

of the right ramus of a mandible with teeth of a horse identified by Jean Hough as *Equus lambei* Hay. Miss Hough is quoted as stating that she considered *E. lambei* to be a subspecies of *E. caballus*. The jaw was evidently derived from adjoining terrace deposits consisting of outwash graded to the outermost recognizable moraines along the Chandalar River in the southern foothills of the Brooks Range. Péwé *et al.* correlate these moraines with the Illinoian Glaciation (1965, Fig. 3).

¹Walrus tusks have been found on several occasions during drift-mining of Second Beach, an auriferous beach deposit of Sangamon age at Nome, which form the type deposits of the Pelukian transgression of Hopkins (this volume). In 1956, walrus tusks were exposed and collected during stripping of estuarine deposits of Pelukian (Sangamon) age at Nome in preparation for gold dredging at deeper levels; these specimens were given to the University of Alaska by Carl Glavinovitz.

REFERENCES

- Frick, C. 1937. Horned ruminants of North America: *Am. Mus. Nat. Hist. Bull.*, v. 69, 669 p.
- Gilmore, C. W. 1908. Smithsonian exploration in Alaska in 1907 in search of Pleistocene fossil vertebrates: *Smithsonian Misc. Coll.*, v. 51 (Publ. 1807), 38 p.
- Hopkins, D. M., F. S. MacNeil, and Estella B. Leopold. 1960. The coastal plain at Nome, Alaska: a late Cenozoic type section for the Bering Strait region: *Repts., 21st Internat. Geol. Cong. (Copenhagen)*, 1960, pt. 4, p. 46-57.
- Kotzebue, O. von. 1821. A voyage of discovery into the South Sea and Bering's Straits, for the purpose of exploring a northeast passage, undertaken in the years 1815-1818: Longman, Hurst, Rees, Orme, and Brown, London, v. 1, 358 p.
- Maddren, A. G. 1905. Smithsonian exploration in Alaska in 1904, in search of mammoth and other fossil remains: *Smithsonian Misc. Coll.*, v. 49 (Publ. 1584), 117 p.
- McCulloch, D. S., D. W. Taylor, and M. Rubin. 1965. Stratigraphy, non-marine mollusks, and radiometric dates from Quaternary deposits in the Kotzebue Sound area, western Alaska: *Jour. Geology*, v. 73, p. 442-453.
- Péwé, T. L. 1952. Geomorphology of the Fairbanks area, Alaska: Ph.D. thesis, Stanford University, Stanford, Calif., 220 p.
- 1965. Fairbanks area, p. 6-36 in T. L. Péwé, O. J. Ferrians, Jr., D. R. Nichols, and T. N. V. Karlstrom, Guidebook, Field Conf. F, Central and South Central Alaska: *Internat. Assoc. Quaternary Res. (INQUA)*, 7th Cong. (Boulder), 141 p.
- Péwé, T. L., D. M. Hopkins, and J. L. Giddings, Jr. 1965. The Quaternary geology and archaeology of Alaska, p. 355-374 in H. E. Wright, Jr., and D. G. Frey, eds., *The Quaternary of the United States*: Princeton Univ. Press, Princeton, N.J., 922 p.
- Quackenbush, L. S. 1909. Notes on Alaskan mammoth expeditions in 1907 and 1908: *Am. Mus. Nat. Hist. Bull.*, v. 26, p. 87-130.
- Skinner, M. F., and O. C. Kaisen. 1947. The fossil bison of Alaska and preliminary revision of the genus: *Am. Mus. Nat. Hist. Bull.*, v. 89, p. 123-256.
- Wahrhaftig, C. 1958. Quaternary geology of the Nenana River Valley and adjacent parts of the Alaska Range, p. 1-78 in C. Wahrhaftig and R. F. Black, *Quaternary and engineering geology in the central part of the Alaska Range*: U.S. Geol. Prof. Paper 293, 118 p.
- Williams, J.R. 1962. Geologic reconnaissance of the Yukon Flats District, Alaska: U.S. Geol. Survey Bull. 1111-H, p. 289-330.

