



VIRGINIA DIVISION OF MINERAL RESOURCES PUBLICATION 75

THE QUATERNARY OF VIRGINIA — A SYMPOSIUM VOLUME

Edited by J.N. McDonald and S.O. Bird



COMMONWEALTH OF VIRGINIA

DEPARTMENT OF MINES, MINERALS AND ENERGY
DIVISION OF MINERAL RESOURCES

Robert C. Milici, Commissioner of Mineral Resources and State Geologist

CHARLOTTESVILLE, VIRGINIA
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FRONT COVER: Quaternary travertine-marl deposits at Beaverdam Falls, Alleghany County. The falls are approximately 25 feet high (Photograph by David A. Hubbard, Jr.).



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DEPARTMENT OF MINES,
MINERALS AND ENERGY

RICHMOND, VIRGINIA

O. GENE DISHNER, Director

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FOREWARD

The Virginia Division of Mineral Resources celebrated the 150th anniversary of its founding in 1984 and 1985. One of several events sponsored by the Division in commemoration of this anniversary was a Symposium on the Quaternary of Virginia, held in Charlottesville on September 26-28, 1984. This Symposium was designed to meet several important objectives: to summarize the state of knowledge on the Quaternary of Virginia and its environs; to call attention to research underway on the Quaternary of Virginia and to identify problems, priorities, and directions for future work; to assemble scientists, students and layman with interest and expertise in the Quaternary of Virginia and its environs in order to promote and facilitate the exchange of ideas and information on the subject; and to promote new interest in the study of the Quaternary of the region. The program provided a comprehensive overview of the status of knowledge of the Quaternary of Virginia. Knowledge about the megafauna of the region was emphasized in commemoration of Thomas Jefferson's interest in this subject area.

Eight of the thirteen invited papers and ten of the eleven poster papers presented at the Symposium are included in this volume. The keynote address presented by Silvio Bedini entitled "Thomas Jefferson and American Paleontology" was published in 1985. The meeting closed with a field trip to Saltville led by Jerry McDonald (1984).

Contained in this volume are papers dealing with many of the major topical areas of Quaternary studies for Virginia and environs. A general summary of geomorphic processes and an evaluation of evidence for Pleistocene overprints on them are given by Conners, who finds a great need for detailed work on Pleistocene geology in Virginia. Three examples of geomorphic studies included in the present volume are those summarizing differences measured in fans on either side of the Blue Ridge by Kochel and Simmons and on alluvial deposits lying above the Potomac

River and some of its tributaries on selected headwater parts of the drainage basin by Kite, Bell and Armstrong, and on travertine and marl deposits known from the state by Hubbard, Giannini and Lorah. Holman and Fay, in separate papers, present evidence that Pleistocene and modern assemblages of reptiles and amphibians (herptiles) from middle Appalachian localities are harmonious, unlike those of mammals; herptiles appear to have tolerated the extreme changes in climate more easily than mammals. Changes in the composition of plant communities in the Appalachians over the last 23,000 years are described by Delcourt and Delcourt. Remnants of several Arctic and boreal plant species which evidently became established in Virginia during glacial stages exist today in isolated areas near the summits of some of the State's higher mountains as shown by Woodward and Ruska. Two recent studies of Pleistocene vertebrate faunas are included: one from a fissure-fill in Pennsylvania (Fonda and Czebieniak), the other from a fluvial (?) deposit in northern Virginia (Ott and Weems). Eshelman and Grady give detailed descriptions of Quaternary vertebrate localities in Virginia, including lists of bird and mammal species found at these sites. McCary summarizes some of his lifelong work on Paleo-Indians in Virginia by describing the distribution of Clovis projectile points from around the State and notes that nowhere in the State have ancient human activities been found in association with Pleistocene animal remains. Papers by White and Barfield summarize aspects of recent archeological investigations at one of the Saltville sites (44Sm51). Rose uses archeological data and historical accounts by early European observers to document the occurrence and distribution of large mammals in Virginia during the late prehistoric and early historic period. McDonald gives a historical sketch of the development of Quaternary vertebrate paleontology and zooarcheology within Virginia, lists modern work underway on these topics, reviews some of the major features of ongoing field work at Saltville, and recommends more emphasis on vertebrate pa-

leontology and zooarcheology at Virginia universities and museums. A novel idea of Pleistocene extinctions, dwarfism, and deformity resulting from inferred climate-induced decreases in blood supply to the mammalian uterus is presented by McLean. Boaz recounts some of the early ideas on evolution of J. L. Cabell.

The editors here make readers aware of two important bibliographic works on the geology of Virginia, including those dealing with Quaternary geology, that might otherwise be overlooked. One is the matchless product of a supreme effort by J. K. Roberts (1942) and the other is a fine work covering the decade from 1960 to 1969 by Boyd Hoffer (1977). We have compiled a new bibliography on the Quaternary of Virginia for those years to the present not included in the earlier cited works. This reference work was obtained from the GeoRef file of the Dialog System in California. It is on open-file at the Virginia Division of Mineral Resources and can be obtained by writing the Division Librarian.

J. N. McDonald
S. O. Bird, editors

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THE QUATERNARY OF VIRGINIA

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QUATERNARY GEOMORPHIC PROCESSES IN VIRGINIA

John A. Connors¹

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INTRODUCTION

With few exceptions (notably the pioneering work of John T. Hack), relatively little geomorphic research has been done in Virginia in recent decades and only a small part of that has focused directly on the influences of Quaternary climatic fluctuations on denudational and depositional processes. The indispensable volume, *The Qua-*

ternary of the United States, for example, devotes less than two of its 900 pages to "Quaternary processes in the Atlantic Coastal Plain and Appalachian Highlands" (Judson, 1965). The geomorphic literature on the inland areas of Virginia, the focus of this paper, is especially sparse. As will be noted, a handful of recent studies have advanced our knowledge of some aspects of Quaternary geomorphology in Virginia. In addition, research is under way focusing on various alluvial and colluvial deposits, periglacial phenomena, surface accumulations of calcium carbonate (marl, tufa, travertine), and a variety of paleontological and archeological sites.

¹1901 Downey Street, Radford, Virginia 24141

The purpose of this paper is to summarize current knowledge of geomorphic events and processes which appear to be associated with Quaternary climatic changes in Virginia. Unfortunately, little is known about the specific denudational processes influencing landforms and associated deposits, and our understanding of the complex responses of those processes to the many climatic fluctuations of the recent geological past is even more deeply shrouded in mystery. Consequently, recognizing and accurately interpreting the evidence can be very difficult. As a result, much of what follows will of necessity be speculative in nature.

HISTORICAL PERSPECTIVE

To help place our topic in geological perspective, a brief summary of the evolution of the Virginia landscape is offered. For more details, the reader may consult Judson (1975) and Hack (1982).

(1) During the late Precambrian and early Paleozoic eras, low-gradient streams flowed southeast from the Canadian Shield to the ancestral Atlantic Ocean.

(2) During the mid-to-late Ordovician (460-435 million yrs B.P.), this proto-Atlantic Ocean apparently began closing as the ancestral North American continental plate approached the European and African plates, initiating a monumental series of orogenies which were to continue for the next 220 million years. Because this mountain-building activity was centered to the east of today's Appalachian highlands, streamflow across Virginia was eventually reversed towards the west and northwest. The New River's northwesterly flow is apparently an inheritance of these ancient upheavals.

(3) During the Triassic period, a massive thermal convection cell arose within the mantle producing tensional forces in the lithosphere and the gradual rifting apart of North America from Europe and Africa. During the uparching, stretching and faulting associated with early rifting, crustal thinning occurred. As the new Atlantic Ocean widened and the eastern edge of North America withdrew from the center of spreading (the Mid-Atlantic Ridge), the eastern margin of the continent subsided and drainage across Virginia began reversing towards the southeast once again.

(4) The southeasterly drainage reversals probably began some 170 million-years ago in northern Virginia (Potomac River) and have continued to

the present day. A major mechanism in establishing the southeasterly streamflow has been the capture of higher-elevation, northwest-flowing streams by the steeper gradient streams flowing directly southeast to the Atlantic. The New River will fall victim to an impending piracy by tributaries of the Roanoke River in the not-too-distant future, geologically speaking (Figure 1). During all this time, widening of the Atlantic Ocean, uplift of the Appalachian highlands, and the denudation and sculpturing of the Virginia landscape have been progressing more-or-less continuously, albeit at varying rates.

(5) Beginning roughly 55 million years ago, a long cooling trend called the "Cenozoic Decline" began. This trend culminated in the series of dramatic climatic fluctuations which have characterized Earth history during the past 2 million years or so. Table 1 provides some details of the current "Ice Age". In Virginia, the focus of Quaternary studies has been on the most recent 50,000 years or so, especially the Late Wisconsinan glacial stage and the ensuing Holocene interglacial.

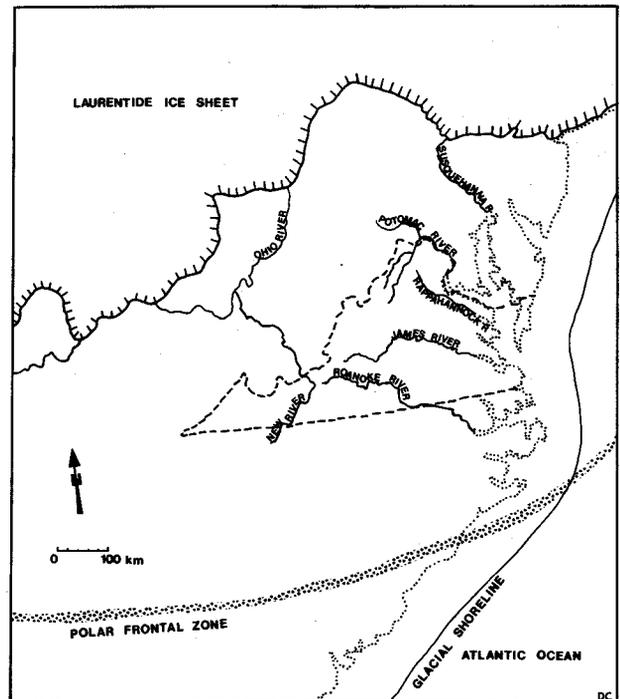


Figure 1. Map showing approximate relation of Virginia to the Laurentide ice sheet, sea level (roughly 395 ft. (120 m) below present mean sea level), and the northern edge of the Polar Frontal Zone during Pleistocene glacial maxima.

Table 1. Outline of Cenozoic glacial chronology.

<i>Years B.P.</i>	<i>Events</i>
70M ^a -65M	Earliest evidence of possible glaciation. Preliminary studies of marine microfossils in Transantarctic Mountains believed to have been carried upslope by glaciers, show glaciation cycles at roughly 70-65M, 50-40M, 30-20M, and 7-3M yr B.P. ^b
55M	Long cooling trend, the "Cenozoic Decline", begins. Apparently related to drift of continents into polar regions. Baffin Bay begins to open allowing cold waters of the Arctic Ocean to enter the Atlantic.
38M	Rapid worldwide temperature decline and formation of near-freezing Antarctic bottom waters.
28M-27M	Good evidence of small, widespread glaciers in Antarctica.
14M-10M	Antarctic Ice Sheet buildup following opening of Drake Passage and full development of the Antarctic South Ring stream.
10M-8M	Antarctic Ice Sheet expands to about half present volume and becomes permanent. Evidence for earliest Cenozoic glaciation in North America.
3.5M	Late Pliocene uplift, including closing of Isthmus of Panama which strengthened Gulf Stream, helped trigger onset of "ice age" climates and circulations. Modern oceanic circulation established by 3.2M yr B.P. Glaciers in Alaska (3.6M yr B.P.) and California (3M yr B.P.)
3.0-2.5M	Pronounced increase in fluctuations between warm and cold climatic episodes. Northward expansion of Antarctic polar front and growth of northern ice sheets. ^c
2.4M	Ice sheets about 2/3 as large as Wisconsin sheets <i>may</i> have existed in North America.
1.8M-1.6M	Beginning of Pleistocene Epoch, based on cold-water, marine fossils.
1.6M-125,000	Because of much conflicting data, no detailed chronology is attempted here. Canada and the northern United States experienced multiple glaciations interspersed with warm interglacial episodes. Good evidence for at least 17 major fluctuations exists in Europe for the last 1.7M yr, based on loess deposits and paleosols. Deep-sea cores indicate at least 21 cycles of glaciation in the last 2.3M yr, based mainly on oxygen-isotope data.
125,000-100,000	Last major interglacial (Sangamon).
85,000	Earliest definitive evidence of Wisconsinan glaciers in North America.
75,000	Start of rapid Wisconsinan ice growth in North America.
70,000-45,000	Mid-Wisconsinan or "Port Talbot" interstade: North American ice sheets retreated to core areas.
25,000	Rapid readvance begins.
23,000	Marked cooling and pond formation at several sites in eastern U. S. between latitudes 34° and 37°N.

Table 1. (cont.)

<i>Years B.P.</i>	<i>Events</i>
20,000-18,000	Maximum extent of Wisconsinan ice sheets: 5.8M mi ² (15M km ²) of land in North America glacier-covered; sea level 395 feet (120 m) lower—Bering Shelf was 620 mi. (1000 km)-wide land mass connecting North America and Asia: firnline averaged about 3280 feet (1000 m) lower than at present in mid-latitudes and temperatures were roughly 3°C colder near oceans and 17°C colder in some mid-continent areas.
18,000-6000	Ice sheets generally in retreat but with many fluctuations, including major readvances of Laurentide sheet at 13.5, 11.8, and 8.2 thousand yr B.P.
16,500	Climatic amelioration beginning in Tennessee.
15,000-14,000	Undeniable evidence of human occupation of North America.
14,000	Rapid rise in sea level begins and continues until about 10,000 yr B.P. Firnline rising: Yellowstone Plateau, San Juan Mountains, Mauna Kea, other areas deglaciated. Pluvial lakes of western U. S. receding.
13,500-8000	Glacial Lake Agassiz in existence.
13,000	24,000 years of drought ending in Florida.
12,500-12,000	Cordilleran Glacial Complex retreats to north of U. S.-Canadian border. Last catastrophic megaflood of Lake Missoula. Last permafrost in Pennsylvania. Warm climate with summer drought on Gulf Coastal Plain.
11,000	Accelerated ablation of ice sheets. Prairie replacing spruce forests in arid parts of Great Plains.
11,000-10,000	Extinction of many species of large vertebrates.
10,400	Lake Algonquin (Georgian Bay-Lake Superior area) began draining northeast into Champlain Sea and Atlantic. Prior to this, most meltwater drained south to Gulf of Mexico.
10,000	“Official” end of Pleistocene and start of Holocene. No break in ongoing climatic adjustments. Deglaciation continues. Vast ice sheet still exists over eastern Canada and sea level is some 66 feet (20 m) below present level. Radiation curves for tilt and precession reinforce each other causing average 7% greater solar radiation than at present and encouraging increased rainfall, slightly warmer temperatures in northern land areas—possibly influenced also by early Holocene expansions of pluvial lakes.
7500	Last readvance of Laurentide ice sheet.
7500-5500	Altithermal interval of exceptionally warm, dry climate in many areas: Lake Bonneville was reduced to a playa; 7000 years ago the prairie/forest border in U. S. midwest was 62 mi. (100 km) east of present location.
6500	Last remnant of Laurentide ice sheet melts on Quebec-Labrador Plateau.
6000	Change from zonal to meridional weather patterns bringing more rain to eastern and central U. S.: slightly cooler; more bogs; pines replace deciduous trees in many areas; flooding more frequent.

Table 1. (cont.)

<i>Years B.P.</i>	<i>Events</i>
5500-0	Neoglaciation: numerous readvances of alpine glaciers with 2 or 3 major advances, each with substages, represented in many mountain ranges. A prelude to the next full glacial?
100-0	Meltbacks of many small alpine glaciers; sea level rises about 0.5 ft. By the mid-1980's, evidence of small increases in mean global temperature and of significant increases in CO ₂ and other "greenhouse" gases in the atmosphere due to human activities leads to growing concern over human impacts on climate.

(Principal sources: Bowen, 1978; Eyles, 1983; Wright, 1983)

^a M = million

^b *Science News*, 1983, vol. 123, p. 6

^c *Science News*, 1986, vol. 129, p. 374

Very little evidence has been uncovered in Virginia which can be related confidently to earlier Quaternary events.

THE QUATERNARY PALEOENVIRONMENT

As an aid in visualizing the environment during a full glacial, imagine driving northeast from Winchester in northern Virginia along Interstate-81 and, in less than four hours driving time (about 180 miles), encountering a great mass of ice blocking the highway. Imagine traveling due west from Winchester along Route 50 and encountering that same wall of ice after 7 or 8 hours driving time (350 highway miles). Such would have been the situation 20,000 years ago. Climates as warm as the present Holocene interglacial probably are characteristic of only about 10 percent of a typical glacial-interglacial cycle. The duration of such a cycle, over the last 500,000 years at least, has been about 100,000 years, and appears to be closely related to the eccentricity of the Earth's orbit about the Sun (Imbrie and Imbrie, 1979).

The great ice mass noted above was part of the Laurentide ice sheet. It rose steeply from its margin to a maximum elevation roughly twice that of Virginia's highest peak. It covered 4 million square miles (10 million km²) of land—a high, almost unbroken, glacial desert stretching northward to well beyond the Arctic Circle. Because so much water was locked up in glaciers, mean sea level was about 395 feet (120 m) lower than at present (Bloom, 1983a). Thus a journey eastward from Winchester 20,000 years ago would have found a broad valley where Chesapeake Bay now exists. In the center of the valley,

the Susquehanna River would be carrying glacial meltwaters and sediments to the Atlantic Ocean whose shoreline lay some 60 miles (97 km) eastward of its present-day position.

Strong katabatic winds, composed of air that was frigid, dry, and heavy, would slide down over the vast Laurentide ice sheet and sweep south and southeast across Virginia towards the Polar Frontal Zone which lay some 180 miles (290 km) south of the Virginia—North Carolina border near latitude 34°N (Figure 1). Along the Polar Frontal Zone, these cold and dry air masses met with warm, moist air masses from the Gulf of Mexico to form a steep north-south temperature gradient. As long as an ice sheet persisted in northeastern North America a fairly strong east-west temperature gradient also existed, and atmospheric circulation across the United States tended to be strongly zonal (from west to east) with little seasonal variation in basic circulation patterns (Knox, 1983). Because of the convergence of westerlies and tropical air masses, precipitation was abundant along the broad Polar Frontal Zone itself and warm-temperate forests similar to those of present-day Virginia existed there during glacials (Delcourt and Delcourt, 1984). In Florida, south of this zone, dry, windy conditions and scrub brush prevailed (Watts, 1983). North of the Polar Front, boreal forest with abundant jack pine and spruce dominated the eastern United States. North of this forest, a fringe of tundra over 93 miles (150 km) wide in places (Watts, 1979) bordered much of the ice sheet itself. Patches of treeless tundra also extended southward along the high Appalachian Mountains to the Smoky Mountains (Wright, 1981). Although minor pockets of permafrost probably existed at higher elevations south of

Pennsylvania, it is very unlikely that sufficient precipitation occurred to allow formation of small glaciers such as those which Berkland and Raymond (1973) suggested were present on Grandfather Mountain, North Carolina. Nival processes associated with snowbanks may well have been operative, but proof of even this is lacking. The lower limits of tundra in Virginia are not known but evidence of Late Wisconsinan tundra at 2620 ft. (800 m) elevation in Maryland (Maxwell and Davis, 1972) and at 3280 ft. (1000 m) in West Virginia (Watts, 1979) suggests it may have extended to similar levels at favorable locations in Virginia.

Detailed temperature and precipitation values for glacial-age Virginia are still conjectural. Current mean annual temperatures range from near 16°C in southeast counties to near 9°C in mountainous counties. Ice-age temperatures were probably on the order of 10°-15° colder overall with very cold winters accounting for most of the difference. Precipitation may have been some 20 to 50 percent less than today during full glacial conditions with a significantly higher percentage of that falling as snow than does today (Delcourt, 1979; Barry, 1983).

GEOMORPHIC PROCESSES AND CLIMATIC CHANGE

We will now pose some questions of major importance to Quaternary geomorphologists, discuss the difficulties, both general and specific, which must be confronted when attempting to answer those questions, and then review the relations between specific processes and Quaternary changes of climate in Virginia.

Among the major questions of concern are these: (1) What were the nature and magnitude of the variations in paleoclimate? (2) When did climatic changes occur in specific locations and what were the durations of the climatic regimes? (3) How do climatic fluctuations influence the various types of processes acting upon the landscape—what is their relative importance and what are the rates at which they progress? (4) What are the resulting impacts upon the landscape, how much evidence of these impacts remains, and how do we recognize that evidence and place it in a meaningful time-frame? (5) How do we apply our knowledge of past and present processes and their known or suspected results to such practical problems as (a) the geological interpretation of known Quaternary fossil and archeological sites; (b) the location of new and potentially rewarding fossil and archeological

sites; (c) improving knowledge of the paleoenvironment; (d) more accurate correlation and dating of Quaternary events and materials; and (e) intelligent land use (e.g.; locating safe waste-disposal sites, stable building sites, good construction materials and dependable water supplies—see Eyles, 1983)?

Three major difficulties are encountered when attempting to unravel paleo-climatic influences on geomorphic processes and landforms.

(1) Singularity of landforms: Like fingerprints, no two landforms are completely identical. It may be possible to identify certain threshold conditions at which an active feature (e.g., slope or stream channel) changes from one equilibrium state to another. However, the uniqueness or "singularity" (Begin and Schumm, 1984) of landforms means that critical parameters quantified at one location cannot be applied with certainty to another locality, even though the environmental settings may appear to be nearly identical.

(2) Meager understanding of contemporary geomorphic processes: Recognizing the processes shaping today's landscapes is far more difficult than it may at first appear. To use one common example, it may be apparent that a rock has been broken down into smaller fragments which now lie scattered along a slope. Problems ensue when we attempt to ascertain exactly what processes caused the breakdown, quantify the contribution of each process involved, and determine when and for how long those processes were operative. Often we are reduced to vague references about "weathering and erosional processes" as a result of our inability to delineate the impacts of such activities as hydration, hydrolysis, oxidation-reduction, frost action, simple solution, overland flow influences, or organic activity.

(3) Extrapolation to past conditions: The difficulties of attempting to apply our limited knowledge of complex interacting processes to the uncertain conditions of the past should be manifest. The task is further complicated by the often profound impacts man has had on vegetative cover (deforestation, farming, grazing), biogeochemical cycles (acid rain, fertilizers, pesticides), streamflow (dams, diversions, accelerated runoff, water table lowering), and the like. For example, the present mechanical sediment load of streams in the eastern United States is probably 4 to 5 times what it was prior to extensive human modification of the land (Meade, 1969).

In spite of such difficulties, Pleistocene stream terraces, buried channels, talus accumulations, lake deposits, distinctive unconformities in sediments and other forms of evidence have been

correlated with specific paleoclimatic intervals in many parts of the world, including numerous locations in the western, central and northeastern United States. In Virginia, however, the imprints of climatic change upon the landscape appear to have been much more subtle, and most correlations to past environments are tentative or unproven. Aside from some late Quaternary sequences in the coastal regions, very few deposits or landforms of any kind in Virginia reveal a clear record of alternating Quaternary environments. This may seem somewhat surprising in view of the numerous climatic fluctuations the area must have experienced during the last 1.5 million years or so.

A fundamental reason for this lack of clear paleoclimatic evidence of a geomorphic nature appears to be that the climatic changes influencing the Virginia terrain generally did not cross major geomorphic thresholds as they did in certain other environments. An important factor in the lack of threshold crossover was the buffering effect of the forests, which maintained their hold on most of the terrain during glacials as well as interglacials. Even though the forest type changed markedly, the influences on slope processes and sediment yield over most of the region may not have changed sufficiently to trigger any major widespread adjustments in basic erosional and depositional processes. As a consequence of this lack of drastic change in surficial processes and the slow ongoing uplift of the Appalachian highlands (Hack, 1982), the terrain as a whole continued to experience denudation during both glacials and interglacials. The constant wearing away of landforms has left behind little concrete evidence of climatic changes for the twentieth century geomorphologist, and evidence of mid-to-early Pleistocene environments is virtually unknown.

A number of estimates of denudational rates have been made. Young's (1969) survey of denudation rate estimates led him to conclude that most areas of steep relief are being lowered from 3.9 to 39 inches (100 to 1000 mm)/1000 yr. Hack (1980) compiled data for the Appalachian region and concluded that the long-term rate of denudation was about 16 inches (40 mm)/1000 yr. Houser (1980, p. 101-102) suggests that solutional processes on the carbonate rocks of the region are responsible for about 5.4 inches (13.5 mm) of that 16 inch (40 mm)/1000 yr total, the rest being attributable to mechanical processes. It should be noted that most of this estimated denudation occurred prior to the Pleistocene Epoch.

Few attempts have been made to quantify possible differences in denudation rates in the Appalachians between Quaternary and Tertiary Periods, or between glacial and interglacial episodes. Denny (1956) estimated that plateau tops in north-central Pennsylvania have been lowered as much as 197 feet (60 m) during the Pleistocene (about 38 mm/1000 yr). Hack (1965) estimated a long-term lowering of 226 feet (69 m)/million yr (69 mm/1000 yr) for Virginia's Shenandoah Valley. Kane (1975) concluded that the current denudation rate of the 613 mi² (1595-km²) Rappahannock River Basin of Virginia had decreased from 0.95 to 0.87 inches (24 to 22 mm)/1000 yr over a recent 20 yr period. The lowering rate in small basins is generally much higher than in large ones—Kane found a 53.5 inches (1358 mm)/1000 yr denudation rate for a small basin of 0.08 mi² (0.2 km²) near Reston, Virginia. Denudation estimates can be used to help explain why deposits of alluvium or colluvium revealing a long history of Quaternary sedimentation are rare in the Appalachian region (e.g., Mills, 1981, p. 218-219).

Although such denudational rates imply a certain gross uniformity of overall effect during the Quaternary, changes in the rates of certain types of weathering, mass wasting, erosion and deposition have undoubtedly taken place during the Quaternary. Evidence for, and some speculation concerning, such changes will now be reviewed for the major surficial processes.

WEATHERING AND MASS WASTING

In a colder climate, such as existed in Virginia during glacials, chemical weathering should be inhibited because lower temperatures decrease the rates of most chemical reactions. Mechanical weathering and mass wasting rates should increase during glacials, mainly through the greater efficacy of frost action. The importance of frost action at cold temperatures appears undeniable, especially where permafrost exists (Washburn, 1980). Where permafrost is not present, and even where mean annual temperatures are above freezing, frost action may still be an important, even dominating, process, but it becomes more difficult to identify positively its effects and isolate them from similar effects of non-cryogenic processes.

Doubts do exist regarding the importance of freeze-thaw action, however. White (1976) advocates hydration shattering as the major process causing the splitting apart and fractionation of

bedrock. Experiments and observations have yet to document that ice is capable of cracking solid rock. Even in a cold environment, it is highly probable that such unjustifiably neglected weathering processes as hydration, hydrolysis, and especially exudation (interstitial salt crystallization) play an important role in preparing the way for, and reinforcing, frost action.

The nature of the deposits and landforms produced will vary with such factors as bedrock lithology and structure, the degree of seasonal temperature change, the amount and distribution of precipitation, and latitude. An understanding of the Pleistocene periglacial environment of Virginia is complicated by the lack of present-day analogues—i.e., a mid-latitude periglacial climate in an area of similar elevation, topography and geology. For example, the angle of the sun is much higher in Virginia than in modern tundra areas such as those of Canada and Siberia. More direct rays of sunlight combined with longer winter days and longer summer nights may have had a significant impact upon freeze-thaw action by increasing the number of freeze-thaw cycles during the year. Aiding this would be the cold dry air which would encourage many more clear sunny days during winter, encouraging melting, and clear cold nights during summer, encouraging freezing.

The rate of diurnal temperature change may also have increased considerably during glacials in Virginia. Rapid freezing causes more efficient near-surface freezing, forming a seal which can significantly increase the forces exerted by the underlying water as it solidifies and expands. In the colder yet drier environment that prevailed during most of the Pleistocene in Virginia, snowbanks may have been quite thin in many places, reducing their insulating capacities and enhancing nival processes (Embleton, 1979).

In the "Ice Age" springtime, the combination of frequent freeze-thaw cycles and abundant water from thawing snow and ground-ice would facilitate the production of detritus and enhance downslope creep and flow of regolith. These activities would tend to produce a thicker regolith, thus reducing slope gradients, increasing stream load and inhibiting stream incision. During interglacials, there would be a reduction in the rate of mass wasting and regolith production, but not a cessation of it. Increased precipitation would yield more runoff, which would winnow fines from slope deposits, increase streamflows, encourage stream incision and lead to steeper slopes (Hack and Goodlett, 1960). That mechanical

weathering and mass wasting did progress at a more rapid rate during glacials is strongly suggested by the observation that periglacial-type features and associated deposits increase in frequency from south to north along the Appalachian highlands and by the sheer abundance of colluvium in certain locations (Mills, 1981).

Much of the geomorphic evidence that has been used to document the former existence of periglacial conditions consists of weathering and mass wasting features such as stone stripes, stone polygons, block fields, and colluvial deposits which show distinct vertical zonations that can be related to past climatic intervals. All these features are present in Virginia and adjacent areas but colluvium with informative vertical zonation is rare—most exposures of residuum and colluvium are notoriously unilluminating (Figure 2). Many of the features once widely assumed to be of relic periglacial origin (Smith, 1949) have been recently shown to be quite active under the present interglacial climate (Hack, 1965; Houser, 1980). A case in point are diamictons.

Diamictons, or diamicts, are nonsorted terrigenous deposits containing a wide range of particle sizes (Flint, 1971, p. 154). The Appalachian region contains extensive diamictons ranging in

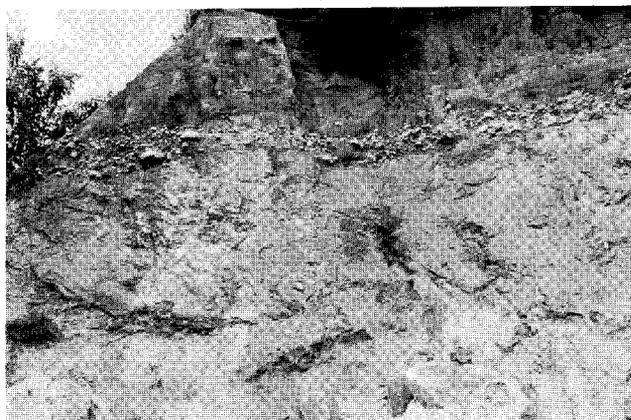


Figure 2. Regolith in borrow pit in Rockingham County, North Carolina along truck route 87 near Eden (Leaksville) in the Piedmont Province, about 3.7 miles (6 km) south of the Virginia border. Cut shows saprolite (decomposed metamorphic bedrock) overlain by a generally fine-grained, poorly sorted material which seems to be mostly colluvium. Upper zone has a very thick deep-red soil profile suggesting all this material may be pre-Quaternary in age. (Photograph taken August 19, 1980)

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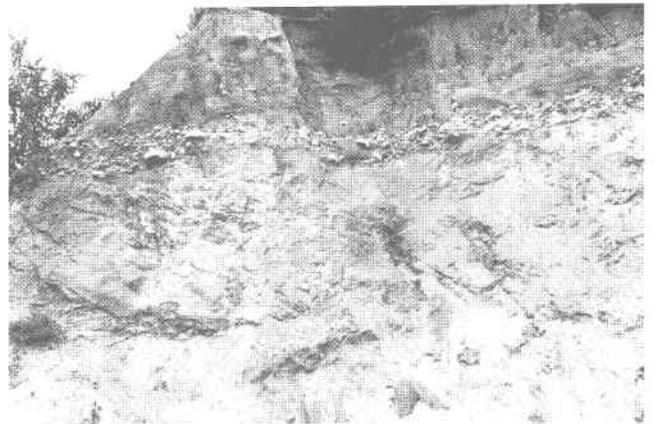


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age from probable Tertiary to contemporary. Most are products of mass wasting. The steep slopes of the Appalachian region are among the most landslide-prone in the nation. During periods of high rainfall, hundreds of debris avalanches, along with mudflows, slumps, flash floods, rockfalls, reactivated earthflows and the like, have been shown to occur (see, for example, Hack and Goodlett, 1960). In August, 1969, Hurricane Camille yielded thousands of mass movements—one study identified 1534 debris “slides” in a 36 mi² (93 km²) area of the Spring Creek drainage basin in eastern West Virginia (Radbruch-Hall and others, 1976). An extreme event such as Camille—28 inches (710 mm) of rainfall in 8 hours—has an estimated recurrence interval of about 1000 years. It produced foot-slope deposits averaging from 12 to 24 inches (30 to 60 cm) in thickness, some containing blocks up to 6 feet (2 m) in diameter (Williams and Guy, 1973). Kochel and others (1982) found evidence for repeated debris avalanching in central Virginia every 700 to 4000 years. Individual events can be recognized using such criteria as buried soils and textural, structural and mineralogical differences between the deposits.

Many of the boulder streams which have been described in the Valley and Ridge southwest of Roanoke are also diamictons. These bouldery accumulations occur in the bottoms of small valleys on the sides of steep ridges, especially where a resistant rock such as the Silurian Tuscarora Sandstone directly overlies a nonresistant unit (Figure 3). Interpretations of the deposits have ranged from alluvium to defunct rock glaciers. Although some may have accumulated by gelifluction and boulder creep under periglacial conditions, most appear to be the product of flash floods and debris flows during intense or “catastrophic” rainfalls (Mills, 1978, 1980a, 1980b). Houser (1980) also concludes that virtually all the colluvial-type deposits in the New River region near Blacksburg are of recent rather than periglacial origin.

However, other diamictons exist, especially at high elevations, which cannot be readily explained by Holocene processes. Michalek (1968) studied many bouldery fan-like colluvial deposits and concluded that most were of periglacial origin. His evidence was that (1) the deposits seem to be undergoing erosion at the present time; (2) the upper ends of many deposits are covered with block fields; (3) no fans were found below about 2300 feet (700 m) elevation; (4) the fans diminish in number and degree of development from north



Figure 3. View of northern slopes of Rich Mountain, showing footslope deposits, some 6.2 miles (10 km) east of Tazewell, Tazewell County, Virginia. Note boulders and blocks along swales at foot of mountain. Are these “boulder streams” Pleistocene deposits with the fines being winnowed by modern fluvial action, or debris flows from rare catastrophic floods of Holocene age, or neither? (Photograph taken June 22, 1980)

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Mills (1981) noted that the great quantity, depth, and apparent age of apron-like diamictons at Grandfather Mountain, North Carolina suggested accumulation under periglacial conditions. These deposits appear older near interfluvies and younger near drainageways. A follow-up study (Mills, 1982) on such bouldery foot-slope deposits seems to document a distinct age differential of at least 10,000 years, based on the percentage of clay, degree of oxidation, and clast weathering in the B-2 soil horizons. Such a contrast in age would be very unlikely had the deposits formed by ongoing random events such as those generated by catastrophic rainfalls.

Features composed of coarse rock fragments and lacking fine interstitial materials have received much attention as paleoclimatic indicators. Many such features occur as large patches of stony rubble covering slopes. Talus, scree, and felsenmeer are all basically unvegetated, or sparsely vegetated, areas covered by large broken fragments of resistant rock (Figures 4 and 5).

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Figure 4. Part of a scree slope near Sherando Lake, Blue Ridge Mountains, Augusta County. Quartzite blocks lie on steep southeast-facing slopes at about 2000 feet (610 m) elevation. Evidence indicates this slope is currently quite active. (Photograph taken June 12, 1984)



Figure 5. Large dislocated blocks of resistant metabasalt along the Greenstone Trail, Blue Ridge Parkway, Augusta County. This location is just a few miles from the scree of Figure 4 and several hundred feet higher in elevation. Large block to left is about 20 feet (6 m) high with a large cleft behind it. Unlike many screes, such large-scale blocks in the poorly developed felsenmeer or rock city-type areas of Virginia appear to be inactive periglacial relics. (Photograph taken June 13, 1984)

Slopes covered by talus and scree are typically steep, usually over 25° , and the rock fragments tend to be of moderate size, often averaging around 8 inches (20 cm) in mean diameter. Talus is derived directly from a cliff at the head of the deposit while scree lacks an immediately adjacent cliff. Felsenmeer, or block fields (blockfields) are

gently sloping (usually less than 15°) or even flat areas, and the blocks are typically larger in mean size than talus or scree, often a meter or more in diameter. If the rocks form a linear body extending down a hillside, "block stream" or some similar term is often used. If blocks are rounded, "boulder field" or "boulder stream" are appropriate terms. As with many groups of landforms, these patches of broken rocks appear to be part of a suite of gradational features and deciding on the most appropriate term for some sites can be difficult.

Generally, the gently-sloping, very coarse-grained felsenmeer-type features appear to be periglacial in origin and inactive in today's climate. They are very well developed in Pennsylvania, where several are popular tourist attractions, and become less frequent, less distinct, and more poorly developed southward along the Appalachians. Among the better known felsenmeer in Pennsylvania are the Devil's Race Course, Devil's Potato Patch, Blue Rocks Block Field, and the Hickory Run Boulder Field (Geyer and Bolles, 1979). The latter may be the largest such feature in the eastern United States, measuring 400 x 1800 feet (122 x 549 m) in areal extent. The Blue Rocks Block Field, which is at least 59 feet (18 m) deep in places and contains blocks of Tuscarora Sandstone up to 39 feet (12 m) long, was interpreted as a product of creep and gelifluction during the Wisconsin glacial by Potter and Moss (1968) who noted its close resemblance to gelifluction sheets and terraces in Alaska. More recently, Psilovikos and van Houten (1982) came to the same basic conclusion after studying the Ringing Rocks field along the Delaware River in eastern Pennsylvania. Felsenmeer require the presence of massive, resistant bedrock with quite widely spaced, distinct joints. Where the resistant rock strata are sufficiently thick, and well-developed, widely spaced joints are present, enormous blocks the size of boxcars or small buildings (Figure 6) may become detached and migrate downslope by a process called cambering, which is especially effective in a periglacial environment (Eyles, 1983, p. 122). Huge blocks, especially if isolated, may also result from the unearthing of large corestones from deeply weathered saprolite (Hupp, 1983). In the resistant bedrock itself, deeply weathered joints and slightly displaced blocks may form the deep narrow passageways of "rock cities." Similar features include periglacial tors, castellated rocks, boulder caves, and assorted fissures and clefts (Figure 5). Geyer and Bolles (1979) provided



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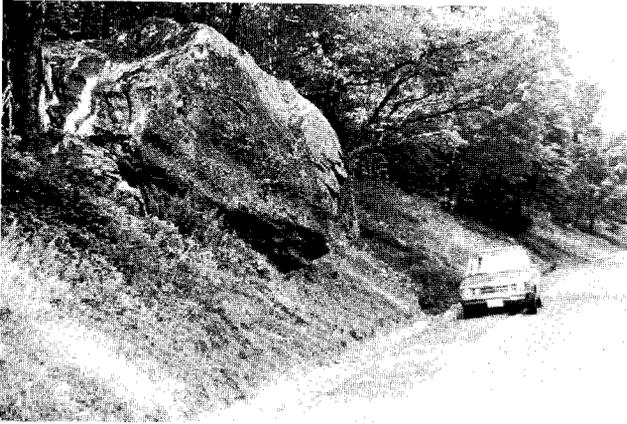


Figure 6. Large isolated boulder along Skyline Drive (near Mile 79) in Shenandoah National Park. No cliffs are nearby and slopes in the forest above the boulder are gentle. A case of periglacial boulder creep, unearthing of a corestone, or both . . . , or something completely different? (Photograph taken June 13, 1984)

descriptions and photographs of many such features, with periglacial action frequently cited as critical to their origin. Most of these phenomena reveal a heavy lichen cover, exhibit deeply pitted and weathered rock surfaces, and show no sign of present activity, attesting to their relic nature.

In contrast, scree slopes, which are especially common along steep slopes in the northern Blue Ridge and Valley and Ridge provinces of Virginia (Figure 4), frequently show such evidence of current activity as (1) tilted trees and scree-inundated shrubs at the base of the slope; (2) abundant fresh rock surfaces and other evidence of recent turnover; (3) less than 75 percent lichen cover; (4) depressions or hollows on the scree surface; (5) broad tumescences or bulges along lower scree slopes; (6) recent rock-slide tracks and scars on slopes below the scree; (7) damming of scree behind large logs or other blockages on the slope; and (8) frequent scars or deformations on trees located on or adjacent to the scree slopes (Hack, 1965; Hupp, 1983).

Where scree slopes and felsenmeer-type features are found in the same area, the scree generally occupies steeper slopes at lower elevations. It appears that many scree slopes are currently undergoing downward migration by a series of complex mass movements as indicated by slide tracks and scars near the bottom of the scree slope. More stable slopes are evident at and beyond the upper part of the slope. Scree is separated from upslope outcrops of the scree-

forming bedrock by forests which are older near the outcrop than lower on the slope (Hupp, 1983).

In addition to resistant upslope bedrock with suitable joint or fracture patterns, the development of large "stone patch" phenomena is apparently favored by the presence of a nonresistant rock underlying the slopes below the resistant formations. In Virginia the nonresistant bedrock is often a shale or other clay-rich material such as the Upper Ordovician Martinsburg Formation. The impermeable nature of such rock limits downward infiltration of water, leading readily to saturated conditions in the overlying colluvium. The pore pressure which develops within the unconsolidated regolith greatly decreases its cohesion. In steeply-sloping treeless scree and talus areas, gravitational attraction can overcome the weakened cohesive forces during periods of heavy or extended rainfall, causing slope failures, especially at the base of the slopes where saturation and pore pressures are greatest. Recent movements of scree on northern Massanutten Mountain have been shown to coincide with periods of heavy rainfall and high streamflow (Hupp, 1983). The numerous "blow-out pits" (landslide headwall hollows or "cirques") which have been observed on scree slopes following heavy downpours attest to the importance of this process. Basal lubrication and sliding along the clay-rich underbase, interstitial water flow (piping), and freeze-thaw may also play a roll in modern as well as glacial-age activity along such slopes. It is generally believed that formation of talus and scree was more effective during glacials and that many presently active scree slopes are merely remnants of the more extensive block-covered slopes of a colder climate.

Freeze-thaw activity may encourage movement along rock-strewn slopes in several ways. Early season snowfall packs in around blocks. Melting, penetration and refreezing of the water occurs, replacing air spaces with ice which, unlike air, is a good conductor of heat. The result is accelerated heat loss from the block field or scree, encouraging ever deeper freezing. Water seeping downslope along the surface between the impermeable underlying material and the colluvium will freeze beneath the barren rubble causing additional expansion and pressure. In the springtime, the upper part of the ice surrounding the blocks will melt and be replaced by stagnant air which helps to insulate the lower ice and retard its melting (Hack and Goodlett, 1960). Even today, ice has been found in Virginia scree as late as July, and in some deep crevasses or block caves

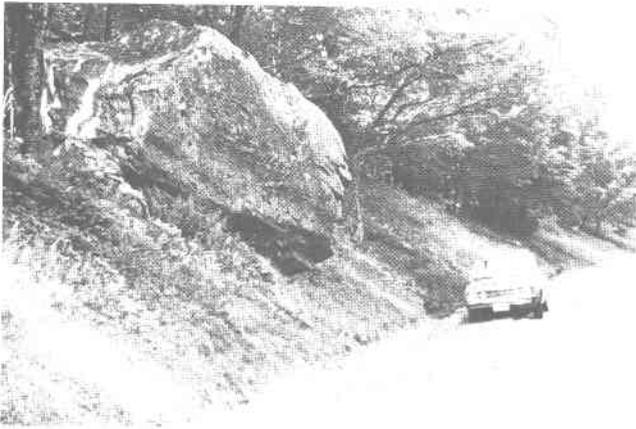


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of New York and New England, it may persist all summer. Thus it is quite probable that patches of permafrost existed in Virginia during glacials. Part of a scree slope cemented and rendered impermeable by such persistent ice forms a barrier to downslope subsurface water seepage, causing locally high pore pressures and encouraging failure (e.g., a rock avalanche) at that place on the scree slope. Even without development of such frozen barriers, the ground saturation of slopes and the frequent refreezing during the periglacial regimes would enhance both the production of more blocks and downslope movements.

Other periglacial-related features occurring in

Virginia include sorted stone polygons, nets, stripes, and steps. The larger of these forms (roughly a meter or more in width or diameter) are generally regarded as periglacial relics (Clark, 1968). Some of the smaller features may be currently active. Table 2 lists a number of such features and indicates the probability of finding them in Virginia. Clark (1984) reports that studies on such features are nearing completion at Whitetop Mountain and Interior, Virginia and other locations. It is hoped that radiocarbon and thermoluminescence dating of critical soil horizons will begin to yield a chronology which can be applied to such phenomena.

Table 2. Occurrence of relic periglacial features in Virginia.

<i>Feature</i>	<i>Occurrence in Virginia</i>
Felsenmeer (blockfields)	yes
Rock cities	yes; small compared to those further north.
Large cambered blocks	yes
Scree and talus slopes	yes; considerable ongoing activity.
Sorted and stone polygons, nets and stripes	yes; small forms may be active at high elevations.
Tors	yes; other origins possible; some active.
Rock glaciers	improbable.
Cryoplanation terraces	probable.
Thermokarst depressions	improbable.
Pingos	highly improbable.
Palsas (palsen)	improbable; easily destroyed - preservation unlikely.
Ice-wedge polygons and casts	highly improbable.
Soil-wedge polygons	improbable.
Periglacial involutions (frost-heaved soils)	yes; origins may be questionable.
Gelifluction fans, lobes, aprons, terraces	yes; difficult to distinguish from Holocene mass wasting features.
Periglacial soil mounds	probable; origins of such features remains debatable.
Ice-rafted clasts in alluvium.	yes.

FLUVIAL PROCESSES

The impacts of climatic change upon fluvial processes are highly complex. Even within a single region, a given change may produce stream erosion in one drainage basin while inducing deposition in another. Factors influencing stream response to a given shift in climate include vegetation, relief, steepness and orientation of slopes, size and shape of the drainage basin, nature of bedrock and regolith, topographic texture, and geomorphic setting. The last named factor may include such processes as active uplift, subsidence, volcanic or thermal phenomena, loess deposition, sea-level changes in coastal regions, and the like. Basically, anything that alters the load-discharge ratio of a stream is likely to trigger some response by the stream (Flint, 1971, p. 304-313).

It is commonly held that in most mid-latitude continental areas a colder climate will induce stream aggradation by increasing stream load—a result of larger quantities of clastic sediment being supplied to streams by glaciers, wind, and/or increased rates of mechanical weathering and mass wasting. Many areas do indeed contain distinctive terraces and alluvial deposits, often of regional extent and clearly contemporaneous with cold glacial episodes.

More directly, climatic changes alter the distribution and magnitude of runoff, causing profound changes in stream behavior, especially in more arid regions. For example, as mean annual precipitation increases from zero, rapid increases in runoff, flood potential and sediment yield result (Knox, 1983). When rainfalls totaling from 12-20 inches (300-500 mm) per year are reached, sediment yield is at a maximum and the desert begins to change to grassland. As precipitation increases beyond this major threshold, increased vegetation density helps stabilize slopes and retard runoff, leading to a very pronounced reduction in flashflooding and sediment yield. At 31-35 inches (800 to 900 mm) of rainfall per year, forests begin to take over from the grassland. Forests are slightly more effective in dampening flood effects and sediment yield than grasslands, perhaps because they are less severely impacted by fires and overgrazing. As rainfall increases beyond about 35 inches (900 mm) per year, forest cover persists and rivers are no longer as responsive to such phenomena as heavy rainfalls and climatic changes as they are in more arid areas.

This scenario helps explain why Quaternary climatic changes did not yield more pronounced

effects in Virginia where the mean annual rainfall is about 47 inches (1200 mm) per year. Distinct terraces and alluvial deposits which can be attributed to climatic change are very rare in the central and southern Appalachians and processes currently operative can explain most such features. Many stream terraces in the Valley and Ridge province appear to be a product of stream piracy in which a stream forced to erode through resistant bedrock is eventually intersected or captured by another which has incised more deeply by exploiting a zone of nonresistant rock. The result is a lowering of base level for the captured stream, often followed by accelerated downcutting and the development of straths and alluvial terraces along the valley (Figure 7).

Hack (1965) describes another, more subtle type of piracy in which streams flowing from rugged mountain terrain onto broad valleys in Virginia deposit fans and aprons at the base of the mountains. Streams which flow only upon the less resistant rocks of the valley lack both the high load of the mountain streams and their foot-slope deposits. Eventually such a stream, or a tributary thereof, will capture a higher-level mountain stream. This stream now takes on the load of the mountain stream, becomes aggradational, and will itself eventually be pirated in a

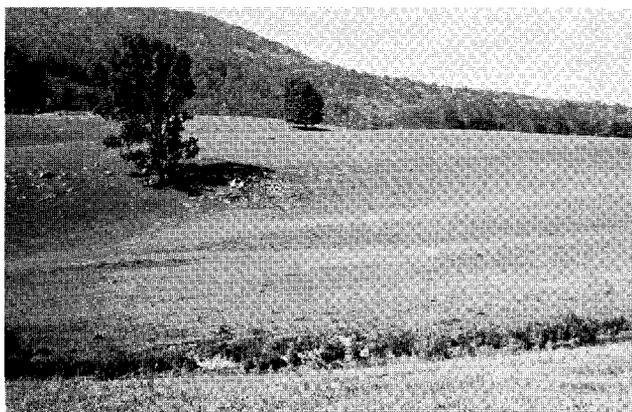


Figure 7. Terrace-like features (stratigraphic benches, straths, alluvial terraces?) along east side of Big Walker Creek Valley southwest of the State Route 42/52 junction, Bland County, Virginia. Are these and similar features found around the state related to bedrock control, base level variations controlled by stream piracies, changes in the rate of downcutting in water gaps, or changes in stream regimen caused by climatic variations? (Photograph taken June 8, 1984)

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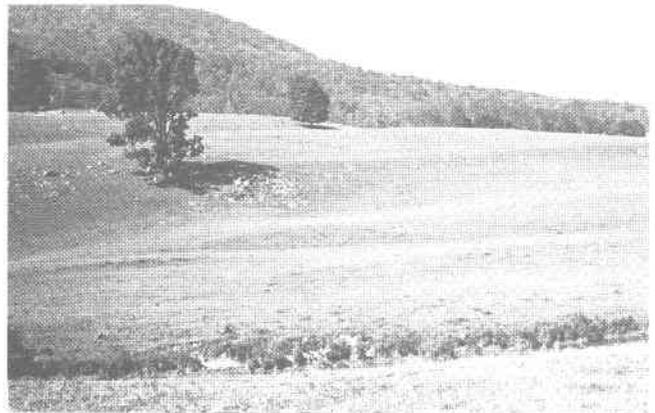


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similar fashion. The overall result is a continuing denudation of the region in a very complex, dynamic fashion which can leave behind numerous terrace remnants and alluvial deposits of widely varying ages. As Hack notes, although climatic change probably altered somewhat the rates of fluvial activity, no fundamental change in basic procedures occurred and clear evidence of various climatic regimes is difficult to recognize in the alluvial sequences.

The influence of catastrophic rainfalls is also important to an understanding of fluvial processes. As noted above, many boulder streams found along small first and second order stream valleys are apparently formed by debris flows and flash floods (Mills, 1980b). Such deposits may be gradational between colluvium and alluvium. Kochel and Johnson (1984) conclude that many humid-temperate "alluvial" fans in central Virginia are actually debris avalanche deposits built up during infrequent storms occurring about once every 3000 to 6000 years. Heavy runoff tends to redistribute the fan deposits by eroding material at the fan head and depositing it on the lower slopes.

Major floods along larger streams may drastically alter the valley floor and stream channel (Hack and Goodlett, 1960), stripping away vegetation, piling up deposits which may later form terraces, and even destabilizing the stream, altering its behavior for years to come. In some stream systems, such events, with recurrence intervals of several hundred years, may have more geomorphic impact than all lesser events combined. Differentiating the effects of such episodic events from possible climatic effects is a major challenge that needs to be met if alluvial sequences are to be accurately interpreted.

One important influence of a cold climate on fluvial systems in Virginia would probably be a reduction, perhaps the near-elimination, of intense and catastrophic rainfall events. Because the Polar Frontal Zone was well to the south of Virginia during glacial maxima, little warm moist air could mix with the cold dry westerlies flowing across the state. Such conditions should help stabilize streams and reduce their erosion and sediment transportation rates. At the same time, production and migration of loose rubble over most of the terrain was probably greater than during warm periods. As the shift from colder to warmer climate occurred and warm moist air masses began following the Polar Front as it moved northward, rainfall would increase. The initial effect might have been increased

deposition as heavy rainfalls destabilized rubble-covered slopes which then delivered excessive amounts of sediment to streams. These related events may help explain the extensive alluviation which apparently took place along the Little Tennessee River during the later stages of glacial-interglacial and stadial-interstadial transition periods (Delcourt, 1980). Following such a transitional phase, the more frequent occurrences of large river discharges would tend to lead to more rapid downcutting than occurred during the colder periods. Generally, records indicate that wetter climates tend to induce stream incision and drier climates stream aggradation (Knox, 1983).

At higher elevations in Virginia, lengthy periods of subfreezing temperatures and extensive areas of frozen ground were probably common during glacial winters. Where the snowpack is shallow, vegetation sparse, and temperatures sufficiently cold, the regolith may be invaded by dense impermeable ice ("concrete frost") which may persist through part or all of the summer (Dunne and Leopold, 1978, p. 167). Under such conditions, wintertime discharge along mountain streams may cease. As in many cold regions today, much of the annual streamflow may have been discharged during the spring melting period. Runoff would be rapid over the frozen ground and springtime floods, some triggered by breakup of ice jams along rivers, would be common. The magnitude of these floods and their impacts would in all probability be far less than those from a Hurricane Camille, however, and clear-cut evidence of such past processes is rare. One indication of such events may be the anomalously large, striation-bearing clasts found in Pleistocene deposits along the lower reaches of many major Appalachian rivers such as the James and Rappahannock (Wentworth, 1928; Flint, 1971, p. 312-313). The clasts are very similar to those found in today's Arctic streams where river ice action is vigorous. Such clasts seem to occur only in sediments deposited during cold climatic intervals, and their size and abundance decrease from the Susquehanna River south to the Roanoke River.

