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A Predictive Model to Differentiate the Fruit Bats *Cynopterus brachyotis* and *C.* cf. *brachyotis* Forest (Chiroptera: Pteropodidae) from Malaysia Using Multivariate Analysis

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Vijaya K. Jayaraj, Charlie J. Laman, and Mohd T. Abdullah (2012) A predictive model to differentiate the fruit bats *Cynopterus brachyotis* and *C.* cf. *brachyotis* Forest (Chiroptera: Pteropodidae) from Malaysia using multivariate analysis. *Zoological Studies* **51**(2): 259-271. Field discrimination of *Cynopterus brachyotis* and *C.* cf. *brachyotis* Forest (as designated by Francis 2008) in southern Thailand, Peninsular Malaysia, and Borneo is problematic. These 2 forms are sympatric in this region but are confined to different habitat types: *C. brachyotis* inhabits open habitats, orchards, and agricultural areas, while *C.* cf. *brachyotis* Forest is confined to primary and old secondary forests. In this study, we attempted to develop prediction models to identify both *C. brachyotis* and *C.* cf. *brachyotis* Forest in this region based on multivariate statistics. Two predictive models were generated using a canonical discriminant function, and it was found that 5 characters can be used to accurately identify museum vouchers of *C. brachyotis* and *C.* cf. *brachyotis* Forest. Four characters are needed for field identification of these 2 forms of *Cynopterus* in southern Thailand, Peninsular Malaysia, and Borneo. A review of the current taxonomy and classification indicated that there is a need to describe the 6 existing forms of the *C. brachyotis* complex in the Indo-Malayan region. This will aid conservationists, field ecologists, and taxonomists in taxonomic- and conservation-related decisions about this species complex.
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Key words: *Cynopterus brachyotis*, Discriminant function analysis, Habitat type.

The genus *Cynopterus* F. Cuvier 1824, commonly known as dog-faced fruit bats or short-nosed fruit bats are widely distributed in the Indo-Malayan region (Corbet and Hill 1992). The taxonomic status of this genus has undergone many revisions, and the most recent classification by Simmons (2005) lists 7 species in this genus: *C. brachyotis* (Müller, 1838); *C. horsfieldii* Gray, 1843; *C. luzoniensis* Peters, (1861); *C. minutus* Miller, 1906; *C. nusatenggara* Kitchener and Maharadatunkamsi, 1991; *C. sphinx* (Vahl, 1797); and *C. tithaecheilus* (Temminck, 1825). Discriminating between species in this genus is often problematic given the many variations and overlap between species representatives across a geographical gradient. Work such as that by Bumrungsri and Racey (2005) is often done to discriminate similar sympatric species in this genus.

The nominate *C. brachyotis* type specimen was described by Müller (1838), but currently the status of *C. brachyotis* is uncertain, as recent studies indicated that it may actually be a complex of species (Campbell et al. 2004). Corbet and Hill

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(1992) listed 19 synonyms of *C. brachyotis*, but Simmons (2005) recognized only seven of them, with most of them lacking data on their status and current distribution. Abdullah (2003) compared morphological measurements of *Cynopterus* from various sources (Andersen 1912, Hill and Thonglongya 1972, Lekagul and McNeely 1977, Medway 1978, Hill 1983, Payne et al. 1985, Kitchener and Maharadatunkamsi 1991 1996, Ingle and Heaney 1992, Nor 1996) and found that a lot of morphological measurements overlap within and between species across its distribution. This species is widely distributed throughout Southeast Asia (Fig. 1) and can be found at areas up to 1600 m in elevation in Borneo (Lekagul and McNeely 1977, Medway 1978, Bergmans and Rozendall 1988, Corbet and Hill 1992, Peterson and Heaney 1993, Abdullah 2003). It can be found in many habitats (but most frequently in disturbed forest) including lower montane forest, dipterocarp forest, gardens, mangroves, and strand vegetation.

Francis (1990) found that there were forearm length differences in *C. brachyotis* caught in primary forests and that from secondary habitats in Sepilok, Sabah. This observation was later investigated by Abdullah et al. (2000) and Abdullah (2003) using molecular and external morphometric data on samples from Borneo and Peninsular Malaysia to the southern tip of Thailand. Results of those studies showed that 2 forms of *C. brachyotis* inhabited 2 contrasting habitats (in Peninsular Malaysia and Borneo). The larger form was found to inhabit open areas, whereas the smaller form was confined to primary forests. Abdullah et al. (2000) postulated that these differences found in *C. brachyotis* are based on ecological differences in the habitats they occupy. Later Campbell et al. (2004) reexamined the species complex using different genetic markers and discovered 4 additional distinct lineages in the *C. brachyotis* complex scattered in the Indo-Malayan region. These 4 lineages are respectively found in India, Myanmar, Sulawesi, and the Philippines. Abdullah and Jayaraj (2006) later performed a cluster analysis on the type specimen of *C. brachyotis* using morphological measurements described by Müller (1938), and the results showed that the nominate *C. brachyotis* was clustered with the larger form of *C. brachyotis*.

A recent study using microsatellites and 2 mitochondrial (mt)DNA genes by Fong (2011) showed congruent findings with Abdullah et al. (2000), Abdullah (2003), Campbell et al. (2004 2006), and Julaihi (2005) of the existence of 2 *C. brachyotis* lineages in southern Thailand, Peninsular Malaysia, and Borneo. The morphometrics of this species also showed same findings but there were misclassifications of some samples (Jayaraj et al. 2004 2005). Campbell et al. (2007) also reviewed the morphological and ecomorphological aspects of this species using multivariate statistics and found that the wing loading and aspect ratio was not an informative character that can be used to differentiate the 2 forms of *C. brachyotis*. Another study on flight parameters also showed similar results (Menon 2007).

