MORPHOLOGICAL VARIATION IN *EONYCTERIS SPELAEA* (CHIROPTERA: PTEROPODIDAE) FROM THE GREATER AND LESSER SUNDAS ISLANDS, INDONESIA AND DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT

Morphological variation in the cave fruit bat, Eonycteris spelaea *from Indonesia and the Philippines was examined using both univariate and multivariate statistical analyses based on measurements of 22 skull characters and 15 external body characters from 270 adult specimens. Other non-meristic characters were also examined.*

Multiple regression analyses indicated strong sexual dimorphism in both skull and external body characters. Almost all measured characters differed significantly between islands. Thirteen of the 37 characters were also influenced by the age of adults.

Four distinct morphological groups of E. spelaea *were recognised using discriminant function analysis following the removal of the effects of age and sex on the measurements considered. These were: Jawa/Sumatera Group, Lesser Sunda/Philippines Group, Sulawesi Group and Kalimantan Group. These morphological groups were considered subspecifically distinct; the Kalimantan Group is herein described as a new subspecies.*

INTRODUCTION

The cave fruit bat, *Eonycteris spelaea* (Dobson, 1871) is a medium size (weight *ca.* 53 - 84 g) member of the family Pteropodidae and subfamily Macroglossinae (Corbet and Hill 1992, Hill and Smith 1984). It is characterized by an elongate facial rostrum; second finger without claw; presence of a kidney-shaped gland on each side of the anus; small and triangular shaped upper incisors; and small premolars and molars. It is distributed widely from southwest and north India, through south China, Andaman Is, Myanmar (Burma), Malaya, Philippines, Sumatera, Jawa, Kalimantan, Sulawesi, Bali, Lombok, Sumba, Timor and Halmahera (Corbet and Hill 1992, Honacki *et al.* 1982, van Strien 1986). Additionally, vertebrate surveys in the Outer and Inner Banda Arc islands of south and eastern Indonesia conducted by Dr. D. J. Kitchener and his colleagues from the Western Australian Museum and the Museum Zoologicum Bogoriense, between 1987 and 1993, collected specimens from Sumbawa, Rinca, Pantar and Alor Islands, Nusa Tenggara.

The taxonomic status of the subspecies of *Eonycteris* is still in question (Hill 1983), largely as a consequence of lack of material (Goodwin 1979).

Previous diagnoses of these subspecies were based on minor differences, such as loss of M_3, depth of rostrum, pelage colour and some slight differences in overall body, skull and teeth size. Andersen (1912) reviewed the genus *Eonycteris* and recognised three species: *E. spelaea* (Dobson, 1871); *E. major* Andersen, 1910 and *E. rosenbergii* (Jentink, 1889).

The taxonomic status of *E. rosenbergii* is contentious. For example, Andersen (1912) and Bergmans and Rozendaal (1988) described it as a valid taxon that was distinguished from the other forms by a heavy rostrum, pelage colour slightly different and by having M_3 frequently missing. Others considered it an aberrant *E. spelaea* (Miller 1907, Tate 1942). Bergmans and Rozendaal (1988) and Corbet and Hill (1992) considered *rosenbergii* as a subspecies of *E spelaea*, while Honacki *et al.* (1982) and van Strien (1986) considered it a species.

Lawrence (1939) described *E. s. glandifera* from Luzon Island, the Philippines; it was characterised by tawny, russet or ochraceous tawny throat pelage in males. She considered that specimens from Sumatera were also *E. s glandifera*. Tate (1942), however, referred the Sumatera specimens to *E. s. spelaea* but stated that specimens from Bali were of similar colour to *glandifera*.

Currently only one species, *E. spelaea*, and the following subspecies of *E. spelaea* are generally recognised (Lawrence 1939, van Strien 1986, Bergmans and Rozendaal 1988, Kitchener *et al.* 1990, Corbet and Hill 1992):

E. s . spelaea (Dobson, 1871)

North India, Burma, South China, Thailand, Malaya, Sumatera, Borneo and Jawa.

E. s. glandifera Lawrence, 1939

Philippines, Palawan, Borneo (?), Central and South Sulawesi (?), Muna, Bali, Lombok, Sumba and Timor.

E. s. rosenbergii (Jentink, 1889)

North Sulawesi.

The present study investigates the morphological variation between island populations of *E. spelaea* from Indonesia and the Philippines; and describes their subspecific taxonomy.

MATERIALS AND METHODS

A total of 270 adult specimens from 15 islands in Indonesia and two islands in the Philippines were examined. Islands refer to populations, with the exception of the Philippines where Negros and Leyte were combined into one population. The collection locality, sample sizes and sex of the specimens for this study are given in Table 1 and Figure 1.

Table 1. Localities sampled and number of specimens of *Eonycteris spelaea* for this study

Taxon	Island	Locality	Loc.code	Longitude	Latitude	Sample Size		
						♂	♀	Total
E. spelaea spelaea	Sumatera	Ketambe	1	97°25'48"E	4°13'40"N	2	2	4
		Bukit tinggi	2	100°21'24"E	0°18'36"S	0	1	1
		Pariaman	3	100°20'00"E	0°39'00"S	0	2	1
		Padang	4	100°18'45"E	0°58'04"S	1	2	3
		Lempur	5	101°24'00"E	2°14'00"S	2	1	3
		Curup	6	102°30'56"E	3°27'26"S	1	0	1
		Kota Agung	7	104°36'17"E	5°30'14"S	1	0	1
		Pulau Panggung	8	104°44'14"E	5°18'07"S	2	3	5
		Sukaraja Tiga	9	104°51'39"E	5°05'12"S	0	1	1
		Jampang	10	105°17'10"E	5°12'56"S	1	1	2
		Jabung	11	105°38'00"E	5°28'00"S	3	6	9
E. spelaea spelaea	Jawa	Labuan	12	105°49'00"E	6°21'12"S	1	2	3
		Banten	13	106°09'49"E	6°01'21"S	2	0	2
		Ciampea	14	106°41'10"E	6°32'10"S	3	4	7
		Pameungpeuk	15	107°43'05"E	7°38'43"S	0	1	1
		Garut	16	107°52'56"E	7°12'00"S	0	1	1
		Randudongkal	17	109°18'30"E	7°06'00"S	1	0	1
		Cilacap	18	109°00'34"E	7°43'45"S	0	1	1
		Ketapang	19	114°24'00"E	8°07'00"S	1	0	1
E. spelaea winnyae subsp.nov	Kalimantan	Tanah Merah	20	117°29'08"E	3°43'43"N	0	2	2
		Long Iram	21	115°37'43"E	0°00'51"S	2	0	2
		Samarinda Ulu	22	116°58'30"E	0°23'00"S	1	2	3
		Samarinda	23	117°05'30"E	0°26'00"S	2	0	2
		Hantakan	24	115°26'05"E	2°44'21"S	0	2	2
E. spelaea rosenbergii	Sulawesi	Maros	25	119°35'00"E	4°59'00"S	5	2	7
		Bonto Maccini	26	119°56'00"E	5°28'30"S	0	4	4
		Bantaeng	27	119°56'00"E	5°30'00"S	2	0	2
		Bonto Manai	28	119°59'00"E	5°29'00"S	2	0	2
		Solie Soppeng	29	119°52'23"E	4°17'38"S	1	0	1
		Poso	30	120°48'00"E	1°20'10"S	1	0	1
		Kendari	31	122°36'00"E	3°52'21"S	2	0	2
		Tanjung Nipa	32	122°40'54"E	3°55'38"S	1	0	1
E. spelaea glandifera	Bali	Gilimanuk	33	114°26'00"E	8°11'00"S	1	0	1
		Klampok	34	114°30'00"E	8°13'44"S	2	2	4
		Jimbaran	35	115°10'00"E	8°46'00"S	1	1	2
		Candi Dasa	36	115°35'00"E	8°31'00"S	1	0	1
E. spelaea glandifera	Lombok	Pelangan	37	115°56'00"E	8°48'00"S	7	0	7
		Kuta	38	116°17'00"E	8°55'00"S	15	11	26
		Suranadi	39	116°14'00"E	8°33'30"S	5	8	13
		Batu Koq	40	116°26'00"E	8°19'30"S	5	10	15
E. spelaea glandifera	Sumbawa	Meranti	41	117°01'15"E	8°33'00"S	3	0	3
		Taliwang	42	116°48'10"E	8°51'15"S	1	0	1
		Belo	43	116°50'00"E	8°52'00"S	2	1	3
		Meraran	44	116°51'00"E	8°41'30"S	1	1	2
		Teluk Santong	45	117°53'30"E	8°43'40"S	2	0	2
		Plampang	46	117°52'15"E	8°55'15"S	3	0	3
		Empang	47	118°05'00"E	8°53'15"S	4	0	4
		Waworada	48	118°49'15"E	8°42'30"S	6	3	9
E. spelaea glandifera	Rinca	Kampung Rinca	49	119°40'00"E	8°39'00"S	1	1	2
E. spelaea glandifera	Sumba	Bondokodi	50	119°08'00"E	9°35'00"S	2	1	3
		Waikelosawah	51	119°29'00"E	9°36'00"S	3	2	5
		Waikabubak	52	119°31'30"E	9°38'00"S	0	2	2
		Umalulu	53	120°34'00"E	9°54'00"S	0	1	1
		Melolo	54	120°38'00"E	9°51'30"S	0	1	1
E. spelaea glandifera	Flores	Labuhan Bajo	55	119°55'00"E	8°33'00"S	4	0	4
		Longko	56	120°30'00"E	8°35'00"S	3	5	8
		Woloaru	57	121°54'00"E	8°42'00"S	1	3	4
		Maumere	58	122°15'00"E	8°37'00"S	1	1	2
		Larantuka	59	122°59'00"E	8°21'00"S	0	3	3
E. spelaea glandifera	Adonara	Horowura	60	123°09'00"E	8°20'00"S	8	7	15
E. spelaea glandifera	Lembata	Belang	61	123°22'00"E	8°26'00"S	2	2	4
		Boto	62	123°23'00"E	8°31'00"S	1	4	5
		Merdeka	63	123°31'00"E	8°22'00"S	2	1	3
		Lamakera	64	123°20'00"E	8°35'00"S	0	1	1
E. spelaea glandifera	Pantar	Bakalang	65	124°18'00"E	8°14'00"S	1	1	2
E. spelaea glandifera	Alor	Apui	66	124°43'00"E	8°15'00"S	2	2	4
E. spelaea glandifera	Timor	Baumata	67	123°43'00"E	10°11'00"S	6	11	17
		Camplong	68	124°00'00"E	9°58'30"S	1	0	1
E. spelaea glandifera	Negros	Mt. Talinis	69	123°11'00"E	9°23'00"N	0	3	3
		Dumaquete	70	123°11'00"E	9°22'00"N	2	0	2
E. spelaea glandifera	Leyte	Inopacan	71	124°47'00"E	10°45'00"N	3	0	3