In summary, the responses of fluvial systems in the Virginia highlands to climatic changes are complex and poorly understood. Evidence of fluvial processes during cold glacial intervals is often subtle and difficult to distinguish from the effects of catastrophic Holocene rainfall events and non-climatic influences such as stream piracy. It is probable that aggradation tended to dominate

along most streams during, and especially at the close of, colder and drier episodes and degradation tended to prevail during warmer, wetter intervals.

PROCESSES OF CAVERN AND KARST DEVELOPMENT

The utility of karst terrain in providing clues to climatic changes is somewhat controversial (Jennings, 1981) but, in general, appears to be limited. Wells and Gutierrez (1981) report that changes in base level may be reflected as changes in slope along longitudinal profiles of karst streams, but dating and relating the previous base levels to specific climatic intervals is very difficult in most areas.

Straths and terraces along major rivers often represent former extended base levels. In nearby soluble rocks, large integrated cavern systems sloping gently towards the base level may have existed. The cave systems developed slightly below and roughly parallel to the water table which was graded to local river levels. The vast Flint Ridge Mammoth Cave system in Kentucky, which is some 310 miles (500 km) in length and still being extended, shows seven primary levels which are correlated with terrace remnants and horizontally extended surface landforms controlled by base levels of the Ohio River during late Tertiary and Pleistocene time. The higher the cave levels, the older they appear to be. When the number of levels is compared with available ages for travertine and sediments, there appears to be about half as many cave levels as glacial-interglacial cycles. Hess and Harmon (1981) suggest a complex series of responses involving excavation of cave passages and cave sediment during interglacials when the Ohio River was downcutting, thus lowering base levels and increasing the hydraulic gradient in the caves. This excavation phase would be followed by partial infilling of the lower cave levels by sediment during glacials when base level was higher because of alluviation along the Ohio River. It appears that two interglacials are required for base level to get low enough for complete removal of the sediment in the existing cave and the initiation of a new cycle of cave development at a lower level.

Increased rainfall in an area should favor increased solution of carbonate rock and more rapid accumulation of residual debris on the surface. However, recognition of such changes in the terra rossa or other karst regolith is very difficult.

Springs, seeps or streams heading in carbonate rocks frequently precipitate calcium carbonate at favorable locations. The resulting deposits can sometimes grow to impressive size, extending for miles along streambeds, building outward to form waterfalls, or accumulating as mounds and fans (Figure 8). These deposits suggest extensive subsurface circulation of waters and dissolution of carbonate bedrock. Deposition is favored where the water stream spreads out, allowing more CO₂ loss, more evaporation, and more algae and moss growth (which takes CO₂ from the water), all of which tend to cause CaCO₃ precipitation. Tufa deposits may therefore record periods of deposition, stagnation, or erosion which can be related to climatic variations. Tufa, as well as travertine formations in caves, may also yield valuable climatic information from entrapped pollen and other fossil material, fluid inclusions, isotopic variations in minerals, and embedded clastic materials.

Many tufa and travertine deposits, as well as clastic cave sediments, have been dated using radiocarbon, thorium-uranium, and remnant plaeomagnetism techniques (Latham, 1981). Results are very encouraging, with ²³⁰Th/²³⁴U dating of travertine and tufa providing the most abun-



Figure 8. Meadow Creek Falls near New Castle, Craig County, Virginia. This creek drains the eastern part of Sinking Creek Valley, a large breached anticline underlain by limestones. The falls are on Silurian sandstones, but the presence of carbonate rocks upstream is evident along the creek—the upper part of the falls seen here flows over a large tufa mound some 30 feet (10 m) high. Most tufa buildups are not so obvious, but they may contain valuable clues to the paleoenvironment. (Photograph taken August 26, 1982)

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dant and reliable data, most of it for the last 150,000 years (Hening and others, 1983). The dates clearly show variations in calcite growth rates through time. The data may then be correlated with chronologies obtained from terrigenous sediments, deep-sea cores and other sources.

Flint (1971, p. 301-302) noted that caves had been under-exploited as a source of information on paleoclimates. While still true, the situation is improving, in some cases with rather surprising results. For example, field observations on limestones in New York and elsewhere indicate that some caves have formed since the retreat of the Wisconsin ice sheet (White, 1979). This is supported by model calculations showing that a fracture about 25 micrometers wide can evolve into a subterranean flow path or conduit of about 5 mm diameter in some 3000 years. Concentrated, turbulent groundwater flow along such a conduit can then enlarge it to a full-scale cave passage of about 3 feet (1 m) diameter in less than 10,000 years. This indicates that cave networks at given levels can indeed be formed in the time span represented by favorable climatic regimes of the Quaternary, and fits in nicely with the theory of Hess and Harmon (1981) described above.

Speleothem formation is generally favored by increases in rainfall and vegetation cover. The vegetation is important because water must absorb considerable carbon dioxide to be capable of dissolving significant amounts of the limestone or dolomite it moves through, and because the major source of the carbon dioxide is organic activity in soils. When water seeping through the ground enters the air in a vadose cave, carbon dioxide is lost and calcite is deposited as travertine. Should the water entering the cave still be capable of corrosion, however, existing speleothems may experience dissolution instead of precipitation of calcite.

In the arid southwestern United States, increased rainfall and vegetation cover favored speleothem growth during glacials. In most localities around the world, however, it is the interglacials which clearly correspond to periods of increased speleothem growth (Gascoyne, 1981; Glazek and Harmon, 1981; Hennig and others, 1983). During glacials, colder temperatures reduce vegetation growth rates along with bacterial and auto-oxidative processes in the soil, thus limiting the carbon dioxide available to infiltrating water. In some areas, including Virginia, decreased precipitation would have an additional inhibiting influence. During very cold periods, speleothem growth may come to a virtual halt

because of reduced precipitation as rain, increased ground ice which limits infiltration, and greatly decreased biotic activity.

In some caves, suites or generations of speleothems can be distinguished (Hennig and others, 1983). Their differing physical characteristics are probably related to differing climatic regimes. Abrupt changes in the nature of cave decorations, such as abundant calcite crystals or globularites below a certain level, shelf-like projections of travertine, or abandoned rimstone deposits usually indicate former water levels in the cave which may reflect climatic conditions.

The travertine bands in speleothems yield information for dating, as noted above, and also for paleotemperature determination. Most speleothems, especially stalagmites and flowstone, contain 0.05 to 0.5 percent trapped water, representing the water which formed the travertine in the past. Oxygen and hydrogen isotope ratios for the entrapped water and coexisting calcite allows temperatures at the time of deposition to be successfully calculated in many cases (Flint, 1976; Yonge, 1981). Travertine may be richer in iron oxides during warmer, moister periods. Zones of dirty travertine may correlate to drier, dustier cave environments when speleothem growth was minimal. Such dirty flowstone may possess a stronger remnant paleomagnetism, aiding dating efforts (Latham, 1981).

Considerable controversy has surrounded the interpretation of speleothems composed of minerals other than calcite, especially aragonite. Many have contended that aragonite tends to crystallize only in higher-temperature caves (above 13-17°C) (Flint, 1971, p. 303-304; Sweeting, 1973; p. 188). Moore (1956) believed caves in the western United States reflected this, with more calcite speleothems at high latitudes and more aragonite at lower latitudes. However, additional studies indicate that aragonite deposition may be complicated by numerous factors other than temperature (Hill, 1976, p. 89), and the value of using it as a paleoenvironment indicator remains to be proven.

Large quantities of elastic debris ranging from clays to huge breakdown blocks are common in caves. Surficial material washed into caves may contain clues to the paleoenvironment. For example, Flint (1971, p. 303) notes that rounding and calcite coatings on sand grains may be related to precipitation. Thick, massive clay fills in caves may contain thin bands of charcoal washed in following forest fires on the surface. Wood, shells, bones and other informative and datable material

may be preserved in cavern sediment, or even encased in travertine. In New York, cave sediments from glacial periods tend to be lower in organic content and higher in soluble components than those from interglacials (Mylroie, 1979). Rockfall debris beneath near-surface domes, breccia zones in cave sediments, or coarser zones of talus near entrance pits may reflect increased frost action and correlate with colder periods. Reworked eolian sediment may be found in caves and might correspond to a warm, dry interval.

Variations in cave passageways include inner channels cut into a cave floor, horizontal galleries not related to bedrock variations, potholes, and knickpoints. Such features often result from changes in water levels, solution rates, water temperature and load, and the like, and some have been linked to Pleistocene climate changes (Sweeting, 1973, p. 155-157).

Unfortunately, little concrete information of the above type is available from Virginia. But in view of the information reviewed above and the abundance of caves in the state, the potential of cave studies for yielding valuable paleoenvironmental information should not be underestimated.

COASTAL AND EOLIAN PROCESSES

A detailed examination of the intensively studied coastal regions of Virginia and adjacent areas is beyond the scope of this paper and no attempt will be made to review the many recent contributions and controversies relating to the Quaternary geology of this region. Rather, a very brief overview of major coastal zone events of importance to surficial processes is offered to complete our perspective of Quaternary geomorphology in Virginia.

Fluctuating sea levels have produced complex sequences of transgressive and regressive deposits and associated landforms in the coastal lowlands of Virginia. Quaternary sediments and various relic terraces or "flats", scarps, strandlines, bars and related features in the coastal zone provide evidence of past sea levels (Bloom, 1983a, 1983b; Farrell, 1979; Johnson, and others 1982; Pilkey and Evans, 1981). Superimposed upon the many sea-level responses to the growth and ablation of glaciers were slow tectonic uplift, seaward tilting, and glacio-isostatic influences.

Sea levels were quite close to those of the present during past interglacials, but when ice sheets were at their maximum extent, sea level was some 395 feet (120 m) lower than at present.

In Virginia, the continental shelf was not actually exposed to the current sub-sea 395-foot-depth contour because the massive Laurentide ice sheet to the north had caused isostatic crustal depression. Hence net submergence of coastal plain features off the Virginia coast may be only 195 - 262 feet (60-80 m) rather than 395 feet. Between 16,000 and 10,000 yrs B.P., crustal rebound caused by the retreat of the Laurentide ice sheet may have caused emergence (regression) along the Virginia coast even as rising sea levels were inundating coastal landscapes along the south Atlantic coast (Bloom, 1983a, p. 219; Clark, 1981).

Mastodons and mammoths roamed the broad windswept coastal plain during glacials. River valleys, lagoons, estuaries, barrier islands, and other features undoubtedly existed over extensive areas of the present continental shelf, but the reworking of deposits by wave activity during ensuing transgressions has extensively altered such features. The cold Labrador Current from the North Atlantic dominated the coastal waters of Virginia during glacials creating a climate more like present-day Nova Scotia than Virginia Beach, with sea temperatures some 6-8°C colder in August than at present (Imbrie and others 1983).

Wind is an important agent in coastal areas today, especially on barrier islands, which total some 69,000 acres (28,000 hectares) in Virginia. Data on eolian effects during the Pleistocene in Virginia are limited. Small sand dune areas were apparently present on parts of the Virginia Coastal Plain during the dry, windy glacials, and thin loess deposits along with ventifacts are scattered about. Among the beach ridges, spits, flats and other abandoned coastal zone features of Virginia are the shallow, circular-to-elliptical depressions called "Carolina Bays", most of which are now believed to be Pleistocene relics of eolian origin (Pettry and others, 1979).

SUGGESTIONS FOR THE QUATERNARY FOSSIL HUNTER

Because much of the interest in Quaternary geology in inland Virginia has centered about vertebrate fossils, the location of potentially productive Quaternary fossil sites merits special attention. Even if a promising site or deposit contains no vertebrates, it is likely to yield other useful information about the paleoenvironment, such as spores, pollen, invertebrate fossils, buried soils, and valuable stratigraphic and sedimentological data. Some general suggestions follow.

(1) Alluvium and colluvium: Although most subaerial deposits of this type lack fossils, rapid burial or special conditions may allow preservation of organisms, including some megafauna. The stratigraphy of any thick depositional sequence, if exposed, may provide valuable information about past processes, even if no fossils are present. Unfortunately, as noted previously, continuing denudation has tended to limit major accumulations which contain sequences of past glacial and interglacial deposits. The base level for most Wisconsinan alluvium was probably very close to current floodplain levels and distinguishing Holocene from Pleistocene deposits may be difficult. The best preservation of old alluvium tends to be on limestone or dolomite. Because of their solubility, most drainage is internal (Figure 9), greatly reducing surface runoff and erosion of surficial materials (Hack, 1965; Houser, 1980). Where carbonate bedrock lies close to the base of mountainous areas, thick colluvial and alluvial deposits are likely to be preserved, but vertebrate fossil finds in such deposits are rare. In eastern Virginia, low-lying marshy environments along coasts and river valleys may have entrapped and preserved numerous animals during glacials, but these locations are now beneath the Atlantic Ocean.

(2) Depressions: Natural lake basins in unglaciated areas such as Virginia are rare, but where



Figure 9. Small, flat-floored karst depression (polje) near Dublin, Pulaski County. A spring-fed stream flows into a swallow hole near its center and exposes several meters of fill. Old topographic maps show this area as a lake. Such a location might yield useful information about late Quaternary climates and life forms. (Photograph taken April 10, 1980)

found, their lacustrine sediments provide an ideal site for fossil preservation. The well-known Saltville Valley (Figure 10) is an excellent example of special conditions giving rise to a classic fossil locality. Saltville lies along a typical strike valley eroded upon the nonresistant Maccrady Formation of Mississippian age. Evidence indicates that a sizable river flowed through the Saltville section of the valley until about 14,500 yr B.P. when piracy of the old "Saltville River" occurred (McDonald and Bartlett, 1983; Stocking and others 1979). Shallow lakes have existed at Saltville almost continuously since then. The origin of the lake depressions is uncertain. Three possibilities are (a) subsidence caused by dissolution of evaporite beds in the underlying Maccrady Formation; (b) mass wasting and colluvium build-up in the water gap immediately north of the valley; (c) alluvial deposition, perhaps during a flood, along the North Fork of the Holston River which occupies the valley immediately north of the water (now a wind) gap. The presence of the lake, plus both fresh and salt water springs, attracted many late Quaternary mammals—and later, humans—to the Saltville Valley.

(3) Caves and fissures: Most residuum and saprolite are unproductive and uninformative. However, where deep fissures have been weathered into bedrock (usually limestone or dolomite), filled with residuum and exposed in river canyons, quarries



Figure 10. View north across Saltville Valley, Smyth County, Virginia's most famous vertebrate fossil locality. Stream piracy and creation of a shallow lake made this an ideal area for the preservation of late Quaternary fossils and prehistoric human artifacts. (Photograph taken June 25, 1984)

(1) Alluvium and colluvium: Although most subaerial deposits of this type lack fossils, rapid burial or special conditions may allow preservation of organisms, including some megafauna. The stratigraphy of any thick depositional sequence, if exposed, may provide valuable information about past processes, even if no fossils are present. Unfortunately, as noted previously, continuing denudation has tended to limit major accumulations which contain sequences of past glacial and interglacial deposits. The base level for most Wisconsinan alluvium was probably very close to current floodplain levels and distinguishing Holocene from Pleistocene deposits may be difficult. The best preservation of old alluvium tends to be on limestone or dolomite. Because of their solubility, most drainage is internal (Figure 9), greatly reducing surface runoff and erosion of surficial materials (Hack, 1965; Houser, 1980). Where carbonate bedrock lies close to the base of mountainous areas, thick colluvial and alluvial deposits are likely to be preserved, but vertebrate fossil finds in such deposits are rare. In eastern Virginia, low-lying marshy environments along coasts and river valleys may have entrapped and preserved numerous animals during glacials, but these locations are now beneath the Atlantic Ocean.

(2) Depressions: Natural lake basins in unglaciated areas such as Virginia are rare, but where



Figure 9. Small, flat-floored karst depression (polje) near Dublin, Pulaski County. A spring-fed stream flows into a swallow hole near its center and exposes several meters of fill. Old topographic maps show this area as a lake. Such a location might yield useful information about late Quaternary climates and life forms. (Photograph taken April 10, 1980)

found, their lacustrine sediments provide an ideal site for fossil preservation. The well-known Saltville Valley (Figure 10) is an excellent example of special conditions giving rise to a classic fossil locality. Saltville lies along a typical strike valley eroded upon the nonresistant Maccrady Formation of Mississippian age. Evidence indicates that a sizable river flowed through the Saltville section of the valley until about 14,500 yr B.P. when piracy of the old "Saltville River" occurred (McDonald and Bartlett, 1983; Stocking and others 1979). Shallow lakes have existed at Saltville almost continuously since then. The origin of the lake depressions is uncertain. Three possibilities are (a) subsidence caused by dissolution of evaporite beds in the underlying Maccrady Formation; (b) mass wasting and colluvium build-up in the water gap immediately north of the valley; (c) alluvial deposition, perhaps during a flood, along the North Fork of the Holston River which occupies the valley immediately north of the water (now a wind) gap. The presence of the lake, plus both fresh and salt water springs, attracted many late Quaternary mammals—and later, humans—to the Saltville Valley.

(3) Caves and fissures: Most residuum and saprolite are unproductive and uninformative. However, where deep fissures have been weathered into bedrock (usually limestone or dolomite), filled with residuum and exposed in river canyons, quarries



Figure 10. View north across Saltville Valley, Smyth County, Virginia's most famous vertebrate fossil locality. Stream piracy and creation of a shallow lake made this an ideal area for the preservation of late Quaternary fossils and prehistoric human artifacts. (Photograph taken June 25, 1984)

and so forth, they provide a likely place for fossil finds. Similar conditions exist among the deep clefts of some large felsenmeer or rock city areas. Karst shafts (Figure 11) and collapsed or filled-in cave entrances, as well as the caves themselves, represent other places worth investigating. Tufa and other mineral deposits are common near springs and along certain rivers in Virginia (Figure 8; Hubbard and others, this volume) and may yield useful data.

SUMMARY

Although the Quaternary paleoenvironments did not alter the terrain of Virginia as drastically as they did in many regions, their imprints are clearly present in some areas, especially at high elevations and in coastal areas. It is also apparent that currently active processes are capable of producing or maintaining many features once thought to be of relic periglacial origin. The Quaternary climatic changes influenced the rate, areas of operation, and relative effectiveness of surficial processes but did not alter the basic denudational pattern that has prevailed for tens of millions of years in Virginia.

With the possible exception of the coastal zone, modern geomorphological research in Virginia is still in its infancy. More precise knowledge of specific weathering processes and how they in-



Figure 11. Pig Hole, Giles County. This 119-foot-deep karst shaft in Middle Ordovician limestone provides access to some 2460 feet (750 m) of cave passages. Pits, crevasses, and caves have good entrapment potential and commonly contain human artifacts, fossils, and geomorphic evidence of climatic change. (Photograph taken August 19, 1981)

fluence slope development and relate to erosional and mass wasting processes is needed. Studies of recent variations in fluvial processes and drainage development such as stream captures, strath and terrace formation, and lithologic and structural influences should also prove productive. Caves are in special need of serious scientific study.

As understanding of modern surficial processes and landforms expands, we will be better able to assess the impacts of past climatic changes, recognize evidence of such changes, and apply our knowledge to a plethora of related fields of interest from Quaternary fossil sites to modern land use planning.

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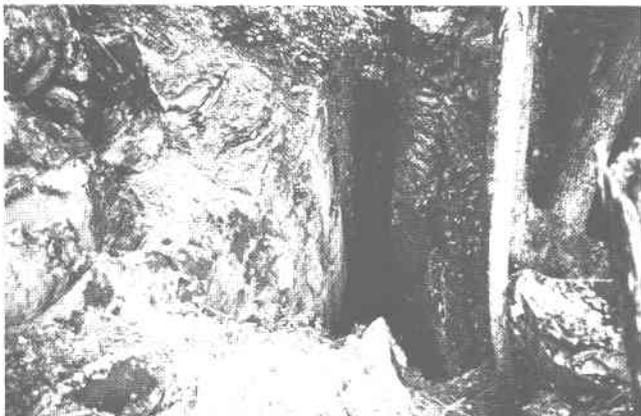


Figure 11. Pig Hole, Giles County. This 119-foot-deep karst shaft in Middle Ordovician limestone provides access to some 2460 feet (750 m) of cave passages. Pits, crevasses, and caves have good entrapment potential and commonly contain human artifacts, fossils, and geomorphic evidence of climatic change. (Photograph taken August 19, 1981)

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**LATE QUATERNARY VEGETATIONAL CHANGE IN THE
CENTRAL ATLANTIC STATES**

Hazel R. Delcourt¹

Paul A. Delcourt²

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ABSTRACT

We review the changes in vegetation, climate, and geomorphic regimes in the central Atlantic states region (36° to 41°N, 74° to 84°W) over the past 23,000 years since the onset of the last full glacial interval. Examination of gradients in late Pleistocene and Holocene plant and animal com-

munities indicates that vegetational disequilibrium and disharmonious faunal assemblages occurred from 13,000 to 10,000 yr B.P. During that time, climatic amelioration and dynamic landscape changes occurred with the transition from colluvial to alluvial geomorphic regimes. The Valley and Ridge Physiographic Province served as a major migrational corridor for plant species at the transition from late Pleistocene to Holocene conditions. Holocene vegetation has shifted from cool-temperate to warm-temperate forests, reflecting climatic warming, continued northward migrations of warm-temperate plant taxa, and, in the Atlantic Coastal Plain, the rise in sea level. Future research priorities include establishing a network of radiocarbon-dated late Quaternary pollen and plant-macrofossil sites in the Allegheny Plateau, Valley and Ridge, Blue Ridge, Piedmont, and Atlantic Coastal Plain physiographic provinces of Virginia and surrounding states.

¹Program for Quaternary Studies of the Southeastern United States, Graduate Program in Ecology and Department of Botany, University of Tennessee, Knoxville, Tennessee 37996.

²Program for Quaternary Studies of the Southeastern United States, Graduate Program in Ecology and Department of Geological Sciences, University of Tennessee, Knoxville, Tennessee 37996.

INTRODUCTION

Studies of late Quaternary vegetational history in the unglaciated southeastern United States were pioneered in Virginia, with one of the earliest studies that of Lewis and Cocke (1929) in the Dismal Swamp (Figure 1). Despite the early emphasis upon understanding the late Quaternary history of vegetation and climate along the Atlantic seaboard, relatively few radiocarbon-dated, late Quaternary palynological sites have been studied within the state of Virginia (Figure 1; Table).

In this paper, we review the available literature concerning late Pleistocene and Holocene plant-fossil studies in Virginia and the surrounding region of the central Atlantic states. We restrict our review to the time interval within which radiocarbon analysis allows vegetational reconstructions to be made based upon an absolute time scale, with the greatest emphasis upon biotic changes since the onset of the last full glacial period, from 23,000 yr B.P. to the present. We summarize vegetational changes for each of the five physiographic provinces represented in the state of Virginia, including the Allegheny Plateau, the Valley and Ridge, the Blue Ridge, the Piedmont, and the Atlantic Coastal Plain. In order to characterize changes in vegetation and climate within the context of these broad physiographic divisions, we draw upon late Quaternary palynological sites from areas surrounding Virginia and located between 36° and 41° N latitude and between 74° and 84° W longitude (Figure 1). We discuss (1) the relationship of late Pleistocene vegetational and faunal gradients to habitat availability and migrational corridors; (2) biotic responses to climatic amelioration during the late glacial and early Holocene intervals; and (3) patterns and processes in Holocene vegetational development. Finally, we indicate important future directions for research in Quaternary vegetational history of Virginia and its surrounding region.

VEGETATION OF THE LATE WISCONSIN FULL GLACIAL INTERVAL (23,000 TO 16,500 YR B.P.)

No pollen or plant-macrofossil sites yet studied within the state of Virginia date from the Late Wisconsin full glacial interval, 23,000 to 16,500 yr B.P. We can infer full glacial vegetation for portions of Virginia from palynological evidence from several sites nearby in Maryland, Delaware, and North Carolina that have radiocarbon dates from this time interval.

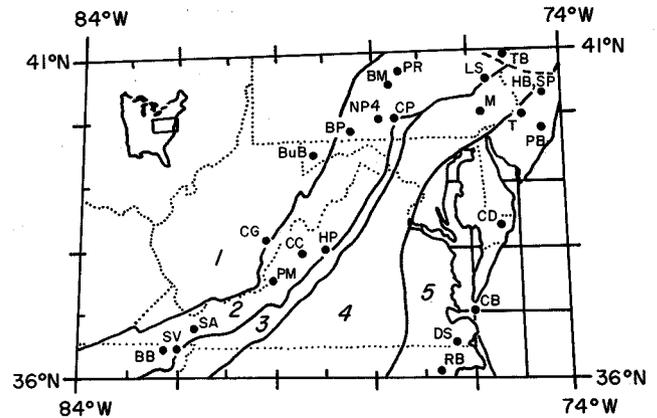


Figure 1. Map of late Quaternary sites discussed in text. Letter codes for the palynological sites are referenced in the Table. Four faunal sites include: NP4, New Paris No. 4, PA (Guilday and others, 1964); CC, Clark's Cave, VA (Guilday and others, 1977); SA, Saltville Valley, VA (Ray and others, 1967); and BB, Baker Bluff Cave, TN (Guilday and others, 1978). The dashed line corresponds to the full glacial limit of the Laurentide Ice Sheet. Physiographic regions discussed in the text are numbered as follows: (1) Allegheny Plateau; (2) Valley and Ridge; (3) Blue Ridge; (4) Piedmont; and (5) Atlantic Coastal Plain.

Buckle's Bog, Maryland (Maxwell and Davis, 1972), is located at 2670 feet (814 m) elevation along a broad ridge on the Allegheny Plateau (Figure 1, Table). The site is an alluvial glade, with 8.5 feet (258 cm) of clay and peat representing the time interval from 19,000 yr B.P. to the present. During the full glacial interval, the vegetation of the Allegheny Plateau was alpine tundra dominated by sedges (Cyperaceae), grasses (Gramineae), and other herbs. Low pollen-influx values (generally less than 2000 grains·cm⁻²·yr⁻¹) indicate that trees were absent at elevations above approximately 1480 feet (450 m) (Maxwell and Davis, 1972).

On the central Atlantic Coastal Plain, full glacial pollen spectra are available from three areas. Near Trenton, New Jersey (Figure 1) a pollen spectrum dating 16,700 yr B.P. (Sirkin and others, 1970) is dominated by pine (*Pinus*), with grass, birch (*Betula*), and spruce (*Picea*), indicating taiga vegetation (an open boreal woodland). Peat lenses buried by sand dune sheets on the Delmarva Peninsula of Maryland (Figure 1) date from 23,300 to 17,800 yr B.P. (Sirkin and others, 1977; Denny and others, 1979). These peat lenses contain a pollen assemblage consisting of pine, spruce, northern shrubs,

Table. Major late Quaternary palynological sites in the central Atlantic states.

SITE NAME, STATE	CODE	LAT. NORTH degrees/min.	LONG. WEST degrees/min.	TIME RANGE	DEPOSITIONAL ENVIRONMENT	POLLEN ANALYST	PUBLICATIONS
Bear Meadows, Pa.	BM	40 30	77 45	Early to late Holocene	Montane bog or glade	A. Kovar	Kovar (1965)
Big Pond, Pa.	BP	39 46	78 33	Early to late Holocene	Pond with perched water table	W. Watts	Watts (1979)
Buckle's Bog, Md.	BuB	39 34	79 16	Full glacial to late Holocene	Montane bog or glade	J. Maxwell	Maxwell and Davis (1972)
Central Delmarva Peninsula, Md.	CD	38 20	75 20	Early Wisconsin to early Holocene	Carolina bays	L. Sirkin	Sirkin and others (1977); Denny and others (1979)
Chesapeake Bay Entrance, Va.	CB	36 58	76 07	Late glacial to late Holocene	Estuary	J. Terasmae	Harrison and others (1965)
Cranberry Glades, W.V.	CG	38 12	80 17	Late glacial to late Holocene	Montane bog or glade	P. Sears; P. Martin; W. Watts	Watts (1979)
Cridler's Pond, Pa.	CP	39 58	77 33	Late glacial to late Holocene	Pond with perched water table	W. Watts	Watts (1979)
Dismal Swamp, Va.	DS	36 35	76 26	Early to late Holocene	Coastal swamp	D. Whitehead	Lewis and Cocke (1929); Whitehead (1972); Whitehead and Oaks (1979)

Table. (cont.)

SITE NAME, STATE	CODE	LAT. NORTH	LONG. WEST	TIME RANGE	DEPOSITIONAL ENVIRONMENT	POLLEN ANALYST	PUBLICATIONS
Hack Pond, Va.	HP	37 59	79 00	Late glacial to late Holocene	Karst sink	A. Craig	Craig (1969)
Helmetta Bog, N.J.	HB	40 23	74 26	Early to late Holocene	Eolian-deflation basin	W. Watts	Watts (1979)
Longswamp, Pa.	LS	40 29	75 40	Early to late Holocene	Karst sink	W. Watts	Watts (1979)
Marsh, Pa.	M	40 06	75 45	Late glacial to late Holocene	Montane bog or glade	P. S. Martin	Martin (1958)
Panther Run Pond, Pa.	PR	40 48	77 25	Late glacial to late Holocene	Montane bog or glade	W. Watts	Watts (1979)
Pine Barrens Bog, N.J.	PB	39 43	74 30	Early to late Holocene	Alluvial swamp	L. Florer (Heusser)	Florer (1972)
Potts Mountain Pond, Va.	PM	37 36	80 08	Early to late Holocene	Pond with perched water table	W. Watts	Watts (1979)
Rockyhock Bay, N.C.	RB	36 10	76 41	Early Wisconsin to late Holocene	Carolina bay	D. Whitehead	Whitehead (1981)
Saltville Valley, Va.	SA	36 52	81 46	Late glacial to late Holocene	Montane bog or glade	W. Benninghoff; H. Delcourt	Ray and others (1967); this study
Shady Valley Bog, Tn.	SV	36 32	81 56	Early to late Holocene	Montane bog or glade	F. Barclay	Barclay (1957)
Szabo Pond, N.J.	SP	40 24	74 29	Early to late Holocene	Eolian-deflation basin	W. Watts	Watts (1979)
Tannersville Bog, Pa.	TB	41 02	75 16	Late glacial to late Holocene	Kettle-block basin	W. Watts	Watts (1979)
Trenton, N.J.	T	38 20	75 20	Early Wisconsin to early Holocene	Eolian-deflation basin	L. Sirkin	Sirkin and others (1977); Denny and others (1979)

and upland herbs indicative of a cold, dry taiga environment in which ephemeral bogs and thaw lakes formed and were subsequently filled by drifting sand.

Farther south on the Coastal Plain of northeastern North Carolina, Rockyhock Bay (Figure 1, Table) records vegetational changes dating from 27,700 yr B.P. to the present (Whitehead, 1981). During the full glacial interval, pollen assemblages at Rockyhock Bay were dominated by 75 percent to 90 percent jack pine (northern *Diploxylon Pinus*), with spruce and a mixture of herbs that indicate an unstable landscape with patches of taiga vegetation interspersed with the exposed surfaces of active sand dunes (Whitehead, 1981).

Although no full glacial pollen sites are known from the Valley and Ridge, Blue Ridge, or Piedmont provinces in the region, we infer that alpine tundra was restricted to highest elevations of the Allegheny Plateau and the Blue Ridge Mountains, with a relatively open boreal forest extending eastward at lower elevations to the Coastal Plain (Delcourt and Delcourt, 1981).

VEGETATION OF THE LATE WISCONSIN LATE GLACIAL INTERVAL (16,500 TO 12,500 YR B.P.)

On the Allegheny Plateau of Maryland, alpine tundra persisted throughout the late glacial interval and was replaced by open spruce woodland after 12,700 yr B.P. (Maxwell and Davis, 1972). Farther south, at Cranberry Glades, an alluvial glade located at 3375 feet (1029 m) elevation on the Allegheny Plateau of West Virginia (Figure 1), alpine tundra persisted until 12,200 yr B.P. (Watts, 1979).

Six sites in the Valley and Ridge Province date from the late glacial interval (Figure 1). The Tannersville, Pennsylvania, site (Figure 1) is a kettleblock depression formed during the retreat of the Laurentide Ice Sheet. From about 14,000 yr B.P. to 13,300 yr B.P., the newly deglaciated landscape was poorly drained, with extensive wetlands dominated by sedges. At 13,300 yr B.P., trees of spruce, aspen (*Populus* cf. *tremuloides*), cedar (*Juniperus* type), and shrubs of green alder (*Alnus crispa*) invaded and stabilized the glacial moraines (Watts, 1979). Between 13,300 and 12,500 yr B.P., the vegetation changed in composition from taiga to closed boreal forest dominated by spruce, pine, fir (*Abies*), and birch. Similarly, at Longswamp, Pennsylvania (Figure 1), in the periglacial zone adjacent to the southernmost limit of glacial advance, late glacial grass-dominated tundra with arctic herbs such as *Dryas integrifolia* and *Sagina* cf. *nodosa*

and shrubs of crowberry (*Empetrum* cf. *nigrum*) and shrub birch (*Betula glandulosa*) persisted until approximately 12,500 yr B.P., when an open, boreal spruce woodland established (Watts, 1979). To the south, along the unglaciated portion of the Valley and Ridge, at Crider's Pond, Pennsylvania (Figure 1; 950 feet, 290 m, elevation), late glacial vegetation was characterized by a boreal forest dominated by spruce, with minor amounts of jack pine but no evidence of tundra herbs (Watts, 1979). Between 13,000 and 12,500 yr B.P., balsam fir (*Abies balsamea*), tree birch, alder, and willow (*Salix*) established locally within the boreal forest.

In the Valley and Ridge Province of Virginia, several sites provide evidence of late glacial vegetation. Hack Pond, a karst pond located at 1480 feet (451 m) elevation at 38° N latitude in the Shenandoah Valley of northern Virginia (Figure 1), dates from greater than 13,000 yr B.P. to the present (Craig, 1969). During the late glacial interval, the vegetation was a closed spruce-pine forest. After 12,700 yr B.P., white pine (*Pinus strobus*), birch, alder, and oak (*Quercus*) established within the forests (Craig, 1969).

The oldest radiocarbon-dated, continuous record of late Quaternary sediment accumulation and vegetational change available from the Valley and Ridge Province of Virginia is represented by the section from the Saltville Valley (Figures 1, 2; Table). Alluvial glades at 1722 feet (525 m) elevation within the Saltville Valley date from 15,500 to 2000 yr B.P. During the late glacial interval, from 15,500 to 12,500 yr B.P., the vegetation was a species-rich mosaic of boreal coniferous and hardwoods forests. Sandstone ridges in the uplands were occupied by jack pine, aspen (*Populus balsamifera* and *P. tremuloides* type), tree birch, and oak. Ash (*Fraxinus*), maples (*Acer pensylvanicum* and *A. saccharum*), beech (*Fagus grandifolia*), hickory (*Carya*), elm (*Ulmus*), and cherry (*Prunus*) occupied mesic slopes. Within the poorly-drained alluvial bottomlands, dominant trees included red spruce (*Picea rubens*) and balsam fir with tamarack (*Larix*) (Figure 2). Open glades were locally dominated by boreal shrubs, grasses, and sedges, with a rich assemblage of herbs indicative of both boreal woodlands and marshes.

Late glacial vegetation on the Piedmont is represented only at Marsh, Pennsylvania (Figure 1). The Marsh site, a small alluvial swale located within 53 miles (85 km) of the ice margin at 41° N latitude, dates to approximately 13,600 yr B.P. (Martin, 1958). The late glacial pollen assemblage from this site was dominated by nonarboreal pollen types, including primarily sedges and grasses, with

substantial representation of pollen of northern Diploxylon pines. Minor amounts of spruce, fir, birch, and willow were also present in the pollen assemblage. The vegetation growing in the vicinity of the Marsh site during the late glacial period has been interpreted as on the ecotone between taiga and tundra, the latter represented by herbs such as *Polemonium*, *Saxifraga* cf. *oppositifolia*, and *Polygonum bistortoides* (Martin, 1958).

In a pollen spectrum dated 13,200 yr B.P. from the Coastal Plain at Trenton, New Jersey (Figure 1), co-dominance of pine, spruce, and birch with grass reflected late glacial taiga persisting approximately 30 miles (50 km) south of the glacial limit (Sirkin and others, 1970). In the central Delmarva Peninsula of Maryland and Delaware (Figure 1), peat lenses interbedded within the Parsonsburg Sand have been radiocarbon-dated between 16,300 and 13,400 yr B.P. (Sirkin and others, 1977; Denny and others, 1979). The pollen spectra document taiga dominated by pine, spruce, and birch, with herbs in the grass, sedge, and aster families.

A pollen spectrum from sediments at the mouth of Chesapeake Bay, Virginia (Figure 1), dates from 15,280 yr B.P. (Harrison and others, 1965). The pollen assemblage is interpreted as a relatively open, coniferous boreal forest dominated by pine, with spruce and nonarboreal pollen important (Harrison and others, 1965).

On the Coastal Plain of North Carolina, approximately 310 miles (500 km) south of the glacial margin, late glacial pollen assemblages were characterized by relatively low pollen influx of 2000 to 5300 grains·cm⁻²·yr⁻¹, persistence of high percentages of jack pine pollen, and continuous representation of fir pollen (Whitehead, 1981). Spruce pollen percentages increased after 16,000 yr B.P. and remained relatively high throughout the late glacial interval, and tamarack was present. The vegetation of the central Atlantic Coastal Plain thus remained in pine-spruce taiga during the late glacial interval (Whitehead, 1981).

During the late glacial interval, a tundra zone generally occurred within 30 to 53 miles (50 to 85 km) of the ice margin (Martin, 1958; Watts, 1979; Pewe, 1983), and alpine tundra extended at high elevations southward along the Allegheny Plateau at least as far south as Cranberry Glades, West Virginia (Watts, 1979). Alpine tundra may also have persisted through the late glacial interval at higher elevations of the Blue Ridge Province into the southern Appalachian Mountains (Delcourt and Delcourt, 1981).

In the Valley and Ridge Province, a pronounced gradient in both physiognomy and composition of

vegetation occurred during the late glacial period. To the north, tundra occurred near the ice margin at Tannersville Bog and Longswamp. Coniferous taiga occurred farther south at Crider's Pond, and closed, species-poor boreal forest dominated by spruce occurred at Hack Pond in the Shenandoah Valley of Virginia. In southwestern Virginia, closed, species-rich boreal forest of spruce, fir, and pine with numerous cool-temperate species of hardwood trees and shrubs characterized the Saltville Valley throughout the late glacial interval.

The late glacial vegetation of the Piedmont Province remains largely unknown, as only the Marsh record is available, identifying the position of the tundra-taiga ecotone.

The central Atlantic Coastal Plain, from central New Jersey to as far south as northeastern North Carolina, was characterized by species-poor taiga throughout the late glacial interval.

VEGETATION OF THE HOLOCENE INTERVAL (12,500 YR B.P. TO THE PRESENT)

For convenience, we distinguish three major time intervals of the Holocene: (1) the early Holocene interval, from 12,500 to 8500 yr B.P.; (2) the middle Holocene interval, from 8500 to 4000 yr B.P.; and (3) the late Holocene interval, from 4000 yr B.P. to the present (Delcourt and Delcourt, 1985).

After 12,500 yr B.P., open spruce woodland was replaced by closed boreal forest on the Allegheny Plateau of Maryland. At Buckle's Bog, the early Holocene boreal forest was composed of spruce, pine, fir, ash, hornbeam (*Carpinus/Ostrya* type), and oak (Maxwell and Davis, 1972). By 10,500 yr B.P., white pine, birch, and hemlock (*Tsuga*) established in the vicinity of Buckle's Bog within a mixed conifer-northern hardwoods forest.

During the middle Holocene, white pine was gradually replaced by hemlock and oak. Hemlock decreased in abundance approximately 3000 yr B.P., and plant succession following the hemlock decline resulted in late Holocene forest communities dominated by oak, chestnut (*Castanea dentata*), beech, and hickory (Maxwell and Davis, 1972).

At Cranberry Glades on the Allegheny Plateau of West Virginia, mixed conifer-northern hardwoods forests were predominant from 12,200 to 4900 yr B.P. Early Holocene forests at Cranberry Glades were dominated by hemlock, with birch, oak, and hornbeam. After the collapse of hemlock populations at 4900 yr B.P., upland forests were dominated by oak, birch, and hickory, with beech and chestnut. Within the last 4500 years, spruce

populations have reexpanded near the site (Watts, 1979).

At Tannersville Bog, within the Valley and Ridge of Pennsylvania, closed boreal forest of pine, spruce, and fir persisted from 12,500 to 11,500 yr B.P. (Watts, 1979). With the arrival of white pine and paper birch (*Betula papyrifera*), an early-successional, mixed conifer-northern hardwoods forest replaced the boreal forest after 11,500 yr B.P. At about 9800 yr B.P., oak and hemlock populations expanded as white pine and paper birch diminished. Hemlock declined at 4600 yr B.P., resulting in a change in forest composition to dominance by pine, birch, oak, and chestnut. Within the last 4000 years, hemlock, spruce, and tamarack populations increased locally (Watts, 1979). Although the composition has shifted in terms of relative dominance of tree taxa, the mixed conifer-northern hardwoods forest type persisted in the vicinity of Tannersville Bog throughout the Holocene.

In contrast to Tannersville Bog, early Holocene vegetation at Longswamp, Pennsylvania, was boreal forest dominated by jack pine, with some fir, birch (*Betula populifolia*), and oak (Watts, 1979). Jack pine dominated from 12,000 to 6000 yr B.P., after which it was replaced by forests of oak and chestnut. The patterns of Holocene vegetation observed at Longswamp are similar to those recorded farther to the west at Panther Run Pond (Figure 1). At Panther Run Pond, closed boreal forest with spruce, fir, and jack pine dominated from 12,600 until about 6400 yr B.P. (Watts, 1979). In the late Holocene, boreal species were replaced by oak, chestnut, hemlock, white pine, and black gum (*Nyssa sylvatica*) (Watts, 1979). At Bear Meadows Bog, located near Panther Run in central Pennsylvania (Figure 1), early Holocene boreal forest of pine, spruce, fir, and tamarack was replaced in the middle Holocene by oak, chestnut, hemlock, beech, and black gum (Kovar, 1965).

At Crider's Pond in south-central Pennsylvania, closed boreal forest of jack pine, spruce, fir, and birch persisted until 9000 yr B.P. (Watts, 1979). After 9000 yr B.P., oak forest with hickory and hemlock replaced the pine forest. Hemlock populations were reduced at about 4500 yr B.P., followed by minor reexpansion in Diploxylon pine in the late Holocene interval. Big Pond, to the southwest of Crider's Pond (Figure 1), contains a Holocene record dating from the last 11,000 years (Watts, 1979). At Big Pond, Holocene vegetational changes were similar to Crider's Pond in timing and sequence of replacement of boreal forest species by temperate forests, with oak, chestnut, and black gum replac-

ing boreal conifers after 9000 yr B.P. (Watts, 1979).

In the Shenandoah Valley of Virginia, the sequence of vegetational changes during the Holocene was similar to that occurring in southern Pennsylvania. At Hack Pond, boreal coniferous forest dominated by jack pine, white pine, and spruce persisted from 12,700 to 9000 yr B.P. (Craig, 1969). From 9000 yr B.P. to the present, temperate forests have been dominated by oak, chestnut, and hickory. Hemlock was present locally until about 4500 yr B.P. White pine and southern Diploxylon pine (*Pinus rigida*) expanded into upland sites during the past 4500 years (Craig, 1969).

Potts Mountain Pond, at 3576 feet (1090 m) elevation in the Valley and Ridge of west-central Virginia (Figure 1), has a radiocarbon-dated pollen sequence that extends from 11,100 yr B.P. to the present (Watts, 1979). At Potts Mountain Pond, early Holocene mixed coniferous-northern hardwoods forest of oak, white pine, spruce, fir, and birch persisted until about 9000 yr B.P. (Watts, 1979). Boreal conifers became locally extinct after 9000 yr B.P. and were replaced by oak, chestnut, black gum, and hickory. White pine reexpanded locally in the late Holocene (Watts, 1979).

In the Saltville Valley of southwestern Virginia, from 12,500 to about 10,000 yr B.P., a mixed conifer-northern hardwoods forest was dominated by oak, spruce, white pine, and jack pine, with hemlock, fir, birch, hornbeam, and maples (Figure 2). From 10,000 to 4700 yr B.P., hemlock dominated the forests. Hemlock populations collapsed 4700 years ago, and were replaced by oak, ash, and chestnut (Figure 2).

Shady Valley Bog, located in northeastern Tennessee (Figure 1), dates from approximately 10,000 yr B.P. to the present (Barclay, 1957). At Shady Valley Bog, hemlock was the forest dominant from 10,000 yr B.P. to the middle Holocene interval. The decline in hemlock populations at Shady Valley probably occurred at the same time as in Saltville Valley, between 5000 and 4500 yr B.P. Late Holocene forests of Shady Valley were predominantly oak, hickory, and chestnut. During the late Holocene interval, there was a minor reexpansion of spruce and fir locally within Shady Valley (Barclay, 1957).

No Holocene pollen or plant-macrofossil records are yet available for the Blue Ridge Province of Virginia or its immediate vicinity. On the Piedmont, the Marsh record from Pennsylvania (Martin, 1958) indicates that boreal forests were replaced in the early Holocene interval by mixed conifer-northern hardwoods forest of pine, hem-

lock, birch, and oak. Deciduous forest of oak and chestnut established in the middle and late Holocene intervals.

On the central Atlantic Coastal Plain, Holocene vegetational changes were influenced by changes in climate and sea level. Two sites in north-central New Jersey, Helmetta Bog and Szabo Pond (Figure 1), record vegetational changes over the past 11,000 years (Watts, 1979). In the early Holocene interval, from 11,400 to 9000 yr B.P., the vegetation at Helmetta and Szabo ponds was boreal forest of spruce and pine, with shrub birch (*Betula glandulosa*). After 9000 yr B.P., spruce populations became locally extinct, and both white pine and southern Diploxylon pine (*Pinus rigida*) established. Oak increased between 9000 and 8500 yr B.P. After 8500 yr B.P., the forests were dominated by oak, with hickory, black gum, and southern Diploxylon pine (Watts, 1979). In the Pine Barrens region of southern New Jersey (Figure 1), southern Diploxylon pines and oaks have codominated for the last 10,500 years (Florer, 1972). Traces of pollen of cool-temperate and boreal species such as spruce, hemlock, and birch persisted until about 10,000 yr B.P. (Florer, 1972). At Trenton, New Jersey (Figure 1), a pollen spectrum dated 10,800 yr B.P. was dominated by pine, with minor amounts of spruce and hemlock; however, spectra dating between 5100 and 2800 yr B.P. reflect middle to late Holocene oak-pine forests on the Coastal Plain (Sirkin and others, 1970). Farther to the south, on the central Delmarva Peninsula of Maryland, pollen spectra dating 9000 and 8900 yr B.P. contain pollen assemblages codominated by oak, pine, and birch, with traces of spruce, hemlock, black gum, and hickory.

At the entrance to the modern Chesapeake Bay (Figure 1), radiocarbon dates are available from sediments at 11,600 and 10,300 yr B.P. (Harrison and others, 1965). Pollen spectra associated with these dates indicate that 11,600 years ago, a mixed conifer-northern hardwoods forest dominated by pine, spruce, fir, hemlock, birch, willow, and oak occupied the outer Coastal Plain at 37° N latitude. After 10,300 yr B.P., forest composition shifted to a temperate assemblage dominated by oak and southern Diploxylon pine.

The development of Holocene vegetation on the outer Coastal Plain of Virginia has been studied extensively at the Dismal Swamp (Figure 1). The swamp developed at the mouth of a drowned river valley as sea level rose during the postglacial interval. The rate of peat accumulation in this freshwater swamp and marsh complex is tied to the rise in sea level and its stabilization at modern

levels approximately 6000 years ago. Although the oldest radiocarbon date available is 8900 yr B.P., peat apparently began to accumulate as early as 12,000 yr B.P. (Whitehead, 1972; Whitehead and Oaks, 1979). The pollen record from the Dismal Swamp shows four intervals of major vegetational change. From 12,000 to about 10,600 yr B.P., open boreal forests of northern Diploxylon pine occurred with minor populations of spruce, birch, and oak. Between 10,600 and 8200 yr B.P., the vegetation changed to a mixed conifer-northern hardwoods forest as beech and hemlock migrated into the area and as birch and oak expanded their populations. Between 8200 and 3500 yr B.P., the vegetation was dominated by oak, with minor populations of southern Diploxylon pine, bald cypress (*Taxodium distichum*), hickory, and sweetgum (*Liquidambar styraciflua*). At about 3500 yr B.P., a minor rise in sea level resulted in a rise of the regional groundwater table and an expansion in the size of Dismal Swamp. Swamp forests of bald cypress, Atlantic white cedar (*Chamaecyparis thyoides*), tupelogram (*Nyssa aquatica*), and red maple (*Acer rubrum*) expanded over the area of Dismal Swamp. The upland vegetation of the Coastal Plain of Virginia was dominated by oak and southern Diploxylon pine during the late Holocene interval (Whitehead and Oaks, 1979).

At Rockyhock Bay, on the outer Coastal Plain of northeastern North Carolina, jack pine-dominated taiga persisted until about 10,000 yr B.P. (Whitehead, 1981). After 10,000 yr B.P., jack pine and spruce were replaced by more dense forests of southern Diploxylon pine, white pine, oak, hickory, hornbeam, birch, beech, and hemlock. This closed, mixed forest persisted until about 5000 yr B.P., when it was replaced by a warm-temperate assemblage including southern Diploxylon pine, oak, bald cypress, tupelogram, red maple, and magnolia (*Magnolia*).

LATE QUATERNARY GRADIENTS IN PLANT AND ANIMAL COMMUNITIES

The central Atlantic states region has been characterized as an area of both vegetational disequilibrium and disharmonious faunal assemblages during the late Pleistocene and early Holocene (Watts, 1979; Delcourt and Delcourt, 1983; Lundelius and others, 1983; Graham and Lundelius, 1984). Were the latitudinal gradients in composition of flora and fauna comparable during the late Pleistocene and early Holocene intervals? Can we interpret the past plant and animal communities

in terms of the changing late Quaternary climate and geomorphic environments?

North-to-south gradients in distribution and composition of vegetation during the late Pleistocene in the central Atlantic states were constrained with respect to physiography, geomorphic regime, and climate. During the late Pleistocene, severe periglacial conditions occurred adjacent to the southern margin of the Laurentide Ice Sheet across all physiographic provinces represented in the central Atlantic states (Péwé, 1983). Discontinuous permafrost extended along the Allegheny Plateau as far south as West Virginia and along the Blue Ridge Province as far south as North Carolina and Tennessee (Delcourt and Delcourt, 1981; Delcourt and Delcourt, 1985). At lower elevations within the Valley and Ridge Province, under climatic conditions that were less severely cold than those prevalent at higher elevations, colluvial processes moved regolith and rock debris downslope. This regime of accelerated mass wastage resulted in the rapid filling of poorly-drained depressions with mineral sediment. In the northern portion of the Valley and Ridge Province, in central Pennsylvania, the late Pleistocene landscape was characterized by extensive patches of open ground, with a mosaic of tundra and taiga communities. Geomorphic disturbances would have continually "reset" plant succession, resulting in a predominance of early-successional or pioneer communities of herbs and shrubs. Farther to the south, from central to southwestern Virginia, the landscape was predominantly closed boreal forest, with more-open patches of muskegs developed within poorly-drained valley bottoms. The increase in richness of plant species in boreal forests from Hack Pond to the Saltville Valley may reflect the areal development of mid- and late-successional forests on more stable landscapes. The frequency and intensity of geomorphic disturbances were greater at 38° N latitude than they would have been at 36° N during the late Pleistocene.

In eastern North America, climatic amelioration began at latitudes of 34° to 36° N as early as 16,500 yr B.P. (Delcourt and Delcourt, 1984). During the late-glacial interval, populations of temperate tree species increased along the southern edge of the boreal forest at sites located at low elevations in western and middle Tennessee, Georgia, and South Carolina (Delcourt and Delcourt, 1984). In the Allegheny Plateau and Blue Ridge physiographic provinces, persistence of severely cold climate and frequent disturbance by active geomorphic processes such as freeze-thaw churning of soil (Péwé,

1983) maintained alpine tundra and inhibited establishment of tree populations throughout the late glacial interval. The periglacial, alpine-tundra environment would have been an effective barrier to migrations of boreal and temperate plant species both east and west of the Valley and Ridge Province.

Within the central Atlantic states, both geomorphic processes and vegetational patterns and processes were locked into a fundamentally glacial climatic regime until approximately 12,500 yr B.P. At lower elevations, two environmental regimes were dominant throughout the late Pleistocene: (1) unglaciated landscapes of the Valley and Ridge Province were shaped by colluvial processes; and (2) land surfaces within the Atlantic Coastal Plain were modified by eolian processes.

The high peaks of the Blue Ridge Mountains served as an orographic barrier that screened moisture from eastward-moving storms. The moisture and unstable regolith were transported downslope, westward into the Valley and Ridge Province and eastward onto the Piedmont. The landscapes of the Valley and Ridge were modified by freeze-thaw processes, where localized disturbances such as debris avalanches, solifluction lobes, and the flow of block streams created open patches of exposed sediments within an otherwise closed boreal forest (see Conners, this volume). These geomorphic episodes of mass-wastage increased the area maintained in pioneer herb and shrub communities, as well as in early-successional forest.

Within the Appalachian Mountains, the change from glacial to interglacial climatic conditions occurred between 13,000 and 12,000 yr B.P.; this corresponded with the transition from a colluvial to a fluvial geomorphic regime. As a result, during the Holocene, the overland flow of water by sheet-wash was less effective in erosion and transport of mineral debris. As the geomorphic threshold from colluvial to alluvial processes was passed, trees colonized the former colluvial surfaces and closed forests were able to establish on stabilized upland slopes. The extensive root systems of the trees and thick organic litter accumulating beneath the forest canopy would have further inhibited erosion of the soil. During the Holocene, concentration of alluvial activity within well-defined stream networks maintained treeless openings within the vegetation only within alluvial glades (wet meadows) and bogs. Sediment that filled ponds, glades, and bogs changed from inorganic to organic-rich at the transition from late glacial to early Holocene conditions (Maxwell and Davis,

1972; Watts, 1979), reflecting decreased colluvial activity and increased rates of peat growth in these environments.

