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Geographic Variation of the Large Red Flying Squirrel, *Petaurista albiventer* (Gray, 1834) (Rodentia: Sciuridae), with a Description of a New Subspecies in Southwestern China

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SL and ZF conceived the study. SL designed the study, analyzed the data, wrote the paper.

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Subspecies, Geographic variation, Statistic analysis, ***Petaurista albiventer*****, Morphometry.**

ABSTRACT

The large red flying squirrel *Petaurista albiventer* mainly inhabits northern Pakistan eastward to southwestern China, stretching across the whole southern Himalayan mountains. However, relatively little work has been performed on mapping its geographic variations in China. In this study, we used 45 *P. albiventer* specimens from Xizang and Yunnan in China to conduct multivariate analyses and calculate coefficients of differences on cranial measurements, together with a comparison of pelage characteristics. Results indicated that the allopatric samples from Xizang were obviously different from all those previously defined in Yunnan. Therefore, we describe them as new subspecies *P. a. muzongensis* subsp. nov. Discussion on the relationships between the differentiation of *P. albiventer* and its environmental evolution in southwestern China are also provided.

INTRODUCTION

The large red flying squirrel *Petaurista albiventer* (Gray, 1834), which was first recorded as *Pteromys albiventer* in its type locality Nepal, inhabits northern Pakistan eastward through India and Nepal into southwestern China, where it is located in the Himalayan temperate forests at elevations of 1350 m to the upper tree line limit at about 3000 m (Ellerman, 1940; Ellerman and Morrison-Scott, 1950; Ellerman, 1961; Corbet and Hill, 1992; Roberts, 1977; Thorington *et al*., 2012; Wang, 2003).

Ellerman (1940) accepted this species as *P. albiventer* in the *albiventer* section of genus *Petaurista*, and emphasized "much redder in general coloration than any member of the *philippensis* section"; however, Ellerman and Morrison-Scott (1950) accepted it as *P. petaurista albiventer*, with Peng and Wang (1981), Feng *et al*. (1986), Corbet and Hill (1992), Roberts (1977), Thorington and Hoffmann (2005) and Thorington *et al*. (2012) also listing it as *P. p. albiventer* or as a synonym of *P. petaurista* (Pallas, 1766). Wang (2003) listed it as *P. albiventer*.

Based on molecular data, Oshida *et al*. (2004) and Yu *et al*. (2006) strongly supported that *P. albiventer* was appreciably different from *P. petaurista* and *P. philippensis* (Elliot, 1839) and should be a valid species of *Petaurista*. In regards to pelage characteristics, the most significant difference between *P. albiventer*, *P. petaurista* and *P. philippensis* is their dorsal pelage, with that of *P. albiventer* being a deep chestnut-red with creamy-white guard hairs scattered on half its back, with a few distributed on the shoulders and head, that of *P. petaurista* being reddish-brown without creamy-white guard hairs, and that of *P. philippensis* being dark gray or black with numerous creamy-white guard hairs scattered on the back, shoulders and head (Fig. 1). Accordingly, based on molecular data and pelage characteristics, we support that *P. albiventer* is a valid species.

According to research on pelage characteristics, Peng and Wang (1981) named *P. petaurista nigra* Wang, 1981 as a new subspecies, with the type locality in Qiqing, Gongshan, Yunnan. Later, Wang (2003) listed it as *P. albiventer nigra*, along with *P. a. yunanensis* (Anderson, 1879), *P. a. grandis* Swinhoe, 1862, *P. a. hainana* G. Allen, 1925, and *P. a. chayuensis* Feng and Zheng, subsp. nov. as five subspecies of *P. albiventer*. However, others consider *P. yunanensis* to be a synonym of *P. philippensis* (Corbet and Hill, 1992; Thorington and Hoffmann, 2005). Previous research calculated differences of 13.16% between *P. philippensis grandis* and *P. petaurista albiventer* in cyt *b* gene sequences (Oshida *et al*., 2004), with *P. hainana*

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Fig. 1. Comparison of the pelage characteristics of *Petaurista albiventer*, *Petaurista philippensis* and *Petaurista petaurista*.

deemed a distinct species and "*P. grandis* closely related to *P. petaurista* rather than to *P. philippensis* or *P. albiventer*" (Yu *et al*., 2006). As for *P. a. chayuensis*, the name has not been published with any diagnostic characteristics or designated type specimen, and thus, according to Article 16. 4 of the International Code of Zoological Nomenclature (4th Edition), it is invalid. That is to say, until now, only *P. albiventer nigra* has been described as a valid subspecies in China.