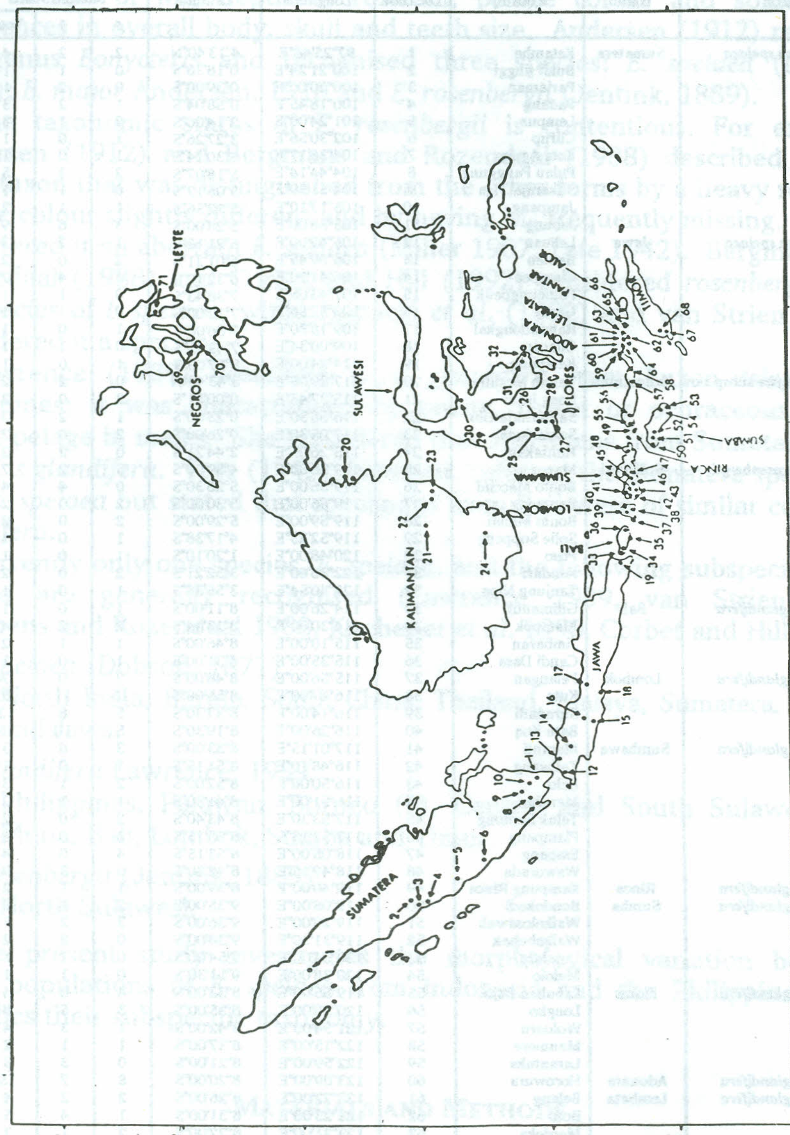


Figure 1. Localities of *Eonycteris spelaea* examined in this study.
For explanation of locality codes see Table 1.

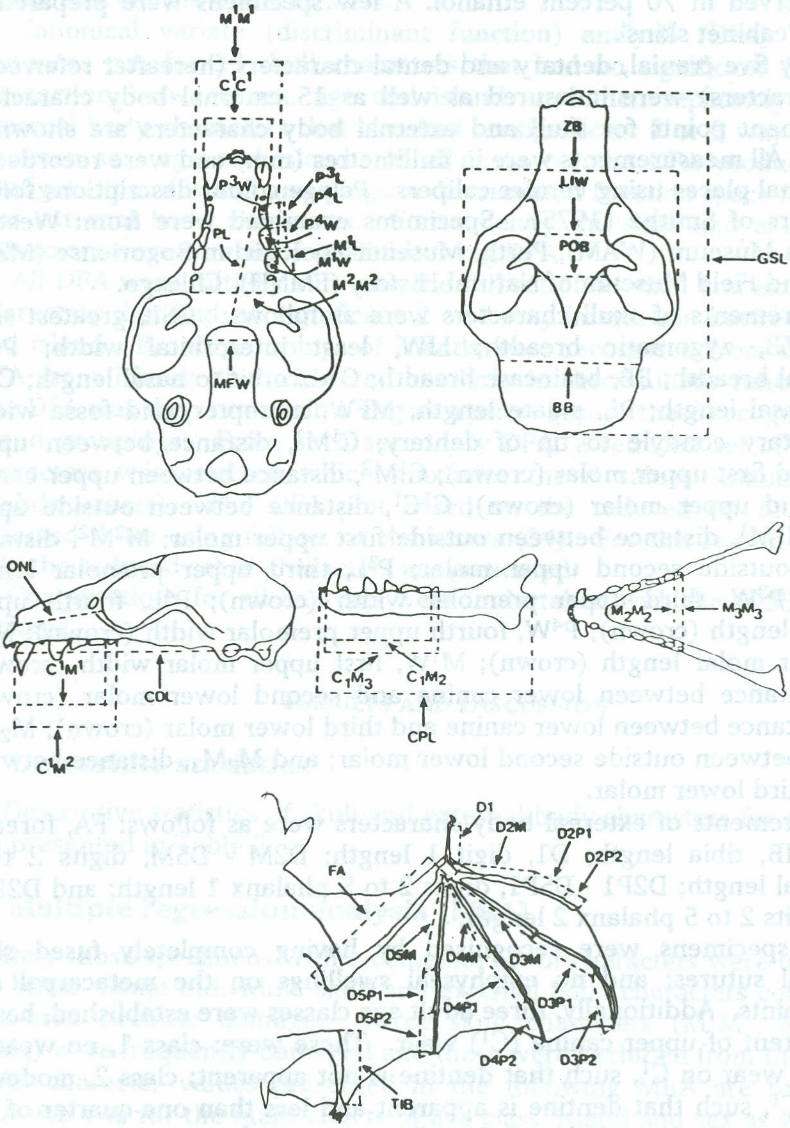


Figure 2. Measurement points for skull and external body characters of *Eonycteris spelaea.* See text for description of measurement codes.

Bats were mainly captured by mist nets, although several specimens were obtained from local people. The specimens were fixed in 10 percent formalin and preserved in 70 percent ethanol. A few specimens were prepared as scientific 'cabinet skins'.

Twenty five cranial, dentary and dental characters (hereafter referred to skull characters) were measured as well as 15 external body characters. Measurement points for skull and external body characters are shown in Figure 2. All measurements were in millimetres (mm) and were recorded to two decimal places using vernier calipers. Pelage colour descriptions follow the colours of Smithe (1975). Specimens examined were from: Western Australian Museum (WAM), Perth; Museum Zoologicum Bogoriense (MZB), Bogor; and Field Museum of Natural History (FMNH), Chicago.

Measurements of skull characters were as follows: GSL, greatest skull length; ZB, zygomatic breadth; LIW, least interorbital width; POB, postorbital breadth; BB, braincase breadth; ONL, orbit to nasal length; CDL, condylobasal length; PL, palate length; MFW, mesopterygoid fossa width; CPL, dentary condyle to tip of dentary; C^1M^1, distance between upper canine and first upper molar (crown); C^1M^2, distance between upper canine and second upper molar (crown); C^1C^1, distance between outside upper canine; M^1M^1, distance between outside first upper molar; M^2M^2, distance between outside second upper molar; P^3L, third upper premolar length (crown); P^3W, third upper premolar width (crown); P^4L, fourth upper premolar length (crown); P^4W, fourth upper premolar width (crown); M^1L, first upper molar length (crown); M^1W, first upper molar width (crown); C_1M_2, distance between lower canine and second lower molar (crown); C_1M_3, distance between lower canine and third lower molar (crown); M_2M_2, distance between outside second lower molar; and M_3M_3, distance between outside third lower molar.

Measurements of external body characters were as follows: FA, forearm length; TIB, tibia length; D1, digit 1 length; D2M - D5M, digits 2 to 5 metacarpal length; D2P1 - D5P1, digits 2 to 5 phalanx 1 length; and D2P2 - D5P2, digits 2 to 5 phalanx 2 length.

Adult specimens were recognised by having completely fused skull basicranial sutures; and no epiphyseal swellings on the metacarpal and phalanx joints. Additionally, three adult age classes were established, based on the extent of upper canine (C^1) wear. These were: class 1, no wear or very little wear on C^1, such that dentine is not apparent; class 2, moderate wear on C^1, such that dentine is apparent and less than one-quarter of the tooth is worn away; and class 3, heavily worn on C^1, with more than one-quarter of tooth worn away.

Variation due to sex, age classes and island, as well as interactions between these factors, were examined by multiple regression analysis (MRA) on each character. Based on these findings, all characters were then scaled to remove the effect of sex and/or age. Each individual's character value was scaled by adding or deducting with the coefficient of regression obtained from the one way MRA.

Canonical variate (discriminant function) analysis (DFA) was in all instances run for 20 skull characters that had no significant 2 or 3 way interaction between sex, age and island; and then separately for all 14 external body characters that also had no significant 2 or 3 way interaction between sex, age and island. In all instances the DFA produced similar configuration of island groupings in discriminant function space for the skull and external body characters. Consequently the skull and external body characters were combined in all following DFA.

All DFA were initially run with the full set of 34 skull and external body characters that had no significant 2 or 3 way interaction between sex, age and island. Broad groupings of islands were recognised from these initial DFA from islands that clustered similarly in discriminant function space. The DFA was then run again using as a *priori* groups these recognised broad island groupings. From such secondary DFA, a reduced set of five to six characters was selected which maximize the F values (minimize Wilks' lambda values). The DFA plot based on the reduced set of characters reflected those using full set of characters (34). For this reason DFA using only the reduced set of characters are presented.

Computations for all analyses were undertaken with the SPSS statistical package.

RESULTS AND DISCUSSION

1. Univariate statistics

Descriptive statistics of skull and external body characters for each taxon are presented in Table 2.

2. Multiple regression analysis (MRA).

Only those specimens with a complete set of characters were included in the MRA. Some individual skull and external body characters could not be measured because damage. Three skull characters (M^1M^1, M^2M^2 and M_3M_3) were frequently damaged and these were excluded from the MRA.

All character values presented in the following MRA are raw values. MRA was run for the main effects of age class, island and sex as well as the interaction between these factors.' The results are presented in Table 3. Because of a large number of characters examined (37), weakly significant ($0.01<p<0.05$) might be expected to have occured by chance alone. As a consequence, only associations with $p<0.01$ were considered significant in the following analyses.

Table 2. Raw data of skull and external body measurements (mm) for *Eonycteris spelaea* males and females combined, followed in brackets by adjusted values for each taxon.
$\overline{X}$ = mean; SD = standard deviation; MIN = minimum; MAX= maximum and N = sample size.

Taxon		Character							
		BB	C^1C^1	C^1M^1	C_1M_2	C^1M^2	C_1M_3	CDL	CPL
Eonycteris spelaea spelaea	$\overline{X}$	14.52 (14.54)	7.27 (7.37)	10.44 (10.47)	12.21 (12.27)	11.67 (11.71)	13.27 (13.34)	29.17 (29.32)	25.90 (26.00)
	SD	0.37 (0.36)	0.33 (0.23)	0.38 (0.35)	0.51 (0.40)	0.40 (0.35)	0.60 (0.45)	0.89 (0.74)	0.81 (0.71)
	MIN	13.65 (13.64)	6.63 (6.92)	9.63 (9.75)	11.14 (11.45)	10.86 (11.01)	11.99 (12.33)	27.55 (28.01)	24.18 (24.56)
	MAX	15.25 (15.15)	7.87 (7.77)	11.26 (11.18)	13.31 (13.15)	12.57 (12.51)	14.41 (14.11)	31.20 (30.85)	27.45 (27.48)
	N	48	44	45	46	45	42	48	48
Eonycteris spelaea glandifera	$\overline{X}$	14.80 (14.80)	7.45 (7.48)	10.93 (10.94)	12.88 (12.91)	12.25 (12.26)	14.04 (14.06)	30.77 (30.82)	27.35 (27.38)
	SD	0.43 (0.42)	0.43 (0.32)	0.38 (0.37)	0.50 (0.45)	0.43 (0.41)	0.55 (0.50)	0.96 (0.87)	0.89 (0.83)
	MIN	13.79 (13.78)	6.56 (6.75)	10.10 (10.15)	11.78 (11.67)	11.25 (11.36)	12.94 (12.74)	28.56 (28.41)	25.18 (25.50)
	MAX	16.04 (15.94)	8.61 (8.45)	12.09 (11.99)	14.49 (14.29)	13.58 (13.46)	15.61 (15.37)	33.40 (33.05)	30.04 (29.75)
	N	187	181	174	185	177	178	180	188
Eonycteris spelaea rosenbergii	$\overline{X}$	14.80 (14.76)	7.33 (7.27)	10.97 (10.94)	12.90 (12.85)	12.23 (12.20)	14.00 (13.93)	30.60 (30.51)	27.31 (27.23)
	SD	0.36 (0.36)	0.40 (0.31)	0.33 (0.30)	0.46 (0.38)	0.39 (0.34)	0.52 (0.42)	0.77 (0.74)	0.63 (0.59)
	MIN	13.74 (13.86)	6.63 (6.52)	10.35 (10.47)	11.97 (12.24)	11.56 (11.63)	13.01 (13.01)	29.32 (29.17)	26.31 (26.19)
	MAX	15.49 (15.61)	8.11 (7.87)	11.46 (11.58)	13.80 (13.60)	12.73 (12.88)	14.91 (14.67)	31.89 (31.79)	28.38 (28.32)
	N	20	20	20	20	20	20	20	20
Eonycteris spelaea winnyae subsp.nov	$\overline{X}$	14.38 (14.40)	6.98 (7.05)	9.62 (9.64)	11.34 (11.39)	10.80 (10.84)	12.27 (12.31)	27.18 (27.34)	24.25 (24.33)
	SD	0.38 (0.34)	0.36 (0.22)	0.41 (0.36)	0.51 (0.37)	0.44 (0.38)	0.62 (0.42)	0.88 (0.59)	0.75 (0.44)
	MIN	13.74 (13.63)	6.59 (6.76)	9.05 (9.19)	10.50 (10.78)	10.13 (10.28)	11.23 (11.57)	26.01 (26.50)	23.14 (23.60)
	MAX	14.81 (14.71)	7.74 (7.50)	10.43 (10.33)	12.06 (11.90)	11.57 (11.45)	13.16 (12.92)	28.41 (28.06)	25.21 (24.92)
	N	11	11	11	11	11	11	10	11

