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Hypsodonty of Dipodidae (Rodentia) in Correlation with Diet Preferences and Habitats

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Abstract The evolution of molar teeth from low-crowned
(brachyodont) to high-crowned (hypsodont) has traditionally
been recognized as a response to increasing tooth wear due to
endogenous (e.g., fiber, silica) and/ or exogenous (e.g., dust,
grit) properties of ingested food. Recent work indicates that
the mean hypsodonty level of large herbivorous land mamma-
lian communities is a strong predictor of precipitation in their
habitats. For small mammals, however, the research is still in
an early stage. This study performed comparative studies of
hypsodonty on 26 extant dipodid species with and without
consideration of phylogeny. The results confirm the role of
diet in shaping the cheek tooth crown height in Dipodidae.
The significant relationship of investigated environmental vari-
ables with hypsodonty may be partly due to phylogenetic
effects. Nonetheless, the mean hypsodonty of dipodid com-
munities has significant relationship with regional climatic
variables. Hence, the hypsodonty of dipodids also has great
potential to be a regional climate proxy.

Keywords Dipodidae · Hypsodonty · Diet · Habitat ·
Phylogeny · Climate

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Introduction

The evolution of morphological characters may be forced by
biotic or abiotic factors, or a mixture of both (Benton 2009).
Testing the relationship between biotic/abiotic factors and
characters by comparative analyses, especially phylogenetic
comparative analyses, can be used to infer evolutionary adap-
tation (Garland et al. 2005). One of the key traits in mammals
is crown height of molars. High-crowned molars have inde-
pendently evolved in a number of mammalian lineages, such
as in rodents, ungulates, marsupials, and lagomorphs, and
have traditionally been interpreted as adaptation for increased
amounts of abrasive material in the diet (Simpson 1953; Janis
1988; Janis and Fortelius 1988; Williams and Kay 2001; Janis
et al. 2002; Bargo et al. 2006; Mendoza and Palmqvist 2007;
Jardine et al. 2012).

For large mammals, especially ungulates, hypsodonty has
formed the basis of widespread paleoecological interpretation
over the past 150 years (Damuth and Janis 2011). In order to
further resolve presumed causes of abrasive wear, a large
number of comparative analyses have been performed
(Axmacher and Hofmann 1988; Janis 1988; Skogland 1988;
Williams and Kay 2001; Janis et al. 2002; Bargo et al. 2006;
Strömberg 2009; Mendoza and Palmqvist 2007; Ozaki et al.
2010). Moreover, the quantitative relationship of hypsodonty
of living ungulate species with the known ecological factors

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has confirmed that the mean hypsodonty of large herbivorous land mammalian communities is a strong predictor of precipitation in their habitats (Damuth et al. 2002; Fortelius et al. 2002; Janis et al. 2004; Eronen et al. 2010a, b; Liu et al. 2012). For small mammals, however, the evolution of tooth morphology in relation to diet and habitats remain poorly explored. Williams and Kay (2001) pointed out that both food and non-diet grit play a role in shaping the evolution of cheek tooth crown height in small mammals. However, Jardine et al. (2012) suggested that the ingestion of grit and soil may be more important. Both of the studies on rodents have found that the fossorial habit is also an important factor in relating to the increase of molar crown height. The adaptive interpretation of hypsodonty for small mammals is possibly more complicated than ungulates due to their broader diets and more diversified life modes, especially when a large number of taxa are considered. However, it remains unclear if the relations between mean hypsodonty and precipitation demonstrated by large mammals can be applied to small mammals. Comparative methods are the most common and productive means for elucidating past evolutionary processes (Garland et al. 2005). Thus, lots of comparative methods have been used, but there is a limitation in these methods. The correlations between traits and ecological variables may be biased by the potential similarity of closely related species (Felsenstein 1985; Harvey and Pagel 1991). In other words, it may improperly raise the degrees of freedom in the statistical model and cause overstatement of the significance in hypothesis tests if species were statistically independent (Felsenstein 1985). In order to control confounding effects of phylogeny, several statistical techniques have been developed (e.g., Felsenstein 1985; Grafen 1989). One of the most commonly used phylogenetic comparative methods is phylogenetic generalized least squares (PGLS) (Grafen 1989; Martins and Hansen 1997). This approach is used to test whether there is a relationship between two (or more) variables while accounting for the fact that lineage is not independent. Phylogenetic approaches take advantage of increasingly complete phylogenies for many important groups, and have the ability to integrate studies of the evolution of organismal function and ecology (Gavrilets and Losos 2009). However, one of the main disadvantages of these methods is that the reliable phylogenetic information is hard to obtain for a large group that includes many clades.

