FOSSIL FLORAS FROM THE PENNSYLVANIAN-PERMIAN CUTLER GROUP OF SOUTHEASTERN UTAH

by

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ABSTRACT

Fossil plants have been collected and described from strata near the Pennsylvanian-Permian boundary in three areas of San Juan County, Utah. Collections made near Indian Creek east of Canyonlands National Park comprise mainly tree fern foliage and sphenopsids from one stratigraphic level, and large logs of conifers with rare conifer foliage from a higher level. A site on Lime Ridge west of Bluff, Utah, yielded abundant large branches of walchian conifers together with calamitaleans and cordaitalean foliage. Sites in Valley of the Gods State Park, west of Lime Ridge, produced mainly stems, with variable occurrences of foliage. Most of the stems are calamitalean or the large tree fern *Caulopteris*, but a single medullosan pteridosperm specimen also was found, as were several small fragments of the lycopsid *Sigillaria*. Tree fern foliage, *Pecopteris*, rare neuropterid foliage, and fragments of leaf-bearing conifer branches also were identified. Thus, our collections contain a mixture of plants adapted to seasonally dry conditions (conifers and possibly cordaitaleans) and those requiring wet substrates (calamitaleans, tree ferns, lycopsids and pteridosperms). Red beds, dune sands, loess, and gypsum indicate aridity, on average, but with intervals of more humid conditions. The combination implies an arid eolian depositional system traversed at times by streams sourced on the Uncompahgre highland.

INTRODUCTION

Floras of the Pennsylvanian-Permian transition are broadly represented across the equatorial regions of the supercontinent of Pangea (e.g., Kerp and Fichter, 1985; Tidwell, 1988; Hunt and Lucas, 1992; Blake and others, 2002; Roscher and Schneider, 2006; Wagner and Álvarez-Vázquez, 2010; Blake and Gillespie, 2011; Lupia and Armitage, 2013; Opluštil and others, 2013; Tabor and others, 2013; Wang and Pfefferkorn, 2013). The content of these floras is similar, especially in the Euramerican areas, which stretch from the present-day western United States through Eastern Europe (figure 1). Many taxa typical of Euramerican floras also occur in Chinese/Cathaysian assemblages (Hilton and Cleal, 2007). On average, these floras reflect the long-term, multi-million-year trend of increasing aridity that characterized much of the Pangean tropics beginning in the late Middle Pennsylvanian (Cecil, 1990), particularly in the central and western areas. However, the floras also reveal a considerable amount of spatio-temporal variability in expression of this trend. In western Pangea in particular, especially in areas some distance north of the equator, the long-term aridification trend may have been reversed in the short term by a limited period of increased moisture input around the Pennsylvanian-Permian boundary (Tidwell, 1988; Soreghan and others, 2002).

This article describes fossil plants from three areas in San Juan County, Utah, from approximately the Pennsylvanian-Permian boundary. These floras are of interest for several reasons. Perhaps most importantly is their paleogeographic position, in far western Pangea. Based on sedimentary patterns and studies of paleosols, this area experienced extreme aridity through most of the later Pennsylvanian, but apparently experienced a return of sufficient moisture during latest Pennsylvanian and earliest Permian to dramatically alter the regional environments before arid conditions returned (Soreghan and others, 2002; Tabor and Poulsen, 2008; Jordan and Mountney, 2012). The period of resurgent moisture was wet enough to support some species typically found in wetland floras of the same age, in the more central parts of the Pangean supercontinent. The floras found in San Juan County are mixed, including species typical of seasonally dry environments as well as the wetland taxa. Mixed assemblages strongly suggest an overall landscape of seasonal moisture limitation, within which the wetland taxa were confined to parts of the landscape with high-water tables, such as the margins of rivers and streams or low-lying parts of floodplains. Such places are also the most favorable for preservation, thus making the wetland plants "more apparent" than might be expected were the fossil flora drawn proportionally from all habitats on the landscape of the time. It is difficult to account for the presence of taxa adapted to periodically dry substrates within overall wetland landscapes characterized by humid

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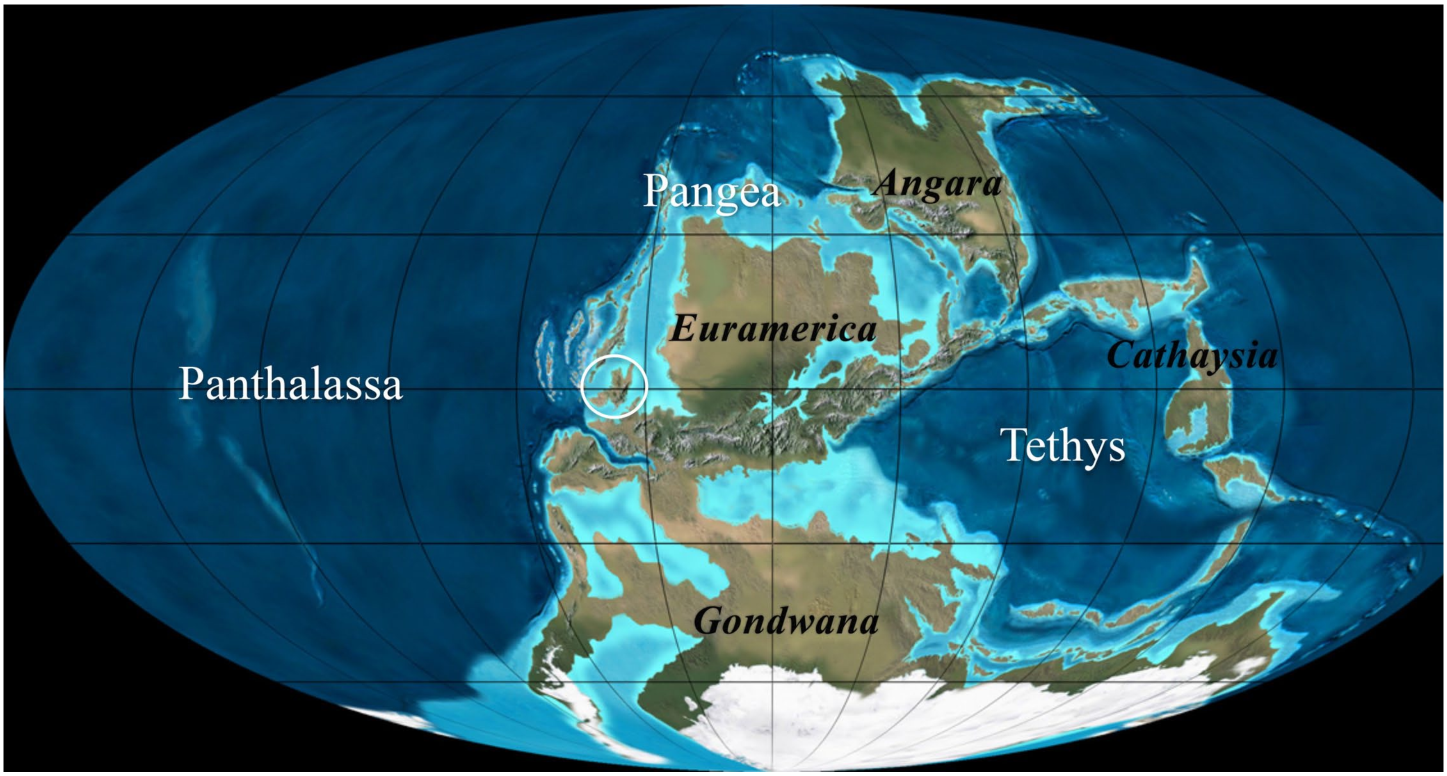