Table 2. Continued

Taxon		Character							
		GSL	LIW	M^1L	M^1M^1	M^1W	M_2M_2	M^2M^2	M_3M_3
Eonycteris spelaea spelaea	$\overline{X}$	34.31 (34.53)	6.61 (6.72)	2.26 (2.23)	9.01 (9.08)	1.18 (1.18)	8.71 (8.71)	8.64 (8.70)	8.82 (8.83)
	SD	0.96 (0.76)	0.33 (0.28)	0.14 (0.14)	0.31 (0.30)	0.06 (0.06)	0.29 (0.29)	0.31 (0.30)	0.25 (0.25)
	MIN	32.73 (33.22)	5.75 (5.97)	2.04 (2.03)	8.46 (8.57)	1.01 (1.01)	8.22 (8.23)	8.00 (7.99)	8.42 (8.39)
	MAX	36.83 (36.38)	7.31 (7.30)	2.60 (2.59)	9.56 (9.59)	1.32 (1.32)	9.29 (9.30)	9.18 (9.30)	9.45 (9.37)
	N	44	46	45	39	45	40	38	36
Eonycteris spelaea glandifera	$\overline{X}$	36.29 (36.36)	6.98 (7.05)	2.34 (2.31)	9.17 (9.24)	1.25 (1.25)	8.92 (8.93)	8.83 (8.88)	9.05 (9.07)
	SD	1.17 (1.03)	0.36 (0.33)	0.15 (0.14)	0.35 (0.34)	0.08 (0.08)	0.34 (0.34)	0.37 (0.36)	0.32 (0.32)
	MIN	33.45 (33.51)	6.13 (5.94)	1.93 (1.95)	8.28 (8.41)	1.06 (1.06)	8.09 (8.10)	7.88 (7.98)	8.14 (8.17)
	MAX	39.87 (39.42)	8.11 (8.06)	2.77 (2.76)	9.89 (10.01)	1.51 (1.51)	9.65 (9.68)	9.77 (9.76)	9.73 (9.78)
	N	182	188	176	167	176	179	172	163
Eonycteris spelaea rosenbergii	$\overline{X}$	35.99 (35.88)	7.10 (7.14)	2.35 (2.30)	8.96 (9.02)	1.32 (1.31)	8.63 (8.64)	8.53 (8.56)	8.75 (8.78)
	SD	0.79 (0.77)	0.33 (0.33)	0.12 (0.11)	0.20 (0.21)	0.10 (0.10)	0.27 (0.28)	0.21 (0.23)	0.26 (0.27)
	MIN	34.30 (34.79)	6.25 (6.47)	2.11 (2.10)	8.66 (8.68)	1.16 (1.16)	8.26 (8.27)	8.22 (8.21)	8.35 (8.37)
	MAX	37.19 (37.54)	7.67 (7.62)	2.54 (2.48)	9.39 (9.41)	1.51 (1.51)	9.12 (9.13)	9.14 (9.13)	9.29 (9.32)
	N	20	20	19	19	19	20	19	20
Eonycteris spelaea winnyae subsp.nov	$\overline{X}$	32.05 (32.28)	6.65 (6.73)	2.04 (2.02)	8.59 (8.66)	1.04 (1.04)	8.30 (8.30)	8.29 (8.33)	8.40 (8.40)
	SD	0.96 (0.62)	0.32 (0.27)	0.19 (0.18)	0.31 (0.29)	0.10 (0.10)	0.32 (0.30)	0.35 (0.34)	0.30 (0.27)
	MIN	30.59 (31.17)	6.13 (6.40)	1.81 (1.80)	8.12 (8.26)	0.85 (0.85)	7.78 (7.83)	7.85 (7.84)	7.80 (7.87)
	MAX	33.43 (32.98)	7.15 (7.16)	2.45 (2.38)	9.05 (9.17)	1.20 (1.20)	8.81 (8.78)	8.79 (8.77)	8.82 (8.74)
	N	10	11	11	10	11	11	11	10

Table 2. Continued

Taxon		Character							
		MFW	ONL	P^3L	P^3W	P^4L	P^4W	PL	POB
Eonycteris spelaea spelaea	$\overline{X}$	4.54 (4.54)	10.86 (10.96)	1.91 (1.90)	0.86 (0.87)	2.01 (2.00)	1.20 (1.20)	16.32 (16.34)	7.69 (7.62)
	SD	0.17 (0.18)	0.52 (0.46)	0.14 (0.12)	0.05 (0.05)	0.12 (0.12)	0.06 (0.06)	0.51 (0.46)	0.41 (0.39)
	MIN	4.16 (4.16)	9.70 (10.00)	1.62 (1.65)	0.77 (0.77)	1.76 (1.76)	1.08 (1.08)	15.19 (15.34)	6.80 (6.97)
	MAX	4.92 (4.92)	12.19 (12.00)	2.25 (2.19)	1.04 (1.04)	2.26 (2.26)	1.32 (1.32)	17.37 (17.21)	8.35 (8.52)
	N	47	45	48	48	47	47	48	48
Eonycteris spelaea glandifera	$\overline{X}$	4.59 (4.59)	11.74 (11.79)	2.00 (1.98)	0.93 (0.94)	2.12 (2.11)	1.26 (1.26)	17.29 (17.27)	7.77 (7.76)
	SD	0.22 (0.22)	0.56 (0.51)	0.12 (0.11)	0.06 (0.06)	0.12 (0.12)	0.07 (0.07)	0.56 (0.55)	0.55 (0.51)
	MIN	3.96 (3.97)	10.06 (10.43)	1.71 (1.73)	0.79 (0.79)	1.84 (1.81)	1.07 (1.07)	15.70 (15.74)	6.06 (6.40)
	MAX	5.20 (5.20)	13.37 (13.18)	2.30 (2.25)	1.06 (1.08)	2.45 (2.43)	1.46 (1.46)	18.88 (18.72)	9.13 (8.98)
	N	188	186	185	185	184	184	185	188
Eonycteris spelaea rosenbergii	$\overline{X}$	4.45 (4.46)	11.88 (11.85)	2.11 (2.07)	0.99 (1.00)	2.17 (2.15)	1.39 (1.39)	17.02 (16.95)	7.97 (8.04)
	SD	0.18 (0.18)	0.42 (0.33)	0.12 (0.11)	0.07 (0.07)	0.11 (0.11)	0.08 (0.08)	0.57 (0.53)	0.57 (0.53)
	MIN	4.15 (4.15)	11.06 (11.25)	1.82 (1.84)	0.88 (0.88)	1.90 (1.89)	1.23 (1.23)	15.83 (15.97)	6.98 (7.15)
	MAX	4.79 (4.79)	12.54 (12.42)	2.29 (2.23)	1.12 (1.12)	2.32 (2.29)	1.53 (1.53)	17.80 (17.81)	8.81 (8.76)
	N	20	20	20	20	20	20	20	20
Eonycteris spelaea winnyae subsp.nov	$\overline{X}$	4.45 (4.45)	10.12 (10.20)	1.79 (1.78)	0.83 (0.83)	1.84 (1.83)	1.09 (1.09)	15.27 (15.29)	8.08 (8.02)
	SD	0.24 (0.25)	0.47 (0.28)	0.10 (0.10)	0.04 (0.05)	0.11 (0.11)	0.07 (0.07)	0.37 (0.31)	0.39 (0.42)
	MIN	4.15 (4.16)	9.32 (9.62)	1.64 (1.59)	0.73 (0.73)	1.68 (1.68)	0.97 (0.97)	14.74 (14.76)	7.38 (7.33)
	MAX	4.87 (4.88)	10.64 (10.46)	1.94 (1.92)	0.88 (0.90)	1.97 (1.96)	1.23 (1.23)	15.83 (15.67)	8.72 (8.57)
	N	10	11	11	11	11	11	11	11

Table 2. Continued

Taxon		Character							
		ZB	D1	D2M	D2P1	D2P2	D3M	D3P1	D3P2
Eonycteris spelaea spelaea	$\bar{X}$	20.31 (20.53)	17.83 (18.05)	31.61 (31.92)	8.83 (8.89)	6.63 (6.79)	47.27 (47.64)	30.03 (30.24)	37.96 (38.55)
	SD	1.40 (0.80)	0.99 (0.93)	1.32 (1.23)	0.50 (0.50)	0.42 (0.42)	1.37 (1.35)	1.23 (1.15)	2.13 (2.00)
	MIN	18.29 (18.69)	16.18 (16.62)	29.30 (29.82)	7.93 (7.89)	5.97 (6.03)	44.78 (45.25)	27.77 (28.15)	33.71 (34.81)
	MAX	23.35 (22.22)	20.49 (20.43)	35.34 (35.22)	9.98 (9.94)	7.50 (7.70)	51.41 (51.23)	32.82 (32.94)	42.90 (42.94)
	N	45	47	48	48	48	48	48	48
Eonycteris spelaea glandifera	$\bar{X}$	21.16 (21.06)	20.64 (20.77)	33.34 (33.56)	9.45 (9.49)	7.59 (7.73)	49.79 (50.02)	32.00 (32.12)	41.57 (42.02)
	SD	1.38 (0.90)	1.03 (0.99)	1.55 (1.51)	0.53 (0.53)	0.60 (0.58)	1.87 (1.81)	1.34 (1.31)	2.24 (2.19)
	MIN	18.61 (18.52)	17.28 (17.73)	29.91 (30.70)	8.07 (8.13)	6.28 (6.40)	43.88 (45.00)	28.09 (28.79)	35.90 (36.77)
	MAX	24.21 (23.08)	23.81 (23.68)	38.38 (38.26)	10.86 (10.90)	9.55 (9.62)	54.66 (55.13)	35.27 (35.22)	47.77 (47.81)
	N	176	186	188	188	188	188	187	188
Eonycteris spelaea rosenbergii	$\bar{X}$	21.49 (21.02)	21.12 (21.17)	33.25 (33.35)	9.55 (9.56)	7.49 (7.61)	51.02 (51.10)	32.58 (32.58)	43.03 (43.36)
	SD	1.11 (0.74)	1.52 (1.53)	1.50 (1.48)	0.60 (0.59)	0.61 (0.60)	1.75 (1.63)	1.16 (1.17)	1.98 (1.89)
	MIN	19.75 (19.49)	19.04 (18.98)	30.64 (30.79)	8.47 (8.43)	6.37 (6.50)	47.49 (47.96)	29.60 (29.72)	39.62 (40.01)
	MAX	23.47 (22.34)	23.80 (23.67)	35.87 (36.37)	10.68 (10.64)	8.62 (8.68)	54.09 (53.91)	34.59 (34.51)	47.11 (47.15)
	N	20	20	20	20	20	20	20	20
Eonycteris spelaea winnyae subsp.nov	$\bar{X}$	19.27 (19.54)	17.25 (17.41)	29.50 (29.75)	8.15 (8.20)	6.55 (6.68)	44.57 (44.88)	28.60 (28.78)	36.05 (36.51)
	SD	1.14 (0.57)	1.25 (1.08)	1.42 (1.16)	0.71 (0.64)	0.51 (0.42)	1.47 (1.08)	0.98 (0.66)	1.60 (1.40)
	MIN	18.09 (18.79)	15.33 (15.78)	27.21 (27.73)	7.20 (7.31)	5.83 (6.07)	42.26 (43.38)	27.37 (27.84)	33.61 (33.65)
	MAX	21.06 (20.50)	18.97 (18.91)	31.57 (31.72)	9.06 (9.08)	7.26 (7.37)	46.21 (46.52)	29.91 (29.70)	38.71 (37.98)
	N	9	11	11	11	11	11	11	11

