

A COMPOSITIONALLY UNIQUE VOLTZIAN CONIFER-CALLIPTERID FLORA FROM A CARBONATE-FILLED CHANNEL, LOWER PERMIAN, ROBLEDO MOUNTAINS, NEW MEXICO, AND ITS BROADER SIGNIFICANCE

WILLIAM A. DIMICHELE¹, DAN S. CHANEY¹, HOWARD FALCON-LANG², HANS KERP³, CINDY V. LOOY⁴, SPENCER G. LUCAS⁵, KARL KRAINER⁶ AND SEBASTIAN VOIGT⁷

¹ Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, USA; ² Department of Earth Sciences, Royal Holloway, Egham, Surrey TW20 0EX, UK; ³ Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität Münster, Heisenbergstraße 2, 48149 Münster, Germany; ⁴ Department of Integrative Biology and Museum of Paleontology, University of California, 3060 Valley Life Sciences Building #3140, Berkeley, California 94720, USA;

⁵ New Mexico Museum of Natural History and Science, 1801 Mountain Rd. NW, Albuquerque, NM 87104, USA;

⁶ Institute of Geology and Paleontology, University of Innsbruck, Innsbruck A-6020 Austria; ⁷ Urweltmuseum GEOSKOP, Burg Lichtenberg (Pfalz), Burgstraße 19, D-66871 Thallichtenberg, Germany

Abstract—Among the Early Permian deposits in Prehistoric Trackways National Monument, Robledo Mountains, is a limestone-filled paleochannel in the Community Pit Formation, discovered by Jerry MacDonald. The paleochannel, which is ~ 140 m wide and 5-6 m maximum depth, contains a complex fill sequence, indicating a seasonally dry climate, and two distinct fossil plant assemblages. The base of the channel is a limestone conglomerate that contains permineralized logs and charcoal attributable to indeterminate waldchian conifers. The middle channel fill consists of multiple lenses of lime mudstone with a sparse brackish-to-marine water invertebrate fauna and a macroflora consisting largely of an undescribed voltzian conifer and the callipterid *Lodevia oxydata*; the deposit also contains in situ fossil roots, indicating at least sporadic plant colonization of the micritic muds. The upper portion of the channel fill is a micritic, gypsiferous lime mudstone that lacks macrofossils.

The significance of this deposit, despite its low diversity, lies in the great caution it presents regarding interpretations of evolutionary patterns based on direct reading of the terrestrial fossil record. This is indicated by the spatio-temporal occurrences of the two rare elements that make up the mid-channel flora. The voltzian conifer is the earliest member of this evolutionary lineage yet described, extending the known range by approximately 25 million years from the previously known occurrence, which itself extended the range approximately 10 million years. Similarly, the geographic range of *Lodevia oxydata* at the Late Pennsylvanian-Early Permian transition, is extended nearly 2500 km, from its previously most westerly known occurrence in West Virginia, USA. Together with the only other report from the Rotliegendes of Poland, it gives this species a total known range, based on these three widely separated and localized occurrences, of approximately 9000 km on today's earth. Clearly, prior to the latest Permian, when such conifers were abundant, the voltzians were significant tropical landscape elements somewhere, but have been incorporated into the fossil record rarely and thus their early history remains largely unknown. For the callipterid, temporal continuity throughout its known range cannot be established, so it cannot be determined if the plant occupied the full range at any given time, or only portions thereof. Nonetheless, the geographic sparseness of its appearances, in light of the high density of plant remains from the sites where it does occur, indicate that its fossil record also is highly incomplete. Such patterns of occurrence, if used in conjunction with indicators of climate and environment, serve to support inferences about where and under what conditions these plants lived and the kinds of taphonomic factors that influenced their preservation.

INTRODUCTION

There are instances, in the course of geological fieldwork, when the hand of fortune reveals the unanticipated and, often, the unimagined. Such discoveries may have significance that goes far beyond their seemingly miniscule spatio-temporal scope. They can open the way to consider possibilities not previously envisioned, and change understandings of pattern and process in significant ways.

