

Taxonomy of *Rhinolophus simplex* Andersen, 1905 (Chiroptera : Rhinolophidae) in Nusa Tenggara and Maluku, Indonesia

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Abstract – *Rhinolophus simplex simplex* Andersen, 1905 was collected for the first time from Bali, Nusa Penida, Moyo, Sangeang, Rinca, Flores, Lembata, Alor and Sumba islands. Additionally, specimens were collected from Lombok, Sumbawa. Other forms of *R. simplex* were collected from Timor, Savu, Roti, Semau and Kai Kecil islands. *Rhinolophus simplex parvus* Goodwin, 1979 is restricted to Timor Island; *Rhinolophus simplex keyensis* Peters, 1871 occurs on Kai Kecil Island. *Rhinolophus simplex* subsp. nov. is described on the basis of its morphology. It occurs on Savu, Roti and Semau islands.

Protein electrophoresis reveals that populations of *Rhinolophus simplex* show levels of genetic variation that are near the mammalian average. Genetic differentiation of populations is low.

INTRODUCTION

Rhinolophus simplex was described by Andersen (1905) from Lombok I., Nusa Tenggara. Since then it has been considered a species by Corbet and Hill (1980, 1986, 1991); Honacki *et al.* (1982); van Strien (1986) and Tate and Archbold (1939). Koopman (1982), however, considered that *R. simplex* and the closely allied Maluku species: *R. keyensis keyensis* Peters, 1871; *R. k. annectens* Sanborn, 1939; *R. truncatus* Peters, 1871 and *R. nanus* Andersen, 1905 might well be subspecies of *R. megaphyllus* Gray, 1834. Hill (1992) supported this latter view and considered the above forms, along with *R. robinsoni* Andersen, 1918 and *R. megaphyllus thaianus* Hill, 1992 (Thailand) and *R. klossi* Andersen, 1918 (Malaya), as subspecies of *R. megaphyllus*.

Hill (1992) concluded that the major difference between the above forms was in the width of the sella, especially the base, and in the degree of inflation of the median anterior rostral swellings. He considered the forms from New Guinea and Australia and the forms *thaianus*, *robinsoni* and *klossi* from Thailand, have a wide sella and prominent, almost hemispherical narial swellings; in the Maluku forms the sella is a little narrower, but the narial swellings remain well developed; and in the Lesser Sunda island forms both sella and narial swellings are least developed.

Vertebrate surveys by the Western Australian Museum, in collaboration with the Museum Zoologicum Bogoriense, throughout Java, Lesser

Sunda islands and Maluku Tenggara, between 1987 and 1992, resulted in the collection of extensive series of specimens, closely related to *R. simplex*. Additionally a series of *R. borneensis parvus* Goodwin, 1979 (placed as a subspecies of *R. celebensis* by Hill 1992) was collected from Timor.

This paper reports on an examination of morphological and genetic variation among these specimens and on a comparison of this variation with a series of *R. megaphyllus* from Queensland, Australia. A small collection of *R. borneensis importunus* from Java are included for reference.

MATERIALS AND METHODS

A total of 117 adult specimens was examined from a number of islands in Indonesia and Queensland, Australia (see Figure 1 for locality of specimens). They are listed in the "Specimens Examined" section. All these specimens are currently lodged in the Western Australian Museum (WAM). At the completion of this series of surveys half of all the WAM specimens, including the holotype, will be lodged in the Museum Zoologicum Bogoriense, Bogor.

Thirty two measurements of skull, dentary and dental characters and 18 of external characters (all in mm) were recorded from adult specimens (see Figure 2, caption). The skull, dentary and dental characters were measured to an accuracy of 0.01mm, while the external characters were measured to an accuracy of 0.1mm.

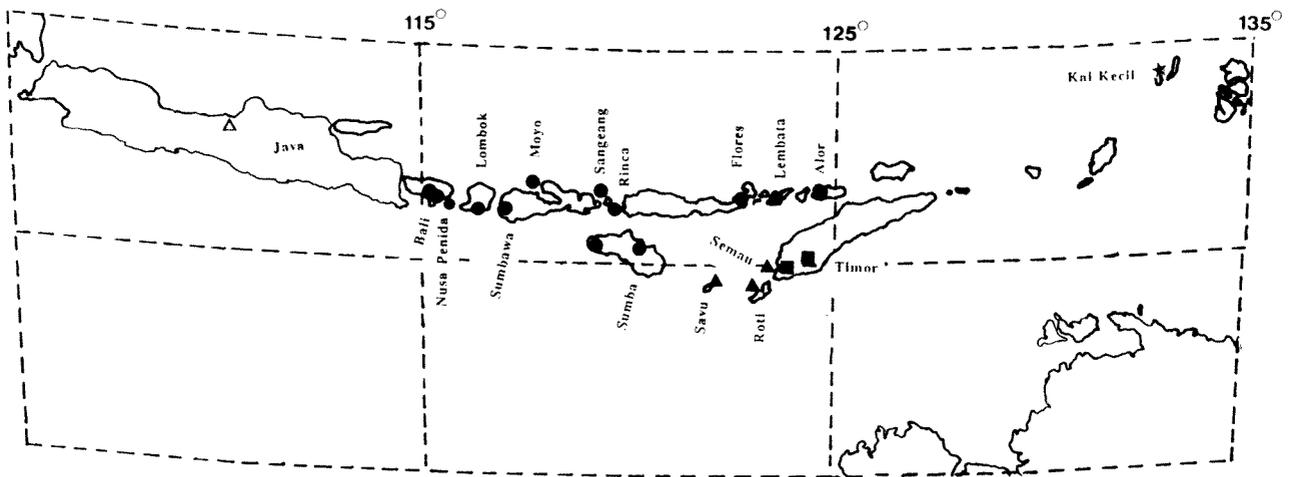


Figure 1 Locality of *Rhinolophus simplex* and *R. borneensis* specimens used in this study. ●, *Rhinolophus simplex simplex*; ■, *R. s. parvus*; ★, *R. simplex keyensis*; ▲, *R. simplex* subsp. nov.; and △, *Rhinolophus borneensis importunus*.

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill and Smith (1984). Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. Additionally two adult age classes were established based on extent of wear on M² hypocone as follows: young adult, no wear or little wear such that the worn area is still elevated above the unworn hypocone basin; for adults, worn surface area of hypocone below level of unworn hypocone basin.

The effect of sex, adult age classes and taxon on skull, dental and external characters was investigated by stepwise multiple regressions on taxon, sex and age for five taxa. These were *Rhinolophus megaphyllus* (Queensland); *R. borneensis importunus* (Java); *R. simplex simplex* (Bali, Nusa Penida, Lombok, Sumbawa, Moyo, Sangeang, Rinca, Flores, Lembata, Alor and Sumba); *R. simplex parvus* (Timor) and *R. simplex* subsp. nov. (Savu, Roti and Semau). *R. simplex keyensis* was not included because the sample size was so small. Further, for the three *R. simplex* subspecies considered, the effect of sex, age and island on skull dental and external measurements was examined using multiple regressions. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Canonical variate (discriminant) analysis (DFA) was computed on skull and external characters separately, with males and females combined, using the SPSS PC⁺ program.

Cellogel electrophoresis of homogenised liver was used to investigate genetically determined protein variation using the techniques described in Richardson *et al.* (1986). This permitted the investigation of variation at 30 presumptive loci.

Genetic variation was assessed on 101 specimens, including some that were juvenile and not included in the morphometric analyses. The proteins scored, with Enzyme Commission Numbers and Locus Symbols in parenthesis, were: aconitate hydratase (E.C.4.2.1.3; *Acon-1* & *Acon-2*), adenosine deaminase (E.C.3.5.4.4; *Ada*), carbonate dehydratase (E.C.4.2.1.1; *Ca*), diaphorase (E.C.1.8.1.4; *Dia*), enolase (E.C.4.2.1.11; *Enol*), fructose-1, 6-diphosphatase (E.C.3.1.3.11; *Fdp*), fumarate hydratase (E.C.4.2.1.2; *Fum*), glucose-6-phosphate dehydrogenase (E.C.1.1.1.49; *G6pd*), glyceraldehyde-3-phosphate dehydrogenase (E.C.1.2.1.12; *Gapd*), guanine deaminase (E.C.3.5.4.3; *Gda*), aspartate aminotransferase (E.C.2.6.1.1; *Got-1* and *Got-2*), α glycerophosphate dehydrogenase (E.C.1.1.1.8; α *Gpd*), glucose-phosphate isomerase (E.C.5.3.1.9; *Gp-1*), isocitrate dehydrogenase (E.C.1.1.1.42; *Idh-1* and *Idh-2*), lactate dehydrogenase (E.C.1.1.1.27; *Ldh-1* and *Ldh-2*), malate dehydrogenase (E.C.1.1.1.37; *Mdh-1* and *Mdh-2*), mannose-phosphate isomerase (E.C.5.3.1.8; *Mpi*), purine nucleoside phosphorylase (E.C.2.4.2.1; *Np*), peptidase (E.C.3.4.13.11; *Pep-A*; E.C.3.4.11.4; *Pep-B*; E.C.3.4.13.11; *Pep-C1* and E.C.3.4.13.9 *Pep-D*), 6-phosphogluconate dehydrogenase (E.C.1.1.44; *6Pgd*), phosphoglucomutase (E.C.5.4.2.2; *Pgm*), superoxide dismutase (E.C.1.15.1.1; *Sod*).

Chi-square was used to test for significance of contingency tables. Tables were reduced when more than a quarter of the cells had expected values less than 2. When expected numbers were small after the tables were reduced to 2 × 2, exact probabilities were computed using twice the probability of the observed tail. Methods used to estimate heterozygosity within populations and genetic distances between populations were those of Nei (1978). These produce "unbiased" estimates. *F*-statistics were computed by the method of Weir and Cockerham (1984), which take into account

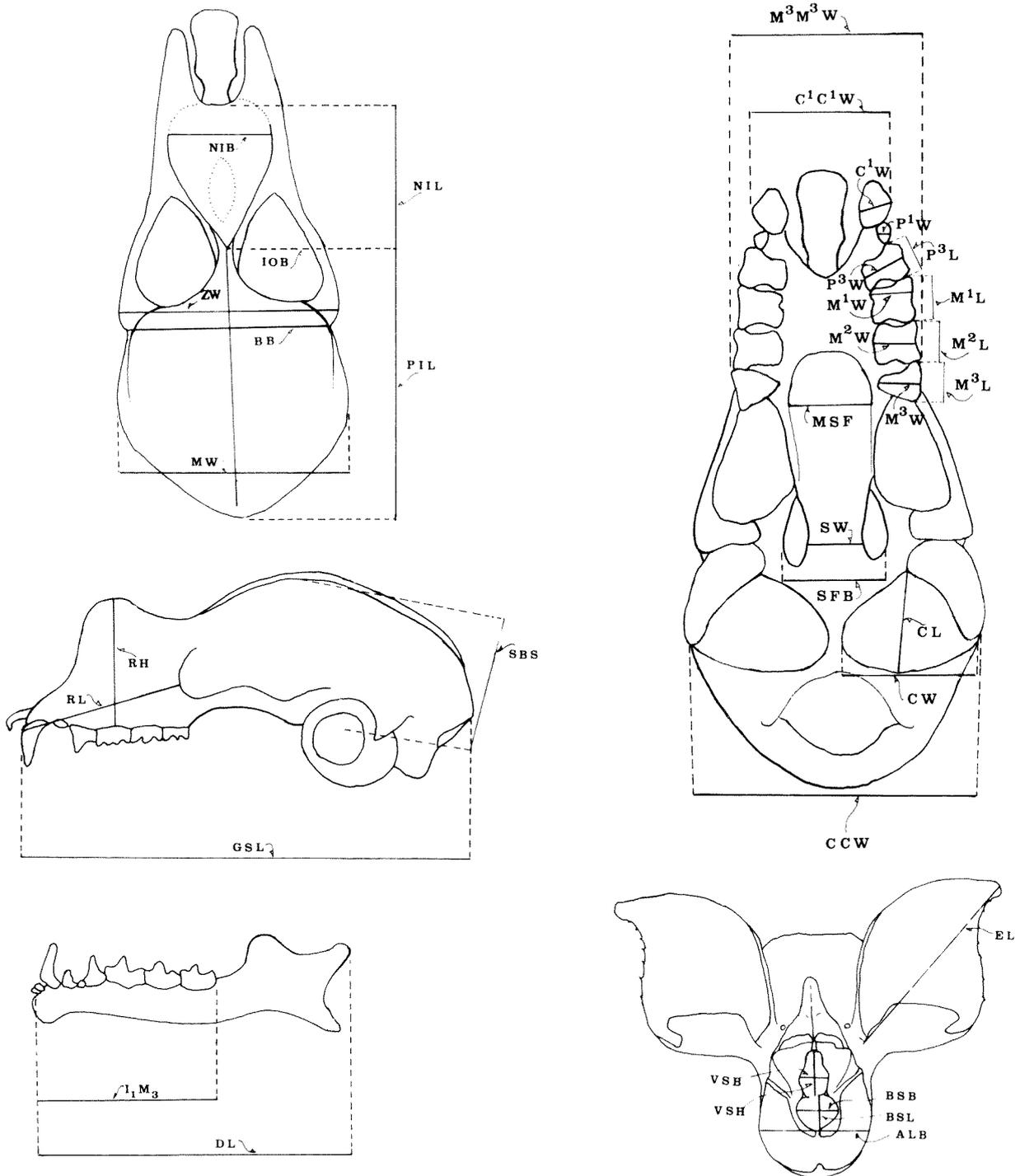


Figure 2 Skull and external measurements referred to in text and their recording points. GSL, greatest skull length; BB, braincase breadth; ZW, zygomatic width; MW, mastoid width; SBS, cranial height – excluding lambdoidal crest; RH, rostrum height – M¹ alveoli to narial crest; RL, rostrum length – orbit anterior edge to maxillary anterior edge; IOB, minimum interorbital breadth; NIL, nasal inflation length – from above junction to nares; NIB, lateral narial inflation breadth; MSF, mesopterygoid fossa breadth; SW, sphenoid/pterygoid bridge basal breadth; SFB, sphenorbital fissure maximum breadth; CW, maximum cochlea breadth; CL, cochlea length; CCW, outside cochleae width; M³M³W, outside M³M³ width (cusp); C¹C¹W, outside C¹C¹ basal width (cusp); C¹W, C¹ width (cusp); P¹W, first upper premolar width; P³L, last upper premolar length; P³W, last upper premolar width; M¹L, M¹W, M²L, M²W, M³L and M³W; first, second and third upper molar length and width, respectively; C¹M³L, upper canine to M³ length (cusp); I₁M₃L, lower tooth row length (cusp); DL, dentary length – condyle to premaxilla anterior edge; SV, snout to vent length; TV, tail to vent length; EL, ear length; TIB, tibia length; PES, pes length; FA, forearm length; D2M, digit 2 metacarpal length; D3M, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4M, digit 4 metacarpal length; D4P1, digit 4 phalanx 1 length; D4P2, digit 4 phalanx 2 length; ALB, maximum anterior noseleaf breadth; BSL, basal sella length; BSB, maximum basal sella breadth; VSH, vertical sella height; and VSB, maximum vertical sella breadth.