In this study, we implemented a typical morphometric analysis, including skull morphometrics and comparison of pelage characteristics, to study the geographic variation of *P. albiventer* in southwestern China. We also discussed the relationships between the differentiation of *P. albiventer* and its environment in southwestern China.

MATERIALS AND METHODS

Data collection

The specimens used in this study are preserved in the Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences (CAS) (Kunming, China), and the Institute of Zoology (IOZ), CAS (Beijing, China). The numbers and collection localities of the specimens examined are listed in the Appendix.

A total of 45 specimens were studied, including 14 males, 12 females, and 19 specimens without recorded sex. Twenty-two specimens had intact skulls, which could be used for the statistical analyses. All specimens were considered as adults due to their erupted molars and M^2 crown with longitudinal worn dentine link (Lu *et al*., 1987). In total, 15 cranial measurements were taken with a digital caliper with the greatest possible accuracy (0.01 mm), including: greatest length of skull (GLS), condylobasal length (CBL), basal length (BL), occipitonasal length (ONL), palatal length (PL), length of palatal bridge (PBL), length of incisive formina (LIF), breadth of incisive formina (BIF), length of upper tooth row (LUTR), length of upper molars (LUM), maximum upper molars breadth (GUMB), heigth of coronoid process of mandible (HCPM), length of lower molar row (LLMR), lower tooth row (LTR), mandibular height (MH) (Fig. 2).

In addition, four external measurements were taken from the specimen records directly, including: head and body length (HB), tail length (TL), hind foot length (HFL), and ear length (EL). Because these measurements were taken by different collectors, they were not included in the multivariate analyses or coefficients of differences (CDs).

Data analysis

The 15 cranial measurements were first log-transformed, with sexual dimorphism analysis (for the 21 intact skull samples with recorded sex) then performed. Without assuming a prior group, overall similarities and differences of the 15 cranial measurements among the samples were assessed through principal component analyses (PCA), and lastly the groups identified via PCA were assigned with names. The CDs (Mayr, 1969) between the groups were calculated using the equation: CD = (Mb − Ma) / (SDa + SDb), where Mb is the mean of population b, Ma is the mean of population a, SDa is the standard deviation of population a, and SDb is the standard deviation of population b. The PCA was performed using SPSS version 17.0 (SPSS Inc., Chicago, IL, USA).

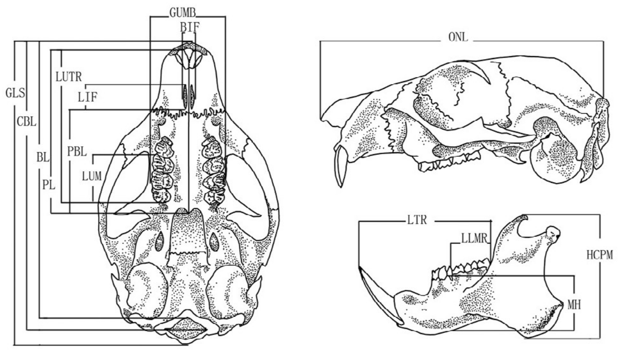

Fig. 2. Sketch map indicating 15 cranial measurements in the study. GLS, greatest length of skull; CBL, condylobasal length; BL, basal length; ONL, occipitonasal length; PL, palatal length; PBL, length of palatal bridge; LIF, length of incisive formina; BIF, breadth of incisive formina; LUTR, length of upper tooth row; LUM, length of upper molars; GUMB, maximum upper molars breadth; HCPM, heigth of coronoid process of mandible; LLMR, length of lower molar row; LTR, lower tooth row and MH, mandibular height.

