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Source: Journal of Vertebrate Biology, 72(22066)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.22066

Journal of
Vertebrate Biology

Open Access

J. Vertebr. Biol. 2023, 72: 22066

DOI: 10.25225/jvb.22066

RESEARCH PAPER

Bone size and its effect on body mass in *Eothenomys miletus* from the Hengduan Mountain region

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▸ **Received 27 November 2022; Accepted 20 December 2022; Published online 31 January 2023**

Abstract. Morphological characteristics are closely related to habitat characteristics; habitat differences drive morphological differentiation, resulting in intraspecific and interspecific differences. In the present study, it was shown that body mass and body length in *Eothenomys miletus* from five regions: (Dali (DL), Jianchuan (JC), Lijiang (LJ), Xianggelila (XGLL) and Deqin (DQ)) of Hengduan Mountain, showed differentiation in bone morphological indices. The length of the sternum in *E. miletus* in JC is smaller than that in XGLL, and the length of the lumbar vertebrae is smaller than that in XGLL and DQ. The length of other trunk bones and limb bones of *E. miletus* in DL, JC and LJ at low latitudes and high temperatures were longer than in XGLL and DQ at high latitudes and low temperatures. Principal component analysis associated XGLL and DQ populations and cluster analysis divided the populations from five regions into two categories. The increase in bone length and mass correlated with increased body mass in *E. miletus*. Change in bone length does not conform to Bergmann's Law, which was affected by altitude, average annual temperature and latitude. Moreover, food, terrain, and living habits may also affect bone morphology in *E. miletus*.

Key words: Bergmann's law, Hengduan Mountain, morphological differentiation, bone

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Introduction

The body mass of mammals is affected by the interaction of genetic and environmental factors, with a series of genes and complex signal pathways in the body regulating the size and proliferation of cells, affecting the size of organs and tissues and thus influencing body mass (Galloni & Edgar 1999, Longo et al. 2004). The study of phenotypic differentiation effectively describes phylogenetic and taxonomic patterns (Boussange & Pellissier 2022). Morphological characteristics are closely related to habitat characteristics; habitat differences drive morphological differentiation, and this differentiation underpins intraspecific and interspecific differences (Cardini 2016, Shakya et al. 2022). The Hengduan Mountain region is a typical north-south oriented mountain range in China, with distinctive geological landforms and rich biodiversity (Wang et al. 2022). Due to its topology and geographical location, it has great significance in many disciplines, such as biology, geography, geology and hydrology, and represents one of the biodiversity hotspots of the world (Rana et al. 2022). The Yunnan red-backed vole, *Eothenomys miletus*, is an endemic species in the Hengduan Mountain region, where it lives in shallow tunnels. The Hengduan Mountain region has a changeable climate, rich vegetation and complex terrain, which provides conditions for the phenotypic differentiation and variation in body

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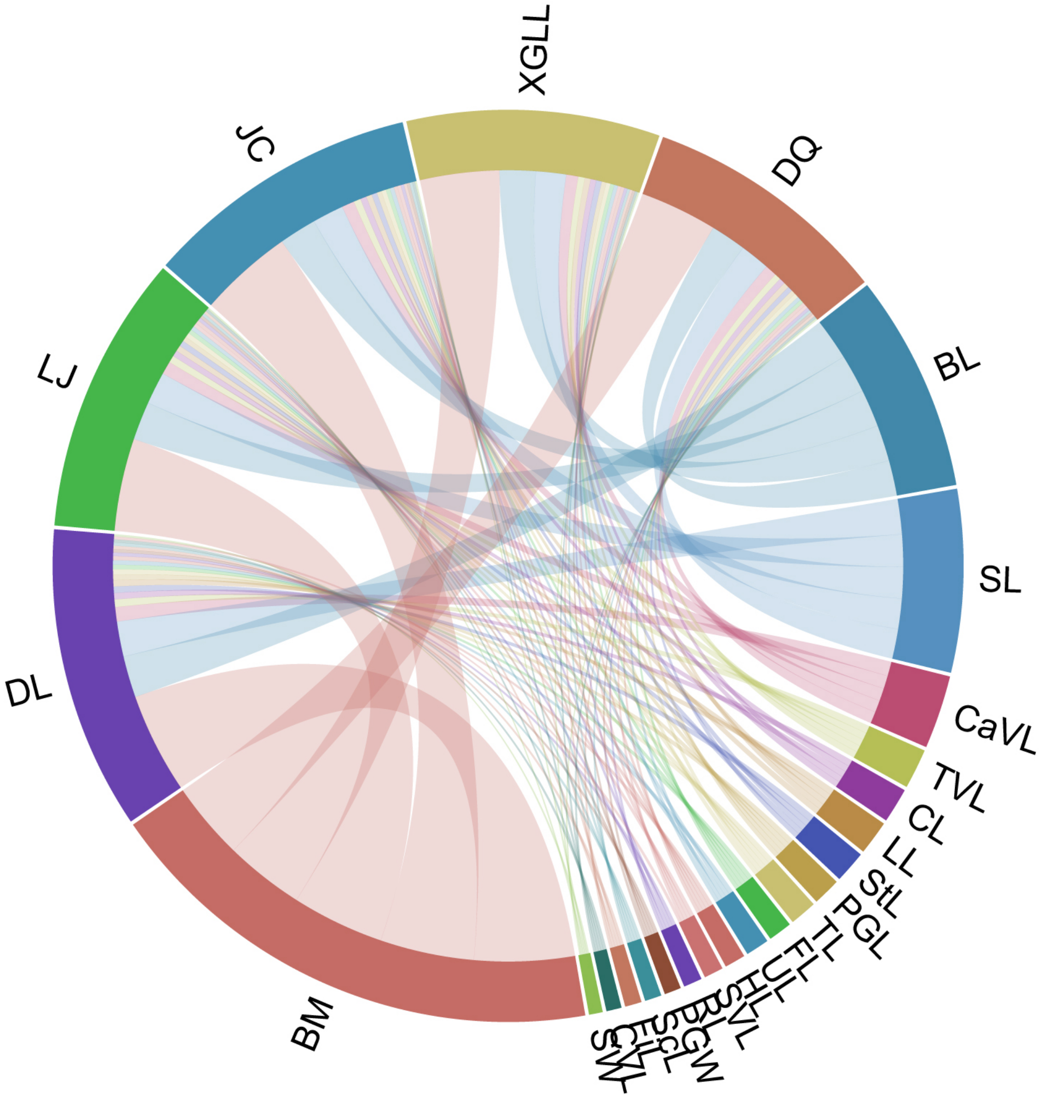

Fig. 1. Chord diagram of body mass, body length and bone length.

mass of *E. miletus* (Zhu et al. 2008). Previous studies showed that *E. miletus* inhabiting different regions of Hengduan Mountain were adapted to the different environmental conditions in the region through variation in body mass, liver mass, digestive tract mass and morphology (Zhang et al. 2018).

