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Evidence for the diet and habitat of two late Pleistocene mastodons from the Midwest, USA

Hilary H. Birks[a]*, Bas van Geel[b], Daniel C. Fisher[c], Eric C. Grimm[d], Wim J. Kuijper[e], Jan van Arkel[b], Guido B.A. van Reenen[b]

[a]Department of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Postboks 7803, N-5020 Bergen, Norway
[b]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, the Netherlands
[c]Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, 1105 North University Ave., Ann Arbor, Michigan 48109-1085, USA
[d]Department of Earth Sciences, University of Minnesota, Minneapolis, Minnesota 55455, USA
[e]Naturalis Biodiversity Center, Postbus 9517, 2300 RA Leiden, the Netherlands

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Abstract

We analyzed intestinal contents of two late-glacial mastodons preserved in lake sediments in Ohio (Burning Tree mastodon) and Michigan (Heisler mastodon). A multi-proxy suite of macrofossils and microfossils provided unique insights into what these individuals had eaten just before they died and added significantly to knowledge of mastodon diets. We reconstructed the mastodons' habitats with similar multi-proxy analyses of the embedding lake sediments. Non-pollen palynomorphs, especially spores of coprophilous fungi differentiated intestinal and environmental samples. The Burning Tree mastodon gut sample originates from the small intestine. The Heisler mastodon sample is part of the large intestine to which humans had added clastic material to anchor parts of the carcass under water to cache the meat. Both carcasses had been dismembered, suggesting that the mastodons had been hunted or scavenged, in line with other contemporaneous mastodon finds and the timing of early human incursion into the Midwest. Both mastodons lived in mixed coniferous-deciduous late-glacial forests. They browsed tree leaves and twigs, especially *Picea*. They also ate sedge-swamp plants and drank the lake water. Our multi-proxy estimates for a spring/summer season of death contrast with autumn estimates derived from prior tusk analyses. We document the recovered fossil remains with photographs.

Keywords: Diet; Late glacial; Macrofossils; Mastodons; Midwest, USA; Non-pollen palynomorphs; Pollen

INTRODUCTION

The extinct American mastodon, *Mammut americanum*, is a common member of the late Pleistocene mammalian fauna of North America, and it is especially abundant in the Great Lakes region with hundreds of known occurrences (for a recent overview of sites, see Widga et al., 2017). Many of these specimens derive from the late-glacial Bølling-Allerød chronozone (14.7–12.9 cal ka BP [before 1950]; Rasmussen et al., 2014). The time window for the extinction of mastodons is estimated by Widga et al. (2017) to be 12,790–12,520 cal yr BP, in the early Younger Dryas chronozone. In the upper Midwest, USA, the vegetation at the time of mastodon abundance was mixed coniferous-deciduous woodland, reconstructed from pollen assemblages, with no apparent modern analogs (but see Birks, 2003). It was dominated by *Picea* and *Larix*, associated with various deciduous trees, especially *Fraxinus nigra* (Williams et al., 2001, 2004; Dyke, 2005; Gonzales et al., 2009; Gill et al., 2012). The abundance of *Fraxinus nigra* indicates a wet climate with high winter precipitation (Gonzales et al., 2009). However, elsewhere in North and Central America, mastodons are associated with other kinds of vegetation and habitats (e.g., Halligan et al., 2016).

The American mastodon would have been a keystone herbivore in late Pleistocene terrestrial ecosystems, so any new information on its paleobiology, and especially its diet, may help elucidate its paleoecology and may shed light on the cause of its extinction near the end of the Pleistocene. Some early comments on mastodon diet were based on reports of material identified as "stomach contents" associated with specimens preserved in lacustrine settings (e.g., Dreimanis, 1968), but there was generally little evidence provided for the anatomical source of these samples or

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*Corresponding author at: Department of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Postboks 7803, N-5020 Bergen, Norway. E-mail address: hilary.birks@uib.no (H.H. Birks).

information concerning the season or cause of death. There are also reports on mastodon fecal material (e.g., Laub et al., 1994; Newsom and Mihlbachler, 2006), often in association with skeletal remains. Fecal material, assuming it is correctly attributed, is a legitimate indicator of some aspect of mastodon diet, but the macrofossil assemblage could be biased toward more indigestible components of what was actually ingested, such as twig remnants. Some of the other components of the meal may possibly be detected by aDNA analysis of the purported fecal material. Other important sources of information on mastodon diet have been studies of stable isotope composition of mineralized tissues (generally suggesting a C3-dominated, or "browsing" diet, of leaves, twigs, and bark; Koch et al., 1998), studies of tooth morphology (e.g., Saunders, 1996) and microwear textures (Green et al., 2005, 2017; Smith and DeSantis, 2018), reports of phytoliths recovered from dental calculus (Gobetz and Bozarth, 2001), and plant remains in a "molar socket" (Teale and Miller, 2012). Direct evidence of the composition of ingested material from preserved intestinal contents is extremely rare but has been reported (e.g., Lepper et al., 1991). Here we make multiproxy analyses of intestinal contents from the two mastodon sites investigated by Lepper et al. (1991) and Bearss and Kapp (1987) to provide direct insight into what mastodons actually ingested. Comparative analyses of the lake sediments surrounding the remains indicate the habitats of the mastodons and the availability of food plants. The intestinal contents provide additional clues about the season of death. Thus, we aim to reconstruct the habitats of the two mastodons and their food preferences.

The Burning Tree mastodon, Ohio

The Burning Tree site is a small infilled pond in a depression within the till of the St. Johns lobe of the Wisconsinan (last) glaciation, which probably melted prior to 15,000 yr ago (Shane, 1989). The bones identified as coming from a single almost fully grown male mastodon were discovered in 1989 during mechanical excavation of the <0.5 ha pond on an undulating moraine in Licking County, Ohio (39°58′45″N, 82°27′10″W; 274 meters above sea level [m asl]) (Lepper et al., 1991) (Fig. 1). Organic and clastic deposits overlying the till were 3.6 m thick.

The macrofossil assemblage from the lake sediment associated with the bones contained abundant seeds of aquatic plants (Lepper et al., 1991). Pollen spectra were dominated by *Picea*, *Abies*, and *Pinus*, characteristic of late-glacial forests along the southern margin of the Wisconsinan ice sheet in midcontinental North America (e.g., Dyke, 2005). These trees are characteristic of the boreal and boreal-nemoral biomes in North America today. The Burning Tree site is currently in the temperate forest biome, and the landscape is largely agricultural.

The material interpreted as intestinal contents was encountered as a coherent, cylindrical mass of plant material

Figure 1. (color online) Map showing the locations of the Burning Tree and Heisler mastodon sites in Ohio and Michigan, respectively.

about 60 cm long and 12 cm in diameter and was recovered during excavation of a sequence of ribs and thoracic vertebrae. It was distinguished by a distinct color (reddish brown) and pungent odor different from that of the surrounding lake sediment (Lepper et al., 1991). There was a distinct parting between the cylinder and the adjacent lake sediment, indicating that there had been no effective commingling of these materials. The entire cylinder of reddish-brown material was collected, as well as a comparative sample of the surrounding lake sediment.

In contrast to the lake sediments, the cylinder contained grassy material, mosses, and nonconiferous twigs and far fewer remains of aquatic plants. It was interpreted as part of the intestine containing the remains of the mastodon's recently ingested food. The occurrence of *Carex* spp. and fen-herb seeds in this sample led to the inference that the mastodon died in late summer. This was supported by analyses of laminar features in tusk dentin (Lepper et al., 1991).

Bacteriological analyses showed that the lake sediment contained taxa known to occur in sediment and/or freshwater environments, whereas the cylindrical mass included species common in mammalian intestinal tracts (Lepper et al., 1991). More refined microbiological analysis by Rhodes et al. (1998) was more quantitative and uncovered greater bacterial diversity. Enterobacteriaceae characteristic of intestines were found by culture and confirmed by DNA and ribosomal sequencing. They predominated in the cylindrical mass of plant material but were rare in the surrounding sediment. This provided strong support for the hypothesis of the intestinal origin for the cylindrical sample. More information on the Burning Tree mastodon is provided in the Supplementary Materials.

The Heisler mastodon, Michigan

Bearss and Kapp (1987) describe the discovery of the Heisler mastodon. It was found in 1984 in Clarence Township of Calhoun County, Michigan (42°23′21″N, 84°44′16″W; 287 masl) (Fig. 1), by Lester and James Heisler while laying tile to improve drainage of a small depression approximately 40 m in diameter in a cultivated field. The natural vegetation of the area would be temperate deciduous forest, but the land is currently cultivated. The depression was an internally drained late Pleistocene lacustrine basin within the till of the Saginaw lobe of the Wisconsinan ice sheet. Beneath the zone of degraded, cultivated peat, the sedimentary sequence extended downward through unweathered peat, peaty marl, marly gyttja grading into gray clay, and finally sands and gravels overlying till. The studied material was recovered from a depth of about 1.5 to 2 m in peaty marl.

