# MORPHOMETRIC VARIATION OF ISLAND POPULATIONS OF *Macroglossus* spp. (Chiroptera : Pteropodidae)

## Agustinus Suyanto[1], Darrel J. Kitchener[2], L.H. Schmitt[3], and Norah K. Cooper[2]

[1]Museum Zoologicum Bogoriense/Division of Zoology, Research Centre for Biology - LIPI
Indonesian Institute of Sciences, P.O. Box 25, Cibinong 16911, Indonesia;
email: suyanto@lipi.go.id, asujan2002@yahoo.com
[2]Department of Anatomy and Human Biology, UWA, Nedlands-Perth, WA 6009, Australia
[3]Western Australian Museum, Perth, WA 6000, Australia

## Abstract

*A total of 395 skulls and skins of* Macroglossus *were examined, mostly from Indonesia, and some from Philippines, Papua New Guinea and Australia. The use of discriminant function analysis recognized six broad groups of island populations of* Macroglossus: *The Jawa group (Nias, Sumatera, Jawa, Bali and Nusa Penida Is.), the Nusa Tenggara group (Lombok, Sumbawa, Moyo, Komodo, Rinca, Sumba, Flores, Adonara, Lembata, Pantar, Alor, Timor, Semau, Roti, Sabu, Kalimantan, Western Australia, New Britain, New Ireland and Buru), the Sulawesi group (Sulawesi only), the Siberut group (Siberut only), the New Guinea group (New Guinea only) and the Philippine group (Philippines only). The Jawa group is represented by* M. sobrinus *Andersen, 1911; the other groups* M. minimus *(Geoffroy, 1810). Within* M. sobrinus, *four subspecies were recognized. These were* M. s. sobrinus *(Jawa and Sumatera);* M.s. fraternus *(Siberut);* M. s. subsp. nov. A *(Bali and Nusa penida); and* M. s. subsp. nov. B *(Nias). Within* M. minimus, *six subspecies were recognized, these were* M. m. minimus *(Nusa Tenggara and Western Australia);* M. m. nanus *(New Britain and New Ireland);* M. m. lagochilus *(Kalimantan, Buru and Madura);* M. m. microtus *(New Guinea);* M. m. fructivorous *(Philippines) and* M. m. meyeri *(Sulawesi). The taxa can be separated by discriminant function and univariate analysis of continuously varying characters, in conjunction with the anteroventral ossification projecting forwards from the dentary symphysis and the fleshy protuberance supported on the distal end of the lips by this ossification.*

**Key Words**: Fruit-bats, *Macroglossus* spp., Population Variation, Morphology, Zoogeography, Indonesia, Philippines, New Guinea, Australia.

## Introduction

Since September 1987, Kitchener and his colleagues from Western Australian Museum and Research Center for Biology, Indonesian Institute of Sciences, Bogor have conducted vertebrate surveys of islands in the Outer and Inner Banda Archs, Indonesia. Numerous specimens of *Macroglossus* were collected from many islands in these Arcs. These collections form the basis for this study on morphometric variation among islands populations of *Macroglossus*. This study has two principle objectives. First, document the nature of the morphometric variation among the various island populations and determine the taxonomic status of these populations and second, review the geographic, past historic and climatic factors which may influence the nature of this variation.

This study is also a part of wider study involving the authors, which has its main objective the investigation of the nature of morphological and genetic changes

within a number of selected species within the region which have a range of differing distribution patterns. Factors affecting this variation may be important in the determination of broad-scale biographic boundaries. Such boundaries include Wallace line between Bali and Lombok, which is classically considered as the boundary between the Oriental and Australian biogeographical region (Mayr, 1944 and Simpson, 1977)

*Macroglossus* is a small, fruit-bat, and is a member of the family Pteropodidae and subfamily Macroglossinae (Hill and Smith, 1984) which spread widely from Sikkim (India) east through Myanmar (Burma), Thailand, Vietnam, Malaysia to the Solomon and Northwern part of Australia (Hill, 1983 and Koopman, 1989). *Macroglossus* is an important component of tropical ecology because they are essential pollinators of many mangrove trees and other tropical plants, particularly economic plants such as durian (*Durio zibethinus*), petai (*Parkia speciosa*), banana (*Musa* spp.) (Start and Marshall 1976; McKean 1983; Kitchener *et al.*, 1990b). Further, because of their practical importance in both the ecology of mangroves, and tropical forest trees, it is important for the conservation of these ecosystem to resolve the contention which exists concerning the taxonomic status of *Macroglossus.*

This study is expected  to be able to resolve some of the existing systematic confusion within *Macroglossus*, because it uses multivariate statistical techniques not previously applied to this problem. Further, we have available to us for study specimens from the following islands not previously examined by other authors: Sumbawa, Moyo, Komodo, Flores, Adonara, Rinca, Lembata, Alor, Pantar, Sumba, Roti, Sabu Is and Western Australia.

Taxonomic status of *Macroglossus*

According to Andersen (1912) there are two distinct species of *Macroglossus* F. Cuvier, 1824, however the diagnosis of these two species appears to be based only on the direction of nares, and the presence or absence of median vertical groove on the upper lip. *Macroglossus minimus* E. Geoffroy, 1810 has nares directed,  more outward than forward and no median vertical groove. While *Macroglossus lagochilus* Matschie, 1899 has nares directed half outward and has a median vertical groove. Briefly, the distribution of *Macroglossus* is as follow: Two subspecies are recognized, based on overall body size. These are: *Macroglossus minimus minimus* E. Geoffroy, 1810  which distributed in Jawa (incl. Madura) and Kangean Is.,Sumatera, Malay Peninsula (Peninsular Malaysia), and possibly Timor. *Macroglossus minimus sobrinus* K. Andersen, 1912 which distributed in Malay Peninsula (Peninsular Malaysia), Sumatera, Nias, Jawa (Tasikmalaya and Kediri), and possibly Tenasserim (Sitang R., Burma (Myanmar), Siam (Thailand), and Darjeeling (India). Four subpecies of *Macroglossus lagochilus* are recognized based on the size of premolars and molars, rostrum and ear. These are *M. lagochilus lagochilus* Matschie, 1899 which is distributed in Borneo, Cagayan Sulu, Philipines (Tablas, Samar, Panay, Cuyo, Negros), Sanghir Is., Celebes (Sulawesi:

Menado, Kema, Amurang), Moluccas (Buru, Ambon, Ceram, Banda Is.). *M. lagochilus nanus* Matschie, 1899 which is distributed in Mysol, W. New Guinea, Bismarck Archipelago, Key (Kei) Is. And Aru Is. *M. lagochilus pygmaeus* K. Andersen, 1912 which is distributed in Murray Is. and Torres Straits. *M. lagochilus microtus* K. Andersen, 1912 which is distributed in Solomon Is.: Florida and Guadalcanar Is.

Taylor (1934) considered *M. lagochilus lagochilus* from the Philippines, as a separate species of *Macroglossus fructivorous*. However, Heany and Rabor (1982) considered *M. fructivorus* to be synonym of *M. minimus*.

Chasen (1940), Tate (1942), and Laurie & Hill (1954) followed Andersen's classification of *Macroglossus*. But Chasen (1940) referred *M. lagochilus lagochilus* to *M. minimus minimus* from Malaysian Peninsula and *M. m. sobrinus* from Nias I. Unfortunately, Chasen did not explain the basis for this judgment. He recorded *M. minimus minimus* from Bali I, and added new subspecies *M. m. fraternus* from Sipora and Siberut Is., Mentawai Is. While Laurie and Hill (1954) added records of *M. l. lagochilus* from Mysol and Admiralty Is. *M. lagochilus microtus* from Bougainville and San Christoval (Solomon Is.). Goodwin (1979), who added the record of *M. lagochilus* from Timor, was unable to differentiate Malayan *sobrinus* and *lagochilus* from Malaya (West Malaysia), Sulawesi and the Solomon Is. based on the direction of the nares.

