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Description of a new species of *Cynopterus* (Chiroptera: Pteropodidae) from Nusa Tenggara, Indonesia.

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Abstract

The taxonomy of small (forearm length <75 mm) members of the '*Cynopterus* Section' of Andersen (1912) is examined. *Cynopterus nusatenggara* sp. nov. is described from Lombok, Sumbawa, Moyo and Komodo Is. *C. minutus* Miller, 1906 is a species from Nias I., Sumatra, Java, Borneo and Sulawesi. *C. luzoniensis* (Peters, 1861) is from Sulawesi, Philippines and adjacent small islands; *C. brachyotis* (Müller, 1838) is redefined; its distribution includes Sri Lanka, Peninsula Malaysia, Penang I., Singapore I., Sumatra, Borneo, Pulau Laut (I.), Bunyu I., Java, Pulau Dua (I.), Madura I., and Bali I. *C. sphinx* is widely distributed from Sri Lanka, India, through Burma, Malaya, Sumatra, Borneo, Java, Sulawesi and many small islands. Within these species are recognisable geographic forms requiring further clarification.

Introduction

Recent vertebrate biological surveys in Nusa Tenggara, Indonesia, carried out by us, in conjunction with colleagues from the Western Australian Museum and Museum Zoologicum Bogoriense, resulted in the collection of an undescribed form of *Cynopterus* on Lombok, Sumbawa, and Moyo islands. Specimens of this form are also present in collections from Komodo I., Nusa Tenggara. The determination of the taxonomic status of this form is the substance of this paper.

According to Tate (1942), morphological differences, apart from overall size, between members of *Cynopterus* are not clearly definable. He stated that even in size, considerable overlap exists between every species in Andersen's (1912) listing of the dimensions of *Cynopterus* spp. Further, he notes that within a series from one locality, pelage colour is frequently variable. Tate (1942) does, however, allow that Andersen's (1912) separation of his '*Cynopterus* Section' and '*Niadus* Section' within this genus is based on seemingly consistent characters. Members of the '*Cynopterus* Section' were seen to differ from those in the '*Niadus* Section' by the oval rather than squarish outline of their cheek teeth, but more particularly by the absence or poor development of surface cusps on P_4 and M_1. Only *C. archipelagus* Taylor, 1934 was considered by Tate (1942) to be difficult to place in these 'Sections' because from its description it appeared to be somewhat intermediate between the 'Cynopterus' and 'Niadus' Sections.

The new form from Nusa Tenggara is clearly a member of the '*Cynopterus* Section' and as such is compared to members of this group in this paper. While this comparison is based on morphology, because the traditional approach has resulted in unsatisfactory diagnoses (Tate 1942), and not withstanding Hill (1983: 118), we have used a

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multivariate statistical approach to assist the diagnosis of this new form and its morphologically close congeners. As a result of these comparisons this new form is herein described as a new species.

Members of the *'Cynopterus Section'* of Andersen (1912)

Andersen (1912: 596) lists 30 proposed names for *Cynopterus* — of which he recognised only 16 as taxonomically valid forms. Since then six new forms have been named: *Cynopterus sphinx babi* Lyon, 1916; *C. archipelagus* Taylor, 1934; *C. terminus* Sody, 1940; *C. brachyotis concolor* Sody, 1940; *C. b. altitudinis* Hill, 1961; and *C. sphinx serasani* Paradiso, 1971.

There has been no comprehensive review of *Cynopterus* since Andersen (1912) whose classification of this group was followed by both Chasen (1940) and Tate (1942), except for the following: the placement of *C. major* Miller, 1906 as a subspecies of *C. sphinx* Vahl, 1797 by Chasen (1940) and the removal of *C. pagensis* Miller, 1906 from synonymy with *C. s. angulatus* and its placement as a subspecies of *C. brachyotis* by both Chasen (1940) and Tate (1942).

