THE EVOLUTION OF BIPEDALISM IN JERBOAS (RODENTIA: DIPODOIDEA): ORIGIN IN HUMID AND FORESTED ENVIRONMENTS

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Mammalian bipedalism has long been thought to have arisen in response to arid and open environments. Here, we tested whether bipedalism coevolved with environmental changes using molecular and paleontological data from the rodent superfamily Dipodoidea and statistical methods for reconstructing ancestral characteristics and past climates. Our results show that the post-Late Miocene aridification exerted selective pressures on tooth shape, but not on leg length of bipedal jerboas. Cheek tooth crown height has increased since the Late Miocene, but the hind limb/head-body length ratios remained stable and high despite the environmental change from humid and forested to arid and open conditions, rather than increasing from low to high as predicted by the arid-bipedalism hypothesis. The decoupling of locomotor and dental character evolution indicates that bipedalism evolved under selective pressure different from that of dental hypsodonty in jerboas. We reconstructed the habitats of early jerboas using floral and faunal data, and the results show that the environments in which bipedalism evolved were forested. Our results suggest that bipedalism evolved as an adaptation to humid woodlands or forests for vertical jumping. Running at high speeds is likely a by-product of selection for jumping, which became advantageous in open environments later on.

KEY WORDS: Adaptation, bipedalism, convergent function, decoupled evolution, humid environments.

Bipedalism, which evolved independently in three major extant mammalian lineages of primates, kangaroos, and rodents, has long been thought to have arisen in those groups convergently as an adaptation to arid and open environmental conditions (Savage and Russell 1983; Hafner and Hafner 1988; Cerling 1992; Djawdan 1993; Ruff et al. 1993; Ruff and Walker 1993; deMenocal 1995; Potts 1998; Archer et al. 1999; Klein 1999; Burk and Springer 2000; Cerling et al. 2011; Wood and Harrison 2011). In primates and kangaroos, bipedalism has been shown to be an adaptation critical for survival during environmental changes associated with
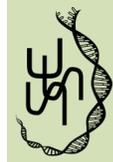
the spread of open grasslands (Cerling 1992; deMenocal 1995; Potts 1998; Klein 1999; Burk and Springer 2000; Cerling et al. 2011; Wood and Harrison 2011). In rodents, bipedalism evolved independently in four different lineages: jerboas in the superfamily Dipodoidea of Asia and North Africa, Heteromyidae of North America, Pedetidae of central and southern Africa, and Australian hopping mice and gerbils in the superfamily Muroidea of the Old World and Australia (Berman 1985). Studies have suggested that bipedalism also evolved in the different rodent groups as an adaptation to open and arid environments, similar to bipedalism in humans and kangaroos (Savage and Russell 1983; Hafner and Hafner 1988). To date, however, the association between bipedal locomotion and environmental changes has not been rigorously tested in rodents.

The superfamily Dipodoidea offers an excellent model system to study the evolution of bipedalism in rodents. This superfamily consists of three major lineages—birch mice, jumping mice, and jerboas—which exhibit a progressive series of adaptations toward a bipedal, saltatorial lifestyle (Ellerman 1941). Birch mice are quadrupedal and nonsaltatorial, and have no specialization in their hind limb structures, whereas jumping mice are primarily quadrupedal jumpers whose hind limbs are greatly elongated compared to those of birch mice (Ellerman 1941; Nowak 1999; Shenbrot et al. 2008). In contrast, jerboas are strictly bipedal hoppers, characterized by the extreme elongation of the hind limbs as well as the reduction and fusion of foot elements (Ellerman 1941; Nowak 1999; Shenbrot et al. 2008). These patterns are important because they supply a set of independent datapoints required for statistical analysis of trait evolution.

The three dipodoid lineages differ in dental types and in their habitats. Birch mice, inhabiting humid forests and woodlands in Eurasia, have brachydont and bunodont cheek teeth, which are characterized by low-crown height and well-developed cusps (Ellerman 1941; Nowak 1999; Shenbrot et al. 2008). Jumping mice, which comprise three living genera (*Eozapus*, *Zapus*, and *Napaeozapus*), possess mesodont cheek teeth (Ellerman 1941). Among them, *Eozapus* is distributed in forested areas of southwestern China, whereas *Zapus* and *Napaeozapus* are distributed across the forests, woodlands, and meadows in North America (Nowak 1999; Hall 2001). In contrast, bipedal jerboas, which are characterized by high-crowned cheek teeth with well-developed lophs, are widely distributed across arid zones in Asia and North Africa (Nowak 1999). As a result, jerboa bipedalism has long been regarded as an adaptation to dry and open habitats.

Here, we investigate the evolution of jerboa bipedalism using comparative methods based on an integrated analysis of molecular, morphological, climatic, and paleontological data. Our results indicate that the available molecular and paleontological evidence

are congruent, and support the conclusion that jerboa bipedalism evolved in humid and forested environments before critical aridification took place in the Late Miocene. This scenario contradicts the longstanding hypothesis that bipedalism evolved in mammals as a means of rapidly traversing dry and open landscapes, although bipedalism in jerboas was ultimately used for this purpose when environmental conditions changed. The findings of the present study suggest that mammalian bipedalism can evolve in either arid and open environments, as in primates and kangaroos, or humid and forested environments, as we show here for jerboas, implying that similar adaptive responses can result from different selective constraints.