Pelage comparisons

According to the PCA and CD analysis results, pelage characteristics of each group were described in detail, and based on significant differences between groups, a key for each was determined.

RESULTS

Sexual dimorphism and principal component analyses

As noted above, 21 intact skull samples (10 males and 11 females) had recorded sex data. Tests of equality of group means between the male and female groups indicated no significant differences for any of the 15 cranial variables (Table I).

Since sexual dimorphism was not observed for the 15 cranial variables, we used them to conduct PCA, resulting in eigenvalues for the first three principal components of 9.52, 1.98, and 1.06, respectively, which accounted for 83.71% of total variance. Most measured characteristics had high positive loadings on the first principal component, suggesting that this component (63.46% of the total variance) represented size variation among samples. The second principal component (13.18% of variance) was strongly correlated with LUM and LLMR (factor loadings > 0.80), whereas the third principal component (7.07% of variance) was correlated primarily with BIF (factor loadings > 0.80) (Table II). Figure 3 shows the plots of *P. albiventer* samples on principal component factors 1 *vs.* 2 and 2 *vs.* 3, respectively.

Table I.- Tests of equality of group means by gender.

Variables	Wilks' Lambda	*F*	*d.f.1*	*d.f.2*	*p*
GLS	1.00	0.02	1	19	0.89
CBL	0.99	0.20	1	19	0.66
BL	0.99	0.20	1	19	0.66
ONL	0.98	3.35	1	19	0.07
PL	1.00	0.00	1	19	0.99
LUTR	0.99	0.20	1	19	0.66
LUM	1.00	0.10	1	19	0.76
LIF	0.98	0.49	1	19	0.49
BIF	0.99	0.24	1	19	0.63
GUMB	0.92	1.56	1	19	0.23
PBL	1.00	0.06	1	19	0.81
HCPM	0.96	0.82	1	19	0.38
LLMR	0.99	0.15	1	19	0.70
LTR	1.00	0.08	1	19	0.79
MH	0.96	0.90	1	19	0.36

Variable codes are given in the text and Fig. 2, significant difference level ($p < 0.05$).

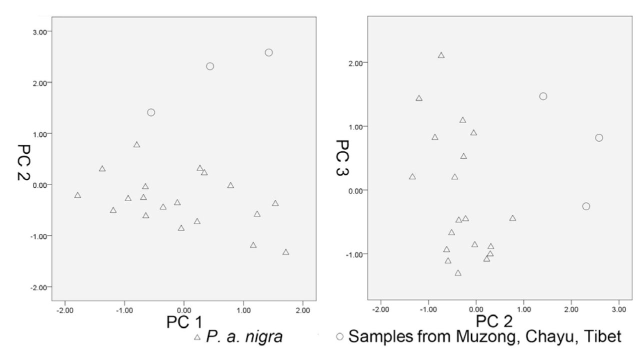

Fig. 3. Scatterplots of the samples for principal component factors 1 *vs.* 2 and 2 *vs.* 3, respectively.

Figure 3 indicates that the samples formed two different groups, one composed of samples of *P. a. nigra* from western and northwestern Yunnan, including Bijiang, Gongshan, Lianghe, Lushui, Tengchong, Yingjiang, Weixi, and Zhongdian, and the other composed of samples from Muzong, Chayu and Tibet. We calculated the CDs and compared pelage characteristics between them.

Table II.- Factor loadings and percentage of variance explained for principal component analysis.

Variables	Principal component (PC)		
	1	2	3
GLS	0.86	0.06	0.42
CBL	0.90	0.11	0.37
BL	0.90	0.17	0.34
ONL	0.85	0.06	0.42
PL	0.92	0.08	0.33
PBL	0.80	0.39	0.10
LIF	0.06	-0.76	0.20
BIF	0.27	0.07	0.88
LUTR	0.87	0.14	0.26
LUM	0.26	0.87	0.28
GUMB	0.59	0.22	0.50
HCPM	0.61	0.44	0.07
LLMR	0.32	0.85	0.26
LTR	0.91	0.16	0.08
MH	0.80	0.40	-0.26
Eigenvalues	9.52	1.98	1.06
Variance explained (%)	63.46	13.18	7.07

Variable codes are given in the text and Fig. 2, the extraction method used was principal component analysis, and the rotation method was Varimax with Kaiser Normalization.

