



Revising Palynostratigraphic Concepts in the Raton Basin a Half-century after R.H. Tschudy's Pioneering Work: A New Pollen Proxy for the Campanian-Maastrichtian Stage Boundary and Reevaluation of the Famous K-PG Fern-Spore Spik

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REVISING PALYNOSTRATIGRAPHIC CONCEPTS IN THE RATON BASIN A HALF-CENTURY AFTER R.H. TSCHUDY'S PIONEERING WORK: A NEW POLLEN PROXY FOR THE CAMPANIAN- MAASTRICHTIAN STAGE BOUNDARY AND A REEVALUATION OF THE FAMOUS K-PG FERN-SPORE SPIKE

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ABSTRACT — R.H. Tschudy pioneered palynostratigraphy in the Raton Basin nearly a half-century ago and established two key precedents: (1) that the Campanian-Maastrichtian stage boundary should be placed at or near the first appearance datum (FAD) of *Kurtzipites* and (2) that the Cretaceous-Paleogene (K-Pg) boundary fern-spore spike signaled the comparatively rapid recovery of ferns following the K-Pg impact event. In light of new discoveries, revisions to these key concepts are proposed. First, correlation between the Raton Basin and the Rock Springs uplift in Wyoming indicates that the pollen proxy for the Campanian-Maastrichtian stage boundary should be moved lower, to within the uppermost part of the *Trudopollis meekeri* Zone (formally defined as an Interval Zone between the FAD of *Aquilapollenites striatus* and the LAD of *T. meekeri*). Second, the apparent association of *Cyathidites* spores with *Anemia*-like schizaeaceous foliage and *Laevigatosporites* spores with thelypteridaceous foliage in the Raton Basin suggests that it was not a general property of ferns, such as the ability to regenerate rapidly from short-lived spores or rhizomes in the soil spore bank, which conferred an advantage in the harsh, post-impact world of the earliest Danian. The long-term viability of modern *Anemia*, *Lygodium*, and *Thelypteris* spores contrasts with that of modern cyatheaceous and *Blechnum* ferns (the taxa traditionally associated with the dominant fern spores at the K-Pg boundary), presumably accounting for the monotaxial nature of the two-phase fern-spore spike in the Raton Basin. Thus, spores of these ferns could have survived a decade-long impact winter, which has been suggested to have caused a mass-extinction event among dicot angiosperms.

INTRODUCTION

Beginning 45 years ago, R.H. Tschudy pioneered palynostratigraphy in the Raton Basin of northeastern New Mexico and south-central Colorado. Here, he established two key precedents that would later become widely recognized chronostratigraphic markers in both western North America and globally: (1) placement of the Campanian-Maastrichtian stage boundary at the first appearance datum (FAD) of *Kurtzipites* (Tschudy, 1973) and (2) correlation between the abrupt disappearance of Cretaceous angiosperm pollen and an earliest Paleocene (Danian) fern-spore spike (Orth et al., 1981; Tschudy et al., 1984). The former concept would later be formalized by Nichols and Sweet (1993) in recognizing the Campanian-Maastrichtian stage boundary in western North America, whereas the latter concept would later be applied globally (Vajda and Bercovici, 2014). Since these pioneering studies, there have been two major advances in the biostratigraphy of the Raton Basin: (1) the discovery that the Campanian-Maastrichtian stage boundary can be placed in the upper part of the Pierre Shale throughout the Raton Basin (Sealey and Lucas, *this volume*) and (2) the discovery that *Anemia*-like schizaeaceous foliage and thelypteridaceous foliage may have produced the dominant fern spores in the two-phase Cretaceous-Paleogene (K-Pg) fern-

spore spike in the Raton Basin (Berry, 2019). Therefore, the objective of this study is two-fold: (1) to select a new pollen proxy for the Campanian-Maastrichtian stage boundary in the Raton Basin and (2) to evaluate the implications of the discovery that the traditional familial affinities of the dominant fern spores in the two-phase K-Pg boundary fern-spore spike in the Raton Basin, *Cyathidites* (Cyatheaceae) and *Laevigatosporites* (Blechnaceae), are likely incorrect.

