

Differentiation in cranial variables among six species of *Hylopetes* (Sciurinae: Pteromyini)

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Abstract: There is some discrepancy in the classification of different species of *Hylopetes*, particularly regarding systematic status of *H. electilis* and *H. phayrei* and their relationship to other species. In the present study, for the first time we have brought together six of the nine *Hylopetes* species and performed statistical analysis of 14 measurable cranial variables, analyzing in total 89 specimens, including *H. electilis*, *H. alboniger*, *H. phayrei*, *H. lepidus*, *H. spadiceus*, and *H. nigripes*. Both univariate and multivariate analysis results indicate that *H. electilis* can not only be obviously distinguished from *H. phayrei*, but also clearly differs from the other four *Hylopetes* species. These results sustain the contention that *H. electilis* is neither a synonym nor subspecies of *H. phayrei*, but should be considered a distinct and valid species. Subsequently, a straightforward discussion on the biogeography of *Hylopetes* in southeastern Asia gives further insight into the differentiation and variety of species belonging to this genus.

Keywords: *Hylopetes*; Morphology; Cranial variables; Statistical analysis; Species

The genus *Hylopetes* (Thomas, 1908) mainly inhabits mountain forests in Asia, ranging from the Himalayas to the Greater Sunda Islands, and including areas of Nepal, China, Indochina, Philippines, Malaysia, and Indonesia (Corbet & Hill, 1992; Hoffmann et al, 1993; Nowak, 1999; Thorington & Hoffmann, 2005). Initially, *Hylopetes* was regarded as a subgenus of *Sciuropterus* (Thomas, 1908), but, based on Pocock's (1923) studies on the morphology of baculum, it was elevated to a full genus. This view, that the arrow-tailed flying squirrel *Hylopetes* in the eastern extreme of the Himalayas and southeastern Asia is a valid genus from the small Kashmir flying squirrel *Eoglaucomys* (A. H. Howell, 1915) in the western Himalayas, has been sustained by subsequent morphological and molecular studies (Nowak, 1999; Oshida et al, 2004; Thorington et al, 1996).

Based on several dental and cranial characteristics as well as external structures, different taxonomists have described varying numbers of *Hylopetes* species (Allen, 1940; Corbet & Hill, 1992; Ellerman, 1940; Ellerman & Morrison-Scott, 1950; Hoffmann et al, 1993; Nowak, 1999; Thorington & Hoffmann, 2005). To date, the maximal number of *Hylopetes* species was put at 13 (Ellerman, 1940), though the latest accepted result is 9

(Thorington & Hoffmann, 2005).

Allen (1940) described two subspecies of *Pteromys* (*Hylopetes*) *alboniger* (Allen, 1925), and listed the Hainan flying squirrel as *Pteromys electilis* (Allen, 1925). Ellerman (1940) listed 13 *Hylopetes* species, including *H. platyurus* (Jentink, 1890), *H. spadiceus* (Blyth, 1847), *H. phayrei* (Blyth, 1859), *H. alboniger* (Hodgson, 1836), and *H. nigripes* (Thomas, 1893) etc., but the Hainan flying squirrel from Namfong, Hainan Island, China was regarded as *Petinomys electilis* (Allen, 1925). Ellerman & Morrison-Scott (1950) accepted the same results of *Petinomys electilis* as Ellerman (1940), however, they listed only five *Hylopetes* species, including *H. spadiceus*, *H. phayrei*, *H. alboniger*, *H. fimbriatus* (Gray, 1837), and *H. sagitta* (Linnaeus, 1766). The last two species were emended in later studies: *H. fimbriatus* was listed as *Eoglaucomys fimbriatus* and *H. sagitta* was replaced by *H. lepidus* (Horsfield, 1822) in the results of Thorington &

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Hoffmann (2005). Corbet & Hill (1992) regarded *H. p. electilis* as subspecies of *H. phayrei*, and *Sciuropterus platyurus* was accepted as the synonym of *H. lepidus* (Horsfield, 1822), resulting in their listing of ten *Hylopetes* species, except for *H. fimbriatus* and *H. baberi* (Blyth, 1847), which were arranged as *Eoglaucmys fimbriatus*, and *H. platyurus* (Thorington & Hoffmann, 2005). The rest of the eight *Hylopetes* species were the same as the results of Thorington & Hoffmann (2005).

