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Pliocene-Recent Holarctic marmots: overview

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Marmots are one of the ancient group of mammals. Originated at the end of Miocene in the New World the genus *Marmota* survives to the Recent time. During its long history a number of migration events can be recorded on the base of paleontological data. The first invasion occurred at the Late Miocene and the next in the Pliocene when marmots widely distributed across Eurasia. From that time Eurasia probably became a new diversification centre of marmots though in North America continued to be a region for marmot speciation. New marmot invasions from North America occurred as well during the Pleistocene. The list of extant and extinct marmots is given.

KEY WORDS: *Marmota*, diversity, distribution, Holarctic, Pliocene-Recent.

INTRODUCTION

Marmots belong to the family Sciuridae, subfamily Marmotinae, which includes Tamiins and Citellins as well. As compared with the latter, marmots are a relatively young group. First true marmot records are known from the late Middle Miocene of North Amercia (Clarendonian), in contrast to other groups of Sciuridae which appeared in North America much earlier, in the Late Eocene, Chadronian.

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Originated in North America, sciurids dispersed over the Old World. Thus, occasional finds dated to Oligocene are known from Europe and Central Asia (DEVYATKIN 1981, LI & TING 1983, HÖCK et al. 1999). In the course of long history of sciurids there were probably several events of migration from North America to Eurasia and, in all probability, back again.

There is no general agreement as to the origin and ancestors of the genus *Marmota*. It has been suggested that this rodent group is close to the northamerican genus *Paenemarmota* and probably derived from *Protospermophilus* (BLACK 1963). However, it was shown that both genera are far from marmots (REPENNING 1962, KOENIGSWALD 1990).

The most ancient taxon, *Marmota vetus* (Marsch 1871) is known from the latest Middle Miocene (Clarendonian) site Loup Fork Beds in northern Nebraska; and another Late Miocene (Hemphilian) species *Marmota minor* (Kellogg 1910) was found in Thousand Creek site, Humboldt County, in Nevada (BLACK 1963). The next archaic species *Marmota sawrockensis* Hibbard 1964 was recorded in Sawrock and Buis Ranch sites (Kansas and Oklahoma). This species belongs to the transitional Hemphilian-Blancan faunas (the earliest Blancan or Hemphilian-Blancan, which corresponds to the early stage of Ruscinian or Early Pliocene) (SAVAGE & RUSSELL 1983). These data allow to conclude that North America was the home range of the genus *Marmota*.

Some investigators, however, were of opinion that this genus originated in Central Asia (BAZHANOV 1947), in Western Mongolia in particular (SCALON 1950).

Another disputable issue is the environments where ancient marmots first appeared. There is still agreement on the kind of terrain (plain and mountains) and type of landscape (forest or steppe) initially inhabited by marmots. ZIMINA & GERASIMOV (1980) pointed to HAMILTON's (1934) suggestion that marmots were initially forest animals and colonized open treeless territories later. Conversely, BAZHANOV (1947) and ANDRUSHKO (1955) are of opinion that appearance of ancient marmots in Asia was connected with plain steppe, and only later they penetrated into mountain regions. Following the opinion of BANNIKOV (1954), BIBIKOV (1989) mentioned mountains as initial landscapes for marmot group.

MARMOT DIVERSITY AND THEIR MIGRATION EVENTS

Based on the Miocene marmot records in North America, KOENIGSWALD (1990) was of the opinion that Eurasian species are immigrants from the New World. Clearly, marmotins developed and diversified in North America, as evidenced by paleontological data. The analysis of extant taxa and fossil records gives grounds for supposition that marmot invasions from North America to Eurasia occured repeatedly during the Late Cenozoic.

It is known that a land bridge existed between Eurasia and North America at the second half of Late Miocene; it served as a migration way from Old to New World and back for cervids, proboscidians, lagomorphs and other group of mammals, including marmots (SHOTWELL 1956, TOBIEN, 1976, VISLOBOKOVA 1990).

It is not inconceivable that the first true marmot invasion could happened during the Late Miocene as suggested by their first record in Asia. SHEVYREVA (1968) mentioned marmot specimens close to the New World *Marmota vetus* from the Saryblak formation in Zaissan Depression of Kazakhstan.

The next marmot migration event might have happened at the end of Early Pliocene-beginning of Middle Pliocene, when the next Beringian land bridge appeared. It may be assumed that marmots could reach at that time as far as the south of Siberia. In particular, fossil remains of the Middle Pliocene *Marmota tologoica* are known from Transbaikalian sites of Tologoi 1 and Beregovaya (VERESHCHAGIN et al. 1960, RAVSKI et al. 1964, IVAN'EV 1966, ERBAJEVA 2003, ALEXEEVA 2005). This species was a characteristic form of the hipparion faunas, which inhabited the savanna like forest steppe. At that time in the region featured temperate warm and rather dry climate and mosaic type landscapes. In all probability, marmots, in common with ochotonids and cementless voles *Villanyia,* were steppe dwelling animals inhabiting open landscapes with scarce shrubs.

