



A low diversity, seasonal tropical landscape dominated by conifers and peltasperms: Early Permian Abo Formation, New Mexico

William A. DiMichele^{a,*}, Dan S. Chaney^a, W. John Nelson^b, Spencer G. Lucas^c,
Cindy V. Looy^a, Karen Quick^d, Wang Jun^e

^a Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, United States

^b Illinois State Geological Survey, 615 East Peabody Drive, Champaign, IL 61820, United States

^c New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104, United States

^d Box 106, Shafter, TX 79845, United States

^e Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, People's Republic of China

Received 30 January 2006; received in revised form 27 November 2006; accepted 29 November 2006

Available online 23 February 2007

Abstract

Walchian conifers (*Walchia piniformis* Sternberg, 1825) and peltasperms similar to *Supaia thinnfeldioides* White and cf. *Supaia anomala* White dominate floodplain deposits of a narrow stratigraphic interval of the middle Abo Formation, Lower Permian of central New Mexico. The plant fossils occur in thinly bedded units up to two meters thick, consisting of coarse siltstone to very fine sandstone with clay partings. Bedding is primarily tabular, thin, and bears rare ripple marks and trough cross beds. Bedding surfaces display mud cracks, raindrop imprints, horizontal and vertical burrows of invertebrates, and footprints of terrestrial vertebrates. These features indicate intermittent and generally unchannelized stream flow, with repeated exposure to air. Channels appear to have cannibalized one another on a slowly subsiding coastal plain. Conifers are dominant at three collecting sites and at three others *Supaia* dominates. Although each of these genera occurs in assemblages dominated by the other, there are no truly co-dominant assemblages. This pattern suggests alternative explanations. Landscapes could have consisted of a small-scale vegetational patchwork dominated almost monospecifically in any one patch, meaning that these plants could have coexisted across the landscape. On the other hand, conifer and supaoid dominance could have been temporally distinct, occurring during different episodes of sedimentation; although in the field there are no noticeable sedimentological differences between conifer-dominated and *Supaia*-dominated channel deposits, they may represent slightly different climatic regimes. The considerable morphological differences between conifers and *Supaia* suggest that the floristic patterns are not a taphonomic effect of the loss of a significant part of the original biodiversity. In general, the climate under which this vegetation developed appears to have been relatively warm and arid, based on the geology (pervasive red color [oxidation], calcrete in paleosols, and abundant mud cracks evidencing ephemeral flow in streams) and biology (low floristic diversity, xeromorphic plant physiognomies).

© 2006 Elsevier B.V. All rights reserved.

Keywords: *Walchia*; *Supaia*; Paleocology; Permian; New Mexico; diversity

* Corresponding author.

E-mail address: dimichel@si.edu (W.A. DiMichele).

1. Introduction

The flora of the Early Permian Abo Formation of New Mexico is noted for its generally low diversity and monotony over a broad region. Dominance by conifers is common, particularly in sandstone and coarse siltstone deposits. Here, we describe an Abo flora dominated almost exclusively by walchian conifers and probable peltasperms of the genus *Supaia*. The plants occur in a stratigraphic interval approximately 6 to 18 m thick composed of clastic sediment, primarily sandstone, deposited by broad, shallow channels and in sheet floods. The deposits crop out in an area of roughly 5 km² at the northern end of the Oscura Mountains in Socorro County, central New Mexico (Fig. 1). These deposits are of interest because the low species richness can be placed in an environmental context that does not suggest significant taphonomic sorting or bias. The original vegetation appears to have consisted of spatially persistent patches, lasting perhaps hundreds of years. Deposits of the Abo Formation from other areas in central New Mexico, particularly from the middle Abo redbeds, have an essentially identical flora (e.g. Ash and Tidwell, 1982; Hatchell et al., 1982; Hunt, 1983). Such broad, spatio-temporal floristic similarity suggests widespread, low-diversity vegetation consistent with a semi-arid climate (Mack, 2003). The association of Permian walchian conifers with seasonal moisture regimes has been noted elsewhere (Ziegler et al., 2002) and is consistent with increased seasonality in the tropical regions.

The fossil-plant bearing deposits in the northern Oscuras present an opportunity to sample fossils from nearly the same stratigraphic horizon across a large area. It is unusual to identify a non-marine deposit from such a narrow stratigraphic horizon, other than a swamp deposit or ash bed, that can be traced for some distance and characterized sedimentologically. This is particularly true in deposits of Permian age, where there are few detailed ecological reconstructions (e.g., Bonner, 2004). The vegetation of Paleozoic terrestrial landscapes generally is reconstructed from many small, stratigraphically disconnected sampling sites, which limits understanding of the spatial scale of compositional variation. Such widespread, parautochthonous assemblages generally sample vegetation from little more than 50 m away from the site of deposition (Wing and DiMichele, 1995). Furthermore, “analytical time averaging” (Behrensmeyer et al., 1992), the process of combining samples from slightly-to-widely different time intervals into a single sample, can confound understanding of short-term variation in plant community composition in

the fossil record. The deposits described here thus permit us to look somewhat more broadly at a landscape than typically is possible.

2. Geological setting

The floras under study occur in the Abo Formation of Early Permian age. They were collected near the northern end of the Oscura Mountains in southeastern Socorro County, New Mexico (Fig. 1). The Oscura Mountains, a fault block range that formed during the mid-to-late Cenozoic, have about 1000 m of vertical relief along their precipitous, west-facing scarp. The face of the range exposes Proterozoic granite overlain by a Paleozoic sedimentary section that generally dips eastward. Lower Permian strata cap the dip-slopes on the gently inclined northern and eastern flanks of the range (Wilpolt and Wanek, 1951) (Figs. 2A and 3A).

The Abo Formation is a succession of red, terrestrial mudstone, siltstone, and sandstone that is widespread in central New Mexico (Lee and Girty, 1909; Needham and Bates, 1943; Wood and Northrup, 1946). The Abo disconformably (?) overlies the Bursum Formation (Fig. 2A), which consists of non-marine mudstone, sandstone, and conglomerate alternating with marine shale and limestone (Lucas and Krainer, 2004). Conformably overlying the Abo is the Yeso Formation, consisting of mostly terrestrial siltstone and sandstone, intercalated with massive to bedded gypsum and laterally extensive beds of marine limestone and dolostone.

Direct evidence for the age of the Abo is meager. Zonation of its land plants and vertebrates is poorly established. The only reported occurrence of biostratigraphically useful fossils in the Abo is fusulinids in a limestone-pebble conglomerate of the upper Abo in the type locality in northeastern Socorro County, near Abo Pass. These fossils were identified “as *Pseudofusulina* similar to species from middle Wolfcampian horizons” (M.L. Thompson in Kottowski et al., 1956, p. 52). The Bursum Formation, below the Abo, spans the Carboniferous–Permian boundary and is time transgressive from middle Virgilian to early Wolfcampian time (Wilpolt et al., 1946; Otte, 1959; Kottowski, 1963; Kottowski and Stewart, 1970; Wahlman and King, 2002; Lucas and Krainer, 2004; Utting et al., 2004; Schneider et al., 2004). At its type locality, 12 to 14 km west of our collecting sites, the Bursum yields an early Wolfcampian (basal Permian) fusulinid fauna (Lucas et al., 2002a); fossil cockroach remains also support a Wolfcampian (early Asselian) age (Schneider et al., 2004). A tongue of the Abo Formation extends into marine limestone in the upper–middle part of the Hueco

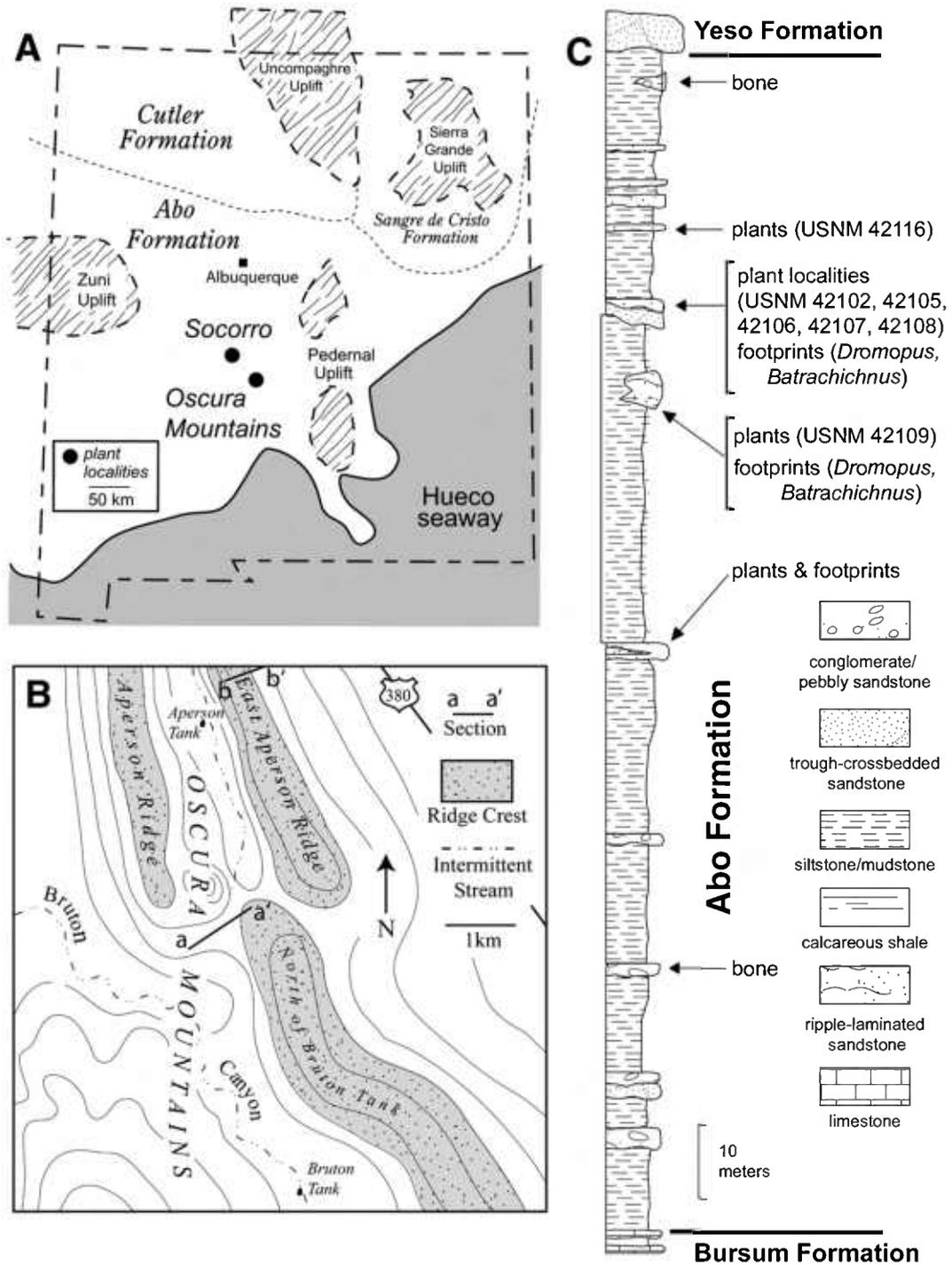


Fig. 1. Geography and geology of fossil collections. Area in gray=Hueco seaway. (A) Location of main collecting area (Oscura Mountains) and ancillary collecting area (East of Socorro) in relation to major penecontemporaneous highlands. (B) Collecting areas in the northern Oscura Mountains. Stratigraphic sections shown by a–a' and b–b' are referenced in text. (C) Composite stratigraphic section of the Abo Formation in the northern Oscura Mountains based on sections noted in (1B) and showing stratigraphic position of fossil plant collections.

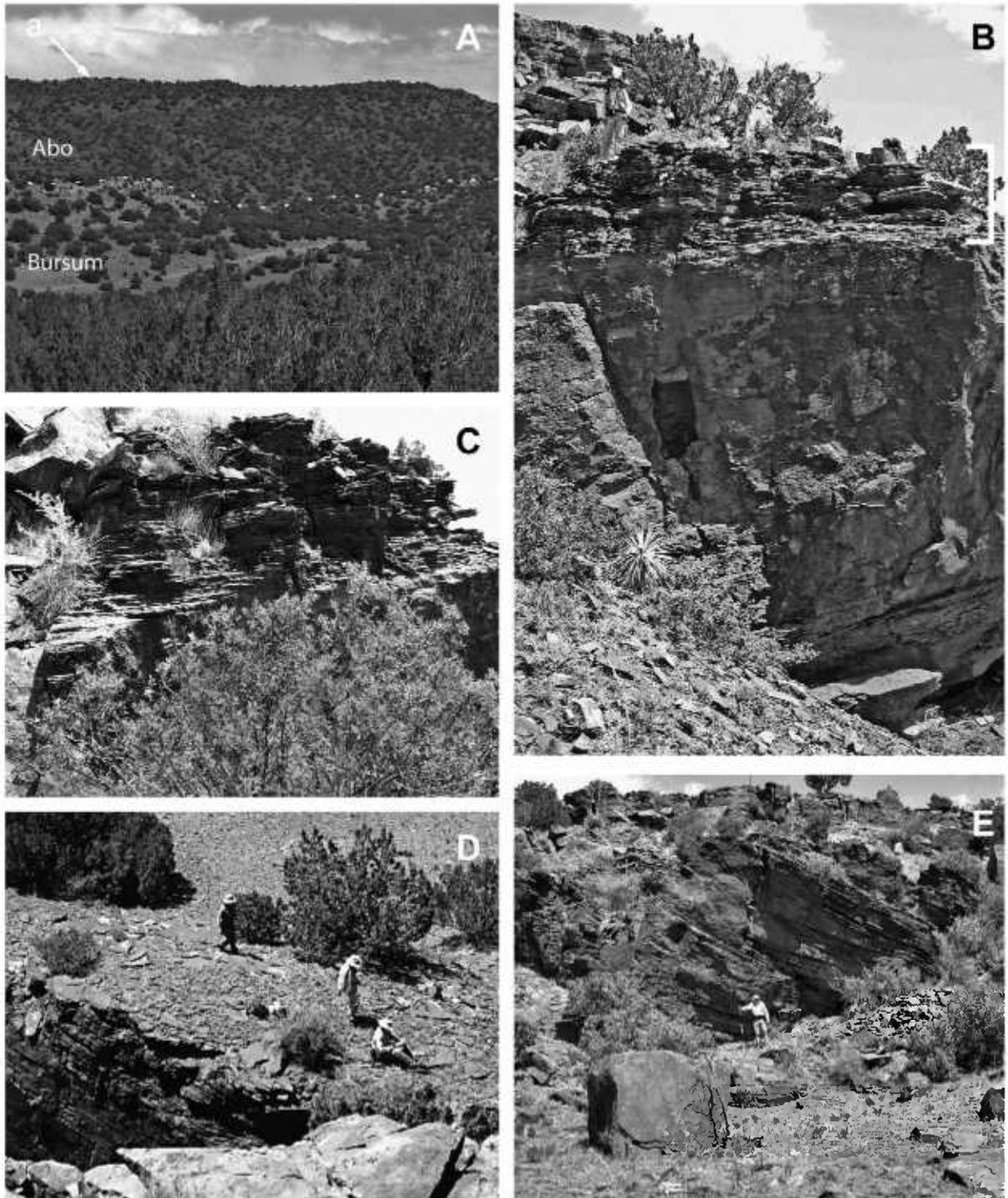


Fig. 2. UNSM locality 42105, North of Bruton Tank. (A) Ridge line above Bruton Tank. White arrow denotes location of *in situ* collections. Contact between the Bursum and Abo formations, indicated by dashed white line, can be seen at the transition from light color to dark color in the middle of the hill slope. (B) Sandstone channel fill. Plant fossils were collected from the thinly bedded siltstone in the upper part, marked by the white bracket, above massive sandstone. (C) Closer view of finely bedded plant–fossil-bearing siltstone. (D) Surface view of plant bearing finely bedded siltstone demonstrating platy nature of the deposit. Photographer and collectors are on same bed. The collectors are on a large, recent slump block. (E) Paleochannel margin, rotated by recent slumping. Deepest part of the channel is to the left in the photograph.

