2012

Biodiversity and Evolutionary Development of Oligocene-Pliocene Lagomorphs (Lagomorpha, Mammalia) of Mongolia

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Erforsch. biol. Ress. Mongolei (Halle/Saale) 2012 (**12**): 47–54

Biodiversity and evolutionary development of Oligocene-Pliocene lagomorphs (Lagomorpha, Mammalia) of Mongolia

M.A. Erbajeva

Abstract

Lagomorphs (pikas and hares) are an ancient group of small mammals originated in Asia in the Paleocene-Eocene. The earliest evidence of their presence in Mongolia is dated to the Early Oligocene. The taxa flourished during the Late Oligocene, Miocene and Pliocene; at the Late Pliocene they were reduced both in their diversity and in abundance. No data on lagomorph are known from the Pleistocene and Holocene, though there are 7 taxa of lagomorphs present in the modern fauna. Altogether, more than 50 lagomorph species, extinct at present, are known to have existed in Mongolia since the Oligocene through the Late Pliocene.

Key words: Lagomorpha, biodiversity, dispersal, Oligocene, Miocene, Pliocene, Mongolia

1. Introduction

The presented materials on the Oligocene-Pliocene lagomorphs have been obtained by extensive studies of localities in Mongolia, specifically of the Valley of Lake (Central Mongolia) and Shamar and Bural Obo localities (Northern Mongolia) (ERBAJEVA 1988, ERBAJEVA & DAXNER-HOCK 2001).

Central Asia is known to have been a centre of the lagomorph origin which dates from the late Paleocene – early Eocene (GUREEV 1964, DAWSON 1967). The earliest records on stem group of lagomorphs are known from the Paleocene – the beginning of the early Eocene (MATHEW & GRANGER 1923, BOHLIN 1951, LI 1965, DASHZEVEG & RUSSEL 1988, LI & TING 1985, SHEVYREVA 1994, ASHER et al. 2005, LOPEZ MARTINEZ 2008). During the last decade some early Eocene lagomorphs were discovered in India and regarded as leporid-like forms on the basis of their ankle bones; the closest to them are archaic lagomorphs from of China identified by calcanei bones and dated to middle Eocene (ROSE et al. 2007). The middle Eocene fossils are also known from Kyrgyzstan (AVERIANOV 1991, SHEVYREVA 1995, AVERIANOV & LOPATIN 2005).

In the middle Eocene the lagomorph order increases in abundance and diversity. Among the fossils several genera have been identified, such as *Lushilagus, Shamolagus, Gobiolagus, Dituberolagus, Hypsimilus, Dawsonolagus, Strenulagus, Desmatolagus, Aktashmys*. Judging from their wide variety, one may safely suggest an appearance of different lagomorph families. So, the first 7 genera of the listed above may be attributed to the Leporidae family, while the last two genera – *Desmatolagus* and *Aktashmys* – to families Palaeolagidae and Mimotonidae respectively (LI 1965, ZHAI 1977, TONG LEI 1987, MENG & HU 2004, MENG et al. 2005, AVERIANOV & LOPATIN 2005, LI et al. 2007). All the above mentioned lagomorph taxa were inhabitants of Asia. There is material evidence of lagomorphs migrating from Asia to North America in the early Eocene using the Beringian land bridge as a passway (ZOOGEOGRAPHY 1974, DAWSON 2007). The land bridge, however, did not persist for long; the connection between the two continents was broken and they became separated by the sea (HOPKINS 1959). Since the middle Eocene lagomorphs of the New World evolved under conditions of isolation. Such a situation appeared favorable enough for the evolutionary development and diversification of the taxa in North America. Dominant were endemic leporid genera *Tachylagus, Mytonolagus, Megalagus, Chadrolagus* and

Litolagus, whereas *Paleolagus* were rather scarce and ochotonids did not exist on the American continent at that time (DAWSON 2007).

