



Early Permian plant megafossils from Carrizo Arroyo, central New Mexico

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EARLY PERMIAN PLANT MEGAFOSSILS FROM CARRIZO ARROYO, CENTRAL NEW MEXICO

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Abstract—A variety of plant fossils, including diverse forms of foliage, have been found in the Red Tanks Member of the Madera Formation of Late Pennsylvanian and Early Permian age in Carrizo Arroyo of the Sierra Lucero area of New Mexico. The flora includes *Lepidophloios*, *Asterophyllites grandis*, *Asterophyllites charaeformis*, *Annularia stellata*, *Annularia sphenophylloides*, *Sphenopteridium manzanitanum*, *Macroneuropteris scheuchzerii*, *Neuropteris* sp., *Mixoneura* sp., *Cyclopteris trichomaniodes*, *Rhachiphyllum schenkii*, *Autunia conferta*, *Arnophyton kuesii*, *Phasmatocycas kansana*, *Cordaites principalis*, *Cordaites angulosostratus*, *Cordaites palmaeformis*, *Cordaianthus* sp., *Samaropsis pseudofluitans*, *Cordaicarpus* sp., *Walchia piniformis*, *Walchia schneiderii*, *Walchianthus* sp., *Ernestiodendron* sp., *Gomphostrobus bifidus*, and *Charliea manzanitana*. The assemblage is dominated by *Autunia conferta*, *Walchia piniformis*, *Sphenopteridium manzanitanum*, and various species of *Cordaites*. The fossil flora and associated fauna indicate that most of the Red Tanks Member is most likely earliest Permian in age. The Red Tanks flora appears to be an example of a transitional flora that developed as the once widespread Palaeophytic flora disappeared because of increasing dryness near the end of the Paleozoic Era.

INTRODUCTION

In contrast to the large number of upper Paleozoic floras known from the Midcontinent and eastern United States, little is known about the plant megafossils from strata of this age in the western continental United States. Therefore, the flora from the Red Tanks Member of the Madera Formation of central New Mexico is a very important addition to our knowledge of Permian plants.

Plant fossils were first discovered in the Red Tanks Member in Carrizo Arroyo by Kenneth Kietzke during the spring of 1975 while he was a geology student at the University of New Mexico. Subsequently, he collected a large number of plant and other fossils (insects, eurypterids, and other invertebrates) from the main fossil-bearing horizon and then informed Dr. Barry Kues at the University of his discovery. Kues and Kietzke returned to the locality, made additional collections, and then published a summary of their findings in 1976. In the spring of 1976, both Drs. S. R. Ash and W. D. Tidwell were invited to work on this flora, and subsequently a selection of the plant fossils were loaned to them for study. Preliminary investigation of the collections resulted in the publication of a series of papers about the flora (Tidwell and Ash, 1980; Ash and Tidwell, 1982; 1987). More recently, Dr. Spencer Lucas and his associates from the New Mexico Museum of Natural History have reopened the quarry and collected more plant fossils, some of which are described in this paper.

GEOLOGIC BACKGROUND

The Red Tanks Member was initially established as the upper member of the Madera Formation in the Lucero uplift area by Kelley and Wood (1946). It represents a transition from Upper Pennsylvanian, dominantly marine strata lower in the Madera, to the Wolfcampian (earliest Permian) nonmarine, continental redbed sequence (Abo Formation) that overlies it. The Red Tanks Member thus contains strata deposited in alternating marine and nonmarine environments.

In Carrizo Arroyo, the Red Tanks is approximately 125–135 m thick, and consists of a wide variety of lithologies, including several relatively thin beds of gray marine limestone, limestone conglomerate, and shale, interbedded with generally thicker beds of red, green and maroon shale, sandstone, siltstone, and arkose (Kues and Kietzke, 1976). These units represent a variety of shifting nonmarine and marginal marine environments, including mudflat, lagoon/estuary, beach, and, particularly in the lower half of the member, coastal swamps associated with a prograding delta system.

The basal 8–9 m of the Red Tanks (unit I of Kues and Kietzke, 1976) is a regressive sequence of gray marine shales and ledge-forming limestones containing a pronounced limestone-pebble conglomerate near its base, overlain by a thin black shale. The shale is in turn overlain by about 15 m of unfossiliferous red/maroon/green blocky claystone, a

characteristic Red Tanks lithology. However, Kues and Kietzke (1976) recognized that this interval could as easily be considered as the upper beds of the underlying Atrasado Member. The remainder of the lower half of the Red Tanks, below a prominent sequence of marine limestones and shales about in the middle of the member, consists of strata indicating a prograding deltaic environment. This sequence includes a thin coaly bed about 33 m above the base of the member and a predominantly graygreen shale interval about 6 m thick approximately 40–50 m above the member base (unit 10 of Kues and Kietzke, 1976). Most fossils described in this paper occur in several horizons of this unit, associated with a nonmarine fauna that includes insects (Kukalova-Peck and Peck, 1976; Rowland, 1997), eurypterids (Kues and Kietzke, 1981), branchiopods, and unornamented ostracods. A limited number of plant fossils also occurs in the “underclay” just beneath a thin coaly bed, lower in the section. The upper half of the Red Tanks is predominantly nonmarine beds of red and green shale and mudstone, with a few minor, thin, transgressive intervals bearing marine or marginal marine invertebrates. The contact of the Red Tanks with the overlying Abo Formation is at the top of the highest marine limestone.

The age of the Red Tanks Member has been subject to debate. Originally considered as Late Pennsylvanian by Kelley and Wood (1946), this member was placed entirely in the Virgilian by Kottowski (1960) and Armstrong et al. (1979). They consider it to be stratigraphically below the Wolfcampian Bursum Formation, which crops out some distance to the east. The similarity of these two units, in lithology and stratigraphic position immediately below the Abo, however, led some earlier workers (e.g., Bates et al., 1947; Read and Wood, 1947; Jicha and Lochman-Balk, 1958) to suggest that the Red Tanks was equivalent to the Bursum and therefore Wolfcampian in age. Based on a preliminary examination of the marine megafauna, Kues and Kietzke (1976) concluded that the Red Tanks was no older than late Virgilian and extended into the Wolfcampian. As paleontological studies of both plants and invertebrates of the Red Tanks has progressed, the ages of various intervals of the Red Tanks have become better defined.