Figure 1. Paleogeographic reconstruction of Pangea and major oceanic areas at the approximate time of the transition from the Pennsylvanian to Permian. Study area marked by white circle. Map courtesy of Ron Blakey, Colorado Plateau Geosystems, Inc.

climates; in contrast, localized wetter areas, within otherwise seasonally dry backgrounds, are commonly found and permit wetland-plant survival in isolated patches or narrow corridors—as in the western United States today.

Herein we report floras from three areas in present day San Juan County, Utah: Lime Ridge, Valley of the Gods, and Indian Creek (figure 2). These floras, composed predominantly of walchian conifers, calamitaleans and marattialean tree ferns, complement a richer and better-preserved flora described by Tidwell (1988) from the Moab area northeast of Indian Creek. In addition, we note evidence for widespread vegetation, even in areas where no macroflora has been identified (or preserved).

GEOLOGY

Tectonic Setting

The localities discussed in this paper are situated in the southwestern part of the Paradox Basin, a Pennsylvanian-age feature that underlies much of southwestern Colorado and southeastern Utah (figure 2). The Paradox Basin is a intraforeland flexural basin (Barbeau, 2003) separated from the Uncompahgre Uplift to the northeast by a major fault zone. Development commenced during the Middle Pennsylvanian, when cyclic carbonate, evaporite, and clastic strata, more than 2 kilometers thick in places, accumulated in the nearly land-locked basin. By Late Pennsylvanian time, tectonism was winding down and sedimentation outstripped subsidence. During the Pennsylvanian-Permian transition, the study area became the site of fluvial, eolian, and restricted marine sedimentation under a climatic regime that fluctuated from arid to subhumid (Baars and Stevenson, 1981; Dubiel and others, 1996; Soreghan and others, 2002).

Stratigraphy

Stratigraphic nomenclature applied to latest Pennsylvanian and earliest Permian rocks in the Paradox Basin is complex, and some aspects remain controversial. A full exposition is beyond the scope of this paper, but see Soreghan and others (2002) and Huntoon and others (2002). Broadly speaking, during the Late Pennsylvanian time dominantly marine strata gradually gave way to alternating layers of gray marine limestone and red terrestrial siliciclastics, with the latter increasing through time. Various authors applied the names Honaker Trail, Rico, and Elephant Canyon formations to the transitional rocks. Proximal to the systemic boundary, the succession consists entirely of red beds that have been assigned to the Cutler Group or Formation. Unit boundaries are time transgressive and intertongue on a large scale (figure 2). As discussed briefly below, the fossil floras highlight some ambiguities in the way time horizons have been drawn through the various, often environmentally distinct strata.

Lime Ridge and Valley of the Gods

Our collections from Valley of the Gods and north of Snake Canyon at Lime Ridge, southern San Juan County,

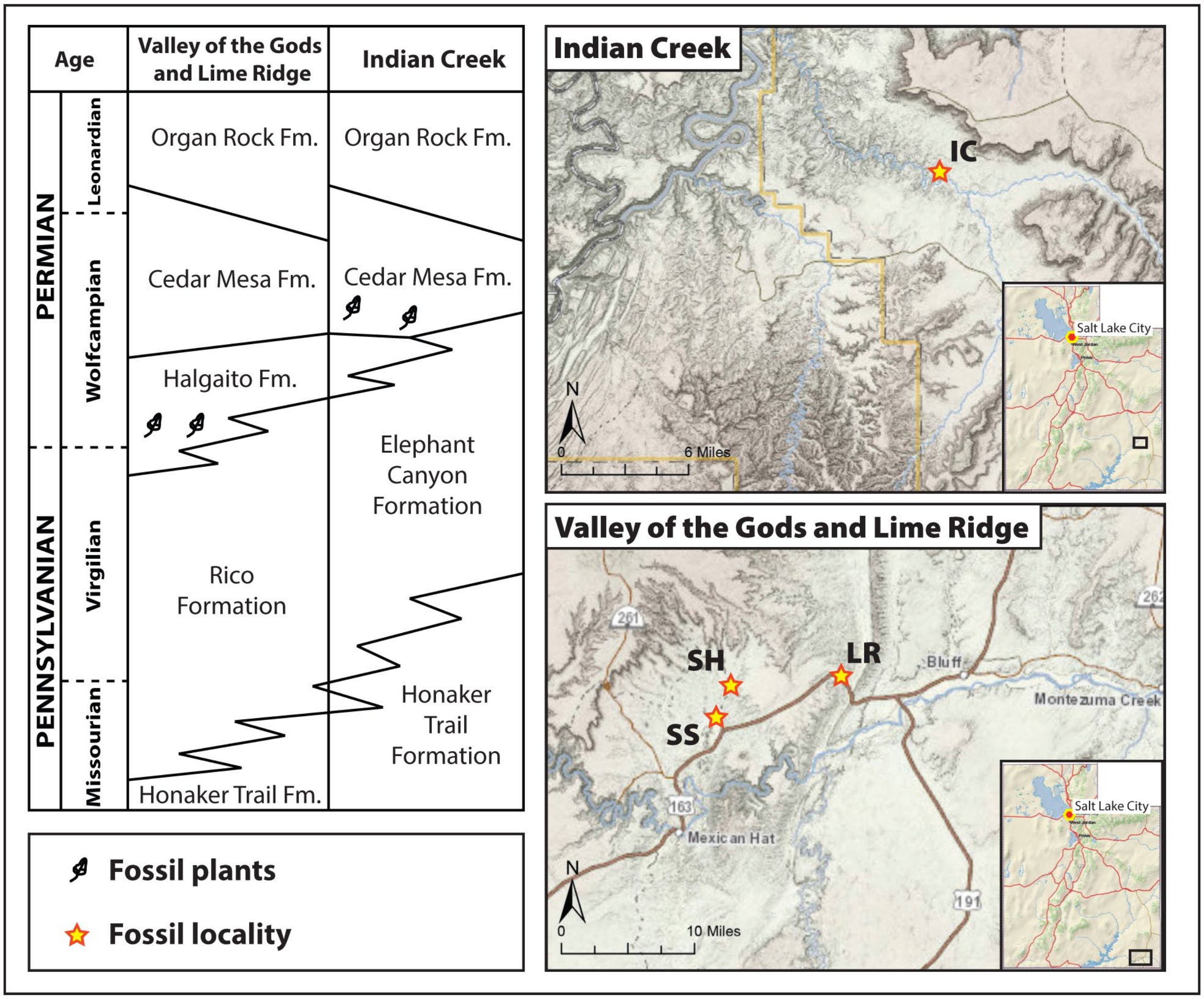

Figure 2. *Stratigraphic terminology used and geographic location of samples discussed and in this paper. IC = Indian Creek, LR = Lime Ridge, SH = Setting Hen, SS = Seven Sailors.*

