THE OHIO JOURNAL OF SCIENCE

Vol. 68 | NOVEMBER, 1968 | No. 6

EXTINCTION OF MASTODONS IN EASTERN NORTH AMERICA: TESTING A NEW CLIMATIC–ENVIRONMENTAL HYPOTHESIS[1, 2]

A. DREIMANIS

Department of Geology, University of Western Ontario

ABSTRACT

More than 600 late Wisconsin mastodon occurrences are known from the glaciated and periglacial portions of eastern North America. Most of of them have been found in poorly drained lowlands, swamps, and valleys, and on the continental shelf. Of the 28 radiocarbon-dated mastodon bones or associated wood from the entire area of eastern North America, 80 percent are 9,000–12,000 years old. Spruce forests or open woodlands have been indicated by palynologic investigations of 18 mastodon sites; wood or cones of spruce and trees associated with spruce forests have been found at ten sites.

This evidence and the distribution pattern of mastodons near the northern boundary of the area of their occurrences suggest that the mastodons of eastern North America were associated with open spruce woodlands or spruce forests. Their extinction was probably initiated by the rapidly increasing dryness 10,000–11,000 years ago, which caused first the retreat of the spruce forests into the moister lowlands and finally their disappearance from the area occupied by mastodons. A migration of mastodons from the relict spruce enclaves toward the more northerly located spruce forests was hampered because these two areas were probably separated by a rapidly expanding belt of pine and hardwood forests over the better-drained morainic, kame, and dune areas in the Great Lakes Region.

INTRODUCTION

The late Pleistocene extinction of mastodons (*Mastodon americanus* or *Mammut americanus*), like the extinction of other large mammals, has been and still is a puzzle. Martin (1958) states that "Most authors who have reviewed the problem reduce it to the outcome of an interaction of all factors that can limit animal populations—predation, competition, parasitism, climatic change, evolutionary lag during environmental stresses, and also the effect of man". Some, for instance Osborn (1942), Williams (1957), and particularly Martin (1958, 1968), emphasize the role of man, while others, e.g. Eiseley (1943), Skeels (1962), Drumm (1963), Russell (1965), Guilday (1968), and Hester (1968), blame it on climatic and ecologic changes, and Slaughter (1968) suggests "out of step" mating as the main cause for their extinction. While recognizing that multiple causes contributed to the extinction of mastodons, the author (Dreimanis, 1967a) proposed a new climatic and environmental hypothesis when discussing the occurences of mastodons in Ontario. The following opinions based upon local evidence were incorporated in this hypothesis: 1) the mastodons preferred open spruce woodlands or spruce forests; 2) their extinction was initiated by a reduction and disappearance of spruce forests due to a rapidly increasing dryness 10,000–11,000 years ago; 3) when their preferred habitat became considerably reduced, the mastodons could not find their way to the northern boreal spruce forests, being separated from them by a wide belt of pine and hardwood forests which meanwhile had developed over the better drained morainic areas of southern Ontario.

[1]This paper was presented at the 1967 Annual Meeting of the Geological Society of America, New Orleans (Dreimanis, 1967b), and is supplemented by new data, published after this meeting.

[2]Manuscript received April 2, 1968.

In order to test this hypothesis in a much larger area than southern Ontario, the eastern marginal zone of the North American continental glaciation, extending from the Great Lakes to the Atlantic shelf, was chosen for study, for the following reasons:

(1) This was an area in which mastodons were abundant during the last thousand years before their extinction, judging from the stratigraphic position of mastodon bones and the radiocarbon dates. Approximately 90 percent of all radiocarbon-dated mastodon sites of North America occur here (table 1).

(2) The Great Lakes region provides some of the most complete information on the environment around the mastodon sites, because plant remains, particularly pollen, have been investigated from 18 sites (table 4).

(3) All the information on food which was found in the rib cages or in the teeth of mastodons has also been derived from this region, particularly from New York state (table 2).

MAIN SOURCES OF INFORMATION

Reports on mastodon sites in the region extending from the Great Lakes to the Atlantic shelf are scattered through numerous publications. Many of the older references are not accessible to an average reader, and therefore mainly summary reports will be quoted here. The compilations by Baker (1920), Hartnagel and Bishop (1921), and Hay (1923 and 1924) contain an abundance of data published or gathered up to the 1920's, while information on newer occurrences and those overlooked by the above authors may be found particularly in the regional reports of Sternberg (1930 and 1963), MacAlpin (1940), Osborn (1942), Skeels (1962), Drumm (1963), Forsyth (1963), Russell (1965), Ogden (1965), Whitmore et al. (1967), and Dreimanis (1967a). There are also several discussions of individual sites, those by Robinson and Krynine (1938), Livingstone (1951), Williams (1957), Hatt (1963), Oltz and Kapp (1963), Stoutamire and Benninghoff (1964), Gooding and Ogden (1965), Wittry (1965), and Ray et al. (1967). The radiocarbon date lists (see table 1 for references) also contain new valuable information. Another summary report (Brown and Cleland, 1968) is in press.

DISTRIBUTION OF MASTODONS

When all the known late and postglacial mastodon occurrences are plotted on a map, they cluster in two main areas: 1) south of the Great Lakes, and 2) along the Atlantic Coast (fig. 1). It is realized that this map is only an approximation of the actual distribution of the mastodon remains, because of incomplete information on their occurrences due to various reasons. However most discoveries of mastodons have been reported by farmers from areas where digging of ditches and ponds has taken place. Therefore, if no finds have been reported from a large area of active farming, for instance southern Ontario, the boundary of the mastodon occurrences in this area must be reasonably correct.

Over 600 occurrences of postglacial mastodons have been reported from the glaciated area south of the Great Lakes, their greatest numbers being in southern Michigan (Skeels, 1962; Wittry, 1965), northern and central Indiana (Hay, 1923; and Wayne, personal communication), northern and central Ohio (Forsyth, 1963), southwestern Ontario (Dreimanis, 1967a), and northwestern New York state (Drumm, 1963). This region extends northwestward, though with decreasing abundance of mastodon sites, as far as southern Saskatchewan, according to Hay (1924) and Sternberg (1963). Most of the northwesterly occurrences (outside fig. 1) may be older than late-Wisconsin, judging from the stratigraphic position of the bones, which are found mainly in gravels.

