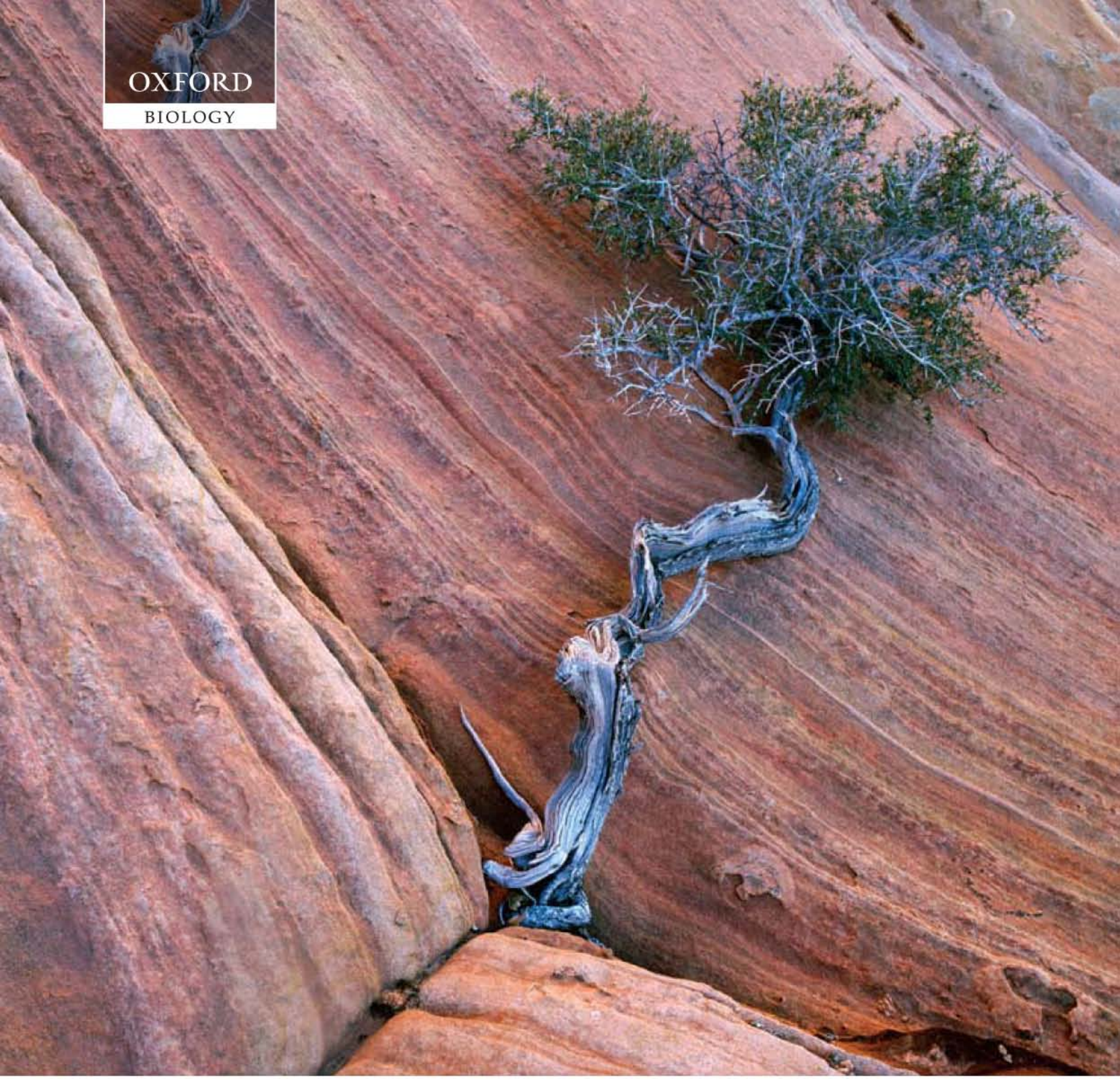

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Pikas, hares, and rabbits (Lagomorpha)

Conrad A. Matthee
Evolutionary Genomics Group, Department of Zoology, University of Stellenbosch, Stellenbosch, 7602 South Africa (cam@sun.ac.za)

Abstract

The pikas, hares, and rabbits (~90 species) are grouped into two families, Ochotonidae and Leporidae, within the mammalian Order Lagomorpha. Based on several molecular studies, the estimated time of divergence of these two families has varied between 30.4 and 51.0 million years ago (Ma), with an average of 40 Ma. Climatic shifts during the Eocene–Oligocene transition may have been responsible for this divergence.

The pikas, hares, and rabbits (Fig. 1) are united into the monophyletic Order Lagomorpha based on the presence of a second peg-like upper incisor and foot morphology showing a unique calcaneal canal running diagonally through the lagomorph calcaneus (*1*). Based on the latter observation, which is also present in lagomorph fossils, it has been proposed that the order has had a long evolutionary separation from other related mammalian orders such as the Rodentia (*1–3*). The Lagomorpha currently comprises two extant families, the Ochotonidae (pikas, 30 species and one genus) and Leporidae (rabbits and hares, 60 species and 11 genera) (*4*).

