Ann. Naturhist. Mus. Wien	108 A	165–171	Wien, September 2007

Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications

Editor: Gudrun DAXNER-HÖCK

5. Lagomorpha (Mammalia): preliminary results

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Manuscript submitted on May 18th 2006,
the revised manuscript on February 2nd 2007

(With 1 text-figure and 1 table)

Abstract

The detailed study of lagomorphs from the Valley of Lakes yielded 45 different taxa from 88 Early Oligocene to Late Miocene localities. Lagomorphs of the Valley of Lakes belong to 3 families. The most abundant and diverse groups are palaeolagins and ochotonids.

Introduction

Lagomorphs are one of the ancient mammalian groups known from the Paleogene of Central Asia (MCKENNA & BELL 1997). They are significant elements of the Mongolian Cenozoic faunas, as well as in those of the Valley of Lakes. The first information on Paleogene lagomorphs was obtained by the Central Asiatic Expeditions of the American Museum of Natural History (AMNH) under the leadership of R.C. ANDREWS in 1923–1924. Later, large samples of the Oligocene lagomorphs were collected by the Soviet-Mongolian Paleontological Expeditions during 1948-1949 and by the Polish-Mongolian Expeditions during the 1960s. These materials were analyzed by GUREEV (1960, 1964) and SYCH (1975).

The material studied in this paper was collected by a joint Austrian-Mongolian project (FWF-P: 10505-GEO) during fieldwork from 1995–1997 in more than 90 localities. The preliminary list of lagomorphs, which included 26 species from 87 Oligocene-Miocene localities, was given by ERBAJEVA and DAXNER-HÖCK (2001). Further detailed studies increased this number to 45 species (Tab. 1).

Most of the material from the localities in the Valley of Lakes is represented by isolated teeth; however, there are some fragments of lower jaws and fragments of skull with different types of teeth or without teeth. To recognize and to define more precisely lagomorph taxa from Mongolia, the holotypes of several Asian lagomorph species were

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studied for comparison, in particular in the following collections: AMNH, New York (site Hsanda Gol); Paleontological Institute RAS (PIN RAS), Moscow (site Tatal Gol); Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing (several Oligocene and Miocene sites, and type collections of Sino-Swedish Expeditions, collected and studied by Birger BOHLIN 1937 and 1942); National Museum of Natural History (NMNH), Paris (site San-tao-ho or Saint-Jacques); Claude Bernard University (UCBL), Lyon, Villeurbanne, France (European lagomorphs).

Detailed studies and comparative analyses of the taxa from Mongolia with the species from other localities of Central Asia revealed the existence of a high variety of lagomorphs in the Valley of Lakes, especially within the genus *Desmatolagus*. Twenty-four different species are referred to this genus. A relatively high species diversity also occurs in the genus *Sinolagomys*, which includes 10 species. In this paper, *Ochotonolagus argyropulo* from Tatal Gol described by GUREEV (1964) is not considered as a valid taxon, but a synonym of *Sinolagomys majori*.

Leporid fossils are quite scarce in the Valley of Lakes because they are represented mainly by isolated lower teeth. In a preliminary paper (ERBAJEVA & DAXNER-HÖCK 2001) they were classified as *Gobiolagus* sp. However, their comparison with the type species and samples from San-tao-ho showed that such leporids belong to the genus *Ordolagus* DE MUIZON, 1977.

A few isolated teeth are close to the European amphilagins, and they are referred to the genera *Amphilagus* and *Eurolagus*.

Among Mongolian lagomorphs, representatives of the genus *Bohlinotona* DE MUIZON, 1977 have been found. They belong to two different taxa, differ from the nominative species *Bohlinotona pusilla* (TEILHARD DE CHARDIN, 1926), and were referred to new species.

