

Alexander Averianov
Zoological Institute, RAS, St. Petersburg

Pleistocene lagomorphs of Eurasia

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In the Pleistocene of Eurasia three species of Prolagidae, 17 species of Ochotonidae and 16 species of Leporidae are known. The species diversity of lagomorphs gradually increased during the Pleistocene and in the late Pleistocene was the same as Recent. Some relict genera became extinct during the early Pleistocene (*Pliopentalagus*, *Alilepus*), others in the Middle Pleistocene (*Ochotonoides*, *Hypolagus* and *Sericolagus*). At least two lagomorph species became extinct during the Holocene (*Prolagus sardus* and *Ochotona transcaucasica*). The Pleistocene was not a critical period in the evolution of Lagomorpha. The extinction was caused by global cooling and was restricted to relict taxa mostly. During the Pleistocene intensive speciation took place in the genera *Ochotona*, *Oryctolagus* and *Lepus* in the Old World, and *Sylvilagus* in the New World. The Recent time is the period of flourishing and biological progress of phylogenetically young groups of lagomorphs (*Ochotona*, Leporinae), which started in the late Pliocene and continued during all the Pleistocene.

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Correspondence: Alexander Averianov, Zoological Institute, Russian Academy of Sciences, 199034 St. Petersburg, Russia. e-mail: sasha@AA1923.spb.edu

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INTRODUCTION

The Pleistocene is characterised by the most complete fossil record for many groups of modern mammals. Here we can trace the origin and early evolution of some recent species. However, the taxonomic approach applied to the recent mammals is sometimes difficult to apply to Pleistocene forms. The lagomorphs is a good example of such disparity between systematics of Pleistocene and recent forms. The taxonomy of all recent species and subspecies is largely based upon external characters (pelage), and, to a lesser extent, on some cranial and dental characters. The majority of Pleistocene remains of lagomorphs are just isolated and fragmented bones, determination of which is based exclusively on their absolute size and on few dental characters, specifically on the structure of the third lower premolar (p3). However, the variation of these characters in recent lagomorphs populations is not really understood.

Here we fall sometimes into circular thinking, when our determination of Pleistocene forms is greatly influenced by the current taxonomy of recent species and we then use these paleontological data for the reconstruction of the history of recent species and their phylogenetic relationships.

In my report I will briefly review the Pleistocene fossil record for the Eurasiatic lagomorphs and will try to elucidate how these data really help us to understand the evolutionary history of the recent taxa and to solve some current taxonomic problems in the field. I provide these data to emphasise some important gaps in the fossil record and to settle up the perspectives for the future work. This review is based on the unpublished taxonomic revision of both fossil and recent lagomorphs, carried out by the author.

All the Pleistocene taxa of lagomorphs could be easily divided into two major groups. The first includes the relict taxa, which became extinct during the Pleistocene or Holocene, or which are close to extinction nowadays. The other group includes taxa which underwent biological progress during the Pleistocene and which flourish now. The latter group includes species of the three genera, namely *Oryctolagus*, *Lepus* and *Ochotona*.

REVIEW OF SPECIES

Relict taxa

A few lineages of the common Mediterranean Neogene ochotonid-like lagomorph *Prolagus* have survived in the Pleistocene (Fig. 1). *Prolagus figaro figaro* LOPEZ MARTINEZ, 1975 is known from the type locality only, Middle Pleistocene Capo Figaro in Sardinia, Italy (Lopez Martinez & Thaler 1975). It is charac-

terised by a large size, a weak or absent crochet, and an enlarged protoconulid, exceeding the size of protoconid. A similar but somewhat smaller lagomorph, *Prolagus figaro depereti* LOPEZ MARTINEZ, 1975, was reported from the Early Pleistocene locality Bagur 2 in Spain (Lopez Martinez 1989). Otherwise it is known from the Ruscinian of France and Spain. The *Prolagus* from the Middle Pleistocene locality Montagnola in Italy, described as *P. sardus* by Fondi (1970, 1972), probably should be referred to the Villafranchian Italian species *Prolagus savagei* BERZI, 1967, contra Lopez Martinez (1989), who referred this material to the Ruscinian French and Spanish *P. michauxi* LOPEZ MARTINEZ, 1975. The holotype of *P. savagei* and few other known p3 of *Prolagus* from the Italian Villafranchian (Berzi 1967; Rook & Masini 1990) lack a crochet, which is represented in some specimens in the Montagnola population and in *P. michauxi*.



