

MORPHOLOGICAL DIFFERENTIATION AMONG THREE SPECIES OF FLYING SQUIRRELS (GENUS *HYLOPETES*) FROM SOUTHEAST ASIA

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The genus *Hylopetes* consists of 8 or 9 species of small flying squirrels. There has been much nomenclatural confusion over 3 of these species: *H. platyurus* (the gray-cheeked flying squirrel), *H. spadiceus* (the red-cheeked flying squirrel), and *H. lepidus* (the pink-cheeked flying squirrel). To address this taxonomic problem, we examined museum specimens and quantified pelage coloration, tail shape, and a number of craniodental characters. A discriminant analysis of craniodental variables discriminated among the 3 species and allocated all specimens correctly ($P < 0.00001$). We found that simple ratios of craniodental measurements coupled with pelage coloration characters can assist in the identification of these problematic species, although tail shape was not useful for discrimination. Based on our results as well as historical accounts and what is known about the biogeographical patterns of the region, we provide a description and discussion of the distributions for these species.

Key words: biogeography, *Hylopetes lepidus*, *Hylopetes platyurus*, *Hylopetes spadiceus*, morphometrics, nomenclature, Sciuridae, systematics

The genus *Hylopetes* comprises a group of small flying squirrels, all native to Southeast Asia. Corbet and Hill (1992) identified 8 species (excluding the 2 forms of *Eoglaucomys* they listed as species of *Hylopetes*), whereas Thorington and Hoffmann (2005) recognized 9 species. This discrepancy in species number stems from a long history of nomenclatural confusion in the literature over several of these species. Following the usage of Thorington and Hoffmann (2005), these species are *H. lepidus* (the pink-cheeked flying squirrel), *H. platyurus* (the gray-cheeked flying squirrel), and *H. spadiceus* (the red-cheeked flying squirrel), and they are the subject of this study.

We note that different taxonomic arrangements lead to different zoogeographic conclusions. The potential zoogeographic barriers of interest are the Sunda Strait, between Java and southern Sumatra (van den Bergh et al. 2001); the Strait of Malacca, between Sumatra and the Malay Peninsula; the Isthmus of Kra on the Malay Peninsula, dividing the Sunda and Indochina floras and faunas (Hughes et al. 2003; Woodruff 2003); the Java Sea, separating Java from Borneo; and the South China Sea, separating the Malay Peninsula from Borneo. Each of these appears to have been a barrier for some species in

spite of the fluctuations in sea level that caused all the islands to be joined into a single Sundaland, broadly connected with the Asian mainland during glacial periods of the Pleistocene (Haq et al. 1987; Voris 2000). During these glacial periods, Sundaland had major river systems (Voris 2000), different rainfall patterns, and probably different habitats (Bird et al. 2005; van der Kaars 2001; van der Kaars and Dam 1995; Visser et al. 2004), which could have maintained the isolation of different populations of flying squirrels. For example, there was probably a broad stretch of savanna on the Sunda shelf during the last glacial maximum period of low sea level (Bird et al. 2005; Heaney 1991), which would be expected to be a barrier to flying squirrels. These patterns also need to be integrated into the study of the historical biogeography of Southeast Asia (Wiens and Donoghue 2004). Understanding the zoogeographic patterns of these flying squirrels and the rest of the Sunda fauna requires, first of all, taxonomic clarity that is unfortunately not yet available for these flying squirrels.

A brief review of the literature illustrates the problems presented by this group. Chasen (1940) recognized that there were 2 species of *Hylopetes* on the Malay Peninsula. He called the larger species *H. sagitta spadiceus*, conspecific with the species found on Java (*H. sagitta* Linnaeus). This is a misnomer for *H. lepidus*, according to Ellerman and Morrison-Scott (1955), because Linnaeus' type specimen of *Sciurus sagitta* is a completely different species—thought to be *Petinomys*, perhaps *P. genibarbis*. Because *H. lepidus* is the oldest name and the type locality for it is Java, the Javan animals are, by

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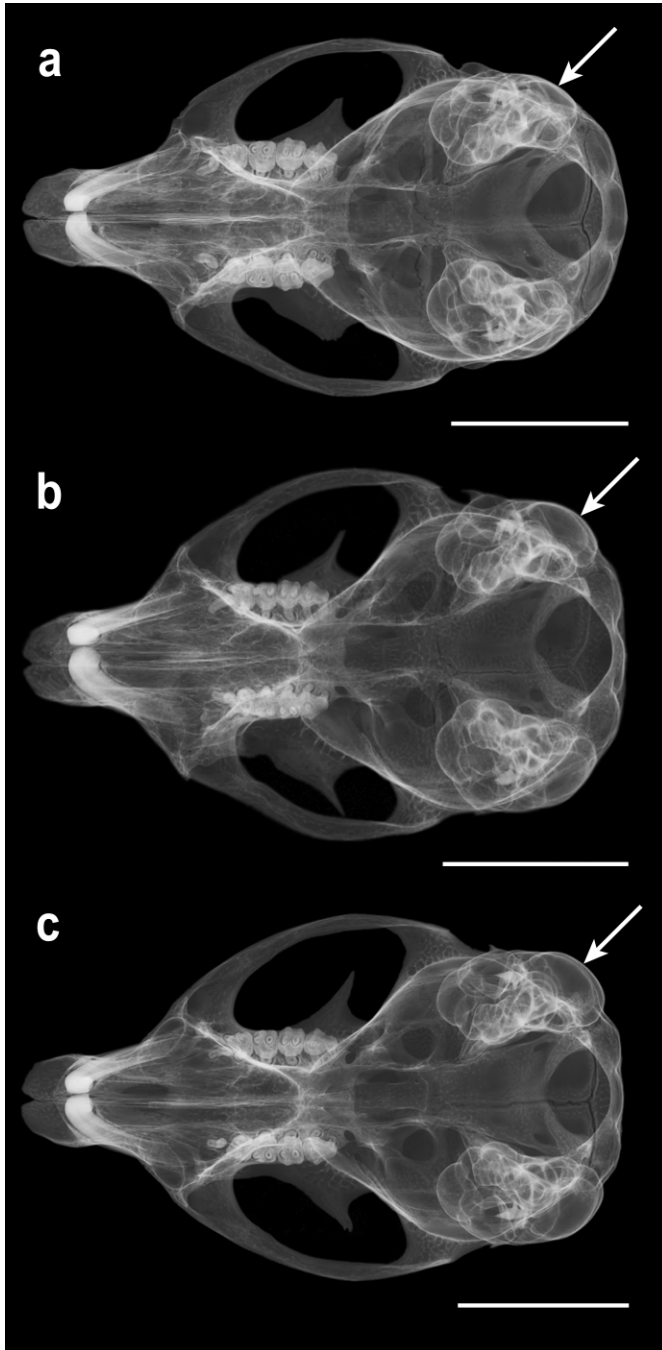


