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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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DiMichele; Cindy Looy, Ph.D.

**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.

UNIVERSITY OF CALIFORNIA, BERKELEY

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SANTA BARBARA • SANTA CRUZ

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DEPARTMENT OF INTEGRATIVE BIOLOGY  
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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,

A handwritten signature in black ink, appearing to read "Cindy Looy".

Cindy Looy

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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-raided 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

1 **Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial**

2 **Pangaea: Paleoecology and evolutionary significance**

3

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5 Daniel Vachard<sup>6</sup>, Dan S. Chaney<sup>7</sup>, Scott D. Elrick<sup>8</sup>, Dori L. Contreras<sup>9</sup>, Francine Kurzawe<sup>1</sup>,

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## 24 **Abstract**

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



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

50

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

52

### 53 **1. Introduction**

54 During the early Permian, the Earth went through a transition from a globally cool to  
55 warm climate (Montañez et al., 2007; Tabor and Poulsen, 2008; Montañez and Poulsen, 2013),  
56 which resulted in prominent vegetational changes. Based on a global dataset, Rees et al. (2002)  
57 recognized four distinctly different floral realms during early Permian (Sakmarian) time: (1) a  
58 Gondwanan realm characterized by glossopterids in temperate regions of the Southern  
59 Hemisphere (Cúneo, 1996; Tewari et al., 2012); (2) a Euramerican realm characterized by  
60 walchian conifers, peltasperms and ferns in a seasonally dry tropical setting (Kerp et al., 1990;  
61 Zeigler et al., 2002); (3) a Cathaysian realm characterized by lycopsids, sphenopsids and ferns in  
62 the humid tropical islands bordering the western Tethys (Hilton and Cleal, 2007; Wang et al.,  
63 2012); and (4) a poorly resolved Angaran realm characterized by cordaitaleans in Northern  
64 Hemisphere temperate mid-latitudes (Meyen, 1982, 1988; Gomankov, 2009). Transitional  
65 vegetation also has been identified at the boundaries of these realms (Broutin et al., 1998;  
66 Berthelin et al., 2003; LePage et al., 2003). This global floral realm architecture had much earlier  
67 origins in the Carboniferous (Chaloner and Meyen, 1973), though the lycopsid-rich wetland  
68 biome, so typical of the Carboniferous Euramerican equatorial regions, was almost completely  
69 absent there by the early Permian (e.g., Kerp and Fichter, 1985; Kerp, 1996; DiMichele et al.,

70 2009; Opluštil et al., 2013; Tabor et al., 2013) and survived in Cathaysia (Hilton and Cleal, 2007;  
71 Wang et al., 2012; Wang and Pfefferkorn, 2013).

72 The Euramerican floral realm, of which the flora reported here is a part, is the best known  
73 of the Permian seasonally dry vegetation types. Assemblages have been described from the  
74 southwestern U.S.A., eastern U.S.A., eastern Canada, North Africa, western Europe, and the  
75 Ukraine (e.g., Florin, 1938-1945; Doubinger, 1956; Kerp et al., 1990; Kerp, 1996; Broutin et al.,  
76 1998; Blake et al., 2002; Zeigler et al., 2002; DiMichele et al., 2007; Galtier and Broutin, 2008;  
77 Blake and Gillespie, 2011; Rößler et al., 2012; Tabor et al., 2013), all of which lay within 10  
78 degrees of the paleoequator (Rees et al., 2002). According to Zeigler et al. (2002), the so-called  
79 walchian conifers are the most characteristic, abundant and widespread plants in this early  
80 Permian seasonal tropical vegetation.

81 Walchian conifers (walchian *Voltziales sensu* Rothwell et al., 2005) were the earliest  
82 conifers to appear in the fossil record and were characterized by a plagiotropic branching pattern  
83 and narrow, triangular to linear, needle-like leaves (e.g., Hernandez-Castillo et al. 2003;  
84 Rothwell et al., 2005). Their ovulate ovuliferous dwarf shoots were organized in cones or fertile  
85 zones. Walchian dwarf shoots had numerous sterile scales interspersed with a few sporophylls,  
86 which showed at least some indication of radial symmetry. Distinctly different and evolutionarily  
87 more derived are the voltzian conifers or voltzian *Voltziales (sensu* Rothwell et al., 2005). They  
88 were trees with an irregular branching pattern (orthotropic) and bifacial ovate, lanceolate to  
89 linear medium-sized leaves (e.g., Clement-Westerhof, 1988; Rothwell et al., 2005). Just like the  
90 walchian conifers, these conifers also produced ovuliferous cones or fertile zones. The sterile  
91 scales and sporophylls in their ovuliferous dwarf shoots, however, were partly to completely  
92 fused, and the whole structure was bilaterally symmetrical and more or less flattened in one

93 plane (e.g., Clement-Westerhof, 1987; Looy and Stevenson, 2014). During the Permian, both of  
94 these groups are largely confined to the Euramerican floral realm, although there are reports of  
95 walchian Voltziales from transitional assemblages (Cathaysia: Liu and Yao, 2013; possibly  
96 Angara: LePage et al., 2003).

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

113         This flora from the middle portions of the channel fill differs entirely from  
114 contemporaneous early Permian western Pangean floras preserved in the Abo Formation and its  
115 equivalents (Hunt, 1983; DiMichele et al, 2013a). These floras are known from coastal plain,

116 siliciclastic red-bed deposits, which crop out widely from the northern to the southernmost parts  
117 of New Mexico, through the central part of the state (Lucas et al., 2013), including in the  
118 Robledo Mountains (Mack et al., 2010; Voigt et al., 2013). They are dominated by walchian  
119 conifers, with local occurrences of the peltasperm *Supaia thinnfeldioides* (DiMichele et al., 2007,  
120 2012), rare callipterid peltasperms and isolated occurrences of other taxa more common in  
121 assemblages from other Permian equatorial regions (Kerp and Fichter, 1985; Galtier and Broutin,  
122 2008; Opluštil et al., 2013; Tabor et al., 2013).

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

129

## 130 **2. Geological context**

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

139 paleontological collections at the NMMNHS as collecting localities NMMNH 3016 and 7981  
140 (these are NMNH localities USNM 43550–43554 and 43563).

141

## 142 *2.1. Stratigraphy and age*

143         The fossil plant assemblages, discussed herein, occur in the lower Permian Hueco Group,  
144 which comprises, from base to top, the Shalem Colony, Community Pit, Robledo Mountains, and  
145 Apache Dam formations (Kottlowski, 1960; Mack and James, 1986; Lucas et al., 1998a, b;  
146 Krainer et al., 2003, 2009; Voigt et al., 2013). The fossils are from 10–15 m above the base of  
147 the local section of the approximately 91-m-thick Community Pit Formation, which means they  
148 are from the lower part of the formation (Figure 2). Based on the current state of our knowledge,  
149 summarized below, the age of the fossil plant assemblage in the lowermost Community Pit  
150 Formation of PTNM is late Asselian. It is bracketed by earliest Asselian fusulinids in the  
151 underlying Shalem Colony Formation and is positioned ca. 40 m below a bed containing (?)latest  
152 Asselian fusulinids in the middle part of the Community Pit Formation, and Sakmarian–early  
153 Artinskian strata in the middle to upper part of the Community Pit Formation (Krainer et al.,  
154 2009; Voigt et al., 2013; Falcon-Lang et al., 2014).

155

### 156 *2.1.1. Biostratigraphic findings*

157         Below the plant-bearing beds, immediately below the Community Pit Formation,  
158 fusulinids and smaller foraminifers are found in the Shalem Colony Formation. These  
159 foraminifers indicate, in regional terminology, an early Wolfcampian age (Needham, 1937;  
160 Lucas et al., 2002; Krainer et al., 2009). On the international time scale, this falls somewhere

161 within the latest Gzhelian–earliest Asselian interval, i.e., the Carboniferous-Permian boundary  
162 (Henderson et al., 2012a).

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

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

183 al., 2013), which suggests that the correlative Community Pit Formation may be, in its  
184 uppermost part, of early Artinskian age.

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

194

## 195 2.2. *General paleoenvironmental interpretation*

196 The Community Pit Formation is a mixed siliclastic-carbonate unit, containing variably  
197 fossiliferous beds of dolomudstone, lime mudstones and wackestones, and siliciclastic shale  
198 (Figure 2; Krainer et al., 2003, 2009; Mack et al., 2013). It was deposited in a shallow marine to  
199 supratidal setting (the Hueco Seaway) on the western margin of the intracratonic Orogrande  
200 Basin (Lucas et al., 1998a, b; Voigt et al., 2013) at a paleolatitude of about 2°N (Tabor et al.,  
201 2008). Elsewhere in Doña Ana County, the unit contains a somewhat restricted marine fauna,  
202 and red/green-mottled caliche paleosols are developed at a few intervals (Krainer et al., 2003,  
203 2009; Lucas et al., 2002; Mack et al., 2010). Fifty kilometers north of Doña Ana County, this  
204 same stratigraphic interval comprises only red bed alluvial facies of the Abo Formation  
205 (DiMichele et al., 2007; Lucas et al., 2012). Therefore, during the Early Permian the location of

206 the PTNM lay close to the fluctuating Hueco Seaway coastline (Mack and James, 1986), with  
207 alluvial plains to the north (Lucas et al., 2012).

208         In a PTNM section that largely comprises the Community Pit Formation, Mack et al.  
209 (2013) identified six supratidal and shallow marine facies. They compared the overall  
210 paleoenvironment with semi-arid portions of the present-day Trucial Coast of Abu Dhabi,  
211 highlighting the presence of gypsum. This interpretation of climate as semi-arid is consistent  
212 with regional studies of paleosols (Mack, 2003; Tabor et al., 2008; Mack et al., 2010). However,  
213 the remains of large fossil trees, which would have required a good water supply, occur at  
214 several intervals in the formation (Tidwell and Munzing, 1995; Falcon-Lang et al., 2014). There  
215 are three possibilities to explain this apparent inconsistency: (1) Regional climate was, in fact,  
216 semi-arid to arid, but there were localized poorly drained, groundwater-dependent habitats dotted  
217 across the landscape (cf. DiMichele et al., 2006), where arborescent vegetation could flourish  
218 despite the aridity. (2) Regional climate was overall somewhat wetter, allowing the geographic  
219 co-occurrence of minor evaporites with large trees, as seen, for example in the present-day  
220 southern Mediterranean region (cf. Francis, 1984). (3) Regional climate oscillated between  
221 wetter and drier phases, the large trees being associated with the former climate states and the  
222 evaporites with the latter (cf. Parrish and Falcon-Lang, 2007).

223

### 224 **3. Paleoenvironment of the fossil site**

225         The fossil site, reported here, occurs within a 5-6 m deep channel cut into a succession of  
226 shale, limestone and dolomite at NMMNH locality 7981 (Figure 3A). The channel cuts down  
227 from a horizon c. 15.5 m above the base of the Community Pit Formation section (Figure 2, 3A).  
228 Measured on an east-west outcrop, sub-perpendicular to the channel axis, the apparent channel



229 width is about 140 m (Figure 4). The eastern channel margin appears steeper than the western  
230 margin, but this may be an artifact of outcrop orientation. In addition, the western margin is  
231 truncated by a fault. Seven sections (A - G) were measured across the channel (Figure 4). Three  
232 distinct units fill the channel; the lower two contain fossil-plant assemblages of different kinds.

233

### 234 *3.1. Lower unit*

235 The basal unit, which occurs only in the central part of the channel (Figure 4, sections B-  
236 E), comprises a lens of limestone pebble-to-cobble conglomerate, 0.05-1.1 m thick, and contains  
237 Plant Assemblage 1. This rudstone is dominated by sub-angular to sub-rounded, elongate clasts  
238 of gray-orange lime mudstone, 20-150 mm long, and accumulations of detrital crinoids and  
239 bryozoans (locally comprising multiple, cemented, randomly arranged fossil fragments, clearly  
240 reworked from underlying beds), within a poorly sorted matrix of medium- to coarse-grained  
241 mixed carbonate-siliciclastic sandstone and mudstone. Specimens of coalified tree-trunks, up to  
242 0.17 m diameter, co-occur with cubic, sub-rounded, 20-50 mm diameter blocks of charcoaled  
243 wood (Plant Assemblage 1) in the basal rudstone.

244

### 245 *3.2. Middle unit*

246 The middle unit, up to 4 m thick, is more laterally extensive, and extends beyond the  
247 margins of the underlying conglomeratic lag, which is confined to the central, basal portion of the  
248 channel. Lime mudstone beds, up to 1.4 m thick, with undulatory or wavy lamination are the  
249 most prominent macroscopic feature of this unit (Figure 3B, C). In thin section, these beds are  
250 planar laminated, partly bioturbated lime mudstone with minor low-angle scours filled with  
251 slightly coarser grained carbonate material. They also include calcareous siltstones with rare thin

252 layers of very fine-grained sandstone (~ 5 to 10%), composed of quartz and subordinate feldspar  
253 silt-size detrital grains, some of which appear to be wind-blown (Figure 5). The silt- and sand-  
254 sized layers contain abundant recrystallized carbonate skeletons and small amounts of detrital  
255 dolomite (Figure 5). Most common are hollow, needle-like skeletons ~30 to 60  $\mu\text{m}$  in diameter  
256 and up to 0.5 mm long, which are recrystallized sponge spicules (Figure 5C), oriented parallel to  
257 bedding planes. There also are subordinate ostracodes and smaller foraminifers (*Tuberitina*,  
258 *Syzrania?*, and nodosinelloid forms) (Figure 5D) and probably other, completely recrystallized  
259 fragments that cannot be identified. Non-skeletal grains are small peloids (Figure 5A). The silt-  
260 sized and sand-sized material indicates transport by weak currents and deposition in a shallow,  
261 restricted environment.