In the Atlantic region, the greatest density of mastodon finds is in a lowland (Orange County, New York) surrounded by mountains. This lowland opens eastward to the Atlantic shelf, where several tens of mastodon teeth have been

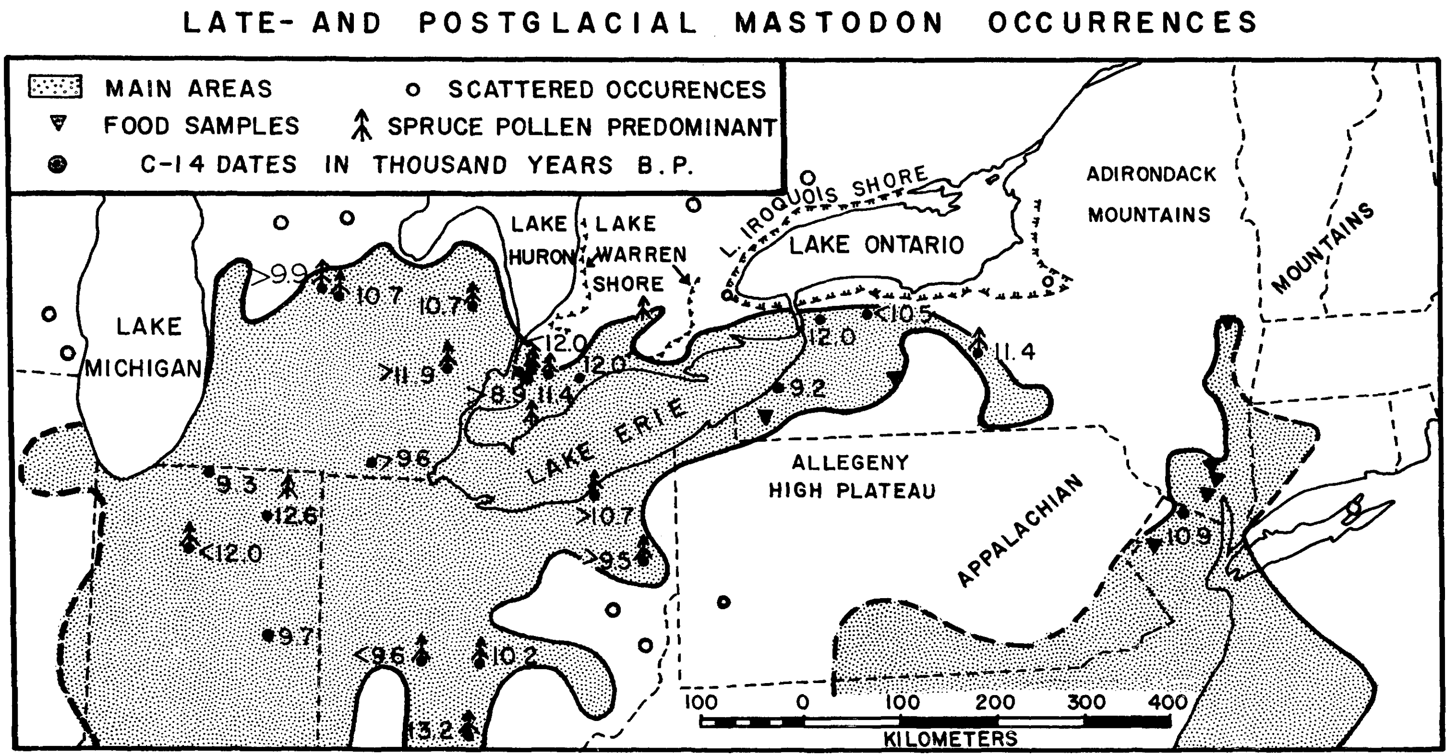

FIGURE 1. Late- and postglacial mastodon occurrences in that part of eastern North America where most information on their food, associated pollen, and radiocarbon dates is available. The dashed boundary line is based mainly upon Hay (1923), the solid boundary upon various more recent sources (see text).

found recently (Whitmore *et al.*, 1967). Part of the Atlantic shelf area of mastodon occurrences is outside of figure 1; it extends northeastward into Nova Scotia, where three finds have been reported on land (Livingstone, 1951).

The mastodon occurrences of the Great Lakes and of the Atlantic regions are separated by a belt of the Appalachian mountains and high plateaus where mastodon remains are rare. Only a few have been reported from scattered valleys in Massachusetts, Connecticut, New York state, New Jersey, Pennsylvania, and Virginia (Hay, 1923; Robinson and Krynine, 1939; Ray *et al.*, 1967).

Both main mastodon regions shown on figure 1 become connected farther to the south, and they continue so as far as the Gulf of Mexico and Florida. The farther south from the glaciated area, the more uncertain is the stratigraphic position of the mastodon remains: most of them appear to be older than late Wisconsin, judging from their descriptions (Hay, 1923 and 1924).

It is clear from figure 1 that the Great Lakes did not form a barrier to the northward expansion of mastodons. In southwestern Ontario, which is north of Lake Erie, their occurrences are as abundant as in the adjoining areas south of the lakes (crossing of Lake Erie basin has been discussed by Dreimanis, 1967a).

When the maps of the mastodon occurrences in Michigan (Skeels, 1962) and in Ontario (Dreimanis, 1967a) are super-imposed on the glacial map (Flint *et al.*, 1959), the northern boundary of the main mastodon areas coincides in many places with the southern border of some of the largest sandy areas. In general, mastodon occurrences are less abundant in sandy and gravelly kame, outwash, and dune areas. They are found mainly in lowlands, valleys, and swampy terrains. Lundelius (1968) has observed the same relationship in Texas. A better preservation of bones in organic sediments and possibly a greater concentration in stream deposits may be partly responsible for the greater abundance of mastodon finds in the above terrains. However the high resistance of mastodon teeth to weathering would preserve them reasonably well on higher ground, where they are also found.

Not all of the lowlands are rich in mastodon finds. Thus a striking difference exists between two adjoining lake basins—those of Lake Erie and Lake Ontario. In southwestern Ontario eighty percent of the mastodon occurrences are on the poorly drained Lake Warren plain of the Erie basin (Dreimanis, 1967a), which emerged more than 12,000 years B.P. (Dreimanis, 1964, Lewis *et al.*, 1966). To the east, in the Lake Ontario basin, mastodons are nearly absent from the Lake Iroquois plain, which emerged 1000–2000 years later (Karrow *et al.*, 1961; Terasmae's comment on the GSC–270 date, 10,390 ± 160 B.P., in Dyck *et al.*, 1966), while they are abundant on the adjoining older lake plains and moraines of northwestern New York (Drumm, 1963). The probable reason for this difference in mastodon abundance on the two lake plains will be discussed later.

The distribution pattern of the late Wisconsin mastodons throughout the once-glaciated area (fig. 1) leads to the following conclusions:

(1) In the same range of geographic latitude, near the northern boundary of their occurrences, mastodon remains are conspicuously less abundant in the well drained sandy areas, particularly on kames and dunes, and they are absent or very rare on mountainous terrain.