Bergmann's and Allen's Laws explain the phenotypic differentiation of thermoregulating animals in adapting to cold and hot environments. Bergmann's Law predicts that thermoregulating animals at high latitudes and in low-temperature environments will have larger body sizes and a reduced surface area, which is conducive to cold resistance. In contrast, thermoregulating animals at low latitudes and in high-temperature environments are predicted to have smaller body sizes and a relatively larger surface area conducive to heat dissipation (Bergmann 1847). Furthermore, as a derivation of Bergmann's Law, Allen's Law predicts that the limbs, tails or ears of thermoregulating animals will be larger as an additional adaptation to temperature regulation in warm climates (Allen 1877). Previous studies showed phenotypic differences in body indices and skull morphology in *E. miletus* from five regions in the Hengduan Mountain region. Variation in body size and skull characteristics in *E. miletus* was not consistent with Bergmann's Law, but the variation in its appendages conformed to Allen's Law (Ren et al. 2020a, b). However, the phenotypic differentiation in *E. miletus* mainly focused on the study of its skull morphology. At the same time, the morphological differentiation of the whole body skeleton will also affect the body mass of the entire organism. Some studies have shown that the bone morphology of Australian marsupials was significantly related to body mass, reflecting allometric growth (Martin et al. 2019). In general, with relatively long bones, the insertion area of muscles was relatively large, both bone weight and muscle volume affected the weight

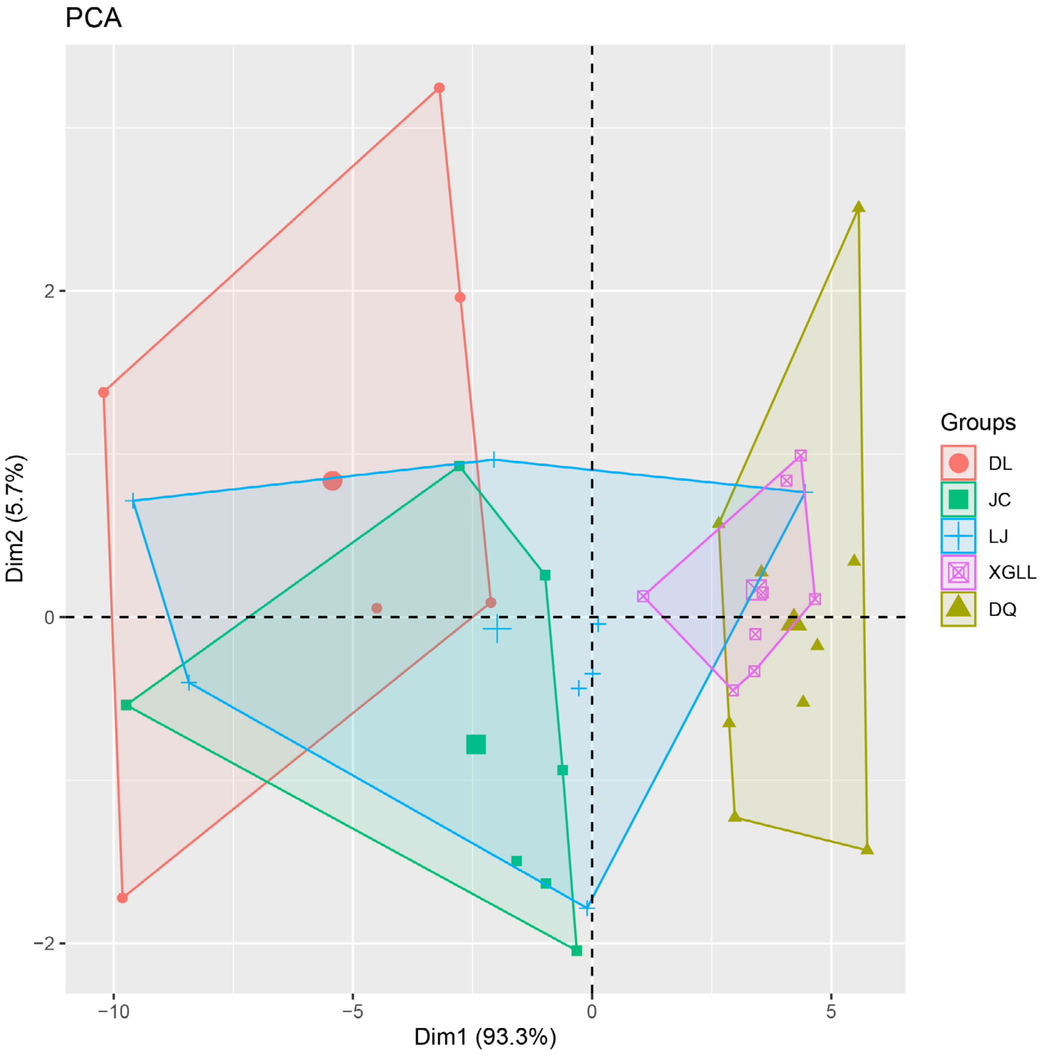

Fig. 2. Principal Component Analysis of body mass, body length and bone length.

of individuals, and stronger individuals had stronger limbs (Etienne et al. 2020, Zhou & Lui 2020). On this basis, the present study measured and analysed the whole-body bone indices in *E. miletus* to explore the influence of bone morphology on body shape and to test whether bone morphology indices conformed with Bergmann's Law in *E. miletus*.

Material and Methods

Samples

A total of 38 healthy, non-breeding adult *Eothenomys miletus* were captured in Dali (DL), Jianchuan (JC), Lijiang (LJ), Xianggelila (XGLL) and Deqin (DQ) from the Hengduan Mountain region in the summer of 2022. The sample number and climate characteristics of each sampling point are detailed in Table 1. The climatic data used in the analysis were for 2022 and were downloaded from the National Meteorological Science Data Center (http://data.cma.cn/).

