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Intestinal Contents of a Late Pleistocene Mastodont from Midcontinental North America

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Salvage excavations of a nearly complete and remarkably well-preserved skeleton of an American mastodont (*Mammut americanum*) in Licking County, Ohio, yielded a discrete, cylindrical mass of plant material found in association with articulated vertebrae and associated ribs. This material is interpreted as intestinal contents of the mastodont and paleobotanical analyses indicate that the mastodont diet included significant amounts of low, herbaceous vegetation. Enteric bacteria (*Enterobacter cloacae*), isolated from a sample of this material, are believed to represent survivors or descendants of the intestinal microflora of the mastodont. This is the first report of the isolation of bacteria associated with late Pleistocene megafauna.

INTRODUCTION

Explanations of late Pleistocene megafaunal extinctions depend, in large measure, on ecological data for the various species involved. Dietary evidence, especially, must be an integral component of any comprehensive understanding of the extinction process. For some taxa, such as mammoths (*Mammuthus* sp.), there is good evidence for diet, including dessicated dung balls (Davis *et al.*, 1984) and gut contents of carcasses preserved in permafrost (Vereshchagin and Baryshnikov, 1984). For mastodonts (*Mammut americanum*), dietary evidence is meager. There are reports of masses of plant material associated with mastodont skeletons in peat (e.g., Warren, 1852; Garland and Cogswell, 1985; Laub, 1990; R. W. Graham, personal communication, 1990); however, there has been little published analysis of such material. This

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paper reports the occurrence of mastodont intestinal contents recovered in primary context and identified on the basis of multiple lines of evidence, some of which are adduced here for the first time.

The Burning Tree mastodont was uncovered in December 1989, during mechanical excavation of a small pond for a golf course in Licking County, Ohio (Fig. 1). The bones of this individual occurred within fibric and hemic peat (Fig. 2) in a small (<0.5 ha) wetland on a gently undulating late-Wisconsinan end moraine (N 39°58′45″ lat., W 82°27′10″ long.). Retention of many articular relationships (Fig. 2) indicates that soft tissue was present when the bones were introduced into the shallow-water sediments; however, displacement of sets of articulated elements relative to one another indicates some postmortem disturbance of the carcass. The skeleton is complete except for both thyrohyoids, most phalanges and sesamoids, the left patella, the right femur, tibia, and fibula, and all but two (ca. tenth and fourteenth, out of about 24) caudal vertebrae posterior to the eighth. The bones of the mastodont are in pristine condition, with no evidence of subaerial weathering and few unambiguous indications of damage by carnivores or scavengers. Tusk dimensions, state of skeletal development, and state of molar eruption and wear (Laws' relative age class XIX; Laws, 1966) suggest that this is an almost fully grown male.

Two 3.6-m sediment cores were taken through the organic and clastic lake deposits to the underlying till. The organic sediments are dominated by autochthonous materials rich in sedimentary pigments. Low iron to manganese ratios, bands of ferrous sulfide, and high carotenoid levels indicate

FIG. 1. Aerial view of the Burning Tree mastodont site, Licking County, Ohio, on December 14, 1989. The mastodont was recovered from the dark area in the center of the photograph, behind and beneath the extended arm of the backhoe.

FIG. 2. Mastodont bones *in situ* showing articulated cervical vertebrae, two humeri, and semiarticulated foot bones. A scale is provided by the boot print which is approximately 30 cm long.

a strongly anaerobic environment throughout the period of basin filling. Littoral and planktonic diatoms are common as well as shallow water copepods and cladocerans. The pollen profile for the entire core sequence is dominated by spruce (*Picea*), fir (*Abies*), and pine (*Pinus*) pollen characteristic of late-glacial and early postglacial forests at the southern margin of the Wisconsinan ice sheets in midcontinental North America (Shane, 1987; Watts, 1983).

