Southern Limits of the Late Pleistocene Euro-Siberian Faunal Complex in East Asia

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Many new findings of animal remains, representatives of the Late Pleistocene Euro-Siberian faunal complex, have been made over the past 15 years. The author lists the southernmost and southeasternmost sites of such animals as the mammoth, the woolly rhinoceros, the giant deer, the elk, the Asiatic wild ass, the Przewalkii horse and the prehistoric bison.

The geographic positions of those sites indicate that in the Late Pleistocene the Euro-Siberian faunal complex was distributed in East Asia from Japan and Korea to Hebei Province in China, and in the south to northeast Sychuan.

During the last Wurm glaciation the range of distribution expanded not only to the north, where typical mammal representatives crossed the Bering Land Bridge, but also to the south and southeast. When migrating across the Tatar Land Bridge to Sakhalin, Hokkaido and other islands, the animals, to a certain extent, drove out the representatives of the Sino-Malayan fauna inhabiting the region since the Middle Pleistocene.

A distinct trend has developed in recent years to report available data on Quaternary paleontology in the form of a short résumé. Although the present résumé of extreme southern findings on the representatives of the Late Pleistocene of Euro-Siberian faunal complexes is of a preliminary nature, all the graphically represented materials furnished here clearly show how much deeper our knowledge is than in 1955, when publications on this problem last appeared (Flerov et al., 1955).

The southern limit of distribution of Late Pleistocene Euro-Siberian faunal complexes in East Asia is not only interesting from the biostratigraphic correlation point of view. This limit is intimately associated with the problem of migration of mammals across the Late Pleistocene Tatar Bridge connecting the Asian continent with Sakhalin, Hokkaido and other Japanese islands in the epoch that apparently coincided with the Wurm depression of sea level that prevailed far to the west.

It is possible to trace a Euro-Siberian faunal complex from the Atlantic to the Pacific Ocean even in the Middle Pleistocene, which corresponds to the West European Holstein. Typical Middle Pleistocene Euro-Siberian complexes possessed an "interglacial" character. They were represented by different species of elephants of the group Paleoloxodon—*P. antiquus sensu lato* (with sub-species) in the western and central regions and *P. namadicus* s. l. in East and South-East Asia, together with different types of rhinoceros of the mercoid group—*Dicerorhinus*—*D. kirchbergensis* (*hemitoechus*) *binagadensis* in the western and central parts of the geographic range and *D. choukoutiens nipponicus* in the Far East. In the Middle Pleistocene this complex is also represented by the Palearctic genus *Megaloceros* with its Far East sub-genus *Sinomegaceros* (Fig. 1).
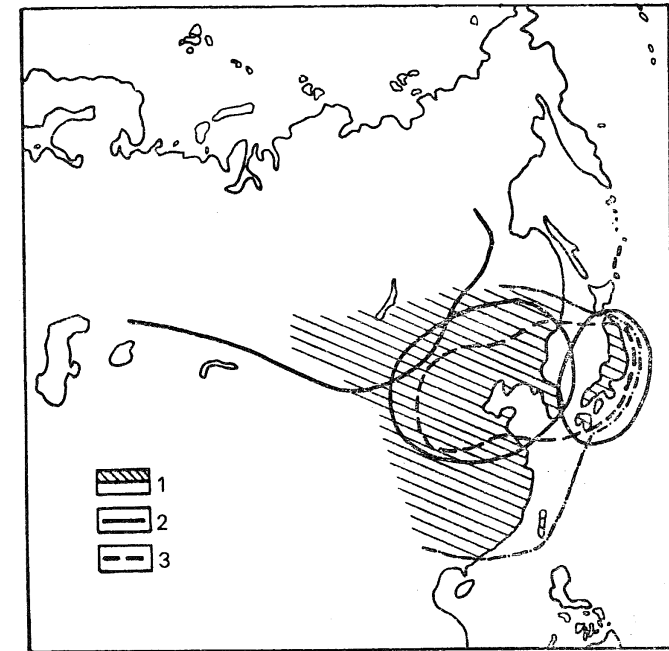

Fig. 1. Distribution of species of Middle Pleistocene Euro-Siberian faunal complex in East Asia (Middle Pleistocene tentatively corresponds to Holstein of West Europe).
1—Group *Paaleoloxodon namadicus*; 2—Mercoid tribe *Dicerorhinus*; 3—Group of early *Sinomegaceros*.

Chzou-koudyan (No. 1 synantropic site in China) and the bone bed of proboscideans in Kuzuu, Japan (lower horizons) are typical faunal sites of the Middle Pleistocene Euro-Siberian complex in East Asia.

The situation in the Far East (as also in the west) radically changed in the Late Pleistocene period, which corresponds to the maximum of the last

glaciation period. In this region the population of Paleoloxodons was replaced by populations of late *Mammonteus primigenius* (Blum.). Mammoths had their most extensive distribution in East Asia, and they not only migrated across the Beringian Land Bridge repeatedly, which at that time gave rise to forms of the genus *Archidiskodon*, but also across the Tatar Land Bridge (Fig 2).

The region of distribution of the woolly rhinoceros, namely *Coelodonta antiquitatis* (Blum.), covered an extensive territory of East Asia from Far North-East Siberia to the Chinese province of Heilun-shan and to the south—right up to Henan province.
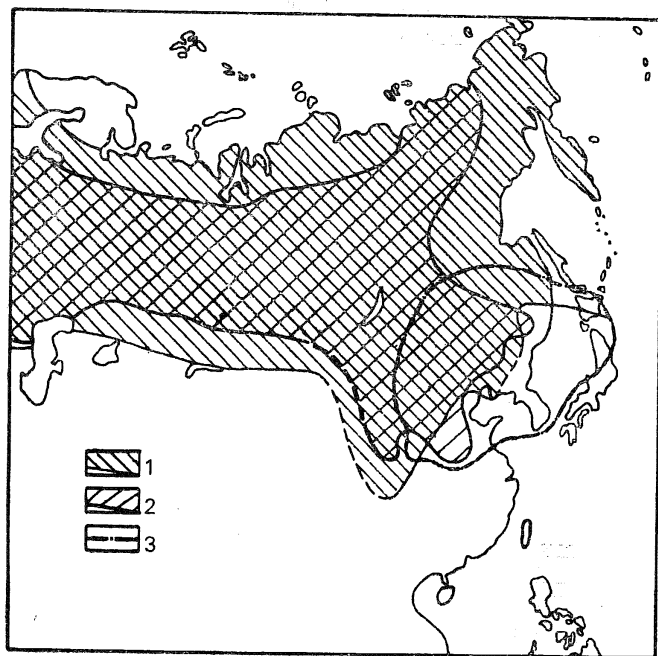

Fig. 2. Distribution of species of Late Pleistocene Euro-Siberian faunal complex in East Asia (last glacial epoch).

1—*Mammonteus primigenius* (Blumenbach); 2—*Coelodonta antiquitatis* (Blumenbach); 3—*Megaloceros* (*Sinomegaceros*) *ordosianus* (Young).

During this period *Bison priscus* s. l. also attained maximum distribution in East Asia. The southern limit of distribution of the bison extended from the Caspian right across to Japan.

Populations of late *Sinomegaceros* were distributed in the Japanese islands, North and Central China and southward right down to Henan province.

The wide dispersion of Euro-Siberian faunal complexes to the south noted in the Late Pleistocene of East Asia can be understood only as a result of

glaciation over extensive regions of northern Euro-Siberia. Glaciation took place as a result of the unique relief of this country (particularly the Tsinlin Mountains) and the extension of a huge area of this continent to the north. Typical sites of Late Pleistocene fauna of the Euro-Siberian complex in East Asia are the Harbina region (Panlachengtse, Fuliaerhtzi, Guxiangtung*), the Saraossogol region (Ordos, China) and the Hanaidzuma region (Japan).

Turning now to the southern limit of distribution of some characteristic Late Pleistocene mammals in East Asia, it will be noticed that the appended schematic maps do not cover the entire area; they only cover the extreme southern points from where fossils have so far been collected.

I. MAMMONTEUS PRIMIGENIUS (BLUMENBACH). MAMMOTH

Large numbers of sites with fossil remains of *Mammonteus primigenius* were discovered in the areas in question during the last two decades. On the basis of the latest publications and materials in various institutions it will be possible to give a tentative delineation of the southern limit of distribution of mammoths as follows (Fig. 3).

One site with fossils of *Mammonteus primigenius* is known from Hokkaido; a second site has not yet been properly established**.

1. Erimo Cape, Hokkaido (Minato, M.M., 1955).

The following are related to the extreme southern sites on the continent:
2. Hegan, Heiluntszyan (Chow, M.M. et al., 1959)***.
3. Youngfengzheng, Huachuan (Chow, M.M. et al., 1959).
4. Dagudunhe, Zhulian (Chow, M.M. et al., 1959).
5. Mnshan' (Chow, M.M. et al., 1959).
6. Vantsin, Girin (Chang, C.K., 1964).
7. Shangyixiang, Yan'tszi (Chow, M.M. et al., 1959).
8. Yan'tszi (Chow, M.M. et al., 1959).
9. Lyukhe (Chow, M.M. et al., 1959).
10. Longwangtang (Chow, M.M. et al., 1959).
11. Chaoyan (Chow, M.M. et al., 1959).
12. Chaoyango, Chifyn (Chow, M.M. et al., 1959).
13. Xuanhua (Chow, M.M. et al., 1959).
14. Tszygan, Sychuan' (Pei, W.C. and Woo, J.K., 1957).