Most of the bones at this site are derived from one young male mastodon. They occurred in multiple clusters across the pond basin, most of which consisted of disarticulated bones, although when bones of a given cluster were identified, they were found to represent several discrete portions of the carcass, each made up of several bones (Fisher, 1987). The material interpreted as intestinal contents of the Heisler mastodon was found in 1985, not in association with skeletal units suggestive of an abdominal derivation (as in the case of the Burning Tree mastodon), but with one of the few clusters of bones that retained primary articular relationships among bones comprising a set of anatomically disjunct skeletal units. The putative intestinal material consisted of a zone of finely ground plant debris several centimeters thick in most places, surrounding the lateral and lower aspect of a hemispherical mass of sand and gravel about 30 cm in plan diameter (see figs. 1B and 2 in Rhodes et al., 1998). This hemisphere is inferred to have originally been a spheroidal mass of sand and gravel, surrounded on all sides by a zone of finely ground plant debris, all retained within tissue of the large intestine. The lower portion of this spheroidal mass would have settled into the fine-grained, anoxic sediment of the pond bottom and was preserved as an intact hemispherical feature, but protracted exposure of the upper portion to oxygenated pond water allowed intestinal tissue to decompose and some of the plant debris and juxtaposed sediment to be dispersed, leaving a roughly horizontal surface of truncation. Two more examples of this type of feature occurred elsewhere at the Heisler site. In each case, the sand and/or gravel was anomalous within the pond setting and had no physical connection to any lower stratigraphic unit such as would be expected for a sedimentary dike.

The hypothesis we are working with is that the masses of sand, gravel, and associated plant debris were "clastic anchors" (Fisher, 1989, 1995, 1996; Rhodes et al., 1998; see the Supplementary Materials) made by humans introducing clastic material into sections of the mastodon's large intestine, after emptying at least some of its normal contents (Rhodes et al., 1998), as part of a strategy of underwater meat storage (Fisher, 1995). Remaining intestinal contents formed the layer of plant debris around the clastic material. The pollen content of the plant debris associated with a clastic anchor was analyzed by R.O. Kapp and G. Snyder (cited in Fisher, 1996) and compared with the pollen assemblage in the surrounding sediment. Surprisingly, although the dominant pollen type in the peaty marl was *Picea*, no *Picea* pollen was found in the anchor-associated zone of plant debris (Fisher, 1989, 1996). An independent analysis of the record of dentin apposition in a tusk of the Heisler mastodon suggested it had died in the autumn (Fisher, 1987), a season when *Picea* pollen would not have been common. Analyses by R.I. Ford (personal communication 1992 to D.C. Fisher) showed that the material contained remains of female *Picea* cones, interpreted as late-autumn forage. See the Supplementary Materials for further information.

Microbiological analysis by Rhodes et al. (1998) on samples from the Heisler site supported the hypothesis that the peripheral zone of plant debris (surrounding clastic material) was intestinal in origin, although fewer taxa could be cultured than from the Burning Tree material. Accordingly, the contrast between the intestinal material and the surrounding sediment was not as strong as that observed for comparable materials at the Burning Tree site.

METHODS

Our approach was to investigate the diet of our mastodon specimens by multiproxy microfossil and macrofossil analyses of the intestinal contents. Similar analyses of the embedding sediments were used to determine the environments in which they lived. Besides pollen, we also analyzed non-pollen palynomorphs (NPPs; van Geel, 2001; van Geel and Aptroot, 2006), plant macrofossils, and Mollusca, in order to obtain more complete environmental reconstructions and to be able to improve the comparison between intestinal contents and lake sediments. A similar approach was used by Lepper et al. (1991) on the material from the Burning Tree site, but our analyses are more detailed and use more proxies. We also document our data photographically (Figs. 2–6).

Samples of the Burning Tree intestinal contents (three aliquots totaling >50 g) and of the surrounding lake sediment (one aliquot >150 g) were selected for the present study from a frozen archive retained in the laboratory of D.C. Fisher since the time of original recovery. There was plenty of material remaining for our analyses. In contrast, the succession of studies attempting to characterize the Heisler intestinal material has significantly depleted the frozen sample archive. We were nonetheless able to select ~100 g from the peripheral zone of plant debris (attempting to exclude clastic material) and ~50 g from the surrounding peaty marl.

Microfossil preparation followed the standard method of Fægri and Iversen (1989). Macrofossil samples were prepared following Mauquoy and van Geel (2007). Identification and ecological interpretation of NPPs followed van Geel (1978), Pals et al. (1980), van Geel and Aptroot (2006), and van Geel et al. (1981, 1989, 2003). Molluscs collected during the macrofossil analysis were identified using Clarke (1981) and Dillon et al. (2013). Bryophytes were identified using Crum and Anderson (1981), Lawton (1971), Nyholm (1975), and Vitt and Buck (2001). Taxonomic nomenclature follows Flora of North America Editorial Committee (1993+); Angiosperm Phylogeny Group IV (2016); Index Fungorum Partnership (2017); Guiry and Guiry (2017); Flanders Marine Institute (VLIZ) (2017); Royal Botanic Gardens, Kew, and Missouri Botanical Garden (2013); and van Soest et al. (2017). Photographs were made by J. van Arkel, using a Nikon D2Xs digital camera mounted on a bellows with Zeiss Luminar lenses or with a Micro-Nikkor 60/2.8 lens (macrofossils in glycerine or dry) or mounted on a Zeiss Universal microscope with Nomarski-DIC (microslides). For enhanced depth of field, several photographs were combined using Helicon Focus and Adobe Photoshop software (focus stacking). Plates were composed in Adobe InDesign.

Table 1. Radiocarbon dates from the Heisler and Burning Tree mastodon sites.

Material	Lab no.	Age (^{14}C yr BP)	Age (cal yr BP)[a]
Heisler mastodon			
Plant debris, gut contents	Beta-39043[b]	11,380 ± 130	13,476–13,009
Bone collagen, XAD-purified[*] gelatin hydrolysate	NSRL-282/AA-6979[b]	11,770 ± 110	13,825–13,361
Burning Tree mastodon			
Deciduous twigs, gut contents	Pitt-0832[b,c]	11,450 ± 70	13,440–13,140
Deciduous twigs, gut contents	Beta-38241/ETH-6758[b,c]	11,660 ± 120	13,747–13,275
Bone collagen, XAD-purified[*] gelatin hydrolysate	NSRL-283/AA-6980[b]	11,390 ± 80	13,397–13,085
Bone collagen, unpurified	Pitt-0830[c]	10,860 ± 70	12,917–12,666

[a] The 95.4% range, calibrated with OxCal 4.3.2 (Bronk Ramsey, 2009) with the IntCal13 calibration curve (Reimer et al., 2013).
[b] Reported in Rhodes et al. (1998).
[c] Reported in Lepper et al. (1991).
[*] XAD is a registered trademark of the Dow Chemical Company.

Table 2. Burning Tree mastodon, microfossils (pollen, spores, and non-pollen palynomorphs).

		Intestinal contents		Lake sediment	
Taxon[a]	Element	Number[b]	Percent[b,c]	Number[b]	Percent[b,c]
Upland plants					
Quercus	Pollen	59	21.0 (25.4)	23	6.0 (8.6)
Picea	Pollen	56	19.9 (24.1)	119	31.1 (44.7)
Fraxinus (mainly *F. nigra*-type)	Pollen	21	7.5 (9.1)	40	10.4 (15.0)
Ulmus	Pollen	18	6.4 (7.8)	8	2.1 (3.0)
Betula	Pollen	17	6.0 (7.3)	14	3.7 (5.3)
Pinus	Pollen	12	4.3 (5.2)	8	2.1 (3.0)
Corylus	Pollen	11	3.9 (4.7)	9	2.3 (3.4)
Salix	Pollen	4	1.4 (1.7)	6	1.6 (2.3)
Ostrya/Carpinus	Pollen	4	1.4 (1.7)	2	0.5 (0.8)
Fagus	Pollen	3	1.1 (1.3)	-	-

Table 2. (*Continued*)

