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A Review of the Distribution of Holarctic Recent Mammals

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A REVIEW OF THE DISTRIBUTION OF HOLARCTIC RECENT MAMMALS

ROBERT L. RAUSCH


GEOLOGICAL EVIDENCE, reviewed recently by Hopkins (1959), indicates that Eurasia and North America are segments of a single land mass that has been intermittently divided during the Cenozoic era by inundation of the Bering-Chukchi platform lying between what are now Alaska and northeast Siberia. The concept of a single land mass is also supported by many biogeographical data. At higher latitudes, the Recent biota of the two continents are strikingly similar, as has been pointed out by Hultén (1937), Walters (1955), Lindroth (1957), Johansen (1956, 1958), and others. It is the purpose of this paper to review the species of Recent mammals that evidently have a Holarctic distribution with some reference to the effects of the Würm (Wisconsin) glaciation upon their distributional pattern.

The Bering-Chukchi platform was above sea level at least during early and late Würm time. During the glacial maximum of this age, more than 35,000 years ago, with the sea about 100 meters below its present level, the platform was evidently exposed in its entirety and comprised an isthmus approximately 1,600 kilometers in north-south extent between the two continental segments (Hopkins, 1959). The use in the past of the term “land bridge” for this connection is perhaps unfortunate, since by connotation it implies a narrow corridor. At the time of maximum exposure of the Bering-Chukchi platform, this isthmus was approximately equal in width to the present north-south dimension of Alaska.

The limits of Pleistocene glaciation have been mapped for North America by Flint and others (1945) and summarized for Eurasia by Charlesworth (1957) and Berg (1958). Farrand (1961) has published a map incorporating the available information on glaciation in northeast Siberia, and a detailed glacial map of Alaska has been prepared by Karlstrom (1961). It has been established that there are extensive unglaciated areas in both Alaska and northeast Siberia, and, according to Hopkins (1959), the Bering-Chukchi platform was never invaded by glacial ice. The platform, in combination with the adjacent unglaciated regions of what are now northeast Siberia and Alaska, made up an area of vast size during the glacial maximum of Würm age. It is known that an arctic climate prevailed in the amphiberingian region during

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Würm time, for paleobotanical studies have disclosed evidence only of species characteristic of the tundra biome. Forests never advanced into the Bering-Chukchi platform (Hopkins, 1959, 1960).

A result of the glacial advances of Würm age was a southward shifting of biotic zones on the continents, with consequent modification of the geographic distribution of many northern species (Charlesworth, 1957). For example, Microtus gregalis Pallas and Dicrostonyx torquatus Pallas occurred in England (compare Hinton, 1926; Zeuner, 1958). Dicrostonyx (D. torquatus; see below) has been found as far south as Pennsylvania (Guilday and Doutt, 1961). The musk ox, Ovibos moschatus (Zimmermann), reached the Netherlands (Hooijer, 1960) and the midwestern United States (Dillon, 1956). The study of Pleistocene marmots by Wehrli (1935) made known the occurrence of Marmota marmota Linnaeus beyond the Rhine, and of the now central Asian M. bobak Müller in middle Germany. Numerous examples of this kind might be cited.

Many species of mammals, not considered further here, had become extinct by the end of the Pleistocene epoch. Excepting these, Zeuner (1958) found that the analysis of upper Pleistocene mammalian faunas of Europe disclosed only Recent species. He stated (p. 381), “It is important to note that, in spite of abundant fossil material, no new species is known to have arisen since the Last Interglacial. 150,000 years have not produced any new species among the mammalia of Europe, though a fair number of subspecies appear to have arisen during this period.” Although arctic and high-boreal species of mammals largely disappeared from the lower latitudes as the glaciers receded, from all indications the environment of the mammals inhabiting the unglaciated refugia at higher latitudes was not much changed. Simpson (1947) pointed out that only “cold temperate to boreal” species were involved in the latest dispersal from the amphiberingian region; this “filter” effect has been discussed by Lindroth (1957), who emphasized that few species of organisms requiring a temperate or warmer climate are common to both North America and Eurasia. Hence, when the Bering-Chukchi platform was inundated, and the amphiberingian refugium was bisected, the species of mammals occurring on both sides of the resulting strait must have been arctic and high-boreal forms.