At the end of Eocene – beginning of Oligocene Europe was linked to Asia by the Turgai land bridge across which the first invasion of lagomorphs into Europe occurred (ZOOGEOGRAPHY 1974). It happened during so called "Grande Coupure" (great break) event. The earliest European lagomorph was recognized as *Desmatolagus* sp. (LOPEZ MARTINEZ, THALER 1974). Supposedly, the environment in Europe became favorable for the lagomorph to evolve and diversify. New genera – *Titanomys, Amphilagus* and *Piezodus* – appeared in Europe in the late Oligocene, the first two of them survived through middle Miocene, and *Piezodus* became the ancestor form for the genus *Prolagus*. The genera *Piezodus* and *Prolagus* represent specific lagomorphs with pika adaptations; they are considered to belong to the family Prolagidae spanning the interval from the Late Oligocene through the Holocene.

Ochotonids represented by such endemic forms as *Marcuinomys, Lagopsis, Paludotona*, *Proochotona*, *Albertona* (LOPEZ MARTINEZ 1986), appeared in Europe at the beginning of Miocene and flourished till the middle of Pliocene. In contrast to them, leporids were very scarce in Europe at that time; they developed since the latest Miocene through Pliocene and Pleistocene and continue to exist at present.

In Asia finds of lagomorph fossils are abundant and diversified. Below we discuss the evolution of some most abundant taxa in Mongolia using also data from adjacent areas of China, Transbaikalia and Kazakhstan. The purpose of this study is to review the diversity and development of the Oligocene-Pliocene lagomorphs in Mongolia; we do not consider the later stage of their evolution because of the gap in Pleistocene and Holocene fossil record.

2. Material and methods

The studied specimens belonging to more than 40 taxa were collected from numerous (> 80) localities in the Valley of Lakes. Rodent assemblages used as the basis for stratigraphy permitted to distinguish 7 biozones (DAXNER-HOECK, BADAMGARAV 2007). Data on lagomorphs are in good agreement with these biostratigraphic units. A number of localities in Mongolia provided materials dated to the Pliocene (DEVIATKIN 1981, ZAZHIGIN 1989).

All the investigated materials from the Valley of Lakes are housed in the Natural History Museum in Vienna (NHMW). Lagomorph fossils from the localities Shamar, Orkhon and Bural Obo are kept at the Geological Institute RAS, Moscow.

3. Biodiversity and development of lagomorphs of Mongolia in context of Global events

The Eocene-Oligocene boundary was marked by significant changes in climate and biota of the Northern Hemisphere, the mild subtropical climate changing to warm and moderately continental one. A gradual cooling at the Oligocene beginning is indicated by a decrease in number of tropical and subtropical plants and their replacement by those typical of temperate belt all over northern Eurasia (AKHMETIEV 1993).

The cooling resulted in appearance of open landscapes and, as a consequence, in an essential reorganisation of biocenoses in Asia, and particularly in Mongolia. The early Oligocene is noted for complete disappearance of some stem groups of lagomorphs (typical of the Eocene in Asia), along with some archaic genera of leporids, such as *Lushilagus, Shamolagus, Dituberolagus, Hypsimilus, Dawsonolagus, Strenulagus, Aktashmys*. However, a number of lagomorph genera – *Gobiolagus*, *Desmatolagus, Zaissanolagus, Ordolagus* that included advanced species – continued to exist and flourished through the Oligocene.

Altogether the Oligocene-Miocene fauna of Mongolia includes more than 40 lagomorph species belonging to at least 3 families – Leporidae, Palaeolagidae and Ochotonidae.

The dominant forms of the Early Oligocene lagomorph fauna were evidently desmatolagins characterized by both abundance and diversity of species. The first appearance of ochotonids is recorded at that time, though they were very rare. Equally scarce were leporids noticeably decreased in number as compared with the preceding faunas of the Eocene when they rather abundant and diversified. So pikas and hares were in subordinate position in the Early Oligocene fauna.

