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Introduction: Historical Perspectives FLINT

PART I: GEOLOGY

GLACIATED AREAS EAST OF THE ROCKY MOUNTAINS

Quaternary Geology of Northern Great Plains LEMKE, LAIRD, TIPTON, LINDVALL
Glaciation of Minnesota and Iowa WRIGHT, RUHE
Outline of Glacial Geology of Illinois and Wisconsin FRYE, WILLMAN, BLACK
Pleistocene Geology of Indiana and Michigan WAYNE, ZUMBERGE
Pleistocene Deposits of the Erie Lobe GOLDTHWAIT, DREIMANIS, FORSYTH, KARROW, WHITE
Quaternary Geology of New York MULLER
The Quaternary of New England SCHAFER, HARTSHORN

UNGLACIATED EASTERN AND CENTRAL UNITED STATES

The Atlantic Coastal Plain and the Appalachian Highlands in the Quaternary RICHARDS, JUDSON
Résumé of the Quaternary Geology of the Northwestern Gulf of Mexico Province BERNARD,
LEBLANC
The Pleistocene in Nebraska and Northern Kansas REED, DREESZEN, BAYNE, SCHULTZ
Quaternary of the Southern Great Plains FRYE, LEONARD

WESTERN UNITED STATES

Glaciation of the Rocky Mountains RICHMOND
The Cordilleran Ice Sheet of the Northern Rocky Mountains and Related Quaternary History
of the Columbia Plateau RICHMOND, FRYKELL, NEFF, WEIS
Nonglacial Quaternary Geology of the Southern and Middle Rocky Mountains SCOTT
Snake River Plain MALDE
Quaternary Geology of the Great Basin MORRISON
Quaternary Geology of the Southwest KOTTELOWSKI, COOLEY, RUHE
The Quaternary of the Pacific Mountain System in California WAHRHAFTIG, BIRMAN
The Glacial History of Western Washington and Oregon CRANDELL
The Quaternary Geology and Archaeology of Alaska PÉWÉ, HOPKINS, GIDDINGS

ZOOGEOGRAPHY AND EVOLUTION

QUATERNARY MAMMALS OF NORTH AMERICA

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THE CONSPICUOUS fossil remains of large extinct animals such as mastodons and ground sloths have long held the public interest. Fossils of Quaternary mammals both large and small are common in most parts of North America, but they have not been studied so intensively as those of the earlier Cenozoic. The special advantages that study of Quaternary mammals offers are a relatively full record, the possibility of establishing detailed phyletic lineages, and the opportunity to draw on a vast reservoir of knowledge of ecology, morphology, general biology, and geographic distribution of the living fauna.

The known fossil record of Pleistocene mammals is more nearly complete than that of any other group. Figure 1 shows the distribution of the major faunal localities in North America, herein defined to exclude the Neotropical Region (compare with the much smaller number of Tertiary localities shown by Savage, 1958, Fig. 2). The wide geographic occurrence of the sites and the short time range of many genera and species make mammals the most useful means of correlation within the Quaternary over wide areas of North America. The abundant fossil record, coupled with the fact that so many genera are still living (Table 1), offers hopes for rich synthesis of data from fossil and living mammals.

Previous summaries of North American Quaternary mammals by Hay (1923, 1924, 1927) and Hibbard (in Flint, 1957, p. 458-467; Hibbard, 1958) show the progressive acceleration in knowledge that has been accomplished in the last 25 years by bulk screen-washing or sifting of fossiliferous matrix. In the past 37 years, 49 of 155 genera have been added to the known Quaternary record; 10 are large mammals but 39 are small, being mostly insectivores, bats, and rodents. Despite this progress the knowledge of the North American record lags far behind that of Europe (Flint, 1957, p. 451-455; Fejfar, 1961), even allowing for the different density of paleontologists. Comprehensive taxonomic works on North American Quaternary mammals are rare (Frick, 1937; Klingener, 1963; Osborn, 1936-42;

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Simpson, 1941, 1945; Skinner and Kaisen, 1947; Stock, 1925).

The history of mammalian paleontology in North America is largely one of emphasis on comparative morphology, phylogeny, and origin of higher categories. This has led generally to emphasis on the earlier Tertiary record and to the lack of integration of related aspects of geology and biology. We believe that the study of fossil mammals in general, and particularly of Quaternary mammals, must provide a synthesis if it is to be more than descriptive morphology and phylogenetic speculation. Hence we have only briefly summarized the basic data of geographic and stratigraphic occurrences (Fig. 1, Table 2), and we discuss more fully the promising avenues for future research. Common names of all genera mentioned in the text are shown on Table 2.

CHRONOLOGY

SCOPE OF PLEISTOCENE

General agreement in defining the Pliocene-Pleistocene boundary is lacking. Application of potassium-argon radiogenic dates and geomagnetic reversal sequences may bring a consensus in the next decade. Our placement of the lower limit of the Pleistocene is based upon the earliest paleontologic evidence of markedly cooler climate in mid-latitudes. The few radiogenic dates now available (Evernden *et al.*, 1964) imply that the base of the Pleistocene as we define it is probably 2-3 million years old.

Mammalian evidence for recognition of the end of the Pleistocene in North America is based on extinction of such large species as elephants, mastodons, camels, large peccaries (*Mylohyus* and *Platygonus*), *Cervalces*, the larger *Bison*, Woodland MuskoX (*Symbos*), Giant Beaver (*Castoroides*), ground sloths, and horses. The gradual extinction of these species occurred through an interval of at least 10,000 years (Hester, 1960); some probably lived as recently as 4000 years B.C. The most conspicuous changes in the North American mammalian fauna thus occurred after the Wisconsin glaciation.

Four chronologies are especially significant for correlation of Quaternary events. They are provided by (a) the biostratigraphic record of land mammals; (b) glacial-interglacial climatic fluctuations, inferred from many sources besides physical-stratigraphic data; (c) geomagnetic-re-