Sample handling

The captured *E. miletus* were euthanised after weighing their body mass (BM) and body length (BL). Dissecting scissors and pointed nose tweezers were used to remove each animal's coat and large muscles. All internal organs were removed, with particular care taken to avoid bone damage (Lin 2017). The sample was placed in boiling water for 50 min, and the remaining muscle was carefully removed from the skeleton using tweezers and anatomical needles. After processing, bones were dried in an oven at 70 °C for 24 h (Wan et al. 2022).

Bone data measurement and calculation

Measurements were taken of cranial length (CL), spinal length (SL), cervical vertebra length (CVL), thoracic vertebra length (TVL), lumbar vertebra length (LL), sacral vertebra length (SVL), caudal vertebra length (CaVL), sternal length (StL), scapula length (ScL), scapula width (SW), pelvic girdle length

Table 1. Main condition for five populations of *Eothenomys miletus.*

Region	Sample number	Wind speed/ m/s	Altitude/m	Annual average temperature/°C	Latitude/°	Precipitation/mm
DL	6	1.88	2,217	19.70	24.90	597.00
JC	7	1.88	2,590	13.90	26.43	987.30
LJ	8	3.00	2,478	12.60	26.87	975.00
XGLL	8	1.13	3,321	5.50	27.90	984.20
DQ	9	2.13	3,459	4.70	28.35	633.70

(PGL), pelvic girdle width (PGW), humeral length (HL), radial length (RL), ulnar length (UL), femoral length (FL), tibial length (TL), fibular length (FiL), and ulnar olecranon length (UOL) (accurate to 0.01 cm); radial and ulnar middle width (URMW), humeral middle width (HMW), femoral middle width (FMW) and tibial and fibular middle width (TFMW) (Wi, accurate to 0.01 cm); ulnar and radial length (URL), humeral length, femoral length, tibial and fibular length (TFL) (Li, accurate to 0.01 cm); ulnar and radial mass, humeral mass, femoral mass, tibial and fibular mass (mi, accurate to 0.0001 g). Because the epiphysis of the two segments of the radius and ulna is conglutinated, when measuring the middle width, mass and length, it is treated as a single bone. The shape of the upper part of the tibia and fibula changes irregularly. Therefore, when measuring the thickness of the middle part, the two bone unions at the lower end are taken. Also, the shape of the upper part of the tibia and fibula changes irregularly. Therefore when measuring the middle width, the two bone unions at the lower end are taken. Based on these measurements, the following indices were calculated: 1) olecranon index: OI = ulnar olecranon length/ulna length (the olecranon is the insertion area of the triceps brachii, and the triceps brachii is the extensor of the upper arm. A high olecranon index means a strong stretching force of the forelimbs); 2) robust index: RI = W_i/L_i (the robust index represents the climbing and running ability of animals to a certain extent); 3) Weight percentage: $D_i = m_i/\sum_{i=1}^{4} m_i \times 100\%$ (Lin et al. 2007).

Statistical analysis

Differences in body mass and morphological indicators between the different sexes of *E. miletus* in the same region were not significant, so all data were pooled for analysis. The SPSS software package

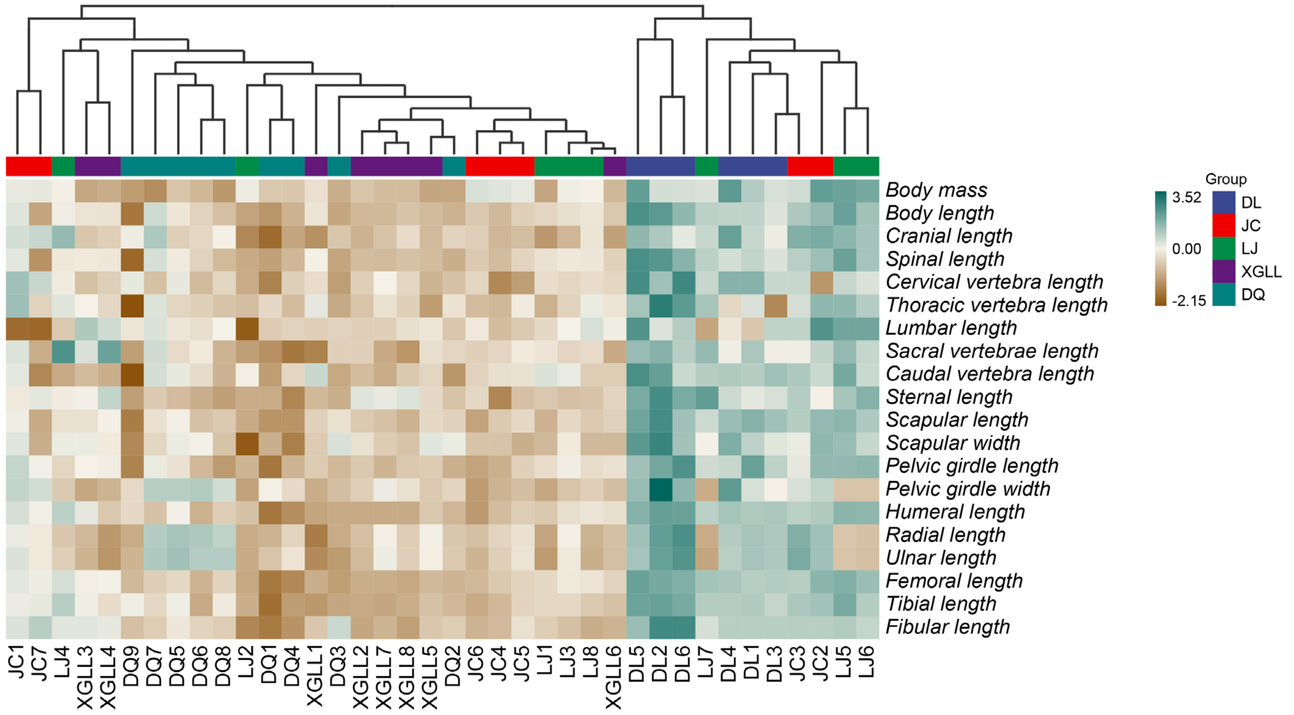

Fig. 3. Cluster analysis of body mass, body length and bone length.

