

Fern spore viability considered in relation to the duration of the Cretaceous-Paleogene (K-Pg) impact winter. A contribution to the discussion

KEITH BERRY

Science Department, Hoehne Re-3 School District, Hoehne, Colorado, 81046, U.S.A.;
 e-mail: keith.berry@hoehnesd.org

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ABSTRACT. The Cretaceous-Paleogene (K-Pg) boundary Chicxulub impact is supposed to have produced a nearly decade-long impact winter which resulted in a mass-extinction event among dicot angiosperms but which left pteridophytes comparatively unaffected. Dicot angiosperms subsequently recovered from the soil seed bank following an episode of global deforestation, although this recovery took centuries. Pteridophytes, on the other hand, are supposed to have recovered within months of the impact event, due to the characteristic, short-term viability of fern spores in the soil bank – an interpretation consistent with the assumption that the dominant fern spore at the K-Pg boundary fern spore spike, *Cyathidites* Couper, was produced by cyatheaceous foliage. At the K-Pg boundary section near Sugarite, New Mexico, however, *Cyathidites* spores are more likely to have been produced by schizaeaceous foliage, which produces spores capable of germinating after spending about a decade or more in the soil and which already commanded similar depositional settings in western North America during the Maastrichtian. Therefore, the protracted – millennial – timescale for fern dominance in the earliest Danian could be related to the unique ecology of schizaeaceous ferns that recovered from a persistent spore bank in a habitat that they already dominated, presumably by suppressing the colonization of angiosperms.

KEYWORDS: K-Pg boundary, mass extinction, impact winter, *Cyathidites*, Cyatheaceae, Schizaeaceae, fern spore spike, spore viability

INTRODUCTION

The patterns of pteridophyte and dicot angiosperm recovery across the Cretaceous-Paleogene (K-Pg) boundary appear paradoxical. On one hand, the characteristic short-term viability of fern spores in the soil bank is supposed to indicate that the fern spore spike associated with the K-Pg mass extinction event occurred within a few months of the K-Pg impact (Sweet 2001, Spicer & Collinson 2014). On the other hand, a severe, decade-long impact winter is supposed to have caused a mass extinction event among dicot angiosperms (Blonder et al. 2014, Spicer & Collinson 2014, Vajda & Bercovici 2014, Field et al. 2018). Sweet (2001: 135), for example, concluded that the short-term viability of fern spores in the soil bank precluded “an initial period of near blackout

and freezing” like that predicted under Pope et al.’s (1994) model of a nearly decade-long impact winter, although this impact winter is supposed to have not only selectively filtered dicot angiosperms but also delayed their recovery for several centuries (Blonder et al. 2014, Spicer & Collinson 2014, Clyde et al. 2016, Field et al. 2018).

Due primarily to modern conservation efforts, the long-term viability of fern spores in the soil bank has been studied extensively. Based on these studies, Spicer & Collinson (2014: 119) observed, “Fern spores have limited viability in the soil spore bank, with proven longevities typically measured in months or at most years. In the case of seeds, however, viabilities can be much longer, often exceeding a decade or

more.” The dominant fern spores in the K-Pg fern spore spike, *Cyathidites diaphana* (Wilson & Webster) Nichols & Brown and *Laevigatosporites haardtii* (Potonie & Venitz) Thomson & Pflug, are typically attributed to cyathea-ceous ferns and blechnaceous ferns, respectively (Vajda et al. 2001, Ocampo et al. 2007, Nichols & Johnson 2008, Spicer & Collinson 2014, Vajda & Bercovici 2014). Although non-chlorophyllous fern spores characteristically exhibit long-term viability as compared to chlorophyllous spores (Lloyd & Klekowski 1970), cyathea-ceous spores are notable exceptions (Mehra & Gupta 1986, Ford & Fay 1999). It is well known that *Cyathea* Smith spores can remain viable for more than a year in cold storage, although these spores completely lose viability by three years (Fig. 1A; Simabukuro et al. 1998a). Therefore, under natural conditions the viability of *Cyathea* spores in the soil bank is typically measured on the order of weeks or months rather than years (Page 1979, Mehra & Gupta 1986, Simabukuro et al. 1998a, b, 2000, Ford & Fay 1999, Goller & Rybczyński 2007, Marcon et al. 2014). The results of these studies clearly indicate that the recovery of cyathea-ceous ferns from the soil spore bank probably took place within the first few months after the K-Pg impact (Sweet 2001, Spicer & Collinson 2014); however, this may not have been possible, due to global darkness and freezing (e.g. Pope et al. 1994, Galeotti et al. 2004, Vellekoop et al. 2014, 2016, Bardeen et al. 2017). Indeed, non-photosynthetic saprophytes may have thrived in the first two years after the K-Pg impact (Vajda & McLoughlin 2004, 2007, Ocampo et al. 2007), when photosynthesis was prevented by soot and other aerosols (Fig. 1A; Bardeen et al. 2017).

