Vertebrate paleontology

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Introduction

When the United States last hosted a congress of the International Quaternary Union (INQUA), Wright & Frye (1965) edited the well-known volume The Quaternary of the United States. There were five chapters on vertebrates including "Quaternary Mammals" by Hibbard *et al.* (1965) and "Quaternary Reptiles" by Auffenberg & Milstead (1965). In the subsequent four decades new developments altered the practice of vertebrate paleontology. A fundamental obvious achievement, yet easily overlooked, consisted of doubling the number of Quaternary fossil localities and vastly augmenting the fossil samples. A quantum increase in microvertebrate samples stemmed from Hibbard's (1949) revolutionary introduction of efficient screening techniques. The resulting progress can be measured by the fact that virtually all species of mammals now living in North America are recorded as fossils, and that approximate geographic distributions of many can be credibly mapped back into the past. Other advances came with the deep-sea definition of glacial and interglacial cycles (marine oxygen isotope stages, MIS), improved methods of dating bone and fossil deposits, new electronic databases, access to ancient DNA, improved methods of phylogenetic reconstruction, and use of isotopic signatures in studies of diet and taphonomy. We briefly comment on the impact of these new facets.

North America is extraordinarily diverse eco-geographically. There is therefore a strong tendency to develop separate regional traditions in studying the succession of vertebrates from the Quaternary. This tendency is reinforced by the simple fact that nature provides different resources in each region. For this reason we devote the last part of this review article to some paleontological highlights from individual states and regions.

Biostratigraphy and Chronostratigraphy

Half a century ago Savage (1951) extended North American Land Mammal Ages (NALMA) into the Quaternary by characterizing the Irvingtonian and Rancholabrean. He led the way in providing NALMA with stage definitions and formal stratotypes. Distinguishing these NALMA from one another, and also the Irvingtonian from the preceding Blancan (largely Pliocene), still receives considerable emphasis. It remains traditional among this continent's Quaternary paleontologists to consider the Pliocene as well as the Pleistocene and Holocene. Thus, their purview generally spans nearly five million years.

Biostratigraphers studying the terrestrial faunal succession in North America embrace two somewhat different philosophies. Some emphasize an Oppelian approach in which overlapping range zones of multiple taxa characterize an assemblage. Others rely more heavily on a single widespread taxon, most often a "geologically instantaneous" intercontinental immigrant, to define a biochron.

Arvicoline rodents characterize the Oppelian approach in Eurasia and North America. Since these small grazers are diverse within the three Holarctic continents, evolved rapidly, and are easily identified by their molar teeth, they have excellent potential for biostratigraphic correlation and stage definition. As noted, widespread use of Hibbard's (1949) screening techniques amplified the availability of rodents in the North American record. One arvicoline biochronology for North America divides the Blancan & Irvingtonian into eight subdivisions (Repenning, 1987).

One serious limitation is that arvicolines often have narrower ecological tolerances and more limited distributions than many large mammals. For example, several proposed arvicoline zones turn out to be restricted to the High Plains. Similarly, Porcupine Cave in south-central Colorado (Fig. 1) has produced a rich assemblage of arvicolines at an elevation of 2900 m, yet that fauna does not readily correlate with other assemblages of similar age from farther east and at lower elevations (Bell & Barnosky, 2000).

North American Quaternary paleontologists generally support the quest for stage-defining immigrants because of that system's simplicity (Woodburne, 1987). *Mammuthus* (mammoths) define the Irvingtonian and *Bison* the Rancholabrean in North America (Savage, 1951). The first mammoths appear in North America fairly early in the

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Fig. 1. Entrance to Porcupine Cave, south central Colorado, 2900 m, 1988.

Pleistocene. The strongest association of North American mammoths with radiometric dates occurs in the Rock Creek local fauna, Texas, where the fossiliferous sediments are overlain by the 1.2-myr Cerro Toledo ash. Other early mammoths occur interbedded with 1.4-myr Guaje Pumice in the Santa Fe Formation in New Mexico, and just above the 1.36-myr Bruneau Basalt in Idaho. In Nebraska, early mammoths occur in the Rushville and Gordon local faunas of early Irvingtonian age. The largest sample of early *Mammuthus* comes from the Leisey Shell Pit in Florida (Fig. 2), with an estimated age of 1.5 myr (Hulbert *et al.*, 1995). The appearance of *Mammuthus* in North America was essentially contemporaneous over the whole continent, with differences in first appearance dates in various regions attributable to discontinuous deposition and the vagaries of associating productive fossil sites with good dates.

Fig. 2. Leisey Bone Bed overlying marine mollusks, Hillsborough County, Florida, 1983.

A problem similar to the restriction of certain arvicoline biochrons to the High Plains may also occur for the first appearance of *Bison* as the definition of the Rancholabrean. The genus was present in Alaska very early in the Pleistocene, but appeared much later south of the Laurentide Ice Sheet (Bell *et al.*, in press). A second difficulty stems from the late Blancan appearance of *Bison* recently reported from horn cores in two Florida sites (McDonald & Morgan, 1999). Possibly these two horn cores represent other bovids; their identification must be more fully discussed.

The oldest well-determined and well-dated *Bison* records from conterminous United States represent long-horned species. These are from American Falls, Idaho, the Mt. Scott local fauna in Meade County, Kansas, and the Ten Mile Hill beds near Charleston, South Carolina. The Idaho occurrence is estimated to be 200,000 yr old. It is found in lake sediments that accumulated behind a lava dam with a much younger K/Ar date of 72,000 yr (Pinsof, 1991). The Mt. Scott local fauna is estimated to be about 160,000 yr old. The South Carolina *Bison* is dated at about 240,000 yr by a U/Th date of interbedded corals (Szabo, 1985).

The end of the Rancholabrean NALMA is readily defined by the great extinction of most megafauna at 13,000 cal yr B.P. (ca. 11,000 ^{14}C yr B.P.). Specialists who prefer the Oppelian approach characterize the Rancholabrean by the association of modern insectivores, rodents, and carnivores with the now-extinct megafauna. The importance and impact of that extinction episode are discussed below.

A major concern of Hibbard *et al.* (1965) was to correlate fossil mammals with the four glacial and three interglacial cycles then recognized, and to reconstruct environmental conditions for them. It is now clear from deep-sea cores and their oxygen isotopic stages that there were about 20 major climatic fluctuations in the last 2 myr (Ruddiman & Wright, 1987). Consequently, efforts to correlate vertebrate faunal history with continental glacial episodes were abandoned. Now the great divide lies at about 50,000 years ago. Younger faunas generally can be dated accurately by ^{14}C; older faunas, representing 90% of Quaternary time, must be dated by other chronostratigraphic techniques.

The best approaches to dating older faunas are multidisciplinary, for example, integrating radiometric dates of tephra layers with paleomagnetic profiles and faunal evolution. The best example of such work, in a remarkably long section, comes from the Anza Borrego Desert in southern California (Fig. 3). There terrestrial sediments from the upper part of the Imperial Formation and the entire Palm Spring Formation attain a thickness of more than 4000 m, as a consequence of tectonic subsidence of the Salton Trough. Based on 150 magnetic samples from the area, Johnson *et al.* (1983) identified 12 paleomagnetic intervals spanning the upper Gilbert, the Gauss, and the lower Matuyama magnetic chrons. These were cross-correlated with one tephra that yielded a K/Ar date of 2.3 myr and with the rich biostratigraphic framework spanning Blancan and Irvingtonian NALMA (Cassiliano, 1999).

In Florida and South Carolina the primary biostratigraphic determinations of Blancan and Irvingtonian terrestrial faunas are supplemented by interfingering relationships with marine deposits. For example, at Macasphalt Shell Pit near Sarasota, Unit 4 yields about 100 species of terrestrial and freshwater vertebrates of late Blancan age. Because this unit is bracketed by many other units bearing a rich marine fauna, it was possible to conduct an integrative geochronological study combining magnetostratigraphy and strontium isotope history, along with ostracod, mollusk, and mammal biochronologies (Jones *et al.*, 1991).

Vertebrate history in the latest Quaternary is greatly illuminated by new methods of applying ^{14}C dating to amino acids in bone. This contrasts with earlier methods that provided dates associated with bone or bracketing the age of the bone. In 1965 it was recognized that dates on bone were unreliable. The organic fraction was often contaminated by foreign proteins from rootlets or humic acid, and the inorganic fraction was susceptible to postdepositional isotopic exchange. In the late 1980s, two major breakthroughs radically improved bone dating, one technological and the other methodological. First, accelerators in tandem with mass spectrometers (TAMS) could directly measure the ^{14}C in a sample, thus requiring only small samples (micrograms vs. kilograms). An individual rodent tooth can now be dated, whereas previously an ungulate limb bone might have been required (Stafford *et al.*, 1991). Also, a direct measurement of ^{14}C, rather than the decay rate of this radioactive isotope by scintillation counters, yields a more precise date. In the initial phases of TAMS dating, standard errors for samples between 15,000 and 20,000 yr old were several hundred years. More recently, strengthening of the AMS magnets improved precision in that age range to give standard errors of less than 50 years.