Materials and Methods
CANNON BONE OF BIPEDAL JERBOAS

The cannon bone is a highly developed element in the hind foot of bipedal jerboas, and is fused from the three central metatarsals (Fig. S1E–G). This bone element is unique to jerboas because among all small mammals, only bipedal jerboas possess a cannon bone (Ellerman 1941; Nowak 1999). The earliest known cannon bone fossils have been discovered from Middle Miocene deposits of China and Mongolia about 13 Mya, and were always found to be associated with tooth remains of *Protalactaga*, the only known jerboa genus found in Early and Middle Miocene deposits in northwestern China and surrounding areas, where screen washing has been applied extensively to collect tooth fossils of small mammals for decades (Young 1927; Qiu 1996, 2000; Zazhigin and Lopatin 2000; Meng et al. 2008; Wu et al. 2009; Sun et al. 2010).

Zazhigin and Lopatin (2000) reported one almost intact and four fragmentary metatarsals from the Lower Subformation of the Oshin Formation of Mongolia, which has a Middle Miocene age of about 13 Mya; these specimens are assigned to *Protalactaga grabaui* because they were found with the dental fossils of *P. grabaui* (Zazhigin and Lopatin 2000). This study uses the intact cannon bone fossil described by Zazhigin and Lopatin (2000), which is 24.6 mm in length. Young (1927) reported an almost complete cannon bone fossil, which was found with the dental fossils of *Paralactaga andessoni* from the Late Miocene Wayaopu locality in Jingchuan of Gansu, China. Schaub (1934) reconstructed the length of the cannon bone of Young (1927) to be 35.5 mm by comparing with the complete cannon bones of extant jerboas. Zazhigin and Lopatin (2001) reported two complete metatarsals with dental fossils of *Stylodipus iderensis* from the Lower Pliocene Upper Khirgis-Nur Subformation of Mongolia. These two metatarsals are 29.3 mm and 29 mm in length, respectively. This study takes the average length of these two cannon bones, 29.15 mm, for relevant analyses.

Statistical Analysis

DIFFERENCE OF CANNON BONE/HEAD-BODY LENGTH RATIOS BETWEEN BIPEDAL JERBOAS AND NONJERBOA SPECIES

This analysis was conducted by using the phylogenetic generalized least squares (GLS) model for continuous characters in the program BayesTraits (Pagel 1999). Our hypothesis is that the hind foot/head-body length ratios in bipedal jerboas are distinct from other rodents. Two independent Markov Chain Monte Carlo (MCMC) runs were carried out for two different hypotheses, with one hypothesis based on a linear regression model and the other an extended model that included a dummy variable to separate jerboas from other rodents (phylogenetic analysis of covariance [ANCOVA]). The program calculated the natural logarithm of the harmonic mean of the likelihoods for each hypothesis. The two hypotheses were compared by a calculation of the Bayes Factor (Raftery 1996). A Bayes Factor greater than two is positive evidence, greater than five is strong evidence, and greater than 10 is very strong evidence for the hypothesis (Raftery 1996).

The hind foot length and head-body length ratios in dipodids, zapodids, and sicistids are provided in Table S1, and the measurements of the hind foot length and head-body length of extant dipodoids are provided in Table S2.

ESTIMATION OF HEAD-BODY LENGTH FROM THE M1 LENGTH FOR FOSSIL JERBOAS

The length was estimated using the phylogenetic GLS model for continuous characters in the program BayesTraits (Pagel 1999). Our hypothesis is that there is a correlated evolution between the first lower molar (m1) length and head-body length in dipodoids, and thus the head-body length of fossil jerboas can be predicted from their m1 length. First, one MCMC run was conducted without fossil data to test for correlated evolution between m1 length and head-body length in dipodoids. Based on living taxa sampled, the analysis supports the conclusion that m1 length and head-body length are strongly correlated in the course of dipodoid evolution, with a R^2 value of 0.71. A second MCMC run was conducted to estimate the head-body length of fossil jerboa species—$P.$ $grabaui$, $Paralactaga$ $anderssoni$, and $S.$ $iderensis$—from their m1 length, and from sampling the last 1000 posterior samples of Alpha (intercept), Beta (slope), and Lambda (phylogenetic signal) parameters from the first run. The results of these estimates are provided in Figure S2 and Table S3.

The m1 length of the three fossil species is based on the report of Zazhigin and Lopatin (2000), Zazhigin and Lopatin (2001), and (Young 1927). The m1 lengths of extant and fossil dipodoids are provided in Table S4. The original measurements on m1 length in modern dipodoid species are provided in Table S5.

ANALYSIS OF CHANGE OF LOCOMOTOR CAPABILITY AND TOOTH CROWN HEIGHT IN JERBOAS

The cannon bone length and head-body length ratios of fossil and extant jerboas were analyzed to determine the change of the leg length during jerboa evolution. The change of the leg length, in turn, traditionally is thought to reflect change in running capability (Hildebrand 1988). In addition, the cheek tooth crown height/length ratios were analyzed to reveal the evolution of dental character changes in jerboas from the Middle Miocene to the Recent. Our hypothesis is that m1 has undergone directional evolution, increasing height with time, whereas cannon bone length has remained static. We tested this hypothesis with a multiple regression model in the program JMP (SAS Institute 2005). The dental crown height/length ratios are provided in Table S6.