FIG. 1.—X-rays of crania of 3 species of *Hylopetes* showing the swelling of the mastoid portion of the temporal bone (arrow). A) *H. lepidus*, B) *H. platyurus*, and C) *H. spadiceus*. Scale bars = 10 mm.

definition, *H. lepidus*. Chasen (1940) considered the smaller of the 2 species on the Malay Peninsula to be *H. platyurus* Jentink—the same as the species on northern Sumatra. Ellerman (1940) and Ellerman and Morrison-Scott (1951) reversed this arrangement and considered the smaller animals to be conspecific with those on Java, hence *H. lepidus platyurus*, and the larger ones on the Malay Peninsula to be a distinct species—*H. spadiceus*. In his report on the Robinson collection, Hill (1960) followed Ellerman and Morrison-Scott in calling the

larger species *H. spadiceus* and the smaller species *H. lepidus platyurus*. Subsequently, Hill (1962) provided quantitative data to support the conclusion that the species on Java is the same as the smaller species on the Malay Peninsula. Muul and Liat (1971) reverted to the Chasen arrangement, that *H. lepidus* is the larger species on the Malay Peninsula and *H. platyurus* is the smaller but gave the alternative arrangement in parentheses. Askins (1977) did the same, giving the name *H. lepidus* to the larger species in Thailand. Thorington et al. (1996) contended that the smaller species on the Malay Peninsula is *H. platyurus*, the larger species is *H. spadiceus*, and that *H. lepidus* should be restricted to the animals from Borneo and Java. In this arrangement, *H. lepidus* differs from the other 2 species in the degree of inflation of the mastoid portion of the temporal bone (herein called the mastoid bone). There is less inflation of the mastoid in *H. lepidus* than in the other 2 species (Fig. 1). However, they provided no quantitative data to support this contention. Here, we tested the arrangement accepted by Thorington and Hoffmann (2005), against the conclusion of Hill (1962) that *H. platyurus* and *H. lepidus* are conspecific, with similar mastoid inflations. To do this, we compared and contrasted morphometrics and pelage coloration of museum specimens from various localities in Southeast Asia.

MATERIALS AND METHODS

We examined 140 specimens representing 30 localities (Appendix D). These specimens consist of skins and associated skulls from the holdings of the American Museum of Natural History, New York City (AMNH) and the Smithsonian Institution, Washington, D.C. (USNM). Standard external dimensions, as given by the collector, were transcribed from skin tags: head and body length (HBL), ear length (EL), and hind-foot length (HFL).

We quantified the pelage coloration of the cheek and the base of the tail (ventral). We developed categories by 1st examining all available study skins of the 3 species and determining the range of pelage color variation (e.g., cheeks varied from nearly white to orange-red). We photographed specimens that represented the 2 color extremes for the cheek and the base of tail (the same specimen was not necessarily photographed for both characters) as well as a series of intermediate specimens along the coloration gradient. We assembled color plates for each of the 2 pelage coloration characters, against which we scrutinized each study skin to arrive at a score.

The color of the cheek was recorded in 7 categories, the following 4 plus 3 intermediate categories (1.5, 2.5, and 3.5), according to the following descriptions and with examples given in parentheses: 1 = gray (e.g., USNM 488620, 488621); 2 = tinges of ochre (e.g., AMNH 106701, 106702; USNM 488643, 489466); 3 = ochre (e.g., AMNH 101439; USNM 488640, 480641); and 4 = ochraceous orange (e.g., USNM 489460, 489483). The color at the base of the tail also was recorded but with 2 additional categories (4.5 and 5.0). These are described here with examples in parentheses: 1 = gray (e.g., USNM 488620, 488636); 2 = tinges of ochre (e.g., USNM 488630, 488631); 3 = ochre (e.g., AMNH 101436, 101437; USNM

104627, 489481); 4 = ochraceous orange (e.g., AMNH 101440, 101441; USNM 488640, 480641); and 5 = orange-red (e.g., USNM 123932, 489460).

Hill (1962) suggested that the species differed in the degree of tapering of the tail, so we took a series of tail measurements to quantify tail shape. First, the length of the tail was measured on the skin from the base to the tip, excluding the hairs at the tip (TL). Tail-width measurements were then taken at 10%, 25%, 50%, 75%, and 90% (TW10%, TW25%, etc.) of this length. Width measurements were taken across the tail from the tip of the hairs on the right side to the tip of the hairs on the left side. At 50%, the lengths of the individual hairs were also measured (HL50%).

Crania were viewed under a magnifying lamp, and the 18 cranial and 3 dental measurements were taken by the 1st author (NLR) to the nearest 0.01 mm using a pair of handheld digital calipers accurate to 0.03 mm (Max Cal, Fred V. Fowler Company, Newton, Massachusetts). These measurements (Fig. 2) included occipitonasal length (ONL); zygomatic breadth (ZB); breadth of braincase (BCB), just behind the zygomatic arches; breadth behind postorbital process (POB), least width behind the postorbital process; breadth across occipital condyles (OCB), least width across dorsal portion of articular processes on exoccipital bones; interorbital breadth (IOB), least width taken between the lateral sides of the frontal bones, relatively deep into orbits, not on the edge of the supraorbital ridges; depth of braincase (BCD), from the basioccipital to the midsagittal junction of the parietals; length of nasals (NL); breadth of nasals (NB); postpalatal length (PPL), from the midnotch of the basioccipital to the posterior edge of the palate; length of bony palate (BPL), measured from the posterior end of the left incisive foramen to the posterior edge of the palate; length of diastema (DL), from the posterior surface of the left incisor to the enamel–dentin junction of the left P4; length of left incisive foramen (IFL); breadth across incisive foramina (IFB), breadth at the premaxillary–maxillary suture; breadth of bony palate (BPB), measured between the lateral surfaces of the maxillary bones lateral to the 1st molars; length of left maxillary tooththrow from P4 to M3 (TRL), measured at the occlusal surface; width of M1 (M1B), greatest width of the upper right M1; depth of incisor (ID), anterior–posterior diameter of the right upper incisor; length of auditory bulla (BL), measured from the posterior bevel of the right auditory bulla to the notch (at the junction of the opaque bone of eustachian tube and the translucent bone of the tympanic capsule); mastoid length (ML), a diagonal measurement, from the anterior edge of the right mastoid process, where it meets the auditory bulla, to the medial edge, where the mastoid portion of the temporal bone meets the occipital bone; and interseptal breadth (ISB), the distance between the 2 septa in the right bulla.

