



Inferring divergence times within pikas (*Ochotona* spp.) using mtDNA and relaxed molecular dating techniques

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ARTICLE INFO

Article history:

Received 1 April 2008

Revised 15 May 2009

Accepted 28 May 2009

Available online 6 June 2009

Keywords:

Ochotona

Pika

Relaxed molecular clock

cyt *b*

ND4

Nearctic pikas

ABSTRACT

Although several studies have recently addressed phylogenetic relationships among Asian pikas (*Ochotona* spp.), the North American species have been relatively neglected and their monophyly generally unquestioned or assumed. Given the high degree of intraspecific diversity in pelage and call structure, the recent identification of previously unrecognized species of pika in Asia, and the increasing evidence for multiple trans-Beringian dispersals in several small mammal lineages, the monophyly of North American pikas warrants reexamination. In addition, previous studies have applied an externally calibrated rate to examine the timing of diversification within the genus. This method has been increasingly shown to return results that, at the very least, are overly narrow in their confidence intervals, and at the worst can be entirely spurious. For this study we combined GenBank sequences from the mitochondrial genes *cyt b* and ND4 with newly generated sequence data from *O. hyperborea* and *O. collaris* to investigate the origin of the North American lineages and the timing of phylogenetic diversification within the genus *Ochotona*. Specifically, we address three goals (1) summarize and reanalyze the molecular evidence for relationships within the genus using statistically supported models of evolution; (2) add additional sequences from *O. collaris* and *O. hyperborea* to rigorously test the monophyly of North American pikas; (3) examine the timing of the diversification within the genus using relaxed molecular clock methods. We found no evidence of multiple trans-Beringian dispersals into North America, thereby supporting the traditional hypothesis of a single invasion of North America. We also provide evidence that the major splits within the genus occurred in the Miocene, and the Nearctic pikas diverged sometime before the Pleistocene.

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1. Introduction

Pikas (Lagomorpha: Ochotonidae; *Ochotona*) comprise 30 species of territorial, small-bodied herbivores currently found in the northern hemisphere (Smith et al., 1990; Hoffmann and Smith, 2005). Thought to have diverged from their sister lineage Leporidae (rabbits and hares) sometime after the K/T boundary (65 mya; but see Bininda-Emonds et al., 2007), pikas are one of the least speciose of any of the families in the superorder Glires (Orders Lagomorpha and Rodentia). Pikas are generalist herbivores adapted to steppe and alpine environments. Extant species (genus *Ochotona*) exhibit high intraspecific variation in pelage and vocalizations but few differences between species (Corbet, 1978; Smith et al., 1990; Erbaeva, 1994). Consequently, their taxonomy has been, and continues to be, poorly resolved (Hoffmann and Smith, 2005).

Two recent molecular studies have explored phylogenetic relationships within *Ochotona* using DNA sequence data. The first (Yu et al., 2000) sampled two mitochondrial genes (1383 bp of ND4 and 1140 bp of cytochrome *b*) from 19 extant species, focusing mainly on the timing and divergence of Asian *Ochotona*. Yu et al. (2000) recovered three main subgroups of pika: a northern subgroup, a shrub-steppe dwelling subgroup, and a mountain subgroup. Largely based on this work, *Ochotona* was grouped into three subgenera (Table 1) by Hoffmann and Smith (2005). While the Yu et al. (2000) analysis provides an important foundation for understanding pika systematics, it included very few intraspecific samples from broadly separated localities and failed to include a number of potentially important species, particularly *O. collaris* (North America) and *O. pusilla* (Eurasia). A second molecular study was recently conducted by Niu et al. (2004), incorporating more taxa but shorter fragments of *cyt b* (~402 bp). As ochotonid taxonomy can be complex and species often misidentified (Smith et al., 1990), the inclusion of additional species and intraspecific samples is important. However, larger taxonomic sampling frequently requires larger molecular datasets to provide sufficient phylogenetic

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Table 1
Subgenera and fossil record of extant Ochotona species.

Subgenus ^a	Species	First known fossil occurrence	
<i>Conothoa</i>	<i>O. brookei</i>	Late Pliocene ^b	
	<i>O. erythrotis</i>		
	<i>O. forresti</i>		
	<i>O. gaoligongensis</i>		
	<i>O. gloveri</i>		
	<i>O. himalayana</i>		
	<i>O. iliensis</i>		
	<i>O. koslowi</i>		Pleistocene ^c
	<i>O. ladacensis</i>		
	<i>O. macrotis</i>		Middle Pleistocene ^d
	<i>O. muliensis</i>		
	<i>O. nigritia</i>		
	<i>O. roylei</i>		
	<i>O. rutilla</i>		
<i>Ochotona</i>	<i>O. cansus</i>	Middle Pleistocene ^e	
	<i>O. curzoniae</i>		
	<i>O. dauurica</i>		
	<i>O. huangensis</i>		
	<i>O. nubrica</i>		
	<i>O. pusilla</i>		Late Pliocene ^e
	<i>O. rufescens</i>		
	<i>O. tibetana</i>		Late Pleistocene ^f
	<i>O. thomasi</i>		
	<i>Pika</i>		<i>O. alpina</i>
<i>O. argentata</i>			
<i>O. collaris</i>		Late Pleistocene ^f	
<i>O. hoffmanni</i>			
<i>O. hyperborea</i>		Late Pleistocene ^e	
<i>O. pallasi</i>			
<i>O. princeps</i>		Middle Pleistocene ^g	
<i>O. turuchanensis</i>			

^a Hoffmann and Smith (2005).

