Geoscience Canada

Methods in Quaternary Ecology #12. Vertebrates

C. S. Churcher et M. C. Wilson

Volume 17, numéro 2, june 1990

URI : https://id.erudit.org/iderudit/geocan17_2art01

Aller au sommaire du numéro

Éditeur(s)

The Geological Association of Canada

ISSN

0315-0941 (imprimé)
1911-4850 (numérique)

Découvrir la revue

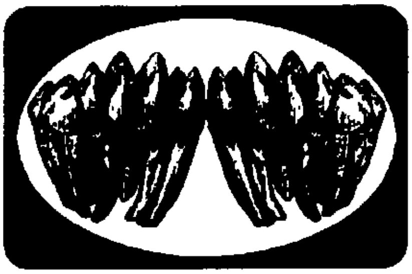
Citer cet article

Churcher, C. S. & Wilson, M. C. (1990). Methods in Quaternary Ecology #12. Vertebrates. *Geoscience Canada*, *17*(2), 59–78.

Résumé de l'article

The original fascination of scholars with Quaternary vertebrates was more related to their sometimes astonishing size and characteristics than to their value in paleoenvironmental reconstruction. The dominant place occupied by Quaternary vertebrates in the paleontological literature owes much to the high visibility of larger species as well asto our own affinity with the Mammalia. Nevertheless, it is clear that vertebrate fossils have enormous potential in the reconstruction of ancient climates and environments. This po-tential extends to the detection of unusual environmental parameters, such as extentand severity of seasonal stresses and even such a specific factor as depth of winter snow. Although many of the larger Quaternary mammals became extinct, modern analogues exist for a large number of fossil forms, allowing inferences of temperature,moisture, substrate, vegetative cover or presence of particular food plant species. Further, the study of small vertebrates, whether mammals or other species, allows paleontologists to make similar inferences based on animals that are relatively tied to one place and cannot migrate as do large ungulates orbirds. Information obtained from these dis-parate sources can serve as a primary suiteof proxy environmental data, as a cross-check on other proxy sources, or as an element to be used in complex transfer functions employing input from multiple proxysources. As methods are refined, the potential for dating bones and teeth directly through radiocarbon, amino-acid racemization, electron spin resonance, uranium-series or other methods should ensure that vertebrate remains will also be of great value in establishing absolute time-sequences of local and regional environmental changes.

Articles



Methods in Quaternary Ecology #12. Vertebrates

C.S. Churcher
Department of Zoology
University of Toronto
Toronto, Ontario M5S 1A1

M.C. Wilson
Department of Geography
University of Lethbridge
Lethbridge, Alberta T1K 3M4

Summary

The original fascination of scholars with Quaternary vertebrates was more related to their sometimes astonishing size and characteristics than to their value in paleoenvironmental reconstruction. The dominant place occupied by Quaternary vertebrates in the paleontological literature owes much to the high visibility of larger species as well as to our own affinity with the Mammalia. Nevertheless, it is clear that vertebrate fossils have enormous potential in the reconstruction of ancient climates and environments. This potential extends to the detection of unusual environmental parameters, such as extent and severity of seasonal stresses and even such a specific factor as depth of winter snow. Although many of the larger Quaternary mammals became extinct, modern analogues exist for a large number of fossil forms, allowing inferences of temperature, moisture, substrate, vegetative cover or presence of particular food plant species. Further, the study of small vertebrates, whether mammals or other species, allows paleontologists to make similar inferences based on animals that are relatively tied to one place and cannot migrate as do large ungulates or birds. Information obtained from these disparate sources can serve as a primary suite of proxy environmental data, as a cross-check on other proxy sources, or as an element to be used in complex transfer functions employing input from multiple proxy sources. As methods are refined, the potential for dating bones and teeth directly through radiocarbon, amino-acid racemization, electron spin resonance, uranium-series or other methods should ensure that vertebrate remains will also be of great value in establishing absolute time-sequences of local and regional environmental changes.

Introduction

Vertebrate paleontology has a relatively long pedigree as compared with other Quaternary paleoecological disciplines. Early interest in Quaternary vertebrates can, in part, be attributed to the large size and high visibility of many mammalian fossils, coupled with a fascination with "antediluvial giants" and other quasi-scientific pursuits. Association of artifacts with remains of extinct animals heightened interest before, and especially during, the early Darwinian era. Direct use of fossil vertebrates in reconstructing Quaternary paleoenvironments was well established by the late 19th century.

The subphylum Vertebrata comprises five major chordate groups, all amply represented by fossilized hard parts: Pisces (fishes), Amphibia (amphibians), Reptilia (reptiles), Aves (birds) and Mammalia (mammals). In terms of the modern world fauna, fishes are by far the most diverse and numerous group, but are mainly marine and thus of lesser importance in the Quaternary nonmarine record. Early taxonomists treated Pisces as a single class, but currently the fishes are placed in three or more classes (*e.g.*, Agnatha, Chondrichthyes and Osteichthyes), while retaining as classes the other vertebrate groups listed above. Mammalian remains, because of their abundance, ubiquity and ease of preservation, dominate the literature on vertebrate paleontology. Mammoths and other "Quaternary giants" are awe-inspiring and have attracted the disproportionate attention of public and scientists alike. On the other hand, microvertebrate fossils are, in many cases, more informative about past environments than are the larger forms; these include the remains of such diverse groups as Rodentia (rodents), Chiroptera (bats), Insectivora (shrews and moles) and a host of small birds, amphibians and fishes.

Vertebrates have enormous potential in reconstructions of paleoclimates, substrate characteristics, vegetation cover, food chains, evolutionary changes, biostratigraphy and general paleoenvironments of a given time period. Vertebrate species display extraordinary size variation: mammals range in length from about 55 mm for the smallest shrew *(Microsorex hoyi)* to about 30 m for the blue whale *(Sibbaldus musculus)*. The animals' size and mobility are important considerations in paleoenvironmental reconstruction, so that interpretations can range from the local environmental level on the basis of microvertebrate fossils to broad regional interpretations based on the presence of large, mobile animals such as bovids (cattle, bison and relatives) or proboscideans (elephants and mammoths).

Vertebrate fossils are usually directly preserved hard parts, such as bones, teeth and occasionally muscle, hair and hornsheaths (Figure 1). Indirect evidence includes trace fossils or ichnites (footprints, skin casts or burrows), nests such as middens of woodrats *(Neotoma)* or dens of hyenas *(Crocuta* or *Hyaena)*, tooth marks or distinctive bone breakage patterns left by predators and scavengers, coprolites or droppings and owl pellets that may contain bones and hair of other vertebrates. Mummified remains of animals may be encountered in dry caves and other arid environments; examples are the North American camel *(Camelops hesternus)* or the Australian marsupial wolf *(Thylacinus cynocephalus)*. Frozen carcasses have been found in permafrost; they include the woolly mammoth *(Mammuthus primigenius)* and woolly rhinoceros *(Coelodonta antiquitatis)* from Siberia, and long-horned bison *(Bison priscus)* from Fairbanks, Alaska from frozen "muck" or organic silt overlying gold-bearing gravel (Guthrie, 1990; Harington, 1990). These provide more complete evidence of morphology, colour, preserved external and internal soft parts, and stomach contents. Similar soft-part preservation occurs in woolly rhinoceros remains from salt-, tannin- and petroleum-impregnated deposits in Poland (Kurtén, 1968) and in human remains from northern European bogs (Glob, 1969). The detection and specific identification of blood residue on stone tools (Loy, 1983) has opened up a new and important area of study.

This paper presents a general introduction to Quaternary vertebrate paleontology, particularly in the context of research undertaken in North America. The nature and potential sources of vertebrate remains, and field sampling techniques are discussed. Evolutionary and zoogeographic patterns can be deduced through analysis of fossil bones, and vertebrate remains play an important role in biostratigraphy. For further details on Quaternary vertebrates in North America see books or papers by Auffenberg and Milstead (1965), Graham (1986), Graham and Semken (1987), Harington (1984a,b), Hibbard (1958, 1970), Hibbard *et al.* (1965), Kurtén and Anderson (1980), Lundelius *et al.* (1983, 1987) and Semken (1983).

Historical Development

Bones of large fossil mammals were viewed by Teutonic peoples as the remains of trolls from the underworld, by the Chinese as remains of devils or dragons and by the ancient Greeks as those of the Cyclops. Later, Christian mythology suggested that they were the remains of victims of Noah's Flood who failed to get into the ark. For example, a fossil skeleton of the large salamander *Andrias scheutzeri* was named *Homo diluvii testis*, literally "Man, witness of the flood." This interpretation, while fanciful, was an attempt to integrate fossil evidence with an hypothesized earlier climatic-environmental event, a "world-wide" flood that destroyed and altered the landscape and its biotas.

Detailed studies of vertebrate paleontology began with Baron Georges Cuvier and Alexandre Brongniart in France. They recognized a succession of vertebrate faunas, but saw them as separated by pervasive catastrophes and extinctions. "Catastrophism" of a sort is seen in current concepts of the importance of asteroidal impacts in causing mass extinctions. Specialized studies of vertebrate groups followed close on the heels of Cuvier's pioneering work. Smith (1817) was one of the first to recognize that there was a stratigraphic framework in which fossils acted as indicators of similar strata and thus relative ages and vertical relationships. The study of fishes, begun by Cuvier (1812), was continued by Agassiz (1833-1844), still a basic reference to the field. Reptiles and Quaternary mammalian fossils, especially "vanished giants" *sensu lato*, were studied in Great Britain by Buckland (1824, 1836), Mantell (1825), Owen (1846, 1849-1884) and Dawkins (1878), whose work was continued by Reynolds (1939).

North American Quaternary vertebrate explorations began in the late 18th century near Big Bone Lick, Kentucky, the first fossiliferous deposit with a recognized complex fauna in North America. The description of animals such as the extinct ground sloth by Thomas Jefferson (1799), mastodon *(Mammut americanum)* and giant bison *(Bison latifrons)* by Peale (1803a,b) attracted great public interest. Jefferson mistakenly believed that the ground sloth *Megalonyx* was a giant carnivore, on the evidence of its isolated huge claws. Some of the material from Big Bone Lick was transported to the fledgling Natural History Museum in London, England, ultimately to be studied by Owen or Dawkins. Rembrandt Peale, who was both an artist and gifted amateur naturalist, excavated the first complete skeleton of a mastodon at Newburgh, New York, with his brothers Charles and Titian, in 1801. Peale did a large oil painting of the excavation showing the bones, the lifting mechanism for removing the soil, and himself holding forth about the discovery.

During these early years, the reconstruction of paleoclimates and paleoecology was uncertain and rudimentary, but, in Canada, for example, J.W. Dawson (1878, 1883) recognized that the Gulf of St. Lawrence and the Ottawa Valley had been inundated by the Champlain Sea. Discoveries of vertebrate fossils (Harington and Occhietti, 1988), including fishes (Dawson, 1891), seals (Dawson, 1878; Leidy, 1856; Lyell, 1845) and whales (Billings, 1870; Dawson, 1883), played a role in reconstructing the Champlain Sea's environment. Even then, misidentification of one seal until the 1970s prevented geologists and biologists from realizing how cold this sea was (Harington, 1984b). Agassiz (1850) brought to North America an expertise in glacial sequences and land forms, learned in the Swiss Alps, as well as his experience with fossil fishes, and recognized a sequence of proglacial lakes in central North America partly on the basis of the fishes in the lake silts. By the late 19th Century, it was well understood that climatic change had been dramatic during the Pleistocene (Dawson, 1893; Wright, 1890).

During the late 19th and early 20th centuries, A.P. Coleman worked assiduously in southern Ontario and collected many vertebrate fossils, especially from the Toronto area (Coleman, 1901), with the specific goal of reconstructing ancient climates. Adding excursions to the Prairies and Quebec, he formulated a sequence of glacial events that paralleled the sequence being described for the European Pleistocene. He showed that climatic change had involved cyclic glacial and interglacial events, with anywhere from two to five cycles represented. Many attempts have since been made to correlate vertebrate faunas with the glacial/interglacial sequences in both the Old and New Worlds (see Flint, 1971). The greatest problem with this biostratigraphic approach is that definition of faunal stages depends on the presumption of a well-established and dated geological chronostratigraphic equivalent. The utility of the concept of a "Kansan" or a "Nebraskan" fauna, for example, can readily be questioned as the geological stratigraphic names in their type areas have been abandoned (Richmond and Fullerton, 1986).

Early Quaternarists were primarily interested in the stratigraphic relationships of

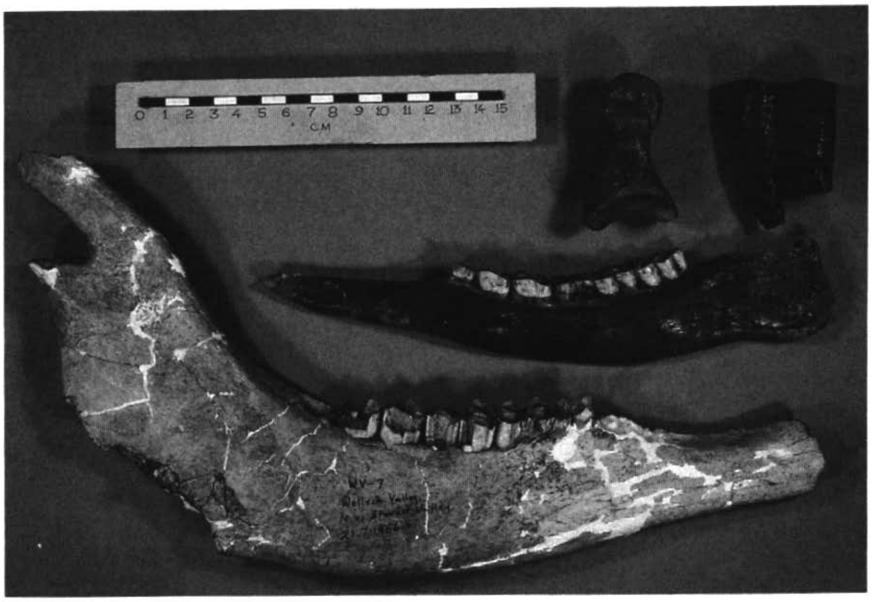


Figure 1 *Quaternary fossils from the South Saskatchewan River Valley, Alberta and Saskatchewan. Top left: extinct camel* (Camelops hesternus) *lower molar, Kansan age, Island Bluff, Medicine Hat; top right: giant sloth* (Nothrotheriops shastense) *toe bone (proximal phalanx), Kansan age, Low Bluff, Medicine Hat; centre: caribou* (Rangifer tarandus) *dentary, Sangamonian or Middle Wisconsinan age, Mitchell Bluff, Medicine Hat; bottom: camel* (Camelops minidokae) *dentary, Jaw Face Section, Wellsch Valley site, Stewart Valley.*

depositional units, and in fossils as indicators of age (and occasionally of environment). Later workers became more interested in the morphological succession of specific lineages of fossils, *e.g.*, horses (Scott, 1913; Simpson, 1951) or mammoths (Osborn, 1936-1942), and thus in the evolutionary sequences, phylogenies and dispersal histories of individual groups. Only later were biotas regularly seen as assemblages from which meaningful deductions about paleoenvironments could be made; this view depended upon uniformitarian thinking (Hutton, 1795) based in analogies from modern examples. In recent decades, bone *assemblages* have become the preferred time indicators, displacing individual index fossils from their previously pre-eminent perch as the key to the ages of strata.