The monotypic pikas have a northern hemisphere distribution with most taxa confined to Asia, where the uplifting of the Tibet Plateau probably played a major role in the diversification of taxa (*5*). The 11 genera of rabbits and hares have a nearly global distribution (Holarctic, Ethiopian excluding Madagascar, northern Neotropical and Oriental) and their diversification is more than likely due to a series of dispersal and vicariance events that could be correlated to the formation and disappearances of intercontinental landbridges (*6*). From a paleontological perspective, evidence suggests either an Asian or North American origin for the order, but the pinpointing of the exact location is hampered by a scattered fossil record for the early and middle Eocene (*7*). It has been postulated that the first expansion of Leporidae occurred in North America during the Miocene (*7*), a notion supported by at least two recent fossil discoveries (*8, 9*), whereas the Ochotonidae probably originated in Asia. Here I review the available information on the timing of the Ochotonidae and Leporidae divergence.

The fossil record of the Lagomorpha dates back to at least 45 Ma (*1, 7*) and the oldest fossil member of the Ochotonidae is known from the early Oligocene of Mongolia ~33–32 million years ago (*10*). Erbajeva (*11*) proposed that during this same period the Leporidae and the Ochotonidae started to diverge from each other and although this date falls within the 40–30 million years suggested by Dawson (*7*), it is more recent than the 50 million years proposed by Benton (*12*). Analyses of 58 presumptive structural allozyme loci estimated the time of divergence between the Leporidae and the Ochotonidae at 37.5 Ma (*13*). Using seven gene regions (mtDNA and nuclear introns), the age of the divergence among the families was estimated at 31.7–29.0 Ma in Bayesian and maximum likelihood analyses that used multiple calibration points and allowed for heterogeneity in molecular evolutionary parameters among genes (*6*). The 95% credibility interval in this study was estimated

Fig. 1 A Riverine Rabbit (*Bunolagus monticularis*) from South Africa. Credit: T. Camacho, Science Photo Library/Images of Africa/Okapia.

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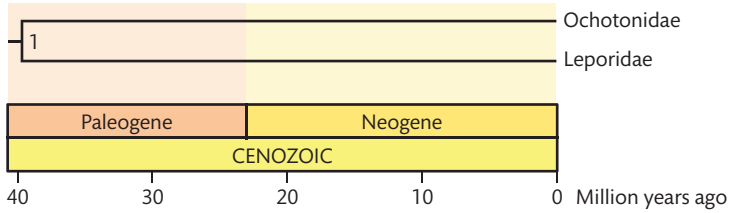

Fig. 2 A timetree of pikas, hares, and rabbits (Lagomorpha). Divergence times are shown in Table 1.

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) between lagomorph families.

Timetree		Estimates							
Node	Time	Ref. (*6*)		Ref. (*13*)		Ref. (*14*)		Refs. (*15, 16*)	
		Time	CI	Time	CI	Time	CI	Time	CI
1	39.6	30.4	39–22	37.5	–	38.9	39–36	51.0	67–35

Note: Node times in the timetree represent the mean of time estimates.

to be 39.3–22.4 Ma. Using the same methodology and sequences derived from the mtDNA genome only, the date was estimated at 38.9 Ma, ranging from 39.9 to 36.3 Ma (*14*).

Using a larger data set that underpinned a broader study dealing with the diversification of Placentalia, the date for the leporid/ochotonid split was estimated at 51.0 Ma, with a large credibility interval of ±16 million years (*15, 16*). The discrepancy in these molecular dates is likely due to the inconsistencies in calibration points (constraints). The Springer *et al.* (*15*) study used a single Euarchontoglires calibration point (mouse and rat) which was repeated in the Murphy *et al.* (*16*) study, while the Matthee *et al.* (*6*) investigation focused specifically on leporid evolution used six time constraints within Glires. The Horner *et al.* (*14*) study used four lagomorph constraints. Although Matthee *et al.* (*6*) allowed different loci to have different patterns of evolutionary change, the divergence time among the Leporidae and Ochotonidae was constrained to be within 40–20 Ma (*6*). Horner *et al.* (*14*) likewise biased the estimate by constraining the divergence of the lagomorph families to between 40 and 35 Ma.

The exact date of the split between the Ochotonidae and the Leporidae remains controversial (Table 1), but consensus suggests that the two lagomorph families diverged at some point between the late Eocene (~45 Ma) and early Oligocene (~30 Ma) (Fig. 2). The Eocene–Oligocene boundary (~34 Ma) is characterized by sudden climatic shifts in global temperatures (a warming trend was immediately followed by cooling events) (*17*) culminating in large changes in mammalian diversity (*18*). It is probable that the Eocene–Oligocene transition also contributed toward the diversification of the Lagomorpha. Furthermore it is believed that the pikas followed a diversification trend throughout the Oligocene where they subsequently spread from Asia to North America (and also later to Africa) to become most numerous during the Miocene (25 fossil genera) (*10*). The Leporidae, on the other hand, did not show a similar diversification trend until the middle Miocene (~15 Ma) at which point the Ochotonidae decreased in diversity and the Leporidae began an increase in diversity (*6*).

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