Hill (1983) briefly stated his classification of a number of forms of *Cynopterus* in the Indo-Australian region which took into consideration his earlier treatment of some members of this genus (e.g. Hill and Thonglongya 1972). Hill's (1983) classification offers some considerable departures from previous ones. For example, he considered *titthaecheilus* a species and removed it from its placement as a subspecies of *C. sphinx* where it had been placed by earlier workers. He also removed *angulatus, scherzeri, babi* and *pagensis* from *C. brachyotis,* where they had been placed as a subspecies by Chasen (1940) and Tate (1942), and listed them instead as a subspecies of *C. sphinx.* Hill (1983) also lists *major* as a subspecies of *C. titthaecheilus* rather than of *C. sphinx.* He also recognised *C. terminus* as a possible valid species rather than a subspecies of *C. sphinx* as it was considered by Sody (1940).

We largely follow the classification of Hill (1983) except we consider *C. minutus* Miller, 1906 is a species and not a subspecies of *C. brachyotis. C. luzoniensis* (not treated by Hill (1983)), is considered a species and not a synonym of *C. b. brachyotis* as listed by Andersen (1912).

We consider the '*Cynopterus* Section' to now comprise the following members:

'*Cynopterus* Section' (Andersen, 1912)

Cynopterus sphinx sphinx (Vahl, 1797)	Sri Lanka, peninsular and N.E. India, Burma
C. s. scherzeri Zelebor, 1869	Car Nicobar I.
C. s. serasani Paradiso, 1971	Serasan I., Natuna I.
C. s. babi Lyon, 1916	Babi I.
C. s. gangeticus Andersen, 1910	C., N.W. India
C. s. pagensis Miller, 1906	Mentawai Is