Studies of the plant megafossils from unit 10 (Ash and Tidwell, 1982, 1987, and herein) indicate a Wolfcampian age for most of the Red Tanks, as do the palynomorphs (see Traverse, this volume). Durden (1984) assigned a Sakmarian (Early Permian) age to insects recovered from unit 10 at Carrizo Arroyo. Kietzke (1983) noted a change from dominantly Pennsylvanian to dominantly Early Permian ostracod species above unit 3, about 27 m above the base of the member.

Among the bivalves of the Red Tanks, *Myalina (Orthomyalina) subquadrata* Shumard, which ranges from late Virgilian to early Wolfcampian in the Midcontinent region (Newell, 1942), is present just above the coaly bed, about 35 m above the base. Higher in the section, the marine interval near the middle of the Red Tanks contains *Septimyalina burmai* Newell and *Pseudomonotis hawni* (Meek and

Hayden), both restricted to the Wolfcampian in the Midcontinent (Newell, 1937, 1942). *Septimyalina burmai* is also present in the Bursum Formation ("lower Abo Formation" of Newell, 1942) in the southern Frontozo Mountains near Abo Pass, which also contains a fairly diverse fusulinid fauna indicative of an early Wolfcampian age. These and other bivalves strongly suggested that most or all of the Red Tanks is Wolfcampian rather than Virgilian in age (Kues, 1984). Brachiopods of the middle marine unit are abundant but have not yet been studied; however, several taxa have distinct Permian rather than Pennsylvanian affinities, and are unknown in typical Virgilian brachiopod faunas of northern and central New Mexico. The Red Tanks gastropod fauna is closely similar to that of the Laborcita Formation in southern New Mexico, which is entirely Wolfcampian in age (Steiner and Williams, 1968; Kues, 1991), again suggesting a similar age for the Red Tanks Member.

Fusulinids are generally the most biostratigraphically useful marine fossils for the late Paleozoic, but to date the only fusulinid species reported for the Red Tanks was *Triticites ventricosa* (Read and Wood, 1947), a species which at that time was interpreted broadly and considered to have a Virgilian to Wolfcampian range. Kues and Kietzke (1976) collected fusulinids from near the base of the Red Tanks, mostly from the lowest 6 m of the member, with a few specimens from their unit 5, about 27 m above the base. These were submitted to Gregory Wahlman, Amoco Production Company, for study, who (Wahlman, written communication to BSK, Feb. 1, 1984) concluded that they are an advanced, latest Virgilian form of *Triticites*, possibly a new species related to *T. subventricosus* or to the Wolfcampian *T. ventricosus/T. meeki* group. This suggests that the lower 25–30 m of the Red Tanks may be late Virgilian. Conversely, Lucas with Heinz Kozur collected fusulinids from unit 1 of Kues and Kietzke (1976) and submitted them to Garner Wilde who (written comm., 19 October 1993) identified *Triticites arcuosooides* Ross, *T. whetstonensis* Ross and Tyrrell, and *T. cf. T. bensonsensis* Ross and Tyrrell, to which he assigned a middle Virgilian age. Kozur (written comm., 1994) identified the conodont as *Streptognathus ruzencevi* Kozur, a Gzhelian, but not latest Gzhelian taxon, which also confirms a possible middle, not late, Virgilian age. The other faunal and floral evidence indicates that the remainder (upper 75–80%) of the Red Tanks section is early Wolfcampian. Thus, based on the available evidence, a reasonable choice for the position of the Pennsylvanian-Permian boundary is at or a little below the coaly bed (top of unit 6 of Kues and Kietzke, 1976) at Carrizo Arroyo.

PALEOBOTANICAL SYSTEMATICS

Lycophytes

The lycophytes, such as *Lepidodendron* (the scale tree) and *Sigillaria*, were mostly tree-like and were an important component of the late Paleozoic floras. Only one lycopod specimen, however, has been collected so far from this flora. The stem fragment, 40 mm long by 25 mm wide, is similar to *Lepidophloios*. The specimen consists of *Lepidophylloides*-type leaves attached to wider than higher leaf bolsters (Figs. 1A, 2A), that are spirally arranged on the stem. DiMichele (personal comm., 1999) noted that *Lepidophloios* has not been reported from Upper Pennsylvanian–Lower Permian strata west of the Appalachian Mountains.

Sphenophytes

Two species of both *Asterophyllites* and *Annularia* are examples of the sphenophytes in this flora. *Asterophyllites* and *Annularia* are the leaf genera of arborescent calamitean forms. The leaves are borne in whorls at the nodes or joints of the stem or branches (Tidwell, 1998). Calamites is related to the living and fossil *Equisetum*. The latter is commonly known as horsetail or joint grass.

Asterophyllites grandis Sternberg is represented by two incomplete specimens, one of which has only one whorl (Figs. 2G, 3H). The 11 linear-lanceolate leaves making up the whorl are 12 mm long, whereas the specimens of *A. charaeformis* (Stnbg.) Geoppert are small (1–2 mm long) and consist mostly of ultimate branches with attached whorls of 6–8 leaves. Both of these species occur throughout the Pennsylvanian

(Abbott, 1958).

The two species of *Annularia* are *A. stellata* (Schlo.) Wood and *A. sphenophylloides* (Zenk.) Gutbier. *Annularia stellata* has a variable leaf form, with leaves that vary in size and number in the whorl (Fig. 2B). The leaves are 12 mm long, with their widest part being near the middle of the mucronate leaf. The specimen of *A. sphenophylloides* (Zenk.) Gutbier consists of two whorls attached to an axis and smaller than most specimens of this species (Fig. 1B). Each whorl contains as many as six spatulate leaves that vary from being of equal length (2 mm) in one whorl to a somewhat unequal length (2–3 mm) in the other. The leaves of *A. sphenophylloides* are much smaller than those of *A. stellata*. Interestingly, they are often collected together in other floras as well as this one (Crookall, 1969). The stratigraphic range for these two *Annularia* species is from middle Pennsylvanian to the Lower Permian (Abbott, 1958; Gothan and Remy, 1957).