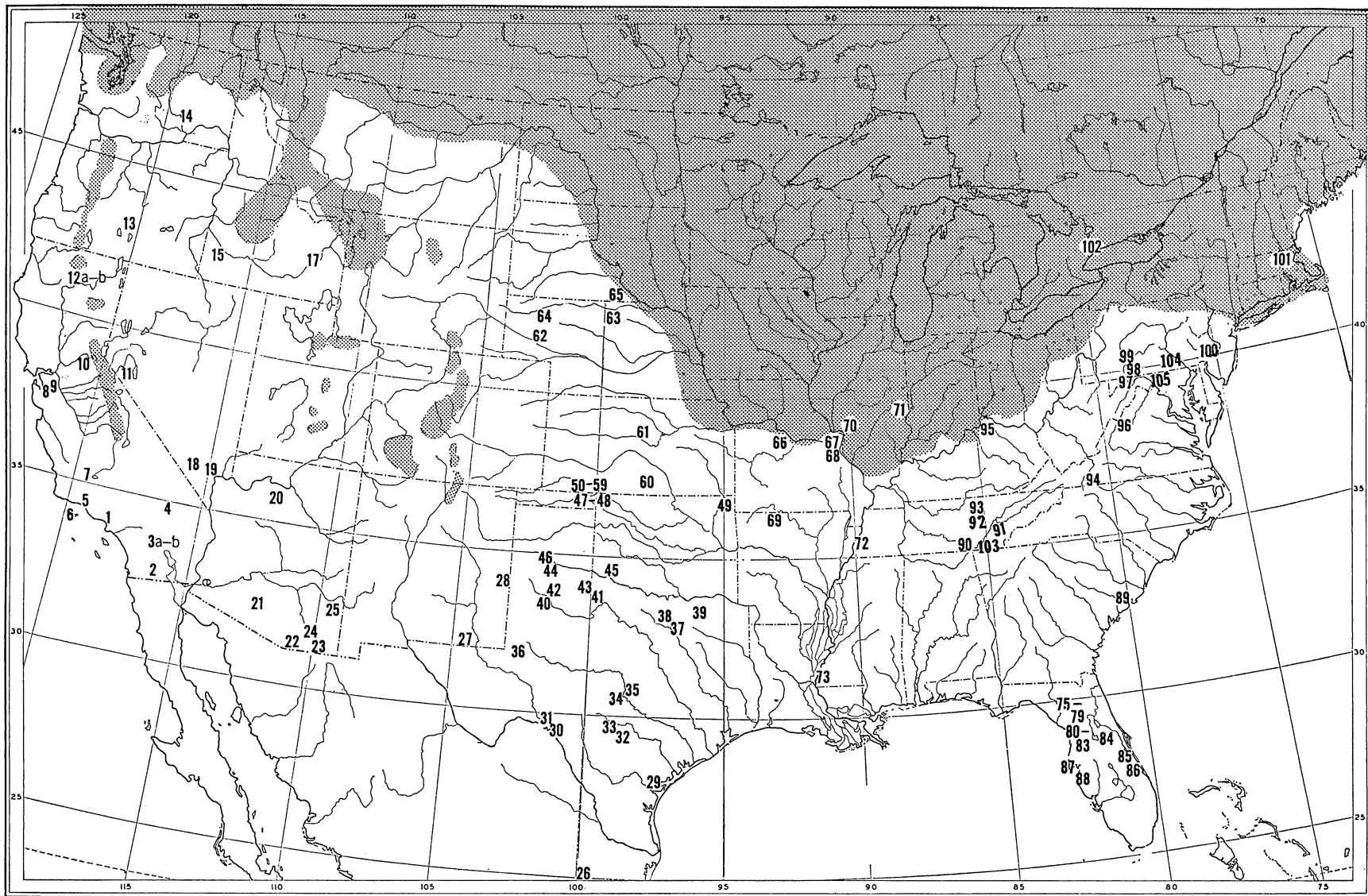


Figure 1. Major faunal sites.

Most of the well-known sites for Pleistocene mammalian assemblages in North America are indicated by numbers, on Figure 1, that correspond with the following list. Following the name of the locality is the age according to the following designations: (LB) Late Blancan, (Ir) Irvingtonian, and (R) Rancholabrean

for those faunas not correlated with the glacial and interglacial stages; and (N) Nebraskan, (A) Aftonian, (LA) Late Aftonian, (K) Kansan, (EK) Early Kansan, (LK) Late Kansan, (Y) Yarmouth, (I) Illinoian, (LI) Late Illinoian, (S) Sangamon, (LS) Late Sangamon, (W) Wisconsin, (EW) Early Wisconsin, (MW) Mid-

dle Wisconsin, and (LW) Late Wisconsin for those faunas where the glacial chronology is used. C¹⁴ dates are included where available. Further information on dates can be found in references cited or in the appropriate date lists cited in *Radiocarbon* (1959-1963). The last number for each locality designates the paper in the list of references that provides an introduction to the literature on each locality. Thus the publications cited are not necessarily the most important ones, but they include comprehensive bibliographies.

In general, only extensive assemblages have been mapped and listed here. The

numerous sites for individual specimens and old collections (often lacking minimal field data) are accessible through summaries by Hay (49, 50, 52). The bibliographies by Hay (53) and Camp *et al.* (14), the latter thoroughly indexed, provide a key to more recent discoveries. Sellards (128) discusses many sites not included here, where Man occurs with Pleistocene vertebrates. Stippled pattern is approximate maximum extent of Pleistocene glaciers. Base map from Goode Base Map Series, Department of Geography, University of Chicago, copyright by the University of Chicago.

- | | | |
|--|---|--|
| 1. Rancho La Brea (R), 149 | 37. Moore Pit (R: Humble, O-235 and 236 37,000 B.P.), 138 | 71. Polecat Creek (LW), 31 |
| 2. Vallecito Creek (Ir), 158 | 38. Clear Creek (MW: SM-534, 28,840 ± 4,740 B.P.), 140 | 72. Island 35 (LW?), 159 |
| 3a. Bautista (Ir), 27 | 39. Ben Franklin (LW: Loc. 5, SM-532, 9,550 ± 375 B.P.; Loc. 4, SM-533, 11,135 ± 450 B.P.), 139 | 73. Itchtucknee River (W), 93, 137 |
| 3b. San Timoteo (LB), 27 | 40. Slaton (R), 97 | 74. Santa Fe River Assemblage (LB and R), 10 |
| 4. Manix Lake (R), 78 | 41. Gilliland (LK), 69 | 75. Hornsby Spring and Sink (W: 9,880 ± 270 B.P.), 5, 21 |
| 5. Carpinteria (R), 160 | 42. Blanco (LB), 78, 96 | 76. Haile (R), 86, 116 |
| 6. Channel Islands (R), 147 | 43. Pasley Ranch (R), 20 | 77. Arredondo (R), 2, 5, 9 |
| 7. McKittrick (R), 125 | 44. Rock Creek (LK), 155 | 78. Devil's Den (LW?), 3 |
| 8. Livermore Valley (Ir? and R), 120 | 45. Holloman (LK), 98 | 79. Williston (R), 116 |
| 9. Irvington (Ir), 120 | 46. Cita Canyon (LB), 79, 85 | 80. Reddick (R), 42, 116 |
| 10. Hawver Cave (R), 145 | 47. Berends (I), 71, 80, 143 | 81. Saber-tooth Cave (R), 73 |
| 11. Wichman (LB), 89 | 48. Doby Springs (I), 71, 80, 101, 144 | 82. Rock Spring (W), 115, 116 |
| 12a. Samwell Cave (R), 145 | 49. Afton (R), 47, 50 | 83. Melbourne (W), 113, 115, 116 |
| 12b. Potter Creek Cave (R), 145 | 50. Deer Park (A), 57, 62 | 84. Vero (W), 156 |
| 13. Fossil Lake (R), 77 | 51. Sanders (LA), 62, 84 | 85. Seminole Field (W), 2, 4, 12, 113, 116, 132 |
| 14. White Bluffs (LB and later), 151 | 52. Seger Gravel Pit (EK), 58 | 86. Bradenton Field (W), 112 |
| 15. Grand View (LB), 64, 90, 161 | 53. Cudahy (LK), 57, 108 | 87. Ashley River (Mixed), 1 |
| 17. American Falls (R), 15, 76 | 54. Borchers (Y), 57, 63, 84 | 88. Little Salt River Cave (W?), 94 |
| 18. Tule Springs (R), 45, 130 | 55. Butler Spring (I), 71, 80, 101, 141 | 89. Craighead Caverns (W?), 94 |
| 19. Gypsum Cave (R), 44 | 56. Mt. Scott (LI), 67, 80, 84, 101, 142 | 90. Saltpetter Cave (W?), 94 |
| 20. Anita (LB), 48 | 57. Cragin Quarry (S), 23, 57, 71, 80 | 91. Robinson Cave (LW) |
| 21. Ventana Cave (R), 16 | 58. Jinglebob (LS), 60, 71, 80, 84 | 92. Early's Pits (LW), 38 |
| 22. Papago Springs Cave (R), 135 | 59. Jones (W: M-1103, > 30,000 B.P.), 57, 71 | 93. Big Bone Lick (W), 124 |
| 23. Naco (R), 46 | 60. Dixon (N), 62 | 94. Natural Chimneys (LW), 39 |
| 24. Curtis Ranch (LB or Ir), 32 | 61. Rezacabek (I), 55 | 95. Cumberland Cave (R), 35, 85, 117 |
| 25. Tusker (Ir), 22 | 62. Broadwater-Lisco (A), 6, 123 | 96. New Paris Sinkholes (LW: Y-727, 11,300 ± 1,000 B.P.), 40 |
| 26. San Josecito Cave (W), 119 | 63. Sand Draw (A), 65, 95 | 97. Frankstown Cave (R), 37 |
| 27. Burnet Cave (W), 122 | 64. Hay Springs Assemblage (Ir and R), 123 | 98. Port Kennedy (Ir), 61, 85, 114, 132 |
| 28. Blackwater Draw (LW), 128 | 65. Roosevelt Lake (R), 36 | 99. Harvard (LW), 118 |
| 29. Sinton (EW), 51 | 66. Eron Sink (W), 100, 132 | 100. Don Beds (S), 49 |
| 30. Centipede Cave (LW), 88 | 67. Cherokee Cave (R), 134 | 101. Little Airplane Cave (W), 105 |
| 31. Damp Cave (LW), 88 | 68. Herculaneum (W), 103 | 102. Bootlegger Sink (LW) |
| 32. Friesenhahn Cave (LW), 24, 47, 99 | 69. Conard Fissure (Ir and R), 11, 85 | 103. Cavetown (W), 47 |
| 33. Cave Without A Name (LW), 106 | 70. Alton (R), 47 | |
| 34. Miller's Cave (LW: A-326, 7,200 ± 300 B.P.), 107 | | |
| 35. Longhorn Cavern (LW), 106, 129 | | |
| 36. Scharbauer (LW), 33 | | |