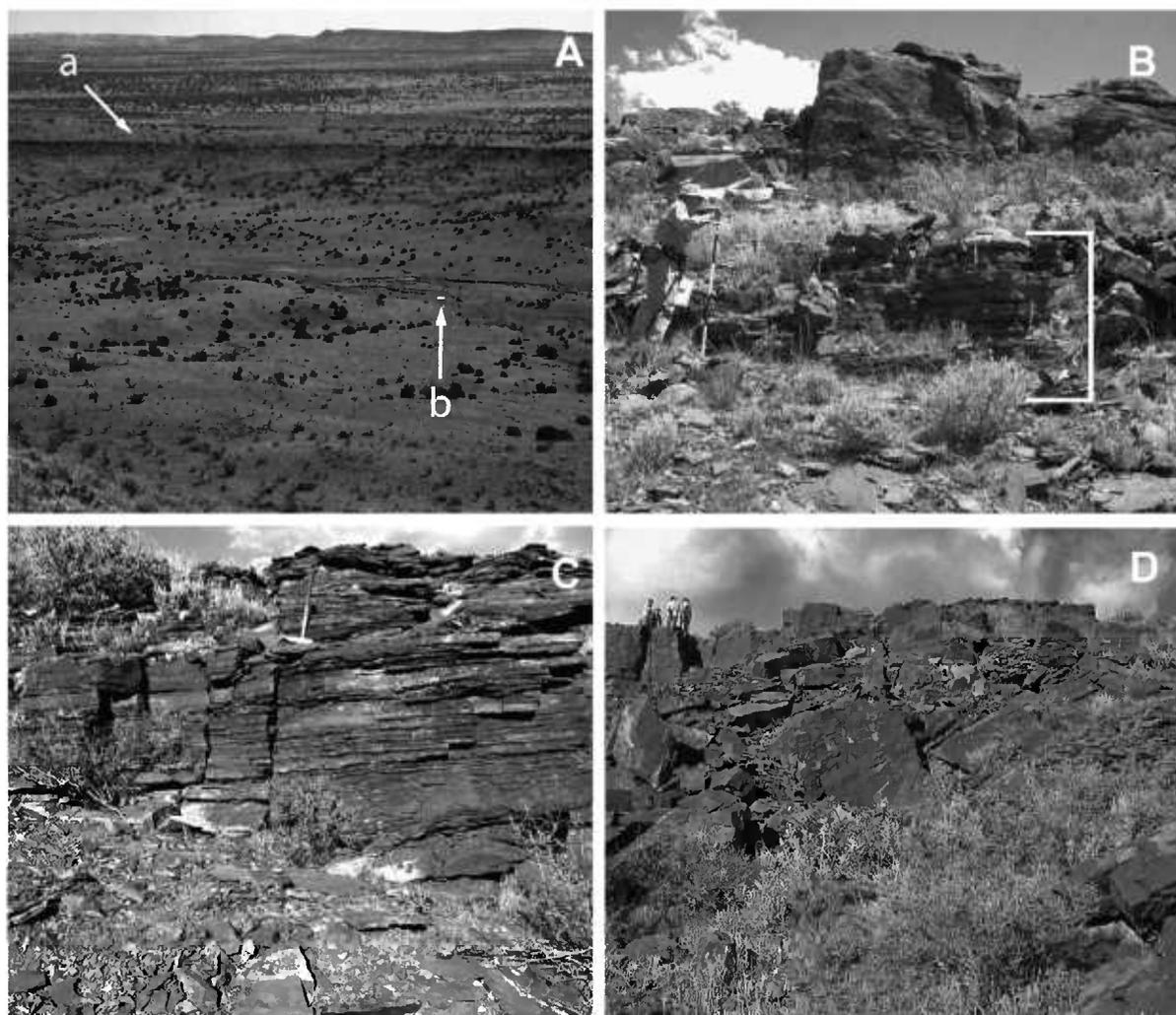


Fig. 3. Plant-bearing deposits. (A) Ridge east of Aperson Tank. a — Ridge line along which plant deposits were found *in situ*. b — Vehicle for scale. (B) USNM locality 42019, Southeast of Aperson Tank. Plant bearing beds marked by white bracket. (C) USNM locality 42107, Aperson Ridge #2. Platy fossil–plant-bearing interbedded siltstone and mudstone. (D) USNM locality 42107, Aperson Ridge #2. General aspect of collecting locality.

Formation in the Robledo Mountains just northwest of Las Cruces, New Mexico, about 170 km south of our study area (Kottlowski et al., 1956; Meyer, 1966; Lucas et al., 1995a,b). The Abo tongue there has been dated as late Wolfcampian on the basis of ammonoids and brachiopods (Kues, 1995), ostracods and other microfossils (Kietzke and Lucas, 1995), and conodonts (Kozur and LeMone, 1995). Fusulinids and other marine invertebrates of the Hueco provide fairly secure correlation to the middle (Neal Ranch) and upper (Lenox Hills) portions of the standard Wolfcampian Series in the Glass Mountains of West Texas (Thompson, 1954; Kottlowski et al., 1956; Otte, 1959; Meyer, 1966; Lucas et al., 1998; Lucas and Krainer, 2002; Wahlman and King, 2002; Lucas et al., 2002b; Seager

and Mack, 2003). These studies indicate that the Abo is mostly of middle to late Wolfcampian age, although an early Wolfcampian age cannot be ruled out in some places. The Yeso Formation, overlying the Abo, has yielded a Leonardian brachiopod and mollusc fauna in south-central New Mexico (Kottlowski et al., 1956). In terms of the international standard Permian section, the Hueco (and Abo) represent late Asselian, all or most of the Sakmarian, and possibly early Artinskian time.

Although exact correlation is not possible, the fossil plants described here occur in the upper-middle part of the Abo Formation, and thus are likely to be similar in age to the Abo tongue in the Robledo Mountains.

During Wolfcampian time, the study area was a gently sloping coastal plain on the northern edge of a

marine embayment in the Orogrande Basin, in which the Hueco Group was deposited (Fig. 1). The region is now generally considered to have been tropical in latitude (e.g. Ziegler et al., 1997). The Ancestral Rocky Mountains orogeny took place mainly during Pennsylvanian time but continued locally into the Early Permian (Kottowski and Stewart, 1970). The resulting uplifts, including the Defiance-Zuni, Uncompaghre, Pedernal and Joyita, all exposed Precambrian crystalline rocks, which are the source of coarse arkose and conglomerate in the lower Abo. Portions of the Pedernal and Uncompaghre uplifts remained active sediment sources throughout Abo deposition (Thompson, 1942; Meyer, 1966; Ross and Ross, 1986; Kluth, 1986; Little, 1987; Mack and Dinterman, 2002).

3. Fossil-bearing deposits

3.1. Description

Fossil plants were collected at six sites in the Oscura Mountains study area (Table 1). In addition, we collected similar paleofloras from five sites east of Socorro, 48 km to the southeast of the Oscura Mountains. These ancillary collections were made at Gallina Well in Cañoncito de la Uva, from which Hunt (1983) previously described a flora, and Cerrillos del Coyote, at roughly the same stratigraphic level, middle Abo Formation, as those found in the Oscura Mountains. Although the lithologic setting and inferred mode of deposition are similar for plant deposits in the Oscura Mountains and in the ancillary study areas, precise correlation to the fossil plant localities outside of the Oscura Mountains could not be done with certainty.

Consequently, the additional collections serve only as points of comparison.

In the study area of the northern Oscura Mountains (Fig. 1), the Abo is approximately 156 m thick. Plant fossils and tetrapod footprints are present in the upper half of the Abo Formation. Wilpolt and Wanek (1951) reported the Abo to be about 241 m thick in the central Oscura Mountains, but this thickness is not confirmed by measurement of the Abo section documented here (Fig. 1). In ancillary exposures near Cerrillos del Coyote and Gallina Well, east of Socorro, much of the Abo is composed of mudstone. This rock is dark reddish brown, very silty (grading to siltstone), massive to weakly fissile, and commonly bears blocky structure and large listric, slickensided fractures, features indicative of ancient soil formation. Paleosols in the Abo Formation and coeval rocks were described by Eberth and Miall (1991), Mack (2003), and Mack et al. (2003) and were used as the basis for interpreting environments of deposition and paleoclimate. We observed many of the soil features described by these authors in roadcuts through the upper Abo Formation on U.S. Rt. 380, a few kilometers north of our plant-collecting localities as well as in the ancillary study areas near the Cerros de Amado about 8 km east of Socorro, New Mexico.

All fossil plants from the Oscura Mountains came from an interval of siltstone and ledge-forming sandstone in the upper part of the Abo (Figs. 1–3). The fossiliferous deposits are exposed along two prominent ridge lines that form a triangle, about 5 km north–south and 1.5 km east–west (at the northern base). The collections identified as Aperson Ridge #1 (USNM locality 42106) and Aperson Ridge #2 (USNM locality 42107) come from the upper part of a single sandstone

Table 1

Plant taxa occurrences at sampling localities. X=present, more than two specimens in the collection; –=absent; *n*=1 and *n*=2 refer to representation in the collection by 1 or 2 specimens respectively

USNM	O 42107	O 42106	O 42109	O 42110	O 42108	O 42105	C 42100	C 42101	G 42111
Locality Name	Aperson Ridge 2	Aperson Ridge 1	SE of Aperson Tank	East of Aperson Tank	South Aperson Ridge	Bruton Tank	Cerillos del Coyote 2	Cerillos del Coyote 1	Gallina Well A
Walchia	<i>n</i> =2	X	–	–	X	X	X	X	X
Supaia thinnfeldioides	X	–	X	X	X	<i>n</i> =1	X	–	<i>n</i> =1
Supaia anomala	X	–	–	–	–	–	–	–	–
Narrow pinnules	X	–	X	X	–	–	–	–	–
Calamites sp.	–	–	–	–	–	–	–	–	–
Sphenophyllum sp.	X	–	–	–	–	–	–	–	–
Peltaspernum sp.	X	–	X	–	X	–	–	–	–

USNM locality numbers beginning with the letter 'O' are from the Oscura Mountains, those beginning with the letter C are from Cerrillos del Coyote, and the one beginning with G is from Gallina Well. See text for details.

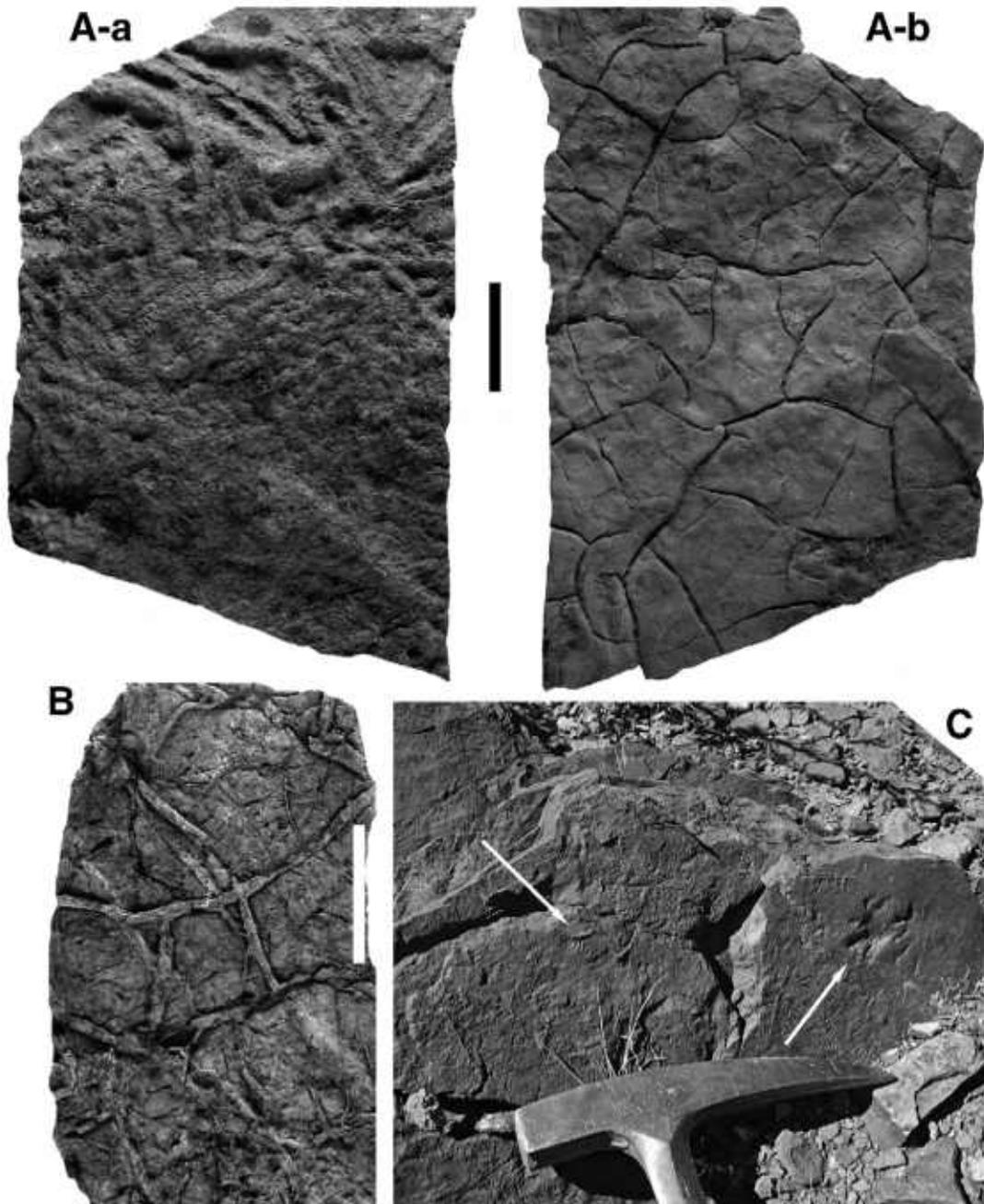


Fig. 4. Sedimentary features and trace fossils associated with plant fossils in laminated siltstone beds. (A) USNM specimen 498848, Aa and Ab, opposite faces of specimen with conifer fossils on one face and mud cracks in clay drape on the opposite face. (B) USNM specimen 498849, Mud cracks in relief (casts). (C) Footprints of terrestrial vertebrate in clay drape of siltstone, in situ. Geologic hammer for scale. Scale bars=5 cm.