Thus, the goal of this study is at smaller scales (e.g., within specific families) to provide a comprehensive test of the evolution of hypsodonty in a specific family, Dipodidae, by combining diet data, environmental data, and phylogenetic information. Dipodids are optimal subjects to test the adaptive significance of hypsodont for the following reasons: 1. They show diverse crown height (Shenbrot and Potapova 1982; Shahin 1999; Ungar 2010), and the increase of crown height has been used as an indicator of environmental change towards drier and more open condition (Wu et al. 2014). 2.

They demonstrate prominent habitat diversity ranging from the forest- and meadow-dwelling mouse-like birch mice and jumping mice to the arid-dwelling saltatorial jerboas (Lebedev et al. 2013; Zhang et al. 2013). 3. They are monophyletic with well-resolved phylogenetic relationships (Pisano et al. 2015). Here, we focus on the following two questions: (1) Is the hypsodonty of Dipodidae related to diet and/ or environment? (2) Can the mean hypsodonty of dipodid community be used to estimate regional climatic factors (precipitation and temperature)? These analyses are based on two hypotheses: specialist herbivores have higher hypsodonty indices than those feeding on leaves and/or seeds and those feeding on fruits and/or animals; species living in the more open and arid regions have higher hypsodonty indices than those inhabiting closer and wetter environments.

Materials and Methods

Materials

Twenty-six out of the 51 species belonging to 13 out of the 16 genera of Dipodoidea listed by Holden and Musser (2005) were analyzed (see Table 1).

Crown Height Data

The crown height data were obtained from two sources: first, newly measured for seven species (minimum four specimens per species) on the specimens housed in the Institute of Zoology, Chinese Academy of Sciences (IOZCAS), and second, cited from Shenbrot and Potapova (1982) and Shenbrot et al. (2008) for the other 19 species (see supplementary material Table 1 in the Appendix). The specimens from IOZCAS have been measured with the method of Shenbrot and Potapova (1982) for only relatively unworn, newly erupted teeth, from the uppermost point between the roots to the upper edge of the crown. The species of Sicista were only defined as brachydontoid by observations (Shenbrot et al. 2008). Hypsodonty has been quantified using indices that isolate allometric changes in tooth morphology: Hypsodonty Index (HI). HI is unworn crown height divided by length in this study. Four categories of HI were classified: brachydont with a ratio less than 0.8, submesodont with a ratio of 0.8–1.3, mesodont with a ratio of 1.3–2.0, and hypsodont with a ratio > 2.0, respectively. The four HI categories were assigned values of 1, 2, 3, and 4, respectively, for the following analyses.

Diet Data

The species are classified into five dietary categories mainly according to Shenbrot et al. (2008) and Samuels (2009): insectivore, omnivore, granivore, generalist herbivore, and specialist herbivore. In our study, the insectivore Euchoreutes naso has

Table 1 Summary of hypsodonty index, diet, and the habitats of 26 extant species in Dipodidae

Species	HI	Diet	Forest	Forest-woodlands	Steppe	Alpine-meadows	Semi-desert	Desert
Sicista kazbegica	1	1	——					
Sicista kluchorico	1	1	——					
Sicista caucasica	1	1	——					
Sicista concolor	1	1	- - -			——		
Sicista tianschanica	1	1	- - -		- - -	——		
Sicista subtilis	1	1		- - - - - -	- - -		- - -	
Sicista strandi	1	1		- - - - - -	- - -			
Sicista pseudonapaea	1	1				- - -	——	
Eozapus setchuanus	1	3	——		- - - - - -	- - -		
Cardiocranius paradoxus	1	2		·············			——	- -
Salpingotus kozlovi	1	2			- - -		——	- -
Allactaga major	2	1	·········	- - - - - -	- - -		- - -	- -
Allactaga elater	2	2		- - - - - -	- - -		- - - · -	—
Euchoreutes naso	2	0			·············		——	- -
Dipus sagitta	2	3		- - - - ·········			- - - -	—
Allactaga balikunica	2	1			·············		——	·
Allactaga sibirica	2	1	·········	- - - - - - ·	·············		—	—
Allactaga bullata	2	1			·············	——	·········	
Stylodipus telum	3	3		- - -			- - - -	-
Stylodipus andrewsi	3	3		············· - - -			——	
Jaculus blanfordi	3	3		·············			·············	——
Eremodipus lichtensteini	3	3					·············	——
Allactodipus bobrinskii	3	4					·············	——
Pygeretmus zhitkovi	3	4		- - -			- - - · -	—
Pygeretmus pumilio	3	4		- - -			- - - - -	—
Paradipus ctenodactylus	4	4					·············	——

