

Morphological variation in *Miniopterus pusillus* and *M. australis* (sensu Hill 1992) in southeastern Asia, New Guinea and Australia

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Abstract – The morphology of 366 specimens of small (forearm <45 mm; cranial mastoid width <7.9 mm) *Miniopterus* from Indonesia, Philippines, New Guinea and Australia was examined, with the assistance of univariate and multivariate statistical analyses.

Four species (*M. pusillus*, *M. australis*, *M. paululus* and *M. shortridgei*) are recognised. Each of these species differentiates into recognisable forms, mostly named, but a new subspecies is described for *M. paululus* from Selaru island. Indeterminate subspecies are recognised for *M. pusillus* from Alor, Roti and Seram islands; *M. australis* from Kai island; and *M. shortridgei* from islands in the Outer Banda Arc and Wetar island.

There was no marked sexual dimorphism among populations of these species, except in cranial height, where males were larger.

These are the first records of *M. pusillus* on Lombok, Sumbawa, Alor and Roti islands; and of *M. shortridgei* on Madura, Lombok, Sumbawa, Alor, Roti, Semau, Savu, Wetar and Selaru islands.

INTRODUCTION

According to Hill in Corbet and Hill (1992), the small species of *Miniopterus* in eastern Indonesia, Philippines, New Guinea and Australia which have a forearm length of less than 45 mm and a mastoid width less than 7.9 mm, comprise only the two species: *M. australis* Tomes, 1858 and *M. pusillus* Dobson, 1876. Hill (1983) tabulated several cranial, dentary and external body measurements of a number of populations of *M. australis* and *M. pusillus*. He stated that these species were sympatric over much of their distributional overlap. Where they occur together they can be distinguished by "the slightly greater external size of *pusillus*". However, according to Hill (1983) the literature contains many examples of these two species being misidentified.

A number of taxa have been recognised among the small species of *Miniopterus* in or adjacent to Indonesia, Philippines, New Guinea and Australia. These are listed below, along with their type localities:

- Miniopterus australis australis* Tomes, 1858 – Loyalty islands (but see Hill 1983: 171–173)
- M. australis shortridgei* Laurie and Hill, 1957 – Kalipoetjang, Tji – Tandoei R., south Java
- M. a. minor* Laurie and Hill, 1954 – Kalipoetjang, Tji – Tandoei R., south Java
- M. tibialis* (Tomes, 1858) – Ambon island, Maluku Tenggara

M. paululus Hollister, 1913 – Guimaras island, Philippines

M. macrocneme Revilliod, 1914 – New Caledonia and Loyalty islands

M. witkampii Sody, 1930 – Lobang Ipoe, Koetai, eastern Kalimantan, Borneo

M. pusillus Dobson, 1876 – Nicobar island

M. solomonensis Maeda, 1982 – Malaita and San Christobal, Solomon islands

There has been considerable confusion as to the taxonomic relationships among these taxa. For example Tate (1941) stated that "*witkampii* is a synonym of *pusillus*" and "*macrocneme* from Loyalty islands is apparently synonymous with *australis*". However, Petersen (1981b) and Hill (1983) associated *macrocneme* with *pusillus*, while Maeda (1982) associated *macrocneme* with the *Miniopterus fuscus* group of species.

Hill (1983) and Hill in Corbet and Hill (1992) considered *tibialis*, *witkampii*, *paululus*, *shortridgei* and *solomonensis* as subspecies of *M. australis*.

Tate (1941) considered *australis* synonymous with *paululus*; an opinion supported by Sanborn (1952) and considered possible by Hill (1983). Sanborn (1952) also thought it likely that *tibialis* was a synonym of *australis*. Petersen (1981a) disagreed somewhat and suggested that *paululus* and *shortridgei* were distinct from *australis*. Maeda (1982) and Koopman (1982) considered *paululus* a species; and the former



Figure 1 Map showing locality names referred to in text.

author placed *shortridgei* in synonymy with *paululus*.

Expeditions throughout Java, Nusa Tenggara and Maluku Tenggara by staff from the Western Australian Museum and Museum Zoologicum Bogoriense between 1987–1994 resulted in an extensive collection of small *Miniopterus* that were representative of *M. australis* and *M. pusillus* (*sensu* Hill in Corbet and Hill 1992). These specimens came from the islands of: Java, Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Kai, Selaru (Tanimbar), Timor, Semau, Roti, Savu and Seram. These recent collections, in conjunction with existing collections from Borneo, Philippines, Papua New Guinea and Australia (Queensland and New South Wales), (see Figure 1 for collection localities) allow for a fresh appraisal of the taxonomy of small *Miniopterus* in this region. This paper reports on such an appraisal, particularly with the view of evaluating the uncertain taxonomic status of most populations and particularly of the previously unreported populations from Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Selaru, Semau, Roti and Savu islands (Figure 1).

MATERIALS AND METHODS

For the morphometric analyses, 366 adult *Miniopterus* specimens from Java, Borneo, 13 islands in Nusa Tenggara and Maluku Tenggara, Philippines, Papua New Guinea and Australia were measured and analysed statistically, using both univariate and multivariate analyses.

Adult condition was judged to be when there was no swelling of the epiphyses of the wing metacarpals or phalanges. Adults were further subdivided into young adults (no wear at distal end of upper canine, or if worn dentine not exposed) and old adults (worn upper canine with dentine exposed).

The measurements (all in mm) were recorded from each specimen using vernier calipers as follows: GSL, greatest skull length; BCL, basicranial length; PL, palatal length; ICD, intercochlear distance; MW, mastoid width; MFB, mesopterygoid fossa breadth; CH, cranial height; LIB, least interorbital breadth; ZW, zygomatic width; BB, braincase breadth; C¹M³, upper maxillary tooth row cusp length; C¹C¹, distance between upper canines at basal labial surface; M³M³, distance between

upper third molar cusps, at labial surface; M²L, upper second molar cusp length; M²B, upper second molar cusp breadth; I₁M₃, lower tooth row cusp length and DL, dentary length from condyle to anterior most point; SVL, snout to anus length; TVL, distal point of tail to anus length; EL, ear length; TIB, tibia length; FA, forearm length; D2-5MC, digits 2-5 metacarpal length; and D3P1-3, digit 3 phalanx 1-3 length.

Sexual dimorphism of 17 cranial, dentary and dental characters (referred to collectively as skull characters) and 12 external body characters of *Miniopterus* specimens was investigated by standard multiple regression (where all effects were assessed simultaneously) of each character on sex and population, with skull and external body characters run separately. Specimens preserved and lodged in the Western Australian Museum's collection from each island, and from Queensland and New South Wales (Australia) were regarded as separate populations. Additionally two distinct forms of small *Miniopterus* were recognised *a priori* as occurring on some islands (Java, Lombok, Sumbawa, Alor, Selaru, Semau, Roti and Seram). Where this occurred, each form on the island was considered a separate population. These forms were clearly recognisable as a larger and smaller form.

Only the populations represented by both the two adult age types and both sexes present were included in these analyses. For the skull characters these were: Java (large form), Lombok island (small), Lombok island (large) Sumbawa island (small), Semau (small), Savu, Selaru (small) and Queensland. For the external characters these populations were: Borneo, Sumbawa (small), Lombok (large), Semau (small), Savu, Selaru (large), Queensland and New South Wales. The difference in the populations used in these analyses results from damage to skulls but not external body characters, or the converse. Graphical inspection of raw data using plots from regression analyses gave no indication of heteroscedasticity.

After first examining for the influence of adult age and/or sex on characters Discriminant Function Analyses (DFA) were run separately for measurements of skull and external characters. Characters that were age or sex dependent, or which had a significant interaction between age and sex, or which had a number of missing cases, were excluded from these analyses.

Populations, as identified above, that had clearly overlapping clusters in discriminant function space were combined as a group. Groups so recognised were then run again with DFA but using a subset of five most influential characters; these subsets were chosen so as to minimise the value of Wilks' Lambda (How *et al.* 1996). In all cases this subset of five characters provided a similar grouping of islands to that when the DFA used the full set of

characters. For this reason only the DFA based on such a subset of characters are presented.

Statistical analyses were performed using SPSS-PC+ (Norusis, 1986).

Specimens examined were from a number of museums. These museums are denoted by a prefix code before the specimen number as follows: WAM, Western Australian Museum; JM, Queensland; M, Australian Museum; and CM, CSIRO, Australia. Most specimens have both a skull and spirit carcase; those affixed with 'S' have a skull only and with 'E', spirit carcase only.

RESULTS

Multiple regressions

Because of the number of associations tested, the level of statistical significance is set at $P < 0.01$.

Skull characters – There were significant interactions in the full model in two characters: palatal length (sex, age, population and sex, population) and M² breadth (age, population). Only cranial height was sexually dimorphic with males of all populations being on average larger ($F_{1,104} = 7.304$, $P = 0.008$). Age was not significantly associated with any character. All characters differed significantly at $P < 0.001$ between populations, except greatest skull length; the characters with the highest F values were C¹M³ length, M³M³ distance C¹C¹ distance and dentary length (Table 1a).

External body characters – There were no significant interactions in the full model, nor was there any significant association of any of the characters with either sex or age. However, all characters were highly significantly ($P < 0.001$) associated with population, particularly tibia length and digit 3 and 5 metacarpal lengths (Table 1b).

Discriminant Function Analyses (DFA)

(a) *Skull characters* – five skull characters were omitted from all DFA. Two of these were omitted because a number of individuals had missing values (mesopterygoid fossa breadth and zygomatic width), two because of significant interactions between main effects (palatal length and M² breadth) and cranial height and one because it was sexually dimorphic.

A DFA using a subset of five of the remaining 12 characters (M³M³ distance, braincase breadth, C¹M³ length, C¹C¹ distance and dentary length) was run for all populations. This analysis extracted four significant functions which explained a total of 98.6% of the variation and allowed 40.4% of specimens to be allocated to their correct group. Three major groupings of these populations were apparent from the plot of Functions 1 and 2 (Figure 2a). Combinations of other Discriminant Functions

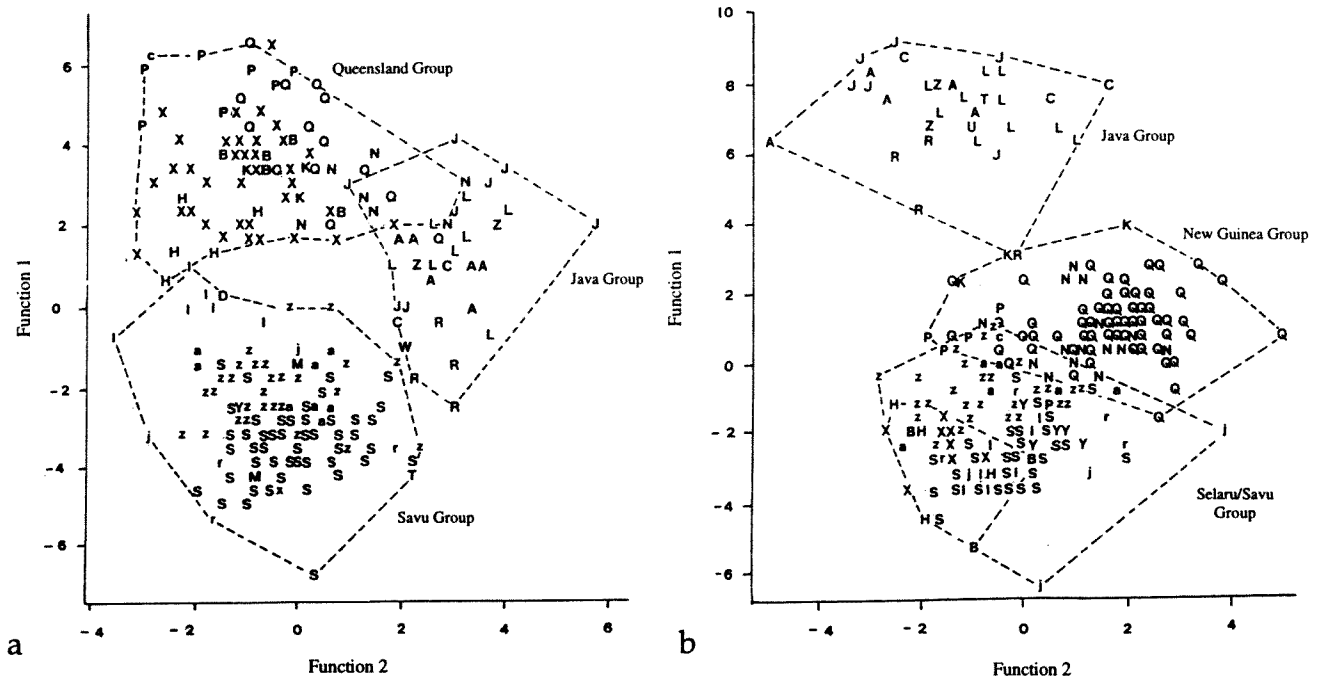


Figure 2 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and all localities for adult *Miniopterus* [15 Indonesian islands, Philippines, Papua New Guinea and Australia (Queensland and New South Wales separately)]. Locality codes are as follows (when two forms are on the same island the larger form is capitalised): Borneo, B; Java, J and j; Madura, D; Lombok, L and l; Sumbawa, Z and z; Moyo, M; Alor, A and a; Wetar, W; Selaru, X and x; Kai, K; Seram, C and c; Timor, T; Semau, Y; Roti, R and r; Savu S; Philippines, H; Papua New Guinea, P; Queensland, Q; and New South Wales, N.

do not clarify further these major groups. These groups are: *Java Group* [Java (large), Alor (larger form), Seram (large), Lombok (large), Roti (large) and Sumbawa (large)]; *Queensland Group* [Queensland, New South Wales, Papua New Guinea, Borneo, Seram (small form), Philippines, Kai, Selaru (large)]; and *Savu Group* [Savu, Alor (small), Madura, Java (small), Lombok (small), Moyo, Roti (small), Timor, Wetar, Selaru (small), Semau and Sumbawa (small)].

The DFA on external body characters (see below) indicated that two clear sub-groupings of populations occurred in the Queensland Group. Consequently, after dividing the Queensland Group into two Groups (New Guinea and Selaru), a DFA was run using a subset of five skull characters (see Table 2a) and the following four *a priori* population groupings: *Java Group* (as above); *New Guinea Group* (Papua New Guinea, Queensland, New South Wales, Kai and Seram (small)); *Selaru Group* [Selaru (large), Philippines and Borneo]; and *Savu Group* (as above).

This DFA extracted three significant functions. Function 1, which separated the Savu Group from the other groups, explained 83.2% of the variance (Figure 3a). The canonical variate coefficients with the highest values on Function 1 were braincase breadth, C^3M^3 length and M^3M^3 distance (Table 2a). Function 2, which separated the Java Group from

the Selaru Group, also partially separated the Java Group, explaining 15.6% of the variance. The coefficients with the highest values on Function 2 were braincase breadth, M^3M^3 distance and M^2 length. Plots of other combinations of Functions 1 to 3 did not further clarify these four groupings.