Taxon[a]	Element	Intestinal contents Number[b]	Intestinal contents Percent[b,c]	Lake sediment Number[b]	Lake sediment Percent[b,c]
Cupressaceae	Pollen	2	0.7 (0.9)	-	-
Juglans cinerea	Pollen	1	0.4 (0.4)	-	-
Abies	Pollen	1	0.4 (0.4)	+	+
Tilia	Pollen	1	0.4 (0.4)	+	+
Carya	Pollen	+	+	2	0.5 (0.8)
Celtis	Pollen	+	+	-	-
Populus	Pollen	-	-	8	2.1 (3.0)
Alnus	Pollen	-	-	3	0.8 (1.1)
Rhamnus	Pollen	-	-	1	0.3 (0.4)
cf. *Viburnum*	Pollen	-	-	1	0.3 (0.4)
Acer saccharum	Pollen	-	-	+	+
Tsuga	Pollen	-	-	+	+
Poaceae	Pollen	49	17.4 (21.1)	117	30.5 (44.0)
Asteraceae subf. Asteroideae undiff.	Pollen	9	3.2 (3.9)	12	3.1 (4.5)
Artemisia	Pollen	3	1.1 (1.3)	1	0.3 (0.4)
Amaranthaceae	Pollen	1	0.4 (0.4)	1	0.3 (0.4)
Humulus	Pollen	9	3.2 (3.9)	8	2.1 (3.0)
Thalictrum	Pollen	-	-	+	+
Pollen sum		281 (232)		383 (266)	
Aquatic and fen plants					
Cyperaceae	Pollen	62	22.1 (26.7)	46	12.0 (17.3)
Typha latifolia	Pollen	10	3.6 (4.3)	3	0.8 (1.1)
Menyanthes trifoliata	Pollen	3	1.1 (1.3)	2	0.5 (0.8)
Nuphar	Pollen	2	0.7 (0.9)	2	0.5 (0.8)
Nymphaeaceae (HdV-127)	Suberized basal cells of mucilaginous hair	5	1.8 (2.2)	68	17.7 (25.6)
Rubiaceae	Pollen	2	0.7 (0.9)	-	-
Sparganium-type	Pollen	1	0.4 (0.4)	3	0.8 (1.1)
Nymphaeaceae (HdV-129)	Trichosclereids	-	-	3	0.8 (1.1)
Potamogeton-type	Pollen	-	-	3	0.8 (1.1)
Sagittaria	Pollen	-	-	2	0.5 (0.8)
Potentilla-type	Pollen	-	-	1	0.3 (0.4)
Ranunculaceae	Pollen	-	-	1	0.3 (0.4)
Rosaceae undiff.	Pollen	-	-	1	0.3 (0.4)
cf. *Brasenia*	Pollen	-	-	1	0.3 (0.4)
Vascular cryptogams					
Polypodiophyta (monolete, psilate)	Spore	7	2.5 (3.0)	2	0.5 (0.8)
Huperzia lucidula	Spore	1	0.4 (0.4)	-	-
Equisetum	Spore	-	-	1	0.3 (0.4)
Polypodiophyta (monolete, verrucate)	Spore	-	-	1	0.3 (0.4)
Pteridium aquilinum	Spore	-	-	1	0.3 (0.4)
Selaginella selaginoides	Spore	-	-	+	+
Nonpollen palynomorphs					
Habrotrocha angusticollis (HdV-37)	Lorica	13	4.6 (5.6)	-	-
Clasterosporium caricinum (HdV-126)	Hyphopodium	77	27.4 (33.2)	19	5.0 (7.1)
Sordaria-type (HdV-55A)	Ascospore	26	9.3 (11.2)	6	1.6 (2.3)
HdV-200	Fungal cell cluster	4	1.4 (1.7)	9	2.3 (3.4)
Sporormiella-type (HdV-113)	Ascospore	1	0.4 (0.4)	-	-
Amphisphaerella dispersella (HdV-310)	Ascospore	1	0.4 (0.4)	-	-
Cercophora-type (HdV-112)	Ascospore	-	-	+	+
Tetraedron minimum (HdV-371)	Cell	-	-	188	49.1 (70.7)
Botryococcus	Colony	2	0.7 (0.9)	154	40.2 (57.9)
HdV-128B	Algal spore?	9	3.2 (3.9)	9	2.3 (3.4)
HdV-128A	Algal spore?	4	1.4 (1.7)	133	34.7 (50.0)
Pediastrum	Colony	-	-	65	17.0 (24.4)
Scenedesmus	Colony	-	-	15	3.9 (5.6)
HdV-225	Algal spore?	-	-	10	2.6 (3.8)

Table 2. (*Continued*)

		Intestinal contents		Lake sediment	
Taxon[a]	Element	Number[b]	Percent[b,c]	Number[b]	Percent[b,c]
Characeae	Oospore fragment	-	-	1	0.3 (0.4)
Transeauina[d]	Zygospore	-	-	1	0.3 (0.4)
Spirogyra scrobiculata-type (HdV-342)	Zygospore	-	-	+	+
Porifera (HdV-220)	Spicule	-	-	11	2.9 (4.1)

[a] "HdV" refers to types recognized by the Hugo de Vries-Laboratory, University of Amsterdam (Miola, 2012).
[b] Plus sign (+) indicates type was observed in scans of the slide but not encountered during the quantitative count.
[c] Percentages were calculated on the sum of terrestrial pollen. Percentages in parentheses exclude Poaceae from the calculation sum.
[d] Formerly called *Debarya* Wittrock, 1872; now shown to be an illegitimate homonym of *Debarya* Schulzer, 1866 (Ascomycota) (Guiry, 2013).

RESULTS

Dating

We obtained no new radiocarbon dates from the mastodons. Calibration of previous radiocarbon ages on both mastodons (Table 1) places them within Greenland interstadial 1 (Bølling-Allerød chronozone). For the Heisler mastodon, the radiocarbon date on plant debris in the intestinal contents is ~400 younger than the direct date on XAD-purified bone collagen, and a χ^2 test indicates that these dates are not the same at the 95% level of significance (carried out in OxCal 4.3.2; Bronk Ramsey, 2009). We do not have a good explanation for the discrepancy, although contamination with younger material might have occurred during excavation or by diffusion of younger humic acids from the overlying sediments. Nevertheless, both dates fall within the Bølling-Allerød chronozone. For the Burning Tree mastodon, the date on unpurified collagen is ~500 yr younger than the date on XAD-purified collagen suggesting likely contamination with younger materials. A χ^2 test indicates that the XAD-purified collagen and two dates on twigs in the intestinal contents are similar at the 95% significance level. In fact, all dates except the one on unpurified collagen fall within the Allerød chronozone.

Microfossil and macrofossil results

Burning Tree

Because the pollen samples from the Burning Tree site have unusually high values of Poaceae relative to other late glacial sites in the upper Midwest, USA, we suspect overrepresentation of local aquatic Poaceae (*Zizania, Glyceria*). Therefore, microfossil percentages have been calculated with and without Poaceae in the pollen sum (Table 2). Many of the macrofossils are illustrated in Figures 2–4.

Microfossils from the Burning Tree mastodon intestinal contents are listed in Table 2. *Quercus*, *Picea*, *Fraxinus*, *Ulmus*, *Betula*, *Pinus*, and *Corylus* are the commonest arboreal-pollen taxa in the intestinal sample, with minor contributions of *Abies*, *Fagus*, *Juglans*, Cupressaceae, *Salix*, and *Tilia*. Some wetland and aquatic taxa are present (*Typha latifolia*, *Nuphar*, and *Botryococcus*, as well as probable algal spore types HdV-128A and HdV-128B), but the numbers of these taxa are much lower than in the environmental sample from the lake deposit. Some algae (*Pediastrum*, *Scenedesmus*, and *Tetraedron minimum*) that were extremely common in the lake deposit are absent in the intestinal sample. Spores of the coprophilous fungus *Sordaria*-type are particularly common. The hyphopodia of the fungus *Clasterosporium caricinum* were growing on epidermis of *Carex* species (van Geel and Aptroot, 2006). *Habrotrocha angusticollis* is a rotifer common in wet mossy habitats.

The macrofossil record from the Burning Tree mastodon intestinal contents (Table 3, Fig. 2) shows that the animal consumed leaves and twigs of *Betula*, Pinaceae, and *Salix*. Herbaceous taxa are present such as *Glyceria* and various Cyperaceae (with the fungal parasite *Clasterosporium caricinum*), as are semiaquatic and aquatic taxa such as *Calliergon giganteum*, *Menyanthes trifoliata*, Alismataceae, *Potamogeton*, *Najas*, Characeae, *Gloeotrichia*, and *Eunapius fragilis* (sponge gemmulae).

The microfossil assemblage of the Burning Tree lake deposit (Table 2) suggests a predominantly forested landscape dominated by *Picea* associated with *Quercus*, *Fraxinus*, *Betula*, and *Corylus*, and with lesser amounts of *Pinus*, *Ulmus*, *Populus*, *Salix*, *Alnus*, *Carya*, *Ostrya/Carpinus*, *Rhamnus*, and cf. *Viburnum*. Upland herbaceous taxa (*Artemisia*, other Asteraceae, and Amaranthaceae) show relatively low values. Cyperaceae and Poaceae dominate the herbaceous taxa. The local aquatic environment is represented by the macrophytes *Nuphar*, cf. *Brasenia*, *Potamogeton*, *Sagittaria*, *Sparganium*, and *Typha*, together with NPPs, including the algae *Tetraedron minimum*, *Botryococcus*, *Pediastrum*, and *Scenedesmus*, spicules of Porifera, and probably algal spore types HdV-128A and HdV-128B.

The macrofossil record of the Burning Tree lake deposit (Table 3, Figs. 3 and 4) shows that *Betula*, Pinaceae, and *Salix* were growing nearby. The bryophytes point to a moist, calcareous habitat. *Meesia triquetra* is a rich fen indicator, while *Rhizomnium punctatum* and *Calliergon giganteum*

Figure 2. (color online) (1–19) Burning Tree, macrofossils from intestinal contents. (1, 2) Leaf fragments cf. *Salix*. (3) *Salix* sp., fruit. (4) *Betula* sp., fruit (wings not preserved). (5) Pinaceae, needle epidermis with stomata. (6) *Glyceria* sp., fruits. (7–9) Cyperaceous epidermis showing mycelium and hyphopodia of parasitic fungus *Clasterosporium caricinum* (HdV-126). (10) Broken fungal fruit-body with two ascospores. (11) Three-septate ascospore from fruit-body (10). (12) Cyperaceous epidermis. (13) Unidentified seed. (14) Alismataceae, seed. (15) *Potamogeton* sp., fruit. (16) *Menyanthes trifoliata*, seeds. (17) Various Cyperaceae. (18) *Carex* sp., utricle. (19) *Habrotrocha angusticollis*, lorica.