Pteridospermophytes (seed ferns)

Pteridospermophytes, commonly called seed ferns, are extinct plants with leaves like ferns, but they reproduced by seeds rather than spores, as do ferns. Seed ferns are represented in this flora by nine genera based on their foliage. These are *Sphenopteridium* Schimper, *Macroneuropteris* Cleal, Shute, and Zodrow, *Neuropteris* (Brongn.) Sternberg, *Odontopteris* Brongniart, *Mixoneura* Weiss, *Cyclopteris* Brongniart, *Rhachiphyllum* Kerp, *Autunia* Krasser emend. Kerp, and *Arnophyton* Ash and Tidwell.

?Lyginopterid

Sphenopteridium manzanitanum Mamay is one of the more common components of this flora. Specimens of this type of sphenopteroid foliage are similar to those described from nearby Kinney quarry of Late Pennsylvanian age (Mamay, 1992). The largest bipinnate frond in the collection is 26 cm long and 14 cm wide, with a robust rachis 10 mm wide. The pinnae of the frond are composed of partially dissected to more deeply clefted or lobed pinnules, generally attached to the

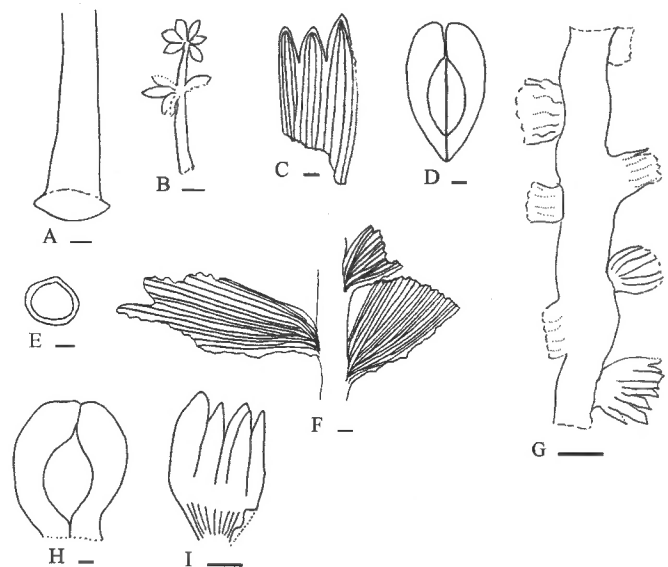


FIGURE 1. A, A leaf of the *Lepidophloios*-like specimen with an attached bolster. Note the wider than tall shape of the bolster. B, *Annularia sphenophylloides* (Zenk.) Gutbier. Two whorls of spatulate leaves attached to an axis. C, *Charliea manzanitana* Mamay. A terminal portion of a leaf illustrating three lobes and veins fusing near the lobe apices. D, *Samaropsis pseudofluitans* Weiss. Note the narrow wing around the nucellus. E, *Cordaicarpus* sp. Note the narrow wing around the nucellus. F, *Charliea manzanitana* Mamay. A series of leaves showing their attachment to the axis. The leaves are incomplete. G, *Cordaianthus* sp. The incomplete cone axis with lateral dwarf or short shoots of sterile scales. H, *Samaropsis* sp. ovule with a wing of uniform width. I, A synangium from the microsporangiate structure. Note the "finger"-like sporangia fused at their bases. (Bars = 1 mm).