Phylogenetic Trees and Divergence Times

The phylogenetic tree and molecular dating results adopted by this study are derived from Wu et al. (2012). We used the program Mesquite version 2.5 (Maddison and Maddison 2007) to manually place the three fossil species—$P.$ $grabaui$, $P.$ $anderssoni$, and $S.$ $iderensis$—into the BEAST consensus tree. This new tree was used for estimating the head-body length of the above species by incorporating relatedness in the phylogenetic GLS regression model. The position of the three species on the tree was based on their first appearance in the fossil record and their relationships to extant jerboa groups. $Protalactaga$ is regarded as the sister taxon to all other jerboas, $Paralactaga$ is placed in Allactaginae, and $S.$ $iderensis$ is grouped with its extant relative $Stylodipus$ $telum$ (Zazhigin and Lopatin 2000, 2001; Wu 2010).

Paleoenvironmental Reconstruction

Since the Early Miocene, fossil occurrences of jerboas are widespread across Neogene localities in northwestern China and surrounding areas. To understand the habitat preferences of early jerboas, we reconstructed the paleoenvironmental conditions from the Early Oligocene to the Late Miocene using floral and faunal data from northwestern China.

We collected paleofloral data from 27 plant assemblages that were compiled from 14 sites in northwestern China (Tables S7 and S8). We assembled mammalian faunal data from the Middle Miocene Tunggur Formation ($\sim$13 Mya) of Nei Mengol, China (Wang et al. 2003) (Table S9).

We applied the calibrated coexistence approach (CA_{cal}) to reconstruct the mean annual temperature (MAT) and mean annual precipitation (MAP) based on the coexistence intervals of climatic

parameters for the selected sites (Mosbrugger and Utescher 1997; Utescher et al. 2009). The CA_{cal} method relies on the presence–absence of plant taxa, and is less sensitive to taphonomic filtering than both assemblage- and leaf physiognomy-based approaches (Mosbrugger and Utescher 1997; Pross et al. 2000). The coexistence intervals of climatic parameters are considered as the comparable environmental conditions of a given fossil location, which were calculated using the ClimStat program (Utescher et al. 2009). Identification of fossil pollen and spores for nearest living relative (NLR) in this study was based on Song et al. (1999). Fossil taxa having relic NLRs or not useful in determining climatic tolerances are excluded from the reconstruction process. The biome types were assessed according to the annual temperature and precipitation reconstructed from the CA_{cal} analysis (Ricklefs 2008). The Köppen aridity index ($AI_{Köppen}$) of each site was calculated using the following equation: $AI_{Köppen} = MAP/(MAT + 33)$(Quan et al. 2013).

The absolute species numbers of ungulates with different dietary types were investigated to infer the paleoenvironments of the Tunggur Formation. The identification of dental types of large herbivorous mammals in the Tunggur Fauna is based on the dataset derived from the Neogene Old World (NOW) database (Fortelius 2008). The NOW database classifies the dentitions of ungulate mammals into three major types—brachydont, mesodont, and hypsodont, and the criteria of the identification are based on the ratio of crown height to the length of the second molars (Fortelius et al. 2006). Taxa with no dental trait information were omitted from this analysis. In total, 17 ungulate species from the Tunggur Fauna were included in this study (Table S10). The community structure of modern ungulates and its relationship with present-day environmental conditions was based on Janis et al. (2004).

Taphonomic variation and climatic mosaicism is locally important in determining habitat suitability for individual species. However, this small-scale variation is challenging to assess over large geographic and temporal scales such as those used in our study. In addition, studies that cover large geographic areas and time scales are less susceptible to small-scale effects of local climatic variation than more restricted studies (Greenwood and Wing 1995; van Dam 2006; Utescher et al. 2009). Hence, we consider effect of local ecological patchiness and environmental mosaicism to be largely outside the scope of this study due to the large geographic and temporal scale of our analysis.

Results
### DECOUPLING OF DENTAL AND LOCOMOTOR EVOLUTION IN JERBOAS
The earliest known fossil record of jerboas is represented by separate molars from the lower part of the Suosuoquan Formation of the Early Miocene about 21 Mya (Fig. S3). However, the locomotor pattern of Early Miocene jerboas remains unknown, since no postcranial materials have been discovered so far. *Protalactaga grabaui* from the Middle Miocene represents the earliest known jerboas that probably employed a bipedal mode of locomotion, evidenced by the development of cannon bones in their hind feet (Young 1927; Zazhigin and Lopatin 2000). The cannon bone contributes to the extreme elongation of the hind limbs of jerboas: their hind foot length is about as long as half of their head-body length (Fig. 1). The discovery of cannon bone fossils that are associated with the dental remains of *P. grabaui* from the Middle Miocene deposits about 13 Mya provides fossil evidence to support the conclusion that jerboas acquired bipedality before 13 Mya.