In recent years, discoveries in the plant fossil record of what might be termed “outliers,” either biogeographically or stratigraphically, have increased awareness that much more of evolutionary interest was happening outside the preservational window of the fossil record than anticipated. Major lineages have been shown to have evolved earlier and appeared in geographic locations quite distinct from what their zeniths in the fossil record might indicate. As a few examples, consider the discovery of the typically Late Triassic, high southern latitude genus *Dicroidium* in Late Permian, equatorial latitudes (Kerp et al., 2006; Abu Hamad et al., 2008); the appearance of *Dioonitocarpidium*, another Late Triassic and Early Jurassic taxon, in the Early Permian equatorial realm (DiMichele et al., 2001); or the occurrence of a voltzian conifer in the latest Early Permian (Looy, 2007), a lineage previously known, and abundantly so, no earlier than the Late Permian. Other examples of either early or unexpectedly late occurrences can be extended to the Peltaspermales, both of the group as a whole (Kerp, 1988) and of the more derived, typically Mesozoic forms with radially symmetrical reproductive morphologies (Kerp et al., 2001), or even to the wholesale survival of a Middle Pennsylvanian-type Euramerican wetland flora into the Early Permian of the Cathaysian realm of western Pangea (Hilton and Cleal, 2007; Wang et al., 2012). All of these occurrences, and many others, suggest that great caution is necessary when using the

fossil record of terrestrial organisms as a direct chronicle of first and last occurrences or as a template for a direct reading of the course of evolutionary history.

Here we report a small limestone-filled, channel-form deposit of Early Permian age from Prehistoric Trackways National Monument, in the Robledo Mountains of southern New Mexico. This channel is filled with carbonate sediments preserving plant fossils that greatly extend the stratigraphic and geographic ranges, respectively, of two taxa: the so-called “voltzian” voltzian conifers and the callipterid *Lodevia oxydata*. These discoveries are important not only for understanding the evolutionary histories and biogeographies of these particular taxa. They serve as indications of just how great are the gaps in our understanding of ancient landscape dynamics and how we must be prepared to work among data sets and models as we develop mechanistic explanations of pattern.

GENERAL GEOLOGICAL CONTEXT

The fossil deposit under consideration was discovered by Mr. Jerry MacDonald, who first noted fossil wood (MacDonald, 1994). Later, one of the authors (SGL) found plant macrofossils in association with the wood while preparing a detailed measured section through this stratigraphic interval (Lucas et al., 1998a, b).

The channel is located in the Robledo Mountains in Doña Ana County, south-central New Mexico (Fig. 1). This exposure is within the Prehistoric Trackways National Monument, managed by the US Bureau of Land Management. Stratigraphically, it is within the Community Pit Formation of the Hueco Group (Fig. 1), which can be age-constrained, based on a variety of paleontological lines of evidence, particularly fusulinids, conodonts and ammonoids, to between the late Asselian and early Artinskian, Early Permian (Falcon-Lang et al., submitted).

