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Taxonomic diversity of Late Cenozoic Asian and North American ochotonids (an overview)

Margarita A. Erbajeva, Jim I. Mead, Nadezhda V. Alexeeva, Chiara Angelone, Sandra L. Swift

ABSTRACT

Ochotonids (pikas) are an ancient group of mammals originating in the Oligocene of Asia and flourishing in the Miocene of the Old World. During the Pliocene they reduced both their diversity and abundance, Only the Pleistocene genus *Ochotona* survived to the present. Their current geographic diversity is concentrated in Asia, where 28 species exist today. Outside of Asia, ochotonids are represented by one living species in Europe and two living species in North America.

There were likely three main immigrations to North America since the Miocene: (1) at the beginning of the Miocene represented by the appearance of *Oreolagus*; (2) at the Miocene- Pliocene boundary represented by the appearance of *Ochotona spanglei;* and (3) during the Early Pleistocene with the appearance of *Ochotona whartoni,* and small pikas close to the "*Ochotona pusilla* group". Extant, endemic North American species appear in the Pleistocene.

Plain-Language Summary

Margarita A. Erbajeva, Geological Institute, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia 670047. erbajeva@gin.bscnet.ru
Jim I. Mead, Department of Geosciences, East Tennessee State University, PO Box 70267, Johnson City, Tennessee 37614, USA. mead@etsu.edu
Nadezhda V. Alexeeva, Geological Institute, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russia 670047. ochotona@online.ru
Chiara Angelone, Universita di Roma Tre, 00146 Roma, Italy. angelone@uniroma3.it
Sandra L. Swift, Department of Geosciences, East Tennessee State University, PO Box 70267, Johnson City, Tennessee 37614, USA. swifts@etsu.edu

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INTRODUCTION

The family Ochotonidae (Lagomorpha) includes 16 extinct genera and one extant genus (*Ochotona*). Studies indicate that the ochotonids show general evolutionary trends in the cheek teeth. These trends include a shift toward rootlessness and hypsodonty, increasing complexity in the enamel structure of the P^3 and P_3, increasing depth of the hypostria of P^4-M^2, and widening of the talonids of P_4-M_2 from narrow to wide (Erbajeva 1994).

Morphological examination of cranial and postcranial skeletons of both extinct and living taxa indicates that the main external features of ochotonids remained invariable for a long time (Gureev 1964; Polyakova and Erbajeva 1974; Erbajeva 1994). Current data suggest that the principal ochotonid adaptations developed in the Oligocene and have mostly been retained. Based on similar dental structures in fossil and modern pikas, it is likely that fossil forms had similar ecologic requirements (e.g., open landscapes, grass diet) (Gureev 1964; Erbajeva 1988; Mead and Spaulding 1995).

MATERIALS

Recent and fossil specimens examined for this study belong to: Geological Institute of the Siberian Branch RAS, Ulan-Ude; Institute of Plant and Animal Ecology USC, Yekaterinburg; Zoological Institute RAS, Saint Petersburg, Russia and Institute of Geology SB RAS, Yakutsk (Russia); American Museum of Natural History, New York; Smithsonian Institution, Washington, D.C.; Carnegie Museum of Natural History, Pittsburgh; Denver Museum of Nature and Science; and the University of California, Museum of Paleontology (USA).

The systematic organization of fossil species presented below is based on the morphology of preserved skulls, mandibles and teeth, and on biometric studies. Most living species, in addition to the mentioned characters, were diagnosed according to external features such as body ratio or pelage. The comparative analysis of living and extinct species is based mainly on the tooth structures and in part on preserved fragments of skull and mandibles for fossil forms.

We follow the standard *Ochotona* dental morphology outlined by Erbajeva (1988). In a whole more than 2000 specimens of living pikas and approximately 650 specimens of fossil *Ochotona* were examined from mentioned above Institutions.

