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Morphological variation among eastern Indonesian island populations of *Hipposideros bicolor* (Chiroptera: Hipposideridae), with descriptions of three new subspecies

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Abstract – *Hipposideros bicolor* (Temminck, 1834) is recorded for the first time in the Indonesian Lesser Sunda islands of Sumbawa, Selaru, Sumba, Savu, Roti and Timor. Morphological comparisons of cranial, dentary, dental and external body characters and univariate and multivariate statistical analyses of measurements of these characters were carried out on 76 adult specimens from six islands in the Lesser Sundas and, for comparison, with specimens from Java and Peninsula Malaysia.

This study reveals that *H. bicolor* differentiates morphologically into three subspecies, which are described herein. These subspecies, and an indeterminate subspecies from Sumbawa island, are closer phenetically to *H. b. bicolor* from Java than to *H. b. atrox* from Peninsula Malaysia.

INTRODUCTION

Hill (1963) characterised the *Hipposideros bicolor* group by the following features: small to moderate body size; large broadly rounded ears, normally with an internal fold or thickening of the membrane of the ear at the antitragal lobe; elongate and narrow skull; unspecialised auditory region; upper incisors weak with outer lobe obsolescent or obsolete. The taxonomy of *H. bicolor* and closely related forms has been confused since the work of Andersen (1918). Hill in Corbett and Hill (1992) considered the *bicolor* group in the Indo-Malay region comprised 22 species.

Hill (1963), in his classical review of *Hipposideros*, recognised the following forms of *H. bicolor*:

H. bicolor bicolor (Temminck, 1834)	North West Java, Banka island
H. b. javanicus Sody, 1937	Central Java
H. b. pomona Andersen, 1918	Southern India
H. b. gentilis Andersen, 1918	North India, Sikkim, Burma
H. b. sinensis Andersen, 1918	South China, Hainan, Thailand, Indochina
H. b. atrox Andersen, 1918	Malay Peninsula, Terutau island, Tioman island, Sumatra
H. b. major Andersen, 1918	Enggano island
H. b. erigens Lawrence, 1939	Mindoro island Philippines
H. b. macrobullatus Tate, 1941	South Sulawesi

Hipposideros javanicus was first placed in synonymy with *H. b. bicolor* by Tate (1941) and this was later supported by Hill (1983) following his examination of an additional Javanese specimen of this subspecies. Hill *et al.* (1986) stated that "the forms *pomona, gentilis* and *sinensis* were probably conspecific". Hill in Corbet and Hill (1992) confirmed this and placed *gentilis* and *sinensis* as subspecies of *H. pomona*. Hill *et al.* (1986) agreed with Strien (1986) and Bergmans and van Bree (1986) that *H. macrobullatus* was a species. Hill in Corbet and Hill (1992) stated that *H. b. major* may be synonymous with *H. b. atrox*; he considered that in Indonesia the forms of *H. bicolor* were *H. b. atrox* (Nias and Enggano islands, Sumatra) and *H. b. bicolor* (Bangka island, Java, Flores island and possibly Timor island and Kangean island (Hill and Rozendaal 1989)). With regard to their presence on Timor island Goodwin (1979) examined three specimens from Tutuala, on the northeastern tip of East Timor, which he was unable to assign to subspecies.

Kitchener and Maharadatunkamsi (1995) described a unique form of *Hipposideros* of the *H. bicolor* group from Sumbawa island, based on a single skull and two carcasses. They could not confidently ascribe it to a species on the material available but it was closest to *H. bicolor* in overall

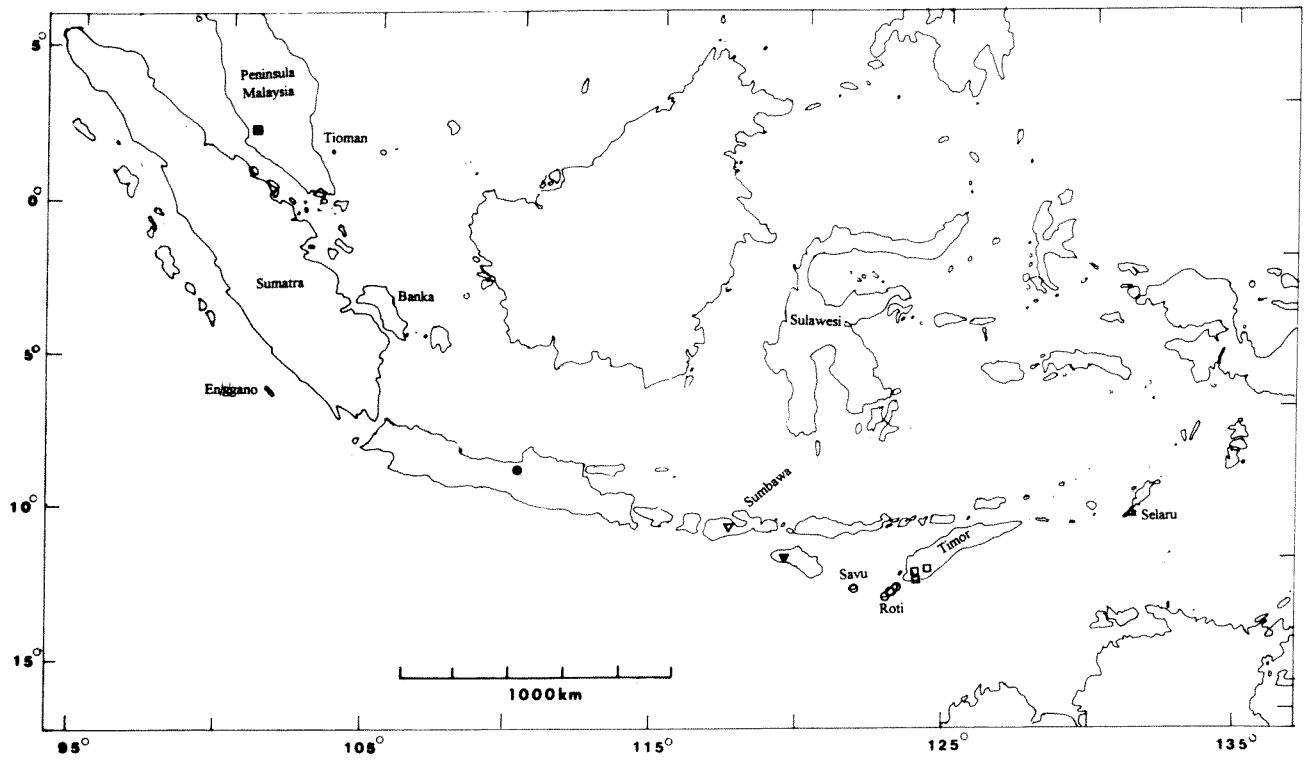

Figure 1 Locality of *Hipposideros bicolor* specimens used in this study, ■, *H. b. atrox*; ●, *H. b. bicolor*; Δ, *H. b. tanimbarensis* subsp. nov.; □, *H. b. hilli* subsp. nov.; O, *H. b. selatan* subsp. nov.; ∇, *H. b.* subsp. indet. and ▼, Sumba specimen.

dimensions. *H. bicolor* is also reported from nearby Flores island by Hill and Rozendaal (1989).

More recently, collections of *H. bicolor* have been made from the following islands in the Lesser Sunda group: Selaru (Tanimbar Is), Timor, Roti, Savu, Sumba - see Figure 1 map. These specimens exhibit some morphological differences from the described forms of *H. bicolor*. This paper reports on an examination of this morphological variation, particularly that of taxonomic significance.

MATERIALS AND METHODS

76 adult specimens from six islands in the Lesser Sunda group and from Java and Peninsula Malaysia were measured.

Adult condition was judged by an absence of swelling of the epiphyseal joints of the wing metacarpals and phalanges.

The description of the colour of the pelage and patagia, where they follow Smithe (1975), are capitalised.