Taphonomic Considerations

The compound origin of a single death assemblage (thanatocoenosis) may not be obvious. Attempts to reconstruct communities are perturbed by differential transportation of skeletal elements, admixture of taxa from different communities, or by mixing through redeposition of fossils from deposits of different ages (Behrensmeyer, 1984; Efremov, 1940). Terrestrial vertebrate remains found in marine deposits illustrate processes of long-distance transport and reworking. Inclusion of an ungulate in an assemblage dominated by fish and other aquatic fossil forms, as well as rodents, might at first elicit less suspicion. The variety of possibilities available for such occurrences has given rise to the concept of "proximal" and "distal" taxa in mixed assemblages, the former representing animals resident in the area of deposition and the latter those that resided elsewhere and were included because of postmortem transportation processes (Shotwell, 1955). These are clearly extremes in a continuum, because the distance of transport must influence the quality of preservation.

The elements of a corpse may not remain closely associated and are unlikely to do so if it remains exposed on the surface for long. Scavengers may remove elements or consume some and damage others, in the process scattering elements over a wide area (Sutcliffe, 1970). Weathering (differential heating/cooling, freeze/thaw, chemical attack, eolian abrasion) may alter a bone's surface and destroy minor features; most important, it can split sutures and crack shafts of longbones. The extent of weathering can be used, in retrospect, to judge the length of exposure time (Behrensmeyer, 1978). Flowing water, whether in sheets on featureless surfaces or as streams or rivers, collects and sorts unburied skeletal elements for deposition. Sorting occurs in the same way that other sedimentary particles are segregated; bones in such an environment can be viewed as nothing more than unusually shaped grains of sediment (Figure 2). Sheets of water from a sudden intense thunderstorm can carry large bones and even small boulders across a gently sloping surface and leave them in local hollows as collections of isolated elements, without any articular relations and representing a mixed thanatocoenosis. Once buried, these accumulations occur in depressions on the ancient surface.

It is not possible in this space to review the entire field of vertebrate taphonomy. Readers are referred to other reviews (Shipman, 1981; Behrensmeyer, 1984; M.V.H. Wilson, 1988) for more information. As an example, we will consider the effects of fluvial transport (Figures 3 and 4). Rivers receive carcasses of drowned animals or can entrain carcasses from the floodplain during floods or through lateral cutting on meanders. These remains can be transported far downstream, through floating of bloated carcasses or through more complex processes (M.V.H. Wilson, 1988). The skeleton will become mechanically disarticulated by current action unless, through desiccation, the skeleton has become "armoured" within its hide. Small bones similar in width and length behave as small pebbles and roll along the river bottom, bouncing in the current and being carried great distances. Large bones, in which there are fat-filled cavities, have a density significantly less than that of water, and tend to roll about their long axes, which become oriented at right angles to the current. As long as the bottom is even and the current moderately strong, such bones will move downstream. Bones or elements that have large air-filled cavities, such as sinuses in the skull, or a cavity that may be filled with either fat or gases from decomposition, may

Figure 2 *Fossil bison skullroof (frontlet) with right horncore, old adult individual, Bighill Creek Formation, Bow River Valley, Alberta (ca. 11,000 years B.P.). Fluvial transport has abraded the end of the right horncore, broken off the left horncore, and thinned bone on the frontal surface to expose sinuses. Comparative measurements of such waterworn specimens are untrustworthy and statistical treatment is unreliable based on specimens from such environments.*

float on the surface and may therefore be carried farther than those that move along the river bottom. Portions of the structure that hang down from the centre of buoyancy, such as horns, antlers or facial bones, will drag or hit against the bottom or any projecting rocks, and may be broken away (Figure 2). Thus crania are often separated from facial regions and the ornamentations are damaged or absent, especially in the ungulates. Irregular structures, such as pelvic girdles, broken skulls with antlers or horns, or mandibles, have little flotation ability because they lack large cavities. Some bones are too heavy and large for a stream to roll or move by force, and their projections lodge in the bottom sediments. However, human skulls tend to behave like air-filled balls and float for long distances (Boaz and Behrensmeyer, 1976). Elements that lodge on the bottom are transported the least distance and are frequently buried by bottom sediments almost as soon as they are disarticulated from the carcass. Because bone is less dense than the minerals of the associated sediment grains, sorted bones will generally be larger than the sedimentary matrix in which they are buried. Given knowledge of the densities of bone and sediment grains, hydraulic equivalencies can be computed and associations broadly predicted. A seeming exception to the rule of relative size is the occurrence of tiny bones in pebble or cobble gravels, but this in fact parallels the processes producing bimodality in conglomerates.

The sorting and redistribution of skeletal elements downstream in a river bed is a study in itself (*e.g.*, Boaz and Behrensmeyer, 1976; Frison and Todd, 1986; Shipman, 1981). Small, dense pieces (such as isolated teeth or fragments of broken longbone shaft) and large, awkward elements (such as antlers or pelves) move only short distances before they are deposited. Teeth and small bone fragments may, under the right circumstances, travel farther, in which case they can become so abraded as to be indistinguishable in shape from the associated pebbles. Small, but light, bones such as carpals and tarsals move well and can become similarly abraded, but most often are trapped in sand or fine gravel. Longbones with resistant shafts and extensive lumina or fat-filled cavities roll along the bottom, while skulls with sinuses or braincases filled with gases from decomposition float easily. Thus, it is almost inconceivable that many elements of a skeleton will remain close together after significant transport. Most elements that have been transported will show signs of abrasion or breakage from contact with the substrate (Figure 5). After they become lodged in the bottom, exposed areas are still subject to damage from contact with other transported grains, ranging from fractures by cobble impact to "sand-blasting" by finer grains. The ends, or epiphyses, of longbones are formed of softer cancellous bone than the shafts, or diaphyses, which are constructed of dense compact bone; after extensive transport, this differential resistance to erosion means that a bone will have lost its significant articular characters. Even lightly abraded bones will give lower than expected articular measurements, while some will be reduced to cylinders lacking articular ends. Such abraded cylinders are also produced by scavengers chewing on the soft articular ends and "rasping" out the softer internal structure with their roughened tongues (Binford, 1981) (Figure 6), so varied taphonomic pathways can lead to similar ends. Microscopic analysis of surface characteristics may be necessary to resolve such ambiguities.

Bones are deposited whenever the current slacks, reducing transporting ability. Slower currents occur near the bottom and sides of a river due to frictional drag. Thus, a bone that is travelling over a smooth surface in mid-stream will move farther and faster than one near the stream's margin. The current is also slack or weak on the inside of a meander curve, so that bones and other sediment tend to be deposited on point bar surfaces (Figure 7). Fossil bones in the Old Crow Basin represent complex depositional histories (Morlan, 1980). Today, the Old Crow River is reworking its old sediments through lateral channel migration and, because its exit from the basin is still lowering, is winnowing the bones from the basin fill, transporting them along its bottom and, when in flood, carrying them up and onto point bars on major river bends, where they are available for recovery by scientists.

Taphonomic factors can influence the identification of paleospecies. In a group with features (*e.g.*, horn-cores) that continue to change with age, it becomes necessary to compare samples of similar population composition. In bison, for example, a gravel pit "population", reflecting alluvial transport of animals accumulated through attritional mortality, would ideally, and because of the nature of the attritional mortality profile, be rich in juvenile and very old individuals (Reher, 1970; Voorhies, 1969). Because juvenile skulls are fragile and more susceptible to damage in fluvial transport, the "population" will be dominated by old individuals (Figure 2). A population of comparable antiquity from a drive-kill site, such as a buffalo jump or trap, would be rich in animals from the intervening age groups, would be dominated by females, and would contain numerous immature calves and even foetal bones (Figure 8). Adult males from the bison kill would typically exhibit more slender horn cores than would males from the alluvial gravels, because the average individual age of the former would be significantly younger (Wilson, 1978). This is one of several factors that led to oversplitting of fossil bison species during the past 100 years. Reliable comparisons can only be made of faunas or samples that have similar

Figure 3 *Pleistocene horse* (Equus *sp.) rib in bedding plane or paleosurface of a river bar. Note that the rib is associated with a change in depositional texture marking the surface of a paleo-bar form. Sangamonian or Mid-Wisconsinan deposits at Mitchell Bluff, South Saskatchewan River Valley, Medicine Hat, Alberta.*

Figure 4 *Pleistocene horse* (Equus *sp.) toe bone (proximal phalanx) in sand deposits. Note that the bone is larger than the surrounding matrix grains demonstrating its lesser density. Sangamonian or Mid-Wisconsinan deposits at Mitchell Bluff, South Saskatchewan River Valley, Medicine Hat, Alberta.*

Figure 5 *Extinct horse* (Equus ?conversidens) *metapodial or cannon bone in cobble gravels. Note ends worn to show cancellous inner structure and broken shaft from loading by gravels. Kansan age, Low Bluff, South Saskatchewan River Valley, Medicine Hat, Alberta.*

taphonomic histories or that have been corrected to compensate for known differences.

Detailed study of the depositional environment and reconstruction of the taphonomic history of a bone occurrence are necessary prerequisites to paleoenvironmental inferences. As noted earlier, some occurrences may be obviously disharmonious, but others may be more intriguing than suspicious. A mountain goat *(Oreamnos americanus)* from a prairie point bar deposit might elicit discussion of changing ecological preferences if a researcher does not take time to consider the implications of its depositional context.

Fossil Material

Fossils have traditionally been considered to be the hard parts remaining from an animal after death and decomposition of the soft parts, but there are other possibilities. Horn-sheaths, eggshells or feathers may be preserved or traces may remain that also attest to the existence of an organism (*e.g.*, burrows, footprints, nests or tooth marks). Such shed elements as antlers and deciduous teeth resemble trace fossils in not requiring the death of the organism to enter the geological record. In general, robust elements preserve better than others and are less distorted or broken. Large elements are differentially preserved because of their strength and because, even when fragmented, their parts

Figure 6 *Fossil bison metacarpals (or front limb cannon bones) showing action of scavenging canids (dogs or wolves).* ***Left****: anterior surface of mature metacarpal showing extensive scoring by teeth;* ***centre****: (posterior surface), exposure of cancellous bone at both ends of bone;* ***right****: anterior surface of immature metacarpal reduced to cylinder by removal of articular ends' cancellous tissue. Left and right, Hitching Post Ranch site, Alberta, about 3500 years old. Centre, Late Pleistocene gravels, Peace River area, Alberta. Note differing scales.*

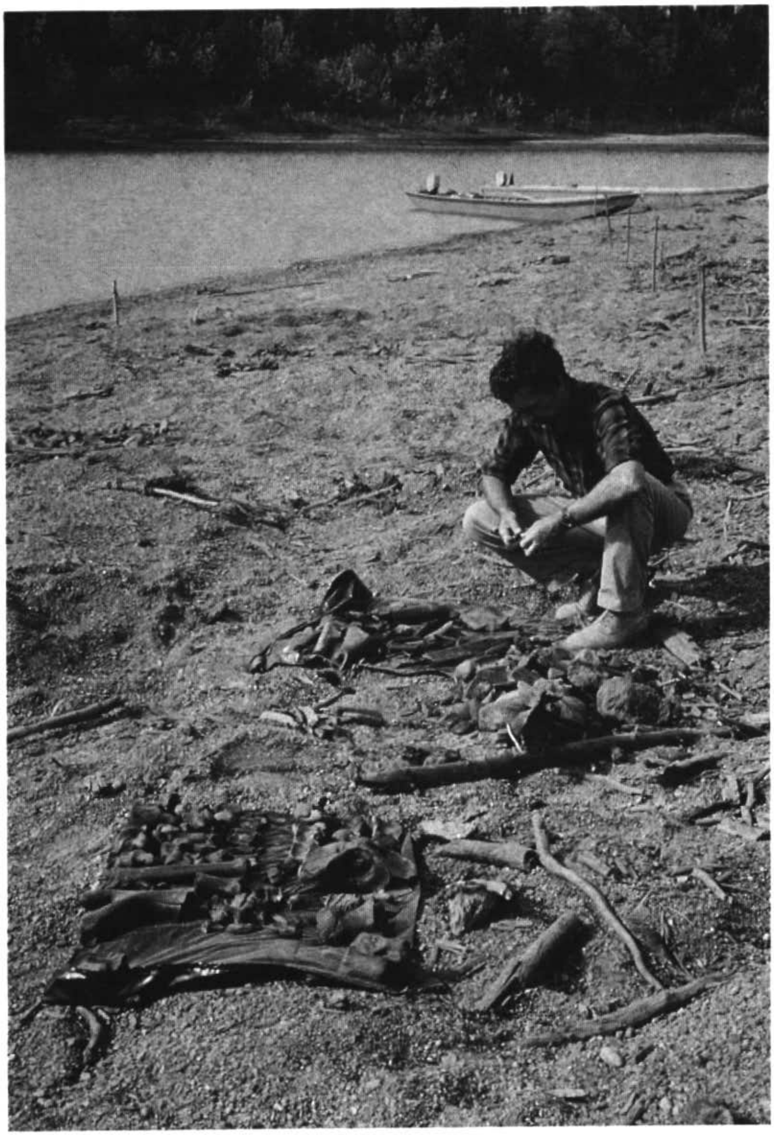


Figure 7 *Old Crow River Locality 11A, Yukon Territory. Pointbar with bones and wood derived from reworking of cutbanks. Specimens have been collected from surface of sands and fine gravels composing the bar.*

Figure 8 *Fossil foetal or neonatal bison bones, Reservoir Gully site, Medicine Hat, Alberta (ca. 1000 years B.P.).* **Left to right:** *metacarpal, vertebral spine, tarsal (ectocuneiform) and metatarsal (cannon bone of hind limb). These are from primary deposition in an archaeological site; such fragile elements would likely be destroyed in fluvial transport.*

may be preserved as well as or better than smaller and lighter whole elements. Dense cortical bone preserves better than lighter structures, and cancellous articular bone preserves less well and with more distortion than heavier dense shaft bone. Thus, fossil vertebrate evidence is biased toward the remains of large robust animals or elements in any environment where there has been a reasonably high level of transporting energy (for example, a beach or river bed), while small, lightly built animals are best known from areas of quiet deposition (for example, backswamps, lakes or swales). Delicate structures may also be preserved where an animal has died in primary position, as in the case of a rodent or frog hibernating in its burrow. The bias toward large animals is compounded by their greater visibility in the field and such factors as fluvial sorting (Dodson, 1973), but such a bias can be overcome through planned use of special recovery techniques (see below).

