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The spore conundrum: Does a dung fungus decline signal humans' arrival in the Eastern United States?

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ABSTRACT

Sporormiella is a fungus that grows on animal dung as part of its life cycle. A decline of *Sporormiella* reproductive spores in stratified Late Glacial pond sediments in Ohio, northern Indiana, and New York has been interpreted as a signal of regional extinction of megafauna due to human predation between 14,800 and 13,900 cal BP. However, this interpretation is undermined by two salient evidential problems. First, numerous skeletons of mastodonts and mammoths in these areas date between 12,500 and 10,700 rcybp (14,500–12,700 cal BP). Megaherbivores were thriving and expanding their range into recently deglaciated areas when the fungal spore evidence implies that they were instead functionally extinct. Second, the archaeological record of human activity in these areas prior to 13,000 cal BP is sparse to non-existent. The fungal spores have not been unambiguously attributed to megafauna (as opposed to small mammals or birds), and the subsequent changes in regional vegetation at 13,900 cal BP may have been caused by changes in precipitation and carbon dioxide levels, rather than relaxed herbivory.

1. Introduction: the Paleoecological implications of *Sporormiella* spores

Sporormiella is a fungus that grows on animal dung as part of its life cycle. It not only thrives on the feces of mammals of varying size but also has been recovered from the dung of the extinct giant birds of New Zealand (Wood et al., 2011). In the 1980s Owen Davis realized that the fluctuations through time of the reproductive spores of *Sporormiella* could be interpreted as a proxy index of changes in the relative numbers of megafauna. In cores taken from lake sediments in Colorado, California, and Idaho, the spores rose to a peak frequency just before 11,000 rcybp (13,000 cal BP) only to decrease abruptly ca. 10,800 rcybp (12,800 cal BP) (Davis, 1987; Davis and Shafer, 2006). The spores only reached pre-crash levels again when cattle-ranching began in this region in the 19th century. Davis observed that the fungus decline coincided precisely with the abrupt demise in the Southwest of such megafauna as giant sloth and mammoth.

More recently, an abrupt Late Glacial decline of *Sporormiella* also has been observed in samples of stratified pond sediments located east of the Mississippi, in Ohio and northern Indiana (Gill et al., 2009, 2012) and in New York (Robinson at al. 2005; Robinson and Burney, 2008). These researchers also tracked the frequencies of pollen and charcoal particles in the same samples; the data allow them to construct a compelling scenario of megafaunal extinction. Something, possibly human predation, initiated a reduction of the populations of megaherbivores ca. 14,800 cal BP, and 1000 years later they were much diminished, perhaps near extinction (Fig. 1). Released from browsing pressure, plants that had been kept in check by the big herbivores multiplied and rapidly changed the composition of the woodlands. Vegetation that previously had cycled through the giant mammals' guts now accumulated on the landscape, providing fuel for either natural or human-ignited fires, which suddenly became more frequent as evidenced by the uptick in charcoal particles.

2. Contradictory evidence of later megafaunal extinction

However, there are two glaring problems with this scenario. First, numerous skeletons of mastodonts and mammoths, both from the southern Great Lakes and southeastern New York (mainly in Orange County), date between 12,500 and 10,700 rcybp (14,500–12,700 cal BP) (Table 1, Fig. 2). One might infer from this relative abundance that unusually large numbers of animals were dying after 14,500 cal BP (Boulanger and Lyman, 2014), or that the peculiar microenvironments (such as kettle ponds) conducive to fossil preservation became more widespread in that period. The

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increased survival of skeletons might also be partially attributable to either changing seasons of mortality or a reduction in the population of scavengers. However, the most parsimonious inference is that the proboscidean population was actually expanding. All of those live animals inevitably ended up as dead animals and so a larger population of carcasses was available for the fortuitous preservation of a small fraction of them.