*Names of Chinese sites not found in the big Soviet World Atlas were retained in English in order to avoid inaccuracy in transliteration into the Russian script (Editor's note).

**A fossil molar of *Mommonteus primigenius* from another site in Hokkaido has the same color as the fossils from Harbina and possibly from Heiluntszyan. Besides this doubtful find, another molar was found at the bottom of Tsugar Strait (reported by Hasegawa, National Scientific Museum, Tokyo).

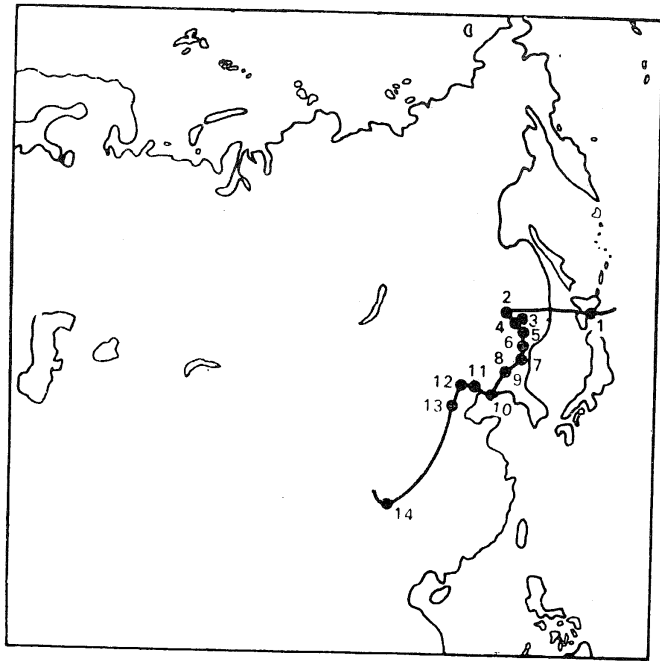***Chinese papers were translated by Ting-Kuo-Li, Berlin.

Fig. 3. Southern limit of distribution of mammoths—*Mammonteus primigenius* (Blumenbach) in East Asia in Late Pleistocene. Here and afterwards names of sites are numbered for easy reference in text (Editor's note).

II. COELODONTA ANTIQUITATIS (BLUMENBACH). WOOLLY RHINOCEROS

The schematic map (Fig. 4) giving the southern limit of distribution of *Coelodonta antiquitatis* in East Asia in the Late Pleistocene at once shows the progress of our knowledge in recent years. According to the new finds the southern limit of distribution of rhinoceros runs from the Harbina region to Lanchzhoi (Hansu province).

1. Vantsin, Girin (Chang, C.K., 1964).
2. Wukeshu, Zhoujiayoufang (Chow, M.M. et al., 1959).
3. Yushu, Jilin (Chow, M.M. et al., 1959).
4. Yushuhsien, Kirin (Pei, W.C., 1956).
5. Chienping District, Liaoning (Woo, J.K., 1961).
6. Chzhoukoudyan', locality 24 (Chia, L.P., Chao, T.K. and Li, Y.H., 1959).
7. Wuzhutai, Xintai, Shan'dun (Wu, Kh.Z. and Zong, G.F., 1973).
8. Sin'tsai, Henan' (Pei, W.C., 1956).
9. Sharaossogol, Ordos (Boule, M. and Teilhard, P., 1928).
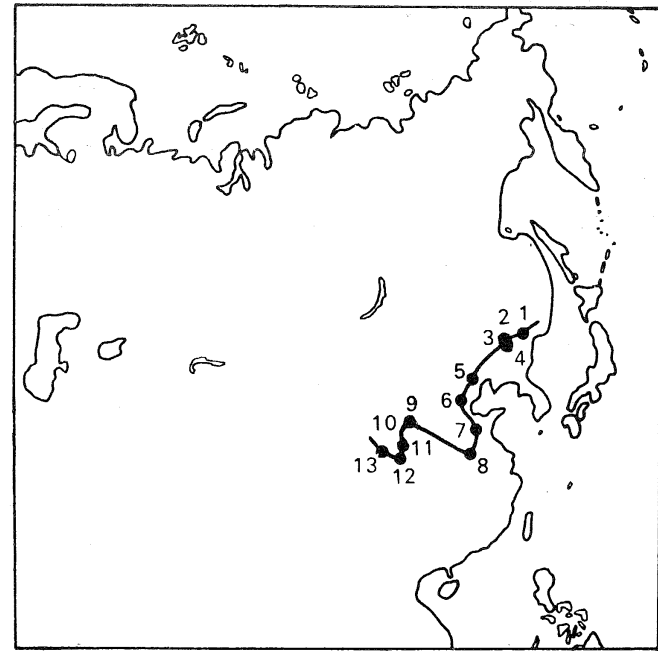10. Siki, Ninsya (Chow, B.S., 1961).

Fig. 4. Southern limit of distribution of woolly rhinoceros—*Coelodonta antiquitatis* (Blumenbach)—in East Asia in Late Pleistocene.

11. Kingyang, Hansu (Hu, C.K., 1962).
12. Toutaoyuan, Yenyang (Hsieh, H.H., 1960).
13. Sochinssu, Lan'chzhoi, Hansu (Chow, M.M., 1959).

Both the species—*Mammonteus primigenius* and *Coelodonta antiquitatis*—are typical of the Late Pleistocene. They had similar distribution in the south of the Far East. As before, the problem of the eastern limit of migration of the rhinoceros in eastern Siberia remains unsolved. On the basis of the pale-ontological data, *Coelodonta antiquitatis* is not found to extend up to the eastern coastal plains of Siberia and it never crossed the Beringian or Tatar Land Bridge (Fig. 2). If the limited distribution of the woolly rhinoceros to the east is to be explained by the ecological peculiarities of the animal it can be compared with *Elasmotherium*. *Elasmotherium* was the Middle Pleistocene Central Asian rhinoceros which throughout its history never extended beyond the coastal Atlantic or Pacific Ocean. This distribution might be explained by the specific ecology of *Elasmotherium*. In contrast to the latter, *Coelondonta antiquitatis* in Europe migrated to the Atlantic and to the North Arctic Ocean in Far North Siberia.

III. MEGALOCEROS (SINOMEGACEROS) ORDOSIANUS (YOUNG). LATE PLEISTOCENE EAST ASIATIC GIANT DEER

The following typical forms of the Late Pleistocene Euro-Siberian faunal complex, such as *Megaloceros* (*Sinomegaceros*) *ordosianus* (Young), representative of Palearctic deer, never reached the New World and did not cross the Yangtze River to the south.

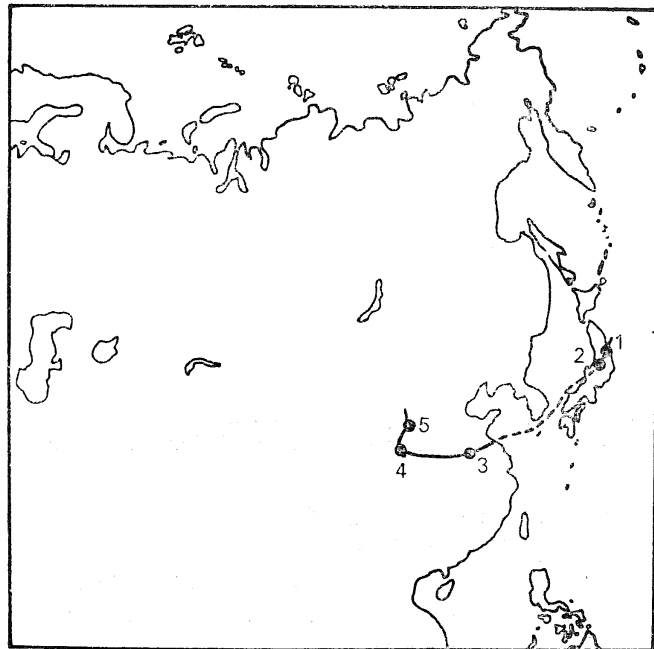The southernmost site of this deer is shown in the map (Fig. 5).

Fig. 5. Southern limit of distribution of giant deer *Megaloceros* (*Sinomegaceros*) *ordosianus* (Young) and *Megaloceros* (*Sinomegaceros*) *ordosianus minor* Kamei in East Asia in Late Pleistocene.

Dwarfed sub-species of giant deer, *Megaloceros* (*Sinomegaceros*) *ordosianus minor* Kamei, detected at the following sites, are known from Japan.
1. Kanamori, Hanaidzumi (Matsumoto, H. and Mori, H., 1956; Kamei, T., 1958, 1961).
2. Totchu, prefektura Nagano (Kamei, T., 1961).

Seven more fossil-bearing sites of *Sinomegaceros* (Kamei, 1961) are known from Japan. Some of them may well belong to the above dwarf form.

The following sites marking the southern extremity of distribution of *Megaloceros* (*Sinomegaceros*) *ordosianus* (Young) are reported from the Asiatic continent:

3. Sin'tsai (Pei, W.C., 1956; Kahlke, H.D., 1957).
4. Sifoungchen, Tsin'yan (Ting, M.L., Kao, F.T. and An, T.S., 1965).
5. Sharaossogol, Ordos (Boule, M., Breuil, H., Licent, E. and Teilhard, P., 1928; Teilhard, P. and Pei, W.C., 1941; Kahlke, H.D., 1957).