BRACKETING THE CAMPANIAN-MAASTRICHTIAN STAGE BOUNDARY USING POLLEN MARKERS: CORRELATION BETWEEN THE ROCK SPRINGS UPLIFT, WYOMING, AND THE RATON BASIN

Correlation between the Western Interior and the Global Standard Stratotype Section and Point (GSSP) for the Campanian-Maastrichtian stage boundary places this boundary at the base of the *Baculites baculus* ammonite zone (Cobban et al., 2006). Tschudy (1973) suggested the base of the *B. baculus* Zone was correlated with the FAD of the palynomorph *Kurtzipites trispissatus* and, therefore, placed the Campanian-Maastrichtian stage boundary near the top of the Vermejo Formation (Fig. 1A, B, C) in its type area in New Mexico (Nichols and Sweet, 1993; Nichols, 1994). However, the stage boundary is

actually known to lie within the upper part of the Pierre Shale (Fig. 1A) in this region (Sealey and Lucas, *this volume*). Therefore, a new pollen marker for the stage boundary is required.

Within the Raton Basin, the uppermost part of the *Trudopollis meekeri* Zone encompasses the Campanian-Maastrichtian stage boundary (Fig. 1A). Tschudy (1973) placed the top of this zone slightly above the top of the Trinidad Sandstone (Fig. 1A), which, in the type area of the Vermejo Formation, contains the index inoceramid “*Cataceramus*” *barabini* (Sealey and Lucas, *this volume*). “*C.*” *barabini* is a marker for the *Baculites eliasi*-*B. baculus* Zones in the Western Interior (Walaszczyk et al., 2001). Although Nichols (1994) described *T. meekeri* as not extending into the lower Maastrichtian and as being restricted to the late (but not latest) Campanian *Aquilapollenites quadrilobus* Zone, the top of this zone is actually found within the uppermost part of the Almond Formation (Fig. 2A, B) at a stratigraphic position higher than the base of the *B. baculus* Zone in the area of the Rock Springs Uplift, Wyoming (Fig. 2C; Gill et al., 1970; Stone, 1973; Lynds and Slattery, 2017). Thus, the uppermost part of the *T. meekeri* Zone also encompasses the Campanian-Maastrichtian stage bound-

ary in this area as well (Fig. 2), and actually lies within the lower part of Nichols’ (1994) *Aquilapollenites striatus* Interval Zone (Lynds and Slattery, 2017). The FAD of *Aquilapollenites striatus* is within the highest unit of the Kaiparowits Formation in southern Utah (Miller et al., 2013), which has been dated at 74.21 ± 0.18 Ma (Roberts et al., 2005). Therefore, the uppermost part of the *Trudopollis meekeri* Zone, which is here defined formally as an Interval Zone between the FAD of *A. striatus* and the LAD of *T. meekeri* (Fig. 2A), closely brackets the 72.1 Ma Campanian-Maastrichtian stage boundary (Figs. 1, 2). For the purposes of this study and for correlation between northern New Mexico and Wyoming where the FAD of *Kurtzipites* is much too high and the FAD of *Wodehouseia* is not a useful marker given the geographic restriction of this taxon to areas further north (Stone, 1973; Tschudy, 1973; Sweet, 1994), the uppermost part of the *T. meekeri* Zone is selected as a new proxy for the stage boundary. This determination is consistent with the informal conventions of other researchers, who previously used the LAD of *T. meekeri* as a provisional marker for the Campanian-Maastrichtian stage boundary in west-central Alberta, Canada (Fanti and Catuneanu, 2009).

