THE FIRST SPECIMEN OF *ANNULARIA SPINULOSA* STERNBERG FROM THE LOWER PERMIAN ABO FORMATION, NEW MEXICO, AND IMPLICATIONS FOR RARITY IN THE PLANT FOSSIL RECORD

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Abstract—We document the first record of *Annularia* cf. *spinulosa* from the red-bed facies of the lower Permian Abo Formation in New Mexico. The record is in the Cañon de Espinoso Member of the Abo Formation northeast of Socorro and is associated with a low diversity tetrapod footprint assemblage dominated by *Dromopus* and a low diversity paleofloral assemblage dominated by *Supaia*. Calamitaleans are generally rare in the Abo Formation, which is unusual for floras of this age, even in western Pangea. The discovery of *Annularia* cf. *spinulosa* indicates that these plants likely were represented by small numbers and were widely dispersed within the Abo landscape, which was dominated throughout its known extent by walchian conifers and *Supaia*.

INTRODUCTION

Rarity is a matter of long-standing interest to ecologists, who have commented extensively upon its various forms and their significance to understanding ecological spatial patterns and dynamics (e.g., Rabinowitz, 1981; Krukeberg and Rabinowitz, 1985; Gaston, 1994; Magurran, 2003). Discussion of the rarity concept continues, with various perspectives (e.g., Frank 2016), including important considerations in conservation biology (e.g., Hartley and Kunin, 2003; Lennon et al., 2004). Rarity of species in modern floras can take many different forms – for example, widespread but uncommon everywhere vs. absent at all but one of many sampling sites, but abundant where it occurs, etc. Thus, the term requires explicit qualification when used.

Rarity has been widely considered in paleontology, where it takes on all of the same spatial forms as in the modern world (e.g., Buzas et al., 1982). Added, of course, is the matter of rarity in time, which has much the same variety of patterns as rarity in space, adding an additional complication to the basic use of the term. Furthermore, in paleontology, rarity of particular species, particular habitat specialists, climatically restricted taxa, or taxa of certain kinds of construction, may be reflections of taphonomic processes – e.g., from the lack of easily preservable parts, to growth in environments unfavorable to preservation, to architectures, in the case of plants that produce few deciduous organs (e.g., Scheihing, 1980; McKinney, 1997). These taphonomic considerations can greatly complicate determination of the relationship between fossil patterns and original ecology (see, for example, discussions in Bashforth et al., 2010, 2011, 2014).

Our objective in this note is to record the first occurrence of *Annularia* cf. *spinulosa* Sternberg from the lower Permian Abo Formation of New Mexico. This occurrence is noteworthy because the Abo has been intensively examined over the length and breadth of its outcrop area, from south-central to north-central New Mexico (Mack and James, 1986; Mack et al., 1995, 2010; Baltz and Myers, 1999; Lucas et al., 2012a, 2013, 2014, 2015a). Consequently, it has been well characterized stratigraphically, sedimentologically and paleoenvironmentally. In addition, it has been intensively prospected for plant fossils throughout this same area, and a number of floras have been published, summarized below.

Despite this sampling, the calamitaleans have proven to be rare elements in the Abo Formation. This is a puzzling result, given the depositional environment of the Abo, which is strongly fluvial and indicative of at least intermittent wetland development. The calamitaleans are one of the most widespread groups of late Paleozoic plants, found commonly and often in abundance in deposits from Pennsylvanian coal basins (for recent discussions, see Thomas, 2014; Falcon-Lang, 2015), where widespread wetland conditions were present intermittently and for long periods of time (thousands to tens of thousands of years at a stretch). In addition, they remain common elements during periods of drier climate in coal basins of central Pangea and in areas of relatively high ground water in otherwise relatively arid areas of far western Pangea (e.g., Tidwell, 1988; DiMichele et al., 2014).

GEOLOGY

The specimen under consideration was collected from the Abo Formation, a lithostratigraphic unit that crops out throughout most of central New Mexico (Lucas et al., 2013) (Fig. 1). The Abo is of early Permian age, primarily Wolfcampian but extending into the early Leonardian; in international terms this is Sakmarian through early Artinskian. The age is constrained by marine fossils of the Hueco Group, which intertongues with Abo-equivalent rocks in southern New Mexico (e. g., Krainer et al., 2009; Vachard et al., 2015; Lucas et al., 2015b).

