



Geometric Morphometry of Skulls Characteristics of Nine Species of *Eothenomys*

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ABSTRACT

Eothenomys were the inherent species in Hengduan Mountains region, which had special status in *Microtus*, Arvicolinae. In order to investigate the geometric morphometrics of the craniums and mandible in nine species of *Eothenomys* (*E. fidelis*, *E. melanogaster*, *E. chinensis*, *E. proditor*, *E. custos*, *E. cachinus*, *E. eleusis*, *E. miletus* and *E. olitor*), ANOVA analyses, principal components analysis, thin plate spline, UPGMA and Multidimensional Scaling were used. The results showed that there had significant differences in skull shapes of centroid size in *Eothenomys*. Orbital cavity and alveolar region had significant differences in intraspecific skulls, some differences were shown in interspecific skulls, such as the point between the anterior tip of suture nasal and premaxilla, anterior tip of suture between nasal and premaxilla, anterior and posterior most ventral points of the upper incisor alveolus, and coronoid process, angular process ascending ramus and condylar process on the mandible. The genus *Eothenomys* could be classified into two subgenera. Moreover, it was inferred that the varieties of skulls characteristics in *E. miletus*, *E. eleusis*, *E. cachinus* and *E. melanogaster* were main influenced by temperature and humidity; *E. olitor*, *E. custos* and *E. chinensis* were main influenced by diet. Thus, the environmental factors (temperature, humidity and diet) may lead to the difference of geometric morphometry of skulls characteristics in *Eothenomys*.

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Authors' Contribution

WLZ conceived of the study and participated in its design, coordination and drafted the manuscript. XYR and DZ carried out the morphometry of skulls characteristics and drafted the manuscript.

Key words

Geometric morphometric, Cranium, Mandible, *Eothenomys*, Ecological adaptation.

INTRODUCTION

Morphological characteristics of small mammals were variable and likely to be affected by age or geographic factors, such as altitudinal and latitudinal (Renaud *et al.*, 2010). Previously studies showed that there had geographical gradients of cranial (Fadda and Corti, 2001), mandibular (Duarte *et al.*, 2000) and dental shape (Renaud, 1999) in mammals. Taxonomic differentiations were commonly associated with morphological divergences (Renaud and Michaux, 2003); now more and more geometric morphometry variations of skulls were reported (Auffray *et al.*, 2009; Renaud and Auffray, 2010).

Morphometrics is a method for the quantitative description, variation, analysis and interpretation of shape, which is a fundamental area of research in biology (Rohlf, 1990; Meng *et al.*, 2018). Unlike the traditional approaches, the geometric method is aimed at comparison of the shapes themselves (Pavlinov, 2001). Traditional morphometrics were restricted to univariate comparisons of individuals' linear measurements to bivariate plots (Janzekovic and

Krystufek, 2004). The geometric morphometric techniques have several advantages over the traditional approaches (Hautier *et al.*, 2009; Auffray *et al.*, 2009), which used all the information available about the land mark location, while adhering to the geometric definition of shape rigorously (Loy *et al.*, 1996). Land marks of homologous points allow the visualization of shape changes among samples (Capanna *et al.*, 1996).

Eothenomys were the inherent species in Hengduan Mountains region (Zheng, 1993), which had special status in *Microtus*, Arvicolinae. *Eothenomys* were useful for palaeoecological, palaeoclimatical, palaeogeographical and evolutionary indicators because they had abundant in fossil and archaeological records (Andrews, 1990). Still now, it is not possible to accurately identify all species in *Eothenomys* by using traditional methods. There were still several unsolved problems in the taxonomy of *Eothenomys* and this leads to search for different methods such as DNA studies (Luo *et al.*, 2004) or karyotypes (Ma and Jiang, 1996). In order to investigate the geometric morphometrics of the craniums and mandible in nine species of *Eothenomys* (*E. fidelis*, *E. melanogaster*, *E. chinensis*, *E. proditor*, *E. custos*, *E. cachinus*, *E. eleusis*, *E. miletus* and *E. olitor*), ANOVA analyses, principal components analysis, thin plate spline, UPGMA and Multidimensional

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Scaling were used in the present study. We hypothesized that there may had differences of skulls characteristics of nine species of *Eothenomys*, and these difference of geometric morphometry of skulls characteristics were mainly for adaptation to their habitats, respectively.