Preserved Elements for Major Vertebrate Groups

Fishes

Typical material can include complete skeletons, whether articulated or disturbed but having all parts associated, as flattened whole animals on bedding planes of fine-grained sediments. Good examples are the well-preserved skeletons in calcareous nodules from Champlain Sea deposits at Green Creek near Ottawa (McAllister *et al.*, 1981). Burrows or nests, as for aestivating lungfish *(Ceratodus)*, may be preserved. A desiccating pond or mass kills associated with volcanic ashfalls or anoxic conditions may give rise to the preservation of remains of many individuals. Isolated bones or clusters of bones such as heavy spines, vertebrae or disarticulated head or gill arch elements, scales and teeth (*e.g.*, shark, pike, sturgeon) may accumulate in small current eddies, either in freshwater streams or lakes, or beaches, or in backwaters and swales.

Amphibians

Remains of amphibians may include complete or disarticulated skeletons of adults or larvae, often flattened on bedding planes. Isolated bones, usually limb-bones, vertebrae or disarticulated skull elements, including tooth-bearing elements, may be encountered. Fine-grained sediments may preserve footprints. Sediments of desiccating ponds or winter hibernacula, the latter ranging from burrows in soft sediment to cavities in coarse rubble, provide another opportunity for the preservation of amphibian remains (Bayrock, 1964).

Reptiles

Material includes bones and teeth, occasionally skulls with many elements associated, and (rarely) complete skeletons or major portions of a skeleton. Isolated bones usually include disarticulated skull elements, longbones or vertebrae, scutes or carapace fragments (*e.g.*, turtles), and isolated shed teeth in groups that replace teeth (*e.g.*, crocodilians). Egg-shell fragments, gizzard stones (gastroliths), burrows or nests, tooth marks, or footprints record past reptilian activity. Quaternary reptilian remains are often small isolated elements because modern reptiles tend to be small, except for Crocodilia and the largest Chelonia, Lacertilia and Squamata. Like the remains of amphibians, reptilian remains may occur in aggregations deposited in eddies of small streams and in assemblages of articulated or partially articulated elements from winter hibernacula, usually cavities in coarse rubble or fractured bedrock.

Birds

Material includes isolated bones and, rarely, whole skulls, limbs or skeletons (*e.g.*, Steadman and Miller, 1987; Harington, 1990), as their light bones are easily crushed or fragmented. Egg shell fragments and occasionally whole eggs, and rarely nests or burrows, may be found in fossil sequences. Regurgitated stomach debris (owl-pellets)(Figure 9), sometimes in massive form if beneath a roost, or debris beneath a raptor's nest, reflect diet of the roosting predator. Further analyses of bones contained in the regurgitated debris are informative as to microfauna in the area, and may record the presence of smaller birds. Feathers and their impressions or footprints, generally of wading forms, may also be preserved.

Mammals

Material includes either whole or fragmentary bones, such as skulls, limb girdles, partial vertebral columns and limbs, depending upon the energy of the depositional environment, and may be well water-rounded in high energy deposits. Teeth often preserve better than other bones (Figure 10), but can be fragmented due to cracking and splitting under alternating temperature or water stresses and drying. Whole animals or complete skeletons are rare unless they are aquatic forms and were deposited in water. They may be entombed in permafrost terrain as in the case of the Beresovka and other Siberian mammoths *(Mammuthus primigenius)*(Heintz and Garutt, 1965; Sokolov *et al.*, 1986), or woolly rhinoceros *(Coelodonta antiquitatis)* (Vereschagin and Baryshnikov, 1962), or buried in burrows (*e.g.*, hyena, *Crocuta* sp. (Sutcliffe, 1970)). Mummified remains occur in arid environments: *e.g.*, the camel *Camelops hesternus* in the American Southwest (Martin and Guilday, 1967; Romer, 1929), the marsupial wolf *Thylacinus cynocephalus* in Western Australia (Merrilees, 1970), and the aodad or Barbary sheep *Ammotragus lervia* in Egypt (Osborn and Helmy, 1980). Partially articulated or associated skeletons may be found in archaeological sites, particularly at kill sites. Partial skeletons may exist in pellets of raptorial birds or in burrows, nests or middens. The nests

Figure 9 *Owl pellet containing rodent and bird bones, bound together with matted hair. Note unbroken longbones, vertebrae, and parts of skull. Length of pellet is 4.5 cm. (Photograph by M.B. Smith).*

Figure 10 *Waterworn partial mammoth* (Mammuthus primigenius) *tooth. Note cobble-like form with transverse grinding ridges worn smooth within general outline and broken right margin. Late Pleistocene (probably Late Wisconsinan) gravels at West Peace River, Alberta. This specimen is in the Peace River Centennial Museum.*

Figure 11 *Modern woodrat (=packrat) midden, Three Forks area, Montana. The midden is composed mainly of juniper* (Juniperus *sp.) and other shrub twigs and small branches, with mammal, bird and reptile bones, and pieces of paper and plastic.*

Figure 12 *South Saskatchewan River, north of Medicine Hat, Alberta, showing slumping exposing tills, sands, and gravels to left (south) at Mitchell Bluff and pointbar formation to right (north) downstream from Island Bluff in distance.*

Figure 13 *Extinct bison* (Bison latifrons) *skull in stratified sands and minor gravels of Mitchell Bluff, South Saskatchewan River, Medicine Hat, Alberta, Sangamonian or Middle Wisconsinan age. Back of skull is to left, with occipital condyle and auditory bulla visible. Top of skull is sheared through the sagittal plane. Nasals, teeth, maxillae, and premaxillae were removed before deposition and right side of skull was removed with slumping of slope.*

themselves may be rich in plant remains that are valuable in paleoenvironmental reconstruction, as in Arctic ground squirrel nests (Harington, 1984a) or woodrat middens in arid areas (Figure 11) (van Devender, 1987; Wells, 1976). Tooth marks caused by carnivore chewing (Haynes, 1980) or rodent gnawing, as well as footprints, and feces as coprolites provide additional evidence of past mammal activity. Under the right circumstances (minimal transportation and rapid burial, as, for example, at an archaeological kill site) even the bones of unborn (foetal) animals may be preserved (Wilson, 1974)(Figure 8).

Figure 14 *Extinct camel* (Camelops hesternus) *cannon bone or metacarpal in sandy silt at Lindoe Bluff, South Saskatchewan River, Medicine Hat, Alberta. Possibly Illinoian age. Note horizontal attitude and arcuate rotational breaks from slumping matrix.*

Figure 15 *Large vertebrate bones from a Late Quaternary assemblage. The specimens are all metacarpals (or front limb cannon bones) from extinct large hoofed mammals, collected from the Bighill Creek Formation, Bow River Valley, Alberta, (ca. 11,000 years B.P.). From left to right: camel* (Camelops hesternus), *bison* (Bison b. antiquus), *small horse* (Equus conversidens) *and large mountain sheep* (Ovis canadensis catclawensis).

Collecting and Laboratory Techniques

Locating Fossils

Ground that has been exposed by gravel-pit operations, road making or other construction activities may yield fossils that have suffered little weathering after being exposed to wind, rain, sun and temperature changes. Other erosional environments lacking trees or lower vegetation, such as river cuts, arid or desert environments, beaches and cliffs, may also yield fossils (Figure 12). However, these exposures, especially those in deserts and savannahs, usually have a rigorous climate and rapid weathering of the fossils may take place. Fossils may be found *in situ* in vertical exposures where they protrude from the matrix (Figure 13), may be exposed on the erosional surfaces of beaches or river benches, or may be exposed and often weathered and fragmented by the actions of the weather and of tree or shrub roots when there is intermittent vegetation and a deflated surface.

The best matrices in which to locate fossils are alluvial sands, gravels, silts or clays, or eolian sand or loess, where rapid burial occurs before severe weathering or breakage and dispersal (Figures 14 and 15).However, the major drawback to most of these matrices is the high probability of disarticulation and dispersal by scavengers or currents. Likely exposures may be located from a distance through fieldglasses. Amateurs, most often people working close to the ground (*e.g.*, farmers, gravel pit operators, construction workers), may inform scientists of the presence of fossils in places known to them. Examination of the exposure must be on site, by foot or on hands and knees, and in a thorough and methodical manner. Prospecting potential sites is best done when the sun is not too high, or the temperature too hot, as the recognition of small fossils is less easy when conditions are trying. Even the location of large fossils under such conditions is less effective, and a return to the same site when conditions are better usually will reveal specimens that have been overlooked.

Vertebrate fossils are often found in gravel pits in Canada, especially those in the Prairies or southern Ontario. Marine mammal remains are abundant in Quaternary deposits on raised beaches in Arctic Canada (Harington, 1990). Glacial outwash gravels are usually barren of fossils, and so those of the Yukon, northern Prairies or Ontario and Quebec seldom produce vertebrates. Most fossils found in gravel pits are water-worn or crushed or both, due to the ball-mill effect of rolling cobbles and their weight in compaction. Fossils found in bogs or silts or sands may be better preserved, but may be less obvious as the matrix obscures them and is not always clean. Sands or minor gravels provide an ideal preservational environment in that they are not deposited by a high-energy flow, do not contain the larger cobbles that may damage the bones, are not usually acidic so as to denature the bones or teeth, and are easy to excavate either by hand or mechanically. Sand lenses in gravel pits often contain the best preserved vertebrate fossils, often associated with mollusc shells and other invertebrate remains.

Fossils can also occur within concretions, as at Green's Creek, near Ottawa, Ontario. Here a variety of fish, small invertebrates and even some terrestrial vertebrates are found together with leaves and seeds within concretions (McAllister *et al.*, 1981, 1988). A fine collection of these concretions is kept in the Division of Palaeobiology, Canadian Museum of Nature (formerly National Museum of Natural History) in Ottawa.

If a slope is examined and a broken piece of a fossil is found at the foot of the slope, the areas below and above the first-found piece should be carefully examined to locate either other broken pieces that could extend the specimen or the source in the vertical face from which either the whole specimen or the pieces that lay on the slope may have been derived. This process applies to talus slopes in quarries, at the foots of cliffs or man-made cuttings, and similar natural scarps such as Scarborough Bluffs, Toronto, or the high cut-banks along many prairie rivers. Where the talus slope is extensive, it should be carefully walked along the base, where the rocks are large, but where large bones may "float" on the surface and be easily seen. Next, the prospector should walk the slope along horizontal lines at about one-metre vertical intervals, while searching the slope surface nearest to his or her face. When a specimen is located, the prospector must not act precipitately and move over areas of the slope that have not been prospected. Fragments of fossils may lie just under the surface of the talus slope and a prudent prospector will winnow through these surficial layers by hand or with small hand tools seeking other fragments that may be hidden.

When the slope has been completely prospected, a series of footprints may be seen in lines along the contours of the slope, and all areas will have been examined (Figure 16). If there is a vertical scarp above the talus, as on a cliff or in a quarry, it should be carefully examined from a short distance, preferably not more than a metre, and usually two passes are required to examine both the basal section of the face and that higher up. The prospector will thus pass backward and forward across the upper level of the talus while both the top level of the talus and the scarp face are fully examined.

Macrovertebrates

The recovery of elements of large vertebrate fossils, those that have survived mainly intact, and are entombed within a soft matrix, requires removal of the surrounding matrix and exposure of the fossil. This may be done using hand tools such as stiff putty knives, pointing trowels, awls, and paint bushes, or even small spades or shovels, with larger spades, shovels and picks used to remove excessive overburden. Once a fossil is located, it should be carefully exposed by first removing any overhanging or overlying overburden, working down through the matrix until it is grossly exposed, and then removing the final matrix that closely adheres to the bones with small handtools and brushes. Specimens preserved in permafrost are less accessible and, rather, may need to be melted out of the permafrost before removal. Only when a specimen has been completely isolated from the matrix may an attempt to lift it be contemplated. Examination and experience will tell whether the bone is cracked or weak, and whether it may be lifted intact without added support. If it may be lifted as it is preserved, it is often prudent to place the fossil in a sealed plastic bag, so that it will not dry out too quickly, and will be less likely to crack or warp as it dessicates. The field number and any notes relevant to the fossil, such as orientation, level or association with other fossils should be noted. The fossil should now be double-bagged, with a separate label with the essential data placed between the two bags; double bagging prevents the labels from becoming water-logged or destroyed by mildew or mold.

Should a fossil be poorly preserved or so large that it might break when lifted, it should be jacketed. This is provided by a plaster jacket moulded around the fossil and the immediately surrounding matrix (Figure 17). The fossil is exposed as described above, but does not have to be exposed in all detail. It is exposed on a pedestal that is undercut all around, somewhat resembling a mushroom. A separator is laid over the fossil, usually consisting of a number of layers of wet tissue, paper towelling, or the like, so that the plaster jacket will not adhere to the fossil. The separating material should be carefully shaped around the fossil and packed into depressions to help stabilize it within the jacket for transport. Strips of burlap or sacking, about four to six inches wide, are soaked in a thin mix of plaster of Paris and laid over the separator so as to overlap each other and form a web-like support. Under very hot field conditions, rock salt may be added to the plaster and water to adjust the setting characteristics of the plaster. The ends are tucked round the margins and into the undercut edge. Should the fossil be massive or very dense, then supporting rods, either wood or metal, may be cut to shape, fitted to the uneven contours, or bent to fit, and smoothed in place with some of the remaining wet plaster. Before the internal plaster and the supporting pieces are too dry, a second layer of plaster-soaked strips is arranged over the supports and into the undercut margin. The cast is then marked with the specimen number, possibly the locality if it is not inherent in the field number, possibly the date, and the fact that this side is the TOP. This last is important, as it will tell the preparator which side to open first! The whole is now allowed to dry for at least 24 hours and sometimes longer, until the plaster is firm.