IV. ALCES ALCES (LINNAEUS). MOOSE

Several years ago it was established that fossils of *Alces alces* (L.) were present in the Late Pleistocene deposits of Japan. They were detected at the following sites (Fig. 6):
1. Kumiyashi—Do Caves, prefectura Gifu (Hesegawa, Y. and Matsushima, Y., 1968).
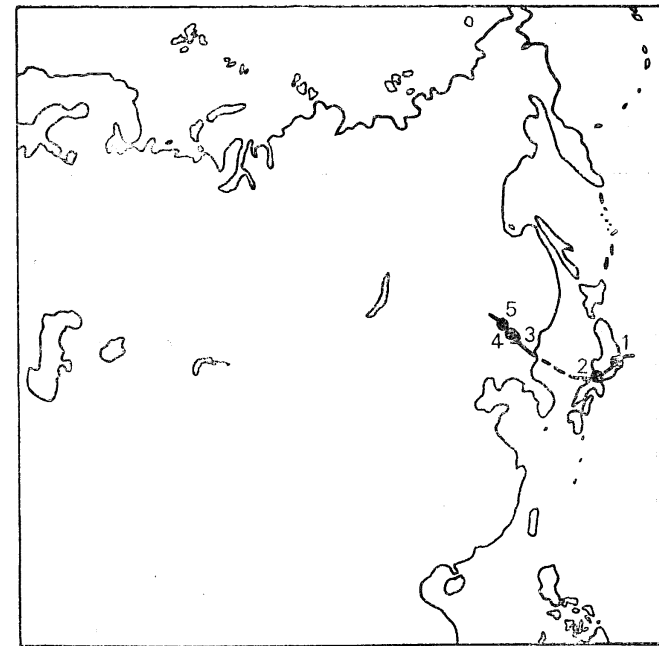2. Kavaraguchi, prefectura Kanagawa (Hasegawa, Y. and Matsushima, Y., 1968).

Fig. 6. Southern limit of distribution of moose—*Alces alces* (Linnaeus) in East Asia in Late Pleistocene.

The extreme southerly sites of moose on the Asian continent are the following:
3. Yushu, Jilin (Chow, M.M. et al., 1959).
4. Wukeshu, Zhoujiayoufang (Chow, M.M.).
5. Harbin (Tokunaga, S. and Naora, N., 1934).

On the basis of the fossils so far known, the Japanese sites of the Late Pleistocene *Alces alces* (L.) are considered to be the southernmost in the Far East.

V. EQUUS HEMIONUS PALLAS, DZHIGETAI, KULAN

Equus hemionus nipponicus Shikama and Onuki, Japanese Late Pleistocene "Kulan"

Of the family of horses, *Equus hemionus nipponicus* Shikama and Onuki, a more or less dwarfed sub-species *Equus hemionus* Pallas, is found to have been distributed all over Japan in the Late Pleistocene period. Fossil remains are known from the following sites (Fig. 7):

1. Jinomori, Ofunato, prefectura Ivate (Shikama, T. and Onuki, Y., 1962).
2. Sakashita, Takata, prefectura Ivate (Shikama, T. and Onuki, Y., 1962).
3. Omine, Tajiri-machi, Toda-gun, prefectura Miyagi (Shikama, T. and Onuki, Y., 1962).

The southern limit of distribution of Late Pleistocene *Equus hemionus* Pallas includes the following sites on the Asian continent:
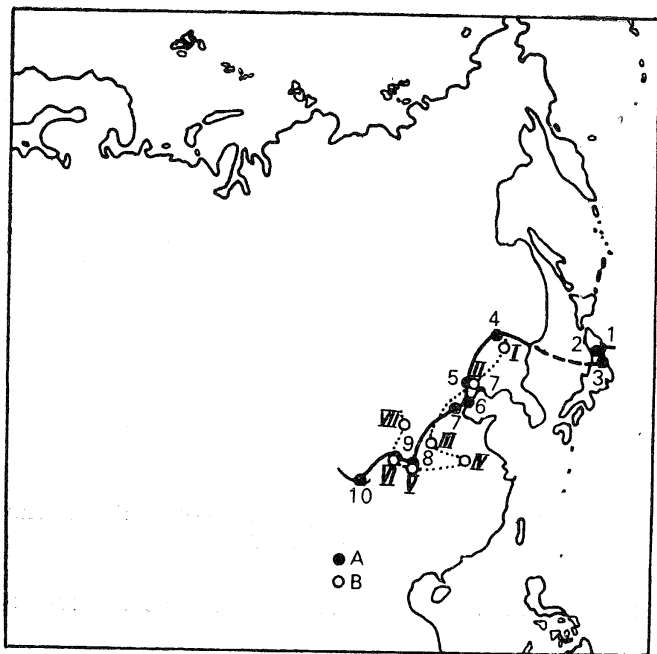

Fig. 7. Southern limit of distribution of Kulans [(*Equus hemionus* Pallas and *Equus hemionus nipponicus* Shikama and Onuki)—(A) and Przewalskii horses (*Equus przewalskii* Polyakov)—(B) in eastern Asia during Late Pleistocene.

4. Harbin (Tokunaga, S. and Naora, N., 1934).
5. Chienping, Liaoning (Woo, J.K., 1961).
6. Chaotsun, Chen'an, Hebei (Pei, W.C., Huang, W.P., Chiu, S.L. and Meng, H., 1958).
7. Chzhoukoudyan', Upper caves (Pei, W.C., 1940).
8. Lan'tyan', Shen'si (Dai, E.J. and Chi, H.G., 1964).
9. Kingyang, Hansa (Ting, M.L., Kao, F.T., An, T.S., Chu, X.T. and Li, C.L., 1965).
10. Sochinssu, Lan'chzhoi, Hansa (Chow, M.M., 1959).

VI. EQUUS PRZEWALSKII POLYAKOV—MONGOLIAN WILD HORSE

The Przewalskii horse in the Late Pleistocene most probably never crossed the Tatar Land Bridge. Fossil remains of this small horse are confined to the Asian continent. Figure 7 shows the southernmost occurrence.

I. Yushu, Jilin (Chow, M.M. et al., 1959).
II. Chienping, Liaoning (Woo, J.K., 1961).
III. Nanlian, Houma, Shan'si (Wang, T.Y., Li, Y.J. and Hu, J.R., 1959).
IV. Sin'tsai, Henan (Pei, W.C., 1956).
V. Lan'tyan', Shen'si (Dai, E.J. and Chi, H.G., 1964).
VI. Kingyang, Hansu (Hu, C.K., 1962).
VII. Sharaossogol, Ordos (Boule, M. and Teilhard, P., 1928).

VII. BISON PRISCUS (BOJANUS) S.L. (WITH SEVERAL SUB-SPECIES)

Late Pleistocene, Euro-Siberian bison

Recently fossil remains of *Bison priscus* Boj. s.l. were detected on Hokkaido Island as well as in Kanamori, Hanaidzumi, Japan (Fig. 8).

1. Around Urakawa, Hokkaido (Hasegawa, Y., Obata, I., Honda, H. and Fugichima, Y., 1972).
2. Kanamori Hanaidzumi (Matsumoto, H., Mori, H., 1956).

On the continent the southernmost fossil remains of bison are the following:

3. Yushu, Jilin (Chow, M.M. et al., 1959).
4. Wakeshu (Chow, M.M. et al., 1959).
5. Chienping, Lyaodun (Woo, J.K., 1961).
6. Lan'tan', Shen'si (Dai, E.J. and Chi, H.G., 1964).

From the above résumé on the southern limits of distribution of some mammals which are typical elements of the Euro-Siberian faunal complex in eastern Asia, it can be noted that this line ran from Japan and Korea up to
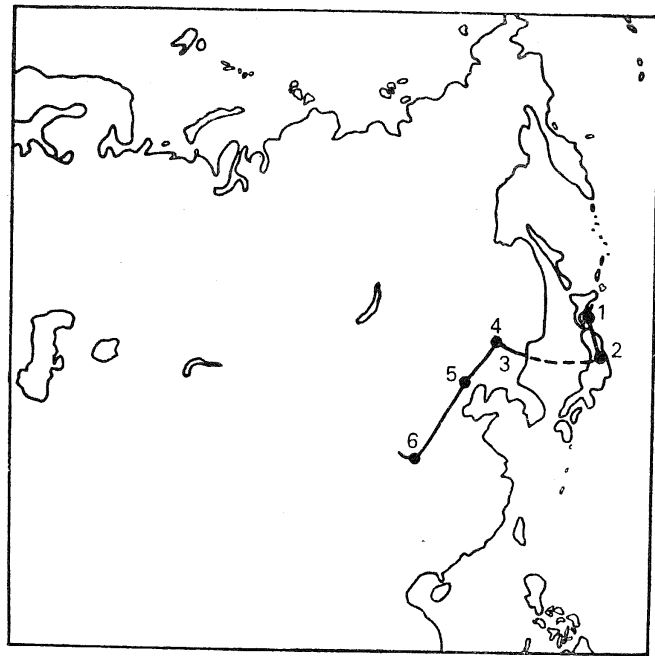
Fig. 8. Southern limit of distribution of *Bison priscus* Bojanus sensu lato (with several sub-species) in eastern Asia during Late Pleistocene.