The second, methodological improvement involved selecting individual amino acids for dating (Stafford *et al.*, 1982). Dates from organic molecules, found in a wide variety of compounds like humates, were rejected in favor of

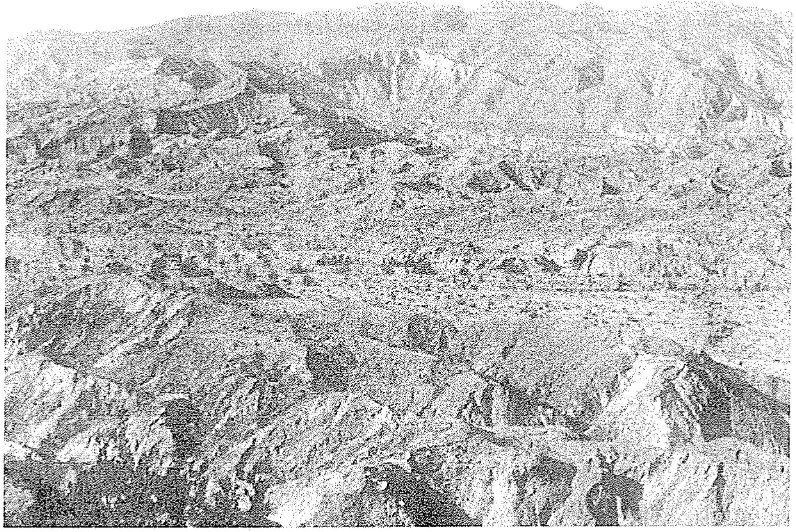

Fig. 3. The long succession of fossiliferous terrestrial sediments in the Anza Borrego Desert, California, 1991.

those from proline and hydroxyproline, which are generally intrinsic to bone. Examination of other isotope ratios, especially nitrogen, can help determine if isotopic exchange is a problem. Finally, filtering collage samples though an inert resin known as XAD-2 allows sample purification without requiring separation of specific amino acids (Stafford *et al.*, 1988, 1999). Thus, technological and methodological advancements in bone ^{14}C-dating provide a far more precise and more accurate chronology.

Biogeography

As the chronological framework improved and vertebrate samples increased in number, paleontologists gave greater emphasis to distribution patterns at several different scales. On the broadest scale, intercontinental dispersals of vertebrate species are of great interest, especially because their magnitude and frequency seem to have increased during the Pliocene and Pleistocene. Shifts in intracontinental vertebrate species ranges have major implications for climatic and ecological history.

Intercontinental dispersals had major impacts on the history of North American vertebrates, especially during the Quaternary Period when these effects seem to have accelerated. Trans-Beringian interchange greatly influenced the character of the North American vertebrate fauna, with increasingly larger percentages being derived from Eurasia from the Pliocene into the Holocene. By Irvingtonian time, the North American mammal fauna had incorporated the influence of treeless tundra-like environments as indicated by the immigration of *Soergelia* (a muskox) and diverse arvicolines, including red-backed voles (*Clethrionomys*), brown lemmings (*Lemmus*), and collared lemmings (*Dicrostonyx*), as well as Caribou (*Rangifer*). Other taxa such as elk (*Cervus*), meadow and prairie voles (*Microtus*), and mammoths (*Mammuthus*) may not be critical indicators of tundra but they do reflect open environments that support ample supplies of grass. For this reason, some paleoecologists have referred to this environment as arctic steppe (Guthrie, 1982). Some Eurasian immigrants, including *Bison*, *Saiga*, *Praeovibos*, *Alces*, and *Xenocyon*, were prevented, for reasons not fully understood, from migrating south of the Laurentide Ice Sheet. Many paleontologists consider the Alaskan-Yukon fauna effectively non-North American, and affiliate it more closely with the Olyorian of Siberia, at least until after the Brunhes magnetochron (Bell *et al.*, in press).

The Great Interamerican Interchange is noted for dispersing more terrestrial vertebrates southward from North America than northward from South America. Nonetheless, during the late Blancan, about 3 myr ago, a substantial group of South American immigrants reached this continent (Webb, 1991). Perhaps the most exotic among them were three families of shelled edentates including a small armadillo (*Dasypus*), a giant armadillo (*Pampatherium*), and the tank-like glyptodont (*Glyptotherium*). Ground sloths of three sizes, representing three different families, also dispersed northward. The ground sloth, *Megalonyx*, notable historically for having been studied by Thomas Jefferson in the White House, spread very widely, even into Alaska. Large rodents including capybaras (*Neochoerus* and *Hydrochoerus*) and porcupines (*Erethizon*) also moved north. The only large ungulate to come against the tide of northern forms was a toxodont genus (*Mixotoxodon*), unless one wishes to count the aquatic manatees (*Trichechus*) as a kind of ungulate. The vampire bats (*Desmodus*) presumably followed some large Neotropical mammals that they regularly parasitized. Finally, the most astonishing immigrant, previously known from the Tertiary of southern South America, was a flightless predatory bird (*Titanis*) that stood more than 3 m tall. Four additional genera from the Neotropical Realm appeared in the early Irvingtonian, notably opossums (*Didelphis*), a small ground sloth (*Nothrotheriops*), a small glyptodont (*Pachyarmatherium*), and a giant anteater (*Myrmecophaga*). Still other important tropical groups, including many kinds of birds, rodents and monkeys, reached Central America without leaving a fossil record (Webb & Rancy, 1996).

Avian migrations on both intercontinental and intracontinental scales constitute another major feature of vertebrate biogeography. Although these migrations are often attributed to Quaternary climatic events, new evidence suggests that they began by the middle Miocene (Steadman & Martin, 1984). Strong global cooling with increased seasonality at mid and high latitudes during the Miocene (Zachos *et al.*, 2001) intensified the differentiation of temperate and boreal vegetation zones in North America (Graham, 1999, p. 267). These effects triggered the diversification of passerines, including migratory forms (Becker, 1987; Olson, 1989, 2001). Late Miocene and early Pliocene evidence consists of genera whose living species are migratory passerines, for example the sparrow (*Ammodramus*) from the late Clarendonian to early Hemphillian of Kansas (Steadman, 1981) and a bunting (*Passerina*) from the late Hemphillian of Chihuahua, Mexico (Steadman & Martin, 1984). This latter record gains chronological credence because the estimated divergence time among living *Passerina* species based on mtDNA is 2.4–3.7 myr (Klicka *et al.*, 2001).

Much of the modern long-distance migration from the Nearctic to the Neotropics involves nine-primaried oscines (warblers, tanagers, buntings, sparrows, and orioles; Emberizidae *sensu lato*). Unfortunately, this group of songbirds is very difficult to characterize at the species level with postcranial osteology, and therefore is poorly represented in the published fossil record. This problem might be partially offset in the future by analyses of ancient DNA (selected late Quaternary fossils only) and a larger investment of time in passerine comparative osteology. The ~20 Quaternary glacial-interglacial cycles (the past 1.8 myr) represent the coolest interval in the history of living genera and species of birds. Long-distance migration may have involved more species of birds, traveling over longer distances, during warm (interglacial) intervals than during times of expanded continental ice sheets. When most of North America north of 40°N was covered with ice during the last glacial maximum, the latitudinal extent of long-distance migration must

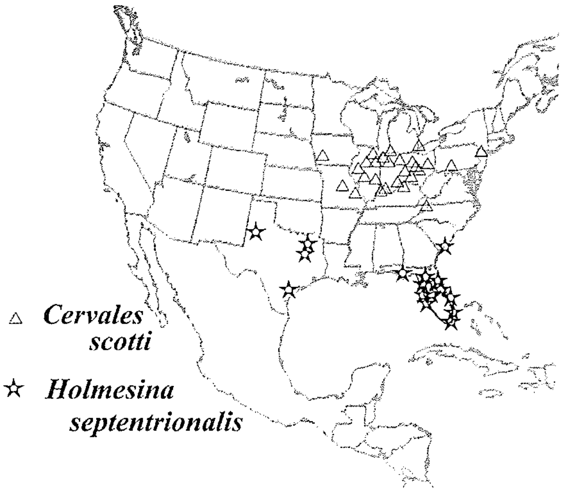

Fig. 4. FAUNMAP I shows the distribution in the U.S. of two late Pleistocene mammalian species, Cervalces scotti and Hokmesina septentronalis, during the Wisconsin Glaciation. Database as of June 25, 1993. Map redrawn from original provided courtesy of Illinois State Museum.

have been substantially shorter than today for the various migratory waterfowl, raptors, shorebirds, and passerines that currently nest north of 40°N. Likewise when currently arid parts of the western United States were filled with major lakes during the glacial maxima (Bachhuber, 1992), there may have been major alternatives to the four principle flyways followed today by migratory birds.

It is increasingly evident that mammals also exhibit interesting intracontinental dispersal patterns, presumably in response to climate change. Such range shifts helped Hibbard *et al.* (1965) distinguish their presumed glacial and interglacial faunas. Today digital databases like FAUNMAP (1994) greatly facilitate detailed biogeographic analyses (Figs 4 and 5). Replacing earlier efforts such as Martin & Hoffmann (1987) is a relational attribute database that utilizes the Geographic Information System (GIS) at the Illinois State Museum to map changes through time. The records can track individual species, species groups, or any other combination of parameters in the database. FAUNMAP I compiles information on location, geological and numerical ages, species composition, archaeological associations, and taphonomic data on faunas in the 48 contiguous United States for the last 40,000 years (FAUNMAP, 1994). More recently, FAUNMAP II has extended geographic coverage to include Alaska and Canada, and has extended the chronologic scope back through the Blancan NALMA.