Habitat*: The solid line indicates the percentage of the habitat type is more than 50 %; the dashed line: 50 %–10 %; the dotted line: less than 10 %. For more detail information see supplementary material Table 2 in the Appendix

95 % insects in its diet composition (Sokolov et al. 1996; Clark et al. 2006). The omnivores have both plant and animal matter in their diet; the granivores mainly feed on seeds, and occasionally eat other fruits and plant parts as well; the generalist herbivores eat primarily plant matter, including mostly soft leafy vegetation or seeds (including less fibrous plant matter); and the specialist herbivores take primarily plant matter, mostly fibrous or difficult to process plants (e.g., grass, bark, or roots).

Ordered states for dietary data were scored as 0 = Insectivore, 1 = Omnivore, 2 = Granivore, 3 = Generalist herbivore, and 4 = Specialist herbivore. The specific dietary information came from published literature sources (Ma et al. 1987; Sokolov et al. 1996; Gromov 2002; Zhang et al. 2007; Miljutin 2006, 2008; Shenbrot et al. 2008; Narisu and Wu 2009; Quéré et al. 2009; Smith et al. 2010). Some of the dietary data were obtained from qualitative description, but most of the data were from quantitative analysis of the stomach contents with wild-caught individuals.

Habitat Data

Habitat data contain habitat types, climate variables (annual precipitation and annual temperature), and geographic ranges. For analysis of habitats of each species, we used the map of

terrestrial ecoregions of the World (Olson et al. 2001). Ecoregions and climate data for estimations of temperature and precipitation were extracted for each occurrence point of each analyzed species using ArcGIS Desktop 10.3. Ecoregions were grouped into six habitat types including (a) forest, (b) forest-steppe and open woodlands, (c) steppe, (d) alpine meadows, (e) semi-desert and, (f) desert. As the distribution of each species usually covers more than one habitat type, we have showed the percentage of different habitat types for all species in three classes: (a) ≥50 %, (b) 50 %–40 %, and (c) <10 % (Table 1). The geographic ranges of these species are based on occurrence point data. The data were compiled by G. Shenbrot using museum specimens (obtained from Global Biodiversity Information facility (GBIF; http://www.gbif.org) and during museum visits), available publications, and personal field observations.

In order to test the relationships between HI and climatic factors, we also obtained bioclimatic variables from Hijmans et al. (2005; available online at http://www.worldclim.org) with DIVA-GIS 7.5 (Hijmans et al. 2012). WorldClim is a set of global climate layers (climate grids) with different spatial resolutions; from 30 s ($0.93 \times 0.93 = 0.86$ km^2 at the equator) to 2.5, 5, and 10 min ($18.6 \times 18.6 = 344$ km^2 at the equator) (interpolations of observed data, representative of 1950–2000).

Phylogenetic Data

The phylogenetic data for extant dipodid taxa used in the present study are derived from Pisano et al. (2015), excluding the species not related in this study with Mesquite 3.04 (see Fig. 1). The species on the tree of Pisano et al. (2015) that was assigned as *Sicista napaea* has been revised as *S. pseudonapaea* in this paper as a result of discussion of G. Shenbrot with collectors that field identification of the specimens as *S. napaea* was erroneous.

Analysis Methods

1. Correlation of HI with diet and environment

Firstly, we calculated the mean HI in different habitats and dietary preference with histogram analyses (Fig. 1). For further analyses, traditional correlation analyses and phylogenetic generalized least squares regression were conducted. For diet, we conducted traditional analyses with non-parametric correlation coefficient (Spearman); for climatic variables (annual precipitation and mean annual temperature), Pearson correlation analysis was performed. Before the phylogenetic generalized least squares regression, the strength of phylogenetic signal of hypsodonty index in dipodid group was tested with Blomberg's K (Blomberg et al. 2003). The traditional statistical analyses were employed with SPSS 17.0. The
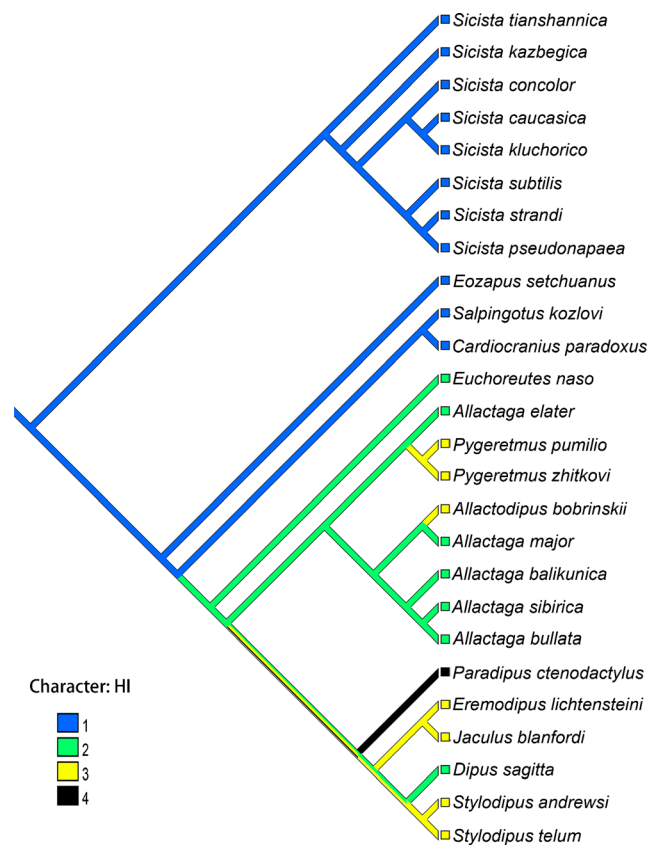