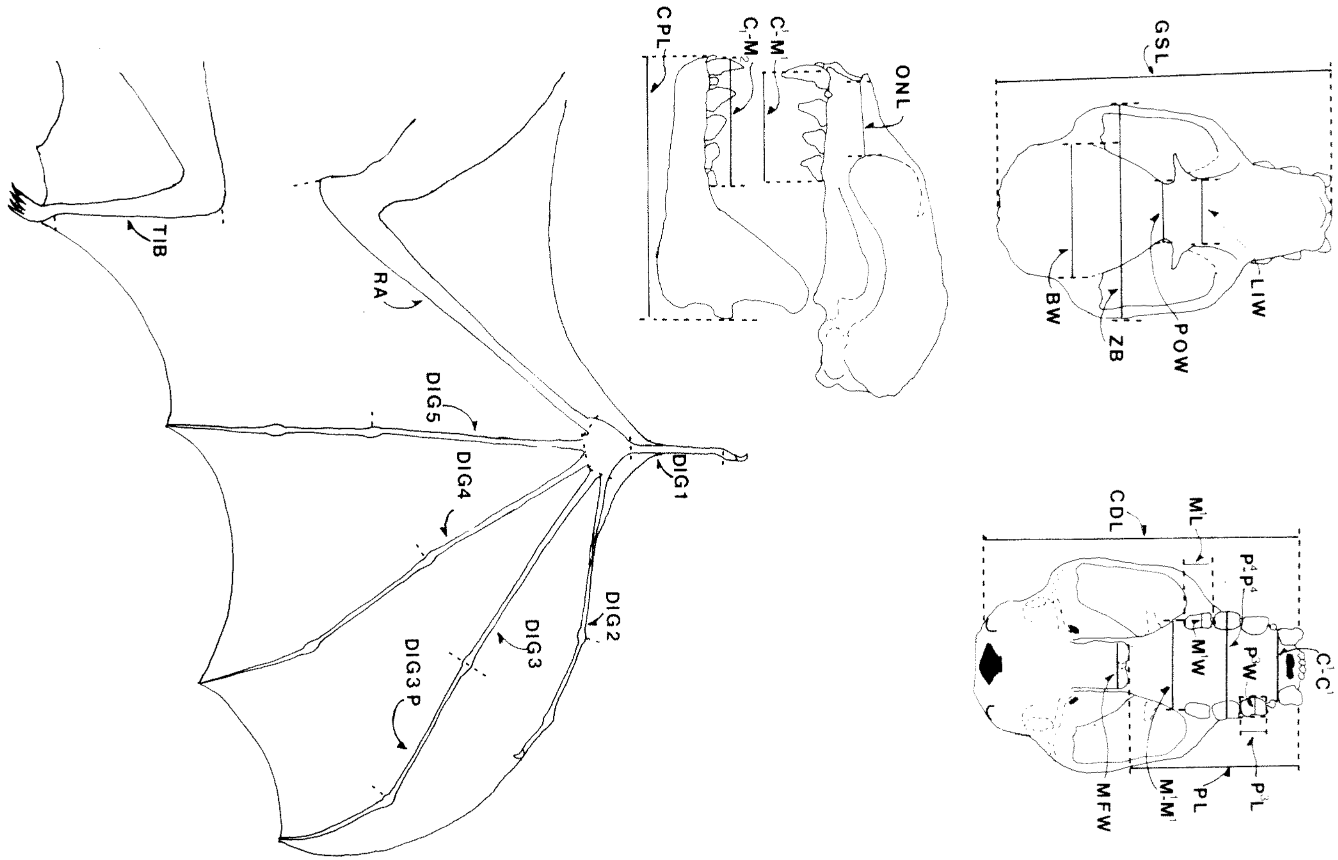


Figure 1 Measurement points for skull and externals of *Cynopterus* spp.
BW, braincase width; CDL, condylobasal length; CPL, dentary condyle to tip of dentary; GSL, greatest skull length; PL, palate length; POW, postorbital width; LIW, least interorbital width; MFW, mesopterygoid fossa width; ONL, orbit to nasal length; ZB, zygomatic breadth; C^1-C^1, outside upper canine breadth (alveoli); P^4-P^4, outside fourth upper premolar breadth (alveoli); M^1-M^1, outside fourth upper molar breadth (alveoli); C^1-M^1, upper canine to first molar length (alveoli); C_1-M_2, lower canine to second lower molar length (alveoli); P^3W, third upper premolar width (crown); P^3L, third upper premolar length (crown); M^1L, first upper molar length (crown); M^1W, first upper molar width (crown); C^1-M^1 upper canine to first upper molar length (alveoli), C_1-M_2, lower canine to second lower molar length (alveoli); DIG1, digit 1 length; DIG2-DIG5, metacarpal length of digits 2 to 5; DIG3P, digit 3, phalanx 1 length; RA, radius length; TIB, tibia length.

C. s. angulatus Miller, 1898	N. Burma to S. China, Hainan I., Vietnam, Lankawi I., N. Malaya, Sumatra, Krakatau Is, Verlaten I. (?), Borneo, Sulawesi, Sangeang I. (?)
Cynopterus brachyotis brachyotis (Müller, 1838)	S. Burma to Vietnam, Malaya, Sumatra, Borneo and many small associated islands, Bawean I.
C. b. altitudinis Hill, 1961	Malayan highlands
C. b. concolor Sody, 1940	Enggano I.
C. b. insularum Andersen, 1910	Kangean I., Mata Siri I.
C. b. javanicus Andersen, 1910	Java, Madura I., Bali I.
C. b. ceylonensis Gray, 1870	Sri Lanka
C. b. brachysoma Dobson, 1871	Andaman Is
Cynopterus minutus Miller, 1906	Nias I., Sumatra, Java, Borneo, Sulawesi
Cynopterus luzoniensis (Peters, 1861)	Philippines, Sulawesi, Peleng I. (?), Talaud I. (?)
Cynopterus titthaecheilus titthaecheilus (Temminck, 1825)	Sumatra; Krakatau I., Sebesi I., Lombok I.
C. t. major Miller, 1906	Nias I.