Results from general descriptive statistics, mtDNA, microsatellites, and morphometric studies showed congruency of the existence of 2 divergent forms of *C. brachyotis*. As Abdullah and Jayaraj's (2006) study showed that the larger form was indeed the assigned *C. brachyotis*, it is apparent that the small form may be a new species of *Cynopterus* yet to be described. However, a recent taxonomy of the *Cynopterus* by Simmons (2005) did not include this new form, and Francis (2008) assigned *C.* cf. *brachyotis* Sunda to the large form of *C. brachyotis* commonly found in open areas and *C.* cf. *brachyotis* Forest to the small form of *C. brachyotis* commonly found in primary forests. For

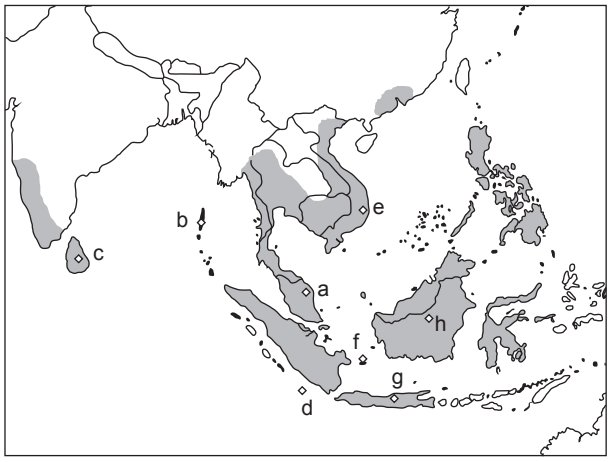

Fig. 1. Distribution of 8 subspecies of *C. brachyotis* in the Indo-Malayan region (Mickelburgh et al. 1992, Simmons 2005). (a) *C. b. altitudinis* found in highlands of the Main Range, Peninsular Malaysia; (b) *C. b. brachysoma* found in the Andaman Is.; (c) *C. b. ceylonensis* found in Sri Lanka; (d) *C. b. concolor* found on Enganno I.; (e) *C. b. hoffeti* found in Vietnam; (f) *C. b. insularum* found in the Kangean Is. and Laut Kecil Is.; (g) *C. b. javanicus* found in Bali, Java, Madura, and Penidah; and (h) *C. b. brachyotis* found in Bangka, Belitung, Borneo, Lombok, the Nicobar Is., Peninsular Malaysia, the Philippines, Singapore, Sulawesi, Sumatra and Thailand.

the easy interpretation of this paper, we assign *C. brachyotis* as the known large form as verified by Abdullah and Jayaraj (2006), and *C.* cf. *brachyotis* Forest as the new undescribed form found in primary forests.

In terms of forearm length differences, Francis (1990) showed that *C. brachyotis* has a mean forearm length of 62.1 mm (*n* = 22) and *C.* cf. *brachyotis* Forest has a mean forearm length of 58.4 mm (*n* = 21). Abdullah (2003) reported that the forearm length of *C.* cf. *brachyotis* Forest was 59.43 (± standard deviation (SD) 2.70) mm, and *C. brachyotis* had a mean forearm length of 63.87 (± 5.02) mm. Campbell et al. (2006) used a forearm length of 63.8 (± 1.6) mm to identify *C. brachyotis* and a forearm length of 59.5 (± 1.7) mm to identify *C.* cf. *brachyotis* Forest.

The high reliance on forearm length to distinguish these 2 forms is problematic as various authors have reported different forearm length measurements used for differentiation. The development of additional characters to differentiate these 2 forms would be useful in the field, as this will aid field ecologists in accurately identifying both *C. brachyotis* and *C.* cf. *brachyotis* Forest in southern Thailand, Peninsular Malaysia, and Borneo. Thus, in this study, we attempted to further describe detailed morphometric variations that exist in the genus *Cynopterus* from Peninsular Malaysia and Borneo using multivariate statistics. The approach was to develop a classification function that can be used to differentiate *C. brachyotis* and *C.* cf. *brachyotis* Forest in the field and verify museum specimens.

MATERIALS AND METHODS

In total, 74 specimens (10 individuals of *C. horsfieldii*, 34 individuals of *C. brachyotis*, 29 individuals of *C.* cf. *brachyotis* Forest, and 1 individual of *Eonycteris major*) were used in this study. These specimens were either collections from field sampling done in various localities within Borneo and Peninsular Malaysia or museum samples from the zoological museum at Universiti Malaysia Sarawak (Sarawak, Malaysia) and the Department of Wildlife and National Parks (PERHILITAN) Museum (Pahang, Malaysia). Due to a limited number of samples of *Cynopterus*, we opted to focus on the problem of differentiating *C. brachyotis* and *C.* cf. *brachyotis* Forest using multivariate statistics. Only specimens of *C. brachyotis* and *C.* cf. *brachyotis* Forest previously confirmed by Abdullah (2003) and Fong (2011) using DNA sequences of the partial Cytochrome *b* (700 bps) and Cytochrome Oxidase 1 (486 bps) were used in this study.

Twenty-eight morphological measurements (skull, dental, and external morphological measurements; Fig. 2) were recorded following Kitchner et al. (1995) and Jayaraj et al. (2004 2005). Abbreviations for the characters measured are as follow: BL, bulla length; C1BW, canine tooth basal width; C1C1B, breadth across both canine outside surfaces; C1M3L, canine molar length or maxillary tooth row length; CW, cranial width; DBC, distance between cochleae; DL, dentary length; D3MCL, 3rd digit metacarpal length; D4MCL, 4th digit metacarpal length; D5MCL, 5th digit metacarpal length; D3P1L, 3rd digit 1st phalanx length; D3P2L, 3rd digit 2nd phalanx length; EL, ear length; GBPL, greatest basial pit length; GSL, great skull length; IOW, interorbital width; M3L, 3rd molar tooth crown length; M3W, 3rd molar tooth crown width; M3M3B, breadth across outside surfaces of both 3rd molar teeth; MW, mastoid width; PES, pes length; PL, palatal length; POW, postorbital width; PPL, postpalatal length; RL, radius length; TL, tibia length; TVL, tail to ventral length; and ZW, zygomatic width. Bat skulls were extracted after morphological data were collected following Nargorsen and Peterson (1980).