Figure 1. Approximate distribution of lagomorph relict taxa in the Pleistocene of Eurasia: **1** - *Prolagus figaro*, **2** - *Prolagus sardus*, **3** - *Prolagus savagei*, **4** - *Hypolagus beremendensis brachygnathus*, **5** - *Caprolagus hispidus*, **6** - *Caprolagus lapis*, **7** - *Sericolagus brachypus*, **8** - *Ochotonoides complicidens*, **9** - *Hypolagus schreuderae*, **10** - *Alilepus zhoukoudianensis*, **11** - *Pliopentalagus progressivus*, **12** - *Pentalagus funessi*.

However, the variation of p3 in *P. savagei* is not adequately known and it looks preferable to refer all the peninsular Italian Pleistocene *Prolagus* to this species.

The Pleistocene-Holocene *Prolagus sardus* (WAGNER, 1829) from Corsica, Sardinia and adjacent smaller islands was one of the largest species of *Prolagus*. It was surviving on the small island of Tavolara off the Sardinian coast as late as the eighteenth century (Kurtén 1968).

Another European relict Pleistocene lagomorph was a rabbit *Hypolagus beremendensis* (PETÉNYI, 1864). The Pleistocene populations are referred to the subspecies *H. b. brachygnathus* KORMOS, 1934, which had gradually evolved from the Pliocene *H. b. beremendensis* (PETÉNYI, 1864). It differs from the latter by its larger size and by dominance of more complicated variants of P2 and p3 (Fladerer & Reiner 1996). Apparently all European localities with the last *Hypolagus* remains (Podumci, Betfia 5, Varbezhnitsa and others) should be dated to the Cromer interglacial (Gunz-Mindel); and these rabbits are not known from Mindel-Riss deposits. If so, extinction of this species was probably connected with the Mindel (=Oka) Glaciation (IV criosuperclimatem according to Zubakov 1986).

In Asia a greater number of relict lagomorphs have survived during the Pleistocene, especially in southern Asia where the climate was more favourable than in Europe. The ochotonid *Ochotonoides complicidens* (BOULE & TEILHARD DE CHARDIN, 1928), which was widespread during the Pliocene was living in China at least by the Middle Pleistocene. Early Pleistocene remains are known from Qinghai Province (Zheng *et al.* 1985), Middle Pleistocene remains exclusively from Gansu and Shaanxi Provinces (Chow & Li 1965; Zheng 1976; Xue 1981; Wang 1988). The large ochotonid with complicated p3 from the Late Pleistocene of Sanjiacun, Yunnan

Province, China, described as *Ochotona* sp. 1 (Qiu *et al.* 1984), could be referred to this species and thus represents its last fossil record.

The relict Pliocene-Pleistocene rabbit *Hypolagus schreuderae* TEILHARD DE CHARDIN, 1940 was originally described from the Early Pleistocene Locality 18 (=Yangshaozun) near Beijing, China, where it was represented by a number of skulls and at least one skeleton (Teilhard de Chardin 1940). This species is also known from the Early Pleistocene of Hebei Province (Cai 1989). It is characterised by a large size and a complicated P2 with three folds on the anterior side.

The rabbit *Alilepus zhokoudianensis* CHENG, CAO, TIAN & LI, 1995 is known from the type locality only, the Early Pleistocene beds of Zhokoudian near Beijing, China (Cheng *et al.* 1995). In Europe the last undoubted remains of *Alilepus* are known from the Early Villafranchian (Odessa catacombs: *A. ucrainicus* GUREEV, 1964). The p3 of this species was not figured, so the attribution of the type material to this genus remains to be demonstrated.

The Plio-Pleistocene rabbit *Sericolagus brachypus* (YOUNG, 1927) is known from the Early to Middle Pleistocene of northern and north-eastern China (Young 1927, 1935; Teilhard de Chardin & Young, 1931; Teilhard de Chardin 1940; Zheng 1976; Zhang *et al.* 1993). This species is possibly an offshoot of the *Alilepus* lineage. It is characterised by the primitive postcranial morphology and a relatively derived structure of the p3, where advanced *Nekrolagus*-like p3 pattern (with the postero-internal fold closed into the enamel lake) was present together with the usual *Alilepus*-like morphotype (Averianov 1996).