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

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

274

275 *3.3. Upper unit*

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

279

280 *3.4. Paleoenvironmental interpretation*

281 There are several possible explanations for the incision of the fossil-bearing channel and  
282 its subsequent filling, primarily with carbonate, which must be treated as temporally independent  
283 phenomena. The occurrence of an incised channel system, albeit unique in the region,  
284 necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine  
285 shelf and to cause channel incision. Most incised features of this nature have been recognized in  
286 non-marine, siliciclastic depositional settings; however, a few examples have been reported in  
287 carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003).  
288 The term “incised channel” (rather than incised valley) is the most appropriate descriptor for the  
289 feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and  
290 5-6 m deep) with a low aspect ratio (about 25:1).

291 There are several possible causes of base-level change. Eustatic lowering of sea-level is,  
292 perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation  
293 may have been deposited sometime during one of several intervals of inferred Permian southern  
294 hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al.,  
295 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event,  
296 resulting in a global lowering of sea level, additional evidence of incision in the area might be  
297 expected at this same horizon, which is widely traceable within the mostly carbonate portion of

298 the Community Pit Formation. However, such evidence has not been found by us or reported  
299 elsewhere.

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

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

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

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

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

335           Above this basal lag, lime mudstones formed under brackish to nearly marine salinities,  
336 with strong suggestions of periods of standing or sluggishly moving water. The salinity and  
337 carbonate accretion are most likely reflective of base-level rise and the invasion of the channel  
338 by marine waters, mixed to some small degree with continued freshwater runoff from the  
339 surrounding terrestrial landscape. A change from a sub-humid to a semi-arid climate is indicated.  
340 However, it is likely that water cover was maintained most of the time, given evidence of  
341 syndepositional occupation of surfaces within the channel by vascular plants and the

342 incorporation of plant remains into the limestone matrix, which consisted of actively  
343 forming/accumulating carbonate muds.

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

352

#### 353 **4. Isotopic analyses of the middle unit**

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

357

##### 358 *4.1. Methodology*

359         Thick sections (~200  $\mu\text{m}$  thick) of two hand samples from the middle unit were studied  
360 petrographically under transmitted light and cathodoluminescence in order to identify calcite  
361 fabrics and textures. Thick sections of the two samples were microdrilled for stable ( $50 \mu\text{g} \pm 10$   
362  $\mu\text{g}$  samples) and radiogenic isotope (0.5 gm) analysis using a Merchantek automated  
363 microdrilling system.

364         Samples (n=10) for stable isotope analysis were roasted at 375° C under vacuum for 30

365 minutes to remove organics and subsequently reacted in 105% phosphoric acid at 90° C in either  
366 a common acid bath on a GVI Optima Stable Isotope Ratio Mass Spectrometer (SIRMS) or a  
367 Gilson Multicarb Autosampler system (individual acid injection vials) interfaced with an  
368 Elementar Isoprime Mass Spectrometer housed in the UC Davis Stable Isotope Laboratory. CO<sub>2</sub>  
369 gas was analyzed in dual inlet mode and values were corrected using the Craig correction to  
370 account for the <sup>17</sup>O contribution (Craig, 1957) and to an internal standard and reported relative to  
371 the Vienna Pee Dee Belemnite (VPDB). Both systems provide  $\delta^{13}\text{C}$  precision of  $\pm 0.04\text{‰}$  and  
372  $\delta^{18}\text{O}$  precision of  $\pm 0.06\text{‰}$ .

373         Microdrilled samples (n=2) for strontium isotope analyses were prewashed with 1 M  
374 ammonium acetate in order to remove Sr associated with absorbed (on clays) or included  
375 noncarbonate phases (Montañez et al., 2000). Strontium was isolated using Spex cation ex-  
376 change resin and microliter columns attached to a channel pump. <sup>87</sup>Sr/<sup>86</sup>Sr ratios were measured  
377 in solution mode on a Nu MC-ICPMS in the Interdisciplinary Center for Plasma Mass  
378 Spectrometry, UC Davis. Values are typically normalized to a nominal value for NIST standard  
379 SRM987 of 0.710249. SRM987 for the measurement period averaged 0.710249 (2 $\sigma$  =  
380 0.000035) based on standards analyzed during this period.

381

## 382 *4.2. Results*

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

385

## 386 *4.3. Paleosalinity interpretation*

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

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



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

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

421

## 422 **5. Plant Assemblages**

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

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

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

448                   The flora comprises adpressed megafloral remains and a few weakly calcified tree-trunks  
449 are preserved in micritic limestone. Adpressed megafloral remains are present at multiple levels  
450 (Figure 3B, C) in discontinuous limestone lenses, each up to 30–50 mm thick and traceable for  
451 several meters along strike. Within these lenses, there are variable concentrations of randomly  
452 oriented plant fragments, ranging from comminuted plant debris to fragments 10–30 cm in  
453 breadth (however, we note that this is a minimum size estimate because it is difficult to obtain  
454 large slabs of material). Identifiable material comprises three-dimensionally preserved

455 adpressions and partially cutinized leaves. Associated with these foliar remains, there are also  
456 open-to-somewhat-denser networks of roots of variable diameter, which crosscut laminations and  
457 are in growth position.

458

### 459 *5.1. Material and methods*

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

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

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

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

481

## 482 5.2. *Voltzian conifers*

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

489 Morphotype A is represented by five isolated shoots (Figure 6A), two of which have the ultimate  
490 tips of the branch preserved. Leaves are bifacially flattened (cf. Type II leaves; de Laubenfels,  
491 1953), and are oblong in shape with obtuse apices. Leaf widths (W) range from 2 to 3.5 mm.  
492 Leaf lengths (L) are difficult to measure, due to overlap among them, and are at least 20 - 25  
493 mm. L:W ratios range from 7 to 11, calculated on a per leaf basis. Leaves depart from the stem at  
494 angles from 15 to 40°, and are straight to slightly incurved when viewed in profile. Leaves are  
495 highly imbricate, particularly on the branch tips, resulting in a distinct "tufted" appearance.  
496 Details of the leaf attachment and axis diameter are obscured by overlapping leaves.

497 Morphotype B is represented by four isolated shoots, and three other specimens  
498 preserving two or three orders of branching (Figure 6B). Branching is orthotropic, with higher  
499 order branches occurring in the axils of persistent leaves at angles of 55°. Leaves are tetragonal  
500 in cross section (Type I leaves: de Laubenfels, 1953), and attached helically to the stem by

501 thickened cushions that are distinctly rhomboidal in shape (Figure 6B). Leaves taper slightly  
502 from the point of attachment to obtuse apices. Leaf length is 15 - 30 mm, and leaf width reduces  
503 from 2.5 - 3.5 mm at the point of attachment to about 2 - 2.5 mm mid-leaf (L:W ratios: 6 - 9).  
504 The angle of leaf departure from the stem axis is variable (average 55°), with the leaves mostly  
505 straight in side profile, but occasionally slightly incurved. Leaves on thicker branches depart at  
506 the higher angles, and are more reflexed in profile.

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

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

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

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

535         Late Paleozoic conifer classification is based on a combination of morphology and  
536 internal and cuticular anatomy of stems, leaves, pollen cones, and ovuliferous structures (such as  
537 ovuliferous cones and fertile zones) (e.g., Clement-Westerhof, 1984, 1987, 1988; Rothwell et al.,  
538 1997, 2005). Several features of the novel conifer material reported here allow it to be referred to  
539 voltzian conifers. First, their foliar morphotypes show generally bifacial ovate, lanceolate to  
540 linear medium-sized leaves, which are characteristic of voltzians. Second, foliar morphotypes B  
541 and D show orthotrophic branching, also characteristic of voltzians, but distinct from the  
542 plagiotrophic walchians (Rothwell et al., 2005). Third, the sterile scales and sporophylls in the  
543 dwarf-shoots are fused, more or less flattened in one plane, and show a bilaterally symmetrical  
544 organization. At this point in time, it is uncertain how many taxa these four leaf morphotypes  
545 represent. Heterophylly does occur in voltzian conifers, and generally involves differences in leaf  
546 size, shape in face view, and apex shape. Voltzians are, however, relatively consistent in leaf

547 characters like mode of attachment, features of leaf bases and shape in cross-section.  
548 Morphotypes B and C might represent a single taxon, but we have no confirmatory evidence for  
549 that, such as attachment to a common branch. The leaves of morphotypes A and D are both  
550 bilaterally flattened, but arise at different angles, and have different kinds of attachment.  
551 Collection of further material is required to answer this question. More material is also needed to  
552 ensure that we have collected the full range of the diversity of conifer foliage in this flora.

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

558

### 559 5.3 *Callipterid foliage* – *Lodevia oxydata*

560         The other dominant taxon in the flora is an unusual callipterid (occurring in 34 out of 114  
561 quadrats; frequency 29.8 %). The material shows considerable morphological variation and  
562 encompasses immature and mature pinnae (Figure 7A-E). Included among the suite of specimens  
563 are pinnae with remarkably robust axes bearing slightly decurrent, pinnately lobed to segmented,  
564 pinnules. Pinnule lobes typically have blunt tips, particularly those forming the pinnule apex.  
565 The venation is pronounced with an indistinct, sometimes slightly flexuous midvein with widely  
566 spaced, steeply ascending lateral veins inserted at angles of 20-30°; lateral veins fork once or  
567 twice, depending on the segmentation with a single vein per lobe. The suite of specimens shows  
568 a number of noteworthy phenologic features. For example, some fronds show pinnae preserved  
569 in the process of unfolding (Figure 7A), a developmental pattern found in other callipterid taxa

570 (e.g., Kerp, 1988). Still others comprise young, immature pinnules (Figure 7E), and a few  
571 unusual mature specimens exhibit pinnules with irregularly curled edges (Figure 7D). Another  
572 axis has a swollen base (Figure 7C), which usually indicates that complete fronds were abscised.

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

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

584

#### 585 5.4. Roots

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

591 The identity of these roots is unknown, although it is possible to narrow down their  
592 affinities, which are most likely with seed plants. They share some features with pteridospermous



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

604         In consideration of the likely seed plant affinities of the roots, the most important point  
605 they highlight is that rooting of the lime mudstones took place contemporaneously with or very  
606 shortly after the entombment of the aerial remains of conifers and *Lodevia* in this same limey  
607 mud. Because these roots are in and ramify through the limestone, and because of the rate at  
608 which subaerially lime mud hardens and becomes effectively impenetrable to roots, and because  
609 there is no evidence within these beds of brecciation associated with long-term pedogenesis and  
610 development of terra rosa type residual siliciastic soils, it is most likely that the roots were  
611 derived from the voltzian conifers and/or the callipterids, though whether one or both cannot be  
612 determined. The possibility remains, of course, that they were derived from an additional kind of,  
613 most likely, seed plant that left no other macrofossil record. The likely contemporaneity or near  
614 contemporaneity of the aerial debris and roots also suggests that the plants in question were  
615 growing on these limey muds while they were water covered. The combination of physical

616 sedimentological evidence, isotopic values of the lime muds, the brackish-to-marine invertebrate  
617 fauna also present within the sediment, and the necessity for incorporation of aerial debris and  
618 roots into the muds prior to solidification, strongly suggests growth of these plants in waters of  
619 brackish to near-marine salinities.

620

#### 621 5.5. *Other rare taxa*

622 All other taxa are rare and include walchian conifers (*Walchia* sp., n = 7 quadrats) (Figure  
623 7F), some small seeds of indeterminate affinity (n = 7), which may be related to one of the  
624 conifers or pteridosperms, the sphenopsid *Annularia spicata* (Gutbier) Schimper (n = 1; Figure  
625 7F), and a putative fern, cf. *Sphenopteris* (n = 1). A small number of weakly calcified tree-trunks  
626 (up to 0.18 m diameter) associated with the addressed remains comprise pycnoxylic coniferopsid  
627 wood that is too coarsely re-crystallized for more accurate determination.

628

### 629 **6. Discussion**

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

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

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

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

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

659 In addition to being physically unusual, this channel deposit contains an exceptional  
660 flora. That flora includes the earliest known voltzian conifers, extending the range of the lineage  
661 downward from the Kungurian-Roadian boundary to the Asselian-Sakmarian, approximately 25

662 million years. It also includes a rare species of callipterid, *Lodevia oxydata*, now known from  
663 Poland, the Appalachian Basin, and New Mexico, all in deposits of earliest Permian age. Both of  
664 the common plants indicate the existence of vegetation types rarely preserved in the geological  
665 record, or perhaps rarely sampled because of the unlikely nature of the host deposits, despite  
666 what appear to have been long stratigraphic ranges and broad geographic distributions.