are from the Halgaito Formation (figures 2 and 3). In Valley of the Gods, the Halgaito and overlying Cedar Mesa Sandstone have eroded to pinnacles and buttes that have been given fanciful names such as Santa Claus and Rudolph, De Gaulle and His Troops, and Rooster Butte. These natural sculptures are reminiscent of those in the better-known Monument Valley to the south in Arizona, but there the pinnacles are carved from the younger Organ Rock Formation and De Chelly Sandstone.

Variously classified as a formation, member, or tongue of the Cutler Group or Formation (Baker and Reeside, 1929; O’Sullivan, 1965; Dubiel and others, 1996), the Halgaito is 70-120 meters thick and consists of predominantly red mudstone, siltstone, sandstone, and minor conglomerate (figure 3). Below the Halgaito is the Rico Formation, a unit of terrestrial red beds alternating with thin but widespread layers of fossiliferous marine limestone. The Rico-Halgaito contact is time transgressive. Above the Halgaito is the Cedar Mesa Sandstone, which undergoes a marked facies change between Valley of the Gods and Lime Ridge. In the type area north of Valley of the Gods, the Cedar Mesa Sandstone is predominantly an eolian facies of cliff-forming sandstone that is light colored, fine grained, and exhibits giant-scale cross-bedding. Within a few kilometers eastward, the Cedar Mesa Sandstone changes to interbedded sandstone, mudstone, siltstone, gypsum, and thin layers of cherty limestone. A measured section through the Cedar Mesa Sandstone at Lime Ridge is 257 to 278 meters thick, depending on the choice of upper contact.

The age of the Halgaito Formation is loosely constrained. According to Vaughn (1962), its vertebrates point to Wolfcampian (early Permian) age. Invertebrate fossils from the uppermost Rico limestone beds favor a Late Pennsylvanian age, but an earliest Permian age cannot be ruled out (O’Sullivan, 1965).

A Halgaito section measured north of Snake Canyon at Lime Ridge (figures 3 and 4.1) is 76 meters thick and contains about 50% sandstone that is light gray to medium reddish brown, very fine to fine grained, and calcareous. Low-angle cross-bedding and ripple marks are common, as are shallow channels. Other features include mud cracks, indistinct burrows and root traces, and zones of carbonate nodules (pedogenic?). Most sandstone apparently represents deposits of small streams, which is where plant

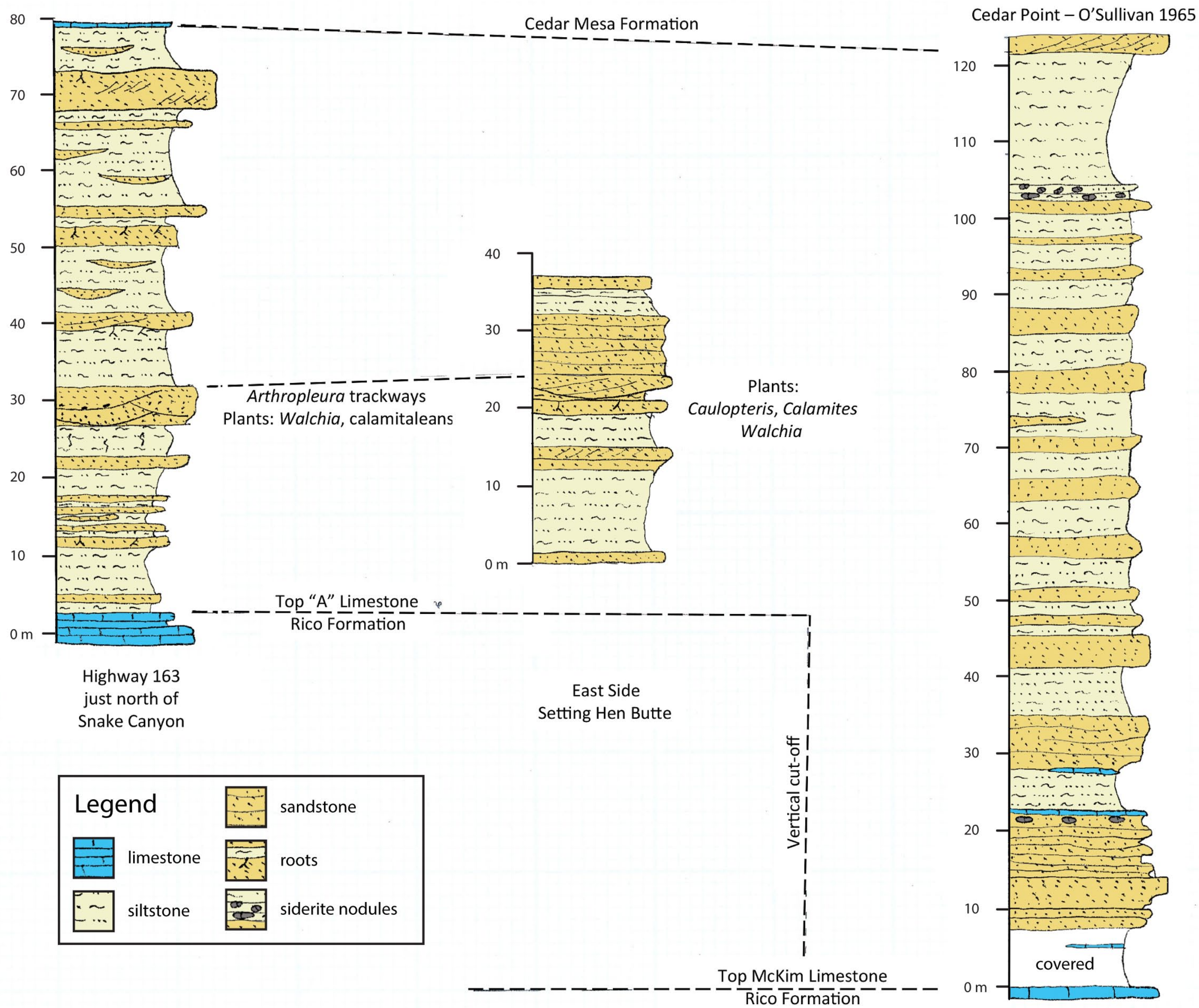

Figure 3. *Measured lithological sections from the east flank of Lime Ridge (Highway 163, just north of Snake Canyon), Setting Hen Butte (Valley of the Gods) and Cedar Point. Scale in meters.*

fossils are preserved (figure 4.2), but a few massive beds may represent accumulations of wind-blown sand and silt. Separating sandstone beds are intervals of mudstone and siltstone, largely red to brown with gray mottling. Some beds have blocky structure and indistinct roots and burrows, suggestive of weak soil development. Beds of massive siltstone, especially a prominent orange bed near the base of the Halgaito, may have formed as eolian deposits (loess). Beds of silty, micritic limestone less than 20 centimeters thick and lenses of intraformational conglomerate are rare constituents.

