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Preliminary Morphometric Analysis of *Aethalops aequalis* Populations in Sabah and Sarawak, Malaysian Borneo

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ABSTRACT.– *Aethalops aequalis* was previously recorded as a subspecies of *A. alecto* in Borneo. They are difficult to distinguish by external morphology as Malaysian *Aethalops* species are similar in size. The objective of this study was to characterize the morphological differences within the Malaysian *A. aequalis* populations based upon the evaluation of seven selected populations in Borneo. To this end, 11 skull and 11 dental characters were examined and analyzed using SPSS software. Six of these characters were found to be polymorphic across populations, with CM1 being the strongest character in most of the extracted functions followed by IM1, both of which are dental characters that relate to the lower jaw length. Character CM1 was generally shorter in most of the Southwest Sarawak populations compared to the Northeast Sarawak and Sabah populations. *Aethalops aequalis* from Sabah and Sarawak possessed a single skull morphotype and mountain isolation is, or has not yet been a sufficient barrier to lead to morphological divergence. The body and skull sizes were not affected by altitude or elevations, with *A. aequalis* possessing a single morphotype in Malaysian Borneo. In conclusion, little morphological variation was detected within and among the different geographical populations of *A. aequalis* in Sabah and Sarawak. The few differences found are likely to have arisen via natural selection driven adaptation to the new environment.

KEY WORDS: **Morphometric, *Aethalops aequalis*, Malaysian Borneo, skull, dental, single morphotype**

INTRODUCTION

Aethalops aequalis, or the Bornean pigmy fruit bat, is endemic to mountaintops in Borneo and is found at elevations of more than 1000 m above seal level (Kitchener et al., 1990). *Aethalops aequalis* differs morphologically from *A. alecto*, although it was previously classified as a subspecies of *A. alecto* (see Faisal et al., 2008a). However, the two species are difficult to differentiate from each other by observation of the external morphology alone, especially for specimens from Malaysia as both of them are very similar in size. *Aethalops aequalis* is also easily confused with the indigenous sister genus species, *Chironax melanocephalus*. The most obvious visible character to distinguish between C. *melanocephalus* and *A. aequalis* is that *A. aequalis* has a single pair of lower incisors whilst *C. melanocephalus* has two pairs.

Aethalops aequalis are endemic to Borneo Island (Kitchener et al., 1993; Maharadatunkamsi and Zein, 2006) and are widely distributed across the Malaysia Borneo region (Faisal et al., 2008a; Tingga, 2010). The difference in the abundance of *A. aequalis* between mountains ranges is most probably due to the differences in food resources. Indeed, food abundance, or the availability of specific food items, has been suggested to be one of the important factors limiting the species diversity of local fruit

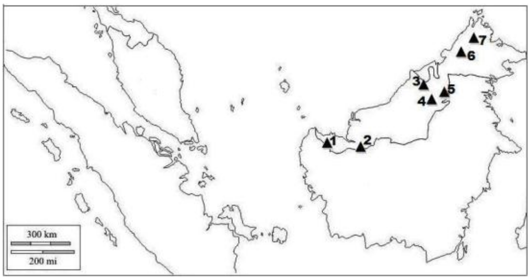

FIGURE 1. Location of the sampling sites representing the seven *A. aequatis* populations surveyed in Malaysian Borneo from three regions as: Southwest Sarawak region (1= Mt. Penrissen, 2 = Mt. Pueh), Northeast Sarawak region (3 = Mt. Mulu, 4 = Mt. Murud and 5 = Bario) and Sabah (6 = Mt. Kinabalu and 7 = Mt. Trus Madi)

bats within old-growth Palaeotropical rainforests (Hodgkison et al., 2004). The implications are important for the conservation of fruit bats species in Malaysia since most fruit bats require relatively large habitat areas in order to locate a continuous supply of sufficient suitable food (Hodgkison et al., 2004). Apart from that, the destruction of suitable habitat, typically for the purposes of human development, in the mountain areas is an increasingly serious problem and concern. Proper mitigation should be taken into account as the endemic mountain organisms are at risk.

The morphological analysis of *A. aequalis* by direct eye observation based solely on its external morphology characteristics is rather inadequate, in as much as it lacks clear distinctive characters. Therefore, skull morphometric analysis is probably the best way to explore differences in morphological characteristics among the Malaysia Bornean species. In addition, there is a lack of detailed morphometric studies of *A. aequalis* within Malaysian Borneo, and thus the existence or level of regional variation is unknown for these populations.

Since *A. aequalis* is widely distributed throughout Borneo, it was hypothesized that there could be more than one form of skull morphotype of *A. aequalis*. Therefore, in this study the skull and dental characteristics of *A. aequalis* were examined using a total of 22 standard characters (11 dental and 11 cranial) to determine if there is any significant difference in the skull morphology of *A. aequalis* among and within populations from Sabah and Sarawak in Malaysian Borneo.