The lower Abo Formation (Scholle Member) consists of interbedded thick mudstones with strong pedogenic overprints, incised by channel-form coarser deposits varying from conglomerates to siltstones. The upper Abo Formation (Cañon de Espinoso Member) is dominated by sheet-like fine-grained sandstones and siltstones separated by mudstone deposits with pedogenic overprints. The sandstone/siltstone beds are of meter-scale thickness, often have intraformational gravel bottoms, but are otherwise of uniform grain size, with thin clay layers in the upper 10-30% of their thickness. They also may be pedogenically altered in their upper parts. The clay drapes often entomb plant fossils and preserve footprints and trackways of tetrapods and invertebrates, mudcracks and raindrop imprints.

The plant-bearing site, USNM (National Museum of Natural History, Smithsonian Institution, Washington, D. C.) 42265, is a 1-2 m thick bench of fine-grained, ripple-laminated sandstone that is part of a series of benches of varying thickness, interbedded with largely covered, finer grained intervals that make up most of the slope on which it is exposed (Fig. 2.1). The bench occurs near the top of a ridge (Fig. 2.2) on the Bureau of Land Management's property northeast of Socorro, New Mexico. Fossil plant remains mainly were recovered from float surrounding the site (Fig. 2.3), but *in situ* plants were found in the upper parts of the bed. The upper portion consists of interbedded siltstones and clay drapes, the latter frequently mudcracked (Fig. 2.4, 2.5). A low diversity tetrapod footprint assemblage (mostly of the lacertoid track *Dromopus*) is present at the site.

Physical features and local geology suggest that the deposit is in the upper part of the Cañon de Espinoso Member about 17 m below the contact with the overlying Arroyo de Alamillo Formation of the Yeso Group (Fig. 1). The Wolfcampian-Leonardian boundary is in the upper part of the Abo Formation (Lucas et al 2015c), but cannot be placed precisely in the Abo Formation section in Socorro County. However, given the stratigraphically high position in the Abo Formation of USNM locality 42265, it is almost certainly of early Leonardian age.

In toto, the various aspects of these deposits suggest sheet flow in shallow, wide channels, filling and thus shallowing upward though time. Water flow appears to have been intermittent in the latter phases of sediment accumulation, accompanied by periodic exposure. Fossil plant remains are rare but, as elsewhere in the upper Abo Formation, are concentrated in the upper portions of siltstone benches. Here, the plants are frequently covered by clay or are mixed with clays and mud clasts (Fig. 3).

