

## The *Myotis adversus* (Chiroptera: Vespertilionidae) species complex in Eastern Indonesia, Australia, Papua New Guinea and the Solomon Islands

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**Abstract** – Comparison of cranial, external and bacular morphology and univariate and multivariate statistical analyses of 149 specimens, previously attributed to *Myotis adversus* (Horsfield, 1824) was carried out on specimens principally from eastern Indonesia and Australia. These comparisons indicated the existence of a complex of three species and six subspecies. These taxa are as follows: *Myotis a. adversus* (Java I., Nusa Penida I., Kangean I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Timor I., Savu I.); *Myotis adversus tanimbarensis* subsp. nov. (Yamdena I.); *Myotis adversus wetarensis* subsp. nov. (Wetar I.); *Myotis moluccarum moluccarum* (Western Australia, Seram and Papua New Guinea; and possibly also including the form from Solomon I.); *Myotis moluccarum richardsi* subsp. nov. (Queensland, Northern Territory) and *Myotis macropus* (Victoria and South Australia).

These above taxa have not previously been reported from Nusa Penida I., Kangean I., Sumbawa I., Moyo I., Lembata I., Pantar I., Alor I., Savu I., Yamdena I., and Wetar I.

Multiple regression analysis indicated that while the skull, dentary and dental characters of the above *Myotis* were not significantly influenced by sex, many of the wing measurements were influenced by sex. Almost all characters were very significantly ( $P < 0.001$ ) influenced by locality, but there was no significant interaction between sex and locality.

### INTRODUCTION

*Myotis adversus* (Horsfield, 1824) is a medium sized member of the subgenus *Leuconoe* Boie, 1830 that is characterised by unusually large feet. The species has a wide distributional range from Taiwan, Malaysia, Greater Sunda Islands (Sumatra, Java and Borneo), Lesser Sunda Islands (Flores), Karimata Island, Togian Islands, Peleng Island; Talaud Islands, Maluku Region (Seram, Ambon, Kai Islands), Solomon Islands, New Hebrides and Australia. Over its range it is morphologically very variable; some of this variation has been recognised taxonomically.

A number of authors have reviewed or commented upon the taxonomy of *Myotis adversus* (Tate 1941; Phillips and Birney 1968; Medway 1977; Findlay 1972; Hill 1983; Hill in Corbet and Hill 1992). The subspecies of *M. adversus* generally recognised are:

*Myotis adversus adversus* (Horsfield, 1824) – Java, Lesser Sunda Islands, Malaysia (?);

*M. a. taiwanensis* Arnäck-Christie Linde, 1908 – Taiwan;

*M. a. carimatae* Miller, 1906 – Borneo, Karimata Island;

*M. a. moluccarum* (Thomas, 1915) – Sulawesi, Maluku Region, New Guinea;

*M. a. solomonis* (Troughton, 1929) – Solomon Islands;

*M. a. orientis* Hill, 1983 – New Hebrides; and

*M. a. macropus* (Gould, 1855) – South Australia

Hill (1983) followed Phillips and Birney (1968) in placing *M. a. solomonis* in synonymy with *M. a. moluccarum*.

There is some contention as to the subspecific status of the Australian form of *Myotis adversus*. Dobson (1878) compared the types of *Vespertilio macropus* with *Vespertilio adversus* and concluded that he was "quite unable to discover any difference. Both agree in dentition, in the form of the head and ears, and in all other respects". Thomas (1915) agreed with Dobson (1878) that the type of *V. macropus* cannot be distinguished from Javanese *V. adversus*. However, Thomas (1915) incorrectly stated that the type of *V. macropus* was from Western Australia, when it was in fact from South Australia (Mahoney and Walton 1988).

Thomas (1915) included a specimen from Port Essington, Northern Territory, Australia, in his description of *Leuconoe moluccarum* and noted that

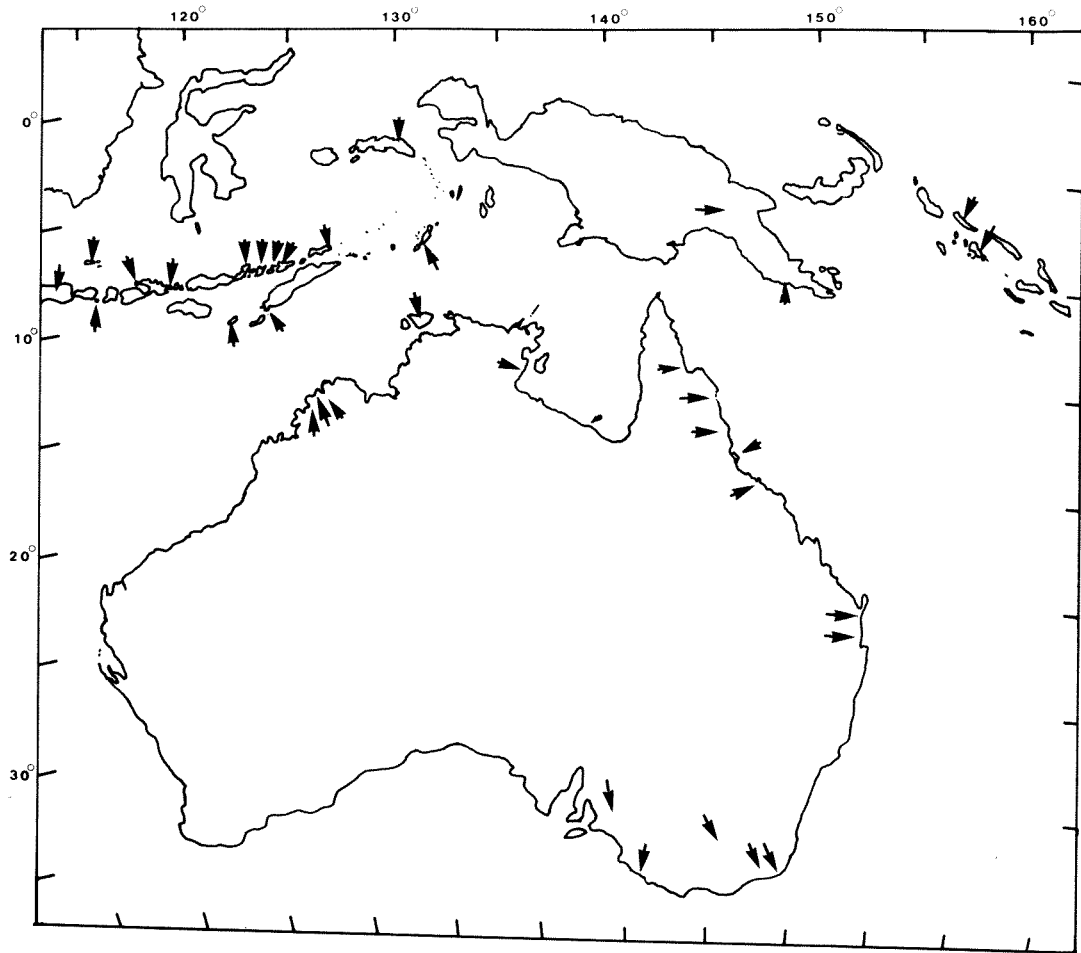


Figure 1 Locality of *Myotis* specimens examined in this study.

this form is very decidedly smaller than *M. adversus macropus* (from South Australia). Tate (1952) examined three specimens of *Myotis* (*Leuconoe*) from Cairns, Northern Queensland, Australia, and although they were of similar size to *Myotis adversus moluccarum* from New Guinea, he considered them representative of *M. adversus macropus*, rather than *M. a. moluccarum*.

Koopman (1984:12) also considered that only one subspecies of *Myotis adversus* (*macropus*) occurred in Australia and stated that its distribution extended from "northeastern Western Australia around the northern and eastern coasts to southeastern South Australia but apparently nowhere extending far inland" Richards (1983) and Mahoney and Walton (1988) recognised *M. a. moluccarum* from Northern Australia and *M. a. macropus* from south and eastern Australia.

A number of terrestrial vertebrate faunal surveys in Nusa Tenggara and the Maluku Tenggara regions of Indonesia, between November 1987 and November 1993, were carried out jointly by staff of the Western Australian Museum and Museum Zoologicum Bogoriense. These surveys resulted in extensive collections of *Myotis adversus* (*sensu lato*) on islands from which they had not previously

been recorded. These recent collections bridge the previous distributional gap between the Oriental and Australian *M. adversus* (*sensu lato*) and allow for a reappraisal of the taxonomy of some of the forms of *M. adversus*.

This paper reports on a taxonomic reappraisal of *Myotis adversus* (*sensu lato*), based on a morphological examination of specimens principally from eastern Indonesia and Australia.

#### MATERIALS AND METHODS

A total of 149 specimens (listed in the specimens examined section) was examined from a number of localities in the Indonesian and Australo-papuan region (Figure 1). These were from Java (2), Nusa Penida (6), Kangean Island (1), Sumbawa Island (5), Moyo Island (1), Flores Island (3), Lembata Island (1), Pantar Island (1), Alor Island (38), Wetar Island (18), Yamdena Island (8), Seram Island (1), Timor Island (1), Savu Island (4), Papua New Guinea (2), Solomon Islands (2), Queensland (12), Northern Territory (2), Western Australia (22), New South Wales (1), Victoria (14) and South Australia (4). All the specimens from Indonesia are currently lodged in the Western Australian

Museum (WAM prefix). At the completion of the project holotypes of new taxa and half the other specimens will be returned to Museum Zoologicum Bogoriense. Other specimens were borrowed from the British Museum, Natural History (BMNH), Queensland Museum (JM), Australian Museum, Sydney (AM), Museum of Victoria (C) and South Australian Museum (SAM).

Twenty measurements of skull, dentary and dental characters and 14 external characters (all in mm) were recorded to 0.1 mm for external characters and 0.01 mm for the other characters.

The measurements recorded were: GSL, greater skull length; CBL, condylobasal length; BB, braincase breadth, ZW, zygomatic width; MW, mastoid width; CH, cranial height; RL, rostrum length; AOW, width between anteorbital foramen; LIB, least interorbital breadth; PPL, postpalatal breadth; MFB, mesopterygoid fossa breadth; BUL, bulla length (excluding cochlear process); C<sup>1</sup>C<sup>1</sup>W, width between outer surface of upper canines (at level of alveoli); M<sup>3</sup>M<sup>3</sup>W, width between outer surface of upper last molars (at level of alveoli); I<sup>1</sup>M<sup>3</sup>L, length between anterior edge of I<sup>1</sup> alveoli to posterior edge of M<sup>3</sup> alveoli; C<sup>1</sup>M<sup>3</sup>L, length between anterior edge of C<sup>1</sup> alveoli to posterior edge of M<sup>3</sup> alveoli. M<sup>2</sup>B, M<sup>2</sup> crown breadth; DL, dentary length from condyle to I<sub>1</sub> anterior alveoli edge, I<sub>1</sub>M<sub>3</sub>L, length between anterior I<sub>1</sub> alveoli edge to posterior M<sub>3</sub> alveoli edge; SVL, tip of rhinarium to anus length; TV, distal tip of tail to anus length; EL, ear length; TIB, tibia length; PES, pes length; FA, forearm length; D3M, D4M and D5M – digit 3 to 5 metacarpal length; D3P1, D4P1, D5P1 – digit 3 to 5 phalanx 1 length; D3P2, D4P2 – digit 3 and digit 4 phalanx 2 length.

Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with all cranial sutures fused and without swelling on the epiphyseal joints of the wing digits.

The effect of sex and island on all characters, except zygomatic width (values missing from many specimens) was examined by multiple regressions for those localities with both sexes present (Java, Nusa Penida, Sumbawa, Alor, Wetar, Yamdena, Savu Western Australia, Queensland, Victoria and South Australia for males – and the same group for females, except Java). Examination of the residuals from regression analysis gave no indication of heteroscedasticity. Because of the number of associations being tested in the multiple regression analysis the level of significance was set at P<0.01,

Stepwise canonical variate (discriminant function) analyses (DFA) were run for all skull, dentary and dental characters for males and females combined after first testing for sexual dimorphism. External measurements were

analysed separately from these other characters and localities were grouped following the groups indicated by the DFA of the skull, dentary and dental characters. In all instances DFA was run using all characters and each island as a group. These islands were then placed into broader groups and the DFA repeated using all characters and these new broad groupings. From this latter

**Table 1** Multiple regression on sex and locality (see text) of *Myotis* for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. For explanation of character codes see Materials and Methods section. Probability levels are \*, 0.05>p>0.01; \*\*, 0.01>p>0.001; and \*\*\*, p<0.001.

Table 1a			
Character	Main Effects		Interaction Sex. Location
	Sex	Location	
GSL	0.066	24.034***	0.472
CBL	0.716	21.410***	0.485
BB	0.828	27.613***	0.527
MW	0.675	17.075***	0.671
CH	0.130	10.944***	1.053
RL	0.556	15.126***	0.524
AOB	0.365	11.587***	1.539
LIB	4.828*	11.956***	1.723
PPL	3.744	10.593***	1.667
MFB	6.091*	6.262***	2.429*
BUL	0.396	9.946***	1.518
C <sup>1</sup> C <sup>1</sup> W	0.239	2.519*	0.400
M <sup>3</sup> M <sup>3</sup> W	1.476	25.723***	0.685
C <sup>1</sup> M <sup>3</sup> L	2.563	26.264***	0.856
I <sup>1</sup> M <sup>3</sup> L	2.504	24.405***	0.743
M <sup>2</sup> B	0.948	2.389*	0.448
ANRAM	0.000	14.651***	0.453
DL	0.163	23.486***	1.181
I <sub>1</sub> M <sub>3</sub> L	1.230	25.747***	1.206
d.f.	1,87	9,87	9,87

Table 1b			
Character	Main Effects		Interaction Sex. Location
	Sex	Location	
SVL	0.987	3.003**	1.142
TV	0.745	12.689***	1.228
EL	0.005	41.009***	0.786
TIB	5.011*	35.391***	1.854
PES	0.038	25.312***	1.009
FA	11.784**	48.818***	1.027
D3M	11.059**	36.414***	1.157
D3P1	7.668**	73.116***	1.992
D3P2	2.917	35.852***	1.069
D4M	9.448**	33.668***	1.460
D4P1	6.556*	26.135***	1.062
D4P2	1.400	10.579***	0.653
D5M	9.713**	34.009***	1.677
D5P1	6.915*	8.008***	1.083
d.f.	1,91	8,91	8,91

**Table 2** Measurements, in mm, for (a) skull, dentary and dental characters, and (b) external characters (see Materials and Methods for explanation of character codes) of adult *Myotis adversus* (all populations); *M. a. adversus* (Java I; Kangean Is, Nusa Penida I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Timor I., Savu I.); *M. a. tanimbarensis* subsp. nov. (Yamdena I.); *M. a. wetarensis* subsp. nov. (Wetar I.); *Myotis adversus* subsp. indet. (New South Wales); *Myotis moluccarum* (all populations); *M. m. moluccarum* (Western Australia, Papua New Guinea, Seram I.); *M. m. richardsi* subsp. nov. (Queensland, Northern Territory); *M. moluccarum* (Solomon Is) and *Myotis macropus* (Victoria, South Australia). N = sample size; SD = standard deviation; MIN = minimum; and MAX = maximum.