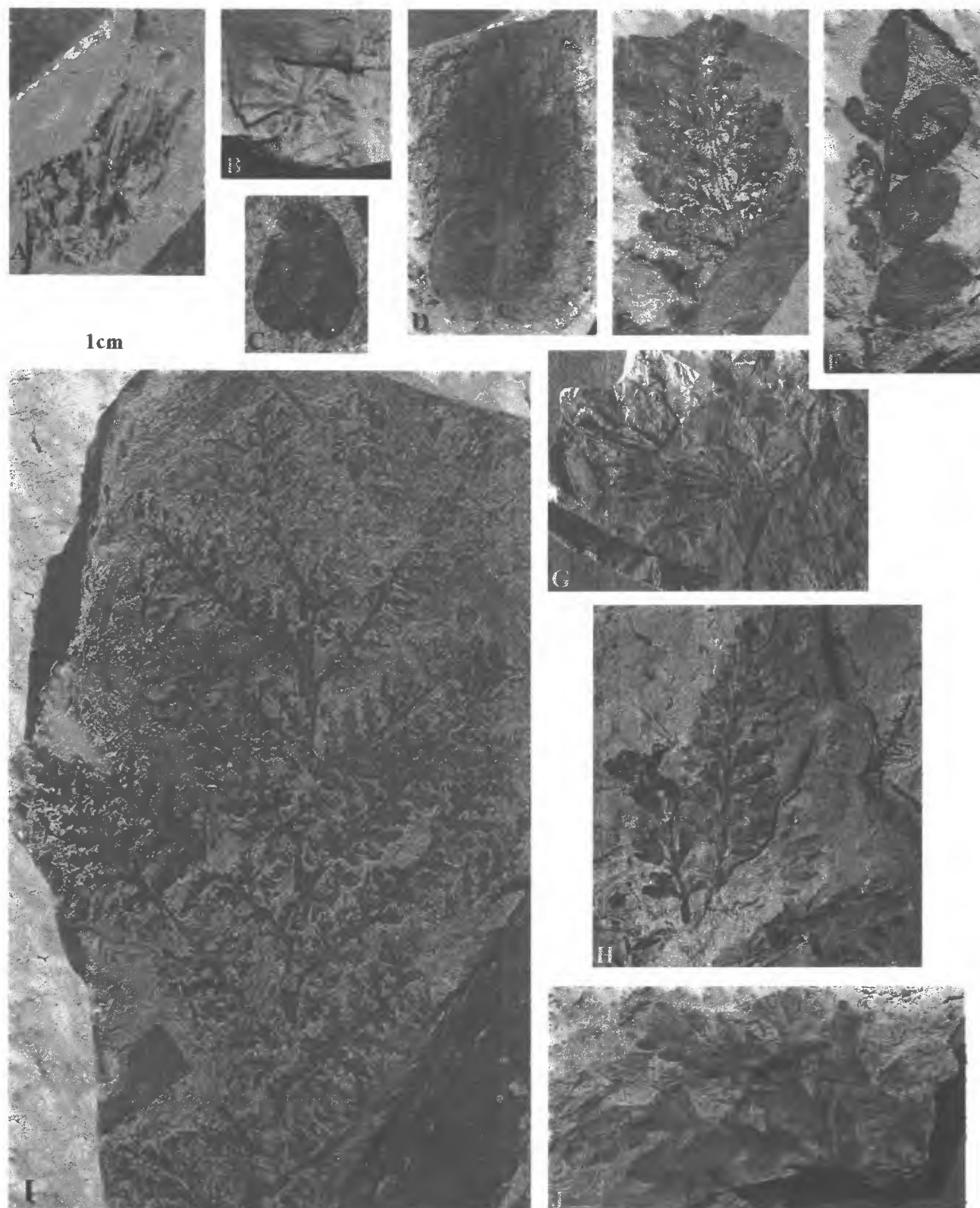


FIGURE 2. **A**, *Lepidophloios*-like specimen. Leaves attached to the bolsters of this stem fragment. **B**, *Annularia stellata* (Schlo.) Wood. A whorl of leaves. **C**, *Cyclopteris trichomanoides* Brongniart. Single pinnule. Note the radiating veins. **D**, *Macroneuropteris scheuchzerii* (Hoffm.) Cleal, Shute, and Zoderow. Single pinnule. Note the large size, midvein, and heart-shaped base. **E**, *Sphenopteridium manzanitanum* Mamay. A portion of a frond segment with compact foliage composed of broadly attached, closely spaced, irregularly lobed pinnules. **F**, *Mixoneura* sp. Distal portion of a pinna showing pinnule shape and attachment. **G**, *Asterophyllites grandis* Sternberg. Specimen with two whorls attached to an axis. Note the leaves of the lower whorl overlapping the whorl above. **H**, *Arnophyton kuesii* (Ash and Tidwell) Ash and Tidwell. Illustration of the nearly complete juvenile fern-like plant. **I**, *Sphenopteridium manzanitanum* Mamay. Distal portion of a large frond bearing several pinnae on each side of the primary rachis. **J**, *Rhachiphyllum schenkii* (Heyer) Kerp. Portion of frond with attached pinnae.