14. On the Origin of the Mammalian Fauna of Canada

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It has been known for quite a long time that the faunal composition of the Palearctic is very similar to that of the Nearctic. This is especially true with respect to the mammalian faunas of Northeastern Siberia and Canada, as many zoogeographers and paleogeographers have noted (Baker, 1920; Romer, 1933; Colbert, 1937; Stirton, 1951; Jelinek, 1957; Zeuner, 1959). With the exception of a few purely American endemics, such as American porcupines, raccoons, and American deer, most of which are descended from South American groups, the mammal species in Canada are of Asiatic origin. Recent paleontological research has demonstrated not only similarity of the present Palearctic and Nearctic faunas but also their very great similarity throughout a considerable part of the Anthropogene Period.

The Pleistocene mammals of Siberia and northwestern North America are well known (Scott, 1937; Frick, 1937; Simpson, 1947; Gromov, 1948; Hibbard, 1958; Vangengeim, 1961). Therefore, after a few general remarks, I shall pass on to a review of the factors that determined the formation of the present-day mammalian faunas of North America.

The skeleton of a vertebrate animal gives a very complete idea of the organism, and permits one to reconstruct the functional importance of individual parts of the animal as well as its general structure and biology. Because they are represented in abundance and variety in modern faunas and in many fossil faunas, mammals provide extremely rich material for the understanding and reconstruction of extinct communities. Many mammal species are strictly associated with definite environmental conditions, so that they are very important for interpreting landscapes of the past. The great variety of biological types represented, and of ecological niches occupied, make mammals perfect indicators of landscapes. The intimate interrelationships that exist between herbivorous mammals and the flora permit one to make a more reliable judgment concerning the vegetation that

existed when a certain species was living. One must not forget that the slightest change in the composition of the vegetation serving as food, or in the method of food procurement or mode of movement of a mammal species, is reflected by evolutionary changes in the bony structure. All of these factors make mammals, as compared with other animals, among the best objects of study in paleogeographic reconstructions. For this reason, mammals provide extensive and abundant data concerning the role of Beringia in the faunistic history of North America and eastern Asia, and serve as an excellent basis for the interpretation of the factors in the development of the modern faunal complexes in these two regions.

A determination of routes, directions, and rates of dispersal is essential to an analysis of penetrative migrations of complete faunas. In establishing the routes, we simultaneously distinguish the obstacles, many of which result from geological transformations, that hinder migration of either the entire fauna or of some of its components. It is necessary, therefore, to determine the tempo or rate of migration of separate species as well as of entire faunas. It is quite obvious that dispersals across Beringia at times of intercontinental connection between Asia and America differed for different species, as each overcame the obstacles in its individual way. For example, elephants, bison, musk-oxen, sheep, and many species of deer crossed from Asia into North America comparatively easily. Saiga and yak, on the other hand, were unable to disperse past Alaska, the obstacles beyond proving to be insuperable for them; these inhabitants of open country did not enter the mountainous and forested areas of Canada. Woolly rhinoceros, musk deer, and squirrels were also unable to overcome the barriers they found on their way; since they were forest dwellers, the open, treeless country was impassable.

The Bering Land Bridge

Recent studies lead us to assume that the Bering Land Bridge has appeared and vanished repeatedly during the Cenozoic Era (Hopkins, 1959 and this volume; Flint and Brandtner, 1961; Saidova, 1961). The earliest Cenozoic connection across this bridge took place during the Paleocene, at a time when there was a double link with America—eastward from Asia and westward from Europe. However, the animal migrations that took place at that remote time are of little importance for the understanding of the later history of the fauna and of the formation of the present-day faunal complexes. It is now definitely established that the Indo-Malayan, African,

and Neotropical faunas had acquired their present character by the end of the Pliocene Epoch, while the Palearctic, Nearctic, and Alpine faunas were formed only during the Anthropogene. Consequently, my discussion will be confined to tracing Anthropogene events that affected mammals in Eastern Asia and North America.

