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Hipposideros diadema (Chiroptera Hipposideridae) in the Lesser Sunda Islands, Indonesia: taxonomy and geographic morphological variation.

D.J. Kitchener*, R.A. How*, N.K. Cooper*, and A. Suyanto+.

Abstract

A morphological study, using multivariate statistical analyses, was carried out on 157 specimens of *Hipposideros diadema* from the Lesser Sunda Is, Borneo, Java, Thailand, Peninsula Malaysia, Philippines, New Guinea, Solomon Is, Bismark Is, and Australia.

This study indicates that two forms of *H. diadema* occur in the Lesser Sunda Is: *H. d. nobilis* (Horsfield, 1823) — Borneo, Java, Bali, Nusa Penida, Lombok; and *H. d. diadema* (Geoffroy, 1813) — Sumbawa, Moyo, Sumba, Flores, Roti, Savu and Timor.

Hipposideros diadema is sexually dimorphic for skull, dentary and dental characters; for many measurements males average slightly larger than females. Female *H. d. diadema* show a cline in overall skull size with a trend to increase from west to east along the Lesser Sunda island chain.

Hipposideros diadema subspecies morphologically similar to the Lesser Sunda subspecies were reviewed taxonomically, redescribed and diagnosed against each other. These were *H. d. masoni* (Dobson, 1872) — Thailand, Malay Peninsula; *H. d. griseus* (Meyen, 1833) — New Guinea, Philippines; *H. d. reginae* Troughton, 1937 — Queensland, Australia; and *H. d. oceanitis* — Solomon and Bismarck Is.

There are three phenetic groupings in the *H. diadema* subspecies considered, based on external and skull measurements combined. *Hipposideros d. diadema, H. d. reginae* and *H. d. masoni* form one group; *H. d. griseus* and *H. d. oceanitis* a second group; and *H. d. nobilis* clusters separately.

Introduction

Extensive surveys of the terrestrial vertebrate fauna of a number of islands in the Lesser Sunda chain have been carried out as a collaborative effort between the Western Australian Museum and Balitbang Zoologi, Indonesia. These surveys, which were begun in September 1987, still continue. They have resulted in the collection of specimens of *Hipposideros diadema* (E. Geoffroy, 1813) from Bali, Nusa Penida Lombok, Sumbawa, Moyo, Flores, Sumba, Roti, Savu and Timor islands — as well as Java.

Tate (1941) summarised information on the subspecies of *H. diadema* known at that time from across its distribution in the Indo-Australian region. Hill (1963) more comprehensively reviewed the taxonomy of *H. diadema* and recognised 16 subspecies. Since then additional subspecies have been described by Phillips (1967) from the Solomon Islands and McKean (1970) from the Northern Territory, Australia.

* Western Australian Museum, Francis Street, Perth, Western Australia.

+ Balitbang Zoologi, LIPI, Jalan Ir. H. Juanda 9, Bogor, Indonesia, 16122.

Currently the following subspecies of *H. diadema* are generally recognised (Hill 1963; Phillips 1967; McKean 1970; Koopman 1982, 1984).

Hipposideros diadema diadema (Geoffroy, 1813) Timor I.; Lombok I.; Bali I.; Kangean I.; Sumbawa I.; Java.
H. d. masoni (Dobson, 1872) — Burma (Tenasserim); Indochina (Annam; Tonkin); Thailand; Malay Archipelago; Borneo; Sumatra and Nias I.
H. d. nicobarensis (Dobson, 1871) — Nicobar I.
H. d. enganus Andersen, 1907 — Engano I.
H. d. natunensis Chasen, 1940 — Bunguran I., N. Natuna Is.
H. d. griseus (Meyen, 1833) — Luzon, Philippine Is.
H. d. speculator Andersen, 1918 — Kalao Is, Flores Sea, south of Sulawesi.
H. d. ceramensis Laurie & Hill, 1954 — Seram, Buru Is.
H. d. euotis Andersen, 1905 — Batchian I.
H. d. pullatus Andersen, 1905 — Haveri, Papua New Guinea.
H. d. custos Andersen, 1918 — Ara, Kei Is.
H. d. mirandus Thomas, 1914 — Manus I, Admiralty Is.
H. d. trobrius Troughton, 1937 — Kiriwina I., Trobriand Is.
H. d. oceanitis Andersen, 1905 — Guadalcanal I., Fauro, Vella Lavella, Ysabel, Bougainville I. (Papua New Guinea).
H. d. demissus Andersen, 1909 — San Christoval I., E. Solomon Is.
H. d. malaitensis Phillips, 1967 — Malaita I., Solomon Is.
H. d. reginae Troughton, 1937 — Queensland, Australia.
H. d. inornatus McKean, 1970 — Northern Territory, Australia.

Hipposideros diadema diadema was considered by Andersen (1905) to occur on both Timor and Java. He noted that the holotype of the nominate subspecies was from Timor and that a skin from Timor closely agrees with Geoffroy's figure and description. However, Andersen (1905) noted that Javan specimens of *H. d. diadema* may average larger than those from Timor — and cautioned that Horsfield's (1823) name for the Javan and Balinese form (*nobilis*) may be valid. Goodwin (1979) also observed that the Javan and Balinese forms of *H. diadema* tended to have larger forearms than those from Timor. He stated that a "larger series of specimens from Java and Timor must be compared before it can be determined whether or not the populations on those islands were consubspecific". But, he concluded by agreeing with Hill (1963) that they were consubspecific and that the form '*nobilis*' should be synonymised with *H. d. diadema*.

Our extensive collections of *H. diadema* from the Lesser Sunda Islands showed considerable morphological variation and appeared to include several distinct forms. To identify these forms we compared them to closely related subspecies. These comparisons form the substance of this paper. Because these investigations have a bearing on some previous taxonomic judgments, this paper also rediagnoses the subspecies considered herein. All taxonomic judgements are the sole responsibility of the senior author.

Methods

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill (1963) and Hill and Smith (1984). Pelage descriptions when following the colour terminology of Ridgway (1912) are capitalised.

Skull characters

Twenty four measurements of skull characters and eight of external characters (all in mm), and weight (in gms) were recorded from adults specimens (Figure 1, caption). Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. All measurements were recorded with dial calipers to two decimal places.

Specimens Examined

One hundred and fifty seven adult specimens of *Hipposideros diadema* were measured from: Thailand, Malay Peninsula, Borneo, Java, Lesser Sunda Is, Philippines, Solomon Is, Bismarck Is and Australia. They are listed in the "Specimens Examined" section.

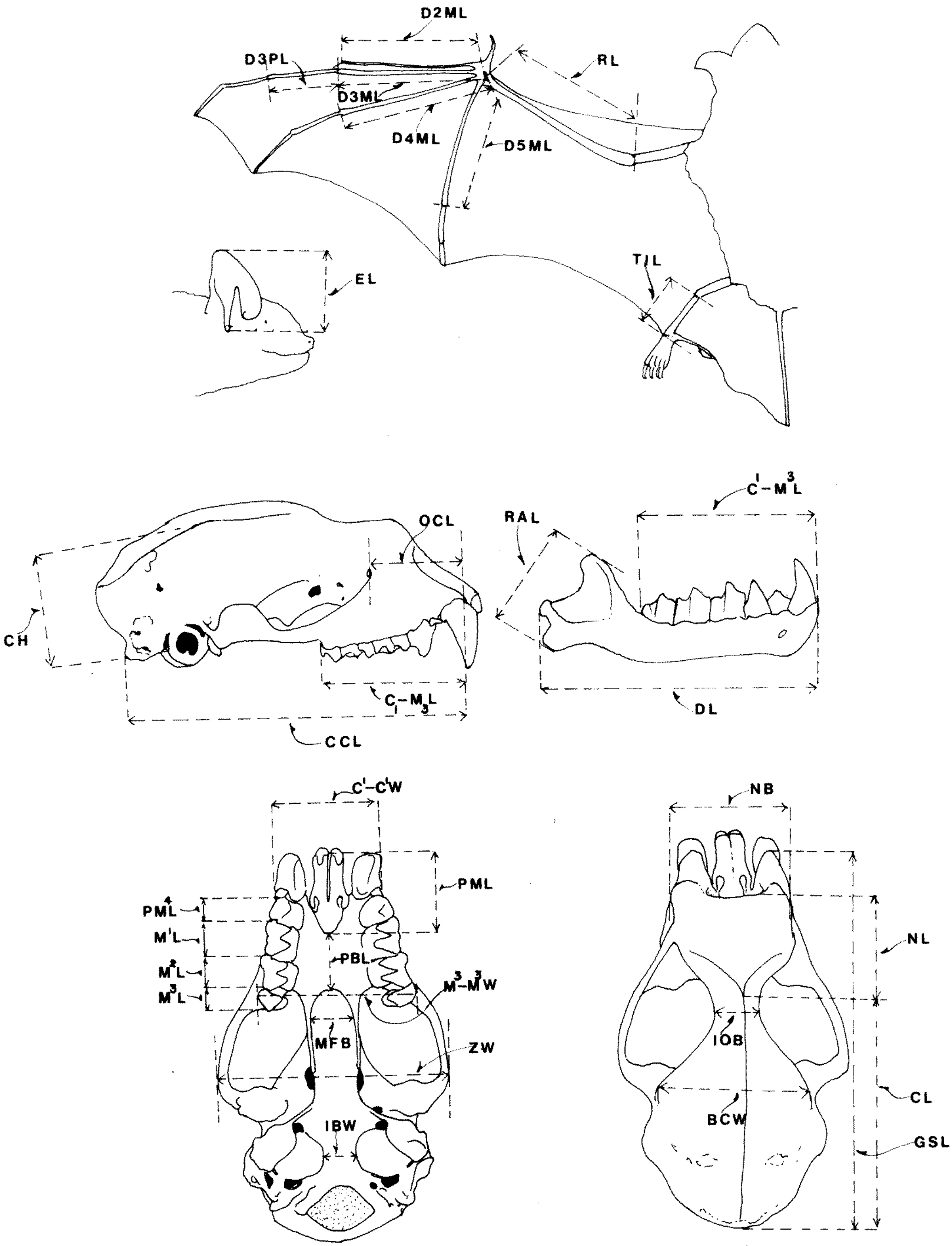
We examined specimens representative of the following taxa *sensu* Hill (1963): *H. d. masoni; H. d. griseus; H. d. pullatus; H. d. oceanitis; H. d. reginae; H. d. demissus* and *H. d. inornatus*. The distribution of these specimens is shown in Figure 1. Additionally we examined specimens of other principal species in the *H. diadema* group of Hill (1963) (*H. dinops; H. lankadiva* and *H. commersoni*). From our examination of these specimens and of the literature we consider the forms *demissus* and *inornatus*, are not closely related to the other subspecies of *H. diadema*. For this reason the small *demissus* and *inornatus* forms are not included in this paper.

To denote the institutional origins of specimens their catalogue numbers are prefixed by the following abbreviations:

WAM : Western Australian Museum, Perth
MZB : Museum Zoologicum Bogoriense (Balitbang Zoologi), Bogor
AM : Australian Museum, Sydney
JM : Queensland Museum, Brisbane
AMNH : American Museum of Natural History, New York
FMNH : Field Museum of Natural History, Chicago
S : Smithsonian Institute, Washington

Morphometric Analyses

Sexual dimorphism was analysed by MANOVA and ANOVA using a two factor analysis for measurements of skull and external characters separately for the factors: island groupings, and sex.


D2ML
D3PL
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D4ML
D5ML
RL
EL
TIL
C^1-M^3L
OCL
RAL
CH
C_1-M_3L
CCL
DL
C^1-C^1W
PML
PM^4L
M^1L
M^2L
M^3L
PBL
M^3-M^3W
MFB
ZW
IBW
NB
NL
IOB
BCW
CL
GSL

◀ **Figure 1** Skull and external measurements referred to in text and their recording points. GSL — greatest skull length, posterior lambdoidal crest to maxilla at C^1 dorsal base; CCL — condylocanine length, condyle to maxilla at C^1 dorsal base; CL — cranial length, posterior sagittal crest to supraorbital bifurcation point; NL — nasal length, posterior supraorbital crest point to rostral swelling anterior median edge; NB — nasal breadth, at posterodorsal contact of zygomatic with rostral swelling; CH — cranial height; IBW — distance between cochlea; PBL — palatal bridge length; MFB — mesopterygoid fossa breadth; OCL —orbit to canine length, orbit anteromost point to maxilla at C^1 dorsal base; IOB —minimum interorbital breadth; ZW — zygomatic width; BCW —braincase breadth, at point above zygomatic junction with braincase; DL — dentary length, condyle to dentary distal tip; RAL — tip ascending ramus to tip angular process length; C^1-C^1W —width outside upper canines at alveoli; M^3-M^3W — width outside upper third molar cusps; C^1-M^3L and C_1-M_3L — upper and lower maxillary toothrow length, at alveoli; PM^4L — second upper premaxillary cusp length; M^1L, M^2l and M^3L — first to third upper molar cusp length; PML — premaxilla length; RL — radius length; D2ML to D5ML — digit 2 to 5, metacarpal lengths; D3PL — digit 3, phalanx 1 length; TIL — tibia length; EL — ear length and WT — weight.

Principal component analysis (using varimax rotation) and canonical variate (discriminant) analysis were performed on external characters (with males and females combined) and for skull characters (males and females separately).

A euclidian distance matrix was subjected to a hierarchical cluster analysis using the unweighted pair group method using arithmetic averages (UPGMA).

Several skull and external characters were excluded from the above analyses. This was because many specimens lacked values for these characters and consequently had they been included the number of cases available would have been sharply reduced. The excluded characters were weight and ear length. These measurements could not be accurately recorded from specimens prepared as 'cabinet skins'. Additionally the length of the premaxillary was excluded. It was recorded for general description purposes only. It could not be measured as precisely as other skull characters because it varied considerably in its curvature.

Variation in size of skull (males and females separate) and external (males and females combined) characters was examined in *H. diadema diadema* from Lombok, Sumbawa, Flores, Sumba, Roti, Savu and Timor Is. Ear length was included as a variable in these analyses because all specimens of *H. d. diadema* examined were "alcoholic" specimens. The principal component Factor 1 score was taken to represent overall size of skull and external characters and related to both latitude and longitude using a stepwise multiple regression analysis. Additionally, greatest skull length, radius length, and weight, representing specific measurements of size, were compared in the same way with latitude and longitude. All statistical procedures were carried out on a NEC 286 computer using the SPSS/PCL+K programme.

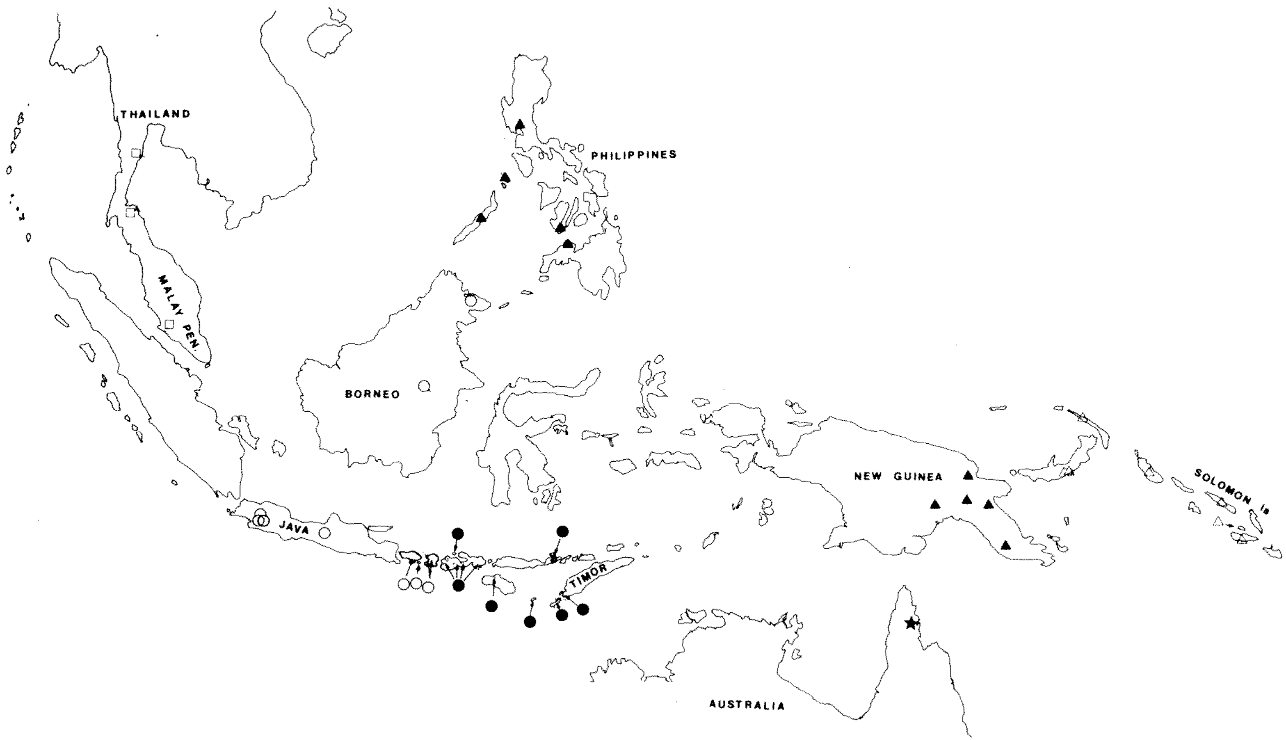


Figure 2 Location of specimens of *Hipposideros diadema* subspecies used in this study. *Hipposideros d. diadema* (●); *H. d. nobilis* (○), *H. d. griseus* (▲); *H. d. reginae* (★); *H. d. masoni* (□); and *H. d. oceanitis* (△).

Systematics

The specimens of *Hipposideros diadema* available to us from the Lesser Sunda Islands are resolved into two subspecies, *H. diadema diadema* (Geoffroy, 1813) from Sumbawa, Moyo, Flores, Sumba, Savu, Roti and Timor; *H. diadema nobilis* (Horsfield, 1823) from Borneo, Java, Bali, Nusa Penida and Lombok. We diagnose and describe these two subspecies against the following related subspecies, which we also redescribe: *H. d. griseus* (Meyen, 1833) from Philippines and Papua New Guinea; *H. d. oceanitis* Andersen, 1909 from the Solomon and adjacent islands (Ysabel, New Ireland, New Britain, Guadalcanal, Bougainville, Florida islands); *H. d. reginae* Troughton, 1937 from Queensland, Australia; and *H. d. masoni* (Dobson, 1872) from Peninsular Malaysia and Thailand.

Description of these forms is presented prior to the multivariate statistical analysis which in part assisted in their recognition.

Hipposideros diadema diadema (Geoffroy, 1813)

Table 1; Figures 3-9, 13-14

Rhinolophus diadema diadema Geoffroy [Saint-Hilaire] É. 1813 Sur un genre de chauve — souris, sous le nom de rhinolophes. Ann. Mus. Hist. Nat. Paris, 20: 263, pls 5,6.

Type: Paris Museum MHNP 918, skin with skull *in situ*, collected by Péron and Lesueur.

Type locality: Timor.

Specimens examined: (see Appendix 1)

Diagnosis

Hipposideros d. diadema differs from *H. d. nobilis* in having its anterior noseleaf larger; tibia shorter relative to ear length (Figure 3); canines smaller and more slender and teeth generally smaller. For example: ♂♂ C^1-M^3 length 11.5 (10.9-12.2) *v.* 12.3 (11.3-13.1); M^2 length 2.7 (2.2-3.2) *v.* 3.0 (2.7-3.3) and ♀♀ C^1-M^3 11.2 (10.4-11.6) *v.* 11.9 (11.0-12.5); M^2 length 2.8 (2.3-3.1) *v.* 3.0 (2.7-3.2). Maxillary tooth rows generally closer together relative to greatest skull length (Figure 6a, b); cranium generally shorter relative to nasal length (Figure 7a, b); zygomatic width generally narrower relative to nasal length (Figure 8a, b).

It differs from *H. d. griseus* in averaging larger in all external and skull measurements (Table 1); nasal breadth absolutely larger: ♂♂ 9.5 (9.0-10.0) *v.* 8.5 (8.1-8.9) and ♀♀ 9.5 (9.1-9.9) *v.* 8.4 (7.9-9.0); nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. reginae* by averaging larger in all external measurements (Table 1), e.g., radius length 85.9 (81.7-90.2) *v.* 81.2 (74.1-84.5); tibia length 34.4 (31.4-36.7) *v.* 29.8 (27.4-31.5); ear longer relative to radius length (Figure 4); tibia longer relative to metacarpal 3 length (Figure 5); molar rows generally narrower closer together relative to greatest skull length (Figure 6a, b).

It differs from *H. d. masoni* in that the tibia averages longer 34.4 (31.4-36.7) *v.* 31.4 (29.7-33.1); ear averages longer 32.1 (30.0-34.6) *v.* 27.0 (25.2-28.2); tibia longer relative

Figures (3-12) Univariate plots of external (males and females combined) and skull characters (**a**, male and **b**, female) adult *Hipposideros diadema*. Code for *H. diadema* subspecies as for Figure 2.

