

TWO EARLY PERMIAN FOSSIL FLORAS FROM THE ARROYO DE ALAMILLO FORMATION OF THE YESO GROUP, SOCORRO COUNTY, NEW MEXICO

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Abstract—We report fossil plants and traces from the Arroyo de Alamillo Formation of the Yeso Group, a lithologic succession of siltstone, sandstone, and minor dolostone and gypsum of early Permian (early Leonardian/late Artinskian) age. These Yeso strata formed under a semi-arid to arid climate regime on a vast coastal plain, conditions generally unfavorable for the preservation of fossil remains. Two fossil plant assemblages were collected from a single outcrop in Socorro County, New Mexico, ~9 and ~13 m above the base of the Arroyo de Alamillo Formation. The lower of the two assemblages occurs in a mud-draped, tabular siltstone bed, approximately 1 m in thickness; the mud drape accounts for the upper 1 cm of the bed. This bed is similar to much of the underlying Abo Formation and is interpreted to have formed in a playa lake. Plant remains are concentrated in the mud drapes and occur with animal trackways, mudcracks, and “raindrop” imprints. Identified plants include the walchian conifer, *Brachyphyllum tenue*, and remains tentatively identified as a coniferophyte similar to *Dicranophyllum*, but lacking key features of that genus. The upper plant assemblage is ~4 m above the first. Plant remains are present in a 0.5 m thick, fine-grained sandstone bed. Planar bedded and lacking trough cross bedding, with climbing ripples, we interpret this deposit as a small-scale sheet flood, unchannelized flow, into a standing water pond, possibly an oasis in an otherwise arid, sand-rich landscape. The fossil plants occur in a small area approximately 2 m in width and 30 cm in depth, length limited by the erosional boundaries of the outcrop to about 3 m. With the exception of a few specimens, all plant remains can be assigned to the peltasperm (callipterid) *Autunia naumanii*. Single specimens are tentatively identified as the peltasperm *Arnhardtia scheibei* and reproductive organs. These are among the youngest occurrences of plant fossils so far reported in the early Permian of western Pangea.

INTRODUCTION

Plant fossils occur frequently, if not abundantly, in Wolfcampian and, in more northerly areas, early Leonardian strata in New Mexico. These beds are of late Gzhelian, Asselian, Sakmarian, and earliest Artinskian age in international terms, all of early Permian age. They represent some of the westernmost vegetation populating the supercontinent of Pangea at that time. Most of the fossils are known from the Abo Formation and its equivalents (Hunt, 1983; DiMichele et al., 2007, 2013a), occurring through the central part of the state from the south, close to the regional oceanic shoreline, to northern areas in the Taos trough (southern Sangre de Cristo Mountains) and Zuni Mountains, in more distal locations. The Abo Formation is a succession of siliciclastic red beds, consisting of thick intervals of mudrock intercalated with calcareous paleosols, tabular siltstone/ sandstone sheet-flood deposits, and small, generally lenticular sandstone- and conglomerate-filled channel deposits, particularly in its lower portions (the Scholle Member), transitioning to tabular siltstones/sandstones and paleosols in its upper part (Cañon de Espinosa Member) (Lucas et al., 2005, 2013a). The Abo Formation is succeeded in a conformable contact by the Yeso Group, the basal-most unit of which in central New Mexico is the Arroyo de Alamillo Formation (Lucas et al., 2005). Plant-fossil occurrences rapidly diminish into the Yeso Group and are reported, at present, only from a few locations (e.g., Koll and DiMichele, 2013; Lucas, 2014), although a few others are now known.

In general, the Abo Formation flora is of low diversity and composed monotonously of walchian conifers of various kinds and the peltasperm *Supaia* (e.g., DiMichele et al., 2007, 2012). In its upper portions, however, other plants begin to appear uncommonly, such as the peltasperm *Autunia conferta*. These appearances of new forms continue into the Yeso Group, and are the basis of this report. Even with the appearance of new kinds of plants, early Permian floras of New Mexico remain of

markedly lower diversity and greater persistence of composition through time than those found 800 km to the east in Texas, of equivalent age.

Because of the induration of Abo and Yeso strata, excavations for fossils is difficult. Fieldwork focuses on the surface discovery of macrofossil remains of plants or animals, or on discovery of trace fossils, and is generally serendipitous. Discoveries come about through recognition of likely kinds of strata, in combination with careful exploration of an area. Search image is important, as is experience. Such are the two fossil floras described here. One is from an Abo-type deposit, a tabular siltstone with clay-drapes formed in as a playa-lake; this deposit also contains an ichnofauna of arthropod walking traces and vertebrate footprints. The other, the more unusual of the two, is from a thin sandstone bed that may have formed as a shallow flood channel entering an ephemeral water body. Although only separated by 3 m, the two fossil-bearing strata are floristically and taphonomically distinct.

GEOLOGICAL SETTING

Stratigraphy and Depositional Environments

The stratigraphic section at the Yeso plant localities (Fig. 1) encompasses the transition from the Abo Formation to the overlying Arroyo de Alamillo Formation of the Yeso Group (Cather and Colpitts, 2005). The lower part of the section encompasses the upper 6.4 m of the Abo Formation, a succession of reddish-brown silty mudstone that contains dispersed carbonate nodules intercalated with relatively thin (0.2-0.5-m-thick) ledges of sandy, pedogenic calcrete. These are typical floodplain overbank and paleosol deposits of the Abo Formation (e. g., Lucas et al., 2013a).

The base of the Arroyo de Alamillo Formation is a 0.3-m-thick bed of thinly laminated and mudcracked dolomite. This bed is overlain by a bed of reddish brown siltstone that is 2.6 m thick and that, in turn, is incised into by an overlying

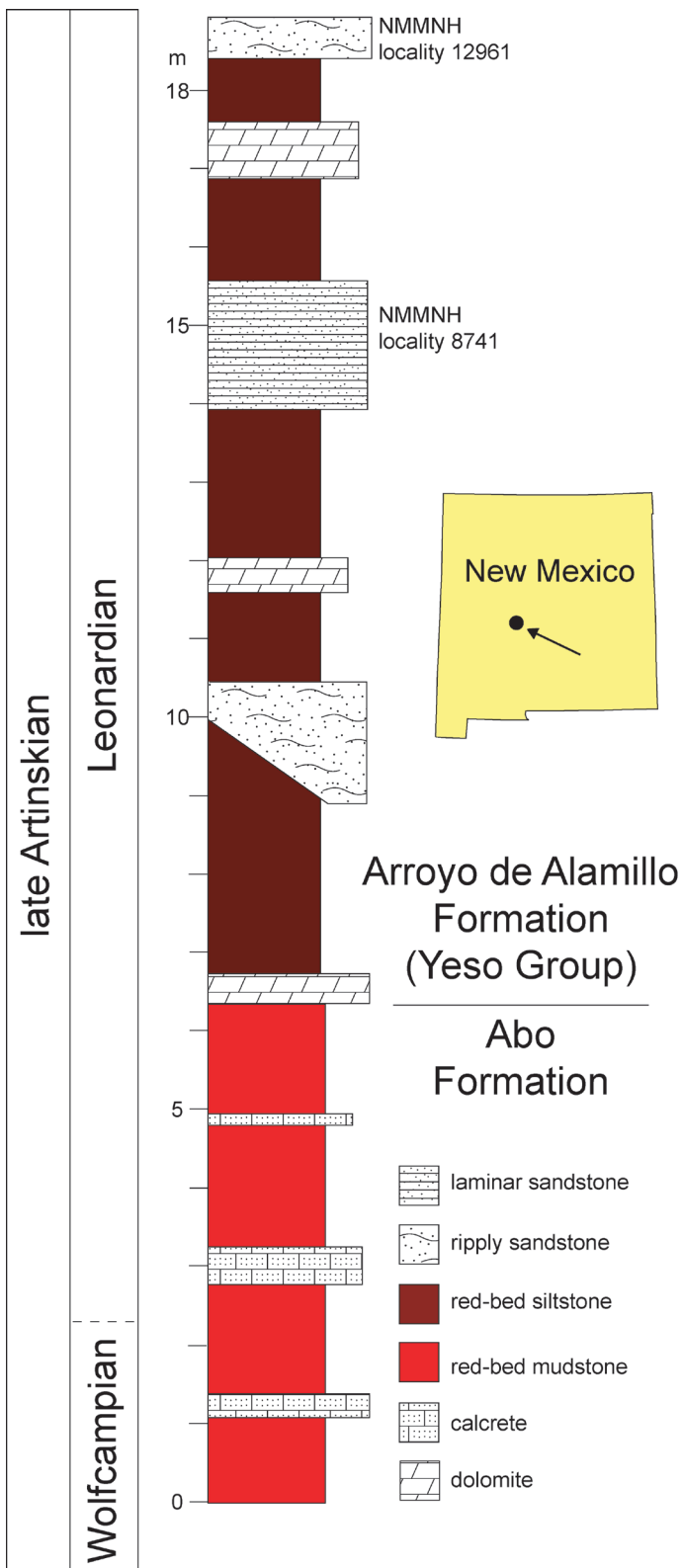


FIGURE 1. Index map and stratigraphic section showing location of the L8741 and L12961 fossiliferous beds and their time stratigraphic positions.