**Table 2a**

Taxon		GSL	CBL	BB	ZW	MW	CH	RL	AOB	LIB
<i>Myotis adversus</i> (all populations)	N	73	73	73	63	73	73	73	73	73
	MEAN	16.55	15.13	8.11	10.40	8.56	6.35	4.85	4.48	4.06
	SD	0.30	0.30	0.13	0.21	0.17	0.13	0.17	0.14	0.10
	MIN	15.72	14.47	7.70	9.60	8.08	5.89	4.34	4.12	3.85
	MAX	17.20	15.85	8.40	10.75	8.91	6.64	5.22	4.76	4.31
<i>Myotis adversus</i> <i>adversus</i>	N	46	46	46	45	46	46	46	46	46
	MEAN	16.58	15.10	8.14	10.43	8.58	6.36	4.85	4.44	4.06
	SD	0.25	0.25	0.12	0.18	0.17	0.13	0.14	0.11	0.11
	MIN	15.79	14.59	7.87	9.81	8.19	6.06	4.50	4.12	3.85
	MAX	17.13	15.68	8.40	10.75	8.91	6.64	5.13	4.72	4.31
<i>Myotis adversus</i> <i>tanimbarensis</i>	N	8	8	8	3	8	8	8	8	8
	MEAN	16.14	14.79	8.07	10.07	8.29	6.22	4.65	4.45	4.06
	SD	0.28	0.27	0.17	0.40	0.13	0.14	0.21	0.12	0.11
	MIN	15.72	14.47	7.70	9.60	8.08	5.89	4.34	4.32	3.87
	MAX	16.66	15.31	8.27	10.30	8.52	6.35	4.92	4.66	4.08
<i>Myotis adversus</i> <i>wetarensis</i>	N	18	18	18	14	18	18	18	18	18
	MEAN	16.71	15.37	8.04	10.43	8.62	6.38	4.94	4.61	4.12
	SD	0.23	0.24	0.11	0.11	0.09	0.11	0.15	0.16	0.07
	MIN	16.34	14.92	7.81	10.21	8.49	6.20	4.66	4.16	4.01
	MAX	17.20	15.85	8.25	10.62	8.83	6.61	5.22	4.76	4.26
<i>Myotis adversus</i> subsp. indet	N=1	15.94	14.64	8.16	9.74	8.53	6.25	4.67	4.48	3.97
<i>Myotis moluccarum</i> (all populations)	N	37	37	37	34	37	37	37	37	37
	MEAN	15.64	14.48	7.81	10.06	8.24	6.08	4.46	4.22	3.85
	SD	0.34	0.38	0.18	0.30	0.24	0.18	0.17	0.14	0.12
	MIN	14.98	13.80	7.48	9.50	7.90	5.82	4.17	3.89	3.53
	MAX	16.37	15.39	8.19	10.76	8.91	6.59	4.92	4.51	4.20
<i>Myotis moluccarum</i> <i>moluccarum</i>	N	22	22	22	22	22	22	22	22	22
	MEAN	15.48	14.29	7.70	9.92	8.13	6.01	4.36	4.16	3.87
	SD	0.23	0.19	0.10	0.20	0.15	0.13	0.11	0.08	0.09
	MIN	14.98	13.97	7.48	9.50	7.90	5.84	4.17	4.00	3.71
	MAX	15.82	14.59	7.86	10.28	8.41	6.32	4.62	4.32	4.07
<i>Myotis moluccarum</i> <i>richardsi</i>	N	13	13	13	13	13	13	13	13	13
	MEAN	15.95	14.87	8.01	10.32	8.49	6.17	4.62	4.36	3.88
	SD	0.31	0.35	0.11	0.28	0.23	0.23	0.15	0.09	0.13
	MIN	15.39	14.27	7.85	9.74	8.12	5.82	4.38	4.21	3.71
	MAX	16.37	15.39	8.19	10.76	8.91	6.59	4.92	4.51	4.20
<i>Myotis moluccarum</i> (Solomon Is)	N	2	2	2	2	2	2	2	2	2
	MEAN	15.33	14.00	7.69	9.75	8.01	6.10	4.37	3.91	3.64
	SD	0.36	0.28	0.18	0.17	0.11	0.04	0.09	0.03	0.06
	MIN	15.07	13.80	7.56	9.63	7.93	6.07	4.30	3.89	3.59
	MAX	15.58	14.20	7.82	9.87	8.09	6.12	4.43	3.93	3.68
<i>Myotis macropus</i>	N	15	15	15	12	15	15	15	15	15
	MEAN	16.75	15.66	8.36	10.70	8.70	6.46	4.84	4.58	4.05
	SD	0.46	0.46	0.17	0.38	0.18	0.22	0.21	0.21	0.11
	MIN	16.18	14.91	8.14	10.20	8.48	6.19	4.51	4.32	3.88
	MAX	17.76	16.58	8.70	11.42	9.15	6.87	5.23	5.03	4.20

Table 2a (continued)

PPL	MFB	BUL	C <sup>1</sup> C <sup>1</sup> W	M <sup>3</sup> M <sup>3</sup> W	I <sup>1</sup> M <sup>3</sup> L	C <sup>1</sup> M <sup>3</sup> L	M <sup>2</sup> B	AMRAM	DL	I <sub>1</sub> M <sub>3</sub> L
73	73	73	73	73	73	73	73	73	73	73
5.43	2.26	2.96	4.61	6.80	7.34	6.20	1.73	4.38	12.04	7.90
0.12	0.11	0.11	0.12	0.17	0.17	0.14	0.06	0.15	0.23	0.18
5.17	1.98	2.69	4.33	6.32	7.01	5.90	1.58	4.02	11.43	7.44
5.70	2.52	3.18	4.87	7.06	7.75	6.43	1.87	4.70	12.54	8.20
46	46	46	46	46	46	46	46	46	46	46
5.41	2.28	2.96	4.62	6.82	7.34	6.22	1.71	4.42	12.06	7.93
0.14	0.10	0.09	0.11	0.14	0.14	0.12	0.05	0.15	0.20	0.16
5.19	2.11	2.82	4.33	6.57	7.01	5.92	1.58	4.02	11.63	7.54
5.67	2.52	3.17	4.87	7.06	7.61	6.43	1.79	4.70	12.54	8.18
8	8	8	8	8	8	8	8	8	8	8
5.41	2.27	2.96	4.61	6.82	7.34	6.04	1.70	4.41	12.05	7.94
0.14	0.11	0.10	0.12	0.14	0.14	0.14	0.05	0.15	0.21	0.15
5.30	1.98	2.72	4.34	6.32	7.03	5.90	1.62	4.03	11.43	7.44
5.51	2.28	2.98	4.77	6.70	7.37	6.32	1.79	4.36	12.12	7.90
18	18	18	18	18	18	18	18	18	18	18
5.49	2.31	3.01	4.63	6.89	7.45	6.25	1.79	4.39	11.70	7.64
0.10	0.07	0.11	0.11	0.09	0.14	0.11	0.04	0.13	0.23	0.15
5.17	2.11	2.69	4.44	6.70	7.22	6.06	1.74	4.13	11.43	7.44
5.70	2.42	3.18	4.85	7.02	7.75	6.43	1.87	4.50	12.12	7.90
5.38	2.08	3.13	4.46	6.60	7.04	5.96	1.62		11.73	7.64
37	37	33	37	37	37	37	37	37	37	37
5.29	2.14	2.82	4.49	6.41	6.92	5.88	1.66	4.15	11.52	7.56
0.14	0.08	0.14	0.10	0.14	0.15	0.17	0.07	0.21	0.33	0.20
4.97	1.90	2.58	4.22	6.19	6.68	5.66	1.41	3.77	11.06	7.30
5.62	2.28	3.07	4.68	6.76	7.32	6.38	1.80	4.74	12.32	8.15
22	22	22	22	22	22	22	22	22	22	22
5.28	2.13	2.77	4.50	6.36	6.85	5.79	1.65	4.03	11.32	7.46
0.12	0.06	0.10	0.08	0.10	0.10	0.08	0.07	0.09	0.18	0.11
4.97	2.01	2.58	4.40	6.19	6.68	5.66	1.41	3.77	11.06	7.30
5.51	2.23	3.01	4.68	6.58	7.06	5.96	1.79	4.21	11.69	7.71
13	13	9	13	13	13	13	13	13	13	13
5.34	2.17	2.96	4.50	6.51	7.03	6.03	1.68	4.35	11.86	7.74
0.14	0.08	0.12	0.11	0.16	0.16	0.18	0.08	0.22	0.27	0.23
5.11	2.08	2.77	4.33	6.26	6.74	5.77	1.58	4.00	11.43	7.35
5.62	2.28	3.07	4.67	6.76	7.32	6.38	1.80	4.74	12.32	8.15
2	2	2	2	2	2	2	2	2	2	2
5.05	1.97	2.62	4.28	6.31	6.83	5.82	1.67	4.08	11.20	7.40
0.07	0.09	0.06	0.08	0.01	0.13	0.11	0.05	0.21	0.17	0.12
5.00	1.90	2.58	4.22	6.30	6.74	5.74	1.63	3.93	11.08	7.31
5.10	2.03	2.66	4.34	6.31	6.92	5.90	1.70	4.23	11.32	7.48
15	15	15	15	15	15	15	15	15	15	15
5.67	2.26	3.05	4.63	6.94	7.54	6.42	1.71	4.50	12.39	8.18
0.17	0.09	0.12	0.22	0.21	0.24	0.19	0.11	0.16	0.36	0.24
5.35	2.13	2.85	4.35	6.64	7.13	6.12	1.56	4.23	11.87	7.79
5.95	2.44	3.27	5.18	7.37	7.93	6.76	1.89	4.83	13.10	8.60