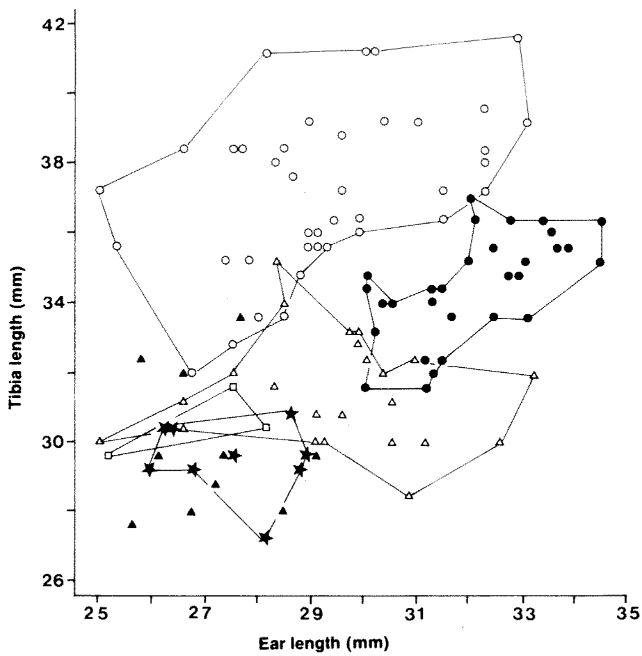


Figure 3 — tibia length v. ear length.

to metacarpal 3 length (Figure 5); ear longer relative to radius length (Figure 4); distance between molar rows further apart relative to cranial length (Figure 10 a, b). In ♀♀ only zygomatic width smaller relative to nasal length (Figure 8b).

It differs from *H. d. oceanitis* in that it averages larger in almost all external and skull measurements and weight (Table 1), e.g., radius length 85.9 (81.7-90.2) *v.* 76.5 (71.7-80.4), metacarpal 4 length 61.6 (57.8-64.8) *v.* 54.0 (48.7-56.9); greatest skull length ♂♂ 30.5 (29.1-31.5) *v.* 28.9 (26.4-29.9) and ♀♀ 30.0 (28.7-31.5) *v.* 29.1 (28.5-30.1); C^1-M^3 length, ♂♂ 11.5 (10.9-12.2) *v.* 10.7 (9.6-11.3) and ♀♀ 11.2 (10.4-11.6) *v.* 10.7 (10.0-11.2); three rather than two large supplementary leaflets on nose; radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); nasals wider relative to their length (Figure 9a, b).

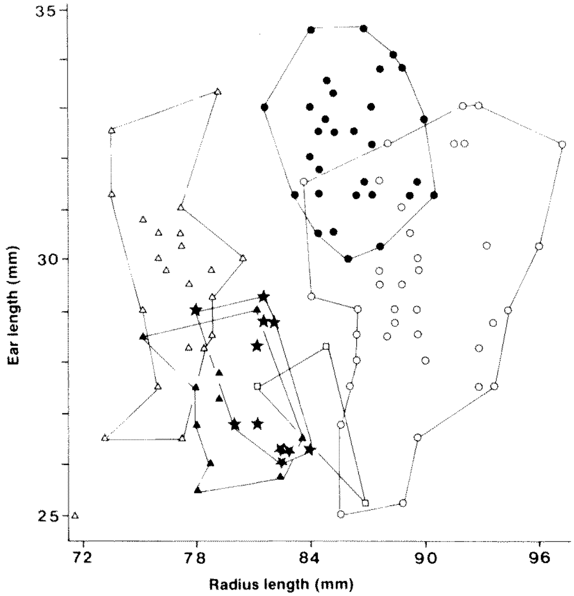


Figure 4 — ear length **v.** radius length.

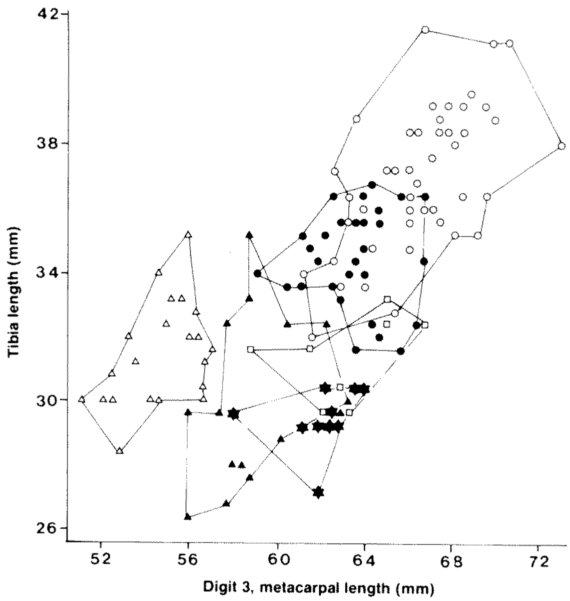


Figure 5 — tibia length **v.** metacarpal length, digit 3.

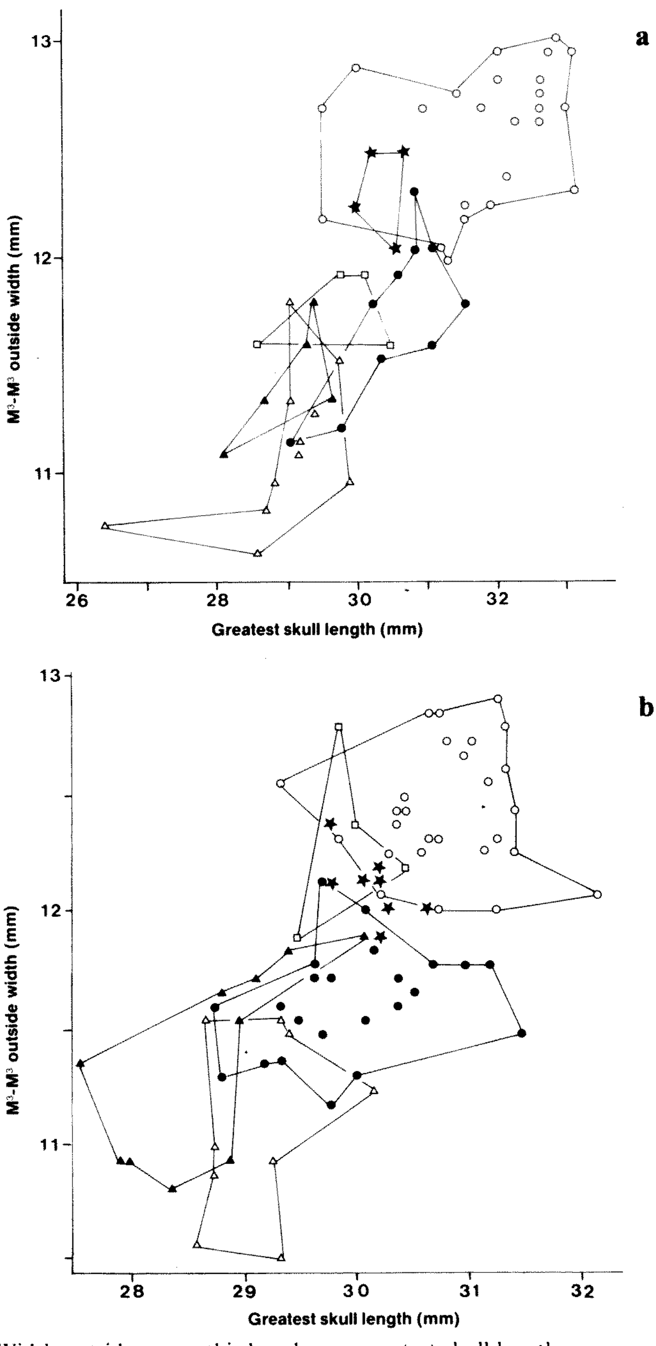


Figure 6a, b — Width outside upper third molars *v*. greatest skull length.

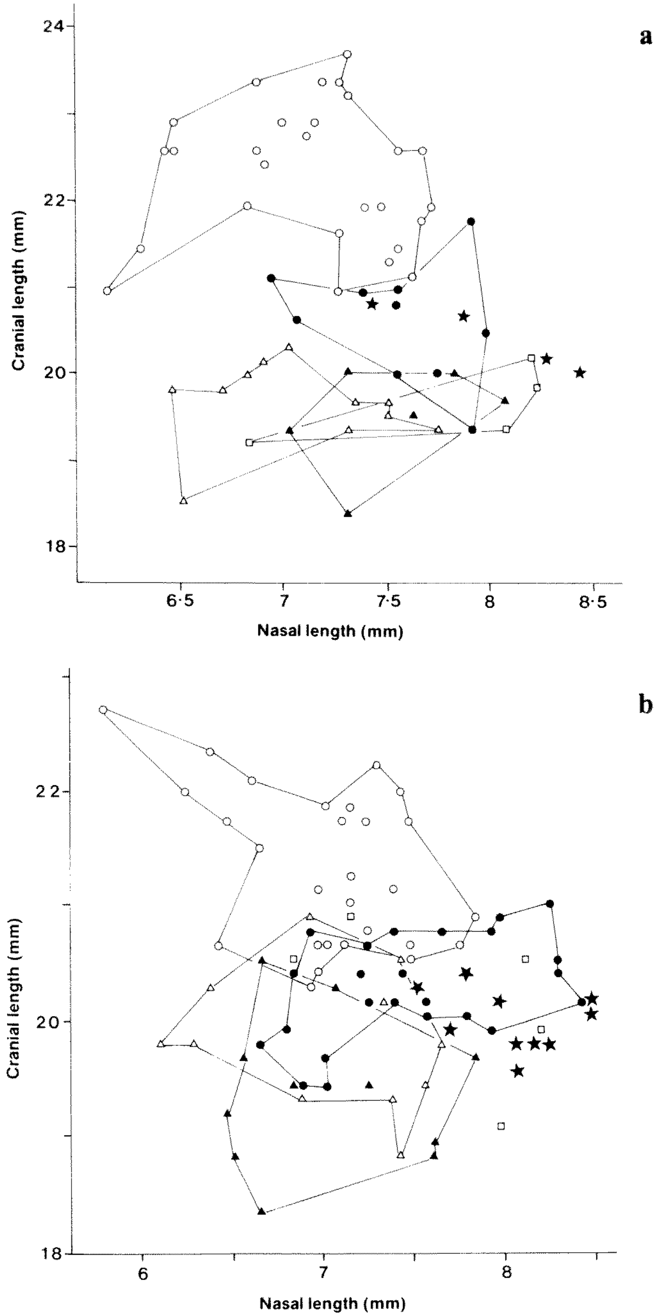


Figure 7a, b — cranial length *v.* nasal length.

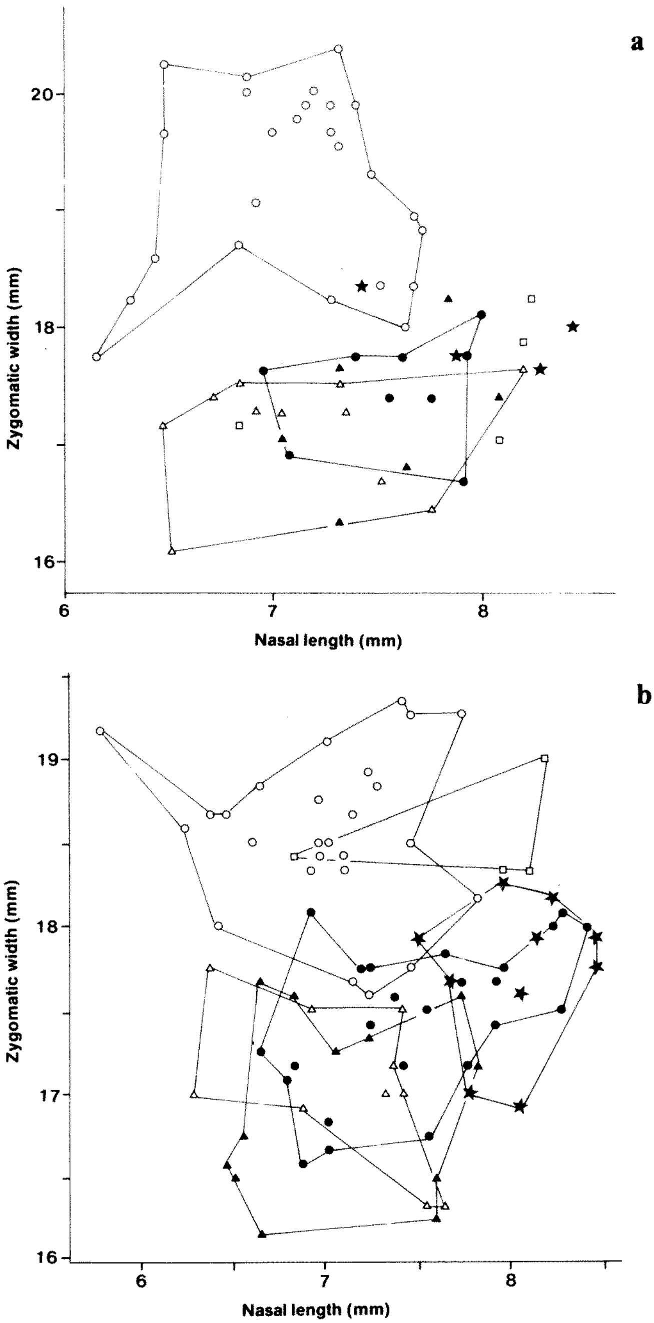


Figure 8a, b — zygomatic width *v.* nasal length.

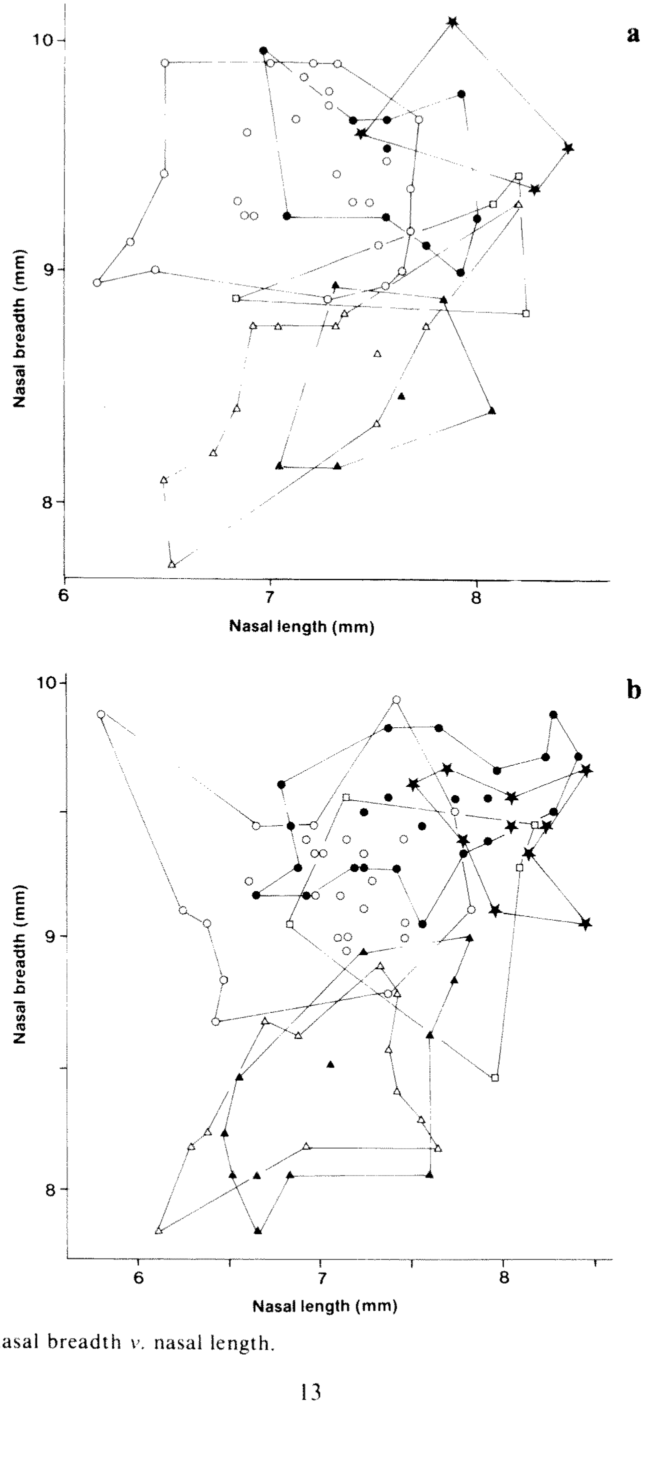


Figure 9a, b — nasal breadth *v.* nasal length.

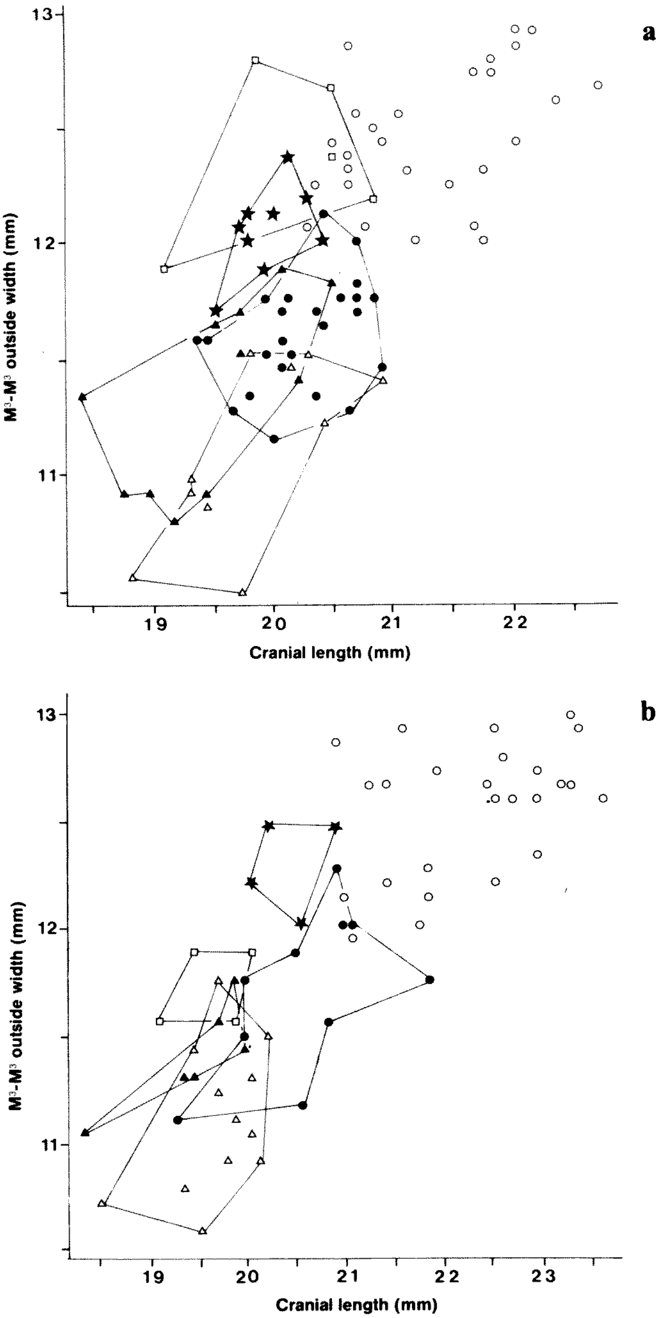


Figure 10a, b — width outside upper third molars *v.* cranial length.

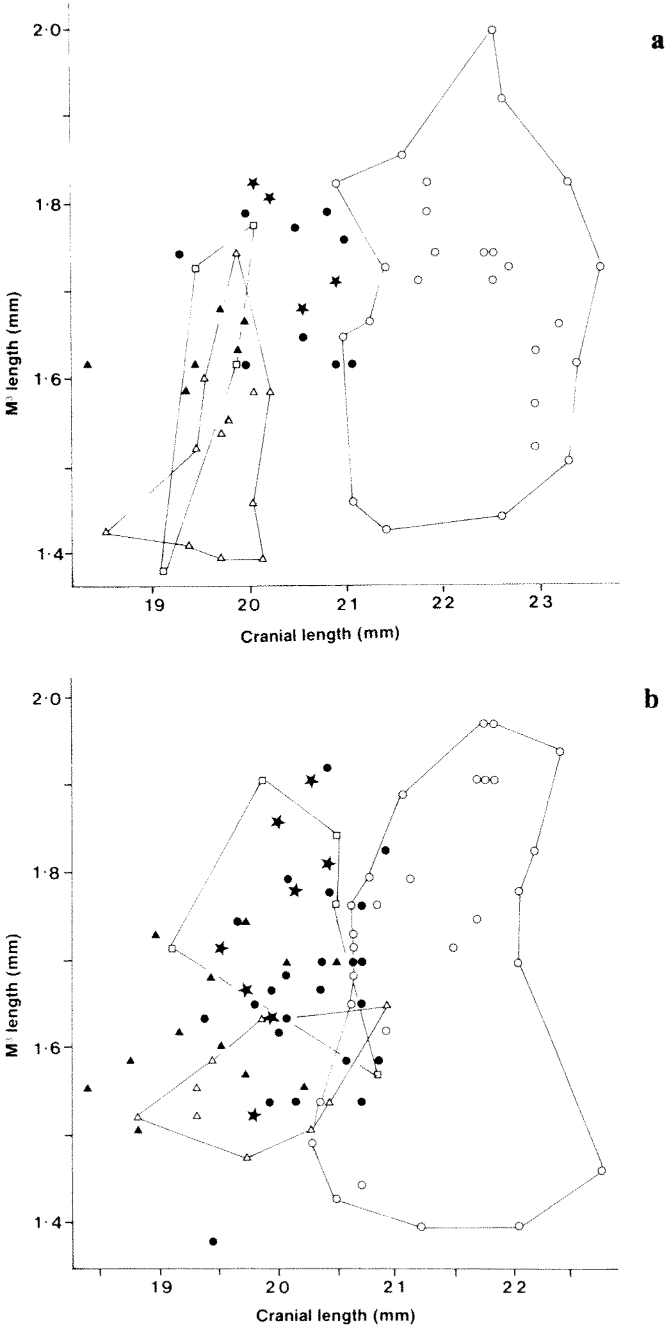


Figure 11a, b M³ length *v.* cranial length.

