动 物 学 研 究 2012，Apr. 33(2): 119−126 CN 53-1040/Q ISSN 0254-5853
Zoological Research DOI：10.3724/SP.J.1141.2012.02119

Cranial morphometric study of four giant flying squirrels (*Petaurista*) (Rodentia: Sciuridae) from China

LI Song[1,*], YU Fa-Hong[2], LÜ Xue-Fei[3, 4]

(1. *State Key Laboratory of Genetic Resources and Evolution*, *Kunming Natural History Museum of Zoology*, *Kunming Institute of Zoology*, *the Chinese Academy of Sciences*, *Kunming* 650223, *China*; 2. *ICBR*, *University of Florida*, *Gainesville*, *FL* 32610, *USA*; 3. *Institute of Zoology*, *the Chinese Academy of Sciences*, *Beijing* 100101, *China*; 4. *Graduate School of the Chinese Academy of Sciences*, *Beijing* 100049, *China*)

Abstract: The present study revisited the controversial taxonomic status of *Petaurista yunanensis*, *P. philippensis*, *P. hainana*, and *P. petaurista* by using a considerably extended set of morphometrical characters (26 cranial variables from 60 adult specimen skulls). The results revealed no sexual dimorphism in any of the four species but confirmed significant craniometric differences among the four species in both the principal components analysis (PCA) and discriminant function analysis (DFA), with the greatest distinction observed between *P. petaurista* and other *Petaurista* species. Both univariate and multivariate analysis indicated that the morphological differences between *P. yunanensis* and *P. philippensis* were less than that between *P. philippensis* and *P. hainana*. The morphometric results were concordant in geographic patterns with mtDNA data from previous studies and indicated that *P. petaurista*, *P. hainana, P. philippensis*, and *P. yunanensis* could be recognized as valid species.

Key words: *Petaurista;* Cranial variables; Statistical analysis; Species

中国四种鼯鼠的头骨形态学

李 松[1,*], 俞发宏[2], 吕雪霏[3, 4]

（1. 中国科学院昆明动物研究所遗传资源与进化国家重点实验室, 昆明动物博物馆, 云南 昆明 650223; 2. 美国佛罗里达大学 生物技术研究中心, 佛罗里达 32610, 美国; 3. 中国科学院动物研究所, 北京 100101; 4. 中国科学院研究生院, 北京 100049）

摘要：针对长期以来有关鼯鼠分类地位的争议, 该研究基于查看、测取 60 号鼯鼠成体头骨(每号头骨测取 26 个可量性状)共计 1 560 个数据, 运用多变量、单变量分析方法, 对鼯鼠属(*Petaurista*)中的 *P. yunanensis, P. philippensis, P. hainana* 以及 *P. petaurista* 头骨可测量数据进行了统计学分析, 以探讨上述 4 种鼯鼠的头骨形态差异以及 *P. yunanensis* 和 *P. hainana* 的分类地位。结果显示：(1)上述可测量头骨性状在该 4 种鼯鼠中不存在性二型现象; (2)上述 4 种鼯鼠在所测量的头骨性状上两两间均存在显著差异; (3)*P. philippensis* 与 *P. hainana* 之间的头骨形态差异程度远大于 *P. yunanensis* 与 *P. philippensis* 之间的差异。该结果在宏观统计分析水平上为上述 4 种鼯鼠的种地位有效性提供了佐证, 与前人基于分子水平(mtDNA)的种地位有效性研究结果相似。

关键词：鼯鼠属; 头骨变量; 统计分析; 物种
中图分类号：959.837; Q954.54+2 **文献标志码：**A **文章编号：**0254-5853-(2012)02-0119-08

Giant flying squirrels (*Petaurista*) occur in lowlands and mountains up to 4 000 m in East and Southeast Asia from Pakistan and Kashmir. Currently, eight to ten forms are commonly accepted as valid *Petaurista* species, with each divided into various forms or subspecies (Corbet & Hill, 1992; Wang, 2003; Thorington & Hoffmann, 2005). Because various species and subspecies with significant geographical variations are included within this genus, the taxonomy and the intra- and inter-specific phylogenetic relationships remain unclear and inconclusive. Several taxonomic studies and more than 18 *Petaurista* forms, subspecies, or species have been

Received date: 2011-07-25; Accepted date: 2011-11-20
Foundation items: National Natural Science Fund of China (30970332); National Basic Research Program of China (973 Program) (2007CB411600); Natural Science Found of Yunnan Province (2007C099M); Special Subjects Funds of National Natural Science Fund of China (J0930004)
* Corresponding author (通信作者), E-mail: lis@mail.kiz.ac.cn
收稿日期：2011-07-25；接受日期：2011-11-20

described on the basis of dental and cranial characteristics and external structures (Allen, 1940; Corbet & Hill, 1992; Ellerman, 1940; Hoffmann et al, 1993; Wang, 2003; Zhang et al, 1997).

