V, 1) or *Oligocarpia* cf. *gutbieri* (Plate V, 2), *Sphenopteris biturica* (Plate V, 3), cf. *Nemejcopteris feminaeformis*, and cf. *Senftenbergia plumosa*. We attribute most specimens simply to *Sphenopteris* indet., with some notation of pinnule shape (e.g., Plate V, 4). As with marattialean foliage, delicate small fern remains were sometimes found preserved as charcoal (Plate V, 5).

Medullosan pteridosperms are quantitatively significant elements in all three collections. Two taxa are common to all three: *Neurodopteris auriculata* (Plate VI, 1, 2) and *Odontopteris subcrenulata* (Plate VI, 5, 6). Both species

are common in Late Pennsylvanian and early Permian assemblages of Euramerica. Four morphotypes were identified from single specimens. A single pinnule occurs in the USNM collection with neuropterid shape and with ultimate-vein reticulations in the apical region (Plate VI, 3, 4); similar rare, isolated pinnules were found in Upper Pennsylvanian strata of New Mexico, and tentatively identified as *Reticulopteris* (DiMichele et al., 2017). A single specimen with odontopterid pinnule shape, venation, and widely spaced ultimate veins was found in the WPA/NPL collections; we identify this tentatively as *Odontopteris schlotheimii* (Plate VI, 7). Two specimens with foliage of the *Eusphenopteris*-type occur in the USGS collection.

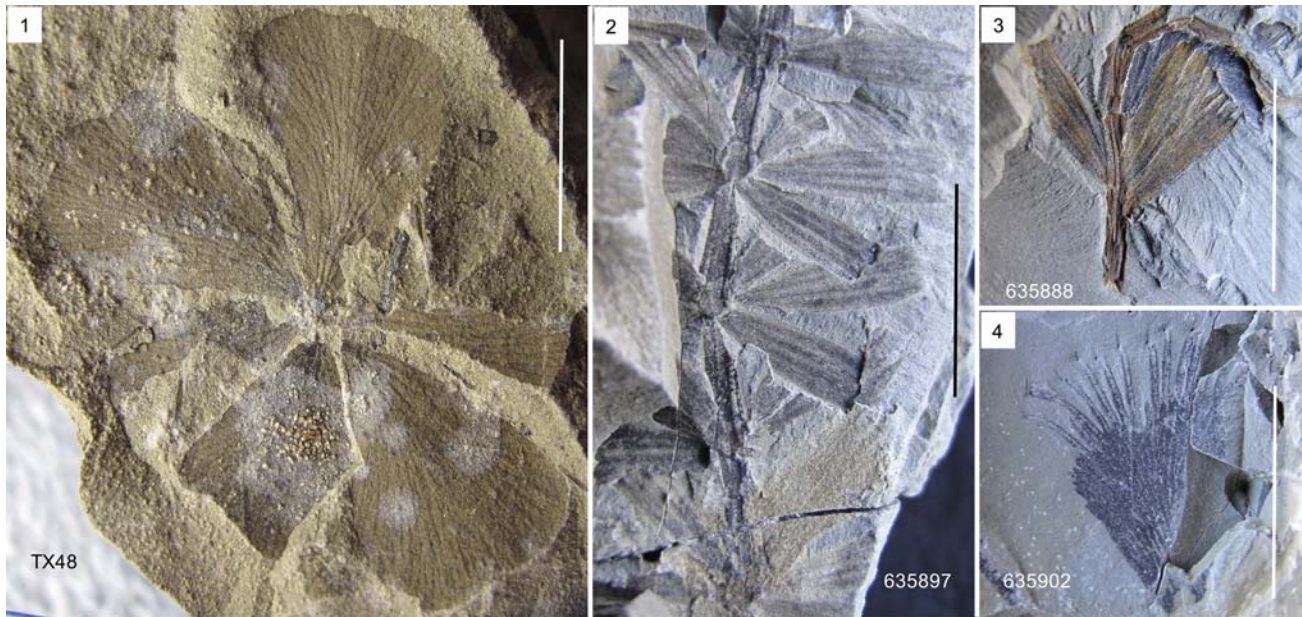


PLATE III *Sphenophyllum*. (1) *S. verticillatum*, NPL TX48. (2) *S. angustifolium*, USNM 635897. (3) *S. angustifolium*, USNM 635888, USNM locality 40600. (4) *S. thonii*, USNM 635902. Scale bars = 1 cm. (Note added in proof: Specimens identified as *Sphenophyllum verticillatum* are more likely *S. miravallis* Vetter).

One is similar to, and may actually be, *Odontopteris subcrenulata*; however, the pinnae are short and the pinnules show a certain degree of marginal lobing more typical of *Eusphenopteris* (Plate VI, 8). The other specimen is much larger, has three lobed pinnules (or short, trifoliate pinnae), and is similar to the much older, Atokan (Duckmantian-Bolsovian) species *E. trifoliolata* (Plate VI, 9). Among the WPA/NPL collections were three highly distinctive *Remia pinnatifida* specimens, including reproductive structures and sterile foliage in attachment (Plates VI, 10 and VII, 4). The affinities of this plant are uncertain, and it has been attributed both to the pteridosperms and to the ferns (Kerp et al., 1991); we treat it here as an *incertae sedis*, possible pteridosperm.

Dispersed, likely pteridospermous reproductive structures are common in all three collections. Specifically attributable to medullosan pteridosperms were a few small, ovoid, ribbed seeds, 1–2 cm in length, with evidence of a compression border, probably the remains of a sarcotesta; they are of the *Trigonocarpus* type (Plates VI, 13 and VII, 5). The most common kind of seeds in all the collections, but found abundantly in the USGS and USNM collections, were small, ovoid to nearly round seeds, 5–7 mm in length, with a thin compression border or lacking a compression border entirely. They were frequently found in masses (Plate VII, 3), as if they were produced and dispersed synchronously. Less commonly encountered, but also found in all three collections, and occurring in small masses, sometimes in charcoalified preservation, were small, distinctly horned seeds; the two horns emanate from the apical region of the nearly round seed body and diverge

nearly horizontally (Plate VI, 11, 12); perhaps these appendages facilitated wind dispersal. Associated with these seeds were small, four-parted whorls of bracts, which we assume to have been part of the same parent reproductive organ, although the original organization of this structure is not known. Somewhat like these, but distinct in a number of ways, are two presumed polleniferous reproductive structures, one each from the USGS and USNM collections (Plate VII, 1, 2). Interpretation of the structures is difficult, but they appear to consist of whorled clusters of 10–12 free, fusiform bracts, each cluster borne at the end of a short, <1-mm-long peduncle; three to four of these whorls are themselves born in a whorl or pseudowhorl at the end of a long, unadorned stalk. They are likely pteridospermous polleniferous organs.

There are several additional taxa or plant remains of uncertain or possible seed-plant affinities in the assemblages. *Sphenopteris germanica* (Plate VII, 6–8) is a major component of all three collections. This plant is either a seed plant or a fern and may be a small, centrally rooted groundcover species of open landscapes or understories (Ash and Tidwell, 1986; *Arnoldia kuesii* is likely a juvenile of *Sphenopteris germanica*). *Taeniopteris* is a form taxon that includes both ferns and seed plants. The few specimens of larger size, as were found in the Sanzenbacher collections (Plate VII, 9), are likely of seed-plant affinity. A single smaller specimen with relatively highly branched venation (Plate VII, 10) is similar to forms of *Taeniopteris* found in the later early Permian and may be a form of leaf associated with reproductive parts of the plant. One distinctive leaf occurs in the USGS collections with

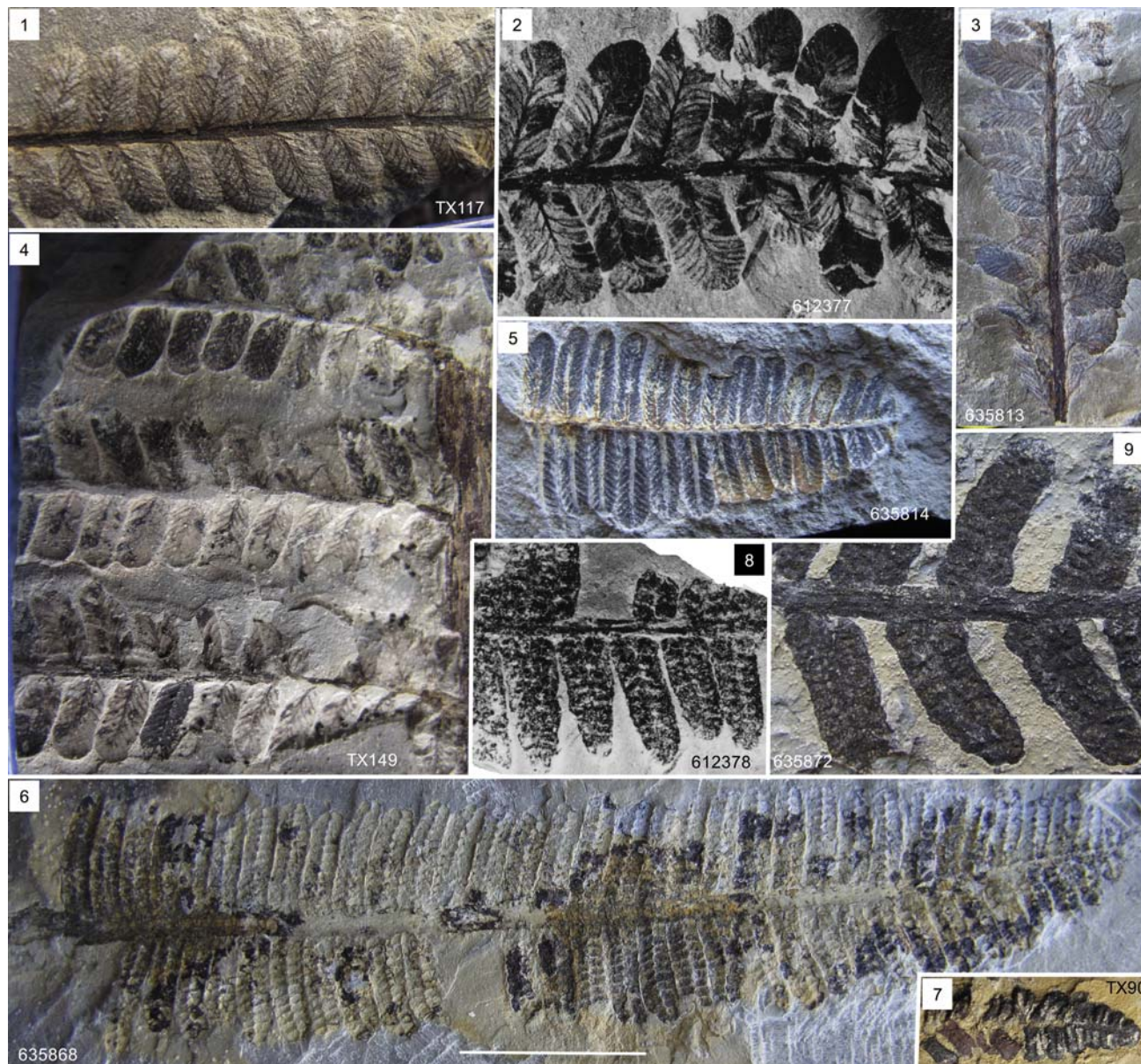


PLATE IV Marattialean fern foliage. (1) *Pecopteris monyi*, NPL TX117. (2) *P. monyi*, USNM 612377. (3) *P. monyi*, USNM 635813. (4) *P. monyi* or *P. hemitelioides*, NPL TX149. (5) *P. hemitelioides*, USNM 635814. (6) *P. cf. permica*, USNM 635868. (7) *Pecopteris* sp., charred preservation. NPL TX90. (8) Fertile marattialean foliage (*Asterotheca* sp.), USNM 612378. (9) Fertile marattialean foliage, USNM 635872. All specimens at same magnification; scale bar in image 6 = 1 cm.

