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Title: Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangaea: Paleoecology and evolutionary significance

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Abstract: The Pennsylvanian-Permian transition has been inferred to be a time of significant glaciation in the Southern Hemisphere, the effects of which were manifested throughout the world. In the equatorial regions of Pangea, the response of terrestrial ecosystems was highly variable geographically, reflecting the interactions of polar ice and geographic patterns on atmospheric circulation. In general, however, there was a drying trend throughout most of the western and central equatorial belt. In western Pangea, the climate proved to be considerably more seasonally dry and with much lower mean annual rainfall than in areas in the more central and easterly portions of the supercontinent. Here we describe lower Permian (upper Asselian) fossil plant assemblages from the Community Pit Formation in Prehistoric Trackways National Monument near Las Cruces, south-central New Mexico, U.S.A. The fossils occur in sediments within a 140-m-wide channel that was incised into indurated marine carbonates. The channel filling can be divided into three phases. A basal channel, limestone conglomerate facies contains allochthonous trunks of walchian conifers. A middle channel fill is composed of micritic limestone beds containing a brackish-to-marine fauna with carbon, oxygen and strontium isotopic composition that provide independent support for salinity inferences. The middle limestone also contains a (par)autochthonous adpressed megaflora co-dominated by voltzian conifers and the callipterid Lodevia oxydata. The upper portions of the channel are filled with muddy, gypsiferous limestone that lacks plant fossils. This is the geologically oldest occurrence of voltzian conifers. It also is the westernmost occurrence of L. oxydata, a rare callipterid known only from the Pennsylvanian-Permian transition in Poland, the Appalachian Basin and New Mexico. The presence of in situ fine roots within these channel-fill limestone beds and the taphonomic constraints on the incorporation of aerial plant remains into a lime mudstone indicate that the channel sediments were periodically colonized by plants, which suggests that these species were tolerant of salinity, making these plants one of, if not the earliest unambiguous mangroves.

Cover Letter, for Editor only

UNIVERSITY OF CALIFORNIA, BERKELEY

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Dear David Bottjer,   May 10, 2015

The revised manuscript "Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangaea: paleoecology and evolutionary significance" was just uploaded on the Paleo3 website. In this paper we present early Permian fossil plant assemblages from the Prehistoric Trackways National Monument, New Mexico. This is the geologically oldest occurrence of voltzian conifers, the westernmost occurrence of a rare seed fern, and possibly evidence for mangroves. We were pleased to hear that the manuscript only needed minor revisions, and some additional analysis. In the revision notes below we explain how and where each point of the reviewers' and editors' comments has been incorporated, and indicated the changes in an annotated version of the revised manuscript. We hope you will find the revised paper acceptable for publication.

Kind regards,

Cindy Looy

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Revision Notes
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REVIEWER 1

Reviewer: Stable isotope geochemistry of the limestones in the channel structure are used as part of the greater argument for brackish to marine water associated with emplacement of the channel limestones and during in-situ plant growth (section 3.2; lines 282-299). The immensity of geological and palaeontological evidence presented for the marine to brackish conditions makes the interpretation of the stable carbon and oxygen isotope permissible, but the presentation of data and arguments surrounding them are under-developed. To be more precise:

Reviewer: No methods of analysis are presented.

Response: A new section describing the methodology of the isotopic analyses was added (4.1 methodology).

Reviewer: $d^{18}O$ and $d^{13}C$ values are presented as ranges, but there is no indication of how many analyses were completed and over which range they represent.

Response: The new methodology section 4.1 includes the number of samples used in for stable isotope analyses, and their values.

Reviewer: There is no presentation of stable isotope data either in Table or graphical form within the manuscript. I strongly recommend that this be included in a revised MS because it helps the reader to understand the meaning/substance of the data ranges and their distributions.

Response: A new section describing the data of the stable isotope data was added (4.2 Results), and presented in a new table (Table 1).

Reviewer: Line 285: "d13C compositions" should be "d13C values"

Response: This was changed in the text.

Reviewer: Line 290: "eariest " should be "earliest".

Response: This was changed in the text.

Reviewer: Lines 262-263: "…, proximal to land given clear evidence for wind-blown detrital material." What evidence, and why is it so clear?

Response: This part of the sentence was removed.

REVIEWER 2

Reviewer: In Page 29, Line 662, you stated "…Preserved cuticle on both conifer and callipterid foliage indicates rapid burial…." I wonder why you did not analyze the cuticle for the identification of these plants remains.

Response: Only a few of the conifers have cuticles preserved, after maceration it became clear the material was too oxidized to recognize epidermal characteristics. We clarified this in the manuscript by adding "Some specimen have cuticles preserved, unfortunately they do not preserve epidermal patterns" to the text. The callipterids do not have cuticle preserved. In a few patchy areas, the epidermal pattern of *Lodevia oxydata* can be recognized as impressions of the inside of the cuticle in the fine-rained sediment. The cuticle was initially preserved, but disappeared later in the process as a result of oxidation.

Reviewer: It has been well known that together occurrence of callipterids and conifers are only occasional. Therefore, the co-occurrence of callipterids and conifers has been always interesting and it would be really appreciated if the authors could provide better detailed information of the conifers, particularly the taxonomy. It is very likely possible to tell what exactly these conifers could be based on cuticle anatomy, with respect to the authors' team, of whom Hans Kerp and Cindy Looy have particularly worked a lot on the systematics of this group including cuticle anatomy. On the other hand, *Lodevia oxydata* as the element of callipterids in the assemblage has got a specific identification. Although these conifers are constrained as voltzian conifers, a more detailed determination rather than "Morphotype A, B, C, D" is very much expected, which is possible if you have got cuticles.

Response: *Lodevia oxydata* has a striking morphology, and for that reason relatively easy to recognize. To be absolutely sure of our case we compared it to a new image of the type specimen, and asked Manfred Barthel for a second opinion. Things are different in that regard for the conifers. A relatively low number of specimens were collected, the morphological differences between the specimens are relatively high, and the cuticles are not well-preserved. At this stage we prefer not to assign these conifers to a particular conifer taxon.

Reviewer: I would recommend to add a few photos to show the "Flora 1" (walchian conifer wood) in this article. Although this flora has been or will be described in detail elsewhere, it is better for a reader's convenience to have a quick look of the whole floral assemblages, as an independent publication.

Response: A detailed treatment of this flora has been published (Falcon-Lang et al., 2014), and we included the information on flora 1 here for sake of completeness. Instead of adding photo's of the walchian wood from the lower unit we decided to minimize the text of this part of the flora further.

Reviewer: Page 5, line 110, "…until now only known only from similar aged exposures in central Europe…" may be one "only" will be better ok.

Response: The second "only" was removed.

Reviewer: In Page 5, Line 95, the citation for Cathaysian conifers "(Cathaysia: Hernandez-Castillo et al., 2001" . It would be better to add a citation of the article: LIU Lujun and YAO Zhaoqi, 2013. "The conifer-remains from the Permian of South China". Acta Palaeontologia Sinica, 52(2): 182-201. (In Chinese with English summary.)

Response: The reviewer is correct. The Liu and Yao article was added to the text.

Reviewer: Page 6, line 136, it is better to give the full name for the abbreviation “NMMNHS” and “NMNH” when they occur for the first time in the text.

Response: Both full names are currently given when used for the first time.

Reviewer: Page 11, line 239, 245, you wrote “Plant Assemblage #1”, whereas in Page 12, line 272, you wrote “Plant Assemblage 2”, should this be “Plant Assemblage #2” for consistence of wording?

Response: The # sign was removed.

Reviewer: Page 24, line 534, “...by the authors in their combined over 200 person-years of field work...” I wonder if this is a mistake of “200 person-months” or “20 person-years”? “200 person-years of field work” in this region by the present authors is somewhat doubtful.

Reviewer: “200 person-years of field work” was changed to “many years”.

Highlights

An early Permian conifer-callipterid dominated megaflora from New Mexico is described

The flora includes the oldest occurrence of voltzian conifers

The flora grew on margins of a highly saline channel and was rooted within lime muds

The isotope composition of the associated fauna support the salinity inferences

The growth habitat is unusual and suggests mangrove habits for one or more taxa

Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangaea: Paleoecology and evolutionary significance

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Abstract

The Pennsylvanian-Permian transition has been inferred to be a time of significant glaciation in the Southern Hemisphere, the effects of which were manifested throughout the world. In the equatorial regions of Pangea, the response of terrestrial ecosystems was highly variable geographically, reflecting the interactions of polar ice and geographic patterns on atmospheric circulation. In general, however, there was a drying trend throughout most of the western and central equatorial belt. In western Pangea, the climate proved to be considerably more seasonally dry and with much lower mean annual rainfall than in areas in the more central and easterly portions of the supercontinent. Here we describe lower Permian (upper Asselian) fossil plant assemblages from the Community Pit Formation in Prehistoric Trackways National Monument near Las Cruces, south-central New Mexico, U.S.A. The fossils occur in sediments within a 140-m-wide channel that was incised into indurated marine carbonates. The channel filling can be divided into three phases. A basal channel, limestone conglomerate facies contains allochthonous trunks of walchian conifers. A middle channel fill is composed of micritic limestone beds containing a brackish-to-marine fauna with carbon, oxygen and strontium isotopic composition that provide independent support for salinity inferences. The middle limestone also contains a (par)autochthonous adpressed megaflora co-dominated by voltzian conifers and the callipterid *Lodevia oxydata*. The upper portions of the channel are filled with muddy, gypsiferous limestone that lacks plant fossils. This is the geologically oldest occurrence of voltzian conifers. It also is the westernmost occurrence of *L. oxydata*, a rare callipterid known only from the Pennsylvanian-Permian transition in Poland, the Appalachian Basin and New Mexico. The presence of in situ fine roots within these channel-fill limestone beds and the taphonomic constraints on the incorporation of aerial plant remains into a lime mudstone indicate

that the channel sediments were periodically colonized by plants, which suggests that these species were tolerant of salinity, making these plants one of, if not the earliest unambiguous mangroves.

Keywords: Permian, estuary, voltzian conifers, callipterids, mangrove, New Mexico

1. Introduction

During the early Permian, the Earth went through a transition from a globally cool to warm climate (Montañez et al., 2007; Tabor and Poulsen, 2008; Montañez and Poulsen, 2013), which resulted in prominent vegetational changes. Based on a global dataset, Rees et al. (2002) recognized four distinctly different floral realms during early Permian (Sakmarian) time: (1) a Gondwanan realm characterized by glossopterids in temperate regions of the Southern Hemisphere (Cúneo, 1996; Tewari et al., 2012); (2) a Euramerican realm characterized by walchian conifers, peltasperms and ferns in a seasonally dry tropical setting (Kerp et al., 1990; Zeigler et al., 2002); (3) a Cathaysian realm characterized by lycopsids, sphenopsids and ferns in the humid tropical islands bordering the western Tethys (Hilton and Cleal, 2007; Wang et al., 2012); and (4) a poorly resolved Angaran realm characterized by cordaitaleans in Northern Hemisphere temperate mid-latitudes (Meyen, 1982, 1988; Gomankov, 2009). Transitional vegetation also has been identified at the boundaries of these realms (Broutin et al., 1998; Berthelin et al., 2003; LePage et al., 2003). This global floral realm architecture had much earlier origins in the Carboniferous (Chaloner and Meyen, 1973), though the lycopsid-rich wetland biome, so typical of the Carboniferous Euramerican equatorial regions, was almost completely absent there by the early Permian (e.g., Kerp and Fichter, 1985; Kerp, 1996; DiMichele et al., 2009; Opluštil et al., 2013; Tabor et al., 2013) and survived in Cathaysia (Hilton and Cleal, 2007; Wang et al., 2012; Wang and Pfefferkorn, 2013).

The Euramerican floral realm, of which the flora reported here is a part, is the best known of the Permian seasonally dry vegetation types. Assemblages have been described from the southwestern U.S.A., eastern U.S.A., eastern Canada, North Africa, western Europe, and the Ukraine (e.g., Florin, 1938-1945; Doubinger, 1956; Kerp et al., 1990; Kerp, 1996; Broutin et al., 1998; Blake et al., 2002; Zeigler et al., 2002; DiMichele et al., 2007; Galtier and Broutin, 2008; Blake and Gillespie, 2011; Rößler et al., 2012; Tabor et al., 2013), all of which lay within 10 degrees of the paleoequator (Rees et al., 2002). According to Zeigler et al. (2002), the so-called walchian conifers are the most characteristic, abundant and widespread plants in this early Permian seasonal tropical vegetation.

Walchian conifers (walchian Voltziales *sensu* Rothwell et al., 2005) were the earliest conifers to appear in the fossil record and were characterized by a plagiotropic branching pattern and narrow, triangular to linear, needle-like leaves (e.g., Hernandez-Castillo et al. 2003; Rothwell et al., 2005). Their ovulate ovuliferous dwarf shoots were organized in cones or fertile zones. Walchian dwarf shoots had numerous sterile scales interspersed with a few sporophylls, which showed at least some indication of radial symmetry. Distinctly different and evolutionarily more derived are the voltzian conifers or voltzian Voltziales (*sensu* Rothwell et al., 2005). They were trees with an irregular branching pattern (orthotropic) and bifacial ovate, lanceolate to linear medium-sized leaves (e.g., Clement-Westerhof, 1988; Rothwell et al., 2005). Just like the walchian conifers, these conifers also produced ovuliferous cones or fertile zones. The sterile scales and sporophylls in their ovuliferous dwarf shoots, however, were partly to completely fused, and the whole structure was bilaterally symmetrical and more or less flattened in one plane (e.g., Clement-Westerhof, 1987; Looy and Stevenson, 2014). During the Permian, both of these groups are largely confined to the Euramerican floral realm, although there are reports of walchian Voltziales from transitional assemblages (Cathaysia: Liu and Yao, 2013; possibly Angara: LePage et al., 2003).

This report describes a distinct assemblage of early Permian (late Asselian) plant macrofossils from the Robledo Mountains in southern New Mexico. These fossils are preserved in an unusual depositional setting, a small channel filled with muddy, brackish-to-marine limestone, bordering a seaway. The assemblage includes *in situ* roots, which provide evidence of plant growth in the lime muds, under saline conditions higher than freshwater. Regional climate appears to have been periodically semi-arid to perhaps even arid (Tabor and Montañez, 2004; Tabor et al., 2008; Mack et al., 2010, 2013; Tabor et al., 2013). The bottom portion of the channel contains a flora dominated by walchian conifer logs, preserved in a locally sourced, conglomeratic lag deposit, probably emplaced during channel incision or initial backfilling phases. The middle portion is a lime mudstone in which the dominant floral elements are vegetative and reproductive remains of voltzian conifers and the callipterid *Lodevia*. This is the earliest record of voltzian conifers, considerably extending the range of the lineage from its previously oldest known occurrence near the early-middle Permian boundary (Looy, 2007; Looy and Stevenson, 2014). It also is the westernmost occurrence of *Lodevia oxydata*, until now known only from similar aged exposures in central Europe and the Appalachian Basin (Kerp and Haubold, 1988; DiMichele et al., 2013b).

This flora from the middle portions of the channel fill differs entirely from contemporaneous early Permian western Pangean floras preserved in the Abo Formation and its equivalents (Hunt, 1983; DiMichele et al, 2013a). These floras are known from coastal plain, siliciclastic red-bed deposits, which crop out widely from the northern to the southernmost parts of New Mexico, through the central part of the state (Lucas et al., 2013), including in the Robledo Mountains (Mack et al., 2010; Voigt et al., 2013). They are dominated by walchian conifers, with local occurrences of the peltasperm *Supaia thinnfeldioides* (DiMichele et al., 2007, 2012), rare callipterid peltasperms and isolated occurrences of other taxa more common in assemblages from other Permian equatorial regions (Kerp and Fichter, 1985; Galtier and Broutin, 2008; Opluštil et al., 2013; Tabor et al., 2013).

Other compositionally unusual assemblages of plants not dominated by walchians have been reported from the early Permian of the Euramerican equatorial region (e.g., DiMichele et al., 2001, 2004), one of which was characterized by voltzian conifers (e.g., Looy, 2007). These assemblages, often known from isolated occurrences, such as the one reported here, strongly suggest the existence of tropical biomes distinct from that dominated by walchian conifers, perhaps reflecting different patterns of rainfall seasonality or habitat quality.

2. Geological context

The fossiliferous deposit we describe here crops out in the Prehistoric Trackways National Monument (PTNM) near Las Cruces, Doña Ana County, south-central New Mexico, U.S.A. (Lucas et al., 2011, Hunt et al., 1993; MacDonald, 1994; Lucas and Heckert, 1995; Lucas et al., 1998ab, 2011; Minter and Braddy, 2009) (Figure 1). Map coordinates for the new fossil site are on file at the New Mexico Museum of Natural History and Science (NMMNHS), Albuquerque, New Mexico, and the National Museum of Natural History (NMNH), Washington, D.C. Only a few fossil plant assemblages have been previously reported from PTNM (Voigt et al., 2013; Falcon-Lang et al., 2014). The new material described here is housed in the paleontological collections at the NMMNHS as collecting localities NMMNH 3016 and 7981 (these are NMNH localities USNM 43550–43554 and 43563).

2.1. Stratigraphy and age

The fossil plant assemblages, discussed herein, occur in the lower Permian Hueco Group, which comprises, from base to top, the Shalem Colony, Community Pit, Robledo Mountains, and Apache Dam formations (Kottlowski, 1960; Mack and James, 1986; Lucas et al., 1998a, b; Krainer et al., 2003, 2009; Voigt et al., 2013). The fossils are from 10–15 m above the base of the local section of the approximately 91-m-thick Community Pit Formation, which means they are from the lower part of the formation (Figure 2). Based on the current state of our knowledge, summarized below, the age of the fossil plant assemblage in the lowermost Community Pit Formation of PTNM is late Asselian. It is bracketed by earliest Asselian fusulinids in the underlying Shalem Colony Formation and is positioned ca. 40 m below a bed containing (?)latest Asselian fusulinids in the middle part of the Community Pit Formation, and Sakmarian–early Artinskian strata in the middle to upper part of the Community Pit Formation (Krainer et al., 2009; Voigt et al., 2013; Falcon-Lang et al., 2014).

2.1.1. Biostratigraphic findings

Below the plant-bearing beds, immediately below the Community Pit Formation, fusulinids and smaller foraminifers are found in the Shalem Colony Formation. These foraminifers indicate, in regional terminology, an early Wolfcampian age (Needham, 1937; Lucas et al., 2002; Krainer et al., 2009). On the international time scale, this falls somewhere within the latest Gzhelian–earliest Asselian interval, i.e., the Carboniferous-Permian boundary (Henderson et al., 2012a).

Above the plant-bearing beds biostratigraphically significant fusulinids were discovered from a packstone (Bed 51, Figure 2). This bed was positioned 53.5 m above the base of the Community Pit Formation at NMMNH locality 7981, and positioned ca. 40 m above the plant beds (equivalent to beds 18–20, Figure 2). The fusulinids include *Pseudoschwagerina beedei* Dunbar and Skinner 1936, *Pseudoschwagerina* cf. *P*. *rhodesi* Thompson 1954 and *Paraschwagerina* sp. with phrenothecae (= *Paraschwagerina* aff. *P*. *phrenesa* Wilde 2006 or *Paraschwagerina* aff. *P*. *fax* Thompson and Wheeler 1946). Based on correlations across New Mexico (Wilde, 2006), we interpret these occurrences as indicative of a late or even latest Nealian (i.e., late to latest Asselian) age. We note that although *Paraschwagerina* specimens with phrenothecae first appear in the uppermost Lenoxian (lower Artinskian) strata of New Mexico (Wilde, 2006), they are present much earlier in the McCloud Limestone of the Klamath Terrane in northern California (Zone C of Skinner and Wilde, 1965), in rocks that are probably equivalent to the early Asselian. Therefore, their presence in the Community Pit Formation is not inconsistent with the age indicated by *Pseudoschwagerina*.