unit. Fossils from sites North of Bruton Tank (USNM localities 42102–float and 42105) and South Aperson Ridge (USNM locality 42108) come from the upper part of the lower of two ledge-forming sandstones. Specimens from Southeast of Aperson Tank (USNM

locality 42109) come from poorly exposed, thin-bedded sandstone that underlies the main ledge-former.

At the southernmost locality, North of Bruton Tank (Fig. 2), abundant conifers occur in laminated to very thinly bedded sandstone, which occurs in the upper

2–3 m of an overall more massive sandstone up to 13 m thick. The channel has an abrupt northern margin (Fig. 2E), but its width and orientation were not determined.

At the northwestern (Aperson Ridge #1 and #2) and southwestern (South Aperson Ridge) localities, fossils occur intermittently in laminated to very thinly bedded sandstone at the top of a laterally extensive (several km²) ledge-forming unit, 3 to 5 m thick (Fig. 3).

In the above localities, ledge-forming sandstones are dominantly very fine grained and display planar, wavy, and ripple cross laminations together with crossbedding in sets mostly less than 50 cm thick, rarely up to 1 m thick. Shallow scour-and-fill structures have at most about 1 m of relief. Small lenses of fine to medium sandstone and intra-formational conglomerate (siltstone, mudstone, and carbonate rip-up clasts) are found in some scours. Sand body types are either simple broad or multistory sheets (using the terminology of Blake and Gubitosa, 1984).

The fossils at the Southeast of Aperson Tank site were collected from thin planar to thin wavy (ripple) bedded, mud-cracked sandstone with horizontal burrows. The plant-bearing sandstone has a maximum visible thickness of 1.5 m, although neither contact is exposed. It is separated from overlying ledge-forming sandstone by a 3 m thick covered interval. The ledge-former may be the same sandstone that yields fossils at Aperson Ridge #1, #2, and South Aperson Ridge sites. The depositional environment of Southeast of Aperson Tank cannot be determined, although its general morphology is similar to that at other sites.

3.2. Paleoenvironmental inferences

The Abo Formation section in the northern Oscura Mountains is readily divided into two distinct units (Fig. 1), as is evident elsewhere in the Abo of central New Mexico (e.g., Lucas and Zeigler, 2004). The lower unit of the Abo Formation (~50 m thick) is interbedded mudstones and arkosic pebbly sandstone and conglomerate. The mudstones contain numerous calcrete nodules and, at some horizons, the nodules are coalesced to form ledges. The sandstones are either single story or multistory ribbons that display abundant crossbeds and scour-and-fill features. Fossil bone occurs in some conglomeratic lags at the bases of channel fills.

The upper part of the Abo Formation (~100 m thick) is very fine-grained to fine-grained sandstone interbedded with siltstones. The siltstones have sparse calcrete nodules and a few lenses of intraformational conglomerate that contain bone fragments. The sand-

stones are either broad simple or multistory sheets that are ripple laminated to small-scale trough crossbedded. They yield numerous footprints of tetrapods (Fig. 4C), mostly of small temnospondyl amphibians (*Batrachichus*) and captorhinomorph reptiles (*Dromopus*), and all the plant fossils discussed here.

The change in sandstone architecture evident in the lower and upper units of the Abo Formation reflects the difference between classic meandering channel deposits (lower unit) and unchannelized sheetflood deposits (upper unit). These sheetflood deposits are similar to those described by Seager and Mack (2003) in the Abo Formation in the Caballo Mountains, which they characterized as having formed on a broad alluvial plain traversed by highly sinuous streams carrying a bed load of silt to very fine sand. The Caballo sheetfloods resulted in sheet-like bodies 3 to 7 m thick and hundreds of meters wide that exhibit both single and multi-story channels with lateral accretion sets.

We infer that the climate of the study area at the time of Abo deposition was warm and semi-arid to subhumid,

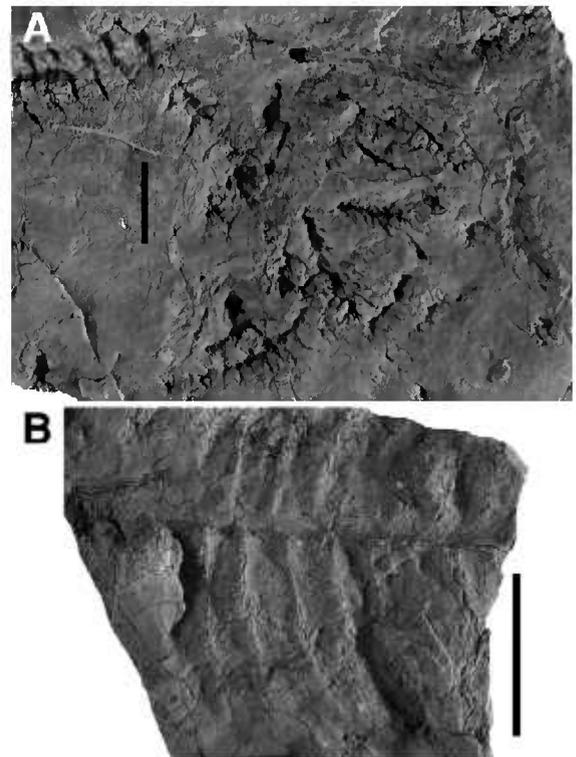


Fig. 5. Sedimentary features associated with plant fossils in laminated siltstone beds. (A) USNM specimen 498850, Conifer remains impressed originally into soft claystone demonstrating contemporaneity of plant and sediment deposition. Scale = 5 cm. (B) USNM specimen 498851, *Supaia* frond covered with clay drape, which was then desiccated. Scale = 5 cm.

with pronounced wet and dry seasons, as determined by Mack et al. (1991), Mack (2003), and Mack et al. (2003) from studies elsewhere in New Mexico. New Mexico lay within 10° of the equator during Wolfcampian time with annual rainfall in the range of 30 to 100 cm (Mack, 2003). These climatic interpretations are based upon characteristics of paleosols, plant and animal fossils, and sedimentary features. The climate of New Mexico became increasingly arid during Leonardian time, as evident by presence of gypsum and eolian sand-dune deposits in the Yeso and Glorieta formations (Mack and Dinterman, 2002; Mack, 2003).

The plant-bearing deposits have a sheet-like geometry, which may have resulted from lateral migration of fluvial channels, either meandering or braided, or possibly from a combination of small channels and unchanneled sheet floods along a muddy coastal plain. Lateral accretionary bedding, indicative of meandering channel deposits, was not observed. Plants were preserved during waning stages of flood activity, shortly prior to abandonment. From outcrop exposures, channels are estimated to be about 10 m in depth. Deposits of

a partially preserved channel at the Aperson Ridge site were 12 m thick and 100 or more meters in width (not accurately determinable). At other collecting sites, channel deposits were measured at 7 m or less in thickness. At least two channel margins were observed (Fig. 2E) on outcrop, indicating that the plant-bearing beds are not part of one contemporaneous deposit, but rather part of a complex of channel sequences and sheet floods at approximately the same stratigraphic level. This suggests the landscape was created by small channels that cannibalized and reworked sediment from the local floodplain, similar to that described from the Abo Formation in southern New Mexico (Mack et al., 2003; Seager and Mack, 2003). Such a landscape is indicative of low rates of subsidence (i.e., a lack of creation of accommodation space) (Blakey and Gubitosa, 1984).

The lithology that yields plants is essentially the same in all of these plant-bearing deposits of the study area. The plants occur in flaggy bedded to laminated, very fine sandstones to siltstones with intercalated clay laminae. The sandstones are calcareous and well

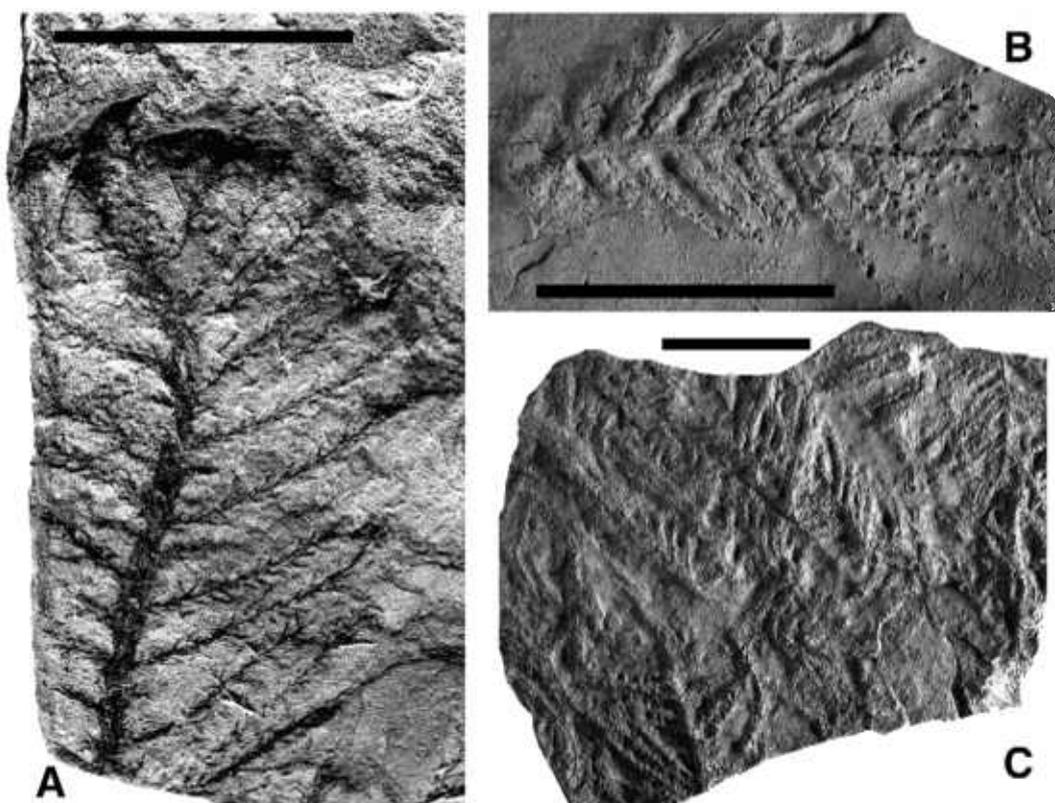


Fig. 6. Conifer specimens all attributable to *Walchia* sp. (A) USNM specimen 498852, Carbonaceous compression. Magnification $\times 1.0$. (B) USNM specimen 498853, Three-dimensional mold, originally in soft clay. Magnification $\times 1.0$. (C) USNM specimen 520392, Three-dimensional cast preservation in relief. Magnification $\times 0.5$. All scale bars=5 cm.

cemented. The plant-bearing beds are everywhere between 1.5 and 2.5 m thick (Figs. 2 and 3).

The thin sandstones and siltstone beds within the plant-bearing interval are primarily planar laminated to unlaminated; ripple cross laminations are rare, and trough cross bedding was not identified in the plant-bearing beds. The sandstone–siltstone beds are separated by claystone laminae up to 1 cm thick (Fig. 3C). Also, within the plant-bearing intervals, the surfaces of both sandstone–siltstone beds and clay interbeds–drapes frequently display polygonal mud-cracks (Fig. 4Ab, B), indicating exposure to the sun shortly after deposition and while still moist. Fig. 4Aa and Ab are opposite sides of a single, 2 cm thick siltstone bed, with a dense mat of plants on the lower side and mudcracked muds on the upper side. Also common are simple horizontal burrows less than 1 cm in diameter. In addition, rare raindrop imprints and the footprints (ichnogenera *Batrachichnus* and *Dromopus*) of small terrestrial tetrapods, were identified in some places (Fig. 4C).

The bedding and associated features of these rocks indicate that stream flow, flooding, and sediment transport were intermittent. During flood stages, coarser sediments were carried in traction. Clays were deposited during the waning stages of flow, which were usually followed by subaerial exposure of bar tops. Similar deposits in the Abo Formation of southern New Mexico were interpreted by Mack et al. (2003) as crevasse-splay and levee deposits. However, in the area of the present study, no evidence of meandering streams or rooted levees was detected, suggesting a plexus of small channels on a low-relief, possible braid plain with bars and areas of standing water.

The density of plant remains on any fossiliferous surface varies from a few, isolated specimens to densely matted branches and foliage. In addition, plants may occur on a few surfaces or many in succession. At the North of Bruton Tank locality, for example, plants occur on nearly every surface through more than 2.1 m of thinly bedded, mud-cracked sandstone–siltstone (Fig. 2B–E). In many cases, the plant fossils evidence deposition contemporaneously with muds, forming deep imprints, where foliage was incorporated into the soft sediment (Fig. 5A). In some cases plant remains were covered by thin layers of mud that were then cracked by exposure to the sun (Fig. 5B). Fossil roots are rare or absent at most sites.