When the first half-jacket is dry, rods, chisel, spades, or crowbars are driven below the fossil through the matrix pedestal, and the matrix with the fossil lifted from its bed and turned over so that it rests on the plaster top. The inverted matrix base below the specimen is now pared down until either the fossil is exposed or the excavator believes that the

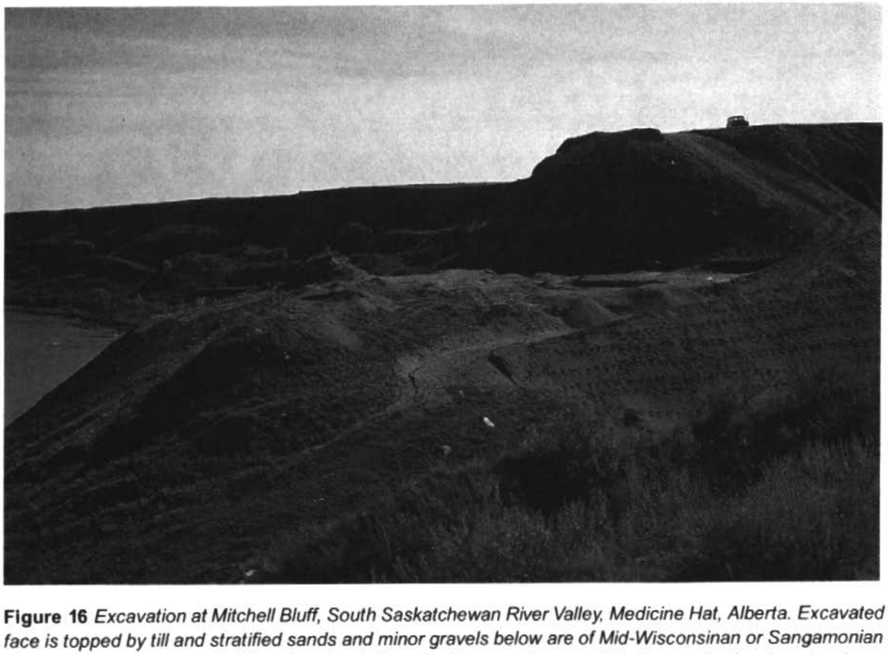


Figure 16 *Excavation at Mitchell Bluff, South Saskatchewan River Valley, Medicine Hat, Alberta. Excavated face is topped by till and stratified sands and minor gravels below are of Mid-Wisconsinan or Sangamonian age. Sandy soil has been bulldozed to the right and as there are bones within the sands, the slope has been walked to search for them. The pattern of footprints illustrates the procedure described in the text.*

fossil might be damaged by removal of too much matrix and loss of strength. One is always weighing the advantages of strength against the disadvantages of weight, especially when the fossil may have to be carried some distance. The exposed base is now wrapped in another double set of plaster-soaked strips, sometimes with additional reinforcing rods, as was the top, and allowed to dry.

Microvertebrates

Remnants of small vertebrates such as rodents, rabbits, small birds, lizards, snakes and fish are often scattered as small isolated elements within a granular matrix such as sand. These items are almost impossible to locate and recover individually in the field and alternative methods have been devised. The matrix, which may be easily friable, as sand, or may be more massive, as clay or marl, is gently shaken, if dry and friable, or washed, if resistant to disintegration unless wet, through a sieve, allowing the fine parts of the matrix to pass through the mesh and retaining the sandy grains or small fossils. The size of the mesh may be varied to catch the size of items desired, but the finer the mesh, the slower is the sieving process. Whichever method is used, care and patience are required to recover the smaller fossils which may be a few millimetres in diameter and as few as two or three in a cubic metre of matrix!

Frames with a cross-handle on top and mesh on the bottom are made of wood, so that they may float. Robust timber is required. Plywood splits easily and often delaminates with continued use in wet washing. The handles are placed diagonally across the frame to give rigidity and the mesh is fastened to the bottom with nails and square battens. The mesh at the bottom may have to take considerable weight for a brief time, and steel mesh rather than copper, aluminum or nylon is preferred. If very heavy loads are anticipated, then battens should be fixed below the mesh and screwed into the sides from below.

The matrix to be washed is conveyed to a source of water, often a stream or river, and portions placed in each frame. If the matrix is solid, the frames with matrix may be placed in the edge of a stream to soak and disintegrate. Large-scale screening operations can introduce much sediment into a stream and may violate local pollution laws, so one should be familiar with appropriate regulations. It should be mentioned that, as the sediment blocks disintegrate, it is not unusual for the fines to slip through the mesh or float out in the current if the frames are submerged, and for the load in a frame to be so reduced that the frame may float away with the remaining concentrate. Thus, it is best to link the frames together with rope. If the fines do not pass easily through the mesh, they may be assisted by moving the frame gently up and down in the water, or gently massaging the matrix against the screen. This should be done carefully as rocks or pointed fossils may penetrate the screen and, once there is a hole in the mesh, it is impossible to estimate how many microfossils may pass through the hole in a stream of water. After the fine silty portion of the matrix has been washed away, the concentrated small grains are laid out on sheets to dry before being bagged. While drying, it is imperative to ensure that the drying concentrate is not blown away by gusts of wind. Heavy rocks around the edge of the sheet or baulks of timber along the edges and between the drying samples both hold the sheets in place and reduce the effect of the wind in removing the dried concentrate. The concentrate is then taken back to the laboratory for examination under a binocular microscope.

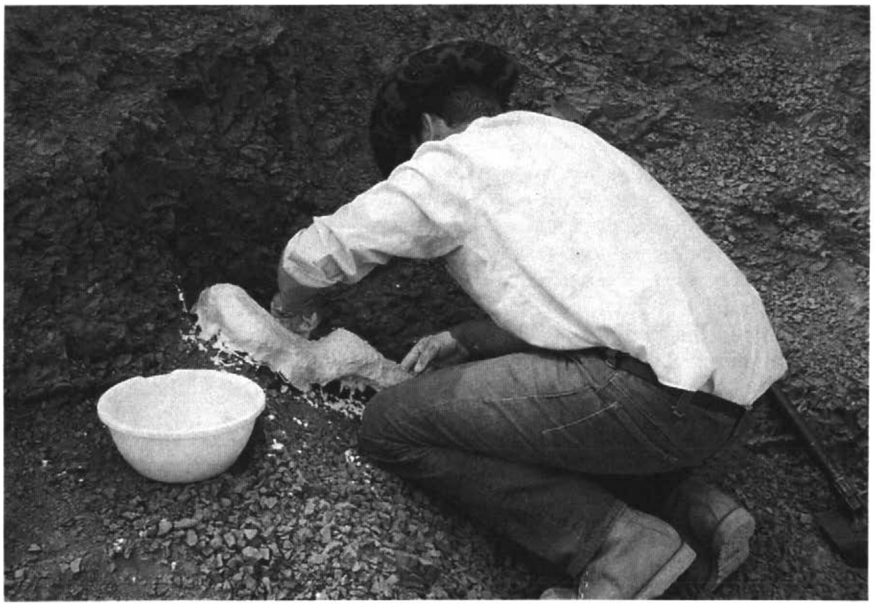


Figure 17 *Field jacketing of fossil bone with burlap and plaster. In this small-scale example, a thin slurry of plaster has been mixed in a bowl and the burlap soaked in it and wrapped around the exposed fossil. Note the undercut edge of the plastered specimen and that the burlap has been tucked under it. The jacket is being shaped and smoothed around the specimen, and will be labelled with field number and "TOP".*

The sorts of fossils that may be recovered from such washing may be isolated small mammal teeth, small vertebrae of fish or mammals, partial longbones or spines of small mammals and fish, and possibly invertebrate exoskeletal fragments, mollusc shells, and plant remains in some deposits.

Dry screening may also be carried out, either using hand-held screens such as the traditional circular ones once common in farms for sifting grain, or the more modern ones pioneered by archaeologists. It is possible to use a series of progressively finer screens to sort the items by size and to retain the smallest remains without their being mixed with the larger items that might crush them. Often the screen is suspended from a frame, like a small child's swing, and swung to and fro by handles. The matrix may also be gently tossed within the frame, or the materials massaged through the mesh. If the mesh is fine, additional support may be given by backing the fine mesh with a coarser mesh, such as chicken wire. The concentrate is bagged for eventual examination in the laboratory.

Laboratory Techniques

As soon as a fossil is safely in the laboratory, the task of preparing it so that it will not deteriorate further, and so that it will yield its biological information to researchers begins. As the fossils come in from the field, they should be checked against the field numbers, and provisionally accessioned. Should any be missing, it is best to know this as soon as possible as it may be possible to retrieve any that are missing or at least save one the trouble of looking for it years later when memories are faint.

Preparation

Basic preparation involves cleaning and restoring the fossil, followed by its stabilization and preservation. Cleaning is accomplished by the use of hand tools such as dental picks, small stiff and soft brushes (*e.g.*, old toothbrushes), acid development if the matrix is amenable to acid removal without harming the fossil, and cleaning with ultrasound. The acids used are dilute weak acids. Glacial acetic acid diluted to 10% by volume in tap water will remove a carbonate matrix or encrustation without weakening any of the phosphate bonds in bones or teeth. At all times the fossils should be prepared so that they do not become too fragile, consistent with their use and storage conditions.

The fossil is cleaned as far as possible. If it is a single element such as an isolated bone or tooth that has not been damaged, it may only require some scraping and brushing before the stabilizer is applied. Stabilizer should be used only if absolutely necessary as stabilizer will limit future use of the fossils for dating or any further analysis. If a fossil is broken into a number of pieces, it may be possible to glue the parts back together to restore its original shape and size. However, when gluing broken fossils back together, the greatest care must be exercised to see that the joints are clean and fit snugly with the minimum of glue to prevent any distortion. It is an axiom of modern museum conservation that specimens should not be irreversibly restored (*e.g.*, using epoxy). A polyvinyl acetate plastic dissolved in acetone or amyl acetate is reasonably suitable and commercially available as household cement. Even when a specimen is not entire, it is frequently worthwhile to glue as much of it back together as possible for convenience of storage as well as to provide the greatest amount of evidence. Fossils that are in more than one piece often get separated. Should the specimen be a complex, such as a skull, it may be broken into many pieces by crushing. If it had to be retrieved without being jacketed, it may be that each piece has first to be cleaned and given a light dose of preservative. If it was collected as a unit within a plaster jacket, the jacket should be laid on sturdy table, propped up with sandbags, with its TOP uppermost. The field notebook should be consulted to see if there were any noteworthy aspects of the preservation or jacketing that suggest that the opening should be carried out in any particular way. With these strictures in mind, the plaster is cut around the rim of the upper surface and the "lid" lifted off. If the jacket has been properly made, the lid should separate easily from the fossil through the separating tissue layers. The fossil is then carefully exposed as the matrix is removed piecemeal. If the fossil is fragmented, but its pieces fit well together, it may be feasible to reconstruct units of the specimen as one proceeds to remove the matrix, but care must be taken to see that distortion does not occur if the eventual units are to be reassembled. As preparation proceeds, the sides of the jacket are removed, and the bone(s) or elements recovered, stabilized, and reassembled.

Preservation

Bones that have retrieved without any jacketing should be dried out slowly, if wet, and preserved. Quick drying will result in drying the ouside more quickly than the inside, thus setting up internal stresses, and will result in longitudinal cracks in dense shafts and distortion of flat bones or thin areas. Exposure for 30 to 45 minutes daily and then rebagging will allow drying to occur over four to six weeks, and the loss of water at each exposure will be sufficiently small that the moisture content will equalize itself within the fossil during the bagged periods. When a fossil is completely dry, it may be very light and fragile. It is then advisable to soak into it applications of a thinned stabilizer such as alcohol-thinned PVA glue, acetone-thinned household cement, or one of the proprietory brands such as "Gelva". It is always good to seek the advice of an experienced conservator, if in doubt. The preservative should not be too thick as it will not sink into the pores of the bone and may lift the surface as it hardens, thus damaging the fossil. The first and second application should seem to have little effect on the porous bone, but gradually a fine sheen will be seen on the surface and the solution will sink into the bone more slowly. This should signal the preparator that the bone's pores are filling with the solution and that a final coating with a non-hygroscopic solution is all that is required. Water-based stabilizers are not recommended as they expand and contract with variations in the atmospheric humidity, thus working the fossil and eventually causing its structural failure. At this point, it may be convenient to inscribe the catalogue number on the specimen. Numbers can be written in permanent ink on light bone or, if the bone is dark, a white panel is painted on in a paint that is not miscible with the stabilizer and then the number is inscribed. "Magic markers" should be avoided because many have light-sensitive ink that fades through time.

Concentrate Sorting

The dry fossil concentrate is placed in trays, usually fairly small to fit under a binocular microscope, and the concentrate is distributed in a thin layer. This is then examined under the binocular microscope, with either a small probe used to winnow the fossils from the rock debris or a pair of fine forceps for removing the fossils as they are found. The fossils are retained in vials for later identification and mounting.

Each fossil is identified as far as possible and, if it is important, catalogued. Often, bulk catalogue numbers are given to the many fragments that are retrieved, but are not noteworthy. An important microscopic fossil, such as a rodent tooth, may be mounted on the end of a pin with a small blob of glue. Each pin is then stuck into the inside end of a cork, which is stopped into a small plastic or glass vial. The vial can be labelled with a label either on the inside or the outside, and the cork may have a short identification number on it so that specimens and their identities are not confused. The vials may be stored in boxes or drawers for convenience. An alternative is the use of "card vials" which allows storage of fossils (Fitzgerald, 1986).

Labelling and Cataloguing

Each specimen should be accompanied by a label that gives field number and final accession number (which should be written on the fossil if possible), its identification, collector, date and place of collection, rock unit or stratigraphic level, and other important data. This information should also be kept in a ledger or master catalogue, where all specimens are entered by number, with all pertinent data, and any publications or exceptional aspects also noted. By going to the master catalogue, one should be able to learn all that is known of a fossil's history without actually examining it.

Data pertaining to a fossil, such as black-and-white or colour photographs, tables of measurements, line illustrations, maps, sectional diagrams, records of radiocarbon dates performed on it or on associated materials, publications referring to it, or similar evidence resulting from its use after preparation, should be kept on file and noted in the master catalogue as being available. Likewise, a record of the geological evidence should be available, including the field notes, and any important rock samples, and taphonomic evidence as to its depositional history, disease, or the effect of other animals' chewing or burrowing on it. Because other workers will use fossils and come to diverging conclusions, it is often difficult to keep the later reference data complete or up-to-date.

Applications

Paleoenvironmental Reconstructions

Vertebrates reflect an impressive array of parameters in reconstruction of past environments (*e.g.*, Davis, 1987; Graham and Semken, 1987; Harington, 1984a,b), and differ dramatically in the degree to which they can be used to reconstruct paleoenvironments. Terrestrial vertebrates range from large and highly mobile forms (*e.g.*, large ungulates) to small species of limited mobility (*e.g.*, rodents or salamanders). The former are useful in reconstructing communities on a regional scale, such as grassland *versus* forest, even though they may have the ability to move across ecotones in the course of a year. Many are, in fact, migratory, with the wildebeest *(Connochaetes taurinus)* of East Africa being one of the best-known examples (Vesey-Fitzgerald, 1960). Microvertebrates may provide specific microenvironmental information relating to substrate, cover type, and even particular food plant species (Auffenberg and Milstead, 1965). Thus, in a paleoenvironmental study one cannot treat all species as of equal analytical weight. Efforts at quantitative analysis of bone assemblages are becoming more widely used (Graham, 1976; Grayson, 1984; R.A. Martin, 1984; Rhodes and Semken, 1986). It should be possible to apply transfer functions comparable to those used by palynologists in the not-too-distant future.