(2) Mastodon remains are nearly absent from a lake plain (Lake Iroquois) which emerged approximately 10,500 years B.P., but are abundant on an older lake plain (Lake Warren) which became a land habitat more than 12,000 years B.P.

RADIOCARBON DATES

At least twenty-eight late Wisconsin and post-glacial mastodon sites have been dated by the radiocarbon method in eastern North America, using either bones and tusks or plant remains closely associated with the bones (table 1). For various reasons, particularly contamination and sampling of material which was not contemporaneous with the bones, several of the youngest dates have been rejected as nonreliable (Hester, 1960; Skeels, 1962; Dreimanis, 1967a; and Martin, 1968). The remaining dates from twenty-six sites (fig. 2) range from approximately 15,000 to 9,000 years B.P.; more than three quarters of them are between 9,000 and 12,000 years B.P. A rapid decline is noticeable in the numbers of dated mastodons around 9,000 years B.P.

The bone collagen dates may be slightly too young due to contamination by humic acids (Haynes, 1968; Martin, 1968). If these dates are excluded, then the decline in the numbers of dated mastodon occurrences begins even earlier, at about 10,000 years B.P. (fig. 2).

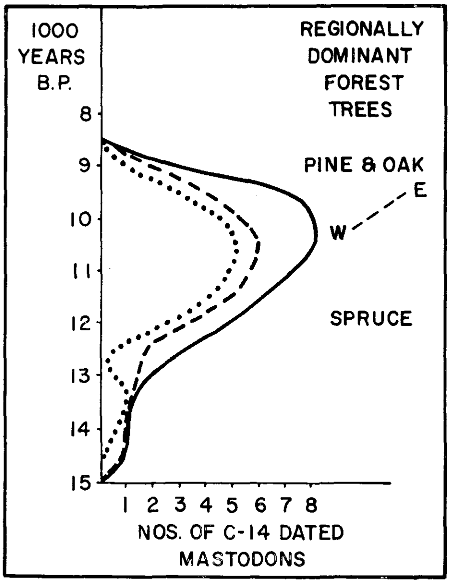

FIGURE 2. Frequency curves of the radiocarbon-dated mastodon sites of eastern North America: a) solid line—all dates from Table 1, b) dashed line—dates on plant remains, c) dotted line—dates on those sites where spruce pollen predominates (Table 4). For the drawing of these graphs, whenever the published dates of mastodon sites are interpreted as being older or younger than the most probable time when the mastodon died, the values of the published dates have been decreased or increased respectively for half a millennium. On the right side: the time of predominance of the major forest components, according to pollen data, and the approximate west-east (W–E) time-boundary for the change from the spruce to the pine dominance.

FOOD AND HABITAT OF MASTODONS

Though mastodons have been described as browsing inhabitants of boreal forests by Osborn (1942), Skeels (1962), Drumm (1963), Russell (1965), Wittry (1965), Dreimanis (1967a), and Martin and Guilday (1968), this conclusion is based mainly upon the nature of their teeth. The only quantitative investigations that have been done were on the pollen content of the sediments surrounding or underlying the bones; all other information is qualitative.

Stomach Contents

Plant remains have been found in large quantities in the rib cages of some

TABLE 1

Radiocarbon dates of postglacial mastodons, eastern North America

Location (Name of mastodon)	Material dated	Relationship of date to age of mastodon	Radiocarbon date (B.P.)	Laboratory code	Reference on radiocarbon date
Indiana:					
Cromwell, Noble Co.	Wood	Too young	*5,300±400	M–138	Crane, 1956
(Richmond Mastodon)	Tusk	Equivalent or minimum date	12,630±1000	M–139	Crane & Griffin, 1958
Elkhart, Elkhart Co.	Tusk	Equivalent or minimum date	9,320±400	M–694	Crane & Griffin, 1961
Muncie, Delaware Co.	Wood	±Equivalent	9,755±300	W–325	Rubin & Alexander, 1958
Wells Farm, Fulton Co. (Wells Mastodon)	Wood underneath bones	Maximum date	12,000±450	I–586	Trautman, 1963
Kentucky:					
Bigbone Lick	Wood	±Equivalent	10,600±250	W–1358	Levin *et al.*, 1965
Michigan:					
Clifford Twp.,	Peat	±Equivalent	10,739±400	M–1746	Crane & Griffin, 1968
Lapeer Co.	Mandibles	Too young	9,900±400	M–1778	Crane & Griffin, 1968
(Rappuhn Mastodon)	Wood	Equivalent	10,750±400	M–1780	Crane & Griffin, 1968
	Wood	Equivalent	10,750±400	M–1781	Crane & Griffin, 1968
	Wood	Equivalent	10,400±400	M–1782	Crane & Griffin, 1968
	Tusk	Too young	9,250±350	M–1783	Crane & Griffin, 1968
Emerson Twp., Gratiot Co. (Smith Mastodon)	Tooth	Equivalent or minimum date	10,700±400	M–1254	Crane & Griffin, 1965
Pontiac Twp., Oakland Co.	Plant remains in tusk socket	Minimum date	11,900±350	Texas Bionucl. 8013260000	Stoutamire and Benninghoff, 1964
Russell Farm, Lapeer Co.	Tusk	Too young	*5,950±300	M–347	Crane and Griffin, 1959
Seneca Twp.,	Tusk-inside	Too young	*7,070±240	M–280	Crane and Griffin 1958
Lenavee Co.	Tusk-outside	Too young	*7,820±450	M–281	
	Wood above bones	Minimum date	9,568±1000	M–282	Crane, 1956
Washtenaw Co.	Tusk, partly mineralised	Too young	*6,300±500	M–67	Crane, 1956
Serville Twp., Gratiot Co. (Thaller Mastodon)	Bones and tusk	Slightly younger	9,910±350	M–1739	Crane and Griffin, 1968
New Jersey:					
Highland Lakes area, Sussex Co.	Peat	±Equivalent	10,890±200	L–231	Broecker and Kulp, 1957