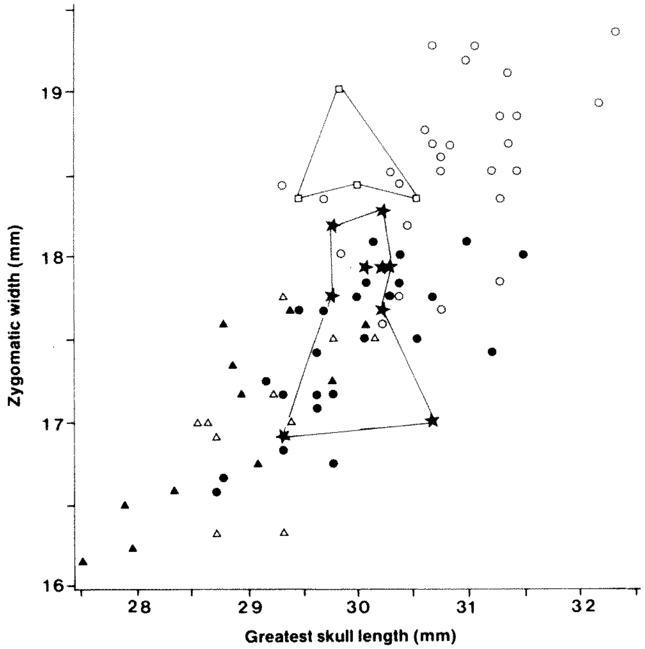


Figure 12b — zygomatic width *v.* greatest skull length.

Description

Externals (Table 1, Figures 3, 4, 5).

Moderately heavy (29.5-60.0) with moderately long forearm (81.7-90.2) and metacarpal 2-5 length; tibia moderately long (31.4-36.7); ear long (30.0-34.6) broad at base and sharply pointed with posterior margin behind the tip very gently concave; noseleaf well developed with three large supplementary leaflets (sometimes divided) always present; usually a fourth small leaflet present; anterior leaf large, greatest width up to 12, reaching anteriorly to distal point of lip, no anterior median emargination but usually this margin slightly scalloped and with a tiny median fleshy anterior projection; internarial septum very slightly thickened anteriorly but not inflated; narial lappets large, margins scalloped, when bent mesially will cover at least three-quarters of nostril opening; nostrils slightly pocketed; intermediate leaf expanded vertically to *c.* 6, prominent median keel terminating at apex to slight to obvious moderately sharp projection flanked laterally by two lower evenly curved projections, slightly narrower (*c.* 9 wide) than anterior leaf; posterior leaf slightly wider (*c.* 13) than anterior leaf, projects well above intermediate leaf, upper edge semicircular with faint gently arched median section sometimes apparent, supported by distinct median septum and two weak lateral septa.

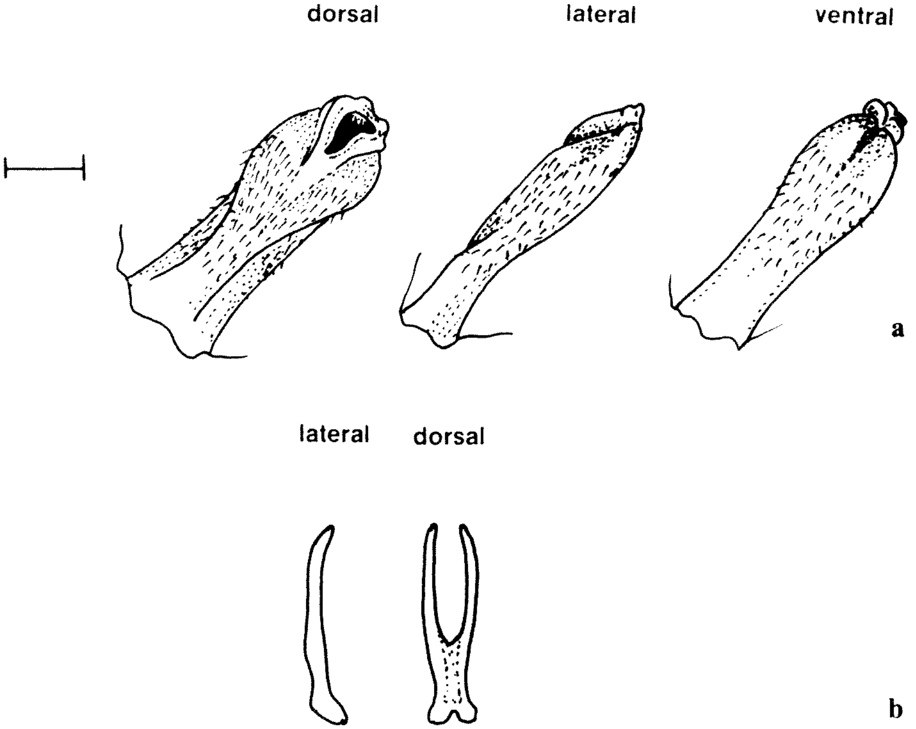


Figure 13 (**a**) Dorsal, lateral and ventral view of glans penis, with prepuce removed, of *H. d. diadema* from SW Timor (WAM M38086). (**b**) dorsal and lateral view of baculum of WAM M38086. Scale line 2 mm.

Pelage

Pelage with distinct colour pattern that is similar in specimens collected from throughout its range. Hair of face, rostrum, chin, throat, top of head, neck and shoulders, and occasionally as a mantle reaching to lumbar region a pale Vinaceous-Buff (light buff) to Wood Brown (pale brown); this colour from distal parts of hair, whereas basal half of hair a darker Buffy Brown to Olive Brown. Remainder of dorsum a contrastingly darker colour ranging from Snuff Brown (light-orange brown) to Clove Brown (dark brown); these hairs tricoloured with basal one-third same colour as distal parts; the middle part similar in colour to shoulder mantle. Pale wide Cartridge Buff to Pale Olive Buff stripe along each dorsal lateral margin in contact with plagiopatagium from femur almost to humerus. A tuft of hair coloured as for the lateral stripe present at both anterior and posterior base of humerus. Occasionally distinct spots or a marbled appearance occur on lower dorsum; these are also same colour as lateral stripe. On ventral surface paler hairs at base of humerus merge to form distinct lateral patches which occasionally spread almost to top of chest. Abdomen and majority of chest a darker colour ranging from Avellaneous (pale pink brown) to Brownish Olive. Usually paler fur of middle part of hair, which approximate colour of chin, emerges on abdomen to produce a marbled effect.

Penis and Baculum

Penis *c.* 9 long; prepuce covered with long hairs which exceed distal end by up to 3; prepuce opening distal; preputial sheath connects to glans base about 4.5 from distal end, glans dorsoventrally flattened (Figure 13a); urethral groove anterodorsal with low lateral lips which have two slight distal protuberances; small spines cover middle section of glans.

Baculum with shape of tuning fork; bifurcating distal arms connect a fragile base (*c.* 0.7 wide) which is about one third the total length (*c.* 2.6) (Figure 13b). These distal arms support lips of urethral groove.

Skull, dentary, dentition (Table 1, Figure 14a)

Moderate length skull (28.7-31.5) with well developed sagittal and lamboidal crests; supraorbital ridges extending forward from anterior point of sagittal crest usually poorly but occasionally moderately well developed, terminating anteriorly at posterolateral margin of rostrum occasionally as a low protuberance; posterior triangle of supraorbital ridge encloses shallow frontal depression; rostrum profile slightly rounded from dorsal aspect; rostral swelling with moderately inflated paired eminences on either side separated by shallow groove, anterior eminences approximately twice surface area of posterior ones, occasionally also low small lateral eminence obvious; zygomatic width moderate (16.6-18.7); mastoid large squarish in dorsal profile, minimum orbital distance moderate (3.3-3.9); premaxilla level with or slightly exceeding canine anterior edge; premaxilla ventral junction with maxilla U-V shaped; anterior palatal foramina slit-like, enclosed within premaxilla or occasionally anterior edge of maxilla closing posterior edge of foramina; mesopterygoid fossa moderately wide (3.3-4.2); sphenoid bridge partially, and occasionally completely, obscuring large sphenorbital foramen when viewed from ventral aspect; median pterygoid groove slight, vomer occasionally projects slightly posterior of postpalatal margin; pterygoids, moderately long, base wide; cochlea width exceeds distance between cochlea; I^1 bilobed, outer lobe reduced, inner lobe taller sharply sloping mesially; upper incisors occasionally in contact, C^1 moderate size, base moderately wide, internal cingulum moderate but does not form an anterior basal cusplet, occasionally a minute posterior basal cusplet; PM^2 moderately large, separates C^1 from PM^4, slightly extruded and nestles in posterior notch of C^1; PM^4 large, encircled by slight to moderate cingulum, usually with cusplet on mid-point of lingual cingulum; M^{1-2} with moderately developed protocone with its posterior edge in contact with metacone base, hypocone moderate, slight internal cingulum; toothrows close together (M^3-M^3W 11.1-12.3), M^3 posterior cusp obsolescent, approximately one-third only of prematacristid present; I_1 bilobed, outer lobe two-thirds crown area of inner lobe; I_2 trilobed, crown area twice that of I_1; C_1 moderately large, cingulum moderately well developed, forms miniscule posterobasal cusplet; PM_2 buccal area almost diamond shaped, two-thirds that of PM_4, PM_4 cusp posterointernal ridge with slight to moderate basal cusp, encircled by moderate cingulum as is M_{1-3}; dentary robust, ventral edge below toothrow slightly arched beneath M_3 then horizontal to PM_2, usually moderately arched ventrally below C_1 (only very slightly in M35210-Savu) to form a keel before rising gently to base of incisors; ascending ramus broadly triangular, erect, angular process broadly rectangular and terminates lateral to condyloid process.

Hipposideros diadema nobilis (Horsfield, 1823)

Table 1; Figures 3-9, 11 and 14

Rhinolophus nobilis Horsfield, T. 1823. Zoological researches in Java and the neighbouring islands, London No. 6, Pl. vii.

Hipposideros diadema vicarius Andersen, K. 1905. On *Hipposideros diadema* and its closest allies. Ann. Mag. nat. Hist. (7) 16: 499, Sarawak.

Types: Two "co-types", skins, in British Museum, Natural History, BM 79.11.21.83.

Type locality: Java.

Specimens examined (see Appendix 1).

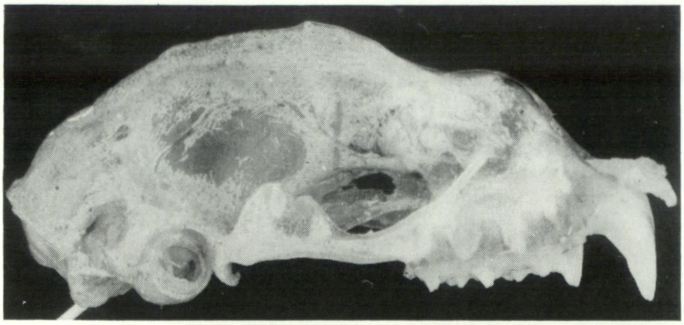
Diagnosis

Hipposideros d. nobilis differs from *H. d. diadema* in having its anterior noseleaf smaller; tibia longer relative to ear length (Figure 3), its canines larger and more robust and teeth generally larger. For example, ♂♂ C^1-M^3 length 12.3 (11.3-13.1) *v.* 11.5 (10.9-12.2); M^2 length 3.0 (2.7-3.3) *v.* 2.7 (2.2-3.2) and ♀♀ C^1-M^3 11.9 (11.0-12.5) *v.* 11.2 (10.4-11.6); M^2 length 3.0 (2.7-3.2) *v.* 2.8 (2.3-3.1); molar tooth rows generally further apart relative to greatest skull length (Figure 6a, b); cranium generally longer relative to nasal length (Figure 7 a, b); zygomatic width relative to nasal length generally larger (Figure 8a, b).

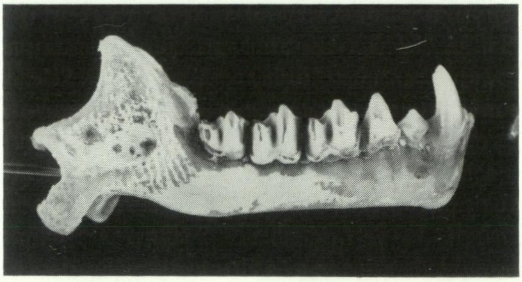
It differs from *H. d. griseus* in having its anterior noseleaf relatively smaller; external and skull measurements and weight averaging larger (in some cases without overlap); (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 79.2 (71.6-85.6); tibia length 36.5 (30.1-41.8) *v.* 30.3 (26.5-35.1); ear length 29.3 (25.0-33.1) *v.* 27.1 (25.5-29.1); greatest skull length ♂♂ 31.9 (29.5-33.2) *v.* 29.1 (28.0-29.6) and ♀♀ 30.8 (29.3-32.3) *v.* 28.7 (27.5-30.1); C^1-M^3 ♂♂ 12.3 (11.3-13.1) *v.* 10.7 (10.3-11.0) and ♀♀ 11.9 (11.0-12.5) *v.* 10.8 (10.2-11.4); cranium longer relative to nasal length (Figure 7 a, b), nasals wider relative to their length (Figure 9 a, b).

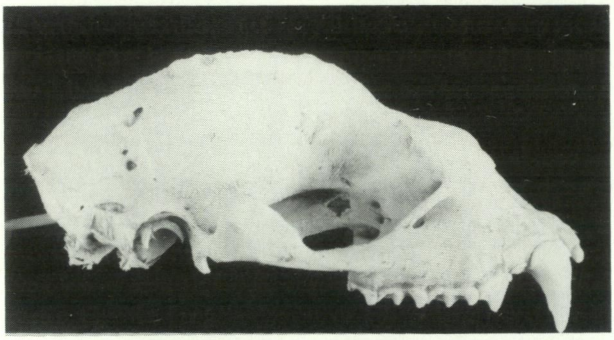
It differs from *H. d. reginae* in having its anterior noseleaf relatively smaller; averaging larger in all external measurements (Table 1) e.g., radius length 88.3 (76.9-97.0) *v.* 81.2 (74.1-84.5) and tibia length 36.5 (30.1-41.8) *v.* 29.8 (27.4-31.5); tibia longer relative to ear length (Figure 3); radius longer relative to ear length (Figure 4);

Figure 14 Dorsal, ventral and lateral view of skull and dentary of adult female (**a**) *Hipposideros diadema diadema* (WAM 38080, Timor; (**b**) *H. d. nobilis* (WAM 30022, Java).

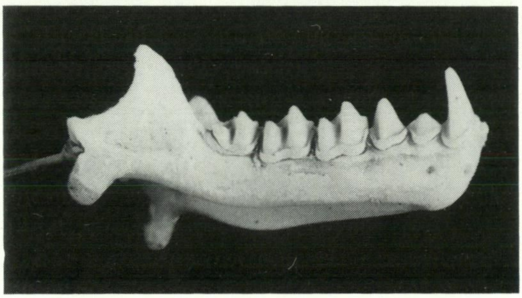


a





b



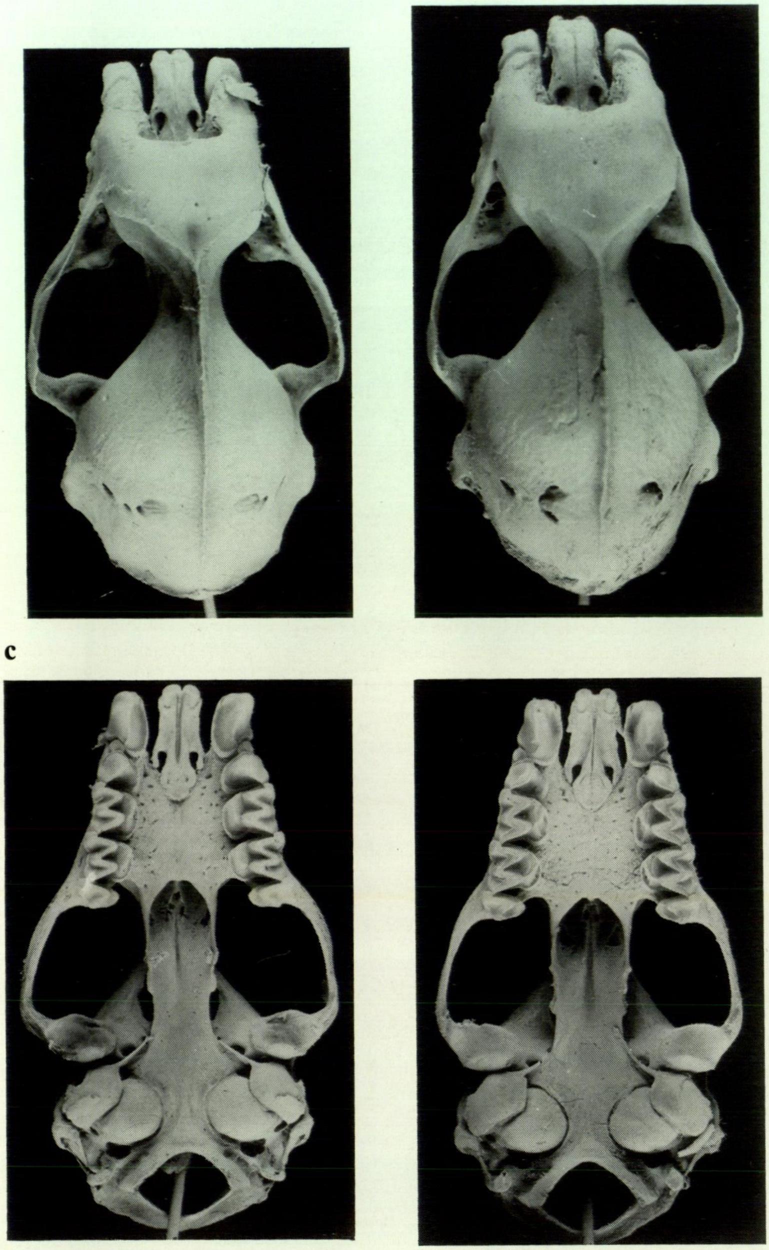
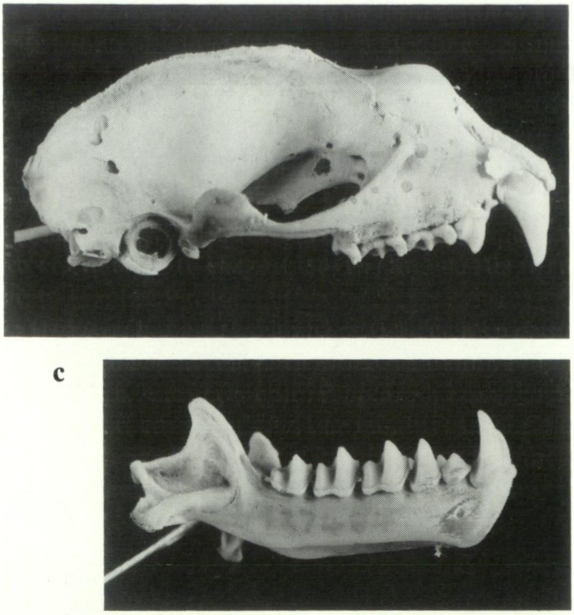
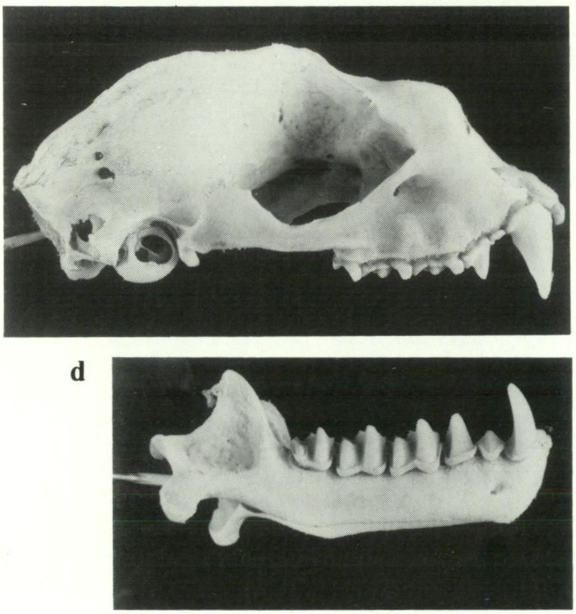


Figure 14 (cont.) Dorsal, ventral and lateral view of skull and dentary of adult female (**c**) *H. d. griseus* (WAM 27484, Papua New Guinea), (**d**) *H. d. reginae* (JM 2453, Queensland).