On the Atlantic Coastal Plain, cold and dry climatic conditions occurred during the late Pleistocene within the rain shadow of the Appalachian Mountains. Extensive eolian activity during the full glacial and late glacial intervals resulted in the reworking of sand across the land surface, for example, the Parsonsburg Sand layer that mantles the central Delmarva Peninsula (Denny and others, 1979). The migration of sand dunes and sheets would have generated gaps within the boreal forest and maintained open taiga across the landscape. Driven by wind, water currents eroded shores of lakes and ponds and thus created oriented Carolina Bays, i.e., elongate, shallow lakes with sand dunes developing along their southeastern margins (Whitehead, 1981). The combination of eolian disturbance and nutrient-poor quartzose substrates was a limiting factor for primary productivity within upland taiga distributed from central New Jersey to North Carolina. The central Atlantic Coastal Plain remained in a glacial climatic regime until about 10,500 yr B.P. because of the maritime influence of the cold Labrador Current extending along the Atlantic Coast as far south as South Carolina (Delcourt and Delcourt, 1984).

After 12,500 yr B.P., boreal taxa spread both northward onto newly deglaciated terrain and to higher elevations within the Allegheny Plateau and the Blue Ridge Province. Temperate taxa expanded northward along migration routes that followed the Valley and Ridge corridor and the Atlantic Coastal Plain. The combination of climatic amelioration, fundamental changes in geomorphic regimes, and plant-species migrations northward resulted in vegetational disequilibrium and dynamically changing landscapes during the early Holocene interval, particularly between 12,500 and 10,000 yr B.P. (Delcourt and Delcourt, 1983).

Four sites with late Pleistocene faunal information within the Valley and Ridge Province extending from Pennsylvania to Tennessee provide some of the best-dated evidence available concerning late Pleistocene faunal gradients (Lundelius and others, 1983; Guilday, 1984). From north to south, these sites include New Paris No. 4, central Pennsylvania; Clark's Cave, western Virginia; Saltville, southwestern Virginia; and Baker Bluff Cave, northeastern Tennessee (Figure 1).

Pleistocene fauna from Saltville date between 15,500 and 13,600 yr B.P. (Ray and others, 1967; McDonald, this volume). The species-rich assemblage of proboscidians, musk oxen, and caribou is

consistent with the paleoecologic reconstruction of boreal forest and poorly-drained muskegs within the Saltville Valley during the late glacial interval.

The three remaining sites contain assemblages of small mammals that date from approximately 12,000 to about 10,000 yr B.P. (Guilday, 1984; Guilday and others, 1978). Guilday and others (1978) document a latitudinal gradient in composition of small mammals from these sites. Although boreal, temperate, and grassland mammals were reported at each site, their relative abundances changed systematically with latitude. At New Paris No. 4, the assemblage of small mammals indicated a mixture of tundra and taiga environments (Guilday and others, 1964). At Clark's Cave, the microtines were characteristic of dense boreal forests (Guilday and others, 1977). The faunal assemblage at Baker Bluff Cave was compatible with a boreal, mixed coniferous-deciduous woodland. From north to south, a climatic gradient from boreal to temperate conditions was inferred (Guilday and others, 1978). The fossil assemblages contained species of mammals whose modern ranges do not overlap, and therefore have been called disharmonious assemblages. These assemblages lacked good modern analogs and have been interpreted as evidence for more equable climatic conditions during the late Pleistocene, with reduced seasonal extremes (Lundelius and others, 1983; Graham and Lundelius, 1984). In part, the north-to-south gradient in geomorphic processes also maintained the fine-grained character of environmental heterogeneity of the late Quaternary Appalachian landscapes.

The disharmonious assemblages of fossil mammals appear to reflect the response of mammalian communities to major climatic amelioration during the late glacial and early Holocene intervals, as well as the increased diversity of habitats that resulted from both widespread geomorphic and vegetational instability. The vegetational disequilibrium (Delcourt and Delcourt, 1983) resulted from northward migrations of plant species along the Valley and Ridge corridor, as well as from changes in disturbance regimes with the transition from colluvial to alluvial geomorphic processes. With the shift 10,000 years ago to a landscape modified predominantly by alluvial processes, the vegetational mosaic changed from the Pleistocene pattern (an open patchwork of tundra, open glades, and boreal forests) to a Holocene pattern of predominantly closed, temperate deciduous forests.

The regional vegetation continued to change throughout the past 10,000 years because of subsequent northward migrations of warm-temperate trees, the expansion of coastal swamps related to

the rise of sea level to its modern position about 6000 years ago, and relatively minor Holocene climatic change. However, the magnitude of environmental changes through the middle and late Holocene intervals was not as great as that characterizing the transition from the late glacial to the early Holocene.

DIRECTIONS FOR FUTURE RESEARCH

From this summary of late Quaternary vegetational changes known from the central Atlantic states, it is apparent that very little information is available for several major physiographic regions. No sites with full glacial sequences of pollen or plant-macrofossil assemblages have yet been studied in the Blue Ridge, Valley and Ridge, or Piedmont provinces of Virginia. Patterns of vegetational change are yet poorly understood for the central portion of the Atlantic Coastal Plain, with only the pioneering studies of Dismal Swamp representing the state of Virginia. Future research should concentrate upon establishing a network of radiocarbon-dated sites with detailed paleoecologic studies throughout this critical region.

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**THE KNOWN HERPETOFAUNA OF THE LATE QUATERNARY
OF VIRGINIA POSES A DILEMMA**

J. Alan Holman¹

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ABSTRACT

Although the mammalian fauna of the late Pleistocene of Virginia contains extinct species and species that indicate boreal climatic conditions, the late Pleistocene herpetofauna appears almost identical to what it is today. This dilemma is discussed, and future Pleistocene herpetological studies are suggested.

INTRODUCTION

Among the most compelling problems of the late Pleistocene are the rapid extinction of the mammalian megafauna, the postulated rapid change in the climate, and ways in which the spread of humankind might be related to the two previous events. Paleoherpetological studies reflect directly or indirectly on all of these questions. Thus, the purpose of the present paper is to examine and reflect upon the record of amphibians and reptiles from the late Pleistocene

of Virginia and to suggest directions for future paleoherpetological studies.

Although few reports on Virginia's late Pleistocene amphibians and reptiles have been done, implications from these reports pose a serious dilemma. Although Virginia's late Pleistocene mammalian fauna contains extinct forms and forms that suggest boreal conditions, the herpetofauna appears to be almost identical to what it is today. The implications of this dilemma will be given after the review of previous studies that follows.

LATE PLEISTOCENE HERPETOFAUNAL
STUDIES IN VIRGINIA

Workers heretofore involved in late Pleistocene herpetofaunal studies in Virginia are, in chronological order: Olaf A. Peterson, Neil D. Richmond, Helen McGinnis, John E. Guilday, Leslie P. Fay, J. A. Holman, and Jerry N. McDonald. Compared to avian and mammalian remains, herpetological fossils are quite difficult to identify. Thus it is not surprising that a few misidentifications of herpetological remains, or objects thought to be herpetological remains, were made. These early misidentifications led to some

¹Museum, Michigan State University, East Lansing, Michigan 48824

confusion in previous interpretations of Pleistocene faunas and events.

O. A. Peterson (1917) reported "a large crocodile tooth" associated with the remains of a mastodon in a "fossil-bearing alluvial deposit" at Saltville, Virginia. This report led to much confusion. Anyone trying to discuss the faunal association of the Saltville deposit had to either postulate some complex reason to account for the presence of the crocodile in a predominantly boreal fauna, or to consider the fauna hopelessly heterochronic. N. D. Richmond (1963) pointed out that the "crocodile tooth" was actually a fossil invertebrate, most likely an orthoceran cephalopod that had eroded out of a lower Paleozoic limestone in the area, and had washed into the site as a part of the gravel in which the Pleistocene mammals were found. Ray, Cooper and Benninghoff (1967) demonstrated that the specimen was an aberrant mandibular tusk of a mastodon, *Mammot americanum* (Kerr).

Later N. D. Richmond (in Guilday, 1962) identified a Coachwhip Snake (*Masticophis flagellum*) and an Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) based on vertebral remains from the late Pleistocene Natural Chimneys site, Augusta County, Virginia. These species are not found in Virginia today although they do range north to near its southern border (Conant, 1975). L. P. Fay (1984) restudied the snake material from the Natural Chimneys site and suggested that the fossil material assigned to *Masticophis flagellum* should be reassigned to *Coluber constrictor*, a species that lives in the area today. This change was based on the fact that Fay was unable to find characters to separate isolated *Masticophis* and *Coluber* vertebrae, and on modern zoogeographic grounds. Fay also changed the identification of *Crotalus adamanteus* to *Crotalus horridus*, the latter species also being a modern resident of the area. This change was based on the low vertebral neural spine of the fossil, a character which readily separates *C. horridus* from *C. adamanteus*.

Only three sites in Virginia thus far have yielded significant published herpetofaunas. These are the Natural Chimneys site in Augusta County, Clark's Cave in Bath County, and the Saltville site in Smyth County, Virginia.

The Natural Chimneys site, 1 mile (1.6 km) west of Mt. Solon, Augusta County, Virginia, was excavated by Carnegie Museum field parties from 1949 through 1961. The site lies at an elevation of 1329 to 1476 feet (405 to 450 m). The bones are thought to have been derived from the

prey of raptors that frequented the feature. The location, geology, and description of the site are found in Guilday (1962). Herpetological remains detailed in Guilday's paper were identified by Neil D. Richmond. Richmond identified two salamanders, five anurans, two turtles, one lizard, and ten snakes from the site. Fay (1984) restudied the Natural Chimneys herpetofauna and added three salamanders, six anurans, one lizard, and seven snakes to the list. Fay eliminated the southern extralimital forms *Masticophis flagellum* and *Crotalus adamanteus* from the list in Guilday (1962). Noteworthy is the fact that the little ground skink, *Scincella lateralis*, is known as a fossil only from the Natural Chimneys site (Fay, 1984). The Natural Chimneys herpetofauna is listed in the Table.

The Clark's Cave deposits, 7.4 miles (12 m) southwest of Williamsville, Bath County, Virginia, was excavated in the early 1970's by field parties from the Carnegie Museum. The site was discovered in 1972. The site lies at an elevation of 1480 feet (448 m). The bones are thought to have been derived from the prey of raptors. A quite detailed account of the regional setting and history of the site is given in Guilday and others (1977). Helen McGinnis identified the amphibians and John E. Guilday identified the reptiles reported in this paper. This herpetofauna included two salamanders, seven anurans, two lizards, and two snakes. Fay (1984) added seven salamanders, three anurans, one turtle, and twenty snakes to the list. The Clark's Cave herpetofauna is also listed in the Table.

The Saltville site, Smyth County, Virginia, has yielded vertebrate fossils for more than two centuries (McDonald, 1984). The site lies at an elevation of about 1720 feet (525 m). A description of the site and previous research there is given by McDonald (1984). Amphibians and reptiles from the Saltville site were collected mainly by field parties from Radford University which were directed by J. N. McDonald during 1980 to 1984. A report on amphibians and reptiles of the Saltville site (Holman and McDonald, 1985) detailed two salamanders, two anurans, two turtles, and two snakes. The Saltville herpetofauna is also listed in the Table.

DISCUSSION

Late Pleistocene amphibians and reptiles have been studied much less thoroughly than mammals. This is probably the result of two factors. First, fossil amphibians and reptiles often are

Table. The Late Pleistocene Herpetofauna Of Virginia. *

Scientific Name	Vernacular Name	Natural Chimneys	Clark's Cave	Saltville
<i>Cryptobranchus alleganiensis</i>	Hellbender	0	0	+
<i>Notophthalmus viridescens</i>	Eastern Newt	+	+	+
<i>Ambystoma (maculatum group)</i>	Mole Salamander	+	+	0
<i>Ambystoma opacum</i>	Marbled Salamander	0	+	0
<i>Ambystoma tigrinum</i>	Tiger Salamander	+	0	0
<i>Desmognathus sp.</i>	Dusky Salamander	+	+	0
<i>Plethodontini sp.</i>	Woodland Salamander	+	+	0
<i>Gyrinophilus porphyriticus</i>	Spring Salamander	0	+	0
<i>Pseudotriton sp.</i>	Red Salamander	0	+	0
<i>Scaphiopus holbrooki</i>	Eastern Spadefoot	+	+	0
<i>Bufo americanus</i>	American Toad	+	+	0
<i>Bufo woodhousei fowleri</i>	Fowler's Toad	+	+	+
<i>Hyla chrysoscelis</i> or <i>H. versicolor</i>	Gray Treefrog	+	0	0
<i>Hyla crucifer</i>	Spring Peeper	0	+	0
<i>Rana catesbeiana</i>	Bullfrog	+	+	0
<i>Rana clamitans</i>	Green Frog	+	+	0
<i>Rana palustris</i>	Pickerel Frog	+	+	0
<i>Rana cf. Rana pipiens</i>	Northern Leopard Frog	+	+	+
<i>Rana sylvatica</i>	Wood Frog	+	+	0
<i>Chelydra serpentina</i>	Snapping Turtle	+	0	+
<i>Graptemys geographica</i>	Map Turtle	0	+	0
<i>Terrapene carolina</i>	Eastern Box Turtle	+	0	0
<i>Chrysemys picta</i>	Painted Turtle	0	0	+
<i>Sceloporus undulatus</i>	Eastern Fence Lizard	+	+	0
<i>Scincella lateralis</i>	Ground Skink	+	0	0
<i>Eumeces ? Eumeces laticeps</i>	Broadhead Skink	0	+	0
<i>Nerodia erythrogaster</i>	Plainbelly Water Snake	+	0	0
<i>Nerodia sipedon</i>	Northern Water Snake	+	+	+
? <i>Regina septemvittata</i>	Queen Snake	0	+	0
<i>Storeria occipitomaculata</i>	Redbelly Snake	+	+	0
<i>Storeria dekayi</i>	Brown Snake	0	+	0
<i>Thamnophis sauritus</i>	Eastern Ribbon Snake	+	+	0
<i>Thamnophis sirtalis</i>	Common Garter Snake	+	+	0
<i>Virginia valeriae</i>	Earth Snake	0	+	0
<i>Carphophis amoenus</i>	Worm Snake	+	+	0
<i>Diadophis punctatus</i>	Ringneck Snake	+	+	0
<i>Heterodon platyrhinos</i>	Eastern Hognose Snake	0	+	0
? <i>Tantilla coronata</i>	Southeastern Crowned Snake	0	+	0
<i>Coluber sp. or Masticophis sp.</i>	Racer or Coachwhip Snake	+	+	0
<i>Opheodrys aestivus</i>	Rough Green Snake	0	+	0
<i>Opheodrys vernalis</i>	Smooth Green Snake	0	+	0
<i>Cemophora coccinea</i>	Scarlet Snake	0	+	0
<i>Elaphe guttata</i>	Corn Snake	+	+	0
<i>Elaphe obsoleta</i>	Rat Snake	+	+	+
<i>Lampropeltis getulus</i>	Common King Snake	+	+	0
<i>Lampropeltis calligaster</i>	Mole Snake	0	+	0
<i>Lampropeltis triangulum</i>	Milk Snake	+	+	0
<i>Crotalus horridus</i>	Timber Rattlesnake	+	+	0

*Indeterminate genera are not listed in one locality if they are specifically identified in one of the other localities. + = present; 0 = absent.

represented by small, fragile bones that may be rare or overlooked at fossil sites. Second, herpetological fossils are more difficult to identify than the mammalian jaws and teeth traditionally studied by vertebrate paleontologists. For the second reason many workers have hesitated to identify herpetological remains for fear of making mistakes. Nevertheless, herpetological information is quite important in the study of late Pleistocene paleoecology.

Hibbard (1960) first realized the significance of crocodylians and large land tortoises in the interpretation of Pliocene and Pleistocene climates. He also believed (personal communication) that information gathered from the study of smaller amphibians and reptiles would yield important data about Pliocene and Pleistocene climates. He reasoned that these ectotherms would be much more sensitive to environmental changes than mammals and thus would be much more indicative of climatic change. Another point is that most amphibians and reptiles of the late Pleistocene represent living species whose ecological tolerances are fairly well known.

Unfortunately, herpetological evidence from Pleistocene faunas has sometimes been misinterpreted. Many Pleistocene faunas contain herpetological species that today would not be ecologically compatible with the mammalian species of the fauna (Lundelius and others, 1983). Workers sometimes disregarded these herpetological species, believing that they were modern intrusions into the fauna, and based their paleoclimatic interpretations on the mammalian component only.

Actually, one usually can recognize quite easily intrusions of herpetological elements into a fauna, and I wish to emphasize that none of the late Pleistocene Virginia amphibians and reptiles listed here are considered to be modern intrusions. Intrusive herpetological forms may be recognized on the basis of three criteria that follow. (1) Intrusive forms are almost always burrowers such as Mole Salamanders of the genus *Ambystoma* or burrowing anurans such as *Scaphiopus*. (2) Bones of intrusive forms are usually of a different color and density than those of the fossils of the deposit. (3) Intrusive forms usually consist of suspiciously complete skeletons, unlike fossils of a deposit which usually consist of isolated bones.

Another mistake that was made, especially in the interpretation of southeastern Pleistocene herpetofaunas, was to reason that when ecologically incompatible forms were present in the

fauna that the deposit was heterochronic. This reasoning undoubtedly grew out of the ingrained belief that solution features in the southeast quite often contained mixtures of Miocene, Pliocene, or Pleistocene fossils, or mixtures of fossils of various Pleistocene ages. The fact is that most solution deposits in the southeast contain rather restricted Pleistocene faunas, occasionally Pliocene faunas, and rarely Miocene faunas; very rarely is there a scrambled mixture of these faunas of different ages. The only mixed fossils that regularly occur are the readily identifiable invertebrate fossils redeposited from the limestones that previously contained these forms. Webb (1974) and Holman (1976) have shown that almost all known southeastern Pleistocene faunas in solution features such as caves and sinkholes are not heterochronic but represent fairly restricted units of time.

The fact that solution features in the southeastern United States almost always contain fossil faunas representing restricted units of time merely follows the basic paleontological principle that in order to have fossilization, some type of immediate burial must occur. The scenario that occurs is as follows. (1) Animal remains are trapped in or carried into solution features by raptors or carnivores, and (2) rapid sedimentation occurs to lead to the fossilization of the bones. This would explain why some solution features contain vertebrate fossil remains, while other seemingly identical ones are barren of fossils. Again, there is no evidence that the late Pleistocene deposits in Virginia that have amphibians and reptiles reported from them contain heterochronic faunas, and therefore we must conclude that a herpetofauna of such a deposit was contemporaneous with the mammalian fauna.

Another important factor to consider (Russell W. Graham, personal communication) with regard to faunas with ecologically incompatible members is that there are practically no mammalian faunas from archeological or paleontological sites in the Holocene that have ecologically incompatible members, yet these assemblages are presumably subjected to the same taphonomic processes as the late Pleistocene ones. Unfortunately, there is practically no published information on the herpetofaunas of the Holocene.

The realization by Hibbard (1960) that faunas that he studied from the High Plains, especially those from southwestern Kansas, were unit faunas, and had ecologically incompatible forms in them, led him and subsequent authors (Dalquest, 1965; Dalquest and others, 1969; Hibbard, 1970;

Hibbard and Taylor, 1960; Martin and Neuner, 1978; Slaughter, 1967, 1975; Slaughter and Hoover, 1963; and Taylor, 1965) to form a Pleistocene "climatic equability hypothesis". The climatic equability hypothesis explained the former co-occurrence of extralimital northern and southern forms that are considered climatically incompatible today, as follows. It was reasoned that mild winters would account for the presence of extralimital southern species, and that cooler summers would account for the presence of extralimital northern species. This hypothesis was based mainly on mammals from the Pleistocene of the central and southern Great Plains, but giant tortoises of the genus *Geochelone* were considered especially important in indicating very mild winters when these reptiles were present in faunas.

The term "disharmonious communities" recently has been used widely to describe communities that have species in them that would be ecologically incompatible today. Lundelius and others (1983) provide a comprehensive discussion of disharmonious communities and their relationship to the Pleistocene climatic equability hypothesis based on terrestrial vertebrate faunas in the United States from 25,000 to 10,000 years before the present.

With specific reference to fossil herpetofaunas, Holman (1976) suggested that ecologically incompatible amphibians and reptiles in late Pleistocene deposits in Florida, Georgia, and Mississippi could be explained on the basis of the climatic equability hypothesis. A more comprehensive review of Pleistocene herpetofaunas of eastern and central North America (Holman, 1980) did not support the classical concept of alternating warm-dry, cool-moist glacial and interglacial climates. On the contrary, the herpetological evidence generally indicated Pleistocene climates south of the glacial limits were warmer or more equable than today until at least very late Pleistocene times.

But what do the amphibians and reptiles thus far identified from the Pleistocene of Virginia indicate regarding the climate of the time? With only a few exceptions, the late Pleistocene amphibians and reptiles occur in the same areas today and none of them is extinct. Two of the extralimital forms, *Ambystoma tigrinum* and *Rana cf. pipiens* (Table) are probably absent from the area today because of local edaphic changes (Fay, 1984). These forms also may indicate the individualistic response of species to their own tolerances, as emphasized by Russell W. Graham

(personal communication). The other extralimital forms, *Graptemys geographica*, *Scincella lateralis*, *Nerodia erythrogaster*, *Tantilla coronata*, and *Cemophora coccinea* occur south of the Virginia Pleistocene localities (Table; Conant, 1975). Thus, based on the herpetofauna alone, one would assume that the climate was nearly the same or perhaps slightly warmer than today in the late Pleistocene of Virginia.

On the other hand, the mammalian fauna of the Natural Chimneys, Clark's Cave, and Saltville contains so many boreal species that previous workers have postulated a boreal climate and boreal vegetation for Virginia in the late Pleistocene (Guilday, 1962; Guilday and others, 1977). Based on the herpetological evidence from these sites, I cannot emphasize enough that we must take a critical look at the environmental reconstructions based on the mammals.

First, a boreal-type summer climate seems impossible. Stuart (1979) pointed out that a mean July temperature well in excess of 18°C appears necessary for the European Pond Tortoise, *Emys orbicularis*, to breed successfully in Europe. This is why no turtle populations are able to maintain themselves in southern England, which has a cool equable climate that lacks enough warm weather in the summer for turtle eggs to hatch. Certainly the four species of late Pleistocene Virginia turtles (*Chelydra serpentina*, *Chrysemys picta*, *Graptemys geographica*, and especially *Terrapene carolina*) would not have been able to have successful hatching of eggs in an area with a boreal summer climate. Moreover, the large number of egg-laying snakes found in the three Virginia late Pleistocene faunas would have had similar problems reproducing in a boreal summer climate. These species include *Carphophis amoenus*, *Diadophis punctatus*, *Heterodon platyrhinos*, *Tantilla coronata*, *Coluber constrictor*, *Opheodrys aestivus*, *Opheodrys vernalis*, *Cemophora coccinea*, *Elaphe guttata*, *Elaphe obsoleta*, and *Lampropeltis getulus*. The egg-laying lizards *Sceloporus undulatus*, *Scincella lateralis*, and *Eumeces laticeps* provide further evidence that summers must consistently have had periods of much warmer temperatures than occur in boreal areas today.

To repeat, these reptiles are not intrusive elements in the faunas and were contemporaneous with the fossil mammal species of Natural Chimneys, Clark's Cave and Saltville (Fay, 1984; Holman and McDonald, 1985). Therefore, it would seem appropriate to suggest other climatic and vegetational models to replace the boreal one that

has been based almost entirely on the mammalian fauna.

Russel W. Graham (personal communication) believes that the mammalian forms did not react to environmental change as "community units", but rather that each species responded to environmental modifications according to their own tolerance limits. Moreover, he believes that northern mammals forced into southern communities by the glaciation became intergrated with the resident biota, creating the disharmonious community. He believes an equable climate would then maintain this assemblage. The herpetofauna, on the other hand, at the latitude of Virginia, would not appear as mixed as the mammalian fauna, for it contains no strictly northern herpetological species. Thus a boreal climate is not indicated for the late Pleistocene of Virginia.

Dreimanis (1968) suggested that changes in vegetational structure and composition rather than shifting ecological zones may have occurred in the late Pleistocene. This composite vegetational situation may have allowed for the simultaneous occurrence of northern and temperate species.

A second part of the herpetological dilemma is that although many late Pleistocene mammalian genera and species became extinct in Virginia (and elsewhere in the world), thus far no extinct amphibian or reptile taxon has been reported from the late Pleistocene of Virginia (Table). In fact, only a very few extinct herpetological species are known from the late Pleistocene of the entire United States, and the status of at least one of these is in doubt (Lundelius and others, 1983).

Certainly numbers of some herpetological species have dwindled in historic times, and some forms today may be on the verge of extinction because of the destruction of habitats by humans. But it is important to note that amphibians and reptiles appear to have been able to cope admirably with the same conditions that drove many mammalian taxa to extinction. Whatever biological attributes these cold-blooded species have, they evidently have fitted them well for changes that took place in the late Pleistocene and Holocene.

More Late Pleistocene Studies are Needed.—It is clear that the study of late Pleistocene-early Holocene amphibians and reptiles in Virginia is yet in its infancy. It is beyond the scope of this paper to list all of the known localities in Virginia containing herpetofaunas, but Ralph E. Eshelman has provided me with a list of 17 such

localities. Moreover, the important Saltville site continues to yield herpetological fossils. Holocene herpetofaunas are especially in need of study to determine whether amphibians and reptiles show modern community structure as do the mammals.

In future studies, more taphonomic work needs to be done such as establishing whether the accumulation of bone results from raptor or predator activities, hibernating activities of the amphibians and reptiles involved, or from other causes.

More fossil material is needed from existing faunal units to confirm some of the previous herpetological identifications. Most snakes have been identified on the basis of isolated vertebral remains, and small natricine and colubrine genera are especially difficult to identify on the basis of such material (Holman, 1981).

Finally, data on minimal critical temperatures necessary for various reptile eggs to hatch would be most enlightening and helpful in the study of the ecology and distribution of late Pleistocene reptile species. It would appear that these data would provide an unprecedented chance to postulate critical mean summer temperatures in the late Pleistocene.

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Leslie P. Fay kindly allowed me to cite the late Pleistocene herpetofaunal lists from the Natural Chimneys and Clark's Cave sites from his doctoral dissertation at Michigan State University, and he provided thought-provoking conversations about paleoherpetological problems. Letters and fossil material sent by Neil D. Richmond in the late 1950's initiated my thinking about late Pleistocene herpetological problems in the Appalachian Region. Ralph E. Eshelman, Fred Grady, Russell W. Graham, and Jerry N. McDonald read drafts of this paper and provided valuable comments and materials. I thank all of these gentlemen for their help without which this paper could not have been written.

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**QUATERNARY VERTEBRATE LOCALITIES OF VIRGINIA
AND THEIR AVIAN AND MAMMALIAN FAUNA**

Ralph Eshelman¹ and Frederick Grady²

“The varying degrees in our understanding of the evolution of the Late Wisconsin fauna is a function of the geographic and chronologic density of the fossil localities. The known faunas are not evenly distributed spatially or temporally but are clustered in those areas and time periods on which intensive research programs have been focused. Thus, the late Pleistocene [and Holocene] faunas of some areas and times are better known than those of others” (Lundelius and others, 1983, p. 311).

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¹Calvert Marine Museum, Solomons, Maryland, 20688, and Research Associate, Department of Paleobiology, National Museum of Natural History, Washington, D. C., 20560.

²Department of Paleobiology, National Museum of Natural History, Washington, D. C., 20560.

ABSTRACT

There are 77 Quaternary vertebrate localities in the state of Virginia from which 100 taxa of birds and 93 taxa of mammals have been identified. While many localities are represented by single specimens, there are several significant local faunas containing numerous specimens representing both marine and terrestrial environments. Karst features, such as caves and fissures, account for 74 percent of the sites. The depositional environment, age, and distribution of Virginia's Quaternary vertebrate localities are discussed, and Virginia's late Pleistocene and 16th Century mammalian faunas are identified and compared.

INTRODUCTION

Early European settlers in Virginia occasionally found Quaternary vertebrate fossils. In 1686 John Banister exhibited large bones and teeth from the interior of Virginia to John Clayton (Goode, 1901; Simpson, 1942, 1943; Ewan and Ewan, 1970). Osborn (1939) noted that Samuel Maverick in 1636 reported fossil bones from 18 feet below the surface of the James River 60 miles above its mouth; however, these specimens were probably Miocene in age. Over one hundred years later, Thomas Jefferson (1787) noted proboscidean remains from the now well-known Saltville locality near the North Fork of the Holston River (Ray and others, 1967).

During the 19th Century, fossil finds consisted for the most part of isolated specimens, some of which are preserved in the U. S. National Museum of Natural History (USNM) collections. The first record of a marine mammal of Quaternary age from Virginia was recorded in a scholarly publication by Mitchill and others (1827). Cope (1867) provided the first published record of Quaternary vertebrates from a cave within the present borders of the state of Virginia.

However, it was not until the middle of the 20th Century that systematic searches for fossil vertebrates were made in Virginia. Two institutions, the Carnegie Museum of Natural History (CMNH) and USNM, made concerted efforts to recover Quaternary vertebrates. Even so, most of the fossils that have been collected remain unstudied and the localities unpublished. Kurtén and Anderson's (1980) *Pleistocene Mammals of North America* noted only three significant localities in Virginia and made passing reference to four others.

The purpose of this paper is to record the avian and mammalian fossil sites of Quaternary age in

Virginia that have been studied or are under study, to establish the late Pleistocene and 16th Century faunas compiled from these localities, and to discuss the zoogeography, age, and environmental reconstruction based on the evidence provided by these faunas. The term "16th Century fauna" as used here refers to the fauna that existed in Virginia, just prior to the arrival of the first European settlers in the Middle Atlantic region.

The number of Quaternary localities (published and unpublished) in Virginia reported in this paper is 77. These sites are listed in Table 1, which also provides information about their location, depositional environment, agent(s) of accumulation, age and method of dating, and sources of data on them. Figures 1 and 2 show the locations of these sites. We follow the format of Lundelius and others (1983) to facilitate comparison with records for the rest of the United States. The Quaternary amphibian and reptilian fossils from Virginia have been studied by Fay (1984; and this volume) and Holman (this volume).

The following institutional designations are used throughout: ANSP, Academy of Natural Sciences of Philadelphia; CMNH, Carnegie Museum of Natural History; NJSM, New Jersey State Museum; RU, Radford University; and USNM, United States National Museum, Department of Paleobiology.

DEPOSITIONAL ENVIRONMENTS AND VIRGINIA QUATERNARY VERTEBRATE LOCALITIES

Table 2 is a list of depositional environments from which Quaternary birds and mammals are known or could be expected to be recovered. This table includes all localities in Table 1, listed by their

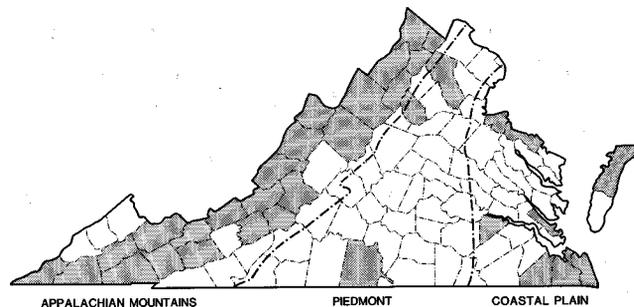


Figure 1. Map of Virginia, showing the three major physiographic regions of Virginia and the counties (shaded) from which Quaternary birds and mammals have been recovered.

Table 1. Virginia localities from which Quaternary birds and mammals have been identified.

Local Fauna	Location	Depositional Environment	Agent(s) of Accumulation	Age and Method of Dating	Notes and References
1. Abingdon	Washington Co.	Salt spring?	Natural accumulation	Late Pleistocene, extinct taxon	Prout, 1860; Hay, 1923
2. Arcadia Cave #1 and #2	Botetourt Co.	Cave	Owl	Early Holocene, based on faunal assemblage	CMNH coll. unpublished data
3. Back Creek Cave #1 (aka Cook Cave)	Bath Co.	Rockshelter, owl roost	Owl	Late Pleistocene/early Holocene, based on faunal assemblage	Guilday and others, 1977; CMNH coll. unpublished data
4. Back Creek Cave #2 (aka Sheets Cave)	Bath Co.	Rockshelter, owl roost	Owl	Late Pleistocene/early Holocene, based on faunal assemblage	Guilday and others., 1977; Jones and others., 1984; CMNH coll. unpublished data
5. Back Creek Cave #3	Bath Co.			Holocene	CMNH coll. unpublished data
6. Bill Neff Cave (aka Susan's Big Mouth Cave)	Rockingham Co.			Holocene?	USNM coll. unpublished data
7. Blacksburg	Montgomery Co.				Handley and Patton, 1947
8. Cedar Hill Cave	Rockingham Co.	Cave			USNM coll. unpublished data
9. Chesapeake City				Late Pleistocene, extinct taxon	USNM coll. unpublished data
10. City Point	Prince George Co.		Natural accumulation	Late Pleistocene, extinct taxon	Hay, 1923
11. Clark's Cave	Bath Co.	Cave	Owl	Late Pleistocene, based on faunal assemblage	Guilday and others, 1977; Jones and others, 1984
12. Cliff Cave #2 (Station B)	Giles Co.	Cave	Owl	Early Holocene, based on faunal assemblage	CMNH coll. unpublished data
13. Comers Cave	Page Co.	Cave		Recent?	Guilday, 1982b
14. Continental Shelf	Offshore	Ocean Bottom	Natural accumulation	Late Pleistocene, extinct taxa	Whitmore and others, 1967; USMN coll. unpublished data
15. Covington	Alleghany Co.		Natural accumulation	Late Pleistocene, extinct taxa	Hay, 1923
16. Crab Orchard Cave	Tazewell Co.	Cave	Cultural accumulation	Holocene, based on faunal assemblage and human association	Clark, 1979 unpublished data
17. Darty Cave	Scott Co.	Cave	Owl	Level 1 = late Pleistocene/Holocene?; level 2-4 = early Holocene, based on faunal assemblage	CMNH coll. unpublished data
18. Deep Creek Pit	City of Chesapeake	Alluvium	Natural accumulation	Late Pleistocene, based on ¹⁴ C dates of 18,780 ± 630 and 16,830 yr B.P. on <i>Mammuth americanum</i> tusk fragment. Wood date 0.3 m above tusk at > 38,000 yr B.P.	Stuckenrath and Mielke, 1972; USMN coll. unpublished data

Table 1. (cont.)

Local Fauna	Location	Depositional Environment	Agent(s) of Accumulation	Age and Method of Dating	Notes and References
19. Denniston	Halifax Co.			Late Pleistocene, extinct taxon	Hay, 1923
20. Early's Cave (aka Early's Pit, Ivanhoe?)	Wythe Co.	Cave		Mid Pleistocene?, based on faunal assemblage	Cope, 1869a, b; Hay, 1923; Guilday, 1962b; Jones and others, 1984
21. Eclipse	City of Suffolk	Marine sediments	Natural accumulation	Pleistocene?	Olsen and Blow, USNM coll. unpublished data
22. Edinburg Fissure	Shenandoah Co.	Fissure		Late Pleistocene (Illinoian?), based on faunal assemblage	USNM coll. unpublished data
23. Edom	Rockingham Co.		Natural accumulation	Late Pleistocene, extinct taxon	Hay, 1923
24. Eggleston Fissure	Giles Co.	Fissure		Late Pleistocene, based on faunal assemblage	CMNH coll. unpublished data
25. Ely Cave (aka Gilley?)	Lee Co.	Cave	Natural accumulation/cultural accumulation	Holocene?, based on human association	Allen, 1885
26. Fairview Beach (aka Belvedere)	King George Co.			Pleistocene, based on extinct taxa	NJSM coll. unpublished data
27. Gardner's Cave	Wythe Co.	Cave		Late Pleistocene, based on faunal assemblage	Guilday, 1962b; Eshelman, USNM coll. unpublished data
28. Gillespie's Cliff Cave	Tazewell Co.	Cave	Owl	Mixed — late Pleistocene and Holocene, based on faunal assemblage	CMNH coll. unpublished data
29. Glade Cave	Augusta Co.	Cave		Holocene	Eshelman, unpublished data
30. Holston Vista Cave	Washington Co.	Cave	Owl?	Late Pleistocene/Holocene, based on faunal assemblage	CMNH coll. unpublished data
31. Hot Run	Frederick Co.	Spring/alluvium	Natural accumulation	Pleistocene, based on ^{14}C of $11,550 \pm 165$ yr B.P. on <i>Mammot</i> molar	Ott and Weems, this volume
32. Hot Springs	Bath Co.	Spring	Natural accumulation	Late Pleistocene, extinct taxon	Hay, 1923
33. Jasper Saltpeter Cave	Lee Co.	Cave		Mid Pleistocene (Illinoian?), based on faunal assemblage	Guilday, 1979; Jones and others, 1984; CMNH coll. unpublished data
34. Keyser Farm	Page Co.		Cultural accumulation	Late Holocene (Woodland Period), based on faunal assemblage and human association	Manson and others, 1943
35. Klotz Quarry Cave #5	Giles Co.	Cave	Owl	Late Pleistocene, based on faunal assemblage	CMNH coll. unpublished data
36. Kumis	Roanoke Co.				Handley and Patton, 1947
37. Lane Cave	Scott Co.	Cave		Late Pleistocene, based on extinct taxon	Holsinger, 1967

Table 1. (cont.)

Local Fauna	Location	Depositional Environment	Agent(s) of Accumulation	Age and Method of Dating	Notes and References
38. Limeton	Warren Co.				Clark, 1938, 1939
39. Loop Creek Quarry Cave	Russell Co.	Cave	Owl	Late Pleistocene/early Holocene, based on faunal assemblage	CMNH coll. unpublished data
40. Luray Caverns	Page Co.	Cave			Hovey, 1882
41. Meadowview Cave	Washington Co.	Cave		Late Pleistocene, based on faunal assemblage	Guilday and Parmalee, 1972; Jones and others, 1984; Klippel and Parmalee, 1984; CMNH coll. unpublished data
42. Metomkin and other barrier island	Accomack Co.	Ocean beach	Natural accumulation	Late Pleistocene, extinct taxon	Mitchill and others, 1827; Hay, 1923; USMN coll. unpublished data
43. Natural Chimneys (aka Brown's Cave and Cave of the Wooden Steps)	Augusta Co.	Cave, owl		Mid-Pleistocene?, based on faunal assemblage	Guilday and Bender, 1960; Wetmore, 1962; Guilday, 1962a; Guilday and Parmalee, 1972; Jones and others, 1984; Fay, 1984; Anderson, 1984
44. New Castle	Craig Co.				Handley and Patton, 1947
45. New Quarry Cave	Smyth Co.	Cave			USNM coll. unpublished data
46. Newport	Giles Co.				Handley and Patton, 1947
47. Pembroke Railroad Cave #1	Giles Co.	Cave		Late Pleistocene, based on faunal assemblage	CMNH coll. unpublished data
48. Pembroke Railroad Cave #2	Giles Co.	Cave		Late Pleistocene, based on faunal assemblage	CMNH coll. unpublished data
49. Paul Penleys Cave	Bland Co.	Cave			CMNH coll. unpublished data
50. Rass Hole (aka Corbett's)	Highland Co.	Cave		Late Pleistocene, extinct taxon	CMNH coll. unpublished data
51. Ripplemead Quarry	Giles Co.	Fissure	Owl, and other natural accumulation	Late Pleistocene/Holocene, based on faunal assemblage	Weems and Higgins, 1977; Jones and others, 1984
52. Ruffner's Cave #2	Page Co.	Cave		Holocene, based on faunal assemblage	Grady, USNM coll. unpublished data
53. Saltville	Smyth Co.	Alluvial, lacustrine, paludal	Natural accumulation	Late Pleistocene, based on nine ¹⁴ C dates ranging from 27,000 to 10,050 yr B.P.	Peterson, 1917; Pickle, 1946, Ray and others, 1967; Guilday and Parmalee, 1972; Guilday, 1982a; McDonald and Bartlett 1983; McDonald 1984; CMNH, RU and USMN coll. unpublished data

Table 1. (cont.)

Local Fauna	Location	Depositional Environment	Agent(s) of Accumulation	Age and Method of Dating	Notes and References
54. Shenandoah Caverns	Shenandoah Co.	Cave			Grady, USNM coll. unpublished data
55. Shires Saltpeter Cave	Craig Co.	Cave		Late Pleistocene/Holocene, based on faunal assemblage	CMNH coll. unpublished data
56. Skyline Caverns	Warren Co.	Cave		Late Pleistocene, based on faunal assemblage	USNM coll. unpublished data
57. Spurey Cave	Madison Co.	Cave	Natural accumulation	Holocene?, based on faunal assemblage	Eshelman, USNM coll. unpublished data
58. Staunton	Augusta Co.	Fissure	Natural accumulation	Late Pleistocene, extinct taxon	Hay, 1923
59. Strait Canyon	Highland Co.	Fissure	Natural accumulation	Late Pleistocene, based on ¹⁴ C date of 29,870 +1800/-1400 yr B.P.	Guilday, 1982b; Anderson, 1984; Fay, 1984; Jones and others, 1984; Guilday and others, unpublished data CMNH and USNM colls. unpublished data
60. Stratford Hall	Westmoreland Co.	Fluvial?	Natural accumulation	Late Pleistocene, extinct taxon	USNM coll. unpublished data
61. Thessalia	Giles Co.				Handley and Patton, 1947
62. Toms Brook	Shenandoah Co.	Cave		Holocene	USNM coll. unpublished data
63. Unknown	Clarke Co. exact provenience unknown	Cave?		Late Pleistocene, based on faunal assemblage	USNM coll. unpublished data
64. Unknown	Augusta Co. exact provenience unknown			Late Pleistocene, extinct taxon	Hay, 1923; ANSP coll. unpublished data
65. Unnamed Cave	Smyth Co.	Cave		Late Pleistocene/Holocene, based on faunal assemblage	RU coll. unpublished data
66. Unnamed fissure (Archeological site 44WR61)	Warren Co.	Fissure	Carnivore den?	Holocene, based on faunal assemblage	Haynes, 1978
67. Varner's Cave	Highland Co.	Cave			Grady, USNM coll. unpublished data
68. Vickers Cave	Washington Co.	Cave		Pleistocene (Illinoian?), based on faunal assemblage	Guilday, 1971a; CMNH coll. unpublished data
69. Virginia Beach (near)	Exact provenience unknown			Late Pleistocene, extinct taxon	USNM coll. unpublished data
70. Virginia Caverns (near New Market)	Rockingham or Shenandoah Co.	Cave		Holocene, based on human association	McGill, 1933
71. Wade Site	Halifax Co.		Cultural accumulation	Late Holocene (Woodland Period), based on faunal assemblage and cultural material	Stevens, 1979

Table 1. (cont.)

Local Fauna	Location	Depositional Environment	Agent(s) of Accumulation	Age and Method of Dating	Notes and References
72. Warrenton	Fauquier Co.			Late Pleistocene, extinct taxon	Hay, 1923
73. Will Farleys Cave	Washington Co. Cave		Owl?	Late Pleistocene?, based on faunal assemblage	CMNH coll. unpublished data
74. Williamsburg (near)	York Co.		Natural accumulation	Late Pleistocene, extinct taxon	Mitchell, 1818; Hay, 1923
75. Williamsburg (near)	York Co.			Late Pleistocene, based on extinct taxon	G.H. Johnson, unpublished data
76. Winding Stairs Cave	Scott Co. Cave			Late Pleistocene, based on faunal assemblage	CMNH coll. unpublished data
77. Womack Pit	City of Virginia Beach	Marine rip-tide channel	Natural accumulation	Late Pleistocene, based on faunal assemblage	Ray and others, 1968

Note: fourteen specimens from the USNM collection listed in Table 2 are not included here because their exact provenience is unknown. There are also another 17 cave faunas in the CMNH collections for which we have no faunal data and these localities are, therefore, not included in this table.

respective depositional environment, as well as 14 isolated specimens listed by catalog number for which no locality number has been assigned. Eleven depositional environments are recorded in order of decreasing frequency of representation at fossil-bearing localities in Virginia. Though no fossil records are known from eolian deposits such as beach dunes, they are to be expected.

Caves, fissures, and, to a lesser degree, rockshelters are the sites that have been studied most systematically in Virginia. These same features probably provide the most promise for new Quaternary vertebrate localities since Virginia has no less than 2300 known limestone caves, fissures, and rockshelters (Holsinger, 1975). Caves commonly contain abundant fossil vertebrates because they provide good environments of preservation and accumulate bones from such sources as roosting-

raptor pellets, packrat middens, naturally trapped animals, and fluvial/colluvial deposits. Regurgitated owl pellets containing the remains of small vertebrates collected in the immediate area of the roost are probably the most important sources of cave bone. Natural Chimneys, Clark's Cave, and the Back Creek caves are examples of Virginia caves that contain significant bone accumulations deposited by predatory birds. Caves, other than natural traps, also present a taphonomic bias in that small vertebrates are usually well represented whereas large vertebrates are frequently represented by one or only a few individuals whose remains are widely scattered over the site (Lundelius and others, 1983).

Woodrats or packrats are well known for their habit of collecting odd objects, including bones and teeth, and often including them in their cave nests. Woodrats may be responsible for the few large bones and teeth from Natural Chimneys. Guilday and Hamilton (1978) suggested similar woodrat accumulation for some West Virginia caves. Strait Canyon and Edinburg Fissure, at least in part, consist of natural trap deposits, while Gardner's Cave and Rass Hole contain bones of large mammals that probably washed into the deposit by natural processes. Other caves, such as Ely, and many rockshelters contain what might be, in part, accumulations attributable to human activities.

Springs are known to attract vertebrates (Shiner, 1983). The marshy environment common to many springs may serve as a trap, and at springs, prey species may be attacked by predators which have staked out such strategic locales. Salt licks such

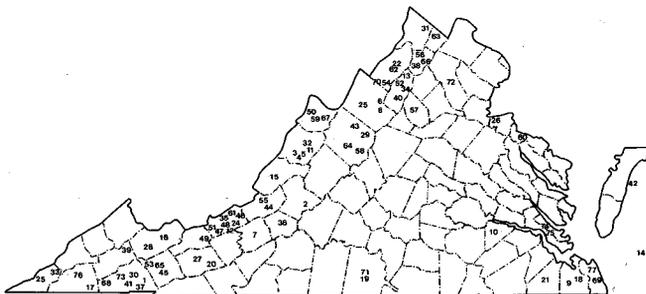


Figure 2. Map of Virginia, showing the location of sites listed in Table 1.

Table 2. Quaternary depositional environments where bird and mammal fossils have been or might likely be recovered in Virginia.

Depositional Environment ¹	Representative Localities ²	Isolated Specimens not given Locality Numbers ³
A. Terrestrial		
Caves (42)	2, 4, 5, 6, 8, 11, 12, 13, 16, 17 20, 25, 27, 28, 29, 30, 33, 35, 37, 38?, 39, 40, 41, 43, 45, 47, 48, 49, 50, 52, 54, 55, 56, 57, 62, 63?, 65, 67, 68, 70, 73, 76	USNM 1645 <i>Mylohyus nasutus</i> USNM 18201 <i>Equus</i> sp.
Fissures (6)	22, 24, 51, 58, 59, 66	
Rockshelters (2)	3, 4	
Springs (including hot and salt springs) (3)	1?, 31, 32,	
Fluvial (streams and river deposits) (4)	18, 26?, 53, 60?	
Lacustrine or paludal deposits (1)	53	
Eolian (sand dune, loess deposits) (0)		
Marsh or peat (1)	10 ^a	USNM 8808 <i>Mammut americanum</i> (swamp)
Archeological context (4)	16, 25, 34, 71	USNM 521 <i>Canis</i> sp.
B. Marine		
Shallow sea bottom (3)	14, 21, 77	USNM 23787 <i>Symbos</i> sp. USNM 187576 <i>Mammut americanum</i> USNM 214824 <i>Mammut americanum</i> USNM 214943 <i>Mammut americanum</i> USNM 243748 <i>Bison</i> sp. USNM 243753 <i>Mammuthus</i> sp. USNM 243926 <i>Mammuthus</i> sp. USNM 243927 <i>Mammuthus</i> sp. USNM 299711 <i>Mammut americanum</i>
Beach (barrier island) (2)	42, 69?	
C. Unknown (13)		
	7, 9, 15, 19, 23, 36, 44, 46, 61, 64, 72, 74, 75	USNM 336566 Artiodactyl vertebra

¹ Number of included sites shown in parenthesis.

² Numbers refer to localities listed in Table 1.

³ Depositional environment known but exact provenience unknown.

^a See Hay (1923, p. 352)

as the one at Saltville and thermal springs such as those at Hot Springs are highly attractive to vertebrates, especially mammals. Salt is an attractant in its own right while thermal springs may provide refuge and water during harsh winters. Classic examples of such environments are Big Bone Lick, Kentucky and the geyser basins of Yellowstone National Park, Wyoming. Reeves (1932) noted more than 90 thermal springs from northwestern Virginia and adjacent parts of West Virginia; water temperatures range up to 105° F in these springs.

Virginia's barrier islands have produced a few fossil vertebrates, including walrus (*Odobenus*) and giant beaver (*Castoroides*). The latter (USNM 215021) is believed to have washed from a drowned peat deposit just offshore of Metomkin Island. Clam, scallop, and bottom-fish dredge-boats commonly pull up fossil mammalian bones from the continental shelf (Whitmore and others, 1967). To date, bison (*Bison*), musk ox (*Symbos*), mammoth (*Mammuthus*), and mastodon (*Mammut*) remains have been dredged from the continental shelf. Eshelman recovered an artiodactyl vertebra frag-

ment (USNM 336566) in water 142 feet deep just off the Cherrystone Channel in Chesapeake Bay, Virginia. Such finds, no doubt, date from full glacial periods when sea level was lower and the continental shelf and the bottom of what is now Chesapeake Bay were exposed. Borrow pits within the Coastal Plain in places reveal marine and fluvial deposits containing Quaternary vertebrates (Ray and others, 1968).

Finally, Semken (1983) points out the potential of archeological sites for increasing information about the history of Holocene vertebrates (Rose, this volume). The growing interest in fossils and continuing construction activity within Virginia no doubt will result in the discovery of additional Quaternary fossil localities in the future.

DISTRIBUTION OF QUATERNARY VERTEBRATE LOCALITIES

For the present discussion Virginia is divided into three physiographic regions: the Coastal Plain, the Piedmont, and the Appalachian Mountains (Figure 1). Quaternary fossils have been recovered from the Coastal Plain and especially from karst features in the Appalachian Mountains. Although Hay (1923, p. 352) reported that "none are known anywhere in the Piedmont Plateau," he did note an unidentified horse tooth from Denniston, Halifax County (Table 1: locality 19), in the Piedmont. Each county from which Quaternary birds and mammals have been recovered is shaded in Figure 1. Of Virginia's 95 counties and 41 independent cities, 32 counties and 4 cities are known to have yielded Quaternary fossils. There are 65 localities in the Appalachian Mountain region, 11 in the Coastal Plain and 1 in the Piedmont region. Nearly every county within the Appalachian Mountains from which caves are known, has yielded fossils. Only a few counties in the Coastal Plain have so far produced Quaternary vertebrate fossils, and only one county in the Piedmont has done so. Though fossil records are rare from the Coastal Plain and Piedmont, the potential is great for adding to the Quaternary vertebrate history of these regions through the discovery of new localities. Certainly there are more sites like the Womack borrow pit (Ray and others, 1968) to be found.

Though it was not the intent of this paper to do a systematic search of faunal studies from archeological sites, additional data about the presence and distribution of prehistoric vertebrates in Virginia can be gleaned from the study of such localities. Keyser Farm (Table 1: locality 34; Manson, MacCord, and Griffin, 1943) yielded an associated fauna

of ten taxa. MacCord (1973a) reports deer and turkey from the Hirsh Site, and elk, deer, bear, fox, raccoon, and wolf (dog?) from the Hidden Valley Rockshelter (MacCord, 1973b). From Bath County alone, Clark reported 32 prehistoric Indian sites (Guilday and others, 1977, p. 78). The potential for studies of vertebrates in such areas is rich. Clark (1979) reported 26 known Indian burial caves and 40 known prehistoric rockshelter sites in Virginia.

ZOOGEOGRAPHY

Our discussion on zoogeography will be limited primarily to the mammalian fauna. Virginia falls within the *Symbos-Cervalces* Pleistocene Faunal Province of Martin and Neuner (1978) characterized by the presence of *Symbos*, *Cervalces*, *Castoroides*, and *Sangamona*. Graham (1979) also recognized Pleistocene faunal provinces and included Virginia as a part of the Eastern Mammalian Region, which is characterized by *Blarina* sp., *Tamias striatus*, *Synaptomys cooperi*, *Castoroides ohioensis*, *Symbos* sp., *Bootherium* sp., and *Mylohyus* sp.

It is difficult to make paleozoogeographical and paleoenvironmental comparisons between late Pleistocene and Recent mammalian faunas for an area as large as Virginia. Virginia has 40,815 square miles of land ranging in elevation from sea level to over 5700 feet. The maximum dimension of the State is over 500 miles, ranging from open ocean to mountains. The late Pleistocene fauna spans perhaps 500,000 years, assuming the Illinoian fauna is represented in known collections, while the 16th Century fauna spans only 100 years. Yet, by contrasting the late Pleistocene and European contact (16th Century) faunas of Virginia and by looking at extirpated forms as listed in Table 3, some general trends can be discerned. Late Pleistocene taxa whose Recent distributions, based on Hall's (1981) work on mammals and Robbins' and others (1966) work on birds, do not range into Virginia today and are considered extirpated. Guilday (1982a) lists four categories for the late Pleistocene fauna of the mid-Appalachian region: (1) extinct species, (2) present-day boreal forms, (3) present-day midwestern forms, and (4) species still living in the area.

Extirpated forms which now live in more northerly areas include: sharp-tailed grouse (*Pediacetes phasianellus*), spruce grouse (*Dendragapus canadensis*), gray jay (*Perisoreus canadensis*), magpie (*Pica pica*), rock ptarmigan (*Lagoptus* cf. *mutus*), pine grosbeak (*Pinicola* cf. *enucleator*), glaucous gull (*Larus hyperboreus*), common murre (*Uria*

Table 3. Taxonomic list of Quaternary birds and mammals of Virginia showing distribution of species by locality.

