

Skull Morphology of Four Species of Zokors (Rodentia, Myospalacinae)

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ABSTRACT

Zokors are one of the subterranean rodents in the subfamily Myospalacinae. Extant zokors include two major genera, *Eospalax* and *Myospalax*, which can be distinguished by skull shape. However, due to few available studies on skull morphology of zokors, the interspecific differentiation of their skulls is still unclear. To differentiate among species and to describe the sexual dimorphism within each species, we measured morphological variation using one-way analysis of variance and cluster analysis in four species of zokor including *Eospalax cansus*, *Eospalax rothschildi*, *Eospalax baileyi*, and *Myospalax aspalax*. We also used principal component analysis and dichotomy to explore key measurements which could reflect skull differences to the maximum. In addition, we tested the correlations between environmental factors and skull measurements for each species. The results of variance analysis indicated that three zokors showed male-biased sexual size dimorphism except for *E. baileyi*. We also found that there were significant differences of linear measurements among four species. The results of cluster analysis showed that the four species of zokors divided into two branches, one including *E. cansus* and *E. rothschildi*, the other *E. baileyi* and *M. aspalax*. The results of principal component analysis showed that the variables that contribute to the first principal component were related to skull size, and the variables which contribute to the second principal component were different between sexes. Thus, linear measurements that reflect the skull size such as cranial length, basal length and cranial base could be key measurements for cluster and classification. Zygomatic breadth could be considered as quantifiable differences between the two genera *Eospalax* and *Myospalax*. We suggest that the clustering patterns could be related to climate and geographical factors. Finally, it was found that most of the skull measurements were positively correlated with latitude but negatively correlated with annual mean temperature and precipitation, which follows Bergmann's rule. This work provides a significant reference value to scholars who apply themselves to pest control and to the classification and identification of zokors using morphology.

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Authors' Contribution

All authors contributed to the study design. YZ, SR and MX collected samples and analyzed the data. YZ prepared the first draft of the manuscript. YZ, NL and XZ performed the experiments. CH and XN revised the article.

Key words

Cluster, Morphology, Skull, Zokor.

INTRODUCTION

Zokors are subterranean rodents in the subfamily Myospalacinae. They live most of their lives in underground tunnels and eat roots and stems of plants in woodland, which cause great losses on forestry (Fan and Shi, 1982; Zhang *et al.*, 2003). Much attention has been paid to genetic differentiation of zokors at the molecular level (Su *et al.*, 2013; Zou *et al.*, 2020), however, morphological data which can be used as a supplement to molecular data are scarce. Besides, there have been controversies in morphological classification and identification of zokor (Su *et al.*, 2015). What are the morphological differences between both sexes and among zokor species, and whether these differences could be used as a basis for classification

are still unclear (Liu *et al.*, 2018). Knowing the ecological differences of zokor species is not only beneficial to better understand the speciation and differentiation, but also provide important reference for further morphological classification and control.

The main distribution areas of zokors are China, Russia, and Mongolia (Luo *et al.*, 2000). Extant zokors can be divided into two genera according to differences of occipital morphology, *i.e.*, *Myospalax* (flat occiput), and *Eospalax* (convex occiput) (Zheng, 1994; Norris *et al.*, 2004). The four species studied here includes the flat occiput type *Myospalax aspalax*, and the convex type *Eospalax cansus*, *Eospalax baileyi* and *Eospalax rothschildi*. Due to the convergent and parallel evolution induced by subterranean lifestyles (Lacey *et al.*, 2001; Flynn, 2009), there are many similarities among different species of zokors. However, there also exists some distinct interspecific and even intraspecific differentiation among geographical populations (Tang *et al.*, 2009; Lu *et al.*, 2013). However, the intraspecific and interspecific differences of

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zokors based on linear measurements were not clarified yet (Liu *et al.*, 2018). And the correlations between these differences and ecological variables were still unclear. Therefore, linear measurements of morphology of zokors are needed to investigate morphological variation within and among zokor species.

The mammalian skull is relatively strong and stable in an adult organism (Dressino *et al.*, 1997; Stumpp *et al.*, 2016). It is usually employed in the research field of morphological evolution, classification, and identification of mammals (Assis *et al.*, 2017). Subterranean mammals undergone the selective pressure underground, and their skulls are influenced by natural selection in the evolutionary process (Lacey *et al.*, 2001; Marcy *et al.*, 2016). By comparing the skull morphology in five species of rodents (zokor was included), Tai *et al.* (2001) found that subterranean rodents including *Lasiopodomys mandarinus* (Cricetidae) and *E. cansus* (Spalacidae) have larger zygomatic breadth and longer checktooth row compared to above-ground relatives. Larger zygomatic breadth could attach more masseter and longer checktooth row could increase chewing surface, which was related to fiber-rich food including underground roots and stems. Zhu (2014) found that the subterranean *L. mandarinus* has strong lower incisor and degraded orbita compare to the aboveground *L. brandtii*, and it was inferred that the skull morphology of *L. mandarinus* was adaptability to digging tunnels with incisors and deterioration of vision of subterranean rodents. The differences in skull morphologies enable to reflect the morphological variations of mammals and exhibit a differentiation of species (Alvarez *et al.*, 2015). Most phenotypes under selective pressures of environment tend to show interspecific differences among geographical populations (Garnier *et al.*, 2005; Caumul *et al.*, 2005). The research on these differences is of great importance to understanding population differentiation, speciation, and for taxonomy.

The zokor has gradually adapted to underground life in both morphology and physiology (Wang *et al.*, 2012), such as small eyes (Zhang and Liu, 1994), strong forelimbs (Lin *et al.*, 2007), and high content of hemoglobin in blood (Wei and Wei, 2001). Due to controversies in classification and identification by morphology, interest in intraspecific and interspecific differentiation of zokors is increasing (Liu *et al.*, 2018; Su *et al.*, 2018). By analyzing the morphological measurements of body and skull of *E. baileyi*, Su *et al.* (2018) found male-biased sexual size dimorphism (SSD) in *E. baileyi*, which may be related to the patterns of digging between two sexes. In addition to quantifying the impact of phylogeny and sex on zokor morphology, Lu *et al.* (2013) highlighted the importance of ecology. Their study found a distinct pattern among geographical populations based on the morphological characteristics of *E. cansus*. By analyzing the differentiation of plateau zokors distributed in Qinghai, Gansu, and Sichuan provinces, the eight populations of zokors were found clustered into two groups: one was the zokors from Gansu province, the other was formed of those from Qinghai and Sichuan provinces (Tang *et al.*, 2009). Additionally, significant differences were found among these eight populations: the cranial length, length of upper cheek tooth row, and diastema length were major measurements valuable in analyzing skull variation. Su *et al.* (2018) suggested that isolation and ecological factors were the major causes for extant patterns. However, due to few studies on skull morphology of zokors, it is unclear how to distinguish the skull of different zokor species and sexes and whether their morphological varies with ecological variables. It is of great importance to define the differentiation patterns of species of zokors at a morphological level.