Univariate statistical analyses and analyses of variance were computed with Excel 2003 (Microsoft Corporation, Redmond, Washington). Principal component analyses and canonical variate analyses were computed with SYSTAT, version 9 (SYSTAT Software Inc., Chicago, Illinois). Ratios were computed from 3 variables, which were important discriminators in the canonical analysis. The 3 variables were summed,

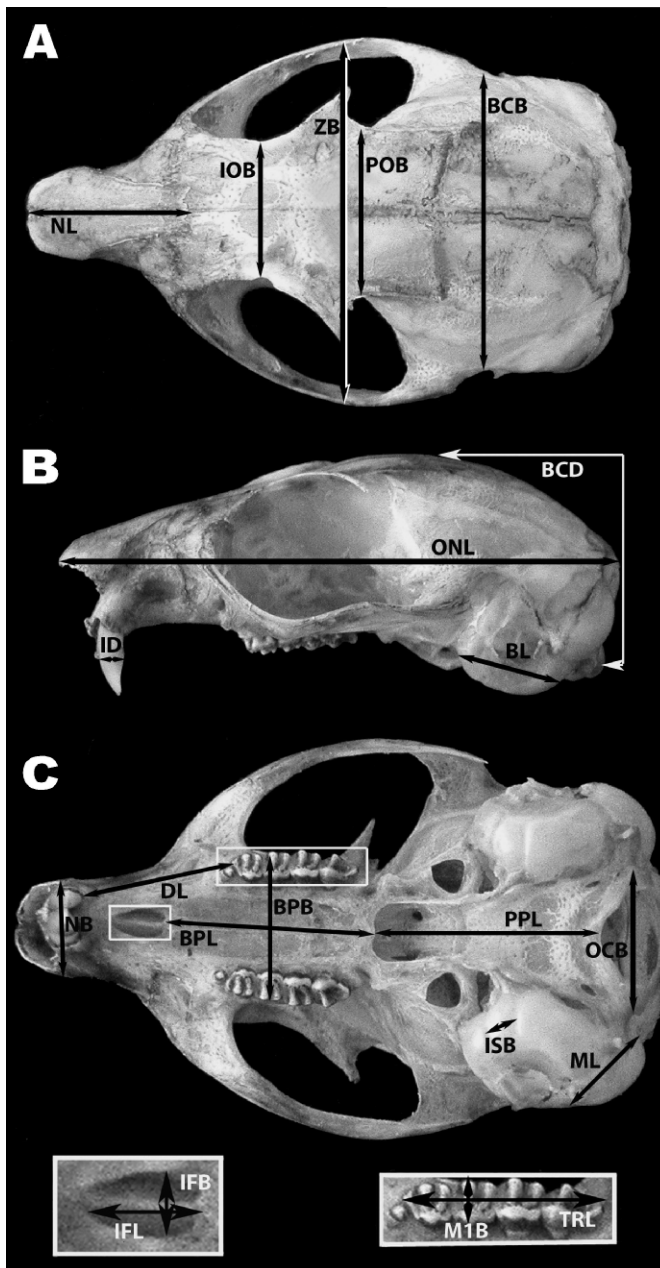


FIG. 2.—Images of cranium of *Hylopetes spadiceus* (USNM 481114; ONL = 35.09 mm) showing measurements taken. A) Dorsal view, B) lateral view, and C) ventral view. Abbreviations of measurements are given in the “Materials and Methods.”

and the ratio of each to the sum was computed. Thus these ratios are members of the Mosimann family of shape ratios, which have desirable characteristics (Jungers et al. 1995; Mosimann 1970). Computed ratios were expected to have a Cauchy distribution, which lacks a defined mean and standard deviation. However, the distributions of our data approximated normal, and we computed means and standard deviations accordingly. (In the 2 samples examined, 66% and 70% of the ratios were within 1 standard deviation of the mean and 95% were within 2 standard deviations of the mean.)

Correct and incorrect classifications were based on a jack-knifed classification matrix in the canonical variate analyses.

TABLE 1.—Descriptive statistics for external measurements, measurements of tail width, and craniodental measurements (all in millimeters) of 3 species of *Hylapetes*, with uncorrected probability assessments of interspecific differences. Under a Bonferroni correction, 5*, 4*, and probably 3* are significant. Variable abbreviations are defined in the “Materials and Methods” and are shown in Fig. 2.