Petaurista are widely distributed in China and more than ten distinct species are recognized (Corbet & Hill, 1992; Wang, 2003; Zhang et al, 1997). However, several of these species are referenced with very few specimens or based solely on skins with no corresponding skulls (Allen, 1940; Ellerman, 1940), and some are actually the synonyms or subspecies of either the *P. petaurista* complex or the *P. philippensis* complex due to intraspecific geographic variations across their distributions in Asia.

Corbet & Hill (1992) treated *P. albiventer* in Pakistan and southwest China as the synonym of *P. petaurista* and recognized *P. philippensis* as a distinct species consisting of many forms formerly assigned to *P. petaurista*, including forms distributed in Taiwan (*P. grandis*), southwest Yunnan (*P. yunanensis*), and Hainan (*P. hainana*). After comparing the pelage and cranial characteristics of *P. petaurista* and *P. hainana*, Huang et al (1995) considered *P. hainana* to be a valid species, but Wang (2003) treated *P. hainana* as a subspecies of *P. yunanensis*. Thorington & Hoffmann (2005) treated all *Petaurista* forms as eight valid species instead of nine as suggested by Corbet & Hill (1992), but they accepted the specific validity of *P. philippensis* and the subspecies status of *P. yunanensis* and *P. hainana*. Patterns of genetic variations observed in the complex of *P. philippensis* based on cytochrome *b* genes indicated that *P. hainana, P. albiventer*, and *P. yunanensis* could be distinct species (Yu et al, 2006). Some forms included in *P. philippensis* warranted separate specific rank based on molecular data (Oshida et al, 2000a, b; Yu et al, 2006), but without further evidence from morphometric data, much remains to be done to ascertain conclusively these specific conclusions.

Most recent phylogenetic studies have focused on molecular data analysis, but tracing changes in morphological characters is also an important way to evaluate the distribution of the characters on which those taxonomic units are based. Morphometric data are important to understand biological phenomena and have been used to evaluate cranial, dental, and body measurements of many mammals (Muñoz-Muñoz & Perpinan, 2010; Slábová & Frynta, 2007; Zelditch et al, 2004). Quantitative analysis of intra- and inter-specific variations at the morphological level is useful for detecting patterns of geographic variations and delimiting intra- or inter-specific evolutionary units. To date, however, there are currently no published reports of quantitative analysis based on morphological characteristics that would allow the identification of the morphotypes in the complex of *P. philippensis* and *P. petaurista*.

To discuss the taxonomic relationships of *P. philippensis*, *P. yunanensis*, *P. hainana*, and *P. petaurista* and test previous taxonomic hypotheses, the present study conducted a comprehensive morphometric study on the above Chinese *Petaurista* species based on samples subsequently collected from southwest Yunnan and the Island of Hainan, China. Multivariate analyses were used to produce an overview of the associations between morphological variables and species patterns and discuss the taxonomic implications of these flying squirrels. Our morphometric study could be complementary to studies of variations of DNA sequences in flying squirrels.

1 Materials and Methods

1.1 Specimens and data collection

According to the taxonomic assignments of Allen (1940) and Zhang et al (1997), a total of 60 intact adult skull specimens of *P. petaurista, P. yunanensis, P. hainana,* and *P. philippensis* were examined for morphometric study (Append. I). These specimens are from the Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, CAS) (Kunming, China), the Institute of Zoology, Chinese Academy of Sciences (IOZ, CAS) (Beijing, China), and the Guangdong Entomological Institute (GDEI) (Guangzhou, China).

Twenty-six cranial variables taken with a digital caliper to the nearest 0.01 mm were used in the morphometric analysis as described by Musser (1979), Musser & Heaney (1992), Xia et al (2006), and Yang et al (2005), and depicted in Fig. 1 following Huang's description (1995). The variables measured included: maximum length of skull (GLS), condylobasal length (CBL), basal length (BL), occipito-nasal length (ONL), palatal length (PL), length of palatal bridge (PBL), length of upper tooth row (LUTR), length of upper molars (LUM), maximum upper molars breadth (GUMB), rostral length (ROL) and breadth (ROB), auditory bulla length (ABL) and breadth (ABB), breadth of zygomatic plate (BZP), breadth of occipital condyles