elongate, ovoid shape, widely spaced parallel veins that converge toward the apex, and a scoop-shaped apical region (Plate VII, 11). We attribute this specimen to *Yuania* (Wang and Chaney, 2010), a noeggerathialean known from early through late Permian, in both China and Euramerica. This leaf is very similar to *Yuania taeniata*, known from the middle early Permian in north central Texas (described as *Russellites taeniata* by Mamay, 1968). Two distinctive but problematic specimens were found on the same hand-sample in the USGS collection (Plate VIII, 1, 2); they presumably are identical taxonomically. The specimens

have a deeply lobed, almost fringed margin. At the base, each lobe is narrow, tapers to a point and is supplied by a single vein. Near the apex, the lamina is mostly fused with a marginal fringe of pointed, narrow lobes. Each marginal extension is supplied by a single vein, but venation in the laminar segment appears to have a decurrent insertion on the midvein, to fork repeatedly near the base, and less commonly in the ascending veins, and to be, overall, sparse. These specimens compare most closely with more complete remains described as *Dioonitocarpidium* sp. by DiMichele et al. (2001) from rocks of latest early Permian

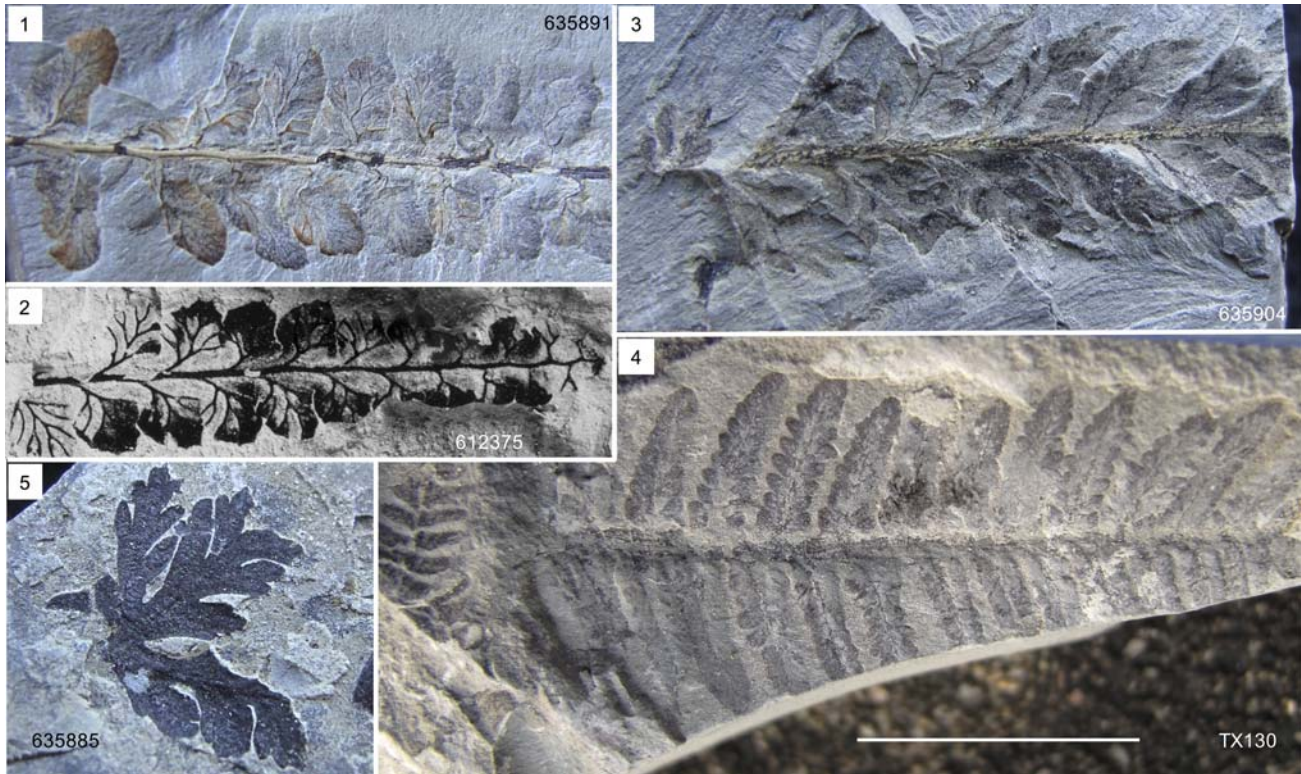


PLATE V Sphenopterid ferns. (1) *Oligocarpia gubieri*, USNM 635891. (2) *Oligocarpia* cf. *gubieri*, USNM 612375. (3) *Sphenopteris biturica*, USNM 635904. (4) *Sphenopteris* sp., NPL TX130. (5) *Sphenopteris* sp., charred preservation, USNM 635885. All specimens at same magnification; scale bar in image 4 = 1 cm.

(Kungurian) age, also in north central Texas. The specimen illustrated in [Plate VIII, 1](#), in particular, bears a striking resemblance to the specimen illustrated in Fig. 6 of the [DiMichele et al. \(2001\)](#) report, representing the lower part of this organ, suggested to be a cycad megasporophyll. If these are, indeed, *Dioonitocarpidium*, the age of first occurrence of this plant is pushed back an additional 25 million years, or so, the prior early Permian occurrence pushing that time of first appearance back from the Late Triassic. A single fragmentary specimen was found that we have tentatively attributed to cf. *Psymgophyllum* ([Plate VIII, 3](#)). It is approximately 13 cm in length and, were it fully preserved, could have been as much as 10 cm in width. Venation is dense, although relatively coarse.

All three assemblages are rich in callipterids, a group of peltasperms, likely derived from callistophytalean pteridosperms ([Meyen, 1987](#); [Naugolnykh and Kerp, 1996](#)). *Autunia conferta* ([Plate IX, 1](#)) was the most common callipterid, dominant or codominant in all three collections. The representative specimens were of typical form, with relatively short, rectangular pinnules, a sunken midvein with an arched lamina, and steep ultimate venation. Of lesser abundance, but present in all collections, is *Rhachiphyllum schenkii*, characterized by club-shaped pinnules of flat aspect that fuse in the distal parts of a pinna into large pinnules

([Plate IX, 2–4](#)); as with *Autunia*, the midvein may be offset in the pinnule, and the ultimate venation ascends steeply. A few specimens were found in all three collections that are attributable either to *Lodevia* sp. or *Autunia naumanii* ([Plate IX, 5](#)); in fragmentary preservation, small pieces of the sterile foliage of these species can appear similar.

The coniferophytes constitute the final group that occurs abundantly in one or more of the macrofloral assemblages. The most abundant of these are plagiotropic penultimate branches and ultimate shoots of walchian conifers, which occur in significant numbers in the USGS and WPA/NPL collections. Conifer taxonomy is challenging due to convergence in leaf form among different species and the difficulty in correlating dispersed vegetative remains with specific reproductive structures ([Visscher et al., 1986](#)). Cuticle can assist identifications, but cuticle preparations have proven difficult with most north central Texas plant remains. The most abundant walchian morphotype is characterized by relatively long, lax leaves ([Plate X, 1, 2](#)). Also present in small numbers are specimens of with short, densely packed leaves; these may be of two types, one with relatively broad leaves that have rounded apices ([Plate X, 3](#)) and one with triangular leaves that have acuminate tips ([Plate X, 4](#)). A single specimen of suspect *Dicranophyllum* was found in the WPA/NPL collection ([Plate X, 5](#)); this leaf

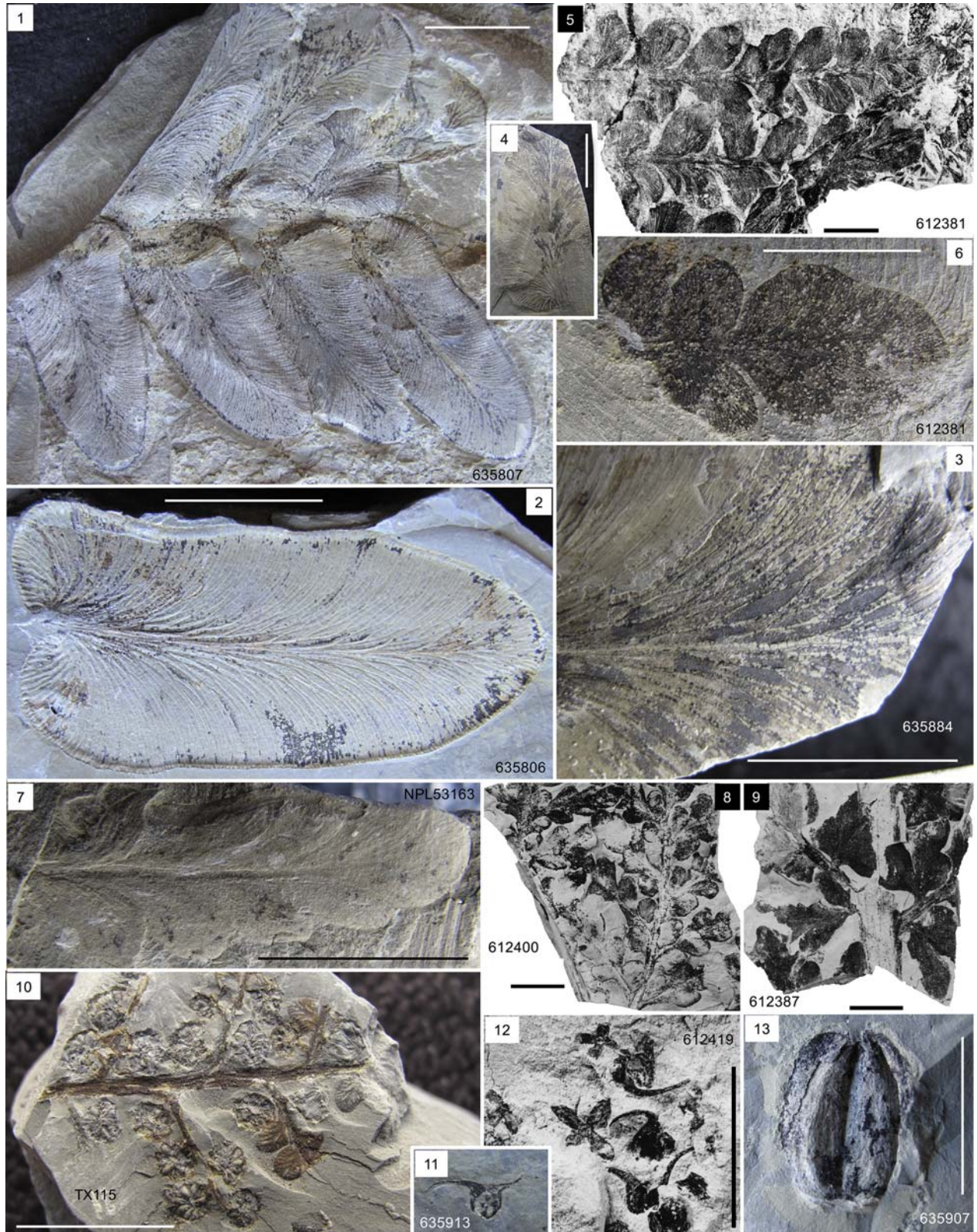


PLATE VI Pteridosperms. (1) *Neurodopteris auriculata*, USNM 635807. (2) *Neurodopteris auriculata*, USNM 635806. (3 and 4) UN neuropterid with reticulate venation. USNM 635884. (5) *Odontopteris subcrenulata*, USNM 612381. (6) *Odontopteris subcrenulata*, USNM 612381. (7) *Odontopteris* sp., possibly *O. schlothemii*, NPL 53163. (8) Unidentified pteridosperm, possibly *Eusphenopteris*, USNM 612400. (9) *Eusphenopteris* sp., USNM 612387. (10) *Remia pinnatifida*, NPL TX115. (11) Unidentified seed, USNM 635913 at same magnification as (12). (12) Unidentified seeds and associated bract whorls, USNM 612419. (13) *Trigonocarpus* sp. USNM 635907. Scale bars = 1 cm.