MATERIALS AND METHODS

Samples

All specimens used in the present study were from the Kunming Institute of Zoology. 179 skulls were photographed with a Nikon camera, the crania and mandibles were analyzed separately, 469 photographs were taken and subsequently analyzed (Table I). Different landmark numbers were used to describe the configurations of the skulls (Table II).

Measurement of skulls characteristics

Landmarks were digitized on standardized pictures of the dorsal, lateral and ventral views of the cranium, and latera view of the mandibles (Fig. 1). Landmarks were marked on the digital picture of skull using TPSDIG2 (Rohlf, 1990; Rohlf and Slice, 1990). In order to avoid bias due to measurement errors, each sample was measured sixth independently. All the landmarks showed good repeatability.

Statistical analysis

Group differences of the morphometric variables were performed by ANOVA analyses with SPSS (13.0). Principal component analysis (PCA) was applied to

investigate phenetic relationships. Shape differences were visualized with transformation grids using thin plate spline (TPS) algorithm (Bookstein, 1991). Pair-wise procrustes distances were calculated between group averages using Morphologika² v2.5 program. Procrustes distance matrix was served as the basis to calculate a similarity tree using the UPGMA method in the PHYLIP program package (Felsenstein, 2009). Multidimensional Scaling, weight matrix and Hierarchical Cluster analysis were used whole skull shapes of nine species with four faces.

Table I.- Numbers of samples examined from different species.

	Cranium			Mandibles
	Dorsal	Lateral	Ventral	
<i>E. miletus</i>	15	11	14	9
<i>E. olitor</i>	1	1	1	1
<i>E. proditor</i>	5	5	6	4
<i>E. custos</i>	4	5	5	5
<i>E. chinensis</i>	4	4	3	2
<i>E. cachinus</i>	21	6	6	2
<i>E. melanogaster</i>	29	26	63	32
<i>E. eleusis</i>	35	31	59	37
<i>E. fidelis</i>	5	4	5	3

Table II.- Numbers of landmark.

	Cranium			Mandibles
	Dorsal	Lateral	Dorsal	
No.	26	30	36	16



Fig. 1. Different view of *Eothenomys* cranium and mandible with landmarks.