Repeated migrations of mammals from Asia into North America took place during the Pleistocene across a Beringian isthmus that formed and disappeared several times. Saidova's study of benthonic foraminifera in the bottom sediments of Bering Sea and the North Pacific indicates that synchronous uplift of the ocean floor and lowering of sea level have brought the Beringian isthmus into existence at least three times during the Pleistocene; the earliest of these events corresponds to the Kansan or Mindel Glaciation (Saidova, 1961, and this volume).

During times of Anthropogene emergence, it is assumed that the Bering Land Bridge was an area of wide plains with low hills and sparse woodlands, affording an opportunity for numerous mammals to migrate from Asia to North America (Flerow and Zablockii, 1961). This environment was such that most northern species of mammals could migrate across the land bridge, with the exception of those animals that inhabit forested mountains. The musk deer, whose ancestors lived in warm, humid, forested areas and probably migrated north and became adapted to cold climates and forested mountains as early as the second half of the Pliocene, is an example of a mammal that did not succeed in crossing the Bering Land Bridge. Neither the musk deer nor the squirrel (*Sciurus*) has migrated even to Kamchatka, since Kamchatka is separated from their main area of development by an expanse of open, treeless country. Conversely, the fact that the Rocky Mountain goat (*Oreamnos*) is derived from Asiatic ancestors suggests that those ancestors were adaptable to the plains of the Bering Land Bridge and that this goat was transformed into a true Alpine form only recently, at the beginning of the Pleistocene. The absence in Alaska of the woolly rhinoceros (*Coelodonta antiquitatis*) is also explained by the nature of the Bering Land Bridge. Rhinoceroses were confined to forest-steppe and forest areas that had a shrubby undergrowth. The woolly rhinoceros apparently did not inhabit open steppes; it would seem that this animal could not feed on harsh steppe grass, but browsed on trees, shrubs, and other soft fodder. Their remains are much rarer in the north of Eastern Siberia than in the south, where they are very numerous. Evidently in the northern part of their range in Eastern Siberia, they found the necessary food only in narrow belts along the rivers.

Nature of Faunal Dispersal

As already mentioned, when speaking of the migration of entire faunas, one must realize that it is not the fauna that is moving; instead, we are observing a movement of biocoenotically related complexes of organisms. Both now and in the past, orographic, ecological, and morphological barriers played a major role affecting the dispersal of terrestrial animals. Some species of a faunal complex can expand into new territories and adjust themselves to new conditions relatively easily; others move slowly and have to reconstruct their ecology and morphology quite appreciably. Forms that have lived for a long period in the area of their origin can change little and only slowly when physical geographic conditions change slightly. On the other hand, that part of the population that migrates early into areas of contrasting conditions often begins to change rapidly as it adjusts itself to the new environment. The resulting morphological lability—the ability of the organism to acquire new adaptations rapidly—is a decisive factor in determining potentialities for migration and expansion into new areas. In other words, the more easily the organism is able to adjust itself to varying conditions, the more readily it can expand its range.

The prior presence in a new territory of ecological analogues is of great importance. For example, the numerous forms of Antilocapridae that developed in North America during the Miocene and the greater part of the Pliocene were full analogues of the deer of Europe and Asia, and occupied biotopes in North America that corresponded to those occupied by deer in the Old World. With the extinction of the majority of genera and species of Antilocapridae during the second half of the Pliocene came an explosive development and dispersal of deer in America (Flerow, 1950).

The main mass of migrants moved from Asia to America, and only a few moved from America to Asia. Most of the "Americans" achieved but limited penetrations into northeastern Asia, and only reindeer, musk-oxen, and a few others established large territories in northern Asia and Europe. The explanation for this east-west imbalance seems to lie in the fact that the principal ecological niches in Asia were already occupied by an abundant and varied mammalian fauna. The thermophile forms that had inhabited the forests of North America at the beginning of the Pleistocene were pushed southward with the appearance of the continental ice sheet in Canada. When the ice sheet disappeared, the American endemics were unable to adjust rapidly enough to reoccupy the newly deglaciated area. This permitted Asiatic immigrants to disperse explosively.

Composition and Relationships of the North American Fauna

The present fauna of North America has a dual affinity to the Palearctic fauna. One component consists of species very similar to or even conspecific with species in Eastern Siberia; in some cases identical subspecies are present in both regions. Another component consists of taxa undoubtedly closely related to Asiatic forms but differing specifically or even generically.