667

## 668 6.2. Flora 1: Walchian and other coniferous wood.

669 The earliest vegetation from the PTNM limestone channel deposit for which we have  
670 evidence is preserved as coalified tree-trunks and charcoaled wood fragments in the calcirudite  
671 at the base of the channel (Falcon-Lang et al., 2015). The specimens examined have walchian  
672 conifer affinity. Species that are part of the large complex of walchian Voltziales are by far the  
673 most commonly encountered kinds of conifers in Euramerican fossiliferous deposits of latest  
674 Pennsylvanian and early Permian age (e.g., Kerp and Fichter, 1985; Clement-Westerhof, 1988;  
675 Kerp, 1996; Ziegler et al., 2002; Hernandez-Castillo et al., 2001, 2009; Rothwell et al., 2005;  
676 Looy 2013; Looy and Duijnste, 2013). They are dominant elements in the red siltstones that  
677 make up much of the Community Pit Formation and its more inland equivalent, the Abo  
678 Formation (DiMichele et al., 2007, 2013a), which crops out in a long north-south band on the  
679 margin of the Rio Grande rift and elsewhere, throughout central New Mexico (Lucas et al., 2012,  
680 2013).

681 The source of the walchian logs is most likely from the margins of the channel and  
682 perhaps from the surrounding floodplain, though we detected no paleosol evidence of a lateral,  
683 subaerially exposed surface. These trees are preserved in what is arguably the wettest phase of  
684 channel development, during which there were periodically high flow volumes and little or no

685 carbonate precipitation. The predominance of walchians is consistent with their preservation in  
686 other kinds of Hueco Group (e.g., in the Robledo Mountains Formation, which immediately  
687 overlies the Community Pit Formation) environmental settings, specifically the siliciclastic  
688 redbed siltstones, which also suggest seasonality of moisture under a climate that was at most dry  
689 subhumid. If the drop in sea level in this area is attributed to glacio-eustasy, the trees were  
690 growing at times of near-glacial maximum (Falcon-Lang and DiMichele, 2010).

691

### 692 6.3. *Voltzian-callipterid vegetation*

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

702 It is probable that one or both of the taxa that comprise this flora were growing in contact  
703 with saline water. This assertion is supported by several aspects of the flora, its taphonomy and  
704 the attributes of the deposit itself. The lime mudstones—wackestones in which the plants occur  
705 have only weak bedding and are not brecciated or fractured. Thus, the organic remains had to be  
706 deposited in that substrate while it was both soft and still accumulating. There are large  
707 fragments of branches and leafy shoots among the fossilized plant parts, suggesting limited

708 transport and, thus a local, parautochthonous origin. Preserved cuticle on both conifer and  
709 callipterid foliage indicates rapid burial. The lime muds are rooted, and the roots are clearly *in*  
710 *situ* and transgressed the substrate while it was still soft enough to be penetrated. The shape of  
711 the root masses and the character of the rock matrix suggest that they did not enter along cracks  
712 in already lithified limestone. Roots are not found in the overlying limestone beds, so it can be  
713 assumed that they originated from plants growing on or immediately adjacent to the lime muds  
714 within the channel. However, an origin from one specific plant taxon or the other, or both cannot  
715 be ascertained. The stable and radiogenic isotopic and invertebrate paleontological evidence both  
716 indicate accumulation of the lime muds under brackish-to-marine salinities.

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

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

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

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

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

754

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1131



1132 **FIGURE CAPTIONS**

1133 Figure 1. County map of New Mexico highlighting the location of the PTNM in Doña Ana  
1134 County, where the fossils were obtained (index map: location of New Mexico in the  
1135 U.S.A.).

1136 Figure 2. Measured section of the Community Pit Formation. Beds are numbered. The  
1137 fossiliferous site discussed in this paper is indicated as NMMNH locality 7981.

1138 Figure 3. Fossiliferous, limestone filled channel. A., Eastern margin of channel. Channel base is  
1139 indicated by arrows. The main fossil excavation was carried out at the eastern channel  
1140 margin; B., Excavation at site A (Fig. 4) to show the nature of the mid-channel lithology,  
1141 a dense, micritic limestone. Geological hammer for scale; C., Exposure of mid-channel  
1142 micritic limestone in western portion of channel. White arrow indicated a calcified tree  
1143 trunk. Scale increments 1 foot (30.5 cm).

1144 Figure 4. Geology of the limestone-filled channel in the Community Pit Formation at NMMNH  
1145 locality 7891, showing correlated measured sections through channel. Solid lines  
1146 demarcate correlatable surfaces. Surface 1 is the base of the channel. Surface two  
1147 separates the middle-channel fill, containing the voltzian conifer-callipterid flora, from  
1148 the upper channel fill, which is devoid of plant macrofossils. Surface 3 marks the top of  
1149 the channel fill.

1150 Figure 5. Common limestone microfacies of the middle channel-fill limestone. Thin section  
1151 photographs all under plane light. A., Fine-grained calcareous sandstone containing few  
1152 foraminiferans; B., Calcareous siltstone with rare foraminiferans; C., Indistinctly  
1153 laminated calcareous siltstone containing sponge spicules; D., Calcareous siltstone with

1154 rare foraminiferans (a particularly conspicuous example can be seen in the center of the  
1155 slide). Scale bars = 0.5 mm.

1156 Figure 6. Addressed conifer foliar morphotypes, and an ovuliferous cone and dwarf shoot of a  
1157 voltzan conifer in Plant Assemblage 2; A., Ultimate shoot of Morphotype A, scale: 10  
1158 mm, NMMNH P68185; B., A branch system of Morphotype B with three orders of  
1159 branching, scale: 10 mm, NMMNH P68186; C., Part of a shoot of Morphotype C  
1160 (Specimen in right hand corner), scale: 10 mm, NMMNH P68187; D., A branch system  
1161 of Morphotype D with two orders of branching, scale: 5 mm, NMMNH P68188; E.,  
1162 Mature ovuliferous cone with bract–dwarf shoot complexes helically arranged around  
1163 axis, scale: 5 mm, NMMNH P68189; F, Flattened dwarf shoot with partly fused base, and  
1164 six obtuse scales, scale: 10 mm, NMMNH P68190.

1165 Figure 7. Addressed callipterids, voltzian conifers and sphenopsids in Plant Assemblage 2; A.,  
1166 Callipterid, *Lodevia oxydata*, showing unfolding frond, scale: 25 mm, NMMNH P68191;  
1167 B., Callipterid, *Lodevia oxydata*, showing typical mature foliage, scale: 10 mm, NMMNH  
1168 P68192; C., Swollen base (possible abscission surface) of callipterid, *Lodevia oxydata*,  
1169 scale: 10 mm, NMMNH P68193; D., Callipterid, *Lodevia oxydata*, showing desiccated  
1170 appearance with curled tips to pinnules, scale: 10 mm, NMMNH P68194; E., Callipterid,  
1171 *Lodevia oxydata*, showing immature foilage, scale: 10 mm, NMMNH P68195; F.,  
1172 Sphenopsid, *Annularia spicata*, scale: 4 mm, NMMNH P68196; G., Walchian foliage,  
1173 scale: 5 mm, NMMNH P68197; H., Fine network of branching gymnosperm roots, of  
1174 probable callipterid affinity, scale: 10 mm, NMMNH P68198.

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1176

1177 **TABLE CAPTIONS**

1178

1179 Table 1. Stable and radiogenic isotope compositions of the Community Pit Fm.

1180

1181 Table 2. Quantitative quadrat data for addressed megafloal assemblages (Plant Assemblage 2) in  
1182 the middle unit of the incised channel (using methodology of Pfefferkorn et al., 1975).

1 **Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial**

2 **Pangaea: Paleocology and evolutionary significance**

3

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24 **Abstract**

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

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

51

52 | **Keywords:** Permian, estuary, voltzian conifers, callipterids, mangrove, New Mexico

53

## 54 | 1. Introduction

55 | During the early Permian, the Earth went through a transition from a globally cool to  
56 | warm climate (Montañez et al., 2007; Tabor and Poulsen, 2008; [Montañez and Poulsen, 2013](#)),  
57 | which resulted in prominent vegetational changes. Based on a global dataset, Rees et al. (2002)  
58 | recognized four distinctly different floral realms during early Permian (Sakmarian) time: (1) a  
59 | Gondwanan realm characterized by glossopterids in temperate regions of the Southern  
60 | Hemisphere (Cúneo, 1996; Tewari et al., 2012); (2) a Euramerican realm characterized by  
61 | walchian conifers, peltasperms and ferns in a seasonally dry tropical setting (Kerp et al., 1990;  
62 | Zeigler et al., 2002); (3) a Cathaysian realm characterized by lycopsids, sphenopsids and ferns in  
63 | the humid tropical islands bordering the western Tethys (Hilton and Cleal, 2007; Wang et al.,  
64 | 2012); and (4) a poorly resolved Angaran realm characterized by cordaitaleans in Northern  
65 | Hemisphere temperate mid-latitudes (Meyen, 1982, 1988; Gomankov, 2009). Transitional  
66 | vegetation also has been identified at the boundaries of these realms (Broutin et al., 1998;  
67 | Berthelin et al., 2003; LePage et al., 2003). This global floral realm architecture had much earlier  
68 | origins in the Carboniferous (Chaloner and Meyen, 1973), though the lycopsid-rich wetland  
69 | biome, so typical of the Carboniferous Euramerican equatorial regions, was almost completely

70 | absent there by the early Permian (e.g., Kerp and Fichter, 1985; Kerp, 1996; [DiMichele et al.](#),  
71 | [2009](#); Opluštil et al., 2013; Tabor et al., 2013) and survived in Cathaysia (Hilton and Cleal, 2007;  
72 | Wang et al., 2012; Wang and Pfefferkorn, 2013).

73 |         The Euramerican floral realm, of which the flora reported here is a part, is the best known  
74 | of the Permian seasonally dry vegetation types. Assemblages have been described from the  
75 | southwestern U.S.A., eastern U.S.A., eastern Canada, North Africa, western Europe, and the  
76 | Ukraine (e.g., Florin, 1938-1945; Doubinger, 1956; Kerp et al., 1990; Kerp, 1996; Broutin et al.,  
77 | 1998; Blake et al., 2002; Zeigler et al., 2002; DiMichele et al., 2007; Galtier and Broutin, 2008;  
78 | Blake and Gillespie, 2011; Rößler et al., 2012; Tabor et al., 2013), all of which lay within 10  
79 | degrees of the paleoequator (Rees et al., 2002). According to Zeigler et al. (2002), the so-called  
80 | walchian conifers are the most characteristic, abundant and widespread plants in this early  
81 | Permian seasonal tropical vegetation.

82 |         Walchian conifers (walchian Voltziales *sensu* Rothwell et al., 2005) were the earliest  
83 | conifers to appear in the fossil record and were characterized by a plagiotropic branching pattern  
84 | and narrow, triangular to linear, needle-like leaves (e.g., Hernandez-Castillo et al. 2003;  
85 | Rothwell et al., 2005). Their ovulate ovuliferous dwarf shoots were organized in cones or fertile  
86 | zones. Walchian dwarf shoots had numerous sterile scales interspersed with a few sporophylls,  
87 | which showed at least some indication of radial symmetry. Distinctly different and evolutionarily  
88 | more derived are the voltzian conifers or voltzian Voltziales (*sensu* Rothwell et al., 2005). They  
89 | were trees with an irregular branching pattern (orthotropic) and bifacial ovate, lanceolate to  
90 | linear medium-sized leaves (e.g., Clement-Westerhof, 1988; Rothwell et al., 2005). Just like the  
91 | walchian conifers, these conifers also produced ovuliferous cones or fertile zones. The sterile  
92 | scales and sporophylls in the [ir ovuliferousse](#) dwarf shoots, however, were partly to completely

93 fused, and the whole structure was bilaterally symmetrical and more or less flattened in one  
94 plane (e.g., Clement-Westerhof, 1987; Looy and Stevenson, 2014). [During the Permian, b](#)Both  
95 of these groups are largely confined to the Euramerican floral realm, although there are reports of  
96 walchian Voltziales from transitional assemblages (Cathaysia: ~~[Hernandez-Castillo et al., 2001](#)~~;  
97 [Liu and Yao, 2013](#); possibly Angara: LePage et al., 2003).

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

114 This flora from the middle portions of the channel fill differs entirely from  
115 contemporaneous early Permian western Pangean floras preserved in the Abo Formation and its



116 equivalents (Hunt, 1983; DiMichele et al, 2013a). These floras are known from coastal plain,  
117 siliciclastic red-bed deposits, which crop out widely from the northern to the southernmost parts  
118 of New Mexico, through the central part of the state (Lucas et al., 2013), including in the  
119 Robledo Mountains (Mack et al., 2010; Voigt et al., 2013). They are dominated by walchian  
120 conifers, with local occurrences of the peltasperm *Supaia thinnfeldioides* (DiMichele et al., 2007,  
121 2012), rare callipterid peltasperms and isolated occurrences of other taxa more common in  
122 assemblages from other Permian equatorial regions (Kerp and Fichter, 1985; Galtier and Broutin,  
123 2008; Opluštil et al., 2013; Tabor et al., 2013).

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

130

## 131 **2. Geological context**

### 132 ***2.1 Geological setting***

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

139 | [\(NMNH\), Washington, D.C.](#) Only a few fossil plant assemblages have been previously reported  
140 | from PTNM (Voigt et al., 2013; Falcon-Lang et al., 2014a). The new material described here is  
141 | housed in the paleontological collections at the [NMMNHS New Mexico Museum of Natural](#)  
142 | [History and Science, Albuquerque, New Mexico](#) as collecting localities NMMNH 3016 and 7981  
143 | (these are [National Museum of Natural History-NMNH](#) localities USNM 43550–43554 and  
144 | 43563).