Table 2b

Taxon		SVL	TV	EL	TIB	PES	FA	D3M	D3P1	D3P2	D4M	D4P1	D4P2	D5M	D5P1
<i>Myotis adversus</i> (all populations)	N	71	71	71	71	71	71	71	71	71	71	71	71	71	71
	MEAN	48.2	42.4	16.7	19.0	11.5	42.6	41.8	17.8	16.1	40.4	11.7	10.3	38.9	10.0
	SD	2.6	3.4	0.8	0.7	0.5	1.4	1.6	0.9	0.9	1.6	0.6	0.8	1.4	0.5
	MIN	42.6	33.4	14.1	16.1	10.2	38.0	37.6	15.5	13.2	35.4	9.6	8.3	34.4	8.8
	MAX	55.0	48.4	18.2	20.6	12.5	45.2	44.6	20.2	18.2	42.8	13.4	12.1	41.8	11.6
<i>Myotis adversus</i> <i>adversus</i>	N	46	46	46	46	46	46	46	46	46	46	46	46	46	46
	MEAN	48.4	43.1	17.1	19.0	11.7	42.4	41.7	18.0	16.2	40.4	11.8	10.4	39.1	10.1
	SD	2.5	2.8	0.6	0.6	0.5	1.1	1.3	0.8	0.8	1.3	0.5	0.8	1.2	0.5
	MIN	43.3	35.7	15.5	17.4	10.7	40.1	38.2	16.2	14.7	37.1	10.7	8.4	36.0	9.0
	MAX	55.0	48.4	18.2	20.0	12.5	44.4	44.4	20.2	18.2	42.8	13.4	12.1	41.8	11.6
<i>Myotis adversus</i> <i>tanimbarensis</i>	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	MEAN	46.8	36.6	15.6	18.5	11.0	41.2	39.7	16.7	14.7	38.4	11.0	9.2	36.7	9.2
	SD	2.8	3.0	0.3	0.4	0.6	1.1	1.4	0.5	0.6	1.6	0.5	0.5	1.4	0.4
	MIN	42.6	33.4	15.2	18.0	10.2	39.9	37.6	16.1	13.9	35.9	10.3	8.5	35.1	8.8
	MAX	49.9	40.1	16.1	19.3	11.8	43.2	42.1	17.3	15.3	40.9	11.6	9.7	39.3	9.8
<i>Myotis adversus</i> <i>wetarensis</i>	N	17	17	17	17	17	17	17	17	17	17	17	17	17	17
	MEAN	48.3	43.2	16.4	19.5	11.3	43.8	43.1	18.1	16.5	41.3	11.7	10.6	39.6	9.9
	SD	2.9	3.0	0.4	0.6	0.4	0.8	0.9	0.6	0.6	0.9	0.3	0.6	0.8	0.3
	MIN	42.7	36.2	15.8	18.7	10.8	42.3	41.4	16.8	15.6	39.6	11.0	9.2	38.5	9.5
	MAX	51.5	47.1	17.4	20.6	12.0	45.2	44.6	18.7	17.7	42.5	12.2	11.6	40.7	10.4
<i>Myotis adversus</i> subsp. indet.	N=1	49.3	39.6	14.1	16.1	10.5	38.0	37.8	15.5	13.2	35.4	9.6	8.3	34.4	9.0
<i>Myotis</i> <i>moluccarum</i> (all populations)	N	37	37	37	37	37	37	37	37	37	37	37	37	36	37
	MEAN	45.0	38.1	15.1	16.7	9.8	38.2	37.2	14.2	13.4	36.6	10.1	8.7	35.4	9.3
	SD	3.3	2.1	0.6	0.6	0.5	1.2	1.1	0.6	0.8	0.9	0.5	0.7	0.9	0.3
	MIN	34.8	34.3	13.8	15.6	8.6	35.4	34.0	12.7	11.2	35.0	9.0	6.7	33.7	8.6
	MAX	54.3	42.4	16.0	18.1	11.0	41.0	39.1	15.7	15.2	38.5	11.5	10.3	37.1	10.2
<i>Myotis</i> <i>moluccarum</i> <i>moluccarum</i>	N	22	22	22	22	22	22	22	22	22	22	22	22	21	22
	MEAN	45.2	38.1	15.4	16.7	9.9	37.7	36.8	14.1	13.1	36.3	10.1	8.8	35.2	9.3
	SD	2.0	2.1	0.5	0.6	0.6	1.1	1.2	0.6	0.6	0.8	0.4	0.6	0.8	0.4
	MIN	41.2	34.3	14.2	15.6	8.6	35.4	34.0	12.7	11.2	35.0	9.0	7.9	33.7	8.6
	MAX	49.0	42.1	16.0	18.1	10.8	39.7	38.4	15.1	14.1	37.6	10.8	10.3	36.6	9.9
<i>Myotis</i> <i>moluccarum</i> <i>richardsi</i>	N	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	MEAN	45.5	37.9	14.6	16.8	9.8	38.8	37.7	14.2	13.5	37.0	10.1	8.6	35.6	9.4
	SD	4.1	2.3	0.5	0.5	0.5	1.1	0.9	0.5	0.9	0.9	0.3	0.8	1.1	0.3
	MIN	37.1	35.3	13.8	16.1	9.0	37.0	35.8	13.4	11.8	35.3	9.4	6.7	33.7	9.0
	MAX	54.3	42.4	15.2	17.8	11.0	41.0	39.1	15.0	15.2	38.5	10.5	9.9	37.1	10.2
<i>Myotis</i> <i>moluccarum</i> (Solomon Is)	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	MEAN	39.1	37.5	14.7	16.7	9.8	39.6	37.3	15.0	14.2	36.2	10.6	8.4	35.3	9.3
	SD	6.2	3.5	0.1	0.3	0.4	1.1	1.1	0.9	0.3	1.6	0.4	0.0	1.4	0.3
	MIN	34.8	35.1	14.6	16.5	9.5	38.8	36.5	14.4	14.0	35.1	10.3	8.4	34.3	9.1
	MAX	43.5	40.0	14.7	17.0	10.0	40.4	38.1	15.7	14.5	37.3	10.8	8.4	36.2	9.5
<i>Myotis macropus</i>	N	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	MEAN	47.1	38.8	15.2	17.5	11.0	40.3	39.4	14.8	14.1	38.3	10.4	9.3	36.9	9.8
	SD	2.6	2.3	0.5	0.5	0.7	1.1	1.2	0.7	0.5	1.34	0.7	0.9	1.1	0.4
	MIN	41.7	34.4	14.3	16.5	9.9	38.2	37.2	13.7	13.1	36.7	9.1	6.6	35.0	9.4
	MAX	50.5	43.4	15.8	18.3	12.3	41.8	41.1	15.8	14.9	40.5	11.4	10.0	38.2	10.7

analysis a reduced set of 5-10 characters was selected. It is the DFA based on this reduced set of characters that is discussed in the text, because in all instances they provided similar discriminant function plots to those of the complete set of characters. These reduced set of characters were selected in all these analyses because the sample size of the smallest *a priori* group selected approximated, or was less than, the number of characters in the analysis. This reduced set of characters was chosen because they provided values that minimise Wilk's lambda. The statistical software used throughout was SPSS PC+.

## RESULTS AND DISCUSSION

### Univariate statistics

Multiple regressions were run separately for skull, dentary and dental characters, excluding zygomatic width which was missing values from many specimens, and external characters because these analyses utilised different sets of locations and sample sizes.

#### Skull, dentary and dental characters

*Sex.* No characters were significantly influenced by sex alone, although least interorbital breadth and mesopterygoid fossa breadth were weakly associated with sex ( $F_{1,87} = 4.828$ ;  $P = 0.031$  and  $F_{1,87} = 6.091$ ;  $P = 0.016$ , respectively) (Table 1a).

*Location.* All characters, except  $C^1C^1$  width and  $M^2$  breadth were very significantly ( $P < 0.001$ ) influenced by location alone (Table 1a).

*Interaction.* There were no significant interactions, although there was a weak interaction between sex and location for mesopterygoid fossa breadth ( $F_{9,87} = 2.429$ ;  $P = 0.016$ ) (Table 1a).

#### External characters

*Sex.* A number of characters representing wing size were influenced by sex alone, with females being larger than males. These characters were forearm length ( $F_{1,91} = 11.784$ ;  $P = 0.001$ ); digit 3 metacarpal length ( $F_{1,91} = 11.059$ ;  $P = 0.001$ ); digit 3 phalanx 1 length ( $F_{1,91} = 7.668$ ;  $P = 0.007$ ); digit 4 metacarpal length ( $F_{1,91} = 9.448$ ;  $P = 0.003$ ); and digit 5 metacarpal length ( $F_{1,91} = 9.713$ ;  $P = 0.003$ ) (Table 1b).

*Location.* All characters were significantly ( $P < 0.001$ ) influenced by location alone. The lack of significant interaction between sex and location indicates that the relationship between wing size of male and females was consistent for all locations.

Mean, standard deviation, minimum and maximum values and sample size for each locality are presented in Table 2 for skulls, dentary and dental characters (2a) and external body characters

(2b) for all characters examined for the locations or location groupings determined in this study to have taxonomic significance. Values for males and females are combined for both the skull, dentary and dental characters and for the external characters. Although most of the wing measurements for females were larger than those of the males, these differences were generally greatly exceeded by the differences between islands or groups of islands.

### Multivariate analyses

In the subsequent DFA of skull, dentary, dental and external characters, males and females were combined. This is appropriate for the skull, dentary and dental characters because they were not significantly influenced by sex. It is less satisfactory for the external characters because many of the wing measurements were influenced by sex. For this reason, the location groupings (possibly representative of putative taxa) were selected on the basis of the skull, dentary and dental characters. The external characters were then placed into location groupings as for the skull and other characters. It was considered that the loss of distinction between the recognised island groupings, or taxa, based on their external measurements, would be minimal because location differences far exceeded sex differences for most of the external characters (Table 1b).

#### All locations – skull, dentary and dental characters

DFA was run on a reduced set of 10 selected characters (listed in Table 3a) for all locations. Three groupings of locations were apparent. These were:

- (i) The Lesser Sunda Group (Java I., Kangean I., Nusa Penida I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Wetar I., Yamdena I., Timor I., Savu I., New South Wales);
- (ii) The Western Australian Group (Western Australia, Northern Territory, Queensland, Seram, Papua New Guinea and Solomon Islands); and
- (iii) The Victorian Group (Victoria, South Australia).

A DFA using the above 10 characters and these three *a priori* groupings extracted two highly significant Functions. Function 1 explained 72.2% of the variance and Function 2, 27.8%.

A total of 97.6% of individuals were classified to their correct group. Misclassifications were in the Lesser Sunda Group, with one specimen from this group allocating to the Victorian Group and two specimens to the Western Australian Group.

Function 1 separated both the Lesser Sunda Group and the Victorian Group from the Western Australian Group (Figure 2a). The characters

**Table 3** Canonical Variate Function coefficients for the three locality groups: Lesser Sunda; Western Australian; and Victorian (see text for clarification). Standardised values followed by (in brackets) unstandardised values for (a) 10 skull and dental characters and (b) seven external characters. For explanation of character codes see Materials and Methods section.

**Table 3a**

Character	Function 1	Function 2
M <sup>3</sup> M <sup>3</sup> W	0.5469 (3.3069)	0.1786 (1.0802)
BB	0.0790 (3.1840)	0.4706 (3.1285)
LIB	0.1569 (1.4119)	-0.1350 (-1.2154)
PPL	0.3856 (2.8807)	0.0581 (0.4341)
C <sup>1</sup> C <sup>1</sup> W	-0.5574 (-4.2458)	0.0018 (0.0134)
GSL	1.2016 (3.5616)	-1.8370 (-5.4449)
CBL	-1.9381 (-5.5309)	2.1724 (6.1994)
RL	0.1723 (0.9570)	-0.9471 (-5.2606)
I <sup>1</sup> M <sup>3</sup> L	0.7461 (4.3581)	0.5446 (3.1809)
M <sup>2</sup> B	-0.0812 (-1.1189)	-0.4262 (-5.8712)
Constant	-58.8462	-22.3024
Variation		
Explained (%)	72.2	27.8

**Table 3b**

Character	Function 1	Function 2
D3P1	0.5373 (0.7249)	-0.7477 (-1.0087)
FA	0.0894 (-0.0752)	0.8681 (0.7301)
D5P2	0.4108 (-0.9332)	0.6058 (1.3762)
TIB	0.3731 (0.6049)	-0.3616 (-0.5862)
D3P2	0.3885 (0.5117)	-0.1650 (-0.2174)
D3M	-0.0544 (-0.0414)	0.4549 (0.3458)
EL	0.3825 (0.5846)	0.0720 (0.1100)
Constant	-35.8578	-23.6352
Variance		
Explained (%)	94.6	5.4

loading most heavily (>0.5) on this Function were: condylobasal length; greatest skull length; I<sup>1</sup>M<sup>3</sup> length; C<sup>1</sup>C<sup>1</sup> width; and M<sup>3</sup>M<sup>3</sup> breadth (Table 3a). Function 2 separated the Victorian Group from both the Lesser Sunda Group and the Western Australian Group. The characters loading most heavily (>0.5) on this Function were: condylobasal length; greater skull length; rostrum length; and I<sup>1</sup>M<sup>3</sup> length (Table 3a). It appears that the Western Australian Group will be distinguished from the other two groups on overall size, particularly skull length, palatal breadth and tooth row length. The Victoria Group separated from the other two groups on a shape difference involving the relationship between condylobasal and greatest skull length, and tooth row length. The Lesser Sunda Group separated from the other two groups on a combination of the above characters.

#### All locations – external characters

DFA was run on a reduced set of seven

characters (listed in Table 3b) using the three above location groupings determined for the skull, dentary and dental characters. This DFA extracted two very significant Functions (Figure 2b). Function 1 explained 94.6% of the variance and Function 2, 5.4%. A total of 95.5% of individuals were classified to their correct group; two specimens from the Victorian Group were misclassified to the Western Australian Group and three specimens from this latter group were misclassified to the Victorian Group.

Function 1 separated the Lesser Sunda Group from both the Western Australian and Victorian Groups. The character loading most heavily (>0.5) on Function 1 was digit 3 phalanx 1 length (Table 3b). Function 2 partially separated the Victorian and Western Australian Groups. The characters loading most heavily (>0.5) on Function 2 were: forearm length; digit 3 phalanx 1 length; and digit 5 phalanx 2 length. (Table 3b). This suggested that these three groups can be separated by aspects of the wing structure, particularly digit 3 phalanx 1 length.

#### The Lesser Sunda Group – skull and dental characters

DFA was run on a reduced set of five skull and dental characters (listed in Table 4a) for all island locations in the Javan Group. Three groupings of islands were apparent. These were:

- (i) The Alor Group (Java, Kangean, Nusa Penida, Sumbawa, Moyo, Flores, Lembata, Pantar, Alor, Timor and Savu);
- (ii) Wetar; and
- (iii) Yamdena.

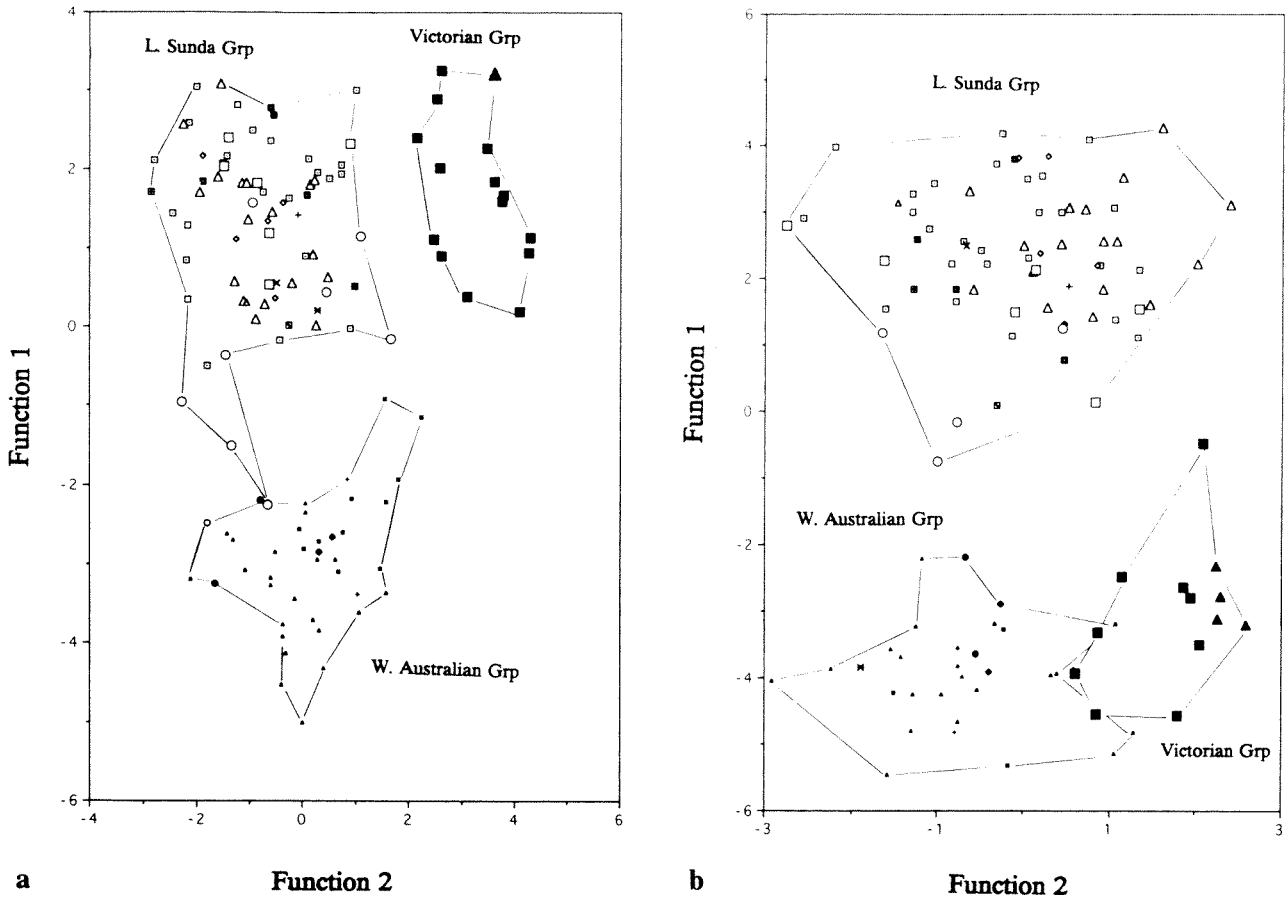
The single New South Wales specimen was left unallocated.