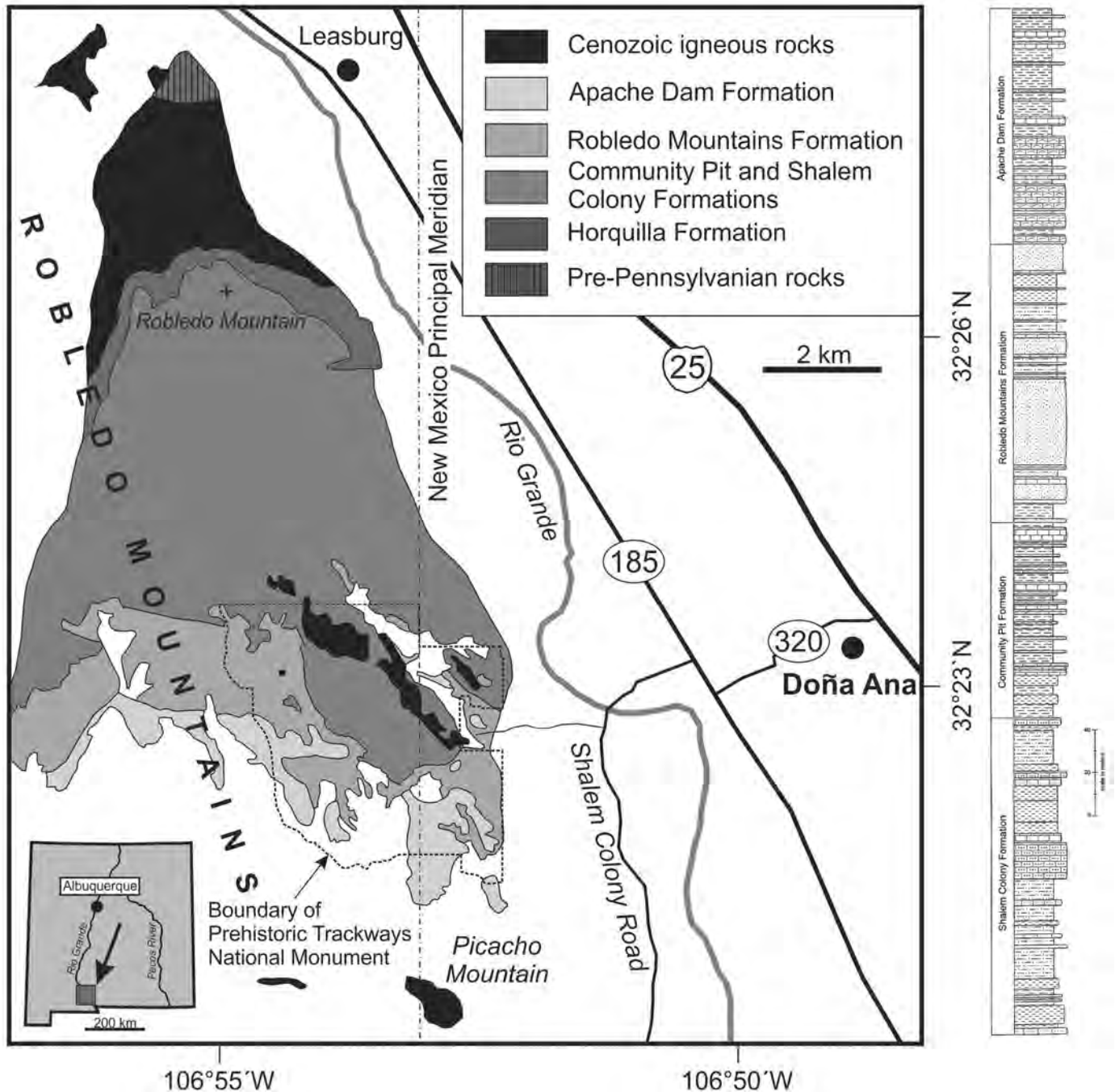


FIGURE 1. Location of the Prehistoric Trackways National Monument in southern New Mexico, within the Robledo Mountains. The fossiliferous channel deposit is within the lower part of the Community Pit Formation.

The Community Pit Formation is correlative with the lower part of the Abo Formation, which crops out prominently throughout central New Mexico (Lucas et al., 2011, 2013).

Throughout most of its outcrop area, the Abo Formation consists entirely of terrestrial red beds – mostly channelized siltstones and sandstones within and between pedogenically overprinted siltstones and, in some cases, claystones (volumetrically, most of the Abo Formation is mudrock). Rare carbonates represent either thin non-marine limestones or calcareous pedogenic horizons. Paleosols indicate a seasonal climate, likely dry subhumid to semiarid (Mack et al., 2010; Tabor et al., 2008). In south-central New Mexico, Early Permian terrestrial red beds interfinger with marine rocks of the Hueco seaway (Mack and James, 1986). These rocks comprise the mixed terrestrial-marine, siliclastic-carbonate Hueco Group, consisting of (in ascending order) the Shalem Colony, Community Pit, Robledo Mountains and Apache Dam formations (Lucas et al., 1998b, 2002). Paleosols and depositional

environments suggest a climatic background that was semi-arid on average (Mack et al., 2003, 2013). At the time of deposition, the area of Hueco Group deposition was peri-equatorial, perhaps 2° North (Tabor et al., 2008).

The Abo Formation flora (Hunt, 1983; DiMichele et al., 2001, 2012, 2013a) is composed nearly entirely of walcian conifers and the probable peltasperm, *Supaia* (White, 1929; Wang, 1997), with rare occurrences of the callipterids *Autunia conferta* and *Rhachiphyllum schenkii*, sphenophylls, peccopterid ferns, the pteridosperm *Neuropteris*, and the possible cycadophyte *Taeniopteris*. This flora is entirely different from that of the carbonate-filled channel in the Robledo Mountains, with which it is broadly contemporaneous.