The foraminifer *Pseudovermiporella* has been identified from the middle and upper part of the Community Pit Formation elsewhere in Doña Ana County. Based on the First Appearance Datum (FAD) of this species, Krainer et al. (2009) inferred a Sakmarian age. This assignment was based on correlation with the FAD of this genus in successions of the Carnic Alps of Austria (Vachard and Krainer, 2001; Krainer et al., 2009). Formerly dated as Sakmarian (Forke, 1995), this interval is now placed in the early Artinskian based on conodonts and fusulinids (Davydov et al., 2013), which suggests that the correlative Community Pit Formation may be, in its uppermost part, of early Artinskian age.

Conodonts obtained from the middle part of the Robledo Mountains Formation, immediately overlying the Community Pit Formation, indicate an assignment to the late Wolfcampian (Lucas et al., 1998a, b, 2002); this is equivalent to a late Artinskian age (Henderson et al., 2012) on the international time scale. An Artinskian age for the Robledo Mountains Formation also is inferred based on the occurrence of the small fusulinid *Pseudoreichelina* throughout the formation (Krainer et al., 2009). This genus, however, ranges into middle Leonardian strata in Central America (Guatemala, northern Mexico), and the southwestern USA (New Mexico, Texas and Nevada) (Vachard et al., 1997), suggesting a Kungurian upper age limit (Henderson et al., 2012a).

2.2. General paleoenvironmental interpretation

The Community Pit Formation is a mixed siliclastic-carbonate unit, containing variably fossiliferous beds of dolomudstone, lime mudstones and wackestones, and siliciclastic shale (Figure 2; Krainer et al., 2003, 2009; Mack et al., 2013). It was deposited in a shallow marine to supratidal setting (the Hueco Seaway) on the western margin of the intracratonic Orogrande Basin (Lucas et al., 1998a, b; Voigt et al., 2013) at a paleolatitude of about 2ºN (Tabor et al., 2008). Elsewhere in Doña Ana County, the unit contains a somewhat restricted marine fauna, and red/green-mottled caliche paleosols are developed at a few intervals (Krainer et al., 2003, 2009; Lucas et al., 2002; Mack et al., 2010). Fifty kilometers north of Doña Ana County, this same stratigraphic interval comprises only red bed alluvial facies of the Abo Formation (DiMichele et al., 2007; Lucas et al., 2012). Therefore, during the Early Permian the location of the PTNM lay close to the fluctuating Hueco Seaway coastline (Mack and James, 1986), with alluvial plains to the north (Lucas et al., 2012).

In a PTNM section that largely comprises the Community Pit Formation, Mack et al. (2013) identified six supratidal and shallow marine facies. They compared the overall paleoenvironment with semi-arid portions of the present-day Trucial Coast of Abu Dhabi, highlighting the presence of gypsum. This interpretation of climate as semi-arid is consistent with regional studies of paleosols (Mack, 2003; Tabor et al., 2008; Mack et al., 2010). However, the remains of large fossil trees, which would have required a good water supply, occur at several intervals in the formation (Tidwell and Munzing, 1995; Falcon-Lang et al., 2014). There are three possibilities to explain this apparent inconsistency: (1) Regional climate was, in fact, semi-arid to arid, but there were localized poorly drained, groundwater-dependent habitats dotted across the landscape (cf. DiMichele et al., 2006), where arborescent vegetation could flourish despite the aridity. (2) Regional climate was overall somewhat wetter, allowing the geographic co-occurrence of minor evaporites with large trees, as seen, for example in the present-day southern Mediterranean region (cf. Francis, 1984). (3) Regional climate oscillated between wetter and drier phases, the large trees being associated with the former climate states and the evaporites with the latter (cf. Parrish and Falcon-Lang, 2007).

3. Paleoenvironment of the fossil site

The fossil site, reported here, occurs within a 5-6 m deep channel cut into a succession of shale, limestone and dolomite at NMMNH locality 7981 (Figure 3A). The channel cuts down from a horizon c. 15.5 m above the base of the Community Pit Formation section (Figure 2, 3A). Measured on an east-west outcrop, sub-perpendicular to the channel axis, the apparent channel width is about 140 m (Figure 4). The eastern channel margin appears steeper than the western margin, but this may be an artifact of outcrop orientation. In addition, the western margin is truncated by a fault. Seven sections (A - G) were measured across the channel (Figure 4). Three distinct units fill the channel; the lower two contain fossil-plant assemblages of different kinds.

3.1. Lower unit

The basal unit, which occurs only in the central part of the channel (Figure 4, sections B-E), comprises a lens of limestone pebble-to-cobble conglomerate, 0.05-1.1 m thick, and contains Plant Assemblage 1. This rudstone is dominated by sub-angular to sub-rounded, elongate clasts of gray-orange lime mudstone, 20-150 mm long, and accumulations of detrital crinoids and bryozoans (locally comprising multiple, cemented, randomly arranged fossil fragments, clearly reworked from underlying beds), within a poorly sorted matrix of medium- to coarse-grained mixed carbonate-siliciclastic sandstone and mudstone. Specimens of coalified tree-trunks, up to 0.17 m diameter, co-occur with cubic, sub-rounded, 20-50 mm diameter blocks of charcoalified wood (Plant Assemblage 1) in the basal rudstone.

3.2. Middle unit

The middle unit, up to 4 m thick, is more laterally extensive, and extends beyond the margins of the underlying conglomeratic lag, which is confined to the central, basal portion of the channel. Lime mudstone beds, up to 1.4 m thick, with undulatory or wavy lamination are the most prominent macroscopic feature of this unit (Figure 3B, C). In thin section, these beds are planar laminated, partly bioturbated lime mudstone with minor low-angle scours filled with slightly coarser grained carbonate material. They also include calcareous siltstones with rare thin layers of very fine-grained sandstone (~ 5 to 10%), composed of quartz and subordinate feldspar silt-size detrital grains, some of which appear to be wind-blown (Figure 5). The silt- and sand-sized layers contain abundant recrystallized carbonate skeletons and small amounts of detrital dolomite (Figure 5). Most common are hollow, needle-like skeletons ~30 to 60 µm in diameter and up to 0.5 mm long, which are recrystallized sponge spicules (Figure 5C), oriented parallel to bedding planes. There also are subordinate ostracodes and smaller foraminifers (*Tuberitina*, *Syzrania*?, and nodosinelloid forms) (Figure 5D) and probably other, completely recrystallized fragments that cannot be identified. Non-skeletal grains are small peloids (Figure 5A). The silt-sized and sand-sized material indicates transport by weak currents and deposition in a shallow, restricted environment.

In addition to the carbonate muds, the middle unit contains poorly exposed siliciclastic shale beds and a single, thin calcarenite lens, 0.14 m thick and several meters wide confined to the central part of the channel and some medium- to coarse-grained siliciclastic sand that shows climbing ripple cross-laminations.

Macrofossils and traces in the middle unit include scattered pterinopectinid bivalves and rare lingulid brachiopods, and horizons with vertical burrows. The low-diversity of the invertebrate fossil assemblage and overall fine-grained nature of the muddy carbonates is typical of restricted marine or brackish depositional environment. Also present at multiple horizons are rooted zones associated with the adpressed megaflora (Plant Assemblage 2 described in section 5). A few weakly calcified tree-trunks, up to 0.18 m diameter and > 1.4 m long, occur in the undulatory beds. These logs have an orientation sub-perpendicular to the channel margins. Rare fragments of wood also are identifiable in thin sections of the limestone matrix.

3.3. Upper unit

The uppermost channel-fill unit is a distinctive yellow dolomite, up to 1.2 m thick, showing prominent calcite-filled vugs and nodular gypsum (Figure 4). No macrofossils were identified in this portion of the channel fill.

3.4. Paleoenvironmental interpretation

There are several possible explanations for the incision of the fossil-bearing channel and its subsequent filling, primarily with carbonate, which must be treated as temporally independent phenomena. The occurrence of an incised channel system, albeit unique in the region, necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine shelf and to cause channel incision. Most incised features of this nature have been recognized in non-marine, siliciclastic depositional settings; however, a few examples have been reported in carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003). The term “incised channel” (rather than incised valley) is the most appropriate descriptor for the feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and 5-6 m deep) with a low aspect ratio (about 25:1).

There are several possible causes of base-level change. Eustatic lowering of sea-level is, perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation may have been deposited sometime during one of several intervals of inferred Permian southern hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al., 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event, resulting in a global lowering of sea level, additional evidence of incision in the area might be expected at this same horizon, which is widely traceable within the mostly carbonate portion of the Community Pit Formation. However, such evidence has not been found by us or reported elsewhere.

It is also possible that rapid, local base-level change could have been triggered by tectonism, given the location of the PTNM in the intracratonic Orogrande Basin. The PTNM is positioned close to and on the subsiding side of a line separating active uplift and erosion from subsidence in this region. Although most of the active tectonism was in the early Wolfcampian, the age of this deposit and the duration of the tail end of that tectonism are sufficiently unconstrained that this must remain an active possibility.

Finally, autogenic processes are another possibility, but these must operate within a larger eustatic or tectonic framework whereby local base-level had been lowered already. Were base-level/sea-level already low, on a landscape that generally experienced little rainfall, it is possible that there were few drainages, particularly in a low-gradient coastal environment. In this scenario, the channel may have originated by avulsion or stream capture, particularly if base-level lowering happened in combination with an increase in regional moisture regime.

The central portion of the channel contains a basal rudstone composed of pebbles and cobbles of marine limestone and faunal detritus, clearly well indurated at the time of its erosion and deposition. Thus, it does not appear to represent a submarine channel. The small size of the channel, and the fact that the only sedimentary particles in it are of local origin from within the areas of the immediate drainage basin, suggest a seasonally dry climate at the time of incision, and a relatively small overall drainage area (Feldmann et al., 2005). There must, however, have been sufficient moisture to promote plant growth proximate to the channel, indicated by moderate-sized logs in the basal channel fill, and to bring about incision in the first place.

The filling of the channel appears to comprise several phases. Clearly, early on in particular, there were periods of active transport of sedimentary particles, whereas at other times the channel appears to have been significantly less active to stagnant and possibly to have had portions subaerially exposed. The middle unit lime muds and their invertebrate fossils may have been washed in from seaward, by the backfilling tidal waters. This may have occurred once the fluvially incised channel was flooded by tidal waters during base level/sea-level rise. Gypsum in the later stages of channel filling suggests an increasingly drier climate with time.

The fill sequence suggests a base-level rise. The basal conglomeratic lag, including permineralized, partially to completely fusinized logs, indicates sufficient moisture on the landscape to support trees, and water movement in the channel during its periods of flow to cause significant erosion and to move, at least periodically, large sedimentary particles. The combination of intraformational gravels and logs, preserved partially or wholly as charcoal, is consistent with a semi-arid to dry sub-humid climate (Cecil and Dulong, 2003). The basal lag was emplaced either during the more active parts of water flow in the channel or during the early phases of transgression.

Above this basal lag, lime mudstones formed under brackish to nearly marine salinities, with strong suggestions of periods of standing or sluggishly moving water. The salinity and carbonate accretion are most likely reflective of base-level rise and the invasion of the channel by marine waters, mixed to some small degree with continued freshwater runoff from the surrounding terrestrial landscape. A change from a sub-humid to a semi-arid climate is indicated. However, it is likely that water cover was maintained most of the time, given evidence of syndepositional occupation of surfaces within the channel by vascular plants and the incorporation of plant remains into the limestone matrix, which consisted of actively forming/accumulating carbonate muds.

The final sediments in the channel are lime mudstones with gypsum cements, lacking any evidence of vascular plants nearby or living on the surface. The lack of plant debris cannot be interpreted to mean that plants were not growing in or around the channel. Absence of evidence not being evidence of absence, plants may no longer have been present on the landscape or conditions may have been unfavorable for the accumulation and preservation of organic matter, or both. One must keep in mind that most sediments formed in fully terrestrial or coastal transitional settings lack terrestrial fossils, even if all other indicators are consistent with the presence of vegetation and fauna.

4. Isotopic analyses of the middle unit

In order to more tightly constrain the extent of marine influence on the lime mudstones of the middle unit, carbon, oxygen, and strontium isotopic analyses were carried out on microdrilled samples of the carbonate samples from the middle unit.

4.1. Methodology

Thick sections (~200 µm thick) of two hand samples from the middle unit were studied petrographically under transmitted light and cathodoluminescence in order to identify calcite fabrics and textures. Thick sections of the two samples were microdrilled for stable (50 µg ±10 µg samples) and radiogenic isotope (0.5 gm) analysis using a Merchantek automated microdrilling system.

Samples (n=10) for stable isotope analysis were roasted at 375° C under vacuum for 30 minutes to remove organics and subsequently reacted in 105% phosphoric acid at 90° C in either a common acid bath on a GVI Optima Stable Isotope Ratio Mass Spectrometer (SIRMS) or a Gilson Multicarb Autosampler system (individual acid injection vials) interfaced with an Elementar Isoprime Mass Spectrometer housed in the UC Davis Stable Isotope Laboratory. CO_2 gas was analyzed in dual inlet mode and values were corrected using the Craig correction to account for the ^{17}O contribution (Craig, 1957) and to an internal standard and reported relative to the Vienna Pee Dee Belemnite (VPDB). Both systems provide $\delta^{13}C$ precision of ± 0.04‰ and $\delta^{18}O$ precision of ± 0.06‰.

Microdrilled samples (n=2) for strontium isotope analyses were prewashed with 1 M ammonium acetate in order to remove Sr associated with absorbed (on clays) or included noncarbonate phases (Montañez et al., 2000). Strontium was isolated using Spex cation ex-change resin and microliter columns attached to a channel pump. $^{87}Sr/^{86}Sr$ ratios were measured in solution mode on a Nu MC-ICPMS in the Interdisciplinary Center for Plasma Mass Spectrometry, UC Davis. Values are typically normalized to a nominal value for NIST standard SRM987 of 0.710249. SRM987 for the measurement period averaged 0.710249 (2σ = 0.000035) based on standards analyzed during this period.

4.2. Results

The well-preserved micrites have average $\delta^{18}O$ and $\delta^{13}C$ compositions –of -3.0‰ (2 std err. of 0.2‰) and 1.1 ‰ (2 std err. of 0.1‰), respectively (Table 1).

4.3. Paleosalinity interpretation

Given the earliest Permian age of the carbonates, these values support a dominantly marine environment. However, these stable isotopic values indicate that the lime muds likely did not form in pure seawater given typical Midcontinent and Panthalassan seawater compositions during this time (Grossman et al. 2008). Seawater $\delta^{18}O$ in the Pennsylvanian and early Permian likely ranged between -1 and 0‰ (Came et al., 2007) given the occurrence of ice sheets in southern Gondwana. The $\delta^{18}O$ composition of low-latitude coastal river water likely was in the range of -1 to -4‰ (cf. Bowen and Wilkinson, 2002), and perhaps a few per mil lower if the climate was monsoonal (Rozanski et al., 1993). Notably, the $\delta^{18}O$ of low latitude, coastal waters can be enriched by several per mil over open ocean seawater (Swart and Price, 2002), a scenario compatible with the tropical epicontinental environment of the study area. Thus, accounting for oxygen isotope fractionation between water and calcite at 25° ±3°C, the micritic $\delta^{18}O$ compositions are compatible with formation in waters over a range of salinities (i.e., fresh to fully marine).

Carbonate $\delta^{13}C$ values, in contrast, provide constraints on the depositional waters in the channel. Seawater $\delta^{13}C$ from the latest Ghzelian through earliest Sakmarian in western Euramerica was +4‰ ±0.5‰. The measured $\delta^{13}C$ values, which are 2 to 3‰ lower than contemporaneous seawater, can be explained by an input of a maximum of 10-20% freshwater. This assumes a freshwater $\delta^{13}C$ composition of -8 to -10‰, which is typical of tropical coastal rivers and associated with subhumid to semi-arid climates and moderate density vegetation (Mook and Tan, 1991). Although lowland tropical rivers draining carbonate terrains can be ^{13}C-enriched due to interaction with the carbonates along the flow path, the observed fossil flora indicate a likely source of locally derived ^{12}C-enriched terrestrial C to the channel waters.

A measured average Sr isotopic composition (n=2) of the laminated lime mudstone facies of 0.708571 (Table 1) is slightly more radiogenic than middle to late Asselian seawater ($^{87}Sr/^{86}Sr$ of 0.70785 to 0.70790; Henderson et al., 2012b). Application of the measured carbonate $^{87}Sr/^{86}Sr$ ratios and Sr concentrations (180 ppm ±32 ppm) to a Sr isotope—[Sr] fluid mixing model (Ingram and DePaolo, 1993) suggests that the fluid from which the carbonate precipitated could accommodate up to 17% freshwater.

The assumption of brackish conditions is thus reasonable for the inferred semi-arid to arid terrestrial paleoenvironment of the study interval. Furthermore, if the channel formed as part of a coastal tidal channel complex, then the measured $\delta^{13}C$ values could record the enhanced contribution to the seawater DIC of ^{12}C-enriched C locally derived from levee banks and/or interdistributary ponds. This finding provides independent confirmation of salinity estimates inferred from invertebrate fauna.

5. Plant Assemblages

The Community Pit Formation floras encompass two distinct assemblages that occur in different facies of the channel. The lowermost flora, consisting solely of the woody remains of walchian conifers, is representative of the widespread, Late Pennsylvanian-Early Permian seasonally dry biome described from many localities across the Euramerican equatorial region (Rees et al., 2002; Zeigler et al., 2002; Bashforth et al., 2014; DiMichele, 2014). The flora preserved in the middle unit of the channel contains a unique assemblage, dominated by a voltzian conifer and a callipterid, unknown in combination from any other locality in Euramerica and preserved under environmental conditions suggestive of a tolerance of high-salinity substrates of one or both taxa.

Details of the lowermost flora have been described by Falcon-Lang et al. and are only be briefly précised here. It includes coalified tree-trunks and charcoalified wood preserved in the basal rudstone. Four specimens of charcoal, which was the only material to preserve anatomical detail, were examined. These specimens are housed in the collections of the New Mexico Museum of Natural History and Science under catalogue numbers NMMNH P68181 – P68184, and comprise pycnoxylic wood that conforms to the Type II Paleozoic wood of Doubinger and Marguerier (1975). These specimens are essentially identical to the wood-type *Macdonaldodendron* Falcon-Lang, Kurzawe et Lucas, which was described from higher in the Community Pit Formation (Falcon-Lang et al., 2014). This wood is considered to be of walchian-conifer affinity. Other woods considered or confirmed to be of walchian affinity are similar to the study specimens (Reymanowna, 1962; Lemoigne and Tyroff, 1967; Tidwell and Munzing, 1995).