The image brought to mind by these deposits is one of dense stands of vegetation growing amidst small intermittent streams. Good preservation of large fronds and branches indicates transport only a short distance from the site of growth and probably within the basic habitat of the parent vegetation. Hence, the deposits are parautochtho-

nous. During stream flow and sheet flooding, moving, sediment-laden water picked up twigs and branches that broke off dead or living plants and carried them a short distance. Flow does not appear to have been very powerful, given the size of many fossil-plant remains.

4. Fossil flora

Fossil plant diversity in the collections from the Oscura Mountains is exceptionally low, given the geographic breadth, thickness, and sedimentary character of the plant-bearing deposits. Only four, possibly five taxa, based on vegetative organs, have been identified in the deposits that comprise this study. These taxa are *Walchia* Sternberg sp. indet. (Figs. 6 and 7), *Supaia thinnfeldioides* White (Figs. 8–11, 16), cf. *Supaia anomala* White (Figs. 12–15), *Sphenophyllum* Koenig sp. indet. (Fig. 17), and possibly *Calamites* Schlotheim sp. indet. In addition, other kinds of plant organs are present rarely, including cones belonging to conifers (Fig. 7B) and *Peltaspermum*-like reproductive organs of peltasperms (Fig. 16). The flora is essentially identical in Abo deposits from nearby areas, of similar age and depositional character (e.g., Hunt, 1983). A few conifer specimens perhaps attributable to *Otovicia hypnoides* (Brongniart) Kerp et al. (1990) and a single specimen of

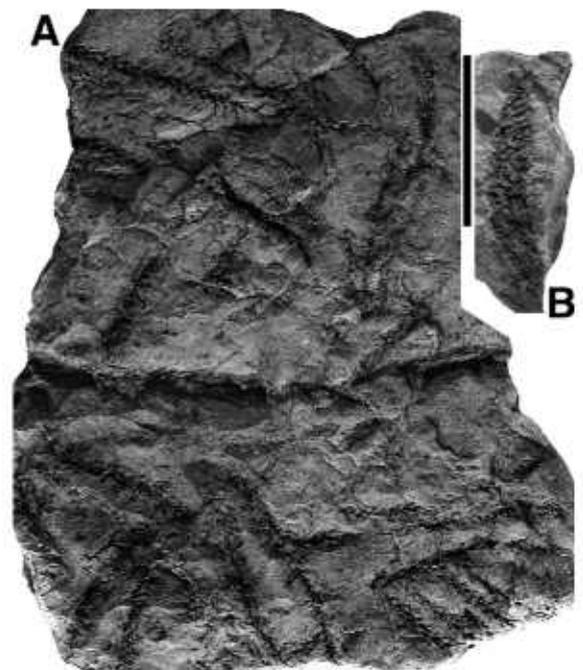


Fig. 7. Conifer remains. (A) USNM specimen 520394, Specimen demonstrates the density of *Walchia* sp. material typical of many bedding surfaces in laminated siltstone deposits. (B) USNM specimen 520395, Conifer cone. Scale bar=5 cm.

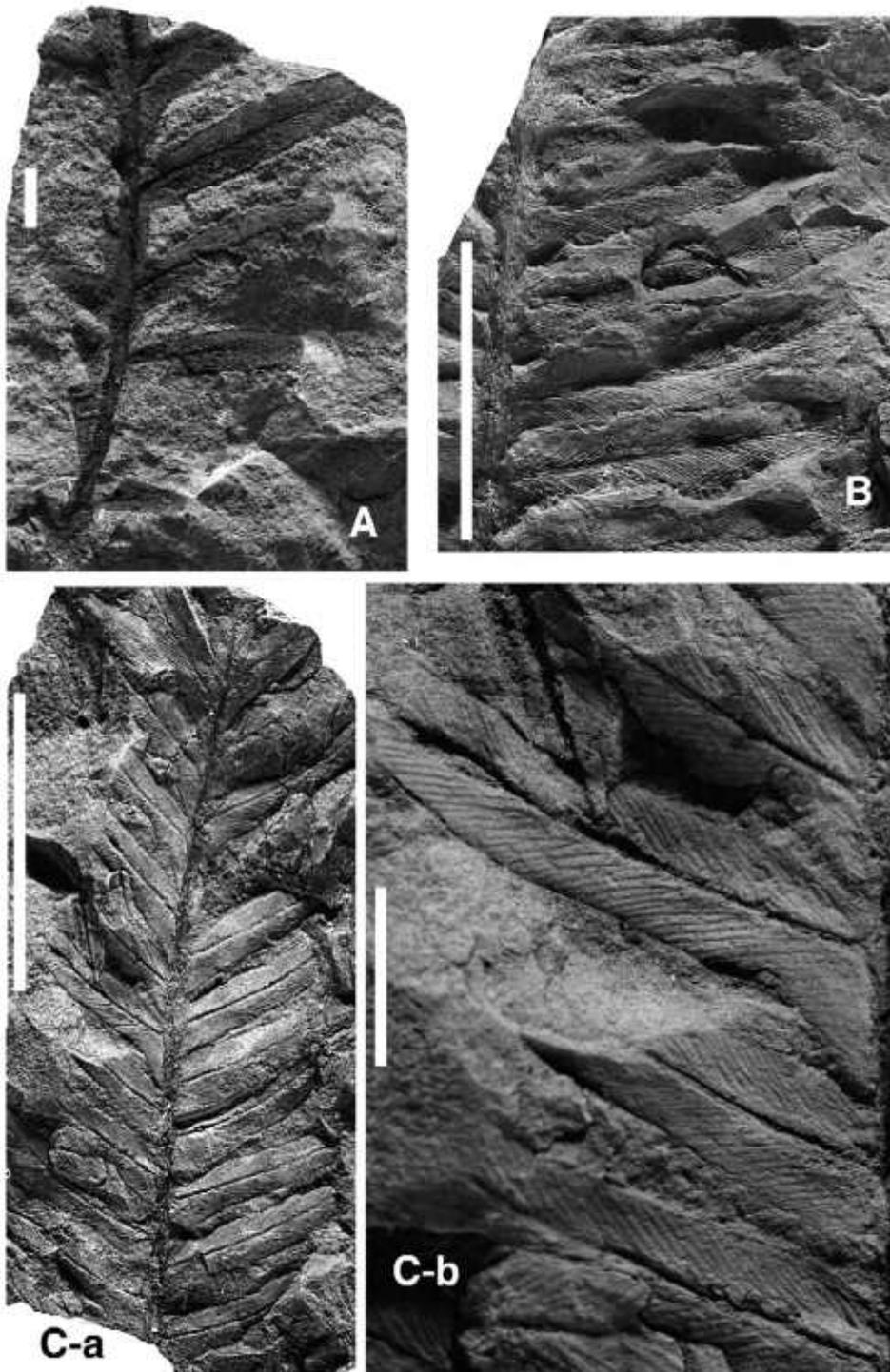


Fig. 8. *Supaia thinnfeldioides*. General aspect of frond pinnules and gross morphology. (A) USNM specimen 324599, *Supaia thinnfeldioides* from the Hermit Shale flora of the Grand Canyon. Originally illustrated in White (1929) as Plate 15, Fig. 2. Scale bar=1 cm. (B) USNM specimen 520414. Scale bar=5 cm. (C) USNM specimen 520414. Ca Scale bar=5 cm. Cb USNM 520415 Detail of venation. Scale bar=1 cm.

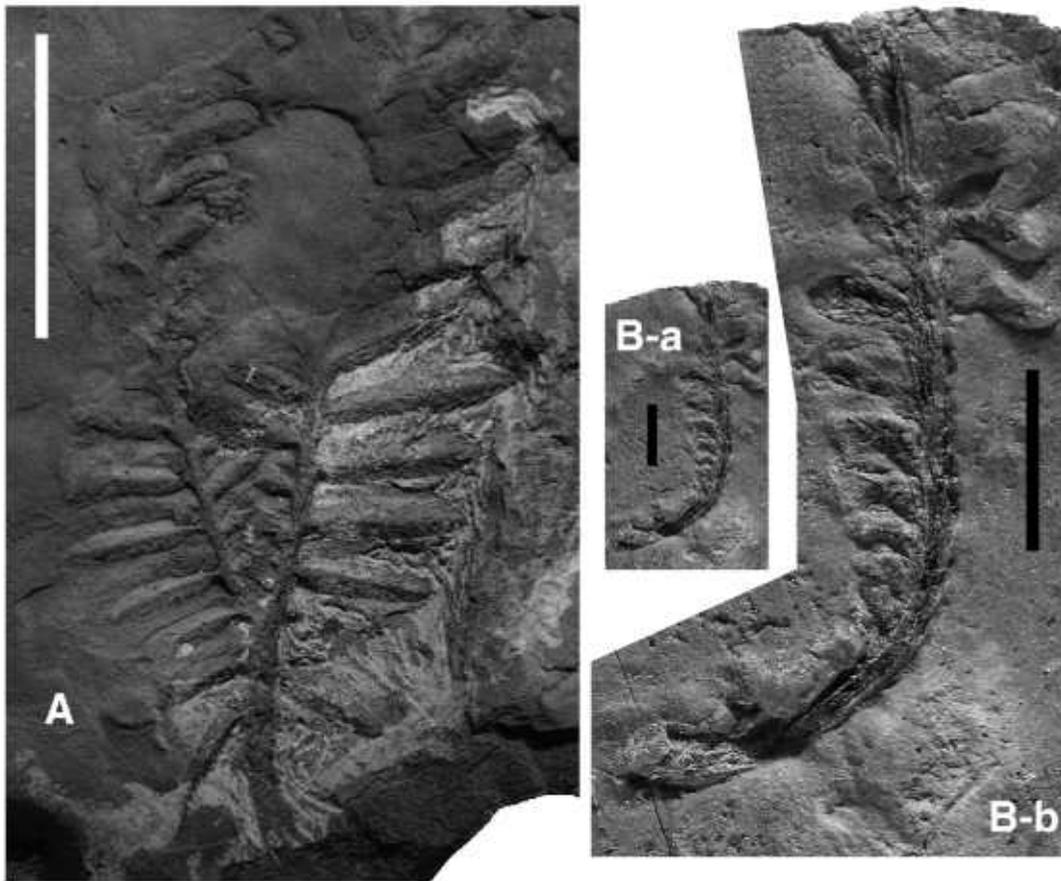


Fig. 9. *Supaia thinnfeldioides*. (A) USNM specimen 520407, Small complete frond showing basal fork. Abo Pass area. See White (1929) for drawing of comparable frond. Scale bar=5 cm. (B) USNM specimen 520416, Small complete frond that does not show a basal fork. Ba Scale bar=1 cm. Bb Scale bar=1 cm.

a reproductive structure similar to *Phasmatocycas kansanus* Mamay (Fig. 18) have been found at these ancillary exposures.

4.1. *Walchia Sternberg sp. indet.*

Conifer branches bearing leaves are probably the most commonly encountered fossil-plant remains in the Abo Formation, reported from numerous localities (e.g., Hunt, 1983; Lucas et al., 1995a,b). Such branches, generally preserved as compressions and impressions, sometimes as molds, can be assigned to *Walchia* sp. Specimens of this form were found in abundance in this study. They typically consist of whole or partial branches with frond-like, planar form bearing permanently attached leaves that were small and narrow, but dorsi-ventrally flattened, and acropetally curved in an S-shape (Figs. 6 and 7). Rare conifer-like cones found in these deposits may be both of pollen- and ovule-bearing types and are likely associated with *Walchia* sp.

The growth habit of *Walchia* appears to have been broadly similar to some species of extant *Araucaria*, such as *A. heterophylla* (Norfolk Island Pine), which has plagiotropic branches arranged in whorls or tight spirals produced periodically and separated by long trunk segments. By all indications, *Walchia* branches were abscised from the trunk; complete branches are often found and may occur in dense mats. Hernandez-Castillo et al. (2003) argued that walchian trees were small in stature, approximately 2 m in height. They base this on a detailed study of stem and branch sizes in *Thucydia mahoningensis*, from the Missourian of Ohio. However, they found only a single stem specimen with attached branches. Larger stems with attached branches with walchian foliage have been reported from Permian deposits of Nova Scotia (Ziegler et al., 2002), suggesting larger trees by that time. Ziegler et al. (2002) noted that the relatively small diameter of walchian branches, on the order of 5–7 mm, and the presence of branch scars on larger diameter stem segments, may be

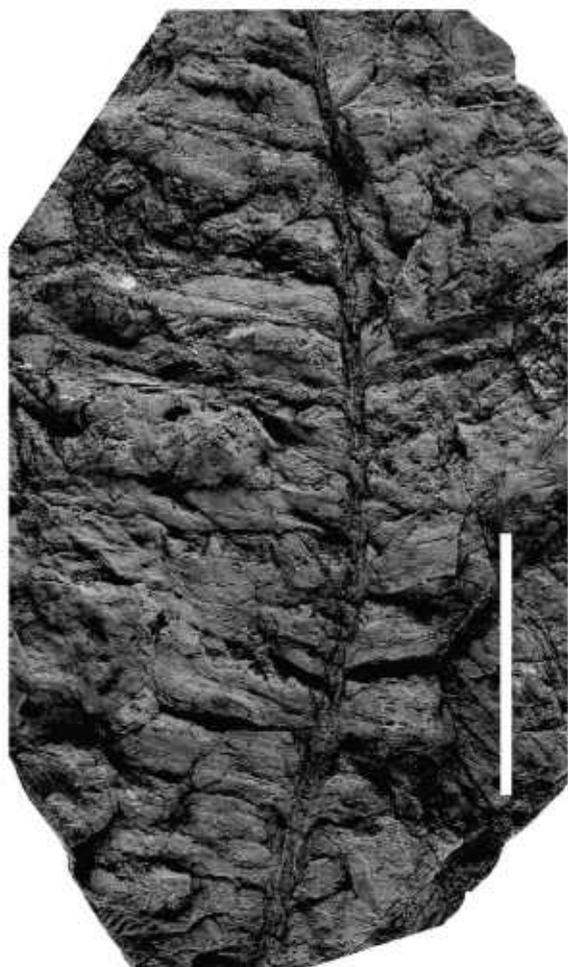


Fig. 10. *Supaia thinnfeldioides*. USNM specimen 520425. Partially preserved large frond. Scale bar=5 cm.

indicative of deciduous-branch attachment near the apical parts of trees, with branches being shed lower on the trunk as growth proceeded. Thus, it is not only possible but likely that there were a variety of sizes among species attributable to the walchian conifers, although present evidence does not unambiguously indicate trees of large stature. At the present time, we cannot determine the size of the New Mexico material.