PALEOCHANNEL-FILL GEOLOGICAL SETTING

The study site consists of a small paleochannel filled principally with carbonates. Paleozoic plant fossils are known and reported from

both marine and non-marine carbonates (e.g., DiMichele et al., 2013b), but such an environmental setting is not one from which such fossils are generally expected or sought. Micritic carbonates are primarily biogenic precipitates forming under climatic conditions chemically conducive to such activity – primarily strongly seasonally dry settings with high evapotranspiration, but with regular influxes of carbonate-rich waters. Such precipitates “set up,” that is they harden rapidly following exposure to air or to flushing by fresh water (e.g., Larrahondo et al., 2011), subsequent to which the incorporation of plant debris would be excluded. Thus, plant remains found as fossils in such carbonate muds had to be incorporated into the substrate while it was still under aqueous cover. Under such conditions, the growth environment of the parent plants was most likely one from which fossilized organic remains are rarely found.

The top of the paleochannel lies approximately 15.5 m above the local base of the Community Pit Formation. It is approximately 140 m wide and 5-6 m deep. The width is an approximation because of possible obliquity in the angle across which the paleochannel face is exposed by erosion. The paleochannel is somewhat asymmetrical in shape, with the eastern edge being steeper and more deeply incised than the western margin.

The paleochannel fill consists of three distinct facies. (1) In a restricted area in the center, and deepest portion of the channel, the 0.05-1.1 m thick fill is composed of an intraformational conglomerate composed mainly of marine limestone clasts most likely derived from the channel walls and local drainage basin. This unit also contains the remains of fossilized logs of walchian conifers, partially to completely preserved as charcoal (Fig. 2.1). (2) The middle unit is up to 4 m thick and consists of micritic limestone beds containing a sparse macrofauna of linguloids and pectinids, a microfauna of ostracodes, foraminiferans and possibly sponge spicules, and a macroflora dominated by voltzian conifers and the callipterid *Lodevia oxydata* (Fig. 2.2), and including unidentifiable tree trunks. This interval also contains scattered occurrences of fossilized fibrous root masses, which appear to have been preserved in situ, indicating rooting into the carbonate muds during the time of active accretion. (3) The uppermost 1.2 m of the

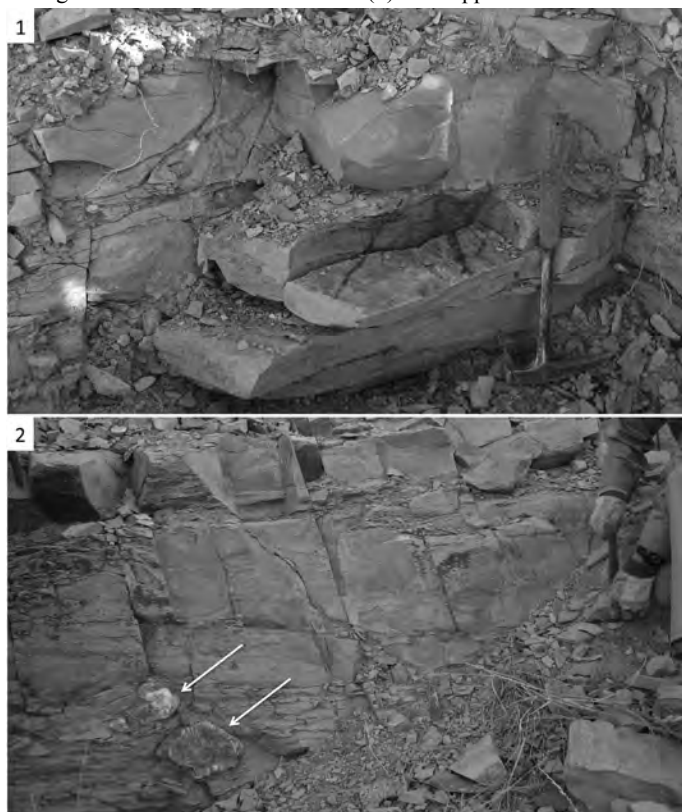


FIGURE 2. Geology of channel-fill deposit. 2.1, Micritic carbonates from mid-channel with plant fossils, visible on bedding surface. Hammer is 40 cm in length. 2.2, Lower portion of channel fill with silicified coniferophyte stems (white arrows) and micritic carbonates of middle channel fill above.

channel is filled with a dolomite containing gypsum nodules that lacks fossils.