The analyses resulting from FAUNMAP I demonstrated that each species responded to environmental change individually in accordance with its own tolerance limits. This reconstruction differs fundamentally from the wholesale shift of life zones and assemblages proposed in the older literature (e.g. Blair, 1965). Faunal provinces defined statistically during the latest Pleistocene are different from those that exist today. Finally, the analyses by the FAUNMAP Working

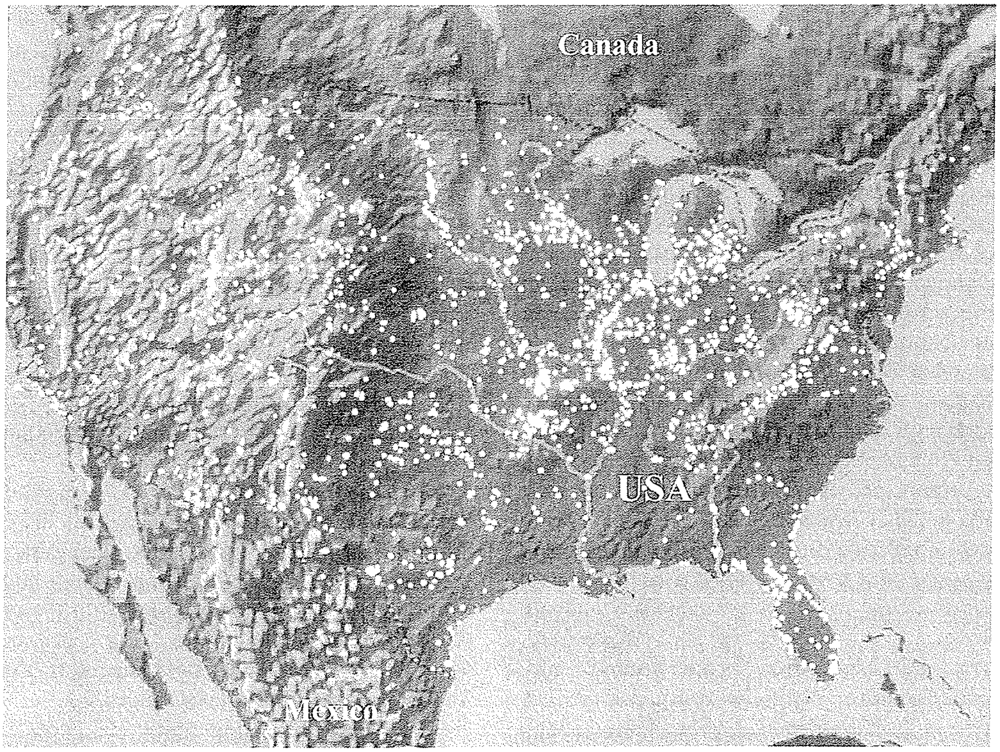

Fig. 5. FAUNMAP I sites in database as of June 25, 1993. Map photo courtesy of Illinois State Museum.

Group (1996) showed that late Pleistocene faunas and environments were more heterogeneous that those of the Holocene. This richness extends beyond the loss attributable to large mammal extinctions, discussed below, and is evident among the smaller vertebrates in every region where latest Pleistocene faunas have been adequately sampled.

Non-Analog Faunas and Taphonomy

Glacial-interglacial shifts in climate rearranged the composition of plant communities and consequently that of vertebrate faunas as well. It is not surprising that one of the great floristic conclusions from palynological studies, that plant species shifted individualistically, is also reflected in vertebrate faunas (FAUNMAP Working Group, 1996). In these studies, communities did not appear to move in lock-step, but appeared to pull apart in very complex patterns (Owen-Smith, 1989).

In each region of North America, one can track in detail the latest Pleistocene shifts of plants. Throughout the west, high-elevation conifers lived at much lower elevations during glacial times than today. On the other hand, by Holocene time the late Pleistocene pinyon-juniper woodlands of the southwest were replaced by desert scrub (Betancourt *et al.*, 1990). In most of the northeastern United States, a decline in spruce (*Picea*) and an increase in oak (*Quercus*) are two of the most striking vegetational changes during the transition from the late Pleistocene to the Holocene (Davis & Shaw, 2001; Jackson *et al.*, 1997). This represents the replacement of a largely coniferous woodland with a mixture of hardwoods and conifers, the latter consisting largely of pine (*Pinus*) and/or hemlock (*Tsuga*) rather than spruce. Some of the warmer floral elements, such as hickories (*Carya*) and black gum (*Nyssa*), did not reach New England until several millennia after the oaks. The late Pleistocene fossil plant data from eastern North America also suggest that open wooded habitats, variously called woodlands, parklands, or savannas, were more widespread than the closed-canopy forests that, in the absence of logging, characterize much of the region today. Quite possibly, the open character of these forests reflects the impact of North America's large mammals, especially mammoths and mastodons. Conversely, the present density of pristine forests may represent an abnormal aspect attributable to the missing megafauna (Graham & Grimm, 1990; Owen-Smith, 1989).

The individualistic response resulted in late Pleistocene vertebrate assemblages that, as already pointed out by Hibbard (1960, 1970), frequently consist of extant taxa that do not overlap geographically today. For instance, one finds arctic and boreal voles (*Clethrionomys*, *Phenacomys*, and various species of *Microtus*), lemmings (*Dicrostonyx*, *Lemmus* and *Synaptomys*), and shrews (*Sorex*) associated with temperate forest-dwelling woodrats (*Neotoma*), squirrels (*Sciurus* and *Tamias*), and shrews (*Cryptotis* and *Blarina*), also accompanied by grasslands taxa such as ground squirrels (*Spermophilus*), prairie dogs (*Cynomys*), and pocket gophers (*Thomomys* and/or *Geomys*). Such associations have been called variously "disharmonious," "out-of-step," or "non-analog" faunas. Recent studies have confirmed this by directly ^{14}C-dating individual bones of non-analog taxa from the same stratigraphic horizon (Stafford & Semken, 1990; Stafford *et al.*, 1999). In other words, these faunas represent true paleocommunities reflecting environments that no longer exist (Graham, 1985, 1986; Graham *et al.*, 1987; Semken, 1988; Stafford *et al.*, 1999).

In other instances, ranges of mammalian species move together through time, suggesting that some communities do remain coherent (Lyons, 2003). A good example consists of late Pleistocene sites in the northern Great Plains that contain modern tundra analogs. Of particular interest is the fauna from Prairieburg, Cedar County, Iowa where the most common mammal, *Lemmus sibiricus*, is associated with other tundra taxa that include collared lemming (*Dicrostonyx torquatus*), singing vole (*Microtus miurus*), and arctic ground squirrel (*Spermophilus undulatus*), but no grassland or forest taxa (Foley & Raue, 1987). As expected, such true tundra faunas lived immediately south of the Wisconsinan ice sheet during full-glacial time.

Another small but intriguing set of full-glacial sites in the Great Plains sample the modern prairie fauna. Present analogs for these sites are located well to the north of their recovery location, and support the conclusion of Stewart (1987) that Wisconsinan faunas of the Central and Northern Great Plains are composed of steppe and boreal taxa. Typical examples include the Domebo fauna (Slaughter, 1965) in Oklahoma; the Jones (Davis, 1987), Robert (Schultz, 1967), and Trapshoot (Stewart, 1987) in Kansas; the Lang/Ferguson (Martin, 1987) in South Dakota; and the Agate Basin (Walker, 1987) in Wyoming.

A very pressing question concerns whether the well-studied faunal patterns of the last glacial termination might approximate patterns from earlier glacial cycles. At least one analog of a modern prairie fauna with much greater antiquity has been recognized in the Sandahl local fauna of Irvingtonian age (Semken, 1966). Two well-studied examples from the late Irvingtonian with long stratigraphic records occur in south-central Colorado. These are the sites in the San Luis Valley studied by Rogers *et al.* (1992) and the work of Bell & Barnosky (2000) at Porcupine Cave (Fig. 1), discussed further below. Ongoing analyses reveal non-analog faunas that persisted through glacial/interglacial transitions, even while they experienced substantial extinction of small species (Barnosky *et al.*, 1996). Nonetheless, the Porcupine Cave samples show that numbers of species within trophic levels have not changed, indicating a modicum of stability, at least in these montane settings.

Another rich microvertebrate fauna samples an even earlier interval in the midcontinent. This is the study of Martin *et al.* (2002) detailing the Deer Park fauna in Meade County, Kansas, during its transition from wetter to drier conditions within a glacial interval in the late Blancan. As discussed below, the numbers of rodents, and even the role of arvicolines, were roughly comparable then to the present rodent fauna of southwestern Kansas.