Start (unpublished data) has examined and studied *Macroglossus* from Peninsular Malaysia. He stated that Andersen's (1912) diagnostic characters for *Macroglossus* from that region are inappropriate. According to Start, rostrum size, teeth size and general size of *M. minimus* and *M. lagochilus* are very similar. In addition he found that in preserved specimens the presence or absence of the internarial groove may be difficult to determine and that direction in which the nares face can be altered by preservation. Start considered other characters to be more diagnostic, as well as difference in their habitat preferences. Based on the following characters: presence of well defined thickened glandular collar across the throat and its colour; presence or absence of the projection of mandibular symphysis; dept of mandible at the canine compared to at the first incisor; and position of anterior edge of lacrimal pit toward posterior edge of molar two, he referred *Macroglossus minimus sobrinus* K. Andersen, 1912 to *Macroglossus sobrinus* (K. Andersen, 1912). He considered *M. sobrinus* occurs inland from the lowlands to over 1800 m a.s.l., but never in mangroves. He referred *Macroglossus lagochilus lagochilus* Matschie, 1899 to *Macroglossus minimus* (Geoffroy, 1810) which occurs in mangrove. Consequently, the distribution of *M. minimus* is restricted to coasts and offshore islands. His notion is followed by Lekagul and McNeely (1977) and Medway (1978). But Kitchener *et al.* (1987, 1990a) and McKean (1983) observed that *M. minimus* in Australia and Lombok I. occurs in various kinds of habitat and altitudes. Hill (1983) reviewed in detail the taxonomic status of *Macroglossus*. He confirmed the division of *Macroglossus* into two species, *M. sobrinus* and *M. minimus*. He supported the opinion that the direction of the nares and the upper lip median groove are not useful diagnostic

characters. Hill (*loc. cit.*), briefly summarized the species and subspecies of *Macroglossus* as follows: *Macroglossus minimus* (Geoffroy, 1810), *M. m. lagochilus* Matschie, 1899 which is distributed in S. Thailand, S. Vietnam, Sirhassen I. (?), Sri Buat I. (?), Bunguran I., North Natuna Is., Borneo to Philippine Is., Sulawesi, Peleng and Sanghir Is., and Molucca Is; *M. m. minimus* (Geoffroy, 1810) which is distributed in Jawa, Bali, Madura and Kangean Is.; *M. m. nanus* Maschie, 1899 which is distributed in Aru Is., Kei Is., Mysol Is., New Guinea, Bismarck Archipelago, Admiralty Is., Queensland, Australia; *M. m. pygmaeus* Andersen, 1911 which is distributed in Murray I. and Torres Straits; *M. m. microtus* Andersen, 1911 which is distributed in Bougainville, San Christobal, Guadalcanal, Florida and Solomon Is. *Macroglossus sobrinus* Andersen, 1911: *M. s. sobrinus* Andersen, 1911 which is distributed in Burma, and Thailand to Sumatera, Nias I., Krakatau I. and Jawa; *M. s. fraternus* Chasen & Kloss, 1927 which is distributed in Sipora and Siberut Is., Mentawai Is.

Koopman (1989) agreed with Hill's (1983) taxonomic treatment of *Macroglossus*, except for the occurrence of *Macroglossus minimus* in Jawa. Koopman (*loc. cit.*) examined 26 specimens from six localities on Jawa and did not record a single *M. minimus*. Kitchener *et al.* (1990a) recorded *M. minimus minimus* from Lombok Is. and McKean (1972) considered that *M. lagochilus pygmaeus* and *M. lagochilus microtus* were synonyms of *M. lagochilus nanus*.

## Materials and Methods

Most of specimens used for this study were collected by us and our colleagues from W. A. Museum and Museum Zoologicum Bogoriense, from 27 islands and its vicinity, using mist nets. The collection localities are shown in Figure 1.

The specimens were fixed in 10% formalin and preserved in 70% ethanol except specimens from Sumatera, Buru, partly Jawa and partly Kalimantan were dry specimens. Specimens examined were from following institution:
WAM: Western Australian Museum, Perth, Western Australia.
MZB: Museum Zoologicum Bogoriense, Bogor, Indonesia.
AM: Australian Museum, Sydney, New South Wales.

A total of 395 specimens were examined. Fifty five skulls, dentary and dental (skull characters) were measured, as well as 20 external characters (Figure 2. to 6.). Sixty nine measurements from continuous characters were in millimeters (mm) and were recorded to two decimal places using digital calipers. For dry specimens, data of ear and body length follow the measurements written on the label. T test was applied to avoid bias caused by the different procedure of measurements on mixed specimens from Jawa and Kalimantan. If there was not any differences, the data included in the analysis. We did not use the measurements of specimens from Sumatera, since all of them are dry specimens, the data on ear and body length were

not comparable. Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill and Smith (1984). Six measurements were based on observation follows Andersen (1912) and Start (unpublished data).
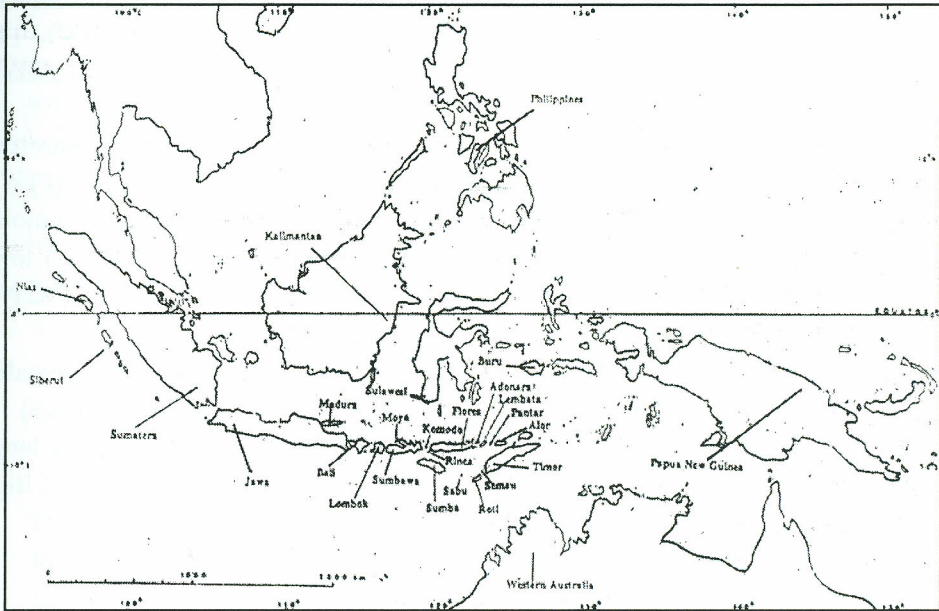


Figure 1. Map showing island where *Macroglossus* specimens were collected for the morphological study.

Specimens included in the statistical analysis are only those with complete set of measurements. Some skulls and external measurements could not be taken because of skull or body damage.

All data were arranged in such a manner for use in the next analysis of skull and external characters by using SPSS (computer program).

Before all subsequent analysis, the correctness and abnormality of values were examined by using MANOVA and RESIDUAL analysis. Any value having residual over 2.5 will be checked for its correct measurement, sex, age and location. After checking any value having residual over 8 subsets:

1.  Overall skull, greatest skull length (GSL), zygomatic breadth (ZB) and condylo canine length (CCL),

2.  Braincase, post palatal length (PPL), skull height (SH), braincase width (BCW), bulla length (BL), basisphenoid width (BSW), foramen magnum width (FMW), inter orbital breadth (IOB) and post orbital breadth (POB),

3.  Rostral and facial, palatal length (PL), upper canine inner distance ($C^1C^1$), upper molar2 molar2 inner distance ($M^2M^2$), upper premolar4 premolar4 inner distance

($P^4P^4$), inter lacrimal pit (ILP), rostral length (RL), mesopterygoid fossa width (MF), the presence of internarial hroove (IG) and median vertical groove (MVG),

4. Upper teeth, upper tooth row (C1M2U), upper canine length (C1LU), upper canine width (C1WU), upper premolar1 length (P1LU), upper premolar1 width (P1WU), upper premolar3 length (P3LU), upper premolar3 width (P3WU), upper premolar4 length (P4LU), upper premolar4 width (P4WU), upper molar1 length (M1LU), upper molar1 width (M1WU), upper molar2 length (M2LU), upper molar2 width (M2WU), the position of upper molar2 toward orbit point (M2U),

5. Lower teeth, lower canine length (C1LL), lower canine width (C1WL), lower tooth row (C1M3L), lower premolar1 length (P1LL), lower premolar1 width (P1WL), lower premolar3 length (P3LL), lower premolar3 width (P3WL), lower premolar4 length (P4LL), lower premolar4 width (P4WL), lower molar1 length (M1LL), lower molar1 width (M1WL), lower molar2 length (M2LL), lower molar2 width (M2WL), lower molar3 length (M3LL), lower molar3 width (M3WL),

6. Mandible, mandible length (ML), coronoid height (CH), dentary dept (DD), mandible symphises length (MSL) and the degree of projection of keeled symphises (KS),

7. Wing, fore-arm length (FA), digit1 metacarpal (DIG1M), digit1 phalanx length (DIG1P), digit2 metacarpal length (DIG2M), digit2 phalanx1 length (DIG2P1), digit2 phalanx2 length (DIG2P2), digit3 metacarpal length (DIG3M), digit3 phalanx1 length (DIG3P1), digit3 phalanx2 length (DIG3P2), digit4 metacarpal length (DIG4M), digit4 phalanx1 length (DIG4P1), digit2 phalanx2 length (DIG4P2), digit5 metacarpal length (DIG5M), digit5 phalanx1 length (DIG5P1), digit5 phalanx2 length (DIG5P2),

8. External, snout vent length/body length (SVL), tibia length (TIB), pes length (PES), ear length (EAR), and the presence of throat glands (TG).

