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Lagomorphs (Mammalia) from the Pleistocene of Eurasia

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Abstract—Thirty seven species belonging to three families of lagomorphs (Prolagidae, Ochotonidae, and Leporidae) from the Pleistocene of Eurasia are reviewed.

INTRODUCTION

The Lagomorpha is a mammalian order, phylogenetically close to the Rodentia. The earliest representatives are known from the Early Eocene of Asia. As early as the Oligocene, the Lagomorpha showed marked adaptive radiation, and they were relatively diverse (at the generic level) in the Miocene. In the Pliocene, the number of genera decreased somewhat; however, a large number of new species appeared in phylogenetically young groups (*Ochotona* and Leporinae).

This study gives a review of Pleistocene species of Lagomorpha from Eurasia based on a revision of the order. To date, only general reviews of the Pleistocene Lagomorpha from Europe (Kurten, 1968; Corbet, 1986) and North America (Kurten and Anderson, 1980) have been published. This paper focuses mainly on finds accurately determined to species. The references mainly comprise studies containing descriptions and (or) figures of Pleistocene Lagomorpha. The lower boundary of the Pleistocene is accepted based on the upper boundary of the paleomagnetic Olduvai Event (ages of 1.6–1.7 Ma).

SYSTEMATIC PALEONTOLOGY

Family Prolagidae Gureev, 1962

The Prolagidae is a compact group of pikalike lagomorphs arising in the Early Miocene predominantly in the Mediterranean Region (Europe; North Africa; Asia Minor; and, possibly, in the region of Lake Baikal). Late members of the family (genus *Prolagus* Pomel, 1853) are characterized by increased premolar foramen, hypsodont dentition, reduced m3, isolated hypconulid on m2 (this tooth consists of three prisms), increased p3 bearing an isolated anteroconid by the retention of a number of primitive features on the upper cheek teeth. Three species are known from the Pleistocene.

Prolagus savagei Berzi, 1967, Late Pliocene to Early Pleistocene of Italy (holotype, from Arondelli; Early Villafranchian). The species was also recorded in the Late Villafranchian of Upper Valdarno (levels Oliv-

ola and Tasso) and in the Middle Pleistocene of Montagnola (Fondi, 1972; Rook and Masini, 1990).

Prolagus figaro Lopez Martinez, 1975, Pliocene to Middle Pleistocene of Italy, France, and Spain (holotype, from Capo Figari, Sardinia; Middle Pleistocene).

Prolagus sardus (Wagner, 1829), Pleistocene to Holocene; islands in the Mediterranean Sea, Sardinia (*P. s. sardus*), Corsica (*P. s. corsicanus*), and neighboring small islands (holotype, from Cagliari, Sardinia; Pleistocene). The species became extinct in the historical period and possibly lived to 1774 in Tavolara Island near Sardinia (see Kurten, 1968).

Family Ochotonidae Thomas, 1897

Small and medium-sized lagomorphs. P4 is completely molarized. M1 and M2 lack traces of a crescent. M3 is absent. There arise one internal, and two external reentrant folds on p3; the group occurred predominantly in Asia and developed there beginning at the Early Oligocene; it was also found in Europe and North America; two endemic genera occurred in the Miocene of Africa.

Ochotonoides complicidens (Boule et Teilhard de Chardin, 1928), Pliocene to Middle Pleistocene of Mongolia, China, and Transbaikalia (holotype, from the Gansu Province, China; Pliocene). These pikas are similar to Recent *Ochotona*, being distinguished from the latter by larger size and complicated structure of p3. They were found in the Early Pleistocene of Yangshaozun (=Locality 18), Heshui, Hanshui, Houhe, You, etc. (Pei, 1939; Teilhard de Chardin, 1940; Zheng, 1976; Xue, 1981; Wang, 1988; Liu and Zheng, 1997) and in the Middle Pleistocene of Lantian (Chow and Li, 1965) and probably survived to the Late Pleistocene ("*Ochotona* sp. 1" from Sanjiacun, see Qiu *et al.*, 1984).