In the late Oligocene ochotonids attributable to the genus *Sinolagomys* (Ochotonidae) became increasingly diversified and widely spread over Asia. Sinolagomyins are known from a number of Oligocene localities – Hsanda Gol, Tatal Gol and Alak-Nur – in Mongolia, as well as from Chinese sites Ulan-Tatal, Shargaltein Tal, Taben Buluk and from Djungarian site Ulungur (BOHLIN 1937, 1942; GUREEV 1964, DEVYATKIN 1981, HUANG 1989, TONG 1989, ERBAJEVA 2007). The late Oligocene was marked by the first appearance of new lagomorph taxa *Bohlinotona* (DE MUIZON 1977), though it was not abundant then.

Of the archaic ochotonids belonging to the genus *Sinolagomys*, there are known *Sinolagomys tatalgolicus*, *S. kansuensis, S. gracilis*. They are characterized by the presence of cheek teeth with reduced roots, as well as a simple feature of p3 consisting of one conid with antero-external fold with or without cement; trigonids of p4-m2 are much wider than talonids. At the end of Oligocene ochotonids became completely rootless (*Sinolagomys ulungurensis*, *S. major*). Leporids (the genus *Ordolagus*) were still scarce.

The beginning of Miocene was marked by further changes of the environments, with an increasing continentality and aridity of climate. They resulted in that open landscape became widely expanded in the high latitudes of Northern Hemisphere and a new component of zonal structure – the steppe zone – came into being. The wide occurrence of various steppes and forest-steppes in Northern Asia (SINITSIN 1962) led to significant changes in mammalian faunas of Mongolia, in particular in lagomorphs. The genera *Bohlinotona* and *Ordolagus* disappeared completely, however a few species of the genus *Desmatolagus* persisted. Ochotonids were subjected to an essential reorganization: the earlier Oligocene synolagomyin taxa were replaced by advanced rootless species *Sinolagomys pachygnathus* (LI QIU 1980); the latter featured evergrowing, high crowned cheek teeth, more complicated structure of p3, much more wider talonids of p4-m2 (in comparison with the earlier taxa), the talonid width being equal to that of the trigonid.

Other rootless ochotonid genera – *Bellatona* and *Alloptox* – appeared for the first time. The genus *Bellatona* may be classified among Asian endemic form, as it occurred only in Asia, in particular in China, Mongolia and Kazakhstan. It completely disappeared by the middle Miocene.

In contrast to it, the genus *Alloptox* was much more diversified and exceeded the above genera both in number of species and abundance. In the middle Miocene it dispersed rapidly westwards across Eurasia. It reached as far as Hungary in Europe, Turkey in Asia Minor, and North Africa (ANGELONE & HIR 2012, WESSELS et al. 2003). It also expanded its range eastwards up to Japan (TOMIDA 2012).

Lagomorph fauna of Mongolia includes also the genus *Amphilagus*; that is an evidence for some European taxa being able to migrate eastwards due to the lack of barriers for mammalian dispersal across Eurasia. Lagomorphs occupied a vast area from France in the west through Kazakhstan, Siberia, Mongolia and China to Japan in the east (ERBAJEVA 2007, TOMIDA & GODA 1993). At the beginning of Late Miocene *Amphilagus* became extinct.

There are no data available on the leporid occurrence in Mongolia, whereas the genus *Tsaganolagus* is known in China, *Hypolagus* in Kazakhstan and Eastern Europe and *Alilepus* in Europe (CHOMENKO 1914, GUREEV 1964, LI 1978, ERBAJEVA 1982, 1994). Along with climatic

change towards cooling and aridization synchronous to global event known as the Messinian crisis, forests became gradually reduced in area, while grassland and steppe expanded. Such paleoenvironmental conditions were favorable for the origination of new genera *Ochotonoma, Ochotonoides* and *Ochotona* and their radiations over Eurasia.