To obtain characters which are important in discriminating the group, the DFA was run on each subset of characters using island as the *a priori* grouping and the first two characters that minimize Wilk's lambda value were selected for the overall combined DFA analysis. Selected characters which have abnormal distribution residual value were transformed into log. Then selected characters were analyzed by multiple regression for one to three factors interaction. If many characters selected had sex or age differences then all value were adjusted by adding the different mean value. Further any variable which has 2 or 3 way interaction was excluded for Discriminant Function Analysis (DFA).

## Result and Discussions

### 1. Univariate Analysis

None of the 14 characters were significantly influenced by sex. All characters were very significant (P<0.001) and were influenced by island (Table 1).

Table 1. Multiple regression of *Macroglossus* based on 14 skull, dentary, dental and external body characters for the six broad island groups. Significance of F values are as follows: * = P<0.05, * * = P,0.01, * * * = P<0.001.

| | MAIN EFFECT | | | INTERACTION | | | |
|---|---|---|---|---|---|---|---|
| | **SEX** | **AGE** | **ISLAND** | **SEX.AGE. ISLAND** | **SEX. AGE** | **SEX ISLAND** | **AGE ISLAND** |
| BSW | 2.91 | 0.48 | 18.16*** | 0.62 | 0.47 | 1.32 | 1.47 |
| C1M2U | 1.36 | 1.62 | 31.21*** | 1.19 | 1.64 | 1.10 | 1.19 |
| C1M3L | 2.87 | 2.97 | 41.39*** | 1.49 | 3.14 | 1.60 | 1.20 |
| CCL | 3.38 | 1.91 | 51.48*** | 0.87 | 1.28 | 1.60 | 1.20 |
| DIG1P | 0.19 | 0.01 | 26.23*** | 0.83 | 0.45 | 0.87 | 0.68 |
| FA | 0.41 | 1.27 | 28.64*** | 1.14 | 1.00 | 0.95 | 0.94 |
| GSL | 2.37 | 2.25 | 62.12*** | 0.71 | 1.40 | 0.51 | 0.77 |
| ML | 2.81 | 2.46 | 66.42*** | 0.87 | 2.94 | 0.84 | 0.79 |
| P4P4 | 1.13 | 1.73 | 10.23*** | 1.13 | 3.60 | 1.48 | 1.00 |
| P4WL | 0.30 | 0.99 | 4.51 *** | 0.44 | 0.25 | 0.45 | 0.48 |
| PPL | 2.84 | 1.96 | 20.58*** | 1.31 | 3.36 | 1.27 | 1.47 |
| RL | 4.35 | 3.20 | 66.12*** | 0.67 | 2.67 | 0.74 | 0.97 |
| SVL | 0.04 | 0.19 | 35.11*** | 1.06 | 0.12 | 0.85 | 1.56 |
| TIB | 1.41 | 2.0 | 13.06*** | 0.81 | 1.67 | 1.39 | 1.12 |

Table 2. The mean, standard deviation, minimum and maximum values and sample size from each of the broad island groups recognized by DFA on the selected five characters (see text for explanation of character codes).

| GROUP | | RL | DIG1P | FA | TIB | C1M3L |
|---|---|---|---|---|---|---|
| JAWA | X | 9.64 | 8.96 | 44.73 | 17.47 | 10.15 |
| | SD | 0.52 | 0.51 | 1.53 | 0.98 | 0.47 |
| | MIN | 8.74 | 7.63 | 7.63 | 15.26 | 9.10 |
| | MAX | 10.67 | 10.30 | 10.30 | 19.32 | 11.13 |
| | N | 71 | 72 | 70 | 72 | 72 |
| NUSA TENGGARA | X | 7.56 | 8.86 | 40.09 | 17.09 | 8.58 |
| | SD | 0.39 | 0.48 | 1.14 | 0.75 | 0.44 |
| | MIN | 6.70 | 7.63 | 37.29 | 15.24 | 7.65 |
| | MAX | 8.59 | 10.46 | 43,74 | 19.30 | 10.14 |
| | N | 258 | 258 | 258 | 258 | 250 |

*Table 2. Continued*

| GROUP | | RL | DIG1P | FA | TIB | CIMBL |
|---|---|---|---|---|---|---|
| PHILIPPINES | X | 8.28 | 10.10 | 44.38 | 18.42 | 9.98 |
| | SD | 0.33 | 0.29 | 0.91 | 0.60 | 0.32 |
| | MIN | 7.66 | 9.49 | 43.28 | 17.61 | 9.32 |
| | MAX | 8.72 | 10.42 | 45.95 | 19.08 | 10.41 |
| | N | 8 | 8 | 8 | 8 | 8 |
| NEW GUINEA | X | 8.96 | 9.49 | 41.18 | 16.39 | 9.85 |
| | SD | 0.50 | 0.50 | 1.74 | 0.86 | 0.58 |
| | MIN | 7.68 | 8.56 | 37.74 | 15.13 | 8.37 |
| | MAX | 9.65 | 10.19 | 43.37 | 17.64 | 10.52 |
| | N | 15 | 15 | 15 | 15 | 14 |
| SIBERUT | X | 12.53 | 10.25 | 50.49 | 20.77 | 12.22 |
| | SD | 0.38 | 0.38 | 1.44 | 0.61 | 0.46 |
| | MIN | 11.95 | 9.24 | 48.75 | 19.67 | 11.72 |
| | MAX | 13.27 | 10.76 | 52.16 | 21.56 | 13.15 |
| | N | 13 | 13 | 13 | 13 | 13 |
| SULAWESI | X | 7.66 | 10.68 | 41.51 | 17.79 | 9.37 |
| | SD | 0.28 | 0.49 | 0.87 | 0.54 | 0.40 |
| | MIN | 7.17 | 9.51 | 39.77 | 16.81 | 8.68 |
| | MAX | 8.17 | 11.76 | 43.60 | 18.64 | 10.30 |
| | N | 29 | 29 | 29 | 29 | 29 |