Burneys—Otisville and Hyde Park. Bones of a stag-moose (*Cervalces scotti*) were recovered from another sampled site, Pawelski Farm. The Otisville mastodont was dated directly to 10,970 ± 40 rcybp. The Hyde Park mastodont was dated, also on collagen from a tusk, to 11,480 ± 50 rcybp. A pine cone found nearby was dated to 11,230 ± 50 rcybp. The Pawelski Farm stag-moose was dated to 12,180 ± 50 rcybp. It was stratified above the level where the *Sporomiella* decline was observed. An additional complication at this site is the incongruous dating of sediment samples overlying the bones to 13,083 ± 86 and 11,212 ± 79 rcybp. At Hyde Park, the top and bottom of the 180 cm-thick deposit yielded nearly identical dates: 12,484 ± 64 rcybp at the top (on sediment), and 12,460 ± 50

Table 1
Selected radiocarbon dates (rcybp) for proboscideans in the upper Midwest.

	Date	Lab#	Sample
Mastodonts			
Ohio			
Burning tree	10,860 ± 70	(PITT-830)	bone collagen
	11,390 ± 80	(NSRL-283)	bone collagen
	11,470 ± 90	(PITT-841)	wood
	11,720 ± 110	(Beta-35045)	*Picea* wood
	11,450 ± 70	(PITT-832)	plant remains
Cole	10,950 ± 40	(Beta-165219)	bone collagen
	10,880 ± 50	(Beta-165220)	bone collagen
Wisconsin			
Deerfield	10,780 ± 60	(CAMS 24944)	bone collagen
	10,910 ± 60	(CAMS 24428)	bone collagen
	11,140 ± 60	(CAMS 24945)	bone collagen
Fenske	11,230 ± 50	(CAMS 72137)	filtered bone collagen (femur)
	11,220 ± 40	(CAMS 72253)	filtered bone collagen (femur)
Michigan			
Grandville	10,920 ± 190	(Beta-15265)	bone collagen (tusk)
	11,320 ± 140	(Beta-15266)	bone collagen (cranium)
St John's	11,970 ± 80	(Beta-78626)	[material not specified]
Shelton	10,970 ± 130	(Beta-10303)	*Picea* wood
	10,020 ± 80	(Beta-13312)	*Picea* wood
	11,770 ± 110	(Beta-14266)	*Picea* wood
	11,960 ± 110	(Beta-9083)	*Picea* wood
	12,320 ± 110	(Beat-9084)	*Picea* wood
Thaller	9990 ± 350	(M-1739)	bone (tusk)
	11,200 ± 400	(M-1743)	overlying gyttja
Pleasant Lake	10,395 ± 100	(Beta-1388)	wood in tusk pulp cavity
	12,845 ± 165	(Beta-1389)	wood under mandible
Heisler	11,770 ± 110	(AA-6979)	bone collagen
Powers	11,220 ± 310	(Beta-9482)	bone collagen (rib)
Illinois			
Perry	11,700 ± 60	(Beta-270214)	bone collagen
Lima Lake (Andrew Farm)	10,775 ± 35	(A1120)	enamel bioapatite
Aurora	(Mastodont 1)		
	11,130 ± 30	(UCIAMS 19329)	dentin
	10,980 ± 60	(CAMS 110994)	dentin
	10,190 ± 25	(UCIAMS 19321)	enamel
	10,430 ± 40	(CAMS 110992)	enamel
	(Mastodont 2)		
	11,320 ± 50	(A 0549)	dentin
Brewster Creek	11,455 ± 35	(UCI 22177)	dentin
Hawthorne	12,248 ± 40	(NZA 26128)	dentin
Indiana			
Kolarik	11,760 ± 280	[lab not reported]	
Fort Wayne	11,280 ± ?	[lab not reported]	
Overmyer	10,055 ± 40	(NZA 29627)	filtered collagen
	10,032 ± 40	(NZA 29243)	enamel
	12,575 ± 260	(UGa-2774)	underlying wood
Lewis	11,160 ± 90	(ISGS-2220)	rib, total organic content
Wells	12,000 ± 450	(I-586)	wood
Mammoths			
Illinois			
Lincoln College			
M. primigenius	11,648 ± 36		dentin
	[average of NZA 26218 (11,635 ± 45) and NZA 27739 (11,670 ± 60)]		

The disparity between the fungal and skeletal evidence is more starkly evident in New York than in the upper Midwest. No actual faunal remains were recovered from the pond sediments that were sampled by Gill et al. In contrast, mastodont bones were excavated from two of the four New York sites studied by Robinson and the