TABLE 1

Late Cenozoic Genera of Non-marine Nearctic Mammals
(Counts in the two right-hand columns exclude a few marginal genera that are dominantly Neotropical. The number of genera known as fossils is taken from Table 2)

	Late Pliocene	Early Pleistocene (= post-Pliocene Blancan)	Irvingtonian	Rancholabrean	Wisconsin (= late Rancholabrean)	Living and known also as fossil	Living (with or without fossil record)
Marsupialia	0	0	0	1	1	1	1
Insectivora	7	5	6	9	9	9	10
Chiroptera	1	2	3	12	12	12	23
Primates	0	0	0	1	1	1	1
Edentata	1	3	5	8	8	1	1
Lagomorpha	5	2	4	3	3	3	4
Rodentia	27	25	28	40	39	35	41
Carnivora	19	21	21	22	21	17	20
Proboscidea	4	4	4	4	3	0	0
Perissodactyla	2	3	4	4	4	0	0
Artiodactyla	6	8	13	24	23	9	10
Total	72	73	88	128	124	88	111

versal sequences, which yield a relative chronology that is becoming tied to dates in years (Cox *et al.*, this volume); and (d) potassium-argon radiogenic dates (Evernden *et al.*, 1964). The correlation of these chronologies with each other and with the record of marine sediments and sea-level changes will gain from and richly benefit the study of fossil mammals for the foreseeable future.

Most of the well-known sites of Pleistocene mammalian assemblages in North America are indicated by number in Figure 1, the caption of which provides an entrance to the literature. The faunas we exclude as late Pliocene are Tehama, Tulare, and San Joaquin (California); Hagerman and Sand Point (Idaho); Benson (Arizona); Rexroad and Bender (Kansas); and Red Corral (Texas).

NORTH AMERICAN LAND-MAMMAL AGES

Successive phases in evolution of the North American mammalian fauna are the basis of the land-mammal ages. The most recent three of these are the Blancan, Irvingtonian, and Rancholabrean (Hibbard, 1958; Savage, 1951; Wood *et al.*, 1941). Table 2 shows the combinations of restricted ranges, as based on the first and last appearances that characterize these ages. Outside of central North America, a given fauna is assignable to a land-mammal age even though its place in glacial chronology can scarcely ever be established. Recent potassium-argon radiogenic dates (Evernden *et al.*, 1964) can be correlated roughly with the mammalian ages and thus indirectly with glacial-interglacial events. At present only the earliest Blancan faunas (about 2.5 to 4 × 10⁶ years old) seem to be Pliocene, *i.e.* older than the earliest recognized continental glaciation that reached mid-latitudes. These faunas also are pre-Villafranchian according to the occurrence in North Amer-

ica of more primitive members of phyletic series whose later members occur in Villafranchian faunas of Europe. Such series are the following:

Ogmodontomys → *Cosomys* → *Mimomys* (s.s.)
Nekrolagus → *Oryctolagus* and *Lepus*

CORRELATION OF MAMMALIAN FAUNAS WITH GLACIAL SEQUENCE

The Great Plains region of central North America is the only area where faunas older than the limit of C¹⁴ dating have been related to glacial-interglacial changes. Most information comes from the intensively studied Meade Basin of southwestern Kansas (Hibbard, 1963b; Hibbard and Taylor, 1960; Taylor, 1960). Correlation of this local faunal and stratigraphic sequence with glacial chronology is based on (a) inferred climatic changes correlated with glacial-interglacial fluctuations, and (b) recognition of lithologic units in southwestern Kansas that can be correlated with those of the glaciated region.

The sequence of diversified vertebrate and invertebrate faunas from southwestern Kansas and the climatic shifts inferred from them (Fig. 2) is the basis for recognizing glacial and interglacial intervals in this area. The magnitude of the faunal shifts, in a vast region of little relief, favors the interpretation that the climatic changes affected most of North America and were probably associated with changes in global circulation. In the southern Great Plains there is evidence of four major episodes of cooler climate separated by three intervals of warmer climate. These intervals are matched with the traditional four glaciations and three interglaciations of the Mississippi Valley.

The petrographically distinctive Pearlette ash (Powers *et al.*, 1958; Swineford, 1949) occurs widely but discontinuously in the Great Plains and is associated at many places with vertebrate and molluscan fossils of the Cudahy fauna, including representatives of many northern or even boreal species (Hibbard, 1949, 1960; Paulson, 1961). These northern elements, and the contrast between this fauna and the immediately younger interglacial Borchers local fauna, indicate that the Pearlette ash is of glacial age. In northwestern Iowa the Pearlette ash occurs stratigraphically above till judged to be Kansan and below Loveland loess (Condra *et al.*, 1950, p. 22-24; Frye *et al.*, 1948).

The Loveland loess in Iowa is younger than Illinoian till and older than Iowan till (Kay and Graham, 1943, p. 50). It has been traced from Iowa westward into Nebraska (Condra *et al.*, 1950; Lugin, 1962) and southward to southern Kansas (Frye and Leonard, 1952, p. 118), where much of the Kingsdown Formation (Cragin, 1896) is correlative with it (Hibbard, 1955a, p. 188; Hibbard *et al.*, 1944). In the Meade Basin the Kingsdown Formation has yielded the Mt. Scott local fauna of late Illinoian glacial age (Hibbard, 1963b) and the Cragin Quarry local fauna of early Sangamon interglacial age (Hibbard and Taylor, 1960), and it is capped by a caliche bed that is interpreted as the Cca horizon of a pedocal soil that formed when the Sangamon soil developed in more humid areas to the north and east. The Sangamon soil has been recognized widely on top of Loveland loess in Kansas and Nebraska (Frye and Leonard, 1952, p. 119-123).