Despite lengthy and protracted debate, there remains several disagreements and uncertainties as to the taxonomy of this polymorphic genus. Among the most contentious include *H. electilis* in Hainan Island, China and *H. alboniger*, *H. phayrei*, *H. platyurus*, *H. spadiceus*, and *H. nigripes*, which have had a complicated taxonomic history due to intraspecific geographic variation in their distributions across Asia (Corbet & Hill, 1992; Hoffmann et al, 1993; Rasmussen & Thorington, 2008; Roberts, 1997; Thorington & Hoffmann, 2005). Despite the controversies, to date no attempt has been made to investigate the differences in measurable skull variables among these groups.

Morphometric data has been used to evaluate cranial, dental, and body measurements of various wild populations of mammals, and the resulting statistic analysis of variations on the morphological level has been proved useful in detecting patterns of geographic variations and delimiting intra- or inter-specific evolutionary units (Li et al, 2008; Li et al, 2012; Munoz & Perpignan, 2010; Slabova & Frynta, 2007; Zelditch et al, 2004). Because the specimens of *Hylopetes* are undoubtedly exiguous, we based our analysis on 89 specimens of 6 *Hylopetes* species. Principal components analysis (PCA) was performed to compare skull measurable variables among them, and furthermore, special attention was paid to the taxonomic status of Hainan flying squirrel from Namfong, Hainan Island, China, which has been listed as either a synonym or subspecies of *H. phayrei* (Corbet & Hill, 1992; Hoffmann et al, 1993; Thorington & Hoffmann, 2005).

MATERIALS AND METHODS

Samples

A total of 89 specimens of *Hylopetes* were examined and used for statistical analysis, including 39 females, 44 males, and 6 specimens of unknown sex (Appendix A). Adults were classified based on phalange ossification and dental patterns. All specimens used in this study were deposited in the American Museum of Natural History (New York, AMNH); the National Museum of Natural History (Washington DC, USNM); the Institute of Zoology, Chinese Academy of Sciences (IOZ, CAS) (Beijing, China); and the Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KNHMZ, KIZ, CAS) (Kunming, China). In total, 14 measurable cranial

variables (Figure 1) taken with a digital caliper to the nearest 0.01 mm were used in statistic analysis.

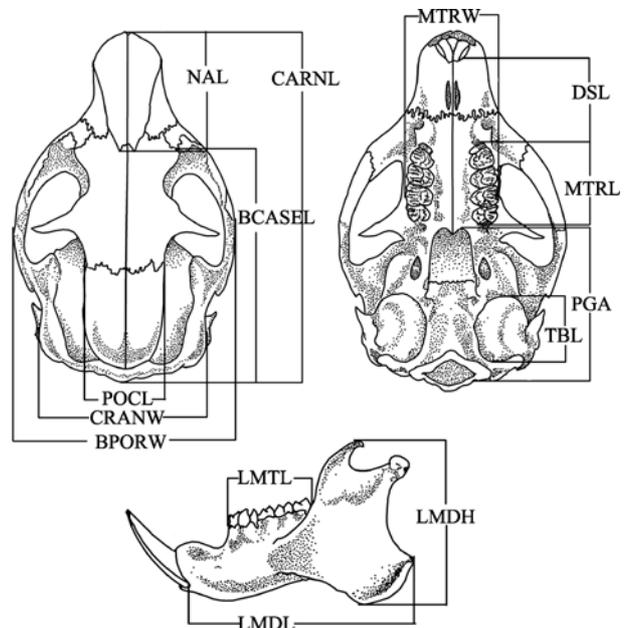


Figure 1 Measurements of 14 cranial variables used in the study

Data analysis

Statistical analysis of the morphometric study, which included sexual dimorphism, multiple comparisons, and principal component analysis (PCA) were performed using SPSS 11.0 (SPSS Inc., Chicago, USA). First, all variables were transformed into natural logarithms to eliminate the bias effect on large measurements in statistical analysis (D'elia & Pardinas, 2004). Then, Kaiser-Meyer-Olkin Measure of Sampling Adequacy (KMO) and Bartlett's Test were performed in order to test if the data were fit for analysis. Statistical differences were considered significant where $P < 0.05$.