145

## 146 | 2.1. Stratigraphy and age

147 | The fossil plant assemblages, discussed herein, occur in the lower Permian Hueco Group,  
148 | which comprises, from base to top, the Shalem Colony, Community Pit, Robledo Mountains, and  
149 | Apache Dam formations (Kottlowski, 1960; Mack and James, 1986; Lucas et al., 1998a, b;  
150 | Krainer et al., 2003, 2009; Voigt et al., 2013). The fossils are from 10–15 m above the base of  
151 | the local section of the approximately 91-m-thick Community Pit Formation, which means they  
152 | are from the lower part of the formation (Figure 2). Based on the current state of our knowledge,  
153 | summarized below, the age of the fossil plant assemblage in the lowermost Community Pit  
154 | Formation of PTNM is late Asselian. It is bracketed by earliest Asselian fusulinids in the  
155 | underlying Shalem Colony Formation and is positioned ca. 40 m below a bed containing (?)latest  
156 | Asselian fusulinids in the middle part of the Community Pit Formation, and Sakmarian–early  
157 | Artinskian strata in the middle to upper part of the Community Pit Formation (Krainer et al.,  
158 | 2009; Voigt et al., 2013; Falcon-Lang et al., 2014a).

159

### 160 | 2.1.1. Biostratigraphic findings

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

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

181 The foraminifer *Pseudovermiporella* has been identified from the middle and upper part  
182 of the Community Pit Formation elsewhere in Doña Ana County. Based on the First Appearance  
183 Datum (FAD) of this species, Krainer et al. (2009) inferred a Sakmarian age. This assignment

184 was based on correlation with the FAD of this genus in successions of the Carnic Alps of Austria  
185 (Vachard and Krainer, 2001; Krainer et al., 2009). Formerly dated as Sakmarian (Forke, 1995),  
186 this interval is now placed in the early Artinskian based on conodonts and fusulinids (Davydov et  
187 al., 2013), which suggests that the correlative Community Pit Formation may be, in its  
188 uppermost part, of early Artinskian age.

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

198

## 199 2.2. General paleoenvironmental interpretation

200 The Community Pit Formation is a mixed siliclastic-carbonate unit, containing variably  
201 fossiliferous beds of dolomudstone, ~~limestone~~ [lime mudstones and wackestones](#), and siliciclastic  
202 shale (Figure 2; Krainer et al., 2003, 2009; Mack et al., 2013). It was deposited in a shallow  
203 marine to supratidal setting (the Hueco Seaway) on the western margin of the intracratonic  
204 Orogrande Basin (Lucas et al., 1998a, b; Voigt et al., 2013) at a paleolatitude of about 2°N  
205 (Tabor et al., 2008). Elsewhere in Doña Ana County, the unit contains a somewhat restricted  
206 marine fauna, and red/green-mottled caliche paleosols are developed at a few intervals (Krainer

207 et al., 2003, 2009; Lucas et al., 2002; Mack et al., 2010). Fifty kilometers north of Doña Ana  
208 County, this same stratigraphic interval comprises only red bed alluvial facies of the Abo  
209 Formation (DiMichele et al., 2007; Lucas et al., 2012). Therefore, during the Early Permian the  
210 location of the PTNM lay close to the fluctuating Hueco Seaway coastline (Mack and James,  
211 1986), with alluvial plains to the north (Lucas et al., 2012).

212 In a PTNM section that largely comprises the Community Pit Formation, Mack et al.  
213 (2013) identified six supratidal and shallow marine facies. They compared the overall  
214 paleoenvironment with semi-arid portions of the present-day Trucial Coast of Abu Dhabi,  
215 highlighting the presence of gypsum. This interpretation of climate as semi-arid is consistent  
216 with regional studies of paleosols (Mack, 2003; ~~Tabor, 2007~~; Tabor et al., 2008; Mack et al.,  
217 2010). However, the remains of large fossil trees, which would have required a good water  
218 supply, occur at several intervals in the formation (Tidwell and Munzing, 1995; Falcon-Lang et  
219 al., 2014a). There are three possibilities to explain this apparent inconsistency: (1) Regional  
220 climate was, in fact, semi-arid to arid, but there were localized poorly drained, groundwater-  
221 dependent habitats dotted across the landscape (cf. DiMichele et al., 2006), where arborescent  
222 vegetation could flourish despite the aridity. (2) Regional climate was overall somewhat wetter,  
223 allowing the geographic co-occurrence of minor evaporites with large trees, as seen, for example  
224 in the present-day southern Mediterranean region (cf. Francis, 1984). (3) Regional climate  
225 oscillated between wetter and drier phases, the large trees being associated with the former  
226 climate states and the evaporites with the latter (cf. Parrish and Falcon-Lang, 2007).

227

### 228 **3. Paleoenvironment of the fossil site**

229

230 | *3.1 Sedimentary facies*

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

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

240

241 | *3.1.1 Lower unit*

242 |         The basal unit, which occurs only in the central part of the channel (Figure 4, sections B-  
243 | E), comprises a lens of limestone pebble-to-cobble conglomerate, 0.05-1.1 m thick, and contains  
244 | Plant Assemblage #1. This rudstone is dominated by sub-angular to sub-rounded, elongate clasts  
245 | of gray-orange lime mudstone, 20-150 mm long, and accumulations of detrital crinoids and  
246 | bryozoans (locally comprising multiple, cemented, randomly arranged fossil fragments, clearly  
247 | reworked from underlying beds), within a poorly sorted matrix of medium- to coarse-grained  
248 | mixed carbonate-siliciclastic sandstone and mudstone. Specimens of coalified tree-trunks, up to  
249 | 0.17 m diameter, co-occur with cubic, sub-rounded, 20-50 mm diameter blocks of charcoalfied  
250 | wood (Plant Assemblage #1) in the basal rudstone.

251

252 | *3.1.2 Middle unit*

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

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

273 Macrofossils and traces in the middle unit include scattered pterinopectinid bivalves and  
274 rare lingulid brachiopods, and horizons with vertical burrows. The low-diversity of the  
275 invertebrate fossil assemblage [and overall fine-grained nature of the muddy carbonates](#) is typical

276 | of ~~a brackish to~~ restricted marine or brackish depositional environment. Also present at multiple  
277 | horizons are rooted zones associated with the addressed megaflora (Plant Assemblage 2  
278 | described in section ~~4.2.5~~). A few weakly calcified tree-trunks, up to 0.18 m diameter and > 1.4  
279 | m long, occur in the undulatory beds. These logs have an orientation sub-perpendicular to the  
280 | channel margins. Rare fragments of wood also are identifiable in thin sections of the limestone  
281 | matrix.

282

283 | ~~3.4.3.~~ *Upper unit*

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

287

288 | ~~3.6.4.~~ *Paleoenvironmental interpretation*

289 |       There are several possible explanations for the incision of the fossil-bearing channel and  
290 | its subsequent filling, primarily with carbonate, which must be treated as temporally independent  
291 | phenomena. The occurrence of an incised channel system, albeit unique in the region,  
292 | necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine  
293 | shelf and to cause channel incision. Most incised features of this nature have been recognized in  
294 | non-marine, siliciclastic depositional settings; however, a few examples have been reported in  
295 | carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003).  
296 | The term “incised channel” (rather than incised valley) is the most appropriate descriptor for the  
297 | feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and  
298 | 5-6 m deep) with a low aspect ratio (about 25:1).

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299 There are several possible causes of base-level change. Eustatic lowering of sea-level is,  
300 perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation  
301 may have been deposited sometime during one of several intervals of inferred Permian southern  
302 hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al.,  
303 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event,  
304 resulting in a global lowering of sea level, additional evidence of incision in the area might be  
305 expected at this same horizon, which is widely traceable within the mostly carbonate portion of  
306 the Community Pit Formation. However, such evidence has not been found by us or reported  
307 elsewhere.

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

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

320 The central portion of the channel contains a basal rudstone composed of pebbles and  
321 cobbles of marine limestone and faunal detritus, clearly well indurated at the time of its erosion

322 and deposition. Thus, it does not appear to represent a submarine channel. The small size of the  
323 channel, and the fact that the only sedimentary particles in it are of local origin from within the  
324 areas of the immediate drainage basin, suggest a seasonally dry climate at the time of incision,  
325 and a relatively small overall drainage area (Feldmann et al., 2005). There must, however, have  
326 been sufficient moisture to promote plant growth proximate to the channel, indicated by  
327 moderate-sized logs in the basal channel fill, and to bring about incision in the first place.

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

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

343 Above this basal lag, lime mudstones formed under brackish to nearly marine salinities,  
344 with strong suggestions of periods of standing or sluggishly moving water. The salinity and

345 carbonate accretion are most likely reflective of base-level rise and the invasion of the channel  
346 by marine waters, mixed to some small degree with continued freshwater runoff from the  
347 surrounding terrestrial landscape. A change from a sub-humid to a semi-arid climate is indicated.  
348 However, it is likely that water cover was maintained most of the time, given evidence of  
349 syndepositional occupation of surfaces within the channel by vascular plants and the  
350 incorporation of plant remains into the limestone matrix, which consisted of actively  
351 forming/accumulating carbonate muds.

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

360

### 361 **3.24.- Isotopic analyses of the middle unit**

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

365

#### 366 4.1. Methodology

367 Thick sections (~200  $\mu\text{m}$  thick) of two hand samples from the middle unit were studied

368 [petrographically under transmitted light and cathodoluminescence in order to identify calcite](#)  
369 [fabrics and textures. Thick sections of the two samples were microdrilled for stable \(50  \$\mu\text{g} \pm 10\$](#)   
370  [\$\mu\text{g}\$  samples\) and radiogenic isotope \(0.5 gm\) analysis using a Merchantek automated](#)  
371 [microdrilling system.](#)

372 [Samples \(n=10\) for stable- isotope analysis were roasted at 375° C under vacuum for 30](#)  
373 [minutes to remove organics and subsequently reacted in 105% phosphoric acid at 90° C in either](#)  
374 [a common acid bath on a GVI Optima Stable Isotope Ratio Mass Spectrometer \(SIRMS\) or a](#)  
375 [Gilson Multicarb Autosampler system \(individual acid injection vials\) interfaced with an](#)  
376 [Elementar Isoprime Mass Spectrometer housed in the UC Davis Stable Isotope Laboratory. CO<sub>2</sub>](#)  
377 [gas was analyzed in dual inlet mode and values were corrected using the Craig correction to](#)  
378 [account for the <sup>17</sup>O contribution \(Craig, 1957\) and to an internal standard and reported relative to](#)  
379 [the Vienna Pee Dee Belemnite \(VPDB\). Both systems provide  \$\delta^{13}\text{C}\$  precision of  \$\pm 0.04\%\$  and](#)  
380  [\$\delta^{18}\text{O}\$  precision of  \$\pm 0.06\%\$ .](#)

381 [Microdrilled samples \(n=2\) for ~~s~~Strontium isotope analyses were prewashed with 1 M](#)  
382 [ammonium acetate in order to remove ~~Sr~~ associated with absorbed \(on clays\) or included](#)  
383 [noncarbonate phases \(Montañez et al., 2000\). Strontium was isolated using Spex cation ex-](#)  
384 [change resin and microliter columns attached to a channel pump. <sup>87</sup>Sr/<sup>86</sup>Sr ratios were measured](#)  
385 [in solution mode on a Nu MC-ICPMS in the Interdisciplinary Center for Plasma Mass](#)  
386 [Spectrometry, UC Davis. Values are typically normalized to a nominal value for NIST standard](#)  
387 [SRM987 of 0.710249. SRM987 for the measurement period averaged 0.710249 \( \$2\sigma =\$](#)   
388 [0.000035\) based on standards analyzed during this period.](#)

389  
390 [4.2. Results](#)

391 ~~In order to assess the extent of marine influence on the lime mudstones of the middle unit,~~  
392 ~~carbon and oxygen isotopic analyses were carried out on microdrilled samples of the carbonate~~  
393 ~~interval.~~ The well-preserved micrites have average  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  compositions ~~between -2.7 to~~  
394 ~~of -3.0‰ (2 std err. of 0.2‰) 2.4‰ and 1.2 and 1.41.1 ‰ (2 std err. of 0.1‰)‰, respectively~~  
395 (Table 1).

#### 397 4.3. Paleosalinity interpretation

398 Given the earliest Permian age of the carbonates, these values support a dominantly  
399 marine environment. However, these stable isotopic values indicate that the lime muds likely did  
400 not form in pure seawater given typical Midcontinent and Panthalassan seawater compositions  
401 during this time (Grossman et al. 2008). Seawater  $\delta^{18}\text{O}$  in the Late Carboniferous Pennsylvanian  
402 and early Permian likely ranged between -1 and 0‰ (Came et al., 2007) given the occurrence of  
403 ice sheets in southern Gondwana. The  $\delta^{18}\text{O}$  composition of low-latitude coastal river water  
404 likely was in the range of -1 to -4‰ (cf. Bowen and Wilkinson, 2002), and perhaps a few per mil  
405 lower if the climate was monsoonal (Rozanski et al., 1993). Notably, the  $\delta^{18}\text{O}$  of low latitude,  
406 coastal waters can be enriched by several per mil over open ocean seawater (Swart and Price,  
407 2002), a scenario compatible with the tropical epicontinental environment of the study area.  
408 Thus, accounting for oxygen isotope fractionation between water and calcite at  $25^\circ \pm 3^\circ\text{C}$ , the  
409 micritic  $\delta^{18}\text{O}$  compositions are compatible with formation in waters over a range of salinities  
410 (i.e., fresh to fully marine).