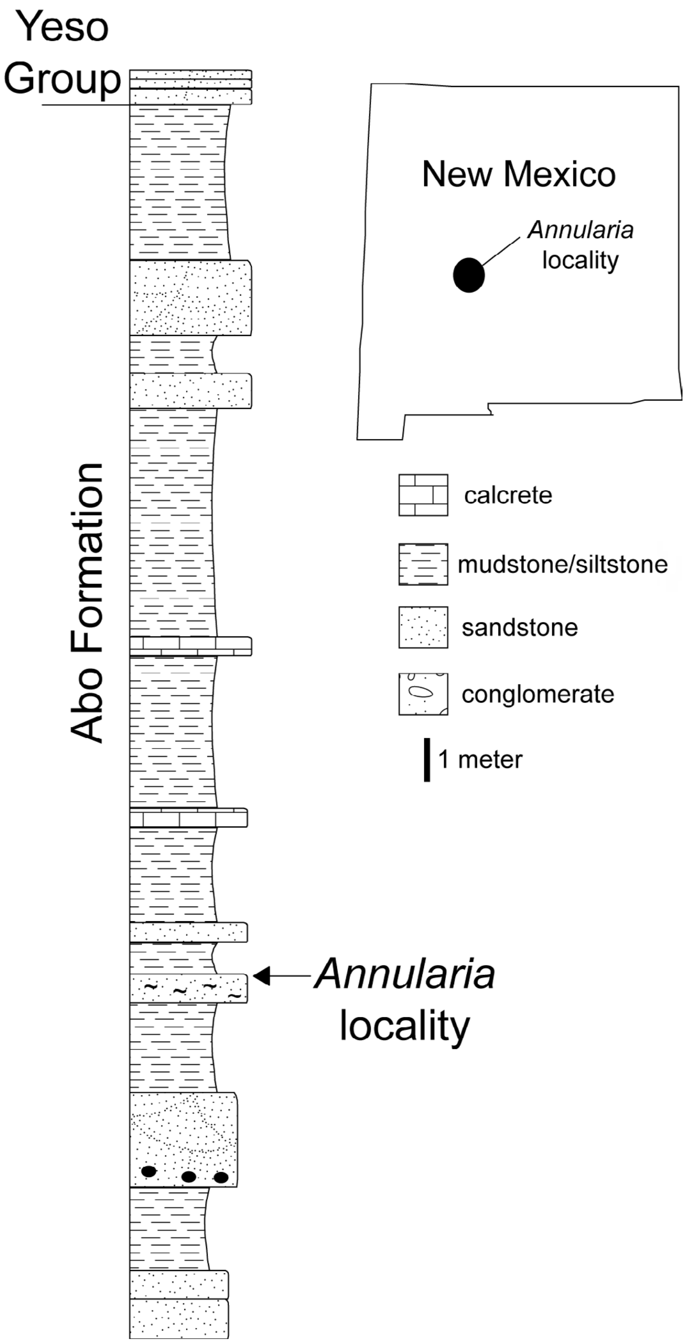

FIGURE 1. Index map and measured stratigraphic section at the Abo Formation fossil locality that yielded the specimen of *Annularia* documented here. Stratigraphic section modified from Lucas et al. (2009).

PALEONTOLOGY

The flora at this location is dominated by *Supaia thinnfeldioides* White (Fig. 3), with smaller numbers of specimens attributable to *Supaia anomala* White, and *Walchia* Ewing, the latter with closely adpressed leaves, similar to Morphotype I of Looy and Duijnstee (2013). One of the *Supaia* specimens is of particular interest, illustrated in Figure 3.2 (we thank Hermann Pfefferkorn for pointing out these features, which we missed!). It appears that a small stem, about 3.5 cm in diameter is present in the lower left portion of the figure. From this suspect stem, delicate root-like elements (R) emanate. A thin line running from the base of the leaf (L) to the stem, at the point of the arrow labeled (S), offers a vague suggestion of attachment.

Based on their fragmentary nature, disposition in the sediment, and association with clay drapes and mudcracked surfaces, most of the plant remains appear to be transported to some degree. However, the small sediment-infilled stem, the roots, and small, associated *Supaia* leaf are identical to features described by DiMichele et al. (2012) from the Abo Formation, which they interpreted as an in situ *Supaia* stand growing in a streamside environment subject to intermittent flood disturbance. This specimen makes it unlikely that the other, relatively large, disconnected plant parts were transported long distances. We thus interpret the assemblage as a mixture of autochthonous and parautochthonous plant remains.

The focus of this paper is a single specimen of calamitalean foliage that was found in float. This specimen consists of three adjacent whorls of leaves, likely attached to a single branch (Fig. 4). Individual whorls, although fragmentary and partially obscured, are symmetrical and nearly round in outline, approximately 4.5 cm in diameter. Whorls consist of up to 25-30, single veined leaves that are approximately 2 cm long, and mainly fusiform in shape, with perhaps some slight expansion distally (Fig. 4.2). Leaves appear to be attached to nodal regions, preserving some of the nodal plates. The nodal areas are wide, approximately 1 cm in diameter. These features are similar to those of *Annularia spinulosa* Sternberg (see Barthel, 2000, 2004, 2015). Certain identification is problematic because of the poor state of preservation, and we confine our identification to *Annularia* cf. *spinulosa*. The taxonomy of calamitalean foliage is in need of revision. This is illustrated by the name *Annularia spinulosa*, which has been proposed for a subset of foliage often attributed to *A. stellata* (Schlotheim) Wood (Barthel, 2000), a taxonomic name that has been used for a wide variety of morphological forms that, as used in the literature, likely encompasses more than one natural species (e.g., Kerp, 1984).

DISCUSSION

The preservation of the specimens we have attributed to *Annularia* cf. *spinulosa* is not the best, which is one of the reasons our identification is tentative. The central area of each whorl, in particular, is unusual in being relatively large, and slightly broken and/or incomplete. This might lead to questions about the species identification of the specimen, or even its affinities with *Annularia*. Comparison with the specimens illustrated by Barthel (2004, fig. 17; 2015, figs. 6 – the lectotype, 62 and 64) is instructive in this regard. In this suite of specimens, stems bearing *A. spinulosa* foliage can be seen to be slightly expanded at the nodes. Additionally, the leaf whorls tend to have been flattened onto the bedding surface, suggesting that in life the whorls were borne in nearly the same plane as the branch axis, which was borne close to horizontal on the main stem. The combination of nodal swelling and slight compressional distortion during preservation leads to exposure of the nodal-plate region and, often, slight fracturing or incomplete exposure (partial covering by sediment). The central region of many of the leaf whorls illustrated by Barthel (2015) also is similar to those in the Abo Formation specimens. Thus, by comparison with these Rotliegend specimens, we feel some confidence in the identification.