EPOCHS	MAMMALIAN AGES	GLACIAL AGES	FAUNAS	CLIMATES AND SIGNIFICANT GEOLOGIC DATA	FAUNAL SHIFTS		
					Cool - summer elements	Mild - winter elements	
RECENT			Living	Mesothermal, semiarid, continental	Many formerly sympatric species now allopatric	Sigmodon hispidus	
PLEISTOCENE	RANCHOLABREAN		erosional unconformity				
		Wisconsin	Jones	Microthermal, subhumid, continental	Ambystoma, neotenic Sorex cinereus Citellus richardsoni Microtus pennsylvanicus	none	
		Sangamon	Jinglebob	Mesothermal, humid maritime	Sorex cinereus Microtus pennsylvanicus	Ambystoma, metamorphosed Terrapene llanensis Oryzomys fossilis	
			Cragin Quarry	Semi-arid Mesothermal, subhumid, maritime	Geochelone Terrapene llanensis Holbrookia texana	Crotaphytus collaris Phrynosoma modestum Notiosorex crawfordi Dasypterus gollitheri	
		Illinoian	Mt. Scott	Microthermal, subhumid, maritime?	Sorex arcticus S. cinereus S. palustris Microtus pennsylvanicus	Terrapene llanensis Blarina b. carolinensis Oryzomys fossilis	
			Butler Spring	Microthermal, subhumid, continental?	Perca flavescens Ambystoma, neotenic Sorex cinereus Microtus pennsylvanicus	none	
	IRVINGTONIAN	Yarmouth	Borchers	Semi-arid Mesothermal, subhumid, maritime	Ambystoma, metamorphosed Geochelone Sigmodon hilli Spilogale cf. S. ambarvalis	none	
		Kansan	Cudahy	Pearlette ash bed Microthermal, subhumid, maritime	Ambystoma, neotenic Sorex cinereus S. lacustris S. megapalustris	Microsorex pratensis Synaptomys (Mictomys) Microtus paroperarius	none
			Seeger			No climatically significant species	
	BLANCAN	Aftonian	Sanders	Mesothermal, subhumid, maritime	Some warm-temperate and subtropical elements from Rexroad fauna absent	Ambystoma, metamorphosed Sigmodon intermedius Bensonmys meadensis Pliolemmus antiquus	
			Deer Park	Semi-arid Mesothermal, maritime		Geochelone Pliopotamys meadensis Pliolemmus antiquus	
		Nebraskan	Unnamed			No climatically significant species	
		PLIOCENE		Bender	erosional unconformity Mesothermal, subhumid, maritime	none	Mammalian fauna not published
	Rexroad			caliche bed Semi-arid Mesothermal, subhumid, maritime	none	Geochelone rexroadensis Notiosorex jacksoni Baiomys spp. Sigmodon intermedius	Nerteroeomys minor Bassariscus casei

Figure 2. Late Cenozoic faunal shifts and inferred climatic changes in the southern Great Plains.

BIOGEOGRAPHY

Changes in geographic distribution of species through geologic time are usually accompanied by morphological changes. Hence biogeography is scarcely separable from evolution. We consider three aspects of these topics: faunal shifts, which are changes in distribution associated with ecological changes but with little taxonomic differentiation; historical biogeography, involving changes in distribution over much of North America (including the Bering Straits area), associated with some taxonomic differentiation; and evolution, in which geographic distribution is relatively insignificant.

FAUNAL SHIFTS

The fossil record is so discontinuous that virtually no well-documented evolutionary sequence of American Pleistocene mammals have been described. Even at the generic level the number of first appearances seems to be correlated with the number of known localities (Table 3). One of the principal reasons for the discontinuous record is the large-scale faunal shifts that include such occurrences as tapirs in Pennsylvania (Simpson, 1945), ground sloths in Alaska (Stock, 1942), and boreal lemmings in the southern Great Plains (Hibbard, 1949).

The most detailed studies of Pleistocene faunal sequence come from the Great Plains, mainly southwestern Kansas and northwestern Oklahoma. A general hypothesis of major climatic shifts in this region has been developed by Hibbard and Taylor (Hibbard, 1944, 1949, 1960, 1963b; Taylor, 1960, 1965; Hibbard and Taylor, 1960). The inferred climatic sequence explains a wide variety of data, such as the former association of species that are now allopatric (living in widely separated areas), the repetitive stratigraphic occurrence of species, and the present-day relic occurrence of others. It applies to (and is drawn from) such diverse groups as fishes, amphibians, reptiles, birds, mammals, and mollusks. The same hypothetical climates are unlikely to have occurred outside central North America, but they unify so many facts and interpretations in this area that they will be a useful tool for future research.

Climate can affect individual mammals directly by lethal extremes of temperature or by drought, but its effects on species or genera of mammals through geologic time are probably indirect, acting through the soils and vegetation of the habitat. Smaller mammals, with a narrower range of habitat and individual home range than the larger carnivores or herbivores, are influenced more by the microclimate in which they live than by regional climatic change (Burt, 1958). Hence it is reasonable and a justification of uniformitarian interpretations that the ecological conclusions drawn from rodents and insectivores are similar to those drawn from the associated lower vertebrates, mollusks, and plants. The consistency of inferences from different elements of late Cenozoic biotas in the Great Plains is decisive proof (and the only test possible) of the validity of the method.

Figure 2 summarizes the latest Cenozoic sequence of faunas and inferred climates in southwestern Kansas (see Taylor, this volume, for a similar summary of associated

TABLE 3

Earliest North American Records of Eurasian Immigrants

GENERA	EARLIEST RECORDS
<i>Ursus</i>	Late Blancan (Loc. 46)
<i>Mammuthus</i>	Late Kansan (Loc. 45)
<i>Preptoceras?</i>	Late Kansan (Loc. 44)
<i>Bison</i>	Illinoian (Loc. 48)
<i>Smilodon</i>	Irvingtonian (Loc. 100)
<i>Gulo</i>	Irvingtonian (Loc. 100)
<i>Euceratherium</i>	Irvingtonian (Loc. 9)
<i>Cervalces</i>	Rancholabrean (Loc. 99)
<i>Rangifer</i>	Wisconsin (Hibbard, 1958)
<i>Oreamnos</i>	Wisconsin (Hibbard, 1958)
<i>Ovibos</i>	Wisconsin (Hibbard, 1958)
<i>Ovis</i>	Wisconsin (Hibbard, 1958)
<i>Alces</i>	Wisconsin (Hibbard, 1958)
<i>Bos</i>	Wisconsin (Hibbard, 1958)
<i>Saiga</i>	Wisconsin (Hibbard, 1958)
<i>Bootherium</i>	Wisconsin (Loc. 95)
<i>Symbos</i>	Wisconsin (Loc. 95)

mollusks). The climatic interpretations are drawn from a variety of organisms, including mammals. These interpretations are the simplest possible based on the assumption that fossils imply past habitats like those of their living morphological equivalents. A consistent application of this assumption suggests that present-day climates, with their seasonal extremes of temperature and aridity, are geologically atypical, even of the Pleistocene. Most of the specific fossil associations would be inexplicable if the climate of the present were taken as the key to the past. But if different distributions of precipitation and seasonal extremes are considered as separate variables, seemingly anomalous associations of species are rationalized.

The first major southward faunal shift of ecological significance is shown by some of the mammals of the Cudahy fauna (Hibbard, 1949, p. 1421) of late Kansan age. Some living species of mammals of the Boreal Subregion extended their ranges southward during Illinoian and/or Wisconsin time. Their remains have been recovered in southern localities, e.g. *Ovibos*, Muskox (Fig. 3); *Microtus xanthognathus* (Fig. 4); *Sorex arcticus* (Fig. 5); and *Dicrostonyx*, Collared Lemming (Fig. 6). Remains of *Sorex cinereus*, Masked Shrew, and *Synaptomys cooperi*, Bog Lemming, are found as far south as San Josecito Cave, Mexico (Fig. 1, Loc. 26); and *Sorex palustris*, Northern Water Shrew, is known from Oklahoma, Kansas, and north-central Tennessee (Fig. 1, Loc. 48, 56, and 93).

The Yellow-cheeked Vole (*Microtus xanthognathus*) and the Rock Vole (*M. chrotorrhinus*) lived in the same area in Pennsylvania and Virginia (Fig. 4) during late Wisconsin time; they now live in widely separated areas in Boreal North America. Guilday (1963) recovered fossil remains of *Dicrostonyx* (*Misothermus*) *hudsonius*, Labrador Collared Lemming, in Pennsylvania (Fig. 6). He considered the present tundra population of this species to be a probable relic of a former Holarctic pre-Wisconsin distribution.