We collected fossil plants from the Halgaito: (1) on the east flank of Lime Ridge along U.S. Highway 163, (2) near Setting Hen Butte in Valley of the Gods, and (3) near Seven Sailors Butte in Valley of the Gods. As best we can determine, all three sites occur between 20 and 25 meters above the base of the Halgaito, and thus are in the same plant-bearing interval of small channels (figure 3). The host rock in all cases is fine-grained, thin- to medium-bedded sandstone sometimes having clay drapes along bedding surfaces, which enhance fossil preservation. It is arranged in a series of crosscutting shallow channels, each a meter or so deep and 10 to 20 meters wide. It cannot be established, however, that the channel deposits at Lime Ridge belong to the same southwest trending, sandstone-filled channel or channel complex identified at both Setting Hen Butte and Seven Sailors Butte (figures 2, 3, and 5.1-5.3). Shark teeth and unidentified bone fragments occur in the basal conglomerate of a channel near Seven Sailors Butte; the original environment of deposition of these vertebrate remains cannot be established given their preservation in channel-lag deposits. *Diplichnities*, the trackway of a giant myriapod, was collected at Lime Ridge (Chaney and others, 2013).

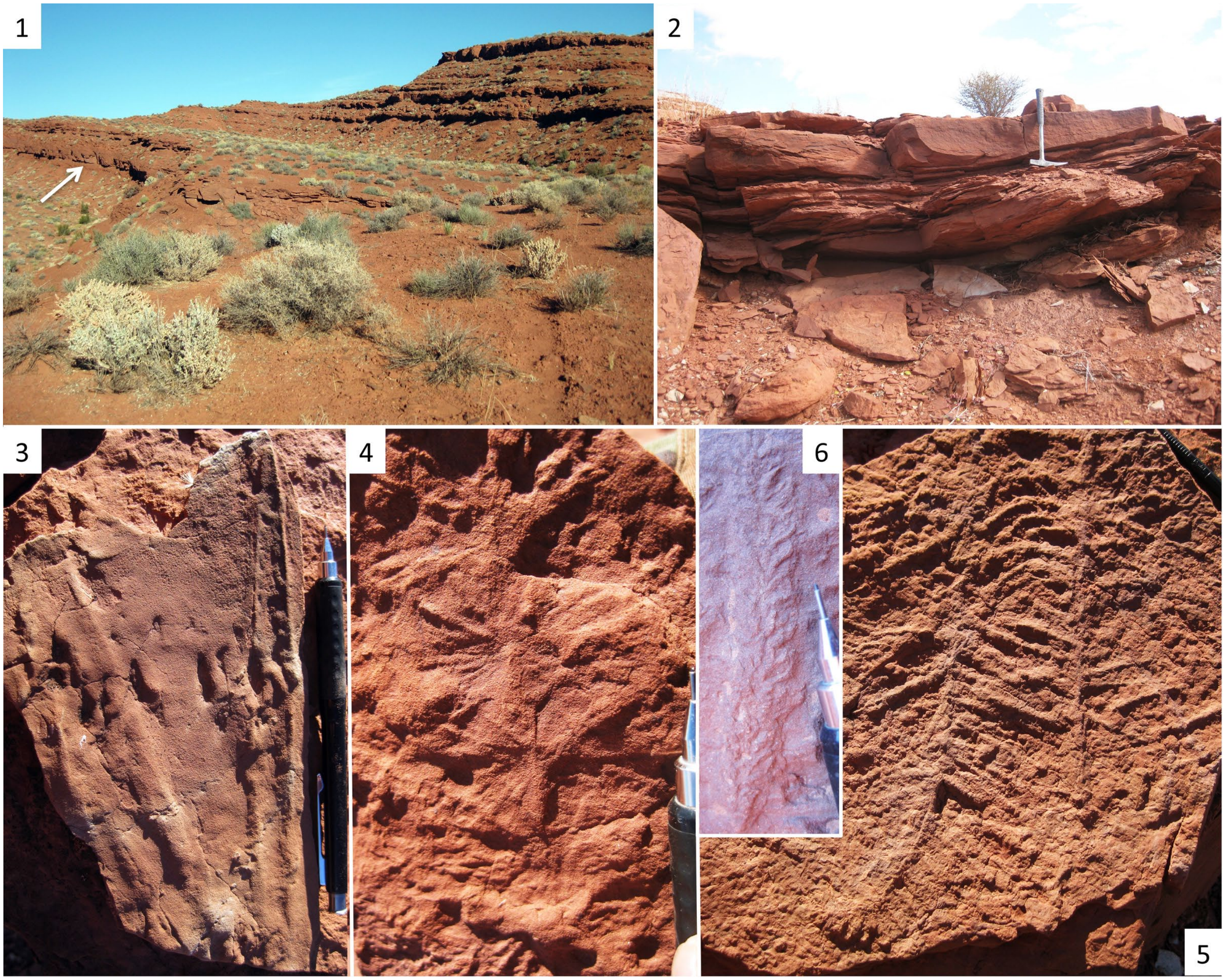

Figure 4. *East flank of Lime Ridge. 1. General view of the fossil-bearing channel deposit, from which plant collections (USNM locality 43579) were made, forming the low ridge in the lower portion of the outcrop (white arrow). 2. Detail of fossiliferous channel sediments, comprising a trough-shaped sandstone-filled scour. 3.* Cordaites *sp. foliage. USNM559863. 4.* Annularia *sp. USNM559862. 5.* Walchia *sp. Mat of branches, including a branch base (center left). Pencil barrel for scale in upper right corner. USNM559864. 6.* Walchia *sp. Ultimate branchlet. Field photograph.*

Indian Creek

Indian Creek is a northwest-flowing tributary of the Colorado River in northern San Juan County. Our collections were made near the stream approximately 19 kilometers northeast of the junction of the Green and Colorado Rivers (figure 2).

Plant fossils occur in rocks that Huntoon and others (1982) mapped as "undivided Cutler-Cedar Mesa Sandstone transition." For brevity, we refer to this unit as the Cedar Mesa Sandstone. Most of our collections came from the basal 10 meters of the Cedar Mesa Sandstone, but two collections of mineralized logs were made 20 to 30 meters above the base. Plant compression fossils occur in thin-bedded siltstones, which fill scours and are intercalated with thin, trough-shaped beds of sandstone. These lie immediately above rooted, calcic Vertisols and below cross-bedded sandstones of possible eolian origin (figures 6.1-6.4). The plant-bearing deposits appear to constitute a floodplain sequence.