Various species of *Annularia* were widespread throughout Euramerica during the Pennsylvanian and early Permian. The work of Barthel, cited here, on Rotliegend specimens, indicates that *A. spinulosa* was present during the Late Pennsylanian and into the early Permian in the central Pangean regions that are now Europe. The species, mostly reported as *A. stellata*, appears in a sampling of additional floras from across Europe, including Scotland (Wagner, 1983), Spain (Amerom et al., 1993), Germany (Kerp and Fichter, 1985), the Czech Republic (Šimůnek and Martínek, 2009) and Romania (Popa, 1999). Where illustrated, these specimens conform to the concept of *A. spinulosa* (Popa, 1999, illustrates a specimen of *Asterophyllites longifolius* (Sternberg) Brongniart that appears to be *Annularia spinulosa*, including having a large nodal region). However, not all these floras include illustrations. There are, of course, many reported assemblages of latest Pennsylvanian or Permian age that do not contain this species, but there is no quantitative assessment of its relative frequency or of the species with which it is most commonly associated. Stratigraphically, the Abo Formation encompasses a considerable interval of time, from the mid-Sakmarian through the early Artinskian (Lucas et al., 2013). Thus, considering the distribution of this species in Europe, its occurrence in the Abo Formation is not unprecedented. However, the reported specimen is from the upper Abo, Cañon de Espinoso Member, which is younger than the Lower Rotliegend and equivalent strata.

The reported specimen of *Annularia* cf. *spinulosa* is the only example of calamitalean foliage thus far reported in the literature from the red beds of the Abo Formation. The Abo also includes gray beds, and the flora of the red beds and gray beds differs (DiMichele et al.,