We propose four key hypotheses that we are testing: (1) whether sexual size dimorphism exist in four zokor species? (2) whether there are significant differences among four species, and which measurements are distinctly

Table I.- Information of sampling area of zokor.

Sampling locality	Species	Code	Longitude (°E)	Latitude (°N)	Altitude (m)	Annual temp. (°C)	Annual precipitation (mm)	Sample size (male/female)
Ecological garden in Jingyuan county	<i>E. cansus</i>	JY	106.3521	35.5145	1932	6.9	641.5	56 (17/39)
Xingzi forest in Zhenba county	<i>E. rothschildi</i>	ZB	108.0207	32.5008	1624	13.8	1300	8 (0/8)
Baiyan village in Xixiang county	<i>E. rothschildi</i>	XX	107.5572	32.8181	1460	14.4	1150	8 (4/4)
Dalianyin town in Weichang county	<i>M. aspalax</i>	WC	117.0529	42.0821	1477	3.3	430	25 (13/12)
Hougou village in Huangyuan county	<i>E. baileyi</i>	HY	101.8395	36.4512	3224	3.0	408.9	8 (3/5)

different among four species? (3) whether exist some key measurements of skull which may be expected to be the basis of classification? (4) whether there exist correlations between environmental factors of habitation and morphological differentiation? In this study, the morphological differentiation of zokors were measured by comparing the skull morphology based on linear measurements of *E. cansus*, *E. baileyi*, *E. rothschildi* and *M. aspalax*. This method is easy to apply and the 22 measurements measured in this method enables reflect the size and shape. This work provides a significant reference value to scholars who apply themselves to pest control and to the classification and identification of zokors using morphology.

MATERIALS AND METHODS

Specimen collection

We collected 105 living adult zokors from five locations. The adult zokor were identified according to its body size and the wear degree of molars (Li and Wang, 1992; Wang *et al.*, 1996). Zokors were captured by living traps placed underground during March to November of 2016 to 2017. Animals were euthanized humanely by ether. The skulls were removed with scissors, and then carefully collected in a sealed bag with labels. The details of sampling locations and species are listed in Table I where break down samples by species and sex. In fact, *E. cansus* and *M. aspalax* are easy to sample because their density of population is larger, and *E. cansus* is the most widely distributed species in China. However, the sample size of *E. baileyi* and *E. rothschildi* were small. *E. baileyi* is difficult to obtain because the density of population is small. *E. rothschildi* who lives in hills is hard to find because we have to catch them by excavating soil instead of living traps placed underground.

Preparation and measurement of skull specimens

The preparation process of skull specimens follows the methodology outlined in the literature (Li *et al.*, 2017). 22 linear measurements were taken on the specimens using a digital caliper. The original data were stored in Supplementary Table I. The 22 measurements of skull and their abbreviations are presented in Table II. The definition of 22 measurements was in described by Xia *et al.* (2006) and Yang *et al.* (2005).

Data analyses

To test whether sexual size dimorphism exist in four zokor species (Hypothesis 1), the t-test was applied if the data conformed to normal distribution and homogeneity of variance. To make the data conform to normal distribution,

the data of skull measurements which did not conform to normal distribution were converted using the normal score method. The differences of skull between males and females of four zokor species were detected separately by independent sample T-test on 22 measurements. If there were significant differences between two sexes in skull indexes, male and female specimens were separated for next analysis.

Table II.- The 22 measurements of skull and their abbreviations.

Measurement	Abbreviation
Breadth of auditory bulla	BAB
Basal length	BL
Breadth of nasal bone	BNB
Cranial base	CB
Cranial height	CH
Cranial length	CL
Greatest mastoid breadth	GMB
Length of auditory bulla	LAB
Length of diastema in lower jaw	LDL
Length of diastema in upper jaw	LDU
Length of lower cheek tooth row	LLC
Length of lower jaw	LLJ
Length of median palatal	LMP
Length of nasal bone	LNB
Length of upper cheek tooth row	LUC
Orbital length	OL
Orbital space	OS
Outer width of upper molars	OWU
Space between auditory bulla	SAB
The least space between forehead crest	SFC
The least space between parietal crest	SPC
Zygomatic breadth	ZB

To test whether there are significant differences among four species, and which measurements are distinctly different among four species (Hypothesis 2), the analysis of variance was applied if the data conformed to normal distribution and homogeneity of variance. The differences in skull morphology among populations were detected by one-way analysis of variance (ANOVA) and multiple comparisons with a Bonferroni correction (reduced alpha) on 22 measurements. We mainly focused on *E. cansus* and *M. aspalax* due to sufficient samples of these two species. Furthermore, k-means cluster analysis (Kaufman *et al.*, 1990) was applied to differentiating the skull morphology by species. The differences of skull between branches were detected by ANOVA based on the results of cluster analysis.

To test whether exist some key measurements of skull which may be expected to be the basis of classification (Hypothesis 3), principal component analysis (PCA) were applied to exploring representative measurements. Furthermore, dichotomy was used to select the minimum number of linear measurements for cluster analysis, which lead to the same cluster results as the cluster results in this study. Details were shown in [Supplementary Table II](#). Choosing half of the numbers of total measurements at a time, the number of linear measurements were narrowed down step by step. Measurements were chosen based on more contribution to the first two principal component and more variations among species. Key measurements with significant differences among species or between

genera were selected according to the results of multiple comparison or ANOVA.

To test whether there exist correlations between environmental factors of habitation and morphological differentiation (Hypothesis 4), we have collected climatic and geographical data of sampling sites from local county annals ([Table I](#)). Altitude, longitude, latitude, annual mean temperature, and annual precipitation were included. The coordinates of trapped zokors retrieved with GPS for each zokor, and the margins of error for the corresponding environmental datasets are less than 1 km radius. The correlations between these factors and skull measurements were analyzed by using the Pearson Correlation Coefficient ([Zhang *et al.*, 2018](#)).