Based on mapped elevation change and structural dip of 2° to the northeast, the Cedar Mesa Sandstone is approximately 120 meters thick in the collecting area. This unit is composed of sandstone, siltstone, and mudstone in various shades of red. The lower half of the formation is roughly 90% sandstone in beds as thick as 20 meters, which erode to a series of joint-bounded buttes and monoliths. Most of the sandstone is light colored, fine grained, well sorted, and exhibits cross-bedding in sets many meters thick. Interpreted as eolian dunes, these strata locally contain gypsum crystal casts, chert formed in interdune sabkhas, and logs of silicified wood. Other sandstone in the lower Cedar Mesa Sandstone is deeper reddish brown and displays low-angle

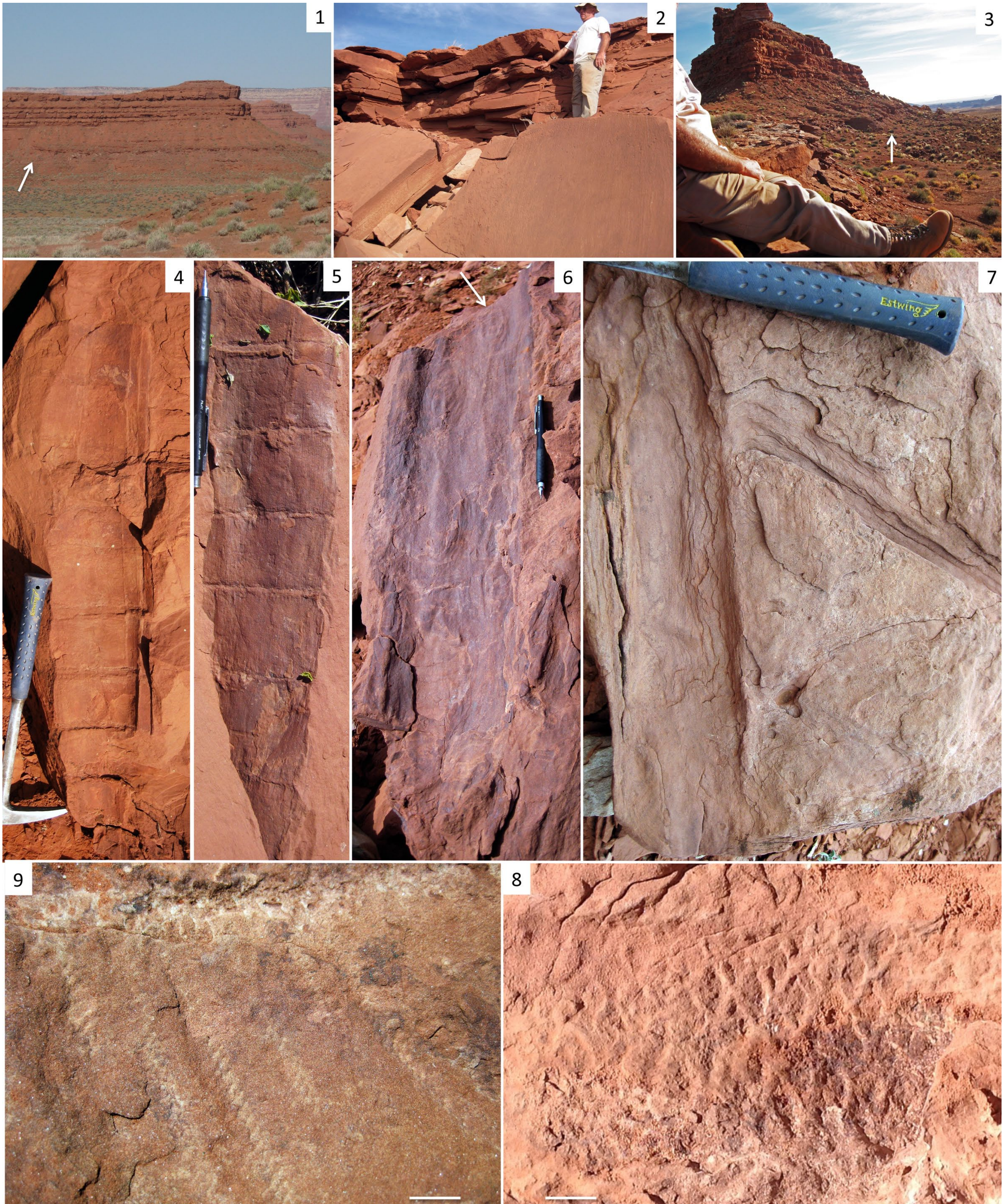

***Figure 5.** Valley of the Gods. 1. Seven Sailors Butte. Fossiliferous channel edge marked by white arrow. Channel deposits extend to the right as resistant ledge. 2. Setting Hen Butte. Tabular, planar-laminated sandstone from which* Walchia *sp. (5.9) was collected. 3. Setting Hen Butte. View of fossiliferous channel, base marked by white arrow. 4.* Calamites gigas. *Field photograph. 5.* Calamites gigas. *Field photograph. 6.* Caulopteris *sp. USNM559861. 7. Medullosan pteridosperm stem with reflexed leaf petiole; a less obvious petiole is present in the lower part of the stem. Field photograph. 8.* Sigillaria brardii. *Scale = 1 centimeter. Field photograph. 9.* Walchia *sp. Scale = 1 centimeter. Field photograph.*