Other named forms placed in synonomy with above taxa are as follows:

Cynopterus duvaucelii (E. Geoffroy, 1828)	Sumatra
C. brevicaudatum (E. Geoffroy, 1828)	Sumatra
C. diardi (E. Geoffroy, 1828)	Sumatra
C. marginatus philippensis Gray, 1870	Philippines
C. m. cumingii Gray, 1870	Philippines
C. montanoi Robin, 1881	Malacca (Kessang)
C. pusillus (E. Geoffroy, 1803)	India
C. marginatus (E. Geoffroy, 1810)	India (Bengal)
C. m. ellioti Gray, 1870	India (Dharwar, S. Bombay)
C. fibulatus (Vahl, 1797)	India (Tranquebar)
C. minor Revilliod, 1912	S.E. Sulawesi
C. archipelagus Taylor, 1934	Philippines (Polillo I.)

The forms *duvaucelii* and *brevicaudatum* were described (as *Pachysoma*) from specimens collected in Sumatra by Diard and Duvaucel. According to Andersen (1912: 619) they are "both absolutely indeterminable from the descriptions; they may be any one of the four forms of *Cynopterus* occurring on Sumatra, though judging only from the published measurements" . . . "are most probably either *C. b. angulatus* or *C. b. brachyotis*. Types probably not in existence." The forms *philippensis*, *cumingii* and *montanoi* were considered by Andersen (1912) to be synonymous with *C. b. brachyotis*. He further synonymised *pusillus*, *marginatus*, *ellioti*, and *fibulatus* with *C. s. sphinx* and *C. diardi* with *C. titthaecheilus*.

Cynopterus minor is known only from the holotype from Lambuja, S.E. Sulawesi. Hill (1983) considered that with a forearm of 53 mm it may be a young adult or an unusually small *C. brachyotis*, a view supported by Bergmans and Rozendaal (1988).

Cynopterus archipelagus from the Philippines is known only from the holotype which is a juvenile and is probably only an aberrant specimen of the more common *Cynopterus* sp. on Luzon (*C. luzoniensis* (see also Heaney *et al.* 1987)).

Some members of the '*Cynopterus* Section' are clearly distinct from the new species from Nusa Tenggara. *Cynopterus titthaecheilus* occurs sympatrically with it but it is much larger. This restricted the comparison of the new species in this study to members of *C. sphinx* and *C. brachyotis*. However, investigation of *C. brachyotis* (*s.l.*) from Sumatra, Java and Borneo indicated its occurrence at several localities with a distinct form, attributed by us to *C. minutus* (previously known only from Nias I.). Because the form *minutus* retained morphological distinctness from both *C. b. javanicus* and *C. b. brachyotis* in approximate sympatry, it is considered a species. Further, the small form of *Cynopterus* examined from the Philippines is not considered conspecific with *C. brachyotis* but is *C. luzoniensis*.

Consequently the new species of *Cynopterus* from Nusa Tenggara is herein diagnosed against *C. sphinx*, *C. brachyotis*, *C. minutus* and *C. luzoniensis*.

Materials and Methods

Specimens Examined

These specimens came from the following institutions (the abbreviations of which prefix specimen numbers listed in Appendix I):

WAM = Western Australian Museum, Perth
MZB = Museum Zoologicum Bogoriense, Bogor
ZRC = Zoological Reference Collection, University of Singapore
BMNH = British Museum (Natural History), London
AMNH = American Museum, Natural History, New York

Measurements (in mm)

Twenty measurements of skull, dentary and dental characters (hereafter referred to as skull characters) and 8 of external characters and weight, where it was available (in gms), were recorded from adult specimens listed in Appendix I. Measurement points for skull and external characters are shown in Figure 1.

Specimens were judged adult if the skull basioccipital suture was closed and phalangeal joints of wing bones were not swollen.

Pelage and skin colour

These colours were determined using Ridgway (1912). Where Ridgway's terms are used the colours are capitalised. However, some of these terms are not immediately recognisable and are translated (in brackets) into simpler words.

