FOSSIL IMPRINT • vol. 80 • 2024 • no. 2 • pp. 312–318

NATIONAL MUSEUM

OVERVIEW OF CENOZOIC EURASIAN LAGOMORPH BIOCHRONOLOGY AND RADIATION

MARGARITA A. ERBAJEVA[1,*], URSULA B. GÖHLICH[2], LAWRENCE J. FLYNN[3], NADIA V. ALEXEEVA[1]

[1] Dobretsov Geological Institute, Siberian Branch RAS, Ulan-Ude, Russia; e-mail: sinolag@mail.ru.
[2] Natural History Museum Vienna, Geological-Paleontological Department, Vienna, Austria.
[3] Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA.
*corresponding author

Erbajeva, M. A., Göhlich, U. B., Flynn, L. J., Alexeeva, N. V. (2024): Overview of Cenozoic Eurasian lagomorph biochronology and radiation. – Fossil Imprint, 80(2): 312–318, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Ochotonidae and Leporidae are two living families belonging to the Order Lagomorpha, an ancient group of mammals originating in the Paleogene of Asia. Those families diversified in the Oligocene and Miocene. More primitive stem lagomorphs inhabited Asia during a time of tropical environmental conditions. A Mid-Cenozoic change towards more continental and arid climate in parallel with Antarctic glaciation resulted in significant reorganisation of paleoenvironmental and climatic conditions in Asia and involved the opening of terrestrial connections between Asia, Europe, and North America, allowing faunal exchanges. This promoted diversification and speciation of lagomorphs in the northern continents. Pronounced lagomorph turnover is documented for Central Mongolia, with new data obtained for the Baikalian region as well as adjacent areas. The earliest lagomorphs were represented by archaic stem genera including paleolagids. These were successively replaced by modern Ochotonidae and Leporidae that flourished during the Miocene and Pliocene. The diversity and abundance of ochotonids and leporids decreased during the Pleistocene and of ochotonids, only the pika genus *Ochotona* survived to the present.

Key words: Lagomorpha, Ochotonidae, Leporidae, biochronology, biodiversity, late Cenozoic, Eurasia

Received: May 23, 2024 | Accepted: September 9, 2024 | Issued: December 20, 2024

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:89B3B598-22E3-434C-A472-BED5C7DBF295

Introduction

Lagomorphs are one of the ancient groups of mammals of Asian origin (Gureev 1964, Dawson 1967). Diversity within the Order Lagomorpha supports the recognition of six families: Strenulagidae Averianov et Lopatin, 2005; Mimotonidae Li, 1977; Palaeolagidae Dice, 1929; Prolagidae Gureev, 1960; Leporidae Fischer, 1814; and Ochotonidae Thomas, 1897. Among these, only two families persist: Ochotonidae comprising only the living pika *Ochotona*, and Leporidae with eleven extant genera (Pavlinov 2003).

Early Asian Lagomorphs

The earliest record of the Order Lagomorpha is known from the Paleocene of Central Asia (Asher et al. 2005). At that time the climate in Asia was warm and humid, with mesophytic vegetation and broad-leaved forests (Akhmetiev 1993). Such conditions enabled the Paleogene stem Mimotonidae to differentiate. During the Eocene increased diversity of lagomorphs developed in both Asia and North America. In Asia, early Eocene taxa include *Shamolagus*, *Arnebolagus*, and *Aktashmys* (Averianov and Lopatin 2005, Lopatin and Averianov 2006, 2020). Of these, *Shamolagus* persisted into the middle Eocene and was joined by the lagomorph genera *Lushilagus*, *Dawsonolagus*, *Hypsimylus*, *Strenulagus*, and *Gobiolagus* (Zhai 1977, Li and Ting 1983, Zhang et al. 2001, Li et al. 2007). Recorded in the Eocene of North America are the distinct genera *Mytonolagus*, *Procaprolagus*, *Megalagus*, *Tachylagus*, *Chadrolagus*, and *Palaeolagus* (McKenna and Bell 1997).

By the close of the Eocene, the climate in Asia became more arid, with continental conditions due to the influence of the Antarctic glaciation (Wolfe 1971, Baldermann et al. 2021). This resulted in reduced diversity of archaic lagomorphs near the Eocene-Oligocene transition, but a few lineages continued as derived species of *Gobiolagus* and the genus *Desmatolagus*, and the last of the paleolagids (Meng et al. 2005).

At the Eocene-Oligocene transition, with the "Grande Coupure" event more than 20 mammal lineages including the archaic lagomorph *Desmatolagus* invaded Europe (López-

DOI 10.37520/fi.2024.023

Martínez and Thaler 1974). Under favorable conditions the success of the invaders resulted in the diversification of the new endemic genera *Titanomys* and *Piezodus*, and *Amphilagus* which then flourished in Europe (Tobien 1974, 1975, Heissig and Schmidt-Kittler 1975, Mörs and Kalthoff 2010).

Significant paleoenvironmental change in the Oligocene of Asia involving aridity developed in the Northern Hemisphere from the Caspian Sea across south Kazakhstan as far as Mongolia (Akhmetiev 1993). The climate trended towards continental conditions, forested areas decreased, and open landscapes became more widely distributed. Due to global environmental change, significant biotic reorganisation may be observed across Central Asia (Harzhauser et al. 2017). The characteristic Eocene genus *Gobiolagus* was replaced by the basal leporid *Ordolagus*, but the genus *Desmatolagus* increased both in species diversity and abundance and became dominant among small mammals in the Oligocene of Asia (Bohlin 1937, Li and Qiu 1980, Tong 1989, Wang and Qiu 2000, Bendukidze et al. 2009, Meng et al. 2013, Erbajeva 2016).