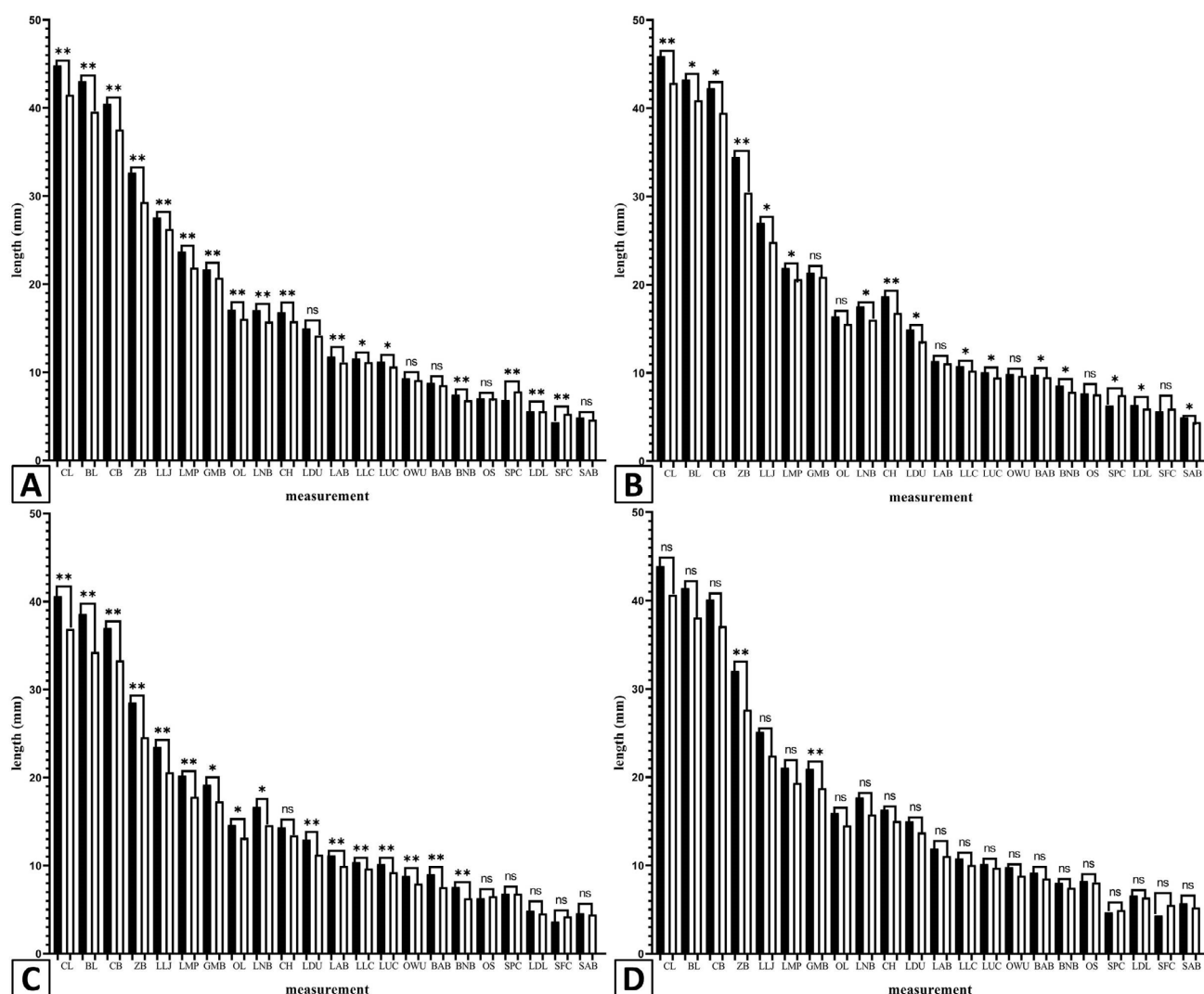


Fig. 1. The skull differences between two sexes based on 22 skull morphological indexes. A, *E. cansus*; B, *M. aspalax*; C, *E. rothschildi*; D, *E. baileyi*. The samples in black and white represent males and females, respectively. * represents highly significant difference ($p < 0.05$); ** represents significant difference ($p < 0.01$) and ns represents no significant difference ($p > 0.05$).

All of the above analyses were conducted through SPSS 20.0 software. The significant and the highly significant levels were 0.05 and 0.01, respectively (Xue, 2008; Feng, 2015).

RESULTS

Skull differences between males and females

The differences between males and females of four species of zokors (*E. cansus*, *M. aspalax*, *E. rothschildi* and *E. baileyi*) were shown in Figure 1. The results in Figure 1A showed that there were 17 measurements with significant differences between the two sexes in *E. cansus*. They were CL, BL, CB, CH, LNB, BNB, ZB, LMP, GMB, LAB, LLC, SPC, SFC, LUC, LLJ, LDC and OL. Except for the SPC and SFC, the other 15 measurements in males were larger than those of females.

There were 16 measurements with significant differences between two sexes in *M. aspalax* (Fig. 1B). They were CL, BL, CB, CH, LNB, BNB, ZB, LMP, BAB, SAB, LLC, SPC, LUC, LLJ, LDU and LDL. Except for SPC, the other 15 measurements in males were larger than that of females.

There were 16 measurements with significant differences between two sexes in *E. rothschildi* (Fig. 1C). They were CL, BL, CB, LNB, BNB, ZB, LMP, OWU, GMB, LAB, BAB, LLC, LUC, LLJ, LDU and OL. All 16 measurements in males were larger than that of females. However, there are only 4 males and only 12 females for this species.

There were only two measurements with significant differences between both sexes in *E. baileyi*, that were

ZB and GMB; these two measurements in males were larger than those of females (Fig. 1B). There were 18 measurements in males were larger than those of females. However, the differences were not significant. However, the sample size of *E. baileyi* is very small because there are only 3 males and only 5 females.

Figure 1 shows that male skulls are significantly larger than female skulls in three out of the four zokor species. Therefore, we analyzed male and female specimens separately for the next step analysis.

Skull differences among different geographical populations

Analyzed by one-way analysis of variance (ANOVA), it is shown that there are 17 measurements and 21 measurements with significant differences among populations in males and females, respectively. The results in males and females are illustrated in Figures 2 and 3, respectively. Compared with males, there were more distinct differences among species in females. It is shown that there were 11 and 8 measurements with significant differences between *E. cansus* and *M. aspalax* in males and females, respectively. Compared with *M. aspalax*, *E. cansus* has larger LLC and LUC, smaller ZB, OWU, BNB.

Cluster analysis of male skulls

Cluster analysis of four species of zokors was conducted according to the mean values of 22 measurements. The results for males are shown in Figure 4A. The zokors in four geographical populations were divided into two major branches: branch A represents populations composed of *E. cansus* and *E. rothschildi*, and branch B represents populations composed of *E. baileyi* and *M. aspalax*.