A total of 88.5% of individuals were allocated to their correct population grouping. Only four of the 115 individuals from the Savu Group were misclassified; three to the Java Group and one to the Selaru Group. Three of the 28 Java Group individuals were misclassified; one to the Selaru Group and two to the New Guinea Group. Most misclassifications were between the New Guinea and Selaru Group: with seven of 44 individuals from the Selaru Group to the New Guinea Group and seven of the 32 individuals from the New Guinea Group to the Selaru Group and five to the Java Group.

(b) *External body characters* – Snout to vent length and tail length were omitted from all DFA because these two measurements could not be recorded with the accuracy of other body measurements.

A DFA using a subset of five of the remaining characters (tibia length, digit 5 metacarpal length, digit 3 phalanx 2 and 3 lengths and ear length) was run for all populations. This analysis extracted four significant functions and allowed 46.1% of specimens to be allocated to their correct group.

Table 1 The F-values from multiple regressions on sex, age and population and their interactions for eight populations of adult *Miniopterus* (see text) from Indonesia, Philippines, New Guinea and Australia. (a) skull characters and (b) external body characters. There were no significant interactions for external body characters. Probability levels are: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Table 1a.

Character	Main Effects			Interactions			
	sex	age	population	sex. age. population	sex. age. population	sex. population	age. population
GSL	0.340	0.047	0.659	0.076	0.036	0.118	0.0310
BCL	3.639	0.297	7.206***	1.400	0.354	0.611	0.559
PL	0.016	0.430	9.126***	7.335***	0.988	3.584**	1.627
ICD	0.709	1.003	4.647***	0.912	0.181	0.878	0.516
MW	5.844*	4.870*	28.130***	0.351	0.002	1.123	0.974
MFB	2.294	0.480*	8.626***	0.934	0.475	1.809	0.753
CH	7.304**	0.409	33.762***	0.157	2.238	1.220	0.896
LIB	1.068	0.352	12.040***	1.012	1.324	1.327	0.755
ZW	3.881	1.106	40.474***	0.423	0.032	1.215	0.897
BB	3.184	0.891	32.967***	1.800	0.012	1.432	0.993
C ¹ M ³	3.916	1.169	64.008***	0.889	1.856	1.076	2.118
C ¹ C ¹	2.833	0.899	40.560***	0.433	0.827	2.811*	2.433*
M ³ M ³	0.753	0.139	61.856***	0.807	2.500	1.375	1.421
M ² L	0.346	0.023	15.718***	0.996	5.135*	1.606	1.680
M ² B	1.720	0.962	13.997***	1.513	2.524	1.276	4.315**
I ₁ M ₃	0.000	0.191	4.366***	0.051	0.241	0.160	0.306
DL	2.950	0.287	40.254***	0.197	0.099	1.145	0.986
d.f	1,104	1,104	7,104	3,104	1,104	6,104	6,104

Table 1b.

Character	Main effects		
	Sex	Age	Population
SVL	0.084	0.414	4.921***
TV	0.164	0.003	20.452***
EL	0.001	0.175	6.257***
TIB	4.358*	2.670	110.245***
FA	0.150	0.183	52.655***
D2MC	0.040	0.352	49.097***
D3MC	1.134	1.779	75.844***
D3P1	0.005	0.243	10.850***
D3P2	2.551	2.308	32.301***
D3P3	0.000	0.004	15.092***
D4MC	0.005	0.042	5.748***
D5MC	0.245	0.419	99.903***
d.f	1,163	1,163	7,163

Three major groupings of these populations are apparent and these are displayed in a plot of Functions 1 and 2 (Figure 2b). These major population groupings were (using the above terminology): Java Group; New Guinea Group; and Selaru Group and Savu Group (combined).

However, because individuals in the Savu group were distinguishable on skull characters from the Selaru Group, the DFA was based on a subset of five external body characters (see Table 2b) and the four *a priori* groups of Java, New Guinea, Selaru and Savu. This analysis extracted three significant functions. Function 1, which explained 82.2% of the variance, separated the New Guinea Group from the other groups and partially separated the Selaru Group from the Java Group (Figure 3b). The

characters with high coefficient values on Function 1 were tibia length and digit 5 metacarpal length (Table 2b). Function 2, which partially separated the Java Group from the other groups, explained 14.1% of the variance. The characters with high coefficient values on Function 2 were tibia length, forearm length, digit 5 metacarpal length, and digit 3 phalanx 2 length. A total of 85.4% of individuals were classified to their correct population with, as expected, most misclassifications between the Savu and Selaru Groups. In the Java Group, 91% of the 104 individuals were correctly classified; misclassifications were 3% to the Savu Group and 6% to the Selaru Group. Only one of the 34 New Guinea Group individuals was misclassified (to the Savu Group). In the Savu Group, 81% of the 138 individuals were correctly classified; misclassifications were 6% to the Java Group and 13% to the Selaru Group. In the Selaru Group, 73% of the 33 individuals were correctly classified; misclassifications were 3% to the Java Group and 24% to the Savu Group.

Morphological variation within major population groups

Considerable subclustering was apparent among populations within the major population groups

Table 2 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and four *a priori* population groups (Java, New Guinea, Selaru and Savu, see text) of adult *Miniopterus*. (a) skull and (b) external body characters. Character codes described in text.

Character	Function 1	Function 2	Function 3
M ³ M ³	0.4561 (4.2094)	0.5107 (4.7141)	-1.0065 (-9.2902)
BB	0.5034 (4.0535)	-0.8807 (-7.0924)	-0.0011 (-0.0090)
C ¹ M ³	0.4950 (4.8138)	0.0246 (0.2390)	0.9945 (9.6701)
M ² L	0.0671 (1.7091)	0.4871 (12.4004)	0.2347 (5.9744)
BCL	-0.3644 (-2.4652)	-0.0583 (-0.3945)	0.1357 (0.9178)
Constant	-64.9332	9.2704	-11.4014
Variance explained (%)	83.2	15.6	1.2

Character	Function 1	Function 2	Function 3
D5MC	0.4417 (0.5051)	0.8880 (1.0155)	-0.6030 (-0.6896)
TIB	0.7515 (1.3791)	-1.2043 (-2.2101)	0.0481 (0.0882)
EL	-0.0805 (-0.1534)	0.2661 (0.5069)	0.8922 (1.6992)
D3P2	-0.0606 (-0.0564)	-0.6566 (-0.6114)	0.1673 (0.1558)
FA	-0.0698 (-0.0677)	0.9035 (0.8776)	0.4292 (0.4169)
Constant	-31.9806	-20.2784	-16.5598
Variance explained (%)	82.2	14.1	3.7

(Java, New Guinea, Selaru and Savu), both in skull and or external body characters. This variation was also examined using DFA.

The Java Group

Skull characters – a DFA based on all the Java Group populations and using a subset of five skull characters extracted two significant functions which combined explained 85% of the variance with 68.6% of individuals allocated to their correct population; no clear subgroups of these populations was detected.

External body characters – a DFA based on all Java Group populations and using a subset of five external body characters (ear length, digit 3 phalanx 1-3 and digit 5 metacarpal length) extracted two significant functions in which 74% of individuals were allocated to their correct population. The

Table 3 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected external body characters and three *a priori* populations subgroups (Western, Southeastern and Seram) of adult *Miniopterus* in the Java Group (see text).

Character	Function 1	Function 2
EL	0.9077 (3.1093)	0.6362 (2.1794)
D3P3	0.7261 (1.5434)	0.0583 (0.1240)
D5MC	0.9224 (0.8365)	-1.2242 (-1.1102)
D3P1	-0.6927(-1.6310)	0.5464 (1.2867)
TIB	-0.3667 (-0.3847)	0.4827 (0.5064)
Constant	-46.8639	-6.0525
Variance explained (%)	74.7	25.3

configuration of these populations in discriminant function space was very similar to Figure 4 but with a marginal overlap between the populations nominated as the western and southeastern forms on that figure. From this DFA the following population groups were recognised: *Western subgroup* (Java, Lombok, Sumbawa); *Southeastern subgroup* (Alor and Roti); and *Seram subgroup* (Seram island)

A DFA based on these three subgroups (Western, Southeastern and Seram) and using a subset of five external body characters (see Table 3) extracted two significant functions. Function 1, which explained 74.7% of the variance, separated the Seram subgroup from both the Western and Southeastern subgroups (Figure 4). All characters, except tibia length, had high canonical variate coefficients on Function 1 (Table 3). Function 2, which explained 25.3% of the variance, separated the Southeastern subgroup from both the Western and Seram subgroups. The characters with high coefficient values on Function 2 were digit 5 metacarpal length, ear length and digit 3 phalanx 1 length. A total of 94.1% of individuals were classified to their correct population subgroup. Misclassification only occurred in the Southeastern subgroup where two of the 10 individuals in this group were allocated to the Western subgroup.

The New Guinea Group

Skull Characters – a DFA based on all populations in the New Guinea Group and using a subset of five skull characters (see Table 4a) extracted three significant functions which explained a combined

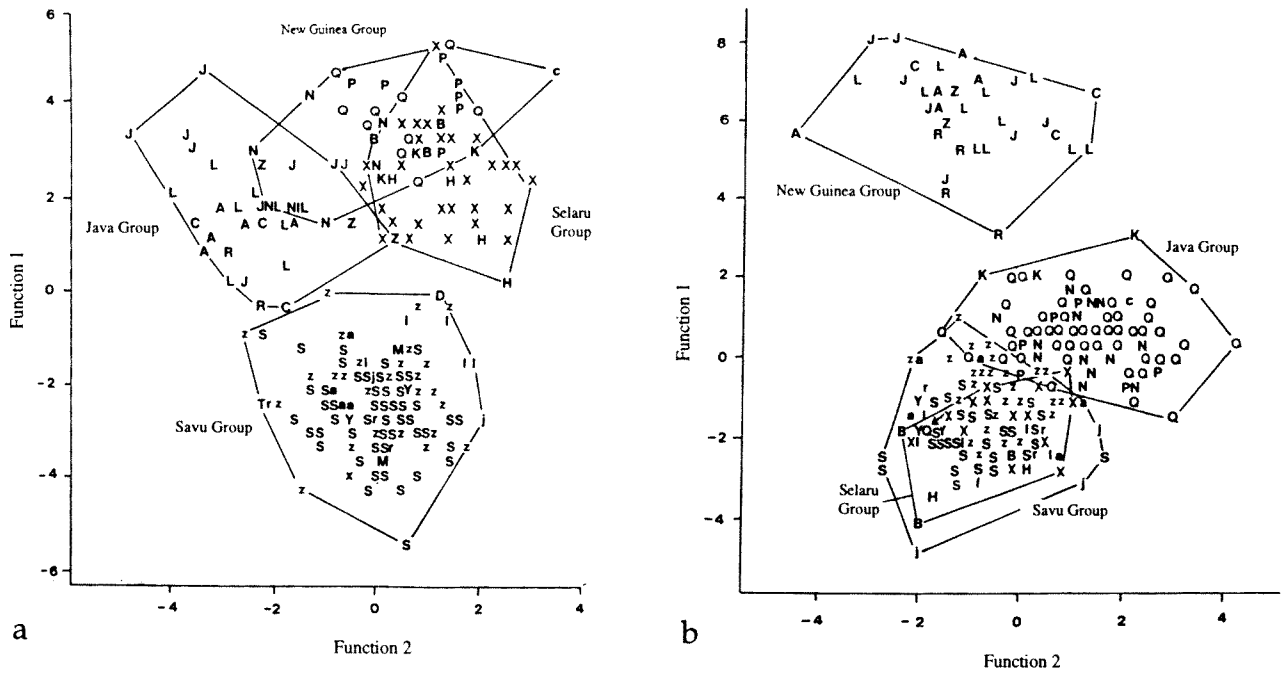


Figure 3 Plot of DFA Functions 1 and 2 based on five (a) skull (b) external body characters and four *a priori* groupings of localities (Java, New Guinea, Selaru and Savu Groups, see text) of adult *Miniopterus*. Locality codes as for Figure 2.

97.9% of the variance. Only 77.1% of individuals were classified to their correct population subgroup. Function 1, which explained 58.5% of the variance, separated the Papua New Guinea

population from both the Kai and New South Wales populations (Figure 5a). The characters with high (>0.5) coefficient values were C1M3 length, dentary length and greatest skull length (Table 4a). Function 2, which explained 24.9% of the variance, separated the Kai population from the others. The character with the highest coefficient value on Function 2 was intercochlear distance (Table 4a). Function 3, which explained 14.5% of the variance, did not noticeably separate further these populations.

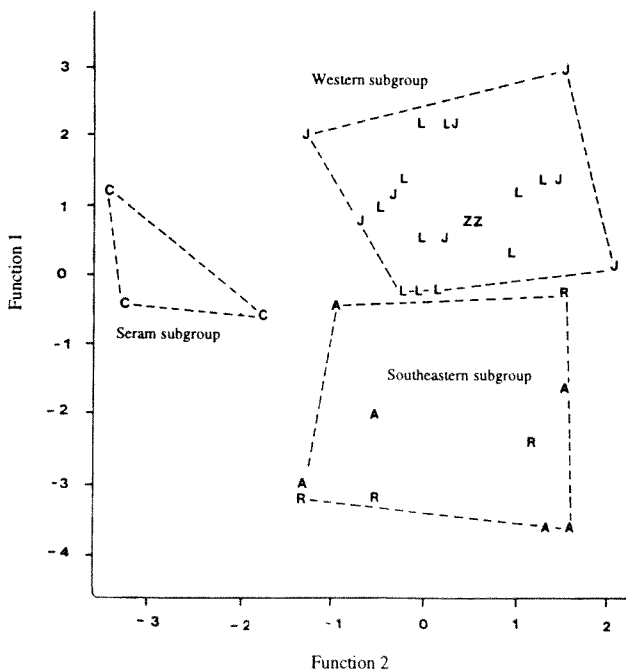


Figure 4 Plot of DFA Functions 1 and 2 based on five external body characters and all Java Group populations (see text) for adult *Miniopterus*. Locality codes as for Figure 2. Three subgroups of populations are apparent from this analysis (Western, Southeastern and Seram).

External characters – a DFA based on all populations in the New Guinea Group and using a subset of five external body characters (see Table 4b) extracted three significant functions which combined explained 97.7% of the variance. Only 56.7% of individuals were classified to their correct population. Function 1, which explained 65.4% of the variance, separated the Papua New Guinea population from the Kai and New South Wales populations and partially so from the Queensland population (Figure 5b). The characters with high coefficients (>0.5) on Function 1 were digit 3 phalanx 1 length, ear length and tibia length (Table 4b). Function 2, which explained 24.3% of the variance, separated the Kai population from the other populations (Figure 5b). The character with the highest coefficient on Function 2 was tibia length (Table 4b). Function 3, which explained 9.3% of the variance did not noticeably further separate these groups.