Scientific Name	Common Name	Locality number (s)
AVES	BIRDS	
Gaviiformes	loons	
1. <i>Gavia</i> sp.	loon sp. unidentified	21
Podicipediformes	grebes	
2. <i>Podilymbus podiceps</i>	pieb-billed grebe	11, 59
3. <i>Podiceps auritus</i>	horned grebe	77
Pelecaniformes	pelicans, etc.	
4. <i>Morus bassanus</i>	gannet	21, 77
5. <i>Phalacrocorax auritus</i>	double-crested cormorant	77
Ardeiformes	herons	
6. <i>Botaurus lentiginosus</i>	American bittern	11
Anseriformes	waterfowl	
7. <i>Olor columbianus</i>	whistling swan	34
8. <i>Branta bernicla</i>	brant	77
9. <i>Anas</i> cf. <i>A. platyrhynchos</i> or <i>A. rubripes</i>	mallard or black duck	11
10. <i>Anas discors</i>	blue-winged teal	43
cf. <i>Anas discors</i>		11
11. cf. <i>Anas crecca</i>	green-winged teal	11
12. <i>Bucephala albeola</i>	bufflehead	43
cf. <i>Bucephala</i> sp.		59
13. <i>Lophodytes cucullatus</i>	hooded merganser	11
cf. <i>Lophodytes cucullatus</i>		59
14. <i>Mergus</i> sp.	merganser	11
15. <i>Oxyura jamaicensis</i>	ruddy duck	11
Anatid	ducks, unidentified	12, 59
Accipitriformes	diurnal raptors	
16. <i>Cathartes aura</i>	turkey vulture	34
17. <i>Accipiter cooperii</i>	cooper's hawk	3
18. <i>Accipiter striatus</i>	sharp-shinned hawk	11, 43, 59
19. <i>Buteo lineatus</i>	red-shoulder hawk	43
<i>Buteo</i> cf. <i>B. lineatus</i>		59
20. <i>Buteo jamaicensis</i>	red-tailed hawk	43
cf. <i>Buteo jamaicensis</i>		59
21. <i>Buteo platypterus</i>	broad-winged hawk	43
<i>Buteo</i> cf. <i>B. platypterus</i>		11
22. <i>Haliaeetus leucocephalus</i>	bald eagle	34

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
23. <i>Falco sparverius</i>	American kestrel	11
Accipitrid	hawks, unidentified	11
Galliformes	gamebirds	
24. <i>Colinus virginianus</i>	bobwhite quail	4, 11, 43, 59
25. #cf. <i>Dendragapus canadensis</i>	spruce grouse	4, 11, 43, 59
26. <i>Bonasa umbellus</i>	ruffed grouse	4, 11, 43, 59
cf. <i>Bonasa umbellus</i>		3
<i>D. canadensis</i> or <i>B. umbellus</i>		4, 11
27. # <i>Lagopus</i> cf. <i>mutus</i>	rock ptarmigan	4, 11
# <i>Lagopus</i> sp.	ptarmigan	4
28. # <i>Pediocetes phasianellus</i>	sharp-tailed grouse	3, 4, 43
cf. # <i>Pediocetes phasianellus</i>		4, 11
Tetraonid	grouse, unidentified	11
29. <i>Meleagris gallopavo</i>	wild turkey	11, 30, 34, 43, 71
cf. <i>Meleagris gallopavo</i>		59
Ralliformes	marsh birds	
30. # <i>Grus americana</i>	whooping crane	43
31. <i>Rallus limicola</i>	Virginia rail	59
cf. <i>Rallus limicola</i>		11
32. <i>Porzana carolina</i>	sora	11
33. <i>Gallinula chloropus</i>	common gallinule	11
Rallid	rails, unidentified	11
Charadriiformes	shore-birds, gulls and auks	
34. <i>Pluvialis dominica</i>	American golden plover	11
35. <i>Charadrius vociferus</i>	killdeer	43
36. cf. <i>Actitis macularia</i>	spotted sandpiper	11, 59
37. <i>Erolia minutilla</i>	least sandpiper	43
38. <i>Capella gallinago</i>	common snipe	11
39. <i>Philohela minor</i>	American woodcock	11, 43, 59
40. cf. <i>Tringa solitaria</i>	solitary sandpiper	11
41. <i>Bartramia longicauda</i>	upland plover	43
42. cf. <i>Limosa</i> , ? sp.	godwit	11
43. <i>Captotrophorus semipalmatus</i>	willet	43
Scolopacid	sandpiper/plover unidentified	11
44. # <i>Larus hyperboreus</i>	glaucous gull	77
45. + <i>Pinguinus impennis</i>	great auk	77
46. # <i>Uria aalge</i>	common murre	77
Alcid	auks, unidentified	21

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
Columbiformes		
	pigeonlike birds	
47. + <i>Ectopistes migratorius</i>	passenger pigeon	3, 4, 11, 43, 59
Cuculiformes		
	cuckoos	
48. <i>Coccyzus</i> sp.	cuckoo, unidentified	11
Strigiformes		
	owls	
49. <i>Otus asio</i>	screech owl	4, 11
50. <i>Bubo virginianus</i> ; <i>Strix?</i> or <i>Bubo?</i>	great horned owl owl	11, 59 3
51. <i>Asio</i> cf. <i>A. flammeus</i> or <i>A. otus</i> cf. <i>Asio</i> sp.	short-eared or long-eared owl; eared owl unidentified	11 59
52. <i>Aegolius acadicus</i>	saw-whet owl	4
Strigid	owls, unidentified	4
Caprimulgiformes		
	goatsuckers	
53. <i>Chordeiles minor</i>	common nighthawk	11
54. <i>Chaetura pelagica</i>	chimney swift	11
Coraciiformes		
	rollerlike birds	
55. <i>Megaceryle alcyon</i>	belted kingfisher	11, 43
Piciformes		
	woodpeckers	
56. <i>Colaptes auratus</i> cf. <i>Colaptes auratus</i>	flicker	4, 11, 59 4, 43
57. <i>Dryocopus pileatus</i>	pileated woodpecker	11
58. <i>Melanerpes carolinus</i> cf. <i>Melanerpes carolinus</i>	red-bellied woodpecker	43 11
59. <i>Melanerpes erythrocephalus</i>	red-headed woodpecker	4, 43
60. <i>Sphyrapicus varius</i>	yellow-bellied sapsucker	11
61. <i>Dendrocopos villosus</i>	hairy woodpecker	4, 11, 43
62. <i>Dendrocopos pubescens</i>	downy woodpecker	11
Picid	woodpecker, unidentified	4, 11
Passeriformes		
	perching birds	
63. <i>Sayornis phoebe</i>	eastern phoebe	43
64. <i>Empidonax</i> sp.	flycatcher	11
65. <i>Contopus virens</i>	eastern wood pewee	43
66. <i>Eremophila alpestris</i>	horned lark	11
67. <i>Petrochelidon pyrrhonota</i>	cliff swallow	11, 43
68. # <i>Perisoreus canadensis</i>	gray jay	11, 43
69. <i>Cyanocitta cristata</i> cf. <i>Cyanocitta cristata</i>	blue jay	4, 11, 43 11

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
70. <i>Corvus brachyrhynchos</i> cf. <i>Corvus</i> sp.	common crow crow	11 3, 59
71. # <i>Pica pica</i>	black-billed magpie	43, 59
72. <i>Parus</i> sp.	chickadee, unidentified	11
73. <i>Parus bicolor</i>	tufted titmouse	11
74. <i>Sitta canadensis</i>	red-breasted nuthatch	11, 43
75. <i>Certhia familiaris</i>	brown creeper	11
76. <i>Cistothorus</i> cf. <i>C. platensis</i>	short-billed marsh wren	11
77. <i>Toxostoma rufum</i> cf. <i>Toxostoma rufum</i>	brown thrasher	43 11
78. <i>Catharus</i> sp.	thrush	11
79. cf. <i>Sialia sialia</i>	eastern bluebird	11
80. <i>Turdus migratorius</i>	robin	11, 43
81. <i>Hylocichla</i> sp.	thrush	43
82. cf. <i>Anthus spinoletta</i>	water pipit	11
83. <i>Bombycilla cedrorum</i>	cedar waxwing	11
84. cf. <i>Dendrocia coronata</i>	myrtle warbler	11
85. <i>Seiurus</i> sp.	waterthrush	11
86. <i>Vermivora chrysoptera</i> Parulid	golden-winged warbler warblers, unidentified	4 11
87. <i>Dolichonyx oryzivorus</i>	bobolink	11
88. cf. <i>Sturnella</i> sp.	meadowlark	11
89. <i>Agelaius phoeniceus</i>	red-winged blackbird	11, 43, 59
90. <i>Molothrus ater</i>	brown-headed cowbird	43
91. <i>Melospiza melodia</i>	song sparrow	43
92. <i>Zonotrichia albicollis</i>	white-throated sparrow	43
93. cf. <i>Icterus spurius</i>	orchard oriole	11
94. <i>Piranga</i> sp.	tanager	11
95. cf. <i>Carpodacus purpureus</i>	purple finch	3
96. cf. # <i>Pinicola enucleator</i>	pine grosbeak	4, 11
97. <i>Loxia</i> sp.	crossbill	4, 11
98. <i>Pooecetes gramineus</i>	vesper sparrow	11
99. <i>Junco hyemalis</i> <i>Junco</i> sp.	slate-colored junco junco	4, 11 43
100. <i>Passerella iliaca</i> Fringillid Passeriform Aves	fox sparrow sparrows, unidentified passerines, unidentified birds, unidentified	43 11 4 3, 4, 17, 20, 24, 28, 35

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
MAMMALIA	MAMMALS	
Marsupialia	pouch-bearing mammals	
1. <i>Didelphis virginiana</i>	common opossum	34, 36, 44, 46, 66, 71
Insectivora	shrews and moles	
2. <i>Sorex arcticus</i>	Arctic shrew	4, 11, 30, 43
3. <i>Sorex cinereus</i>	masked shrew	3, 4, 11, 30
<i>Sorex cf. S. cinereus</i>		43
<i>Sorex cinereus</i> or <i>S. longirostris</i>	masked or southeastern shrew	59
4. <i>Sorex dispar</i>	long-tailed shrew	4, 11, 30, 59
5. <i>Sorex fumeus</i>	smoky shrew	3, 4, 11, 30, 43, 59
<i>Sorex cf. S. fumeus</i>		33
6. <i>Sorex palustris</i>	water shrew	11, 30, 43
<i>Sorex sp.</i>		11, 12, 24, 28, 30, 35, 47
7. <i>Microsorex hoyi</i>	pygmy shrew	11, 30, 35, 43, 47
8. <i>Blarina brevicauda</i>	short-tailed shrew	3, 4, 11, 30, 33, 43, 59
<i>Blarina cf. B. brevicauda</i>		20
<i>Blarina sp.</i>		12, 17, 22, 24, 30, 35, 41, 47, 56, 73
9. <i>Cryptotis parva</i>	least shrew	43
Soricid	shrews, unidentified	8, 22, 39
10. <i>Parascalops breweri</i>	hairy-tailed mole	3, 4, 11, 12, 17, 30, 33, 43, 59, 73
11. <i>Scalopus aquaticus</i>	eastern mole	4, 11, 43, 66
<i>Scalopus sp.</i>		30
12. <i>Condylura cristata</i>	star-nosed mole	3, 4, 11, 30, 33, 39, 43, 59
Chiroptera	bats	
13. <i>Myotis lucifugus</i> or <i>M. sodalis</i>	little brown bat	4, 11
<i>Myotis cf. M. lucifugus</i>		30, 43
14. <i>Myotis keenii</i>	Keen's bat	11, 43
<i>Myotis keenii</i> or <i>M. grisescens</i>		4, 30
15. <i>Myotis grisescens</i>	gray bat	4
16. <i>Myotis leibii</i>	small-footed bat	4, 11
<i>Myotis sp.</i>		3, 4, 30, 33, 35, 54
17. <i>Pipistrellus subflavus</i>	eastern pipistrelle	11, 33, 43, 59, 67
<i>Pipistrellus sp.</i>		4
18. <i>Lasiomycteris noctivagans</i>	silver-haired bat	51
19. <i>Eptesicus fuscus</i>	big brown bat	3, 4, 11, 30, 33
<i>Eptesicus cf. E. fuscus</i>		43
<i>Eptesicus sp.</i>		12, 30, 35, 43
20. <i>Plecotus cf. townsendii</i>	big-eared bat	11
<i>Plecotus sp.</i>		4, 33
21. <i>Lasiurus borealis</i>	red bat	11
<i>Lasiurus cf. L. borealis</i>		43
Chiropteran	bats, unidentified	6, 12, 20, 22, 40, 47, 56, 70
Edentata	armadillos and sloths	
22. <i>Megalonyx jeffersonii</i>	Jefferson's ground sloth	37
<i>Megalonyx cf. M. jeffersonii</i>		20, 53

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
23. # <i>Dasyppus</i> cf. * <i>D. bellus</i>	beautiful armadillo	41
Lagomorpha	hares and rabbits	
24. # <i>Ochotona</i> sp.	pika	33
25. cf. <i>Sylvilagus transitionalis</i>	New England cottontail	11
26. <i>Sylvilagus floridanus</i>	Eastern cottontail	34, 44, 46
<i>Sylvilagus</i> sp.	cottontail rabbit	43, 52, 54, 66
cf. <i>Sylvilagus</i> sp.		12
27. <i>Lepus americanus</i>	snowshoe hare	4, 11, 22, 43
<i>Lepus</i> sp.		30
Leporid	hares and rabbits, unidentified	3, 4, 8, 16, 17, 27, 28, 30, 35, 41, 43, 47, 48, 57, 62, 63, 73
Rodentia	rodents	
28. <i>Tamias striatus</i>	eastern chipmunk	3, 4, 11, 33, 43, 54
<i>Tamias</i> cf. <i>T. striatus</i>		20, 30
<i>Tamias</i> sp.	chipmunk, unidentified	12
29. # <i>Eutamias minimus</i>	least chipmunk	11
<i>Eutamias</i> sp.		4
30. <i>Marmota monax</i>	woodchuck	3, 4, 6, 11, 30, 33, 34, 43, 44, 63, 66
<i>Marmota</i> cf. <i>M. monax</i>		20
<i>Marmota</i> sp.		12, 17, 24, 28, 35, 41, 76
31. # <i>Spermophilus tridecemlineatus</i>	thirteen-lined ground squirrel	3, 4, 11, 30, 43
<i>Spermophilus</i> sp.		30
cf. <i>Spermophilus</i> sp.		39
32. <i>Sciurus carolinensis</i>	gray squirrel	33, 34, 43
<i>Sciurus</i> cf. <i>S. carolinensis</i>		14
<i>Sciurus carolinensis</i> or <i>S. niger</i>	gray or fox squirrel	3, 30
<i>Sciurus</i> sp.		17, 30
33. <i>Tamiasciurus hudsonicus</i>	red squirrel	3, 4, 11, 12, 33
<i>Tamiasciurus hudsonicus</i>	Pleistocene red squirrel	43
*cf. <i>T. h. tenduoidens</i>		
34. <i>Glaucomyz volans</i>	southern flying squirrel	11, 43
<i>Glaucomyz</i> cf. <i>G. volans</i>		3, 4, 17, 20, 30
35. <i>Glaucomyz sabrinus</i>	northern flying squirrel	11, 30, 43
<i>Glaucomyz</i> cf. <i>sabrinus</i>		3, 4
<i>Glaucomyz</i> sp.	flying squirrel, unidentified	3, 12, 20, 28, 33, 47
<i>Tamias</i> or <i>Glaucomyz</i>	squirrels, unidentified	11
Sciurid	squirrels, unidentified	2, 17, 22, 28, 35, 39, 41, 47, 48, 63, 73
36. <i>Castor canadensis</i>	beaver	3, 17, 20, 22, 34, 43, 46, 51, 62
37. + <i>Castoroides ohioensis</i>	giant beaver	42, 43
Castorid	beaver, unidentified	47
38. <i>Peromyscus maniculatus</i>	deer mouse	3, 4, 11, 43
<i>Peromyscus</i> cf. <i>P. maniculatus</i>		43, 59
39. <i>Peromyscus leucopus</i>	white-footed mouse	3, 4, 7, 11
<i>Peromyscus</i> cf. <i>P. leucopus</i>		30, 43
<i>Peromyscus</i> sp.		3, 4, 6, 12, 17, 22, 24, 35, 43, 59, 62, 63, 67, 73

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
40. <i>Neotoma floridana</i>	eastern woodrat	3, 4, 11, 30, 33, 43, 59, 67
<i>Neotoma</i> cf. <i>N. floridana</i>		20
<i>Neotoma</i> sp.	woodrat unidentified	2, 4, 12, 17, 22, 24, 28, 35, 39, 47, 48, 62, 73, 76
41. <i>Clethrionomys gapperi</i>	red-backed vole	3, 4, 11, 12, 17, 24, 30, 33, 35, 39, 41, 43, 47, 51, 59, 73
42. <i>Phenacomys intermedius</i>	heather vole	3, 4, 11, 59
<i>Phenacomys</i> cf. <i>P. intermedius</i>		43
<i>Phenacomys</i> sp.		17, 30, 39, 41
43. <i>Microtus pennsylvanicus</i>	meadow vole	3, 4, 11, 13, 24, 30, 33, 43
<i>Microtus</i> cf. <i>M. pennsylvanicus</i>		20, 41, 59
44. <i>Microtus chrotorrhinus</i>	rock vole	3, 4, 11, 24, 30, 33, 43
<i>M. pennsylvanicus</i> or <i>M. chrotorrhinus</i>		3, 4, 17, 33, 35, 43
45. # <i>Microtus xanthognathus</i>	yellow-cheeked vole	3, 4, 11, 22, 28, 30, 43, 63
46. <i>Microtus pinetorum</i>	woodland vole	3, 4, 11, 67
<i>Microtus pinetorum</i> or <i>M. ochrogaster</i>	woodland or prairie vole	17, 24, 30, 33, 39, 41, 43, 47, 59
<i>Microtus</i> sp.	voles, unidentified	6, 8, 12, 22, 28, 30, 33, 35, 47, 56, 57, 62, 63
47. # <i>Neofiber *leonardi</i>	extinct round-tailed muskrat	59
Microtid	microtine, unidentified	2
48. <i>Ondatra zibethicus</i>	muskrat	3, 11, 29, 34, 43, 59, 71
<i>Ondatra</i> sp.		17, 22, 53
49. <i>Synaptomys cooperi</i>	southern bog lemming	3, 11, 17, 24, 30, 33, 35, 39, 43, 47, 59
<i>Synaptomys</i> cf. <i>S. cooperi</i>		41
50. # <i>Synaptomys borealis</i>	northern bog lemming	3, 4, 11, 12, 24, 33, 43, 59
<i>Synaptomys</i> cf. <i>S. borealis</i>		30
<i>Synaptomys</i> sp.	bog lemming, unidentified	28, 33, 35
51. <i>Zapus hudsonicus</i>	meadow jumping mouse	11, 43, 59
<i>Zapus</i> sp.	jumping mouse, unidentified	30, 33
52. <i>Napaeozapus insignis</i>	woodland jumping mouse	11, 24, 43, 59
53. <i>Erethizon dorsatum</i>	porcupine	11, 17, 30, 43, 59, 66
Cetacea	whales and porpoises	
54. # <i>Eschrichtius glaucus</i>	gray whale	42
Cetacean	whales and porpoise, unidentified	77
Carnivora	flesh-eaters	
55. <i>Canis</i> cf. * <i>C. dirus</i>	dire wolf	11
56. <i>Canis lupus</i>	gray wolf	43, 51
57. <i>Canis latrans</i>	coyote	22
58. <i>Canis familiaris</i>	domestic dog	34
<i>Canis</i> sp.	dogs, unidentified	3, 22, 26, 40, 66
59. <i>Urocyon cinereoargenteus</i>	gray fox	34, 51, 66
60. <i>Vulpes vulpes</i>	American red fox	4
<i>Vulpes</i> sp.		43
Canid	dogs and foxes, unidentified	25, 35, 47, 59, 66

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
61. <i>Ursus americanus</i> <i>Ursus</i> cf. <i>U. americanus</i> <i>Ursus</i> sp.	black bear	3, 6, 11, 22, 27, 34 43 20, 26, 30, 38, 41, 44, 55
Ursid	bears, unidentified	35, 40, 48
62. <i>Procyon lotor</i> <i>Procyon</i> cf. <i>P. lotor</i>	raccoon	3, 11, 34, 43, 46, 52 54, 66 17, 20, 30, 73
63. <i>Martes americana</i> <i>Martes</i> cf. <i>M. americana</i>	marten	11, 17, 43 39
64. <i>Martes pennanti</i> <i>Martes</i> cf. <i>M. pennanti</i>	fisher	3, 17, 51 43
65. <i>Mustela rixosa</i>	least weasel	3, 4, 11, 43
66. # <i>Mustela erminea</i>	ermine	11
67. # <i>Mustela frenata</i> <i>Mustela</i> cf. <i>M. frenata</i> <i>Mustela erminea</i> or <i>M. frenata</i>	long-tailed weasel	34 43 11
68. <i>Mustela vison</i> <i>Mustela</i> sp.	mink weasels, unidentified	4, 11, 12, 17, 43 12
69. <i>Mephitis mephitis</i>	striped skunk	8, 11, 34, 43, 44, 46, 66
70. <i>Spilogale putorius</i>	eastern spotted skunk	20, 51
71. <i>Lutra canadensis</i>	river otter	34
72. + <i>Panthera?</i> or <i>Felis *atrox</i>	indeterminate large cat	2, 38, 40
73. <i>Felis concolor</i>	mountain lion	34
74. <i>Lynx rufus</i> <i>Lynx?</i> sp.	bobcat indeterminate small cat	34 17, 39, 43
75. # <i>Odobenus rosmarus</i>	Atlantic walrus	42, 77
76. <i>Halichoerus grypus</i> Carnivorans	gray seal carnivores, unidentified	77 20, 77
Proboscidea	mastodons, gomphotheres and elephants	
77. + <i>Mammuth americanum</i>	american mastodon	1, 10, 14, 15, 18, 23, 31, 32, 53, 59, 65, 74
78. + <i>Mammuthus primigenius</i> + <i>Mammuthus</i> sp.	woolly mammoth mammoths, unidentified	14, 53 14, 72
Perissodactyla	odd-toed hooved herbivores	
79. <i>Equus *complicatus</i> <i>Equus</i> cf. * <i>E. complicatus</i>	complex-toothed horse	1, 59 20
80. <i>Equus</i> cf. * <i>E. fraternus</i> <i>Equus</i> sp.	brother horse horses, unidentified	31 9, 18, 19, 20, 51, 53, 58 60, 65, 73
81. + <i>Tapirus</i> cf. * <i>T. veroensis</i> <i>Tapirus</i> sp.	vero tapir tapirs, unidentified	59 20, 22, 38, 51, 73, 76
Artiodactyla	even-toed hooved herbivores	
82. + <i>Mylohyus nasutus</i> <i>Mylohyus</i> sp.	long-nosed peccary peccaries, unidentified	59 3, 20, 22, 26, 43, 47, 51, 73
83. + <i>Platygonus compressus</i>	flat-headed peccary	20, 31, 66

Table 3. (cont.).

Scientific Name	Common Name	Locality number (s)
84. + <i>Platygonus vetus</i> <i>Platygonus</i> sp.	Leidy's peccary peccaries, unidentified	68 27, 45, 50, 56, 65
85. # <i>Cervus elaphus</i> <i>Cervus</i> cf. <i>C. elaphus</i> cf. <i>Cervus</i> sp.	elk	11, 34, 61 59 17
86. <i>Odocoileus virginianus</i> cf. <i>Odocoileus virginianus</i> <i>Odocoileus</i> sp.	white-tailed deer deer, unidentified	4, 16, 20, 31, 34, 43, 53, 59, 66, 71 11, 40 2, 17, 24, 35, 47, 49, 62, 73
87. + <i>Sangamona?</i> sp.	fugitive deer	47, 76
88. #cf. <i>Alces alces</i>	moose	59
89. +? <i>Cervalces</i> sp.	extinct moose	22, 53
90. # <i>Rangifer tarandus</i>	caribou	17, 24, 35, 53
91. # <i>Bison</i> sp. Bovid	bison	14, 20, 26, 31, 53, 69 20
92. + <i>Symbos cavifrons</i> + <i>Symbos</i> sp.	woodland musk ox	53, 59 14
93. + <i>Bootherium</i> sp. Ovibovine	Harlan's musk ox extinct musk ox, undetermined	53 14, 53

+ extinct genus

* extinct species

extirpated from Virginia

aalge), gannet (*Morus bassanus*), arctic shrew (*Sorex arcticus*), yellow-cheeked vole (*Microtus xanthognathus*), northern bog lemming (*Synaptomys borealis*), heather vole (*Phenacomys intermedius*), pika (*Ochotona princeps*), least chipmunk (*Eutamias minimus*), ermine (*Mustela erminea*), walrus (*Odobenus rosmarus*), gray seal (*Halichoerus grypus*), moose (*Alces alces*), and caribou (*Rangifer tarandus*). Extirpated forms which now live in the west include the whooping crane (*Grus americana*), 13-lined ground squirrel (*Spermophilus tridecemlineatus*), and bison (*Bison bison*). In addition, pika, least chipmunk, sharp-tailed grouse, and gray jay, listed as northern forms, also can be listed as western.

Animals now extinct which lived in Virginia in late Pleistocene time include: great auk (*Pinguinus impennis*), passenger pigeon (*Ectopistes migratorius*), Jefferson's ground sloth (*Megalonyx jeffersonii*), beautiful armadillo (*Dasypus bellus*), roundtail water rat (*Neofiber leonardi*); dire wolf (*Canis dirus*), extinct large cat (*Panthera* or *Felis atrox*), American mastodon (*Mammuthus americanum*), woolly mammoth (*Mammuthus primigenius*), complex-toothed horse (*Equus complicatus*), brother horse (*Equus fraternus*), Vero tapir (*Tapirus ve-*

roensis), long-nosed peccary (*Mylohyus nasutus*), flat-headed peccary (*Platygonus compressus*), fugitive deer (*Sangamona fugitiva*) (Churcher, 1984 questioned the validity of this taxon), extinct moose (*Cervalces scotti*), woodland muskox (*Symbos cavifrons*), and Harlan's muskox (*Bootherium* sp.).

All of the taxa listed above became extinct in the late Pleistocene except the great auk and passenger pigeon which became extinct during the historic period. Though no fossil record of the species exists in Virginia, the Carolina parakeet (*Conuropsis carolinensis*) is another species that became extinct during the historic period. Not surprisingly, the late Pleistocene mammalian and avian fauna of Virginia show a marked association with the Recent northern fauna. Perhaps surprising, however, is the presence of forms with southern affinity - the beautiful armadillo (*Dasypus bellus*) and the roundtail water rat (*Neofiber leonardi*).

Table 4 compares Virginia's late Pleistocene mammals with the State's "potential" 16th Century mammals. Using this approach one can negate the effects of European introduction of exotic taxa such as *Rattus* and *Mus* as well as possible extirpation of original faunal elements such as *Ectopistes*, *Conuropsis*, *Cervus*, and *Bison*. Guilday (1963,

Table 4. Comparison of the terrestrial mammalian fauna of Virginia in the late Pleistocene and in the 16th Century, with inferred feeding habits.

Late Pleistocene Fauna	Feeding Habits	Potential ¹ 16th Century Fauna
	omnivore	<i>Didelphis virginiana</i>
<i>Sorex arcticus</i>	insectivore	<i>Sorex longirostris</i>
<i>Sorex cinereus</i>	insectivore	<i>Sorex cinereus</i>
<i>Sorex dispar</i>	insectivore	<i>Sorex dispar</i>
<i>Sorex fumeus</i>	insectivore	<i>Sorex fumeus</i>
<i>Sorex palustris</i>	insectivore	<i>Sorex palustris</i>
<i>Microsorex hoyi</i>	insectivore	<i>Microsorex hoyi</i>
	insectivore	<i>Blarina talmalestes</i>
<i>Blarina brevicauda</i>	insectivore	<i>Blarina brevicauda</i>
<i>Cryptotis parva</i>	insectivore	<i>Cryptotis parva</i>
<i>Parascalops breweri</i>	fossorial carnivore	<i>Parascalops breweri</i>
<i>Scalopus aquaticus</i>	fossorial carnivore	<i>Scalopus aquaticus</i>
<i>Condylura cristata</i>	fossorial carnivore	<i>Condylura cristata</i>
<i>Myotis lucifugus</i>	aerial insectivore	<i>Myotis lucifugus</i>
<i>Myotis keenii</i>	aerial insectivore	<i>Myotis keenii</i>
<i>Myotis grisescens</i>	aerial insectivore	<i>Myotis grisescens</i>
<i>Myotis leibii</i>	aerial insectivore	<i>Myotis leibii</i>
	aerial insectivore	<i>Myotis sodalis</i>
<i>Pipistrellus subflavus</i>	aerial insectivore	<i>Pipistrellus subflavus</i>
<i>Lasionycteris noctivagans</i>	aerial insectivore	<i>Lasionycteris noctivagans</i>
<i>Eptesicus fuscus</i>	aerial insectivore	<i>Eptesicus fuscus</i>
<i>Plecotus townsendii</i>	aerial insectivore	<i>Lasiurus cinereus</i>
<i>Lasiurus borealis</i>	aerial insectivore	<i>Lasiurus borealis</i>
	aerial insectivore	<i>Nycticeius humeralis</i>
	aerial insectivore	<i>Plecotus rafinesquii</i>
<i>Megalonyx jeffersonii</i>	large insectivore	
<i>Dasypus bellus</i>	medium insectivore	
<i>Ochotona</i> sp.	small grazer	<i>Sylvilagus palustris</i>
<i>Sylvilagus transitionalis</i>	small grazer	<i>Sylvilagus transitionalis</i>
<i>Sylvilagus floridanus</i>	small grazer	<i>Sylvilagus floridanus</i>
<i>Lepus americanus</i>	small grazer	<i>Lepus americanus</i>
<i>Tamias striatus</i>	small granivore	<i>Tamias striatus</i>
<i>Eutamias minimus</i>	small granivore	
<i>Marmota monax</i>	medium semi-fossorial herbivore	<i>Marmota monax</i>
<i>Spermophilus tridecemlineatus</i>	small semi-fossorial herbivore	
<i>Sciurus carolinensis</i>	arboreal granivore	<i>Sciurus carolinensis</i>
	arboreal granivore	<i>Sciurus niger</i>
<i>Tamiasciurus hudsonicus</i>	arboreal granivore	<i>Tamiasciurus hudsonicus</i>
<i>Glaucomys volans</i>	arboreal granivore	<i>Glaucomys volans</i>
<i>Glaucomys sabrinus</i>	arboreal granivore	<i>Glaucomys sabrinus</i>
<i>Castor canadensis</i>	semi-aquatic herbivore	<i>Castor canadensis</i>
<i>Castoroides ohioensis</i>	semi-aquatic herbivore	
	small granivore	<i>Reithrodontomys humulis</i>
<i>Peromyscus maniculatus</i>	small herbivore	<i>Peromyscus maniculatus</i>
	small herbivore	<i>Ochrotomys nuttalli</i>

Table 4. (cont.)

Late Pleistocene Fauna	Feeding Habits	Potential ¹ 16th Century Fauna
<i>Peromyscus leucopus</i>	small herbivore	<i>Peromyscus leucopus</i>
	small herbivore	<i>Peromyscus gossypinus</i>
<i>Phenacomys intermedius</i>	small herbivore	<i>Sigmodon hispidis</i>
<i>Neotoma floridana</i>	small herbivore	<i>Oryzomys palustris</i>
<i>Clethrionomys gapperi</i>	small herbivore	<i>Neotoma floridana</i>
<i>Microtus pennsylvanicus</i>	small herbivore	<i>Clethrionomys gapperi</i>
<i>Microtus chrotorrhinus</i>	small herbivore	<i>Microtus pennsylvanicus</i>
<i>Microtus xanthognathus</i>	small herbivore	<i>Microtus chrotorrhinus</i>
<i>Microtus pinetorum</i>	small herbivore	
<i>Neofiber leonardi</i>	semi-aquatic herbivore	<i>Microtus pinetorum</i>
<i>Ondatra zibethicus</i>	semi-aquatic herbivore	
<i>Synaptomys cooperi</i>	herbivore	<i>Ondatra zibethicus</i>
<i>Synaptomys borealis</i>	herbivore	<i>Synaptomys cooperi</i>
<i>Zapus hudsonicus</i>	herbivore	
<i>Napaeozapus insignis</i>	herbivore	<i>Zapus hudsonicus</i>
<i>Erethizon dorsatum</i>	herbivore	<i>Napaeozapus insignis</i>
<i>Canis dirus</i>	medium-sized carnivore	? <i>Erethizon dorsatum</i>
<i>Canis lupus</i>	medium-sized carnivore	
<i>Canis latrans</i>	medium-sized carnivore	<i>Canis lupus</i>
<i>Urocyon cinereoargenteus</i>	medium-sized carnivore	
<i>Vulpes vulpes</i>	medium-sized carnivore	<i>Urocyon cinereoargenteus</i>
<i>Ursus americanus</i>	large omnivore	? <i>Vulpes vulpes</i>
<i>Procyon lotor</i>	medium-sized carnivore	<i>Ursus americanus</i>
<i>Martes pennanti</i>	small carnivore	<i>Procyon lotor</i>
<i>Mustela rixosa</i>	small carnivore	<i>Martes pennanti</i>
<i>Mustela erminea</i>	small carnivore	<i>Mustela rixosa</i>
<i>Mustela frenata</i>	small carnivore	
<i>Mustela vison</i>	small carnivore	<i>Mustela frenata</i>
	small carnivore	<i>Mustela vison</i>
<i>Mephitis mephitis</i>	medium-sized omnivore	<i>Lutra canadensis</i>
<i>Spilogale putorius</i>	medium-sized omnivore	<i>Mephitis mephitis</i>
<i>Felis sp.</i>	medium-sized omnivore	<i>Spilogale putorius</i>
<i>Lynx rufus</i>	medium-sized omnivore	<i>Felis concolor</i>
<i>Mammut americanum</i>	large herbivore	<i>Lynx rufus</i>
<i>Mammuthus primigenius</i>	large herbivore	
<i>Equus complicatus</i>	large herbivore	
<i>Equus fraternus</i>	large herbivore	
<i>Tapirus veroensis</i>	large herbivore	
<i>Mylohyus nasutus</i>	medium-sized omnivore	
<i>Platygonus compressus</i>	medium-sized omnivore	
<i>Cervus elaphus</i>	large herbivore	<i>Cervus elaphus</i>
<i>Odocoileus virginianus</i>	large herbivore	<i>Odocoileus virginianus</i>
<i>Sangamona sp.</i>	large herbivore	
<i>Alces alces</i>	large herbivore	
<i>Cervalces sp.</i>	large herbivore	

Table 4. (cont.)

Late Pleistocene Fauna	Feeding Habits	Potential ¹ 16th Century Fauna
<i>Rangifer tarandus</i>	large herbivore	
<i>Bison</i> sp.	large herbivore	<i>Bison bison</i>
<i>Symbos cavifrons</i>	large herbivore	
<i>Bootherium</i> sp.	large herbivore	
? <i>Homo sapiens</i>	large herbivore	<i>Homo sapiens</i>

¹By potential is meant the fauna to be expected today without the effect of colonization by Europeans.

1971b, and 1982a) thought that bison, which are absent from archeological sites in Virginia, were transient in the Appalachian Mountains. We do not dispute the possibility that Indians affected the prehistoric mammal fauna; we are only trying to negate the effects of European culture on the fauna and identify a "potential" natural mammalian fauna. Table 4 lists each taxon by inferred feeding habit. The late Pleistocene mammalian fauna consists of 85 taxa including Paleo-Indians (*Homo sapiens*). The 16th Century fauna, including man, consists of 73 taxa (Guilday and others, 1977, list 68 and Guilday, 1982a, listed 75 mammalian taxa from the mid-Appalachian region). Fifteen taxa from the late Pleistocene fauna are extinct, these include twelve herbivores, two carnivores and one omnivore. Twenty-six taxa in the late Pleistocene fauna are not present in the 16th Century fauna; twenty of these are herbivores. Thirteen taxa listed for the 16th Century fauna are not known for the late Pleistocene of Virginia; of these, four are bat species and five are cricetid species. Additionally, four species, otter (*Lutra canadensis*), fox squirrel (*Sciurus niger*), southeastern shrew (*Sorex longirostris*), and Indiana Myotis bat (*Myotis sodalis*) are possibly present in the late Pleistocene fauna of Virginia, but they have not yet been identified positively.

Guilday (1982a) notes that for the mid-Appalachian area the late Pleistocene mammalian fauna was more diverse, especially for the browsing and grazing herbivores, than the Recent fauna. Table 4 indicates that this statement appears to be true for Virginia.

Assuming that the greater number of cricetine rodent species in the 16th Century fauna, as compared to the late Pleistocene fauna (seven versus two), is not an artifact of collecting bias or identification error, a glaring disparity in cricetine representation during these two periods is evident. In contrast, there are ten microtine rodents in the

late Pleistocene fauna and only six in the 16th Century fauna. Microtines are characteristic of more northern or boreal environments than are cricetines. The pattern of microtine occurrence in Virginia is consistent with the inferred climatic differences between the late Pleistocene and the Holocene. Eshelman (1975) demonstrated similar changes in cricetine/microtine proportions that were correlated with cooler and warmer climates of Pleistocene glacials and interglacials, respectively.

The New Paris No. 4 fauna in Pennsylvania (Guilday and others, 1964) illustrates this pattern of changing cricetine/microtine proportions correlated with climatic changes in the region. Microtines account for 80 percent of the total individuals identified in the lower levels, but only 34 percent in the younger, upper levels (dated at 11,300 ± 100 yr B.P.). The associated faunas suggest that boreal climate existed when the lower levels were deposited, and that this changed to a more temperate climate when the upper levels were deposited. Graham (1976) shows that the taxonomic diversity of microtines during the late Pleistocene decreases from the northeast to the southwest across the U. S. This trend parallels this same cline seen today, but the group was less diverse in the late Pleistocene than it is today. Graham (1976) notes that the diversity of shrews also increased over this time period. However, for Virginia there are eight shrew taxa in the late Pleistocene and nine in the 16th Century fauna (Table 4). This count on shrew species could reflect bias in collecting and identification errors.

Though the opossum (*Didelphis virginiana*) is listed from six localities in Table 3, three occurrences (36, 44, 46) are from sites with uncertain age determinations. Localities 66 and 71 are assumed to be Holocene sites based on associated fauna. The sixth site, Keyser Farm (Table 1: locality 34), is a Woodland Period archeological site which

is dated between 1000 BC and 1600 AD. The opossum may not have been present in Virginia during the late Pleistocene. In addition to the six localities listed in Table 3 for the porcupine (*Erethizon dorsatum*), Ray and Lipps (1970) refer to three unpublished occurrences of porcupine in Virginia (Ray, personal communication, indicates that specimens from these localities are under study at the University of Tennessee). Guilday (1962a) states the spotted skunk (*Spilogale*) and the opossum (*Didelphis*) are suspected of being post-Pleistocene additions to Virginia. Table 3 concurs with Guilday's observation for the opossum, but the occurrence of *Spilogale* at Clark's Cave indicates that the spotted skunk was present in the late Pleistocene.

The reduction in number of mammalian species from the late Pleistocene to the Holocene has been noted by several researchers (Martin, 1967; Martin and Webb, 1974; Graham, 1976, 1979). Semken (1983, p. 192) summarized this phenomenon as follows: "The Pleistocene fauna of the United States was characterized by a combination of (1) extinct megavertebrates and (2) extant temperate megavertebrates and microvertebrates in association with (3) now disjunct large and small northern species. The Holocene fauna of temperate regions generally is composed of the second category only." The data provided here indicate that this general observation is accurate for Virginia.

QUATERNARY ENVIRONMENTAL RECONSTRUCTION BASED ON MAMMALIAN FOSSILS

During maximum Wisconsinan glaciation from approximately 18,000 yr B.P. to just prior to the Pleistocene/Holocene boundary at 10,000 yr B.P., the environment of Virginia was boreal. It was during this period that the large extinct herbivores listed in Table 4 such as *Mammuthus americanum*, *Mammuthus primigenius*, and specialized herbivores such as *Megalonyx jeffersonii*, *Platygonus compressus*, *Mylohyus nasutus*, and *Tapirus veroensis* existed. Smaller extirpated boreal forms listed in Table 4 include *Sorex arcticus*, *Ochotona* sp., and *Microtus xanthognathus*. These forms existed, possibly sympatrically, within a spruce/jackpine/fir, birch parkland interspersed with woody shrubs and grasses which covered the entire State (Delcourt and Delcourt, 1981). This unique, extinct, coniferous parkland has no modern counterpart. In mountain areas of the State, tundra may have existed. There, *Rangifer tarandus* would have been more plentiful. In the grassy areas of the boreal

parkland *Equus fraternus*, *E. complicatus*, *Bootherium* sp., *Symbos cavifrons*, and *Bison* sp. would have been prevalent.

It was also during this time that sea level was more than 300 feet below its present level, thus exposing much of the continental shelf from where *Mammuthus* and *Mammuthus* teeth have been recovered by bottom-dredge fishing boats. The area of the Chesapeake Bay would have contained the large valley of the proto-Susquehanna River and its tributaries. Here Paleo-Indians, no doubt, found shelter and food. Post-glacial warming changed this setting remarkably. Sea level slowly rose to its present stand, and the primarily coniferous forest of Virginia described above was succeeded by a deciduous forest blanket. By early Holocene time the State was covered by a vast, closed-canopy deciduous forest in which the mammalian fauna consisted dominantly of forest product consumers, insectivores, and carnivores (Guilday, 1984) (Table 4).

The forest-product consumers consisted of browsers such as the large herbivores: *Cervus elaphus*, *Odocoileus virginianus*, and *Alces alces*. Mast feeders (nut eaters) included the arboreal granivores: *Sciurus carolinensis*, *Tamiasciurus hudsonicus*, *Glaucomyz volans*, and *Glaucomyz sabrinus*. Grazing animals (grass eaters) were restricted to what were mainly temporary grasslands. These were small rodents and rabbits including: *Sylvilagus transitionalis*, *Sylvilagus floridanus*, *Lepus americanus*, *Synaptomys cooperi*, *Synaptomys borealis*, *Microtus pennsylvanicus*, and *Microtus pinetorum*. *Bison* sp. was probably transient or relatively uncommon because of restricted grasslands during the Holocene.

Insectivores which fed upon insects of the deciduous forest consisted of shrews and bats and included *Sorex dispar*, *Microsorex hoyi*, *Blarina brevicauda*, *Cryptotis parva*, *Myotis keenii*, *Myotis leibii*, *Pipistrellus subflavus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Plecotus townsendii*, *Lasiurus borealis*, and *Dasypus bellus*. Moles, such as *Scalopus aquaticus* and *Condylura cristata*, which are listed in Table 4 as fossorial carnivores, eat insects.

Fresh-water mammals of late Pleistocene/early Holocene time were *Castor canadensis*, *Castoroides ohioensis*, *Ondatra zibethicus*, and *Neofiber leonardi*. Finally, carnivores which preyed upon many of the above species were: *Canis dirus*, *Canis lupus*, *Vulpes vulpes*, *Martes pennanti*, *Mustela vison*, *Felis* sp., and *Lynx rufus*.

It should be pointed out, that the late Pleistocene fauna of Table 4 did not coexist sympatrically at

any one time nor did all these forms inhabit every part of what today is Virginia.

DISHARMONIOUS FAUNAS AND THEIR POSSIBLE CAUSES

Lundelius and others (1983, p. 311) states: "Various taxonomic groups of vertebrates from a given site frequently suggest different and sometimes contradictory paleoenvironmental reconstructions; for example, in the Appalachian area mammalian faunas and some birds indicate 'boreal' conditions, but the herpetofaunas and other birds from the same locality indicate a climate similar to that of today or even milder."

Fay (1984) studied the herptiles of Strait Canyon (Table 1: locality 59) and notes that climatic conditions 30,000 years ago were nearly identical to those of modern western Virginia.

Holman (this volume) states: "Although Virginia's late Pleistocene mammalian fauna contains extinct forms and forms that suggest boreal conditions, the herpetofauna appears to be almost identical to what it is today." Why would amphibians and reptiles (ectotherms) characteristic of mild environments coexist with birds and mammals (homiotherms) many of which are characteristic of boreal environments? Following is a discussion which may help to explain this disparity.

The identification of some fossil specimens might be inaccurate because of the fragmentary nature of the specimens and the lack of adequate modern comparative materials. Bird remains that are commonly misidentified include hawks, eagles, and grouse (Lundelius and others, 1983). Grouse are commonly cited as being indicative of "boreal" conditions. While such errors of identification might contribute to the problem of apparent ecological incompatibility among species, within a given fauna, the identification of remains of many boreal mammal species (e.g., caribou, pika, yellow-cheeked vole, and rock vole) is comparatively easy. Guilday and Parmalee (1972) and Guilday and Hamilton (1978) notes that the heather vole is easily identified even in very young individuals. Though some misidentifications might have been made, most identifications probably are reliable. Classic exceptions to this expected standard are Prout's (1860) description of a juvenile mastodon tooth from King's Salt Works, near Abingdon, Virginia, as that of a titanotherium and Peterson's (1917) identification of a juvenile proboscidean tusk from Saltville as the tooth of a crocodillian (Ray and others, 1967). Additional confusion can be expected because the taxonomy of some mammalian groups

is in need of restudy and thus there must remain some question as to the specific identifications of certain forms, such as species within *Equus* and *Mammuthus*.

A second plausible explanation for seemingly disharmonious faunas could be faunal compression caused by continental glaciers moving south in the late Pleistocene. "That the fauna of glaciated territory was forced southward or eliminated does not imply that the boreal fauna completely replaced a more southern faunal type or that the area south of the ice front was appreciably colder than at present. This view holds that an admixture of ecologically segregated boreal and austral elements existed, possibly almost side by side, near the ice front but within unglaciated territory" (Smith, 1957, p. 207).

Guilday (1971a), however, argue that latitudinal and altitudinal shifting of life zones in response to Quaternary climatic oscillations cannot fully explain the disharmonious faunas known from the late Pleistocene. For example, Guilday (1971a) points out that using the present distribution of the round-tail water rat (*Neofiber alleni*) as a southerly climatic indicator could lead to "serious error". Its present range may be restricted by competition with the larger muskrat (*Ondatra zibethicus*), rather than by climate. In the Pleistocene, however, closely related water rodents were apparently sympatric. During Kansan, Sangamian, and Illinoian times the extinct muskrat (*Ondatra annectens*) and a species of water rat, *Neofiber* sp., were evidently sympatric at Trout and Hamilton caves, West Virginia and *O. hiatidens* and *Neofiber* sp. were sympatric at Port Kennedy Cave, Pennsylvania.

Ray and others (1968) point out that the gannet (*Morus bassamus*) and gray seal (*Halichoerus grypus*) apparently were breeding in southeastern Virginia, far south of their present range, during the late Pleistocene. These records might suggest that coastal Virginia had cooler temperatures during the late Pleistocene, being similar, perhaps, to that of Nova Scotia today. But Ray and others (1968) point out that more recent natural and human influences on the region (e.g., destruction of favorable coastal breeding habitat by sea level stabilization, port activity, etc.) also could have been important contributing factors to their extirpation from Virginia.

Today the pika (*Ochotona princeps*) is confined to the northern Rocky Mountains, yet the genus is known from six sites in the Appalachian Mountains, including Jasper Saltpeter Cave (Table 1: locality 9). Guilday (1979) points out that pikas

(*Ochotona*) from the Pleistocene of the eastern United States may be a separate species with environmental requirements different from the western form and/or that modern pikas are confined to their present niche by interspecific competition, thus its present range is limited by "competitive factors rather than physiological or anatomical strictures" (Guilday, 1979, p. 442).

Weems and Higgins (1977) attempt to explain the disharmonious Ripplemead Quarry (Table 1: locality 51) fauna as an accumulation that included Pleistocene forms (including tapir, horse, and peccary) that had survived into the Holocene, thus allowing a mixture of boreal and temperate species. Semken (1983) and Mead and Meltzer (1984) reviewed purported records of Holocene faunas containing Pleistocene taxa that have been dated radiogenically and argue that records of such postulated late survivals are rare if valid at all.

Guilday (1971a) and Lundelius and others (1983) pointed out that several taxa from the Appalachian region show a positive Bergmann's Response, that is, the tendency for members of a species to increase in size with increasing latitude through its range. A southward shift of cooler climates is inferred for Pleistocene glaciations. Several species, such as *Ondatra* (Nelson and Semken, 1970) and *Blarina* (Graham and Semken, 1976; Jones and others, 1984), were larger during late Pleistocene than they are at the same areas today; the late Pleistocene forms from the U. S. are comparable to those living in Canada today. Guilday (1984, p. 254) noted "nine species of mammals have undergone a Holocene size reduction, while four have increased in size within the [Appalachian] area during the last 11,000 years, paralleling, for the most part, modern latitudinal size clines." Thus size analyses may support a claim of overlap of southern and boreal types.

Many researchers have attempted to explain incompatible, "allopatric" or "disharmonious" faunas (Semken, 1974) by the "climatic equability hypothesis" which maintains that more equable climates (cooler summers and warmer winters) in the Pleistocene allowed seemingly unnatural associations of northern, western, and southern forms (Hibbard, 1960; Dalquest, 1965; Slaughter, 1967, 1975; Dalquest and others, 1969; Hibbard, 1970; Holman, 1976, 1980; Martin and Neuner, 1978). Dreimanis (1968) argued that late Pleistocene changes in the structure and composition of plant communities rather than shifting ecological zones may have allowed the sympatry of northern and temperate mammals and temperate herpetological forms.

Graham (1976, 1979) and King and Graham (1981) noted that animal distributions are primarily determined by either the distribution of plant foods on which they depend or on the distribution of prey species. King and Graham (1981, p. 133) stated "animals show varying tolerances by the range of habitats in which they can exist. . . If each species reacted individually in response to environmental change through time as they have been shown to do through space, then plant communities would be constantly changing and their species composition would not necessarily be the same as modern analogs." Thus, because individual species of a community react independently to environmental changes, it is not always appropriate to apply characteristics of modern communities to the reconstruction of past environments. This model was elaborated and termed "coevolutionary disequilibrium" by Graham and Lundelius (1984).

Thus Holman's (this volume) dilemma of why the Virginia herpetofauna does not suggest the boreal environmental interpretation that many of the birds and mammals do, may be explained by their individual response to change. Amphibians and reptiles (ectotherms) apparently were little affected by the modern plant community changes from the late Pleistocene to Recent, while birds and mammals (homoiotherms) were more affected.

Semken (1983) points out that several species including *Erethizon dorsatum*, *Martes pennanti*, *Spermophilus tridecemlineatus*, *Clethrionomys gapperi*, and *Tamiasciurus hudsonicus* apparently had more extensive ranges until a few hundred years ago. The modern faunal distribution cannot be attributed wholly to climatic change associated with deglaciation since many small mammals were strongly affected by (a) climatic change during the Holocene, (b) pre-Columbian cultural patterns, and (c) European settlement (Semken, 1983). Thus, even within relatively short periods of geological time and in the absence of major climatic changes, range changes among vertebrate species can occur sufficiently to create new disharmonious faunas.

AGE INTERPRETATION OF VIRGINIA'S QUATERNARY LOCALITIES

Table 3 lists all of the Virginia fossil vertebrate localities giving their presumed ages as either late Pleistocene (Wisconsinan) or Holocene. A few of the human-associated sites, such as Keyser Farm (Table 1: locality 34), can be placed within the Woodland Indian Period based on associated cultural material. Gardner's Cave, Edinburg Fissure, and possibly part of Jasper Saltpeter Cave and

Strait Canyon Fissure suggest early Wisconsinan or even Illinoian ages. Virginia has not yielded a rich middle Pleistocene fauna such as Trout Cave, West Virginia; Cumberland Cave, Maryland, or Port Kennedy Cave, Pennsylvania. Jones and others (1984) listed Early's Cave (Table 1: locality 20) as mid-Pleistocene and Strait Canyon (Table 1: locality 59) as early Wisconsinan. More detailed study and more radiometric age determinations of the known faunas of Virginia (only 4 of the 77 localities reported in this paper have been dated radiometrically) are needed before better chronologic interpretations can be made.

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EARLY MAN IN VIRGINIA¹Ben C. McCary²

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ABSTRACT

The Archeological Society of Virginia's survey of fluted projectile points, carried out since 1947, has recorded more than 700 such points from within the State. Over 85 percent of these records are from the Piedmont and Tidewater areas south of the James River, as are most of the known Clovis sites in Virginia. A significant outlying concentration of projectile point records focuses upon Smyth County, southwestern Virginia. Radiocarbon dated Clovis sites from eastern North America fall between 11,120±180 and 10,190±300 yrs B.P.

¹In this article the terms Early Man and Paleo-Indian have the same meaning and refer specifically to the Clovis complex, the earliest culture found in Virginia, which dates to between 12,000 and 10,000 yrs B.P.

²Professor Emeritus of Modern Languages, Lecturer in Anthropology, College of William and Mary, Williamsburg, Virginia 23185

INTRODUCTION

The distinctive fluted point associated with the Clovis culture has been found in every state in the continental United States and in parts of Canada. No prototype of it has been found in Europe or Asia. Therefore, it apparently originated in the present forty-eight contiguous United States. Clovis points usually have parallel or slightly convex sides. The base in most cases is concave. One major characteristic is the presence of flutes on the proximal or basal faces which extend about one-fourth to one-half of the length of the points. There are no notches in the basal area.

Based on ¹⁴C-dated sites, the Clovis culture seems to have appeared soon after 12,000 yrs B.P. According to Haynes (1970), there is some meager evidence of pre-Clovis migrations to America, but the representative tools of these possibly earlier migrants are too poorly known to make comparisons with Clovis tools.

Interest in Paleo-Indians in Virginia was stimulated to a great extent by various archeological finds made in the western part of the United

States from 1927 to the 1950's. The Dent site, found near Dent, Colorado in 1932, is generally accepted as the first site which yielded, in 1936 and 1937, Clovis fluted points found in association with mammoth remains. The Blackwater No. 1 locality, New Mexico, in 1936 and 1937 yielded the type specimens from which is derived the name Clovis fluted point (Wormington, 1957). As more sites were found in the western part of the United States it became apparent that these early hunters covered much territory in pursuit of large animals, such as the mammoth, mastodon, camel, horse, and other members of the late Pleistocene fauna. Associated with the skeletal remains at the kill sites were distinctive projectile points which, as already stated, became known as Clovis fluted points.