The rabbit *Pliopentalagus progressivus* LIU & ZHENG, 1997 is known by two teeth from the Late Pliocene - Early Pleistocene fillings in Henan Province, China (Liu & Zheng 1997).

The genus *Pliopentalagus* was characteristic for the Ruscinian of Eurasia. This lineage is nowadays represented by the relict Amami rabbit *Pentalagus furnessi* (STONE, 1900) inhabiting two small islands of the Ryukyu Archipelago, Japan, where its fossil remains are known from the Late Pleistocene and Holocene deposits (Tomida *et al.* 1990; Tomida & Otsuka 1993).

Another recent relict of an ancient lineage is the hispid hare *Caprolagus hispidus* (PEARSON, 1839) distributed along the southern Himalayan foothills. It is descendant of the Villafranchian *Caprolagus sivalensis* FORSYTH MAJOR, 1899 from Pakistan. The genus was also represented in the Early Pleistocene of Java by *Caprolagus lapis* (HOOIJER, 1964), known from isolated teeth from Sangiran (Hooijer 1964; Dawson 1971). From the recent species it differs by a somewhat less complicated p3 morphology.

Oryctolagus

The genus *Oryctolagus* includes two extinct species, *O. lacosti* (POMEL, 1853) and *Oryctolagus laynensis* LOPEZ MARTINEZ, 1977 (Fig. 3). The former was distributed in the Early Villafranchian - Middle Pleistocene of France, Spain, and Portugal, the latter is restricted to the early Villafranchian of Spain. The distinction between these two species is not clear and they may be synonymous. Fossil remains attributed to the Recent European rabbit *Oryctolagus cuniculus* (LINNAEUS, 1758) are known since the Early Pleistocene in numerous localities in central and southern Europe and possibly in northern Africa (Donard 1981; Callou 1995).

The European rabbits of the Mindel-Riss epoch are attributed to the subspecies *O. c. lunellensis* DONARD, 1981, those of the Riss epoch to *O. c. grenalensis* DONARD, 1981. The Wurmian European rabbits are referred to the recent subspecies *O. c. huxleyi* HAECKEL,