Morphometric analyses

Only adults with complete data sets were included in the statistical appraisal. Means, standard deviations and ranges were computed for skull and external body (wing and tibia) characters. Sexual dimorphism was examined using a two factor MANOVA of each of the skull and external characters for the factors, species and sex.

Principal component analysis, based on a correlation matrix of all measured characters using varimax rotation, was performed. The first three principal component scores were examined. This *a priori* clustering procedure did not produce any definable species group clusters so the data are not presented. Canonical variate (discriminant) analysis was then performed on all measured characters for the species as recognised by us.

Measured characters important in discrimination between these *Cynopterus* spp. using both stepwise discriminant function analysis and examination of characters in the canonical variate analysis which weigh heavily on one or more functions. Univariate plots of all combinations of characters seen as important were examined to detect single combinations of characters to discriminate between species.

In the case of individual *Cynopterus* that cannot be classified to species using the diagnostic descriptions supplied, they may be classified by calculating their canonical variate coefficients using Table 2 and plotting their coefficients on Figures 24 and 25.

All the above analyses were performed using both z-values and unscaled values, but because results were very similar only those from unscaled data are presented. All analyses were performed on a COMPAQ computer using SPSS/PC+.

***Cynopterus nusatenggara* sp. nov.**

(Table 1: Figures 2-15)

Holotype

WAM M31335 (field number S222); currently the holotype is in the Western Australian Museum, but its final lodgement will be the Museum Zoologicum Bogoriense, Bogor, Indonesia. Adult female, teats enlarged but not lactating; skull and mandible separate; carcass with tongue intact, fixed in 10 percent formalin and preserved in 70% ethanol; skin prepared as a cabinet specimen. Blood and liver samples held in ultrafreezer at Western Australian Museum.

Type Locality

Desa Belo, Jerewah, West Sumbawa Island, Nusa Tenggara Barat, Indonesia (8°52'S, 116°50'E); mist netted by D.J. Kitchener, R.A. How and Maharadatunkamsi on 15 May 1988 from the boundary between dense, tall, mixed evergreen lowland rainforest and ricefields at an altitude of ± 40 m (Figure 2).

Paratypes

Listed in Appendix I.

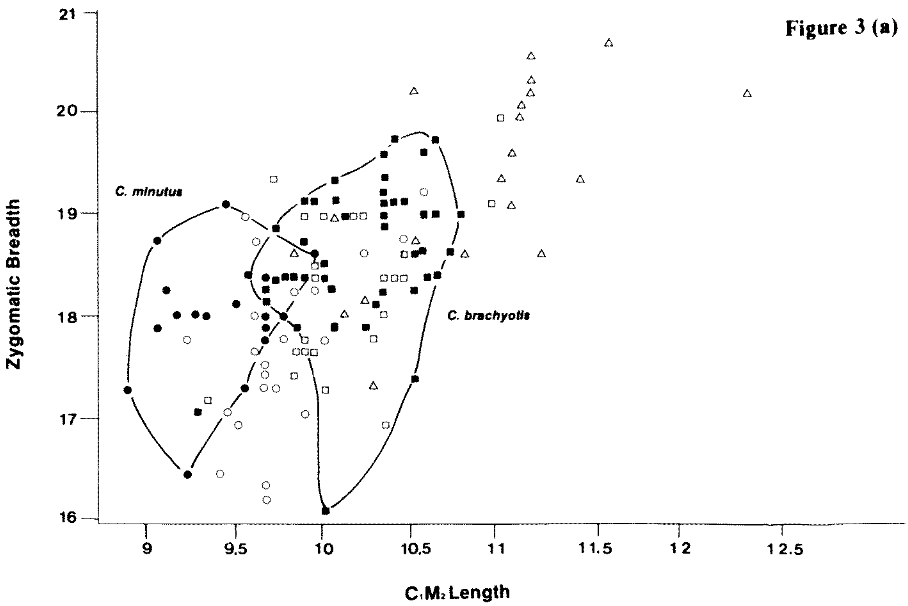
Diagnoses

Cynopterus nusatenggara differs from *C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis* in having margin of ear without white or light coloured edge — this white trim is particularly noticeable on anterior margin of ear of these other species, (except for

Figure 2 Photograph of type locality of *Cynopterus nusatenggara*. Capture site was at boundary of rice fields and lowland rainforest near Desa Belo, West Sumbawa.