## 2. Discriminant Function Analysis (DFA)

### 2.1. All Islands Separate

The DFA of the 14 selected characters for all islands separately as the *a priori* groups produced six broad island groups. However, many islands are represented by only a few specimens, and considerably less than the number of characters. Therefore, to minimize over-fitting of the data, this DFA was repeated using only the five characters that minimize Wilk's lambda. These five characters were: ML;DIG1P;TIB; SVL;and P4WL. The analysis using variables also clearly shows the six broad groups on function 1 and 2 (Figure 2). These broad groups were 1) The Jawa Group (Bali, Nusa Penida, Jawa, Nias and Sumatera). (2) The Nusa Tenggara Group (Kalimantan, Buru, Adonara, Alor, Flores, Moyo, Madura, Komodo, Lembata, Lombok, Pantar, Rinca, Roti, Semau, Sumba, Sumbawa, Sabu, Timor, Western Australia, New Britain and New Ireland). (3) The Sulawesi Group (Sulawesi only). (4) The Siberut Group (Siberut only). (5) The New Guinea Group (New Guinea only). (6) The Philippine Group (Philippines only). The mean, standard deviation (SD), minimum and maximum of characters for the above six island groups are presented in Table 2. Visual inspection of this table indicates considerable difference between means of many characters between these broad groupings.
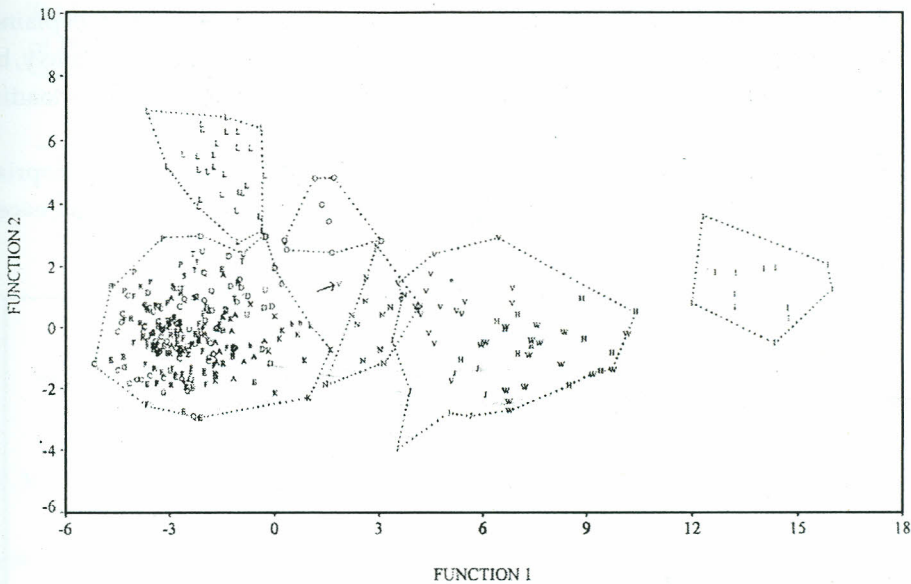
FUNCTION 1

Figure 2. Plot of canonical variate functions 1 and 2 of all islands and 5 characters of *Macroglossus*. Locality code for all figure 4 to 16.

| A : Sumbawa | K : Kalimantan | U : Roti |
|---|---|---|
| B : Moyo | L : Sulawesi | V : Bali |
| C : Sumba | M : Buru | W : Jawa |
| D : Lombok | N : Papua New Guinea | X : Komodo |
| E : Flores | 0 : Philippines | Y : Rinca |
| F : Lembata | P : Western Australia | Z : Semau |
| G : Adonara | Q : Timor | b : New Britain |
| H : Sumatera | R : Pantar | i : New Ireland |
| I : Siberut | S : Alor | n : Nusa Penida |
| J : Nias | T : Sabu | w : Madura |

## 2.2. Jawa, Siberut, Nusa Tenggara, Sulawesi, New Guinea and Philippine Groups

Next, a DFA based on the 14 characters using the above six broad groups as the *a priori* groupings was computed. These functions allocated 94.0% of all individuals to their correct group.

This analysis was then repeated using a reduced set of five characters (RL, DIG1P, FA, TIB and C1M3L), selected from the above analysis to minimize Wilk's lambda. This was done because the number of characters (14) substantially exceeds the smallest group sample size (Siberut, N=8). This analysis with five characters produced very similar clustering to the DFA that was run with 14 characters. The following description is based on this analysis using five characters.

Function 1, which accounted for 81.1% of the variation, separated the Siberut, Jawa and the Nusa Tenggara groups (Figure 3). The characters loading most heavily on this function (ie with standardized canonical discriminant function coefficients

greater than 0.5 were RL, FA and C1M3L see Table 3). Function 2, which explained 13.9%, separated the Sulawesi Group from four of the other five groups completely, but only partially separated it from the Philippine Group. The only character loading heavily (>0.5) was DIG1P.

A total of 90.9% of individuals were correctly classified to their appropriate island group (Table 4). A low of misclassification occurred in all island groups, except Siberut where 100% of individuals were correctly classified.
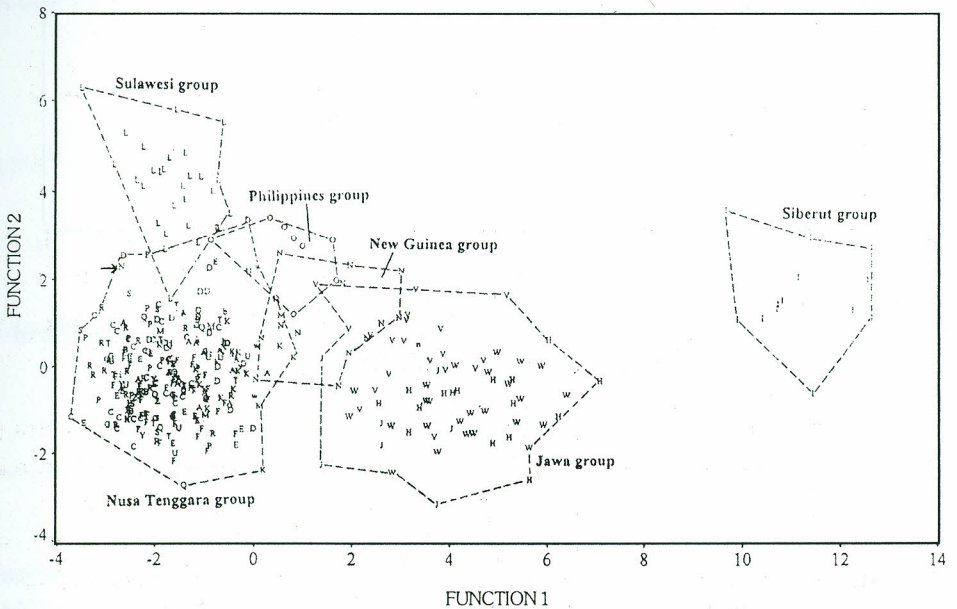


Figure 3. Plot of canonical variate functions 1 and 2 of 6 island groups and five characters of *Macroglossus* (for code to localities see Figure 2).

Table 3. Standardized and unstandardized (in brackets) canonical discriminant function coefficient of the first two significant functions for *Macroglossus* spp. Specimens, separated into 6 broad groups and based on five characters (sex and age classes combined).

| CHARACTER | FUNCTION 1 | | FUNCTION 2 | |
|---|---|---|---|---|
| RL | 0.9327 | (2.0276) | 0.0427 | (-0.6976) |
| FA | 0.6405 | (0.3131) | 0.2360 | (-0.2755) |
| C1M3 | 0.6235 | (-0.7288) | 0.3946 | (1.2748) |
| DIG1P | 0.0995 | (-0.3087) | 0.8787 | (1.9315) |
| TIB | 0.2274 | (0.06638) | 0.2998 | (0.2269) |
| Constant | -27.2817 | | -16.0213 | |
| Variance explained (%) | 81.1 | | 13.9 | |

Table 4. Classification results from DFA of 6 broad groups of island populations of *Macroglossus* using a reduced set of 5 characters.

| ACTUAL GROUP | No. of cases | Predicted Group membership (%) | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| Siberut (1) | 13 | 100 | 0 | 0 | 0 | 0 | 0 |
| Jawa (2) | 69 | 0 | 89.9 | 0 | 10.1 | 0 | 0 |
| Sulawesi (3) | 29 | 0 | 0 | 96.6 | 0 | 0 | 3.4 |
| New Guinea (4) | 14 | 0 | 0 | 7.1 | 78.6 | 14.3 | 0 |
| Philippines (5) | 8 | 0 | 0 | 0 | 0 | 75.0 | 25.0 |
| Nusa Tenggara (6) | 250 | 0 | 0 | 1.2 | 5.6 | 2.0 | 91.2 |

Percent of "grouped" cases correctly classified: 90.9%.

## 2.3. Variation within the Jawa Group

A DFA based on 13 of the 14 selected characters (excluding SVL measurements, because the important Sumatera sample comprised "cabinet skins" only, see Section 1.2.) for the Jawa Group revealed three distinct clusters (Figure 4). These three subgroups were Nias, Jawa/Sumatera, and Bali/Nusa Penida. A total of 73.9% of individuals were correctly classified to their appropriate groups.

The above DFA was repeated using the above three subgroups as *a priori* groups, and based on a subset of five characters selected from the above analysis to minimize Wilk's lambda. The five characters were: FA, ML, P4WL, TIB and DIG1P, This analysis produced a similar plot to the previous one (Figure 5). Function 1, which explained 77% of the variation, separated Bali/Nusa Penida from both the Nias and Jawa/Sumatera subgroups. Function 2, which explained 23% of the variation, separated Nias from the other two subgroups.