MATERIALS AND METHODS

In this study, seven mountains were selected as sampling areas so as to cover the maximum geographical and topographical separation (to maximize the chance of finding morphological polymorphisms) along with geographically local populations for comparison. The selected sites were Mount (Mt.) Penrissen and Mt. Pueh as representative for Southwest Sarawak region; Mt. Mulu, Mt. Murud and Bario (Northeast Sarawak region) and Mt. Kinabalu and Mt. Trus Madi (Sabah group) (Fig. 1).

Typically, and on average, ten standard mist nets in average were set up across the forest trails and forest edges from approximately 700 m to 2113 m above sea level. The mist nets were checked from about 18:00 hours till midnight and left open until 07:00 hours the following morning. Each particular net was shifted to a new area if it was unsuccessful in capturing bats. Each captured bat was placed in a single cloth bag and brought back to the main base camp for identification and processing. Selected individuals were euthanised using chloro-form and were preserved either as dry or

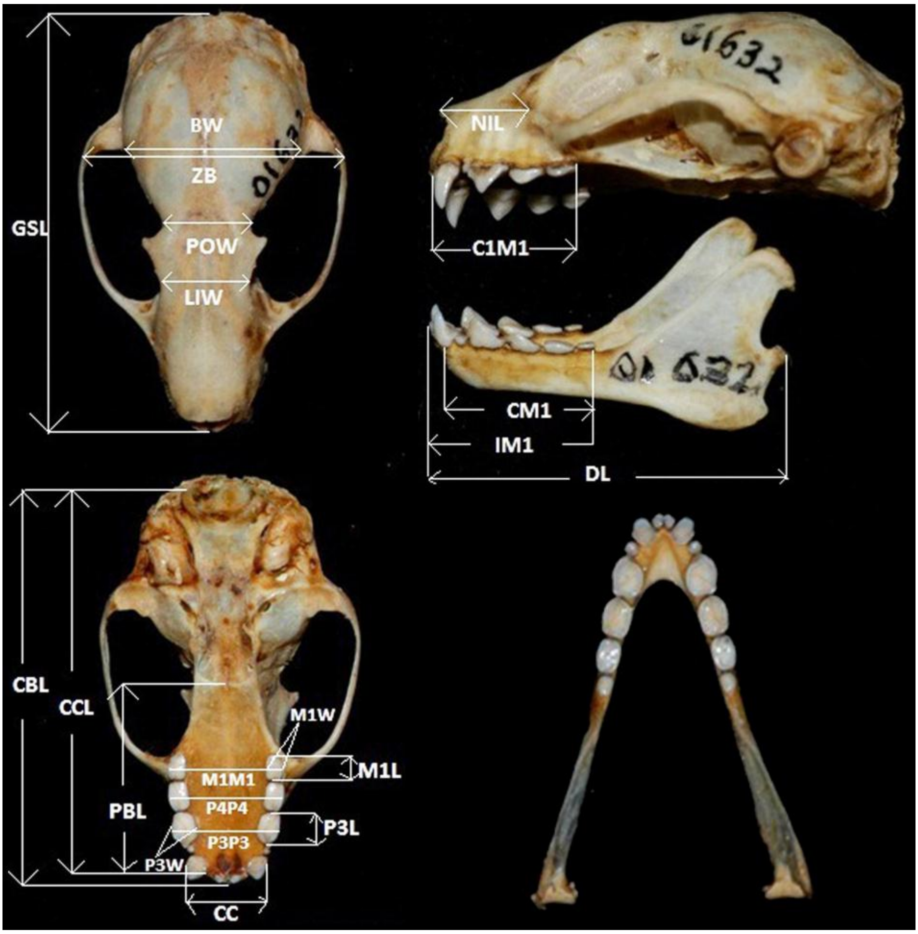

FIGURE 2. Schematic showing the measurement points for the 11 cranial and 11 dental characters of *A. aequalis*.

wet specimens whereas, others were released back to the forest.

Identification of bats was based on the work of Payne et al. (1985) while the works of Allen (1938) and Hill (1966) were used for further details of the external and internal morphology. Important external measurements were measured using a Mitaka digital caliper and bats were weighed using a Pasola spring balance. The external characters measured were the lengths of the forearm (FA), ear (E), tibia (TB), hind foot (HF) and head body (HB). Determination of the developmental status as juvenile/adult was performed by observing the epiphyseal-diaphyseal fusion on the third, fourth and fifth metacarpals (Kunz, 1988). Every individual was determined for its sex. Additional voucher samples were examined from the Universiti Malaysia Sarawak Zoological Museum (Abdullah et al., 2010).

Skulls were extracted from 65 adult individuals and then subjected to morphometric analyses. The 22 skull and dental measurements that were taken from each individual followed that of Kitchener et al. (1993) for both the external and internal characters (Fig. 2). The 11 skull characters measured were the greatest skull length (GSL), braincase width (BW), zygomatic breadth (ZB), postorbital width (POW), least interorbital width (LIW), condylocanine length (CCL), condylobasal length (CBL), orbit to nasal length (NIL), mesopterygoid fossa width (MFW), palatum length (PBL) and the dentary length (DL). The 11 dental characters measured were the distance between upper canine and first upper molar (C1M1), third upper premolar length (P3L), third upper premolar width (P3W), distance between outside third upper premolar (P3P3), distance between outside fourth upper premolar (P4P4), distance between outside first upper molar (M1M1), first upper molar length (M1L), first upper molar width (M1W), distance between outside upper canine (C1C1), distance between lower incisor and second lower molar (IM1) and the distance between lower canine and second lower molar (CM1). These 22 measurements are shown schematically in Figure 2.