ANALYSIS OF INTESTINAL CONTENTS

During the excavation of some of the ribs and associated thoracic vertebrae, excavators noted an elongate mass of organic material (ca. 60 × 12 cm) distinguished from the surrounding dark brown peat by its reddish-brown color and pungent odor. Due to its location and distinctive properties this material was provisionally identified as gut contents. During sampling the material separated cleanly from the surrounding peat leaving a cylindrical impression in the matrix. Samples of this gut material and adjacent peat differ markedly in floral composition. The gut sample has a larger proportion of unidentified, highly fragmented florets (spike or raceme), possibly of a swamp grass, along with a matted mass of leaves, moss (including *Calliergon* sp.) and nonconiferous twigs. These twigs are small (mean length = 20 mm, SD = 6 mm, N = 14) and most lack bark and exhibit sheared ends. The peat sample consists of many amorphous plant materials including twigs of widely varying sizes (conifer as well as deciduous), rootlets, portions of leaves (both small, narrow monocot leaves and fragments of veined dicot leaves), small plant stem parts, small to medium sized (1–3 mm) fragments of wood charcoal (notably absent in the gut sample), and a small number of florets similar to those found in the gut sample.

Seeds are abundant in both samples, but they constitute a much lower proportion of the gut sample. In addition, the percentages of various taxa were quite distinct. The gut sample includes an abundance of small (1 mm diameter) seeds tentatively identified as clover (*Trifolium?*), as well as sedges (*Carex* sp., *C. crawei, C. hystericina,* and *Cladium mariscoides*) and naiads (*Najas flexilis* and *N.* sp.) with lesser amounts of pondweed (*Potamogeton* sp.), waterlily (*Nymphaea tuberosa*), and pigweed (*Amaranthus* sp.). In contrast, the peat sample was dominated by thousands of naiad seeds (*Najas flexilis*) and a greater variety of other species including pondweeds (*Potamogeton natans?, P. diversifolius?,* and *P. spirillus?*), sedges (*Carex comosa?, C. awuatilis?,* and *C.* sp.), waterlily (*Nymphaea tuberosa*), marsh St.-John's wort (*Hypericum virginicum* var. *Fraseri*), spikerush (*Eleocharis* sp.), rush (*Juncus* sp.), burreed (*Sparaganium chorocarpum?*), flatsedge (*Cyperus* sp.), and an unidentified carbonized seed.

All of the plant species represented in the gut sample by seeds flower in midsummer and set seed by late summer to early autumn indicating an early autumn death for the mastodont. Analysis of incremental lamination in tusk dentin, following methods described by Fisher (1988), confirms this inference.

Pollen grains recovered from interstices on the occlusal surfaces of the molar dentition provide independent dietary information. Although pollen and other particulate matter may have been introduced anytime between the eruption of the tooth and the excavation of the skeleton, it seems likely that such materials would have accumulated during the mastication of plant matter. Cementum was removed from the third molars and additional material was scraped from cavities in the dentine of the second molars. Pollen grains were recovered by (1) digestion with 10% HCl, (2) extraction with 70% alcohol, (3) digestion with warm 10% KOH, and (4) subsequent isolation by standard treatment for peat samples.

The yield of pollen was understandably meager; only 68 pollen grains were recovered from 25 g of material. Herbaceous species, particularly sedges, grasses, and aquatic plants, account for 62% of the pollen assemblage. In addition, small numbers of moss and sphagnum spores were recovered. While perhaps not a direct reflection of diet, this pollen spectrum differs significantly from baseline regional pollen spectra, which show an overwhelming predominance of spruce, fir, and pine for this time period, with a nonarboreal component of less than 10% (e.g., C. J. Woltemade, unpublished data).

RADIOCARBON AGE

Radiocarbon analysis of bone collagen from the mastodont yielded an age of 10,860 ± 70 yr B.P. (Pitt-0830; Table 1); however, bone collagen dates typically are younger than dates from other organic materials (Meltzer and Mead, 1983, p. 132; R. Stuckenrath, personal communication, 1990). Dates of 11,660 ± 120 yr B.P. (Beta-38241/ETH-6758) and 11,450 ± 70 yr B.P. (Pitt-0832) were obtained from nonconiferous twigs and other organic matter from the presumed gut contents, and these statistically equivalent dates should provide a more accurate age of the mastodont. Large twigs and branches of spruce recovered in association with the skeleton yield dates which are up to 1000 yr older, indicating that the skeleton sank into older deposits.

