# LANDSCAPE PALEOECOLOGY AND MEGAFAUNAL EXTINCTION IN SOUTHEASTERN NEW YORK STATE

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*Abstract.* Stratigraphic palynological analyses of four late Quaternary deposits comprise a landscape-level study of the patterns and processes of megafaunal extinction in southeastern New York State. Distinctive spores of the dung fungus *Sporormiella* are used as a proxy for megafaunal biomass, and charcoal particle analysis as a proxy for fire history. A decline in spore values at all sites is closely followed by a stratigraphic charcoal rise. It is inferred that the regional collapse of a megaherbivory regime was followed by landscape transformation by humans. Correlation with the pollen stratigraphy indicates these developments began many centuries in advance of the Younger Dryas climatic reversal at the end of the Pleistocene. However, throughout the region, the latest bone collagen dates for *Mammut* are considerably later, suggesting that megaherbivores lasted until the beginning of the Younger Dryas, well after initial population collapse. This evidence is consistent with the interpretation that rapid overkill on the part of humans initiated the extinction process. Landscape transformation and climate change then may have contributed to a cascade of effects that culminated in the demise of all the largest members of North America's mammal fauna.

*Key words: dung fungi; extinctions; fire history; human impacts; mastodons; megafauna; microscopic charcoal; paleoecology; palynology; pollen;* Sporormiella; *Younger Dryas.*

## INTRODUCTION

Disagreement prevails over what drove the late Pleistocene extinctions in North America (Martin and Steadman 1999, Grayson and Meltzer 2003). In spite of clear associations between an expanding paleolithic (Clovis) culture and the extinct mammal fauna, more conclusive evidence for overkill is lacking. Although the geochemical record indicates that both developments coincide with rapid climate swings, particularly in the North Atlantic at ca. 11 000 radiocarbon years before present ($^{14}$C yr BP) (Alley et al. 2003), the order of events has been blurred by fluctuating levels of atmospheric $^{14}$C. The latter resulted in ''plateaus'' and ''cliffs'' in the radiocarbon calibration curve (Fiedel 1999).

However, the North American episode is but one of several pulses of extinction worldwide, first taking large vertebrates (megafauna) on continental landmasses late in the Pleistocene and proceeding with island losses for the next 10 millennia. This later phase encompasses historic time, now affecting medium and small vertebrates. Each of these episodes of extinction has occurred in step with initial dispersal of anatomically modern humans out of Africa (Martin and Steadman 1999).

Absolute dates at least broadly constrain the above North American timeline, which may be resolved by analyzing microfossil stratigraphies at a landscape level. On a local scale, rates and geographic patterns of faunal extirpation and cultural activity then can be considered in light of proposed causes of megafaunal extinction, as outlined in Table 1 (also see Appendix).

Simpson (1953) noted that when a novel invader rapidly drives another species to extinction by competition, chances are against finding the two forms at the same stratigraphic level. Furthermore, rare taxa tend to ''disappear'' from the fossil record before the time of actual extinction (Signor and Lipps 1982). Conversely, human remains and artifacts, which similarly may be rare initially, would not be expected to ''appear'' until some time after actual human arrival. We have used, therefore, proxy measures that may be more sensitive to these factors than the conventional fossil and archaeological record alone.

As well as contributing to a reconstruction of vegetational and environmental patterns, stratigraphic pollen studies here include spore counts of the dung fungus, *Sporormiella* as a measure of large herbivore biomass. *Sporormiella* spore percentages have been found to rise following the introduction of grazing animals in historic times. Spores are usually abundant in Pleistocene sediments but scarce or absent for most Holo-

TABLE 1. Proposed causes of megafaunal extinction in North America.

| Hypoth-esis | Type | Source | Rate | Pattern | Process | Comments |
|---|---|---|---|---|---|---|
| $H_1$ | climate change | Graham and Lundelius (1984), Guthrie (1984) | slow? | A mosaic vegetation pattern becomes zonal; extinctions follow climate gradient. | Climate change leads to less hospitable environments for certain large species that fail to adapt. | |
| $H_2$ | environmental insularity | King and Saunders (1984) | slow? | Extinction follows as boreal forest recedes northwards. | Rapid expansion of deciduous forest reduces available habitat. | Applies only to extinction of American mastodon |
| $H_3$ | rapid climate change: the Younger Dryas | Berger (1991) | rapid | Follows Younger Dryas onset at ea. 11 000 ^{14}C yr BP | As $H_1$, but change is more drastic and develops rapidly. | |
| $H_4$ | blitzkrieg, or rapid overkill | Martin (1984) | rapid | A wave proceeds through a region. | Naïve fauna rapidly hunted to extinction. | |
| $H_5$ | protracted overkill | Whittington and Dyke (1984), Fisher (1997) | slow | Slow wave, or mosaic pattern of megafaunal collapse | Initially naïve fauna; overexploitation eventually causes collapse. | |
| $H_6$ | predator pit | Janzen (1983) | rapid | Wave through a region | Humans and native predators each contribute to collapse. | |
| $H_7$ | second-order predation | Whitney-Smith (2001) | moderately rapid | Pulsed | Interactions between humans, carnivores, herbivores, and vegetation. | |
| $H_8$ | three-stage overkill | Alroy (2001) | rapid | Pulsed | Overkill sufficient to explain pattern. | |
| $H_9$ | clovis age drought | Haynes (1991) | rapid | Severe but temporary vegetation change following human arrival, at ea. 11 000 ^{14}C yr BP | Aridification, rapidly amplifying predation by humans. | |
| $H_{10}$ | hypervirulent disease | MacPhee and Marx (1997) | very rapid | Panzootic disease pattern | Infectious disease with trans-generic virulence. | |
| $H_{11}$ | keystone megaherbivores | Owen-Smith (1987), Zimov et al. (1995), Schüle (1990) | not specified | Landscape transformation and fire follow megafaunal collapse. | Megaherbivores, which maintain open forest, are removed by humans or disease. | Fire regime changes as forests close and fuel loads rise (Schüle 1990) |
| $H_{12}$ | great fire | Humbert (1927), Miller et al. (1999) | rapid | Simultaneous throughout large regions | Landscape transformation by anthropogenic fire. Extirpation follows loss of forage. | Proposed for Madagascar; applicable to North America |
| $H_{13}$ | synergy | Burney (1993a, b, 1999), Diamond (1984) | slow | Mosaic pattern of extinctions | Human and natural causes interact. | |

cene samples (Davis 1975, 1987, Davis and Shafer 2002). High percentages of *Sporormiella* on mammoth dung have tied this coprophilous fungus to the extinct megafauna (Davis et al. 1984), and although spores may be found on the dung of rabbits and small rodents, elevated values in modern sediments appear to be exclusively associated with a high density of large herbivores (Davis 1987, Burney et al. 2003).

Stratigraphic charcoal studies as a measure of regional fire occurrence may also detect the onset of cultural activity in a variety of geographic contexts (Burney 1997). Such work has traced early landscape transformation by humans on landmasses bordering the north Atlantic, northern Europe, Australia, South America, Madagascar, and oceanic islands of the Pacific and Caribbean (Singh et al. 1981, Burney 1987, Burney et al. 1994, 1995, Athens 1997, and references in Grayson 2001). The onset of anthropogenic conflagration often can be distinguished from natural trends in burning: a sharp peak in microscopic charcoal values of at least an order of magnitude is typically followed by one to two millennia of lower concentrations that are nevertheless considerably above background levels. For reasons outlined above, such palynological markers tend to put human activity centuries or sometimes millennia earlier than direct archaeological evidence.

This study examines fossil records from the upper Wallkill Valley and the Hudson Lowlands of southern New York State (Fig. 1), an area covered by the Laurentide ice sheet at Last Glacial Maximum. Sediment dates from near the terminal moraine, at least 45 km further south, suggest that deglaciation was well underway by 18 750 $^{14}$C yr BP (Muller and Calkin 1993). Terrestrial and meltwater drainage northward became impounded by the retreating glacier, forming a succession of periglacial lakes in the Wallkill Valley of up to 90 km$^2$ in area, eventually draining into Glacial Lake Albany (Connally et al. 1989), which would have inundated the Hudson Lowlands during its earliest stages (Dineen 1986). It has been estimated that the glacial margin receded into the upper Hudson Valley by 13 000 $^{14}$C yr BP, (Connally and Sirkin 1973) but a review of available age data suggests the deglacial chronology in New York is still not tightly constrained (Muller and Calkin 1993). Isostatic rebound eventually led to the southward drainage of Lake Albany into the Atlantic, but the Wallkill River continues to flow north and much of its upper reaches are surrounded by extensive mucklands. Proximity to the melting glacier has meant that sedimentary basins of this region had a high rate of sediment accumulation encompassing the presumed "extinction window."

### Methods

Fossils of extinct Pleistocene megafauna were recovered from well-stratified subphreatic sites at Otisville, Hyde Park, and Pawelski Farm (Fig. 1 and Table 2). A medium-sized lake, Binnewater Pond, while not
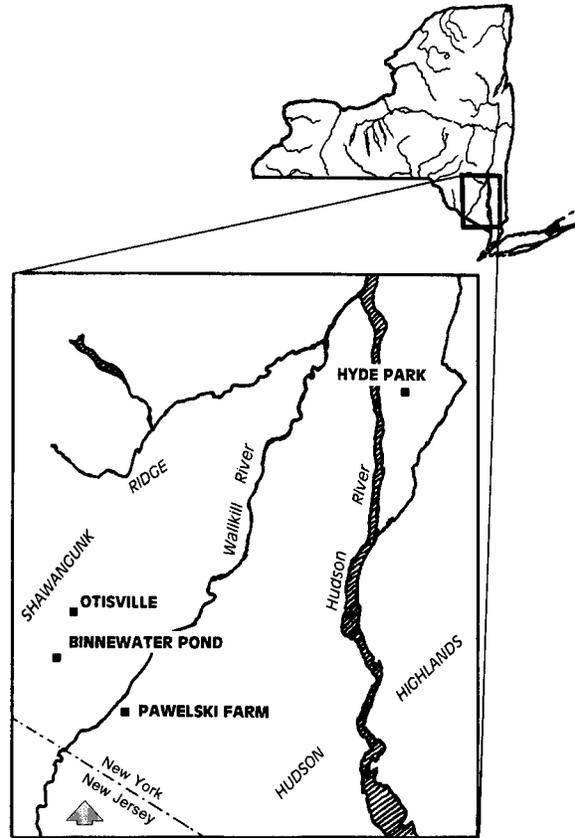


Fig. 1. Location of sites in southeastern New York State, USA.

known to be a megafaunal site, has a long sedimentary record with good temporal resolution.

Each of the megafaunal sites was examined through cores and worked as an open excavation (Table 2). A cone of depression in the water table was maintained with a gasoline-powered pump while work was underway (Burney et al. 2001). Sediment sequences were described and samples removed directly from a cleaned vertical face of the excavation trench. An open-sided bucket auger sampled below the level of open excavation, allowing for descriptions of sediments and subsampling in the field. Lake sediments were recovered with a 5 cm diameter modified Livingstone piston corer.

In the laboratory, separate subsamples were taken for pollen/charcoal processing, loss-on-ignition (LOI) determinations using the Dean method (Dean 1974), and $^{14}$C dating. Pollen/charcoal subsamples were stored in vials under refrigeration; $^{14}$C samples were oven-dried and stored in airtight containers at room temperature.

Pollen processing followed standard methods (Faegri et al. 1989); digests were suspended in glycerol for permanent liquid slide mounts. At least 400 grains of tree and shrub pollen were counted per sample using

TABLE 2. Characteristics of New York State sites.

| Site | General location | Latitude, longitude | Elevation (m) | Type of feature | Megafaunal remains | Sampling method |
|---|---|---|---|---|---|---|
| Pawelski Farm | Wallkill Valley "Black Dirt" | 41°20′02″ N, 74°25′45″ W | 122 | large wetland | *Cervalces scotti* | excavation and bucket auger |
| Binnewater Pond | Wallkill Valley | 41°24′36″ N, 74°33′07″ W | 256 | lake | | piston core |
| Otisville | Wallkill Valley | 41°28′23″ N, 74°31′10″ W | 230 | small wetland | *Mammut american-um* | excavation and bucket auger |
| Hyde Park | Mid-Hudson Valley: Hudson Lowlands | 41°46′48″ N, 73°53′38″ W | 74 | wetland | *Mammut american-um* | excavation and bucket auger |

400× magnification; a 1000× (oil immersion) lens was employed for difficult determinations.