Mid-Cenozoic Lagomorphs of Central Mongolia

A pronounced lagomorph turnover can be observed in Central Mongolia. Abundant fossil materials known from more than 30 sites located in the Valley of Lakes provide important information on the sequence of Oligocene to Miocene lagomorph assemblages (Daxner-Höck and Badamgarav 2007, Erbajeva 2007, Daxner-Höck et al. 2013, Erbajeva and Daxner-Höck 2014, Daxner-Höck and Göhlich 2017).

In the region of Central Mongolia two lagomorph genera typified the early Oligocene. The genus *Desmatolagus* was dominant in contrast to *Ordolagus* and we conclude that they were adapted to rather humid conditions with shrubs and dense vegetation. Cooler climate and more semi-arid conditions led to the development of open landscapes inhabited by the early ochotonid genera *Sinolagomys* and *Bohlinotona*, although they were not numerous. Desmatolagins continued as diverse species including *Desmatolagus gobiensis*, *D. orlovi*, *D. youngi*, *D. robustus*, *D. shargaltensis* and *D. chinensis*. The increasing aridity resulted in the widening of open landscapes.

The diversity and distribution of steppe-dwelling ochotonids increased in the Early Miocene. The rooted genus *Bohlinotona* with the archaic species *Bohlinotona pusilla* illustrated an early stage in the ochotonid evolutionary line. Probably it exploited less arid conditions with soft vegetation. In contrast, later more advanced and rootless species *B. mongolica* may have been adapted dentally to drier conditions with tougher vegetation. *Bohlinotona* occupied the territory of Northern China and Mongolia together with the more modern ochotonid genus *Sinolagomy*s. The distribution area of the latter reached farther westward into Kazakhstan. The genus *Sinolagomys* demonstrates a relatively high diversity of species in Central Asia: *Sinolagomys tatalgolicus*, *S. kansuensis*, *S. major*, *S. ulungurensis*, *S. gracilis*, *S. badamae* and *S. pachygnathus* (Bohlin 1937, Li and Qiu 1980, Huang 1987, Tong 1989, Erbajeva et al. 2017).

During the Oligocene-Miocene transition significant reorganisation of the paleoenvironment and biota of Eurasia occurred. Cooling and increasing aridity led to expansion of open landscape (Baldermann et al. 2021). After the end of the Oligocene, desmatolagins vanished and became extinct, and the archaic ochotonid *Bohlinotona* disappeared completely. Some *Sinolagomys* species persisted past the late Oligocene and the derived rootless species *S. ulungurensis* and *S. pachygnathus*, flourished in the Early Miocene. Hypsodont teeth in *Sinolagomys* may have been an adaptation to feeding on harsh grass that had become widely distributed in northern Asia.

Mid-Cenozoic Lagomorphs of Europe

In the late Oligocene of Europe, the stem lagomorph genus *Amphilagus* including *Amphilagus antiquus* Pomel, 1853, *A. ulmensis* Tobien, 1974 and *A. wuttkei* Mörs et Kalthoff, 2010 flourished. During the Early Miocene *Amphilagus* diversified and became widely distributed in western and central Europe (Engesser 1972, Topachevsky 1987, Angelone 2009, Harzhauser et al. 2011, Fostowicz-Frelik et al. 2012). By the Middle Miocene *Amphilagus* invaded Asia extending eastwards into Kazakhstan, Mongolia, eastern Siberia and Japan (Tomida and Goda 1993, Erbajeva 2013, Erbajeva et al. 2016).

While European genera of basal origin (*Titanomys*, *Piezodus*, and *Prolagus*) continued to diversify during the Early Miocene (Tobien 1974, 1975) new ochotonid genera *Eurolagus*, *Albertona*, *Marcuinomys*, and *Lagopsis* (Mein and Adrover 1982, López-Martínez 1986) appeared. Of these, the only advanced genus to thrive successfully in Europe was *Lagopsis* (Bucher 1982); other ochotonids in contrast were uncommon.

The Miocene Steppe Lagomorphs of Asia and Europe

In Asia, new steppe-dwelling ochotonid species of the genera *Bellatona* and *Alloptox* are recorded in the Miocene. The genus *Bellatona* included three species – *Bellatona kazakhstanica*, *B. yanghuensis* and *B. forsythmajori*, the first of which is known from the Early Miocene and the second from the Middle Miocene and restricted to China, Mongolia and Kazakhstan (Dawson 1961, Zhou 1988, Erbajeva 1988, Qiu 1996, Erbajeva and Bayarmaa 2021a). In contrast, the genus *Alloptox* flourished and was distributed more widely from Japan (Tomida 2012) and China in the east through Mongolia (Erbajeva and Bayarmaa 2021b), and Kazakhstan, to the south into Pakistan (Flynn et al. 1997, Wessels et al. 2003), and to the west as far as Asia Minor (Turkey), Hungary and even North Africa (Ünay and Sen 1976, Sen 1990, Angelone and Hir 2012).