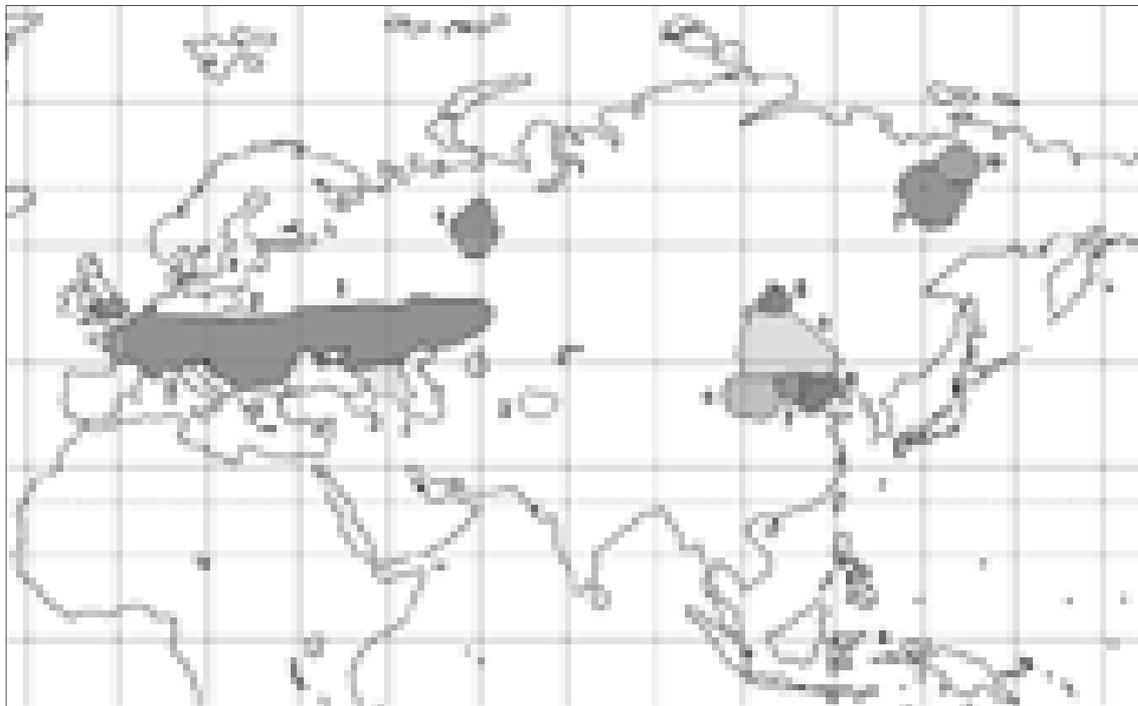


Figure 2. Approximate distribution of the *Ochotona* species in the Pleistocene of Eurasia: **1** - *O. pusilla*, **2** - , **3** - *O. rufescens*, **4** - *O. azeica* and *O. transcaucasica*, **5** - *O. dodogolica* and *O. zasuchini*, **6** - *O. tibetana*, **7** - *O. hyperborea*, **8** - *O. kozłowi*, **9** - *O. dauuica*, **10** - *O. whartoni*

1874 (Donard 1981). All these subspecies differ mostly in size. According to the traditional taxonomic works there are from two to six recent subspecies of *O. cuniculus*, all differing in size and pelage characteristics. The recent craniometric analysis of *O. cuniculus* showed that variation in size occurred in a continuous cline, so there is no evidence for separation of this species into subspecies (Sharples *et al.* 1996). However, the mitochondrial DNA analysis of 13 rabbit populations reveals two geographically separated maternal lineages, the divergence of which goes back to 2.5 My (Monnerot *et al.* 1994), so at least two recent geographic subspecies of *O. cuniculus* could be maintained.

Lepus

The reliable Early Pleistocene records of the genus *Lepus*, with p3 or P2 described, are known from Moldavia, Ukraine, Russia and Austria (Sukhov 1976; Shushpanov 1977;

Fladerer 1987). All these remains belong to small-sized hares similar in size with the recent *L. capensis*. The species attribution of these materials is not clear.

The fossil record of variable hare *Lepus timidus* LINNAEUS, 1758 can be traced since the Middle Pleistocene (Kurtén 1968; Von Koenigswald 1972). Nowadays it inhabits the forest and Arctic zones of Eurasia. The recent range of *L. timidus* differs considerably from its Pleistocene range. In Western Europe the variable hare is now restricted to the northern latitudes (Fenno-Scandia, Ireland, Scotland) and to the Alps (subspecies *L. t. varronis*). This distribution pattern is apparently connected both with the climatic change of the Holocene and with the competitionary displacing of this species by the brown hare, *L. europaeus*. During the Pleistocene the distribution of *L. timidus* was confined to Europe (Fig. 4), but since the Holocene its range greatly