Unless otherwise noted, pollen zones have been assigned using stratigraphically constrained cluster analysis (CONISS) on the square-root transformed data, using Edwards and Cavalli-Sforza's chord distance. Only taxa comprising at least 5% of the upland pollen sum in at least one sample have been included in the cluster analysis. *Sporormiella* spore counts are presented as a percentage of the combined aquatic and upland pollen sum.

Samples for charcoal analysis were treated using a modification of the Winkler nitric acid process (Winkler 1985) to remove pyrite. Resulting digests were washed through 250-μm sieves to remove macrofossils and macroscopic charcoal before hydrogen fluoride treatment. Calibrated tablets of *Lycopodium* spores were added before the final residues and were suspended in glycerine jelly for permanent slide mounts.

Charcoal residues were counted at 400× magnification using an eyepiece reticule so as to measure the two-dimensional projected area of individual fragments, reported as $\mu m^2/cm^3$. Morphology and texture of microscopic charcoal fragments are reported here as either graminoid (derived from cuticles of grasses and sedges) or amorphous (from woody and broadleaf plant types; Goldberg 1986, Burney 1987). Particles whose smallest dimension exceeded 250 μm are recorded as number of particles/$cm^3$.

### Absolute dates

To construct a chronology of latest occurrences, radiocarbon dates have been obtained on megafaunal remains excavated from these sites (Table 2) or alternatively from museum specimens of the same region. Plant macrofossils or sediment samples were dated to help establish the stratigraphic chronology in cores and excavations.

### RESULTS

#### Binnewater pond

*Sediment description.*—A dark greenish-gray humic silty clay (Munsell color 10Y 4/1) forming the lower

unit contains abundant algal and humic material. A gradual contact at about 11.2 m forms the lower boundary of a nearly uniform black gyttja (Munsell color 5Y 2.5/2) that continues to the sediment-water interface. The subsampled face of the core revealed close laminations in the lower unit that were most apparent in the samples dried for $^{14}$C dating. Plant macrofossils are very sparse, but pollen is abundant, with excellent preservation throughout the sequence.

*Pollen stratigraphy.*—

1. *Zone I.*—*Pinus* (pine) and *Picea* (spruce), in that order, dominate the pollen spectrum (Fig. 2). Pollen of broadleaf taxa is less important, but *Alnus* (alder) rises to 8%, while *Salix* (willow) and *Quercus* (oak) each attain 5%. Cyperaceae (sedges) are relatively abundant, up to 15% of the total. *Artemisia* (sage), *Thalictrum* (meadow rue), and Poaceae (grasses) each attain almost 5%. The date of 22 850 ± 90 $^{14}$C yr BP (all values are reported as mean ± SD) is on sediment which is not a basal sample and thus does not necessarily mark the lower strata of Zone I.

2. *Zone II.*—A steady rise and peak in *Picea* replaces *Pinus* as the dominant taxon just before the middle of this interval. However, by the upper boundary, *Pinus* steadily recovered, once again outnumbering *Picea*, whose values dropped below 10%. *Abies* (fir) and *Betula* (birch) rise rapidly to peak at over 10% and 13% respectively. *Quercus* shows a rise and decline, peaking mid-zone at 15%. Herbaceous taxa become less important toward the upper part of the zone. Five internally consistent radiocarbon dates within Zone II range from 13 210 ± 90 to 11 494 ± 91 (Table 3 and Fig. 2).

3. *Zone III.*—*Pinus* shows a decrease, while *P. strobus* (white pine) appears fairly abruptly at the bottom of the zone, beginning a continuous regional presence lasting for thousands of years. *Picea* recovers and remains at about 15% before declining sharply to zero at the top. *Abies* peaks and also drops to zero at the top while *Quercus* declines to below 5%. *Alnus* and *Betula* rise rapidly to 25% and >30% respectively across Zone III before declining abruptly at the top.
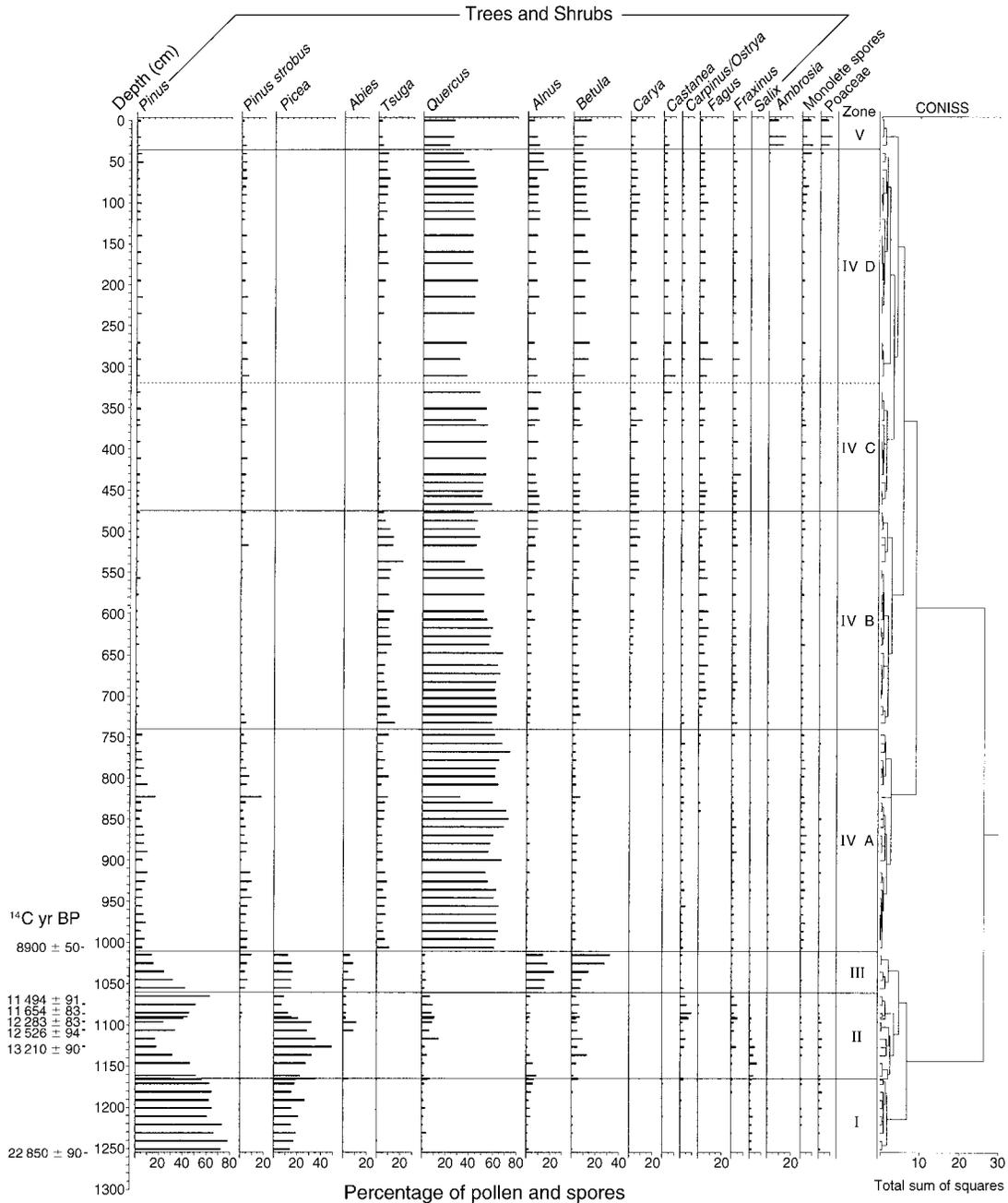
FIG. 2.   Diagram showing percentage of the total pollen and spores at each depth for major pollen and spore types for Binnewater Pond, New York, USA. Cluster analysis used is constrained incremental sum of squares (CONISS).

4. *Zone IVa.*—A sediment date of 8900 ± 50 $^{14}$C yr BP marks the bottom of this unit. Zone IVa thus is characterized by the rapid rise of thermophilous species, particularly *Quercus* which jumps to >60%, a level maintained more or less until the present. *Betula* and *Alnus* remain at low levels through the entire zone. *Pinus* remains <10%, dropping <5% at the top. *Ulmus* (elm) appears, maintaining a steady 3–4% through the late Holocene. A slight rise in *Pinus strobus* pollen occurs at the top of Zone III.

5. *Zone IVb.*—first *Fagus* (beech) and then *Carya* (hickory) become important. *Tsuga* (hemlock) declines to less than 1%.

6. *Zone IVc.*—*Tsuga* remains at <1% throughout, and appears to be replaced principally by *Pinus strobus*. *Castanea* (chestnut), occasionally present in low numbers since Zones I and II, becomes an important component of the assemblage toward the top of Zone IVc. Cyperaceae (sedges) reach values not seen since the late Pleistocene.

TABLE 3. Radiometric dates.

| Lab no. | Site/ source | $^{14}$C yr BP ± SD† | Calibrated calendar age at 2σ | Material | Pretreatments | Method | δ$^{13}$C | Stratigraphic provenance (cm) |
|---|---|---|---|---|---|---|---|---|
| β 71069 | Otisville | 11 640 ± 60 | 13 850–13 420 | wood (stems) | acid and alkali | AMS‡ | −27.8 | 75–85 |
| β 71070 | Otisville | 12 340 ± 70 | 15 410–14 100 | wood (stems) | acid and alkali | β-decay | −26 | 115–125 |
| β 71071 | Otisville | 11 970 ± 70 | 15 100–13 650 | wood (stems) | acid and alkali | β-decay | −27.2 | 135–145 |
| β 153148 | Otisville | 14 300 ± 50 | 17 480–16 800 | sediment | acid and alkali | AMS | −26.5 | 461–501 |
| β 157491 | Binnewater Pond | 8900 ± 50 | 10 190–9880 | sediment | acid and alkali | AMS | −30 | 1004.5–1005.5 |
| AA45688 | Binnewater Pond | 11 494 ± 91 | 13 830–13 150 | sediment | acid and alkali | AMS | −28.6 | 1073.5–1074.5 |
| AA45687 | Binnewater Pond | 11 654 ± 83 | 14 000–13 330 | sediment | acid and alkali | AMS | −28.5 | 1085.5–1086.5 |
| AA45685 | Binnewater Pond | 12 283 ± 83 | 15 390–13 860 | sediment | acid and alkali | AMS | −29 | 1095–1096 |
| AA45686 | Binnewater Pond | 12 526 ± 94 | 15 560–14 150 | sediment | acid and alkali | AMS | −29.6 | 1105–1106 |
| β 157492 | Binnewater Pond | 13 210 ± 90 | 16 380–15 370 | sediment | acid and alkali | AMS | −29.4 | 1125–1126 |
| β 153148 | Binnewater Pond | 22 870 ± 90 | NA§ | sediment | acid and alkali | AMS | −26 | 1255–1256 |
| β 141061 | Pawelski Farm | 12 180 ± 60 | 15 285–13 845 | bone (phalanx) | collagen extraction with alkali | AMS | −20.0 | 160–200 |
| AA45690 | Pawelski Farm | 11 212 ± 79 | 13 450–12 990 | sediment | acid and alkali | AMS | −23.5 | 129.5–130.5 |
| AA45689 | Pawelski Farm | 13 083 ± 86 | 16 210–15 080 | sediment | acid and alkali | AMS | −23.2 | 154.5–155.5 |
| β 135234 | Hyde Park | 11 480 ± 60 | 13 805–13 165 | tooth enamel (tusk) | collagen extraction with alkali | AMS | −22.7 | |
| AA46612 | Hyde Park | 12 484 ± 64 | 15 490–14 150 | sediment | acid and alkali | AMS | −26.6 | 9.5–10.5 |
| AA46613 | Hyde Park | 13 280 ± 75 | 16 430–15 540 | sediment | acid and alkali | AMS | −26.5 | 34.5–35.5 |
| NZA12584 | Temple Hill (NY State Museum # V100) | 11 000 ± 80 | 13 173–12 661 | bone (scapula) | collagen extraction and gelatinization | AMS | −21.3 | |

† Radiocarbon years before present (where present is 1950), corrected for isotopic fractionation.
‡ Accelerator mass spectrometry.
§ Not applicable because the date is beyond the range for calibration to calendar years.