Systematics

In the present paper I follow the classification of the order Lagomorpha given by GUREEV (1964). Accordingly, the order includes, in addition to Leporidae and Ochotonidae, the family Palaeolagidae. The classification of lagomorphs is based mainly on the structure of skull and cheek teeth and, in recent forms, also on the pelage coloration and chromosomes number.

The fauna from the Valley of Lakes includes representatives of three families: Leporidae, Palaeolagidae and Ochotonidae.

The family Palaeolagidae consists of two subfamilies – Palaeolaginae and Amphilaginae. The representatives of the subfamily Palaeolaginae are the most diverse in number of species and abundant in number of specimens. They are characterized by the rather low crowned cheek teeth, of which the upper ones have three roots, two smaller external and larger internal. Lower teeth consist of trigonid and talonid and also a third conid (lophid), which existed as a usual in young individuals. The representatives of the second subfamily Amphilaginae are rather scarce and they appeared at the beginning of the Miocene.

The family Ochotonidae appeared in the Middle Oligocene and consists of two subfamilies - Synolagomyinae and Ochotoninae. Synolagomyinae are particularly abundant and include several species which differ from desmatolagins in lacking cheek teeth roots; moreover, their tooth crown is much higher than in desmatolagins. Ochotoninae first appeared in the Early Miocene and are represented by the genus *Alloptox*, which in the Late Miocene is replaced by the genus *Ochotona*. These genera are characterized by rootless evergrowing cheek teeth, high tooth crown, equal width of trigonids and talonids on P_4 and M_2 and in upper teeth hypostria that became deeper.

Leporids are represented by the sole genus *Ordolagus.*

Some lagomorph taxa are given in open nomenclature because their fossils are represented only by isolated teeth.

Biostratigraphy
(Tab. 1)

The chronological and stratigraphic distribution of lagomorphs are arranged according to the biozonation of Cenozoic sediments established in Central Mongolia by DAXNER-HÖCK et al. (1997) and HÖCK et al. (1999). Seven biozones (A; B; C; C/1; D; D/1; E) were recognized, each of them characterized by specific rodent assemblages, lithostratigraphic positions and geological age (controlled by Ar/Ar-dating).

In this stratigraphic succession, the desmatolagins are the oldest group and they are dominant throughout the Oligocene, surviving up to the Early Miocene. The Early Oligocene faunas include only representatives of the genus *Desmatolagus*, among which *D.* cf. *vetustus*, a survivor of Late Eocene, is worthy of mention.

The leporid remains are scarce in the Oligocene faunas of the Valley of Lakes; they belong to the genus *Ordolagus*. In the Asian Eocene, however, leporids were rather diverse and abundant; the faunas included the genera *Strenulagus*, *Lushilagus*, *Shamolagus*, *Dituberolagus* and *Gobiolagus*, which did not survive to the Oligocene (MENG et al. 2005).

The ochotonids appeared in the Middle Oligocene. They were represented by the genera *Bohlinotona* and *Sinolagomys* of the subfamily Sinolagomyinae, a characteristic element of the Middle and Late Oligocene and Early Miocene faunas of Central Mongolia. At the beginning of the Miocene, a new genus (*Bellatona*) of sinolagomyins and of ochotonins (*Alloptox*) appeared in the fauna. For the Early and Middle Miocene stage, a high diversity and a significant variety of lagomorphs are characteristic. They belong to 18 different taxa of 6 genera - *Desmatolagus*, *Amphilagus*, *Eurolagus*, *Sinolagomys*, *Bellatona* and *Alloptox* (Table 1). Toward the Late Miocene the diversity of lagomorphs decreased and all Paleogene and Early Neogene genera disappeared, whereas the new genus *Ochotona* appeared in the faunas and survived to the Recent.