A cluster analysis using Euclidean distances with the unweighted pair-groups method average (UPGMA) was performed to construct a morphometrics-based phylogeny and confirm the initial grouping of samples (Everitt 1993). The *E. major* measurements were used as the outgroup for this analysis. Data of confirmed groupings were then subjected to a *t*-test to check for sexual dimorphism. Levene's test for equality of variances was used as a selection criterion for the assumption of equal or unequal variances prior to the *t*-test (Zar 1984). The normality of the data was checked using a normal probability plot and the Shapiro-Wilk test. The assumption of homoscedasticity was tested using Box's M test, and the assumption of multicolinearity was checked by observing the tolerance value for all independent variables (Joseph et al. 1992). Next, the data were subjected to a stepwise discriminant function analysis following Joseph et al. (1992) and Manly (1994). Two separate analyses were performed: 1) using a combination of all available characters and 2) using only external morphological characters. Data were analyzed using Minitab 2002 v13.2 (2006 Minitab, Pine Hall

Rd State College, PA, USA) and SPSS vers. 13 (SPSS, Chicago, IL, USA).

RESULTS

The UPGMA cluster analysis (Fig. 3) shows th groupings of *Cynopterus* spp. based on morphological measurements. Based on the phylogram, there are 3 major clades consisting of *C. horsfieldii*, *C.* cf. *brachyotis* Forest, and *C. brachyotis*. Of the 28 characters examined, 3 characters (IOW for *C. horsfieldii* and D3MCL and D5MCL for *C. brachyotis*) were found to be sexually dimorphic (Table 1). The means and standard deviations (SDs) of all characters are shown in table 2. PES was $\log_{10}$-transformed to achieve normality, whereas PPL, PL, and TL were excluded from the analysis as these data did not follow a normal distribution either prior to or after transformation to achieve normality. Box's M statistics had a value of 23.406 (probability of $p = 0.483$, $p > 0.001$) indicating homoscedasticity. Thus, the data were analyzed using a pooled covariance matrix for classification. Multicolinearity among the independent variables was not present, as tolerance values for all variables were > 0.10.

For analysis of all remaining characters, the stepwise method identified 1 discriminant function (Function 1) that was statistically significant based

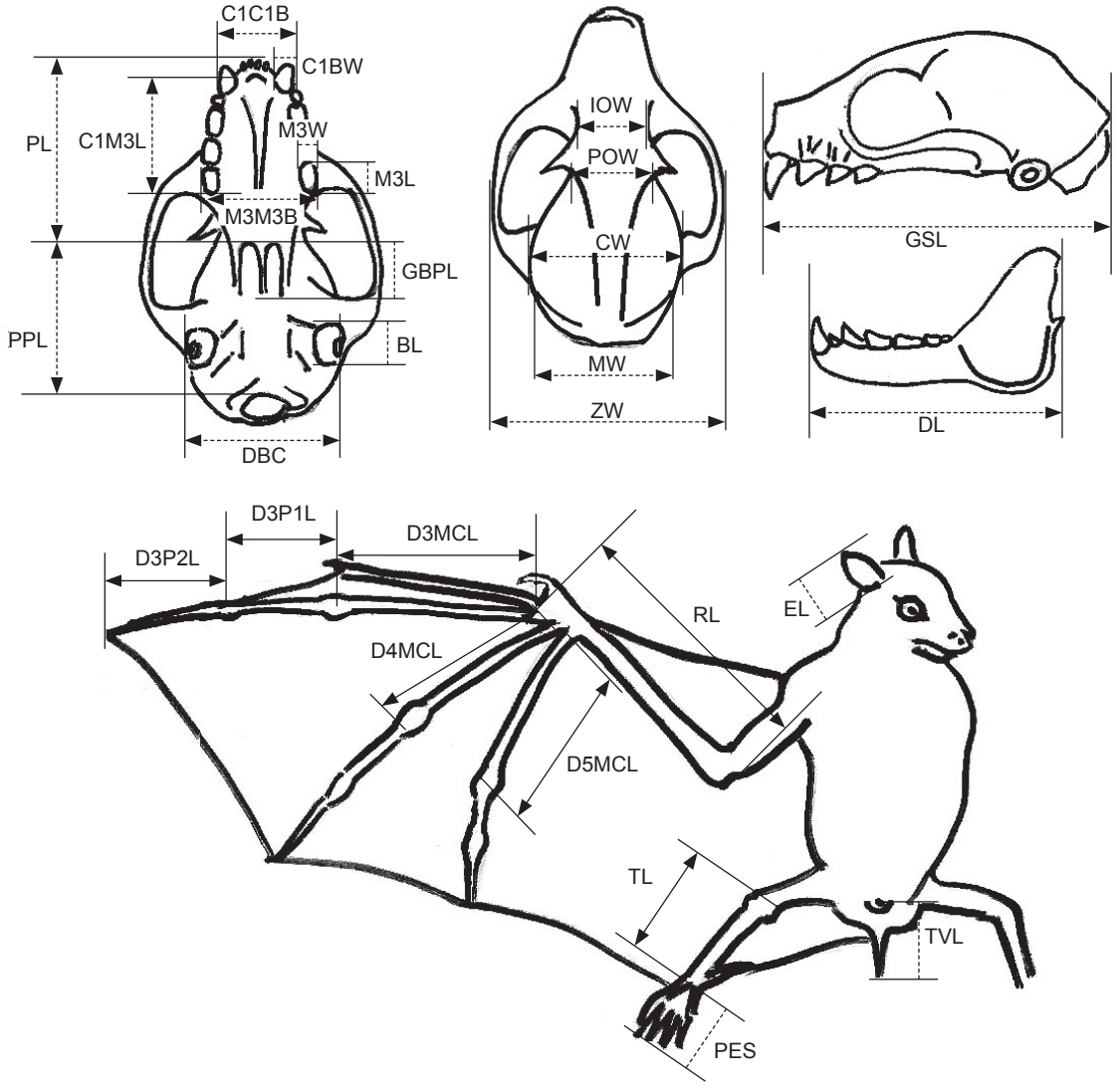

Fig. 2. Skull, dental, and external measurements taken during this study. The abbreviations of body measurements please refer to "MATERIALS AND METHODS" section.