In this current paper, we focus our attention on the peculiar flora from the middle beds of the channel. This flora has been described in brief by DiMichele et al. (2015), with an emphasis on its stratigraphic implications. Here, we detail the morphology and paleoecology of the plants and their broader evolutionary implications.

The flora comprises adpressed megafloral remains and a few weakly calcified tree-trunks are preserved in micritic limestone. Adpressed megafloral remains are present at multiple levels (Figure 3B, C) in discontinuous limestone lenses, each up to 30–50 mm thick and traceable for several meters along strike. Within these lenses, there are variable concentrations of randomly oriented plant fragments, ranging from comminuted plant debris to fragments 10–30 cm in breadth (however, we note that this is a minimum size estimate because it is difficult to obtain large slabs of material). Identifiable material comprises three-dimensionally preserved adpressions and partially cutinized leaves. Associated with these foliar remains, there are also open-to-somewhat-denser networks of roots of variable diameter, which crosscut laminations and are in growth position.

5.1. Material and methods

A total of 155 rock specimens were collected, each showing at least one adpressed plant fragment. Collections were made at four separate sites (Figure 4, sections A - C and E) spanning the entire channel width over an outcrop distance of 120 m, with a fifth collection (comprising four sub-collections) obtained as random samples from float. Two specimens of calcified tree-trunk were also collected, and for each specimen, standard TS, RLS, and TLS petrographic thin sections were made, and viewed using an Olympus binocular BH-5 microscope.

The proportional abundance of taxa was quantified using a variant of the method of Pfefferkorn et al. (1975), in which each hand specimen is treated as a "quadrat," with each taxon occurring on that quadrat counted only once, regardless of the number of individual specimens or fragments of specimens present (Table 2). Comminuted plant debris and other indeterminate fragments were excluded from such counts,; however, gymnosperm axes of uncertainty affinity and invertebrates were included. The dominance and diversity data reported below are based on the three largest collections only, which include the majority (n = 114) of the specimens (sections C, E and float; localities USNM 43550, 43554, and NMMNH SGL-09-136, respectively), and represent the frequency of occurrence of each taxon as a proportion of the number of quadrats in those counts. For rare taxa, the number of occurrences in the entire collection is reported.

Specimens are housed in the Paleobotanical Collections of the New Mexico Museum of Natural History and Science, Albuquerque, NM (NMMNH) and the United States National

Museum of Natural History, Smithsonian Institution (USNM). Illustrated or traced specimens are stored in the Paleontological Type and Illustrated Collections of the NMMNH under the catalog numbers NMMNH P68185 - P68346.

5.2. *Voltzian conifers*

By far the most common plant remains present in the megafloral assemblages are those of voltzian conifers (occurring in 78 out of 114 quadrats; frequency 68.4 %), of which four foliar morphotypes (A - D) and a single ovuliferous cone are present (Figure 6). These morphotypes are distinguished based on details of leaf attachment to the stem, overall leaf shape, leaf profile, length to width ratio (L:W) of the leaves, and leaf angle of departure from the stem. Some specimen have cuticles preserved, unfortunately they do not preserve epidermal patterns. Morphotype A is represented by five isolated shoots (Figure 6A), two of which have the ultimate tips of the branch preserved. Leaves are bifacially flattened (cf. Type II leaves; de Laubenfels, 1953), and are oblong in shape with obtuse apices. Leaf widths (W) range from 2 to 3.5 mm. Leaf lengths (L) are difficult to measure, due to overlap among them, and are at least 20 - 25 mm. L:W ratios range from 7 to 11, calculated on a per leaf basis. Leaves depart from the stem at angles from 15 to 40°, and are straight to slightly incurved when viewed in profile. Leaves are highly imbricate, particularly on the branch tips, resulting in a distinct ”tufted” appearance. Details of the leaf attachment and axis diameter are obscured by overlapping leaves.

Morphotype B is represented by four isolated shoots, and three other specimens preserving two or three orders of branching (Figure 6B). Branching is orthotropic, with higher order branches occurring in the axils of persistent leaves at angles of 55°. Leaves are tetragonal in cross section (Type I leaves: de Laubenfels, 1953), and attached helically to the stem by thickened cushions that are distinctly rhomboidal in shape (Figure 6B). Leaves taper slightly from the point of attachment to obtuse apices. Leaf length is 15 - 30 mm, and leaf width reduces from 2.5 - 3.5 mm at the point of attachment to about 2 - 2.5 mm mid-leaf (L:W ratios: 6 - 9). The angle of leaf departure from the stem axis is variable (average 55°), with the leaves mostly straight in side profile, but occasionally slightly incurved. Leaves on thicker branches depart at the higher angles, and are more reflexed in profile.

Morphotype C is represented by four isolated foliar shoots (Figure 6C). Leaves are tetragonal in cross section, and attached to the stem on rhomboidal leaf cushions (cf. Type I leaves: de Laubenfels, 1953). Leaves are distinguished from those of Morphotype B primarily by having a distinctly falcate profile, and by showing a greater degree of taper from the base to the tip of the leaf. Leaves depart at a high angle (average 60°), then curve inward toward the supporting axis. There is considerable variation in the absolute size of leaves within this morphotype, varying from 6 - 20 mm in length and 1 - 3.5 mm in width (L:W ratios: 5 - 9; ratio calculated per leaf). One relatively small specimen, which is similar in all other leaf characteristics, represents the tip of a branch, and may be juvenile foliage.

Morphotype D is represented by one, relatively large, branched specimen (Figure 6D). Ultimate branches occur in the axils of persistent leaves, and the overall branching pattern is orthotropic. Leaves have decurrent attachments to the stem, with the decurrent portions of the bases thick and clearly distinguishable for the entire length of the internode. Leaves depart from the stem at angles commonly up to 90°. It should be noted, however, that there is a high degree of variation that may have been influenced by taphonomic processes, such as drying of the material prior to deposition. Leaves are slightly more than 20 mm long, and 1.2 - 2 mm wide (resulting a distinctively high L:W ratio of 12.5) and have a straight profile with an obtuse apex.

The leaves are dorsiventrally flattened in cross section (cf. Type II leaves: de Laubenfels, 1953), with a thick, fleshy appearance. Leaves on the thicker, higher order axis appear more lax; however, again, this could reflect taphonomic processes, such as differential drying of dead foliage prior to incorporation into the sediment.

The ovulate cone associated with these foliar morphotypes is compound with bract-ovuliferous dwarf shoot complexes helically arranged around the axis (Figure 6E). Bracts are narrow and elongate with an obtuse apex and slightly bend toward the cone axis. Dwarf shoots, which have an axillary position, are flattened and bilaterally symmetrical with five to six partially fused, similarly shaped, oblong sterile scales and/or sporophylls with obtuse apices (Figure 6F). The base of the dwarf shoots is stalk-like, and given their size and position on the cone, dwarf shoots are likely partially fused with the bract.

Late Paleozoic conifer classification is based on a combination of morphology and internal and cuticular anatomy of stems, leaves, pollen cones, and ovuliferous structures (such as ovuliferous cones and fertile zones) (e.g., Clement-Westerhof, 1984, 1987, 1988; Rothwell et al., 1997, 2005). Several features of the novel conifer material reported here allow it to be referred to voltzian conifers. First, their foliar morphotypes show generally bifacial ovate, lanceolate to linear medium-sized leaves, which are characteristic of voltzians. Second, foliar morphotypes B and D show orthotrophic branching, also characteristic of voltzians, but distinct from the plagiotrophic walchians (Rothwell et al., 2005). Third, the sterile scales and sporophylls in the dwarf-shoots are fused, more or less flattened in one plane, and show a bilaterally symmetrical organization. At this point in time, it is uncertain how many taxa these four leaf morphotypes represent. Heterophylly does occur in voltzian conifers, and generally involves differences in leaf size, shape in face view, and apex shape. Voltzians are, however, relatively consistent in leaf characters like mode of attachment, features of leaf bases and shape in cross-section. Morphotypes B and C might represent a single taxon, but we have no confirmatory evidence for that, such as attachment to a common branch. The leaves of morphotypes A and D are both bilaterally flattened, but arise at different angles, and have different kinds of attachment. Collection of further material is required to answer this question. More material is also needed to ensure that we have collected the full range of the diversity of conifer foliage in this flora.

We note that the earliest voltzian conifers described to date are *Lebowskia grandifolia* and *Manifera talaris* from the uppermost lower Permian–lowermost middle Permian of north-central Texas (Looy, 2007; Looy and Stevenson, 2014). Therefore, the novel conifer morphotypes from Plant Assemblage 2 extend the temporal range of this clade into the early Permian (late Asselian), and represent the oldest known occurrence of voltzian conifers.

5.3 Callipterid foliage – Lodevia oxydata

The other dominant taxon in the flora is an unusual callipterid (occurring in 34 out of 114 quadrats; frequency 29.8 %). The material shows considerable morphological variation and encompasses immature and mature pinnae (Figure 7A-E). Included among the suite of specimens are pinnae with remarkably robust axes bearing slightly decurrent, pinnately lobed to segmented, pinnules. Pinnule lobes typically have blunt tips, particularly those forming the pinnule apex. The venation is pronounced with an indistinct, sometimes slightly flexuous midvein with widely spaced, steeply ascending lateral veins inserted at angles of 20-30°; lateral veins fork once or twice, depending on the segmentation with a single vein per lobe. The suite of specimens shows a number of noteworthy phenologic features. For example, some fronds show pinnae preserved in the process of unfolding (Figure 7A), a developmental pattern found in other callipterid taxa (e.g., Kerp, 1988). Still others comprise young, immature pinnules (Figure 7E), and a few unusual mature specimens exhibit pinnules with irregularly curled edges (Figure 7D). Another axis has a swollen base (Figure 7C), which usually indicates that complete fronds were abscised.

Axes of small to medium size (up to 28 mm in diameter) co-occur with this foliar material and are sometimes found in organic connection with it, suggesting that leaves may have been retained on branches for some time. This was observed in 16 quadrats.

Pinnae and associated axes are identified as *Lodevia oxydata* (Göppert) Haubold et Kerp based on their broad, stiff rachial axes and bluntly ending pinnules (Kerp and Haubold, 1988). Pinnules are up to 3.2. cm long, which is larger than in other *Lodevia* species. The pinnule is composed of segments that widen markedly towards their tips. Segment tips and pinnule apices are very blunt, and not rounded. The pinnules, overall, appear "flat," and the rachial axes are robust. Also, compared to other *Lodevia* species, the basal pinnules in *L. oxydata* are quite large. The absence of large diameter axes, despite the existence of quite a large collection, suggests that *L. oxydata* may have been a shrub.

5.4. Roots

Among the remaining adpressed material, only roots occurring in growth position (n = 17 quadrats) are common, being found in all four *in situ* collections. Roots comprise dense, interwoven networks and more extensive, open systems (Figure 7H). They show four, or more, orders of branching, the largest being c. 25 mm in diameter, the smallest < 1 mm in diameter. They ramify irregularly, side-axes being disposed at variable angles to the higher-order axes.

The identity of these roots is unknown, although it is possible to narrow down their affinities, which are most likely with seed plants. They share some features with pteridospermous root systems, which have a similar indeterminate growth pattern (Rothwell and Whiteside, 1974; Stull et al., 2012). Although roots attributable to Paleozoic conifers are poorly known, modern forms have root morphologies similar to those of other seed plants. What these roots are not likely to be is equally as enlightening as what they might be. They are not typical rooting features of arborescent and herbaceous lycopsids (Dawson, 1868; Jennings et al., 1983; Pigg, 1992). Nor are they calamitalean roots, such as *Pinnularia* and *Myriophyllites*, which show side-branches disposed perpendicular to primary axes and comprise discontinuous size-class orders of branching (Dawson, 1868; Taylor et al., 2009). Neither do they appear to be marattialean tree-fern root systems, which are networks of generally relatively straight, unforked, larger roots (4 - 6 mm diameter, but often larger: Ehret and Phillips, 1977; Mickle, 1984; Millay, 1997) that commonly form dense networks in isolated clumps (Falcon-Lang, 2006).

In consideration of the likely seed plant affinities of the roots, the most important point they highlight is that rooting of the lime mudstones took place contemporaneously with or very shortly after the entombment of the aerial remains of conifers and *Lodevia* in this same limey mud. Because these roots are in and ramify through the limestone, and because of the rate at which subaerially lime mud hardens and becomes effectively impenetrable to roots, and because there is no evidence within these beds of brecciation associated with long-term pedogenesis and development of terra rosa type residual siliciastic soils, it is most likely that the roots were derived from the voltzian conifers and/or the callipterids, though whether one or both cannot be determined. The possibility remains, of course, that they were derived from an additional kind of, most likely, seed plant that left no other macrofossil record. The likely contemporaneity or near contemporaneity of the aerial debris and roots also suggests that the plants in question were growing on these limey muds while they were water covered. The combination of physical sedimentological evidence, isotopic values of the lime muds, the brackish-to-marine invertebrate fauna also present within the sediment, and the necessity for incorporation of aerial debris and roots into the muds prior to solidification, strongly suggests growth of these plants in waters of brackish to near-marine salinities.

5.5. Other rare taxa

All other taxa are rare and include walchian conifers (*Walchia* sp., n = 7 quadrats) (Figure 7F), some small seeds of indeterminate affinity (n = 7), which may be related to one of the conifers or pteridosperms, the sphenopsid *Annularia spicata* (Gutbier) Schimper (n = 1; Figure 7F), and a putative fern, cf. *Sphenopteris* (n = 1). A small number of weakly calcified tree-trunks (up to 0.18 m diameter) associated with the adpressed remains comprise pycnoxylic coniferopsid wood that is too coarsely re-crystallized for more accurate determination.

6. Discussion

There are certain aspects of the PTNM limestone channel deposit, recited here, that frame the paleoecological interpretation of its biota.

(1) The geological setting. The basic setting is a channel cut into a limestone platform, thus indicative of some lowering of base level at least locally. The channel is narrow, shallow and asymmetrical. There are, as far as we know, no other incised channels identified anywhere in the surrounding geological exposures of the Community Pit Formation in the Prehistoric Trackways National Monument, which has been thoroughly scouted for more than a decade by Jerry MacDonald (1994), the discoverer of the deposit, and numerous other geologists (e.g., Lucas et al., 1998a, b, 2011; Mack et al., 2013; Falcon-Lang et al., 2014).

(2) The host lithologies. The channel is filled primarily with lime muds, the benches of which are separated by thin siliciclastic parting beds. The fill can be subdivided into three units. The basal channel fill, present only in the center of the channel, as typical of a lag deposit, is conglomeratic and includes plant remains, mainly coniferous tree trunks. The middle unit is composed of lime mudstone lenses separated by thin siliciclastic beds, and hosts the majority of adpression plant fossil remains. The upper unit is a lime mudstone with scattered gypsiferous nodules.

(3) The biota. A brackish-to-marine water invertebrate fauna was found in the lower two units of the channel fill, consistent with the isotopic compositions of the carbonate matrix. Trunks of walchian conifers occur in the basal lag deposit and many of these are preserved as charcoal. The middle unit contains a flora dominated numerically by undescribed voltzian conifers, with subdominant numbers of the callipterid *Lodevia oxydata*. These aerial remains occur intermixed with in situ roots that appear to have a seed-plant affinity.

It must be emphasized that this is an extremely unusual deposit, of a type rarely encountered by the authors in their combined many years of fieldwork. Limestone filled, terrestrial channels are uncommon. The closest analogue may be limestone-filled lakes that formed under semi-arid to occasionally arid climates, such as those that typify Late Pennsylvanian and early Permian exposures in the Appalachian Basin of the eastern USA (e.g., Montañez and Cecil, 2013), from which plant fossils (callipterids, tree ferns) are known and reported (e.g., DiMichele et al., 2013b).

In addition to being physically unusual, this channel deposit contains an exceptional flora. That flora includes the earliest known voltzian conifers, extending the range of the lineage downward from the Kungurian-Roadian boundary to the Asselian-Sakmarian, approximately 25 million years. It also includes a rare species of callipterid, *Lodevia oxydata*, now known from Poland, the Appalachian Basin, and New Mexico, all in deposits of earliest Permian age. Both of the common plants indicate the existence of vegetation types rarely preserved in the geological record, or perhaps rarely sampled because of the unlikely nature of the host deposits, despite what appear to have been long stratigraphic ranges and broad geographic distributions.

6.2. Flora 1: Walchian and other coniferous wood.

The earliest vegetation from the PTNM limestone channel deposit for which we have evidence is preserved as coalified tree-trunks and charcoalified wood fragments in the calcirudite at the base of the channel (Falcon-Lang et al., 2015). The specimens examined have walchian conifer affinity. Species that are part of the large complex of walchian Voltziales are by far the most commonly encountered kinds of conifers in Euramerican fossiliferous deposits of latest Pennsylvanian and early Permian age (e.g., Kerp and Fichter, 1985; Clement-Westerhof, 1988; Kerp, 1996; Ziegler et al., 2002; Hernandez-Castillo et al., 2001, 2009; Rothwell et al., 2005; Looy 2013; Looy and Duijnstee, 2013). They are dominant elements in the red siltstones that make up much of the Community Pit Formation and its more inland equivalent, the Abo Formation (DiMichele et al., 2007, 2013a), which crops out in a long north-south band on the margin of the Rio Grande rift and elsewhere, throughout central New Mexico (Lucas et al., 2012, 2013).

The source of the walchian logs is most likely from the margins of the channel and perhaps from the surrounding floodplain, though we detected no paleosol evidence of a lateral, subaerially exposed surface. These trees are preserved in what is arguably the wettest phase of channel development, during which there were periodically high flow volumes and little or no carbonate precipitation. The predominance of walchians is consistent with their preservation in other kinds of Hueco Group (e.g., in the Robledo Mountains Formation, which immediately overlies the Community Pit Formation) environmental settings, specifically the siliciclastic redbed siltstones, which also suggest seasonality of moisture under a climate that was at most dry subhumid. If the drop in sea level in this area is attributed to glacio-eustasy, the trees were growing at times of near-glacial maximum (Falcon-Lang and DiMichele, 2010).

6.3. Voltzian-callipterid vegetation

A plant assemblage entirely distinct from that preserved in the basal channel-lag deposits is represented by fossils preserved in the middle unit of the channel fill. Here, accumulations of randomly-oriented adpressions, associated with calcified tree-trunks and *in situ* fossil roots, occur within lime mudstones and wackestones, with biogenic grains that indicate a brackish-to-marine origin. The plant assemblage is dominated by a low-diversity flora consisting of undescribed voltzian conifers (Figure 6) and subdominant amounts of the callipterid *Lodevia oxydata* (Figure 7A-E). A few specimens suggest the presence of walchians (Figure 7G), calamitaleans (Figure 7F) and small ferns as rare elements. The plants are preserved mainly as compressions and have variably preserved cuticle on the outer surfaces.

It is probable that one or both of the taxa that comprise this flora were growing in contact with saline water. This assertion is supported by several aspects of the flora, its taphonomy and the attributes of the deposit itself. The lime mudstones—wackestones in which the plants occur have only weak bedding and are not brecciated or fractured. Thus, the organic remains had to be deposited in that substrate while it was both soft and still accumulating. There are large fragments of branches and leafy shoots among the fossilized plant parts, suggesting limited transport and, thus a local, parautochthonous origin. Preserved cuticle on both conifer and callipterid foliage indicates rapid burial. The lime muds are rooted, and the roots are clearly *in situ* and transgressed the substrate while it was still soft enough to be penetrated. The shape of the root masses and the character of the rock matrix suggest that they did not enter along cracks in already lithified limestone. Roots are not found in the overlying limestone beds, so it can be assumed that they originated from plants growing on or immediately adjacent to the lime muds within the channel. However, an origin from one specific plant taxon or the other, or both cannot be ascertained. The stable and radiogenic isotopic and invertebrate paleontological evidence both indicate accumulation of the lime muds under brackish-to-marine salinities.

