Geographic variation of the Perny's Long-nosed squirrels (*Dremomys pernyi*) (Milne-Edwards, 1867) (Rodentia: Sciuridae) from southwestern China based on cranial morphometric variables

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ABSTRACT. A sample of 114 specimens of *Dremomys pernyi* was investigated, 73 of which had intact skulls and were subjected to multivariate, coefficient of difference (C. D.), and cluster analyses. Results indicate that 4 subspecies (groups) of *Dremomys pernyi* inhabit southwestern China: *D. p. pernyi* in the center and western Sichuan province and central and northwestern Yunnan province; *D. p. flavior* in the areas ranging from the southwestern Guangxi province, southwestern Guizhou province to the southern Yunnan province (east of Honghe River); *D. p. howelli* in the western Yunnan province (west of Nujiang River); and one new group (*D. pernyi* Wuliangshan group) in the Wuliangshan areas (between the Honghe River and the Lancangjiang River), Jingdong, Yunnan province. The results also probe into the relationships between subspecies differentiation of *D. pernyi* and the geographic structure and evolution in southwestern China.

KEY WORDS : Geographic variation, Subspecies, Numerical analysis, *Dremomys pernyi*, Morphometry

INTRODUCTION

Perny's Long-nosed squirrel *Dremomys pernyi* (Milne-Edwards, 1867) mainly lives in southern China (including Tibet and Taiwan), but also occurs in northern Vietnam, northern Myanmar, and parts of northeastern India.

With regard to subspecies differentiation, ALLEN (1940) listed 6 subspecies: *D. p. pernyi*, *D. p. flavior* (Allen, 1912), *D. p. howelli* (Thomas, 1922), *D. p. senex* (Allen, 1912), *D. p. modestus* (Thomas, 1916), and *D. p. calidior* (Thomas, 1916); ELLERMAN (1940) added 5 more subspecies: *D. p. griselda* (Thomas, 1916), *D. p. chintalis* (Thomas, 1916), *D. p. lichiensis* (Thomas, 1922), *D. p. mentosus* (Thomas, 1922), and *D. p. imus* (Thomas, 1922); ELLERMAN & MORRISON-SCOTT (1950) recognized only 3 subspecies: *D. p. pernyi*, *D. p. imus*, and *D. p. owstoni* (Thomas, 1908); MOORE & TATE (1965) indicated that there were 6 subspecies, comparable with the former results. They argued that *D. p. griselda*, *D. p. lichiensis*, and *D. rufigenis lentus* (A.B. Howell, 1927) were synonyms of *D. p. pernyi*, *D. p. mentosus* and *D. p. imus* were synonyms of *D. p. howelli*, *D. p. modestus* was a synonym of *D. p. senex*, *D. p. chintalis* was a synonym of *D. p. calidior*, and agreed on *D. p. owstoni* and *D. p. flavior* as being valid subspecies; CORBET & HILL (1992) only listed all of subspecies names but provided no further discussion.

Clearly, there has been disagreement as to the subspecies differentiation of *D. pernyi*, and also the geographic variation of the species has been studied insufficiently. Therefore, based on the analysis of cranial morphometric variables, we attempted a more detailed analysis of the geographic variation of *D. pernyi* in southwestern China. Additionally, we discuss the relationships between geographic variation in *D. pernyi* and the geological changes in this area.

MATERIALS AND METHODS

Data collection

This study was conducted at Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, CAS) (Kunming, China), and based on the mammal collections of the Museum of Vertebrates of KIZ, CAS, and the Institute of Zoology, Chinese Academy of Sciences (IOZ, CAS) (Beijing, China). Numbers and collection localities of specimens that were examined in the study are listed in the Appendix.