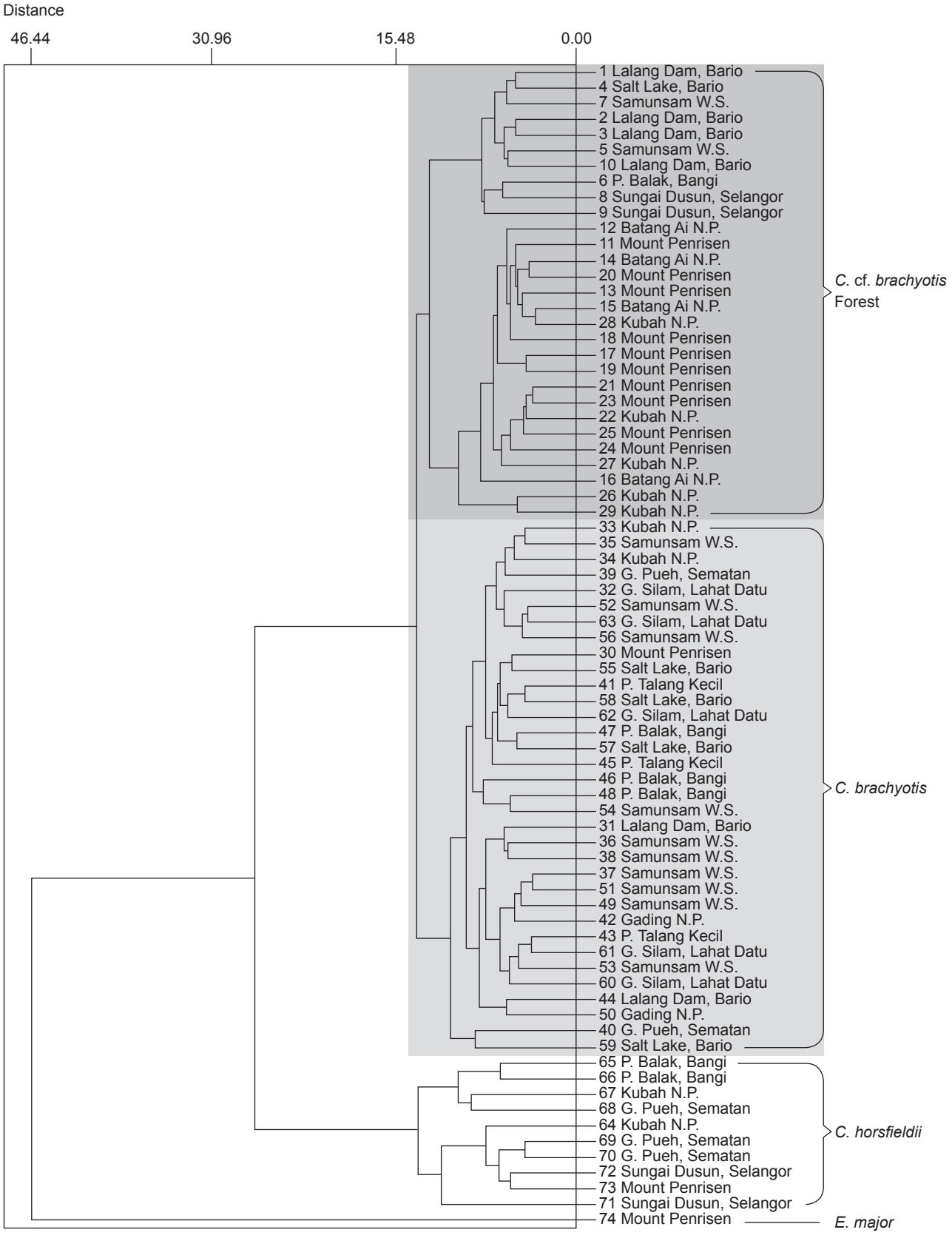

Fig. 3. UPGMA cluster analysis of *Cynopterus* spp.

on Wilks' lambda (Table 3), and 6 characters (GBPL, M3L, M3W, TVL, D3P2L, and RL; Table 4) were generated from the stepwise procedure. The characters with the highest weight on function 1 were RL (0.957) and M3L (0.506), whereas M3L (3.912) and M3W (-3.454) had the highest discriminant loadings. All 6 characters determined by the stepwise procedure produced a discriminant function with an accuracy rate of 100% (see accuracy rates, Table 5).

For analysis of only external morphological characters, the stepwise method identified a discriminant function (Function 1) that was statistically significant (Table 6) with 4 characters (TVL, D3P1L, D3MCL, and RL; Table 7) generated from the stepwise procedure. The character with the highest weight and loading was RL (weight = 1.240; loading = 0.706), while D3MCL (-0.731) had the 2nd-highest weight. All 4 characters determined by the stepwise procedure produced a discriminant function with an accuracy rate of 96.8% (see accuracy rates, Table 8).

A histogram of the discriminant scores of the discriminant function for all characters

Table 1. Sexual dimorphism test using a *t*-test for equality of means (equal/unequal variances; only sexually dimorphic characters are shown)

	C. horsfieldii	*C. brachyotis*	
Character	IOW	D3MCL	D5MCL
t	3.434	1.346	1.113
d.f.	8	32	32
Significance (2-tailed *)	0.009	0.021	0.090
Conclusion	sexually dimorphic	sexually dimorphic	sexually dimorphic

Characters are defined in "MATERIALS AND METHODS".