lenticular sandstone that has climbing ripple laminae and ranges in thickness from 0.3 to 1.6 m. Another reddish brown siltstone bed (1.1 m thick) follows and is overlain by another thinly laminated and mudcracked dolomite bed (0.4 m thick). Overlying reddish brown siltstone is 1.8 m thick and is overlain by a bed that is 1.6 m thick of thinly laminated siltstone and very fine sandstone. This bed hosts locality 8741 and is lenticular on strike (laterally) over 10 m.

Many laminae in this bed are clay draped, and some display mudcracks and what are likely raindrop impressions. At locality 8741, besides the plant fossils described below, there is a rich ichnoassemblage dominated by arthropod walking traces (such as *Diplichnites* and *Diplopodichnus*) and tetrapod footprints (mostly reptile, such as *Varanopus* and *Erpetopus*). This bed and the trace fossil assemblage are very similar to a bed in the Leonardian Choza Formation near Abilene, Texas, which Minter et al. (2007) interpreted as a playa-lake deposit. We also interpret as a playa-lake deposit the bed that hosts locality 8741. Thinly laminated siltstones and sandstones indicate episodic input of sediment into a standing body of water, likely by an ephemeral stream(s) along the lake margin. However, eolian transport of sediment into the lake may also have taken place. Suspended mud in the lake would have settled to form clay drapes after the initial input of silt and sand-sized grains into the waterbody. Mudcracks, raindrop impressions and the tracks indicate periodic subaerial exposure when the lake dried out.

Above the playa-lake deposit are 1.3 m of reddish brown siltstone overlain by a third, laminar dolomite (0.7 m thick). Another siltstone bed (0.8 m thick) follows, and the section is capped by a 0.5-m-thick sandstone bed that hosts locality 12961. This sandstone has thick tabular to wavy beds that encompass climbing ripples. Modern erosion has greatly limited the lateral extent of this bed, but its lack of crossbedding and lack of evident incision suggests it represents unchanneled flow (sheetflooding) on the floodplain.

Both plant localities described here are present within the context of regional lower Yeso Group deposition, which took place on an arid coastal plain between the DeChelly erg to the north/northwest and the northwestern shelf of the Delaware basin to the southeast (Fig. 2; see Mack and Dinterman, 2002; Lucas et al., 2013b). Clearly, the fossiliferous beds described here represent relatively wet microenvironments on this coastal plain.

Age of the Deposits

Various age constraints place the Abo-Yeso strata at locality 12961 in the early Permian (Lucas et al., 2015). At the top of the Arroyo de Alamillo Formation, stratigraphically about 100 m above locality 12961, conodonts indicate an early Leonardian (middle Kungurian) age, and regional correlations place the Leonardian base (which is in the upper Abo Formation) in the late Artinskian (Lucas et al., 2022). Thus, locality 12961 is most likely of early Leonardian/late Artinskian age (Fig. 1).

Permian plant biostratigraphy of Euramerica is at least an order of magnitude less resolved than for the Pennsylvanian (Cleal, 2018). This is largely a consequence of a long-term environmental shift beginning in the Pennsylvanian and continuing through the transition to the Permian (e.g., Kerp, 1996; DiMichele et al., 2008; DiMichele et al., 2020; Cleal and Cascales-Miñana, 2021; Marchetti et al., 2022) that resulted in increasing habitat heterogeneity and concomitant vegetational differentiation. The Pennsylvanian-age wetland paleo-species pool was broadly uniform over a vast area of the former Euramerican Pangea. Its fossil record is well documented (e.g., Wagner and Alvarez-Vázquez, 2010; Opluštil et al., 2022) because it is so well and widely preserved in association with coal beds. The more xeromorphic plants comprise several species pools as a consequence of the landscape heterogeneity

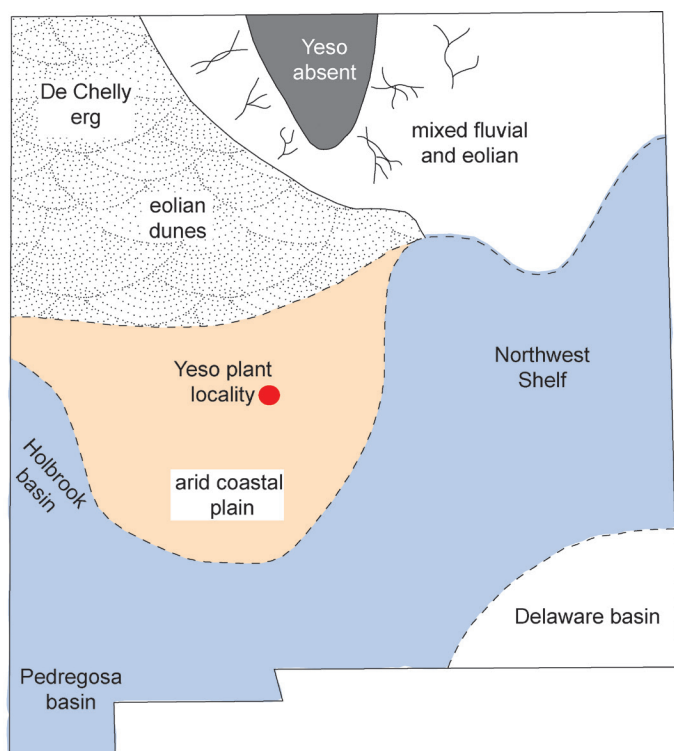


FIGURE 2. Paleogeography and depositional systems of the lower Yeso Group (modified from Lucas et al., 2013b).

that emerges under seasonal tropical drought. Furthermore, these species pools are neither as abundant nor even remotely as well preserved as the pool of wetland species. The result is a range of drought tolerant floras that are not as spatially uniform as the wetland flora, not as well studied, nor yet organized into a finely resolved stratigraphic framework (e.g., Kerp, 1988; Cleal, 2018).

PALEOBOTANY

Locality 8741: Red-Bed Deposit

Two plant-fossil morphotypes were found at Locality 8741. The more common of these were various sized branch fragments that resemble the conifer taxon *Brachyphyllum*. This genus, common and diverse in the Mesozoic, has been described in the Permian both by White (1929) and Mamay (1967). The former of Wolfcampian age from Arizona, the latter from early Leonardian age strata of Texas. The other specimens are of questionable affinity, similar in some respects to the coniferophyte *Dicranophyllum* but lacking crucial features.

Brachyphyllum tenue

The conifer remains found at L8741 (Fig. 5) are characterized by slender branches on which are inserted closely adpressed, triangular leaves that do not flex away from the stem in the sigmoidal shape seen in most walchian conifers. The leaves are so closely adpressed that on some specimens their presence only becomes clear with careful observation. Leaves are largest on the main lateral branch axes, up to 4 mm in length and 1 mm in width. On the ultimate branches the leaves are smaller, about half the size of those on the main lateral branch axes, about 1.5-2 mm in length and 0.4-0.6 mm in width. Leaves are broadest at the base and taper to an acuminate apex; they have a weakly expressed, abaxial central ridge. The leaves are slightly curved laterally/adaxially, conforming to the curvature of the parent axis. Only the abaxial face of each leaf is exposed, outwardly facing, so that successive leaves overlap slightly – they are partially imbricate. Branches likely were borne

plagiotropically. The ultimate branchlets are widely spaced and somewhat flexuous, giving the branches a very sparse, almost “stick-like” appearance.