Coefficients of differences (CDs)

The CD comparisons for the 15 cranial variables between *P. a. nigra* and the Muzong samples showed that the CDs of LUM and LLMR were larger than 1.28 (Table III).

Comparison of pelage characteristics

The specimens from Muzong (Chayu, Tibet) could be distinguished from *P. a. nigra* by the following pelage characteristics: 1, no or few creamy-white guard hairs on the back, compared with creamy-white guard hairs on the waist and buttock areas, but those of *P. a. nigra* distribute forward on the neck and head areas; 2, base of the ear area mainly rufous-brown (or grey-brown occasionally), compared with white (or light grey-brown); 3, back of the feet brown black, with a rufous-brown shade on the back of the front feet, compared with deep black brown; 4, tail not as black, but with a rufous-brown shade (Fig. 4).

Table III.- Comparison of coefficients of differences (CDs) between *Petaurista albiventer nigra* and Muzong samples.

Variables	CD	Variables	CD	Variables	CD
GLS	0.51	PBL	0.64	GUMB	0.37
CBL	0.52	LIF	0.52	HCPM	0.87
BL	0.65	BIF	0.47	LLMR	4.72
ONL	0.53	LUTR	0.51	LTR	0.45
PL	0.64	LUM	5.58	MH	0.60

Italicized values denote measurements greater than 1.28, variable codes are given in the text and Fig. 2.

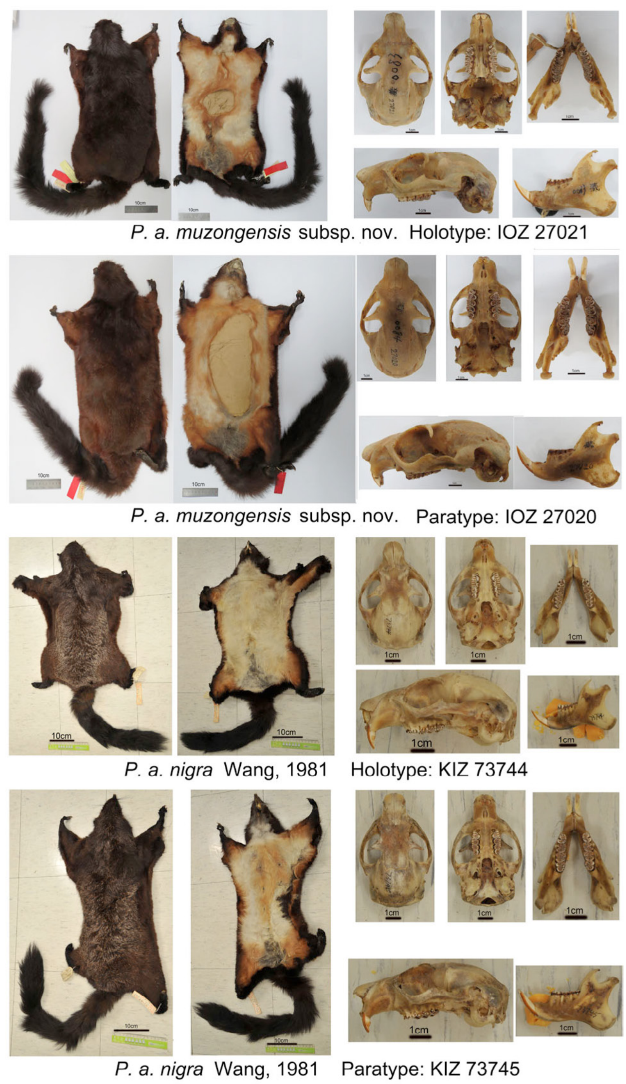

Fig. 4. Type specimens of *Petaurista albiventer muzongensis* Li and Feng, subsp. nov. and *Petaurista albiventer nigra*.