The Tests of Equality of Group Means (by Wilks' Lambda) was used to assess the sexual dimorphism of each group. In order to evaluate variations between samples, multiple comparisons (by Least-Significant Difference) between taxa were performed for all 14 cranial measurements. The associations between cranial measurable characters and species were assessed by multivariate analysis of the PCA. PCA based on the variance-covariance matrix of the log-transformed variables was performed to identify variables that account for maximum variation in the data set, and to represent distances between major groups in order to assess the specific relationships among the individuals. The eigenvector scores describing the relative significance of each variable to principal components were used to compare the cranial morphological similarities and differences. The PCA scatter-plot visually represents the variation among different individuals of the samples (Figure 2).

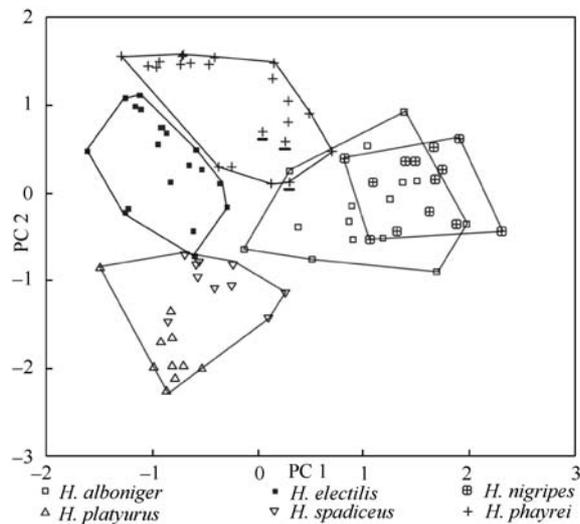


Figure 2 Plots of six *Hylopetes* species samples on the principal components factors 1 and 2

RESULTS

The means and standard deviation (*SD*) of 14 measurable cranial variables of *Hylopetes* are presented in Table 1. The results of KMO is 0.946 and that of *P* of Bartlett's Test of Sphericity is 0.000, together

confirming that the data garnered in the morphometric study were fit for PCA analysis. The Tests of Equality of Group Means for 83 samples showed no sexual dimorphism in all 14 cranial variables in the 6 *Hylopetes* species (Table 2). Table 3 presents the results of multiple comparisons on all 14 cranial variables between the species of *Hylopetes*.

Multivariate analysis was based on principal components analysis. In PCA, eigenvalues for the first three principal components were 12.161, 0.740 and 0.541 respectively, accounting for 96.014% of the total variance (Table 4). The first principal component factor (PC1) accounted for 86.867% of the total original variance and most variables had high positive loadings, suggesting the size variation in the samples. The second principal component (PC2) accounted for 5.284% of the total variance and is strongly correlated with TBL, with factor loadings >0.9. Along the third principal component factor (PC3), which accounts for 3.863% of the total variance, the main morphological variable contributing to this association is PORCL, with factor loadings >0.9.

Because the eigenvalue of the first principal components was 12.161, and the third was much lower (0.541), we used PC1 and PC2 to make the PCA scatterplot (Figure 2).

Table 1 Cranial variable measurements of *Hylopetes* (mean±*SD*)/range. Variable codes explained in Figure 1