FOSSIL FLORA

There are two distinct floras in the strata that compose the paleochannel. These floras are preserved in different facies, are compositionally distinct and preserved differently. They appear to be derived from spatio-temporally distinct kinds of vegetation and to reflect growth of the plants under different kinds of environmental conditions.

The older flora consists entirely of logs and wood fragments, some preserved as charcoal, and located exclusively in the basal-most conglomeratic unit. The anatomical characteristics of those specimens that could be studied, which are preserved mainly as charcoaled wood, indicate a walchian conifer affinity. In the absence of pith and detailed vascular features, a more confident assignment cannot be made. These specimens are described in detail in Falcon-Lang et al. (this volume). Walchian conifers are common and widespread in Early Permian deposits throughout western equatorial Pangea. The walchian conifer stem *Macdonaldodendron* Falcon-Lang, Kurzawe & Lucas (Falcon-Lang et al., 2014), has been described from allochthonous specimens preserved in offshore carbonate facies of the Community Pit Formation, but 50 or more meters above the carbonate channel-fill horizon.

The second flora is preserved in the middle unit of the paleochannel fill, in a micritic lime mudstone. Specimens are sparse and variably disposed within the micrites, and include foliage, branch fragments with attached foliage, carbonate permineralized trunks, and in situ fossil fibrous roots. The majority of the specimens are attributable to an undescribed form of voltzian voltzialean conifer (Fig. 3.1). These specimens consist of several vegetative morphotypes, some of which are probably assignable to the same species, and rare specimens of reproductive structures. Less abundant, but nonetheless common, is foliage of the callipterid plant *Lodevia oxydata* (Göppert) Haubold & Kerp (Fig. 3.2). Also notable in this assemblage are masses of taxonomically unattributable fibrous roots that must have penetrated the carbonate muds while they were still soft – and hence, almost certainly, water covered (Fig. 3.3). Rare elements of the flora include a few specimens of sphenopterid fern foliage, some fragmentary remains possibly assignable to *Walchia* sp., and a single specimen attributable to the sphenopsis *Annularia spicata* (Gutbier) Schimper. This flora is described in greater detail in Falcon-Lang et al. (submitted).

DISCUSSION

The fossil floras discussed herein are of importance for several reasons: depositional environment, inferred environmental circumstances, and floristic composition. All descends from the first – the peculiar depositional context of the fossils. The presence of fossil plants in micritic carbonate deposits may not be as unusual as it first appears; however, this is not a search image that most field-oriented researchers have in mind, and, consequently, may be frequently overlooked. An equally unusual example of a fossil deposit is one from the Middle Permian of North Texas, described in the literature as South Ash Pasture (DiMichele et al., 2004), which is preserved in a small, siltstone-filled channel that is incised into thick, primary gypsum beds and is overlain by oolitic limestone. Basically, the South Ash Pasture deposit would have been overlooked or bypassed for detailed examination but for the fortuitous find of fossil wood by a property owner. There is no simple “cure” for this problem, other than the prescription of “more field work.”

The fossil deposit in the Robledos is preserved in a small, incised paleochannel, cut through marine carbonate and siliciclastic strata (Fig. 4). The channel is, as far as we can determine, an isolated feature and thus unlikely to have resulted from channel switching. It may signal a drop in base level as an initiator of incision. Whether the change in base level was due to a eustatic sea-level drop or local to regional tectonism cannot be determined satisfactorily from the evidence at hand. Eustasy, in particular, should have had a widespread effect. Mapping throughout the Prehistoric Trackways National Monument has not revealed any additional features of this nature in the same stratigraphic interval. The Asselian-Sakmarian time period, however, was within the Early Permian glacial interval (Montañez et al., 2007; Fielding et al., 2008), so a eustatic cause must remain a possibility. Tectonism is a significant unknown in this instance. The Robledo Mountains area was in the then tectonically active Orogrande Basin, though a more broadly visible physical fingerprint might be expected were local tectonism the cause