The hypothesized stability of most amphibian and reptile faunas in the North American Quaternary record was recently called into question. Traditionally, the stability of herpetofaunas was seen as their major distinction from later Cenozoic mammalian faunas. "If there is any one thing that characterizes the reptiles of the entire last half of the Cenozoic it is their stability" (Auffenberg & Milstead, 1965, p. 557). Recently, however, Bell & Gauthier (2002) cast serious doubt on this generalization by noting that present geography played a key role in the identification of most Quaternary herp specimens. Now that the circularity of this approach is clear, paleoherpetologists have adopted a more rigorous approach to their identifications, using the principles of phylogenetic systematics.

This more rigorous approach, however, leads to a practical problem in herpetofaunal taxonomic resolution. Using current understanding of morphological synapomorphies, the majority of herpetofaunal elements cannot be identified to species. This was first demonstrated for snakes from Papago Springs Cave in Arizona by Czaplewski *et al.* (1999). More recently, it also became evident in an exhaustive study of morphology and taxonomic utility of the ilium in North American toads of the genus *Bufo* (Bever, 2002). A sustained effort must be made to seek out morphological synapomorphies in the skeletal elements typically recovered from the fossil record. In many cases, this will simply mean re-evaluating traditionally utilized characters in the context of broader phylogenetic comparisons. New synapomorphies have incisively delineated the fossil distribution of various species of horned lizards, genus *Phrynosoma* (Norell, 1989).

These preliminary results are leading some Quaternary paleontologists to reconsider the herpetofaunal stability hypothesis and to undertake fundamental new character analyses. Meanwhile many herps can be paleoecologically informative even without species-level resolution. For example, fossil tortoises in areas north of their modern distribution definitely carry climatic significance (King & Saunders, 1986). The patterns of many such changing Quaternary distributions are indicated by Holman (1995) and by Bell & Gauthier (2002).

Taphonomy, meaning the processes of site formation and modification after burial, is another factor that must be considered in non-analog faunas. As shown by an extensive literature developed during the last two decades (e.g. Behrensmeyer & Hill, 1980; Bonnichsen & Sorg, 1989; Haynes, 1991), mixing processes before and after deposition are major concerns. Before a fossil assemblage can be considered non-analog, the contemporaneity of its members should be demonstrated by ^{14}C dating. In the study by Stafford *et al.* (1999) a considerable number of supposed non-analog faunas failed this test. Other important taphonomic factors are sample size and distribution of elements. Poorly sampled faunas may incorrectly appear to have modern analogs.

Extinctions and Conservation

Abrupt loss of nearly all large late Pleistocene land mammals in the Americas constitutes one of the unresolved mysteries in the history of life. The first concerted effort to search for the cause of this event was an INQUA symposium (Martin & Wright, 1967). The symposium documented the scope and speed of the great megafaunal extinction in North America, with loss of at least 35 genera of large mammals ca. 13,000 cal yr B.P. The roster of losses includes armadillos, glyptodonts, four families of ground sloths, giant beavers, capybaras, lions, pumas, sabertooths, peccaries, llamas, camels, pronghorns, musk-oxen, goats, horses, mammoths, mastodons, and gomphotheres (Alroy, 1999; Graham & Lundelius, 1984; Martin & Steadman, 1999). That symposium found no clear resolution between the two major causal hypotheses, climate change and human hunting. A central position on megafaunal extinctions was that of Kurtén & Anderson (1980, p. 363): "No one cause can account for it; rather a mosaic of adverse conditions prevailed... making the [megafauna] vulnerable to environmental pressures, including man, the hunter, who probably delivered the *coup de grace* to some of the megafauna between 12,000 and 9000 years ago." Another major effort to comprehend late Quaternary extinctions (Martin & Klein, 1984) still found this issue unresolved in North America, although on balance the efficacy of human environmental modification had gained many adherents in a global perspective.

While most accounts of late Quaternary extinctions feature the three dozen species of large mammals, it is also important to consider other groups. Although the North American herpetofaunal record does not disclose the loss of many species during the Pleistocene, southward restriction and ultimate loss of giant tortoises, genus *Hesperotestudo*, constitutes one striking herpetofaunal example. It is not generally appreciated that the number of avian generic extinctions in the latest Quaternary is about half of that affecting mammals. Most affected were carrion-feeders such as condors, vultures, storks, eagles, and caracaras, as well as other commensals that depended on large mammals (Steadman & Martin, 1984). Thus, extinction of large mammalian herbivores set off a trophic cascade that also wiped out large carnivores and scavengers, including many kinds of large birds.

Brown (1995) noted that large body size may be associated with extinction episodes via two major causal connections. First, large organisms have fewer individuals on any given landscape, and thus any environmental perturbations are more likely to degrade their numbers below the threshold for survival. Secondly large animals have more severe life history constraints, including low litter size and long intervals between reproduction. Even so, not every large mammal species became extinct. It will be useful to determine if some special life history features permitted bison, black bears, pronghorns, and several kinds of deer, goats, and sheep to survive? Kiltie (1984) suggested that study of breeding schedules and reproductive rates may explain the survival of the bovids and cervids noted above. Fisher (1987, 1996) reads from individual mammoth and mastodont tusks a wealth of information about life histories, the season of death, and possible distinction between human and climatic population pressures. Frison's work (e.g. 1992) with such prey species as mammoth and bison in Paleoindian contexts points an essential direction in which megafaunal population studies must evolve. Reconstruction of life histories in critical fossil populations holds the secret of how each species slides into extinction.

Two primary schools continue to vie for a complete explanation of the late Pleistocene vertebrate extinctions. One of these, as noted above, features the vast and various environmental shifts that coincided with the last deglaciation in North America. The other, emphasizing the role of human hunters, was formally presented by Paul S. Martin in a 1965 INQUA symposium as the "Overkill Hypothesis" (Martin, 1967). This concept was later amended to the "Blitzkrieg Hypothesis" (Martin & Klein, 1984). It makes the testable prediction that the appearance of Paleoindians in North America should be essentially concurrent with the megafaunal extinction. It does not follow, however, that a close correlation in time, now somewhat dubious, would demonstrate a causal relationship.

Computer simulations of North American megafaunal extinction by Alroy (2001) present a perfect challenge for more population studies of extinct megafauna. His analyses go well beyond previous attempts to model Paleoindian populations as they colonized the New World, adding interactions among declining herbivore species and population-level responses of large herbivores as they were presumably hunted. Alroy's model seems quite robust in most parameters, and correctly predicts the timing of the mass extinction, without resorting to local or *ad hoc* environmental scenarios. It is nonetheless a model that needs to be iteratively tested with revised records from FAUNMAP (FAUNMAP Working Group, 1996).

Another extinction hypothesis, articulated by MacPhee & Marx (1997), connects indirectly with the arrival of humans. When Paleoindians entered North America their dogs brought a series of diseases new to the resident mammal fauna. The major difficulty with this hypothesis is that it will be very difficult to test. The search for evidence has concentrated in the frozen ground of Beringia, and it is difficult to see how it can be extended into lower latitudes.

Still another hypothesis that begins with the human impact on mammoths (*Mammuthus*) and mastodonts (*Mammut*) is the "Keystone Species Hypothesis" of Norman Owen-Smith (1989), developing from his extensive experience with African ungulate communities. If human hunters rapidly and repeatedly decimated proboscidean populations, the reduction and ultimate demise of these great (keystone) herbivores would produce a cascade of detrimental changes depriving other herbivores in that ecosystem of their primary resources. This model might be refuted if it were shown that the proboscideans were among the last of the megafauna to go extinct.

Whatever the cause, the terminal Pleistocene extinction of large mammals and birds removed from the Americas vast faunas resembling African game parks. With increasing precision the megafaunal extinction episode is documented at ca. 13,000 cal yr B.P., that is during the last 1% of Quaternary time. Preliminary studies by Stafford *et al.* (1999) precisely dating of the youngest megafauna suggest that the extinctions may have occurred within a few hundred years. That perspective explains why Quaternary vertebrate extinction studies are beginning to merge with conservation studies. Graham & Grimm (1990) point out that studies of past habitat and climate change often illuminate conservationists' studies of present and future change. For example, a re-examination of the paleoecology of the endangered black-footed ferrets (*Mustela nigripes*) shows that they often lived without prairie dogs, contrary to the view (based only on historic observations) that *Cynomys* was their "obligate" prey (Owen *et al.*, 2000). Quaternarists must participate in modeling past and present species ranges, habitats, and genetic makeup to represent the full potential range of niche parameters. Such a combined approach of past and present perspectives gives the best hope for understanding and managing future faunal change.

Isotopes, Ecology, and Diet

Recognition that stable isotopes in bone retain a reliable record of an animal's diet opened a major new field of study illuminating both evolutionary and ecological aspects of ancient vertebrates. Ratios between ^{12}C and ^{13}C in tooth enamel establish the alternative photosynthetic pathways (C_3 or C_4) for different types of plants herbivores have eaten. The following example helps to explain the sympatry between three proboscideans that were the most abundant taxa at the West Palm Beach Site in the late Wisconsinan of south Florida. There Koch *et al.* (1998) showed that 92% of the diet of *Mammuthus columbi* consisted of C_4 grasses, while 90% of that of *Mammut americanum* was C_3 (presumably browse). The third proboscidean, the Neotropical gomphothere (*Cuvieronius tropicus*), consumed 49% C_4 grasses, exactly the intermediate strategy predicted by resource partitioning theory. Similarly, MacFadden *et al.* (1999) employed carbon isotopes to demonstrate a substantial (and partly unexpected) spread among feeding strategies of hypsodont horses in the late Hemphillian Palmetto Fauna of central Florida.