For a time, it appeared that maps of sympatry would be a central element in paleoecological studies. Maps of the modern distribution of still-extant species identified in a Late Quaternary fauna would be superimposed, and the area in which all or most overlapped (the area of sympatry) would be taken as the best modern analogue for past environmental conditions at the site. While this approach retains utility, it embodies several assumptions: for example, differential dispersal rates of colonizing species are ignored, modern ranges are assumed to (but frequently, in reality, do not) document physiological limits, and possible microevolutionary change in habitat preference is discounted. Graham and Semken (1987), while reaffirming the power of this approach, warned against uncritical over-use of maps of sympatry, urging researchers to employ other methods as well and, in particular, to analyze the implications of a fauna species-by-species, integrating the environmental data afterward. Baseline species-by-species studies of the modern equivalents are an obvious prerequisite; in fact, they are seldom available in the detail desired. One exception might be the study of Champlain Sea fishes (McAllister *et al.*, 1988).

Substrate

Certain species are useful indicators of specific ecological niches or local environmental parameters. Substrates, such as the character of geological deposits and bedrock, and the soils developed within them, are important constraints for burrowing species. In general, burrowing vertebrates reflect soft, uncompacted soils, often sands or loams. Some insectivores (*e.g.*, moles) and rodents (*e.g.*, pocket gophers) are more highly specialized and efficient burrowers than their relatives and can take advantage of more challenging substrates. Pocket gophers *(Geomys* and *Thomomys)* possess specialized front teeth and powerful clawed feet, and the ability to close the mouth behind the teeth. Like moles, they effectively extend their burrows in order to forage underground. Burrowing ground squirrels *(Spermophilus)* and prairie dogs *(Cynomys)* lack these specializations and, while they also use teeth and claws in burrowing, they do so less efficiently and do much of their foraging above ground. Substrate is also reflected in foot structures of larger forms, such as ungulates. For example, hoof structures of mountain goat *(Oreamnos americanus)* and caribou *(Rangifer tarandus)* differ dramatically: the former concentrates its weight upon a relatively small surface for rock climbing, while the broadly splayed large hooves of the latter are developed for locomotion on soft unconsolidated substrates. Similarly, the insulated and cushioned "hooves" (pads) of camels are ideal for locomotion on hot sand, but are relatively delicate and quickly wear down on angular rocky or gravelly surfaces. Furthermore, it is likely that direct loading and compaction by trampling of tundra habitats by mammoths and other large mammals could have caused dramatic changes in vegetation and associated microvertebrate faunas (Guthrie, 1982).

Paleoclimates

Vertebrates are useful indicators in paleoclimatic reconstructions, through either their known direct requirements (temperature, availability of water) or indirect requirements (changes in vegetation or substrate). For example, thawing of permafrost in peatland terrain would render a formerly productive area physically impassible to most large ungulates, resulting in a lower diversity of species (Guthrie, 1990). Climatic warming, which might contribute to high biotic diversity and productivity, could, in this case, produce a substrate change that would offset any adaptive advantages conferred by temperature. Paleoclimatic information is not restricted to land vertebrates, as freshwater fishes are sensitive to changes in water temperature (Cross, 1970). Unfortunately, it is difficult to isolate the interrelated variations in temperature, atmospheric humidity, and seasonal extremes, but it may not always be necessary to do so. Many modern vertebrate adaptations depend upon the interaction of several factors. For example, an index of snow severity involving both depth and low temperatures has proved more informative than either parameter alone in understanding year-to-year variations in populations of white-tailed deer *(Odocoileus virginianus*; Ozoga and Gysel, 1972; Verme, 1968). The past record of this species in areas near the margin of its range could be used, in part, as a proxy record of snow severity (Wilson and Hills, 1984). Such an approach may not hold for all species, as the rapidity with which species respond to environmental changes can vary according to variations in species mobility. Even though a vast area of suitable range may open up, such as through deglaciation, a given species can only move into this territory at a rate governed by its dispersal ability (Hoffman and Jones, 1970). Consequently, there can be considerable lag between time of climatic change, habitat availability and occupation of new territory.

Bones and teeth provide a record of physiological changes as a result of fluctuating climatic factors during the life of an individual animal. Paleopathological studies can therefore reveal environmental as well as behavioural information. Dental pathologies (growth arrests, or hypoplasias) in *Bison*, for example, record seasonal stresses such as winter severity and summer droughts. The time of stress is detectable on the basis of the location of the hypoplasia on the tooth crown (M.C. Wilson, 1988). Climatic conditions associated with composition of vegetation are reflected in the carbon isotope composition of bone collagen in herbivores (Chisholm *et al.*, 1986; Land *et al.*, 1980: Tieszen *et al.*, 1979). A temporal record of environmental change can be reconstructed in a stratified site where a single species is well represented (*e.g.*, McKinnon, 1986). Changes through time in rates of bison tooth attrition also reflect changes in quality of forage (M.C. Wilson, 1988). Changes in tooth wear over large geographic distances may reflect either temporal or environmental differences, or both, and may be impossible to distinguish in the record. Climatic stresses can also cause disruptions in population structure, producing unusual recruitment or survivorship curves (M.C. Wilson, 1974; Reher, 1978; Reher and Frison, 1980).

Vegetation Communities

Dietary specializations in many species are known and are reflected in dental structure (*e.g.*, high-crowned teeth in grazing forms) and can in many cases be inferred for fossil species (Janis, 1984; Solounias and Dawson-Saunders, 1987). The high-crowned/low-crowned dental conformation for the grazer/browser relationship is not infallible, however, and must be used with caution (Graham and Semken, 1987). Direct recovery of vegetable food remains from crevices in enamel folds or tooth fossettes or otherwise in close association with a fossil is possible on occasion and allows more sophisticated dietary analyses (Akersten *et al.*, 1988; Voorhies and Thomasson, 1979), as does analysis of dessicated dung (coprolites) from exceptional environments such as dry caves (Mead *et al.*, 1986a,b). Dental microwear patterns can also indicate the type of diet that an animal eats (Walker *et al.*, 1978). Vegetation also provides protection for many vertebrates, either in the form of cover to hide in, or as a broken background to camouflage an otherwise distinct outline. Reconstruction of protective cover types depends upon analogies from modern forms, and evolutionary behavioural changes pose a problem with this approach. The habitat requirements for many species can be very specific, especially for arboreal forms such as tree squirrels (*Sciurus* and allies) and most primates, which can provide a reliable indication of past vegetation or cover types. Some species can be highly destructive of vegetation, influencing the distribution of other species; a good example is destruction and trampling of trees by elephants in Africa today.

There are times when vegetational reconstruction on the basis of the bones of animals is successful (Graham, 1976; Land *et al.*, 1980; Guthrie, 1982; Rhodes and Semken, 1986). In fact, vertebrate remains can at times be better than pollen in vegetation reconstructions, because vertebrate remains can be identified to species level with considerable accuracy, and, with the exception of some fluvial sequences, vertebrates are often of more local origin as opposed to pollen which can be derived from great distances (Guthrie, 1990). Many pollen records are incomplete from the northern Great Plains because of the paucity of permanent lakes during the early postglacial period, but abundant vertebrate remains from alluvial gravels deposited during this time are dominantly grazing forms, indicating an open steppe or steppe-tundra (Churcher, 1968, 1975; Wilson and Churcher, 1978, 1984). Pollen evidence is beginning to confirm this (Barnosky, 1989; Barnosky *et al.*, 1987; MacDonald, 1989).

Clinal Variation and Microevolution

Many living species are polytypic, varying clinally in size, colour, and bodily proportions over geographic distances. Populations that differ significantly in such characters are regarded as taxonomic subspecies, with arbitrary lines drawn between them to segment the clines. Given that neighbouring subspecies overlap morphologically, especially in the area of the imposed boundary, taxonomists can only identify individuals as to subspecies with respect to the collecting locality and expected range boundaries. Joysey (1972) has argued persuasively that Late Quaternary chronoclines should be segmented for fossil remains by establishing arbitrary temporal boundaries analogous to the geographical boundaries within neospecies. This has the salutary effect of making subspecies three-dimensional (both areally and temporally distributed) and more amenable to incorporation into micro-evolutionary schemes. Other paleontologists have considered that subspecies based on morphological details are impossible to recognize in the fossil record as they are overshadowed by sexual, age and individual variation, because of the general paucity of materials or small sample sizes, or unreliable stratigraphic correlations.

Clinal variation throughout time (Figure 18) has been documented for such disparate groups as rodents and lagomorphs (Davis, 1987; Purdue, 1980), carnivores (Klein and Scott, 1989), proboscideans (Churcher, 1986; Maglio, 1973) and artiodactyls such as bison (Wilson, 1974, 1980) and white-tailed deer (Purdue, 1989; Purdue and Styles, 1986). Direct environmental influences can be implicated for some modern clines; for example, Purdue (1989) related size variation in squirrels (*Sciurus* spp.) and cottontail rabbits (*Sylvilagus floridanus*) to an east-west moisture gradient. Range boundaries frequently represent not sudden environmental changes, but the attainment of a threshold value on an environmental gradient (*e.g.*, mean winter temperature). Temporal variations in the location of the threshold isopleth are reflected in extensions and contractions of range as, for example, along the northern boundary of the range of the pronghorn antelope (*Antilocapra americana*) where occasional severe winters cause dramatic population reductions and range contraction, but during the intervening mild years the range can expand dramatically into marginal areas. Certain sequences suggesting morphological change through time at one locality may be related directly to geographic displacement or clines, as in the case of *Sciurus* spp. and *Sylvilagus floridanus* (Purdue, 1980) and short-tailed shrews, *Blarina* spp. (Graham and Semken, 1976; Jones *et al.*, 1984), and thus need not mark true evolutionary changes (Koch, 1986). Displacement of the cline in the opposite direction would bring back the original morph (body type) to the locality in question, and apparent trends in one area could be balanced by conservatism of morphology elsewhere. However, some chronoclines seem to represent true pervasive evolutionary change, as in *Bison* (Wilson, 1974, 1978, 1980), muskrat, *Ondatra* spp. (L.D. Martin, 1984; Nelson and Semken, 1970), and mammoths, *Mammuthus* spp. (Churcher, 1986; Maglio, 1973). Geist (1971) argued for a strong phenotypic component in this, linked to dispersal history and dietary trends, in which case the "evolution" would be reversible under appropriate conditions, but McDonald (1981) argued that changes in bison chronology were beyond simple phenotypic variation. Given the evidence for modern environmental influences in fostering clinal variation, there is much potential in using chronoclinal shifts to infer changing paleoenvironments.

When both spatial and temporal variation are documented for extinct forms, as for the elk-moose *Cervalces* (Figure 19), inference of the causative factors is difficult in the absence of direct analogues in modern forms. However, examination of paleoenvironmental associations can reveal correlations of value. Morphological change is only one possible response to environmental change. An animal's body shape may be conserved if a species migrates to an area that approximates its former environment. Migration, then, is another possible response to environmental change.

Extinctions

An important area in which paleoecological studies of vertebrates are pre-eminent is in the search for causes of Quaternary extinctions, which differentially affected megavertebrates (Martin and Klein, 1984). Such ecological factors as habitat destruction, lessened availability of nutritious vegetation, and disruption of feeding strategies probably were involved; these could have resulted from changes in seasonal climate patterns changing the length and severity of seasonal minima (Graham, 1986). These considerations do not negate the possibility that human hunters administered the *coup de grâce* to many species. Authors debating the case for human agency must clearly distinguish the *process* of extinction from the *event* of extinction: the killers of the last few mammoths did not necessarily play a role in bringing them to the brink of extermination.

Local extirpation or outright extinction are the extreme results of environmental change that exceeds the ability of a species to adapt. It should also be remembered that modern ranges do not necessarily reflect the physiological limits of species, but can be influenced by inter-specific competitive exclusion, predation (especially by humans), or other factors. Even today the ranges of some species are poorly known. Careful baseline studies of modern distribution and physiological adaptations are required for more detailed paleoecological reconstructions. If the modern ranges are themselves undergoing change (*e.g.*, some species are still dispersing into territory opened up by deglaciation millenia ago), the establishment of a modern "baseline" can be difficult.

Biostratigraphy

A major change in this century has been the establishment of a time-scale, to which sites' faunas or individual taxa can be related. Such chronological control has allowed more complete paleoenvironmental reconstructions to be made with multifaceted analysis of fossil remains. Current emphasis, given an ability to date materials and sites directly by

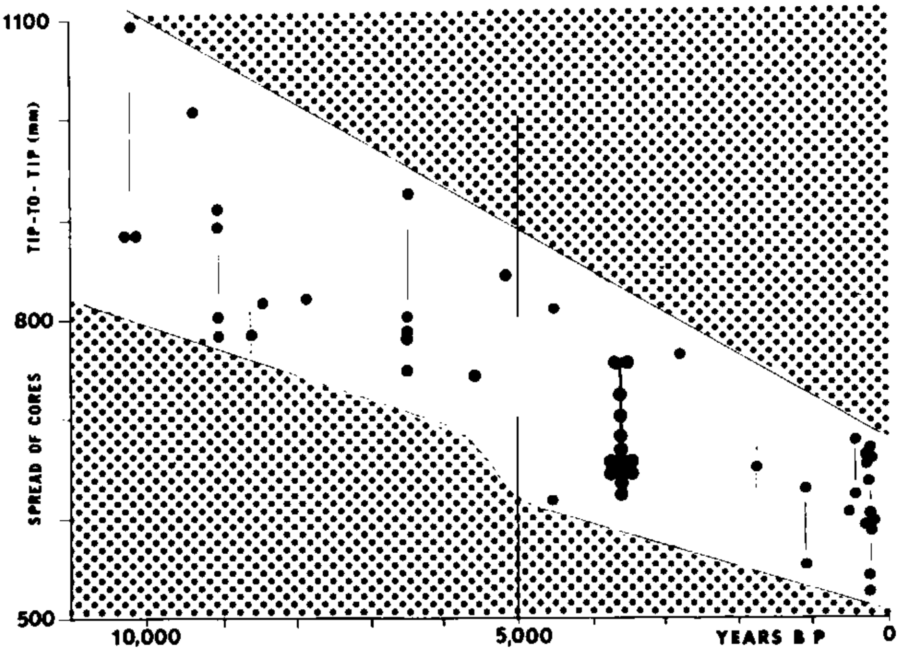


Figure 18 *Chronoclinal variation in* Bison *horncore spread (tip-to-tip) on the northern Great Plains, from 11,000 years B.P. to present. Adapted from Wilson (1980) with additional unpublished data.*

radiometric, paleomagnetic, or other means, allows the fine-resolution study of the rapidity of environmental change and microevolutionary change, millennium by millennium, with standard errors of less than 200 years for most of the Holocene. It is now possible to document with great precision chronoclinal trends as well as events of dispersal and extinction; given dated sequences from disparate areas we can now search for "critical dates" of change that reflect widespread paleoclimatic or other paleoenvironmental changes (*e.g.*, Bryson *et al.*, 1970). However, the lack of a reliable chronological control covering most of the Quaternary is still one of the greatest problems for vertebrate paleontologists. Only when there are better dating techniques and agreement among geologists and their interpretations, will it be possible to refine the vertebrate time-scale.