c



d

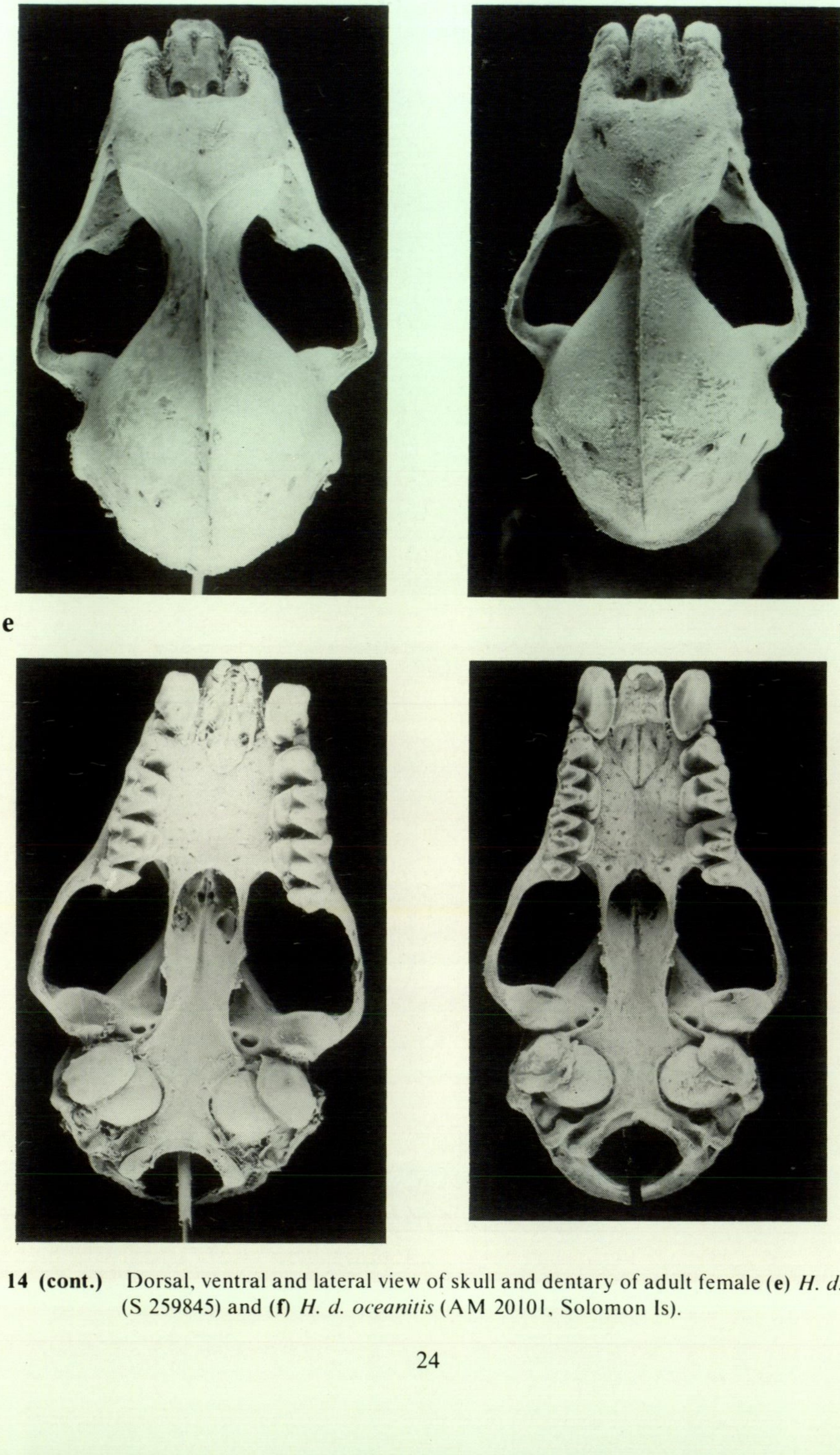
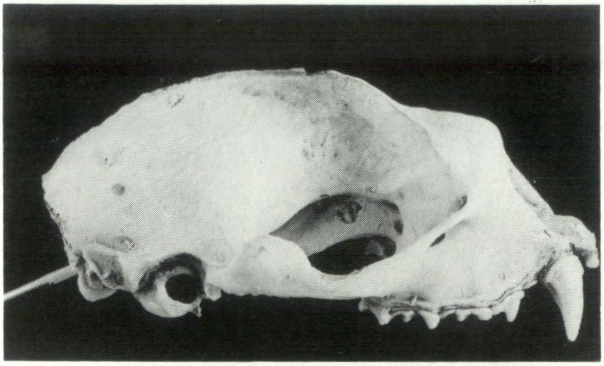
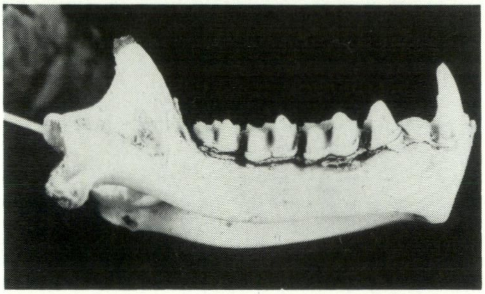
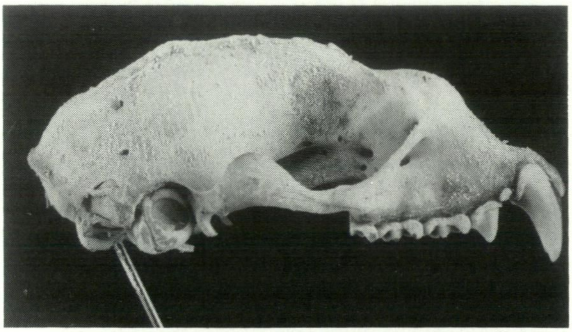


Figure 14 (cont.) Dorsal, ventral and lateral view of skull and dentary of adult female (**e**) *H. d. masoni* (S 259845) and (**f**) *H. d. oceanitis* (AM 20101, Solomon Is).

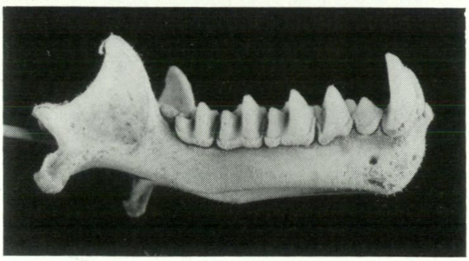


e





f



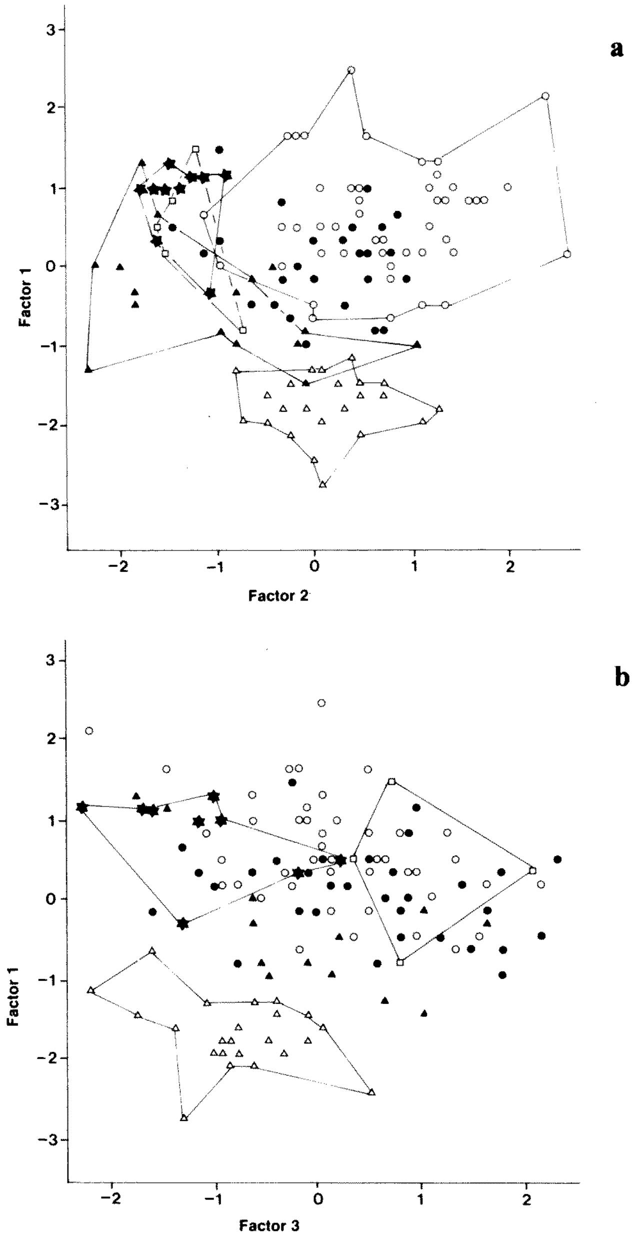


Figure 15 Principal component analysis based on external measurements of *Hipposideros diadema* specimens used in this study. (**a**) Factor 1 *v.* 2 and (**b**) Factor score 1 *v.* 3. Subspecies symbols as for Figure 2.

tibia longer relative to metacarpal 3 length (Figure 5). Most skull, dental and dentary characters average larger, e.g., greatest skull length ♂♂ 31.9 (29.5-33.2) v. 30.4 (30.0-30.7) and ♀♀ 30.8 (29.3-32.3) *v*. 30.0 (29.3-30.7); C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v*. 11.6 (11.3-11.8) and ♀♀ 11.9 (11.0-12.5) v. 11.4 (11.0-11.7); nasals shorter relative to their breadth (Figure 9a, b).

It differs from *H. d. masoni* in having its anterior noseleaf relatively smaller; averages larger in all external measurements (Table 1) e.g., radius length 88.3 (76.9-97.0) *v*. 85.0 (80.2-90.2); tibia longer relative to both ear length (Figure 3) and metacarpal 3 length (Figure 5). Most skull and dental measurements (except minimum interorbital distance and nasal length) average larger (Table 1) e.g., C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v*. 11.5 (11.2-11.7) and ♀♀ 11.9 (11.0-12.5) v. 11.6 (11.4-12.0); molar rows further apart relative to greatest skull length (Figure 6a, b); cranial length greater relative to M^3 length (Figure 11a, b).

It differs from *H. d. oceanitis* in having its anterior noseleaf relatively smaller; three rather than two large supplementary nose leaflets; averages much heavier 50.9 (40.0-67.0) *v*. 36.4 (30.2-42.0); larger in all external measurements, often with no overlap (Table 1) e.g., radius length 88.3 (76.9-97.0) *v*. 76.5 (71.7-80.4), tibia length 36.5 (30.1-41.8) *v*. 31.5 (28.6-35.0); tibia longer relative to ear length (Figure 3); radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); larger in all skull measurements (Table 1), e.g., greatest skull length ♂♂ 31.9 (29.5-33.2) *v*. 28.9 (26.4-29.9) and ♀♀ 30.8 (29.3-32.3) *v*. 29.1 (28.5-30.1); C^1-M^3 length ♂♂ 12.3 (11.3-13.1) *v*. 10.7 (9.6-11.3) and ♀♀ 11.9 (11.0-12.5) *v*. 10.7 (10.0-11.2); molar rows wider apart relative to greatest skull length (Figure 6a, b); nasals wider relative to their length (Figure 9a, b); cranial length greater relative to M^3 length (Figure 11 a, b); zygomatic width larger relative to nasal length (Figure 8a, b).

Description

Externals (Table 1, Figures 3, 4, 5)

Heaviest of subspecies considered (40.0-67.0); wing dimensions largest of subspecies with radius 76.9-97.0 and metarcapal digit 5 51.6-62.8; tibia large (30.1-41.8); ear length moderate (25.0-33.1); anterior noseleaf tends to be narrower than *H. d. diadema* (up to 10) and does not project as far anteriorly; posterior leaf with weak median septum and two faint lateral septa. Other descriptions as for *H. d. diadema*.

Pelage

Pattern of colouration similar to *H. d. diadema* but in some specimens the pale lateral dorsal stripe and pale ventral patch at base of humerus indistinct or absent. Also paler area on head and mantle considerably reduced. There is considerable colour variation even on a single island. For example, on Lombok I. predominant darker dorsal colours range from orange brown to dark sepia while lighter colours range from pale cream to dark buff.

Table 1 Measurements, in mm, (see Figure 1 caption for code to characters) for adult *H. diadema diadema; H. d. nobilis; H. d. griseus; H. d. reginae; H. d. masoni; H. d. oceanitis*. N, sample size; X, mean; SD, standard deviation; MIN, minimum; MAX, maximum (a) skull characters (males and females separate); (b) external characters (males and females combined).

Table 1a Males		GSL	CCL	CL	NL	NB	CH	IBW	PBL	MFB	OCL	IOB	ZW
H. d. diadema	N	11	10	11	11	11	11	11	11	11	11	11	11
	X	30.5	27.3	20.6	7.6	9.5	8.2	2.3	5.2	3.7	7.5	3.6	17.6
	SD	0.68	0.69	0.68	0.33	0.31	0.34	0.22	0.42	0.3	0.38	0.2	0.55
	MIN	29.1	25.9	19.3	6.9	9.0	7.7	2.0	4.5	3.3	7.1	3.3	16.7
	MAX	31.5	28.1	21.8	8.0	10.0	8.7	2.7	6.1	4.2	8.4	3.9	18.7
H. d. nobilis	N	27	26	27	27	27	27	27	27	27	27	27	27
	X	31.9	28.3	22.3	7.1	9.4	8.5	2.7	5.7	3.6	8.0	3.4	19.2
	SD	1.01	0.80	0.80	0.45	0.34	0.33	0.28	0.52	0.30	0.52	0.21	0.85
	MIN	29.5	26.3	20.9	6.2	8.9	8.0	2.2	4.5	2.9	6.4	3.1	17.5
	MAX	33.2	29.5	23.6	7.7	9.9	9.6	3.2	7.4	4.2	8.7	4.0	20.5
H. d. griseus	N	6	6	6	6	6	6	6	6	6	6	6	6
	X	29.1	25.5	19.5	7.5	8.5	7.7	2.3	4.8	3.4	6.7	3.5	17.3
	SD	0.59	0.44	0.58	0.39	0.33	0.31	0.28	0.30	0.18	0.24	0.31	0.66
	MIN	28.0	24.7	18.4	7.0	8.1	7.3	1.8	4.3	3.1	6.4	3.1	16.4
	MAX	29.6	26.0	20.0	8.1	8.9	8.2	2.6	5.2	3.7	6.9	3.9	18.3
H. d. reginae	N	4	4	4	4	4	4	4	4	4	4	4	4
	X	30.4	27.4	20.4	8.0	9.6	8.2	2.7	5.3	3.7	7.4	3.8	18.0
	SD	0.31	0.38	0.36	0.45	0.31	0.11	0.26	0.26	0.08	0.34	0.19	0.35
	MIN	30.0	26.9	20.1	7.4	9.4	8.0	2.4	5.0	3.6	7.0	3.6	17.6
	MAX	30.7	27.7	20.9	8.5	10.1	8.2	3.0	5.6	3.7	7.8	4.0	18.4
H. d. oceanitis	N	12	11	12	12	12	11	11	12	11	12	12	11
	X	28.9	25.5	19.7	7.2	8.6	8.0	2.5	5.4	3.4	6.7	3.5	17.1
	SD	0.89	0.78	0.46	0.52	0.41	0.38	0.20	0.62	0.17	0.43	0.18	0.51
	MIN	26.4	23.6	18.6	6.5	7.8	7.4	2.3	4.9	3.0	5.8	3.1	16.0
	MAX	29.9	26.5	20.3	8.2	9.3	8.5	2.9	6.5	3.7	7.5	3.8	17.6
H. d. masoni	N	4	4	4	4	4	4	4	4	3	4	4	4
	X	29.7	26.5	19.6	7.8	9.1	8.1	2.5	5.2	3.6	7.4	3.6	17.6
	SD	0.86	0.43	0.43	0.67	0.29	0.44	0.22	0.53	0.04	0.42	0.50	0.57
	MIN	28.5	26.0	19.1	6.8	8.8	7.5	2.2	4.5	3.6	7.0	2.9	17.1
	MAX	30.5	27.0	20.1	8.3	9.4	8.5	2.8	5.8	3.6	8.0	4.0	18.2

Table 1a Males (cont.)

		BCW	DL	RAL	C^1-C^1W	M^3-M^3W	C^1-M^3L	C_1-M_3L	PM^4L	M^1L	M^2L	M^3L	PML
H. d. diadema	N	11	11	11	11	11	11	11	11	11	11	11	11
	X	12.0	22.6	9.4	8.1	11.7	11.5	13.9	2.2	2.8	2.7	1.7	6.6
	SD	0.44	0.58	0.33	0.26	0.36	0.37	0.30	0.26	0.16	0.33	0.08	0.44
	MIN	11.2	21.8	8.9	7.8	11.1	10.9	13.5	1.8	2.5	2.2	1.6	6.0
	MAX	12.6	23.3	9.9	8.6	12.3	12.2	14.4	2.6	2.9	3.2	1.8	7.2
H. d. nobilis	N	27	27	27	27	26	27	27	27	27	27	27	27
	X	12.5	23.9	9.9	8.5	12.6	12.3	14.9	2.4	3.1	3.0	1.7	6.9
	SD	0.52	0.73	0.57	0.46	0.30	0.44	0.44	0.20	0.13	0.15	0.14	0.47
	MIN	11.5	21.8	9.0	7.6	11.9	11.3	14.0	2.0	2.8	2.7	1.4	6.0
	MAX	13.4	24.8	11.5	9.2	13.0	13.1	15.6	2.8	3.3	3.3	2.0	7.8
H. d. griseus	N	6	6	6	6	6	6	6	6	6	6	6	6
	X	11.6	21.3	9.2	7.5	11.4	10.7	13.1	2.0	2.7	2.7	1.6	6.2
	SD	0.78	0.50	0.50	0.28	0.24	0.27	0.21	0.15	0.1	0.12	0.04	0.21
	MIN	10.4	20.8	8.3	7.0	11.1	10.3	12.9	1.7	2.5	2.5	1.6	6.0
	MAX	12.7	22.0	9.8	7.8	11.8	11.0	13.5	2.1	2.8	2.9	1.7	6.5
H. d. reginae	N	4	3	4	3	4	4	3	4	4	4	4	4
	X	11.9	22.5	9.2	8.0	12.3	11.6	13.9	2.0	2.9	2.9	1.8	6.7
	SD	0.28	0.83	0.21	0.09	0.25	0.23	0.45	0.14	0.16	0.17	0.07	0.26
	MIN	11.6	21.6	9.0	8.0	12.0	11.3	13.5	1.9	2.7	2.6	1.7	6.4
	MAX	12.2	23.3	9.5	8.1	12.5	11.8	14.4	2.2	3.0	3.0	1.8	6.9
H. d. oceanitis	N	11	12	12	12	12	12	12	12	12	12	12	12
	X	11.9	21.3	9.2	7.4	11.1	10.7	13.1	1.9	2.7	2.7	1.5	5.7
	SD	0.31	0.69	0.46	0.35	0.35	0.49	0.44	0.14	0.19	0.15	0.10	0.63
	MIN	11.4	19.6	8.4	7.0	10.6	9.6	12.1	1.7	2.5	2.3	1.4	4.7
	MAX	12.4	22.1	9.8	8.2	11.8	11.3	13.6	2.2	3.1	2.9	1.7	6.6
H. d. masoni	N	4	4	4	4	4	4	4	4	4	4	4	4
	X	11.8	22.4	9.2	7.5	11.7	11.5	13.8	2.2	2.9	3.0	1.6	6.5
	SD	0.62	0.27	0.35	0.37	0.20	0.21	0.12	0.17	0.09	0.09	0.18	0.22
	MIN	11.0	22.1	8.9	7.0	11.6	11.2	13.7	2.0	2.8	2.9	1.4	6.2
	MAX	12.3	22.7	9.6	7.8	11.9	11.7	13.9	2.4	3.0	3.1	1.8	6.8

Table 1a Females		GSL	CCL	CL	NL	NB	CH	IBW	PBL	MFB	OCL	IOB	ZW
H. d. diadema	N	25	25	25	25	25	25	25	25	25	25	25	25
	X	30.0	26.8	20.3	7.5	9.5	8.2	2.4	5.0	3.6	7.2	3.8	17.5
	SD	0.69	0.62	0.42	0.52	0.23	0.32	0.16	0.24	0.24	0.34	0.18	0.46
	MIN	28.7	25.6	19.4	6.7	9.1	7.5	2.0	4.4	3.2	6.6	3.4	16.6
	MAX	31.5	28.1	21.0	8.4	9.9	8.8	2.6	5.6	4.3	7.9	4.0	18.1
H. d. nobilis	N	28	28	28	28	28	28	28	28	28	28	28	28
	X	30.8	27.4	21.3	7.0	9.2	8.3	2.7	5.5	3.6	7.7	3.5	18.6
	SD	0.66	0.63	0.68	0.46	0.29	0.33	0.22	0.32	0.29	0.43	0.24	0.49
	MIN	29.3	26.3	20.3	5.8	8.7	7.6	2.2	4.9	3.0	6.9	3.2	17.6
	MAX	32.3	28.9	22.7	7.8	10.0	9.3	2.9	6.1	4.1	8.6	3.9	19.4
H. d. griseus	N	12	12	12	12	12	11	12	12	12	12	12	12
	X	28.7	25.4	19.5	7.1	8.4	7.9	2.3	4.7	3.2	6.8	3.6	16.9
	SD	0.80	0.76	0.63	0.51	0.39	0.23	0.23	0.33	0.23	0.45	0.19	0.57
	MIN	27.5	24.6	18.4	6.5	7.9	7.5	2.0	4.2	2.8	6.3	3.3	16.1
	MAX	30.1	26.6	20.5	7.8	9.0	8.2	2.7	5.4	3.6	7.7	3.9	17.7
H. d. reginae	N	10	10	10	10	10	10	10	10	10	10	10	10
	X	30.0	26.8	20.0	8.0	9.4	8.1	2.5	5.4	3.6	7.2	3.9	17.7
	SD	0.39	0.49	0.28	0.31	0.21	0.21	0.24	0.56	0.11	0.22	0.18	0.44
	MIN	29.3	26.1	19.6	7.5	9.1	7.8	2.2	4.7	3.4	6.8	3.6	16.9
	MAX	30.7	27.4	20.5	8.5	9.7	8.4	2.9	6.7	3.8	7.5	4.1	18.3
H. d. oceanitis	N	11	11	11	12	12	11	12	12	11	12	12	10
	X	29.1	25.8	19.8	7.0	8.4	7.8	2.5	5.0	3.4	6.7	3.4	17.1
	SD	0.53	0.43	0.60	0.53	0.31	0.18	0.20	0.39	0.21	0.32	0.13	0.47
	MIN	28.5	25.0	18.8	6.1	7.9	7.6	2.2	4.6	3.2	6.0	3.2	16.3
	MAX	30.1	26.6	20.9	7.6	8.9	8.1	2.9	6.0	3.8	7.2	3.6	17.8
H. d. masoni	N	5	5	5	5	5	5	5	5	5	5	5	5
	X	30.1	26.8	20.2	7.7	9.2	8.1	2.6	4.9	3.6	7.4	3.9	18.6
	SD	0.44	0.61	0.69	0.61	0.44	0.18	0.24	0.35	0.24	0.19	0.12	0.33
	MIN	29.4	26.2	19.1	6.9	8.5	7.8	2.2	4.6	3.3	7.2	3.7	18.3
	MAX	30.5	27.6	20.9	8.2	9.6	8.3	2.9	5.4	3.9	7.7	4.0	19.0

Table 1a Females (cont.)