Southward and southwestward retractions of ranges of ecological significance during the later Pleistocene are shown by the present distribution of *Dasypterus*, Yellow Bat (Fig. 4); *Hydrochoerus*, Capybara; *Oryzomys*, Rice Rat (Fig. 3); *Neofiber*, Water Rat (Fig. 1, Loc. 40, 61, and

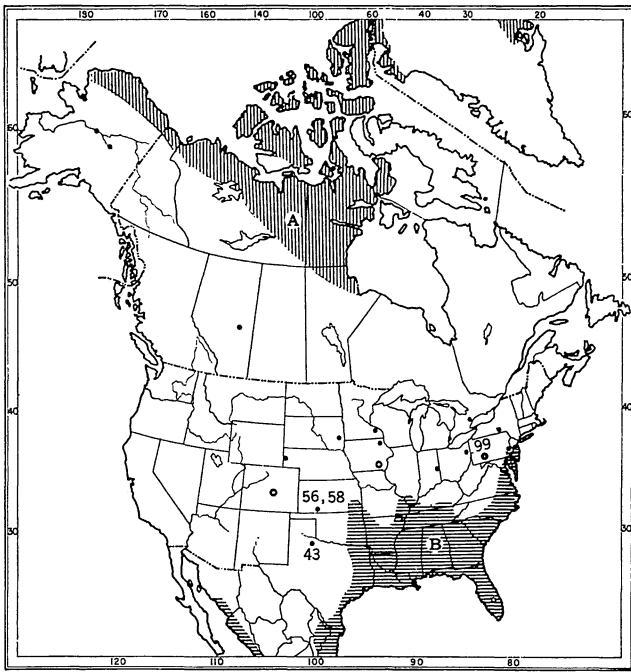


Figure 3. Recent distribution (A) of the Muskox, *Ovibos moschatus*, with fossil records (99, and unnumbered circles). Open circles indicate questionable identifications. Data from reference citations 28, 43, 49, 50, 52, 83. Northerly portion of the Recent distribution (B) of the Marsh Rice Rat, *Oryzomys palustris* (including *O. couesi*, fide E. R. Hall, 1960, *Southw. Nat.*, v. 5, No. 3, p. 171-173), with fossil records for *O. fossilis* (43, 56, 58). Data from reference citations 20, 43, 60, 67. *Oryzomys palustris* is known also from several post-Pleistocene prehistoric localities, not mapped, east of the Mississippi River and north of its modern limits.

100); *Conepatus*, Hognose Skunk (Fig. 5); *Felis pardalis*, Ocelot (Fig. 7); *Panthera onca*, Jaguar (Fig. 8).

The presence of maritime climates and extensive broad, marshy, undissected valleys seems to have provided the habitat for the northern ranges of the Capybara, Rice Rat, and Water Rat.

Neofiber, the Water Rat, is a good example of a form whose range has become greatly restricted because of the lack of habitat or because of competition with *Ondatra*, the Muskrat, or for both reasons (Birkenholz, 1963). *Neofiber* is not closely related to *Ondatra*, and in middle Pleistocene faunas (Port Kennedy Cave, Fig. 1, Loc. 100, and Rezabek, Fig. 1, Loc. 61) these two forms were associated, although at the present time their ranges do not overlap. It is of interest to note that the range of the Jaguar during the Pleistocene has been approximately that of the peccaries.

Westward shifts in ranges are shown by *Mormoops*, Leaf-chinned Bat (Fig. 6); *Desmodus*, Vampire Bat (Fig. 1, Loc. 26, 78, 79, and 82); *Citellus*, Ground Squirrel (Fig. 1,

Loc. 93, 96, 97, 98, and 104); *Taxidea*, Badger (Fig. 1, Loc. 97 and 100); *Conepatus*, Hognose Skunk (Fig. 5); and *Ochotona*, Pika (Fig. 7).

HISTORICAL BIOGEOGRAPHY

The Nearctic Region (Canada, continental United States, northern Mexico, including the central plateau but not the coastal lowlands on either side) is inhabited by 111 genera of mammals. These have various patterns of distribution and are variably distinct from the mammals of the Palearctic and Neotropical Regions. The most marked endemism is at the family level: the pronghorn (Antilocapridae) and sewellel (Aplodontidae) are restricted to the Nearctic. At the other extreme 21 species may be common to North America and Eurasia (Rausch, 1963), and many more to the southern Nearctic and the Neotropical Regions. These different patterns of distribution and different degrees of endemism imply different histories. The Cenozoic (mainly pre-Quaternary) differentiation and spread of the North American families and many genera of mammals have been summarized by Burt (1958), Savage (1958), and Simpson (1947). We comment on the Quaternary spread of mammals (a) between the Neotropical and Nearctic Regions, (b) between the Palearctic and Nearctic Regions in the Bering Straits area, and (c) within the Nearctic.

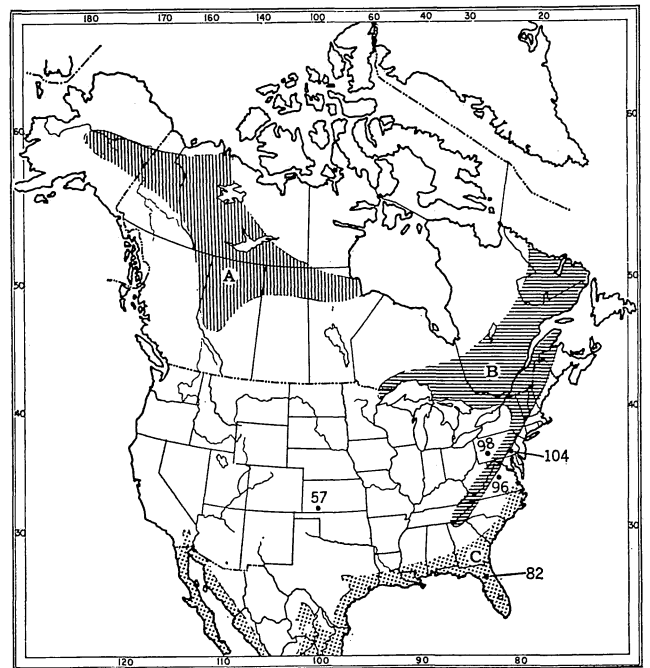


Figure 4. Recent distribution (A) of the Rock Vole, *Microtus chrotorrhinus*, with fossil records (96, 98, 104), (B) of the Yellow-cheeked Vole, *M. xanthognathus*, with fossil records (96, 98, 104), and the northerly portion of the Recent distribution (C) of the yellow bat, *Dasypterus*, with fossil records (57, 82). Data from reference citations 39, 42-43, 71.

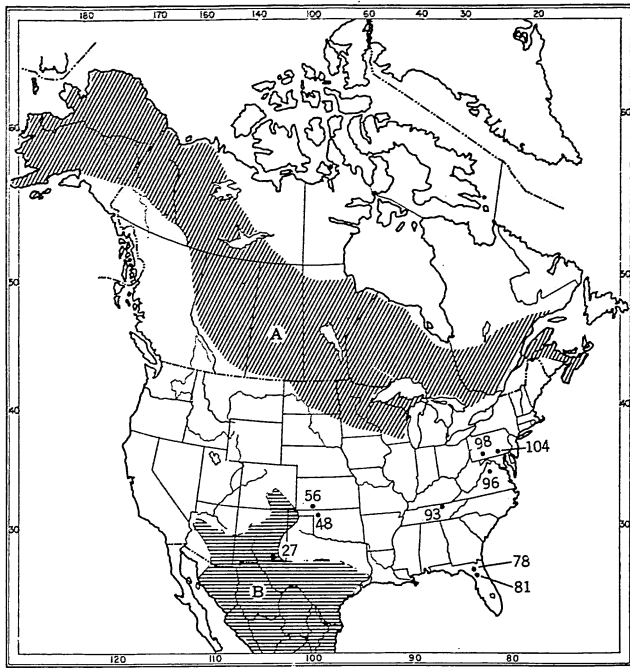


Figure 5. Recent distribution (A) of the Arctic Shrew, *Sorex arcticus*, in North America, with fossil records (48, 56, 93, 96, 98, 104), and the northerly portion of the Recent distribution (B) of the Hognose Skunks, *Conepatus* (including the nominal species *C. mesoleucus* and *C. leuconotus*) with fossil records (27, 78, 81). Data from reference citation 43 and from those cited under each locality in the explanation to Fig. 1.