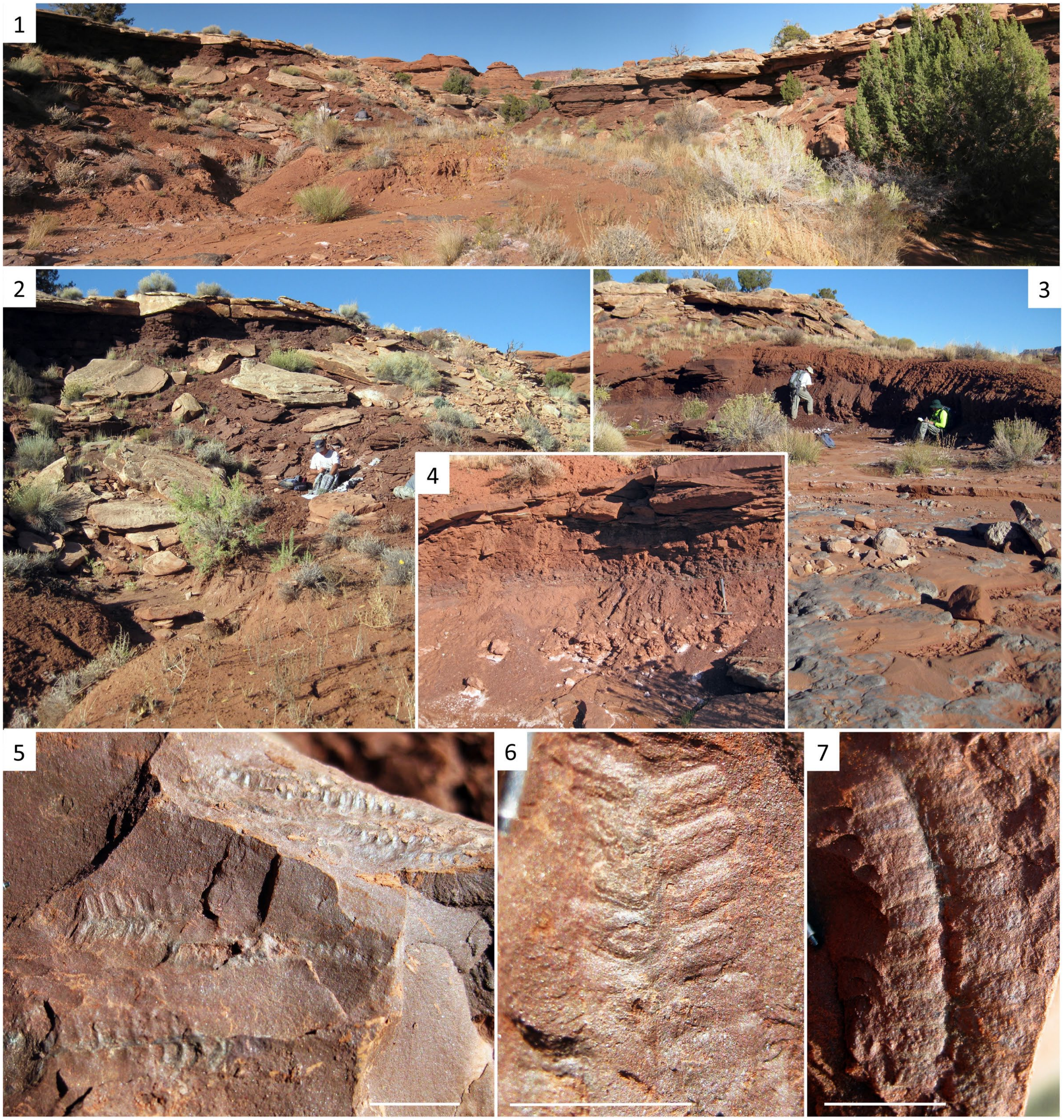

Figure 6. *Indian Creek. 1. Collecting area USNM locality 43582. Collections made in left side of area. 2. Collecting site USNM locality 43582, closeup. 3. Collecting area USNM locality 43577. 4. Collecting site locality 43577, closeup. Plants come from clayey shale immediately below the sandstone ledge. 5.* Pecopteris *sp., showing three pinnae. USNM559865. 6.* Pecopteris *sp. Closeup of central pinna illustrated in 6.5. 7. Fertile pecopterid,* Asterotheca *sp., pinna fragment. USNM559866. Scale bars in 5-7 = 1 centimeter.*

cross-bedding along with cut-and-fill features characteristic of fluvial channels. Less resistant to erosion, most mudstone and siltstone is also dark reddish brown, non-fissile, and non-fossiliferous. Locally, deposits of laminated to thinly bedded shale and siltstone have yielded fossil foliage and stems.

Underlying the Cedar Mesa Sandstone at Indian Creek is the Elephant Canyon Formation, which consists of terrestrial red beds alternating with thin but widely traceable beds of marine limestone (Baars, 1962, 1991). The upper contact is drawn at the top of the stratigraphically highest limestone (Huntoon and others, 1982). The Elephant Canyon resembles the Rico Formation, but evidently is younger, as the Elephant Canyon intertongues southward with the Halgaito Formation and yields both Virgilian and early Wolfcampian fusulinids (Loope and others, 1990; Sanderson and Verville, 1990). On this basis, fossil plants from the basal Cedar Mesa Sandstone are definitely Permian, and likely are younger than those from Lime Ridge and Valley of the Gods.

FOSSIL FLORAS

Floras from all three sites are noteworthy for containing a distinct wetland element. This finding contrasts with the abundant evidence of Late Pennsylvanian and early Permian climatic aridity over large areas of western Pangea, exemplified by extensive deposits of loess, dune sands and evaporites (e.g., Langford and others, 2008; Tabor and Poulsen, 2008; Sur and others, 2010; Dubois and others, 2012; Jordan and Mountney, 2012). The typically xeromorphic, seasonally dry floral component of our floras varies in abundance, type of preservation, and implications about the landscape in which it existed. Although none of these fossils are museum-quality "trophies", they yield valuable insights into the landscape and climate of western equatorial Pangea during this time.

All collections described in this paper are housed in the U.S. National Museum of Natural History, Paleobotanical Collections, under the following locality numbers:

1. Lime Ridge—43579
2. Setting Hen Butte—43580-43581
3. Seven Sailors Butte—43583-43686
4. Indian Creek lower level—41414-41419, 41652, 43577, 43582
5. Indian Creek upper level—41413, 41420, 43578

Lime Ridge

The flora from the shallow-channel complex at the Lime Ridge site is dominated by walchian conifers, but also contains a significant component of calamitaleans, including foliage, and rare cordaitalean foliage (figures 4.3-4.6). Walchian specimens occur as fragments of branches and as whole lateral branch systems, sometimes densely matted. They are present throughout the site on many bedding surfaces. Walchians correlate closely with physical environmental indicators of seasonal aridity (Falcon-Lang and Bashforth, 2005; Bashforth and others, 2014), mostly likely dry subhumid to semiarid climates (sensu Cecil and Dulong, 2003). Calamitalean fossils, including large branches with attached foliage, are common. Although these fossils are not well enough preserved for specific identification, their ovoid foliage whorls and large number of leaves resemble *Annularia carinata*. Cordaitalean foliage shows characteristic strap-shaped, elongate leaves with bluntly pointed tips but, again, cannot be identified to the species level. On the basis of thousands of observations from across Euramerica over the past 150 years, calamitaleans can be regarded confidently as preferring habitats with high soil moisture. The group is complex, however, and many of the species, such as those found in the deposits described here, appear to have been able to colonize rapidly shifting substrates (Gastaldo, 1992), including within active rivers, and to have been able to grow in the wetter parts of otherwise dry landscapes (DiMichele and others, 2006). Cordaitaleans, in contrast to both walchian conifers and calamitaleans, are, as a group, exceptionally widespread in their environmental preferences, growing everywhere from swampy wetlands and peat-forming settings to upland areas (e.g., Falcon-Lang and Bashforth, 2005; Opluštil and others, 2009; Raymond and others, 2010).