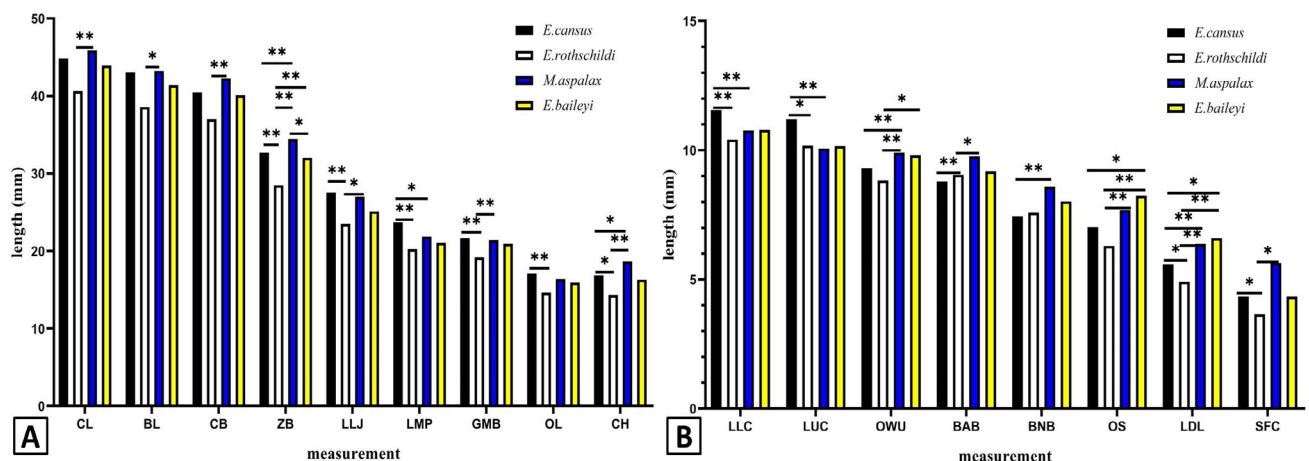


Fig. 2. Skull differences of males among populations based on ANOVA and multiple comparison. A, CL, BL, CB, ZB, LLJ, LMP, GMB, OL, CH; B, LLC, LUC, OWU, BAB, BNB, OS, LDL, SFC. * represents highly significant difference ($p < 0.05$) and ** represents significant difference ($p < 0.01$).

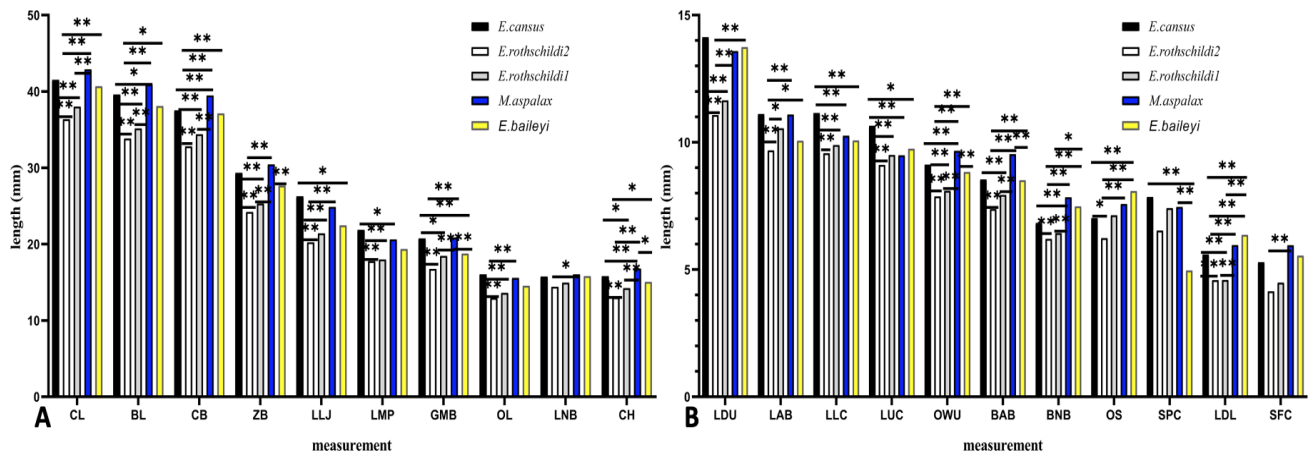


Fig. 3. Skull differences of females among populations based on ANOVA and multiple comparison. **A**, CL, BL, CB, ZB, LLJ, LMP, GMB, OL, LNB, CH; **B**, LDU, LAB, LLC, LUC, OWU, BAB, BNB, OS, SPC, LDL, SFC. * represents highly significant difference ($p < 0.05$) and ** represents significant difference ($p < 0.01$).

It was found that there were 12 measurements with significant differences between the two branches by ANOVA: CL, CB, BL, CH, BNB, ZB, OS, OWU, BAB, LLC, SFC, LUC and LDL. Except for LLC and LUC, the other eleven measurements were all higher in branch B than branch A, which indicated that the skull size in branch B was larger than that of branch A because these measurements all reflect skull size. However, the molars in branch A are larger than those of branch B.

The differences within branches were detected by ANOVA. In branch A, there were significant differences between *E. cansus* and *E. rothschildi* in 15 measurements, which were all larger in *E. cansus* than of *E. rothschildi*. These measurements were CL, CB, BL, CH, ZB, LMP, OWU, GMB, LAB, LLC, LUC, LDL, LLJ, LDU and OL. It was shown that the skull and molar size in *E. cansus* was larger than those of *E. rothschildi*. In branch B, there were four measurements with significant differences between *E. baileyi* and *M. aspalax*. These measurements were CH, ZB, LAB and BAB. Except for LAB, the other three measurements were larger in *M. aspalax* than that of *E. baileyi*, which indicated that the skull shape was different in the two species, and that the breadth and height of skull of *M. aspalax* were larger than that of *E. baileyi*.

Cluster analysis of female skull

The cluster analysis results of females are shown in Figure 4B. The five geographical populations of zokors are divided into two major branches, branch A which represents mixed populations composed of *E. cansus* and *E. rothschildi*, and branch B which represents mixed populations composed of *E. baileyi* and *M. aspalax*. It was found that there were 13 measurements with significant

differences between the two branches by ANOVA: CL, CB, BL, CH, BNB, ZB, OS, OWU, BAB, LLC, SFC, LUC and LDL. Except for LLC and LUC, the other eleven measurements were all higher in branch B than branch A, which indicated that the skull size in branch B was larger than that of branch A because these measurements all reflect skull size. However, the molars in branch A are larger than those of branch B.

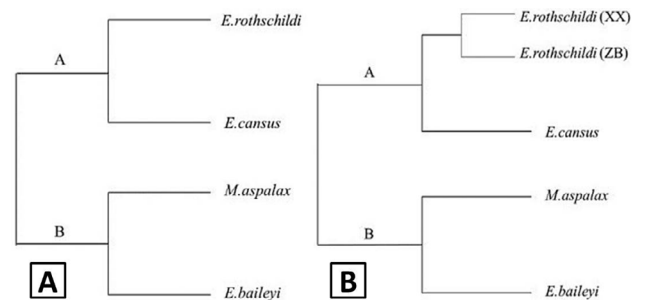


Fig. 4. Skull indexes clustering. **A**, males; **B**, females.