7. *Zone IVd*.—*Tsuga* makes a gradual recovery to early Holocene levels by mid-zone, but is not as strongly represented as in the mid-Holocene. *Castanea* continues to rise, along with *Fagus* and *Betula*, all of which peak at ~12% in the lower part of this zone, partially replacing *Quercus*, which falls to 30% for the first time since the late glacial. By mid-zone, *Quercus* has returned to >40%.

8. *Zone V*.—A rapid rise in Poaceae from near zero to 10% and the first appearance of ruderal species such as *Plantago* (plantain) mark the lower boundary of this zone. Monolete spores also show a steep rise, as does *Ambrosia* (ragweed). The percentage of all tree pollen declined relative to upper Zone IVd. *Quercus* drops to 20% and is paralleled by decreases in *Fagus*, *Carya*, *Tsuga*, and *Pinus strobus*. The only tree species to exhibit an increase from Zone IVd is *Betula*.

Sporormiella.—Spores of the dung fungus *Sporormiella* spp. maintain high values, at 3–5% (Davis 1987) throughout Zone I (Fig. 3). A steep decline begins at the bottom of Zone II, dropping to less than 0.5% by the middle and reaching 0% at the top of this unit. Above this horizon, *Sporormiella* is mostly absent, occasionally reaching 0.5% until the late Holocene, where in upper Zone IVd and lower Zone V, it climbs to 1% for the first time since the late Pleistocene.

*Charcoal*.—Throughout Zone I, graminoid charcoal is either absent or at a very low level, while other microscopic charcoal concentrations average below 2 × 10$^6$ μm$^2$/cm$^3$ (see Fig. 3). Graminoid charcoal increases to 5 × 10$^6$ μm$^2$/cm$^3$ at the bottom of Zone II, amorphous charcoal to 15 × 10$^6$ μm$^2$/cm$^3$ and total charcoal reaches 20 × 10$^6$ μm$^2$/cm$^3$, an order of magnitude rise overall. The subsequent pattern of charcoal
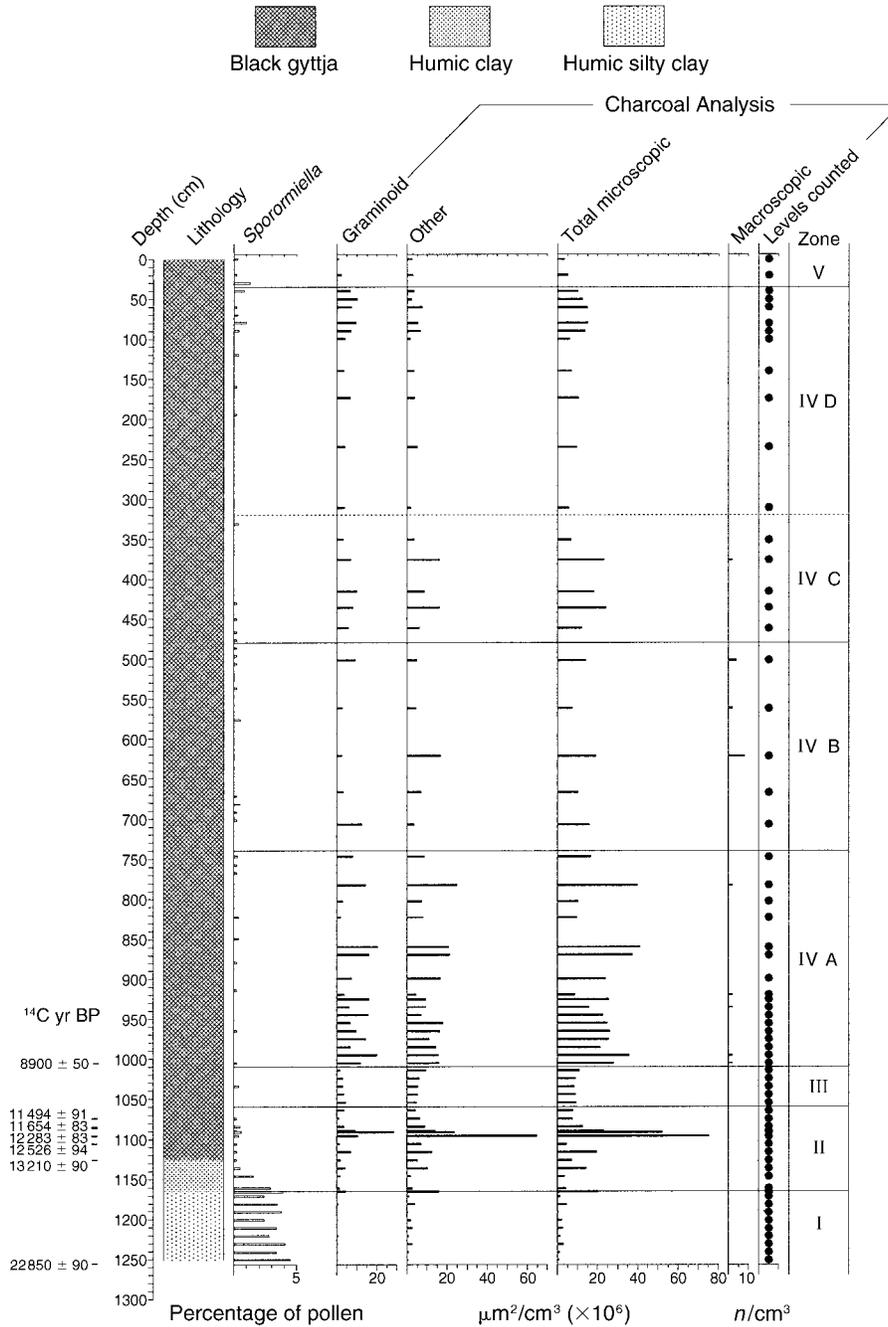
Fig. 3. *Sporormiella* and charcoal for Binnewater Pond. Spore values are expressed as a percentage of pollen sum (upland plus aquatic). Microscopic charcoal is expressed as projected area on slide per volume of sediment. Macroscopic charcoal (>250 μm) is expressed as number of particles (*n*) per volume of sediment.

concentrations is erratic for the lower half of Zone II, averaging $10 \times 10^6$ μm$^2$/cm$^3$ until mid-zone, when it rises abruptly again to $75 \times 10^6$ μm$^2$/cm$^3$. Amorphous charcoal rises earliest, followed closely by graminoid charcoal. By the upper part of Zone II and throughout Zone III, total charcoal settles to a steady level of about $10 \times 10^6$ μm$^2$/cm$^3$, with the graminoid fraction con-

tributing somewhat less than 50%. The lower boundary of Zone IVa is marked by a rise of total microscopic charcoal to $>20 \times 10^6$ μm$^2$/cm$^3$, a pattern that characterizes the remainder of Zone IV, with graminoid charcoal often contributing >50% of the total. In Zone V, total charcoal falls to values not recorded since Zone I and lower Zone II.
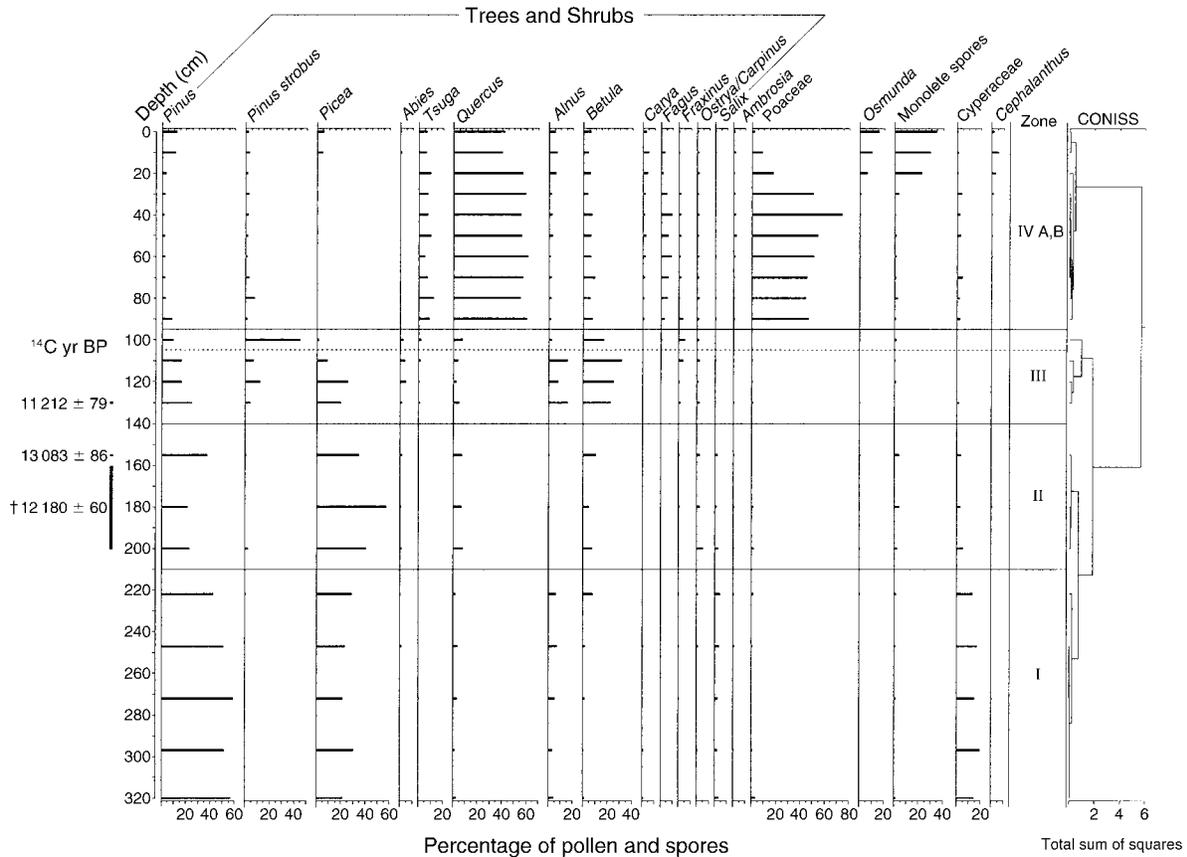
FIG. 4. Diagram showing percentage of the total pollen and spores at each depth for major pollen and spore types for Pawelski Farm, New York, USA. The dagger symbol indicates date for the *Cervalces* skeleton. Cluster analysis used is constrained incremental sum of squares (CONISS). The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

### *Pawelski* Cervalces *site*

Beginning in 1996, annual ditch maintenance on the Pawelski farm in the Black Dirt Region of Orange County had uncovered several unusual bones and pieces of antler. Once the source was located, systematic excavation in 1999 revealed the skeleton of a male *Cervalces scotti*, or stag moose (Scott 1885), lying between 170 cm and 200 cm below the surface. A plug of compact bone extracted from a proximal phalanx yielded an accelerator mass spectrometry (AMS) collagen date of $12\,180 \pm 60$ $^{14}$C yr BP (Table 3).

Sediment samples were taken at 10 cm intervals directly from a cleaned face of the drainage ditch, above the bone-bearing layer. Sediment below the bottom of the ditch was sampled with a bucket auger. Subsamples for pollen and charcoal were taken at ~25-cm intervals for the lower part of this sequence.