DESCRIPTION OF NEW SUBSPECIES

Petaurista albiventer muzongensis Li and Feng, subsp. nov.

Holotype:

IOZ 27021, ♂, adult, collected 7 August 1973, from Muzong, Chayu, Tibet, China, elevation 2,300 m.

Paratype:

IOZ 27020, ♀, adult, collected 7 August 1973, from Muzong, Chayu, Tibet, China, elevation 2,300 m.

Specimens examined:

1 ♂♂ and two (no recorded sex) pelage specimens without skulls from Xizang.

Etymology:

This new subspecies is named according to the type locality.

Diagnosis:

Few or no creamy-white guard hairs on the back, base of the ear area mainly rufous-brown (or grey-brown occasionally), back of the front and hind feet brown black, with a rufous-brown shade on the back of the front feet, tail not as black as that of *P. a. nigra,* but with a rufous-brown shade.

Description:

P. a. muzongensis subsp. nov. exhibits several distinct and apparently stable characteristics: (1) general dorsal color chestnut-red, deeper on the forebody and narrower on the waist and buttock areas, changing from chestnut-red to reddish-brown from the back center to the flank, with few to no creamy-white guard hairs on the back; (2) underparts ochraceous buff (hair base yellow-white, and tip yellow-brown), center area deeper, anus area grey-brown, throat white or white-grey, chin brown with a deep brown spot on its center area; (3) muzzle and sides mainly brown-black, but with a reddish shade, crown and nape nearly the same as the back, but the forehead deeper, cheeks rufous-brown, base of the ear area mainly rufous-brown (or grey-brown occasionally), orbits blackish-brown, and ear brown without tufts; (4) flanks reddish-brown, and back and belly clearly distinguished; (5) back of the front and hind feet brown-black, but with a rufous-brown shade on the back of the front feet, pads developed; (6) tail brown-black, with a rufous-brown shade.

Synonyms:

Pteromys albiventer albiventer, Gray, Illustr. Zool., pl. xviii; *Petaurista petaurista nigra* Wang, 1981, New Mammals from the Gaoligong Mountains (1), Acta Theriologica Sinica, Vol. 1, No. 2, 169-170.

Measurements

see Table IV for external and skull of type specimens of *Petaurista albiventer muzongensis* subsp. nov.

Table IV.- Measurements (mm) of external and skull of type specimens of *Petaurista albiventer muzongensis* Li and Feng, subsp. nov.

Specimen	Holotype	Paratype	Specimen	Holotype	Paratype
Sex	**Male**	**Female**	**Sex**	**Male**	**Female**
HB	476	480	LIF	4.08	3.70
TL	530	480	BIF	3.28	3.84
HFL	82	82	LUTR	38.86	39.85
EL	45	47	LUM	18.03	18.46
GLS	78.51	81.90	GUMB	20.68	22.18
CBL	73.30	77.15	HCPM	33.80	35.58
BL	68.62	72.06	LLMR	18.89	19.75
ONL	78.37	81.65	LTR	36.62	38.04
PL	41.34	42.67	MH	13.44	13.86
PBL	28.43	29.50			

Variable codes are given in the text and Fig. 2, HB, head and body length; TL, tail length; HFL, hind foot length; EL, ear length.