Table 2. Continued

Taxon		Character							
		D4M	D4P1	D4P2	D5M	D5P1	D5P2	FA	TIB
Eonycteris spelaea spelaea	$\overline{X}$	46.45 (46.88)	24.90 (25.20)	23.10 (23.61)	43.05 (43.50)	19.77 (19.94)	17.54 (17.80)	69.25 (69.86)	30.32 (30.66)
	SD	1.33 (1.23)	0.96 (0.91)	1.36 (1.28)	1.46 (1.36)	0.89 (0.86)	1.14 (1.09)	2.54 (2.34)	1.65 (1.58)
	MIN	44.16 (44.83)	23.25 (23.66)	20.65 (21.40)	40.03 (40.83)	17.39 (17.69)	14.73 (15.15)	64.31 (65.43)	27.84 (27.77)
	MAX	49.62 (49.77)	26.85 (26.80)	26.36 (26.48)	46.99 (46.80)	21.90 (21.76)	20.23 (20.12)	75.82 (75.45)	34.46 (33.85)
	N	48	48	48	48	48	48	48	48
Eonycteris spelaea glandifera	$\overline{X}$	49.15 (49.44)	26.65 (26.87)	25.58 (25.99)	45.54 (45.85)	21.26 (21.36)	19.71 (19.88)	73.50 (73.90)	33.31 (33.45)
	SD	1.86 (1.81)	1.25 (1.21)	1.41 (1.33)	1.87 (1.79)	1.11 (1.08)	1.15 (1.11)	2.74 (2.62)	1.78 (1.59)
	MIN	43.75 (44.35)	23.93 (24.35)	21.65 (22.40)	40.51 (41.66)	19.12 (19.21)	16.93 (17.12)	65.35 (67.04)	28.37 (28.85)
	MAX	53.78 (53.82)	29.93 (29.88)	30.52 (30.64)	50.27 (50.66)	24.90 (24.76)	22.95 (22.84)	81.25 (82.37)	37.44 (36.75)
	N	188	188	188	188	188	188	188	187
Eonycteris spelaea rosenbergii	$\overline{X}$	49.87 (50.02)	26.97 (27.10)	25.33 (25.66)	45.81 (45.96)	21.19 (21.21)	20.02 (20.10)	74.43 (74.57)	33.33 (33.18)
	SD	1.79 (1.70)	1.13 (1.07)	1.30 (1.38)	1.63 (1.57)	0.77 (0.75)	0.97 (0.97)	2.59 (2.56)	1.97 (1.92)
	MIN	46.37 (46.67)	23.97 (24.28)	22.32 (22.67)	42.43 (42.59)	19.77 (19.86)	17.81 (18.23)	70.20 (70.40)	28.97 (29.11)
	MAX	53.39 (53.25)	29.36 (29.31)	27.41 (28.16)	49.23 (49.04)	23.40 (23.26)	21.86 (22.28)	80.90 (80.53)	37.66 (37.05)
	N	20	20	20	20	20	20	20	20
Eonycteris spelaea winnyae subsp.nov	$\overline{X}$	43.65 (44.00)	23.29 (23.54)	21.62 (22.03)	40.04 (40.40)	18.14 (18.28)	16.00 (16.22)	65.46 (65.96)	28.16 (28.45)
	SD	1.62 (1.21)	0.90 (0.55)	1.01 (0.73)	1.77 (1.31)	0.73 (0.54)	1.23 (1.00)	2.52 (1.83)	1.97 (1.41)
	MIN	41.32 (42.43)	22.04 (22.80)	20.40 (21.15)	36.95 (38.10)	16.73 (17.03)	14.26 (14.69)	61.44 (62.56)	25.17 (25.87)
	MAX	45.74 (45.91)	25.03 (24.55)	23.65 (23.29)	42.44 (42.60)	18.88 (18.92)	17.79 (17.47)	69.06 (68.59)	30.81 (30.20)
	N	11	11	11	11	11	11	11	11

Table 3. Multiple regression of skull and external body characters (raw data) of *Eonycteris spelaea* by adult age class, island and sex.

Character	Age	Island	Sex	Age, Island	Age, Sex	Island, Sex	Age, Island, Sex
Skull							
BB	0.09	7.96 ***	35.54 ***	1.27	0.24	0.91	0.81
C^1C^1	4.76 **	10.76 ***	305.92 ***	0.66	3.36	0.86	1.29
C^1M^1	0.66	17.67 ***	29.16 ***	1.14	0.02	1.54	0.62
C_1M_2	0.16	19.67 ***	117.57 ***	1:16	0.83	2.09 *	0.28
C^1M^2	1.41	21.07 ***	44.17 ***	1.27	0.35	1.60	0.81
C_1M_3	0.03	19.85 ***	124.32 ***	1.42	1.05	2.53 **	0.52
CDL	3.47 *	35.19 ***	117.25 ***	1.49	2.66	1.40	1.81
CPL	1.15	36.11 ***	97.00 ***	1.40	1.76	0.99	1.40
GSL	6.53 **	34.47 ***	137.39 ***	1.60	6.57 *	1.73 *	1.26
LIW	3.80 *	5.85 ***	60.34 ***	0.61	1.73	0.66	1.39
M^1L	2.20	5.69 ***	12.92 ***	1.45	2.17	0.86	1.31
M^1W	0.04	11.04 ***	2.23	0.47	0.06	1.13	0.50
M_2M_2	1.57	9.17 ***	6.80 *	1.07	0.87	0.94	0.20
MFW	0.00	1.62	0.07	1.05	3.28	0.96	0.95
ONL	1.95	21.71 ***	100.79 ***	1.16	3.45	1.02	1.83
P^3L	0.63	7.00 ***	41.69 ***	1.08	1.35	1.16	1.14
P^3W	1.13	11.65 ***	10.27 **	0.49	0.65	0.95	0.44
P^4L	1.52	7.10 ***	2.04	0.85	1.67	0.86	1.07
P^4W	0.33	16.17 ***	2.37	0.96	0.32	1.04	0.27
PL	0.57	25.27 ***	37.11 ***	1.79 *	1.87	1.05	1.08
POB	12.59 ***	2.25 **	10.87 **	0.72	2.27	0.79	0.68
ZB	17.93 ***	7.06 ***	385.91 ***	0.96	29.97 ***	0.77	1.45
External Body							
D1	1.20	40.91 ***	40.38 ***	1.16	0.01	1.03	0.55
D2M	3.84	17.10 ***	23.19 ***	1.67	0.38	0.67	0.81
D2P1	0.98	12.72 ***	6.85 **	0.72	2.72	0.91	1.28
D2P2	5.10 **	17.33 ***	15.63 ***	1.15	0.35	1.53	0.90
D3M	8.30 ***	23.82 ***	19.41 ***	2.38 **	0.16	1.31	0.56
D3P1	3.73 *	22.46 ***	27.65 ***	1.36	0.13	0.71	0.96
D3P2	5.12 **	28.26 ***	23.99 ***	1.43	0.89	1.05	0.25
D4M	6.12 **	27.24 ***	28.71 ***	2.08 *	0.49	1.49	0.40
D4P1	8.01 ***	26.60 ***	26.82 ***	1.58	0.17	1.03	0.65
D4P2	9.41 ***	30.23 ***	32.31 ***	1.21	0.44	1.31	0.51
D5M	5.34 **	24.46 ***	37.66 ***	1.76 *	0.52	1.58	0.84
D5P1	3.38 *	25.09 ***	25.80 ***	1.67	0.01	0.64	0.95
D5P2	6.62 **	34.82 ***	34.87 ***	1.30	0.42	0.97	0.20
FA	4.16 *	24.32 ***	41.74 ***	1.47	0.60	0.98	0.78
TIB	8.27 ***	23.85 ***	69.69 ***	1.54	0.72	0.92	1.12

Remarks : Significance of F values are as follows: * = $p<0.05$, ** = $p<0.01$ and *** = $p<0.001$.

2.1. Age classes.

From Table 3, only four of 22 skull characters (C^1C^1, GSL, POB and ZB) were significantly associated with the age classes, ZB also had a significant interaction with both age and sex. This significant interaction of ZB related to the fact that in age class 1, the average values for both male and female were close (♂ 20.74, ♀ 19.72); whereas in age class 2 and 3, the differences were greater (♂ 22.22, ♀ 19.88; and ♂ 22.46, ♀ 20.24).

Nine of 15 external body characters (D2P2, D3M, D3P2, D4M, D4P1, D4P2, D5M, D5P2 and TIB) were significantly influenced by the adult age classes (Table 3). Among these characters, D3M also had an interaction with both age class and island. This interaction resulted from the average values of D3M age class 3 in Sumatera being smaller than those of age class 1 and 2 (46.14 *v.* 47.20 and 47.07); age class 3 averages were smaller than those of age class 2 in Flores (49.00 *v.* 49.35); Adonara (49.00 *v.* 49.86)and Timor (52.25 *v.* 52.39); and in Bali and Sumba where age class 1 averages were greater than those of class 2 (48.88 *v.* 47.28 and 52.53 *v.* 51.67, respectively). The remaining ten islands had D3M values that averaged larger in sequence according to the age classes, with age class 3 always the greatest.

2.2. Island.

All skull and external body characters, except MFW, differed significantly, most of them at $p<0.001$ (Table 3). This indicated that the differences in morphology between these islands were considerable.

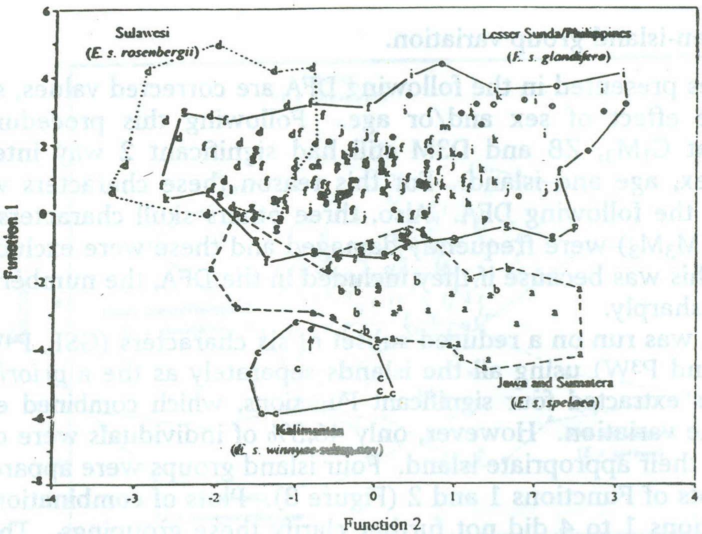
Among these characters, only C_1M_3 had an interaction with both island and sex. This related to the fact that in all islands males averaged larger than females, except for Philippines where females averaged larger than males (14.09 *v.* 13.19).

2.3. Sex.

Seventeen of the 22 skull characters were significantly associated with sex, many at the 0.1% level of significance (Table 3). All external body characters were similarly significantly associated ($p<0.01$) with sex. These results indicated that most characters were sexually dimorphic in both skull and external body characters.

3. Canonical variate (discriminant function) analysis (DFA).

Only those specimens with a complete set of characters were included in the DFA.