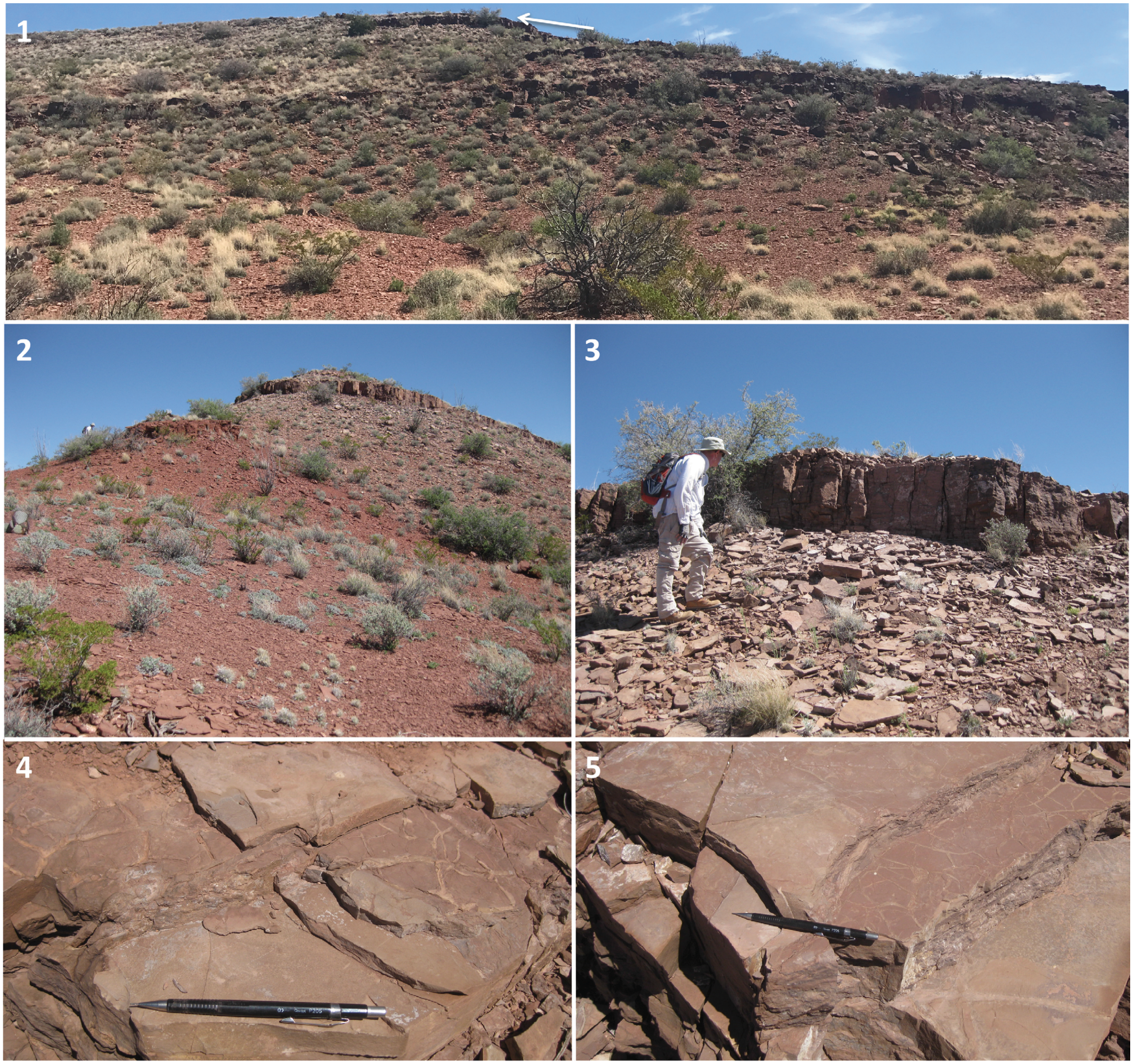

FIGURE 2. Progressively closer views of USNM locality 42265. **1.** Succession of resistant siltstone benches intercalated with less resistant, slope-forming mudstones. White arrow indicates bench containing plant fossils. **2.** View of two successive siltstone benches separated by less resistant mudstones. Plant-bearing bench at top of hill. **3.** Plant-bearing bench. **4-5.** Upper portion of plant-bearing bench in which plant-fossils and animal trackways are found concentrated in clay partings/drapes. Note mudcracked surfaces between thicker beds of siltstone.

2013). *Annularia spicata* and *Asterophyllites equisetiformis* have been reported from the gray facies (Lucas et al., 2012b; DiMichele et al., 2013). Calamitalean stems have been reported in both facies types; common in the gray facies, but rare in the red beds.

The flora of the Abo red beds and equivalent units in New Mexico has now been described in a series of publications (e.g., Hunt, 1983; DiMichele et al., 2007, 2012, 2015, 2017; Voigt et al., 2013, 2015; Rinehart et al., 2015). In total, these publications report on field work done throughout most of the outcrop area of the Abo Formation and include collections from approximately 200 field locations. For any given site where plant fossils were found, dozens of additional sites were prospected without producing any plant remains. Thus, the Abo red beds are among the most intensively investigated fossil-plant-bearing strata in the western part of the former Pangean supercontinent. In a 2013 summary of the known flora, DiMichele et al. (2013) reported red-bed plant collections from 172 sites. The most commonly occurring plants, based on the number of collecting sites at which they occur (82 of 172), are walchian conifers, corresponding to at least 5 different morphotypes. The second most common taxa are species of the genus *Supaia* (28 of 172 sites), overwhelmingly represented by *Supaia thinnfeldioides* (25 of 28 occurrences). Callipterids, represented mainly by *Autunia conferta*, occur at 9 sites. All other taxa are rare, including calamitalean stem remains, which were found at two sites only; calamitalean foliage was not found. More detailed studies of relatively large floras from single sites or multiple sites in a confined area (e.g., Hunt, 1983; DiMichele et al., 2015) typically report no calamitalean remains.

The Abo flora is one typical of environments with strong edaphic filters, keeping diversity very low and selecting strongly against plants with preferences or requirements for wet substrates throughout much of the year. Nonetheless, the extreme rarity of calamitalean stem and foliar remains is unusual for paleoequatorial fossil-plant assemblages of late