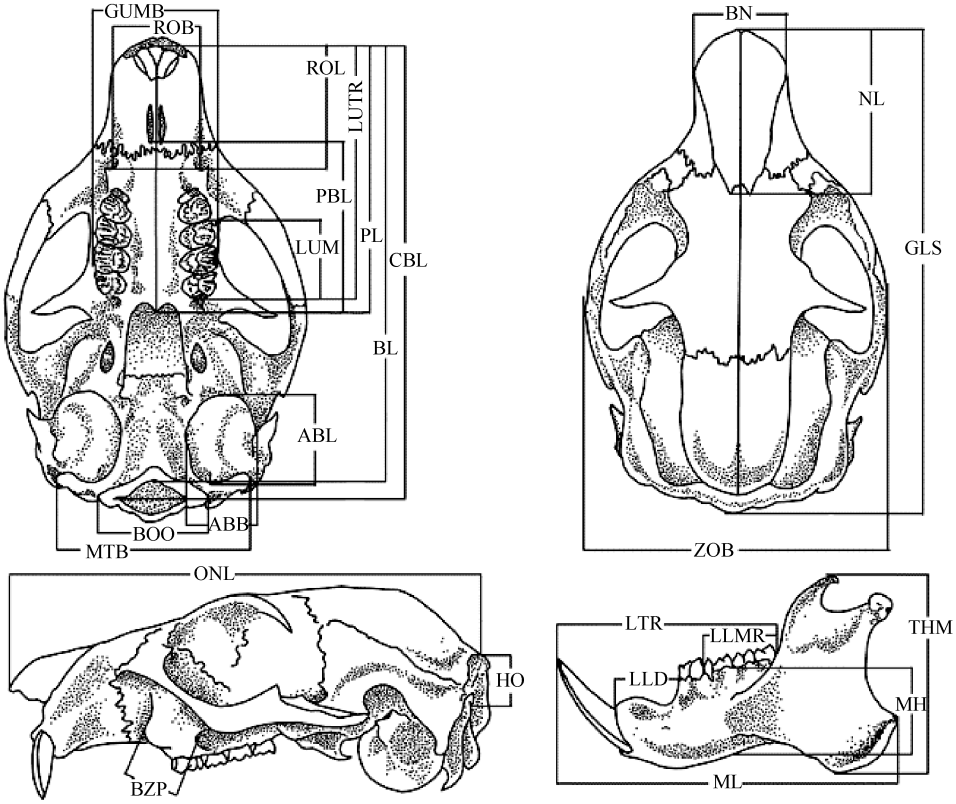

Fig. 1 Illustration of the 26 cranial variables used in the study

(BOO), height of occipital (HO), zygomatic breadth (ZOB), mastoid breadth (MTB), nasal length (NL) and breadth (BN), mandible length (ML), height of mandible (THM), length of lower diastema (LLD), length of lower molar row (LLMR), length of lower tooth row (LTR), and mandibular height (MH). In addition, the head and body length (HB), tail length (TL), hind foot length (HFL), and ear length (EL), which were compared to the original measurements labeled on the skins by the collectors.

1.2 Data analysis

Statistical analyses were performed using SPSS version 11.0 (SPSS Inc., Chicago, IL, USA). All variables were transformed into logarithms to eliminate the bias effect of large measurements in multivariate analysis (D'Elía & Pardiñas, 2004). Statistical differences were considered significant at $P<0.05$.

In this study, all related data were subjected to one-way ANOVA for calculating mean±*SD*. *T*-test was used to assess the sexual dimorphism between male and female groups by comparing the group means of cranial measurements. Multiple comparisons between taxa were made for all 26 cranial measurements to evaluate variations between samples. Multivariate analyses, including principal components analysis (PCA) and discriminant function analysis (DFA), were carried out to evaluate the degree of similarity and dissimilarity in cranial structures between the putative species and to determine how the taxa were related when all cranial characters measured are considered simultaneously.

The PCA is based upon the variance-covariance matrix of the log-transformed variables. The eigenvector scores describing the relative significance of each variable to the principal components were used to compare the cranial morphological similarities and differences. The PCA scatter-plot visually represented the variation among different individuals of the samples. The DFA was performed to investigate the integrity of the pre-defined groups and to predict group membership of specimens with the linear models of variables. Based on the derived discriminant functions, each individual was allocated to the group with nearest centroid, and the proportion of individuals allocated to each group was calculated.

2 Results

Mean±*SD* of 4 external and 26 cranial variables for the four taxa are presented in Tab. 1.

Tab. 1 Four external and 26 cranial measurements of four species of *Petaurista*: (mean±*SD*)/range

	GLS	CBL	BL	ONL	PL	PBL	LUTR	LUM
P. yunanensis	77.16±2.73	71.55±2.51	66.29±2.58	76.90±2.70	40.08±1.72	26.97±1.06	37.57±1.36	12.46±0.42
n=15	71.67−81.56	67.79−75.68	62.24−70.53	71.64−81.09	37.55−43.05	25.05−28.59	35.73−39.80	11.68−13.06
P. philippensis	79.10±2.01	73.93±2.14	68.60±2.09	78.70±2.08	41.82±1.47	28.10±1.32	38.94±1.13	12.46±0.47
n=21	75.35−82.71	69.10−77.75	64.44−72.39	74.96−82.77	39.11−43.80	26.13−30.64	37.27−40.77	11.67−13.29
P. hainana	73.45±1.90	68.92±1.80	63.83±1.77	72.82±1.83	39.05±1.20	25.35±0.92	36.14±1.12	11.16±0.31
n=17	68.96−76.68	65.19−72.04	60.34−66.86	68.59−75.52	36.93−41.25	23.96−27.29	34.04−37.99	10.58−11.78
P. petaurista	63.25±2.12	59.40±2.00	55.05±1.84	62.84±2.24	33.64±1.54	22.23±1.25	30.88±0.98	9.92±0.43
n=7	60.16−66.43	56.98−62.67	52.69−58.30	59.39−66.14	32.26−35.86	20.25−23.80	29.72−32.34	9.15−10.42