CLASSIFICATION OF THE FAMILY OCHOTONIDAE

Five families are recognized in the order Lagomorpha: Mimolagidae Erbajeva, 1986, Leporidae Gray, 1821, Palaeolagidae Dice, 1929, Prolagidae Gureev, 1960, and Ochotonidae Thomas, 1897. The family Ochotonidae includes two subfamilies, Sinolagomyinae Gureev, 1960 and Ochotoninae Thomas, 1897. The chronologic range of Sinolagomyinae is Oligocene to Miocene. Ochotoninae is known from the Miocene – Recent. The classification of genera (after Erbajeva 1994, modified with new data from Sen, 2003) is as follows:

Ochotonidae Thomas, 1897
- Sinolagomyinae Gureev, 1960
  - *Sinolagomys* Bohlin, 1937
  - *Austrolagomys* Stromer, 1926
  - *Kenyalagomys* MacInnes, 1953
  - *Oreolagus* Dice, 1917
  - *Bellatona* Dawson, 1961
  - *Heterolagus* Crusafont, Villata, and Truyols, 1955
  - *Bellatonoides* Sen, 2003
- Ochotoninae Thomas, 1897
  - *Marcuinomys* Groizet, 1839
  - *Lagopsis* Schlosser, 1884
  - *Albertona* Lopez-Martinez, 1986
  - *Alloptox* Dawson, 1961
  - *Paludotona* Dawson, 1959
  - *Proochotona* Chomenko, 1914
  - *Ochotonoides* Teilhard de Chardin and Young, 1931
  - *Pliolagomys* Erbajeva, 1983 in Agadjanian and Erbajeva, 1983
  - *Ochotonoma* Sen, 1998
  - *Ochotona* Link, 1795

THE DIVERSITY OF OCHOTONIDS AND THEIR EVOLUTIONARY DEVELOPMENT

Subfamily Sinolagomyinae

The earliest ochotonids referred to the genus *Sinolagomys* are recognized from Oligocene deposits in China and Mongolia (Bohlin 1937, 1942; Gureev 1964). The genus flourished in eastern Asia from the middle Oligocene through early Miocene (Gureev 1964; Li and Qiu 1980; Tong 1989). Oligocene taxa are characterized by having reduced roots, cheek teeth with closed crown bases, with rather high crown, hypostria of the upper cheek teeth nearly half of the tooth width, and talonids of lower teeth being much narrower trigonids (Erbajeva 1994, figure 2).

At the beginning of the Miocene ochotonids were widespread. A number of new genera of Sinolagomyinae appeared in Europe (*Heterolagus*), Africa (*Kenyalagomys* and *Austrolagomys*), North America (*Oreolagus*), and Asia (*Bellatona* and *Bellatonoides*). *Sinolagomys,* represented by new Miocene species, persisted in Asia. *Heterolagus* and *Austrolagomys* appeared at the end of early Miocene. All Miocene taxa differ from the Oligocene in their lack of cheek tooth roots, higher crowns, nearly equal widths of trigonids and talonids on P_4-$M_{2,}$, and deeper hypostria in the upper teeth.

Sinolagomys, *Kenyalagomys*, and *Oreolagus* became extinct the end of the Middle Miocene (Dawson 1965; Janvier and Muizon 1975; Li and Qiu 1980). *Bellatona* and *Bellatonoides* survived until the Late Miocene. By the end of the Late Miocene all genera in Sinolagomyinae became extinct.

Subfamily Ochotonodnae

The earliest record of subfamily Ochotoninae is from the early Miocene, after which members of both ochotonid subfamilies evolved in parallel throughout the Miocene (Erbajeva 1994).

It seems likely that Ochotoninae derived from primitive *Bellatona*-like ancestors described by Qiu (1996). All Ochotoninae are characterized by rootless cheek teeth except *Marcuinomys,* which has teeth with closed crown bases similar to *Sinolagomys kansuensis*. However, *Marcuinomys* differs from the latter by having more a complex structure of the most diagnostic teeth (P_3 and P^3). By the end of Early Miocene all ochotonid cheek teeth are rootless and hypsodont.

Alloptox, of the early Miocene of Asia (Li 1978), has a tooth structure similar to European genera (*Marcuinomys*, *Albertona*, and *Lagopsis*; Lavocat 1951; Bucher 1982; Lopez Martinez 1986) suggesting that arid, continental climate and paleoenvironmental conditions of the Middle Miocene was favorable for pikas of the genera *Alloptox* and *Lagopsis* the diverse species of which is evident. They scattered in Asia and Europe, respectively, whereas the primitive specialized taxa *Marcuinomys* and *Albertona* disappeared.