Variables	<i>H. alboniger</i> <i>n</i> =15	<i>H. electilis</i> <i>n</i> =22	<i>H. nigripes</i> <i>n</i> =13	<i>H. platyurus</i> <i>n</i> =10	<i>H. spadiceus</i> <i>n</i> =10	<i>H. phayrei</i> <i>n</i> =19
CRANL	48.52±3.02 42.79–52.9	38.56±0.99 36.41–39.96	51.50±2.70 45.59–55.28	31.90±0.88 30.87–33.26	35.58±0.80 34.58–36.87	40.65±2.56 37.51–46.61
BCASEL	35.24±3.59 30.17–41.4	30.32±0.93 28.47–31.61	41.08±1.37 38.06–42.94	25.65±0.84 24.20–27.00	29.12±0.58 28.35–29.72	32.44±2.13 30.04–37.61
CRANW	21.98±0.62 20.97–22.98	18.21±0.44 17.44–18.93	22.58±0.52 21.93–23.46	16.38±0.39 15.81–17.02	17.67±0.29 17.33–18.35	18.84±1.12 17.13–20.91
BPORW	30.56±1.83 26.84–33.3	23.50±0.77 22.23–24.74	32.10±0.91 30.14–33.06	19.55±0.53 18.77–20.25	21.79±0.66 20.98–23.04	24.91±1.80 21.97–28.34
PORCL	11.51±0.79 10.07–12.89	11.20±0.65 9.84–12.41	11.71±0.77 10.06–13.10	9.78±0.52 9.23–10.63	10.20±0.57 9.38–11.26	10.10±0.64 9.03–11.50
PGA	19.63±1.37 17.11–21.34	15.42±0.60 14.35–16.17	20.79±0.96 18.40–22.00	13.66±0.44 13.12–14.58	15.40±0.64 14.20–16.64	16.65±1.20 15.43–19.07
NAL	14.35±1.36 11.90–16.20	10.66±0.72 9.27–12.22	16.17±0.85 14.14–17.42	9.06±0.41 8.18–9.53	10.15±0.48 9.37–10.93	11.67±1.13 9.97–13.94
TBL	8.79±0.52 8.20–10.16	8.55±0.51 7.52–9.25	9.30±0.46 8.63–9.96	6.64±0.30 6.31–7.21	7.40±0.17 7.12–7.59	9.43±0.47 8.45–10.14
DSL	10.21±1.06 8.12–11.64	8.15±0.40 7.42–8.95	10.46±0.77 8.53–11.81	6.42±0.38 5.97–6.98	7.33±0.40 6.39–7.80	8.79±0.77 7.53–10.48
MTRL	10.41±0.73 8.00–11.06	7.98±0.24 7.45–8.42	12.40±0.50 11.77–13.18	5.92±0.23 5.62–6.28	7.47±0.32 7.01–8.19	8.49±0.51 7.73–9.82
MTRW	12.86±0.54 11.89–13.97	9.96±0.28 9.35–10.45	12.96±0.29 12.46–13.44	7.74±0.27 7.32–8.03	8.66±0.40 8.27–9.55	10.33±0.56 9.42–11.60
LMDL	28.69±2.13 25.65–33.57	20.63±0.78 19.42–21.97	32.28±2.07 28.32–35.33	18.51±0.77 17.48–19.73	21.25±0.79 20.26–22.60	23.53±2.84 18.46–28.00
LMDH	18.42±1.56 14.41–20.22	14.22±0.62 13.36–15.42	21.05±1.20 19.06–22.80	11.38±0.64 10.38–12.34	13.02±0.64 12.01–14.01	14.82±1.09 13.61–17.55
LMTL	10.18±0.41 9.50–10.87	7.55±0.23 7.19–8.04	11.77±0.66 11.04–13.56	5.49±0.22 5.18–5.82	6.70±0.20 6.46–7.13	8.26±0.44 7.72–9.36

Figure 2 indicates PC1-PC2 scatter plots of principal component analysis. Inspection of Figure 2, samples of *H. electilis*, *H. platyurus*, *H. spadiceus*, and *H. phayrei* are distinguished from each other to form their distinct groups, showing different morphological characteristics of their skulls. However, results showed that samples of *H. alboniger* and *H. nigripes* are quite close to one another with considerable overlap, suggesting that *H. alboniger* shares similar measurable skull characteristics with *H. nigripes*. An interesting result was that the three samples named *H. electilis* from Chiang Mai, Thailand (labeled as “±” in Figure 2) are separated from those from Namfong, Hainan Island, but scatter in the samples of *H. phayrei*, hinting that the samples of *H. electilis* from Chiang Mai, Thailand should be more similar with those of *H. phayrei* in measurable skull characteristics.