Ochotona dodogolica Erbajeva, 1966, Early Pleistocene of Transbaikalia (holotype, from Dodogol, Buryatia; Early Pleistocene). The species is represented by relatively complete specimens, including a fragmentary skull (Polyakova and Erbajeva, 1974; Erbajeva, 1988).

Ochotona azerica Gadzhiev et Aliev in Erbajeva, 1988 [the name proposed earlier by Aliev (1969) is invalid], Middle Pleistocene of Transcaucasia (holo-

type, from Acheulean beds of Azykh Cave, Azerbaijan). The species is poorly known, but probably valid. It is distinguished from the geographically close species, *O. rufescens*, by relatively larger anterior segment of p3.

Ochotona transcaucasica (Vekua, 1967), Early Pleistocene to Holocene (?) of Transcaucasia (holotype, from Mousterian beds of Tsopi Cave, Georgia). The species is distinguished from *O. azerica* by its larger size and is similar to *O. rufescens* in the relatively small anterior segment of p3 that is widely fused with the posterior segment. It was found in the Early Pleistocene of Azykh Cave, Azerbaijan (Markova, 1982; Erbajeva, 1988); Middle Pleistocene of Treugol'naya Cave, Stavropol Region; the Late Pleistocene of Tsopi Cave, Georgia and Taglar Cave, Azerbaijan (Vekua and Shidlovskii, 1958; Vekua, 1967). In Armenia, it probably survived to the Holocene (Averianov and Baryshnikov, 1993).

Ochotona zasuchini Erbajeva, 1988, Early Pleistocene of Transbaikalia. To date, the species is represented only by the holotype (Zasukhino, Buryatia, beginning of the Early Pleistocene); it is distinguished by its larger size.

Ochotona polonica Sych, 1980, Early Pliocene to Early Pleistocene (?) of Poland (holotype, from Zamkova Dolna Cave, Late Ruscian). Pikas from the Late Pliocene to Early Pleistocene of Poland are commonly assigned to this species (see review, Wolsan 1989, 1990), although such identification is not substantiated and the necessary characters are usually absent. *O. polonica* is a poorly understood species, the validity of which is questionable.

Ochotona whartoni Guthrie et Matthews, 1971, Early to Late (?) Pleistocene of Alaska, Canada, and Yakutia. It is distinguished by its large size. In Eurasia, it was found only in the Middle Villafranchian of Yakutia (Erbajeva and Belolyubskii, 1993); it possibly also occurred in the Pleistocene.

Ochotona alpina (Pallas, 1773), Late Pleistocene to Recent; predominantly highland regions of Russia, Kazakhstan, Mongolia, and China. Fossil specimens from the Late Pleistocene of the Chusovaya River (Gromov, 1957a), referred to as this species, probably belong to *O. hyperborea*.

Ochotona hyperborea (Pallas, 1811), Late Pliocene to Recent; highland taiga belt of Russia, China, Korea, and Japan. The species was found in the Middle Pleistocene of Jinniushan, China, and in the Late Pleistocene of Mamontova Gora (30-meter-high terrace), Yakutia (Agadjanian, 1972; Zhang *et al.*, 1993).

Ochotona pallasi (Gray, 1867), Late Pliocene to Recent of Kazakhstan, Russia, Mongolia, and China. The presence of this species was indicated in the Early Pleistocene of the upper reaches of the Lena River; however, the material was not described. These specimens may belong to *O. filippovi* (see below).

Ochotona dauurica (Pallas, 1776), Early Pleistocene to Recent; desert steppes of Russia, Mongolia, Kazakhstan, and China. In the Early Pleistocene, it was recorded in Tologoi, Transbaikalia (*O. d. gureevi* Erbajeva, 1966; see Erbajeva, 1988); in the Middle to Late Pleistocene, in several localities of China, the material was not described.