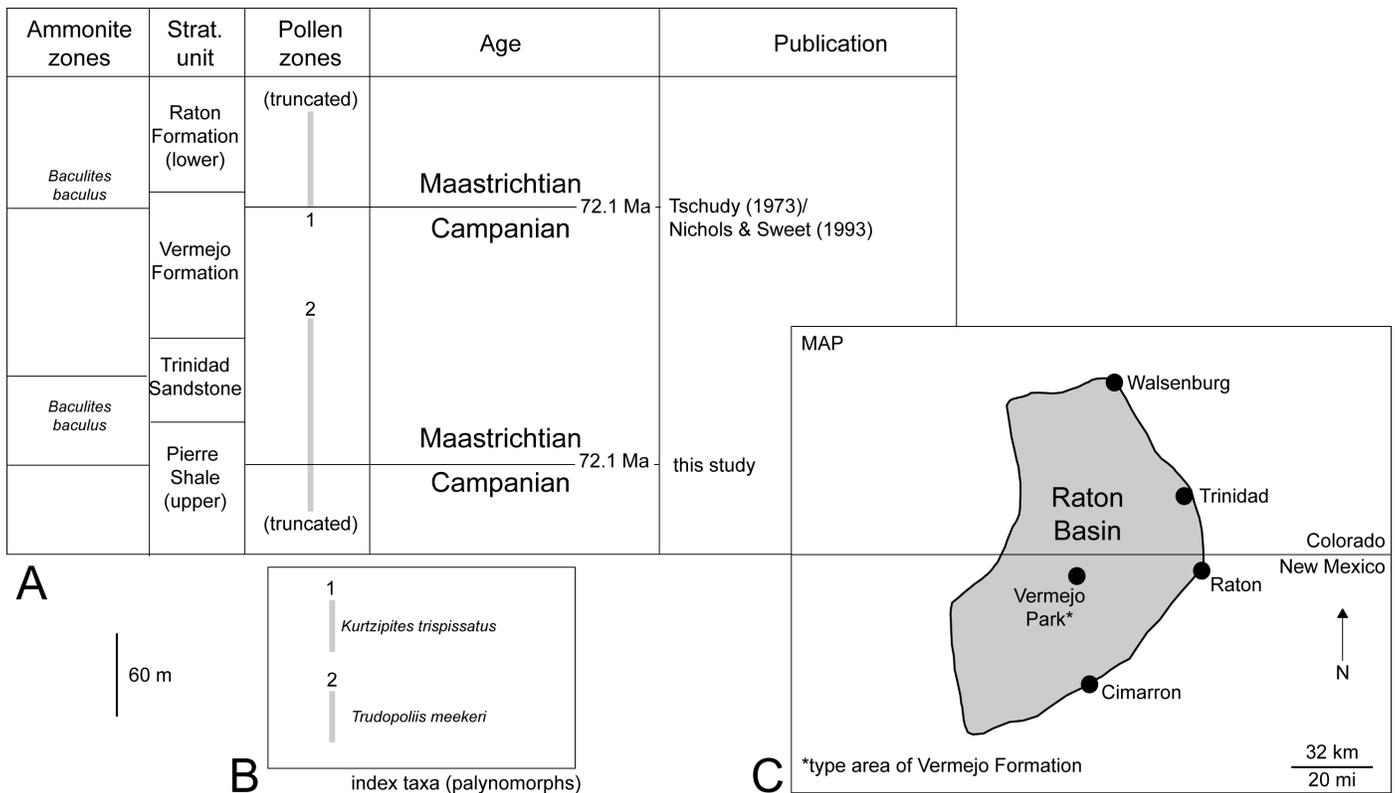


FIGURE 1. **A**) Diagram illustrating the projected position of the base of the *Baculites baculus* ammonite zone (Campanian-Maastrichtian stage boundary) near the top of the Vermejo Formation according to Tschudy (1973) and Nichols and Sweet (1993) relative to palynostratigraphic markers, FAD of *Kurtzipites trispissatus* (1) near the top of the Vermejo Formation, LAD of *Trudopollis meekeri* (2) in the lower part of the Trinidad Sandstone, and the actual position of the base of the *B. baculus* zone in the upper part of the Pierre Shale. Tschudy (1973) correlated the base of the *Baculites baculus* Zone with the FAD of *Kurtzipites trispissatus* in the Raton Basin, placing the Campanian-Maastrichtian stage boundary near the top of the Vermejo Formation. However, the base of the *B. baculus* Zone actually lies within the upper part of the Pierre Shale (Sealey and Lucas, *this volume*). Therefore, the stage boundary actually lies within the upper part of the *Trudopollis meekeri* Zone. **B**) Key to index palynomorphs. **C**) Inset map illustrating the location of Tschudy’s (1973) study area in the type area of the Vermejo Formation (asterisk) within the Raton Basin of northeastern New Mexico and south-central Colorado.