A DFA, using both the above five characters and the three above *a priori* island groupings, extracted two very significant Functions. Function 1 explained 65.1% of the variance and Function 2, 34.9%. A total of 88.9% of specimens were allocated to their correct group. Misclassifications were as follows: Two of the Alor Group were misclassified to Yamdena; three to Wetar. Two from Wetar were misclassified to the Alor Group and one to Yamdena.

The single specimen from New South Wales was classified to the Yamdena population.

Function 1 almost completely separated the Alor Group from the Yamdena population (Figure 3a). The characters loading heavily (>0.5) on Function 1 were M<sup>3</sup>M<sup>3</sup> width; anteorbital foramen breadth; M<sup>2</sup> breadth; and mesopterygoid fossa breadth (Table 4a). Function 2 partially separates the Wetar population from both the Alor Group and the Yamdena population (Figure 3a). The character loading heavily on Function 2 was M<sup>2</sup> breadth.





**Figure 2** Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined and based on three locality groups: Lesser Sunda, Western Australian and Victorian (see text for clarification) for (a) 10 skull, dental and dentary characters; and (b) seven external characters. Locality codes are as follows: □, Alor I.; ◆, Papua New Guinea; ■, Savu I.; ◇, Sumbawa I.; +, Northern Territory; □, Flores I.; ○, Seram I.; ●, Solomon Is; ☒, Java I.; +, Kangean Is; ▩, Lembata I.; X, Moyo I.; X, New South Wales; □, Pantar I.; ■, Queensland; △, Wetar I.; ▲, South Australia; △, Timor I.; ■, Victoria; ▲, Western Australia; and ○, Yamdena I.

*The Lesser Sunda Group – externals*

DFA was run on a reduced set of five characters (listed in Table 4b) using the above three island groupings that were determined for the skull, dentary and dental characters. This DFA extracted two very significant Functions. Function 1 explained 61.7% of the variation and Function 2, 38.3%. A total of 88.2% of individuals were classified to their correct island group. Misclassifications were as follows: Three individuals from the Alor Group to the Yamdena population, four individuals from the Alor Group to the Wetar population; and one individual from the Wetar Group to the Yamdena population. All Yamdena individuals were correctly classified. Function 1 partially separated the Yamdena population from both the Alor Group and the Wetar population (Fig 3b). The character loading heavily (>0.5) on Function 1 was ear length (Table 4b). Function 2 separated the Yamdena and Wetar populations (Fig. 3b). The character loading heavily (>0.5) on Function 2 was forearm length (Table 4b).

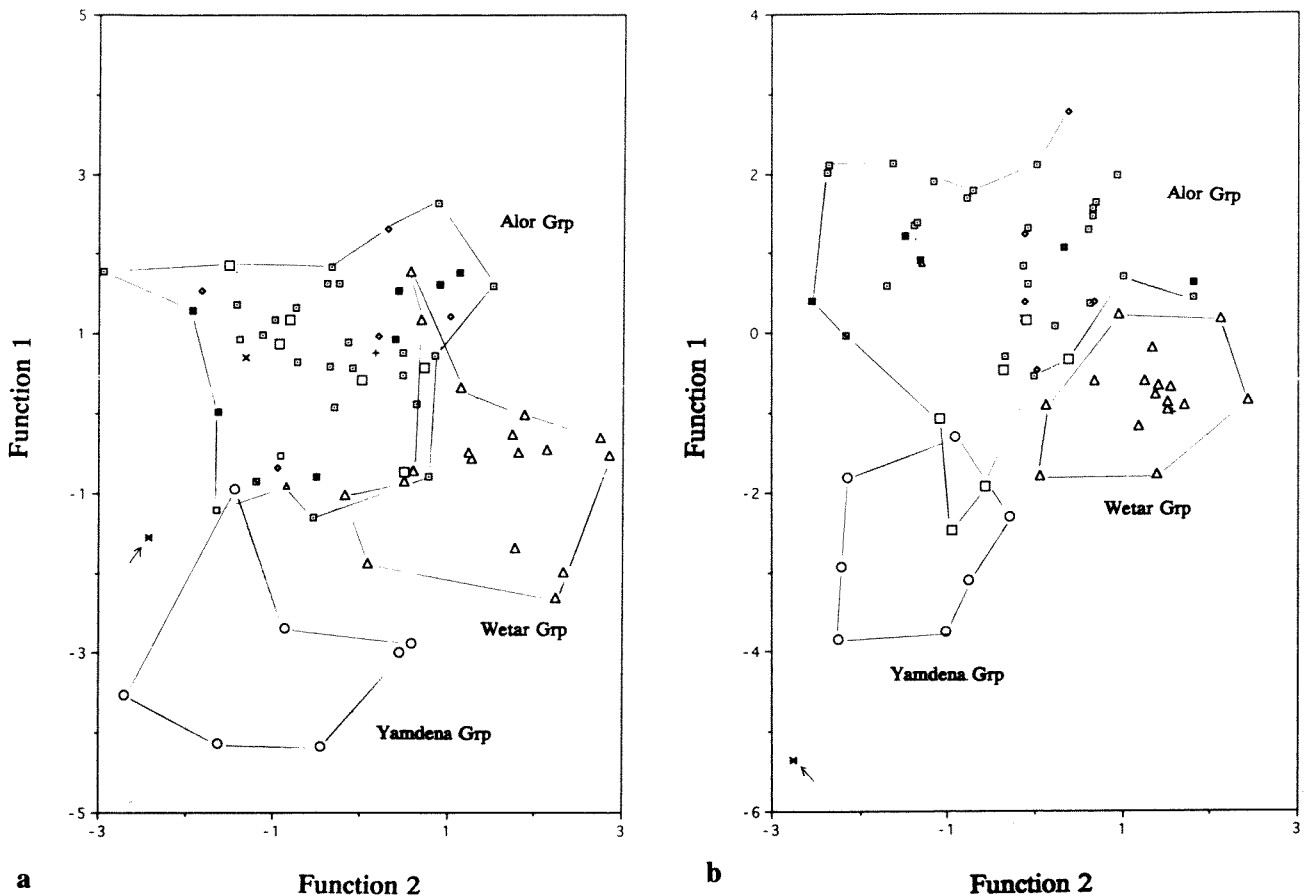
*The Western Australian Group – skull, dentary and dental characters*

DFA was run on all characters, except zygomatic breadth (missing in a number of specimens), for all locations. Four groups were identified. These groups were:

- (i) Western Australia;
- (ii) Queensland and Northern Territory;
- (iii) Solomons; and
- (iv) Papua New Guinea and Seram

The DFA run with these four groups and using all characters, extracted two significant Functions. Function 1 explained 67.4% of the variance and Function 2, 28.7% (Figure 4a). A total of 95% of individuals were classified to their correct group. Misclassifications were in the Queensland/NT Group, where one specimen classified to Western Australia and one to the Papua New Guinea/Seram Group.

A DFA was run again using a reduced set of five characters (dentary length, anteorbital foramen



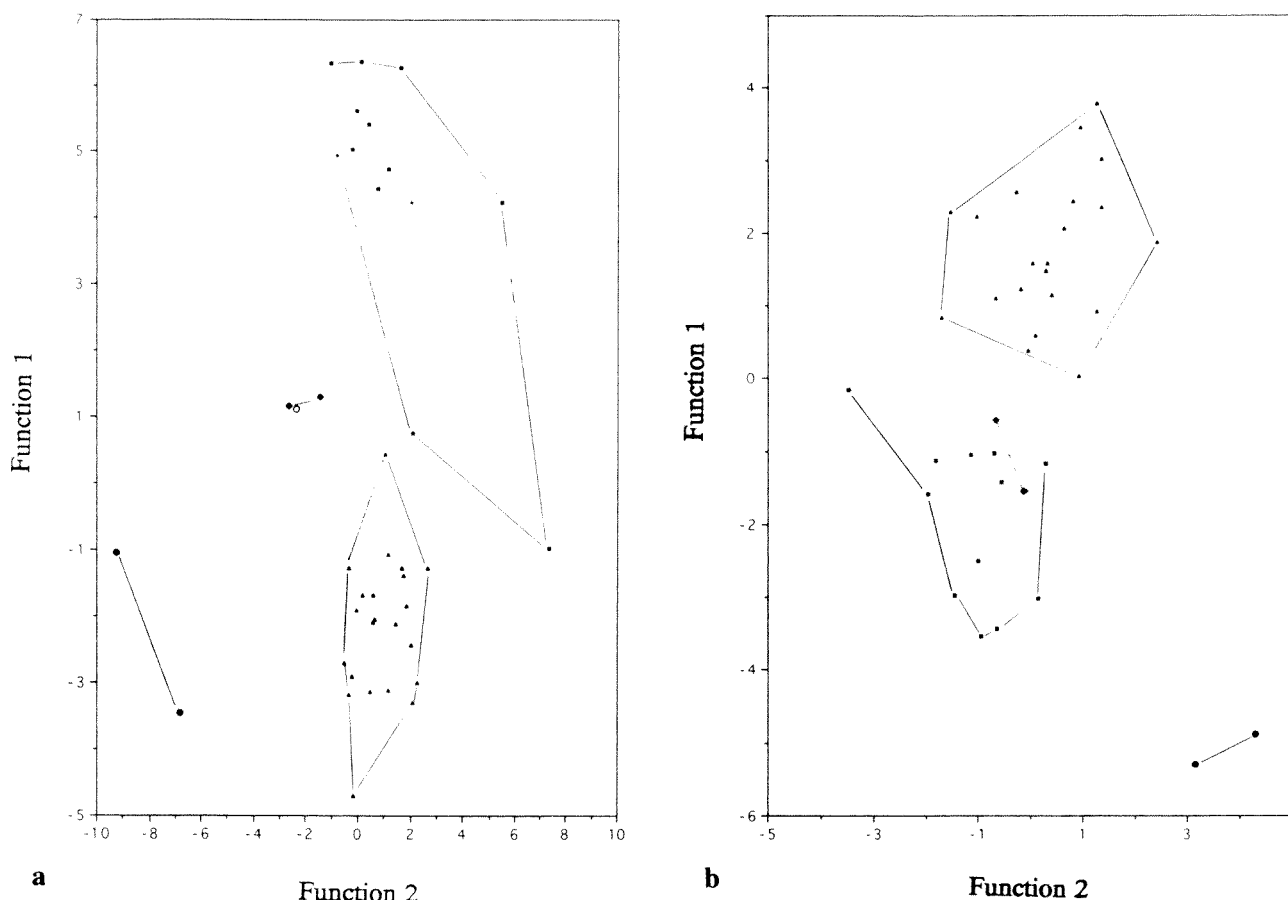
**Figure 3** Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined, based on the following three island groups in the Lesser Sundas: Alor, Wetar and Yamdena. The NSW specimen (arrowed) was unallocated (see text for clarification) for (a) five skull and dental characters and (b) five external characters. Locality codes as for Figure 2 captions.

width,  $M^2$  breadth, least interorbital breadth,  $C^1C^1$  width) selected from the above analysis and using the Western Australia and Queensland/Northern Territory Groups only. The Solomon Island sample ( $N=2$ ) and the Papua New Guinea/Seram sample ( $N=3$ ) were too small to include as groups – so these latter specimens were included in this analysis as unallocated specimens. This analysis extracted a highly significant function with 97.1% of individuals classified to their correct group. Only one specimen was misclassified between these two groups: one from the Western Australian Group was misclassified to the Queensland/NT Group (Figure 5a). On this Function the two Solomon Island specimens allocated to the Western Australian Group while the PNG/Seram individuals were intermediate. The characters loading heavily ( $>0.5$ ) on Function 1 and which were influential in discriminating between the Western Australian Group and the Queensland/NT Group were anteorbital foramen width, dentary length and  $C^1C^1$  width (Table 5a).

#### *The Western Australian Group – externals*

A DFA was run on all characters for the island groupings identified in the earlier DFA analysis on

skull, dentary and dental characters (WA, Qld/NT, Solomons, PNG/Seram). This latter analysis extracted two significant Functions. Function 1 explained 77.6% of the variance, and Function 2 20.6% (Figure 4b). A total of 89.5% of individuals were classified to their correct group. Misclassifications were as follows: one Western Australian Group individual to the Queensland/NT Group and three of this latter group to the Western Australian Group. A DFA was again run using a reduced set of five characters (ear length, forearm length, digit 4 metacarpal length, digit 4 phalanx 2 length and digit 5 metacarpal length) selected from the above analysis and using the Western Australia and Queensland/Northern Territory Groups only. The Solomon Island sample ( $N=2$ ) and the Papua New Guinea sample ( $N=2$ ) were too small to include as groups – so these were included in this analysis as unallocated specimens. This analysis extracted a highly significant Function with 100% of individuals classified to their correct group. On this Function both the two Solomon Island specimens and the Papua New Guinea specimens allocated to the Queensland/NT Group (Figure 5b). The characters loading heavily ( $>0.5$ ) on Function 1, and which were influential in



**Figure 4** Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined based on the following four locality groupings in the Western Australian Group: Western Australia; Queensland/Northern Territory; Papua New Guinea/Seram; and Solomon Is for (a) all skull characters except zygomatic breadth, and (b) all external characters. Locality codes as for Figure 2 caption.

discriminating between the Western Australian Group and the Queensland/NT Group, were forearm length, ear length, digit 5 metacarpal length and digit 4 phalanx 2 length (Table 5b).