Ochotona koslowi (Buechner, 1894), Middle Pleistocene (?) to Recent of China. Two fragmentary skulls from a site of Peking men, Zhoukoudian (Middle Pleistocene), were referred to as *O. koslowi* and *Ochotona* cf. *koslowi* (Young, 1934; Pei, 1936). These skulls notably differ from those of Recent *O. koslowi* (Erbajeva, 1988, p. 184–185). Notwithstanding the differences indicated, fossil pikas and *Ochotona koslowi* are rather similar in measurements and in convex frontal part of skull. Similar pikas are relatively abundant in Zhoukoudian (Li and Ji, 1981); however, additional material was not described. *O. koslowi* was also recorded in the Late Pleistocene of China.

Ochotona pusilla (Pallas, 1769), Late Pliocene to Recent. In the Pleistocene, it occurred in Great Britain, Netherlands, France, Switzerland, Italy, Yugoslavia, Germany, Hungary, Poland, Czechoslovakia, Austria, Romania, Ukraine, Russia and Kazakhstan. Nowadays, it occurs in steppe regions from the Volga River and the Southern Ural Mountains to the boundary of China (Russia and Kazakhstan). The following extinct subspecies were distinguished.

O. p. lazari (Kretzoi, 1941) is represented by only the holotype (Gombasek, Czechia; Early Pleistocene).

"*O. p. veterior*" Kretzoi in Janossy, 1969 [nomen nudum] (Solymar, Hungary; Middle Pleistocene); the name is invalid.

O. p. spelaea (Owen, 1846), holotype, from Kent's Hole, Great Britain; Late Pleistocene; probably, all specimens of small pikas from the Middle and Late Pleistocene of Europe (except for the Crimea and Caucasus) should be assigned to this subspecies. The material was described in the following localities: Middle Pleistocene: la Fage (France), Belvédère (Netherlands), and Varbezhnitsa (Bulgaria) (Chaline, 1975; Kolfschoten, 1985; Popov, 1988); Late Pleistocene: Kent's Hole (Great Britain), Niksloch (Austria), Pillisszanto and Subalyuk (Hungary), Veternica and Pecine u Brini (Croatia), Gornja Bijambarska (Bosnia), Smolucka Cave (Serbia), Żalasia (Poland), Novgorod Severskii and Mezhirichi (Ukraine), and Starye Duruitory and Brynzeny-1 (Moldova) (Owen, 1846; Kormos, 1916; Mottl, 1938; Lozan, 1970; Malez, 1963, 1966, 1968, 1979; Rekovets, 1985; Bochenski *et al.*, 1985; Dimitrijević, 1988; Erbajeva, 1988; Rekovets and Topachevsky, 1988; Fladerer, 1992).

O. p. liubini Erbajeva et Baryshnikov in Erbajeva, 1988, holotype, from Mousterian beds of Barakavskaya Cave, Krasnodar Region; Late Pleistocene. The subspecies is only known from the type locality.

O. p. tanaitica Erbajeva, 1988, holotype, from Alimov's Shelter, Crimea; Holocene. The subspecies was also found in the Late Pleistocene of the Crimea Peninsula, in the Adzhi Koba locality (Gromov, 1961; Erbajeva, 1988).

In the present state of understanding of small pikas, the specimens from the Late Pleistocene of the Ural Mountains and the adjacent area should be assigned to the Recent subspecies *O. p. pusilla* (Pallas, 1768). The material was described in the following localities: Nizhnie Karmalki, Lower Don, Stolbovoi Grotto, Medvezh'ya Cave, Mal'kovo, Nitsa, and Verkhnyaya Alabuga (Gromov, 1957a, 1957b; Kuz'mina, 1965, 1971, 1975; Maleeva and Federyagina, 1984).

Ochotona filippovi Erbajeva, 1999, Early Pleistocene of the northern part of the Baikal Region. The species is presented by few specimens from Podymakhino in the Irkutsk Region (Erbajeva, 1999). In the structure of p3, the species combines the characters of *O. pusilla* and *O. rufescens*. It is probably similar to the ancestors of American *O. princeps* and *O. collaris* (Erbajeva, 1999).