Sangeang I. population, tentatively attributed to *C. sphinx*); it differs in that the surfaces of metacarpals and phalanges are not strikingly lighter than patagia colour and so do not form such contrasting lines against wing membranes; hair of head contrastingly darker than hair of back, whereas these other species have hair of head the same colour or only slightly darker; it differs in that P^3 lingual cusp connected to base of taller labial cusp by a commissure than runs at right angles to axis of molar row, or slightly forward of this angle (Figure 13a) (except for the Sangeang I. population, tentatively attributed to *C. sphinx*). In these other *Cynopterus* spp. this commissure is angled posterior of this right angle (Figure 13b). It also differs in having P^4 with low lingual cusp separated from its labial cusp by a basin that is frequently raised between these cusps and slopes gently from this raised surface both anteriorly and posteriorly but not forming a definite ridge between these cusps (Figure 13a) as in these other *Cynopterus* spp. (Figure 13b).

It also differs from *C. sphinx* in that it averages smaller for all measurements except P^3W and M^1L in females (Table 1): e.g., ♀♀-GSL 28.1 (26.0-29.9) *v.* 30.3 (28.1-32.9), C_1-M_2 9.9 (9.3-10.6) *v.* 11.0 (9.9-13.1), RAD 59.9 (55.1-64.8) *v.* 65.7 (58.1-75.8); ♂♂-GSL 28.3 (27.2-29.7) *v.* 30.4 (28.7-33.7), C_1-M_2 10.1 (9.3-10.6) *v.* 11.1 (10.1-12.8), RAD 59.3 (54.7-61.9) *v.* 65.1 (59.2-75.0). This size difference is illustrated by the plot of ZB *v.* C_1-M_2 (Figure 3); BW smaller relative to M^1W (Figure 4); GSL shorter relative to DIG 1 (Figure 5); and posterolabial corner of P4 generally much more square.



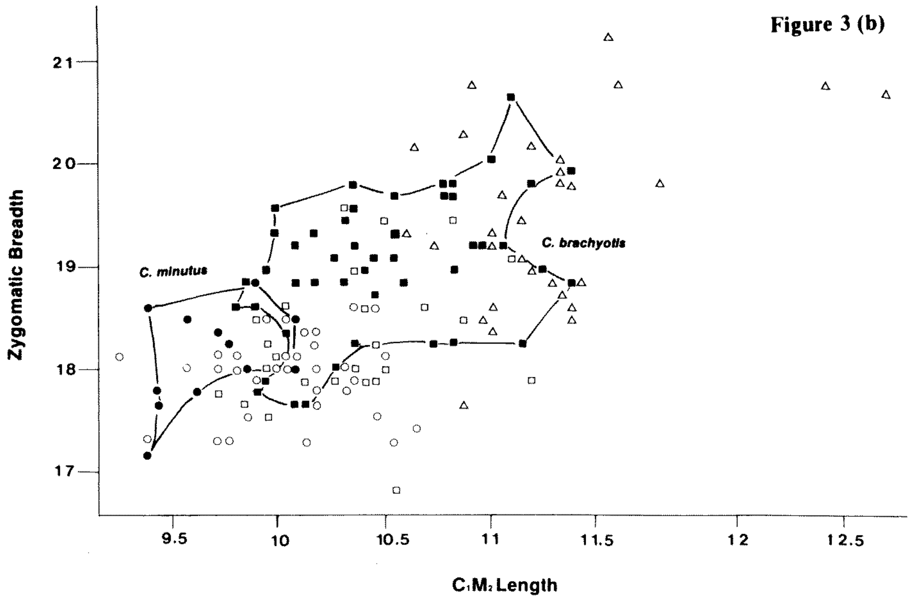


Figure 3-11 Bivariate plots of selected skull and body measurements for five species of *Cynopterus* (a) females, (b) males. O, *C. nusatenggara*; △, *C.* sphinx; ■, *C. brachyotis*; ●, *C. minutus* and □, *C. luzoniensis.*

