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MORPHOMETRICAL COMPARISON ON BACULA OF *PETAURISTA ALBORUFUS* AND *P. PETAURISTA* (RODENTIA: SCIURIDAE) FROM TAIWAN[1]

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Bacular measurements were compared in order to provide fundamental information on morphology and speciation of giant flying squirrels, *Petaurista alborufus* and *P. petaurista* from Taiwan. The baculum of *P. alborufus* showed no morphological difference from that of *P. petaurista.* Based on principal components analysis, *P. alborufus* has a greater magnitude on Component I than *P. petaurista.* In other words, the former has a larger bacular structure in simultaneous multivariate space than the latter. Discriminant functions to identify *P. alborufus* and *P. petaurista* were also constructed. This study agrees with Patterson's suggestion (1983) that selection forces may work on both body size and baculum size.

Petaurista alborufus and *P. petaurista* are two folivorous, arboreal and nocturnal species of giant flying squirrels (genus *Petaurista*) from Taiwan (McCullough, 1974; Nowak and Paradiso, 1983). They occur at elevation from 1,100 to 3,600 m and from 300 to 2,200 m respectively (McCullough, 1974).

Pocock (1923) studied the bacula of some species of flying squirrels, subfamily Petauristinae, and proposed that bacula are as variable in this subfamily as in the whole family of squirrels, the Sciuridae. Also, he provided a figure of the bacula of *P. phillippensis* and described it as:

> "long, stout bone, gradually narrowing from the base to slightly expanded and upturned distal end, which when viewed from the front, is seen to be shaped rather like the widened spout of jug, the lower rim of the spout being evenly rounded."

This is the only literature describing the baculum of *P. petaurista.*

Bacula of other sciurids have been

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studied by Thomas (1915), Wade and Gilbert (1944) and Burt (1957, 1960). Also, bacula have been employed as a criterion for age determination on squirrels (Kirkpatrick and Barnett, 1957). Geographic variation of bacula has been studied in *Eutamias* by Patterson (1984), and in *Dipodomys* by Best and Schnell (1974) and Best (1981). Patterson and Thaeler (1982) proposed that different bacular morphologies probably reflect different behavioral and neuroendocrinological responses from the female during copulation. Patterson (1983) found evidence for the hypothesis that the baculum has a precise function in species-specific reproduction, and thereby exposes to direct selection. Therefore, the reproductive isolation mechanism might be explained by bacular differences between *P. alborufus* and *P. petaurista*, especially in sympatric populations (Marler, 1957).

This study compared bacular measurements of *P. alborufus* and *P. petaurista* by applying multivariate statistical analyses in order to provide fundamental information on morphology and speciation of *P. alborufus* and *P. petaurista* in Taiwan. Based on multivariate statistical analyses, this study also constructed discriminant functions to identify *P. alborufus* and *P. petaurista*. Further research on the basis of molecular, cytological, and behavioral analyses will help to refine the systematic and evolutionary relationships of these taxa.

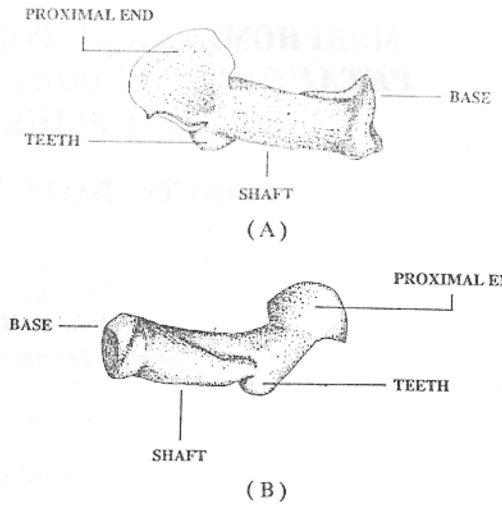

Fig. 1. (A) left lateral and (B) right lateral view of baculum of *Petaurista*.