DISCUSSION

Based on the specimens from Namfong, Hainan Island, China, Allen (1925) first described a valid species named *Pteromys (Petinomys) electilis*, but later on review classified it as *Pteromys electilis* (Allen, 1940). Later studies by Ellerman (1940) and Elleuman & Morrison-Scott (1950) continued to use *Petinomys electilis* as the scientific name for this species, and emphasized the species distribution on Hainan Island, China. However, based on their understanding of its two septa in each bulla, Corbet & Hill (1992) listed the group in *Hylopetes*. While Corbet & Hill (1992) narrated significant differences on pelage characteristics between

H. electilis and *H. phayrei*, they still opted to list it as belonging to *H. phayrei*, while placing *H. p. electilis* as its subspecies. More succinctly put, the validity of the Hainan flying squirrel, *H. electilis*, has been controversial for quite a long time (Corbet & Hill, 1991, 1992; Ellerman, 1940; Hoffmann et al, 1993; Nowak, 1999; Thorington & Hoffmann, 2005; Wang, 2003; Zhang et al., 1997).

The validity of various measurable cranial variables in distinguishing between species and species groups in *Hylopetes* has been critical in several studies. For example, Rasmussen & Thorington (2008) discussed the distributions for *H. platyurus*, *H. spadiceus*, and *H. Lepidus* using similar methods. In the present study, we performed statistical analyses on 14 measurable cranial variables from 22 samples of *H. electilis*, 19 of which came from Namfong, Hainan Island, China, in order to compare them with the samples of other five other validated *Hylopetes* species. The results showed significant difference between *H. electilis* and the other five *Hylopetes* species (Table 3), indicating it could be distinguished from other five species by using measurable skull variables. Similarly, though Figure 2 indicates that samples of *H. electilis* from Namfong, Hainan Island could be clearly distinguished from those of other five *Hylopetes* species, we found that they were closest to samples of *H. phayrei*, as opposed to the other four *Hylopetes* species. This result not only sustains the idea that *H. electilis* on Hainan Island should be a valid species, but it also may explain the reasons why there were so many systematic disagreements between *H. electilis* and *H. phayrei*.

Table 2 Tests of Equality of Group Means (by Wilks' Lambda) for Sexual Dimorphism

	Wilks' Lambda	F	df1	df2	P
CRANL	0.998	0.193	1	81	0.662
BCASEL	0.996	0.332	1	81	0.566
CRANW	1.000	0.022	1	81	0.884
BPORW	0.999	0.074	1	81	0.787
PORCL	0.995	0.443	1	81	0.507
PGA	0.999	0.090	1	81	0.765
NAL	1.000	0.038	1	81	0.846
TBL	1.000	0.000	1	81	0.991
DSL	0.996	0.308	1	81	0.580
MTRL	0.998	0.154	1	81	0.696
MTRW	1.000	0.008	1	81	0.930
LMDL	0.998	0.148	1	81	0.701
LMDH	0.992	0.645	1	81	0.424
LMTL	0.998	0.159	1	81	0.691

Variable codes are explained in Figure 1. Significant difference level: ** $0 < P < 0.001$, * $0.001 < P < 0.05$.

Table 3 Multiple Comparisons (by Least-Significant Difference) of all 14 cranial variables between the six *Hylopetes* species