In the Late Miocene, ochotonids underwent tremendous changes. All Sinolagomyinae and the Ochotoninae genera *Alloptox* and *Lagopsis* became extinct. Some new forms appeared, such as *Paludotona* in Europe and *Proochotona* in Eurasia, but they survived only to the end of Late Miocene and beginning of the Early Pliocene, respectively (Dawson 1959; Chomenko 1914). At the end of Late Miocene three genera, *Ochotonoides, Ochotonoma*, and *Ochotona*, appeared in Asia, and *Pliolagomys* appeared in Eurasia to middle Pliocene (Kretzoi 1959; Sen 1998; Topacewski and Scorik 1977; Erbajeva 1988). At the beginning of Pliocene the geographic range of ochotonids shrank, with all African forms becoming extinct. Concurrently, *Ochotona* migrated to North America (*Ochotona spanglei* Shotwell 1956) and to Europe (*Ochotona* sp. from Maritsa) (de Bruijn et al. 1970).

During the Pliocene *Ochotonoides* (three species)*, Pliolagomys* (three species) and *Ochotona* (36 species) flourished. They were represented by a number of species having wide distributions in Eurasia, from Hungary, Romania and Moldavia in the west, to North China in the east. They differed much in body size and tooth morphology. *Ochotonoides* and *Pliolagomys* are characterized by complicated structures of the P_3 (Erbajeva 1988, figures 21-23). These genera became extinct in the Late Pliocene, and only *Ochotona* survives to the present. The latter had a wide distribution in Eurasia from the Late Miocene through Pleistocene and in North America from the Early Pleistocene through Recent (Erbajeva 1988). This genus with simple structure of P_3 was represented by a number of species differing by the variations of teeth size (corresponding to body size), from large to medium and small among ochotonids (Erbajeva 1994, figure 6; Erbajeva and Zheng 2005).

OCHOTONID DEVELOPMENT AND HISTORY IN EURASIA

The genus *Ochotona* was represented in Eurasia by several species differing in size: large forms - *Ochotona lagreli*, *O. guizhongensis*, *O. chowmincheni, O. gudrunae, O. ursui*, *O. gromovi*, *O. tologoica*, *O. transcaucasica*, *O. magna, O. zasuchini*, *O. zazhigini, O. zhangi*; medium-sized forms - *Ochotona antiqua*, *O. plicodenta, O. lingtaica, O. dodogolica*, *O. polonica, O. nihewanica*, *O. agadjianiani, O. tedfordi*; and small-sized forms - *Ochotona minor*, *O. sibirica*, *O. valerotae, O. horaceki, O. dehmi, O. youngi, O. Gracilis*, and others.

Ochotona lagreli, O. guizhongensis, *O. chowmincheni,* and *O. minor* are Late Miocene forms distributed in China and Mongolia; they never appeared in the Pliocene (Schlosser 1924; Qiu 1987; Erbajeva and Daxner-Hoeck 2001; Erbajeva 2003; Erbajeva and Zheng 2005; Erbajeva et al. 2006). During the Pliocene in Asia *Ochotona* was distributed from Transcaucasia in the west through Kazakhstan, Transbaikalia, and Mongolia to China in the east. Representative species include

Ochotona agadjianiani, O. gromovi, *O. intermedia, O. sibirica, O. nihewanica, O. plicodenta, O. lingtaica, O. youngi, O. gracilis, O. gudrunae,* and *O. zazhigini* a.o. (Zheng 1982; Agadjanian and Erbajeva 1983; Erbajeva 1994; Zheng and Zhang 2000; Erbajeva and Zheng, 2005; Erbajeva et al. 2006). In the Europe, mainly in the east, *Ochotona ursui* (Dacic Basin*,* Romania), *Ochotona* sp. (Maritsa, Greece), *Ochotona antiqua* (Moldavia, Ukraine and the Russian Plain), and *O. polonica* (Zamkowa Dolna, Poland) are recognized (Simionescu 1930; de Bruijn et al. 1970; Sych 1980; Erbajeva and Shushpanov 1988).

The Pleistocene is characterized by the development and diversity of small pikas of the "*O. pusilla*" group, the history of which began at the end of Pliocene-beginning of Pleistocene, approximately 2.00-1.67 Ma. The species attributed to this group are characterized by archaic (plesiomorphic) features of their cheek teeth such as wide confluence between the anteroconid and posteroconid in the $P_{3,}$ and by small size.