A series of 114 specimens were studied, 73 of which had intact skulls and were suitable for quantitative analyses. Specimens that were used in the study were all adults. Four external measurements; head and body length (HB), tail length (TL), hind foot length (HFL) and ear length (EL) were recorded from original labels attached to skins. Since these measurements may show considerable interobserver variation, they were not included in our analyses. Skull variables were recorded as described previously by MUSSER (1979), MUSSER & HEANEY (1992). All 15 cranial measurements were taken with a digital caliper to its greatest accuracy (0.01mm): greatest length of skull (GLS); condylobasal length (CBL); basal length (BL); rostral length (ROL); upper tooth row (UTR); the first upper molar length (FUML); palatal length (PL), the distance from the anterior edge of the premaxillary to the posterior edge of the palatine; postpalatal length (PPL), the distance from the posterior edge of the palatal to the anterior edge of the foramen magnum; interorbital breadth (IOB); zygomatic breadth (ZOB); length of diastema (LDS); breadth of incisive foramen (BIF); length of incisive foramen (LIF); lower tooth row (LTR); height of Mandibular (HM).

Data analysis

Based on the 15 variables described above, principal component analyses (PCA) were conducted to highlight differences in skull shape between the samples. This technique combines the variables to show the maximum variation between individuals without assuming prior grouping based on putative subspecies identification. The coefficient of difference between groups (C. D.; MAYR, 1969) was calculated using the following equation: C. D.=(M_b-M_a)/(SD_a+SD_b); where M_b is the mean of population b, M_a is the mean of population a, SD_a is the standard deviation of population a, and SD_b is the standard deviation of population b.

Squared Euclidean distances between the group centroids were calculated using Mahalanobis distances and were subjected to cluster analysis by Hierarchical Cluster methods. Statistical analyses were performed using SPSS version 11.0 (SPSS Inc., Chicago, IL, USA).

Because no holotypes could be examined in this study, the different subspecies were identified based on their collection sites. The type specimen of *D. p. pernyi* was from Moupin, Sichuan, China, collected by Perny and *D. p. pernyi* mainly occurs in western Sichuan; the type specimen of *D. p. howelli* was from S. W. of Tengyueh, extreme western Yunnan, China, collected June 4, 1912, by E. B. Howell; the type specimen of *D. p. flavior* was from Mongtz, southeastern Yunnan, China, collected in 1911 by H. Orii (MOORE & TATE, 1965).

In order to establish if there is sexual dimorphism in *D. pernyi*, an analysis on both sexes was first performed.

RESULTS

Test on sexual dimorphism in *D. pernyi*

68 out of 73 samples had information concerning their sex, and they were classified into a male (38 specimens) and a female group (30 specimens). Tests of Equality of Group Means were performed, and the results indicated that none of skull variables showed significant differences between males and females (Table 1). In other words, there is no sexual dimorphism in these 15 cranial dimensions in *D. pernyi*.

TABLE 1

Tests of Equality of Group Means for males and females. Variable codes are given in the text

Variables	Wilks' Lambda	F	df1	df2	Sig.
GLS	1.000	0.016	1	66	0.898
CBL	0.999	0.076	1	66	0.898
BL	0.999	0.068	1	66	0.795
ROL	1.000	0.027	1	66	0.871
UTR	0.998	0.105	1	66	0.747
FUML	0.990	0.648	1	66	0.424
PL	0.996	0.234	1	66	0.630
PPL	0.999	0.084	1	66	0.898
IOB	0.999	0.096	1	66	0.757
ZOB	1.000	0.021	1	66	0.887
LDS	1.000	0.023	1	66	0.879
BIF	0.987	0.883	1	66	0.351
LIF	0.998	0.102	1	66	0.751
LTR	0.994	0.400	1	66	0.529
HM	1.000	0.007	1	66	0.933

Sig. level<0.05

Multivariate analysis

As noted above, 73 individuals with intact skulls were available that could be assessed by principal component analyses (PCA). Eigenvalues for the first three principal components were 11.17, 1.06 and 0.94 respectively, accounting for 87.79% of the total variance. Most characteristics had high positive loadings on the first principal component, suggesting that this component (74.45% of the total variance) represents size variation in the sample, with specimens increasing in size from left to right. The second principal component (7.09% of variance) is strongly correlated with BIF and LIF (factor loadings>0.50). The third principal component (6.26% of variance) is correlated primarily with FUML and PL (factor loadings>0.50) (Table 2). Table 2 indicates that PPL is the only variable, which is negatively correlated with the third PC, and it suggests that Wuliangshan specimens are the smallest and the *D. howelli's* are the largest in absolute dimension (Table 4).