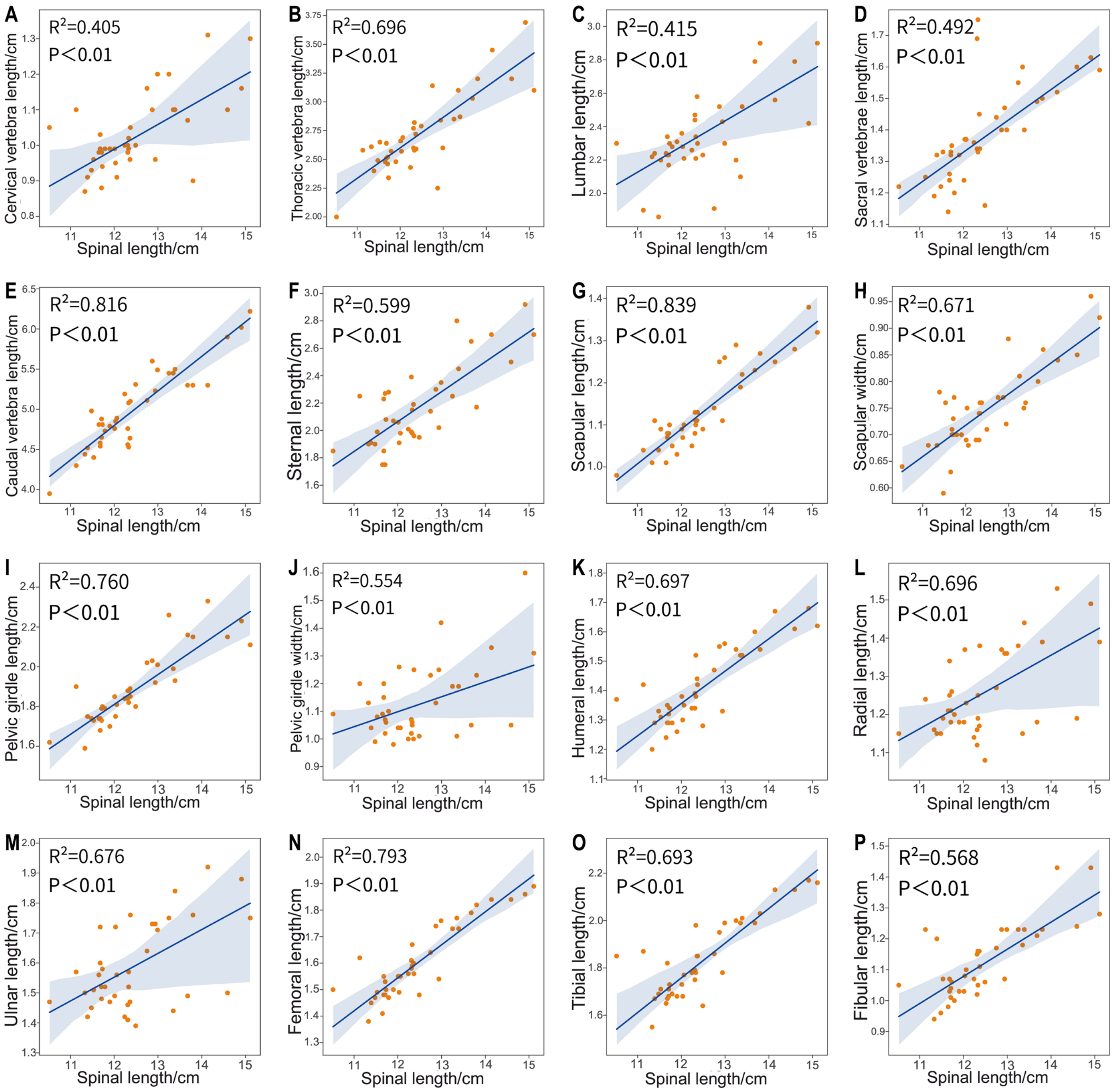

Fig. 4. Linear regression analysis of spine length and A) cervical vertebra length; B) thoracic vertebra length; C) lumbar length; D) sacral vertebrae length; E) caudal vertebra length; F) sternal length; G) scapular length; H) scapular width; I) pelvic girdle length; J) pelvic girdle width; K) humeral length; L) radial length; M) ulnar length; N) femoral length; O) tibial length; P) fibular length.

(ver. 26.0) was used to conduct ANOVA for body mass and body length, and one-way ANCOVA was conducted for 18 bone morphological indices, including cranial length and spine length, with body length as the covariate. Principal Component Analysis (PCA) and cluster analysis based on 20 groups of sample data were undertaken. Spearman's correlation was used to test the correlation of environmental variables with skeletal morphological indices, based on predictions of Bergmann's Law. Linear regression was used to calculate the relationship between spine length and 16 bone morphological indices, including the length of cervical vertebra and thoracic vertebra, as well as the relationship between total bone mass and body mass. Multiple linear regressions were used to examine the relationship of altitude, annual average temperature and temperature to bone morphological indices. Finally, regression coefficients were used to measure the influence of environmental factors on bone morphological indices. Kruskal-Wallis rank sum test and Dunn's test were used as post-hoc tests to identify differences in URMW, HMW, FMW, TTMW, URL, TFL, ulnar and radial sturdiness (URI), humeral sturdiness (HRI), femoral sturdiness (FRI), tibia and fibula sturdiness (TFRI), UOL, OI.

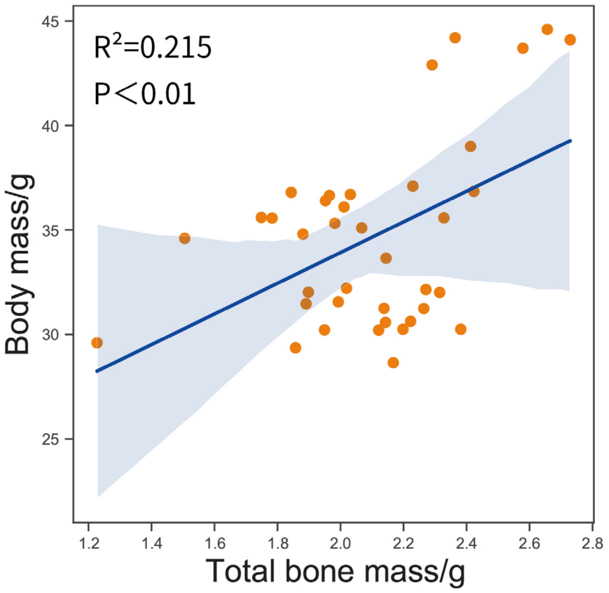

Fig. 5. Linear regression analysis of total bone mass and body mass.