Measurements were as follows: GSL, greatest skull length; CB, braincase breadth; ZW, zygomatic width; MW, mastoid width; RL, rostrum length; LIB, least interorbital breadth; TBL, tympanic bulla length; ILD, interlachrymal distance; CL, cochlea length; CW, intercochlear distance; C^1B, upper canine breadth at base; P^3B, second upper premolar cusp breadth; M^3B, last upper molar cusp breadth; M^1M^3L, upper molar row cusp length; C^1M^3L, upper canine to last upper molar cusp length; M^3M^3W, width across M^3 to M^3 from outer alveoli edge; I_1M_3L, lower tooth row length; DL, dentary length; SVL, snout to vent length; TVL, tail to vent length; EL, ear length; TIL, tibia length; FA, forearm length; D2-5 MC, digits 2 to 5 metacarpal length; D3-5 P1, digits 3 to 5 phalanx 1 lengths; D3-5 P2, digits 3 to 5 phalanx 2 lengths; ANB, anterior noseleaf maximum breadth; PNB, posterior noseleaf maximum breadth.

Sexual dimorphism of all cranial, dentary, dental and body characters that were measured was investigated by standard multiple regression analyses (where all effects were assessed simultaneously of each character on sex and island). Graphical inspection of raw data using plots from regression analyses gave no indication of heteroscedasticity.

Stepwise Canonical Variate (Discriminant Function) analyses were run for all cranial, dentary, dental and external body characters measured for both sexes combined.

RESULTS

Multiple regressions

Localities included in these analyses were from Peninsula Malaysia, Java, Selaru, Timor, Roti, Savu and Sumba islands.

The analyses showed that there were no significant interactions between locality and sex for

Table 1 Multiple regressions on sex and localities (Peninsula Malaysia, Java, Sumbawa, Selaru, Timor, Roti, Savu and Sumba islands) of *Hipposideros bicolor* for (a) cranial, dentary and dental characters and (b) external body characters. F values are presented for the main effects only; there were no significant ($P<0.05$) interactions. For explanation of character codes see Materials and Methods section. Significance levels are *, $P<0.05$; ** $P<0.01$; and *** $P<0.001$.

Table 1a

Character	Sex	Locality
GSL	5.668*	9.054***
MW	2.069	2.067
RL	4.901*	3.936**
CW	0.005	3.839**
LIB	2.802	10.957***
CB	0.176	4.709**
TBL	0.063	0.941
ILD	0.232	16.740***
CL	1.139	0.384
M^3M^3W	5.792*	9.936***
C^1B	2.116	10.239***
P^3B	0.065	4.266**
M^1M^3L	0.008	0.044
M^3B	4.073	3.580**
C^1M^3L	0.279	6.521***
DL	0.655	10.843***
I_1M_3L	1.673	6.254***
d.f.	1,41	6,41

Table 1(b)

Character	Sex	Locality
SVL	0.492	2.039
TVL	6.897*	3.571**
EL	0.123	4.110**
TIL	5.877*	1.441
FA	2.805	3.826**
D2MC	0.269	4.050**
D3MC	2.859	5.351***
D3P1	2.116	11.586***
D3P2	0.556	1.034
D4MC	2.513	5.141***
D4P1	5.675*	7.026***
D4P2	0.018	0.977
D5MC	0.751	4.521**
D5P1	5.718*	5.093***
D5P2	3.116	2.207
ANB	1.826	1.592
PNB	2.231	3.715**
d.f.	1,55	6,55

either cranial, dentary, dental or external body characters. However, the following characters were significantly sexually dimorphic at $0.05> P> 0.01$: greatest skull length; rostrum length; outside M^3-M^3 width; tail to vent length; tibia length and both digit 4 and digit 5 phalanx 1 length. However, considering the number of interactions being tested, these were only weakly significant interactions (Table 1a, b).

Most cranial, dentary, dental and external body characters differed significantly at ($P< 0.01$) with locality except: mastoid width; tympanic bulla length; cochlea length; upper molar row length; snout to vent length; tibia length; digits 3, 4 and 5 phalanx 2 length and anterior noseleaf breadth (Table 1a, b). This indicated the existence of considerable morphological variation among the populations. This variation is also apparent in the descriptive statistics presented in Table 2 for groupings of these island populations.

Discriminant Function Analysis (DFA)

Analyses of cranial, dentary and dental characters were run separately from those of external body characters. Both sexes were combined in these analyses. Characters excluded from the analyses were: zygomatic width (frequently damaged and some missing cases); greatest skull length; rostrum length; outside M^3-M^3 width; tail to vent length; tibia length; digit 4 phalanx 1 length and digit 5 phalanx 1 length (sexually dimorphic).

Initially, DFA were run for all characters, but because many of the groupings of populations had fewer individuals than there were characters measured, DFA in all cases were also run with a subset of five characters. These five characters were selected to provide values that minimised Wilk's lambda (How *et al.* 1996). In all cases the reduced set of five characters provided groupings of individuals in discriminant function space that were similar to those based on the complete set of characters. For this reason, only the DFA based on five characters are detailed below.

Cranial, dentary and dental characters

The DFA based on five characters (lachrymal breadth, least interorbital breadth, dentary length, P^3 breadth and I_1M_3 length) and using as groups each island and the Peninsula Malaysia population, extracted three significant functions which indicated the presence of four putative groups as follows: Selaru; Timor; Roti/Savu; Peninsula Malaysia - with the few Java and Sumba specimens not clearly allocated (Figure 2a, b). The relatively high proportion (89.7%) of individuals that were classified to their correct locality indicated that these groups were robust.

The DFA based on the above four groups, with

Table 2 Measurements, in mm, for (a) cranial, dentary and dental characters and (b) external body characters (see Materials and Methods for explanation of character codes) of adult *Hipposideros bicolor atrox; H. b. bicolor, H. b. tanimbarensis* subsp. nov.; *H. b. hilli* subsp. nov., *H. b. selatan* subsp. nov. and specimens of *H. bicolor* from Sumba island (referred to *H. b. tanimbarensis*) and Sumbawa island (*H. bicolor* subsp. indet.). $\bar{x}$, mean; SD, standard deviation; Min, minimum; Max, maximum and N, sample size.