Several isotopes other than C also contribute insights into vertebrate paleoecology. Stable isotopes of N document the degree of carnivory of an animal and whether it has fed on marine organisms. $^{87}Sr/^{86}Sr$ ratios have varied through Earth history, and that ratio in most instances faithfully records the geological substrate inhabited by an organism. For example, the enamel of *Mammut americanum* from Florida registered levels too high to represent the Gulf Coastal Plain sedimentary environments. The only likely explanation is that they migrated northward across the Fall Line to granitic terrain (Hoppe *et al.*, 1999).

Finally, the oxygen isotopic composition of bone is determined by the source and temperature of the water utilized by an animal. Such data can provide a significant key to microclimatic patterns. Rubenstein *et al.* (2002) used oxygen isotopes to link the breeding and wintering ranges of a migratory songbird. Fisher (1987) applied such analysis to successive lamellae in proboscidean tusks to determine their seasonal growth patterns and to determine the season of death. In a broader application, Smith & Patterson (1994) utilized oxygen isotope ratios to assess climatic history of successive fish faunas from lake beds in the Glenns Ferry Formation of Idaho. In another long-term stratigraphic study, Rogers & Wang (2002) traced a late Matuyama shift in climate by proxy evidence extracted from dental enamel of pocket gophers (*Thomomys*).

Phylogenetic Studies and DNA

Phylogenetic studies have advanced substantially in two different modalities. The first involves theoretical advances, such as showing how molecular and morphological data can be integrated and studying patterns of faunal dynamics (Webb & Barnosky, 1985). The second advances have come via methodological innovations, such as cladistic analysis using new software such as PAUP (Phylogenetic Analysis Using Parsimony), and Norell's (1989) work on fossil and recent iguanid lizards. As a result, many of the evolutionary patterns that were interpreted as orthogenetic evolution several decades ago are now seen as bushes with many branches (e.g. Guthrie, 1970, for *Bison*; Steadman, 1980, for turkeys; and Martin & Barnosky, 1993, for a sampler of other groups). Such tree-like patterns are more concordant with our current understanding of the complexity of evolutionary systems in geological time.

The increasing possibility of obtaining and amplifying DNA from late Pleistocene and Holocene fossil bones offers an exciting supplement to more traditional phylogenetic methods used by vertebrate paleontologists. Although such studies are still in their infancy, ancient DNA evidence is profoundly reshaping perceptions of phylogenetic patterns. Quaternary vertebrate populations often offer an ideal halfway house between modern samples and ancient fossil samples. For instance, in her study of pocket gophers (*Thomomys talpoides*), Hadly (1997) shows no change in their genetics in spite of major spatial shifts. Evidently, their body size changes are due entirely to phenotypic plasticity and not to migration. On the other hand voles (*Microtus*) in the same settings show substantial shifts in their DNA.

Genetic studies of modern vertebrates have also helped unravel evolutionary and biogeographic shifts in populations during the rapid environmental changes of the Quaternary. *Puma concolor* extends the entire length of both American continents, thus occupying the largest range of any New World land mammal. It surely lived in North America first, extending its range into South America during the Pliocene-Pleistocene Great American Interchange. Yet the North American *Puma* populations share a remarkably homogeneous genome, in contrast with the several genetically diverse subspecies in Central and South America (Culver *et al.*, 2000). These authors conclude that North America lost its puma population and later was recolonized from a reservoir in eastern South America. Genetics thus demonstrates that the mountain lion is the fifth large cat swept away in North America's late Pleistocene extinction episode, the others being two sabercats (*Smilodon fatalis* and *Dinobastis serus*), the North American cheetah (*Miracinonyx truman*), and the American lion (*Panthera atrox*). It is also possible to include the jaguar (*Panthera onca*) as the sixth large cat species so eclipsed, for it experienced at least a substantial southward range reduction at the end of the Wisconsinan.

DNA from permafrost-preserved bones of brown bears in northwestern North America (eastern Beringia), integrated with modern samples, reveals a very complex history of local extinctions, reinvasions, and possible competition with the extinct short-faced bear (*Arctodus*). "Late Pleistocene histories of mammalian taxa may be more complex than those that might be inferred from the fossil record or contemporary DNA sequences alone" (Barnes *et al.*, 2002, p. 2267).

Morphological studies can be effectively combined with ancient DNA comparisons to better distinguish simple phenotypic shifts from fundamental evolutionary changes. Speciation events may be frequently produced by climatic shifts during the Quaternary, but these require a more direct demonstration of genetic discontinuity than traditional speculative models often present. Klicka *et al.* (2001) clearly demonstrate rapid genomic evolution among buntings (genus *Passerina*) during the Quaternary. Similarly, Martin's (1979) morphological work on populations of cotton rats (genus *Sigmodon*) documents highly punctuated evolution. Many more careful studies combining genetic and morphometric evidence are needed before generalizations about evolutionary rates and patterns are warranted.

Some Regional Highlights

Long stratigraphic sequences with superpositional control provide an ideal basis for working out the continental succession of Pliocene and Pleistocene vertebrate faunas. Fortunately there are about ten such sections, mainly in western North America. These include the Anza-Borrego Desert (Fig. 2) and the San Timoteo Badlands in California; the San Pedro Valley and the Gila River Valley in Arizona and western New Mexico; the Snake River Plain of Idaho; the Ringold Formation in Washington; Meade County, Kansas; and several sections in Nebraska. These sections provide a framework for biostratigraphic and biochronologic correlation of the many other unique fossil localities that have been studied across the United States. Some highlights of current research are presented below by states and regions.

Alaska

Increasingly, Quaternary paleontologists have recognized that the far north, beyond the continental glaciers, must be considered separately from temperate North America. Its denomination as eastern Beringia emphasizes its ecological continuity with western Beringia, especially during glacial intervals when sea level was low. The large mammals of Beringia, dominated by *Equus*, *Bison*, *Rangifer*, and *Mammuthus*, extended all the way into southern France and northern Spain, where they appear in lifelike color on the walls of Lascaux and Altamira (Guthrie, 2001). During the past 30 years, the mammoth steppe has been characterized by Guthrie (1990) and others as a fossil ecosystem quite different from the present tundra, taiga, and muskeg, which cannot support such a vast grazing fauna. An abundance of grass and forbs, along with a climate of drastically limited snowfall, supported immense multispecies herds, of which woolly mammoth was the keystone species. In eastern

Beringia the drainage routes trended westward, directing migratory corridors from Canada into Asia and back.

Only after an ice-free corridor opened southward, at the very end of the Pleistocene, did surviving elements of the Beringian fauna enter temperate North America (including the lower 48 states). Among the wave of new species that appeared in the latest Pleistocene and early Holocene, filtering in from Alaska, were humans, wolves, grizzly bear, elk, moose, and bison. This is a bit confusing in cases where an older sibling species was already present: for example, *Canis dirus* was supplanted by *Canis lupus*, and native *Cervalces* was followed by immigrant *Alces*. It is intriguing to note that a few of the mammoth steppe species had already edged through to ranges south of the great ice sheets, including such wide-ranging herbivores as caribou (*Rangifer*) and muskoxen (*Ovibos*) and also the giant lion (*Felis leo atrox*).

The Prince of Wales Island off southeastern Alaska has an extensive karstland in the Tongass National Forest. Large collections of vertebrates from On Your Knees Cave represent the mid-Wisconsin interstade and the last glacial maximum (Heaton *et al.*, 1996). Sediments of the earlier period yield evidence of denning carnivores, including black bear (*Ursus americanus*), brown bear (*Ursus arctos*), Arctic fox (*Alopex lagopus*), and river otter (*Lontra canadensis*), as well as caribou (*Rangifer tarandus*), a bovid (*Saiga* or *Oreamnos*), and abundant rodents, including hoary marmot (*Marmota caligata*), heather vole (*Phenacomys intermedius*), long-tailed vole (*Microtus longicaudus*), and brown lemming (*Lemmus trimucronatus*). This fauna suggests a variety of local landscapes with the last species indicating expanding tundra conditions at the approach of the last glacial maximum. The best indicator of the latter time is the ringed seal (*Phoca hispida*), which represents the presence of land-fast sea ice. Apparently, foxes scavenged remains of these and also harbor seal (*Phoca vitulina*) and Steller's sea lion (*Eumatopias jubatus*).

Great Basin

The unique basin-and-range physiography of the Great Basin has a clear influence on the geographic distribution of the extant flora and fauna. Furthermore, this geographic setting interacted in a dramatic manner with climatic change at the end of the Pleistocene. Brown (1978) proposed that boreal mammal and bird species extended widely across lowland areas during the late Pleistocene when boreal vegetation extended to lower elevations. As temperatures warmed during the transition to the Holocene, boreal biota retreated to higher elevations where they ultimately became isolated and in some cases suffered local extirpation. There was no possibility of subsequent colonization of these "montane islands" by boreal land mammals from "continental sources" such as the Rocky Mountains or Sierra Nevada. A similar pattern was suggested for birds (Johnson, 1978).