Hebei Province, China. To the south it extended right up to the northeastern province of Szechwan during the Late Pleistocene.

During the last glacial epoch (Wurm, on the Alpine scale) typical mammals of the Euro-Siberian faunal complex not only crossed the Beringian Land Bridge in the north but also the Tatar Land Bridge. In Japan they were more or less concentrated as a Late Pleistocene association of Sino-Malayan type which migrated into Japan along the earlier southern Land Bridge during the early phase of the Middle Pleistocene.

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Some New Data on Faunal Exchange across the Bering Land Bridge

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The author compares some Eurasian and North American gallinaceous birds and small mammals on the basis of osteological, paleontological considerations.

From this point of view, among the smaller Tetraonids, unambiguously of North American origin, the reinvasion by members of the genus *Lagopus* may be conceived as two waves, similar to that of man. New paleontological finds originating from Middle Europe speak of the Eurasiatic origin of Hazel grouse (members of the genera *Tetrastes* and *Bonasa*). The close relation of the Eastern Asiatic and North American spruce grouse (*Falcipennis* and *Canachites*) is proved by a detailed osteological comparison.

Some newly found remains of the members of the small mammal family Eomyidae, especially *Leptodontomys*, in Europe show great similarity with North American forms.

Finally the odontological features of the Eurasian and North American sagebrush voles (*Lagurus*) are compared, showing peculiar specialization.

The discussions and papers on the problem of faunal exchange across the Bering Land Bridge are so extensive that it is practically impossible to cover the entire literature dealing with this problem. These papers deal with individual faunistic elements which are known from different stratigraphic horizons starting from the Paleogene through the Late Quaternary period. Moreover, extensive connections between the flora and fauna of the two continents have been detected. Sampling the literature on this complex problem, we became aware of a glaring fact: two vertebrate groups have not received the attention they deserve.

The first group comprises birds. The study of birds is interesting not only in the context of zoogeographic analysis but also from the paleontological and osteological points of view.

The second such group comprises certain small mammals. The results of

The Role of Beringian Land in the Development of Holarctic Mammalian Fauna in the Late Cenozoic

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Comparative study of Old and New World living and fossil mammals is a traditional source of information on the Beringian interrelations of the Holarctic faunas. But in recent times paleontological evidence directly from the area of exchange, i.e. from the Far North-East of the USSR and from Alaska, is especially important. The first Early and Middle Pleistocene mammalian localities have been discovered here recently, the first Late Pliocene finds have been made, and the studies in the paleogeography of this area show remarkable progress. But correlation of mammal-bearing deposits with the marine sequence of the Bering Strait zone making the stages of disruption of the land connection is rather difficult due to the different tectonic and paleogeographic history of this zone and the rest of the region of continental shelf and the peripherical lowlands of the Arctic coasts of Asia and North America. This vast region that had the major role in the history of Beringian faunal exchange, it is proposed to name Beringida. The narrow active zone of Beringida within which the land bridge and the strait alternately appeared we name Beringia.

The main stages of faunal evolution in Beringida are discussed— Middle-Late Pleistocene, Early Pleistocene and Late Pliocene. Present evidence suggests that during the Late Cenozoic the fauna of Beringida (including Alaska) developed as one. The stages of disruption of the land connection in the narrow zone of Beringia had a relatively minor role in the history of this fauna. The early development of cooling in the high latitudes caused the evolution of subarctic mammalian fauna in Beringida. Since the Early Pleistocene this fauna can be considered as cryoxerotic ("periglacial"). Due to the progressive general cooling of the Holarctic climate the cold-resistant Beringidan species had the opportunity of dispersal to the temperate latitudes of both continents.

Recent data support A. Turgarin's idea of the autochthonous evolution of the cold-resistant ("Arctic") fauna within Beringida. During the Late Cenozoic we must consider Beringida not as a land bridge across which an intercontinental faunal exchange took place, but as an independent (though closely related to the Palearctic) region in which a peculiar fauna evolved that repeatedly dispersed into the Old and New worlds.

TRADITIONAL AND NEW SOURCES OF INFORMATION ON BERINGIAN CONNECTIONS OF HOLARCTIC MAMMALS

The problem of Beringian land is one of the fundamental problems of the zoogeography and history of Holarctic fauna. The notable similarity of recent fauna of Eurasia and North America gave rise to the concept of the Bering Land Bridge and it is still a basic source of knowledge of trans-Beringian connections of Palearctic and Nearctic mammals. The use of modern methods of systematics and zoogeography including genetic connections (Vorontsov, Lyapunova, 1973) makes the extrapolation of relations of past and present forms more objective so that the present approach becomes possible. The second traditional source of information is the comparative analysis of well-studied fossil fauna of the temperate latitudes of Eurasia and America. This method gave and still gives very valuable knowledge of the history of Beringian connections (Simpson, 1947; Kurtén, Tobin and others—this collection). Research on the phylogeny of groups, representing the Old and New worlds, is especially important in this context.

It is now not only possible to conceive of a faunistic exchange for a prolonged period but also to subdivide it into several phases (Repenning, 1967). The traditional sources of information, however, cannot guarantee the necessary details of the history of faunal connections. Despite the great advance in the study of the relations of recent mammals of the Old and New worlds, the historical interpretation of the chronology of these data was always an unsurmountable factor and remains a weak link even today. Even the study of recent species from the Beringian region itself offers a better insight into the history of the first ten thousand years.

Phylogenetic study of representatives of Palearctic and Nearctic forms from Late Cenozoic deposits in the temperate latitudes of both continents can establish the time of migration only within wide limits. This is because the correlation of deposits including the fauna in different hemispheres is quite tentative in nature. Besides, many representatives of Palearctic and Nearctic forms are separated from each other by distinct morphological discontinuity. It is possible that only the intermediate forms served as Beringian immigrants; but they are not known to us.

Studying the fauna of temperature latitudes, paleontologists got used to regarding the Beringian land as a reliable transport route which allowed transfer of animals from one continent to the other. The best postulate in this respect was that the Bering landmass acted as "a cold filter". This led to a deviation from the actual natural conditions for this extensive country with its unique landscape and animal population.

Without detracting from the significance of the two traditional approaches it can thus be said that further progress in decoding Beringian faunal ex-

change is not possible without specific paleontological studies in the Beringian land. This is in fact the new significant source of information and during the last decade it has yielded quite interesting data. But it is also encountering considerable difficulties.

PRINCIPAL PROGRESS AND DIFFICULTIES IN STUDYING PALEONTOLOGICAL EVIDENCE OF THE BERINGIAN LANDMASS

The discovery of Middle Pleistocene (Péwé, Hopkins, 1967) and Early Pleistocene (Sher, 1967, 1971; Guthrie, Matthews, 1971) mammalian fauna in North-East Asia and Alaska can be considered a very important achievement of the past decade. Only fauna of the Upper Paleolithic-Early Labreinian stages are known so far throughout the Polar Holarctic regions. Their ages are not more than 100-200 thousand years. Therefore the fossils of the most recent years in fact opened a new era in the study of Bering land connections between the Old and New worlds.

During the last few years immense progress has been achieved in correcting the paleogeographic picture of the Far North in the Late Cenozoic period. Earlier concepts were replaced and it was accepted that coniferous-broadleaved forests became extinct even earlier (toward the beginning of the Pliocene) (Baranova et al., 1968; Biske and Baranova—this collection). Similarly the age of taiga forest of recent type (Early Pliocene, Hopkins et al., 1971) and the even earlier appearance of a Holarctic belt and formation of permafrost were established (Sher, 1971; Arkhangelov, Sher, 1973; Kartashova, 1974). These new geological and paleogeographic data completely revise our thinking about the setup when faunal exchange took place between the continents in the Late Cenozoic period.

The process of decoding the natural conditions of the Late Pleistocene period has advanced considerably. The conformity of fauna in the north of the two continents as a whole was responsible for this. The development and better insight of the theory of cryoxerotic (periglacial, tundra-steppe type) biocenosis was promoted not only by geological and paleontological studies but also by the study of recent relict steppe families of the North-East USSR (Yurtsev, 1974). For some reason this theory was for long denied recognition in North America. But with the publication of the paper by R.D. Guthrie containing his paleoecological analysis of the Late Pleistocene fauna of Alaska and earlier similar representatives this theory received its due place (Guthrie, 1968a, b). While introducing significant modifications and corrections into the generalized model of faunistic exchanges across the Bering Land Bridge, all these data did not, however, offer a detailed chronology of the exchange. This is connected with certain paradoxical situations that appeared in the course of the rapid accumulation of geological materials on the Bering Strait region.

A series of terraces, containing marine sediments and fixing the epoch when the Bering Land Bridge was absent, was established on both sides of the strait. However, the formations of continental origin in the strait regions were studied very poorly. In particular, mammalian fossils, except for singular finds of Late Pleistocene age, were not reported in them. Even singular exceptions of this rule, such as the Cape Deceit section on the coast of Kotsev Gulf with three horizons of different ages containing mammalian fauna, threw little light on the problem of correlation. The only marine bed in this region belongs to the Late Pleistocene Pelukian transgression (Guthrie, Matthews, 1971).