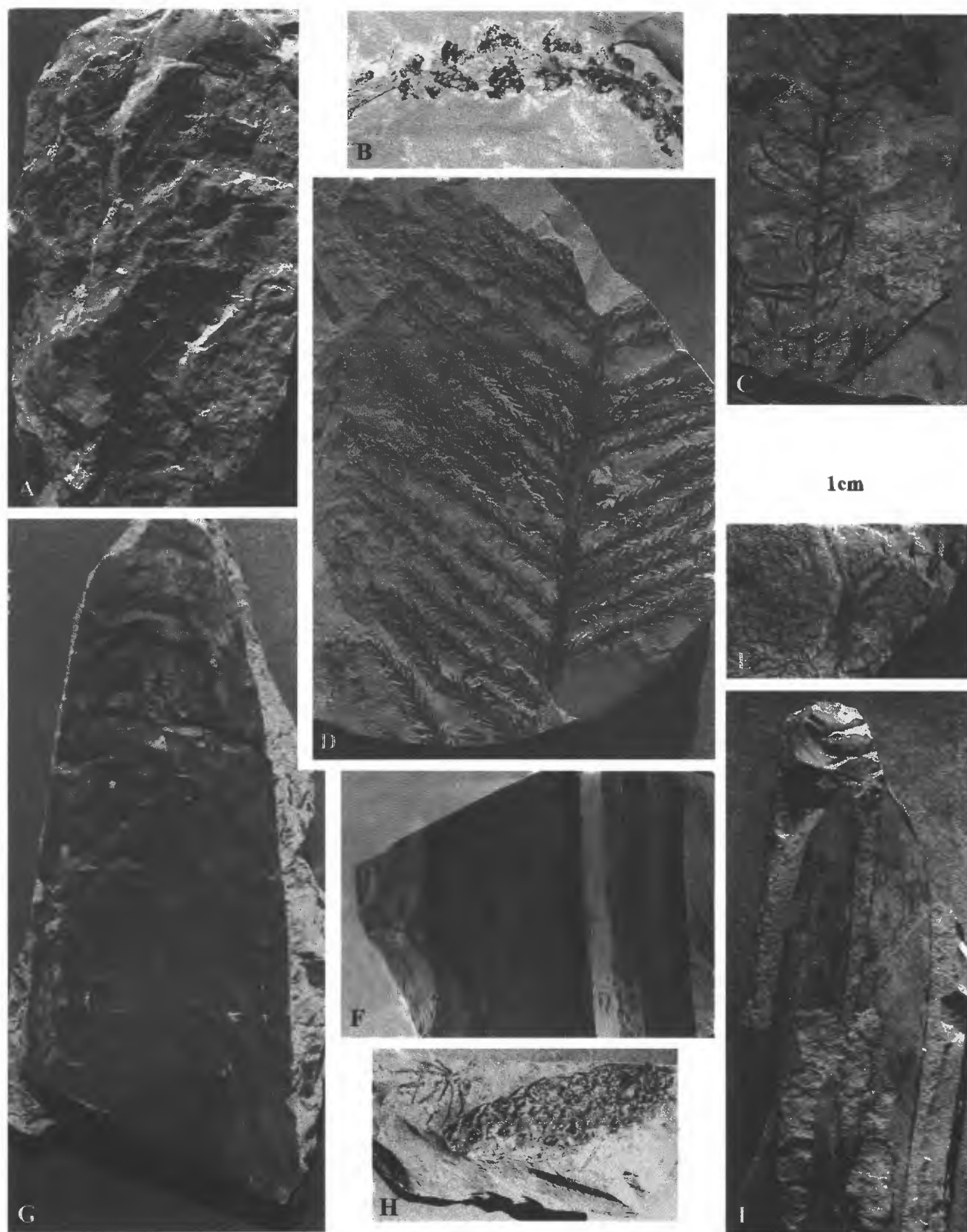


FIGURE 3. **A**, *Autunia conferta* (Stnbg.) Kerp. Portion of rachis with attached pinnae. **B**, *Phasmocycas kansana* Mamay. Part of the fertile axis with sessile attached oval-shaped ovules. **C**, *Walchia schneiderii* Zeiller. Specimen showing widely spaced needle-like leaves arising from an ultimate branch. **D**, *Walchia piniformis* (Schlo.) Sternberg. An ultimate branch with attached penultimate branches. The spirally arranged, decurrent, sickle-shaped leaves arise from the penultimate branches. **E**, *Gomphostobus bifidus* (Gein.) Potonie. An isolated leaf with its characteristic forked tip. **F**, *Cordaites principalis* (Germ.) Geinitz. Portion of a large leaf that has split. **G**, *Cordaites angulosostratus* Grand 'Eury. The characteristic broad, rounded apex of this species that has not split. **H**, *Walchianthus* sp. Note apices or tips of the distal portion of the microsporophylls are not divided. The whorl of leaves is *Asterophyllites grandis* Sternberg. **I**, *Cordaites palmaeformis* Goeppert. Note the deeply lacinated apex of this leaf.

rachis by constricted short stalks (Figs. 2E, 2I). The venation is obscure due to the thick lamina of the pinnules, but appears to be dichotomous. The equal dichotomizing rachial segments of this species reported from the Kinney quarry (Mamay 1992) have not been uncovered in this flora. As pointed out by Mamay and Mapes (1992), this taxon resembles *Sphenopteris elegans* Brongniart. However, they separated them on the presence of the dichotomously divided rachial segments and the lack of a prominent midvein in *Sphenopteridium manzanitanum* that is not present (dichotomous segments) or is present (has a midvein) in *Sphenopteris elegans*.

Medullosans

Fossils now attributed to *Macroneuropteris* (*Neuropteris*) *scheuchzerii* (Hoffm.) Cleal, Shute, and Zedrow, were once assigned to *Neuropteris*, a poorly circumscribed artificial genus that obviously included several natural genera. On the basis of cuticular studies and gross morphology, Cleal et al. (1990) recognized nine genera in the complex of fossils assigned to *Neuropteris*. Of the nine, only *Neuropteris* and *Macroneuropteris* occur in the Carrizo Arroyo flora.

Most specimens assigned to *Macroneuropteris scheuchzerii* in this flora are detached, but are specifically recognizable pinnules (Fig. 2D). Their relatively large size (50–65 mm long by 25 mm wide), lanceolate shape with heart-shaped bases and bluntly pointed to somewhat rounded apices, are distinctive. However, the stiff epidermal hairs, characteristic of this species, have not been observed on these specimens. The cyclopteroid basal lobe or lobes on these fossils are a further point of distinction (Mamay and Mapes, 1992). Crookall (1959) has reported *Macroneuropteris scheuchzerii* as ranging from Westphalian A to D in Great Britain, Gothan and Remy (1959) indicate the range as Westphalian B to D, and Read and Mamay (1964) list the species occurring in their Zone 12, which is uppermost Pennsylvanian. It now appears that the range extends into the Early Permian.

An incomplete specimen with three linear-lanceolate shaped pinnules is the only definite specimen of *Neuropteris* in this collection. The pinnules have crenulate margins that converge to a bluntly pointed apex, but their bases are not preserved. The venation is typically neuropteroid. Based on the shape of the pinnules, their venation, and crenulate margins, they are very similar to *N. pseudoblissi* Potonie, a species common in the uppermost Pennsylvanian and Lower Permian of Germany (Remy and Remy, 1959).

Two incomplete fronds having only a portion of the secondary pinnae represent an unidentified species of *Mixoneura* (Fig. 2F). Pinnules comprising the pinnae are oval to somewhat rounded, with rounded apices and bases (Fig. 4C). The bases are often restricted, resulting in a short, decurrent stalk. The age of *Mixoneura* is Pennsylvanian, extending into the Permian.

Cyclopteris trichomanoides Brongniart is represented in the flora by four specimens of detached pinnules. The orbicular to tongue-shaped pinnules lack a midvein, but contain numerous, crowded veins radiating from the point of pinnule attachment (Fig. 2C). The veins divide two or more times before reaching the pinnule margins. These specimens may well represent the basal pinnules of *Macroneuropteris scheuchzerii*.

A very small specimen of a microsporangiate structure is also present in the flora. The synangiate structures comprising this specimen have restricted bases and are attached laterally to a geniculate rachis. They resemble a hand with the microsporangia as like "fingers." The microsporangia are separate from one another in their distal portions and only fused together at their restricted bases (Fig. 1I). No microspores or pollen grains are preserved. These structures are similar to *Telangiopsis*, which has sporangia clustered and fused at their bases to form cup-like structures. The synangia on the specimen from Red Tanks differs in having restricted bases rather than a broad base like the synangiate structures of *Telangiopsis*.