In summary, three broad and distinct locality groups were apparent from DFA. These were: (i) the islands of Java, Nusa Penida, Kangean, through Nusa Tenggara to the southwestern islands of Maluku Tenggara, and possibly to New South Wales; (ii) central Maluku, northern Australia, Papua New Guinea to the Solomon Islands; and (iii) southeastern Australia. Further, within the first two of these broad locality groups are a further six recognisable locality subgroups.

These locality groups and subgroups represent putative taxa. These grouped populations of *Myotis* include the following named forms of *Myotis adversus*: *adversus*; *moluccarum*; *macropus*; and *solomonis*. The following taxonomic section allocates these above named forms to their appropriate locality group, describes and rediagnosis the previously named taxa, and proposes and describes three new subspecies to represent unnamed and morphologically distinct populations.

## TAXONOMY

### *Myotis adversus* (Horsfield, 1824)

*Vespertilio adversus* Horsfield, 1824: 2 unnumbered pages

#### Diagnosis

*Myotis adversus* differs from *Myotis moluccarum* in averaging larger in all skull, dental and dentary characters, although none absolutely so (Table 1). For example, greatest skull length 16.55 (15.72–17.20) 73 v. 15.64 (14.98–16.37) 37; braincase breadth 8.11 (7.70–8.40) 73 v. 7.81 (7.48–8.19) 37; zygomatic width 10.40 (9.60–10.75) 63 v. 10.06 (9.50–10.76) 34; I<sup>1</sup>M<sup>3</sup> length 7.34 (7.01–7.75) 73 v. 6.92 (6.68–7.32) 37; and dentary length 12.04 (11.43–12.54) 73 v. 11.52 (11.06–12.32) 37. Greatest skull length generally larger relative to both condylobasal length and braincase breadth (Figures 6 a,b, respectively); and I<sup>1</sup>M<sup>3</sup> length generally greater relative to braincase breadth (Figure 7). It also averages larger in all external measurements. For example ear length 16.7 (14.1–18.2) 71 v. 15.1 (13.8–16.0) 37; tibia length 19.0 (16.1–20.6) 71 v. 16.7 (15.6–18.1) 37; forearm length 42.6 (38.0–45.2) 71 v.

**Table 4** Canonical Variate Function coefficients for the three island groups in the Lesser Sundas; Alor; Wetar and Yamdena; The NSW specimen was unallocated. (see text for clarification). Standardised values followed by (in brackets) unstandardised values for (a) five skull and dental characters and (b) five external characters. For explanation of character codes see Materials and Methods section.

Character	Function 1	Function 2
M <sup>3</sup> M <sup>3</sup> W	0.7386 (5.6645)	0.1247 (0.9561)
M <sup>2</sup> B	-0.5573 (-11.4639)	0.6636 (13.6526)
AOB	-0.6868 (-5.3612)	0.3379 (2.6373)
MFB	0.5213 (5.2694)	0.0790 (0.7985)
I <sub>1</sub> M <sub>3</sub>	0.3722 (2.5111)	0.3305 (2.2301)
Constant	-26.4963	-61.3732
Variance		
Explained (%)	65.1	34.9

Character	Function 1	Function 2
EL	0.6592 (1.2682)	-0.0433 (-0.0833)
FA	-0.1511 (-0.1473)	1.0635 (1.0371)
TV	0.3056 (0.1069)	0.3314 (0.1160)
D4P1	0.3745 (0.7524)	-0.4339 (-0.8719)
PES	0.3451 (0.7368)	-0.1338 (-0.2857)
Constant	-36.7853	-34.2812
Variance		
Explained (%)	61.7	38.3

38.2 (35.4–41.0) 37; tibia length 19.0 (16.1–20.6) 71 *v.* 16.7 (15.6–18.1) 37; and digit 3 phalanx 1 length 17.8 (15.5–20.2) 71 *v.* 14.2 (12.7–15.7) 37. Forearm length and digit 3 phalanx 1 length both larger relative to digit 5 phalanx 2 length (Figures 8 a,b).

*Myotis adversus* differs from *Myotis macropus* in having skull, dental and dentary measurements that average smaller (except for rostrum length, least interorbital breadth and mesopterygoid fossa breadth). For example, greatest skull length 16.55 (15.72–17.20) 73 *v.* 16.75 (16.18–17.76) 15; brain case breadth 8.11 (7.70–8.40) 73 *v.* 8.36 (8.14–8.70) 15; zygomatic width 10.40 (9.60–10.75) 63 *v.* 10.70 (10.20–11.42) 12; greatest skull length generally larger relative to both condylobasal length and braincase breadth (Figures 6 a,b). It averages smaller in all external measurements (except digit 5 phalanx 2), and digit 3 phalanx 1 is of larger absolute size. For example, ear length 16.7 (14.1–18.2) 71 *v.* 15.2 (14.3–15.8) 13; tibia length 19.0 (16.1–20.6) 71 *v.* 17.5 (16.5–18.3) 13; forearm length 42.6 (38.0–45.2) 71 *v.* 40.3 (38.2–41.8) 13 and digit 3 phalanx 1 17.8 (15.5–20.2) 71 *v.* 14.8 (13.7–15.8) 13.

***Myotis adversus adversus* (Horsfield, 1824)**

*Vespertilio adversus* Horsfield, 1824: 2 unnumbered pages

**Syntypes**

Include Natural History Museum, London, No. 79.11.21.123; adult female; carcass in alcohol, skull separate.

**Type locality**

Java Island.

**Diagnosis**

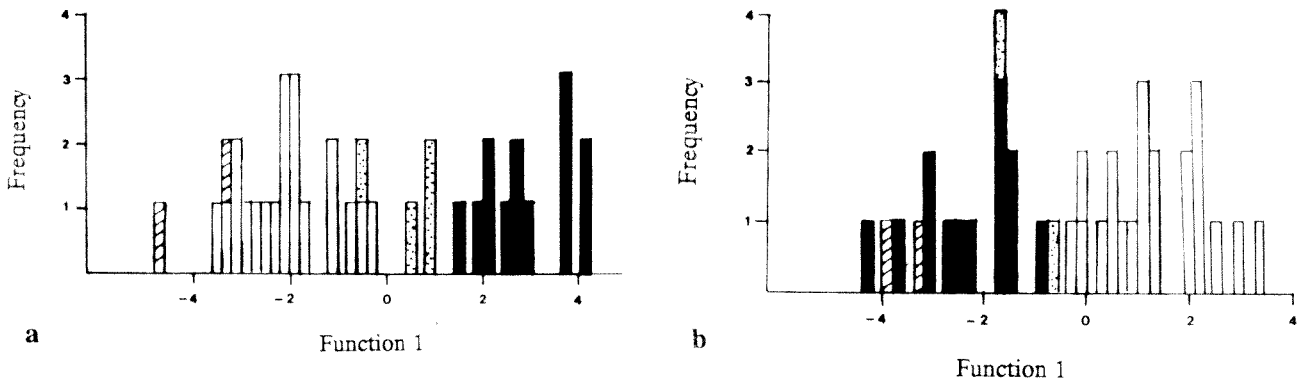
*Myotis adversus adversus* differs from *Myotis adversus tanimbarensis* subsp. nov. in having skull, dental and dentary measurements averaging larger, except anteorbital foramen width (Table 1). For example, greatest skull length 16.58 (15.79–17.13) 46 *v.* 16.14 (15.72–16.66) 8; zygomatic width 10.43 (9.81–10.75) 45 *v.* 10.07 (9.60–10.30) 3; I<sub>1</sub>M<sub>3</sub> length 7.34 (7.01–7.61) 46 *v.* 7.34 (7.03–7.37) 8. M<sup>3</sup>M<sup>3</sup> breadth generally larger relative to anteorbital foramen width (Figure 9). It also differs in having all external measurements averaging larger. For example, ear length 17.1 (15.5–18.2) 46 *v.* 15.6 (15.2–16.1) 7; forearm length 42.4 (40.1–44.4) 46 *v.* 41.2 (39.9–43.2) 7 digit 5 metacarpal length 39.1 (36.0–41.8) 46 *v.* 36.7 (35.1–39.3) 7. Ear length larger relative to pes length (Figure 10).

*Myotis adversus adversus* differs from *Myotis adversus wetarensis* subsp. nov. in having a generally longer ear 17.1 (15.5–18.2) 46 *v.* 16.4 (15.8–17.4) 17; generally shorter tibia 19.0 (17.4–20.0) 46 *v.* 19.5 (18.7–20.6) 17; forearm length 42.4

**Table 5** Canonical Variate Function coefficients for the two locality groups: Western Australia and Queensland/Northern Territory (Solomon Island, Papua New Guinea and Seram specimens were unallocated in the analysis). Standardised values followed by (in brackets) unstandardised values for (a) five skull, dentary and dental characters and (b) five external characters. For explanation of character codes see Materials and Methods section.

Character	Function 1
AOB	1.0628 (12.4574)
DL	0.9365 (4.3094)
C'C'W	-0.5684 (-6.2501)
M <sup>2</sup> B	-0.4277 (-5.6417)
Constant	-64.8959

Character	Function 1
EL	1.0160 (2.3247)
FA	-1.3872 (-1.3330)
D5M	0.8001 (0.8595)
D4P2	0.5285 (0.7537)
Constant	-21.4448



**Figure 5** Histogram of Function 1 coefficients from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined, based on the two locality groupings: Western Australia, □; and Queensland/Northern Territory, ■; the Solomon Is, ▨; Papua New Guinea and Seram ▩. Specimens were unallocated for (a) five skull, dentary and dental characters and (b) five external characters.

(40.1–44.4) 46 *v.* 43.8 (42.3–45.2) 17 and digit metacarpal lengths. Anteorbital foramen width generally shorter relative to M<sup>3</sup>M<sup>3</sup> width (Figure 9).

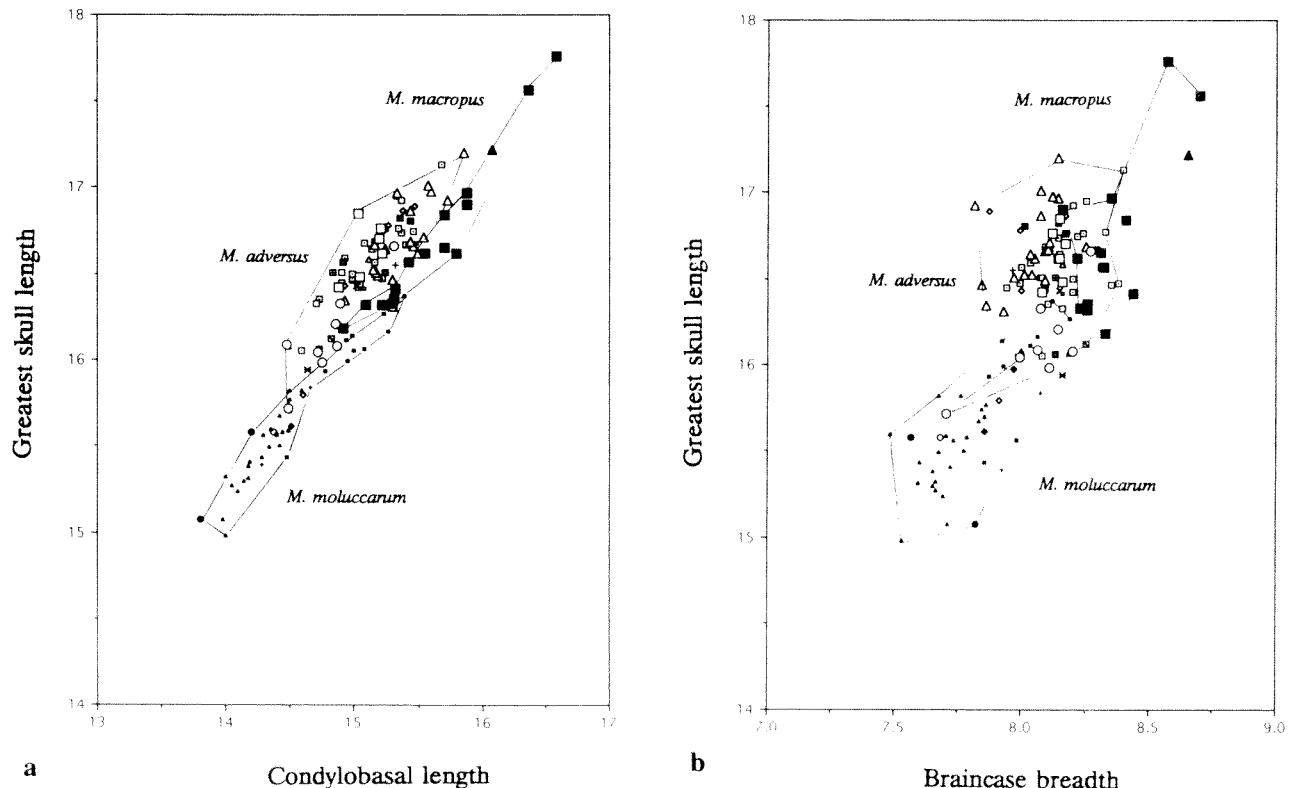
**Description**

*Skull and dentition*

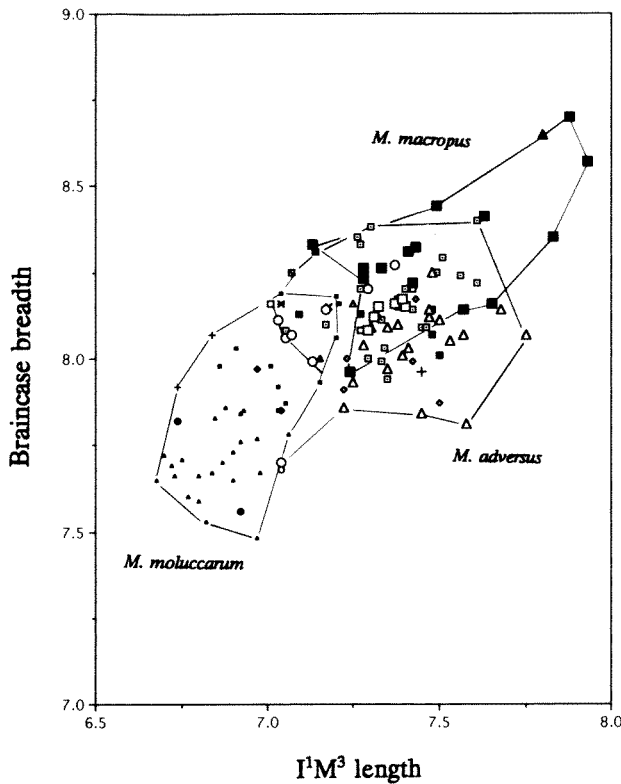
Moderate size skull (see Table 1); rostrum rises gently posteriorly to parietal midpoint; slight sulcus in anterior part of frontal but posterior to interorbital midpoint frontal flat; cranium broad with moderate laterodorsal inflation; sagittal and lambdoidal crest absent to faint; nuchal area low domed; supraoccipital projects moderately posterior to nuchal area; infraorbital foramen oval,

with broad bar separating it from orbital cavity; zygoma moderately high and of even breadth; mesopterygoid moderately broad, partially conceals sphenorbital fissure in some specimens; anterior palate broadly incised, posterior edge of the emargination reaches almost to C<sup>1</sup> midpoint; palate shelf extends posterior almost to midpoint between M<sup>3</sup> posterior edge and tympanic bulla anterior edge; palate posterior to M<sup>3</sup> posterior edge fragile, with thin median process projecting slightly ventrally from its surface and slightly beyond its posterior margin; presphenoid usually with slight sulcus; basisphenoid with moderate anterolateral depression for cochlea.