Table 2a – cranial, dentary and dental characters

Island	Variable	GSL	MW	RL	CW	LIB	CB	ZW	TBL	ILD	CL	M^3M^3W	C^1B	P^3B	M^1M^3L	M^3B	C^1M^3L	DL	I_1M_3L
H.b. atrox	$\bar{x}$	17.32	9.23	3.38	1.83	2.83	8.54	9.58	2.55	4.50	2.51	6.26	0.95	1.06	3.90	1.42	6.35	11.56	7.27
	S.D.	0.26	0.18	0.15	0.10	0.07	0.17	0.12	0.16	0.06	0.05	0.15	0.08	0.03	0.13	0.13	0.09	0.09	0.13
(Peninsula	Min	17.10	9.11	3.28	1.73	2.77	8.37	9.45	2.43	4.47	2.45	6.13	0.87	1.04	3.75	1.30	6.30	11.47	7.12
Malaysia)	Max	17.61	9.43	3.56	1.92	2.90	8.71	9.67	2.73	4.57	2.55	6.42	1.02	1.09	3.98	1.56	6.45	11.64	7.37
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
H.b. bicolor	$\bar{x}$	18.21	9.25	3.59	1.90	2.88	8.61	9.17	2.54	4.75	2.54	6.10	0.98	1.07	3.91	1.33	6.39	11.73	7.51
	S.D.	0.06	0.12	0.13	0.15	0.01	0.16	0.18	0.01	0.00	0.03	0.01	0.03	0.08	0.12	0.01	0.07	0.01	0.08
(Java)	Min	18.17	9.16	3.50	1.80	2.87	8.49	9.04	2.53	4.75	2.52	6.09	0.96	1.01	3.82	1.32	6.34	11.72	7.45
	Max	18.25	9.33	3.68	2.01	2.88	8.72	9.30	2.54	4.75	2.56	6.11	1.00	1.13	3.99	1.33	6.44	11.73	7.56
	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
H.b. subsp. indet.	$\bar{x}$	18.36	9.05		1.63	2.84	8.81	9.42	2.64		2.64	5.94	1.05	1.16	3.90	1.21	5.70	12.06	7.56
	S.D.	–	–		–	–	–	0.01	–		–	–	–	–	–	–	–	–	–
(Sumbawa)	Min	18.36	9.05		1.63	2.84	8.81	9.41	2.64		2.64	5.94	1.05	1.16	3.90	1.21	5.70	12.06	7.56
	Max	18.36	9.05		1.63	2.84	8.81	9.43	2.64		2.64	5.94	1.05	1.16	3.90	1.21	5.70	12.06	7.56
	N	1	1		1	1	1	2	1		1	1	1	1	1	1	1	1	1
H.b.	$\bar{x}$	17.66	9.21	3.45	1.76	2.58	8.53	9.08	2.64	4.52	2.50	5.82	0.97	1.00	3.81	1.42	6.31	11.54	7.37
tanimbarensis	S.D.	0.24	0.10	0.19	0.11	0.07	0.14	0.17	0.10	0.06	0.11	0.13	0.03	0.06	0.07	0.11	0.11	0.15	0.09
	Min	17.16	9.03	3.05	1.52	2.45	8.23	8.75	2.41	4.42	2.25	5.46	0.92	0.89	3.70	1.19	6.14	11.24	7.14
(Selaru)	Max	17.98	9.41	3.89	1.92	2.71	8.76	9.26	2.87	4.63	2.74	5.97	1.04	1.12	3.96	1.53	6.53	11.78	7.58
	N	18	18	18	17	18	18	18	18	18	18	17	18	18	18	18	18	18	18
H.b. hilli subsp.	$\bar{x}$	17.29	9.10	3.39	1.63	2.77	8.32	8.77	2.60	4.53	2.53	5.73	0.88	0.93	3.71	1.38	6.12	11.11	7.09
	S.D.	0.19	0.13	0.15	0.14	0.08	0.11	0.10	0.12	0.08	0.10	0.10	0.03	0.04	0.10	0.11	0.10	0.17	0.22
(Timor)	Min	16.82	8.73	3.11	1.36	2.61	8.14	8.49	2.43	4.36	2.35	5.54	0.82	0.87	3.46	1.10	5.95	10.79	6.69
	Max	17.78	9.31	3.71	1.84	2.96	8.61	8.96	2.94	4.77	2.73	5.94	0.96	1.02	3.92	1.60	6.39	11.39	7.52
	N	27	27	27	27	27	27	27	26	27	27	25	27	26	27	27	27	27	27
H.b. selatan subsp.	$\bar{x}$	17.59	9.15	3.30	1.71	2.79	8.44	9.00	2.68	4.81	2.57	5.87	0.95	0.99	3.81	1.28	6.20	11.42	7.11
nov.	S.D.	0.18	0.13	0.26	0.13	0.11	0.12	0.12	0.07	0.09	0.13	0.12	0.05	0.06	0.11	0.16	0.11	0.15	0.19
	Min	17.35	8.98	2.96	1.55	2.60	8.24	8.85	2.55	4.69	2.40	5.63	0.86	0.94	3.66	1.11	6.04	11.23	6.83
(Roti/Savu)	Max	17.85	9.30	3.64	1.93	2.95	8.59	9.15	2.75	4.93	2.74	5.99	1.01	1.08	3.98	1.53	6.33	11.67	7.35
	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
H.b. subsp. cf. *tanimbarensis* (Sumba)	N=1	17.89	9.17	3.41	2.01	2.74	8.62	9.23	2.58	4.63	2.56	5.94	0.99	1.02	4.11	1.41	6.53	11.69	7.17

Table 2b – external body characters

Island	Variable	SVL	TVL	EL	TIL	FA	D2MC	D3MC	D3P1	D3P2	D4MC	D4P1	D492	D5MC	D5P1	D5P2	ANB	PNB
H.b. atrox	$\bar{x}$	43.1	29.2	19.0	18.9	43.1	35.8	32.0	17.4	18.7	33.7	10.6	9.1	31.5	12.7	10.9	4.9	5.4
	S.D.	2.6	1.6	1.2	0.6	1.0	1.0	1.0	0.4	0.8	0.6	0.4	0.3	1.0	0.4	0.3	0.3	0.4
(Peninsula	Min	39.4	27.4	17.4	18.5	42.3	34.6	31.2	16.9	17.9	33.3	10.1	8.7	30.5	12.2	10.4	4.6	5.0
Malaysia)	Max	45.3	31.2	20.3	19.8	44.5	37.0	33.4	17.9	19.7	34.6	10.9	9.5	32.9	13.2	11.1	5.1	6.0
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4
H.b. bicolor	$\bar{x}$	48.2	31.1	19.0	20.7	44.8	36.8	34.4	18.4	18.6	36.6	11.0	9.0	34.8	13.4	11.7	4.6	4.8
	S.D.	0.5	1.0	0.2	0.4	0.1	0.8	0.1	0.9	1.5	0.5	0.2	0.6	0.5	0.3	0.8	0.4	0.1
(Java)	Min	47.8	30.4	18.8	20.4	44.7	36.2	34.3	17.8	17.6	36.2	10.9	8.6	34.5	13.2	11.1	4.3	4.7
	Max	48.5	31.8	19.1	21.0	44.8	37.3	34.4	19.0	19.7	36.9	11.2	9.4	35.2	13.6	12.3	4.8	4.9
	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
H.b. subsp. indet.	$\bar{x}$	49.3	31.6	20.2	21.1	46.6	38.0	34.5	19.0	20.4	36.9	11.2	9.4	35.6	13.4	12.4	5.0	5.7
	S.D.	0.1	4.2	0.8	0.4	0.5	0.6	0.1	0.1	1.2	0.9	0.2	0.2	0.4	0.1	0.3	0	0
(Sumbawa)	Min	49.2	28.6	19.7	20.8	46.2	37.6	34.4	18.9	19.5	36.2	11.1	9.2	35.4	13.4	12.2	5.0	5.7
	Max	49.4	34.6	20.8	21.4	46.9	38.4	34.6	19.1	21.2	37.5	11.4	9.5	35.9	13.5	12.6	5.0	5.7
	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
H.b. tanimbarensis	$\bar{x}$	45.1	32.2	20.6	19.4	42.9	35.9	32.5	18.0	18.8	35.0	10.4	9.1	33.5	12.6	11.5	4.8	5.6
	S.D.	1.8	2.3	0.6	0.5	1.0	0.8	0.5	0.5	1.0	0.6	0.3	0.4	0.7	0.4	0.4	0.3	0.2
(Selaru)	Min	41.8	27.2	19.5	18.5	40.3	34.5	31.0	17.2	15.4	33.6	1.0	8.5	32.0	12.1	10.8	4.1	5.1
	Max	48.2	35.5	21.8	20.5	45.0	37.5	33.3	18.9	19.8	36.4	11.0	9.8	34.9	13.3	12.3	5.2	5.9
	N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	24	24
H.b. hilli subsp.	$\bar{x}$	44.2	30.9	20.0	19.2	42.3	35.6	32.1	17.1	18.4	34.5	10.0	8.8	33.6	12.2	11.1	4.6	5.4
	S.D.	1.9	2.1	0.8	0.6	0.9	0.9	0.7	0.5	0.9	0.8	0.3	0.5	0.7	0.4	0.5	0.4	0.3
(Timor)	Min	38.1	26.7	18.0	18.2	40.8	33.5	30.3	16.3	16.4	32.7	9.4	6.6	32.3	11.4	10.0	3.8	4.5
	Max	47.6	35.1	22.2	20.8	44.4	37.4	33.4	17.9	20.0	36.0	10.5	9.6	34.8	13.1	12.1	5.2	6.0
	N	34	31	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34
H.b. selatan subsp.	$\bar{x}$	45.4	32.1	20.6	19.2	42.7	34.8	31.7	17.2	18.9	33.5	10.2	9.0	33.0	12.6	11.2	4.8	5.8
nov.	S.D.	1.0	2.3	0.5	0.5	0.8	0.7	0.8	0.7	0.9	0.8	0.4	0.6	0.8	0.5	0.4	0.3	0.4
	Min	44.5	29.0	19.6	18.5	41.6	34.0	30.4	16.1	17.2	32.0	9.5	8.3	31.7	11.9	10.5	4.5	5.4
(Roti/Savu)	Max	47.3	35.6	21.4	19.8	43.7	35.8	33.0	18.1	20.0	34.6	10.6	10.3	33.8	13.2	11.8	5.2	6.5
	N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	8
H.b. subsp. cf. *tanimbarensis*	N=1	43.1	36.5	20.8	20.6	45.1	38.6	34.9	18.1	19.9	36.8	10.6	9.4	35.6	13.1	12.4	4.9	5.9
(Sumba)																		