Figure 3. (color online) (20–38) Burning Tree, macrofossils from lake deposit. (20, 21) *Picea*, winged seeds. (22) *Betula* sp. (?), catkin with anthers. (23, 24) Pinaceae, anthers. (25) Coniferous needle, epidermis with stomata. (26) *Salix* sp., bud. (27) *Betula* sp., fruit (wings not preserved). (28) Unidentified seeds. (29) *Zizania* sp., fruits. (30) *Salix* sp., epidermis. (31) *Sparganium* sp., fruits. (32) Alismataceae, seed. (33) *Typha* sp., fruit. (34) *Potamogeton* sp., leaf tip. (35) *Nuphar* (*N. microphyllum* or *N. variegatum*), seeds. (36) *Menyanthes trifoliata*, epidermis. (37) *Eleocharis* sp., fruits with perianth. (38) various Cyperaceae.

suggest a swampy, open fen carr. *Campylium stellatum* and *Calliergonella cuspidata* are also species of calcareous mires. *Zizania aquatica*, *Menyanthes trifoliata*, various Cyperaceae, *Sparganium*, *Typha*, and Alismataceae probably occurred in the littoral zone along the lakeshore, while *Potamogeton*, *Najas*, *Nuphar*, and Characeae were growing in the lake. Chironomids, *Cristatella mucedo*, and Porifera were also part of the lake ecosystem.

Table 3. Burning Tree mastodon, presence of macrofossils.

Taxon	Element	Intestinal contents[a]	Lake sediment[a]
Trees and shrubs			
Pinaceae	Needle epidermis with stomata	X (5)	
Salix sp.	Fruit	X (3)	
Salix sp.	Leaf fragments	X (1, 2)	
Betula sp.	Fruit	X (4)	X (27)
Betula sp.	Catkin with anthers		X (22)
Pinaceae	Needle epidermis with stomata		X (25)
Picea	Seed		X (20, 21)
Pinaceae	Anther		X (23, 24)
Salix sp.	Bud		X (26)
Salix sp.	Epidermis		X (30)
Aquatic and wetland plants			
Cyperaceae	Epidermis	X (12)	
Carex sp.	Utricle	X (18)	
Glyceria sp.	Caryopsis	X (6)	
Menyanthes trifoliata	Seed	X (16)	
Menyanthes trifoliata	Epidermis	X	X (36)
Alismataceae	Seed	X (14)	X (32)
Cyperaceae	Achene	X (17)	X (38)
Cyperaceae	Epidermis with *Clasterosporium caricinum*	X (7-9)	X
Najas flexilis	Seed	X	X
Potamogeton sp.	Leaf fragment	X	X (34)
Potamogeton sp.	Fruit	X (15)	X
Eleocharis sp.	Achene		X (37)
Najas marina	Seed		X
Nuphar sp.	Seed		X (35)
Sparganium sp.	Fruit		X (31)
Typha sp.	Seed		X (33)
Zizania sp.	Caryopsis		X (29)
Unidentified			
Unidentified	Woody twig	X	
Unidentified	Seed	X (13)	X (28)
Aquatic and wetland bryophytes			
Calliergon giganteum	Stem, leaf	X	X (39, 40)
Calliergonella cuspidata	Stem, leaf		X
Campylium stellatum	Stem, leaf		X
Meesia triquetra	Stem, leaf		X (41)
Rhizomnium punctatum	Stem, leaf		X
Scorpidium revolvens	Stem, leaf		X (42, 43)
Fungi			
Cenococcum	Ectomycorrhizal roots	X	
Fungi undiff.	Fruit-body with ascospores	X (10, 11)	
Algae			
Characeae	Oospore	X	X
Cyanobacteria			
Gloeotrichia	Colony	X	
Invertebrates			
Habrotrocha angusticollis	Lorica	X (19)	
Eunapius fragilis	Gemmule	X	X (46, 47)
Chironomidae	Head capsule		X
Cristatella mucedo	Statoblast		X
Porifera undiff.	Gemmule		X (44, 45)
Prionocera sp.	Head capsule		X (48)
Other			
Sand		X	

[a] Numbers in parentheses refer to illustrations in Figures 2–4.

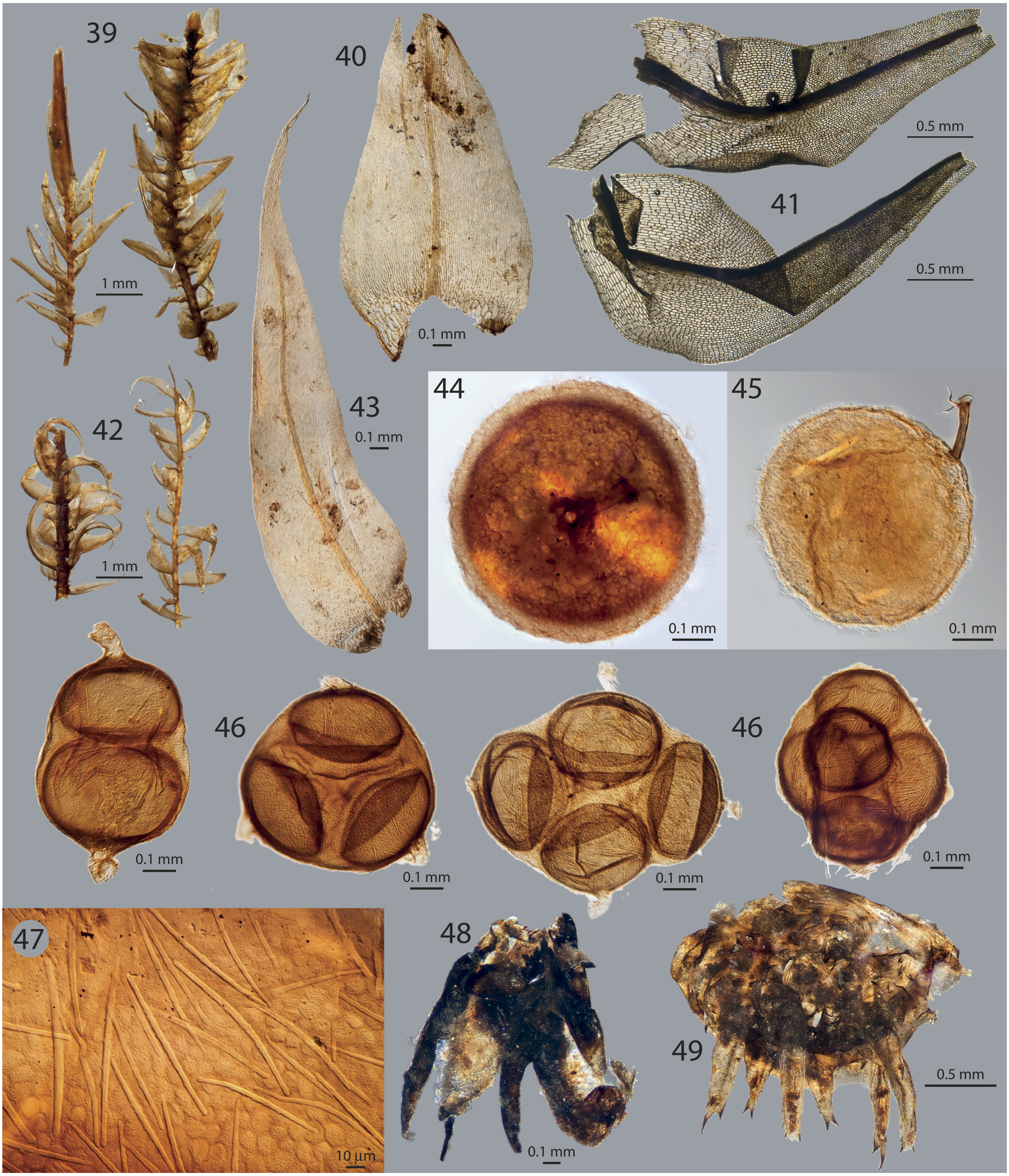

Figure 4. (color online) (39–49) Burning Tree, macrofossils from lake deposit, continued. (39, 40) *Calliergon giganteum*. (41) *Meesia triquetra*. (42, 43) *Scorpidium revolvens*. (44, 45) Gemmulae of freshwater sponges. (46) *Eunapius fragilis*, gemmulae. (47) Wall of gemmula of *Eunapius fragilis*. (48) *Prionocera* sp., head capsule. (49) Unidentified zoological object.