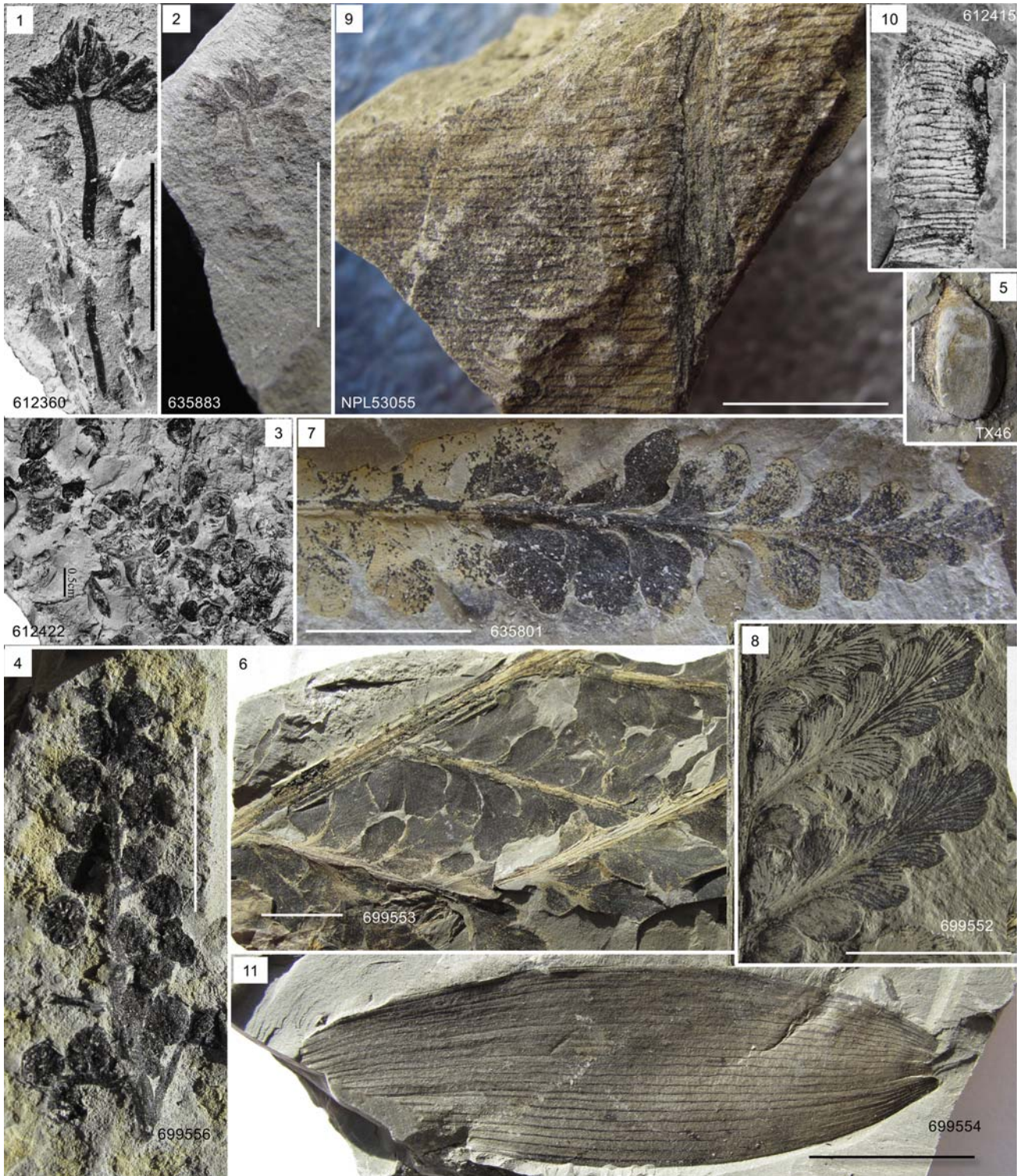


PLATE VII Reproductive structures and *incertae sedis*. (1) Unidentified reproductive organ, USNM 612360. (2) Unidentified reproductive organ, USNM 635883. (3) Seed mass, USNM 612422. (4) *Remia pinnatifida*, USNM 699556. (5) *Trigonocarpus* sp., NPL TX46. (6) *Sphenopteris germanica*, USNM 699553. (7) *Sphenopteris germanica*, USNM 635801. (8) *Sphenopteris germanica*; a rare specimen showing venation clearly, USNM 699552. (9) *Taeniopteris* sp., NPL 53055. (10) *Taeniopteris* sp., USNM 612415. (11) *Yuania* sp., similar to *Y. taeniata*, USNM 699554. Scale bars = 1 cm, except Fig. 3, scale bar = 0.5 cm.

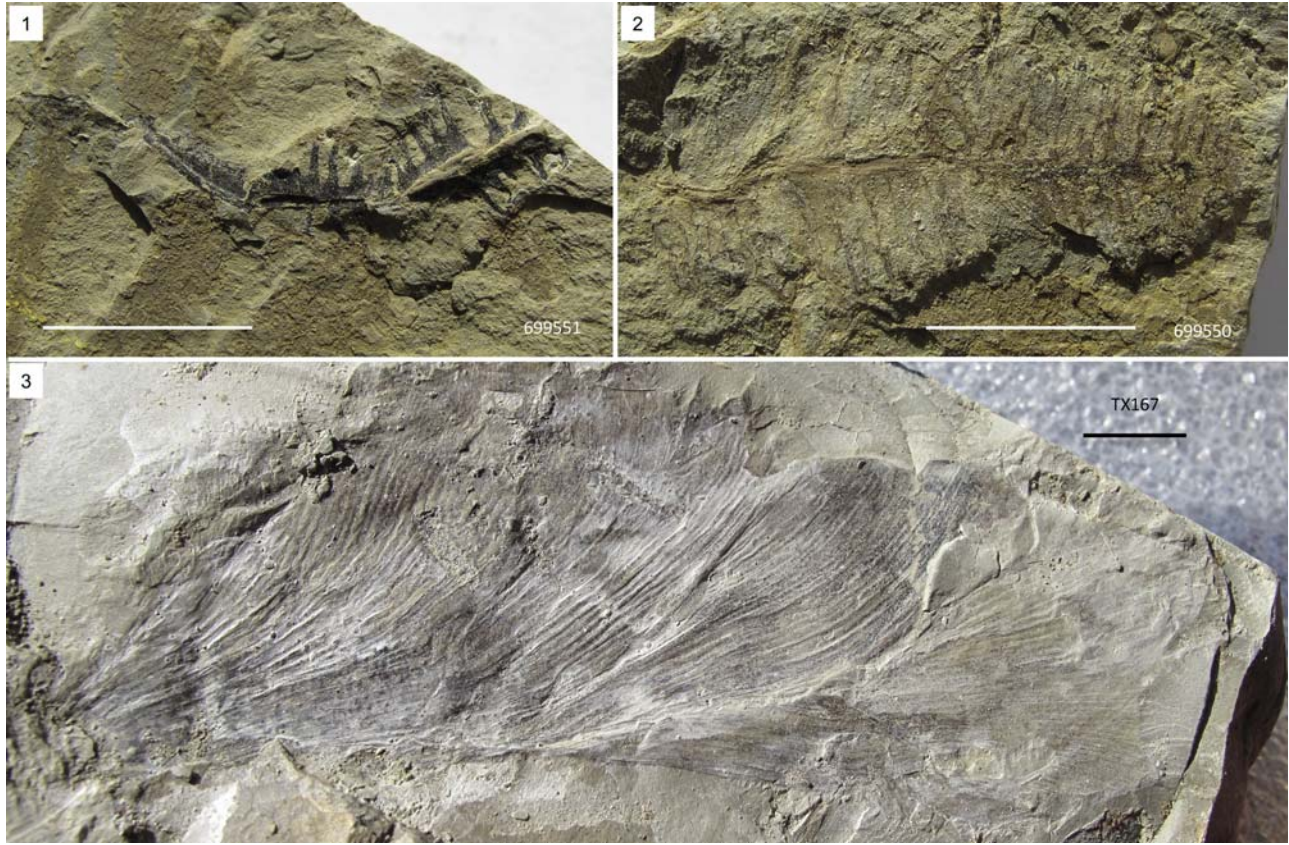


PLATE VIII Incertae sedis. (1) Problematic plant, cf. *Dioonitocarpidium* sp., base of leaf/sporophyll, USNM 699551. (2) Unidentified plant, cf. *Dioonitocarpidium* sp., distal portion of leaf/sporophyll, USNM 699550. (3) Cf. *Psymphyllum* sp., NPL TX167. Scale bars = 1 cm.

fragment was long, forked, and had the well-marked, double veins typical of the genus. Bracts typical of conifer cones were mostly of two types, a simple form (Plate X, 6) and of a forked type similar to *Gomphostrobus* sp. (Plate X, 7). A few specimens of small conifer cones were found, possibly polliniferous (Plate X, 8). The other major group of coniferophytes are the cordaitaleans. This group is frequently underestimated in fossil assemblages because the leaves can be difficult to differentiate from stems and leaf axes of pteridosperms and marattialean ferns, which are often longitudinally striated. Cordaitaleans are most abundant in the USNM collection, which also contains the fewest conifers. In that collection, remains include leaves (Plate X, 9) and rare specimens of the cordaitalean reproductive structure *Cordaitanthus* (Plate X, 10). A variety of winged seeds, usually attributed to either conifers or callipterids, occurs in all three collections; these could not be tied to specific plants, and the range of variation is illustrated in Plate X, 11–15.