Perhaps the simplest interpretation that can be made of this deposit is that it formed in a quiet, abandoned or largely abandoned channel, perhaps as a lake deposit or as a sluggish drainage into a coastal embayment. The lime mud almost certainly is of microbial and algal origin. In order for invertebrates, plant parts and roots to be preserved in the lime mud, a shallow, persistent water cover was required, at least during those times when aerial material was being incorporated. Lime muds such as these harden and develop surface crusts quickly when exposed subaerially. If these crusts were thin, that is if periods of water cover exceeded those of exposure, plants could recolonize the surfaces and roots could “punch through” the crustose surfaces. The key attributes then as they affect the vascular plant assemblage are high salinity, high pH, fluctuating but semi-persistent water cover, and high rates of evaporation and transpiration.

The voltzian conifers in this deposit are the earliest known (late Asselian) representative of this evolutionary lineage, significantly extending the known stratigraphic range downward from the Kungurian-Roadian (Early-Middle Permian) boundary in Texas (Looy, 2007; Looy and

Stevenson, 2014). These previously oldest voltzian conifers occur in deposits interpreted, like the PTNM limestone channel deposit, to have formed under dry-subhumid to semi-arid conditions. They were part of an assemblage that included conifer and cycad taxa with an overall late Permian (Zechstein/Wuchiapingian) to Mesozoic aspect (DiMichele et al., 2001).

The other common plant in the mid-channel assemblage is *Lodevia oxydata*. This is a very rare species that has only been described twice previously in the fossil record. Both previous occurrences are from near the Pennsylvanian-Permian boundary in (1) the Rotliegend of Lower Silesia, Poland (Göppert, 1864-65) and (2) the Dunkard Group of the Central Appalachian Basin, U.S.A. (DiMichele et al., 2013b). The New Mexico occurrence extends the geographic range of this taxon across the entire breadth of the Euramerican realm. In the Appalachians, *L. oxydata* is known from limestone beds lacking evidence of marine influence (Montañez and Cecil, 2013) at two, closely adjacent, localities, interpreted as having formed under a semi-arid to dry subhumid climate regime (DiMichele et al., 2013b). The Rotliegend specimen is from a very different environmental setting, occurring in an inland basin located far from the nearest marine influence and not characterized by either arid conditions or any evidence of elevated salinity.

In summary, the deposit described here indicates the existence of a previously unknown type of late Paleozoic plant assemblage. This assemblage is of low diversity, consisting of two abundant seed-plant species and a few rare taxa. Its habitat of growth, on the margins of and rooted within the lime muds of a shallow, highly saline channel, is most unusual and suggests a mangrove habit for one or both of the dominant forms. The discovery of such deposits involves a great deal of luck and indicates the necessity for continued field studies and examination of even unlikely looking sedimentary-rock strata.

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FIGURE CAPTIONS

Figure 1. County map of New Mexico highlighting the location of the PTNM in Doña Ana County, where the fossils were obtained (index map: location of New Mexico in the U.S.A.).

Figure 2. Measured section of the Community Pit Formation. Beds are numbered. The fossiliferous site discussed in this paper is indicated as NMMNH locality 7981.

Figure 3. Fossiliferous, limestone filled channel. A., Eastern margin of channel. Channel base is indicated by arrows. The main fossil excavation was carried out at the eastern channel margin; B., Excavation at site A (Fig. 4) to show the nature of the mid-channel lithology, a dense, micritic limestone. Geological hammer for scale; C., Exposure of mid-channel micritic limestone in western portion of channel. White arrow indicated a calcified tree trunk. Scale increments 1 foot (30.5 cm).

Figure 4. Geology of the limestone-filled channel in the Community Pit Formation at NMMNH locality 7891, showing correlated measured sections through channel. Solid lines demarcate correlatable surfaces. Surface 1 is the base of the channel. Surface two separates the middle-channel fill, containing the voltzian conifer-callipterid flora, from the upper channel fill, which is devoid of plant macrofossils. Surface 3 marks the top of the channel fill.

Figure 5. Common limestone microfacies of the middle channel-fill limestone. Thin section photographs all under plane light. A., Fine-grained calcareous sandstone containing few foraminiferans; B., Calcareous siltstone with rare formaniferans; C., Indistinctly laminated calcareous siltstone containing sponge spicules; D., Calcareous siltstone with

rare foraminiferans (a particularly conspicuous example can be seen in the center of the slide). Scale bars = 0.5 mm.

Figure 6. Adpressed conifer foliar morphotypes, and an ovuliferous cone and dwarf shoot of a voltzan conifer in Plant Assemblage 2; A., Ultimate shoot of Morphotype A, scale: 10 mm, NMMNH P68185; B., A branch system of Morphotype B with three orders of branching, scale: 10 mm, NMMNH P68186; C., Part of a shoot of Morphotype C (Specimen in right hand corner), scale: 10 mm, NMMNH P68187; D., A branch system of Morphotype D with two orders of branching, scale: 5 mm, NMMNH P68188; E., Mature ovuliferous cone with bract–dwarf shoot complexes helically arranged around axis, scale: 5 mm, NMMNH P68189; F, Flattened dwarf shoot with partly fused base, and six obtuse scales, scale: 10 mm, NMMNH P68190.

Figure 7. Adpressed callipterids, voltzian conifers and sphenopsids in Plant Assemblage 2; A., Callipterid, *Lodevia oxydata*, showing unfolding frond, scale: 25 mm, NMMNH P68191; B., Callipterid, *Lodevia oxydata*, showing typical mature foliage, scale: 10 mm, NMMNH P68192; C., Swollen base (possible abscission surface) of callipterid, *Lodevia oxydata*, scale: 10 mm, NMMNH P68193; D., Callipterid, *Lodevia oxydata*, showing desiccated appearance with curled tips to pinnules, scale: 10 mm, NMMNH P68194; E., Callipterid, *Lodevia oxydata*, showing immature foilage, scale: 10 mm, NMMNH P68195; F., Sphenopsid, *Annularia spicata*, scale: 4 mm, NMMNH P68196; G., Walchian foliage, scale: 5 mm, NMMNH P68197; H., Fine network of branching gymnosperm roots, of probable callipterid affinity, scale: 10 mm, NMMNH P68198.

TABLE CAPTIONS

Table 1. Stable and radiogenic isotope compositions of the Community Pit Fm.

Table 2. Quantitative quadrat data for adpressed megafloral assemblages (Plant Assemblage 2) in the middle unit of the incised channel (using methodology of Pfefferkorn et al., 1975).

Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangaea: Paleoecology and evolutionary significance

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Abstract

The Pennsylvanian-Permian transition has been inferred to be a time of significant glaciation in the Southern Hemisphere, the effects of which were manifested throughout the world. In the equatorial regions of Pangea, the response of terrestrial ecosystems was highly variable geographically, reflecting the interactions of polar ice and geographic patterns on atmospheric circulation. In general, however, there was a drying trend throughout most of the western and central equatorial belt. In western Pangea, the climate proved to be considerably more seasonally dry and with much lower mean annual rainfall than in areas in the more central and easterly portions of the supercontinent. Here we describe lower Permian (upper Asselian) fossil plant assemblages from the Community Pit Formation in Prehistoric Trackways National Monument near Las Cruces, south-central New Mexico, U.S.A. The fossils occur in sediments within a 140-m-wide channel that was incised into indurated marine carbonates. The channel filling can be divided into three phases. A basal channel, limestone conglomerate facies contains allochthonous trunks of walchian conifers. Preservation as charcoalified wood indicates that these trees were subject to periodic fires. A middle channel fill is composed of micritic limestone beds containing a brackish-to-marine fauna with carbon, and oxygen and strontium isotopic composition that provide independent support for salinity inferencesalso indicative of brackish-to-marine conditions. The middle limestone also contains a (par)autochthonous adpressed megaflora co-dominated by voltzian conifers and the callipterid *Lodevia oxydata*. The upper portions of the channel are filled with muddy, gypsiferous limestone that lacks plant fossils. This is the geologically oldest occurrence of voltzian conifers. It also is the westernmost occurrence of *L. oxydata*, a rare callipterid known only from the Pennsylvanian-Permian transition in Poland, the Appalachian Basin and New Mexico. The presence of in situ fine roots within these

channel-fill limestone beds~~s~~ and the taphonomic constraints on the incorporation of aerial plant remains into a lime mudstone indicate that the channel sediments were periodically colonized by plants, which suggests that these species were tolerant of salinity, making these plants one of, if not the earliest unambiguous mangroves.

Keywords: Permian, estuary, voltzian conifers, callipterids, mangrove, New Mexico

1. Introduction

During the early Permian, the Earth went through a transition from a globally cool to warm climate (Montañez et al., 2007; Tabor and Poulsen, 2008; Montañez and Poulsen, 2013), which resulted in prominent vegetational changes. Based on a global dataset, Rees et al. (2002) recognized four distinctly different floral realms during early Permian (Sakmarian) time: (1) a Gondwanan realm characterized by glossopterids in temperate regions of the Southern Hemisphere (Cúneo, 1996; Tewari et al., 2012); (2) a Euramerican realm characterized by walchian conifers, peltasperms and ferns in a seasonally dry tropical setting (Kerp et al., 1990; Zeigler et al., 2002); (3) a Cathaysian realm characterized by lycopsids, sphenopsids and ferns in the humid tropical islands bordering the western Tethys (Hilton and Cleal, 2007; Wang et al., 2012); and (4) a poorly resolved Angaran realm characterized by cordaitaleans in Northern Hemisphere temperate mid-latitudes (Meyen, 1982, 1988; Gomankov, 2009). Transitional vegetation also has been identified at the boundaries of these realms (Broutin et al., 1998; Berthelin et al., 2003; LePage et al., 2003). This global floral realm architecture had much earlier origins in the Carboniferous (Chaloner and Meyen, 1973), though the lycopsid-rich wetland biome, so typical of the Carboniferous Euramerican equatorial regions, was almost completely absent there by the early Permian (e.g., Kerp and Fichter, 1985; Kerp, 1996; DiMichele et al., 2009; Opluštil et al., 2013; Tabor et al., 2013) and survived in Cathaysia (Hilton and Cleal, 2007; Wang et al., 2012; Wang and Pfefferkorn, 2013).

The Euramerican floral realm, of which the flora reported here is a part, is the best known of the Permian seasonally dry vegetation types. Assemblages have been described from the southwestern U.S.A., eastern U.S.A., eastern Canada, North Africa, western Europe, and the Ukraine (e.g., Florin, 1938-1945; Doubinger, 1956; Kerp et al., 1990; Kerp, 1996; Broutin et al., 1998; Blake et al., 2002; Zeigler et al., 2002; DiMichele et al., 2007; Galtier and Broutin, 2008; Blake and Gillespie, 2011; Rößler et al., 2012; Tabor et al., 2013), all of which lay within 10 degrees of the paleoequator (Rees et al., 2002). According to Zeigler et al. (2002), the so-called walchian conifers are the most characteristic, abundant and widespread plants in this early Permian seasonal tropical vegetation.

Walchian conifers (walchian Voltziales *sensu* Rothwell et al., 2005) were the earliest conifers to appear in the fossil record and were characterized by a plagiotropic branching pattern and narrow, triangular to linear, needle-like leaves (e.g., Hernandez-Castillo et al. 2003; Rothwell et al., 2005). Their ovulate ovuliferous dwarf shoots were organized in cones or fertile zones. Walchian dwarf shoots had numerous sterile scales interspersed with a few sporophylls, which showed at least some indication of radial symmetry. Distinctly different and evolutionarily more derived are the voltzian conifers or voltzian Voltziales (*sensu* Rothwell et al., 2005). They were trees with an irregular branching pattern (orthotropic) and bifacial ovate, lanceolate to linear medium-sized leaves (e.g., Clement-Westerhof, 1988; Rothwell et al., 2005). Just like the walchian conifers, these conifers also produced ovuliferous cones or fertile zones. The sterile scales and sporophylls in their ovuliferous~~se~~ dwarf shoots, however, were partly to completely fused, and the whole structure was bilaterally symmetrical and more or less flattened in one plane (e.g., Clement-Westerhof, 1987; Looy and Stevenson, 2014). During the Permian, bBoth of these groups are largely confined to the Euramerican floral realm, although there are reports of walchian Voltziales from transitional assemblages (Cathaysia: Hernandez-Castillo et al., 2001 ; Liu and Yao, 2013; possibly Angara: LePage et al., 2003).

This report describes a distinct assemblage of early Permian (late Asselian) plant macrofossils from the Robledo Mountains in southern New Mexico. These fossils are preserved in an unusual depositional setting, a small channel filled with muddy, brackish-to-marine limestone, bordering a seaway. The assemblage includes *in situ* roots, which provide evidence of plant growth in the lime muds, under conditions of high salinitysaline conditions higher than freshwater. Regional climate appears to have been periodically semi-arid to perhaps even arid (Tabor and Montañez, 2004; Tabor, 2007; Tabor et al., 2008; Mack et al., 2010, 2013; Tabor et al., 2013). The bottom portion of the channel contains a flora dominated by walchian conifer logs, preserved in a locally sourced, conglomeratic lag deposit, probably emplaced during channel incision or initial backfilling phases. The middle portion is a lime mudstone in which the dominant floral elements are vegetative and reproductive remains of voltzian conifers and the callipterid *Lodevia*. This is the earliest record of voltzian conifers, considerably extending the range of the lineage from its previously oldest known occurrence near the early-middle Permian boundary (Looy, 2007; Looy and Stevenson, 2014). It also is the westernmost occurrence of *Lodevia oxydata*, until now– only known only from similar aged exposures in central Europe and the Appalachian Basin (Kerp and Haubold, 1988; DiMichele et al., 2013b).

This flora from the middle portions of the channel fill differs entirely from contemporaneous early Permian western Pangean floras preserved in the Abo Formation and its equivalents (Hunt, 1983; DiMichele et al, 2013a). These floras are known from coastal plain, siliciclastic red-bed deposits, which crop out widely from the northern to the southernmost parts of New Mexico, through the central part of the state (Lucas et al., 2013), including in the Robledo Mountains (Mack et al., 2010; Voigt et al., 2013). They are dominated by walchian conifers, with local occurrences of the peltasperm *Supaia thinnfeldioides* (DiMichele et al., 2007, 2012), rare callipterid peltasperms and isolated occurrences of other taxa more common in assemblages from other Permian equatorial regions (Kerp and Fichter, 1985; Galtier and Broutin, 2008; Opluštil et al., 2013; Tabor et al., 2013).

Other compositionally unusual assemblages of plants not dominated by walchians have been reported from the early Permian of the Euramerican equatorial region (e.g., DiMichele et al., 2001, 2004), one of which was characterized by voltzian conifers (e.g., Looy, 2007). These assemblages, often known from isolated occurrences, such as the one reported here, strongly suggest the existence of tropical biomes distinct from that dominated by walchian conifers, perhaps reflecting different patterns of rainfall seasonality or habitat quality.

2. Geological context

~~*2.1 Geological setting*~~

The fossiliferous deposit we describe here crops out in the Prehistoric Trackways National Monument (PTNM) near Las Cruces, Doña Ana County, south-central New Mexico, U.S.A. (Lucas et al., 2011, Hunt et al., 1993; MacDonald, 1994; Lucas and Heckert, 1995; Lucas et al., 1998ab, 2011; Minter and Braddy, 2009) (Figure 1). Map coordinates for the new fossil site are on file at the ~~NMMNHS~~ New Mexico Museum of Natural History and Science (NMMNHS), Albuquerque, New Mexico, and the ~~NMNH~~ National Museum of Natural History

(NMNH), Washington, D.C.~~.~~ Only a few fossil plant assemblages have been previously reported from PTNM (Voigt et al., 2013; Falcon-Lang et al., 2014~~a~~). The new material described here is housed in the paleontological collections at the NMMNHS ~~New Mexico Museum of Natural History and Science, Albuquerque, New Mexico~~ as collecting localities NMMNH 3016 and 7981 (these are ~~National Museum of Natural History~~ NMNH localities USNM 43550–43554 and 43563).

2.1. Stratigraphy and age

The fossil plant assemblages, discussed herein, occur in the lower Permian Hueco Group, which comprises, from base to top, the Shalem Colony, Community Pit, Robledo Mountains, and Apache Dam formations (Kottlowski, 1960; Mack and James, 1986; Lucas et al., 1998a, b; Krainer et al., 2003, 2009; Voigt et al., 2013). The fossils are from 10–15 m above the base of the local section of the approximately 91-m-thick Community Pit Formation, which means they are from the lower part of the formation (Figure 2). Based on the current state of our knowledge, summarized below, the age of the fossil plant assemblage in the lowermost Community Pit Formation of PTNM is late Asselian. It is bracketed by earliest Asselian fusulinids in the underlying Shalem Colony Formation and is positioned ca. 40 m below a bed containing (?)latest Asselian fusulinids in the middle part of the Community Pit Formation, and Sakmarian–early Artinskian strata in the middle to upper part of the Community Pit Formation (Krainer et al., 2009; Voigt et al., 2013; Falcon-Lang et al., 2014~~a~~).

2.1.1. Biostratigraphic findings

Below the plant-bearing beds, immediately below the Community Pit Formation, fusulinids and smaller foraminifers are found in the Shalem Colony Formation. These foraminifers indicate, in regional terminology, an early Wolfcampian age (Needham, 1937; Lucas et al., 2002; Krainer et al., 2009). On the international time scale, this falls somewhere within the latest Gzhelian–earliest Asselian interval, i.e., the Carboniferous-Permian boundary (Henderson et al., 2012a).

Above the plant-bearing beds biostratigraphically significant fusulinids were discovered from a packstone (Bed 51, Figure 2). This bed was positioned 53.5 m above the base of the Community Pit Formation at NMMNH locality 7981, and positioned ca. 40 m above the plant beds (equivalent to beds 18–20, Figure 2). The fusulinids include *Pseudoschwagerina beedei* Dunbar and Skinner 1936, *Pseudoschwagerina* cf. *P. rhodesi* Thompson 1954 and *Paraschwagerina* sp. with phrenothecae (= *Paraschwagerina* aff. *P. phrenesa* Wilde 2006 or *Paraschwagerina* aff. *P. fax* Thompson and Wheeler 1946). Based on correlations across New Mexico (Wilde, 2006), we interpret these occurrences as indicative of a late or even latest Nealian (i.e., late to latest Asselian) age. We note that although *Paraschwagerina* specimens with phrenothecae first appear in the uppermost Lenoxian (lower Artinskian) strata of New Mexico (Wilde, 2006), they are present much earlier in the McCloud Limestone of the Klamath Terrane in northern California (Zone C of Skinner and Wilde, 1965), in rocks that are probably equivalent to the early Asselian. Therefore, their presence in the Community Pit Formation is not inconsistent with the age indicated by *Pseudoschwagerina*.