This model sets up predictions that can be tested by examining the fossil record of boreal mammals in the Great Basin. Four predictions are the following: (1) boreal mammals now isolated on Great Basin mountains must have occupied lowland valleys in the past; (2) boreal mammals now found only on certain ranges were present on others in the past; (3) boreal mammals no longer occuring in the Great Basin were there in the past; and (4) no Holocene colonizations by boreal mammals. These predictions have been supported elegantly by analyses of various late Pleistocene and early Holocene mammal faunas from the Great Basin (e.g. Grayson, 1987, 1993; Heaton, 1990, 1999; Mead & Mead, 1989; Mead *et al.*, 1992).

Abundant data derived from such diverse sources as ice cores, speleothems, and lake sediments indicate that similar climatic cycles extend into the Great Basin's past throughout the Quaternary (e.g. Winograd *et al.*, 1992). Thus, the boreal faunal dynamics outlined by Brown (1978) and supported by paleontological studies spanning the Pleistocene/Holocene boundary ought to be extended into earlier ages.

Recent recognition of a Middle Pleistocene (Irvingtonian mammal age) fauna from Cathedral Cave in the eastern Nevada is thus of particular significance (Bell, 1995). The cave entrance has an elevation of 1950 m and opens near the mouth of a steep canyon overlooking the Snake Valley, assuring that fossils within its sediments were derived from a wide range of elevations. Taphonomic vectors probably included raptorial carnivoran mammals, raptorial birds, and woodrats. The latter are rodents of the genus *Neotoma* with a proclivity to incorporate natural objects from their surroundings into their large well-cemented nests. Woodrat nests have provided an extraordinarily rich record of Great Basin biota during the past 40,000 years (Betancourt *et al.*, 1990). Preliminary studies of the extraordinarily rich Cathedral Cave vertebrates indicate that its arvicoline rodent assemblage is essentially identical to that of the Porcupine Cave in Colorado, discussed further below. Evidently Cathedral Cave extends the record of Great Basin faunal dynamics, with cycles of lowland expansion and montane isolation, back to an interval between 750,000 and 850,000 years ago (Bell & Barnosky, 2000).

In the canyon country of Utah dry alcoves provide the first intact boli of *Mammuthus columbi* along with dung blankets representing several other extinct ungulates. These digesta, dating to as recently as 11,670 ^{14}C yr B.P., include plant macrofossils, hair, and insect fauna (Davis *et al.*, 1985).

Idaho

A great wealth of late Pliocene material comes from the Glenns Ferry Formation in the western Snake River Plain. The focus of classic and current research is the local fauna especially the famous "Horse Quarry" where more than 200 individuals of the early horse, *Equus simplicidens*, have been recovered (Fig. 6). Additionally, 112 other species of vertebrates are known, making Hagerman the richest known Blancan fauna. A series of younger faunas, including Froman Ferry and Tyson Ranch, in the Glenns Ferry Formation document the transition to the Irvingtonian land mammal age. In addition to terrestrial faunas, this formation includes extensive fish faunas associated with ancient Lake Idaho (Smith &

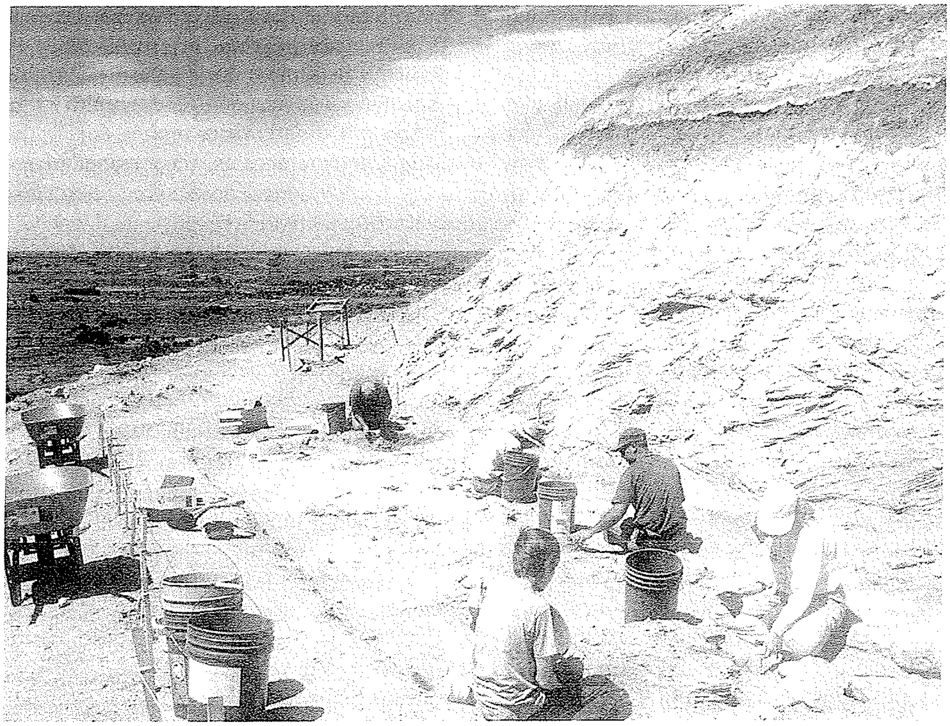

Fig. 6. Excavations at Hagerman Horse Quarry, Hagerman, Idaho, 1997.

Patterson, 1994). Subsequently, the modern Snake River drainage was created by capture of that lake by the Columbia River system.

A wealth of later Quaternary faunas are associated with the eastern Snake River Plain, most notably the American Falls fauna of last-interglacial age (Pinsof, 1991). Recently described from a higher elevation near the Wyoming border is the Booth Canyon fauna. Among distinctive features of this fauna is the higher proportion of the extinct muskox, *Bootherium bombifrons*. Finally, from the northern part of the state, at Tolo Lake, is a recent excavation of a large death assemblage (representing more than ten individuals) of Columbian mammoth, *M. columbi*, in association with *Bison antiquus*.

Colorado

A critical new site for middle Pleistocene paleontology in the Rocky Mountain region and adjacent parts of the Great Basin is Porcupine Cave in the central Rocky Mountains of Colorado (Fig. 1). The cave is situated at 2900 m in a large intermontane basin and presumably sampled a wide range of the ambient faunas in that area through the time duration of the accumulated sediments. Age assessments were based on paleomagnetic data and the known temporal ranges of recovered fauna, especially the arvicoline rodents (Bell & Barnosky, 2000). The arvicoline rodent fauna consists of at least seven extinct taxa including *Phenacomys* cf. *gryci*, *Mimomys* cf. *virginianus*, *Mictomys* cf. *meltoni*, *Allophaiomys pliocaenicus*, *Microtus* (=*Terricola*) *meadensis*, *Microtus paroperarius*, and an extinct and extant morphotypes of sagebrush vole, *Lemmiscus*. The estimated age of the middle portion of the Pit Locality is between 750,000 and 850,000 yr (Barnosky, 2003; Bell & Barnosky, 2000). This same suite of arvicoline rodents, presumably representing a unique biochronologic signature, appears in Cathedral Cave, Nevada, discussed above.

Wyoming

Paleontological work in the Yellowstone ecosystem, one of the largest virtually intact temperate ecosystems on Earth, helps bridge the gap between the fossil record and the present. With the time dimension thus expanded, one can develop new insights into how future climates will influence the ecology and evolution of the native western biota. Holocene cave sites, especially Lamar Cave and Waterfall Locality, sample over 80% of the present Yellowstone vertebrate fauna (Hadly, 1999). Lamar Cave contains over 10,000 identified mammal specimens representing 41 species. There are about as many avian specimens, but identifications are still in progress. Besides skeletal remains, isotopic and genetic samples are studied. Some of the findings are as follows:

(1) The late Holocene fauna still exists within 5–7 km of the fossil sites.
(2) Small mammal abundances fluctuate in the same manner as trapping studies today.

(3) Habitat generalists retain more constant population abundances than do habitat specialists during periods of cliimatic change.
(4) Relative abundances in these sites correlate well with estimates of effective populations size derived from genetic variation studies.
(5) Species persist through long periods of time with similar abundances, suggesting stable community assembly rules (within this time frame).
(6) Body sizes of mammals respond to climatic change by increasing during cold periods, while amphibian body sizes get smaller.
(7) Migration rates estimated from genetics are lower than expected in pocket gophers and higher than expected in voles.
(8) Elks and wolves are long-term natives of the Yellowstone fauna.
(9) Well-sampled fossil sites can more comprehensively document the local fauna than many trapping studies today.