Morphometric analyses were implemented using the Statistical Package Social Science, SPSS (version 15.0, SPSS Inc., 2006). Data were tested for sexual dimorphism using univariate analysis with main effects interaction (Sum of square type III) with a confidence interval of 95%. Characters that showed a significant difference between the sexes were excluded from any further analysis of the pooled (gender independent) samples from each population. Each dataset was checked for its conformation the assumptions or a parametric distribution using both Minitab (version 14.0, Minitab Inc., 2004) and SPSS (version 15.0, SPSS Inc. 2006) with the Kolmogorov-Smirnov goodness of fit test parameter at a significance level of $P < 0.05$. Data distribution was standardized using $\log_{10}$ transformation following Krebs (1999).

Discriminant Function Analysis (DFA) with a stepwise method and graphical representation from canonical variate analysis were conducted for multivariate statistical analysis. Groupings in the DFA analysis were performed according to the species' localities and matrices within group correlations were used.

RESULTS

Univariate analyses.– The sample size, mean, minimum and maximum of external measurements of studied species and the skulls' morphological measurements from seven observed localities were recorded (Tables 1 and 2). The number of examined females exceeded that of males and at two localities no males were available in the analyzed samples. Thus the data were pooled for both sexes, and hence the 22 characters were first screened on the separate sexes within each population for any sex-dependent polymorphism (sexual dimorphism), with any characters showing sexual dimorphism being excluded from analysis of gender-pooled samples.

Four of the 22 examined characters were found to be sexually dimorphic, namely GSL ($p = 0.006$), C1M1 ($p = 0.018$), PBL ($p = 0.037$) and DL ($p = 0.034$) (Table 3). With pooled datasets of female and male bats, four characters (CCL, $p = 0.019$; CBL, $p = 0.023$; P3W, $p = 0.001$; and PBL, $p = 0.008$) differed significantly between the seven populations observed. The same four characters plus also GSL showed a significant interaction between sex and locality. This indicates that these five characters (CCL ($p = 0.036$, CBL ($p = 0.020$), P3W ($p = 0.002$), PBL ($p = 0.004$) and GSL ($p = 0.049$)) are either significantly

TABLE 1. Sample numbers and gender at each locality (population) surveyed and their external morphological characters (mean and size range)

Population	Sex	No.	Forearm (mm)	Ear (mm)	Tibia (mm)	Hind foot (mm)	Head-Body (mm)
Mt. Penrissen	Male	7	43.68	10.40	16.48	8.58	64.62
			(40.9-45.7)	(8.95-11.82)	(15.76-18)	(8-9.66)	(61.1-69)
	Female	4	43.15	10.87	14.66	8.97	65.03
			(40.17-44.94)	(9.97-10.36)	(13.51-15.75)	(7.87-10.46)	(61.44-70)
Mt. Pueh	Male	-	-	-	-	-	-
	Female	2	38.11	10.36	15.28	8.75	67
			(32.0-44.22)	(9-11.71)	(15-15.55)	(8.5-9)	
Mt. Mulu	Male	3	43.53	-	15.57	7.72	-
			(42.67-44.22)		(15.27-16.13)	(7.3-8.05)	
	Female	6	42.92	-	15.48	8.43	-
			(41.63-45.4)		(14.76-16.46)	(8.25-8.72)	
Mt. Murud	Male	7	44.05	10.26	15.12	7.27	60.15
			(42.16-45.34)	(8.61-11.59)	(11.43-16.66)	(6.23-8.3)	(55.52-64.78)
	Female	16	43.76	10.72	15.82 (14.95-	9.94	61.49
			(41.48-46.18)	(9.32-12.11)	16.95)	(9.56-10.26)	(58.73-64.44)
Bario	Male	1	44.0	12.0	16.0	-	72
	Female	2	45.85	10.5	16.1	-	67
			(43.7-48)	(10-11)	(15.2-17)		(59-750
Mt. Kinabulu	Male	4	44.37	10.74	13.79	8.45	60.06
			(42.94-45.53)	(9.86-11.52)	(12.39-14.6)	(7.29-10.41)	(56.16-63.65)
	Female	8	44.12	11.24	14.77	8.53	60.68
			(42.18-46.98)	(10.67-11.630	(12.09-16.5)	(7.73-9.77)	(56.89-63.95)
Mt. Trus Madi	Male	-	-	-	-	-	-
	Female	6	43.86	9.74	16.5	7.49	64.24
			(43.16-44.59)	(7.51-10.87)	(16.07-17.09)	(7.01-7.88)	(59.14-68.42)

different between genders in the same locality or between the same gender from different localities.