High-precision dating of bioevents at the K-Pg boundary is fraught with difficulties and is therefore largely based on inference (Nichols & Johnson 2008). At the present time, high-precision dating of the K-Pg boundary fern spore spike indicates that it occurred within a century of the K-Pg impact event and lasted for about a millennium (Clyde et al. 2016, Field et al. 2018). Although the initial pattern of plant recovery across the K-Pg boundary was viewed as analogous to pioneer succession following an ecological disaster (Tschudy et al. 1984), the protracted – millennial – timescale for fern dominance is enigmatic and may not be attributable to typical, seral succession (Wolfe & Upchurch 1987, Spicer & Collinson 2014).

DISCUSSION

Although the dispersed-spore species *Cyathidites diaphana* is often stated to be a cyathea-ceous fern, there is no evidence to support this interpretation (Nichols 1995). Within the Raton Basin of northeastern New Mexico, *Anemia*-like schizaeaceous foliage collected from the K-Pg boundary section at Sugarite is associated with dispersed *C. diaphana* spores (Fig. 1B; Berry 2019, Berry et al. in press). *Anemia*-like schizaeaceous foliage is known to have been capable of producing psilate, *Lygodium*-like trilete spores presently classified in the dispersed-spore genus *Cyathidites* (Chandler 1955, 1963, Balme 1995, Collinson 2001, Trivett et al. 2006, Berry 2019, Berry et al. in press), and numerous authors have suggested that spores presently classified as *C. diaphana* were produced by *Anemia*-like schizaeaceous foliage in particular (Warter 1965) or schizaeaceous foliage in general (Bolkhovitina 1961, Hedlund 1966, Kroeger 1995). Moreover, Chandler (1963) suggested that the species of fern foliage collected from the K-Pg boundary at Sugarite, “*Anemia*” *elongata* (Newberry) Knowlton, probably produced spores presently classified as *Cyathidites* (Fig. 1B; Balme 1995, Berry 2019, Berry et al. in press). Only two fern megafossils that have been collected from the Raton Formation are known (1) to have been capable of producing the dominant spores at the K-Pg boundary fern spore spike and (2) to have survived the K-Pg impact (Berry 2019, Berry et al. in press); therefore, there is strong support for the hypothesis that *Anemia*-like schizaeaceous foliage collected from the K-Pg boundary section at Sugarite produced the *Cyathidites* spores observed in this section (Berry 2019), particularly since thelypteridaceous fern thickets can be linked to *Laevigatosporites*-dominated palynofloral assemblages farther up the section (Berry et al. in press). For all of these reasons, it is necessary to reconsider the hypothesis that the dominant spores in the K-Pg boundary fern spore spike were short-lived because of their alleged affinity to cyathea-ceous ferns.

Fern species show considerable variation in spore viability. Spores of most species remain viable for only a few months, although spores of a few, rare species remain viable for more than a decade (Nayar & Kaur 1971, Spicer & Collinson 2014). The exceptional viability of these spores is on par with that of seeds of many

dicot angiosperms (Spicer & Collinson 2014). When stored at the same temperature (4°C) as relatively long-lived spores of a cyatheaaceous species, which completely lost viability by the third year of storage (Simabukuro et al. 1998a), *Anemia* Swartz spores remained viable for more than 30 years (Fig. 1A; Nester-Hudson 2011). Under natural conditions, *Anemia* spores characteristically exhibit “extreme viability” of 20 years or more (Fig. 1A; Schraudolf 1986: 271). Although apparently not as extreme as *Anemia*, *Lygodium* Swartz spores (Fig. 1A) are also known to remain viable for a number of years (Laage 1907, Sussman 1965, Ferriter 2001, Hutchinson et al. 2006, Sebesta et al. 2016), as they have been documented to remain viable for at least eight years in the soil bank (Hutchinson & Langeland 2006, Rowe & Lockhart 2011). Likewise, spores of *Mohria* Swartz (Fig. 1A) are known to remain viable for at least eight years (Atkinson 1960; also see Laage 1907, Sussman 1965).