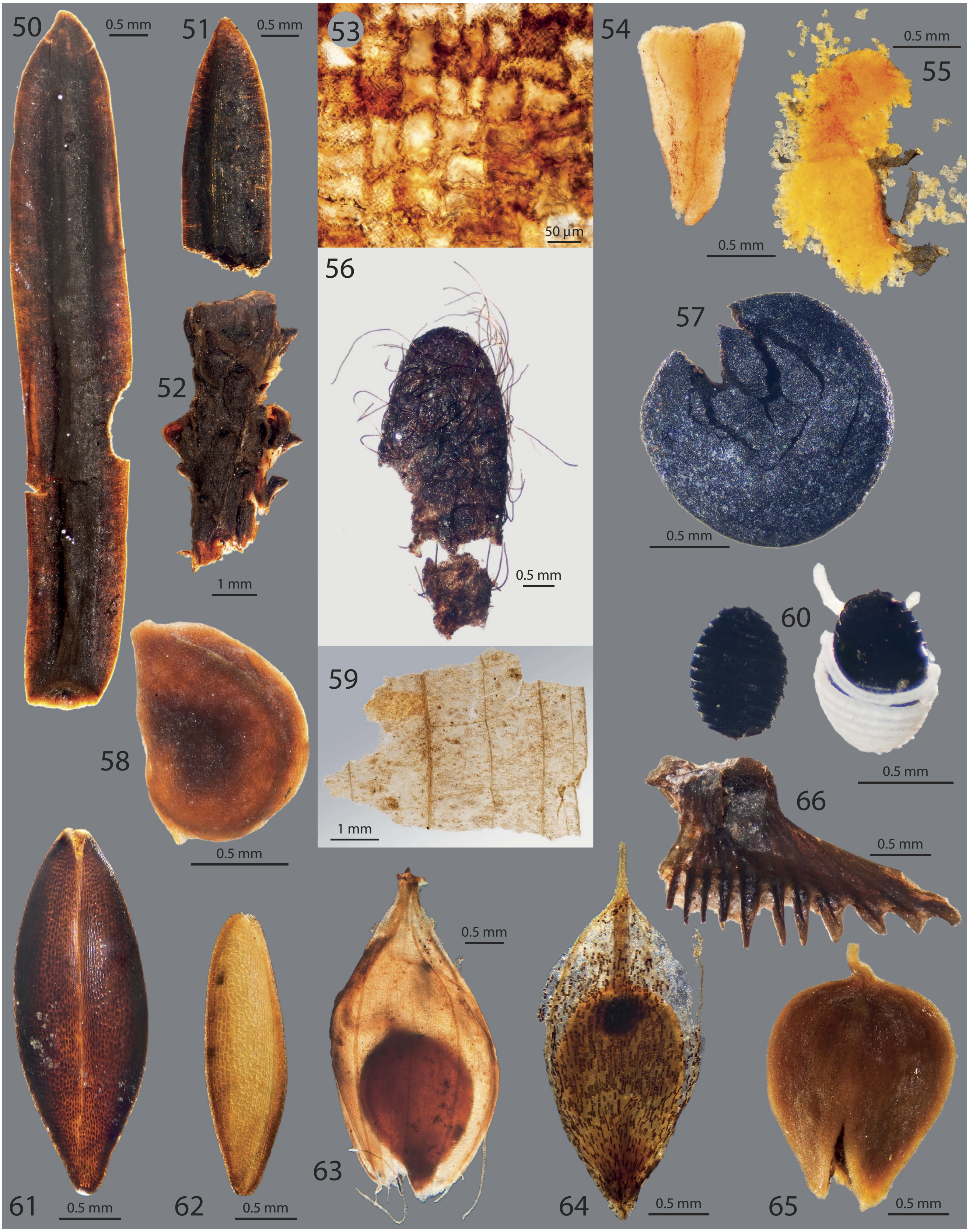

Figure 5. (color online) (50–66) Heisler, macrofossils from intestinal contents. (50, 51) *Picea*, needle fragments. (52) Twig with leaf scars. (53) Pinaceae, periderm. (54, 55) *Picea* pollen sacs (54: full of pollen; 55: after squashing, showing separate pollen grains). (56) Mycorrhizal root tip (incomplete) of *Cenococcum geophilum*. (57) *Cenococcum geophilum*, sclerotium (broken). (58) *Potamogeton* sp., fruit. (59) *Potamogeton*, leaf fragment. (60) Characeae, oospores. The right one showing part of the calcium carbonate coating. (61) *Najas marina*, seed. (62) *Najas flexilis*, seed. (63) *Carex* cf. *rostrata*, utricle with fruit. (64) *Carex nigra* type, utricle with fruit. (65) *Carex rostrata* type, fruit. (66) *Perca* sp., praeoperculum.

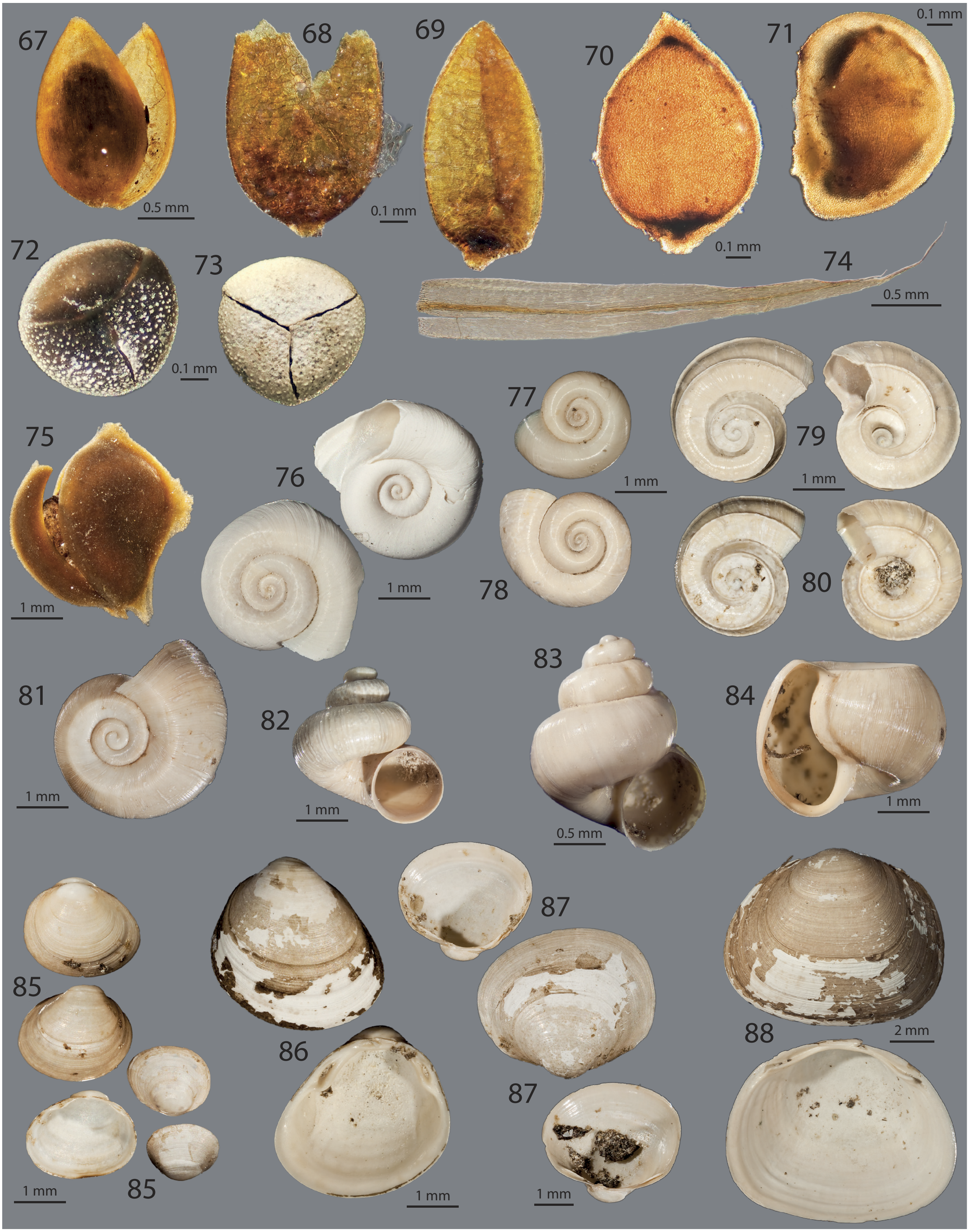

Figure 6. (color online) (67–74) Heisler, macrofossils from intestinal contents, continued. (67) *Viola* sp., seed. (68, 69) *Juncus* sp., seeds. (70) cf. *Urtica*, fruit. (71) cf. *Comarum palustre*, fruit. (72, 73) *Selaginella* cf. *selaginoides*, macrospores. (74) *Sarmentypnum exannulatum*, leaf. (75–88) Heisler, macrofossils from lake deposit. (75) *Potamogeton* sp., fruit. (76) *Gyraulus* sp. (77, 78) *Gyraulus parvus*. (79, 80) *Valvata tricarinata*. (81, 84) *Heliosoma anceps*. (82) *Valvata sincera sincera*. (83) *Amnicola* sp. (85) *Pisidium* sp. (86) *Pisidium* cf. *compressum*. (87) *Sphaerium* sp. (88) *Sphaerium rhomboideum*.