Normality test and data transformation.– Analysis of each dataset with both software packages (SPSS and MiniTab v14.0) produced concordant results, with the majority of the analyzed characters (14/22, or 12/18 after exclusion of the four sexually dimorphic characters) revealing a non-parametric data distribution, although this decreased to 13/22 and 11/18, respectively, at the $p > 0.05$ level (Table 4). All data were standardized using $\log_{10}$ transformation to avoid any occurrence of bias in response to some non – normality distribution (Krebs, 1999).

Discriminant Function Analysis (DFA).– The accuracy rate of correctly classifying each bat irrespective of its gender with respect to its locality (population) based on the 18 non-sexually dimorphic characters was 85.5%. In applying the stepwise method, six statistically significant discriminant functions were extracted based on the Wilks' Lambda values (Table 5).

The Wilks' Lambda statistic for the test of function 1 through 6 (Wilks' lambda = 0.030) was highly significant ($p = 0.009$), whereas the other five tests of function (function 2 through 6, function 3 through 6, function 4 through 6, function 5 through 6 and function 6) were all insignificant (Table 5). Function 1 accounted for 37.9% of the variation between populations, whilst functions 2, 3, 4, 5 and 6 accounted for

TABLE 2. Mean ± standard deviation, minimum and maximum of morphological values of *A. aequalis* for each locality.

Character		**Mt Pen**	**Mt Kn**	**Mt Mrd**	**Mt TMd**	**Mt Mu**	**Bar**	**Mt Pu**
GSL	**X±SD**	23.72±0.769	23.39±0.663	23.20±0.755	23.56±0.244	23.31±0.555	22.67±0.746	23.32±0.863
	Min	22.23	22.44	21.33	23.17	22.35	21.94	22.71
	Max	24.65	24.44	24.26	23.8	23.95	23.43	23.93
BW	**X±SD**	10.59±0.321	10.80±0.320	10.61±0.295	10.60±0.483	10.61±0.297	10.56±0.354	10.48±0.304
	Min	10.16	10.18	10.07	9.82	10	10.26	10.26
	Max	11.23	11.3	11.36	11.03	10.98	10.95	10.69
ZB	**X±SD**	15.03±0.453	14.72±0.787	14.74±0.782	14.96±0.415	14.38±0.500	14.46±0.765	15.01±0.714
	Min	14.37	13.67	12.78	14.46	13.79	13.75	14.5
	Max	15.94	16.08	16.4	15.27	15.34	15.27	15.51
POW	**X±SD**	5.29±0.400	5.39±0.438	5.31±0.397	5.16±0.307	5.49±0.234	5.73±0.115	5.12±0.078
	Min	4.64	4.85	4.64	4.87	5.22	5.6	5.06
	Max	5.9	6.02	6	5.68	5.91	5.8	5.17
LIW	**X±SD**	5.060.294	4.91±0.192	4.92±0.329	4.97±0.107	4.94±0.271	4.93±0.189	5.01±0.007
	Min	4.8	4.53	4.28	4.84	4.6	4.72	5
	Max	5.84	5.15	5.84	5.13	5.43	5.09	5.01
CCL	**X±SD**	20.20±0.795	20.17±0.825	19.86±0.459	19.60±0.531	20.72±0.496	19.77±0.595	20.09±0.113
	Min	19.23	19.4	19.26	19.26	19.9	19.27	20.01
	Max	21.79	22.26	20.6	20.53	21.46	20.43	20.17
CBL	**X±SD**	20.73±1.152	20.20±1.010	20.21±0.756	19.81±0.286	21.14±0.512	20.13±0.510	21.43±1.053
	Min	19.46	19.26	19.2	19.46	20.22	19.62	20.68
	Max	22.26	22.32	22.26	20.18	21.74	20.64	22.17
NIL	**X±SD**	4.79±0.344	4.57±0.231	4.74±0.197	4.65±0.206	4.91±0.396	4.88±0.156	4.69±0.233
	Min	3.9	4.05	4.28	4.41	4.53	4.77	4.52
	Max	5.11	4.96	5.05	4.87	5.47	4.99	4.85
C1M1	**X±SD**	7.23±0.364	7.01±0.2454	6.93±0.323	6.83±0.352	7.08±0.350	7.18±0.142	6.92±0.510
	Min	6.52	6.66	6.3	6.51	6.5	7.05	6.56
	Max	7.81	7.42	7.57	7.22	7.43	7.33	7.28
P3L	**X±SD**	1.85±0.167	1.76±0.129	1.85±0.123	1.91±0.087	1.94±0.180	1.78±0.225	1.89±0.071
	Min	1.54	1.61	1.62	1.79	1.52	1.55	1.84
	Max	2.04	1.94	2.05	2.02	2.17	2	1.94
P3W	**X±SD**	1.30±0.076	1.29±0.079	1.26±0.076	1.32±0.104	1.38±0.027	1.42±0.012	1.25±0.057
	Min	1.21	1.21	1.21	1.23	1.35	1.41	1.21
	Max	1.41	1.44	1.46	1.47	1.42	1.43	1.29
P3P3	**X±SD**	6.50±0.183	6.48±0.146	6.40±0.254	6.49±0.124	6.43±0.307	6.44±0.115	6.18±0.014
	Min	6.15	6.14	5.82	6.29	5.79	6.31	6.17
	Max	6.76	6.75	6.79	6.61	6.79	6.53	6.19
P4P4	**X±SD**	6.78±0.338	6.58±0.263	6.67±0.315	6.63±0.123	6.85±0.231	6.58±0.025	6.51±0.156
	Min	6.4	6.13	6.13	6.49	6.53	6.55	6.4
	Max	7.23	7.22	7.27	6.79	7.22	6.6	6.62
M1M1	**X±SD**	6.78±0.308	6.75±0.246	6.71±0.304	6.58±0.121	6.80±0.245	6.51±0.065	6.69±0.021
	Min	6.42	6.5	6.16	6.42	6.42	6.44	6.67
	Max	7.28	7.29	7.29	6.76	7.11	6.57	6.7
M1L	**X±SD**	1.06±0.082	1.13±0.112	1.14±0.092	1.10±0.106	1.19±0.125	1.18±0.068	1.13±0.141
	Min	0.89	1	0.92	0.97	1.04	1.1	1.03
	Max	1.19	1.39	1.27	1.23	1.37	1.23	1.23
M1W	**X±SD**	1.03±0.066	1.04±0.042	1.01±0.069	1.04±0.022	1.00±0.056	1.07±0.029	0.94±0.113
	Min	0.93	0.98	0.88	1.01	0.93	1.05	0.86
	Max	1.15	1.11	1.18	1.07	1.09	1.1	1.02