Neotropical-Nearctic relationships. The fossil record in Central America and Mexico is so little known that times of faunal interchange in Pliocene and Pleistocene times can scarcely be defined. Some groups of ultimate South American ancestry (hystricomorph rodents and edentates) extended their ranges northward into the Nearctic Region during this time. Quaternary events may have had little effect on these genera except in changing the limits of habitable areas during glaciations.

Some genera that are now Neotropical (for example, the peccaries and tapir, *Tapirus* [*Tapirella*]) occurred during Quaternary time far north of their present range. They are most reasonably regarded not as tropical or subtropical elements in Quaternary faunas but as genera that were once widespread in the southern Nearctic Region and that have been extinguished in much of their range by late Quaternary climatic changes.

Palearctic-Nearctic relationships. During late Pliocene and Quaternary times the spread of mammals between the Old and New Worlds could only have occurred in the Bering Straits region, although for the early Tertiary we cannot categorically exclude faunal connections around the North Atlantic. The clearest paleontologic evidence is the appearance in North America of groups with ancestors in

Eurasia. Such immigrations are particularly noticeable at the family level (Elephantidae and Bovidae) but range through lower taxonomic ranks. Table 3 summarizes the earliest known occurrences of genera that probably entered North America as the same or closely related genera during Quaternary or immediately pre-Quaternary times. A recent study by Kurtén (1963) points the way toward future refinements.

Zoogeographical studies of living and fossil mammals (Burt, 1958; Rausch, 1963; Savage, 1958; Simpson, 1947; Stokes and Condie, 1961) have cast light on the approximate times and range of habitats in Quaternary faunal dispersal in the Bering Straits region. Direct paleontologic and stratigraphic evidence in the Seward Peninsula athwart the path of mammalian spread has become available only recently (Hopkins, 1959a, b).

Table 3 shows that half of the immigrant genera listed have an earliest known record in the Wisconsin. These genera are predominantly those characteristic or tolerant of arctic-alpine environments. The relative predominance of fossil deposits in Alaska of Wisconsin age is partly responsible for the first records of such forms, but the relative severity of Wisconsin-age climates is probably a significant cause also. Fossils of latest Pleistocene mammoth, bison, and horse in a region then vegetated with



Figure 6. Recent mainland distribution (A) of the Collared Lemming, *Dicrostonyx groenlandicus*, (B) of the Labrador Collared Lemming *D. hudsonius*, with fossil record (98), and the northerly portion of the Recent distribution (C) of Peters' Leaf-chinned Bat, *Mormoops megalophylla*, with fossil record (84). Data from reference citations 40, 43, 116. Rausch (1963) regards the above forms of *Dicrostonyx* as conspecific with *D. torquatus*.

tundra (Hopkins, 1959b) show that many of these mammals could have crossed the emergent Bering-Chukchi Platform during a time of lowered sea level in the late Pleistocene.

An earlier immigration that will be of significance both to regional stratigraphy in North America and to chronology of the Bering Straits region is that of *Mammuthus*. Two separate stocks of this genus seem to have entered North America. The later was *M. primigenius*, the Woolly Mammoth, during the Rancholabrean. The earlier was the stock first seen as *Mammuthus haroldcooki* in Kansas and Oklahoma in late Kansan deposits. It may have given rise to all later American species except *M. primigenius*. These early mammoths were not boreal animals; they are rare in southwestern Kansas (Hibbard, 1953) and in Oklahoma (Meade, 1953), and are common in the Seymour Formation of north-central Texas (Hibbard, in preparation). The passage of these animals across the Bering Strait during a glacial interval seems most unlikely, and yet the morphological grade of the first immigrants seems to preclude a Pliocene age. Perhaps the early Pleistocene of our definition precedes the early Pleistocene of Hopkins' (1959a) usage.

Intra-Nearctic relationships. The present patterns of distribution and the composition of the living fauna are the

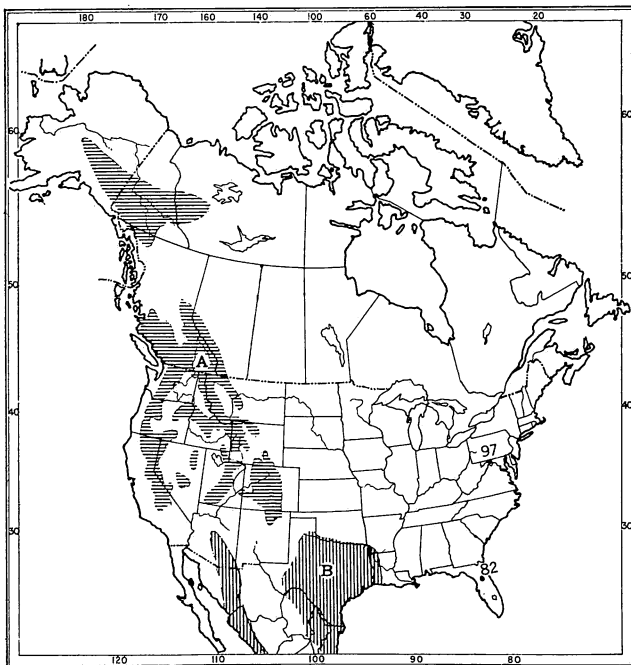


Figure 7. Recent distribution (A) of the Pika, *Ochotona* (*Pika*), in North America, with fossil record (97), and the northerly portion of the Recent distribution (B) of the Ocelot, *Felis* (*Leopardus*) *pardalis*, with fossil record (82). Data from reference citations 35, 43, 116.

The fossil *Ochotona* belongs to the subgenus *Pika* on the basis of partial separation of the incisive and palatine foramina.

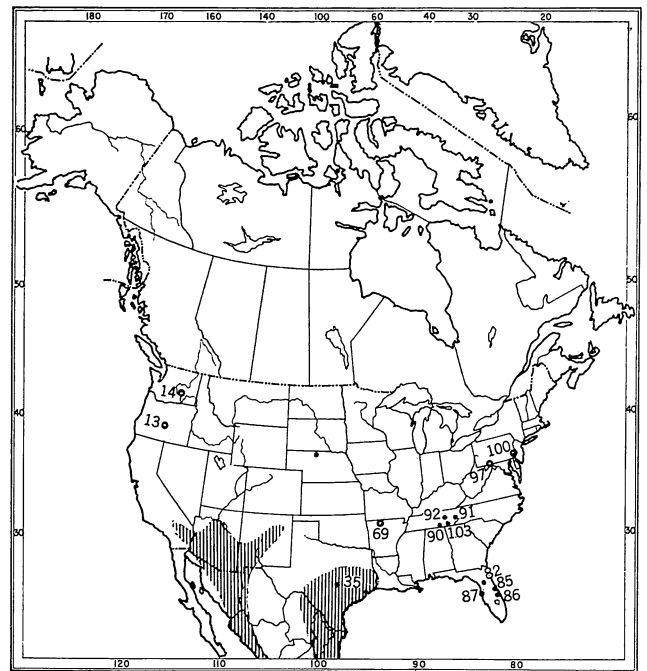


Figure 8. Northerly portion of the Recent distribution of the Jaguar, *Panthera* (*Jaguaris*) *onca*, with fossil records including *P. (J.) onca augusta* but excluding *P. (J.) atrox*. The locality in Nebraska represented by the unnumbered solid circle is the type locality ("Niobrara River") for *P. (J.) onca augusta*. Open circles indicate questionable identifications. Data from reference citations 43, 94, 105, 129, 131.

product of extinction and evolution as well as of considerable restrictions in distribution. Such changes can be studied most effectively by synthetic biogeographic studies of the type made by Blair (1958) and Neill (1957). The frequent disagreements about the chronology of range changes and about the age of a given pattern of distribution indicate that biogeography is unlikely to be a fruitful area of research without an objective method of analyzing its data.