Walker (1987) presented the first broad review of late-glacial faunas in the Wyoming Basin based on ~70 localities. The vertebrate samples and their stratigraphic contexts range from the long chronological coverage of Natural Trap Cave in the northern Bighorn Mountains to small faunas associated with four cultural levels in the Agate Basin of northeastern Wyoming. The full-glacial samples are marked by such tundra species as *Ovibos moschatus*, *Rangifer tarandus*, *Ovis canadensis*, and abundant *Dicrostonyx torquatus*, this last species exteding some 2000 km south of its present range. The common large grazers are *Mammuthus columbi*, *Camelops hesternus*, *Equus conversidens*, and *Bison antiquus*. The associated large carnivores, *Arctodus simus* (short-faced bear), *Ursus arctos* (grizzly bear), *Miracinonyx trumani* (American cheetah), and *Felis atrox* (American lion), exhibit adaptations for open habitats and were presumably predators on the large grazers.

South Dakota

In the town of Hot Springs, South Dakota a sediment-filled sinkhole occurs within carbonate deposits of the Spearfish Formation. During the last glaciation, thermal artesian water formed a pond which trapped remains of more than 50 juvenile and young adult males of *Mammuthus columbi*. In addition, 37 other vertebrate species have been recovered including *Arctodus simus*, *Camelops* sp. and *Hemiauchenia macrocephala* (Agenbroad *et al.*, 1990).

Kansas

The Meade Basin in Kansas is once more a critical center of research on the succession of Pliocene and Pleistocene vertebrates, recalling the heyday of Hibbard and his hard-working crews. Critical new evidence of a rich late Blancan microfauna adds a slightly younger facies to the classic Deer Park assemblage (Martin *et al.*, 2002). An abundance of *Baiomys* in Kansas during the Blancan, and its subsequent retreat to Mexico and the southwestern United States, suggests a slightly drier regime during that earlier interval. Minus aquatic species, the number of rodent species (18) from southwestern Kansas some 3 myr ago closely resembled that living there today.

The next-younger sample of the Borchers Badlands fauna boasts critical relationships between superposed localities and dated tephra. The Borchers site lies directly on the Huckleberry Ridge Ash, which has a radiometric date of 2.10 myr and records the last appearances in the region of the dwarf cotton mouse (*Sigmodon minor*) and the giant tortoise (*Geochelone*). An early Irvingtonian fauna from Nash 72 Quarry (Fig. 6), which lies 2.5 m above Huckleberry Ridge ash, records the first-known appearance of *Microtus* in the Meade Basin (Eshelman & Hibbard, 1981). Many fundamental patterns of rodent evolution and systematics seem to be centered in the rich faunal sequence from Meade County, Kansas.

Missouri Valley

In Missouri and Iowa, intensive waterscreening of matrix from 95 Holocene sites, most with cultural associations, has yielded 78 vertebrate species. Archaeological chronology permits subdivision of some sites into 50-yr intervals with a resultant 147 interpretable faunules. Paleoenvironmental analysis of these data suggests that: (1) Holocene conditions started on the western plains and transgressed eastward over a 1000-yr period; (2) the altithermal intensified in western Iowa between 8400 and 6350 yr B.P., but did not affect eastern Iowa forests during this interval; and (3) the drought predicted for the western United States approximately A.D. 1200 also impacted the plains. The faunas associated with sites occupied during this time and into the beginning of the Little Ice Age indicate dominance of Pacific air, a cool dry air mass, over the region. Although rainfall was reduced, decreased evaporation/transpiration partially balanced this effect so that human settlements persisted on the North Central Plains (Semken & Falk, 1987). A number of sites within the Northern Plains contained one or two mammalian species that presently are allopatric by up to 160 km, a configuration that is typical for Holocene local faunas.

Texas

In the southern Great Plains one crosses the Llano Estacado southeasterward onto the Edwards Plateau which is bounded on the east and south by the Balcones Escarpment. The plateau is underlain by flat-lying, mid-Cretaceous limestones in which numerous solution caves record the vertebrate biota of that area over a considerable portion of the Pleistocene. Careful study of more than 40 cave faunas has illuminated patterns of faunal change during the last 25,000 years (Lundelius, 1967). In addition, Fyllan and Kitchen Door caves produce faunas of Irvingtonian age in sediments with reversed remnant magnetism (Holman & Winkler, 1987; Taylor, 1982). The age of the Fyllan Cave Local Fauna is estimated to be about 830,000 yr. The fauna contains a number of extinct taxa including *Dasypus bellus*, *Aztanolagus agilis*, *Atopomys texensis*, *Allophaiomys* sp., and *Ondatra annectans*. It also has at least six extralimital taxa including *Synaptomys cooperi*, *Glaucomys cf. G. volans*, *Notiosorex*, and *Tapirus* sp. The fauna indicates a warm climate more humid that present but without the present climatic extremes.

One of the earliest studied faunas is from Friesenhahn Cave. It provides unusually well-preserved specimens, including articulated skeletons of *Homotherium serum*, *Mylohyus nasutus*, and *Sylvilagus*. In addition, there are skeletons of juvenile (probably neonates) of *Homotherium* as well as complete ontogenetic series of the dentition (Rawn-Schatzinger, 1992). An older unit also contains large numbers of teeth and bones of young *Mammuthus* exhibiting putative tooth marks that may represent the work of *Homotherium*.

Most of the Pleistocene faunas date from the last glacial maximum and contain three groups of species: extinct taxa, extant extralimital taxa, and extant taxa that still occur in the area. Level 3 from Laubach Cave, with a date of 23,230 ± 490 ^{14}C yr B.P. thus precedes the last glacial maximum and contains a few taxa such as *Tremarctos* sp., *Didelphis virginiana*, and *Glyptotherium* sp. not represented in most of the younger faunas (Lundelius, 1985). It also contains the only record of the Mexican free tailed bat, *Tadarida brasiliensis*, older than 2000 yr B.P. (Toomey, 1993).

The Pleistocene faunas of the Edwards Plateau share a great many extinct taxa with faunas of other areas of North America. The common widespread forms include *Canis dirus*, *Mammuthus*, *Paramylodon*, *Megalonyx*, *Smilodon*, antilocaprids, *Bison antiquus*, *Camelops*, *Hemiauchenia*, and *Equus* sp. They lack eastern forms such as *Bootherium*, *Castoroides*, and *Cervalces* and Rocky Mountain taxa such as *Nothrotheriops* and *Euceratherium*. A few taxa such as *Mammut*, *Glyptotherium* and *Chlamytherium*, which are widespread in faunas from the Gulf Coastal Plain and eastern North America, are found only along the eastern edge of the Edwards Plateau. Few examples of western taxa are known from the western edge of the plateau, an exception being *Navahoceras* from Cueva Quebrada in Val Verde County (Lundelius, 1984).

The extant taxa from the Pleistocene faunas show much the same pattern as the extinct ones. Carnivores, many rodents, and insectivores are shared with many faunas from other areas. Extralimital species include *Sorex cinereus*, *Synaptomys cooperi*, *Tamias striatus*, *Microtus pennsylvanicus*, and *Microtus ochrogaster*. The extralimital forms are now found in areas to north and east of the Edwards Plateau that have more mesic climates. To date no species from the Rocky Mountains are known from deposits on the Edwards Plateau.

The deposits in many of the Texas caves contain Holocene deposits with abundant fossils. The longest continuous sequence, from about 17,000 years ago to the present, is in Hall's Cave, Kerr County, Texas (Toomey, 1993). This shows the expected change from mesic to more xeric conditions about 10,000 years ago, with the disappearance of the extinct and many extralimital taxa. It also shows fluctuation in the percentages of several environmentally sensitive species. For example, changing proportions of *Notiosorex* (desert shrew) and *Cryptotis* (little short tailed shrew) indicate a relatively dry period between 11,600 and 10,125 ^{14}C yr B.P. From 10,125 to 9200 ^{14}C yr B.P. conditions were more mesic. This was followed by long period of gradual drying until about 2000 ^{14}C yr B.P. when there was return to conditions similar to present.

Florida

The richest Quaternary faunas in eastern North America come from diverse sedimentary deposits along the eastern Gulf of Mexico and the southern Atlantic Coastal Plain, spanning a broad range of Pliocene and Pleistocene formations. The richest example is an early Irvingtonian fauna from Leisey Shell Pits on the southeastern edge of Tampa Bay. There an extensive bonebed lying between marine shell beds produced some 50,000 catalogued specimens, including the richest early Pleistocene samples of sabercats, mammoths, tapirs, llamas, and many others from more than 100 vertebrate species. Its estimated age of about 1.5 myr is based on integrating mammalian biostratigraphy, marine mollusk biostratigraphy, magnetostratigraphy and Sr-isotope stratigraphy (Hulbert *et al.*, 1995).

Possibly the most diverse late Blancan vertebrate site is Inglis 1A at the mouth of the Withlacoochee River (Figs 7 and 8). Although only a small sinkhole, this site provides the most complete census of the mingled interamerican fauna thus far available. The site evidently sampled a subtropical savanna that extended around the Gulf of Mexico and expanded markedly during a low sea level of the latest Pliocene. The herpetofauna consists of 47 species which indicate "a mixed habitat of mature longleaf pine with xeric hammock interspersed" (Meylan, 1982, p. 67). Many of the species at Inglis 1A still live in similar associations along the belt of relatively xerophytic habitats in the central uplands of Florida. Study of these stable associations over a span of nearly 3 myr can illuminate present conservation efforts in these threatened habitats today.