Some 80 years ago, many Quaternary geologists identified strata by their contained index fossils (Savage, 1951). There are, at least in terms of the degree of time resolution demanded by Quaternary scientists, no worldwide terrestrial index fossils. An additional problem is that vertebrates have always been less abundant than invertebrates. Absence of a given species could as easily reflect sampling biases or accidents of preservation as it could any environmental, physiological, competitive or extinction factor. Thus, with terrestrial fossils, it became necessary to have a suite of index species before an age could be suggested. This procedure was codified in a series of "Land Mammal Ages" for the Tertiary and Quaternary, in which the indicator species were included. For example, the presence of mammoths (genus *Mammuthus*) in North America indicates an age of about 2.3 million years ago or less (Churcher, 1986; Harington, 1984a), whereas the presence of bison (*Bison* spp.) indicates an age of 1.2 million years or less in northern North America and considerably less (<400,000 years ago) in the south (Graham and Semken, 1987; Harington, 1984a,b). Both of these genera originated in Eurasia and arrived in North America by migration, providing convenient sudden appearances in the record. Alternatively, horses (genus *Equus*) evolved in North America. Fossils of equid teeth, which are intergradational between the ancestral genus *Piohippus* and its descendant *Equus*, pose a problem in assigning stratigraphic ages. Only broad age limits of perhaps a few hundred thousand years can be used.

At present, even Land Mammal Ages are considered insufficiently reliable or too coarse in temporal resolution; if a deposit yields an extensive fauna it is designated as a local fauna and is then matched taxon by taxon with temporal distributions established on evidence from other sites, as has been done for several parts of North America (Churcher, 1984; Lundelius *et al.*, 1987; Harington, 1978; Kurtén and Anderson, 1980) (Figure 20). The best possible fit is made and any discrepancies are checked for errors in identification. If the discrepancies are confirmed, it can then be considered that the species in question were present earlier or later than previously recorded, or that they changed their geographic distribution through time (so that their previously established temporal range remains valid for one area but not for another; in effect, being time transgressive). The latter is known to have happened in Recent faunas either through human introduction of exotics, as in the case of opossums *(Didelphis virginianus)* released in California, or through colonization without human intervention, as in the northward range extension of opossums into Ontario and British Columbia, of fishes in the Great Lakes (Stewart and Lindsay, 1983), or the colonization of South America and then North America by cattle egrets *(Bubulcus ibis)* from Africa.

Whenever there has been a major faunal change, the recovered faunas are often con-

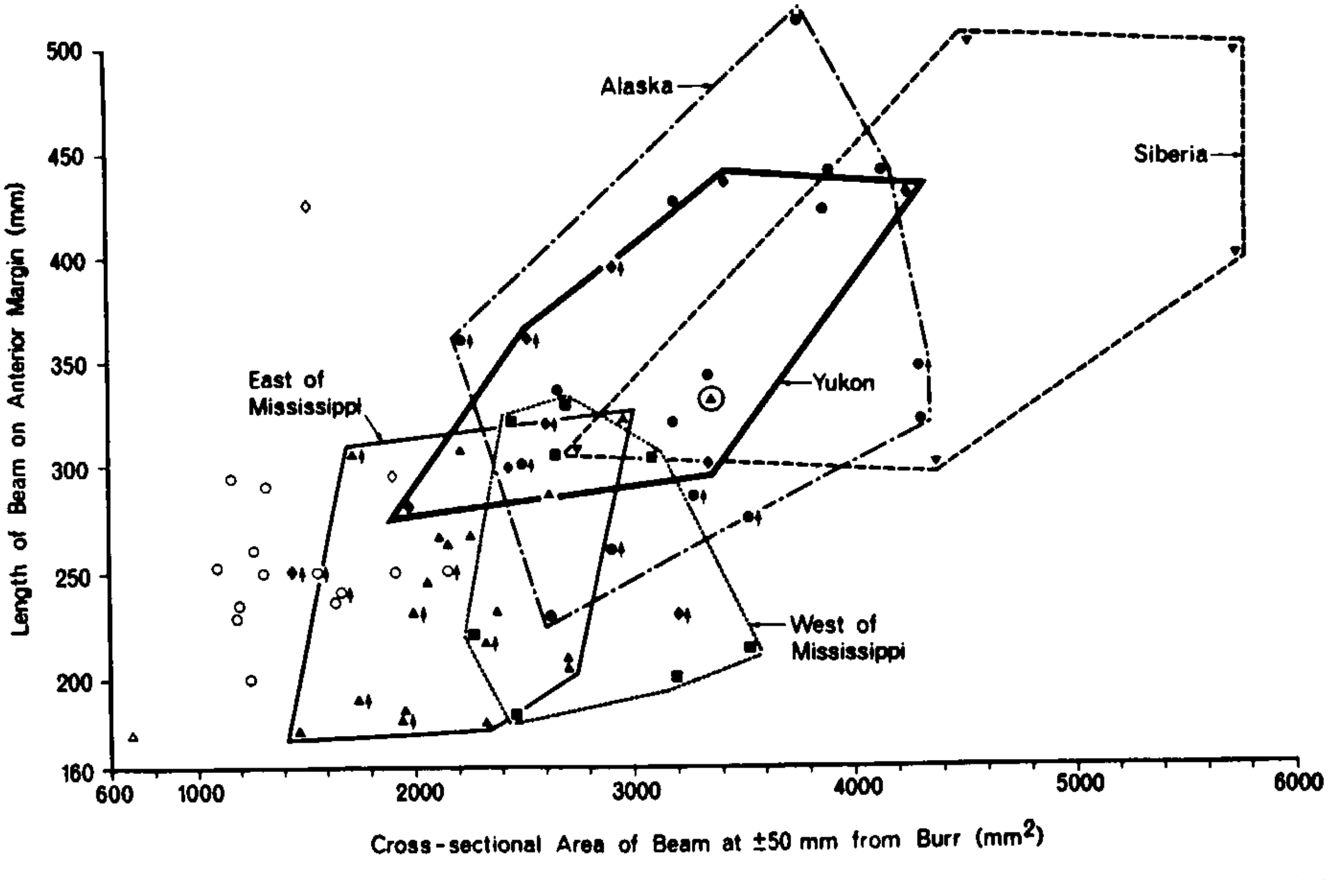


Figure 19 *Geographic clinal variation in antler beam of the extinct elk-moose* (Cervalces). *Antlers derived from presumed adult males are indicated by solid symbols, those from young males by open circles. Arrows indicate plots for which length of beam is minimal. Polygons outline plots from geographic areas. (Taken from Churcher and Pinsof, 1987).*

fusing or contradictory, because there can be different "faunal facies" in deposits that are apparently correlative or geographically contiguous. Thus, where contacts between riverine, riparian forest, grassland, and rocky hillslope or mountain environments are narrow or marked, only the more mobile and ecologically tolerant species will appear in more than one habitat and thus in the representative deposits. Animals with limited mobility, either because of small size or because of structural limitations, will be better indicators of local environments. However, a mechanism of transport and deposition that samples several environments (*e.g.*, a river passing through different vegetational communities) can accumulate mixed "faunas" that did not co-exist in life (Shotwell, 1955). Animals that undertake seasonal migration may reside sequentially in different environments and may therefore exhibit specific adaptations for each; environmental changes with metamorphosis in amphibians are an obvious example, but other groups (*e.g.*, birds) require specific habitats during the period in which young are dependent upon their parents for protection and feeding. Seemingly productive vegetational communities might become unattractive in winter because of snow cover, causing occupants to move to otherwise less favorable communities and resulting in seasonal mixing of species that occupy distinct areas in summer.

Many authors have described Pleistocene faunas that exhibit unusual associations of forms that seemingly represent markedly different, and hence contradictory, environments. These "disharmonious faunas" could, in part, represent artificial associations, like those described above, but are frequent enough to have elicited hypotheses that the environments in which they lived were not like any of the present day. An example of such a disharmonious fauna from a northern Alabama cave includes northern species (caribou, *Rangifer tarandus*; marten, *Martes americana*; fisher, *Martes pennanti*; and brown bear, *Ursus americanus*), western species (prairie chicken, *Tympanuchus cupido*; and thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*), and southern species (extinct armadillo, *Dasypus bellus*; extinct tapir, *Tapirus* cf. *veroensis*; jaguar, *Panthera onca*; and extinct peccary, *Platygonus compressus)* (Churcher *et al.*, 1988). Even discounting the extinct species, this assemblage has no modern counterpart. Such an unusual fauna, if not taphonomically mixed, could signal a vegetational community no longer represented, seasonal alterna-

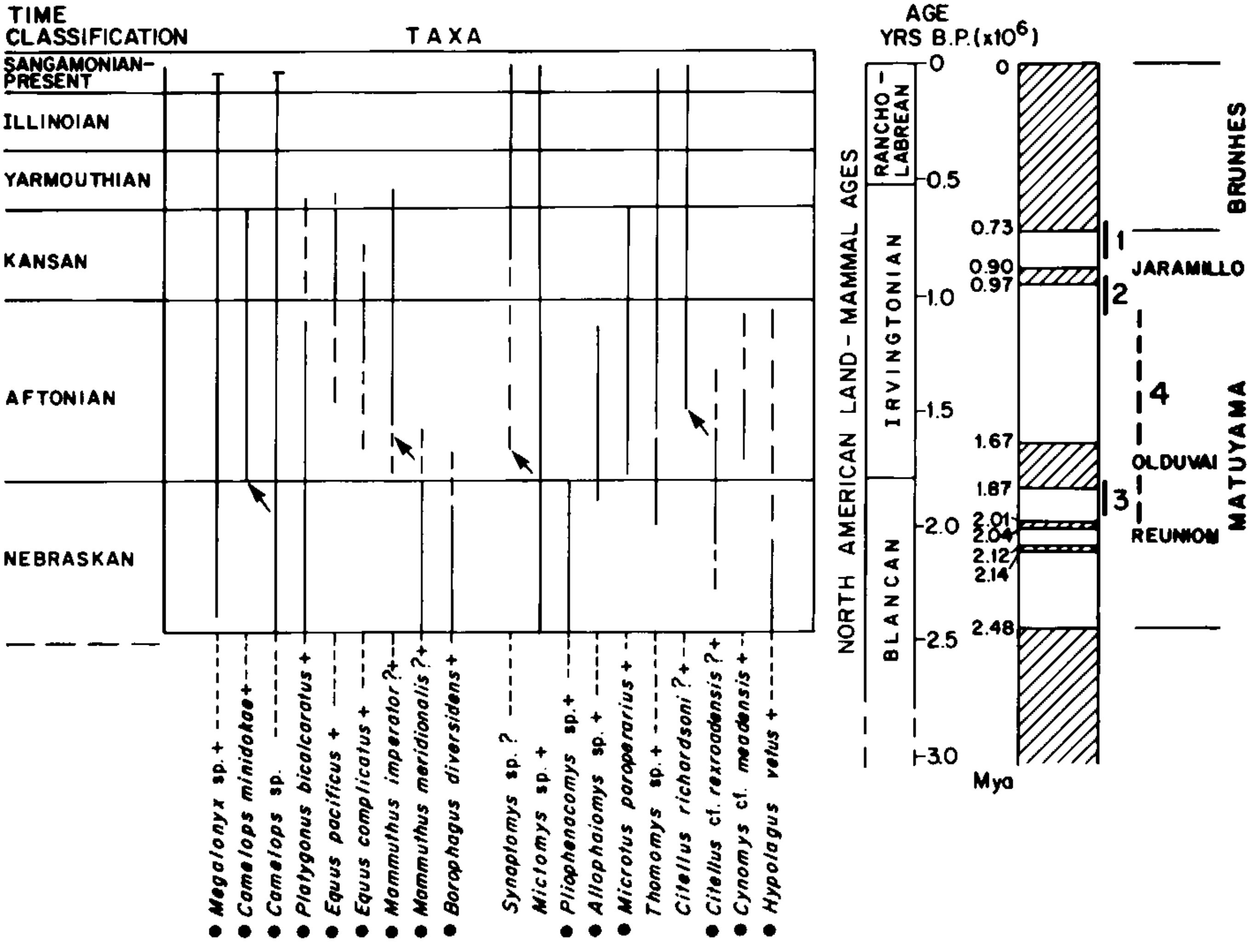


Figure 20 *An example of the taxonomic data available for faunal dating of a site, in this case the Wellsch Valley site near Stewart Valley, Saskatchewan. Taxa with dots before their names are extinct, though they may have relatives that survive to the present. Those with pluses (+) after their names are present in the Wellsch Valley record; diagonal arrows (➘) indicate replacement or derivation of taxa, an important consideration if identification is difficult. Age ranges of taxa as documented at other sites are shown as solid lines. Land-mammal ages and magnetic polarity events are shown at right; normal polarity is shaded and reversed polarity is white. Lines 1 to 4 on right show possible ages for Jaw Face section at Wellsch Valley based on combined faunal, paleomagnetic and stratigraphic considerations; alternatives 1 and 4 are preferred over 2 and 3. The potential temporal range for the Wellsch Valley Local Fauna appears to fit best within the Aftonian, with the caveat that the utility of early glacial/interglacial temporal units is itself in question (see text, p. 60).* Borophagus *and* Pliophenacomys *suggest an older age for the fauna or later persistence of these taxa than formerly documented. (Modified after Barendregt* et al., *in preparation).*

tion of discrete fauna, or any number of other possibilities (see Graham, 1986; Graham and Semken, 1987). Most importantly in terms of the present paper, it reinforces the need for studies of entire assemblages, rather than interpretation based on a single "indicator" species.