Table 2. Means and standard deviations (SDs) of all characters used in this analysis

	Cynopterus cf. *brachyotis* Forest		*C. brachyotis*		Overall	
Character	Mean	S.D.	Mean	S.D.	Mean	S.D.
GSL	27.39	0.76	28.45	0.88	27.92	0.97
IOW	5.60	0.32	5.92	0.36	5.76	0.37
POW	6.32	0.60	6.48	0.65	6.40	0.63
CW	12.06	0.39	12.39	0.36	12.23	0.41
MW	12.23	0.40	12.66	0.43	12.45	0.47
ZW	17.93	0.79	18.40	0.80	18.16	0.82
DBC	5.62	1.07	4.72	0.79	5.17	1.04
BL	2.60	0.58	2.18	0.42	2.39	0.55
GBPL	6.95	0.93	5.72	0.90	6.34	1.10
C1BW	1.61	0.24	1.44	0.20	1.52	0.24
C1C1B	5.92	0.29	6.05	0.30	5.99	0.30
M3M3B	8.37	0.36	8.44	0.36	8.40	0.36
C1M3L	8.94	0.39	9.10	0.28	9.02	0.34
M3L	1.83	0.11	1.95	0.14	1.89	0.14
M3W	1.25	0.15	1.18	0.13	1.21	0.14
TVL	11.40	1.95	11.47	2.63	11.43	2.29
EL	14.48	1.34	14.67	1.29	14.58	1.31
D3P1L	26.63	1.37	28.38	1.25	27.51	1.57
D3P2L	33.75	2.32	36.19	2.42	34.97	2.65
D3MCL	41.47	1.76	43.06	1.71	42.27	1.90
D4MCL	38.87	1.40	40.94	1.63	39.91	1.83
D5MCL	39.64	1.43	42.31	1.44	40.98	1.96
RL	58.08	1.40	63.55	2.04	60.82	3.26
LogPES	1.02	0.04	1.04	0.07	1.03	0.06

Characters are defined in "MATERIALS AND METHODS".

(Fig. 4) showed that *C. brachyotis* and *C.* cf. *brachyotis* Forest formed distinct groups, whereas the histogram of the discriminant scores of the discriminant function for only external morphological characters (Fig. 5) showed some misclassifications (2 individuals). The discriminant functions based on the unstandardized canonical coefficient functions (Tables 3, 7) can be used

Table 3. Wilks' lambda test of discriminant function 1 (with all available characters)

Wilks' lambda	Chi-squared	Eigenvalue	Percent of variance
0.157	94.412	5.368	100%
Cumulative percent	**Canonical correlation**	***d.f.***	**Significance ****
100%	9.18	6	0.00

Table 4. Standardized and unstandardized canonical discriminant function coefficients (with all characters)

Character	Function 1	
	Standardized	Unstandardized
GBPL	-0.371	-0.405
M3L	0.506	3.912
M3W	-0.481	-3.454
TVL	-0.346	-0.149
D3P2L	0.350	0.148
RL	0.957	0.546
Constant	-	-37.326

Characters are defined in "MATERIALS AND METHODS".

Table 5. Classification results (pooled covariance matrix) of the stepwise discriminant function analysis (with all available characters)

		Group	Predicted group membership		Total
			1	2	
Original	Count	1	29	0	29
		2	0	34	34
	Percent	1	100%	0%	100%
		2	0%	100%	100%
Cross-validated[a]	Count	1	29	0	29
		2	0	34	34
	Percent	1	100%	0%	100%
		2	0%	100%	100%

Both 100% of the original and cross validated. [a]grouped cases were correctly classified.

Table 6. Wilks' lambda test of discriminant function 1 (with external morphological characters)

Wilks' lambda	Chi-squared	Eigenvalue	Percent of variance
0.195	96.337	4.188	100%
Cumulative percent	**Canonical correlation**	***d.f.***	**Significance ****
100%	0.897	4	0.00

Table 7. Standardized and unstandardized canonical discriminant function coefficients (with external morphological characters)

Character	Function 1	
	Standardized	Unstandardized
TVL	-0.479	-0.216
D3P1L	0.572	0.442
D3MCL	-0.731	-0.433
RL	1.240	0.706
Constant	-	-34.507

Characters are defined in "MATERIALS AND METHODS".

Table 8. Classification results (pooled covariance matrix) of the stepwise discriminant function analysis (with external morphological characters)

		Group	Predicted group membership		Total
			1	2	
Original	Count	1	32	2	34
		2	0	29	29
	Percent	1	94.1%	5.9%	100%
		2	0%	100%	100%
Cross-validated[a]	Count	1	32	2	34
		2	0	29	29
	Percent	1	94.1%	5.9%	100%
		2	0%	100%	100%

Both 96.8% of the original and cross-validated. [a]grouped cases were correctly classified.

as a tool to determine whether a specimen is *C. brachyotis* or *C.* cf. *brachyotis* Forest. The predictive models are as follows:
for all remaining characters

$$\hat{y} = -0.405a + 3.912b - 3.454c - 0.149d + 0.148e + 0.546f - 37.326 \text{ (constant)} \quad (a)$$

and for only external morphological characters

$$\hat{y} = -0.216d + 0.442 - 0.433h - 0.706f - 34.507 \text{ (constant)}; \quad (b)$$

where $\hat{y}$ is the discriminant score (a negative score indicates *C.* cf. *brachyotis* Forest and a positive score indicates *C. brachyotis*), *a* is the GBPL, *b* is the M3L, *c* is the M3W, *d* is the TVL, *e* is the D3P2L, *f* is the RL, *g* is the D3P1L, and *h* is the D3MCL.