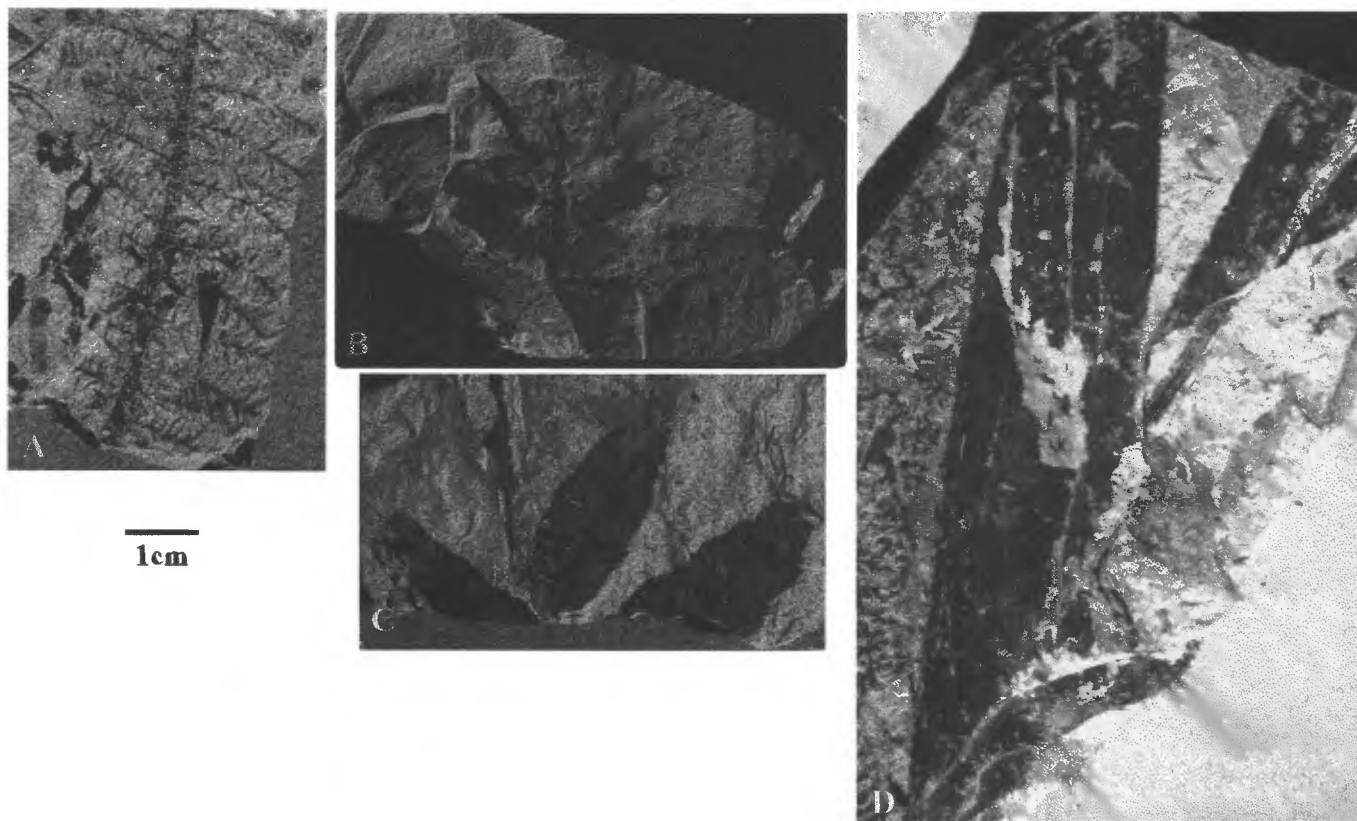


FIGURE 4. A, *Ernestiodendron?* sp. A pinnately branched shoot system with penultimate branches arising alternately to suboppositely. Note the needle-like leaves arching downward. B, *Charliea manzanitana* Mamay. Specimen with several leaves attached to an axis. Figures 1C, F were drawn from this specimen. C, *Neuropteris* sp. Note the three pinnules without bases due to preservation. D, *Cordaites principalis* (Germ.) Geinitz. Leaf split into two parts.

Peltasperms

Callipteris has been found to have been preoccupied by a modern fern. Consequently, species formerly assigned to the genus have been placed in other genera such as *Rhachiphyllum* for some sterile forms and *Autunia* for fertile types (Kerp, 1988; Kerp and Haubold, 1988). These two genera are present in this flora.

Specimens of *Rhachiphyllum schenkii* (Heyer) Kerp consist of bipinnate fronds with subopposite pinnae. Pinnules of this species are highly variable, ranging from oblong to linear-lanceolate in shape and 10–25 mm long to 3–7 mm wide in size (Fig. 2J). They also vary from entire-margined to lobed. The midvein arches from the decurrent pinnule base to 2/3–4/5 distance to pinnule apex. The secondary veins divide five times before striking the margins. The intercalary pinnules on the main rachis between the pinna that are typical of the callipterids are similar to the other pinnules on the frond. *Rhachiphyllum schenkii* apparently grew under relatively humid conditions according to Kerp (1988), who based this on the association of *R. schenkii* and the giant horsetail, *Calamites gigas*, at the Sobernheim locality of the Saar-Nahe region in Germany, and on the very thin lamina of the pinnules of *R. schenkii*. The stratigraphic range of *R. schenkii* is from Upper Pennsylvanian into Lower Permian. It is most common in the Lower Permian.

Fronds of *Autunia conferta* (Stnbg.) Kerp are bipinnate with suboppositely attached pinnae. Pinnules arise decurrently and obliquely from the pinna rachis and have thick laminae (Fig. 3A). The crenate-to-straight-margined, ovate-shaped pinnules are 5–10 mm long and 3 mm wide. Midveins are strong and sunken, a distinction between this species and *R. schenkii*, whose midveins are not. Intercalary pinnules occur in two rows on the rachis between the pinnae. The megasporophylls in the fertile specimen are isolated rather than being attached to the axis. They are bilaterally symmetrical, with strong ribs radiating from the petiole. Anterior margins are crenate. Stratigraphically, *A. conferta* was once considered to be an index fossil of the Lower Permian (Read and Mamay, 1964). However, more recently it has been collected in strata of Late Pennsylvanian age. It has been reported from the upper Dunkard Group immediately above the Washington coal in West Virginia and from an equivalent horizon in Ohio (Cross et al., 1996).