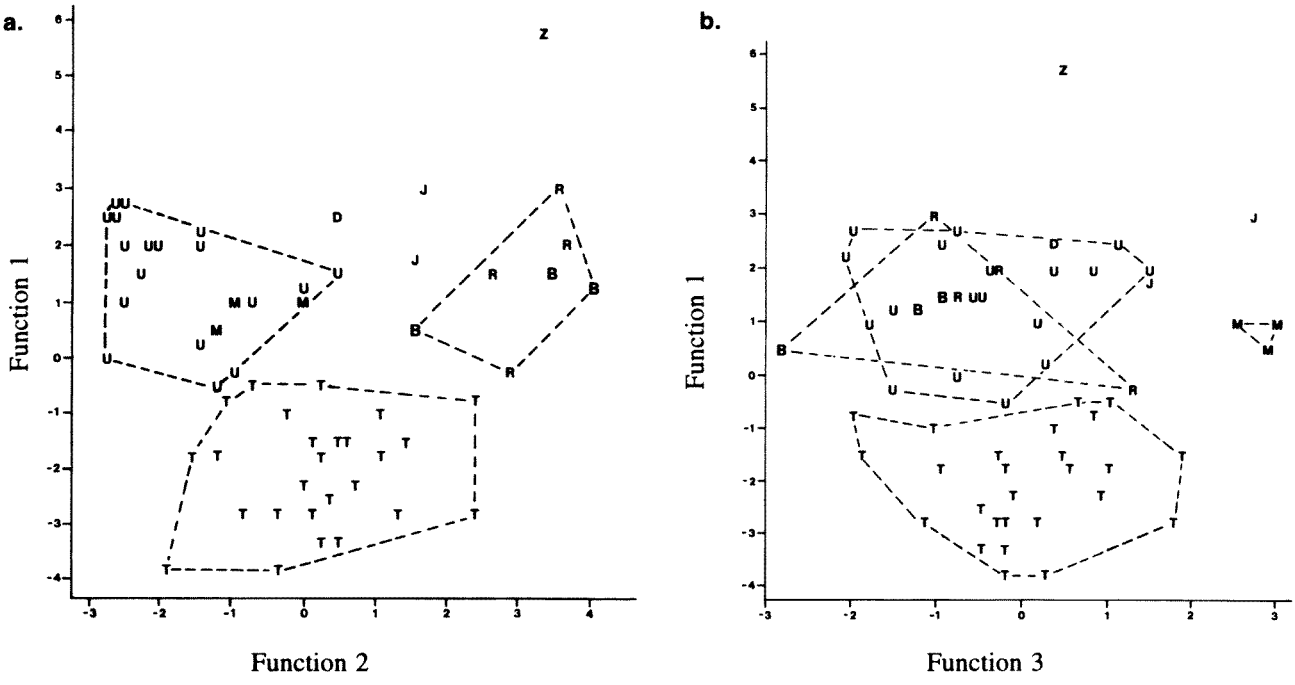

Figure 2 Canonical Variate Analysis among each island and the Peninsula Malaysia population of *Hipposideros bicolor* and based on a subset of five cranial, dentary and dental characters (see text). Population codes are as follows: B, Savu island; D, Sumba island; J, Java island; M, Peninsula Malaysia; R, Roti island; T, West Timor; U, Selaru island; and Z, Sumbawa island. (a) plots of Functions 1 and 2, and (b) plots of Functions 1 and 3.

Table 3 Canonical variate function coefficients from analysis based on four groupings of *Hipposideros bicolor* populations (Selaru, Timor, Roti/Savu and Peninsula Malaysia) and on a subset of five characters for (a) cranial, dentary and dental characters and (b) external body characters. See Materials and Methods for explanation of character codes.

Table 3a

Character	Function 1	Function 2	Function 3
ILD	–0.0567 (–0.7527)	1.0084 (13.3952)	–0.3758 (–4.9920)
DL	0.8646 (5.4397)	0.3208 (2.0181)	0.4812 (3.0276)
LIB	–0.5959 (–7.0866)	–0.0927 (–1.1022)	0.8110 (9.6452)
P^3B	0.4464 (8.2084)	0.0402 (0.7392)	0.4569 (9.4022)
I_1M_3L	–0.1004 (–0.5628)	–0.6067 (–3.4003)	–0.2244 (–1.2573)
Constant	–42.7810	–57.2068	–36.7831
Variation explained (%)	56.8	35.3	7.9

Table 3b

Character	Function 1	Function 2	Function 3
D3P1	–0.8525 (–1.7123)	0.6319 (1.2693)	0.2407 (0.4834)
D5MC	1.5099 (2.0338)	0.3248 (0.4374)	0.5502 (0.7411)
FA	–0.5068 (–0.5340)	–0.5134 (–0.5410)	0.3127 (0.3294)
EL	0.3661 (0.4960)	0.5985 (0.8109)	0.4401 (0.5962)
D4MC	–0.3931 (–0.5320)	0.2409 (0.3259)	–1.3309 (–1.8010)
Constant	–6.9297	–41.3082	29.342
Variation explained (%)	60.2	27.2	12.6

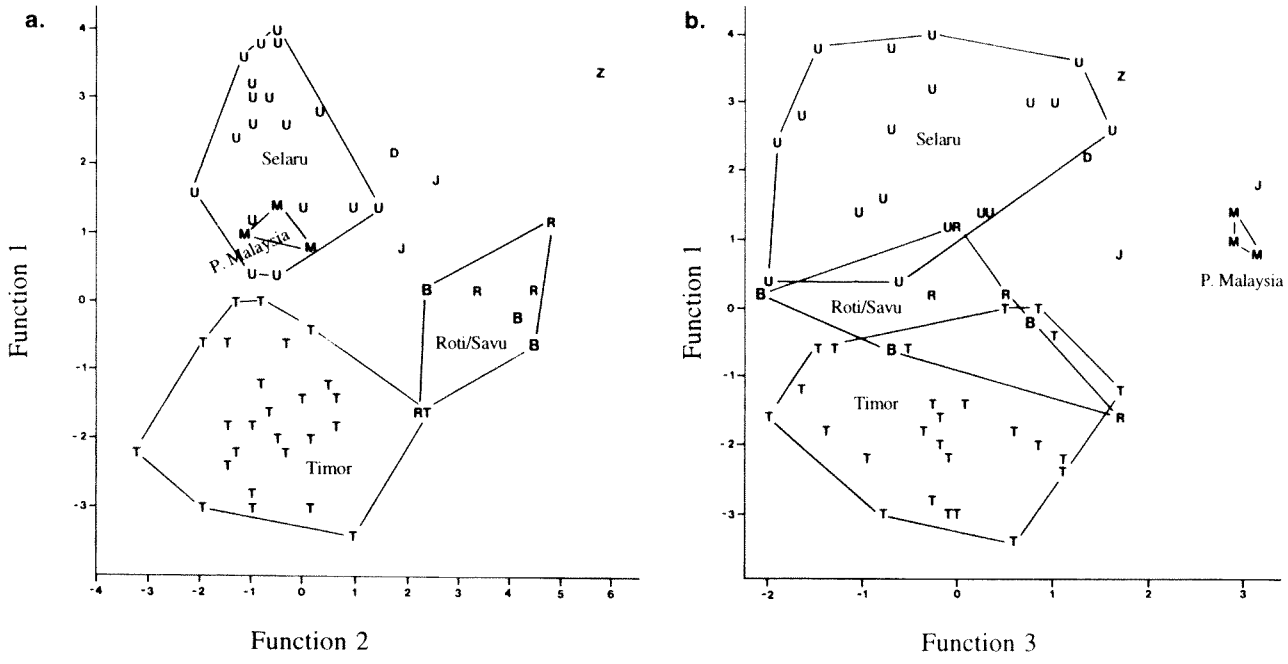

Figure 3 Canonical Variate Analysis among four population groupings of *Hipposideros bicolor* (Selaru, Timor, Roti/Savu and Peninsula Malaysia) - with the few Sumba, Sumbawa and Java specimens unallocated - and based on a subset of five cranial , dentary and dental characters (see text). (a) plots of Functions 1 and 2 and (b) plots of Functions 1 and 3. Population codes as for Figure 2.

the two Java specimens and single Sumba and Sumbawa specimens unallocated, and again using the above five characters, extracted three significant functions which allocated 98.2% of the specimens to their correct group. Function 1, which explained 56.8% of the variance, separated the Selaru and Malay Peninsula Group from the Timor Group (Figure 3a). The characters with high coefficients (>0.5) on Function 1 were dentary length and least interorbital breadth (Table 3a). Function 2 (35.3% of variance) separated the Roti/Savu Group from the Selaru, Malay Peninsula and Timor Groups (Figure 3a). The character with the highest coefficient (>0.5) on Function 2 was interlachrymal distance (Table 3a). Function 3 (7.9% of variance) separated the Malay Peninsula Group from the other three groups (Figure 3b). The character with the highest coefficient on Function 3 was least interorbital breadth (Table 3a). Of the unallocated specimens, one of the Javanese specimens allocated to the Peninsula Malaysia Group and the other to the Roti/Savu Group; the Sumba and Sumbawa specimens allocated to the Selaru Group.