Fig. 1 Phylogeny of Dipodidae after Pisano et al. (2015). *Sicista napaea* was revised as *Sicista pseudonapaea* (see text for explanation), and the species not used in this study are excluded. HI was mapped on the tree with Mesquite 3.04

phylogenetic generalized least squares regression and K-value testing were conducted with the caper package (Orme et al. 2011) and the picante package (Kembel et al. 2010), respectively, in R version 3.0.2 (R Core Team 2013).

Correlation between Mean HI of Dipodid Community and Regional Climatic Factors

To test the relationship between mean HI of dipodid community and regional climatic factors, we converted point data for species to a grid format with a resolution of 0.5° latitude and longitude for grid cells (~55 km at the equator, 8050 cells), and recorded all species present within each grid cell to calculate the mean HI. Then, the data of all 19 bioclimatic variables were converted to the gridded format based on extent and resolution of the gridded format of the species distribution data. After this conversion, we exported all the grid cells to a matrix format that contained both the mean HI data and bioclimatic data.

We used both Pearson correlation analysis (Table 4) and spatial autoregressive analysis with spatial simultaneous autoregressive SAC model (Table 5) to test the relationship

between mean HI of dipodid community and regional climatic factors. In the spatial autoregressive analysis, the weight matrix was constructed using the k-nearest neighbors.

The grid conversion was conducted with software DIVA-GIS 7.5 (Hijmans et al. 2012); the Pearson analyses were performed with SPSS 17.0, and spatial autoregressive analyses with Package 'spdep' in R version 3.0.2 (R Core Team 2013; Bivand and Piras 2015).

Results

Table 1 and Fig. 2 provide the summary statistics of HI, diet, and habitat types of 26 extant species of Dipodidae. A clear tendency can be seen that the diet and distribution ranges shift from predominantly omnivorous taxa in forest to herbivorous taxa in desert with increasing crown height in Tables 1 and 2. Moreover, herbivores always have higher hypsodont indices than omnivores and granivores in any given habitats (Fig. 2).

Results for traditional correlation and phylogenetic generalized least squares regression analyses are presented in Table 3. In the correlation analysis, diet, annual precipitation, and temperature all show significant correlations with hypsodonty index ($p < 0.001$, $p = 0.001$, and p < 0.001, respectively). Before phylogenetic generalized least squares regression analyses, we tested the strength of phylogenetic signal (Table 2). K greater than one implies that closer relatives have more similar value of HI than expected under Brownian motion evolution so that the PGLS is appropriate. When phylogenetic effects were taken into account, the regression result ($p = 0.0009$) still indicates there is a significant correlation

Table 2 Output from the test of phylogenetic signal

Functional traits	K	P
HI	1.171	0.001

For detailed description of K statistics see Blomberg et al. (2003)

between HI and diet. However, PGLS of the annual precipitation and temperature are not significant ($p = 0.1628$, and $p = 0.0606$, respectively) (Fig. 3b, c).

Table 4 shows the relationships of mean HI of the dipodid community with all 14 bioclimatic variables. The results suggest that hypsodonty levels of the dipodid community have significant correlations with precipitation and temperature. The strongest correlation of mean HI was recorded with precipitation of the warmest quarter and maximum temperature of the warmest period (Figs. 4 and 5). It's important to note that there is a stronger correlation in warm periods than in cold periods.