Tab. 1: Stratigraphic distribution of lagomorphs from the Valley of Lakes

			Oligocene				Miocene			
		Taxa	A	B	C	C/1	D	D1/1	D1/2	E
Palaeolagidae	Palaeolaginae	*Desmatolagus* cf. *vetustus*	+							
		Desmatolagus gobiensis	+	+	+					
		Desmatolagus cf. *gobiensis*	+	+	+	+	+			
		Desmatolagus sp. (aff. *gobiensis*)		+						
		Desmatolagus cf. *robustus*		+						
		Desmatolagus sp. (aff. *chinensis)*	+		+	+				
		Desmatolagus youngi	+	+						
		Desmatolagus cf. *youngi*	+	+			+			
		Desmatolagus sp. (aff. *youngi)*	+							
		Desmatolagus ex gr. *youngi*	+							
		Desmatolagus orlovi			+					
		Desmatolagus cf. *orlovi*	+	+	+		+			
		Desmatolagus sp. (aff. *orlovi)*		+						
		Desmatolagus ex gr. *orlovi*					+			
		Desmatolagus sp. (aff. *simplex)*			+					
		Desmatolagus cf. *simplex*					+			
		Desmatolagus sp. 1	+	+	+		+			
		Desmatolagus sp. 2	+		+					
		Desmatolagus sp. 3	+		+					
		Desmatolagus sp.	+	+	+	+	+			
		Desmatolagus sp. A		+	+					
		Desmatolagus sp. (aff. *periaralicus)*			+					
		Desmatolagus cf. *shargaltensis*			+					
	Amphi laginae	*Amphilagus* sp. 1					+			
		Amphilagus sp. 2					+			
		Amphilagus sp. 3					+			
		Eurolagus aff. *fontannesi*					+			
Leporidae		*Ordolagus* cf. *teilhardi*		+	+					
		Ordolagus sp.		+						
Ochotonidae	Sinolagomyinae	*Bohlinotona* sp. (large)		+		+				
		Bohlinotona sp. (small)			+	+				
		Sinolagomys cf. *major*		+	+	+	+			
		Sinolagomys cf. *kansuensis*			+		+			
		Sinolagomys sp. A			+					
		Sinolagomys sp. AB				+				
		Sinolagomys ulungurensis					+			
		Sinolagomys cf. *ulungurensis*				+	+			
		Sinolagomys sp.		+		+	+			
		Bellatona cf. *kazakhstanica*					+			
		Bellatona sp.						+		
	Ochotoninae	*Alloptox minor*					+	+		
		Alloptox gobiensis						+	+	
		Alloptox cf. *gobiensis*							+	
		Ochotona lagreli								+
		Ochotona minor								+

Paleoenvironmental implications

The mammal faunal analysis and the study of evolutionary development of different lagomorph lineages show that the significant reorganizations in the lagomorph complex as well as in terrestrial biota of the Central Asia took place in the Paleogene.

The whole area of Northern Eurasia in the Paleocene was dominated by thermophilic forest vegetation of tropical and subtropical types (Zoogeography 1974). Such types of paleolandscapes continued to exist during the Eocene. They were occupied by warm-adapted mammals that preferred forest and swamp biotopes. Among the lagomorphs in Late Eocene faunas, leporids were rather abundant; they were dominant forms, whereas desmatolagins were scarce at that time (Meng et al. 2005). One feasible scenario is that rooted leporids and low crowned desmatolagins were inhabitants of subtropical open woodland with meadows. Progressive cooling and aridization, which started from the Middle Eocene and continued through the Early Oligocene, resulted in a gradual decrease in temperature. Deep subtropical forests vanished and open landscapes with open woodland and xerophytic vegetation appeared; the climate became moderately warm (Zoogeography 1974; Berggren & Prothero 1992). This paleoenvironmental reorganization led to the disappearance of archaic leporids, which are absent in the Early Oligocene lagomorph fauna. At that time, desmatolagins became a dominant and diverse group among lagomorphs. Among large mammals, the inhabitants of subtropical forest and swamp biotopes decreased and those of open landscapes appeared (Zoogeography 1974). The continuation of progressive cooling during the Middle Oligocene caused diversification of small mammals, in particular of lagomorphs. Besides the desmatolagins, three additional new taxa appeared in the fauna. Leporids are scarce, represented by species with high crowned rootless evergrowing teeth. The genus *Sinolagomys* includes rootless *S. major* and rooted small *Sinolagomys* sp. The genus *Bohlinotona* is represented by rooted forms, but the morphological structures of their teeth show a tendency towards lengthening of the tooth crown, as evidenced by its significant curvature. Lack of roots and a tendency towards hypsodonty indicate the adaptation of lagomorphs to open landscapes and to feeding on grass. With gradual aridization of the climate, the distribution of open landscapes expanded. All Asian ochotonids of the genera *Sinolagomys* and *Bohlinotona* lack teeth roots; they became steppe dwellers of xerophytic areas. At the Late Oligocene and during the Early and Middlle Miocene, the numbers of desmatolagins significantly decreased, and the diversity of amphilagins and ochotonids increased (Fig. 1). The latter were represented at that time by the genera *Amphilagus*, *Eurolagus*, *Sinolagomys*, *Bellatona* and *Alloptox*. Further aridization and cooling resulted in disappearance of archaic species at the Late Miocene. The only genus, *Ochotona*, a typical steppe inhabitant, appeared and became dominant.