	<i>H. alboniger</i> ~ <i>H. electilis</i>		<i>H. alboniger</i> ~ <i>H. nigripes</i>		<i>H. alboniger</i> ~ <i>H. platyurus</i>		<i>H. alboniger</i> ~ <i>H. spadicus</i>		<i>H. alboniger</i> ~ <i>H. phayrei</i>	
	Mean difference	<i>P</i>	Mean difference	<i>P</i>	Mean difference	<i>P</i>	Mean difference	<i>P</i>	Mean difference	<i>P</i>
CRANL	0.097	0.000**	-0.029	0.001**	0.180	0.000**	0.131	0.000**	0.075	0.000**
BCASEL	0.063	0.000**	-0.068	0.000**	0.136	0.000**	0.081	0.000**	0.034	0.000**
CRANW	0.081	0.000**	-0.011	0.072	0.129	0.000**	0.094	0.000**	0.067	0.000**
BPORW	0.112	0.000**	-0.022	0.006*	0.193	0.000**	0.146	0.000**	0.088	0.000**
PORCL	0.014	0.120	-0.006	0.529	0.071	0.000**	0.054	0.000**	0.058	0.000**
PGA	0.103	0.000**	-0.024	0.008*	0.156	0.000**	0.106	0.000**	0.071	0.000**
NAL	0.126	0.000**	-0.053	0.000**	0.197	0.000**	0.149	0.000**	0.089	0.000**
TBL	0.010	0.165	-0.026	0.003*	0.120	0.000**	0.072	0.000**	-0.031	0.000**
DSL	0.096	0.000**	-0.010	0.418	0.200	0.000**	0.142	0.000**	0.065	0.000**
MTRL	0.113	0.000**	-0.077	0.000**	0.242	0.000**	0.142	0.000**	0.086	0.000**
MTRW	0.109	0.000**	-0.003	0.591	0.221	0.000**	0.172	0.000**	0.095	0.000**
LMDL	0.142	0.000**	-0.051	0.000**	0.187	0.000**	0.130	0.000**	0.087	0.000**
LMDH	0.111	0.000**	-0.059	0.000**	0.208	0.000**	0.150	0.000**	0.094	0.000**
LMTL	0.130	0.000**	-0.062	0.000**	0.270	0.000**	0.182	0.000**	0.092	0.000**
CRANL	-0.126	0.000**	0.083	0.000**	0.034	0.000**	0.021	0.001**	0.209	0.000**
BCASEL	-0.131	0.000**	0.073	0.000**	0.018	0.062	0.028	0.001**	0.205	0.000**
CRANW	-0.092	0.000**	0.047	0.000**	0.012	0.049*	0.014	0.005*	0.140	0.000**
BPORW	-0.135	0.000**	0.081	0.000**	0.034	0.000**	-0.023	0.001**	0.216	0.000**
PORCL	-0.021	0.033*	0.056	0.000**	0.039	0.000**	0.044	0.000**	0.077	0.000**
PGA	-0.128	0.000**	0.052	0.000**	0.002	0.800	-0.032	0.000**	0.180	0.000**
NAL	-0.179	0.000**	0.070	0.000**	0.022	0.082	-0.037	0.001**	0.250	0.000**
TBL	-0.037	0.000**	0.109	0.000**	0.061	0.000**	-0.042	0.000**	0.146	0.000**
DSL	-0.107	0.000**	0.103	0.000**	0.045	0.001**	-0.031	0.004*	0.210	0.000**
MTRL	-0.191	0.000**	0.128	0.000**	0.028	0.002*	0.027	0.000**	0.320	0.000**
MTRW	-0.113	0.000**	0.111	0.000**	0.062	0.000**	0.014	0.013*	0.225	0.000**
LMDL	-0.194	0.000**	0.045	0.001**	-0.011	0.362	0.055	0.000**	0.239	0.000**
LMDH	-0.171	0.000**	0.096	0.000**	0.038	0.001**	0.017	0.055	0.267	0.000**
LMTL	-0.192	0.000**	0.139	0.000**	0.051	0.000**	0.038	0.000**	0.332	0.000**
CRANL	0.160	0.000**	0.104	0.000**	-0.049	0.000**	-0.105	0.000**	-0.056	0.000**
BCASEL	0.150	0.000**	0.103	0.000**	-0.055	0.000**	-0.102	0.000**	-0.047	0.000**
CRANW	0.105	0.000**	0.078	0.000**	-0.035	0.000**	-0.062	0.000**	-0.027	0.000**
BPORW	0.169	0.000**	0.111	0.000**	-0.047	0.000**	-0.105	0.000**	-0.058	0.000**
PORCL	0.060	0.000**	0.065	0.000**	-0.017	0.162	-0.012	0.239	0.004	0.641
PGA	0.130	0.000**	0.096	0.000**	-0.050	0.000**	-0.084	0.000**	-0.034	0.000**
NAL	0.202	0.000**	0.142	0.000**	-0.048	0.002*	-0.108	0.000**	-0.060	0.000**
TBL	0.098	0.000**	-0.004	0.552	-0.048	0.000**	-0.151	0.000**	-0.103	0.000**
DSL	0.152	0.000**	0.075	0.000**	-0.058	0.000**	-0.134	0.000**	-0.076	0.000**
MTRL	0.220	0.000**	0.164	0.000**	-0.100	0.000**	-0.155	0.000**	-0.055	0.000**
MTRW	0.176	0.000**	0.099	0.000**	-0.049	0.000**	-0.126	0.000**	-0.077	0.000**
LMDL	0.182	0.000**	0.138	0.000**	-0.057	0.000**	-0.100	0.000**	-0.043	0.001**
LMDH	0.209	0.000**	0.154	0.000**	-0.058	0.000**	-0.113	0.000**	-0.055	0.000**
LMTL	0.244	0.000**	0.154	0.000**	-0.088	0.000**	-0.177	0.000**	-0.089	0.000**

Variable codes are explained in Figure 1. **: $0 < P < 0.001$, *: $0.001 < P < 0.05$.