Ochotona rufescens (Gray, 1842), Middle Pleistocene (?) to Recent; mountains of Turkmenistan, Iran, Afghanistan, and Pakistan. Pikas from the Middle Pleistocene of Sel'-Ungur Cave (Kyrgyzstan) described as "*Ochotona alaica*" (Erbajeva, 1988; Volozheninov and Krakhmal', 1989) and probably specimens from the Middle Pleistocene of Emirkaya-2 (Turkey) (Montuire *et al.*, 1994) belong to this species.

Ochotona rutila (Severtzov, 1873), Middle Pleistocene (?) to Recent of Pamir and Tien Shan (Tadjikistan, Kyrgyzstan, Uzbekistan, Kazakhstan, and Afghanistan). Fossil specimens were recorded in the Late Pleistocene of Uzbekistan, but were not described.

Ochotona macrotis (Guenther, 1875), Late Pliocene to Recent; high-mountain areas of Central Asia, including Tadjikistan, Kyrgyzstan, Kazakhstan, Afghanistan, Pakistan, India, Nepal, Bhutan, and China. Fossil specimens were found in the Middle Villafranchian of Kazakhstan, but were not recorded in the Pleistocene.

Ochotona thibetana (Milne-Edwards, 1871), Late Pliocene to Recent of China, Myanmar, Bhutan, and India. Fossil specimens were found in the Early Pleistocene of Yangshaozun (=Locality 18) and in the Middle Pleistocene of Heshui, China (Teilhard de Chardin, 1940; Zheng, 1976).

Family Leporidae Fischer, 1817

Large and medium-sized lagomorphs. Teeth are hypsodont. P3 is entirely molarized in advanced species. M3 is present; m3 consists of two segments. The group is known since the Late Oligocene. The main adaptive radiation of the family occurred in the Neogene of North America. The relationships between Oligocene Asiatic leporids (genus *Ordolagus* de Muizon, 1977) and American forms are uncertain; this is proba-

bly a lateral evolutionary lineage of the family. Adaptive radiation of Asiatic leporids (subfamily Leporinae) occurred after the immigration of members of the genus *Alilepus* Dice, 1917 (Middle Miocene, Early Vallesian, MN 9; coincided with the emergence of *Hipparion* in the Old World) from North America. In the Late Miocene (Turolian, MN12–MN13), the genus *Hypolagus* Dice, 1917 (subfamily Archaeolaginae) entered Eurasia; however, this did not result in adaptive radiation at the generic level, although the genus occurred there up to the Middle Pleistocene. In the Late Miocene (Turolian, approximately 6 Ma) the Leporinae entered Africa.

Hypolagus schreuderae Teilhard de Chardin, 1940, Late Pliocene to Early Pleistocene of China; holotype, from the Early Pleistocene of Yangshaozun (=Locality, 18). The species is represented by relatively complete specimens (skeleton and a series of skulls) from the type locality (Teilhard de Chardin, 1940). Isolated teeth were also found in the Early Pleistocene of Nihewan (Cai, 1989). The species is characterized by large measurements and a complicated P2 (three folds on the anterior side).

Hypolagus beremendensis (Petényi, 1864), Early Pliocene to Middle Pleistocene of Poland, Netherlands, Germany, Austria, Czechia, Hungary, Romania, Croatia, Israel, Turkey, Georgia, Moldova, Ukraine, Russia, and Kazakhstan. A characteristic subspecies of the Pleistocene is *H. b. brachygnathus* Kormos, 1934, a direct descendant of Pliocene *H. b. beremendensis* (Petényi, 1864); it is distinguished from the latter by larger measurements and by the prevalence of complicated morphotypes of P2 and p3 (see Fladerer and Reiner, 1996). The specimens were described from the following Pleistocene localities: Early Pleistocene: Schernfeld (Germany), Villany 3 (Hungary), Betfia 13 (Romania), Chlum 6 (Czechia), Deutsch-Altenburg (Austria), Chishmikiioi (Moldova), and Cherevychnoe (Ukraine); Middle Pleistocene: Podumci (Croatia), Betfia 5 (Romania), Varbezhnitsa (Bulgaria), and Emirkaya-2 (Turkey) (Kormos, 1934a; Kowalski, 1958; Fejfar, 1961; Dehm, 1962; Terzea and Jurcsak, 1969; Terzea, 1973; Shushpanov, 1977; Fladerer, 1984, 1987; Popov, 1988; Montuire *et al.*, 1994).