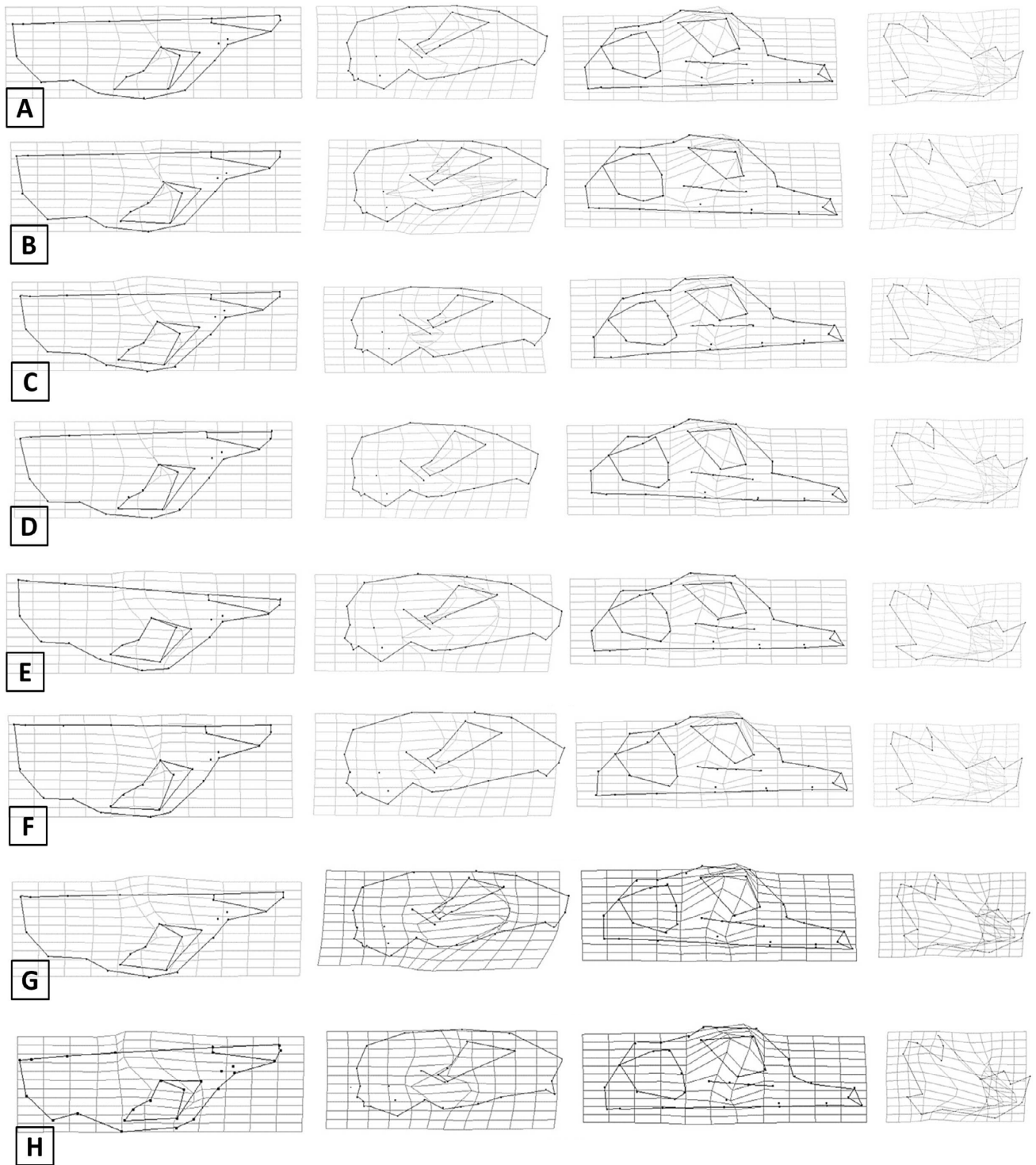


Fig. 2. Deformation grids on four faces were generated thin plate spline (TPS) algorithm, which show the shape differences associated with the particular canonical variate in different species. A, *E. fidelis*; B, *E. melanogaster*; C, *E. chinensis*; D, *E. proditor*; E, *E. custos*; F, *E. cachinus*; G, *E. eleusis*; H, *E. miletus*.

RESULTS

ANOVA analyses showed that there had significant differences in skull shape among species in centroid size (Table III). Principal component analysis also showed that significant differences were found among nine species. On the dorsal view of the cranium, the first and second PC cumulative variance explained 86%, *E. melanogaster* is clearly separated from all other species. On the lateral view of the cranium, the first and second PC cumulative variance explained 86%, which was classified into two parts, one part included *E. eleusis*, *E. cachinus* and *E. miletus*, another part included *E. melanogaster*, *E. custor*, *E. fidelis* and *E. proditor*. On the ventral view of the cranium, the first and second PC cumulative variance explained 87%; *E. melanogaster* is clearly separated from all other species. On the lateral view of the mandibles, the

first and second PC cumulative variance explained 82%, *E. miletus*, *E. melanogaster* and *E. chinensis* were clearly identifiable. Thin plate spline (TPS) analysis showed that the shape differences associated with the particular canonical variety in different species, which were mostly in orbital cavity and alveolar region (Fig. 2).

Table III.- ANOVA for the cranial size of *Eothenomys* (significant values are in *italics*).

		Sum of squares	df	F	P
Cranium	Dorsal	2164573	8	22.435	0.000
	Lateral	543761.9	8	9.367	0.000
	Ventral	2158279	8	11.730	0.000
Mandibles		271992.1	8	4.998	0.000