During the Late Miocene, the climate of the Northern Hemisphere became gradually drier and cooler. The average annual temperature continued to decrease. Open landscapes with true steppes became widespread and provided the main habitat for different species. New records previously noted as *Proochotona* occur in eastern Europe (Khomenko 1914,

Argyropulo 1948, Gureev 1964, Lungu 1981). Čermák (2016) determined that these represent early *Ochotona*. The genus *Proochotona* is not valid, and the first evidence of *Ochotona* is Miocene.

By the Late Miocene in Europe the insular endemic ochotonid *Paludotona* Dawson, 1959 differentiated but it was confined in the Tusco-Sardinian Bioprovince.

The Late Neogene of Asia

The close relative of *Ochotona*, *Bellatonoides eroli* flourished in Asia Minor (Sen 2003). By the Late Miocene *Ochotona* spread throughout Asia, demonstrating high species diversity: *O. lagreli*, *O. minor*, *O. tedfordi*, *O. chowmincheni*, *O. guizhongensis*, *O. ozansoyi* (Schlosser 1924, Ji et al. 1980, Sen 2003, Erbajeva et al. 2006). *Ochotonoides* and new genus *Ochotonoma* also differentiated by the Pliocene as *Ochotonoides teilhardi* (Wu and Flynn 2017), and as *Ochotonoma anatolica* (Sen 1998). At the Late Miocene-Early Pliocene transition, the genus *Ochotona* invaded the New World (*O. spanglei* of Shotwell 1956).

North American leporids had differentiated during the Early and Middle Miocene, and dispersed to northern Asia in the Late Miocene. They spread apparently widely throughout northern Eurasia as *Hypolagus* and *Alilepus* (Flynn et al. 2014). Leporids dispersed into Africa and South Asia after 8 Ma (López-Martínez et al. 2007, Winkler et al. 2011, Flynn et al. 2019).

While Late Miocene *Alilepus* spread across Eurasia, the leporid *Nesolagus* differentiated in South China (Jin et al. 2010) by around 8 Ma. Leporids became rather diverse in the Pliocene but were not numerous. They represent, in addition to *Hypolagus* and *Alilepus*, the genera *Pliopentalagus*, *Trischizolagus*, *Nuralagus*, and *Oryctolagus*. *Pentalagus* clearly differentiated by the end of the Pleistocene in Japan (Tomida and Otsuka 1993).

Further gradual cooling in the Northern latitudes and orogenic processes resulted in prominent environmental reorganization in Eurasia during the Pliocene. Most of the Miocene ochotonid diversity diminished, however, the genera *Ochotonoides* and *Ochotona* survived. During the Pliocene, peculiar lagomorph species of the genus *Prolagus* proliferated in the Mediterranean region. This group, here defined as the distinctive Prolagidae, includes more than 25 species occurring mostly in Europe. A few records extended into northern Africa (Geraads 1994, Sen et al. 2024) and Asia Minor. The time range of *Prolagus* is Early Miocene through Holocene.

During the Pliocene, diverse species of the genera *Ochotonoides* and *Ochotona* occupied Eurasia. In Eastern Europe the new genus *Pliolagomys* appeared and spread quickly eastwards. *Pliolagomys* flourished through the Pliocene and came to occupy the vast plain territories of Eurasia, from Romania, Moldavia and the Ukraine eastward as far as western Siberia and Kazakhstan. Species of the genus *Ochotonoides* were widely distributed across much of Asia from China, Transbaikalia, and Mongolia westward to Kazakhstan (Erbajeva 1988). Most genera disappeared by the end of the Early Pleistocene, but *Ochotona* survives up to modern times.

The Success of the Pika

Although *Ochotona* first appeared in the Late Miocene, the main features of the skull and the structure of the teeth remained unchanged to the present. During the Pliocene, *Ochotona* flourished mostly in Asia, but is recorded in the Early Pliocene (MN 14) of Europe (at Maritsa; Bruijn de et al. 1970). We suppose that Late Pliocene environments favored species diversity of pikas distributed all over Eurasia. The huge number of species of many sizes indicates preference of different habitats: *Ochotona antiqua*, *O. pseudopusilla*, *O. ursui*, *O. galatica*, *O. valerotae*, *O. polonica*, *O. dehmi*, *O. horaceki*, *O. kormosi* in Europe, and *O. gudrunae*, *O. gromovi*, *O. tologoica*, *O. intermedia*, *O. plicodenta*, *O. lingtaica*, *O. zasuchini*, *O. zazhigini*, *O. zhangi* in Asia (Erbajeva and Zheng 2005, Erbajeva 2016). A few extinct ochotonids occur in North America in addition to *Ochotona spanglei*, such as *O. whartoni* and *O.* cf. *princeps*. The latter was widely distributed in the great intermountain basins of western North America during the Early and Middle Pleistocene (Mead et al. 2004). The distribution area of *O. whartoni* was mainly the western Arctic and Alaska (Guthrie and Matthews 1971) but the species spread into northeast Asia (Kolyma Lowland; Erbajeva and Belolyubski 1993).