		BCW	DL	RAL	C^1-C^1W	M^3-M^3W	C^1-M^3L	C_1-M_3L	PM^4L	M^1L	M^2L	M^3L	PML
H. d. diadema	N	25	25	25	25	25	25	25	25	25	25	25	25
	X	11.9	22.0	9.2	7.9	11.6	11.2	13.6	2.2	2.8	2.8	1.7	6.8
	SD	0.38	0.57	0.38	0.30	0.25	0.29	0.26	0.18	0.13	0.20	0.11	0.36
	MIN	11.3	20.7	8.5	7.4	11.2	10.4	12.9	1.7	2.5	2.3	1.4	6.0
	MAX	12.6	23.1	10.0	8.3	12.1	11.6	14.0	2.4	3.1	3.1	1.9	7.3
H. d. nobilis	N	28	28	28	28	28	28	28	28	28	28	28	28
	X	12.1	23.0	9.5	8.2	12.4	11.9	14.4	2.3	3.0	3.0	1.7	6.6
	SD	0.48	0.52	0.37	0.35	0.28	0.35	0.39	0.23	0.12	0.14	0.18	0.35
	MIN	11.3	22.1	8.7	7.4	12.0	11.0	13.4	1.9	2.7	2.7	1.4	5.7
	MAX	13.0	24.1	10.3	8.8	12.9	12.5	15.2	2.9	3.2	3.2	2.0	7.2
H. d. griseus	N	12	12	12	12	11	12	12	12	12	12	12	12
	X	11.5	21.1	8.6	7.4	11.4	10.8	13.0	2.0	2.7	2.6	1.6	6.1
	SD	0.45	0.63	0.44	0.48	0.40	0.37	0.43	0.13	0.17	0.23	0.08	0.40
	MIN	10.7	19.9	7.6	6.8	10.8	10.2	12.5	1.7	2.4	2.3	1.5	5.5
	MAX	12.4	21.9	9.0	8.5	11.9	11.4	13.8	2.1	3.0	3.0	1.8	6.9
H. d. reginae	N	10	10	10	10	10	10	10	10	10	10	10	10
	X	11.8	22.3	8.9	7.8	12.1	11.4	13.8	1.9	2.7	2.8	1.7	6.3
	SD	0.20	0.36	0.30	0.17	0.18	0.18	0.19	0.11	0.12	0.10	0.11	0.45
	MIN	11.5	21.7	8.4	7.5	11.7	11.0	13.5	1.7	2.5	2.6	1.5	5.4
	MAX	12.1	22.8	9.3	8.1	12.4	11.7	14.0	2.1	2.9	3.0	1.9	6.8
H. d. oceanitis	N	11	12	12	12	10	12	12	12	12	12	12	12
	X	11.6	21.6	9.1	7.4	11.1	10.7	13.3	1.9	2.7	2.7	1.6	6.0
	SD	0.40	0.44	0.52	0.33	0.37	0.32	0.27	0.16	0.09	0.12	0.06	0.52
	MIN	11.1	20.8	8.0	6.8	10.5	10.0	12.8	1.6	2.6	2.5	1.5	4.9
	MAX	12.4	22.2	9.7	7.9	11.5	11.2	13.8	2.1	2.9	2.9	1.7	6.9
H. d. masoni	N	5	5	5	5	5	5	5	5	5	5	5	5
	X	12.0	22.4	9.4	7.8	12.4	11.6	13.9	2.2	3.0	3.0	1.8	6.4
	SD	0.35	0.73	0.34	0.16	0.36	0.22	0.21	0.15	0.12	0.13	0.13	0.29
	MIN	11.4	21.7	9.1	7.7	11.9	11.4	13.6	1.9	2.9	2.8	1.6	6.0
	MAX	12.4	23.3	9.8	8.1	12.8	12.0	14.1	2.3	3.2	3.2	1.9	6.8

Table 1b:		WT	RL	D2ML	D3ML	D3PL	D4ML	D5ML	TIL	EL
H. d. diadema	N	26	36	36	36	36	36	36	36	34
	X	47.2	85.9	67.1	63.6	28.6	61.6	56.0	34.4	32.1
	SD	6.88	2.17	2.36	1.88	1.28	1.55	1.38	1.46	1.28
	MIN	29.5	81.7	61.1	59.3	25.5	57.8	53.1	31.4	30.0
	MAX	60.0	90.2	71.6	67.0	31.1	64.8	58.4	36.7	34.6
H. d. nobilis	N	37	55	54	54	54	54	54	55	39
	X	50.9	88.3	70.0	66.3	29.1	63.3	58.2	36.5	29.3
	SD	6.36	3.98	2.88	2.67	1.33	2.53	2.35	2.54	2.01
	MIN	40.0	76.9	63.6	61.2	26.5	58.0	51.6	30.1	25.0
	MAX	67.0	97.0	76.0	73.2	32.5	70.0	62.8	41.8	33.1
H. d. griseus	N	11	18	18	18	18	18	18	17	10
	X	38.0	79.2	62.7	59.5	26.6	57.3	52.4	30.3	27.1
	SD	6.81	3.89	3.11	2.53	1.40	2.26	2.20	2.58	1.15
	MIN	27.0	71.6	57.9	56.0	24.5	54.1	49.1	26.5	25.5
	MAX	51.0	85.6	68.6	65.2	29.9	60.8	56.7	35.1	29.1
H. d. reginae	N	2	13	13	13	13	12	13	12	12
	X	46.0	81.2	65.1	62.2	25.9	59.0	54.0	29.8	27.5
	SD	2.83	2.68	1.8	1.5	0.82	1.29	1.49	1.06	1.25
	MIN	44.0	74.1	61.4	58.1	24.7	55.6	50.6	27.4	25.9
	MAX	48.0	84.5	68.0	64.2	27.2	60.4	56.2	31.5	29.3
H. d. oceanitis	N	13	24	24	24	24	24	24	24	24
	X	36.4	76.5	57.3	54.6	25.2	54.0	50.3	31.5	29.5
	SD	3.48	2.14	1.94	1.76	0.92	1.80	1.81	1.54	1.88
	MIN	30.0	71.7	52.2	50.9	23.5	48.7	46.1	28.6	24.9
	MAX	42.0	80.4	60.4	57.0	26.9	56.9	53.6	35.0	33.2
H. d. masoni	N	2	6	8	8	8	8	8	8	3
	X	44.1	85.0	67.2	63.2	28.7	60.5	56.2	31.4	27.0
	SD	2.97	3.76	2.38	2.48	1.72	2.72	2.53	1.31	1.60
	MIN	42.0	80.2	64.3	58.8	25.9	57.3	53.7	29.7	25.2
	MAX	46.2	90.2	71.0	66.9	30.9	66.0	60.7	33.1	28.2

Penis and Baculum

Penis similar to *H. d. diadema*; baculum same general shape as *H. d. diadema* but with flexing on arms variable: almost straight in specimen from Borneo and more 'flexed' in specimen from Lombok; size similar to *H. d. diadema* with total length 2.06-2.51 and basal width 0.52-0.79.

Skull, dentary, dentition (Table 1, Figure 14b)

Large robust skull, greatest skull length (29.3-33.2) with well developed sagittal and lambdoidal crests; supraorbital ridges extending forward from anterior point of sagittal crest usually moderately well developed, terminating anteriorly at posterolateral margin of rostrum as a moderate to marked protuberance which gives rostrum a squarish aspect from dorsal view; posterior triangle of ridge encloses a slight to moderate frontal depression; groove separating rostral eminences moderate; zygomatic width large (17.5-20.5); mastoid moderate; C^1 very large and robust. I^1 bilobed and frequently with a third outer cusplet, inner cusp larger and taller but more vertical than in *H. d. diadema*; toothrows wide apart (M^3-M^3W 10.8-13.0). Other skull characters are as for *H. d. diadema*.

Hipposideros diadema griseus (Meyen, 1833)

Table 1; Figures 3-7, 9-10 and 14

Rhinolophus griseus Meyen, F.J.F., 1833, Beiträge zur zoologie gesammelt auf einer Reise um die Erde. Abh. Nova Acta Akad. Caes. Leop. Carol. Halle 16, 2: 608, Pl. 46.

Hipposideros diadema anderseni Taylor, E.H., 1934, Philippine Land Mammals, Monogr. Philipp. Bureau of Science Manila, 30, 43 — Bunguran Island, North Natuna Islands.

Hipposideros diadema pullatus Andersen, K., 1905. *Hipposideros diadema* and its closest allies, Ann. Mag. nat. Hist. (7) 16, 498 — Haveri, Papua New Guinea.

Type: not allocated.

Type locality: Luzon, Philippine islands.

Specimens examined: See Appendix I.

Diagnosis

Hipposideros d. griseus differs from *H. d. diadema* in averaging smaller in all external and skull measurements (Table 1); nasal breadth absolutely smaller: ♂♂ 8.5 (8.1-8.9) *v.* 9.5 (9.0-10.0) and ♀♀ 8.4 (7.9-9.0) *v.* 9.5 (9.1-9.9); nasals shorter relative to their length (Figure 9a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; external and skull measurements and weight averaging smaller (in some cases without overlap) (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 88.3 (76.9-97.0); tibia length 30.3 (26.5-35.1) *v.* 36.5 (30.1-41.8); ear length 27.1 (25.5-29.1) *v.* 29.3 (25.0-33.1); greatest skull length ♂♂ 29.1 (28.0-29.6) *v.* 31.9 (29.5-33.2) and ♀♀ 28.7 (27.5-30.1) *v.* 30.8 (29.3-32.3); C^1-M^3 ♂♂ 10.7 (10.3-11.0) *v.* 12.3 (11.3-13.1) and ♀♀ 10.8 (10.2-11.4) *v.* 11.9 (11.0-12.5). Cranial length smaller relative to nasal length (Figure 7a, b).

It differs from *H. d. reginae* in being generally slightly smaller in external characters (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 81.2 (74.1-84.5) and much smaller in skull and dental characters e.g. greatest skull length ♂♂ 29.1 (28.0-29.6) *v.* 30.4 (30.0-30.7) and ♀♀ (28.7 (27.5-30.1) *v.* 30.0 (29.3-30.7); nasal breadth ♂♂ 8.5 (8.1-8.9) *v.* 9.6 (9.4-10.1) and ♀♀ 8.4 (7.9-9.0) *v.* 9.4 (9.1-9.7); C^1-C^1 width ♂♂ 7.5 (7.0-7.8) *v.* 8.0 (8.0-8.1) and ♀♀ 7.4 (6.8-8.5) *v.* 7.8 (7.5-8.1); C^1-M^1 length ♂♂ 10.7 (10.3-11.0) *v.* 11.6 (11.3-11.8) and ♀♀ 10.8 (10.2-11.4) *v.* 11.4 (11.0-11.7); molar row (M^3-M^3W) narrower relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in being generally smaller in wing measurements (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 85.0 (80.2-90.2) and metacarpal 5 length 52.4 (49.1-56.7) *v.* 56.2 (53.7-60.7); much smaller, skull, dental and dentary characters (Table 1) particularly: nasal breadth ♂♂ 8.5 (8.1-8.9) *v.* 9.1 (8.8-9.4) and ♀♀ 8.4 (7.9-9.0) *v.* 9.2 (8.5-9.6); orbit to canine length ♂♂ 6.7 (6.4-6.9) *v.* 7.4 (7.0-8.0) and ♀♀ 6.8 (6.3-7.7) *v.* 7.4 (7.2-7.7); dentary length ♂♂ 21.3 (20.8-22.0) v. 22.4 (22.1-22.7) and ♀♀ 21.1 (19.9-21.9) v. 22.4 (21.7-23.3), and C^1-M^3 length ♂♂ 10.7 (10.3-11.0) *v.* 11.5 (11.2-11.7) and ♀♀ 10.8 (10.2-11.4) *v.* 11.6 (11.4-12.0); molar row width (M^3-M^3W) much narrower relative to cranial length (Figure 10a, b) and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. oceanitis* in having three rather than two large supplementary nose leaflets; averages larger in all wing measurements but shorter in tibia and ear lengths (Table 1) e.g., radius length 79.2 (71.6-85.6) *v.* 76.5 (71.7-80.4); tibia length 30.3 (26.5-35.1) v. 31.5 (28.6-35.0); and ear length 27.1 (25.5-29.1) v. 29.5 (24.9-33.2); ear length generally shorter relative to radius length (Figure 4); and metacarpal 3 longer relative to tibia length (Figure 5).

Description

Externals (Table 1, Figures 3, 4, 5)

Small, body weight 27.0-51.0; radius length 71.6-85.6 and other wing measurements small; tibia short (26.5-35.1); ear short (25.5-29.1); noseleaf large, greatest width up to 11.5, shape of anterior, intermediate and posterior leaves as for *H. d. diadema*. Other descriptions as for *H. d. diadema.*

Pelage

Pattern of coloration very similar to *H. d. diadema* but with shoulder patch a more distinct triangular shape. The darker dorsal colours range from Clove Brown to Snuff Brown while the ventral colours range from cream to pinkish buff.

Penis and Baculum

Both penis and baculum similar in size and shape to *H. d. diadema*; baculum with total length *c.* 2.0 and basal width c. 0.6.

Skull, dentary, dentition (Table 1, Figure 14c)

Moderate length skull (27.5-30.1; cranial length short relative to nasal length; rostrum profile from dorsal aspect varies from rounded (AM 19554) to squarish (FM 80371) with a range of intermediate shapes; rostral eminences more inflated in Papua New Guinea specimens than in *H. d. diadema* but Philippine specimens as for *H. d. diadema*; nasals narrow (7.9-9.0); M^{1-2} with small hypocone; distance between toothrows narrow (M^3-M^3W 10.8-11.9).

Other skull characters are as for *H. d. diadema.*

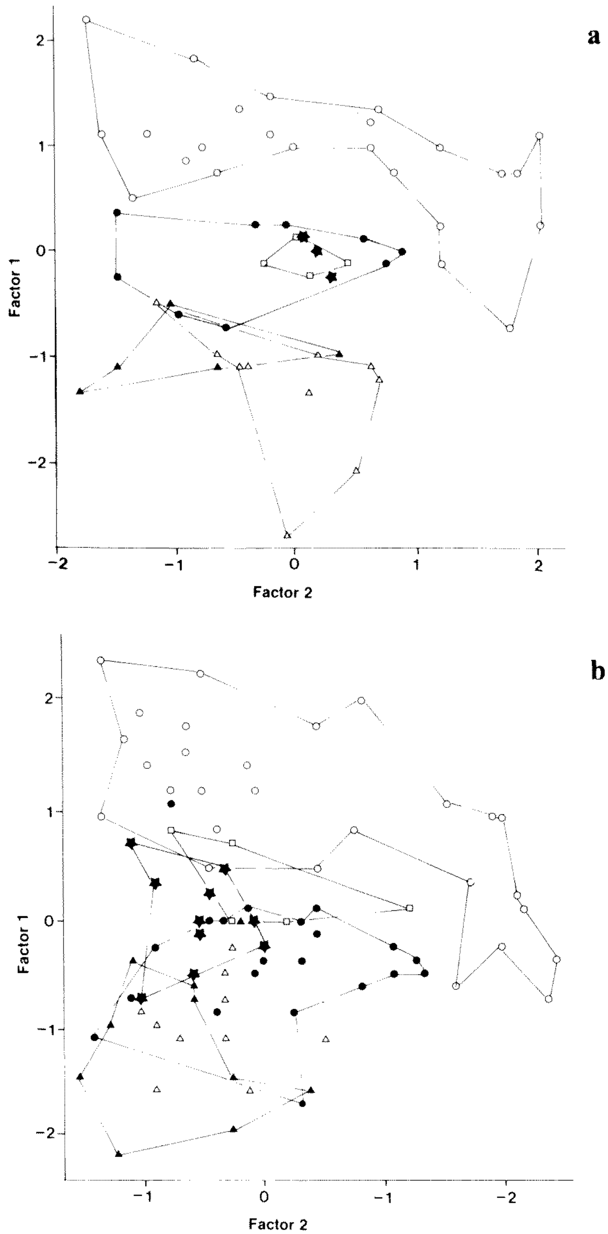


Figure 16 Principal component analysis based on skull measurements of the subspecies of *H. diadema* examined, showing the first two Factors. Subspecies codes as for Figure 2. (**a**) males; (**b**) females.

Hipposideros diadema reginae Troughton, 1937

Table 1; Figures 3-10, 12 and 14

Hipposideros diadema reginae Troughton, E. Le G., 1937. Six new bats (Microchiroptera) from the Australian region, Aust. Zool., 8: 275.

Holotype: Australian Museum AM 1243, male. Wet skin and skull.

Type locality: Bloomfield River, Cooktown area, Queensland.

Specimens examined: See Appendix 1.

Diagnosis

Hipposideros d. reginae differs from *H. d. diadema* by averaging smaller in all external measurements (Table 1) e.g., radius length 81.2 (74.1-84.5) *v*. 85.9 (81.7-90.2); and tibia length 29.8 (27.4-31.5) *v*. 34.4 (31.4-36.7); ear shorter relative to radius length (Figure 4); tibia shorter relative to metacarpal 3 length (Figure 5); distance between molar rows generally wider relative to greatest skull length (Figure 6a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; averages smaller in all external measurements (Table 1) e.g., radius length 81.2 (74.1-84.5) v. 88.3 (76.9-97.0); and tibia length 29.8 (27.4-31.5) v. 36.5 (30.1-41.8); tibia shorter relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); tibia shorter relative to metacarpal 3 length (Figure 5); most skull characters average smaller e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v*. 31.9 (29.5-33.2) and ♀♀ 30.0 (29.3-30.7) *v*. 30.8 (29.3-32.3); C^1-M^3 length ♂♂ 11.6 (11.3-11.8) *v*. 12.3 (11.3-13.1) and ♀♀ 11.4 (11.0-11.7) *v*. 11.9 (11.0-12.5); nasal longer relative to their breadth (Figure 9a, b).

It differs from *H. d. griseus* in being generally slightly larger in external characters (Table 1) e.g. 81.2 (74.1-84.5) *v*. 79.2 (71.6-85.6) and larger in skull and dental characters e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v*. 29.1 (28.0-29.6) and ♀♀ 30.0 (29.3-30.7) *v*. 28.7 (27.5-30.1); nasal breadth ♂♂ 9.6 (9.4-10.1) *v*. 8.5 (8.1-8.9) and 9.4 ♀♀ (9.1-9.7) *v*. 8.4 (7.9-9.0); C^1-C^1 ♂♂ 8.0 (8.0-8.1) v. 7.5 (7.0-7.8) and ♀♀ 7.8 (7.5-8.1) *v*. 7.4 (6.8-8.5); C^1-M^3 length ♂♂ 11.6 (11.3-11.8) *v*. 10.7 (10.3-11.0) and ♀♀ 11.4 (11.0-11.7) *v*. 10.8 (10.2-11.4); distance between molar row wider relative to cranial length and greatest skull length (Figures 10a, b and 6a, b, respectively; and nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in having externals that average smaller (except ear length) (Table 1) e.g. radius length 81.2 (74.1-84.5) *v*. 85.0 (80.2-90.2); in ♂♂ distance between molar rows wider relative to cranial length and greatest skull length (Figures 10a and 6 a, respectively); ♀♀ zygomatic width smaller relative to nasal length and greatest skull length (Figure 8b and 12b, respectively).