5.1.2 Palynofloral Composition

The Sanzenbacher palynoflora is dominated by pteridosperm pollen with subdominant conifers. Typical wetland species are uncommon. Select elements are illustrated in

Plate XI. Table 6.2 summarizes the main palynomorphs and their affinities with major plant groups. The morphotaxon *Vesicaspora* is by far the most abundant pollen type in all three samples. Some forms correspond to *Vesicaspora wilsonii* (Plate XI, 12), some to an unnamed “globose form” (Plate XI, 13), and others to *Vesicaspora ovata* (*Scheuringpollenites ovatus*) or have no clear species affinity. Continuous variation among these forms renders it difficult to break them into distinct species. Although *V. wilsonii* was produced by members of the Pennsylvanian family Callistophytaceae (Millay and Taylor, 1979), these Permian forms probably represent peltasperms, quite likely *Autunia*. *Vesicaspora* and *Falcisporites/Alisporites* are associated with Permian and Triassic peltasperms (see review in Zavialova and Van Konijnenburg-van Cittert, 2011). Subdominants include the peltasperm *Wilsonites* (Plate XI, 14), representing at least in part *Sphenopteris germanica* (Remy and Rettschlag, 1954). Also subdominant is the problematic taxon *Anguisporites intonsus* (Plate XI, 10). Although originally described as a trilete spore, its protosaccate exine more closely resembles seed plant prepollen, and we treat it here as such, following Ravn (1986). Conifer prepollen (Plate XI, 20) is relatively uncommon but persistent. At least three morphospecies are recognized



PLATE IX Callipterids. (1) *Autumia conferta*, USNM 536561. (2) *Rhachiphyllum schenkii*, USNM 612390. (3) *Rhachiphyllum schenkii*, USNM 612396. (4) *Rhachiphyllum schenkii*, USNM 612392. (5) *Cf. Lodevia* sp., USNM 635866. Scale bars = 1 cm.

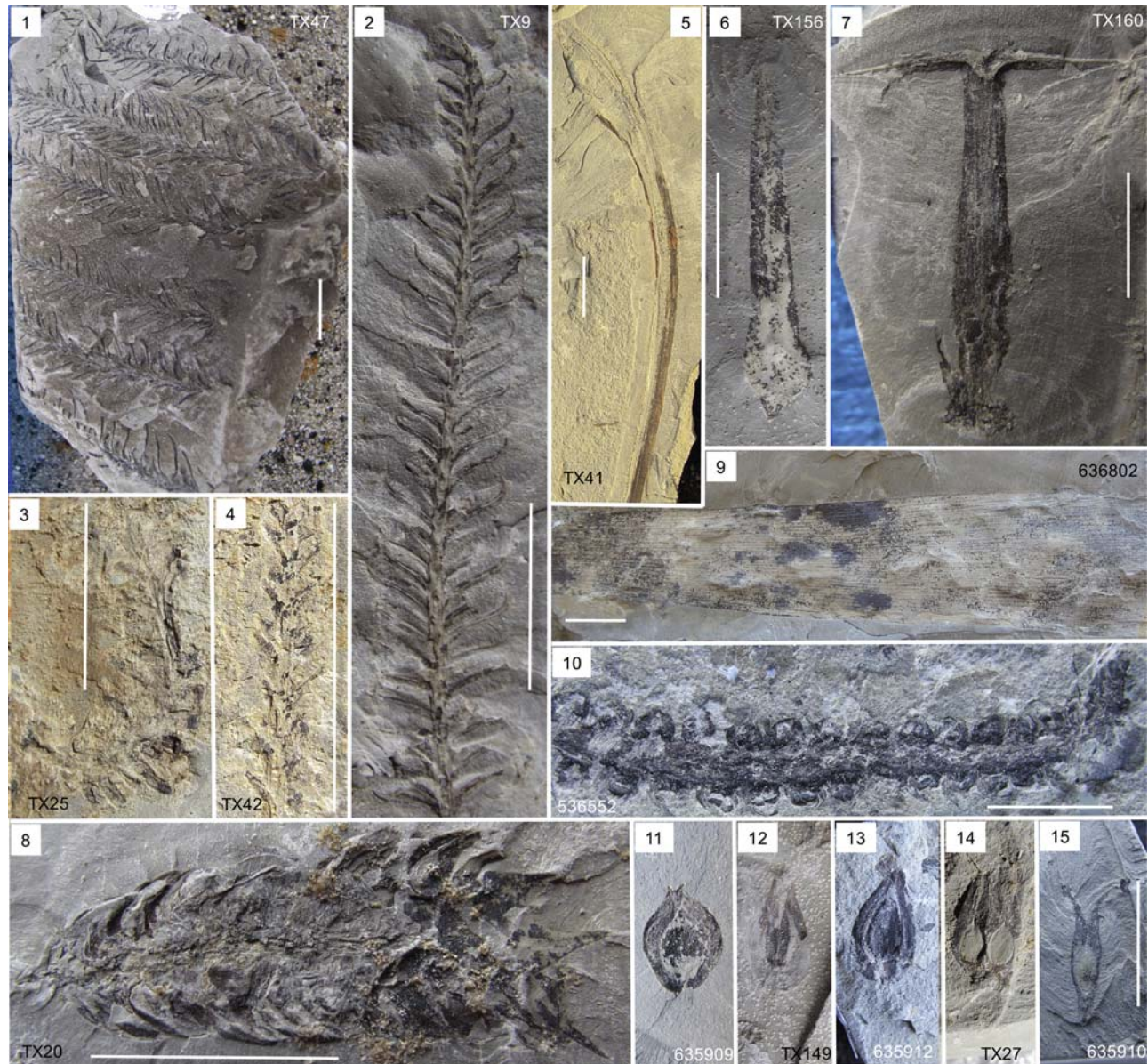


PLATE X Coniferophytes. (1) *Walchia* sp., NPL TX47. (2) *Walchia* sp., NPL TX9. (3) *Walchia* sp., NPL TX25. (4) *Walchia* sp., NPL TX42. (5) *Dicranophyllum* sp., NPL TX41. (6) Conifer cone bract, NPL TX156. (7) Conifer cone bract *Gomphostrobus bifidus*, NPL TX160. (8) Conifer cone, probably polleniferous, NPL TX20. (9) *Cordaites* sp., USNM 636802. (10) *Cordaitanthus* sp., USNM 536552. (11–15) Seeds of various forms with wings or horns that suggest affinities with coniferophytes or callipterids; all same magnification, scale bar in image 15. (11) USNM 635909. (12) NPL TX149. (13) USNM 635912. (14) NPL TX27. (15) USNM 635910. Scale bars = 1 cm.

(*Potonieisporites novicus*, *Potonieisporites bhardwajii*, *Potonieisporites simplex*), but we consider the morphological criteria used to separate those species to be of dubious taxonomic value and therefore made no attempt to separate them in pollen counts.

Other elements in the palynoflora are relatively uncommon. Most notable are probable spores of Marattiales (Plate XI, 5), as well as many other spore morphotypes not reflected in the macrofossil record, probably representing herbaceous ferns (Plate X, 6–9). Cordaitalean prepollen

(Plate XI, 17), lycopsid microspores (*Crassispora*, *Cadiospora* [Plate XI, 1, 2], and *Endosporites*), and sphenopsis spores (Plate XI, 3, 4) are relatively rare, matching their rarity in the macrofossil assemblages. Non-taeniate bisaccate pollen is also relatively rare. Taeniate forms (*Striatoabieites*, *Vittatina*, *Protohaploxylinus*) (Plate XI, 15, 16) are uncommon. They are believed to represent dryland gymnosperms, although their precise affinities are unknown in the Euramerican realm; they become abundant and diverse in the Permian. Pollen of medullosan pteridosperms,