DISCUSSION

General discussion of statistical results

Based on the cluster analysis, a clear division (approximately 15.48% distance, based on estimates from the graph) was observed between *C. brachyotis* and *C.* cf. *brachyotis* Forest. Visual observations of samples during field sampling indicated that adult *C. brachyotis* can be vaguely identified due to the brown fur with a pronounced yellowish or reddish tinge, and these bats usually have a forearm of > 60 mm. Adults of *C.* cf. *brachyotis* Forest have a smaller body size with duller coloration and usually have a forearm length of < 60 mm.

Comparison with previous bat surveys (Timoh 2006, Fukuda et al. 2008) and personal observations indicate that *C. brachyotis* was sampled across a wide variety of vegetation types with different capture rates, whereas *C.* cf. *brachyotis* Forest was confined to primary forests. Capture rates of *C. brachyotis* were 44% in secondary forests, 41% in orchards, and 72% in oil palm plantations (Fukuda et al. 2008). The high capture rate in oil palm plantations is probably associated with the abundance of oil palm fruit, i.e., a food source (Fukuda et al. 2008). We also speculated that this abundant food source would also likely increase the life expectancy of *C. brachyotis* in oil palm plantations as many older individuals were captured (with distinct reddish-brown fur on their shoulders and worn out or missing teeth in most individuals) in Timoh's (2006) study.

In this study, the analyses revealed that the RL, M3L, and M3W had the highest discriminant loading and weight, and this was reflected by the importance of these characters during the identification process. The RL or forearm length is one of the characters useful in identifying bats, especially fruit bats of the family Pteropodidae. This character was also previously used to differentiate *C. brachyotis*, *C.* cf. *brachyotis* Forest, and other *Cynopterus* in Malaysia (Abdullah et

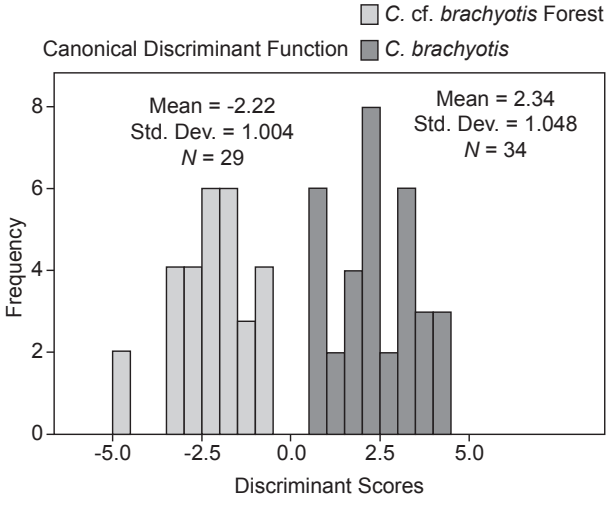

Fig. 4. Histogram of discriminant scores of both *C. brachyotis* and *C.* cf. *brachyotis* Forest for all available characters.

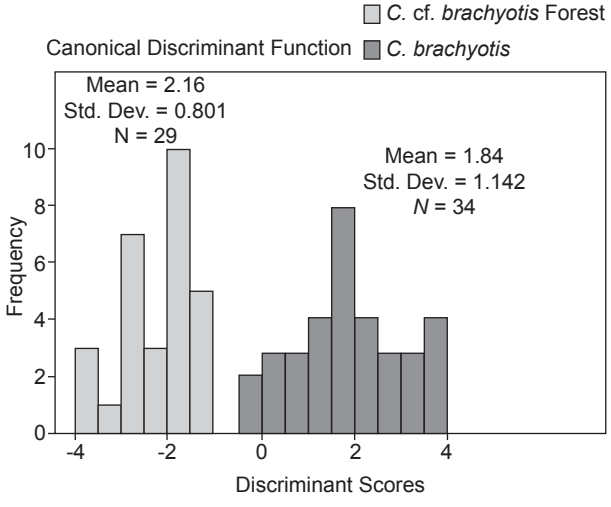

Fig. 5. Histogram of discriminant scores of both *C. brachyotis* and *C.* cf. *brachyotis* Forest for external morphological characters.

al. 2000, Abdullah 2003, Campbell et al. 2004 2006 2007, Jayaraj et al. 2004 2005, Fong 2011). Although M3L and M3W are not generally used for species identification, molar differences in *C. horsfieldii*, *C sphinx*, and *C. brachyotis* are a key character which can be used to differentiate these 3 species of *Cynopterus* in Malaysia. The D3MCL and D3P1L both contribute to the length and size of the wings, and this may reflect the habitats that both species occupy.

The cluster and discriminant function analyses showed that *C. brachyotis* and *C.* cf. *brachyotis* Forest populations are morphologically distinct, congruent with previous results using molecular methods (Abdullah 2003, Campbell et al. 2004 2006, Julaihi 2005, Fong 2011). Although the topology of the dendogram generated by the cluster analysis was not similar to previous molecular studies, it was able to differentiate *C. brachyotis* from *C.* cf. *brachyotis* Forest. The different topologies might be a reflection of the morphological appearances of these bats. Morphologically both *C. brachyotis* and *C.* cf. *brachyotis* Forest look similar, whereas *C. horsfieldii* is very much larger with distinct cusps on the lower premolar and 1st lower molar; these characteristics are not present in *C. brachyotis* or *C.* cf. *brachyotis* Forest.

The prediction models developed will be particularly useful in accurately identifying *C. brachyotis* and *C.* cf. *brachyotis* Forest in Malaysia. Specifically function (a) can be used to verify museum specimens, and function (b) will be more appropriate for field identification. Function (a) requires cranial, dental, and external morphological measurements; thus, unverified museum specimens can be identified once the skull is extracted, reducing the cost of validating the species using molecular tools. Although having a lower accuracy rate, function (b) can be used in the field as only external morphological characters are needed to identify the species. If needed, however, a tissue sample via skin scraping or a wing punch can be taken for species verification in the lab. An accurate identification method will definitely aid ecologists, conservationists, and law enforcement officials in studying and conserving this species complex.