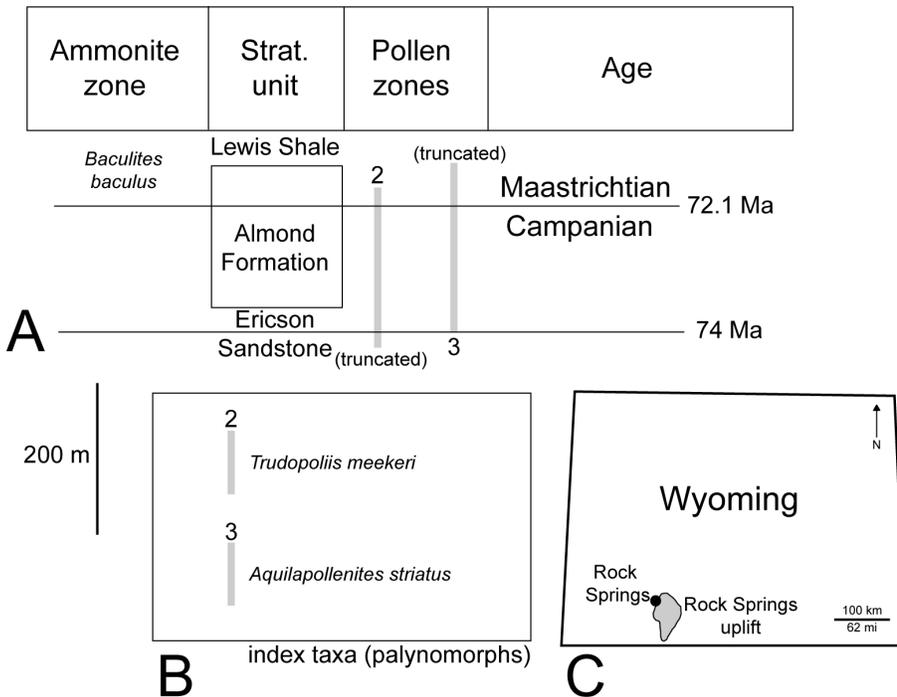


FIGURE 2. **A**) Diagram illustrating the position of the base of the *Baculites baculus* ammonite zone (Campanian-Maastrichtian stage boundary) in the upper part of the Almond Formation according to Gill et al. (1970) and Lynds and Slattery (2017) relative to palynostratigraphic markers, LAD of *Trudopollis meekeri* (2) near the top of the Almond Formation and FAD of *Aquilapollenites striatus* (3) below the Almond Formation. As in the Raton Basin (Fig. 1), in the area of the Rock Springs Uplift, Wyoming, the highest part of the *Trudopollis meekeri* Zone encompasses the Campanian-Maastrichtian stage boundary as defined by ammonite biostratigraphy. **B**) Key to index palynomorphs. **C**) Inset map illustrating the location of the Rock Springs uplift in southwestern Wyoming, where Gill et al. (1970) conducted ammonite biostratigraphy, and Stone (1973) conducted palynostratigraphy.

RE-ENVISIONING THE K-PG FERN-SPORE SPIKE IN THE RATON BASIN

Tschudy et al. (1984) compared the pattern of plant succession across the K-Pg boundary in the Raton Basin with the pattern of plant recovery on the Krakatau Islands following the 1883 volcanic eruption, which effectively sterilized these islands and established the concept that the K-Pg boundary fern-spore spike signaled the relatively rapid recovery of ferns following the impact event. Although this concept is still widely accepted today (Nichols and Johnson, 2008; Vajda and Bercovici, 2014), it is important to point out that the monotaxial nature of the global K-Pg fern-spore spike apparently does not signal the general recovery of ferns after the K-Pg impact event, as Tschudy et al. (1984) envisioned, but instead signals a highly specific bioevent on a scale unanticipated by Tschudy et al.'s (1984) study (Vajda and Bercovici, 2014; Bercovici and Vellekoop, 2017). Clarke (1963), for example, reported dozens of fern-spore species in the coals of the Maastrichtian Vermejo Formation, although only two of these are represented in the K-Pg boundary fern-spore spike in the overlying Raton Formation.

Traditionally, the dominant fern spores at the K-Pg boundary have been attributed to Cyatheaceae or a *Blechnum*-like fern (Vajda et al., 2001; Ocampo et al., 2007). Within the Raton Basin, Wolfe and Upchurch (1987) proposed an association