The distribution of the Early Pleistocene ochotonids in Eurasia expanded west and northeast relative to the Pliocene distribution. Fossil records of pikas in Europe are known from France (*Ochotona valerotae*, Valerots site), Germany (*Ochotona dehmi*, Schernfeld), Slovakia (*Ochotona horaceki,* Honce), Hungary (*Ochotona* sp., Ostramos 2,), and the Ukraine and Russian Plain (*Ochotona pseudopusilla*). Records in Asia are from west and east Siberia (*Ochotona* sp., Scorodum, Romanovo, Kizikha sites, *O. filippovi*, Podymakhino) and Yakutia (*Ochotona* cf. *whartoni* and *Ochotona* sp., Krestovka section). *Ochotona* continues to be rather abundant in Transbaikalia, Mongolia and Northern China (Dehm 1962; Gureev 1964; Janossy 1986; Zheng and Zhang 2000; Erbajeva et al. 2001; Cermak 2004; Erbajeva and Zheng 2005; Erbajeva 2005). During Middle and Late Pleistocene, successive glacial and interglacial phases resulted in episodic paleoenvironmental changes. With changes of climate towards cool and dry conditions, open landscapes became widespread. At that time vast territories in Eurasia were occupied by steppe-tundra (also called the Mammoth-Steppe). Throughout the Pleistocene, Asia was broadly connected with Europe, with no barriers to faunal interchange (e.g., ice sheets). This connection is illustrated by broad migrations of Asian-steppe faunal elements, such as ochotonids, jerboas, lagurids, and others to Europe. In Transcaucasia a geographically restricted population of large-sized pika, *Ochotona transcaucasica,* existed.

A wide geographic radiation of *Ochotona pusilla* occurred. A broad area of Eurasia was occupied by a number of taxa of the subspecies level distributed from southern England through the Netherlands, France, northern Italy in the west, Transcaucasia in the south, and to the Prebaikal region of Siberia in the east. From postglacial times through the Holocene, climate change led to moderately warm conditions and the reestablishment of forest and grasslands. Likely, as a result of these changing climate conditions, *Ochotona pusilla* became more restricted in its distribution. Holocene fossil remains are not known in Europe except in Crimea (Gromov 1961), the southern Urals (Smirnov 1993), and Hungary (Kordos 1978). The modern species (Fig. 1) is mainly steppe dweller, range of which includes a small part of Eastern Europe in the right side of Middle Volga river valley (approximately 54° N), through Northern Kazakhstan to the border of China. The modern range includes a small part of Eastern Europe, mainly steppe habitats of middle Volga river valley (approximately 54° N), through Northern Kazakhstan to the border of China.

REVIEW OF NORTH AMERICAN PIKAS OF THE PAST

The earliest *Ochotona* found in North America is *Ochotona spanglei* Shotwell that immigrated to the Western Hemisphere during the latest Miocene or early Pliocene (Shotwell 1956). Following this event, there is a gap of approximately three million years in the known North American record of *Ochotona*. The next possible immigration of ochotonids took place in the earliest Pleistocene via the Bering Land Bridge. At that time, vast areas of Siberia were inhabited by small and large forms of *Ochotona*. *Ochotona* near *Ochotona whartoni* is known from East Siberia (Zayarsk site) to the Kolyma Range area and in North America from Cape Deceit, Alaska, and the Old Crow River Basin (Guthrie and Matthews 1971; Harington 1978; Erbajeva and Belolubsky 1993; Storer 2004).

Fossil remains of small pikas from the middle Pleistocene (Irvingtonian Land Mammal Age) are known from Cumberland and Trout Caves in the central Appalachians, a region not occupied by pikas at present (Guilday 1979; Mead 1987). According to recent data, small pikas survived in this region until the late Pleistocene, and fossils are known from an additional five caves (Kurten and Anderson 1980; Mead and Grady 1996). Other

FIGURE 1. *Ochotona pusilla* Pallas, 1768. Original drawing (paint) of (by) V.A.Vatagin (Table II, after S.I. Ognev, The mammals of USSR and adjacent countries, vol. IV, USSR Academy of Sciences Press, Moscow – Leningrad, 1940. 615 p.).

Irvingtonian ochotonids, close to the Cumberland and Trout Cave forms, are known from lower layers of the Pit and the Velvet Room in Porcupine Cave, Colorado (Mead et al. 2004). However, ochotonid remains from upper levels of the Velvet Room are similar to *Ochotona princeps*. Most localities containing fossil ochotonids are situated in western North America, areas now occupied by *O. princeps* (Grayson 1977, 1987; Mead 1987; Mead and Spaulding 1995; Hafner 1993; Hafner and Sullivan 1995).