Pliopentalagus progressivus Liu et Zheng, 1997, Late Pliocene or Early Pleistocene of China (holotype, from filled karstic pits near Taizishan). The species is represented by two isolated teeth from the type locality (Liu and Zheng, 1997). It is distinguished from the Pliocene species of the genus by larger measurements and deep folds on p3.

Pentalagus furnessi (Stone, 1900), Late Pleistocene to Recent, Amami Oshima and Tokunoshima islands of the Ryukyu Archipelago, Japan. Fossil specimens were found in the Late Pleistocene of Kojima, Tokunoshima Island (Tomida and Otsuka, 1993).

Alilepus zhokoudianensis Cheng, Cao, Tian, et Li, 1995, Early Pleistocene of China (holotype, from the

middle part of the Early Pleistocene of Zhoukoudian Cave). The species is known from the type locality only (Cheng *et al.*, 1995); it is a relict form. In Europe, the latest reliable *Alilepus*, *A. ucrainicus*, was recorded in the Early Villafranchian of the Odessa Catacombs (Gureev, 1964). Hares from the Khapry and Liventsovka localities (Rostov Region; Middle Villafranchian), previously identified as *Lepus* sp. and *Alilepus* sp., probably belong to the genus *Alilepus*.

Sericolagus brachypus (Young, 1927), Late Pliocene to Middle Pleistocene of China; holotype, from Sanjiadian (=Locality, 60); Early Pleistocene. Fossil material was described in the following localities: Early Pleistocene: Shuangyinzi (=Locality 2), Yangshaozun (=Locality 18), Shouyang (=Locality 20), Heshui, and Zhoukoudian; Middle Pleistocene: Jinniushan (Young, 1927, 1935; Teilhard de Chardin and Young, 1931; Bohlin, 1942a, 1942b; Teilhard de Chardin, 1940; Zheng, 1976; Zhang *et al.*, 1993; Cheng *et al.*, 1995; Averianov, 1996).

Caprolagus lapis (Hooijer, 1964), Early Pleistocene of Java, Indonesia (holotype, from Sangiran, Java; Early Pleistocene). The species is represented by isolated teeth from the type locality (Hooijer, 1964; Dawson, 1971). It is distinguished from the Recent *C. hispidus* (Pearson, 1839) from India by a relatively simple structure of p3.

Oryctolagus lacosti (Pomel, 1853), Late Pliocene to Middle Pleistocene of France, Spain, and Portugal (holotype, from Perrier, France; Early Villafranchian). Fossil specimens were found in the Middle Pleistocene of Bagur 2 and Aridos 1, Spain (Lopez Martinez *et al.*, 1976; Lopez Martinez, 1980a).

Oryctolagus cuniculus (Linnaeus, 1758), The Common Rabbit. Early Pleistocene to Recent of Central and Southern Europe and North Africa. Fossil rabbits were recorded in numerous Pleistocene localities of Europe, see reviews by Donard (1981) and Callou (1995). The most important localities were found in the Middle Pleistocene: Lunel-Viel, Pech de l'Azé, Combe-Grenal, and Gavaudun (France); Ambrona and Huéscar 1 (Spain); and Montagnola (Italy); and in the Late Pleistocene: Grimaldi (Italy), Le Morin and Pont d'Ambon (France), and Cueva Millan (Spain) (Serres *et al.*, 1839; Boule, 1919; Fondi, 1972; Mazo *et al.*, 1985; Donard, 1981; Sesé, 1986; Alvarez *et al.*, 1992). Rabbits from the Mindel-Riss are distinguished as a separate subspecies, *O. c. lunellensis* Donard, 1981; those from Riss, as *O. c. grenalensis* Donard, 1981; and Würm rabbits are assigned to the Recent subspecies *O. c. huxleyi* Haeckel, 1874 (Donard, 1981).