Table 1 Measurements, in mm, (see Figure 2 caption for code to characters) for adult *Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s. parvus*, *R. simplex* subsp. nov. and *R. borneensis importunus*. N, sample size; \bar{X} , mean; SD, standard deviation; min, minimum; max, maximum. (a) skull, dentary and dental characters and (b) external characters; males and females combined.

		GSL	BB	ZW	MW	SBS	RH	RL	IOB	PIL	NIL	NIB	MSF	SW	SFB	CW	CL
<i>R. megaphyllus</i>	N	14	15	15	15	13	15	15	15	14	15	15	14	15	15	15	15
	\bar{X}	19.53	8.88	9.60	9.32	6.84	6.33	6.61	2.63	11.35	5.80	5.55	2.86	1.65	3.24	3.58	3.19
	SD	0.43	0.18	0.24	0.19	0.25	0.27	0.20	0.10	0.30	0.31	0.19	0.16	0.12	0.16	0.10	0.10
	Min	18.60	8.55	9.05	9.00	6.40	5.85	6.25	2.50	10.65	5.25	5.20	2.55	1.40	2.80	3.40	2.90
	Max	20.00	9.15	10.00	9.55	7.25	6.70	6.90	2.85	11.75	6.25	5.80	3.10	1.85	3.50	3.75	3.35
<i>R. simplex simplex</i>	N	47	49	49	47	48	48	48	49	48	49	49	43	47	46	49	49
	\bar{X}	17.66	7.96	8.73	8.48	5.97	5.60	5.95	2.35	10.41	5.23	4.93	2.39	1.37	2.79	3.45	3.03
	SD	0.42	0.20	0.25	0.17	0.32	0.18	0.27	0.12	0.32	0.21	0.17	0.12	0.10	0.15	0.13	0.08
	Min	16.75	7.40	8.05	8.05	5.40	5.25	5.40	2.10	9.60	4.65	4.60	2.06	1.10	2.50	3.20	2.90
	Max	18.45	8.45	9.15	8.80	6.80	6.10	6.50	2.60	11.00	5.65	5.50	2.60	1.60	3.10	3.75	3.20
<i>R. simplex keyensis</i>	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	\bar{X}	17.63	8.05	8.78	8.40	5.93	5.73	6.00	2.30	10.40	5.35	4.85	2.58	1.42	2.90	3.55	3.05
	SD	0.18	0.21	0.18	0.07	0.32	0.25	0.14	0.07	0.57	0.64	0.28	0.25	0.04	0.07	0.0	0.07
	Min	17.50	7.90	8.65	8.35	5.70	5.55	5.90	2.25	10.00	4.90	4.65	2.40	1.40	2.85	3.55	3.00
	Max	17.75	8.20	8.90	8.45	6.15	5.90	6.10	2.35	10.80	5.80	5.05	2.75	1.45	2.95	3.55	3.10
<i>R. simplex parvus</i>	N	13	13	13	13	13	13	13	13	13	13	13	10	13	13	12	12
	\bar{X}	16.87	7.53	8.34	8.14	5.62	5.23	5.59	2.20	10.17	4.57	4.55	2.34	1.40	2.75	3.28	2.97
	SD	0.29	0.15	0.13	0.18	0.35	0.18	0.13	0.11	0.24	0.28	0.11	0.07	0.12	0.08	0.11	0.09
	Min	16.50	7.20	8.08	7.79	5.10	5.00	5.40	2.04	9.75	4.20	4.35	2.20	1.16	2.60	3.10	2.85
	Max	17.30	7.75	8.57	8.49	6.20	5.65	5.80	2.38	10.50	5.00	4.75	2.45	1.60	2.90	3.40	3.10
<i>R. simplex</i> subsp. nov.	N	26	27	26	26	27	28	28	28	27	28	28	23	27	27	27	27
	\bar{X}	15.95	7.11	7.71	7.67	5.57	5.06	5.23	2.07	9.52	4.57	4.41	2.27	1.28	2.58	3.17	2.86
	SD	0.50	0.29	0.34	0.26	0.35	0.23	0.23	0.11	0.33	0.20	0.17	0.14	0.07	0.11	0.09	0.11
	Min	15.30	6.60	7.25	7.25	4.75	4.65	4.85	1.90	9.00	4.20	4.10	2.05	1.15	2.35	3.00	2.70
	Max	17.10	7.65	8.40	8.20	6.40	5.55	5.70	2.30	10.25	4.95	4.80	2.50	1.40	2.80	3.40	3.15
<i>R. borneensis importunus</i>	N	9	10	9	10	9	10	10	10	9	10	9	10	9	8	9	10
	\bar{X}	19.2	8.67	9.72	9.08	6.43	6.10	6.41	2.34	11.55	5.07	5.26	2.74	1.59	2.89	3.54	3.06
	SD	0.50	0.25	0.19	0.19	0.25	0.18	0.31	0.14	0.44	0.19	0.13	0.08	0.09	0.16	0.09	0.08
	Min	18.50	8.20	9.45	8.85	5.90	5.75	5.85	2.10	10.50	4.75	5.05	2.60	1.40	2.70	3.45	2.90
	Max	19.80	8.95	10.00	9.40	6.70	6.40	6.80	2.60	11.95	5.26	5.40	2.80	1.70	3.20	3.70	3.20

Table 1 (continued)

		CCW	M ³ M ³ W	C ¹ C ¹ W	C ¹ W	P ¹ W	P ³ L	P ³ W	M ¹ L	M ¹ W	M ² L	M ² W	M ³ L	M ³ W	C ¹ M ³ L	I ₁ M ₃ L	DL
<i>R. megaphyllus</i>	N	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	14
	\bar{X}	4.90	7.16	7.86	1.26	0.49	1.08	1.51	1.57	1.55	1.62	1.66	1.55	1.57	7.34	8.52	12.65
	SD	0.24	0.24	0.23	0.08	0.05	0.04	0.10	0.07	0.10	0.07	0.08	0.06	0.06	0.18	0.22	0.34
	Min	4.40	6.70	7.30	1.05	0.40	1.00	1.30	1.50	1.35	1.50	1.55	1.50	1.45	7.05	8.05	12.05
	Max	5.20	7.40	8.10	1.40	0.60	1.15	1.70	1.70	1.70	1.75	1.75	1.70	1.70	7.65	8.80	13.05
<i>R. simplex simplex</i>	N	48	48	48	48	48	48	48	49	49	49	49	48	48	47	47	5
	\bar{X}	4.40	6.34	7.48	1.08	0.42	0.98	1.36	1.42	1.37	1.41	1.43	1.31	1.38	6.65	7.80	11.64
	SD	0.19	0.17	0.22	0.07	0.06	0.05	0.11	0.06	0.10	0.06	0.07	0.06	0.07	0.18	0.21	0.30
	Min	3.90	5.80	6.85	0.95	0.30	0.90	1.10	1.30	1.20	1.25	1.25	1.20	1.15	6.30	7.40	11.00
	Max	4.80	6.65	8.05	1.30	0.55	1.05	1.55	1.50	1.70	1.50	1.60	1.45	1.50	7.10	8.30	12.35
<i>R. simplex keyensis</i>	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	\bar{X}	4.25	6.33	7.57	1.20	0.50	1.00	1.50	1.48	1.55	1.35	1.48	1.25	1.42	6.60	7.68	11.70
	SD	0.07	0.18	0.04	0.0	0.0	0.0	0.0	0.04	0.0	0.0	0.04	0.07	0.04	0.14	0.25	0.28
	Min	4.20	6.20	7.55	1.20	0.50	1.00	1.50	1.45	1.55	1.35	1.45	1.20	1.40	6.50	7.50	11.50
	Max	4.30	6.45	7.60	1.20	0.50	1.00	1.50	1.50	1.55	1.35	1.50	1.30	1.45	6.70	7.85	11.90
<i>R. simplex parvus</i>	N	12	13	11	13	13	13	13	13	13	13	13	13	13	13	13	12
	\bar{X}	3.88	5.92	7.10	1.02	0.40	0.89	1.25	1.35	1.29	1.38	1.35	1.24	1.30	6.29	6.38	10.95
	SD	0.15	0.15	0.13	0.08	0.06	0.05	0.10	0.07	0.09	0.06	0.05	0.05	0.08	0.17	0.17	0.29
	Min	3.70	5.60	6.90	0.90	0.30	0.80	1.05	1.20	1.15	1.30	1.30	1.15	1.20	6.10	6.18	10.50
	Max	4.10	6.10	7.35	1.15	0.55	1.00	1.40	1.45	1.40	1.50	1.45	1.30	1.40	6.60	6.68	11.25
<i>R. simplex subsp. nov.</i>	N	28	28	24	28	28	28	28	28	28	28	28	28	28	28	26	23
	\bar{X}	3.82	5.54	6.82	0.95	0.33	0.84	1.13	1.24	1.19	1.26	1.26	1.14	1.19	5.86	6.76	10.28
	SD	0.21	0.19	0.18	0.07	0.07	0.04	0.09	0.05	0.07	0.07	0.08	0.06	0.07	0.26	0.26	0.30
	Min	3.40	5.20	6.50	0.85	0.15	0.80	1.00	1.15	1.10	1.15	1.15	1.05	1.10	5.55	6.30	9.80
	Max	4.25	5.90	7.10	1.10	0.45	0.95	1.35	1.35	1.35	1.40	1.45	1.30	1.40	6.40	7.30	10.90
<i>R. borneensis importunus</i>	N	10	10	9	10	10	10	10	10	10	10	10	10	10	10	10	9
	\bar{X}	4.80	6.97	7.87	1.30	0.51	1.09	1.53	1.64	1.53	1.64	1.60	1.48	1.54	7.31	8.56	12.63
	SD	0.19	0.19	0.21	0.07	0.06	0.05	0.08	0.05	0.08	0.05	0.08	0.04	0.06	0.22	0.14	0.30
	Min	4.50	6.60	7.50	1.15	0.40	1.00	1.45	1.55	1.45	1.55	1.50	1.40	1.45	6.90	8.35	12.10
	Max	5.05	7.25	8.10	1.40	0.60	1.15	1.70	1.70	1.70	1.70	1.75	1.50	1.65	7.60	8.75	12.95

