EARLY PERMIAN FLORA, DOÑA ANA MOUNTAINS, SOUTHERN NEW MEXICO, WITH SPECIAL CONSIDERATION OF TAXONOMIC ISSUES AND ARTHROPOD DAMAGE

WILLIAM A. DIMICHELE₁, SPENCER G. LUCAS², DAN S. CHANEY₁, MICHAEL P. DONOVAN¹, HANS KERP³, REBECCA A. KOLL⁴ and CINDY V. LOOY⁵

₁Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC, 20560, USA; -email: dimichel@si.edu; ²New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104, USA; ³Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität Münster, Heilenbergstraße 2, 48149 Münster, Germany; ⁴Department of Biology, University of Florida, Gainesville, FL 32611, USA; ⁵Department of Integrative Biology, University of California Museum of Paleontology, University of California Herbarium, University of California, Berkeley, CA 94720, USA

Abstract—Plant fossils were collected from nine sites, and noted at several others, in Lucero Arroyo and its immediate tributaries in the Doña Ana Mountains, north of Las Cruces, in southern New Mexico. The strata hosting the plant fossils are assigned to the Robledo Mountains Formation and are of early Permian (Leonardian/Artinskian) age. The succession comprises, primarily, siltstones and sandstones deposited in active or abandoned stream channels. The plant-fossil material is allochthonous at each collecting site. Most of the collections are small, consisting of <10 specimens; three are larger, consisting of between 19 and 98 specimens. The flora is heavily dominated by coniferous, xeromorphic seed-plant foliage; based on the number of sample-site occurrences, conifers and cordaitaleans were the most widespread plants, and likely dominated the landscape. In the larger collections, however, greater diversity was found, and peltaspermous, or presumed peltaspermous, genera were found, including _Rhachiphyllum_, _Supaia_ (and/or possibly _Glenopteris_), _Auritifolia_, _Gigantopteris_, and _Supaia anomala_. A lectotype for _Supaia anomala_ is formally designated herein, and the species is transferred to the genus _Auritifolia_, based on its gross morphology and, particularly, its venation. The flora also contains rare examples of calamitaleans, small ferns, and the noeggerathelaean _Yuania_. Arthropod damage was found to be rare and includes several examples of galling and margin feeding on the lamina, primarily of _Auritifolia_ and gigantopterids. The flora likely occupied a seasonally arid landscape, but one with one or more intervals of substantial rainfall.

INTRODUCTION

Floras of early Permian age are found throughout western Pangea, including modern-day Mexico (Weber, 1997), New Mexico (Tidwell and Ash, 2004; DiMichele et al., 2007; 2013), Arizona (Lucas, personal observation), Utah (Tidwell, 1988; DiMichele et al., 2014), and Colorado (White, 1912), and in the west central region, now Texas, Oklahoma (Read and Mamay, 1964; DiMichele et al., 2000, 2001, 018; Chaney and DiMichele, 2007), and Kansas (Sellards, 1900a; Warren, 1969). Although a number of these floras have been documented, they are less well known than those more centrally located in Pangea, from the Appalachian Basin of the USA to Britain and continental Europe (e.g., Wagner, 1983; Wagner and Martinez Garcia, 1982; Kerp and Fichter, 1985; Wagner and Lyons, 1997; Kerp et al., 1989; Popa, 1999; Šimůnek and Martínek, 2009; Uhl and Jasper, 2016; Opluštil et al., 2017). Floras from these widely separated areas of Euramerica share the common occurrence of abundant conifers, and other taxa, odontopterids for example, that frequently occur with the xeromorphic forms. The more mesomorphic to hygromorphic elements, however, are much less prominent in western Pangea, early Permian floras than in more centrally located regions. The western Pangean floras tend to contain some distinct elements, shared in common with later, middle and late Permian floras of the Angaran and Cathaysian paleogeographic regions. These shared plant groups include supaioids, comoids and gigantopterids, among other elements. The western fossil floras are dominated almost universally by xeromorphic taxa, with notable exceptions, where marattialean ferns and calamitaleans are particularly abundant – perhaps reflecting local variation in environmental and preservational conditions.

Hovering above this general pattern is a large scale “taphonomic megabias” (Behrensmeyer et al., 2000) that is an especially prominent factor in terrestrial deposits of the late Paleozoic. This megabias is the almost complete absence of late Paleozoic “upland” environments, particularly those located far from basins, as a result of the action of erosion over the long time spans separating the Paleozoic from the Recent (Looy et al., 2014). Ecological dynamics and evolutionary events in “extrabasinal” areas (sensu Pfefferkorn, 1980), are inferred but require special circumstances. Narrow basins, surrounded by steep-sided terrain, may foster the transport of plant remains from the slope habitats into the basin (e.g., Broutin et al., 1990; Opluštil and Cleal, 2007; Cleal et al., 2017). In such intermontane settings, climatic fluctuations may create conditions that increase the likelihood for plant remains to be transported from seasonally dry areas into basinal lowlands (e.g., Falcon-Lang, 2004; Falcon-Lang et al., 2009; Bashforth et al., 2014; Uhl and Jasper, 2016); as discussed by Cecil and Dulong (2003), and supported by data from tropical river sediment discharge measurements (Cecil et al., 2003), seasonally dry climates are the most likely to host high sediment transport. Most unusual of all, upland areas, and the plant remains buried there, may be preserved when certain tectonic peculiarities rapidly lower upland areas, allowing them to be buried and preserved (e.g., Opluštil, 2005). Examples of these phenomena are not common in the fossil record, even though most Pennsylvanian and early Permian basins regularly experienced seasonally dry climates (associated with glacial-interglacial oscillations). This is in large part because the potential for the preservation of organic matter was at its lowest point during these seasonally dry intervals (Gastaldo and Demko, 2011), requiring locally wet conditions for burial.

There are some notable reminders of this taphonomic megabias reported from the fossil record. Consider, for example, the many unusual, Angaran-type taxa reported by Broutin (1974, 1977, 1986) from a flora found in the vicinity of Guadalcanal,
Spain; specimens such as these may indicate a largely unknown flora of moisture-limited substrates, widespread across much of Pangea. The existence of largely unseen floras across extensive segments of the supercontinent has been discussed by Falcon-Lang et al. (2009, 2015), based on the discovery of both stratigraphically and temporally unexpected elements preserved in channel deposits in the Illinois Basin and in New Mexico. Findings such as these are “red flags” that should temper any attempt to reconstruct evolutionary phenomena from direct readings of the terrestrial fossil record, and that similarly challenge our ability to reconstruct and understand biogeographic patterns in the deep past.

It has been a goal of the authors of this paper to find and report floras from western Pangea. Such data are needed in order to expand our understanding of the vegetation from this part of the supercontinent, and to provide a platform from which we can make more informed interpretations of late Paleozoic plant evolution in response to environmental change. In this study, we examine a relatively small but unusual flora, particularly noteworthy for the peltaspermous elements that compose a major part of it. In this instance, we add an additional perspective, that of arthropod activity associated with this flora. In combination, the plant and animal components suggest growth of the flora in a seasonally strongly dry environment, one that likely was subhumid (sensu Cecil, 2003) but with a moist period for part of the year, in keeping with other early Permian floras from this region of Pangea.

**GEOLOGY**

**Location and Stratigraphy**

The Doña Ana Mountains are a westward-tilted fault block just north of Las Cruces in Doña Ana County, New Mexico (Fig. 1). The oldest rocks exposed in the range are strata long assigned to the Bursum? and Hueco formations (Kottlowski, 1960; Seager et al., 1976; Mack et al., 2003). These strata were reasigned (Fig. 2), regionally, to (in ascending order) the Panther Seep Formation and the Hueco Group, the latter consisting of the Shalem Colony, Community Pit, and Robledo Mountains formations (Krainer et al., 2005; Lucas et al., 2015). The uppermost of these units, the Robledo Mountains Formation, previously assigned to the Abo Member (or “tongue”) of the Hueco Formation (Mack, 2007; Mack et al., 2010), includes nonmarine siliciclastic red beds that yield plant fossils and vertebrate footprints (Lucas et al., 1995a).

Strata of the Hueco Group in the Doña Ana Mountains have the following attributes. The lowermost Shalem Colony Formation is ~ 63 m thick, and consists mostly of dark gray, bioclastic wackestone-mudstone and shale. The Community Pit Formation is at least 160 m thick, and is mostly shale and brownish-weathered calcareous mudstones. The Robledo Mountains Formation is at least 60 m thick, composed mostly of terrestrial red-bed siltstones and fine sandstones, shale, and marine limestones. These are the “shelf facies” of previous workers. Their “basin facies” comprise faulted strata of the Community Pit Formation or strata of the Panther Seep Formation, which underlies the Shalem Colony Formation in the Doña Ana Mountains. These Panther Seep strata are at least 64 m thick and consist of thick shale slopes interbedded with thinbedded limestones, sandy limestones and thin intraformational conglomerates.

**Robledo Mountains Formation Lithology**

In this paper, we focus specifically on fossil floras from the Robledo Mountains Formation in the Doña Ana Mountains, which is a 60 m thick succession of partly covered shale intervals (62.2%) with intercalated siltstone/sandstone (15.5%) and limestone (22.3%). The shale is greenish and dark gray in the lower part, but greenish and red in the upper part. Red shale occurs particularly in the elastic sequence of units 67-74 (Fig. 3). Shale units are up to 4.2 m thick (unit 22), but are mostly < 1.5 m.

The basal fine-grained sandstone of the Robledo Mountains Formation locally is 1.3 to 4 m thick and displays well-developed trough crossbedding. Intercalated siltstones/fine-grained sandstones are mostly red, but also greenish (units 27, 31, 38 and 42), and up to 1.3 m thick (unit 42). In the siltstones, ripple lamination is a common sedimentary structure, but horizontal lamination is also observed. Coarse-grained siltstones and fine-grained sandstones are trough crossbedded, representing small channel fills. The red-bed sandstones yield plant fossil impressions and tetrapod footprints indicative of a terrestrial paleoenvironment (Lucas et al., 1995a).

Intercalated limestones are 0.1 to 1.2 m thick, mostly < 1 m. Individual limestone beds are up to 0.8 m thick. Most common are dark gray, yellowish brown weathered micritic limestones, which are frequently bioturbated. These limestones are composed of bioclastic mudstone/wackestone, and rarely of crinoidal packstone (unit 60) and grainstone. Some beds contain gastropods (units 35, 46, 48, 52). Two coquina layers (units 19, 21) occur near the base. Silty limestones also are present. In the upper part of the section the limestone intercalations are gray and micritic, containing some ostracods.

These strata formed in a low-energy, shallow marine, partly restricted environment with locally coarser siliciclastic influx. The red-bed sequence of units 67-74 represents a nonmarine facies (muddy coastal plain with intercalated fluvial channels).

**Plant-Fossil Collecting Sites**

Most plant fossils were collected principally from three parts of the Robledo Mountains Formation in Lucero Arroyo or its immediate tributaries. Location information for these collections is on file at the National Museum of Natural History. The stratigraphic positions of the plant-fossil bearing deposits conform broadly to the lower (units 2-17), middle (units 67-72), and uppermost (units 74-83) portions of the section (Fig. 3). All collecting sites were identified in the field in accordance with the Doña Ana Mountains stratigraphic sections published by Mack et al. (2010, figs. 6-7), and correspond to siltstones 2 and 3 in the lower portion, 7 and 8 in the middle portion, and 11 in the upper portion. Our measured sections were made independently of those of Mack et al. (2010), and an exact correlation was not possible. Two additional collections were made in a small arroyo to the north of Lucero Arroyo, identified by MacDonald (1994) informally as “Ripple Track Draw.” These two localities could not be correlated with the Lucero Arroyo section, but are within the Robledo Mountains Formation.