The results of spatial autoregressive analysis are listed in Table 5. Both ρ and λ parameters are statistically significant, which suggests the presence of significant spatial autocorrelation in both the lagged dependent variable and residuals. When the spatial autocorrelation was taken into account, coefficients remain statistically significant except for the mean temperature of wettest quarter and precipitation of coldest quarter.

Discussion

Both traditional and phylogenetic analyses clearly show that diet plays an important role in the development of high-crowned teeth in dipodids. It means that species feeding on more intrinsically abrasive plant materials have higher hypsodonty indices than those feeding on less abrasive foods (Fig. 2a). This result is similar to that based on South American rodents and ungulates analyses (Williams and Kay 2001). It should be noted that the insectivorous taxon, *Euchoreutes naso*, has a relatively higher crown (mesodont) than expected. For this species, high cusps may contribute to the measured height of the tooth crown, and are more likely to relate to tooth function rather than tooth durability (Damuth and Janis 2011). Additionally, we cannot overlook the influence of vertical distribution of foraging micro-habitats (feeding height) as an additional explanation for evolutionary changes in molar crown height in rodents. Williams and Kay (2001) suggested that arboreal species have higher crown than terrestrial/ semi-aquatic species. However, this conclusion is not applicable to dipodids (all ground-surface foragers). The generalist herbivore, *Eozapus setchuanus*, which has never been recorded in low vegetation habitats (Quéré et al. 2009), has a low-crown height (brachydont). In this case, lower molar crowns could be attributed to the fact that this species lives in higher feed position where dust could be less than in the
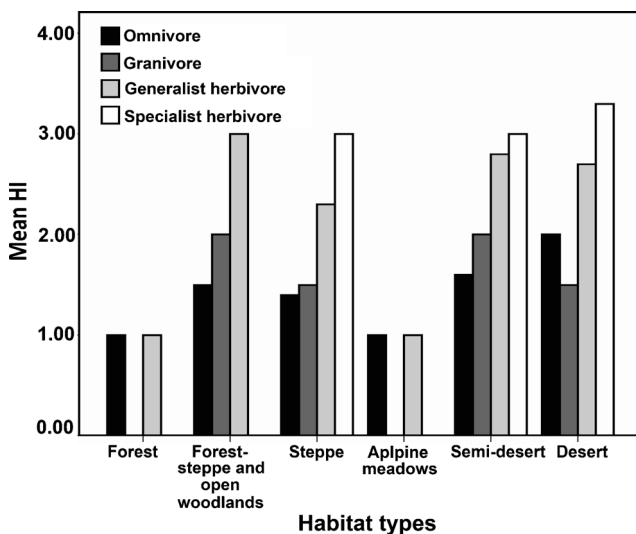

Fig. 2 Histogram of mean HI of the different dietary group in six habitat types. It shows the relationship of HI to diet and habitat type in 25 species of extant Dipodidae. *Euchoreutes naso* was excluded from the analysis. On the horizontal axis habitats have been arranged from left to right in order of increasing openness, from closed forests to desert

Table 3 Summary statistics for Pearson correlation and phylogenetic regressions

Variables (n = 26)	Correlation analyses[*]		Phylogenetic generalized least squares regression	
	P-value	r	P-value	Slope
HI vs Diet	<0.001	0.672	0.0009	1.242
HI vs mean Annual Precipitation	0.001	-0.606	0.1628(n.s.)	-0.0024
HI vs mean Annual Temperature	<0.001	0.712	0.0606(n.s.)	-0.0528

(n.s.) not significant

Correlation analyses[*]: For diet and environmental variables, Spearman and Pearson correlation coefficient have been used, respectively. See text for more detail information