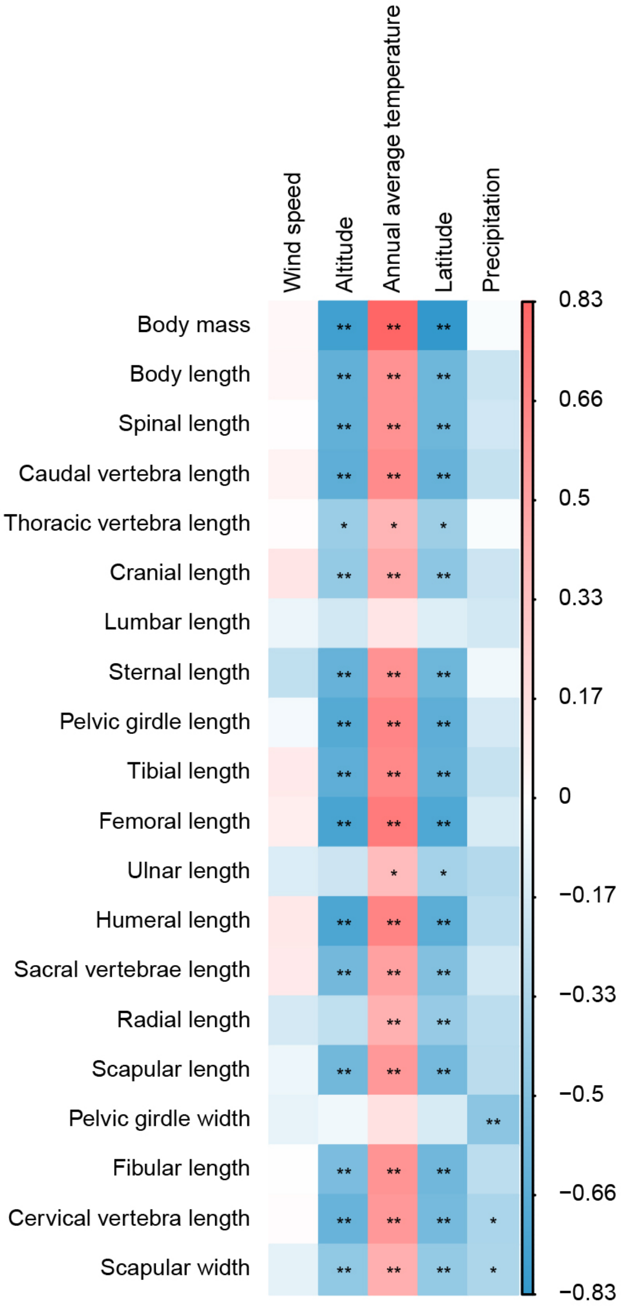

Fig. 6. Correlation analysis between body mass, body length, bone length and climate (*$P < 0.05$, **$P < 0.01$).

Results

Body mass, body length and bone morphological indices

Body mass, body length, cervical vertebra length and scapula length in *E. miletus* from the five regions showed significant differences (body mass: F = 12.928, $P < 0.001$; body length: F = 7.458, $P < 0.001$; cervical vertebra length: F = 4.460, $P = 0.006$; scapula length: F = 4.672, $P = 0.004$). In addition, there were significant differences in scapula width, humeral length, radial length, ulnar length, femoral length (scapula width: F = 2.894, $P = 0.038$; humeral length: F = 3.131, $P = 0.028$; radial length: F = 2.964, $P = 0.034$; ulnar length: F = 2.741, $P = 0.046$; femoral length: F = 3.651, $P = 0.015$). The sternal length in JC was smaller than that in XGLL, and the lumbar vertebra length was smaller than that in XGLL and DQ. Among the other bone morphological indices, DL, JC and LJ were larger than in XGLL and DQ (Fig. 1).

Principal component analysis

The first principal component accounted for 93.3%, and the second principal component accounted for 5.7%. Although there was a slight overlap between LJ, XGLL and DQ, it can be seen that XGLL and DQ mostly overlapped, while DL, JC and LJ overlapped to a certain extent (Fig. 2).

Cluster analysis

Although there were LJ individuals between DQ and XGLL, and XGLL individuals between DL and LJ, it may be due to the differences in wild individuals. In general, *E. miletus* from DL, JC and LJ at low latitude and high temperature clustered together, while *E. miletus* from XGLL and DQ at high latitudes and low temperatures clustered together (Fig. 3).

Linear regression analysis of spine length and other bone morphological indices

The length of the spine was highly significantly and positively correlated with the length of the cervical vertebra (Fig. 4A), thoracic vertebra (Fig. 4B), lumbar vertebra (Fig. 4C), sacral vertebra (Fig. 4D), caudal vertebrae (Fig. 4E), sternum (Fig. 4F), scapular (Fig. 4G), pelvic girdle (Fig. 4I), humerus (Fig. 4K), radius (Fig. 4L), ulna (Fig. 4M), femur (Fig. 4N), tibia (Fig.