	<i>H. lepidus</i>		<i>H. platyurus</i>		<i>H. spadiceus</i>		Probability ^a		
	$\bar{X} \pm SD$	<i>n</i>	$\bar{X} \pm SD$	<i>n</i>	$\bar{X} \pm SD$	<i>n</i>	1	2	3
HBL	134.00 ± 4.96	20	116.65 ± 7.22	20	145.75 ± 9.62	93	5*	4*	5*
EL	19.10 ± 0.97	20	15.85 ± 0.93	20	18.28 ± 1.27	89	5*	2*	5*
HFL	26.45 ± 1.57	20	23.90 ± 1.25	20	27.34 ± 1.56	89	5*	—	5*
TL	120.75 ± 7.37	20	91.38 ± 7.40	16	127.10 ± 8.57	93	5*	—	5*
TW10%	25.39 ± 3.60	18	18.55 ± 2.76	20	26.07 ± 3.92	95	5*	—	5*
TW25%	27.44 ± 3.60	18	20.45 ± 3.72	20	28.21 ± 4.21	95	5*	—	5*
TW50%	24.89 ± 3.96	19	16.32 ± 2.87	19	24.49 ± 3.82	96	5*	—	5*
HL50%	18.42 ± 1.92	19	14.11 ± 1.88	18	18.64 ± 2.56	96	5*	—	5*
TW75%	19.95 ± 2.93	19	13.94 ± 2.97	17	20.70 ± 3.55	93	5*	—	5*
TW90%	15.26 ± 3.14	19	10.60 ± 3.14	15	16.26 ± 3.00	91	3*	—	5*
ONL	34.02 ± 0.90	19	31.95 ± 0.90	18	35.38 ± 1.04	82	5*	5*	5*
ZB	21.09 ± 0.79	13	19.76 ± 0.63	16	21.67 ± 0.81	77	4*	—	5*
BCB	16.33 ± 0.49	18	16.20 ± 0.29	18	17.09 ± 0.45	89	—	5*	5*
POB	9.92 ± 0.45	20	9.74 ± 0.43	20	10.21 ± 0.61	89	—	—	2*
OCB	7.82 ± 0.24	20	7.57 ± 0.18	20	7.99 ± 0.26	91	3*	2*	5*
IOB	8.09 ± 0.54	20	8.05 ± 0.37	20	7.89 ± 0.52	89	—	—	—
BCD	11.46 ± 0.37	18	10.64 ± 0.32	19	11.48 ± 0.45	87	5*	—	5*
NL	9.33 ± 0.34	19	8.71 ± 0.61	18	9.84 ± 0.65	80	3*	2*	5*
NB	5.10 ± 0.35	16	4.92 ± 0.30	17	5.24 ± 0.40	83	—	—	2*
PPL	11.60 ± 0.47	19	10.63 ± 0.43	20	12.07 ± 0.58	89	5*	2*	5*
BPL	11.14 ± 0.58	19	9.95 ± 0.38	20	11.66 ± 0.48	89	5*	4*	5*
DL	7.68 ± 0.58	20	7.26 ± 0.34	20	8.22 ± 0.46	88	2*	4*	5*
IFL	2.41 ± 0.26	19	2.19 ± 0.20	20	2.33 ± 0.27	92	2*	—	—
IFB	1.36 ± 0.25	19	1.35 ± 0.14	20	1.45 ± 0.18	91	—	—	—
BPB	8.29 ± 0.26	20	7.64 ± 0.22	20	8.58 ± 0.43	92	5*	2*	5*
TRL	6.60 ± 0.13	20	5.42 ± 0.16	20	6.75 ± 0.23	89	5*	2*	5*
M1B	1.75 ± 0.10	20	1.51 ± 0.08	20	1.75 ± 0.09	91	5*	—	5*
ID	1.70 ± 0.13	20	1.63 ± 0.12	20	1.71 ± 0.12	90	—	—	2*
BL	6.65 ± 0.56	20	6.62 ± 0.23	20	7.24 ± 0.28	93	—	5*	5*
ML	4.55 ± 0.33	19	5.02 ± 0.25	20	5.69 ± 0.29	92	4*	5*	5*
ISB	2.72 ± 0.36	19	2.39 ± 0.43	20	2.47 ± 0.40	93	—	—	—

^a Probabilities: 5* $P < 0.00001$; 4* $P < 0.0001$; 3* $P < 0.001$; 2* $P < 0.01$; $-P > 0.01$. These are probabilities of the following hypotheses: 1. *H. lepidus* = *H. platyurus*, 2. *H. lepidus* = *H. spadiceus*, and 3. *H. platyurus* = *H. spadiceus*.

Reported misclassifications based on ratios were determined from the actual distributions of the individual ratios.

RESULTS

Table 1 lists the means and standard deviations of the external measurements, tail-width measurements, and craniodental measurements of the 3 species. In addition, Table 1 lists the uncorrected significance levels for each 2-species comparison (columns labeled 1, 2, and 3). If each 2-species comparison ($n = 93$) was subjected to the Bonferroni correction, the comparisons listed as 5* ($P < 0.00001$) and 4* ($P < 0.0001$) would be significant at the level $P < 0.01$, and the comparisons listed as 3* ($P < 0.001$) would be significant or verge on significance at the level $P < 0.05$. This is probably an overcorrection for these intercorrelated measurements, but we do not consider the uncorrected probability level 2* ($P < 0.01$) to be significant.

We scored cheek coloration and color at the base of the tail, and these scores are shown in Fig. 3. Most specimens of *H. platyurus* had gray cheeks and were scored as 1.0. Most specimens of *H. lepidus* had pinker cheeks and were scored as

2.0 or 2.5. The cheeks of specimens of *H. spadiceus* were the pinkest, and more than 50% were scored as 3.0–4.0. There was overlap between all 3 pairs of species, although the median and mode of the scores were all different.

Hairs at the base of the tail were similarly scored with similar results. Most of the specimens of *H. platyurus* were scored as 1.0–2.5. Specimens of *H. lepidus* were most frequently scored 3.0 or 3.5, whereas more than 70% of the specimens of *H. spadiceus* were scored 3.5–4.5. As with cheek coloration, there was considerable overlap among the 3 species in coloration at the base of the tail.

The tail-width measurements showed that *H. platyurus* has a significantly narrower tail than do the other 2 species, which are not significantly different from one another. When tail-width measurements are divided by tail length (measured on the skin, not taken from the label), there are no significant differences among the species in relative tail width. Thus, the width of the tail of *H. platyurus* exhibits the same proportions relative to its length as do the other 2 species (results not shown). When tail-width measurements are divided by the average tail width, there is also no difference among the 3

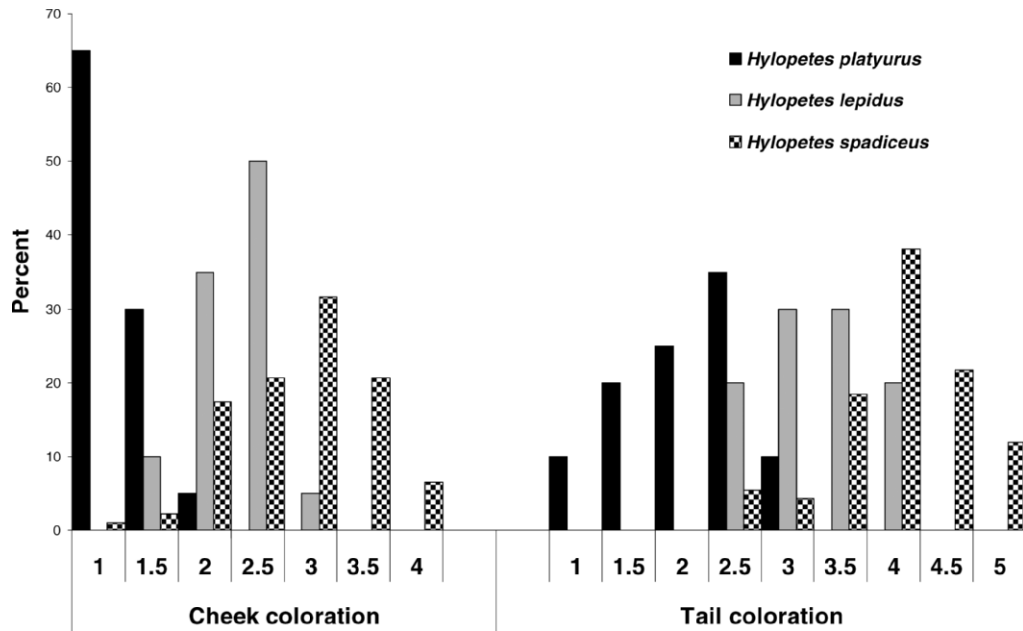


FIG. 3.—Bar graph showing the pelage coloration of the cheek and ventral base of the tail in 3 species of *Hylopetes*. The scoring ranges from 1 (gray) to 5 (orange-red) as described in the “Materials and Methods.” Sample sizes were as follows: *H. lepidus* = 20, *H. platyurus* = 20, *H. spadiceus* = 100.