In branch A, there were significant differences between *E. cansus* and *E. rothschildi* in 21 measurements except for SAB. These measurements were all larger in *E. cansus* than that of *E. rothschildi*. It was shown that the skull and molar size in *E. cansus* was larger than that of *E. rothschildi*. In branch B, there were seven measurements showing significant differences between *E. baileyi* and *M. aspalax*. These were CH, ZB, SAB, OWU, GMB, BAB and SPC. Except for LAB, the other six measurements were higher in *M. aspalax* than that in *E. baileyi*, demonstrating that the breadth and height of the skull of *M. aspalax* are larger than those of *E. baileyi*.

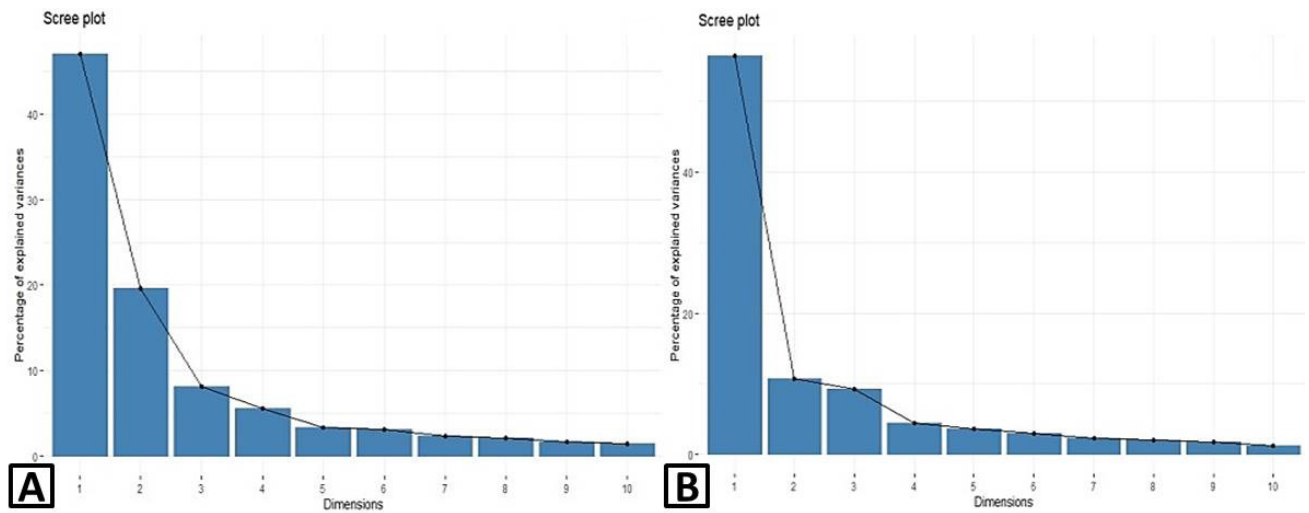


Fig. 5. Contribution proportion of the first ten principal components. A, male; B, female.

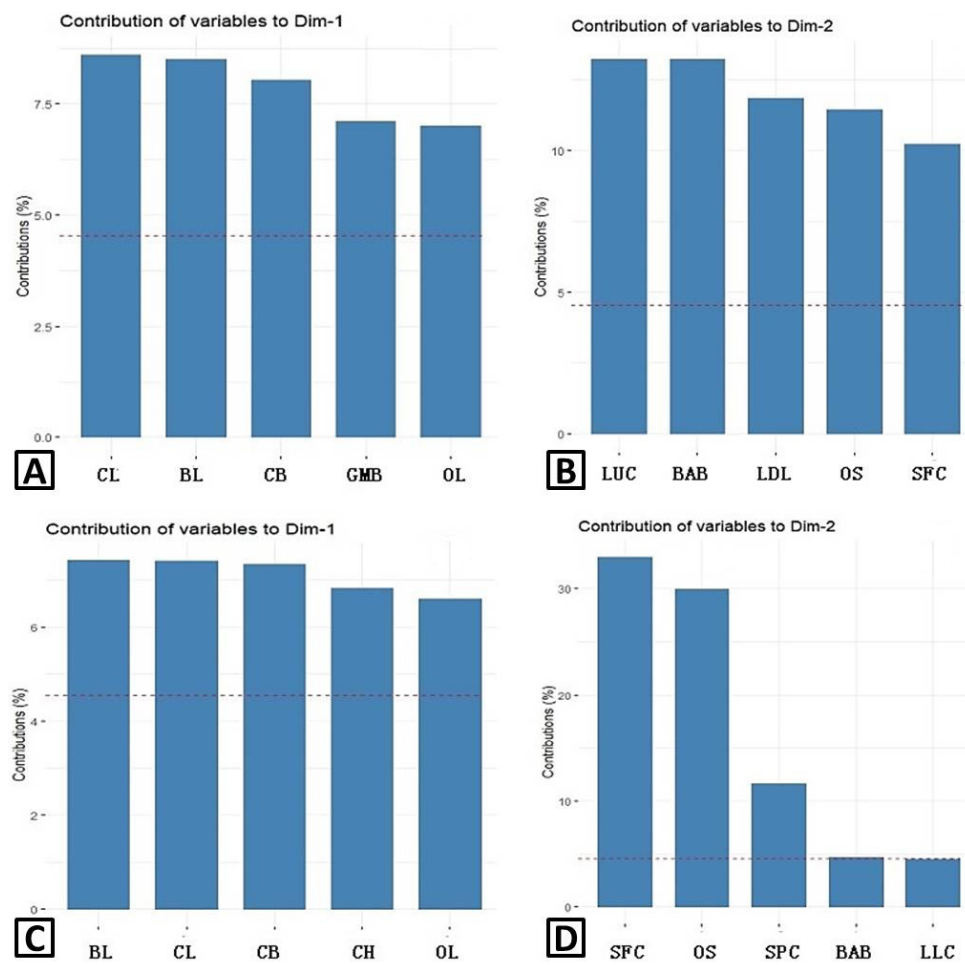


Fig. 6. Contribution of variables to the first two principal components. A, male (variables to Dim-1); B, male (variables to Dim-2); C, female (variables to Dim-1); D, female (variables to Dim-2).

Principal component analysis

The results of principal component analysis (PCA) are shown in Figures 5, 6 and 7. In males, the eigenvalue of the first four principal components was greater than 1, and the cumulative contribution proportion to the total variation was 80.23%. The contribution to variance of the first four principal components were 47%, 19.6%, 8.16%, and 5.5%, respectively (Fig. 5A). The variables which have the main contribution to the first principal component were CL, BL and CB (Fig. 6A). These variables were parallel to the first principal component and were positively correlated with the first principal component (Fig. 7A). The variables which have the main contribution to the second principal component were LUC, BAB, LDL, OS and SFC (Fig. 6B). Three variables including BAB, OS, SFC were proximately parallel to the second principal component and four measurements were positively correlated with the second principal component except for LUC (Fig. 7A).