	GUMB	ROL	ROB	ABL	ABB	BZP	BOO	HO
P. yunanensis	20.25±0.89	16.61±1.07	15.64±0.82	13.28±0.72	10.17±0.45	8.20±0.66	18.27±0.77	8.43±0.79
n=15	18.70−21.46	14.94−18.14	13.94−16.85	12.22−14.62	8.83−10.61	6.94−9.12	17.00−19.67	6.87−9.76
P. philippensis	20.43±0.79	17.63±0.81	16.56±0.72	14.81±0.67	11.18±0.48	7.73±0.43	18.58±0.88	8.53±0.57
n=21	19.07−22.57	16.05−18.93	15.36−18.11	13.73−15.76	10.50−12.41	6.60−8.74	17.48−20.22	7.47−9.57
P. hainana	19.26±0.72	15.88±0.76	16.12±0.73	14.27±0.36	10.53±0.63	6.67±0.46	17.48±0.82	9.45±0.69
n=17	18.14−20.57	14.06−17.34	14.51−17.30	13.60−14.91	9.36−11.48	5.96−7.66	15.57−18.62	8.27−10.72
P. petaurista	16.60±0.46	12.72±0.51	13.81±0.65	13.19±0.38	9.33±0.48	6.04±0.35	14.39±0.53	7.61±0.24
n=7	16.05−17.46	12.09−13.30	12.65−14.53	12.81−13.88	8.54−9.78	5.53−6.53	13.51−15.00	7.34−8.04

	ZOB	MTB	NL	BN	ML	THM	LLD	LLMR
P. yunanensis	51.00±1.74	29.34±1.11	23.82±1.56	15.15±1.00	53.96±2.09	31.88±1.19	10.30±0.81	13.66±0.45
n=15	48.18−54.40	27.26−31.24	20.59−26.05	13.94−16.91	49.54−57.31	29.95−34.00	8.95−12.01	13.13−14.66
P. philippensis	51.42±1.72	30.05±1.31	24.34±1.46	15.30±0.96	54.82±1.33	32.23±1.23	10.82±0.65	14.03±0.56
n=21	46.48−54.73	27.71−32.11	21.98−27.34	13.53−17.40	52.31−57.68	29.61−34.64	9.42−11.94	13.16−15.37
P. hainana	49.09±1.24	27.58±1.07	22.76±1.23	14.61±0.61	50.92±1.21	30.08±1.25	10.21±0.53	12.53±0.35
n=17	46.79−51.34	25.96−29.39	20.89−24.71	13.38−15.50	48.81−52.71	27.96−32.40	8.97−10.88	11.83−13.12
P. petaurista	41.34±1.10	22.67±0.92	19.47±1.31	11.13±0.47	43.42±1.11	26.08±1.07	8.52±0.42	10.74±0.26
n=7	39.16−42.50	21.54−23.65	17.84−21.15	10.39−11.71	42.08−44.93	24.65−28.04	7.82−9.20	10.39−11.16

	LTR	MH	HB	TL	HFL	EL
P. yunanensis	35.64±1.21	12.21±0.65	443.07±26.80	528.69±49.19	82.93±4.91	44.14±3.32
n=15	33.95−37.19	11.38−13.80	420.00−520.00	440.00−620.00	75.00−92.00	40.00−52.00
			n=14	*n*=13	*n*=14	*n*=14
P. philippensis	36.99±1.18	12.31±0.52	459.53±33.17	549.95±41.89	83.42±7.74	49.21±4.20
n=21	34.98−39.89	11.02−12.95	384.00−530.00	470.00−620.00	65.00−100.00	42.00−58.00
			n=19	*n*=19	*n*=19	*n*=19
P. hainana	34.21±0.87	11.61±0.41	413.63±27.29	486.31±30.60	77.00±5.21	41.59±4.12
n=17	32.35−35.41	10.88−12.32	348.00−450.00	400.00−520.00	70.00−90.00	30.00−47.00
			n=16	*n*=16	*n*=17	*n*=17
P. petaurista	28.96±0.83	9.77±0.25	337.50±3.54	360.00±0.00	60.00±0.00	42.00±0.00
n=7	27.81−29.90	9.35−10.06	335.00−340.00	360.00−360.00	60.00−60.00	42.00−42.00
			n=2	*n*=2	*n*=2	*n*=2

Variable codes are given in the text and Fig. 1.

2.1 Univariate analysis

Univariate comparison revealed that the means of all variables were significantly different and, in general, tended to become progressively larger from *P. petaurista*, *P. hainana*, *P. yunanensis,* to *P. philippensis.* The *t*-tests of Equality of Group Means on 54 (30 males, 24 females) out of 60 specimens indicated there was no sexual dimorphism in the 26 cranial variables in the four *Petaurista* groups (Tab. 2). Quantitative pairwise comparisons of all cranial variables between taxa indicated that *P. yunanensis* was morphologically similar to *P. philippensis*, with 11 cranial measurements showing no significant difference ($P>0.05$) (Tab. 3). Also, five cranial variables were not significantly different between *P. yunanensis* and *P. hainana*.