Remarks : (a) Sumatera, (b) Jawa, (c) Kalimantan, (d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 3. Plot of cannical variate (discriminant) Functions 1 and 2 based on six selected characters for all islands.

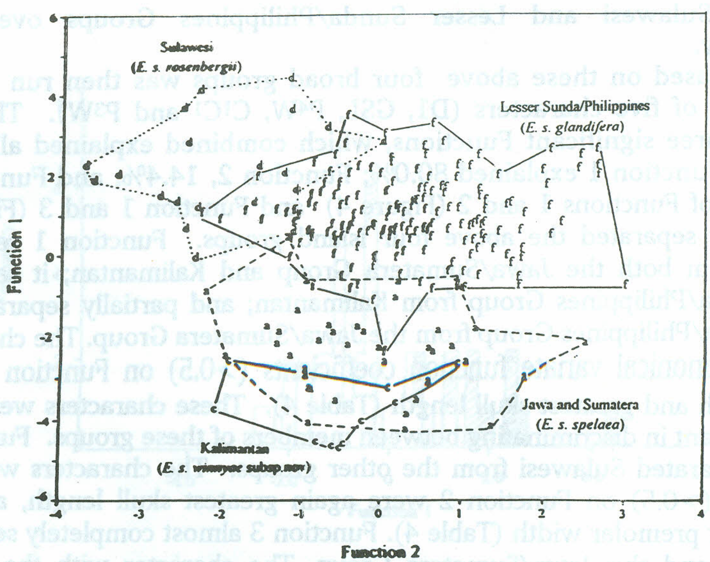


Figure 4. Plot of cannical variate (discriminant) Functions 1 and 2 based on five selected characters for four islands.
(Jawa and Sumatera, Lesser Sunda/Philippines, Sulawesi and Kalimantan)

3.1. Between-island group variation.

All values presented in the following DFA are corrected values, scaled to remove the effect of sex and/or age. Following this procedure, MRA showed that C_1M_3, ZB and D3M still had significant 2 way interactions involving sex, age and island. For this reason these characters were not included in the following DFA. Also, three others skull characters (M^1M^1, M^2M^2 and M_3M_3) were frequently damaged and these were excluded from the DFA. This was because if they included in the DFA, the number of cases will reduce sharply.

The DFA was run on a reduced subset of six characters (GSL, P^4W, C^1C^1, D1, D2P1 and P^3W) using all the islands separately as the a *priori* groups. This analysis extracted four significant Functions, which combined explained 96.1% of the variation. However, only 46.3% of individuals were classified correctly to their appropriate island. Four island groups were apparent from the DFA plots of Functions 1 and 2 (Figure 3). Plots of combinations of the other Functions 1 to 4 did not further clarify these groupings. These four groups were as follows:

1. Jawa/Sumatera Group
2. Lesser Sunda/Philippines Group
3. Sulawesi Group
4. Kalimantan Group.

Only the Sulawesi and Lesser Sunda/Philippines Groups overlapped substantially.

A DFA based on these above four broad groups was then run using a reduced set of five characters (D1, GSL, P^4W, C^1C^1 and P^3W). This DFA extracted three significant Functions, which combined explained all of the variation. Function 1 explained 80.0%; Function 2, 14.4%; and Function 3, 5.6%. Plots of Functions 1 and 2 (Figure 4) and Function 1 and 3 (Figure 5) most clearly separated the above four island groups. Function 1 separated Sulawesi from both the Jawa/Sumatera Group and Kalimantan; it separated Lesser Sunda/Philippines Group from Kalimantan; and partially separated the Lesser Sunda/Philippines Group from the Jawa/Sumatera Group. The characters with high canonical variate function coefficients (>0.5) on Function 1 were digit 1 length and greatest skull length (Table 4). These characters were likely to be important in discriminating between members of these groups. Function 2 partially separated Sulawesi from the other groups. The characters with high coefficients (>0.5) on Function 2 were again greatest skull length, and also fourth upper premolar width (Table 4). Function 3 almost completely separated Kalimantan and the Jawa/Sumatera Group. The character with the highest coefficient on Function 3 was greatest skull length (Table 4). Greatest skull length, which represented overall skull size, was clearly an important character to discriminate between members of all four broad island groups.

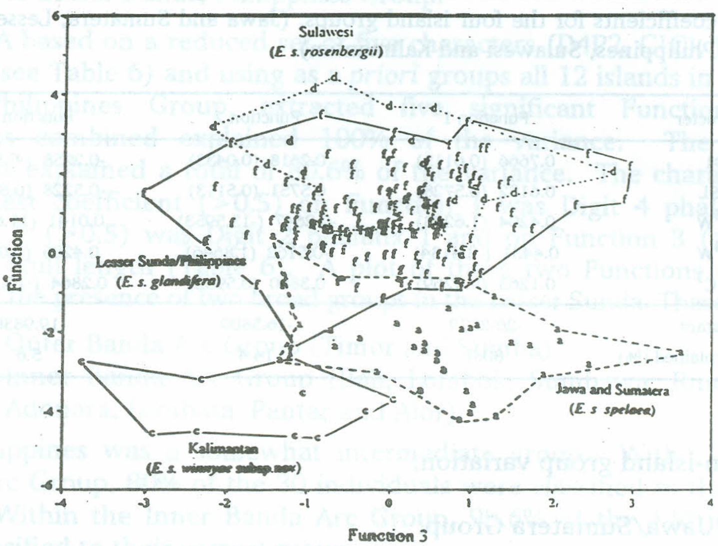
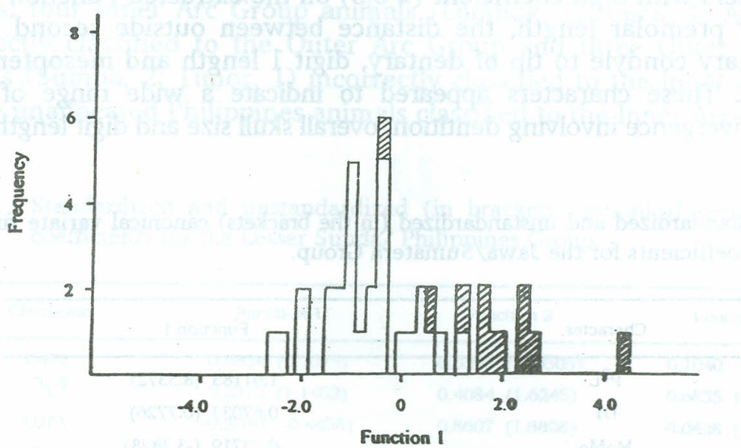


Figure 5. Plot of cannical variate (discriminant) Functions 1 and 3 based on five selected characters for the same four island groups listed in Figure 4.



Remarks : Sumatera, ☐ ; and Jawa, ▨ .

Figure 6. Frequency histogram of Function 1 based on five selected characters for the Jawa/Sumatera groups.

Table 4. Standardized and unstandardized (in brackets) canonical variate function coefficients for the four island groups. (Jawa and Sumatera, Lesser Sunda/ Philippines, Sulawesi and Kalimantan).

Character	Function 1	Function 2	Function 3
D1	0.7666 (0.6115)	0.2618 (0.0433)	-0.2258 (-0.8673)
GSL	0.6182 (0.5728)	0.5751 (0.5113)	0.5228 (0.8987)
P^3W	0.4204 (1.6288)	-0.2647 (-13.5953)	0.0141 (11.6178)
P^4W	0.4431 (-2.4134)	-0.5162 (1.8646)	0.4285 (0.0412)
C^1C^1	0.1263 (9.9269)	0.3880 (0.5962)	0.2864 (-10.2708)
Constant	-26.2579	-16.5809	-19.9830
Variation explained (%)	80.0	14.4	5.6

3.2. Within-island group variation.

3.2.1. The Jawa/Sumatera Group.

A DFA was run based on a reduced set of five characters (Table 5) and using as a *priori* group the two islands of Jawa and Sumatera. This analysis extracted a very significant Function. Of the cases, 92.3% of individuals classified correctly to their appropriate island (Figure 6). This indicated a substantial degree of morphological differentiation between these islands. The characters with high coefficient (>0.5) on the extracted Function were: third upper premolar length, the distance between outside second lower molar, dentary condyle to tip of dentary, digit 1 length and mesopterygoid fossa width. These characters appeared to indicate a wide range of morphological divergence involving dentition, overall skull size and digit length.

Table 5. Standardized and unstandardized (in the brackets) canonical variate function coefficients for the Jawa/Sumatera Group.

Character	Function 1
P^3L	1.01183 (8.5372)
D1	0.67033 (0.7726)
M_2M_2	-0.93719 (-3.3828)
MFW	-0.61903 (-3.7280)
CPL	0.76565 (1.2174)
Constant	-15.5954
Variation explained (%)	100

3.2.2. The Lesser Sunda/Philippines Group.

A DFA based on a reduced set of five characters (D4P2, C^1C^1, D2P1, GSL and BB, see Table 6) and using as a *priori* groups all 12 islands in the Lesser Sunda/Philippines Group, extracted five significant Functions. These Functions combined explained 100% of the variance. The first two Functions explained a total of 80.6% of the variance. The characters with the highest coefficient (>0.5) on Function 1 was Digit 4 phalanx 2, on Function 2 (>0.5) was Digit 2 phalanx 1 and on Function 3 (>0.5) was greatest skull length (Table 6). A plot of these two Functions (Figure 7) indicated the presence of two broad groups in the Lesser Sunda. These were:

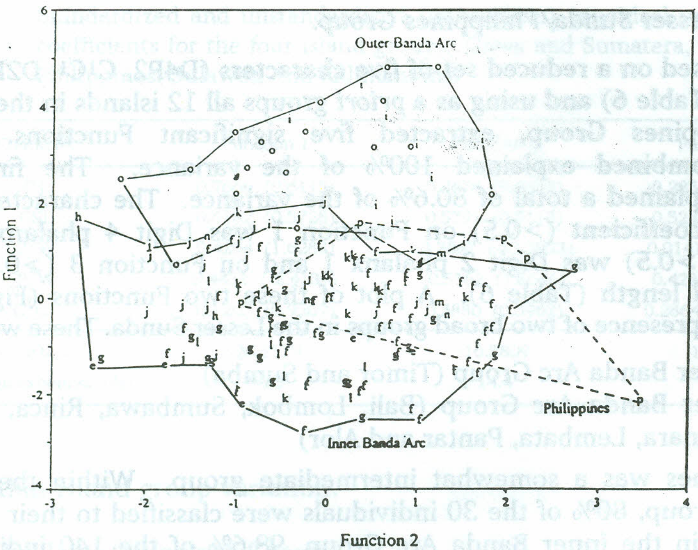
1. Outer Banda Arc Group (Timor and Sumba)
2. Inner Banda Arc Group (Bali, Lombok, Sumbawa, Rinca, Flores, Adonara, Lembata, Pantar and Alor)

The Philippines was a somewhat intermediate group. Within the Outer Banda Arc Group, 80% of the 30 individuals were classified to their correct group. Within the Inner Banda Arc Group, 98.6% of the 140 individuals were classified to their correct group.

A DFA was then run on a reduced set of five characters (listed in Table 7) using as a *priori* groups the two above island groups: the Outer Banda Arc and the Inner Banda Arc; with Philippines unallocated. This DFA extracted a highly significant Function with 95.7% of individuals classified correctly to their appropriate island arc group (Figure 8). Misclassifications were as follows: four Inner Arc Group animals (Lombok, 1; Rinca, 1; Adonara, 2) incorrectly classified to the Outer Arc Group and three Outer Arc Group animals (Sumba, 2; Timor, 1) incorrectly classified to the Inner Arc Group. All five unallocated Philippines animals classified to the Inner Arc Group.