Table 1 (continued)		SV	TV	EL	TIB	PES	FA	D2M	D3M	D3P1	D3P2	D4M	D4P1	D4P2	ALB	BSL	BSB	VSH	VSB
<i>R. megaphyllus</i>	N	15	15	15	15	15	14	15	15	15	15	15	15	15	15	12	11	13	15
	\bar{X}	47.2	24.1	19.4	19.1	8.3	46.9	35.1	32.9	13.5	19.9	34.5	10.2	12.1	9.0	2.5	3.1	4.4	2.2
	SD	2.5	2.1	0.8	0.6	0.3	0.7	0.7	0.6	0.4	0.8	0.6	0.4	0.5	0.6	0.3	0.4	0.3	0.2
	Min	42.6	20.9	17.6	17.5	7.4	45.8	33.3	31.9	12.7	18.1	33.5	9.8	11.3	7.7	2.0	2.7	3.7	1.8
	Max	51.1	28.0	20.6	20.1	8.6	48.1	36.0	34.1	14.0	21.2	35.6	10.7	12.8	9.6	2.9	4.0	5.1	2.7
<i>R. simplex simplex</i>	N	49	49	49	48	49	48	48	49	49	49	49	49	49	49	39	38	40	47
	\bar{X}	43.2	21.1	17.7	18.2	7.6	41.9	31.4	29.5	12.3	19.1	30.3	8.8	11.8	8.1	2.3	2.5	3.9	2.0
	SD	1.5	2.0	1.0	0.7	0.4	1.3	1.4	1.0	0.6	0.9	1.1	0.4	0.6	0.5	0.2	0.2	0.2	0.2
	Min	39.9	18.1	14.4	16.0	6.1	39.0	28.7	27.1	11.0	17.1	27.5	7.5	10.5	7.2	1.8	2.1	3.2	1.7
	Max	46.6	26.2	19.6	19.7	8.4	44.9	35.6	31.8	13.7	21.0	32.8	9.9	13.1	9.3	2.7	3.1	4.3	2.4
<i>R. simplex keyensis</i>	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	\bar{X}	42.7	18.7	18.9	16.8	7.3	41.4	31.1	28.5	11.7	19.0	30.0	8.9	11.0	9.2	2.7	2.8	4.5	2.4
	SD	1.2	2.2	1.7	0.1	0.0	0.1	0.2	0.5	0.4	0.1	0.9	0.1	0.2	0.5	0.4	0.4	0.0	0.4
	Min	41.8	17.2	17.7	16.7	7.3	41.4	31.0	28.2	11.4	19.0	29.4	8.8	10.9	8.8	2.4	2.6	4.5	2.1
	Max	43.5	20.3	20.0	16.9	7.3	41.5	31.3	28.9	11.9	19.1	30.7	9.0	11.1	9.5	2.9	3.1	4.5	2.7
<i>R. simplex parvus</i>	N	13	12	13	13	13	13	12	12	13	12	12	13	13	13	13	13	13	13
	\bar{X}	37.7	20.1	16.1	17.3	7.7	40.1	29.9	27.9	11.6	17.2	28.7	8.3	10.9	7.4	1.9	2.5	3.4	1.9
	SD	1.2	2.2	0.4	0.6	0.5	0.8	0.7	1.0	0.4	0.5	0.9	0.3	0.4	0.3	0.2	0.1	0.3	0.1
	Min	35.4	17.0	15.4	16.5	6.8	38.2	28.6	26.8	10.9	16.2	27.7	7.8	10.3	7.0	1.6	2.3	3.1	1.6
	Max	39.7	23.8	16.6	18.5	8.3	41.3	31.1	30.2	12.3	18.0	30.5	8.5	11.8	7.8	2.2	2.7	4.0	2.0
<i>R. simplex subsp. nov.</i>	N	28	28	28	28	28	27	28	28	28	28	28	28	28	21	16	15	16	24
	\bar{X}	38.2	20.3	16.7	15.2	6.4	37.4	27.6	26.3	10.3	16.2	26.7	7.9	9.8	7.6	2.3	2.4	3.6	1.9
	SD	1.7	1.8	0.8	0.8	0.3	0.9	1.0	0.8	0.5	0.8	0.9	0.3	0.8	0.4	0.2	0.2	0.3	0.2
	Min	35.6	18.0	15.0	14.0	5.9	35.8	26.1	24.8	9.5	14.7	24.6	7.5	8.4	6.8	2.0	2.2	3.3	1.6
	Max	42.8	24.3	18.3	16.6	7.1	39.1	29.5	27.6	11.4	18.4	28.5	8.5	11.4	8.8	2.6	2.7	4.2	2.1
<i>R. borneensis importunus</i>	N	10	10	10	10	10	9	10	10	10	10	10	10	10	10	9	9	10	10
	\bar{X}	45.7	23.8	19.4	19.9	9.3	44.4	32.3	30.3	13.0	20.7	31.7	9.3	12.7	9.0	2.5	2.6	4.5	2.1
	SD	2.4	2.3	0.54	0.9	0.4	1.0	1.1	0.9	0.5	1.0	1.2	0.4	0.6	0.3	0.2	0.2	0.3	0.1
	Min	40.8	19.0	18.7	18.3	8.4	42.4	29.9	28.4	12.1	18.7	29.1	8.5	11.6	8.6	2.2	2.2	4.1	1.9
	Max	48.1	26.9	20.4	21.1	9.7	45.5	33.6	31.3	13.6	22.1	33.3	10.0	13.6	9.4	3.0	2.8	5.0	2.2

sample size variation. Cluster analysis used the UPGMA method of Sneath and Sokal (1973). All statistical analyses were undertaken with Genstat 5 (Genstat 5 Committee 1987) and Biosys-1 (Swofford and Selander 1989).

MORPHOLOGY: STATISTICS

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size of each taxon are presented in Table 1 for (a) skull, dentary and dental characters and (b) external characters

Multiple regressions

Multiple regressions were run for skull, dentary and dental characters and external characters on sex and adult age for five taxa (*R. borneensis*, *R. megaphyllus*, *R. simplex simplex*, *R. s. parvus* and *R. s. subsp. nov.*). Additionally, multiple regression was run for the *R. simplex* group alone for skull and external characters on sex, adult age and island. In these analyses, islands with small sample size were omitted because either a sex or adult age category was absent. The results of these analyses are presented in Tables 2 and 3.

In the following discussions, because of the large number of interactions being tested, the level of significance was set at $P < 0.01$.

All 5 taxa – skulls

Sex. From Table 2a, eight characters (greatest skull length, GSL; braincase breadth, BB; rostrum height, RH; rostrum length, RL; outer cochlear width, CCW; upper maxillary tooth row length, C¹M³L; lower tooth row length, I¹M³L and dentary length, DL) showed a significant relationship with sex alone ($P < 0.000$ – $P = 0.002$). Also there was a significant interaction for outer M³M³ width for sex, age and taxon ($P = 0.009$). This interaction resulted from subadult females being smaller than subadult males in *R. megaphyllus* and females being slightly smaller than males in *R. s. parvus* and *R. borneensis*.

Age. Rostrum height, RH; showed a significant ($P = 0.003$) relationship with age alone. Outer M³M³ width also had a significant interaction between age, sex, and taxon ($P = 0.009$), as discussed above.

Taxon. All skull characters, except M³ width, had a significant relationship ($P < 0.001$) with taxon. These relationships were consistent between the sex and age groupings; the only significant interaction was between sex, age and taxon ($P = 0.009$) for outer M³M³ width, as discussed above, clearly there is a considerable extent of morphological distinctness among these taxa.

All 5 taxa – externals

Sex and age. There were significant relationships with snout to vent length, SV, both with sex alone

($P < 0.001$) and age alone ($P < 0.007$) and with interactions between sex and age and sex and taxon (Table 2b).

Taxon. All characters were significantly related to taxon ($P < 0.001$), except basal sella length (BSL).

R. simplex group – skulls

Sex. No character had a significant relationship with sex alone, although there was a significant interaction between age, sex and island ($P = 0.005$ and $P = 0.002$, respectively) for braincase breadth BB and M² width, M²W. For BB, this resulted from young adult females being larger than old adult females on Roti I., and males being larger than females on Moyo and Flores, whereas on other islands they were approximately the same size, For M²W, young adult males were larger than old adult males on Flores and young adult males were larger than young adult females on Savu I., whereas on other islands they were approximately the same size. Also, for P¹ width, P¹W, there was a significant interaction between sex and island ($P = 0.008$) which resulted from females being larger than males on Savu I., whereas on other islands they were approximately the same size.

Age. No character had a significant relationship with age alone. But there were significant interactions for BB and M²W between sex, age and island, as discussed above.

Island. All 30 characters had a significant relationship with island alone, most at $P < 0.001$. These relationships were consistent for sex and age categories except for braincase breadth, M² width, and P¹ width which had interactions between age and or sex and island, as discussed above.

Clearly, there was marked morphological differences among the island populations of *R. simplex*.

R. simplex group – externals

Sex and age. The only significant relationship was the interaction between sex and island for ear length, EL (Table 3b). This resulted from the Rotinese sample where males had greater ear lengths than females, whereas on other islands they were subequal.

Island. All characters except ear length, EL; maximum anterior noseleaf breadth, ALB, and maximum basal sella breadth, BSB, were significant, most at $P < 0.001$. The only significant interaction was again between sex and island for ear length (Table 3b) as discussed above.

Multivariate analyses

5 taxa analysis

Canonical variate (discriminant) analysis (DFA) was carried out on five taxa (*R. megaphyllus*, *R.*

Table 2 Multiple regressions on taxon (*Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s parvus*, *R. simplex* subsp. nov. and *R. borneensis importunus*), sex and age for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. Significance levels are *, $0.05 > p > 0.01$; **, $0.01 > p > 0.001$; and ***, $p < 0.001$.

Table 2a

Character	Main Effects			Interactions			
	Sex	Age	Taxon	Sex. Age	Sex. Taxon	Age. Taxon	Sex. Age. Taxon
GSL	** 7.167	3.325	*** 128.719	0.099	0.779	0.753	0.833
BB	*** 11.472	* 4.116	*** 155.075	0.235	0.778	0.416	0.402
ZW	3.798	1.783	*** 127.417	0.060	0.350	0.162	1.240
MW	* 6.635	1.952	*** 133.256	0.358	0.259	0.248	2.249
SBS	1.445	0.487	*** 26.914	0.009	0.785	0.767	0.511
RH	*** 11.602	** 9.752	*** 64.575	0.280	0.843	0.710	1.640
RL	*** 11.100	1.294	*** 80.190	0.355	2.222	0.805	1.848
IOB	.696	.904	*** 25.446	0.932	0.856	0.982	0.898
PIL	0.206	0.960	*** 48.550	0.705	0.355	0.538	0.563
NIL	1.717	0.314	*** 34.673	2.103	0.160	0.165	1.253
NIB	* 7.064	0.756	*** 88.723	0.832	0.543	0.332	* 3.993
SW	0.536	0.728	*** 23.096	2.803	1.786	1.136	1.340
SFB	0.908	0.930	*** 29.172	2.802	0.879	0.472	0.560
CW	0.177	0.106	*** 20.200	0.839	0.308	0.666	0.360
CL	0.288	0.248	*** 23.949	2.588	0.644	0.443	0.864
CCW	** 9.626	* 6.572	*** 63.086	0.125	0.753	0.353	* 4.005
M ² M ² W	3.631	0.778	*** 156.608	0.230	1.114	0.745	** 5.091
C ¹ W	0.152	0.000	*** 31.014	3.093	1.208	1.130	1.907
P ¹ W	0.062	0.599	*** 13.425	1.258	1.741	2.065	* 3.510
P ³ L	0.444	0.079	*** 59.942	* 6.123	0.322	1.179	2.854
P ³ W	0.375	0.003	*** 29.514	2.202	0.365	0.670	0.931
M ¹ L	0.223	0.785	*** 68.903	0.628	0.240	0.589	1.007
M ¹ W	0.105	0.619	*** 21.441	0.904	0.610	0.257	0.743
M ² L	0.244	0.047	*** 63.528	0.104	0.894	1.121	0.626
M ² W	3.792	1.159	*** 41.020	1.011	1.367	0.459	1.168
M ³ L	0.746	0.038	*** 59.181	* 4.298	0.802	0.901	1.700
M ³ W	0.679	2.183	1.720	* 6.084	1.125	0.706	1.081
C ¹ M ² L	** 8.473	1.459	*** 116.743	0.000	0.305	0.637	* 3.323
I ₁ M ₃ L	** 9.751	* 5.077	*** 112.654	3.117	1.500	0.684	3.078
DL	** 10.616	2.973	*** 144.502	0.015	1.092	1.165	2.409
DEGREES OF FREEDOM	1,71	1,71	4,71	1,71	4,71	4,71	2,71

Table 2b

Character	Sex	Main Effects		Sex. Age	Interactions		Sex. Age. Taxon
		Age	Taxon		Sex. Taxon	Age. Taxon	
SV	*** 15.293	** 7.898	*** 40.602	** 7.900	** 5.050	2.188	2.307
TV	0.257	2.221	** 5.135	0.019	0.514	1.982	0.624
EL	0.083	0.003	*** 14.580	0.001	0.309	0.412	0.067
TIB	0.662	0.290	*** 48.605	0.269	1.402	1.398	1.326
PES	0.847	0.440	*** 59.904	0.005	0.505	0.573	1.163
FA	0.206	0.173	*** 77.969	3.968	1.403	0.609	0.960
D2M	0.381	0.137	*** 47.522	0.290	1.241	0.486	1.121
D3M	0.002	0.084	*** 55.055	1.323	1.162	0.927	1.142
D3P1	0.348	3.552	*** 41.778	0.884	1.388	1.112	1.485
D3P2	0.468	0.733	*** 34.810	0.001	1.831	1.926	0.093
D4M	0.751	0.737	*** 78.263	1.460	2.230	1.571	1.380
D4P1	1.229	0.055	*** 52.247	1.843	2.900	0.892	2.660
D4P2	2.259	1.882	*** 27.121	0.711	1.768	1.225	1.513
ALB	2.217	2.987	*** 15.412	0.134	0.346	1.688	0.112
BSL	0.601	0.567	2.120	0.057	0.487	0.562	0.607
BSB	2.481	0.165	*** 11.389	0.142	1.086	1.312	0.834
VSH	1.135	0.002	*** 17.864	2.984	2.412	1.344	1.169
VSB	0.062	0.311	** 5.624	1.748	0.363	0.319	0.282
DEGREES OF FREEDOM	1,59	1,59	4,59	1,59	4,59	4,59	2,59

borneensis importunus, *R. simplex simplex*, *R. s. parvus* and *R. simplex* subsp. nov.). *Rhinolophus s. keyensis* was included in this analyses but unallocated because of its small sample size (N = 2). Both sex and age groups were combined. However, this analysis was carried out only after deleting nine skull characters shown in the multiple regression analysis to be significantly ($P < 0.01$) influenced by sex or age (GSL, BB, RH, RL, CCW, M³M³W, C¹M³L, I¹M³L, DL, see Table 2a). Also MSF, and C¹C¹B were deleted because too many individuals had these values missing. The skull analyses used was with this reduced set of 21 characters.

Similarly, the DFA of external characters was run following deletion of snout to vent length, SVL, because there were significant ($P < 0.01$) interactions between sex and age for this character (Table 3b).

Skulls. The DFA for the five taxa was first run using the reduced set of 21 characters and using islands as the *a priori* grouping. When these islands were grouped to represent the five above taxa the configuration of the taxon clusters in discriminate

function space was very similar. However, because the number of individuals in some taxa was less than the number of characters measured (*R. borneensis*, 8; *R. megaphyllus*, 15) a reduced set of characters was used in the analysis. Of the 21 characters used in the DFA of the five taxa as the *a priori* groups, five were chosen because they provided values that minimise Wilk's Lambda. The plots of the discriminant functions 1 to 3, based on the reduced set of five characters (mastoid width, MW, supraorbital length, NIL; M¹ length, M¹L; zygomatic width, ZW; and sphenorbital fissure width, SFB) produced very similar plots to the above analyses, and so only these are presented and discussed below.

The DFA produced three significant canonical functions. These three functions combined explained 99.9 percent of the variance (Table 4a) with function 1, 86.9 percent; function 2, 10.2 percent and function 3, 2.8 percent. A total of 95.3 percent of individuals were correctly classified to their appropriate taxon. Only five individuals were

Table 3 Multiple regressions for *Rhinolophus simplex* (*R. s. simplex*, *R. s. parvus* and *R. s. subsp. nov.*) on island, sex, and age for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. Significance levels as for Table 2.