MATERIALS AND METHODS

Collection and preparation of specimens

One hundred and twelve bacula of giant flying squirrels were purchased in Hsangming, Kaohsiung, Taiwan, R. O. C. from September 1983 to August 1984. Specimens are now deposited in the Smithsonian Institute, Washington D. C., U. S. A.. Bacula cut from fresh carcasses were air dried, and then soft tissues were removed. Four bacular measurements were made to the nearest 0.1 mm using dial calipers, i. e. bacular length (BL): greatest length of balculum (Best and Schnell 1974); bacular width (BW): the greatest width of bacular shaft (Best and Schnell, 1974); bacular height of the proximal end (BHPE): greatest height of proximal end of bacula; and bacular height of base (BHB): greatest width of the posterior end of bacula (Fig. 1). Bacular weight (BWT) was measured in milligrams. Measurements were taken until the same reading was obtained. Age was determined using six classes of molor tooth wear (Day, 1987).

Analyses

Five bacular characters were examined for normality using histograms, means, and standard deviations (BMDP7D, Dixon, 1985). Only adult specimens (tooth wear classes II–VI) were used for analysis (Day, 1987). Principal component analysis of individuals was based on the correlation matrix (Sneath and Sokal, 1973) and calculated with BMDP4M (Dixon, 1985)

R-technique analysis upon dispersion of variables was performed. Uncorrelated linear functions were constructed to explain the variation within the sample population. Test of sphericity reduced the number of components to be interpreted (Pimentel, 1979). The percentage of variance of each variable judged which coefficients should be interpreted (Pimentel, 1979). Component correlation analysis was the Pearson product-moment correlation of the original data with component scores of each component. A small component correlation coefficient might indicate that the coefficients were not significant (Pimentel, 1979; Somers, 1986).

Stepwise discriminant analysis was carried out using BMDP7M (Dixon, 1985). The variables with the largest F-value were entered into a discriminant model if this F-value exceeded a default value of four in BMDP7M (Srivastava and Carter, 1983). Three groups were recognized in stepwise discriminant analysis: LENA, bacula of *P. alborufus* (N=9); A-GRANDIS, bacula of *P. petaurista* tooth wear classes II and III (N=36); B-GRANDIS, bacula of *P. petaurista* tooth wear classes IV to VI (N=78). The stepwise discriminant analysis was used to develop the joint discriminant functions.

RESULTS

Principal components analysis

Male flying squirrels were divided into three groups for the purpose of analyzing bacular measurements. Group LENA contained all *P. alborufus* specimens. Group A-GRANDIS contained *P. petaurista* belonging to tooth wear classes II and III. Group B-GRANDIS contained the tooth wear classes IV to VI of *P. petaurista*. The correlation between tooth wear classes and the five bacular measurements were all not significant ($r_{0.05}$=0.33). Univariate ANOVA indicated that all five bacular characters were significantly different among the three groups (Table 1, p<0.01). *P. alborufus*

Table 1

Summary statistics for untransformed measurements of five bacular characters from nine *P. alborufus* and 104 *P. petaurista*

	LENA		A-GRANDIS		B-GRANDIS	
Characters	Mean	SE	Mean	SE	Mean	SE
BL	96.44	1.23	78.02	.63	81.74	.41
BHB	42.23	1.91	32.66	.56	36.42	.32
BHPE	55.33	1.09	50.21	.43	50.02	.28
BW	12.33	.37	11.28	.18	12.00	.12
BWT	6782.22	447.85	4123.97	173.60	5521.46	103.15

	F	p
MANOVA		
ALL	21.72	0.0000
BL	97.48	0.0000
BHB	37.38	0.0000
BHPE	18.11	0.0000
BW	7.14	0.0012
BWT	39.37	0.0000

*: Characters are defined in text.

Table 2
Eigenvalues of principal component analysis based on correlation matrix and the test of sphericity for five bacular characters from nine *P. alborufus* and 104 *P. petaurista*

Components	Eigenvalue	Cumulative proportion of variance	Sphericity chi-square
1	3.0637	.6127	75.08*
2	.9122	.7952	29.64*
3	.5467	.9045	2.96*
4	.2778	.9610	—
5	.1990	1.0000	—

*: Significant at $p<0.05$.

had a larger bacular structure than *P. petaurista*. A multivariate analysis confirmed that there were significant differences in a simultaneous character among the three groups (Table 1, MANOVA, $p<0.01$).