In the course of jerboa evolution, their dental structures underwent a steady increase in crown height, and morphologically shift from bunodont and brachydont to lophodont and hypsodont condition beginning in the Late Miocene (Figs. 2 and 3). The change of dental structure in jerboas coincides with an environmental shift from humid and forested to arid and open conditions since the Late Miocene in the Asian interior.

Exant bipedal jerboas have high-crowned molars with well-developed lophs, an adaptation to the dietary ecology of the extremely dry and open ecosystem dominated by C4 fibrous plants (Fig. 2A, B). However, fossil jerboas living in the Early Miocene, Middle Miocene, and the early part of the Late Miocene still possessed brachydont and bunodont cheek teeth, suggesting a dietary adaptation for succulent C3 vegetation in their early history (Fig. 2C, D). The measurements of cheek tooth crown height show that the crown height/length ratio of primitive jerboas such as *Protalactaga* remained low and did not increase during the Early and Middle Miocene (Figs. 3, S4). The primitive dental condition of *Protalactaga* is consistent with the relative humid forest/woodland environments in the Asian interior during the Early and Middle Miocene. Subsequently, the crown height of cheek teeth started to increase after the Late Miocene in jerboas (Figs. 3, S4). Importantly, the evolutionary transition in dental structures from brachydonty and bunodonty to hypsodonty and lophodonty in jerboas coincides with the post-Late Miocene aridification in the Asian interior toward increasingly drier and cooler conditions and the expansion of C4 fibrous plants (Fig. 4; Cerling et al. 1997; Fortelius and Zhang 2006; Liu et al. 2011; Eronen et al. 2012; Zhang et al. 2012).

A phylogenetically controlled ANCOVA shows that distinctive differences evolved in the hind foot/head-body length ratios between bipedal jerboas and quadrupedal jumping mice and birch mice (Fig. 1A). Birch mice have the lowest ratio, around 24%, in keeping with their quadrupedal and nonsaltatorial type of locomotion, whereas in jumping mice, this ratio increases to around 34%, consistent with their dual quadrupedal and
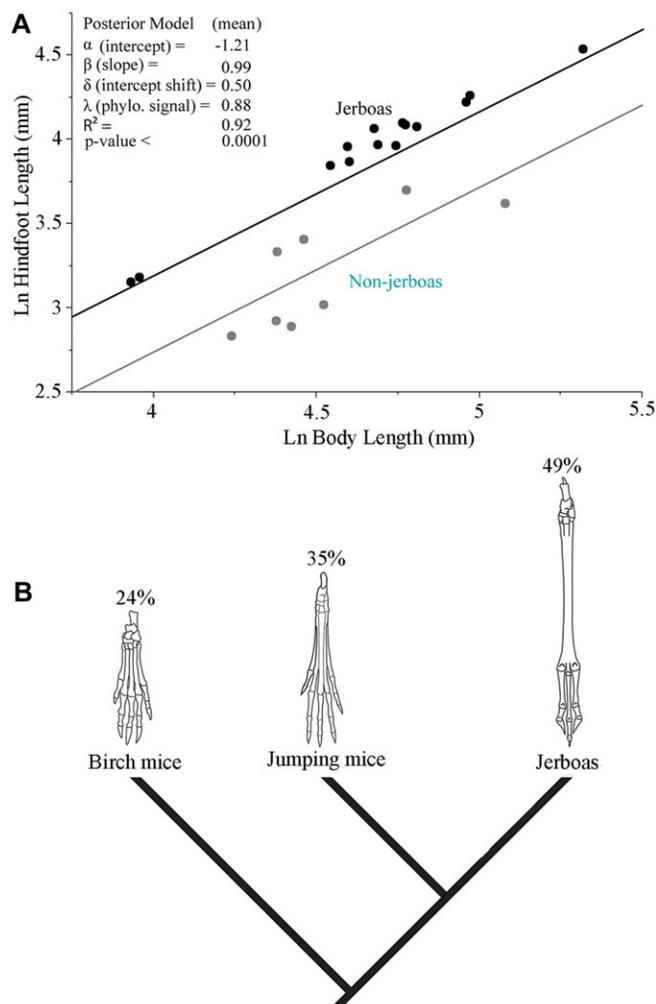
Figure 1. Jerboas show a distinct relationship between hind foot length and head-body length compared with other nonjerboa rodents. **(A)** The average of the Bayesian posterior phylogenetic generalized least square regression lines is shown. The multiple regression model, which includes a dummy variable that shifts the intercept creating two lines (jerboas are the black line, and nonjerboas are the gray line), is preferred over a single regression model by a Bayes Factor test of 13.9. **(B)** The elongation of the cannon bone contributed to the high hind foot/head-body length ratios in bipedal jerboas. Numbers indicate the hind foot/head-body length ratios for each of the corresponding groups. The skeletal structures of the hind foot showed in this figure are not to scale and are based on Berman (1985) and Lyon (1901), respectively.

saltatorial locomotor abilities (Fig. 1B). However, this ratio increases dramatically in bipedal jerboas, with an average ratio of 49% (Fig. 1B). Particularly, the great elongation of metatarsal bones contributes mainly to their high hind foot/head-body length ratio (Fig. 1B).