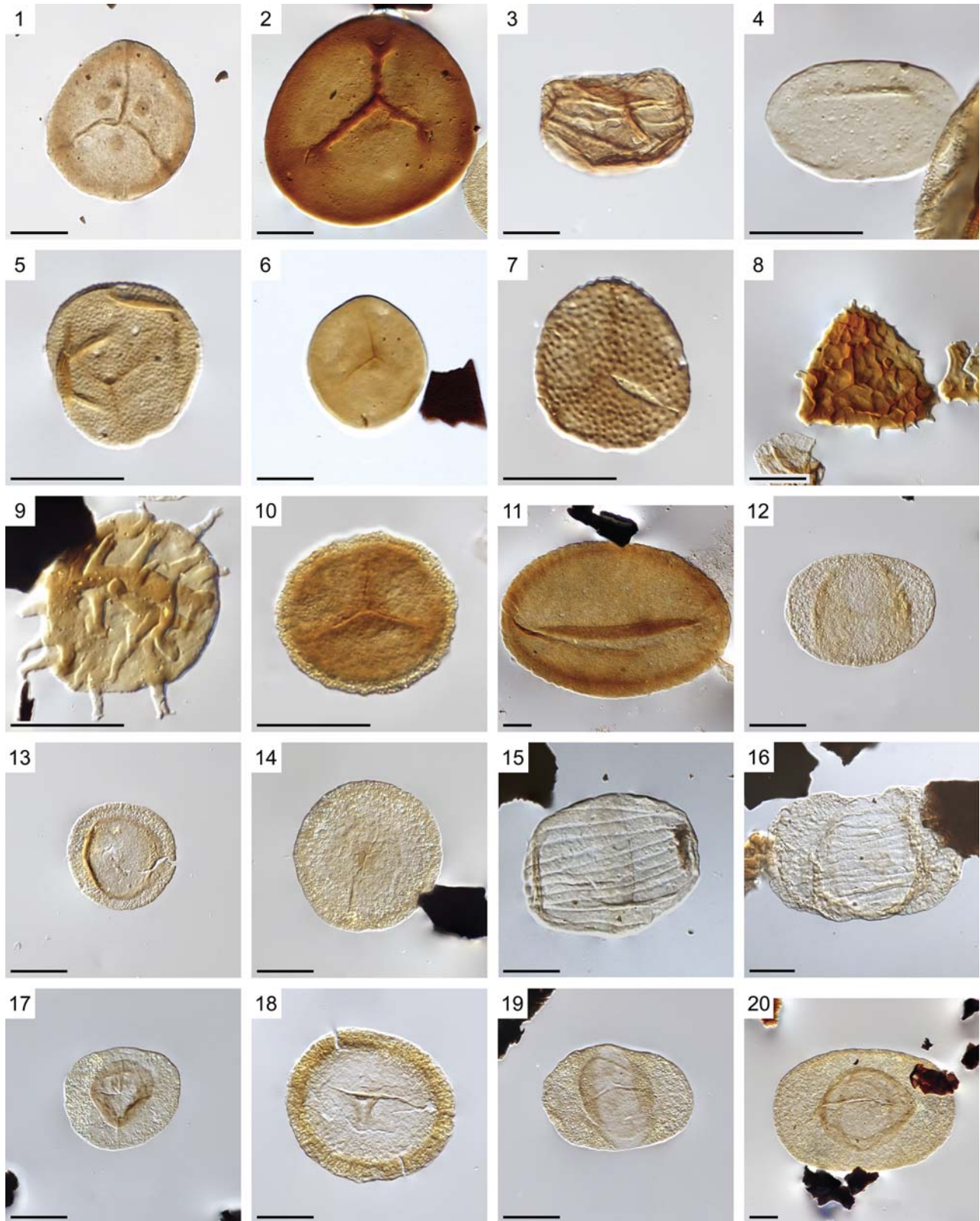


PLATE XI Palynomorphs. Specimen names are followed by locality number (if USGS or USNM; no locality number is given for NPL), slide number and England Finder graticule coordinates. (1) *Crassispora kosankei* (USGS 9999, slide 1, R50-1). (2) *Cadiospora magna* (NPL531778B-1, G32-3). (3) *Columnisporites ovalis* (USGS 9999, slide 1, F59). (4) *Laevigatosporites medius* (USNM 40600, slide 1, V19-2). (5) *Cyclogranisporites minutus* (USNM 40600, slide 1, J19-3). (6) *Punctatisporites* cf. *P. nudus* (USGS 9999, slide 1, O56-4). (7) *Anapiculatisporites* sp. (NPL53178B-1, G18-4). (8) *Triquitrites* cf. *T. sculptilis* (USNM 40600, slide 1, K19). (9) *Raistrickia protensa* (NPL53178B-1, K19-1). (10) *Anguisporites intonsus* (USNM 40600, slide 1, T19-1). (11) *Schopfipollenites ellipsoides* (NPL53178A-1, R25-3). (12) *Vesicaspora* cf. *V. wilsonii* (NPL53178B-1, V22). (13) *Vesicaspora* sp. "globose" (NPL53178B-1, V19). (14) *Wilsonites* cf. *W. delicatus* (NPL53178B-1, L20). (15) *Vittatina costabilis* (USGS 9999, slide 1, M52-4). (16) *Striatoabietites richteri* (USGS 9999, slide 1, N61-3). (17) *Florinites mediapudens* (NPL53178B-1, U21). (18) *Cannanoropollis* cf. *C. janaki* (USNM 40600, slide 1, Q21-1). (19) *Illinites unicus* (USNM 40600, slide 1, C18-2). (20) *Potonieisporites novicus* (NPL53178B-1, G20-1). Scale bars = 20 μ m.

Schopfipollenites, is rare but present in all three collections. Medullosan pre-pollen is usually rare in dispersed palynofloras. It is unusually large, up to 500 μm in length (Taylor, 1978), and consequently has a much faster settling velocity in air compared with wind-dispersed palynomorphs, restricting its area of dispersal (Schwendemann et al., 2007). Large size and low pollen production are also probably correlated; it also likely renders grains more susceptible to fragmentation during transport, deposition, and preparation (significantly, grains in the Sanzenbacher flora tend to be whole).

One unexpected note is the presence of *Cannanoropollis* (Plate XI, 18) in the palynoflora. This pollen type characterizes Gondwanan palynofloras and is associated with the southern hemisphere conifer family Ferugioladaceae (Archangelsky and Cuneo, 1987). Nonetheless, it is common enough in the Sanzenbacher flora to make it difficult to dismiss as a waif. The apparent presence of *Cannanoropollis* in the Sanzenbacher flora points up a shortcoming of palynology: dispersed spores and pollen exhibit considerable homoplasy because they possess a relatively small character set. Therefore, it is possible that these specimens do not represent Ferugioladaceae but instead another, perhaps unrelated, group.

5.2 Quantitative Composition of the Flora

5.2.1 Macroflora Quantitative Composition

Forty-four taxonomic entities are recognized among the three macrofloral collections (Table 6.1); 38 of these may be considered, broadly, to be proxies for biological species or species groups (Table 6.3). Descriptions of dominance-diversity patterns are based on this redacted group of taxa; reproductive organs were excluded from the overall taxonomic count if they duplicated a more abundant vegetative organ. On the basis of the redacted taxonomic list (Table 6.3), one species, *Autunia conferta*, occurs at an average frequency of >20%. Five taxa, *Walchia* sp., *Sphenopteris germanica*, marattialean foliage, *Neurodontopteris auriculata*, and calamitalean stem remains occur at an average frequency between 5% and 10%. The remainder of the assemblage occurs, on average, at <5% frequency, although specific taxa may be >5% in one collection. Twelve taxa occurred once, which accounts for approximately 32% of the biological-species proxy taxa composing the flora.

There is considerable variability in abundance among the three collections, including among those taxa with the highest average frequencies of occurrence. This variability can be gauged with the coefficient of variation (CV [the standard deviation/mean]) of the mean of each taxon's frequency of occurrence. We have multiplied the CV by 10 in Table 6.3 to make differences more obvious; lower CVs

mean lower variance. CVs range from 2.1 to 17.3. Only five of 38 taxa in the assemblage have CVs <5, and only two of these, *Autunia conferta* and *Sphenopteris germanica*, are among the six taxa with average frequencies >5%. Twelve taxa are present in all three collections, including five of the six with the highest average frequencies. Ten occur in two collections, and 15 taxa, or 39.5% of the biological-species proxy taxa in the flora, occur in only one collection.

The three macrofloral samples have similar dominance-diversity distributions (Fig. 6.2). These similarities include their patterns of taxonomic richness, as well as the abundance distribution of that richness, by taxonomic group. However, because of the fragmentation of plant remains, the quadrat method presents some challenges in computing relative abundances in those cases where different organs of the same plant are tabulated separately. Because the different kinds of organs occurred on many of the same quadrats at Sanzenbacher, their frequencies cannot be combined confidently into a single, common abundance estimate, and they are presented separately. There are two groups with this problem in the current analysis. The first is the calamitalean sphenopsids. The species richness of these plants is best resolved by their foliage, which is distinctive, and three foliage species occur at Sanzenbacher. Calamitalean stem remains can be more common than foliage, however, as they are in one of the Sanzenbacher collections (NPL), and these are less diverse, often difficult to separate taxonomically when fragmentary, and thus generally cannot be united confidently with particular types of foliage. Thus, stems and foliar remains are tabulated separately. Similarity in the frequencies of the stems and foliage in the NPL collections points to an abundance in the range of 11%–16% as a reasonable estimate. A similar problem is presented by marattialean fern foliage, which occurs as both sterile and fertile remains that can be difficult to correlate, especially if the fertile remains are not particularly well preserved. This is illustrated by the USNM collection in which fertile and sterile marattialean foliage are both present at >5%, suggesting that the general abundance of these plants in the collection is within this range. Fertile and sterile marattialean remains present independent, complementary estimates of the frequency of occurrence rather than composing a single, additive occurrence.

All three macrofloral collections have similar patterns of richness, from 22 to 25 species-proxy taxa. In each, the great majority of taxa, approximately 80% in each collection, are rare, occurring on <5% of the quadrats counted, with the largest single category being $n = 1$ occurrence. Two of the three dominance-diversity curves (USGS, USNM) show a basic hollow-curve distribution of dominance, with a single species occurring on approximately 20%–30% of the quadrats, followed, in descending order, by three or four additional species with >5% frequency of

TABLE 6.3 Plant Taxa Representing Proxy Biological Species or Groups Composing the Sanzenbacher Macroflora

	USGS 9999	USNM 40600	TXNPL 1161	Avg Freq	CV × 10
<i>Autunia conferta</i>	30.3	22.5	18.0	23.6	2.6
<i>Walchia</i> sp.	6.4	0.3	19.3	8.7	11.2
<i>Sphenopteris germanica</i>	10.2	5.5	7.0	7.6	3.2
<i>Pecopteris</i> spp.	2.5	15.8	2.0	6.8	11.5
<i>Neurodopteris auriculata</i>	3.8	11.3	3.7	6.2	6.9
<i>Calamites</i> stems	0.0	0.3	15.7	5.3	16.8
<i>Annularia spicata</i>	0.0	0.0	11.0	3.7	17.3
<i>Odontopteris subcrenulata</i>	7.3	1.0	2.0	3.4	10.0
<i>Rhachiphyllum schenkii</i>	3.5	2.3	4.0	3.3	2.8
<i>Cordaites</i> sp.	1.3	4.8	1.0	2.4	9.0
cf. <i>Lodevia</i>	2.2	2.6	1.7	2.2	2.1
<i>Sphenophyllum thonii/verticillatum</i>	2.2	1.0	1.3	1.5	4.3
cf. <i>Sphenopteris</i> sp. 1	1.0	3.2	0.0	1.4	11.9
cf. <i>Oligocarpia</i> sp.	1.6	2.3	0.0	1.3	9.0
<i>Sphenophyllum</i> sp.	0.6	2.6	0.0	1.1	12.5
cf. <i>Danaeites</i> sp.	1.0	2.3	0.0	1.1	10.6
<i>Asterophyllites equisetiformis</i>	0.6	1.9	0.3	1.0	8.8
<i>Pecopteris hemitelioides</i>	0.3	0.3	2.0	0.9	11.0
cf. <i>Autunia conferta</i>	1.3	0.6	0.0	0.6	10.0
<i>Remia pinnatifida</i>	2.0	0.0	1.0	0.5	9.4
<i>Odontopteris</i> sp.	0.0	0.0	1.3	0.4	17.3
<i>Sphenopteris</i> sp.4	0.0	0.6	0.7	0.4	8.7
<i>Peltaspermum</i> sp.	0.6	0.6	0.0	0.4	8.7
<i>Taeniopteris</i> sp.	0.6	0.0	0.3	0.3	9.9
<i>Sphenopteris (Pecopteris)</i> sp.3	0.0	0.0	0.7	0.2	17.3
cf. <i>Sphenopteris</i> sp. 2	0.3	0.3	0.0	0.2	8.7
Cf. <i>Psymphyllum</i> sp.	0.0	0.0	0.3	0.1	17.3
<i>Dicranophyllum</i> sp.	0.0	0.0	0.3	0.1	17.3
<i>Pecopteris</i> cf. <i>monyii</i>	0.0	0.0	0.3	0.1	17.3
Neuropterid-reticulate venation	0.0	0.3	0.0	0.1	17.3
<i>Neuropteris</i> spp.	0.0	0.3	0.0	0.1	17.3
<i>Annularia carinata</i>	0.0	0.3	0.0	0.1	17.3
cf. <i>Nemejcopteris feminaeformis</i>	0.0	0.3	0.0	0.1	17.3
cf. <i>Eusphenopteris trifoliolata</i>	0.3	0.0	0.0	0.1	17.3
<i>Sphenophyllum oblongifolium</i>	0.3	0.0	0.0	0.1	17.3
cf. <i>Senftenbergia plumosa</i>	0.3	0.0	0.0	0.1	17.3
<i>Yuania</i> sp.	0.3	0.0	0.0	0.1	17.3
Unknown leaf	0.3	0.0	0.0	0.1	17.3

Numerical columns 1 to 3 represent the frequencies of quadrat occurrences in each individual collection. Numerical column 4 is the average frequency in the three collections. Numerical column 5 is the coefficient of variation (CV; standard deviation/mean, ×10) of each taxon in the three collections.