Valley of the Gods

Collections from Valley of the Gods (figure 5.4-5.9) consist mostly of large axes (stems) preserved as casts in sandstone, along with rare fragments of foliage. The most abundant stems belong to *Calamites gigas*, a large diameter calamitalean thought to have lived under conditions of moisture stress (see Barthel and Rößler, 1996; Naugolnykh, 2005). Also common at Setting Hen and Seven Sailors Buttes are large diameter stems of marattialean tree ferns, of the *Caulopteris* type. The most diagnostic feature of *Caulopteris* is leaf scars (one of which is marked by a white arrow in figure 5.6) arranged helically around the stem (if arranged in two opposite rows the stems would be attributable to *Megaphyton*). A few fragments of *Pecopteris*, tree-fern foliage occur in association with the stems. A single stem attributable to a medullosan pteridosperm (figure 5.7) was found at Seven Sailors Butte. This stem is > 7 centimeters in diameter and is characterized by persistent, attached basal portions of fronds (one of which can be seen clearly and one of which is hinted at lower on the stem); the locations of other possibly attached leaf bases are weakly marked, as can be typical of these stems. No unequivocal pteridosperm foliage was identified at Valley of the Gods, though some poorly preserved specimens of possible pteridosperm affinity were found.

Small bits of other wetland plants were identified from Valley of the Gods. Most significant are a few specimens of the wetland lycopsid *Sigillaria* (figure 5.8). These are most likely *S. brardii*, effectively the only species of *Sigillaria* in the Late Pennsylvanian and Permian. Pfefferkorn and Wang (2009) demonstrated that the deeper roots of *S. brardii* allowed this species to tolerate drought better than the other giant lycopsids.

Also identified from Valley of the Gods are a few specimens of walchian conifers (figure 5.9). All poorly preserved, these specimens came from fissile, planar-laminated sandstone that occupied broad, shallow troughs within a channel (figure 5.2). Such occurrences indicate that walchians were present on the landscape, probably in interfluves where moisture deficits would be most strongly amplified under a prevailing, background seasonally dry climate regime.

In addition to actual fossils, sedimentary features at Valley of the Gods suggest widespread plant colonization of the landscape. For example, a flaggy siltstone bed near Setting Hen Butte contains more than 100 vertical, cylindrical features that penetrate the entire 15 centimeter thickness of the bed. Consistently about 4 centimeters in diameter, these cylinders have haloes of gray against the red background, suggesting chemical reduction caused by organic matter (figure7). Although these might be roots, their random spacing and lack of dense clumps (as might be expected from roots emanating from a stem base), together with occurrence of a paleosol directly below, suggests that the cylinders represent small, upright stems that were partially buried in sediment. DiMichele and others (2012) described similar features (attributed to the probable peltasperm, *Supaia*) from the lower Permian Abo Formation of New Mexico.

Indian Creek

The twelve small collections made along Indian Creek consist of two principal components, marattialean tree-fern foliage and stems of sphenophyllalean sphenopsids. The tree-fern foliage (figs. 6.5-6.7) is both vegetative (*Pecopteris*) and fertile (*Asterotheca*). No species determinations could be made with confidence, on the basis of the specimens preserved. Tree ferns are common elements of wetland floras from both peat and mineral substrates. They produced large numbers of small, highly dispersible spores, giving them prodigious colonization abilities. As a consequence, they were elements of many different kinds of landscapes, as long as there were wet substrate areas present that could be reached by their wind-dispersed spores.

One of the channel scours also contains abundant, silicified coniferophyte logs (Stanesco and others, 2002). These logs appear to have been transported and may represent a "log jam", such as those reported from older rocks in the eastern U.S. and Canada (e.g. Gastaldo and Degges, 2007; Gibling and others, 2010). The conifer *Walchia* also was found in sandstone from beds at this stratigraphic level.

DISCUSSION

Pennsylvanian-Permian boundary floras from the San Juan County, Utah region are few in number but significant indicators of vegetation in western equatorial Pangea. The region was strongly influenced by winds off the Panthalassa Ocean to the west, as well as by periodic climatic and sea-level changes induced by Southern Hemisphere, high latitude glaciation (reviewed in Tabor and Poulsen, 2008; see also Soreghan and others, 2002; Montañez and others, 2007). In general, floras discussed herein are consistent with a long-recognized trend toward increasing tropical aridity throughout the entire Euramerican region, within which there were shorter episodes of wetter climate, perhaps less than 1-3 million years in duration (Tabor and Poulsen, 2008).

A wetter episode (at least dry sub-humid) proposed to occur near the Pennsylvanian-Permian boundary in the Colorado Plateau (Soreghan and others, 2002) is consistent with the floras we describe in this paper. This period of increased moisture may be associated with cycles of glaciation at high elevations within the Ancestral Rocky Mountains, in the Uncompahgre highlands (Soreghan and others, 2008), fueled by a combination of cold temperatures and periodic increases in moisture delivery to the area. If cycles of mountain glaciation occurred across the Pennsylvanian-Permian boundary in the Ancestral Rockies, and we acknowledge that such proposals are controversial, they could account for the periodic occurrence of wetland floras—or of any kind of floras—intercalated with intervals of extreme aridity. The close spatial physical proximity of sand dunes and flood-plain soils and channels, such as at Indian Creek (Stanesco and Campbell, 1989), may not necessarily be indicative of contemporaneity. Rather, the paleosols and channels preserving wetland plants might more likely represent periods of perennial to intermittent stream flow, accompanied by channel incision into, and floodplain development on, landscapes of stabilized dune fields during wet, cold, glacial intervals. The dunes may have become active again during warmer, arid interglacial intervals. Under such depositional conditions, bounding surfaces within the eolian deposits would mark periods of stabilization, caused either by rising water tables or increased precipitation.

Pennsylvanian-Permian boundary floras from New Mexico (Tidwell and others 1999; DiMichele and others, 2004; DiMichele and Chaney, 2005; DiMichele and others, 2010) and Utah (Mamay and Breed, 1970; Tidwell, 1988) are similar to those reported here, and reveal a mix of plants typical of both wetlands and dry substrates. Such floras do not require widespread wet climates. Rather, they suggest that the prevailing climate was one of seasonal, locally severe, drought, within which there were wet areas capable of supporting certain kinds of wetland plants, particularly those with high dispersal capabilities and capacities to tol-