Fossil cannon bones have been found with *P. grabaui* from the Middle Miocene, with *P. anderssoni* from the Late Miocene, and with *S. iderensis* from the Early Pliocene (Young 1927; Zazhigin
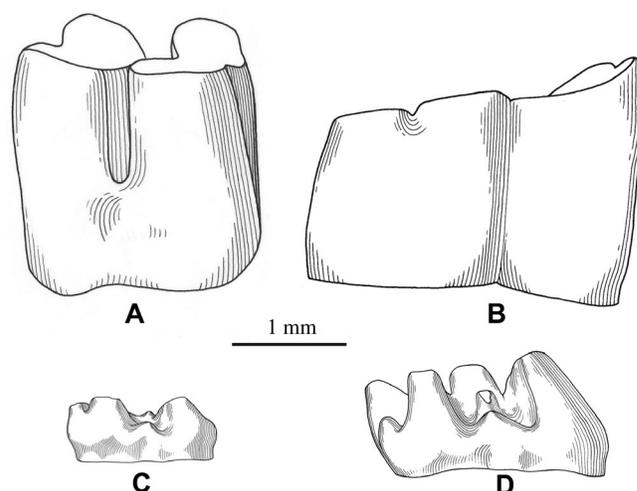

Figure 2. Comparison of dental structure of the first lower molar (m1) of fossil and extant jerboas in lateral view. **(A)** Right m1 of extant three-toed jerboa—*Jaculus orientalis* (AMNH 70004). **(B)** Left m1 of extant five-toed jerboa—*Allactaga mongolica* (AMNH 84157). **(C)** Right m1 of the fossil three-toed jerboa—*Dipus* sp. (IVPP V16905.2), from the beginning of the Late Miocene of the middle bed of Dingshanyanchi Formation, Xinjiang, China (Wu et al. 2012). **(D)** Left m1 of primitive jerboa—*Protalactaga grabaui* (IVPP V1037.9), from the Middle Miocene, around 13 Mya of Tunggur Fauna, Nei Mongol, China (Qiu 1996). MCZ, Museum of Comparative Zoology of Harvard University; AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, the Chinese Academy of Sciences.

and Lopatin 2000, 2001). Based on the strong correlation between the m1 tooth length and head-body length in extant jerboas, the head-body lengths of *P. grabaui*, *P. anderssoni*, and *S. iderensis* were estimated from their m1 length and their phylogenetic position (Fig. S2; Table S3). In as much as the cannon bone/head-body length ratio reflects the hind foot/head-body length ratio, it is striking that this ratio has remained quite stable from early fossil jerboas to their extant relatives (Fig. 3). This observation supports the conclusion that there was little selective pressure on jerboas to increase their leg length from the Middle Miocene to the Recent, suggesting that early jerboas probably had already acquired a bipedal hopping capability similar to that of their modern relatives.

The Origin of Jerboa Bipedalism in a Humid and Warm Climatic Phase

According to the results from a recent molecular phylogenetic analysis, dipodoids underwent a stepwise transition from quadrupedal to bipedal locomotion, with facultative bipedality retained in modern jumping mice as an intermediate stage (Wu et al. 2012). According to the estimated dates (Wu et al. 2012), bipedal
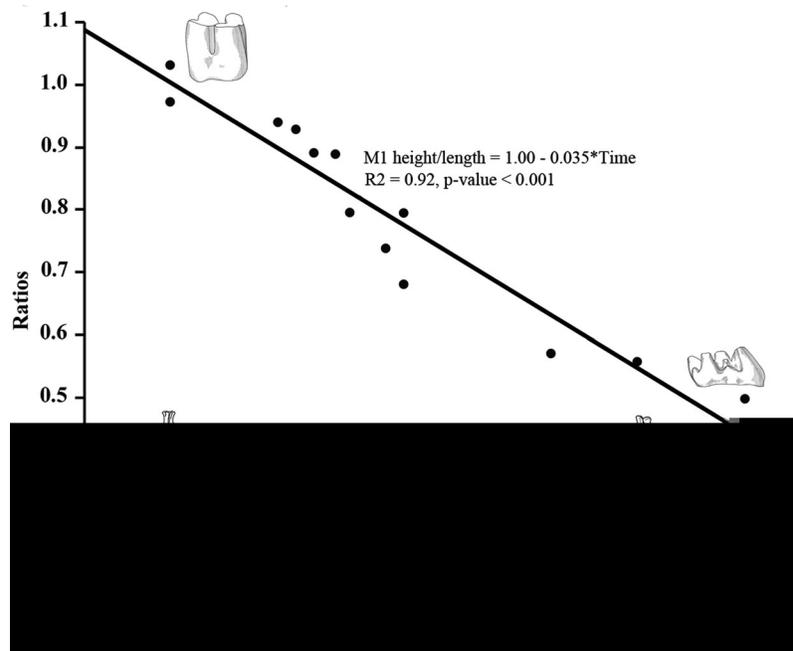
Figure 3. Change of tooth shape (m1 height and width) and leg shape (cannon bone length) over time. The lines represent the maximum likelihood least squares regression lines relating the ratios of m1 height to width and cannon bone length to head-body length to time. These lines show substantial change in tooth morphology over the past 15 million years, whereas the evolution of the cannon bone has been static over the same interval. Although the oldest three points in the m1 plot appear to fall on a more horizontal line, a single regression model is preferred using Akaike weights (w_i = 0.95 for the single regression and w_i = 0.05 for a multiple regression model that introduces a change in slope). For regression model of m1 ratio, intercept SE = 0.02 and slope SE = 0.003. For the regression model of cannon bone ratio, intercept SE = 0.004 and slope SE = 0.001. The cannon bones used in the figure are based on Zazhigin and Lopatin (2000)