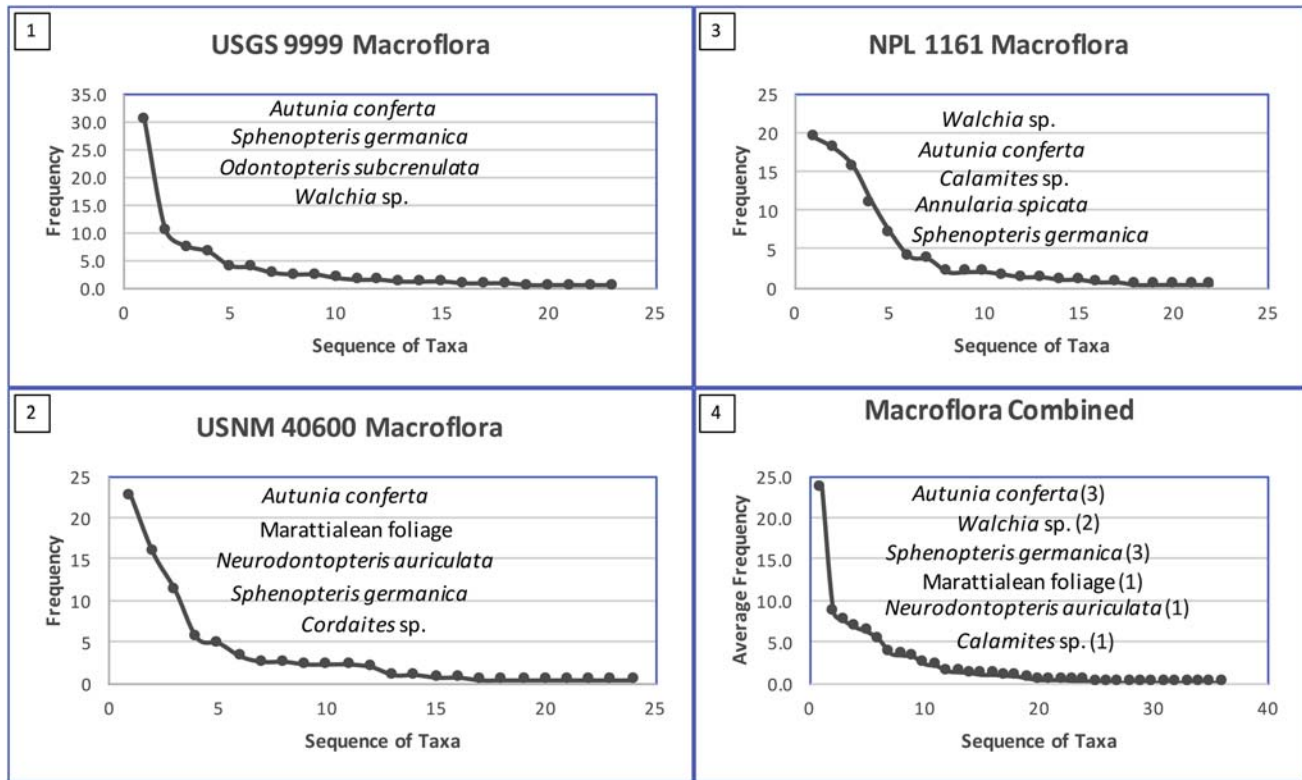


FIGURE 6.2 Dominance-diversity distribution of Sanzenbacher macrofloral collections. Taxa of >5% frequency are listed in order of abundance for each curve. (1) USGS 9999. (2) USNM 40600. (3) NPL 1161. (4) Average frequencies of the three individual collections.

occurrence. All remaining taxa occur at <5% frequency. The NPL collection differs sharply from the pattern of the other two. In it, the three most common taxa are of approximately equal frequency, at 15%–20%; this may be an analytical artefact that resulted from field sampling decisions, as discussed later.

On closer inspection, the differences in dominance distribution among the three collections become even more apparent. The USGS collection is strongly dominated by one species that occurs on >30% of the quadrats, with the following three subdominant taxa comprising 5%–11% frequency. The USNM collection is less monotypically dominated, with three species at >10% frequency and another two at approximately 5% or greater (treating the marattialean fern sterile and fertile foliage as independent frequency estimates of the same group). The NPL collections, in contrast to the others, have three taxa between approximately 16% and approximately 19%; only two additional taxa occur at >5% frequency, and one is calamitalean foliage, which duplicates the occurrence of stem remains at higher frequency.

When the taxonomic composition of these collections is considered, sharp differences emerge. *Autunia conferta* is the most consistently abundant, ranking first in two of the

three (USGS and USNM) and second in the third (NPL). Walchian conifers dominate the NPL collection, occur at slightly more than 5% of the USGS collection, and are a minor element of the USNM collection. *Sphenopteris germanica* occurs consistently in all three collections at >5% frequency. However, other significant taxa, those occurring at >5% average frequency, are present in only one assemblage: marattialean ferns, calamitalean sphenopoids, the pteridosperm species *Odontopteris subcrenulata* and *Neurodopteris auriculata*, and cordaitalean foliage.

5.2.2 Palynological Quantitative Composition

The quantitative composition of the palynological floras is summarized in Table 6.4 for the major groups and Table 6.5 for the detailed breakdown. As noted earlier, pteridosperms dominate the flora, accounting on average for 70%–80% of each assemblage. Most of this abundance is accounted for by species of *Vesicaspora*, which is present at approximately 30%–50% of each flora and probably can be attributed to the callipterids. *Wilsonites* spp., attributable to the peltasperms, and *Anguisporites intonsus*, of uncertain but likely seed plant affinity, also are common elements. Other relatively abundant elements include marattialean fern spores

TABLE 6.4 Major Palynological Groups, Palynomorph Counts, and Percentage of Total Count for Each of the Three Sanzenbacher Samples

Taxa	USGS 9999		USNM 40600		NPL 53178B	
	Group Count	Group %	Group Count	Group %	Group Count	Group %
Lycopsids	5	1.66	3	1.00	4	1.33
Sphenopsids	9	2.99	3	1.00	4	1.33
Marattiales	9	2.99	28	9.36	26	8.67
Other ferns	16	5.32	6	2.01	8	2.67
Cordaitaleans	5	1.66	7	2.34	5	1.67
Conifers	10	3.32	14	4.68	20	6.67
Pteridosperms	234	77.74	219	73.24	211	70.33
<i>Anguisporites intonsus</i>	37	12.29	50	16.72	19	6.33
<i>Vesicapora</i> spp.	144	47.84	95	31.77	145	48.33
<i>Wilsonites</i> spp.	29	9.63	60	20.07	18	6.00
Taeniaties	13	4.32	19	6.35	22	7.33
TOTAL	301	100	299	100	300	100

Pteridosperms are subdivided into the most abundant taxa. Taeniaties encompass ? Voltziales and Peltaspermales, not including *Vittatina*. Major groups in bold typeface; individual pteridosperm taxa in italics.

(~3%–9% abundance), conifer pollen (~3%–5% abundance), and taeniaties, pollen of uncertain affinity but thought to be from dryland plants (~4%–7% abundance).

Sample size emphasizes a distinct advantage of the palynofloral record. At least 64 distinct taxa occur in a mere 900-grain count. We project total diversity to exceed 100 taxa in the many thousands of grains available for observation. Most elements of the palynoflora are rare (Table 6.5). Thirty-eight taxa are present in only one of three collections, which is approximately 60% of the flora. Twenty-one of these single site occurrences are represented by a single grain, 33% of the flora. Many of these rare elements are thought to be derived from small ferns, but such patterns of rarity are found in all the major groups of plants.

6. DISCUSSION

Three principal points can be made about the Sanzenbacher flora. The first has to do with sampling of fossil floras: the three, separate Sanzenbacher collections, all made from the same strata at the same location, differ significantly. The second point addresses the relationship between macroflora and palynoflora: recent studies have found these two to differ in unexpected ways (Mander et al., 2010; Looy et al., 2014; Looy and Hotton, 2014). However, at Sanzenbacher, they appear to be broadly congruent. The final point is the similarity of the Sanzenbacher flora to floras of presumed similar age elsewhere in the United States and western

Europe, indicative of broad geographic ranges and extensive species populations across the Pangean equatorial region.

6.1 Collecting

The Sanzenbacher collections offer a rare opportunity to assess paleobotanical sampling biases. Although the three collections were made successively 20 and 30 years apart, there was overlap, and discussion, among the collectors. Witte, the original lead collector and supervisor of the 1940s WPA crew, directed Mamay to the site in 1961; Mamay returned to the site in 1991 with three of the authors, thus ensuring continuity of collecting location and strata. In addition, the three collections are of similar size, each approximately 250 hand-sample specimens.

We can speak directly to the 1991 USNM collection, which was made in the course of 1 day by four collectors who worked alongside each other. The collection is effectively unbiased: plants were relatively sparse in the matrix, and anything that looked even remotely identifiable was collected. Given what we know of Mamay's collecting methods elsewhere (the USNM holdings abound with his collections, and we had ample opportunity to discuss his methods in the field and in the museum collections), he retained everything regardless of completeness or perceived taxonomic significance. Thus, the 1961 USGS collection resembles the 1991 USNM collection in terms of lithofacies, the size range of specimens, and specimen quality.

TABLE 6.5 Palynoflora Quantitative Data From Each of the Three Sanzenbacher Collections

	USGS 9999-1	USNM 40600-1	NPL 53178B-1
Taxa	Count	Count	Count
Lycopsids			
<i>Crassispora kosankei</i>	2		
<i>Endosporites globiformis</i>	3		
<i>Cadiospora magna</i>		3	4
Sphenopsids			
<i>Calamospora</i> cf. <i>breviradiatus</i>		2	
<i>Columinisporites ovalis</i>	9	1	3
<i>Laevigatosporites minor</i>			1
Marattiales			
<i>Cyclogranisporites</i> cf. <i>minutus</i>		2	
<i>Cyclogranisporites obliquus</i>			1
<i>Cyclogranisporites</i> indet.		2	5
<i>Dictyomonolites</i> sp.			1
<i>Fabasporites</i> cf. <i>pallidus</i>		8	5
<i>Laevigatosporites medius</i>		4	4
<i>Punctatisporites glaber</i>		1	
<i>Punctatosporites</i> cf. <i>granifer</i>		2	
<i>Punctatisporites</i> cf. <i>minutus</i>		1	
<i>Punctatosporites minutus</i>		8	5
<i>Punctatisporites/Punctatosporites</i> indet.	6		4
<i>Punctatisporites obesus</i>	2		
<i>Punctatisporites</i> cf. <i>nudus</i>			1
<i>Leioaletes circularis</i>	1		
Other Ferns			
<i>Anapiculatasporites</i> sp. A (G18/4)			1
<i>Camptotriletes triangularis</i>	2		
<i>Convolutispora</i> cf. <i>florida</i>	1		
<i>Convolutispora mellita</i>	1		
<i>Convolutispora</i> sp. B (W19)		1	
<i>Convolutispora</i> sp. C (F19)			1
<i>Deltoidospora sphaerotriangula</i>	5		
<i>Granulatisporites</i> indet.			1
<i>Lophotriletes microsaetosus</i>	1		
<i>Raistrickia</i> cf. <i>aculeata</i>			1
<i>Raistrickia</i> cf. <i>protensa</i>			1
<i>Raistrickia</i> indet.	1	1	1
<i>Savitrissporites nux</i>	1		

TABLE 6.5 Palynoflora Quantitative Data From Each of the Three Sanzenbacher Collections—cont'd

	USGS 9999-1	USNM 40600-1	NPL 53178B-1
Taxa	Count	Count	Count
<i>Triquitrites sculptilis</i>	2	3	1
<i>Verrucosiporites verrucosus</i>	1		1
<i>Verrucosiporites cf. insuetus</i> (Q18/2)		1	
Cordaitaleans			
<i>Cannanoropollis cf. janakii</i>		1	1
<i>Florinites millottii</i>	2		
<i>Florinites mediapudens</i>		1	
<i>Florinites occultus</i>		1	
<i>Florinites</i> indet.	3	4	4
Conifers			
<i>Tinnulisporites microsaccus</i>	1		
<i>Potonieisporites</i> species complex	9	14	20
Seed Ferns			
<i>Alisporites cf. plicatus</i>			2
<i>Colatisporites decorus/Anguissporites intonsus</i>	37	50	19
<i>Falcisporites cf. stabilis</i>	2		
<i>Falcisporites cf. zapfei</i>	5	4	5
<i>Falcisporites</i> indet.	2		2
<i>Klausipollenites cf. staplinii</i>	3		
<i>Paravesicaspora splendens</i>	2		
<i>Platysaccus cf. papilionis</i>	4	4	
<i>Platysaccus cf. saarensis</i>	1	6	19
<i>Pityosporites</i> 'clepsydroid'	1		
<i>Schopfipollenites ellipsoideus</i>	4		1
<i>Vesicapora</i> species complex	144	95	145
<i>Wilsonites</i> species complex	29	60	18
Taeniates			
<i>Illinites unicus</i>	6	5	7
<i>Illinites cf. talchirensis</i>			1
<i>Kosankeisporites cf. elegans</i>	1		
<i>Protohaploxypinus</i> sp. A			4
<i>Striatoabieites richteri</i>	3	12	4
<i>Strotersporites communis</i>			1
<i>Vittatina costabilis</i>	1	1	3
<i>Vittatina lata</i>	1	1	2
TOTAL	299	300	300

Numbers represent the counts of each palynomorph taxon identified.