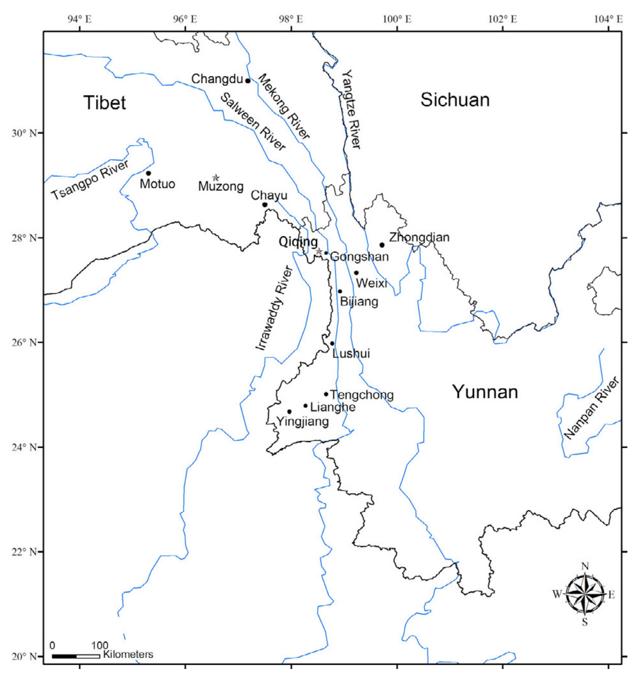

Fig. 5. Geographic localities of samples examined in this study (star indicates type locality).

External and cranial measurements of *P. a. muzongensis* subsp. nov. and *P. a. nigra* are listed in Table V, and it shows most measurement features overlap between the two subspecies with exceptions of LUM and LLMR. Figure 4 indicates the type specimens of *P. a. muzongensis* subsp. nov. and *P. a. nigra*.

Table V. Measurements (mm) of external and skull variable measurements (mm) of *Petaurista albiventer* subspecies.

Varia-bles	Subspecies	
	P. a. muzongensis	*P. a. nigra*
HB	465.33±22.03 (440~480)	441.44±24.13 (420~520)
TL	496.67±28.87 (480~530)	537.24±51.67 (440~620)
HFL	81.67±0.58 (81~82)	81.94±5.31 (70~92)
EL	46.00±1.00 (45~47)	44.56±3.46 (40~52)
GLS	79.45±2.14 (77.94~81.90)	77.07±2.48 (71.67~81.56)
CBL	74.15±2.68 (72.00~77.15)	71.53±2.34 (67.79~75.68)
BL	69.45±2.31 (67.68~72.06)	66.38±2.41 (62.24~70.53)
ONL	79.22±2.14 (77.63~81.65)	76.77±2.49 (71.64~81.09)
PL	41.69±0.86 (41.06~42.67)	40.14±1.56 (37.55~43.05)
PBL	28.51±0.94 (27.61~29.50)	27.22±1.07 (25.05~28.64)
LIF	3.31±0.38 (2.75~4.33)	4.96±0.56 (4.02~5.85)
BIF	3.64±0.31 (3.28~3.84)	3.31±0.38 (2.75~4.33)
LUTR	38.85±1.01 (37.84~39.85)	37.69±1.28 (35.73~39.80)
LUM	17.99±0.50 (17.47~18.46)	12.56±0.48 (11.68~13.60)
GUMB	20.99±1.07 (20.11~22.18)	20.29±0.80 (18.70~21.46)
HCPM	34.04±1.44 (32.73~35.58)	31.83±1.11 (29.95~34.00)
LLMR	19.00±0.70 (18.36~19.75)	13.70±0.42 (13.13~14.66)
LTR	36.79±1.18 (35.70~38.04)	35.75±1.13 (33.95~37.19)
MH	13.21±0.80 (12.32~13.86)	12.33±0.65 (11.38~13.80)

Variable codes are given in the text and Fig. 2. Values are mean ± std. dev. with the range given in parentheses. HB, head and body length; TL, tail length; HFL, hind foot length; EL, ear length.

KEY TO THE SUBSPECIES OF *P. ALBIVENTER*

1. Creamy-white guard hairs on waist and buttock areas, and distributed forward on the neck and head areas, with a white (or light grey-brown) area under the base of the ear---------------------------------------*P. a. nigra*
2. Few or no creamy-white guard hairs on the back, base of the ear area mainly rufous-brown (or grey-brown occasionally)------------*P. a. muzongensis* subsp. nov.

Figure 5 shows the geographic localities of the samples examined in the study.