The above analyses indicated that while the Papua New Guinea population had diverged from the New South Wales population; the Queensland population was both geographically and

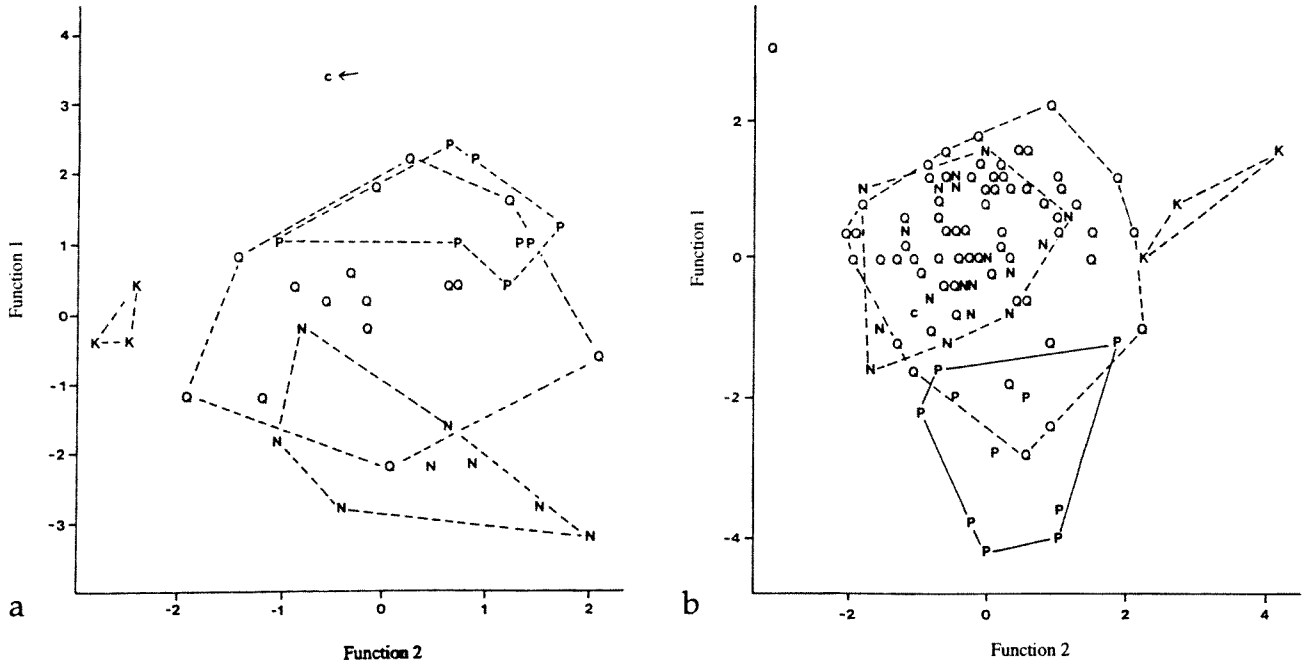


Figure 5 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and the four New Guinea Group populations (New Guinea, Queensland, New South Wales and Kai island) for adult *Miniopterus*. Locality codes as for Figure 2.

morphologically intermediate between them. The Kai population, represented by only three specimens, appeared to form a subgroup separate from the Papua New Guinea, Queensland and New South Wales populations.

The Selaru Group

Skull characters – a DFA based on the three

populations of Borneo, Philippines and Selaru as *a priori* groups and using a subset of five skull characters (see Table 5a) extracted two significant functions. Function 1, which explained 91.9% of the variance, separated all three populations (Figure 6a). All five characters had high coefficient values on Function 1 (Table 5a) which suggested that overall skull size was important in separating these

Table 4 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and four populations (Kai, New Guinea, Queensland and New South Wales) of adult *Miniopterus* in the New Guinea Group (see text). (a) skull and (b) external body characters.

Character	Function 1	Function 2	Function 3
C'M ³	0.6378 (7.4690)	0.4619 (5.4096)	-1.1766 (-13.7785)
GSL	-0.5034 (-3.2171)	0.4439 (2.8372)	1.2120 (7.7464)
ICD	-0.3369 (-4.7289)	0.6065 (8.5132)	-0.5549 (-7.7884)
M ² L	0.2055 (6.5967)	-0.4442 (-14.2600)	0.3979 (12.7725)
DL	0.6463 (4.4046)	-0.1149 (-0.7831)	0.3511 (2.3927)
Constant	-42.0322	-53.1482	-64.9240
Variance explained (%)	58.5	24.9	14.5

Character	Function 1	Function 2	Function 3
D3P3	0.8337 (1.7967)	-0.0900 (-0.1940)	0.3421 (0.7371)
TIB	0.5286 (1.3082)	0.7407 (1.8334)	-0.2608 (-0.6454)
EL	-0.5818 (-0.9738)	-0.0746 (-0.1249)	-0.1564 (-0.2617)
D3P2	-0.1913 (-0.2285)	-0.2253 (-0.2691)	1.0794 (1.2896)
FA	-0.3811 (-0.4763)	0.4637 (0.5796)	0.0278 (0.0347)
Constant	2.0761	-42.6074	-25.740
Variance explained (%)	65.4	24.3	9.3

Table 5 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and three populations (Borneo, Philippines and Selaru) of adult *Miniopterus* in the Selaru Group (see text). (a) skull and (b) external body characters.

Table 5a Character	Function 1	Function 2
I_1M_3	0.7940 (8.0915)	0.5475 (5.5792)
BB	-0.9966 (-7.7188)	1.0001 (7.7461)
MW	0.8575 (6.2331)	-0.4952 (-3.5995)
M^3M^3	-0.8138 (-8.5414)	0.1177 (1.2358)
C^1C^1	0.7086 (7.3221)	-0.1008 (-1.0413)
Constant	-26.8162	-67.7533
Variance explained (%)	91.9	8.1

Table 5b Character	Function 1	Function 2
EL	0.5450 (1.3966)	0.0426 (0.1091)
D3P1	-0.3955 (-0.8599)	0.8448 (1.8368)
D3P3	0.6162 (0.8501)	-0.6363 (-0.8780)
D2MC	-1.1344 (-1.2697)	-0.2616 (-0.2928)
D3P2	0.8204 (2.4340)	0.4129 (1.2249)
Constant	-28.7462	13.3848
Variance explained (%)	86.8	13.2

populations. Function 2, which explained 8.1% of the variance, separated the Borneo and Philippine populations. The characters with high (>0.5) coefficients on Function 2 were braincase breadth and I_1M_3 length. A total of 94.1% of individuals

were classified to their correct population. All individuals in the Borneo and Philippine populations and all but three of the 42 individuals from the Selaru population were correctly classified; these three Selaru individuals were misclassified to the Philippine population.

External characters— a DFA, based on the three populations of Borneo, Philippines and Selaru as *a priori* groups and using a subset of five external body characters (see Table 5b), extracted two significant functions. Function 1, which explained 86.8% of the variance, separated the Selaru population from both the Philippine and Borneo populations (Figure 6b). All five characters, except digit 3 phalanx 1 length, had high (>0.5) coefficient values (Table 5b). Function 2, which explained 13.2% of the variance, separated the Borneo and Philippine populations. The characters with high (>0.5) coefficients on Function 2 were digit 3 phalanx 1 and 3. A total of 97% of individuals were classified to their correct populations. All individuals in the Borneo and Philippine populations were correctly classified; a single Selaru individual was misclassified to the Borneo population.

The Savu Group

Skull characters – a DFA based on all populations in the Savu Group and using a subset of five characters (dentary length, M^3M^3 distance, intercochlear distance, mastoid width and C^1M^3 length) extracted four significant functions, which combined explained 98.1% of the variation. There

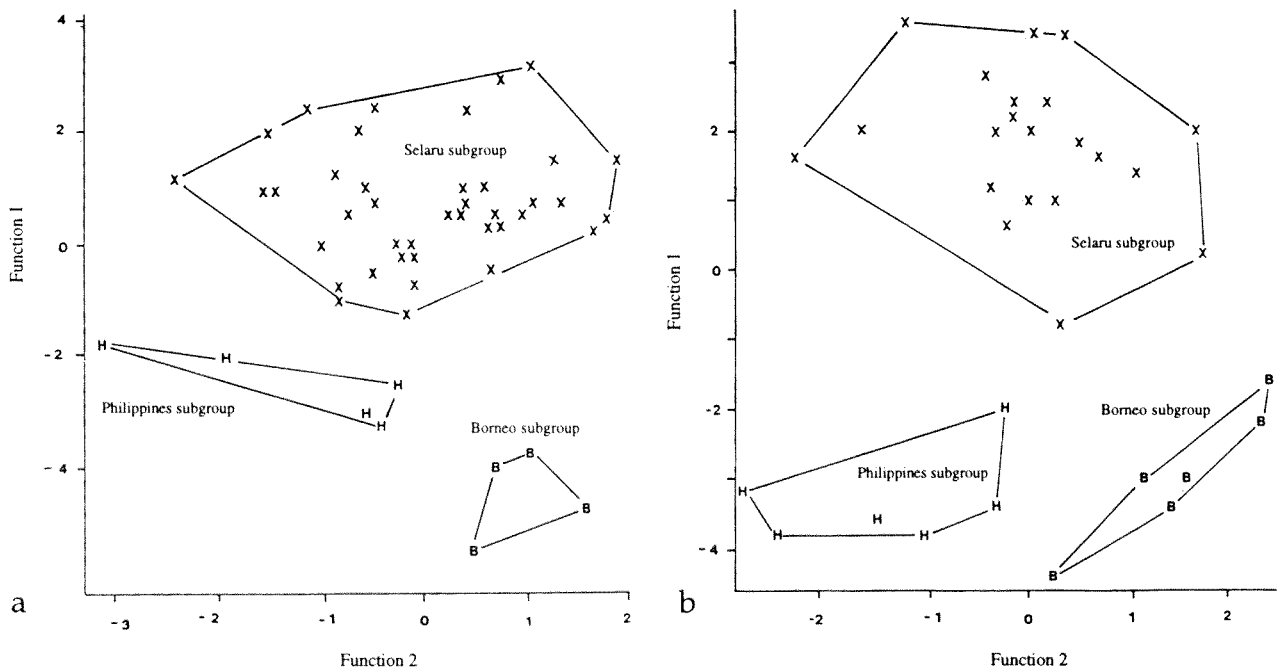


Figure 6 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and the three Selaru Group populations (Borneo, Philippines and Selaru) for adult *Miniopterus*. Locality codes as for Figure 2.

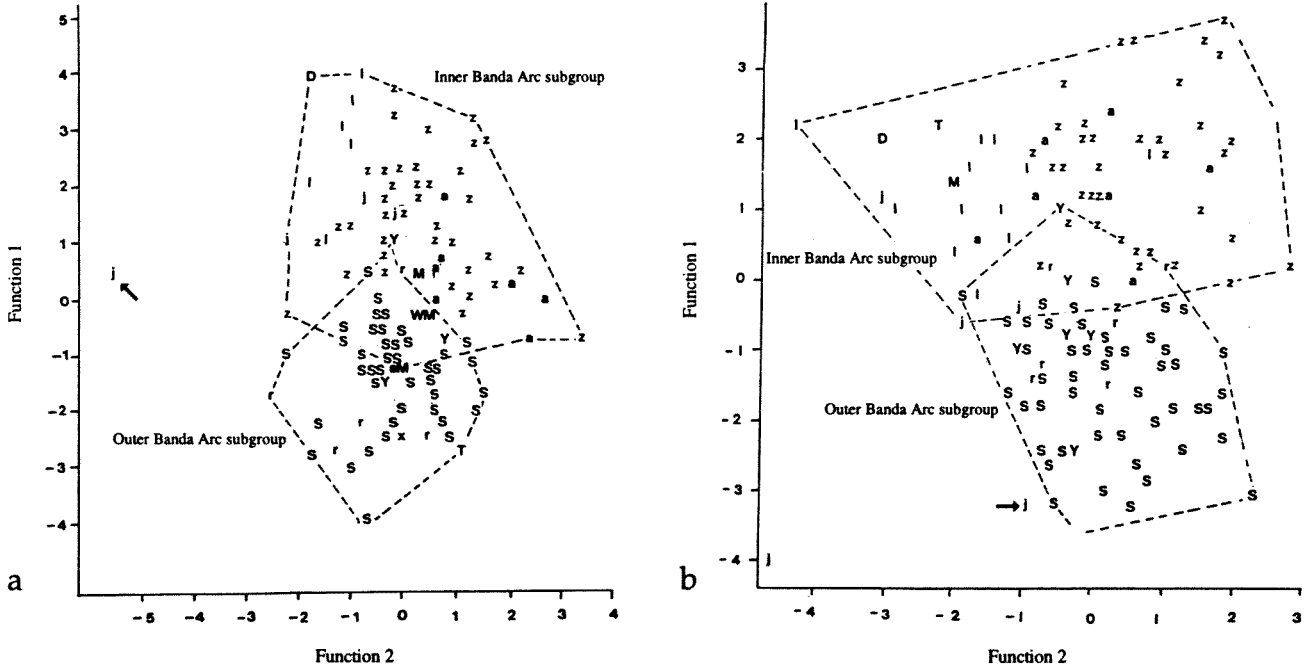


Figure 7 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and all the island populations in the Savu Group (see text) for adult *Miniapterus*. Locality codes as for Figure 2.

was, however, considerable overlap between these populations, with only 45.2% of individuals classified to their correct population. The plots of combinations of Functions 1 to 3, which combined explained 92.5% of the variance, indicated that some morphological substructuring occurs among these populations. For example, Function 1 which

explains 67.6% of the variance, separated most of the populations in the Inner Banda Arc group of islands from the populations in the Outer Banda Arc islands (Figure 7a). Plots of combinations of other functions do not noticeably clarify further these groupings.

Table 6 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and two *a priori* subgroupings of the 12 island populations (Inner and Outer Banda Arc, with Wetar island included in the latter subgroup) of adult *Miniapterus* in the Savu Group (see text). (a) skull and (b) external body characters.

Character	Function 1
DL	0.6507 (4.4852)
ICD	0.5579 (6.8625)
MW	-0.7147 (-5.8647)
C ¹ M ³ L	0.6320 (8.0696)
M ² L	0.2319 (6.1311)
Constant	-54.7709

Character	Function 1
D3P2	1.0514 (1.3822)
D3P1	-0.4575 (-1.1849)
D5MC	0.9814 (1.4285)
M3MC	-0.8619 (-1.1053)
EL	-0.3023 (-0.7236)
Constant	-22.0157

A DFA based on the two subgroups identified above, namely the *Inner Banda Arc subgroup* (Java, Madura, Lombok, Sumbawa, Moyo, Alor) and the *Outer Banda Arc subgroup* (Timor, Roti, Semau, Savu, Wetar and Selaru) and using a subset of five characters (see Table 6a) extracted a significant function (Figure 8a) which classified 91.2% of individuals to their correct population subgroup. A total of 93.8% and 88.7% of individuals in the Outer Banda Arc and Inner Banda Arc subgroups, respectively, were correctly classified. Individuals that were misclassified in the Outer Banda Arc subgroup comprised the following numbers of individuals: Roti, 1; Semau, 1; and Savu, 2. Inner Banda Arc misclassifications were as follows: Java, 2; Moyo, 1; Sumbawa, 2; and Alor, 2. All characters had high coefficient values on Function 1 (Table 6a).