Table 3a

Character	Sex	Main Effects		Sex. Age	Interactions		Sex. Age. Island
		Age	Island		Sex. Island	Age. Island	
GSL	0.044	0.458	41.595	6.347	2.615	1.226	7.697
BB	0.117	3.417	44.800	6.416	3.439	5.126	9.171
ZW	0.008	0.434	42.519	3.626	2.658	0.972	5.708
MW	0.091	6.843	51.452	7.087	3.796	1.288	6.800
SBS	0.000	0.140	3.796	0.316	1.553	0.425	0.558
RH	2.826	0.262	9.135	1.928	0.513	0.514	5.024
RL	0.134	0.045	31.389	1.377	3.429	1.099	0.138
IOB	0.246	1.130	9.576	1.452	0.591	0.713	0.933
PIL	0.334	0.869	14.320	1.778	0.615	1.082	3.382
NIL	0.003	0.843	18.056	2.770	1.767	0.985	0.159
NIB	0.031	0.275	28.287	1.499	3.256	1.126	1.882
SW	1.053	1.376	4.973	0.022	1.417	2.335	0.259
SFB	1.533	2.395	2.584	1.533	1.422	0.268	2.228
CW	0.001	1.339	6.148	0.209	0.778	0.549	0.952
CL	0.011	0.864	8.179	2.401	2.036	0.795	0.311
CCW	2.615	0.604	20.927	0.075	0.805	0.160	0.391
M ³ M ³ W	0.482	1.273	46.851	5.092	1.704	0.978	4.591
C ¹ W	1.008	0.021	4.858	0.021	0.142	0.542	0.110
P ¹ W	1.404	5.953	14.556	0.005	4.348	3.014	1.157
P ³ L	0.273	0.673	17.219	0.006	0.334	3.251	0.268
P ³ W	0.154	1.042	13.061	1.042	1.109	0.582	0.155
M ¹ L	0.424	0.832	26.398	2.055	2.001	2.654	2.921
M ¹ W	0.872	0.000	5.539	0.000	2.406	1.533	0.058
M ² L	0.709	0.709	10.628	1.971	0.847	0.194	1.784
M ² W	1.919	1.161	8.432	6.848	0.926	0.618	11.323
M ³ L	0.003	3.193	11.674	0.163	1.317	0.642	0.127
M ³ W	0.129	0.517	11.120	2.068	1.255	1.550	0.389
C ¹ M ³ L	0.353	0.353	51.854	1.411	1.352	0.177	4.332
I ₁ M ₃ L	0.315	0.013	73.172	0.617	1.427	0.479	2.521
DL	0.014	0.047	66.467	2.620	2.465	1.218	6.367
DEGREES OF FREEDOM	1,26	1,26	5,26	1,26	4,26	4,26	1,26

Table 3b

Character	Sex	Main Effects		Sex. Age	Interactions		Sex. Age. Island
		Age	Island		Sex. Island	Age. Island	
SV	0.176	0.069	28.275	0.150	0.520	0.694	2.084
TV	0.284	2.670	3.109	0.413	1.036	1.862	0.420
EL	0.098	0.063	1.798	0.004	5.505	2.437	4.712
TIB	0.005	0.083	41.150	0.926	0.281	0.365	1.472
PES	0.116	0.040	12.590	0.904	0.917	0.912	0.818
FA	0.543	1.035	24.474	1.183	0.838	0.931	3.275
D2M	0.532	0.000	17.119	1.075	0.543	0.770	1.490
D3M	0.072	1.232	14.872	1.342	0.547	0.679	0.249
D3P1	1.012	0.124	15.439	0.000	1.498	0.608	0.209
D3P2	0.799	1.046	17.561	0.199	0.880	0.426	0.002
D4M	0.402	3.601	33.937	4.652	2.621	1.614	1.607
D4P1	4.457	0.012	13.284	1.016	2.557	0.866	0.019
D4P2	0.041	0.157	17.845	2.890	0.379	0.922	5.557
ALB	0.000	0.583	2.459	0.055	1.251	1.045	0.018
BSL	0.094	0.165	4.530	1.108	0.073	1.021	1.099
BSB	0.932	0.007	0.699	1.916	0.533	1.302	5.935
VSH	0.115	0.490	8.392	3.426	1.103	0.692	2.510
VSB	0.580	5.218	2.924	0.205	0.294	1.351	0.381
DEGREES OF FREEDOM	1,23	1,23	5,23	1,23	3,23	4,23	1,23

incorrectly classified: Four *R. simplex* sp. nov. were classified as *R. s. parvus* and one *R. s. simplex* was classified as *R. s. parvus*.

The plot of functions 1 and 2 most clearly separates the taxa (Figure 3a) and plots of other combinations of functions 1–3 do not further clarify graphically this separation. From Figure 3a, the *R. borneensis* and *R. megaphyllus* clusters are clearly separate on function 2 and these two species clearly cluster separately from the *R. simplex* subspecies on function 1. Further, the *R. simplex* subspecies clusters, which partially overlap, separate on function 1. The unallocated *Rhinolophus s. keyensis* grouped closely with *R. s. simplex*.

The character loading most heavily (>0.5) on function 1 and which is presumed an important discriminant between *R. borneensis*, *R. megaphyllus* and *R. simplex*, and among the *R. simplex* subspecies, was M¹ length (Table 4a). The characters loading heavily (>0.5) on function 2 and

presumed important in discriminating between *R. borneensis* and *R. megaphyllus* were supraorbital length, NIL, and zygomatic width, ZW (Table 4a).

Externals. The DFA for the five taxa was first run using the reduced set of 17 characters and using island as the *a priori* grouping. When these islands were grouped to represent the five above taxa the configuration of the taxon clusters in discriminant function space was very similar to that produced above. However, because the number of individuals in some taxa was less than the number of characters measured (e.g. *R. borneensis*, 9; *R. megaphyllus*, 12) fewer characters were used in the analysis. Five the 17 characters used in the DFA as the *a priori* groups were selected (forearm length, FA; pes length, PES; vertical sella height VSH; digit 4, phalanx 1 length, D4P2) for analysis because they provided values that minimise Wilk's Lambda. These five characters produced similar DFA plots to those from the 17 characters. Only the DFA

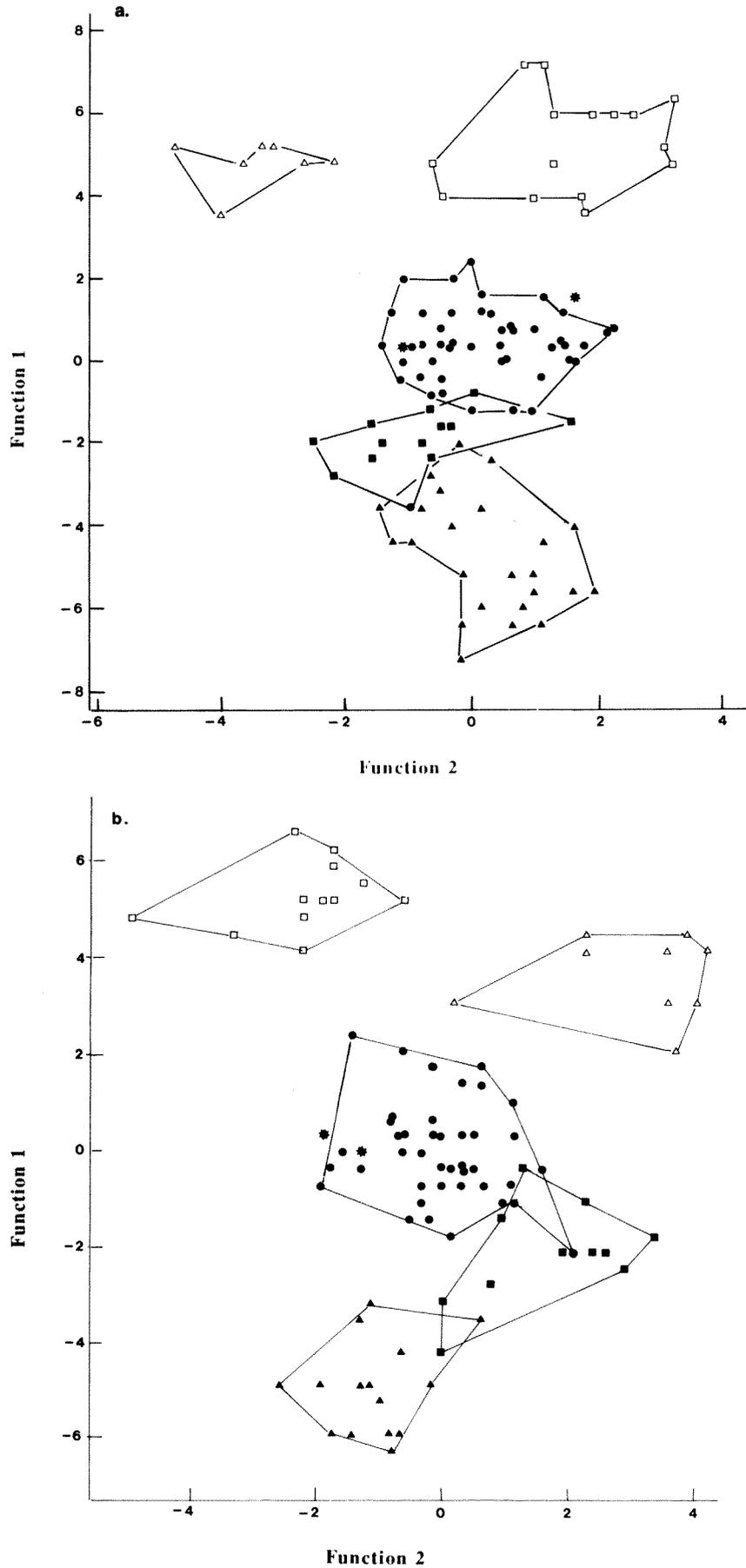


Figure 3 Canonical variate analysis grouped by taxon (*Rhinolophus megaphyllus*, □; *R. simplex simplex*; *R. s. parvus*; *R. s. subsp. nov.*; and *R. borneensis importunus*) based on (a) skull, dentary and dental characters and (b) external characters, for functions 1 and 2. Other taxon symbols as for Figure 1 caption.

Table 4 Canonical variate function coefficients for the five taxa: *Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s. parvus*, *R. s. subsp. nov.* and *R. borneensis parvus*. *R. s. keyensis* unallocated. Standardised values, followed by (in brackets) unstandardised values. (a) skull and dental; (b) external characters.**Table 4a**

Character	Function 1	Function 2	Function 3
MW	0.3517 (1.7477)	0.4891 (2.4302)	0.6221 (3.0911)
NIL	0.2224 (0.9304)	0.7231 (3.0253)	-0.7308 (-3.0575)
M'L	0.5114 (8.5400)	-0.4025 (-6.7206)	-0.1993 (-3.3275)
ZW	0.3518 (1.3538)	-0.8787 (-3.3811)	-0.4380 (-1.6854)
SFB	0.1374 (0.9804)	0.4699 (3.3522)	0.7509 (5.3568)
CONSTANT	-45.9212	-6.4634	-6.3208
VARIATION EXPLAINED (%)	86.9	10.2	2.8

Table 4b

Character	Function 1	Function 2	Function 3
FA	0.6108 (0.5706)	-0.1597 (-0.1492)	-0.1565 (-0.1462)
PES	0.2590 (0.7415)	1.0000 (2.8640)	-0.4652 (-1.3324)
VSH	0.3455 (1.2204)	-0.2507 (-0.8854)	0.2965 (1.0471)
D4P2	-0.1158 (-0.1892)	0.2766 (0.4519)	1.1051 (1.8054)
D4M	0.3276 (0.3474)	-0.6520 (-0.6915)	-0.1803 (-0.1912)
CONSTANT	-42.6952	3.4166	-2.7095
VARIATION EXPLAINED (%)	77.3	16.6	4.1

based on this reduced set of five characters are presented and discussed below.

The DFA produced four significant canonical functions. These functions combined explained 100 percent of the variance (Table 4b) with function 1, 77.3 percent; function 2, 16.6 percent; function 3, 4.1 percent and function 4, 2.0 percent. A total of 95.6 percent of individuals was correctly classified to their appropriate taxon. Four specimens were incorrectly classified. One *R.s. subsp. nov.* was classified as *R.s. parvus*, one *R.s. parvus* was classified as *R.s. subsp. nov.* and two *R.s. simplex* were classified as *R.s. parvus*.

The plot of functions 1 and 2 and functions 1 and 3 most clearly separates the taxa (Figure 3b) and plots of other combinations of functions 1–4 does not further clarify graphically this separation. From Figure 3b, *R. borneensis*, *R. megaphyllus*, *R.s. simplex* and *R.s. subsp. nov.* cluster separately on function 1 with *R.s. parvus* also clustering separately from *R. megaphyllus* and *R. borneensis* on this function.

Additionally *R. megaphyllus* clusters separately from both *R.s. parvus* and *R. borneensis* on function 2. The unallocated *R. simplex keyensis* specimens cluster close to *R. s. simplex*.

The character loading most heavily (>0.6) on function 1, which is presumed to be a most important discriminant between most of these taxon, was forearm length (Table 4b). the characters loading heavily (>0.6) on function 2, and presumed important discriminants between *R. megaphyllus* and both *R.s. parvus* and *R. borneensis*

were pes length, PES, and digit 4 metacarpal length, D4M (Table 4b).

R. simplex analysis

A DFA was carried out on the three subspecies of *R. simplex* (*R.s. simplex*, *R.s. parvus*, and *R. s. subsp. nov.*) after combining both sex and age groups. This analysis was carried out for skulls, dentary and dental characters only after deleting three skull characters shown by the multiple regression analysis to be significantly ($P < 0.01$) influenced by sex or age (BB, P¹W, and M²W, see Table 3a). Also, MSF and C¹C¹W were deleted because too many individuals had these values missing. The skull analyses was then run with the reduced set of 25 characters.

Similarly the DFA of external characters was run after deletion of ear length from the analysis because there was a significant ($P < 0.01$) interaction between sex and island for this character (Table 3b).