External body characters

The DFA based on five characters (digit 3 phalanx 1 length, digit 4 metacarpal length, forearm length, ear length and digit 2 metacarpal length), and using as groups each island population and the Peninsula Malaysia population, extracted four significant functions but with only 61.8% of individuals classified to their correct locality. Bivariate plots of these functions did not reveal the descrete clusters apparent for the cranial, dentary and dental characters, although there was partial separation between the Timor and Selaru Groups (Figure 4).

A DFA was run based on five characters (digit 3 phalanx 1 length, digit 5 metacarpal length, digit 4 metacarpal length, ear length and forearm length) and using as groups those identified in the earlier cranial, dentary and dental analysis. This DFA extracted three significant functions with 80.3% of individuals classified to their correct groups. There was considerable overlap between the Timor and Selaru Groups, with 11.8% of individuals from the Timor Group misclassified to the Selaru Group. A total of 37.5% of the Roti/Savu Group were misclassified to either the Selaru Group (12.5%) or the Timor Group (25.0%). Of the ungrouped specimens, the two from Sumbawa and the two from Java grouped with the Selaru Group; the single specimen from Sumba island grouped with the Selaru Group. Only the Peninsula Malaysia Group was discrete. Function 1, which explained 60.2% of the variance, separated the Peninsula Malaysia Group from the other groups and from the unallocated Sumbawa, Java and Sumba specimens (Figure 5). The characters with high coefficients (> 0.5) on Function 1 were digit 5 metacarpal length, digit 3 phalanx 1 length and forearm length (Table 3b). Function 2 (27.2% of variance) also separated the Peninsula Malaysia

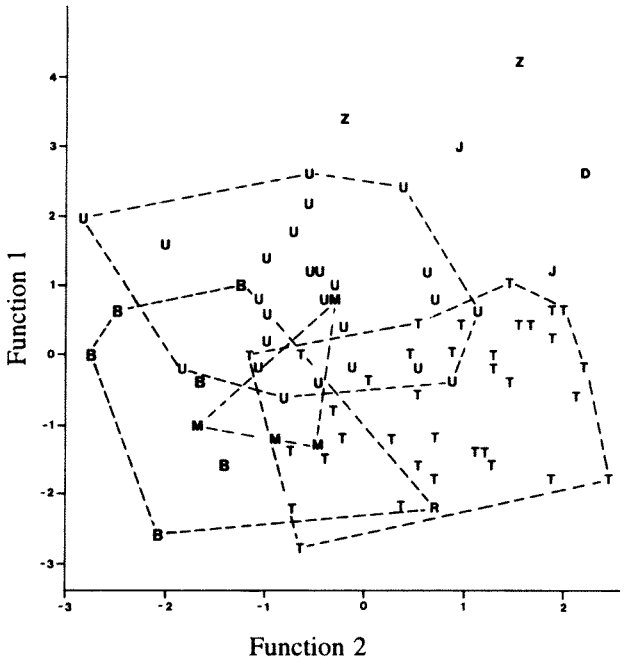

Figure 4 Plots of Functions 1 and 2 from Canonical Variate Analysis among each island population and the Peninsula Malaysia populations of *Hipposideros bicolor* and based on a subset of five external characters (see text). Population codes as for Figure 2.

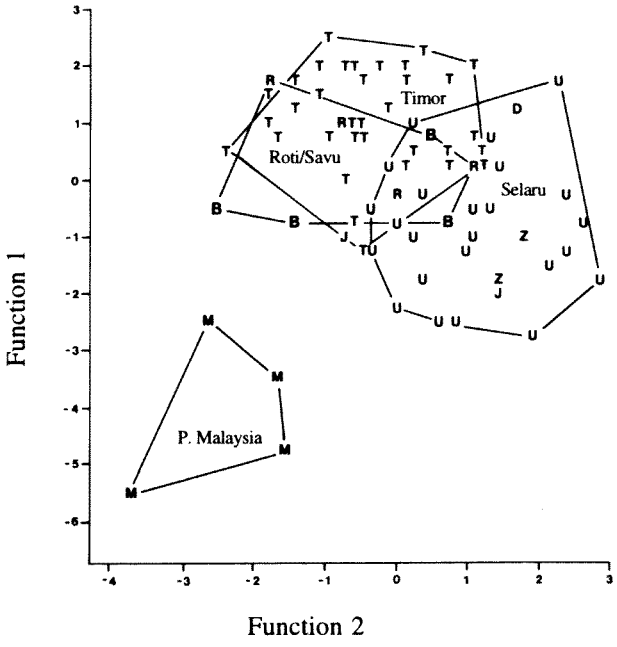

Figure 5 Plots of Functions 1 and 2 from Canonical Variate Analysis among four population groupings (Selaru, Timor, Roti/Savu and Peninsula Malaysia) - with the few Sumba, Sumbawa and Java specimens unallocated - and based on a subset of five external body characters. Population codes as for Figure 2.

Group from the Selaru Group and partially separated it from the Timor Group; it also partially separated the Timor and Roti/Savu Groups from the Selaru Group (Figure 5). The characters with high coefficients (>0.5) on Function 2 were digit 3 phalanx 1, ear length and forearm length. Function 3 (12.6% of variance) also separated the Malay Peninsula Group from the Roti/Savu Group. The characters with high coefficients (>0.5) on Function 3 were digit 4 and 5 metacarpal lengths (Table 3b).

In summary, the above statistical analyses indicated that the specimens of *H. bicolor* from the Lesser Sunda islands differed morphologically in both cranial, dentary, dental and external body characters from *H. bicolor atrox* from Peninsula Malaysia and also on cranial, dentary and dental characters from *H. b. bicolor* from Java. However, among this island chain the populations were further differentiated on cranial, dentary and dental characters into three clear forms (Timor, Selaru and Roti/Savu). The two Sumbawa island specimens grouped closely with those from Selaru island on external body morphology but on cranial, dentary and dental morphology the single specimen available for study was not closely associated with any of the other specimens. The Sumba island specimen is clearly closely associated with the Selaru form on cranial, dentary and dental characters and is tentatively referred to that form. The Sumbawa specimens, described in detail by Kitchener and Maharadatunkamsi (1995), are not referred to any of these Lesser Sunda subspecies. These two specimens agree in size with the measurements of a single specimen from Ruteng, Flores island reported in Hill and Rozendaal (1989). Further specimens will probably allow recognition of the Sumbawa and Flores form as a unique subspecies.

The following section formally recognises three new subspecies of *H. bicolor* in the Lesser Sunda islands.

SYSTEMATICS

Hipposideros bicolor tanimbarensis subsp. nov., Kitchener

Holotype

Western Australian Museum (WAM) No. M44287; adult female; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; collected by Ir. Ibnu Maryanto (Museum Zoologicum Bogoriense) and Ron Johnstone, Western Australian Museum), on 25 April 1993.

Type locality

Wesuri Cave, near Adaut, Selaru island, Tanimbar Island Group (8°09'S, 131°08'E); at sea level.

Paratypes (all from type locality)

12♀♀, 12♂♂; WAM (M43818, M44248-9,

M44252, M44254, M44259, M44261-8, M44271-2, M44275-6, M44279, M44281-3, M44286, M44290).