411 Carbonate  $\delta^{13}\text{C}$  values, in contrast, provide constraints on the depositional waters in the  
412 channel. Seawater  $\delta^{13}\text{C}$  from the latest Ghzelian through earliest Sakmarian in western  
413 Euramerica was  $+4\text{‰} \pm 0.5\text{‰}$ . The measured  $\delta^{13}\text{C}$  values, which are 2 to 3‰ lower than

414 contemporaneous seawater, can be explained by an input of a maximum of 10-20% freshwater.  
415 This assumes a freshwater  $\delta^{13}\text{C}$  composition of -8 to -10‰, which is typical of ~~rivers draining~~  
416 ~~carbonate systems and for freshwater systems in lowland region~~ tropical coastal rivers bordering  
417 ~~erations~~ and associated with subhumid to semi-arid climates and moderate density vegetation  
418 (Mook and Tan, 1991). Although lowland tropical rivers draining carbonate terrains can be  $^{13}\text{C}$ -  
419 enriched due to interaction with the carbonates along the flow path, the observed fossil flora  
420 indicate a likely source of locally derived  $^{12}\text{C}$ -enriched terrestrial C to the channel waters.

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

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

433

#### 434 **45. Plant Assemblages**

435 The Community Pit Formation floras encompass two distinct assemblages that occur in  
436 different facies of the channel. The lowermost flora, consisting solely of the woody remains of

437 walchian conifers, is representative of the widespread, Late Pennsylvanian-Early Permian  
438 seasonally dry biome described from many localities across the Euramerican equatorial region  
439 (Rees et al., 2002; Zeigler et al., 2002; Bashforth et al., 2014; DiMichele, 2014). The flora  
440 preserved in the middle unit of the channel contains a unique assemblage, dominated by a  
441 voltzian conifer and a callipterid, unknown in combination from any other locality in Euramerica  
442 and preserved under environmental conditions suggestive of a tolerance of high-salinity  
443 substrates of one or both taxa.

444           Details of the lowermost flora have been described by Falcon-Lang et al. and are  
445 only be briefly précised here. (20154b — in press) and will only be touched on briefly here. It  
446 includes coalified tree-trunks and charcoalfied wood preserved in the basal rudstone. Four  
447 specimens of charcoal, which was the only material to preserve anatomical detail, were  
448 examined. These specimens are housed in the collections of the New Mexico Museum of Natural  
449 History and Science under catalogue numbers NMMNH P68181 – P68184, and comprise  
450 pycnoxylic wood that conforms to the Type II Paleozoic wood of Doubinger and Marguerier  
451 (1975). These specimens are essentially identical to the wood-type *Macdonaldodendron* Falcon-  
452 Lang, Kurzawe et Lucas, which was described from higher in the Community Pit Formation  
453 (Falcon-Lang et al., 2014). This wood is considered to be of walchian-conifer affinity. Other  
454 woods considered or confirmed to be of walchian affinity are similar to the study specimens  
455 (Reymanowna, 1962; Lemoigne and Tyroff, 1967; Tidwell and Munzing, 1995).

456  
457           ~~Rather~~In this current paper, we, we focus our attention on the peculiar flora from the  
458 middle beds of the channel. This flora has been described in brief by DiMichele et al. (2014~~—in~~

459 ~~press~~), with an ~~emphasis-focus~~ on its stratigraphic implications. Here, we detail the morphology  
460 and paleoecology of the plants and their broader evolutionary implications.

461

462

#### 463 *4.1 Flora 1: Walchian conifer wood*

464 ~~Coalified tree trunks and charcoaled wood are preserved in the basal rudstone. Hand~~  
465 ~~lens observations indicate that the coalified tree trunks are entirely devoid of cellular anatomy,~~  
466 ~~so only the well-preserved charcoal was studied in detail (Falcon Lang et al., 20154b). Material~~  
467 ~~studied comprised four specimens, housed in the collections of the New Mexico Museum of~~  
468 ~~Natural History and Science under catalogue numbers NMMNH P68181–P68184. All four~~  
469 ~~specimens are pyenoxylic wood attributable to a single morphotype, which conforms to the Type~~  
470 ~~II Paleozoic wood of Doubinger and Marguerier (1975). These specimens are essentially~~  
471 ~~identical to the wood type *Macdonaldodendron* Falcon Lang, Kurzawe et Lucas, which was~~  
472 ~~described from higher in the Community Pit Formation (Falcon Lang et al., 2014a). This wood is~~  
473 ~~considered to be of walchian conifer affinity. Other woods considered or confirmed to be of~~  
474 ~~walchian affinity are similar to the study specimens (Reymanowna, 1962; Lemoigne and Tyroff,~~  
475 ~~1967; Tidwell and Munzing, 1995).~~

476

#### 477 *4.2 Flora 2: Voltzian conifers and *Lodevia callipterids**

478 ~~The flora comprises a~~Adressed megafloal remains and a few weakly calcified tree-  
479 trunks are preserved in micritic limestone, ~~from the middle unit of the channel fill.~~Adressed  
480 megafloal remains are present at multiple levels (Figure 3B, C) in discontinuous limestone  
481 lenses, each up to 30–50 mm thick and traceable for several meters along strike. Within these



482 lenses, there are variable concentrations of randomly oriented plant fragments, ranging from  
483 comminuted plant debris to fragments 10–30 cm in breadth (however, we note that this is a  
484 minimum size estimate because it is difficult to obtain large slabs of material). Identifiable  
485 material comprises three-dimensionally preserved impressions and partially cutinized leaves.  
486 Associated with these foliar remains, there are also open-to-somewhat-denser networks of roots  
487 of variable diameter, which crosscut laminations and are in growth position.

488  
489 *5.1. Material and methods*

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

496 The proportional abundance of taxa was quantified using a variant of the method of  
497 Pfefferkorn et al. (1975), in which each hand specimen is treated as a “quadrat,” with each taxon  
498 occurring on that quadrat counted only once, regardless of the number of individual specimens or  
499 fragments of specimens present (Table 24). Comminuted plant debris and other indeterminate  
500 fragments were excluded from such counts; however, gymnosperm axes of uncertainty affinity  
501 and invertebrates were included. The dominance and diversity data reported below are based on  
502 the three largest collections only, which include the majority (n = 114) of the specimens (sections  
503 C, E and float; localities USNM 43550, 43554, and NMMNH SGL-09-136, respectively), and

504 represent the frequency of occurrence of each taxon as a proportion of the number of quadrats in  
505 those counts. For rare taxa, the number of occurrences in the entire collection is reported.

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

511

512 54.2.1. *Voltzian conifers*

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

519 Morphotype A is represented by five isolated shoots (Figure 6A), two of which have the  
520 ultimate tips of the branch preserved. Leaves are bifacially flattened (cf. Type II leaves; de  
521 Laubenfels, 1953), and are oblong in shape with obtuse apices. Leaf widths (W) range from 2 to  
522 3.5 mm. Leaf lengths (L) are difficult to measure, due to overlap among them, and are at least 20  
523 -25 mm. L:W ratios range from 7 to 11, calculated on a per leaf basis. Leaves depart from the  
524 stem at angles from 15 to 40°, and are straight to slightly incurved when viewed in profile.  
525 Leaves are highly imbricate, particularly on the branch tips, resulting in a distinct "tufted"  
526 appearance. Details of the leaf attachment and axis diameter are obscured by overlapping leaves.

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

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

546           Morphotype D is represented by one, relatively large, branched specimen (Figure 6D).  
547 Ultimate branches occur in the axils of persistent leaves, and the overall branching pattern is  
548 orthotropic. Leaves have decurrent attachments to the stem, with the decurrent portions of the  
549 bases thick and clearly distinguishable for the entire length of the internode. Leaves depart from

550 | the stem at angles commonly up to 90°. ~~however, it~~ should be noted, ~~however,~~ that there is a  
551 | high degree of variation that may have been influenced by taphonomic processes, such as drying  
552 | of the material prior to deposition. Leaves are slightly more than 20 mm long, and 1.2-2 mm  
553 | wide (resulting a distinctively high L:W ratio of 12.5) and have a straight profile with an obtuse  
554 | apex. The leaves are dorsiventrally flattened in cross section (cf. Type II leaves: de Laubenfels,  
555 | 1953), with a thick, fleshy appearance. Leaves on the thicker, higher order axis appear more lax;  
556 | however, again, this could reflect taphonomic processes, such as differential drying of dead  
557 | foliage prior to incorporation into the sediment.

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

565 |         Late Paleozoic conifer classification is based on a combination of morphology and  
566 | internal and cuticular anatomy of stems, leaves, pollen cones, and ovuliferous structures ~~(such~~  
567 | as ovuliferous cones and fertile zones) (e.g., Clement-Westerhof, 1984, 1987, 1988; Rothwell et  
568 | al., 1997, 2005). Several features of the novel conifer material reported here allow it to be  
569 | referred to voltzian conifers. First, their foliar morphotypes show generally bifacial ovate,  
570 | lanceolate to linear medium-sized leaves, which are characteristic of voltzians. Second, foliar  
571 | morphotypes B and D show orthotrophic branching, also characteristic of voltzians, but distinct  
572 | from the plagiotrophic walchians (Rothwell et al., 2005). Third, the sterile scales and sporophylls

573 in the dwarf-shoots are fused, more or less flattened in one plane, and show a bilaterally  
574 symmetrical organization. At this point in time, it is uncertain how many taxa these four leaf  
575 morphotypes represent. Heterophylly does occur in voltzian conifers, and generally involves  
576 differences in leaf size, shape in face view, and apex shape. Voltzians are, however, relatively  
577 consistent in leaf characters like mode of attachment, features of leaf bases and shape in cross-  
578 section. Morphotypes B and C might represent a single taxon, but we have no confirmatory  
579 evidence for that, such as attachment to a common branch. The leaves of morphotypes A and D  
580 are both bilaterally flattened, but arise at different angles, and have different kinds of attachment.  
581 Collection of further material is required to answer this question. More material is also needed to  
582 ensure that we have collected the full range of the diversity of conifer foliage in this flora.

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

588

589 ~~54.3.2.2~~ *Callipterid foliage* – *Lodevia oxydata*

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590 The other dominant taxon in the flora is an unusual callipterid (occurring in 34 out of 114  
591 quadrats; frequency 29.8 %). The material shows considerable morphological variation and  
592 encompasses immature and mature pinnae (Figure 7A-E). Included among the suite of specimens  
593 are pinnae with remarkably robust axes bearing slightly decurrent, pinnately lobed to segmented,  
594 pinnules. Pinnule lobes typically have blunt tips, particularly those forming the pinnule apex.  
595 The venation is pronounced with an indistinct, sometimes slightly flexuous midvein with widely

596 spaced, steeply ascending lateral veins inserted at angles of 20-30°; lateral veins fork once or  
597 twice, depending on the segmentation with a single vein per lobe. The suite of specimens shows  
598 a number of noteworthy phenologic features. For example, some fronds show pinnae preserved  
599 in the process of unfolding (Figure 7A), a developmental pattern found in other callipterid taxa  
600 (e.g., Kerp, 1988). Still others comprise young, immature pinnules (Figure 7E), and a few  
601 unusual mature specimens exhibit pinnules with irregularly curled edges (Figure 7D). Another  
602 axis has a swollen base (Figure 7C), which usually indicates that complete fronds were abscised.

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

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

614

#### 615 ~~54.2.4.~~ *Roots*

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616 Among the remaining adpressed material, only roots occurring in growth position (n = 17  
617 quadrats) are common, being found in all four *in situ* collections. Roots comprise dense,  
618 interwoven networks and more extensive, open systems (Figure 7H). They show four, or more,

619 orders of branching, the largest being c. 25 mm in diameter, the smallest < 1 mm in diameter.

620 They ramify irregularly, side-axes being disposed at variable angles to the higher-order axes.

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

634         In consideration of the likely seed plant affinities of the roots, the most important point  
635 they highlight is that rooting of the lime mudstones took place contemporaneously with or very  
636 shortly after the entombment of the aerial remains of conifers and *Lodevia* in this same limey  
637 mud. Because these roots are in and ramify through the limestone, and because of the rate at  
638 which subaerially lime mud hardens and becomes effectively impenetrable to roots, and because  
639 there is no evidence within these beds of brecciation associated with long-term pedogenesis and  
640 development of terra rosa type residual siliciastic soils, it is most likely that the roots were  
641 derived from the voltzian conifers and/or the callipterids, though whether one or both cannot be

642 determined. The possibility remains, of course, that they were derived from an additional kind of,  
643 most likely, seed plant that left no other macrofossil record. The likely contemporaneity or near  
644 contemporaneity of the aerial debris and roots also suggests that the plants in question were  
645 growing on these limey muds while they were water covered. The combination of physical  
646 sedimentological evidence, isotopic values of the lime muds, the brackish-to-marine invertebrate  
647 fauna also present within the sediment, and the necessity for incorporation of aerial debris and  
648 roots into the muds prior to solidification, strongly suggests growth of these plants in waters of  
649 brackish to near-marine salinities.