Skulls. The DFA for the *R. simplex* subspecies was first run using the reduced set of 25 characters and using islands as the *a priori* groupings. When these islands were then grouped to represent the three taxa *R. s. simplex*, *R. s. parvus* and *R. s. subsp. nov.* (*R. s. keyensis* unallocated), the configuration of the taxon clusters in discriminant function space was similar to that produced above. However, as the number of characters was considerably larger than the number of individuals in one taxon group (*R. simplex parvus*, 12) a reduced set of five characters

Table 5 Canonical variate functions coefficients for the three subspecies of *Rhinolophus simplex* (*R. s. simplex*, *R. s. parvus*, *R. s. subsp. nov.*). *Rhinolophus s. keyensis* unallocated. Standardised values, followed by (in brackets) unstandardised values (a) skull and dental; (b) external characters.

Table 5a

Character	Function 1	Function 2
I ₁ M ₃ L	1.2760 (5.8790)	-0.9938 (-4.5787)
C ¹ M ³ L	-0.8948 (-4.4169)	1.0576 (5.2205)
M ³ M ³ W	0.1955 (1.1858)	0.8975 (5.4438)
CB	0.4427 (3.8282)	0.2631 (2.2755)
NIB	0.2770 (1.6894)	-0.4586 (-2.7968)
CONSTANT	-42.6169	-27.1418
VARIATION EXPLAINED (%)	75.4	24.6

Table 5b

Character	Function 1	Function 2
TIB	0.4414 (0.6271)	-0.4069 (-0.5781)
SV	0.9602 (0.6010)	0.6795 (0.4506)
PES	0.3907 (1.1571)	-0.8443 (-2.5005)
D4P1	0.4708 (1.3476)	0.4592 (1.3145)
VSH	0.6294 (3.3753)	0.0508 (0.2722)
TV	-0.5209 (-0.2470)	0.1439 (0.0682)
BSB	-0.5409 (-2.5337)	0.3179 (1.4891)
CONSTANT	-50.4099	-6.9463
VARIATION EXPLAINED (%)	85.4	14.6

was selected on the basis that they provided values that minimise Wilk's lambda. The plots of the discriminant function 1 and 2 based on this reduced set of five characters (lower, tooth row length, I₁M₃L; upper maxillary tooth row length, C¹M³L; outer M³M³ width, M³M³W; cranium breadth, CB; and nasal inflation breadth, NIB) produced very similar plots to the above analyses, and so only these are presented and discussed below.

The DFA produced two significant canonical functions. Function 1 explained 75.4 percent of the variance and function 2, 24.6 percent (Table 5a). A total of 100 percent of individuals were correctly classified to their appropriate subspecies. The plot of function 1 and 2 (Figure 4a) clearly separates the subspecies: *simplex*, *parvus* and *subsp. nov.* with the unallocated *keyensis* grouping with *simplex*. Function 1 separates all three allocated subspecies clusters and function 2 partially separates *R. s. simplex* from both *R. s. parvus* and *R. s. subsp. nov.* and completely separates the *R. s. parvus* and *R. s. subsp. nov.* clusters.

The characters loading most heavily (>0.8) on function 1 and presumed important discriminants between the three allocated subspecies, were lower tooth row length, I₁M₃L, and upper maxillary tooth row length, C¹M³L (Table 5a). Characters loading most heavily on function 2 (>0.8) and presumed particularly important in discriminating between *R. s. parvus* and *R. s. subsp. nov.* included, in

addition to the above two characters, outer M³M³ width, M³M³W (Table 5a).

Externals. The DFA for the *R. simplex* subspecies was first run using the reduced set of 17 characters and using islands as the *a priori* groupings. When these islands were then grouped to represent the three allocated *R. simplex* subspecies (see above), the configuration of the taxon clusters in discriminant function space was similar to that produced above. However, because the number of characters was larger than the number of individuals in one taxon group (*R. simplex parvus*, 12) a reduced set of seven characters was selected (tibia length, TIB; snout to vent length, SV; pes length, PES; digit 4, phalanx 1 length, D4P1; vertical sella breadth, VSB; tail to vent length, TV; basal sella breadth, BSB) using the method for skulls above; this produced similar DFA plots to those produced using the 17 characters. Only the DFA based on this set of seven characters are presented and discussed below.

The DFA produced two significant canonical functions. Function 1 explained 85.4 percent of the variance and function 2, 14.6 percent (Table 5b). A total of 100 percent of individuals were correctly classified to their appropriate subspecies. The plot of functions 1 and 2 (Figure 4b) clearly separates the subspecies, with the unallocated *keyensis* again grouping with *R. s. simplex*. Function 1 separates all three subspecies clusters and function 2 separates *R. s. parvus* and *R. s. subsp. nov.*

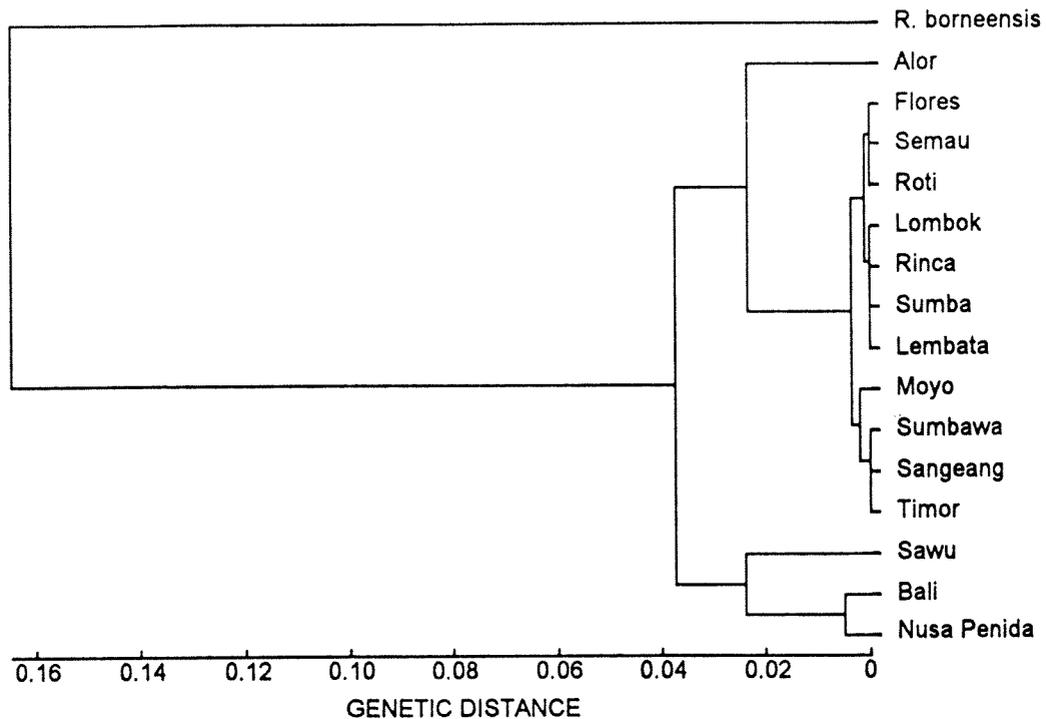


Figure 5 Dendrogram computed by UPGMA from the genetic distance (Nei standard distance, unbiased) between island populations of *Rhinolophus simplex* and *R. borneensis* from Java.

The characters loading most heavily (>0.6) on function 1 and presumed important discriminants between *R.s. simplex* and both *R. s. parvus* and *R.s. subsp. nov.* are snout to vent length, SV and vertical sella height, VSH (Table 5b). Characters loading most heavily on function 2 (>0.6) and presumed important discriminants between *R. s. parvus* and *R.s. subsp. nov.* are snout to vent length and pes length, PES (Table 5b).

GENETICS

The gene frequencies are presented in Table 6. Fifteen of the 30 loci scored showed variation within islands. The genotype frequencies for all occurrences of polymorphism within an island did not differ significantly from the Hardy-Weinberg expectations. Mean heterozygosity levels are presented at the bottom of Table 6. They fall within the usual range observed for mammalian populations (Nevo, Beiles and Ben-Shlomo 1984).

Much of the variation within *Rhinolophus simplex* was due to inter-island differences. *F*-statistics revealed four loci that had F_{ST} greater than 0.1. These were *Acon-2* (0.83), *Idh-2* (0.63), *Pep-D* (0.16) and *6Pgd* (0.22). The mean F_{ST} over all loci was 0.42 with bootstrapped 95% confidence limits of 0.09 and 0.67. However, for most loci, there was little or no variability within or between islands and the unbiased Nei genetic distances between islands was low, being generally less than 0.04 (Table 7). These distances, together with those estimated from a sample of 18 individuals of *R. borneensis*

from Java were subjected to cluster analysis and the resultant dendrogram is presented in Figure 5. This dendrogram reveals the integrity of *R. simplex* as a species distinct from *R. borneensis*.

SYSTEMATICS

Rhinolophus simplex simplex Andersen, 1905

Rhinolophus simplex Andersen, K., 1905: 76, Pl. 3.

Holotype

British Museum No. 97.4.18.4, adult female, in alcohol, collected June 1896 by A. Everett.

Type locality

Lombok I., Nusa Tenggara, altitude 2500 ft (ca. 830 m).

Diagnosis

Rhinolophus s. simplex differs from both *R. simplex parvus* and *R. simplex subsp. nov.* in averaging larger in all skull, dental and dentary measurements, except for the posterior width of the sphenoid/pterygoid bridge; SW, and external measurements, except pes length, PES, and basal sella length, BSL, (Tables 1a, b). It differs almost absolutely from *R.s. subsp. nov.* in tibia length and forearm length (see Table 1). I_1M_3 longer relative to outside cochleae width, nasal inflation breadth, C^1M^3 length and outer M^3M^3 width (Figures 6, 7a, b, c, respectively). It differs from *R.s. parvus* in having snout to vent length longer relative to pes

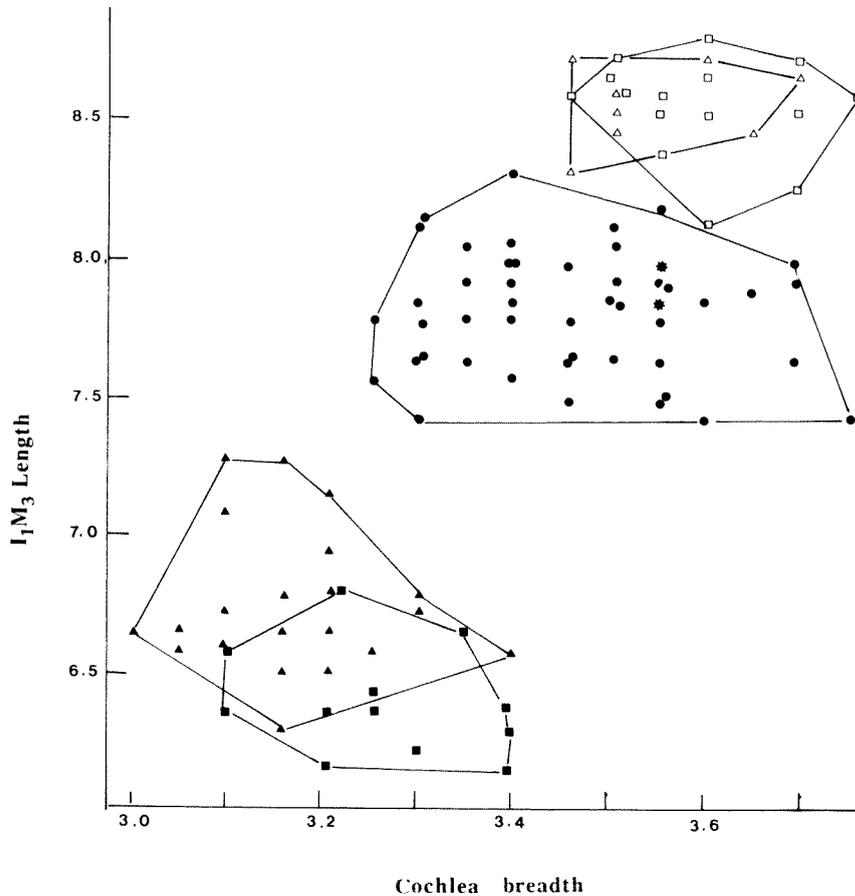


Figure 6 Plot of lower tooth row length, I_1M_3 , versus cochlea breadth, CW, for *Rhinolophus simplex* subspecies, *R. megaphyllus* (□) and *R. borneensis importunus*. Other taxon symbols as for Figure 1.

length (Figure 8).

It is approximately the same size as *R. s. keyensis*. For example: greatest skull length 17.66 (16.75–18.45) *v.* 17.63 (17.50–17.25), zygomatic width 8.73 (8.05–9.15) *v.* 8.78 (8.65–8.90) and forearm length 41.9 (39.0–44.9) *v.* 41.4 (41.4–41.5)]. It differs from *keyensis* in having a smaller sella, with vertical sella height absolutely shorter 3.9 (3.2–4.3) *v.* 4.5 (4.5–4.5) and vertical sella breadth averaging narrower 2.0 (1.7–2.4) *v.* 2.4 (2.1–2.7).

Description

Skull and dentition

Rhinolophus s. simplex is larger than *R. s. parvus* and *R. s. subsp. nov.* (Table 1). Specimens show some variation in overall size and shape, but most of this variation may be found in a single population, for example, Moyo I. This can be appreciated by the wide distribution of the values for Moyo I. for the functions 1 and 2 scores from the DFA within the *R. s. simplex* cluster (Figure 4a). This is also true for those characters that were not quantified such as the size and shape of the anterior rostral swellings and the juxtaposition of the upper and lower vestigial premolar with the other premolars.

The junction of the supraorbital ridges is usually behind the mid-point of the orbital cavity but occasionally it is anterior to that point. The median anterior rostral swellings also vary considerably in size and extent of inflation in relation to the supraorbital length (Figure 9); some individuals, from throughout the range of *R. s. simplex* approximate the large size and inflation of the two individuals of *R. s. keyensis* from the eastern Kai Kecil I. The size and extent of crowding of the vestigial upper and lower premolar was extremely variable. Usually the anterior upper premolar was in contact with the canine but its contact with the posterior premolar was extremely variable. The lower vestigial premolar varied from being located almost in the tooth row between the anterior and posterior premolar, sometimes not in solid contact with these adjacent premolars, to being totally extruded such that the anterior and posterior premolars are in contact.