between *Stenochlaena*-like fern foliage (Blechnaceae) and the dominant spores at the K-Pg boundary fern-spore spike (Upchurch et al., 2007). However, other researchers rejected this notion as *Stenochlaena* could not have produced the dominant fern spores at the two-phase, fern-spore spike in the Raton Basin (Collinson, 2001; Nichols and Johnson, 2008). Within Wolfe and Upchurch's (1987) phase-1 megafloral assemblage (Figs. 3A, B), Lee and Knowlton (1917) also collected an *Anemia*-like schizaeaceous fern (Fig. 3C), which is presently attributed to "*Anemia*" *elongata* (Berry, 2019). Chandler (1963) specifically posited that this species of *Anemia*-like schizaeaceous foliage could have produced smooth (psilate), *Lygodium*-like spores, which are classified by Balme (1995) in the dispersed spore genus *Cyathidites* (Fig. 3C), based on the proposed correspondence between sterile foliage ("*Anemia*" *elongata*) with fertile foliage bearing intact sporangia and spores ("*A.*" *poolensis*). This interpretation is in accordance with the views of other researchers, such as Warter (1965), who suggested that spores presently attributed to *C. diaphana* (Kroeger, 1995), the dominant fern spore in the first phase of the fern-spore spike in the

Sugarite coal zone (Spicer and Collinson, 2014), could have been produced by *Anemia*-like schizaeaceous foliage (Berry, 2019). Likewise, the dominant *Laevigatosporites* spore (Fig. 3C) in the second phase of the fern-spore spike in the Raton Basin, which has been classified as *L. haardtii* by some researchers (e.g., Nichols, 2002), has also been posited to have been produced by thelypteridaceous foliage (Collinson, 2002). This is in accordance with the recovery of *L. haardtii* (= *L. ovatus*, Nichols, 2002) spores from the sporangia of thelypteridaceous foliage (Stockey et al., 2006), which is very similar to thelypteridaceous foliage (Fig. 3C) collected from the Raton Basin (Postnikoff, 2009; Manchester, 2014; Berry, 2019).

The taphonomic pathways of fern spores and fern foliage are characteristically disparate, of course, so the hypothesis that dispersed spores were produced by co-occurring foliage is, in most cases, highly speculative unless bolstered by the recovery of fertile foliage with intact sporangia containing spores. However, the hypothesis outlined above (i.e., that dispersed spores belonging to *Cyathidites* and *Laevigatosporites* were produced by *Anemia*-like schizaeaceous foliage and thelypteridaceous foliage, respectively (Berry, 2019), is bolstered by several observations. First, although the two-phase K-Pg boundary fern-spore spike is relegated to a centimeter-scale rather than a meter-scale interval throughout the Raton Basin (Nichols and Johnson, 2008; Vajda and Bercovici, 2014), the