Close study shows that a substantial part of the first group consists of taxa characteristic of northern latitudes in North America, including Alaska and part of Canada. The northern group includes the forest bison (*Bison priscus athabascaae*), snow sheep (*Ovis nivicola*), musk-ox (*Ovibos moschatus*), moose (*Alces alces americanus*), New World elk or wapiti (*Cervus elaphus canadensis*), brown bear (*Ursus arctos middendorffi*), ermine (*Mustela erminea richardsoni*), weasel (*Mustela nivalis rixosa*), wolverine (*Gulo gulo luscus*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), arctic hare (*Lepus timidus*), lemmings (*Dicrostonyx torquatus*, *Lemmus sibiricus*), and voles (*Microtus oeconomys*, *Clethrionomys rutilus*).

The second and less closely related group, on the other hand, consists of taxa distributed chiefly in the southern part of North America. The ranges of the species included in this group extend either across southern Canada and the United States or through the Rocky Mountains south of Alaska. The second group includes the plains bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), Rocky Mountain goat (*Oreamnos montanus*), grizzly bear (*Ursus horribilis*), black bear (*Ursus americanus*), American badger (*Taxidea taxus*), skunks (*Mephites* and others), coyote (*Canis latrans*); swift and kit fox (*Vulpes velox*, *macrotis*), bobcat (*Lynx rufus*).

As I suggested earlier, this dual similarity is explainable by differences in the glacial history in North America and Northeastern Siberia. Glaciation in Northeastern Siberia has consisted only of relatively small ice sheets and local alpine glaciers, and vast areas remained that were inhabited by a varied mammalian fauna, including the bisons. On the other hand, enormous areas in North America, including all of Canada, were subjected to glaciation for a lengthy period of time (Flint, 1947), and these areas were unsuitable for mammal life. Asiatic mammals that had migrated to North America before the maximum glaciation were cut off from their original homeland and lost all connection with it. Furthermore, they were

pushed southward to the area of the present United States and were forced into new environments quite different from the northern landscapes. This resulted in rapid evolution and the acquisition of specific adaptations to the new conditions. During the retreat and disappearance of the continental glaciers in Canada, a new migration of Asiatic mammals across the Beringian isthmus took place. This history of immigration, evolution in isolation, and renewed immigration is illustrated by the history of sheep and bison, and explains the twofold degree of similarity to Asiatic mammalian faunas.

The sheep that migrated to America prior to the maximum glaciation were closely related to the living Asiatic argali (*Ovis ammon*). During the glaciation, they were forced southward and there evolved into the distinctly different American bighorn sheep (*Ovis canadensis*), which retains, however, many features of its Asiatic ancestor. Later, another Asiatic species, the Siberian snow sheep (*Ovis nivicola*), entered North America and dispersed southward along the Rocky Mountains to northern British Columbia. Its modern range includes areas on both sides of Bering Strait but does not merge with that of *Ovis canadensis*.

An even more striking illustration of the effect of the differences between Siberian and North American glaciation is provided by the history of the bison (Skinner and Kaisen, 1947; Flerow and Zablozki, 1961). The early stages in the history of the bison are not yet clearly understood. However, an Asiatic origin is indicated by the fact that the earliest records of the genus are represented by *Bison sivalensis* (Falconer) Lidekker in the late Pliocene Siwalik deposits of India and by *B. paleosinensis* Chardin and Piveteau in the Late Pliocene Nihowan fauna of China.^a During early Pleistocene time, bison dispersed into the temperate zone of Asia and Europe. At this time, short-horned forms, including first *B. tamanensis* Vereshchagin and the later *B. priscus schoetensaki* Freudentberg,^b are found in southern Europe as far north as the north Caucasus (Predkavkazie). By middle Pleistocene time, bison apparently disappeared completely in southern Asia but became widely distributed across Europe, northern Asia, and northern North America as a large, long-horned form, *B. p. crassicornis* Richardson. During this long period, extending from the end of the Mindel-

^a The *Bison*-bearing levels in the Siwalik Series and the Nihowan fauna are correlated by other authors in this volume with the Villafranchian Stage of Europe and are assigned by them to the Lower Pleistocene. Ep.