Western Hemisphere immigrants similar to the "*O. pusilla*" group dispersed to the central Appalachians in the east and Rocky Mountains in the west at the Middle Pleistocene (Guilday 1979; Mead et al. 2004). Pleistocene North American pikas might have inhabited open, lowland landscapes. According to Grayson (1987, p. 359), "*Ochotona princeps* became extinct in the lowlands of the northern half of the Great Basin" around 7,000 years ago. Moreover, in this region some sites with ochotonid remains are found 35 to 280 km from their present distribution (Grayson 1987). The distribution of pikas in the Great Basin likely was reduced due to a climatic shift towards warmer and drier conditions in the Holocene. It may be possible that the rapid explosion of the herbivorous arvicolid rodents, which became the main competitors of pikas, led to a restriction of the ochotonid distribution in Asia, in particular in the Transbaikal area (Erbajeva 1988, 1994). Changing climates likely restricted the pika to the montane 'islands' in the west and led to their extinction in the east. Gradually pikas became inhabitants of mountains of varying altitude and talus-dwellers. Today, *Ochotona princeps* lives mainly in mountains at lower latitudes, whereas *O.collaris* inhabits a wide range of altitudes at higher latitudes, including lowlands (Youngman 1975).

COMPARISON BETWEEN LIVING ASIAN AND NORTH AMERICAN PIKAS

Ochotona princeps and *O. collaris* of North America and *O. alpina* and *O.hyperborea* of Asia were once considered to be a single species based on skull morphology and external features (Argyropulo 1948; Gureev 1964; Corbet 1978). These same species are considered distinct, based on chromosomal data. Because they share the number of chromosomes (2n = 68), a closer phylogenetic relationship was hypothesized for *Ochotona pusilla* and the North American species (*Ochotona princeps* and *O. collaris*) (Vorontsov and Ivanitskaya 1973). This hypothesis is supported by the fossil record and by the presence of plesiomorphic features shared in *Ochotona pusilla* in some P_3 of both North American species. It may be suggested that *Ochotona pusilla, O. collaris* and *O. princeps* likely had the same ancestral form, the divergence of which took place at least by the earliest Pleistocene. The oldest ancestral taxon probably was similar to the pikas from Cumberland and Trout Caves as well as from Porcupine Cave, having small size and a wide confluence between anteroconid and posteroconid. It is reasonable to suggest that the development of the living forms, at least of *Ochotona princeps*, probably occurred during the end of Middle or beginning of Late Pleistocene. As noted above, ochotonid remains from the upper levels of the Velvet Room are similar to *Ochotona princeps*.

Comparisons between recent *Ochotona pusilla, O. collaris,* and *O. princeps* show that they differ significantly in their size, pelage, biology, skull morphology, tooth structure, ear bones, baculum morphology, and behavioral data. They differ as well by diversity of their habitats and elevations. *Ochotona pusilla* is a burrowing steppe-dwelling animal; in arid and desert steppes it is generally found in wet biotopes with thick grass and bushes mainly in Northern Kazakhstan (Ognev 1940; Gureev 1964). Today *Ochotona princeps* is talus-dwelling species distributed in mountainous area of West North America (Smith 1974, 1981). *Ochotona collaris* is also a typical rock and talus-dwelling pika, distributed in the mountains of central and southern Alaska and northwestern Canada (Broadbooks 1965).

CONCLUSIONS

Ochotonids originated in Central Asia during the Oligocene, flourished during Miocene and Pliocene and decrease their diversity during Pleistocene.

The first dispersal of the genus *Ochotona* into the Europe occurred at the beginning of Pliocene.

There have been repeated migration events to the North America.

The first ochotonid' invasion into the Western Hemisphere occurred at the beginning of Miocene when *Oreolagus* appeared.

The next immigration occurred during the late Miocene (Hemphillian), recorded with the first appearance of the genus *Ochotona*.

The ancestral forms of the living pikas migrated to North America at the beginning of Early Pleistocene and they distributed as far south and east west as the Appalachians and Colorado.

The earliest Irvingtonian pikas are closer to pikas of "O. pusilla" group, having some plesiomorphic characters.

Recent North American pikas differ significantly from *Ochotona pusilla* by their external features and their habitat.

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