^b Cai (1989).

^c Li et al. (2006).

^d Erbajeva and Zheng (2005).

^e Erbajeva (1994).

^f Harington (1978).

^g Mead (1987).

resolution. Recent morphological (Lissovsky, 2003) and molecular (Lissovsky et al., 2007) studies have also been conducted on the Palearctic members of the subgenus *Pika*. Phylogenetic analyses by Lissovsky et al. (2007) incorporated greater sampling within the *O. alpina*–*hyperborea* complex, resulting in the recognition of the morphologically, ecologically, and genetically distinct species, *O. turuchanensis*. Lissovsky (2003) and Lissovsky et al. (2007) also suggested the presence of at least one additional species, *O. scorodumovi*, which may be conspecific with *O. mantchurica*.

1.1. Nearctic pikas

In North America, two allopatric species of pika are currently recognized—*O. collaris* and *O. princeps*—which have been traditionally defined on the basis of geographic isolation, size of auditory bullae, and pelage characteristics (Nelson, 1893; Hall, 1951; Broadbooks, 1965; MacDonald and Jones, 1987). The many similarities between the two species led some authors to synonymize *O. collaris* and *O. princeps*, along with the Palearctic *O. hyperborea*, with the Palearctic species *O. alpina* (e.g., Broadbooks, 1965; Corbet, 1978). Weston (1981) used morphometric data to show distinct differences between the North American taxa, with *O. princeps* more closely resembling the Asian species. In terms of intraspecific variation, *O. princeps* includes 36 recognized subspecies and a much patchier distribution than the monotypic *O. collaris* (Hall, 1981). This may be an artifact of disproportionate research efforts over the past century, as *O. princeps* has been more frequently studied than *O. collaris* (MacDonald and Jones, 1987; Smith and

Weston, 1990). While subspecific differentiation within *O. collaris* has been suggested (Baker, 1951), it has yet to be thoroughly investigated. It may also reflect true levels of intraspecific variation, possibly resulting from events of historical population fragmentation within *O. princeps* or a more recent bottleneck within *O. collaris* (Hafner, 1994; Hafner and Sullivan, 1995).

1.2. Biogeography and fossil history

Currently, pika diversity is highest in Asia (28 species), with only two species in North America. The current distribution and diversity of the pikas is a fraction of that seen during their peak in the Miocene, with fossils representing multiple genera known from localities as far apart as north Africa, eastern North America, and western Europe (Dawson, 1967). Pleistocene records exist for steppe pika (*O. pusilla*) in Great Britain, although this species is now known only from the central Russian steppes and northern Kazakhstan (Erbajeva, 1994; Fisher and Yalden, 2004; Smith et al., 1990).

Pikas are known from North American localities as early as the Miocene (in Oregon; Shotwell, 1956), and as far south as California, as far east as Virginia in the Pleistocene (Kurtén and Anderson, 1980; Erbajeva, 1994; Mead and Grady, 1996). Several North American species have been described, including a relatively large form (*O. whartoni*) from Alaska and the Yukon Territory (Mead, 1987; Guthrie and Matthews, 1971). A smaller species, possibly *O. collaris*, is thought to have been sympatric (although perhaps not contemporary) with *O. whartoni* (now extinct; Guthrie and Matthews, 1971; Harington, 1978; Weston, 1981; Mead, 1987). Distribution maps of *O. princeps* and *O. collaris* have been used to suggest allopatric speciation in separate refugia during the Wisconsinan glaciation (Guthrie, 1973; Harington, 1978). This scenario would imply that *O. collaris* and *O. princeps* diverged within North America after a single dispersal across the Bering Land Bridge from Asia. However, similar assumptions about the Alaska marmot (*Marmota flaviventris*) and the hoary marmot (*M. caligata*), also North American alpine specialists with similarly allopatric distributions, proved incorrect, as molecular data suggest that the Alaskan marmot is the result of an independent colonization and is actually more closely related to Asian species (Steppan et al., 1999).

1.3. Current objectives

Pikas exhibit a great deal of intraspecific morphological diversity and relatively low interspecific diversity, making it unreasonable to use a single sample per putative species as a proxy for that species. An increasing number of studies have demonstrated the importance of sampling multiple individuals from multiple species to understand the evolutionary history and taxonomic limits of a species (Peters et al., 2005). Using a single individual, or geographically clumped sample from multiple individuals, could fail to capture paraphyly or polyphyly resulting from introgression, hybridization, and/or incomplete lineage sorting of ancestral polymorphisms (Peters et al., 2007). As many talus-dwelling species live in patchily distributed habitat with disjunct populations (Smith et al., 1990), they may be likely to contain cryptic lineages. Several of the most recently described species of pika are talus-dwelling, and very geographically restricted (e.g., *O. iliensis*, Li and Smith, 2005; *O. argentata*, Erbajeva and Ma, 2006). Little is known about the potential for pika species to hybridize, but rabbits and hares show evidence of introgression or hybridization between species (Alves et al., 2003). While denser taxonomic sampling is important, it necessitates increasing the number of characters to improve resolution and nodal support (Jansa et al., 2006).

Statistical and computational phylogenetic methods have greatly improved over the past few years, and we sought to utilize

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