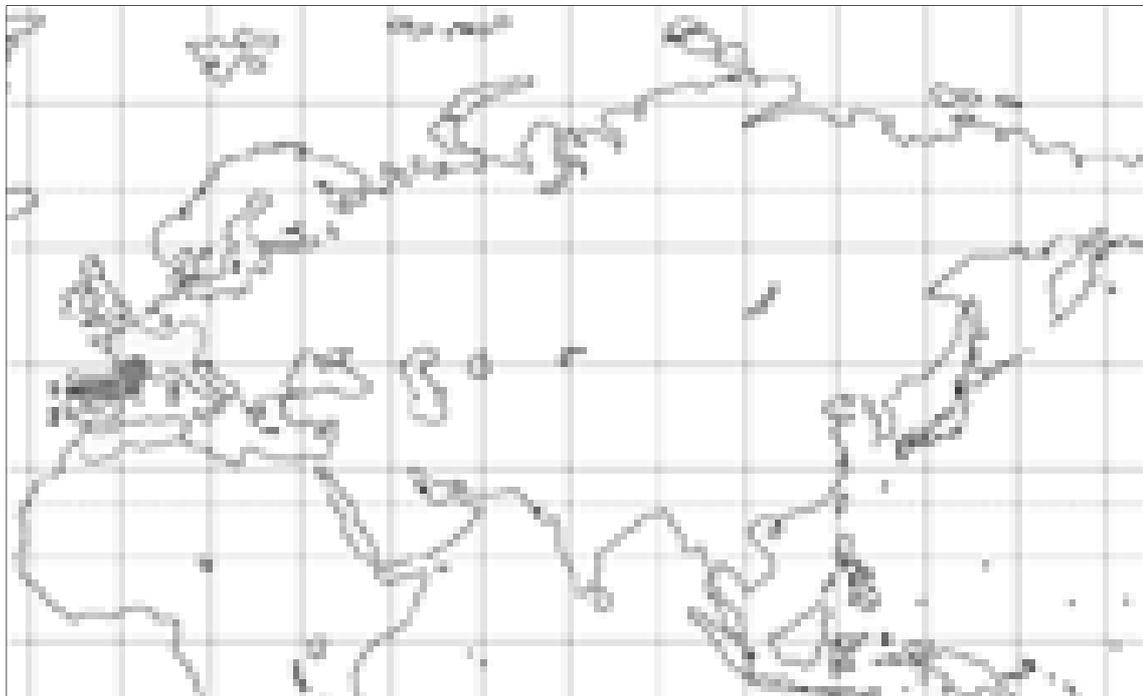


Figure 3 Approximate distribution of the *Oryctolagus* species in the Pleistocene of Eurasia: **1** - *O. lacosti* **2** - *O. laynensis* **3** - *O. cuniculus*

extended to the east up to the Pacific Ocean; this was connected with the disappearance of the periglacial steppe and its replacement by forests.

The Middle Pleistocene European records of the variable hare can probably be referred to the subspecies *L. t. praetimidus* KRETZOI in Janossy, 1969, which was characterised by very large size (Janossy 1969). In the Late Pleistocene remains of *L. timidus* are known from more than hundred localities in Spain, Portugal, France, Belgium, Great Britain, Italy, Switzerland, Germany, Austria, Czech, Poland, Yugoslavia, Hungary, Moldavia, western Ukraine and Crimea. Sometimes they are found in the great abundance, like in the Madlerian beds of the Kesslerloch cave in Switzerland where remains of at least 1000 individuals were collected (Heierli 1907; Koby 1960). Apparently all continental European records of variable hare could be referred to the subspecies *L. t. wuermensis* KOPY, 1960. The Late Pleistocene variable hare from Great Britain was somewhat larger (Sanford 1869; Hinton 1909) and could be separated as the subspecies *L. t. anglicus* HINTON, 1909.

The Late Pleistocene *L. t. ponticus* AVERIANOV, 1994 is known from several localities on the Crimea peninsula (Averianov 1994). Late Pleistocene records of the variable hare from Moldavia can probably be referred to the same subspecies.

The extinct Late Pleistocene Don hare *Lepus tanaiticus* GUREEV, 1964 inhabited the periglacial zone of Eastern Europe and Northern Asia. It differs from *L. timidus* by the structure of dentary and p3 (Averianov 1999). The species could be divided into three subspecies: *L. t. gmelini* AVERIANOV & KUZMINA, 1993 from the Wurmian 2/3 of central Russia, *L. t. tanaiticus* GUREEV, 1964 from the Wurmian 3 of Central Russia, Ukraine, Ural Mountains and northern Kazakhstan, and *L. t. vereschagini* AVERIANOV, 1995 from the

Wurmian 3 (Sartanian) of Yakutia, Eastern Siberia (Averianov & Kuzmina 1993; Averianov 1995, 1999). These subspecies differ mostly in size.

The Early Pleistocene *Lepus valdarnensis* Weithofer, 1889 from Italy was a relatively large hare, possible close to *L. europaeus* and *L. capensis* (subgenus *Eulagos* GRAY, 1867), differing from them mostly in less developed ability for fast running (it has relatively shorter distal limb bones). By some authors it was referred to the genus *Oryctolagus* and synonymised with *O. lacosti* (POMEL, 1853). The species is reliably known only from the Late Villafranchian of Italy (Weithofer 1889; Bosco 1900; Forteleoni 1974).

The Late Pliocene - Recent cape hare *Lepus capensis* LINNAEUS, 1758 inhabits savannahs, deserts, steeps, and mountain regions of Africa, Spain, the Near East, and Central Asia. The recent distribution of *L. capensis*, compared to the Pleistocene range, is restricted only in Europe (now it is absent from Italy, Germany, and Hungary). This may be connected with the disappearance of the steeps here in the Holocene. It cannot be excluded that Pleistocene remains from Italy referred to *L. capensis* are actually belonging to *L. corsicanus* DE WINTON, 1898, which is now considered as a distinct species (Palacios 1996). Similarly, all Spanish Pleistocene records of the cape hare could be referable to *L. granatensis* ROSENHAUER, 1856. The oldest fossil records of *L. capensis* are known from the Upper Pliocene of Eastern Africa. This species was reported from more than 20 localities in Spain, Italy, Germany, Hungary, northern Caucasus, Kazakhstan, Middle Asia, Altai Mountains, southern Western Siberia, Transbaikalia and China. Two fossil subspecies of the Cape hare can be currently recognised. *L. c. terraerubrae* KRETZOI, 1956 is a poorly known subspecies to which a few isolated teeth from the Middle Pleistocene of Germany, Hungary, Rumania, Italy, and Croatia could be referred (Kormos 1934;