In the upper portion of the formation, given similarities to deposits from that part of the section in Lucero Arroyo, including small sandstone-filled channel-like features with cordaitalean leaf mats, and an absence of charcoal and marine invertebrates. All collections also appear to have been drawn from deposits with various characteristics of small channels, including their basic channel form with scoured bases, trough cross-beds, intraformational basal conglomeratic lags, and plant fossil remains disposed at angles in the matrix, indicating rapid deposition from suspension or traction during periods of waning flow. At some sites, fossil leaves, particularly the structurally coriaceous leaves of cordaitaleans, were preserved in dense mats, through tens of centimeters of siltstone or sandstone matrix. In the lower part of the section only, and in association with the fossil plant remains, fossil charcoal, an indicator of local fires, was found at USNM localities 41669, 42271, 41670, and clams, spirorbids, linguloids, and fish scales, indicators of possibly brackish conditions, were found at USNM localities 41669, 41670.

USNM locality 41669 (Fig. 4A) is from the lowest part of the Robledo Mountains Formation, Siltstone 2 of Mack et al.
FIGURE 1. Location of the Doña Ana Mountains in southern New Mexico, showing location of Lucero Arroyo and position of the stratigraphic section in Figure 3. Modified from Krainer et al. (2005).

(2010). The plant-fossil bearing deposit was of channel form, and included various thin beds of mixed lithological character. These beds include red-stained siltstone with cordaitalean leaf mats, siltstone with a substantial clay component and abundant invertebrate shell remains, possibly linguloids (Fig. 4B), in which conifers and cordaitaleans were noted, and a layer of conglomeratic matrix in which the callipterid *Rhachiphyllum* was noted. Large, charred wood fragments also were present.

USNM locality 42271 is in a well indurated, buff to yellow siltstone that caps the top of a low ridge (Fig. 4C). The unit is thickly bedded, and the beds are largely horizontal to the extent it could be seen in the limited vertical outcrop exposures (Fig. 4D). Plant fossils, which are often preserved as large fragments, occur in localized concentrations. Due to the limited exposure and the general similarity in grain size, color and bedding of many of the siltstones in the local area, the extent of the plant-bearing unit could not be clearly delimited. The fossiliferous bed appears to be a channel-form deposit, possibly subject to intermittent flooding between periods of standing water. No evidence was found suggesting estuarine conditions. The bed accords with the top of Siltstone 2 or the bottom of Siltstone 3, in the terminology of Mack et al. (2010). The collection from this bed is the largest of the Dona Ana collections made by us. The flora is dominated by xeromorphic seed plants, principally
supaioids. Woody charcoal (Fig. 4E) is present, intermixed with the plant remains.

USNM locality 41670 (Fig. 4F) is the uppermost of the three collecting sites in the lower part of the Robledo Mountains section, conforming to Siltstone 3 of Mack et al. (2010). Plant remains were sparsely distributed, but jumbled and angularly disposed in a buff to yellow, well indurated matrix of lithologically heterogeneous siltstone and fine-grained sandstone. The deposit contained rare charcoal, the remains of shelly invertebrates and fish scales. The deposit is of channel-form, with a gravel lag at the base, in which seed remains were the most abundant types of fossils. The deposit appears to represent a flashy discharge channel, possibly estuarine, in which plant material was deposited episodically and rapidly. At USNM locality 42272, also within the Siltstone 3 interval, remains of permineralized (silicified) wood were found, but were not accompanied by any adpression fossils.

Two small collections were made in the upper middle portion of the Robledo Mountains Formation, corresponding to Siltstone 7 (USNM locality 42276) and Siltstone 8 (USNM locality 42272) of Mack et al. (2010). Conifer remains were sparse at both locations (only one specimen was collected from 42272) but were the most common plant fossil remains. At locality 42276 (Fig. 5A), the fossiliferous siltstone bed contained thin layers of carbonate and/or gypsum within, which conforms with the lithological description of Siltstone 7 by Mack et al. (2010). At locality 42276 (Fig. 5B, C), plant fossil remains were found in thickly bedded, buff to yellow siltstone that had high specific gravity due to enrichment of iron in the matrix. The deposit was spatially restricted and clearly channel-form; this can be seen particularly in Figure 5C, where beds thin laterally. Plant fossil remains were found at the bottom of this deposit.

The highest collecting site in the Doña Ana Mountains, Lucero Arroyo section is USNM locality 42273 (Fig. 5D), attributed to Siltstone 11 of Mack et al. (2010). Cordaitalean leaves constituted the only plant fossils identified (see Fig. FIGURE 3. Measured section of part of the Community Pit and Robledo Mountains formations in the Doña Ana Mountains. This is section C from Krainer et al. (2005). Note that the upper part of the Robledo Mountains Formation is faulted out.
FIGURE 4. USNM sampling locations in the lower Robledo Mountains Formation. See text for details. A, USNM 41669. B, Nonmarine bivalves in siltstone from USNM 41669. USNM specimen 713253. Scale bar = 1 cm. C, USNM 42271. General overview of outcrop area. D, USNM 42271. Exposure of plant-fossil-bearing strata. Hammer in foreground is 40.5 cm in length; the coated portion of the handle is 19 cm long. E, Charcoal fragment from USNM 42271. USNM specimen 713298. Scale bar = 1 cm. F, USNM 41670. General overview of outcrop area.
7°C), and these occurred in mats, without preferred orientation, through a thickness of >10 cm. The fossiliferous matrix is, as at many of the other sites, a buff to yellow siltstone or fine-grained sandstone that is made fissile by the presence of abundant fossil leaves, along which the rock tends to split. Plant fossil remains were concentrated in a small area, possibly the base of a channel fill.

As noted above, two collections were made in a small arroyo to the north of Lucero Arroyo. These could not be tied directly into the Lucero Arroyo stratigraphic section. These are denoted USNM locality 43574 (Fig. 5E) and USNM locality 43587. At both locations, only cordaitalean leaves and conifer remains were identified. At Locality 43574, cordaitalean leaves were preserved in mats without preferred orientation, through >10 cm of bedding. At Locality 43587, cordaitalean leaves again occurred through >10 cm of matrix, but with some indications of current alignment. Both deposits appear to represent channel fillings, sluggish or with current activity sufficient, at least intermittently, to align plant remains.

**COLLECTING AND QUANTIFICATION METHODS**

Plant fossil remains were preserved as impressions in well-indurated siltstones or fine-grained sandstones at most collecting sites. As a result, most collecting was done by surface pickup, or limited splitting of hand specimens taken from portions of outcrops long exposed to weathering. Some degree of weathering made the rock fracture more easily, and also made the fossils themselves more visible by enhancing their contrast with the matrix. Attempts to split poorly weathered fossiliferous matrix usually met with little success. Consequently, all but one of the collections are relatively small in terms of number of hand samples collected.

The induration of the siliceous matrix at many of the collecting sites also made preparation of the fossils difficult. Attempts at degagement with needles or with a vibratool often resulted in breakage or damage to the specimen. As a consequence, little preparation was carried out, even though, as can be seen from the illustrated specimens, some preparation would be desirable. In addition, we found no evidence of cuticular remains, which might have helped with interpretation of some of the plant fossil remains.

All collections were quantified, using the methods of Pfefferkorn et al. (1975), as modified, for example, by Bashforth and Nelson (2015) or Bashforth et al. (2016). In this method, each hand sample surface of a collection is treated as a sampling quadrat (thus, opposite sides of a slab are treated as distinct quadrats), and the presence of a taxon is recorded only once for that quadrat, regardless of the number of individual specimens. Counterpart surfaces are excluded. Barren surfaces are recorded, but not used in the total quadrat count; a count of barren surfaces is revealing with regard to the density of the fossils in the matrix, recognizing that completely barren specimens uncovered during excavation would not have been collected or recorded. Very large specimens may be divided into more than one sampling quadrat.

The result of this counting technique is a frequency distribution, recording the number of sampling-quadrat occurrences for each taxon. Conversion of the occurrence data to percentage occurrence is calculated by dividing the number of quadrat occurrences of a taxon by the total number of informative quadrats. Hypothetically, each taxon could occur on every surface, so the percentage occurrences observed (frequencies of occurrence) for all taxa in a collection usually will not sum to 100%. Seeds (often broken down by morphotype), wood fragments, axes, roots and unidentifiable plant remains (including comminuted plant debris) also are recorded as categories. As a result, because some quadrats contained only debris, unidentifiable axis remains, or roots, the total occurrence percentage of identifiable leaf and stem taxa may add up to <100%. Occurrences of animal remains and charcoal also are recorded, but these counts are kept separate from the plant fossil counts because they may occur on surfaces barren of plant-fossil remains, and thus could inflate the total number of quadrats considered informative. Counts also are not easily combined because of the potential for the occurrence of more than one taxon on each quadrat (hand-sample) surface. Thus, for example, combining several species of one group, say conifers, into a single conifer occurrence number, will not produce a true frequency unless there had been no quadrat-occurrence overlap among occurrences of the different taxa. In some instances, this problem has been addressed through notes taken during the quantification process.

Despite these drawbacks, the quadrat method is a way to assess rapidly the basic dominance-diversity structure of an assemblage. It circumvents problems associated with “what to count” brought about by compound leaves (does one tree-fern pinnule count as much as one conifer branch?), the preservation of some taxa (e.g., lycopsids) largely as stem remains, and the difficulties in connecting reproductive organs to vegetative remains. Counting methods work best when the assemblage being analyzed is composed of similar-sized plant remains that have similar degrees of fragmentation (e.g., floras consisting of well preserved remains of broad-leaved angiosperms, or of early terrestrial floras composed dominantly of stick-like axial remains). Comparisons of count vs. quadrat sampling (e.g., DiMichele et al., 1991) indicate that similar dominance-diversity sequences are calculated, but that the quadrat method tends to elevate the abundance estimates of rare taxa and reduce the estimated abundances of common taxa, compared to simple counting of remains (Wing and DiMichele, 1995). Neither method is “correct,” the objective of each is to estimate biomass as represented in the original plant community from which the remains are derived.

The results of the quantitative analyses are presented in Table 1. Because of the small size of the samples in most instances, we present only the raw count data, not converted to percentages. The collections are organized stratigraphically, with oldest at the bottom. However, again, the small size of most collections means that stratigraphic ranges of taxa are almost certainly not complete, which is why we treat the flora as if drawn from a single species pool.

We examined the plant fossils for evidence of arthropod herbivory and assigned damage types (DTs) based on shared morphological characteristics using the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira et al., 2007). We described all of the damage by host plant. However, we did not perform quantitative analyses on the DT data, because of the small plant fossil sample sizes at each locality.

**FLORA**

**Pteridophytes**

**Calamitaleans**

The remains of pteridophytes are extremely rare in the Doña Ana Mountains collections. Calamitalean stems were found at two collecting localities, represented by three specimens. They were identified by the regular ribbing of the axes and by the presence of nodes at which the ribs terminated (Fig. 6A-D). The rib ends from adjacent internodes alternate. The ribs in one large specimen (Fig. 6A, B) are particularly wide, and terminate in irregularly elongate ends, forming a somewhat irregular node. These features suggest an affinity with *Calamites gigas* Brongnari. It has been suggested that *C. gigas* had a non-clonal, free-standing growth habit (Barthel and Rößler, 1996) and lived in seasonally dry, moisture-limited habitats (Barthel and
TABLE 1. Stratigraphic distribution of USNM collection sites and their plant, animal, and taphonomic-indicator components. Quantitative methods report the number of hand-sample quadrats on which an object category was observed (see text for methodological details).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>43587</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>43574</td>
<td>6</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42273</td>
<td>5</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42272</td>
<td>4</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42276</td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>41670</td>
<td>34</td>
<td>18</td>
<td>2</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42277</td>
<td>3</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42271</td>
<td>140</td>
<td>56</td>
<td>2</td>
<td>90</td>
<td>16</td>
<td>35</td>
<td>1</td>
<td>2</td>
<td>10</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>41669</td>
<td>25</td>
<td>13</td>
<td>1</td>
<td></td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>11</td>
<td>4</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occurrences</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td></td>
<td>7</td>
<td>18</td>
</tr>
<tr>
<td>Summed Qs</td>
<td>221</td>
<td>91</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>91</td>
<td>16</td>
<td>39</td>
<td>4</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>33</td>
<td>12</td>
<td>9</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>27</td>
<td>5</td>
<td>38</td>
<td>12</td>
<td>11</td>
<td>1</td>
<td>9</td>
<td>2</td>
</tr>
</tbody>
</table>
localities, and at one additional site from which a collection could not be made. Thus, where plant fossil remains were found, conifers almost always were part of the assemblage. In the three collections with the largest sample size (25, 34, and 140 informative hand-sample surfaces), frequencies of conifer remains are <1%, ~20% and ~30%, respectively, thus not dominating any collection. The remains are almost entirely small fragments of foliated, vegetative branches; no diagnostic reproductive remains were identified.