2.2 Multivariate analysis

In PCA, the eigenvalues for the first three principal components were 20.62, 1.64 and 0.85, respectively, accounting for 88.91% of the total variance (Tab. 4). Most characteristics with high positive loadings on the first principal component suggested that this component (79.32% of the total variance) represented size variation within the samples. All specimens on the first principal component were clustered as three groups, *P. petaurista*, *P. hainana*, and the group of *P. yunanensis* and *P. philippensis* with considerable overlaps. The second principal component (6.32% of the total variance) was strongly correlated with ROB, ABL, ABB, and BZP (loadings>0.50), and the third principal component (3.27% of the total variance) was correlated primarily

Tab. 2 *t*-tests of Equality of Group Means for male and female (variable codes are given in the text and Fig.1)

	Wilks' Lambda	*F*	*df*1	*df*2	*P*
GLS	0.982	0.964	1	52	0.331
CBL	0.976	1.274	1	52	0.264
BL	0.980	1.087	1	52	0.302
ONL	0.981	1.021	1	52	0.317
PL	0.988	0.636	1	52	0.429
PBL	0.998	0.099	1	52	0.754
LUTR	0.993	0.386	1	52	0.537
LUM	0.994	0.297	1	52	0.588
GUMB	0.983	0.924	1	52	0.341
ROL	1.000	0.006	1	52	0.939
ROB	0.959	2.214	1	52	0.143
ABL	0.986	0.746	1	52	0.392
ABB	0.978	1.191	1	52	0.280
BZP	0.956	2.368	1	52	0.130
BOO	0.993	0.377	1	52	0.542
HO	0.996	0.233	1	52	0.632
ZOB	0.967	1.775	1	52	0.189
MTB	0.993	0.359	1	52	0.552
NL	0.998	0.106	1	52	0.746
BN	0.994	0.291	1	52	0.592
ML	0.992	.432	1	52	0.514
THM	0.955	2.438	1	52	0.124
LLD	0.986	0.739	1	52	0.394
LLMR	0.999	0.071	1	52	0.791
LTR	0.994	0.322	1	52	0.573
MH	0.981	0.988	1	52	0.325

$P<0.05$

with HO (loadings>0.50) (Tab. 4). The first two principal components separated all specimens as four distinct groups (Fig. 2).

The DFA identified the major patterns of morphological divergence in the crania among the four *Petaurista* groups. The variation pattern reflected by the first two discriminant functions was consistent with the morphological variations observed in the PCA, and all samples were clearly clustered as four distinguishable groups based on the 1st and 2nd discriminant functions (Fig. 3). In specimen reclassification by DFA, all individuals were properly assigned to their original groups on the basis of the studied measurements. Fig. 4 is the geographic distributions of all *Petaurista* samples used in this study.

3 Discussion

One contentious issue regarding the Chinese *Petaurista* is the taxonomic status of *P. yunanensis*, *P. philippensis*, *P. hainana*, and the populations of *P. petaurista* in China, which have long been controversial (Corbet & Hill, 1992; Ellerman, 1940; Ellerman & Morrison-Scott, 1950; Hoffmann et al, 1993; Huang et al,