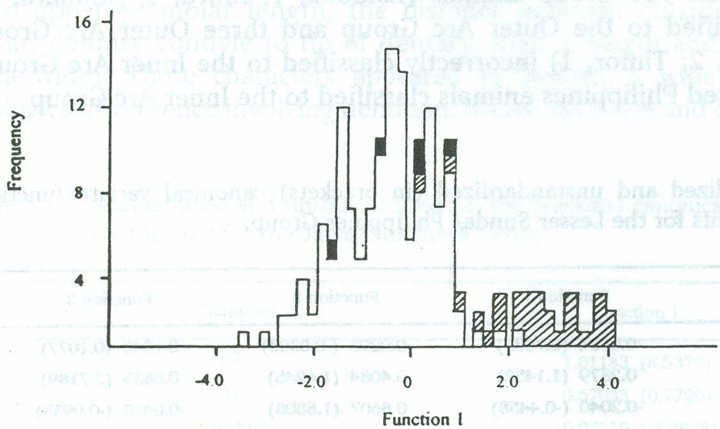
Table 6. Standardized and unstandardized (in brackets) canonical variate function coefficients for the Lesser Sunda/ Philippines Group.

Character	Function 1	Function 2	Function 3
D4P2	0.6834 (0.7075)	-0.0293 (-0.0303)	0.1040 (0.1077)
C^1C^1	0.2879 (1.1452)	0.4084 (1.6245)	0.6835 (2.7189)
D2P1	-0.2040 (-0.4458)	0.8607 (1.8808)	-0.0428 (-0.0935)
GSL	0.2613 (0.3242)	-0.2217 (-0.2750)	1.0639 (1.3198)
BB	0.3483 (0.9909)	-0.4832 (-1.3746)	0.4106 (1.1682)
Constant	-49.1844	1.1135	8.2684
Variation explained (%)	67.6	13.0	8.8



Remarks : (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 7. Plot of cannical variate (discriminant) Functions 1 and 2 based on five selected characters for the Lesser Sunda/Philippines Group.



Remarks : Outer Banda Arc ; Inner Banda Arc ; Philippines

Figure 8. Frequency histogram of Functions 1 based on five selected characters for the Outer and Inner Banda Arc Groups, with Philippines unallocated.

The character with the highest coefficient (>0.5) was digit 4 phalanx 2 length, suggesting that this character was an important discriminant between the Inner and Outer Banda Arc forms. Other important discriminating characters were first upper molar width, mesopterygoid fossa width, braincase breadth and condylobasal length, suggesting that skull characters were also influential in separating the Inner and Outer Banda Arc groups.

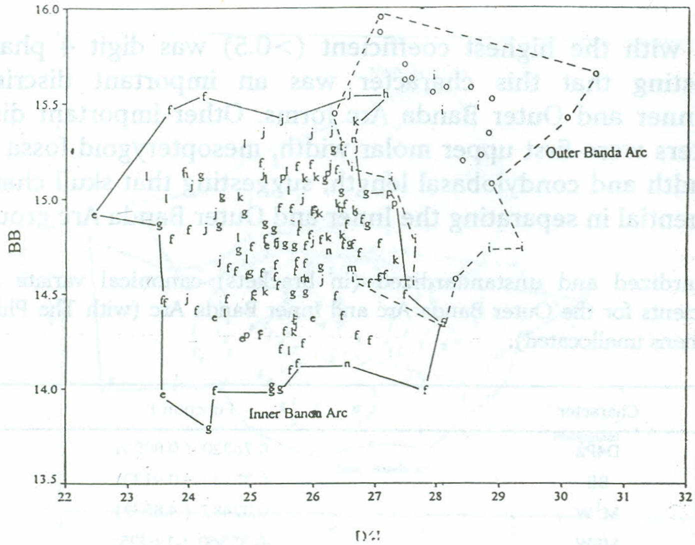
Table 7. Standardized and unstandardized (in brackets) canonical variate function coefficients for the Outer Banda Arc and Inner Banda Arc (with The Philippines specimens unallocated).

Character	Function 1
D4P2	0.76320 (0.8055)
BB	0.35133 (0.9133)
M^1W	0.37487 (4.8537)
MFW	-0.35360 (-1.6225)
CDL	0.29944 (0.4222)
Constant	-46.0914
Variation explained (%)	100

Among the Outer Banda Arc islands of Timor and Sumba there was considerable overlap of individuals in discriminant function space (Figure 7). This indicated that these two populations were morphologically similar. Also, among the island populations of the Inner Banda Arc, almost all individuals from the array of islands in this arc were encompassed by the cluster of individuals from the island with the largest sample size (Lombok Island). This suggested that little morphological differentiation had occurred within the Inner Banda Arc Islands. Support for this view was obtained by DFA of the Inner Banda Arc Islands using the same characters (D4P2, C^1C^1, D2P1, GSL and BB) that were used for the DFA of all 12 islands in the Lesser Sunda/Philippines Group. This DFA showed that only 27.0% of the individuals classified correctly to their appropriate island.

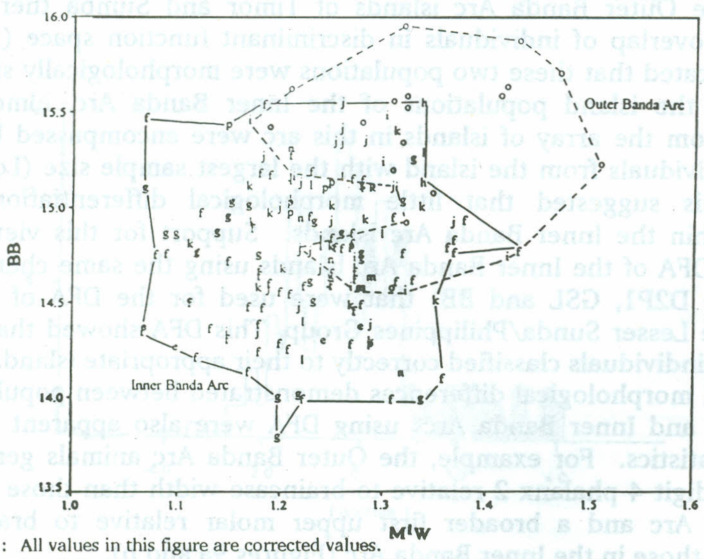
The broad morphological differences demonstrated between populations in the Outer and Inner Banda Arcs using DFA were also apparent in the univariate statistics. For example, the Outer Banda Arc animals generally have longer digit 4 phalanx 2 relative to braincase width than those in the Inner Banda Arc and a broader first upper molar relative to braincase breadth than those in the Inner Banda Arc (Figures 9a and b).

The morphological association of the Philippines population with those of the Inner Banda Arc islands, Lesser Sunda, requires further examination. Biogeographically, this association is not logical in that there is no obvious



Remarks : All values in this figure are corrected values.
(e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 9a. Bivariate plot of BB and D4P2 of *Eonycteris spelaea* from the Outer and Inner Banda Arc Groups.



Remarks : All values in this figure are corrected values.
(e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 9b. Bivariate plot of BB and M^1W of *Eonycteris spelaea* from the Outer and Inner Banda Arc Groups.

pathway for the Philippines *E. spelaea* to have moved to Lesser Sunda Islands, particularly when compared to the obvious movement routes available from the large Sundaic islands via Bali to these Inner Banda Arc islands. This morphological similarity between the Philippines and Lesser Sunda populations may be an example of convergence. Resolution of the problem requires a genetic comparison between these populations; this comparison is important because if the Philippines population is proven to be genetically distinct then the Lesser Sunda population would need to be renamed.

3.2.3. The Sulawesi Group.

This group comprised individuals from eight localities. Seven of these localities were from the southern part of Sulawesi and one from central Sulawesi. These specimens clustered reasonably tightly (Figure 3).

A number of specimens (7) from the Lesser Sunda/Philippines Group were allocated to this group. These were from the islands of Lombok (2), Sumbawa (3), Adonara (1) and Timor (1). Also, seven of the 20 Sulawesi specimens classified to the Lesser Sunda/Philippines Group.

It is possible that the dispersed cluster of the Sulawesi group individuals in discriminant function space may result from the presence of two taxa on that island: *E. s. rosenbergii* and possible *E. s. glandifera*. To evaluate this possibility a DFA was run between the Sulawesi group and the Lesser Sunda/Philippines group. This DFA, based on five selected characters (see

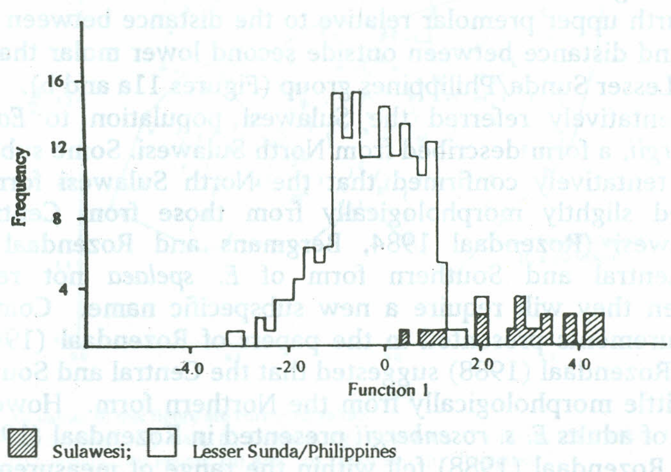


Figure 10. Frequency histogram of Function 1 based on five selected characters for the Sulawesi and Lesser Sunda/ Philippines Groups.

Table 8) extracted a single function with 96.3% of all individuals allocated to their correct group (Figure 10). This indicated these two groups are considerably separated.

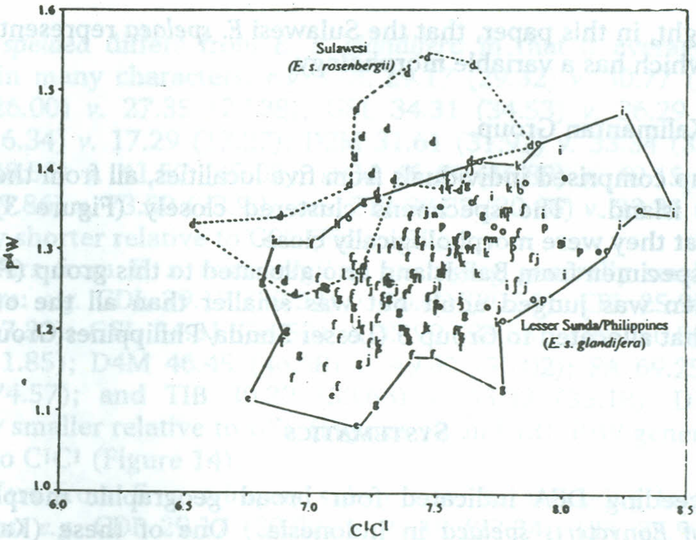
The misclassification involved three specimens (15.0%) from Sulawesi which were classified to the Lesser Sunda/ Philippines group and 4 specimens (2.3%) from the Lesser Sunda/ Philippines group were classified to the Sulawesi group. The characters with high coefficient (>0.5) on this Function were: fourth upper premolar width, phalanx 2 length of digit 3, phalanx 2 length of digit 4, distance between outside upper canine and distance between outside second lower molar (Table 8).

Table 8. Standardized and unstandardized (in the brackets) canonical variate function coefficients for the Sulawesi and Lesser Sunda/Philippines groups.

Character	Function 1
P^4W	0.95601 (13.3690)
D3P2	0.86386 (0.4141)
D4P2	-0.65274 (-0.4960)
C^1C^1	-0.63231 (-2.0028)
M_2M_2	-0.40333 (-1.2164)
Constant	4.1408
Variation explained (%)	100

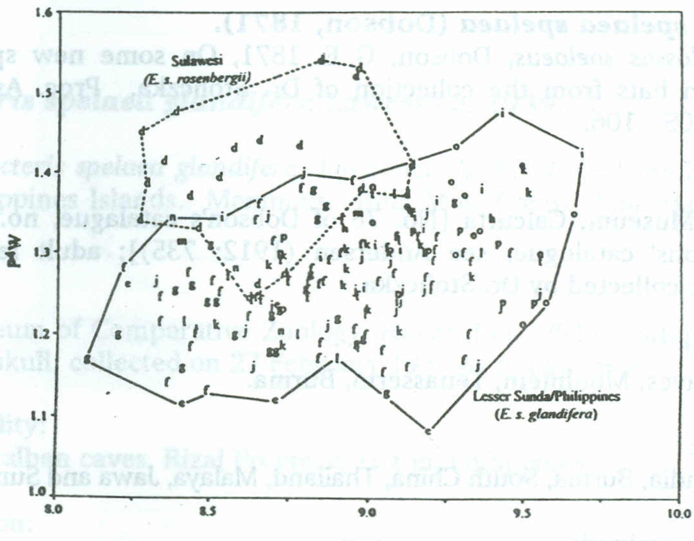
The separation between populations in Sulawesi and *E. s. glandifera* were also apparent using univariate statistics. For example, the Sulawesi animals have wider fourth upper premolar relative to the distance between outside upper canine and distance between outside second lower molar than those animals in the Lesser Sunda/Philippines group (Figures 11a and b).