Table 4 Factor loadings of the principal component analysis

Variables	PC1	PC2	PC3
CRANL	0.869	0.389	0.288
BCASEL	0.851	0.403	0.223
CRANW	0.875	0.262	0.346
BPORW	0.872	0.345	0.313
PORCL	0.295	0.112	0.945
PGA	0.910	0.307	0.214
NAL	0.912	0.284	0.214
TBL	0.373	0.915	0.107
DSL	0.775	0.523	0.214
MTRL	0.844	0.363	0.304
MTRW	0.801	0.416	0.367
LMDL	0.935	0.222	0.174
LMDH	0.886	0.326	0.279
LMTL	0.819	0.417	0.321
Eigenvalues	12.161	0.740	0.541
Variance explained (%)	86.867	5.284	3.863

Variable codes are explained in Figure 1.

Both a variety of previous studies as well as the present study have established that the Hainan flying squirrel, *H. electilis*, is restricted to Hainan Island, China (Ellerman, 1940; Ellerman & Morrison-Scott, 1950), and we thought that the channel isolation may have accelerated its absolute evolution. Based on molecular data, Jorgensen & Demarais (1999) and Oshida et al (2000) discussed the close genetic relationship and the recent divergence between *H. electilis* and *H. phayrei*. Their results suggest that these populations rapidly extended the ranges to their present distributions in a relatively short time (Jorgensen & Demarais, 1999; Oshida et al, 2000). Based on our current findings and the previous data, we recommend further correlative ecology studies on *H. electilis* and *H. phayrei* should be performed in order to gather more data that would help explain their adaptation process, and in doing so explain their phenotypic differentiation.

Additionally, three samples of *H. electilis* (labeled as “±” in Figure 2) from Chiang Mai, Thailand, were found to be not only clearly different from those of *H. electilis* from Namfong, Hainan Island, China, but they also scatter within samples of *H. phayrei* to form a close group (Figure 2). Based on the results of pelage comparison between *H. electilis* and *H. phayrei*, while Corbet & Hill (1992) listed the former as *H. p. electilis* while also emphasizing some significant differences in pelage characteristics between the two (Corbet & Hill, 1992). Our results also indicate that samples of *H. electilis* from Hainan Island could differ from those of *H. phayrei* samples from mainland in terms of skull

measurable characteristics (Figure 2), and likewise support their earlier results that *H. electilis* is distributed across Hainan Island, China. (Ellerman, 1940; Ellerman & Morrison-Scott, 1950).

The ultimate results from our statistical analysis of the skull characteristics sustains the argument that *H. electilis* is neither a synonym nor subspecies of *H. phayrei*, but a valid species in its own right. As for *H. platyurus*, although it was accepted as the synonyms of *H. lepidus* (Corbet & Hill, 1992), Figure 2 indicates that specimens of *H. platyurus* could be completely separated from five other *Hylopetes* species, similarly illustrating that it likely must also belong to a valid *Hylopetes* species. Unfortunately, without specimens of *H. lepidus* to serve as a comparison, the data collected in the present paper is suggestive but not conclusive, therefore we cannot definitively state whether *H. platyurus* is a synonym of *H. lepidus* or not. Further studies with more specimens may help further settle the ongoing debates regarding the taxonomy.