In the Late Pleistocene the pika *Ochotona* decreased both in abundance and species diversity. Gradually it showed reduced area of distribution in Eurasia probably due to the appearance of trophic and habitat competitors, namely another typically herbivorous group, the different arvicolids of the subfamily Microtinae. It is possible to suppose that given high explosive radiation, the diverse arvicolid species became successful in ochotonid habitats of various landscapes – steppes, meadows, open forests and others. Probably various arvicolid taxa occupied the favorable niches of ochotonids pushing them out of their habitat and becoming dominant forms. Ochotonids decreased both in diversity and numbers, few ochotonid species are known in late Pleistocene faunas of Eurasia. These are fossil ancestors of living pikas such as *Ochotona* cf. *alpina*, *O.* cf. *hyperborea*, *O. dauurica*, *O.* cf. *rufescens* recorded in Asia. However, during the Late Pleistocene the small species *Ochotona pusilla* did disperse widely in the west to the vast plain territories of southern England, central Spain, the Netherlands, France, Italy and Greece. The species was successful throughout temperate Eurasia, as far east as the Prebaikal region of East Siberia (Laplana et al. 2015, Erbajeva 2008). At present, this species persists only in Northern Kazakhstan and in the restricted steppe of the Upper Volga River of Russia (Erbajeva 1988). More than 40 extinct species of *Ochotona* are known in the world, but 29 species persist to the Present (Smith et al. 2018).

Acknowledgements

We dedicate this paper to the memory of Prof. Oldřich Fejfar for his tremendous contributions to morphological and evolutionary studies of small mammals.

We thank Prof. I. Horáček and other colleagues for the invitation to contribute to this volume. We are grateful to

Text-fig. 1. O. Fejfar and M. Erbajeva on the field excursion of the 2nd Paleontological Colloqiuum in Weimar, Germany, 1966.

Gudrun Daxner-Höck for her professional support and advice. Special gratitude we express to Dr. Jan Wagner for careful editing. We would like to thank reviewers for helpful comments. This work was performed within the framework of state assignments of the Dobretsov Geological Institute SB RAS (project no. FWSG-2021-0003).

References

Angelone, Ch., (2009): The Early Vallesian Vertebrates of Atzelsdorf (Late Miocene, Austria). 6. Lagomorpha. – Annalen des Naturhistorischen Museums in Wien, A, 111: 515–518.

Angelone, Ch., Hír, J. (2012): *Alloptox katinkae* sp. nov. (Lagomorpha: Ochotonidae) westernmost Eurasian record of the genus from the early Middle Miocene vertebrate fauna of Litke 2. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 214: 1–10. https://doi.org/10.1127/0077-7749/2012/0227

Akhmetiev, M. A. (1993): Fitostratigrafiya kontinental'nykh otlozheniy paleogena I miotsena vnetropicheskoy Azii [Phytostratigraphy of the Paleogene and Miocene continental deposits of non-tropical Asia]. – Trudy, Geologicheskiy institute RAN [Transactions, Geological Institute Russian Academy of Sciences], 475: 1–143. (in Russian)

Argyropulo, A. I. (1948): Obzor retsenthykh vidov semeystva Lagomyidae Lilljeb., 1886 (Lagomrpha, Mammalua) [A review of Recent species of the family Lagomyidae Lilljeborg, 1886 (Lagomorpha, Mammalia)]. – Trudy Zoologicheskogo instituta An SSSR [Proceedings of the Zoological Institute of the USSR], 7: 124–128. (in Russian)

Asher, R. J., Meng, J., Wible, J. R., McKenna, M. C., Rougier, G. W., Dashzeveg, D., Novacek, M. J. (2005): Stem Lagomorpha and antiquity of Glires. – Science, 307: 1091–1094. https://doi.org/10.1126/science.1107808

Averianov, A. O., Lopatin, A. V. (2005): Eocene Lagomorphs (Mammalia) of Asia: 1. *Aktashmys* (Strenulagidae fam. nov.). – Paleontological Journal, 39(3): 308–317.

Baldermann, A., Wasser, O., Abdullayev, E., Bernasconi, S., Lohr, S., Wemmer, K., Piller, W. E., Rudmin, M., Richoz, S. (2021): Paleo-environmental evolution of Central Asia during the Cenozoic: new insights from the continental sedimentary archive of the Valley of Lakes (Mongolia). – Climate of the Past, 17(5): 1955–1972. https://doi.org/10.5194/cp-17-1955-2021

Bendukidze, O. G., de Bruijn, H., van den Hoek-Ostende, L. (2009): A revision of Late Oligocene associations of small mammals from the Aral Formation (Kazakhstan) in the National Museum of Georgia, Tbilissi. – Palaeodiversity, 2: 343–377.

Bohlin, B. (1937): Oberoligozäne Säugetiere aus dem Shargaltein-Tal. Sino-Swedisch Expedition. – Palaeontologia Sinica, N. S., Ser. C, 3: 1–66, 2 pls.

Bruijn, H. de, Dawson, M. R., Mein, P. (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). I, II, and III. – Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B, 73(5): 535–584.

Bucher, H. (1982): Étude des genres *Marcuinomys* Lavocat et *Lagopsis* Schlosser (Lagomorpha, Mammalia) du Miocène inférieur et moyen de France. Implications biostratigraphiques et phylogénétiques. – Buletin du Muséum National d'Histoire naturelle, Ser. 4, Sec. C, 4(1/2): 43–74.

Čermák S. (2016): The Late Miocene species *Ochotona kalfense* (Mammalia, Lagomorpha) of Moldova: The oldest European record of the genus in the context of the earliest Ochotoninae. – Comptes Rendus Paleovol, 15: 927–940. https://doi.org/10.1016/j.crpv.2016.04.010

Daxner-Höck, G., Badamgarav, D. (2007): Geological and Stratigraphic Setting. – Annalen des Naturhistorischen Museums in Wien, A, 108: 1–24.