4.2. *Supaia thinnfeldioides* White

Fossilized remains of probable peltaspermous foliage are nearly as common in our collections as are remains of fossil conifers. These remains are most similar to *Supaia thinnfeldioides* White (1929). They consist of fragments of a compound leaf that may be forked near the base (Fig. 9A), above the petiole. Pinnules are free (Fig. 8A), decurrent (Fig. 8A, B), sometimes with a

slightly auriculate base (Fig. 8C). Veins are straight, depart at an angle from the well developed midrib, and may fork before reaching the margin (Fig. 8B, C). Veins in the decurrent base originate directly from the midrib (Fig. 8Cb). The apices of the pinnules are acute and attenuated, although no drip-tip like extensions are present. Pinnules are generally narrow, some as wide as 1.5 cm. Pinnules remain free up to the apex of the frond where those adjacent to the single terminal pinnule may be slightly fused (pinnatifid).

Taxonomic assignment of these leaves is made problematic by the similarity of species in several genera described from the Permian tropics. Included in this group are *Supaia thinnfeldioides* White (1929), the type species of the genus, *Protoblechnum wongii* Halle (1927), *Glenopteris splendens* Sellards (1900), *Compsopteris adzvensis* Zalesky (the genus as emended by Naugolnykh, 1999), and *Brongniartites* Zalesky (1927), although similarities to this latter genus are less than to some species of the other genera (Naugolnykh, 1999, also notes that the name *Brongniartites* is invalid). In a review of this group, Naugolnykh (1999) proposed that Early Permian fossils identified as *Compsopteris* from Europe, North America and China, are probably referable to other genera, particularly *Supaia* or *Glenopteris*. *Compsopteris* is of Late Permian age from the north-temperate Angaran floral realm.

It is difficult to distinguish *Supaia*, *Glenopteris*, and *Protoblechnum* based solely on gross frond morphology, especially if specimens are fragmentary (DiMichele et al., 2005). In his description of *Supaia*, White (1929) commented at length on its similarities to *Protoblechnum* as described by Halle (1927). Halle (1927) had admitted to assigning Chinese material to *Protoblechnum* with some reservation, given that the name was originally applied by Lesquereux (1879) to North American material of Pennsylvanian age. White (1929) was of the opinion that Halle (1927) had misattributed the Chinese material to *Protoblechnum*. Although Halle described *Protoblechnum wongii* fronds as “sometimes bifurcating once” (p. 135), White insisted that in his examination of *Protoblechnum* specimens, no signs of frond bifurcation were visible. He thus suggested that the Chinese material should have been assigned to *Glenopteris*, which Sellards (1900) described as pinnatifid and tapering to apex and base, making no note of frond bifurcation. However, since that time, frond bifurcation in *Protoblechnum* has been thoroughly documented (Sze, 1955; Sun et al., 1999). The shape of the pinnule bases in *P. wongii* are similar to those of *Glenopteris splendens* in being flared in some specimens. Based on the material illustrated by

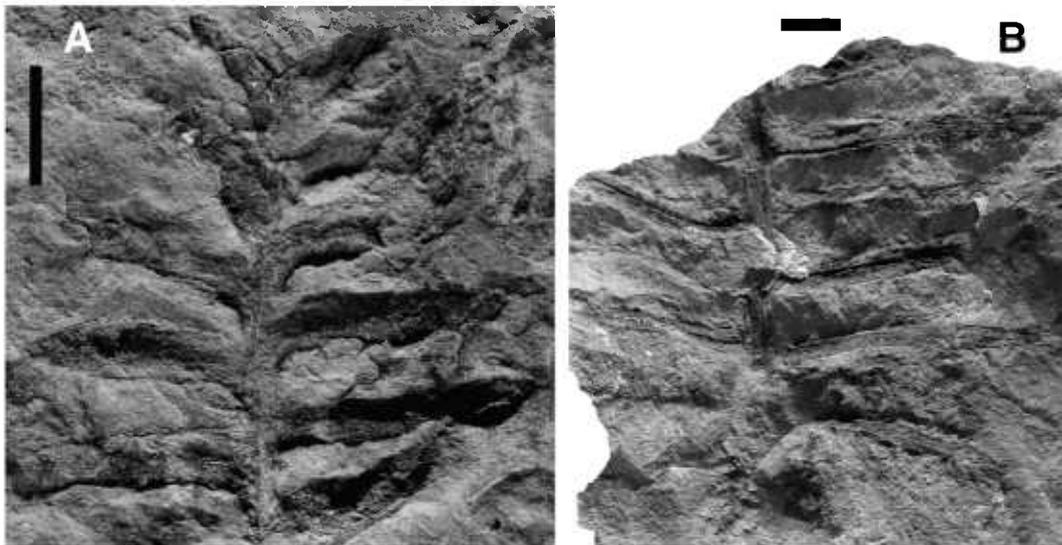


Fig. 11. Probable specimens of *Supaia thinnfeldioides*. These specimens are compressed in such a manner that the full width of the pinnule is not preserved. (A) USNM specimen 520418. (B) USNM 520419. Scale bars = 1 cm.

Sellards (1900), however, it is difficult to rule out frond bifurcation in *Glenopteris*, again confounding some of the simple ways in which these genera supposedly could be distinguished.

In the large amount of material recovered during this study, no bifurcate frond axes were found to which clearly identifiable foliage was attached. However, rare examples of bifurcate axes were found in association

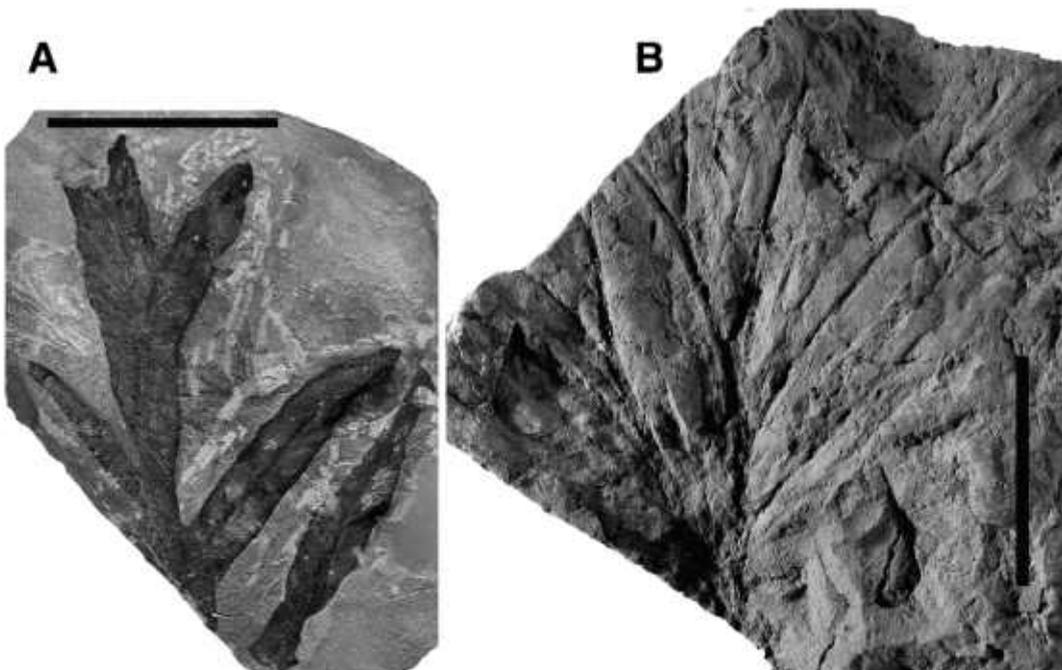


Fig. 12. *Supaia anomala*. (A) USNM specimen 324583, Specimen from Hermit Shale flora of the Grand Canyon, illustrated by White (1929) as Plate 21, Fig. 1, showing terminal portion of leaf. Specimen has been retouched to emphasize the lamina. Specimens of *S. anomala* are difficult to photograph and retouching of some specimens is necessary to allow them to be distinguished from the rock matrix. (B) USNM specimen 520413, Specimen illustrating bipartite architecture and repeated forking of the lamina. Not retouched. For both specimens, Scale bar = 5 cm.



Fig. 13. *Supaia anomala*. USNM specimen 520420. (Aa) Original, unretouched specimen. (Ab) Retouched specimen illustrating the repeated forking of the lamina and the bipartite nature of the leaf architecture. This is a large specimen; Scale bar=7 cm.

with laminate foliage of the peltaspermous type, and these were within the size range of bifurcate fronds known from elsewhere in rocks of Early Permian age from the western US. From this we presume that these leaves were likely once bifurcate.

Consequently, the most confident assignment that can be made is to *Supaia thinnfeldioides*, though the material is quite comparable to both *Glenopteris*

splendens Sellards and *Protoblechnum wongii* Halle based on gross morphology. Both *Supaia* and *Glenopteris* were first described from rocks of Early Permian age in the western U.S.: *Supaia* from Arizona, and *Glenopteris* from Kansas, adding greater likelihood to these taxonomic attributions than to *Protoblechnum*.

The peltaspermous nature of these fronds is suggested by the occurrence of several specimens of peltate organs

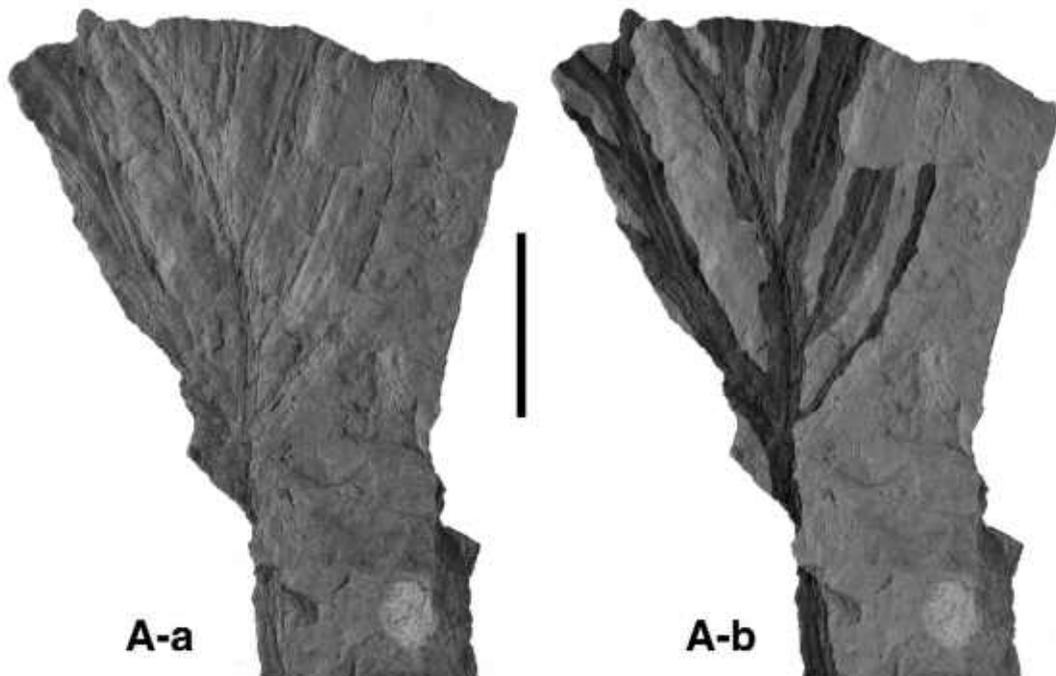


Fig. 14. *Supaia anomala*. USNM specimen 520421. (Aa) Original specimen, unretouched. (Ab) Retouched specimen illustrating the bipartite nature of the lamina. Note in particular the laminar lower portion, which may be the petiole; the base is not preserved to confirm this interpretation. Scale bar=5 cm.

(Fig. 16) similar in form to those described as *Peltaspermum* by Naugolnykh and Kerp (1996). These occur only in association with supaioids and not in sediments where conifers dominate to the exclusion of peltasperms. These specimens are round with radial striations and a central area suggesting attachment to a stalk. They are broadly similar in form to the (possibly synonymous [Kerp, 1988]) peltaspermous reproductive organs *Sandrewia* (Mamay, 1975) and *Autunia* (Kerp, 1988).

Several foliage specimens were found preserved so that the full width of the pinnule laminae is not exposed (Fig. 11). These are illustrated here because they are comparable to specimens illustrated by DiMichele et al. (2000) from the late Early Permian of West Texas, which were not identified, but which possibly are *Supaia* and occur in near-shore environments in association with *Taeniopteris*, *Delnortea*, and the likely peltasperm, *Comia*.

White (1929) characterized *Supaia* as a complex of small, “herbaceous” plants. In fact, there is no definitive evidence of the growth architecture of any of the *Supaia* species. The architecture of the forked fronds is consistent with small-tree or liana habit. However, the abundance and large size of the foliage in the study site deposits (Figs. 10 and 15), the clearly compound nature of individual leaves, the probable abscission of the

foliage, and its occurrence to the exclusion of other kinds of plants, suggests an origin from trees or shrubs.