650

#### 651 54.2.5. Other rare taxa

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652 All other taxa are rare and include walchian conifers (*Walchia* sp., n = 7 quadrats) (Figure  
653 7F), some small seeds of indeterminate affinity (n = 7), which may be related to one of the  
654 conifers or pteridosperms, the sphenopsid *Annularia spicata* (Gutbier) Schimper (n = 1; Figure  
655 7F), and a putative fern, cf. *Sphenopteris* (n = 1). A small number of weakly calcified tree-trunks  
656 (up to 0.18 m diameter) associated with the addressed remains comprise pycnoxylic coniferopsid  
657 wood that is too coarsely re-crystallized for more accurate determination.

658

#### 659 65. Discussion

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

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



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

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

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

682 It must be emphasized that this is an extremely unusual deposit, of a type rarely  
683 encountered by the authors in their combined ~~many over 200 person~~-years of fieldwork.  
684 Limestone filled, terrestrial channels are uncommon. The closest analogue may be limestone-  
685 filled lakes that formed under semi-arid to occasionally arid climates, such as those that typify  
686 Late Pennsylvanian and early Permian exposures in the Appalachian Basin of the eastern USA

687 (e.g., Montañez and Cecil, 2013), from which plant fossils (callipterids, tree ferns) are known  
688 and reported (e.g., DiMichele et al., 2013b).

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

697

### 698 *5.1. Paleoenvironmental interpretation*

699 ~~There are several possible explanations for the incision of the fossil-bearing channel and~~  
700 ~~its subsequent filling, primarily with carbonate, which must be treated as temporally independent~~  
701 ~~phenomena. The occurrence of an incised channel system, albeit unique in the region,~~  
702 ~~necessitates a fall in base level sufficient to sub-aerially expose carbonates formed on the marine~~  
703 ~~shelf and to cause channel incision. Most incised features of this nature have been recognized in~~  
704 ~~non-marine, siliciclastic depositional settings; however, a few examples have been reported in~~  
705 ~~carbonate-dominated settings (e.g., Johnson and Simo, 2002; Jiang et al., 2003; Tucker, 2003).~~  
706 ~~The term “incised channel” (rather than incised valley) is the most appropriate descriptor for the~~  
707 ~~feature (Gibling, 2006; Falcon-Lang et al., 2009) because it is relatively small (140 m wide and~~  
708 ~~5–6 m deep) with a low aspect ratio (about 25:1).~~

709        There are several possible causes of base level change. Eustatic lowering of sea level is,  
710 perhaps, the hypothesis most likely to be invoked first, given that the Community Pit Formation  
711 may have been deposited sometime during one of several intervals of inferred Permian southern  
712 hemisphere glaciation (middle Asselian-early Artinskian) (Montañez et al., 2007; Fielding et al.,  
713 2008ab; Rygel et al., 2008; Montañez and Poulsen, 2013). Were it due to a eustatic event,  
714 resulting in a global lowering of sea level, additional evidence of incision in the area might be  
715 expected at this same horizon, which is widely traceable within the mostly carbonate portion of  
716 the Community Pit Formation. However, such evidence has not been found by us or reported  
717 elsewhere.

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

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

730        The central portion of the channel contains a basal rudstone composed of pebbles and  
731 cobbles of marine limestone and faunal detritus, clearly well-indurated at the time of its erosion

732 and deposition. Thus, it does not appear to represent a submarine channel. The small size of the  
733 channel, and the fact that the only sedimentary particles in it are of local origin from within the  
734 areas of the immediate drainage basin, suggest a seasonally dry climate at the time of incision,  
735 and a relatively small overall drainage area (Feldmann et al., 2005). There must, however, have  
736 been sufficient moisture to promote plant growth proximate to the channel, indicated by  
737 moderate sized logs in the basal channel fill, and to bring about incision in the first place.

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

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

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

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

771

772 6.5.2. Flora 1: Walchian and other coniferous wood.

773 The earliest vegetation from the PTNM limestone channel deposit for which we have  
774 evidence is preserved as coalified tree-trunks and charcoaled wood fragments in the calcirudite  
775 at the base of the channel (Falcon-Lang et al., 2014b5). The specimens examined have walchian  
776 conifer affinity. Species that are part of the large complex of walchian Voltziales are by far the

777 most commonly encountered kinds of conifers in Euramerican fossiliferous deposits of latest  
778 Pennsylvanian and early Permian age (e.g., Kerp and Fichter, 1985; Clement-Westerhof, 1988;  
779 Kerp, 1996; Ziegler et al., 2002; Hernandez-Castillo et al., 2001, 2009; Rothwell et al., 2005;  
780 Looy 2013; Looy and Duijnste, 2013). They are dominant elements in the red siltstones that  
781 make up much of the Community Pit Formation and its more inland equivalent, the Abo  
782 Formation (DiMichele et al., 2007, 2013a), which crops out in a long north-south band on the  
783 margin of the Rio Grande rift and elsewhere, throughout central New Mexico (Lucas et al., 2012,  
784 2013).

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

795

796 | ~~G5.3. Flora 2:~~ *Voltzian-callipterid vegetation*

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

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

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

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

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

840           The other common plant in the mid-channel assemblage is *Lodevia oxydata*. This is a  
841 very rare species that has only been described twice previously in the fossil record. Both  
842 previous occurrences are from near the Pennsylvanian-Permian boundary in (1) the Rotliegend of  
843 Lower Silesia, Poland (Göppert, 1864-65) and (2) the Dunkard Group of the Central  
844 Appalachian Basin, U.S.A. (DiMichele et al., 2013b). The New Mexico occurrence extends the



845 geographic range of this taxon across the entire breadth of the Euramerican realm. In the  
846 Appalachians, *L. oxydata* is known from limestone beds lacking evidence of marine influence  
847 (Montañez and Cecil, 2013) at two, closely adjacent, localities, interpreted as having formed  
848 under a semi-arid to dry subhumid climate regime (DiMichele et al., 2013b). The Rotliegend  
849 specimen is from a very different environmental setting, occurring in an inland basin located far  
850 from the nearest marine influence and not characterized by either arid conditions or any evidence  
851 of elevated salinity.

852  
853 In summary, the deposit described here indicates the existence of a previously unknown  
854 type of late Paleozoic plant assemblage. This assemblage is of low diversity, consisting of two  
855 abundant seed-plant species and a few rare taxa. Its habitat of growth, on the margins of and  
856 rooted within the lime muds of a shallow, highly saline channel, is most unusual and suggests a  
857 mangrove habit for one or both of the dominant forms. The discovery of such deposits involves a  
858 great deal of luck and indicates the necessity for continued field studies and examination of even  
859 unlikely looking sedimentary-rock strata.

860

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880

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1245 **FIGURE CAPTIONS**

1246 Figure 1. County map of New Mexico highlighting the location of the PTNM in Doña Ana  
1247 County, where the fossils were obtained (index map: location of New Mexico in the  
1248 U.S.A.).

1249 Figure 2. Measured section of the Community Pit Formation. Beds are numbered. The  
1250 fossiliferous site discussed in this paper is indicated as NMMNH locality 7981.

1251 Figure 3. Fossiliferous, limestone filled channel. A., Eastern margin of channel. Channel base is  
1252 indicated by arrows. The main fossil excavation was carried out at the eastern channel  
1253 margin; B., Excavation at site A (Fig. 4) to show the nature of the mid-channel lithology,  
1254 a dense, micritic limestone. Geological hammer for scale; C., Exposure of mid-channel  
1255 micritic limestone in western portion of channel. White arrow indicated a calcified tree  
1256 trunk. Scale increments 1 foot (30.5 cm).

1257 Figure 4. Geology of the limestone-filled channel in the Community Pit Formation at NMMNH  
1258 locality 7891, showing correlated measured sections through channel. Solid lines  
1259 demarcate correlatable surfaces. Surface 1 is the base of the channel. Surface two  
1260 separates the middle-channel fill, containing the voltzian conifer-callipterid flora, from  
1261 the upper channel fill, which is devoid of plant macrofossils. Surface 3 marks the top of  
1262 the channel fill.

1263 Figure 5. Common limestone microfacies of the middle channel-fill limestone. Thin section  
1264 photographs all under plane light. A., Fine-grained calcareous sandstone containing few  
1265 foraminiferans; B., Calcareous siltstone with rare foraminiferans; C., Indistinctly  
1266 laminated calcareous siltstone containing sponge spicules; D., Calcareous siltstone with

1267 rare foraminiferans (a particularly conspicuous example can be seen in the center of the  
1268 slide). Scale bars = 0.5 mm.

1269 Figure 6. Addressed conifer foliar morphotypes, and an ovuliferous cone and dwarf shoot of a  
1270 voltzan conifer in Plant Assemblage 2; A., Ultimate shoot of Morphotype A, scale: 10  
1271 mm, NMMNH P68185; B., A branch system of Morphotype B with three orders of  
1272 branching, scale: 10 mm, NMMNH P68186; C., Part of a shoot of Morphotype C  
1273 (Specimen in right hand corner), scale: 10 mm, NMMNH P68187; D., A branch system  
1274 of Morphotype D with two orders of branching, scale: 5 mm, NMMNH P68188; E.,  
1275 Mature ovuliferous cone with bract–dwarf shoot complexes helically arranged around  
1276 axis, scale: 5 mm, NMMNH P68189; F, Flattened dwarf shoot with partly fused base, and  
1277 six obtuse scales, scale: 10 mm, NMMNH P68190.

1278 Figure 7. Addressed callipterids, voltzian conifers and sphenopsids in Plant Assemblage 2; A.,  
1279 Callipterid, *Lodevia oxydata*, showing unfolding frond, scale: 25 mm, NMMNH P68191;  
1280 B., Callipterid, *Lodevia oxydata*, showing typical mature foliage, scale: 10 mm, NMMNH  
1281 P68192; C., Swollen base (possible abscission surface) of callipterid, *Lodevia oxydata*,  
1282 scale: 10 mm, NMMNH P68193; D., Callipterid, *Lodevia oxydata*, showing desiccated  
1283 appearance with curled tips to pinnules, scale: 10 mm, NMMNH P68194; E., Callipterid,  
1284 *Lodevia oxydata*, showing immature foilage, scale: 10 mm, NMMNH P68195; F.,  
1285 Sphenopsid, *Annularia spicata*, scale: 4 mm, NMMNH P68196; G., Walchian foliage,  
1286 scale: 5 mm, NMMNH P68197; H., Fine network of branching gymnosperm roots, of  
1287 probable callipterid affinity, scale: 10 mm, NMMNH P68198.

1288  
1289

1290 | **TABLE CAPTION**S

1291

1292 | Table 1. Stable and radiogenic isotope compositions of the Community Pit Fm.

1293

1294 | Table 1~~2~~. Quantitative quadrat data for addressed megafloral assemblages (Plant Assemblage #2)

1295 | in the middle unit of the incised channel (using methodology of Pfefferkorn et al., 1975).

1296

Figure 1 Map Flood

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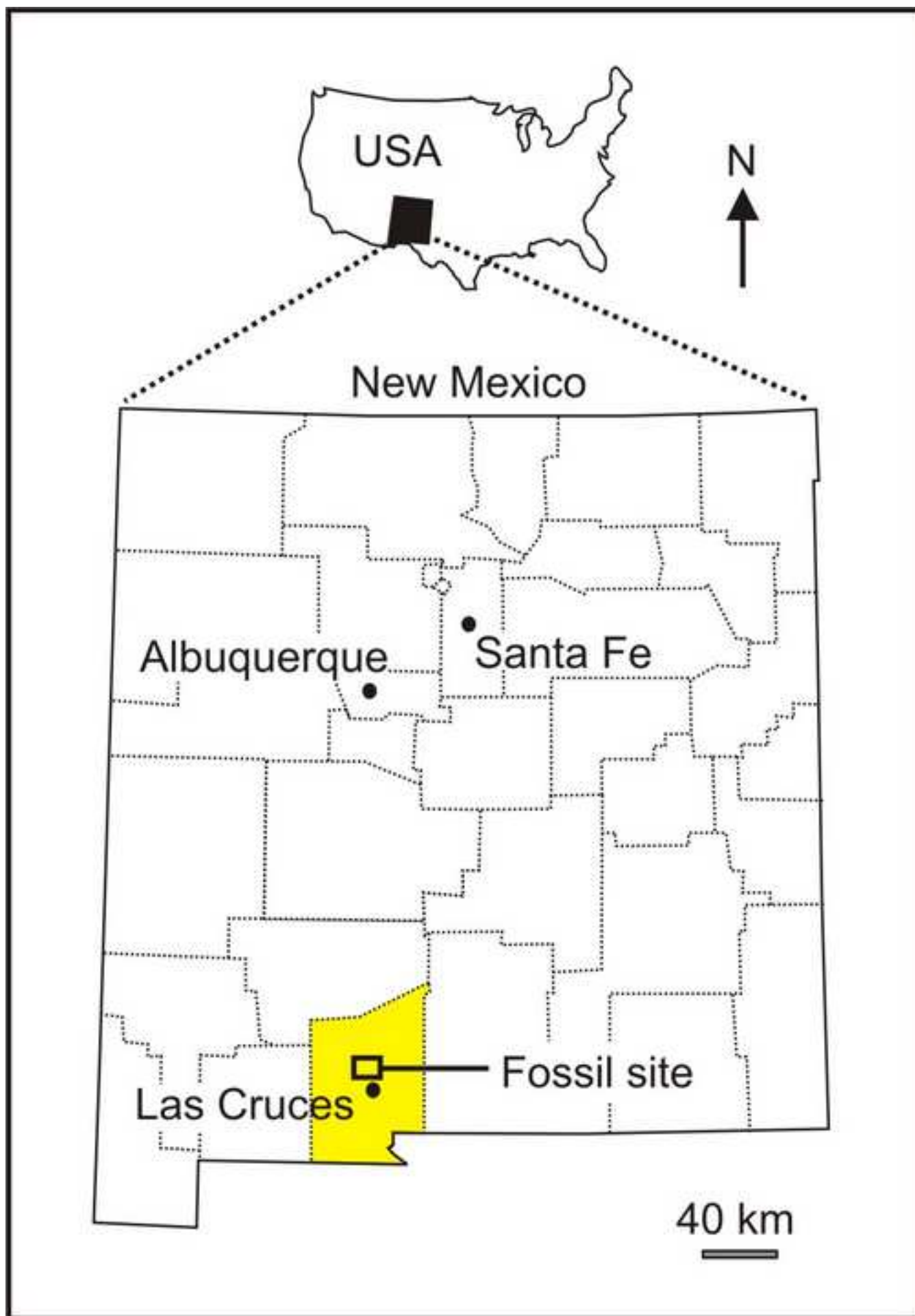