TABLE 2

Factor loadings and percentage of variance explained for principal component analysis. Variable codes are given in the text.

Variables	PC1	PC2	PC3
GLS	**0.866**	0.347	0.273
CBL	**0.851**	0.434	0.227
BL	**0.857**	0.425	0.211
ROL	**0.841**	0.341	0.227
UTR	**0.851**	0.327	0.375
FUML	0.280	0.147	**0.850**
PL	**0.722**	0.330	0.549
PPL	**0.738**	0.388	-0.360
IOB	**0.822**	0.137	0.168
ZOB	**0.900**	0.230	0.170
LDS	**0.839**	0.390	0.224
BIF	0.324	**0.831**	0.003
LIF	0.233	**0.816**	0.315
LTR	**0.832**	0.271	0.396
HM	**0.858**	0.157	0.237
Eigenvalues	11.17	1.06	0.94
Variance explained (%)	74.45	7.09	6.26

Fig. 1 (A, B) shows a plot of the samples of *D. pernyi* on principal components (Fig. 1. A: PC1 versus PC2, Fig. 1. B: PC1 versus PC3).

Inspection of Fig. 1 suggests that the samples are separated into 3 different groups. According to previous results of subspecies differentiation (MOORE & TATE, 1965) and taking into consideration the collecting localities, we find that the samples (*D. p. howelli*) originating from west of the Nujiang River (including Longling, Tengchong, Lushui, and Gongshan) form a clearly separated group. The samples (*D. p. pernyi*) of the western Sichuan province (including Yajiang, Muli, Daofu, and Daocheng) and Yunnan province (including Kunming, Anning, Binchuan, Weixi, and Deqin areas) overlap the

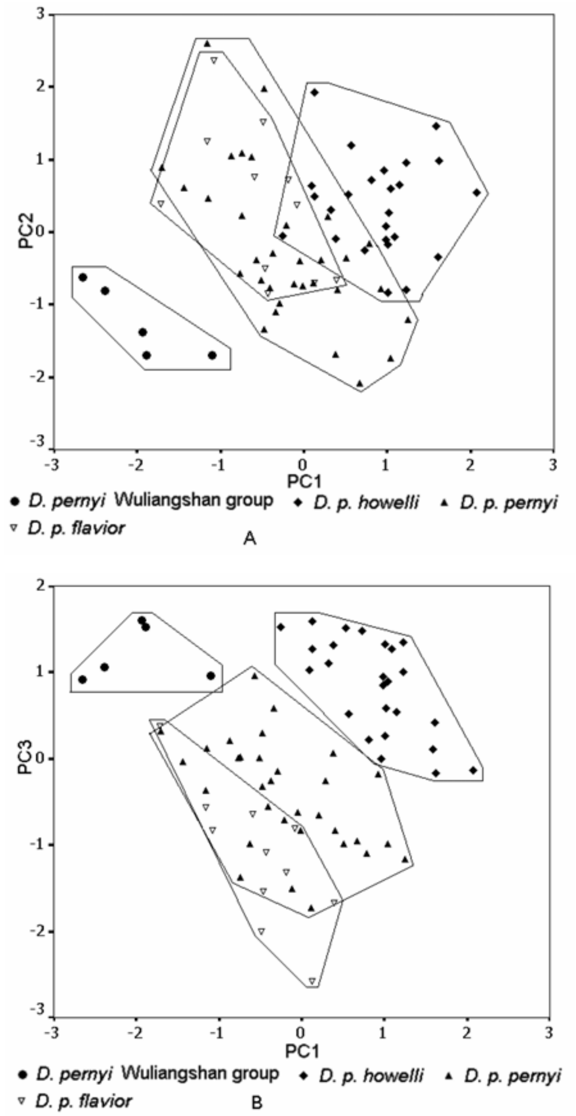

Fig. 1. – Plots of the *D. pernyi* subspecies in multivariate space.