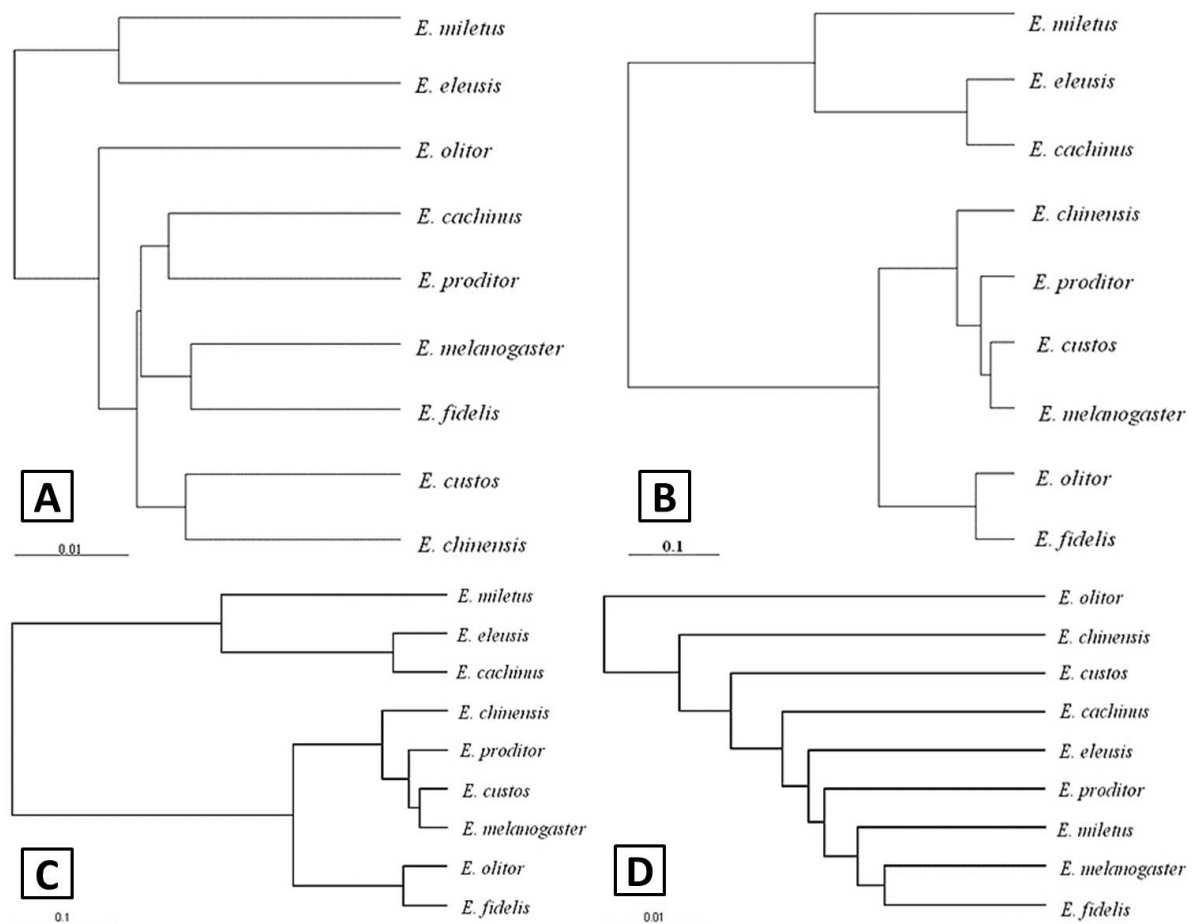


Fig. 3. UPGMA trees showing morphometric affinity among populations calculated from pair-wise procrustes distances between consensus configurations of each species. A, similarities based on the dorsal view of the cranium; B, similarities based on the lateral view of the cranium; C, similarities based on the ventral view of the cranium, D, similarities based on the mandible. The below line was mean procrustes distances.

The similarity three trees showed that *E. miletus* and *E. eleusis* were more closely (Fig. 3A, B, C), *E. melanogaster* and *E. fidelis* were gathered together (Fig. 3A, C), *E. melanogaster* and *E. custos* were gathered together, *E. fidelis* and *E. olitor* were gathered together (Fig. 3B, D). In Multidimensional Scaling analysis, *E. fidelis*, *E. proditor*, *E. olitor*, *E. custos* and *E. chinensis* were above the diagonal (between Dimension 1 and 2); *E. miletus*, *E. eleusis*, *E. cachinus* and *E. melanogaster* were below the diagonal (Fig. 4). Dimension weights plot caudated from weight matrix analyze was revealed that varieties of ventral of the cranium and mandible had effects on Dimension 2, and varieties of lateral and dorsal of the cranium had effects on Dimension 1 (Fig. 5).

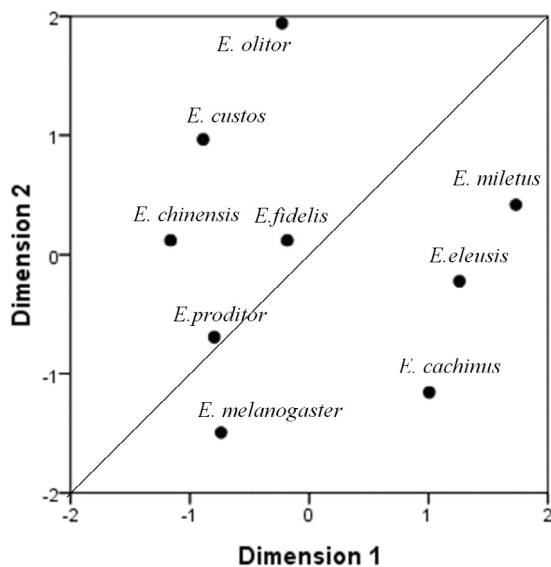


Fig. 4. Scatter plot of Multidimensional Scaling analyzes, using whole skull shape of nine species with four faces.