TABLE 2. Continue.

Character		Mt Pen	Mt Kn	Mt Mrd	Mt TMd	Mt Mu	Bar	Mt Pu
CC	**X±SD**	4.71±0.147	4.54±0.215	4.71±0.179	4.63±0.174	4.64±0.202	4.65±0.150	4.62±0.255
	Min	4.47	4.26	4.23	4.41	4.33	4.48	4.44
	Max	4.92	4.83	4.94	4.88	5.09	4.74	4.8
MFW	**X±SD**	3.16±0.190	3.07±0.239	3.18±0.245	3.06±0.144	3.06±0.222	3.01±0.137	3.07±0.106
	Min	2.89	2.75	2.56	2.83	2.62	2.89	2.99
	Max	3.5	3.5	3.6	3.2	3.32	3.16	3.14
PBL	**X±SD**	11.12±0.472	11.04±0.349	10.72±0.426	10.95±0.231	11.03±0.277	10.23±0.302	10.83±0.530
	Min	10.17	10.46	9.62	10.68	10.48	9.91	10.45
	Max	11.66	11.65	11.44	11.25	11.4	10.51	11.2
IM1	**X±SD**	8.37±0.350	8.06±0.326	8.21±0.323	7.99±0.382	8.20±0.178	8.37±0.232	8.13±0.806
	Min	7.68	7.63	7.6	7.59	7.99	8.12	7.56
	Max	8.8	8.71	8.92	8.41	8.47	8.58	8.7
CM1	**X±SD**	8.02±0.371	7.72±0.298	7.81±0.298	7.67±0.363	7.92±0.220	7.99±0.083	8.06±0.205
	Min	7.18	7.32	7.19	7.23	7.51	7.9	7.91
	Max	8.48	8.15	8.44	8.03	8.18	8.06	8.2
DL	**X±SD**	17.40±0.671	16.96±0.678	16.88±0.739	16.48±0.942	17.19±0.478	16.93±1.321	17.33±1.011
	Min	16.04	15.95	15.12	15.25	16.57	15.64	16.61
	Max	18.19	17.74	18.08	17.82	17.9	18.28	18.04

Kn-Kinabalu, TMd-Trus Madi, Mrd-Murud, Mu-Mulu, Bar-Bario, Pen-Penrissen, Pu-Pueh

27.9%, 13.7%, 11.2%, 5.7% and 3.6%, respectively. All extracted functions explained 100% variance for all 18 characters (Table 6).

Character CM1 was heavily loaded in Function 1 with a canonical discriminant function unstandardized coefficient value of 1.615, with that for function 3, 4 and 6 being 0.885, 1.162 and -0.674, respectively. For function 2 and 5, IM1 was the heaviest character loading, with corresponding values of -1.349 and 0.905, respectively (Table 7).

In Figure 3, functions 1 and 2 clustered the Mt. Mulu population with 100% correctly classified individuals, and Mt. Kinabalu with 90.9% being correctly grouped. Another clustering consisted of Mt. Trus Madi (40%), Mt. Penrissen (9.1%), Mt. Murud (88.9%) and Mt. Kinabalu (one individual with 9.1%). Due to insufficient samples from the Bario and Mt. Pueh populations, inconclusive results were obtained. Thus, although the Bario population formed its own group (100% correctly grouped), this was derived from just two individuals. The Mt. Pueh population with also only two samples, on the other hand was unresolved with one sample closer to the population from Mt Murud and the other individual clustered on its own.