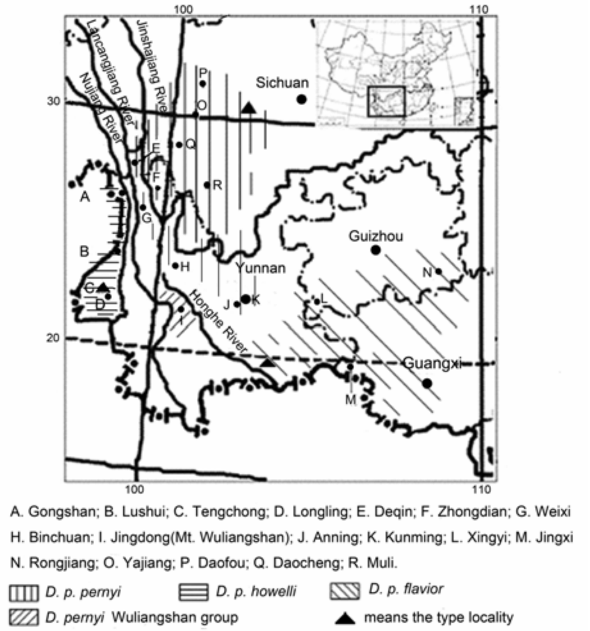

Fig. 2. – The geographic distribution of samples examined in this study.

samples (*D. p. flavior*) of the southwestern Guangxi province (Jingxi area) and the southwestern and southern Guizhou province (Xingyi and Rongjiang areas). These two subspecies also form one group. The most interesting result in this study is that the samples of Mt. Wuliangshan (Jingdong, Yunnan province) are unmistakably separate from the other three subspecies and form a clearly distinct group. Fig. 2 shows the geographic distribution of samples in this study.

TABLE 3

Comparison of Coefficient of Difference (C. D.) between *D. pernyi* Wuliangshan group and other three adjacent subspecies of *D. pernyi* respectively: 1: *D. p. howelli*, 2: *D. p. pernyi*, 3: *D. p. flavior*, 4: *D. pernyi* Wuliangshan group. Variable codes are given in the text.

Variable	1-4	2-4	3-4
GLS	**3.13**	**1.54**	**1.56**
CBL	**2.98**	**1.74**	**1.55**
BL	**2.81**	**1.55**	**1.52**
ROL	**3.30**	**1.37**	1.26
UTR	**3.66**	**1.53**	**1.31**
FUML	**1.67**	0.18	1.06
PL	**2.61**	0.38	0.32
PPL	**2.42**	**2.62**	**2.14**
IOB	**2.68**	**1.36**	0.83
ZOB	**3.89**	**2.18**	**2.03**
LDS	**3.14**	**1.48**	**1.79**
BIF	**1.43**	0.68	0.93
LIF	**2.33**	0.77	0.98
LTR	**2.71**	0.86	0.82
HM	**2.40**	1.09	0.86

Coefficient of Difference (C. D.)

According to the MYAR's theory on subspecies differentiation, the C. D. on the conventional level of subspecific differtiation should be equal to or larger than 1.28. The results of comparison on the C. D. in the skull measurement between *D. pernyi* Wuliangshan group and the other three adjacent subspecies of *D. pernyi* respectively indicate (Table 3): (1) C. D.s of all variables are larger than 1.28 between *D. pernyi* Wuliangshan group and *D. p. howelli*; (2) with the exception of C. D.s for FUML, PL, BIF, LIF, LTR, and HM, the remaining nine C. D.s are larger than 1.28 between *D. pernyi* Wuliangshan group and *D. p. pernyi*; (3) C. D.s of GLS, CBL, BL, UTR, PPL, ZOB, and LDS are larger than 1.28 between *D. pernyi* Wuliangshan group and *D. p. flavior*. Based on these comparisons, it is clear that the samples from the Mt. Wulianshan area markedly differ from the adjacent known subspecies of *D. pernyi*, strongly suggesting that this group should be recognised as a new group within *D. pernyi*.