In females, the eigenvalue of the first four principal component was greater than 1, and the cumulative contribution proportion to the total variation was 80.83%. The contribution proportion of the first four principal component were 56.5%, 10.7%, 9.16% and 4.46%, respectively (Fig. 5B). The variables which have the main contribution to the first principal component were BL, CL and CB (Fig. 6C). These variables were parallel to the first principal component and were positively correlated with the first principal component (Fig. 7B). The variables which have the main contribution to the second principal component were SFC, OS, and SPC (Fig. 6D). These three variables were parallel to the second principal component and were positively correlated with the second

principal component (Fig. 7B).

The variables which contribute to first principal component reflect skull size, which was consistent in both sexes. However, the variables which contribute to the second principal component were different between sexes. Males have more than 60% contribution by LUC, BAB, LDL, OS and SFC to the second principal component. LUC, BAB and LDL were related to the shape of molars and auditory bulla. Females have more than 60% contribution by SFC and OS to the second principal component. SFC and OS were shared in both sexes, but they were more important in females. OS was related to visual range. SFC has less variation among species than most of measurements in females (Fig. 3; Supplementary Table II). It is perhaps indicated that SFC not only reflects the differences but also reflects the commonality among species in females.

Selection of key measurements

For males, at least four measurements are needed to be the basis of cluster based on dichotomy, they are CL, BL, CB and OS (Supplementary Fig. 1). As shown in Figure 2A and B, CL, BL, CB and OS were significantly larger in *M. aspalax* than that of *E. rothschildi*. These four measurements could also be the key measurements differentiating *E. rothschildi* from *M. aspalax*. Besides, there were 13 measurements with differences between two genera (not shown). By exploring the measurements of maximum variation between genera, ZB (Fig. 8A), CH and OS of *M. aspalax* (*Myospalax*) were found significantly different from another three species (*Eospalax*), respectively.

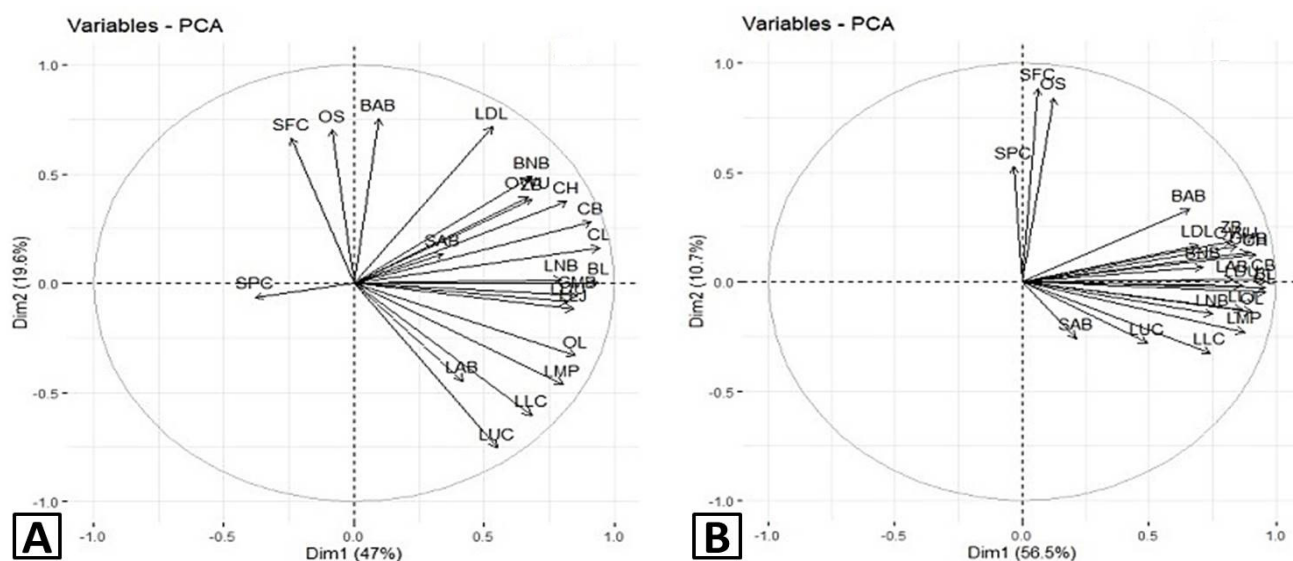


Fig. 7. Correlations between variables and the first two principal components. A, male; B, female.

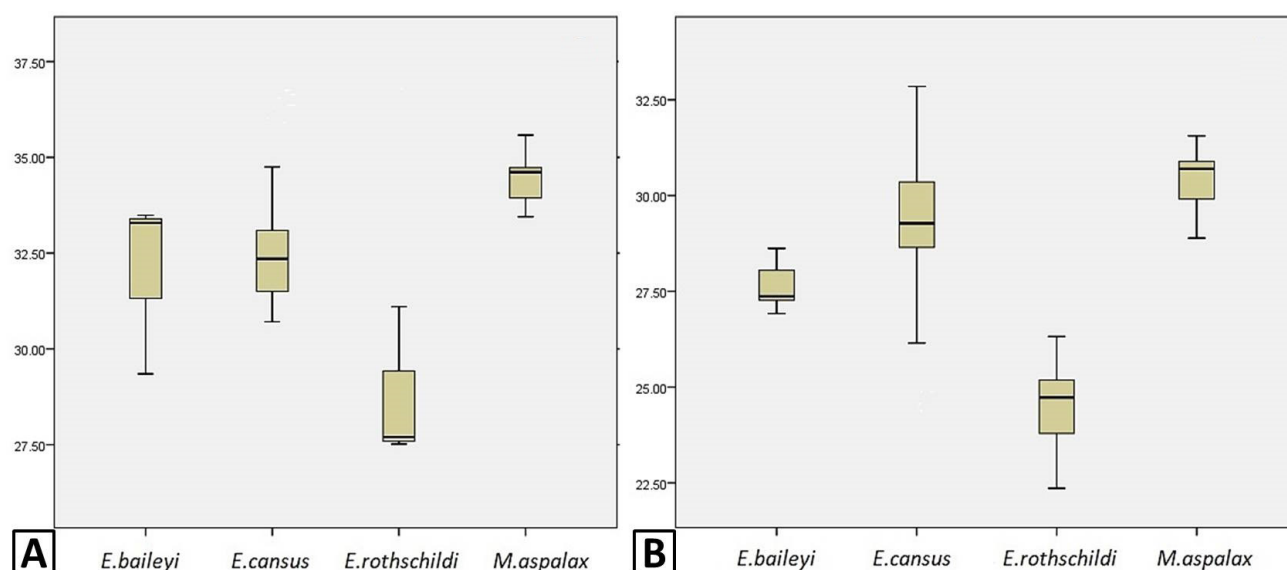


Fig. 8. The box plots of zygomatic breadth among four zokor species. A, males; B, females.