Much of the information about conditions during Pleistocene time has been acquired recently, and there is now a quantity of data to indicate that the Recent mammalian species which occupied the amphiberingian refugium during Würm time are Holarctic in distribution. Consequently, during the last decade taxonomists have found necessary the consideration of a broader species concept, with a reduction in the number of taxa and an increase in the number of species accepted as common to the high-boreal and arctic regions of both continents. Simpson’s (1947, p. 617) statement that “Categories below the genus are too narrow; very few are recorded as common to the two land masses in question,” may now be amended in the light of new information.
TABLE 1

SPECIES OF HOLARCTIC RECENT MAMMALS

<table>
<thead>
<tr>
<th>SPECIES</th>
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<tbody>
<tr>
<td>18. Cervus elaphus Linnaeus, 1758.</td>
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<tr>
<td>19. Alces alces Linnaeus, 1758.</td>
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<tr>
<td>20. Rangifer tarandus Linnaeus, 1758.</td>
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Of the Recent mammals considered here, 21 species (see Table 1) are probably Holarctic in distribution. Among these are eight whose geographic distribution in North America indicates post-Pleistocene dispersal from the amphiberigian region: *Lepus timidus*, *Cistellus undulatus*, *Clethrionomys rutilus*, *Microtus oeconomus*, *Microtus gregalis*, *Lemmus lemmus*, *Dicrostonyx torquatus*, and *Ovis nivicola*. Their ranges in North America are shown in Figures 1–8.

The taxonomic status of three of these species may be questioned. The structural details of the palate described earlier (Rausch, 1953) as serving to differentiate Alaskan material from Eurasian specimens of *M. gregalis* have been seen to vary. Ognev's (1948) conclusion that *M. gregalis* is a Holarctic species is probably correct, as will be shown in findings to be published elsewhere.

The extensive arctic distribution of the brown (Obskii) lemming, *Lemmus sibiricus* (Kerr), has been rather generally accepted. However, Sidorowicz (1960), upon comparing Siberian and Scandinavian material, concluded that the latter is conspecific with *L. lemmus* (Linnaeus). The prior name, *L. lemmus*, is used here provisionally for North American specimens pending further investigation. Chromosome studies such as those of Matthey and Zimmermann (1961) would be useful.
Of the eight species mentioned above, all but *Ovis nivicola* occur extensively in Eurasia; but for an apparently isolated population in the Noril'sk Mountains east of the lower Enisei River, this sheep is found only in the mountains of northeast Siberia as far west as the Lena River and south to the latitude of Lake Baikal, where it ranges west to the upper Angara River (Heptner and others, 1961). If *O. nivicola* (including *O. dalli* Nelson) is specifically distinct from *O. canadensis* Shaw (see Sushkin, 1925; Cowan,
1940), it occupies regions of similar size on the two continents. However, if *O. nivicola* is conspecific with *O. canadensis*, as so considered by Ellerman and Morrison-Scott (1951) and by Heptner and others (1961), it could not be a late- or post-Pleistocene invader of North America. It is regarded as distinct in the present paper.

Their present distribution and paleontological evidence strongly suggest that these eight species originated in Eurasia. If present in the amphiberian refugium during Würm time, portions of their populations would have been
isolated within the eastern segment of the refugium when the isthmus was inundated for the last time around 10,000 years ago. Since all are arctic or high-boreal species, they would have extended their ranges eastward as habitat became suitable behind the receding glaciers. This hypothesis is supported by the fact that these species occur in Alaska around the limits of the former refugium, with the number of species present decreasing progressively toward the east. *Lemmus* has occupied Baffin Island, while *Citellus undulatus* and *Clethrionomys rutilus* have extended their ranges only as far as Hudson Bay.
and the Melville Peninsula. *Lepus timidus, Microtus oeconomus, M. gregalis,* and *O. nivicola* have more restricted ranges. Three species—*L. lemmus,* *C. undulatus,* and *O. nivicola*—have spread rather far down the Rocky Mountains.

Lindroth (1957, p. 264) has pointed out that the strait between Baffin Island and Greenland is the most effective barrier in the entire arctic region to the dispersal of terrestrial animals. It appears that the strait between Baffin Island and the Ungava Peninsula, as well as Hudson Bay, are equally effective
obstacles for the species considered here, for, among these species, only *Dicrostonyx torquatus* is found in Greenland and Ungava. Since it is the best adapted among small rodents for winter activity, its more extensive range might be expected. The collared lemming of Ungava has long been considered a distinct species, *D. hudsonius* (Pallas); however, according to R. S. Peterson (unpublished thesis), who studied series of specimens from Payne River, Ungava, and from Belcher Islands, Hudson Bay, the characters used to distinguish *D. hudsonius* are not constant. (It might be suggested that *Dicrostonyx* became established in Ungava by means of reimmigration from the south, but its presence on many of the arctic islands provides contrary evidence.) Only a single, Holarctic species is recognized here.