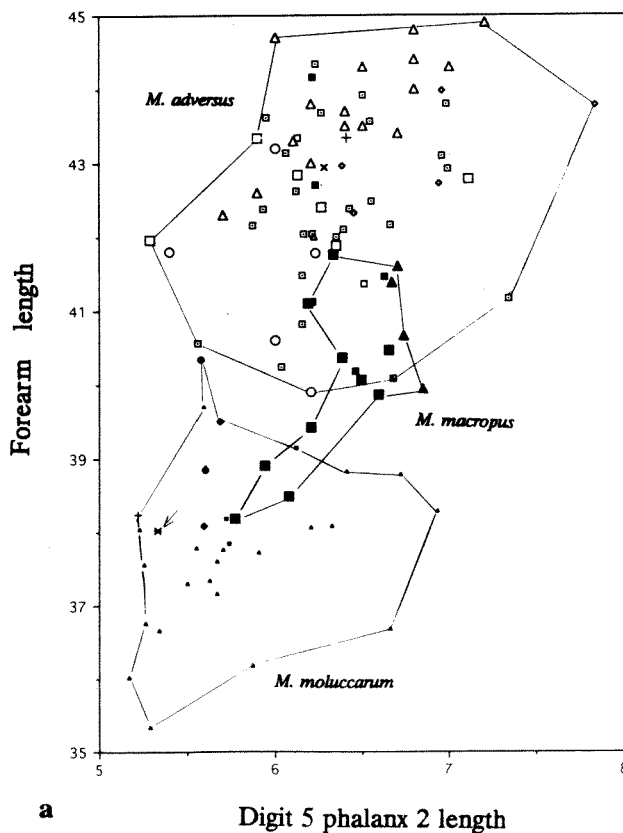
Upper incisors bicuspid with I<sup>2</sup> size half again as



**Figure 6** Plot of greatest skull length *versus* (a) condylbasal length and (b) braincase breadth, for male and female adult *Myotis adversus*, *M. moluccarum* and *M. macropus*. Locality codes as for Figure 2.



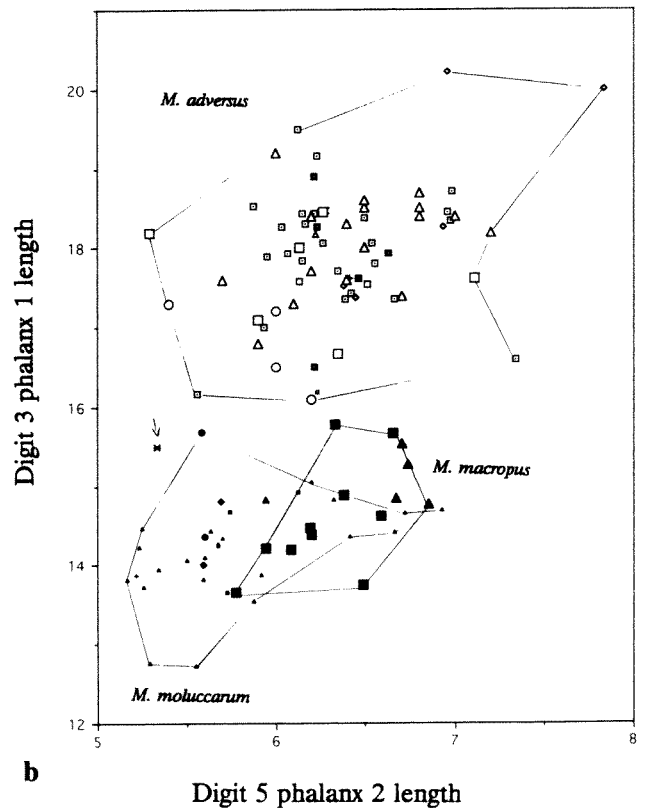
**Figure 7** Plot of braincase breadth versus  $I^1M^3$  length for male and female adult *Myotis adversus*, *M. moluocarum* and *M. macropus*. Locality codes as for Figure 2.



large as that of  $I^1$ ;  $I^1$  posterior cusp two-thirds height of anterior cusp;  $I^2$  labial cusp large, subequal in height to  $I^1$  anterior cusp;  $I^2$  lingual cusp well developed, much shorter than primary cusp, formed by oblique ventral projection of posterior lingual cingulum;  $I^3$  separate from  $C^1$  by a diastema about equal in width to  $I^3$  breadth;  $I_{1-3}$  not imbricate except for slight overlap between  $I_2$  and  $I_3$ ;  $I_{1-2}$  tricuspid;  $I_3$  much larger, its breadth (in tooth row) greater than that of  $I_{1-2}$  – its breadth anteroposteriorly about twice that of  $I_{1-2}$ ;  $I_3$  occlusal surface subterete with four distinct cusps – a larger almost central crown – two smaller lateral (anterolateral one frequently irregular) crowns and a small lingual crown;  $C^1$  lingual face concave, anterior face with groove traversing full length of tooth, posterior face with sharp ridge;  $C_1$  with strong posterior and lingual cingula which frequently project to an anterior and posterior cingular cusplet;  $C_1$  in close contact with  $I_3$  and  $P_1$ .  $P^1$  small, conical, suboval in occlusal view, less than half  $P^4$  height and *ca* one-quarter  $P^4$  size;  $P^3$  conical, minute, *ca* one-sixth  $P^1$  size, in tooth row or partially intruded;  $P^1$  and  $P^4$  cingulum not in contact;  $P_1$  larger than  $P^1$ , *ca* four-fifth  $P_4$  size;  $P_3$  less than one-half  $P_1$  height and *ca* one-third  $P_1$  size, usually intruded from toothrow.

#### Colour

Dorsum Dark Grayish Brown, ventral surface a Blackish Neutral Gray tipped with Pale Neutral Gray. Patagia and ears Dark Grayish Brown.



**Figure 8** Plot of digit 5 phalanx 2 length versus (a) forearm length and (b) digit 3 phalanx 1 length for male and female adult *Myotis adversus*, *M. moluocarum* and *M. macropus*. Locality codes as for Figure 2.

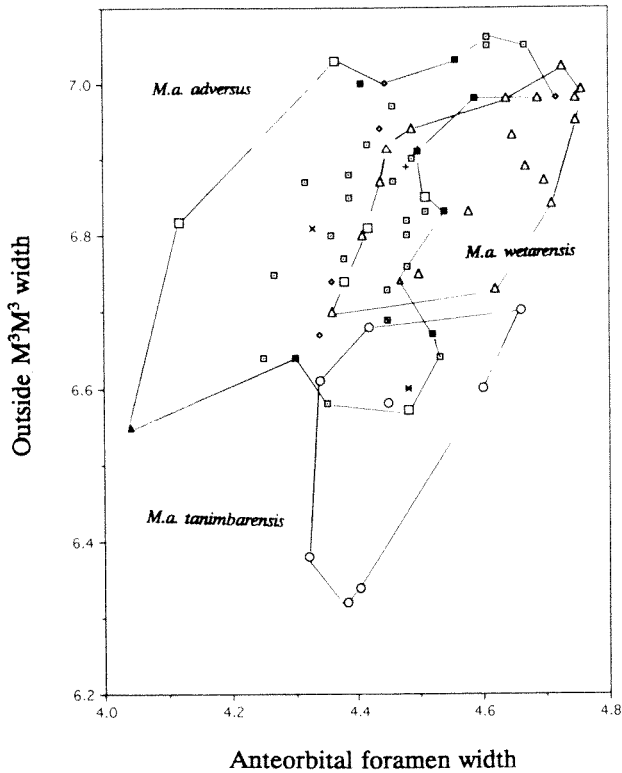


Figure 9 Plot of outside M<sup>3</sup>M<sup>3</sup> width versus anteorbital foramen width for male and female adult *Myotis adversus adversus*, *M. a. tanimbarensis* subsp. nov. and *M. a. wetarensis* subsp. nov. Locality codes as for Figure 2.

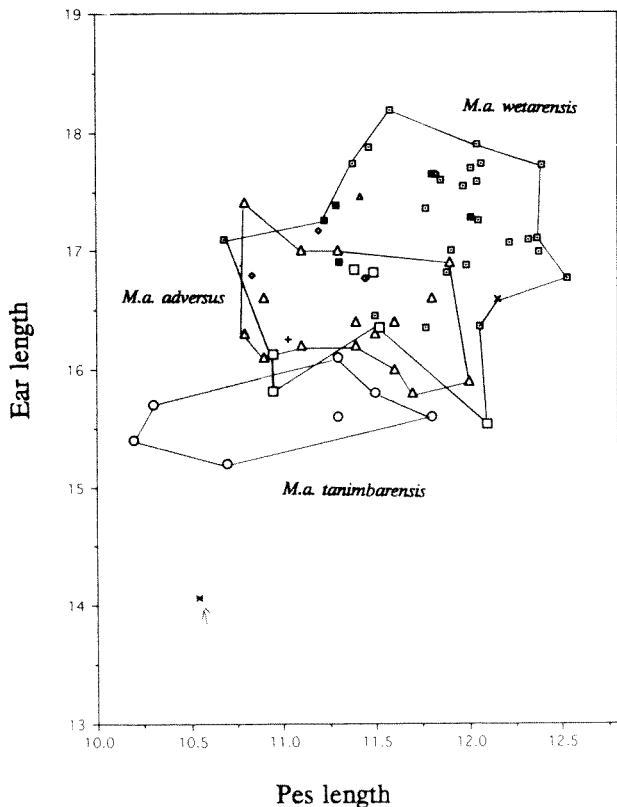


Figure 10 Plot of ear length versus pes length for male and female adult *Myotis a. adversus*, *M. a. tanimbarensis* subsp. nov. and *M. a. wetarensis* subsp. nov. Locality codes as for Figure 2.

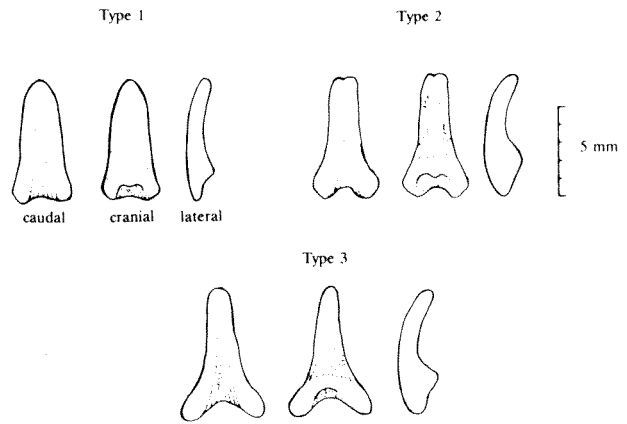


Figure 11 Baculum types: type 1 – *Myotis moluccarum* and *M. macropus*; types 2 and 3 – *M. adversus*.

*Penis and baculum*

Penis ca 3.5 long; glans penis a simple pear shape with ventral urethral slit. Baculum with base bifurcated to lesser or greater extent with distal end narrowing (types 1 or 2, Figure 11). Maximum length (mean, range, N) = 0.70 (0.60–0.83) 5.

**Distribution**

Peninsular Malaysia (?); Java; Kangean Island; Nusa Penida Island and Nusa Tenggara (Sumbawa Island; Moyo Island; Flores Island; Lembata Island; Pantar Island; Alor Island; Timor Island and Savu Island).

***Myotis adversus tanimbarensis* subsp. nov.**  
**Kitchener**

**Holotype**

Museum Zoologicum Bogoriense (MZB) No. 15906; Western Australian Museum (WAM) field No. M43583; adult male, skull separate, carcass fixed in 10% formalin, preserved in 75% ethanol; liver stored at Western Australian Museum in ultrafreeze refrigerator; baculum separate; weight 9 gm; collected by D.J. Kitchener, R.A. How and I. Maryanto on 16 April 1993.

**Type locality**

7 km N. Saumlaki, Yamdena Island, Tanimbar Islands, Maluku Tenggara, Indonesia (7°54'00"S, 13°20'00"E); from large cave lit by large entrance, with deep well to sea.

**Paratypes**

Listed in 'Specimens Examined' section.