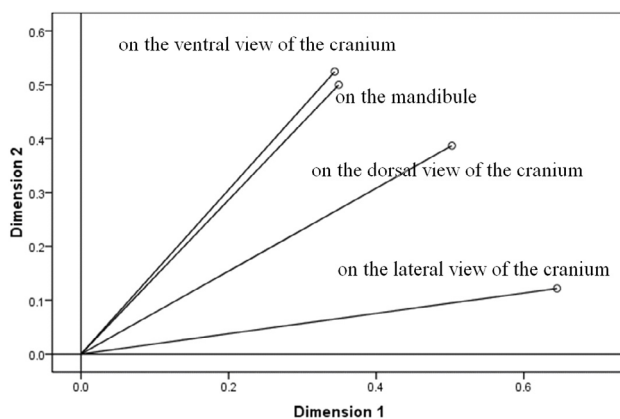


Fig. 5. Plot of dimension weights, using whole skull shape of nine species with four faces.

DISCUSSION

The relationship between taxonomy and geometric morphological characteristics

The classification and identification of the genus *Eothenomys* remained confusion, which was especially typical in the classification studies on this genus. It had been identified as *Clethrionomys rufocanus*: *Clethrionomys* and the *Eothenomys/Caryomys* complex (Hinton, 1926; Allen, 1940; Jones and Johnson, 1965). Allen (1940) further classified the genus *Eothenomys* into three subgenera: *Eothenomys*, *Antelionomys* and *Caryomys*. Musser and Carleton (1993) pointed that *Eothenomys* were reassigned to a genus independently. Wang and Li (2000) classified only two subgenera in *Eothenomys*, *Eothenomys* and *Antelionomys*. In the present study, UPGMA trees showed that the genus *Eothenomys* may classified into two subgenera. In Multidimensional Scaling analysis, *E. fidelis*, *E. proditor*, *E. olitor*, *E. custos* and *E. chinensis* were above the diagonal; *E. miletus*, *E. eleusis*, *E. cachinus* and *E. melanogaster* were below the diagonal, suggesting that the genus *Eothenomys* could classified into two subgenera, which supported the results for Wang and Li (2000).

Historically, genus *Eothenomys* included 14 species, as described by Milne-Edwards (1872), Thomas (1911a, b, 1914, 1921), Allen (1912), Cabrera (1922), Hinton (1923), Tokuda and Kano (1937) and Wang and Li (2000). Furthermore, it was debated about 9 species: *E. shaneius*, *E. regulus*, *E. lemminus*, *E. andersoni*, *E. smithii*, *E. wardi*, *E. fidelis*, *E. Eva* and *E. inez* (Liu and Liu, 2005). Hinton (1923) regarded *Eothenomys* as a distinct genus and described *E. fidelis*. Allen (1924) renamed *Microtus fidelis*. Wang and Li (2000) used *E. fidelis* as a synonym of *E. miletus*. Wang (2003) recognized *E. fidelis* was a distinct species. In the present study, the results showed that only *E. melanogaster* is clearly separated from all other species on cranium and mandible using by principal component analysis. Overlapping is visible between *E. fidelis* and *E. chinensis*, *E. proditor* and *E. miletus* on the dorsal view of the cranium, but *E. miletus* and *E. fidelis* separated clearly from each other as on the lateral view of the cranium. According to UPGMA trees, *E. miletus* appeared to separate from *E. fidelis*, which supported the results those of Wang (2003).

Based on UPGMA trees, *E. miletus* and *E. eleusis* appeared to be more closely related to others (Fig. 3). Although *E. eleusis* and *E. miletus* were proposed as separate subspecies or species (Allen, 1940; Hinton, 1923; Musser and Carleton, 1993; Thomas, 1912a, b; Wang and Li, 2000), the cyt b sequences from these two species were nearly identical (Luo et al., 2004). But Multidimensional Scaling analyzes revealed that they had some distance.

Anterior ventral points of the upper incisor alveolus of *E. miletus* was different from *E. eleusis*. ANOVA analyses showed that significant differences in skull shape were found among species in centroid size. As noted earlier, the radiation of Oriental voles were probably recent, and most likely began about 2 Mya according to the fossil record (Zheng, 1993). The environment can interact to various degrees in mandible morphology (Renaud and Millien, 2001). Based on the above researches, we inferred that the radiation of *E. miletus* and *E. eleusis* began to radiation recently.