Daxner-Höck, G., Göhlich, U. B. (2017): Introduction to special issue "The Valley of Lakes in Mongolia, a key area of Cenozoic mammal evolution and stratigraphy". – Palaeobiodiversity and Palaeoenvironment, 97(1): 1–9. https://doi.org/10.1007/s12549-016-0270-z

Daxner-Höck, G., Badamgarav, D., Erbajeva, M. A., Göhlich, U. B. (2013): Miocene mammal biostratigraphy of Central Mongolia (Valley of Lakes). – In: Wang, X.-M., Flynn, L. J., Fortelius, M. (eds), Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 477–494. https://doi.org/10.7312/columbia/9780231150125.003.0020

Dawson, M. R. (1959): *Paludotona etruria*, a new ochotonid from the Pontian of Tuscany. – Verhandlungen der Naturforschenden Gesellschaft in Basel, 70(2): 157–166.

Dawson, M. R. (1961): On two ochotonids (Mammalia, Lagomorpha) from the later Tertiary of Inner Mongolia. – American Museum Novitates, 2061: 1–15.

Dawson, M. R. (1967): Lagomorph history and the stratigraphic record. – Special Publications, University Kansas, Dept. of Geology, 2: 287–316.

Dice, L. R. (1929): The phylogeny of the Leporidae, with description of a new genus. – Journal of Mammalogy, 10: 340–344. https://doi.org/10.2307/1374124

Engesser, B. (1972): Die obermiozäne Säugetierfauna von Anwil (Baselland). – Tätigkeitsberichte der Naturforschende Gesellschaft Baselland, 28: 37–363.

Erbajeva, M. A. (1988): Pishchukhi kaynozoya: taksonimiya, sistematika, filogeniya [Cenozoic pikas (taxonomy, systematics, phylogeny)]. – Nauka, Moskva [Moscow], 224 pp. (in Russian)

Erbajeva, M. A. (2007): 5. Lagomorpha (Mammalia): Preliminary results. – Annalen des Naturhistorischen Museums in Wien, A, 108: 165–171.

Erbajeva, M. A. (2008): Late Pleistocene small ochotonids of Eurasia with emphasis to the history of *Ochotona pusilla*. – In: Krempaská, Z. (ed.), Volume of abstracts. 6th Meeting of the European Association of Vertebrate Palaeontologists, Spišská Nová Ves, Slovak Republic, 30th June – 5th July 2008. Museum od Spiš, Spišská Nová Ves, pp. 38–40.

Erbajeva, M. A. (2013): New species of *Amphilagus* (Lagomorpha, Mammalia) from the Miocene of the Valley of the Lakes, Central Mongolia. – Paleontological Journal, 47(3): 311–320. https://doi.org/10.1134/S0031030113030040

Erbajeva, M. A. (2016): The Ochotonids of Eurasia: Biochronology and taxonomic diversity. – Biology Bulletin, 43(7): 729–735. https://doi.org/10.1134/S1062359016070062

Erbajeva, M. A., Angelone, Ch., Alexeeva, N. V. (2016): A new species of the genus *Amphilagus* (Lagomorpha, Mammalia) from the Middle Miocene of south-eastern Siberia. – Historical Biology, 28: 199–207. https://doi.org/10.1080/08912963.2015.1034119

Erbajeva, M. A., Baatarjav, B., Daxner-Höck, G., Flynn, L. J. (2017): Occurrence of *Sinolagomys* (Lagomorpha) from the Valley of Lakes (Mongolia). – Palaeobiodiversity and Palaeoenvironment, 97(1): 11–24. https://doi.org/10.1007/s12549-016-0262-z

Erbajeva, M. A., Bayarmaa B. (2021a): Miocene ochotonids of the genus *Bellatona* (Lagomorpha, Mammalia) from Mongolia. – Paleontological Journal, 55(5): 98–106. https://doi.org/10.1134/S003103012105004X

Erbajeva, M. A., Bayarmaa B. (2021b): A Review of the Genus *Alloptox* (Lagomorpha, Ochotonidae) from the Valley of Lakes, Central Mongolia, with the description of a new species. – Paleontological Journal, 55(2): 217–223. https://doi.org/10.1134/S0031030121020040

Erbajeva, M. A., Belolyubskyi, I. N. (1993): First record of *Ochotona wahrtoni* in Kolyma lowland. – Russian Geology and Geophysics, 34(6): 142–144.

Erbajeva, M. A., Daxner-Höck, G. (2014): The most prominent Lagomorpha from the Oligocene and Early Miocene of Mongolia. – Annalen des Naturhistorischen Museums in Wien, A, 116: 215–245.

Erbajeva, M. A., Flynn, L. J., Li, C. K., Marcus, L. (2006): New Late Cenozoic Ochotonids from China. – Beiträge zur Paläontologie, 30: 133–141.