*Sediment description.*—Distinct boundaries delineate three sedimentary units. A dark blue-gray clay (Munsell color: Gley 4/N) forms the lower unit, which contacts a peaty clay (Munsell color: Gley 5/10Y) at 215 cm. The peaty clay extends to 100 cm and includes abundant yellowish-brown, fibrous, plant material which is apparently sedges and broad-leaved plants. The upper unit is a dark peat (Munsell color: 10YR 2/1), typical of the soils of New York's Black Dirt Region.

*Pollen stratigraphy.*—The summary pollen diagram (Fig. 4) includes major types; zones have been established numerically. In this instance, Poaceae and monolete spores have been treated as paludal taxa. Only trace amounts of Poaceae pollen appear in this record during the late Pleistocene, but values abruptly rise to ~40% in Zone IVa, b, represented entirely by grains of a single thin-walled morphotype. Their importance is reduced upsection and near the surface, where monolete spores approach 40%.

1. *Zone I.*—*Pinus* is the principal taxon in this zone, followed closely by *Picea*, and Cyperaceae, but *Alnus*, *Quercus*, and *Salix* are important throughout, each amounting to as much as 5%. *Betula* rises from a trace to above 5% at the top. Pollen tends to be sparse yet adequate, except for the 298-cm sample, for which only ~300 grains were counted in five complete slides. Pres-

ervation is generally good, with grains intact but frequently crumpled, apparently from being supported in a clay matrix.

2. *Zone II.*—*Picea* rises steadily to 55%, dominating the middle of this zone, but *Pinus* recovers toward the top. Sedges decline to low levels early in the section; *Betula* and *Quercus* rise to ~10%. *Ostrya/Carpinus* (hop hornbeam and hornbeam) and monolete spores display a low but significant presence throughout. *Salix* has a lesser presence than earlier, but keeps a steady signal to the top of Zone II. A sediment date of 13 083 ± 86 $^{14}$C yr BP came from near the top of the zone. The *Cervalces* skeleton was found within the boundaries of Zone II.

3. *Zone III.*—*Picea* rises to ~25% mid-zone, but drops to ~10%, delineating a final decline. *Pinus* (undifferentiated) follows the opposite pattern, decreasing somewhat mid-zone and peaking at the top. *Pinus strobus* appears and exceeds 10% at this time, while *Quercus* declines. *Alnus* and *Betula* both rise and fall across this zone and *Tsuga* appears in low numbers at the top. Sediment from the bottom of Zone III dates to 11 212 ± 79 $^{14}$C yr BP.

4. *Zone IVa, IVb.*—*Picea* disappears and *Quercus* jumps to 60%. *Tsuga* rises early within the zone and remains a steady presence of ~10–12%, while *Carya*, *Fagus*, and *Acer* become a significant part of the spectrum. Poaceae rises rapidly from trace amounts to ~60% of the upland and aquatic total, but is replaced in the course of the upper 60 cm by monolete and *Osmunda* fern spores, and to a lesser degree by pollen of *Cephalanthus* (buttonbush), a paludal shrub. *Pinus* drops below 5% by mid-zone but recovers to exceed 10% within 10 cm of the surface. *Pinus strobus* is present at less than 2% throughout Zone IV, with the exception of the 80 cm sample, where it barely exceeded 5%. Absent from most of Zone IV, *Picea* reaches ~5% in the top two samples. *Betula*, which begins to decline in Zone III, now maintains a presence of between ~5% and 10% throughout Zone IV. *Alnus* starts Zone IV at ~2% and does not exceed this low level until the top 30 cm, where it surpasses 5%.

*Sporormiella.*—These spores are present throughout Zone I, reaching 3–4% of the upland and aquatic pollen sum (Fig. 5). In a single sample, for which pollen was also sparse (see remarks on 298 cm sample, above), *Sporormiella* is below 1%, but otherwise is high for the rest of this zone (~3–4%). At the boundary with Zone II, spore values drop to low numbers (~0.5%) for the remainder of Zone II before disappearing at the top. With the exception of some trace amounts observed at two levels toward the center of Zone IV, *Sporormiella* is essentially absent from the rest of the sequence.

*Charcoal.*—Total microscopic charcoal concentrations in Zone I and most of Zone II scarcely exceed 2 × 10$^6$ μm$^2$/cm$^3$. At the top of Zone II, in the 155-cm sample (sediment date:13 083 ± 86 $^{14}$C yr BP), a change in the fire history is marked by a charcoal concentration rise to over 25 × 10$^6$ m$^2$/cm$^3$. Above this, values then decline before rising in the middle of Zone III to ~8 × 10$^6$ μm$^2$/cm$^3$, where graminoid fragments contribute a little over 50%; some macroscopic charcoal also is present. Low levels then persist until the lower portion of Zone IV, where microscopic charcoal rises to 10 × 10$^6$ μm$^2$/cm$^3$. Very low levels mark most of the Holocene record here before rising significantly at 20 cm from the present surface.

### Otisville

Bones of an American mastodon (*Mammut americanum*) were uncovered in 1872 by peat diggers in a small bog at the foot of the eastern slope of the Shawangunk Mountains. The Otisville mastodon skeleton now resides at the Peabody Museum in New Haven, Connecticut. Contemporary newspaper accounts and local inquiries helped relocate the site east of the town of Otisville, New York (Table 2). The profile of the basin was initially traced by transecting the bog with a series of exploratory bucket auger cores so that an appropriately deep section for excavation could be located, avoiding the area disturbed by peat mining. Sediment samples and plant macrofossils were collected based on their stratigraphic provenance. Below 1.6 m depth, sediment sampling continued by using a bucket auger down to 5.12 m, where the auger bottomed out in a gravelly layer, presumably consisting of glacial drift.

*Sediment description.*—An AMS sediment date sets a minimum time of 14 300 ± 50 $^{14}$C yr BP (Table 3), for onset of sedimentation at the Otisville site. A clayey basal gravel contacts an olive gray clay unit (Munsell color 5Y 4/1–4/2) at 465 cm, which becomes a bit darker and more humic as it continues upsection to 320 cm (Munsell color 5Y 3/1–3/2), becoming a humic, silty clay (Munsell color 5Y 4/1–4/2) up to ~90 cm. From this level, peat forms the upper unit, and is dark gray, with clay from ~90 to 75 cm (Munsell color 2.5Y 3/2). Above this, the peat becomes darker up to 45 cm (Munsell color 2.5Y 4/1–4/2). It includes more woody material and less clay. From 45 cm upwards, the unit becomes darker and less woody (Munsell color 2.5 Y 2/0), changing to a dark gray woody peat (Munsell color 10YR 3/1) at ~25 cm below the surface.

A surface sediment sample was taken, but much of the upper 25 cm of the peat unit was disturbed by a mass of roots and so the next sample was taken at 30 cm, and at 10-cm intervals thereafter, to the bottom of the excavated pit. Sampling proceeded below this level by bucket auger.

*Pollen stratigraphy.*—The summary diagram displaying major pollen and spore types for the Otisville site is shown in Fig. 6. A dissimilarity coefficient of ~0.6 clusters the samples into four basic zones, comparable to the pollen stratigraphies of Binnewater Pond and Pawelski Farm.
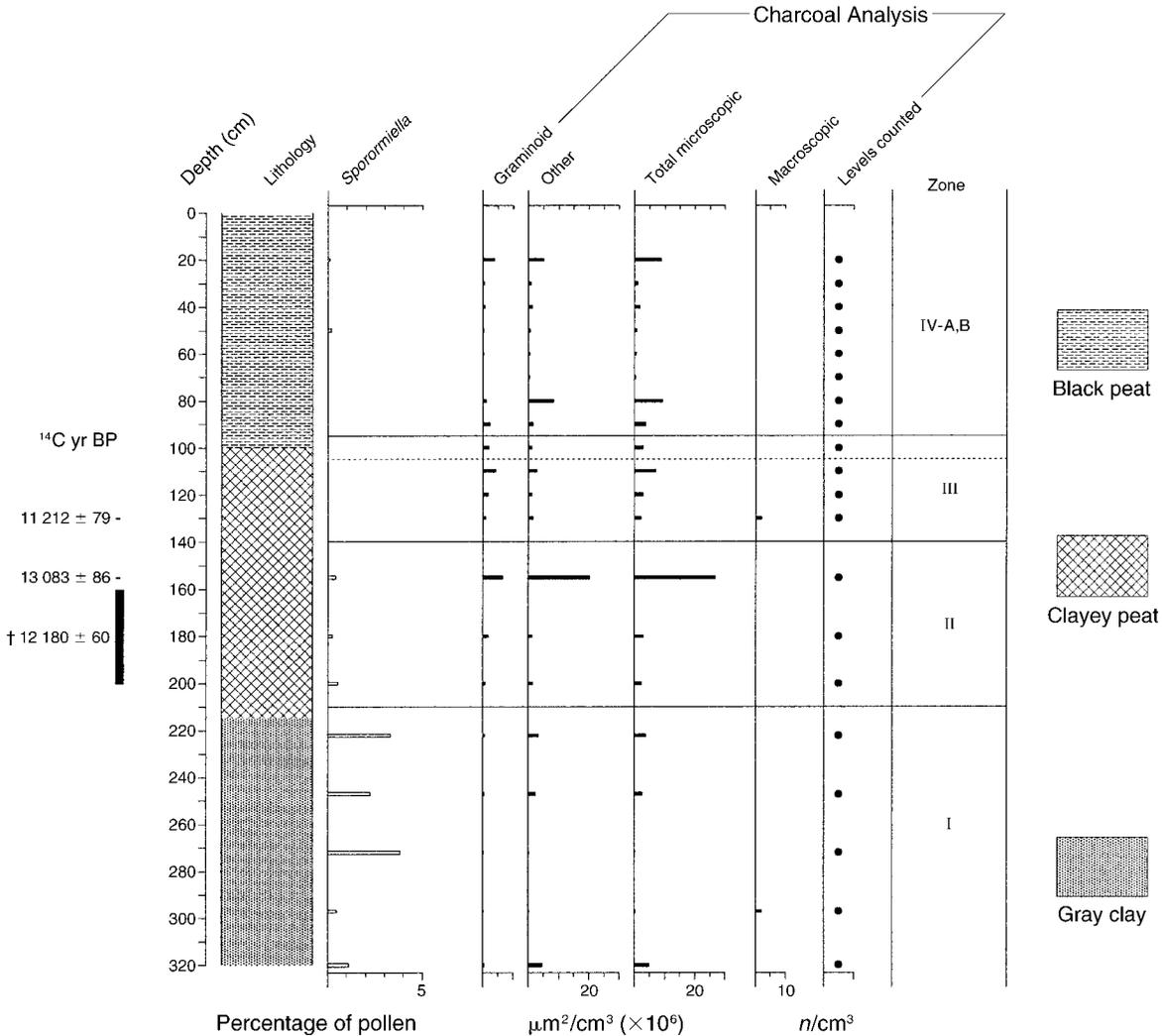
FIG. 5. *Sporormiella* and charcoal for Pawelski Farm. Spore values are expressed as a percentage of pollen sum (upland plus aquatic). Microscopic charcoal is expressed as projected area on slide per volume of sediment. Macroscopic charcoal (>250 μm) is expressed as number of particles (*n*) per volume of sediment. The dagger symbol indicates date for the *Cervalces* skeleton. The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

In addition to the aquatic and paludal taxa that are normally excluded from the upland pollen sum, *Alnus* also is excluded from the Otisville spectra. Alder shrubs are growing abundantly on the bog surface today and polyads of more than 60 *Alnus* grains are found in fossil samples. Monolete spores also are excluded for similar reasons.