Similar specimens also have been described from the New Mexico Abo Formation (DiMichele et al., 2013a, fig. 4), subjacent to the Yeso Group, where they are relatively rare, and where they were reported to occur at 13% of 172 red-bed localities and 10% of 30 gray-bed collecting sites. Like the L8741 specimens, the Abo specimens have closely adpressed, small, triangular leaves and ultimate branches that are relatively widely spaced and somewhat flexuous.

There are two close published comparisons to the Yeso specimens described from the western U.S. One is *Brachyphyllum tenue*, described by David White (1929) from the Hermit Shale of the Grand Canyon, Arizona, likely of Asselian or perhaps Sakmarian age. This species is similar in architecture to the Yeso specimens in its narrow, widely separated ultimate branches. It also has closely adpressed, triangular leaves. A second possibility is *Brachyphyllum(?) densum* described by Sergius Mamay (1967) from beds that today would be considered part of the Lueders Formation of Texas, an early Permian unit of Leonardian, likely Kungurian, age. Mamay (1967) recognized that *Brachyphyllum* had been described primarily from the Mesozoic, which explains his addition of “(?)” following the generic name. White (1929) also described a second *Brachyphyllum* species, *B. arizonicum*, in which the leaves appear to be wider and shorter than those of *B. tenue*. As a noted taxonomic “splitter”, however, White’s two species may be the same, their differences in appearance reflecting preservational factors. Mamay (1967) believed neither to be identical to the specimens he described from Texas. Of these early Permian, western Pangean plants assigned to *Brachyphyllum*, the Yeso specimens are most similar to *B. tenue*, given the openness of the branch architecture. The New Mexico specimens, both those reported here and those known from the Abo Formation, differ from Mamay’s original specimens in the wide spacing and somewhat flexuous architecture of the ultimate branchlets, whereas in the original Texas material the ultimate branchlets are denser and are not flexuous.

All of these specimens, those from Texas, New Mexico, and Arizona, appear to have been deposited under conditions of seasonal drought. In North-Central Texas, the Lueders Formation was deposited during a time of regional sea-level highstand (Holterhoff, 2010). Climate at that time, based on paleosols and the composition of floras, was likely seasonally dry (DiMichele et al., 2006). The Abo Formation and Yeso Group also were deposited under strongly seasonal conditions (e.g., Mack et al., 1991; Lucas et al., 2013b), as also has been suggested for the Hermit Shale (White, 1929).

Indeterminate coniferophyte, possibly related to *Dicranophyllum*

Several specimens were found in the L8741 deposit that consist of foliated axes, 3 to 4 mm in diameter, that bear narrow leaves in what appears to a tight helix (Figs. 6-7). Leaf arrangement is inferred from several specimens that present various views, including the axis in longitudinal and face view (Fig. 6a), the latter reflecting burial of the axis by a thin layer of sediment or, more likely, an imprint of the plant on the mud-draped surface (Fig. 7). In longitudinal section (Fig. 6 a-c, but particularly 6c), it can be seen that the leaves had clasping bases, were of sigmoidal shape, and were borne at angles from nearly horizontal to about 45°. Leaf widths are approximately 1-2 mm (see especially Fig. 6d and Fig. 7); lengths are difficult to determine due to preservational factors but appear to be between 4 and 6 cm. Leaves have a central groove that likely represents a single, sunken midvein; no lateral veins are visible. The leaf apex is acuminate and tapers rapidly near the apex from the full width to the tip (Fig. 6d). The midvein continues to just below

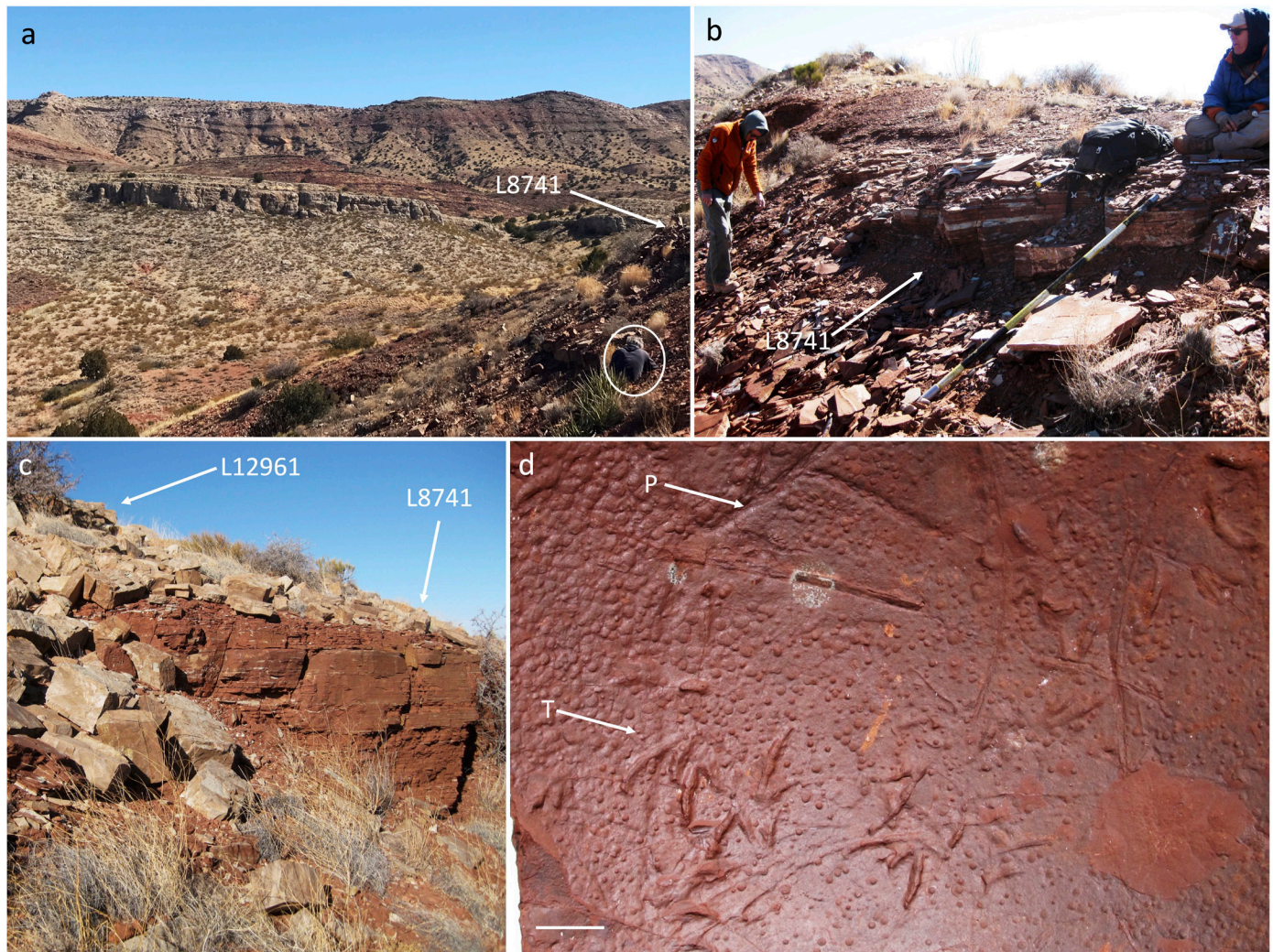


FIGURE 3. Locality 8741 lithology. **a**, View to the northeast from the L8741 hillslope. The location of the fossiliferous bed is at the arrow. Person for scale in the oval. **b**, L8741 fossiliferous bed from which collections were made. **c**, Relative positions of L8741 and L12961 on a slope adjacent to the one from which the fossils were collected. **d**, Mud draped surface from L8741. Surface is covered by cavities interpreted either as raindrop imprints or gas-escape structures. P = plant remains covered by mud. T = vertebrate footprints impressed into the mud surface. Scale bar in d = 1 cm.

the apex. There is no indication that the leaves were forked or that the midvein might be a double strand, which is of relevance to the possible identification of these specimens. Isolated leaves occur, although this observation does not necessarily indicate they were deciduous given that none of the dispersed leaves had basal portions preserved.