Table 4. Heisler mastodon, microfossils (pollen, spores, and non-pollen palynomorphs).

		Intestinal contents		Lake sediment	
Taxon[a]	Element	Number[b]	Percent[b,c]	Number[b]	Percent[b,c]
Upland plants					
Picea	Pollen	253	89.4	171	50.6
Larix	Pollen	15	5.3	-	-
Coniferae	Wood	++	++	-	-
Salix	Pollen	3	1.1	8	2.4
Alnus	Pollen	2	0.7	2	0.6
Betula	Pollen	1	0.4	21	6.2
Quercus	Pollen	1	0.4	26	7.7
Fraxinus (mainly *F. nigra*-type)	Pollen	1	0.4	37	10.9
Corylus	Pollen	1	0.4	3	0.9
Cupressaceae	Pollen	1	0.4	12	3.6
Ostrya/Carpinus	Pollen	-	-	3	0.9
Carya	Pollen	-	-	1	0.3
Celtis	Pollen	-	-	+	+
Populus balsamifera-type	Pollen	-	-	14	4.1
Ulmus	Pollen	-	-	4	1.2
Humulus	Pollen	-	-	8	2.4
Juglans cinerea	Pollen	-	-	1	0.3
Pinus	Pollen	-	-	1	0.3
Acer saccharum	Pollen	-	-	+	+
Shepherdia canadensis	Pollen	-	-	+	+
Poaceae	Pollen	3	1.1	8	2.4
Ambrosia-type	Pollen	2	0.7	8	2.4
Artemisia	Pollen	-	-	6	1.8
Pollen sum		283		338	
Aquatic and wetland plants					
Cyperaceae	Pollen	26	9.1	26	7.7
Typha latifolia	Pollen	4	1.4	2	0.6
Sparganium-type	Pollen	1	0.4	1	0.3
Nymphaea	Pollen	-	-	1	0.3
Nymphaeaceae (HdV-127)	Hair[d]	-	-	3	0.9
Nymphaeaceae (HdV-129)	Trichosclereids	-	-	1	0.3
Potentilla-type	Pollen	-	-	1	0.3
Urtica	Pollen	-	-	1	0.3
Utricularia	Hair	-	-	1	0.3
Vascular cryptogams					
Polypodiophyta (monolete, psilate)	Spore	3	1.1	-	-
Selaginella selaginoides	Spore	2	0.7	-	-
Equisetum	Spore	1	0.4	2	0.6
Nonpollen palynomorphs					
Sordaria-type (HdV-55A)	Ascospore	44	15.5	-	-
Sporormiella-type (HdV-113)	Ascospore	14	4.9	-	-
Glomus cf. *fasciculatum* (HdV-207)	Chlamydospore	7	2.5	-	-
Gelasinospora (HdV-1)	Ascospore	2	0.7	-	-
Cercophora-type (HdV-112)	Ascospore	1	0.4	-	-
Clasterosporium caricinum (HdV-126)	Hyphopodium	1	0.4	3	0.9
Botryococcus	Colony	-	-	148	43.7
Pediastrum	Colony	-	-	34	10.1
Tetraedron minimum (HdV-371)	Cell	-	-	30	8.8
HdV-128B	Algal spore?	5	1.8	-	-
HdV-128A	Algal spore?	7	2.5	7	2.1
HdV-225	Algal spore?	-	-	7	2.1
Scenedesmus	Colony	-	-	3	0.9
Characeae	Oospore fragment	-	-	+	+

Table 4. (*Continued*)

Taxon[a]	Element	Intestinal contents		Lake sediment	
		Number[b]	Percent[b,c]	Number[b]	Percent[b,c]
Porifera (HdV-220)	Spicule	-	-	17	5
Unknown (HdV-223)	Palynomorph	-	-	11	3.3

[a] "HdV" refers to types recognized by the Hugo de Vries-Laboratory, University of Amsterdam (Miola, 2012).
[b] Plus sign (+) indicates type was observed in scans of the slide but not encountered during the quantitative counts.
[c] Percentages were calculated on the sum of terrestrial pollen.
[d] Suberized basal cells of mucilaginous leaf hairs.

Heisler

Picea completely dominates the intestinal-content pollen-spectrum with almost 90% (Table 4) in contrast to the (probably multiannual) pollen spectrum of the Heisler lake deposit. The presence of *Picea* pollen sacs in the macrofossil assemblage suggests overrepresentation of *Picea* pollen, especially if sacs were squashed and broken during preparation. *Larix laricina*, which normally occurs in low percentages in lake sediments, is the second-most common tree-pollen type. Other arboreal taxa show low frequencies only. Among the herbaceous taxa are low percentages of *Sparganium* and *Typha*. Cyperaceae pollen is common, which fits well with the macrofossil record. Fungal spores of the coprophilous *Sordaria*-type and *Sporormiella*-type are common. The latter includes ripe *Sporormia* spores that have developed slits and spores of the closely related *Preussia*, both of which are also coprophilous genera (see van Geel and Aptroot, 2006). The presence of chlamydospores of *Glomus* (formed under the soil surface) shows either that some soil material was ingested or that *Glomus* was introduced with the clastic material. Aquatic taxa are absent, apart from spores of HdV-128A and 128B, but these can also occur in mires (van Geel et al., 1989).

The macrofossil assemblage of the Heisler intestinal sample (Table 5, Figs. 5 and 6) contained *Picea* needle fragments, *Picea* pollen sacs (still filled with pollen), periderm of Pinaceae, wood fragments, and some charcoal. Among the herbaceous taxa were *Carex* species, *Viola* sp., cf. *Juncus*, cf. *Urtica*, cf. *Comarum palustre*, *Equisetum*, and *Selaginella selaginoides*. A variety of aquatic taxa included *Potamogeton*, Characeae, *Najas marina*, *N. flexilis*, Ostracoda, Porifera, and a small fish bone of *Perca* sp. The three recorded moss species point to a rich fen habitat, probably with seepage of alkaline water. The intestinal material of the Heisler mastodon also contained a few mollusc remains: one adult valve of *Sphaerium rhomboideum* and three juvenile valves of cf. *Pisidium* sp. These molluscs may have been introduced during the production of the "clastic anchors," but some molluscs could have been ingested when the Heisler mastodon was drinking water.

The arboreal pollen record of the Heisler lake deposit (Table 4) is dominated by *Betula*, *Fraxinus*, and *Picea*, with some *Quercus*, *Populus*, Cupressaceae, *Corylus*, and *Salix*, whereas *Alnus*, *Ostrya/Carpinus*, *Carya*, *Juglans*, *Pinus*, and *Ulmus* show low values. Upland herbaceous taxa (*Artemisia*, other Asteraceae, and Poaceae) show low percentages only. Aquatic taxa are comparatively rare and include *Utricularia*, Characeae, *Nymphaea*, *Sparganium*, and *Typha*; the algae *Botryococcus*, *Pediastrum*, *Scenedesmus*, and *Tetraedron minimum*; and freshwater sponges.

Apart from some *Picea* needle fragments, the macrofossil record of the Heisler lake deposit is dominated by aquatic taxa, including *Potamogeton*, *Najas*, and Characeae, and a variety of invertebrates: Cladocera, Ostracoda, Bryozoa, Porifera, Chironomidae, and numerous Mollusca (Fig. 6, 76–88; Table 5). The mollusc shells were mostly well preserved and some still had a periostracum (thin organic coating), but some showed (bio) erosion. Some shells could not be identified to species level (e.g., juvenile shells). Many juveniles and some adults of *Valvata tricarinata*, *Helisoma anceps*, and *Gyraulus parvus* were recorded, and two juveniles of *Amnicola* cf. *limosa* were found. Some of the bivalves were still present as double valved. Double shells and valves of *Sphaerium rhomboideum* and *Sphaerium* (*Musculium*) sp. were recorded (possible candidates: *S. lacustre*, *S. partumeium*, and *S. securis*). One valve of *Pisidium* cf. *compressum* and double shells and many valves of *Pisidium* sp. were recorded. Probably some originally double-valved shells were separated during sampling and sieving of the sediment. The assemblage is typical of fresh calcareous waters with muddy substrates and aquatic vegetation occurring today in the boreal forest region of southern Canada and northern USA.

DISCUSSION

Samples from the lake sediments of the mastodon sites probably represent the complete growing seasons of multiple years, especially as the sediments had probably been stirred up by the process of emplacement of the mastodon parts. In contrast, the intestinal samples are expected to represent short time intervals and therefore overrepresent taxa that were flowering or fruiting near the time of death of the animal. In addition, the mastodons may have been selective in their food choice, which may cause additional overrepresentation and underrepresentation of some taxa.

Environments of the mastodons

The microfossil and macrofossil assemblages from the sediments surrounding the mastodon skeletal units indicate their environment, both regionally, with wind-dispersed forest-pollen types such as *Picea*, and more locally, with fen and aquatic taxa. The macrofossils, in particular, are probably locally derived, as they are generally not dispersed far from their source (Birks, 1973) and represent both aquatic and emergent lakeshore vegetation.