Diagnosis

Hipposideros bicolor tanimbarensis differs from *H. b. bicolor* [including also measurements from Hill (1983) and Tate (1941)] in averaging smaller in most cranial, dentary and dental measurements, except for tympanic bulla length and intercochlear distance. For example: absolutely smaller greatest skull length 17.2-18.0 (N = 18) *v.* 18.2-19.0 (3) and least interorbital breadth 2.5-2.7 (18) *v.* 2.9-3.0 (4). Posterior noseleaf breadth larger 5.1-5.9 (24) *v.* 4.7-4.9 (2). Interlachrymal distance narrower relative to dentary length (Figure 6). Dorsal pelage darker, tipped with Fuscous rather than Burnt Umber.

H. b. tanimbarensis differs from *H. b. atrox* in having a narrower: zygomatic width 8.8-9.3 (18) *v.* 9.5-9.7 (3); least interorbital breadth 2.5-2.7 (18) *v.* 2.8-2.9 (3); M^3M^3 width 5.5-6.0 (17) *v.* 6.1-6.4 (3). It has a longer digit 5 metacarpal length relative to forearm length (Figure 7); and narrower least interorbital breadth relative to dentary length (Figure 8). Glans penis distal end sharper and less rounded in craniocaudal view, and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broad and not bilobed; arms of distal bifurcation not as widely spaced or as broad (Figure 10). Dorsal pelage darker, tipped with Fuscous rather than Cinnamon.

H. b. tanimbarensis differs from *H. b. hilli* subsp. nov. in averaging larger in all characters, except least interorbital breadth, interlachrymal distance, cochlea length, and digit 5 metacarpal length.

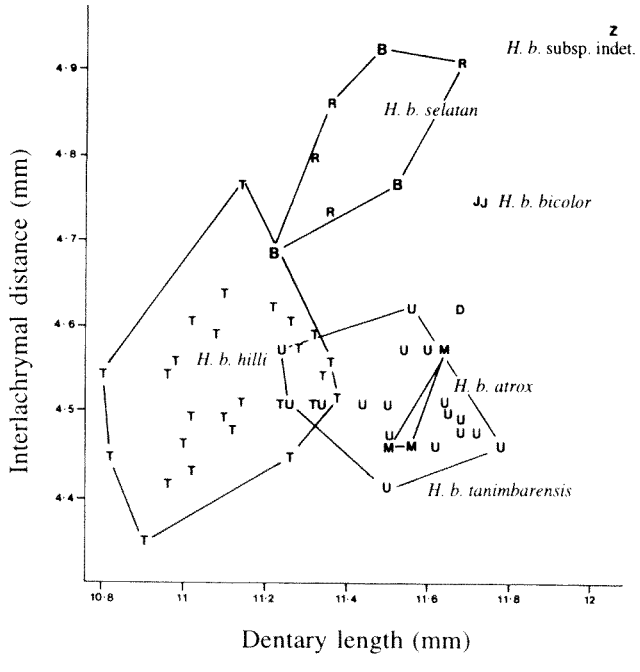

Figure 6 Plot of interlachrymal distance *versus* dentary length for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

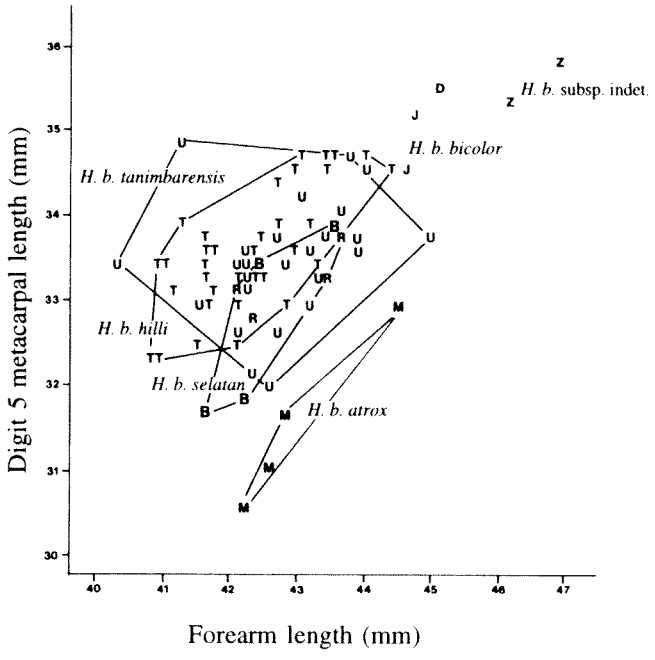

Figure 7 Plot of digit 5 metacarpal length *versus* forearm length for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

Dentary length shorter relative to least interorbital breadth (Figure 8). Dorsal pelage darker, tipped with Fuscous rather than Burnt Umber.

H. b. tanimbarensis differs from *H. b. selatan* subsp. nov. in having a narrower interlachrymal distance 4.4-4.6 (18) *v.* 4.7-4.9 (7) and narrower least interorbital breadth relative to dentary length (Figure 8). Dorsal pelage darker, tipped with Fuscous rather than Burnt Umber.

Description

A moderate sized *H. bicolor* subspecies with greatest skull length 17.66 (17.16-17.98) 18 and forearm length 42.9 (40.3-45.0) 25. For other measurements see Table 2a, b. It agrees closely with the general description of the cranium, dentition and external body characters of this species as described by Hill (1963). *Hipposideros b. tanimbarensis* has zygomata broad, occasionally massive, with superior jugal projection low; zygomatic width narrower than mastoid width 9.08 (8.75-9.26) 18 *v.* 9.21 (9.03-9.41) 18; least interorbital breadth narrow 2.58 (2.45-2.71) 18; crown area of outer lower incisor slightly larger than that of inner lower incisors; anterior lower premolar three-quarters length and half to three-quarters height of posterior lower premolar; and vomer projection into mesopterygoid fossa only slightly thickened.

Pelage of ventral surface Smoke Gray; dorsal surface Smoke Gray base tipped with Fuscous. The patagia Dusky Brown.

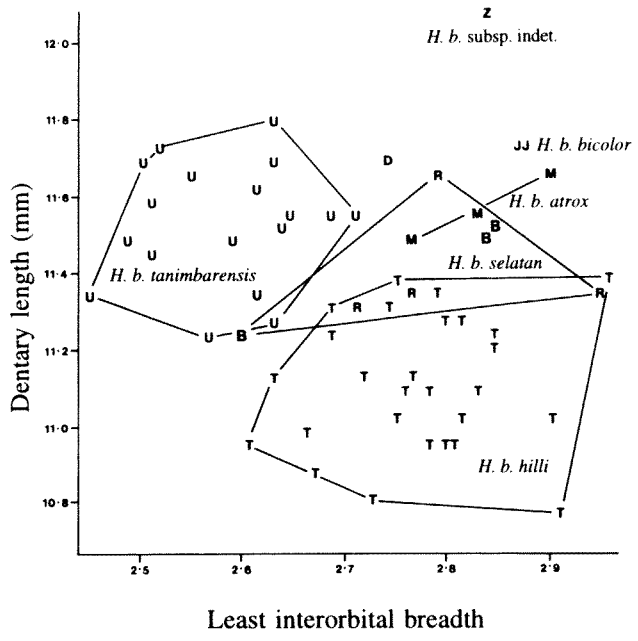

Figure 8 Plot of dentary length *versus* least interorbital breadth for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

Penis *ca.* 7 mm long. Glans penis with distal head of variable shape; in craniocaudal view it ranges from a blunt rod shape (Figure 9b) to an arrow shape (Figure 9c) to a broadly rounded head with median distal slit (Figure 9d). Baculum ca. 3.0-3.2 mm long; base slightly broadened, long narrow shaft with short bifurcated distal tip (Figure 10b,c).

Distribution

Known only from the type of locality at Wesuri Cave, near Adaut, Selaru island, Tanimbar Group.

Etymology

Named after the Tanimbar Group of islands which it inhabits.

Referred Specimen

A single adult female (WAM M30345) mist netted over a river in a large limestone cave at Waikelosawah, Sumba island (9°36'S,119°29'E) is tentatively referred to *H. b. tanimbarensis;* its measurements are presented in Tables 2a, b. On the basis of the more important cranial, dental and dentary measurements the DFA allocated it to *H. b. tanimbarensis*. Its glans penis is similar to Figure 9c; its baculum has a length of 2.74 mm and is similar to Figure 10b.