Cluster Analyses

According to the results of Multivariate analysis and Coefficient of Difference, the samples of Mt. Wuliangshan should be classified as a distinct new group. Cluster analysis of Squared Euclidean distances between the different group centroids calculated using the Mahalanobis distances produced a dendrogram of four groups (Fig. 3).

Fig. 3 shows that *D. p. pernyi* and *D. p. flavior* cluster closely together and form a monophyletic group. This group then clusters with the *D. pernyi* Wuliangshan group to form a group that is clearly separated from *D. p. howelli*.

External and cranial measurements of the four groups of *D. pernyi* are given in Table 4.

TABLE 4

External and cranial measurements of four groups of *D. pernyi*: (Mean ± std. Deviation) / range. Variable codes are given in the text.

	HB	TL	HFL	EL	GLS	CBL	BL	ROL	UTR	FUML
D. p. howelli	188.16±10.63	142.36±15.76	44.40±2.89	20.48±2.12	53.66±1.21	47.34±1.25	44.13±1.21	13.25±0.51	24.87±0.58	2.02±0.08
N=25	174.00-210.00	95.00-165.00	36.00-50.00	17.00-24.00	51.15-56.57	44.28-49.73	40.84-46.27	12.29-14.12	23.71-25.81	1.87-2.17
D. p. pernyi	179.09±12.26	144.44±11.35	42.28±3.30	19.75±3.21	49.68±1.15	43.68±0.98	40.81±1.05	11.87±0.62	22.61±0.56	1.85±0.10
N=32	151.00-200.00	120.00-165.00	35.00-48.00	14.00-25.00	47.47-52.39	41.52-45.97	38.57-42.90	10.77-12.97	21.28-23.62	1.61-2.04
D. p. flavior	175.91±10.10	132.00±14.67	42.73±2.72	20.09±3.67	49.37±0.92	43.56±1.18	40.70±1.03	11.72±0.58	22.27±0.48	1.70±0.15
N=11	162.00-190.00	95.00-150.00	39.00-47.00	10.00-24.00	47.55-50.48	41.83-45.53	39.29-42.18	10.83-12.71	21.56-22.95	1.37-1.88
D. pernyi	156.60±12.22	136.40±4.98	42.00±1.23	20.60±0.55	46.02±1.23	39.66±1.33	37.25±1.24	10.64±0.28	21.03±0.47	1.87±0.01
Wuliangshan group, N=5	137.00-170.00	132.00-145.00	41.00-44.00	20.00-21.00	45.22-48.18	38.63-41.74	36.12-39.15	10.31-10.93	20.52-21.64	1.85-1.89
Total	180.18±13.74	141.30±13.75	43.05±3.10	20.11±2.82	50.75±2.56	44.64±2.46	41.68±2.26	12.24±0.97	23.22±1.37	1.88±0.15
N=73	137.00-210.00	95.00-165.00	35.00-50.00	10.00-25.00	45.22-56.57	38.63-49.73	36.12-46.27	10.31-14.12	20.52-25.81	1.37-2.17

(continue)