The remains are of two principal kinds (Fig. 8), both attributable to walchian conifers, those with plagiotropic branching habits. Based on the remains in the assemblage, these conifers shed their photosynthetic units as penultimate branches, which has been interpreted as an adaptation to life in seasonally dry habitats with periodic fires (Looy, 2013). Neither of these most common forms has the morphology typically identified as Walchia piniformis Sternberg, which has rather small, recurved leaves of gracile form (Visscher et al., 1986; Looy and Duijnstee, 2013). One form resembles what DiMichele et al. (2013, fig. 5.1) identified, informally, as Culmitzschia americana, using that name to encompass specimens similar to those of Lebachia americana Florin. Such specimens (Fig. 8A-B) have relatively straight leaves that are neither closely adpressed to the axis, nor approach a horizontal insertion (see characterization in Hernandez-Castillo et al., 2014, tables 1-2). The other form (Fig. 8C-D) is more robust, and the leaves are slightly more S-shaped, approaching the morphology of Culmitzschia speciosa (Florin) Clement-Westerhof, but not as inflected as typically found in that morphotype (Clement-Westerhof, 1984).

Peltasperms: Callipterids

The likely peltasperm Rhachiphyllum cf. schenkii (Heyer) Kerp was found at low frequency (8-9%) at two localities (Table 1), both in the lower part of the Robledo Mountains Formation. Specimens (Fig. 9) consist of pinnae or pinna fragments bearing pinnules with an inclined insertion, a deeply incised acrosopic base and a strongly decurrent basiscopic base that are weakly confluent with the subjacent pinnule. Pinnule apices are bluntly pointed. The pinnules are 2-3 times longer than wide. The pinnule midvein is thin and surficial, and the pinnule lamina is flat (the lamina is not vaulted, and the midvein is not sunken); the midvein is slightly asymmetrically disposed in the pinnule lamina, inserted slightly beyond the pinnule midline to the acrosopic side, and traverses the pinnule in a slightly retrograde, but straight manner. Lateral veins are fine, steeply disposed, and relatively straight; those in the main pinnule lamina run a great distance toward the apex prior to contacting the margin.

The characteristics of the Doña Ana specimens conform to Rhachiphyllum schenkii as described by Kerp (1988). This fossil plant is very likely of peltaspermalean affinity, although that has not been established by finding reproductive structures in attachment to vegetative foliage, nor has it been established by cuticular evidence. Rhachiphyllum-type foliage has been found in association with Peltaspernum Harris at some collection locations in Europe, discussed by Kerp et al. (2001). In addition, the foliage bears strong similarity to that of some species of Autunia Krasser emend. Kerp, for which definite attachment to peltaspermalean reproductive organs has been established.
(Kerp, 1982). An early Permian occurrence is consistent with the known stratigraphic distribution of this plant in Euramerica.

**Peltasperms: Supaia and the “Supaioid Complex”**

The principal taxonomic problem encountered in this analysis, one that has delayed preparation of a floristic assessment of the collection for over a decade, is the taxonomic determination of the remains of supaioids. These constitute a group of taxa, most of which are very similar in aspects of their foliar gross morphology, making them extremely difficult to differentiate in fragmentary preservation, even when well preserved. DiMichele et al. (2005) referred to these plants as the “supaioid complex,” and, following Wang (1997), Naugolnykh (1999) and earlier workers, suggested that these, and several other groups of plants, common in the early Permian of Euramerica, are likely of peltaspermous affinity. Those taxa most similar to the Doña Ana Mountains specimens are *Supaia thinnfeldioides* White, *Glenopteris* Sellards emend. Krings et al., and *Supaia anomala* White, the latter of which may belong, as we will argue below, in the genus *Auritifolia* Chaney et al.

The similarities and difficulty of differentiating these different genera were clearly recognized by all of the early
FIGURE 8. Walchian conifers. These specimens may represent different size fragments of the same species. 

A, “Culmitzschia” americana. USNM specimen 713251. USNM locality 41669. 

B, “Culmitzschia” americana. USNM specimen 713258. USNM locality 41670. 

C, Cf. Culmitzschia speciosa. USNM specimen 713252. USNM locality 41669. 

D, Culmitzschia speciosa. USNM specimen 713259. USNM locality 41670. Scale bars = 1 cm.
workers who introduced their names (e.g., Sellards, 1900b; White, 1929; Zalessky, 1934), or extended their application (e.g., Halle, 1927). This difficulty continues to the present day, and is reflected in several papers that compare Euramerican, Cathaysian, and Angaran genera (e.g., Wang, 1997; Naugolnykh, 1999; DiMichele et al., 2005; Krings et al., 2005; DiMichele et al., 2007; Chaney et al., 2009; Mamay et al., 2009). A number of these papers discuss the problems in some detail; Naugolnykh (1999) sums up many of the gross morphological differences in a table, and Krings et al. (2005, p. 193) present a concise summary of the matter.

These plants may all belong to a still larger group with global distribution, lineages that have been assigned to different orders but may have deeper shared roots, including the Peltaspermales, Coryspermales, and perhaps other groups of so-called “Mesozoic seed ferns” (e.g., Taylor, E.L. et al., 2006). The roots of this large clade may be at least in the Early Pennsylvanian, should the type specimen of the genus Protoblechnum Lesquereux (Lesquereux, 1879/1880) be accepted as belonging to this complex.

White (1929), for example, at first was of the opinion that the nearest relatives of Supaia are to be found among Gondwanan forms, noting several similar morphotaxa, including Dicroidium Gothan. In his words (White, 1929, p. 58), “…the reference which I was at first disposed to make of the Hermit plants [Supaia] to the genus Dicroidium, most of whose species, as differentiated by Gothan, appear to me plainly congeneric with Supaia, seems to be precluded…” From that point, White goes on to explain his decision to keep Supaia as a distinct genus, based on morphological features such as simple vs. twice pinnate architecture, and odontopteroid vs. alethopteroid pinnule shape and venation. Specimens attributable to the corysperm Dicroidium have recently been found in the Permian of the Middle East (Kerp et al., 2006; Abu Hamad et al., 2008, 2017), which places them in the late Paleozoic equatorial region, and solidifies a possible link with the peltasperms, biogeographically and morphologically. Furthermore, Abu Hamad et al. (2008) noted that Dicroidium-like foliage occurs in the lower Permian and illustrated two specimens, one of them originally illustrated as Gleichenites neesii.

White (1929) also compared his Supaia to Angaran taxa described by Zalessky (1934), including Brongniartites Zalessky. Naugolnykh (1999, p. 693) noted, however, that Brongniartites is an invalid name (already having been occupied for fossil wood at the time of its description), and, furthermore, that it should be subsumed in Compsopteris Zalessky. Naugolnykh (1999) argued that Compsopteris mostly has been misapplied to non-Angaran specimens found throughout Euramerica, specimens he believed may, in fact, be attributable to Glenopteris. Naugolnykh notably drew an exception for the specimens described as Protoblechnum wongii Halle from the Guadalcanal region of Spain, described by Broutin (1977). These specimens are part of a remarkable flora that also contains a number of other elements of Angaran affinity (e.g., see also Broutin, 1974, 1986). The Guadalcanal flora raises some serious questions about our understanding of extrabasinal evolutionary and biogeographic dynamics and
patterns (e.g., Looy et al., 2014). The rarity, in Euramerica, of the fossil-plant assemblage found in this flora suggests that it likely lived in areas outside of depositional basins most of the time, and entered basin environments either rarely, under exceptional circumstances, or, if more frequently, almost always under conditions when preservation potential was very low, such as during times of strong climatic seasonality (Gastaldo and Demko, 2011).

The affinities of the supaioid lineage, including additional groups such as callipterids and perhaps some of the "gigantopterids," are probably with the Peltaspermales. This hypothesis has been based on the widespread co-occurrence of peltaspermalean reproductive structures with vegetative remains of these plants; the evidence for a peltaspermalean affinity of the gigantopterids is weaker than for most of the other groups. More recently, peltaspermalean affinities of a number of suspect peltaspers have been supported by studies comparing their cuticular or epidermal features (e.g., Wang, 1997; Naugolnykh, 1999; Krings et al., 2005; Chaney et al., 2009; Karasev, 2013) with those of well understood peltaspermalean plants, such as Autunia (e.g., Kerp and Barthel, 1996) or Germaropteris (Kustatscher et al., 2014). Wang (1997) found Autunia-like fructifications in association with remains he assigned to Supaia from upper Permian strata of China. Meyen and Migdisova (Kustatscher et al., 2014), Wang (1997) found Autunia-like fructifications in association with remains he assigned to Supaia from upper Permian strata of China. Meyen and Migdisova (Kustatscher et al., 2014), identified a consistent association of Peltaspernum remains with Compsopteris. The peltaspermalean reproductive organ Autunia (originally described as Sandrewia Mamay was placed in synonymy with Autunia by Kerp [1982]), was found in association with Comia Zaleskia and Aurgifolia in Permian strata of Texas (Mamay et al., 2009; Chaney et al., 2009). And, among other lineages, some forms of callipterid foliage have been found in attachment to the peltaspermalean reproductive organ Autunia, leading to the establishment of Autunia as a whole-plant genus (Kerp, 1988); other forms of callipterid foliage are likewise suspected to be peltaspermalean (e.g., Meyen and Migdisova, 1969). Over several years, a fuller picture also has emerged around plants previously assigned to the Mesozoic genus Lepidopteris Schimper, which, based on remains found in the upper Permian of Europe, were correlated with Peltaspernum-type reproductive organs as the basis of a whole-plant genus (Poort and Kerp, 1990). Additional European discoveries led to their classification as the new genus Germaropteris Kustatscher et al. (Kustatscher et al., 2014), which has subsequently been found in lower Permian deposits in Texas (Baumgardner et al., 2016).

Supaia and/or Glenopteris

The most common supaioid remains found in the Doña Ana Mountains collections may represent a single species or two similar species in different genera. One candidate species is Glenopteris splendens Sellards, one of several Glenopteris species described by Sellards (1900b), which Krings et al. (2005) suggest to be part of a single morphological species; Figures 10A-B illustrate Glenopteris specimens from original Kansas localities of Sellards and White, for comparison with the Doña Ana Mountains specimens. The main suspect species is Supaia thinnfeldioides; specimens from White’s (1929) syntype suite are illustrated in Figures 10C-D for comparison with Doña Ana Mountains specimens. Although S. lineatifolia White and S. rigida White are similar to S. thinnfeldioides, the latter is the earlier described species and was designated the type species of the genus by White (1929); S. thinnfeldioides thus has priority should these three be considered variants of a single species. The Doña Ana Mountains remains also are strikingly similar to Protoblechnum wongii Halle, from the Cathaysian flora (Halle, 1927), although we prefer to restrict possible affinities to the more likely western Pangean taxa.

Examples of the Doña Ana Mountain specimens are illustrated in Figures 11-13. Determining species affinity on a case-by-case basis is greatly handicapped by fragmentary preservation and the intergrading nature of morphological features among many specimens. No morphologically unambiguous whole leaves were found. However, one specimen (Fig. 11A) appears to preserve the base of the leaf. If this is the case, the base is robust, and the leaf is unforked, suggesting attribution to Glenopteris splendens. Another specimen (Fig. 11B) also suggests the base of a leaf, but its preservation is unusual, and, although it is likely attributable to the supaioids, details of its morphology are unclear. The rachises in both of these specimens are longitudinally striate. A third specimen (Fig. 11C), also with ambiguous morphology, may be interpreted as a stem, approximately 0.75 cm in diameter, bearing several subopposite leaves with slender petioles and, as seen in the lower part of the specimen, clasping bases; were this to be a supaioid, it again would suggest a Glenopteris affinity in the absence of any evidence of petiolar forking. Leaf tips (Fig. 10D-E) are similar to specimens of Supaia thinnfeldioides and Glenopteris splendens, with somewhat greater similarity to G. splendens. The pinnules shrink abruptly in size near the apex and become weakly confluent. The apical pinnule is small, rounded, and indistinct. More like G. splendens than S. thinnfeldioides, however, the pinnules enlarge at the base and are markedly auriculate in the specimen illustrated in Figure 11E.