The anterior basisphenoid has a marked depression or pit which is much lower than the surface of the basioccipital. This is quite different from the shape of this region in *R. megaphyllus ignifer* where the basioccipital surface runs smoothly into a shallow basisphenoid groove.

The posterior palate margin terminates at M^2 mid

Table 6 Allele frequencies, mean heterozygosity and sample sizes in island populations of *Rhinolophus simplex* and *R. borneensis* from Java. A dash indicates the allele was not detected. The mean heterozygosity and its standard error, and mean number of individuals (N) per locus are shown at the bottom of the table. No variation was detected at the following loci: *Acon-1*, *Ca*, *Enol*, *Fdp*, *Fum*, *Gapd*, *G6pd*, *Got-1*, *Gp-1*, *Idh-1*, *Idh-2*, *Mdh-1*, *Mdh-2*, *Np* and *Pep-C1*.

LOCUS	GENE	ISLAND						
		BALI	N.PENIDA	LOMBOK	SUMBAWA	MOYO	SANGEANG	RINCA
<i>Acon-2</i>	A	-	-	-	-	-	-	-
	B	-	-	-	-	-	-	-
	C	-	-	1.00	1.00	1.00	1.00	1.00
	D	1.00	1.00	-	-	-	-	-
	E	-	-	-	-	-	-	-
<i>Ada</i>	A	-	-	-	-	-	-	-
	B	-	-	-	0.10	-	-	-
	C	1.00	1.00	1.00	0.90	1.00	1.00	1.00
	D	-	-	-	-	-	-	-
<i>Dia</i>	A	-	-	-	0.10	0.05	-	-
	B	1.00	1.00	1.00	0.90	0.95	1.00	1.00
	C	-	-	-	-	-	-	-
	D	-	-	-	-	-	-	-
	E	-	-	-	-	-	-	-
<i>Gda</i>	A	-	-	-	-	-	-	-
	B	-	-	-	-	-	-	-
	C	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>áGpd</i>	A	-	-	-	-	-	-	0.12
	B	-	-	-	-	-	-	-
	C	1.00	1.00	1.00	1.00	1.00	1.00	0.88
<i>Got-2</i>	A	-	-	-	-	-	-	-
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	-	-	-	-	-	-	-
	D	-	-	-	-	-	-	-
<i>Idh-2</i>	A	-	-	-	-	-	-	-
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	-	-	-	-	-	-	-
<i>Ldh-1</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	0.88
	B	-	-	-	-	-	-	0.12
<i>Mpi</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	-	-	-	-	-	-	-
<i>Pep-A</i>	A	-	-	-	-	-	-	-
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	-	-	-	-	-	-	-
	D	-	-	-	-	-	-	-
<i>Pep-B</i>	A	-	-	-	-	0.05	-	-
	B	-	-	-	0.10	0.05	-	-
	C	-	-	-	-	-	-	-
	D	1.00	1.00	1.00	0.80	0.90	1.00	1.00
	E	-	-	-	-	-	-	-
	F	-	-	-	0.10	-	-	-
<i>Pep-D</i>	A	-	-	-	-	-	-	-
	B	-	-	-	-	0.30	-	-
	C	1.00	1.00	1.00	0.80	0.60	1.00	1.00
	D	-	-	-	-	-	-	-
	E	-	-	-	-	-	-	-
	F	-	-	-	0.20	0.10	-	-
	G	-	-	-	-	-	-	-
<i>6Pgd</i>	A	0.44	0.07	0.25	0.50	0.50	0.50	0.12
	B	0.50	0.93	0.75	0.50	0.50	0.50	0.88
	C	-	-	-	-	-	-	-
	D	0.06	-	-	-	-	-	-
	E	-	-	-	-	-	-	-
<i>Pgm</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	-	-	-	-	-	-	-
<i>Sod</i>	A	-	-	-	-	-	-	-
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mean Heterozygosity		0.019	0.005	0.017	0.056	0.046	0.033	0.025
Standard error		0.019	0.005	0.017	0.025	0.026	0.033	0.014
N per locus		9	7	2	5	10	1	4

Table 6 (continued)

SUMBA	FLORES	LEMBATA	ALOR	ISLAND TIMOR	SEMAU	ROTI	SAVU	JAVA
-	-	-	-	-	-	0.04	-	1.00
1.00	1.00	1.00	1.00	1.00	0.12 0.88	- 0.96	-	-
-	-	-	-	-	-	-	0.25 0.75	-
-	-	-	-	-	-	-	-	0.08
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.17 0.50 0.25
-	-	-	-	-	-	-	-	-
1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.80	0.36 0.64
-	-	-	-	-	-	0.04	-	-
-	-	-	-	-	-	-	0.20	-
-	-	-	0.04	-	-	-	-	-
1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00
-	-	0.17	0.05	-	-	-	-	-
1.00	1.00	0.83	0.96	1.00	1.00	1.00	1.00	0.97 0.03
-	-	-	0.04	-	-	-	-	-
1.00	1.00	1.00	0.96	1.00	1.00	1.00	0.92 0.08	0.94
-	-	-	-	-	-	-	-	0.06
-	0.25	0.33	0.73	-	-	-	-	-
1.00	0.75	0.67	0.23 0.04	1.00	1.00	1.00	1.00	1.00
-	-	-	-	-	-	-	-	-
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
-	-	-	-	-	-	-	-	-
1.00	1.00	1.00	0.86 0.14	1.00	1.00	0.96 0.04	0.98 0.02	0.75 0.25
-	-	-	0.04	-	-	-	0.02	-
0.92	1.00	0.83	0.96	1.00	1.00	1.00	0.98	0.09 0.03
-	-	0.17	-	-	-	-	-	-
0.08	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	0.94
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	-
-	-	-	-	-	-	-	-	0.06
-	-	-	-	-	0.17	-	-	-
0.08	-	-	-	-	-	-	-	-
0.92	0.75	1.00	0.46 0.09	0.92	0.66	0.73	1.00	1.00
-	-	-	0.09	-	-	-	-	-
-	0.25	-	0.27 0.09	0.08	0.17	0.27	-	-
-	-	-	-	-	-	-	-	-
0.08	0.25	0.17	-	0.42	0.25	-	-	-
0.84	0.75	0.83	1.00	0.58	0.75	1.00	1.00	0.94
0.08	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	0.06
-	-	-	-	-	-	-	-	-
1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98 0.02	0.97 0.03
-	-	-	-	-	-	-	-	-
1.00	1.00	1.00	1.00	1.00	0.12 0.88	- 1.00	- 1.00	- 1.00
0.022	0.050	0.051	0.059	0.023	0.051	0.023	0.034	0.073
0.013	0.028	0.025	0.029	0.018	0.026	0.014	0.017	0.029
6	2	3	11	6	4	11	20	18

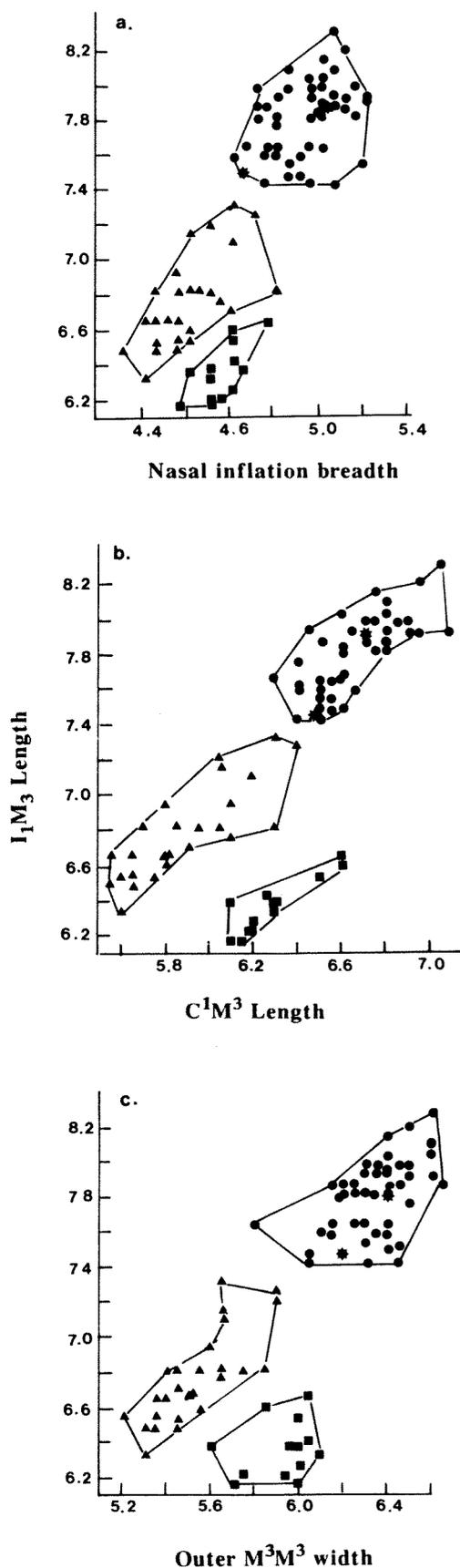


Figure 7 Plot of lower tooth row length, I_1M_3 , versus (a) nasal inflation breadth, NIB; (b) upper maxillary tooth row length, C^1M^3 ; and (c) outer M^3M^3 width, M^3M^3W ; for subspecies of *Rhinolophus simplex*; subspecies symbols as for Figure 1, caption.

point; occasionally there is a slight median postpalatal protuberance but more usually this is a smooth U shape; premaxilla posteriorly terminates at P^3 mid point; sphenoidal/pterygoid bridge obscures anterior sphenorbital fissure when viewed from the ventral aspect; incisors weak, bilobed; M^{1-2} hypocone well developed.

Externals

The external characters are similar to those described by Andersen (1905) for *Rhinolophus simplex*. The anterior noseleaf is moderately wide (8.2) with an obvious anteromedian notch. The vertical sella is longer than the basal sella (4.0 *v.* 2.3), smoothly curved at the apex and not noticeably constricted. Ears are moderately long (17.8), outer apical margin reasonably concave.

Pelage and skin colour

Dorsal pelage of most specimens Fuscous, which is colour of distal one-third of hairs, the basal part of which is Drab. Ventral surface pure Drab.

Occasional specimens of both sex paler, with dorsal surface Russet, which is colour of distal one-third of hairs, the basal part of which is Cream Color. Ventral surface pure Fawn Color. Wing and ears Fuscous.

Baculum

The shape of bacula among *Rhinolophus simplex* largely differs in the extent of the incision in the posteroventral basal margin (Figure 10, Table 8), which ranges from deeply incised in WAM M38252 (Bali I). to slightly concave in WAM M30249 (Sumba I). All these basal types occur in *R. s simplex*.

Distribution

Many islands in the Inner Banda Arc: Bali, Nusa Penida, Lombok, Sumbawa, Moyo, Sangeang, Komodo, Rinca, Flores, Lembata, Alor, Wetar islands and Sumba Island in the outer Banda Arc. Its ability to occupy new habitats, such as defence tunnels build by Japanese during the Second World War, suggest that it is a good colonist and that it probably exists on many other islands in this region.

Rhinolophus simplex keyensis Peters, 1871

Rhinolophus megaphyllus keyensis Peters, W., 1871.

Types

Cotypes, Mus. Berol. No. 3240 and No. 3291.

Type locality

Key-Inseln (= Kai Islands).

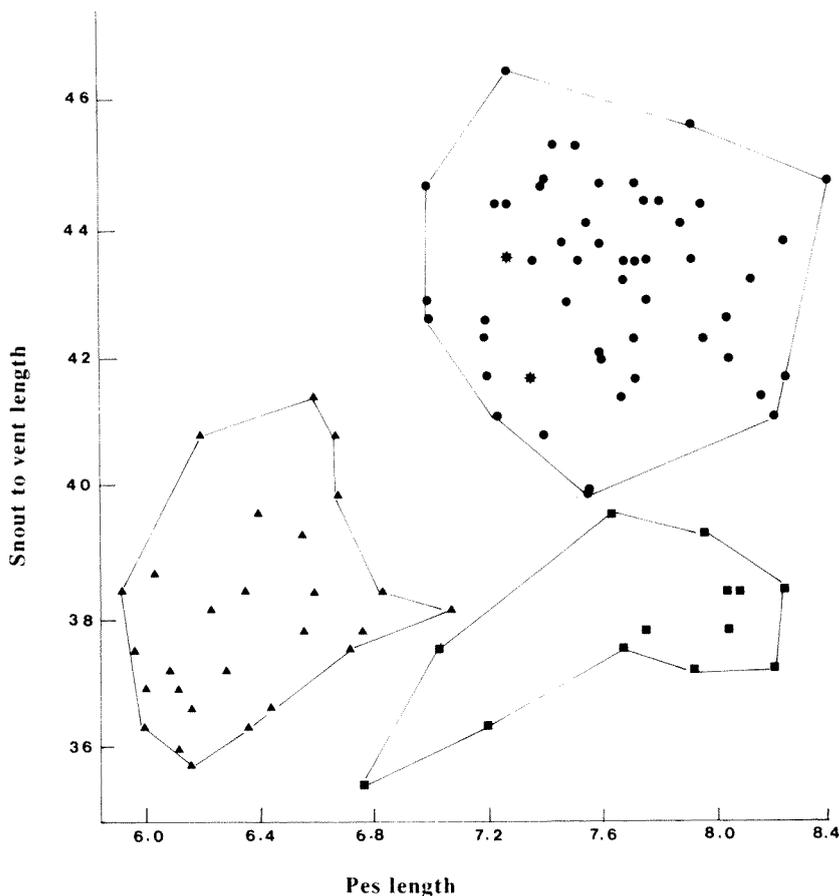


Figure 8 Plot of snout to vent length versus pes length for subspecies of *R. simplex*. Subspecies codes as for Figure 1.