On initial inspection, the preliminary identification of these specimens was, at the generic level, *Dicranophyllum*. However, all described species of *Dicranophyllum*, as far as the authors are aware, have leaves that are forked multiple times and are characterized by a pair of parallel veins in the lower portion of the leaf, prior to the initial dichotomy (e.g. Grand'Eury, 1877; Mamay and Read, 1956; Mamay, 1981; Barthel and Noll, 1999; Van der Pas et al., 2017), traits lacking in the present specimens. In conformance with *Dicranophyllum* is the basic architecture of the plant, which appears to be a slender stem closely invested with leaves, in the fashion of a bottle brush (Barthel and Noll, 1999; Meyer, 2005; Van der Pas et al., 2017).

If this plant is a *Dicranophyllum*, it must be considered a new species thereof, also considering its age, given that the genus is primarily a Pennsylvanian form. A dense stand of upright stems from the Sangre de Cristo Formation, an Abo Formation

equivalent in north-central New Mexico, was attributed to *Dicranophyllum* by Rinehart et al. (2015) but without definitive evidence from foliage in attachment. We must, nonetheless, consider the possibility that this is a new plant of coniferophyte affinity, perhaps related to the Dicranophyllales, but a distinct generic form. This would be in keeping with the appearance of other unusual plants in the upper Abo Formation and lower Yeso Group, such as that described by Koll and DiMichele (2013) or described in the next section of this paper.

Locality 12961: Sandstone Deposit

The plant remains at L12961 were attributable, with just a few exceptions, to a single species, *Autunia naumannii* (Kerp and Haubold, 1988a, b). A few additional specimens of foliage, roots, reproductive organs, and uncertain features occur rarely. Most of the *A. naumannii* specimens are preserved as large fragments, leading us to suspect that had the hard, resistant enclosing rock matrix been more susceptible to splitting along large surfaces, much larger, possibly even entire, fronds might have been recovered.

Autunia naumannii

The dominant plant in the assemblage is similar to *Autunia*



FIGURE 4. Locality 12961 outcrop. **a**, Relative positions of L12961 and L8741 on the hillslope from which the L12961 collection was made. Note that the fossiliferous L12961 bed is truncated on either side. Contact with the underlying paleosol is visible. **b**, L12961 bed at the top of a slope. **c**, Internal structure of the L12961 fossiliferous bed, showing scours and variable thickness of various layers within the thicker deposit. The bed sits directly on a paleosol.

naumannii. This species has been widely reported across tropical Pangea, from the eastern most regions (China; Wang et al., 2014; Wan et al., 2016; Zhou et al., 2017) to West (Texas: Glasspool et al., 2013; New Mexico: DiMichele et al., 2017) and many areas in between (Pennsylvania: DiMichele et al., 2013b; Germany: Kerp and Fichter, 1985; Kerp, 1988; Kerp and Haubold, 1988a). It is associated with environmental indicators of moisture seasonality, but still with moderate soil moisture.

The material found in the Yeso deposit appears to have had small, but robust forked fronds. based on the thickness of some of the frond rachis segments (Fig. 8). The pinnules are small, multilobed, and, in the larger instances, might be considered ultimate pinnae (Figs. 9 - 10). The lobes vary from rounded to elongate (Fig. 10b-d). The pinnules/ultimate pinnae are arranged in a subopposite manner on the penultimate pinnae (Fig. 9a; Fig. 10 a, d-e). Venation is coarse and steeply ascending (Fig. 10), although, due to the coarseness of the sediment, the venation is generally obscure. Small, rounded intercalary pinnules (Fig. 8c; Fig. 9a; Fig. 11 a, b) are present, but are difficult to recognize in most specimens; these are a characteristic and important

diagnostic feature of callipterids. Most of the specimens deviate to some degree from typical *A. naumannii* in having more rounded pinnule lobes than is typical for the species; in this trait it might be considered a subspecies or even a new sister species.

The mono-dominance of a single taxon in this collection suggests that it lined the channel. Furthermore, the size of the remains preserved in the deposit indicates that they likely entered the channel as fresh specimens, not as dried litter, thus probably in a major windstorm that tore off pieces of fronds. This is consistent with other features of the fossil deposit, such as specimens at an angle in the matrix indicating rapid burial, or the absence of seeds (with a single exception), suggesting sediment deposition over a short period during which reproduction was not occurring.

Arnhardtia or *Gracillopteris*

A single specimen was found (Fig. 11c) that has very small, lobed pinnules, perhaps 5 mm in length, with elongate lobes of < 1 mm in length. Pinnules are inserted in an alternate manner. This specimen is similar to, but not definitive of *Arnhardtia scheibei* (compare with figures in Kerp et al, 1990, or plate IV,