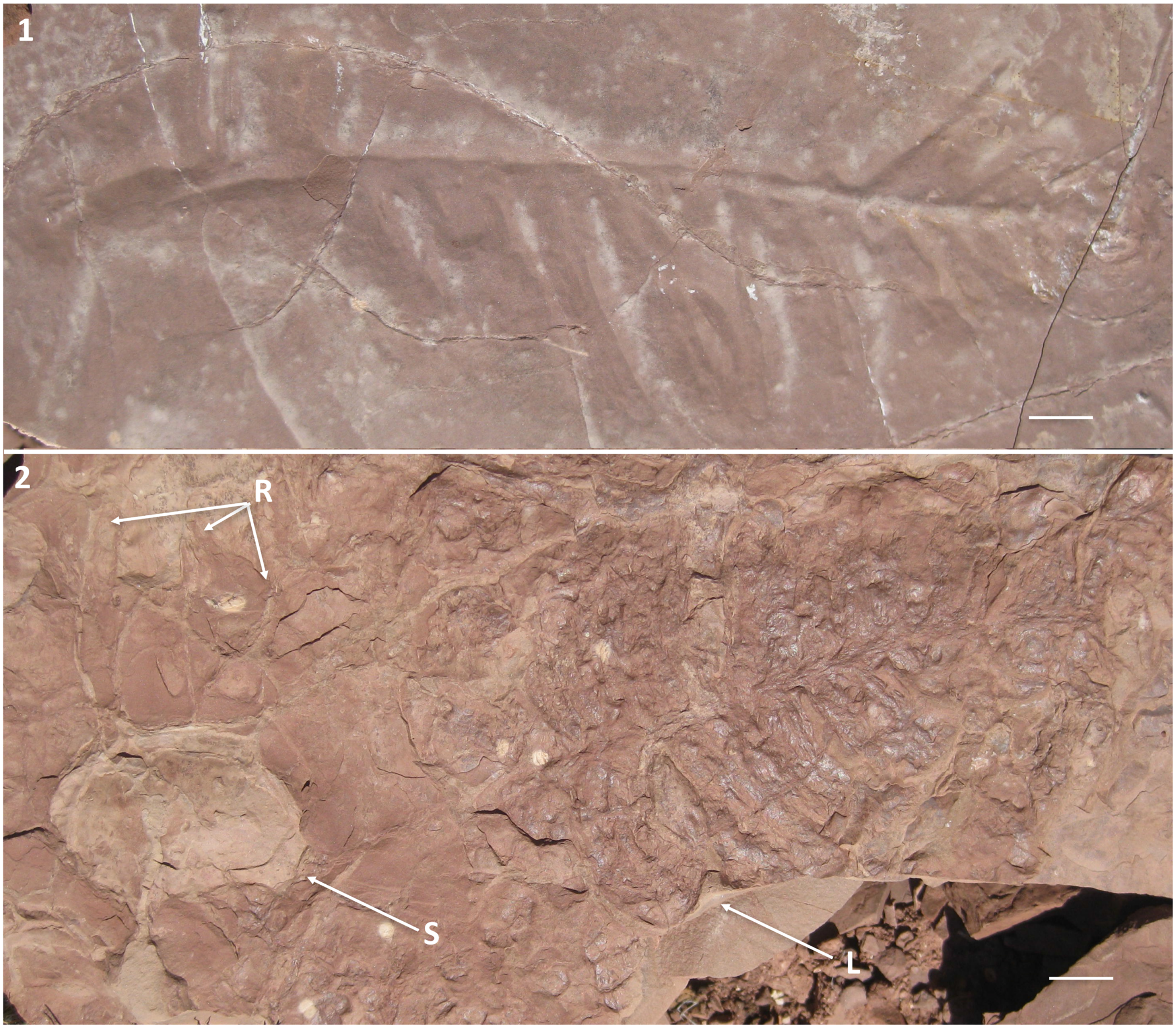

FIGURE 3. *Supaia thinnfeldioides*. **1.** Likely ½ of a forked, roughly symmetrical leaf, embedded in a claystone layer and thus partially obscured. **2.** Small leaf (L) lying on the contact between a siltstone layer and claystone drape, showing the irregularity of the siltstone surface. This leaf is possibly attached to a stem (S) in cross-section from which emanate thin roots (R). Scale bars = 1 cm.

Paleozoic Pangea. The calamitaleans seemingly had the capacity to disperse widely; in addition to being typical elements in wetland floras of late Paleozoic age, they also are found in assemblages otherwise dominated by drought-tolerant plants. They appear, together with the marattialean tree ferns, to have been one of the most widely dispersing groups of plants centered in wetter substrates, and are reported from riverine corridors and lakeside habitats well into the Permian, under seasonally dry climates. Like calamitaleans, remains of marattialean ferns also are extremely rare in the Abo red beds, occurring in only 2% of the plant collections. In light of the rarity of the two most widespread "wetland" floral elements, their near absence in the Abo Formation suggests rather extreme environmental conditions. This is consistent with the relative abundance of *Supaia*, a plant generally found in floras of strongly xeromorphic aspect, interpreted as having lived in environments with a long, intense dry period (White, 1929; Wang, 1997; DiMichele et al., 2007, 2012; Galtier and Broutin, 2008). The Abo depositional environment appears to have varied through time, from a semi-arid coastal plain with well-developed streams, represented by incised channels and thick sandstones, to one dominated by intermittent sheet flow in cryptic channels, with evidence of little or no water at times. Thus, the rarity of calamitaleans, and *Annularia,* in particular, suggests a near absence of suitable habitats for these plants on the original Abo landscape. The rarity, in this instance, does not appear to be a taphonomic happenstance, in which these particular plants were filtered out in the processes of sediment transport and burial of organic remains.