Details of pinnule shape and leaf architecture of the midfrond can be seen in the two specimens illustrated in Figure 12. In both specimens, the pinnules are elongate, with lengths greatly exceeding widths. Pinnule insertions are only slightly angular, with slight decurrence at the base of the midrib. Most pinnules are without basal auriculae, or are only slightly auriculate, and are free from adjacent pinnules. The pinnule base may be slightly constricted, although this appearance is exaggerated by matrix infilling around the pinnule bases, evidently reflecting slight rotation of the pinnules from the horizontal plane in life, leading to some basal irregularities. Pinnule margins are straight to slightly undulate. The midvein is well marked, slightly sunken in the pinnule lamina, and very straight, running to near the pinnule apex, which is bluntly pointed. Both specimens are slightly, but clearly, bent, as if they may have been one-half of a forked leaf. In this bending, and in overall pinnule shape and aspect, the illustrated specimens are broadly representative of the larger population, and affinities with S. thinnfeldioides are suggested.

Lateral venation is very difficult to make out in most of the Doña Ana Mountains specimens (Fig. 13). This may be due to the cortaceous nature of the laminae, reflected in the resistance of the foliage to breakage or folding, and by such features as the sunken midveins. Where lateral veins can be seen, they have a decurrent insertion, and make a relatively narrow angle with the midvein, resulting in a steep trajectory and long course through the lamina (Fig. 13A, C). They appear to dichotomize rarely and vary from unforked to forked no more than twice; fasciculae are weakly developed to absent. In most specimens (e.g., Fig. 13B), the lateral venation is essentially invisible. These venation characteristics are equally attributable to G. splendens or S. thinnfeldioides.

Supaia anomala

When White (1929) described the genus Supaia, he included in it specimens with a broad range of morphology, making clear delimitation of the genus difficult, particularly given the significant morphological overlap of some of White’s Supaia species with some of the taxa mentioned above (specifically Protoblechnum, Compsopteris, Glenopteris, and Brongniartites). In the more fully known of White’s species, e.g., S. thinnfeldioides, and in particular those that overlap with the above-mentioned forms, the main petiole/rachis is forked in
FIGURE 10 (facing page). *Glenopteris splendens* and *Supaia thinnfeldioides* from the original collections of Sellards and White, for comparison with New Mexico specimens. **A**, *Glenopteris splendens* showing apical region; note fork in midvein. USNM specimen 8084. Original Sellards specimen from Banner Kansas. **B**, *Glenopteris splendens* showing unforked base of leaf. USNM 8298cp. Original White specimen from Elmo Kansas. **C**, *Supaia thinnfeldioides*. Note forked petiole. Specimen is large (note scale bar). Part of original syntype suite of White (1929, plate 14). USNM 38030. USGS locality 7880. **D**, *Supaia thinnfeldioides*. Specimen is large (note scale bar). Part of original syntype suite of White (1929, Plate 15.2). USNM 324599. USGS locality 7880. Scale bars = 1 cm, except for image C where scale bar = 20 mm.

FIGURE 11. Either *Supaia thinnfeldioides* or *Glenopteris splendens*. Architecture. **A**, Possible base of leaf (arrow), strongly suggesting a non-forked architecture. USNM 713273cp. **B**, Possible base or lower portion of leaf (arrow), equivocally suggesting a non-forked architecture. USNM 713272. **C**, Axis (stem?) bearing several side axes noted by arrows (solid = unequivocal; dashed = likely but taphonomically obscured). Position and width of main axis is marked by heavy arrows. USNM specimen 713276. **D**, Leaf tip; pinnules increasingly confluent approaching apex. USNM specimen 713274. **E**, Leaf tip; Note rachis dichotomy below apex and steep, non-fasciculate lateral venation. USNM specimen 713278. All specimens from USNM locality 72271. All illustrated at the same magnification. Scale bar below D = 1 cm.

its lower portion, and the majority of the pinnules are inserted on the two resultant rachises (Fig. 10C). This forked architecture could not be demonstrated for all species, however, and their gross morphology allows for the possibility that they were not forked (e.g., *Supaia merriami*, which Krings et al. [2005] note to be virtually identical to *Glenopteris splendens*, which is unforked; Fig. 10B). Additionally, in most of these species, the pinnules are clearly distinct, even if they may be auriculate and slightly connate in some specimens or portions of the leaf; and, furthermore, are generally significantly longer than wide (Fig. 10A, D). Venation in almost all of White’s *Supaia* species is relatively simple in its organization, with veins inserted at an angle and climbing steeply through the pinnule lamina, forking rarely, and not forming distinct fascicles. The relative simplicity of the lateral pinnule venation in White’s species is subject to some question, because of the poor preservation of fine details in most specimens. To the extent that White’s descriptions are accepted, the new species attributed to *Supaia* by Wang (1997) deviate from this morphology in having weakly fasciculate lateral veins. Such vein bundling may be a very important characteristic that casts some doubt on the attribution of the Chinese material to *Supaia*. Distinctly fasciculate veins, as we discuss below, may be diagnostic, at least in some taxa, such as *Comia* and the likely closely related genus, *Auritifolia*. 
FIGURE 12. Either *Supaia thinnfeldioides* or *Glenopteris splendens*. Mid-leaf characteristics. **A-B**, USNM specimen 713280. **C-D**, USNM specimen 713281. Both specimens from USNM locality 42271. Scale bars = 5 mm in A and C, 1 cm in B and D.

FIGURE 13 (facing page). Either *Supaia thinnfeldioides* or *Glenopteris splendens*. Pinnule details. **A**, USNM specimen 713275. Note non-fasciculate, relatively steep ultimate venation. **B**, USNM specimen 713271. Note non-fasciculate steeply disposed ultimate veins. Cause of scalloped margin uncertain. **C**, USNM specimen 713279. Note the lack of visible ultimate veins and somewhat wrinkled lamina, the typical preservation states for specimens of this morphotype. All specimens from USNM locality 72271. Scale bars = 1 cm.
Morphology of *Supaia anomal* Syntypes. Among White’s (1929) *Supaia* species, *Supaia anomal* stands out as very different from the others. White illustrated a number of specimens, which today constitute a suite of syntypes (Fig. 14-16). However, in our opinion, as expressed earlier (DiMichele et al., 2007), these specimens are not necessarily similar enough to constitute a coherent species concept; two are very similar to *S. thinnfeldioide*.* Thus, we restrict our description to those that form what is, in our opinion, a coherent morphotype, noting, however, that there are specimens, encountered in fragmentary preservation, that are difficult to assign and have similarities to each of these morphotypes (e.g., Fig. 18A-B).

Specimens of White (1929) that we consider to be *Supaia anomal sensu stricto* (Figs. 14, 15A-B): USNM 324582 (White, 1929, plate 20, fig. 3), 324583 (White, 1929, plate 21, fig. 1), 324584 (White, 1929, plate 21, fig. 2), 324585 (White, 1929, plate 21, fig. 3), 324588 (White, 1929, plate 24, fig. 4).

Specimens probably assignable to *Supaia anomal sensu
**FIGURE 15.** *Auritifolia* (*Supaia*) *anomala* syntypes of White (1929). A, USNM specimen 324588. Forked basal portion of leaf (arrow). (White, 1929, Plate 24.4). B, USNM specimen 324582. (White, 1929, Plate 20.3). C-D, USNM 324587. We include this specimen tentatively in *Auritifolia anomala*. (White, 1929, Plate 22). All specimens from USGS locality 7880. Scale bars = 1 cm, except in in C, scale bar = 5 mm.

*stricto* (Fig. 15C-D): USNM 324586 (White, 1929, plate 21, fig. 4), 324587 (White, 1929, plate 22).

Specimens of White (1929) that we exclude from *Supaia anomala sensu stricto* (Fig. 16): USNM 38035 (White, 1929, plate 20, fig. 1), and 324581 (White, 1929, plate 20, fig. 2).

Using the restricted suite of specimens, the species consists of a relatively large leaf that has a basal fork, the petiole dividing into two diverging main rachises. The main rachis/midrib is usually relatively straight in most specimens, but may become somewhat zig-zag in the upper portions, each deflection corresponding to the insertion of a laterally borne pinnule. Pinnules have a subopposite insertion, at an approximately 45° angle with the midrib. They are 1-2 cm wide, and, in the main part of the leaf, 7-10 cm or more in length. Pinnule laminae may be slightly undulate, and the margins vary from straight to slightly irregularly wavy. The pinnule apex is triangular and bluntly pointed. Pinnules are decurrent and fused with the adjacent pinnules, forming a broad ribbon of tissue that flanks the main leaf rachis, making the entire leaf appear ribbon-like.

In apical regions, where the midvein/rachis is alternately deflected (zig-zag), it can be difficult to differentiate the rachial wings from the bases of pinnules. The main rachis is wide and slightly sunken in the lamina; the pinnule midveins also are wide, relatively speaking, are slightly recessed in the lamina and extend to near the pinnule apex. Lateral venation is extremely difficult to observe in White’s suite of syntype specimens, in either adaxial or abaxial view, suggesting that the lamina was coriaceous, possibly even slightly succulent. Where there are suggestions of lateral venation, it appears as if the veins are grouped into fascicles, which may correspond to undulations in the pinnule lamina. The apical region of the leaf reveals much about the leaf’s organization and development. In the apical region, the midvein/rachis and flanking lamina undergo a series of back-and-forth, zig-zag dichotomies, terminating with an asymmetrical apical fork, surmounted by small extensions of the midvein/rachis and the lateral lamina. As mentioned below, the lamina continuously flanks the rachis of the leaf, so that the apical division really does not produce two clearly differentiated pinnules but, instead, continuations of the laminate rachis.

**Designation of a *Supaia anomala* lectotype.** White did not designate a holotype. We therefore designate herein USNM specimen 324583 from the syntype suite as the lectotype of *Supaia anomala* White (White, D., 1929, Flora of the Hermit Shale, Grand Canyon, Arizona: Carnegie Institution of Washington Publication 405, p. 1–221; Fig. 14A-B). The specimen is housed in the paleobotanical collections of the National Museum of Natural History, Smithsonian Institution. It is from U. S. Geological Survey paleobotanical locality 7880, Hermit Shale, lower Permian, Arizona, USA.

*Supaia anomala from the Oscura Mountains, New Mexico.* *Supaia anomala* is a prominent component of a flora described from lower Permian strata of the Abo Formation, which crops out...
FIGURE 16. Excluded *Supaia anomala* syntypes of White (1929). We exclude these specimens from *Auritifolia anomala* based on their proportions. They should be considered *Supaia* sp., comparable to *Supaia thinnfeldioide*es. A comparison with White’s (1929) original illustrations indicates that those were skillfully retouched to remove marks made during preparation; as far as we are able to discern, however, no alterations were made in the characteristics of the specimens, unless noted. **A**, USNM specimen 38035. (White, 1929, Plate 20-1). **B**, USNM specimen 324581. (White, 1929, Plate 20-2). Both specimens from USGS locality 7880. Scale bars = 1 cm.