Figure 4 (a)

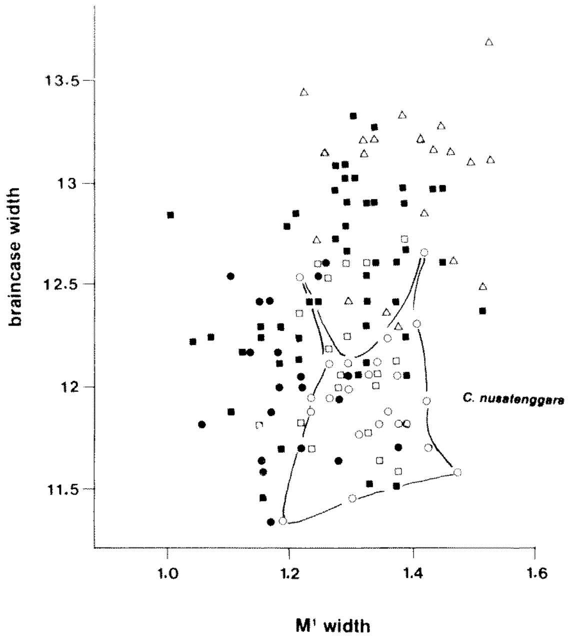
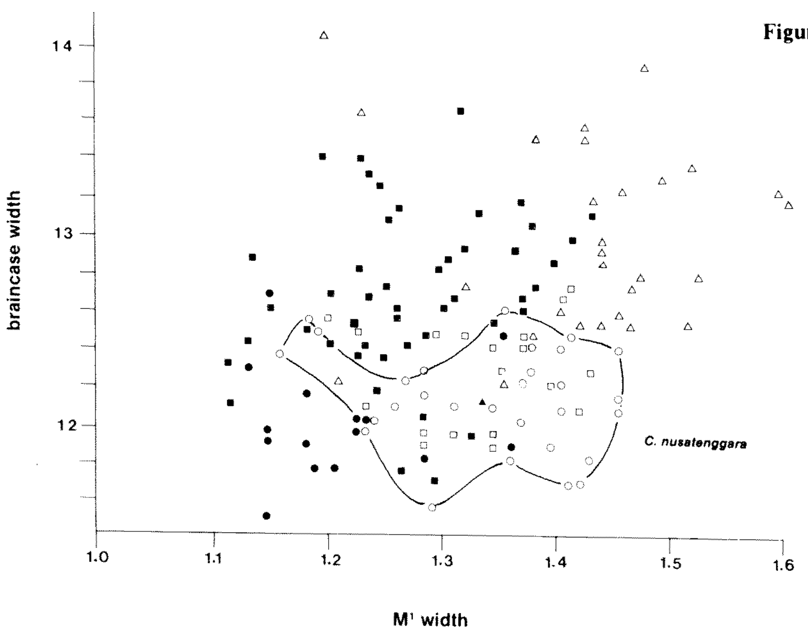


Figure 4 (b)