Body sizes and relation to habitat types of *Cynopterus brachyotis* and *C.* cf. *brachyotis* Forest

Body size can be related to the flight performance of bats as the total body mass is negatively correlated with wing loading, a measure of the ability to navigate around obstacles (Aldridge 1986, Aldridge and Rautenbach 1987, Jones et al. 1993, Rhodes 2002) and maneuverability in cluttered areas (Aldridge and Rautenbach 1987, Jones et al. 1993, Kalcounis and Brigham 1995, Brigham et al. 1997, Rhodes 2002). This can be directly linked to the habitats of both species, with *C. brachyotis* occupying less-cluttered habitats and *C.* cf. *brachyotis* Forest occupying dense areas (Abdullah et al. 2000, Abdullah 2003, Jayaraj et al. 2004 2005). Body size seems to be the discriminating factor in the cluster analysis for effectively discriminating these 2 species, which explains why both species can be separated, but body size per se does not depict the entire picture of the divergence of these bats. In terms of the flight apparatus and dimensions, both species apparently did not undergo the change in wing shape indicated in a recent study by Campbell et al. (2007), but rather a change in body size which might have been due to selective pressures for *C. brachyotis* and *C.* cf. *brachyotis* Forest to fit into their respective habitats. Similarly, Menon (2007) revealed that the aspect-ratio and wing-loading indices cannot be used to differentiate these 2 species in Borneo.

Previous studies (Freeman 1981, Schluter 1993, Wain-Wright 1996) noted that there was a relationship between the structure of the feeding apparatus and diet in bats. As M3W and M3L are associated with feeding and foraging, it was speculated that the shape and dimension of the dentition are associated with the diet. Current knowledge of the diet and foraging behavior of *C. brachyotis* in Malaysia was previously documented by Lim (1970), Phua and Corlett (1989), Fujita and Tuttle (1991), Francis (1994), Funakoshi and Zubaid (1997), Tan et al. (1998), Mohd Azlan et al. (2000), and Hodgkison et al. (2003), but none of those authors focused on differences in the diets and foraging behaviors of *C. brachyotis* and *C.* cf. *brachyotis* Forest. Thus a more-detailed study of the diets and foraging behaviors would shed more light on ecological differences between *C. brachyotis* and *C.* cf. *brachyotis* Forest.

Implications of recent studies for the taxonomic status of the *Cynopterus brachyotis* complex

It was proven by various studies that *C. brachyotis* is a species complex with 6 distinct

lineages. Genetically *C. brachyotis* has 6 forms; 4 geographically distinct lineages respectively from India, Myanmar, Sulawesi, and the Philippines, and 2 sympatric forms (recognized as *C.* cf. *brachyotis* Forest and *C. brachyotis* in this study) in southern Thailand, Peninsular Malaysia, and Borneo. These 2 sympatric forms are found in distinct habitats: *C. brachyotis* is found in open areas, and *C.* cf. *brachyotis* Forest is found in the primary and old secondary forests (Abdullah 2003, Campbell et al. 2004 2006, Jayaraj et al. 2004 2005, Julaihi 2005, Fukuda et al. 2008, Fong 2011). *Cynopterus brachyotis* is the ancestral lineage of all *Cynopterus* in Peninsular Malaysia and Borneo with nucleotide divergence ranging 8%-9%, whereas *C.* cf. *brachyotis* Forest is closely related to *C. horsfieldii*, differing by only a genetic divergence of 3.5% (Abdullah 2003).

This scenario is not new to the taxonomy of *Cynopterus* as *C. nusatenggara* described by Kitchner and Maharadatunkamsi (1991 1996) was also found within *Cynopterus* populations during field sampling on islands of Nusa Tenggara, Indonesia. *Cynopterus* bats are currently represented by 7 species (Simmons 2005), but there are a lot of variations in terms of body size and coloration between and within species. These variations were observed in island populations and highland populations, and are due to differences in vegetation and other ecological factors (see Hill and Thonglongya 1972, Lekagul and McNeely 1977, Medway 1978, Payne et al. 1985, Kitchner and Maharadatunkamsi 1991 1996, Ingle and Heaney 1992, Schmitt et al. 1995, Nor 1996, Abdullah et al. 2000, Storz et al. 2001, Abdullah 2003, Campbell et al. 2004 2006 2007, Jayaraj et al. 2004, Menon 2007, Fukuda et al. 2008, Fong 2011).

Menon (2007) collected an unidentified *Cynopterus* specimen from Satang I., Borneo, Malaysia, and this specimen was later identified using DNA techniques. The forearm length of this *Cynopterus* specimen was 69 mm indicating it was *C. sphinx*, but DNA identification indicated that it was *C. brachyotis* (unpubl. data). A molar examination of the specimen did not show a clear distinction between *C. brachyotis* and *C. sphinx.* Such an observation is the norm when individuals from this genus are collected in a wide range of vegetative types, which indicates that there are high intra- and interspecific variations among *Cynopterus* representatives. The lack of such knowledge indicates the necessity for a current large-scale study on inter- and intraspecific forms of *Cynopterus* across their distribution. Although *C. brachyotis* is widely distributed, information on the current status of the 6 lineages of *C. brachyotis* especially is not clear. Confounded by the non-recognition of these new *C. brachyotis* lineages (Forest, India, Myanmar, Sulawesi, and the Philippines) as distinct species (see Abdullah and Jayaraj 2006), the survival of these rare species may be threatened if no clear and proper planning for conservation is put in place.