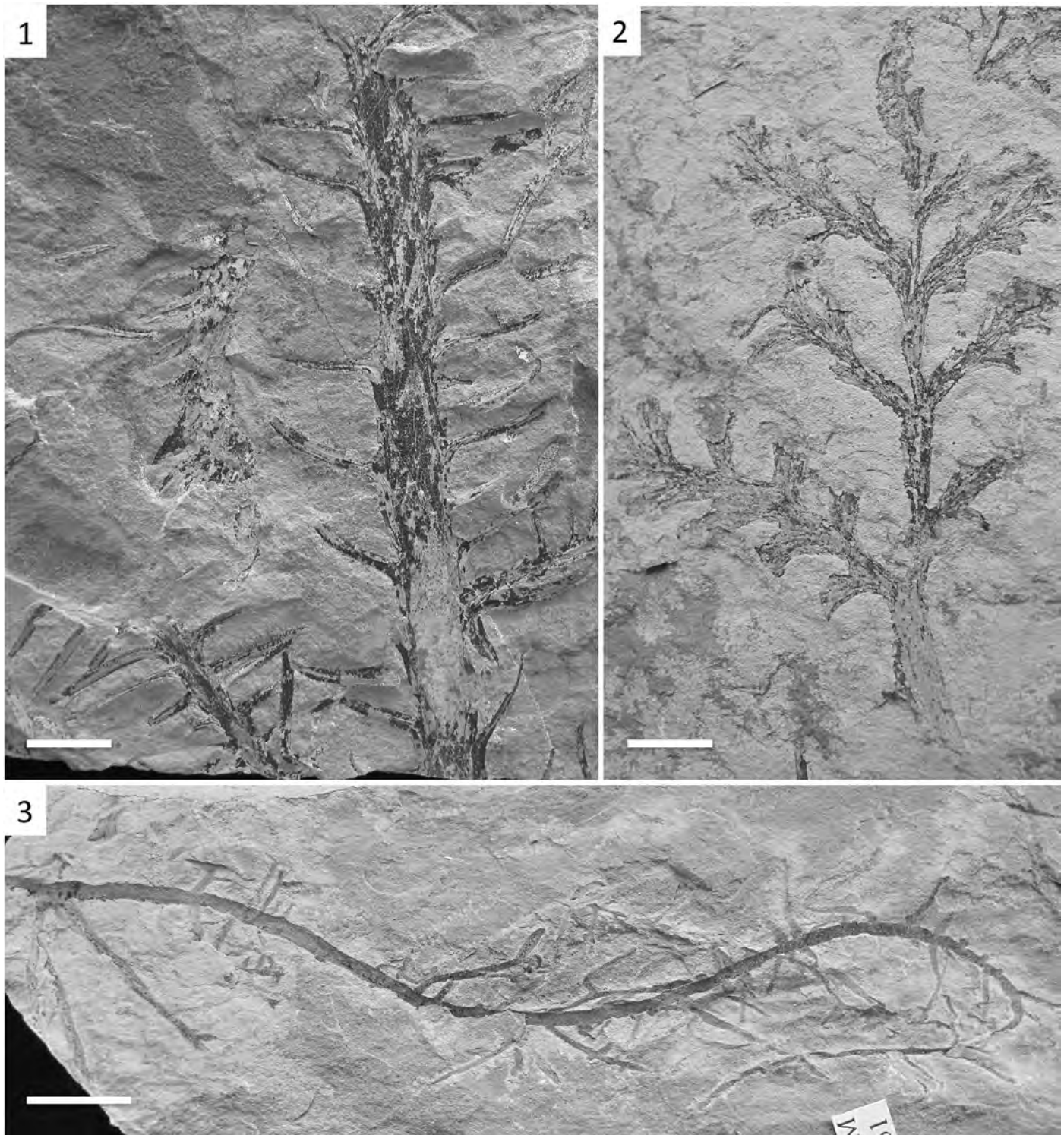


FIGURE 3. Channel-fill plants. **3.1**, Voltzialean conifer branch with attached foliage. NMMNH Specimen P-68872, NMMNH locality 3016 (USNM locality 43550). **3.2**, *Lodevia oxydata*, callipterid foliage. NMMNH Specimen P-68873, NMMNH locality 9123 (USNM locality 43554). **3.3**, Roots of indeterminate affinity. NMMNH Specimen P-68874, NMMNH locality 9124 (USNM locality 43551). All scale bars = 1 cm.