Indolagus nigricollis (F. Cuvier, 1823), Pleistocene to Recent of Pakistan, India, Bangladesh, Sri-Lanka, and Indonesia. Fossil specimens were found in the Pleistocene of Karnul Caves near Madras, India (Lydekker, 1886).

Fossil hares of the genus *Lepus* Linnaeus, 1758 are frequently mentioned in studies of the Lower Pleis-

tocene of Eurasia. In the overwhelming majority of cases, the material is not described. The assignment of early finds to the genus *Lepus* (rather than to the other genera of the Leporidae) requires substantiation.

Among the finds of Early Pleistocene hares assigned with certainty to the genus *Lepus* (in the case where p3 or P2 are available), specimens from the following localities should be mentioned: Chishmikiioi (Moldova), Nogaïsk, Cherevychnoe (Ukraine) (Shushpanov, 1977, 1983), Deutsch-Altenburg (Austria) (Fladerer, 1984), Chui-Atasevo (Bashkiria) (Sukhov, 1976). These fossils belong to small hares, limited in size to the range of variation of Recent *L. capensis* (the lengths of p3 from Moldova and southern Ukraine are 3.2, 3.4, and 3.5). At present, it is impossible to determine what species they belong to. P2 from the Chui-Atasevo locality has two enamel folds on the anterior surface, i.e., a large medial fold and a lingual fold. This distinguishes the tooth from P2 of *Hypolagus* and resembles those of the members of the genus *Lepus*.

Lepus timidus Linnaeus, 1758, The Arctic Hare Middle Pleistocene to Recent. Nowadays the species inhabits forest and tundra zones of northern Eurasia. The Recent range of *L. timidus* substantially differs from its Pleistocene range. In Western Europe, the Arctic hare occurs only in northern latitudes (Fennoscandia, Ireland, and Great Britain) and in the Alps (a distinct form, *L. t. varronis*) that is probably associated with both climatic changes in the Holocene and replacement of this species by the European hare *L. europaeus*. On the contrary, the eastern part of the range of *L. timidus* substantially expanded because of the development of forests throughout a vast area of periglacial steppe and the disappearance of *L. tanaiticus*, formerly a characteristic species of this ecosystem; thus, nowadays it reaches the Pacific coast of Russia.

Early *L. timidus* was found in the Middle Pleistocene of Germany: Gunz-Mindel of Sackdilling, Hundsheim, and Mosbach 2 and Mindel of Sudmerberg 2 (Kurten, 1968; Koenigswald, 1972); Czechia: Gunz-Mindel of Zlatyi Kun' (Kurten, 1968); France: Mindel-Riss of Lunel-Viel (Serres *et al.*, 1839); Hungary: Riss 1 of Solymar (Janossy, 1969, 1986); Ukraine: Riss 2 of Starun' (Kormos, 1934b; Kul'chitskii, 1982); and in Moldova: Middle Acheulean bed III of Starye Duruityro Grotto (David, 1980: *Lepus* aff. *timidus*) and the terminal part of the Middle Pleistocene of Sakharna Cave (Lozan, 1970; Lozan and Skramtai, 1972). Arctic hares from the Middle Pleistocene of Central Europe can be referred to the subspecies *L. t. praetimidus* Kretzoi in Janossy, 1969 (holotype, from Solymar Cave, Hungary; Riss 1), characterized by very large size.

In the Late Pleistocene, *L. timidus* was a common species in Western Europe. Thus, several thousand bones of Arctic hares belonging to more than 1000 individuals were found in the Madeleinian beds of Kesslerloch Cave, Switzerland (Heierli, 1907; Koby, 1960b). Arctic hares were found in more than one hundred Late Pleis-

tocene localities of Spain, Portugal, France, Belgium, Great Britain, Italy, Switzerland, Germany, Austria, Czechia, Poland, Yugoslavia, Hungary, Moldova, Ukraine, and Crimea. Apparently, all Late Pleistocene specimens of Arctic hares from Western Europe, except for Great Britain, should be referred to as the subspecies *L. t. wuermensis* Koby, 1960. The following localities of this subspecies are most important: Kesslerloch (Switzerland); La Vache, Jaurens, and Cotencher (France); Urtiaga (Spain); Moggaster Höhle and Villa-Seckendorff (Germany); and Veternica (Croatia) (Rütimayer, 1875; Studer, 1904; Heierli, 1907; Dubois and Stehlin, 1933; Koby, 1960a; Malez, 1963; Altuna, 1970; Lopez Martinez, 1980b; Koenigswald, 1985; Groiss, 1992).