species (results not shown). This indicates that there is no difference in the tapering of the tail in these 3 species. *H. platyurus* has a shorter, narrower tail than the other 2 species (tail length 77.7% ± 4.6% of head and body length in *H. platyurus*, 87.5% ± 5.3% in *H. spadiceus*, and 90.2% ± 6.1% in *H. lepidus*), but proportional differences within the tail are not supported by our data. The probability levels were not at all close to significant, therefore a type II error is unlikely.

Among the 21 craniodental measurements (Table 1), 16 exhibited a rank pattern of *H. platyurus* < *H. lepidus* < *H. spadiceus*. Of the other 5 measurements, only 1, mastoid length, exhibited a fundamentally different pattern. For this variable, the ranking was *H. lepidus* < *H. platyurus* < *H. spadiceus*. In a stepwise canonical variate analysis based on log-transformed values, 8 variables were removed, leaving 13 discriminating variables (Table 2). The 3 samples were aligned on the 1st axis by size (Fig. 4), and the canonical discriminant functions, standardized by within-group variances, demonstrated that they emphasize length of the toothrow (+0.84), length of the diastema (+0.55), and other length variables as positive values versus interorbital breadth (−0.44), incisor depth (−0.42), and bullar length (−0.37) as negative values (Table 2). This axis separated *H. platyurus* from the other 2 species. On the 2nd axis, there was a strong emphasis on the mastoid length (+0.86) and breadth of braincase (+0.53) versus interseptal width (−0.44), depth of braincase (−0.38), and length of toothrow (−0.36). There was a clear separation of *H. lepidus* from the other 2 species (Fig. 4). All specimens were correctly assigned among the 3 species in a jackknifed classification matrix (Wilkes’ lambda = 0.0137, *d.f.* = 13, 2, 85; approximate *F* = 42.28, *d.f.* = 26, 146, *P* < 0.00001).

A principal component analysis (not shown) based on the same data did not separate the 3 populations effectively. There was extensive overlap between the clusters of points of all 3 species. This is because the largest variances in the matrix are associated with measurements that are poor discriminators among the 3 populations. A principal component analysis (not shown) based on the log-transformed data of 3 variables, which

TABLE 2.—Canonical discriminant functions, unstandardized and standardized, used in stepwise discriminant analysis shown in Fig. 4. Variable abbreviations are defined in the “Materials and Methods.” The largest standardized functions are emphasized in boldface type.

Variable	Canonical discriminant functions		Canonical discriminant functions standardized by within-group variances	
	Factor 1	Factor 2	Factor 1	Factor 2
BCB	9.891	24.402	0.214	0.529
OCB	−7.923	−10.345	−0.256	−0.334
IOB	−7.373	−1.121	−0.437	−0.067
BCD	5.354	−10.960	0.188	−0.385
PPL	10.745	−3.898	0.453	−0.164
DL	10.293	−2.265	0.550	−0.121
IFL	−1.371	−2.812	−0.145	−0.298
BPB	10.942	−0.359	0.332	−0.011
TRL	26.300	−11.050	0.844	−0.355
ID	−5.844	0.529	−0.415	0.038
BL	−10.121	10.572	−0.366	0.382
ML	4.085	16.984	0.206	0.856
ISB	−0.828	−3.018	−0.121	−0.441
Constant	−111.654	−27.266		
Variance explained (%)	73	27		

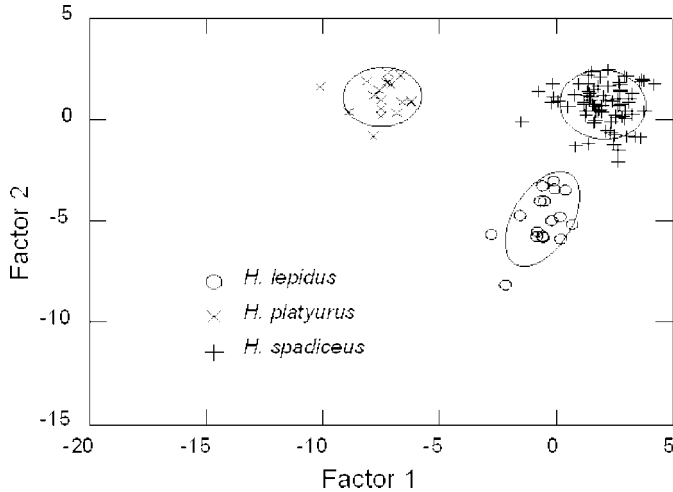


FIG. 4.—Graph of stepwise discriminant analysis performed on 13 log-transformed craniodental variables (see Table 2 for list), providing 100% discrimination among the 3 species of *Hylopetes* (140 specimens, 30 localities).

were important in the canonical discrimination (length of toothrow, length of bulla, and length of mastoid), was much more effective. In this analysis, only 1 specimen of *H. lepidus* overlapped the cluster of *H. spadiceus*, and there was no overlap of either of these species with the cluster of *H. platyurus*.