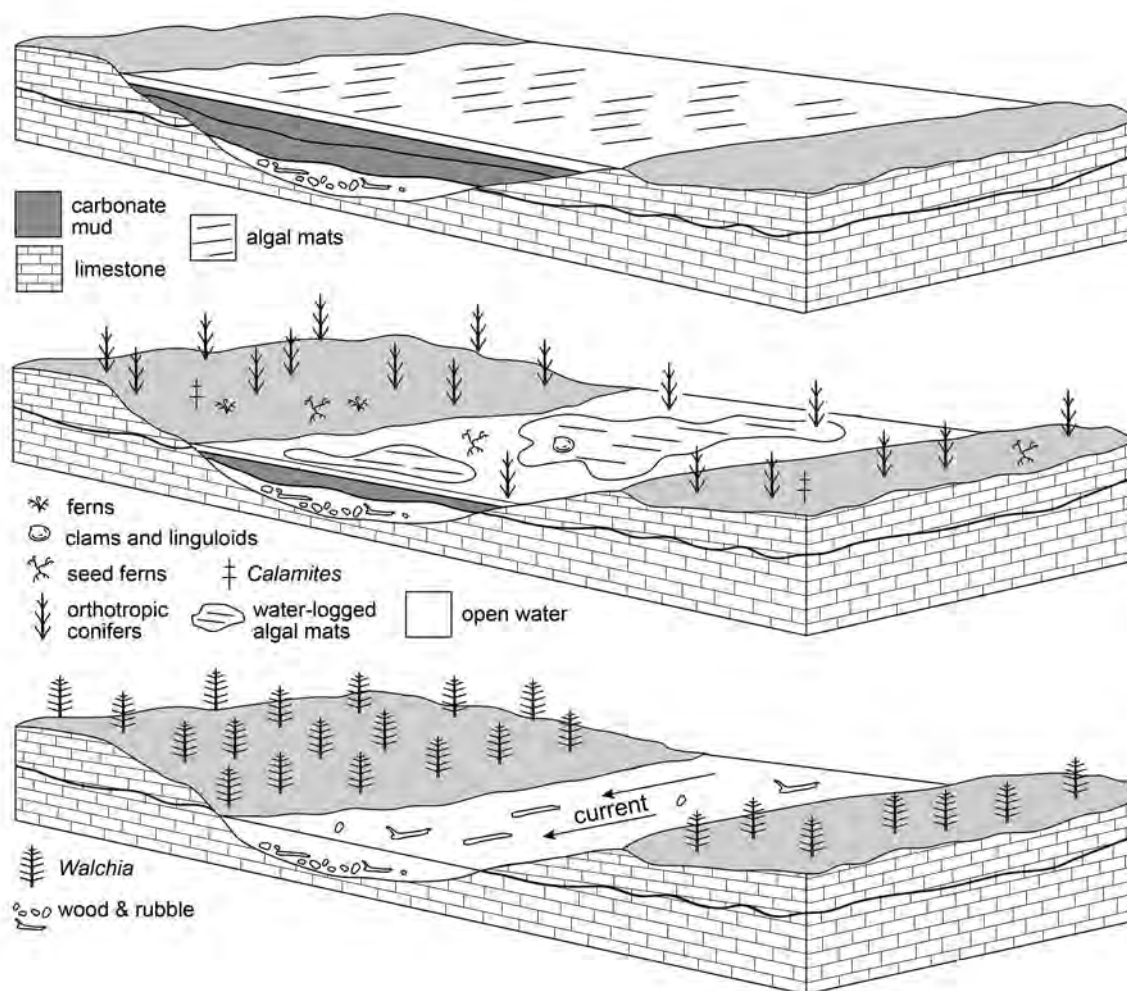


FIGURE 4. Channel-fill progression model. **Bottom.** Active flow during incision phase and early back filling. **Middle.** As the channel fills flow volume decreases and carbonate precipitation ensues; surrounding flora changes and plants are incorporated into the micritic muds. **Top.** Evaporitic conditions intensify in final channel fill phases and gypsum is deposited in association with micritic muds.

of subsidence-initiated channel incision.