CLOVIS CULTURE IN VIRGINIA

My main objective with this paper is to review much of what we have learned since the late 1940's about the wide but, in most cases, thinly spread Clovis culture in Virginia. In the early 1930's, I began examining collections of Indian artifacts throughout Virginia. I was amazed to learn that the number of Clovis points, even in large collections of artifacts from Virginia, was so small.

For example, one collection of approximately 20,000 projectile points had only 6 Clovis points.

The Archeological Society of Virginia was organized in 1940. A few years later it decided to undertake the publication of a *Quarterly Bulletin*. With this established, I announced in the December 1946 issue (Volume 1, Number 2) of the *Quarterly Bulletin* that in collaboration with the Society, I would begin a continuing survey of Clovis points found in Virginia. The entire thirty-four pages of the September 1947 issue of the *Quarterly Bulletin* was devoted to the first fluted-point survey report, which listed and described 126 Clovis points found in Virginia. The results of 23 surveys now have been published in the *Quarterly Bulletin*, giving pertinent information on more than 700 Clovis points found in Virginia (Figure 1).

The interest aroused by the surveys in the Paleo-Indian and his tool kit has led to the discovery of twelve small Clovis sites in Virginia. Six of them have been recorded, and the remaining six are being investigated by their finders and will be recorded at later dates in the *Quarterly Bulletin*.

The largest of the six small sites already recorded has produced approximately 100 Paleo-Indian tools and 12 Clovis points. The smallest of the six sites has yielded about 20 Paleo-Indian

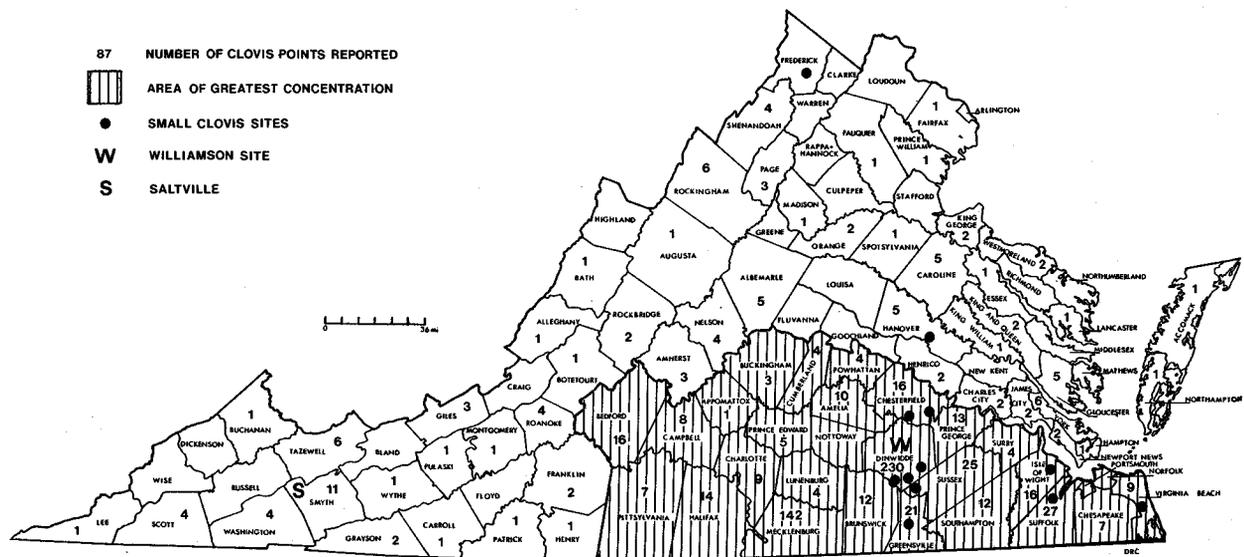


Figure 1. Map of Virginia counties and larger Tidewater cities showing number of Clovis points reported for each political unit. Notice the high concentration of points in the southern Piedmont and Tidewater and in and near Smyth County in southwest Virginia.

tools and 2 Clovis points. The six recorded sites are located in Isle of Wight (1), Dinwiddie (1), Chesterfield (2), and in Sussex (1) counties and the City of Suffolk (1). Adjacent to the Sussex County site, two small outcrops of chert and chalcedony were found. The six small Paleo-Indian sites which are being investigated and have not been recorded in the *Quarterly Bulletin* are located in the following counties: one in Amelia, one in Greensville, three in Dinwiddie, and one in Frederick. The Paleo-Indians wanted to be near good outcrops of cryptocrystalline quartz, and they made efforts to find them. More than half of the twelve small sites just mentioned were located near an outcrop of the preferred lithic materials.

One of the largest and most prolific Paleo-Indian sites in the United States, the Williamson site, was discovered in the summer of 1949 in Dinwiddie County, Virginia (Figure 1). From 1946 to 1949 three survey reports had appeared in the *Quarterly Bulletin*, and the five persons primarily responsible for the discovery of the Williamson site had profited by the helpful information provided by the survey reports. I was fortunate in having been associated with the finding and identification of the site which has now become recognized as one of the largest Paleo-Indian workshop and settlement sites in North America. The Williamson site is about 4.5 miles east of Dinwiddie Courthouse. It lies on an elevated stretch of land between Little Cattail Creek on the north and a very small creek on the south known as Health Meadows. The cultivated land on which the site is widely scattered constitutes more than 75 acres.

I prepared a report on the site that was published in *American Antiquity* in July, 1951. At that date, two years after its discovery, the site had yielded 33 Clovis points, 174 end scrapers, 214 side scrapers, 16 preforms, several graters, and many rough cores (McCary, 1951). Today, one might estimate conservatively that the site has produced 200 Clovis points. One might also estimate that the site has yielded approximately 1200 to 1400 end scrapers, 1000 side scrapers, and other tools in smaller numbers including knives, perforators, graters, spokeshaves, choppers, wedges, drills, and hammerstones (Figures 2-4).

As already stated, the Paleo-Indian preferred cryptocrystalline quartz (chalcedonies, flints, cherts, and jaspers) to other materials for tool making. Evidence indicates that there were probably several outcrops of these preferred lithic

materials on the Williamson site. When the site was discovered in 1949 it was covered with thousands of unutilized flakes and with many large and small cores. The materials provided by the outcrops consist, in layman terms, mainly of variegated chalcedony and chert with cream, gray, brown, and blue colors dominating. A bluish-black chert also occurs there. Small pockets of minute crystals are often found in the chalcedony and chert, and they doubtlessly led to breakage when flaking was attempted. Flakes and cores of white quartz, and of gray and brown quartzite, found in small quantities on the site, could have been of local provenance. Rock crystal, found sporadically as flakes and implements, was probably brought in from sources higher up in the Piedmont area. Petrified wood, represented by very few flakes, could have had its origin in Prince George County which adjoins Dinwiddie County.

The proximity of rivers, creeks, springs, and swamps was desirable to the Paleo-Indian, and the presence of large game played an important part in the selection of a site. The Williamson site probably met most of these requirements. Little Cattail Creek was likely in existence and flowed by the site. Stony Creek was slightly under two miles and Rowanty Creek slightly over two miles away. The Nottoway River was about ten miles to the south and the Appomattox was approximately the same distance to the north. The large game, if not the mastodon, was presumably the deer, the small black bear, and the elk. It should be remembered that no mastodon or mammoth bones have been found in an eastern North American Paleo-Indian habitation site (Gramly, 1982).

Our surveys indicate that there was also a sizable concentration of Paleo-Indians in Mecklenburg County, Virginia, which is about 55 miles southwest, as the crow flies, of the Williamson Paleo-Indian site. Mecklenburg County has yielded about 142 Clovis points found on farms near Chase City and Clarksville. However, no large community site similar to the Williamson site has been found in Mecklenburg County.

It should be noted that the concentration of Clovis points in Mecklenburg County extends into Granville County, North Carolina which adjoins Mecklenburg County. A. D. Capehart of Oxford, North Carolina reported to me in September, 1948, that over a period of years he had collected 62 Clovis points from Granville County (McCary, 1948). Since that time the number of points from Granville County has increased to 96. Alamance

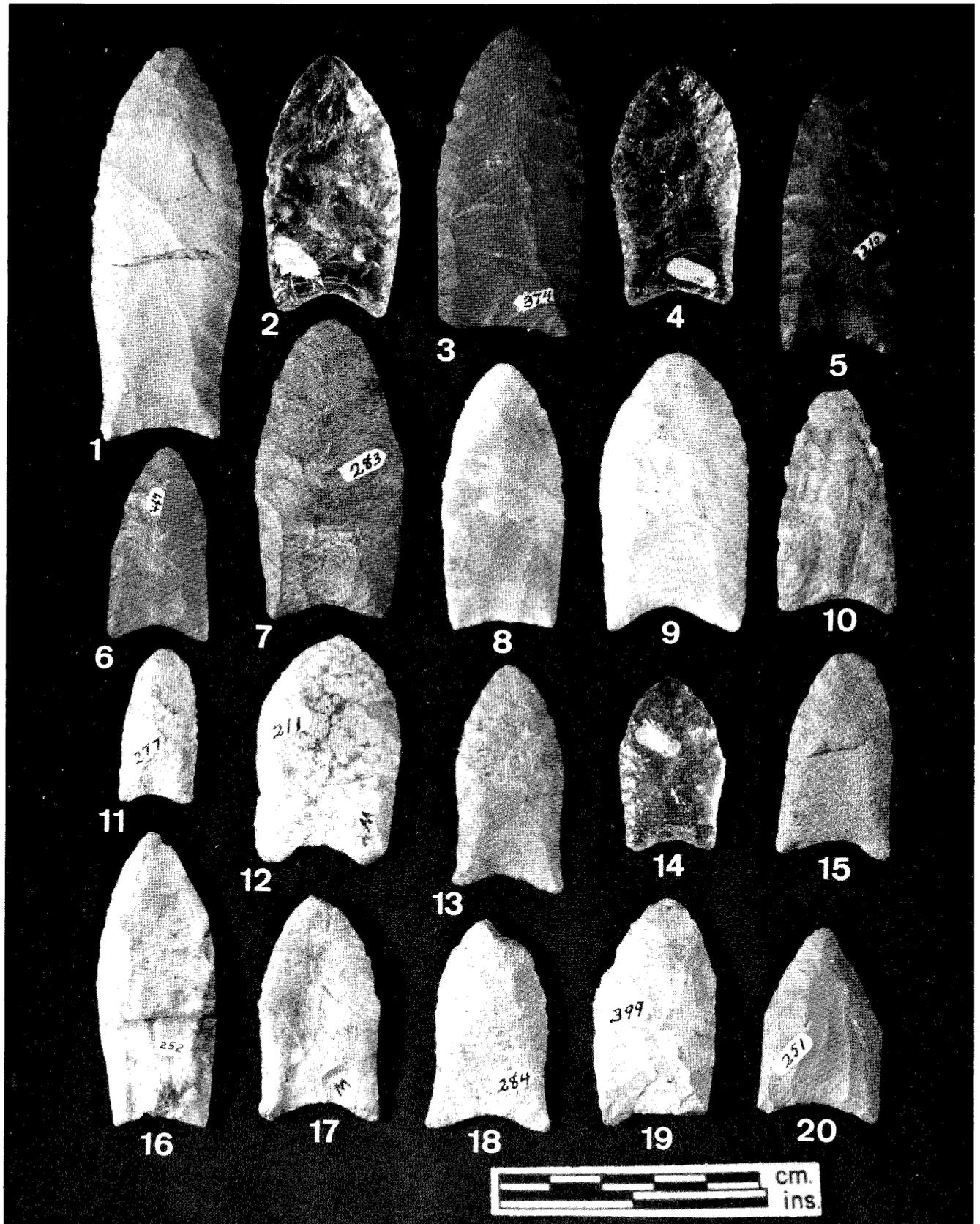


Figure 2. Clovis points from three areas of concentration in Virginia. (1-3) Mecklenburg County; (4-6) Saltville, Smyth County; (7-20) Williamson site, Dinwiddie County.

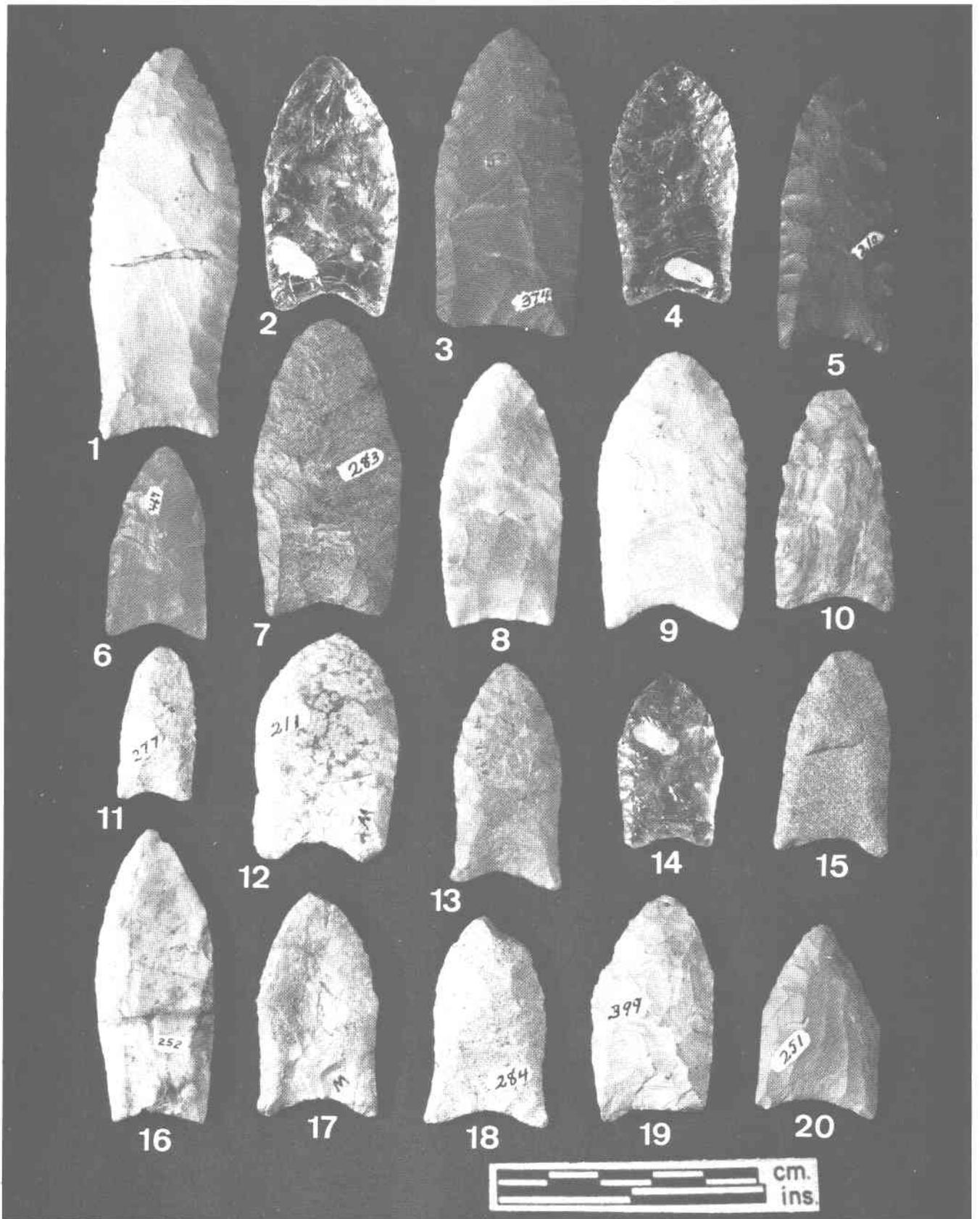


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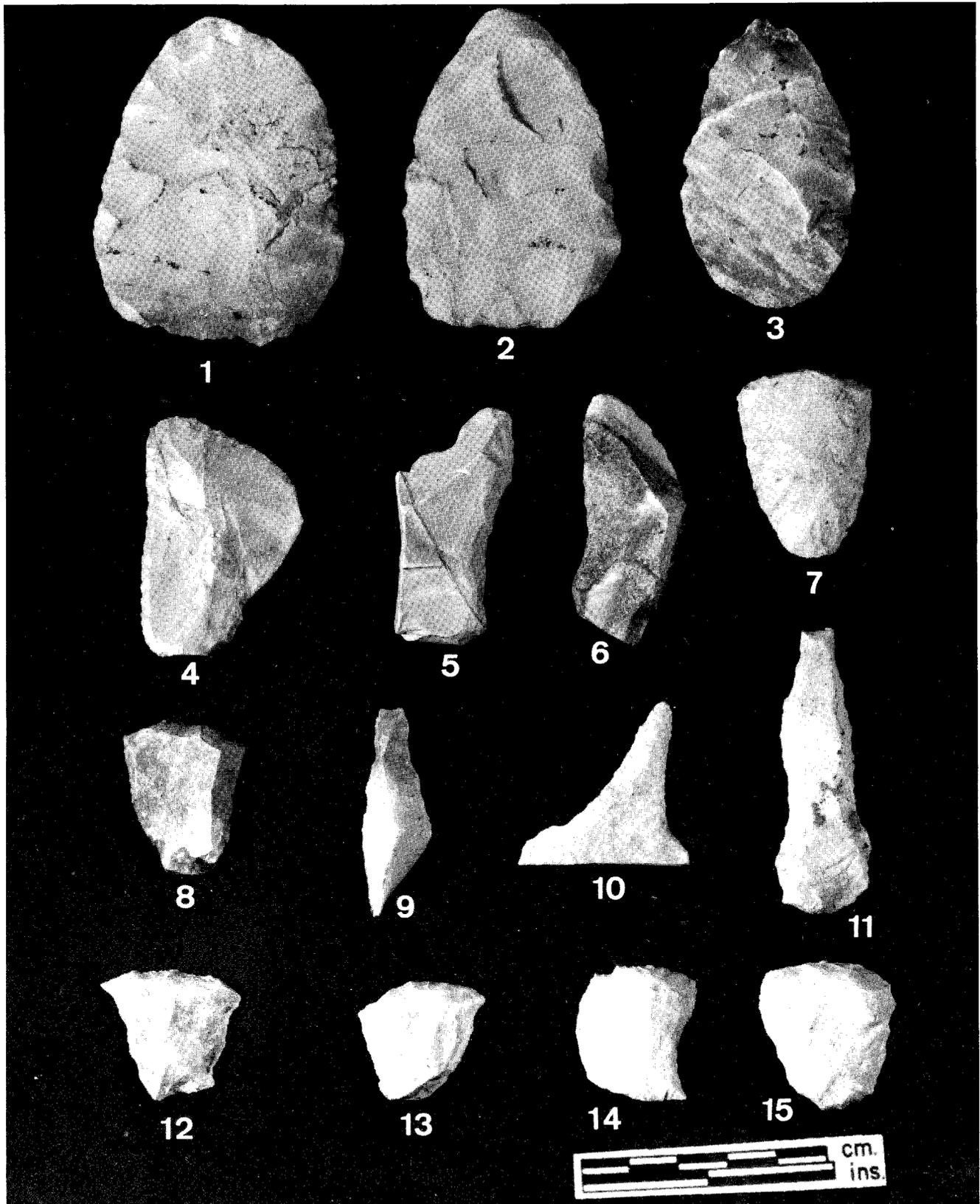


Figure 3. Clovis tools from the Williamson site (A). (1-3) large biface blade knives; (4) side scraper; (5, 6) spokeshaves; (7) distal end of broken Clovis point converted to end scraper; (8) end scraper; (9) twist drill; (10) expanding drill; (11) twist drill; (12-14) end scrapers with gravers; (15) end scraper.

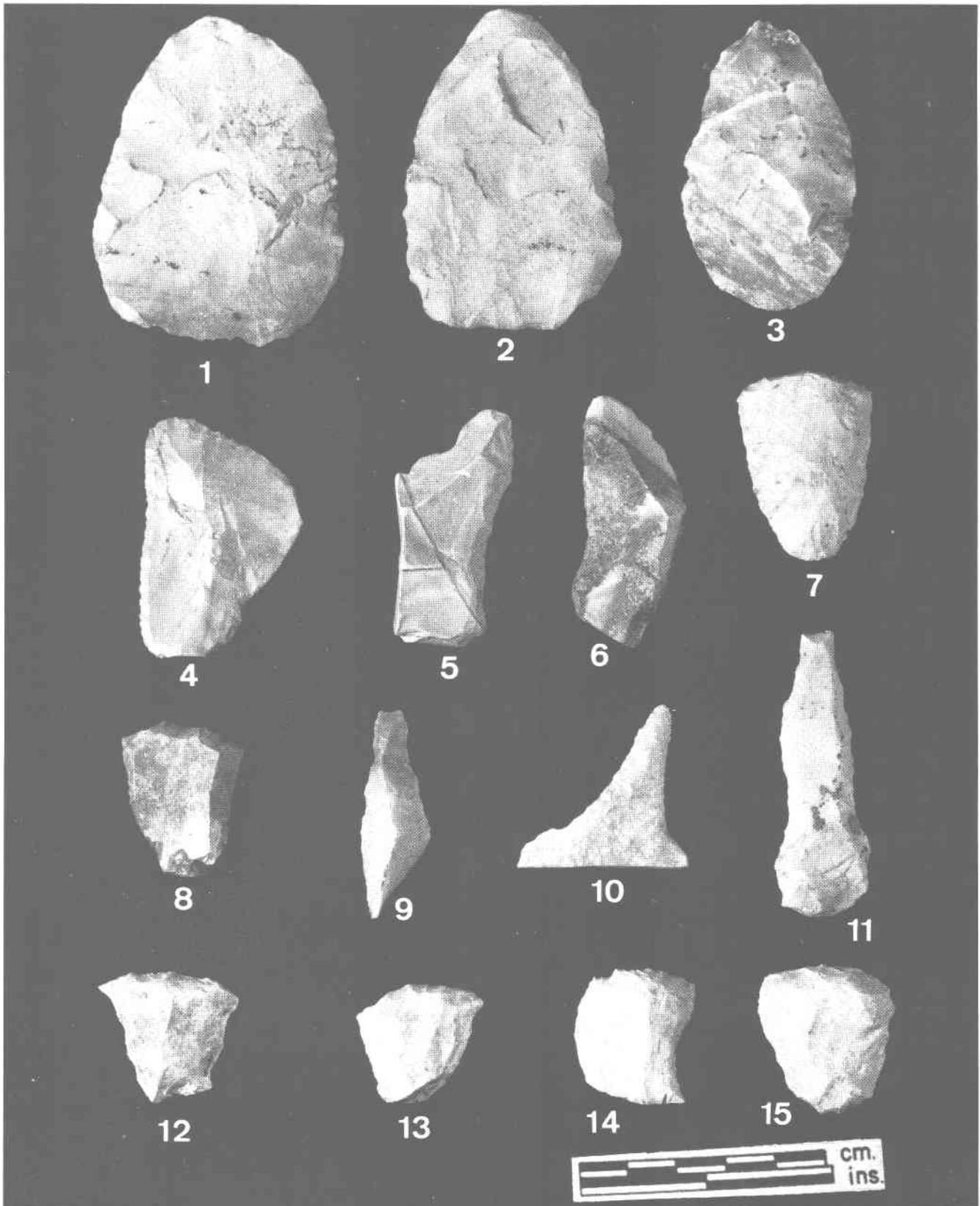


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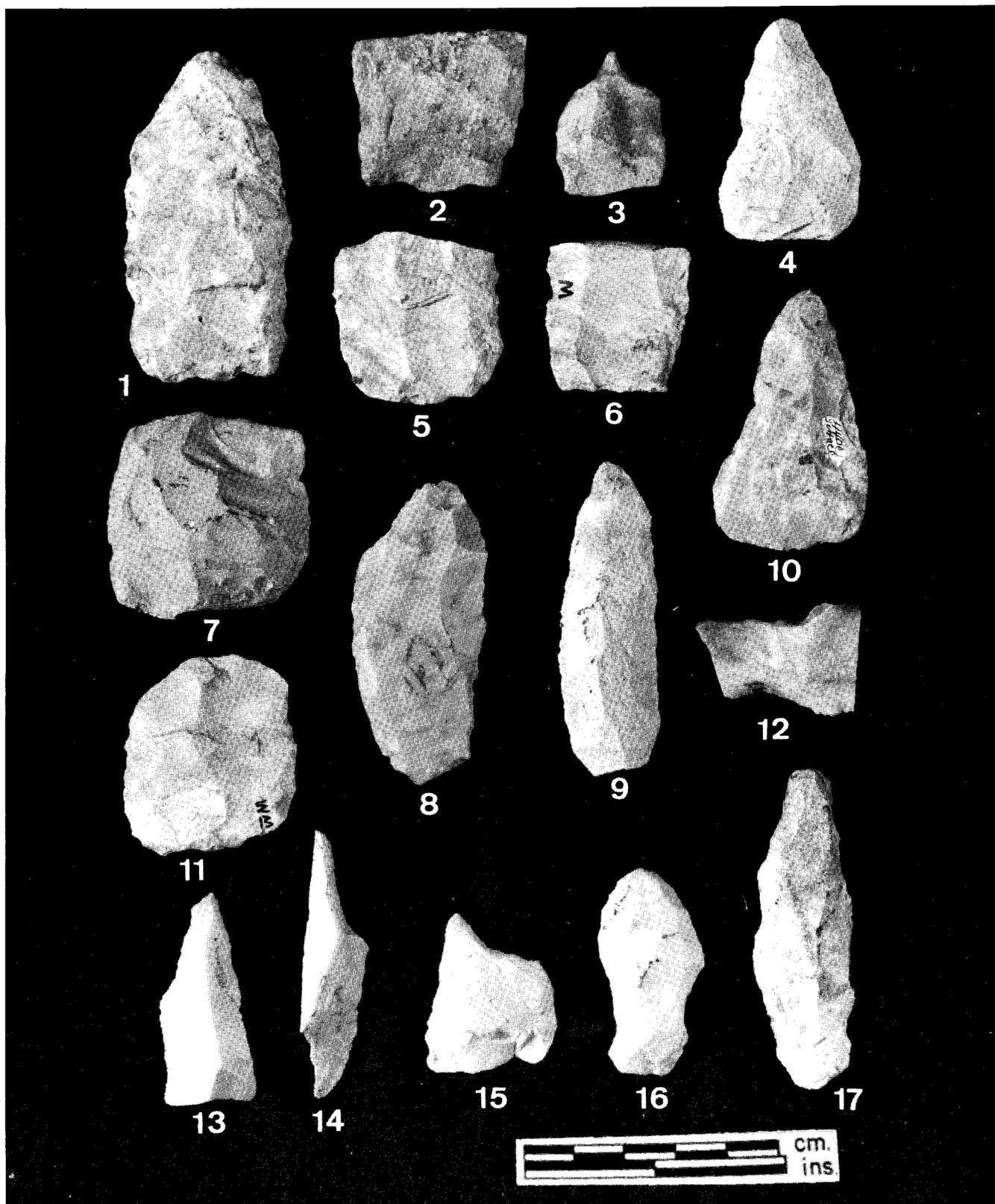


Figure 4. Clovis tools from the Williamson site (B). (1) preform; (2) broken preform; (3) graver; (4) triangular knife; (5, 6) broken preforms; (7) wedge; (8) side scraper; (9) humpback scraper; (10) triangular knife; (11) wedge; (12) two spokeshaves on a flake; (13-15) perforators; (16) scraper with two spokeshaves; (17) humpback scraper.

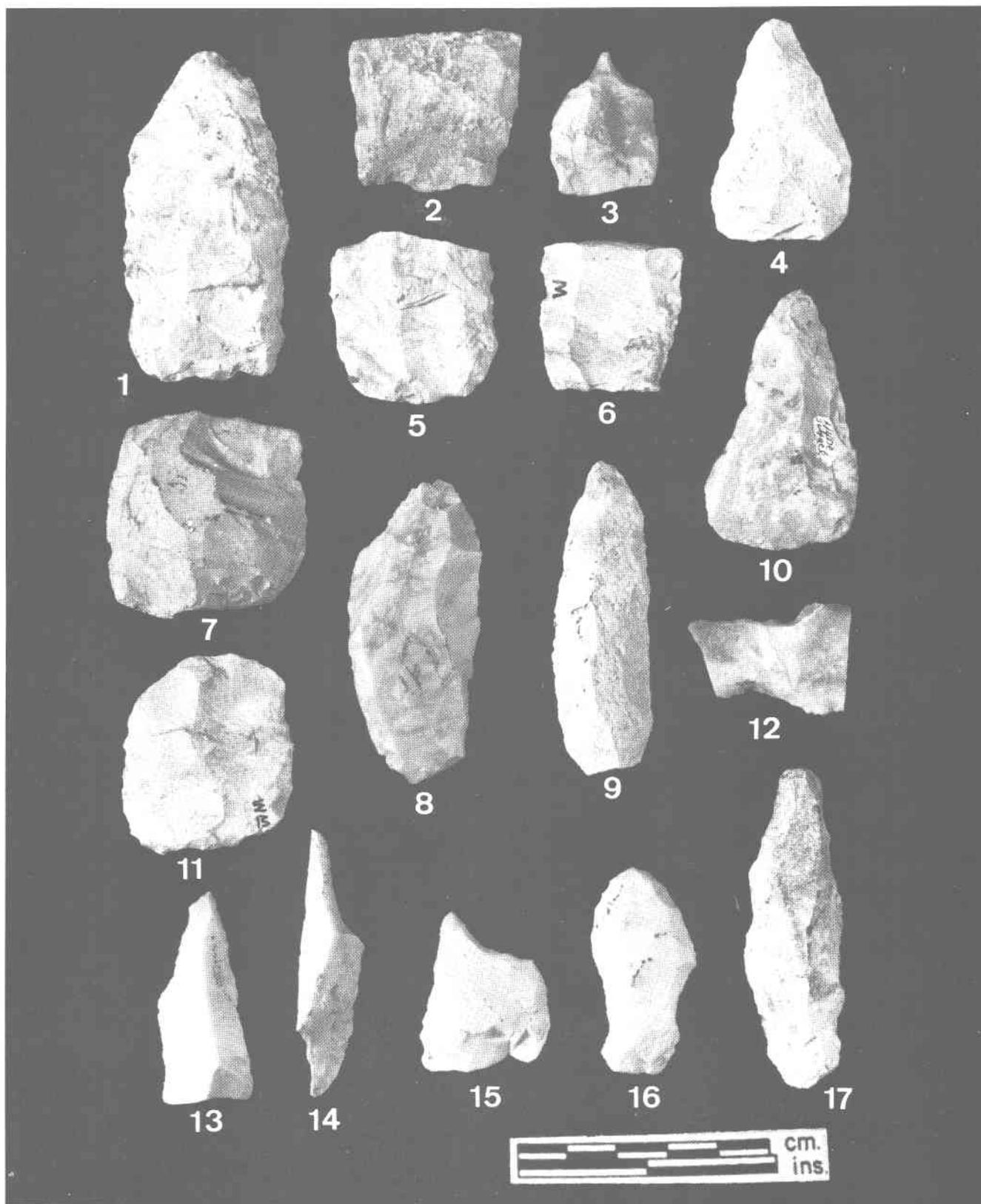


Figure 4. Clovis tools from the Williamson site (B). (1) preform; (2) broken preform; (3) graver; (4) triangular knife; (5, 6) broken preforms; (7) wedge; (8) side scraper; (9) humpback scraper; (10) triangular knife; (11) wedge; (12) two spokeshaves on a flake; (13-15) perforators; (16) scraper with two spokeshaves; (17) humpback scraper.

County, North Carolina has the second largest concentration of Clovis points in the State; this consists only of 12 points. Furthermore, a look at the map showing the distribution by counties of Clovis points found in Virginia (Figure 1) will show that the Paleo-Indians in Virginia preferred living south of the James River, assuming the pattern of reported Clovis points is indicative of the relative distribution of Paleo-Indians in the State. Of the 100 counties in Virginia (including five recently reorganized as cities), 26 counties south of the James River, including Bedford and Pittsylvania at the western boundary, have provided approximately 85 percent of the fluted points recorded for Virginia.

Announcements were made in two early issues of the *Quarterly Bulletin* which aroused great hope and expectation of finding an association between Paleo-Indians and extinct megafauna. R. W. Pickle (see McCary, 1947) of Saltville, Virginia, stated that he had found near Saltville the broken base of a Clovis point "in a sand and gravel stratum bearing numerous mineralized mastodon bones." Pickle (McCary, 1952) reported another find of a Clovis point in Saltville at a depth of 36 to 40 inches "in a sandy like clay soil." A few days later at a still lower depth "a large tooth" identified as that of a young mastodon was found. The article stated that no association between the Clovis points and the mastodon bones and tooth was claimed. We are inclined to believe that it was in both of the finds a case of "so close but still so far," and that the potentiality to prove an "association" at some future date is still in Saltville.

The surveys of Clovis points add proof to the early opinion that Saltville and the surrounding region attracted the Paleo-Indians. The *Quarterly Bulletin* of March 1983, gives the latest count of the distribution by counties of Clovis points found in Virginia (McCary, 1983). It reveals that 11 Clovis points have been reported from Smyth County in which Saltville is located. Tazewell County, adjoining Smyth County on the north, has yielded 6 points and Washington County, adjoining Smyth County on the west, has reported 4 points making a total of 21 Clovis points for the three-county area. All the other sixteen counties in the southwestern tip of the State from Craig, Montgomery, Floyd, and Patrick counties inclusive have produced a total of only 15 Clovis points. Therefore, we cannot discredit the importance of the role that Saltville and its environs might play one day in furthering our understanding of the Paleo-Indian in Virginia.

Excavations were made at the Williamson site between 1972 and 1975 in an effort to obtain suitable material with which to absolutely date the Paleo-Indian occupation. By the end of the summer of 1975 the excavation consisted of 11 completed ten-foot squares and two five-by-ten cuts. Artifacts were prolific in most of the squares. Unfortunately, we found neither recognizable hearths nor datable charcoal samples. We also were unsuccessful in our efforts to find pollen samples. We were disappointed that we did not obtain our major objective which was to date the site. However, further efforts should be made to obtain radiocarbon dates at some of our more promising small sites in the State.

AGE OF CLOVIS CULTURE

Before we look at several radiocarbon dates of Clovis sites in the eastern and northeastern parts of the United States, we should note that it has been pointed out that the ten ^{14}C -dated Clovis sites in the western part of the United States are between 11,000 and 11,500 yrs B.P. (West, 1983).

Pennsylvania, Nova Scotia, and several states in the northeastern part of the United States have Clovis sites which have been radiocarbon dated in recent years. The Debert site in Nova Scotia produced a series of dates with an average date of 10,600 yrs B.P. (MacDonald, 1969). A Paleo-Indian site in western Connecticut, 6LF21, yielded a date of 10,190 \pm 300 yrs B.P. (Moeller, 1980). The Vail site, an encampment site in northwestern Maine, produced a date of 11,120 \pm 180 yrs B.P. (Gramly, 1982). The Shawnee-Minisink site, near Stroudsburg, Pennsylvania, yielded a series of radiocarbon dates which averaged about 10,500 yrs B.P. (Eisenberg, 1978).

Note that the Debert site and the Shawnee-Minisink site are within a few hundred years of being as old as the western Clovis sites. More ^{14}C dates, especially from the east and southeast, might narrow the gap now existing between the radiocarbon ages of eastern and western Clovis sites.

CONCLUSIONS

Some fifty years of recording Clovis fluted points discovered in Virginia has shown clearly and convincingly that the Paleo-Indian makers of these points occurred throughout the State (Figure 1; McCary, 1983). The distribution of points by county and city suggests that the southern Piedmont-southern Tidewater area stands

apart as a region of relatively great Paleo-Indian activity within the State. The most significant concentration of reported Clovis points from the western part of Virginia is from the Smyth-Tazewell-Washington-county area. Site selection by Paleo-Indians was probably influenced by the availability of good water, game, and outcrops of cryptocrystalline quartz.

Ongoing and future excavations of known or suspected Paleo-Indian sites in Virginia should strive to obtain absolute dates for typologically or culturally distinct horizons, and to reconstruct the environments utilized by Paleo-Indians as much as possible with the use of geomorphic, pollen, and faunal data.

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LATE PREHISTORIC AND PROTOHISTORIC LARGE MAMMAL ZOOGEOGRAPHY OF VIRGINIA

Robert K. Rose¹

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ABSTRACT

Evidence derived from 18 late prehistoric (middle and late Woodland Period) archeological sites, from several early historical accounts, and from the current understanding of the distribution of Virginia mammals indicates that the large mammal fauna of the Commonwealth has not changed substantially within the past 4,000 yrs. Some species (e.g., bison, elk, timber wolf, and mountain lion) have been extirpated since the settlement of Virginia by Europeans; some previously extirpated species (e.g., porcupine, coyote, and beaver) have been naturally or artificially reintroduced during the historical period, and others (e.g., woodchuck and red fox) probably have expanded their distributions as a result of changing land-use patterns in the Commonwealth.

¹Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23508.

INTRODUCTION

The purpose of this paper is to evaluate the distribution of the land mammals of Virginia, especially the large mammals, that were present during the late prehistoric and protohistoric periods and to compare them with today's Virginia mammals. The late prehistoric component of Virginia's faunal history, arbitrarily defined as that representing the 2,000 years before European settlement, corresponds approximately with the middle and late Woodland Period. The information on the mammals of this period comes from excavated archeological sites that have been dated either by ¹⁴C methods or by distinguishing pottery or other artifacts associated with the sites or strata. The protohistoric (hereafter called "early historical") record is reconstructed from the writings of early Virginia settlers, explorers, or travelers. Early writings date from slightly before A.D. 1600 and extend into the 18th Century; the later accounts are from the western sections of the Commonwealth, where European

settlement occurred much later than it did on the Coastal Plain. The record of modern Virginia mammals comes from a number of sources: two books on the distribution of Virginia mammals (Bailey, 1946; Handley and Patton, 1947), other compilations (Hamilton and Whitaker, 1979; Hall, 1981), recent literature of mammalogy, and correspondence and conversations with other mammalogists within the Commonwealth.

LARGE MAMMALS

The mammals that were present for the 2,000 years before European settlement were the survivors of the late Pleistocene and early Holocene extinctions that occurred in the region. Information about these extinctions is to be found in other chapters within this volume, especially the papers by Eshelman and Grady, and by McDonald. Other viewpoints on the late Quaternary dynamics of the mammalian faunas of eastern North America are provided by Guilday (1971), Handley (1971), and by the recent excellent book *Pleistocene Mammals of North America* (Kurten and Anderson, 1980). The main point from these reviews is that the large mammal fauna of late Quaternary Virginia suffered extensive extinctions and, as a result, few species of large mammals survived to the late prehistoric period.

When applied to mammals, any definitions of "large" and "small" will have difficulty with universal acceptance. Kurten and Anderson (1980, p. xiv) distinguish between micromammals (orders Insectivora, Chiroptera, Rodentia, and Lagomorpha) and macromammals (orders Edentata, Carnivora, Artiodactyla, Perissodactyla, and Proboscidea). By this system small carnivores such as the weasels, which may weigh as little as 0.1 pounds (50 grams), are macromammals. A more common approach is to define an arbitrary body weight, for example 11 pounds (5 kg) (Snyder, 1978), to differentiate large from small mammals. With this method, many of the small carnivores become small mammals, and some rodents (e.g., beaver, *Castor canadensis*, and woodchuck, *Marmota monax*) become large mammals. Using the body weight criterion, there are only eight species of large mammals in Virginia today, including woodchuck, beaver, red fox (*Vulpes vulpes*), black bear (*Ursus americanus*), raccoon (*Procyon lotor*), river otter (*Lutra canadensis*), bobcat (*Felis rufus*), and white-tailed deer (*Odocoileus virginianus*). The gray fox (*Urocyon cinereoargenteus*), which weighs slightly less than 11 pounds (5 kg), the Virginia opossum

(*Didelphis virginiana*), and the coyote (*Canis latrans*), which has reappeared within the past five years in two western counties (J. Pagels, pers. comm.), might be included by some authors. However defined, the list of large mammals in Virginia is short. In this paper, I have operationally defined "large mammals" as those that were sufficiently large both to be used as food by the Woodland Period Indians and to be observed and recorded in the early historical record. With this method, mammals of squirrel size and larger are included in the study sample.

THE LATE PREHISTORIC RECORD

The best direct information for the 2,000 years before settlement has been derived from the excavations of archeological sites of the Woodland Period. Although there are some difficulties with the use of these records, this is a fruitful and expanding area of research. Since 1968, information from archeological sites has provided a fair estimate of the mammals that were present at the time the sites were occupied. However, several of the papers reviewed here indicate that only a fraction of the faunal remains recovered from the sites had been evaluated. Thus, the information, although accumulating rapidly, is still fragmentary in terms of its utility in reconstructing the distributions of the mammals of the late prehistoric period.

One of the difficulties with the mammal record as determined from archeological sites is that mammal remains tended to be preserved either in caves (which are restricted to western Virginia) or in shell middens in the Piedmont or Coastal Plain regions. Elsewhere, acid soils generally have destroyed the evidence that mammals were present. Consequently, there is an uneven mammal record within the Commonwealth, with several excellent sites in the Valley and Ridge region, some information from sites in the Coastal Plain, and almost nothing from the Piedmont region (Figure). Although mammals living near caves or streams may be overly represented, we are more concerned with knowing what mammals were present during the 2,000 years before settlement than in knowing where they lived. Finally, archeological sites contain samples of mammals biased in favor of large mammals that were taken as food and then preserved in garbage pits, middens, or graves. This bias is not a problem here because we are primarily interested in the larger mammals of the Commonwealth.

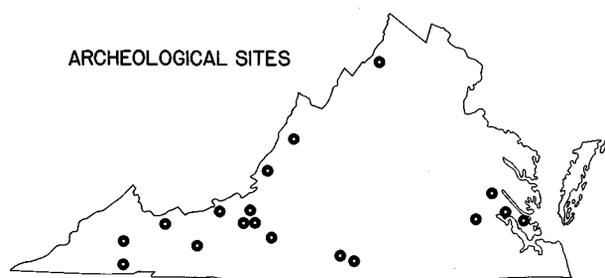


Figure. Location of the 11 montane, 3 piedmont, and 4 coastal plain late prehistoric archeological sites that have been reviewed in this study.

The mammals of the late prehistoric period were similar to those present today (Table 1); each can be assigned clearly to an extant species. The mammals that were collected at several archeological sites included the Virginia opossum, eastern cottontail (*Sylvilagus floridanus*), seven species of rodents (including tree squirrels and beaver), four canids, one bear, one raccoon, three mustelids, two felids, and two cervids, for a total of 22 species. In addition to the species that were present at many sites, several other species including mole, white-footed mouse (*Peromyscus leucopus*), rice rat (*Oryzomys palustris*), meadow vole (*Microtus pennsylvanicus*), porcupine (*Erethizon dorsatum*), spotted skunk (*Spilogale putorius*), and long-tailed weasel (*Mustela frenata*), were recorded at one or two sites. (The "mole" is probably the eastern mole, *Scalopus aquaticus*, the mole with the widest distribution in Virginia today.)

The white-tailed deer is the most common mammal at these sites. This is not surprising because deer probably were abundant throughout Virginia, and because of their large size, each successful hunt provided much food. Conspicuously absent from Table 1 is the American bison, *Bison bison*, although there is one bison tooth known from nearby Currituck County, North Carolina dated about 2,610 yrs B. P. (Painter, 1978). According to early historical accounts, the bison, or American buffalo, was common throughout much of Virginia, except for the Coastal Plain. One explanation for the absence of bison from archeological sites is that montane caves and Coastal Plain shell middens were far removed from places where bison were common. Another explanation is that bison would be too large to carry back to the Indian villages. Consequently, the carcass could have been dismembered at the kill site, and the usable parts carried back to the

village as was often done with deer (Holland, 1979). Under these conditions, it is unlikely that large numbers of bones would be returned to the village and to its garbage pits. Elk (*Cervus elephas*), which are intermediate in size between white-tailed deer and bison, were present at half of the 18 sites that were evaluated in this paper (Table 1).

Beavers and woodchucks were found at most of the 18 sites; both are large and easy to hunt because of their fidelity to lodges and burrows near forest edges, respectively. Foxes, raccoons, and gray squirrels were also common. The flying squirrel (probably southern flying squirrel, *Glaucomys volans*) is a species that might be, but has not been, found at archeological sites. Despite the fact that these squirrels are nocturnal, there are several reports of their presence in the early historical accounts.

In Table 1, the faunas from archeological sites have been grouped according to geographic location, starting in the southwest and moving northward and eastward. The faunas were grouped from west to east in an effort to uncover unusual distributional patterns, but none was revealed. A few species, such as the woodrat (*Neotoma floridana*), today are restricted to the western part of the Commonwealth and they might be assumed to have been similarly restricted during prehistoric times. However, such a pattern of distribution cannot be detected with certainty in this small sample of 18 archeological faunas.

In some studies, notably Benthall's (1979) from Dougherty's Cave in Russell County and Barber's (1981) study of Maycocks Point Shell Midden in Prince George County, good information is available for long time periods. Dougherty's Cave was a stratified site, with the lower layers dating from the middle Archaic Cedar Creek Period (Benthall, 1979). Barber (1981) commented that neither the mammals eaten nor their proportions changed in the ¹⁴C-dated layers at the Maycocks Point location; the maximum established age difference between the layers was about 500 years. These studies reinforce the observation that no readily apparent changes in the mammalian fauna within the past 4,000 years have been revealed from the study of archeological sites.

In sum, the archeological record indicates that between 22 and 29 species have been preserved at one or more sites. White-tailed deer predominate almost everywhere, but the Woodland Period Indians collected mammals of all sizes and

Table 1. Species of mammals recorded at late prehistoric archeological sites in Virginia. "X" indicates presence, "O" indicates a conspicuous absence, and "?" refers to a specimen referable to one taxon but possibly a congener. For scientific names, refer to Table 3.

	Opossum	Cottontail	Chipmunk	Gray squirrel	Fox squirrel	Flying squirrel	Woodchuck	Beaver	Muskrat	Woodrat	Wolf	Dog	Gray fox	Red fox	Black bear	Raccoon	Mink	Skunk	Otter	Mountain lion	Bobcat	White-tailed deer	Elk	Bison
Appalachian Highlands																								
Benthall 1979	X	X	X	X			X	X	X	X					X	X			X			X	X	
MacCord 1981			X	X	X				X				X		X								X	
MacCord & Buchanan 1980				X			X	X	X		X	X	X		X	X	X		X	X	X	X	X	X
Funk 1976				X			X	X			?	X												
MacCord 1972		X	X	X			X	X	X	X		X	X		X	X		X	X	X		X		
Barber & Barody 1977		X					X	X					X		X	X				X		X	X	
Buchanan 1980		X	X				X						X		X							X	X	
MacCord 1976	X	X		X			X	X					X									X	X	
Johnson 1979				X				X					X		X							X	X	
MacCord 1973a		X	X				X	X			?	X	X		X	X		X	X	X	X	X	X	X
MacCord 1973b		X					X	X					X		X							X		
Piedmont																								
Waselkov 1977	X	X		X	X		X	X	X	X		X	X		X	X		X				X	X	X
Stevens 1979	X								X			X		X								X		
Egloff & others 1980	X	X		X	X		X	X	X		X	X				O	X		X			X		
Coastal Plain																								
Barber 1981	X			X	X		X	X	X			X	X	X	X	X				X	X	X	X	
Owen 1969	X	X		X			X	X	X			X	X		X		X					X		
Barber 1978	X	X		X			X	X	X						X							X		
Geier & Barber 1983	X	X					X	X				X			X							X		

of most kinds, even some that might be considered too small to eat.

THE EARLY HISTORICAL RECORD

The written accounts of early settlers in the New World would seem to be excellent sources of information about the contemporary fauna because they describe species actually seen by the observers. However, there are several shortcomings with this information.

(1) Although some of the early settlers were educated in England and some even knew the English biota fairly well, the 16th- and 17th-Century natural philosophers were trained more in Aristotelian principles than in the need for careful observation and description. In fact, "natural history" did not begin in England until the publication of White's *Natural History of Selbourne* in 1789. William Strachey's 1612 manuscript, published under the title *Historie of Travell in Virginia Britania*, is regarded as one of

the best historical sources of this period. Quotes from his (and other) writings will indicate the qualitative nature of the information in the early historical record:

"The Beaver there is as big as an ordinary water dog but his legs exceeding short, his forefeet like a dog's, his hinder like a swan's, his tail somewhat like the form of a racket, bare without hairs, which to eat the Savages esteem a great delicate."

(2) Much of what the early observers described was based upon comparison with mammals of their experience in England. Consequently, our white-tailed deer is described variously as being similar to red, roe, or fallow deer, our rabbits to their hares, and so on. Furthermore, some American mammals, such as opossum and raccoon, had no counterparts in England or Europe. These were often called by their Indian names and described as being similar to rats or monkeys, respectively. The descriptions sometimes were very crude, as seen in another Strachey quote:

"There is a beast they call Aroughcoune, much like a badger, tailed like a fox, and of a mingle black and grayish color, and which useth to live on trees as squirrels do, excellent meat, we kill often of them, the greatest number yet we obtain by trade." Strachey is describing a raccoon.

(3) The writer often relied on second-hand information or hearsay. This is seen in many accounts, such as those of Reverend John Clayton, educated at Oxford University and well known for his scientific investigations before coming to America for two years to serve as Rector to James City Parish from 1684-1686. "Elke, I have heard of them beyond the inhabitants . . .", indicating that elk were absent from the Coastal Plain (Berkeley and Berkeley, 1965). Second-hand accounts are not surprising from a rector, who would have had little reason to travel far and wide, but who would likely be in contact with many people who did travel. We have to rely on the good judgment of the rector to sift fact from fiction, and to record the best information possible. Accounts are most accurate and most believable when the observations are made by the writer.

(4) The early historical accounts are largely from the Coastal Plain, where the earliest settlements occurred. Journeys to the south and west brought back information about the wildlife there, but this information usually became secondhand for the writer of the accounts.

(5) None of the early historical accounts was written by a woodsman.

(6) For a variety of reasons, hyperbole or faulty

metaphors seem to be common features of many early historical accounts. Comments on the size, ferociousness, and numbers of mammals, especially large mammals, are often exaggerated.

"They have diverse beasts fit for provision, the chief are deer, both red and fallow, great store in the country towards the heads of the rivers, though not so many amongst the rivers; in our island about Jamestown are some few, nothing differing from ours in England but that of some of them the antlers of their horns are not so many, our people have seen 200, 100, and 50 in a herd," (Strachey, 1612). Clayton's statement that the "Rachooone, I take it to be a species of a monkie" (Berkeley and Berkeley, 1965) hardly instills confidence in the modern reader that Clayton was a trained scientist of his time. After two years in America, Clayton returned to England and spent the next 40 years of his life as a major and influential spokesman in establishing a picture of the New World in European minds.

With these seemingly casual, vague, and flimsy accounts as the norm, it is remarkable that some wildlife accounts did indicate that careful observations had been made. For example, several writers commented on flying squirrels, small nocturnal rodents that are difficult to observe. Clayton (Berkeley and Berkeley, 1965) reported seeing two kinds of bats, "one a large sort with long ears," and "the other much like the English something larger I think, very common." He must have observed the big-eared bats in the genus *Plecotus*.

The early historical accounts indicate that the mammals first observed by settlers in the 17th Century, and even a century later, did not differ substantially from the faunal lists based on evidence from late prehistoric archeological sites (Table 2). Compared to Table 1, there are some differences; for example, the woodrat, woodchuck, porcupine, and red fox were not reported in historical accounts. Today, the woodrat is restricted to the western part of Virginia and its absence in early historical accounts is not unexpected. However, the woodchuck was present at most archeological sites from the western half of Virginia, but is absent from the eastern sites and from the early historical accounts. The woodchuck would have been easy to observe because it is large, active during the day, prefers forest edges and clearings (even near buildings), and digs large and noticeable holes in the ground. I conclude that the woodchuck was not present in eastern Virginia during the time of the early settlements, but that it has moved eastward in

Table 2. Species of mammals recorded in early historical accounts in Virginia. "X" indicates presence and "?" refers to a specimen referable to one taxon but possibly a congener. For scientific names, refer to Table 3.

	Opossum	Cottontail	Chipmunk	Gray squirrel	Fox squirrel	Flying squirrel	Woodchuck	Beaver	Muskrat	Woodrat	Wolf	Dog	Gray fox	Red fox	Black bear	Raccoon	Mink	Skunk	Otter	Mountain lion	Bobcat	White-tailed deer	Elk	Bison
Clayton 1684 (Berkeley and Berkeley 1965)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hariot 1588			X	X							X	X							X	X	X	X		
Smith 1612 (Arber 1967)	X	X		X	X	X		X	X				X		X	X	X	X						X
Beverley 1705 (Dunbar 1964)																								X
Argall 1613 (Barbour 1972)																								X
Byrd 1728 (Boyd 1929)					X			X							X	X				X	X	X		X
Banister 1678 (Ewan and Ewan 1970)		X	X	X	X	X		X	X				X		X				X		X	X		
Strachey 1612	X	X		X	X			X	X		?	X	X		X	X	X	X	X	X	X	X		X
17th Century (Bruce 1927)	X	X						X			X	X			X	X			X	X		X		

association with the clearing of the land for agriculture. In fact, even today populations do not occur east of Williamsburg. The porcupine probably was common in western Virginia, and it is unclear why the presence of this easily seen and distinctive mammal was not recorded in an early account. The red fox, also missing from these historical accounts, is another species that requires clearings or openings, and its distribution too may have expanded rapidly with the spread of agriculture.

The presence of elk was reported only once in the early historical accounts, and this was the hearsay comment by Clayton. Either elk were not common in the Coastal Plain, or else they were considered to be one of the deer that are similar to "red, roe, or fallow deer." (It is possible that elk were mistakenly called red deer, and white-tailed deer were called fallow deer.) In the absence of careful description, we cannot be sure which explanation is more likely. Elk were present in most archeological sites in the western part

of Virginia, and also at Waselkov's (1977) site in Franklin county and Barber's (1981) site in Prince George County. The latter site is located in the Coastal Plain, but the elk remains were found in Barber's Zone 4, which was dated A.D. 245±90 yrs. Handley and Patton (1947) state that the last specimen of elk was killed in January 1855 by Colonel Joseph Tuley of Clarke County.