The relationship between environment and geometric morphological characteristics

The random differentiation associated with environment were observed in cranial (Fadda and Corti, 2001), mandibular (Duarte *et al.*, 2000; Renaud and Auffray, 2010) and dental shape differentiation (Renaud, 1999; Hautier *et al.*, 2007), geographical gradients (Renaud and Millien, 2001). Shapes in European wood mouse had a latitudinal gradient changing (Renaud and Michaux, 2003; Renaud *et al.*, 2005). *Eothenomys* has been recorded near Trans-Himalayan Tange includes various north-south extending ranges and adjacent mountainous areas on the east skirts of the Qinghai-Tibetan Plateau. The geological configuration of this area was complicated (Li and Wang, 1986). In the present study, skull shapes in *E. melanogaster* was rather smaller, and *E. chinensis* was larger, which was supported for Bergmann's rule (Bergmann, 1847; Mayr, 1942). Moreover, variations of environment could influence the centroid size of *Eothenomys*. On the mandible, *E. proditor* had a higher centroid size, *E. proditor* has been recorded from woodland and meadow around 2800-4200m (Luo *et al.*, 2004), which was inhabited the highest altitude among *Eothenomys*, and the food quality was lower. Other study showed that the intergeneric comparisons between mandible shapes suggested that the latitudinal change in morphology observed within the wood mice may be related to change in diet (Renaud and Michaux, 2003). So, *E. proditor* should diversify their shape of mandible in order to maintain its high-energy demand.

Using thin plate spline analysis, significant morphological differentiations were shown for both orbital cavity and alveolar region in intraspecific skulls. And some differences were interspecific character, such as the point between the anterior tip of suture nasal and premaxilla, anterior tip of suture between nasal and premaxilla, anterior and posterior most ventral points of the upper incisor alveolus, and coronoid process, angular process ascending ramus and condylar process. The main function of the nose is helping animal to breathe. When animal inhale through their nose, air passes through nostrils

into a short and narrow area known as the nasal passage that leads to the back of the pharynx, and down into the windpipe and lungs. The external air that we breathe is also warmed and moistened as it passes through the nose. Therefore, the main difference of interspecies was nasal bone, which may reflect adaptations to temperature and humidity. However, the different of nose could view on lateral and dorsal of cranium, which have a main effect on Dimension 1 in Multidimensional Scaling analysis, and *E. miletus*, *E. eleusis*, *E. cachinus* and *E. melanogaster* were below the diagonal, so it may imply that speciation of four species were main affected by temperature and humidity. Change of premaxilla and mandible were interacted to the quality diet (Renaud and Michaux, 2003, 2007; Duarte *et al.*, 2000; Renaud and Millien, 2001), varieties of ventral of the cranium and mandible had effects on Dimension 2, which may imply that *E. olitor*, *E. custos* and *E. chinensis* were affected by diet quality.

CONCLUSION

In conclusion, there had significant differences in skull shapes of centroid size in *Eothenomys*. The genus *Eothenomys* could be classified into two subgenera. Moreover, the environmental factors (temperature, humidity and diet) may lead to the difference of geometric morphometry of skulls characteristics in *Eothenomys*.

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Statement of conflict of interests

The authors declare that they have no competing interests.

REFERENCE

- Allen, G.M., 1912. Some Chinese vertebrates, Mammalia. *Mem. Mus. Comp. Zool. Harvard College*, **40**: 201-247.
- Allen, G.M., 1924. Microtinae collected by the Asian expedition. *Am. Mus. Nov.*, **133**: 1-13.
- Allen, G.M., 1940. The mammals of China and Mongolia, Part II. *Am. Mus. Nat. Hist.*, **2**: 820-823.
- Andrews, P., 1990. *Owls, caves and fossils*. University of Chicago Press, pp. 196.