It differs from *H. d. oceanitis* in having three rather than two large supplementary nose leaflets; wing measurements average larger (Table 1), e.g. metacarpal 3 length 62.2 (58.1-64.2) *v*. 54.6 (50.9-57.0) and radius length 81.2 (74.1-84.5) *v*. 76.5 (71.7-80.4); tibia generally shorter relative to ear length (Figure 3); radius longer relative to

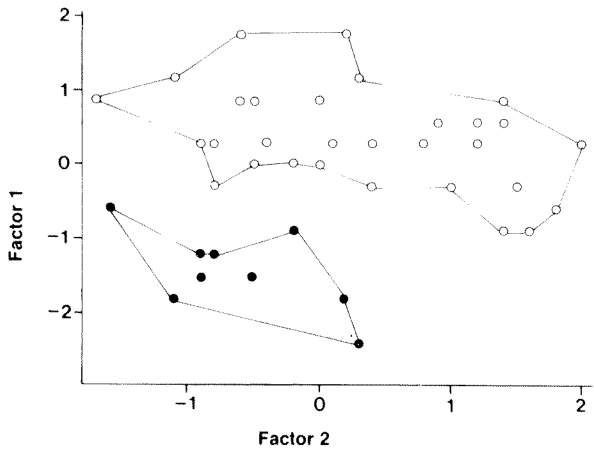


Figure 17 Principal component analysis based on skull measurements of *Hipposideros diadema diadema* from Sumbawa I. and *H. d. nobilis* from Lombok I. showing the first two Factor scores. Subspecies codes as for Figures 2.

ear length (Figure 4); metacarpal 3 longer relative to tibia length (Figure 5); averages larger in almost all skull measurements e.g., greatest skull length ♂♂ 30.4 (30.0-30.7) *v.* 28.9 (26.4-29.9) and ♀♀ 30.0 (29.3-30.7) *v.* 29.1 (28.5-30.1); C^1-M^3 length ♂♂ 12.3 (12.0-12.5) *v.* 11.1 (10.6-11.8) and ♀♀ 11.4 (11.0-11.7) *v.* 10.7 (10.0-11.2); distance between molar rows wider relative to greatest skull length (Figure 6a, b); nasal length greater relative to cranial length (Figure 7a, b) and nasal breadth greater relative to nasal length (Figure 9a, b).

Description

Externals (Table 1, Figures 3, 4, 5)

Moderately heavy (44.0-48.0); radius short (74.1-84.5) and other wing measurements also short; tibia short (27.4-31.5); ear short (25.9-29.3); noseleaf well developed; three large supplementary leaflets but no trace of the fourth leaflet present in *H. d. diadema*; anterior leaf large, greatest width up to 12. Other descriptions as for *H. d. diadema.*

Pelage

Pattern of colouration very similar to *H. d. diadema* but with head, throat and shoulder mantle paler and without darker marking; these paler areas range from Pale Pinkish Cinnamon to Light Pinkish Cinnamon. The lower back is predominantly Saccardo's Umber (brown) marbled with Sepia (dark brown) and Light Pinkish Cinnamon. In contradistinction to the type description of this form by Troughton

(1937), dorsal pale lateral stripes may be prominent, varying from White to Pale Pinkish Buff; occasional patches of these paler colours may also occur on the lower back (e.g. AM 8106). The pelage of the throat is less clearly marked from that of the chest and abdomen which is a slightly darker Isabella Color (light 'pinkish' brown).

Penis and Baculum

Penis with same general shape as *H.d. diadema* but with distal end of glans more pointed and without clearly defined small distal protuberances on lip of urethral groove. Baculum similar shape to *H. d. diadema* but with basin of base slightly deeper so that base in lateral view appears slightly wider, base *c.* 0.6 wide and greatest length *c.* 2.1.

Skull, dentary, dentition (Table 1, Figure 14d)

Moderate length skull (29.3-30.7); posterior triangle of supraorbital ridges enclose moderate to deep frontal depression; nasal profile squarish in dorsal view, long (7.4-8.5) and wide (9.1-10.1); rostal eminences inflated, separated by moderate medial groove; anterior palatal foramina oval, large, with anterior edge of maxilla closing foramina posterior edge, mesopterygoid fossa wide (3.4-3.8). Other characters as for *H. d. diadema.*

Hipposideros diadema masoni (Dobson, 1872)

Table 1; Figures 3-6, 10-11 and 14

Phyllorhina masoni Dobson, G.E. 1872,. Brief descriptions of five new species of Rhinolophine bats, J. Asiat. Soc. Beng. 2: 499.

Holotype: Calcutta Museum. Number 297, body in alcohol, skull separate.

Type locality: Moulmein, Burma.

Specimens examined: See Appendix I.

Diagnosis

Hipposideros d. masoni differs from *H. d. diadema* in that its tibia averages shorter 31.4 (29.7-33.1) *v.* 34.4 (31.4-36.7); ear averages shorter 27.0 (25.2-28.2) *v.* 32.1 (30.0-34.6); tibia shorter relative to metacarpal 3 length (Figure 5); ear shorter relative to radius length (Figure 4); molar rows (M^3M^3W) narrower relative to cranial length (Figure 10a, b).

It differs from *H. d. nobilis* in having a relatively larger anterior noseleaf; averages smaller in all external measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 88.3 (76.9-97.0): tibia shorter relative to both ear length (Figure 3) and metacarpal 3 length (Figure 5). Most skull and dental measurements (except minimum interorbital distance and nasal length) average smaller (Table 1) e.g., C^1-M^3 ♂♂ 11.5 (11.2-11.7) *v.* 12.3 (11.3-13.1) and ♀♀ 11.6 (11.4-12.0) *v.* 11.9 (11.0-12.5); molar rows closer (M^3-M^3W) relative to greatest skull length (Figure 6a, b); cranial length shorter relative to M^3 length (Figure 11a, b).

Table 2: ANOVA of *H. diadema* by sex and island for (a) skull and (b) external characters. Significance of F values are as follows P<.05*, P<.01** and P<.001***

Character		Factor	
(a) SKULL	Sex	Island	Interaction
GSL	7.582**	20.411***	1.722
CCL	4.600	26.699***	2.178*
Cl	2.840	25.791***	2.947*
NL	1.141	7.192***	1.442
NB	0.000	20.605***	1.076
CH	0.069	7.656***	1.554
IBW	1.095	5.537***	0.747
PBL	1.006	6.524***	0.628
MFB	0.023	7.124***	0.425
OCL	6.301*	13.277***	1.158
IOB	5.964*	8.456***	1.012
ZW	1.104	19.085***	1.733
BCW	6.329*	8.139***	1.401
DL	11.015***	29.460***	2.218*
RAL	6.090*	5.878***	1.087
C^1-C^1W	2.139	13.287***	1.106
M^3-M^3W	1.531	31.523***	1.778
C^1-M^3L	10.470**	27.166***	1.087
C_1-M_3L	14.872***	39.354***	1.881*
PM^4L	0.403	11.432***	0.369
M^1L	0.301	12.148***	1.095
ML	1.038	11.282***	0.972
M^3L	0.036	7.413***	0.567
(B) EXTERNALS			
RL	0.175	29.510***	1.254
D2ML	0.196	39.097***	0.924
D3ML	0.198	42.248***	0.810
D3PL	0.173	20.000***	0.795
D4ML	0.019	32.374***	0.571
D5ML	0.234	26.697***	0.684
TIL	0.927	25.011***	1.023

It differs from *H. d. griseus* in being generally larger in wing measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 79.2 (71.6-85.6) and metacarpal 5 length 56.2 (53.7-60.7) — 52.4 (49.1-56.7); much larger skull, dental and dentary characters (Table 1) particularly nasal breadth ♂♂ 9.1 (8.8-9.4) *v.* 8.5 (8.1-8.9) and ♀♀ 9.2 (8.5-9.6) *v.* 8.4 (7.9-9.0); orbit to canine length ♂♂ 7.4 (7.0-8.0) *v.* 6.7 (6.4-6.9) and ♀♀ 7.4 (7.2-7.7) *v.* 6.8 (6.3-7.7); dentary length ♂♂ 22.4 (22.1-22.7) *v.* 21.3 (20.8-22.0) and ♀♀ 22.4 (21.7-23.3) *v.* 21.1 (19.9-21.9); and C^1-M^3 length ♂♂ 11.5 (11.2-11.7) *v.* 10.7 (10.3-11.0) and ♀♀ 11.6 (11.4-12.0) *v.* 10.8 (10.2-10.4); molar row width (M^3-M^3W) wider relative to cranial length (Figure 10a, b); and nasals wider relative to their length (Figure 9a, b).

It differs from *H. d. reginae* in having externals that average larger (except ear length, see Table 1), e.g., radius length 85.0 (80.2-90.2) *v.* 81.2 (74.1-84.5); in ♂♂ molar rows (M^3-M^3W) narrower relative to cranial length (Figure 10a); in ♂♂ molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a); in ♀♀ zygomatic width larger relative to nasal length and greatest skull length (Figures 8b and 12b respectively).

It differs from *H. d. oceanitis* in having three rather than two large nasal leaflets; in being larger in all wing measurements (Table 1) e.g., radius length 85.0 (80.2-90.2) *v.* 76.5 (71.7-80.4); radius longer relative to ear length (Figure 4); metacarpal 3 length longer relative to tibia length (Figure 5); generally larger in skull, dental and dentary characters, particularly nasal length ♂♂ 7.8 (6.8-8.3) *v.* 7.2 (6.5-8.2) and ♀♀ 7.7 (6.9-8.2) *v.* 7.0 (6.1-7.6); zygomatic width ♂♂ 17.6 (17.1-18.2) *v.* 17.1 (16.0-17.6) and ♀♀ 18.6 (18.3-19.0) *v.* 17.1 (16.3-17.8); dentary length ♂♂ 22.4 (22.1-22.7) *v.* 21.3 (19.6-22.1) and ♀♀ 22.4 (21.7-23.3) *v.* 21.6 (20.8-22.2); C^1-M^3 length ♂♂ 11.5 (11.2-11.7) *v.* 10.7 (9.6-11.3) and ♀♀ 11.6 (11.4-12.0) *v.* 10.7 (10.0-11.2); molar rows (M^3-M^3W) wider relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); in ♀♀ zygomatic width larger relative to nasal length (Figure 8b).

Description

Externals (Table 1, Figures 3, 4, 5)

Medium size; weight 42.0-46.2, radius length 80.2-90.2; tibia short 29.7-33.1; ear short; noseleaf well developed with three only supplementary leaflets in the specimens examined; anterior leaf large, maximum diameter up to 11.5. Other descriptions as for *H. d. diadema.*

Pelage

Pattern of colouration very similar to *H. d. diadema.* Overall dorsal colour Clove Brown to Bister and ventral surface Buffy Brown to Tawny Olive. Shamel (1942) describes two colour phases (i) a pale yellow or buff with reddish brown tips to hairs and (ii) pale buff with dark brown tips to hairs of back with much paler brown with lighter tips to abdomenal hairs.

Penis and Baculum

Penis and baculum as for *H. d. diadema.* Baculum base *c.* 0.7, greatest length *c.* 2.1.

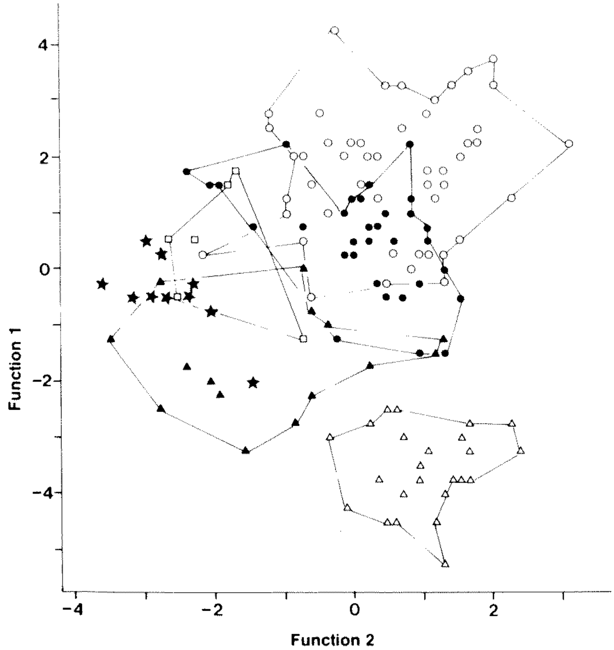


Figure 18 Canonical variate analysis based on external measurements of *Hipposideros diadema* subspecies. Plot of functions 1 and 2 for males and females combined. Subspecies codes as for Figure 2.

Skull, dentary, dentition (Table 1, Figure 14e)

Moderate length skull (28.5-30.5) with well developed sagittal and lambdoidal crests; supraorbital ridges moderately well developed, terminating as slight protuberance at posterolateral margin of rostrum; rostrum profile squarish from dorsal aspect; rostral eminences moderately to well inflated; mesopterygoid width variable; sphenoid bridge partially obscures large sphenorbital foramen; toothrow width variable with females wider than males e.g., M^3-M^3 width ♀♀ 11.9-12.8 and ♂♂ 11.6-11.9; I_1-$_2$ occasionally imbricate (FMNH 98689). Other skull characters as in *H. d. diadema*.

Hipposideros diadema oceanitis Andersen, 1905

Table 1; Figures 3-11 and 14

Hipposideros diadema oceanitis Andersen, K. 1905, On *Hipposideros diadema* and its closest allies, Ann. Mag. nat. Hist. (7)16: 497.

Hipposideros diadema malaitensis Phillips, C.J., 1967, A new subspecies of Horseshoe bat (*Hipposideros diadema*) from the Solomon Islands, Proc. Biol. Soc. Washington 80: 35, — Malaita I.

Holotype: British Museum, Natural History BM 88.1.5.23, adult male, in alcohol.

Table 3 Principal component scores for the first three factors for *Hipposideros diadema* (a) external characters (males and females combined), (b) skull characters (males and females separate).

(a) External characters	Factor 1	Factor 2	Factor 3
RL	0.7149	0.5085	0.3790
D2ML	0.8470	0.3127	0.3920
D3ML	0.8767	0.3056	0.3355
D3PL	0.4658	0.3208	0.8244
D4ML	0.8230	0.3771	0.3808
D5ML	0.7912	0.4642	0.3336
TIL	0.3623	0.8886	0.2655
% variation explained	86.8	5.9	4.0

(b) Factor scores for males, followed by females in brackets

Skull characters	Factor 1	Factor 2	Factor 3
GSL	0.9426 (0.9014)	0.2285 (0.2220)	0.0258 (0.1320)
CCL	0.9426 (0.8790)	0.2153 (0.2589)	0.0549 (0.1872)
CL	0.8774 (0.8171)	0.3200 (0.2772)	—0.2175 (—0.2156)
NL	—0.0403 (—0.0439)	—0.1097 (—0.0717)	0.8062 (0.8167)
NB	0.7126 (0.4266)	0.3746 (0.3596)	0.3333 (0.6229)
CH	0.6133 (0.3400)	0.4925 (0.6600)	0.1051 (0.1616)
IBW	0.2976 (0.4692)	0.5791 (0.3406)	—0.3423 (—0.2031)
PBL	0.5059 (0.6212)	0.1183 (0.0399)	—0.3722 (—0.0949)
MFB	0.2762 (0.1865)	0.7783 (0.6693)	0.2387 (0.4105)
OCL	0.8307 (0.8043)	0.2600 (0.1512)	0.0438 (0.0664)
IOB	—0.1523 (—0.1715)	0.2142 (0.1595)	0.7646 (0.7339)
ZW	0.7986 (0.8054)	0.4438 (0.3941)	—0.1800 (—0.0186)
BCW	0.4728 (0.2325)	0.7699 (0.8448)	—0.0611 (0.1002)
DL	0.9327 (0.8746)	0.2217 (0.2612)	—0.0965 (0.0513)
RAL	0.7054 (0.6526)	0.1868 (0.0922)	—0.1778 (—0.0207)
C^1-C^1W	0.8191 (0.6157)	0.2842 (0.4397)	—0.0054 (—0.0032)
M^3-M^3W	0.8686 (0.7713)	0.2605 (0.3900)	—0.0734 (0.0328)
C^1-M^3L	0.8926 (0.8387)	0.2872 (0.3669)	—0.0449 (0.0494)
C_1-M_3L	0.9509 (0.8865)	0.1343 (0.2687)	—0.1667 (—0.0092)
PM^4L	0.6394 (0.4061)	0.3708 (0.7083)	—0.2487 (—0.0436)
M^1L	0.7018 (0.5932)	0.2215 (0.4393)	—0.3396 (—0.0798)
M^2L	0.7332 (0.5337)	0.1698 (0.4757)	—0.1805 (0.1654)
M^3L	0.5849 (0.6065)	—0.4127 (—0.5559)	0.4515 (0.1622)
% variation explained	58.5 (49.8)	9.3 (10.5)	6.7 (7.2)

Type locality: Guadalcanar (= Guadalcanal), Solomon Islands.

Specimens examined: See Appendix 1.

Diagnosis

Hipposideros d. oceanitis differs from *H. d. diadema* in having two rather than three large supplementary nose leaflets; averages smaller in almost all external and skull measurements and weight (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 85.9 (81.7-90.2), metacarpal 4 length 54.0 (48.7-56.9) *v.* 61.6 (57.8-64.8); greatest skull length ♂♂ 28.9 (26.4-29.9) *v.* 30.5 (29.1-31.5) and ♀♀ 29.1 (28.5-30.1) *v.* 30.0 (28.7-31.5); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 11.5 (10.9-12.2) and ♀♀ 10.7 (10.0-11.2) *v.* 11.2 (10.4-11.6); radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. nobilis* in having two rather than three large supplementary nose leaflets; proportionally larger anterior noseleaf; averages much lighter 36.4 (30.2-42.0) *v.* 50.9 (40.0-67.0); smaller in all external measurements (often with no overlap) (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 88.3 (76.9-97.0), tibia length 31.5 (28.6-35.0) *v.* 36.5 (30.1-41.8); tibia shorter relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); smaller in all skull measurements (Table 1), e.g., greatest skull length ♂♂ 28.9 (26.4-29.9) *v.* 31.9 (29.5-33.2) and ♀♀ 29.1 (28.5-30.1) *v.* 30.8 (29.3-32.3); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 12.3 (11.3-13.1) and ♀♀ 10.7 (10.0-11.2) *v.* 11.9 (11.0-12.5); molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a, b); nasals narrower relative to their length (Figure 9a, b); cranial length smaller relative to M^3 length (Figure 11a, b); zygomatic width small relative to nasal length (Figure 8a, b).

It differs from *H. d. griseus* in having two rather than three large supplementary nose leaflets; averages smaller in all wing measurements but longer in tibia and ear length (Table 1) e.g., radius length 76.5 (71.7-80.4) *v.* 79.2 (71.6-85.6), tibia length 31.5 (28.6-35.0) *v.* 30.3 (26.5-35.1) and ear length 29.5 (24.9-33.2) *v.* 27.1 (25.5-29.1); ear length generally longer relative to radius length (Figure 4) and metacarpal 3 length shorter relative to tibia length (Figure 5).

It differs from *H. d. reginae* in having two rather than three large supplementary nose leaflets; wing measurements average smaller (Table 1) e.g., metacarpal 3 length 54.6 (50.9-57.0) *v.* 62.2 (58.1-64.2) and radius length 76.5 (71.7-80.4) *v.* 81.2 (74.1-84.5); tibia generally longer relative to ear length (Figure 3); radius shorter relative to ear length (Figure 4); metacarpal 3 shorter relative to tibia length (Figure 5); molar rows (M^3-M^3W) narrower relative to greatest skull length (Figure 6a, b); nasal length shorter relative to cranial length (Figure 7a, b) and nasals narrower relative to their length (Figure 9a, b).

It differs from *H. d. masoni* in having two rather than three large supplementary nose leaflets; smaller in all wing measurements (Table 1), e.g., radius length 76.5

Table 4 Standardised and unstandardised (in brackets) canonical variates from the six subspecies of *Hipposideros diadema* considered (a) for external characters (males and females combined, WT and EL excluded) and (b) for skull characters (males and females separate).

(a)

External characters	Function 1	Function 2	Function 3
RL	0.2242 (0.0743)	—0.1900 (—0.0629)	0.5366 (0.1777)
D2ML	0.3174 (0.1228)	—0.6905 (—0.2671)	—0.3461 (—0.1339)
D3ML	0.6869 (0.3005)	—0.0942 (—0.0412)	—0.9451 (—0.4135)
D3PL	0.1452 (0.1165)	0.2772 (0.2225)	0.6969 (0.5593)
D4ML	—0.0760 (—0.0358)	0.1577 (0.0744)	1.5580 (0.7349)
D5ML	—0.2312 (—0.1149)	—0.1540 (—0.0765)	—0.9185 (—0.4564)
TIL	0.0371 (0.0187)	1.2214 (0.6146)	—0.4253 (—0.2140)
Constant	(—28.5045)	(—1.7211)	(—7.6778)
% Variation explained	70.4	22.6	4.4

(b) Skull — (males)

Characters	Function 1	Function 2	Function 3
GSL	—1.9247 (—2.2962)	—1.7695 (—2.1111)	1.1040 (1.3170)
CCL	0.9763 (1.4313)	1.4317 (2.0989)	—2.3769 (—3.4847)
CL	1.1511 (1.7132)	—0.7962 (—1.1850)	0.6982 (—1.6571)
NL	0.1305 (0.3022)	—0.2603 (—0.6029)	—0.2341 (1.6174)
NB	—0.2979 (—0.8450)	1.3318 (3.7771)	—0.3220 (—0.6640)
CH	—0.0041 (—0.0126)	—0.3314 (—1.0124)	0.0596 (—0.9838)
IBW	0.3999 (1.5854)	—0.0252 (—0.0998)	0.1748 (0.2363)
PBL	—0.3295 (—0.7022)	0.3357 (0.7154)	0.3834 (0.3726)
OCL	0.6439 (1.3945)	0.1297 (0.2808)	0.5340 (0.8303)
ZW	—0.6460 (—0.9326)	0.0533 (0.0769)	1.4823 (0.7710)
DL	0.5649 (0.8916)	0.1617 (0.2552)	0.7032 (2.3396)
M^1-M^3W	0.8535 (2.7876)	—0.1150 (—0.3756)	0.6095 (2.2970)
C^1-M^3L	—0.4427 (—1.0885)	0.5647 (1.3887)	—0.4815 (1.4987)
C_1-M_3L	0.6480 (1.6709)	—0.6502 (—1.6766)	0.1250 (—1.2415)
PM^4L	0.2542 (1.3063)	0.1563 (0.8031)	—0.2417 (0.6423)
M^2L	—0.7735 (—3.9982)	—0.1518 (—0.7846)	0.1755 (—1.2492)
M^3L	0.1554 (1.3205)	0.8406 (7.1411)	—2.3769 (1.4910)
Constant	—50.8880	—1.5300	—12.2906
% variation explained	70.9	16.0	7.6

Table 4 cont.