External characters – a DFA based on all populations in the Savu Group and using a subset of five characters (digit 3 phalanx 2, tibia length, ear length, forearm length and digit 3 metacarpal length) extracted three significant functions, which combined explained 95.6% of the variance. There was considerable overlap between these populations with only 57.6% of individuals classified to their correct populations. Plots of Functions 1 and 2 (Figure 7b) revealed most of the separation between these populations, which

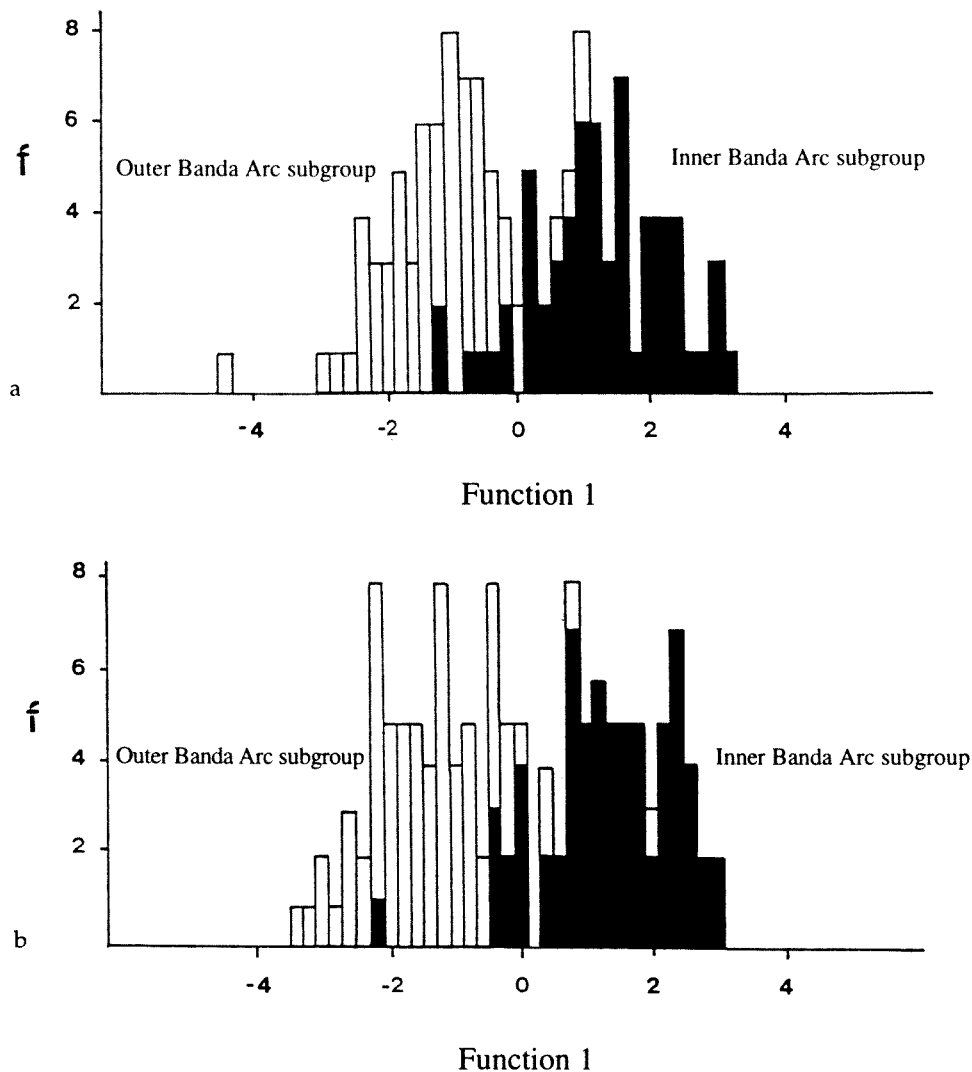


Figure 8 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and two groupings (Inner and Outer Banda Arc, with Wetar island placed in the Outer Banda Arc subgroup) (see text) for adult *Miniopterus*. Locality codes as for Figure 2.

cluster similarly to the populations that were clustered above based on skull characters.

A DFA based on the Inner and Outer Banda Arc subgroups above and using a subset of five external body characters (see Table 6b) extracted a significant function (Figure 8b) which classified 92.7% of individuals to their correct population subgroup. A total of 94.1% and 91.3% of individuals in the Outer Banda Arc and Inner Banda Arc subgroup, respectively, were classified correctly. Numbers of individuals that were misclassified in the Outer Banda Arc subgroup comprised the following: Semau, 1; Roti, 1; Savu, 1; and Timor, 1. The characters that had high coefficient values (>0.5) were digit 3 phalanx 2 length, and both digit 3 and digit 5 metacarpal lengths (Table 6b).

Summary of multivariate analysis

The combination of DFA on skull and external

body measurements of specimens of *Miniopterus* used in this study indicated the presence of considerable morphological differentiation among these island populations. Four distinct groups of populations were identified (Java, New Guinea, Selaru and Savu). The Java Group was the most distinctive and was separated from these other population groups, both in skull and external body characters, but particularly the latter. The Savu Group was separated from the remaining three populations groups on skull characters but could not be separated from the Selaru Group on external body characters. The New Guinea and Selaru Groups were separated principally on external body characters.

All four population groups are recognised as separate species. Within each of these four major population groups there was morphological differentiation, some of which is recognised as

being subspecifically distinct. Named taxa relate to the population groups and subgroups as follows:

Java Group: *Miniopterus pusillus*

Western subgroup: *M. p. pusillus*

Southeastern subgroup: *M. pusillus* subsp. indet. A

Seram subgroup: *M. p.* subsp. indet. cf. *M. pusillus* subsp. indet. A.

New Guinea Group: *Miniopterus australis*

Papua New Guinea/Queensland/NSW subgroup: *M. a. tibialis*

Seram unallocated: *M. a. tibialis*

Kai subgroup: *M. a.* subsp. indet.

Selaru Group: *Miniopterus paululus*

Philippines subgroup: *M. p. paululus*

Borneo subgroup: *M. p. witkampii*

Selaru subgroup: *M. p.* subsp. nov.

Savu Group: *Miniopterus shortridgei*

Inner Banda Arc subgroup: *M. s. shortridgei*

Outer Banda Arc subgroup: *M. s.* subsp. indet.

The following systematic section describes these above taxa using univariate analyses, particularly measurements of means and ranges of characters, but also of bivariate plots of characters that were indicated by DFA to be important. These important characters were recognised as those with high standardised canonical discriminant function coefficients (presented in text) as well those with high loadings (from the pooled- within-groups correlations between discriminating variables and canonical discriminant functions).

TAXONOMY

***Miniopterus pusillus* Dobson, 1876**

M. pusillus Dobson, 1876: 162

M. macrocneme Revilliod, 1914: 360

Lectotype: Wroughton (1918:22) designated specimen number 185, Indian Museum, collected by Stoliczka, as the lectotype.

Type locality: Nicobar islands (see Wroughton 1918:22)

Type locality not listed in Dobson (1876) but he lists specimens (p. 163) of *M. pusillus* collected from Nicobar islands and Madras (apparently by Stoliczka – see Dobson, 1871). Hill (1983) discussed both the choice of lectotype and the type locality (Nicobar islands) by Wroughton (1918) and agrees with him. It appears that both Tate (1941) and Ellerman and Morrison-Scott (1951) were incorrect in selecting a lectotype from Madras.

Diagnosis

Miniopterus pusillus differs from *M. australis*, *M. paululus* and *M. shortridgei* by averaging larger in most external body characters (Table 7b) and with digit 5 metacarpal longer relative to ear length (Figure 9a).

It differs from *M. australis* in being on average larger in all external body characters; for example, in having both a generally longer forearm length 42.6 (36.5–44.3) 35 *v.* 39.2 (37.4–41.6) 107 and tibia

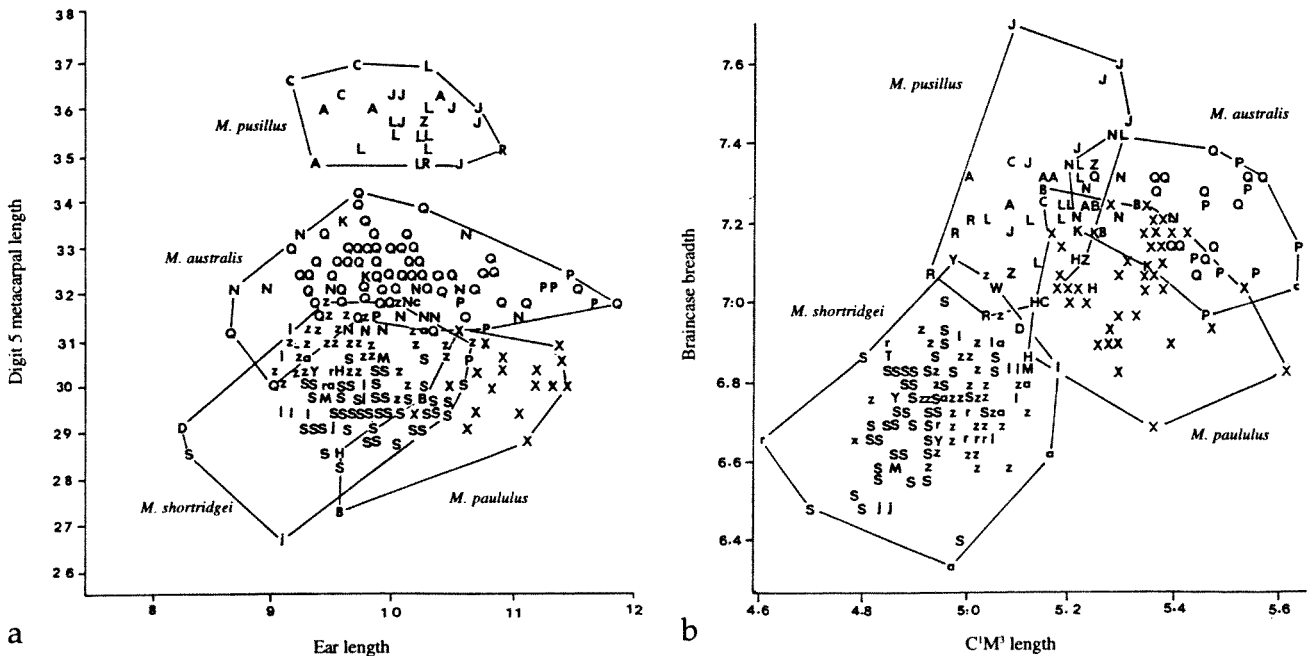


Figure 9 Plot of (a) digit 5 metacarpal length (mm) versus ear length (mm) and (b) braincase breadth (mm) versus C'M³ length (mm) for all populations of adult *Miniopterus* considered (*pusillus*, *australis*, *paululus* and *shortridgei*). Locality codes as for Figure 2.

length 19.0 (14.7–20.3) 35 v. 15.9 (14.8–17.3) 107. It also is on average smaller in all skull characters (Table 7a), except cranial height, least interorbital breadth and braincase breadth; for example, greatest skull length 13.5 (12.9–14.0) 35 v. 14.0 (13.5–14.4) 36 and C¹M³ length 5.2 (4.9–5.3) 35 v. 5.4 (5.2–5.6) 36. Also upper molar row generally shorter relative to braincase breadth (Figure 9b).

It differs from *M. paululus* in being on average larger in all external body characters except ear length; for example, forearm length 14.0 (13.5–14.4) 36 v. 37.1 (34.2–38.7) 34 and tibia length 19.0 (14.7–20.2) 35 v. 15.0 (13.9–15.6) 34. Tail to vent length absolutely larger 44.8 (39.7–51.2) 34 v. 34.8 (31.2–39.0) 34. It is on average smaller in all skull characters, except mastoid width, cranial height, least interorbital breadth and braincase breadth (Table 7a). For example, greatest skull length 13.5 (12.9–14.0) 35 v. 13.8 (13.1–14.3) 53 and cranial height 5.8 (5.6–6.3) 34 v. 5.5 (5.2–5.7) 53. Upper molar cusp row generally shorter relative to braincase breadth (Figure 9b).

It differs from *M. shortridgei* in averaging larger in all skull and external body characters. For example, forearm length 42.6 (36.5–44.3) 35 v. 36.8 (33.3–39.3) 148; tibia length 19.0 (14.7–20.2) 35 v. 15.0 (13.4–16.4) 150; greatest skull length 13.5 (12.9–14.0) 35 v. 13.3 (12.6–13.8) 135; and C¹M³ length 5.2 (4.9–5.3) 35 v. 5.0 (4.6–5.2) 137. Braincase breadth usually greater relative to upper molar cusp row length (Figure 9b).

Miniopterus pusillus pusillus Dobson, 1876

Lectotype and type locality: stated above.

Specimens examined: Indonesia; Java Island – Cibereum, 6°44'S, 107°00'E, WAM M(27160-4) 2 ♀ ♀ 3 ♂ ♂. Kiskenda, 7°06'S, 110°16'E, WAM M(39322, 39327, 39371) 3 ♂ ♂. Lombok Island – Bang Kang, 8°30'S, 116°10'E, WAM (M35850-54, 35857-8, 35868, 35873, 35876, 35960) 8 ♀ ♀, 3 ♂ ♂. Sumbawa Island – Batu Tering, 8°48'S, 117°22'E, WAM M31453 ♀. Desa Sangeang, 8°18'S, 118°56'E, WAM M(31547-8) 2 ♂ ♂.

Diagnosis

Miniopterus p. pusillus differs from *M. pusillus* subsp. A (see below) by averaging larger in all external body and skull characters, except for digit 3 phalanx length, mesopterygoid fossa breadth and M² breadth, which are subequal in length (Table 7a, b). For example, forearm length 42.8 (40.5–44.1) 21 v. 42.0 (36.5–44.3) 11; tibia length 19.2 (18.2–20.2) 21 v. 18.6 (14.7–20.0) 11; greatest skull length 13.6 (13.2–14.0) 22 v. 13.4 (12.9–13.8) 10; M³M³ distance 5.5 (5.3–5.7) 22 v. 5.3 (5.1–5.5) 10. Ear generally longer relative to digit 3 phalanx 3 length (Figure 10).

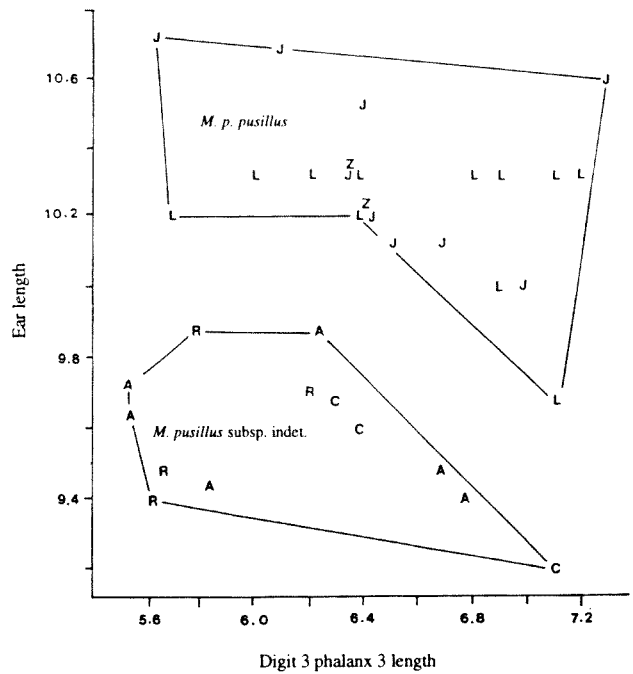


Figure 10 Plot of ear length (mm) versus digit 3 phalanx 3 length (mm) for island populations of adult *Miniopterus pusillus pusillus* and *M. p. macrocneme*. Island codes as for Figure 2.