^b *B. cesaris* Schlottheim, 1821, has priority over *B. priscus* Bojanus, 1827, and *B. pallasi* Baer, 1823. However, both *B. cesaris* and *B. pallasi* are *nomen oblitum*, and I retain *B. priscus*.

Riss Interglaciation into the beginning of the Riss-Würm Interglaciation, landscape conditions were more or less uniform, the range of bison was continuous across Holarctica, and no substantially different species appeared.

Bison priscus crassicornis migrated from Asia to America before the Riss (or Illinoian) Glaciation. During this glaciation they were forced southward out of Canada to the present area of the United States, where they evolved into the giant species *B. latifrons* Harlan. This southern population was completely isolated from the northern group, which continued to live in Asia, Beringia, and Alaska. The ancestor of the modern plains bison, *B. alleni* Marsh then developed in the southern part of the United States, and this form evolved into the steppe bison of the Wisconsin Glaciation (*B. bison antiquus* Leidy) and finally into the living post-Pleistocene *B. bison bison* Linnaeus.

To the north, in Alaska and Siberia, the long-horned bison (*B. priscus crassicornis*) persisted through much of the late Pleistocene, but by the end of the Wisconsin (or Würm) Glaciation, bison began gradually to become smaller throughout Holarctica. Their horns became shorter, as well, and the long-horned *B. p. crassicornis* was replaced by the short-horned *B. p. priscus* Bojanus, which was equally holarctic in distribution and which also failed to produce distinct local forms.

With the withdrawal of the Wisconsin ice sheet, bison again penetrated into Canada from Alaska and Beringia to the northwest. However, like other late Pleistocene Asiatic immigrants, the northern bison dispersed only into the MacKenzie River basin and failed to reach the Hudson Bay region and eastern Canada. These areas probably were cleared of ice later than other parts of Canada and therefore remained unsuitable for such mammals as bison, moose, and wapiti. The presence of Hudson Bay also affected the climate and created very severe environments.

At the end of the Würm (or Wisconsin) Glaciation, the range of bison began to shrink and disintegrate, and by the beginning of the Holocene was completely disrupted. Bison became extinct over enormous areas and persisted only in parts of Europe, Eastern Siberia, Alaska, Canada, and the United States. The isolated populations began to differentiate, resulting in the wisent (*Bison bonasus*) of Europe, the large wood bison (*B. priscus athabascae*) of Eastern Siberia, Alaska, and Canada, and the plains bison (*B. bison bison*) of the United States. Further isolation in Europe produced a reduction from the moderate horn length of the ancestral wisent (*B. bonasus major* Hilzheimer) to the short-horned Lithuanian bison (*B. b.*

bonasus Linnaeus) and Caucasus bison (*B. b. caucasicus* Satunin). *B. b. major* was once present in the Caucasus and in Transcaucasia, but later its range diminished, and *B. b. caucasicus* persists only on the western half of the main ridge of the Caucasus.

Eastern Siberia, Alaska, and Canada were inhabited by the big *B. priscus athabascæ* Rhoads, but a very small, short-horned endemic race evolved in an extreme northern part of Eastern Siberia isolated from the general range of the species by mountain ranges. This subspecies occupied lowlands adjoining the Arctic Ocean in the Lena, Indigirka, and Kolyma River basins and became extinct during the post-Würm thermal maximum.