Three principal components were chosen included 90.5% of total variance (Tables 2 and 3). BL, BHB, BW, and BWT were the four characters with the highest magnitude of coefficients on the first axis. Components II and III were bipolar (i.e. eigenvector has both positive and negative coefficient shape factors). BHPE had the highest coefficient (.822) for component II (Table 3). The sphericity test (Pimentel, 1979) of PCAs indicated that the first three components contain nontrivial information (Table 2). Four characters (BL, BHB, BW, BWT) correlated significantly with the first component from correlation matrix (Table 3, $r_{0.05}=0.184$; Pimentel, 1979), by conducting component correlation analysis.

Component I explained 61.27% of the total variance (Tables 2 and 3). In terms of the contribution made by each character, only BHPE contributed more of its total variance to component II

Table 3
Principal components, component correlations and percentage of variance for each variable based on the correlation matrix of bacular characters from nine *P. alborufus* and 104 *P. petaurista*

Characters*	Principal component			Component correlations**			Percentage of the variance			
	I	II	III	I	II	III	I	II	III	TV***
BL	.835	.231	−.351	.85	.80	.38	94.9	2.2	3.0	2.3
BHB	.887	−.193	−.233	.86	.37	.41	97.4	1.4	1.2	2.5
BHPE	.498	.822	.239	.16	.10	.97	50.6	47.3	2.1	1.4
BW	.754	−.304	.557	.28	.93	.12	87.0	4.3	8.7	2.0
BWT	.881	−.232	−.039	.74	.53	.07	97.9	2.0	0.0	2.4
Variance				3.1	.9	.5				
% of total				61.3	18.3	10.9				

*: Characters are defined in text.
**: $r_{0.05}=0.184$.
***: The total variance (TV) for the first 3 components of each variable (Pimentel, 1979).

(Table 3). There were highly significant differences among the three groups for components I and III ($p<0.01$).

Discriminant analysis

Using a stepwise discriminant analysis (BMDP7M, Dixon, 1985) on bacular characteristics, three classification functions were constructed.

$$AG = 5.67846\,BL + 6.35921\,BHPE + 4.79540\,BW - 0.00935\,BWT - 390.10206$$

$$BG = 5.86463\,BL + 6.22484\,BHPE + 4.47633\,BW - 0.00789\,BWT - 401.56282$$

and

$$L = 7.09593\,BL + 6.82826\,BHPE + 2.58096\,BW - 0.00740\,BWT - 523.00136$$

were classification functions for determining A-GRANDIS, B-GRANDIS, and LENA respectively. By subtraction methods described by Srivastava and Carter (1983), a discriminant system with two discriminant functions was formulated as:

$$Z1 = AG - BG = -0.18617\,BL + 0.13437\,BHPE + 0.31907\,BW - 0.00146\,BWT + 11.40676$$

$$Z2 = AG - L = -1.41747\,BL - 0.46905\,BHPE + 2.21444\,BW - 0.00195\,BWT + 132.89931$$

where Z1, Z2 are canonical variables. Four bacular characters (i.e., BL, BHPE, BW, and BWT) out of five were chosen with high F-values ($F>4.0$). Jackknifed classification percentages for group A-GRANDIS, group B-GRANDIS, and group LENA were 66.7%, 76.9% and 100% respectively.

Standard canonical discriminant functions were:

$$C1 = -0.89877\,BL - 0.29026\,BHPE + 1.40513\,BW - 0.00128\,BWT + 21.90641$$

$$C2 = +0.29427\,BL + 0.66759\,BHPE - 0.37758\,BW - 0.00310\,BWT - 11.43945$$

Means were (1.09828, 0.63346), (−0.3610, −0.47671), and (−4.49849, 0.69783) for A-GRANDIS, B-GRANDIS, and LENA respectively.