Florida and the southern Appalachians produce rich samples of fossil birds, several of which exemplify "disharmonious" faunas, like those of small mammals described above. Major changes in distribution during the Quaternary are evident for many extant, non-resident species, including certain hawks, grouse, columbids, and corvids (Emslie, 1998; Lundelius *et al.*, 1983; Parmalee, 1992; Steadman, 2001). A common feature of these displaced avifaunas from the southeast is that they now live well to the north or west, often in grassland or northern coniferous habitats.

From the Plio-Pleistocene of Florida (Blancan through Rancholabrean land mammal ages), Emslie (1998) listed 93 species of non-passerine birds, 24 species of probable resident passerines, and only five species of probable Nearctic/Neotropical migrant passerines, the latter consisting of two thrushes, a catbird, warbler, and bunting.

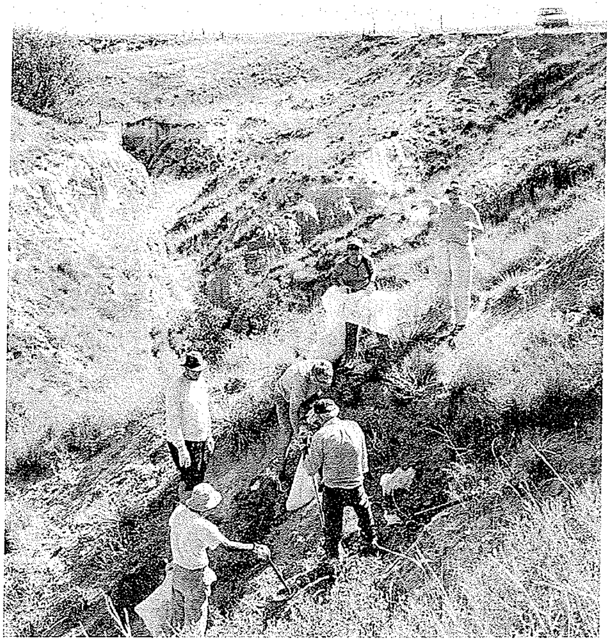

Fig. 7. Nash 72 Quarry, 3.5 m above the Huckleberry Ridge ash, seen in background. Meade County, Kansas, 2000.

Of the 122 species of birds from the Blancan through Rancholabrean of Florida, 21 (17%) are extinct, namely a cormorant, anhinga, stork, teratorn, three condors, duck, three eagles, accipitrid vulture, cracid, turkey, two rails, phorusracid, woodcock, pigeon, and two owls (Emslie, 1998). The six extinct genera from Florida (the teratorn *Teratornis*, condor *Aizenogyps*, duck *Anabernicula*, eagle *Amplibuteo*, accipitrid vulture *Neophronotops*, and phorusrhacid *Titanis*) have all been found elsewhere in North America. Just as is the case with living species today, many of the largest extinct taxa of Pleistocene birds were very widespread.

Appalachian Mountains and Allegheny Plateau

The Appalachian Mountains and Allegheny Plateau have been famous for their caves and associated Quaternary fossil-bearing deposits since the classic studies of Edward Cope and Joseph Leidy. A century passed before a Carnegie Museum team carried out the first detailed excavation of one of these sites, New Paris No. 4 (Guilday *et al.*, 1964). Their stratigraphic transect ranged from latest Wisconsinan through Holocene time. The late Wisconsinan fauna included arctic species such as caribou, yellow-cheeked vole, and collared lemmings, well south of their modern distributions, along with more southern taxa such as peccary, spectacled bear and beautiful armadillo, north of their implied distribution. This and other Appalachian sites also exhibited plains species, including thirteen-lined ground squirrel and plains pocket gopher well east of their present ranges and Rocky Mountain alpine taxa, notably the pika, in the Appalachians. Level-by-level maps, possibly the first paleoecological centerfolds, show the constriction in biogeographical distribution of species up section. The changing vertebrate faunules imply a succession of landscapes from boreal forest parkland to boreal forest, and then, after a quantum reduction in the early Holocene, to mixed forest and finally to the present deciduous forest conditions. Guilday *et al.* (1964) also integrated a level-by-level palynological analysis with paleoenvironmental interpretations based on fossil vertebrates.

Fig. 8. Screenwashing at Inglis 1A, Mouth of Withlacoochee River, Florida, 1974. Photo by Howard C. Converse, Jr.

Outlook Prospectus

There are still many unresolved issues, raised by Hibbard *et al.* (1965), that continue to challenge Quaternary vertebrate paleontologists. First, ^{14}C dating is generally limited to the last 50,000 yr. For deposits and faunas between this age and approximately 200,000 yr ago, there are no techniques that have been accepted as completely reliable for determining age. Electron spin resonance dating of enamel, optically stimulated resonance dating of sand grains, U-series dating of bone, and young age ranges of ^{40}Ar–^{39}Ar dating, each may become a more reliable clock for the great range of environments studied by Quaternary vertebrate paleontologists. Perhaps one of these methods will provide the key to accurately dating the boundary between the Irvingtonian and Rancholabrean NALMA.

There are also unresolved questions about the dispersal of species between and within continents. Perhaps the most intriguing concerns the ecogeographic barrier that frequently prohibited faunal continuity between Beringia and temperate latitudes of North America. Paleontologists have not yet identified clearly which mechanisms led to its occasional breakdown, chronicled by the sudden influx of Eurasian boreal beasts into the conterminous United States. Looking southward, reciprocal faunal mingling between North America and South America, and the changing ecological signatures that these migrations represent, require much refinement, especially in the American tropics (Webb & Rancy, 1996).

Finally, the cause of Pleistocene extinctions remains hotly debated (Alroy, 2001; Martin & Klein, 1984). The popular press attempts to capture the debate with three buzzwords, "Chill, kill, and ill." The prospect of fuller resolution depends on developing refined ecological and population studies of individual species and their communities. Only at that level can future extinction models be rigorously tested. The same work projected from the Quaternary into the future will also provide important insights into vertebrate conservation strategies.

Many of these issues point to the need for more complete faunal data from a broader spectrum of time and space. North American vertebrate paleontologists have undertaken FAUNMAP as a partial answer to this need, but there is still a loud call for tighter integration of floristic with faunistic data.

Dedication

This review reminds us that the work of paleontologists, as in many branches of historical science, is cumulative. It prompts us to honor the generations of dedicated scholars and scientists who have laid the foundations upon which we continue to build. Here we dedicate our work to four outstanding Quaternary vertebrate paleontologists who illuminated our paths.

Claude W. Hibbard (Fig. 9) stands out as the most productive Quaternary vertebrate paleontologist in North America, both in the field and in the museum. Björn Kurtén and Elaine Anderson undertook their magnificent synthesis in the 1970s, when the discipline had become perhaps too kaleidoscopic. The resulting volume on "North American Quaternary Mammals" inspired the entire profession and gave it new impetus. John E. Guilday, predecessor in the eastern region, led an extraordinarily productive team to new levels of multidisciplinary environmental reconstruction based on meticulously excavated spelean systems.

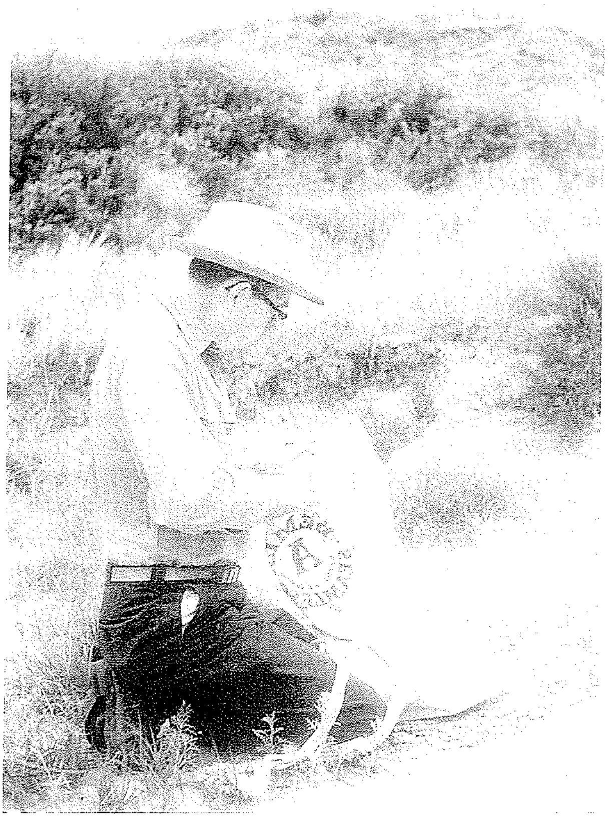

Fig. 9. Claude W. Hibbard preparing burlap strips for a plaster jacket, Blancan deposits at Hagerman, Idaho, 1973. Photo by Mick Hagger.

Even as we dedicate this chapter to these four predecessors, we note that there were many other key participants. Kurtén & Anderson (1980) cited 45 institutional collections and 124 professional colleagues as contributors to the success of their enterprise. More than ever, the best practices in Quaternary vertebrate paleontology continue to require collaboration of many scholars with diverse expertise.

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