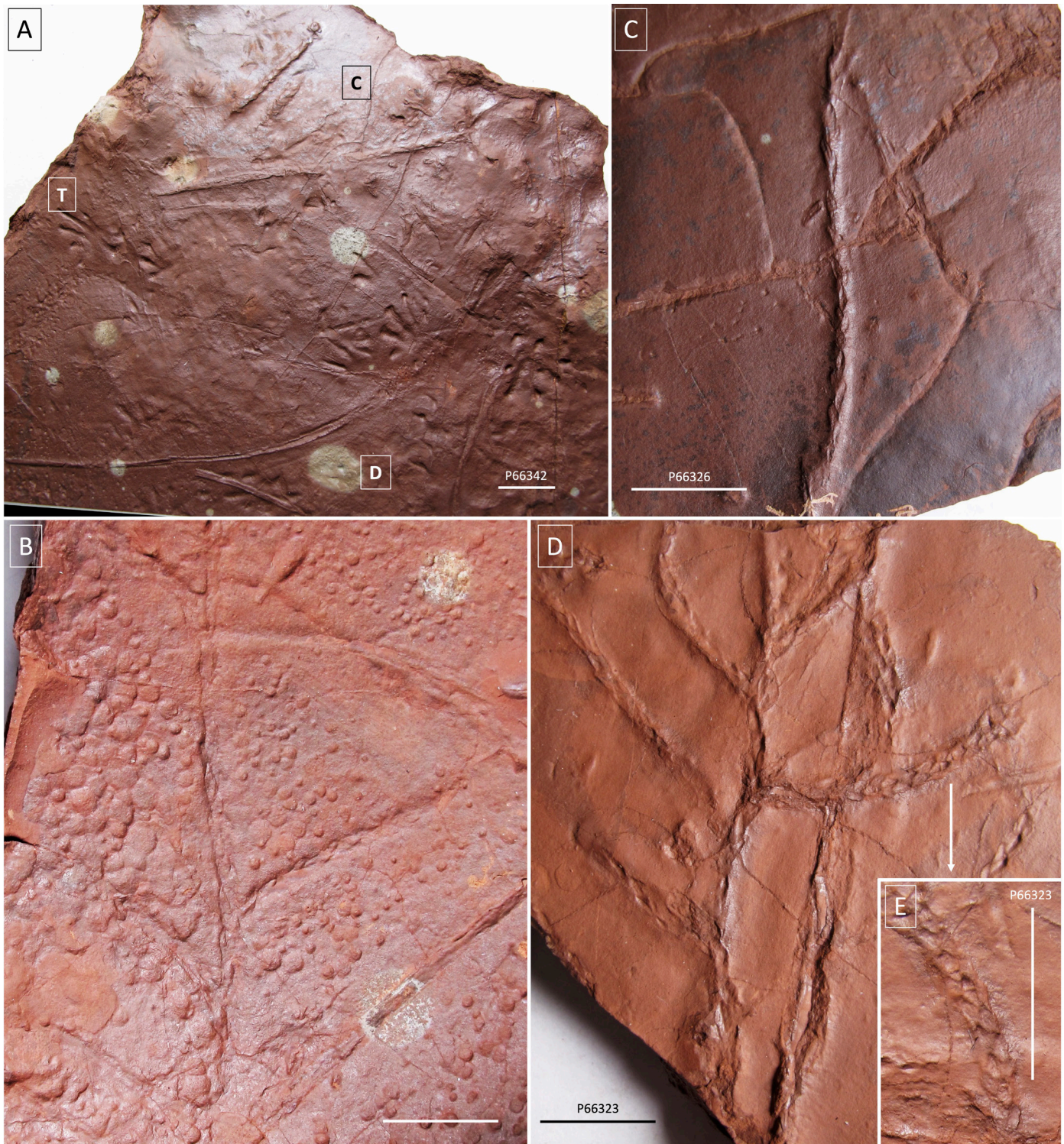


FIGURE 5. Locality 8741. Coniferophytes. **A**, Mud drape on siltstone bed with a vertebrate trackway (T), scraps of conifer *Brachyphyllum tenue* terminal branchlets (C), and leaves of cf. *Dicranophyllum* (D). NMMNHS P66342. **B**, *Brachyphyllum tenue* branch surrounded by raindrop imprints. **C**, *Brachyphyllum tenue* terminal branchlet enclosed in a mud drape that later cracked, a crack passing through the specimen. NMMNHS P66326. **D**, *Brachyphyllum tenue* lateral branch. White arrow points to enlargement of ultimate branchlet in E. NMMNHS P66323. Scale bars = 1 cm.

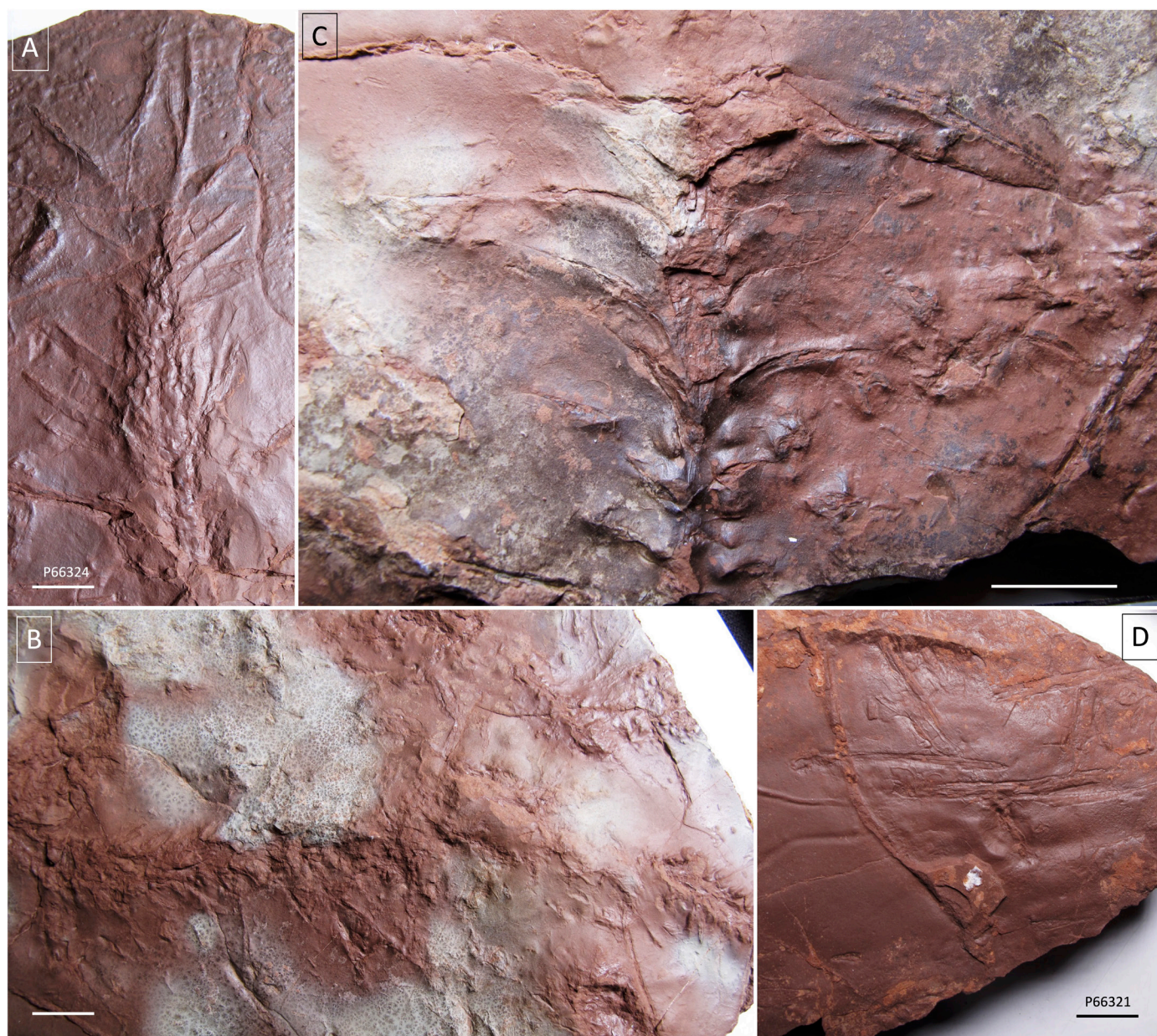


FIGURE 6. Locality 8741. Coniferophyte, cf. *Dicranophyllum* sp. **A**, Branch fragment preserved in a mud drape. Stem has attached leaves and exposed leaf bases. The leaf at the top of axis indicates that the lateral leaves are likely much longer than they appear. **B**, Branch fragment with attached leaves, preserved in siltstone. Leaves may be truncated. **C**, Branch fragment preserved in mud drape. Details include claspings leaf bases and helical disposition of leaves. **D**, Leaf fragments in mud drape; they appear to have a single, central vein. NMMNHS P66321. Scale bars = 1 cm.

fig. 5 of Šimůnek and Martinek, 2009) or *Gracillopteris* (Kerp et al., 1991). Both genera were segregated from *Callipteris* by Kerp and Haubold (1988a).

Miscellaneous Specimens

Several miscellaneous plant remains were recovered from the L12961 excavation. The most common of these were fragments of fine roots (Fig. 11d). Such root remains do not appear to penetrate the substrate and likely were washed in with sediment and other plant remains.

A few specimens were found on which there were scattered small, sporangia or synangial clusters (Fig. 12 a-b), possibly part of callipterid pollen organs. These organs clearly consist of several parts, which either represent several elongate sporangia of a synangium or are parts of the wall of a single sporangium that split longitudinally. An indication of a possible synangial

origin can be seen in Figure 12b, at the arrow, which may be one of these dispersed units in transverse section, indicating that it has 4-5 chambers.

Only a single ovule/seed was found among the L12961 plant remains (Fig. 12c). This seed is radiospermic and elongate (6 mm long and a maximum of 3.4 mm wide). It has a medial ridge. The lack of seeds in this collection may be an indication of the timing and rate of deposition of the sediment, occurring rapidly and during a season of the year when the main flora was not in a reproductive mode, expected to be temporally constrained in a seasonal climate.