Tab. 3 Multiple Comparisons between the four study species

Variables	*P. yunanensis* vs *P. philippensis*		*P. yunanensis* vs *P. hainana*		*P. yunanensis* vs *P. petaurista*		*P. philippensis* vs *P. hainana*		*P. philippensis* vs *P. petaurista*		*P. hainana* vs *P. petaurista*	
	Mean Difference	*P*	Mean Difference	*P*	Mean Difference	*P*	Mean Difference	*P*	Mean Difference	*P*	Mean Difference	*P*
GLS	0.011*	0.015	0.021**	0.000	0.086**	0.000	0.032**	0.000	0.097**	0.000	0.065**	0.000
CBL	0.016*	0.002	0.016*	0.003	0.081**	0.000	0.033**	0.000	0.097**	0.000	0.065**	0.000
BL	0.015*	0.003	0.016*	0.002	0.081**	0.000	0.031**	0.000	0.095**	0.000	0.064**	0.000
ONL	0.010*	0.027	0.024**	0.000	0.088**	0.000	0.034**	0.000	0.098**	0.000	0.064**	0.000
PL	0.019*	0.001	0.011	0.058	0.076**	0.000	0.030**	0.000	0.095**	0.000	0.065**	0.000
PBL	0.018*	0.008	0.027**	0.000	0.084**	0.000	0.045**	0.000	0.102**	0.000	0.057**	0.000
LUTR	0.015*	0.002	0.017*	0.001	0.085**	0.000	0.032**	0.000	0.100**	0.000	0.068**	0.000
LUM	0.001	0.911	0.048**	0.000	0.099**	0.000	0.047**	0.000	0.099**	0.000	0.051**	0.000
GUMB	0.003	0.542	0.022*	0.001	0.086**	0.000	0.025**	0.000	0.089**	0.000	0.064**	0.000
ROL	0.026*	0.001	0.019*	0.018	0.116**	0.000	0.046**	0.000	0.142**	0.000	0.096**	0.000
ROB	0.025*	0.001	0.013	0.070	0.054**	0.000	0.011	0.103	0.078**	0.000	0.067**	0.000
ABL	0.047**	0.000	0.032**	0.000	0.002	0.771	0.015*	0.012	0.050**	0.000	0.034**	0.000
ABB	0.041**	0.000	0.014	0.065	0.038**	0.000	0.027**	0.000	0.079**	0.000	0.052**	0.000
BZP	0.025*	0.015	0.089**	0.000	0.132**	0.000	0.065**	0.000	0.107**	0.000	0.043*	0.002
BOO	0.007	0.293	0.019*	0.007	0.104**	0.000	0.027**	0.000	0.111**	0.000	0.084**	0.000
HO	0.006	0.578	0.051**	0.000	0.043*	0.005	0.044**	0.000	0.049*	0.001	0.094**	0.000
ZOB	0.003	0.462	0.016*	0.001	0.091**	0.000	0.020**	0.000	0.094**	0.000	0.075**	0.000
MTB	0.010	0.090	0.027**	0.000	0.112**	0.000	0.037**	0.000	0.122**	0.000	0.085**	0.000
NL	0.009	0.311	0.019*	0.044	0.088**	0.000	0.029*	0.002	0.097**	0.000	0.068**	0.000
BN	0.004	0.600	0.015	0.083	0.133**	0.000	0.020*	0.017	0.138**	0.000	0.118**	0.000
ML	0.007	0.114	0.025**	0.000	0.094**	0.000	0.032**	0.000	0.101**	0.000	0.069**	0.000
THM	0.005	0.383	0.025**	0.000	0.087**	0.000	0.030**	0.000	0.092**	0.000	0.062**	0.000
LLD	0.022*	0.023	0.003	0.767	0.082**	0.000	0.025*	0.008	0.103**	0.000	0.079**	0.000
LLMR	0.012*	0.018	0.037**	0.000	0.104**	0.000	0.049**	0.000	0.116**	0.000	0.067**	0.000
LTR	0.016*	0.001	0.018**	0.000	0.090**	0.000	0.034**	0.000	0.106**	0.000	0.072**	0.000
MH	0.003	0.583	0.022*	0.002	0.096**	0.000	0.025**	0.000	0.100**	0.000	0.075**	0.000

*: $P<0.05$; **: $P<0.001$

Tab. 4 Factor loadings and percentage of variance explained for principal component analysis (variable codes are given in the text and Fig. 1)

Variables	PC1	PC2	PC3
GLS	0.898	0.347	0.221
CBL	0.868	0.379	0.212
BL	0.876	0.388	0.227
ONL	0.904	0.336	0.201
PL	0.841	0.422	0.224
PBL	0.872	0.347	0.024
LUTR	0.889	0.375	0.192
LUM	0.944	0.164	-0.016
GUMB	0.839	0.250	0.330
ROL	0.820	0.420	0.151
ROB	0.535	0.586	0.470
ABL	0.129	0.895	0.207
ABB	0.393	0.766	0.085
BZP	0.833	-0.608	-0.028
BOO	0.847	0.279	0.258
HO	0.084	0.191	0.943
ZOB	0.852	0.250	0.370
MTB	0.882	0.307	0.265
NL	0.745	0.357	0.317
BN	0.757	0.339	0.389
ML	0.919	0.291	0.219
THM	0.875	0.260	0.208
LLD	0.709	0.401	0.372
LLMR	0.914	0.275	-0.002
LTR	0.883	0.391	0.157
MH	0.838	0.288	0.242
Eigenvalues	20.62	1.64	0.85
Variance explained (%)	79.32	6.32	3.27