Aspects of the NPL collection, on the other hand, suggest a focus on particularly fossil-rich zones within the exposure, not accompanied by intentional taxonomic or specimen-size filtering on outcrop but, rather, a focus on productive layers at the expense of less productive zones. A very large number of specimens appear to be from a layer <10 cm thick that, on one surface and through several millimeters of sediment, preserves *Annularia spicata* in great abundance as branches with attached leaves. The obverse side of these specimens contains abundant calamitalean axes, many of which may have been subterranean rhizomes. This is suggested by the hackly texture of the lithological matrix around the calamitalean axes, possibly reflective of bioturbation by the axes themselves, and by associated roots. Another suite of WPA specimens contains abundant, large, branch fragments of *Walchia* sp., preserved in a coarser grained matrix than any found in the USGS or USNM collections. This horizon, too, appears to have been a focal point of collecting based on comments in Witte's report for period ending January 27, 1941 (see comments in Section 3) and on Mamay's 1961 field notes, which indicate an increase in siltstone and sandstone toward the top of the exposures. The result is the elevation of abundance of certain taxa in the NPL collection far beyond their abundances in the other two collections.

Another important consideration from this study is the effect of sample size. A 250-specimen sample is relatively typical of many early Permian plant collections, both USNM and USGS, held by the National Museum of Natural History. Our examination of the major NPL collections, in addition to those from Sanzenbacher made by Witte, suggests that this is true for most of them, too. When examined in terms of taxonomic richness, the three Sanzenbacher samples are similar: USGS = 25, USNM = 25, NPL = 22, of the total 38 proxy biological species entities. There are, however, 12 taxa or >30% of the flora among the three collections that occur only once. In addition, only *Autunia conferta* occurs at >10% frequency in all three collections, and only *A. conferta*, *Sphenopteris germanica*, and *Neurodopteris auriculata* have a CV ($\times 10$) of <10 among those species with average frequencies >5%. Only four taxa in the entire Sanzenbacher sample have a CV <5, which indicates great variation in abundance from one collection to the next. The message is relatively straightforward: the more collecting that is done, the more closely the samples will approximate the composition of the population – a statistical truism. The differences among the three Sanzenbacher collections, however, in both most frequent and rare components, suggests that the total collection of approximately 750 specimens is not yet large enough to capture either the full taxonomic richness of the population or more than the most basic aspects of the dominance-diversity structure.

Similar conclusions pertaining to sample size and perceived diversity can be drawn from large collections acquired elsewhere in the Permo-Carboniferous section of north central Texas. Examples include the underlying coal-bearing Markley Formation (DiMichele et al., 2006; Taber et al., 2013b), as well as most from the Leonardian Albany Group, and the Leonardian Clear Fork Formation (as defined by Nelson et al., 2013). Other late Paleozoic studies also have examined variation among collections made from the same bed at different, but nearby, sites or at different levels, thus preserving sedimentological context (e.g., Wnuk and Pfefferkorn, 1987; Wing and DiMichele, 1995; Pryor and Gastaldo, 2000; Bashforth et al., 2011, 2014, 2016). In general, these studies, all of wetland deposits, have encountered low species richness but also variation from one site to another, and often from one level to another in the same bed. This variation is likely a result of the combination of taphonomic processes such as transport and sorting but also of patchiness of plants on the landscape.

6.2 Macroflora-Palynoflora Comparison

Reconstruction of a paleoflora from dispersed palynomorphs is a complicated endeavor. The composition of a given palynological sample is affected by a host of factors, including vegetation structure, phenology, life habit, pollination mode, relative abundance, position on the landscape, and depositional environment. Palynological samples are almost always time-averaged, in that they represent multiple depositional events occurring over an unknown interval of time, in contrast to the “moment-in-time” snapshots of macrofloral assemblages. The task of reconstruction is further complicated by relatively poor taxonomic resolution of many palynomorph taxa, especially relative to macrofloral taxa. [For more detailed discussion of these limitations, see Looy and Hotton (2014).] Nevertheless, palynofloras have the distinct advantage of drawing from a larger source pool compared with macrofloras, and they provide a far larger sample size, which gives a more complete picture of the total vegetation.

The Sanzenbacher palynoflora is largely congruent with the macroflora: pteridosperms are dominant, conifers subdominant, and wetland species uncommon. The most common morphotaxon, *Vesicaspora*, representing peltasperms, closely matches the abundance of this group in the macroflora, particularly represented by the callipterids *Autunia conferta* and *Rhachiphyllum schenkii*. Among the subdominants, *Wilsonites*, ranging from approximately 6% to 20% of the palynoflora, is reflected in the common occurrence of *Sphenopteris germanica* in the macroflora, present at >5% frequency in all three collections. The problematic taxon *Anguisporites intonsus* (~6%–17% of the flora) cannot be compared well with the macroflora

due to its unknown affinities. Conifer prepollen, *Potoniaesporites*, represented by at least two morphospecies, is relatively uncommon but always present, ranging from 3% to almost 7% of the palynoflora. The greatest palynofloral and macrofloral abundance of walchian conifers occurs in the NPL 1161 samples. The abundance of calamitaleans in the NPL 1161 macroflora is not matched in the palynoflora, however, which may reflect the overrepresentation of this group in the macroflora, as discussed earlier.

Most elements of the palynoflora are uncommon. This generally includes probable spores of Marattiales, although these are most abundant and diverse in USNM 40600, which also has the most abundant marattialeans remains in the macroflora. Many of the rare spore morphotypes probably represent herbaceous ferns, which are similarly rare in the macroflora. A similar pattern can be found in the palynomorphs of cordaitaleans and lycopsids.

Incongruence between macrofloral and palynofloral assemblages does occur. For example, lycopsids are rare but persistent in the palynofloral assemblage (*Cadiospora*, *Crassispora* = *Sigillaria*; *Endosporites* = *Chaloneria*) but do not occur in the macroflora. *Schopfipollenites* (= *Medullosaceae*) is rare but present in all three assemblages, in contrast to the importance of medullosans in the macrofossil assemblages. The reasons for this latter mismatch are not clear but probably relate to the large size of medullosan prepollen, as noted earlier.

We did not attempt to characterize the entire flora for this analysis. Nonetheless, the notably higher diversity of the palynological taxa shows that the macroflora significantly underestimates total floral diversity. Rare palynomorphs likely represent plants rare on the landscape, those occupying interfluves, and those growing at different times (due to seasonal variation or short-term fluctuations in weather patterns). In contrast, herbaceous forms, which may be present in the palynoflora, are less likely to be represented in the macroflora compared with arborescent plants (e.g., Scheihing, 1980; Scheihing and Pfefferkorn, 1984).

6.3 Broader Context of the Sanzenbacher Flora

6.3.1 Palynoflora in Context

Pennsylvanian-Permian transition palynofloras of the Euramerican province display broadly similar patterns: relict Pennsylvanian wetland taxa in coals and conifer/seed-fern dominance in siliciclastic rocks. Palynofloral assemblages from the uppermost Pennsylvanian siliciclastic beds in Texas (Gupta, 1977; Pashuck and Gupta, 1979; Looy and Hotton, 2014) and from Pennsylvanian-Permian strata

of New Mexico (Utting et al., 2004; Utting and Lucas, 2010) are similar to the Sanzenbacher palynoflora. All contain significant quantities of *Potoniaesporites* spp., *Vesicaspora* spp., including the globose form, non-taeniate bisaccates (*Platysaccus* spp., *Pityosporites* spp.), and relatively small numbers of taeniate pollen (notably *Vittatina costabilis*, *Illinites unicus*, *Striatoabieites richteri*). The enigmatic palynomorph *Anguisporites intonsus* (sometimes reported as *Colatisporites decorus*) is also a common component of these floras. Marattialian spores (*Punctatisporites minutus*, *Punctatosporites* spp., *Cyclogranisporites aureus*, *Cyclogranisporites minutus*, *Laevigatosporites medius*, *Laevigatosporites ovatus*) are also present, as well as such herbaceous fern taxa as *Convolutisporites* spp., *Lophotriletes commisuralis*, *Raistrickia* spp. *Triquitrites sculptilis*, *Triquitrites* spp., and *Deltoidospora* (*Leiotriletes*) spp. These latter taxa are typical of Late Pennsylvanian assemblages and tend to be abundant in coals and subordinate in siliciclastics. Curiously, *Savitrissporites nux*, which otherwise disappears at the top of the Bolsovian, is described as common in the latest Pennsylvanian of Canyon del Cobre, New Mexico (Utting and Lucas, 2010). *Savitrissporites nux* also appears (rarely) in the Sanzenbacher palynoflora, where its occurrence could be dismissed as reworking, except for its possible correlation with the Canyon del Cobre assemblage.

Most of the palynological studies of Upper Pennsylvanian and lower Permian strata in Kansas, Arizona, and Oklahoma have not attempted to describe a complete assemblage but have rather focused on distinctive species (literature summarized in Lupia and Armitage, 2013). Nevertheless, many of the species described in these reports are a close match to those in the Sanzenbacher assemblage. Lupia and Armitage (2013) also present their own analysis of cores from north central Oklahoma ranging in age from Gzhelian through Kungurian (Virgilian through Leonardian). They do not present taxonomic details, but the overall pattern appears quite similar to that seen at Sanzenbacher. For example, monosaccate prepollen (*Potoniaesporites*) and nontaeniate pollen are moderately abundant, in contrast to taeniate pollen, which does not become abundant until significantly higher in the section, near the top of the Wolfcampian. We have noticed a similar pattern in samples from north central Texas (Hotton and Looy, unpublished data). A notable difference can be seen in the high percentage of trilete spores reported from the lower Asselian Grenola Formation (Lupia and Armitage, 2013). This could be due to sampling of a wet interval, or it could be because the authors treat *Anguisporites* as a trilete spore – without taxonomic and sedimentological details, the pattern is difficult to interpret.