New York:					
Byron, Genesee Co.	Twigs underneath bone	Maximum date	10,450±400	W-1038	Ives *et al.*, 1964
Cheery Tavern, Erie Co.	Wood	±Equivalent	12,000±300	W-507	Rubin and Alexander, 1960
Kings Ferry, Cayuga Co.	Wood	±Equivalent	11,410±410	Y-460	Deevey *et al.*, 1959
Sheridan, Chautauqua Co.	Rib	±Equivalent or minimum date	9,200±500	M-490	Crane and Griffin, 1959
Ohio:					
Hallsville, Ross Co. (Pontius Farm Mastodon)	Wood	±Equivalent	13,180±520	OWU-220	Ogden and Hay, 1967
Johnstown, Licking Co.	Wood	±Equivalent	10,192±163	OWU-141	Ogden and Hay, 1967
New Chambersburg (Cole Mastodon)	Wood	Minimum date	9,460±305	OWU-194	Ogden and Hay, 1967
Novelty, Geauga Co.	Peat above bones	Minimum date	10,654±188	OWU-129	Ogden and Hay, 1965
Somerford Twp. Madison Co. (Orleton Farms Mastodon)	Wood underneath bones	Maximum date	9,600±500	M-66	Crane, 1956
Ontario:					
Rodney, Campbell farm	Wood	±Equivalent	11,400±450	S-29	McCallum and Dyck, 1960
	Vegetable muck	±Equivalent	12,000±500	S-30	McCallum and Dyck, 1960
Thamesville	Collagen of bones	±Equivalent or minimum date	11,380±170	GSC-611	Lowdon and Blake, 1968
Tupperville, Ferguson farm	Gyttja in skull cavities	Too young	*6,230±240	S-16	McCallum and Dyck, 1960
	Collagen of bones	Minimum date	8,910±150	GCS-614	Lowdon and Blake, 1968
Tupperville, Perry farm	Detrital plants underneath bones	Maximum date	12,000±200	S-172	McCallum and Wittenberg, 1965
	Plants underneath bones	Maximum date	11,800±170	GSC-211	Dyck *et al.*, 1966
Alabama:					
Demopolis Dam, Sumter Co.	Wood	±Equivalent	14,650±500	W-1571	Ives *et al.*, 1967
Louisiana:					
West Feliciana Parish	Wood	±Equivalent	12,740±300	W-944	Levin *et al.*, 1965

*These dates are considerably too young either because of contamination or due to dating of material which was much younger than the mastodon bones.

mastodon skeletons: for instance, seven bushels of plant material, which has been considered to be the stomach contents, was discovered at the Hackettstown, New Jersey, site (Hay, 1923). Small samples of plant remains have been investigated from seven mastodon sites (table 2:S). Four of the samples contained mostly twigs, in three cases identified as coniferous, in two as hemlock, in one as cedar, though the latter may be questioned (J. L. Forsyth, personal communication), because of the similarity between the wood of cedar and of spruce. Nonvascular plants are mentioned in three reports on stomach contents, leaves in two. However, these are only random identifications, without any quantitative data, and all of them are from relatively southerly locations within the entire region under discussion.

TABLE 2

Food of Mastodons

Location (Name of mastodon)	M: food, recovered from the mouth S: stomach content, found in the rib cage	Reference
New Jersey:		
Hackettstown, Warren Co.	S: wood of hemlock and cedar	Hay, 1923
New York:		
Chester, Orange Co.	S: coarse vegetable stems and films	Hartnagel and Bishop, 1921
Cohoes, Albany Co.	M: twigs of larch	Hartnagel and Bishop, 1921
Jamestown, Chautauqua Co.	S: twigs of cone-bearing trees	Hay, 1923
Newburgh, Orange Co., (Warren Mastodon)	S: terminal branches of coniferous trees, later identified as hemlock, and finely divided leaves	Drum, 1963
Temple Hill, Orange Co.	S: broken twigs and plant remains	Hartnagel, 1921
Wayland, Steuben Co.	S: swamp plants and mosses	Hartnagel, 1921
Ohio:		
New Cambersburg (Cole Mastodon)	M: resins and tars with high pollen percentage of spruce, some pine, grass, and composites	Ogden and Hay, 1967
Virginia:		
Wythe Co.	S: reeds, twigs, and grass or leaves	Hay, 1923

Mouth

Examination of material adhering to teeth collected at two sites (table 2:M) has produced larch twigs, and resins and tars.

Plant Remains Associated with Mastodon Bones

Wood and other macroscopic plant remains have been found associated with mastodon bones in many places, but they have been identified from only ten sites (table 3). Remains of spruce were recovered from all ten sites, accompanied by tamarack in two, and cedar (possibly spruce ?) and willow from one site each.

While the macroscopic remains belonged to the local vegetation of the places where the mastodons died, the associated pollen grains must have come from the entire surrounding area. Pollen has been investigated from 18 sites (table 4). Spruce pollen predominates in sixteen sites. Pine dominates in two, but, because of overproduction of the pine pollen, spruce was probably the main tree present, even in these cases. Peat dredged from the Atlantic continental shelf where several mastodon teeth have been found (Whitmore, et al., 1967) contains mainly spruce pollen (Emery *et al.*, 1965); it has been dated at 11,000 ± 350 years B.P. (W-1491).

All of the above pollen assemblages also contain various amounts of pine (jack pine, where the species has been identified), and in most of them also are minor quantities of oak, fir, larch, alder, and willow. The nonarboreal pollen, mainly Cyperaceae and Compositae, varies from one to eighty-five percent of the arboreal pollen. Most authors who have interpreted the pollen data from the mastodon sites, or from their vicinity, have concluded that open spruce woodlands or spruce forests formed the dominant vegetation in the surrounding area (Sears and Clisby, 1952; Cox, 1959; Oltz and Kapp, 1963; Stoutamire and Benninghoff, 1964; Emery *et al.*, 1965; Gooding and Ogden, 1965; Ogden, 1965; Ogden and Hay, 1965 and 1967; Cleland, 1966; Dreimanis, 1967a).

TABLE 3

Macroscopic plant remains, associated with mastodon bones (outside their mouths and rib cages)

Location (Name of mastodon)	Plant remains	Reference
Michigan:		
Alma, Gratiot Co.	Fruits of tamarack and black spruce	Hay, 1923
*Burlington Twp., Lapeer Co. (Rappuhn Mastodon)	Spruce cones	Wittry, 1965
*Emerson Twp., Gratiot Co. (Smith Mastodon)	Spruce wood and needles; seeds, particularly of *Potamogeton*	Oltz and Kapp, 1963
*Pontiac Twp., Oakland Co. (Pontiac Mastodon)	Wood and twigs of white spruce, willow and tamarack	Hatt, 1963
New York:		
*Cheery Tavern, Erie Co.	Cones, spruce wood	Muller, 1965
East Coldenham, Orange Co.	Wood of red cedar and spruce (underneath the mastodon bones)	Hay, 1923
New Dorp, Richmond Co.	Cones of white spruce	Hay, 1923
Ohio:		
*Hallsville, Ross Co. (Pontius Farm Mastodon)	Spruce wood	Ogden and Hay, 1967
*Johnstown, Licking Co.	Spruce wood	Ogden and Hay, 1967
*New Chambersburg (Cole Mastodon)	Spruce wood	Ogden and Hay, 1967

*Radiocarbon dates of these mastodons are in table 1.