As follows from the paleontological data, marmots penetrated into Eastern Europe at that time; in the Western Ukraine they inhabited savanna-like landscapes (TATARINOV 1969) which were widely distributed then in Northern Eurasia.

In North America contemporary species was recognized as *Marmota arizonae* Hay 1921.

Based on abundant paleontological data, it is possible to assume that Eurasia became a new diversification centre of marmots during the Pliocene. At the end of Late Pliocene they were of widespread occurrence in Eurasia. They are known from a number of sites in the south of Eastern Europe, such as Port Katon, Il'inka, Uryv 4 (AGADJANIAN 1970, MARKOV 1976). In Asia their remains are known in Klochnevo I, Western Transbaikalia (*Marmota* sp.) and in Northern Korea (*Marmota tomanensis*) (TOKUNAGA & MORRI 1939, ERBAJEVA 1998).

It may be suggested with fair confidence that highly diversified and widely distributed marmots could easily populate southern regions of Eurasia. Some of them could occupy mountain regions and became adapted to mountains of the Central and Middle Asia and to elevated regions in Europe. They are believed to become ancestral forms of some modern Eurasian mountain taxa, such as *Marmota himalayana, M. menzbieri* (now restricted in range), *M. caudata* (with peculiar primitive features) and others.

The next new invasion of marmots from New World to Eurasia could have happend during the Early Pleistocene when an extensive faunal exchange between these two continents took place. At present *Marmota monax* has a wide range in North America, from eastern Alaska to eastern Labrador, to southern shore of the Hudson Bay and to the Rocky Mountains and Great Plains. Fossil remains of this species were identified at 25 Pleistocene-Holocene localities from Arkansas to Pennsylvania, the earliest occurrences being dated to late Irvingtonian (Cumberland and Trout Caves) (KURTEN & ANDERSON 1980). It may be safely suggested that ancient forms of this species — inhabitants of forests — could migrate to Eurasia and populate woodland regions with open biotopes; they could be ancestors of some recent species such as *M. baibacina* and *M. kastschenkoi*. At that time in Eurasia marmots probably continued their diverisification and migrated further westwards.

Their extinct forms are known in Western Europe from Gran Dolina in Atapuerca (Spain), Podumci and Tatinja Draga (Croatia), Montousse 5 (France), Deutsch Altenburg (Austria) (MAUL 1990, CUENCA BESCOS et al. 1999, PAUNOVIC & RABEDER 2000, CUENCA BESCOS & CANUDO 2006).

In Asia the Early Pleistocene marmots are known from localities Zasukhino 2 and 3, Western Transbaikalia, Siberia; from Nalaikha, Mongolia; from Choukoutien 18, China (TEILHARD DE CHARDIN 1940, ZHEGALLO et al. 1982, ERBAJEVA 2003).

Another extant species *Marmota flaviventris* is distributed over vast areas in North America. Its range, however, was more wider in the past; its fossil remains have been recovered from a number of Pleistocene-Holocene localities far south of its present range (HOWELL 1915, LANGE 1956, HARRIS 1970, ANDERSON 1974). Recently the fossils have been recorded in the Irvingtonian sites of Colorado (Badger Room, Pit, Gypsum room a.o.) (BARNOSKY et al. 2004, SHABEL et al. 2004).

At the Middle Pleistocene marmotins were widely distributed in Eurasia though they were not abundant. *Marmota bobak paleoplanicola* was described by GROMOV et al. (1965) in the faunas of the south of Eastern Europe. In Asia, in Northern China *Marmota* cf. *bobak* of that age has been recovered from Choukoutien 1; and *Marmota mantchurica*, *M. robusta* and *M. bobac sibiricus* are known from Ku-Hsiang-Tung near Harbin, Manchoukuo (Northern China) (TOKUNAGA & NAORA 1939). The remains of *Marmota caudata* subsp. foss. were found in Tajikistan at the archaeological site Aman-Kutan, the Zeravshan range. In Western Transbaikalia *Marmota sibirica nekipelovi* close to the modern *M. sibirica* was described by ERBAJEVA (1966). More scarce fossil remains of marmot with dominant characters of *M. camtschatica* were collected in Western Transbaikalia (Zasukhino 8) too (AGADJANIAN & ERBAJEVA 1983). Based on the paleontological data from this area it can be assumed that the formation of both recent taxa (*Marmota sibirica* and *M. camtschatica doppelmayri*) took place at that time.