As shown in Fig. 1, inhabitants of woodland forests, mainly desmatolagins, gradually decreased from the Early Oligocene towards the Early Miocene because open landscapes expanded considerable during the Middle Oligocene through the Late Miocene in Central Asia. Ochotonids, being steppe dwellers, increased in number and diversity from the Late Oligocene to the end of the Miocene.

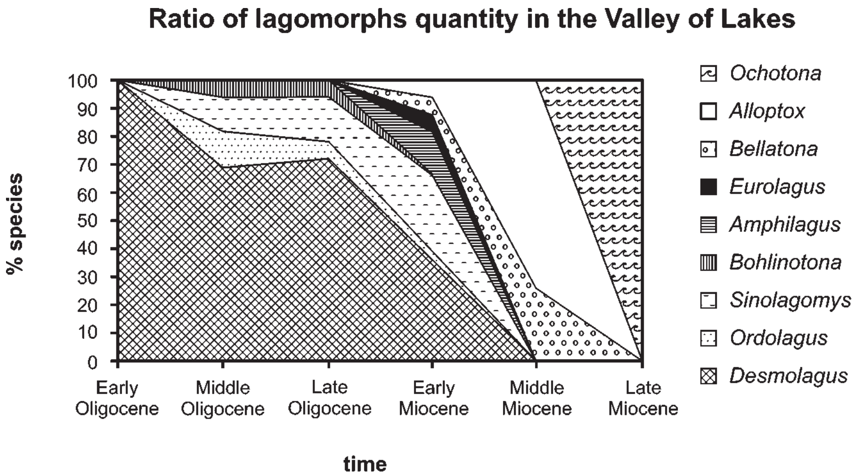

Fig. 1: Lagomorph composition showing dynamics of Oligocene-Miocene landscapes.

Acknowledgments

The research on Mongolian lagomorphs was supported by the Austrian Science Fund (FWF) grant P-10505-GEO and P-15724-N06 in part by the Russian Fund of Basic Research, current grant N 05-05-97212. I am grateful to G. Daxner-Höck for professional assistance and valuable discussion on Mongolian faunas, I thank Mrs. Eva Höck for her important help with collections. The author thanks colleagues from several Institutions for help to study lagomorph collections: Ch. Li, W. Wu, Zh. Qiu, Sh. Zheng, (IVPP, Beijing, China); R. Tedford, L. Marcus, M. McKenna (AMNH, New York, USA); M. Hugueney, P. Mein (UCBL, Lyon, Villeurbanne, France); S. Sen (MNHN, Paris, France); V. Reshetov, A. Lopatin (PIN RAS, Moscow). I thank the reviewer for valuable comments.

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