Finds of the genus *Ochotonoma* are scanty in eastern Asia; however, it was characteristic of the Pliocene in Central Europe and Asia Minor (SEN 2003, ERBAJEVA & ZHENG 2005).

Peculiar large sized ochotonid attributed to the genus *Ochotonoides* appeared at the end of late Miocene and flourished through the late Pliocene. Besides Mongolia, they inhabited Northern China, Western Transbaikalia and Kazakhstan. In the early Pleistocene they disappeared in Asia completely (ZHENG 1982, ERBAJEVA 1988).

In the late Miocene, under conditions of arid and cool climate, the expansion of steppe provided a favorable environment for development of the highly diversified genus *Ochotona* inhabiting Asia. Most species, including *Ochotona lagrellii*, *O. minor, O. tedfordi, O. magna, O. chowmincheni*, were confined to China and Mongolia, and only *Ochotona guizhongensis* penetrated as far westwards as Northern Kazakhstan (ERBAJEVA 2003, ERBAJEVA et al. 2006).

Ochotonid diversification in Mongolia and in the adjacent regions of Transbaikalia continued during the Pliocene. They were represented by *Ochotona gromovi, O*. cf. *lingtaica, O. sibirica, O. intermedia, O. tologoica, O. zazhigini, O.* cf. *nihewanica, O. zasuchini* known from a number of sites in Mongolia and the Transbaikal area (ERBAJEVA 1988). The leporids dated to the Pliocene belong to the genus *Hypolagus*; they occurred in rather small quantities and disappeared completely at the Pliocene-Pleistocene transition.

Further climatic changes towards greater cooling and aridity led to significant re-organisations in paleovegetation and mammal faunas of Central Asia in the late Pliocene. The most thermophilic elements disappeared from the flora with an expansion of steppes. Ochotonids decreased in diversity and abundance. In all probability, it was connected with the explosive radiation and spreading of arvicolids – the main trophic competitors to herbivorous ochotonids. There are no data as yet on the lagomorph presence in Mongolia during the Pleistocene and Holocene.

The modern Mongolian lagomorph fauna includes *Lepus timidus*, *L. tolai*, *L. tibetanus* and some ochotonids – *Ochotona daurica, O. alpina*, *O. hyperborea, O. hoffmani* and *O pallasi.*

Conclusions

1. Lagomorphs originated in Central Asia in the Paleogene and flourished during the Oligocene, Miocene and Pliocene.
2. Altogether more than 50 lagomorph species, extinct at present, are known to exist in Mongolia since the Oligocene through the late Pliocene.
3. The early Oligocene fauna was dominated by *Desmatolagus* represented by more than 10 taxa, while leporids and ochotonids held a subordinate position.
4. Ochotonids first appeared in the late Oligocene and reached their maximum diversity during the Miocene; towards the end of Pliocene all the ochotonid genera became extinct with the only exception of the still extant genus *Ochotona*.
5. The genus *Ochotona* came into being in the late Miocene and was distinguished for high diversity during the Pliocene; there are no data on the lagomorph presence in Mongolia during the Pleistocene and Holocene.
6. Leporids in Mongolian fauna were scarce during both the Oligocene and Pliocene.
7. At present 3 species of hares and 5 species of ochotonids are known to dwell in Mongolia.

Acknowledgement

I am greatful to Annegret and Michael Stubbe for the invitation and financial support to attend the Conference and to contribute to this volume. I extend my gratitude to Gudrun Daxner-Höck, Mathias Harzhauser and Ursula Göhlich for the nice opportunity to study exceptional fossil lagomorph materials from Mongolia in Vienna (NHMW).

This research has been supported by FWF-P:10505-GEO, by FWF-project: P-23061-N19 and grants of RFBR, Nr. 12-04-00081, and in part Nr. 12-05-98000, 11-05-00677.

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The young staff of the symposium organization office, from left: Markus Wall, Hannes Becher, Oliver Lindecke, Uta Stuhr, Uta Schwarz-Olbrich, Martin Kluschke.