Arnophyton kuesii (Ash and Tidwell) Ash and Tidwell represents a nearly complete juvenile, fern-like plant (Fig. 2H). It consists of a horizontal rhizome with roots, a short, thick, upright aerial branch, and a tuft of dimorphic leaves (Ash and Tidwell, 1986a, b). This species may represent the juvenile form of *Rhachiphyllum schenkii*.

Cycadophytes

The cycadophytes contain the living or true cycads and their fossil representatives. Two specimens of the cycadalean *Phasmatozycas kansana* Mamay found in Carrizo Arroyo consist only of the fertile basal axis and attached ovules. The specimens are about 10 cm long, with an axis that is about 1 cm wide and longitudinally striated. The ovules are oval, about 2 mm wide by 2 mm long, and are sessile on the axis (Fig. 3B). In an early paper, some of these fossils were assigned to *Phasmatozycas* sp. by Ash and Tidwell (1982, fig. 15). *Phasmatozycas* is considered to be a member of the lineage of cycads derived from the seed ferns (Mamay, 1973; Kerp, 1983). The alternating glands and taeniopterid distal lamina that Mamay (1973) and Gillespie and Pfefferkorn (1986) observed in specimens of this genus are not present in our material. The fossils originally assigned to *Phasmatozycas* came from Permian strata assigned to Floral Zone 14 of Read and Mamay (1964).

Coniferophytes

Cordaites

Cordaites, depending on the species, were large trees that attained heights of 100 m or were small, many branched shrubs. They are the sister group of the conifers, and thus, their closest relatives. This group is represented in the Red Tanks flora by a series of incomplete leaves of three species of *Cordaites*, *C. principalis* (Germ.) Geinitz (Fig. 3F), *C.*

angulosostraitus Grand 'Eury (Fig. 3G), and *C. (Dorycordaites) palmaeformis* Goeppert (Fig. 3I), a partially preserved *Cordaianthus* strobilus, and detached ovules or seeds assigned to *Samaropsis* or *Cordaicarpus*.

Large, elongated, strap-like leaves with parallel venation of 1–5 (usually 2–3) thin veins between pairs of coarser veins are characteristic of both *C. principalis* and *C. angulosostraitus*. Shape of the leaf and apex distinguishes *C. angulosostraitus* from *C. principalis* (Crookall, 1970). The former is characterized by a rather elongate-oval leaf shape with a broader, more rounded apex that rarely splits, and thus, differs from the latter which has a narrower, more pointed leaf, that commonly splits (Fig. 4D). Leaves of *C. palmaeformis* in this flora are narrow, with only the apices being preserved. Veins in this species are fine, parallel, undivided, and of equal width. The species is noted for having more or less deeply lacinated leaves, which appear in the larger specimens in the flora.

The *Cordaianthus* specimen consists of an incomplete axis with a lateral arrangement of the dwarf or short shoots (Fig. 1G). It is not known conclusively whether this strobilus is ovuliferous or polleniferous, although it is most likely the latter, as no megasporophylls are attached.

Samaropsis occurs in this flora as isolated, flattened seeds, that are generally ovate and 10 mm long by 5–7 mm wide with a broad wing that completely surrounds the nucleus. The specimens where the wing is narrow near the base and widens upwards near the micropyle have been assigned to *S. pseudofluitans* Weiss (Fig. 1D), whereas those with more uniformly wide wings are placed in *S. sp.* (Fig. 1H).

Cordaicarpus is a genus used for ovules or seeds commonly attributed to *Cordaites*, although they may represent seed ferns as well (Fig. 1E). The specific limits of this genus are not well defined (Cridland et al., 1963). Therefore, the specimens from the Red Tanks flora are not referred to any particular species.

Conifers

Conifers, typically called evergreens, are the most common gymnospermous plants. They are characterized by scaly, broad, or needle-like leaves, as on *Pinus*. Conifers are one of the dominant fossil types in the Red Tanks flora. They are represented by four genera: *Walchia* with two species, *Walchianthus*, ?*Ernestiodendron*, and *Gomphostrobus*.

The two species of *Walchia* are *W. piniformis* (Schlo.) Sternberg and *W. schneiderii* Zeiller. Several specimens of pinnately branched axes of *W. piniformis* have been collected (Fig. 3D). The branches bear overlapping, decurrent, falcate-shaped leaves that are spirally arranged around the branch. The leaves are from 2–7 mm long by 0.25–0.5 mm wide. The species ranges from the Upper Pennsylvanian into the Permian (Gothan and Remy, 1957). The specimens of *Walchia schneiderii* are very incomplete, consisting of ultimate branches arising alternately to suboppositely from the penultimate branch. Needle-like leaves, 11–13 mm long by 0.5 mm wide, are attached alternately to oppositely on the ultimate branches (Fig. 3C). The leaves are widely spaced and typically arise at an acute angle, although some are perpendicular. *Walchia schneiderii* is Upper Pennsylvanian to Lower Permian in age (Cridland et al., 1963; Cridland and Morris, 1963).

Several specimens in this flora are considered to be pollen cones assignable to *Walchianthus* (45–65 mm long by 15–20 mm wide). They consist of cone axes bearing numerous, spirally arranged, flattened microsporophylls (Fig. 3H). Each microsporophyll has an upturned distal portion that partially overlaps the base of the one above. These distal portions or segments are narrowly triangular to subtriangular in shape with a somewhat rounded base and an entire, acute apex. Although rather large, these cones are assumed to be polleniferous. There is no indication of ovulate structures having been present, and the distal portion of the microsporophylls are entire rather than having bifid tips like the bracts of walchiaceous ovuliferous cones.