In terms of biogeography, the existing recognized *Cynopterus* species of *C. brachyotis*, *C. horsfieldii*, *C. luzoniensis*, *C. minutus*, *C. nusatenggara*, *C. sphinx*, and *C. tithaecheilus* are distributed in the Indo-Malayan region and their distributions overlap. Simmons (2005) listed their distributions as follow: *C. brachyotis* is distributed in Sri Lanka, India, Nepal, Burma, Thailand, Cambodia, Vietnam, South China, Malaysia, the Nicobar and Andaman Is., Borneo, Sumatra, Sulawesi, Magnole, Sanana, Sangihe I., and Talaud I. with possible occurrence in the Palawan region of the Philippines; *C. horsfieldii* is limited to Thailand, Cambodia, Peninsular Malaysia, Borneo, Java, Sumatra, the Lesser Sunda Is., and adjacent small islands; *C. luzoniensis* is found in Sulawesi, the Philippines, and adjacent small islands; *C. minutus* is found in Sumatra, Java, Borneo, and Sulawesi; *C. nusatenggara* is found in Lombok, Moyo, Sumbawa, Sangeang, Komodo, Flores, Sumba, Adonara, Lembata, Pantar, Alor, and the Wetar Is.; *C. sphinx* is found in Sri Lanka, Pakistan, Bangladesh, India, South China, Southeast Asia including Burma, Vietnam, Cambodia, Peninsular Malaysia, Sumatra, and possibly in Borneo; and *C. tithaecheilus* is found in Sumatra, Java, Bali, Lombok, Timor, and adjacent small islands.

In Malaysia; however, only 5 species of *Cynopterus* coexist together, i.e., *C. horsfieldii*, *C. sphinx*, *C. brachyotis*, *C. minutus*, and *C.* cf. *brachyotis* Forest. *Cynopterus horsfieldii*, *C. brachyotis*, and *C.* cf. *brachyotis* Forest have a high geographic distributional overlap (Abdullah 2003, Campbell et al. 2004 2006 2007), but *C.* cf. *brachyotis* Forest's distribution extends farther north into Thailand, Vietnam, and probably Cambodia and Laos (Campbell et al. 2004 2006). Ecologically, *C. sphinx* and *C. brachyotis* are common in open habitats, orchards, and agricultural areas, whereas *C. horsfieldii* and *C.* cf. *brachyotis* Forest are found in primary and old secondary forests in Peninsular Malaysia and southern Thailand. *Cynopterus* cf. *brachyotis* Forest is also rare in Peninsular Malaysia, as its

occurrence is dictated by the existence of primary and old secondary forests. *Cynopterus sphinx* is found in both habitat types, but declines in number near forest edges (Campbell et al. 2006). Similar observations were found in Borneo, but with the exclusion of *C. sphinx* as records of this species occurring in Borneo are only from Central Kalimantan (Payne et al. 1985, Abdullah et al. 1997), and to date, there are no recent records of this species in Malaysian Borneo. The occurrence of *C. minutus* in Borneo is still in question, as there is little information on it, but a recent survey by Benda (2010) did record *C. minutus* in Sabah. The forearm length of *C. minutus* captured in his study was 54.3-58.1 (mean, 55.69, SD, 1.644) mm (n = 5), which is slightly smaller but overlaps with forearm length measurements of *C.* cf. *brachyotis* Forest in Abdullah (2003), Campbell et al. (2004 2006 2007), Jayaraj et al. (2004 2005), Jayaraj (2009), and Fong (2011).

As Abdullah and Jayaraj's (2006) preliminary investigation of the nominate specimen of *C. brachyotis* revealed that the type specimen of *C. brachyotis* described by Müller (1838) is the larger form, it is apparent that the remaining *C. brachyotis* lineages (Forest, India, Myanmar, Sulawesi, and the Philippines) require further study to clarify their phylogenetic positioning and taxonomic status. To date, there are more than 10 studies (see Abdullah et al. 2000, Abdullah 2003, Campbell et al. 2004 2006 2007, Jayaraj et al. 2004 2005, Julaihi 2005, Abdullah and Jayaraj 2006, Jayaraj 2009, Fong 2011) that have validated the existence of *C.* cf. *brachyotis* Forest, but there are no published studies on the remaining *C. brachyotis* lineages in the Indo-Malayan region. Thus, a complete phylogenetic tree of all 7 recognized species and recorded divergent forms of *Cynopterus* (including the 6 divergent forms of *C. brachyotis*) should be generated to clarify the taxonomic status of all *Cynopterus* spp. in the Indo-Malayan region. Clarification of *C. luzoniensis* from Sulawesi and Palawan is also needed, as there is the possibility that the Sulawesi and Philippine forms of *C. brachyotis* previously described by Campbell et al. (2004) could possibly be *C. luzoniensis*, or these 2 *C. brachyotis* forms may differ from *C. luzoniensis* altogether. Finally, because *C. minutus* is recognized as a distinct species (Simmons 2005), there is a need to check the status of this species in Borneo as little information is available.

Two models to differentiate *C. brachyotis* and *C.* cf. *brachyotis* Forest were developed using multivariate statistics with a high accuracy rate of of identifying both *C. brachyotis* and *C.* cf. *brachyotis* Forest. Based on the 1st prediction model (function a), 6 chara-cters are needed to accurately differentiate *C. brachyotis* from *C.* cf. *brachyotis* Forest in southern Thailand, Peninsular Malaysia, and Borneo. This model would be more appropriate for use on museum specimens as skull and dental characters are needed for the calculation. The 2nd prediction model (function b) can be used during field sampling, as only external morphological measurements are needed for identification. These prediction models can subsequently be used by bat biologists to correctly identify adult *C. brachyotis* forms in southern Thailand, Peninsular Malaysia, and Borneo, thus aiding in research and conservation efforts of both *C. brachyotis* and *C.* cf. *brachyotis* Forest in this region. Further suggestions on taxonomic research of this species complex should include verification of multiple genetic markers, examination of detailed morphometrics, and a review of the taxonomic status of the 6 existing *C. brachyotis* forms in the Indo-Malayan region. Conservation of this species complex needs to be carefully planned in order to ensure that all 6 divergent forms do not go extinct, as these are suspected of being undescribed species in the Indo-Malayan region.

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