4.3. Cf. *Supaia anomala* White

A number of specimens were found with ribbon-like lamina and a pseudopalmate architecture (Figs. 12–14), bearing a strong similarity to *Supaia anomala* White (1929). The petiole is possibly laminated for all or part of its length (Fig. 14). The main rachis forks approximately equally then divides asymmetrically along each of the two main segments an additional three to five times. Each division gives rise to nearly discrete pinnules to the outer side of each fork, the ultimate pinnules arising from a nearly equal dichotomy (Figs. 12 and 14); the lamina is slightly constricted at the base of each lateral pinnule. The venation, as in other peltasperms of the Early Permian, departs the midvein at a high angle, about 45°; the veins may be slightly convex in their path to the margin of the lamina and may branch one to several times. Lamina width varies from less than 1 cm to more than 2 cm. In a specimen found in isolation in a siltstone bed above those from which the main Oscura Mountains floras were collected, nearly complete leaves occur on opposite sides of a rock specimen 3 cm thick, and may be attached to a common

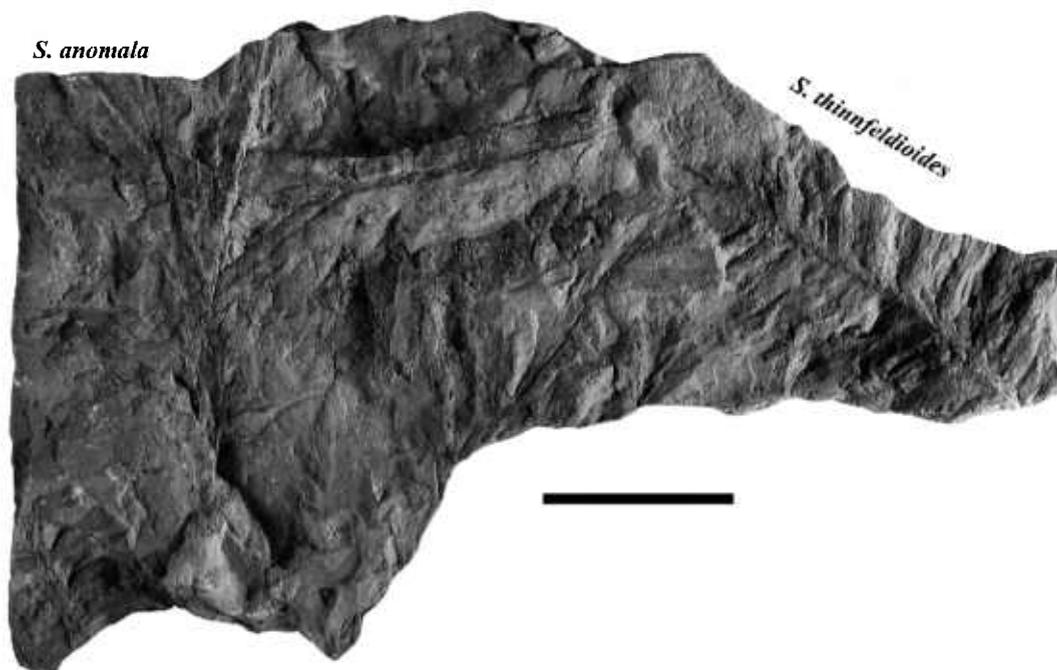


Fig. 15. USNM specimen 520422. Specimen with both *Supaia thinnfeldioides* and *Supaia anomala*. Scale bar=5 cm.

axis. There is no indication that any of these specimens are attached as terminal portions to frond segments with pinnate pinnule architecture.

The closest comparable Permian plant to these specimens is *Supaia anomala* of White (1929) (Fig. 12A is from White's original suite of *S. anomala* specimens), although our specimens compare only to a portion of the material White assigned to this species. We treat this comparison with caution because of the way in which this species was originally circumscribed; White may have combined two morphologically distinct plants.

In his monograph of the Hermit Shale flora, White (1929) described nine species of the new genus, *Supaia*. After an examination of White's original material, housed at the National Museum of Natural History, Smithsonian Institution, we believe White oversplit his suite of specimens, creating too many species. He may have been misled by highly variable preservation of his fossils. White himself states, (pp. 61 and 62)

“On account of the variation of the pinnules in the parts of the pinna, the differences due to the relative stages of maturity of the specimens, the nascent stage of development of the genus, and the highly fragmentary character and xerophytic phase of the material collected, the specific differentiation of the Hermit specimens is difficult.”

He further remarks,

“At the same time it now seems probable that the number of species of *Supaia*... will be increased.”

This all seems to come down to a matter of taxonomic philosophy — lumping vs. splitting. White may have lumped into *Supaia* some forms that are not encompassed within the morphological variation attributed to the genus *Supaia*, as he originally described it. On the other hand, White apparently also oversplit the species-level taxonomy within the genus *Supaia*.

Perhaps the best example of this problem is White's species *Supaia anomala*. He characterized this species as having large pinnately arranged pinnules with typically linear, ribbon-like laminae. The pinnules are thick, with obscure venation and crenulate margins. Most of the specimens attributed to this species by White fit his description. However, only one of the typically pinnate specimens has even a hint of an incomplete apical region. To remedy this deficiency, White added several specimens that appeared to be “terminal” portions of fronds. Their addition to the *S. anomala* suite was based, presumably, on pinnule size and slight crenulation of the margin, given that they lack the pinnate pinnule arrangement found in the rest of the suite of specimens. The “terminal” pinnule morphology in these specimens, is a repeatedly forked linear, ribbon-

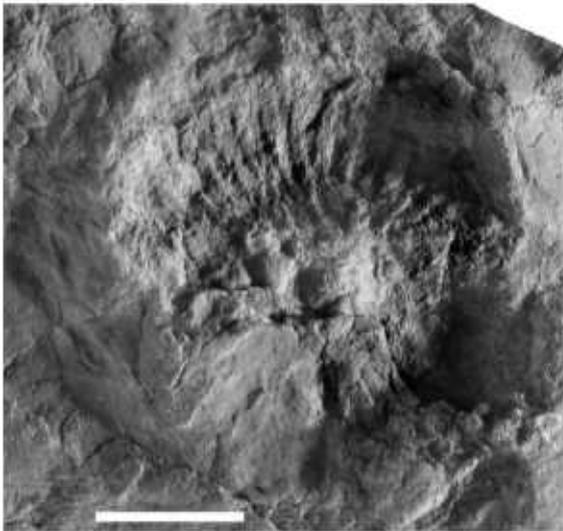


Fig. 16. *Peltaspermum* sp. USNM specimen 420417. *Peltaspermum*-like reproductive structure, typically associated with plants assignable to the Peltaspermales. Scale bar=1 cm.

like lamina (in White's terms: "apex of the pinna slightly sympodially dichotomous in distant, oblique, narrow, short-linear pinnules, the linear or narrowly lingulate terminal being more or less deeply cut in one or two very short lobes at some distance below the rather obtuse apex"). It is possible that White has lumped together here a typical *Supaia* (the pinnate specimens) with something entirely different (the "sympodially dichotomous" specimens). He notes that this species is "suggestive of older Mesozoic floras," with nothing comparable known in the Permian outside of the Hermit Shale flora. Our *S. anomala*-like specimens clearly indicate that this morphotype is distinct and might even be considered a separate genus (with several species), given its differences in architecture from the other species of *Supaia*.

4.4. *Sphenophyllum* sp.

Several small, fragmentary specimens consist of jointed axes of less than 4 mm in diameter with faintly visible ribs. No laminate foliage was visible on the bedding plane surface, although there were clear indications of foliage buried in the sediment at right angles to the bedding plane surface. The largest of these specimens appears to be a mass of axes, possibly a single plant or clone, deposited on a soft mudstone surface (Fig. 17 represents two sides of the same hand specimen). Based on size and physical characteristics, these specimens appear to be a species of *Sphenophyllum*.

Without foliar features, a further taxonomic assignment is not possible. These are the only examples in this flora of a plant generally considered to be ground-cover and they may have grown in wetter stream margins rather than throughout the area covered by the dominant vegetation.

4.5. *Calamites* sp.

A single specimen of a ribbed axis approximately 1 cm wide and slightly more than 1 cm in length, but lacking a clear node, is questionably assigned to *Calamites*.

4.6. cf. *Phasmatoxycas kansanus* Mamay

A single specimen was found in float at the Gallina Well locality, east of Socorro, with gross morphology and size approximating *Phasmatoxycas kansanus* (Fig. 18). This genus and species were described by Mamay (1973) from the Early Permian of Texas, who believed them to be early cycads. *P. kansanus* consists of a broad *Taeniopteris*-type lamina with ovules or seeds apparently borne on the abaxial side, attached to either side of the midrib. These features can be seen clearly on the specimen, even though details of venation cannot be determined. Axsmith et al. (2003) have re-examined specimens of this genus and have concluded that its cycad affinities are problematic. *Phasmatoxycas* has been associated with *Taeniopteris* sterile foliage, which has not been identified in our collections from New Mexico.

5. Patterns of plant distribution

Collections in the Oscura Mountains were made *in situ* from six distinct sites. In addition, float blocks bearing fossil plants were collected on debris slopes below each fossiliferous outcrop. Plant distribution, by collecting locality in the Oscura Mountains and in the ancillary collecting localities east of Socorro, is summarized in Table 1. The most conspicuous characters of each collecting site were the following.

1. Each site was dominated overwhelmingly by either walchian conifers or supaioid peltasperms, but codominance did not occur. In fact, overlap was minimal between these taxa in the collections made *in situ*. Rarely a specimen of conifer might occur within a peltasperm-dominated assemblage, or vice versa. And, on occasion, a specimen of the opposite group would appear in float, where accessible sample size was larger. Dominance at a site was consistent

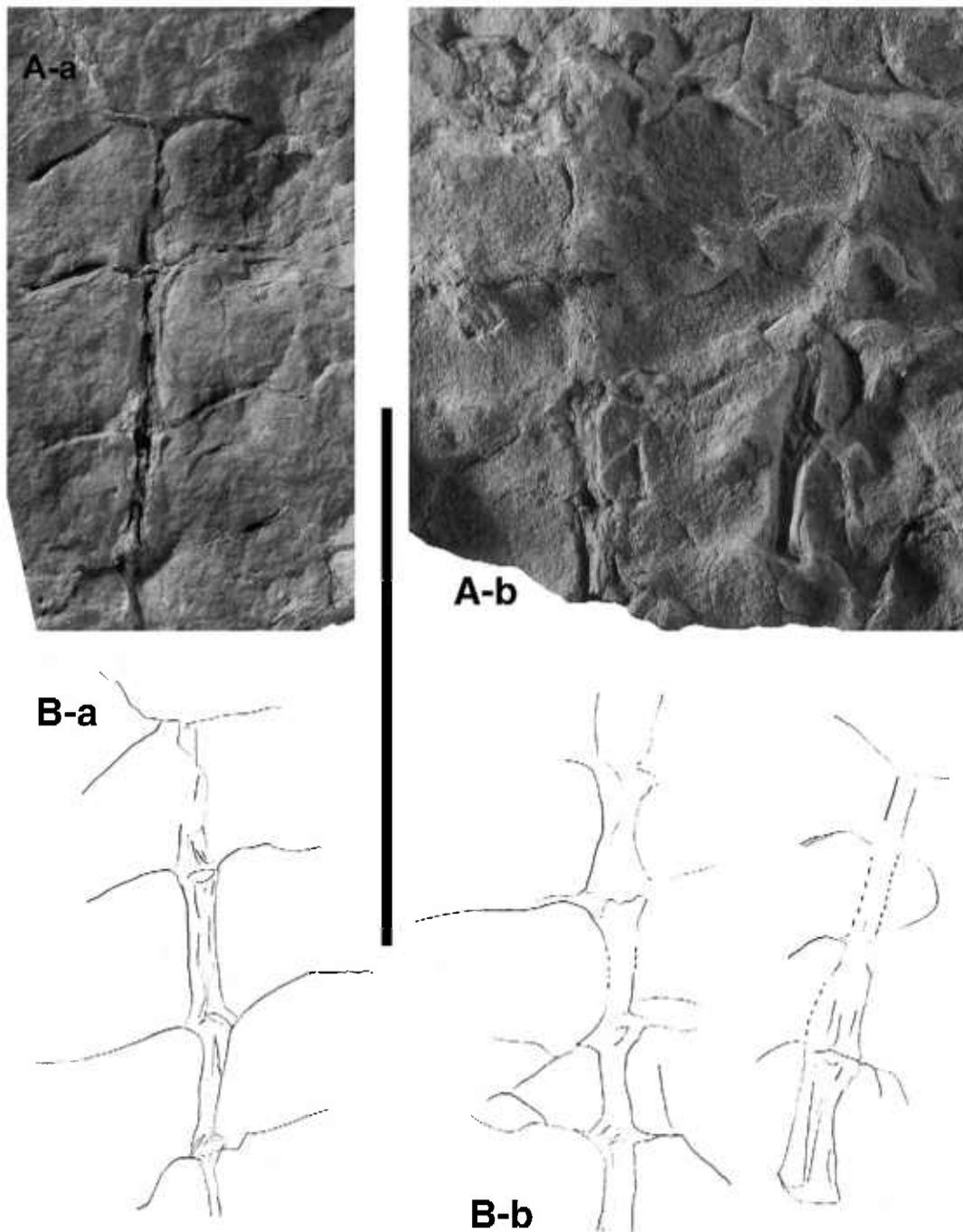


Fig. 17. *Sphenophyllum* sp. preserved as impression originally in soft clay. USNM specimen 520423. Aa and Ab represent opposite sides of the same specimen Ba and Bb are camera lucida drawings of the same specimens. Scale bar=5 cm.

through the entire thickness of accumulated sediment. The plant-bearing sandstones appeared to be a single story at each site.

2. Plant fossils occurred through a thickness of up to 3 m of flaggy bedded siltstones with interbedded thin

claystones, the latter generally as drapes. These flaggy bedded siltstones were always at the tops of thicker sandstone bodies, where rock body geometry could be observed, thus likely representing the final phases of sheet floods or channel flow into low lying



Fig. 18. cf. *Phasmatocycas kansanus* sp. USNM specimen 520424. Impression, probably of adaxial surface with seeds/ovules visible on either side of the midrib of the lamina. Gallina Well locality, East of Socorro. Scale bar=1 cm.

areas of standing water. Associated with the plant fossils were multiple layers of animal tracks and trails, numerous desiccation-cracked surfaces, surfaces imprinted with rain drops, and interbedded mud drapes, all indicators of intermittent flooding, waning flow, and subaerial exposure.

3. Conifer-dominated and peltasperms-dominated deposits can occur in close physical proximity, such as less than 50 m apart at Aperson Tank Ridge #1 and #2 localities. These assemblages may have accumulated contemporaneously in close proximity, or they may have been deposited in separate flooding events on a slowly subsiding landscape where streams were canalizing sediments on the local landscape, thus making these deposits appear lateral to one another instead of stacked on one another in multistory sequences.
4. Similar distributions of plants in siltstone–claystone interbedded sequences were seen in the ancillary collecting areas east of Socorro, Gallina Well (USNM 42111, 42117, 42118) and Cerrillos del Coyote (USNM 42100, 42101). At each of these sites, deposits tended to be dominated by either walchian conifers or peltasperms, although there were occasional co-occurrences within a deposit dominated by one taxonomic group or the other. Although these could not be correlated directly with the Oscura Mountains deposits, the basic depositional patterns and patterns of plant occurrences are the same in both areas.