We have tentatively referred the Sulawesi population to *Eonycteris spelaea rosenbergii,* a form described from North Sulawesi. Some subsequent workers have tentatively confirmed that the North Sulawesi form of *E. spelaea* differed slightly morphologically from those from Central and Southern Sulawesi (Rozendaal 1984, Bergmans and Rozendaal 1988). Should the Central and Southern form of *E. spelaea* not represent *rosenbergii,* then they will require a new subspecific name. Comparison between measurements presented in the papers of Rozendaal (1984) and Bergmans and Rozendaal (1988) suggested that the Central and Southern *E. spelaea* differ little morphologically from the Northern form. However, all measurements of adults *E. s. rosenbergii* presented in Rozendaal (1984) and Bergmans and Rozendaal (1988) fell within the range of measurements in this study present in Table 2 for the 20 specimens of *E. spelaea* measured from Central and South Sulawesi.



Remarks : All values in this figure are corrected values.
(d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 11a. Bivariate plot of P^4W and C^1C^1 of *Eonycteris spelaea* from the Sulawesi and Lesser Sunda/Philippines Groups.



Remarks : All values in this figure are corrected values.
(d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 11b. Bivariate plot of P^4W and M_2M_2 of *Eonycteris spelaea* from the Sulawesi and Lesser Sunda/Philippines Groups.

It is thought, in this paper, that the Sulawesi *E. spelaea* represent a single subspecies which has a variable morphology.

3.2.4. The Kalimantan Group.

This group comprised individuals from five localities, all from the eastern part of the island. The specimens clustered closely (Figure 3), which indicated that they were morphologically close.

A single specimen from Bali Island also allocated to this group (Figure 3). This specimen was judged adult but was smaller than all the other Bali specimens that allocated to Group 3 (Lesser Sunda/Philippines Group).

SYSTEMATICS

The preceeding DFA indicated four broad geographic morphological groupings of *Eonycteris spelaea* in Indonesia. One of these (Kalimantan Group) is unnamed subspecies and herein described as a new subspecies. The following systematics section describes the differences between the geographic groups of *E. spelaea* using univariate descriptors to facilitate the identification and classification of specimens.

***Eonycteris spelaea spelaea* (Dobson, 1871).**

Macroglossus spelaeus, Dobson, G E. 1871, On some new species of Malayan bats from the collection of Dr. Stoliczka. Proc. Asiat. Soc. Beng. 105 - 106.

Holotype:

Indian Museum, Calcutta [No. 78 of Dobson's catalague, no. 100*a* of Andersons' catalague, see Andersen (1912: 735)]; adult female, in alcohol; collected by Dr. Stoliczka.

Type locality:

Farm caves, Moulmein, Tenasserin, Burma.

Distribution:

North India, Burma, South China, Thailand, Malaya, Jawa and Sumatera.

Specimens examined:

Listed in Appendix 1.

Diagnosis (mean values; raw data, followed in the brackets by adjusted values - see Table 2)

E. s. spelaea differs from *E. s. glandifera* in that it averages generally smaller in many characters: *e.g.* CDL 29.17 (29.32) *v.* 30.77 (30.82); CPL 25.90 (26.00) *v.* 27.35 (27.38); GSL 34.31 (34.53) *v.* 36.29 (36.36); PL 16.32 (16.34) *v.* 17.29 (17.27); D2M 31.61 (31.92) *v.* 33.34 (33.56); D3P2 37.96 (38.55) *v.* 41.57 (42.02); D4M 46.45 (46.88) *v.* 49.15 (49.44); FA 69.25 (69.86) *v.* 73.50 (73.90); and TIB 30.32 (30.66) *v.* 33.31 (33.45). D1 generally shorter relative to GSL (Figure 12).

It differs from *E. s. rosenbergii* in averaging generally smaller in most characters: *e.g.* CDL 29.17 (29.32) *v.* 30.60 (30.51); CPL 25.90 (26.00) *v.* 27.31 (27.23); GSL 34.31 (34.53) *v.* 35.99 (35.88); ONL 10.86 (10.96) *v.* 11.88 (11.85); D4M 46.45 (46.88) *v.* 49.87 (50.02); FA 69.25 (69.86) *v.* 74.43 (74.57); and TIB 30.32 (30.66) *v.* 33.33 (33.18). D1 and P^4W generally smaller relative to GSL (Figures 12 and 13). P^4W generally smaller relative to C^1C^1 (Figure 14).

It differs from *E. s. winnyae* subsp. nov. in averaging larger in most characters: *e.g.* CDL 29.17 (29.32) *v.* 27.18 (27.34); CPL 25.90 (26.00) *v.* 24.25 (24.33); GSL 34.31 (34.53) *v.* 32.05 (32.28); D4M 46.45 (46.88) *v.* 43.65 (44.00); D5M 43.05 (43.50) *v.* 40.04 (40.40); FA 69.25 (69.86) *v.* 65.46 (65.96); and TIB 30.32 (30.66) *v.* 28.16 (28.45). GSL larger relative to D1, P^4W and P^3W (Figures 12, 13 and 15). The dorsalateral cranium less inflated.

Eonycteris spelaea glandifera Lawrence, 1939.

Eonycteris spelaea glandifera, Lawrence, B. 1939, Collections from The Philippines Islands. Mammals. Bull. Mus. Comp. Zool. Harv. 86: 28 - 73.

Type:

Museum of Comparative Zoology, Harvard no. 35159; adult male, skin and skull; collected on 27 February 1937 by B. Lawrence.

Type locality:

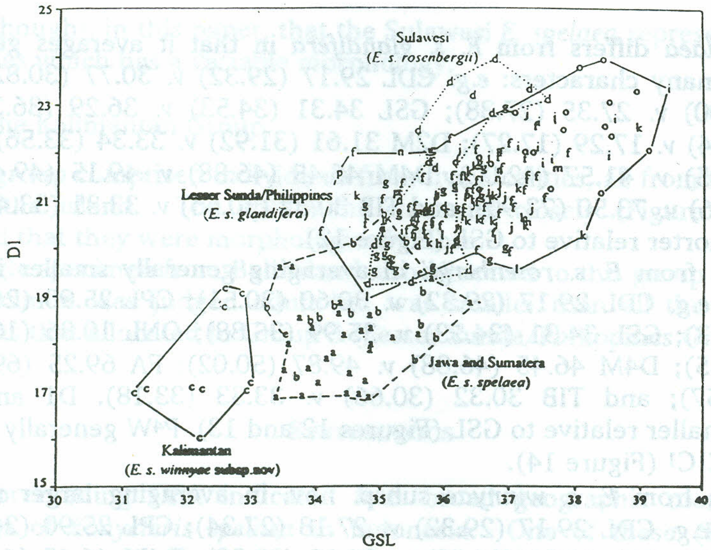
Montalban caves, Rizal Province, Luzon, Philippines.

Distribution:

Philippines, Palawan, Muna, Bali, Lombok, Sumbawa, Rinca, Sumba, Flores, Adonara, Lembata, Pantar, Alor and Timor.

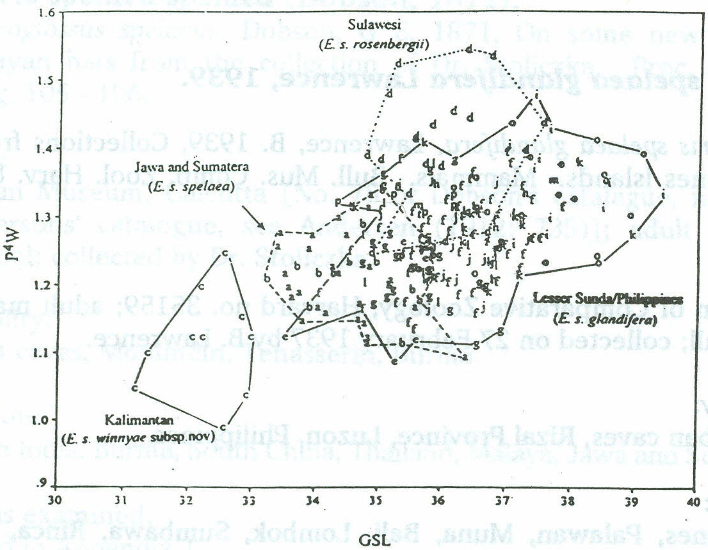
Specimens examined:

Listed in Appendix 1.



Remarks : All values in this figure are corrected values.
(a) Sumatera, (b) Jawa, (c) Kalimantan, (d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 12. Bivariate plot of D1 and GSL of *Eonycteris spelaea* considered in this study.



Remarks : All values in this figure are corrected values.
(a) Sumatera, (b) Jawa, (c) Kalimantan, (d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 13. Bivariate plot of P^4W and GSL of *Eonycteris spelaea* considered in this study.

Diagnosis (mean values; raw data, followed in the brackets by adjusted values - see Table 2)

E. s. glandifera differs from *E. s. spelaea* in the characters as described in the diagnosis of *E. s. spelaea*.

It differs from *E. s. rosenbergii* in averaging slightly larger in many skull characters: *e.g.* CDL 30.77 (30.82) *v.* 30.60 (30.51); GSL 36.29 (36.36) *v.* 35.99 (35.88); and PL 17.29 (17.27) *v.* 17.02 (16.95). Most external body characters average slightly smaller than *rosenbergii*, except : D2M 33.34 (33.56) *v.* 33.25 (33.35); D2P2 7.59 (7.73) *v.* 7.49 (7.61); D4P2 25.58 (25.99) *v.* 25.33 (25.66) and D5P1 21.26 (21.36) *v.* 21.19 (21.21). P^4W generally smaller relative to GSL (Figure 13). C^1C^1 generally larger relative to P^4W (Figure 14).

It differs from *E. s. winnyae* subsp. nov. in being absolutely larger in some characters: CDL 30.77 (30.82) *v.* 27.18 (27.34); CPL 27.35 (27.38) *v.* 24.25 (24.33); GSL 36.29 (36.36) *v.* 32.05 (32.28); ONL 11.74 (11.79) *v.* 10.12 (10.20); D3P2 41.57 (42.02) *v.* 36.05 (36.51); FA 73.50 (73.90) *v.* 65.46 (65.96); and TIB 33.31 (33.45) *v.* 28.16 (28.45). GSL longer relative to P^3W (Figure 15). The dorsalateral cranium less inflated.

***Eonycteris spelaea rosenbergii* (Jentink, 1889).**

Callinycteris rosenbergii, Jentink, F A. 1889, On a new genus and a new species in the Macroglossine group of bats. Notes Leyden Mus. 11: 209 - 212.

Type:

Leyden Museum RMNH no.27427, male subadult, skull extracted, collected by H. von Rosenberg.

Type locality*):

Tulabolo, Gorontalo, North Celebes, Indonesia (0°31' N, 123°16' E).

*) From Rozendaal (1984).