Table III.- The correlations between 22 measurements and environmental factors.

M	AMT	AP	Alt	Long	Lat
CL	-0.557**	-0.608**	-0.022	0.303**	0.520**
CB	-0.611**	-0.634**	-0.046	0.375**	0.589**
BL	-0.564**	-0.602**	-0.022	0.268**	0.486**
CH	-0.634**	-0.650**	-0.130	0.460**	0.650**
BNB	-0.541**	-0.527**	-0.070	0.492**	0.644**
LNB	-0.340**	-0.360**	0.024	0.177	0.316**
ZB	-0.636**	-0.666**	-0.068	0.376**	0.597**
LMP	-0.355**	-0.423**	0.042	-0.038	0.153
OS	-0.535**	-0.527**	0.244*	0.185	0.449**
SAB	-0.144	-0.152	0.210*	-0.080	0.046
OWU	-0.690**	-0.710**	-0.027	0.408**	0.655**
GMB	-0.580**	-0.652**	-0.022	0.189	0.436**
BAB	-0.619**	-0.633**	-0.159	0.555**	0.722**
LAB	-0.451**	-0.525**	0.200*	-0.030	0.246*
LLC	-0.232*	-0.315**	0.105	-0.202*	-0.022
SFC	-0.400**	-0.390**	-0.035	0.281**	0.404**
SPC	0.113	0.065	-0.276*	0.019	-0.081
LUC	-0.101	-0.184	0.146	-0.301**	-0.155
LDL	-0.772**	-0.760**	0.273**	0.267**	0.626**
LLJ	-0.469**	-0.539**	-0.021	0.087	0.298**
LDU	-0.509**	-0.559**	0.167	0.032	0.305**
OL	-0.460**	-0.523**	0.243	0.054	0.277**

For abbreviations, see Table II. M, measurement; AMT, annual mean temperature; AP, annual precipitation; Alt, altitude; Lat, latitude; Long, longitude. *represents significant difference ($p < 0.05$); **represents highly significant difference ($p < 0.01$).

For females, at least four measurements are needed to be the basis of cluster based on dichotomy, they are CL, BL, CB and LLC (Supplementary Fig. 2). As is shown in Figure 3A and B, CL, BL, CB and LLC were significantly larger in *E. cansus* than that of *E. rothschildi*. CL, BL and CB were significantly larger in *M. aspalax* than that of *E. rothschildi*, and were also significantly larger in *E. baileyi* than that of *E. rothschildi*. These three measurements could also be the key measurements differentiating *E. rothschildi* from the other three species because of the smallest measurements of CL, BL and CB in *E. rothschildi*. Besides, there were 14 measurements with differences between two genera (not shown). By exploring the measurements of maximum variation between genera, ZB (Fig. 8B) and OWU of *M. aspalax* (*Myospalax*) were found significantly different from another three species (*Eospalax*), respectively.

Correlation analysis between skull morphology and environmental factors

The data of sexes were pooled for correlation analysis. The correlations between 22 measurements and environmental factors were shown in Table III. It was indicated that most measurements were significantly correlated with latitude, annual mean temperature, and annual precipitation.

Seventeen of the skull measurements were positively correlated with latitude, and these measurements all reflect skull and auditory bulla size. However, the correlations were slight, and the maximum Pearson correlation coefficient between OWU and latitude was 0.655.

Twenty skull measurements were negatively correlated with annual mean temperature, and the maximum Pearson correlation coefficient between LDL and annual mean temperature was -0.772.

Nineteen skull measurements were negatively correlated with annual precipitation; the maximum Pearson correlation coefficient between LDL and annual mean temperature was -0.760. Some of the skull measurements highly correlated annual mean temperature and annual precipitation were CB, CH, ZB, OWU.

DISCUSSION

Skull differences between males and females

We have shown that four zokor species had differences between males and females, however, the most important differences were related to skull size. We also found that *E. cansus*, *E. rothschildi*, and *M. aspalax* were with sexual size dimorphisms (SSD) because there are significant differences between males and females in most measurements of these three species. Sexual size dimorphism (SSD) is a common phenomenon in the natural world (Han and Fu, 2013; Noonan *et al.*, 2016). Males and females of the same species are different in many morphological aspects, and they have different physiological characteristics (Ralls, 1977; Fairbairn and Roff, 2006). These differences include body size (Rudoy and Ribera, 2017), sexual organs (Glucksmann, 1974), behaviors (Turgeon *et al.*, 2016), and even hair color (Cooper *et al.*, 2016). Sex size dimorphism include different types, male-biased sex size dimorphism (MBSSD) and female-biased sex size dimorphism (FBSSD) (Wu *et al.*, 2014). MBSSD can be seen in most mammals, represented by the body size of males being larger than that of females (Kinahan *et al.*, 2007; Hudson and Fu, 2013). In this study, a male-biased SSD (MBSSD) could be seen in all of the species we studied except *E. baileyi* because the male skulls were larger than the female skulls. The MBSSD of zokor found in this study and in previous study (Su *et al.*, 2017) indicated that the sex of zokor could be inferred roughly based on body size which could be inferred from skulls.

The sexual selection hypothesis provides one reasonable explanation for MBSSD, suggesting that large males might compete more effectively for mating opportunities and thus obtain better reproductive success (Blanckenhorn *et al.*, 2007; Stillwell *et al.*, 2010). On the other hand, "increased-energy" hypothesis (Shillington and Peterson, 2002) may explain the MBSSD in zokors (Su *et al.*, 2018). This hypothesis was originally explained by Bergmann (1847): animals in cold regions have been observed to be bulkier than individuals of the

same species in warm regions because larger bodies can conserve energy more competently due to their smaller surface-to-volume ratio. For zokors, males and females often live alone. Males dig tunnels intercepting with the female burrows during breeding seasons (Zhang, 2007). Furthermore, the home range of male zokors (1790 ± 720 m²) is significantly larger than that of females (260 ± 112 m²; Zhang *et al.*, 1993); These activities in male zokors, such as extra digging (Zhang, 2007), longer digging time (Wang *et al.*, 2000) and home range keeping increase the energy expenditure. These behavioral differences between two sexes may result in more energetically demands of males, which generate selective pressures on male traits of morphology. Therefore, a functional evolutionary mechanism by increasing body and skull size might be not only beneficial to males to conserve energy expenditure but also enables them to efficiently perform their various daily life tasks.