Quaternary restrictions of range are known in many genera. The gopher, *Geomys*, and shrew, *Blarina*, which formerly occurred west of the continental divide but are now eastern (Hibbard, 1959; White and Downs, 1961) probably were affected by the regional disappearance of their habitat. Late Pleistocene aridity that deprived them of moist soil and humus is a plausible cause. In other cases the reasons remain obscure.

EVOLUTION

The Pleistocene fossil record of mammals in North America is more nearly complete than that of any other class of organisms. As shown in Table 4, only 20% of the extant genera are unrepresented as fossils. Despite this relatively full record, the phyletic development of practically no

TABLE 4

First and Last Appearances of Late Cenozoic Mammalian Genera Shown in Tables 1 and 2 (N = number of localities that are shown in Fig. 1. Late Pliocene localities are listed in the text under Scope of Pleistocene)

	First appearance		Last appearance	
	Per- cent	Number	Per- cent	Number
Late Pliocene (N = 9)	52	37 of 72	18	13 of 72
Early Pleistocene (= post-Pliocene)				
Blancan (N = 14)	19	14 of 73	23	17 of 73
Irvingtonian (N = 14)	36	32 of 88	12	10 of 88
Rancholabrean (N = 81)	40	50 of 128	31	40 of 128
Wisconsin (N = 59)	25	31 of 124	30	36 of 124
Living	20	22 of 111	—	—

species has been documented. Evidently changes in habitat and geographic range have added to the other gaps in the record caused by geologic and human factors.

PHYLETIC SEQUENCES

The better-documented phyletic sequences include species of the Jumping Mouse, *Zapus*, and of the White-footed Mouse, *Peromyscus*. Klingener (1963) described a series of four successional subspecies leading from the late Pliocene *Zapus sandersi rexroadensis* to the Recent *Zapus hudsonius* (Fig. 9). Hibbard (1955a, p. 212; Hibbard and Taylor, 1960, p. 175) found that the Sangamon *Peromyscus progressus* is closely related to the living *P. leucopus* but has more primitive tooth characters. *P. leucopus* may therefore have evolved during the latest Sangamon and Wisconsin.

Less well documented but plausible lineages have been inferred for several other genera of mammals. These phyletic lines are the simplest and shortest that are consistent with the available fossil record and the data of comparative anatomy, and hence their errors will prove mainly due to oversimplification. Such synthesis of fossil interpretation with data from related fields, and the discovery of more fossils, will favor the inference of longer stratigraphic ranges and of slower rates of change and geographic spread. Students of evolution, biogeography, and Pleistocene stratigraphy should understand that the mammalian evolutionary sequences are only the simplest interpretations of a fragmentary record. Such phyletic lines have been proposed, mainly on dental characters, in many genera of which we list only a sample.

1. Hibbard (1963a) has interpreted evolution of some rabbit genera as taking place in the early Pleistocene—*Sylvilagus*, *Caprolagus*, *Oryctolagus*, and *Lepus* from a "pro-*Sylvilagus*" stock.

2. The stratigraphic succession of fossil mammoths is consistent with an interpretation of progressive increase in number of enamel plates in the teeth. Hibbard (1953) suggested that the oldest known American species, *Mammuthus haroldcooki* from the late Kansan of southwestern Kansas and Oklahoma, is ancestral to *M. imperator*.

3. Kurtén (1963) has discussed Old World–New World lineages in the saber-toothed cats of the *Homotherium-Dinobastis* and *Megantereon-Smilodon* lines and in the black bears of the *Ursus thibetanus-U. americanus* line.

A possible example of apparent evolutionary change that results only from ecological changes has been described by Hibbard (1963b). Stratigraphically distinct samples of the Short-tailed Shrew, *Blarina*, represent different-sized animals that would be ascribed to an evolving lineage in conventional study. Similar differences can be found in the large northern and small southern subspecies of *Blarina brevicauda*, and associated faunas support the interpretation that the observed morphological differences are due to shifts of a cline.

MODERNIZATION OF QUATERNARY FAUNA

The progressive modernization of the Quaternary Nearctic mammalian fauna has taken place through the evolution of new genera and species from autochthonous stocks, through immigration from the Neotropical and Palaearctic Regions, through elimination by absolute extinction, or through extinction of widespread groups in the Nearctic Region but with survival elsewhere, e.g. camels and horses.

The only extant species known from pre-Quaternary deposits is the badger, *Taxidea taxus*, in the Rexroad local fauna. The known fossils include only lower jaws, and if a skull is found it will probably reveal specific differences. Even if not, the generalization that mammalian species are of Quaternary origin is valid. (The modernization of genera and species in the faunal sequence of southwestern Kansas

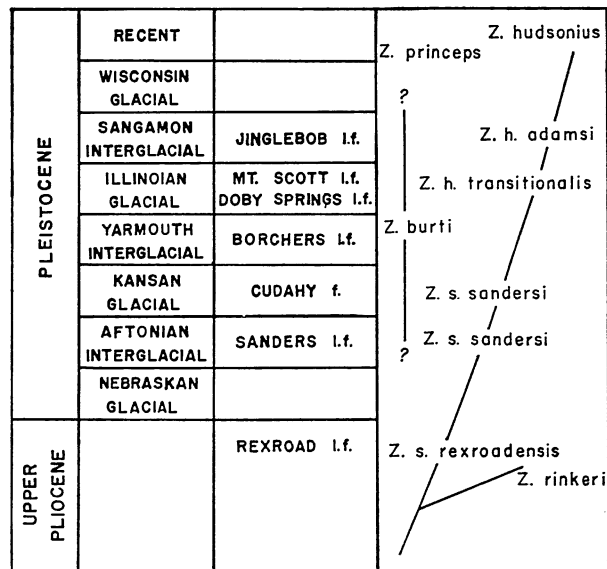


Figure 9. Evolution of the species and subspecies of the jumping mouse, *Zapus*, after Klingener (1963). The Pleistocene fossils are from localities 48, 51, 53, 54, 56, and 58 (Fig. 1) in southwestern Kansas and adjacent Oklahoma, but *Zapus* lives only farther north and east in the Great Plains.

has been contrasted by Taylor, this volume, with the record of mollusks.)

Taking the stratigraphic ranges (Table 2) at face value one might wrongly infer the evolution of many new genera during the Pleistocene. The ecologic replacement of some genera by others, the inverse correlation of number of known fossil localities with age, and the immigration of animals into areas where fossiliferous sediments have been preserved are all more likely causes of the known range than taxonomic evolution.

The following pairs of genera occur in successive strata, with no zone of overlap or with a relatively short interval of joint occurrence. Their morphologic differences are great enough to preclude ancestral-descendant relationship, but their similarities are such that they may have overlapped ecologically. In such cases the first appearance of the younger genera in the fossil record may be due primarily to ecological replacement.

OLDER GENERA		YOUNGER GENERA
<i>Plesippus</i> (zebrine)	} replaced by	<i>Equus</i> s.s., large horse
<i>Nannippus</i> (three toed)		
<i>Stegomastodon</i>	replaced by	<i>Mammuthus</i> , mammoth
<i>Capromeryx</i>	replaced by	<i>Antilocapra</i> , pronghorn
<i>Hypolagus</i>	replaced by	<i>Sylvilagus</i> , rabbit and <i>Lepus</i> , hare
<i>Pliophenacomys</i>		
<i>Arctodus</i>	replaced by	<i>Ursus</i> (brown and grizzly bear but not the black bear)

The correlation of first appearance of genera with number of known fossil localities is evident in Table 4. This shows that a very high percentage of Pleistocene first appearances could be due entirely to quality of the fossil record, without any evolutionary changes or immigration from outside areas.

The fossil record is so scanty, particularly in Alaska and adjacent areas, that we do not know when groups arrived or how much of their taxonomic differentiation took place after their arrival and before their earliest record as fossils. Study of these immigrants can be carried out most effectively by biogeographic studies such as those by Stokes and Condie (1961) on *Ovis* or by Rausch (1963) on the mammals of the Bering Straits area.