It has long been noted that cyatheaaceous spores require light for germination, whereas schizaeaceous spores (e.g. *Anemia*, *Lygodium*, and *Mohria*) characteristically exhibit dark germination of spores (Life 1907, Nester & Coolbaugh 1986, Schraudolf 1986, Lott et al. 2003, Ospina et al. 2015). *Cyathea* spores germinate poorly under red light, with the highest frequency of germination occurring under white light or shorter-wavelength light (Simabukuro et al. 1998a, b, Ospina et al. 2015, Suo et al. 2015). This implies that *Cyathea* spores germinate on or near the surface (Simabukuro et al. 1998a, b, Suo et al. 2015); that is consistent with the observation that these spores lose viability rapidly (Mehra & Gupta 1986, Ford & Fay 1999). In contrast, dark germination of schizaeaceous spores is well understood to be a product of antheridiogen effects, which facilitate the relatively rapid mass germination of long-dormant spores in soil banks pending the initial exposure of some spores, which then mature, to red light (Nester 1985, Nester & Coolbaugh 1986, Schraudolf 1986, Chiou & Farrar 1997, Lott et al. 2003, Suo et al. 2015). Nester (1985: 4) observed, “Red light is an absolute requirement for spore germination in the schizaeaceous ferns.” As red light penetrates farther into the soil than other wavelengths of visible light, red light can reach regenerative plant tissues, such as spores, buried centimeters beneath the surface (Mo et al.

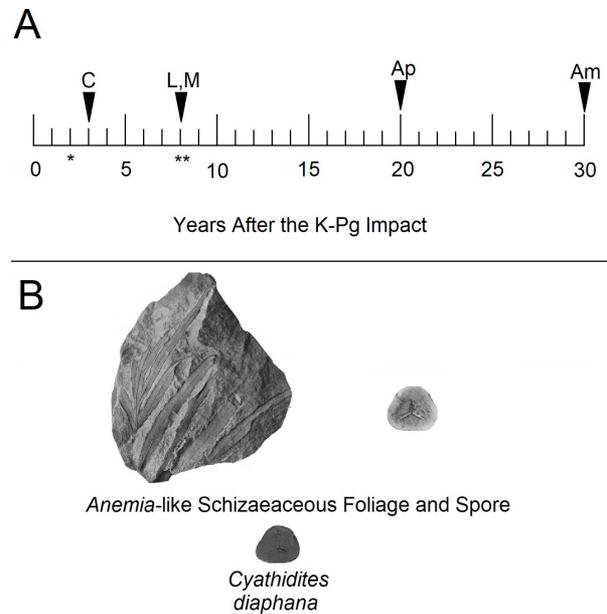


Fig. 1. A. Timescale for events following the K-Pg boundary Chicxulub impact, relative to proven longevities of fern spores. Single asterisk (*) denotes the end of the non-photosynthetic phase of terrestrial recovery (saprophyte dominance) or the end of global darkness (Ocampo et al. 2007, Bardeen et al. 2017). Double asterisk (**) denotes the end of the nearly decade-long K-Pg impact winter according to Pope et al. (1994) and Bardeen et al. (2017), based on the settling times of sulfuric acid aerosols and soot aerosols, respectively. C denotes the complete loss of viability of *Cyathea delgadii* Sternberg spores under cold (4°C) storage (Simabukuro et al. 1998a). Such multi-year viability for *Cyathea* spores is unusual, as most spores lose viability within weeks or months (Mehra & Gupta 1986, Ford & Fay 1999). L and M denote the long-term viability of *Lygodium microphyllum* Brown and *Mohria caffrorum* Linnaeus spores (Atkinson 1960, Rowe & Lockhart 2011). Ap denotes the long-term viability of *Anemia phyllitidis* (Linnaeus) Swartz spores in the soil bank (Schraudolf 1986). Am denotes the long-term viability of *Anemia mexicana* Klotzsch spores under cold (4°C) storage (Nester-Hudson 2011). **B.** Illustration of *Anemia*-like schizaeaceous foliage collected from the K-Pg boundary section near Sugarite, New Mexico, adapted from Lee and Knowlton (1917). Drawing of *Anemia* spore based on photograph of *A. poolensis* Chandler spores by Rouse (1962: pl. 3, figs 25, 26). The fern collected from the K-Pg boundary section near Sugarite is supposed to have produced spores similar to these (Chandler 1963). Indeed, these spores closely match *Cyathidites diaphana* (Wilson & Webster) Nichols & Brown spores (Rouse 1962, Warter 1965, Berry 2019), which are associated with *Anemia*-like schizaeaceous foliage in the K-Pg boundary section near Sugarite. Drawing of *C. diaphana* spore adapted from a photograph by Vajda et al. (2013: fig. 4.5)