In Canada, the post-Pleistocene history of bison has been one of range reduction and extinction similar to that in Eurasia. This history follows the same pattern seen in musk-ox (*Ovibos moschatus*), which became extinct throughout Palearctica and were preserved only in North America and Greenland, where the periglacial conditions to which they were adapted are still present. Even in North America, the musk-ox gradually disappeared west of the MacKenzie River and retreated eastward nearer to the glaciated areas, a process that has continued into historic time. Similarly, the range of forest bison shrank eastward, and the species finds its last refuge in the forests of the Great Slave Lake region of Canada (Seton, 1886, 1912, 1927; Flerow in Adlerberg *et al.*, 1935; Raup, 1935; Soper, 1939, 1941; Fuller, 1962) in an area of severe climatic conditions in which small patches of prairies are present in the taiga forest. These prairie patches apparently approach the character of the cold forest-steppes that were once widely developed in Siberia, Alaska, and Canada at the end of the Pleistocene and during the early Holocene. All features characterizing this big Canadian wood bison indicate its very close morphological affinity with the extinct Pleistocene and early Holocene species of the so-called "primary bison," *Bison priscus* (Rhoads, 1898).

We can say confidently that the typical Pleistocene mammals of north-eastern Asia were unable to survive the period of the Holocene thermal maximum and the resulting change in the vegetation. The formation of *Sphagnum* associations (muskegs) in northern regions deprived most species of large herbivorous animals (including horses, oxen, and many species of deer and antelope) of their main source of forage. Rhinoceroses and mammoths became extinct at the same time and probably for the same reason. Only the musk-ox and the wood bison survived this crisis in America, persisting in areas where remnants of Pleistocene landscapes were preserved. These "living fossils," once contemporaries of the mammoth, survived to the present time as the last representatives of the Pleistocene fauna.

REFERENCES

- Adlerberg, G. P., B. S. Vinogradov, N. A. Smirnov, and C. C. Flerow. 1935. Zveri Arktiki (Arctic mammals): Leningrad, 579 p.
- Baker, F. C. 1920. The life of the Pleistocene or Glacial Period: Univ. Ill. Bull., v. 17, no. 41, 476 p.
- Colbert, E. H. 1937. The Pleistocene mammals of North America and their relations to Eurasian forms, p. 173-184 in G. G. MacCurdy, ed., Early Man: Lippincott, New York, 363 p.
- Flerow, C. C. 1950. Morfologiya i ekologiya olenobraznykh v protsesse ikh evolyutsii (Morphology and ecology of deerlike animals and processes of their evolution): Akad. Nauk SSSR, Materialy po chetvertichnomu periodu SSSR (Data on the Quaternary Period) Bull. 2, p. 50-69.
- Flerow, C. C., and M. A. Zablockii. 1961. O prichinakh izmeneniia areala bizonov (On the reasons for the change in the range of bison): Bull. Moskva Ob-va Ispytatelei Prirody Otd. Biologii, v. 46, p. 99-109.
- Flint, R. F. 1947. Glacial geology and the Pleistocene Epoch: Wiley, New York, 589 p.
- Flint, R. F., and F. Brandtner. 1961. Climatic changes since the last Interglacial: Am. Jour. Sci., v. 259, p. 321-328.
- Frick, C. 1937. Horned ruminants of North America: Am. Mus. Nat. Hist. Bull., v. 69, 669 p.
- Fuller, W. A. 1962. The biology and management of the bison of Wood Buffalo National Park: Canadian Wildlife Serv., Wildlife Mgmt. Bull. Ser. 1, no. 16, 52 p.
- Gromov, V. I. 1948. Paleontologicheskoe i arkhologicheskoe obosnovanie stratigrafii kontinental'nykh otlozhenii chetvertichnogo perioda na territorii SSSR (Paleontological and archaeological bases of the stratigraphy of continental deposits of the Quaternary Period in the territory of the USSR): Akad. Nauk SSSR, Tr. Geol. Inst., Bull. 64, Ser. Geol. No. 17, 519 p.
- Hibbard, C. W. 1958. Summary of North American Pleistocene mammalian local faunas: Papers Michigan Acad. Sci., Arts, and Letters, v. 43, p. 3-32.
- Hopkins, D. M. 1959. Cenozoic history of the Bering Land Bridge: Science, v. 129, p. 1519-1528.
- Jelinek, A. J. 1957. Pleistocene faunas and early man: Papers Mich. Acad. Sci., Arts, and Letters, v. 42, p. 225-237.
- Raup, H. M. 1935. Botanical investigations in Wood Buffalo Park: Nat. Mus. Canada Bull. 74, Biol. Ser. 20, 174 p.
- Rhoads, S. N. 1898. Notes on living and extinct species of North American Bovidae: Proc. Acad. Nat. Sci., Philadelphia, v. 49, p. 483-502.
- Romer, A. S. 1933. Pleistocene vertebrates and their bearing on the problem of human antiquity in North America, p. 49-81 in D. Jenness, ed., The American aborigines, their origin, and antiquity: Toronto Univ. Press, 396 p.
- Saidova, H. M. 1961. Ekologiya foraminifer i paleogeografiya dal'nevostochnykh morei SSSR i severo-zapadnoi chasti Tikhogo Okeana (Ecology of foraminifera and paleogeography of the Far East Seas of the USSR and the north-western part of the Pacific Ocean): Akad. Nauk SSSR, Inst. Okeanologii, 232 p.
- Scott, W. B. 1937. A history of land mammals in the Western Hemisphere, 2d ed.: Macmillan, New York, 786 p.