In the Late Pleistocene of Great Britain, there was a substantially larger Arctic hare assigned to the subspecies *L. t. anglicus* Hinton, 1909. It was described from Hutton and Ightham caves (Sanford, 1869; Hinton, 1909).

L. t. ponticus Averianov, 1994, Late Pleistocene of the Crimea (holotype, from Syuren' 1; Aurignacian). It was described in several localities (Dal', 1928; Gromov, 1961; Averianov, 1994). Arctic hares from the Late Pleistocene of Moldova (Lozan, 1970) probably belong to this subspecies.

Lepus tanaiticus Gureev, 1964, Late Pleistocene, periglacial zone of Eastern Europe and Northern Asia (holotype, from the Late Paleolithic Site Kostenki 4, Voronezh Region). Three subspecies were distinguished.

L. t. gmelini Averianov et Kuzmina, 1993, Late Pleistocene (Würm 2/3) of Russia (holotype, from the Paleolithic Site Kostenki 14). The subspecies was only recorded in a humus horizon of the Kostenki Sites (Averianov, Kuz'mina, 1993). It is distinguished from the type subspecies by smaller measurements.

L. t. tanaiticus Gureev, 1964, Late Pleistocene (Würm 3) of Russia, Ukraine, and Northern Kazakhstan (Russian Plain and Ural Mountains). The main localities are Mezhirichi, Novgorod Severskii (Ukraine), Kostenki, Betovo, Nizhnie Karmalki, and Sungir' (Russia) (Vereshchagin and Gromov, 1952; Sukachev *et al.*, 1966; Gureev, 1964; Rekovets, 1985; Rekovets and Topachevsky, 1988; Averianov and Kuz'mina, 1993; Averianov, 1999).

L. t. vereschagini Averianov, 1995, Late Pleistocene, Yakutia (holotype, from Paleolithic Site Berelekh, Yakutia; Sartanian Time). Localities: Berelekh, Aldan River, Adycha River, Dyuktai Grotto, and Mamontova Gora (30-meter-high terrace) (Agadjanian, 1972; Averianov, 1995).

Lepus valdarnensis Weithofer, 1889, Early Pleistocene of Italy (lectotype, from the Late Villafranchian of Upper Valdarno); a large hare, probably closely related to the European hare and Cape hare (subgenus *Eulagos* Gray, 1867) and distinguished by a lesser developed ability for high-speed running (relatively

short limb bones). Some researchers place it in the genus *Oryctolagus*, a synonym of *O. lacosti* (Pomel, 1853). This question demands additional study. Reliable specimens were registered from only the Late Villafranchian of Italy (Weithofer, 1889; Bosco, 1900; Forteleoni, 1974).

Lepus capensis Linnaeus, 1758, The Cape Hare. Early Pleistocene to Recent; savanna, desert, steppe, and highland regions of South, East, and North Africa; Spain; Arabian Peninsula; Near East and Central Asia. The recent range of *L. capensis* has decreased in comparison with the Pleistocene range only in Europe (to date, the species does not inhabit Italy, Germany or Hungary). This may be associated with the disappearance of steppe landscapes in this area in the Holocene. The earliest examples of the species were found in the Late Pliocene of East Africa. Fossil material was described from the localities of Eurasia dated as Middle Pleistocene, Sel'-Ungur (Kyrgyzstan) and Aridos 1 (Spain), and the Late Pleistocene, Teshik-Tash (Uzbekistan) (Gromova, 1949; Lopez Martinez, 1980a; Volozheninov and Krakhmal', 1989).