Bison were reported in some of the early historical accounts (Table 2). Handley and Patton (1947) contend that "when the settlers first came, the bison . . . was quite common throughout the State, at least down to the edge of the Coastal Plain." Dunbar (1964) believed that the 45 place names involving "buffalo" are helpful in finding the former distribution of the bison in Virginia; none was located well into the Coastal Plain. Barbour (1972) reported a June 1613 letter from Captain Samuel Argall that described seeing "a great store of cattle (bison)" grazing along the banks of the Rappahannock River "about 65 leagues" from the Chesapeake Bay. This location

was probably close to the Fall Line between the Piedmont and the Coastal Plain. According to Handley and Patton (1947), the last bison was killed in Virginia in the 1790's.

Other extirpations recorded by Handley and Patton (1947) include the fisher, *Martes pennanti* (probably in the 1890's), pine marten, *Martes americana* (probably in the 1830's or 1840's), porcupine (1899), timber wolf, *Canis lupus* (1912), mountain lion, *Felis concolor* (which were hunted in the 1880's), beaver (about 1910), and white-tailed deer in 44 western and central counties (about 1905). Some of these species, notably the white-tailed deer and beaver, have been reestablished and are doing well today throughout the Commonwealth under the protection of regulated hunting and trapping.

MODERN MAMMALS OF VIRGINIA

The current mammalian fauna of Virginia is similar to that which was present 400 years ago when the early European settlements were established, minus the extirpations mentioned above. There have been a few additions, including Old World murid rodents (Norway rat, *Rattus norvegicus*, and house mouse, *Mus musculus*), the hispid cotton rat, *Sigmodon hispidus*, which has moved northward and eastward during historical times and was first recorded in Virginia in 1940, and the South American nutria, *Myocastor coypus*, which has moved into the southeastern corner of Virginia after escaping from domestication in Louisiana during the 1930's. As discussed above, it is likely that the woodchuck, and especially the red fox, have expanded their distributions substantially since the onset of European settlement. Some other species have been introduced, such as the Sika deer (*Cervus nippon*) and horse (*Equus caballus*) on Assateague Island and the black-tailed jackrabbit (*Lepus californicus*) on Cobb Island, but these are considered to be localized exotics and not part of the local fauna. Table 3 lists the modern mammals of Virginia arranged according to their probable distribution within the Commonwealth.

In conclusion, the mammals of late prehistoric, early historical, and today's Virginia are similar. In fact, the mammalian fauna does not seem to have changed much during the past 4,000 years. This picture of constancy during this period is consistent with the findings of Delcourt and Delcourt (this volume) that neither the climate nor the vegetation of Virginia has changed substantially during the last 4,000-5,000 years. Each

Table 3. Virginia mammals and their likely distributions within the Commonwealth, taken from Hall (1981), *The Mammals of North America* and Hamilton and Whitaker (1979) *Mammals of Eastern North America*, using the nomenclature of Jones, Carter, and Genoways (1979).

Distribution is statewide for:

- Didelphis virginiana*, Virginia opossum
- Sorex longirostris*, southeastern shrew (absent in mtns?)
- Microsorex hoyi*, pygmy shrew
- Blarina brevicauda*, short-tailed shrew
- Cryptotis parva*, least shrew
- Scalopus aquaticus*, eastern mole
- Condylura cristata*, star-nosed mole
- Myotis lucifugus*, little brown bat
- Myotis keenii*, Keen's myotis
- Lasionycteris noctivagans*, silver-haired bat
- Pipistrellus subflavus*, eastern pipistrelle
- Eptesicus fuscus*, big brown bat
- Lasiurus borealis*, red bat
- Lasiurus cinereus*, hoary bat
- Nycticeius humeralis*, evening bat (east of mtns?)
- Plecotus rafinesquii*, Rafinesque's big-eared bat
- Sylvilagus floridanus*, eastern cottontail
- Tamias striatus*, eastern chipmunk (except southern Va.?)
- Marmota monax*, woodchuck (except Southeastern Va.)
- Sciurus carolinensis*, gray squirrel
- Tamiasciurus hudsonicus*, red squirrel (except Coastal Plain and southern Piedmont)
- Glaucomys volans*, southern flying squirrel
- Castor canadensis*, beaver (extirpated, reestablished)
- Reithrodontomys humulis*, eastern harvest mouse
- Peromyscus leucopus*, white-footed mouse
- Ochrotomys nuttalli*, golden mouse (except northern Va.)
- Microtus pennsylvanicus*, meadow vole
- Microtus pinetorum*, woodland vole
- Ondatra zibethicus*, muskrat
- Rattus norvegicus*, Norway rat (introduced from Europe)
- Mus musculus*, house mouse (introduced from Europe)
- Zapus hudsonius*, meadow jumping mouse
- Canis lupus*, gray wolf (extirpated)
- Vulpes vulpes*, red fox (except extreme SE Va.?)
- Urocyon cinereoargenteus*, gray fox
- Procyon lotor*, raccoon
- Mustela frenata*, long-tailed weasel
- Mustela vison*, mink

Mephitis mephitis, striped skunk (except extreme SE Va.?)

Lutra canadensis, river otter (now east of mtns.)

Felis concolor, mountain lion (probably extirpated)

Felis rufus, bobcat

Cervus elephas, wapiti (or elk) (extirpated)

Odocoileus virginianus, white-tailed deer

Bison bison, bison ("buffalo"), except SE Va. (extirpated)

Distribution in Appalachian highlands for:

Sorex cinereus, masked shrew

Sorex palustris, water shrew

Sorex fumeus, smoky shrew

Sorex dispar, long-tailed or rock shrew

Parascalops breweri, hairy-tailed mole

Myotis grisescens, gray myotis

Myotis velifer, cave myotis

Myotis sodalis, Indiana or social myotis

Plecotus townsendii, Townsend's big-eared bat

Sylvilagus transitionalis, New England cottontail

Lepus americanus, snowshoe hare (endangered)

Sciurus niger, fox squirrel

Glaucomys sabrinus, northern flying squirrel (endangered)

Peromyscus maniculatus, deer mouse (N. Va.)

Neotoma floridana, eastern woodrat (N. Va.)

Clethrionomys gapperi, southern red-backed vole

Microtus chrotorrhinus, rock vole (status undetermined)

Napaeozapus insignis, woodland jumping mouse

Erethizon dorsatum, porcupine (extirpated)

Canis latrans, coyote (extirpated, recent immigrant)

Martes americana, marten (extirpated)

Martes pennanti, fisher (extirpated, recent immigrant)

Mustela nivalis, least weasel

Spilogale putorius, eastern spotted skunk

Distribution in southern Piedmont and Coastal Plain for:

Blarina carolinensis, southern short-tailed shrew

Oryzomys palustris, marsh rice rat

Sigmodon hispidus, hispid cotton rat

Distribution in southeastern Virginia for:

Lasiurus seminolus, Seminole bat

Lasiurus intermedius, northern yellow bat

Sylvilagus palustris, march rabbit (Tidewater only)

Peromyscus gossypinus, cotton mouse (Tidewater only)

Myocaster coypus, nutria, introduced from South America, southern Va. only

Distribution in Appalachian highlands and southeastern Virginia only for:

Synaptomys cooperi, southern bog lemming

Ursus americanus, black bear

species present in the archeological record is readily assignable as a Virginia mammal known from the historical period, although that species might now be extinct in Virginia (e.g., the timber wolf). As more and more archeological sites are excavated, the former distribution and status of some species is certain to become better known. Although some species have been extirpated from Virginia since European settlement began and others have expanded their distributions within Virginia in response to changing land-use patterns, the mammalian fauna appears to have remained remarkably static during the past four millennia.

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ON THE STATUS OF QUATERNARY VERTEBRATE PALEONTOLOGY AND ZOOARCHEOLOGY IN VIRGINIA

Jerry N. McDonald¹

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ABSTRACT

The first vertebrate fossils found in North America by Europeans were recovered in Virginia; scientific archeology in North America was initiated in Virginia, and Thomas Jefferson—possibly the most influential patron of vertebrate paleontology during its formative years—was a native son. However, a strong, enduring tradition in the study of Quaternary vertebrates did not develop in Virginia. Amateur and professional

collecting and study of prehistoric Quaternary vertebrates, though, has been increasing since the middle of the 20th Century and is currently being conducted on an unprecedented level. Extensive collecting has been carried out in the western part of Virginia. Descriptions of some of the collections have been published, along with a few more extensive analyses of selected local faunas. The Carnegie Museum of Natural History and the Smithsonian Institution have been most responsible for this increased activity. Some institutions in Virginia are becoming increasingly active, but broad-based institutional support within the State for the developing professional and lay

¹P.O. Box 4098, Newark, Ohio 43055

interest in Quaternary vertebrates is needed to heighten awareness and appreciation of these resources.

INTRODUCTION

A growth of interest in the study of prehistoric Quaternary vertebrates of Virginia has occurred since the middle of the 20th Century, and has included significant work in both vertebrate paleontology and zooarcheology. The collecting of faunal materials from various depositional contexts has dominated this work within the State during the last three decades. These collections have indicated clearly and convincingly that substantial quantities of prehistoric Quaternary vertebrate remains are to be found within Virginia. Comparatively few of the faunas that have been collected since 1950 have been described in the literature, and very few have been the subject of detailed paleoecological, zoogeographical, or evolutionary analyses (Eshelman and Grady, this volume).

This paper assesses the status of the study of prehistoric Quaternary vertebrates of Virginia. *Representative* activity in both vertebrate paleontology and zooarcheology, as determined from a search of the literature of the last eight years, examinations of collections, and personal interviews, is the foundation for this assessment. The assessment is restricted to work on vertebrate faunas of the *prehistoric* period. It is *not* intended to be an exhaustive treatment of the history of vertebrate paleontology or zooarcheology within Virginia (see Eshelman and Grady, this volume, and Rose, this volume, for more detailed historical surveys). Rather, this represents an effort to describe current patterns and conditions of work on the Quaternary vertebrates of Virginia.

The body of this paper is divided into four sections. The characteristics of the present interest in Quaternary vertebrates are better understood if seen in historical context, so a brief review of the place of studies of prehistoric Quaternary vertebrates in Virginia is presented. Current activity patterns in vertebrate paleontology and zooarcheology are then treated separately because these fields have had different histories, even though work within each may converge to provide complementary insights into faunal patterns and dynamics. Modern activity is influenced by the amount and type of institutional support provided paleontologists and zooarcheologists, so a review of the major facets of institutional support and regulation within the State that affects

the study of Quaternary vertebrates is provided. Several recommendations are made that might improve the conditions for the appreciation and study of Quaternary vertebrates in Virginia.

HISTORICAL CONTEXT

Several important discoveries of vertebrate fossils were made in Virginia during the colonial period. The earliest fossil vertebrate remains recovered by Europeans from Anglo-America were reported in 1636 by Samuel Maverick as having been found about 60 miles upstream of the mouth of the James River, in Virginia. These were reportedly whale bones, probably of Miocene age (Simpson, 1942, 1943; Eshelman and Grady, this volume). During his fourteen years in Virginia (1678-1692), John Banister collected several vertebrate fossils from marine deposits in the Tidewater region of the colony, and he obtained "some" teeth from the interior of Virginia "found in the Hills beyond the Falls of the James River at least a Hundred and fifty Miles up into the Country" (Ewan and Ewan, 1970). The latter were probably delivered to Banister at or near "The Falls" (modern Richmond) by Indians from the western Piedmont or Appalachian Mountains, although the specimens could have been acquired by the Wood or Batts expeditions to the Valley and Ridge in 1654 and 1671, respectively. There is no good reason to believe, however, that these teeth were of the ground sloth *Megalonyx jeffersonii* as was suggested by Goode (1901), since the remains of numerous other large vertebrates also have been found in western Virginia (Ray and others, 1967; Eshelman and Grady, this volume). By the 1740's, the occurrence of vertebrate fossils in Virginia was sufficiently well-known to allow Catesby to write that in "all parts of Virginia, at the Distance of Sixty Miles, or more (from the sea)... are frequently found the *Vertebras*, and other Bones of Sea Animals." (Catesby, 1743, vol. 2, Appendix p. vii, quoted in Simpson, 1942, p. 134). At about this same time, in 1739, Charles Le Moyne, the second Baron de Longueuil, collected some proboscidean remains near the south side of the Ohio River above modern Louisville, Kentucky. Whether Longueuil or subsequent French and British collectors of fossils in this area recovered the first fossils from Big Bone Lick is equivocal, but within three decades of Longueuil's visit, Big Bone Lick—then a part of Virginia—had emerged as the most important and well-known source of Quaternary vertebrate remains in eastern North America (Simpson, 1942, 1943). Arthur Campbell sent Thomas Jefferson a

mastodon tooth from the Saltville Valley in 1782, thereby identifying that locality, located in what is today southwest Virginia, as a source of Quaternary vertebrate fossils (Boyd, 1952; Jefferson, 1787).

If the lengthy record of vertebrate fossil discoveries in Virginia was inadequate to establish a tradition of curiosity about and study of these objects, the presence, genius, and energy of native son Thomas Jefferson might have effected a focused interest in natural history in Virginia such as was occurring in some of the more northerly British colonies late in the 18th and early in the 19th centuries. Lacking the educational and fiscal resources typical of some European countries, the American colonies/states late in the 18th Century could not compete effectively with the Europeans in many academic fields. In natural history, however, American scientists could make original contributions and gain international respect in doing so, and at the same time dispel notions—such as some of those of Buffon, which particularly irritated Jefferson—that American biota was inferior to or otherwise less spectacular than that of Europe (Jefferson, 1787; Oleson, 1976). Jefferson made many contributions to the development of vertebrate paleontology in America: he published the first scientific paper describing (inaccurately) a fossil vertebrate from and in America (Jefferson, 1799), he proffered critical response to Buffon's notions about American vertebrates (including humans) (Jefferson, 1787), and he used the influence of his high offices to support the collection, dissemination, and study of vertebrate fossils from America—including the collecting of some of the first fossils by Americans from what is now the western United States (Osborn, 1929; Simpson, 1942; Bedini, 1985). Jefferson is also considered the person first responsible for conducting a systematic, problem-oriented archeological excavation and the first to publish results of such an excavation (Jefferson, 1787; Brose, 1973; Stoltzman, 1973). Jefferson supported the development of learned societies concerned with advancing natural philosophy, exploration in search of new forms of natural objects and areas, and progressive state-supported educational systems and curriculum development wherein, ultimately, most basic training in the natural sciences in the United States came to be offered (Simpson, 1942; Bedini, 1985).

Despite the role of Virginia in the early development of natural sciences in colonial and early national America, however, strong widespread interest in this field failed to materialize within the Colony and State. The social and economic organ-

ization of Virginia was not conducive to the development of a social environment in which the study of natural science could become well established. The population of Virginia was dispersed. Towns were few and usually provided only essential administrative and economic services. In the absence of populous, economically complex urban centers with critical masses of interested persons, broad-based interest in the natural sciences did not develop (Ewan, 1976). Virginians with an interest in vertebrate paleontology either had to culture this interest on their own or join learned societies that had become established elsewhere, such as at Charleston, South Carolina, or the principal port cities from Philadelphia to Boston (Ewan, 1976). Since these societies were organized to function by the direct participation of members rather than by publication of transmitted information, relatively few Virginians were able to be functional members. Jefferson, perhaps the most visible exception, was able to participate more fully in learned societies, especially those of Philadelphia, since his duties as Secretary of State, Vice President, and President of the United States (1789-1809), and president of the American Philosophical Society (1797-1814), kept him in or near that city much of the period 1789-1814 (Kiger, 1963; Greene, 1976; Bedini, 1985).

After Jefferson's return to Virginia in 1809, he devoted much time and energy to the establishment of a comprehensive public education system in Virginia (Patton, 1906; Bedini, 1985). As a result of his (and others') efforts, the University of Virginia was established by the Virginia Legislature in 1819 and began instruction in 1825. The general public education system, however, was not established until 1870. In the meantime, various other private and institutional programs developed to provide elementary and more advanced education to the general populace of Virginia. For the most part, however, these were apprenticeships, military schools, or church-sponsored academies or colleges that were concerned either with providing practical vocational training or academic training in subjects other than the natural sciences (Heatwole, 1916; Bell, 1930; Buck, 1952). Natural philosophy and related subjects were represented for extended periods only at the University of Virginia and the College of William and Mary. The creation of the Virginia Geological Survey in 1835, with William Barton Rogers as its first director and its location at Charlottesville, *was* a progressive act that assured that geological investigation would be carried out (Roberts, 1942). The Survey was concerned primarily with describing and mapping the geol-

ogy of the state and in determining its economic resources, and vertebrate paleontology did not become an important area of investigation. The establishment of the Virginia Agricultural and Mechanical School (modern VPI&SU)—the largest educational institution to be developed during the second half of the 19th Century in Virginia—was made possible by the federally funded land-grant college program and was intended primarily for practical training in agricultural and mechanical skills (Buck, 1952; Dabney, 1971). Instruction in vertebrate paleontology and archeology, therefore, traditionally has not been a part of general education curricula in Virginia.

The practice of vertebrate paleontology in North America shifted near mid-19th Century from learned societies to the newly created Smithsonian Institution (1846) in Washington, D. C. and several universities and other institutions in the northeastern states (Greene, 1976; Voss, 1976). At this time, the exploration of western territories was focusing the attention of vertebrate paleontologists on the west (Lanham, 1973). Virginia—along with most of the eastern United States—received relatively little attention from vertebrate paleontologists during the late 19th Century (Eshelman and Grady, this volume).

More attention has been paid to Virginia's fossil localities during the 20th Century, especially by the Carnegie Museum of Natural History (Pittsburgh, Pa.), as part of its systematic investigation of the Quaternary vertebrate paleontology of the middle and southern Appalachians (e.g., Peterson, 1917; Guilday, 1962; Guilday and others, 1977). The Smithsonian Institution has also shown heightened interest in Virginia's Quaternary vertebrates during the 20th Century (Ray and others, 1967; Ray and others, 1968). The activity of both institutions increased during the 1960's and in doing so called attention to the fact that there are many productive paleontological sites of Quaternary age in Virginia worthy of professional scientific attention. As a result, scientists in Virginia have become increasingly active in recent years in collecting and describing Quaternary vertebrate remains.

Archeology was developing as a distinct discipline during the 19th Century also, but in this field, too, Virginia was the scene of much less activity than some nearby states. Virginia sites received only peripheral attention during the era of Mound Builder investigations and, later, during the southeastern river basin surveys (Carr, 1877; Fowke, 1894; Brose, 1973; Stoltman, 1973). Professionally directed archeological investigations took place in Virginia during the Depression under federally

funded programs but on a smaller scale than in some other eastern states and with emphasis on the historical archeology of Jamestown. One outgrowth of the increased visibility of professionally conducted archeology in Virginia during the Depression was the creation of the Archeological Society of Virginia in 1940. Two years later, in 1942, this Society commenced publication of the *Quarterly Bulletin*, which, after a tenuous start, has been the principal journal dealing with archeology in Virginia. The *Quarterly Bulletin* was joined in 1963 by *The Chesopiean*, publication of the Chesopiean Archaeological Association.

Since the 1960's, archeology in Virginia has become increasingly professionalized. Several colleges and universities now offer undergraduate training in archeology, although opportunities for graduate training in prehistoric archeology remain limited. The Council of Virginia Archaeologists was organized in 1975 to further the aims of professional archeology in the State. Another important development was the creation of the Virginia Historic Landmarks Commission (VHLC) in 1966. This Commission was responsible for surveying, registering, and encouraging the protection of Virginia's archeological sites and, through the Virginia Commissioner of Archaeology, was charged with enforcing the provisions of the subsequently passed Virginia Antiquities Act (1977), the principal body of legislation dealing with the prehistoric human record in Virginia. The VHLC became the Virginia Division of Historic Landmarks (VDHL) in 1985; the Director of the Division is now charged with enforcing the provisions of the Virginia Antiquities Act and the more recent (1979) Cave Protection Act.

QUATERNARY VERTEBRATE PALEONTOLOGY IN VIRGINIA

Recent work on Quaternary vertebrates in Virginia has been characterized by the recovery of specimens on an unprecedented scale. The Carnegie Museum of Natural History is clearly the leader in this activity, having collected at numerous locations throughout western Virginia. Several thousand specimens from in and near the Saltville Valley of southwest Virginia have been collected by and for the Smithsonian Institution, while other smaller collections have been made by workers from other institutions. Several local faunas have been described. Excavations are underway at at least three sites within the State. Overall, professional work with Quaternary vertebrates is increasing, a communication and field support network

is developing, and public awareness and interest is growing. Note is made, however, that many workers are located at out-of-state institutions, that there is no functional repository within the State where specimens are being curated and studied, and that there is no worker employed by a Virginia institution whose professional responsibilities lie primarily with the collection, curation, or study of Quaternary vertebrates. Also, there is remarkably little information available to the public to inform them about the animal life of the Quaternary or to satisfy or stimulate their curiosity about this subject area. John Guilday, the central figure in the Quaternary vertebrate paleontology of the Appalachians, died in November 1982, and with him passed much of the momentum, experience, and knowledge for continued work in this region.

The Carnegie Museum of Natural History has a lengthy tradition of interest in the study of Quaternary vertebrates of the middle and southern Appalachian Mountains. One of the most ambitious and far-sighted programs for the study of Appalachian Quaternary vertebrates is the systematic sampling of local faunas throughout the region by employees and friends of the Carnegie Museum. This program was initiated by John Guilday in the 1950's. Field surveying and collecting was carried out by Carnegie staff members—most notably Harold Hamilton with the assistance of his associates, especially Robert E. Whitemore (Johnson City, Tn.) and Lois Miller (Pittsburgh, Pa.). This program has resulted in the sampling of hundreds of local faunas, almost exclusively from karst and karst-like features, from Georgia and Alabama to Pennsylvania and Ohio. Forty-eight local faunas from Virginia have been collected by the Carnegie Museum, mostly under this program of systematic sampling, and therefore mostly from the western counties (Table 1, Figure 1). This program is continuing, and additional sites in Virginia have been identified for sampling (H. Hamilton, personal communication).

The Carnegie sampling program has produced what is unquestionably the most important collection of late Quaternary faunas from eastern North America with which can be addressed important systematic, ecological and zoogeographical questions (see, e.g., Guilday, 1962; Guilday and others, 1977; Fay, 1984a, 1984b, this volume; Holman, this volume). Spatial variations in faunal composition for any given period will allow inferences about latitudinal gradients in species distribution and community composition and structure throughout the middle and southern Appalachians. Similar variations in intraspecific morphology allows in-

ferences about chorocline variation in character expression. Temporal changes in the composition or intraspecific morphology of stratified faunas permit inferences about faunal turnover and chronocline variation. The correlation of patterns of composition and morphology among several stratified sites could permit unusual opportunities to document and interpret faunal changes on a regional scale during the environmentally dynamic late Quaternary. Major problems facing the analysis of these local faunas are the lack of manpower to study them in a timely fashion, and the lack of precise temporal and compositional control so typical of faunas from karst features which limits the extent to which relatively precise time/space ecological and zoogeographic patterns can be documented.

The Saltville Valley, located in Smyth and Washington counties, is a large subaerial site containing a number of different fossil-bearing depositional units. This locality has been known as a source of remains of late Quaternary mammals for more than 200 years (McDonald, 1984a). The first record of a fossil from this area is contained in a letter from Arthur Campbell to Thomas Jefferson, dated November, 1782 (Boyd, 1952), probably a response to Jefferson's appeal for information about the natural curiosities of Virginia. Olaf Peterson of the Carnegie Museum obtained a small collection of fossils at Saltville in 1917. The first scientifically motivated excavation took place in 1966-67 as a joint venture between Virginia Polytechnic Institute and the Smithsonian Institution with the paleontological aspect of this work being directed by Clayton E. Ray (Smithsonian Institution). Salvage excavations in 1978 and 1980 by Charles Bartlett, Jr., led to the involvement of this author in excavations at Saltville in the fall of 1980. In recognition of the Saltville locality's potential to yield abundant information on diverse aspects of the late Quaternary history of the middle Appalachian region, the Saltville Project was initiated in 1982. This project is a multidisciplinary investigation of the Quaternary history of the locality that currently involves sixteen specialists from eight institutions in three countries.

The Saltville locality, defined as the Saltville Valley and its environs within a radius of about 6 miles, contains a large variety of depositional environments, including those of caves, fissures, sinkholes, springs (one with an associated tufa deposit), streams, a lake-marsh-bog system, and colluvium. Several different features, representing the karst, tufa, colluvium, lotic, and lentic deposits, are known to be fossiliferous. The most productive

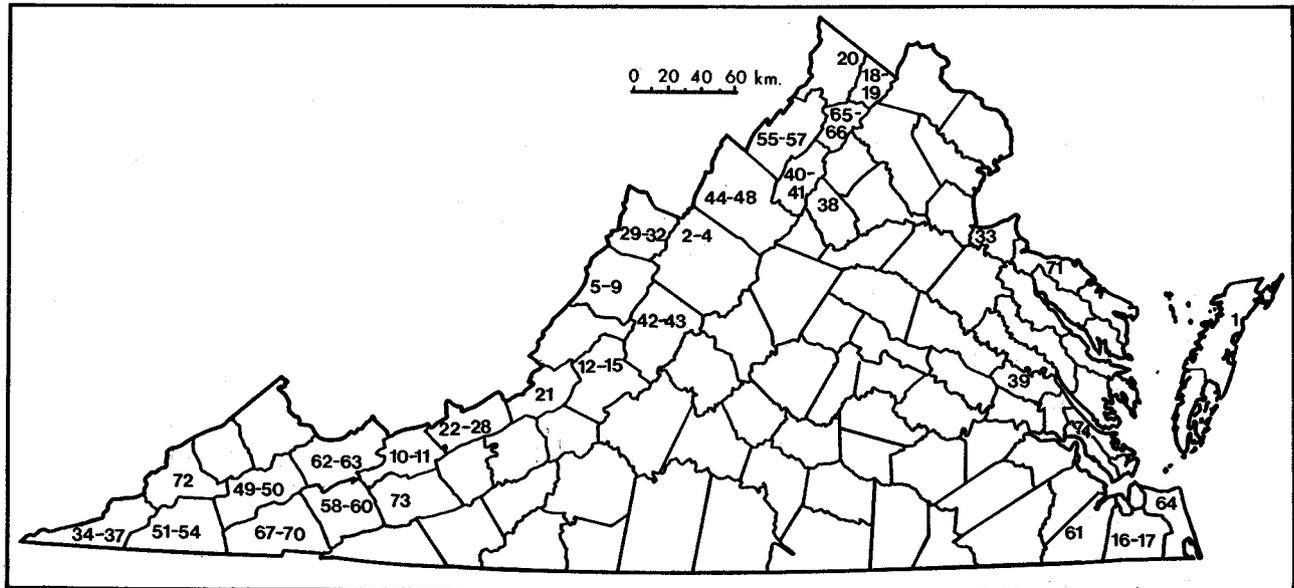


Figure 1. Unpublished Quaternary vertebrate faunas in Virginia. The county locations of faunas listed in Table 1 are identified here by number.

deposits discovered to date are the fluvial sediments associated with the extinct Saltville River (ca. 27,000-13,500 yrs B.P.) and the lacustrine deposits associated with extinct Lake Totten (ca. 13,500-140 yrs B. P.). These well-stratified deposits occur over much of the bottom of Saltville Valley. The groundwater that occurs in the valley bottom is saline, and that condition, along with the fact that the Lake Totten deposits are massive clays characterized by low permeability, has resulted in an extremely good environment of preservation for the entombed fossils. The variety of depositional environments at this locality provides opportunity to recover information collected by various depositional processes, each with a different sampling bias. This variety of sampling, in turn, should permit a more complete and balanced assessment of the late Quaternary history of the region than would be possible with data from only a single site or type of depositional environment. The lentic and lotic sediments found in the valley bottom appear to represent relatively continuous deposition for approximately the last 15,000 years, and more intermittent deposition over the preceding 12,000 years. These sediments, therefore, potentially offer a continuous biotic record for the last 15,000 years and a periodic one for the last 27,000 years. Subaerial stratified sites containing proven fossil resources are rare in the Appalachians, as are sites that span as much time as do the Saltville Valley deposits. The Saltville Valley

is significant, therefore, as a proven source of vertebrate fossils and contemporaneous biophysical information spanning much of the environmentally dynamic late Wisconsin-Holocene transition (see, e.g., McDonald and Bartlett, 1983; McDonald, 1984a, 1984c, 1985, in press; Barfield, this volume; Delcourt and Delcourt, this volume; White, this volume; Holman and McDonald, in press).

Other sites in Virginia producing Quaternary vertebrate fossils and currently being studied include the Hot Run site in Frederick County and an unnamed site in Warren County. The Hot Run Site, being worked by James Ott (University of Maryland), appears to be a shallow subaerial deposit that includes remains of several extinct taxa of large mammals, along with those of domesticated forms (Ott and Weems, this volume). Samuel Bird (Virginia Division of Energy) and Walter Wheeler (University of North Carolina) have recently collected and are now studying remains of small mammals, birds, and fishes from a cave deposit in Warren County (S. O. Bird, pers. comm.).

Information has been published on faunas from at least six Virginia sites during the last eight years. Weems and Higgins (1977) described a fauna containing at least 33 vertebrate species found in a fissure near Ripplemead in Giles County. Gary Haynes (1978) reported thirteen genera/species, mostly mammalian, recovered from a small fissure in Warren County. Most of the remains came from

Table 1. Unpublished Quaternary vertebrate faunas from Virginia¹

<i>Locality</i>	<i>County/City</i>	<i>Estimated Age</i>	<i>Repository²</i>
1. Metompkin Island	Accomack Co.	Pleistocene	USNM
2. Glade Cave	Augusta Co.	?Holocene	USNM
3. Natural Chimneys	Augusta Co.	Late Pleistocene	UT
4. Unnamed Locality	Augusta Co.	(not stated)	ANSP
5. Back Creek Cave #1	Bath Co.	(not stated)	CMNH
6. Back Creek Cave #2	Bath Co.	(not stated)	CMNH
7. Back Creek Cave #3	Bath Co.	Holocene	CMNH
8. Clark's Cave	Bath Co.	Late Pleistocene	UT
9. Rope Burn Cave	Bath Co.	(not stated)	CMNH
10. Bane's Cave	Bland Co.	Late Holocene	CMNH
11. Paul Penley's Cave	Bland Co.	(not stated)	CMNH
12. Arcadia #1	Botetourt Co.	Pleistocene/Holocene	CMNH
13. Arcadia #2	Botetourt Co.	Pleistocene/Holocene	CMNH
14. Arcadia Little Cave	Botetourt Co.	?Holocene	CMNH
15. Springwood Bluff	Botetourt Co.	(not stated)	CMNH
16. Deep Creek	Chesapeake (City)	Pleistocene	USNM
17. Unnamed Locality	Chesapeake (City)	Late Pleistocene	USNM
18. Calmes Neck Cave	Clarke Co.	Holocene	CMNH
19. Unnamed Cave	Clarke Co.	(not stated)	USNM
20. Hot Run	Frederick Co.	Quaternary	UM
21. Shires Saltpeter Cave	Craig Co.	Late Pleistocene/ Holocene	CMNH
22. Cliff Cave #2	Giles Co.	Late Pleistocene/ Holocene	CMNH
23. Eggleston Cliff Cave	Giles Co.	Holocene	CMNH
24. Eggleston Fissure	Giles Co.	Late Pleistocene	CMNH
25. Klotz Quarry Cave	Giles Co.	Late Pleistocene/ Holocene	CMNH
26. Pembroke Railroad Cave #1	Giles Co.	Pleistocene	CMNH
27. Pembroke Railroad Cave #2	Giles Co.	?Pleistocene/Holocene	CMNH
28. Ripplemead Quarry	Giles Co.	Late Pleistocene	CMNH
29. Rass Hole (= Corbertt's Cave)	Highland Co.	Late Pleistocene/ Holocene	CMNH
30. Saltpeter (Arbegast) #5	Highland Co.	Holocene	CMNH

Table 1. (cont.)

<i>Locality</i>	<i>County/City</i>	<i>Estimated Age</i>	<i>Repository²</i>
31. Strait Canyon	Highland Co.	Pleistocene	CMNH/ USNM
32. Varner's Cave	Highland Co.	Holocene	CMNH/ USNM
33. Belvedere Beach	King George Co.	Late Pleistocene/ Holocene	NJSM
34. Carter Cave	Lee Co.	(not stated)	CMNH
35. Jasper Saltpeter Cave	Lee Co.	Late Pleistocene/ Holocene	CMNH
36. Skylight Cave	Lee Co.	Holocene	CMNH
37. Wallen Creek Cave	Lee Co.	Holocene	CMNH
38. Spurey	Madison Co.	Modern	USNM
39. Lanexa	New Kent Co.	Pleistocene	CMNH
40. Comers Cave	Page Co.	?Modern	CMNH
41. Ruffner's #2	Page Co.	Holocene	USNM
42. Collierstown Fissure	Rockbridge Co.	Holocene	CMNH
43. Fishbone Cave West	Rockbridge Co.	(not stated)	CMNH
44. Bill Neff Cave	Rockingham Co.	Quaternary	USNM
45. Cedar Hill Cave	Rockingham Co.	Quaternary	USNM
46. Monger Cave	Rockingham Co.	Holocene	CMNH
47. Round Hill Cave	Rockingham Co.	Pleistocene	CMNH
48. Wheelbargers Cave	Rockingham Co.	Holocene	CMNH
49. Loop Creek Quarry Cave	Russell Co.	Late Pleistocene/ Early Holocene	CMNH
50. River Bend Cave	Russell Co.	?Holocene	CMNH
51. Darty Cave	Scott Co.	Early Holocene	CMNH
52. Roadcut Cave	Scott Co.	Pleistocene/ Holocene	CMNH
53. Taylor Cave	Scott Co.	(not stated)	CMNH
54. Winding Stairs Cave	Scott Co.	?Late Pleistocene	CMNH
55. Edinburg Fissure	Shenandoah Co.	Quaternary	USNM
56. Shenandoah Cavern	Shenandoah Co.	Holocene	USNM
57. Toms Brook	Shenandoah Co.	Holocene	USNM
58. New Quarry Cave	Smyth Co.	Quaternary	USNM
59. Saltville	Smyth Co.	Quaternary	CMNH/ USNM
60. Unnamed Cave	Smyth Co.	Quaternary	USNM
61. Eclipse Beach	Suffolk (City)	?Pleistocene	USNM
62. Crab Orchard Cave	Tazewell Co.	Modern	VRCA
63. Gillespie's Cliff Cave	Tazewell Co.	(not stated)	CMNH

Table 1. (cont.)

<i>Locality</i>	<i>County/City</i>	<i>Estimated Age</i>	<i>Repository²</i>
64. Virginia Beach	Virginia Beach (City)	Pleistocene	USNM
65. Skyline Caverns	Warren Co.	Late Pleistocene	USNM
66. Unnamed Cave	Warren Co.	Quaternary	VDMR
67. Holston Vista Cave	Washington Co.	Late Pleistocene/Holocene	CMNH
68. Meadowview Cave	Washington Co.	Pleistocene/Holocene	CMNH
69. Vicker's Cave	Washington Co.	(not stated)	CMNH
70. Will Fraley's Cave	Washington Co.	Late Pleistocene	CMNH
71. Stratford Hall	Westmoreland Co.	?Pleistocene	USNM
72. Parson's Cave	Wise Co.	Holocene	CMNH
73. Gardner's Cave	Wythe Co.	(not stated)	CMNH
74. Unnamed Subaerial Site	Yorktown (City)/York Co.	Late Pleistocene	CWM

¹ Most of these faunas are not described in the literature. Some, such as Clark's Cave (Guilday and others, 1977; Fay, 1984a), Natural Chimneys (Guilday, 1962; Fay, 1984a), Ripplemead Quarry (Weems and Higgins, 1977), Saltville (Peterson, 1917; Ray and others, 1967; McDonald and Bartlett, 1983; Holman and McDonald, in press) and Strait Canyon (Fay, 1984b) have been published in part, but substantial quantities of undescribed specimens are known for all but Clark's Cave and Natural Chimneys.

² The repositories of unpublished collections are listed in this column, as follows: ANSP = Academy of Natural Sciences of Philadelphia; CMNH = Carnegie Museum of Natural History; CWM = College of William and Mary; NJSM = New Jersey State Museum; UM = University of Maryland (James Ott collection); UT = McClung Muesum, University of Tennessee; USNM = United States National Museum of Natural History; VDMR = Virginia Division of Mineral Resources; VRCA = Virginia Research Center for Archaeology.

the upper 2-3 inches of the excavated sediments. All identified genera and species are extant. The presence of porcupine (*Erethizon* sp.) and red fox (*Vulpes* sp.) within the fauna is noteworthy for zoogeographic reasons, because these taxa might not have been present in Virginia at the time of European contact (Pagels, 1979; Rose, this volume).

McDonald and Bartlett (1983) described and figured the partial associated skeleton of an extinct muskox (cf. *Symbos* sp.) from Saltville, and Holman and McDonald (in press) have described a herpetofauna containing ten taxa from the same locality. The latter paper, which described samples collected from radiometrically dated stratigraphic units, concluded that the modern herpetofauna of the Saltville area has probably been in place for at least 13,500-15,000 years. Fay (1984a, b; this volume) and Holman (this volume) have analyzed several late Wisconsin-Holocene herpetofaunas from the middle and southern Appalachians, including those from Strait Canyon, Natural Chim-

neys, Clark's Cave, and Saltville in Virginia. Their findings are that herptiles, unlike plants and higher vertebrates, appear to have been relatively unaffected by the environmental dynamics that characterized the region during the late Wisconsin-Holocene. Although unpublished, much work on the Strait Canyon fauna had been completed by John Guilday at the time of his death. Hopefully, someone will soon finish and publish his work on this important fauna.

ZOOARCHEOLOGY IN VIRGINIA

Zooarcheology is a recently-developed subdiscipline of archeology which is still undergoing rapid transformation and increased specialization, particularly as it relates to regional and cultural-level research design, data analysis and theory building in archeology (Hesse and Wapnish, 1985). Robison (1978) reviewed the development of zooarcheology

in North America, tracing the development of the subdiscipline from an initial concern with merely identifying some or all species (especially mammals and easily recognized birds and reptiles) recovered from a site, through increased quantification of the identified remains and application of these data to specific ecological questions (such as butchering techniques and seasonal hunting patterns), to a modern orientation that integrates zooarcheological data into the holistic analysis of local and regional cultures and their dynamics (such as analyses of intersite functions, or class/ethnic composition of the population). For all its potential and dynamics, however, zooarcheology is based upon the recovery and study of faunal remains from archeological contexts. Faunal remains must be regarded *before excavation* as integral parts of the archeological record, recognized as artifacts during survey and excavation activities, excavated with the same full provenance data as other artifacts, properly stored, and made accessible to researchers, if there is to be zooarcheological analyses or insights at any level of complexity or sophistication. There presently exists substantial variation in the way that faunal remains from

archeological sites in Virginia are perceived and handled. Professional archeologists and many amateur archeologists routinely excavate faunal remains as parts of the complete site record, whereas at the other extreme some excavators save few if any faunal remains.

Most published reports on prehistoric archeology done in Virginia by professional or amateur archeologists appear in the *Quarterly Bulletin* of the Archeological Society of Virginia. Most of the site reports published in this journal during the last seven years have included mention of faunal remains. Many sites, especially open air sites older than middle Woodland age (1,500 yr B.P.), rarely yield faunal remains; most such materials, if ever they were present at a site, have decomposed in Virginia's humid mesothermic environment. For cave, rockshelter, and middle or late Woodland sites, however, faunal remains often are not collected by excavators or they are not described in site reports, possibly because they are not considered important, they have not been identified, or they are assigned lower priority than other artifacts. Site reports that include mention of faunal remains (Figure 2) typically include a short list

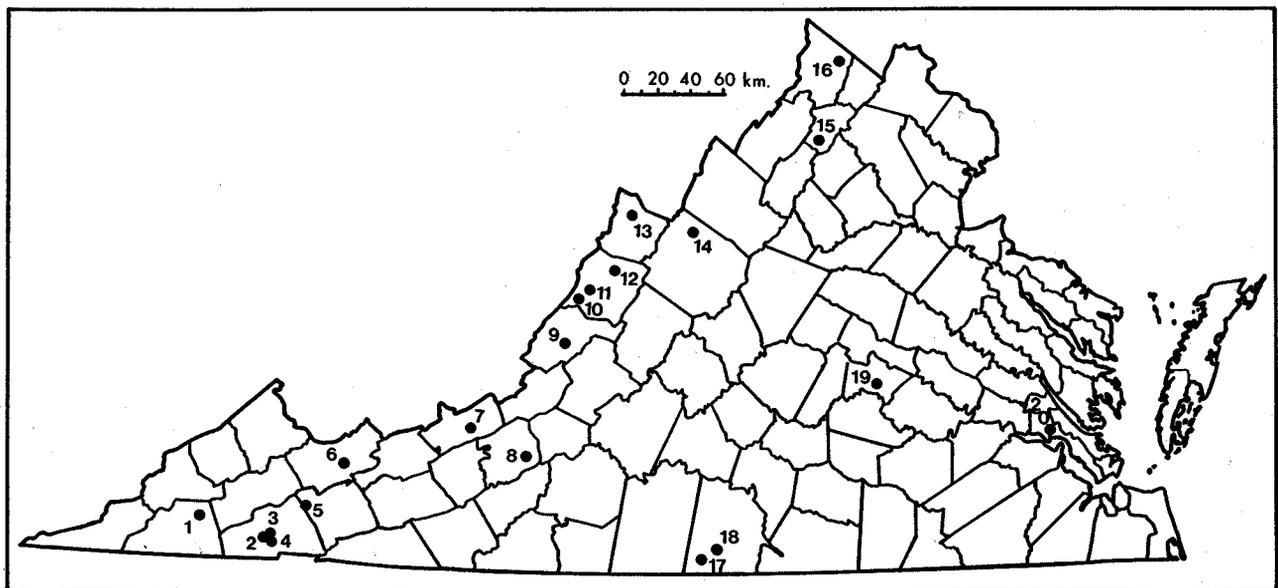


Figure 2. Recently published paleontological and zooarcheological localities in Virginia. The localities are: 1 - Flanary (44Sc13); 2 - White (44Wg37); 3 - Arrington (44Wg27); 4 - Sullins (44Wg12); 5 - Saltville; 6 - Crab Orchard (44Tz1); 7 - Ripplemead Fissure; 8 - Hall (44My33); 9 - Hercules (44Ay40); 10 - Gathright Dam area; 11 - Hidden Valley area; 12 - Clark's Cave; 13 - Strait Canyon; 14 - Natural Chimneys; 15 - Unnamed cave (44Wr61); 16 - Hot Run; 17 - Wade (44Ha34); 18 - Reedy Creek (44Ha22); 19 - Hertzler (44Po3); 20 - College Creek (44Jc27).

of species—usually under “subsistence”—and identification of tools or other artifacts made from faunal elements. Most faunal lists are biased toward mammals (Table 2) and toward species with easily identifiable characters at that. Among recent publications, only in Barber’s analysis of the College Creek Site (44Jc27), which was intended as a methodological paper, and in Coleman’s description of the Reedy Creek Site (44Ha22), do mammals constitute less than one half the listed taxa (Barber, 1978a, Coleman, 1982). Faunal remains were quantified in about one third of the surveyed reports containing faunal data (Table 2). Only one surveyed report (Egloff and Reed, 1980) dealt with the functional analysis of faunal remains. Stratigraphic context was not provided for most reported faunal remains, due in great part—but not exclusively—to the fact that specimens from most sites were collected on or near the surface, usually from the plow zone. Buchanan’s faunal data for the Hall Site (44My33) contains the most detailed stratigraphic data among the sites listed in Table 2 (Buchanan, 1980). The major reason that more zooarcheological work is not reported upon probably is because of the fact that few amateur or professional archeologists working on Virginia’s prehistory are sufficiently well trained in zooarcheology to identify and analyze faunal remains.

Michael Barber (Thomas Jefferson National Forest and Radford University), the only zooarcheologist in Virginia that works regularly with prehistoric faunal collections, has addressed several methodological problems before the Virginia archeological community. In a 1978 paper he presented rationale and procedures for developing a comparative collection, pointing out that the first step in faunal analysis was the accurate identification of the specimens recovered, and that a type collection of “core species” was a necessity for identifying animal remains (Barber, 1978b). In another 1978 paper, Barber attempted to demonstrate temporal differences in resource exploitation by comparing the faunal assemblages from three different excavation units of middle to late Woodland, late Woodland, and historic ages (Barber, 1978a). Later, working with three historic site assemblages, Barber challenged the notion that small sample size could not provide meaningful insight into the ecological dynamics of sites. His conclusion that small faunal assemblages could provide useful information about cultural lifeways, such as yielding a list of the minimum number of species used by the site occupants and revealing subtle details of their culture, was also a declaration

that *any* zooarcheological data, if accurately recorded and reported, might be useful (Barber, 1981).

A small number of analytical and theoretical studies dealing with the aboriginal use of vertebrates in Virginia have been published recently. E. Randolph Turner (Virginia Research Center for Archaeology) described the ecological function of an intertribal buffer zone situated astride the Fall Line during the early part of the 17th Century. He presented evidence suggesting that this contested zone probably served as an important source of game (especially deer), and further theorized that overexploitation of the deer population in the Tidewater region had possibly occurred as early as the middle of the late Archaic Period (Turner, 1978). Holland (University of Virginia) drew upon ethnohistoric sources to document and analyze the protohistoric fire hunt, from which analysis—using distribution patterns of pottery from archeological sites—he postulated the existence of other prehistoric buffer zones in Virginia (Holland, 1979). McDonald (1984b) studied 97 partial mandibles of whitetail deer (*Odocoileus virginianus*) from the 17th Century (ca. A.D. 1600-1635) Trigg Site (44My3) (Buchanan, 1984), from which were obtained data on the sex and age of the harvested population, the presence of dental abnormalities, and patterns of seasonal hunting. The Trigg Site deer population was relatively old, females outnumbered males, and the deer were hunted throughout the year. The implications of this pattern are that the deer population was relatively large, and hunters could be relatively selective with a high probability of hunting success at any season. Henry Miller (St. Marys City, Md.) studied faunal assemblages from fifteen early historic sites along the lower James and Potomac rivers in Virginia and Maryland in order to test hypotheses predicting how human subsistence patterns change in frontier settings (Miller, 1984). He found that diet patterns changed significantly during the 17th Century from a seasonally changing, generalist reliance upon diverse wild and domestic animals to a more specialized, simplified pattern. Although Miller’s study does not deal strictly with prehistoric zooarcheology, it documents the presence of certain species in Virginia at or soon after European contact; it develops a model useful to the study of subsistence change among aboriginal populations entering a frontier or a new “exploitation zone”; and it represents a modern, sophisticated approach to the study of faunal remains from archeological sites wherein model building, theory testing, and

Table 2. Vertebrate remains from prehistoric archeological sites reported in the *ASV Quarterly Bulletin*, 1978-1984

Site Name and Number	Source	Subsistence ¹				Tools ²	Other ³	Age ⁴
		M	B	R/A	F			
1. Hercules 44Ay40	Johnson, 1979	6	1	1/0	0	X	number of bones	1W
2. Hidden Valley Rockshelter 44Ba31	Geier, 1981	3	0	0/0	0	X	----	1W
3. Gathright Dam-Lake Moomaw-Hidden Valley area, Bath Co.	Geier, 1983	7	1	1/0	0	-	----	1W
4. Reedy Creek 44Ha22	Coleman, 1982	8	2	4/2	4	X	number of bones by level and taxon	1W
5. Wade Site 44Ha34	Stevens, 1979	5	1	1/0	2	X	(Red Fox)	Indet. (mA-1W)
6. College Creek 44Jc27	Barber, 1978a	8	1	5/0	4	-	Species abundance, MNI; element, side age and sex of deer remains	mW-H
7. Hall Site 44My33	Buchanan, 1980	7	1	3/0	1	X	relatively good stratigraphic record; wet screened	1W
8. Hertzler Site 44Pa3	MacCord and Livesay, 1982	5	0	1/0	0	X	----	1W
9. Flanary Site 44Sc13	MacCord, 1979	2	1	1/0	0	X	----	1W
10. Crab Orchard Site 44Tzl	Egloff and Reed, 1980	5	1	1/0	0	X	limited analysis of butchering	1W
11. Sullins Site 44Wg12	MacCord, 1981	7	1	1/0	0	X	number of elements and percent of total; number of specimens by species and feature	1W
12. Arrington Site 44Wg27	Bartlett, 1980	3	1	2/0	0	X	----	e-mW
13. White Site 44Wg37	Bartlett, 1979	1	0	0/0	0	X	----	mA-1W

¹ M = Mammals; B = Birds; R/A = Reptiles/Amphibians; F = Fish. The number in each column indicates the number of taxa reported for each class/group considered by the authors of the report to have been used as a food resource by the aboriginal population.

² An X in this column indicates that tools (or other artifacts) made from faunal elements were identified as such in the report.

³ Noteworthy aspects of the collecting, analysis, or reporting procedure, or the content of the fauna.

⁴ Age of the site: A = Archaic; W = Woodland; H = Historic; e = Early; m = Middle; l = Late.

the characteristics and dynamics of regional cultures are addressed.

INSTITUTIONAL SUPPORT OF STUDIES

Ownership of prehistoric faunal remains in Virginia lies with the landowner—private citizens or corporations, or local, state, or federal governments. The intent of both the state and federal governments is to protect their faunal resources in order to assure maximum public benefit from the removal (if necessary) and study of these materials. In order to collect or excavate specimens from federal land, permits must be obtained from the federal agency with local jurisdiction. Archeological collecting and excavating on state lands, and any collecting or excavating in caves (except *by* the owner), must be permitted by the Virginia Division of Historic Landmarks. In addition, the state agency with local jurisdiction may require a separate permit, and permission of the landowner is also required for removing materials from caves owned by local governments or private citizens. The federal and state governments retain ownership of materials excavated under federal or state permit. Ownership of materials originating on private, county, or municipal land lies with the landowner but may be transferred at the discretion of the landowner. Since most land in Virginia is owned by local governments or privately, there is little legal control by the state or federal governments over the exploitation or destruction of subaerial archeological or paleontological sites. As a result, much information of scientific value is lost regularly, especially to construction activities, unscientific collecting procedures, and commercial trafficking in specimens, because of inadequate concern for or awareness of the significance of these resources on the part of the landowners or collectors.

Responsibility for the professional level collecting and study of faunal remains in Anglo-America has traditionally rested with scholars affiliated with colleges and universities or museums of natural history. Unfortunately, there is no vertebrate paleontologist or zooarcheologist position on the faculty of any Virginia institution of higher education, nor is any regularly listed course offered in either of these areas at the college or university level. There are a few faculty members that do research in the vertebrate paleontology of Virginia, but this is not their principal academic area of responsibility. No full-time faculty member is known to be conducting research on zooarcheology. Academic training in vertebrate paleontology and

zooarcheology for students in Virginia institutions is limited, and takes the form of seminars, field courses, special topics courses, and independent study.

A similar deficiency in institutional interest in prehistoric Quaternary vertebrates exists among museums in Virginia. Virginia has many museums (Virginia Association of Museums, 1984) but, until 1985, the State was without a museum of natural history. The three largest public museums of science in the State are young institutions: The Peninsular Science and Nature Center (1966) in Hampton, the Science Museum of Virginia (1969) in Richmond, and the Roanoke Valley Science Museum (1970) in Roanoke. None of these science museums offers topical exhibits in Quaternary vertebrate paleontology or zooarcheology, nor does any collect, store, or support research in these areas. In fact, these museums normally do not accept donations of fossils or zooarcheological specimens; typically such offerings will be referred to or passed on to another museum—such as the Smithsonian Institution—or, if accepted, are placed “in the attic.” There is no good prospect for this condition to change in the near future, given the fiscal constraints and administrative orientation of each museum. Yet, it must be realized that the regional and national museums, such as the Carnegie and National museums of natural history, cannot continue to accept specimens and collections that are better suited to state-level museums (see, e.g., Adams, 1985).

The most promise for institutionally supported progress in the study of prehistoric faunal remains in Virginia lies with the new Virginia Museum of Natural History. This venture, directed by Noel Boaz and located in the City of Martinsville, opened to the public on June 2, 1985. The conceptual strengths of this institution lie in its being directed by an active research scientist and its orientation toward scientific collecting and research from its inception. This museum offers Virginia its first museum of natural history and a complete museum in that it will promote collecting, research and public education in the natural sciences.

The Virginia Research Center for Archaeology (VRCA) was created as a unit of the Virginia Historic Landmarks Commission in 1966, but did not become functional until 1976 (Outlaw, 1982). The VHLC, in conjunction with VRCA, administered the provisions of the Virginia Antiquities Act and, later, the Virginia Cave Protection Act (Code of Virginia, Title 10, chapters 12.1 and 12.2, respectively), the principal bodies of state legislation dealing with the archeological and paleobiological

resources of Virginia. The VDHL, through VRCA, now enforces the provisions of these acts. The VRCA holds what is probably the largest publicly-owned comparative collection of faunal specimens for use by zooarcheologists in the State, but even so it is of limited value in many respects, being strongest on small mammals but weak on other groups and its collections are generally inadequate for documentation of individual variation, age differences, and sexual dimorphism. VRCA has been faced with substantial fiscal reductions since 1981 and, among other adjustments, recently has had to limit the development and use of this collection. The Department of Anthropology, College of William and Mary, also has an inactive comparative collection of faunal specimens. The study of zooarcheological material in Virginia, therefore, requires the worker to have a personal collection, to rely upon collections of institutions outside Virginia, or to rely upon published identification guides or personal knowledge of osteological or dental characters.