Several specimens of *A. naumannii* were found that have unusually modified margins of the terminal parts of several adjacent pinnules (Fig. 12d-e). On these pinnules, the margin appears swollen and divided into multiple radial segments. It

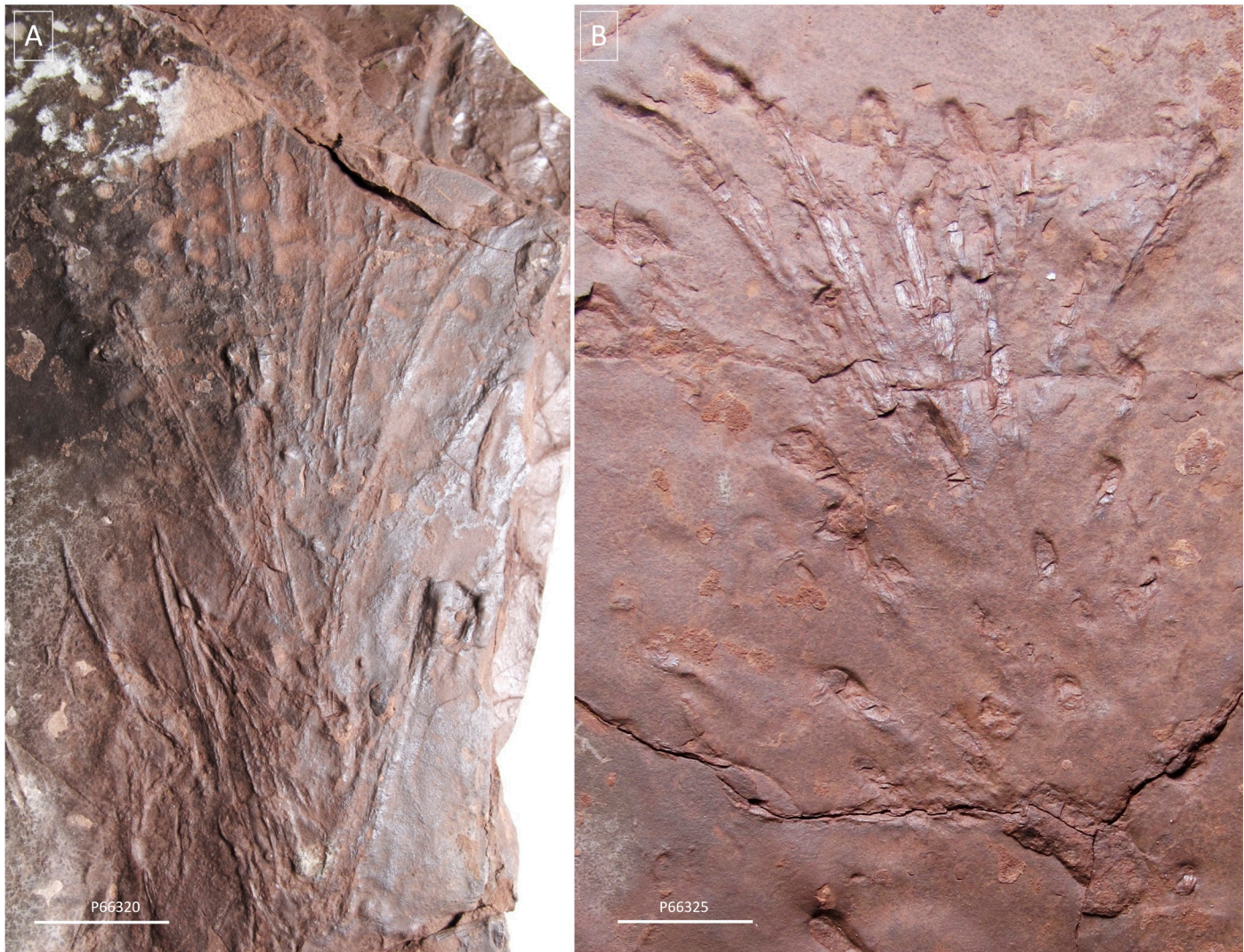


FIGURE 7. Locality 8741. Coniferophyte, cf. *Dicranophyllum* sp. **A**, Axis with attached leaves preserved in mud drape. Leaves are approximately 1.5 mm wide, 3 cm long, have acuminate tips, and a single midvein or midvein region. NMMNHS P66320. **B**, Axis with attached leaves preserved in, and partially projecting through, a mud drape. Leaves are about 2-2.5 mm wide, 4.5 cm long, have a single vein, and acuminate tips. NMMNHS P66325. Scale bars = 1 cm.

is possible, given pinnule shape and size, that the seemingly thickened margins are enrolled. Morphology similar to this was discussed by Kerp (1988) for *Autunia conferta*, where he points out earlier work in which such morphology was misinterpreted as representing reproductive organs. Personal observation (Kerp, unpublished) indicates that such thickening is known to occur in some other callipterids, a result of marginal folding, creating a “rim”.

DISCUSSION

The collections reported here are representative of a pattern seen elsewhere in the upper Abo Formation and lower Yeso Group – the appearance of plant types either not found in older strata or rare there. In this instance, two different kinds of depositional environment were found in close physical proximity, separated on outcrop by approximately 3 m of reddish brown siltstone, laminar dolomite, and siltstone, which indicates a temporal separation likely of thousands of years. Only rare or unusual elements occur in these deposits, including *Brachyphyllum tenue* and a *Dicranophyllum*-like plant in the red-bed playa-lake deposit and *Autunia naumannii* in the shallow, sheet-flood sandstone. Both possibly formed on an arid landscape, particularly the upper deposit containing *A. naumannii*. The

Yeso Group records regional, western Pangean drying and the development of vast sand seas by the time of the deposition of the overlying Glorieta Sandstone (Mack and Dinterman, 2002; Lucas et al., 2013b). Plants clearly grew on this landscape, but likely in restricted areas adjacent to streams, possibly in oases.

The two deposits described here are very different from a taphonomic perspective. In the playa-lake deposit, L8741, a flood, evidently of short duration, carried a few organic remains into a playa lake. Following the initial introduction of coarser sediments, a period of quiescence occurred during which fine clays settled from suspension. During this latter time, the plant remains carried in suspension settled with the clays and either were incorporated into the sediment (as in Fig. 3d) or were impressed into the muds, thus leaving only surface features (as in Fig. 7b). The playa surface then became exposed and, while still soft, animals transgressed it, and final drops of rain may have impressed themselves upon it. The animals could not have come from too far away, nor could the buried vegetation have been transported over too great a distance given that the playa was of rather limited width and any of the flood events that filled it likely intense and of short duration. In some ways similar, the fine sandstone deposit, L12961, appears to have been a sheet flow, one in which the sediment was deposited