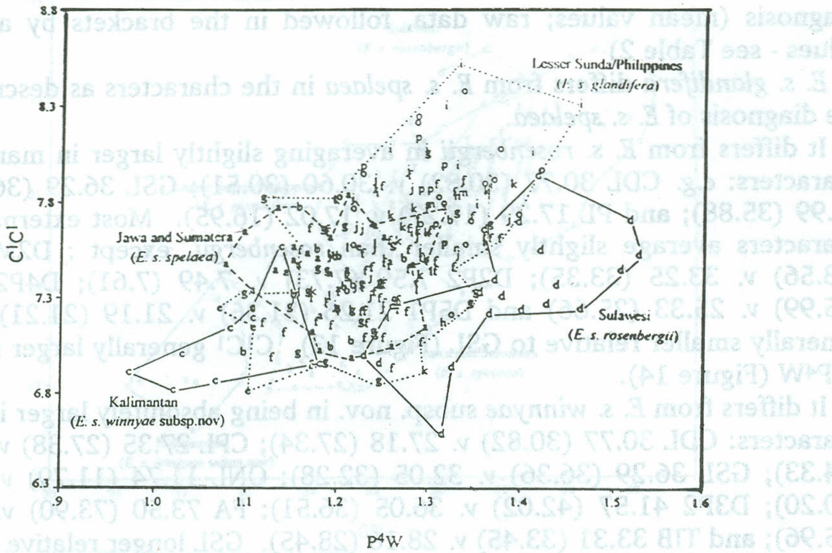
Distribution:

Sulawesi.

Specimens examined:

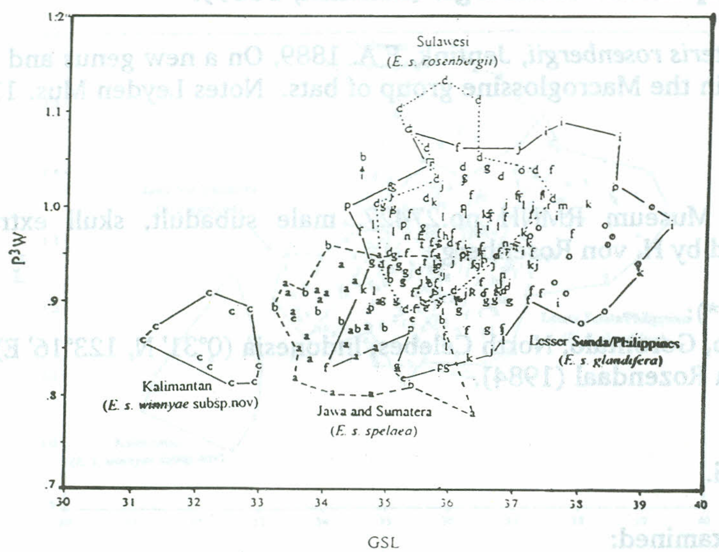
Listed in Appendix 1.

Diagnosis (mean values; raw data, followed in the brackets by adjusted values - see Table 2)



Remarks : All values in this figure are corrected values.
(a) Sumatera, (b) Jawa, (c) Kalimantan, (d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 14. Bivariate plot of C^1C^1 and P^4W of *Eonycteris spelaea* considered in this study.



Remarks : All values in this figure are corrected values.
(a) Sumatera, (b) Jawa, (c) Kalimantan, (d) Sulawesi, (e) Bali, (f) Lombok, (g) Sumbawa, (h) Rinca, (i) Sumba, (j) Flores, (k) Adonara, (l) Lembata, (m) Pantar, (n) Alor, (o) Timor and (p) Philippines

Figure 15. Bivariate plot of P^3W and GSL of *Eonycteris spelaea* considered in this study.

E. s. rosenbergii differs from both *E s. spelaea* and *E. s. glandifera* as described in the previous diagnosis of those two subspecies.

It differs from *E. s. winnyae* subsp. nov. in that it averages larger in most skull characters: *e.g.* C^1M^2 12.23 (12.20) *v.* 10.80 (10.84); CDL 30.60 (30.51) *v.* 27.18 (27.34); CPL 27.31 (27.23) *v.* 24.25 (24.33); and GSL 35.99 (35.88) *v.* 32.05 (32.28). Absolutely larger in some external body characters: D3P2 43.03 (43.36) *v.* 36.05 (36.51); D5M 45.81 (45.96) *v.* 40.04 (40.40); FA 74.43 (74.57) *v.* 65.46 (65.96); and TIB 33.33 (33.18) *v.* 28.16 (28.45). P4W larger relative to C^1C^1 (Figure 14). The dorsolateral cranium less inflated.

It differs from *E. s. spelaea, E. s. glandifera* and *E. s. winnyae* subsp. nov by having a more tapered rostrum and cheek teeth that were squarer in occlusal view.

E. spelaea winnyae Maharadatunkamsi and Kitchener subsp. nov.

Holotype:

Museum Zoologicum Bogoriense MZB No. 16004 (Western Australian Museum field number M 37381); adult female, skull and dentaries removed; carcase fixed in 10 percent formalin and preserved in 70 percent ethanol.

Type locality:

Desa Air Putih, Kecamatan Samarinda Ulu, East Kalimantan, Indonesia (0°23'00'S, 116°58'30'E); collected using mist net on 5 September 1991 from a banana plantation by Drs. A. Suyanto MSc.

Distribution:

Kalimantan

Specimens examined:

Listed in Appendix 1.

Diagnosis (mean values; raw data, followed in the brackets by adjusted values - see Table 2)

E. s. winnyae differs from *E. s. spelaea, E. s. glandifera* and *E. s. rosenbergii* as indicated in the earlier diagnosis of those subspecies.

Description

E. s. winnyae is the smallest of the four subspecies of *E. spelaea* (Table 2). The overall shape of its cranium and external body characters are similar to the nominate subspecies. Its rostrum is moderately long and is gently arched dorsally to a moderately inflated dorsocranial region. It has shelder canines and molars that in occlusal view tend to be more oval in outline than the others subspecies of *E. spelaea*.

The pelage colour is described separately for males and females. Females have a ventrum with the distal two-third of hairs a 'grizzled cream' with a base drab. The dorsum has hairs with distal tips of 'grizzled cream' and a base of olive brown. The head is olive brown. The males have a ventrum with a 'grizzled cream' hairs at one-third of distal tip and a base of drab. The gular hairs are olive brown, tipped with clay colour and the dorsum is as for the females. These colours may be found in the other forms of *E. spelaea*.

Etymology

Named after the senior author's wife, Winny, in recognition of her unfailing encouragement and understanding during this study.

ACKNOWLEDGEMENTS

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Appendix 1. Specimens examined (all adults).

Sumatera:

Bukit Tinggi: ♀ MZB 9756.
Curup: ♂ MZB 13258.
Jabung: ♂♂ MZB 11471, 11485, 11527; ♀♀ MZB 11473-4, 11526, 11528, 11531-2.
Jampang: ♂ MZB 11174; ♀ MZB 11177.
Ketambe: ♂♂ MZB 13145, 13217; ♀♀ MZB 13143-4.
Kota Agung: ♂ MZB 9698.
Lempur: ♂♂ MZB 13232, 13234; ♀ MZB 13233.
Pulau Panggung: ♂♂ MZB 11023-4; ♀♀ MZB 11025, 11038, 11225.
Padang: ♂ WAM 37038; ♀♀ WAM 37031, 37033.
Pariaman: ♀ WAM 37173.
Sukaraja Tiga: ♀ MZB 10842.

Jawa:

Banten: ♂♂ MZB 9618, 10679.
Ciampea: ♂♂ MZB 9596-8; ♀♀ MZB 9602, 9608-9, 9611.
Cilacap: ♀ MZB 3221.
Garut: ♀ MZB 12123.
Ketapang: ♂ WAM 39847.
Labuan: ♂ MZB 13068; ♀♀ MZB 13111, 13117.
Pameungpeuk: ♀ MZB 11291.
Randudongkal: ♂ MZB 12385.

Kalimantan:

Hantakan: ♀♀ MZB 11701-2.
Long Iram: ♂♂ MZB 13518, 13528.
Samarinda Ulu: ♂♂ WAM 37361, 37378; ♀ MZB 16004 (WAM 37381).
Samarinda: ♂ WAM 37349; ♀ WAM 37348.
Tanah Merah: ♀♀ WAM 12661-2.

Sulawesi:

Bantaeng: ♂♂ WAM 33093, 33282.
Bonto Maccini: ♀♀ WAM 33310, 33313, 33316, 33318.
Bonto Manai: ♂♂ WAM 33385, 33393.
Kendari: ♂ MZB 12625.
Maros: ♂♂ MZB 13187, 15310, WAM 33158, 33184, 33188; ♀♀ MZB 13192, 13202.
Poso: ♂ MZB 13703.
Solie Soppeng: ♂ MZB 13655.
Tanjung Nipa: ♂♂ MZB 12627-8.

Bali:

Candi Dasa: ♂ WAM 38600.
Gilimanuk: ♂ WAM 39903.
Jimbaran: ♂ WAM 39959; ♀ WAM 39951
Klampok: ♂♂ MZB 9614-5; ♀♀ MZB 9612-3.

Lombok:

Batu Koq: ♂♂ WAM 30820-1, 33722, 33724-5; ♀♀ WAM 30988-9, 33641-2, 33646, 33649, 33651-3, 33675.

Kuta: ♂♂ WAM 30819, 30822-3, 30825, 31093, 31109, 33600, 33608, 33613, 33615, 33669-73; ♀♀ WAM 31078, 31083, 31085-6, 31091, 31095, 31097, 33605, 33622, 33677-8.

Pelangan: ♂♂ WAM 30831, 30836, 33603, 33617, 33619-20, 33624.

Suranadi: ♂♂ WAM 30818, 30833, 31022, 33601, 33602, ♀♀ WAM 30834, 31030, 31039, 33638-40, 33686, 33688.

Sumbawa:

Belo: ♂♂ WAM 31313, 31325; ♀ WAM 31352.

Empang: ♂♂ MZB 13767, 13870.

Meranti: ♂♂ WAM 31190, 31213-4.

Meraran: ♂ WAM 31250; ♀ WAM 31251.

Plampang: ♂♂ MZB 13762, 13765, 13891.

Taliwang: ♂♂ MZB 12822, 13752-3.

Teluk Santong: ♂♂ WAM 31406, 31414

Waworada: ♂♂ WAM 31657, 31660, 31665-6, 31673-4; ♀♀ WAM 31658, 31669-70.

Rinca:

Kampung Rinca: ♂ WAM 32922; ♀ WAM 32924.

Sumba:

Bondokodi: ♂♂ WAM 30481, 30484; ♀ WAM 30842.

Melolo: ♀ WAM 30514.

Umalulu: ♀ WAM 30570.

Waikabubak: ♀♀ WAM 30340, 30367.

Waikelosawah: ♂♂ WAM 30397, 30401, 30408; ♀♀ WAM 30336, 30399.

Flores:

Labuan Bajo: ♂♂ WAM 32965, 32976, 32978, 32980.

Larantuka: ♀♀ WAM 32102, 32110, 32132.

Longko: ♂♂ WAM 32840, 32881, 32899; ♀♀ WAM 32830, 32835, 32845, 32850, 32890.

Maumere: ♂ WAM 32100, ♀ WAM 32101.

Woloaru: ♂ WAM 32086; ♀♀ WAM 32040-2.

Adonara:

Horowura: ♂♂ WAM 32470, 32480-2, 32494, 32497, 32506, 32509; ♀♀ WAM 32466, 32477, 32493, 32495, 32498, 32503, 32504.

Lembata:

Belang: ♂♂ WAM 32177, 32182; ♀♀ WAM 32206, 32236.

Boto: ♂ WAM 32412; ♀♀ WAM 32402, 32411, 32422, 32434.

Lamakera: ♀ MZB 13390.

Merdeka: ♂♂ WAM 32258, 32271; ♀ WAM 32256.

Pantar:

Bakalang: ♂ WAM 37720; ♀ WAM 37733.

Alor:

Apui: ♂♂ WAM 37928, 37940; ♀♀ WAM 37939, 37942.

Timor:

Baumata: ♂♂ WAM 30179, 30183-4, 30186, 30195, 30197; ♀♀ WAM 30072, 30180, 30182, 30188, 30190-3, 30198, 30200, 30207.

Camplong: ♂ WAM 30220.

Negros:

Dumaguete: ♂♂ FMNH 158482, 162333.

Mount Talanis: ♀♀ FMNH 142690, 142693, 142696.

Leyte:

Inopacan: ♂♂ FMNH 161426, 161436-7.