It differs from *M. pusillus* subsp. indet. cf. *M. p.* subsp. indet. A from Seram island by averaging smaller in most external body characters, and larger in most skull characters (Table 7a, 7b). For example, forearm length 42.8 (40.5–44.1) 21 v. 43.4 (42.9–43.7) 3; ear length 10.3 (9.7–10.7) 21 v. 9.5 (9.2–9.7) 3; greatest skull length 13.63 (13.16–14.02) 22 v. 13.35 (13.27–13.42) 3 and C¹M³ length 5.20 (5.04–5.32) 22 v. 5.13 (5.08–5.15) 3. Ear longer relative to digit 3 phalanx 3 length (Figure 10).

Distribution

Lombok, Sumbawa (this study); Nicobar Islands (type locality); Madras, Thailand, Hong Kong, Java and Sumatra (Hill 1983, Hill in Corbet and Hill 1992).

Miniopterus pusillus subsp. indet. A

Specimens examined: Indonesia; Alor Island – Kalabahi, 8°14'S, 124°32'E, WAM M(37567E, 37875, 37886E, 37904-7) 7 ♂ ♂. Roti Island – Baa, 10°44'S, 123°06'E, WAM M(35357, 35359E, 35387S, 123°06'35402, 35404) 5 ♀ ♀. Seram island – Manusela, 3°10'S, 129°36'E, WAM M(34719, 34724, 34726) 3 ♀ ♀.

Diagnosis

Miniopterus pusillus subsp. indet. A and the referred specimen from Seram island differs from *M. p. pusillus* as described in the earlier diagnosis of that subspecies.

Table 7 Measurements of adult (males and females combined) *Miniopterus pusillus*, *M. australis*, *M. paululus* and *M. shortridgei* and their subspecies and unnamed forms and population Group and subgroup names from this study (a) cranial, dentary and dental and (b) external body characters. 0, mean; SD, standard deviation; MIN, minimum; MAX, maximum and N, sample size. Character codes defined in text.

Table 7a - Skulls		GSL	BCL	PL	ICD	MW	MFB	CH	LIB	ZW	BB	C ¹ M ³	C ¹ C ¹	M ³ M ³	M ² L	M ² B	I ¹ M ³	DL
<i>Miniopterus pusillus</i> (Java Group)	\bar{x}	13.53	5.18	5.16	1.23	7.64	1.68	5.83	3.48	7.48	7.27	5.16	3.93	5.44	1.21	1.40	6.55	9.59
	SD	0.27	0.16	0.16	0.06	0.20	0.14	0.16	0.11	0.21	0.16	0.10	0.14	0.13	0.04	0.06	0.12	0.19
	MIN	12.92	4.85	4.72	1.11	7.00	1.39	5.55	3.23	6.83	6.96	4.93	3.57	5.09	1.12	1.29	6.30	9.25
	MAX	14.02	5.46	5.43	1.38	8.07	1.94	6.25	3.68	7.88	7.71	5.32	4.12	5.69	1.29	1.56	6.86	10.04
	N	35	31	33	34	35	29	34	35	30	35	35	35	35	35	35	33	35
<i>M. p. pusillus</i> (Western subgroup)	\bar{x}	13.63	5.21	5.19	1.24	7.72	1.66	5.88	3.51	7.57	7.31	5.20	3.98	5.49	1.22	1.41	6.60	9.65
	SD	0.25	0.15	0.14	0.07	0.16	0.15	0.16	0.11	0.16	0.17	0.08	0.12	0.10	0.04	0.07	0.10	0.18
	MIN	13.16	5.01	4.99	1.11	7.29	1.39	5.62	3.23	7.22	7.07	5.04	3.64	5.28	1.17	1.29	6.41	9.34
	MAX	14.02	5.46	5.43	1.38	8.07	1.94	6.25	3.68	7.88	7.71	5.32	4.12	5.69	1.29	1.56	6.86	10.04
	N	22	21	22	22	22	19	22	22	22	17	22	22	22	22	22	22	20
<i>M. pusillus</i> subsp. indet A (Southeastern subgroup)	\bar{x}	13.36	5.08	5.08	1.22	7.49	1.73	5.71	3.43	7.32	7.20	5.08	3.83	5.34	1.18	1.38	6.49	9.53
	SD	0.24	0.20	0.21	0.04	0.21	0.09	0.11	0.10	0.24	0.12	0.10	0.14	0.13	0.04	0.05	0.12	0.19
	MIN	12.92	4.85	4.72	1.17	7.00	1.58	5.55	3.32	6.83	6.96	4.93	3.57	5.09	1.12	1.29	6.30	9.25
	MAX	13.79	5.38	5.35	1.31	7.77	1.84	5.92	3.58	7.56	7.33	5.23	3.98	5.50	1.27	1.43	6.62	9.76
	N	10	7	8	9	10	7	9	10	10	10	10	10	10	10	10	10	10
<i>M. pusillus</i> subsp. indet A (Seram subgroup)	\bar{x}	13.35	5.21	5.08	1.20	7.60	1.66	5.82	3.44	7.48	7.19	5.13	3.89	5.43	1.17	1.42	6.50	9.43
	SD	0.08	0.01	0.08	0.07	0.06	0.08	0.11	0.02	0.10	0.18	0.04	0.08	0.10	0.03	0.08	0.08	0.08
	MIN	13.27	5.20	4.99	1.12	7.55	1.60	5.69	3.42	7.37	6.99	5.08	3.81	5.32	1.15	1.40	6.41	9.34
	MAX	13.42	5.22	5.14	1.26	7.66	1.75	5.90	3.46	7.54	7.34	5.15	3.96	5.49	1.20	1.45	6.55	9.48
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>M. australis</i> (New Guinea Group)	\bar{x}	14.00	5.28	5.40	1.24	7.72	1.75	5.76	3.42	7.59	7.21	5.40	3.99	5.67	1.30	1.48	6.80	10.00
	SD	0.19	0.11	0.14	0.08	0.18	0.07	0.13	0.08	0.16	0.11	0.12	0.10	0.14	0.04	0.06	0.15	0.20
	MIN	13.48	5.00	5.08	1.08	7.03	1.61	5.47	3.30	7.20	6.96	5.20	3.84	5.34	1.21	1.33	6.57	9.67
	MAX	14.44	5.46	5.74	1.39	8.02	1.87	6.02	3.60	7.91	7.41	5.63	4.27	5.98	1.38	1.56	7.12	10.38
	N	36	33	33	35	36	30	36	36	31	36	36	36	35	36	36	36	36
<i>M. a. tibialis</i> (P.N.G. subgroup)	\bar{x}	14.05	5.31	5.51	1.26	7.62	1.80	5.77	3.43	7.57	7.15	5.51	4.02	5.78	1.30	1.50	6.93	10.16
	SD	0.12	0.06	0.12	0.07	0.25	0.04	0.14	0.09	0.17	0.13	0.06	0.09	0.10	0.02	0.02	0.06	0.11
	MIN	13.94	5.24	5.36	1.16	7.03	1.75	5.47	3.32	7.30	6.96	5.44	3.90	5.65	1.27	1.47	6.85	9.99
	MAX	14.21	5.38	5.74	1.33	7.86	1.87	5.90	3.60	7.82	7.34	5.63	4.14	5.98	1.33	1.53	7.00	10.31
	N	8	7	7	7	8	6	8	8	8	8	8	8	8	8	8	8	8
<i>M. a. tibialis</i> (Queensland/NSW subgroup)	\bar{x}	14.03	5.28	5.37	1.25	7.78	1.74	5.76	3.41	7.60	7.25	5.37	3.98	5.63	1.29	1.48	6.77	9.97
	SD	0.17	0.11	0.13	0.08	0.13	0.08	0.14	0.08	0.17	0.09	0.11	0.11	0.14	0.04	0.05	0.14	0.20
	MIN	13.73	5.00	5.08	1.10	7.53	1.61	5.48	3.30	7.20	7.06	5.20	3.84	5.34	1.21	1.36	6.57	9.67
	MAX	14.44	5.46	5.57	1.39	8.02	1.87	6.02	3.57	7.91	7.41	5.56	4.27	5.91	1.38	1.56	7.09	10.38
	N	24	22	22	24	24	20	24	24	20	24	24	24	23	24	24	24	24

<i>M. australis</i> subsp. indet. (Kai subgroup)	\bar{x}	13.64	5.17	5.27	1.13	7.55	1.70	5.76	3.43	7.58	7.13	5.27	3.97	5.71	1.30	1.38	6.64	9.78
	SD	0.16	0.10	0.02	0.07	0.05	0.03	0.08	0.07	0.07	0.05	0.07	0.03	0.02	0.04	0.05	0.09	0.06
	MIN	13.48	5.06	5.25	1.08	7.51	1.68	5.69	3.37	7.53	7.08	5.21	3.94	5.70	1.26	1.33	6.57	9.71
	MAX	13.80	5.25	5.29	1.21	7.60	1.73	5.85	3.50	7.66	7.16	5.35	4.00	5.73	1.34	1.42	6.74	9.83
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>M. a. tibialis</i> (Seram subgroup)	\bar{x}	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MIN	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	MAX	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	N	1	1	1	1	1	1	1	1	1	-	1	1	1	1	1	1	1
<i>M. paululus</i> (Selaru Group)	\bar{x}	13.81	5.20	5.32	1.23	7.55	1.77	5.49	3.37	7.48	7.07	5.31	3.92	5.67	1.31	1.45	6.68	9.88
	SD	0.23	0.14	0.46	0.09	0.15	0.09	0.12	0.09	0.19	0.14	0.11	0.11	0.09	0.04	0.05	0.13	0.17
	MIN	13.07	4.91	4.79	1.05	7.18	1.57	5.21	3.11	6.76	6.68	5.05	3.66	5.44	1.25	1.32	6.37	9.18
	MAX	14.29	5.74	8.06	1.38	7.88	1.91	5.74	3.58	7.75	7.31	5.62	4.13	5.88	1.40	1.56	6.96	10.26
	N	53	43	43	53	53	42	53	53	50	53	53	52	53	53	53	52	51
<i>M. p. paululus</i> (Philippine subgroup)	\bar{x}	13.66	5.06	5.31	1.15	7.38	1.65	5.41	3.25	7.56	6.97	5.16	3.80	5.61	1.28	1.45	6.46	9.78
	SD	0.13	0.05	0.19	0.04	0.08	0.06	0.10	0.08	0.12	0.11	0.08	0.03	0.04	0.02	0.05	0.06	0.14
	MIN	13.49	5.00	5.15	1.11	7.28	1.57	5.30	3.11	7.44	6.84	5.05	3.76	5.56	1.26	1.40	6.37	9.58
	MAX	13.81	5.12	5.58	1.21	7.47	1.73	5.53	3.31	7.75	7.10	5.25	3.84	5.65	1.30	1.53	6.51	9.95
	N	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
<i>M. p. witkampii</i> (Borneo subgroup)	\bar{x}	13.94	5.13	5.25	1.18	7.47	1.69	5.49	3.36	7.66	7.23	5.25	3.81	5.70	1.33	1.38	6.53	9.82
	SD	0.27	0.18	0.12	0.05	0.09	0.03	0.06	0.08	0.10	0.05	0.06	0.12	0.08	0.02	0.05	0.06	0.15
	MIN	13.52	4.91	5.14	1.11	7.34	1.65	5.44	3.27	7.54	7.17	5.15	3.66	5.61	1.30	1.32	6.42	9.61
	MAX	14.29	5.28	5.43	1.23	7.59	1.73	5.60	3.46	7.72	7.29	5.33	3.94	5.79	1.35	1.44	6.57	9.97
	N	5	4	5	5	5	4	5	5	3	5	5	4	5	5	5	5	5
<i>M. p. graysonae</i> (Selaru subgroup)	\bar{x}	13.81	5.23	5.33	1.24	7.58	1.80	5.50	3.38	7.46	7.06	5.33	3.95	5.67	1.31	1.46	6.72	9.90
	SD	0.23	0.13	0.52	0.09	0.15	0.07	0.13	0.08	0.20	0.13	0.10	0.10	0.10	0.04	0.05	0.10	0.17
	MIN	13.07	4.98	4.79	1.05	7.18	1.67	5.21	3.21	6.76	6.68	5.17	3.72	5.44	1.25	1.34	6.51	9.18
	MAX	14.27	5.74	8.06	1.38	7.88	1.91	5.74	3.58	7.72	7.31	5.62	4.13	5.88	1.40	1.56	6.96	10.26
	N	43	34	33	43	43	33	43	43	42	43	43	43	43	43	43	42	41
<i>M. shortridgei</i> (Savu Group)	\bar{x}	13.28	5.04	4.89	1.15	7.23	1.66	5.32	3.26	7.02	6.74	4.96	3.63	5.20	1.20	1.35	6.27	9.34
	SD	0.19	0.16	0.21	0.09	0.14	0.10	0.12	0.08	0.17	0.13	0.10	0.11	0.11	0.04	0.05	0.13	0.19
	MIN	12.57	4.37	3.47	0.92	6.60	1.40	4.96	3.08	6.28	6.32	4.61	3.38	4.86	1.10	1.16	5.79	8.81
	MAX	13.81	5.43	5.35	1.40	7.52	1.90	5.73	3.46	7.53	7.10	5.18	3.96	5.55	1.30	1.49	6.58	9.76
	N	135	119	121	134	132	124	137	137	134	137	137	135	137	137	137	135	132
<i>M. shortridgei</i> (Inner Banda Arc subgroup)	\bar{x}	13.37	5.12	4.93	1.18	7.25	1.72	5.30	3.27	7.08	6.76	5.02	3.65	5.24	1.22	1.37	6.33	9.47
	SD	0.18	0.12	0.15	0.09	0.13	0.07	0.12	0.08	0.17	0.12	0.08	0.12	0.12	0.04	0.05	0.10	0.16
	MIN	12.74	4.83	4.64	0.99	6.72	1.55	4.96	3.08	6.44	6.32	4.81	3.38	4.96	1.12	1.16	6.10	9.00
	MAX	13.81	5.40	5.35	1.40	7.52	1.90	5.63	3.46	7.53	7.08	5.18	3.96	5.55	1.30	1.47	6.58	9.76
	N	66	58	60	66	64	61	67	67	67	65	67	67	67	67	67	66	64
<i>M. shortridgei</i> (Outer Banda Arc subgroup)	\bar{x}	13.19	4.97	4.86	1.11	7.20	1.61	5.33	3.25	6.96	6.72	4.90	3.61	5.15	1.19	1.33	6.21	9.22
	SD	0.17	0.15	0.26	0.07	0.14	0.09	0.11	0.08	0.15	0.13	0.08	0.10	0.08	0.04	0.05	0.12	0.14
	MIN	12.57	4.37	3.47	0.92	6.60	1.40	5.06	3.10	6.28	6.39	4.61	3.40	4.86	1.10	1.20	5.79	8.81
	MAX	13.51	5.43	5.34	1.27	7.43	1.82	5.73	3.42	7.22	7.10	5.05	3.87	5.31	1.29	1.49	6.46	9.50
	N	69	61	61	68	68	63	70	70	69	70	70	68	70	70	70	69	68