Zooarchaeology

An almost separate subdiscipline of Quaternary paleontology is the burgeoning field of faunal interpretation of remains from archaeological sites, known by the names of "zooarchaeology", "archaeozoology" or "faunal analysis". It is beyond the scope of this paper to discuss this important area of research in detail. The indisputable association of artifacts with extinct faunas, and later with hominids that could be seen to differ from modern humans, validated the concept that humans had co-existed with extinct mammals and had an evolutionary history that included a "human" (toolmaker) stage of more than one million years' duration. This period is often known as the "Anthropogene" in Europe and the Soviet Union in recognition of sequences of fossil hominids and of stone tool industries that established that humans had evolved in a manner similar to that of the rest of the biotic world. In North America the involvement of Barnum Brown in the excavations at Folsom, New Mexico firmly cemented the link between archaeology and vertebrate paleontology that continues to this day. Analysis of the animal remains associated with human remains or occupational sites has developed dramatically in the past thirty years, building especially upon the pioneering work of vertebrate paleontologist T.E. White (1952-55). It boasts distinctive methodologies (*e.g.*, Grayson, 1984; Klein and Cruz-Uribe, 1984) and extensive cross-links with taphonomy (*e.g.*, Binford, 1981; Morlan, 1980), and tool analysis (Loy, 1983), subdivisions for each of the taxonomic groups and biotic provinces and, in some cases, for culturally mediated divisions (*e.g.*, fish, bird, or mammal studies; Old World *versus* New World; Neolithic *versus* Paleolithic or Industrial; Classical Greek *versus* Roman, Egyptian or Mesopotamian; sedentary *versus* transhumance).

Concluding Remarks

Clearly, study of Quaternary vertebrate faunas has played, and will continue to play, an important part in Quaternary ecology. Fruitful areas of future research will include refinements in the use of vertebrates as biostratigraphic tools, more attention paid to the record of microvertebrate remains, and co-ordinated studies of all biotic remains from single sites containing vertebrate fossils for more complete paleoenvironmental reconstructions.

References

Agassiz, L., 1833-1844, Recherches sur les poissons fossiles, 5 vols: Neuchatel, 1420 p. With supplement, Monographie des poissons fossiles du vieux grès rouge ou systéme Devonien [Old Red Sandstone] des Iles Britanniques et de Russie, 171 p.

Agassiz, L., 1850, Lake Superior. Its physical character, vegetation, and animals: Gould, Kendall and Lincoln, Boston, 428 p.

Akersten, W.A., Foppe, T.M. and Jefferson, G.T., 1988, New source of dietary data for extinct herbivores: Quaternary Research, v. 30, p. 92-97.

Auffenberg, W. and Milstead, W.W., 1965, Reptiles in the Quaternary of North America, *in* Wright, H.E., Jr. and Frey, D.G., eds., The Quaternary of the United States: Princeton University Press, Princeton, New Jersey, p. 557-568.

Barendregt, R.W., Thomas, F.F., Irving, E., Stalker, A. MacS. and Churcher, C.S., in preparation, Stratigraphy and paleomagnetism of the Jawface Section, Wellsch Valley Site, Saskatchewan.

Barnosky, C.W., 1989, Postglacial vegetation and climate in the northwestern Great Plains of Montana: Quaternary Research, v. 31, p. 57-73.

Barnosky, C.W., Anderson, P.M. and Bartlein, P.J., 1987, The northwestern U.S. during deglaciation: vegetational history and paleoclimatic implications, *in* Ruddiman, W.F. and Wright, H.E., Jr., eds., North America and Adjacent Oceans during the Last Deglaciation: Decade of North American Geology Series, v. K-3, Geological Society of America, Boulder, Colorado, p. 289-321.

Bayrock, L.A., 1964, Fossil *Scaphiopus* and *Bufo* in Alberta: Journal of Paleontology, v. 38, p. 1111-1112.

Behrensmeyer, A.K., 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 4, no. 2, p. 150-162.

Behrensmeyer, A.K., 1984, Taphonomy and the fossil record: American Scientist, v. 72, p. 558-566.

Billings, E., 1870, On bones of a whale lately discovered in Cornwall, Ontario.: Canadian Naturalist and Quarterly Journal of Science, New Series, v. 5, p. 438-439.

Binford, L.R., 1981, Bones: Ancient men and modern myths: Academic Press, New York, 320 p.

Boaz, N.T. and Behrensmeyer, A.K., 1976, Hominid taphonomy: transport of human skeletal parts in an artificial fluviatile environment: American Journal of Physical Anthropology, v. 45, p. 53-60.

Bryson, R.A., Baerreis, D.A. and Wendland, W.M., 1970, The character of late-glacial and post-glacial climatic changes, *in* Dort, W., Jr. and Jones, J.K., Jr., eds., Pleistocene and Recent Environments of the Central Great Plains: University of Kansas, Department of Geology, Special Publication No. 3, p. 53-74.

Buckland, W., 1824, Notice on the *Megalosaurus*, or great fossil lizard of Stonesfield: Transactions of the Geological Society of London, Series 2, v. 1, p. 390-396.

Buckland, W., 1836, Geology and mineralogy considered with reference to natural theology, 2 vols.: Bridgewater Treatises No. 6, London.

Chisholm, B.S., Driver, J., Dube, S. and Schwarcz, H.P., 1986, Assessment of prehistoric bison foraging and movement patterns via stable-carbon isotope analysis: Plains Anthropologist, v. 31, p. 193-205.

Churcher, C.S., 1968, Pleistocene ungulates from the Bow River gravels at Cochrane, Alberta: Canadian Journal of Earth Sciences, v. 5, p. 1467-1488.

Churcher, C.S., 1975, Additional evidence of Pleistocene ungulates from the Bow River gravels at Cochrane, Alberta: Canadian Journal of Earth Sciences, v. 12, p. 68-76.

Churcher, C.S., 1984, Faunal correlations of Pleistocene deposits in western Canada, *in* Mahaney, W.C., ed., Correlation of Quaternary Chronologies: GeoBooks, Norwich, United Kingdom, p. 145-158.

Churcher, C.S., 1986, A mammoth measure of time: molar compression in *Mammuthus* from the Old Crow Basin, Yukon: Current Research in the Pleistocene, v. 3, p. 61-64.

Churcher, C.S., Parmalee, P.W., Bell, G.L. and Lamb, J.P., 1988, Caribou from the Late Pleistocene of northwestern Alabama: Canadian Journal of Earth Sciences, v. 67, p. 1210-1216.

Churcher, C.S. and Pinsof, J.D., 1987, Variation in the antlers of North American *Cervalces* (Mammalia; Cervidae): review of new and previously recorded specimens: Journal of Vertebrate Paleontology, v. 7, p. 373-397.

Coleman, A.P., 1901, Glacial and interglacial beds near Toronto: Journal of Geology, v. 9, p. 285-310.

Cross, F.B., 1970, Fishes as indicators of Pleistocene and Recent environments in the Central Great Plains, *in* Dort, W., Jr. and Jones, J.K., Jr., eds., Pleistocene and Recent Environments of the Central Great Plains: University of Kansas, Department of Geology, Special Publication No. 3, p. 241-257.

Cuvier, G., 1812, Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusiers animaux dont les revolutiones du globe on détruit les espéces, 4 vols., Paris.

Davis, L.C., 1987, The mammalian record for Late Pleistocene and Holocene environmental changes in the Central Great Plains of the United States, *in* Graham, R.W., Semken, H.A., Jr. and Graham, M.A., eds., Late Quaternary Mammalian Biogeography of the Great Plains and Prairies: Illinois State Museum Scientific Papers, v. 22, p. 88-143.

Dawkins, W.B., 1878, Monograph of the British Pleistocene Mammalia, a preliminary treatise on the relation of the Pleistocene Mammalia to those now living in Europe: Palaeontographical Society Monographs, pt. A, p. i-xxxviii.

Dawson, J.W., 1878, Note on a fossil seal from the *Leda* clay of the Ottawa valley: Canadian Naturalist, New Series, v. 8, p. 340- 341.

Dawson, J.W., 1883, On portions of the skeleton of a whale from gravel on the line of the Canadian Pacific Railway, near Smith's Falls, Ontario: Canadian Naturalist, New Series, v. 10, p. 385-387.

Dawson, J.W., 1891, Note on a fossil fish and marine worm found in the Pleistocene nodules of Green's Creek on the Ottawa: Canadian Record of Science, v. 4, p. 86-88.

Dawson, J.W., 1893, The Canadian Ice Age: W.V. Dawson, Montreal, 301 p.

Dodson, P., 1973, The signficance of small bones in paleoecological interpretation: University of Wyoming Contributions to Geology, v. 12, p. 15-19.

Efremov, I.A., 1940, Taphonomy: a new branch of paleontology: Pan-American Geologist, v. 74, p. 81-93.

Fitzgerald, G.R., 1986, The card-vial system for the storage of small vertebrate fossils, *in* Waddington, J. and Rudkin, D.M., eds., Workshop on Care and Maintenance of Natural History Collections: Royal Ontario Museum, Life Sciences Miscellaneous Publications, p. 81-83.

Flint, R.F., 1971, Glacial and Quaternary Geology: John Wiley and Sons, New York, 553 p.

Frison, G.C. and Todd, L.C., 1986, The Colby Mammoth Site: Taphonomy and archeology of a Clovis kill in northern Wyoming: University of New Mexico Press, Albuquerque, 238 p.

Geist, V., 1971, The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*: Quaternary Research, v. 1, p. 283-315.

Glob, P.V., 1969, The Bog people: Iron Age man preserved; translated by R. Bruce-Mitford: Cornell University Press, Ithaca, New York, 200 p.

Graham, R.W., 1976, Late Wisconsin mammalian faunas and environmental gradients of the eastern United States: Paleobiology, v. 2, p. 343-350.

Graham, R.W., 1986, Plant-animal interactions and Pleistocene extinctions, *in* Elliott, D.K., ed., Dynamics of Extinction: John Wiley and Sons, New York, p. 131-154.

Graham, R.W. and Semken, H.A., Jr., 1976, Paleoecological significance of the short-tailed shrew *(Blarina)*, with a systematic discussion of *Blarina ozarkensis*: Journal of Mammalogy, v. 57, p. 433-449.

Graham, R.W. and Semken, H.A., Jr., 1987, Philosophy and procedures of paleoenvironmental studies of Quaternary mammalian faunas, *in* Graham, R.W., Semken, H.A., Jr. and Graham, M.A., eds., Late Quaternary Mammalian Biogeography of the Great Plains and Prairies: Illinois State Museum, Scientific Papers, v. 22, p. 1-17.

Grayson, D.K., 1984, Quantitative Zooarchaeology: Academic Press, Orlando, 202 p.

Guthrie, R.D., 1982, Mammals of the mammoth steppe as paleoenvironmental indicators, *in* Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E. and Young, S.B., eds., Paleoecology of Beringia: Academic Press, New York, p. 307-326.

Guthrie, R.D., 1990, Frozen Fauna of the Mammoth Steppe: the story of Blue Babe: University of Chicago Press, Chicago, 323 p.

Harington, C.R., 1978, Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence: National Museum of Natural Sciences, Ottawa, Syllogeus 15, 105 p.

Harington, C.R., 1984a, Mammoths, bison and time in North America, *in* Mahaney, W.C., ed., Quaternary Dating Methods: Elsevier, Amsterdam, p. 299-309.

Harington, C.R., 1984b, Quaternary marine and land mammals and their paleoenvironmental implications — some examples from northern North America, *in* Genoways, H.H. and Dawson, M.R., eds., Contributions to Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication no. 8, p. 511-525.

Harington, C.R., 1990, ed., Canada's Missing Dimension: Science and history in the Canadian Arctic Islands: Canadian Museum of Nature, Ottawa, Vol. 1.

Harington, C.R. and Occhietti, S., 1988, Inventaire systematique et paléoécologie des mammifères marins de la mer de Champlain (fin de Wisconsinien) et de ses voies d'accès: Géographie physique et Quaternaire, v. 42, p. 45-64.

Haynes, G., 1980, Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones: Paleobiology, v. 6, p. 341-351.

Heintz, A. and Garutt, 1965, Determination of the absolute age of the fossil remains of mammoth and woolly rhinoceros from the permafrost of Siberia by the help of radio carbon (C^{14}): Norsk Geologisk Tidsskrift, v. 45, p. 73-79.

Hibbard, C.W., 1958, Summary of North American Pleistocene mammalian faunas: Papers of the Michigan Academy of Science, Arts and Letters, v. 43, p. 3-32.

Hibbard, C.W., 1970, Pleistocene mammalian local faunas from the Great Plains and Central Lowland provinces of the United States, *in* Dort, W., Jr. and Jones, J.K., Jr., eds., Pleistocene and Recent Environments of the Central Great Plains: University of Kansas, Department of Geology, Special Publication no. 3, p. 395-433.

Hibbard, C.W., Ray, D.E., Savage, D.E., Taylor, D.W. and Guilday, J.E., 1965, Quaternary mammals of North America, *in* Wright, H.E., Jr. and Frey, D.G., eds., The Quaternary of the United States: Princeton University Press, Princeton, New Jersey, p. 509-525.

Hoffman, R.S. and Jones, J.K., Jr., 1970, Influence of Late-Glacial and Post-Glacial events on the distribution of Recent mammals on the northern Great Plains, *in* Dort, W., Jr. and Jones, J.K., Jr., eds., Pleistocene and Recent Environments of the Central Great Plains: Department of Geology, University of Kansas, Special Publication No. 3, p. 355-394.

Hutton, J., 1795, Theory of the earth, with proofs and illustrations: Edinburgh.

Janis, C.M., 1984, The use of fossil ungulate communities as indicators of climate and environment, *in* Brenchley, P., ed., Fossils and Climate: John Wiley and Sons, New York, p. 85-104.

Jefferson, T., 1799, A memoir on the discovery of certain bones of a quadruped of the clawed kind in the western parts of Virginia: Transactions of the American Philosophical Society, v. 4, p. 246-260.

Jones, C.A., Choate, J.R. and Genoways, H.H., 1984, Phylogeny and paleobiogeography of short-tailed shrews (genus *Blarina*), *in* Genoways, H.H. and Dawson, M.R., eds., Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication No. 8, p. 56-148.

Joysey, K.A., 1972, The fossil species in space and time: some problems of evolutionary interpretation among Pleistocene mammals, *in* Joysey, K.A. and Kemp, T.S., eds., Studies in Vertebrate Evolution: Winchester Press, New York, p. 267-280.

Klein, R.G. and Cruz-Uribe, K., 1984, The Analysis of Animal Bones from Archaeological Sites: University of Chicago Press, Chicago, 266 p.

Klein, R.G. and Scott, K., 1989, Glacial/Interglacial size variation in fossil spotted hyenas *(Crocuta crocuta)* from Britain: Quaternary Research, v. 32, p. 88-95.