Marine terraces extend to the west for 200-300 km from Bering Strait. Buried marine deposits are found at some distance farther, whereas reliable marine sediments are absent from Ayon Island. They are absent from the marine coastal depressions, i.e. at the point where rich mammalian fauna are known at various Pleistocene horizons. Thus the zones of development of marine sediments and sections with mammalian fauna are regionally disconnected and correlation of the history of continental fauna with the history of transgression is quite difficult.

A simplified assumption was to be found in literature on Bering land. This propounded that the regression in the strait region corresponded with glaciation and transgression took place during the interglacial period. But it is established that certain transgressions coincided with glaciations, whereas others coincided with warming of the climate (Petrov, 1966). And the glaciations themselves were mainly localized in the strait region, in Chukotka and Alaska. Consequently, the climato-stratigraphic data do not make correlation of the transgression zones with more westerly regions any easier.

Therefore the regions which taper right into the Bering Strait bear information mainly about stages when there was no connection between the continents and hence there is no history of mammalian fauna. First of all, the regions where these fauna are studied are widely separated; secondly, they appreciably differed from the strait region in their own history, which showed no scope for glaciation, nor did they stand very high above sea level. Can these territories be included within the Beringia region? This problem requires special attention.

GEOGRAPHICAL SETUP OF BERINGIAN LAND (TWO CONCEPTS). BERINGIA AND BERINGIDA

At the beginning of this century zoogeography helped in the framing of the idea of an extensive hypothetical landmass connecting Asia with America. From the beginning our understanding of the Bering landmass had twofold significance in the zoogeographic sense in the USSR. P.P. Sushkin (1925), A.Ya. Turarinov (1929), B.K. Shtegman (1936) regarded Beringia not only

as a bridge between the continents, i.e. as a path for faunal exchange, but also as a region where new types of fauna appeared (tundra and taiga-types)*. Thus Beringia stood for a quite extensive zoogeographic region and not a specific paleogeographic country, whose history was so far little known.

In light of recent data a distinct contrast between the dynamic zone of the Beringia isthmus (or Bering Strait) and the rest of the more stable shelf region was established. Recent floras bring this contrast out more distinctly (Yurtsev, 1970). As a result of the complex and unique geographic conditions of the Bering isthmus, occurring at the junction of two continents and two oceans, it can be surmised that rapid historical development occurred here. It was a combination of oceanic elements of varied origin with continental relict elements that accumulated in the isthmus region after repeated phases of extension of the landmass. The Lena-Kolyma depression in the northern extremity belongs to the opposite zone. This is a fragment of Polar shelf and shows many things in common with North Angarida in the botanical and geographic sense. On this basis B.A. Yurtsev (1973, 1974) suggested excluding almost the entire East Siberian shelf and marginal depressions of Polar coastal regions from the geographic framework of Beringia. He suggested delimiting Beringia in the sector occurring between the hilly right bank of the Kolyma (and the valley extending below water level) to the west and the lower course of the Mackenzie River to the east.

This area was named by B.A. Yurtsev "Great Beringia" or "Beringian Holarctic Sector". He subdivided still narrower zones in it, such as "Little Beringia" (for the limiting regression epoch) and the "Central Beringian Subsector" (from transgressional epochs). The boundary between these zones lies to the south of the Amguema River to the west and Cape Barrow to the east. According to B.A. Yurtsev the Beringian landmass and Beringian isthmus fall within this geographie framework. The Asian territory of the Beringian landmass is bound, with respect to the position of the coastline, by two limits—by the Kolyma River mouth and the Amguema confluence. The spatial framework of Beringia—a paleogeographic country whose center lay in the dried-up Bering Strait (Yurtsev, 1973)—might have changed within this framework.

The concept of a "narrow" Beringia, suggested by B.A. Yurtsev, is an altogether new idea and differs from the classical concept of A.Ya. Tugarinov and other zoogeographers. We believe that B.A. Yurtsev did not properly evaluate the important role of a large part of the East Siberian shelf and the Lena-Kolyma marginal depressions in the history of Beringian connections.

The recent position of the coastline can be regarded as one of the deepest transgressions that took place in the Pleistocene. Possibly this condition

*In this context the zoogeographic understanding of Beringia is homologous with the botanical-geographic understanding of the Eoarctic (Tolmachev, 1932-35).

largely determines the unique nature of the present-day flora of the Beringian sector. The transgressing sea extended right up to the Anyui-Chukotka uplands and isolated the coastal lowland from the Bering Strait. However, from the peculiarities of shelf relief, the connection of these two regions can be established even when the sea level was rather low.

Let us illustrate this idea by examples relating to the past epoch of continental connection, whose paleogeography is usually reconstructed on the basis of present-day bathymetry of the shelf. By notionally lowering the sea level by only 50 m, and not by 100 m or 200 m as is normally done, two narrow dry isthmuses are caused to appear in the Bering Strait (Greager, McManus, 1967). A huge landmass is exposed along the north coast. The minimum extension of this landmass is 400 km from north to south and the maximum extension nearly 800 km. This landmass as a whole appears in the strait region, leaving the Chukotka basin underwater and nearly covering the Alaska shelf north of 70° latitude N. The Siberian and Alaskan shelves are divided to the north only by a narrow patch of Chukotka basin which is the northern section of Hope Sea Bella canyon. Together with the plains of the bordering lowlands, the shelf landmass 50 m below sea level forms a region which almost equals the whole of North-East Asia in area (Fig. 1).
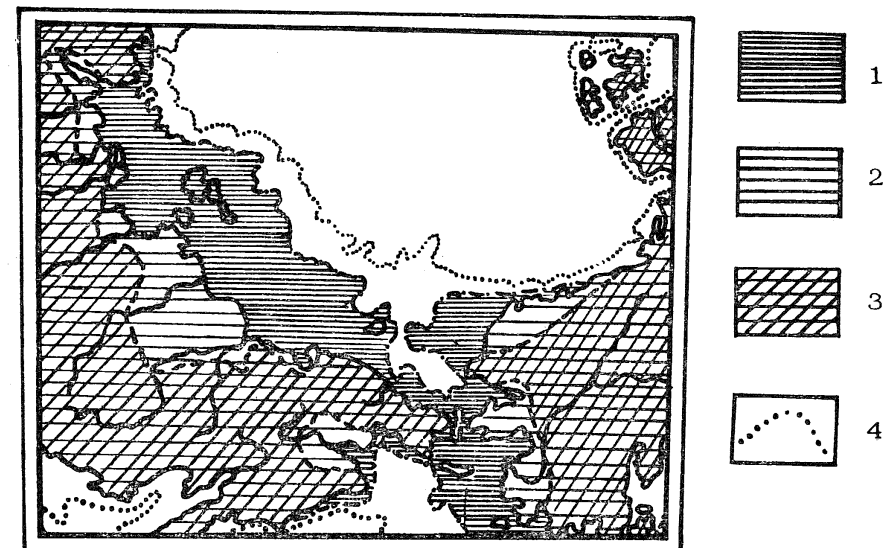

Fig. 1. Configuration of Bering land with lowering of sea level by 50 m below present-day level.

1—Dried-up portion of shelf; 2—Marginal depressions of continents; 3—Regions of mainly hilly relief; 4—Boundary of continental shelf (at 200 m isobath). Isobath 50 m is shown in hypsometric map of USSR on 1: 2,500,000 scale as well as in maps in paper by Greager and McManus (1967).

Moreover, if the sea level fell by only 35 m before the land connections (land bridge) appeared there would have existed an extensive and continuous band of Arctic depression extending from Taimyr to Wrangel Island (Greager, McManus, 1967, Fig. 4). The shelf protruding out of the sea contained an extreme depression zone of organic composition, dominated by families of vegetation and animals of the types found to predominate over here. The biocenosis of the North Siberian plain extended over wide bands of marginal depressions right up to the Bering Strait even before the land bridge could appear. It gave rise to a constant potential of continental type which quickly covered the continents at the time of connection. Faunal exchange across the isthmus from the outset was under the influence of this potential. Therefore we arrive at a conclusion as to the definite role of the marginal depressions of the polar coast of East Siberia inhabited by fauna in the history of Bering faunal exchange. This is fully confirmed even today by paleontological data on the identity of the mammalian fauna of these depressions with those of Alaska*.

This important role of the marginal plains of East Siberia was enhanced by the more stable continental regime of this zone in the Pleistocene. Geological and paleontological data suggest that transgression in this zone did not extend farther south of the present-day coastline and in all probability did not cover the shelf completely. Even the easternmost outpost of the shelf landmass, known as the Wrangel Islands, does not include any Pleistocene marine terrace (Kiryushina, 1955). It is interesting that faunistic data show that the Wrangel Islands were connected with the continent during some of the transgressions in the strait region (Patrovskii, Yurtsev, 1970).

All these facts lead us to the idea that by analyzing the history of this part of the Holarctic the entire continental shelf from Taimyr to Alaska in the marginal continental depressions tapering into it should be regarded as a single country. A relatively narrow dynamic zone is isolated within this extensive country. The sea level varied in this zone and land bridge and strait alternated. The impact of wind and the waterbody of the Pacific Ocean (in particular, the appearance of glaciation on the landmass) operated to some degree or other. Spatially this zone corresponds with B.A. Yurtsev's Central Beringia Sub-sector; it is confined within the latitude of the Amguema River mouth and the western extremity of the Chukotka basin in Asia.