It is highly probable that periglacial conditions of the Late Pleistocene with cold and dry climate was favorable for marmots; the latter became a permanent component of the Old World faunas (as follows from their presence in abundance in many localities in Eurasia). In Europe *Marmota primigenia* Kaup, *M. bobak paleorossica* I. Grom., *M*. cf. *bobak, M*. cf. *marmota* are recorded (KRETZOI 1954, CHALINE 1972, ZIMINA & GERASIMOV 1980, KALTHOFF 1999). Vast areas in Asia, from Northern Caucasus, through Kazakhstan, West Siberia, Transbaikalia and Northern China to the Chukchi Peninsula in the North East, were inhabited by extinct marmots similar to the modern species; and the most of them are found within the area of their recent distribution. Northernmost finding of extinct *Marmota camtschatica vaskovskii* occurred in north-eastern part of Anadyr Range.

In the New World, Late Pleistocene-Holocene records of extant species *M. flaviventris* and *M. monax* are known from a number of sites in North America, as it was mentioned above.

The modern Holarctic marmot fauna contains 15 species: two are known in Europe, six in North America and eight in Asia (Table 1).

Analysis of the distribution area, biogeographic history and ecology of extant marmots has shown the most of species being mountain inhabitants. Thus, *Marmota himalayana* (Hodgson 1841) occupies high mountain forest-steppe, steppe and deserts of the Central Asia: from western Kunlun to eastern

Table 1.

Classification of marmots († extinct species).

Order Rodentia Bowdich 1821
Family Sciuridae Fischer de Waldheim 1817
Subfamily Marmotinae Pocock 1923
Tribe Marmotini Pocock 1923
Genus *Marmota* Blumenbach 1779

Marmota himalayana (Hodgson 1841)
† *M.* cf. *himalayana robusta* (Milne-Edwards 1870)
Marmota bobak (Müller 1776)
† *M. bobak paleoplanicola* (I. Gromov 1965)
† *M. b. paleorossica* (I. Gromov 1965)
Marmota baibacina (Kastschenko 1899)
Marmota sibirica (Radde 1862)
† *M. sibirica nekipelovi* Erbajeva 1966
Marmota camtschatica (Pallas 1811)
† *M. camtschatica vaskovskii* I. Gromov 1965
Marmota menzbieri (Kaschkarov 1925)
Marmota marmota (Linnaeus 1758)
Marmota caligata (Eschscholz 1829)
Marmota olympus (Merriam 1898)
Marmota vancouverensis (Swartz 1911)
† *Marmota vancouverensis* (subfoss.) (Swartz 1911)
Marmota caudata (Geoffroy 1844)
† *M. caudata* subsp.? (foss.) (I. Gromov 1965)
Marmota flaviventris (Audubon & Bachman 1841)
† *M. flaviventris* Audubon & Bachman (foss.)
Marmota monax (L. 1758)
† *M. monax hessi* Simpson 1949
Marmota broweri Hall & Gilmore 1934
Marmota kastschenkoi (Stroganov & Judin 1956)
† *Marmota vetus* (Marsch 1871)
† *Marmota minor* (Kellogg 1910)
† *Marmota sawrockensis* Hibbard 1964
† *Marmota arizonae* Hay 1921
† *Marmota tologoica* Ivanijev 1966
† *Marmota tomanensis* Tokunaga & Morri 1939
† *Marmota mantchurica* Tokunaga & Naora 1939
† *Marmota primigenia* (Kaup 1839)

Nanshan, and ranges of Sichuan and Yunnan, as well as Tibet and Hymalaya (Gromov et al. 1965). Another species *Marmota caudata* (Geoffroy 1844) inhabits alpine meadows of Tien Shan, Pamir, Hindu Kush and Kashmir, while *Marmota menzbieri* Kaschkarov 1925 occupies a limited area in alpine zone of Tien Shan high mountains. Yet another Asian species *Marmota camtschatica* (Pallas 1811) occurs in high mountains of East Siberia, southern Yakutia and the north-east of Asia (Kolyma and Kamchatka uplands), though it has never been found in North America. Extinct northernmost marmot *Marmota camtschatica vaskovskii* was found on north-eastern part of Anadyr range (Gromov et al. 1965).

The European species *Marmota marmota* (Linnaeus 1758) occupied alpine meadows of Western and Central Europe (the Alps and High Tatra).