In an attempt to obtain simpler discriminators between the 3 species while reducing the importance of size itself, we examined combinations of small numbers of variables. The same 3 variables used in the smaller principal component analysis (length of toothrow, length of bulla, and length of mastoid) were summed, and each variable was divided by the sum (Table 3). The length of toothrow is a good measure of size in these species, so the computed variables were expected to discriminate on the basis of bulla length or mastoid length, with size partially removed. All 3 computed variables discriminated the sample of *H. platyurus* from *H. lepidus*; 2 of them also discriminated the other combinations of species. One variable (length of toothrow/total) provided 100% correct classifications of the individuals to species. The other 2 variables (length of

bulla/total and mastoid length/total) were not as successful at classifying individuals to the correct species. An additional 5 ratios of variables were computed: length of mastoid/length of bulla, interorbital breadth/length of toothrow, interorbital breadth/length of diastema, interorbital breadth/mastoid length, and breadth of braincase/depth of braincase (Table 4). The ratio of interorbital breadth/length of toothrow discriminated between the species effectively, and it allowed efficient classification of individuals to the correct species with misclassifications of 1 of 19 *H. lepidus* and 1 of 20 *H. platyurus* in 1 test, and 0 of 20 *H. platyurus* and 4 of 86 *H. spadiceus* in another test. Another ratio, interorbital breadth/mastoid length, provided the best contrast between *H. lepidus* and *H. spadiceus*, with misclassifications of 1 of 18 *H. lepidus* and 4 of 86 *H. spadiceus*. These were all post hoc classifications, but we expect these ratios to assist with species identification for a majority of specimens.

DISCUSSION

Hill (1962) used cranial measurements to discriminate *H. spadiceus* from the combined *H. lepidus* of Java (*H. lepidus lepidus*) and the *Hylopetes* of Sumatra and the Malay Peninsula (which he called *H. lepidus platyurus*). He clearly discriminated between the 2 groups with a graph of greatest length of auditory capsule (x-axis) versus the ratio of bulla width to greatest length of auditory capsule (y-axis). However, there is little or no discrimination on the y-axis; all the discrimination is accounted for on the x-axis. Because his “total length of auditory capsule” is taken “from the most anterior point of the tympanic bulla to the most posterior point of the inflated external mastoid portion of the periodic” (Hill 1962:724), we contend that it combines the smaller *H. platyurus*, which has a larger mastoid region, with the larger *H. lepidus*, which has a smaller mastoid region. To avoid this problem, we took separate measurements of the length of the bulla and a diagonal length measuring the length of the mastoid portion of the temporal bone.

Our study clearly separates the 3 populations, which we treat as distinct species. A canonical variate analysis based on 13

TABLE 3.—Relative lengths of maxillary toothrow, excluding P3 (TRL), auditory bulla (BL), and mastoid (ML) in 3 species of *Hylopetes*. Total = TRL + BL + ML. The first 3 rows of data represent mean ± SD and are followed by results produced from 1-way analyses of variance.

Species	Total	TRL/total	BL/total	ML/total
<i>H. lepidus</i> (n = 19)	17.67 ± 0.41	0.373 ± 0.011	0.369 ± 0.008	0.257 ± 0.014
<i>H. platyurus</i> (n = 20)	17.06 ± 0.53	0.318 ± 0.008	0.388 ± 0.006	0.294 ± 0.009
<i>H. spadiceus</i> (n = 88)	19.65 ± 0.59	0.343 ± 0.011	0.368 ± 0.008	0.289 ± 0.009
<i>H. lepidus</i> versus <i>H. platyurus</i>	F = 16.3 df. = 1, 37 P < 0.001	F = 345 ^a df. = 1, 37 P < 0.00001	F = 63.5 df. = 1, 37 P < 0.00001	F = 98.5 df. = 1, 37 P < 0.00001
<i>H. lepidus</i> versus <i>H. spadiceus</i>	F = 195 df. = 1, 105 P < 0.00001	F = 119.8 df. = 1, 105 P < 0.00001	F = 0.460 df. = 1, 105 P = 0.49912	F = 145 df. = 1, 105 P < 0.00001
<i>H. platyurus</i> versus <i>H. spadiceus</i>	F = 329 df. = 1, 106 P < 0.00001	F = 95.9 df. = 1, 106 P < 0.00001	F = 101.5 df. = 1, 106 P < 0.00001	F = 5.27 df. = 1, 106 P = 0.024

^a Dividing line between *H. lepidus* and *H. platyurus* is 0.342; misclassified 0 of 19 *H. lepidus* and 0 of 20 *H. platyurus*.

TABLE 4.—Ratios of selected craniodental measurements for 3 species of *Hylopetes*. The first 6 rows of data represent mean \pm SD (n) and are followed by results produced from 1-way analyses of variance. ML = Mastoid length; BL = length of auditory bulla; IOB = interorbital breadth; TRL = length of maxillary toothrow, excluding P3; DL = length of diastema; BCB = breadth of braincase; BCD = depth of braincase.

Species	ML/BL	IOB/TRL	IOB/DL
	IOB/ML	BCB/BCD	
<i>H. lepidus</i>	0.698 \pm 0.049 (n = 19)	1.225 \pm 0.087 (n = 19)	1.060 \pm 0.09 (n = 19)
	1.790 \pm 0.160 (n = 18)	1.440 \pm 0.040 (n = 16)	
<i>H. platyurus</i>	0.759 \pm 0.030 (n = 20)	1.485 \pm 0.071 (n = 20)	1.110 \pm 0.05 (n = 20)
	1.610 \pm 0.110 (n = 20)	1.520 \pm 0.050 (n = 18)	
<i>H. spadiceus</i>	0.778 \pm 0.088 (n = 93)	1.168 \pm 0.084 (n = 86)	0.960 \pm 0.070 (n = 85)
	1.390 \pm 0.100 (n = 88)	1.490 \pm 0.050 (n = 85)	
<i>H. lepidus</i> versus <i>H. platyurus</i>	F = 22.2	F = 105.29 ^a	F = 5.60
	F = 18.28	F = 36.45	
	$d.f.$ = 1, 37	$d.f.$ = 1, 37	$d.f.$ = 1, 37
	$d.f.$ = 1, 36	$d.f.$ = 1, 32	
	P < 0.00003	P < 0.00001	P = 0.023
	P < 0.001	P < 0.00001	
<i>H. lepidus</i> versus <i>H. spadiceus</i>	F = 14.5	F = 7.12	F = 31.56
	F = 195.73 ^b	F = 15.73	
	$d.f.$ = 1, 110	$d.f.$ = 1, 103	$d.f.$ = 1, 102
	$d.f.$ = 1, 104	$d.f.$ = 1, 99	
	P < 0.001	P < 0.01	P < 0.00001
	P < 0.00001	P < 0.001	
<i>H. platyurus</i> versus <i>H. spadiceus</i>	F = 0.878	F = 243.24 ^c	F = 95.80
	F = 73.92	F = 6.48	
	$d.f.$ = 1, 111	$d.f.$ = 1, 104	$d.f.$ = 1, 103
	$d.f.$ = 1, 106	$d.f.$ = 1, 101	
	P = 0.35	P < 0.00001	P < 0.00001
	P < 0.00001	P = 0.012	

^a Dividing line 1.370; misclassified 1 of 19 *H. lepidus* and 1 of 20 *H. platyurus*.