FIGURE 17. Specimen originally attributed to *Supaia anomala* by DiMichele et al. (2007, fig. 13Ab, USNM specimen 520420). We reject that identification here. Image from DiMichele et al. (2007) used with permission of Elsevier Scientific Publishers BV.
FIGURE 18. Auritifolia anomala transitional, uncertain and typical specimens. A, Specimen with characteristics more like Supaia thinnfeldioides/Glenopteris splendens than A. anomala, including size and venation of pinnules, but with a well developed striate, winged rachis and short confluent pinnules. USNM specimen 713283. B, Specimen of uncertain affinity, but with some features A. anomala. USNM specimen 713286. C, Typical A. anomala: note pinnule surface undulations and rachis deflection at top of image. USNM specimen 713294. D, Typical A. anomala. USNM specimen 713291. All specimens from USNM locality 42271. Scale bars = 1 cm.
in the Oscura Mountains, in central New Mexico (DiMichele et al., 2007, figs. 12-15). These strata are broadly coeval to those of the Robledo Mountains Formation in Lucero Arroyo of the Doña Ana Mountains. If the assignment of the specimens designated *Supaia anomala* in that paper is accepted, the specimens reveal a great deal more about the morphology of the leaf, particularly its architecture, than the suite of specimens described by White (1929). However, the specimens are significantly larger than any in White’s original Hermit Shale syntype suite and therefore show features that are not evident in the type material; we thus now question the assignment to *S. anomala* of some of the material illustrated as that species by DiMichele et al. (2007).

Similarities between the White (1929) specimens and most of those from the Oscura Mountains, as described by DiMichele et al. (2007), include the following: (1) a ribbon-like lamina flanking the main rachises of the leaf; (2) subopposite insertion of pinnules that originate from what appear to be dichotomies in the ribbon-like leaf rachis; (3) broad and long pinnules, the bases of which may be slightly constricted, and the laminae of which form a continuum with the laminae flanking the main rachis; (4) somewhat zig-zag rachial dichotomies in the distal regions of the leaves; and (5) overall relatively large size of the leaves, tens of centimeters in length and width.

Distinct and different aspects of the Oscura Mountains specimens are present only in the larger specimens, particularly the one illustrated in DiMichele et al. (2007, fig. 13, USNM specimen 520420; re-illustrated here as Fig. 17), which is more than 40 cm in width and lacks the basal portion. If this specimen is accepted as *Supaia anomala*, the leaf has a pinnate architecture with a basal fork (suggested by, but not visible in the specimen), followed by additional rachial/laminar dichotomies. Such architecture would require that most of the specimens attributable to *S. anomala* from both the Hermit Shale and Doña Ana Mountains be fragments drawn largely from more apical regions of leaves. However, there is no evidence in any specimens, from the Hermit Shale, the Doña Ana Mountains, or among the other specimens from the Oscura Mountains, of further dichotomies in the pinnules themselves, as seems to be the case in specimen 520420. Neither has its ovobinate pinnule shape been observed in any of the suites of specimens from these other areas. Thus, we here exclude this specimen from *Supaia anomala* and suggest that the earlier attribution was in error. At present, the affinities of this specimen must remain uncertain.

In contrast, the specimen illustrated in DiMichele et al. (2007, fig. 14, USNM specimen 520421), which is also relatively large, may represent the lower portions of a specimen (so designated by White, 1929, p. 62, line 14), appear to represent the lower portions of a *Supaia anomala* leaf. If so, the morphology possibly demonstrates a basalar dichotomy in the rachis and its flanking lamina. The only other specimen of *S. anomala* known to us that demonstrates such a dichotomy is that illustrated by White (1929, plate 24, fig. 4, USNM specimen 324588), reillustrated here as Figure 15A.

**Supaia anomala in the Doña Ana Mountains Collections.**

Numerous specimens from a single collecting locality (USNM 42271) in Lucero Arroyo conform morphologically to White’s *Supaia anomala* in its syntype concept, as described above; examples are illustrated in Figures 18C, 18D and 19-21. In terms of the most basic, gross morphological aspects of the leaf, these specimens are ribbon-like, with the leaf lamina running continuously along the main rachis and into the pinnules without constriction or interruption (Figs. 18C-D, 19A-B). The leaves likely terminate in a series of apical rachial dichotomies (Fig. 19C). Pinnule laminae are flat (Figs. 18C, 19A-B) to distinctly undulate (Fig. 20A-C) and have slightly sunken, well marked midribs (Fig. 21A).

Unlike White’s specimens, in which ultimate venation is mostly obscure, many of those from the Doña Ana Mountains have distinct venation in the pinnules, and that venation is strongly fasciculate (Figs. 20B-E, 21B-C). The fascicles broadly conform to undulations in the pinnule laminae, where such undulations are present (Fig. 20B-C). Each fascicle has a central vein that persists about two-thirds of the distance to the pinnule margin, where it breaks up into numerous ultimate, tertiary veins (Figs. 20D-E, 21B-C), which undergo several further dichotomies. Most of the tertiary veins, and their derivatives, produced from the terminal end of the midvein reach the pinnule margin. However, most of the tertiary veins produced lateral to the midvein, in the lower and middle portion of the pinnule lamina, do not reach the margin. Rather, they come into contact with tertiary veins from the adjacent fascicle, but it is not clear if they fuse. Additionally, some of these tertiary veins appear to anastomose within the fascicle, although it is difficult to determine if these are actual vein anastomoses or taphonomic happenstance, resulting from the desiccation and formation of wrinkles in the lamina, which was thick and may have desiccated prior to burial in sediment.

The only plants of possible peltaspermous affinity known to us with a venation pattern similar to that seen in these Doña Ana Mountains specimens are attributable to *Auritifolia waggoneri* (see Chaney et al., 2009, figs. 3, 5). Also, as in the Doña Ana Mountains leaves, the pinnules of *A. waggoneri* may be undulate, with the undulations conforming to the position of the fascicles. Importantly, the leaves of *A. waggoneri* undergo a series of zig-zag rachial dichotomies in the upper portions of the leaf, terminating in two (large) apical pinnules (Chaney et al., 2009, fig. 8). As a final similarity between *Supaia anomala* and *A. waggoneri*, the pinnules in *A. waggoneri* may be basally fused to the adjacent pinnules, forming somewhat of a wing laterally to the main rachis, although this is not nearly as well developed as in *S. anomala*. *Supaia anomala* also bears comparison to *Comia*, and, in particular, *Comia craddockii* (Mamay et al., 2009), which also has distinctly fasciculate venation, although the veins in *Comia* all reach the margin of the pinnule and do not anastomose (see Mamay et al., 2009, fig. 9, which is a reproduction of the Zalessky, 1934 line drawing of the type specimen; and see figures and line drawings of other species from the lower Permian of Texas in that paper). Also, as in *C. craddockii*, the pinnules of *S. anomala* appear to be smallest at the base and in the upper parts of the leaf, reaching maximum dimensions in the central portion.

**Reassignment of Supaia anomala to Auritifolia.** Based on the aforementioned observations and discussion, we believe *Supaia anomala* is sufficiently distinct from other species assigned to *Supaia* by White (1929), as represented by the type species, *S. thinfeldoioides* (so designated by White, 1929, p. 62, line 14), to be removed from the genus. Furthermore, *S. anomala* shares several critical characteristics with *Auritifolia* and fits well in that genus. Making this separation is a step toward consolidating the morphological features of *Supaia* and restricting/refining to some extent the overlaps among *Supaia* and several other taxa of the supaioid complex.

**Auritifolia anomala** (White) DiMichele, Lucas, Chaney, Donovan, Kerp, Koll, and Looy

**Emended diagnosis:** Petiolate, forked leaf, main rachis dichotomizing in lower 1/3 of leaf. Pinnules borne suboppositely on two derivative rachises, each principal rachis forking once to several times in apical region. Rachis consisting of ribbon-like lamina flanking the petiole and two derivative rachises. Multiple, laterally borne pinnules inserted at approximately a 45° angle to rachis. Pinnules in larger leaves 1-2 cm in width and typically 10 cm or more in maximum length, shorter at leaf base, elongating in the central region, becoming short again in upper portions. Pinnule laminae continuous with the laminar regions flanking rachis, giving the leaf an overall ribbon-like appearance. Each ultimate rachis terminating in a pair of unequal pinnules that appear as simple extensions of rachis and flanking laminae.
FIGURE 19. Auritifolia anomala. A, Mid-leaf specimen of typical aspect. USNM specimen 713295. B, Specimen of image A at lower magnification to show contrast in form between Supaia thinnfeldioides/Glenopteris splendens, at top, and A. anomala at bottom. USNM specimen 713295. C, Specimen apical region of leaf; note forked rachial vein and lateral laminar wings (arrow). USNM specimen 713292cp. Both specimens from USNM locality 42271. Scale bars = 1 cm.

Pinnule surfaces variably undulatory, undulations conforming to lateral vein fascicles. Pinnule margins straight to somewhat irregular, terminating in a bluntly pointed apex. Main rachial vein and pinnule veins sunken in lamina, but pinnule laminae not distinctly vaulted, suggesting thick, coriaceous laminar construction. Lateral veins organized in fascicules. Central, secondary vein reaching through approximately 2/3 of pinnule lamina, breaking up into tertiary veins that reach pinnule margin. Additional tertiary veins, originating directly from fascicular midvein, do not reach pinnule margin but abut tertiary veins from adjacent fascicle. Intrafascicular anastomoses present; interfascicular anastomoses possible.


**Lectotype (designated herein):** United States National Museum specimen 324583.

**Type Locality:** Hermit Shale Formation, Supai Group, lower Permian (Cisuralian), Grand Canyon, Arizona, U.S.A.

**Gigantopterids**

Several specimens in the Doña Ana Mountains collections can be attributed with certainty to the gigantopterids, whereas two others are of problematic morphology but may belong to this group. These specimens are restricted to two collecting
localities, USNM 41669 and USNM 42271, both among the larger collections (Table 1). The “gigantopterids” sensu lato are a phylogenetically enigmatic group of plants. Recent reviews of this group, which address some of the taxonomic and biogeographic problems, include Glasspool et al. (2004a), Booi et al. (2009) and Koll et al. (2017). Among those publications, Glasspool et al. (2004a) reanalyzed the Chinese specimens on which the gigantopterid concept is based, and recommended restricting the group to *Gigantopteris* and *Gigantonoclea*, pending a thorough reevaluation of the entire plexus of taxa traditionally placed in this group.

In a broad sense, the gigantopterids sensu lato have two principal centers of distribution, one in Cathaysia and nearby peri-Tethyan areas, in eastern Pangea, and the other in the western Pangean regions of Euramerica. Although specimens from these two areas have been assigned to many of the same genera, it is not clear to what extent morphological similarities are due to evolutionary convergence vs. common ancestry. Koll et al. (2017) suggested that there are, indeed, sufficient similarities to justify recognition of several shared genera. On the other hand, as these authors note, there clearly are some genera that are not shared, and others where convergence seems
FIGURE 21. *Auritifolia anomala*. A-B, Specimen of typical aspect with well developed fasciculate venation, particularly visible in enlargement image B. USNM specimen 713296. B is a composite digital image. C, Pinnule tip with well developed ultimate vein fascicles; also note spheroidal arthropod galls (arrows, DT247). USNM 713289. Both specimens from USNM locality 42271. Scale bars = 1 cm.
to underlie similarities in morphology. Evolutionarily, the group is distinct in its complex, anastomosing venation, some of which is notably angiosperm like (Glasspool et al., 2004b), and in the biogeochernistry of some Cathaysian forms, also similar to that of angiosperms (Taylor D.W. et al., 2006).

**Cf. Zeilleropteris Koidzumi**

Mamay (1986) described two new species of gigantopterids, previously assigned tentatively by Read and Mamay (1962) to *Gigantopteridium* Schenk. One of these species, with four orders of venation, was assigned to *Zeilleropteris* Koidzumi, as *Zeilleropteris wattii* Mamay. Two years later, Mamay (1988) described a second morphotype from the early Permian of Texas, which he assigned to *Gigantonoclea* Koidzumi, based on small fragments with complex, reticulate venation; the venation might be interpreted as representing four orders of vein branching, although the reticulations are so numerous, and the mesh they form so compact, that such counting of vein orders seems superfluous and uninformative.