With the group of recent invaders of North America might also be included *Ochotona collaris* because of its distributional pattern (Fig. 1) and because recent Palearctic affinities are suggested by some of its parasites. (The possible zoogeographic significance of parasitic helminths was recognized early by von Ihering [1902], but surveys in northern regions still are not complete enough to make full use of such information.) It has been noted that the nematodes parasitic in *O. collaris* belong to genera found in Eurasian species of *Ochotona*, but thus far unknown from the Rocky Mountain *O. princeps* (Richardson) (see Rausch, 1960). Data on fleas also indicate the recent Palearctic origin of this pika (Holland, 1958, 1963).
Isolated populations of small mammals are found on various arctic islands: for instance, *Lemmus* on St. George Island, Pribilof Group, Wrangel Island, Novosibirsk Islands; *Dicrostonyx* on St. Lawrence, on the Aleutian Islands of Unalaska and Unmak, Novaya Zemlya, Novosibirsk Islands; *Clethrionomys* on St. Lawrence Island; *Microtus* on Unalaska, St. Lawrence, and St. Matthew Islands; *Sorex* on St. Lawrence and on St. Paul, Pribilof Group (see Vinogradov and Gromov, 1952). Differentiation in these isolated populations is not unexpected, since the rate of genetic drift is related to the size of the breeding population, and high-amplitude fluctuations in numbers sometimes result in very low densities on such islands. Some of the islands, such as the Pribilofs and the St. Matthew Islands lying in deeper water near the edge of the Bering–Chukchi platform, evidently would have been connected with the refugium only during early Würm time. The changes that have taken place in the mammals found on the more remote islands, however, appear in general to have been no greater than those that have occurred among the mammals on St. Lawrence Island, which must have been one of the last to be separated from the refugium. These insular mammals commonly have been considered specifically distinct from those of the two continents, but this concept appears in most cases to be invalid. The period of isolation has been too short to allow differentiation beyond the subspecific level.

A series of experimental crossings of some of the small mammals may provide further understanding of their affinities. Fertile hybrids have been obtained from the following combinations (Rausch, unpublished data): *Lemmus*, Point Barrow, Alaska, and St. George Island, Pribilof Group; *Dicrostonyx*, Point Barrow, Alaska, and Unmak Island, Aleutian Islands; *Microtus oeconomus*, St. Lawrence Island and Kenai Peninsula, Alaska. Attempts are in progress with *Lemmus* from Point Barrow and from Sweden. Shvarts and others (1960) succeeded in obtaining fertile hybrids from two subspecies of *Microtus gregalis*, using animals originating about 1,000 kilometers apart.

The affinities of another insular mammal, *Microtus abbreviatus* Miller, endemic on the St. Matthew Islands, have not been sufficiently investigated. This vole, clearly of the subgenus *Microtus*, not *Stenocranius* as frequently has been stated, may be conspecific with *M. middendorffi* Poliakov, of northern Siberia, according to Matthey and Zimmermann (1961).

Besides the eight species considered above to be comparatively recent invaders of North America, thirteen additional species appear to be Holarctic. These have extensive geographic distributions on both continents: *Sorex arcticus*, *S. caecutiens* (or *S. cinereus*; compare van den Brink, 1953, and Stroganov, 1957); *Castor fiber*, *Canis lupus*, *Alopex lagopus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela erminea*, *M. nivalis*, *Gulo gulo*, *Cervus elaphus*, *Alces alces*, and *Rangifer tarandus*. With only three exceptions, the Eurasian and...
North American populations of these are separated by the width of Bering Strait. The range of *Alces alces* encompasses the boreal zone of both continents, with extensions into the Arctic. *Castor fiber* is usually limited to the taiga but is frequently found north of the tree line. It is absent in eastern Siberia (Dezhkin, 1961), but Siivonen (1956) observed that the European form and the introduced North American form freely intergrade in the wild state in Finland. *Cervus elaphus* has the southermmost range of any of these species, and the Eurasian and North American populations are the most disjoint of any of the species considered here. However, they are recognized as being conspecific; in fact, Flerov (1952) concluded that one subspecies, *C. elaphus canadensis*, occurs both in western North America and in Eurasia.

The distributional status of four additional species (Table 2) is uncertain, and they are possibly Holarctic: *Marmota marmota*, *Felis lynx*, *Ochotona hyperborea*, and *Martes martes*. The relationships of the marmots are not well understood (see Moore, 1961), although the North American *M. caligata* (Eschscholtz) has been considered conspecific with *M. marmota* by Ellerman and Morrison-Scott (1951), Rausch (1953), and others. *M. camtschatica* Pallas, whose Siberian range is almost identical with that of *Ovis nivicola* (see Bobrinskii and others, 1944), is of particular interest, as is the form occurring in the Brooks Range, Alaska (Rausch, 1953). The North American forms share few species of parasites with those in Eurasia. The position of *Felis lynx* can be elucidated by studies of material from Siberia (Kurtén and Rausch, 1959). The degree of relationship between *Ochotona hyperborea* and *O. collaris* should be investigated further. The former occurs throughout eastern Siberia, including the Chukchi Peninsula. Hagmeier (1961) has suggested that *Martes americana* (Kerr) may be conspecific with *M. martes* and *M. zibellina* Linnaeus. Apparently the latter may be excluded from this possibility, since it differs significantly from the other two in the form of the penile bone (Novikov, 1956). Whether this difference is constant in fully adult animals is a point to consider.

As new paleontological and geological data become available, our species concepts will be further refined. It may then be possible to confirm some of the conclusions presented herein and to modify them.
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