The foraminifer *Pseudovermiporella* has been identified from the middle and upper part of the Community Pit Formation elsewhere in Doña Ana County. Based on the First Appearance Datum (FAD) of this species, Krainer et al. (2009) inferred a Sakmarian age. This assignment was based on correlation with the FAD of this genus in successions of the Carnic Alps of Austria (Vachard and Krainer, 2001; Krainer et al., 2009). Formerly dated as Sakmarian (Forke, 1995), this interval is now placed in the early Artinskian based on conodonts and fusulinids (Davydov et al., 2013), which suggests that the correlative Community Pit Formation may be, in its uppermost part, of early Artinskian age.

Conodonts obtained from the middle part of the Robledo Mountains Formation, immediately overlying the Community Pit Formation, indicate an assignment to the late Wolfcampian (Lucas et al., 1998a, b, 2002); this is equivalent to a late Artinskian age (Henderson et al., 2012) on the international time scale. An Artinskian age for the Robledo Mountains Formation also is inferred based on the occurrence of the small fusulinid *Pseudoreichelina* throughout the formation (Krainer et al., 2009). This genus, however, ranges into middle Leonardian strata in Central America (Guatemala, northern Mexico), and the southwestern USA (New Mexico, Texas and Nevada) (Vachard et al., 1997), suggesting a Kungurian upper age limit (Henderson et al., 2012a).

2.2. General paleoenvironmental interpretation

The Community Pit Formation is a mixed siliclastic-carbonate unit, containing variably fossiliferous beds of dolomudstone, ~~limestone~~lime mudstones and wackestones, and siliciclastic shale (Figure 2; Krainer et al., 2003, 2009; Mack et al., 2013). It was deposited in a shallow marine to supratidal setting (the Hueco Seaway) on the western margin of the intracratonic Orogrande Basin (Lucas et al., 1998a, b; Voigt et al., 2013) at a paleolatitude of about 2ºN (Tabor et al., 2008). Elsewhere in Doña Ana County, the unit contains a somewhat restricted marine fauna, and red/green-mottled caliche paleosols are developed at a few intervals (Krainer et al., 2003, 2009; Lucas et al., 2002; Mack et al., 2010). Fifty kilometers north of Doña Ana County, this same stratigraphic interval comprises only red bed alluvial facies of the Abo Formation (DiMichele et al., 2007; Lucas et al., 2012). Therefore, during the Early Permian the location of the PTNM lay close to the fluctuating Hueco Seaway coastline (Mack and James, 1986), with alluvial plains to the north (Lucas et al., 2012).

In a PTNM section that largely comprises the Community Pit Formation, Mack et al. (2013) identified six supratidal and shallow marine facies. They compared the overall paleoenvironment with semi-arid portions of the present-day Trucial Coast of Abu Dhabi, highlighting the presence of gypsum. This interpretation of climate as semi-arid is consistent with regional studies of paleosols (Mack, 2003; ~~Tabor, 2007;~~ Tabor et al., 2008; Mack et al., 2010). However, the remains of large fossil trees, which would have required a good water supply, occur at several intervals in the formation (Tidwell and Munzing, 1995; Falcon-Lang et al., 2014~~a~~). There are three possibilities to explain this apparent inconsistency: (1) Regional climate was, in fact, semi-arid to arid, but there were localized poorly drained, groundwater-dependent habitats dotted across the landscape (cf. DiMichele et al., 2006), where arborescent vegetation could flourish despite the aridity. (2) Regional climate was overall somewhat wetter, allowing the geographic co-occurrence of minor evaporites with large trees, as seen, for example in the present-day southern Mediterranean region (cf. Francis, 1984). (3) Regional climate oscillated between wetter and drier phases, the large trees being associated with the former climate states and the evaporites with the latter (cf. Parrish and Falcon-Lang, 2007).

3. Paleoenvironment of the fossil site

~~3.1 Sedimentary facies~~

The ~~new~~ fossil site, reported here, occurs within a 5-6 m deep channel cut into a succession of shale, limestone and dolomite at NMMNH locality 7981 (Figure 3A). The channel cuts down from a horizon c. 15.5 m above the base of the Community Pit Formation section (Figure 2, 3A). Measured on an east-west outcrop, sub-perpendicular to the channel axis, the apparent channel width is about 140 m (Figure 4). The eastern channel margin appears steeper than the western margin, but this may be an artifact of outcrop orientation. In addition, the western margin is truncated by a fault.

Seven sections (A - G) were measured across the channel (Figure 4). Three distinct units fill the channel; the lower two contain fossil-plant assemblages of different kinds.

3.1.~~1~~ Lower unit

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The basal unit, which occurs only in the central part of the channel (Figure 4, sections B-E), comprises a lens of limestone pebble-to-cobble conglomerate, 0.05-1.1 m thick, and contains Plant Assemblage #1. This rudstone is dominated by sub-angular to sub-rounded, elongate clasts of gray-orange lime mudstone, 20-150 mm long, and accumulations of detrital crinoids and bryozoans (locally comprising multiple, cemented, randomly arranged fossil fragments, clearly reworked from underlying beds), within a poorly sorted matrix of medium- to coarse-grained mixed carbonate-siliciclastic sandstone and mudstone. Specimens of coalified tree-trunks, up to 0.17 m diameter, co-occur with cubic, sub-rounded, 20-50 mm diameter blocks of charcoalified wood (Plant Assemblage #1) in the basal rudstone.

3.~~1.~~2. Middle unit

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The middle unit, up to 4 m thick, is more laterally extensive, and extends beyond the margins of the underlying conglomeratic lag, which is confined to the central, basal portion of the channel. Lime mudstone beds, up to 1.4 m thick, with undulatory or wavy lamination are the most prominent macroscopic feature of this unit (Figure 3B, C). In thin section, these beds are planar laminated, partly bioturbated lime mudstone with minor low-angle scours filled with slightly coarser grained carbonate material. They also include calcareous siltstones with rare thin layers of very fine-grained sandstone (~ 5 to 10%), composed of quartz and subordinate feldspar silt-size detrital grains, some of which appear to be wind-blown (Figure 5). The silt- and sand-sized layers contain abundant recrystallized carbonate skeletons and small amounts of detrital dolomite (Figure 5). Most common are hollow, needle-like skeletons ~30 to 60 µm in diameter and up to 0.5 mm long, which are recrystallized sponge spicules (Figure 5C), oriented parallel to bedding planes. There also are subordinate ostracodes and smaller foraminifers (*Tuberitina*, *Syzrania*?, and nodosinelloid forms) (Figure 5D) and probably other, completely recrystallized fragments that cannot be identified. Non-skeletal grains are small peloids (Figure 5A). The silt-sized and sand-sized material indicates transport by weak currents and deposition in a shallow, restricted environment. ~~, proximal to land given clear evidence for wind-blown detrital material.~~

In addition to the carbonate muds, the middle unit contains poorly exposed siliciclastic shale beds and a single, thin calcarenite lens, 0.14 m thick and several meters wide confined to the central part of the channel and some medium- to coarse-grained siliciclastic sand that shows climbing ripple cross-laminations.

Macrofossils and traces in the middle unit include scattered pterinopectinid bivalves and rare lingulid brachiopods, and horizons with vertical burrows. The low-diversity of the invertebrate fossil assemblage and overall fine-grained nature of the muddy carbonates is typical of ~~a brackish to~~ restricted marine or brackish depositional environment. Also present at multiple horizons are rooted zones associated with the adpressed megaflora (Plant Assemblage 2 described in section ~~4.2~~ 5). A few weakly calcified tree-trunks, up to 0.18 m diameter and > 1.4 m long, occur in the undulatory beds. These logs have an orientation sub-perpendicular to the channel margins. Rare fragments of wood also are identifiable in thin sections of the limestone matrix.

3.~~1.~~3. Upper unit

The uppermost channel-fill unit is a distinctive yellow dolomite, up to 1.2 m thick, showing prominent calcite-filled vugs and nodular gypsum (Figure 4). No macrofossils were identified in this portion of the channel fill.

3~~6~~.4~~1~~. Paleoenvironmental interpretation

There are several possible explanations for the incision of the fossil-bearing channel and its subsequent filling, primarily with carbonate, which must be treated as temporally independent phenomena. The occurrence of an incised channel system, albeit unique in the region, necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine shelf and to cause channel incision. Most incised features of this nature have been recognized in non-marine, siliciclastic depositional settings; however, a few examples have been reported in carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003). The term “incised channel” (rather than incised valley) is the most appropriate descriptor for the feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and 5-6 m deep) with a low aspect ratio (about 25:1).

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There are several possible causes of base-level change. Eustatic lowering of sea-level is, perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation may have been deposited sometime during one of several intervals of inferred Permian southern hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al., 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event, resulting in a global lowering of sea level, additional evidence of incision in the area might be expected at this same horizon, which is widely traceable within the mostly carbonate portion of the Community Pit Formation. However, such evidence has not been found by us or reported elsewhere.

It is also possible that rapid, local base-level change could have been triggered by tectonism, given the location of the PTNM in the intracratonic Orogrande Basin. The PTNM is positioned close to and on the subsiding side of a line separating active uplift and erosion from subsidence in this region. Although most of the active tectonism was in the early Wolfcampian, the age of this deposit and the duration of the tail end of that tectonism are sufficiently unconstrained that this must remain an active possibility.

Finally, autogenic processes are another possibility, but these must operate within a larger eustatic or tectonic framework whereby local base-level had been lowered already. Were base-level/sea-level already low, on a landscape that generally experienced little rainfall, it is possible that there were few drainages, particularly in a low-gradient coastal environment. In this scenario, the channel may have originated by avulsion or stream capture, particularly if base-level lowering happened in combination with an increase in regional moisture regime.

The central portion of the channel contains a basal rudstone composed of pebbles and cobbles of marine limestone and faunal detritus, clearly well indurated at the time of its erosion and deposition. Thus, it does not appear to represent a submarine channel. The small size of the channel, and the fact that the only sedimentary particles in it are of local origin from within the areas of the immediate drainage basin, suggest a seasonally dry climate at the time of incision, and a relatively small overall drainage area (Feldmann et al., 2005). There must, however, have been sufficient moisture to promote plant growth proximate to the channel, indicated by moderate-sized logs in the basal channel fill, and to bring about incision in the first place.

The filling of the channel appears to comprise several phases. Clearly, early on in particular, there were periods of active transport of sedimentary particles, whereas at other times the channel appears to have been significantly less active to stagnant and possibly to have had portions subaerially exposed. The middle unit lime muds and their invertebrate fossils may have been washed in from seaward, by the backfilling tidal waters. This may have occurred once the fluvially incised channel was flooded by tidal waters during base level/sea-level rise. Gypsum in the later stages of channel filling suggests an increasingly drier climate with time.

The fill sequence suggests a base-level rise. The basal conglomeratic lag, including permineralized, partially to completely fusinized logs, indicates sufficient moisture on the landscape to support trees, and water movement in the channel during its periods of flow to cause significant erosion and to move, at least periodically, large sedimentary particles. The combination of intraformational gravels and logs, preserved partially or wholly as charcoal, is consistent with a semi-arid to dry sub-humid climate (Cecil and Dulong, 2003). The basal lag was emplaced either during the more active parts of water flow in the channel or during the early phases of transgression.

Above this basal lag, lime mudstones formed under brackish to nearly marine salinities, with strong suggestions of periods of standing or sluggishly moving water. The salinity and carbonate accretion are most likely reflective of base-level rise and the invasion of the channel by marine waters, mixed to some small degree with continued freshwater runoff from the surrounding terrestrial landscape. A change from a sub-humid to a semi-arid climate is indicated. However, it is likely that water cover was maintained most of the time, given evidence of syndepositional occupation of surfaces within the channel by vascular plants and the incorporation of plant remains into the limestone matrix, which consisted of actively forming/accumulating carbonate muds.

The final sediments in the channel are lime mudstones with gypsum cements, lacking any evidence of vascular plants nearby or living on the surface. The lack of plant debris cannot be interpreted to mean that plants were not growing in or around the channel. Absence of evidence not being evidence of absence, plants may no longer have been present on the landscape or conditions may have been unfavorable for the accumulation and preservation of organic matter, or both. One must keep in mind that most sediments formed in fully terrestrial or coastal transitional settings lack terrestrial fossils, even if all other indicators are consistent with the presence of vegetation and fauna.

~~3.2~~4. **Isotopic analyses of the middle unit**

In order to ~~assess the~~ more tightly constrain the extent of marine influence on the lime mudstones of the middle unit, carbon, oxygen, and strontium isotopic analyses were carried out on microdrilled samples of the carbonate ~~lithofacies~~samples from the middle unit.

4.1. Methodology

Thick sections (~200 µm thick) of two hand samples from the middle unit were studied petrographically under transmitted light and cathodoluminescence in order to identify calcite fabrics and textures. Thick sections of the two samples were microdrilled for stable (50 µg ±10 µg samples) and radiogenic isotope (0.5 gm) analysis using a Merchantek automated microdrilling system.

Samples (n=10) for stable isotope analysis were roasted at 375° C under vacuum for 30 minutes to remove organics and subsequently reacted in 105% phosphoric acid at 90° C in either a common acid bath on a GVI Optima Stable Isotope Ratio Mass Spectrometer (SIRMS) or a Gilson Multicarb Autosampler system (individual acid injection vials) interfaced with an Elementar Isoprime Mass Spectrometer housed in the UC Davis Stable Isotope Laboratory. CO_2 gas was analyzed in dual inlet mode and values were corrected using the Craig correction to account for the ^{17}O contribution (Craig, 1957) and to an internal standard and reported relative to the Vienna Pee Dee Belemnite (VPDB). Both systems provide $\delta^{13}C$ precision of ± 0.04‰ and $\delta^{18}O$ precision of ± 0.06‰.

Microdrilled samples (n=2) for strontium isotope analyses were prewashed with 1 M ammonium acetate in order to remove Sr associated with absorbed (on clays) or included noncarbonate phases (Montañez et al., 2000). Strontium was isolated using Spex cation exchange resin and microliter columns attached to a channel pump. $^{87}Sr/^{86}Sr$ ratios were measured in solution mode on a Nu MC-ICPMS in the Interdisciplinary Center for Plasma Mass Spectrometry, UC Davis. Values are typically normalized to a nominal value for NIST standard SRM987 of 0.710249. SRM987 for the measurement period averaged 0.710249 (2σ = 0.000035) based on standards analyzed during this period.

4.2. Results

~~In order to assess the extent of marine influence on the lime mudstones of the middle unit, carbon and oxygen isotopic analyses were carried out on microdrilled samples of the carbonate interval.~~ The well-preserved micrites have average $\delta^{18}O$ and $\delta^{13}C$ compositions ~~between -2.7 to -~~ –of -3.0‰ (2 std err. of 0.2‰) ~~2.4‰~~ and ~~1.2 and 1.4~~1.1 ‰ (2 std err. of 0.1‰)~~‰~~, respectively (Table 1).

4.3. Paleosalinity interpretation

Given the earliest Permian age of the carbonates, these values support a dominantly marine environment. However, these stable isotopic values indicate that the lime muds likely did not form in pure seawater given typical Midcontinent and Panthalassan seawater compositions during this time (Grossman et al. 2008). Seawater $\delta^{18}O$ in the ~~Late Carboniferous~~Pennsylvanian and early Permian likely ranged between -1 and 0‰ (Came et al., 2007) given the occurrence of ice sheets in southern Gondwana.– The $\delta^{18}O$ composition of low-latitude coastal river water likely was in the range of -1 to -4‰ (cf. Bowen and Wilkinson, 2002), and perhaps a few per mil lower if the climate was monsoonal (Rozanski et al., 1993). Notably, the $\delta^{18}O$ of low latitude, coastal waters can be enriched by several per mil over open ocean seawater (Swart and Price, 2002), a scenario compatible with the tropical epicontinental environment of the study area. Thus, accounting for oxygen isotope fractionation between water and calcite at 25° ±3°C, the micritic $\delta^{18}O$ compositions are compatible with formation in waters over a range of salinities (i.e., fresh to fully marine).

Carbonate $\delta^{13}C$ values, in contrast, provide constraints on the depositional waters in the channel. Seawater $\delta^{13}C$ from the latest Ghzelian through earliest Sakmarian in western Euramerica was +4‰ ±0.5‰. The measured $\delta^{13}C$ values, which are 2 to 3‰ lower than contemporaneous seawater, can be explained by an input of a maximum of 10-20% freshwater. This assumes a freshwater $\delta^{13}C$ composition of -8 to -10‰, which is typical of ~~rivers draining carbonate systems and for freshwater systems in lowland regions~~tropical coastal rivers ~~bordering cratons~~ and associated with subhumid to semi-arid climates and moderate density vegetation (Mook and Tan, 1991).~~–~~ Although lowland tropical rivers draining carbonate terrains can be ^{13}C-enriched due to interaction with the carbonates along the flow path, the observed fossil flora indicate a likely source of locally derived ^{12}C-enriched terrestrial C to the channel waters.

A measured average Sr isotopic composition (n=2) of the laminated lime mudstone facies of 0.708571 (Table 1) is slightly more radiogenic than middle to late Asselian seawater ($^{87}Sr/^{86}Sr$ of 0.70785 to 0.70790; Henderson et al., 2012b). Application of the measured carbonate $^{87}Sr/^{86}Sr$ ratios and Sr concentrations (180 ppm ±32 ppm) to a Sr isotope—[Sr] fluid mixing model (Ingram and DePaolo, 1993) suggests that the fluid from which the carbonate precipitated could accommodate up to 17% freshwater. ~~This~~

The assumption of brackish conditions is thus reasonable for the inferred semi-arid to arid terrestrial paleoenvironment of the study interval. ~~Moreover, if~~Furthermore, if the channel formed as part of a coastal tidal channel complex, then the measured $\delta^{13}C$ values could record the enhanced contribution to the seawater DIC of ^{12}C-enriched ~~terrestrial~~ C locally derived from levee banks and/or interdistributary ponds. This finding provides independent confirmation of salinity estimates inferred from invertebrate fauna.

~~4~~5. Plant Assemblages

The Community Pit Formation floras encompass two distinct assemblages that occur in different facies of the channel. The lowermost flora, consisting solely of the woody remains of walchian conifers, is representative of the widespread, Late Pennsylvanian-Early Permian seasonally dry biome described from many localities across the Euramerican equatorial region (Rees et al., 2002; Zeigler et al., 2002; Bashforth et al., 2014; DiMichele, 2014). The flora preserved in the middle unit of the channel contains a unique assemblage, dominated by a voltzian conifer and a callipterid, unknown in combination from any other locality in Euramerica and preserved under environmental conditions suggestive of a tolerance of high-salinity substrates of one or both taxa.

Details of the lowermost flora have been described by Falcon-Lang et al. and are only be briefly précised here. (20154b – in press) and will only be touched on briefly here. It includes coalified tree-trunks and charcoalified wood preserved in the basal rudstone. Four specimens of charcoal, which was the only material to preserve anatomical detail, were examined. These specimens are housed in the collections of the New Mexico Museum of Natural History and Science under catalogue numbers NMMNH P68181 – P68184, and comprise pycnoxylic wood that conforms to the Type II Paleozoic wood of Doubinger and Marguerier (1975). These specimens are essentially identical to the wood-type *Macdonaldodendron* Falcon-Lang, Kurzawe et Lucas, which was described from higher in the Community Pit Formation (Falcon-Lang et al., 2014). This wood is considered to be of walchian-conifer affinity. Other woods considered or confirmed to be of walchian affinity are similar to the study specimens (Reymanowna, 1962; Lemoigne and Tyroff, 1967; Tidwell and Munzing, 1995).