The characters loading heavily (>0.5) on Function 1 were TIB, FA and DIG1P. The characters loading heavily (>0.5) on Function 2 were FA and P4WL (Table 5). A total of 94.3% of individuals were correctly classified to their appropriate groups. A low level of misclassification occurred in each of the three island groups.

## 2.4. Variation within the Nusa Tenggara Group

A DFA based on 13 characters (run without SVL to enable the inclusion of the important Buru specimens which were missing this measurements) extracted five significant functions. At least three broad subgroups were apparent (Figure 6). These were (I) Kalimantan Subgroup (Kalimantan, Buru and Madura); (ii) New Britain Subgroup (New Britain and New Ireland); and (iii) Lombok Subgroup (Nusa Tenggara islands, Western Australia).

When DFA was run on a reduced subset of five characters (BSW, TIB, C1M3L, FA and P4WL) and three *a priori* groups defined selected from this analysis to minimise Wilk's Lambda, it produced three clusters similar to those in Figure 6 and 7.
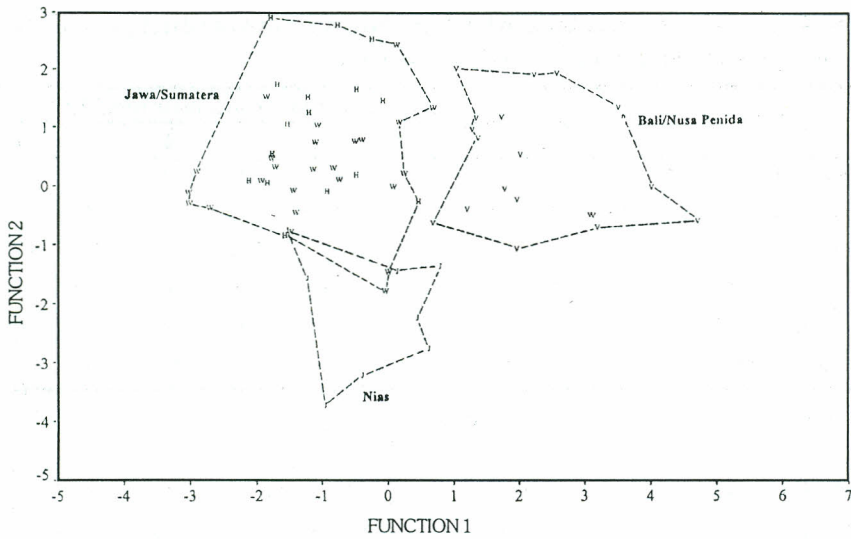
Figure 4. Plot of canonical variate functions 1 and 2 of all islands and 14 characters (minus SVL) of *Macroglossus sobrinus* (code, see Figure 2).
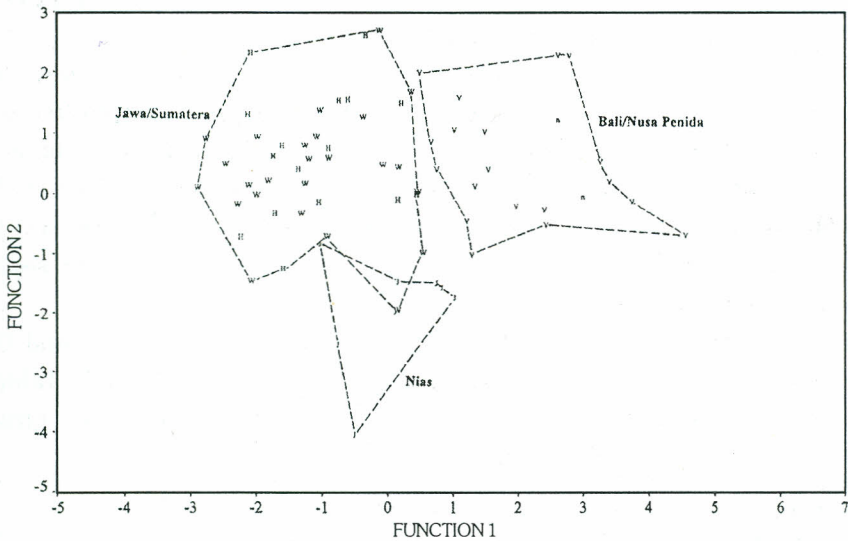


Figure 5. Plot of canonical variate functions 1 and 2 of three island groups and five characters of *Macroglossus sobrinus* (code, see Figure 2).

This DFA extracted two significant functions. Function 1, which explained 91.9% of the variation, separated the Lombok Subgroup from both the New Britain and Kalimantan Subgroups. The characters loading most heavily (>0.5) on function 1 were TIB and C1M3L (Table 6). Function 2, which explained 8.1% of the variation, completely separated the New Britain and Kalimantan Subgroups. The characters loading most heavily (>0.5) on function 2 were FA and C1M3L (Table 6). A total of 96.3% of specimens

were classified in their correct group. Of the Kalimantan Subgroup, two individuals were incorrectly classified to the Lombok Subgroup and another to the New Britain Subgroup. Of the Lombok Subgroup, six of the 212 specimens were incorrectly classified to the Kalimantan Subgroup. All the New Britain Subgroup were correctly classified.
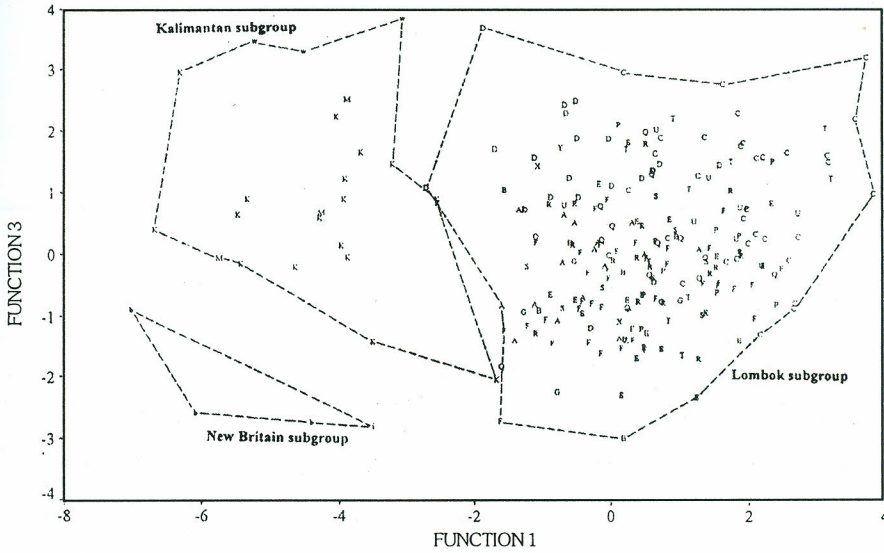


Figure 6. Plot of canonical variate functions 1 and 3 of all islands and 13 characters for the Nusa Tenggara group (code, see Figure 2).
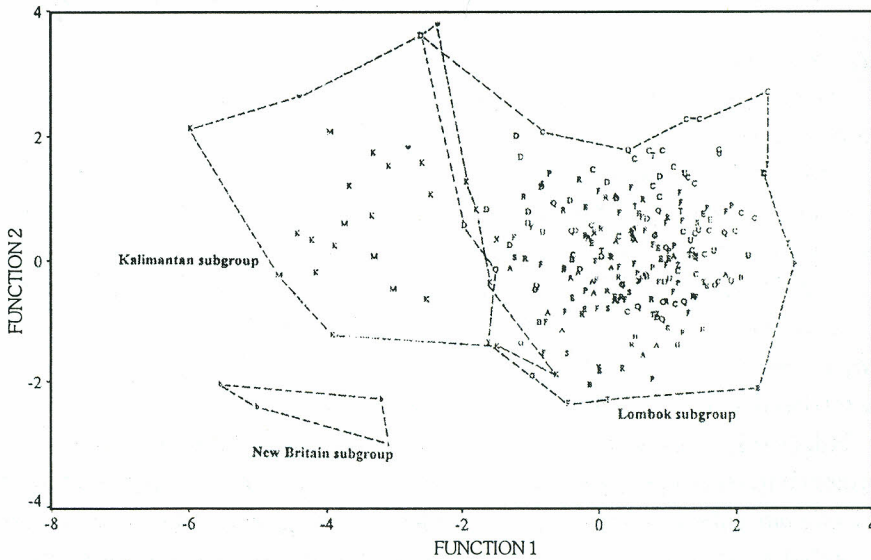


Figure 7. Plot of canonical variate functions 1 and 2 of three groups (see text) based on a selected set of 5 characters for the Nusa Tenggara groups (code, see Figure 2).