The palynoflora of the Dunkard Group in the Central Appalachian Basin contains many of the typical Late

Pennsylvanian species described from Sanzenbacher and assemblages of similar age (Clendening, 1975; Eble et al., 2013). Taking into account variance in taxonomic concepts, up to half of the spore morphospecies may be in common between the two floras. However, unlike the Sanzenbacher palynoflora, pollen species such as *Potoniopsis* spp. and *Vesicaspora wilsonii* are extremely sporadic in the upper Dunkard (Greene Formation, of likely Asselian age [Tibert et al., 2011, 2013]) and taeniate forms do not appear until near the top of the Greene Formation. The disparity seems clearly controlled by facies: the Dunkard palynoflora was collected from coals, as noted by Eble et al. (2013), whereas the Pennsylvanian-Permian samples described here are derived from siliciclastic deposits. Further evidence of this coal–siliciclastic disparity comes from an uppermost Pennsylvanian coal from the Bursum Formation, New Mexico, dominated by typical Late Pennsylvanian wetland taxa (although also including significant amounts of *Vesicaspora*) (DiMichele et al., 2016), similar to a coal of similar age described from north central Texas (Looy and Hotton, 2014).

European palynological assemblages display a broadly similar pattern, although specific morphotaxa vary, exaggerated by disparities in palynological nomenclature. The *Vittatina costabilis* zone of Clayton et al. (1977), considered lower Autunian, is characterized by abundant *Potoniopsis* and *Vittatina costabilis* (although not their first appearance) and a pronounced decrease in abundance of typical wetland flora. Typical Permian forms (taeniate bisaccates) and virtual disappearance of monoete spores (= Marattiales and sphenopsids) mark the *Disaccites striatiti* Zone (Clayton et al., 1977), corresponding to the upper Autunian. Similar patterns are seen elsewhere across the Euramerican floral realm.

The Sanzenbacher palynofloral assemblage is most notable for being composed primarily of Late Pennsylvanian palynomorphs. Even so-called Permian elements occur, though rarely, in the Pennsylvanian. The paleobotanist A.T. Cross noted with regard to the Dunkard flora that it was “essentially a reduced remnant of late Pennsylvanian time with a few Permian precursors being introduced” (paraphrased from Clendening and Gillespie, 1972) — this comment can be applied to almost any known Pennsylvanian–Permian transition flora. As has been noted many times before, terrestrial vegetation in the Late Pennsylvanian–early Permian closely tracked climate conditions and is clearly controlled by depositional environment. The absence of novel plant macrofloral or palynofloral taxa at the Pennsylvanian–Permian boundary, here as well as globally, renders it very difficult to define the stratigraphic boundary in terrestrial strata using plant fossils.

6.3.2 Macroflora in Broader Context

The Sanzenbacher flora compares most closely to several floras from the lower part of the Cisuralian Epoch, the

Asselian, and lower Sakmarian Stages, which correlate with the lower Wolfcampian Stage in U.S. regional terminology. Comparability is strengthened by similarity of depositional environments, particularly the absence of coal beds or other lithofacies indicators of extensive wetlands. Three floras from central New Mexico and one from southwest Texas are discussed next, followed by comments on the lower Permian floras known from the eastern United States.

In the United States, the closest comparison, stratigraphically and paleoenvironmentally, is with the flora of Carrizo Arroyo (Tidwell and Ash, 2004), from the Red Tanks Member of the Bursum Formation, central New Mexico. The age of this flora is well constrained by conodonts and fusulinids from limestones (Lucas et al., 2013) to the early Wolfcampian. Environmentally, the Bursum Formation in the Carrizo Arroyo vicinity has been interpreted to be a coastal plain in which the remains of plants and freshwater to terrestrial invertebrates accumulated in standing water, possibly a large lake. Comparison is impeded to some extent by the differences in taxonomic names for what, by comparison of illustrations, appear to be the same taxa. Common elements include *Autunia conferta*, *Walchia schneideri*, *Rhachiphyllum schenkii*, *Sphenopteris germanica*, an *Odontopteris* that is very similar to *O. subcrenulata*, *Dicranophyllum* (identified as lycopsid leaves in the Carrizo Arroyo flora), *Cordaites*, calamitaleans, and possibly *Neurodopteris auriculata*. Carrizo Arroyo has a greater diversity of conifers and includes the noeggerathialean *Charliea*; however, it lacks marattialean foliage, which is part of the Sanzenbacher flora.

A flora from the “Red Magdalena” (terminology of C.B. Read, 1941, notes with USNM collection) also likely is from the Bursum Formation but exposed in Abo Pass, central New Mexico (DiMichele et al., 2017). The deposit probably formed in a brackish-water lagoon surrounding a seasonally dry coastline; brackish-to-marine depositional conditions are suggested by the suite of invertebrates preserved with the plants. Floral overlap with Sanzenbacher is minimal in detail but, as noted for Spanish Queen, later, there is a general similarity in the dominance of taxa regarded as xeromorphic forms, including small numbers of *Rhachiphyllum*, *Taeniopteris*, and *Odontopteris*, within a dominant framework of various walchian conifers, with none like that at Sanzenbacher. No marattialean ferns are present in the “Red Magdalena” collection.

In many respects, the Spanish Queen Mine flora of the terrestrial Abo Formation, also from central New Mexico (Lucas et al., 2012) and of early middle Wolfcampian age (likely Sakmarian), likewise, is similar to Sanzenbacher. The flora occurs in gray siltstones with abundant comminuted plant debris, concentrated in pockets or troughs, and deposited in an active fluvial channel. Similar elements include *Rhachiphyllum schenkii*, *Neurodopteris auriculata*, *Annularia spicata*, *Taeniopteris*, marattialean

foliage, including *Polymorphopteris* sp., and walchian conifers (although different from those of Sanzenbacher). Noncomparable elements include the callipterid *Dichophyllum*, and the medullosan *Alethopteris schneideri*.

An early Wolfcampian flora from the Neal Ranch Formation of Brewster County in southwest Texas (Glasspool et al., 2013) is comparable to Sanzenbacher despite considerable paleoenvironmental differences. The Brewster County plant remains were deposited in a prodeltaic marine setting and are accompanied by marine invertebrate fossils. Like Sanzenbacher, and the above floras from central New Mexico, the Neal Ranch flora is a mixture of plants characteristic of a variety of soil moisture regimens including xeromorphic elements such as walchian conifers (none in common with Sanzenbacher), callipterids (none in common with Sanzenbacher), medullosan pteridosperms (including *Neurodopteris auriculata*), and the *incertae sedis* elements *Taeniopteris* and *Sphenopteris germanica*. However, the flora also includes a large array of wetland plants, such as the lycopsid *Sigillaria*, marattialean ferns, calamitaleans (including *Annularia spicata*), and a variety of small fern foliage.

American floras of similar age but associated with coal beds contrast compositionally with the Sanzenbacher flora. From Carrizo Arroyo in central New Mexico, small numbers of plant macrofossils have been collected immediately above and below a thin coal bed from very close to the Carboniferous–Permian boundary (DiMichele et al., 2016). These are similar to Sanzenbacher in dominance of drought tolerant taxa, primarily walchian conifers, although there is no overlap in species with those from Sanzenbacher, and small numbers of *Rhachiphyllum*, *Taeniopteris*, *Odopteris*, and calamitalean stems are present. Marattialean ferns dominate the coal palynoflora and are present in the palynofloras of mudrocks above and below the coal, but no macrofossils of these plants were found.

From the eastern United States, the flora of the Dunkard Group in West Virginia, Pennsylvania, and Ohio contrasts sharply with all the western U.S., early Wolfcampian assemblages. The age of the Dunkard is debated because it lacks the marine beds and their faunas, used in correlation to regional or global stratigraphies. Recent studies of nonmarine ostracodes suggest an earliest Permian age for the Greene Formation (Tibert et al., 2011, 2013), thus making it of comparable age to Sanzenbacher. The Dunkard flora, however, is overwhelmingly dominated by plants typical of wetland habitats (Blake and Gillespie, 2011), as known from floras in the latest Carboniferous and earliest Permian of Europe (Wagner and Lyons, 1997). Callipterids make their first appearance in the Appalachian Basin in these strata (Washington and Greene Formations of the Dunkard Group: DiMichele et al., 2013) and conifers are known to occur sporadically throughout the Dunkard but also, similarly, sporadically, throughout Upper

Pennsylvanian strata in the Appalachians (Lyons and Darrah, 1989; McComas, 1988; Martino, 2017). Wagner and Lyons (1997) provide a cogent analysis of these records and note that environmental changes during the Carboniferous–Permian transition make this boundary difficult to determine with plant fossils and that the time of appearance of xeromorphic elements across Euramerica is highly variable.

Much more is known of floras from the Carboniferous–Permian transition in Europe than in the United States. The boundary is, again, difficult to identify there due to the extreme continentality of the geological successions, although recent radiometric age dates have been correlated to the floral succession, providing hope for a greatly improved understanding and basis for correlation (Opluštil et al., 2016). Nonetheless, there are well-studied and highly diverse floral successions to which the Sanzenbacher flora is compositionally similar, if less diverse. Recently, Wagner and Álvarez-Vázquez (2010) proposed a new floral zone for the uppermost Carboniferous, the *Annularia spicata* floral zone, to which the Sanzenbacher flora is similar. This would fall under the *Autunia conferta* floral zone as presented in Opluštil et al. (2016), which spans the Carboniferous–Permian boundary in Europe. Comparable floras, differing to varying degrees in the relative abundance of taxa but with the same basic floristic composition, are reported from Scotland (Wagner, 1983), southwestern Spain (Broutin, 1986, Wagner and Mayoral, 2007), northern Spain (Wagner and Martínez García, 1982), France (Steyer et al., 2000), Germany (Kerp and Fichter, 1985; Barthel, 2009), the Czech Republic (Šimůnek and Martínek, 2009; Opluštil et al., 2017), and Romania (Popa, 1999), and this is a small representative selection of published floras.

7. CONCLUSIONS

The Sanzenbacher flora is one of the few early Wolfcampian (Asselian) floras to be reported from north central Texas, an area well known for its Permian vertebrate fossils. As such, it serves as a point of comparison to other floras from the early Permian of western Pangea. Comparison with several described floras indicates considerable variation in space and time. However, similarities also are revealed, including the consistent mixture of plants interpreted to have grown in wetter and more water-stressed substrates. Drought-tolerant taxa, including conifers, callipterids, taeniopterids, and certain of the medullosan pteridosperm groups (particularly *Neurodopteris* and *Neurocallipteris*), occur widely among these floras intermixed with more mesomorphic to hygromorphic plant groups, such as marattialean tree ferns and calamitaleans.

The Sanzenbacher flora is one of many floras collected for the first time by the WPA, during the late 1930s and

early 1940s. These floras guided our initial collecting efforts in north central Texas, and we anticipate future research on other localities discovered by the WPA in Clay County and adjacent counties. It is our hope that this continuing work will further enhance our understanding of early Permian floras and environments.

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