DISCUSSION

All seven populations of *A. aequalis* assayed from Malaysia Borneo were strongly discriminated from each other by the CM1 and IM1 characters, both of which are dental characters that are related to the lower jaw length. Character CM1, which is a strong character in identifying *A. aequalis*, was observed to show distinct differences between the groupings of Mt. Pueh – Mt. Penrissen against group Mt. Murud – Mt. Mulu – Bario –Mt. Trus Madi – Mt. Kinabalu. A longer CM1 indicates the likely consumption of soft food resources which need less powerful jaws to chew, and this was commonly observed in the Mt. Pueh

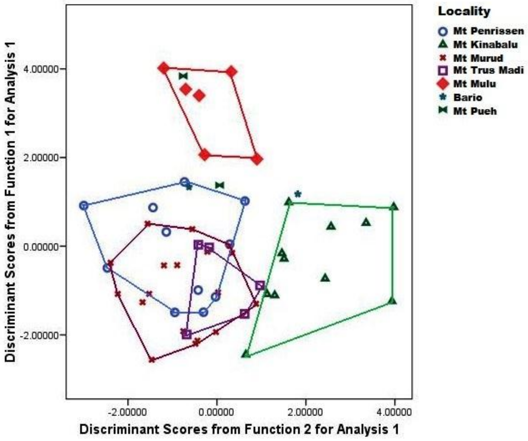

FIGURE 3. Plot of function 1 against function 2, for gender-pooled *A. aequalis* from the indicated seven localities (see Figure 1), without replacing the missing value and with mean based on the 18 non-sexually dimorphic skull characters.

TABLE 3. F values from multiple regression of characters of *A. aequalis* on sex, locality and the interaction of sex and locality.

Character	Sex	Locality	Sex. locality
GSL#	8.071**	1.265	2.188*
BW	0.706	0.684	0.689
ZB	2.527	0.982	1.190
POW	0.609	1.205	1.073
LIW	2.662	0.408	0.612
CCL	0.215	2.780*	2.343*
CBL	2.900	2.681*	2.635*
NIL	1.256	1.532	1.469
C1M1#	5.848*	1.576	1.745
P3L	0.183	1.715	1.532
P3W	0.071	4.518**	3.813**
P3P3	0.691	0.851	0751
P4P4	0.273	1.274	1.073
M1M1	1.288	0.771	0.732
M1L	0.896	1.615	1.414
M1W	0.467	1.444	1.255
CC	0.000	1.364	1.163
MFW	1.065	0.733	0.717
PBL#	4.565*	3.269**	3.418**
IM1	2.862	1.304	1.257
CM1	2.374	1.688	1.578
DL#	4.704*	1.226	1.402

(*), (**) and (***) indicate statistical significance at P < 0.05, P < 0.01 and P < 0.001, respectively. # These four characters were sexually dimorphic and were excluded from the analysis of gender pooled samples.

and Mt. Penrissen populations. These two populations also had a wide range of CM1 lengths. Therefore, these populations were suggested to be very selective in likely their food intake as at lower elevations, there was a higher availability of food resources compared to on the mountaintops. Unlike the Southwest Sarawak group, the Sabah and Northeast Sarawak groups seem to possess a shorter lower jaw in order to consume harder food resources. According to Dumont (2003), based on *Syconycteris autralis*, bats that consume hard fruits will possess characteristics such as a low condyle, relatively tall skull and wide palate. Pteropodid bats extract juice by using their low cusped teeth surrounding a depressed central basin (Walker, 1968). Fruit eaters that consume hard fruits have even blunter teeth than those that mainly consume soft fruits (Anthony and Kay, 1993; Kay and Covert, 1984; Meldrum and Kay, 1997).

With respect to the cranial and dental analysis, the size of the teeth was the main set of characters that could diagnose *A. aequalis*. This is in agreement with Kitchener et al. (1993) who reported that both *A. alecto* and *A. aequalis* were distinctively identifiable based on their cranial and dental measurements, with the strong characters for diagnosis being M1M1 and C1M1. The shape of the skull of *A. aequalis* in most of the observed populations in this study is likely to be to be strongly correlated with the food intake. Previous studies on bats have documented the associations between the bat's cranial morphology and its diet in terms of insects, fruits, nectars and small vertebrates (Dumont, 1997). Fruit feeders are found to have less specific cranial and mandibular morphologies compared to nectar and exudate feeders (Dumont, 1997). The correlation between body size, bite force,

TABLE 4. Normality test for each character.