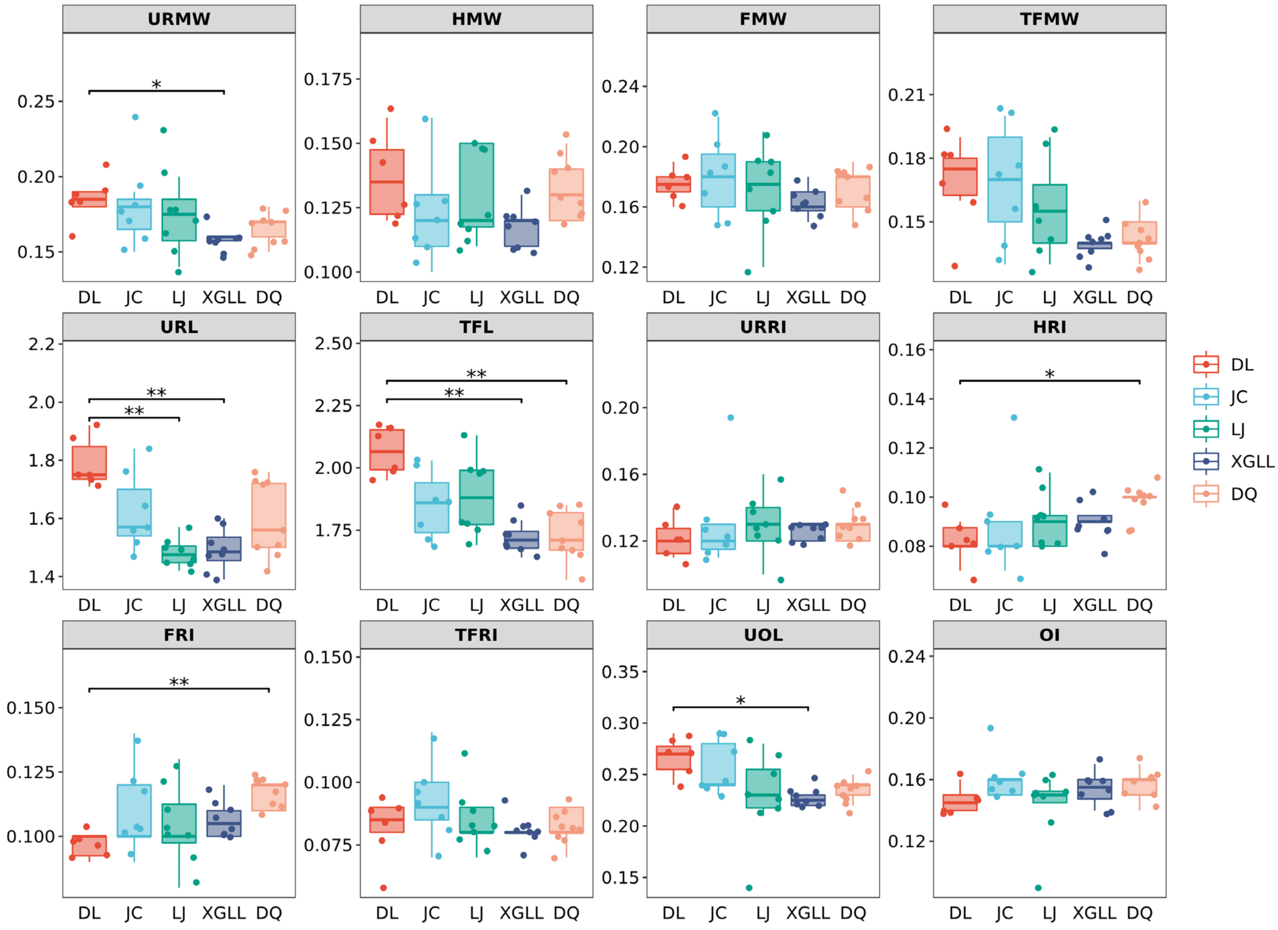

Fig. 7. Boxplots of limb bone indices (*$P < 0.05$, **$P < 0.01$).

4O), fibula (Fig. 4P) and scapular width (Fig. 4H), pelvic girdle width (Fig. 4J), respectively.

Linear regression analysis of total bone mass and body mass

There was a positive correlation between the total bone mass and the body mass ($R^2 = 0.215$, $P < 0.01$); as body mass increased, so did total bone mass (Fig. 5).

Correlation between body mass, body length, bone morphology indices and climate

Body mass, body length, cranial length, sacral vertebra length, caudal vertebra length, humeral length, femoral length, tibial length were positively correlated with wind speed, and lumbar length, sternal length, scapular length, scapular width, pelvic girdle length, pelvic girdle width were negatively correlated with wind speed. Body mass, body length, and the length of trunk bones and limb bones were negatively correlated with altitude, positively correlated with annual average temperature, and negatively correlated with latitude. In addition to body mass, thoracic vertebra length and sternal length, body length, length of other trunk bones and limb bones were negatively correlated with precipitation (Fig. 6).

Limb bone index data

The middle width of the radius and ulna, and tibia and fibula showed significant differences (URMW: $P = 0.036$; TFMW: $P = 0.032$), among which the middle width of radius and ulna in DL and XGLL showed significant differences ($P < 0.05$); the length of ulna and radius, tibia and fibula had highly significant differences (URL: $P = 0.001$; TTL: $P = 0.001$), among them, the length of ulna and radius was significant between DL and XGLL ($P < 0.01$), DL and LJ, and the length of tibia and fibula was significant ($P < 0.01$) between DL and XGLL, DL and DQ; there were significant differences in humeral, femoral robustness index (HRI: $P = 0.023$; FRI: $P = 0.015$), among which there were significant differences in the humeral, femoral robustness index in DL and DQ ($P < 0.05$); there was a significant difference in ulnar olecranon length ($P = 0.006$), among which there was a significant difference between DL and XGLL ($P < 0.05$) (Fig. 7). The weight percentage of the hindlimb bone (WPHB) was higher than the weight percentage of the forelimb bone (WPFB) in the five regions (Fig. 8).

Correlation between robustness index of limb bone and climate

Ulnar and radial robustness index was negatively correlated with altitude and latitude and positively correlated with annual average temperature. Humeral robustness index was highly significantly positively correlated with altitude and latitude and negatively correlated with annual average temperature. Femoral robustness index was significantly positively correlated with altitude and latitude and negatively correlated with annual average temperature. Tibial and fibular robustness index was positively correlated with wind speed, annual average temperature and precipitation and negatively correlated with altitude and latitude (Fig. 9).

Standard coefficients of multiple linear regression analysis between body mass, body length, bone morphology indices and latitude, altitude and annual average temperature.

Regression showed that body mass, cranial length, lumbar length, sacral vertebrae length, pelvic girdle width, radial length, ulnar length, ulnar olecranon length, tibial length, fibular length, robustness index of radius and ulna, olecranon index, robustness index of humerus, robustness index of femur, and robustness index of tibia and fibula were significantly affected by annual average temperature. In addition, body length, spinal length, cervical vertebra length, thoracic vertebra length, caudal vertebra length, scapular length, scapular width, pelvic girdle length, humeral length, femoral length and the total bone mass were significantly affected by latitude (Fig. 10).