- Auffray, J.C., Renaud, S. and Claude, J., 2009. Rodent biodiversity in changing environment. *Kasetsart J.*, **43**: 83-93.
- Bergmann, C., 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Götting. Stud.*, **3**: 595-708.
- Bookstein, F.L., 1991. *Morphometric tools for landmark data*. Cambridge University Press, Cambridge, pp. 435.
- Cabrera, A., 1922. Sobre algunos mamíferos de la China oriental. *Bol. Teal Soc. Españ. Hist. Nat.*, **22**: 162-170.
- Capanna, E., Bekele, A., Capula, M., Castiglia, R., Civitelli, M.V., Codjla, J.T.C. and Fadda, C., 1996. A multidisciplinary approach to the systematics of the genus *Arvicanthis* Leson, 1842 (Rodentia, Murinae). *Mammalia*, **60**: 677-696. <https://doi.org/10.1515/mamm.1996.60.4.677>
- Duarte, L.C., Monteiro, L.R., Von-Zuben, F.J. and Dos-Reis, S.F., 2000. Variation in the mandible shape in *Thrichomys apereoides* (Mammalia: Rodentia): Geometric analysis of a complex morphological structure. *Syst. Biol.*, **49**: 563-578. <https://doi.org/10.1080/10635159950127394>
- Fadda, C. and Corti, M., 2001. Three-dimensional geometric morphometrics of *Arvicanthis*: Implications for systematics and taxonomy. *J. Zool. System. Evolut. Res.*, **39**: 235-245.
- Felsenstein, J., 2009. *PHYMLIP: Phylogeny interface package*, Version 3.69. University of Washington, Seattle, Washington.
- Hautier, L., Bover, P., Alcover, J.A. and Michaux, J., 2007. Microwear pattern, and paleobiology of the extinct Balearic dormouse *Hypnomys morpheus*. *J. Mammal. Evolut.*, **14**: 205-207.
- Hautier, L., Bover, P., Alcover, J.A. and Michaux, J., 2009. Mandible morphometrics, dental microwear pattern, and palaeobiology of the extinct Balearic dormouse *Hypnomys morpheus*. *Acta Palaeontol. Polon.*, **54**: 181-194. <https://doi.org/10.4202/app.2008.0001>
- Hinton, M.A.C., 1923. On the voles collected by Mr. G. Forrest in Yunnan; with remarks upon the genera *Eothenomys* and *Neodon* and upon their allies. *Annls. Mag. Nat. Hist.*, **9**: 145-162. <https://doi.org/10.1080/00222932308632833>
- Hinton, M.A.C., 1926. Monograph of the voles and lemmings (*Microtinae*), living and extinct. *Br. Mus. Nat. Hist.*, **2**: 251-257.
- Janzekovic, F. and Krystufek, B., 2004. Geometric morphometry of the upper molars in European wood mice *Apodemus*. *Folia Zool.*, **53**: 47-55.
- Jones, J.K. and Johnson, D.H., 1965. Synopsis of the lagomorphs and rodents of Korea. *Univ. Kansas Publ. Mus. Nat. Hist.*, **16**: 257-407.
- Loy, A., Dimartion, S. and Capolongo, D., 1996. Patterns of geographic variation of *Talpa romana* (Insectivora, Talpidae). Preliminary result derived from a geometric morphometrics approach. *Mammalia*, **60**: 77-89. <https://doi.org/10.1515/mamm.1996.60.1.77>
- Li, B.Y. and Wang, F.B., 1986. *Basic characteristics of landforms in the northwest Yunnan and southwest Sichuan area*. Beijing Science and Technology Press, Beijing, pp. 174-183.
- Liu, S.Y. and Liu, Y., 2005. Summary of systematic study on *Eothenomys*. *Sichuan J. Zool.*, **24**: 98-103.
- Luo, J., Yang, D.G., Suzuki, H., Wang, Y.X., Chen, W.J., Campbell, K.L. and Zhang, Y.P., 2004. Molecular phylogeny and biogeography of Oriental voles: Genus *Eothenomys* (Muridar, Mammalia). *Mol. Phylogen. Evolut.*, **33**: 349-362. <https://doi.org/10.1016/j.ympev.2004.06.005>
- Ma, Y. and Jiang, J.Q., 1996. The reinstatement of the status of Genus *Caryomys* (Thomads, 1911) (Rodentia: Microtinae). *Acta Zootaxon. Sin.*, **21**: 493-496.
- Mayr, E., 1942. *Systematics and the origin of species*. Columbia University Press, New York, pp. 347-348.
- Meng, Y.X., Wang, G.H., Xiong, D.M., Liu, H.X., Liu, X.L., Wang, L.X. and Zhang, J.L., 2018. Geometric morphometric analysis of the morphological variation among three *Lenoks* of Genus *Brachymystax* in China. *Pakistan J. Zool.*, **50**: 885-895. <http://dx.doi.org/10.17582/journal.pjz/2018.50.3.885.895>
- Milne-Edwards, A., 1872. Description of mammals-footnotes. *Nouv. Arch. Mus. Hist. Nat. Paris*, **7**: 73-100.
- Musser, G.G. and Carleton, M.D., 1993. Family Muridae. In: *Mammal species of the world a taxonomic and geographic reference* (eds. D.E. Wilson and D.M. Reeder). Smithsonian Institution Press, Washington D.C. pp. 501-755.
- Pavlinov, I.Y., 2001. *Geometric morphometrics: A new analytical approach to comparison of digitized images*. Russian Academy of Sciences, pp. 41-90.
- Renaud, S., 1999. Size and shape variability in relation to species differences and climatic gradients in the African rodent *Oenomys*. *J. Biogeogr.*, **26**: 857-865. <https://doi.org/10.1046/j.1365-2699.1999.00327.x>
- Renaud, S. and Auffray, J.C., 2010. Adaptation and plasticity in insular evolution of the house mouse