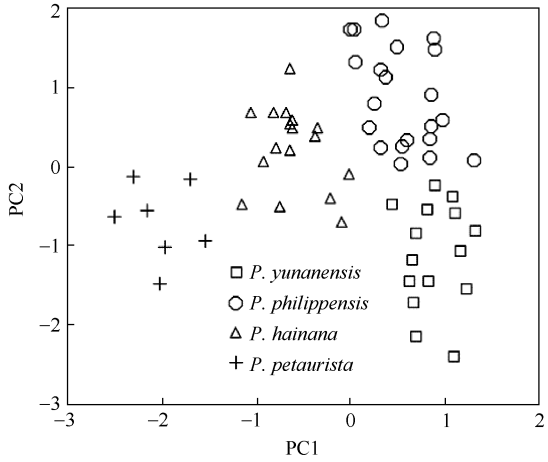

Fig. 2 Scatterplots of the samples in PCA space

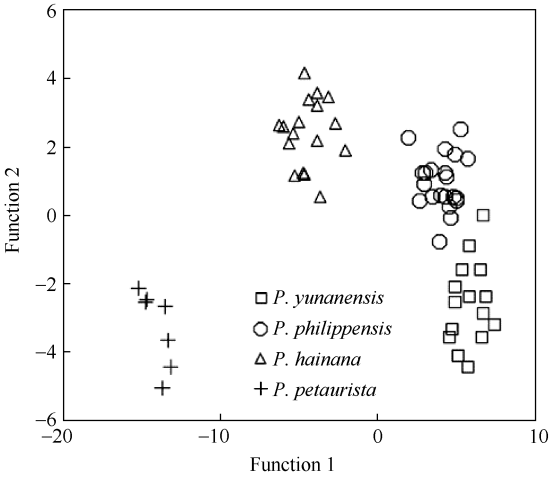

Fig. 3 Plot of the samples of the four *Petaurista* species on discriminant canonical function 1 and 2

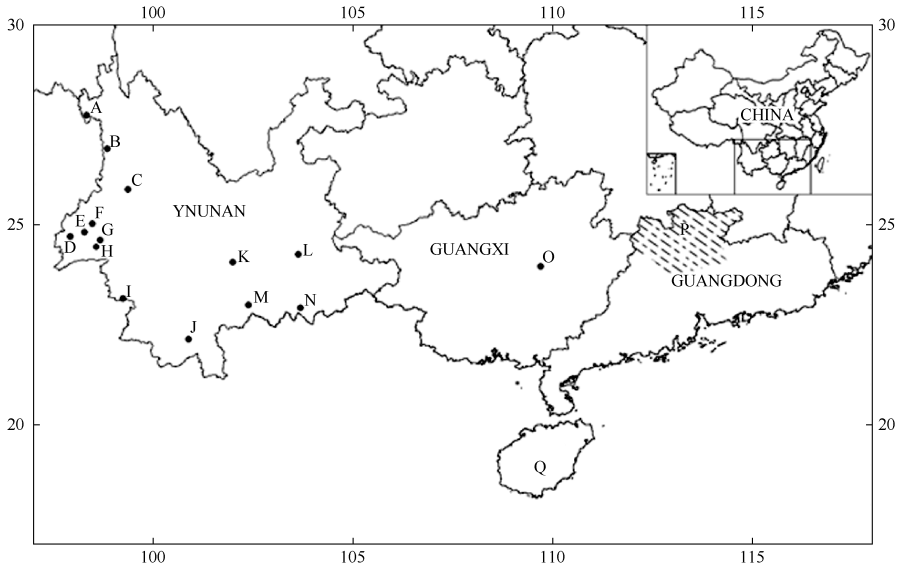

Fig. 4 Geographic distributions of samples used in the study

A: Dulongjiang; B: Bijiang; C: Yunlong; D: Yingjiang; E: Lianghe; F: Tengchong; G: Longling; H: Luxi; I: Cangyuan; J: Xishuangbanna; K: Xinping; L: Mile; M: Lvchun; N: Pingbian; O: Xiangzhou; P: Northern Guangdong; Q: Hainan.

1995; Oshida et al, 2000a, 2000b; Thorington & Hoffmann, 2005; Wang, 2003; Yu et al, 2006). By using a considerably extended set of morphometrical characters (26 cranial variables) and applying multivariate morphometric analyses, results of the present study confirmed the significant craniological differences in *P. petaurista*, *P. hainana*, *P. yunanensis*, and *P. philippensis*, with *P. petaurista* having the most pronounced morphological variations, particularly in metrical components of cranial and body size.

Pelage coloration had been applied for classification of flying squirrels and led to many taxonomical disagreements due to numerous color variations within *Petaurista*, even between different sexes (Allen, 1940; Ellerman & Morrison-Scott, 1950; Oshida et al, 2004b). A series of color variations in pelage were observed among the *Petaurista* forms including both sexes (Allen, 1940; Oshida et al, 2004a), but the pairwise comparison of each of the 26 cranial variables revealed no sexual dimorphism in any of the four groups, implying that the divergence of coloration patterns in forms was due to environmental or genetic fluctuations over time.

Both univariate and multivariate analysis revealed that the skull morphometric characters used in this study were effective for discriminating the four *Petaurista* groups. Our analyses demonstrated that the four morphotypes of *Petaurista* were distinguished by a number of cranial characteristics. The morphometric variables, which caused the major distinction between those groups, were specifically located in the occipital, supraocular, and rostral regions, as well as in the prootic-squamosal length. Patterns of molecular sequence variations from previous studies (Oshida et al, 2000a; Yu et al, 2006) and the cranial morphological differences observed in this study indicate that *P. hainana, P. philippensis*, and *P. yunanensis* could be recognized as three distinct species. These differences were clear and reinforced the existence of three morphotypes of the complex *P. philippensis*; although the degree and form of the morphological differences might be related to their geographical variations. Even though molecular data suggested that *P. philippensis* is closely related to *P. hainana* and significantly distinct from *P. yunanensis* (Yu et al, 2006), many characteristics beyond those related to external morphology and pelage coloration were observed to be held in common between *P. yunanensis* and *P. philippensis*. A good example is the similarity in the pattern of overall cranial structure in multiple comparison analysis. The degree of the morphological variations between *P. yunanensis* and *P. philippensis* was less than that observed between *P. philippensis* and *P. hainana*, with eleven cranial measurements showing no significant difference ($P>0.05$) (Tab. 3). *Petaurista yunanensis* occurs from extreme southwestern Yunnan into Myanmar and Indochina and is extensively sympatric with *P. philippensis* in southwestern China (Wang, 2003; Zhang et al, 1997). The sharing of morphological characteristics between *P. philippensis* and *P. yunanensis* is related to their similar living conditions.