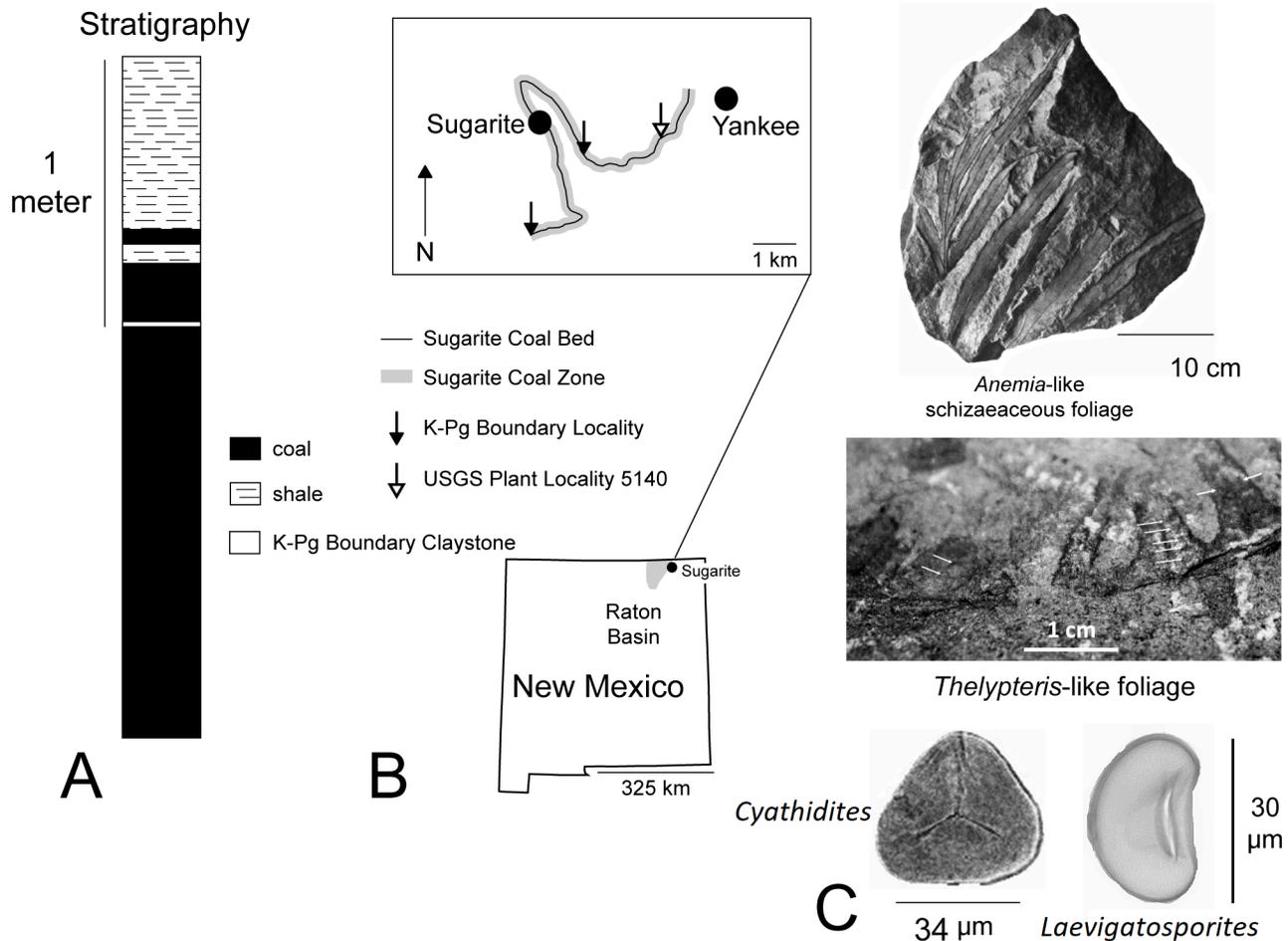


FIGURE 3. **A)** Composite section of K-Pg boundary section near Sugarite, New Mexico, with key to lithologic units. **B)** Map illustrating location of K-Pg boundary localities and USGS Plant Locality 5140 in the Raton Basin, New Mexico, where Lee and Knowlton (1917) collected fern foliage from Wolfe and Upchurch's (1987) phase-1 megafloreal assemblage. **C)** Illustrations of fern megafossils and corresponding fern spores. Illustration of *Anemia*-like schizaeaceous foliage is adapted from Lee and Knowlton's (1917) original illustration of the type specimen of "*Anemia*" occidentalis, which is now regarded as "*A.*" *elongata* (Manchester, 2014). Photograph of *Thelypteris*-like foliage, NMMNH P-80466 (aff. *Speirseopteris*), collected by the lead author from a fern thicket in the upper coal zone of the Raton Formation. Arrows on the photograph indicate once-forking veins (left half of the photograph), which are characteristic of thelypteridaceous foliage, and round sori located on the non-branching veins located on either side of the midvein (right half of the photograph), which are characteristic of *Speirseopteris* (Stockey et al., 2006; Manchester, 2014). Drawing of *Cyathidites* spore based on Berry (2019). Drawing of *Laevigatosporites* spore based on Stockey et al. (2006).

dominant spores in this fern-spore spike also dominate low-diversity palynofloral assemblages in the highest strata of the Raton Formation (e.g., Harrison, 2018). The observation that only two fern megafossils that have been collected from the Raton Formation are known to have both survived the K-Pg mass-extinction event and to have been capable of producing *Cyathidites* and *Laevigatosporites* spores lends credence to the perspective that these dispersed spores are probably not associated with the families (Cyatheaceae and Blechnaceae) traditionally linked with the K-Pg fern-spore spike in the Raton Basin (Berry, 2019). Second, the only ferns recorded from Lee and Knowlton's (1917) Raton megaflorea for which there are currently multiple collections (i.e., several specimens collected from more than a single locality) include ferns presently attributed to *Anemia*-like schizaeaceous foliage ("*Anemia*" *elongata*) and ferns presently attributed to *Speirseopteris*-like thelypteridaceous foliage (Fig. 3C; Lee and Knowlton, 1917; this study). Thus, the two-taxon signal of the K-Pg fern-spore

spike appears to correspond with the pattern of taxonomic diversity in the low-diversity Raton fern megaflorea (Fig. 3C).