Table 7b – Externals

		SVL	TV	EL	TIB	FA	D2MC	D3MC	D3P1	D3P2	D3P3	D4MC	D5MC
<i>Miniopterus pusillus</i> (Java Group)	\bar{x}	44.5	44.8	10.1	19.0	42.6	38.6	39.3	10.1	28.5	6.4	37.7	35.3
	SD	2.6	3.0	0.4	1.0	1.5	1.3	1.3	0.4	1.3	0.5	1.2	1.3
	MIN	38.4	39.7	9.2	14.7	36.5	33.9	33.8	9.1	25.3	5.5	32.6	30.1
	MAX	50.2	51.2	10.9	20.2	44.3	41.1	41.1	11.2	31.3	7.3	39.3	37.0
	N	34	34	34	35	35	35	35	35	35	35	35	35
<i>M. p. pusillus</i> (Western subgroup)	\bar{x}	45.4	45.2	10.3	19.2	42.8	38.7	39.5	10.1	28.6	6.6	38.0	35.6
	SD	2.3	2.9	0.2	0.6	0.9	0.9	0.7	0.4	1.0	0.5	0.6	0.5
	MIN	41.4	39.7	9.7	18.2	40.5	35.5	8.5	9.4	27.0	5.6	36.8	34.9
	MAX	50.2	51.2	10.7	20.2	44.1	41.1	40.7	11.1	31.3	7.3	39.3	37.0
	N	20	21	21	21	21	21	21	21	21	21	21	21
<i>M. pusillus</i> subsp. indet A (Southeastern subgroup)	\bar{x}	43.3	43.9	9.6	18.6	42.0	38.1	38.5	10.2	28.0	6.1	36.9	34.4
	SD	2.2	3.0	0.2	1.5	2.2	1.8	1.9	0.5	1.7	0.5	1.8	1.8
	MIN	38.6	40.1	9.4	14.7	36.5	33.9	33.8	9.1	25.3	5.5	32.6	30.1
	MAX	46.5	50.3	9.9	20.0	44.3	39.8	40.2	11.2	30.2	7.0	38.7	36.3
	N	11	11	10	11	11	11	11	11	11	11	11	11
<i>M. pusillus</i> subsp. indet A (Seram subgroup)	\bar{x}	42.7	45.7	9.5	19.0	43.4	39.4	40.3	9.8	29.3	6.6	38.7	36.6
	SD	4.0	4.3	0.3	0.7	0.5	1.0	1.0	0.3	1.5	0.4	0.1	0.4
	MIN	38.4	42.6	9.2	18.4	42.9	38.3	39.2	9.5	27.6	6.3	38.6	36.2
	MAX	46.2	48.7	9.7	19.7	43.7	40.1	41.1	10.1	30.3	7.1	38.8	37.0
	N	3	2	3	3	3	3	3	3	3	3	3	3
<i>M. australis</i> (New Guinea Group)	\bar{x}	43.1	41.4	10.1	15.9	39.2	34.9	35.6	9.4	25.3	6.3	34.4	32.3
	SD	2.7	3.5	0.6	0.5	0.8	0.9	0.8	0.4	1.0	0.6	0.8	0.7
	MIN	33.9	30.9	8.7	14.8	37.4	31.7	32.8	8.0	21.7	4.4	31.9	30.1
	MAX	50.5	48.9	11.9	17.3	41.6	37.1	37.8	10.9	29.6	7.5	36.3	34.1
	N	89	92	105	107	107	107	107	107	107	106	107	107
<i>M. a. tibialis</i> (P.N.G. subgroup)	\bar{x}	44.7	40.9	10.7	15.9	39.7	35.1	35.8	9.6	25.9	5.4	34.0	31.7
	SD	1.9	3.2	0.7	0.4	0.6	0.7	0.7	0.3	0.8	0.4	0.5	0.6
	MIN	41.5	36.3	9.7	15.2	38.8	33.9	34.4	9.1	24.2	4.8	33.1	30.7
	MAX	47.4	46.3	11.7	16.5	40.4	36.4	36.7	10.2	27.0	6.2	35.1	32.3
	N	10	10	10	10	10	10	10	10	10	10	10	10
<i>M. australis tibialis</i> (Queensland/NSW subgroup)	\bar{x}	42.9	41.6	10.0	15.9	39.1	34.8	35.5	9.4	25.2	6.4	34.1	32.3
	SD	2.7	3.6	0.6	0.4	0.7	0.9	0.8	0.4	0.9	0.5	30.3	0.7
	MIN	33.9	30.9	8.7	14.8	37.4	31.7	32.8	8.0	21.7	4.4	3.6	30.1
	MAX	50.5	48.9	11.9	16.9	40.8	36.6	37.5	10.9	29.6	7.5	36.3	34.1
	N	75	78	91	93	93	93	93	93	93	92	93	93
<i>M. australis</i> subsp. indet. (Kai subgroup)	\bar{x}	43.2	39.9	9.8	17.1	41.1	36.6	37.5	9.7	26.1	6.4	35.6	33.1
	SD	4.0	0.4	0.2	0.2	0.4	0.4	0.5	0.3	1.6	0.1	0.4	0.7
	MIN	40.3	39.5	9.6	16.9	40.8	36.3	37.0	9.5	24.3	6.3	35.2	32.3
	MAX	47.7	40.2	9.9	17.3	41.6	37.1	37.8	10.0	27.3	6.5	35.9	33.7
	N	3	3	3	3	3	3	3	3	3	3	3	3

<i>M. australis</i> subsp. indet. (Kai subgroup)	\bar{x}	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	SD	-	-	-	-	-	-	-	-	-	-	-	-
	MIN	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	MAX	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	N	1	1	1	1	1	1	1	1	1	1	1	1
<i>M. paululus</i> (Selaru Group)	\bar{x}	41.6	34.8	10.5	15.0	37.1	32.4	33.5	9.2	24.6	5.4	32.2	29.8
	SD	1.9	2.2	0.6	0.4	0.8	0.8	0.8	0.5	0.9	0.6	0.8	0.8
	MIN	37.0	31.2	9.6	13.9	34.2	29.9	31.0	8.0	22.3	4.3	29.2	27.3
	MAX	45.1	39.0	11.5	15.6	38.7	34.3	35.5	9.9	26.5	6.7	34.1	31.1
	N	33	34	33	34	34	34	34	34	34	34	34	34
<i>M. p. paululus</i> (Philippine subgroup)	\bar{x}	40.8	35.3	9.7	14.8	37.0	32.4	33.2	8.6	25.3	5.1	32.1	29.6
	SD	2.1	2.0	0.2	0.4	0.7	0.8	0.7	0.2	1.0	0.4	0.8	0.7
	MIN	37.0	32.5	9.6	14.2	35.8	31.5	32.4	8.4	24.2	4.7	31.0	28.4
	MAX	43.2	37.8	10.0	15.4	37.9	33.5	34.4	8.8	26.5	5.9	33.2	30.4
	N	6	6	6	6	6	6	6	6	6	6	6	6
<i>M. p. witkampii</i> (Borneo subgroup)	\bar{x}	40.9	34.5	10.0	14.7	36.3	31.5	32.6	8.7	24.2	6.1	31.4	29.0
	SD	1.7	2.8	0.2	0.5	1.1	1.0	0.9	0.6	1.4	0.5	1.2	0.9
	MIN	38.2	31.2	9.6	13.9	34.2	29.9	31.0	8.0	22.3	5.4	29.2	27.3
	MAX	43.1	38.6	10.3	15.2	37.1	32.3	33.4	9.3	26.0	6.7	32.4	29.8
	N	6	6	6	6	6	6	6	6	6	6	6	6
<i>P. graysonae</i> subsp. nov. (Selaru subgroup)	\bar{x}	42.1	34.8	10.9	15.2	37.4	32.7	33.9	9.5	24.5	5.3	32.4	30.0
	SD	1.9	2.2	0.5	0.3	0.6	0.6	0.6	0.3	0.7	0.4	0.6	0.6
	MIN	38.4	31.9	9.9	14.4	36.5	31.4	32.9	8.9	23.5	4.3	31.5	28.7
	MAX	45.1	39.0	11.5	15.6	38.7	34.3	35.5	9.9	25.6	6.0	34.1	31.1
	N	21	22	21	22	22	22	22	22	22	22	22	22
<i>M. shortridgei</i> (Savu Group)	\bar{x}	39.9	37.2	9.7	15.0	36.8	32.6	33.4	9.1	24.5	5.6	32.1	30.0
	SD	2.16	3.5	0.4	0.5	1.0	1.1	0.9	0.4	1.1	0.5	0.9	0.9
	MIN	33.5	27.3	8.3	13.4	33.3	28.5	29.0	7.4	21.4	3.9	27.8	26.6
	MAX	46.3	64.0	10.8	16.4	39.3	37.9	35.5	10.2	27.4	6.9	34.3	32.0
	N	148	146	140	150	148	148	148	148	148	148	147	147
<i>M. shortridgei</i> (Inner Banda Arc subgroup)	\bar{x}	40.7	36.4	9.6	15.1	37.4	33.1	33.8	9.1	25.3	5.5	32.6	30.6
	SD	2.3	4.3	0.4	0.6	1.0	1.0	0.9	0.4	0.9	0.5	1.0	0.8
	MIN	34.0	27.3	8.3	13.4	33.3	28.5	29.0	7.4	21.4	3.9	27.8	26.6
	MAX	46.3	64.0	10.7	16.4	39.3	35.1	35.5	10.2	27.4	6.6	34.3	32.0
	N	73	72	70	73	72	72	72	72	72	72	71	71
<i>M. shortridgei</i> (Outer Banda Arc subgroup)	\bar{x}	38.7	38.0	9.8	14.8	36.2	32.1	33.0	9.0	23.7	5.7	31.7	29.5
	SD	4.7	2.3	0.4	0.3	0.6	1.0	0.6	0.3	0.6	0.5	0.6	0.5
	MIN	1.0	32.2	8.3	14.2	34.6	30.3	31.5	8.3	22.0	4.6	29.8	27.9
	MAX	42.8	43.9	10.8	15.6	37.7	37.9	34.2	9.5	25.8	6.9	32.9	30.7
	N	76	74	70	77	76	76	76	76	76	76	76	76

Distribution

Alor, Roti and probably Seram (this study) and Timor (Goodwin 1979), Ambon (Hill 1983) and possibly Sulawesi (Hill 1983).

Referred specimens

The three Seram specimens are morphologically slightly distinct from the Alor and Roti populations. However, because they are a small sample their subspecific status could not be assessed.

Remarks: *Miniopterus pusillus* from Ambon/Seram and Kai islands were thought by Maeda (1982) to represent the form *pusillus*, while Hill (1983) considered them *macrocneme*. Goodwin (1979) considered those from Timor island to be *M. pusillus*, whereas Hill (1983) placed them closer to *macrocneme*.

We tentatively ascribed specimens examined by us from Kai island to *M. australis tibialis*. These have measurements very similar to the *M. pusillus* reported by Hill (1983: Table 10) from that island.

Hill (1983) stated that *M. p. macrocneme* differed from *M. p. pusillus* by having longer tibia. In this study the Southeastern subgroup of *M. pusillus*, including specimens from Alor and Roti islands (close to Timor island) and the specimens from Seram (Seram subgroup) had tibia of a very similar length to those from the Western subgroup (Java, Lombok and Sumbawa) – that are *M. p. pusillus*.

Interestingly, the measurements listed by Hill (1983: Table 10) and Goodwin (1979) for *M. pusillus* specimens from Ambon/Seram islands and Timor island, respectively, fall within the range of measurements for the *M. p. pusillus* specimens in our Western subgroup, and are not clearly representative of the form *macrocneme*. Further, the difficulty in attributing specimens in the eastern Indonesian islands to *macrocneme* is further emphasised by the smaller cranial and dental measurements in our Table 7a, b for the Southeastern subgroup (Roti, Alor islands) and those presented by Revilliod (1914) – in his description of *M. macrocneme*. For example, greatest skull length 13.6 (13.2–14.0) 22 v. 14.2 (14.0–14.4) 4; mastoid width 7.7 (7.3–8.1) 22 v. 8.1 (8.0–8.2) 4; C'M³ length 5.2 (5.0–5.3) 22 v. 5.6 (5.5–5.8). Tibia length, for the Southeastern subgroup specimens, however, averaged larger than for *M. macrocneme* (s.s) 19.2 (18.2–20.2) 21 v. 18.3 (17.8–19.0) 50.

Specimens attributed by Hill (1983) to *macrocneme* from areas intermediate (Solomon and New Hebrides Islands, New Guinea) between New Caledonia/Loyalty islands and Alor, Roti, Timor and Seram appeared to indeed represent *macrocneme*. We have not examined specimens of *macrocneme* (s. s.) or sampled these 'intermediate' areas. However, we consider it probable that the forms in both the Seram and Southeastern subgroups will prove to be subspecifically

distinct from both *M. p. pusillus* and *M. p. macrocneme*.

Miniopterus australis Tomes, 1858

M. australis Tomes, 1858: 125

M. tibialis Tomes, 1858

?*M. solomonensis* Maeda, 1982

Lectotype: British Museum, Natural History No. BM(NH) 54.5.19.5, designated by Hill (1983: 172), who provides a detailed discussion of the history relating to the material examined by Tomes.

Type locality: Loyalty Islands.

Diagnosis

Miniopterus australis differs from *M. pusillus* as described in the above diagnosis of that species.

It differs from *M. paululus* in averaging larger in all external body characters, except ear length and digit 3 phalanx 2 length. For example, forearm length 39.2 (37.4–41.6) 107 v. 37.1 (34.2–38.7) 34 and tibia length 15.9 (14.8–17.3) 107 v. 15.0 (13.9–15.6) 34. Digit 5 metacarpal length greater relative to ear length (Figure 9a). Skull size very similar to *M. paululus* but averages slightly larger in all measurements except mesopterygoid fossa breadth and M² length. For example, greatest skull length 14.0 (13.5–18.4) 36 v. 13.8 (13.1–14.3) 53 and C'M³ length 5.4 (5.2–5.6) 36 v. 5.3 (5.1–5.6) 53. Braincase breadth generally greater relative to upper molar row length (Figure 9b).