- mandible. *J. Zool. System. Evolut. Res.*, **48**: 138-150.
- Renaud, S., León, M.P.D., Tafforeau, P. and Zollikofer, C., 2010. Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. *J. Anat.*, **216**: 368-380. <https://doi.org/10.1111/j.1469-7580.2009.01177.x>
- Renaud, S. and Michaux, J., 2003. Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *J. Biogeogr.*, **30**: 1617-1628. <https://doi.org/10.1046/j.1365-2699.2003.00932.x>
- Renaud, S., Michaux, J., Schmidt, D.D., Aguilar, J.P., Mein, P. and Auffray, J.C., 2005. Morphological evolution, ecological diversification and climate change in rodents. *Proc. Biol. Sci.*, **272**: 609-617. <https://doi.org/10.1098/rspb.2004.2992>
- Renaud, S. and Michaux, J., 2007. Mandibles and molars of the wood mouse, *Apodemus sylvaticus*: Integrated latitudinal pattern and mosaic insular evolution. *J. Biogeogr.*, **34**: 339-355. <https://doi.org/10.1111/j.1365-2699.2006.01597.x>
- Renaud, S. and Millien, V., 2001. Intra- and interspecific morphological variation in the field mouse species *Apodemus argenteus* and *A. speciosus* in the Japanese archipelago: the role of insular isolation and biogeographic gradients. *Biol. J. Linn. Soc.*, **74**: 557-569. <https://doi.org/10.1111/j.1095-8312.2001.tb01413.x>
- Rohlf, F.J., 1990. *An overview of image processing and analysis techniques for morphometrics*. Proceedings of the Michigan Morphometrics Workshop, pp. 38-60.
- Rohlf, F.J. and Slice, D.E., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *System. Zool.*, **39**: 40-59. <https://doi.org/10.2307/2992207>
- Thomas, O., 1911a. New Asiatic Muridae. *Annls. Mag. Nat. Hist.*, **8**: 205-209. <https://doi.org/10.1080/00222931108692923>
- Thomas, O., 1911b. *The duke of Bedford's zoological exploration of eastern Asia. XIII. On mammals from the provinces of Kan-su and Sze-chwan, western China*. Proceedings of the Zoological Society of London, pp. 158-180.
- Thomas, O., 1912a. *The duke of Bedford's exploration of eastern Asia. XV. On mammals from the Provinces of Szechwan and Yunnan, western China*. Proceedings of the Zoological Society of London, pp. 127-141.
- Thomas, O., 1912b. On insectivores and rodents collected by Mr. F. Kingdon Ward in N.W. Yunnan. *Annls. Mag. Nat. Hist.*, **8**: 513-519. <https://doi.org/10.1080/00222931208693164>
- Thomas, O., 1914. Second list of small mammals from western Yunnan collected by Mr. F. Kindon Ward. *Annls. Mag. Nat. Hist.*, **8**: 472-475.
- Thomas, O., 1921. A new genus of opossum from southern Patagonia. *Annls. Mag. Nat. Hist.*, **8**: 136-139. <https://doi.org/10.1080/00222932108632494>
- Tokuda, M. and Kano, T., 1937. The alpine Murid of Formosa. *Bot. Zool.*, **5**: 1115-1122.
- Wang, Y.X., 2003. *A complete checklist of mammal species and subspecies in China, A taxonomic and geographic reference*. China Forestry Publishing House, Beijing, China, pp. 234-263.
- Wang, Y.X. and Li, C.Y., 2000. *Mammalia*, Vol. 6, *Rodentia*, Part III: *Cricetidae*. *Fauna sin.* Science Press, Beijing.
- Zheng, S.H., 1993. *Quaternary rodents of Sichuan-Guizhou area, China*. Science Press, Beijing, pp. 123-156.