Fossil material of *L. capensis* was also indicated (without descriptions) in more than 20 Late Pleistocene localities of Spain, Italy, Germany, Hungary, Northern Caucasus, Kazakhstan, Central Asia, Altai, southern part of Western Siberia, Transbaikalia, and China.

L. c. terraerubrae Kretzoi, 1956, Middle Pleistocene of Central Europe (Germany, Hungary, Romania, Italy, and Croatia) (holotype, from Villany 6, Hungary; Gunz-Mindel). The subspecies is poorly understood, isolated teeth were described from the following localities: Nagyarsanyhegy 4 (Hungary), Voigtstedt (Germany), Betfia 5 (Romania), Monte Peglia (Italy), and Podumci (Croatia) (Kormos, 1934a; Kowalski, 1958; Kretzoi, 1965; Terzea and Jurcsak, 1969; Van der Meulen, 1973).

L. c. tolai Pallas, 1778, Late Pliocene(?) to Recent of northern Mongolia, northeastern China, and Transbaikalia. Hares from the Middle Villafranchian of Transbaikalia (Gureev and Erbajeva, 1975) probably belong to this subspecies; some specimens from the Late Pleistocene of China were assigned to the subspecies (Jin *et al.*, 1984).

Lepus europaeus Pallas, 1778, The European Hare. Early Pleistocene to Recent of Europe (except for Scandinavia, Spain, and Ireland), Asia Minor, Transcaucasia, and Kazakhstan. Apparently, the earliest examples of *L. europaeus* were found in the Caucasus, in the Early Pleistocene of the Akhalkalaki locality, in the Acheulean beds of Tsona, Azykh, Treugol'naya, and Kudaro 1 caves; see review (Averianov and Baryshnikov, 1993). Many undescribed specimens referred to as the European hare were indicated in a number of localities of the Middle Pleistocene of Western Europe; the material was described in Hundsheim, Genkingen 2 (Rissian interglacial or Riss-Würm) (Germany), and

Stranska Skala (Czechia) (Freudenberg, 1914; Schirmeisen, 1927; Ziegler, 1995).

Relatively numerous specimens of *L. e. gureevi* I. Gromov, 1952 were found in the Late Pleistocene (Riss or Würm?) of the Binagady locality; some European hares from the Late Pleistocene of Transcaucasia probably belong to this subspecies (Gromov, 1952; Vereshchagin, 1959; Averianov and Baryshnikov, 1993).

L. e. euxinicus Averianov, 1994, Late Pleistocene to Early Holocene of the Crimea (holotype, from Adzhi Koba Cave; Mousterian). The specimens from the Late Pleistocene of Moldova (Lozan, 1970) probably belong to this subspecies of the European hare.

In the Late Pleistocene, *L. europaeus* is relatively common in the southern part of Europe and in Asia; it was found in more than 60 localities of Spain, France, Italy, Yugoslavia, Bulgaria, Hungary, Moldova, Crimea and southern Ukraine, European Russia, Caucasus, and Kazakhstan. Pleistocene finds of *L. europaeus* occur within the Recent range of the species.

Lepus mandshuricus Radde, 1861, Middle Pleistocene to Recent of Far East of Russia and northeastern China. Fossil material was described in the Middle Pleistocene of Jinniushan, China (Zhang *et al.*, 1993); the species was indicated without descriptions in the Late Pleistocene of the Amur Region.

Lepus oiostolus Hodgson, 1840, Early Pleistocene to Recent of the Tibetan Plateau, i.e., eastern India, Nepal, and Western China. Apparently, all specimens of this species from the Early and Middle Pleistocene of China should be assigned to the subspecies *L. o. wongi* Young, 1927 (holotype, from Zhoukoudian; Middle Pleistocene) characterized by larger measurements than the Recent forms. The descriptions of this form were given in the following cases: the Middle Pleistocene of Zhoukoudian, Jinniushan, and Lantian and the Pleistocene of Yenchingkou (Young, 1927, 1930; Colbert and Hooijer, 1953; Chow and Li, 1965; Zhang *et al.*, 1993; Cheng *et al.*, 1995).

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