SUMMARY

Many significant discoveries of prehistoric Quaternary vertebrate remains were made in Virginia during the colonial and early national periods. A strong interest in the natural sciences did not develop in Virginia, however, and as a result, little attention was paid to the prehistoric vertebrate record of the state during the 19th and first half of the 20th centuries. The study of prehistoric Quaternary vertebrates from Virginia by paleobiologists and zooarcheologists began to intensify around the middle of the 20th Century. Paleobiologists at the Carnegie Museum of Natural History and the National Museum of Natural History were most responsible for this increased activity, although archeologists with the College of William and Mary, the University of Virginia, and the Archeological Society of Virginia also made contributions to the development of foundations for subsequent zooarcheological studies within the State. More recently, support for the study of prehistoric Quaternary vertebrates has come from additional educational institutions and government agencies located within and near Virginia. Most work since 1950 has consisted of collecting specimens from a large number of localities, particularly in western Virginia. Some of these collections have been described, with considerable variation in rigor, but most are unstudied. Many more of these collections need to be described in order to make, in the least, basic descriptive in-

formation available for more detailed or generalized studies. Proportionately few analytical, methodological, or theoretical papers, based upon studies of prehistoric local faunas of Virginia, have been published—but these types of studies are increasing and are to be encouraged. The collection of additional materials is continuing, and—increasingly—information on the associated paleoenvironments is also being collected.

Expanded institutional support appears to be necessary if substantial progress is to be realized in the study, appreciation, and protection of Virginia's prehistoric Quaternary vertebrate resources.

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**EMBRYOGENESIS DYSFUNCTION IN THE PLEISTOCENE/HOLOCENE TRANSITION
MAMMALIAN EXTINCTIONS, DWARFING, AND SKELETAL ABNORMALITY**

Dewey M. McLean¹

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¹Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

ABSTRACT

The Pleistocene/Holocene transition, a time of cold, glacial conditions followed by rapid global warming at the end of the last ice age, was a time of fascinating paradoxes. During maximum advance of the Weichselian (European) and Wisconsinan (North America) ice sheets 20,000-18,000 yr B. P., mammalian faunas facing the extreme cold and restricted living space and food reserves seemingly adapted and survived. Then, during the late Wisconsinan period of climatic warming and increasing food supply in the form of expanding grasslands, mammalian faunas experienced one of the most profound extinction events in earth history, the Pleistocene/Holocene transition extinctions, in which many taxa suddenly became extinct and/or dwarfed. Integration of environmental temperatures with modern reproductive physiology identifies a linkage between high ambient air temperatures and reproductive dysfunction and predicts extinctions and dwarfing during periods of rapid warming, including that at the end of the last ice age.

Modern mammals experience reproductive dysfunction in high ambient temperatures, in environmental temperatures that they supposedly have been adapted to for the past several thousand years. High environmental temperatures cause hyperthermia (elevation of core temperature) in female mammals. Hyperthermia, in turn, reduces the flow of blood to the female uterus. Uterine blood flow is a developing embryo's source of water, oxygen, and nutrients and also serves to dissipate heat from the uterus. Reduced uterine blood flow is associated with increased embryo death, dwarfing, and skeletal abnormality. Pleistocene/Holocene transition mammals facing rapidly shifting climatic extremes from maximum cooling during the last ice age to rapid warming could only have experienced reproductive dysfunction in the form of reduced uterine blood flow and consequential damage to developing embryos. Embryogenesis dysfunction was almost certainly commonplace during climatic warming in the Pleistocene/Holocene transition.

INTRODUCTION

The Pleistocene/Holocene transition was a time of fascinating paradoxes. About 20,000-18,000 yr B. P. terrestrial mammalian faunas experienced some of the coldest conditions of the last ice age during maximum advances of the European Weichselian and the American Wisconsinan ice sheets.

Most large herbivores and their carnivore predators survived those extreme conditions of cold and restricted living space and food, etc. Then, at the end of the ice age during the period of most rapid warming, retreat northward of the ice sheets and boreal forests, and increasing food source in the form of rapidly expanding grasslands, occurred one of the most profound extinction events in earth history, the Pleistocene/Holocene mammalian extinctions. At a time when ranges of semitropical species should logically have been expanding, ranges, in fact, were contracting (Martin, 1984). At a time when environmentally rigorous conditions should logically have been relaxing for high latitude mammalian faunas, those mammals experienced the most severe extinctions. Concurrent with the extinctions were widescale dwarfing and skeletal abnormalities. In this paper, I will address these paradoxes via integrating the Pleistocene/Holocene transition climatic warming with mammalian reproductive physiology, expanding upon the linkage between elevated ambient air temperature and reproductive dysfunction that I proposed earlier (McLean, 1981). I account for the paradoxical nature of the extinctions, dwarfing, and skeletal deformation via heat-induced reduction of blood flow to the female uterus and consequent damage to the embryo during various stages of pregnancy. A conclusion that will emerge in this work is that because of the sensitivity of embryos to thermally-induced reduced uterine blood flow, mammals cannot readily adapt to rapid climatic warming. Times of rapid rise in ambient air temperatures are almost inescapably times of embryogenesis dysfunction and, if severe enough, extinction.

PLEISTOCENE/HOLOCENE TRANSITION
CLIMATIC WARMING

About 20,000-18,000 yr B. P., earth was locked in cold, ice age conditions (Figure 1). In Europe, the Weichselian ice sheet reached its maximum extent about 20,000 yr B. P. In North America, the equivalent Wisconsinan ice sheet also reached its maximum extent about 20,000 yr B. P. Extreme cold conditions lasted from about 20,000-18,000 yr B. P. Following the most intense glacial conditions, earth began to warm up gradually until about 14,000 yr B. P. when a more rapid warming began. Based on studies of Coleoptera in northwestern Europe, Coope (1975) suggests large-scale warming between 13,000 to 11,000 yr B. P.; warming during early stages may have been at the rate of 1°C per decade (Figure 2). Deglacial warming in Europe

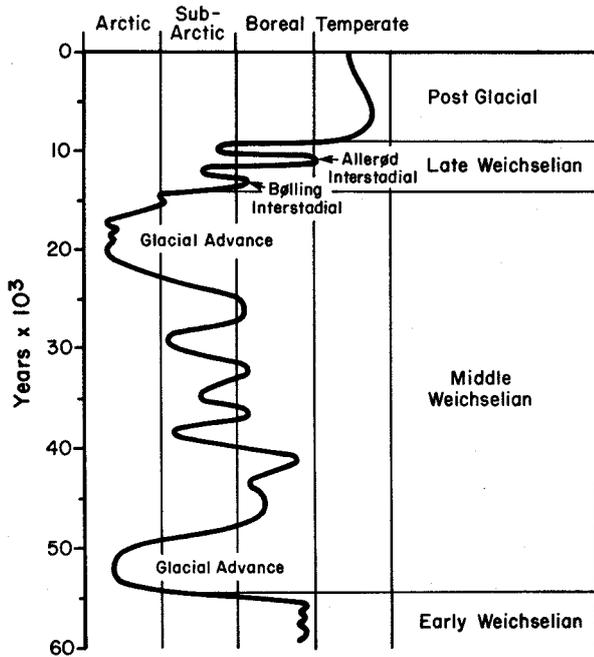


Figure 1. Weichselian climate changes in north-western Europe (adapted from Coope and Sands, 1966).

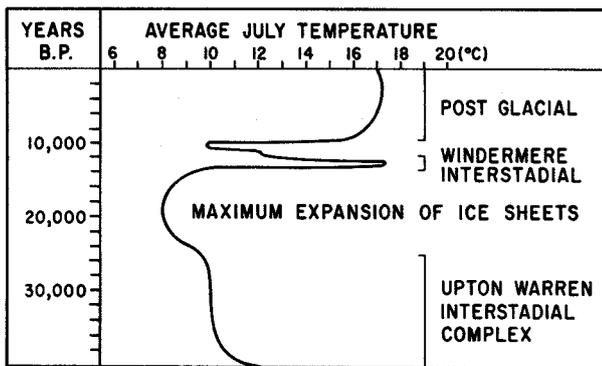


Figure 2. Fluctuations in the average July temperature in lowland Britain as indicated by beetle fauna (after Coope, 1977a, b).

and in the Atlantic Ocean seems to have occurred in two stages. For the high-latitude North Atlantic, Ruddiman and McIntyre (1981) report warming at 13,000-11,000 yr B. P., cooling from 11,000-10,000 yr B. P., and then warming again from 10,000-8,000 yr B. P. Mix and Ruddiman (Kerr,

1983) indicate the same climate change chronology for the equatorial Atlantic, for the North Atlantic and the European continent. Duplessy and others (1981) indicate 6°C warming after 13,000 yr B. P., with a return to cold conditions 11,000-10,000 yr. B. P., and then warming up for good; study at the Bay of Biscay south of the English Channel indicates that one-third of the ice melted between 16,000 and 13,000 yr B. P. For Europe, Wright (1977) indicated the first signs of warming about 13,000 yr B. P.

For North America, the warming was somewhat different; the two stages of warming seen in the Atlantic and European records are not evident in eastern North America (Tom Webb, personal communication) nor in the continental interior. However, the rate of warming was also rapid. Wright (1977) notes that spruce forests that had dominated the Middle West disappeared during an interval from about 12,000 yr B. P. in the modern prairie region to about 10,000 yr B. P. in the region of modern northern coniferous forests. The transition at any locality was abrupt, occurring over just a few hundred years. Webb and Bryson (1972) note that the most profound climatic change in the Wisconsin-Minnesota region was during the Pleistocene/Holocene within a few centuries of 11,300 yr B. P.; at that time the temperature rose about 3.3°C, and the length of the summer season increased by one month.

In the southern United States, the cold, dry Wisconsin climate ended about 14,600 yr B. P. (Watts and Stuiver, 1980). In South Carolina, the boreal coniferous forest was replaced by mesic at about 12,800 yr B. P. Georgia was the southern limit for the Late Wisconsin spruce forest. In the Texas region, Vaughn Bryant (personal communication) suggests a change from boreal to less boreal forests about 15,000-10,000 yr B. P., with no dramatic change at any one locality. In Missouri and Tennessee, pollen of deciduous trees began to appear in spruce-dominated areas about 16,000 yr B. P.; the spruce forests continued their retreat northward, and between 13,500-12,000 yr B. P., the spruce disappeared from Missouri, central Illinois, and Tennessee (King and Saunders, 1984). King and Saunders (1984) note that between 12,000 and 10,000 years ago, the ice retreated north of the Great Lakes. Following the retreating ice, the early pioneering plant communities of spruce woodland and tundra were replaced by a brief episode of pine and then deciduous species. The shift in spruce to pine dominance forms a prominent time-transgressive marker horizon throughout eastern North America (Ogden, 1967).

PLEISTOCENE/HOLOCENE TRANSITION
"GREENHOUSE" CONDITIONS

Cause of the global warming at the end of the last ice age has long been the subject of intense interest. It is now known that the warming at the end of the last ice age was concurrent with a rapid buildup of CO_2 in the atmosphere that did not stop until it reached pre-industrial levels about 10,000 yr B.P. (Figure 3). During the last glaciation, atmospheric CO_2 varied between two levels: (1) 180-200 parts per million (ppm) in very cold conditions and (2) 250-270 ppm in relatively warm periods. Pre-industrial levels were around 260-280 ppm (the pre-1850 level was about 266 ppm; the modern atmosphere contains about 340 ppm). Study of the Dome Ice Core from Antarctica (Figure 4, after Delmas and others, 1980) records low CO_2 values between 22,000-15,000 yr B. P., during the coldest part of the last ice age; the CO_2 values of 0.016 percent were about one-half that of the modern value of 0.033 percent. Neftel and others (1982) indicate that CO_2 -induced greenhouse warming might be involved in control of the ice ages, noting that the increased atmospheric CO_2 contributes significantly to the global warming at the transition from the last glaciation to the Holocene.

The mechanism by which CO_2 is released into the atmosphere is not known; however, an interesting sequence of events seems involved. The suggestion by Imbrie and Imbrie (1980) that variations in the earth's orbit are the fundamental cause of

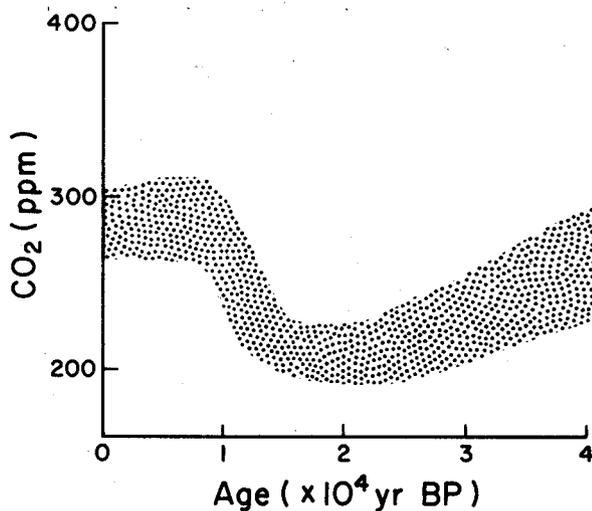


Figure 3. Variations of atmospheric CO_2 over the past 40,000 years (after Neftel and others, 1982).

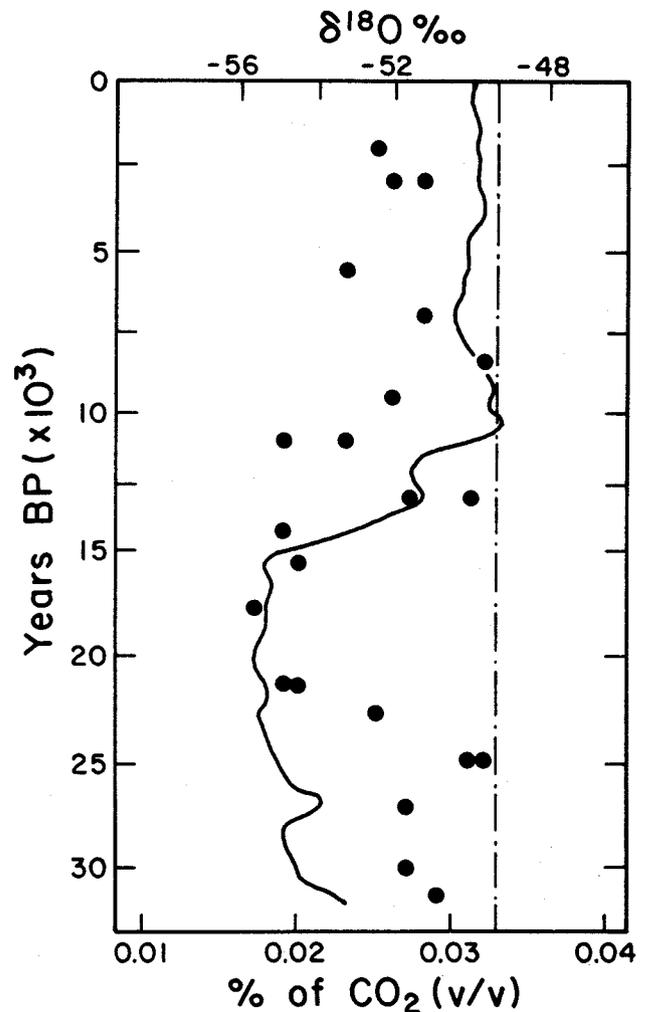


Figure 4. Analysis of percent of CO_2 in air bubbles in the Dome C ice core (Antarctica), plotted against oxygen-18 isotopic values. The dashed line represents modern atmospheric CO_2 content (0.033 percent) (after Delmas and others, 1980).

the succession of Pleistocene ice ages now seems confirmed. Atmospheric CO_2 seems to boost effects of orbital variations. Shackleton and Pisias (1985) indicate that atmospheric CO_2 concentration leads ice volume over the orbital bandwidth, and is forced by orbital changes by a mechanism presently not understood, with a short response time. They further note that variations in atmospheric CO_2 should be seen as part of the forcing of ice volume changes. The order of events suggests that orbital variations

are the primary cause of climate change and that CO₂ exerts intermediate influence.

PLEISTOCENE/HOLOCENE TRANSITION WARMING-EXTINCTION CONNECTION

During maximum advance of the Weichselian and Wisconsinan ice sheets, mammals would have had to adapt to extreme conditions of cold, restricted living space, and diminished food reserves, etc. That most large mammals survived attests to their ability to adapt to cold conditions. Most large-bodied herbivores in North America about 25,000-20,000 yr B. P. and their predators survived the late Wisconsin maximum (McDonald, 1984).

Starting about 18,000 yr B. P. came a relaxation of severe ice age conditions. In North America the ice sheets that had advanced from Canada into the northern United States began retreating northward. Boreal forests that, during coldest conditions, had migrated as far southward as Georgia in the east to Texas in the west began their rapid retreat northward to their modern ranges. Concurrently, grasslands developed in the North American continental interior east of the Rocky Mountains and expanded their area of coverage eastward and northward. Yet, during that time of ameliorating climatic conditions and expanding living space and food reserves, in what would seem to be an emerging "golden age" for mammals, many taxa became extinct, and dwarfing and skeletal abnormalities were widespread. McDonald (1984) notes that the limiting intensity of most selecting forces was relaxed after 18,000 yr. B. P., and that the associated environmental changes should not have produced the cluster of extinctions which occurred.

In fact, nearly two-thirds of North America's genera of large mammals, along with larger-bodied avian and reptilian genera, became extinct during the late Wisconsin and early Holocene. The late Wisconsinan megafauna includes about 49 genera, of which 33 genera (67 percent) became extinct during the Pleistocene/Holocene transition (McDonald, 1984).

That the steepest gradient of Pleistocene/Holocene transition global warming was coupled temporally to global mammalian extinctions, dwarfing, and skeletal abnormality is well documented (Table). Graham and Lundelius (1984) indicate that the critical period of environmental change for most continents seems to have been 10,000 to 12,000 yr B. P. For northeastern North America, Marshall (1984) notes that between 12,000 to 10,000 yr B. P., the ice sheet retreated north of the Great Lakes, pine and deciduous species replaced the spruce woodland, and that *Mammot americanum* became extinct. Between 11,500 to 10,500 yr B. P., the American southwest experienced megafaunal extinctions, and the greatest vegetational-climatic change since the Sangamon interglacial. For the Appalachian region, the terrestrial mid-Appalachian mammalian fauna "crashed" about 10,000 to 12,000 yr B. P. (Guilday, 1984). Central and South America and Africa also experienced large mammal extinctions at about the same time as in the Holarctic about 11,000 yr B. P. (Guthrie, 1984). In terms of geographical bias, the extinctions were more severe in North America than in Europe, Africa, and Asia (Martin, 1984). I will address this phenomenon in the section titled "Geographical Bias In The Pleistocene/Holocene Extinctions: An Explanation."

Table. Calibration of Pleistocene/Holocene transition climate warming on different continents relative to times of extinctions and dwarfing (modified from Marshall, 1984).

LAND AREA	CLIMATE CHANGE (yrs B. P.)	EXTINCTION (yrs B. P.)	DWARFING (yrs B. P.)
Africa	12,000-8,000	12,000-8,000	12,000
Australia	26,000-15,000 16,000-12,000	26,000-20,000 (some 18,000-15,000)	26,000-15,000
Europe	14,000-10,000	12,000-10,000	15,000-12,000
North America	12,000-10,000 12,000-11,000 11,500-10,500	12,000-10,000 11,500-10,500	12,000-10,000 12,000-11,000 11,000-10,000
South America	10,000	12,000-8,000	(known but not well documented)

To summarize to this point, linkage between rapid Pleistocene/Holocene transition climatic warming and extinctions, dwarfing, and skeletal abnormalities is firmly established.

NEW LIGHT ON OLD PARADOXES

Modern ecological and evolutionary theory predict that climatic warming following the maximum glacial advance should have resulted in an increase in megafaunal biomass and diversity; if competitive exclusion at any trophic level was going to produce the extinction of any taxon, it should have done so during the maximum glacial advance 20,000 to 18,000 yr B. P. period when selection was most intense and limiting (McDonald, 1984). The fact that most mammals survived the cold and suffered extinctions during the warming at the end of the last ice age indicates that we need new ways of examining the Pleistocene/Holocene transition extinctions. I attempt to do so by integrating changes in ambient air temperature with reproductive dysfunction via heat-induced damage to developing embryos.

The Pleistocene/Holocene transition extinctions affected mammals large and small, birds, and reptiles. However, several researchers indicate that large mammals were affected most severely of all. Merilees (1984) notes that some process bore more heavily on larger than on smaller mammals. Martin (1984) indicates that large terrestrial mammals were most affected with the extinct genera equaling or exceeding 44 kg (100 lbs), and that the sudden loss of large mammals must mean that large size was a handicap. McDonald (1984) notes that whatever the cause of the extinctions in North America, the phenomenon was continent wide, was selective principally against large mammals, and likely resulted from some ultimate, ubiquitous causal factor that quickly rendered much of the continent's megafauna "unfit."

Two elements are common to the extinctions: global warming and the extreme sensitivity of developing embryos to above-normal heat. High ambient temperature can, by elevating the uterine areas of female mammals, damage developing embryos. Reproductive dysfunction among modern mammals during hot periods, to which they are supposedly adapted, is commonplace (discussion is included in following sections). The rapid global warming at the end of the last ice age would have rendered many taxa "unfit."

Rapid rise in ambient air temperature during the Pleistocene/Holocene transition would have imposed especial hardship on large mammals. Be-

cause large mammals have relatively small surface/volume ratios they would have retained relatively greater body heat than would small mammals during the rapid climatic warming. Small body size, or the ability to reduce body size during the interval of rapid warming by allowing the more ready dissipation of body heat, would have been most advantageous. That the warming was rapid is indicated by King and Saunders (1984) who state that the warming terminating the Pleistocene was faster than any other temperature change since the beginning at the last interglacial stage. Haynes (1984) notes that one of the most abrupt climatic changes came at the end of the Pleistocene about 11,000 yr B. P. Knowledge of modern heat-induced reproductive dysfunction predicts that extinctions, dwarfing, and skeletal abnormalities would have been inescapable during rapid global warming and expansion of grasslands at the end of the last ice age, and especially among the larger mammalian species.

ELEMENTS OF THERMOREGULATION

In ambient temperatures where nearly constant core temperatures can be maintained, mammals are homeothermic; however, the core temperature can vary with changes in ambient air temperature (Figure 5). Within the "Zone of Homeothermy," and at an optimum environmental temperature that is variable depending upon the species and its acclimatization, body heat production is at a minimum in the "Zone of Thermal Neutrality." In the "Zone of Thermal Neutrality" a nearly constant core temperature is maintained with minimal effort

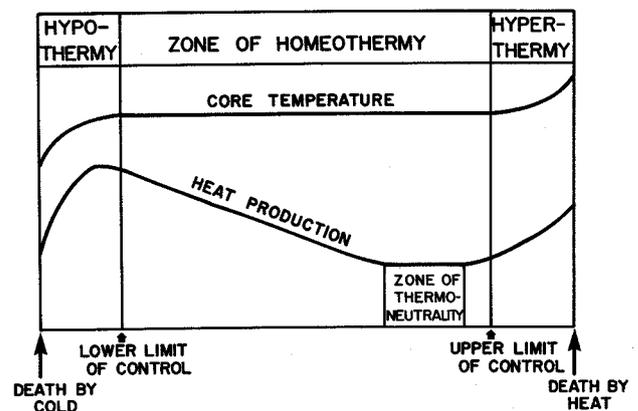


Figure 5. Heat production and core temperature of homeotherms relative to environmental temperatures (modified from Bianca, 1968).

from an animal's thermoregulatory mechanisms. McDowell (1968) notes that the desirable thermal environment for most livestock is between 13 and 18°C.

Mammals produce body heat. In addition, they absorb heat from the sun. Bianca (1968) indicates that cattle may absorb three times as much heat from the sun as they produce by their metabolism. In ruminants, the microorganisms contained in the rumen constitute an extra source of heat, contributing up to 10 percent of an animal's basal heat production.

Studies of domestic mammals show that they undergo diurnal rhythms of body temperature reaching minimum and maximum values in early morning and late afternoon, respectively (Bianca, 1968). Under natural conditions, heat stress occurs in a rhythmic cycle with maxima lasting for a few hours each day. The larger the mammal, the greater the amount of heat stored. Heat stress under natural conditions occurs in a rhythmic 24-hour pattern with maxima lasting only a few hours around mid-day. To avoid thermoregulatory problems generated by retention of excessive body heat, mammals must lose body heat by radiation and convection during the relatively cool night hours. Mammals lose heat from the body to the environment through sensible heat loss (radiation, convection, and conduction), and by behavioral tactics such as seeking appropriate environments, wallowing, sweating, and panting, etc.

In ambient air temperatures rising above those in which an animal's heat production stays within the "Zone of Thermal Neutrality," a thermal steady state cannot be maintained and body temperature will rise continuously, indicating true hyperthermia. An animal will then activate defense reactions against overheating (vasodilatation, sweating, or panting). Ambient air temperatures which cause core temperatures to rise in most domestic mammals are about 28 to 33°C but may be as low as 21 to 24°C in some breeds of lactating cattle (Bianca, 1968). McDowell (1968) indicates that temperatures between 21 and 28°C cause discomfort for an animal, triggering changes in behavior, decreased food intake, and less efficient performance.

Hyperthermia occurs at relatively low environmental temperatures when air humidity and solar radiation are high. With additional heat load, sweating or panting increase; however, cooling derived via these means cannot maintain homeothermy and body temperature begins to rise. At the "Upper Limit of Control" heat defense mechanisms can no longer maintain homeothermy, and

the core temperature rises (the animal becomes hyperthermic). Bianca (1968) indicates the rise in body temperature in turn brings about an increase in the metabolic rate because of the van't Hoff effect which can cause death by heat. The van't Hoff effect, with respect to mammalian heat production, represents the two-to three-fold increase in heat production brought about by a 10°C increase in tissue temperature; i.e., the temperature coefficient, Q_{10} , of mammalian tissues is of the order of 2 to 3. The upper lethal temperature is only a few degrees above normal body temperature; in most species it is 42 to 45°C or only about 3 to 6°C above normal body temperature. However, as will be discussed in the following sections, environmental temperatures far below those required to kill outright via thermoregulatory failure can have great impact upon mammalian bioevolution.

THE HYPERTHERMIA-REDUCED UTERINE BLOOD FLOW CONNECTION

That high environmental temperatures can cause the core temperatures of mammals to increase is well documented (discussed below). Elevated core temperatures in female mammals can, in turn, trigger reproductive dysfunction. Such dysfunction is common every summer in temperatures to which modern mammals are supposedly adapted.

The mechanism by which high ambient temperatures induce reproductive dysfunction is becoming clear. High ambient air temperatures, by inducing hyperthermia in female mammals, reduces the flow of blood to the uterus. Uterine blood flow (UBF) is a developing embryo's source of water, oxygen, nutrients, and hormones (Senger and others, 1967; Bazer and others, 1969; Barron, 1970). In addition, UBF helps to dissipate uterine metabolic heat (Abrams and others, 1971; Gwazdauskas and others, 1974). Brown and Harrison (1981) note that, unlike many body tissues that have autoregulation, the uterus of the pregnant ewe at thermoneutrality is unable to maintain constant blood flow as perfusion pressure decreases (Greiss, 1966; Ladner and others, 1970).

That UBF is affected by environmental heat has been demonstrated in cows fitted with blood flow transducers around a mid-uterine artery, given injections of estradiol, and then placed in shade/no shade conditions. Cows placed in the shade showed a greater resultant rate of increase in UBF than did cows that were denied shade, demonstrating that UBF is affected by thermal stress (Roman-Ponce and others, 1978) (Figure 6). In the subtropical climate of Gainesville, Florida, shade provided

THE HIGH AMBIENT AIR TEMPERATURE-EMBRYOGENESIS DYSFUNCTION CONNECTION

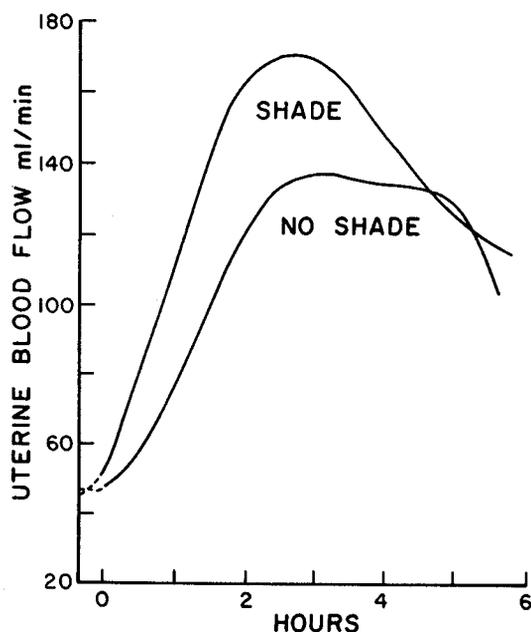


Figure 6. Uterine blood flow responses (ml/min) of cows maintained in shade relative to cows denied shade after injection of estradiol. Cows maintained in the shade had a relatively greater increase in uterine blood flow than did cows denied shade (after Roman-Ponce and others, 1978).

during the summer lowered respiration rates and rectal temperatures of lactating dairy cattle; shade improved both milk yield and reproductive performance over control cattle denied shade (Roman-Ponce and others, 1977); Roman-Ponce and others (1978) state that reduction of UBF in response to thermal stress may elevate temperature of the reproductive tract and prejudice the developing embryo. In the lactating bovine, environmental temperatures above 21.1°C cause deep body temperature to rise (Thatcher, 1974); temperature increase from 21.1 to 35°C caused the conception rate to decline from 40 to 31 percent.

High temperatures also affect reproduction among smaller mammals by reducing the rate of uterine blood flow. Oakes and others (1976) noted a 25-48 percent decrease in UBF of ewes exposed to induced hyperthermia. In warm summer (27°C) in England, Leduc (1972) noted a 46 percent reduction in placental blood flow in rabbits which was associated with an increase in number of runts and dead fetuses.

Hafez (1968) indicates that the effects of temperature on pregnancy and embryonic survival vary with the species, temperature, period of exposure, length of gestation, and stage of pregnancy; extremely high temperatures lower fertility, decrease litter size, increase abortion, and increase fetal resorption. Heat can affect male mammals via damage to spermatozoa, resulting in elevated embryo death (Howarth and others, 1965; Ulberg and Burfening, 1967; Burfening and Ulberg, 1968); however, as Bishop (1964) has indicated, most investigators consider the female responsible for embryonic death.

Ulberg and Sheean (1973) indicate that infertility in females subjected to high environmental temperatures is the result of damage caused by high body temperature acting directly upon the embryo immediately after fertilization (Figure 7). Pregnancy is most sensitive to environmental stress during the period between ovulation and implantation. The sheep zygote is most sensitive to the harmful effect of high ambient temperature during the initial stage of cleavage while in the oviduct (Dutt, 1963). Rectal temperatures taken in sheep and cattle about the time the egg was undergoing the first cell division showed that in both the pregnancy rate decreased with each degree of increase of rectal temperature.

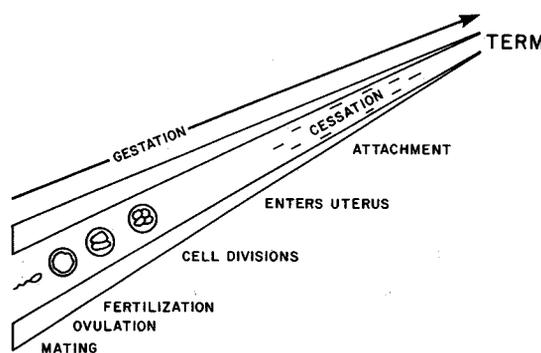


Figure 7. Schematic summarization of a series of sequential physiological events beginning with mating, and proceeding to birth of offspring at term; it is estimated that one-third or more of potential young cease to develop after the embryo enters the uterus (after Ulberg, L. C., and Burfening, P. J., 1967).

Rabbit embryos are also more susceptible to heat damage during first cell division than during the second. Ulberg and Sheean (1973) suggest that heat load on a female while her fertilized eggs are undergoing first cleavage may alter the rates of metabolism within the embryos, perhaps interfering with RNA synthesis. Four-day-old rabbit embryos morphologically abnormal because of heat stress may be capable of initiating an implantation site which is prominent at twelve days of gestation. Slight increase in temperature acting directly on the embryo disorients the mechanism controlling development within the blastomere; thus, whereas cells may continue to develop for a time, perhaps even forming a morphologically normal embryo, they subsequently die. Ulberg and Burfening (1967) note that temperature stress during early developmental stages results in later death of the embryo.

Ulberg and Burfening (1967) indicate that if a slight increase in temperature surrounding the embryo at the time of the first few cell divisions contributes to delayed death, the body temperature of the female near the time of mating should be associated with the chances of success of that mating. Results of their experiments on effects of heat load on reproductive capability of sheep and cows are shown in Figure 8. The authors note that an association between body temperature at the time of mating and embryo survival seems indicated. Alliston and others (1965) note that variation of atmospheric temperature by as little as 1 to 2°C may alter the point in the reproductive process that is affected. According to Woody and Ulberg (1964) control ewes maintained in constant 70°F had significantly higher level of fertility than ewes maintained in a room with a constant 90°F.

Frank Gwazdauskas (Dairy Science, VPI&SU, personal communication) indicates that probably 50 percent of cattle embryos die under natural conditions, with 10 percent loss in the first 4 days and 40 percent loss between 6 to 15 days.

To summarize to this point, if modern hot summer temperatures—to which modern mammals are supposedly adapted—have such profound, and widespread, impact upon mammalian reproductive capability, the cold-adapted mammals of the Pleistocene/Holocene transition facing rapid, and extreme, climatic warming could only have suffered reproductive dysfunction.

PLEISTOCENE/HOLOCENE DWARFING AND SKELETAL ABNORMALITY: A MECHANISM

Concurrent with the mammalian extinctions in the Pleistocene/ Holocene transition was dwarfing

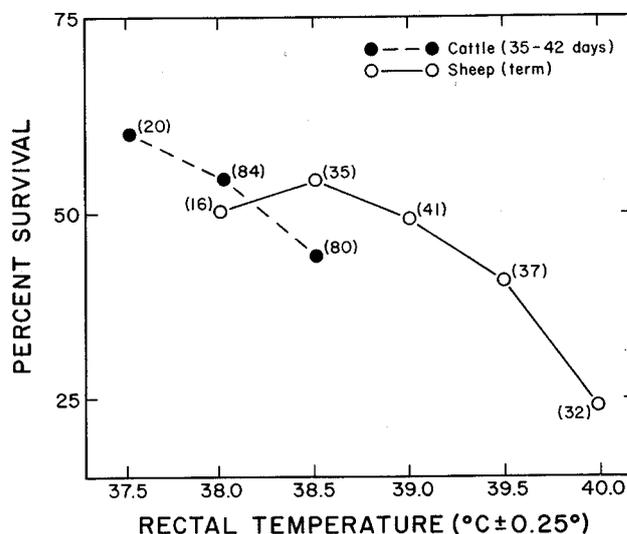


Figure 8. Influence of rectal temperature at the time of mating on embryo survival in sheep and cattle. The value in parentheses represents the number of observations for each temperature group. Note that increase in body temperature reduces survival rate (after Ulberg, L. C., and Burfening, P. J., 1967).

among mammals on a nearly global scale (Table); skeletal abnormalities are also known during the same time period. Marshall (1984) notes that the knowledge that extinction and dwarfing are concurrent processes may provide insight in extinction phenomena, and that if we can identify mechanisms causing a decrease in body size, we can better understand cause of the extinctions, assuming that both extinction and dwarfing are indeed linked to a common causal factor(s). In fact, Pleistocene/Holocene transition extinctions, dwarfing, and skeletal abnormalities seem to have common cause in the rapid increase in ambient air temperatures at the end of the last ice age.

Hafez (1968) notes that environmental temperature is perhaps the most important climatic component affecting prenatal growth. Miniature calves are often born to unadapted European breeds of livestock following a summer of pregnancy in the tropics. Pregnant ewes exposed to high experimental temperatures bore miniature lambs, the reduction in weight being proportional to the length of exposure. Yeates (1958) demonstrated that dwarfing is an effect of temperature and not to reduced feed intake. Heat-induced dwarfs are well-proportioned miniatures, in contrast to the long-legged thin lambs from underfed ewes.

Brown and Harrison (1981) note that intrauterine growth retardation (IUGR) results from exposure

of ewes to high environmental temperature during late gestation, and that since uterine blood flow is a major source of nutrients for the developing fetus, altered placental function because of heat stress may be a contributing factor in ovine IUGR. Their experiments rule out maternal nutrition as a primary cause of fetal dwarfing. Roman-Ponce and others (1976) have reported reduced mid-uterine artery blood flow in response to heat stress in nonpregnant ovariectomized ewes. Brown and others (1976) also reported decreased uterine blood flow during heat stress in pregnant rabbits.

Small lambs resulting from maternal heat stress of 25 or 53 days duration are proportional dwarfs and occur independently of level of nutrition (Brown and others, 1977); dwarfing was not alleviated by increasing the dietary protein of heat stressed pregnant ewes. Dwarfing occurs with maternal heat stress during only the last month of pregnancy. Intrauterine growth retardation, and not disproportional fetal dwarfing, results from late gestation heat stress.

Growth of animals after weaning can also be stunted by high environmental temperatures (Hafez, 1968), the degree of stunting varying with the breed, age, fatness, plane of nutrition, and relative humidity. Growth of European breeds of cattle is depressed at temperatures constantly maintained above 24°C. High temperatures may be lethal to newborn mammals which are not well adapted to withstand high temperatures early in life; lambs and calves are especially susceptible. Lambs between two and seven days of age cannot survive longer than about two hours at 38°C, or more than three hours of solar radiation exposure.

For the phenomenon of dwarfing during the Pleistocene/Holocene transition, all modern large species in North America seem to have experienced size decrease during the Holocene (Gilbert and Martin, 1984). Dwarfing occurred in species that survived and also in those that became extinct, and was concurrent with the extinctions (Guthrie, 1984); some species experienced dwarfing just prior to extinction. Tchernov (1984) reported that most mammals in the Middle East responded directly and quickly to Pleistocene/Holocene transition climatic warming by drastic diminution of body sizes. For the Israel area, Davis (1981) reported that the fox, wild boar, gazelle, goat, and probably aurochs underwent a size reduction at the end of the Pleistocene 10,000-12,000 yr ago; most carnivores in Israel and Lebanon show size reduction in the Pleistocene/Holocene transition (Kurten, 1965). For the Natural Trap Cave area of Wyoming, Gilbert and Martin (1984) indicate that climate change was reflected not in extinction but in size

reduction. Many surviving European mammals have become smaller during postglacial times (Kurten, 1972). Examples include the gigantic Pleistocene brown bear of Europe (that in postglacial times has been reduced in size to the smallest living race of the species *Ursus arctos*), lion, auroch, bison, elk, and red deer, etc. Kurten (1972) reports that dwarfing as a prelude to extinction has been observed in many cases.

For the phenomenon of skeletal abnormalities, Hafez (1968) notes that climatic stress or hyperthermia during pregnancy may cause fetal malformations in some species. The effects of temperature depend upon the stage of pregnancy at the time of exposure, since most malformations occur during organogenesis. The severity of the defects is usually less when heat exposure is delayed until later stages of embryonic development. In hot climates the later maturing parts of the animal body such as the loin and rump are stunted. At sexual maturity, such animals will have smaller pelvic cavities than normal and may produce stillbirth calves because the size of the pelvis is too small for a normal delivery.

Abnormalities were common in Pleistocene/Holocene transition mammalian faunas. Guthrie (1984) suggests that more spectacular than the general postglacial decline in body size was a reduction in size of some body parts. Guthrie (1984) also reports that virtually all mammoths associated with Clovis points in the New World are diminutive and have reduced tusks. McDonald (1984) reports that an unusually high frequency of skeletal abnormalities has been found in *Bison* from 11,000 to 9,000 yr B. P.

To summarize, high environmental temperatures affect modern mammals of all sizes by reducing the flow of blood (UBF) to the female uterus. Reduction of UBF, in turn, results in embryogenesis dysfunction that can be expressed in embryo death, dwarfing, and skeletal/morphological abnormalities. In light of this knowledge, it would seem that dwarfing and skeletal abnormality triggered by warming in the Pleistocene/Holocene transition would have been inescapable. I suggest that the Pleistocene/Holocene transition extinctions, dwarfing, and skeletal abnormalities all have common cause in the climatic warming at the end of the last ice age.

EXPANDING GRASSLANDS AND EXTINCTIONS: A CONNECTION

During the Pleistocene/Holocene transition climatic warming and retreat of ice sheets and boreal forest northward, grasslands began to appear and

expand in the North American interior. According to Guthrie (1984), North American grasslands began to expand across the midcontinent in a roughly triangular area with the base backed up against the Rocky Mountains and the apex heading toward Ohio and Pennsylvania. At the time the grasslands were expanding at their greatest rate from 12,000-10,000 yr B. P., mammoths, horses, and camels, etc., became extinct. Thus occurred one of the most fascinating paradoxes of the Pleistocene/Holocene transition. During a time of warming, and expanding grasslands that would have provided an increasing food source for many herbivores, extinctions occurred. McDonald (1984) touches upon the paradox by noting that modern ecological and evolutionary theory predicts that most environmental changes during the time of extinctions should have produced an increase in megafaunal biomass and diversity, and not extinctions.

However, as noted in the section titled "The Hyperthermia-Reduced Uterine Blood Flow Connection," mammals denied shade suffer reduction in UBF. Concurrent with the expansion of grasslands, woodland areas, that would have provided shade during a time of general climatic warming, were being reduced in size. The reduction of shade would have triggered hyperthermia and UBF reduction among mammals long adapted to cold and shade. Large mammals, because of their relatively small surface/volume ratios, would have been especially affected. Embryogenesis dysfunction was virtually inescapable during the Pleistocene/Holocene climatic warming and expansion of grasslands.

GEOGRAPHICAL BIAS IN THE PLEISTOCENE/HOLOCENE EXTINCTIONS: AN EXPLANATION

Another fascinating paradox of the Pleistocene/Holocene mammalian extinctions is that during relaxation of extremely cold glacial conditions, the higher northerly latitudes should have become relatively congenial to life. Instead, Guthrie (1984) notes that although the late Pleistocene extinctions exhibit a global pattern, they were mainly Holarctic and more dramatic in the northern portions (Alaska and Siberia), whereas the rest of the world was affected more lightly. Webb (1984) indicates that it has long been evident that glacial cycles and their climatic effects were harsher at higher latitudes. That high-latitude mammalian faunas were more affected than low-latitude faunas during the extinctions is expressed by Martin (1984) who notes that during warming from 10,000 to 12,000

yr B. P., the time of the most dramatic extinctions, the range of semitropical species should have been expanding and not contracting. About half the families of large vertebrates that became extinct in temperate North America during the late Pleistocene survive at low latitudes, mainly in the American tropics (Webb, 1984).

In light of modern climate dynamics, that the Pleistocene/Holocene mammalian extinctions would have been more severe in the higher latitudes is predictable. During periods of warming, the higher latitudes heat up relatively more than do the lower latitudinal areas (Figure 9). Thus, during

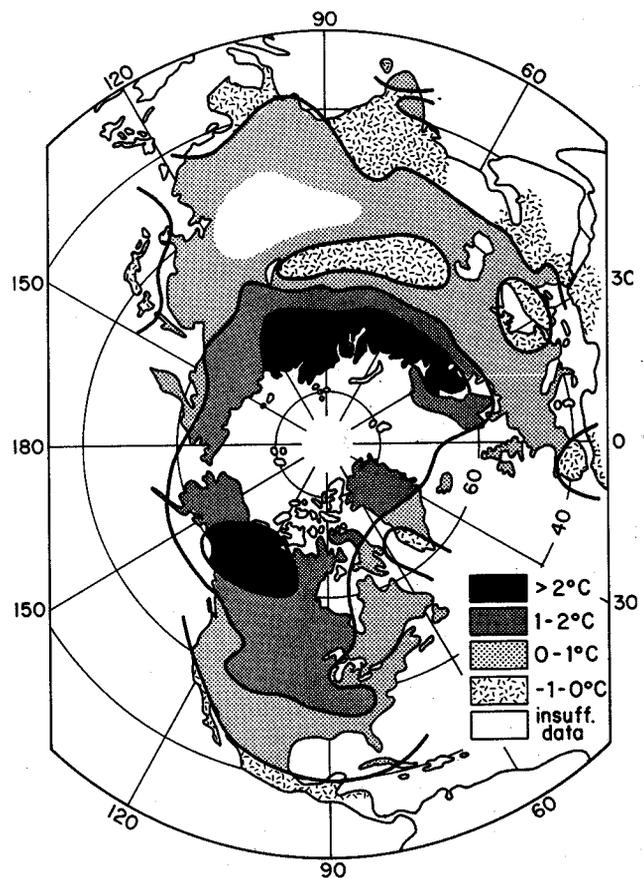


Figure 9. Spatial pattern of mean annual temperature differences (northern hemisphere) between cold- and warm-year groups (after Wigley and others, 1980). Maximum warming occurs in high latitudes and continental interiors, up to more than five times the hemispheric mean increase in a region from Finland across Russia and Siberia to about 90°E. A large part of North America has positive temperature changes of two or more times the hemispheric mean.

warming intervals, high latitude mammals have a relatively greater heat load to have to adapt to.

The cause of the relatively greater degree of warming in high latitudes is suggested in the work of Wigley and others (1980). Comparison of composites of the five warmest years with the five coldest for the period 1925 to 1974 indicates that during warm periods maximum warming occurs in high latitudes and in continental interiors. In a region from Finland to across the northernmost parts of Russia and Siberia to about 90°E, the temperature increase is up to more than five times above the hemispheric mean temperature increase. A large area of northern North America also shows temperature increases of two or more times the hemispheric mean. Apparently, warm periods in the northern hemisphere have intensified high-latitude (50-70°N) westerlies, greater cyclonic activity in the arctic and subarctic regions of the eastern hemisphere, and a westward displacement of the Siberian High in the winter half of the year.

In application to the Pleistocene/Holocene extinctions, the regions showing greatest warming during modern warming intervals in the northern hemisphere coincide with the regions that experienced the most intense patterns of Pleistocene/Holocene extinctions in the northern hemisphere. Conversely, some regions of the northern hemisphere apparently cool down during general northern hemispheric warming. These areas, that include Japan, much of India, an area about Turkey, the Iberian peninsula, North Africa, and a region in central Asia, etc., seem to have been more lightly affected by extinctions.

HEAT-INDUCED EMBRYOGENESIS DYSFUNCTION: EVOLUTIONARY IMPLICATIONS

Grayson (1984) notes that attempts to explain the Pleistocene extinctions are made more difficult because we have no theory that relates organisms to their environment sufficiently to explain any set of vertebrate extinctions. I suggest that high ambient temperatures acting directly upon mammalian embryos explains the cause of the extinctions, dwarfing, and skeletal abnormalities during climatic warming at the end of the last ice age.

This natural linkage between climatic warming and vertebrate reproductive dysfunction shows that mammals are far more sensitive to climate change than has been suspected and may help to explain other mammalian extinction episodes during the Cenozoic. Similar to the most recent (Rancholabrean) extinction episode at the end of the last

ice age, some other major Cenozoic mammalian extinction events seem also to have occurred at the end of ice ages. Webb (1984) correlates the late Hemphillian, late Blancan, and late Irvingtonian extinction events with glacial terminations. Thus, as indicated by the record, climatic warming seems to be more lethal to terrestrial mammalian faunas than does climatic cooling.

The sensitivity of mammals to climatic warming has implications for the future. Today, our burning of the fossil fuels coal, oil, and gas is causing the waste product CO₂ to accumulate in the atmosphere. Atmospheric CO₂ is predicted to double over pre-industrial levels during the next century, causing global warming ("greenhouse" conditions) of perhaps 3°C in the northern hemisphere. Effects of future "greenhouse" conditions upon our civilization have been the subject of lively debate. Topics most discussed have focussed upon rise in sea level associated with melting of polar ice, and the potential shifting of rainfall patterns away from agricultural regions, etc. We even hear that the positive effects of global warming might be beneficial, and even outweigh negative ones. In the sweeping speculations upon our future, the effects of warming operating directly upon mammalian reproductive physiology have been ignored. In light of the sensitivity of modern mammals to high ambient temperatures this would seem to be a serious oversight.

I suggest that the Pleistocene/Holocene mammalian extinctions provide an example for evaluating the impact of a future climatic warming upon modern mammals. Modern mammals are the survivors of the Pleistocene/Holocene extinctions; I suggest that many survived primarily by being able to reduce surface/volume ratios (i.e., by becoming dwarfed), and thus maintain core temperatures conducive to reproductive success at a time when large size was disadvantageous.

During this modern interglacial we are, in effect, living on a "thermal plateau." We have no evidences that modern mammalian faunas can withstand a rise in ambient air temperature by several degrees Celsius over the short span of a few decades. In fact, evidences abound suggesting that we are not as well adapted to this thermal plateau as we might suspect. Every summer, all about us, are clear signs of reproductive dysfunction during hot summer temperatures that we are supposedly adapted to. A rapid elevation of temperatures can only further aggravate reproductive dysfunction, causing the phenomenon to expand in scope and magnitude.

If, as Wigley and others (1980) suggest, certain regions of the northern hemisphere actually heat

up several times above the mean hemispheric temperature increase, the North American land mass could be in for an interesting test of theory. History shows us that during the last time of rapid warming (at the end of the last ice age) that extinctions were the most severe of all in North America. If the Pleistocene/Holocene transition extinctions have a lesson to offer, it is that a future rapid elevation of temperatures to above modern levels might be potentially dangerous, and especially so for mammalian faunas of the North American land mass.

CONCLUSIONS

In the middle 1970's, I became fascinated with involvement of the carbon cycle in evolution of earth's climate and life and began a series of multidisciplinary studies that I hoped might illuminate principles operating in that vast, and essentially unknown, complex. In my early work, I focussed upon the Tertiary/Cretaceous (K-T) transition of about 65 Myr ago because it was rich in information. I soon came to believe that the K-T transition was a time of perturbation of the carbon cycle, and associated CO₂-induced global warming via the so-called "greenhouse" conditions (McLean, 1978). By now, I have linked the K-T transition, the CO₂ buildup, and the global extinctions, to the Deccan Traps flood basalt volcanism, seemingly the largest volcanic event of the Phanerozoic Eon (McLean, 1985a, 1985b, 1985c).

One area of greatest fascination to me was to attempt to discover potential linkage between changes in ambient air temperature and direct effects upon terrestrial vertebrates that might influence bioevolution. Here, I focussed upon the Pleistocene/Holocene transition as the time interval richest in information. Several years ago, I published on such linkage (McLean, 1981); this current paper expands upon my original thesis that hot environmental conditions directly affect reproductive capacity.

In application of modern principles to the Pleistocene/Holocene mammalian extinctions, dwarfing, and skeletal abnormalities, I recognize that the taxa affected reflect vast physiological and morphological diversity, and were spread over vast geographical areas, and variable climatic scenarios. Certainly, overall, many factors (including man) were likely involved in the Pleistocene/Holocene scenario. However, two factors come together in a potent mix, the knowledge of which may have value in paleontology. These are the known rapid Pleistocene/Holocene global warming and the documented sensitivity of mammalian reproduction to

heat. In light of sensitivity of modern mammals to even normally hot summer temperatures, it seems that heat-induced embryogenesis dysfunction would have been inescapable during the Pleistocene/Holocene transition. That the ambient air temperature-embryogenesis dysfunction linkage may have predictive power is hinted at in the several Cenozoic mammalian extinction episodes that occurred during warming at the end of ice ages (Webb, 1984). It is interesting that, similar to the K-T transition, the mammalian extinctions at the end of the last ice age also occurred during global warming associated with CO₂ buildup in the atmosphere.

On a final point, I have avoided critical discussion of other extinction models in this paper. My limited knowledge of the specific Pleistocene/Holocene taxonomic base precludes me being a critic. Instead, I have approached the Pleistocene/Holocene scenario as part of my general studies searching for principles relating to involvement of the carbon cycle in the evolution of life on our planet. As such, all those researchers who have collected, and interpreted, Pleistocene/Holocene data have been my teachers, and have my appreciation for providing me data, and viewpoints, to integrate in my search for "cause" of the most fascinating event I know of in earth history: the Pleistocene/Holocene mammalian extinctions.

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PRELIMINARY OBSERVATIONS ON FLOODPLAIN, TERRACE, AND FAN DEPOSITS IN THE UPPER POTOMAC RIVER BASIN OF VIRGINIA AND WEST VIRGINIA. J. Steven KITE, Alison BELL, and Mark ALLAMONG, Department of Geology and Geography, West Virginia University, Morgantown, WV 26506

Three independent research projects concerning the late Cenozoic stratigraphy and history of the upper Potomac River basin were begun during 1984. Laboratory analyses and compilation of field data have barely begun, so it is not yet possible to present detailed discussions of each project. However, our work to date warrants a preliminary discussion of the alluvial and colluvial deposits in this part of the central Appalachian Mountains.

One project was a reconnaissance of all types of alluvial deposits in the lower Shenandoah Valley, including deposits of the Potomac River, in Berkeley and Jefferson counties, West Virginia and Clarke County, Virginia. In this study area (Figure), widespread post-settlement alluvium with little soil profile development commonly overlies well-developed, buried, pre-settlement soil profiles. The post-settlement alluvium typically is 1.6 to 6.6 feet (0.5 to 2 m) thick, and contains historical artifacts. At one locality the buried pre-settlement soil contains late Woodland Period pottery. In the study area, post-settlement alluvium is not as thick along the Shenandoah

and Potomac rivers as on their tributaries, suggesting that most sediment eroded from hillslopes either is stored on the floodplains of the tributaries, or is transported by the larger streams directly to the lower Potomac.

A scarcity of cut-bank exposures along the Shenandoah and Potomac rivers hampers study of Holocene alluvial history and associated floodplain stratigraphy along these major streams; proper study of the floodplain will require artificially created exposures such as backhoe trenches or archeological excavations, such as those carried out at the Flint Run (Thunderbird) site south of our study area (Segovia and Franco, 1977; Foss, 1977). No distinct Holocene depositional units have been delineated in the present study. In general, modern Potomac River channel gravel is composed of sandstone and chert, with minor carbonate and siltstone clasts, whereas Shenandoah River gravel is composed of quartzite and sandstone, with minor conglomerate, greenstone, and carbonate clasts. In the vicinity of alluvial terraces, up to one-third of modern channel clasts show extensive weathering rinds, indicating reworking of older alluvium. The over-bank facies on modern floodplains is predominantly sandy loam or silty loam, locally broken by gravelly splay deposits. Various soil series occur on the modern floodplains.

At least two pedologically distinct terrace units occur in the lower Shenandoah Valley. Terraces 16 to 65 feet (5 to 20 m) above modern floodplains are characterized by Captina and Ashton soil series. Alluvial gravel in these terraces generally have fewer carbonate and greenstone clasts, but more quartzite and sandstone clasts, than modern floodplain gravel.