Diagnosis

Rhinolophus s. keyensis differs from *R. s. simplex* as diagnosed earlier for this subspecies.

It differs from *R. s. parvus* in averaging larger in all skull, dentary and most external characters (see Table 1). With the following characters it is absolutely larger: ear length, forearm length, maximum anterior noseleaf breadth, basal sella length, vertical sella height, vertical sella breadth, greatest skull length, rostrum length and M¹ width (see Table 1).

It differs from *R. s. amiri* subsp. nov. in averaging larger in most skull, dentary, dental and external characters (see Table 1). With a number of characters it is absolutely larger, for example: forearm length, vertical sella height, greatest skull length, zygomatic width, cranial width and C¹M³ length (see Table 1).

Description

Apart from differences described in the diagnosis of *R. s. simplex*, *R. s. keyensis* is very similar to that species. In the two specimens of *R. s. keyensis* available to us, the juncture of the supraorbital ridge is just posterior to the orbital cavity mid point, supraorbital length greater than nasal inflation breadth (Figure 9); median anterior rostral swellings inflated; anterior upper premolar in contact with both canine and posterior premolar;

lower vestigial premolar extruded from toothrow but still in contact with adjacent premolars – in WAM 42642 the anterior and posterior premolars are not in contact, whereas in WAM M42643 they are in solid contact.

The form of the basiphonoid, palate and dentition is similar to *R. s. simplex*.

Externals

The external characters similar to *R. s. simplex* but anterior noseleaf wider (9.2 *v.* 8.1). The vertical sella taller (4.5 *v.* 3.9) and wider (2.4 *v.* 2.0) with a slightly wider mid part than *R. s. simplex*, smoothly rounded at apex.

Pelage and skin colour and baculum

As described for *R. s. simplex*.

Distribution

Kai Kecil I.

Remarks

This form is only weakly separated from *R. s. simplex*; the subspecific distinction resting solely on the shape and size of its sella. In all other characters it appears to be very close to *R. s. simplex*, as attested to by its closeness to that subspecies in discriminant function space (Figures

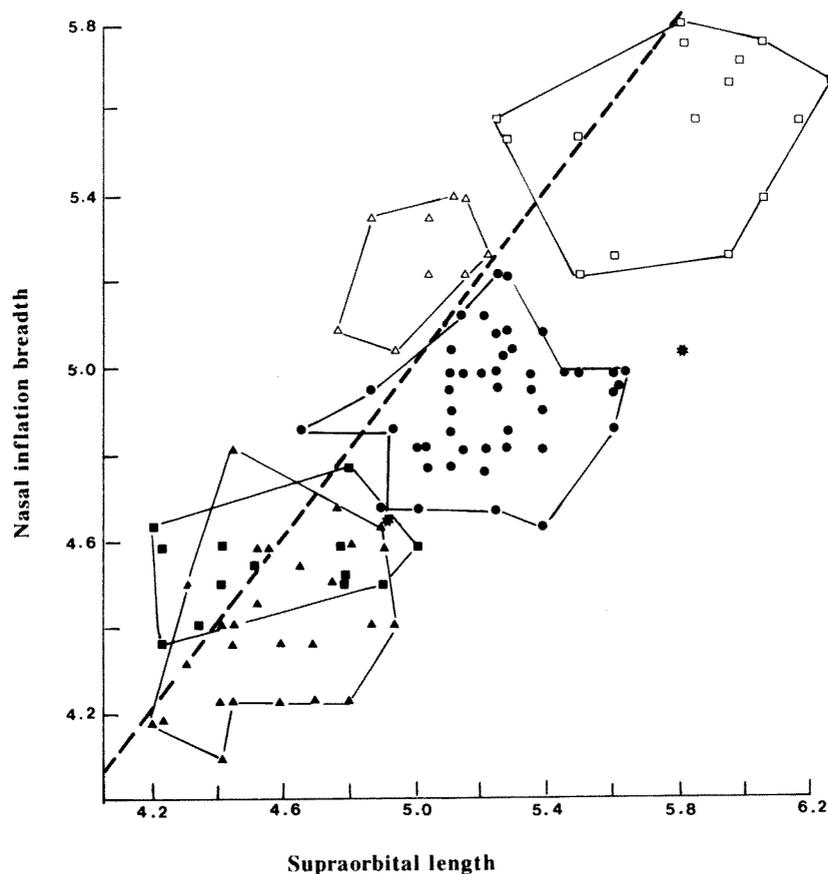


Figure 9 Plot of nasal inflation breadth, NIB, versus supraorbital length, NIL, for the taxa *Rhinolophus simplex simplex*, *R. s. parvus*, *R. s. subsp. nov.* *R. megaphyllus* (□) and *R. borneensis parvus*. The oblique broken line joins values where NIB = NIL. Other taxon symbols as for Figure 1, caption. Following Hill (1992), those forms with values generally below the line should be *R. megaphyllus* while those generally above the line are other species in the 'ferrumequinum' group.

4a, b). Future collections from Tanimbar and Wetar Is may help clarify its taxonomic status with respect to *R. s. simplex*.

Rhinolophus simplex parvus Goodwin, 1979

Rhinolophus borneensis parvus Goodwin, 1979: 102-105.

Holotype

American Museum, Natural History No. 237766, adult male, skin and skull, collected 27 March 1968.

Type locality

Lia Hoo Cave, nr Fatu Maca village, 11 km S Baucau, Timor, altitude ca. 550 m.

Diagnosis

Rhinolophus simplex parvus differs from *Rhinolophus s. simplex* and *R. s. keyensis* as diagnosed earlier for these subspecies.

Differs from *Rhinolophus simplex* subsp. nov. in averaging larger (but with measurements overlapping) in all skull and dentary characters except supraorbital length and lower tooth row

length (Table 1a). Also the relationship between lower tooth row length and : nasal inflation breadth, C^1M^3 length and outer M^3M^3 width differs (Figures 7a,b,c). General body measurements also average larger except those related to facial foliations: maximum noseleaf breadth, basal sella length, vertical sella height, maximum vertical sella breadth.

Description

Apart from differences described in the diagnoses of *R. s. simplex*, *R. s. parvus* is very similar to that subspecies. The skull, however, tends to have the juncture of supraorbital and lambdoidal ridges level with orbital cavity mid point (36%), just posterior (36%) or well posterior from that point (28%); anterior sphenoid/pterygoid bridge tends to obscure more of sphenorbital sinus when viewed from ventral aspect.

Pelage and skin colour also differs slightly. Dorsal pelage Cinnamon Brown, which is colour of distal one-third of hairs, basal part of which is Drab. Ventral surface pure Fawn Color. Wings Grayish Brown, Ears Fawn Color.

Distribution

Timor I. only.

Rhinolophus simplex amiri* Kitchener subsp. nov.*Holotype**

Museum Zoologicum Bogoriense (MZB) No. 15901 (field number WAM M3519; adult female; weight 3.6gm; carcass fixed in 10 percent formalin, preserved in 75 percent ethanol; skull separate; liver in ultrafreeze; collected by D.J. Kitchener on 26 September 1990.

Type locality

Kampung Wawarae, Desa Menia, Savu I., Nusa Tenggara, Indonesia (10°29'S, 121°55'E), collected by hand, from shallow limestone cave, in open woodland, 500 m from sea, altitude 20 m.

Paratypes

Listed in "Specimens examined" section.

Diagnosis

Rhinolophus simplex amiri differs from *R. s. simplex*, *R. s. keyensis* and *R. s. parvus* as described in the earlier diagnoses of these subspecies.

Description

Apart from the differences described in the diagnosis and description of *R. s. simplex* and *R. s. parvus*, *R. s. amiri* is very similar to *R. s. parvus*. The colour of pelage is, however, variable, particularly the Savu specimens. Roti specimens have pelage similar in colour to the usual dark phase of *R. s. simplex*. Semaui specimens are similar to *R. s. parvus*.

Specimens from Savu are distinct and a much paler colour. The dorsal surface has hairs with the basal part Cream Color; on the rump this is tipped with Fuscous which is the dominant colour; on the neck, shoulders and upper back the Fuscous tipping is sparse allowing the Cream Color to appear to provide a vague paler mantle. The chest

and throat pure Cream Color; the abdomen darker because this Cream Color base tipped with Drab.

Distribution

Semaui, Roti, and Savu I., Nusa Tenggara Timur, Indonesia

Etymology

Named after Dr M. Amir, Director, Balitbang Zoologi, LIPI, Indonesia, in recognition for his support of this collaborative research project between 1987 and 1993.

Remarks

Rhinolophus simplex (*R. s. simplex*, *R. s. parvus*, *R. s. amiri* and *R. s. keyensis*) differ from *R. megaphyllus ignifer* in being generally smaller in most skull, dental, dentary and external measurements (see Table 1a, b). For example, greatest skull length 15.30–18.45 v. 18.60–20.00; braincase breadth 6.60–8.45 v. 8.55–9.15; zygomatic width 7.25–9.15 v. 9.05–10.00; nasal inflation breadth 4.10–5.20 v. 5.20–5.80; mastoid width 7.25–8.80 v. 9.00–9.55; outer M³M³ width 5.20–6.65 v. 6.70–7.40; C¹M³ length 5.55–7.10 v. 7.05–7.65; forearm length 35.8–44.9 v. 45.8–48.1. The anterior basisphenoid has a marked depression or pit, rather than a shallow groove that runs smoothly into the basioccipital surface. It also differs in having I₁M₃ length smaller relative to outer cochleae width (Figure 6) and forearm length longer relative to pes length (Figure 11). Baculum base with ventral bifurcated arms much shorter relative to posterior margin of dorsal surface of base (Figure 10).

DISCUSSION

Hill (1992) lists *R. truncatus* Peters, 1871 and *R. nanus* Andersen, 1905 from Bacan I., N. Maluku and Goram I., C. Maluku as a subspecies of *R. megaphyllus*. We have not been able to examine specimens of these forms. However, descriptions of them, along with measurements in Andersen (1905:84), suggest that *R. truncatus* is more allied to

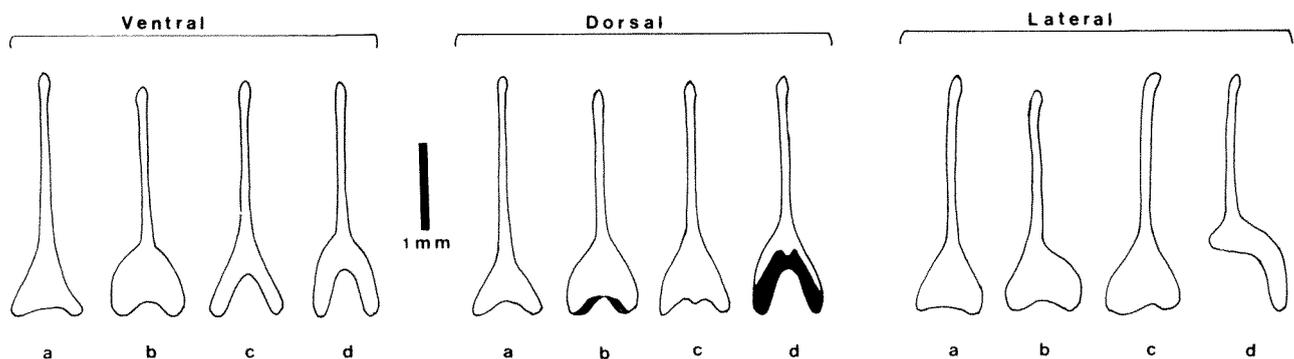


Figure 10 Range of bacula size and shape in *Rhinolophus simplex*, compared to *R. megaphyllus*. (a) *R. s. simplex* (WAM 30249, Sumba); (b) *R. s. subsp. nov.* (WAM M35374, Roti); (c) *R. s. simplex* (WAM M38252, Bali) and (d) *R. megaphyllus* (WAM M29979, Queensland).

Table 7 Nei's unbiased genetic distance between *Rhinolophus simplex* populations and *R. borneensis* from Java.

NUSA PENIDA	0.005							
LOMBOK	0.034	0.033						
SUMBAWA	0.035	0.041	0.000					
MOYO	0.038	0.045	0.004	0.000				
SANGEANG	0.034	0.041	0.000	0.000	0.004			
RINCA	0.038	0.034	0.000	0.004	0.008	0.004		
SUMBA	0.038	0.034	0.000	0.004	0.007	0.005	0.000	
FLORES	0.034	0.033	0.000	0.000	0.000	0.000	0.000	
LEMBATA	0.039	0.036	0.000	0.005	0.009	0.005	0.000	
ALOR	0.070	0.062	0.026	0.030	0.031	0.035	0.026	
TIMOR	0.033	0.038	0.000	0.000	0.002	0.000	0.002	
SEMAU	0.032	0.031	0.000	0.000	0.001	0.002	0.000	
ROTI	0.043	0.035	0.002	0.007	0.010	0.011	0.002	
SAVU	0.028	0.020	0.029	0.038	0.042	0.038	0.030	
JAVA	0.171	0.161	0.162	0.163	0.174	0.172	0.159	
	BALI	NUSA P.	LOMBOK	SUMBAWA	MOYO	SANGEANG	RINCA	

R. megaphyllus whereas the narrower cranium and nasal swellings and overall small size of *R. nanus* are more suggestive of *R. simplex*. However, J.E. Hill (pers. comm.) informed us that the holotype of *R. nanus* is very old and has a damaged skull. Consequently, he considers that the narrowing of the skull of *R. nanus* may well be an artefact because otherwise the skull is very like that of *R. truncatus*.