It differs from *Miniopterus shortridgei* in averaging larger in all external body and skull characters. For example, forearm length 39.2 (37.4–41.6) 107 v. 36.8 (33.3–39.3) 148; tibia length 15.9 (14.8–17.3) 107 v. 15.0 (13.4–16.4) 150; greatest skull length 14.0 (13.5–14.4) 36 v. 13.3 (12.6–13.8) 135; and C'M³ length 5.4 (5.2–5.6) 36 v. 5.0 (4.6–5.2) 137.

Miniopterus australis tibialis (Tomes, 1858)

Vespertilio tibialis Tomes, 1858: 126–127

Holotype: Stated by Tomes (1858: 126) to be exhibited in the Leyden Museum, where it is supposed to still be located (Tate 1941: 575).

Type locality: Ambon ([Amboyna) island, Muluku Tenggara, Indonesia.

Specimens examined: Australia; New South Wales – Bonalbo Colliery, 28°44'S; 152°37'E, CM 877, ♂, S. Bungawalbin, 29°02'S; 153°17'E, AM M22797, ♀, E. Cangai, 29°30'S; 152°29'E, AM M(10920, 12721) 2 ♀, E. Glenreagh, 30°03'S; 152°59'E, AM M12722, ♀, E. Kempsey, 31°05'S; 152°50'E, CM 1831-2, ♀, ♂, S. Limeburners, 31°18'S; 152°57'E, AM M(21446, 21456, 21465, 21476), 3 ♀ ♀, ♂, E. Macquarie, 29°29'S;

150°07'E, AM M9026-7, ♀, ♂, E. Nimbin Rocks, 28°37'S; 153°12'E, CM (10851-3, 10857-9), 3 ♀♀, 3♂♂. Tooloom, 28°37'S; 152°25'E, CM (871, 873-6), 3 ♀♀, 2 ♂♂. Unknown locality, CM921, ♀, E.

Queensland – Barretts Lagoon, 18°03'S; 145°58'E, QM JM8255, ♂, E. Blue Lagoon, 22°44'29"S; 150°38'17"E, CM19095, ♂. Bracewell, 23°54'S; 150°54'E, QM JM(436, S, 437) 2 ♂♂. Bribie Island, 26°57'S; 153°07'E, QLD JM1943E, ♂. Brisbane, Camp Mt, 27°24'S; 152°54'E, QM JM (6870E, 6871) ♀, 1 Sex Unknown. Buthen Buthen, 13°23'S; 143°27'E, QM JM (2450, E, 2473, 2474E), 3 ♂♂. Cape York, Iron Range 165 kms NE of Archer River, 12°44' S; 143°15' E, AM M(16084-5, E) ♀, ♂ Cape York, Rocky River, 13°49'S; 143°28'E, CM 4487, S, ♂. Chillagoe, 17°09'S; 144°31'E, CM 10841, E, ♂. Crab Camp, 22°38'45"S; 150°43'46"E, ANWC19073, S, ♂. Creek on Atherton Rifle Range, 17°16'S; 145°29'E, AM M1680, E, ♂. Creek South of Coen, 14°06'S; 143°12'E, AM M(16082, E, 16086-91, E) 3♀♀, 4 ♂♂. Herberton, Extenuate Mine, 17°26'S; 145°25'E, QLD JM(8420 E, 8421, 8422 E, 8423, 8424 E, 8425, 8426 E, 8429 E) 2 ♀♀ 6 ♂♂. Kuranda, 16°49'S; 145°38'E, CM(5924, 5925-6 E, 5932 E) 3 ♀♀, ♂. Lake Barrine, 17°15'S; 145°38'E, Qld JM1450 E, ♂. Mount Boldy, 4 km West of Atherton, 17°16'S; 145°29'E, AM13610 E, ♀. Oakleigh Colliery, Glencoe section, 27°39'S; 152°36'E, Qld JM416 E, Sex Unknown. Old Irishman Mine, 19°00'S; 146°17'E, Qld JM(1675, 1676 E, 1677, 1678-1680 E), 6 ♀♀. Ravenswood, 20°06'S; 146°53'E, CM(15869 E, 15870-1), 2 ♀♀, ♂. Rockhampton, 23°23'S; 150°30'E, Qld JM(6863-6869, 6873-4 E), M(16451 E, 16794 E), 6 ♀♀, 3 ♂♂, 2 Sex Unknown. Rosella Plains, 18°25'S; 144°28'E Qld JM(2940-1 E), ♀, ♂. Thornton Peak, 16°10'S; 145°23'E, AM M(13293, 13300-5 E), 3 ♀♀, 4 ♂♂. West Claudie Range, 12°44'S; 143°17'E, Qld JM2400, E, ♂. Wombah Railway Tunnel, Via Gin Gin, 25°00'S; 151°57'E, CM(5970, 5972-3, E), 2 ♀♀, ♂. Wongabel State Forest, 17°19'S; 145°29'E, AM M16083, E, ♂. Locality Unknown, 597 E, ANWC 164525, ♀ 1 Sex Unknown.

Papua New Guinea – Putei CM (1990S, 1995E, 1997E, 1998, 1999E, 2000E, 2002, 2010S, 2020S, 2030E, 2031S, 2032E, 2040, 2043S, 2047E) 7 ♀♀, 8 ♂♂.

Seram island, Indonesia: Manusela, 30°10'S, 129°36'E, WAM M34722, ♂.

Diagnosis

Miniopterus australis tibialis differs from *M. australis* subsp. indet. from Kai island in that both Australian and New Guinea specimens have a shorter tibia 15.9 (14.8–16.9) 93 and 15.9 (15.2–16.5) 10, respectively, *v.* 17.1 (16.9–17.3) 3 and a generally shorter forearm length 39.1 (37.4–40.8) 93 and 39.7 (38.8–40.4) 10, respectively, *v.* 41.1 (40.8–41.6) 3. Most other wing measurements are also smaller (Table 7b). Most skull characters are larger (Table

7a). For example, both the Australian and New Guinea specimens have a longer greatest skull length 14.0 (13.7–14.4) 24 and 14.1 (13.9–14.2) 8, respectively, *v.* 13.6 (13.5–13.8) 3.

Distribution

Queensland, New South Wales (Australia), Papua New Guinea and Seram (this study), Ambon (type locality) and probably Sulawesi, Batchian island, Aru island, Beu island, Mayabit Bay, Waigeo, West Irian (Hill 1983).

Remarks

Tomes (1858) described *Vespertilio tibialis* from five specimens, but he noted that it differed little from *Miniopterus blepotis* except that it is a "trifle smaller, and moreover appears to ... differ remarkably in all the specimens in having the extremity of the tibia perfectly free for nearly a third of its length". He provides measurements for one of these specimens as (*in.* and *lin.* converted to mm) lengths of: head and body 63.5; head 14.8, ear 7.4; tragus 4.2; forearm 39.2–40.2; and tibia 14.8. Measurements for the other three adult male specimens from the Nicobars are provided in Dobson (1871). Sanborn (1952: 107) considered that the appearance of the extremity of the tibia in the specimen described by Tomes (1858) almost certainly resulted from the interfemoral membrane not being pinned out such that it curls up along the tibia giving the impression of a "slender shank".

Miniopterus australis subsp. indet.

Three specimens from Desa Elat, Kai island [5°39'S, 132°59'E; WAM M42885 (♀); WAM M42724 (♀) and WAM M42749 (♀)] are distinguished from *M. australis tibialis* as described in the above diagnosis. These specimens are most clearly distinguished by their long tibia (Table 7a, b). They may warrant recognition as a separate subspecies but a larger sample of specimens is required to evaluate their taxonomic status.

Miniopterus paululus Hollister, 1913

M. paululus Hollister, 1913: 311–312

M. witkampii Sody, 1930: 272–273

Holotype: United States National Museum No. 105493. Adult in alcohol, skull removed, collected in December 1887, by J.B. Steere.

Type locality: Guimaras islands, Philippines.

Diagnosis

Miniopterus paululus differs from *M. pusillus* and *M. australis* as described in the above diagnoses for these species.

Miniopterus paululus differs from *M. shortridgei* in averaging larger in all external body and skull characters except digit 3 phalanx 3 length (see Table 7a, b). For example, forearm length 37.1 (34.2–38.7) 34 v. 36.8 (33.3–39.3) 148; ear length 10.5 (9.6–11.5) 33 v. 9.7 (8.3–10.8) 140; greatest skull length 13.8 (13.1–14.3) 53 v. 13.3 (12.6–13.8) 135; and C^1M^3 length 5.3 (5.1–5.6) 53 v. 5.0 (4.6–5.2) 137. Ear length generally longer relative to digit 5 metacarpal length (Figure 9a); and upper molar cusp row generally longer relative to braincase breadth (Figure 9b).

Remarks

Revilliod (1914) diagnosed *M. australis* from *M. pusillus macrocneme* by its tragus which he stated projects anteriorly at its distal end with an almost horizontal, irregular dentate cranial margin; whereas in *macrocneme* the tragus does not project strongly forward and there is no clear dentate cranial margin. We found no such strong anterior margin in the *M. australis* available to us. Hill (1983) stated that specimens of *australis* from more western localities do not have a tragus with this dentate margin.

Miniopterus paululus paululus Hollister, 1913

Holotype and *Type locality*: described above.

Specimens examined: Philippine islands – Leyte island, 10°28'S, 124°45'E, WAM M29040 E, ♀. Majuyod, 9°43'S,

123°10'E, WAM M25874-5, 2 ♀♀. Negros island, 9°20'N, 123°18'E, WAM M29041-3, 3 ♀♀.

Diagnosis

Miniopterus p. paululus differs from *M. p. witkampi* in averaging slightly larger in most wing measurements (Table 7b). For example, forearm length 37.0 (35.8–37.9) 6 v. 36.3 (34.2–37.1) 6 and digit 5 metacarpal length 29.6 (28.4–30.4) 6 v. 29.0 (27.3–29.8) 6. Digit 3 phalanx 3 length generally longer relative to ear length (Figure 11a). It differs in that all skull characters, except palatal length and M^2 breadth, average smaller (Table 7a). For example, greatest skull length 13.7 (13.5–13.8) 5 v. 13.9 (13.5–14.3) 5 and braincase breadth 7.0 (6.8–7.1) 5 v. 7.2 (7.2–7.3) 5. Braincase breadth narrower relative to I_1M_3 length (Figure 11b).

Miniopterus p. paululus differs from *M. p. graysonae* subsp. nov. in averaging slightly smaller in most external body and skull characters, except tail to vent length, digit 3 phalanx 2 length and zygomatic width (Table 7a, b). For example, forearm length 37.0 (35.8–37.9) 6 v. 37.4 (36.5–38.7) 22; tibia length 14.8 (14.2–15.4) 6 v. 15.2 (14.4–15.6) 22; and greatest skull length 13.7 (13.5–13.8) 5 v. 13.8 (13.1–14.3) 43. Ear generally longer relative to digit 3 phalanx 3 length (Figure 11a).

Distribution

Majuyod and Negros island (this study), Guimarás island (type locality), Philippines.

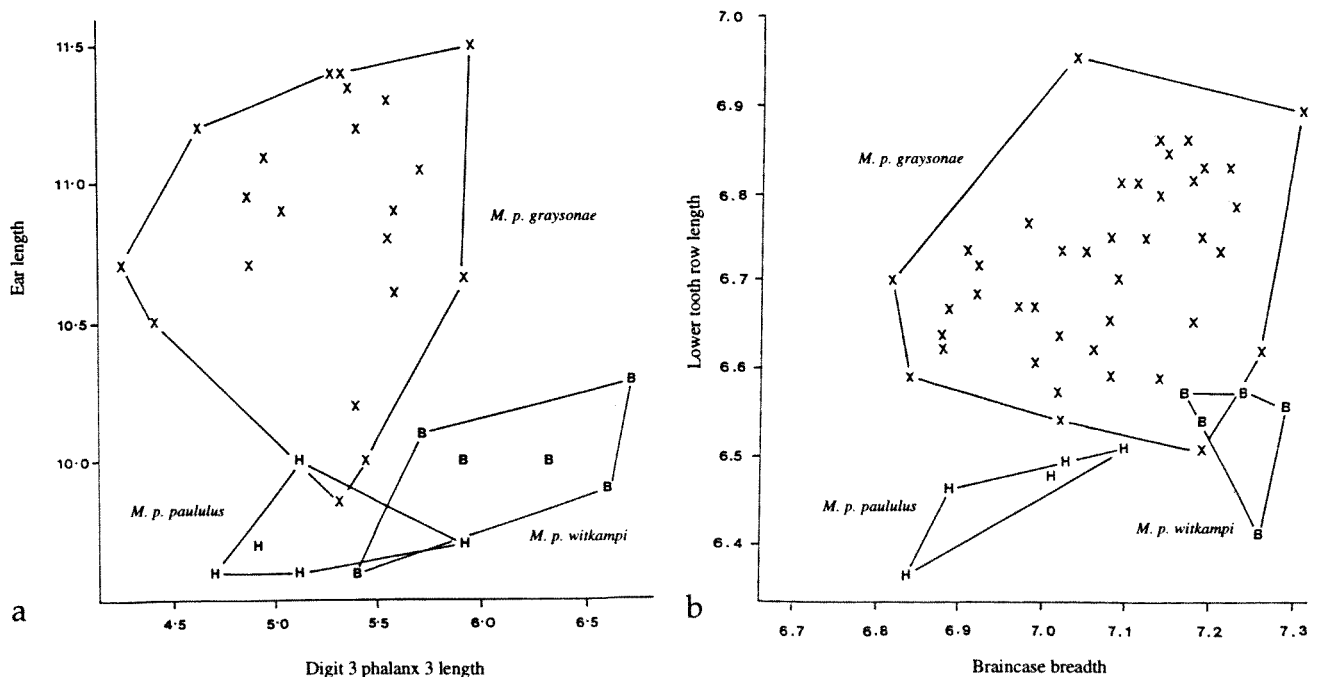


Figure 11 Plot of (a) ear length (mm) versus digit 3 phalanx 3 length (mm) and (b) lower tooth row length (mm) versus braincase breadth for island populations of adult *Miniopterus paululus paululus*, *M. p. witkampi* and *M. p. graysonae* subsp. nov. Island codes as for Figure 2.

Remarks

The forearm length of the type specimen of *M. p. paululus* fall within the range of our measurements of this taxon, but the measurements of the digit 3–5 metacarpal length and most of the skull measurements of the type, except I_1M_3 , are smaller than those presented herein (see Hollister 1913).

***Miniopterus paululus witkampi* Sody, 1930**

M. witkampi Sody, 1930: 272–273

Holotype: The Sody Collection. Ex. Muzeum Zoologicum Bogoriensis No. 422, adult male, collected 24 January 1928.

Type locality: Lobang Ipoe, Koetai, East Kalimantan, Borneo island.

Specimens examined: Borneo Island– Gomantong, Sabah, 5°31' N, 118°04'E, WAM M (26002-6, 26007 E) 3 ♀♀, 3 ♂♂.

Diagnosis

Miniopterus p. witkampi differs from *M. p. paululus* as described in the above diagnosis.