2015). All of these factors suggest that schizaeaceous ferns are generally adapted to recover from the soil spore bank following long periods unfavorable to growth, such as droughts (e.g. Schraudolf 1986). Once established, schizaeaceous ferns often form thickets demonstrating allelopathic and other inhibitory effects, which suppress the colonization of dicot angiosperms and which enhance their invasive potential (Lott et al. 2003, Walker & Sharpe 2010).

Within the extensively studied Meeteetse flora at Big Cedar Ridge (BCR) in Wyoming, Wing et al. (2012) observed *Anemia*-like schizaeaceous fern thickets dominating peat-forming depositional settings in a subtropical coastal habitat. Based on these observations, Wing et al. (2012: 40) concluded that these fern thickets were presumably “neither strongly nutrient limited nor early successional” and that “the evidence from BCR suggests that as late as the latest Campanian, schizaeaceous ... ferns were still able to dominate the vegetation of a habitat they no longer command today: warm coastal wetlands without strong nutrient limitation or frequent disturbance.” Wing et al.’s (2012) latest Campanian age assessment (72.7 ± 1.43 Ma) was based on radiometric dating of the BCR tuff, which preserved the Meeteetse flora; however, they also noted that the Meeteetse Formation at BCR is underlain by the *Baculites grandis* ammonite zone and lies above the base of magnetochron C31r. Therefore, the Meeteetse flora at BCR cannot be older than Maastrichtian in age (Ogg 2012). In fact, the Meeteetse flora must be essentially equivalent in age to the Vermejo Formation, which conformably underlies the K-Pg boundary-bearing unit in northeastern New Mexico (Berry 2019, Berry et al. in press). Consequently, very near the end of the Cretaceous, *Anemia*-like schizaeaceous ferns dominated depositional settings like those observed at the K-Pg boundary section at Sugarite. This suggests that *Anemia*-like schizaeaceous foliage likely produced a persistent soil spore bank in this habitat.

Climate models based on sulfuric acid or soot aerosols predict a K-Pg impact winter lasting about eight years (Pope et al. 1994, Galeotti et al. 2004, Bardeen et al. 2017). Sweet (2001) argued that the short-term viability of fern spores ensured that the K-Pg boundary fern spore spike could not have taken place after such an impact winter. However, this interpretation is based on the premise that the dominant fern spores in the fern spore spike were produced by cyatheaceous ferns, which have short-lived spores (Spicer & Collinson 2014). Based on the results of this study, it is clear that the spores of schizaeaceous ferns (*Anemia*, *Lygodium*, *Mohria*) remain viable for at least eight years (about a decade or more) and could therefore have recovered from the soil bank following a nearly decade-long impact

winter akin to that predicted by Pope et al. (1994) or Bardeen et al. (2017). This interpretation is further bolstered by the red-light requirement for spore germination observed in schizaeaceous ferns (Nester 1985), as red light penetrates centimeters into the soil (Mo et al. 2015) and thus can reactivate viable spores buried for several years (e.g. Leck & Simpson 1987, Lindsay & Dyer 1990, de Groot & During 2013).

Additional support for the hypothesis that the K-Pg boundary fern spore spike occurred after a nearly decade-long impact winter might be drawn from studies of the long-term viability of taxa that could have produced the other dominant spores at the fern spore spike. Collinson (2002) attributed the dominant species of *Laevigatosporites* spore at the K-Pg boundary fern spore spike to thelypteridaceous foliage, and these spores were subsequently collected from the intact sporangia of a thelypteridaceous fern (Stockey et al. 2006). Stockey et al. (2006) described these spores as *L. ovatus* s.l. Wilson & Webster – a taxon widely regarded as a junior synonym for *L. haardtii* (Nichols 2002), the dispersed spore Collinson (2002) attributed to thelypteridaceous foliage. Today, *Thelypteris palustris* Schott spores are known to remain viable in the soil bank for at least a decade and to form a persistent spore bank (Leck & Simpson 1987, Lindsay & Dyer 1990, Bremer 2007, de Groot & During 2013), although there is at least one report of *T. palustris* spores losing viability rapidly under storage conditions (e.g. Ballesteros et al. 2012). Based on these preliminary results, it is plausible that there was potential for long-term spore viability in *Laevigatosporites*, provided that these spores are in fact attributable to a species of thelypteridaceous fern as suggested by Collinson (2002), Berry (2019) and Berry et al. (2019). As the aforementioned viability studies are limited to a single species of thelypteridaceous fern, however, it is unclear whether these results are as generally applicable as those observed among the schizaeaceous ferns.