Hill (1992:100) separated the *R. megaphyllus* species complex (in which he includes *R. s. simplex* and *R. s. keyensis*) from other IndoMalayan species in the *ferrumequinum* group principally on the supraorbital crests combining at a point behind the centre of the orbital cavity; such that the supraorbital length (from junction of crests to nares) is much greater than rather than slightly greater than or equal to the width across the anterior lateral rostral swellings (in our terminology NIL NIB) and the supraorbital depression being larger than it is wide. The association by Goodwin (1979) and Hill (1992) of the form *parvus* with *R. borneensis* and *R. celebensis*, respectively, depended largely on the supraorbital crests of *parvus* merging anterior to the mid point of the orbital cavity. However, in the sample of *parvus* available to us this junction point was variable; sometimes it was level with the point, or just behind or well behind it (an *R. simplex* character). Also the supraorbital length is frequently much greater than the width across the outer lateral rostral swellings (see also Figure 9). Clearly in the form *parvus* (and *amiri*) this latter character is too variable for it to be usefully diagnostic in terms of the association of *parvus*, although it appears to hold true for *R. borneensis* and generally so for *R. megaphyllus* and *R. s. simplex*. Goodwin (1979:104) further considered that *R. simplex* differed from *parvus* in being larger

overall and in having "dentition (that) is somewhat more primitive. The vestigial premolars in both upper and lower jaws are generally not as crowded, but there is some individual variation in this condition" Further, "the sella of *simplex* is slightly constricted and the connecting process is not as prominent". In the specimens available to us there was considerable variation in the extent of crowding in both the upper and lower vestigial premolar, particularly the lower. The lower premolar in both *parvus* and *R. s. simplex* varied in its position from almost being in the toothrow to being completely extruded such that this first and second premolars were in contact. Further we can find no consistent difference between *parvus* and *R. s. simplex* in the shape of either the sella or the connecting process.

We associate the form *parvus* with *R. simplex* rather than with *R. borneensis*, as suggested by Goodwin (1979) or with *R. celebensis* as considered by Hill (1992). This is because of its morphological closeness to *R. simplex* and because, as discussed above, the characters used by these authors to diagnose it from *R. simplex* cannot be substantiated by us. It is also relevant here that our electrophoretic study, using 30 loci, concluded that there was little or no detectable genetic difference between *R. s. simplex*, *R. s. parvus* and *R. s. amiri*. For example the population of *R. s. parvus* (Timor) is not genetically differentiated from several *R. s. simplex* populations (Sangeang, Sumbawa), while two populations of *R. s. amiri* (Roti and Semau) are closer genetically to the majority of the *R. s. simplex* populations than they are to the third population of *R. s. amiri* (Savu). The significance of the apparent clusters within *R. simplex* based on the Nei genetic distance metric is tenuous because it is the product of gene frequency variation at just one or two loci. Thus Alor differentiates due to

Table 7 (continued)

0.000							
0.000	0.000						
0.025	0.006	0.010					
0.002	0.000	0.003	0.029				
0.000	0.000	0.002	0.021	0.000			
0.002	0.000	0.004	0.020	0.006	0.000		
0.030	0.030	0.032	0.057	0.035	0.028	0.030	
0.157	0.166	0.150	0.193	0.169	0.164	0.160	0.151
SUMBA	FLORES	LEMBATA	ALOR	TIMOR	SEMAU	ROTI	SAVU

variability at two loci, *Idh-2* and *Pep-D*, while the Bali-Nusa Penida-Savu cluster is largely due to *Acon-2* allele frequency differences.

Hill (1983) considered that the form *parvus* was very similar to *R. madurensis* Andersen, 1918 from Madura I., a view supported by Bergmans and van Bree (1986) who considered *parvus* synonymous with *R. celebensis madurensis*. We have been unable to examine specimens of the form *madurensis*, but if

parvus is indeed synonymous with *R. celebensis*, then it brings into question the distinction between other species in the *ferrumequinum* group (*sensu* Tate and Archbold 1939).

We have not examined in depth the taxonomic relationships between all the forms of *R. megaphyllus* (*sensu* Hill, 1992). Our conclusions, then, with respect to the specific status of the forms, *R. simplex* (*simplex*, *keyensis*, *parvus* and

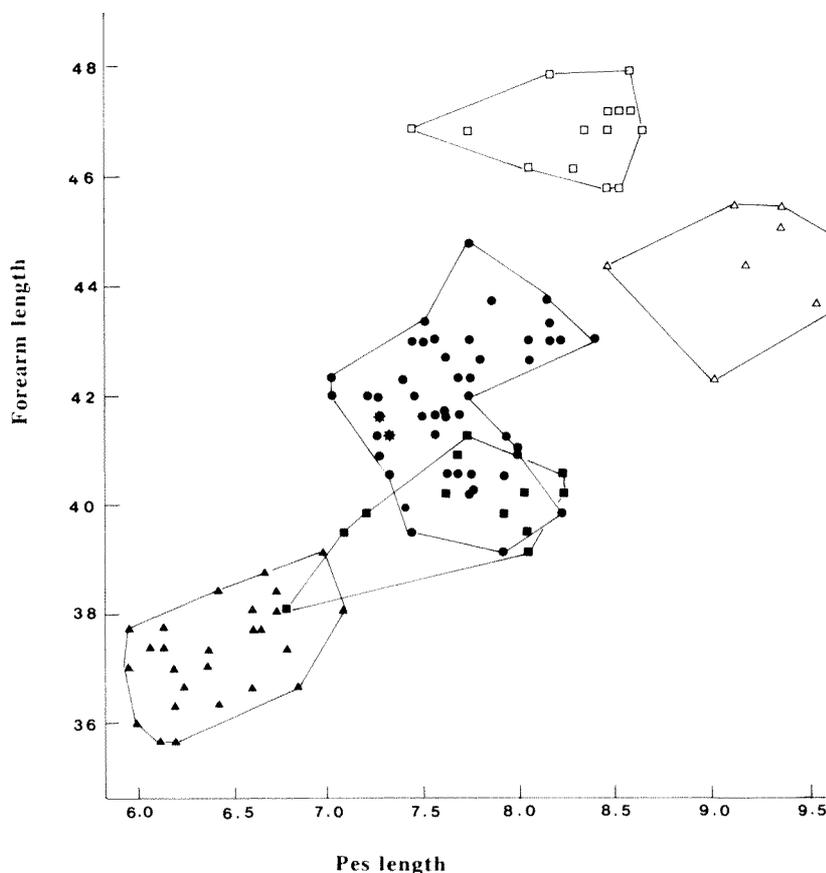


Figure 11 Plot of forearm length versus pes length for *R. simplex* subspecies, *R. megaphyllus* (□) and *R. borneensis*. Other taxa codes as for Figure 1.

Table 8 Mean and range, in mm, and sample size of baculum: greatest length, basal height and basal breadth, for *Rhinolophus simplex* subspecies and *R. megaphyllus*.

	Greatest Length	Basal Height	Basal Breadth	N
<i>R. s. simplex</i>	3.00 (2.67–3.48)	0.85 (0.67–0.99)	0.84 (0.60–0.95)	11
<i>R. s. parvus</i>	2.98 (2.48–3.32)	0.77 (0.76–0.94)	0.78 (0.63–0.97)	3
<i>R. s. amiri</i> subsp. nov.	2.66 (2.64–2.68)	0.74 (0.67–0.85)	0.74 (0.67–0.83)	4
<i>R. megaphyllus</i>	2.70 (2.68–2.72)	0.82 (0.82–0.82)	0.83 (0.78–0.88)	2

amiri), are tentative. Clearly these four forms differ from *R. megaphyllus ignifer* in general size, aspects of the basicranium and shape of basal part of baculum and for *parvus* and *amiri* also in the shape of the rostrum. Some independent support for this decision comes from an electrophoretic study incorporating liver tissue from specimens used in this paper, which shows that Queensland *R. megaphyllus* differs at 17 percent of their electrophoretic loci, including 4 fixed differences, from *R. simplex* (T. Reardon pers. comm.) However, for a complete appraisal of the relationship of these forms with *R. megaphyllus* it would be necessary to compare them in detail with *R. m. megaphyllus* and the smaller forms (*R. m. vandeuseni*) from the islands off northeast New Guinea. These smaller forms of *R. megaphyllus*, which appear to be connected to *R. megaphyllus ignifer* by intermediates (Koopman 1982), are approximately the same size as *R. s. simplex* (see Koopman 1982).

The taxonomic status of the Maluku form *R. annectens* (Wetar I.) is indeterminate. This form is known only from the holotype which we were unable to examine. However, this holotype was examined by J.E. Hill (pers. comm.) who stated that it is a smashed skull, which on size could be *parvus*, or close to it.

Prior to our study, *Rhinolophus simplex* was reported only from Lombok, Sumbawa and Komodo islands, (as *R. s. simplex*); Kai (as *R. s. keyensis*) and Timor (as *R. celebensis parvus*). We have recorded it additionally from Bali, Nusa Penida, Moyo, Sangeang, Rinca, Flores, Lembata, Alor, Sumba, Savu, Roti and Semau. Frequently on these islands it was collected from tunnels built by the Japanese during the Second World War. It was often the only species present in such tunnels.

The occurrence of morphological variation among *Rhinolophus simplex* from some of the Gondwanic islands of the outer Banda Arc (Sumba, Savu, Roti, Semau, Timor and Kai Kecil) reflects similar variation in the microchiropterans *Hipposideros sumbae* and *Taphozous aches* that have been examined from this region (Kitchener and Maryanto 1993; Kitchener *et al.* 1993). The presence on Semau of *R. s. amiri*, a population separated by a narrow water gap of only about three kilometres from *R. s. parvus* on Timor, suggests reduced gene

flow is probably operating between these two populations to maintain these morphological distinctions.

SPECIMENS EXAMINED

Rhinolophus borneensis importunus

INDONESIA

Java I: Kiskenda, 7°6'S, 110°16'E, WAM (M39310–13, M39319–21, M39328, M39354–5, M39361–2, M39367, M39380) (10♂, 4♀).

Rhinolophus megaphyllus ignifer

AUSTRALIA

Queensland: McIlwraith Range, 13°47'S, 142°15'E, WAM M29972 (1♂); Iron Range, 11°37'S, 142°55'E, WAM M29977–86, (6♂♂, 4♀♀); Chillagoe, 17°9'S, 144°31'E, WAM M29973 (1♀); Yarramulla Lava Tunnels, 18°13'30"S, 144°40'30"E, WAM M29974–6 (3♀♀).

Rhinolophus simplex amiri subsp. nov (paratypes)

INDONESIA

Savu I: Desa Menia, 10°29'S, 121°55'E, WAM (M35113, M35117–8, M35120–25, M35127, M35129, M35132–8, M35222, 35260–2) (8♂♂, 15♀♀).

Roti I: Baa, 10°44'S, 123°6'E, WAM (M35351–2, M35370–4, M35376–8, M35380, M35389, M35391–3 (7♂♂, 8♀♀); Sanggoen, 10°43'S, 123°9'E, WAM M35422–3 (2♂♂).

Semau I: Uiasa, 10°10'S, 123°28'E, WAM (M35599, M35604, M35606 (1♂, 2♀♀); Onansila, 10°13'S, 123°30'E, WAM M38014 (1♂).

Rhinolophus simplex parvus

INDONESIA

Timor I: Baumata, 10°11'S, 123°43'E, WAM (M30059, M30096–7, M30123, M30125–6, M30128–40, M30145–7, M30150–2, M30155–7, WAM 30160–2, M30172) (5♂♂, 27♀♀); Panite, 9°50'S, 124°29'E, WAM (M34896, M34897–9, M34960, M34962, M34969–72, M35009) (2♂♂, 10♀♀).

Rhinolophus simplex simplex

INDONESIA

Bali I.: Candi Kuning, 8°7'S, 115°9'E, WAM 38441

(1 ♀); Payongan 8°29'E, 115°15'E, WAM M38424 (1 ♀); Ubud, 8°30'S, 115°16'E, WAM (M38372, M38409) (1 ♂, 1 ♀); Gianyar, 8°23'S, 115°23'E, WAM (M38252-3, M38263, M38265, M38268, M38270, M38273) (3 ♂ ♂, 4 ♀ ♀).

Nusa Penida I: Sampalan, 8°41'S, 115°34'E, WAM (M39580-1, M39584) (3 ♀ ♀).

Lombok I: Ngaln, 8°55'S, 116°17'E, WAM (M31111, M33860-4) (2 ♂ ♂, 4 ♀ ♀).

Sumbawa I: Desa Belo, 8°52'S, 116°50'E, WAM (M31336-7) (1 ♂, 1 ♀); Desa Sangeang, 8°18'S, 118°56'E, WAM (M31601-4, M31619) (1 ♂, 4 ♀).

Moyo I: Brang Kua, 8°14'15"S, 117°36'45"E, WAM (M31912-5, M31921) (3 ♂ ♂, 2 ♀ ♀); Tanjung Pasir, 8°23'15"S, 117°31'30"E, WAM (M31952-3, WAM M31962-4, M31966, M31968-79) (7 ♂ ♂, 12 ♀ ♀).

Sangeang I: 8°13'30"S, 119°00'20"E, WAM M31588 (1 ♂).

Rinca I: 8°39'S, 119°40'E, WAM (M32930-2, M32937-9) (6 ♂ ♂).

Flores I: Daraloeng Baru, 8°33'S, 122°39'E, WAM (M32589-90, M32597-8) (2 ♂ ♂, 2 ♀ ♀).

Alor I: Kalahabi, 8°14'S, 124°32'E, WAM (M37615-7, M37651-2, M37654) (1 ♂, 5 ♀ ♀).

Lembata I: Kampung Merdeka, 8°22'S, 123°31'E, WAM M32286 (1 ♀); Desa Boto, 8°31'S, 123°23'E, WAM M32429-30 (2 ♂ ♂).

Sumba I: Waingapu, 9°37'S, 120°14'E, WAM (M30249-50, M30252-3) (3 ♂ ♂, 1 ♀). Bondokodi 9°35'S, 119°8'E, WAM (M30486, M30492) (2 ♂ ♂).

Rhinolophus simplex keyensis

Kai Kecil I: Tual, 5°38'S, 132°44'E, WAM (M42642-3) (1 ♂, 1 ♀).

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Mrs N. Cooper, Western Australian Museum, ran the computer analyses. Mrs S. Dalton and Mrs Anne Nevin, Western Australian Museum, typed the manuscript.

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