Kowalski 1958; Kretzoi 1965; Terzea & Jurcsak 1969; Van der Meulen 1973). Some remains from the Late Pleistocene of China were referred to the recent subspecies *L. c. tolai* PALLAS, 1778 (Jin *et al.* 1984).

The Early Pleistocene - Recent brown hare *Lepus europaeus* PALLAS, 1778 is distributed now in Europe (except for Scandinavia and Ireland), the Near East, Transcaucasia, and Kazakhstan. Early Pleistocene records of this species were reported from the Caucasus (Averianov & Baryshnikov 1993). Middle Pleistocene remains are known from Germany and Czechoslovakia (Freudenberg 1914; Schirmeissen 1927; Ziegler 1995). The relatively numerous remains of the extinct subspecies of brown hare, *L. e. gureevi* GROMOV, 1952, were described from the Late Pleistocene of Binagady in Azerbaijan (Gromov 1952; Vereschagin 1959; Averianov & Baryshnikov 1993). The extinct *L. e. euxi-*

nicus AVERIANOV, 1994 is known from the Late Pleistocene and Early Holocene of Crimea (Averianov 1994). In the Late Pleistocene *L. europaeus* was quite common in the southern Europe and in Asia. Its remains were reported, but usually not described, from more than 60 localities of Spain, France, Italy, Yugoslavia, Bulgaria, Hungary, Moldavia, Crimea and southern Ukraine, European Russia, the Caucasus, and Kazakhstan. The Pleistocene records of *L. europaeus* do not extend the recent geographic range of the species.

The Middle Pleistocene - Recent Manchurian hare *Lepus mandshuricus* RADDE, 1861 from the Russian Far East and north-eastern China was reported from some Late Pleistocene localities nearby Amur River in Russia and described from the Middle Pleistocene of China (Zhang *et al.* 1993).