CONCLUSION

Since the K-Pg boundary fern spore spike was first described in detail by Tschudy et al. (1984), fern dominance in the earliest Danian has been attributed to the fact that ferns are

“pioneer recolonizers of devastated landscapes, and their proliferation represents a classic example of a ‘disaster flora’ composed of taxa capable of rapidly generating from spores” (Field et al. 2018: 3–4). At the K-Pg boundary section at Sugarite, New Mexico, however, the dominant fern spores at the fern spore spike were likely produced by taxa that could have regenerated from spores nearly a decade after the impact and which already commanded similar depositional settings in western North America during the Maastrichtian, presumably by suppressing the colonization of angiosperms. For these two reasons, the protracted, millennial timescale for fern dominance in the earliest Danian may be accounted for by the unique ecology of *Anemia*-like schizaeaceous ferns, which likely recovered from a persistent spore bank in a habitat that they already commanded in the Maastrichtian.

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REFERENCES

- ATKINSON L.R. 1960. The Schizaeaceae: the gametophyte of *Mohria*. *Phytomorphology*, 10(1): 351–367.
- BALME B.E. 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Paleobot. Palynol.*, 87(2–4): 81–323.
- BALLESTEROS D., ESTRELLES E., WALTERS C. & IBARS A.M. 2012. Effects of temperature and desiccation on ex situ conservation of nongreen fern spores. *Am. J. Bot.*, 99(4): 721–729.
- BARDEEN C.G., GARCIA R.R., TOON O.B. & CONLEY A.J. 2017. On transient climate change at the Cretaceous-Paleogene boundary due to atmospheric soot injections. *Proc. Natl Acad. Sci., USA*, 114(36): 7415–7424.
- BERRY K. 2019. Linking fern foliage with spores at the K-Pg boundary section in the Sugarite coal zone, New Mexico, USA, while questioning the orthodoxy of the global pattern of plant succession across the K-Pg boundary. *Neues Jahrb. Geol. Paläontol.*, 291(2): 159–169.
- BERRY K., LUCAS S.G. & SEALEY P.L., in press, Revising palynostratigraphic concepts in the Raton Basin a half-century after R.H. Tschudy’s pioneering work. In: Ramos F.C., Zeigler K., & Zimmerer M. (eds), *Fall Guidebook of the New Mexico Geological Society*. New Mexico Geological Society, Socorro.
- BLONDER B., ROYER D.L., JOHNSON K.R., MILLER I. & ENQUIST B.J. 2014. Plant ecological shift across the Cretaceous-Paleogene boundary. *PLoS ONE*, 12(9): 1–7.
- BOLKHOVITINA N.A. 1961. Iskopaemye I sovremennye spory aemeystva shizeynykh (Fossil and recent spores in the Schizaeaceae). *Trudy Geologicheskogo Instituta, Akademiya Nauk S.S.S.R.*, 40(1): 1–176.
- BREMER P. 2007. The colonization of a former seafloor by ferns. Ph.D. Thesis, Wageningen University, Wageningen.
- CHANDLER M.E.J. 1955. The Schizaeaceae of the South of England in Early Tertiary times. *Bull. Br. Mus. Nat. Hist.*, 2: 291–314.
- CHANDLER M.E.J. 1963. The lower Tertiary floras of southern England III: the flora of the Bournemouth beds; the Boscombe, and the Highcliff Sands. *British Museum of Natural History, London*.
- CHIOU W-L & FARRAR D.R. 1997. Antheridiogen production and response in Polypodiaceae species. *Am. J. Bot.*, 84(5): 633–640.
- CLYDE W.C., RAMEZANI J., JOHNSON K.R., BOWRING S.A. & JONES M.M. 2016. Direct high-precision U-Pb geochronology of the end-Cretaceous extinction and calibration of Paleocene astronomical timescales. *Earth Planet. Sci. Lett.*, 452(C): 272–280.
- COLLINSON M.E. 2001. Cainozoic ferns and their distribution. *Brittonia*, 53(2): 173–235.
- COLLINSON M.E. 2002. The ecology of Cainozoic ferns. *Rev. Palaeobot. Palynol.*, 119(1–2): 51–68.
- DE GROOT G.A. & DURING H. 2013. Fern spore longevity in saline water: can sea bottom sediments maintain a viable spore bank? *PLoS ONE*, 8(11): 1–11.
- FERRITER A. 2001. *Lygodium* management plan for Florida: a report from the Florida Exotic Plant Council’s *Lygodium* Task Force: First Edition. Florida Exotic Pest Plant Council, Florida, USA.
- FIELD D.J., BERCOVICI A., BERV J.S., DUNN R., FASTOVSKY D.E., LYSON T.R., VAJDA V. & GAUTHIER J.A. 2018. Early evolution of modern birds structured by global forest collapse at the End-Cretaceous mass extinction. *Curr. Biol.*, 28(11): 1825–1831.
- FORD M.V. & FAY M.F. 1999. Spore-derived axenic cultures of ferns as a method of propagation. *Methods Mol. Biol.*, 111: 159–168.
- GALEOTTI S., BRINKHUIS H. & HUBER H. 2004. Records of post-Cretaceous-Tertiary boundary millennial-scale cooling from the western Tethys: a smoking gun for the impact winter hypothesis? *Geology*, 32(6): 529–532.
- GOLLER K. & RYBCZYŃSKI J.J. 2007. Gametophyte and sporophyte of tree ferns in vitro culture. *Acta Soc. Bot. Poloniae*, 76(3): 193–199.