Since this zone is directly connected with the Bering Strait and corres-

*The role of the so-called "Pacific Beringia" (Sher, 1971, p. 130) was perhaps somewhat different, i.e. the shelf landmass to the south of Bering Strait, the south coast of which was subjected to the warm, mild effects of the Pacific Ocean. This coast was the most reliable path of migration for oceanic and, possibly, forest elements. Let us only note that the "southern path" probably had secondary significance and existed only for a short period compared with the "northern path". The greater depth of the shelves of the Bering Sea and its more active history are indirect evidence for this.

ponds with the Bering Land Bridge it would be quite correct to name it Beringia. The entire extensive region of shelf, plain and marginal depressions of the north of East Siberia and America we propose to call Beringida, as it was first named in the Russian language [in the translation by V.L. Bianka of the book by V. Kobel't (1903), p. 13]. It is proposed to preserve the name "Beringian land" as a term that can be freely used.

Therefore Beringida stands for the paleontological country covering the continental shelves of the Laptev, East Siberian, Chukotka and Bering seas together with the marginal depressions of North-East Asia and Alaska tapering into it and the areas surrounding the low hilly regions with extensive depressions (Fig. 2). Despite certain zonal and regional variations of climate
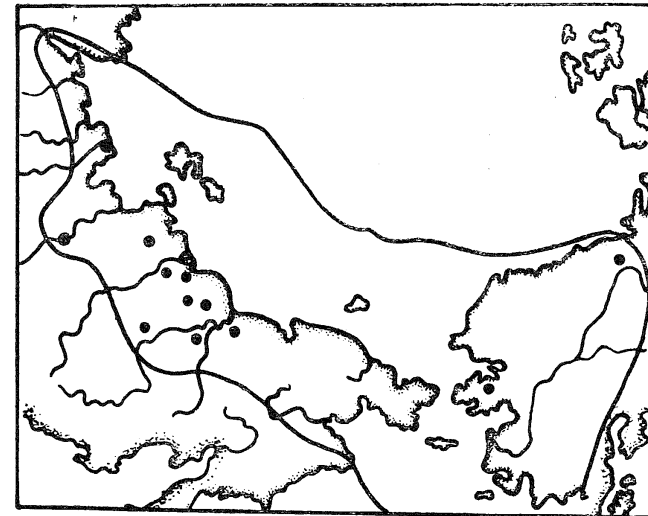

Fig. 2. Distribution of locales of Early Pleistocene mammalian fauna in Beringida territory. Solid line demarcates contour of Beringida as understood by author.

and landscape, inevitable over such an extensive territory, the most distinctive feature of Beringida was its entirety, as represented by the absence of any orographic barrier dividing it. It is also manifested by its generally monotonous landscape and climatic conditions*. Owing to this homogeneity, sedimentation was also homogeneous all over its plain areas throughout the Pleistocene period. Beringida faunas were amazingly similar. Similarly the

*It is clear from this that Beringida is not only spatially but also in its own way different from the "Megaberingia" of B.A. Yurtsev. Megaberingia includes the entire northeast of Asia and northwest of North America. The idea of differentiating it was put forward by B.A. Yurtsev because of its nonhomogeneity (Yurtsev, 1974: 146).

role of the fauna was also the same, not only between Siberia and Alaska but also between the Yano-Kolyma depression, which is now dissected from East Siberia by the arc of the Verkhoyansk Kolyma hill range, and Central Siberia. According to the proposal, Beringida might be considered not only as a country connecting Asia with America, but also as a unique zoogeographic unit with which, as we will try to show hereinafter, the history of sub-arctic fauna is very closely associated. This was very confidently proposed by A.Ya. Tugarinov. As we understand it, Beringia is part of Beringida. It is extremely dynamic and unique because most of its biota and particularly its fauna were subjected to the dominant role of the country as a whole. Hence we feel that these two outwardly contradictory concepts of Beringia—those of A.Ya. Tugarinov and B.A. Yurtsev—can be unified.

Let us now examine the three stages in the faunal development of Beringida—namely, Late Pliocene, Early Pleistocene and the second half of the Pleistocene in which we would include the Middle and Late Pleistocene. For convenience of discussion let us start with the last, which is the oldest and best studied stage, because very little is known about the Pleistocene fauna of Beringida.

CRYOXEROTIC (PERIGLACIAL) FAUNA OF BERINGIDA IN THE SECOND HALF OF THE PLEISTOCENE

In the second half of the Pleistocene, especially in the Late Pleistocene, the mammalian faunas of Beringida are quite well known. They can now be considered to be finally interpreted as faunas of a unique flourishing complex with predominance of herbivorous animals. These were present under a cold, sharply continental climate (Vangengeim, 1961; Sher, 1973; Guthrie, 1968a, b). The enormous fossil remains of herbivorous animals indirectly prove their presence in large numbers. Besides, there are large amounts of direct paleontological evidence as to the existence of an extensive Beringida plain which was covered by treeless vegetation of "tundra-steppe" type with large-scale association of herbaceous plants. Data on the fossil remains of food of Pleistocene mammals are of great interest. Gramineae, various types of grasses and *Artemisia* were the food of the Berezov mammoth, Bytantaiskii rhinoceros, Selerikanskii horse, and bison from the Krestovka River area (Kupriyanova, 1957; Garutt and Metel'tseva, 1970; Metel'tseva, report of Jan. 25, 1972; Sher, 1971).

The intensive development of frost fissures and growth of polygonal and vein-type ice along with extensive growth of associations of grasses show that the climate of the Late Pleistocene differed considerably from the cold, almost snowless winter and quite warm, dry summer. This provided the necessary impulse of heat for the flourishing of steppe vegetation. The landscapes of North-East Yakutia with ultra-continental climatic conditions

(Verkhoyan valley type) are closely similar to the unique Beringida landscapes. This interpretation of landscape-climatic conditions helps to explain not only the flourishing of an extensive population of herbivores, but also the presence of xerophilic species, such as saiga, tinsels, small-skulled fieldvole, insect fauna, such as *Cymindis binotata* F.W. among ground beetles; and *Stepanocleonus* sp. among weevils (Kiselev, 1974). The total absence of cold-resistant fauna can be understood from this point of view. These conditions encourage us to call the Late Pleistocene fauna of Beringida cryoxerotic type.

It is apparent that the presence of such fauna over extensive regions, including the recent islands on the shelf, was possible only because of the appearance of a large continental mass of dried-up shelf. The similarity of the Late Pleistocene fauna of North-East USSR and Alaska is so great that the Bering Strait cannot be considered as a zoogeographic boundary of high rank for this period. Recent faunal similarity of the two sides of the Bering Strait was inherited from this epoch. As a result of this the zoologists expressed their doubts about fixing the boundary of zoogeographic regions between Chukotka and Alaska (Chernyavskii, 1973).

The degree of endemism of Pleistocene fauna of Alaska and the East Siberian lowlands is low, and naturally lower on the Asian side. The problem of endemic forms not crossing over the Bering Strait is a special problem based on the identity of fauna. It can probably be solved with respect to each individual species (woolly rhinoceros, American mastodon; camel, smilodon and others) on the basis of the specific conditions required for its survival. It is to be noted that the entire range of Late Pleistocene endemic forms of Alaska was in all probability very small in numbers. Therefore, out of four locales in the Fairbanks region (Guthrie, 1968a) the faunal remains of mastodons and smilodons are known only from one site. Moreover, each represents less than 0.05 per cent of total individuals. Camels were, perhaps, more characteristic of the cryoxerotic fauna of Alaska and their fossil remains are known from all four sites. Even then they represent more than 0.05 per cent (0.1-0.3 per cent) of the individuals only at two places.

As usual there is no confirmation of the non-entry of the woolly rhinoceros into Alaska. We feel that its extensive distribution in the Beringida territory was due to the availability of fodder. During the last few years the author has observed a wonderful regularity in the distribution of fossil remains of the rhinoceros. Usually the depressions and extensive river valleys are found to be rich sites for Late Pleistocene fauna. Even at such places fossil remains of the rhinoceros are rare (usually less than 1 per cent), although their occurrence is constantly recorded. During the mapping program of VAGT at the Yukagirskii upland the geologists collected at the rate of 5-10 bones from a number of stations close together. Fossil remains of the rhinoceros were practically always present and their relative quantity quite

appreciable. Rhinoceros fossil remains with soft tissues were also reported from the hilly regions (the Bytantai and El'ga rivers). Thus it can be surmised that although the rhinoceros lived in the depressions, a larger number of them lived in the uplands and river valleys where they were not the only dominant species. At present it is difficult to say whether this was associated with more intersected topography having rocky substrata (for example, bolder beds) or with peculiarities of the vegetation. But it would be quite relevant to believe that some still unknown peculiar ecological distribution of the woolly rhinoceros rendered it quite distinct from the horses, bison and other animals that inhabited the western and eastern parts of Beringida. This would also explain why the rhinoceros did not cross the Bering Land Bridge.