(b) Skull (females)

Character	Function 1	Function 2	Function 3
CCL	—0.5966 (—0.9904)	0.4946 (0.8210)	0.1534 (0.2546)
CL	0.0220 (0.0390)	—0.3757 (—0.6667)	0.5771 (1.0241)
NL	—0.1653 (—0.3471)	—0.0063 (—0.0132)	—0.4230 (—0.8881)
NB	—0.3782 (—1.3289)	0.9007 (3.1648)	0.2135 (0.7501)
PBL	0.3864 (1.1029)	—0.0656 (—0.1873)	—0.2026 (—0.5782)
MFB	—0.1423 (—0.5764)	—0.0278 (—0.1125)	0.3464 (1.4032)
IOB	—0.0168 (0.0840)	0.1928 (0.9654)	—0.2098 (—1.0507)
ZW	0.5746 (1.2218)	—0.4504 (—0.9576)	—0.3578 (—0.7608)
DL	0.8122 (1.5054)	—0.2406 (—0.4460)	—0.8968 (—1.6621)
RAL	—0.2762 (—0.6874)	0.0267 (0.0664)	0.4455 (1.1089)
C^1-C^1W	—0.1282 (—0.3941)	0.0611 (0.1880)	0.4555 (1.4006)
M^3-M^3W	0.4333 (1.4427)	0.4910 (1.6347)	—0.8882 (—2.9573)
C_1-M_3L	—0.0167 (0.0505)	—0.0537 (—0.1630)	0.6123 (1.8576)
PM^4L	0.1349 (0.7104)	0.1427 (0.7513)	0.4276 (2.2513)
M^1L	0.2999 (2.3243)	—0.1379 (—1.0684)	0.3483 (2.6989)
M^3L	0.0207 (0.1593)	0.3695 (2.8410)	0.0484 (0.3721)
Constant	—33.6239	—34.9333	—0.5045
% Variation explained	44.6	28.6	17.9

(71.7-80.4) *v.* 85.0 (80.2-90.2), radius shorter relative to ear length (Figure 4); metacarpal 3 length shorter relative to tibia length (Figure 5); generally smaller in skull, dental and dentary characteristics, particularly nasal length ♂♂ 7.2 (6.5-8.2) *v.* 7.8 (6.8-8.3) and ♀♀ 7.0 (6.1-7.6) *v.* 7.7 (6.9-8.2); zygomatic width ♂♂ 17.1 (16.0-17.6) *v.* 17.6 (17.1-18.2) and ♀♀ 17.1 (16.3-17.8) *v.* 18.6 (18.3-19.0); dentary length ♂♂ 21.3 (19.6-22.1) *v.* 22.4 (22.1-22.7) and ♀♀ 21.6 (20.8-22.2) *v.* 22.4 (21.7-23.3); C^1-M^3 length ♂♂ 10.7 (9.6-11.3) *v.* 11.5 (11.2-11.7) and ♀♀ 10.7 (10.0-11.2) *v.* 11.6 (11.4-12.0); molar rows (M^3-M^3W) narrower relative to greatest skull length and cranial length (Figures 6a, b and 10a, b, respectively); in ♀♀ only zygomatic width smaller relative to nasal length (Figure 8b).

Description

Externals (Table 1, Figures 3, 4, 5)

Smallest of the subspecies examined: weight 30.0-42.0, radius length 71.7-80.4, tibia moderately long 28.6-35.0; ear moderately long 24.9-33.2; noseleaf well developed with two large and one small supplementary leaflets; anterior leaflet of the same shape as *H. d. diadema*, greatest width up to 10. Other descriptions as for *H. d. diadema.*

Pelage

Basic pattern of colouration similar to *H. d. diadema* but with much less contrast between the paler and darker parts. In some specimens the paler dorsal lateral stripes are very indistinct as is the posterior margin of the pale shoulder mantle which merges indistinctly with the marbling of the lower back region. The predominant darker colours of dorsal and ventral pelage is Natal Brown (dark orange brown) and Buffy Brown (pale brown), respectively. The paler head, throat and mantle pelage a pinkish brown, and ranges from Avellaneous to Wood Brown. Occasional indistinct paler spots on dorsum, particularly at base of femur and humerus.

Penis and Baculum

Penis and baculum as for *H. d. diadema*. Baculum base *c.* 0.75, greatest length 2.0-2.3.

Skull, dentary, dentition (Table 1, Figure 14f)

Small skull with greatest length (26.4-30.1), well developed sagittal and lambdoidal crests; supraorbital ridges poorly developed, terminating anteriorly in a very low protuberance, posterior triangle encloses moderate frontal depression; rostral profile from dorsal aspect oval, small; rostral eminences well inflated; mastoid triangular shaped in dorsal profile; M^3 posterior cusp obsolescent, prematacristid most reduced of *H. diadema* subspecies considered, represented by a small nub only.

Statistical Analysis: Results and Discussion

(a) Sexual dimorphism

Only the following islands were used in this analysis. They had both males and females well represented.

Island	No. of individuals Skulls		Externals	
	♂♂	♀♀	♂♂	♀♀
Sumbawa Moyo	4	6	4	6
Flores	2	6	2	8
Roti	1	1	2	1
Borneo	2	2	2	2
Java	5	6	5	6
Lombok	16	17	18	17
Nusa Penida	1	1	1	1
Papua New Guinea	4	5	4	4
Philippines	2	5	2	7
Queensland (Aust)	3	10	3	8
Ysabel	2	2	3	—
New Britain	5	7	5	8
Thailand	3	2	1	1

A two factor ANOVA was run for subspecies, sex and island for skull and external characters. From Table 2 there was significant sexual dimorphism in 8 of the 23 skull characters. These were GSL, OCL, IOB, BCW, DL, RAL, C^1-M^3L, C^1-M^3L. The most pronounced dimorphism was in greatest skull length, dentary length, and C1-M3 length. There was no significant dimorphism in external measurements (Table 2). There were very significant ($p << .001$) differences for all measurements between islands for the combined sexes and a weakly significant interaction between sex and island for four skull characters (CCL, CL, DL and C^1-M^3L). The MANOVA also indicated that there was a significant difference between both the sexes (Hotellings Test = 0.577, P = 0.03) and the islands (Hotellings Test = 19.846, $P << .001$), but did not show a significant interaction between these effects (Hotellings Test = 3.940, P = 0.486).

As a consequence, subsequent analysis of *H. diadema* subspecies will combine males and females when external characters are being considered, but will treat males and females separately for skull characters.

(b) Principal component analysis (all specimens)

External characters — seven external characters were used (weight and ear length excluded). The analysis (males and females combined) extracted three factors (Table 3a) which together explained 96.6 percent of the variation (Factor 1 — 86.8, Factor 2 — 5.9 percent and Factor 3 — 4.0 percent). The plot of Factors 1 and 2 (Figure 15a) shows that *H. d. oceanitis* clusters distinctly from the other subspecies, with the separation on Factor 1. This Factor is strongly influenced by the majority of external measurements, except phalanx 1 digit 3 and tibia length and probably reflects its smaller overall body size. Separation between the other species is largely on Factor 2; on this Factor *H. d. nobilis* clusters distinctly from *H. d. griseus, H. d. reginae* and *H. d. masoni* — but these latter three subspecies merge on this Factor. However, *H. d. reginae* and *H. d. masoni* separate on Factor 3 (Figure 15b) which is most strongly influenced by phalanx 1 digit 3 (averages longer in *H. d. masoni*, 28.7 *v.* 25.9). *H. d. nobilis* and *H. d. diadema* cluster together on all Factors; the latter subspecies also are not separable from *H. d. griseus, H. d. reginae* or *H. d. masoni.*

Skull characters. Twenty-three skull characters were used in this analysis (males and females separately).

Males — the PCA extracted three Factors (Table 3b) which combined explained 74.4 percent of the variation (Factor 1 — 58.5 percent, Factor 2 — 9.3 percent and Factor 3 — 6.7 percent). The plot of Factors 1 and 2 (Figure 16a) indicates that several of the subspecies cluster distinctly. Only *H. d. diadema, H. d. reginae* and *H. d. masoni* cluster together; these are not separated by other combinations of Factors 1, 2 or 3. The separation between these subspecies is mainly on Factor 1. Most characters load heavily and positively on this Factor, except nasal length, minimum interorbital distance and distance between cochlea (Table 3b). This suggests that overall size of skull, teeth and dentary are important in separating these groups.

Females — The 3 Factors extracted by the PCA combined explained 67.5 percent of the variation (Factor 1 — 49.8 percent; Factor 2 — 10.5 percent; Factor 3 — 7.2

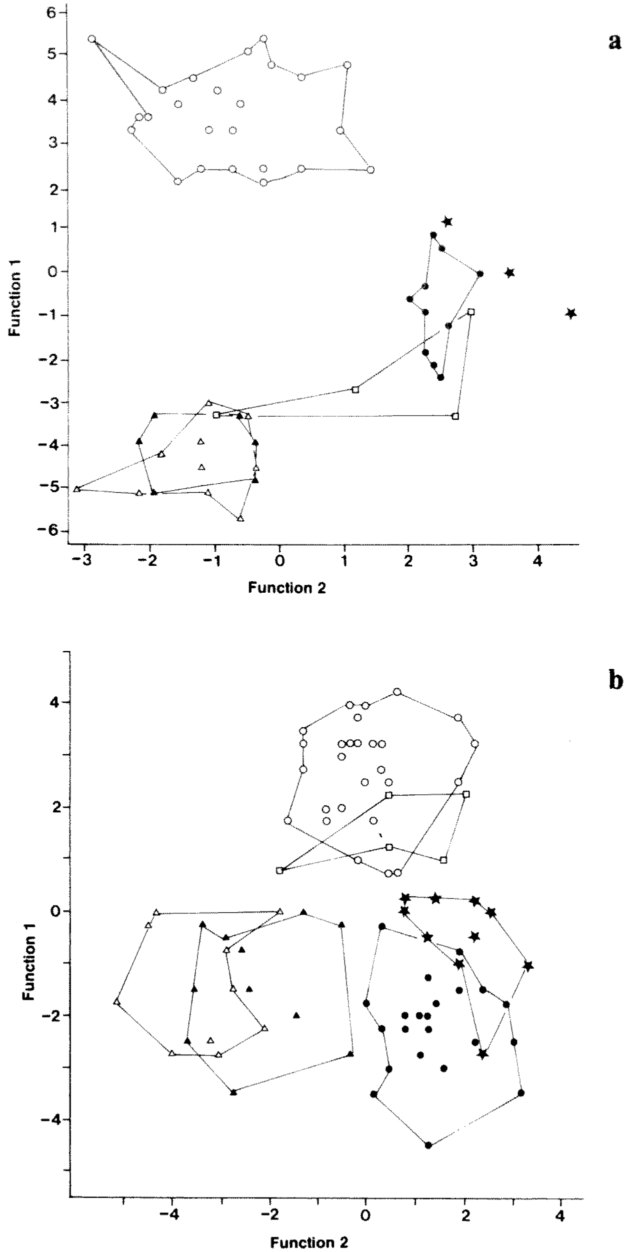


Figure 19 Canonical variate analysis based on skull measurements of *Hipposideros diadema* subspecies. Plot of functions 1 and 2 for (**a**) males and (**b**) females. Subspecies codes as for Figure 2.

percent, Table 3b). The plot of Factors 1 and 2 (Figure 16b) indicate a similar trend to Figure 16a but with the clusters less discrete. Again the separation between these groups is mainly on Factor 1 with characters loading on this Factor as for the males (Table 3b).

(c) Principal Component Analysis (Lombok and Sumbawa specimens only)

The two subspecies of *H. diadema* in the Lesser Sunda Islands interface between the narrow, (14 km) shallow strait between Lombok and Sumbawa (Selat Alas).

The PCA analysis of 23 skull characters (males and females combined) for the Lombok and Sumbawa specimens, representing respectively *H. d. nobilis* immediately to the west and *H. d. diadema* immediately to the east of Selat Alas, extracted three factors. These factors combined explained 73 percent of the variation (Factor 1 — 56.7 percent,; Factor 2 — 10.8 percent; Factor 3 — 5.4 percent). The plot of Factor 1 and Factor 2 (Figure 17) indicates that the closely adjacent Lombok and Sumbawa populations cluster separately and maintain their distinct morphological identity.

(d) Descriminant Function Analysis

(i) *External characters* (males and females combined, excluding weight and ear length)

The first three canonical variate functions, combined explained 97.4 percent of the variance (Table 4a). Function 1, which explained 70.4 percent of the variance, appeared to be most influenced by metacarpal 3 length (D3ML) and then metacarpal 2 length (D2ML); Function 2 (22.7 percent) appeared to be most influenced by tibia length (TIL); and Function 3 (4.4 percent) appeared influenced most by metacarpal 4 (D4ML) but the other characters were also important (Table 4a).

The plot of Functions 1 and 2 (Figure 18) provided the best separation of the *H. diadema* subspecies considered. Plots of Functions 1 and 2 separately with Function 3 did not provide noted further clarification or separation of the groups.

A plot of the first two discriminant functions (Figure 18) reveals separation of *H. d. oceanitis* from the other subspecies. Also *H. d. reginae* is separate from both *H. d. diadema* and *H. d. nobilis* and *H. d. griseus* is separate from *H. d. nobilis*. Function 1 provided complete separation only for *H. d. oceanitis*, but *H. d. nobilis* was also reasonably separate from *H. d. griseus* on that Function. Function 2 provided almost complete separation of *H. d. reginae* from *H. d. oceanitis* and *H. d. nobilis*, it also allowed complete separation between *H. d. masoni* and *H. d. oceanitis.*

Of the cases, 76.4 percent were correctly classified. With *H. d. diadema* 63.9 percent were correctly classified; incorrect classifications were: 16.7 percent as *H. d. nobilis,* 5.6 percent as *H. d. griseus*, 2.8 percent as *H. d. oceanitis* and 11.1 percent as *H. d. masoni.* With *H. d. nobilis* 79.6 percent were correctly classified; incorrect classifications were: 13.0 percent as *H. d. diadema*, 3.7 percent as *H. d. griseus* and 3.7 percent as *H. d. masoni.* With *H. d. griseus* 58.8 percent were correctly classified; incorrect classifications were: 11.8 percent as *H. d. diadema*, 5.9 percent as *H. d.*

nobilis, 17.6 percent as *H. d. reginae* and 5.9 percent as *H. d. oceanitis*. With *H. d. reginae* 81.8 percent were correctly classified; incorrect classifications were: 18.2 percent as *H. d. griseus*. With *H. d. oceanitis* 100 percent were correctly classified. With *H. d. masoni* 66.7 percent were correctly classified; incorrect classifications were: 16.7 percent as both *H. d. griseus* and *H. d. reginae*.

(ii) *Skull characters* (male and female analyses separate, excluding premaxilla length).

Males — The first three canonical variate functions combined explained 94.5 percent of the variation (Table 4b). Function 1 which explained 70.9 percent of the variance, appeared to be most influenced by characters GSL, CCL, CL, OCL, ZW, DL, M^3-M^3W, C^1-M^3L, M^2L. These are characters related to overall size of the skull, teeth and dentary. Function 2 (16.0 percent) appeared most influenced by GSL, CCL, CL, NB, C_1-M_3L, M^3L which relate to overall length of the skull, nasal breadth and length of teeth. Function 3 (7.6 percent) was most influenced by GSL, ZW, DL, M^3-M^3W and M^3L which again relate to overall length and width of skull and dentary and M^3 length (Table 4b).

The plot of Functions 1 and 2 (Figure 19a) provided the best separation of *H. diadema* subspecies. Plots of other combinations of Functions 1, 2 and 3 did not notably clarify the clusters. From Figure 19a it is apparent that *H. d. nobilis* males separated from the other subspecies on Function 1, suggesting that it is distinguished from them by its much larger and more robust skull and dentition. The other subspecies are arranged as a continuum of clusters that separate partially on Function 2. For example, *H. d. oceanitis* separate from *H. d. masoni, H. d. diadema* and *H. d. reginae* but not from *H. d. griseus*. *H. d. masoni* is not separated from either *H. d. diadema* or *H. d. griseus*. Again these would appear to be separated by length of skull, nasal shape and length of teeth.

Of the cases considered, 94.8 percent were classified to their correct subspecies when all three Factors were considered. With *H. d. diadema, H. d. nobilis, H. d. reginae* 100 percent were correctly classified. With *H. d. griseus* 83.3 percent were correctly classified; 16.7 percent were incorrectly classified as *H. d. oceanitis*. With *H. d. oceanitis* 90.9 percent were correctly classified; 9.1 percent were incorrectly classified as *H. d. griseus*. With *H. d. masoni* 75.0 percent were correctly classified; 25.0 percent were incorrectly classified as *H. d. diadema*.

Females — The three canonical variate Functions produced explained 91.1 percent of the variance. Function 1 which explained 44.6 percent of the variance appeared to be most influenced by characters related to overall skull and dentary length (DL, CCL) (Table 4b). Function 2 (28.6 percent) appeared most influenced by characters related to shape of nasal (NB)) and, length and width of skull (CCL, ZW, M^3-M^3W) Function 3 (17.9 percent) appeared most influenced by characters related to length of dentary (DL), cranial length (CL), distance between molar rows (M^3-M^3W) and length of part of lower tooth row (C_1-M_3L).

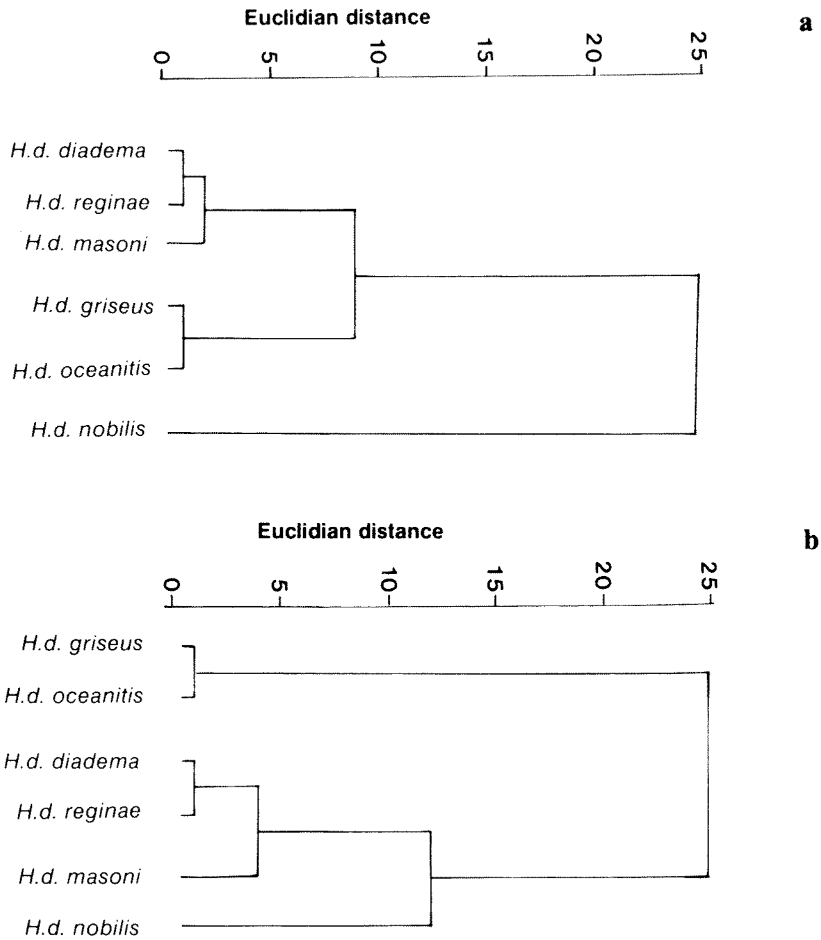


Figure 20 Phenetic relationships of the subspecies of *Hipposideros diadema* examined derived by UPGMA analysis on skull plus external measurements for (**a**) males and (**b**) females.

The plot of Functions 1 and 2 for females (Figure 19b) is similar to males (Figure 19a) (*H. d. masoni* separates from *H. d. nobilis* in discriminant function space when Factor 3 is also considered).