Similar studies confirmed that MBSSD exists in *E. baileyi* (Tang *et al.*, 2009; Su *et al.*, 2017), in *E. cansus* (Lu *et al.*, 2013) and in *M. aspalax* (Bazhenov, 2017). However, distinct SSD was not found in *E. baileyi* in this study, due to the small sample size of this species. More samples of *E. baileyi* should be collected to verify the above conclusion in future research.

Skull differences among four species of zokors

We have shown that three linear measurements (Cranial length, basal length and cranial base) are needed to distinguish between four common species of zokor. The result of PCA has shown that the measurements which contribute to the first principal component mainly related to skull size, which was proved to be positively correlated to body size (Su *et al.*, 2018). It is indicated that the measurements which reflect skull size could be key measurements of morphology. This view is confirmed again based on the selection of key measurements. Cranial length (CL), basal length (BL) and cranial base (CB) could be key measurement for cluster and classification. However, the measurements which contribute the most to the second principal component were different between sexes. The shape of molars and auditory bulla were more important in males. Longer checktooth row and diastema might increase oral cavity volume and be beneficial to digest more plants which meet the needs of more energy of males. Auditory bulla was related to audition (Zhu, 2014), which may be more important in males when they intercepting with the female burrows during breeding seasons. Although zokor has weak vision, its visual system was sensitive to light (Du, 2005). Visual range might be more important in females because females were more aggressive and defensive than males during breeding

seasons (Li *et al.*, 2001). The least space between forehead crest (SFC) might be beneficial to explore the common features among female zokor species, which might be indicators to differentiate zokor from its closely-related species. Although the sample size of *E. rothschildi* was small, we could tell the *E. rothschildi* from another three species based on skull morphology because *E. rothschildi* has the smallest skull size. Compared the differences between *M. aspalax* and *E. cansus*, we have found that the skull of *E. cansus* was more slender than that of *M. aspalax*. This characteristic might be the basis for distinguishing between these two species, which could be measured by ZB, LLC, LUC, OWU and BNB (Figs. 2, 3).

In this study, we have found further evidence of correlations between environmental factors of habitation and morphological differentiation for each zokor species. The morphological differences of zokors are thought to be closely related to climatic and geographical factors (Su *et al.*, 2018; Kang, 2018). Environment is one of the important factors related to morphological variation of organism: to adapt to a living environment, each species might show corresponding geographical differentiation with various aspects of different environmental factors such as climate, soil, and food resources (Geng *et al.*, 2012). *E. baileyi* and *M. aspalax* belong to different genera, and their living environment are also different. *E. baileyi* is endemic to the Qinghai-Tibet Plateau, at high altitudes from 2800-4200m (Fan and Shi, 1982; Zhang and Liu, 2002). *M. aspalax* live mainly in the grasslands, farmlands, and semi-desert areas with lower elevations (Bazhenov, 2017). The cluster analysis of these two species of zokors indicates that they share morphological similarities, such as larger skulls and smaller molars. Combined with climatic and geographical data in Table I, it can be seen that both of their habitats are similar in some aspects such as relatively high latitude, low annual mean temperature, scarce precipitation, and a shortage of food resources. Thus, a specialization may be occurred in morphology, such as the larger body size and the smaller relative surface area, so that heat loss per unit body weight could be decreased as an adaptation to the cold environment. This convergence also follows Bergmann's rule (Bergmann, 1847). Besides, twenty skull measurements were negatively correlated with annual mean temperature, it is suggested that the temperature might be one of the factors influencing skull size. Additionally, there were scarce precipitation (Table I) and hard soils in the habitats of these two species, making it likely difficult for them to dig tunnels (Su *et al.*, 2018). This pressure requires the skulls to adapt by changing the skull shape from wide and short to long because zokor often moves the soil to the ground surface by snout during digging (Li and Wang, 1996; Zhang *et al.*, 2003; Wang and Fan, 1987).

It is demonstrated that the skulls morphology of some subterranean rodents were related to soil hardness (Marcy *et al.*, 2016; Borges *et al.*, 2017). It could also occur in zokor because hard soil might be related to larger skull (Su *et al.*, 2018). This hypothesis is supported by the cranial length and cranial base being larger in *E. baileyi* and *M. aspalax*. However, the molars of *E. baileyi* and *M. aspalax* were smaller than those of *E. cansus* and *E. rothschildi* because *E. cansus* has the largest molars relative to other three species of zokors. Molars are used to grind down the food (Kay, 1975), it is speculated that the food resources of *E. cansus* were relatively abundant so that larger molars were more suitable for higher-proportioned cellulose in the roots and leaves of plants.

Most of measurements of *E. cansus* were significantly larger than those of *E. rothschildi*, whose skull was the smallest of the four species examined in this study. This finding is consistent with previous results that *E. rothschildi* was the smallest species in *Eospalax*, *i.e.*, with smaller skulls and a significantly smaller body size than other species in *Eospalax* (Li and Chen, 1992; Li and Wang, 1996). In the sampling process, we also found that the body size and skull of *E. rothschildi* was significantly smaller than that of other species of zokors. *E. rothschildi* lived in Qinba Mountain area, which was a habitat with high annual mean temperature, plentiful rainfall, mixed evergreen and deciduous broad-leaved forest, and soft soil. In these conditions, it was relatively easy for zokors to dig tunnels (Fan and Shi, 1982). As a result, the skull of *E. rothschildi* might be relatively smaller (Su *et al.*, 2018). Due to its small body size, flexible body, and large area of heat dissipation, *E. rothschildi* could adapt to the environment with abundant food resources and a warm and humid climate (Li and Chen, 1986).

In this study, zygomatic breadth (ZB) could be considered as quantifiable differences between the two genera *Eospalax* and *Myospalax* because zygomatic breadth of *M. aspalax* were larger than those of another three species in both sexes. The genus *Eospalax* was distinctly different from *Myospalax* due to the protrusion of the occipital. The posterior skull of species of *Myospalax* is truncated. The posterior skull of species of *Eospalax* was not truncated, but sloped back obliquely and turned downwards (Li, 1995). This is the most typical characteristic of the two genera *Eospalax* and *Myospalax*. However, these characteristics have not been quantified into specific or measurable measurements. As a result, the conclusions of this study can provide a reference for the further classification of *Eospalax* and *Myospalax* species. To make our results more reliable, more samples of *E. rothschildi* and *E. baileyi* should be collected and supplemented in future studies. In addition,

more morphological measurements with good characters for classification need to be explored and qualified to serve as the basis for the future research on classification and evolution.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animal were followed.

Supplementary material

There is supplementary material associated with this article. Access the material online at: <https://dx.doi.org/10.17582/journal.pjz/20200422090410>

Statement of conflict of interest

The authors have declared no conflict of interests.

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