RatherIn this current paper, we, we focus our attention on the peculiar flora from the middle beds of the channel. This flora has been described in brief by DiMichele et al. (2014 – in press5), with an emphasis focus on its stratigraphic implications. Here, we detail the morphology and paleoecology of the plants and their broader evolutionary implications.

4.1 Flora 1: Walchian conifer wood

Coalified tree-trunks and charcoalified wood are preserved in the basal rudstone. Hand lens observations indicate that the coalified tree-trunks are entirely devoid of cellular anatomy, so only the well-preserved charcoal was studied in detail (Falcon-Lang et al., 20154b). Material studied comprised four specimens, housed in the collections of the New Mexico Museum of Natural History and Science under catalogue numbers NMMNH P68181 – P68184. All four specimens are pycnoxylic wood attributable to a single morphotype, which conforms to the Type II Paleozoic wood of Doubinger and Marguerier (1975). These specimens are essentially identical to the wood-type *Macdonaldodendron* Falcon-Lang, Kurzawe et Lucas, which was described from higher in the Community Pit Formation (Falcon-Lang et al., 2014a). This wood is considered to be of walchian-conifer affinity. Other woods considered or confirmed to be of walchian affinity are similar to the study specimens (Reymanowna, 1962; Lemoigne and Tyroff, 1967; Tidwell and Munzing, 1995).

4.2 Flora 2: Voltzian conifers and Lodevia callipterids

The flora comprises aAdpressed megafloral remains and a few weakly calcified tree-trunks are preserved in micritic limestone. from the middle unit of the channel fill. Adpressed megafloral remains are present at multiple levels (Figure 3B, C) in discontinuous limestone lenses, each up to 30–50 mm thick and traceable for several meters along strike. Within these lenses, there are variable concentrations of randomly oriented plant fragments, ranging from comminuted plant debris to fragments 10–30 cm in breadth (however, we note that this is a minimum size estimate because it is difficult to obtain large slabs of material). Identifiable material comprises three-dimensionally preserved adpressions and partially cutinized leaves. Associated with these foliar remains, there are also open-to-somewhat-denser networks of roots of variable diameter, which crosscut laminations and are in growth position.

5.1. Material and methods

A total of 155 rock specimens were collected, each showing at least one adpressed plant fragment. Collections were made at four separate sites (Figure 4, sections A - C and E) spanning the entire channel width over an outcrop distance of 120 m, with a fifth collection (comprising four sub-collections) obtained as random samples from float. Two specimens of calcified tree-trunk were also collected, and for each specimen, standard TS, RLS, and TLS petrographic thin sections were made, and viewed using an Olympus binocular BH-5 microscope.

The proportional abundance of taxa was quantified using a variant of the method of Pfefferkorn et al. (1975), in which each hand specimen is treated as a “quadrat,” with each taxon occurring on that quadrat counted only once, regardless of the number of individual specimens or fragments of specimens present (Table 21). Comminuted plant debris and other indeterminate fragments were excluded from such counts,; however, gymnosperm axes of uncertainty affinity and invertebrates were included. The dominance and diversity data reported below are based on the three largest collections only, which include the majority (n = 114) of the specimens (sections C, E and float; localities USNM 43550, 43554, and NMMNH SGL-09-136, respectively), and represent the frequency of occurrence of each taxon as a proportion of the number of quadrats in those counts. For rare taxa, the number of occurrences in the entire collection is reported.

Specimens are housed in the Paleobotanical Collections of the New Mexico Museum of Natural History and Science, Albuquerque, NM (NMMNH) and the United States National Museum of Natural History, Smithsonian Institution (USNM). Illustrated or traced specimens are stored in the Paleontological Type and Illustrated Collections of the NMMNH under the catalog numbers NMMNH P68185 - P68346.

54.2.1. *Voltzian conifers*

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By far the most common plant remains present in the megafloral assemblages are those of voltzian conifers (occurring in 78 out of 114 quadrats; frequency 68.4 %), of which four foliar morphotypes (A - D) and a single ovuliferous cone are present (Figure 6). These morphotypes are distinguished based on details of leaf attachment to the stem, overall leaf shape, leaf profile, length to width ratio (L:W) of the leaves, and leaf angle of departure from the stem. Some specimen have cuticles preserved, unfortunately they do not preserve epidermal patterns.

Morphotype A is represented by five isolated shoots (Figure 6A), two of which have the ultimate tips of the branch preserved. Leaves are bifacially flattened (cf. Type II leaves; de Laubenfels, 1953), and are oblong in shape with obtuse apices. Leaf widths (W) range from 2 to 3.5 mm. Leaf lengths (L) are difficult to measure, due to overlap among them, and are at least 20 - -25 mm. L:W ratios range from 7 to 11, calculated on a per leaf basis. Leaves depart from the stem at angles from 15 to 40°, and are straight to slightly incurved when viewed in profile. Leaves are highly imbricate, particularly on the branch tips, resulting in a distinct ”tufted” appearance. Details of the leaf attachment and axis diameter are obscured by overlapping leaves.

Morphotype B is represented by four isolated shoots, and three other specimens preserving two or three orders of branching (Figure 6B). Branching is orthotropic, with higher order branches occurring in the axils of persistent leaves at angles of 55°. Leaves are tetragonal in cross section (Type I leaves: de Laubenfels, 1953), and attached helically to the stem by thickened cushions that are distinctly rhomboidal in shape (Figure 6B). Leaves taper slightly from the point of attachment to obtuse apices. Leaf length is 15 - 30 mm, and leaf width reduces from 2.5 - 3.5 mm at the point of attachment to about 2 - 2.5 mm mid-leaf (L:W ratios: 6 - 9). The angle of leaf departure from the stem axis is variable (average 55°), with the leaves mostly straight in side profile, but occasionally slightly incurved. Leaves on thicker branches depart at the higher angles, and are more reflexed in profile.

Morphotype C is represented by four isolated foliar shoots (Figure 6C). Leaves are tetragonal in cross section, and attached to the stem on rhomboidal leaf cushions (cf. Type I leaves: de Laubenfels, 1953). Leaves are distinguished from those of Morphotype B primarily by having a distinctly falcate profile, and by showing a greater degree of taper from the base to the tip of the leaf. Leaves depart at a high angle (average 60°), then curve inward toward the supporting axis. There is considerable variation in the absolute size of leaves within this morphotype, varying from 6 - 20 mm in length and 1 - 3.5 mm in width (L:W ratios: 5 - 9; ratio calculated per leaf). One relatively small specimen, which is similar in all other leaf characteristics, represents the tip of a branch, and may be juvenile foliage.

Morphotype D is represented by one, relatively large, branched specimen (Figure 6D). Ultimate branches occur in the axils of persistent leaves, and the overall branching pattern is orthotropic. Leaves have decurrent attachments to the stem, with the decurrent portions of the bases thick and clearly distinguishable for the entire length of the internode. Leaves depart from the stem at angles commonly up to 90°. ~~; however, i~~It should be noted, however, that there is a high degree of variation that may have been influenced by taphonomic processes, such as drying of the material prior to deposition. Leaves are slightly more than 20 mm long, and 1.2 - 2 mm wide (resulting a distinctively high L:W ratio of 12.5) and have a straight profile with an obtuse apex. The leaves are dorsiventrally flattened in cross section (cf. Type II leaves: de Laubenfels, 1953), with a thick, fleshy appearance. Leaves on the thicker, higher order axis appear more lax; however, again, this could reflect taphonomic processes, such as differential drying of dead foliage prior to incorporation into the sediment.

The ovulate cone associated with these foliar morphotypes is compound with bract-ovuliferous dwarf shoot complexes helically arranged around the axis (Figure 6E). Bracts are narrow and elongate with an obtuse apex and slightly bend toward the cone axis. Dwarf shoots, which have an axillary position, are flattened and bilaterally symmetrical with five to six partially fused, similarly shaped, oblong sterile scales and/or sporophylls with obtuse apices (Figure 6F). The base of the dwarf shoots is stalk-like, and given their size and position on the cone, dwarf shoots are likely partially fused with the bract.

Late Paleozoic conifer classification is based on a combination of morphology and internal and cuticular anatomy of stems, leaves, pollen cones, and ovuliferous structures (~~,~~ such as ovuliferous cones and fertile zones)~~.~~ (e.g., Clement-Westerhof, 1984, 1987, 1988; Rothwell et al., 1997, 2005). Several features of the novel conifer material reported here allow it to be referred to voltzian conifers. First, their foliar morphotypes show generally bifacial ovate, lanceolate to linear medium-sized leaves, which are characteristic of voltzians. Second, foliar morphotypes B and D show orthotrophic branching, also characteristic of voltzians, but distinct from the plagiotrophic walchians (Rothwell et al., 2005). Third, the sterile scales and sporophylls in the dwarf-shoots are fused, more or less flattened in one plane, and show a bilaterally symmetrical organization. At this point in time, it is uncertain how many taxa these four leaf morphotypes represent. Heterophylly does occur in voltzian conifers, and generally involves differences in leaf size, shape in face view, and apex shape. Voltzians are, however, relatively consistent in leaf characters like mode of attachment, features of leaf bases and shape in cross-section. Morphotypes B and C might represent a single taxon, but we have no confirmatory evidence for that, such as attachment to a common branch. The leaves of morphotypes A and D are both bilaterally flattened, but arise at different angles, and have different kinds of attachment. Collection of further material is required to answer this question. More material is also needed to ensure that we have collected the full range of the diversity of conifer foliage in this flora.

We note that the earliest voltzian conifers described to date are *Lebowskia grandifolia* and *Manifera talaris* from the uppermost lower Permian–lowermost middle Permian of north-central Texas (Looy, 2007; Looy and Stevenson, 2014). Therefore, the novel conifer morphotypes from Plant Assemblage #2 extend the temporal range of this clade into the early Permian (late Asselian), and represent the oldest known occurrence of voltzian conifers.

54.3.2.2 Callipterid foliage – Lodevia oxydata

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The other dominant taxon in the flora is an unusual callipterid (occurring in 34 out of 114 quadrats; frequency 29.8 %). The material shows considerable morphological variation and encompasses immature and mature pinnae (Figure 7A-E). Included among the suite of specimens are pinnae with remarkably robust axes bearing slightly decurrent, pinnately lobed to segmented, pinnules. Pinnule lobes typically have blunt tips, particularly those forming the pinnule apex. The venation is pronounced with an indistinct, sometimes slightly flexuous midvein with widely spaced, steeply ascending lateral veins inserted at angles of 20-30°; lateral veins fork once or twice, depending on the segmentation with a single vein per lobe. The suite of specimens shows a number of noteworthy phenologic features. For example, some fronds show pinnae preserved in the process of unfolding (Figure 7A), a developmental pattern found in other callipterid taxa (e.g., Kerp, 1988). Still others comprise young, immature pinnules (Figure 7E), and a few unusual mature specimens exhibit pinnules with irregularly curled edges (Figure 7D). Another axis has a swollen base (Figure 7C), which usually indicates that complete fronds were abscised.

Axes of small to medium size (up to 28 mm in diameter) co-occur with this foliar material and are sometimes found in organic connection with it, suggesting that leaves may have been retained on branches for some time. This was observed in 16 quadrats.

Pinnae and associated axes are identified as *Lodevia oxydata* (Göppert) Haubold et Kerp based on their broad, stiff rachial axes and bluntly ending pinnules (Kerp and Haubold, 1988). Pinnules are up to 3.2. cm long, which is larger than in other *Lodevia* species. The pinnule is composed of segments that widen markedly towards their tips. Segment tips and pinnule apices are very blunt, and not rounded. The pinnules, overall, appear "flat," and the rachial axes are robust. Also, compared to other *Lodevia* species, the basal pinnules in *L. oxydata* are quite large. The absence of large diameter axes, despite the existence of quite a large collection, suggests that *L. oxydata* may have been a shrub.

54.2.4. Roots

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Among the remaining adpressed material, only roots occurring in growth position (n = 17 quadrats) are common, being found in all four *in situ* collections. Roots comprise dense, interwoven networks and more extensive, open systems (Figure 7H). They show four, or more, orders of branching, the largest being c. 25 mm in diameter, the smallest < 1 mm in diameter. They ramify irregularly, side-axes being disposed at variable angles to the higher-order axes.

The identity of these roots is unknown, although it is possible to narrow down their affinities, which are most likely with seed plants. They share some features with pteridospermous root systems, which have a similar indeterminate growth pattern (Rothwell and Whiteside, 1974; Stull et al., 2012). Although roots attributable to Paleozoic conifers are poorly known, modern forms have root morphologies similar to those of other seed plants. What these roots are not likely to be is equally as enlightening as what they might be. They are not typical rooting features of arborescent and herbaceous lycopsids (Dawson, 1868; Jennings et al., 1983; Pigg, 1992). Nor are they calamitalean roots, such as *Pinnularia* and *Myriophyllites*, which show side-branches disposed perpendicular to primary axes and comprise discontinuous size-class orders of branching (Dawson, 1868; Taylor et al., 2009). Neither do they appear to be marattialean tree-fern root systems, which are networks of generally relatively straight, unforked, larger roots (4 - 6 mm diameter, but often larger: Ehret and Phillips, 1977; Mickle, 1984; Millay, 1997) that commonly form dense networks in isolated clumps (Falcon-Lang, 2006).

In consideration of the likely seed plant affinities of the roots, the most important point they highlight is that rooting of the lime mudstones took place contemporaneously with or very shortly after the entombment of the aerial remains of conifers and *Lodevia* in this same limey mud. Because these roots are in and ramify through the limestone, and because of the rate at which subaerially lime mud hardens and becomes effectively impenetrable to roots, and because there is no evidence within these beds of brecciation associated with long-term pedogenesis and development of terra rosa type residual siliciastic soils, it is most likely that the roots were derived from the voltzian conifers and/or the callipterids, though whether one or both cannot be determined. The possibility remains, of course, that they were derived from an additional kind of, most likely, seed plant that left no other macrofossil record. The likely contemporaneity or near contemporaneity of the aerial debris and roots also suggests that the plants in question were growing on these limey muds while they were water covered. The combination of physical sedimentological evidence, isotopic values of the lime muds, the brackish-to-marine invertebrate fauna also present within the sediment, and the necessity for incorporation of aerial debris and roots into the muds prior to solidification, strongly suggests growth of these plants in waters of brackish to near-marine salinities.

54.2.5. Other rare taxa

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All other taxa are rare and include walchian conifers (*Walchia* sp., n = 7 quadrats) (Figure 7F), some small seeds of indeterminate affinity (n = 7), which may be related to one of the conifers or pteridosperms, the sphenopsid *Annularia spicata* (Gutbier) Schimper (n = 1; Figure 7F), and a putative fern, cf. *Sphenopteris* (n = 1). A small number of weakly calcified tree-trunks (up to 0.18 m diameter) associated with the adpressed remains comprise pycnoxylic coniferopsid wood that is too coarsely re-crystallized for more accurate determination.

65. Discussion

There are certain aspects of the PTNM limestone channel deposit, recited here, that frame the paleoecological interpretation of its biota.

(1) The geological setting. The basic setting is a channel cut into a limestone platform, thus indicative of some lowering of base level at least locally. The channel is narrow, shallow and asymmetrical. There are, as far as we know, no other incised channels identified anywhere in

the surrounding geological exposures of the Community Pit Formation in the Prehistoric Trackways National Monument, which has been thoroughly scouted for more than a decade by Jerry MacDonald (1994), the discoverer of the deposit, and numerous other geologists (e.g., Lucas et al., 1998a, b, 2011; Mack et al., 2013; Falcon-Lang et al., 2014~~a~~).

(2) The host lithologies. The channel is filled primarily with lime muds, the benches of which are separated by thin siliciclastic parting beds. The fill can be subdivided into three units. The basal channel fill, present only in the center of the channel, as typical of a lag deposit, is conglomeratic and includes plant remains, mainly coniferous tree trunks. The middle unit is composed of lime mudstone lenses separated by thin siliciclastic beds, and hosts the majority of adpression plant fossil remains. The upper unit is a lime mudstone with scattered gypsiferous nodules.

(3) The biota. A brackish-to-marine water invertebrate fauna was found in the lower two units of the channel fill, consistent with the ~~stable~~ isotopic compositions of the carbonate matrix. Trunks of walchian conifers occur in the basal lag deposit and many of these are preserved as charcoal. The middle unit contains a flora dominated numerically by undescribed voltzian conifers, with subdominant numbers of the callipterid *Lodevia oxydata*. These aerial remains occur intermixed with in situ roots that appear to have a seed-plant affinity.

It must be emphasized that this is an extremely unusual deposit, of a type rarely encountered by the authors in their combined many ~~over 200 person~~ years of fieldwork. Limestone filled, terrestrial channels are uncommon. The closest analogue may be limestone-filled lakes that formed under semi-arid to occasionally arid climates, such as those that typify Late Pennsylvanian and early Permian exposures in the Appalachian Basin of the eastern USA (e.g., Montañez and Cecil, 2013), from which plant fossils (callipterids, tree ferns) are known and reported (e.g., DiMichele et al., 2013b).

In addition to being physically unusual, this channel deposit contains an exceptional flora. That flora includes the earliest known voltzian conifers, extending the range of the lineage downward from the Kungurian-Roadian boundary to the Asselian-Sakmarian, approximately 25 million years. It also includes a rare species of callipterid, *Lodevia oxydata*, now known from Poland, the Appalachian Basin, and New Mexico, all in deposits of earliest Permian age. Both of the common plants indicate the existence of vegetation types rarely preserved in the geological record, or perhaps rarely sampled because of the unlikely nature of the host deposits, despite what appear to have been long stratigraphic ranges and broad geographic distributions.

~~*5.1. Paleoenvironmental interpretation*~~

~~There are several possible explanations for the incision of the fossil-bearing channel and its subsequent filling, primarily with carbonate, which must be treated as temporally independent phenomena. The occurrence of an incised channel system, albeit unique in the region, necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine shelf and to cause channel incision. Most incised features of this nature have been recognized in non-marine, siliciclastic depositional settings; however, a few examples have been reported in carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003). The term "incised channel" (rather than incised valley) is the most appropriate descriptor for the feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and 5-6 m deep) with a low aspect ratio (about 25:1).~~

There are several possible causes of base-level change. Eustatic lowering of sea-level is, perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation may have been deposited sometime during one of several intervals of inferred Permian southern hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al., 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event, resulting in a global lowering of sea level, additional evidence of incision in the area might be expected at this same horizon, which is widely traceable within the mostly carbonate portion of the Community Pit Formation. However, such evidence has not been found by us or reported elsewhere.

It is also possible that rapid, local base-level change could have been triggered by tectonism, given the location of the PTNM in the intracratonic Orogrande Basin. The PTNM is positioned close to and on the subsiding side of a line separating active uplift and erosion from subsidence in this region. Although most of the active tectonism was in the early Wolfcampian, the age of this deposit and the duration of the tail end of that tectonism are sufficiently unconstrained that this must remain an active possibility.

Finally, autogenic processes are another possibility, but these must operate within a larger eustatic or tectonic framework whereby local base-level had been lowered already. Were base-level/sea-level already low, on a landscape that generally experienced little rainfall, it is possible that there were few drainages, particularly in a low-gradient coastal environment. In this scenario, the channel may have originated by avulsion or stream capture, particularly if base-level lowering happened in combination with an increase in regional moisture regime.