**Diagnosis**

*Myotis adversus tanimbarensis* differs from *Myotis adversus adversus* as detailed in the diagnosis of the latter subspecies.

It differs from *Myotis adversus wetarensis* in averaging smaller in all skull, dentary and dental measurements, except braincase breadth. For example, greatest skull length 16.14 (15.72–16.66) 8 *v.* 16.71 (16.34–17.20) 18; zygomatic width 10.07 (9.60–10.30) 3 *v.* 10.43 (10.21–10.62) 14; I<sup>3</sup>M<sup>3</sup> length 7.34 (7.03–7.37) 8 *v.* 7.45 (7.22–7.75) 18; M<sup>3</sup>M<sup>3</sup> width smaller relative to anteorbital breadth (Figure 9). It also differs in having all external measurements smaller. For example, ear length 15.6 (15.2–16.1) 7 *v.* 16.4 (15.8–17.4) 17; tibia length 18.5 (18.5–19.3) 7 *v.* 19.5 (18.7–20.6) 7; forearm length 41.2 (39.9–43.2) 7 *v.* 43.8 (42.3–45.2) 17; digit 5 metacarpal length 36.7 (35.1–39.3) 7 *v.* 39.6 (38.0–40.7) 17. Ear length shorter relative to pes length (Figure 10).

### Description

The morphology of *M. a. tanimbarensis* is as described earlier for *M. a. adversus* except for differences noted in the earlier diagnosis and as follows: *M. a. tanimbarensis* has the skull at the junction of the parietal and frontal regions more inflated. The baculum of the holotype MZB 15906 was a type 3 (Figure 11) and had a greatest length of 0.71. The dorsal pelage Dusky Brown; ventral surface basal hairs Dusky Brown tipped with Pale Neutral Gray. Patagia and ears Dusky Brown.

### Distribution

Known only from Yamdena Island, Tanimbar Group, Maluku Tenggara, Indonesia.

### Etymology

Named after the Tanimbar Islands.

### *Myotis adversus wetarensis* subsp. nov. Kitchener

### Holotype

Museum Zoologicum Bogoriense (MZB) No. 15907; Western Australian Museum (WAM) field No. M44690; adult female, skull separate, carcase fixed in 10% formalin, preserved in 75% ethanol, weight 13.2 gm; collected by D.J. Kitchener and R.A. How on 23 September.

### Type locality

2 km E. Ipokil, Wetar Island, Maluku Tenggara, Indonesia, (7°45'00"S, 128°48'20"E) from a large sunken cave.

### Paratypes

Listed in 'Specimens Examined' section.

### Diagnosis

*Myotis adversus wetarensis* differs from *Myotis adversus adversus* and *Myotis adversus tanimbarensis* as detailed in those earlier diagnoses.

### Description

The morphology of *M. a. wetarensis* is as described earlier for *M. a. adversus* except for differences noted in the earlier diagnosis. The baculum of WAM 44706 is a type 3 (Figure 11) with maximum length 0.71. The dorsal pelage Dark Grayish Brown; ventral surface with basal hairs Dark Grayish Brown tipped with White; patagium Fuscous.

### Distribution

Known only from Wetar Island, Maluku Tenggara, Indonesia.

### Etymology

Named after Wetar Island.

### *Myotis adversus* subsp. indet.

### Remarks

The single adult male specimen from New South Wales (AM 13250) was classified by DFA to *Myotis adversus tanimbarensis*. While it is closest morphologically to that subspecies, it differs from it in having a skull with the cranium less inflated immediately posterior of the interorbital constriction; longer bulla 3.13 *v.* 2.96 (2.72–2.98) and generally smaller externally (see Table 1). For example, forearm length 38.0 *v.* 41.2 (39.9–43.2); ear length 14.1 *v.* 15.6 (15.2–16.1) 7 and tibia length 16.1 *v.* 18.5 (18.0–19.3) 7. It also has a baculum that is more broadly spatulate (type 1, Figure 11).

### *Myotis moluccarum* (Thomas, 1915)

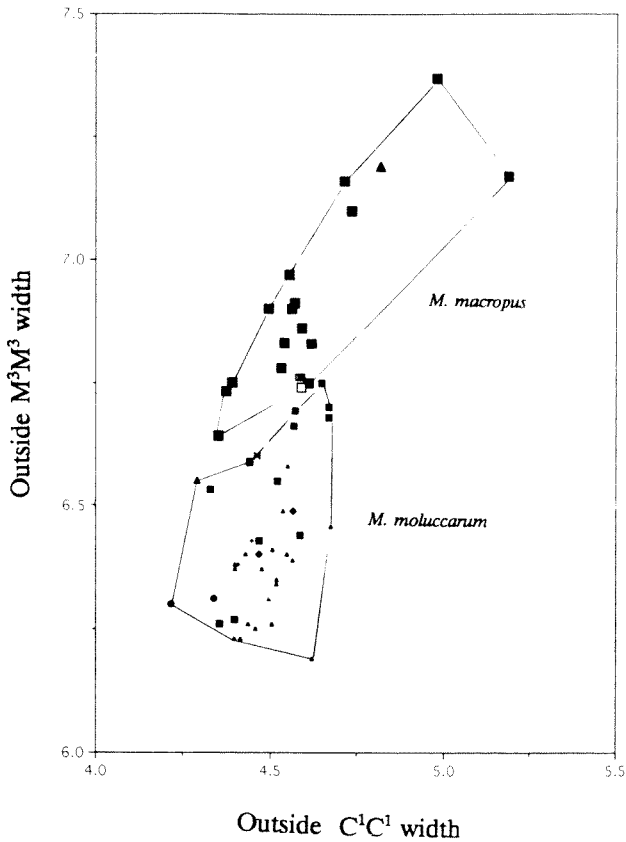
*Leuconoe moluccarum* Thomas, 1915: 170–172.

### Diagnosis

*Myotis moluccarum* differs from *Myotis adversus* as detailed in the earlier diagnoses of the latter species.

It differs from *Myotis macropus* in averaging smaller for all skull, dentary and dental measurements. For example greatest skull length 15.64 (14.98–16.37) 37 *v.* 16.75 (16.18–17.76) 15; braincase breadth 7.81 (7.48–8.19) 37 *v.* 8.36 (8.14–8.70) 15; zygomatic width 10.06 (9.50–10.76) 34 *v.* 10.70 (10.20–11.42) 12; M<sup>3</sup>M<sup>3</sup> width 6.41 (6.19–6.76) 37 *v.* 6.94 (6.64–7.37) 15; I<sup>3</sup>M<sup>3</sup> length 6.92 (6.68–7.32) 37 *v.* 7.54 (7.13–7.93) 15. M<sup>3</sup>M<sup>3</sup> width smaller relative to C<sup>1</sup>C<sup>1</sup> width (Figure 12). It also averages smaller in all external measurements. For example, tibia length 16.7 (15.6–18.1) 37 *v.* 17.5 (16.5–18.3) 13; forearm length 38.2 (35.4–41.0) 37 *v.* 40.3 (38.2–41.8) 13; digit 3 metacarpal 37.2 (34.0–39.1) 37 *v.* 39.4 (37.2–41.1) 13. Forearm length generally longer relative to digit 5 phalanx 2 length (Figure 8a).





**Figure 12** Plot of outer M<sup>3</sup>M<sup>3</sup> width versus outer C<sup>1</sup>C<sup>1</sup> width for *Myotis moluccarum* and *M. macropus*. Locality codes as for Figure 2.

***Myotis moluccarum moluccarum* (Thomas, 1915)**

*Leuconoe moluccarum* Thomas, 1915:

**Holotype**

British Museum No. 10.3.1.29 (original number 854); adult male; skin and skull separate; collected by W. Stalker in July 1909.

**Type locality**

Ara, Kei (= Kai) Islands, Maluku Tenggara, Indonesia.

**Specimens examined**

See 'Specimens Examined' section.

**Diagnosis**

[Our measurements of AM 23420 and SAM 21781, Solomon Is are followed, where available (in brackets) by the mean and range of the holotype measurements of *solomonis* from Troughton (1929) and five specimens listed in Phillips and Birney (1968)].

*Myotis moluccarum moluccarum* differs from *Myotis moluccarum richardsi* subsp. nov. in averaging smaller in all skull, dentary and dental measurements. For example, greatest skull length 15.48 (14.98–15.82) 22 v. 15.95 (15.39–16.37) 13; braincase breadth 7.70 (7.48–7.86) 22 v. 8.01 (7.85–

8.19) 13; zygomatic width 9.92 (9.50–10.28) 22 v. 10.32 (9.74–10.76) 13; P<sup>1</sup>M<sup>3</sup> length 6.85 (6.68–7.06) 22 v. 7.03 (6.74–7.32) 13; braincase breadth narrower than C<sup>1</sup>C<sup>1</sup> width (Figure 13). Ear generally longer relative to digit 5 metacarpal length (Figure 14).

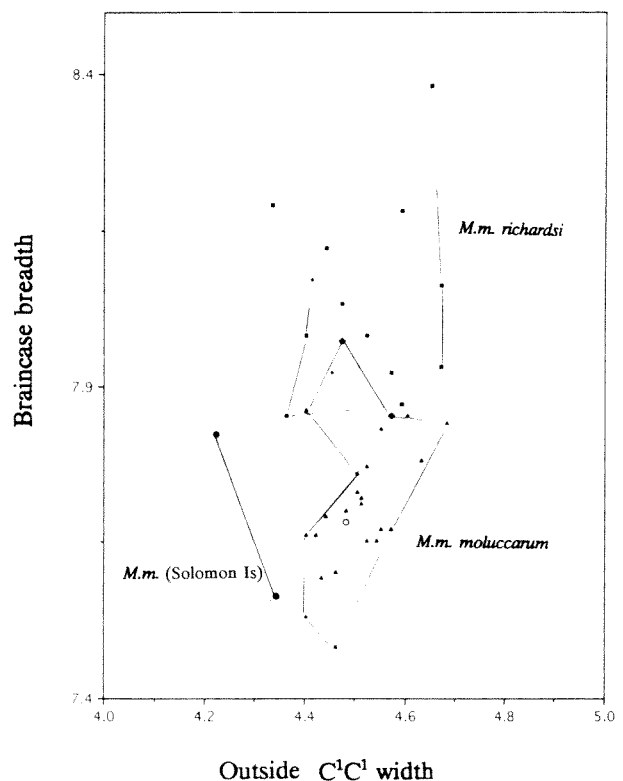
It differs from the Solomon Island form of *Myotis moluccarum* in having both a larger anteorbital foramen width 4.16 (4.00–4.32) 22 v. 3.89–3.93 and C<sup>1</sup>C<sup>1</sup> width 4.50 (4.40–4.68) 22 v. 4.22–4.34 [4.4(4.3–4.4)]. C<sup>1</sup>C<sup>1</sup> width larger relative to braincase breadth (Figure 13). Forearm generally shorter 37.6 (35.4–39.7) 22 v. 38.8–40.4 [39.6 (38.5–41.3)] and a paler ventral pelage.

**Description**

The morphology of *M.m. moluccarum* is as described earlier for *M. a. adversus*, except for differences noted in the earlier diagnosis, and as follows: the median postpalatal spine projects further posteriorly, is broader, and projects less ventrally; mesopterygoid fossa broad with broad external ventral flanges on the pterygoid processes; such that the sphenorbital fissure is almost obscured from the ventral view; and the P<sup>3</sup> is usually well intruded from the tooth row such that P<sup>1</sup> and P<sup>4</sup> cingulum are often in contact.

Baculum with base slightly broadened and distal shaft spatulate (type 1, Figure 11), greatest length 0.71 (0.66–0.78) 3.

Dorsal pelage Burnt Umber; ventral surface basal



**Figure 13** Plot of braincase breadth versus outer C<sup>1</sup>C<sup>1</sup> width for *Myotis moluccarum moluccarum*, *M. moluccarum* (Solomon Is) and *M. m. richardsi* subsp. nov. Locality codes as for Figure 2.

hairs Dark Grayish Brown tipped with Pale Neutral Gray.

#### Distribution

Western Australia, Kai Islands, Seram, Papua New Guinea and probably Ambon.

#### Remarks

The earlier DFA indicated that on skull characters the two Papua New Guinea and the single Seram specimens allocated to the Western Australia *Myotis m. moluccarum*. However, on externals, one of these PNG specimens was intermediate between the Western Australian *M.m. moluccarum* and the Queensland/Northern Territory *M. m. richardsi*; the other PNG specimen allocated to this latter subspecies (there were no external measurements for the Seram specimen).

Direct comparison between the forms of *M. moluccarum* examined in this study with the holotype of this species from the Kai Islands was not possible.

Recent expeditions by us (Kitchener *et al.* 1993a) and by a team from the Australian Museum, also failed to collect *Myotis moluccarum* on the Kai Islands. Comparison of the Western Australian form with measurements of this holotype presented in Thomas (1915) indicated that it was clearly closer in size to this holotype than was the Queensland/Northern Territory form.

The form of *M. moluccarum* from the Solomon Is (*Anamygdon solomonis* Troughton, 1929) appears to be distinct from the other forms of this species. However, because we examined only two specimens we tentatively follow more recent classifications and retain this form in synonymy with *M. m. moluccarum*. It is noted that the P<sup>1</sup> and P<sup>4</sup> cingula of our two Solomon Island specimens were not in contact. In the holotype of *A. solomonis*, Troughton (1929: 91) stated that these two upper premolars were in contact. Their dorsal pelage was Dusky Brown; ventral pelage Burnt Umber with very slight frosting on tips; the venter was not 'pale' as in the other taxa reviewed herein. We did not observe the baculum of the Solomon Island form.

The subspecific taxonomy of *M. moluccarum* remains somewhat obscure, however its clarification will depend on availability for study of more extensive series of specimens from Maluku Tenggara, Papua New Guinea and the Solomon Is.

#### *Myotis moluccarum richardsi* subsp. nov. Kitchener

#### Holotype

Queensland Museum (JM) No. 5335; adult female, skull separate, carcase preserved in 75%

ethanol; collected by P. Myroniuk on 22 December 1985.