ground. Besides that, high and dense vegetation may serve as a filter to dust at the ground level.
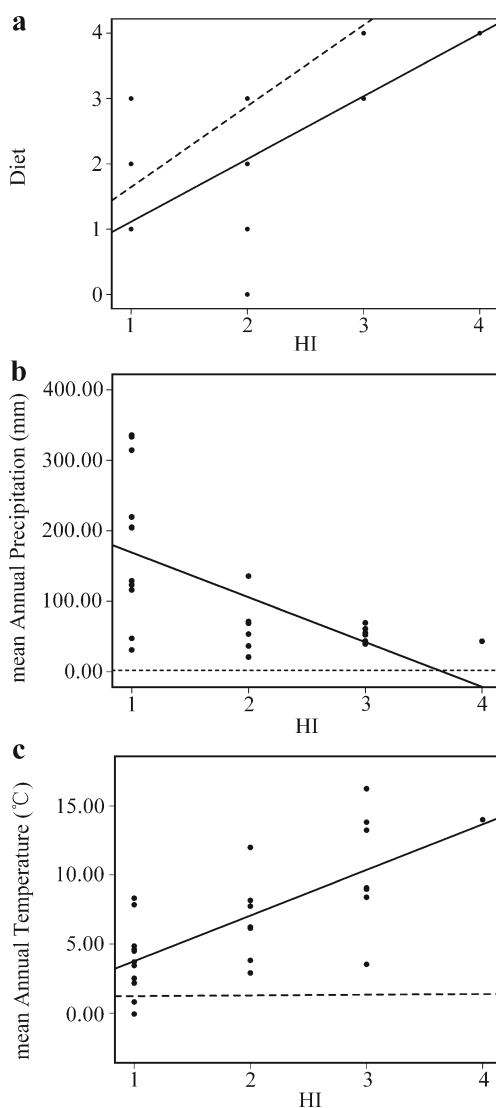
Fig. 3 Scatterplots of (**a**) HI vs diet, (**b**) HI vs mean annual precipitation of distribution region, and (**c**) HI vs mean annual temperature of distribution region. Every point stands for one species. The solid lines and the dotted lines indicate the linear relationship without / with the phylogenetic effect took into account, respectively

Concerning environmental variables, habitat data have been considered for the first time as a factor in analysis of molar crown height in rodents. The habitat variable has been considered as a significant role in the development of hypsodont teeth in ungulates (Janis 1988; Mendoza and Palmqvist 2007). Nonetheless, Williams and Kay (2001) questioned the relationship between habitats and exogenous grit on plant material. However, it is obvious there is more grit loading on plant surfaces in desert than forest in our case. The result here shows that almost all the hypsodont species live mainly in desert and more than half of brachydont species live in the forest and grassland habitats.

Kay et al. (1999) reported strong correlations between the proportion of species of hypsodont sigmodontine rodents at approximately 75 South American localities and climatic variables (e.g., mean annual precipitation and mean annual temperature). In the correlation analysis, our study reaches the same conclusions as Kay et al. (1999). However, the correlations were not statistically significant with phylogeny considered ($P > 0.1$). How

Table 4 Correlation analyses between mean HI and bioclimatic variables

| Bioclimatic variables	P-value	r	(n = 8050)
Annual mean temperature	<0.001	0.48	
Max temperature of warmest period	<0.001	0.59	
Min temperature of coldest period	<0.001	0.37	
Mean temperature of wettest quarter	<0.001	0.21	
Mean temperature of driest quarter	<0.001	0.57	
Mean temperature of warmest quarter	<0.001	0.57	
Mean temperature of coldest quarter	<0.001	0.37	
Annual precipitation	<0.001	-0.45	
Precipitation of wettest period	<0.001	-0.39	
Precipitation of driest period	<0.001	-0.27	
Precipitation of wettest quarter	<0.001	-0.41	
Precipitation of driest quarter	<0.001	-0.27	
Precipitation of warmest quarter	<0.001	-0.52	
Precipitation of coldest quarter	0.1705(n.s.)	-0.05	

(n.s.) not significant
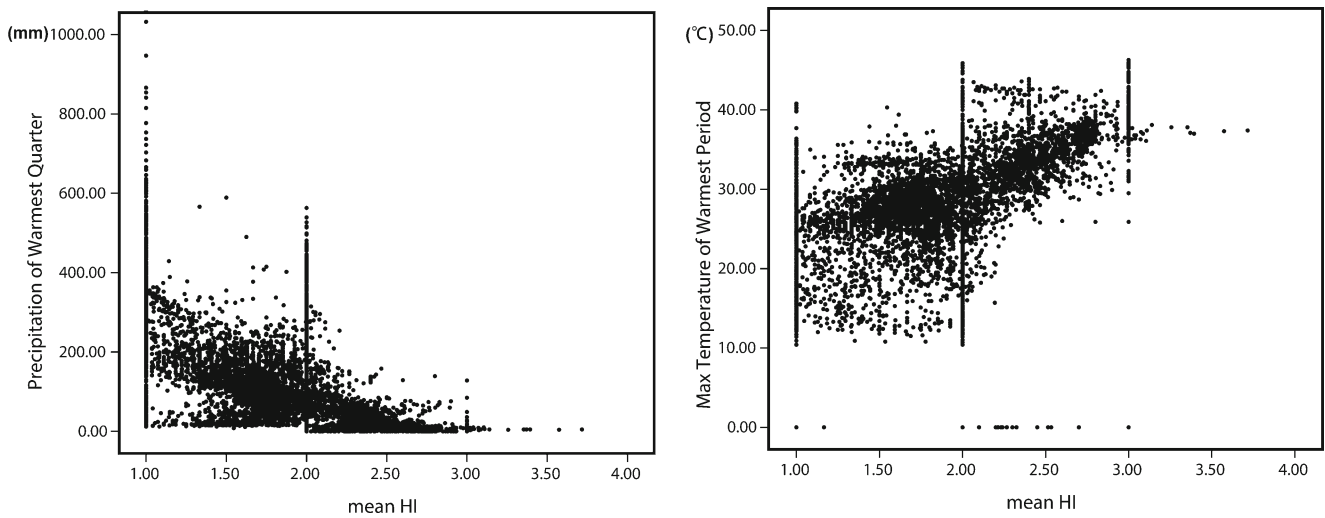
Fig. 4 Scatterplot of the correlation results of mean HI against precipitation of warmest quarter and maximum temperature of warmest period