The central portion of the channel contains a basal rudstone composed of pebbles and cobbles of marine limestone and faunal detritus, clearly well-indurated at the time of its erosion and deposition. Thus, it does not appear to represent a submarine channel. The small size of the channel, and the fact that the only sedimentary particles in it are of local origin from within the areas of the immediate drainage basin, suggest a seasonally dry climate at the time of incision, and a relatively small overall drainage area (Feldmann et al., 2005). There must, however, have been sufficient moisture to promote plant growth proximate to the channel, indicated by moderate-sized logs in the basal channel fill, and to bring about incision in the first place.

The filling of the channel appears to comprise several phases. Clearly, early on in particular, there were periods of active transport of sedimentary particles, whereas at other times the channel appears to have been significantly less active to stagnant and possibly to have had portions subaerially exposed. The middle unit lime muds and their invertebrate fossils may have been washed in from seaward, by the backfilling tidal waters. This may have occurred once the fluvially incised channel was flooded by tidal waters during base level/sea-level rise. Gypsum in the later stages of channel filling suggests an increasingly drier climate semi-arid climate during that phasewith time.

The fill sequence suggests a base-level rise. The basal conglomeratic lag, including permineralized, partially to completely fusinized logs, indicates sufficient moisture on the landscape to support trees, and water movement in the channel during its periods of flow to cause significant erosion and to move, at least periodically, large sedimentary particles. The combination of intraformational gravels and logs, preserved partially or wholly as charcoal, is consistent with a semi-arid to dry sub-humid climate (Cecil and Dulong, 2003). The basal lag was emplaced either during the more active parts of water flow in the channel or during the early phases of transgression.

~~Above this basal lag, lime mudstones formed under brackish to nearly marine salinities, with strong suggestions of periods of standing or sluggishly moving water. The salinity and carbonate accretion are most likely reflective of base-level rise and the invasion of the channel by marine waters, mixed to some small degree with continued freshwater runoff from the surrounding terrestrial landscape. A change from a sub-humid to a semi-arid climate is indicated. However, it is likely that water cover was maintained most of the time, given evidence of syndepositional occupation of surfaces within the channel by vascular plants and the incorporation of plant remains into the limestone matrix, which consisted of actively forming/accumulating carbonate muds.~~

~~The final sediments in the channel are lime mudstones with gypsum cements, lacking any evidence of vascular plants nearby or living on the surface. The lack of plant debris cannot be interpreted to mean that plants were not growing in or around the channel. Absence of evidence not being evidence of absence, plants may no longer have been present on the landscape or conditions may have been unfavorable for the accumulation and preservation of organic matter, or both. One must keep in mind that most sediments formed in fully terrestrial or coastal transitional settings lack terrestrial fossils, even if all other indicators are consistent with the presence of vegetation and fauna.~~

6~~5~~.2. Flora 1: Walchian and other coniferous wood.

The earliest vegetation from the PTNM limestone channel deposit for which we have evidence is preserved as coalified tree-trunks and charcoalified wood fragments in the calcirudite at the base of the channel (Falcon-Lang et al., 2014~~4b~~5). The specimens examined have walchian conifer affinity. Species that are part of the large complex of walchian Voltziales are by far the most commonly encountered kinds of conifers in Euramerican fossiliferous deposits of latest Pennsylvanian and early Permian age (e.g., Kerp and Fichter, 1985; Clement-Westerhof, 1988; Kerp, 1996; Ziegler et al., 2002; Hernandez-Castillo et al., 2001, 2009; Rothwell et al., 2005; Looy 2013; Looy and Duijnstee, 2013). They are dominant elements in the red siltstones that make up much of the Community Pit Formation and its more inland equivalent, the Abo Formation (DiMichele et al., 2007, 2013a), which crops out in a long north-south band on the margin of the Rio Grande rift and elsewhere, throughout central New Mexico (Lucas et al., 2012, 2013).

The source of the walchian logs is most likely from the margins of the channel and perhaps from the surrounding floodplain, though we detected no paleosol evidence of a lateral, subaerially exposed surface. These trees are preserved in what is arguably the wettest phase of channel development, during which there were periodically high flow volumes and little or no carbonate precipitation. The predominance of walchians is consistent with their preservation in other kinds of Hueco Group (e.g., in the Robledo Mountains Formation, which immediately overlies the Community Pit Formation) environmental settings, specifically the siliciclastic redbed siltstones, which also suggest seasonality of moisture under a climate that was at most dry subhumid. If the drop in sea level in this area is attributed to glacio-eustasy, the trees were growing at times of near-glacial maximum (Falcon-Lang and DiMichele, 2010).

6~~5~~.3. ~~Flora 2:~~ Voltzian-callipterid vegetation

A plant assemblage entirely distinct from that preserved in the basal channel-lag deposits is represented by fossils preserved in the middle unit of the channel fill. Here, accumulations of randomly-oriented adpressions, associated with calcified tree-trunks and *in situ* fossil roots,

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occur within ~~micritic limestone~~lime mudstones and wackestones ~~beds~~, ~~which~~ with biogenic grains that indicate a ~~evidence a~~ brackish-to-marine origin. The plant assemblage is dominated by a low-diversity flora consisting of undescribed voltzian conifers (Figure 6) and subdominant amounts of the callipterid *Lodevia oxydata* (Figure 7A-E). A few specimens suggest the presence of walchians (Figure 7G), calamitaleans (Figure 7F) and small ferns as rare elements. The plants are preserved mainly as compressions and have variably preserved cuticle on the outer surfaces.

It is probable that one or both of the taxa that comprise this flora were growing in contact with saline water. This assertion is supported by several aspects of the flora, its taphonomy and the attributes of the deposit itself. The lime mudstones—wackestones in which the plants occur ~~has~~ have only weak bedding and are not brecciated or fractured. Thus, the organic remains had to be deposited in that substrate while it was both soft and still accumulating. There are large fragments of branches and leafy shoots among the fossilized plant parts, suggesting limited transport and, thus a local, parautochthonous origin. Preserved cuticle on both conifer and callipterid foliage indicates rapid burial. The lime muds ~~lime muds~~ are rooted, and the roots are clearly *in situ* and transgressed the substrate while it was still soft enough to be penetrated. The shape of the root masses and the character of the rock matrix suggest that they did not enter along cracks in already lithified limestone. Roots are not found in the overlying limestone beds, so it can be assumed that they originated from plants growing on or immediately adjacent to the lime muds within the channel. However, an origin from one specific plant taxon or the other, or both cannot be ascertained. The stable and radiogenic ~~stable~~ isotopic and invertebrate paleontological evidence both indicate accumulation of the lime muds under brackish-to-marine salinities.

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Perhaps the simplest interpretation that can be made of this deposit is that it formed in a quiet, abandoned or largely abandoned channel, perhaps as a lake deposit or as a sluggish drainage into a coastal embayment. The ~~limestone~~ lime mud almost certainly is of microbial and algal origin. In order for ~~it to stay in a non-cemented state, such that~~ invertebrates, plant parts and roots ~~could~~ to be preserved in ~~it~~the lime mud, a shallow, persistent water cover was required, at least during those times when aerial material was being incorporated. Lime muds such as these harden and develop surface crusts quickly when exposed subaerially. If these crusts were thin, that is if periods of water cover exceeded those of exposure, plants could recolonize the surfaces and roots could “punch through” the crustose surfaces. The key attributes then as they affect the vascular plant assemblage are high salinity, high pH, fluctuating but semi-persistent water cover, and high rates of evaporation and transpiration.

The voltzian conifers in this deposit are the earliest known (late Asselian) representative of this evolutionary lineage, significantly extending the known stratigraphic range downward from the Kungurian-Roadian (Early-Middle Permian) boundary in Texas (Looy, 2007;~~,~~ Looy and Stevenson, 2014). These previously oldest voltzian conifers occur in deposits interpreted, like the PTNM limestone channel deposit, to have formed under dry-subhumid to semi-arid conditions. They were part of an assemblage that included conifer and cycad taxa with an overall late Permian (Zechstein/Wuchiapingian) to Mesozoic aspect (DiMichele et al., 2001).

The other common plant in the mid-channel assemblage is *Lodevia oxydata*. This is a very rare species that has only been described twice previously in the fossil record. Both previous occurrences are from near the Pennsylvanian-Permian boundary in (1) the Rotliegend of Lower Silesia, Poland (Göppert, 1864-65) and (2) the Dunkard Group of the Central Appalachian Basin, U.S.A. (DiMichele et al., 2013b). The New Mexico occurrence extends the geographic range of this taxon across the entire breadth of the Euramerican realm. In the Appalachians, *L. oxydata* is known from limestone beds lacking evidence of marine influence (Montañez and Cecil, 2013) at two, closely adjacent, localities, interpreted as having formed under a semi-arid to dry subhumid climate regime (DiMichele et al., 2013b). The Rotliegend specimen is from a very different environmental setting, occurring in an inland basin located far from the nearest marine influence and not characterized by either arid conditions or any evidence of elevated salinity.

In summary, the deposit described here indicates the existence of a previously unknown type of late Paleozoic plant assemblage. This assemblage is of low diversity, consisting of two abundant seed-plant species and a few rare taxa. Its habitat of growth, on the margins of and rooted within the lime muds of a shallow, highly saline channel, is most unusual and suggests a mangrove habit for one or both of the dominant forms. The discovery of such deposits involves a great deal of luck and indicates the necessity for continued field studies and examination of even unlikely looking sedimentary-rock strata.

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FIGURE CAPTIONS

Figure 1. County map of New Mexico highlighting the location of the PTNM in Doña Ana County, where the fossils were obtained (index map: location of New Mexico in the U.S.A.).

Figure 2. Measured section of the Community Pit Formation. Beds are numbered. The fossiliferous site discussed in this paper is indicated as NMMNH locality 7981.

Figure 3. Fossiliferous, limestone filled channel. A., Eastern margin of channel. Channel base is indicated by arrows. The main fossil excavation was carried out at the eastern channel margin; B., Excavation at site A (Fig. 4) to show the nature of the mid-channel lithology, a dense, micritic limestone. Geological hammer for scale; C., Exposure of mid-channel micritic limestone in western portion of channel. White arrow indicated a calcified tree trunk. Scale increments 1 foot (30.5 cm).

Figure 4. Geology of the limestone-filled channel in the Community Pit Formation at NMMNH locality 7891, showing correlated measured sections through channel. Solid lines demarcate correlatable surfaces. Surface 1 is the base of the channel. Surface two separates the middle-channel fill, containing the voltzian conifer-callipterid flora, from the upper channel fill, which is devoid of plant macrofossils. Surface 3 marks the top of the channel fill.

Figure 5. Common limestone microfacies of the middle channel-fill limestone. Thin section photographs all under plane light. A., Fine-grained calcareous sandstone containing few foraminiferans; B., Calcareous siltstone with rare formaniferans; C., Indistinctly laminated calcareous siltstone containing sponge spicules; D., Calcareous siltstone with

rare foraminiferans (a particularly conspicuous example can be seen in the center of the slide). Scale bars = 0.5 mm.

Figure 6. Adpressed conifer foliar morphotypes, and an ovuliferous cone and dwarf shoot of a voltzan conifer in Plant Assemblage 2; A., Ultimate shoot of Morphotype A, scale: 10 mm, NMMNH P68185; B., A branch system of Morphotype B with three orders of branching, scale: 10 mm, NMMNH P68186; C., Part of a shoot of Morphotype C (Specimen in right hand corner), scale: 10 mm, NMMNH P68187; D., A branch system of Morphotype D with two orders of branching, scale: 5 mm, NMMNH P68188; E., Mature ovuliferous cone with bract–dwarf shoot complexes helically arranged around axis, scale: 5 mm, NMMNH P68189; F, Flattened dwarf shoot with partly fused base, and six obtuse scales, scale: 10 mm, NMMNH P68190.

Figure 7. Adpressed callipterids, voltzian conifers and sphenopsids in Plant Assemblage 2; A., Callipterid, *Lodevia oxydata*, showing unfolding frond, scale: 25 mm, NMMNH P68191; B., Callipterid, *Lodevia oxydata*, showing typical mature foliage, scale: 10 mm, NMMNH P68192; C., Swollen base (possible abscission surface) of callipterid, *Lodevia oxydata*, scale: 10 mm, NMMNH P68193; D., Callipterid, *Lodevia oxydata*, showing desiccated appearance with curled tips to pinnules, scale: 10 mm, NMMNH P68194; E., Callipterid, *Lodevia oxydata*, showing immature foilage, scale: 10 mm, NMMNH P68195; F., Sphenopsid, *Annularia spicata*, scale: 4 mm, NMMNH P68196; G., Walchian foliage, scale: 5 mm, NMMNH P68197; H., Fine network of branching gymnosperm roots, of probable callipterid affinity, scale: 10 mm, NMMNH P68198.

TABLE CAPTIONS

Table 1. Stable and radiogenic isotope compositions of the Community Pit Fm.

Table ~~1~~2. Quantitative quadrat data for adpressed megafloral assemblages (Plant Assemblage #2) in the middle unit of the incised channel (using methodology of Pfefferkorn et al., 1975).

Figure 1 Map Flood

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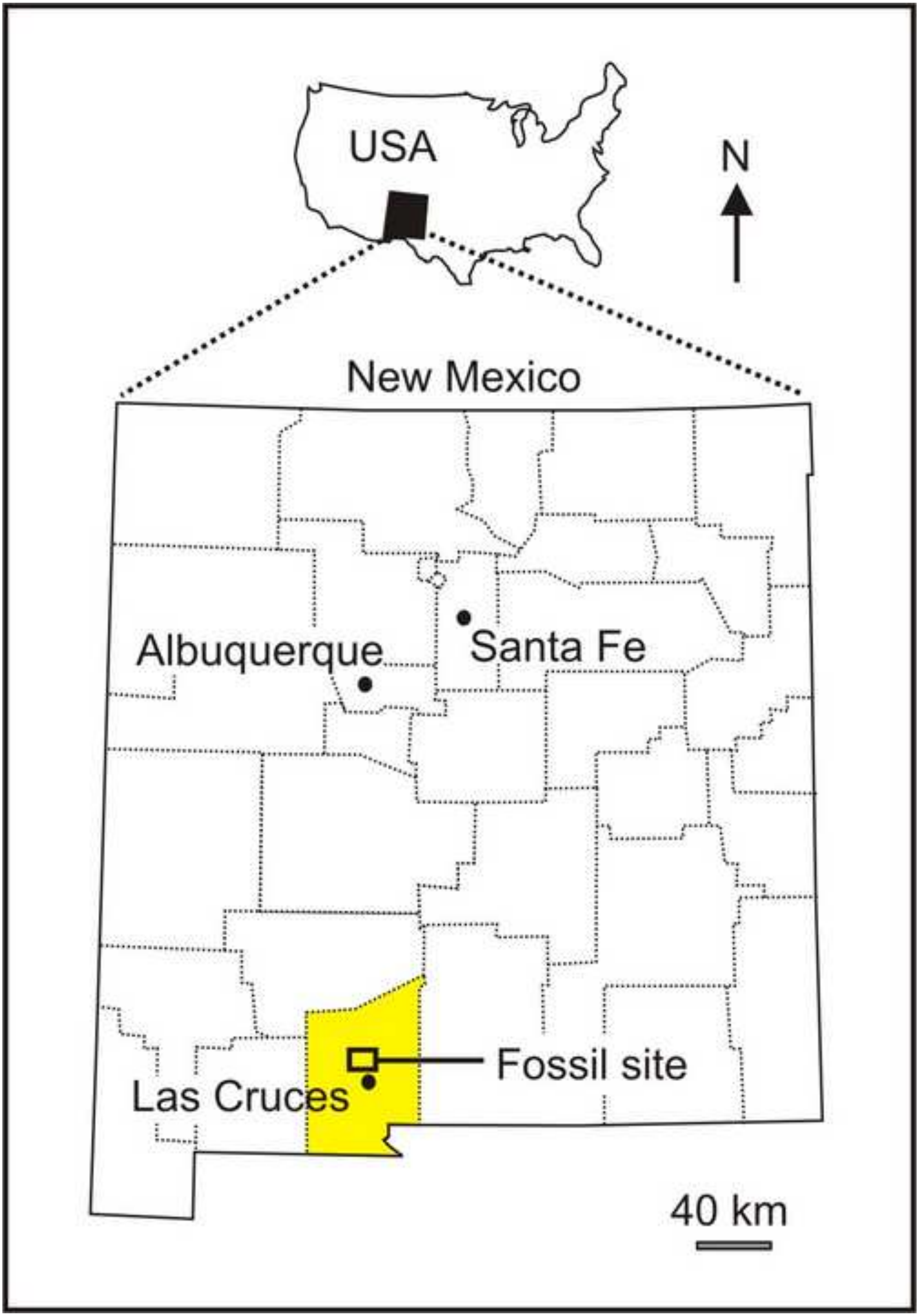

Figure 2 Geology Flood

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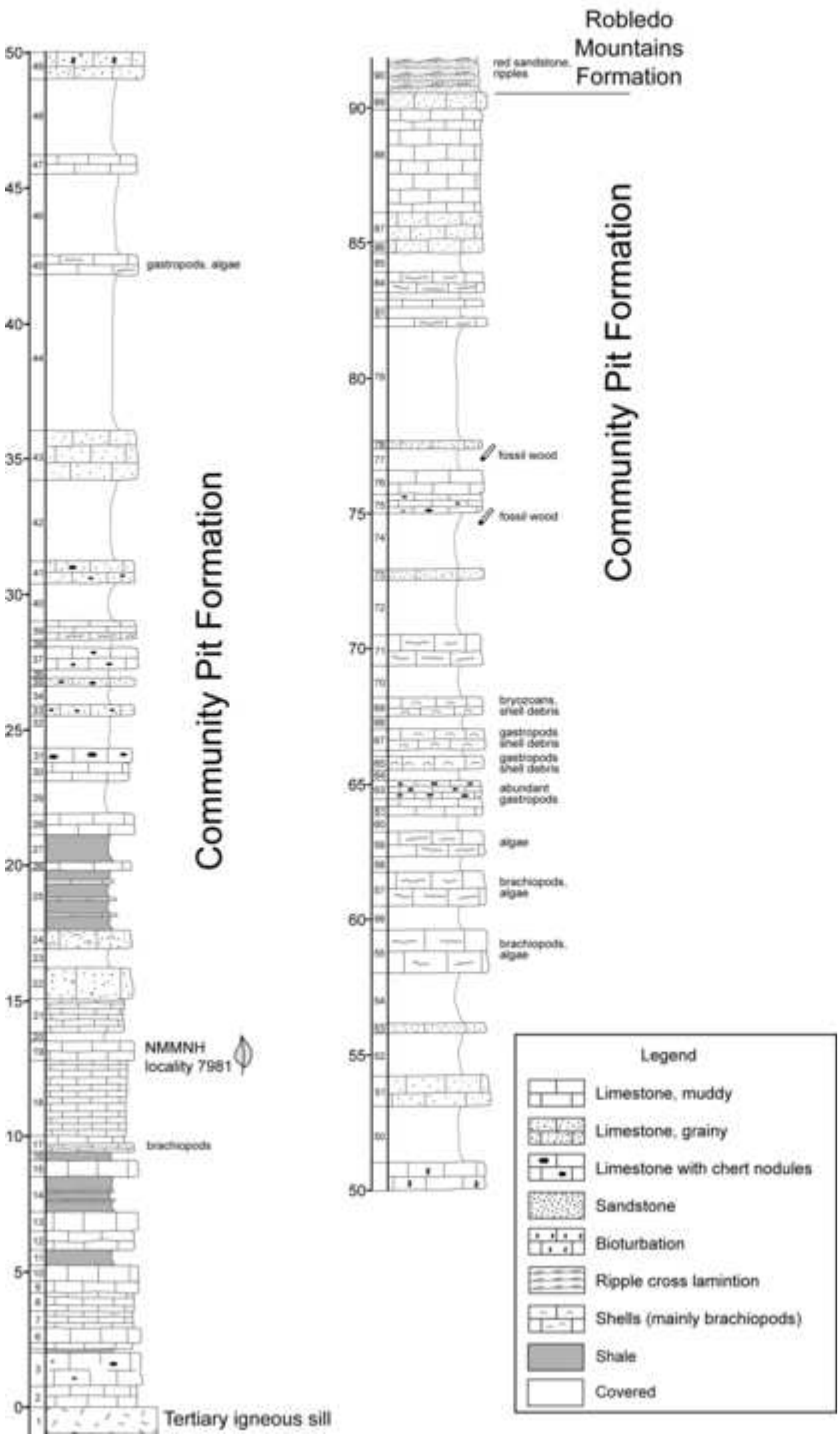