Middle Pleistocene fauna of Beringida are little known compared with those of the Late Pleistocene period. Fauna of this stratigraphic interval are found in the Utkinskii bed in the Malyi Anyui (Sher, 1971) and Mastaa-khskii sands of the Chukchi River in the Kolyma lowland. The Mastaa-khskii sands may be quite extensively distributed in the coastal lowlands. The mammalian fossil remains from Cripple Creek and from other sites belonging to the Illinois (Péwé, Hopkins, 1967) can perhaps be tentatively correlated with the fauna of Alaska. Although the Middle Pleistocene faunas of Beringida are connected with lower stratigraphic horizons than the Late Pleistocene, they can be differentiated only on the basis of several more archaic forms of horse, mammoth, ungulate, lemming and, possibly, moose and musk ox. The rest of this complex is of the same type and the conclusions drawn with regard to the Late Pleistocene fauna of Beringida also apply to it.

The uniformity of Late Pleistocene fauna of the entire Beringida territory is quite high, and in all probability the number of endemic forms in the Illinois fauna of Alaska was not higher than that of the Wisconsin period. The relation of Beringida fauna with the fauna occurring in the interior of Asia and America is quite different. If all the known elements of Beringida fauna are widely distributed in the Late Pleistocene in Asia the temperate latitudes of America did not possess the Beringida forms until this time. Animals like the *Ovibos, Ovis, Dicrostonyx*, living in Alaska in the Illinois period, appeared in the temperate latitudes of America only in the Wisconsin period, and some of them (*Rangifer, Alces*) were totally absent throughout the Pleistocene period. This distinction of the Illinois fauna of Alaska with respect to other American regions can be explained by the fact that the basic boundary between the Palearctic and Nearctic fauna was not the Bering Strait. In fact, the mountains of Western Canada acted as a barrier and thus the absence of an "ice-free corridor" was aggravated for prolonged periods (Hopkins, 1967).

There are groups of animals of Asian origin (*Bison, Clethrionomys, Cerval-*

ces, Bootherium) which appeared for the first time in the central regions of North America during the Illinois period (Hibbard et al., 1965). But either they or their ancestors appeared in Beringida even earlier. Consequently they also surmounted some "restrictions" in the Beringida territory. They were thus late in being distributed beyond the limits of Alaska. These will be dealt with later.

Thus during the second half of the Pleistocene, which is equivalent to the appearance of the Upper Paleolithic complex in Eurasia and the Rancholabrian period in America, the fauna of the whole of Beringida (including Alaska) present us with a complete unit. These are quite intimately associated with Siberian fauna. Their relation with the American fauna is expressed by some Beringida forms which had migrated to the temperate latitudes of North America during the period when the corridor between the Laurentian and Cordillera glaciers* was open. Such migrational phases were perhaps several, or at least two, such as early- and late-Rancholabrian (Repenning, 1967). The cold-resistant nature of Beringida mammals shows that they did not migrate during the climatic optimum of interglacial periods, but mostly during their earlier phases. In all probability the Beringida forms were no competitors during migration over the ice-free periglacial territory. This is one factor that might explain the one-sided movement of the immigrants from Asia (more correctly, from Beringida) into America.

EARLY PLEISTOCENE FAUNA OF BERINGIDA AND MIGRATION TO TEMPERATE LATITUDES

As has been observed earlier, even the first Early Pleistocene finds in Beringida territory oblige us to take another look at this stage of faunal relations between the Old and New worlds. During the past few years the Early Pleistocene Olerskii fauna, known earlier only from the Chukchi River area, have been found practically all over Beringida territory (Fig. 2). They have been detected from the valleys of the Sededema, Krestovka, Kolyma, Alazei, Khomus-Yuryakh and Keremesit rivers. Numerous sites of Olerskii fauna were detected by geologists of the Yakutia Geological Organization in the Central-Yan region; isolated finds were reported from the Omoloy and Lena river valleys. Primitive lemmings of the tribe Dicrostonychini (Zazhigin, this collection), lemmings of the genus *Lemmus*, voles of the Allophaimys group, archaic ox of the genus *Praeovibos* (two species) and reindeer were characteristic representatives of this fauna. All these forms can be considered as autochthonous subarctic and typical for the Olerskii fauna. The second group comprises north boreal, widely distributed species of open lands

*The conclusions of American geologists as to the compact glaciation of northern North America and the joining of the two glacial covers are here accepted as an axiom.

(without forest), known to have existed in the temperate, and cool Mindel faunas of Europe. These occur abundantly in Beringida as well. These are represented by large archaic horses of the sub-genus *Plesippus*, moose from the broad forehead group (genus *Praealces*), bison of the type *B. schoetensacki*, *Zorgeliya* and others. Individual groups of archaic elephants with mammothlike features, a unique type of ground squirrel, shrew, pika and beavers are present here.

It is a pity that the Olerskii fauna of eastern Beringida have been studied even more meagerly. If we go by the preliminary findings of Ch.R. Harrington (reported in Moscow in October, 1973), who is now engaged in study of the Old Crow fauna (upper reaches of the Porcupine River, Yukon territory, Canada), there are such characteristic forms of the Olerskii complex as *Praeovibos*, *Equus* (*Plesippus*) cf. *verae*, *Soergelia*, *Praealces* and other fauna. It would be seen from this list that the fauna of Old Crow can be sharply distinguished from the American fauna beyond Alaska. They are very similar to, if not identical with, the Olerskii fauna.

Thus the Early Pleistocene faunas of the entire Beringida territory do not in any way lag behind the Late Pleistocene faunas in uniformity. This leads us to the conclusion that the whole of Beringida in the Early Pleistocene was inhabited by a uniform type of subarctic fauna. Their extensive geographic distribution (nearly 4000 km from west to east), internal homogeneity, uniqueness and clear separation in time impart to this fauna the significance of a zonal faunal complex.

A multidisciplinary study of the natural conditions of the Early Pleistocene of Beringida showed the period of existence of the Olerskii complex to be marked by a distinctly severe climate. The nature of Olerskii flora, the composition of mammalian and insect faunas together with traces of stable permafrost in Olerskii deposits prove not only the existence of cold subarctic climatic features but also dry climatic features in this area (Kats et al., 1970; Sher, 1971; Giterman, 1973 and others). The sharp predominance of obligate and to a lesser extent facultative tundra species in the composition of beetle fauna, and the quite significant role of xerophylls, such as ground beetles like *Bembidion dauricum* Motsch., *Pterostichus nearcticus* Ltd., and weevils like *Stephanocleonus* cf. *plumbeus* (Lec.), *Morychus* sp. (Matthews, 1974; Kiselev, in press) can be cited as some examples. It can be conceived that the Beringida mammals living under difficult conditions in the Early Pleistocene adapted not only to cold but also to dry climates. This conclusion is of great significance for understanding the source of cryoxerotic (periglacial) fauna, which migrated all over the Holarctic during the second half of the Pleistocene.

Fanning out of the representatives of Beringida fauna into the Old and New worlds was recorded even in the Early Pleistocene period. In temperate latitudes they appear, as a rule, at places with more or less cold phases, for

example, in the Mindel horizons of the Zyussenborn locality (Sher, 1975).

When we consider the New World, we will see that in the Late Kansas, which is comparable with the Mindel of Europe, a whole group of Asiatic immigrants (Hibbard et al., 1965) appeared in the temperate latitudes of North America. Although an understanding of the systematic relationship of these with the Beringida forms requires extensive work it is now possible to assert that practically the entire group of these immigrants is represented in the Early Pleistocene fauna of Beringida. These together with the primitive representatives of gray field mice and archaic elephants having a similarity with the genus *Mammuthus* and hares of the genus *Lepus* were the first species subsequent to the widespread tribe Ovibovini. The earliest fossil remains of the ox in the USA are associated with the late Kansas fauna of Rock Creek in Texas. Description of the species *Proptoceras mayfieldi* from there shows great similarity with the Beringida genus *Soergelia*.

It would be pertinent to deal with the problem of American endemic genera of Asiatic origin (*Sangamona*, *Cervalces*, *Oreamnos*, *Bootherium*, *Symbos*). The origin of at least some of them can be quite reliably associated with those of Beringida. Thus *Cervalces*, sharply differing from *Alces*, is quite close to the widely distributed group of moose (*Praealces*) with broad foreheads in Beringida. *Cervalces* are found in the temperate latitudes of America in the Illinois (Hibbard et al., 1965). It is not yet clear whether *Cervalces* also lived in Alaska or not. In all probability the antler of *C. alaskensis*, described by Ch. Frick (1937), belonged to *Praealces* (Sher, 1971); the same holds for the fossil found by Ch. Harrington in the Old Crow region. If the fossils of the Rancholabreiskii site in Alaska really belong to *Cervalces* (Péwé, Hopkins, 1967; Guthrie, 1968a), it can be surmised that they occurred at the boundary of the Early and Middle Pleistocene as a derivative of the Alaskan population of *Praealces*, which was isolated from the main Beringida geographic range in the course of one of the transgressional phases. Subsequently in Illinois this genus penetrated into the interior of America. If the present-day *Cervalces* was not to be found in Alaska it would mean that its morphological isolation took place in the course of overcoming the barrier which separates Beringida from the main American continent, when adaptation to more temperate climatic conditions took place. The history of the genus *Bootherium* can be assumed to be exactly like this. These are the possible ancestors of one of the numerous forms of Beringida ox.