DISCUSSION

As noted above, it is unquestionable that *P. albiventer* should be a valid *Petaurista* species. In the present study, we found that the specimens stored at KIZ named as *P. a. yunanensis* should be classified as *P. albiventer* due to their dorsal pelage, which is a deep reddish-chestnut with creamy-white guard hairs scattered on half the back, but predominately absent from the shoulders and head, whereas "*yunanensis*" shows "numerous white-tipped hairs giving a frosted effect" (Ellerman, 1961). In their study, Yu *et al*. (2006) stated that *P. yunanensis* (tissues used in molecular study were all collected from KIZ, and thus were actually *P. albiventer*) was a sister group of *P. albiventer* (samples from Pakistan), with differences of only 6.5% in the pairwise comparison of the complete cytochrome *b* gene sequences. However, their discriminant function analysis and PCA morphology results (cranial measurements from specimens deposited in the American Museum of Natural History, National Museum of Natural History, and Chinese Institute of Zoology, not the KIZ specimens used in their molecular analysis) showed that *P. yunanensis and P. philippensis* could not be separated. Thus, their research not only demonstrated that the specimens named as *P. a. yunanensis* in KIZ should be a subspecies of *P. albiventer* apart from those of Pakistan, but also supported the results of Corbet and Hill (1992) and Thorington and Hoffmann (2005) that *P. yunanensis* should be a synonym of *P. philippensis.* Under the same circumstances, Li *et al*. (2012) also used the KIZ "*P. a. yunanensis"* specimens (which should be *P. albiventer*) in their cranial morphometric study of four giant flying squirrels, and demonstrated that *P. albiventer* (rather than *P. yunanensis*) should be a valid species.

The PCA results in the present study showed that the specimens were clustered into two distinct geographic groups: *P. a. muzongensis* subsp. nov. and *P. a. nigra* (Fig. 3). Furthermore, CD analyses indicated that two CDs among the 15 cranial measurements between *P. a. muzongensis* subsp. nov. and *P. a. nigra* exceeded 1.28 (Table III). According to Mayr (1969), CD values on subspecific differentiation should be equal to or larger than 1.28; thus, we concluded that *P. a. muzongensis* subsp. nov. should be a new valid subspecies of *P. albiventer*. Furthermore, pelage comparison between *P. a. muzongensis* subsp. nov. and *P. a. nigra* further sustained their valid subspecies status (Fig. 4), and classification as allopatric populations (Fig. 5). In conclusion, we strongly suggest that *P. a. muzongensis* subsp. nov. should be considered as a valid subspecies of *P. albiventer*.

Unfortunately, the type locality of *P. albiventer* is in Nepal (Gray, 1834), and we do not have the type specimen to compare with *P. a. muzongensis* subsp. nov. Based on their cyt *b* differences (Yu *et al*., 2006), however, we believe that *P. a. nigra* should be a different subspecies from *P. a. albiventer* (6.5% differences in cyt *b* gene sequences between them*)*. Further studies are required to determine the relationship between *P. a. muzongensis* subsp. nov. and *P. a. albiventer,* especially in regards to cranial morphometrics and pelage characteristics.

As shown in Figure 5, the distribution of specimens examined in this study exhibited the highest species diversity not only in China (Chen, 2002), but also the world (Myers *et al*., 2000). The collision of the Indian and Eurasian continental plates led to the high mountains and deep gorges in the area, with these complex environments expediting intra-specific geographic variation. From the view of biogeography, *P. albiventer* inhabits northern Pakistan eastward to southwestern China, stretching across the whole southern Himalayan mountains. However, determining how has it adapted to such complex environments and what mechanisms are responsible for subspecies differentiation still require clarification. Further studies, especially molecular data analyses, should be performed to elucidate the relationships between subspecies differentiation, local adaptation, and geographical evolution.

CONCLUSION

It is concluded from the current study that *P. a. muzongensis* subsp. nov. is a valid subspecies of *P. albiventer*.

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Conflict of interest statement

Authors declared that there is no conflict of interest.

Supplementary Material

There is supplementary material associated with this article. Access the material online at: http://dx.doi.org/10.17582/journal.pjz/2017.49.4.1321.1328

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