Table 5. Standardized and unstandardized (in brackets) canonical discriminant function coefficients of combined characters for the Jawa Group *Macroglossus* based on selected five characters and with three *a priori* subgroups (see text) (sex and age classes combined).

| CHARACTER | FUNCTION 1 | FUNCTION 2 |
|---|---|---|
| TIB | 1.0739 (1.4618) | 0.1189 (0.1619) |
| ML | -0.3619 (- 0.6338) | -0.1464 (-0.2564) |
| DIG1P | 0.5888 (1.3922) | 0.2134 (0.5045) |
| FA | -0.8798 (-0.6551) | 0.7419 (0.5524) |
| P4WL | -0.3648 (-11.2351) | 0.6602 (20.3336) |
| Constant | 8.5391 | -34.6453 |
| Variance explained (%) | 77 | 23 |

Table 6. Standardized and unstandardized (in brackets) canonical discriminant function coefficients of combined characters for the Nusa Tenggara Group *Macroglossus* based on selected five characters and with three *a priori* subgroups (see text) (sex and age classes combined).

| CHARACTER | FUNCTION 1 | FUNCTION 2 |
|---|---|---|
| BSW | -0.4314 (-1.8093) | 0.2140 (0.8976) |
| TIB | 0.9473 ( 1.4052) | -0.2648 (-0.3928) |
| C1M3L | -0.5766 (-1.4635) | -0.5001 (-1.2693) |
| FA | -0.3553 (-0.3183) | 1.0618 (0.9513) |
| P4WL | 0.4268 (13.1639) | 0.3386 (10.4432) |
| Constant | 1.7677 | -26.8026 |
| Variance explained (%) | 91.9 | 8.1 |

### 3. Taxonomy of *Macroglossus*

The analysis of the continuous morphological characters clearly showed that the group from Siberut Island was morphologically the most distinct of the six groups recognized from DFA. It differs from all these other groups by being larger and by having some shape differences. The remaining five groups documented by the DFA, are also reasonably distinct in discriminant function space. The Jawan Group, which consists of the three identifiable populations: Sumatera/Nias, Jawa, Bali and Nusa Penida is also a large group. The Jawan Group and the Siberut Island Group are also linked by the presence of bony projection on the anteroventral surface of the mandible symphysis and a more fleshy medial distal projection of both the upper and lower lip.

Hill (1983) considered the bony projection on the mandible symphysis to be an important character to diagnose the species *M. sobrinus* (anteroventral projection present) and *M. minimus* (absent). This projection, taken in conjuction with the results of the DFA, indicate that a sharp boundary exists between the westernmost groups (from Siberut, Sumatera, Nias, Jawa, Bali and Nusa Penida) and the other group. This boundary is at the narrow strait between Nusa Penida and Lombok. Given this parapatric distribution

the above western groups are considered to be *M. sobrinus* and all other groups are *M. minimus*. The DFA indicates that these two species have a number of subspecies. Most of these subspecies comprise populations that are already named.

The taxonomy of *Macroglossus* in the study region is now considered to be as follows: *Macroglossus sobrinus* which comprises *M. s. sobrinus* (Jawa/Sumatera), *M. s. fraternus* (Siberut), *M. s.* subsp. nov. A (Bali/Nusa Penida), *M. s.* subsp. nov. B (Nias); *Macroglossus minimus* which comprises *M. m. minimus* (Nusa Tenggara/Western Australia), *M. m. nanus* (New Britain/New Ireland), *M. m. lagochilus* (Kalimantan/Buru/Madura?), *M. m. fructivorous* (Philippines), *M. m. meyeri* (Sulawesi), *M. m. microtus* (New Guinea).

The status of *M. m. pygmaeus* from Murray Island in the Torres trait was not examined.

## 4. Identification

*Macroglossus sobrinus* differs from *M. minimus* in being generally larger in many skull, dentary, dental and external body characters. It also has a prominent anteroventral ossified projection of the dentary symphysis and associated fleshy projection of the medial distal part of both the upper and lower lips. Further it differs in having mandible length larger relative to basisphenoid width (Figure 8) and forearm length greater relative to digit 1 phalanx (Figure 9).

The four subspecies of *M. sobrinus* (*fraternus, sobrinus*, subsp. nov. A and subsp. nov. B) are also distinguishable by univariate statistics. *M. s. fraternus* is considerably larger in most skull, dentary, dental and external body characters than the other subspecies of *M. sobrinus. M. sobrinus* subsp. nov. A can be distinguished from both *M. s. sobrinus* and *M. s.* subsp. nov. B by having a larger tibia relative to mandible length (Figure 10). *M. sobrinus* subsp. nov. B can be distinguished from *M. s. sobrinus* by having a smaller forearm length relative to snout to vent length (Figure 11).

The six species of *M. minimus* (*minimus, nanus, lagochilus, microtus, fructivorus* and *meyeri*) can be distinguished by univarite statistics. *M. m. microtus* differs from the other subspecies of *M. minimus* in having a larger digit 1 phalanx length relative to rostral length (Figure 12). *M. m. nanus* differs from *M. m. minimus* in having smaller tibia length relative to C1M3 length (Figure 13). *M. m. nanus* differs from *M. m. lagochilus* in having a shorter forearm length relative to tibia length (Figure 14).

This study clarifies considerably the taxonomic status of *Macroglossus*, which is considered by most authors to comprise two species only. Based on the analysis we tentatively follow the view that only two species are present in the study region. These are *M minimus* and *M. sobrinus*. There is, however, a case for considering *M. fraternus* as a species on morphological grounds because it is much larger than and differs in shape from its most closely related phenetic form, *M. s. sobrinus* from Jawa and Sumatera. Also the form from Sulawesi (*M. m. meyeri*) differs in size and shape from the other subspecies of *M. minimus*; it may warrant recognition as a species.
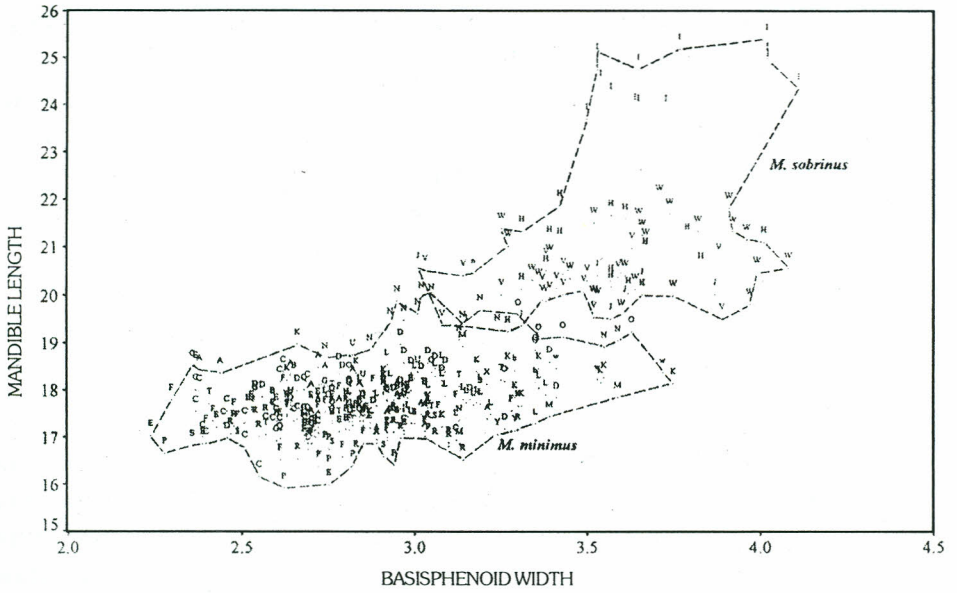
Figure 8. Univariate plot of mandible length *versus* basisphenoid width (code, see Figure 2).
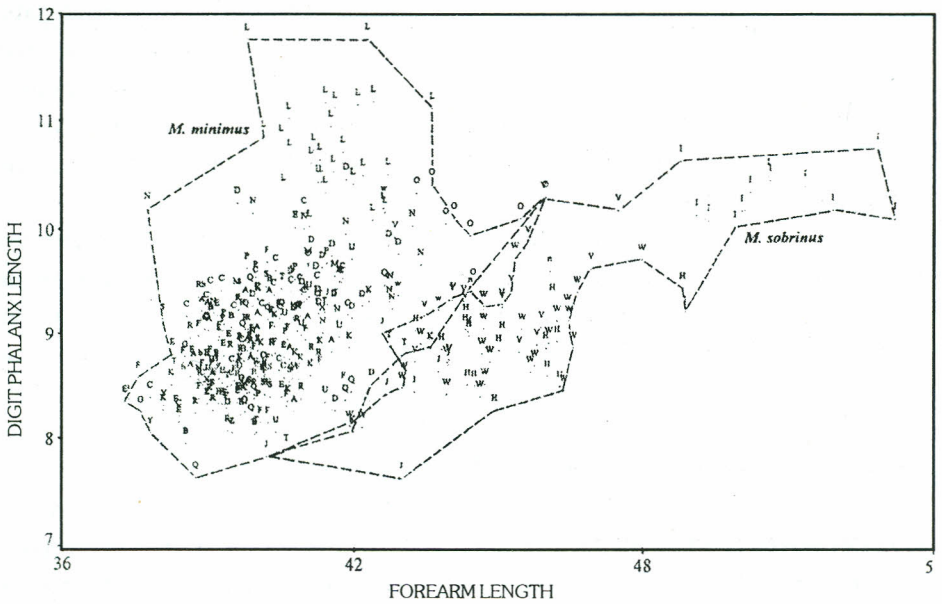