In summary, the occurrence of a single specimen of *Annularia* cf. *spinulosa* adds an additional species to the relatively low species diversity reported from the Abo Formation, which now stands in the mid-30s. It extends the Permian range of this plant into the western reaches of the equatorial region of the Pangean supercontinent. And, it serves as an example of a type of plant that is otherwise common over a broad area, but that can be exceedingly rare in certain kinds of environments where it might otherwise be expected to be present. This example of rarity in the fossil record appears to be reflective of original low abundance and occurrence at a few, widely scattered places on a broad, semi-arid to arid coastal plain.

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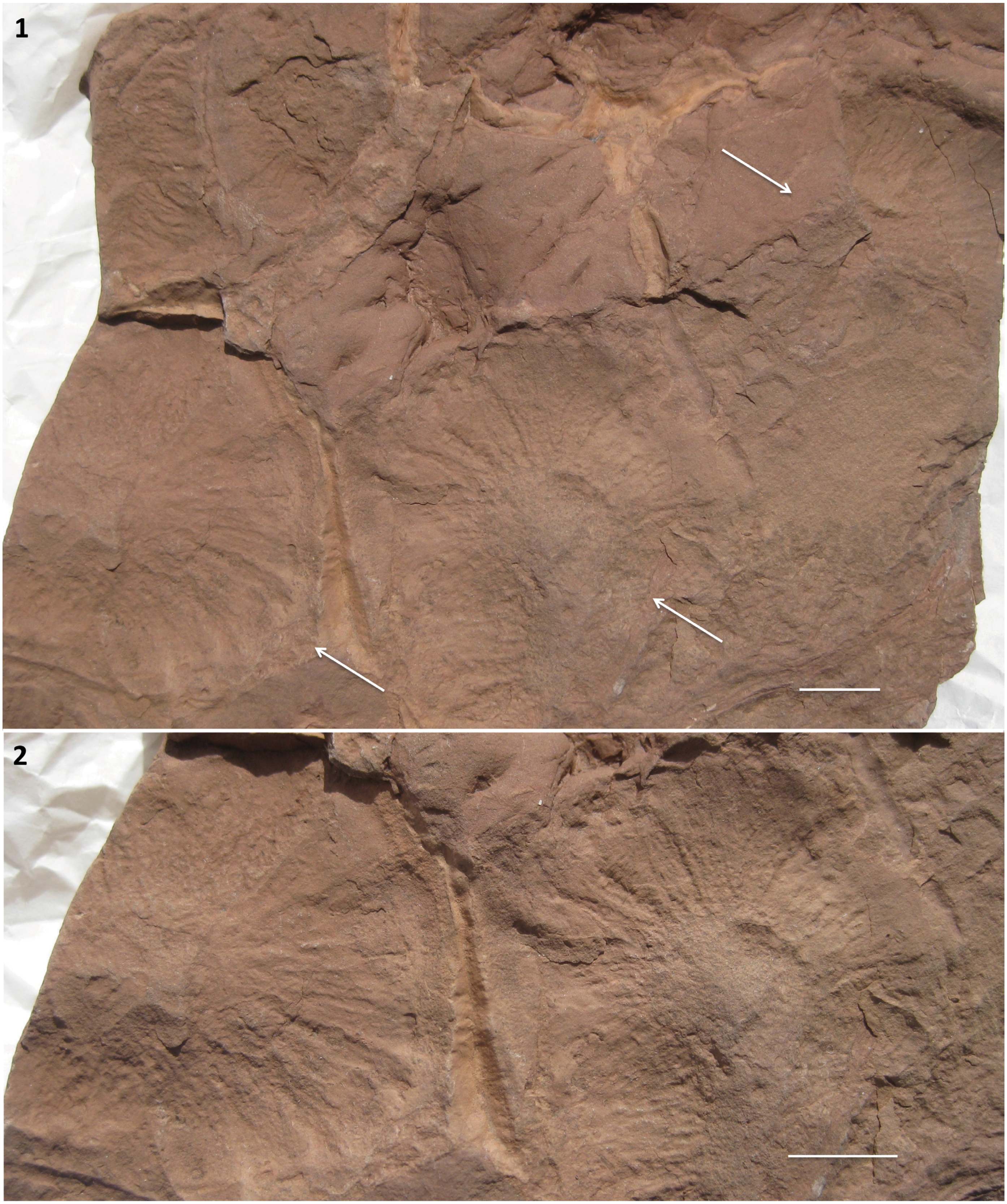

FIGURE 4. *Annularia* cf. *spinulosa* specimen. USNM specimen 637034, USNM locality 42265. 1. Nearly complete specimen showing three whorls of leaves (white arrows) preserved on a claystone layer. The clay became mudcracked after deposition of sediment and leaf remains. 2. Closer view of two best preserved leaf whorls. Scale bars = 1 cm.

for reviews of an earlier version of this paper, which spurred significant improvements.