1. *Zone I.*—*Pinus* and *Picea*, in that order, dominate these late-glacial pollen spectra. Toward the top, *Picea* rises at the expense of *Pinus*. Broadleaf taxa include *Betula*, which exceeds ~15% in the upper part of the zone. *Quercus*, *Salix*, and Poaceae each attain 8–10%. Cyperaceae often exceeds 20%. *Thalictrum* reaches 5%, forming part of a tundra community along with *Artemisia* and other Asteraceae. An AMS date on a

plant macrofossil of 11 970 ± 70 ¹⁴C yr BP marks the top of Zone I.

2. *Zone II.*—*Picea* continues its rise, surpassing *Pinus*. *Betula* rises and peaks before mid-zone, and *Alnus* declines steadily, as noted at the Binnewater and Pawelski sites. *Quercus* and Poaceae form a steady ~5–8%. *Salix* has a similar value, but is somewhat higher at mid-zone. *Abies* and *Pinus strobus* appear. *Artemisia* and *Thalictrum* drop to lower levels, but Poaceae and Asteraceae (high echinate types) have a presence comparable to that of Zone I.

3. *Zone III.*—*Pinus* now dominates the assemblage, followed by *Picea*, which drops out abruptly at the top of this zone. *Alnus* reaches almost 10% and *Betula*, 15%. *Tsuga* appears for the first time and *Quercus* re-
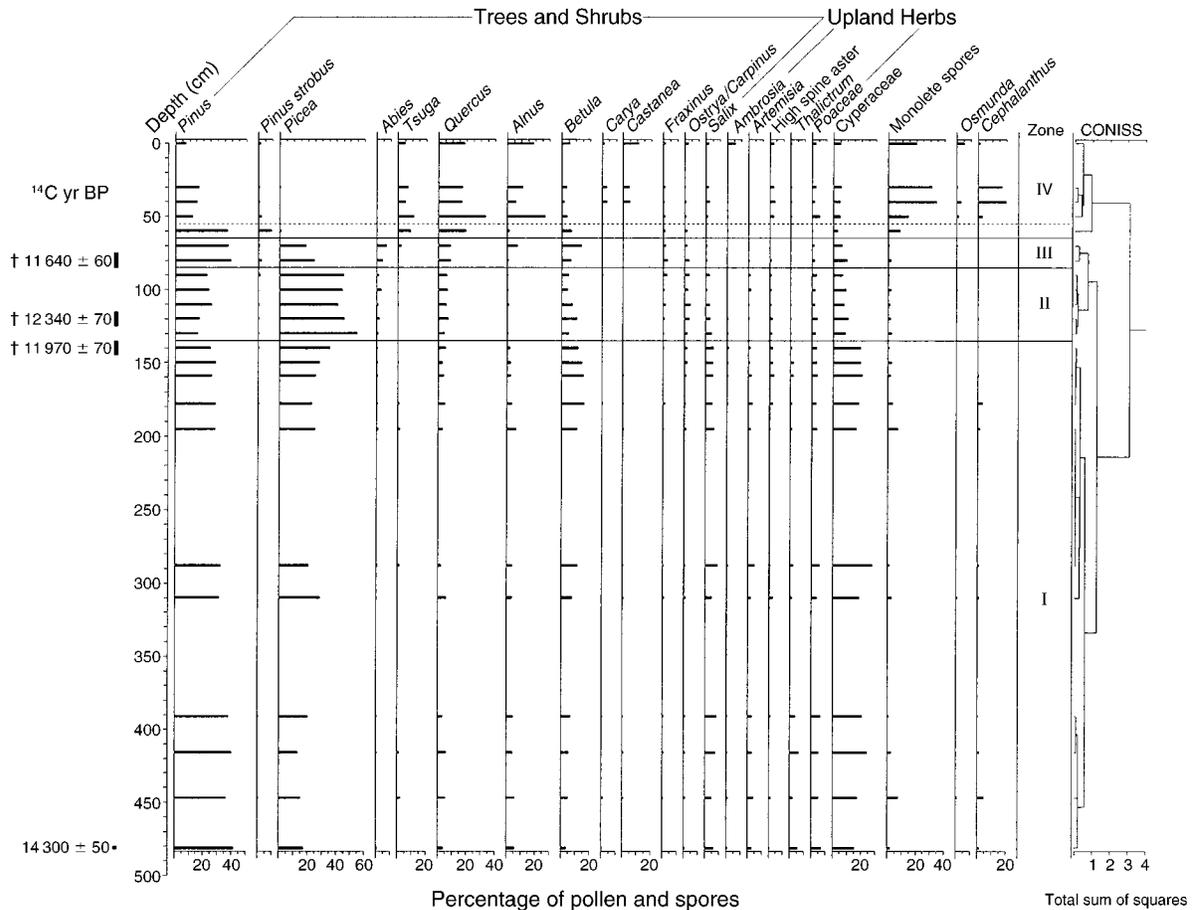
FIG. 6. Diagram showing percentage of the total pollen and spores at each depth for major pollen and spore types for Otisville, New York, USA. Dagger symbols indicate plant macrofossil dates. Cluster analysis used is constrained incremental sum of squares (CONISS). The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

mains at ~8%. A plant macrofossil AMS dated at 11 640 ± 60 $^{14}$C yr BP originated from the lower sample. As in Binnewater Pond and Pawelski Farm, the last appearance of *Picea* may be seen as defining the top of this zone.

4. *Zone IV.—Pinus* continues to dominate at 40%, and at the bottom of this zone *Picea* is absent. *Pinus strobus*, although registering a trace presence earlier, exceeds 10% in the 60-cm sample that forms the bottom of the zone. Above this point *Pinus* falls to 15% and *P. strobus* below 2%. *Quercus* climbs rapidly to 40%, *Betula* drops below 5%, and *Tsuga* rises to 15%. *Carya* and *Castanea* appear midzone and each exceed 5%; monolete spores become abundant.

*Sporormiella.*—The fungal spores associated with dung have a significant presence of ~2–3% throughout Zone I, show somewhat lower values of ~1–2% through Zone II, and fall to their lowest encountered level of ~0.2% near the top. They subsequently recover slightly before disappearing from the record at the top of Zone III. *Sporormiella* then is absent from every

sample above this horizon except for the surface, where it reappears in low numbers. Overall, *Sporormiella* values of the Pleistocene record at Otisville are not as high as at Pawelski Farm or Binnewater Pond, but nevertheless are comparable with those of modern sediments in overstocked areas (Davis 1987, Davis and Shafer 2002). In contrast to other sites, *Sporormiella* maintains a continuous although declining presence at this site through Zone III and finally drops out at the same stratum as *Picea*.

*Charcoal.*—Otisville contains background levels of amorphous charcoal that are many times higher than elsewhere (Fig. 7). From the beginning of sedimentation, at the bottom of Zone I, charcoal concentration is ~50 × 10⁶ μm²/cm³, and even though this level declines to about 20 × 10⁶ μm²/cm³ by the top of Zone I, it rises again to ~35 × 10⁶ μm²/cm³ in Zone II, and averages only slightly less for the remainder of the Late Pleistocene. Macroscopic charcoal appears first in Zone III (Younger Dryas) and then in the surface sample. Microscopic charcoal concentrations rise much later
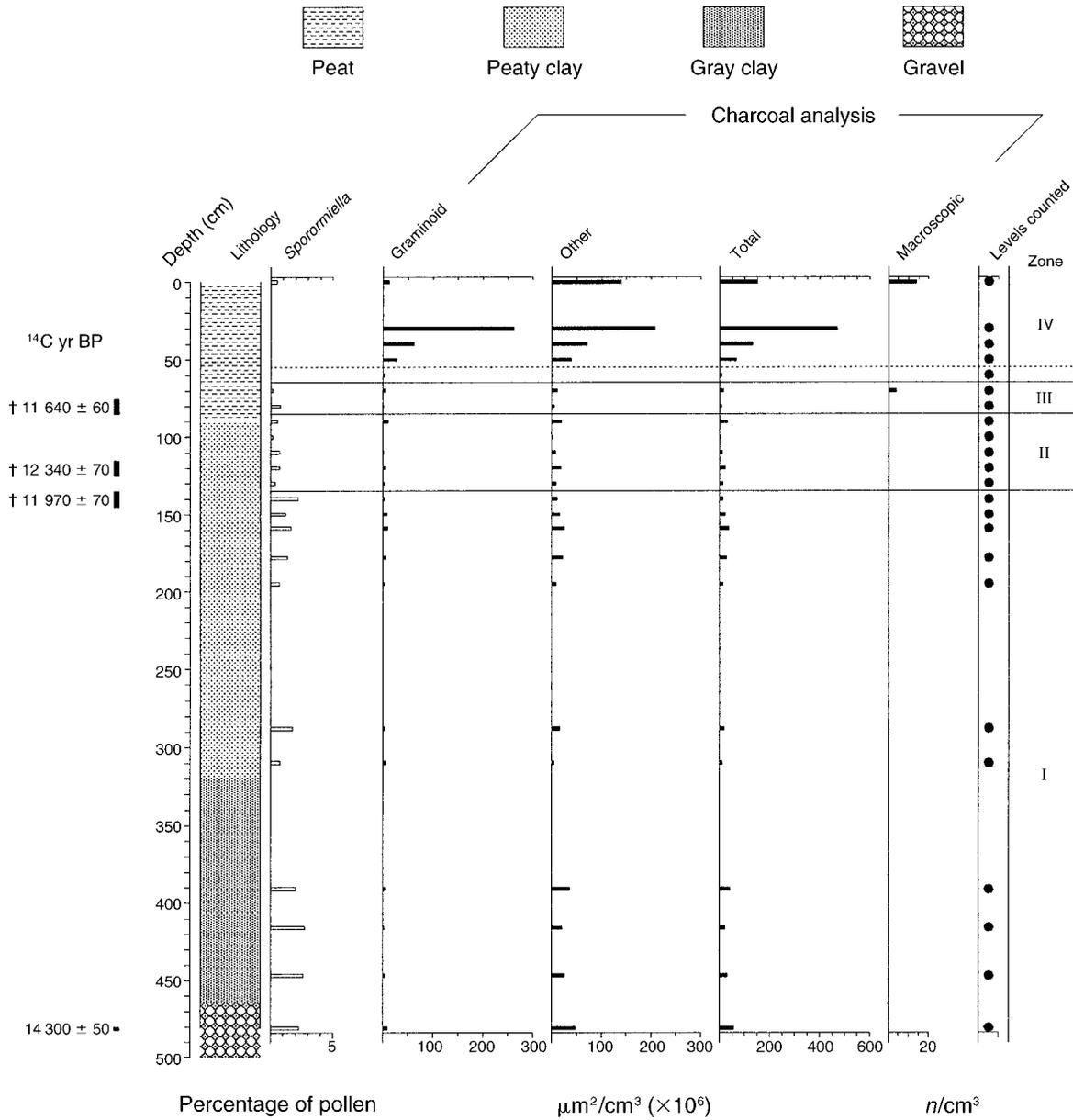
FIG. 7.   *Sporormiella* and charcoal for Otisville. Spore values are expressed as a percentage of pollen sum (upland plus aquatic). Microscopic charcoal is expressed as projected area on slide per volume of sediment. Macroscopic charcoal (>250 μm) is expressed as number of particles (*n*) per volume of sediment. Dagger symbols indicate plant macrofossil dates. The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

than at all other sites, beginning at 50 cm from the surface and coinciding with the *Quercus* peak in Zone IV.

### Hyde Park

During late summer of 1999, a backhoe deepened an artificial pond in a wetland area of suburban Hyde Park, Dutchess County, New York, and encountered the limb bones of a probiscidian. A fragment of tusk recovered from the spoil heap at the site yielded an AMS collagen date of 11 480 ± 60 $^{14}$C yr BP (Table 3). Work stopped

until the following year when arrangements were made to excavate below the water table, permitting more controlled removal of matrix sediments (D. A. Burney and G. S. Robinson, *unpublished manuscript*), which revealed a nearly complete skeleton of an adult male *Mammut americanum*. The thoracic spinal vertebrae, pelvis, and sacrum were substantially articulated and a fully articulated foot was positioned plantar side down in the sediments.