Petaurista hainana was considered a valid species based on both molecular and morphological data (Huang et al, 1995; Yu et al, 2006). Our morphometric results were concordant with mtDNA data of previous research (Oshida et al, 2000a; Yu et al, 2006) and demonstrated the significant differences between *P. hainana* and *P. yunnanensis*/*P. philippensis*. In both PCA and DFA, *P. hainana* was clearly separated from other three groups (Fig. 2, 3), with 21/26 cranial variables being significantly different ($P<0.05$) (Tab. 3). *Petaurista hainana* is confined to tropical forests on Hainan Island of China and *P. philippensis* and *P. yunanensis* are distributed in mountainous coniferous, dry deciduous and evergreen forests at different elevations in western Yunnan of China. The phenotypic divergence of *P. hainana* in relation to *P. philippensis* and *P. yunanensis* is likely associated with their geographical distributions and living conditions and could be viewed as a reflection of adaptations to various ecological niches. The differences in skull morphology suggest that *P. hainana* is neither the synonym of *P. philippensis* nor a subspecies of *P. yunanensis* or *P. petaurista* (Corbet & Hill, 1992; Thorington & Hoffmann, 2005; Wang, 2003), but a valid species in its own right.

The greatest distinction observed was between *P. petaurista* and other *Petaurista* forms. *Petaurista petaurista* displayed a relatively high level of diversity in skull morphology, with 22/26 cranial variables significantly different from *P. hainana*, *P. philippensis,* and *P. yunanensis* at $P<0.001$ level (Tab. 3). Based on 26 morphological cranial variables, the specimens of *P. petaurista* formed a distinct aggregate in both PCA and DFA (Fig. 2,3), consistent with the results of Oshida et al. (2000a) and Yu et al (2006). It is obvious that *P. petaurista*, *P. hainana*, *P. philippensis,* and *P. yunanensis* are taxonomically distinct and distinct valid species.

Acknowledgments: We thank Prof. ZJ FENG, Prof. Y MA, Prof. GQ QUAN and Prof. QS YANG from the Institute of Zoology, the Chinese Academy of Sciences, and Prof. HJ HU and Prof. P YANG from the Guangdong Entomological Institute (GDEI) for their generous help in checking specimens. We extend special thanks to Mr. Kevin Holland of the University of Florida for advice and help on the manuscript.

Append I: specimens examined

Petaurista yunanensis *n*=15

Yingjiang, Yunnan: IOZ 25849(♂). Gongshan, Yunnan: KIZ 73442(♀), 73445(♂), 73744(♂), 73745(♀), 73823(♂), 830207(♀), 90039(♀), 90043(♀), 90051(♂), 90407. Tengchong, Yunnan: KIZ 76348(♀). Lianghe, Yunnan: KIZ 650236(♂), 650237(♂). Bijiang, Yunnan: KIZ 780102(♀).

Petaurista philippensis *n*=21

Xishuangbanna, Yunnan: IOZ 10457(♂), 10458(♂), 10460(♀), 15041(♀), 15042(♀), 15043(♂), 15044(♂), 61-003(♀). Luxi, Yunnan: IOZ 24009(♂), 24010(♀). Mile,

Yunnan: KIZ 84255(♂), 84258(♂), 84300(♂). Lvchun, Yunnan: KIZ 72104(♀).

Longling, Yunnan: KIZ 620028(♂). Cangyuan, Yunnan: KIZ 78053(♂). Pingbian,

Yunnan: KIZ 84117(♂), 84119(♂). Xinping, Yunnan: KIZ 77017(♀). Yunlong,

Yunnan: KIZ 200369(♀). Yunnan: KIZ 92005.

Petaurista hainana *n*=17

Hainan: GDEI 0403(♀), 0404(♂), 0499(♀), 0524(♂), 0611(♀), 0618(♂), 0621(♀),

0622(♂), 0623(♀), 0624(♂), 0625(♂), 0626(♂), 0703(♂), 0704(♂), 0705(♀),

0714(♀), 0717(♀).

Petaurista petaurista *n*=7

Xiangzhou, Guangxi: IOZ 00433(♂). Northern Guangdong: GDEI 2279, 2284, 2286(♀), 2287, 2288(♂), 2289.

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