Character	Kolmogorov-Smirnov		
	Statistic	df	Sig.
GSL	0.125	65	0.013
BW	0.067	65	0.200(*)
ZB	0.096	64	0.200(*)
POW	0.125	65	0.013
LIW	0.123	65	0.016
CCL	0.130	65	0.009
CBL	0.165	65	0.000
NIL	0.088	59	0.200(*)
C1M1	0.128	65	0.010
P3L	0.133	65	0.006
P3W	0.236	65	0.000
P3P3	0.113	65	0.039
P4P4	0.160	65	0.000
M1M1	0.196	65	0.000
M1L	0.061	64	0.200(*)
M1W	0.093	65	0.200(*)
CC	0.114	65	0.034
MFW	0.064	64	0.200(*)
PBL	0.107	64	0.067(**)
IM1	0.079	64	0.200(*)
CM1	0.125	65	0.013
DL	0.074	65	0.200(*)

(*) and (**) indicate not significant at $p > 0.10$ and $0.10 > p > 0.05$, respectively.

TABLE 5. Wilks' Lambda values.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 6	0.030	145.536	108	0.009
2 through 6	0.091	99.318	85	0.137
3 through 6	0.229	61.214	64	0.576
4 through 6	0.399	38.175	45	0.754
5 through 6	0.640	18.501	28	0.913
6	0.837	7.363	13	0.883

TABLE 6. Eigen values.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2.046(a)	37.9	37.9	0.820
2	1.505(a)	27.9	65.7	0.775
3	0.742(a)	13.7	79.5	0.653
4	0.607(a)	11.2	90.7	0.614
5	0.308(a)	5.7	96.4	0.485
6	0.194(a)	3.6	100.0	0.403

[a] First 6 canonical discriminant functions were used in the analysis.

gape width and the physical properties of the dietary fruits was found to be important (Dumont and O' Neal, 2004). Recent findings have shown that the variation in the bat's bite force is influenced more by their body size rather than by specific cranial traits (Aguirre et al., 2002). It was suggested that a high bite force capacity evolved along with a large body size by adaptation of functionally relevant traits associated with jaw musculature instead of cranial shape (Herrel et al., 2008). The overall cranial size, muscle mass and the fiber length of the muscle temporalis were found to be the best predictors for bite force (Herrel et al., 2008).

In a recent study at Mt. Tchabal Mbabo and Tchabal Gandala in Africa, no morphological variation was observed in the local bat species, *Andropadus virens* (Smith et al., 2005), suggesting that mountain isolation alone was insufficient to promote morphological differences. In Malaysia, the different food diversity in the mountains was suggested as a possible factor to drive different *A. aequalis* populations in Mt. Mulu to develop slightly different skull morphologies, rather than that of physical isolation by distance/ mountain topography. Thus new immigrants (colonizers) to Mt. Mulu probably encountered different food sources and or interspecific competition among existent fruit bats forcing them to change to a new diet and so selection for preexisting (rare) changes or new mutations rapidly spread into the population. Thus, at a population level the skull shape and size have evolved from the selective advantage of such adaptations to the new environment of the individuals. Thus, rather than geographical isolation as the main driving force for morphological divergence in the population, it will be differential natural

TABLE 7. Standardised and unstandardised (in brackets) Canonical Discriminant Function Coefficients.

Measurement	**Function**			
	1	**2**	**3**	**4**
BW	0.080 (6.062)	0.793 (59.754)	0.666 (50.177)	-0.019 (-1.403)
ZB	0.036 (1.755)	0.278 (13.481)	-0.806 (-39.112)	-0.148 (-7.178)
POW	-0.094 (-3.109)	0.474 (15.708)	0.568 (18.830)	0.272 (9.011)
LIW	-0.071 (-2.904)	-0.478 (-19.605)	-0.314 (-12.868)	-0.288 (-11.796)
CCL	0.398 (28.789)	-0.157 (-11.366)	-0.170 (-12.313)	-0.018 (-1.333)
CBL	0.412 (22.003)	0.387 (20.660)	0.056 (2.964)	-0.444 (-23.708)
NIL	0.313 (12.375)	-0.101 (-3.996)	0.264 (10.427)	0.302 (11.941)
P3L	0.023 (0.717)	-0.605 (-19.201)	-0.102 (-3.234)	0.485 (15.395)
P3W	0.552 (21.397)	0.102 (3.970)	-0.353 (-13.687)	0.471 (18.281)
P3P3	-0.135 (-10.271)	0.726 (55.210)	-0.272 (-20.697)	0.825 (62.725)
P4P4	0.386 (21.827)	-0.632 (-35.697)	-0.089 (-5.034)	-0.519 (-29.313)
M1M1	-0.175 (-10.095)	-0.147 (-8.483)	0.369 (21.330)	-0.613 (-35.400)
M1L	0.559 (13.988)	0.541 (13.520)	0.777 (19.425)	0.057 (1.416)
M1W	-0.720 (-27.662)	0.303 (11.638)	-0.494 (-18.974)	-0.156 (-5.976)
CC	-0.327 (-18.522)	-0.394 (-22.285)	0.757 (42.832)	0.588 (33.239)
MFW	-0.628 (-19.920)	-0.437 (-13.876)	-0.075 (-2.393)	-0.339 (-10.762)
IM1	-1.222 (-67.236)	-1.349 (-74.242)	0.651 (35.809)	0.958 (52.702)
CM1	1.615 (90.498)	0.986 (55.253)	-0.885 (-49.598)	-1.162 (-65.123)
Constant	(-80.447)	(-48.645)	(-16.247)	(25.993)

selection caused by the ecological differences in the habitat (Smith et al., 2005).