The Doña Ana Mountains specimens are all fragmentary, but they preserve enough of the morphology of the leaf to permit comparison with known forms of gigantopterids, particularly the two mentioned above. They are most similar to *Zeilleropteris wattii*, and fall within the scope of specimens that have been assigned to that species; that said, the concept of *Z. wattii* either has drifted in its application (by us and others), or Mamay’s (1986) original diagnosis was too narrow, confined to only a portion of the natural population, because specimens such as those described and illustrated here in Figure 22, lack crucial features that have been considered typical of the genus *Zeilleropteris*.

Leaf laminae in the Doña Ana specimens are broad and relatively flat, with slightly scalloped margins. Secondary veins depart from the midvein (primary vein) at a slight acroscopic angle, with little or no decurrence in their insertion. They proceed about ¼ of the distance to the margin, in the convex lobes, before giving rise to a terminal spray of tertiary veins. Tertiary veins originate from the secondary veins or directly from the primary vein. Those tertiary veins that originate laterally from the secondary vein are inserted in an opposite-alternate pattern and make an angle of about 30° with the secondary vein. The tertiary veins generally dichotomize one time, sometimes two, and these branches, which may be considered quaternary veins, fuse with one another to form elongate, open meshes. Initial forks of tertiary veins may occur quite close to the insertion point of the vein (thus not confined to the terminal part of a long tertiary vein), and once these veins begin to dichotomize, the matter of what is a tertiary vs. quaternary vein becomes moot.

This pattern of vein branching means that the secondary veins are the central veins of fascicles, and define the most immediately visible aspect of the venation. Tertiary and quaternary veins are visually difficult to separate, although this can be done technically, but their pattern of fusion into elongate meshes means that the main (secondary) vein of a fascicle appears to be flanked by a weakly developed system of reticulate veins.

Quaternary veins fuse with veins from the adjacent fascicle to form a weak suture vein. Suture veins trace a somewhat zigzag path, beginning about 1/3 of the distance from the main midrib (primary vein) and extending to just below the margin, terminating below a shallow sinus.

As mentioned above, these Doña Ana specimens deviate from Mamay’s (1986) original description of *Zeilleropteris wattii*. The tertiary veins are not elongate, dividing into quaternary veins at their tips, close to the location of the suture vein. As a consequence of the absence of elongate, clearly defined tertiary veins, there are not distinct fascicles in the areas of the lamina between adjacent secondary veins. Therefore, there is no inter-tertiary suture vein, as described for *Z. wattii*, in which there were two suture veins, one between adjacent tertiary-vein fascicles and one between adjacent secondary veins and their resultant cloud of tertiary and quaternary veins. Furthermore, the inter-secondary-vein mesh (composed of the nearly undifferentiable tertiary and quaternary veins) does not originate clearly at the junction between the primary vein and the lower of any given pair of secondary veins, strong features of both *Gigantopteridium* and *Zeilleropteris* (Koll et al., 2017). In this latter feature the specimens described here fall somewhere between *Gigantopteridium* Koidzumi and *Evolsonia* Mamay. Because entities with this type of venation have been identified (by us – unpublished) elsewhere in the American southwest, they may point to the existence of a distinct species, or even a new genus. Questions can be raised about the generic assignment of the specimens Mamay (1986) identified as *Zeilleropteris*. The type material of Koidzumi (1936) is small and fragmentary, and thus can be assessed only by its venation. As noted by Mamay, however, the American form has distinctly bifurcate leaf architecture, whereas the architecture of Chinese specimens later assigned to *Zeilleropteris* lacks such a bifurcation and have distinctly lobed margins. The Doña Ana specimens are too incompletely preserved to demonstrate overall leaf architecture.

The Doña Ana specimens also may be compared with *Gigantonoclea*. They differ from this genus in several critical ways. Most importantly, they do not form a looping mesh (well illustrated in Glasspool et al., 2004a); in *Gigantonoclea* the higher order veins loop along the secondary and primary veins, and this is not seen in the Doña Ana specimens. In fact, it is unlikely that the specimens identified by Mamay (1988) are, in fact, *Gigantonoclea*, as indicated by Glasspool et al. (2004a).

They lack some of the critical venation features of the genus and are too incomplete for any such assignment, particularly considering its paleobiogeographic implications. Just what they may be is another matter.

**Possible Gigantopterids of Uncertain Affinity**

Two specimens with gigantopterid-like characteristics (Figs. 23-24) occur at USNM locality 42271. These shared characteristics are most clearly marked at the detailed level of the ultimate venation, which we describe here working backward from the ultimate to the more proximate veins. The most notable feature is the fasciculate organization of the venation, with the ultimate veins contacting those of the adjacent fascicles to form a suture vein. The ultimate veins originate from the central vein of the fascicle, with which they make an approximately 30° angle. The veins branch dichotomously two or three times (they are difficult to discern due to the nature of preservation), and do not appear to anastomose with other veins from the same fascicle. The fascicle midveins are inserted in a longitudinally striate rachis. This venation pattern is most similar to that of *Gigantopteridium* Koidzumi.

The laminar portions of the leaf have distinctly lobate margins that are very deeply incised. The main veins of the fascicles terminate in the lobes; the suture veins terminate in the sinuses. The suture veins may have a decurrent insertion in the main, primary racinal vein of the lamina. They become progressively less well developed toward the lamina margin and dissipate short of the margin. If the suture vein is, indeed, inserted directly in the primary midvein of the lamina, this feature would add a further complication to the identification of these specimens. *Evolsonia texana* is the only North American species in which the suture vein arises midway between two adjacent secondary veins. In contrast, in both *Gigantopteridium* and *Zeilleropteris* the suture vein originates at the junction between the lower secondary and primary vein. Thus, different aspects of the venation in the Doña Ana Mountains specimens offer conflicting indications regarding assignment to known
FIGURE 22. *Cf. Zeilleropteris*. All specimens fragmentary. A, Note insect margin feeding damage (arrow, DT12, close-up in Fig. 28H). USNM specimen 713248. B, USNM specimen 713249. C, USNM specimen 713250. D, USNM specimen 713302. Specimens in A-C from USNM locality 41669. Specimen in D from USNM locality 42271. Scale bars = 1 cm.
FIGURE 23. Gigantopterids of indeterminate affinity. A-B, Note spheroidal arthropod gall with domed central chamber adjacent to the midvein (arrow in image B, DT247). USNM specimen 713284. C-D, Possibly multiple leaves attached to a common stem. Arrow marks lamina that is possibly joined to immediately adjacent lamina on opposite side of putative stem. Enlargement in D to illustrate fasciculate venation and development of suture veins (arrows). USNM specimen 713285cp. Both specimens from USNM locality 42271. Scale bars = 1 cm.

genera. The quality of preservation, however, prevents this uncertainty from being resolved.

Difficulties arise in interpreting the overall morphology of the leaf, which is demonstrated by USNM specimen 713285 (Fig. 23C). In this specimen, several laminate portions of the leaf appear, at first examination, to be suboppositely, pinnately arranged on a central axis, which is either a rachis or a stem. In this interpretation, the laminae would be interpreted either as pinnules of a compound leaf or as simple leaves on a common axis. However, the first lamina on the right (marked by an arrow in Fig. 23C) appears to be inserted on the backside of the main axis, which is twisted or bent at that point. Here, careful examination suggests that the lamina on the right may be attached to the immediately adjacent, fragmentary lamina on the left side of the axis, to form a single leaf with a basal dichotomy. Furthermore, at the left side of the specimen, a pair of laminae is positioned as if the laminae could be parts of a forked leaf, although no connection is preserved. It is difficult to know which, if either, of these interpretations is correct. On a variety of lines of evidence, however, some gigantopterids have been interpreted as vines (H. Li et al., 1994; Seyfullah et al., 2014) or scrambling plants (Simon et al., in press), which, if also the case here, would comport with the small, flexuous aspect of the main axis of this specimen and support its interpretation as a stem.

Without additional material, it is difficult to decide how to classify these specimens. If part of a pinnate leaf, and if accepted
as gigantopterids, they would constitute the first documented pinnate leaves in North American members of this group. If the laminae are portions of forked leaves attached to a common axis they would most likely be attributed to *Gigantopteridium*, although with marginal characteristics not generally seen in that genus; in that case, they might be considered distinct from *Gigantopteridium americanum* (White) Koidzumi.

**Cf. Yuania H.C. Sze**

USNM locality 41670 is the uppermost plant-bearing bed found in the lower part of the Robledo Mountains Formation. The deposit appears to represent a variable-flow, possibly flashy discharge channel fill. Plant fossils were angularly disposed in sandstone; the lower contact is erosional with underlying strata and there is a gravely lag at the base, which was rich in seeds. Among the allochthonous plant fossil remains preserved in this deposit, a morphologically distinctive specimen of uncertain affinity, USNM specimen 713256, is illustrated in Figure 25.

The specimen appears to be a flabellate lamina attached to a woody axis. The lamina is fragmentary, with only its lower portion preserved. In addition, the lamina is partly obscured by the woody axis, the texture of which (the axis) is revealed best under the lighting of the right-hand photograph, and which is > 10 mm in diameter. The lamina seems to have a broad attachment to the axis. This characteristic is further suggested by two arcuate, carbonaceous features seen (Fig. 25, white arrows) in the area of the stem where the partially permineralized woody fabric has broken off (and there may be others, less well exposed, beneath these two). We suspect these arcuate marks may be the basal portions of additional laminae that either are buried in the matrix or were sheared off when the rock split to reveal the fossil remains. The strongly marked lines in the lamina appear to be prominent veins, a number of which enter the lamina base and divide at least twice in an open-dichotomous manner, thus without anatomosing. To the extent the lamina is preserved, these veins run roughly in parallel. Given the prominence of the veins, the relative position of the attached lamina, and markings indicating the possibility of additional attached laminae, vertically disposed relative to one another rather than helically arranged, the lamina may be part of a compound leaf, and the specimen reveals the abaxial side.

This specimen is most similar to *Yuania*, a plant known from strata of similar age in Texas, where it was described as *Russelites* Mamay. Wang and Chaney (2010) later evaluated the morphological aspects of *Yuania* and *Russelites* and determined them to be the same, with *Russelites* being the junior synonym. *Yuania taeniata* (Darrah) X.M. Du and J.N. Zhu is the only described American species (see Mamay, 1968). The Doña Ana Mountains specimen, to the extent it is preserved, although consistent with the features of *Y. taeniata*, lacks certain characteristics necessary for a confident classification, such as the leaf apex and the overall architecture of the leaf-bearing axis. *Yuania* has been associated with reproductive organs, which, together with the basic morphology of the plant, strongly suggest affinities with the Noeggerathiales (Wang et al., 2004), a pteridophytic plant group of uncertain higher order relationships.

**Seeds**

The Doña Ana Mountains flora is strongly dominated by seed-plant remains, and in particular by strongly xeromorphic seed plants. Most of the plants appear to have had thick, leathery leaves, indicated by their obscure venation, and by the fact that the remains resisted mechanical degradation despite being transported together with relatively coarse-grained sediment and under high-volume stream discharge. Very little evidence of pteridophytes was found in the flora. Despite this dominance of known or strongly suspected seed plants, seeds themselves occur on only 12% of the informative quadrats that comprise the entire Doña Ana Mountains collection (Table 1, 27 out of a sample of 221). A selection of the seed types encountered is illustrated in Figure 26.

For the most part, these seeds appear to be radiospermic, with well developed sarcotestal layers, indicated by compression borders, sometimes coaly (e.g., Fig. 26D-E), and in one instance apparently fortuitously preserved in entirety (Fig. 26H-I). Most of these radiospermic seeds are relatively large, about 10 mm in diameter, sometimes greater. Smaller seeds also were encountered, with dimensions of <5 mm (Fig. 26E [at arrow], F-G). In one instance (Fig. 26F), the seed appears to be platypermic and to have a wing. We cannot relate these seeds at present to any foliage taxa. No asymmetrical winged seeds were found, of the type attributable to suspected peltasperms, such as the gigantopterids.

The largest concentration of seeds was found at the bottom of the channel-form deposit, USNM locality 41670. Here, the seeds were largely unsorted with respect to size. Although allochthonous, they may not represent part of the lag deposit of heavier material that was deposited at the bottom of the channel. Rather, their excellent preservation suggests settling from the water column after a (flash) flood, perhaps in a scour area that was filled with standing water. In such an instance, the seeds may give some indication of the diversity found in the vegetation surrounding the site of deposition, rather than reflecting long-distance transport. The size, radiospermic morphology, sarcotestal layers, and apparently strongly developed sclerotestas are indicative of animal or possibly water dispersal.