jerboas diverged from jumping mice in the Late Oligocene around 25.5 Mya (95% credibility interval 18.4–32; node 9, Fig. 4). The basal radiation of crown jerboa groups was estimated to have occurred around 18.4 Mya (95% credibility interval 13.9–23) in the late part of the Early Miocene (node 11, Fig. 4). These results indicate that jerboas most likely acquired bipedalism during the Early Miocene, around 18.4 Mya.

In a global context, except for several short-term cooling phases, the world experienced a relatively warm stage from the Late Oligocene to the middle part of the Middle Miocene, which peaked in the Mid-Miocene Climatic Optimum from 17 to 15 Mya (Zachos et al. 2001; Mosbrugger et al. 2005). To assess the paleoclimatic conditions in northwestern China from the Early Oligocene to the Late Miocene, we reconstructed the regional annual temperature and precipitation based on 27 plant assemblages from 14 sites in northwestern China (Table S11) (Mosbrugger and Utescher 1997; Utescher et al. 2009). Our results indicate that the biomes of the 14 sites were largely temperate deciduous forest and woodland/shrubland (Fig. S5A). We then calculate the Köppen aridity index ($AI_{\text{Köppen}}$) based on the annual temperature and precipitation of each site. The $AI_{\text{Köppen}}$ shows that all 14 sites were (sub-)humid with eight of them extending into semiarid, in-

dicating that the overall regional climate was (sub-)humid from the Early Oligocene until the Late Miocene (Fig. S5B). Therefore, the results of our biome and paleoclimatic analysis are consistent with the general climatic trend in Eurasia (Zachos et al. 2001; Mosbrugger et al. 2005), indicating that the timing of the origin of jerboa bipedalism coincides with a warm and humid climatic phase during the early Neogene, and much earlier than the onset of significant aridification beginning in the Late Miocene (Fig. 4). This finding suggests that jerboa bipedalism evolved in humid environments with various densities of vegetation, rather than in arid and open habitats.

To further decipher the habitat preferences of early jerboas, we investigated composition of mammalian fauna associated with jerboa fossils in the Tunggur Formation. The Tunggur Fauna from the Middle Miocene (~13 Mya) produced abundant mammalian fossils associated with two early jerboa species: *P. grabaui* and *Protalactaga major* (Qiu 1996; Wang et al. 2003). This formation is similar in age to that of the Lower Subformation of the Oshin Formation in Mongolia and to that of the Quantougou Fauna of the Xianshuihe Formation of China (Young 1927; Qiu 1996; Zazhigin and Lopatin 2000; Wang et al. 2003). The two latter formations contained the earliest known cannon bone
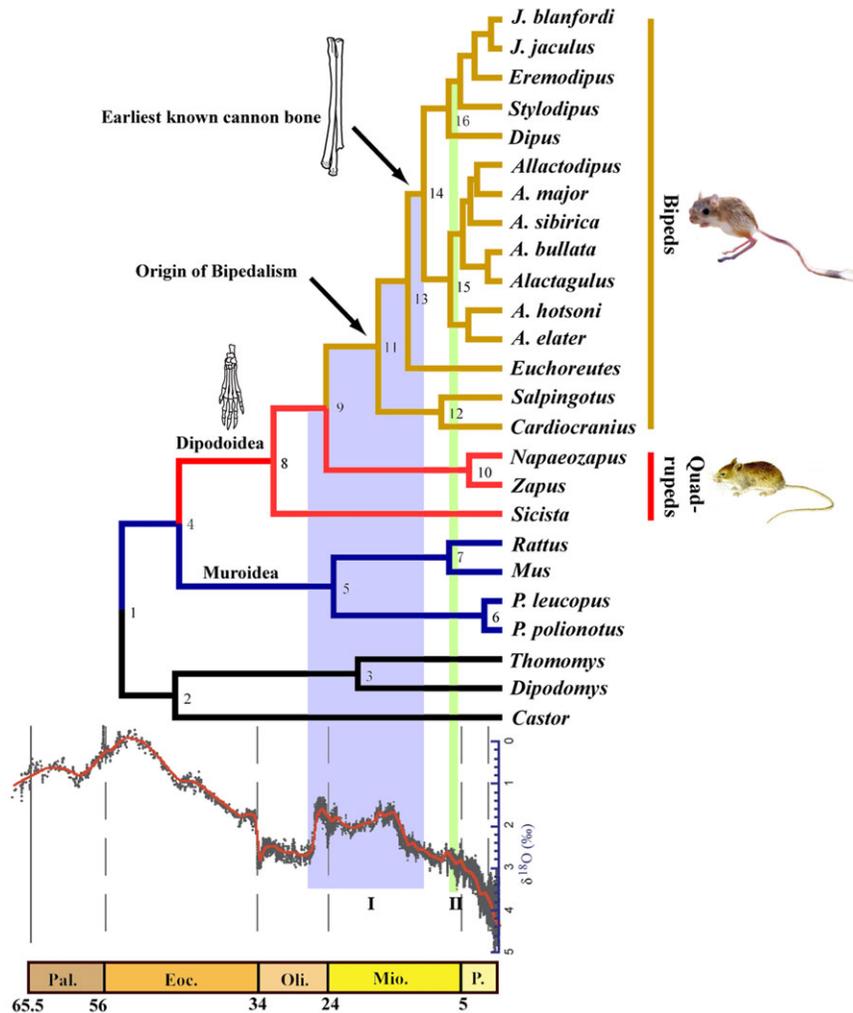
Figure 4. Phylogenetic relationships and divergence times among dipodoid rodents. The phylogenetic tree is based on Wu et al. (2012). (I) A global warm climatic phase from the Late Oligocene until the middle part of the Middle Miocene and (II) the time when C4 plants started to expand (Zachos et al. 2001; Mosbrugger et al. 2005). Note that the timing of the origin of jerboa bipedalism coincides with a warm climatic stage in the Early Miocene, and much earlier than the onset of significant aridification beginning in the Late Miocene. The foot skeletal structure at node 8 indicates the ancestral condition in dipodoid rodents, with separation of metatarsals. The oxygen-isotope record is based on Zachos et al. (2001). The cannon bone used in this figure is based on the report of Zazhigin and Lopatin (2000). Picture of the Chinese Birch Mouse (*Sicista concolor*) used in the figure is based on Smith and Xie (2008). The picture of three-toed jerboa, *Dipus sagittal*, was based on the photo by Shaoyuan Wu in the Gurbantunggut Desert of northern Xinjiang, China.