Discussion

Species living in a specific habitat will adapt to the environment through the differentiation of morphological traits, thereby maximising reproductive success and survival (Zhu et al. 2010). Body mass is a fundamental index of animal body size but is affected by seasonal patterns and food availability and can vary widely. In contrast, bone is a more fixed character than body mass (Daniel et al. 2019). Presently, research on the morphological differentiation of small mammals mainly focuses on the phylogeny and classification of species through the characteristics of skulls (Zhu et al. 2015, Li et al. 2020, Fan et al. 2022). For example, it was shown that the skull morphology of *Myospalax baileyi* in different regions had apparent geographical differentiation, which was affected by habitat isolation and altitude factors (Su et al. 2018). There were significant differences in the size and shape of skulls among different geographic populations of the *Hipposideros armiger*, and regression analysis showed that the geographic changes in the shape of skulls were related to climate factors (Hou et al. 2017). Population differentiation of the skull morphology of Shaanxi *Lepus capensis* may be related to different selection pressures resulting from environmental differences in different regions (Li et al. 2011). In the present study, the body mass and body length of *E. miletus* in DL, JC and LJ were larger than those in XGLL and DQ. PCA and cluster analysis showed that *E. miletus* in DL, JC and LJ clustered together similarly in XGLL and DQ. Compared with XGLL and DQ, DL, JC, and LJ are at a lower latitude, higher temperature and with more abundant food resources, which may be one of the reasons for the body mass gain of *E. miletus* in the three regions. Competition with other species may also play a role. During sampling in DL, JC and LJ, many *Apodemus* were encountered. Both *E. miletus* and *Apodemus* eat plant buds, plant stems and seeds with high water content (Luo et al. 2000), and *E. miletus* may experience selection for a larger body size to enhance its competitiveness with *Apodemus*. An increase in body size might also enhance running speed and predator avoidance.

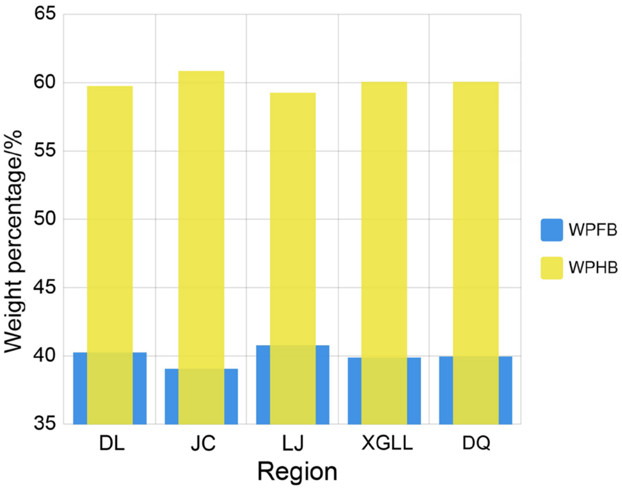

Fig. 8. Weight percentage of forelimb bone and hindlimb bone.

Previous studies found that in the Hengduan Mountain region, *E. miletus* had phenotypic differentiation in body indices and skull morphology, which may be affected by altitude, temperature and food (Ren et al. 2020b). The current study showed that the cervical vertebra length and scapular length differed significantly, as did the scapular width, humeral length, radial length, ulnar length, and femoral length. Sternal length in JC was smaller than that in XGLL, and the lumbar length was smaller

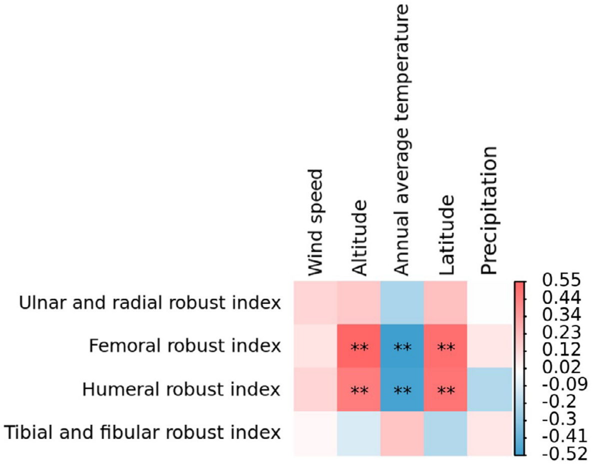

Fig. 9. Correlation analysis between robustness index of limb bone and climate (**$P < 0.01$).

than that in XGLL and DQ, the length of the other trunk bones and limb bones were larger in DL, JC and LJ than that in XGLL and DQ. The length of the spine is directly related to body length of the animals. Although there was no difference in the length of the spine, cervical vertebra length, thoracic vertebra length, lumbar length, sacral vertebrae length and caudal vertebra length in DL, JC and LJ were larger than those in XGLL and DQ. A longer spine means a larger muscle insertion area, resulting in greater body length and bone mass (Amson & Bibi 2021), which corresponds to the body mass of *E. miletus* in the five regions. Linear regression of *E. miletus* in the five regions showed that the total bone mass and body mass had a significant positive correlation; greater body mass is related to greater total bone mass. The longer the spine, the larger the chest cavity formed with the ribs and sternum, the larger the body size, and the higher the upper limit of body mass (Amson & Bibi 2021). Notably, the length and width of the scapula in DL, JC and LJ were larger than those in XGLL and DQ. The scapula provides a larger attachment surface for the muscles involved in the forelimb movement; a larger attachment surface means more muscles, which also affects body mass (Young et al. 2019).