The genera and subgenera *Sylvilagus*, *Lepus*, *Lagurus*, *Microtus*, *Dimobastis*, *Smilodon*, *Mammuthus*, *Equus*, *Mylohyus*, *Camelops*, *Rangifer*, *Alces*, *Antilocapra*, *Bison*, *Oreamnos*, *Symbos*, *Ovibos*, and *Ovis* might have originated as late as early Pleistocene times. If so, they are the highest-ranking groups that are geologically so young. Although mammalian evolution might have been accelerated during the Pleistocene in some groups, this time-span was so short that differentiation hardly ever went beyond the species-group level. If *Ondatra* is derived from *Pliopotamys* this would be the latest origin of a genus that can be documented in the Pleistocene of North America. In general, the Pleistocene record is conspicuous by the

elimination of old stocks rather than the development of new ones.

PROBLEMS

The problems available for future research include a heritage of old, unsolved ones, along with newly raised questions that result from an increase in knowledge in paleontology as well as in other fields.

The most obvious old problem is as old as the study of Quaternary mammals. Why did the most conspicuous extinctions occur so late and after the last glaciation? Recent studies (Hester, 1960; Martin, 1958; Martin *et al.*, 1961) and the application of C¹⁴ dates have provided a wealth of data but no consensus. We suggest that any plausible explanation of late Pleistocene extinction cannot be *ad hoc*, but must also shed light on previous mammalian extinctions, contemporaneous non-mammalian extinctions, and on contemporaneous range changes in organisms that did not become extinct.

Newly apparent topics, and those that can be newly attacked with profit, have come from new techniques as well as the gradual accumulation of data. All problems of Quaternary chronology and correlation, and all topics that involve these matters, will be influenced by the results of C¹⁴ and K/Ar dating and by research on geomagnetic polarity. Study of rates of evolution, of geographic spread, and of regional changes in habitat are particularly dependent upon a refined chronology.

A particularly worthwhile study with worldwide ramifications would be paleoecological analysis of the biota associated with the Pearlette ash. This ash provides a unique, virtually contemporaneous datum throughout much of the Great Plains for a time when a continental ice sheet covered part of northern North America and the climate and its zonation was radically different from that of today. Such a study would require the long-term collaboration of diverse specialists; it thus reflects our belief that knowledge of Quaternary mammals will be most advanced through studies devoted to geology and entire biotas, and not solely to Quaternary mammals.

Examples of a few recent studies that exemplify valuable data gained from a synthetic approach are given below. It is no coincidence that some of the most valuable work is by those not trained as mammalian paleontologists.

The occurrence of beaver-cut wood in peat deposits of New England led Kaye (1962) to suggest that the region in early postglacial time was less swampy than today. If beavers were responsible for providing sites of accumulation for pollen-bearing sediments perhaps they also account for irregularities in pollen stratigraphy.

Late Pleistocene wood rat (*Neotoma*) middens in southern Nevada include twigs and seeds of juniper not now living in the low desert mountains. The relatively large size of the plant remains makes them more significant indicators of local vegetation than windblown pollen; hence Wells and Jorgensen (1964) were able to infer late Pleistocene changes in climate and in distribution of wood rat and juniper woodland.

In an area near Denver, Colorado, Scott (1962, 1963) studied Quaternary history in a particularly thorough way.

The fossil mammals he recorded do not include great diversity of species, but the integration of fossil mammals with geomorphology, buried soils, detailed physical stratigraphy, and the record of other fossil organisms points the way for future research of this kind.

The most abundant and detailed information about glacial-interglacial changes in climate and habitats comes from the Illinoian and Sangamon faunas of southwestern Kansas and northwestern Oklahoma (see references to faunas 47, 48, 55-58). Fossils representing angiosperms, mollusks, fishes, amphibians, reptiles, birds, and mammals provide a wide variety of sources of ecological and stratigraphic data. From these studies far more information about environmental changes has been gained than the study of any one group could yield, and far more information about mammals than a strictly mammalogical study would produce.

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SUMMARY

Only 22 out of 111 living Nearctic mammalian genera are unknown as fossils, so mammals are the best known Quaternary group of animals in North America. The 155 Quaternary genera have restricted and overlapping ranges that are the basis for the Blancan (only the latter part is Quaternary), Irvingtonian, and Rancholabrean mammalian ages. The chronology based on mammals can now be related to those of glacial-interglacial climatic changes, geomagnetic-polarity epochs, and potassium-argon dates, from which it appears that the Quaternary of our definition began about 2.5 million years ago.

The basic data of stratigraphic ranges (177 genera) and geographic occurrences (104 localities) are summarized with 160 references that provide entrance to a much larger literature. Most of the text is devoted to discussion of promising avenues for future research and examples of the kinds of synthetic study that have proved fruitful.

Faunal shifts correlated with glacial-interglacial climatic changes have been documented thoroughly only in the southern Great Plains. Interpretations based on small mammals are consistent with those based on lower vertebrates, mollusks, and plants. Immigration from the Old World via the Bering Straits is most marked among hardy boreal forms that may have crossed when sea level was lower.

In spite of the relatively full fossil record, well-documented phyletic sequences of species are unknown outside the rodents. Although many genera are first known from Quaternary sediments, in practically all cases they probably lived before then. Probably all Recent mammalian species originated during the Quaternary, but generic change was by extinction rather than evolution into new genera.

PART II: BIOGEOGRAPHY

PHYTOGEOGRAPHY AND PALYNOLOGY

- Phytogeography and Palynology of Northeastern United States DAVIS
Problems in the Quaternary Phytogeography of the Great Lakes Region CUSHING
Palynology and Pleistocene Phytogeography of Unglaciaded Eastern North America WHITE-
HEAD
Pleistocene Pollen Analysis and Biogeography of the Southwest MARTIN, MEHRINGER
Plant Geography in the Southern Rocky Mountains WEBER
A Pleistocene Phytogeographical Sketch of the Pacific Northwest and Alaska HEUSSER
The Boreal Bryophyte Flora as Affected by Quaternary Glaciation STEERE
Polyploidy, Distribution, and Environment JOHNSON, PACKER, REESE

ZOOGEOGRAPHY AND EVOLUTION

- Quaternary Mammals of North America HIBBARD, RAY, SAVAGE, TAYLOR, GUILDAY
Avian Speciation in the Quaternary SELANDER
Amphibian Speciation BLAIR
Reptiles in the Quaternary of North America AUFFENBERG, MILSTEAD
Quaternary Freshwater Fishes of North America MILLER
Pleistocene Events and Insects ROSS
The Study of Pleistocene Nonmarine Mollusks in North America TAYLOR
Other Invertebrates—An Essay in Biogeography FREY
Recent Adjustments in Animal Ranges SMITH

GENERAL

- Pleistocene Nonmarine Environments DEEVEY

PART III: ARCHAEOLOGY

- Late Quaternary Prehistory in the Northeastern Woodlands GRIFFIN
An Outline of Southeastern United States Prehistory with Particular Emphasis on the Paleo-
Indian Era WILLIAMS, STOLTMAN
Quaternary Human Occupation of the Plains STEPHENSON
Postglacial Climate and Archaeology in the Desert West BAUMHOFF, HEIZER
Pacific Coast Archaeology MEIGHAN

PART IV: MISCELLANEOUS STUDIES

- Late Quaternary History, Continental Shelves of the United States CURRAY
Isotope Geochemistry and the Pleistocene Climatic Record BROECKER
Quaternary Paleopedology RUHE
Geochemistry of Some Quaternary Lake Sediments of North America SWAIN
Quaternary Paleohydrology SCHUMM
Glaciers and Climate MEIER
Volcanic-Ash Chronology WILCOX
Quaternary Paleomagnetic Stratigraphy COX, DOELL, DALRYMPLE
Tectonics of Quaternary Time in Middle North America KING
Dendrochronology FRITTS
Theoretical Paleoclimatology MITCHELL