^b Dividing line 1.548; misclassified 1 of 18 *H. lepidus* and 4 of 88 *H. spadiceus*.

^c Dividing line 1.340; misclassified 0 of 20 *H. platyurus* and 4 of 86 *H. spadiceus*.

cranial measurements successfully discriminated between the species and classified all specimens correctly. Ratios involving 3 measurements were slightly less successful in discriminating between the 3 species. Similarly, a variety of external characters—relative tail length, cheek coloration, and color at the base of the tail—exhibited major differences between the species, but the overlap between them did not permit 100% correct allocation to species. Tail shape, previously suggested to differ between the species (Hill 1962), was not useful for discrimination.

Our study involved adequate samples from peninsular Malaysia and from Java. We have not seen adequate samples from Sumatra or Borneo. Neither did Hill (1962), who included 2 specimens from Sumatra and 4 specimens from Borneo in his analysis. *H. spadiceus* and *H. platyurus* are sympatric on the Malay Peninsula and on the northern end of Sumatra. This is based on the fact that both *H. platyurus* (Jentink 1890a) and *H. spadiceus sumatrae* (Sody 1949) have their type locality in northern Sumatra. Intergradation between either and *H. lepidus* on Sumatra has not been demonstrated. We hope that our data and analyses will lend themselves to further tests of our hypothesis that the 3 are distinct species.

The occurrence of *H. spadiceus* on Sumatra is poorly supported. Its occurrence in northern Sumatra is based on 2 specimens: the type of *H. spadiceus sumatrae* described by Sody (1949) from Redalong, East Atjeh, and 1 specimen examined

by Hill (1962), from Deli, Medan. In southern Sumatra, the documentation is little better. We examined 1 skin without a skull from Goenoeng Dempo, southwestern Sumatra. We considered this specimen to be *H. spadiceus* because we scored the coloration of the cheek and base of tail 3.0 and 4.0, respectively, like many *H. spadiceus*, but few *H. lepidus* (only 5% and 20%, respectively) and no *H. platyurus*. *Hylopetes aurantiacus* was described by Wagner (1841) from Bangka Island, off the northeast coast of southern Sumatra. In Wagner's (1841) original description, the tail is described as "... cauda plana disticha, castanea," [flat distichous tail, chestnut colored] and elaborated further as "Der Schwanz ist rostig-kastanienbraun; an der Wurzel zu beiden Seiten orange-gelb eingefast." [The tail is rusty-chestnut; bordered at the base on both sides by orange-gold.] We would probably have scored this at 3.5 or 4.0, which excludes *H. platyurus* but does not discriminate between *H. spadiceus* and *H. lepidus*. However, Hill (1962) studied the type specimen and concluded that *H. aurantiacus* is a subspecies of *H. lepidus*. His measurements support this assessment. Jentink (1890b:150, footnote) obtained a specimen from Bangka and illustrated the skull, which has an inflated mastoid region like that of *H. spadiceus* (Fig. 1). Sody (1937) examined 2 specimens with damaged skulls and described them as very similar to the one described by Wagner (1841). We have no basis for identifying these 2 specimens. Our conclusion, based on the observations of Jentink (1890b)

and Hill (1962), is that *H. spadiceus* and *H. lepidus* are sympatric on the island of Bangka.

We examined 4 specimens from Borneo, all of which we considered to be *H. spadiceus*. This is in agreement with Payne and Francis (1985), who reported this species in Borneo, vouchered by 11 specimens. They also reported *H. lepidus platyurus* on Borneo, vouchered by 2 specimens. According to Payne and Francis (1985:248), this species is “known only from G. Kinabalu (1,370 m) in Sabah; and the Kelabit uplands (900–1,070 m) in Kalimantan.” The report of Corbet and Hill (1992) of *H. lepidus* occurring on Borneo appears to be based on Payne and Francis (1985). Thus, *H. spadiceus* and *H. platyurus* both occur on Borneo and reports of *H. lepidus* on Borneo probably refer to what we consider to be *H. platyurus*. However, we note that in peninsular Malaysia, *H. platyurus* occurs in the lowlands below 300 m, but in Borneo it occurs in the uplands, always above 900 m. Upland small mammals on Mount Kinabalu are commonly distinct species (Corbet and Hill 1992).

We provide modified accounts from Thorington and Hoffmann (2005) as summaries of our current best hypotheses about the taxonomy and distribution of these 3 species. Recognized subspecies are presented in boldface type.

Hylopetes lepidus (Horsfield, 1822)

Pink-cheeked flying squirrel.

Type locality.—“... only found in the closest forests of Java,” [Indonesia].

Distribution.—Java and Bangka Island.

Synonyms.—***aurantiacus*** (Wagner, 1841:438).

Comments.—Formerly called *sagitta* Linnaeus, 1766; see Medway (1977:104). Formerly included *platyurus* (Corbet and Hill 1992:316; Hill 1962; Medway 1977:104).

Hylopetes platyurus (Jentink, 1890a)

Gray-cheeked flying squirrel.

Type locality.—Deli, NE Sumatra.

Distribution.—Sumatra, peninsular Malaysia, and Borneo.

Comments.—Formerly included in *lepidus* (Corbet and Hill 1992:316; Hill 1962; Pavlinov et al. 1995).

Hylopetes spadiceus (Blyth, 1847)

Red-cheeked flying squirrel.

Type locality.—“Arracan” [Arakan, Myanmar].

Distribution.—Myanmar, Thailand, southern Vietnam, Sumatra including Bangka Island, peninsular Malaysia, and Borneo.

Synonyms.—*amoenus* (Miller, 1906); *belone* (Thomas, 1908); ***everetti*** (Thomas, 1895); *caroli* Gyldenstolpe, 1920; *harrisoni* (Stone, 1900); ***sumatrae*** Sody, 1949.

Comments.—Includes *harrisoni*; see Medway (1977:105). Formerly included *sipora*; see Hill (1962). Corbet and Hill (1980:137) listed *spadiceus* in *lepidus*, without comment.