It is a pity that we know very little about the interval of time between the existence of the Olerskii complex and the appearance of early variants of Early Paleolithic age. Olerskii deposits are practically everywhere separated by erosion from the overlying Mastaakskii deposits. The reorganization of the fauna themselves at this boundary is quite considerable. It is also possible that a certain warming of climate was confined to this interval. The

Pinakul-Einahnuhtan transgressional phase in Beringida was perhaps confined to this interval of time. It is a fact that the climatic conditions during this transgression were quite severe. Temporary dislocation of the continental connection in Beringia could have contributed to the morphological isolation of certain mammals of eastern Beringida (Alaska).

BERINGIDA FAUNA IN THE LATE PLIOCENE

Pre-Olerskii fauna of Beringida are still poorly studied. But this period of time is so interesting that even scanty and indirect information is of significance.

The first paleontological information on pre-Olerskii Beringida fauna was received from the Cape Deceit locality, situated on the coasts of Kotsev Gulf (Guthrie, Matthews, 1971). This fauna seemed to be identical with those of Olerskii in composition and conditions of habit. Fossils of mammals and insects were obtained from muddy deposits and permafrost. Cape Deceit fauna came into existence under conditions of tundra vegetation. Of 11 mammalian taxa only two do not show close relations with Olerskii fauna, such as the rodents like the fieldmouse *Pliomys* and the marmot *Marmota*. On the basis of the degree of evolution of archaic lemmings such as *Predicrostonyx* (Zazhigin, this collection) and primitive microtine, like the genus *Microtus*, it can be surmised that the Cape Deceit fauna are somewhat older than the Olerskii fauna. R. Guthrie and J. Matthews believe that these fauna are older than the late Kansas of America and can be correlated in age with the Gunz period. It can thus be tentatively suggested that the Cape Deceit fauna belong to the Late Pliocene (according to the official understanding on the USSR scale).

Olerian fauna were detected in 1973 from a horizon occurring in the exposures of the Krestovka River (right-bank tributary of the Kolyma River); this was underlain by a bed containing abundant fossil remains of small mammals*. The paleobotanical characteristics of these beds support the presence of tundra vegetation; certain forms of rodents help to place this part of the Krestovkian section under Upper Pliocene, so that they are synchronous with the Cape Deceit formations.

The resultant subarctic type Early Pleistocene Olerskii complex and the stable nature of the permafrost are indirect proof that the formation of a cold-loving biocenosis had a prolonged pre-Pleistocene history. Analyzing the Early Pleistocene fauna of Beringida, it can be assumed that its Late Pleistocene fauna must have had certain characteristic features which were later inherited in the Pleistocene. Moreover, the difference from fauna of the

*The interpretation in this section, given in an earlier work by the author (Sher, 1971), has been basically revised in light of new data.

same age occurring in temperate latitudes should be more theoretically significant than that in the Pleistocene, when the climatic contrasts between north and south started to moderate because of progressive cooling. Despite its limitations the paleontological data on Alaska and Kolyma confirm this view. Cape Deceit fauna practically cannot be correlated with the well-studied Late Pliocene fauna of the temperate latitudes of North America. Its connection with the Palearctic becomes distinctly apathetic; but even then the uniqueness of this fauna is so great that American paleontologists, in turn, concluded that there had been autochthonous growth of the Beringida mammalian fauna. R. Guthrie and J. Matthews even report on the "Beringian mammalian realm".

How long did the core processes of development of the Beringida fauna last? Although we do not have the relevant paleontological information, series of indirect data suggest that this process continued throughout the Pliocene. Numerous publications of the last few years regarding the appearance of a severe climate, even at the beginning of the Pliocene in the polar zones of the earth (a synopsis of some of the publications is translated in the paper by A.A. Arkhangelov and the author, 1973), also support this idea. It was mentioned above that the concepts of paleobotanists about the Late Pliocene vegetation of the Far North have changed during the last few years. Depletion in the composition of taiga forests took place toward the beginning of the Pliocene. Flora and insect fauna of the Lava Camp site in Alaska, which were there more than 5.7 million years ago, suggest the distribution of cold-resistant biocenosis during this period at higher latitudes (Hopkins et al., 1971).

Despite the extremely fragmentary information on the Late Pliocene fauna of Beringida, the migration of thermophilic faunal elements appears to be improbable. Late Pliocene immigrants had to adapt themselves to the quite severe climatic conditions of Beringida.* They are also supposed to have adapted and undergone changes in course of adjustments to more cold-resistant ways.

The list of mammals of Asiatic origin for the Late Pliocene was first published in America (Repenning, 1967, Table 5; Hibbard et al., 1965). This list included series of boreal forms which probably passed through the "cold filter" of Beringida (*Pliolemmus, Synaptomys*). Recently *Synaptomys* was found in the Upper Pliocene of North Mongolia (Devyatkin, Zazhigin, 1973). Thus the regions of Beringida were inhabited by the north boreal and later by subarctic animals which appeared even in the Pliocene.

*"Advancement" during the development of cold climate to the north should have influenced the flora. Possibly because of this, it is difficult to find the age of the pliocene floras of Beringida, which are considerably younger than the floras of the same age which grew in temperate latitudes.

CONCLUSIONS

Beringida was an extensive plain landmass covering the recent shelf from Taimyr to the Mackenzie River mouth; it also included the present-day marginal lowlands of East Siberia and Alaska. This landmass existed throughout the Pleistocene and, possibly, a considerable part of the Pliocene. A great similarity of mammalian faunas of various parts of Beringida, including Siberia and Alaska, has been detected at all stages of Late Cenozoic history. Practically the same types of fauna were present all over Beringida but they differed from the fauna of temperate latitudes of the same age.

Beringia was the most dynamic sector of Beringida. Intermittent marine transgression separated the American part of Beringida from the rest of the territory, leading to the adaptation of certain mammals in Alaska. However, these discontinuities in time had a relatively insignificant role against the background of the general unity of the fauna of Beringida.

Development of a cold climate at higher latitudes was observed throughout the Pliocene. This led to the formation of tundra vegetation and sub-arctic-type fauna in the Late Pliocene period. Cryoxerotic (periglacial) biocenosis developed here under the influence of a cold, sharply continental climate before the Early Pleistocene period. The amplitude of vegetative changes did not extend beyond the limits of the subarctic (tundra forest, hypoarctic deciduous taiga) during the phases of gradual warming of the climate. Thus subarctic conditions prevailed over Beringida throughout the Pleistocene and part of the Pliocene.

As compared to temperate latitudes, the earlier development of a cold climate in Beringida encouraged the appearance of principally new Holarctic faunal elements which were capable of living under severe climatic conditions. They contained groups of autochthonous subarctic fauna such as lemmings, oxen, reindeer. Individual species of many widely distributed boreal genera are found to have appeared here concurrently.

Beringida species got the chance to migrate into temperate latitudes because of progressive cooling of the climate in the Holarctic during the Late Cenozoic period. This process covered the entire Pleistocene period and the migration took place in several waves in the Old as well as New worlds. The migration of Beringida mammals into the temperate latitudes of America was determined not so much by the presence or absence of the land bridge at this stage; it was in fact much influenced by climate and the paleogeography of the continental regions of North America tapering into Beringida.

Recent data collected from the fossil fauna of Beringida confirm A.Ya. Tugarinov's hypothesis as to the autochthonous buildup of cold-resistant fauna in the territory of this extensive northern landmass. Beringida is an independent zoogeographic unit and fauna of this unit had a prolonged and unique history. They had an important role in the development of the fauna

of the entire Holarctic in the Late Cenozoic period. Therefore, Beringida should not be considered as a land bridge along which migration of mammals from Asia into America took place; it should be treated as an independent region where individual fauna developed, and whence representatives of these fauna migrated into the Old as well as the New worlds.

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Role of the Bering Land Bridge in the Distribution of Esocoid Fishes

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A number of independent intercontinental migrations of esocoid fishes took place in the Holarctic during the Cenozoic. The Eurasian origin of the sub-order Esocoidei is clearly apparent from paleontological evidence. The superfamily Esocoidea (pikes) appeared in Northern Asia and invaded the Nearctic across the Bering Land Bridge twice, before the Middle Miocene and near the end of the Pliocene. The distribution of the superfamily Umbroidea probably occurred in two different ways. Umbridae originated in Europe and migrated into the Nearctic across the North Atlantic Bridge in the Late Eocene or Early Oligocene. The short-term appearance of this family in Asia (in the Oligocene) was the result of its invasion from Europe. Another umbroid branch family, Dalliidae, seems to have migrated to North America via the Bering Land Bridge before the Middle Oligocene. The genus *Dallia* invaded Chukotka from Alaska, most likely during the Early Pleistocene.

Phylogenetic study of esocoids (suborder—Esocoidei) from fossil and recent materials shows that different branches of this group entered North America from Europe several times during the Cenozoic; entry from North America into Europe is recorded only once. Most of these migrations took place through Beringia.

Available paleontological data clearly indicate the Eurasian origin of the esocoids. Thus the super-family Umbroidea is known in Eurasia from the Pliocene, whereas in North America it is known only from the Middle Oligocene; the super-family Esocoidea in the Old World is known from the Oligocene and in the New World from the Late Miocene (see Table).

Study of the phylogeny of these two groups shows that the history of their distribution varied significantly.

The idea of the North American origin of esocoids and their subsequent migration to Europe through Asia is based on their sequential reduction in species variation in recent ichthyofauna on these continents (Banarescu, 1960); but this idea is not supported by the paleontological facts. Now practically all