Figure 2 Geology Flood  
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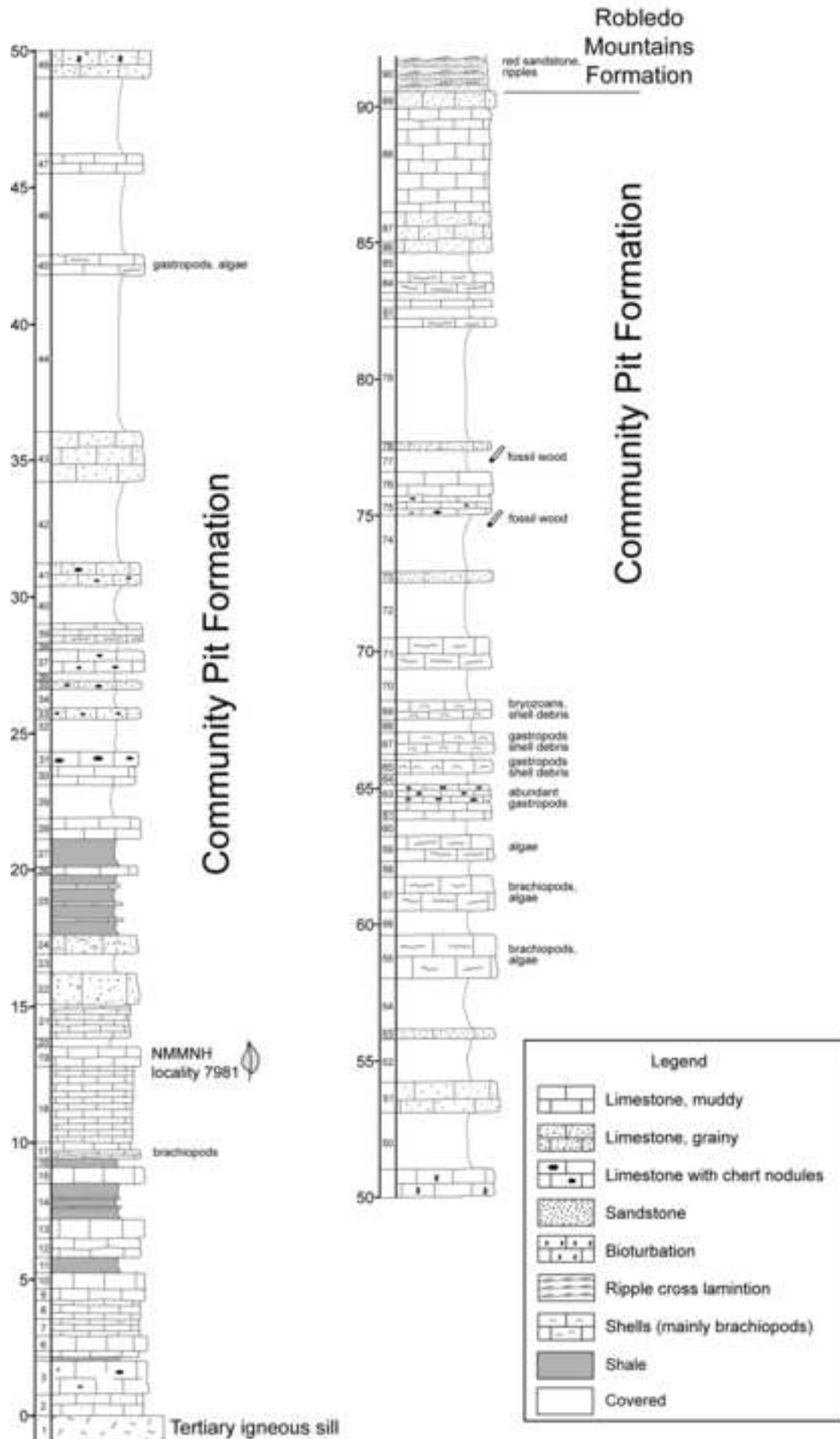


Figure 3 Channel Outcrop Flood  
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Figure 4 Sections Across Channel Flood  
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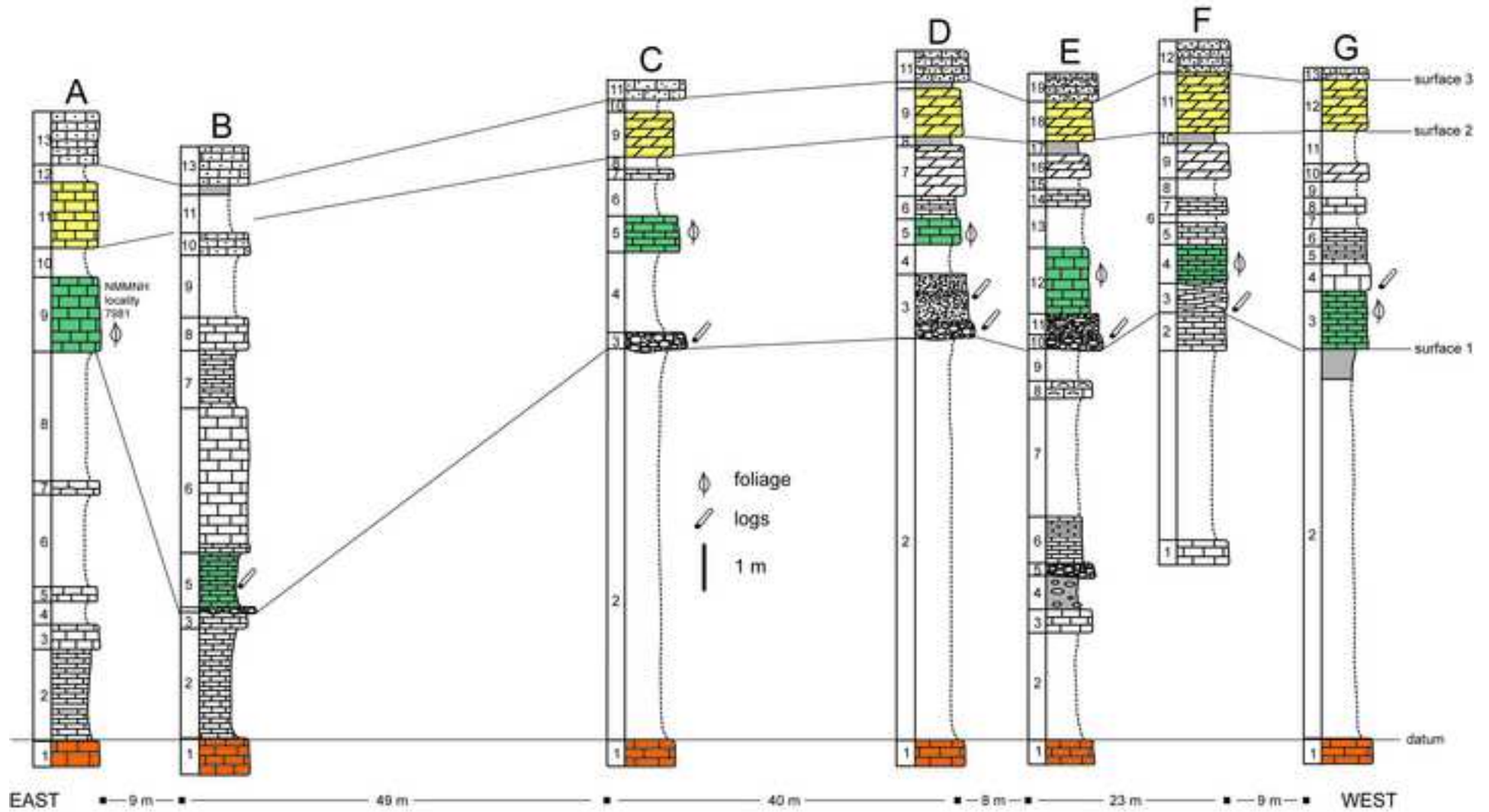