fossils that have been referred to *P. grabaui* (Young 1927; Qiu 2000; Zazhigin and Lopatin 2000), supporting the conclusion that *P. grabaui* probably employed a bipedal mode of locomotion. Among the 17 large ungulate species from the Tunggur Fauna, 14 of them are browsers with brachydont cheek teeth (Table S10). This Fauna has three nonbrachydont forms: one hypsodont rhino and two mesodont bovids (Table S10). The species composition between browsers and grazer/mixed-feeders in Tunggur Fauna is consistent with the species ratio found in present-day forest environments (Janis et al. 2004). These data are also consistent with our biome reconstruction, showing that the environment of Tunggur was a forested landscape (Fig. S5A,

B). Therefore, the analysis of our mammalian faunal composition of Tunggur Formation supports the conclusion that the early bipedal jerboa *P. grabaui* inhabited a relatively humid and forested environment, different from the arid and barren habitats of extant jerboas.

Discussion

Because all modern bipedal rodents inhabit desert or semidesert areas with arid climates, their bipedality has long been regarded as an adaptation to arid and open environments (Hatt 1932; Eisenberg 1975; Savage and Russell 1983; Hafner and Hafner

1988). However, the results of the present study are at odds with this picture.

In the course of jerboa evolution, the development of the highly derived limb structure of the cannon bone appears much earlier than the acquisition of dental hypsodonty and lophodonty, showing that the evolution of locomotor and dental trait in jerboas underwent different patterns of evolution over time (Fig. 3).

The evolution of hypsodonty and lophodonty in ungulate mammals is an adaptive response to increasing environmental dryness and openness (Fortelius 1985; Janis 1988; Solounias et al. 1994; Fortelius and Solounias 2000; Janis et al. 2004). The arid-adapted vegetation in open landscapes contains a large percentage of fibrous elements, demanding high tolerance of abrasiveness in the teeth of mammalian species that feed on them (Fortelius 1985; Janis 1988; Solounias et al. 1994; Fortelius and Solounias 2000). Thus, the change of cheek tooth crown height can reflect the change of dietary ecology that was caused by the climate changes (Fortelius 1985; Janis 1988; Solounias et al. 1994; Fortelius and Solounias 2000; Janis et al. 2004). Interestingly, cheek teeth of jerboas underwent a similar pattern of change from a brachydont and bunodont to a hypsodont and lophodont condition beginning in the Late Miocene (Figs. 2 and 3). The transition of dental morphology in bipedal jerboas is consistent with the shift of climate in the Asian interior from humid and forested toward drier and open conditions since the Late Miocene (Fortelius and Zhang 2006; Liu et al. 2011; Eronen et al. 2012). In contrast, the hind limb/head-body length ratios remained high and stable in jerboas despite environmental changes (Fig. 3). The decoupling of locomotor and dental trait evolution in jerboas supports the conclusion that jerboa bipedalism did not evolve as an adaptation to arid and open habitats, but rather to humid and forested environments.