**Other Reproductive Organs**

**Incertae Sedis Reproductive Organ**

A single specimen of a reproductive organ of uncertain affinity was found at USNM locality 41670, in the lower Robledo Mountains Formation, from which one of the three largest collections was made. This partially three-dimensional specimen is illustrated (Fig. 27A-C) in a series of increasing magnification photographs, in order to show its size and salient features.

The morphology of this specimen is difficult to interpret. It appears to consist of a series of stalked structures, arranged helically on an unseen central axis. The most revealing of these structures is marked by a white arrow in Figure 27B, which clearly shows the disposition of the stalk (suggesting that the apex of the specimen is toward the top of the images, as illustrated), and its termination by an expanded ovoid feature, seen in longitudinal section. Adjacent such ovoid structures indicate that the wall was most likely continuous, and that it extended beyond the central body. It cannot be determined if these extensions formed a continuous ring around the apex of the central body, but it seems clear that they did not enclose it. Close examination of these other ovoid structures reveals what may be several, smaller ovoid structures within them. No bracts are evident in positions subtending these structures.

It is difficult to decide what this specimen represents. Possibilities that seem most likely include seeds, polliniferous organs or some sort of cupule, bearing seeds within. Degagement of the specimen has not been attempted because of the extreme hardness of the matrix and the apparent three-dimensional preservation of the specimen, but further preparation is necessary to clarify the morphological and phylogenetic affinities.

**Peltasperm Reproductive Organs**

Structures similar to the peltasperm reproductive organs *Peltaspernum, Autania*, and *Sandrewia*, were found at one of the Doña Ana Mountains collecting locations, USNM 42271, the single largest collection (Table 1). The specimens are found on
FIGURE 24. Gigantopterids of indeterminate affinity. A-B, Further enlargements of USNM specimen 713285cp. Area enlarged in B is shown by bracket in A. Images show deeply incised margin, fasciculate ultimate venation, development of suture veins (MV=Midvein; SV=Suture Vein); in addition, note ambiguous feature suggesting that the lamina consists of strongly adpressed but free pinnules (upper right of image B: We believe this to be a lighting artefact). USNM locality 42271. Scale bars = 1 cm.
195

FIGURE 25. Cf. *Yuania* sp. A-B. Same specimen under two different lighting angles to emphasize different features. Width of axis more apparent in image B. Arrows indicate locations of arcuate, carbonized features, possibly representing attachment points of pinnules. USNM specimen 713256. USNM locality 41670. Scale bars = 1 cm.

The specimens consist of a strongly ribbed, fan-shaped, or clam-shell-shaped, bilaterally symmetrical lamina, about 1 cm in width. The lamina is thin between the ribs, which we presume to be veins. The ribs terminate in a series of acuminate teeth that fringe the distal margin of the structure. There is no evidence of scars in any of the specimens, where seeds might have been attached, nor is there evidence of microsporangia.

These structures are not fully symmetrical disks, as found in *Peltaspernum* (Kerp et al., 2001). Rather, in their bilateral symmetry, they are more similar to peltaspermous reproductive structures such as *Autunia* or *Sandravia*, which Kerp (1988) has placed in synonymy with *Autunia*. *Autunia* has been linked, by attachment between vegetative foliage and reproductive organs, to the callipterids (Kerp, 1988; Kerp and Haubold, 1988). However, *Autunia* also may be associated with one or more non-callipterid taxa, such as *Supaia*, *Comia*, and *Auritifolia*, a linkage that has been suggested based on repeated co-occurrence (see Mamay et al., 2009; Chaney et al., 2009).

**ARTHROPOD DAMAGE**

Arthropod damage (damage types = DT) associated with the Doña Ana Mountains flora is uncommon and occurs on 10 seed plant leaves and pinnules, including *Supaia thinnfeldiioides* (or *Glenopteris splendens*), *Auritifolia anomala*, cf. *Zeilleropteris*, and the possible gigantopterid (Table 2). We found four DTs in three functional feeding groups: two galling DTs (DT33, DT247), one margin feeding DT (DT12), and one oviposition DT (DT76). All four damage types associated with Doña Ana Mountains plant fossils have been previously documented on floras from the mid-Cisuralian of north-central Texas (Beck and Labandeira, 1998; Labandeira and Allen, 2007; Schachat et al., 2014, 2015). Therefore, this study expands the geographic range of the observed DTs into New Mexico during the early Permian.

**Galling**

Galling is the most common type of herbivory found in this study (eight leaves and pinnules; Table 2) and is associated with *Auritifolia anomala*, *Supaia thinnfeldiioides* (or *Glenopteris splendens*), and the possible gigantopterid. Spheroidal to polylobate galls on *A. anomala* are defined by a
FIGURE 26. Seeds. All seeds except that in image F are radiospermic; the seed in image F is winged and platyspermic. Most of the radiospermic seeds have thin compression borders, indicating the presence of a compressible sarcotesta. All or much of the sarcotesta appears to be well preserved in the specimen illustrated in H-I. Images are divided into two groups. Scale bar for images A-E, H in image D. Scale bar for images F-G, I in image G. Arrow in image E indicates a relatively rare, smaller seed. A, USNM specimen 713260. B, USNM specimen 713262. C, USNM specimen 713263. D, USNM specimen 713264. E, USNM specimen 713261. F, USNM specimen 713287. G, USNM specimen 713288. H-I, USNM specimen 713289. Specimens in A-F from USNM locality 41670. Specimens in G-I from USNM locality 42271. Scale bars = 1 cm.

central domed chamber surrounded by a rim of depressed tissue (DT247, Figs. 21C, 28A-B). Five of these galls are associated with three specimens of *A. anomala*, all positioned adjacent to leaf midveins. The galls are 1.5–1.8 mm long by 1.0–1.3 mm wide, and the encircling depressed rims are 0.2–0.6 mm wide. A similar circular gall also assigned to DT247 has a flattened central chamber instead of a domed chamber. The gall is located adjacent to the midvein of an *A. anomala* pinnule and is bounded by an indented rim (Fig. 28C). The gall is 1.3 mm long by 0.9 mm wide, and the surrounding rim is 0.2–0.3 mm wide.

An oval gall characterized by a flattened chamber delimited by a depressed rim is positioned on the midvein of *Supaia thinnfeldioides* (or *Glenopteris splendens*) (DT247, Fig. 28D). The gall is 1.1 mm long by 0.8 mm wide, with its long axis parallel to the midvein. The depressed rim surrounding the gall is 0.1 mm wide. The gall’s external morphology is very similar to the gall on *Auritifolia anomala* in Figure 28C, but differs in its position on the leaf. On *S. thinnfeldioides*, the gall is located directly on the midvein, and on *A. anomala*, the gall is adjacent to the midvein. A similar ovoidal gall on a fragment of *S. thinnfeldioides* (or *Glenopteris splendens*) is 0.9 mm long by 0.6 mm wide (DT247, Fig. 28F). The gall is bound by a concave rim that is 0.1–0.2 mm wide, although the rim extends to 0.5 mm wide and narrows to a point along the upper left portion of the gall in the view in Figure 28F. Details of the central chamber were lost during preservation.

A second gall morphotype on *Supaia thinnfeldioides* (or *Glenopteris splendens*) is also positioned along the midvein
FIGURE 27. Reproductive organs. A-C, Incertae sedis strobilus. Arrow in image B indicates the most clearly stalked of the structures. USNM 413269, USNM locality 41670. D, Suspected Autunia-type peltaspermous reproductive structure. USNM specimen. 713301. USNM locality 42271. Scale bars = 1 cm.

TABLE 2. Damage types on leaves and pinnules from the Doña Ana Mountains flora.

<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>USNM Locality #</th>
<th>Plant Species</th>
<th>Damage Type</th>
<th>Functional Feeding Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>713248</td>
<td>41669</td>
<td>cf. Zeilleropteris</td>
<td>12</td>
<td>margin feeding</td>
</tr>
<tr>
<td>699030</td>
<td>41670</td>
<td>Supaia thinnfeldioides</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713270</td>
<td>42271</td>
<td>Supaia thinnfeldioides</td>
<td>12, 33</td>
<td>margin feeding, galling</td>
</tr>
<tr>
<td>713292</td>
<td>42271</td>
<td>Auritifolia anomala</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713280</td>
<td>42271</td>
<td>Supaia thinnfeldioides</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713305</td>
<td>42271</td>
<td>Auritifolia anomala</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713306</td>
<td>42271</td>
<td>Auritifolia anomala</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713289</td>
<td>42271</td>
<td>Auritifolia anomala</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>713284</td>
<td>42271</td>
<td>possible gigantopterid</td>
<td>247</td>
<td>galling</td>
</tr>
<tr>
<td>699031</td>
<td>42271</td>
<td>Auritifolia anomala</td>
<td>76</td>
<td>oviposition</td>
</tr>
</tbody>
</table>
FIGURE 28. Arthropod damage, including galls (A-F), possible oviposition marks (G), and margin feeding (H, I). A. Two galls adjacent to the midvein of *Auritifolia anomala* (DT247, USNM loc. 42271, USNM 713306). B. Gall with depressed rim adjacent to the midvein of *A. anomala* (DT247, USNM loc. 42271, USNM 713305). C. Circular gall with flattened center next to the midvein of *A. anomala* (DT247, USNM loc. 42271, USNM 713292). D. Circular gall on the midvein of *Supaia thinfeldioiides* or *Glenopteris splendens* (DT247, USNM loc. 42271, USNM 713280). E. Lenticular gall on the midvein of *S. thinfeldioiides* or *G. splendens* (DT33, USNM loc. 42271, USNM 713270). F. Ovoidal gall on fragment of *S. thinfeldioiides* or *G. splendens* (DT247, USNM loc. 41670, USNM 699030). G. Possible oviposition marks following the midvein of *A. anomala* (DT76, USNM loc. 42271, USNM 699031). H. Margin feeding on a cf. *Zeilleropteris* leaf (DT12, USNM loc. 41669, USNM 713248). I. Margin feeding on *S. thinfeldioiides* or *G. splendens* (DT12, USNM loc. 42271, USNM 713270). Scale bar measurements: A, B, D, E, F, H = 5 mm; C, G, I = 1 cm.

(DT33; Fig. 28E), but has a lenticular shape and lacks a surrounding depressed rim. The gall is 2.3 mm long by 1.2 mm wide, with its long-axis parallel to the mid-vein. Carbonized material is present on portions of the surface of the gall, particularly on the upper-left edge in the view in Figure 28E.

A spheroidal gall with a domed chamber adjacent to the primary vein of a possible gigantopterid (DT247; Fig. 23B) is 2.3 mm long by 2.0 mm wide. The overall appearance of the gall and position on the leaf are similar to the domed DT247 galls associated with *Auritifolia anomala* (Figs. 21C, 28A-B).

**Margin Feeding**

Margin feeding is a type of external foliage feeding where a mandibulate insect excises tissue from the edge of a leaf. Shallow, U-shaped excisions into the leaf margins (DT12) of cf. *Zeilleropteris* and *Supaia thinfeldioiides* (or *G. splendens*) are the only examples of external foliage feeding associated with the Doña Ana Mountains flora. Margin feeding on a cf. *Zeilleropteris* leaf is 3.8 mm wide and 1.4 mm deep with a 0.2–0.5 mm wide reaction rim (Figs. 22A, 28H). On a *Supaia thinfeldioiides* (or *G. splendens*) pinnule, two margin-feeding excisions are present. In the view in Figure 28I, the upper excision is 3.1 mm across and 1.1 mm deep. The excision is surrounded by a 0.5–1.0 mm wide rim of probable necrotic tissue bordered by a 0.2 mm wide black reaction rim. The lower excision is composed of three cusps that are 4.0 mm...
wide combined, 1.5 mm deep, and flanked by a 0.4–0.5 mm rim of necrotic tissue.