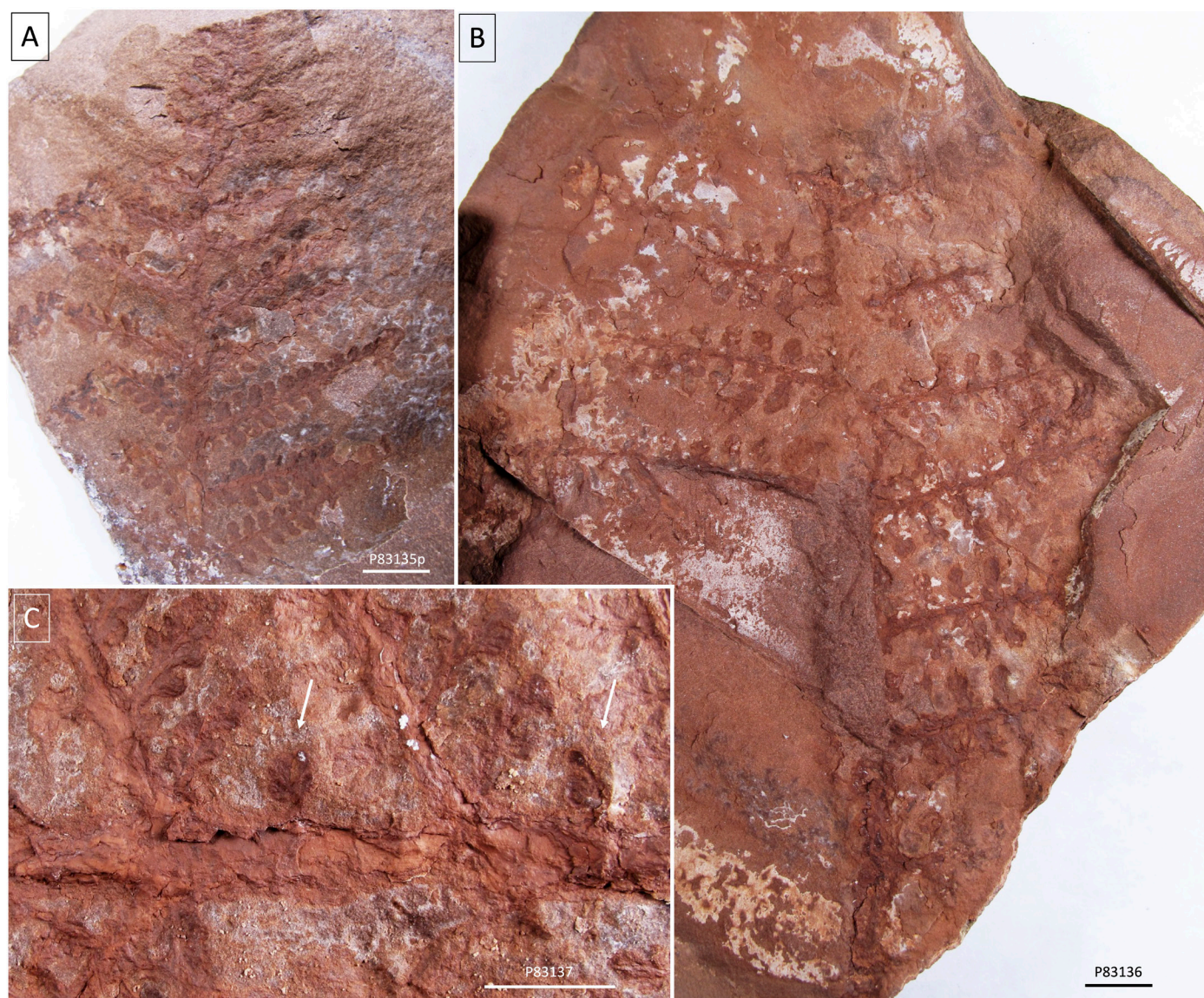


FIGURE 8. Locality 12961. *Autunia naumannii*. **A**, Substantial portion of a frond demonstrating rapid shortening of pinnae distally, and changes in pinnule shape through this transition. P83135 part. **B**, Partial frond that appears to have been large given the main rachis diameter of >1 cm. Pinnules are much more elongate and lobed than in the small frond segment illustrated in image (A). P83136. **C**, Rachis with intercalary pinnules; (arrows) these are often obscure or their occurrence uncertain. P83137. Scale bars = 1 cm.

rapidly in a major storm, incorporating large fragments of plant remains throughout the thickness of the deposit. That the flora was effectively monotypic strongly implies a thick, vegetation composed of *Autunia naumannii*, either lining a preexisting channel, or covering the landscape over which the flood took place. A lack of upright, buried stems suggests that the sheet flow may have followed something like a preexisting arroyo.

In either of these deposits, the central question is where were these plants on the broader landscape given that they are found only in isolation in beds that are themselves rare occurrences? This points to very real concerns about the adequacy of the terrestrial fossil record to provide a representative picture of the regional vegetation (and also likely the fauna) of a time and place under strongly seasonal dry, even semi-arid physical conditions, even if in a basinal lowland. As noted above, the Yeso Group preserves several such one-off deposits containing plant remains of unusual types, of uncertain affinities, implying a complex and heterogeneous regional vegetation (e.g., Koll and DiMichele, 2013). Similar occurrences of plants otherwise

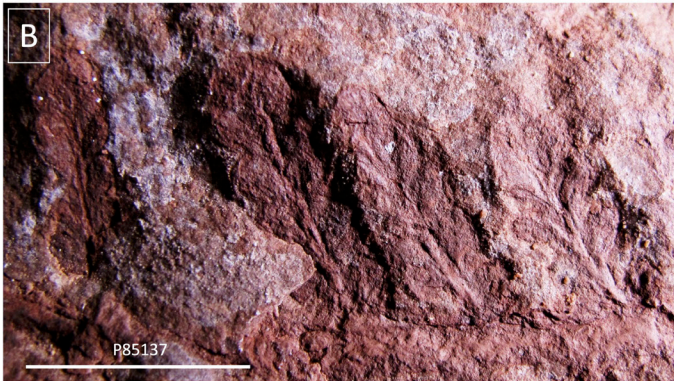
known only from much younger strata, or previously not known at all, have been reported from other areas of western Pangea, such as north-central Texas (e.g., DiMichele et al., 2001; Looy, 2007; Looy and Duijnste, 2020), New Mexico (Falcon-Lang et al., 2015), the southern Alps in Europe (Forte et al., 2017), and the Middle East (e.g., Kerp et al., 2006; Blomenkemper, 2018; Kerp et al., 2021).

From a dynamic perspective, the landscapes from which these seemingly unique, isolated plant occurrences were drawn must have had significant spatial connectivity that is not preserved in the geological record - perhaps excepting the record of paleosols, which tell us some kind of vegetation was out there on the landscape, but not what it was compositionally. Local habitats in disrupted or disturbed environments, those also under moisture stress would have had a patchwork of microhabitats quite different from similar disturbances in a humid or perhumid tropical landscape, such as those found in coal basins of Central Pangea. The rainforest habitats were almost certainly more homogeneous across wide swaths of landscape than more



FIGURE 9. Locality 12961. *Autunia naumannii* foliage. **A**, Apical section of a compound leaf. **B**, Pinna fragment showing shape and venation of pinnules. **C**, Higher magnification of pinnules in image (B). **D**, Pinnule illustrating the continuum between individual pinnules and pinnule lobes on larger ultimate laminar portions. **E**, Pinnae with lobed pinnules in which the lobes are less differentiated than in image (D). **F**, Higher magnification of pinnules in image (E). Scale bars = 1 cm.

FIGURE 10 (facing page). Locality 12961. *Autunia naumannii*. **A**, Nearly complete pinna bearing ultimate laminate segments that could be considered either lobed pinnules or ultimate pinnae bearing small, rounded pinnules. P85137. **B**, Higher magnification image of some ultimate laminate segments illustrated in image (A). P85137. **C**, Ultimate laminate segments illustrating the complexity of differentiating pinnae and pinnules. P85153. **D**, Ultimate laminate segments in which the lobing of the margins is shallow and pinnule identity clear. P85140. **E**, Terminal portion of a main rachis illustrating the rapid diminution of pinna length, and the transition of pinnae to pinnules. **F**, Terminal portion of a main rachis illustrating the rapid diminution of pinna length, and the transition of pinnae to pinnules. In this specimen the pinnules become progressively less lobed as the secondary pinna length diminishes. P85135. Scale bars = 1 cm.