The implications of these distributions for the historical zoogeography of the species are as follows. The Sunda Strait

may have been a barrier for the dispersal of *H. spadiceus* to Java, but it has not been a barrier to the dispersal of *H. lepidus*, which is found on both sides of this strait. This is a common pattern in squirrels; of 9 other species on Java, only 1 does not also occur on Sumatra; of 25 species found on Sumatra, only 9 are found also on Java. Either they did not cross the Sunda Strait, or they subsequently became extinct on Java. Although *H. spadiceus* is reported from both northern and southern Sumatra, *H. lepidus* is restricted to southern Sumatra (Bangka Island), and *H. platyurus* is known only from northern Sumatra. The Malacca Strait has not been a barrier to *H. platyurus* or *H. spadiceus*, which are both found on Sumatra and the Malay Peninsula. This is true for 18 of the other squirrels occurring on Sumatra as well. The Isthmus of Kra has not been a barrier to *H. spadiceus*. The range of *H. platyurus* is restricted to the southern states of Malaysia on the peninsula and does not approach the Isthmus of Kra. Although the isthmus has been an extraordinary boundary for plants and birds (Hughes et al. 2003; Woodruff 2003), 9 of the 25 squirrels occurring on the peninsula south of the isthmus also occur north of the Isthmus of Kra. The South China Sea between peninsular Malaysia and Borneo has not been a barrier to either *H. platyurus* or *H. spadiceus*. This is a common pattern (Meijaard 2003), and 15 other squirrel species also are common to the peninsula and the fauna of Borneo (totaling 34 squirrel species). The Java Sea between Java and Borneo has probably been a barrier to *H. lepidus*, as it probably has been for the other 9 species on Java. Of those that occur both on Java and Borneo, all but one also are found on the Malay Peninsula and may have utilized the South China Sea route. The other one occurs on Java, Sumatra, and Borneo and may have used a route from southeastern Sumatra, through Bangka Island, to southwestern Borneo.

We hope this paper will stimulate other studies of these taxa, with well-identified voucher specimens. Molecular studies generating phylogenies and estimated dates of divergence would test our taxonomic hypotheses and provide estimates of when the water barriers isolated the various squirrel populations on the Malay Peninsula and these Southeast Asian islands. Studies of ecological differences between the species are needed to help explain the differences in geographic patterns and elucidate the historical ecology of the Sunda shelf.

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APPENDIX I

Specimens examined.

Hylopetes lepidus ($n = 20$).—Indonesia, Java, Cheribon, 6.77°S, 108.55°E (AMNH 101431, 101433–101442, 101833–101837, 101921, 103018, 106701, 106702).

Hylopetes platyurus ($n = 20$).—Malaysia, Selangor, Klang, Tanjong Duablas, Kuala Langat Forest Reserve, Bukit Mandol, 2°55'N, 101°34'E, 0–250 feet (USNM 488617, 488620, 488621, 488627, 488630, 488633–488636); Malaysia, Wilayah Persekutuan, Kuala Lumpur, Sungei Buloh, Sungei Buloh Forest Reserve, Bukit Lanjan, 3°10'N, 101°35'E, 500–1,000 feet (USNM 488618, 488619, 488623–488626, 488628, 488629, 488631, 488632).

Hylopetes spadiceus ($n = 100$).—Indonesia, Sumatra, Riau Islands Province, Natuna Islands, Bunguran, 4.00°N, 108.25°E (USNM 104627); Sumatra, Riau Archipelago, Kundur, 0.75°N, 103.43°E (USNM 122883); Sumatra, Goenoeng Tempo, 4.03°S, 103.13°E (AMNH 106641); Indonesia, Borneo, Kalimantan, Ngabang, 0.38°N, 109.95°E (AMNH 106737). Malaysia, Borneo, Sabah, Mount Kinbalu, Tenompok, 6.02°N, 116.50°E, 4,500 feet (USNM 301023); Mount Kinbalu, Bundu Tuhan, 5.97°N, 116.50°E (USNM 292651, 292652); Malaysia, Selangor, Kepong Forest Reserve (USNM

311369); Selangor, Klang, Kanpong Ayer, Kuning Bukit (USNM 481112); Selangor, Bukit Lanjan (USNM 481115); Malaysia, Johor, Segamat, Kudong, 2°30'N, 102°49'E (USNM 481109, 481114, 481116); Segamat, Bekok Tamok, 2°30'N, 102°49'E (USNM 481111); Johor, Kluang, Pengkalan Terek (USNM 481110, 481113); Kluang, Paloh, Labis Forest Reserve, Serandong, 2°17'N, 103°22'E, 250–500 feet (USNM 488638, 488639); Kluang, Bekok, Labis Forest Reserve, Ulu Habong, 2°20'N, 103°08'E, 250–500 feet (USNM 488640–488643); Labis Forest Reserve, Tong Nam Company, 2°20'N, 103°13'E, 250–500 feet (USNM 488644–488646, 488661); Labis Forest Reserve, Kudong, 2°22'N, 103°13'E, 250–500 feet (USNM 488647–488650, 488654–488656, 488663, 488664, 488668, 488669, 489453–489455, 489457, 489458, 489460, 489461, 489470–489477, 489482, 489483, 489489–489492, 489495, 489500, 489501); Labis Forest Reserve, Lenek, 2°20'N, 103°05'E, 250–500 feet (USNM 488651, 489464–489467, 489469); Labis Forest Reserve, Kersiak, 2°27'N, 103°17'E, 500–1,000 feet (USNM 488653, 489493, 489494); Labis Forest Reserve, Tamok, 2°24'N, 103°15'E, 250–500 feet (USNM 488657–488660, 489450–489452, 489478–489481, 489484–489488); Labis Forest Reserve, Batu Empat at mile 4, 2°19'N, 103°10'E, 250–500 feet (USNM 488662); Kluang, Niyor, Labis Forest Reserve, Pengkalan Terek, 2°11'N, 103°19'E, 200–500 feet (USNM 489496–489499). Thailand, Sakon Nakhon, Muang, Phu Pan (USNM 308155); Thailand, Nakhon Si Thammarat, Ban Na, Fhang (USNM 535203); Thailand, Toak Plateau, Tenasserim, 16.32°N, 98.48°E (AMNH 54822); Thailand, Pulo Terutau, 6.58°N, 99.67°E (USNM 123931–123933). Vietnam, Ba Ria-Vung Tau, Con Dao Islands, Con Son Island, Airport Building, 0.5 km S, 8.70°N, 106.58°E, 10 m (USNM 357017, 357018); Vietnam, locality unknown (USNM 258237).