- HEDLUND R.W. 1966. Palynology of the Red Branch Member of the Woodbine Formation (Cenomanian), Bryan County, Oklahoma. *Bull. Oklahoma Geol. Soc.*, 112: 1–69.
- HUTCHINSON J.T. & LANGELAND K.A. 2006. Survey of control measures on old world climbing fern (*Lygodium microphyllum*) in Southern Florida. *Florida Scientist*, 69(4): 217–233.
- HUTCHINSON J.T., FERRITER A., SERBESOFF-KING K., LANGELAND K.A. & RODGERS L. 2006. Old world climbing fern (*Lygodium microphyllum*) management plan for Florida: Second Edition. Florida Exotic Pest Plant Council, Florida, USA.
- KROEGER T.J. 1995. The paleoecologic significance of palynomorph assemblages from the Ludlow, Slope, and Cannonball formations, southwestern North Dakota. Ph.D. Thesis, University of North Dakota.
- LAAGE A. 1907. Bedingungen der Keimung von Farn- und Moossporen. *Beih. Bot. Zentralbl.*, 21(1): 76–115.
- LECK M.A. & SIMPSON R.L. 1987. Spore bank of a Delaware River freshwater tidal wetland. *Bull. Torrey Bot. Club*, 114(1): 1–7.
- LEE W.T. & KNOWLTON F.H. 1917. Geology and paleontology of the Raton Mesa and other regions, Colorado and New Mexico. USGS Professional Paper 101: 1–435.
- LIFE A.C. 1907. Effect of light upon the germination of spores and the gametophyte of ferns. *Missouri Botanical Garden Annual Report*, 1907(18): 109–122.
- LINDSAY S. & DYER A.F. 1990. Fern spore banks: implications for gametophyte establishment: 243–253. In: Rita J. (Ed.), *Taxonomia, biogeografía y conservación de pteridofitos* [Taxonomy, biogeography and conservation of pteridophytes]. Societat d'Historia Natural de les Illes Balears-IME, Palma de Mallorca.
- LOTT M.S., VOLIN J.C., PEMBERTON R.W. & AUSTIN D.F. 2003. The reproductive biology of the invasive ferns *Lygodium microphyllum* and *L. japonicum* (Schizaeaceae): implications for invasive potential. *Am. J. Bot.*, 90(8): 1144–1152.
- LLOYD R.M. & KLEKOWSKI E.J., JR. 1970. Pteridophyta: Evolutionary significance of chlorophyllous spores. *Biotropica*, 2(2): 129–137.
- MARCON C., SILVEIRA T. & DROSTE A. 2014. Germination and gametophyte development of *Cyathea corcovadensis* (Raddi) Domin (Cyatheaceae) from spores stored at low temperatures. *Maringá*, 36(4): 403–410.
- MEHRA P.N. & GUPTA A. 1986. Gametophytes of Himalayan Ferns. P. KAPUR, C-61, Mayapuri Industrial Area Phase II. New Delhi: 1–204.
- MO M., YOKAWA K., WAN Y. & BALUŠKA F. 2015. How and why do root apices sense light under the soil surface? *Front. Plant Sci.*, 6(755): 1–8.
- NAYAR B.K. & KAUR S. 1971. Gametophytes of homosporous ferns. *The Botanical Review*, 37(3): 295–396.