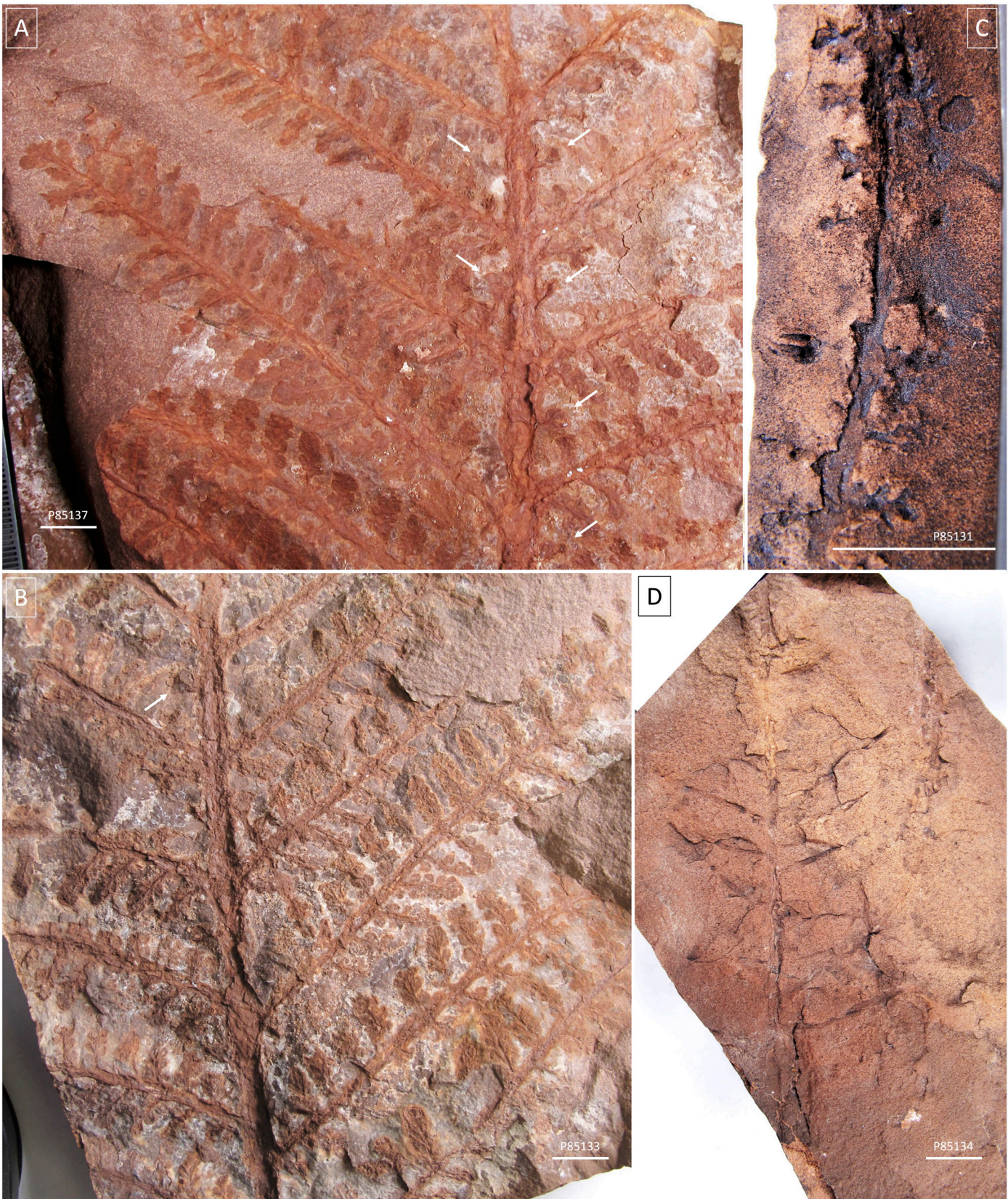


FIGURE 11. Locality 12961. *Autunia naumannii*, cf. *Arnhartdia scheibei*, Roots. **A**, *Autunia naumannii*. Segment of frond showing intercalary pinnules (arrows) and stout construction. P85137. **B**, Frond segment demonstrating stout construction and progressive lobing of pinnules basipetally. P85133. **C**, cf. *Arnhartdia scheibei*. Pinnae bearing small pinnules that are deeply lobed and orthogonal to the pinna axis. Poor preservation prevents positive identification. P85131. **D**, Roots. These do not appear to have been transported but rather to have been introduced transgressively into the sediment after entombment of the plant remains. P85134. Scale bars = 1 cm.

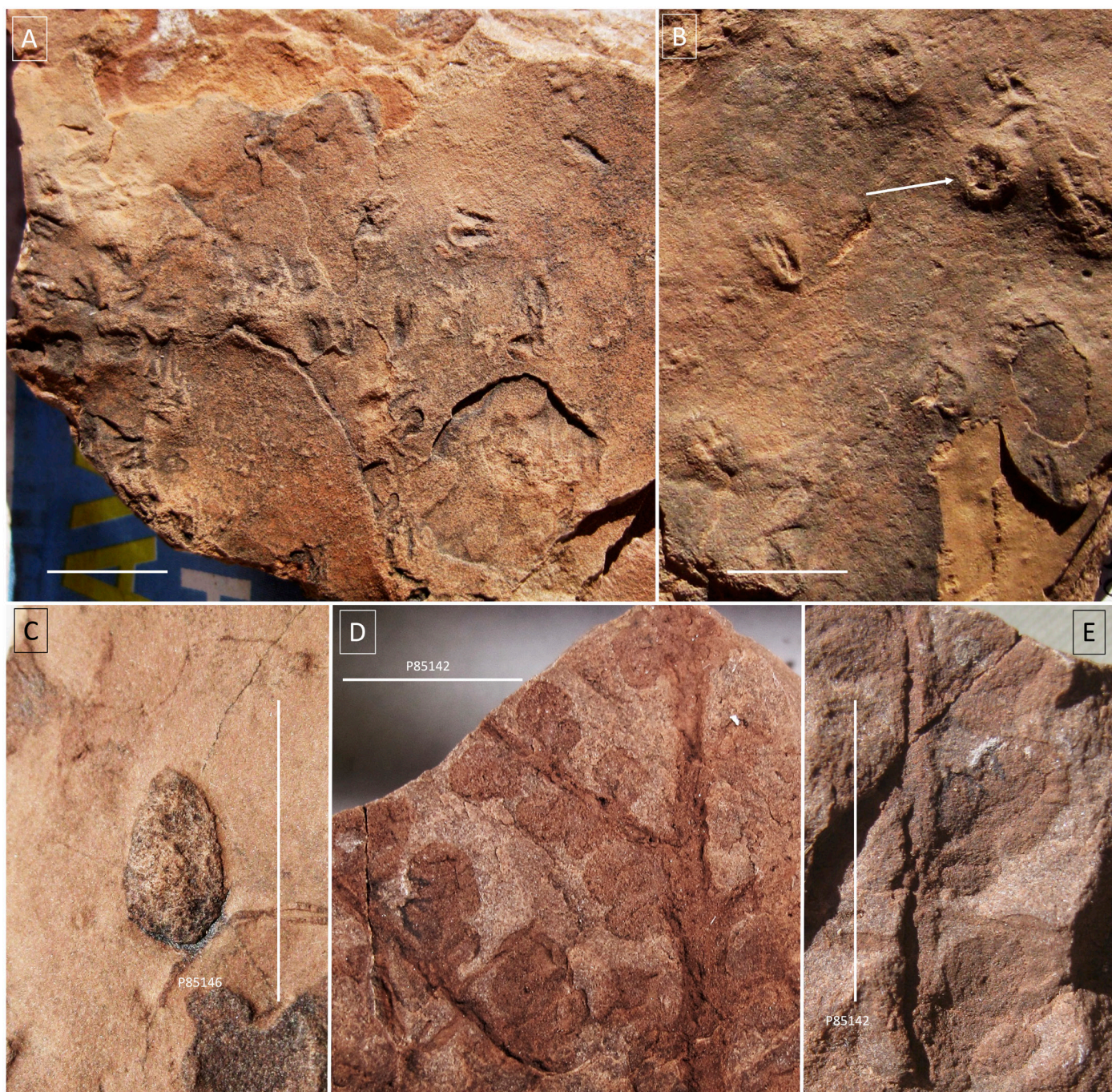


FIGURE 12. Locality 12961. Reproductive organs. **A**, Synangiate pollen organs of uncertain affinity consisting of multiple lobes or chambers. **B**, Synangiate pollen organs of uncertain affinity. Specimen at arrow appears to be exposed in transverse section suggesting multiple chambers, perhaps as many as five. **C**, Small, radiospermic seed or ovule with possible longitudinal ridge. This is the only seed identified in the collection. P85146. **D**, Pinnules, possibly of *Autunia naumannii*, with an unusual apical feature. P85142. **E**, Enlargement of some of the pinnules illustrated in Image (D). Only one such specimen was found in the collections. P85142.

moisture-limited, seasonal landscapes, regardless of disturbance rates and kinds. In contrast, a semi-arid to arid environment likely had greater heterogeneity and, perhaps, less connectivity than an area of vast wetland habitat. From an assembly rules perspective (e.g., Belyea and Lancaster, 1999; Weiher and Keddy, 2002), plants in any given habitat had to: (1) be able to reach the site, (2) be able to survive under the conditions at the site, and (3) be able to compete, whatever that term may mean in detail, against other organisms already at the site, if there were any. It must be presumed that there were sufficient source populations on the landscape to permit a species such as *Autunia naumannii* to colonize a site and appear in an isolated fossil occurrence seemingly out of nowhere. This applies to all such spatially isolated, unique occurrences and indicates that the landscapes were much richer and compositionally diverse than might be guessed from the nature of the fossil record. To explain this requires an inductive leap, perhaps, to claim that the landscape was far richer than the record reveals, but such isolated occurrences permit such an interpretation to be envisioned as a possibility.

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