A comparison with present-day forests suggests that distribution of the trees recorded from each pollen site was probably heterogeneous, depending upon soil and drainage conditions, insolation, and other factors. Black spruce, for instance, prefers moist lowlands, while white spruce, jack pine, and many species of oak grow better on well drained higher ground or slopes. This differentiation probably had already begun in late Wisconsin time, but it became more pronounced as the climate became drier and the summers warmer. The spruce-fir forests retreated into the lowlands and depressions, while the pine and later the pine-hardwoods forests spread over the moraines, kames, and dunes (see also Cleland, 1966).

Thirteen of the palynologically investigated mastodon sites have been dated by the radiocarbon method (tables 1 and 4, figs. 1 and 2). Of these 13 sites, at least eight are older than 10.5 thousand years B.P. According to the current interpretation of palynologic records, spruce was the dominant tree everywhere in the Great Lakes region at that time (Cox, 1959; Davis, 1967; Terasmae, 1961; Ogden, 1965 and 1967; Cushing, 1965; Cleland, 1966). Four of the mastodon sites, where spruce pollen predominated, are dated younger than 10.5 thousand years. If the bone dates are not considered, because of the possible contamination of the collagen by younger humus acids, two sites remain where the radiocarbon dates are on wood. In one of them (Johnstown, Ohio) the mastodon has been dated slightly younger than 10.5 thousand years B.P. (OWU–141: 10, 192±163), but at the other, (Orleton Farms, Ohio) the bones were above wood dated 9,600± 500 years old (M–66). If these two dates are correct, then they suggest persistence of spruce forest enclaves in poorly drained areas, surrounded by pine and hardwoods on better drained terrain.

TABLE 4

Pollen, associated with mastodon bones

Location (Name of mastodon)	Principal pollen in decreasing order of abundance (nonarboreal pollen listed only, if abundant)	Reference
Indiana:		
*Wells Farm, Fulton Co.	Spruce; oak, fir, willow, larch, sedge, grass	Gooding and Ogden, 1965
Michigan:		
*Clifford Twp., Lapeer Co. (Rappuhn Mastodon)	Spruce-fir forest	Crane and Griffin, 1968
*Emerson Twp., Gratiot Co. (Smith Mastodon)	Spruce; pine, oak	Oltz and Kapp, 1963
Pitt Farm, Gratiot Co.	Pine; spruce, oak	Oltz and Kapp, 1963
Pontiac Twp., Oakland Co.	Spruce and nonarboreal pollen; oak, pine	Stoutamire and Benninghoff, 1964
*Serville Twp., Gratiot Co. (Thaller Mastodon)	Spruce pollen zone	Crane and Griffin, 1968
Ohio:		
*Hallsville, Ross Co. (Pontius Farm Mastodon)	Spruce; pine, fir, larch	Ogden and Hay, 1967
*Johnstown, Licking Co.	Spruce, pine, sedge, grass	Ogden and Hay, 1967
*New Chambersburg (Cole Mastodon)	Spruce; fir, pine, birch	Ogden and Hay, 1967
*Novelty, Geauga Co.	Spruce; pine, fir, sedge, grass	Ogden and Hay, 1965
*Somerford Twp., Madison Co. (Orleton Farms Mastodon)	Spruce; pine, grass, fir, oak	Sears and Clisby, 1952
Ontario:		
Harwich Twp.: Toll farm	Spruce; pine, oak, nonarboreal	Dreimanis, 1967
Ingersoll: Bond farm	Spruce; sedge, composites, oak	Dreimanis, 1967
*Thamesville	Spruce	Dreimanis, 1967
*Tupperville: Ferguson farm	Spruce; oak, pine, elm, fir	Dreimanis, 1967
*Tupperville, Perry farm	Spruce; nonarboreal	Dreimanis, 1967
New York:		
*King Ferry, Cayuga Co.	Spruce; pine	Cox, 1959
Virginia:		
Saltville	Pine, spruce; nonarboreal, fir, oak	Ray et al., 1967

*Radiocarbon dates of these mastodons are in table 4.

As all the microscopic plant remains and most of the wood associated with the mastodons indicate the presence of spruce woodlands or forests around them, these were most probably their preferred habitats. Absence of mastodon remains from areas which lack spruce, for instance the Lake Iroquois plain (see further), strengthens this conclusion. Martin and Guilday (1968), however, state that mastodons were not confined to coniferous-forest habitats in the more southerly areas, for instance in central Florida. Unfortunately, there are no published pollen analyses from any of the southern mastodon sites which may indicate the types of plants associated with them.

The information on the food remains is still too meagre to permit drawing definite conclusions on the food preferred by the mastodons, except for the widely accepted concept that they were browsers. Even if mastodons lived in spruce forests, the spruce branches were not necessarily their main food. They may have preferred other plants growing in spruce forests.

CHANGE FROM SPRUCE TO PINE DOMINANCE

Approximately 10,000 to 11,000 years ago, an abrupt change is recorded in pollen diagrams from that part of the Great Lakes Region where the mastodons lived and in the southeastern corner of New York state: the spruce-dominated pollen assemblages gave way to high-pine maxima (Cox, 1959; Cushing, 1965; Gooding and Ogden, 1965; Ogden, 1965 and 1967; Gilliam *et al.*, 1966; J. Terasmae's comment on the GSC–270 date in Dyck *et al.*, 1966; Sirkin, 1967). In New England this event occurred during the following millenium (Davis, 1965 and 1967). The change in pollen content coincided with stratigraphic indications of drier climate, for instance the deposition of wind-blown sand over lake marl at the Wells mastodon site, Indiana (Gooding and Ogden, 1965). At the Ferguson site near Tupperville, Ontario, lacustrine marl, rich in spruce pollen, had dried out some time prior to 8,910±150 years B.P. (GSC–614). All the widespread and consistent palynologic and geologic evidence suggests that the period of dominance of pine pollen represents an increase in dryness and probably also warmer summers (Cox, 1959). An abrupt change in climate approximately 11,000 years ago has also been considered as a result of the investigations of deep-ocean cores (Broecker *et al.*, 1960) and from pollen analyses elsewhere, e.g. in Minnesota (Wright, 1964) and in Texas and New Mexico (Hester, 1968).

In the Lake Ontario basin, the change from spruce to pine dominance coincides with the end of Lake Iroquois (J. Terasmae's comment on the GSC–270 date in Dyck *et al.*, 1966). In the Lake Ontario basin, pine pollen grains dominate in the first organic sediments which were deposited after the lake level had dropped for more than 300 feet. This pollen evidence is given by Karrow *et al.* (1961) for Burlington, Ontario, and by Cox (1959) for Perch Lake, N. Y., at the other end of Lake Ontario. One of the Burlington plant assemblages is dated at 10,150±450 years B.P. (TB–50) (Karrow *et al.*, 1961). The low content or even absence of spruce in pollen sites on the exposed Lake Iroquois bottom, after it had been drained, may be the reason why mastodons did not enter this lake plain (page 260 and 266); if they preferred spruce forests or woodlands, they would not have been attracted to an area devoid of this habitat. However, the topographically similar Warren and other older lake plains, which had emerged much earlier, during the dominance of spruce, were their preferred habitats (Dreimanis, 1967a; also p. 260 of this paper).