Erbajeva, M. A., Zheng, S. (2005): New data on Late Miocene-Pleistocene ochotonids (Ochotonidae, Lagomorpha) from North China. – Acta Zoologica Cracoviensia, 48A (1-2): 93–117. https://doi.org/10.3409/173491505783995734

Fischer [de Waldheim], G. (1814): Zoognosia tabulis synopticis illustrata. Vol. III: Quadrupedum reliquorum, Cetorum et Monotrymatum descriptionem continens. – Nicolai Sergeidis Vsevolozsky, Mosquae [Moscow], xxiv + 732 pp. https://doi.org/10.5962/bhl.title.42225

Flynn, L. J., Barry, J. C., Downs, W., Harrison, J. A., Lindsay, E. H., Morgan, M. E., Pilbeam, D. (1997): Only ochotonid from the Neogene of the Indian Subcontinent. – Journal of Vertebrate Paleontology, 17(3): 627–628. https://doi.org/10.1080/02724634.1997.10011011

Flynn, L. J., Jin C.-Z., Kelley, J., Jablonski, N. G., Ji, X.-P., Su, D. F., Deng, T., Li, Q. (2019): Late Miocene fossil calibration from Yunnan Province for the Striped Rabbit *Nesolagus*. – Vertebrata PalAsiatica, 57(3): 214–224.

Flynn, L. J., Winkler, A. J., Erbajeva, M., Alexeeva, N. V., Anders, U., Angelone, Ch., Čermák, S., Fladerer, F. A., Kraatz, B., Ruedas, L. A., Tomida, Y., Veitschegger, K., Zhang, Z. (2014): The Leporid Datum: A Late Miocene biotic marker. – Mammal Review, 44(3-4): 164–176. https://doi.org/10.1111/mam.12016

Fostowicz-Frelik, L., Nadachowski, A., Kowalewska-Groszkowska, M. (2012): New data on the Miocene stem lagomorph *Eurolagus fontannesi*, and its northernmost record. – Acta Palaeontologia Polonica, 57(1): 1–20. https://doi.org/10.4202/app.2010.0109

Geraads, D. (1994): Rongeurs et Lagomorphes du Pléistocène moyen de la «Grotte des Rhinoceros», Carriere Oulad Hamada 1 à Casablanca, Maroc. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 191(2): 147–172. https://doi.org/10.1127/njgpa/191/1994/147

Gureev, A. A. (1960): Oligocene lagomorphs (Lagomorpha) from Mongolia and Kazakhstan. – In: Flerov, K. K. (ed.), Tertiary Mammals. Paleontological Institute, Transactions, 77(4): 5–34.

Gureev, A. A. (1964): Zaytseobraznye (Lagomorpha) (Fauna SSSR. Mlekopitayushchie, t. 3, vyp. 10) [Lagomorphs (Lagomorpha) (Fauna of the USSR. Mammals, vpl. 3, part 10)]. – Nauka, Moskva [Moscow], Leningrad, 276 pp. (in Russian)

Guthrie, R. D., Matthews, J. W. (1971): The Cape Deceit fauna – Early Pleistocene mammalian assemblage from Alaskan Arctic. – Quaternary Research, 1(4): 474–510. https://doi.org/10.1016/0033-5894(71)90060-3

Harzhauser, M., Daxner-Höck, G., Göhlich, U. B., Nagel, D. (2011): Complex faunal mixing in the early Pannonian paleo-Danube Delta (Late Miocene, Gaweinstal, Lower Austria). – Annalen des Naturhistorischen Museums in Wien, A, 113: 167–208.

Harzhauser, M., Daxner-Höck, G., Erbajeva, M. A., López-Guerrero, P., Maridet, O., Piller, W. E., Göhlich, U. B., Ziegler, R. (2017): Oligocene and early Miocene mammal biostratigraphy of the Valley of Lakes in Mongolia. – Palaeobiodiversity and Palaeoenvironment, 97(1): 219–231. https://doi.org/10.1007/s12549-016-0264-x

Heissig, K., Schmidt-Kittler, N. (1975): Ein primitiver Lagomorphe aus dem Mitteloligozän Süddeutschlands. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, 15: 57–62.

Huang, H. (1987): Fossil ochotonids from the Middle Oligocene of Ulantatal, Nei Mongol. – Vertebrata PalAsiatica, 25(4): 260–282. (in Chinese, English summary)

Ji, H. X., Hsu, C. Q., Huang, W. P. (1980): The Hipparion fauna from Guizong basin, Xizang. – Ser. Scientific Expedition to Qinghai-Sizang Plateau, Xizang Paleontology, 5: 18–32.

Jin, C. Z., Tomida, Y., Wang, Y., Zhang, Y. Q. (2010): First discovery of fossil *Nesolagus* (Leporidae, Lagomorpha) from Southeast Asia. – Science China Earth Science, 53(8): 1134–1140. https://doi.org/10.1007/s11430-010-4010-3

Khomenko, I. P. (1914): La faune meotique du village Taraklia du district de Bendery: Fissipedia, Rodentia, Rhinocerotinae, Equinae, Suidae, Proboscidae – Trudy bessarabskogo obshchestva estestvoispytateley i lyubiteley ectestvoznaniya (Travaux de la Société des Naturalistes et des Amateurs des Sciences Naturelles de Bessarabie), Kishinev, 5: 1–55.

Laplana, C., Sevilla, P., Arsuaga, J. L., Arriaza, M. C., Baquedano, E., Pérez-González, A., López-Martínez, N. (2015): How far into Europe did pikas (Lagomorpha: Ochotonidae) go during the Pleistocene? New evidence from Central Iberia. – PLoS ONE, 10(11): e0140513 (17 pp.). https://doi.org/10.1371/journal.pone.0140513

Li, C. (1977): Paleocene eurymyloids (Anagalida, Mammalia) of Qianshan, Anhui. – Vertabrata PalAsiatica, 15(2): 103–118.