	PL	PPL	IOB	ZOB	LDS	BIF	LIF	LTR	HM
D. p. howelli	27.05±0.54	17.49±0.72	14.34±0.55	27.42±0.78	13.46±0.50	1.82±0.16	3.48±0.29	22.69±0.51	6.24±0.24
N=25	25.85-28.10	15.59-19.21	13.09-15.56	25.96-28.74	12.47-14.60	1.53-2.15	3.01-4.32	22.00-23.69	5.84-6.88
D. p. pernyi	23.96±0.71	17.23±0.52	13.44±0.66	25.64±0.81	11.95±0.49	1.59±0.21	2.98±0.43	20.61±0.61	5.63±0.22
N=32	22.61-25.54	16.09-18.13	11.88-14.62	24.20-27.99	11.00-12.94	1.17-2.02	2.28-4.00	19.51-21.74	5.15-6.20
D. p. flavior	23.82±0.60	17.18±0.74	12.80±0.46	25.02±0.64	12.06±0.40	1.70±0.22	3.05±0.39	20.44±0.46	5.52±0.21
N=11	22.73-24.98	15.90-18.63	12.17-13.63	23.71-25.66	11.24-12.56	1.27-2.02	2.48-3.80	19.76-21.02	5.16-5.91
D. pernyi	23.35±0.88	14.35±0.58	12.22±0.24	22.99±0.36	10.63±0.40	1.32±0.19	2.57±0.10	19.52±0.66	5.16±0.21
Wuliangshan group, N=5	22.34-24.17	13.98-15.38	12.07-12.64	22.71-23.60	10.24-11.20	1.16-1.54	2.51-2.75	18.46-20.03	4.79-5.30
Total	24.96±1.66	17.11±0.98	13.57±0.87	25.98±1.44	12.39±0.97	1.67±0.24	3.14±0.45	21.22±1.23	5.79±0.41
N=73	22.34-28.10	13.98-19.21	11.88-15.56	22.71-28.74	10.24-14.60	1.16-2.15	2.28-4.32	18.46-23.69	4.79-6.88

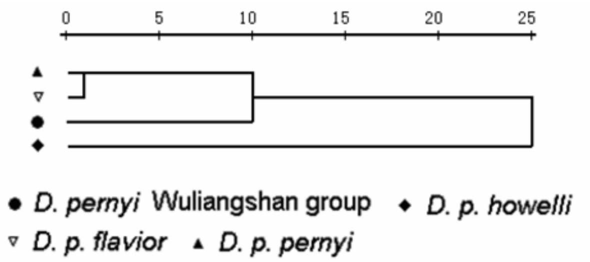

Fig. 3. – Dendrogram from UPGMA cluster analysis of Mahalanobis distances among the four subspecies groups recognized here.

DISCUSSION

Subspecies differentiation of *D. pernyi* in southwestern China

In earlier studies (Allen, 1940; Ellerman, 1940; Ellerman & Morrison-Scott, 1950; Moore & Tate, 1965; Corbet & Hill, 1992), 3 subspecies of *D. pernyi* were recognised in southwestern China: *D. p. howelli*, *D. p. pernyi*, and *D. p. flavior*. On the basis of 15 cranial measurements, the results of multivariate analysis (Fig. 1) confirmed these three subspecies. However, in the present study, one new group was revealed: the *D. pernyi* Wuliangshan group. The group was first suggested by the results of the principal component analyses, and subsequently corroborated by differences in the coefficient of difference (C.D.). The results of cluster analyses (Fig. 3) indicate that *D. p. pernyi* and *D. p. flavior* cluster closely together, and indicates the high degree of similarity in the 15 cranial measurements between the two groups. Moreover, this suggests that these two groups might be closely related. On the other hand, *D. p. howelli* is the most distinct group. As the area of distribution of the *D. pernyi* Wuliangshan group is separated from other subspecies by rivers, it has likely adapted to local environmental characteristics.

Finally, the distribution area of the different groups (Fig. 2) indicates that each of them has its own area of distribution, suggesting that they are geographically different subspecies (groups). We therefore suggest that the samples of Mt. Wuliangshan should be assigned to a separate subspecies of *D. pernyi*, but, more studies, especially molecular data analysis should be performed to confirm this.