EXTINCTION OF MASTODONS

If mastodons preferred spruce forests or woodlands and avoided pine-hardwoods forests, then the rapid reduction of the spruce forests throughout the areas inhabited by mastodons became critical for them. Spruce is more tolerant to poorer drainage than are pine and oak, so the spruce forests persisted longer in swamps and lowlands, thus providing mastodons with scattered refuges. However, these refuges turned eventually into traps, as they became smaller due to increasing dryness, while the surrounding pine-hardwoods forests spread out and became more extensive.

The extinction of mastodons began, according to Dreimanis (1967), at this time, when the spruce forests were gradually disappearing in the area where they lived, and from which the mastodons could not find a way to the northern boreal spruce forests. It is still unknown how extensive were the spruce forests in the north about 10,000 years B.P., as the pollen diagrams from the area immediately north of Lake Huron and Lake Superior are truncated at their base and begin only about 9000 years B.P. (Terasmae, 1968). It is possible that the northward spread of the boreal spruce forests was also hampered by the dryness of climate.

Whether the northern spruce forests were extensive or not, the mastodons were probably separated from them by a wide belt of pine and hardwood forests which meanwhile had developed over the better drained morainic, kame, and dune areas along the northern boundary of the region occupied by the mastodons. The small number of available radiocarbon-dated palynologic investigations in north-central Michigan, central Ontario, and the northern end of the Hudson River valley makes it difficult to test the rate and time of expansion of the pine-hardwoods forest in these areas which could have served as the escape routes for the mastodons. J. Terasmae's pollen diagram from the Galt moraine, near Galt, Ontario (Karrow, 1963), is from a place which is a short distance north of the boundary of the mastodon occurrences. In this diagram the decrease in spruce and increase in jack pine had already begun a few centuries after 11,950 ± 350 years B.P. (TB 59–69), that is, earlier than in the Lake Erie lowlands to the south (Lewis *et al.*, 1966). The Smith mastodon site in Gratiot Co., Michigan, is also near the northern boundary of the mastodon occurrences in Michigan. Here the change from spruce to pine pollen dominance is above that level which has been correlated with the 10,700 ± 400-year-old (M–1254) mastodon (Oltz and Kapp, 1963). Pine pollen grains are abundant (about 30 percent) for some distance below this level, accompanied by more than ten percent hardwoods. In Consaulus Bog, in central New York state, near the northernmost boundary of mastodon occurrences in the Hudson River valley, Cox (1959) has noted a high abundance of pine pollen (30–46 percent) during the spruce maximum (45–55 percent); apparently pines were present even at that time in the surrounding area. No radiocarbon date is available from this site.

The above data from the northern boundary of the mastodon areas suggest that pines and hardwoods were already present or even relatively abundant throughout this area during the spruce maximum. Therefore, the increasing dryness which initiated the rapid expansion of pine and hardwoods farther south must have been equally effective immediately north of the region where mastodons were found, particularly because of the extensive well drained morainic, kame, and sandy areas.

During the culmination of the dry, pine episode, the spruce forests disappeared from the areas occupied by mastodons, probably with the exception of a few small relict areas (for pollen data, see Cox, 1959; Kapp and Gooding, 1964; Gooding and Ogden, 1965; Ogden, 1965 and 1967). This period of dominance of pine became very critical for mastodons. They were probably weakened by the new unaccustomed or unsuitable food. The scattering of the mastodons into the few remaining disjunct spruce forests may have also favored inbreeding and made them more sensitive to diseases. The rapid decline in the numbers of mastodons radiocarbon-dated at 9,000 to 10,000 years B.P. (fig. 2) suggests that, by this time, they had reached that critically low level of population at which any adverse factors might have led to their extinction.

One of these contributing factors may have been the Palaeo-Indians who were probably present in the Great Lakes region at this time (Mason, 1958; Griffin, 1961; Cleland, 1966), and had migrated northeastward as far as Nova Scotia (MacDonald, 1968). According to Wittry (1965), the Rappuhn mastodon in Michigan was probably butchered by humans. Less certain evidence for human association is a possible skinning tool found with a mastodon at the Ferguson farm site at Tupperville, Ontario (Dreimanis, 1961). Williams (1957) discusses various other possible, though not clearly proven associations of man and mastodon outside this area of investigation, and Irvin-Williams (1968) reports evidence for hunting of mastodons at Hueyatlaco in Mexico. The amount of evidence supporting mastodon hunting is still meagre, and Griffin (1968) even doubts that the Palaeo-Indians of the Great Lakes Region hunted mastodons.

SUMMARY

The author's (Dreimanis, 1967a) climatic and environmental hypothesis concerning the extinction of the mastodon has been tested by reviewing the available data on over six hundred mastodon sites from the glaciated region of eastern North America. Radiocarbon dates have been assembled from 28 mastodon sites, palynologic data from 18, information on the food remains in rib cages and on teeth from nine, and associated macroscopic plant remains from ten. From all this information, together with additional palynologic and geologic data, the following inferences are made:

1) Mastodons preferred open spruce woodlands or spruce forests.
2) Their decrease in abundance was preceded by a reduction and disappearance of spruce forests due to a rapidly increasing dryness 10,000 to 11,000 years ago in the Great Lakes region, and probably slightly later farther east.
3) The northward migration of mastodons toward the more northerly located spruce forests was hampered by development of a wide belt of pine and hardwoods forests over the better drained areas of north-central Michigan, central Ontario, and central New York state at the time of the reductions of the spruce forests farther south. This third inference still requires more support from radiocarbon-dated palynologic investigations there. However, the presently available palynologic and geologic information does not contradict this hypothesis.

ACKNOWLEDGMENTS

The author is grateful for the information given, by J. L. Forsyth on the Ohio mastodons, by W. J. Wayne on the Indiana mastodons, and by W. Wittry on several Michigan mastodons.

REFERENCES

Baker, F. C. 1920. Life of the Pleistocene or glacial period as recorded in the deposits laid down by the great ice sheets. Univ. Illin. Bull. 17: 476 p.

Broecker, W. S., and **J. L. Kulp.** 1957. Lamont natural radiocarbon measurements IV. Science 126: 908–919.