The pollen assemblages indicate that the lakes were surrounded by mixed coniferous-deciduous forests dominated by *Picea*, together with *Larix*, characteristic of the late glacial vegetation in the Great Lakes area along with a significant deciduous component, especially *Fraxinus*, mainly *F. nigra*. Deciduous taxa were more frequent in the more southerly site (Burning Tree) in Ohio. Open glades were probably rather rare, as upland-herb pollen types have low percentages. It seems likely that mastodons roamed through the forest, browsing the trees, particularly *Picea*, and foraging and drinking at ponds.

The pollen assemblages from the mastodons' environments are consistent with others from the Great Lakes region for the Allerød chronozone. They represent a vegetation type that was a mixture of *Picea*, *Larix*, and deciduous trees, with especially high values of *Fraxinus nigra*. These assemblages have no modern pollen analog (Overpeck et al., 1992; Williams et al., 2001, 2004; Jackson and Williams, 2004). Although these taxa occur together today in the northern Great Lakes region, the modern assemblages are dominated by *Pinus* and *Betula*, and *Fraxinus nigra* is much less abundant (e.g., Williams et al., 2001, 2004; Grimm and Jacobson, 2004; Gonzales and Grimm, 2009; Gonzales et al., 2009). A modeling study using extended climate-pollen response surfaces suggested that greater precipitation, especially winter precipitation (snow), was a feature during the late glacial period (Gonzales et al., 2009).

Both lakes were surrounded by marginal sedge-swamps dominated by *Carex* spp. and containing other telmatic plants (Tables 2–5). The presence of numerous arboreal macrofossils in the Burning Tree lake sediment indicates a short distance between the sampling site and tree species, and therefore that the marginal lake-swamp was probably less extensive than at the Heisler site or that there was an inflowing stream nearby. The pollen and macrofossil records from Burning Tree suggest that the swamp contained abundant *Salix*, a variety of sedges (*Carex* and *Eleocharis*), and the emergent grass *Zizania aquatica* (wild rice), together with other wet-fen plants. There were also areas of rich fen around the lakes, indicated by the mosses and *Selaginella selaginoides*. These plants indicate calcareous conditions and may have been deposited near the mastodon carcasses through trampling and disturbance.

Lakes were important water sources for mastodons, and the surrounding sedge marshes were grazed. As indicated by the assemblages of aquatic plants, *Najas flexilis, N. marina, Potamogeton* spp., Nymphaeaceae, and *Chara*, the lake waters were calcareous with relatively high conductivity but probably low nutrient status. This is confirmed by the abundance of freshwater mollusca at the Heisler site. The snails and clams typically live in aquatic vegetation and on the muddy bottoms of shallow ponds, as well as in slow-moving rivers with quiet, silt-free, clean, cool, well-oxygenated, and calcium-rich water and abundant macrophytes. *Valvata sincera sincera* prefers larger calcareous lakes, ranging from the shoreline to 15 m depth. *Gyraulus parvus* lives in a variety of permanent and temporary water bodies. There are no indications for transport of shells, so we get a spectrum of the *in situ* mollusc fauna. Land snails of species from marsh or higher banks were absent. Algae such as *Botryococcus*, *Pediastrum*, *Scenedesmus*, and *Tetraedron*, and invertebrates such as Chironomidae, Cladocera, Bryozoa, and sponges, were also part of the lake ecosystems.

Mastodon meals

Yansa and Adams (2012) provided a review of the habitats and diets of mammoths and mastodons in the Great Lakes region of the USA and adjacent Ontario, Canada, as they neared extinction around 13.0 cal ka BP. Our detailed results accord well with their characterization of mastodons as browsers of shrub and tree leaves, including spruce twigs, needles, and bark. They lived in a spruce parkland/sedge wetland environment and later in spruce-dominated forest.

The intestinal samples represent a relatively short time interval (probably only a few days and therefore just part of a season). The assemblages are biased by the specific vegetation of the sites where the animals selected their last meals and their selection of food plants. The microfossil assemblages from the intestinal samples of both mastodons differ from the surrounding lake deposits, especially for non-anemophilous types. Taphonomically, the intestinal contents represent the local vegetation that the mastodons were eating, whereas the lake sediments would have a larger source area and represent the average of several decades of pollen deposition. In most respects, the browsing and grazing behavior of the mastodons was similar. They browsed tree branches and leaves, both conifers and broad leaves, and pulled up herbaceous plants from the lakeshore that included fruits and seeds in the ingested sediment.

At both sites, algae (HdV-128A, *Botryococcus*, *Tetraedron minimum*, *Pediastrum*, and *Scenedesmus*), remains of Nymphaeaceae leaves (HdV-127), and sponge spicules are common in the lake sediments but rare or even absent in the intestinal samples. The absence of aquatic algae such as *Botryococcus*, *Pediastrum*, and *Tetraedron* in the intestinal samples is remarkable. These algae are common in freshwater and bloom in eutrophic conditions when inorganic phosphate and nitrate are high and the water temperature is warm. The aquatic assemblages indicate that the lakes were oligotrophic to mesotrophic, so blooms were probably rare, especially in early spring when the water was cool, which would explain the absence of algae in the intestines. Larger *Pediastrum* values in the sediments are probably derived from the *Pediastrum* population increase in autumn. *Pediastrum* would have been rare in the water in spring, when the mastodon was taking its last drink.

The intestinal samples from both mastodons contained ascospores of the coprophilous *Sordaria*-type and

Table 5. Heisler mastodon, presence of macrofossils.

Taxon	Element	Intestinal contents[a]	Lake deposit[a]
Trees and shrubs			
Picea	Needle	X (50, 51)	
Picea	Pollen sacs	X (54, 55)	
Pinaceae undiff.	Periderm	X (53)	
Spermatophyta undiff.	Wood fragments and woody twigs	X (52)	
Pinaceae undiff.	Needle fragment		X
Upland herbs			
cf. *Urtica*	Fruit	X (70)	
Viola sp.	Seed	X (67)	
Aquatic and wetland spermatophytes			
Carex nigra-type	Achene	X (64)	
Carex cf. *rostrata*	Achene	X (63, 65)	
cf. *Comarum palustre*	Achene	X (71)	
Juncus sp.	Seed	X (68, 69)	
Najas flexilis	Seed	X (62)	
Najas marina	Seed	X (61)	
Potamogeton sp.	Fruit	X (58)	X (75)
Potamogeton sp.	Leaf fragment	X (59)	X
Najas sp.	Seed		X
Aquatic and wetland bryophytes			
Calliergon giganteum	Leaf, stem	X	
Sarmentypnum exannulatum	Leaf	X (74)	
Scorpidium revolvens	Stem, leaf	X	
Vascular cryptogams			
Equisetum	Epidermis fragments	X	
Selaginella cf. *selaginoides*	Megaspore	X (72, 73)	
Fungi			
Cenococcum geophilum	Mycorrhizal roots and sclerotia	X (56, 57)	
Algae			
Characeae	Oospore	X (60)	X
Vertebrates			
Perca sp.	Praeoperculum	X (66)	
Molluscs			
cf. *Pisidium* sp.	Shell	X	
Sphaerium rhomboideum	Shell	X	X (88)
Amnicola sp.	Shell		X (83)
Gyraulus sp.	Shell		X (76)
Gyraulus parvus	Shell		X (77, 78)
Helisoma anceps	Shell		X (81, 84)
Valvata sincera sincera	Shell		X (82)
Valvata tricarinata	Shell		X (79, 80)
Pisidium cf. *compressum*	Shell		X (86)
Pisidium sp.	Shell		X (85)
Sphaerium sp.	Shell		X (87)
Other invertebrates			
Ostracoda	Valve	X	X
Porifera	Gemmule	X	X
Bryozoa	Statoblast		X
Chironomidae	Head capsule		X
Cladocera	Ephippium		X
Other			
Charcoal		X	

[a] Numbers in parentheses refer to illustrations in Figures 5 and 6.

Sporormiella-type fungi. These are absent from the Heisler and infrequent in the Burning Tree lake-sediment samples (Tables 2 and 4), which suggests that the mastodons were consuming herbaceous food with wind-dispersed ascospores from fruit-bodies that developed on nearby feces but that these spores were not dispersed by wind or water from land to lake (e.g., Baker et al., 2013; Gill et al., 2013). Studies of mammoth dung (van Geel et al., 2008, 2011a, 2011b) suggest coprophagy (ingestion of the animal's own dung) by *Mammuthus primigenius*. The presence of fungal fruit-bodies of coprophilous taxa in mammoth feces was of crucial importance in demonstrating coprophagy. Because we did not find fruit-bodies of dung-inhabiting fungi in the mastodon samples, we can only speculate about possible coprophagy of our mastodons. However, the presence of the ascospores of coprophilous fungi can be expected in any sample of vegetation frequented by large herbivores (van Geel et al., 2007), because dung and fruit-bodies will have been present, and dispersed ascospores could thus have been consumed unintentionally. The presence of *Glomus* in the intestine indicates that soil material was ingested, also suggesting that soil was accidentally consumed when vegetation was pulled up.