DISCUSSION

Morphological description of bacula

The baculum of *P. alborufus* is similar in general morphology to that of *P. petaurista* (Fig. 1). The proximal end of the baculum is fan-shaped, which is similar to that of the *Sciurus* genus (Burt, 1960). The proximal end protrudes from the shaft at an angle of 45.3 to 48.3 degrees in *P. petaurista* and 31.8 to 43.2 degrees in *P. alborufus* (N=5 in each). The cartilage of the penis attaches to the proximal end with connective tissue. A groove is visible along the bacular shaft on the right side. The base is concave from an end view, and connects with a ligament that is tubular before dividing into two bundles. There is a prominent tooth-like projection at the bend between the proximal end and the shaft; this structure is also found in *Glaucomys sabrinus* (Burt, 1960). Pocock (1923) reported a baculum of *Petaurista* lacking the proximal end. This specimen was probably a juvenile, since in our sample, bacula of juveniles without the proximal end were not uncommon.

Principal components analysis

Size appears to be the major difference between the bacula of *P. alborufus* and *P. petaurista.* Bacular length could be a very important character for speciation or it could act as an isolating mechanism. Patterson and Thaeler (1982) suggested that baculum length is not correlated to body size, a hypothesis supported by our study. However, our result was not based on a univariate measurement but on the simultaneous distribution of several variables of both body size (Day 1987) and baculum size. We agree with Patterson's suggestion (1983) that selection forces may work on both body size and baculum size at the same time.

Discriminant analysis

Existing keys based on single characteristics are often inadequate for species determination, especially if identification must be made from skeletons only. However quantitative taxonomy based on an analysis of multidimensional characteristics is often reliable.

P. alborufus and *P. petaurista* can be identified by measurements taken on the baculum. Take measurements (BL, BHPE, BW, and BWT) and substitute the values into discriminant functions Z1 and Z2 (not the classification functions AG, BG, and L). If $Z1>0$ and $Z2>0$, then the bacula belong to members of the *P. petaurista* group A. If $Z1<0$ and $Z1<Z2$, then the bacula belong to members of the *P. petaurista* group B. If $Z2<0$ and $Z2<Z1$ then the bacula belong to specimens of *P. alborufus*. Standardized measurements use the standardized discriminant functions C1 and C2, having the same result as nonstandardized functions. However, the jackknifed correction classification percentages were low for *P. petaurista* group A and group B. In other words, there were 33.3% and 23.1% misclassification possibilities for *P. petaurista* group A and group B respectively. The high percentage of misclassification between GROUP A-GRANDIS and B-GRANDIS indicated that variation between the two different age class groups of adults is smaller than between species.

CONCLUSION

Morphometrical analyses of bacular measurements indicated that *P. alborufus* has a larger bacular structure than does *P. petaurista*. The biases and weaknesses of this study are repetitious measuring, uneven coverage of the shape, uncertain positioning when measuring, and non-homologous comparisons (Bookstein *et al.*, 1985). To confirm the morphometrical difference between *P. alborufus* and *P. petaurista*, size-free principal components analysis (Somers, 1986) and box truss measuring method (Bookstein *et al.*, 1985) should be investigated. To more fully understand species differences of these two species of flying squirrels, karyotypic, biochemical, and morphometrical studies on the genus *Petaurista* should be conducted.

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臺灣地區白面鼯鼠與大赤鼯鼠陰莖骨之形值比較

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由臺灣地區白面鼯鼠 (*Petaurista alborufus*) 與大赤鼯鼠 (*P. petaurista*) 陰莖骨的形值比較，以探討二種之間的分種關係。二者陰莖骨的外部形態沒並有差異。但是在主成份分析的第一主成份軸上，白面鼯鼠的座標值比大赤鼯鼠顯著地較大。意卽前者的陰莖骨構造比後者大。並以判別方程式來建立鑑定二者之數學模式。本研究支持 Patterson (1983) 的假說，卽天擇會同時作用於體型及陰莖骨大小。