- NESTER J.E. 1985. Comprehensive investigation of spore germination and antheridiogen chemistry in *Anemia mexicana* Klotzsch. Ph.D. Thesis, Iowa State University, Ames.
- NESTER J.E. & COOLBAUGH R.C. 1986. Factors influencing spore germination and early gametophyte development in *Anemia mexicana* and *Anemia phyllitidis*. *Plant Physiology*, 82(1): 230–235.
- NESTER-HUDSON J. 2011. Spore age as a factor influencing spore viability and gamete development in the fern, *Anemia mexicana*. *Botany 2011: Healing the Planet, The Annual Meeting of Four Leading Scientific Societies*, St. Louis, MO: 146.
- NICHOLS D.J. 1995. Palynostratigraphy in relation to sequence stratigraphy, Straight Cliffs Formation (Upper Cretaceous), Kaiparowits Plateau, Utah. *USGS Bulletin*, 2215-B: 1–21.
- NICHOLS D.J. 2002. Palynology and palynostratigraphy of the Hell Creek Formation in North Dakota: a microfossil record of plants at the end of the Cretaceous: *GSA Special Paper*, 361: 393–456.
- NICHOLS D.J. & JOHNSON K.R. 2008. Plants and the K-T Boundary. Cambridge University Press, Cambridge. *USGS Bulletin*, 2115-B, 21 p.
- OCAMPO A.C., VAJDA V. & BUFFETAUT E. 2007. Unravelling the Cretaceous-Paleogene (KT) turnover, evidence from flora, fauna and geology: 197–219. In: Cockell C., Gillmour I., Koeberl C. (Eds), *Biological Processes Associated with Impact Events*. Springer, Berlin.
- OGG J.G. 2012. Geomagnetic polarity time scale: 85–114. In: Gradstein F., Ogg M., Schmitz M. & Ogg G. (Eds) *The geologic time scale 2012*. Elsevier, Amsterdam.
- OSPINA K.R., BRIONES R. & PÉREZ-GARCÍA B. 2015. Spore germination of three tree fern species in response to light, water potential, and canopy openness. *Am. Fern J.*, 105(2): 59–72.
- PAGE C.N. 1979. Experimental aspects of fern biology: 552–585. In: Dyer A.F. (Ed.) *The Experimental Biology of Ferns*. Academic Press, London.
- POPE K.O., BAINES K.H., OCAMPO A.C. & IVANOV B.A. 1994. Impact winter and the Cretaceous/Tertiary extinctions: results of a Chicxulub asteroid impact model. *Earth and Planetary Science Letters*, 128(3–4): 719–725.
- ROUSE G.E. 1962. Plant microfossils from the Burrard Formation of western British Columbia. *Micropaleontology*, 8(2): 187–218.
- ROWE R. & LOCKHART C. 2011. The invasion of the non-native climbing ferns. *Palmetto*, 28(3): 4–7.
- SCHRAUDOLF H. 1986. Phytohormones and Filicinae: chemical signals triggering morphogenesis in Schizaeaceae: 270–274. In: Bopp M. (Ed.) *Plant Growth Substances 1985*. Springer-Verlag, Berlin.
- SEBESTA N., RICHARDS J. & TAYLOR J. 2016. The effects of heat on spore viability of *Lygodium microphyllum* and implications for fire management. *Southeastern Naturalist*, 15(sp8): 40–50.