Inspection of a cleaned vertical face of the pit showed that while the backhoe may have removed
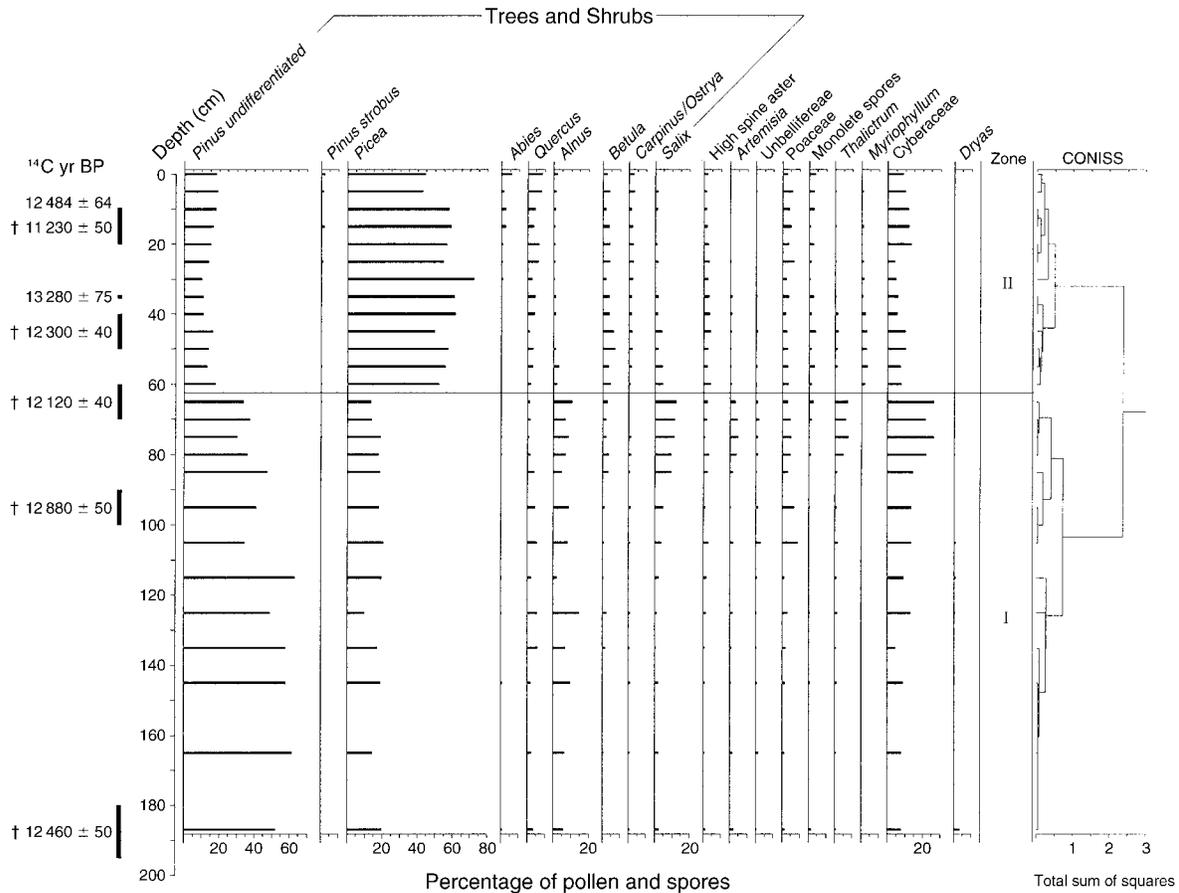
FIG. 8. Diagram showing percentage of the total pollen and spores at each depth for major pollen and spore types for Hyde Park, New York, USA. The dagger symbols indicate plant macrofossil dates. Cluster analysis used is constrained incremental sum of squares (CONISS). The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

much of the upper sedimentary units, the underlying stratigraphy was intact. Samples for microfossil work were removed directly from the face, at 5-cm intervals. A parallel set of large volume samples at 10 cm intervals were taken for macrofossil analysis. Sampling from 100 cm below the sediment surface (below the floor of the excavated pit) was continued at 5-cm intervals using a 7.5-cm bucket auger. Fist-sized cobbles were encountered at 175 cm, requiring the use of a posthole digger to remove material down to 190 cm, at which point the sediment became too indurated for further removal.

*Sediment description.*—The basal sandy gravel includes cobbles of subrounded gray sandstone of 6 cm average diameter. Smaller stones, up to 4 cm diameter, are present in the unit from 175 cm to 160 cm, where a uniform dark bluish gray clay (5B 4/1) is contacted, also uniform in appearance, up to 140 cm where it meets a dark gray clay (5Y 4/1). At 100 cm, the clay becomes more humic, containing some plant fibers and degraded molluscan gravel. It is interrupted at 80 cm by a lens of coarse sand and angular schistose gravel

consisting of clasts up to 1 cm diameter. At 55 cm, on a clear boundary, the humic clay unit meets a grayish brown (Munsell color: 2.5Y5/2) humic silty clay that contains a calcareous molluscan gravel. At about 30 cm, there is a laterally uneven contact with a dark gray-brown silty clay (2.5Y4/2), which includes wood, grass, and sedge fiber; broken snails; and other mollusk shells. Another uneven contact occurs at about 10 cm, characterized as a coarse detrital peat, which bears some clay, but little or no sand. A sediment date of 12 484 ± 64 $^{14}$C yr BP originated from the bottom of the peat member, but a similarly provenanced *Abies* cone scale yielded an AMS date of 11 230 50 $^{14}$C yr BP. A tracing of this peat unit laterally shows that much of its upper part was removed by a backhoe bucket.

*Pollen stratigraphy.*—The entirely late Pleistocene pollen stratigraphy of this site clearly is divided into two pollen zones (Fig. 8).

1. *Zone I.*—*Pinus* dominates throughout, and makes up as much as 60% of the lower part of this zone, where it is followed by *Picea* (19%), *Alnus* (8%), *Quercus* (5%), and *Salix* (2%). Together with the less abundant

Poaceae and *Artemisia*, these latter taxa begin to constitute a larger share in the upper part of the zone. Trilete spores are present earlier; monolete spores and *Lycopodium* sporadically occur throughout the profile. Cyperaceae rise steadily from 10% to 25%. The presence of *Dryas* is entirely within Zone I; it comprises ~3% of the lowest sample and trace amounts are found throughout the zone.

2. *Zone II.*—*Picea* rises abruptly to 55% and exceeds 70% at mid-zone, declining to about 40% towards the top. *Pinus* spp. is less than 20% of the sum, although the occurrence of *Pinus strobus* (haploxylon) is a consistent, if low, presence from the mid-zone on up. *Abies* appears slightly earlier, and exceeds 5% at the top. *Quercus* rises steadily to about 18%. *Betula* and *Carpinus*/*Ostrya* rise and maintain a level of ~5% and 2%, respectively. *Alnus* and *Salix* decline early on but do not disappear. High echinate Asteraceae and Poaceae are present throughout the interval, as in Zone I; *Artemisia* declines but remains in the profile. Monolete spores are present throughout, averaging less than 5%. Cyperaceae is less than 10% at the bottom of Zone II but increases to ~15% upsection. *Myriophyllum* (water milfoil) appears at the bottom, rises ca. 4%, declines at midzone, but is still present at the top.

The sediment date of 13 280 ± 75 $^{14}$C yr BP was taken at 35 cm depth, in the lower half of this zone, but an AMS age on *Picea* needles located ~10 cm below this was 12 300 ± 40 $^{14}$C yr BP (N. G. Miller, *unpublished manuscript*). The following observations suggest that Zone III is missing, along with a portion of Zone II and much of the peat unit of the sedimentary strata. Although *Picea* shows a slight decline near the top the Zone II, *Quercus* has risen to 18% and displays no sign of decline; *Tsuga* remains absent. There is no pronounced rise in *Betula* as in the other described sites that would be expected to mark Zone III. *Alnus*, which has fallen from its strong presence in Zone I, shows no recovery by the top of the sequence.

A particularly rich record of plant macrofossils reported elsewhere (N. G. Miller, *unpublished manuscript*), is in close agreement with the pollen stratigraphy described here.

*Sporormiella.*—In common with the other sites, at Hyde Park, *Sporormiella* has a strong presence throughout Zone I, even exceeding 6% (Fig. 9) at some horizons. At the bottom of Zone II, the spores begin a steady decline, and while never quite reaching zero, values are very low by the top of Zone II, as at Binnewater Pond and Pawelski Farm. Following the initial decline in the middle of Zone II, spores briefly return to 6% in a single sample (25 cm) then drop to a less than 0.5% average for the remainder of the sequence.

*Charcoal.*—Throughout Zone I (Fig. 9), all charcoal is below 1 × 10$^6$ μm$^2$/cm$^3$ and graminoid charcoal is at trace levels. In the lower part of Zone II, an order of magnitude rise occurs. Total microscopic charcoal

concentration at 45 cm is 2.6 × 10$^6$ μm$^2$/cm$^3$, subsequently rising to 28 × 10$^6$ μm$^2$/cm$^3$ at 35 cm, with graminoid and amorphous types at approximately subequal contributions. Charcoal values decline above this, but remain at five to 10 times the average found in Zone I. Macroscopic charcoal first appears at the bottom of Zone II, then rises at 35 cm.

### *Temple Hill mastodon*

One of many mastodons found in Orange County, the Temple Hill specimen was excavated in 1921, after it was encountered during trenching in mucklands about 4 miles (6.4 km) west of Newburgh, New York (Hartnagel and Bishop 1922). The largely complete skeleton is now at the State Museum of New York in Albany. A plug of compact bone removed from the subscapular fossa yielded an AMS age of 11 000 ± 80 $^{14}$C yr BP (Table 3).

## Discussion

### *Biostratigraphy*

The sedimentary histories of each site display key features of the late-glacial pollen stratigraphy of southern New England (Deevey 1939, 1943, Leopold 1956, Davis 1969). This correspondence is most complete for Binnewater Pond, which singly received uninterrupted sedimentation during the late Holocene. Nevertheless, all sites incorporate a microfossil stratigraphy that brackets the extinction window.

Zone I at Binnewater Pond is equivalent to pollen zone A1 of the southern New England sequence. Similarly, Zone II corresponds to zones A2–A3, reflecting the late-glacial rapid warming of the Bölling/Alleröd Interval (Peteet 1992); Zone III is equivalent to A4, now recognized as a vegetational response to the Younger Dryas cooling event in the northeastern United States (Leopold 1956, Peteet et al. 1990, Peteet 1992). In particular, Zone III pollen spectra display a characteristic rise then fall of *Alnus*, that marks the beginning and end of the Younger Dryas across regions from New Jersey to the Atlantic Provinces of Canada (Mayle et al. 1993). Zone IVa matches the C1 pollen zone, a response to the onset of Holocene warming.

Other key points of correspondence that occur in the remainder of the postglacial sequence include the *Tsuga* decline, an event recorded in pollen diagrams from sites throughout the range of *Tsuga canadensis*. Dating to ca. 4800 $^{14}$C yr BP, this ''hemlock decline'' has been attributed to a forest pathogen outbreak, (Davis 1981, Allison et al. 1986), and is a useful stratigraphic marker for correlating sequences across eastern North America.