Li, C., Meng, J., Wang, Y. (2007): *Dawsonolagus antiquus*, a primitive lagomorph from the Eocene Arshanto Formation, Nei Mongol, China. – In: Beard, Ch. K., Luo, Z.-X. (eds), Mammalian paleontology on a Global Stage: Papers in honor of Mary R. Dawson. Bulletin of the Carnegie Museum of Natural History, 39: 97–110. https://doi.org/10.2992/0145-9058(2007)39[97:DAAPLF]2.0.CO;2

Li, C. K., Qiu, Z. D. (1980): Early Miocene mammalian fossils of Xining Basin, Qinghai. – Vertebrata PalAsiatica, 18(3): 198–214.

Li, C. K., Ting, S. Y. (1983): The Paleogene mammals of China. – Bulletin of the Carnegie Museum of Natural History, 21: 1–93. https://doi.org/10.5962/p.228600

Lopatin, A. V., Averianov, A. O. (2006): Eocene Lagomorpha (Mammalia) of Asia: 2. *Strenulagus* and *Gobiolagus* (Strenulagidae). – Paleontological Journal, 40(2): 79–88. https://doi.org/10.1134/S0031030106020110

Lopatin, A. V., Averianov, A. O. (2020): *Arnebolagus*, the oldest eulagomorph, and phylogenetic relationships within the Eocene Eulagomorpha, new clade (Mammalia, Duplicidentata). – Journal of Paleontology, 95(2): 394–405. https://doi.org/10.1017/jpa.2020.94

López-Martínez, N. (1986): The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). VI. The ochotonid lagomorph *Albertona balcanica* n. gen. n. sp. and its relationships. – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, B, 89(2): 177–194.

López-Martínez, N., Likius, A., Mackaye, H. T., Vignaud, P., Brunet, M. (2007): A new lagomorph from the late Miocene of Chad (Central Africa). – Revista Española de Paleontología, 22: 1–20. https://doi.org/10.7203/sjp.22.1.20384

López-Martínez, N., Thaler, L. (1974): Sur le plus ancien Lagomorphe europeen et la "Grande Coupure" Oligocene de Stehlin. – Palaeovertebrata, 6: 234–251.

Lungu, A. N. (1981): Hipparionovaya fauna srednego Sarmata Moldavii [*Hipparion* fauna of middle Sarmatian in Moldova]. – Ministerstvo vyschego i srednego specialnogo obrasovaniya Moldavskoy SSR, Kishinev, 118 pp. (in Russian)

McKenna, M. C., Bell, S. K. (1997): Classification of Mammals. Above the Species Level. – Columbia University Press, New York, 631 pp.

Mead, J. I., Erbajeva, M., Swift, S. L. (2004): Middle Pleistocene (Irvingtonian) *Ochotona* (Lagomorpha, Ochotonidae) from Porcupine Cave. – In: Barnosky, A. D. (ed.), Biodiversity Response to Climate Change in the Middle Pleistocene. The Porcupine Cave Fauna from Colorado. University California Press, Berkeley, Los Angeles, London, pp. 155–163. https://doi.org/10.1525/california/9780520240827.003.0014

Mein, P., Adrover, R. (1982): Une faunule de mammifères insulaires dans le Miocène moyen de Majorque (Iles Baléares). – Geobios, 15: 451–463. https://doi.org/10.1016/S0016-6995(82)80133-2

Meng, J., Hu, Y-M., Li, C. K. (2005): *Gobiolagus* (Lagomorpha, Mammalia) from Eocene Ula Usu, Inner Mongolia, and comments on Eocene lagomorphs of Asia. – Paleontologia Electronica, 8(1.7A): 1–23.

Meng, J., Ye, J., Wu, W. Y., Ni, X. J., Bi, S. D. (2013): A single-point base definition of the Xiejian Age as an exemplar for refining Chinese Land Mammal Ages: Fossil mammals of Asia. – In: Wang, X.-M., Flynn, L. J., Fortelius, M. (eds), Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 124–141. https://doi.org/10.7312/columbia/9780231150125.003.0003

Mörs, T., Kalthoff, D. (2010): A new species of *Amphilagus* (Mammalia, Lagomorpha) from the Late Oligocene lake deposits of Enspel (Westerwald, Germany). – Palaeobiodiversity and Palaeoenvironment, 90: 83–98. https://doi.org/10.1007/s12549-009-0020-6

Pavlinov, I. Y. (2003): Sistematika sovremennykh mlekopitayushchikh [Taxonomy of Recent mammals]. – Sbornik trudov Zoologicheskogo muzeya MGU [Archives of the Zoological Museum of Moscow MSU], 46: 3–297. (in Russian)

Pomel, A. (1853): Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le basisns hydrographique supérieur de la Loire et surtout dans la Valée de son affluent principal. – l'Allier, J. B. Bailliere, Paris, 193 pp.

Qiu, Z. D. (1996): Middle Miocene micromammalian fauna from Tunggur, Nei Mongol. – Science Press, Beijing, 214 pp.

Sen, S. (1990): Miocene lagomorphs from Paşalar, Turkey. – Journal of Human Evolution, 19: 455–461. https://doi.org/10.1016/0047-2484(90)90056-H

Sen, S. (1998): Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia and Lagomorpha. – Geodiversitas, 20: 359–378.

Sen, S. (2003): Lagomorpha. – In: Fortelius, M., Kappelman, J., Sen, S., Bernor, R. L. (eds), Geology and paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York, pp. 163–177.