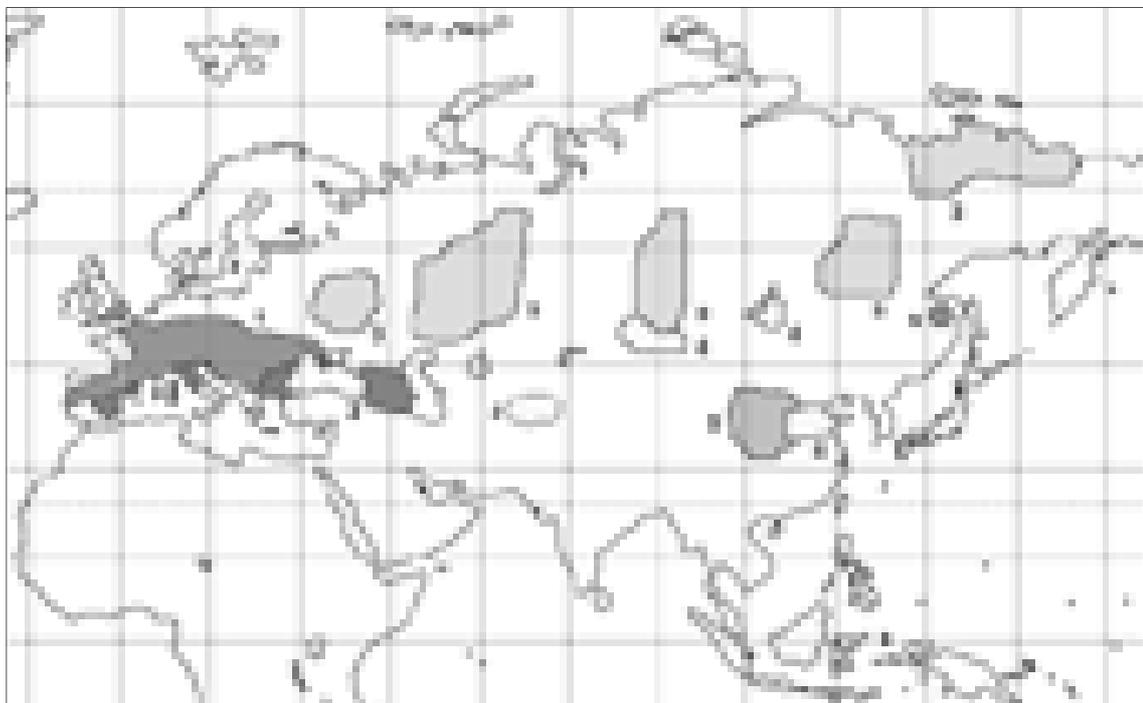


Figure 4 Approximate distribution of the *Lepus* species in the Pleistocene of Eurasia: **1** - *L. timidus*, **2** - *L. europaeus*, **3** - *L. tanaiticus*, **4** - *L. capensis*, **5** - *L. oiostolus*, **6** - *L. mandshuricus*

The Early Pleistocene - Recent woolly hare *Lepus oiostolus* HODGSON, 1840 now inhabits the Tibetan Plateau (eastern India, Nepal, and China). All remains of this species from the Early - Middle Pleistocene of China are probably referable to the extinct subspecies *L. o. wongi* YOUNG, 1927, which was characterised by its larger size relative to the modern subspecies. The remains of this hare are described from a number of Chinese localities (Young 1927, 1930; Colbert & Hooijer 1953; Chow & Li 1965; Zhang *et al.* 1993; Cheng *et al.* 1995).

Ochotona

Another successful group of recent lagomorphs is the genus *Ochotona*, the last representative of the family Ochotonidae. There are several fossil species of *Ochotona* described from the Pleistocene (Fig. 2).

Ochotona azerica GADZHIEV & ALIEV in Erbaeva, 1988 is based on the common material from the Middle Pleistocene of Azykh Cave in Azerbaijan. From the geographically close species *O. rufescens* it differs by a relatively larger anterior segment of p3. Another Caucasian extinct ochotonid is *Ochotona transcaucasica* (VEKUA, 1967), ranging from the Early Pleistocene till probably Holocene (Averianov & Baryshnikov 1993). It has some similarity with *O. rufescens* (the anterior segment of p3 relatively small, broadly fused to the posterior segment).

The type material for *Ochotona polonica* SYCH, 1980 comes from the Late Ruscianian Zamkova Dolna locality in Poland. To this species all pikas remains from the Late Pliocene - Early Pleistocene of Poland are usually attributed (see review in Wolsan 1989, 1990), however, the majority of these materials are not described and such determination needs to be established.

A number of extinct *Ochotona* species were described from Transbaikalia. *Ochotona dodogolica* ERBAJEVA, 1966 and *Ochotona*

zasuchini ERBAJEVA, 1988 are known from the Early Pleistocene. The former species is based on relatively numerous material, including skull fragments (Polyakova & Erbaeva 1974), the latter, larger-sized, is based on one isolated p3 only (Erbaeva 1988).

The Pleistocene American Wharton's pika *Ochotona whartoni* GUTHRIE & MATTHEWS, 1971 was reported from the Middle Villafranchian of Yakutia (Erbaeva & Belolyubskii 1993). This species may have existed in Siberia during the Pleistocene.

A few Recent Eurasian pika species have a known fossil record in the Pleistocene. The northern pika *Ochotona hyperborea* (PALLAS, 1811) was described from the Middle Pleistocene of China (Zhang *et al.* 1993) and the Late Pleistocene of Yakutia (Agadjanian 1972). The Daurian pika *Ochotona dauurica* (Pallas, 1776) was reported from some Middle and Late Pleistocene localities in China, but the material was not described. An extinct subspecies, *O. d. gureevi* ERBAJEVA, 1966, is known from the Early Pleistocene of Transbaikalia (Erbaeva 1988).

Two fragmented skulls from the Middle Pleistocene Zhoukoudian site in China were referred to as *O. koslowi* and *Ochotona cf. koslowi* (Young 1934; Pei 1936). Although these skulls have some differences from the Recent Kozlov's Pika *O. koslowi* (BUECHNER, 1894) (see Erbaeva 1988), they share the convex frontals and are similar in size. *O. koslowi* was reported (but not described) also from the Late Pleistocene of China.