Figure 9. Univariate plot of forearm length *versus* digit 1 phalanx length (code, see Figure 2).
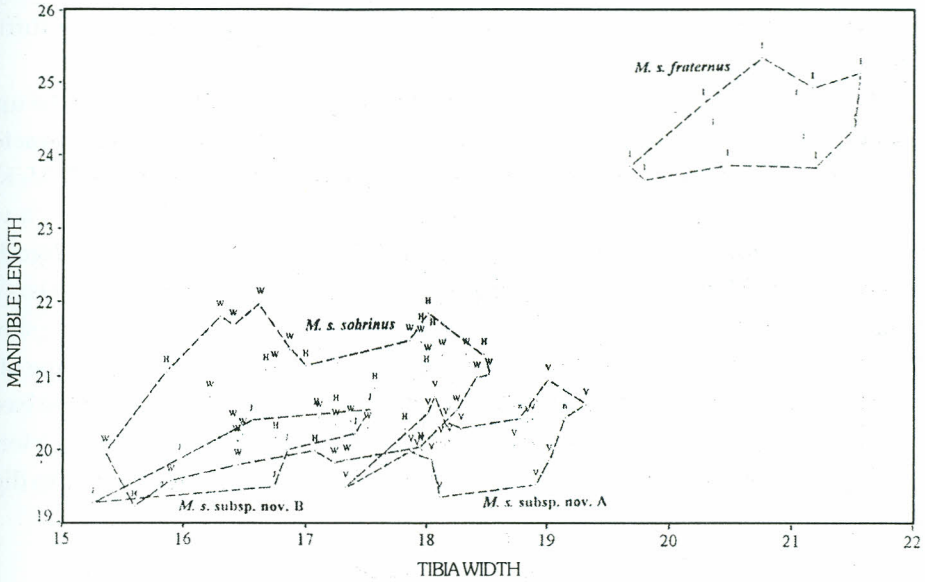
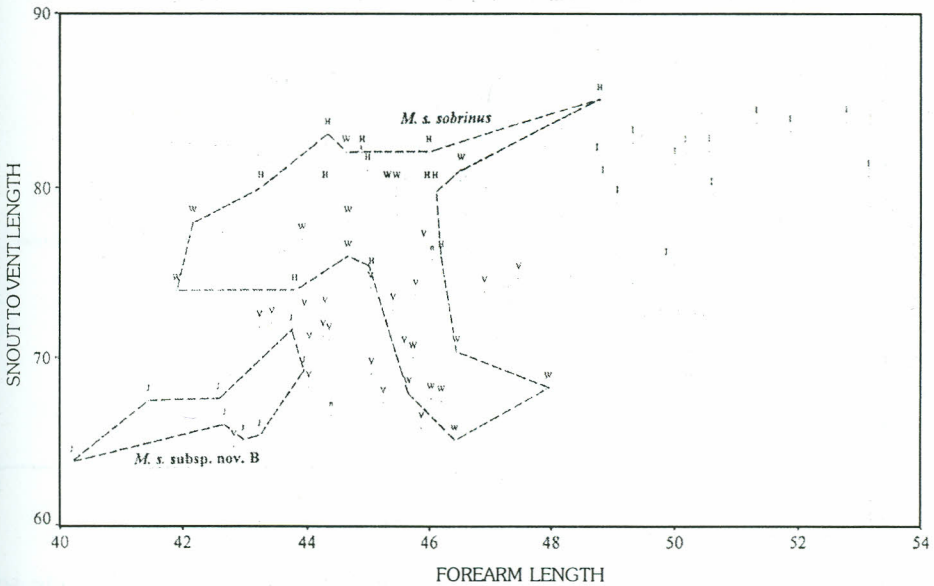Figure 10. Univariate plot of tibia length *versus* mandible length (code, see Figure 2).



Figure 11. Univariate plot of forearm length *versus* snout to vent length (code, see Figure 2).

While all the taxa are distinguishable using multivariate statistical analysis, most are also clearly separable using univariate analysis. Only *M. m. nanus* is difficult to separate (from *M. m. lagochilus*).

We disagree with Andersen (1912) that the median vertical groove on the upper lip is a diagnostic characters for *M. lagochilus* (*M. minimus*), because that character is also sometimes found in *M. sobrinus* subsp. nov. A and B from Nias and Bali. McKean (1972) considered *M. pygmaeus* and *M. microtus* to be synonym of *M. nanus*, a view followed by van Strien (1986) and Corbet & Hill (1992). Hill (1983) treated *M. lagochilus* as a synonym of *M. m. minimus*, a decision supported in this paper, on the basis that both taxa have a mandible that slopes posteriorly beneath the incisors and have shorter rostrum than *M. m. sobrinus sensu* Andersen (1912). We consider that the slope of the mandible is due, in large part, to the absence of projection of a symphysis at the base of the mandible. *M. sobrinus* is also easily diagnosed from *M. minimus* by having a longer mandible length relative to basisphenoid width and a forearm longer relative to digit 1 phalanx length.
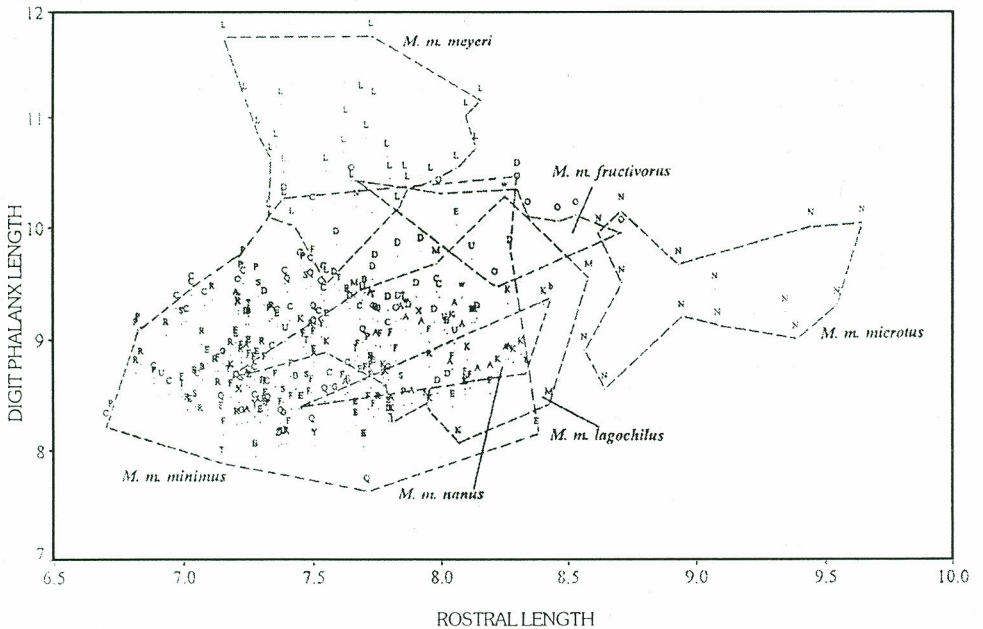