should this difference be interpreted? From the phylogenetic point of view, phenotypes of taxa usually are not statistically independent because they are all related through their hierarchical phylogenetic history. Therefore, it will lead to inflated Type I error rates by treating all data points as statistically independent in traditional interspecific comparative analyses (Felsenstein 1985; Garland et al. 2005). In the present case, the K-value (K>1) suggests that the crown height does exhibit phylogenetic

signals, although hypsodonty has often been considered as an example of convergent adaptation in both extant and extinct mammalian herbivores. The pattern that increasing crown height in response to general environmental and climatic trends from predominantly closed − forested, warm, and wet habitats to open temperate grasslands, to hot desert habitats has been found among many mammal lineages including South American rodents (Kraglievich 1940; Janis 1988; Pascual and Ortiz

Fig. 5 (a) Color-interpolated map of mean HI of 26 extant dipodids; white values indicate lack of data; from greens to reds, they show the successive increase of crown height; (b) Map of current (representative of 1950–2000) maximum temperature of warmest period; and (c) mean annual precipitation where the 26 extant dipodids are distributed; the climate data were downloaded from WorldClim database. The grid map of dipodid distribution ranges converted from the real occurrence points for each species included in the analysis was provided by Shenbrot. See text for explanation
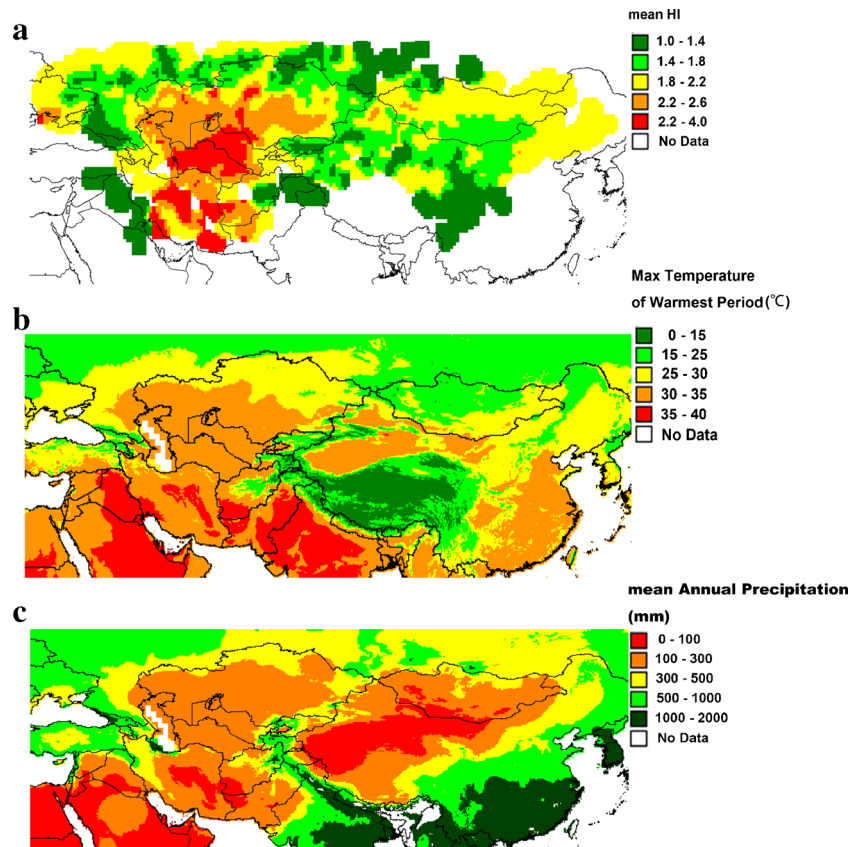
Table 5 The results of maximum likelihood estimation for spatial simultaneous autoregressive SAC models