- SIMABUKURO E.A., DYER A.F. & FELIPPE G.M. 1998a. The effect of sterilization and storage conditions on the viability of the spores of *Cyathea delgadii*. *Am. Fern J.*, 88(2): 72–80.
- SIMABUKURO E.A., DE CARVALHO M.A.M. & FELIPPE G.M. 1998b. Reserve substances and storage of *Cyathea delgadii* Sternb. Spores. *Brazilian Journal of Botany*, 21(2): 149–152.
- SIMABUKURO E.A., ESTEVES L.M. & FELIPPE G.M. 2000. Fern spore rain collected at two different heights at Moji Guaçu (São Paulo, Brazil). *Fern Gazette*, 16(3): 147–166.
- STOCKEY R.A., LANTZ T.C. & ROTHWELL G.W. 2006. *Speirseopteris orbiculata* gen. et. sp. nov. (Thelypteridaceae), a derived fossil Filicalean from the Paleocene of western North America. *Int. J. Plant Sci.*, 167(3): 729–736.
- SUO J., CHEN S., ZHAO Q., SHI L. & DAI S. 2015. Fern spore germination in response to environmental factors. *Frontiers in Biology*, 10(4): 358–376.
- SUSSMAN A.S. 1965. Longevity and resistance of the propagules of bryophytes and pteridophytes. *Encyclopedia of Plant Physiology*, 532(15): 1086–1092.
- SPICER R.A. & COLLINSON M.E. 2014. Plants and floral change at the Cretaceous-Paleogene boundary: three decades on. *GSA Special Paper*, 505: 117–132.
- SWEET A.R. 2001. Plants, a yardstick for measuring the environmental consequences of the Cretaceous-Tertiary boundary event. *Geoscience Canada*, 28(3): 127–138.
- TRIVETT M.L., STOCKEY R.A., ROTHWELL G.W. & BEARD G. 2006. *Paralygodium vancouverensis* sp. nov. (Schizaeaceae): additional evidence for filicalean diversity in the Paleogene of North America. *Int. J. Plant Sci.*, 167(3): 675–681.
- TSCHUDY R.H., PILLMORE C.L., ORTH C.J., GILLMORE J.S. & KNIGHT J.D. 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous-Tertiary boundary, Western Interior. *Science*, 225(4666): 1030–1032.
- VAJDA V. & BERCOVICI A. 2014. The global vegetation pattern across the Cretaceous-Paleogene mass extinction interval: a template for other mass extinction events. *Global and Planetary Change*, 122(2014): 29–49.
- VAJDA V. & MCLOUGHLIN S. 2004. Fungal proliferation at the Cretaceous-Tertiary boundary. *Science*, 303(5663): 1489.
- VAJDA V. & MCLOUGHLIN S. 2007. Extinction and recovery patterns of the vegetation across the Cretaceous-Paleogene boundary – a tool for unraveling the causes of the end-Permian mass-extinction. *Rev. Palaeobot. Palynol.*, 144(1,2): 99–112.
- VAJDA V., RAINE J.I. & HOLLIS C.J. 2001. Indication of global deforestation at the Cretaceous-Tertiary boundary by New Zealand fern spike: *Science*, 294(5547): 1700–1702.
- VAJDA V., LYSON T.R., BERCOVICI A., DOMAN J.H. & PEARSON D.A. 2013. A snapshot into the terrestrial ecosystem of an exceptionally well-preserved dinosaur (Hadrosauridae) from the Upper Cretaceous of North Dakota, USA. *Cretac. Res.*, 46(1): 114–122.
- VELLEKOOP J., ESMERAY-SENLET S., MILLER K.G., BROWNING J.V., SLUIJS A., VAN DE SCHOOTBRUGGE B., SINNINGHE DAMSTÉ J.S. & BRINKHUIS H. 2016. Evidence for Cretaceous-Paleogene boundary bolide “impact winter” conditions from New Jersey, USA. *Geology*, 44(8): 619–622.
- VELLEKOOP J., SLUIJS A., SMIT J., SCHOUTEN S., WEIJERS J.W.H., DAMSTÉ J.S.S. & BRINKHUIS H. 2014. Rapid short-term cooling following the Chicxulub impact at the Cretaceous-Paleogene boundary. *Proc. Natl Acad. Sci., USA*, 111(21): 7537–7541.
- WALKER L.R. & SHARPE J.M. 2010. Ferns, disturbance and succession: 177–219. In: Mehlreter K., Walker L.R., Sharpe J.M. (Eds) *Fern Ecology*. Cambridge University Press, Cambridge: 177–219.
- WARTER J.L.K. 1965. Palynology of a lignite of lower Eocene (Wilcox) age from Kemper County, Mississippi. Ph.D. Thesis. Baton Rouge, Louisiana State University Agricultural and Mechanical College.
- WING S.L., STROMBERG C.A.E., HICKEY L.J., TIVER F., WILLIS B., BURNHAM R.J. & BEHRENSMEYER A.K. 2012. Floral and environmental gradients on a Late Cretaceous landscape. *Ecol. Monographs*, 82(1): 23–47.
- WOLFE J.A. & UPCHURCH G.R. 1987. Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proc. Natl Acad. Sci., USA*, 84(15): 5096–5100.