———, **M. Ewing,** and **B. J. Heezen.** 1960. Evidence for an abrupt change in climate close to 11,000 years ago. Am. J. Sci. 258: 429–48.

Brown, J., and **C. Cleland.** 1968. The Late-glacial and early Postglacial faunal resources in Midwestern biomes newly opened to human adaptation; paper presented at the symposium "Quaternary of Illinois", Urbana, Ill. (in press).

Cleland, C. D. 1966. The prehistoric animal ecology and ethnozoology of the upper Great Lakes region. Mus. Anthropol. Univ. Michigan, Anthropol. Papers 29. 294 p.

Cox, D. D. 1959. Some postglacial forests in central and eastern New York State as determined by the method of pollen analysis. N. Y. State Mus. Bull. 377. 52 p.

Crane, H. R. 1956. University of Michigan radiocarbon dates. I. Science 124: 664–672.

———, and **J. B. Griffin.** 1958. University of Michigan radiocarbon dates II. Science 127: 1098–1105.

———, and ———. 1959. University of Michigan radiocarbon dates IV. Am. J. Sci. Radiocarb. Suppl. 1: 173–198.

———, **and** ———. 1961. University of Michigan radiocarbon dates VI. Radiocarbon 3: 105–125.

———, **and** ———. 1965. University of Michigan radiocarbon dates X. Radiocarbon 7: 123–152.

———, **and** ———. 1968. University of Michigan radiocarbon dates XII. Radiocarbon 10: 61–114.

Cushing, E. J. 1965. Problems in the Quaternary phytogeography of the Great Lakes region, in H. E. Wright, Jr. and D. G. Frey (ed.). The Quaternary of the United States, Princeton Univ. Press. 403–416.

Davis, M. B. 1965. Phytogeography and palynology of northeastern United States, in H. E. Wright, Jr. and D. G. Frey (ed.). The Quaternary of the United States, Princeton Univ. Press. 377–402.
———. 1967. Late-glacial climate in northern United States: a comparison of New England and the Great Lakes region, in E. J. Cushing and H. E. Wright, Jr. (ed.). Quaternary Paleoecology. 11–43.
Deevey, E. S., and **R. F. Flint.** 1957. Postglacial hypsithermal interval. Science 125: 182–184.
———, **L. J. Gralenski,** and **V. Hoffren.** 1959. Yale natural radiocarbon measurements IV. Am. J. Sci. Radiocarb. suppl. 1: 144–172.
Dreimanis, A. 1961. Solving the jigsaw puzzle of the Tupperville Mastodon's life. Globe and Mail, Dec. 6: 7.
———. 1964. Lake Warren and the Two Creeks interval. J. Geol. 72: 247–250.
———. 1967a. Mastodons, their geologic age and extinction in Ontario, Canada. Can. J. Earth Sci. 4: 663–675.
———. 1967b. Extinction of mastodons in eastern North America: a new climatic-environmental theory (abstract). Program, 1967 Annual Meeting of the Geological Society of America, New Orleans: 51–52.
Drumm, J. 1963. Mammoths and mastodons, Ice age elephants of New York. Univ. State New York, State Educ. Dept., State Mus. and Sci. Service. Educ. Leaflet 13. 31 p.
Dyck, W., J. A. Lowdon, J. G. Fyles, and **W. Blake, Jr.** 1966. Geolgocial Survey of Canada radiocarbon dates V. Radiocarbon 8: 96–127.
Eiseley, L. 1943. Archaeological observations on the problem of post glacial extinction. Am. Antiquity 8: 209–217.
Emery, K. O., R. L. Wigley, and **M. Rubin.** 1965. A submerged peat deposit off the Atlantic coast of the United States. Limnology and Oceanography 10., Supplement: R97–R102.
Flint, R. F., R. B. Colton, R. P. Goldthwait, H. B. Willman (ed.). 1959. Glacial map of the United States east of the Rocky Mountains. Geol. Soc. Am.
Forsyth, J. L. 1963. Ice age census. Ohio Conservation Bull. 27, No. 9. 16–19, 31.
Gilliam, J. A., R. O. Kapp, and **R. D. Bogue.** 1967. A Post-Wisconsin pollen sequence from Vestaburg bog, Montcalm County, Michigan. Michigan Acad. Sci., Arts, and Letters, Papers 52. 3–17.
Gooding, A. M., and **J. G. Ogden, III.** 1965. A radiocarbon-dated pollen sequence from the Wells mastodon site near Rochester, Indiana. Ohio J. Sci. 65: 1–11.
Griffin, J. B. 1961. Post-glacial ecology and culture changes in the Great Lakes area of North America. Great Lakes Res. Div., Inst. Sci. and Tech., Univ. Michigan. Publ. 7: 147–155.
———. 1968. The proper study of prehistoric man, paper presented at the symposium "Quaternary of Illinois", Urbana, Ill. (in press).
Guilday, J. E. 1968. Differential extinction during Late-Pleistocene and Recent times, in P. S. Martin and H. E. Wright, Jr. (ed), Pleistocene extinctions: 121–140.
Hartnagel, C. A., and **S. C. Bishop.** 1921. The mastodon, mammoths and other Plestocene mammals of New York State. N. Y. State Mus. Bull. 241 and 242. 110 p.
Hatt, R. T. 1963. The mastodon of Pontiac. Cranbrook Inst. Sci. News Letter 32: 62–64.
Hay, O. P. 1923. The Pleistocene of North America and its vertebrated animals from the States east of the Mississippi River and from the Canadian provinces east of longitude 95°. Carnegie Inst. Wash. Publ. 322. 499 p.
———. 1924. The Pleistocene of the middle region of North America and its vertebrated animals. Carnegie Inst. Wash. Publ. 322a. 385 p.
Haynes, C. V., Jr. 1968. Carbon-14 dates and early man in the New World, in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 267–286.
Hester, J. J. 1960. Late Pleistocene extinctions. Am. Antiquity 26: 58–87.
———. 1968. The agency of man in animal extinction in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 169–192.
Irwin-Williams, C. 1968. Association of early man with horse, camel, and mastodon at Hueyatlaco, Valsequillo (Pueblo, Mexico), in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 337–348.
Ives, P. C., B. Levin, R. D. Robinson, and **M. Rubin.** 1964. U. S. Geological Survey radiocarbon dates VII. Radiocarbon 6: 37–76.
———, ———, **C. L. Oman,** and **M. Rubin.** 1967. U. S. Geological Survey radiocarbon dates IX. Radiocarbon 9: 505–529.
Kapp, R. O., and **A. M. Gooding.** 1964. A radiocarbon-dated pollen profile from Sunbeam Prairie bog, Darke County, Ohio. Am. J. Sci. 262: 259–266.
Karrow, P. F. 1963. Pleistocene geology of the Hamilton-Galt area. Ont. Dept. Mines, Geol. Rept. 16. 68 p.
———, **J. R. Clark,** and **J. Terasmae.** 1961. The age of Lake Iroquois and Lake Ontario. J. Geol. 69: 659–667.
Levin, B., P. C. Ives, C. L. Oman, and **M. Rubin.** 1965. U. S. Geological Survey radiocarbon dates VIII. Radiocarbon 7: 372–398.