6. Discussion

Tropical floristic species richness in the western parts of the late Paleozoic tropics (present day North America, e.g., Ziegler et al., 1997) declined during the transition from the Pennsylvanian to the Permian. This change in richness accompanied a change in the basic flora, a biome transition in the lowland tropics (DiMichele and Aronson, 1992), that reflected a change in ambient climatic conditions from everwet to seasonally dry (Ziegler et al., 2002; DiMichele et al., 2006). Middle Pennsylvanian-type wetland floras survived into the Late Permian in China (Tian et al., 1996; Wang et al., 2003), where high rainfall permitted peat formation and the associated flora to survive climatic changes attendant upon deglaciation during the Early Permian (see papers in Martini, 1997).

Vegetation of seasonally dry environments was rarely so low in overall species richness as that found in the deposits described here from central New Mexico. In fact, there are few plant-bearing deposits described from the Pennsylvanian or Permian tropics with evidence as

described here of such high dominance by one or two species on a regional scale (e.g. Ziegler et al., 2002). Even more peculiar is the clear evidence that, although coexistent, conifers of the *Walchia* type and peltasperms attributable to *Supaia thinnfeldioides* were distinctly patchy in dominance.

6.1. Inferring the physical habitat

The plant bearing portions of sandstone bodies are laterally extensive sheets that are relatively thin (a few meters or less) intercalated with thick slopes of siltstone/mudstone. They are multistoried, and thus represent multiple events. Precise correlation among the several plant localities in the Oscura Mountains is not possible. They appear, however, to fall within a stratigraphic interval less than 15 to 18 m thick. At the North of Bruton Tank locality fossil plants occurred in the upper 3 m of a fining-upward sandstone unit about 13 m thick. The lower 10 m of this sandstone showed planar, ripple, and cross-lamination, including foreset beds up to about 35 cm thick indicative of lateral accretion. In the vicinity of these deposits there is an abrupt channel margin where this sandstone scoured into underlying (poorly exposed) strata. Although only one edge was found, this deposit clearly represents a channel fill. At the localities east and west of Aperson Tank, the plant-bearing sandstone units were thinner and more tabular. The lower contact or relations to enclosing strata were not observed, although distinct biofacies were recognizable, possibly indicating separate depositional events, capturing spatio-temporal differences in the vegetation on the landscape.

The energy of this system is somewhat difficult to estimate because the site of the Oscura Mountains lay on a flat and featureless, muddy coastal plain bordered on the south by the Hueco seaway during deposition of the Abo Formation (see Fig. 1). Mountainous source areas formed the distant skyline 80–160 km or more to the north and northeast. Thus, given distance from the source and low gradient, trunk streams could carry sediment only during heaviest flow. Channel features were observed at the North of Bruton Tank locality. However, the tabular geometry of the deposits east and west of Aperson Tank, and their lack of sedimentary characteristics of channels, suggests that these could be sheet-flow sand bodies, part of a braided system of small channels. The combination of these geometries and sedimentological features suggests that channels laterally migrated and avulsed forming broad sand flats in which much of the flow was unconfined (or unchanneled). The fossil plants and trackways tend to be in the upper parts of the sand sheets in strata with a variety of

ripple and laminated bedding. A few channels appear to have remained active within the complex of sandflats. Plants may have colonized the deposits following disturbance by intense flooding or the areas subject to sheet flooding. Each thin, rippled, tabular sand and overlying mud layer may represent a single sheet flood cycle. The largest clasts in the plant-bearing levels are the plant fossils themselves, which may be the best clue to the flow regime during flood events. Large plant remains must have been moved with the mud, silt, and fine sand. The lack of clear soil development may indicate that plants did not colonize sedimentologically active areas, instead living at the edge of these deposits, or that paleosols were immature and were removed during the erosional phases of each sheet flood.

The presence of mudcracks, horizontal burrows and/or feeding traces, animal tracks, raindrop imprints, and plant impressions on multiple layers in the upper few meters of each deposit requires the passage of enough time for animals to leave their marks and the sediment to dry out before the flood event took place locally. Given the likelihood that this was a region with seasonal climate during the Permian (Mack, 2003; Mack et al., 2003), it is probable that weeks to months elapsed between each flood event and subsequent drying. To form each complete deposit of thinly bedded, mud-cracked sandstone, 1 to 3 m thick, probably required several years to decades. The entire unit composed of multiple sheet sands and small channels may represent a considerable amount of time from hundreds to thousands of years.

6.2. Low species richness: taphonomic bias?

An immediate suspicion arises in the face of these patterns that there must be significant taphonomic biases of some major type that resulted in the loss of all but the most decay resistant fossils from the plant-bearing Abo redbeds. Most Abo environments were not conducive to preserving fossil plants, even though vegetation likely was present based on the presence of rooted horizons and paleosols in otherwise non-fossiliferous sequences. We may surmise that on floodplains, soil development and pervasive oxidation (red = rust) may have destroyed all organic matter, although plant fossils of excellent quality may occur in red claystones and siltstones, such as those from the Early Permian of Texas (DiMichele et al., 2006). In active channels, plant matter may have been carried through and eventually was ground up, decomposed or floated out to sea. Where plants wound up in the bed load, the sand was permeable enough that the plants decayed. Consequently, preservation took place only in back-water areas, such as Cerrillos del Coyote, where

plants occur in tabular sandstone lateral to a small channel, and in intermittent or ephemeral stages of drying streams, such as in the Oscura Mountain deposits described here in detail, where fine clay drapes likely were essential for fossilization, encasing plant pieces and protecting them from oxygen and bacteria.

When examined in detail, however, taphonomic biases do not seem to account for the patterns of extreme dominance and low species richness. First, *Supaia* and *Walchia* are quite different in gross morphology and should have been affected quite differently by extreme sedimentological conditions. The *Supaia* fossils are pinnate, laminate fronds that, although appearing quite leathery in construction, were nonetheless relatively large and should have been more subject to the effects of abrasion during transport than the tough needle-like foliage of *Walchia*. Second, large, complete fronds or branches of both these genera are encountered frequently and often occur as dense mats on mud-draped siltstone surfaces. The large size and density of the fossils indicates local, low-energy transport. Third, fossils occur commonly as three dimensional molds in clay drapes between thin siltstone beds (Figs. 4Aa and 5), suggesting deposition during waning stages of stream or sheet flooding, coincident with the settling of mud from suspension. Such fossils do not occur in the coarser sandstone facies of the sedimentary sequences described here; rather, they are found only in those deposits indicating flashy discharge, possibly deposited in intense storms and floods of short duration. Overall, it would be difficult to make a case for the differential abrasion or decay of an unseen diversity of species, leaving only the well preserved conifers and supaioids.

Most peculiar is the infrequency of calamitalean sphenopsid remains, plants known to have frequented stream sides and environments of sediment aggradation (Gastaldo, 1992). A few specimens were identified, suggestive of larger populations, given the clonal morphologies and dense growth stands in many species of these plants.

Similarly, ground cover plants were largely absent. A few specimens of the sphenopsid *Sphenophyllum* were identified. No other ground cover plants or vines, well represented among the ferns and pteridosperms, were identified in any of the collections made as part of this study or other studies (e.g., Hunt, 1983) from the Oscura Mountains or nearby areas.

A study by Scheihing (1980) may explain the absence of ground cover and the apparently low richness of these floras. Examining an area of the New Jersey pine barrens following a hurricane, he found that roads through the forested areas, which may be considered the equivalent of stream catchments, contained abundant

branches and leaves of the local canopy trees, mostly pine and oak. Ground cover plants, which were conspicuous elements of the forest floor, were virtually absent from the roadways. Scheihing attributed this to the reduction in wind shear by the dense canopy. To the extent that this model is applicable, the Permian forests of the Abo Formation may have been composed of dense and largely monotypic stands of canopy trees locally or even over large areas. The presence of dense mats of large fronds suggests such catastrophic deposition and limited transport, probably in storms, the plant parts settling out with mud as water flow waned. The rare occurrence of ground cover plants in the Abo deposits may reflect a significant taphonomic filter affecting the composition of the fossil-plant assemblages.

6.3. Persistent mono-dominance

The other significant pattern in these deposits is the local dominance of one type of canopy plant within any local deposit. The dominant plant persists at each collecting site through many cycles of siltstone–claystone deposition, each thin, tabular siltstone bed presumably representing one in a series of periodic floods. The periodicity of flooding is made clear by the presence of terrestrial animal tracks, raindrop imprints, and mudcracks in various combinations on many of the surfaces, including those that bear plant fossils. It is difficult to estimate the time encompassed by two or more meters of such platy siltstone at the top of a thicker sandstone, but we presume that the aggregate beds making up each plant-bearing deposit represent a time frame of on the scale of decades at least.

On occasion channel margins were observed within the laterally persistent ledge-forming sandstone, suggesting that the plant-bearing horizon in the Oscura Mountains in fact consists of several to many distinct sand bodies and the depositional events they represent. Plant-bearing sediments may have been deposited over an extended period of time on a coastal plain of low relief and low subsidence, with repeated episodes of channel cutting and sheet flow. At some times, *Walchia* was dominant, at others *Supaia*. Although specimens of these two genera occur together, they possibly attained dominance at different times and perhaps under subtly different climatic conditions, explaining the high dominance of single species in any one local sequence (one temporally distinct deposit) of interbedded muds and silts. Although collected locally, these intervals of dominance may represent more widespread, possibly regional intervals of widespread low diversity forest development. Each rare opportunity for plant preservation

may have captured one temporal interval and the associated dominant plant. In this instance, it is probable that the conifers represent the wetter ends of a climatic gradient, given the abundance of walchian conifers in diverse Permian plant assemblages of North America (e.g., Read and Mamay, 1964; Mamay and Mapes, 1992; DiMichele et al., 2001) and Europe (Kerp and Fichter, 1985), including those with local patches of tree ferns, pteridosperms, and callipterids. In contrast, *Supaia* has rarely been reported as a landscape dominant. Its dominance of the Hermit Shale flora (White, 1929), from which the genus was first described, is unusual. And in this flora, *Supaia* is overwhelmingly the most common plant. Its xeromorphic attributes, such as thick leaf laminae, obscure venation, and generally small size in comparison to related forms, such as the callipterids, in addition to its association with evaporitic sediments, as described by White (1929) for the Grand Canyon specimen suite, suggest that it may have been most common in water-stressed habitats, possibly forming open canopied scrublands.

The alternative to this scenario is a persistently patchy landscape, one in which small areas of conifer-dominated vegetation and areas of peltasperm dominance overlapped little but occurred in close proximity, creating a heterogeneous landscape. This would be possible if the spatial dynamics were controlled largely by opportunistic colonization of heavily disturbed sites followed by exclusion of the other potential dominant by the incumbent. It also may indicate widespread differences in local substrate conditions, perhaps related to the degree of available ground water.

It really is not possible to distinguish between these options based on the evidence at hand. However, the latter seems less likely in light of the sedimentological evidence for multiple shallow channels and swales on a larger sand flat, all at about the same stratigraphic position but not necessarily formed at the same time. In either case, these deposits have no parallel in the literature as regards the high dominance, low species richness, and widespread distribution.

Acknowledgements

We thank Murphy Quick for his assistance in the field. Greg Mack made extensive constructive comments on the manuscript, which are gratefully acknowledged. We thank Allister Rees, Jörg W. Schneider, and an anonymous reviewer for helpful reviews. We acknowledge the Roland W. Brown Fund of the Smithsonian Institution for partial support of this research. Wang Jun acknowledges a grant from the Chinese National Natural Science

Foundation (No.40321202), which contributed to his visit to the US. Cindy Looy acknowledges the Netherlands Organization for Scientific Research. This is a publication 147 of the Evolution of Terrestrial Ecosystems Program at the Smithsonian Institution.

References

- Ash, S., Tidwell, W.D., 1982. Notes on the Upper Paleozoic plants of central New Mexico. New Mexico Geological Society Guidebook, 33rd Field Conference, Albuquerque County I, pp. 245–248.
- Axsmith, B.J., Serbet, R., Krings, M., Taylor, T.N., Taylor, E.L., Mamay, S.H., 2003. The Enigmatic Paleozoic plants *Spermopteris* and *Phasmatocycas* reconsidered. American Journal of Botany 90, 1585–1595.
- Behrensmeyer A.K. Hook, R.W., rapporteurs, 1992. Paleoenvironmental contexts and Taphonomic Modes. In: Behrensmeyer, A.K. et al. (Eds.), Terrestrial Ecosystems through Time. University of Chicago Press, Chicago, pp. 14–136.
- Blakey, R.C., Gubitosa, R., 1984. Controls of sandstone body geometry and architecture in the Chinle Formation (Upper Triassic), Colorado plateau. Sedimentary Geology 38, 51–86.
- Bonner, H., 2004. When bugs were big, plants were strange, and tetrapods stalked the Earth. National Geographic Society, Washington, D.C.
- DiMichele, W.A., Aronson, R.B., 1992. The Pennsylvanian–Permian vegetational transition: a terrestrial analogue to the onshore–offshore hypothesis. Evolution 46, 807–824.
- DiMichele, W.A., Dixon, W.H., Nelson, W.J., Chaney, D.S., Hook, R.W., 2000. An Early Permian coastal flora from the Central Basin Platform of Gaines County, west Texas. Palaios 15, 524–534.
- DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., Nelson, W.J., 2001. An Early Permian flora with Late Permian and Mesozoic affinities from north-central Texas. Journal of Paleontology 75, 449–460.
- DiMichele, W.A., Kerp, H., Krings, M., Chaney, D.S., 2005. The Permian peltasperm radiation: evidence from the southwestern United States. In: Lucas, S.G., Zeigler, K.E. (Eds.), The Nonmarine Permian. New Mexico Museum of Natural History and Science Bulletin, vol. 30, pp. 67–79.
- DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wetspots: the fate and significance of Carboniferous elements in Early Permian coastal plain floras of North-Central Texas. In: Greb, S., DiMichele, W.A. (Eds.), Wetlands Through Time. Geological Society of America Special Publication, vol. 399, pp. 223–248.
- Eberth, D.A., Miall, A.D., 1991. Stratigraphy, sedimentology and evolution of a vertebrate-bearing, braided to anastomosing fluvial system, Cutler Formation (Permian–Pennsylvanian), north-central New Mexico. Sedimentary Geology 72, 225–252.
- Gastaldo, R.A., 1992. Regenerative growth in fossil horsetails following burial by alluvium. Historical Biology 6, 203–219.
- Halle, T.G., 1927. Palaeozoic plants from central Shansi. Paleontologia Sinica, Series A 11 (Fascicle 1), 1–316.
- Hernandez-Castillo, G.R., Rothwell, G.W., Stockey, R.A., Mapes, G., 2003. Growth architecture of *Thucydia mahoningensis*, a model for primitive walchian conifer plants. International Journal of Plant Science 164, 443–452.
- Hatchell, W.O., Blagbrough, J.W., Hill, J.M., 1982. Stratigraphy and copper deposits of the Abo Formation, Abo Canyon area, New