Figure 12. Univariate plot of digit 1 phalanx length *versus* rostral length (code, see Figure 2).
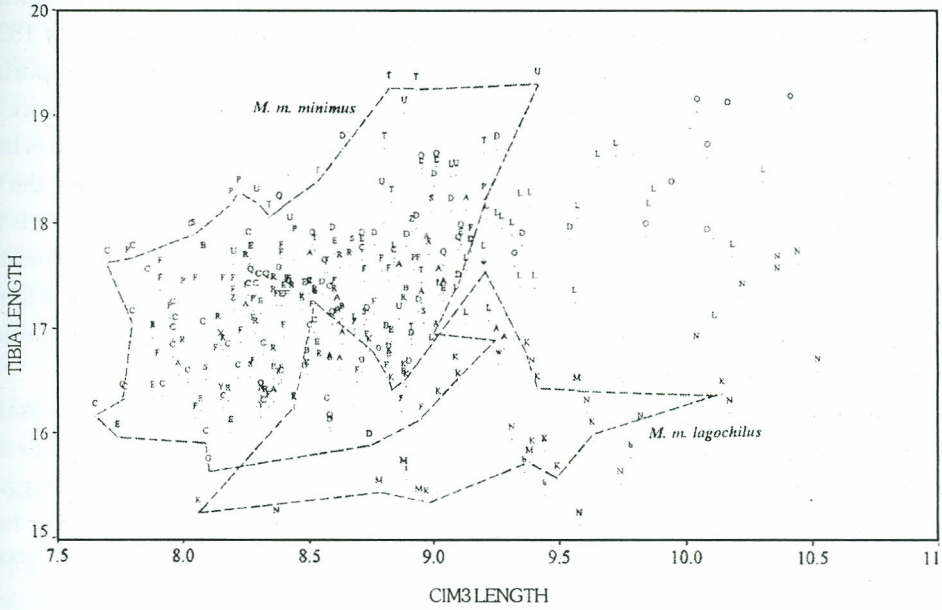
Figure 13. Univariate plot of tibia length *versus* C1M3 length (code, see Figure 2).
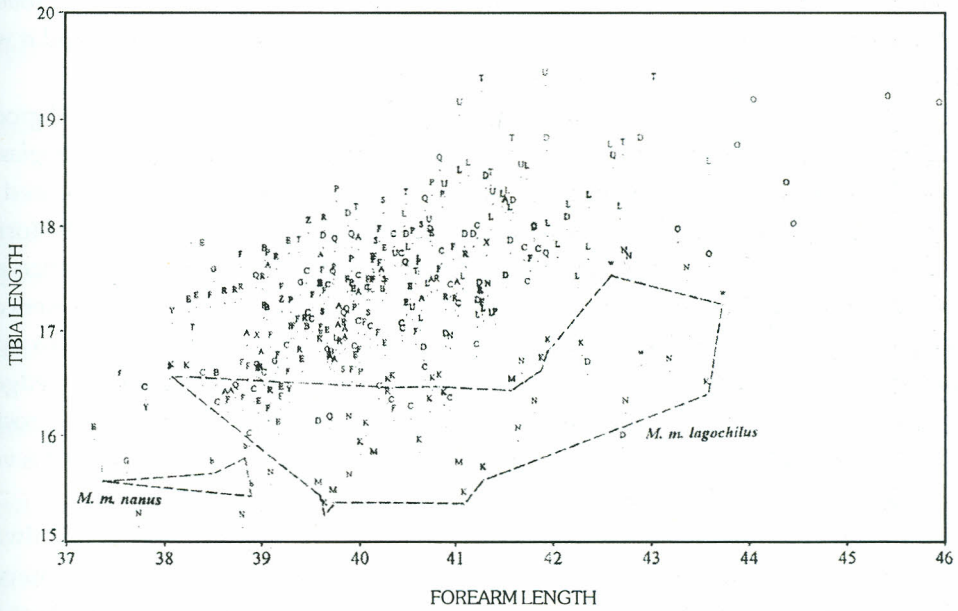


Figure 14. Univariate plot of forearm length *versus* tibia length (code, see Figure 2).

The *Macroglossus* from Siberut I. (*M. s. fraternus*) is the most morphologically divergent form of *Macroglossus*. The sea distance of 120 km and sea depth of 155 m (Heany, 1985) between Siberut I. and Sumatera appears to have been an important barrier to gene exchange between the forms of *Macroglossus* on these islands. Since the home range of *Macroglossus* is approximately 2 km (Start, 1974) and Siberut I. has been separated from Sumatera since at least the middle Pleistocene, at which time the sea level dropped about 160 meters below present levels (Gascoyne *et al.*, 1979), it is not surprising that this ocean has represented a substantial barrier to movement of *Macroglossus*. Similarly the boundary between Nusa Penida and Lombok Islands, involving a narrow water strait of some 22 km, appears to mark the southern boundary between *M. sobrinus* and *M. minimus*.

Other narrow water gaps between islands in Nusa Tenggara do not necessarily appear to have been substantial barriers to gene flow. For example, Kitchener and Maharadatunkamsi (1991) found a similar situation with *Cynopterus nusatenggara*. Because the sea depth of Selat Lombok is 256 m, Bali and Lombok Is may never have been connected by a land bridge during the pleistocene, although Kitchener *et al.* (1990a) indicate that this water gap may have been as narrow as 400 m. During the Pleistocene, the sea level dropped from 137 to 159 m (Donn *et al.*, 1962) and could be more than 230 m (Batchelor, 1979). Heany (1991) considers that in the absence of tectonic activity, land area above the 120 m bathymetric line could be considered dry land about 1800 yr BP. Selat Lombok is long considered an important biogeographic boundary and is well known as the southern part of Wallace's line (Mayr, 1944).

Start (unpublished data) stated that the direction of nares, median vertical groove and rostral size are in appropriate characters to diagnose the species of *Macroglossus* from West Malaysia. This is because the first two characters can be influenced by preservative solution and because rostral measurements overlap between the forms. Instead Start (unpublished data) proposed as diagnostic characters the presence of a thickened glandular collar across the throat (throat gland), the presence or absence of the projection of mandibular symphysis, the depth of mandible at the canine to at the first incisor, and the position of anterior edge of the lacrimal pit to the posterior edge of second molar. The throat gland was not found to be a useful character, although rostral length was. I did not use the depth of the mandible at the first incisor because it is very difficult to measure objectively.

Start (unpublished data) reported that in West Malaysia, *M. minimus* always occur along the coast whereas *M. sobrinus* is found more inland. However, we observed that *M. minimus* occurs from the lowland to the highland. Unfortunately, nowhere did I record two of the forms of *Macoglossus* sympatrically.

Other similar studies on morphological variation in Indonesian Chiroptera also indicate that Wallace's line, between Bali and Lombok Is., is of some importance as a subtle boundary separating sibling species or subspecies. For example, Kitchener

and Maharadatunkamsi (1991) and Kitchener and Maryanto (1993) reported that the distribution of the sibling species pairs *Cynopterus nusatenggara/ C. brachyotis* and *Hipposideros sumbae/ H. larvatus-H. madurae* and the subspecies of *Aethalops alecto* (*alecto* and *boeadii*) (Kitchener *et al.* 1993a) interface between Lombok I. and Bali/ Jawa. However, other sibling species from Jawa and Bali intrude well eastwards into Nusa Tenggara before interfacing with their counterparts. For example, *Taphozous melanopogon* occurs throughout Nusa Tenggara as far east Timor I. when it meets its sibling species *T. achates* (Kitchener *et al.*, 1993b). *Hipposideros diadema nobilis* interfaces with the eastern form *H. d. diadema* between Lombok and Sumbawa Is. (Kitchener *et al.*, 1992) and *Rhinolophus simplex* interface with *R. borneensis/ R. celebensis* between Bali and Jawa (Kitchener *et al.*, 1995). Further, the subspecies of house shrew *Suncus murinus* (*S. m. murinus* and *S. m. mülleri*) interface between Bali and Lombok (Kitchener *et al.*, 1994).

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