Figure 5 Microfacies Flood  
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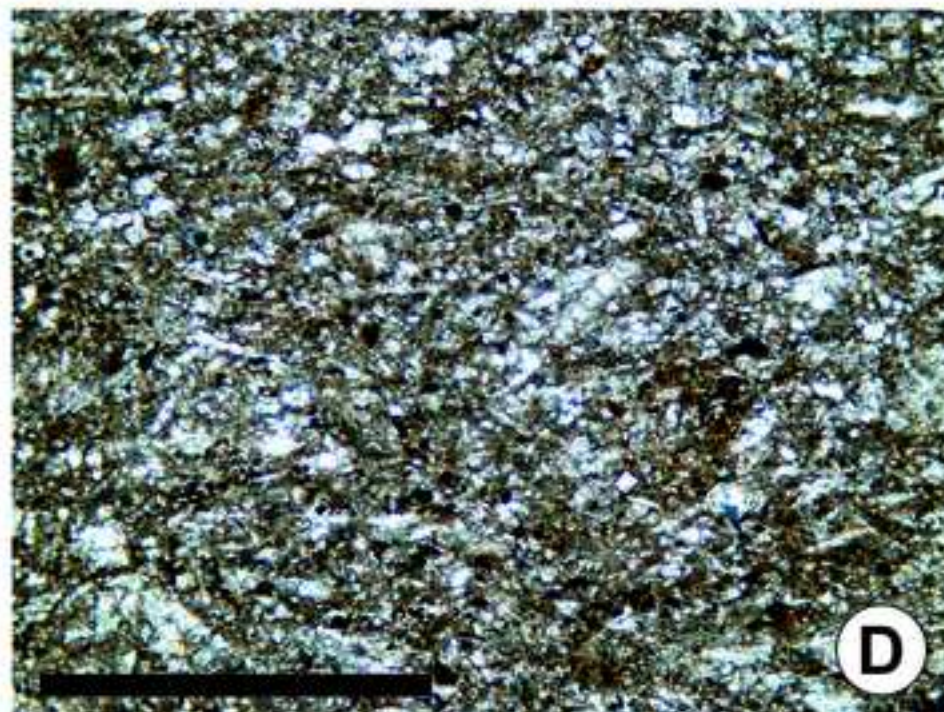
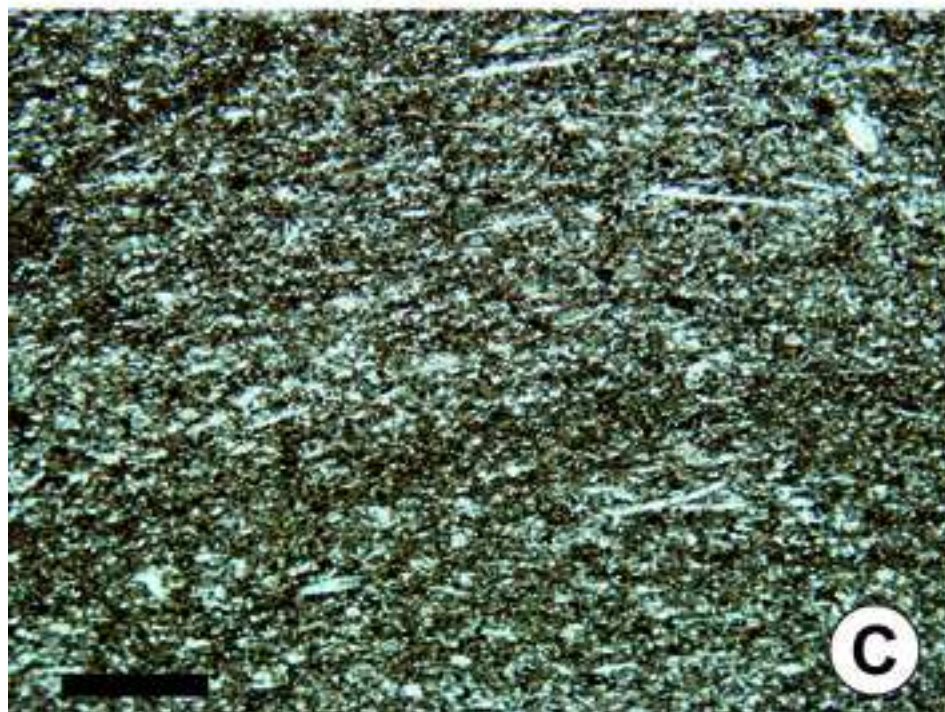
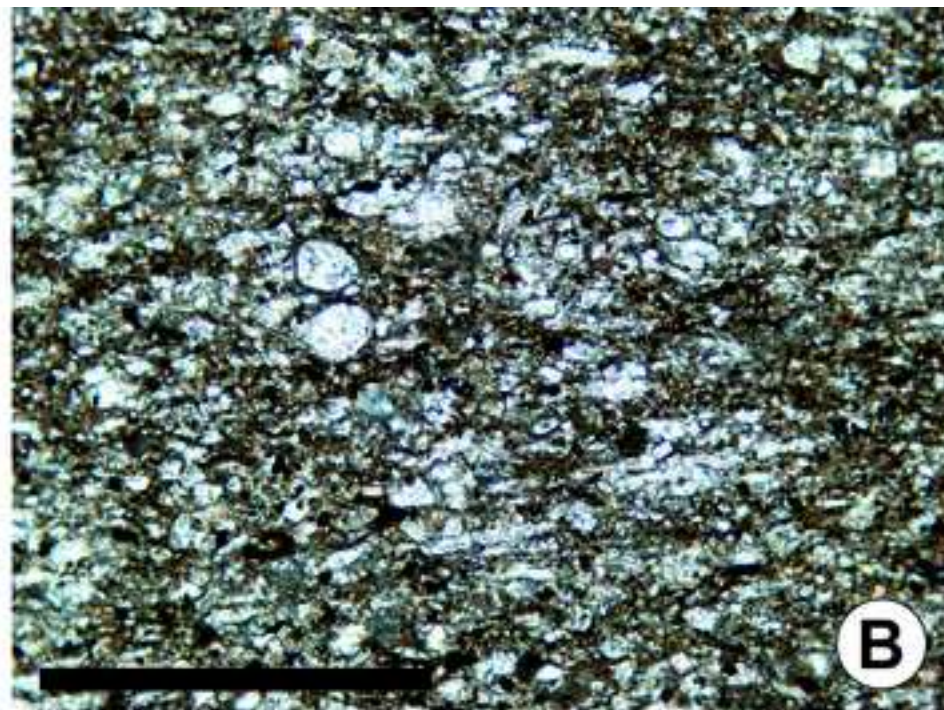
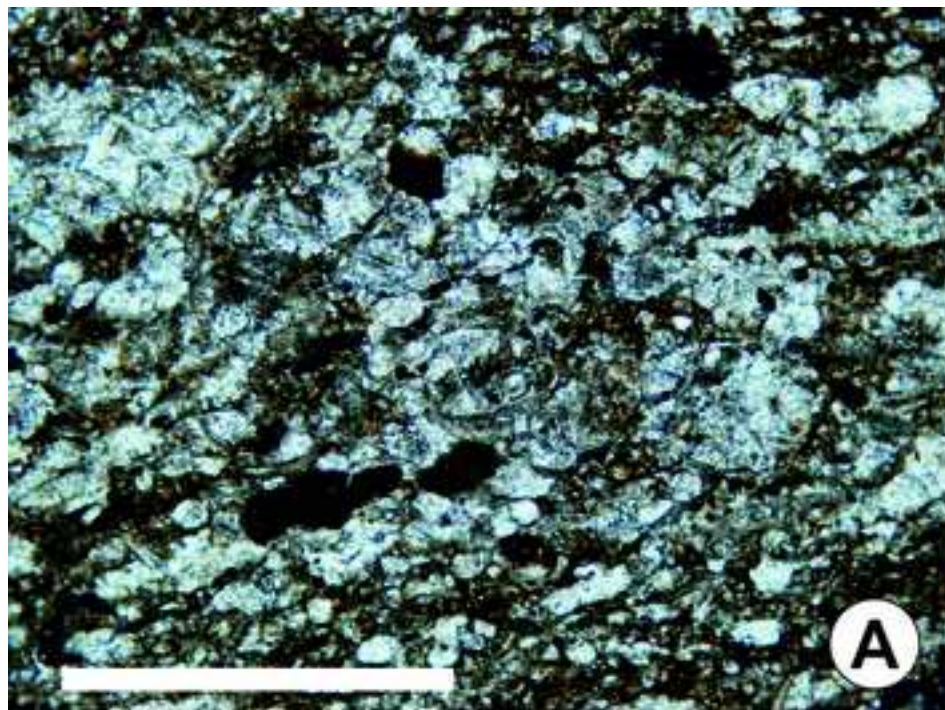


Figure 6 Conifers Flood  
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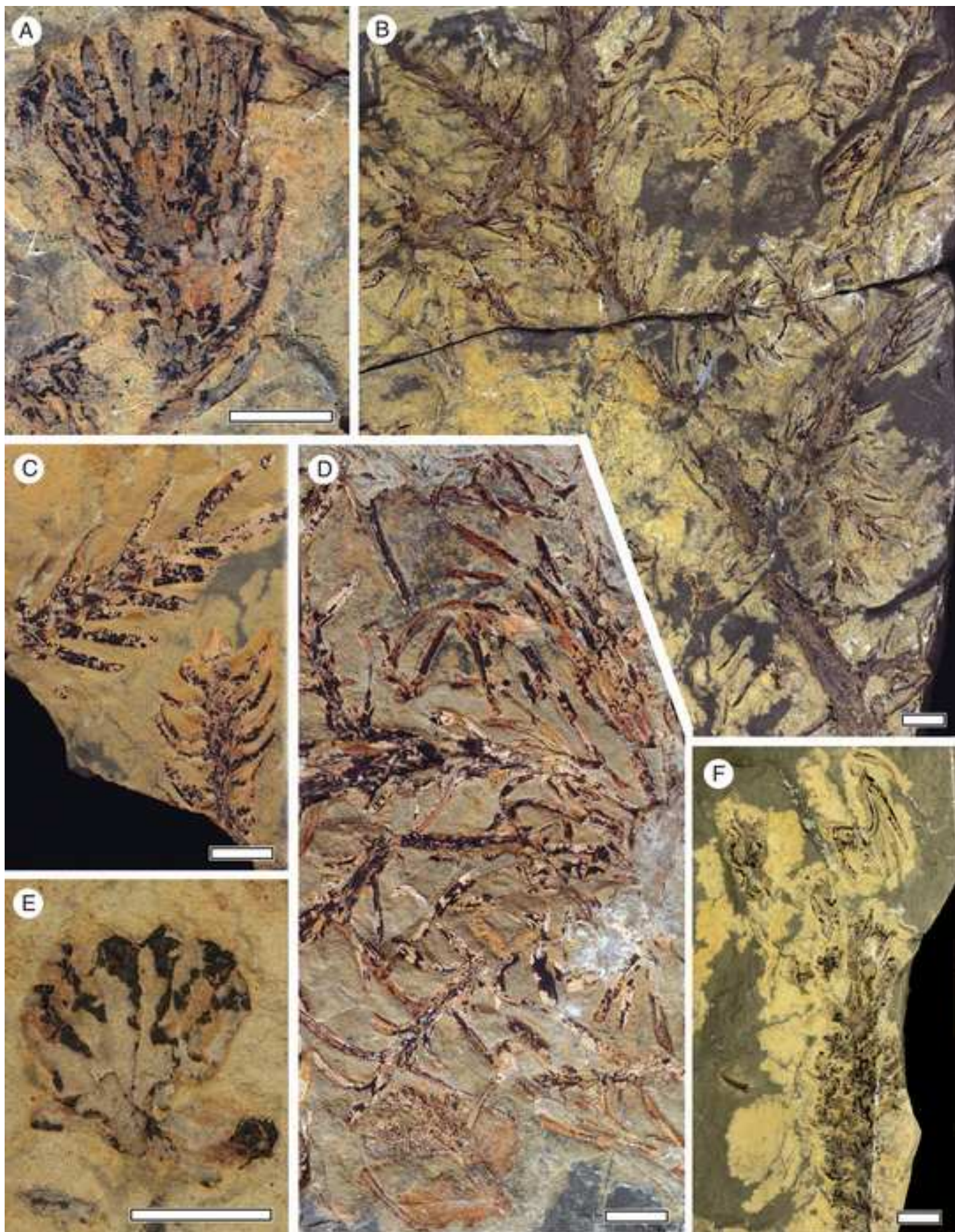
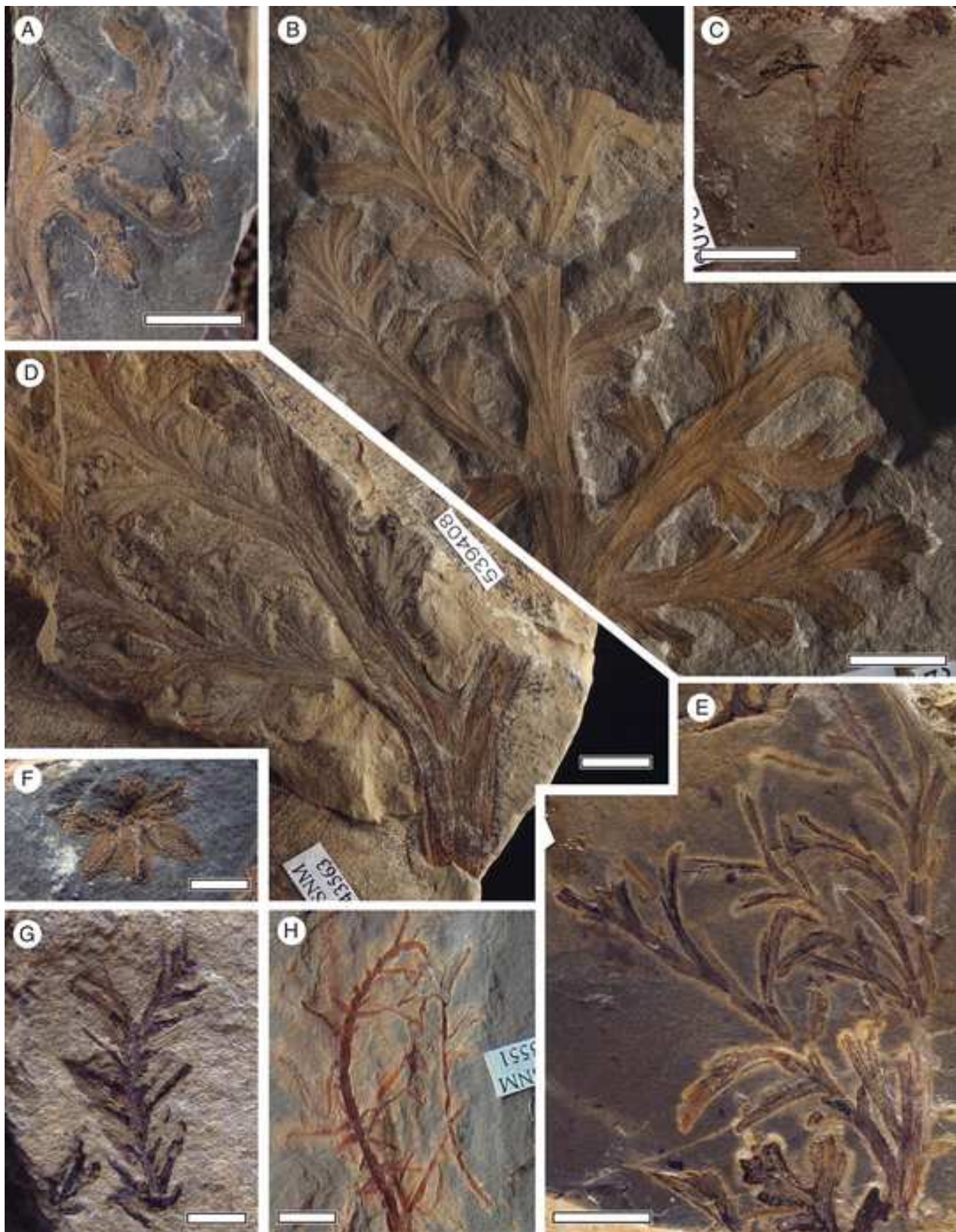


Figure 7 Lodevia Others Flood  
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**Table 1 Isotopes**

[Click here to download Table: Table 1 isotopes.xlsx](#)

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

<b>Sample</b>	<b>d<sup>13</sup>C (‰)</b>	<b>d<sup>18</sup>O (‰)</b>	<b><sup>87</sup>Sr/<sup>86</sup>Sr</b>
<i>SGL-09-136A</i>	1.22	-2.72	0.708562
laminated lime mudstone	1.41	-2.49	0.70858
	1.21	-2.73	
	1.36	-2.41	
<b><i>Sample Average (± 1 S)</i></b>	<b>1.30 (±0.09)</b>	<b>-2.59 (±0.14)</b>	<b>0.708571</b>
<i>SGL-09-136B</i>	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	
<b><i>Sample Average (± 1 S)</i></b>	<b>0.96 (±0.16)</b>	<b>-3.14 (±0.09)</b>	
<b><i>Overall Average</i></b>	<b>1.09</b>	<b>-2.99</b>	—
<b><i>2 Std Err (n=10)</i></b>	<b>0.13</b>	<b>0.24</b>	—

**Table 2 Megafloral data**  
[Click here to download Table: Table 2 Megafloral data.docx](#)

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