Our evidence suggests that jerboas lived in relatively humid and forested environments before the Late Miocene, and in dry and open conditions afterward. During this period of environmental change, bipedal jerboas ceased to be restricted to humid environments and instead exploited their capacity for bipedal locomotion to enter new environments. Continuing adaptation to changing local conditions is evident in the evolution of molar structure from brachydont and bunodont to hypsodont and lophodont, which tracks the environmental change from humid and forested to arid and open conditions. Extant jerboas with hypsodont teeth still live in the same areas once inhabited by Miocene jerboas with brachyodont teeth, a fact consistent with the interpretation that jerboas underwent in situ adaptation to ecological changes.

Three major hypotheses have been proposed as to why bipedalism evolved in rodents: (1) to increase running speed to escape from predators in open environments (Hatt 1932; Bartholomew and Caswell 1951; Eisenberg 1975); (2) to free the forelimbs for efficient food handling (Bartholomew and Gary 1954); (3) to reduce the energetic costs of locomotion (Reichman and Oberstein 1977). Biewener and Blickhan (1988) refuted the third hypothesis for bipedal rodents because their study on North American kangaroo rats shows that high-speed running is energetically expensive and can only be maintained for a short distance for small rodents. This study rejects the first hypothesis because the jerboa bipedality appears not to have evolved as an adaptation to open habitats, but rather to three-dimensional (3D) forests and woodlands. There is no evidence to reject the second hypothesis so far, but it is unlikely that the selective pressures on the forelimbs alone can lead to the extremely specialized structures of the hind limbs in jerboas. The specialization of hind limb structures in jerboas requires a specific adaptive explanation.

Based on the results of the present study, we propose a new hypothesis for bipedal evolution in jerboas. Bipedalism evolved as an adaptation to the structurally complex setting of forests and woodlands, and specifically to increase capability for vertical jumping, rather than to increase speed for horizontal running. Since the Early Miocene when their morphological innovations first arose, jerboas have shared habitats with different groups of quadrupedal rodents: the short-legged birch mice readily climb trees, they are not known to jump, whereas the longer legged jumping mice have an all-purpose morphology that enables them to climb and perform short-range leaps in a complex 3D setting. Based on their bipedal build that confers upon them a superior capability for vertical long-range jumping (but not necessarily climbing), jerboas would have been able to exploit new ecological niches different from those of birch mice and jumping mice. Thus, the highly elongated hind limbs of jerboas likely evolved originally to increase jumping ability. The long hind limbs, in turn, provided jerboas an additional capability of high-speed running, due to the increase of stride length (Jungers 1982; Hildebrand 1988). The capability for fast locomotion for short distances was therefore a by-product of selection for jumping, which became advantageous in open environments later on.

The results of the present study have implications for the nature of convergent evolution. As a basic property of evolution, convergence is the process that similar adaptive responses result from similar selective pressures in distantly related organisms (Losos 2011). However, our results suggest that mammalian bipedalism can arise independently from different environmental conditions. In rodents, bipedalism originated in humid and forested environments, whereas this trait evolved in primates and kangaroos as a response to arid and open habitats. Our finding implies that analogous traits, although often arising from similar selective constraints, can also arise from disparate ones.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Comparison of hind foot structures of dipodoid and nondipodoid rodents.
Figure S2. The correlation between head-body length and the length of the first lower molar (m1) in jerboas.
Figure S3. Crown view of molars of the earliest known jerboa fossils from the Early Miocene (~21 Myr) of the Suosuoquan Formation, Xinjiang, China.
Figure S4. Leverage residual plots for multiple regressions of the same data with Figure 3 (m1 height by m1 width and time, and cannon bone length by head-body length and time) show the same patterns of change in m1 morphology over time and a lack of change in cannon bone length over time.
Figure S5. Reconstruction of biomes and paleoclimatic types of the Asian interior from the Early Oligocene to the Late Miocene based on 27 plant assemblages from 14 sites of northwestern China.
Figure S6. Crown view of molars of *Protalactaga* sp. 1 from the beginning of the Late Miocene of the middle bed of the Dingshanyanchi Formation, Xinjiang, China.
Figure S7. Crown view of molars of *Dipus* sp. 2 from the Late Miocene of the upper bed of the Dingshanyanchi Formation.
Figure S8. Crown view of molars of *Protalactaga* sp. 2 from the late part of the Early Miocene of the Halamagai Formation, Xinjiang, China.
Table S1. Comparison of hind foot/head-body length ratios in extant dipodoids and outgroup taxa (Unit: mm).
Table S2. Measurements of hind foot length and head-body length in extant dipodoids (Unit: mm).
Table S3. Comparison of cannon bone length/head-body length ratios in extant and fossil jerboas (Unit: mm).
Table S4. The m1 lengths and head-body lengths of dipodoids (Unit: mm).
Table S5. Measurements of m1 length in dipodoids (Unit: mm).
Table S6. Comparison of tooth crown height/length ratios in jerboas.
Table S7. List of the 27 palaeofloral assemblages from 14 sites in northwestern China collected for this study.
Table S8. List of plant assemblages of northwestern China and corresponding nearest living relative (NLR).
Table S9. Faunal list of Tunggur Formation (from Wang et al. 2003).
Table S10. List of ungulate species and their dental types of the Tunggur Fauna.
Table S11. Results of the paleoclimatic analysis for each of the selected sites.