Four New World marmots are typical mountain species: *Marmota caligata* (Eschscholz 1829) inhabits mountain tundra and open landscapes of the north-west and west of North America, *Marmota broweri* Hall & Gilmore 1934 is found in Brooks Range of northern Alaska and *Marmota olympus* (Merriam 1898), in alpine zone of the Olymp Peninsula mountains in north-west of North America. The peculiar endemic species *Marmota vancouverensis* (Swartz 1911) is characteristic for high mountains of Vancouver Island.

Several species are inhabitants of the mosaic type landscapes in Eurasia (*M. baibacina*), Asia (*M. sibirica*) and North America (*M. flaviventris*).

Marmota flaviventris (Audubon & Bachman 1841) occurs in the western United States. It occupies arid habitats at low to mid elevations of British Columbia, semi-deserst on the Columbia Plateau and Snake River Plains; in the Great Basin it occurs everywhere in woodlands and at forest openings up to the alpine zone (Frase & Hoffmann 1980).

Marmota baibacina (Kastschenko 1899) inhabits mountain steppes and alpine meadows of West Siberia and Tuva (Russia), north-western Mongolia, eastern Kazakhstan, Kirgizia, north-west Xinjiang in China.

Marmota sibirica (Radde 1862) occupies steppes of plain and low-mountains of Transbaikalia, alpine meadows in Tuva, northern and Central Mongolia, north-west and north-east of China.

The last three species are inhabitants of lowlands. Among them, *Marmota monax* (L. 1758) occupies open biotopes in the forest zone from eastern Alaska to the southern shore of Hudson Bay, eastern Labrador, extending southward into the Rocky Mountains and eastern Great Plains. *Marmota bobak* (Müller 1776) lives in steppes of plain territories of Eastern Europe and northern Kazakhstan, as well as in low-mountains of Mongolia. *Marmota kastschenkoi* (Stroganov & Judin 1956) has limited area of distributions, inhabiting piedmont steppes in the south West Siberia and northern part of the Altai Mountains (Taranenko 2005, 2008).

CONCLUSIONS

The genus *Marmota* has an origination in the late Middle-Late Miocene of North America. During their long history three main westward dispersals occurred: at the Late Miocene, at the late of Early Pliocene and at the Early Pleistocene. From the Pliocene the Eurasia became a new diversification centre of marmots in parallel with North America.

Seventeen fossil taxa are recognized all over Holarctic from the Late Miocene through Holocene and at present time 15 living species are known in modern faunas of the world.

Of 15 extant species, only 9 living species of *Marmota* — *Marmota himalayana*, *M. bobak*, *M. marmota*, *M. caudata*, *M. sibirica*, *M. camtschatica*, *M. flaviventris, M. monax* — have fossil records and subfossil data are known for *M. vancouverensis* (Nagorsen & Cardini 2009) (Tables 1, 2).

Table 2.

Chronological and geographical distributions of the genus *Marmota*.

Geochronology		Europe	Asia	North America
Recent time		*Marmota marmota* *Marmota bobak*	*Marmota himalayana* *Marmota bobak* *Marmota caudata* *Marmota menzbieri* *Marmota baibacina* *Marmota sibirica* *Marmota camtschatica* *Marmota kastschenkoi*	*Marmota caligata* *Marmota flaviventris* *Marmota vancouverensis* *Marmota olympus* *Marmota monax* *Marmota broweri*
Holocene		*Marmota bobak* *Marmota* cf. *bobak*	*Marmota sibirica* *Marmota* sp.	*Marmota monax* *Marmota flaviventris*
Pleistocene	late	*Marmota* cf. *bobak* *Marmota* aff. *bobak* *M. bobak paleoplanicola* *M. bobak paleorossica* *Marmota marmota* *Marmota primigenia* *Marmota* sp.	*Marmota* cf. *sibirica* *M.* cf. *camtschatica* *M. camtschatica vaskovskii* *Marmota* cf. *baibacina* *Marmota* sp.	*Marmota* cf. *flaviventris* *Marmota monax hessi*
	middle	*Marmota primigenia* *Marmota bobak* *Marmota marmota* *Marmota* sp.	*Marmota bobak* *M.* cf. *himalayana robusta* *M. sibirica nekipelovi* *Marmota mantchurica* *Marmota* cf. *caudata* *Marmota* sp.	*Marmota* aff. *monax*
	early	*Marmota* cf. *marmota* *Marmota* cf. *bobak* *Marmota* sp.	*M.* cf. *himalayana robusta* *Marmota* sp.	
Pliocene	late	*Marmota* sp.	*Marmota tomanensis* *Marmota* sp.	
	middle		*Marmota tologoica*	*Marmota arizonae*
	early			*Marmota sawrockensis*
Miocene	late		*Marmota* sp. aff. *Marmota vetus*	*Marmota minor* *Marmota vetus*

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