Hipposideros bicolor hilli subsp. nov. Kitchener

Holotype

Western Australian Museum (WAM) No. M34953; adult male; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate;

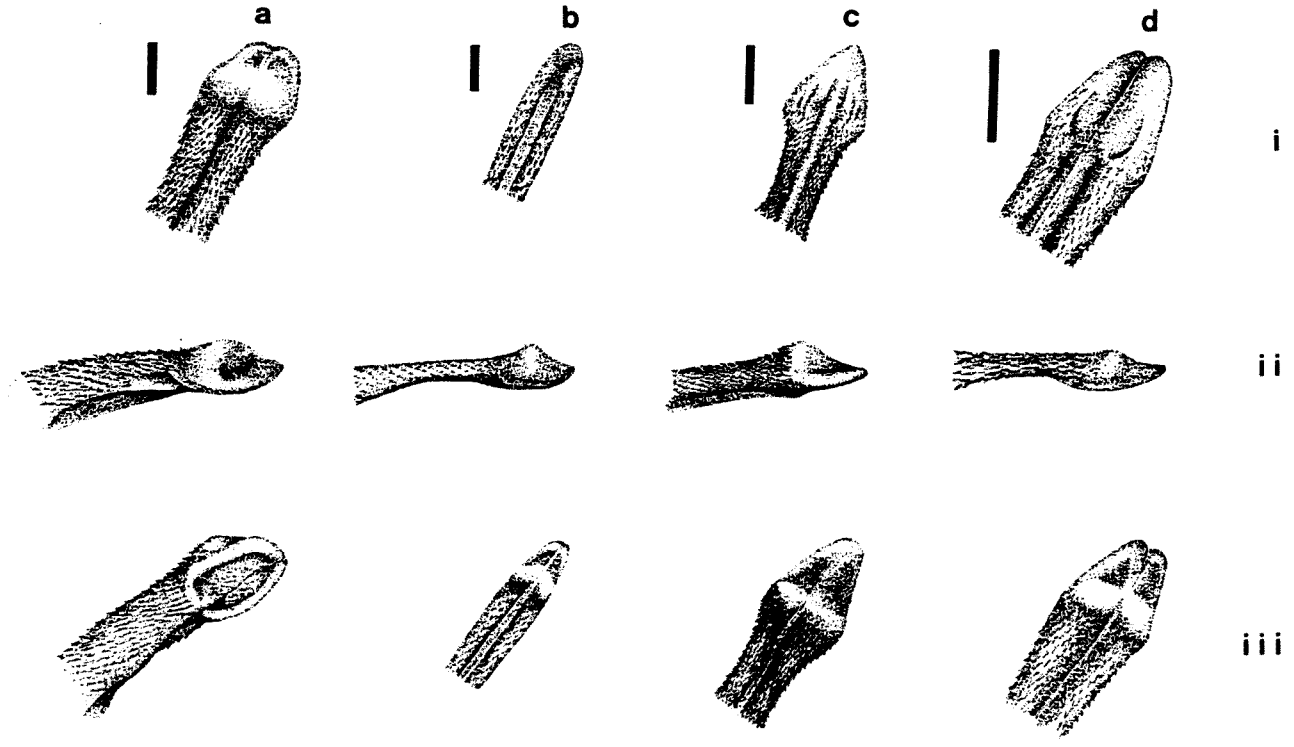

Figure 9 Glans penis of (a) *Hipposideros bicolor atrox* from Peninsula Malaysia (WAM M21159); (b) and (c) *H. b. selatan* subsp. nov. from Roti island (WAM M35375 and WAM M35507, respectively) and (d) *H. b. hilli* subsp. nov. from Timor island (WAM M34959). From (i) cranial, (ii) lateral and (iii) caudal views. Scale lines, 0.5 mm.

collected on 17 October 1990 by Dr Ken Aplin (Western Australian Museum) and Bapak Boeadi (Museum Zoologicum Bogoriense).

Type Locality

Mist netted in a cave at Oimoro, near Panite, West Timor, Nusa Tenggara Timur, Indonesia (9°50'S, 124°29'E); at sea level.

Paratypes

From the following localities on West Timor: Baumata (10°11'S, 123°43'E), 7♀♀, 5♂♂, WAM M(30060, 30098-9, 30107, 30110, 30115-6, 30118-22; Bauraen (10°15'S, 123°43'E), 1♀, WAM M35010; Panite (9°50'S, 124°29'E), 11♀♀ 9♂♂, WAM M(34889-92, 34894, 34951-2, 34954-6, 34958-9, 34961, 34963-5, 34967-8, 34973-4).

Diagnosis

Hipposideros b. hilli differs from *H. b. bicolor* [including also Hill (1983) and Tate (1941) measurements] in averaging smaller in most measurements, except tympanic bulla length, M^3 breadth, ear length and digit 5 metacarpal length. For example, absolutely smaller in both greatest skull length 16.8-17.8 (27) *v.* 18.2-19.0 (3) and forearm length 40.8-44.4 (34) *v.* 44.6-46.8 (6). Dentary length relative to least interorbital breadth shorter (Figure 8).

Hipposideros b. hilli has similar cranial and external body measurements to *H. b. atrox* but differs in having considerably smaller dental measurements (see Table 2a). Dentary length relative to both interlachrymal distance and least interorbital breadth shorter (Figures 6 and 8, respectively). Digit 5 metacarpal length longer relative to forearm length (Figure 7). Glans penis distal end less rounded in craniocaudal view and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broadened and not bilobed, arms of the distal bifurcation not as widely spaced or as broad (Figure 10). Dorsal pelage darker, tipped with Burnt Umber rather than Cinnamon.

Hipposideros b. hilli differs from *H. b. tanimbarensis* as described in the earlier diagnosis of that subspecies.

Hipposideros b. hilli differs from *H. b. selatan* in averaging smaller in most cranial, dental and dentary characters. For example, greatest skull length 17.3 (16.8-17.8) 27 *v.* 17.6 (17.4-17.9) 7. Interlachrymal distance and dentary length generally smaller (Figure 6) and dentary length relative to least interorbital breadth generally smaller (Figure 8).

Description

Hipposideros b. hilli is on average, the smallest form of *H. bicolor* in the Lesser Sunda Islands. It has a greatest skull length of 17.29 (16.82-17.78) 27 and forearm length of 42.3 (40.8-44.4) 34. Other measurements of cranium, dentition, dentary and external body characters (see Table 2a, b) are similar to *H. b. tanimbarensis*. Its zygomatic width is much narrower than the mastoid width 8.77 (8.49-8.96) 27 *v.* 9.10 (8.73-9.31) 27.