Figure 3 Channel Outcrop Flood
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Figure 4 Sections Across Channel Flood

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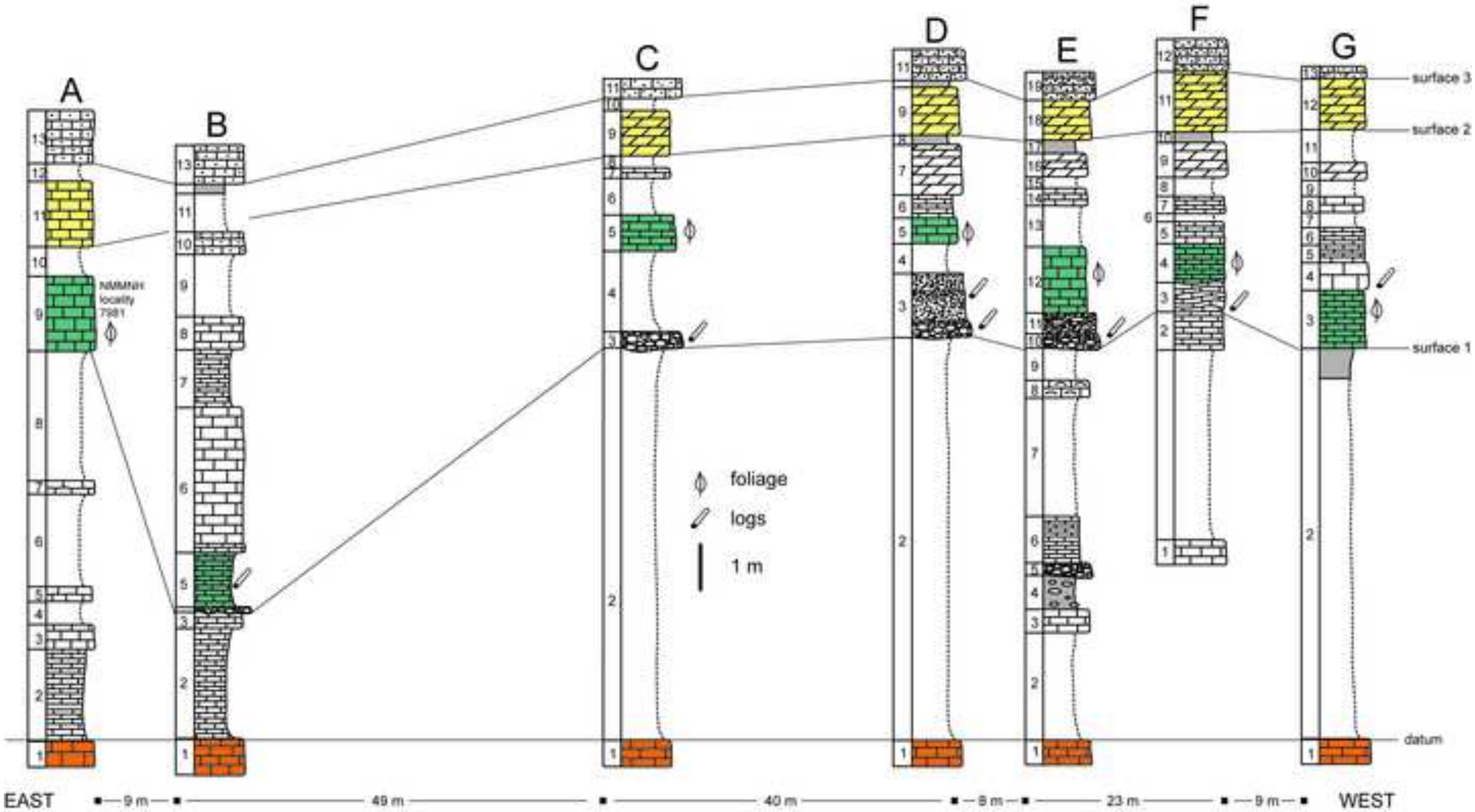

Figure 5 Microfacies Flood

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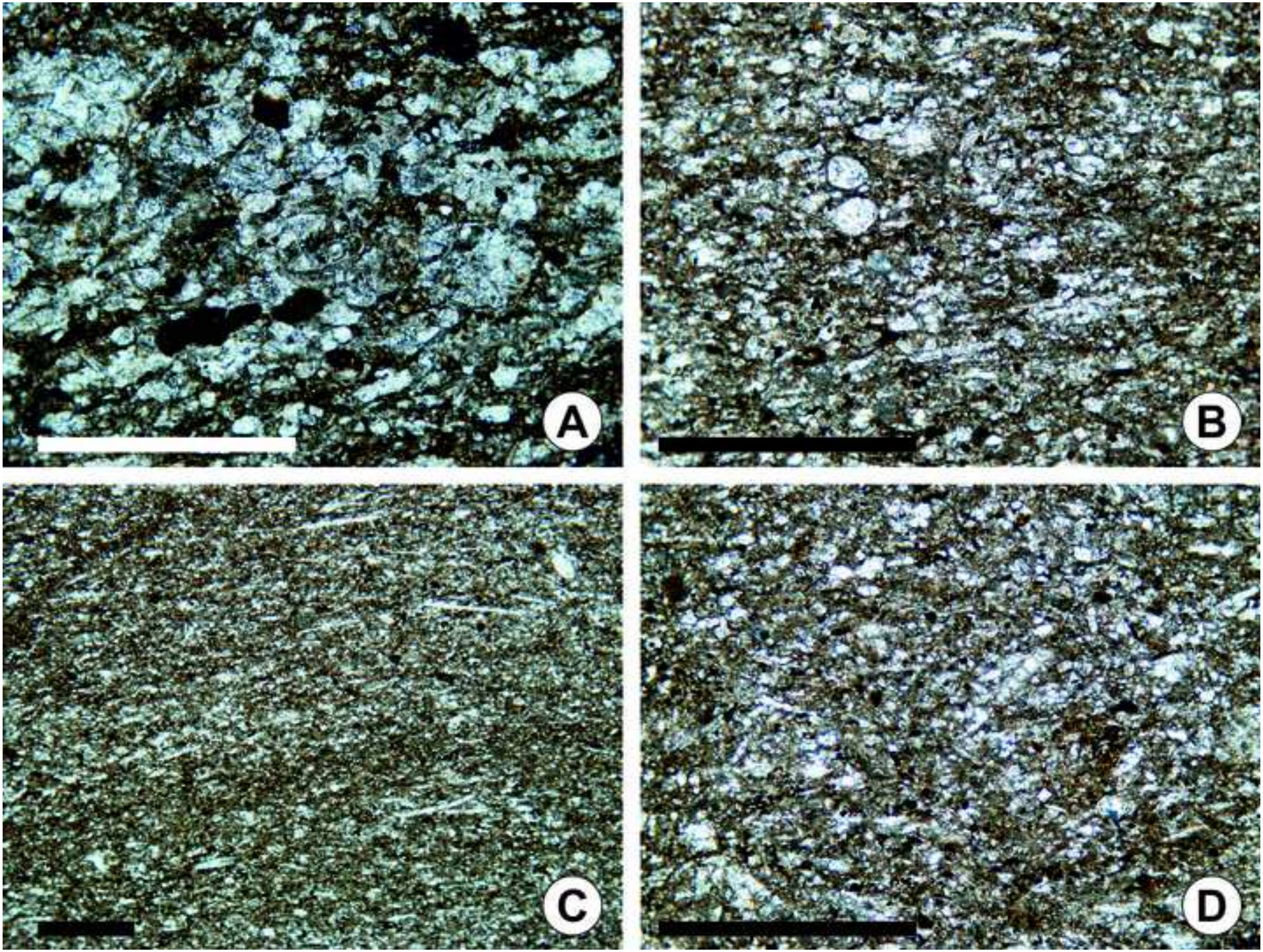

Figure 6 Conifers Flood

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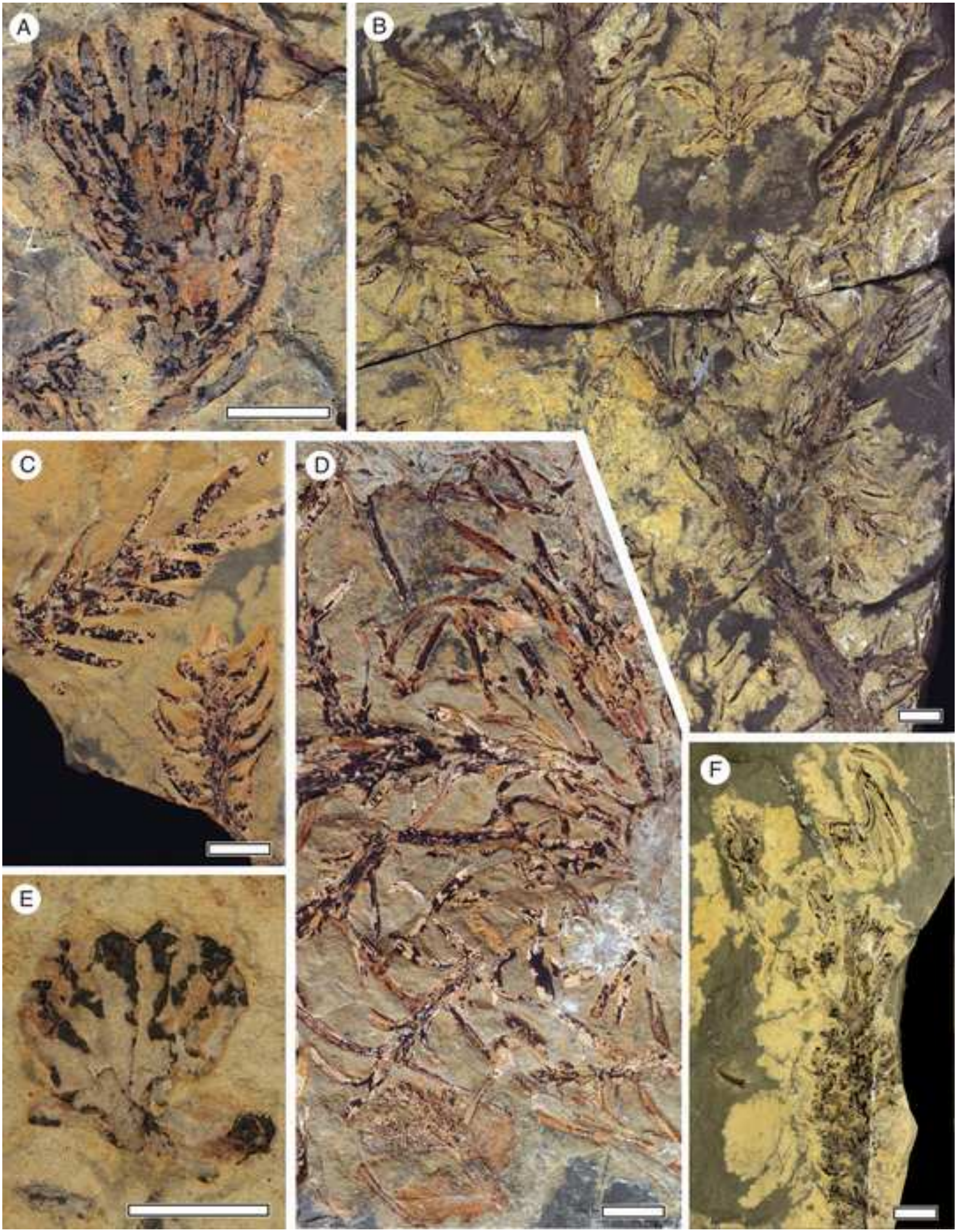

Figure 7 Lodevia Others Flood

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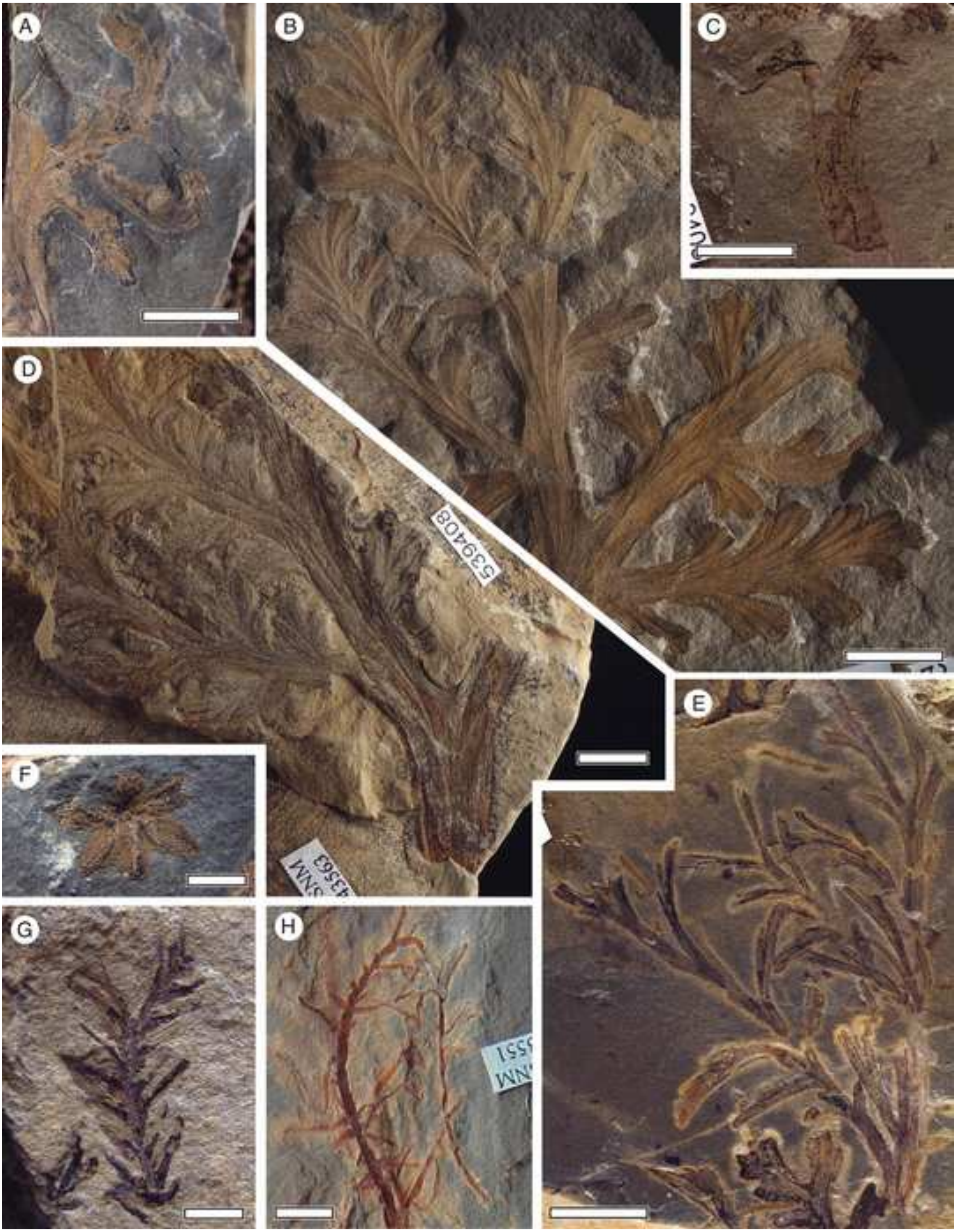

Table 1 Isotopes
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Table 1. Stable and radiogenic isotope compositions of the Community Pit Fm.

Sample	d^{13}C (‰)	d^{18}O (‰)	^{87}Sr/^{86}Sr
SGL-09-136A	1.22	-2.72	0.708562
laminated lime mudstone	1.41	-2.49	0.70858
	1.21	-2.73	
	1.36	-2.41	
Sample Average (± 1 s)	**1.30 (±0.09)**	**-2.59 (±0.14)**	**0.708571**
SGL-09-136B	0.94	-3.66	
siliciclastic lime mudstone	0.95	-3.34	
	0.81	-3.00	
	0.85	-3.18	
	1.22	-3.24	
	0.98	-3.14	
Sample Average (± 1 s)	**0.96 (±0.16)**	**-3.14 (±0.09)**	
Overall Average	**1.09**	**-2.99**	—
2 Std Err (n=10)	**0.13**	**0.24**	—

Table 2 Megafloral data

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	Sites with numerous specimens				Sites with few specimens					
Section	C	E	Random 1	**Tot./Mean**	A	B	Random 2	Random 3	Random 4	**Tot./Mean**
NMMNHS collection	NM2010-05	NM2010-01	SGL09-136	**n/a**	NM2010-03	NM2010-02	NM2010-14	n/a	n/a	**n/a**
USNM locality	43554	43550	n/a	**n/a**	43552	43551	43563	n/a	43553	**n/a**
Quadrats (number)	27	50	37	**114**	7	8	19	6	1	**41**
Voltzian conifer	17	30	31	**78**	0	4	8	5	1	**18**
Frequency (%)	63	60	83.8	**68.9**	0	50	42.1	83.3	100	**55.08**
Lodevia oxydata	3	19	12	**34**	5	3	9	1	0	**18**
Frequency (%)	11.1	38	32.4	**27.2**	71	37.5	47.3	16.7	0	**34.5**
Axes	5	6	2	**13**	1	1	4	0	0	**6**
Roots	3	4	5	**12**	2	2	0	0	0	**4**
Seeds	4	1	1	**6**	0	0	0	1	0	**1**
Walchian conifer	3	1	2	**6**	1	0	1	0	0	**2**
cf. Autunia	0	2	0	**2**	0	0	1	0	0	**1**
Annularia spicata	0	1	0	**1**	0	0	0	0	0	**0**
Sphenopteris sp.	0	1	0	**1**	0	0	0	0	0	**0**
Pterinopectinid bivalve	1	2	0	**3**	0	0	0	0	0	**0**
Lingulid brachiopod	1	0	0	**1**	0	0	0	0	0	**0**