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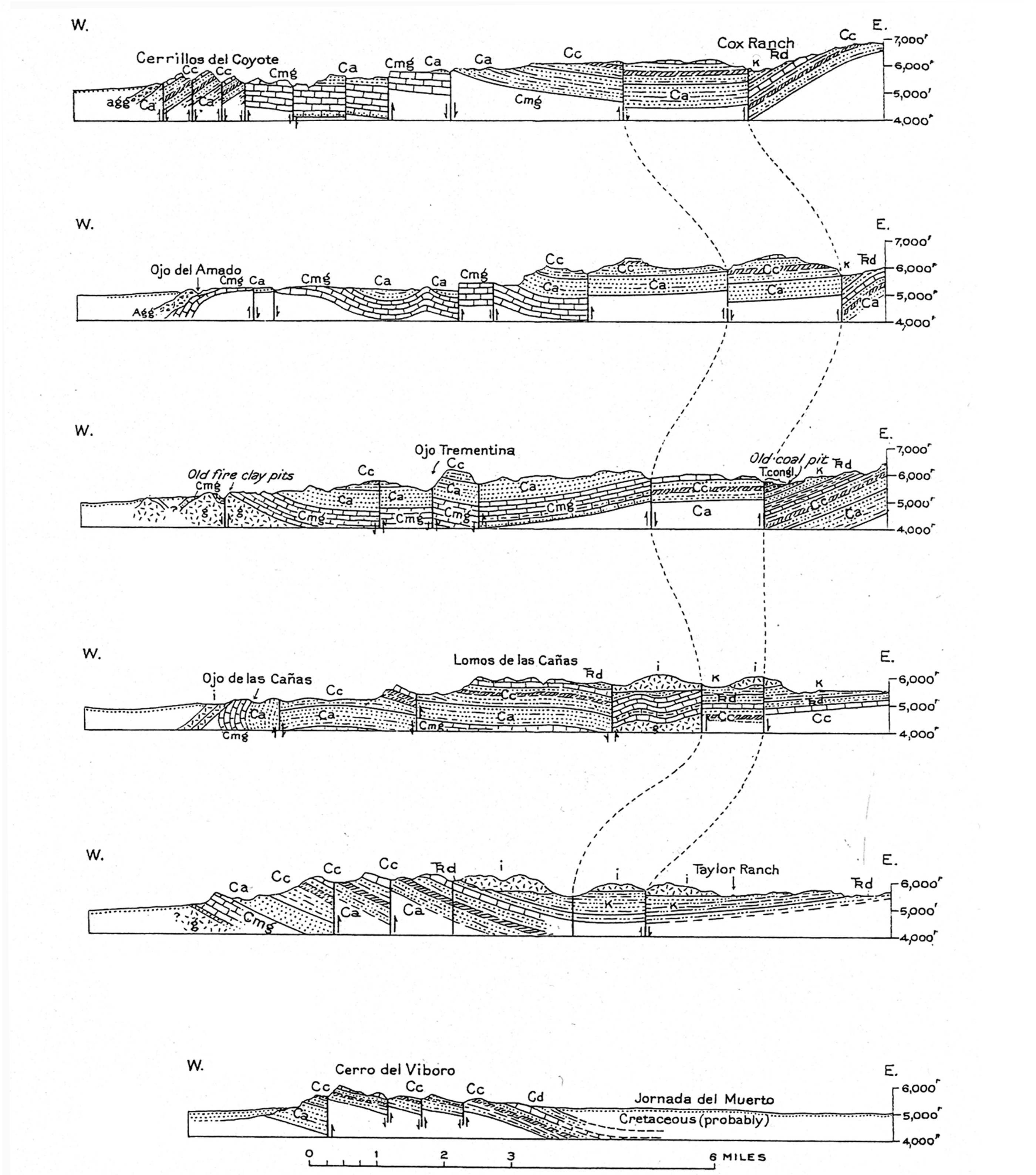

Darton's (1928, pl. 21) cross sections east of Socorro. Units are agg = agglomerate (volcanic); Ca = Abo Sandstone; Cc = Chupadera Formation; Cmg = Magdalena Group; g = granite; i = volcanic flows; K = Upper Cretaceous strata; T = Tertiary conglomerate; Trd = Triassic Dockum(?).