Sen, S., Geraads, D., Pickford, M., Vacant, R. (2024): Pliocene and Pleistocene lagomorphs (Mammalia) from Northwest Africa: New discoveries. – Paleobiodiversity and Paleoenvironments, 104(2): 381–417. https://doi.org/10.1007/s12549-024-00605-6

Schlosser, M. (1924): Tertiary vertebrates from Mongolia – Palaeontologia Sinica, Ser. C, 1(1): 1–119.

Shotwell, J. A. (1956): Hemphilian mammalian assemblage from north-eastern Oregon. – Geological Society of America Bulletin, 67(6): 717–738. https://doi.org/10.1130/0016-7606(1956)67[717:HMAFNO]2.0.CO;2

Smith, A. T., Johnston, C. H., Alves, P. C., Hackländer, K. (eds) (2018): Lagomorphs: Pikas, rabbits, and hares of the World. – John Hopkins University Press, Baltimore, 266 pp.

Thomas, O. (1897): On the genera of rodents: An attempt to bring up to date the current arrangement of the order. – Proceedings of the Zoological Society of London, 1896: 1012–1028. https://doi.org/10.1111/j.1096-3642.1896.tb03097.x

Tobien, H. (1974): Zur Gebissstruktur, Systematik und Evolution der Genera *Amphilagus* und *Titanomys* (Lagomorpha, Mammalia) aus einigen Vorkommen im jüngeren Tertiär Mittel- und Westeuropas. – Mainzer geowissenschaftliche Mitteilungen, 3: 95–214.

Tobien, H. (1975): Zur Gebißstruktur, Systematik und Evolution der Genera *Piezodus*, *Prolagus* and *Ptychoprolagus* (Lagomorpha, Mammalia) aus einigen Vorkommen im jüngeren Tertiär Mittel- und Westeuropas. – Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden, 103: 103–186.

Tomida, Y. (2012): New species of *Alloptox* (Lagomorpha, Ochotonidae), first record of the genus in Japan, and subgeneric distinction. – Paleontological Research, 16: 19–25. https://doi.org/10.2517/1342-8144-16.1.019

Tomida, Y., Goda, T. (1993): First discovery of *Amphilagus*-like ochotonid from the Early Miocene of Japan. – In: Abstracts of the 1993 Annual Meeting of the Paleontological Society Japan, p. 76.

Tomida, Y., Otsuka, H. (1993): First discovery of fossil Amami Rabbit (*Pentalagus furnessi*) from Tokunoshima, Southwestern Japan. – Bulletin of the National Science Museum, 19(2): 73–79.

Tong, Y. (1989): A new species of *Sinolagomys* (Lagomorpha, Ochotonidae) from Xinjiang. – Vertebrata PalAsiatica, 27(2): 103–116.

Topachevsky, I. V. (1987): Novyy vid *Amphilagus* (Lagomorpha, Palaeolagidae) iz srednego sarmata Ukrainy [A new species of *Amphilagus* (Lagomorpha, Palaeolagidae) from the Middle Sarmatian of Ukraine]. – Vestnik Zoologii, 5: 24–30. (in Russian)

Ünay, E., Sen, S. (1976): New species of the genus *Alloptox* in Tortonian of Anatolia. – Bulletin of the Mineral Research and Exploration Institute Turkey, Ankara, 85: 145–149.

Wang, B. Y., Qiu, Z. X. (2000): Micromammal fossils from red mudstone of lower member of Xianshuihe Formation in Lanzhou basin, China. – Vertebrata PalAsiatica, 38(4): 255–273.

Wessels, W., Feifar, O., Pelaez-Campomanes, P., Meulen van der, A., De Bruijn, H. (2003): Miocene small mammals from Jebel Zelten, Libya. – Coloquios de Paleontologia, 1: 699–715.

Winkler, A. J., Flynn, L. J., Tomida, Y. (2011): Fossil lagomorphs from the Potwar Plateau, northern Pakistan. – Palaeontologia Electronica, 14(3): 38A (16 pp.).

Wolfe, J. A. (1971): Tertiary climatic fluctuations and methods of analysis of Tertiary floras. – Palaeogeography, Palaeoclimatology, Palaeoecology, 9: 27–57. https://doi.org/10.1016/0031-0182(71)90016-2

Wu, W.-Y., Flynn, L. J. (2017): The Lagomorphs (Ochotonidae, Leporidae) of Yushe Basin. – In: Flynn, L. J., Wu, W.-Y. (eds), Late Cenozoic Yushe Basin, Shanxi Province, China: Geology and Fossil Mammals. Vol. II: Small Mammal Fossils of Yushe Basin. Springer, Heidelberg, pp. 31–58. https://doi.org/10.1007/978-94-024-1050-1_4

Zhai, R. J. (1977): Supplementary remarks on the Age of Changxiandian Formation. – Vertebrata PalAsiatica, 15(3): 173–176.

Zhang, Z. Q., Dawson, M. R., Huang, X. (2001): A new species of *Gobiolagus* (Lagomorpha, Mammalia) from the Middle Eocene of Shanxi Province, China. – Annales of the Carnegie Museum, 70(4): 257–261. https://doi.org/10.5962/p.316107

Zhou, X. Y. (1988): Miocene ochotonid (Mammalia, Lagomorpha) from Xinzhou, Shaanxi. – Vertebrata PalAsiatica, 26(2): 139–148.