Using all three canonical variate functions 92.0 percent of all cases were correctly classified to their subspecies. With *H. d. diadema* and *H. d. reginae* 100 percent were correctly classified. With *H. d. nobilis* 92.9 percent were correctly classified; 7.1 percent were incorrectly classified as *H. d. masoni*. With *H. d. griseus* 81.8 percent were correctly classified; 18.2 percent were incorrectly classified as *H. d. oceanitis*. With *H. d. oceanitis* 80.0 percent were correctly classified; 20.0 percent were

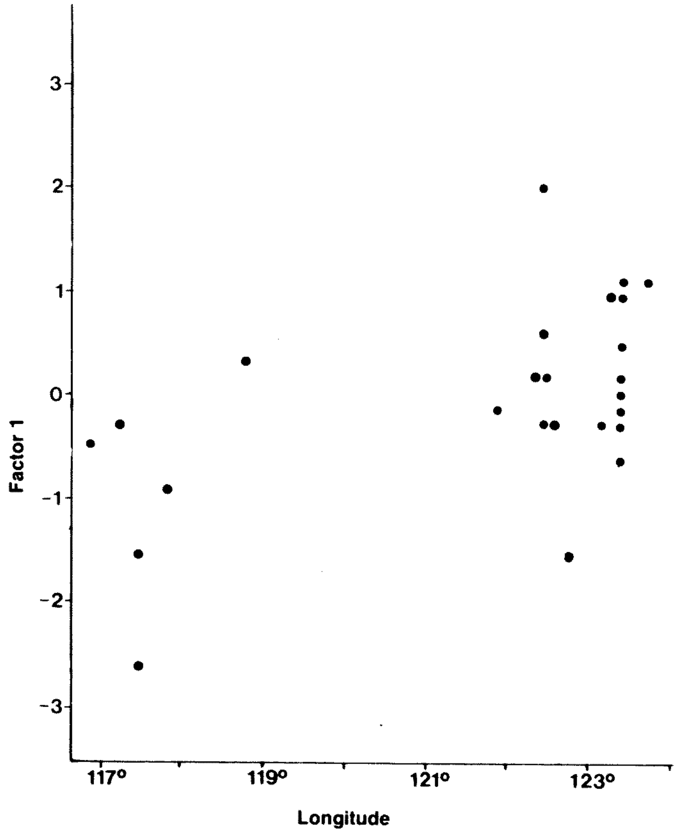


Figure 21 Plot of the first principal component factor score based on skull measurements of individual female *Hipposideros d. diadema* against the longitude of their collection sites.

incorrectly classified as *H. d. griseus*. With *H. d. masoni* 80.0 percent were correctly classified; 20.0 percent were incorrectly classified as *H. d. griseus*.

It appears that *H. d. nobilis* separates from most other subspecies on characters strongly influenced by overall skull and dentary length, but separates from *H. d. masoni* on Factor 3, which is also influenced by C_1-M_3 and width between molar rows (M^3-M^3W). The other subspecies are likely to be separated by the size and shape of their dorsal skull, particularly the nasal region.

Phenetic relationships

The UPGMA analysis of *H. d. diadema* subspecies was run for males and females separately against both skull and external characters separately and combined. These

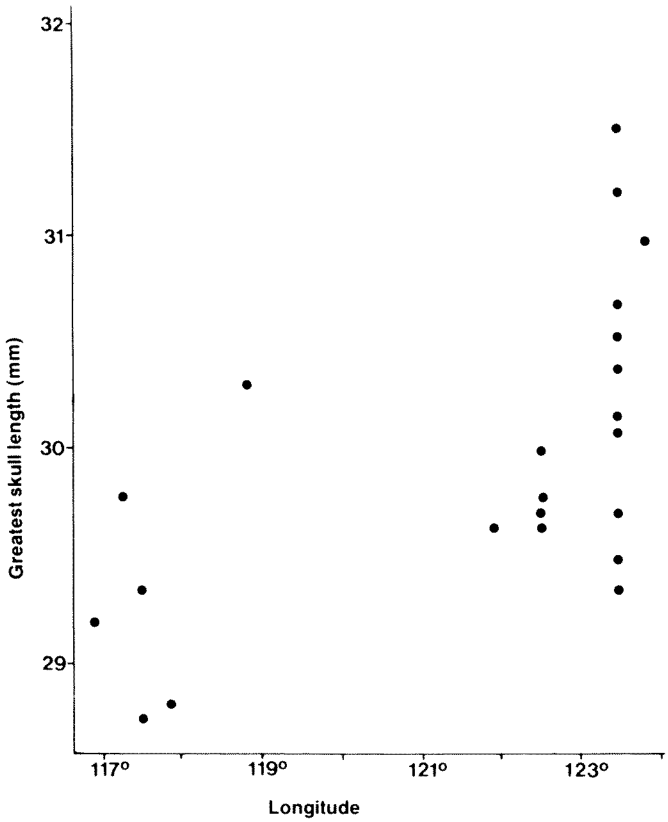


Figure 22 Plot of the greatest skull length of individual female *Hipposideros d. diadema* against the longitude of their collection sites.

two treatments produced very similar dendrograms so we present only the latter results. For males (Figure 20a), *H. d. nobilis* is phenetically very distinct from the other subspecies. The other subspecies fall into two groups. One group closely linking *H. d. griseus* and *H. d. oceanitis* and the other group closely linking *H. d. diadema, H. d. reginae* and *H. d. masoni* but with the latter subspecies slightly less closely related. The relationships for females (Figure 20b) are very similar, to the situation in the males. Once again it closely links *H. d. griseus and H. d. oceanitis* but places this group as distant from the other subspecies. *H. d. nobilis* is again separated from *H. d. diadema, H. d. regina* and *H. d. masoni;* these latter three subspecies again form a tight group, especially *H. d. diadema* and *H. d. reginae.*

Geographic variation in H. d. diadema

Factor 1 of the PCA analysis in the *H. diadema* subspecies considered appears to reflect in large part overall size in skull and external characters of specimens. For this reason the PCA Factor 1 scores of individual specimens was used as a measure of the specimen's overall size. This score was then associated with the specimen's latitude and longitude using stepwise multiple regression analysis. Skulls of males and females were analysed separately. External measurements were combined for males and females. The same analyses were then repeated using greatest skull length, radius length and body weight as direct measurements of size.

Skull characters

Females

Longitude is significantly correlated with the skull Factor scores obtained from PCA of *H. d. diadema* specimens only. ($F_{1,21}$ = 12.745, P = 0.0018) (Figure 21). The equation representing this relationship is Factor 1 score = 0.247 longitude — 29.944 (R^2 = 0.378).

Only longitude is significantly correlated with greatest skull length ($F_{1,23}$ = 12.395, P = .0018) (Figure 22). The equation representing this relationship is greatest skull length = 0.166 longitude + 9.709 (R^2 = 0.350).

These data strongly suggest that in female *H. d. diadema* there is a clinal trend in overall skull size, with greatest skull length increasing from west to east.

Males

There was no significant correlation between Factor scores and longitude (P = 0.22) or latitude (P = 0.97).

Nor is there a significant correlation between greatest skull length and longitude (P = 0.48) and latitude (P = 0.99).

These data suggest that males do not show the cline in skull size which is apparent in females. However, there were only 11 males in this analysis. A larger sample may indicate the same trend in males that is present in females.

External characters

The analysis of external Factor scores against latitude and longitude included ear length as an external characters. There was no significant correlation between Factor scores and longitude (P = 0.30) or latitude (P = 0.45).

Nor was there a significant correlation between weight and longitude (P = 0.18) or latitude (P = 0.76) or between radius length and longitude (P = 0.15) or latitude (P = 0.51).

Discussion

This study clearly demonstrates the existence of at least two morphological forms of *Hipposideros diadema* in the Lesser Sunda Islands. The eastern form (*H. d. diadema*), which ranges from at least Timor to Sumbawa, is smaller and easily diagnosed by skull and external characters from the western form (*H. d. nobilis*). The *a priori* principal component analysis separates *H. d. diadema* and *H. d. nobilis* into distinct clusters. Their morphological distinction is still clear when PCA is applied to populations on Lombok and Sumbawa which are the islands on either side of the distributional interface between these two subspecies. These two islands are separated by a narrow (14 km) shallow strait (Selat Alas). They would have been broadly connected during the late Pleistocene (Kitchener *et al.* 1990a) allowing ready interchange between their populations of *H. diadema*. Further, evidence from Kitchener *et al.* (1990b) suggests that water gaps of this nature are not a barrier to most species of bat in this region. This coupled with the observation that *H. diadema* (? *nobilis*) crossed a 50 km water gap to recolonise Krakatau only 45 years after that island had been sterilised by volcanic eruption (Dammerman 1948), supports the belief that Selat Alas would not constitute a substantial barrier to movement of *H. diadema* between these two islands. Despite the probability of gene exchange between these close populations of *H. diadema nobilis* and *H. d. diadema* these juxtaposed subspecies retain a morphological distinctiveness that placed their males at opposite extremes of the phenetic relationships amongst the closely related subspecies examined. Their females are also considerably separated phenetically.

There is a trend within *H. d. diadema* females for overall skull size to decrease from east to west. This suggests some overall factor such as climate may be operating, because there is a trend towards moister environments from east to west as this island chain emerges from the rain shadow cast by the Australian continent. An increase in size in response to increasing climatic severity (especially aridity) is a trend observed in other bats (Findley and Jones 1967; Findley and Traut 1970; Stebbings 1973).

The westwards step from Sumbawa to Lombok results in *H. d. nobilis* on Lombok having a skull considerably larger than the Sumbawan *H. d. diadema*. This is in spite of the trend which places the Sumbawan population at the smaller end of an east-west cline in overall skull size. Clearly the selection factors operating within *H. d. diadema* to reduce its size from east to west do not have a similar influence on the Lombok *H. d. nobilis*. Perhaps this finding is in keeping with studies (Kitchener and Caputi 1985) on morphological clines in tropical Australian *Scotorepens*. That study indicated that *S. sanborni* shows a strong trend to increase in measures of overall size from west to east. However, in *S. greyii* the trend is reversed. These authors concluded that morphological clines in these species result from a complex interplay of environmental patterns.

In combination, the above observations indicate that the morphological distinctiveness between *H. d. diadema* and *H. d. nobilis* over such a narrow gap may warrant their recognition as separate species. A concurrent electrophoretic study carried out by colleagues at the South Australian Museum, on tissue collected from populations of *H. diadema* on Sumbawa and Lombok may assist with such a taxonomic decision. For the present, we tentatively retain *nobilis* as a subspecies of *H. diadema*.

This study of the taxonomy of the Lesser Sunda *H. diadema* required examination of some morphologically and geographically closely related subspecies. As a consequence, the conclusions of this study have a wider bearing on the subspecific taxonomy of *Hipposideros diadema*. In particular, we differ from most recent authors by placing the New Guinea form, *H. d. pullatus*, in synonymy with *H. d. griseus* from the Philippines. This is because we are unable to distinguish between these subspecies on size and shape, apart from the observation that the paired eminences on the nasal swelling appeared less inflated in specimens from the Philippines. Also we agree with Shamel (1942) that Thailand *H. d. masoni* have slightly longer skulls than those from the Javan form of *H. diadema* (we included some of the same specimens examined by Shamel in this study of *H. d. masoni*). However, we do not agree with Hill (1963) that *H. d. masoni* is consubspecific with the Javan form (*H. d. nobilis*).

The taxonomy of *H. diadema* in the Bismarck and Solomon Is is confused. A number of small subspecies have been described from that region (*H. d. trobrius, H. d. malaitensis, H. d. mirandus, H. d. oceanitis* and *H. d. demissus*). Additionally, Koopman (1982) notes the presence of another distinct form from Misima Island. Phillips (1967), Hill (1968) and Koopman (1982) have all commented on the distributional mosaic of smaller and larger subspecies in this region. We have examined specimens of *H. d. oceanitis* and the smaller *H. d. demissus*. These, and the other smaller forms referred to above, are not closely related to the subspecies of *H. diadema* considered in this paper — nor is the small *H. d. inornatus* from Northern Territory, Australia. The taxonomic status of these smaller forms will be examined in a separate paper.

Hipposideros diadema oceanitis from the Solomon islands is quite distinct from the other subspecies examined in both the Principal Component and Discriminant Function Analyses. However, the UPGMA analysis indicate that it is very closely related to *H. d. griseus* from Papua New Guinea and the Philippines.

Hipposideros diadema reginae from Queensland, Australia is very closely related phenetically to *H. d. diadema* of Nusa Tenggara. This conflicts with the statement by Koopman (1984: 11) that neither of the Australian *H. diadema* subspecies "has any close affinity with the still larger *H. d. diadema* of the Lesser Sundas". It is also reasonably closely related to *H. d. masoni* from Thailand and Malaysia. Together, these populations of *H. diadema* stand apart from those of New Guinea and the Solomon forms. The relationships of *H. d. reginae* suggests that it reached Australia from the Lesser Sundas rather than from the New Guinea-Cape York route.

Koopman (1982) correctly cautioned against the naming of island forms of *H. diadema* without first considering variation within the species over a wide range. *H. diadema* subspecies vary in their morphology over their distribution as demonstrated in this study with *H. d. diadema*. This variation may be expected to be emphasised by the requirement of this species for large caves which presumably restrict their general movements to the locality of such caves — although we have mentioned their ability to move substantial distances on occasions.

Evidence from the Lesser Sundas indicates that these subspecies may have a wide distribution and occupy a number of islands that have never been connected; e.g., the inner and outer Banda island groups. Consequently many small island populations of the subspecific *H. diadema* in the Moluccas, Solomons, Bismarcks and other islands: Nicobar, Engano, Bungaran, Kalao, Kei may, after a comprehensive revision of the species, result in a number of them being recognised as consubspecific with the forms considered herein. This is particularly likely with subspecies on islands on or close to the Sunda Shelf e.g., (*H. d. nicobarensis; H. d. enganus; H. d. natunensis*). If this proves to be the case, then the stability of some of the subspecies names used in this paper may be affected. For example, if the Nicobar I. population were shown to be consubspecific with that from Burma, then *H. d. masoni* would be replaced by *H. d. nicobarensis*. However, other populations of *H. diadema* on small islands were named after 1900. Consequently, the nomenclature of the other subspecies considered here are unlikely to be affected by such synonymy because their names would have priority.

A principal reason for carrying out our series of mammal surveys on islands throughout the Lesser Sundas was to examine distributional trends of species along this island chain and, with selected species, also examine morphological and genetic changes that occur between their populations on different islands. These data, coupled with comparisons between island mammal faunas in the region, will be used to examine the nature of the interface between the Australian and Oriental Biogeographic Regions — traditionally placed between Lombok and Bali. However, a great deal of systematic work remains to be done on mammals of this region before we can clarify its mammalian biogeography. Recent studies suggest that there is much more mammal endemicity in the Lesser Sundas than was previously supposed (Kitchener *et al.* 1990a, b; Kitchener *et al.* 1991a-d); Kitchener and Maharadatunkamsi (1991).

Kitchener *et al.* (1990a, b) suggested that the water gap between Bali and Lombok was not a barrier to the distribution of bats and did not mark an important biogeographic boundary for bats. This study would tend to support this view, with the demarcation between subspecies of *H. diadema* in this region being placed to the east of Lombok.

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Appendix I: Specimens examined. All adults, 'alcoholic' specimens except where the numbers are affixed with S — which are 'cabinet' skins.

Hipposideros d. diadema

INDONESIA

Flores I.:	Ratulodong, 8°11'S, 122°52'E, WAM 32557, WAM 32560, WAM 32562, WAM 32565-7, WAM 32581-2, WAM 32558, WAM 32583 (8 ♀♀, 2 ♂♂).
Moyo I.:	Tanjung Pasir, 8°23'15S, 117°31'30"E, WAM 31950, WAM 31993 (2 ♀♀).
Roti I.:	Baa, 10°44'S, 123°06'E, WAM 35430 (♀); Oeseli, 10°51'S, 123°05'E, WAM 35495-96 (2 ♂♂).
Savu I.:	Menia, 10°29'S, 121°55'E, WAM 35210 (♀).
Sumba I.:	Waikabubak, 9°38'S, 119°31'30"E, WAM 30353-4 (2 ♂♂).
Sumbawa I.:	Batu Dulang, 8°35'S, 117°17'20"E, WAM 31756 (♀); Batu Tering, 8°48'S, 117°22'E, WAM 31138, WAM 31466-7 (3 ♂♂); Desa Bela, 8°52'S, 116°50'E, WAM 31302 (♀); Merente, 8°33'10"S, 117°01'15"E, WAM 31177 (♂); Teluk Santong, 8°43'40"S, 117°53'30"E, WAM 31411 (♀); Waworada, 8°42'30"S, 118°47'30"E, WAM 31672 (♀).
Timor I.:	Lifuleo, 10°18'S, 123°30'E, WAM 38039, WAM 38080-83, WAM 38086, WAM 38087-90 (9 ♀♀, ♂).

Hipposideros d. nobilis

INDONESIA

Bali I.:	c. 8°15'S, 115°00'E, WAM 16170-71 (2 ♀).
Java I.:	Cibodas, 6°45'S, 107°00'E, MZB 10374, MZB 9429, MZB 10375 (♂, 2 ♀♀); Cidalog, 7°14'S, 106°54'E, MZB 12786 (♀); Liampea, 6°32'S, 106°40'E, MZB 9426, MZB 9428 (2 ♀♀); Sukambumi, 7°15'S, 106°50'E, WAM 30022 (♀); Gua Ciampea, 6°32'S, 106°40'E, MZB 14787 (♂); Guharatu (C. Java) MZB 9415, MZB 9410, MZB 943 (3 ♂♂).
Lombok I.:	Kuta, 8°55'S, 116°17'E, WAM 31105, WAM 33765-75, WAM 33900-03 (8 ♂♂, 8 ♀♀); Suranadi, 8°33'30"S, 116°14'E, WAM 33761-4, WAM 35738 (2 ♂♂, 3 ♀♀);

Pringgasela, 8°36′S, 116°29′E, WAM 35741, WAM 35744 (2 ♂♂); Lendi, 8°35′S, 116°31′E, WAM 35729, WAM 35742-3 (2 ♀♀, ♀); Lenele 8°37′S, 116°30′E, WAM 35733, WAM 35747 (2 ♂♂); Tebabian, 8°37′S, 116°30′E, WAM 35736-7 (2 ♀♀); Terowangan Air 8°37′S, 116°30′E, WAM 35731-2, WAM 35735 (1 ♂, 2 ♀♀); Lombok, WAM 35740, WAM 35745 (2 ♂♂).

Nusa Penida I.: 8°45′S, 115°30′E, MZB 14828, MZB 14845 (♂, ♀).

BORNEO

Sabah,

Bode River: Sepagaya Forest Reserve, 5° S52′N, 118°04′E, FMNH 76960 S (♂); Kalimantan, Ritan River (*c.* 0°50′N, 115°45′E), FMNH 44125-6 (♂♀); S. Kalimantan, WAM 27605 S (♀); N. Borneo, AM 6242 (♂).

Hipposideros diadema griseus

PAPUA

NEW GUINEA: Doido, 6°32′S, 144°51′E, AM 15103 (♀); Lawarere, 9°25′S, 147°26′E, AM 15089-90, AM 15095 (2 ♂♂, ♀); Mt Missim, 7° 15′S, 146°47′E, AM 19554 (♂); Tedebeoi Village, AM 19102 S (♀); Waro Swamp, 6°31′S, 143°11′E, AM 15200 S (♂); Baiteta, 5°20′S, 145°44′40″E, WAM 27484, WAM 27486 (2 ♀♀).

PHILIPPINES: Busuanga I., 6 km NE of San Nicolas, 12° 10′N, 120°05′E, S 477700 S, S 477703 S, S 1477715 S (2 ♂♂, 1♀); Luzon I., 4 mi W of Ipo Dam, 14°53′N, 121°08′E, S 304073 S (♀); Clark Air Base, 14°50′N, 120°30′E, S 304074 S, 51304076 S (♂ ♀); Mindanao I., Matam Sapinit Cave, 8°28′N, 123°07′E, FMNH 80371 S (♀); Negros I. **c.** 9°N, 123°00′E, WAM 29051-2 (2 ♀♀); Palawan I. St Pauls Cave, 10° 12′N, 118°50′E, AM 12412 (♀).

Hipposideros diadema reginae

AUSTRALIA

Queensland: Bourne Creek, 13°39′S, 143°03′E, JM 3505 (♀); Buthen Buthen, 13°23′S, 143°27′E, JM 2452-3, JM 2468 (3 ♀♀); c. 5 km WSW of Buthen Buthen, 13°24′S, 143°25′E, JM 2472 (♀); Rocky Scrub, 13°44′S, 143°22′E, JM 3504 (♀); Steenes Shack, 13°46′S, 143° 12′E, JM 2411 (♀); West Claudie River, 12°44′S, 143° 19′E, JM 2383, JM 2402, JM 3507, AM 8106 S, AM 13337, JM 9492 (4 ♂♂, 2 ♀♀); Attack Creek, 13°30′S, 143° 15′E, JM 2419 (♀).

Hipposideros diadema masoni

MALAYSIA: Batu Caves, 3° 16′N, 101°39′E, FMNH 109556 (♀); Bentong, 3°35′N, 101°54′E, FMNH 98689-90 S (2 ♀♀); Kepong Forest Reserve, 3° 12′N, 101°38′E, FMNH 82278 (♂).

THAILAND: Koh Lak, nr Prachuap Khiri Khan, (11°50′N, 99°49′E); S 258945-6 S (2 ♀♀); Seechol, (= Ban Sichon, 9°00′N, 99°56′E, S 255767 S (♂); Thailand, FMNH 48848, (♂).

Hipposideros diadema oceanitis

SOLOMON ISLANDS

NEW GUINEA Ysabel I.:

c. 8 km E Mufu Point, *c.* 8°00S, 159°00′E, AM 3579, AM 3969-71, AM 3974 (3 ♂♂, 2 ♀♀).

Florida Is: Mboli Caves *c.* 9°00′S, 160°00′E, AM 7857 (♂);

Guadalcanal I.: Lavaro Platations, *c.* 9°30′S, 160°00′E, AM 3496 AM 3498 (♀, ♂).

New Ireland I.: nr Lakuramau, 2°54′S, 151°16′E, AM 20089 AM 20091 (2 ♂♂).

New Britain I: Melai, nr Fulleborn, 6°6′S, 150°40′E, AM 20092 (♀); nr Waipo, 5°58′S, 150°43′E, AM 20093 (♀), AM 20095-7 (3 ♀♀), AM 20099-101 (3 ♀♀), AM 20104-5 (2 ♂♂), AM 20107, AM 20109, AM 20111 (3 ♂♂).

Bougainville I.: Bouin District, AM 6578 (♀).

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