The *Ambrosia* horizon, marking the boundary of Zone V, is prevalent throughout the Northeast and much of the Midwest and is understood to be a cultural rather than climatic signal for the late Holocene pollen record. Together with other palynological markers, the rise of
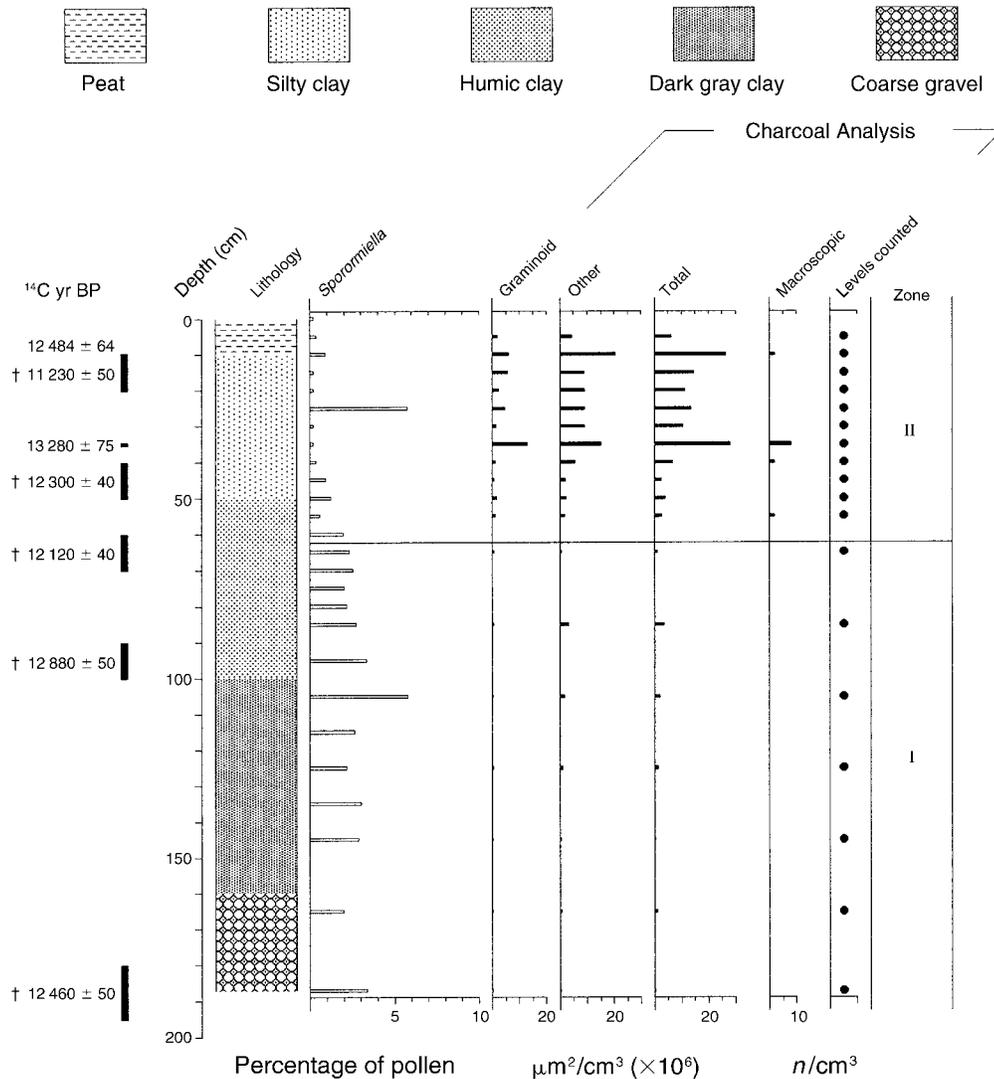
FIG. 9. *Sporormiella* and charcoal for Hyde Park. Spore values are expressed as a percentage of pollen sum (upland plus aquatic). Microscopic charcoal is expressed as projected area on slide per volume of sediment. Macroscopic charcoal (>250 μm) is expressed as number of particles (*n*) per volume of sediment. Daggers indicate plant macrofossil dates. The bars to the left of the *y*-axis indicate the stratigraphic range from which the radiocarbon-dated material was obtained.

*Ambrosia* reflects land-use changes associated with European settlement about 300 years ago in the Northeast (Miller 1973, Russell 1980, Peteet 1992).

Most New England pollen stratigraphies include a "B" or Boreal Zone typically defined by a final *Pinus* peak occurring just above the Younger Dryas. In studies where *P. strobus* or haploxyon pine pollen is displayed separately, the "B- Zone" *Pinus* peak is formed primarily if not exclusively by *P. strobus*, or white pine (Davis 1969). An equivalent of this zone notably is absent from the Binnewater Pond sequence, although it is clearly reflected in two of the other sites of this study.

Although all the sediment dates from the Binnewater core are internally consistent, two are from clay-con-

taining units. Each of these samples had low carbonate content (Robinson 2003), and they were rejected for the following reasons. The date of 22 850 ± 90 $^{14}$C yr BP is not consistent with a location significantly north of the glacial margin until at least ca. 17 000 $^{14}$C yr BP (Connally and Sirkin 1970). The date of 13 210 ± 90 $^{14}$C yr BP is from a pollen stratigraphic horizon correlative with the earliest A2–A3 pollen zone. Other studies from the Wallkill and lower Hudson valley region put this horizon at ca. 12 600 $^{14}$C yr BP (Connally and Sirkin 1970, Peteet et al. 1993, Maenza-Gmelch 1997*a*, *b*). While hard-water error is unlikely in these cases, glacial clay may have introduced "infinite-age" carbon into the organic fraction (Sutherland 1980) and thus invalidated the results.

*Sporormiella* declined at Binnewater Pond at the bottom of Zone II, suggesting an abrupt drop in the density of large herbivores around this site during the early stage of the Bölling/Alleröd late-glacial warming. Near the boundary of Zones IV and V, presumably at around the time of European settlement, *Sporormiella* values surpass any samples since the late Pleistocene. There are two maxima: the first possibly caused by relaxed predation pressure on game animals when native American populations were decimated by epidemics following first European contact. The second peak may mark the subsequent introduction of domestic ungulates (cf. Davis 1975).

Immediately preceding the Late Pleistocene drop in *Sporormiella*, there is an order-of-magnitude rise in both graminoid and other microscopic charcoal. This rise occurs at the boundary of Zones I and II, and may be the first sign of human activity in the region (the second being *Sporormiella* decline). The largest increase in fire frequency appears later, about 60 cm higher, above the middle of Zone II in the Binnewater sequence, at $12\,283 \pm 83$ $^{14}$C BP, on AMS dated sediments, and may be a result of litter accumulation following the depletion of large herbivores. By Zone V, the charcoal data indicate that fire is now reduced in importance to a level not seen for ca. 13 millennia.

At Pawelski Farm, the low concentration of pollen in the lower unit may be due to rapid deposition of clay from glacial melt. The pollen profile of Zone III is indicative of the Younger Dryas chronozone, particularly the unprecedented rise and then fall in *Alnus* pollen spanning the unit. The late glacial and early Holocene pollen stratigraphy correlates well with that of Binnewater Pond, although inspection of Fig. 4 shows that, based on a dissimilarity coefficient of ~0.8 chosen in this case to establish pollen stratigraphic zones, the single sample at 100 cm depth would also qualify as a zone in its own right. By correlation with New England pollen stratigraphy, (Davis 1969), this is the "B-Zone" that is apparently missing or obscured by other taxa in the Binnewater Pond pollen profile. As in New England, it is defined here by a rapid rise of *Pinus strobus* to ~45%. This "boreal" zone is understood to postdate the Younger Dryas chronozone (Peteet et al. 1993), and is demarcated here by a broken line toward the top of Zone III in Fig. 4 and Fig. 5. The striking rise of Poaceae pollen and later of monolete spores is accompanied by aquatics suggesting local changes in the wetland plant community. *Quercus* dominance signals the onset of Holocene warming, followed by other thermophilous species. Today, the top ~30 cm of the peat unit is disk plowed and planted with onions, and yet the uppermost pollen spectra have remained well stratified, suggesting that such disturbance does not significantly mix the sediments vertically. Furthermore, the pollen spectrum at the surface is not modern: the mid-Holocene *Tsuga* decline and the *Ambrosia* horizon are missing. Much of the surface

sediment has been burned off and is regularly deflated by winds, exposing layers laid down at least 5000 years ago. Because of artificial drainage, the surface is dry for much of the year, which explains why it does not sequester a modern pollen rain.

The sediment date marking the Zone II charcoal peak is not consistent with the pollen stratigraphy, which is clearly younger. However, the *Cervalces* skeleton was recovered from 200 cm depth and AMS dated to $12\,180 \pm 60$ $^{14}$C yr BP. Although it is possible that the bones sank into the sediments, the collagen date is consistent with the pollen spectrum of its matrix. Accordingly, the date marks the interval between *Sporormiella* decline at the Zone I–Zone II boundary, and the charcoal peak that occurs ~60 cm above it.

The pollen spectrum of Otisville's Zone II correlates with the Bölling/Alleröd warming, an interpretation supported by the radiometric date of $12\,340 \pm 70$ $^{14}$C yr BP on a plant macrofossil. However, because of radiocarbon anomalies that characterize this time period (Fiedel 1999), the stratigraphic reversal of this date with the later one from Zone I is more apparent than real. When calibrated at 2 sigma the two dates in question overlap by a thousand years (Table 3). Otisville's Zone III is represented by two samples showing a peak in *Betula* and *Alnus*, and establishes the Younger Dryas chronozone.

Otisville's pollen stratigraphy shows a clear *Pinus strobus* spike, equivalent to the boreal or "B Zone" of the New England pollen stratigraphy. It appears at 60 cm depth and cluster analysis (dendrogram, Fig. 6) recognizes it as a zone in its own right from a dissimilarity coefficient of ~0.9. However, at a larger dissimilarity coefficient it clusters with Zone IV, to which we have assigned it here, with a broken line indicating its upper limit.

As elsewhere, the early Holocene warming is marked by a significant rise in *Quercus*, but sedimentation has slowed above this, so the later Holocene is poorly represented. However, all taxa present at 30 cm also appear in the surface sample in roughly the same percentages, the principal exception being *Ambrosia*, constituting ~8% at the surface but barely present at 30 cm. This provides some assurance that root disturbance has not introduced late Holocene material into the lower portion of Zone IV. The abundance of *Ambrosia* and *Castanea* at the surface suggest that it is late Holocene and likely of post-European contact time. Thus, it might have been assigned to Zone V, but as a single sample that did not cluster by the chosen dissimilarity coefficient, we have grouped it with Zone IV.

Otisville's charcoal record indicates that fire was an important element of the local ecology by the time the earliest sediments began to accumulate. When microscopic charcoal concentrations rise, they reach levels not seen at other sites: 210 and $260 \times 10^6$ $\mu$m$^2$/cm$^3$ for amorphous and graminoid types respectively. As a small sedimentary basin, this site would be expected

to receive a strong local signal in its charcoal record. Nevertheless, that record is not one of sporadic and occasional fires that might be over-represented, but of frequent natural fires that are a consistent feature of the local ecology. The first macroscopic charcoal fragments appear somewhat earlier, in upper Zone III, indicating burning close to the site (Patterson et al. 1987). *Sporormiella* remains moderately high (over 1%) during most of late Pleistocene time, up into lower Zone III, before falling to zero at the same time as *Picea*. A reappearance of the spores and *Ambrosia* at the surface suggests introduced livestock and European agriculture. Dairy cattle (of the Mitchell farm) occupied the site at least from the 19th century (H. R. Decker, *personal communication*).

Zone II at Hyde Park encompasses the spruce maximum or A2–A3 zones of the regional pollen stratigraphy (Peteet et al. 1993, Davis 1969, Maenza-Gmelch 1997*a*, *b*) as well as of northern New Jersey (Peteet et al. 1990), reflecting the Bölling/Alleröd warming (Peteet 1992). However, this is not followed by an *Alnus* maximum, indicating that the Younger Dryas is not represented. Pollen and macrofossils of rooted aquatic taxa such as *Myriophyllum* suggest the formation of a shallow pond (N. G. Miller, *unpublished manuscript*).