Correlation analysis showed that the body mass, body length and bone morphological indices were

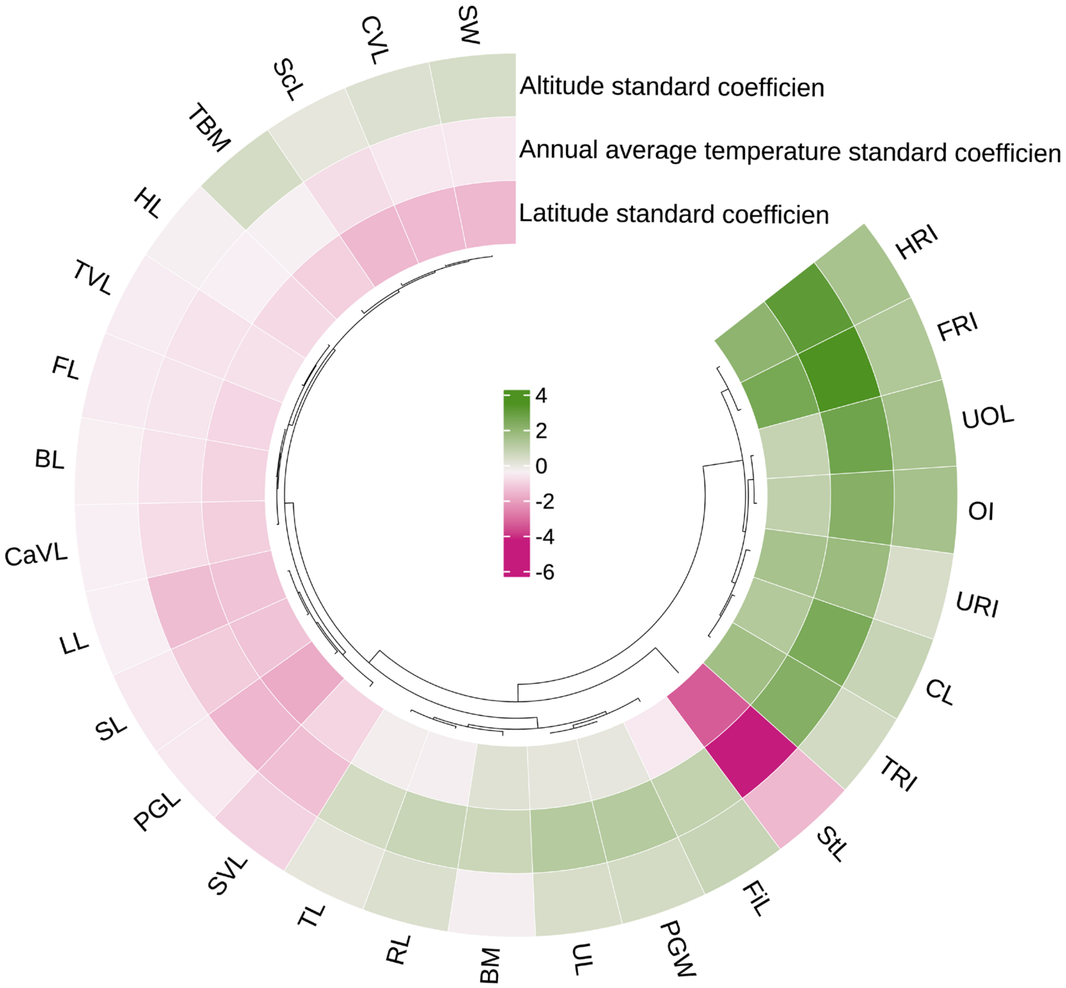

Fig. 10. The standard coefficients of multiple linear regression analysis between body mass, body length, bone morphology indices and latitude, altitude, annual average temperature.

significantly negatively correlated with altitude and latitude and were significantly positively correlated with the annual average temperature, which means that *E. miletus* in the Hengduan Mountain region has greater body mass and body length at low latitudes and in a high-temperature environment, which was not consistent with the Bergman's Law.

The appearance and structure of organs are closely related to body proportions and functional differences, especially concerning locomotor behaviour (Maher et al. 2022). The robustness index of limb bones is an index of the ability of animals to climb, run, dig and forage (Assif & ChirChir 2022). The present results showed significant differences between the five regions in the robustness index of the humerus and the robustness index of the femur; XGLL and DQ were greater than those in DL, JC and LJ. From the point of view of sampling sites, those in DL, JC and LJ comprised almost flat farmland and dams, so the process of obtaining food for *E. miletus* may not involve climbing. However, the two sampling sites in XGLL and DQ were mostly steep hillsides, and the *E. miletus* living in these two regions may be required to actively climb to forage and avoid natural enemies, resulting in a stronger humerus and femur.

Weible's symmetrical morphological formation hypothesis states that the structure of organs and tissues to enable animals to complete specific functions is optimised, such that investment in the distribution of limb bone material reflects adaptive function (Weibel 1991). The relative weight of the hindlimb bone in *E. miletus* in the five regions was greater than that of the forelimb bone. *Eothenomys miletus* lives in shallow tunnels and is better at running and jumping than digging, which requires more robust hindlimb development. In contrast, the activities of *M. baileyi*, which are typical of subterranean rodents, and include foraging, migration and mate finding, are associated with active burrowing activity (Zhang et al. 2020). A previous study showed that the weight percentage of the forelimb of *M. baileyi* was 55.2% (Lin et al. 2007). Linear regression also showed that the length of each part of the trunk and limb bones was positively associated with the length of the spine, and spine length inevitably leads to increased body mass. Therefore, we speculated that the different habitat preferences and activities of *E. miletus* and *M. baileyi* would be reflected by their contrasting bone morphology. Notably, standard coefficients of multiple linear regression analysis showed that, compared with altitude, the body mass, body length, trunk bones length, limb bones length and robustness index of the *E. miletus* were more significantly affected by the annual average temperature and latitude, which may be related to adaptations to the harsh conditions associated with the high altitude and temperature changes in the Hengduan Mountain region.

In conclusion, the present study showed that the body mass and body length of *E. miletus* in the five regions of the Hengduan Mountains varied, with clear differentiation in bone morphological indices. Greater bone length and mass resulted in an increased body mass in *E. miletus*. The change in bone length does not conform to Bergmann's Law and is associated with altitude, average annual temperature and latitude. Differences in diet and habitat appear to be the drivers of bone morphology variation in *E. miletus*.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (no. 32160254), Ten Thousand Talent Plans for Young Top-Notch Talents of Yunnan Province (YNWR-QNRC-2019-047) and Young and Middle-aged Academic and Technical Leaders Reserve Talents Project of Yunnan Province (2019HB013).

Author Contributions

Y.-Q. Liao performed the experiments, analysed the data, and drafted the paper. T. Jia performed experiments and prepared figures and tables. W.-L. Zhu conceived and designed the experiments and approved the final draft.

Data Availability Statement

The data supporting this study's findings are available in the FigShare Digital Repository: https://doi.org/10.6084/m9.figshare.21761429.

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