**Oviposition**

Circular to polylolate marks, possibly representing oviposition sites, follow the midvein and secondary veins of *Auritifolia anomala* (DT76; Fig. 28G). The marks are characterized by a darkened, ragged rim surrounding the presumed ovipositor insertion point and are 0.5–0.9 mm long by 0.2–0.6 mm wide. The reaction rims are 0.1–0.2 mm wide.

**DISCUSSION**

**Geology**

The stratigraphic section of the Hueco Group in the Doña Ana Mountains is strikingly similar to that in the Robledo Mountains, ~ 5 km to the southwest (Lucas et al., 1998, 2015) and in the San Andres Mountains, ~ 20 km to the northeast (Lucas et al., 2002). In all three areas the Shalem Colony Formation (the lower part of Hueco Group, Fig. 2) is characterized by relatively coarse-grained limestones and algal limestones that yield Wolfcampian fusulinids. The overlying Community Pit Formation in all three areas is finer-grained, mostly calcareous mudstones and shales. Above that, the Robledo Mountains Formation is interbedded with marine shale and limestone and siliciclastic red-beds that yield tetrapod tracks and plant fossils. In the Doña Ana Mountains, faulting and erosion have removed the uppermost strata of the Robledo Mountains Formation and overlying Hueco rocks. Thus, in terms of the lithostratigraphy of Seager et al. (1976) in the Doña Ana Mountains, the Shalem Colony Formation is correlative with the Bursum? Formation and lower Hueco Formation, the Community Pit Formation correlates with the middle Hueco Formation, and the gastropod-bearing member and the Abo Tongue is equivalent to the Robledo Mountains Formation (see correlations in Fig. 2).

Biostratigraphic data from the Robledo Mountains (Lucas et al., 2015) indicate that the Shalem Colony is early Wolfcampian, the Community Pit Formation is middle-Wolfcampian-earliest Leonardian, and the Robledo Mountains Formation is early Leonardian (middle Artinskian).

The beds bearing plant fossils indicate proximity to marine conditions in the lower part of the Robledo Mountains Formation. Here, the fossiliferous siltsstones are interbedded with limestones, and may contain invertebrate or fish fossils suggestive of brackish water influences, at least intermittently. No such indicators were found in the upper plant-fossil-bearing beds. Fossil charcoal also was found in the lower three plant-fossil-bearing deposits. Where it was possible to determine from the outcrop exposure, the deposits bearing plant fossils were laid-down in intermittently active channels. We have no evidence of lacustrine or lagoonal, quiet-water sedimentation, at least not among the beds in which plant-fossil remains were found.

Despite the small differences in lithological characteristics, or in the details of the shape and depositional history of the various deposits, most of the collections are too small to permit assessments to be made of temporal, stratigraphic patterns. We therefore treat the assemblage as a single flora. This is in keeping with other studies of floras from Abo Formation, with which the Robledo Mountains Formation is in part correlative, in areas of central and northern New Mexico (see DiMichele et al., 2013). The flora is homogeneous over most of the state, dominated primarily by various conifers, but with a strong admixture of supaoids, particularly those most like *Supaia thinnfeldioides* and *Auritifolia anomala*, as found in the Doña Ana Mountains flora. The Abo Formation subflora reported here is most like that from the Oscura Mountains, some distance to the north (DiMichele et al., 2007).

**Fossil Plants**

The Doña Ana Mountains flora is strongly xeromorphic in aspect and dominated by seed plants or suspected seed plants. The predominant elements are primarily the walchian conifers and cordaitaleans. Secondarily, and restricted primarily to one collecting locality, peltasperm foliar remains were found in some abundance. The most abundant taxa were *Supaia thinnfeldioides* and *Auritifolia anomala*, with smaller numbers of *Rhachiphyllum schencki* and rare occurrences of *Zelneropteris* and an indeterminate gigantopterid. Remains of pteridophytes were extremely rare, consisting of a few fragmentary calamitalean stems and some scraps of foliage likely derived from groundcover ferns.

The specimens that make up the taphoflora are of robust construction, with woody axes and likely leathery, quite stiff leaves, resistant to destruction during transport. Such remains may have stiffened further after death, due to drying. This stiffness is suggested by their frequent three-dimensional disposition in the sediment, and not uncommon position at angles to laminating or bedding surfaces without being notably deformed. More suggestive than definitive (because delicate foliage may also sometimes be similarly preserved), these aspects of the plant-remains-as-sedimentary-particles indicate resistance to breakage, compression, and the ability to tolerate burial without significant distortion. Furthermore, the sedimentary environments in which most of the plant remains were deposited appear to have been shallow streams and possibly crevasse splays within a dynamic fluvial system (Mack et al., 2003). Our observations of the fossiliferous deposits suggest intermittent relatively high sediment loads, indicative of seasonal floods and high discharge rates. That the plant remains were not destroyed under these conditions, or significantly abraded in most instances, testifies both to their sturdy construction and to their likely derivation from microhabitats proximate to the site of burial.

These taphonomic observations suggest that the paleo-flora could be a biased representation of the standing vegetation. The evidence of calamitaleans and small ferns indicates, unequivocally, that there were places on the landscape where moisture-requiring plants lived, confirmed by sedimentological studies (Mack et al., 2003). The presence of these plant fossils also indicates that there were at least some places where groundcover developed, although its density cannot be guessed. Paleosol studies of the Robledo Mountain Formation exposures in the Doña Ana Mountains indicate a seasonal climate during the fluvial phases of sedimentation (Mack et al., 2010), with the water table well below the soil surface for most of the year. These observations are consistent with reports of paleosols from other locations in the equivalent-age Abo Formation, well to the north of the Doña Ana Mountains exposures (Tanner and Lucas, 2017), suggesting broad, regionally uniform climatic conditions.

Although small, the flora is similar to low diversity floras reported from the Robledo Mountains Formation in the nearby Robledo Mountains, also in southern New Mexico, proximate to the Hueco seaway (Voigt et al., 2013; DiMichele et al., 2015). The flora also is effectively identical, compositionally, to more distant floras from areas farther to the north in New Mexico, in the temporally equivalent Abo Formation, (e.g., Hunt, 1983; Lucas et al., 1995b; DiMichele et al., 2007, 2013). Recently acquired evidence suggests that a similar flora also may characterize red beds yet farther to the west in Pangea, in modern-day Arizona. Thus, the flora is characteristic of a spatially extensive, low-diversity vegetation inhabiting much of the coastal region of western Pangea, an area that, due to syndepositional tectonism, was elevationally complex. The flora also shares taxa in common with the Hermits Shale flora of the
Grand Canyon, in Arizona, although the latter is more diverse, but also consists primarily of strongly xeromorphic plants, and is preserved in similar lithofacies (White, 1929). In light of these considerations, the Doña Ana Mountains flora raises our awareness that widespread, low diversity floras may have been the norm in tropical areas throughout much of western Pangea, raising questions that engage us to consider whether these areas truly were of low diversity and compositionally homogeneous over vast spatial domains, or if this pattern reflects some kind of pervasive taphonomic bias.

**Arthropod Damage**

The presence of galls in the Doña Ana Mountains flora expands the geographic and host plant range of DT247 and provides further evidence for the proliferation of foliar galling in the early Permian. Multiple, small-bodied hemipteroid lineages, including some whose modern relatives induce galls today, diversified in the early Permian (Shcherbakov, 2000; Schachat and Labandeira, 2015). In addition, the xeric climate present during much of the early Permian (Montañez and Poulsen, 2013) may have provided equivalent conditions for gall formation, as modern galls may be more common in dry environments (Fernandes and Price, 1992). Together, evidence from plant-arthropod associations, insect body fossils, and paleoclimatic records point to the proliferation of galling as an important functional feeding group during the Permian.

Galls were once thought to have evolved together with angiosperms (Scott et al., 1994; Raman et al., 2005), but increased documentation of Paleozoic galls in recent years has prompted reassessment of the origins of galls (Schachat and Labandeira, 2015). Galls associated with the Doña Ana Mountains flora contribute to the expanding record of foliar galls on Permian seed plants (Schachat and Labandeira, 2015). The earliest possible foliar galls are associated with the liverwort, Metzgeriothallus sharonae, from the Middle Devonian of New York State (Labandeira et al., 2014). The next appearance of possible galls is in the Early Pennsylvanian on the apiculate strobili of Paracalamostachys, a calamitalean from Europe (Amerom, 1973). In the Late Pennsylvanian of the Illinois Basin, holometabolous insect larvae galled Stiptiopteris petiolar fronds of the tree fern Psaronius chasei (Labandeira and Phillips, 1996).

In the early Permian, galls proliferated on new plant groups and plant parts in Euramerica, including medullosan pteridosperms (Stull et al., 2013; Xu et al., 2018), peltasperms (Labandeira et al., 1998), gigantopterids (Schachat et al., 2014, 2015), lycophytes (Stull et al., 2013; Xu et al., 2018), and Walchia (Schachat et al., 2014; Vassilenko, 2011). Damage type 247 galls have previously been documented in two floras from the mid-Cisuralian of north-central Texas (Schachat et al., 2014, 2015). At the Colwell Creek Pond locality, DT247 is associated with Taeniopteris spp., an unaffiliated broad-leaved plant, Auritifolia waggoneri, and the gigantopterid Evolosnia texana (Schachat et al., 2014). Damage type 247 is also associated with Taeniopteris at the Mitchell Creek Flats locality (Schachat et al., 2015).

Marginal feeding damage has been well documented in Paleozoic floras, particularly in the Late Pennsylvanian and Permian. The earliest evidence of margin feeding is cuspatate excisions into the leaf margins (DT12) and apices (DT13) of Metzgeriothallus sharonae, a liverwort from the Middle Devonian of New York State (Labandeira et al., 2014). The next documented appearance of margin feeding is from the Mississippian (Serpukhovian), where DT12 is associated with the pteridosperm Triphylloteperis australis in the Sydney Basin, New South Wales, Australia (Iannuzzi and Labandeira, 2008). In the Pennsylvanian, DT12 occurs on medullosan seed ferns, including Macropteris schueltzii (Müller, 1982; Scott and Taylor, 1983). In the Permian, margin feeding is associated with an array of plants including Euramerican conifers (Looy, 2007), and broad-leaved seed plants from Euramerica (Beck and Labandeira, 1998; Schachat et al., 2014, 2015; Xu et al., 2018), Gondwana (Prevec et al., 2009; Cariglino and Gutiérrez, 2011), and Cathaysia (Glasspool et al., 2003).

Oviposition marks first occur in the fossil record during the Middle (Béthoux et al., 2004) and Late Pennsylvanian (Laß and Hoff, 2014) on plant axes. Oviposition damage on foliar tissue appears to have increased in frequency during the Permian, particularly on glossopterid floras in Gondwana (Prevec et al., 2009; McLoughlin, 2011; Souza Pinheiro et al., 2012; Gallego et al., 2014; Cariglino, in press). Although less common, oviposition marks have also been documented from the Pennsylvanian-Permian transition (Xu et al., 2018) and Permian of Euramerica (Schachat et al., 2014; Vassilenko, 2011).

**ACKNOWLEDGMENTS**

The authors gratefully acknowledge the assistance of Greg Mack and Jerry MacDonald in locating plant-bearing strata for discussions about the interpretation of the environments of deposition. We thank W. John Nelson and Scott D. Elrick for assistance with fieldwork, and Conrad Labandeira for discussions about Permian arthropod herbivory. Arden Bashforth and Jun Wang provided much appreciated thorough, constructive reviews. This work was supported, in part, by a grant from the U.S. Bureau of Land Management to SGL.

**REFERENCES**


Cariglino, B., and Gutiérrez, P.R., 2011, Plant-insect interactions in a Glossopteris flora from the La Golondrina Formation (Guadalupian—Lopingian), Santa Cruz Province, Patagonia, Argentina: Ameghiniana, v. 48, p. 103–112.
Li, H., Tian, B., Taylor, E.L. and Taylor, T.N., 1994, Foliar anatomy of Gigantopteris guizhouensis (Gigantopteridiales) from the Upper