High terraces (more than 66 feet, 20 m, above modern floodplains) are characterized by Monongahela, Braddock, Waynesboro, Thurmont, and Tygart soils; however, at least two areas of Braddock soil near Harpers Ferry are formed on local colluvium. A few isolated terrace surfaces occur more than 213 feet (65 m) above modern floodplains. These very high terraces are not as well developed in the lower Shenandoah Valley as along the South Fork of the Shenandoah, in Warren County, Virginia (Rader and others, 1975). A few exposures of high terrace deposits show a typical sand-over-gravel floodplain sequence, thoroughly modified by pedogenic clay. Most high terrace deposits lack upper sand layers; it is likely the sand was removed by rill or sheet erosion. Other exposures suggest colluvial mixing of sand, gravel, and pedogenic clay. High

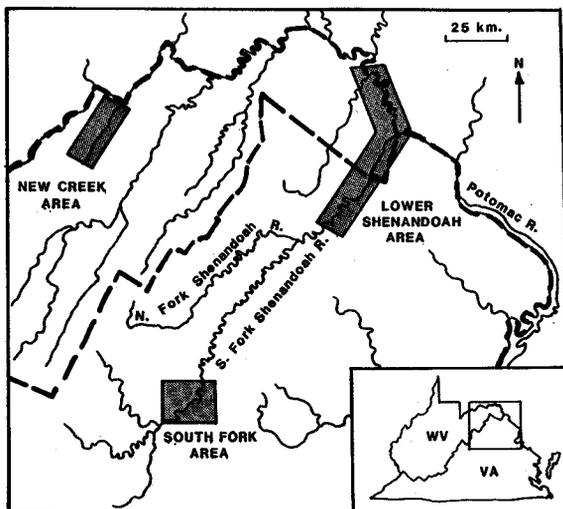


Figure. Study areas.

terrace gravel is mostly quartzite, sandstone, and conglomerate.

The style of terrace destruction is strongly influenced by the underlying bedrock lithology. Terraces formed on shale tend to persist until destroyed by lateral migration of the major stream channel. The alluvial veneers may be almost entirely eroded away, but the underlying shale straths appear resistant to slope processes and first-order stream erosion. High terraces formed on carbonate bedrock generally show sinkholes and colluvial reworking of terrace sediments suggesting that old alluvium commonly is let down by karst solution. Although terraces formed on shale survive as distinct landforms longer than their counterparts on carbonate bedrock, it is likely that alluvium reworked by karst solution may be considerably older.

In the second project, a detailed study along the South Fork of the Shenandoah River in Rockingham County, Virginia, field studies show two types of alluvium: one composed predominantly of channel gravel and sand, the other composed mostly of overbank sand and silt. Most alluvium between the Blue Ridge and the modern river channel appears to be old bedload deposits largely derived from mountain tributaries. The gravel is well exposed and exhibits varied intensities of pedogenesis, especially clay accumulation in the B horizon. One exposure revealed a deeply weathered gravel with many thick weathering rinds on sandstone cobbles, overlying more than 3 feet (1 m) of fine sand and silt, apparently overbank deposits. The soil series associated with these coarser terrace sediments is the Cotacto variant cobbly loam.

Higher benches exist on foot slopes of the Blue Ridge and yield sandy soils which may be remnant terrace material that has undergone extensive erosion. Alternatively, they may be of alluvial-fan origin. Colluvial landforms are found adjacent to these benches and exhibit typical colluvium soil profiles, such as the Laidig soil series which displays a fragipan.

In contrast to the coarse deposits derived from the Blue Ridge, the valley bottom northwest of the river has mostly sand and silt alluvium. Older terraces are well preserved when adjacent to tributaries which supply resistant sandstone and quartzite to the valley floor, producing a coarser alluvial deposit. Fragipan-bearing Monongahela cobbly and sandy loams are typical terrace soils in this area.

Most of the study area is underlain by saprolite developed from Paleozoic carbonate and shale,

creating conditions suitable for long-term preservation of alluvial deposits. Where carbonate bedrock occurs, it weathers beneath the alluvium undergoing pedogenesis, producing a bisequel soil profile. The profile is essentially a Frederick or Lodi clay residual sub-soil capped by a Monongahela soil developed in alluvium. Other soil series formed from older alluvial parent material include the Unison and Shenval pebbly and cobbly loams.

The third study contributing to this paper is a detailed examination of the geomorphology of New Creek Valley in Mineral and Grant counties, West Virginia, a valley containing landforms and deposits typical of smaller valleys of the upper Potomac basin. For most of its length, New Creek flows over shale, which crops out between ridges underlain by resistant sandstone and orthoquartzite. Bedload in New Creek consists of siltstone, sandstone, and orthoquartzite; although shale bedrock underlies the stream bed, no shale clasts were found in the channel. Soils found on the modern floodplain include the Pope, Chagrin, Huntington, and Philo series. Drainage anomalies and wet, clayey depressions in wide areas of the floodplain indicate old meander cut-offs.

Several fans occur between the steep slopes of New Creek Mountain and the stream. These fans are truncated by the stream, and have moderately developed soils. Fan deposits adjacent to moderate slopes on the opposite side of the stream have better developed soil profiles. These fans with well-developed profiles occur in areas shown as residual soils on soil survey maps.

The New Creek Valley contains two individual terraces 23 to 33 feet (7 to 10 m) above modern stream level. These terraces contain alluvium similar to modern channel deposits but altered by the pedogenic processes that have formed Monongahela, Tygart, and Purdy soils.

Higher terraces in New Creek Valley are composed primarily of large rounded sandstone boulders. One location approximately 131 feet (40 m) above modern stream level contains hematite-cemented conglomerate and breccia composed of rounded sandstone cobbles and pebbles, and angular shale and siltstone clasts. Adjacent to the Potomac River, at its confluence with New Creek, there are shale straths mantled by a thin veneer of gravelly alluvium at 197 to 213 feet (60 to 65 m) above modern stream level (Dennison, 1963).

Our three independent projects allow a few generalizations about terraces in the upper Potomac River basin. Terrace deposits are best developed wherever tributaries that carried an

abundant supply of resistant sandstone or quartzite clasts emptied into the major river system. Although terrace deposits differ from modern floodplain deposits in several aspects, these differences can be attributed to post-depositional pedogenesis and erosion. Soil survey maps are useful in identifying the extent of probable terrace deposits, but these soils maps must be field checked before they are of use in the compilation of accurate surficial geology maps.

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QUATERNARY ALLUVIAL FANS IN CENTRAL VIRGINIA. R. Craig KOCHER and David W. SIMMONS, Department of Geology, Southern Illinois University, Carbondale, IL 62901.

Most sedimentological models of modern and ancient alluvial fans have focused on fans formed in arid, humid-glacial, humid-tropical, or humid-periglacial environments. Little attention has been given to alluvial fans developed in humid-temperate areas such as Virginia (Kochel and Johnson, 1984). Significant differences exist in morphology, depositional processes, and facies between the Virginia fans and fans described in other climates. Coarse gravel fans are the dominant depositional landform along piedmont slopes of the Blue Ridge Mountains in west-central Virginia.

Two distinct types of fans have developed during the Quaternary Period on opposite sides of the Blue Ridge Mountains. Active fans east of the Blue Ridge are constructed by infrequent debris avalanching caused by intense rainfall. Inactive fans along the western slopes of the Blue Ridge appear to have been constructed by braided stream processes. Rainfall in excess of 23.6 inches (60 cm) in 8 hours during Hurricane Camille in 1969 triggered hundreds of debris avalanches east of the Blue Ridge in Nelson County (Williams and Guy, 1973). Sediments have accumulated on small debris fans by repeated debris avalanching and debris flows during the Holocene. The debris fans are elongate because of their confinement by steep valley walls in Lovington granite-gneiss bedrock. The locus of deposition on these fans appears to be controlled by the distribution and magnitude of upslope failures. Aerial photographs taken after the Camille storm show that an average of 25 percent of fan surfaces were activated by debris flows. Nelson County debris fan sediments are very poorly sorted cobbles and boulders in a mud matrix and are generally less than 66 feet (20 m) thick. These mud-matrix gravels are thick-bedded and rarely exhibit internal stratification, except for occasional crude bedding and basal imbrication. Inverse grading is common because of high dispersive stresses during emplacement of the sediments by debris flow mechanisms. No significant down-fan facies variations are visible in the debris fan sediments. Lateral variations occur because of the lobate nature of debris deposition on irregular fan surfaces.

The 1969 deposits contain the coarsest clasts in all of the stratigraphic sections observed. Pre-1969 deposits have higher clay content, greater oxidation, and higher quartz/feldspar ratios in the matrix. Depositional units are separated by erosional contacts. Many of the bed surfaces contain paleosols formed on fan paleosurfaces during the time between successive debris flows. These buried soils can be radiocarbon dated. Dating of buried soils in the Davis Creek debris fans indicates that depositional episodes are separated by periods of inactivity ranging from 3,000 to 4,000 years. Correlation of fan stratigraphies in Davis Creek show that deposition has occurred at least three times during the Holocene, most recently in 1969 (Kochel and Johnson, 1984).

Depositional units can be recognized and correlated based on the identification of buried soil horizons, bedding character, clast weathering, and changes in matrix mineralogy with depth.

Table. Comparison of Blue Ridge fans and debris fans.

MORPHOLOGY	BLUE RIDGE FANS	DEBRIS FANS
SIZE	10's km ²	1-2 km ²
SHAPE	fan, bajada	elongate, isolated
GRADIENT	moderate, concave less than 5°	steep, segmented
SOILS	thick surface soil, very old paleosol	more than 5° no surface soils, many paleosols
SEDIMENTOLOGY		
TEXTURE	high Gravel+Sand/Mud	low Gravel+Sand/Mud
MATRIX	sand	mud
FABRIC	imbricated	none
SORTING	poor (locally good)	very poor
ROUNDNESS	subrounded	angular
BEDDING	alt. sand and gravel	crudely developed
SEDIMENTARY STRUCTURES	gravel forsets, channel fills, bars,	occasional inverse grading
RETURN INTERVAL	more continuous	discrete (3,000 yrs+)
DOWN—FAN FACIES	fining down-fan facies more continuous laterally (sheets)	no down-fan trends distinct units lobate, discontinuous in plan debris avalanche debris flow
DOMINANT PROCESSES	braided stream flood surge sheet flood	
AGE	Pleistocene	Holocene

Discrete sedimentation units within the fans are characterized by abrupt changes in the sediment texture and ratios of quartz/feldspar in the matrix. Decomposition of granitic clasts with time yields increasing quartz/feldspar ratios as the feldspars alter to clay minerals. Bulk texture tends to decrease with age as clasts disintegrate. Typically, these decompositional trends are gradual with depth in sediments. However, if weathering is interrupted by catastrophic deposition (i.e. by debris flows) these trends will display abrupt changes with depth. These qualitative indicators of age and depositional activity reinforce the correlations based on radiocarbon dating.

Alluvial fans form an extensive bajada along the western flank of the Blue Ridge that has prograded westward over Cambrian carbonates in the Shenandoah Valley. These Blue Ridge fans are best developed between Grottoes and Vesuvius along the southeastern margin of the Shenandoah Valley. No historical depositional activity has been observed on these fans. Fan sediments are sand matrix, clast supported gravels composed primarily of Antietam quartzite. The Blue Ridge fan gravels are well-imbricated, contain abundant channel fill sequences, and exhibit large-scale planar cross-stratification in many areas. Locally, gravels are well sorted, but overall sorting is poor. These gravels appear to have been deposited by powerful braided streams with insignificant debris flow activity (Table).

Blue Ridge fans are thick relative to the debris fans to the east and typically range in thickness between 65 to 492 feet (20 to 150 m). Distinct down-fan variations occur in grain-size and sed-

imentary structures (Figure). Proximal areas of individual fans and/or bajadas contain coarse, poorly sorted, imbricated boulders deposited by powerful, competent surges. The mid-fan facies is usually the thickest part of the fan and is characterized by imbricated, cross-bedded gravel and sand. In many areas, the gravel appears to be organized into distinct longitudinal bars while the sand beds appear to have been deposited by laterally extensive sheet floods. The Blue Ridge fans grade distally into terrace gravels of the South River and Shenandoah River. Distal fan sediments are dominated by cross-bedded sand and cross-bedded pebble-to cobble-sized gravel. Scattered deposits of mud occur in the distal facies and in inter-fan regions where ponding was likely to have occurred.

Manganese ore has been commercially mined from several of the Blue Ridge fans during the past century (Hack, 1965). The manganese is thought to have developed in the residual soils formed on the underlying carbonate rocks which were buried by prograding fan gravel. Most of the deposits are located in the proximal fan facies, in areas where maximal reworking and placer development would have been expected. Therefore, some of the manganese may have resulted from stratiform placer deposition. Gravel, sand, and clay are being mined from midfan, distal, and inter-fan facies, respectively.

Age relationships for the Blue Ridge fans are somewhat uncertain. No radiocarbon dating has been done on these sediments. Relative ages can be determined based on soil geomorphology and weathering characteristics of the fan sediments. Surface soils are well developed under a fairly

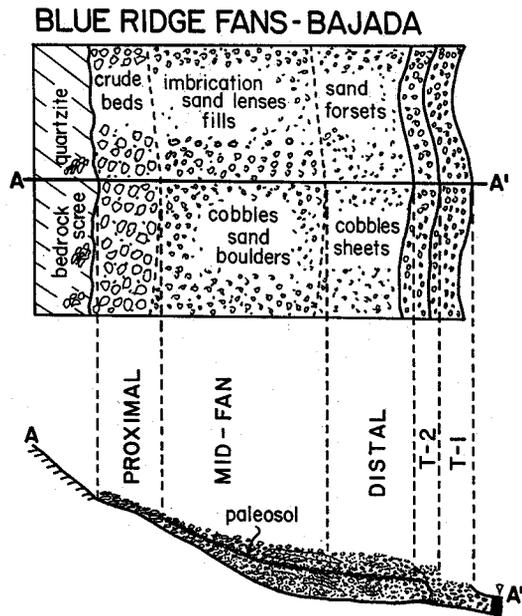


Figure. Schematic facies model for alluvial fans along the western flank of the Blue Ridge. Distal fining is consistent with the interpretation of tractive processes (i.e. braided stream) dominating over suspended processes (i.e. debris flow).

dense forest cover. Development of the thick surface spodosol probably required thousands of years under the present humid-temperate climate. Its presence indicates that there has not been extensive deposition on these fans throughout the late Holocene and perhaps the entire Holocene. Several meters below the surface of the Blue Ridge fans there is a well developed paleosol. This paleosol can be observed in all the sites investigated and is a useful time-stratigraphic marker. The paleosol separates upper gravels having a tan, sandy matrix and unweathered quartzite clasts from lower gravels with a red matrix and rotted quartzite clasts. To form such an extensive paleosol and to permit such decomposition of resistant quartzite clasts require either a very long time (on the order of tens of thousands to millions of years) under present climatic conditions and/or a warmer, more humid paleoclimate under which conditions the soil would have developed more quickly. The lack of paleosols and significant vertical differences in sediment induration and clast weathering throughout the upper gravel indicate that they were deposited rapidly by high frequency flows. The frequency of deposition on these fans may have been annual, i.e., a seasonal climate, or as infrequently as every few tens of years. The

paucity of paleosols indicates that significant periods of inactivity, on the order of hundreds to thousands of years, did not occur. A similar interpretation of continuity of depositional activity can be made for the lower gravel below the paleosol. Therefore, we suggest that there have been at least two episodes of fan construction during the Quaternary, separated by a long period of inactivity which is marked by the prominent paleosol.

In current investigations we are continuing to refine the facies model for humid-temperate alluvial fans and attempting to determine the cause for marked variation of alluvial fans on opposite sides of the Blue Ridge. We hope to determine more precisely the ages of the Blue Ridge fan sediments and to determine how Quaternary climatic changes may have influenced depositional processes on the fans. We speculate that Pleistocene climates may have been more favorable than Holocene ones for braided stream processes. The retreat of the polar front and renewed intrusion of tropical air masses appears to be coincident with, and may be recorded by, the initiation of Holocene debris flow activity on the fans east of the Blue Ridge about 11,000 years ago. At several sites east of the Blue Ridge, Holocene debris fans are entrenched into Pleistocene fan sediments. These Pleistocene sediments are sand matrix gravel that appear similar to the Blue Ridge fan gravel and may record a similar shift in dominant depositional processes from braided stream to infrequent debris flow episodes. If the sedimentological changes through time on these fans are inexplicable by climatic variations, then other causative processes such as neotectonism will have to be explored.

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QUATERNARY TRAVERTINE-MARL DEPOSITS OF VIRGINIA. David A. HUBBARD, Jr., and William F. GIANNINI, Virginia Division of Mineral Resources, P. O. Box 3667, Charlottesville, VA 22903; and Michelle M. LORAH; Department of Environmental Science, University of Virginia, Charlottesville, VA 22903.

Valley and Ridge travertine-marl deposits have been observed in ten Virginia counties (Figure). Occurrences are typically located downstream from faulted and fractured carbonate rocks. Deposits are the result of inorganic and organic precipitation of low magnesium calcite from mixed surface and subsurface waters. CaCO_3 is actively deposited seasonally, but stream erosion is currently outpacing deposition over the yearly cycle at each site. Algal cysts collected near the base of one deposit may indicate Pleistocene deposition. Angiosperm leaf imprints at numerous sites are all of modern tree species. A date between 750 and 1000 A.D. was suggested for projectile point and pottery fragments found in the top of a Frederick County deposit. Deposits have been worked for agricultural lime in four counties with operations continuing at one location. Soil types and topographic signatures show promise for rapid recognition of these features.

Investigations are continuing into the location of additional travertine-marl deposits. Detailed studies are being carried out at two sites by the authors and others.

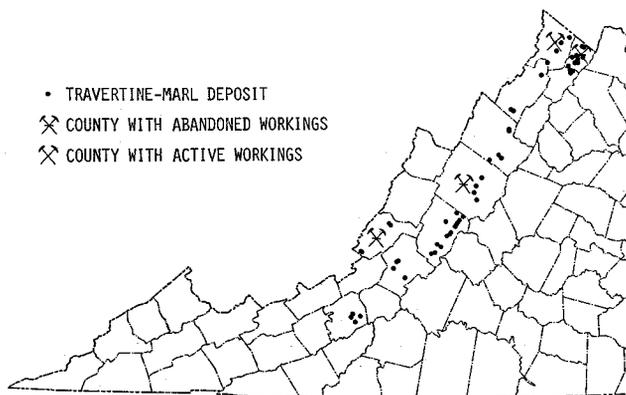


Figure. Distribution of travertine-marl deposits in Virginia. Counties containing sites worked for agricultural lime are indicated.

WISCONSINAN HERPETOFAUNAS OF THE CENTRAL APPALACHIANS. Leslie P. FAY; The Museum, Michigan State University, East Lansing, MI 48824-1045¹

Fossil herptiles of the central Appalachian Mountains do not exhibit the striking Wisconsin-Holocene range adjustments characteristic of some contemporaneous species of birds and mammals. Composite ranges (based on present distributions) of the fossil herptiles are harmonious (all species sympatric) and occur in the central or southern Appalachian region. Most fossil mammal composite ranges are disharmonious (not all species sympatric at present) with 83 percent to 92 percent of the species co-occurring in the central or northern Appalachians. The remaining 8 percent to 17 percent (extirpated from the region some time in the Holocene) co-occur 93 miles (150 km) north of Edmonton, Alberta, over 1860 miles (3000 km) from the Appalachian fossil localities in an area defined by the southern limit of *Microtus xanthognathus* and the northwestern limit of *Spermophilus tridecemlineatus*. This small area of boreal habitat in western Canada is also occupied by many wide-ranging species still present in the Appalachians (56 percent to 84 percent of the fossil faunas, boreal extirpates included; Guilday and others, 1978, and references therein). Thus, the majority of mammals and all herptiles present in the central Appalachians have been in residence since at least the Mid-Wisconsinan (Fay, 1984a), but a few mammals have undergone dramatic range shifts since the Late Wisconsinan. The fossil record for birds is less completely examined but includes current residents plus a minority of species now removed to the boreal forest or arctic tundra. Why are 14 bird and mammal species of boreal to tundra habitat preference found as fossils in central Appalachian accumulations along with representatives of the current temperate fauna? Why were herptiles apparently not affected by the forces that caused other tetrapods to shift their ranges to the north and west from 186 miles (300 km) to 1984 miles (3200 km) at the close of the latest glaciation? Causes responsible for these varying responses

¹ Present address: P.O. Box 141, Winnebago, IL 61088

among and between vertebrate classes have not yet been adequately identified.

Several common misconceptions about herptile ecology block further understanding of this zoogeographic disparity. Disharmonious mammalian fossils are usually accepted as the result of synchronous deposition, but herptiles from the same localities that do not match the ecologic and distributional characteristics of the mammals have often been suspected of being intrusive (Lundelius and others, 1983). Important Wisconsinan Appalachian localities [e.g. New Paris No. 4, Pennsylvania (Guilday and others, 1964) and Ladds Quarry, Georgia (Holman, 1967, 1985)] were judged to be heterochronic assemblages and the significance of the herptile components left in question. The distributional incongruities more likely result from real ecologic or climatic factors, as no evidence for heterochronic deposition has been demonstrated in most localities.

The often repeated assertion that herptiles were more severely affected by glacial-interglacial climatic shifts than were other animals (Aufenberg and Milstead, 1965) is no longer supported. There is no documentation of dislocation of northern or southern forms into the central Appalachians, a maximum 110 mile (177 km) northward migration of "southern" forms, and evidently no resident species were forced to make significant range adjustments (Fay, 1984b).

The assumption that poleward distribution limits of herptiles are governed by cold temperatures is an over simplification that may obscure a great deal of information useful in paleoenvironmental reconstruction. Severity of the cold season is less critical (assuming suitable hibernacula) than duration of the warm season. All boreal North American amphibians and some reptiles are oviparous, limited by warm seasons of sufficient duration and intensity for growth and development of eggs. Adults can avoid unfavorable conditions during the remainder of the year by hibernation.

If the climatic equability hypothesis is accurate in predicting reduced seasonal extremes during glacial stages with regard to interglacials, the cooler summers may not allow sufficient time for incubation of eggs at higher latitudes (as is the case for turtles in Great Britain now and during previous glacial intervals: Stuart, 1979). Yet an essentially modern herpetofauna existed at least as far north as New Paris in southern Pennsylvania at the end of the latest glaciation (Guilday and others, 1964). Apparently, herptiles are able to respond to the shift from "equable" to "non-

equable" climatic regimes more swiftly than mammals, if indeed herptile ranges beyond ice limits were much affected by glacial-interglacial cycles.

Only one Late Wisconsinan Appalachian equable herpetofauna—Ladds, Georgia—has been described. This locality supports the equability hypothesis with two "northern" and two "southern" disharmonious species in an otherwise sympatric herpetofauna characteristic of northern Georgia today (Holman, 1976, 1980, 1985a, 1985b).

Several possible explanations for the lack of dramatic range changes in Wisconsinan herpetofaunas may be advanced based on evolutionary stability (few late Quaternary extinctions or originations) as well as apparent zoogeographic and ecologic stability (Fay, 1984b). (1) Herptiles can adapt more rapidly to climatic change than can mammals. Reptiles and amphibians have a marked capacity for acclimatization to seasonal climatic change, which may allow for physiologic rather than range adjustments over glacial-interglacial intervals. (2) There are fewer eastern North American "boreal" herptiles than mammals available to be displaced southward into the central Appalachians by glaciation. More than twice as many mammal (14) as herptile (4) species are restricted to the area north of the latitude of the New York-Pennsylvania border and east of Lake Winnipeg. (3) As herptiles can be more difficult to identify to species-level than mammals, climatically induced range changes may go unrecognized. Of the taxa just mentioned, all 14 species of mammals are known as fossils, but only one of the four herptiles has been identified as fossils. (4) Clinal morphological changes in space and time are difficult to quantify for herptiles because of the types of bones used in their identification and because herptiles are characterized by indeterminate growth. The record of Bergmann's Response and its climatic importance for Appalachian mammals (Guilday and others, 1978) is unknown and perhaps irrelevant for herptiles. (5) Much of the herpetofauna of the Appalachian region is endemic or has a widespread distribution centered on this region, reflecting both probable center of origin and restricted microhabitat requirements for many of the species. The region may have served as a glacial refugium for herptiles as it was postulated to have been for the eastern deciduous forest (Braun, 1950).

Although the ranges of other animals and plants changed in response to the glacial-inter-

glacial climatic shifts, herptiles of the central Appalachian Mountains were apparently unaffected by physical and biotic alterations over the past 30,000 years.

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LATE PLEISTOCENE FAUNA OF THE HOLLIDAYSBURG FISSURE. Shirley S. FONDA and Andrew P. CZEBIENIAK, Department of Geosciences, Pennsylvania State University, University Park, PA 16803

Excavation of a large vertical fissure 1.2 miles (1.9 km) northeast of Hollidaysburg, Blair County, Pennsylvania, has produced numerous vertebrate and invertebrate fossils of late Pleistocene age. The fissure is exposed in the southeastern wall of an abandoned quarry within the Upper Silurian Keyser Limestone, and is lined with thick drapes of travertine. Descending at least 40 feet (13 m), the fissure is 6 feet (2 m) wide and 18 feet (6 m) long; it was completely filled with rubble from cave breakdown and the weathering of surface material. The upper third of the fissure was filled with limestone blocks. The middle section, containing many blocks embedded in red-brown clay, yielded fragments of a young mastodon (dated by amino-acid racemization at about 12,000 yr B.P.) and numerous smaller animals. The bottom portion was filled with horizontally-bedded, varicolored clays, cave rubble, and well-weathered limestone blocks; several large pockets of fossils and many isolated remains were scattered throughout. An adjacent small cave continuous with the large fissure contained a wide variety of well-preserved bones, including numerous skulls and mandibles, some of which were still articulated. Also, a number of pockets within the travertine drapes contained abundant small vertebrates.

Forty-eight species of mammals were recovered, along with unidentified fish, frog/toad, salamander, snake, turtle, and bird bones. Invertebrates include at least three species of land snails and some insect exoskeletons. Sediment was collected at 2-foot intervals for pollen analysis in the future.

The smaller mammals are represented by most of their skeletal parts, whereas the large mammals, mostly juveniles, are represented in some cases only by a few teeth. Juveniles might have been prone to fall into a fissure through either carelessness or their size, whereas the few teeth might have been carried in by small animals such as pack rats. Other animals probably inhabited the fissure as is suggested by the occurrence of several 0.3-0.5 foot (0.1-0.2 m) layers of snake remains and a few pockets of frog bones. These snake bones were commonly articulated, and the sediment here contained up to 75 percent skeletal remains. The occurrence of many gnawed bones suggests that small rodents also inhabited the fissure.

Of the 48 species of mammals, six are now extinct (*Cervalces* sp., *Mylohyus nasutus*, *Tapirus veroensis*, *Mammot americanum*, *Castoroides ohioensis*, and *Canis dirus*). Although some (13 percent) of the species suggest a boreal habitat, the majority indicate a temperate woodland-meadow environment, somewhat cooler than the present. The more northerly species could represent relict populations.

The mammalian fauna (48 species) is represented by at least 7866 individuals, distributed (number of species, percent of total individuals) as follows: insectivores (6 spp., 23%), bats (2 spp., 0.6%), carnivores (11 spp., 2.2%), rodents (20 spp., 68%), lagomorphs (2 spp., 6%), perissodactyls (2 spp., 0.03%), artiodactyls (4 spp., 0.17%), and proboscideans (1 sp., 0.01%). The greatest number of species and individuals were found in the back portion of the fissure between the 21- and 25-foot (6.5-7.7 m) levels, in the front portion between the 31- and 33-foot (9.5-10.2 m) levels, and in the adjacent small cave.

THE HOT RUN SITE: A NEW PLEISTOCENE VERTEBRATE LOCALITY IN NORTHERN VIRGINIA. James R. OTT and Robert E. WEEMS, Department of Zoology, University of Maryland, College Park, MD 20742 and U. S. Geological Survey, Reston, VA 22092

The Hot Run Site is located in Frederick County, northwest Virginia, on the floor of the Shenandoah Valley. The site contains a diffuse, unstratified deposit composed primarily of sand and clay containing a mixture of late Pleistocene and Holocene vertebrate material. Uncommon elements include lithic artifacts assigned to the

Woodland and Archaic periods. Of the eight species of vertebrates present at the site, three (*Mammot americanum*, *Platygonus compressus*, *Equus* cf. *E. fraternus*, and possibly *Odocoileus virginianus*) are components of the late Pleistocene fauna, while one species (*Bison bison*) is known from the late Holocene. Three species of domestic mammals (*Bos taurus*, *Felis domesticus*, and domestic? sheep/goat) are also represented at the site. The investigation of Hot Run was initiated in 1977 following the discovery of the site by Mr. Jonas Chamberlain and James Ott. The overall research objective is a paleoecological reconstruction of the Hot Run Site during the late Pleistocene and early Holocene.

The Hot Run Site is located on a 13 acre tract of land owned by the V. V. Cutshaw family, 1000 feet (308 m) north of Stephenson, Virginia (39°14'22" North; 78°6'20" West); it is in the Stephenson, Va. Quadrangle, USGS 7.5' series. The site is at an elevation of 590 feet (182 m), and lies within a shallow depression at the confluence of four streams. The site lies east of U. S. Highway 11, south of State Highway 749, and west of the Baltimore and Ohio Railroad tracks. Closure of the 590 foot (182 m) contour line at the railroad bridge delimits the fossil-bearing area. Thus defined, the site extends 590 feet (182 m) north-south and 900 feet (277 m) east-west.

The Hot Run Site lies upon three Ordovician limestone formations: the Lincolnshire, the New Market, and the Oranda/Edinburg.

The presence of fossil material at Hot Run was brought to light through the construction of a pond which now forms the central feature of the site. The pond and its immediate environment have a complex recent history involving four major modifications between 1963 and 1984. Each modification has resulted in considerable change to the physiognomy of the site and each has simultaneously unearthed and buried large quantities of fossil-bearing sediments.

The original excavation of the pond took place circa 1963 and produced a collecting basin of three acres. The pond contained three islands. In August of 1977 the pond was partially drained and dredged and in November of 1980 a large number of the spoil piles created from the 1977 excavation were leveled. The dam was refurbished and the pond filled in the spring of 1984. This final modification flooded the major fossil-bearing areas of the site.

Between August 7 and August 24, 1977 abundant and highly visible fossil material was collected from the surface of the pond's margins.

Following the dredging of the pond on August 24, 1977, material was collected both by searching the surface of the spoil piles and by raking lightly the surface of the spoil piles and searching the disturbed areas. Surface collecting on the largest of the three islands was initiated on August 7, 1977 and continued until May 10, 1980 when a grid system was established on the island and a controlled subsurface excavation was initiated. Twenty quadrates were demarcated and nine were excavated to a depth of 14 inches (35 cm) in the following manner. Quadrates were cleared to a depth of 4 inches (10 cm). This material was then removed to the periphery of the island and washed. The underlying area thus exposed was turned over to a depth of 8 inches (20 cm), raked lightly and washed. This step was repeated with the plowing depth increased to 14 inches (35 cm). Additional fossil material was recovered by walking along the streams associated with the site, raking the stream channels, and examining the stream's substrate.

All vertebrate material recovered was washed in water and permanently labeled. With the exception of materials destined for radiocarbon or amino acid dating, all items were coated with either Duco Cement and Acetone, Elmers glue and water, or Carbowax, depending on their condition. The locations of many, but not all, fossil finds were recorded. For specimens collected on the island the depths at which they were found were also recorded. Sediment was removed from the pulp cavities of *Mammut americanum* molars and from sections of long bones for pollen analysis in the future.

From 1977 through April 1984, over 400 teeth, bones, and skeletal fragments were recovered and identified when possible. In addition, a large number of fragments too small to label and a small amount of lithic material have been recovered. Of the three species assigned to the late Pleistocene, *Mammut americanum* is the most commonly represented and is known from over 80 complete or partial milk teeth, premolars, and molars. In addition, a large number of tooth and tusk fragments, the latter not exceeding 12 inches (30 cm), and a small number of bone fragments, the largest weighing about 2 pounds, have been recovered. A *Mammut americanum* molar submitted to the radiocarbon laboratory of Richard Pardi, Queens College, N. Y., yielded a collagen date of $11,550 \pm 165$ ¹⁴C yr B. P. Other identified species from the late Pleistocene are *Platygonus compressus*, represented by one left calcaneus, one right proximal scapular fragment, one prox-

imal metatarsal fragment, and one left lower canine tooth, and *Equus* cf. *E. fraternus*, known from one complete lower third premolar. *Odocoileus virginianus* is known from three proximal antler fragments, two of which possess the basal surface which unites with the pedicel. The geological ages of these fragments are presently unknown.

Late Holocene species represented at the site include *Bison bison*, known from one left astragalus and one phalanx, and three domestic species: *Felis domesticus*, known from one radius; *Bos taurus*, known from one metatarsal; and domestic ?goat/sheep, known from one tibia.

Lithic materials recovered include the distal portion of an early Archaic knife 2.6 inches (6.5 cm) in length and 1.6 inches (4.0 cm) wide, made of rhyolite. This tool was found during subsurface collecting on the island in juxtaposition with fragments of *Mammut americanum* tusk and bone at the 4 to 8 inch (10-20 cm) depth. A number of worked chert flakes found primarily in black carbonaceous earth at the pond's southeast corner have been assigned to the Woodland Period.

The Hot Run Site appears to be a spring deposit and contains a mixed assemblage of vertebrate and lithic materials spanning at least 11,550 years. Further interpretation of the site must await completion of other studies now underway, including amino acid dating of elements representing the five indigenous species found at the site and analysis of pollen collected from within the *Mammut americanum* molars.

The authors express their appreciation to the V. V. Cutshaw family for extending permission to work on their property for the last 7 years. The Archaic knife was identified by Kurt Carr, Catholic University. Woodland artifacts and vertebrate materials were identified by the respective staffs of the Archeology and Vertebrate Paleontology divisions of the Smithsonian Institution, Washington, D. C. Funds for radiocarbon dating were graciously provided by the Sigma Xi Research Society and are gratefully acknowledged.

A PLEISTOCENE LEGACY: ARCTIC AND BOREAL ELEMENTS IN THE CONTEMPORARY BIOTA OF VIRGINIA. Susan L. WOODWARD and William F. RUSKA, Jr., Department of Geography, Radford University, Radford, VA 24142 and Montgomery County Planning Department, Christiansburg, VA 24073.

Arctic and boreal elements comprise a significant proportion of Virginia's contemporary biota, with the component species often occurring as isolated outliers of more northerly distribution areas. Until rather recently, northern affinities were explained by the migration of arctic and boreal forms southwards along the Appalachian Mountain system into a region where broadleaf deciduous forests had been stable since the Mesozoic. We know now from pollen studies that Virginia's vegetation was greatly affected by Pleistocene climatic changes and that during the last glacial maximum the State was covered by boreal vegetation, with tundra probably occurring on the higher Appalachian summits (Delcourt and Delcourt, 1981). The plant and animal species of these northern communities have, for the most part, retreated upslope and northward during the Holocene. Refugia for arctic and boreal species persist where fortuitous combinations of elevation, geology, and topography harbor cold, wet habitats: mountain summits above 4800 feet (1463 m); treeless summits and north-facing talus slopes; and high elevation areas with impeded drainage (Linzey, 1979; Ogle, 1982, 1984) (Figure). None of the current communities in Virginia truly replicate Pleistocene or Recent arctic and boreal ecosystems; all have been affected by local extinction, speciation and/or the admixture of austral forms.

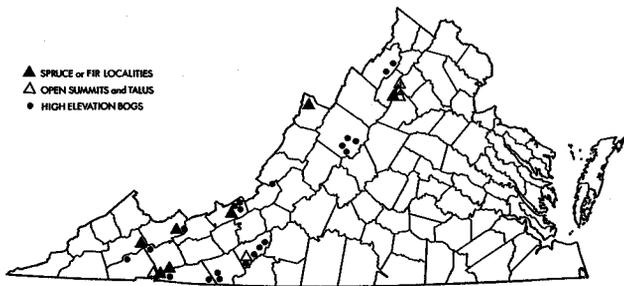


Figure. Refugia for arctic and boreal species in Virginia.

Spruce (*Picea rubens*) and fir (*Abies balsamea* and *A. fraseri*), although much reduced in areal extent by human activity, still occur on a few of the highest peaks and find their best expression on Whitetop Mountain (5520 feet, 1682 m) and Mount Rogers (5729 feet, 1746 m), respectively. Associated with these conifers are such boreal forbs as *Clintonia borealis*, *Maianthemum canadense*, and *Oxalis montana*. Whitetop is also apparently the last refugium in the State for the northern flying squirrel (*Glaucomys sabrinus*).

Open summits provide habitat for several arctic-alpine plants. *Arenaria groenlandica*, *Potentilla tridentata*, and *Trientalis borealis* thrive on the Blue Ridge monadnock, Buffalo Mountain (3971 feet, 1210 m), in Floyd County. Large populations of *Potentilla tridentata* also occur on Whitetop and on Hawksbill Mountain (4049 feet, 1234 m) in Shenandoah National Park.

High elevation sphagnum "bogs" occur in the Blue Ridge and the Valley and Ridge physiographic provinces. In very restricted habitats may be found such boreal species as *Vaccinium macrocarpon* and *Sanguisorba canadensis*. Some bogs in the southern Blue Ridge support relict populations of the bog turtle (*Clemmys muhlenbergi*).

Northern plants are also found outside the more typical "boreal" habitats (Harvill and others, 1977, 1981). Most of these are quite rare; arctic-alpine bearberry (*Arctostaphylos uva-ursi*), for example, has only a single Virginia station. Other rare northern species include *Dalibarda repens*, *Cornus canadensis*, and *Streptopus roseus*.

When trying to interpret disjunct distributions there is always a challenge in distinguishing between relicts and recent long-distance immigrants. In studies of mountain top islands in the Great Basin, Brown (1982) concluded that boreal mammals are relicts of the late Pleistocene, whereas boreal bird populations are maintained by presently high immigration rates. A similar pattern is evident in Virginia; northern mammals have suffered a steady attrition throughout the Holocene and only one species (*Tamiasciurus hudsonicus*) remains today which is not considered rare, threatened, or endangered state-wide (Linzey, 1979). No non-migratory boreal birds occur in Virginia at present, although some are known from the fossil record (Guilday and others, 1977). Populations of migratory boreal bird species occur at high elevations, presumably continually replenished by immigration. Migrant birds may also have played a role in dispersing arctic-alpine forbs to some of the open summits in the

State. The age and origin of these treeless areas are subject to debate and some at least are known to be post-Pleistocene.

ACKNOWLEDGMENTS

The authors wish to thank H. S. Adams of Dabney S. Lancaster Community College (Covington) and S. Croy and D. Allard of The Nature Conservancy (Blacksburg) for providing us unpublished data on the distribution of spruce forests and "bogs" in Virginia.

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- PROJECTILE POINTS FROM A MULTICOMPONENT SITE (44Sm51) IN THE SALTVILLE VALLEY, VIRGINIA. Ellen H. WHITE, Department of Anthropology, University of Virginia, Charlottesville, VA 22903 (Present address: 6349 Mershon St., Philadelphia, PA 19149)
- Projectile points from archeological site 44Sm51 convey a variety of information concerning the presence of prehistoric man in southwestern Virginia's Saltville Valley. This preliminary report—based primarily upon site tests conducted in 1984—illustrates the lengthy record of human presence available at the site, as well as this site's ability to significantly enhance the largely unexplored archeological data base of the valley.
- The Saltville Valley lies in the Valley and Ridge Province of the Appalachian Mountains. Until about 135 years ago, part of the valley supported a lake. The lake had been drained by 1850, after which much of the valley floor was used as pasture land. Salt extraction, the valley's principal commercial activity since late in the 18th Century, and its allied activities—including the construction of pipelines, furnaces, roads, railroads, factories, etc.—have altered the surface sediments over large parts of the valley. Beginning in the 1930's, high pressure injection wells were employed to extract subsurface salt deposits. Salt extraction has seriously undermined the bedrock of the region, causing some areas to subside. Railroad construction, removal of sediment for fill material, and use of the site surface as a parking lot for industrial employees, have further disturbed parts of site 44Sm51.
- Site 44Sm51 is situated on a terrace-like erosional remnant that is now one of the highest surfaces on the valley floor. This feature appears to be composed of colluvial slope wash from the adjacent Little Valley Limestone hills and was probably formed during the (?)Sangamonian Interglacial. The site has been probed sporadically by collectors for several decades. Only recently have professional excavations been undertaken. In 1980, a brief test of the site by archaeologists from the Virginia Research Center for Archeology produced evidence suggesting that it was a small late Woodland Period hamlet (Egloff, 1981). A group from Radford University investigated the stratigraphy of the terrace-like deposit in 1982, at which time a small (?)storage pit and several lithic and ceramic artifacts were recovered. In 1984, workers from Radford Uni-

versity conducted a test excavation at the site to determine the time span represented by archaeological evidence, and to assess the value of the site for further exploration.

The 1984 excavation consisted of sampling twelve 1-m x 1-m quadrants located along three transects crossing the site. In excess of 5,000 artifacts were recovered, including lithic tools, ceramics, and several specimens of non-human bone. Included among these artifacts was a wide range of projectile point types. In all, eighty-three projectile points, most made of chert, were found. Fifty-nine of these points were identified typologically using the standard guides available (Holland, 1970; MacCord and Hranicky, 1979; Swope, 1982); the remaining twenty-four points were incomplete, unfinished, or otherwise unidentifiable. The identified point types included Hardaway (2), Palmer (2), LeCroy-St. Albans (2), Big Sandy (2), Guilford (1), Stanly (1), Morrow Mountain (2), Lamoka (3), Halifax (2), Brewerton (5), Merom (3), Orient Fishtail (2), Fox Creek (1), Bare Island (3), Badin (1), Yadkin (9), Madison (9), Peedee/Pentagonal (2), and Clarksville (7). It is interesting to note that Bare Island, Fox Creek, Orient Fishtail, and Hardaway points are uncommon in the Tennessee River drainage basin of southwest Virginia. Thirty-four of the projectile points identified represent the Woodland Period, while twenty-five points represent the Archaic Period, including early Archaic types transitional from the Paleo-Indian Period. The points suggest, therefore, that this site was used by Indians of various traditions over some 10,000 years.

Clearly, 44Sm51 is a multicomponent site. Additionally, the recent excavations do not imply sedentism, nor that use of the site was restricted to the Woodland Period. On the contrary, the available data suggest that 44Sm51 was a site of transient occupation over an extended period of time, probably as a hunting and fishing station from which the valley bottom resources could be exploited easily. Since 44Sm51 has been excavated only on a trial basis, and since field work was concluded only a short time before this report was prepared, most conclusions are preliminary. Further excavations are needed in order to better understand the time frame, areal extent, and uses of this site.

This research was conducted by Radford University with support from the Town of Saltville and the National Geographic Society (grants 2512 and 2880 to J. N. McDonald).

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TOOLS AND DEBITAGE: CULTURAL DEBRIS FROM A MULTICOMPONENT SITE (44Sm51) IN THE SALTVILLE VALLEY, VIRGINIA. Eugene BARFIELD, Department of Anthropology, Indiana University, Bloomington, IN 47401

For almost two centuries the Saltville Valley of Virginia has been known for its contributions to paleontology. Evidence documenting multi-component human occupation of the Saltville Valley has accumulated for thousands of years. The archaeology of this area, however, has been largely ignored by professional archaeologists until recently. During the summer of 1984, a preliminary investigation of site 44Sm51 was conducted in order to determine the complexity and age of the site and to obtain greater insight into the prehistoric lifestyle of the aboriginal inhabitants of this valley. The following are partial results of the investigations carried out in 1984.

Site 44Sm51 is located on the west side of Saltville Valley on the top and sides of an erosional remnant lying some 23 feet (7 m) above the adjacent valley bottom which, until the middle of the 19th Century, contained a lake and marsh. Preliminary investigation of the sediment forming this terrace suggests that it accumulated during the ?Sangamonian Interglacial (McDonald, 1984). About 79 inches (200 cm) of ?Sangamon-age deposits lie unconformably over the Maccrady Shale (Mississippian) bedrock. Several centimeters of industrial debris—slag from furnaces, cinders from locomotives, gravel from

parking lots for heavy machinery, as well as discards left by collectors—now cover the surface. This site presents at least 32,292 ft.² (3000 m²) of surface suitable for human occupation. The site location provided an excellent view of the water and wildlife below.

Local amateur collectors have known of this site for many years, and valuable information has been lost through their activities. Areas for investigation in 1984 were selected with this in mind. A meter-wide strip was surveyed across the top and side of the hill from south to north for excavation; another meter-wide strip was surveyed east to west. Excavated squares were located where the least disturbance was noted. Twelve 1-m by 1-m squares were opened, but some were found to be so badly disturbed by previous collecting or industrial activity that they were abandoned.

Ten students from several universities as well as volunteers participated in the 1984 Radford University summer field-school. More than one thousand person-hours of labor were devoted to the archaeological field excavations. About 258 ft.³ (7.32 m³) of earth were carefully excavated by trowels, with stratigraphic control, and sifted through one-quarter-inch-mesh screens. Numerous piles of spoil left by collectors also were sifted. Although the artifacts recovered from these spoil piles were out of context, they provided information useful for the preliminary evaluation of this multicomponent site.

Of the twelve one-meter squares tested, six were especially productive. These squares yielded several thousand stone and ceramic artifacts. Tables 1 and 2 describe the categories, lithic composition, and horizontal distribution of cultural debris, exclusive of projectile points,

Table 1. Categories of lithic materials.

Flakes	4655
Shatter	70
Chunks	46
Nodule fragments	5
Unidentified tools	7
Scrapers	10
Drills	5
Hammerstones	4
Utilized flakes	14
Biface	1
Total	4817

Table 2. Lithic materials recovered by quadrant.

SQUARE	CHERT	JASPER	QUARTZ	QUARTZITE	RHYOLITE	CHALCEDONY
62E-86N	305	13	-	3	-	6
62E-97N	1439	47	4	2	44	-
62E-99N	1122	58	5	30	10	39
62E-101N	123	6	2	2	2	-
62E-102N	432	1	1	8	26	1
98E-61N	1001	24	1	8	3	12
Totals	4422	186	13	53	85	58

recovered in 1984. In addition, 134 potsherds were found; most were identified as the limestone tempered late Woodland Period Radford Series.

Projectile points from 44Sm51 suggests that the site was occupied intermittently by several different aboriginal groups over the last 10,000 years (White, this volume). Other tools and lithic residue associated with these occupations suggest that the site was used primarily as a transient hunting station. This conclusion is supported especially by the lithic tools recovered (Table 1) and the large number of small lithic flakes (Table 1), indicating that some tools had been finished or retouched at the site. The lithic material was primarily medium-gray, dark-gray, and black chert—probably obtained from quarries located nearby in the Holston River watershed. The source of jasper, the second-most common material, is not known, although local occurrences have been reported (Cooper, 1964). Additional analyses will be undertaken to determine if discernible patterns of size and distribution of the debitage can be recognized.

This research was conducted by Radford University and was supported by the Town of Saltville and the National Geographic Society (grant 2880 to J. N. McDonald).

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VIRGINIA'S FIRST EVOLUTIONIST: JAMES LAWRENCE CABELL. N. T. BOAZ, Virginia Museum of Natural History, P. O. Box 3991, Martinsville, VA 24115.

The mid-nineteenth century was a confused intellectual battleground of ideas, where the traditional doctrines of the church came into conflict (not for the first or the last times) with scientific notions of man's place in nature. To further charge the environment of debate religious and scientific arguments were adduced on both sides of the political questions of slavery and the contrasting economic systems of South and North.

It was undoubtedly difficult for contemporary natural scientists to avoid the implications of their work for the political questions of the day, but it has been virtually impossible for modern historians of science to analyze the scientific questions without recourse to inferred political motivations involved, particularly of those individuals in the South (e.g. Gould, 1981; Brace, 1982). As interesting as these questions may be, this presentation deals exclusively with the scientific problems.

James Lawrence Cabell, M. D. was Professor of Comparative Anatomy and Philosophy at the University of Virginia for a period of 52 years, from 1837 until his death in 1889. Like his well-known German contemporary, Rudolf Virchow, he combined a strong interest in natural history with important work in public health. Cabell organized the American National Board of Health and served as the president of the American Public Health Association. He was the nephew of Joseph C. Cabell, Jefferson's spokesman in the Virginia General Assembly during the legislation enabling the founding of the University of Virginia (Dabney, 1981, p. 16). For many years he lived in Pavilion II, and is remembered in one of the Chapel windows at the University of Virginia (O'Neal, 1976 p. 63,72).

Cabell wrote a lengthy review of the influential book published in 1854 by Josiah C. Nott and George Gliddon, of Mobile, Alabama, entitled *Types of Mankind*. The review appeared in the *Protestant Episcopal Review and Church Register* of January, 1857. This review was subsequently

expanded and published in New York as a volume of over 300 pages as *The Testimony of Modern Science to the Unity of Mankind*. This volume also reprints an 1857 review by Cabell of *Indigenous Races of the Earth*, by seven authors including Nott and Gliddon, and such notables as Joseph Leidy, Louis Agassiz, and J. Aitken Meigs.

Cabell's motivation in writing these works was clearly to counter the polygenic argument of human origin advanced by Nott and Gliddon, which he considered contrary to both natural science and the biblical Mosaic account. But, as with Darwin two years later, his arguments were based exclusively on scientific data. As he stated (1858, p. 11), "any attempt to fetter the scientific inquirer by the supposed meaning of inspiration, is certain to damage the latter in the estimation of a numerous class of intelligent and learned men." Virginius Dabney (1981, p. 16) credits Cabell with being "ahead of Darwin in publishing a work that recognized the theory of evolution" and by anticipating "by many years Hugo de Vries's theory of mutations." On the other hand, a review of the literature reveals that apparently no modern historian of science has even cited Cabell or his evolutionary work. The present analysis indicates that Cabell was indeed an important figure in the development of evolutionary thought in America, although it is also clear that, unlike Darwin's and Wallace's theory, his formulation lacked the key element of natural selection as the mechanism of evolutionary change.

Cabell (1858, p. 17-19) recognized a species as a group of beings with "constant defining characters" and which had "sprung from a common stock." He argued against the concepts of the influential Samuel George Morton and Louis Agassiz, which held species to be unchangeable, "primordial organic forms." He pointed out that the varieties that were known to exist in species were clear indications of adaptations to different environmental conditions. Cabell therefore understood one of the basic tenets of the Darwinian paradigm to follow, i.e., that variation exists within a species which can act to adapt the species to a particular environment.

Cabell's commitment to evolution—that is, that species change through time—is clear. He states (1858, p. 20) that, ". . . certain *acquired* peculiarities are often reproduced with perfect regularity so as to give rise, within the limits of a single original species, to '*varieties*' marked by characters as '*permanent*' as those which distinguish the species itself. . ." Yet, he did not continue

to the Darwinian conclusion that this evolution would lead to the production of new species. In a footnote, Cabell (1858, p. 21) endorses Dana's definition of a species as "based on a specific amount or condition of concentrated force in the act or law of creation." We may thus conclude that Cabell accepted evolution, but only *within* species, which were themselves created.

Today we would characterize Cabell's evolutionary mechanism, the inheritance of acquired characters, as "Lamarckian." However, Cabell apparently derived most of his belief in this thesis from Johannes Muller of Berlin, a disciple of Goethe and the mentor of Virchow and the anthropologist Hermann Klaatsch. Appendix A in Cabell's book is dedicated to a discussion of Muller's ideas. As Cabell (1858, p. 22-23) discusses it:

The law of the permanency of primordial forms is admitted on all hands to be subject to qualifications. Within certain limits [the species], it adapts itself to various changes in the influences under which the race may subsist. Thus, by carefully changing the food and other agents of vital stimulation, we may modify, to an extent sometimes quite considerable, the outward structural character of many plants and low animal organisms; and these newly acquired characters may then be perpetuated by hereditary transmission, under the influence of the law of assimilation between parent and offspring, even though the causes which originally determined the variation from the primitive type have ceased to operate.

From this passage it is clear that Cabell in no way implied differential survival of offspring, although he recognized, as Darwin did, that variability could be inherited.

Cabell postulated a second manner of variation, what we term "mutations" and what Darwin termed "sports." He stated, "a similar effect [to inheritance of acquired characters] is produced in those cases in which a given variation appears accidentally in a single individual and is then transmitted to his offspring" (Cabell, 1858, p. 23). This idea is the basis for Dabney's (1981) reference to de Vries's theory of mutation, and it is an early, though incorrectly synthesized, realization that mutation is a major contributor to species' variability.

As Darwin, Cabell lacked the Mendelian prin-

ciple of particulate inheritance and thus was faced with the problem presented by the theory of blending inheritance. Cabell noted that in cases of "accidental variations," both sexes must possess the trait if it were not to be lost through admixture in the general population. One must conclude that he considered the inheritance of acquired characters the more important of the forces of evolution.

In lengthy passages on physiology, history, linguistics, and geology that sound remarkably "modern," Cabell argued for the basic unity of the human species. He (1858, p. 317) disputed claims by Sir Richard Owen and Jeffry Wyman that the human races differ as much as the "three species" of orangutan. As is now well known the orangutan consists of a single species, *Pongo pygmaeus*. Cabell's (1858, p. 309) position on the unity of the human species is made clear in a passage comparing Sir Isaac Newton with the rest of humanity:

Can such a "celestial genius" one may reasonably ask, be of the same original parentage with the Bushman, who lives in holes and caves, and devours ants' eggs, locusts and snakes? . . . It should not surprise us that when we contemplate exclusively the patent diversities of races and overlook the less obvious but more significant evidences of a common nature, we should shrink from the conclusion to which a deeper insight into the facts must yet inevitably conduct us.

Cabell's position, of course, has been amply sustained in this regard over the past 126 years.

In conclusion, James Lawrence Cabell clearly was ahead of most of his American contemporaries, including Nott, Gliddon, Agassiz, and Dana, in correctly recognizing many of the central points of evolutionary theory as they were eventually explicated by Darwin and Wallace. As Darwin, he was forced to accept the doctrine of inheritance of acquired characters (Darwin's "pangenes") as an answer to loss of inherited change through "blending" in populations, since neither knew of Mendel's work. Yet, Cabell lacked Darwin's insight that races could be incipient species, and that differential reproduction lay at the base of evolutionary change through time.

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