For a final note regarding geography, it is worth noting that *Hylopetes* are distributed in different zoogeographic subregions of the Oriental region, each with significant geographical variations (Corbet & Hill, 1992; Lekagul & Mcneely, 1988; Zhang et al, 1997). Accordingly, the samples of the six *Hylopetes* species used in this study can be morphologically distinguished as different, distinct groups (Figure 2). *H. alboniger* and *H. phayrei* belong to the Indochinese subregion and overlap extensively in Thailand, Indochina, Burma, and southern China (Corbet & Hill, 1992; Hoffmann et al, 1993; Thorington & Hoffmann, 2005), where the habitat is tropical, subtropical, or evergreen forest, with low elevation (500-1500 m) and within reach of southwest and south monsoons. Additionally, the population of *H. alboniger* occurs in the eastern extreme of the Himalayas and occupies temperate coniferous forest at mid elevations (1 500-3 000 m) or deciduous and subtropical forests at low elevations, while *H. nigripes* is endemic to the Philippines and occurs in subtropical or tropical dry forests (Nowak, 1999). Similar morphological characteristics (Figure 2) between *H. alboniger* and *H. nigripes* may potentially be adaptations to similar living habitats, though again, further studies are needed to explore this possibility.

South China itself is located at the crossroads of southeastern Asia, and has been a thoroughfare for animal dispersal from mainland Asia southward into the Indo-Malayan region. In southeastern Asia, many species have migrated south from Burma and southern China along the forested mountains of the Thai-Burma border into Malaysia, Sumatra, Java, and Borneo (Lekagul & Mcneely, 1988). *H. nigripes*, *H. lepidus*, and *H. spadiceus* inhabits the Sundaic sub region, with subtropical or tropical dry forests. The greatest distinction observed between *H. platyurus* and *H.*

spadiceus and other *Hylopetes* is consistent with discussions about *H. platyurus*, *H. spadiceus*, and *H. lepidus* by Rasmussen & Thorington (2008). However, because the habitats of these Sundaic *Hylopetes* are not well known and the ranges of these flying squirrels are poorly recorded, nearly every new collection will reveal new distribution limits, prompting further research. Based on that reality and the results of the present study, we suggest that future molecular studies on these species' phylogenies may give us more evidence as to the volition of their species status, and the subsequent estimation of divergence times will help us to understand the biogeography of *Hylopetes*, and perhaps give some further insight into larger shifts within the region.

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Appendix I

Specimens examined in this study

H. alboniger n=15

Yunnan, China: IOZ 5507 ♀, 5508 ♂, 15046 ♀; KIZ 00009 ♀, 76311 ♂, 84756, 89011, 90004, 206746, 206745, 640222 ♂, 640227 ♂; AMNH 114884 ♂, 114885 ♂, 114886 ♀;

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- H. electilis* n=22
Hainan, China: AMNH 58138 ♀, 58158 ♀, 58159 ♀, 58160 ♂, 58161 ♀, 58162 ♂, 58163 ♂, 58164 ♀, 58166 ♀, 58167 ♂, 58171 ♂, 58172 ♂, 58176 ♂, 58179 ♀, 58180 ♂, 58181 ♂, 58182 ♀, 58186 ♀, 58198 ♂;
Chiang Mail, Thailand: AMNH 167891 ♀, 167892, 167893 ♂;
- H. nigripes* n=13
Palawan, Philippines: AMNH 242098 ♀, 203314 ♀, 203313 ♂, 203311 ♀, 203309 ♂, 203310 ♂;
USNM 477991 ♂, 477993 ♀, 477996 ♂, 478005 ♀, 478006 ♀, 478007 ♀, 478009 ♂;
- H. platyurus* n=10
Selamgger, W Malaysia: USNM 488617 ♀, 488619 ♀, 488620 ♂, 488623 ♂, 488624 ♀, 488625 ♀, 488626 ♀, 488630 ♂, 488631 ♂, 488633 ♂;
- H. spadiceus* n=10
Johore, W Malaysia: USNM 481109 ♂, 481110 ♀, 481112 ♀, 481114 ♂, 481116 ♂, 488648 ♂, 488638 ♂, 488641 ♀, 488645 ♀, 488646 ♀;
- H. phayrei* n=19
Banlad, Siam: USNM 294888 ♂, 294890 ♂, 294891 ♂, 294892 ♀, 297089 ♀;
Chiang Mai, Siam: USNM 260621 ♀, 260622 ♂, 260624 ♂, 153580 ♀;
Mandalaypopa, Burma: AMNH 163552 ♀, 163553 ♀, 163554 ♂, 163555 ♂, 163557 ♀, 163558 ♀, 163561 ♂, 163559 ♂, 163560 ♂, 163563 ♂.
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