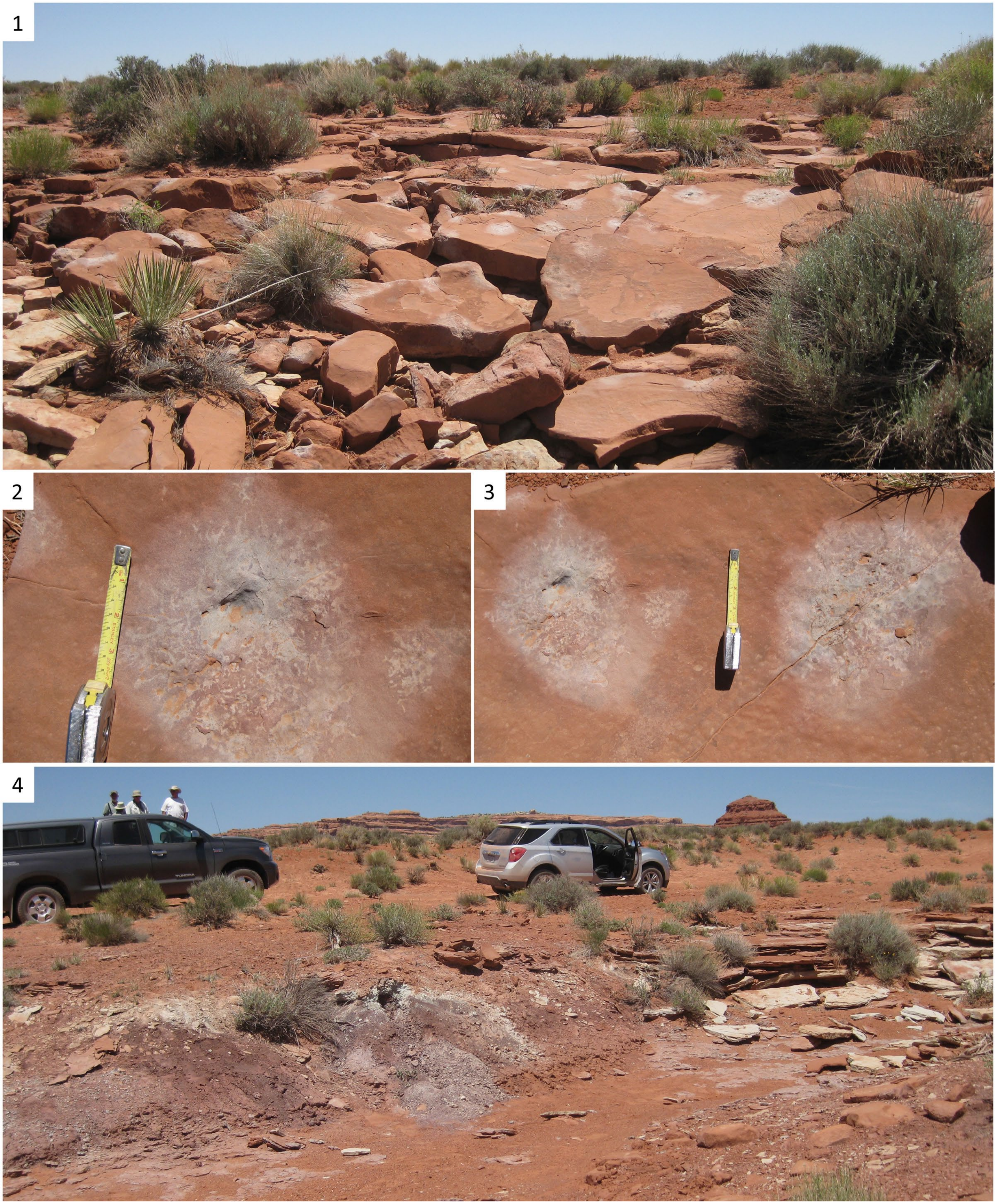

Figure 7. *Valley of the Gods, near Setting Hen Butte. 1. Siltstone surface covered with areas of iron reduction. 2. Detail of reduced area illustrating central core and root-like features surrounding the core area. Scale = 10 centimeters. 3. Pair of reduced areas showing similarity of basic structure. Scale = 10 centimeters. 4. Paleosol below the siltstone bed illustrated in (7.1).*

erate short moisture deficits. The most likely scenario is that a number of perennial streams, sourced in the Uncompahgre highlands, coursed across the coastal plain of the former Paradox Basin en route to the western ocean. At some intervals, perhaps during periods of mountain glaciation as discussed above, these riverine corridors sustained large populations of plants adapted to wetter environments.

Thus, at Valley of the Gods and Lime Ridge, we find fossils of large plants that represent all the major groups of Pennsylvanian wetland plants: tree ferns, calamitaleans, pteridosperms and lycopsids. The lycopsids and pteridosperms are of particular note because they had large dispersal organs (megaspores for *Sigillaria* and large seeds in the case of the pteridosperms) that could not be broadcast widely. This observation implies either permanent western refugial areas for these plants during drought, or rapid expansion of their populations along continuously developed wetland corridors during short intervals of widespread wetness. Tree ferns and calamitaleans could grow in marginally wet areas, giving them the capacity to reach remote or isolated sites with wet soils. The former produced billions of small, highly dispersible spores, which could reach remote wet areas. The latter included many streamside and lake margin specialists, which could recover from repeated disturbances (e.g., Gastaldo, 1992), and thus occupy small, but interconnected corridors with intermittent wetness. As noted above, perennial stream flow in fluvial systems may have, at times, been maintained by ice melting in the Ancestral Rocky Mountains, which provided wetland conditions in an otherwise dry, perhaps arid climate.

Plants reflecting seasonally dry conditions have been reported in floras from the Colorado Plateau from strata as old as Early Pennsylvanian (Tidwell, 1967). Such plants also occur in Pennsylvanian collections from the Midwestern coal fields (Feldman and others, 2005; Falcon-Lang and others, 2009) but only in small channels that show evidence of seasonally dry conditions, developed between periods of coal formation. Their presence in our Utah collections thus is hardly surprising. In fact, such plants probably are greatly under-represented in the fossil record relative to their original dominance of the landscape during the dry phases of glacial-interglacial cycles, when conditions for organic preservation were least favorable (Gastaldo and Demko, 2011).

Trunks of large conifers or cordaitaleans, such as those found at Indian Creek, have been reported elsewhere in the Colorado plateau from rocks of similar age (Condon, 1997; Stanesco and others, 2002). These occurrences suggest that stands of such trees flourished on the Uncompahgre highlands, where they may have received orographic rainfall, perhaps during all parts of glacial-interglacial cycles. These trees may then have spread along permanent streams into the lowlands during episodes of wetter climate.

As a final note, plants from western Pangea are closely allied phylogenetically to groups that occur throughout the equatorial region. This is true both of the wetland and seasonally dry taxa. Although the number of dominant class-level groups, represented by distinct architectures, was more numerous than is typical of modern vegetation, the late Paleozoic tropics nonetheless hosted significantly fewer species, genera, and families than do the modern tropics. In a late Paleozoic world with far lower diversity than today, many individual species, therefore, may have had greater niche breadth than is typical among modern plants. Such resource breadth may have, perhaps to a considerable extent, buffered their populations from environmental changes. Most species had either wind dispersed pollen or spores, which would have contributed to high levels of gene flow and made possible large effective population sizes—these factors may have been among the most important responsible for the lower numbers of species. There are few tests of such hypotheses (but see Raymond and Costanza, 2007), and clearly the late Paleozoic, and the western areas of Pangea, promise to be fertile areas for study of plant evolutionary and ecological dynamics.

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