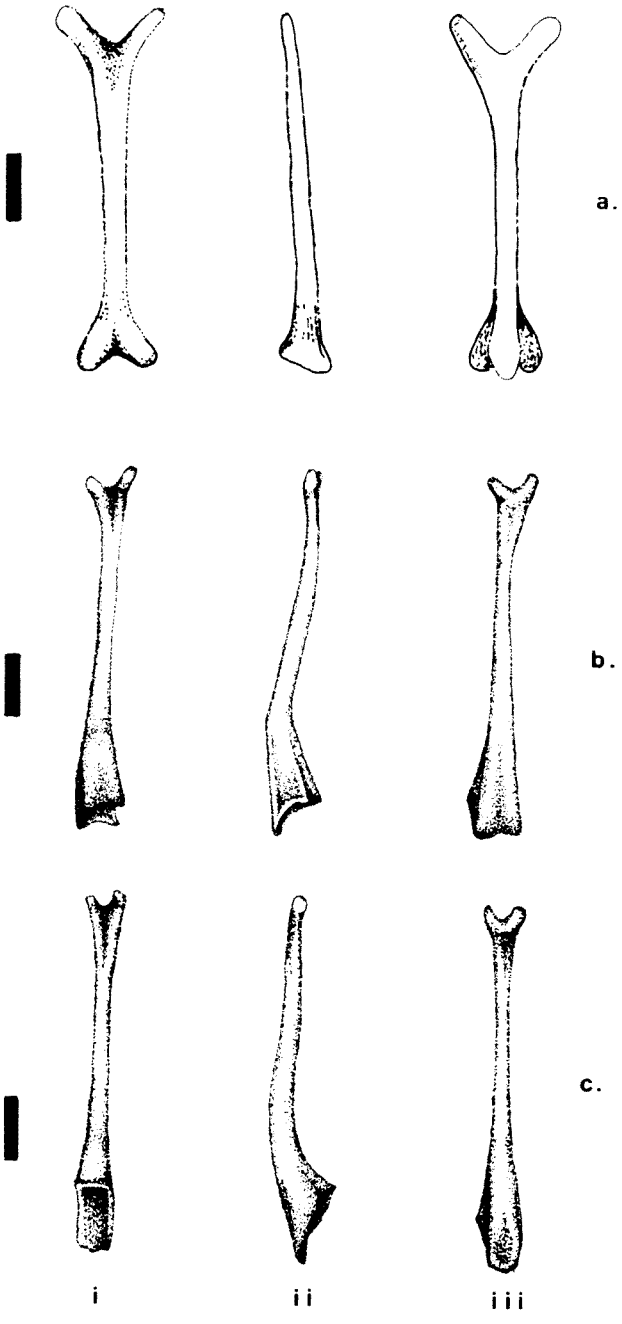

Figure 10 Baculum of (a) *Hipposideros bicolor atrox* from Peninsula Malaysia (WAM M21158), (b) *H. b. selatan* subsp. nov. from Roti island (WAM M35507), and (c), *H. b. hilli* subsp. nov. from Timor island WAM M34959). From (i) caudal, (ii) lateral and (iii) cranial views. Scale lines 0.5 mm.

Pelage colour of the ventral surface Drab. The dorsum Drab tipped with Burnt Umber. Patagia Dusky Brown.

Penis *ca.* 7 mm long. Glans penis with distal head flattened craniocaudally and broadly rounded with a median terminal slit (Figure 9d). Baculum *ca.* 2.8 mm long, slightly broadened at base; shaft long, narrow, slightly flexed in lateral view with short bifurcated distal tip (Figure 10c).

Distribution

Several localities in West Timor (Baumata, Bauraen and Panite), Nusa Tenggara Timur, Indonesia.

Etymology

Named after John Edwards Hill, formerly of the British Museum of Natural History. Although retired he continues to provide generous assistance to the new generations of chiropteran taxonomists.

***Hipposideros bicolor selatan* subsp. nov. Kitchener**

Holotype

Western Australian Museum (WAM) No. M 35421; adult female; 'scientific' skin; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; collected on 9 October 1990 by D.J. Kitchener.

Type locality

Desa Sanggoen, 6 km SW Baa, Roti island, Nusa Tenggara Timur, Indonesia (10°43'S, 123°09'E); collected by hand in a small limestone cave; at sea level.

Paratypes

From Roti island: Kota Baa (10°44'S, 123°06'E), 1♂, WAM M35375; Desa Oeseli (10°51'S, 123°05'E), 2♀♀, WAM M35506-7. From Savu island: Desa Menia (10°29'S, 121°55'E), 1♀, 3♂♂, WAM M(35115, 35119, 35130, 35211).

Diagnosis

Hipposideros b. selatan differs from *H. b. bicolor* [including also measurements from Hill (1983) and Tate (1941)] in averaging smaller in most cranial measurements, except tympanic bulla length, interlachrymal distance and cochlea length, all dental measurements and most external measurements except noseleaf breadth and ear length (see Table 2a). For example, greatest skull length 17.4-17.9 (7) *v.* 18.2-19.0 (3); digit 3 metacarpal length 30.4-33.0 (8) *v.* 34.3-34.4 (2); and forearm length 41.6-43.7 (8) *v.* 44.6-46.8 (6). Posterior noseleaf breadth larger 5.4-6.5 (8) *v.* 4.7-4.9 (2).

Hipposideros b. selatan is similar in overall size to *H. b. atrox* (see Table 2a, b). It differs in having a smaller: zygomatic width 8.9-9.2 (7) *v.* 9.5-9.7 (3) and M^3M^3 width 5.6-6.0 (7) *v.* 6.1-6.4 (3) and larger interlachrymal distance 4.7-4.9 (7) *v.* 4.5-4.6 (3). Interlachrymal distance relative to dentary length larger (Figure 6). Glans penis distal end less rounded in craniocaudal view and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broadened and not bilobed, arms of distal bifurcation not as widely spaced or as broad (Figure 10) Dorsal pelage darker, tipped with Burnt Umber rather than Cinnamon.

Hipposideros b. selatan differs from both *H. b. tanimbarensis* and *H. b. hilli* as described in the earlier diagnoses of these two subspecies.

Description

Approximately the same overall size as *H. b. tanimbarensis* with which it agrees in general form of cranium (apart from differences noted in the earlier diagnosis), dentition and dentary (see Table 2a, b). Greatest skull length 17.59 (17.35-17.85) 17 and forearm length 42.7 (41.6-43.7) 8. Zygomatic width narrower than mastoid width 9.00 (8.85-9.15) 7 *v.* 9.15 (8.98-9.30) 7.

Pelage colour of ventral surface Drab. The dorsum Drab tipped with Burnt Umber. Patagia Dusky Brown.

Penis *ca.* 5 mm long, glans shape variable, with forms ranging from those shown in Figure 9 b, c and d. Baculum ca. 3.2 mm long, with shaft long, bifurcated slightly at distal tip (Figure 10b) but also with bifurcate arms closer together.

Distribution

Roti and Savu islands, Nusa Tenggara Timur, Indonesia.

Etymology

The most southern populations of *H. bicolor*. Selatan is Bahasa Indonesian for southern.

DISCUSSION

Hipposideros bicolor is a widespread Asian species that prior to this study was known to be distributed from mainland Asia (northern India through Assam, Burma, southern China, Thailand, Vietnam, Malay Peninsula) to the southeast islands of Sumatra, Java, to Flores island in the Lesser Sunda Islands, Sulawesi and Philippines and several smaller associated islands. This study confirms that it also extends eastwards along the southern chain of Indonesian islands as far as the Tanimbar Group. In this southern chain of islands it differentiates morphologically into three subspecies which have a stronger phenetic relationship with *H. b. bicolor* of Java rather than

with *H. b. atrox* of Peninsula Malaysia. It may be that the form of *H. bicolor* on Sumbawa island is a further subspecies.

The morphological differentiation of a number of species of micro- and megachiroptera into two or three subspecies in the Lesser Sunda islands has been documented (Kitchener and Suyanto 1996). This morphological differentiation shows some patterns, and as summarised by Kitchener and Suyanto (1996), "reflect the last major glacial (18,000 yr BP) island arrangement (and) suggests that many of these morphological changes, presumably reflecting evolutionary processes, are of relatively recent origin". These authors further state that such differentiation to subspecies tends to occur in the easternmost islands or on islands in the Outer Banda Arc (Sumba, Roti, Savu and Timor). *Hipposideros bicolor* has followed these general patterns and differentiated into subspecies on the easternmost island of Selaru and on islands in the Outer Banda Arc (Timor and Roti/Savu). Interestingly, the single specimen from the island of Sumba in the Outer Banda Arc, appeared to be phenetically closer to the population of *H. bicolor* on Selaru island than to the populations on the isolated islands in the Outer Banda Arc of Roti/Savu and Timor.

Only two studies have examined the association between geographic variables and morphology among bats in the region (Kitchener *et al.* 1992, Kitchener and Maharadatunkamsi 1996). These studies showed that longitude was the most important associate in determining overall skull and body size. In the former study, *Hipposideros diadema* tended to be smaller towards the east contrasting with the latter study on *Cynopterus nusatenggara* which tended to be larger to the east. *Cynopterus nusatenggara* also became larger on more isolated islands. The form of *H. bicolor* on the western island of Sumbawa was much larger than those forms on islands to the east and south - suggesting that this species followed the overall size trend of its congener.

Other specimens examined

Hipposideros bicolor bicolor

Kiskenda, Java (7°06'S, 110°16'E); 2♀♀; WAM M(39314, 39360).

Hipposideros bicolor atrox

Ampang Impounding, Selangor Peninsula Malaysia (3°08'N, 101°46'E); 2♀♀, 2♂♂; WAM M(21158-61).

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