The Late Pliocene - Recent steppe pika *Ochotona pusilla* (PALLAS, 1769) was widely distributed in the Pleistocene. Its remains are known from Great Britain, the Netherlands, France, Switzerland, Italy, Yugoslavia, Germany, Hungary, Poland, Czechoslovakia, Austria, Rumania, Ukraine, Russia, and Kazakhstan (it nowadays lives only in the steppe zone of Russia and Kazakhstan, from

the Volga River till the Ural Mountains). There are several extinct subspecies of the steppe pika. *O. p. lazari* (KRETZOI, 1941) is known by the holotype only from the Early Pleistocene locality of Gombasek in Czechoslovakia. The name "*O. p. veterior*" KRETZOI in Janossy, 1969 [nomen nudum] was applied to the material from Solymar, Uppony 1, and Tarkü in Hungary (Janossy *et al.* 1968; Janossy 1969). *O. p. spelaea* (OWEN, 1846) was originally described from the Late Pleistocene of Great Britain. Apparently this name could be applied to all Late Pleistocene steppe pikas from Europe (except Crimea and the Caucasus). *O. p. liubini* ERBAJEVA & BARYSCHNIKOV in ERBAJEVA, 1988 is known from the type locality only, Moustierian layers of the Barakaevskaya Cave in the northern Caucasus. *O. p. tanaitica* ERBAJEVA, 1988 is known from several Late Pleistocene sites in Crimea (Erbaeva 1988).

The fossil remains of the Afghan pika *Ochotona rufescens* (GRAY, 1842) are known from the Middle Pleistocene sites of Sel' Ungur in Kirghisia (Erbaeva 1988) and Emirkaya-2 in Turkey (Montuire *et al.* 1994). The Moupin pika *Ochotona thibetana* (MILNE-EDWARDS, 1871) was described from the Early and Middle Pleistocene of Gansu and Henan Provinces, China (Teilhard de Chardin 1940; Zheng 1976).

DISCUSSION

The Pleistocene epoch was not a crucial period for the lagomorphs' history. During this epoch the background extinction of some relict taxa, connected with the global cooling, took place. During this time an intensive speciation occurred in phylogenetically young groups of lagomorphs: in the genera *Ochotona*, *Oryctolagus*, and *Lepus* in the Old World and in the genus *Sylvilagus* in the New World.

The Recent fauna of lagomorphs in Europe has, in general, a relict appearance. *Orycto-*

lagus cuniculus and *Lepus timidus* lived here at least since the Early and Middle Pleistocene, respectively. *Lepus corsicanus* (Apennines, Corsica) and *L. granatensis* (Spain) possibly represent a more ancient radiation of hares and are now peripherally restricted in distribution. In contrast, in Asia we see an intensive speciation in the populations of *Lepus timidus* and *Ochotona hyperborea*, which invaded a huge territory of Siberia in the Holocene, leading to the formation of many subspecies in Asia and at least one species in North America (the Arctic hare *Lepus arcticus* ROSS, 1819). A similar intensive speciation process can be expected in the future for the brown hare, which considerably extended its range to the East during past few centuries. This was connected with the declining forest in this area.

The recent centre of the species diversity for pikas is located in Tibet and the Himalayas. Unfortunately, any fossil record for these territories is virtually absent. However, it can be hypothesised that intensive speciation of these mountain pikas took place in the post-Pleistocene epoch. During the Pleistocene their ancestors apparently lived at lower altitudes. Having become adapted to the cold Asiatic steppes they had to migrate to higher mountains with the Holocene warming and subsequent speciation was connected with the range fragmentation and geographic isolation by the mountain ridges. This may be the main reason for the high taxonomic diversity of Tibetan and Himalayan pikas. This scenario looks more suitable than the hypothesis of Mitchell (1981), who considered Tibet as the centre of origin for the genus *Ochotona*.

Concluding, we may see that the known fossil record for the Pleistocene lagomorphs is incomplete in many respects and really does not help much for understanding of the evolutionary history of the Recent species. For the better understanding of this history we need more Pleistocene records, more numerous fossil samples, we need detailed descrip-

tions of all relevant materials and especially we need the study of skull and dentition variation in the Recent and fossil lagomorph populations. This will allow us to make more precise determination of the fossil materials at the species and subspecies levels and to reconstruct the real history of the Recent species.

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