It differs from *M. paululus graysonae* in averaging smaller in all external body characters, except digit 3 phalanx 3 length (Table 7b). For example, forearm length 36.3 (34.2–37.1) 6 v. 37.4 (36.5–38.7) 22 and tibia length 14.7 (13.9–15.2) 6 v. 15.2 (14.4–15.6) 22. Ear length shorter relative to digit 3 phalanx 3 length (Figure 11a). It averages slightly larger in measurement of overall skull size, such as greatest skull length, zygomatic width, braincase breadth and M^3M^3 distance and slightly smaller in other skull measurements such as mastoid width cranial skull height and C^1M^3 length (Table 7a). I_1M_3 length generally shorter relative to braincase breadth (Figure 11b).

Distribution

Koetai, East Kalimantan (type locality), and Gomantong, East Sabah, Borneo island.

***Miniopterus paululus graysonae* subsp. nov.,
Kitchener**

Holotype: Western Australian Museum No. M44339, adult male, weight 5.8 gm, collected by Ir Ibnu Maryanto (Museum Zoologicum Bogoriense) and Mr Ronald Johnstone (Western Australian Museum) on 28 April 1993.

Type locality: Bangruti Cave, near Adaut, Selaru island, Tanimbar Islands Group, Maluku Tenggara, Indonesia, (ca. 8°09'S, 131°08'E), at sea level.

Paratypes: Selaru Island – Adaut, 8°09'S, 131°08'E, WAM M(44319-20, 44322-4, 44325E, 44326, 44327S, 44328-9, 44330S, 44331-3, 44335E, 44336, 44338, 44340-44 S, 44346-7S, 44348E, 44350, 44351S, 44353S,

44354, 44355-7S, 44358, 44359-61S, 44362, 44363S, 44366, 44367S, 44369E, 44371, 44372-4S, 44377S) 20 ♀♀, 24 ♂♂.

Diagnosis

Miniopterus paululus graysonae differs from *M. p. paululus* and *M. p. witkampi* as described in the above diagnoses of these subspecies.

Distribution

Known only from Selaru island, Tanimbar Island Group.

Etymology

Named after Ms Jacky Grayson, who contributed greatly to this paper by removing skulls and recording external body measurements.

***Miniopterus shortridgei* Laurie & Hill, 1957**

Miniopterus australis shortridgei Laurie and Hill, 1957: 128 (renamed)

M. australis minor Laurie and Hill 1954: 72–73

Holotype: British Museum of Natural History No. BM 9.1.5.426 (Collector's no. 1451); adult male; skin (in alcohol) and skull separate; collected by G.C. Shortridge on 3 March 1908.

Type locality: Kalipoetjang, Tji – Tandoei River, south Java.

Specimens examined: Java island – Kiskenda, 7°06'S, 110°16'E, WAM M(39334E, 39353E) ♀, ♂. Sukabumi, 7°15'S, 106°50'E, WAM M(30007, 300010-1), ♀ 2 ♂♂ Madura island – Sampang, 7°13'S, 113°15'E, WAM M39411, ♀♂. Lombok island – Bang Kang, 8°30'S, 116°10'E, WAM M(35855, 35860-1, 35863-4, 35865E, 35866-8, 35870, 35959E, 35961) 8 ♀♀, 2 ♂♂. Sumbawa island – Batu Dulang, 8°35'S, 117°18'E, WAM M (31769-72, 31773S, 31774, 31776-81, 31782S, 31783-4, 31787-5, 31796E, 31797, 31798E, 31800-8, 31812, 31813E, 31814-6, 31818, 31853E, 31854-5) 14 ♀♀, 31 ♂♂ Desa Sangeang, 8°18'S, 118°56'E, WAM M31556 ♂. Moyo island – Sebotok, 8°09' 30" S, 117°37'15" E, WAM M31906, ♀. Tangung Pasir, 8°23'15" S, 117°31'30" E, WAM M31960, ♀. Alor island – Kalabahi, 8°14'S, 124°32'E, WAM M(37518-21, 37543, 37564, 37565E, 37566, 37625, 37627) 4 ♀♀, 6 ♂♂. Roti island – Baa, 10°44' s, 123°06'E, WAM M(35358, 35388) ♀, ♂ Oeseli, 10°51'S, 123°05'E, WAM M(35498, 35500-2) 3 ♀♀, ♂. Savu island – Menia, 10°29'S, 121°55'E, WAM M(35114, 35126, 35128, 35139, 35140S, 35141-2, 35143S, 35144-6, 35147E, 35148-51, 35152S, 35153, 35154-5, 35165-6, 35168-70, 35171E, 35172, 35173E, 35175-6, 35178-9, 35218-20, 35221E, 35223-6, 35228-30, 35231E, 35232-3, 35234E, 35235-9, 35240E, 35241-3, 35245E, 35246-54, 35255E, 38 ♀♀, 30 ♂♂. Timor island – Lifuleo Oisina, 9°18'S, 123°30'E, WAM M38065, ♀. Semau island – Desa Uiasa, 10°10'S,

123°28'E, WAM M(33066E, 33067-8, 33069-71 E), 3 ♀♀, 3 ♂♂ Wetar island – Desa Ipokil, 7°50'S, 126°16'E, WAM M44528, ♀. Selaru island – Adaut, 8°09'S, 131°08'E, WAM M44334 S, ♂.

Diagnosis

Miniopterus shortridgei differs from *M. pusillus*, *M. australis* and *M. paululus* as described in the above diagnoses of these species.

Distribution

Java, Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Selaru (Tanimbar Islands), Timor, Semau, Roti and Savu islands, Indonesia.

Remarks

Laurie and Hill (1954: 72) stated that in the type series of *M. shortridgei* the wing membrane is inserted at the end of the tibia near the heel, and that the *os calcis* with the tail membrane also starts at that point. This was also the case in the specimens we examined from throughout the range of this species. Laurie and Hill (1954: 73) list measurements for the holotype and five paratypes of *M. shortridgei*. They state that the skull is very similar to *M. a. australis* but definitely shorter and that the 16 specimens examined by them had a skull length of 12.8–13.3, C¹M³ length 4.8–5.0 and C¹C¹ breadth 3.2–3.6. Specimens we studied were similar in size, except that C¹C¹ breadth tends to be larger in our sample. Goodwin (1979: 120) provided measurements for a *Miniopterus* from Timor island

which he attributed to *M. a. australis*, but stated that it was "close to *M. a. shortridgei* of Java but averages slightly larger in forearm and certain other measurements". We consider the Timor specimens examined by Goodwin (1979) to be *M. shortridgei*.

However, our DFA and univariate analyses indicated that the Timor specimens differed morphologically somewhat from the nominate form on Java. The specimens from Timor island were grouped, along with those from Savu, Roti, Semau, Wetar and Selaru islands, into an Outer Banda Arc form (the geological origins of Wetar are unclear, see General Discussion); while those from the inner (volcanic) Banda Arc islands of Alor, Moyo, Sumbawa, Lombok, Madura and Java comprised an inner Banda Arc form. This latter form averaged larger in all cranial, dentary and dental characters, except cranial height (Table 7a) and most external body measurements, except tail to vent length, ear length and digit 3 phalanx 3 length (Table 7b). The Inner Banda Arc form also generally had a longer dentary relative to intercochlear distance (Figure 12a) and a generally longer digit 3 phalanx 2 length relative to digit 3 phalanx 1 length (Figure 12b).

GENERAL DISCUSSION

The four species of *Miniopterus* studied (*pusillus*, *australis*, *paululus* and *shortridgei*) showed considerable geographic variation in intraspecific morphology for cranial, dentary, dental (except *M. pusillus*) and external body characters. In the case of

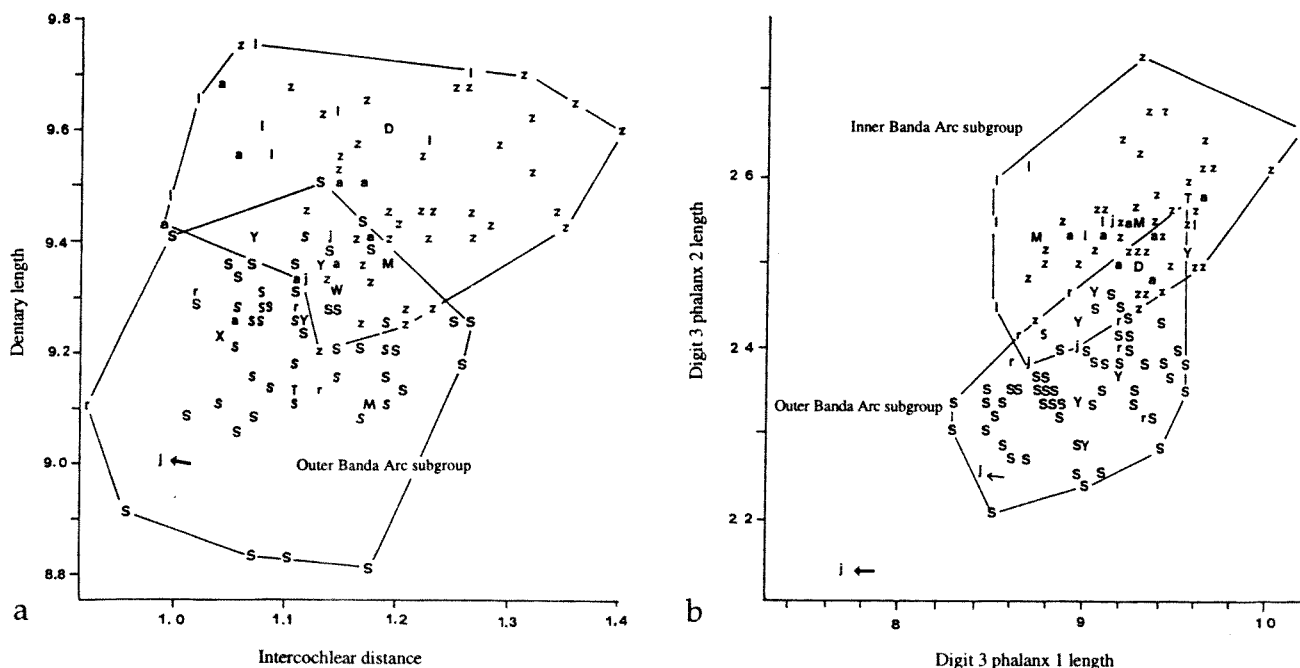


Figure 12 Plot of (a) dentary length (mm) versus intercochlear distance (mm) and (b) digit 3 phalanx 2 length (mm) versus digit 3 phalanx 1 length (mm) for island populations of adult *Miniopterus shortridgei* for the two population subgroupings (Inner and Outer Banda Arc/Wetar island). Island codes as for Figure 2.

the former three species, their intraspecific morphology diverged sufficiently to warrant subspecific status. In the remaining species, *M. shortridgei*, two reasonably distinct forms are recognised. One of these forms is restricted to Java and the volcanic islands of the Inner Banda Arc, which are a volcanic extension of Western Sumatra and Java (Michaux 1991); the other occurs on the gondwanic islands of the Outer Banda Arc, and apparently also on Wetar island. The single specimen from Wetar island is a damaged skull only. A DFA run with a reduced set of variables, so as to include this Wetar island specimen in the analysis as an unallocated specimen, placed it with specimens from the Outer Banda Arc group of islands.

Intraspecific morphological variation in both *M. pusillus* and *M. shortridgei* appeared to be most marked in the general region of Alor and Wetar islands. Interestingly, Alor and Wetar islands, like Roma and Kambing islands, now inactive volcanically, are characterised by reef-limestone terraces uplifted to 500–800 m above sea level (see Hamilton 1979). Perhaps the more recent volcanic activity on Inner Banda Arc islands to the west of Alor island not only impacted on the habitat and faunal assemblages on those islands, but may in some way have favoured the development of a particular bat ecomorph.

The western *M. p. pusillus* (Java-Sumbawa) is larger in all characters than the eastern form, *M. pusillus* subsp. indet. A (Alor and Roti). Further, the Inner Banda Arc form of *M. shortridgei* (Java-Alor) is larger for most characters than the form on the Outer Banda Arc and Wetar island. The region of this differentiation reflects a pattern documented by Kitchener and Suyanto (1996), Kitchener, Konishi and Suyanto (1996) and Kitchener, Packer and Maryanto (1996) who examined intraspecific morphological variation in ten species of bat and a mouse in the region of southern Indonesia between Java and the Kai islands. They noted that morphological differentiation tended to occur in the eastern parts of the distributional range of the species examined, or in the Outer Banda Arc on the islands of Sumba, Roti, Savu, Semaui and Timor. The exceptions to this were two species that morphologically diverged in the western part of this region. These were *Scotophilus collinus* Sody, 1936, which had two forms that diverged between Bali and Lombok islands, and *Hipposideros diadema* (Geoffroy, 1813), which had two subspecies that interfaced between Lombok and Sumbawa islands.

The trend for *M. pusillus* and *M. shortridgei* to become smaller in overall size on the eastern and southern islands in the Lesser Sundas is also observed in seven of the ten bat species referred to above. The exceptions were *Cynopterus nusatenggara* Kitchener and Maharadatunkamsi, 1991 and

Hipposideros sumbae Oei, 1960, which increase in size, and *Scotophilus collinus* Sody, 1936 which shows no clear such trends in morphology. Kitchener and Suyanto (1996) stated that this trend for overall skull and body dimensions to change with longitude, at least for the most eastern islands of Tanimbar and Kai, which have a less severe climate, may in part be influenced by Bergmann's effect. However, within the Lesser Sundas a complex interplay of factors is likely to be involved. This is indicated by the study by Kitchener and Maharadatunkamsi (1996) on *Cynopterus nusatenggara* which showed that most cranial, dentary and external body measurements became larger to the east or on the more isolated islands, and smaller on the islands to the south. However, the cranium and teeth also were smaller on the larger (irregularly shaped) islands.

The two forms of *M. shortridgei* overlap somewhat morphologically, but not particularly so in the region where the islands in the gondwanic outer Banda Arc and volcanic inner Banda Arc are closest. This is between Alor and Timor (the placement of Wetar island in these island Arcs is not clear). For example, a few specimens from the more western islands of Java, Moyo and Sumbawa were misclassified to the Outer Banda Arc form. For this reason, these two forms are not recognised as subspecies. It may well be that examination of further specimens from the region of the interface between these forms (Alor, Timor and Wetar islands) may provide a stronger case for the recognition of them as subspecies.

While the systematic groupings of forms in this paper into species differs somewhat from that of Hill (1983), we place the forms we studied into similar subspecies taxa. We are also doubtful that the eastern Indonesian form of *Miniopterus pusillus* on Timor and associated islands and on Seram (and Ambon) represent the form *macrocneme*. However, we recognised that other taxonomic tools need to be applied to further resolve the taxonomy of this group. Our experience with this genus leads us to agree with Goodwin (1979) that resolution of the taxonomy of many forms of *Miniopterus* is exceedingly difficult because morphological differences between even sympatric species are sometimes minor and that pelage colour is of little taxonomic value.

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