BACTERIOLOGICAL ANALYSIS

To evaluate further the properties of the material provisionally identified as gut contents, a bacteriological investigation was undertaken. Samples of peat and gut material were inoculated into sterile tryptone–yeast extract–glucose broth and sterile thioglycollate broth. After incubation overnight, the samples were turbid, indicating bacterial growth. The broth cultures were streaked onto nutrient agar plates and

TABLE 1. RADIOCARBON AGES FOR THE BURNING TREE MASTODONT SITE, LICKING COUNTY, OHIO

Sample No.	Material	Context	Age (yr B.P.)	Laboratory No.
BTM-002	Spruce wood	Associated with skeleton	12,620 ± 90	Beta-35046
BTM-006	Peat, soil	Associated with skeleton	12,230 ± 70	Pitt-0833
BTM-001	Spruce wood	Associated with skeleton	11,720 ± 110	Beta-35045
BTM-003	Twigs	Gut contents	11,660 ± 120	Beta-38241/ ETH-6758
BTM-004	Organics	Gut contents	11,450 ± 70	Pitt-0832
BTM-007	Beaver gnawed wood		11,470 ± 90	Pitt-0841
BTM-005	Bone, collagen fraction		10,860 ± 70	Pitt-0830

blood agar plates and incubated aerobically and anaerobically. The colonies of bacteria incubated anaerobically all proved to be facultative anaerobes. No strict anaerobes were found on any of the bacteriological media inoculated.

Two colony types of gram-negative bacilli were isolated from the gut sample and identified as *Enterobacter cloacae*. *Enterobacter* species occur naturally in soil and water (Stanier *et al.*, 1976), but *E. cloacae* is the most common member of the genus found in the intestinal tracts of animals (Krieg, 1984).

As a control for our observations on the gut sample, a similar series of tests was run on samples of adjacent peat. Two different strains of gram-negative bacteria were isolated from the peat samples: *Serratia fonticola*, which is found in streams and freshwater environments (Krieg, 1984), and *Citrobacter freundii*, which commonly occurs in soil and water, though it also may be found in the intestinal tract of animals (Krieg, 1984). *E. cloacae* was not isolated from the peat samples. The peat thus contains bacterial taxa that might be expected, independent of the occurrence of a large mammal carcass, whereas the presumed gut material includes a form that is absent in the surrounding peat and that is frequently encountered in animal intestinal tracts. We therefore conclude that the culture obtained from the gut sample is most likely derived from survivors or possibly descendants of the intestinal microflora of the mastodont.

DISCUSSION

The biogeochemical circumstances which promoted excellent preservation of the mastodont skeleton and gut material within the intestines also allowed gut bacteria to persist for 11,000 yr. We believe this is the first report of the isolation of enteric bacteria from late Pleistocene megafauna. Molecular biological comparisons between these bacteria and modern members of the same species will have important implications for the study of evolutionary change in these groups.

As was noted above, there have been other claims in the literature for the recovery of gut contents from American mastodonts (reviewed by Dreimanis, 1968). In several of these cases, gut contents have comprised morphologically discrete masses, but the Burning Tree mastodont gut material is thus far unique in offering evidence of (1) a floral composition that contrasts with that of the surrounding matrix but (2) is compatible with pollen removed from the dentition, (3) a season of death determined from inferred food remains that is confirmed by analysis of tusk laminations, and (4) a bacterial flora that corroborates the hypothesis of an enteric source. Therefore, this appears to constitute the most definitive identification of mastodont gastrointestinal contents.

Mastodonts have been characterized as predominantly browsing animals (Martin and Guilday, 1967), and most previous accounts of gut contents have identified coniferous twigs as a dominant element in their diet (Dreimanis, 1968; Garland and Cogswell, 1985; Laub, 1990). In contrast, intestinal contents of the Burning Tree mastodont are notable for their nonconiferous nature and their inclusion of components suggestive of selective feeding on low, herbaceous vegetation, implying a mixture of browsing and grazing habits. Although generalization from this sample may be premature, the central role played by diet in at least some hypotheses for mastodont extinction (Dreimanis, 1967; Graham and Lundelius, 1984; King and Saunders, 1984) gives such results profound importance for evaluating the overall pattern of late Pleistocene megafaunal extinction.

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