A number of studies suggest that the K-Pg impact event resulted in an impact winter lasting about a decade (Pope et al., 1994, 1997; Pope, 2002; Ocampo et al., 2007; Vellekoop et al., 2014, 2016). Accordingly, this decade-long impact winter has been proposed to have caused profound turnover among the flora of western North America and the globe, resulting in a mass-extinction event among dicot angiosperms (Ocampo et al., 2007; Blonder et al., 2014; Spicer and Collinson, 2014; Vajda and Bercovici, 2014). Relative to pteridophytes, which are suggested to have recovered rapidly from soil spore banks (Sweet, 2001; Spicer and Collinson, 2014), the recovery of dicot angiosperms took about a millennium (Field et al., 2018). Nichols and Johnson (2008) proposed that the recovery of dicot angiosperms was predominantly from soil seed banks. This interpretation is based upon the observation that most fern spores are short-lived in the soil spore bank, so ferns would have to

have regenerated from the soil spore bank within months of the K-Pg impact event (Spicer and Collinson, 2014).

Unlike spores of Cyatheaceae and *Blechnum*, which characteristically lose viability within a matter of weeks within the soil spore bank (Mehra and Gupta, 1986; Ford and Fay, 1999; British Pteridological Society, 2017), spores of *Anemia*, *Lygodium*, and *Thelypteris* are known to exhibit long-term viability in soils. When stored at the same temperature (4°C) as exceptionally long-lived *Cyathea* spores, which were completely unviable by the third year of storage (Simabukuro et al., 1998), spores of a species of *Anemia* remained viable for more than 30 years (Nester-Hudson, 2011). Likewise, spores of another species of *Anemia* are known to remain viable for more than 20 years (Schraudolf, 1986). Both of these extant species produce smooth-walled spores while immature (Dettman and Clifford, 1991; Balme, 1995), which are similar to those produced by extinct, *Anemia*-like schizaeaceous foliage when mature (Chandler, 1963; Collinson, 2001). Likewise, spores of *Lygodium* are known to remain viable in soils for at least eight years (Hutchinson and Langeland, 2006), which is the fastest that the K-Pg impact winter is projected to have ended (Pope et al., 1994; Sweet, 2001). Spores of *Thelypteris* also have germinated after spending at least a decade in the soil spore bank (de Groot and During, 2013; Bremer, 2007). Indeed, long-term viability of these spores is unusual when compared to the viability of most fern spores (Nayar and Kaur, 1971; Spicer and Collinson, 2014) or spores of *Cyathea* and *Blechnum*, in particular. Thus, the monotaxial nature of the two-phase fern-spore spike in the Raton Basin could be due to the fact that the initial phase of plant recovery took longer than Tschudy et al. (1984) assumed based on the recovery pattern on the Krakatau Islands.

CONCLUSIONS

Within the Raton Basin, the highest part of the *Trudopollis meekeri* Zone, which is formally defined as an Interval Zone between the FAD of *Aquilapollenites striatus* and the LAD of *T. meekeri*, is a better proxy for the Campanian-Maastrichtian stage boundary than alternative pollen markers (the FAD of either *Wodehouseia* or *Kurtzipites*). Although the two-phase, K-Pg boundary fern-spore spike in the Raton Basin is traditionally attributed to global proliferation of either Cyatheaceae or Blechnaceae in the earliest Danian, it is likely that the dominant spores in the fern-spore spike in the Raton Basin were produced by *Anemia*-like schizaeaceous ferns and thelypteridaceous ferns. As these ferns appear to exhibit the potential for long-term spore viability relative to *Cyathea* and *Blechnum*, the monotaxial nature of the K-Pg fern-spore spike in the Raton Basin could signal a protracted recovery interval following a nearly decade-long impact winter, which has been hypothesized to have led to the apparently abrupt (i.e., geologically instantaneous) disappearance of Cretaceous dicot angiosperm pollen. If correct, this novel hypothesis could account for the apparent synchronicity in the recovery of ferns and dicot angiosperms with a strong affinity to Lauraceae in the megafossil record of the Raton Basin as both would have recovered from

the soil propagule bank when favorable climatic conditions returned (Berry, 2019). In contrast to the fern-spore spike, there is no palynologic record of the initial recovery of lauraceous palynomorphs as these are rarely preserved in the fossil record (Berry, 2019).

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