- Seton, E. T. 1886. The ruminants of the Northwest: Proc. Can. Inst., Ser. 3, vol. 21, no. 4, fasc. 3, p. 113-117.
- 1912. The Arctic prairies: Constable, London, 415 p.
- 1927. Lives of game animals, v. 3. Doubleday, Doran, New York, 780 p.
- Simpson, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic: Geol. Soc. America Bull., v. 58, p. 613-688.
- Skinner, M. F., and O. C. Kaisen. 1947. The fossil *Bison* of Alaska and preliminary revision of the genus: Am. Mus. Nat. Hist. Bull., v. 89, Art. 3, p. 123-356.
- Soper, J. D. 1939. Wood Buffalo Park; notes on the physical geography of the Park and its vicinity: Geogr. Rev., v. 29, p. 383-399.
- 1941. History, range, and home life of the northern bison: Ecol. Monogr., v. 11, p. 347-412.
- Suirton, R. A. 1951. Principles in correlation and their application to later Cenozoic holarctic continental mammalian faunas: Rept., 18th Internat. Geol. Cong. (London), 1948, pt. 11, p. 74-84.
- Vangengeim, E. A. 1961. Paleontologicheskoe obosnovanie stratigrafii Antropogennykh otlozhenii severo vostochnoi Sibiri (Paleontological basis of the stratigraphy of the Anthropogene deposits of Northeastern Siberia): Akad. Nauk SSSR, Tr. Geol. Inst., Vyp. 48, 182 p. In Russian; English translation of parts available from Am. Geol. Inst.
- Zeuner, F. E. 1959. The Pleistocene Period; its climate, chronology and faunal successions: Hutchinson, London, 447 p.

15. *The Effect of the Bering Land Bridge on the Quaternary Mammalian Faunas of Siberia and North America*

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The history of land connections between Asia and North America, and the effects of such connections on the faunal history of both continents, have occupied the minds of zoogeographers for a long time. And yet many questions remained unanswered because of insufficient knowledge of the fossil faunas of Eastern Siberia, especially of those representing the earlier part of the Anthropogene. Work by the Geological Institute of the Academy of Sciences of the USSR during the past ten years has greatly enlarged our knowledge of the Anthropogene fauna of Eastern Siberia. It appears now that there were at least three periods of intercontinental faunal exchange; at the beginning of the Anthropogene, during the Maximum (Samarov) Glaciation, and, most recently, during the Zyrianka and Sartan Glaciations. The distinction between the last two periods of continental connection is vague, and it may be that the intervening period of separation was short-lived.

Early Anthropogene

According to the Anthropogene faunal record, the earliest connection across Beringia took place in the Villafranchian. Apparently, faunal exchange took place at this time in both directions, although our record seems to indicate that most of the migrating mammals moved from Asia to North America. Introduced to Asia from North America was a horse that was ancestral to the Asian *Equus sanmeniensis-sivalensis* lineage (horses with a long protocone differing from, but contemporary with, *E. stenonis*). We know of no horses of *E. stenonis* type in Asia; they were present only in Europe and Africa, possibly extending eastward as far as Kazakhstan. Apparently, there have been two routes by which horses penetrated the Old