#### Type locality

Gayundah Creek, Hinchinbrook Island, Queensland, Australia (18°22'S, 146°13'E); mist netted over creek in rainforest at sea level.

#### Paratypes

Listed in 'Specimens examined' section.

#### Diagnosis

*Myotis moluccarum richardsi* differs from *Myotis moluccarum moluccarum*, excluding the Solomon Island form, as detailed in the earlier diagnoses of that subspecies.

It differs from the Solomon Island form of *M. moluccarum* in the same way that it differs from *M. m. moluccarum* except that its ears are not notably shorter (see Figure 14 and Phillips and Birney 1968).

#### Description

The morphology of *M.m. richardsi* is as described earlier for *M.m. moluccarum* except for differences noted in the earlier diagnosis and as follows: P<sup>1</sup> and P<sup>4</sup> cingulum occasionally in contact, but usually not. The baculum is also similar to *M.m. moluccarum* from Western Australia (type 1, Figure

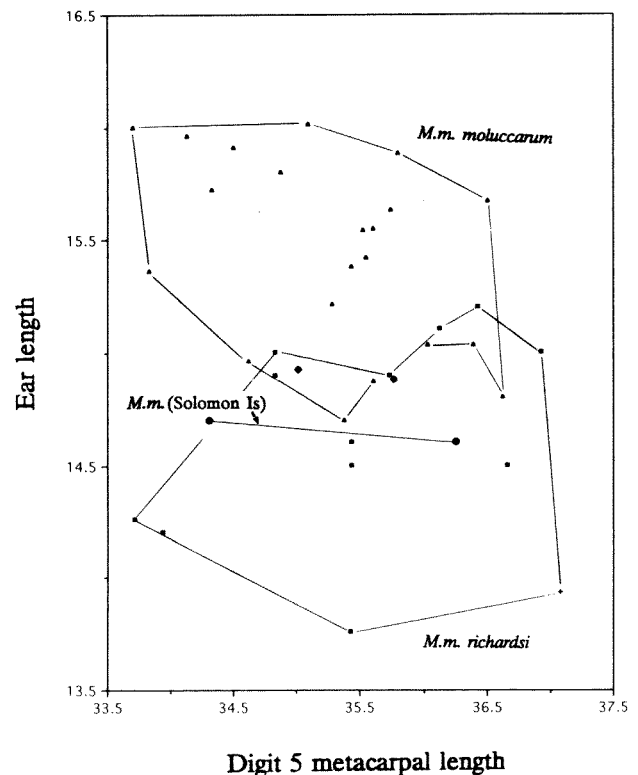


Figure 14 Plot of ear length versus digit 5 metacarpal length for *Myotis moluccarum moluccarum*, *M. moluccarum* (Solomon Is) and *M. m. richardsi* subsp. nov. Locality codes as for Figure 2.

11) – the one extracted had a greatest length of 0.73.

Pelage colour variable – dorsum ranges from Russet to Burnt Umber to Dark Grayish Brown. Ventral surface with basal hairs Cinnamon Brown or Dark Grayish Brown tipped with Pale Neutral Gray, or light Neutral Gray. Patagium and ears Russet or Fuscous.

#### Distribution

Queensland and Northern Territory, Australia.

#### Etymology

Named after Mr Greg Richards for his studies on the chiropteran fauna of Queensland.

#### *Myotis macropus* (Gould, 1855)

*Vespertilio macropus* Gould, 1855: un-numbered page of text.

#### Syntypes

Includes BMNH No. 53.10.22.32; skin ("alcoholic"), skull separate.

#### Type locality

South Australia

#### Specimens examined

See later section.

#### Diagnosis

*Myotis macropus* differs from *Myotis adversus* and *Myotis moluccarum* as detailed in the earlier diagnoses of these species.

#### Description

The morphology of *Myotis macropus* is as described earlier for *Myotis adversus*, except for differences noted in the earlier diagnosis. Also the baculum of the Victorian specimen (C25641) is long (0.81), broad and a spatulate type 1 form (Figure 11) rather than types 2 or 3 typical of *M. adversus*.

#### Distribution

South Australia and Victoria, Australia.

### DISCUSSION

*Myotis adversus* (*sensu lato*) in the study region comprised three species and six subspecies. One specimen from New South Wales also appeared representative of *Myotis adversus* and is morphologically closest to *M. a. tanimbarensis*; it is not allocated to a subspecies.

It appears, then, that all three species in this species complex occur in Australia – *Myotis moluccarum* (northern Australia), *Myotis adversus* (New South Wales) and *Myotis macropus* (southeastern Australia).

*Myotis adversus* is widespread and appears to alter little in morphology from Java through Nusa Tenggara to Alor Island. This is indicated by the fact that the cluster of the large sample of specimens from Alor Island in discriminant function space incorporates all the other islands in Nusa Tenggara (Figure 3a,b). Wetar Island (Maluku Tenggara Administrative province), immediately to the east of Alor Island, is the first population of *Myotis adversus* in this island chain to noticeably diverge morphologically. This divergence was considerable, such that the Wetar individuals that misclassified to the Alor Group based on skull dentary and dental characters, comprised only two of 18 individuals, and based on external characters, only one of 16 individuals.

The Yamdena population (Kepulauan Tanimbar) further to the east again, and part of the outer Banda Arc of islands, also diverged further morphologically from the Alor Group of populations and also was quite distinct from the Wetar population. No individuals in the Yamdena population were misclassified to these other populations in the DFA. It is probably that this morphological divergence of the Wetar and Yamdena populations reflects their relative geographic isolation from other islands to the west. Alor Island, and many of the islands further to the west in the Inner Banda Arc, were either joined or separated by small water gaps during the last glacial maxima about 18,000 yrs BP, when the sea level fell by about 120 m. Wetar Island, however, is separated by a wide stretch of deep water of ca. 900 m depth (Indonesian Naval Hydrographic Survey maps, 1991) (Kitchener *et. al* 1990, Heaney 1991). Yamdena Island, in the Outer Banda Arc, is the most geographically isolated *M. adversus* population (except for the New South Wales specimen, if it is indeed *M. adversus*); further it has never been connected by dry land to these other island populations. However, distance of present day water gaps between populations, or closeness of past connection during the Pleistocene, are not the sole explanation for the morphological divergence of the Wetar and Tanimbar populations. This is because the Timor and Savu populations, which are also isolated geographically, both by relative wide current water gaps and by deep seas, do not appear to have similarly diverged morphologically. Perhaps the slightly drier climate of the Wetar and the wetter climate of Yamdena Islands compared to the islands to the west (Oldeman, 1980) has resulted in differential selection pressures on the morphology of the population of both Wetar and Yamdena Islands.

The distribution of *Myotis adversus* extends from Java along the island chain of the Lesser Sundas as far as Tanimbar only. *Myotis moluccarum* occurs on

the Kai Islands, Seram (and possibly to Peleng Island, Sulawesi and Irian Jaya – see Hill (1983: 160)), New Guinea, the Solomon Islands and northern Australia.

Hill (*loc. cit.*) notes that *M. a. carinatae* from Borneo and Sumatra is very similar to *M. moluccarum* but notes that "only limited material is available for comparison". We have not examined that material.

The distribution of the *Myotis adversus* complex in eastern Indonesia presents a pattern of morphology somewhat different again from those recently reported for other bat species in that region. For example, the form of *Hipposideros diadema* from Java (*nobilis*) reaches Lombok Island, where it interfaces sharply across the sea strait of Sumbawa with the eastern form of *H. diadema* (*diadema*). *Rhinolophus simplex* and *Hipposideros sumbae*, Lesser Sunda endemic species, are widely distributed throughout the Inner Banda Arc but differentiate into identifiable morphological forms on the outer Banda Islands. The pteropodid *Pteropus lombocensis*, endemic to the Lesser Sunda Islands, has a distinct western form (Lombok and Sumbawa Is) and an eastern form which occurs as far east as Alor Island; this eastern form shows some further morphological variation. The pteropodid *Aethalops alecto* has a wide distribution on the mountain tops of Sumatra, Java, Bali and Lombok Islands. However, on these latter two islands it has differentiated morphologically, sufficient to warrant subspecific status (Kitchener and Maryanto 1993, Kitchener *et. al* 1992, 1993 a–d, 1995 a,b). Other studies, by us and our colleagues A. Suyanto and Maharadatunkamsi (unpublished data) on *Scotophilus kuhlii*, *Hipposideros ater*, *Rhinolophus affinis*, *Eonycteris spelaea* and *Macroglossus minimus*, also reveal a variety of distributional patterns of subspecies of chiroptera in Eastern Indonesia which no doubt reflect current geography, recent historic events and current climatic patterns in the region. Clearly, however, there is a complex interaction between all these factors which has resulted in this mosaic of intraspecific morphological differentiation.

#### SPECIMENS EXAMINED

##### *Myotis adversus adversus*

Java: Locality unknown, BMNH (401 405) (♂, ♀).

Kangean Island: Central region, 115°20'S, 6°55'E, MZB13349 (1♂)

Nusa Penida: Karangasari, 8°42'S, 115°35'E, WAM M(39627–839663, 39674, 39680, 39682) (2♂♂, 4♀♀).

Sumbawa Island: Desa Sangeang, 8°18'S, 118°56'E, WAM M (31541, 31546, 31554–5, 31567) (1♂, 4♀♀).

Moyo Island: Sebotok, 8°09'30"S, 117°37'15"E, WAM M 31907 (1♂).

Flores Island: Ratulodong, 8°11'00"S, 122°52'00"E, WAM M (32569, 32574, 32586) (3♂♂).

Lembata Island: Merdeka Hadakewa, 8°22'S, 123°31'E, WAM M 32358 (1♀).

Pantar Island: Batu Bakalang, 8°14'S, 124°18'E, WAM M 37742 (1♂).

Alor Island: Kalabahi, 8°14'S, 124°32'E, WAM M (37523–5, 37527, 37536, 37547, 37553, 37555, 37557, 37581, 37583–4, 37586–7, 37589–91, 37593, 37595–600) (8♂♂, 16♀♀).

Timor Island: Lifuleo Oisina, 10°18'S, 123°30'E, WAM M 38066 (1♂).

Savu Island: Menia, 10°29'S, 121°55'E, WAM M (35256–8, 35265) (1♂, 3♀♀).

##### *Myotis adversus wetarensis* subsp. nov. (all paratypes)

Wetar Island: Desa Ipokil, 7°50'S, 126°16'E, WAM M (44686–7, 44689–94, 44696, 44698–706) (1♂, 17♀♀).

##### *Myotis adversus tanimbarensis* subsp. nov. (all paratypes)

Yamdena Island: Saumlaki, 7°59'S, 131°22'E, WAM M (43581–5, 43589, 43618–9) (7♂♂, 1♀).

##### *Myotis adversus* subsp. indet.

New South Wales: Rocky Creek, 28°39'S, 153°20'E, AM M 13250 (1♂).

##### *Myotis moluccarum moluccarum*

Western Australia: Drysdale R. Nat. Park, 14°40'S, 127°00'E, WAM M (14063–5, 14067–77, 14079) (3♂♂, 12♀♀). Mitchell Plateau, 14°30'00"S, 125°47'20"E, WAM M (15763, 21571, 21582) (2♂♂, 1♀). Surveyors Pool, Mitchell Plateau, 14°40'20"S, 125°43'40"E, WAM M (21509–11) (2♂♂, 1♀). Prince Regent Reserve, 15°49'25"S, 125°37'03"E, WAM M 12255 (1♂).

##### *Myotis moluccarum richardsi* subsp. nov. (all paratypes)

Northern Territory: Melville Island, 11°18'S, 130°27'E, C 953 (sex unknown). Mungejirri Yaalput Waterhole, 14°32'S, 135°15'E, SAM M1810 (1♂).

Queensland: Brisbane, 27°28'S, 153°01'E, JM 2838, (1♀). Dowah Creek, JM (5000, 5003) (2♀♀). Hinchinbrook Island, 18°22'S, 146°15'E, JM 5335 (1♀). Jerona, Ayr, 19°34'S, 147°13'E, JM (7971–2, 7975) (1♂, 2♀♀). Lake Barrine, 17°16'S, 145°35'E, AM M 4901 (1♀). Macleods Creek, Cooktown, 15°26'S, 145°08'E, AM M 13317 (1♀). Noosa Heads,

26°25'S, 153°07'E, JM 9303 (1♂). Peach Creek, 13°41'S, 143°09'E, SAM M 16355 (1♂). Somerset Point, 10°45'S, 142°35'E., JM 5002 (1♀).

Seram Island: Locality unknown, BMNH 428 (1♀)

Papua New Guinea: Port Moresby, 9°27'S, 147°08'3, AM M 18824 (1♂).

Yuro, Central Province, 6°32'S, 144°51'E, AM M 15110 (1♂).

*Myotis moluccarum* (Solomon Islands)

Solomon Islands: Mbeu River. approx 6.5 km NW Tamaneke Village Marovo Lagoon, 8°18'S, 157°45'E, AM M 23420 (1♀). Pavora R. Choiseul Islands, 6°46'S, 156°32'E, AM M 21781 (1♀).

*Myotis macropus*

South Australia: Nildottie, 34°41'08"S, 139°36'36"E, SAM M (13373-6) (2♂♂, 2♀♀).

Victoria: Cloggs Cave, East Buchan, 37°30'S, 148°10'E, C (2986, 3568-70, 3684, 4352) (5♂♂, 1♀).

East Gippsland, (locality unknown) C25904, (♀). Glenelg River, 2 km W of Red Cap Creek, 38°01'S, 140°58'S, C26083 (1♂). Ovens River, 10.4 km NE of Mt Killawarra, 36°09'50"S, 146°13'40"E, C (25653, 25661) (1♂, 1♀). Rocky Creek, 50 km from confluence with Wingham River, 37°43'18"S, 149°29'24"E, C24908 (1♂). Scorpion Block, Nowa Nowa, 37°16'S, 147°58'E, C 26097 (1♀). Steep Bank Rivulet, 9.5 km NW of Wando Bridge, C 24870 (1♀). Goulburn River, 14.6 km SSW of Nathalia, 36°10'15"S, 145°06'40"E, C 25641 (1♂).

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