Relationships between subspecies differentiation of *D. pernyi* and geographical evolution in southwestern China

The study indicates that there are at least 4 subspecies (groups) of *D. pernyi* in southwestern China. The area covered by these subspecies (southeastern Tibet, western Sichuan province, southwestern, western, and northwestern Yunnan province, southwestern Guangxi province, and southwestern Guizhou province) is not only recognized by the highest species diversity in China, but is also well known to include some of the most abundant biodiversity areas in the world (Chen, 2002). In his book, Sun (1996) indicates that many complex geological changes took place in these areas during the Cenozoic, especially from the end of the Tertiary to the early stage of the Pleistocene. The collision of the Indian and Eurasian plates resulted in the drastic uplifting of Tibet-Qinghai plateau and rapid river cutting in these areas. Subsequently, high mountains and deep gorges may have acted as barriers to gene flow and may have promoted elevated rates of speciation. Our results also suggest that rivers function as barriers in subspecies differentiation: the Nujiang River acts as a barrier to separate *D. p. howelli* from other subspecies of *D. pernyi.* The *D. pernyi* Wuliangshan group, on the other hand, is distinctly separated from *D. p. flavior* by the Honghe River.

Zeng (1991) indicated that the (pre-)historic Jinshajiang River would have been a southward flowing river in the earlier Pleistocene, parallel along the Nujiang River and the Lancangjiang River, and continuing southeastward along the Mt. Wuliangshan area. Clark et al. (2004) also considered that the (pre-)historic Jinshajiang River flowed into the Honghe River in its early times, but later changed its flow. In other words, in the early Pleistocene, the (pre-)historic Jinshajiang River flowed into the Honghe River and may have acted as a barrier to separate the Mt. Wuliangshan area from adjacent eastern and northeastern areas (such as Kunming, Anning, and Binchuan areas). During the later geological times, this river changed its flow and became the current Jinshajiang River.

From a biogeographical point of view, subspecies differentiation of *D. pernyi* reflects the isolating effects of rivers, but, in order to estimate the differentiation time of these subspecies, and the current rivers' resultant effects on the subspecies differentiation, molecular data, especially phylogenies of subspecies of *D. pernyi* are needed.

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APPENDIX

Specimens examined in the study

D. p. howelli N=46

Yunnan Province: Longling (KIZ 620021, 620022, 620027); Tengchong (KIZ 539, 548, 565, 598, 601, 650299, 76315); Lushui (KIZ 74011, 74093, 74095, 74127, 74166, 74179, 74197, 74198, 74199, 74240, 74263, 74282, 74283, 74309, 74308, 74334, 74380, 74382); Gongshan (KIZ 73406, 73423, 73446, 73560, 73639, 73640, 73641, 73645, 73683, 73690, 73720, 73721, 73719, 73816, 73819, 73827, 73833, 73864).

D. p. pernyi N=43

Sichuan Province: Yajiang (KIZ 820272, 820277); Muli (KIZ 641, 611, 650092, 650093, 820891); Daofou (KIZ 820841, 820243, 820244); Daocheng (KIZ 810272, 810350, 810356, 810357).

Yunnan Province: Deqin (KIZ 79540, 79565, 79609, 79683, 79454, 79465, 79526); Zhongdian (KIZ 810066, 810424); Binchuan (KIZ 810642, 810643, 810688, 810694, 810695, 810706, 810707); Weixi (KIZ 810517); Kunming (KIZ 630094, 630100, 640204, 640206, 640560, 640561, 640562, 67036, 67037, 76688); Anning (KIZ 63I-0207, 63I-0272).

D. p. flavior N=20

Guizhou Province: Xingyi (KIZ 631022, 631023, 631028, 631036, 631068, 631069, 631072, 631096, 631097, 631098, 631103, 631104, 631106, 631107, 631128, 631200, 631275); Rongjiang (KIZ 630641).

Guangxi Province: Jingxi (IOZ 21460, 21460A).

D. pernyi Wuliangshan group N=5

Yunnan Province: Jingdong, Wuliangshan (KIZ 640040, 640365, 640366, 640372, 640385).

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