The Burning Tree mastodon intestine did not contain overwhelming amounts of *Picea* and *Larix* pollen, and the percentages of deciduous-tree pollen, *Ulmus*, *Fraxinus*, *Corylus*, and Q*uercus*, and Poaceae and Cyperaceae pollen are relatively great compared with the Heisler mastodon. All these taxa flower in spring, so the differences between pollen samples from the intestine and lake sediment are linked to the season of the mastodons' death.

The relatively large amount of Cyperaceae pollen in the intestinal sample of the Burning Tree mastodon may indicate that the sedges were flowering when they were eaten. However, the pollen may have been already deposited within the sedge marsh before it was eaten. The large number of Cyperaceae seeds together with other marsh-plant propagules probably originated from the seeding plants or from sediment hauled out with the sedge plants by the mastodon's trunk. The mastodon also ate a copious quantity of grasses (*Glyceria* and *Zizania*). Poaceae pollen is abundant in the lake sediment, and *Zizania aquatica* fruits (wild rice) were recovered (Table 3; Fig. 3, 29).

The pollen assemblages of trees and upland herbs in the Heisler mastodon spectrum are completely different from the Burning Tree intestinal contents. The Heisler pollen spectrum is dominated by *Picea* pollen, whereas the sediment sample shows many more arboreal taxa (Table 4). The combination of so much *Picea* pollen (accompanied by pollen sacs full of pollen) and more than 5% *Larix* pollen (which was not recorded in the corresponding sediment sample) indicates ingestion during the flowering period and browsing of the Heisler mastodon on young branches with pollinating male cones, especially of *Picea*. The seasonality of *Picea* flowering suggests that the Heisler mastodon died in April or May, but see the "Residual inconsistencies" section. Propagules of aquatic and fen plants that form later in the season also occur (Table 5). The mastodon may have ingested these along with sediment while grazing in a sedge marsh around the lakeshore. It could also have ingested a few propagules of aquatic plants, such as *Chara* oospores and *Najas* seeds, together with some aquatic invertebrate remains and a fish bone, when drinking the more than 100 L of water required each day.

Association with human activity

According to Goebel et al. (2008), the best explanation of available genetic, archaeological, and environmental evidence is that humans colonized the Americas around 15,000 yr BP, immediately after the deglaciation of the Pacific coastal corridor. Humans already lived in the Americas before the Clovis culture developed ca. 13 ka BP (Waters and Stafford, 2007). Humans rapidly migrated eastward along the southern margin of the continental ice sheet, possibly following prey such as mammoth and mastodon (Goebel et al., 2008). Based on adjusted ^{14}C dating and a reevaluation of the record of the Clovis culture, Waters and Stafford (2007) revised the Clovis time range to 13,125 to 12,925 cal yr BP. This overlaps with the age of our mastodons. Within 200 calendar years, Clovis technology spread throughout North America, including the Midwest, though we need to be clear that neither of the sites we focus on here yielded diagnostic Clovis artifacts. Sites of this age showing evidence of pre-Clovis or Clovis human activity are small and may represent mammoth or mastodon kills, short-term camps, or caches. In southeastern Wisconsin, the Schaefer and Hebior mammoth sites provide evidence of proboscidean hunting or scavenging near the margin of the Laurentide Ice Sheet between 14.8 and 14.2 cal ka BP (Joyce, 2006). Disarticulated remains of a single mammoth at both sites were sealed in pond clay and were associated with unequivocal stone artifacts, probably of pre-Clovis type, and the bones bore consistent signs of butchering—cut and pry marks made by stone tools (Overstreet and Kolb, 2003). Disarticulated skeletons of mammoths and mastodons preserved within lake sediments are widespread in the Midwest (Widga et al., 2017). It seems possible that the practice of caching carcasses in small lakes was a common method of preserving the meat (Fisher, 1989, 1995, 2009). In any case, this is the hypothesis within which we currently understand these two otherwise puzzling occurrences of mastodon intestinal contents.

Residual inconsistencies

We are satisfied that most observations made during this study are compatible with one another and with our growing knowledge of the ecology of late-glacial North America. However, some inconsistencies remain. Why did Kapp (cited in Fisher, 1996) find no pollen of *Picea* in the intestinal contents of the Heisler mastodon, whereas we found it to be both abundant and accompanied by anthers? Why did Ford report debris of female conifer cones in his samples of Heisler intestinal contents, whereas we recognized no comparable material? The mastodon bones at the Heisler site are all consistent with a single individual, a young male, so it cannot be reasonable to explain the reported differences by conjecturing that there were intestinal contents from more than one individual. However, we can propose three other potential explanations of these inconsistencies:

First, it is possible that these differences simply reflect the heterogeneity of intestinal material in a large mammal that forages sporadically within a complex habitat with a wide variety of potential foods (Green et al., 2017). Once past the stomach, there would be little tendency for peristaltic movement to homogenize intestinal contents, so we might well acquire a serially diversified picture of this animal's diet. Kapp's material came from one "clastic anchor," but later analyses, including ours, came from a second anchor. Therefore, although they are part of the same intestine, they sample different parts of it. The mastodon might have eaten only one or two *Picea* cones from the previous year, which Ford happened to sample. The abundant *Picea* pollen and anthers we recorded are usually produced in May.

Second, the samples of Heisler intestinal contents used by Kapp, Ford, and Rhodes et al. (1998) were selected early in the history of study of this site, when enough material remained to focus on the outer portion of the peripheral zone of plant debris (intestinal contents), avoiding material close to the sand and gravel that filled the interior of the "clastic anchor." By the time our sample was selected, it was difficult to collect enough mass for analysis while maintaining a safe distance from the clastic material, risking contamination of our sample by inclusion of introduced sediment—and pollen associated with it—that would have been acquired from a substrate just beyond the pond margin without having been ingested by the mastodon. Our sample might thus have included both material ingested by the mastodon and material introduced postmortem by humans during production of a "clastic anchor."

Third, although we have no direct or compelling evidence of coprophagy for mastodons comparable to evidence for woolly mammoths (van Geel et al., 2008, 2011a, 2011b), coprophagy would dramatically increase the potential for observing dietary heterogeneity by combining material ingested by multiple individuals, even during different parts of the year, in a single individual's intestine.

At present, we cannot rule out any of the three hypotheses described previously, but it is worth noting that they are not mutually exclusive. However, another problem is that our botanically based estimates of season of death for at least the Heisler mastodon (and probably the Burning Tree mastodon) differ from the estimates generated by tusk analysis. Tusk dentin accretes along the surface of a proximal pulp cavity throughout life and typically shows an annual cycle of variation in structure and composition that has been seasonally calibrated by finer-scale increment studies and stable isotope analyses (e.g., Fisher, 1987; Koch et al., 1989). The Heisler and Burning Tree mastodons have not been studied with the full range of techniques (e.g., multiple isotope systems and microscale computed tomography; e.g., Fisher et al., 2014) that have been used recently, but both of these specimens were originally reported to show autumn seasons of death (Fisher, 1987; Lepper et al., 1991).

CONCLUSIONS

The combined analysis of macrofossils and microfossils—including NPPs—provides a detailed reconstruction of the late-glacial environment of the Burning Tree and Heisler mastodon sites. Both were surrounded by mixed coniferous-deciduous forest with abundant *Picea*, mixed with more deciduous trees in Ohio than in Michigan. The pollen spectra and radiocarbon dates fit with the known regional vegetation history of the Great Lakes region. The mastodons lived for at least part of the year near lakes surrounded by marginal sedge fens. Both lakes had calcareous oligo-mesotrophic water, with many Mollusca in the Michigan site. Botanical evidence shows that the mastodons browsed on trees and shrubs, with a preference for *Picea*, eating leaves and twigs. They used the marginal sedge fen vegetation extensively (mainly sedges and grasses) as additional forage and drank the lake water. They consumed, probably unintentionally, spores of dung fungi and seeds and fruits of fen plants and aquatic plants such as *Potamogeton* spp. and *Najas* spp., algae, and invertebrates. Intestinal samples are biased by the food choice of the mastodons and by the short time interval they represent, whereas lake sediment samples indicate the composition of terrestrial and aquatic vegetation at the sites. The botanical evidence implies that the seasons of their last meals were late spring or summer, in contrast to tusk structural evidence that indicates their deaths in the autumn. Ascospores of coprophilous fungi and aquatic algae appeared to be important "differentiating taxa" for intestinal samples and sediments surrounding the mastodons.

The diets of mammoths have been relatively well documented from frozen remains in the Arctic. This study uniquely improves our understanding of the diets and the paleoecology of mastodons in North America compared to previous reports on this topic. Diets of two mastodons have been precisely reconstructed from multiproxy analyses of preserved intestinal contents, which provide direct and incontrovertible evidence of what the mastodons ate. They are compared to similar multiproxy analyses of the surrounding lake sediments that reflect the local terrestrial and aquatic vegetation of the mastodons' habitats and therefore the food plants available to them. They were herbivorous and seemed to select twigs and leaves, especially of *Picea*, as well as lakeshore sedges and grasses. The taxa identified in the analyses are presented as photographs, which will allow subsequent redetermination if necessary and will be an aid to future researchers in identifying their fossil specimens.

SUPPLEMENTARY MATERIALS

To view supplementary material for this article, please visit https://doi.org/10.1017/qua.2018.100

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