Aethalops aequalis was not morphologically separated at the population level, but at a geographic level the Northern Borneo group possessed a shorter lower jaw and a narrower ZBL compared to those from Southwest Sarawak. These differences may due to adaptation to the different principally available food resources, resulting from species competition and plant distribution within the new habitat, akin to size and shapes of the bills of the Galapagos Island finches that are optimally effective for their respective diets (Abzhanov, 2010). Thus, the size and shape of the bat skull may have evolved as an adaptation to meet the demands of holding and masticating different food sources depending on the habitat and local competition from other species. This could explain why bats in the population from Mt. Mulu differ from those in the other populations. In general, the isolation of a species by geographical distance or other topographical barriers to panmixis that then limit the gene flow allow fixed differences between populations. However, in contrast, a high gene flow (N*m*: 1.84 – 22.94) was detected in the Mt. Mulu populations of *A. aequalis* (Tingga, 2010) and so it appears that the ecological differentiation was not strong enough to counteract the homogenizing effects of gene flow (Abzhanov, 2010). Overall, *A. aequalis* could be considered as a single morphotype and that it is possible that mountain isolation as an effective barrier to gene flow either does not exist or has not been in place long enough to lead to morphological divergence between populations arising from *de novo* mutations.

It has been suggested that terrestrial mammals, such as tree shrews and squirrels, in the Indomalayan region have acquired morphological differences following the traditional Bergmann’s rule, island – isolation effect and various geographical barriers (Endo et al., 2007). For bats, the skull shape and size have also been

TABLE 7. continue.

5	6
0.052 (3.928)	0.293 (22.060)
-0.161 (-7.825)	0.390 (18.921)
-0.198 (-6.533)	-0.501 (-16.588)
0.123 (5.026)	0.244 (10.028)
0.569 (41.122)	0.354 (25.601)
-0.231 (-12.342)	-0.174 (-9.261)
-0.046 (-1.838)	0.229 (9.037)
-0.408 (-12.953)	0.298 (9.472)
-0.020 (-0.777)	-0.400 (-15.501)
0.172 (13.057)	0.154 (11.690)
0.465 (26.253)	0.296 (16.701)
0.193 (11.142)	0.004 (0.229)
-0.289 (-7.237)	0.197 (4.920)
0.232 (8.904)	-0.122 (-4.672)
-0.395 (-22.346)	0.078 (4.410)
0.220 (6.985)	-0.147 (-4.667)
0.905 (49.790)	-0.337 (-18.534)
-0.494 (-27.677)	-0.674 (-37.746)
(-76.655)	(-41.257)

suggested to be dependent on zoogeographical factors, although the genetic separation may not be obvious since bats are able to freely fly across many such geographical obstacles (Endo et al., 2007). In this study on the populations of *A. aequalis* in Borneo, higher altitude or elevations had no significant effect on the size of the bats or their skull size, and so fails to support (but does not refute) the Bergmann's theory.

Other morphological studies on bats, such as *Penthetor lucasi* (Mohd-Ridwan, 2010), *Rhinolophus affinis* (Maharadatunkamsi et al., 2000), *A. alecto* (Kitchener et al., 1993), *Myotis muricola* (Wiantoro, 2010) and *Eonycteris spelaea* (Maharadatunkamsi et al., 2003), were able to group the bats together according to their respective geographical populations. In addition, a recent study on *P. lucasi* was also able to distinguish bats from different populations using their morphological characters (Mohd-Ridwan, 2010). The insectivorous bat *Kerivoula papillosa* could be identified into two morphological forms, *K. papillosa* type L (large form) and *K. papillosa* type S (small form), and this division is supported by genetic findings (Faisal, 2008b; Hasan, 2009; Faisal et al., 2010). Over a wider geographical aspect, with respect to the morphological variations of insectivorous bats, *M. muricola* clustered into three major groups but these failed to conform to the Wallace's Line as a major barrier (Wiantoro, 2010).

Overall, the two most distinctive characters of *A. aequalis* were both related to their teeth (CM1 and IM1), with CM1 as the main character since most populations were correctly grouped when based on that character. This would suggest that this species of bat requires larger muscles and a wider jaw as to be able to bite with stronger force, which is necessary when consuming harder foods (Dumont, 2007), given that skulls of bats are optimized in order to meet the stress and demands of holding and masticating food (Dumont et al., 2005).

In conclusion, very little morphological variation was detected within and among the populations of *A. aequalis* in Sabah and Sarawak. The small morphological differences noted are probably the result of natural selection upon the bats to survive and adapt to the new environment as an ecologically different area. As a whole, a single morphotype of *A. aequalis* is found in the populations in Malaysia Borneo. Future studies on the association of their mandibles with their bite strength, muscle mass and the type of food resources available and utilized could be conducted on *Aethalops*.

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