- Mexico. New Mexico Geological Society Guidebook, 33rd Field Conference, Albuquerque Country II, pp. 249–260.
- Hunt, Adrian, 1983. Plant fossils and lithostratigraphy of the Abo Formation (Lower Permian) in the Socorro area and plant biostratigraphy of Abo red beds in New Mexico. New Mexico Geological Society Guidebook, 34th Field Conference, Socorro Region II, pp. 157–163.
- Kerp, J.H.F., 1988. Aspects of Permian palaeobotany and palynology. X. The West and Central European species of the genus *Autunia* Krasser emend. (Peltaspermeaceae) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage). Review of Palaeobotany and Palynology 54, 249–360.
- Kerp, J.H.F., Fichter, J., 1985. Die Makrofloren des saarpfälzischen Rotliegenden (?Ober-Karbon-Unter-Perm; SW Deutschland). Mainzer Geowissenschaftliche Mitteilungen 14, 159–286.
- Kerp, J.H.F., Poort, R.J., Swinkels, H.A.J.M., Verwer, R., 1990. Aspects of Permian palaeobotany and palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (?Late Carboniferous– Early Permian; SW-Germany) with special reference to the reproductive biology of the earliest conifers. Review of Palaeobotany and Palynology 62, 205–248.
- Kietzke, K.K., Lucas, S.G., 1995. Some microfossils from the Robledo Mountains member of the Hueco Formation, Dona Ana County, New Mexico. In: Lucas, S.G., Heckert, A.B. (Eds.), Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science, Bulletin, vol. 6, pp. 57–62.
- Kluth, C.F., 1986. Plate tectonics of the Ancestral Rocky Mountains. American Association of Petroleum Geologists, Memoir 41, 353–369.
- Kottlowski, F.E., 1963. Paleozoic and Mesozoic strata of southwestern and south-central New Mexico. New Mexico Bureau of Mines and Mineral Resources, Bulletin 79, 1–100.
- Kottlowski, F.E., Stewart, W.J., 1970. The Wolfcampian Joyita Uplift in central New Mexico. New Mexico Bureau of Mines and Mineral Resources, Memoir 23, 1–31.
- Kottlowski, F.E., Flower, R.H., Thompson, M.L., Foster, R.W., 1956. Stratigraphic studies of the San Andres Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources, Memoir 1, 1–132.
- Kozur, H.W., LeMone, D.V., 1995. The Shalem Colony section of the Abo and upper Hueco members of the Hueco Formation of the Robledo Mountains, Dona Ana County, New Mexico: stratigraphy and new conodont-based age determinations. In: Lucas, S.G., Heckert, A.B. (Eds.), Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science, Bulletin, vol. 6, pp. 39–55.
- Kues, B.S., 1995. Marine fauna of the Early Permian (Wolfcampian) Robledo Mountains member, Hueco Formation, southern Robledo Mountains, New Mexico. In: Lucas, S.G., Heckert, A.B. (Eds.), Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science, Bulletin, vol. 6, pp. 63–90.
- Lee, W.T., Girty, G.H., 1909. The Manzano Group of the Rio Grande valley, New Mexico. U.S. Geological Survey Bulletin 389, 1–141.
- Lesquereux, L., 1879. Description of the coal flora of the Carboniferous formation in Pennsylvania and throughout the United States. Second Geological Survey of Pennsylvania, Report of Progress 1, 1–188.
- Little, G.E., 1987. Subsurface analysis of the (Permian) Abo Formation in the Lucero region, west-central New Mexico. M.S. thesis, New Mexico Institute of Mining and Technology, Socorro, 103 p.
- Lucas, S.G., Krainer, K., 2002. Permian stratigraphy in the Jarilla Mountains, Otero County, New Mexico. New Mexico Geological Society Guidebook, 53rd Field Conference, Geology of White Sands, pp. 211–222.
- Lucas, S.G., Zeigler, K.E., 2004. Permian stratigraphy in the Lucero uplift, central New Mexico. New Mexico Museum of Natural History and Science, Bulletin 25, 71–82.
- Lucas, S.G., Krainer, K., 2004. The Red Tanks Member of the Bursum Formation in the Lucero uplift and regional stratigraphy of the Bursum Formation in New Mexico. New Mexico Museum of Natural History and Science, Bulletin 25, 43–52.
- Lucas, S.G., Anderson, O.J., Heckert, A.B., Hunt, A.P., 1995a. Geology of Early Permian tracksites, Robledo Mountains, south-central New Mexico. In: Lucas, S.G., Heckert, A.B. (Eds.), Early Permian Footprints and Facies. New Mexico Museum of Natural History and Science, Bulletin, vol. 6, pp. 13–32.
- Lucas, S.G., Anderson, O.J., Heckert, A.B., Hunt, A.P., 1995b. Geology of early Permian tracksites, Robledo Mountains, south-central New Mexico. New Mexico Museum of Natural History and Science, Bulletin 6, 13–32.
- Lucas, S.G., Heckert, A.B., Estep, J.W., Cook, C.W., 1998. Stratigraphy of the Lower Permian Hueco Group in the Robledo Mountains, Dona Ana County, New Mexico. New Mexico Museum of Natural History and Science, Bulletin 12, 43–54.
- Lucas, S.G., Krainer, K., Kues, B.S., 2002a. Type section of the Upper Carboniferous Bursum Formation, south-central New Mexico, and the Bursumian Stage. New Mexico Geological Society Guidebook, 53rd Field Conference, Geology of White Sands, pp. 179–192.
- Lucas, S.G., Krainer, K., Kues, B.S., 2002b. Stratigraphy and correlation of the Lower Permian Hueco Group in the southern San Andres Mountains, Dona Ana County, New Mexico. New Mexico Geological Society Guidebook, 53rd Field Conference, Geology of White Sands, pp. 223–240.
- Mack, G.H., 2003. Lower Permian terrestrial paleoclimatic indicators in New Mexico and their comparison to paleoclimate models. New Mexico Geological Society Guidebook, 54th Field Conference, Geology of the Zuni Plateau, pp. 231–240.
- Mack, G.H., Dinterman, P.A., 2002. Depositional environments and paleogeography of the Lower Permian (Leonardian) Yeso and correlative formations in New Mexico. Mountain Geologist 39, 75–88.
- Mack, G.H., Cole, D.R., Giordano, T.H., Schaal, W.C., Barcelos, J.H., 1991. Paleoclimatic controls on stable oxygen and carbon isotopes in caliche of the Abo Formation (Permian), south-central New Mexico, U.S.A. Journal of Sedimentary Petrology 61, 458–472.
- Mack, G.H., Leeder, M., Perez-Arlucea, M., Bailey, B.D.J., 2003. Sedimentology, paleontology, and sequence stratigraphy of Early Permian estuarine deposits, south-central New Mexico, USA. Palaios 18, 403–420.
- Mamay, S.H., 1973. *Archaeocycas* and *Phasmatozycas*, new genera of Permian cycads. U.S. Geological Survey, Journal of Research 1, 687–689.
- Mamay, S.H., 1975. *Sandrewia*, n. gen., a problematical plant from the Lower Permian of Texas and Kansas. Review of Palaeobotany and Palynology 20, 75–83.
- Mamay, S.H., Mapes, G., 1992. Early Virgillian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, 61–85.
- Martini, I.P. (Ed.), 1997. Late Glacial and Postglacial Environmental Changes: Quaternary, Carboniferous, Permian, and Proterozoic. Oxford Univ. Press, New York.
- Meyer, Richard F., 1966. Geology of Pennsylvanian and Wolfcampian rocks in southeast New Mexico. New Mexico Bureau of Mines and Mineral Resources, Memoir 17, 1–123.

- Naugolnykh, S.V., 1999. A new species of *Compsopteris* Zalessky from the Upper Permian of the Kama River Basin (Perm Region). *Paleontological Journal* 33, 686–697.
- Naugolnykh, S., Kerp, H., 1996. Aspects of Permian Palaeobotany and Palynology. XV. On the oldest known peltasperms with radially symmetrical ovuliferous discs from the Kungurian (uppermost Lower Permian) of the Fore-Urals (Russia). *Review of Palaeobotany and Palynology* 91, 35–62.
- Needham, C.E., Bates, R.L., 1943. Permian type sections in central New Mexico. *Geological Society of America Bulletin* 54, 1653–1668.
- Otte Jr., C., 1959. Late Pennsylvanian and Early Permian stratigraphy of the northern Sacramento Mountains, Otero County, New Mexico. *New Mexico Bureau of Mines and Mineral Resources, Bulletin* 50, 1–111.
- Read, C.B., Mamay, S.H., 1964. Upper Paleozoic floral zones and floral provinces of the United States. *U.S. Geological Survey Professional Paper* 454-K, 1–35.
- Ross, C.A., Ross, J.R.P., 1986. Paleozoic paleotectonics and sedimentation in Arizona and New Mexico. *American Association of Petroleum Geologists, Memoir* 41, 653–668.
- Scheihing, M.H., 1980. Reduction of wind velocity by the forest canopy and the rarity of non-arborescent plants in the Upper Carboniferous fossil record. *Argumenta Palaeobotanica* 6, 133–138.
- Schneider, J.W., Lucas, S.G., Rowland, J.M., 2004. The blattida (Insecta) fauna of Carrizo Arroyo, New Mexico — biostratigraphic link between marine and non-marine Pennsylvanian/Permian boundary profiles. *Bulletin, New Mexico Museum of Natural History and Science* 25, 247–261.
- Seager, W.R., Mack, G.H., 2003. Geology of the Caballo Mountains, New Mexico. *New Mexico Bureau of Mines and Mineral Resources, Memoir* 49, 1–136.
- Sellards, E.H., 1900. A new genus of ferns from the Permian of Kansas. *Kansas University Quarterly* 9, 179–189.
- Sun, Bainian, Shen, Guanglong, He, Xilin, 1999. New material of *Protoblechnum* from Permian coal-bearing strata in western Henan. *Earth Science Journal of China University of Geosciences* 24, 161–166 (in Chinese with English summary).
- Sze, H.C., 1955. On a forked frond of *Protoblechnum wongii* Halle. *Scientia Sinica* 4, 201–212.
- Thompson, M.L., 1942. Pennsylvanian System in New Mexico. *New Mexico School of Mines Bulletin* 17, 1–92.
- Thompson, M.L., 1954. American Wolfcampian fusulinids. *University of Kansas Paleontological Contributions, Protozoa, Article* 5, 1–226.
- Tian, B.L., Wang, S.J., Gao, Y.T., Chen, G.R., Zhao, H., 1996. Flora of Palaeozoic coal balls in China. *Palaeobotanist* 45, 247–254.
- Utting, J., Hartkopf-Froder, C., Lucas, S.G., Traverse, A., 2004. Palynological investigation of the Upper Pennsylvanian Red Tanks Member, Bursum Formation, Carrizo Arroyo, New Mexico, U.S.A. *New Mexico Museum of Natural History and Science, Bulletin* 25, 89–96.
- Wang, S.J., Hilton, J.M., Tian, B., 2003. A new species of cardiocarpalean ovule from Early Permian coal balls from north China. *Review of Palaeobotany and Palynology* 123, 303–319.
- Wahlman, G.P., King, W.E., 2002. Latest Pennsylvanian and earliest Permian fusulinid biostratigraphy, Robledo Mountains and adjacent ranges, south-central New Mexico. *New Mexico Bureau of Mines and Mineral Resources, Circular* 208, 1–26.
- White, D., 1929. Flora of the Hermit Shale, Grand Canyon, Arizona. *Publication, vol. 405. Carnegie Institution of Washington*, pp. 1–221.
- Wilpolt, R.H. and Wanek, A.A., 1951. Geology of the region from Socorro and San Antonio east to Chupadera Mesa: Valencia, Torrance, and Socorro Counties, New Mexico. *U.S. Geological Survey, Oil and Gas Investigations Map, OM-121*, 2 sheets, map scale 1:62,500.
- Wilpolt, R.H., MacAlpin, A.J., Bates, R.L., and Vorbe, G., 1946. Geologic map and stratigraphic sections of Paleozoic rocks of Joyita Hills, Los Pinos Mountains, and northern Chupadera Mesa, Valencia, Torrance, and Socorro Counties, New Mexico. *U.S. Geological Survey, Oil and Gas Investigations Preliminary Map*, 61, 1 sheet, map scale 1:62,500.
- Wing, S.L., DiMichele, W.A., 1995. Conflict between local and global changes in plant diversity through geological time. *Palaios* 10, 551–564.
- Wood, G.H. and Northrup, S.A., 1946. Geology of Nacimiento Mountains, San Pedro Mountain, and adjacent plateaus in parts of Sandoval and Rio Arriba Counties, New Mexico. *U.S. Geological Survey, Oil and Gas Investigations Preliminary Map*, 57, 1 sheet, map scale 1:62,500.
- Zalessky, M.D., 1927. Permskaya flora Uralskikh predelov Angaridy. *Trudy Geolkom., Nov. Ser., vol. 176*, pp. 1–52.
- Ziegler, A.M., Hulver, M.L., Rowley, D.B., 1997. Permian world topography and climate. In: Martini, I.P. (Ed.), *Late Glacial and Postglacial Environmental Changes: Quaternary, Carboniferous–Permian, and Proterozoic*. Oxford University Press, New York, pp. 111–146.
- Ziegler, A.M., Rees, P.M., Naugolnykh, S.V., 2002. The Early Permian floras of Prince Edward Island, Canada: differentiating global from local effects of climate change. *Canadian Journal of Earth Sciences* 39, 223–238.