Several specimens of ?*Ernestiodendron* sp. occur in the flora. They represent a pinnately-branched shoot system in which the penultimate branches have lateral ultimate or secondary branches arising alternately to suboppositely (Fig. 4A). The ultimate branches essentially paral-

leaves each other. Overlapping linear leaves with fusiform bases, 13–15 mm long, occur on the penultimate branches. Although some of the needle-like leaves on the ultimate branches are spirally arranged, most are opposite to subopposite in pairs, but somewhat spiral as well. The leaves are separated, flat, sickle-shaped, 1 mm long near the tip of the ultimate branch to 5 mm at their longest on these specimens, and are attached in the plane perpendicular to the branch. They do not overlap and are not decurrent. They arise from the branch acutely, arch slightly upward, flatten outwardly perpendicular to the axes, and then some bend abruptly upward near the needle apices, whereas most simply arch downward. These specimens are similar to *Ernestiodendron*, but are distinct from described *Ernestiodendron* species. Primarily, they differ from *E. filiciforme* (Schlo.) Florin by being larger, not having needles at right angles to the branch, and not arching strongly upward as in *E. filiciforme*. *Walchia piniformis* differs from ?*Ernestiodendron* sp. by having decurrent leaves that are close together and overlapping, and more or less paralleling the branch axis, none of which equal in ?*Ernestiodendron* sp. specimens.

Specimens of *Gomphostrobus bifidus* (Gein.) Potonie consist of isolated leaves that have forked tips which are characteristic of this species (Fig. 3E). The specimens resemble the leaves illustrated by Read and Mamay (1964) as *G. bifidus* from the Permian Abo Formation of central New Mexico. Kerp et al. (1990) mentioned that *Gomphostrobus*-like leaves are known as bracts from walchiaceous ovulate cones as well as foliage of certain conifer branches. They continued to treat *Gomphostrobus* as a form-genus, however, because their material, like that from the Red Tanks flora, could not be correlated with either foliage or cones.

Incertae sedis

Charliea manzanitana Mamay occurs as four small, incomplete specimens of the foliage of this species. One specimen has five leaves still attached to the axis (Fig. 4B). The others are the terminus of leaves. The leaves are helically arranged around the axis. They are persistent, oblong to linear-oblong in shape with constricted, somewhat clasping bases (Fig. 1F). The usually truncated apices divide into 3–4 equal to nearly equal, rounded to bluntly pointed lobes (Fig. 1C). The leaves on these specimens are 20 mm long and 9–11 mm wide. Venation consists of 12–21 narrow, parallel veins, some of which dichotomize. Eventually, 3–4 veins project into each lobe where they converge and fuse near the lobe apex. Another specimen of this genus is new and will be described later. *Charliea manzanitana* was first reported from the Pennsylvanian age Kinney quarry by Mamay (1990).

DISCUSSION

The rarity of calamitalean and lepidodendralean remains, the presence of *Walchia*, ?*Ernestiodendron*, *Cordaites*, and *Autunia conferta*, and the lack of *Pecopteris*, the leaf form of the common swamp dwelling psaronious tree fern, indicate an upland environment for the Red Tanks flora. This flora is noteworthy because it may represent an example of the “Transitional” flora that developed as the once widespread Palaeophytic flora disappeared because of increasing dryness near the end of the Paleozoic (Knoll, 1984). The timing of the change from the Palaeophytic flora to the “Transitional” and the succeeding Mesophytic was not synchronous throughout the world (Knoll, 1984; Traverse, 1988). It began during the Late Pennsylvanian in western North America (Arnold, 1941; Read, 1947; Lyons and Darrah, 1989), where it was essentially completed by about the middle of the Permian period; the change was not complete in the world until late in the Early Triassic of China, however (Knoll, 1984).

According to current thinking, the Palaeophytic flora consisted of plants that inhabited lowland areas, often in association with peat-forming swamps, during most of the Paleozoic. This flora was dominated by mesic plants such as lycophytes, horsetails, and ferns, some of which were giant arborescent forms. During the Pennsylvanian, however, another flora adapted to a more rigorous dry climate began to develop in highland areas. In contrast to the lowland floras, this new flora consisted mostly of seed plants such as conifers, which were adapted to liv-

ing in a seasonally dry climate. This flora could not successfully compete with the Palaeophytic floras then inhabiting the more humid regions, and the remains of the members of the new flora are not commonly found in typical Pennsylvanian floral deposits, especially those associated with coal swamps. Those that are found were most often, but not always (McComas, 1988; Lyons and Darrah, 1989), transported some distance before deposition.

The situation began to change when the lowland floras in some areas came under increasing stress due to increasing dryness during the late Paleozoic (Frederickson, 1972). Consequently, the highland floras began to invade the lowlands, replacing the lowland plants, which were coming under increasing environmental stress. As a result, the remains of the invading plants began to enter the geologic record in North America near the end of the Paleozoic in increasing numbers, while at the same time the numbers of lowland plants declined. The resulting flora, containing a mixture of both indigenous forms and invaders, has been termed “Transitional” by several authors (e.g., Knoll, 1984; Traverse, 1988). In a relatively short time, this “Transitional” flora was replaced by the Mesophytic flora. Because the Red Tanks flora contains only a few characteristic Palaeophytic plants and many Mesophytic-like forms, it appears that the change may have begun earlier in central New Mexico. Read (1947) proposed the term “Cordilleran Flora” for the higher Pennsylvanian floras which showed mesophytic modifications.

Some authors, however, do not believe that “Transitional” floras composed of mixtures of indigenous Palaeophytic forms and invading Mesophytic forms is a valid concept. For example, DiMichele (pers. comm., 1999) considers the “Transitional” floras to be merely due to mixing of florules on the outcrop. In his opinion, once the florules are separated, the discrepancy disappears. Furthermore, he believes that the floral transition occurred gradually when the “Mesophytic” flora migrated into the lowlands during brief intervals of moisture stress, followed by the return of the Paleophytic flora. The seasonally dry periods just got longer and longer until the complete changeover occurred. Research on the transition from the Palaeophytic flora to the Mesophytic flora in the Southwest is, nevertheless, continuing.

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