In terms of glacial-interglacial cycles, there are reasonable expectations that lowstand coastal deposits are among the most likely to be preserved on intermediate-term time scales because they can be buried by marine incursions, isolating organic material from degradation for tens of thousands of years. Such intermediate-term burial gives regional tectonism time to create long-term accommodation space, if the area is within a basinal setting (Gastaldo and Demko, 2011). It might be hypothesized, therefore, that a eustatic rise in sea level following incision would most likely result in preservation of a fossil flora composed of the most commonly encountered taxa found in the area surrounding the deposit. Alternatively, if the cause of channel incision were tectonic, it presents the possibility that accommodation space was created at a portion of the glacial-interglacial cycle not usually conducive to intermediate and long-term preservation of organic debris, such as during high-stand or falling stages of sea level. Under such circumstances, the possibility arises of capturing a terrestrial flora not normally preserved in the fossil record.

Another peculiar aspect of the depositional conditions of the paleochannel fill is the preservation of the mid-channel flora within brackish-to-marine micritic carbonates. The presence of sparse linguloid and pectinid invertebrates, and the composition of the microfauna within the micrites suggests such salinities. This flora is composed of two very unusual taxa, a voltzian voltzialean conifer and *Lodevia oxydata*. In order for these fossils to be incorporated into a micritic mud, the substrate would need to have been soft and actively accumulating. This would require water cover, given that such muds almost certainly reflect the activities of carbonate-generating organisms and that such micrites would have solidified to a concrete-like texture

within a very short time (days to weeks) once exposed to the air or flushed with fresh water. Thus, the plants were either growing on the margins of the paleochannel or, given the presence of fibrous roots in the micritic carbonates, perhaps even in the paleochannel itself, which may have been mostly sediment filled and under shallow water cover during the middle and later phases of backfilling.

The environmental conditions recorded by the paleochannel deposit suggest climatic aridity, during base-level rise and channel filling (Fig. 4). The oldest deposits in the channel are composed of an intraformational, marine-carbonate conglomerate, composed of clasts similar compositionally to the channel walls. This kind of deposit indicates enough moisture on the landscape, at least periodically, to contribute to streams that could locally transport clasts of large size. In addition, the deposit contains some walchian-like coniferophyte logs, which are most likely to have grown under seasonally dry, subhumid to, perhaps, semi-arid climate (Bashforth et al., 2014). This basal-most deposit most likely formed as a lag in the channel bottom during incision or as back-filling was initiated.

The middle part of the paleochannel is composed of micritic carbonates, which appear to be an in situ accumulation of lime mud most likely precipitated by biogenic activity. An environment suitable for such carbonate precipitation would have to have been able to support a community of bacteria and algae capable of creating such sediment, thus wet enough to maintain at least some surface water cover in the paleochannel, but with limited flow volumes compared to the earlier formed deposit. Local soil moisture also had to be sufficient enough to support trees, or at least shrubs, and some groundcover plants, either on the paleochannel margins or in shallow water portions of the channel, or both. The final phase of paleochannel filling (Fig. 4, top

panel) does not contain fossil flora, and the micritic carbonate matrix includes concentrations of gypsum, suggesting that this final phase may have become semi-arid to arid, though the gypsum is not primary and thus may not be a direct reflection of climate at the time of limestone formation. Nonetheless, the paleochannel provides an unusual look at changing environmental circumstances and the vegetational changes that accompanied this.

From the biological viewpoint, the flora from the middle unit of the paleochannel is exceptional. The conifer occurrence extends the range of this evolutionary lineage to an earlier time by approximately 25 million years, the previously earliest occurrence being at the Early-Middle Permian boundary (Looy, 2007). The *Lodevia oxydata* fossils extend the geographic range of that taxon by approximately 2500 km, from an occurrence in the Appalachian Basin (DiMichele et al., 2013b), to a total range, based on only three occurrences (the eastern most from Poland), of over 9000 km (this would, of course, be a still substantial ~ 6000 km in the Early Permian world). These extensions, not the first of their kind, are both remarkable and serve as a warning. Previously reported outlying, early appearances of such plants as *Peltaspermum* (Kerp et al., 2001), *Dioonitocarpidium* (DiMichele et al., 2001), *Dicroidium* (Kerp et al., 2006), or voltzian voltzialean conifers (Looy, 2007) have changed both our understanding of the temporal and biogeographic distributions of these plants. Such patterns of fossil distribution in time and space indicate a great deal of undetected biological dynamics that must be inferred from isolated, often unique occurrences. As such, they serve as points of interaction with models of evolution and its relation to space and time more than they serve as parts of a well represented, direct record of the evolutionary process.

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