Lewis, C. F. M., T. W. Anderson, and **A. A. Berti.** 1966. Geological and palynological studies of Early Lake Erie deposits. Great Lakes Res. Div., Inst. Sci. and Tech., Univ. Michigan, Publ. 15: 176–191.

Livingstone, D. 1951. A new record for the mastodon, *Mastodon americanus* Kerr, from Nova Scotia. Proc. Nova Scotia Inst. Sci. 22: 15–16.

Lowdon, J. A., and **W. Blake, Jr.** 1968. Geological Survey of Canada radiocarbon dates VII. Radiocarbon 10-2: 207–245.

Lundelius, E. L., Jr. 1968. Late-Pleistocene and Holocene faunal history of central Texas, in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 287–320.

Martin, P. S. 1958. Pleistocene ecology and biogeography of North America, in C. L. Hubbs (ed.), Zoogeography. Am. Assoc. Adv. Sci. Publ. 51: 375–420.

———. 1968. Prehistoric overkill, in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 75–120.

———, and **J. E. Guilday.** 1968. A bestiary for Pleistocene biologists, in P. S. Martin and H. E. Wright, (ed.), Pleistocene extinctions: 1–62.

Mason, R. J. 1958. Late Pleistocene geochronology and the Paleo-Indian penetration into the Lower Michigan Peninsula, Mus. Anthropol. Univ. Michigan, Anthropol. Papers II. 48 p.

Muller, E. H. 1963. Geology of Chautauqua County, New York. Pt. II, Pleistocene geology. New York State Mus. Bull. 392. 60 p.

MacAlpin, A. 1940. A census of mastodon remains in Michigan. Michigan Acad. Sci., Arts and Letters, Papers 25: 481–490.

MacDonald, G. F. 1968. Debert: a Paleo-Indian site in central Nova Scotia. Natl. Mus. Canada, Anthropol. Papers 16. 158 p.

McCallum, K. J., and **W. Dyck.** 1960. University of Saskatchewan radiocarbon dates II. Am. J. Sci. Radiocarbon Supp. 2: 73–81.

———, and **J. Wittenberg.** 1965. University of Saskatchewan radiocarbon dates IV. Radiocarbon 7: 229–235.

Ogden, J. G., III. 1965. Pleistocene pollen records from eastern North America. Botan. Rev. 31: 481–504.

———. 1967. Radiocarbon and pollen evidence for a sudden change in climate in the Great Lakes region approximately 10,000 years ago, in E. J. Cushing and H. E. Wright, Jr., (ed.), Quaternary paleoecology: 117–127.

———, and **R. J. Hay.** 1965. Ohio Wesleyan University natural radiocarbon measurements II. Radiocarbon 7: 166–173.

———, and ———. 1967. Ohio Wesleyan University radiocarbon measurements III. Radiocarbon 9: 316–332.

Oltz, D. F., and **R. O. Kapp.** 1963. Plant remains associated with mastodon and mammoth remains in central Michigan. Am. Midland Naturalist 70: 339–346.

Osborn, H. F. 1942. Proboscidea: a monograph of the discovery, evolution, migration an extinction of mastodons and elephants of the world. Am. Museum Press, New York, N. Y., 2 vol. 1675 p.

Ray, C. E., B. N. Cooper, and **W. S. Benninghoff.** 1967. Fossil mammals and pollen in a late Pleistocene deposit at Saltville, Virginia. J. Paleont. 41: 608–622.

Robinson, C. W., and **P. D. Krynine.** 1938. A new mastodon locality at Saltillo, Huntington County, Pa. Proc. Penna. Acad. Sci. 12: 93–96.

Rubin, M., and **C. Alexander.** 1958. U. S. Geological Survey radiocarbon dates IV. Science 127: 1476–1487.

———, and ———. 1960. U. S. Geological Survey radiocarbon dates V. Am. J. Science Radioc. Supp. 2: 129–185.

Russell, L. S. 1965. The mastodon. Roy. Ont. Museum Ser. 6. 16 p.

Sears, P. B., and **K. H. Clisby.** 1952. Pollen spectra associated with the Orleton Farms mastodon site. Ohio J. Sci. 52: 9–10.

Sirkin, L. A. 1967. Late-Pleistocene pollen stratigraphy of western Long Island and eastern Staten Island, New York, in E. J. Cushing and H. E. Wright, Jr. (ed.), Quaternary paleoecology: 249–274.

Skeels, M. A. 1962. The mastodons and mammoths of Michigan. Michigan Acad. Sci., Arts and Letters, Papers 47: 59–65.

Slaughter, B. H. 1968. Animal ranges as a clue to Late-Pleistocene extinction, in P. S. Martin and H. E. Wright, Jr. (ed.), Pleistocene extinctions: 155–168.

Sternberg, C. M. 1930. New records of mastodons and mammoths in Canada. Can. Field-Naturalist 44: 59–65.

———. 1963. Additional records of mastodons and mammoths in Canada. Natl. Mus. Can. Nat. Hist. Papers 19. 11 p.

Stoutamire, W. P., and **W. S. Benninghoff.** 1964. Biotic assemblage associated with a mastodon skull from Oakland County, Michigan. Michigan Acad. Sci., Arts and Letters, Papers 49: 47–60.

Terasmae, J. 1961. Notes on the late-Quaternary climatic changes in Canada. Annals, New York Acad. Sci. 95: 658–675.

———. 1968. Postglacial chronology and forest history in the northern Lake Huron and Lake Superior regions, in E. J. Cushing and H. E. Wright, Jr., Quaternary paleoecology: 45–58.

Trautman, M. A. 1963. Isotopes, Inc. radiocarbon measurements III, Radiocarbon 5: 62–79.

Whitmore, F. C., Jr., K. O. Emery, H. B. S. Cooke, and **D. J. P. Swift.** 1967. Elephant teeth from the Atlantic continental shelf. Science 156: 1477–1481.

Williams, S. 1957. The island 35 mastodon: its bearing on the age of Archaic cultures in the East. Am. Antiquity 22: 359–372.

Wittry, W. 1965. The institute digs a mastodon. Cranbrook Inst. Sci. News Letter 35: 14–19.

Wright, H. E., Jr. 1964. Aspects of the early postglacial forest succession in the Great Lakes region. Ecology 45: 439–448.