	Coefficients (p-value)	ρ (p-value)	λ (p-value)
Annual mean temperature	0.00124839 (3.146e-09)	0.97344 (< 2.22e-16)	0.34094 (< 2.22e-16)
Max temperature of warmest month	0.00172114 (5.129e-14)	0.96961 (< 2.22e-16)	0.34879 (< 2.22e-16)
Min temperature of coldest month	0.00283498 (3.032e-06)	0.32468 (< 2.22e-16)	0.9789 (< 2.22e-16)
Mean temperature of wettest quarter	0.00058704 (0.08439)ns	0.32147 (< 2.22e-16)	0.9799 (< 2.22e-16)
Mean temperature of driest quarter	5.1896e-04 (1.538e-08)	0.97229 (< 2.22e-16)	0.34419 (< 2.22e-16)
Mean temperature of warmest quarter	0.00180505 (8.26e-14)	0.97036 (< 2.22e-16)	0.34667 (< 2.22e-16)
Mean temperature of coldest quarter	0.00067082 (1.369e-05)	0.97631 (< 2.22e-16)	0.33337 (< 2.22e-16)
Annual precipitation	-3.6022e-05 (5.678e-09)	0.9742 (< 2.22e-16)	0.33619 (< 2.22e-16)
Precipitation of wettest month	0.00039137 (0.002221)	0.97827 (< 2.22e-16)	0.32607 (< 2.22e-16)
Precipitation of driest month	-1.4951e-04 (4.381e-07)	0.97577 (< 2.22e-16)	0.3324 (< 2.22e-16)
Precipitation of wettest quarter	-6.3436e-05 (5.959e-08)	0.97511 (< 2.22e-16)	0.33385 (< 2.22e-16)
Precipitation of driest quarter	0.00039137 (0.002221)	0.97822 (< 2.22e-16)	0.32636 (< 2.22e-16)
Precipitation of warmest quarter	-6.7603e-05 (2.349e-08)	0.97315 (< 2.22e-16)	0.34091 (< 2.22e-16)
Precipitation of coldest quarter	-2.4779e-05 (0.2998)ns	0.97991 (< 2.22e-16)	0.32107 (< 2.22e-16)

ns not significant

Jaureguizar 1990; Kay et al. 2002). It may represent a general pattern of correlated evolutionary change rather than a single event. From this perspective, it is hard to deny the relationship between HI and precipitation completely in dipodids.

Compiling all species together at the regional community level, the mean hypsodonty index of dipodids showed significant correlations with precipitation and temperature by both traditional Pearson analysis (non-spatial analysis) and spatial autoregressive analysis. The *p*-values indicate that the null hypothesis, mean HI, and bioclimatic variables in the dipodid community are uncorrelated, is rejected. In other words, changes in mean HI value are closely related to changes in climate variables. Besides that, the general pattern of hypsodonty in the map resembling the modern temperature and precipitation pattern to a great extent (Fig. 5) also supports the result. Our results concur with the strong correlation of hypsodonty index in large mammal communities and annual rainfall (Fortelius et al. 2002; Eronen et al. 2010a, 2010b; Liu et al. 2012). Thus, it can be expected that the hypsodonty index of a mammalian community is an ideal indicator of precipitation and temperature. It is noteworthy that there is a better correlation in warm periods than in cold periods in our analyses, possibly due to hibernations and their regional distribution. There is some discrepancy between HI and rainfall in some regions, such as South Xinjiang of China, where the present precipitation is low but mean HI is also low, with some low-crowned species, such as *Salpingotus kozlovi* and *Dipus sagitta*, distributed in this arid area suggesting that hypsodonty does not necessarily serve as the only morphological adaptation to an arid environment. Liu et al. (2012) showed better accuracy using both hypsodonty and lophs to estimate mean annual precipitation than by either variable alone. Future work to explore more morphological traits is highly expected.

Conclusions

Our study is the first to investigate the relationship of hypsodonty with the diet and environmental variables in dipodids. In addition, phylogenetic and spatial autocorrelation effects have also been taken into account. Some conclusions were obtained as following:

(1) The results clearly show that the dietary preference plays a significant role in shaping the evolution of tooth crown height in Dipodidae.
(2) The significant relationship between hypsodonty and environmental variables may be partly affected by phylogenetic effects.
(3) It appears possible to use the mean HI of dipodid communities as proxy for estimating regional climatic variables. Future work should attempt to integrate information on tooth crown height and other associated traits (e.g., lophs) for more clades of rodents that have evolved high-crowned teeth.

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