Koch, P.L., 1986, Clinal geographic variation in mammals: implications for the study of chronoclines: Paleobiology, v. 12, p. 269-281.

Kurtén, B., 1968, Pleistocene Mammals of Europe: Aldine Publishing Co, Chicago, 317 p.

Kurtén, B. and Anderson, E., 1980, Pleistocene Mammals of North America: Columbia University Press, New York, 422 p.

Land, L.S., Lundelius, E.L., Jr. and Valestro, S., 1980, Isotopic ecology of deer bones: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 32, p. 143-152.

Leidy, J., 1856, Note on the remains of a species of seal, from the Post-Pleistocene deposit of the Ottawa River: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 8, p. 90-91.

Loy, T.H., 1983, Prehistoric blood residues: detection on tool surfaces and identification of species of origin: Science, v. 220, p. 1269-1271.

Lundelius, E.L., Jr., Graham, R.W., Anderson, E., Guilday, J., Holman, J.A., Steadman, D.W. and Webb, S.D., 1983, Terrestrial vertebrate faunas, *in* Porter, S.C., ed., Late Quaternary Environments of the United States, v. 1, The Late Pleistocene: University of Minnesota Press, Minneapolis, Minnesota, p. 311-353.

Lundelius, E.L., Jr., Churcher, C.S., Downs, T., Lindsay, E.H., Schultz, G.E., Semken, H.A., Webb, S.D. and Zakrzewski, R.J., 1987, The North American Quaternary sequence, *in* Woodburne, M.O., ed., Cenozoic Mammals of North America: University of California Press, Berkeley, p. 211-235.

Lyell, C., 1845, Travels in North America in the years 1841-1842, with geological observations in the United States, Canada, and Nova Scotia: 2 vols., Wiley and Putnam, New York.

MacDonald, G.M., 1989, Postglacial palaeoecology of the subalpine forest-grassland ecotone of southwestern Alberta: new insights on vegetation and climate change in the Canadian Rocky Mountains and adjacent foothills: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 73, p. 155-173.

Maglio, V., 1973, Origin and evolution of the Elephantidae: Transactions of the American Philosophical Society, v. 63, p. 1-149.

Mantell, G.A., 1825, Notice on the *Iguanodon*, a newly discovered fossil reptile, from the sandstone of Tilgate Forest, in Sussex: Philosophical Transactions of the Royal Society, v. 115, p. 179-186.

Martin, L.D., 1984, Phyletic trends and evolutionary rates, *in* Genoways, H.H. and Dawson, M.R., eds., Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication No. 8, p. 526-538.

Martin, L.D. and Martin, J., 1987, Equability in the Late Pleistocene: Kansas Geological Survey Guidebook No. 5, p. 123-127.

Martin, P.S. and Guilday, J.E., 1967, A bestiary for Pleistocene biologists, *in* Martin, P.S. and Wright, H.E., Jr., eds., Pleistocene Extinctions: the search for a cause: Yale University Press, New Haven, p. 1-62.

Martin, P.S. and Klein, R.G., 1984, eds., Quaternary Extinctions: A prehistoric revolution: University of Arizona Press, Tucson, 892 p.

Martin, R.A., 1984, The evolution of cotton rat body mass, *in* Genoways, H.H. and Dawson, M.R., eds., Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday: Carnegie Museum of Natural History, Special Publication No. 8, p. 179-183.

McAllister, D.E., Cumbaa, S.L. and Harington, C.R., 1981, Pleistocene fishes *(Coregonus, Osmerus, Microgadus, Gasterosteus)* from Green Creek, Ontario, Canada: Canadian Journal of Earth Sciences, v. 18, p. 1356-1364.

McAllister, D.E., Harington, C.R., Cumbaa, S.L. and Renaud, C.B., 1988, Paleoenvironmental and biogeographic analyses of fossil fishes in peri-Champlain Sea deposits in eastern Canada, *in* Gadd, N.R., ed., The Late Quaternary Development of the Champlain Sea Basin: Geological Association of Canada, Special Paper 35, p. 241-258.

McDonald, J.N., 1981, North American Bison: their classification and evolution: University of California Press, Berkeley, 316 p.

McKinnon, N.A., 1986, Paleoenvironments and Cultural Dynamics at Head-Smashed-In Buffalo Jump, Alberta: The carbon isotope record: M.A. thesis, University of Calgary, Calgary, Alberta, 219 p.

Mead, J.I., O'Rourke, M.K. and Foppe, T.M., 1986a, Dung and diet of the extinct Harrington's mountain goat *(Oreamnos harringtoni)*: Journal of Mammalogy, v. 67, p. 284-293.

Mead, J.I., Agenbroad, L., Davis, O.K. and Martin, P.S., 1986b, Dung of *Mammuthus* in the arid Southwest, North America: Quaternary Research, v. 25, p. 121-127.

Merrilees, D., 1970, A check on the radiocarbon dating of desiccated thylacine (marsupial "wolf") and dog tissue from Thylacine Hole, Nullarbor Region, Western Australia: Helictite, v. 8, p. 39-42.

Morlan, R.E., 1980, Taphonomy and Archaeology in the Upper Pleistocene of Northern Yukon Territory: a glimpse of the peopling of the New World: National Museum of Man Mercury Series, Archaeological Survey of Canada, Ottawa, Paper 94, 380 p.

Nelson, R.S. and Semken, H.A., Jr., 1970, Paleoecological and stratigraphic signficance of the muskrat in Pleistocene deposits: Geological Society of America, Bulletin, v. 81, p. 3733-3738.

Osborn, D.J. and Helmy, I., 1980, The Contemporary Land Mammals of Egypt (including Sinai): Fieldiana (Zoology), New Series, No. 5, 579 p.

Osborn, H.F., 1936-1942, Proboscidea: a monograph of the discovery, evolution, migration, and extinction of the mastodonts and elephants of the world, 2 vols.: American Museum of Natural History, New York, 1675 p.

Owen, R., 1846, A History of British Fossil Mammals and Birds: John van Voorst, London, 560 p.

Owen, R., 1849-1884, A History of British Fossil Reptiles: reprinted from publications of the Palaeontographical Society, etc., London, 4 vols.

Ozoga, J.J. and Gysel, L.W., 1972, Response of white-tailed deer to winter weather: Journal of Wildlife Management, v. 36, p. 892-896.

Peale, R., 1803a, An historical disquisition on the mammoth, or great American incognitum, an extinct, immense, carnivorous animal whose remains have been found in North America: London, 91 p.

Peale, R., 1803b, Account of some remains of a species of gigantic oxen found in America and other parts of the world: Philosophical Magazine, v. 15, p. 325-327.

Purdue, J.R., 1980, Clinal variation of some mammals during the Holocene in Missouri: Quaternary Research, v. 13, p. 242-258.

Purdue, J.R., 1989, Changes during the Holocene in the size of white-tailed deer *(Odocoileus virginianus)* from central Illinois: Quaternary Research, v. 32, p. 307-316.

Purdue, J.R. and Styles, B.W., 1986, Dynamics of mammalian distribution in the Holocene of Illinois: Illinois State Museum, Reports of Investigations No. 41, 63 p.

Reher, C.A., 1970, Population dynamics of the Glenrock bison population, *in* Frison, G.C., ed., The Glenrock Buffalo Jump, 48CO304: Late Prehistoric Period buffalo procurement and butchering on the northwestern plains: Plains Anthropologist, v. 15, no. 50, Memoir No. 7, p. 51-55.

Reher, C.A., 1978, Buffalo population and other deterministic factors in a model of adaptive process on the shortgrass plains, *in* Davis, L.B. and Wilson, M.C., eds., Bison Procurement and Utilization: a symposium, Plains Anthropologist, v. 23, no. 82, Memoir No. 14, p. 23-39.

Reher, C.A. and Frison, G.C., 1980, The Vore Site, 48CK302, a stratified buffalo jump in the Wyoming Black Hills: Plains Anthropologist, v. 25, Memoir No. 16, 190 p.

Reynolds, S.H., 1939, A monograph on the British Pleistocene Mammalia, Volume III, Part VI. The Bovidae: Palaeontographical Society, London, p. 1-65.

Rhodes, R.S., II and Semken, H.A., Jr., 1986, Quaternary biostratigraphy and paleoecology of fossil mammals from the Loess Hills region of western Iowa: Proceedings of the Iowa Academy of Science, v. 93, p. 94-130.

Richmond, G.M. and Fullerton, D.S., 1986, Introduction to Quaternary glaciations in the United States of America, *in* Sibrava, V., Bowen, D.Q. and Richmond, G.M., eds., Quaternary Glaciations in the Northern Hemisphere: Quaternary Science Reviews, v. 5, p. 3-10.

Romer, A.S., 1929, A fresh skull of an extinct American camel: Journal of Geology, v. 37, p. 261-267.

Savage, D.E., 1951, Late Cenozoic vertebrates of the San Francisco Bay region: University of California Publications, Bulletin of the Department of Geological Sciences, v. 28 p. 215-314.

Scott, W.B., 1913, A history of land mammals in the western hemisphere: Macmillan, New York, 693 p.

Semken, H.A., Jr., 1983, Holocene mammalian biogeography and climatic change in the eastern and central United States, *in* Wright, H.E., Jr., ed., Late Quaternary Environments of the United States, v. 2, The Holocene: University of Minnesota Press, Minneapolis, Minnesota, p. 182-207.

Shipman, P., 1981, Life History of a fossil, An introduction to taphonomy and paleoecology: Harvard University Press, Cambridge, 222 p.

Shotwell, J.A., 1955, An approach to the paleoecology of mammals: Ecology, v. 36, p. 327-337.

Simpson, G.G., 1951, Horses: Oxford University Press, New York, 247 p.

Smith, W., 1817, Stratigraphical System of organized fossils: London, 118 p.

Sokolov, V.Y., Dubrovo, I.A., Lebedkina, N.S. and Ponomarenko, N.G., eds., 1986, Yuribeyskiy momont [The Yuribey mammoth]: Iztadel'stvo "Nauka", Moscow, 160 p.

Solounias, N. and Dawson-Sanders, B., 1987, Dietary adaptations and paleoecology of the Late Miocene ruminants from Pikermi and Samos in Greece: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 65, p. 149-172.

Steadman, D.W., and Miller, N.G., 1987, California condor associated with spruce-pine woodland in the Late Pleistocene of New York: Quaternary Research, v. 28, p. 415-426.

Stewart, K.W. and Lindsay, C.C., 1983, Postglacial dispersal of lower vertebrates into the Lake Agassiz region, *in* Teller, J.T. and Clayton, L., eds., Glacial Lake Agassiz: Geological Association of Canada, Special Paper 26, p. 391-419.

Sutcliffe, A.J., 1970, Spotted hyaena: crusher, gnawer, digester and collector of bones: Nature, v. 227, p. 1110-1113.

Tieszen, L.L., Hein, D., Qvortrup, S.A., Troughton, J.H. and Imbamba, S.K., 1979, Use of $\delta^{13}C$ values to determine vegetation selectivity in East African herbivores: Oecologia, v. 37, p. 351-359.

van Devender, T.R., 1987, Paleoclimatic implications for the monsoonal Sonoran Desert of a packrat midden vegetation sequence from the Puerto Blanco Mountains, southwestern Arizona: Quaternary Research, v. 27, p. 51-72.

Vereshchagin, N.K. and Baryshnikov, G.F., 1982, Paleoecology of the mammoth fauna in the Eurasian Arctic, *in* Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E. and Young, S.B., eds., Paleoecology of Beringia: Academic Press, New York, p. 267-279.

Verme, L.J., 1968, An index of winter weather severity for northern deer: Journal of Wildlife Management, v. 32, p. 566-574.

Vesey-Fitzgerald, D.F., 1960, Grazing succession among East African game animals: Journal of Mammalogy, v. 41, p. 161-172.

Voorhies, M.R., 1969, Taphonomy and population dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska: University of Wyoming, Contributions to Geology, Special Paper, v. 1, 69 p.

Voorhies, M.R. and Thomasson, J.R., 1979, Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in an extinct species: Science, v. 206, p. 331-333.

Walker, A., Hoeck, H. and Perez, L., 1978, Microwear of mammalian teeth as indicators of diet: Science, v. 201, p. 908-910.

Wells, P.V., 1976, Macrofossil analysis of wood rat *(Neotoma)* middens as a key to the Quaternary vegetational history of arid America: Quaternary Research, v. 6, p. 233-248.

White, T.E., 1952-1955, Observation on the butchering techniques of some aboriginal peoples, nos. 1 to 9: American Antiquity, v. 17, p. 337-338; v. 19, p. 160-161; v. 19, p. 254-264; and v. 21, p. 170-178.

Wilson, M.C., 1974, The Casper Local Fauna and its fossil bison, *in* Frison, G.C., ed., The Casper Site: a Hell Gap bison kill on the High Plains: Academic Press, New York, p. 125-171.

Wilson, M.C., 1978, Archaeological kill site populations and the Holocene evolution of the genus *Bison*, *in* Davis, L.B. and Wilson, M.C., eds., Bison Procurement and Utilization: A symposium: Plains Anthropolgist, v. 23, Memoir No. 14, p. 9-22.

Wilson, M.C., 1980, Morphological dating of Late Quaternary bison on the northern plains: Canadian Journal of Anthropolgy, v. 1, p. 81-85.

Wilson, M.C., 1988, Bison dentitions from the Henry Smith Site, Montana: evidence for seasonality and paleoenvironments at an Avonlea bison kill, *in* Davis, L.B., ed., Avonlea Yesterday and Today: Archaeology and prehistory: Saskatchewan Archaeological Society, Saskatoon, p. 203-225.

Wilson, M.C. and Churcher, C.S., 1978, Late Pleistocene *Camelops* from the Gallelli Pit, Calgary, Alberta: morphology and geologic setting: Canadian Journal of Earth Sciences, v. 15, p. 729-740.

Wilson, M.C. and Churcher, C.S., 1984, The Late Pleistocene Bighill Creek Formation and its equivalents in Alberta: correlative potential and vertebrate palaeofauna, *in* Mahaney, W.C., ed., Correlation of Quaternary Chronologies: Geo Books, Norwich, United Kingdom, p. 159-175.

Wilson, M.C. and Hills, L.V., 1984, Holocene white-tailed deer *(Odocoileus virginianus)* from the foothills northwest of Calgary, Alberta, Canada: Canadian Journal of Earth Sciences, v. 21, p. 365-371.

Wilson, M.V.H., 1988, Taphonomic processes: Information loss and information gain: Geoscience Canada, v. 15, p. 131-148.

Wright, G.F., 1890, The ice age in North America and its bearings upon the antiquity of man: D. Appleton and Company, New York, 622 p.

Accepted, as revised, 1 June 1990.