Microscopic charcoal particles of Hyde Park Zone I are of small size classes, mostly between 50 to 500 $\mu m^2$ (Robinson 2003). This continues through lower Zone II, suggesting a time of not only less frequent fire, but that charcoal originated from more distant sources (Clark 1988). Larger size classes and macroscopic charcoal of at least 250 $\mu m$ (Fig. 5) take a greater share at 50 cm depth, a pattern indicating local fires (Clark 1988). However, concentrations remain low overall, and consequently by this time fire was not a frequent occurrence. A macrofossil date suggests that after 12 300 $\pm$ 40 $^{14}$C yr BP, fire abruptly became frequent; an increase in average particle sizes also suggests that both local and regional fire contributed to the rise in charcoal concentration. Graminoid (grass and sedge) charcoal accounts for most of the largest size classes. Charcoal rise at Hyde Park stratigraphically follows closely upon *Sporormiella* spore decline in the same manner as observed in the records of Binnewater Pond, Pawelski Farm, and Otisville.

Plant macrofossil dates suggest that *Sporormiella* decline at Hyde Park cannot be much earlier than 12 300 $^{14}$C yr BP (Fig. 9 and N. G. Miller, *unpublished manuscript*). Similar dates from southern New England constrain the corresponding pollen horizon at ca. 12 590 $\pm$ 430 $^{14}$C yr BP (Peteet et al. 1992). The terrestrial record from northwestern Europe places the onset of the Bölling at ca. 13 000 $^{14}$C yr BP (Watts 1980). The significance of an apparently later *Sporormiella* decline at Otisville is addressed below.

An anomaly in the *Sporormiella* record at Hyde Park occurs at 20 cm, where, following initial decline, spore values briefly return to a maximum. Just above this horizon, an *Abies* cone scale is AMS dated only slightly younger than the mastodon itself (Fig. 9). Although this could suggest a brief return of megafauna to this area, a simpler explanation is that the brief influx of *Sporormiella* migrated from the gut of the mastodon that collapsed and died at about this time only ca. 1 m away. In a small sedimentary basin, a high density of spores may have had little opportunity to extensively disperse.

### Hypotheses for extinction

If climate change was the sufficient cause of extinction ($H_1$ in Table 1; see Appendix) we should expect *Sporormiella* to decline at all sites simultaneously. Even at this spatial scale, spore decline is not simultaneous, whether measured by pollen chronostratigraphy or by absolute dates. Of the two sites that have plant macrofossil dates, Hyde Park and Otisville, one shows a *Sporormiella* decline at least a millennium earlier than the other. Most sites record this event earlier or later in pollen Zone II, but at Otisville, *Sporormiella* persists through Zone III, only to disappear at the same time as *Picea* pollen. There is no suggestion at this stage of the formation of a uniform or zonal vegetation pattern (Guthrie 1984). Such a development occurs yet in the future, at ca. 9000 $^{14}$C yr BP, when *Quercus* rapidly dominates regional pollen spectra, suggesting the formation of closed-canopy forest at the beginning of the Holocene

*Sporormiella* data from three of the four sites indicate that large herbivores were in decline at the very time that *Picea* (spruce) was either rising or already dominating regional pollen spectra. This tends to contradict $H_2$, which holds that the American mastodon became so dependent on spruce that it died out as hardwood forests expanded.

At least a millennium elapsed between the earliest local megafaunal collapse (*Sporormiella* decline) and dates for extinct megafauna reported here (Table 3). Recently obtained AMS collagen dates from New York's Fingerlake region are 11 630 $\pm$ 80 $^{14}$C yr BP and 10 840 $\pm$ 60 $^{14}$C yr BP for mastodon, and 10 890 $\pm$ 50 $^{14}$C yr BP for mammoth (P. Nester, *personal communication*). Even if megaherbivores declined rapidly at individual sites, a rapid wave did not sweep through the entire region. These observations weaken all hypotheses predicting a rapid extirpation of megafauna on the regional scale, specifically $H_3$, $H_4$, $H_6$, $H_9$, $H_{10}$, and $H_{12}$ of Table 1. A further difficulty for $H_3$ and $H_9$ is that megafaunal populations appear to have gone into steep decline well before the Younger Dryas climate reversal. Even if large animals were eliminated from wide areas, pockets apparently remained, suggesting a mosaic pattern of extirpation, as expected from $H_5$ and $H_{13}$.

The overkill model of $H_8$ calls for a tripartite pulsed extinction over a period of ca. 1640 years, but the generally unimodal drop in *Sporormiella* values presented

here reflects only one of the two major pulses predicted. The most abundant late occurrences in the northeast region are mastodon, a member of the megaherbivore guild, predicted by this model to disappear in the middle round.

The "second order predation" overkill model cannot account for the repeated conjunction of a terminal *Sporormiella* decline followed by a charcoal rise. $H_7$ predicts that initial overkill of megaherbivores (and possibly carnivores) would be followed by population outbreaks of smaller herbivores that then rapidly exhaust available vegetation. If it was a more regional phenomenon, the spore anomaly at Hyde Park might support $H_7$ and $H_8$.

None of the single-causal hypotheses are of much help in explaining why a drop in *Sporormiella* is followed by a rise in stratigraphic charcoal concentrations. However, $H_{11}$ proposes that large herbivores roaming continental landscapes would have kept fuel loads low by consuming vast quantities of biomass (Schüle 1990). If such animals were removed by some novel factor such as human activities or introduced disease, frequent and intense fires might result.

Synergy ($H_{13}$) incorporates the above view of herbivory and fire but extends the hypothesis to a range of human activities. These activities include hunting and landscape fires that constitute an extinction process that initially would be expected to be relatively slow, but later cumulative and may then be compounded by "natural" environmental shifts. Binnewater Pond, the highest resolution sequence, records a brief, 10-fold rise in charcoal that immediately precedes *Sporormiella* decline. This possibly is the first sign of earliest human settlers locally, who then overexploited available game, undercutting an established herbivory regime, and completing a first stage of landscape transformation. In the second phase, according to charcoal data, accumulating fuel loads develop a potential for more pervasive and frequent fires that appear later. A second well-known prehistoric activity, the deliberate use of fire to clear underbrush and encourage a renewed flush of growth attractive to game (Patterson and Sassaman 1988), could have amplified the earlier developments. Although major environmental shifts mark late-glacial time in the Northeast, a subsequent event could have a multiplied effect for a system already under a sustained assault. We propose that this is why terminal dates of most extinct taxa cluster around the onset of the Younger Dryas chronozone, apparently a millennium or more after people have entered the region. Paleolithic activities may be the underlying and sufficient cause of the observed landscape transformation, but such effects would be compounded by the inevitable climate changes.

It is useful to compare these New York records to Late Holocene deposits in Madagascar, which track environmental and other changes leading up to and following human arrival (Burney et al. 2003). A series of cores from across the island display a diachronous *Sporormiella* decline, commencing in the arid southwest, ca. 2000 years ago. At each site, spore decline is followed by a sharp rise in stratigraphic charcoal, succeeded by the last occurrences of large herbivore taxa. This occurred in a background of climatic aridification that was already well underway prior to the advent of humans.

The Madagascar records also assist resolution of uncertainty regarding the significance of the Zone II charcoal rise at Hyde Park, Pawelski, and Binnewater, when spruce is either dominant or on the decline. The spruce pollen rise, found throughout formerly glaciated parts of the Northeast is considered to mark the transition from periglacial tundra to open conifer woodland (Watts 1983). This development may seem sufficient for fire to become an important factor on the local landscape. In Madagascar, however, a very different set of environmental changes were present, yet a charcoal rise appears linked to spore decline near the time of human arrival.

Stratigraphic charcoal records from the Hudson Highlands that overlook the eastern Wallkill Valley also suggest that environmental changes alone do not account for all the available data. These upland sites would be more prone to lightning strikes, but show a later onset of fire than most of the lowland areas of this study. It took until the early Holocene for fire to play a significant role at Sutherland Pond, at 380 m elevation (Maenza-Gmelch 1997*a*). By contrast, Spruce Pond at 223 m elevation, incipiently records frequent fire in Younger Dryas time (Maenza-Gmelch 1997*b*). Together with Otisville, these records begin to outline a regional fire history that was not tracking climate changes in any simple fashion, but rather suggest a mosaic pattern of change that might be elucidated with further *Sporormiella* studies.

Dates on organic material associated with the earliest fluted point tradition, ca. 11 500 ^{14}C yr BP, are still the most widely accepted interval for human arrival in the Americas south of the ice sheets (Haynes 1969, Fiedel 1999). Generally accepted dates for the settlement of eastern North America remain no earlier than ca. 11 000 ^{14}C yr BP (Dincauze 1993).

The Dutchess Quarry Caves are located in the Wallkill Valley ~8 km northeast of the Pawelski farm and ~13 km southeast of Binnewater Pond. Formed in a dolomitic limestone outcrop, the caves have yielded Paleo-Indian projectile points and remains of the extinct giant beaver, flat-headed peccary, caribou, and other extant vertebrate taxa (Funk 1976, Funk and Steadman 1994). Several AMS ^{14}C ages range from 13 840 ± 80 to 11 670 ± 70 ^{14}C yr BP, on purified collagen from caribou bones recovered from or above stratigraphic units bearing fluted projectile points (Steadman et al. 1997). However, there is no clear association between the cultural material and extinct megafaunal species. Questions remain about the integ-

rity of the Dutchess Quarry Cave stratigraphy. Although the proxy data of this study indicates otherwise, no direct evidence has emerged to place settlement in the region before 11 000 $^{14}$C yr BP.

### SUMMARY AND CONCLUSIONS

Stratigraphic pollen, spore, and microscopic charcoal records from four sites in southeastern New York put a regional focus on the mass extinction of large mammals in North America. The proxy data from four localities show a substantial agreement regarding changes in herbivory and fire regimes that unfolded during the late Pleistocene. A region-wide drop in *Sporormiella* values during the late glacial is associated everywhere with a subsequent rise in stratigraphic charcoal.

Correlation of these data with pollen stratigraphy implies that human alteration of the landscape and megafaunal collapse began significantly before the monumental changes in vegetation that mark the Holocene boundary. Microfossil stratigraphy is supported by the radiocarbon chronology presented here to show that regional fire and herbivory regimes were transformed in advance of the Younger Dryas climatic reversal.

Bone collagen dates on extinct megafauna as late as 11 000 ± 80 $^{14}$C yr BP are seen as the terminal stage of a process in which ecological collapse followed human arrival, leaving severely reduced populations of megafauna that survived to the end of the Pleistocene.

The preceding observations may be used to evaluate the proposed causes of megafaunal extinction in North America (Table 1). Hypotheses that call for an extinction process driven by environmental or climate changes are weakened by the observed chronology. Specifically, $H_1$, $H_2$, and $H_3$, although not soundly refuted, are nevertheless severely weakened by evidence of key environmental changes that postdate the initial megafaunal collapse. By specifically invoking a drought close to Younger Dryas time, $H_9$ also suffers, but the suggestion of a human/climate interaction could apply in a more general sense. In addition, all hypotheses insisting on a rapid rate of extinction, particularly $H_4$, $H_6$, $H_9$, $H_{10}$, $H_{12}$, and to some degree $H_7$, are not supported by evidence presented here. The apparently protracted nature of the extinction process is consistent with $H_5$, $H_8$, $H_{11}$, and $H_{13}$. The data further suggest a mosaic pattern of landscape transformation and extinction at the regional level, which is most consistent with $H_{13}$.

Based on these data, it is tentatively concluded that human activities indeed drove an extinction process that took at least a millennium to complete. Such a reconstruction is now supported by a similar fossil chronology from late Holocene Madagascar, which also is associated with human arrival (Burney et al. 2003). Nevertheless, such inferences should not preclude a role for a number of forces that have been discounted here as primary causes. Once human activities were brought to bear on the system, the effects of "natural" stresses could then have been amplified (Burney 1993*a, b,* 1999). The spore data in particular, suggest an initial blitzkrieg (Martin 1984) as a crippling but not fatal blow. Human use of fire may have amplified the ecological response to a severely reduced herbivory. Climate change appears to have compounded these effects, culminating in the disappearance of all the largest members of the North American mammalian fauna.

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## APPENDIX

A review of the proposed causes of the Late Pleistocene extinctions in North America is presented in ESA's Electronic Data Archive: *Ecological Archives* M075-011-A1.