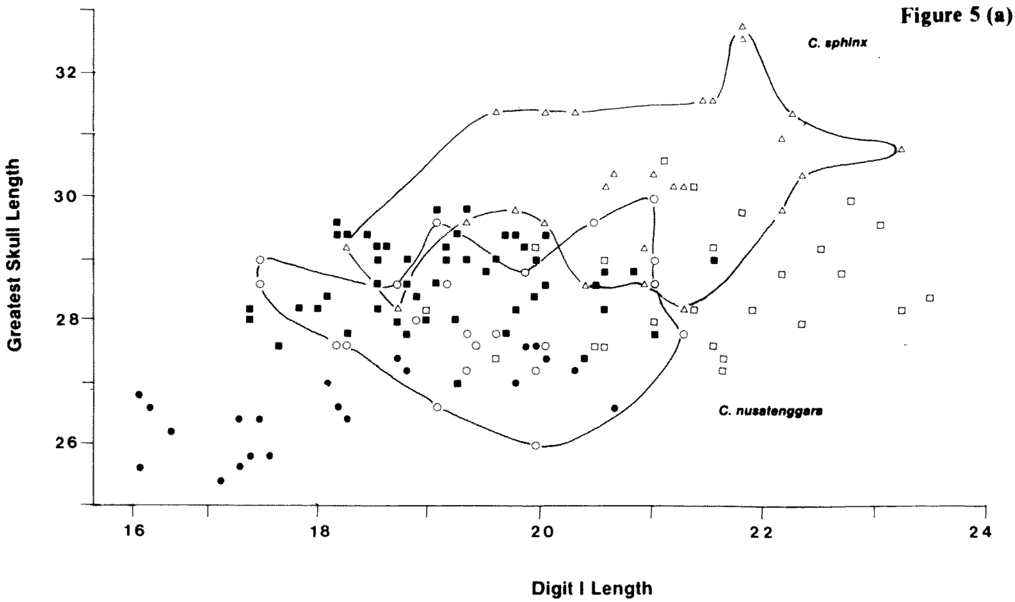


Figure 5 (a)
C. sphinx
C. nusatenggara
Greatest Skull Length
Digit I Length
26
28
30
32
16
18
20
22
24

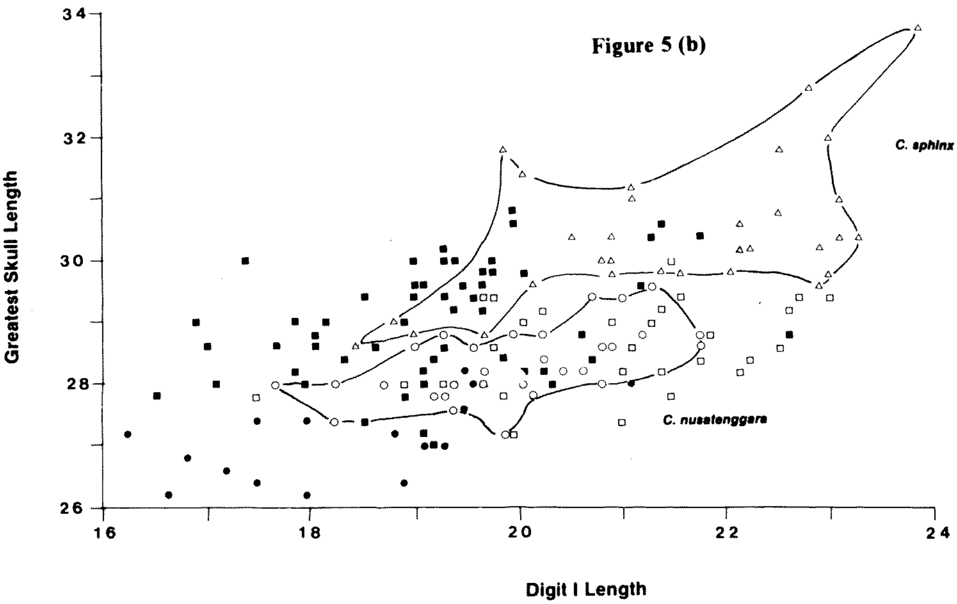


Figure 5 (b)
C. sphinx
C. nusatenggara
Greatest Skull Length
Digit I Length
26
28
30
32
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24

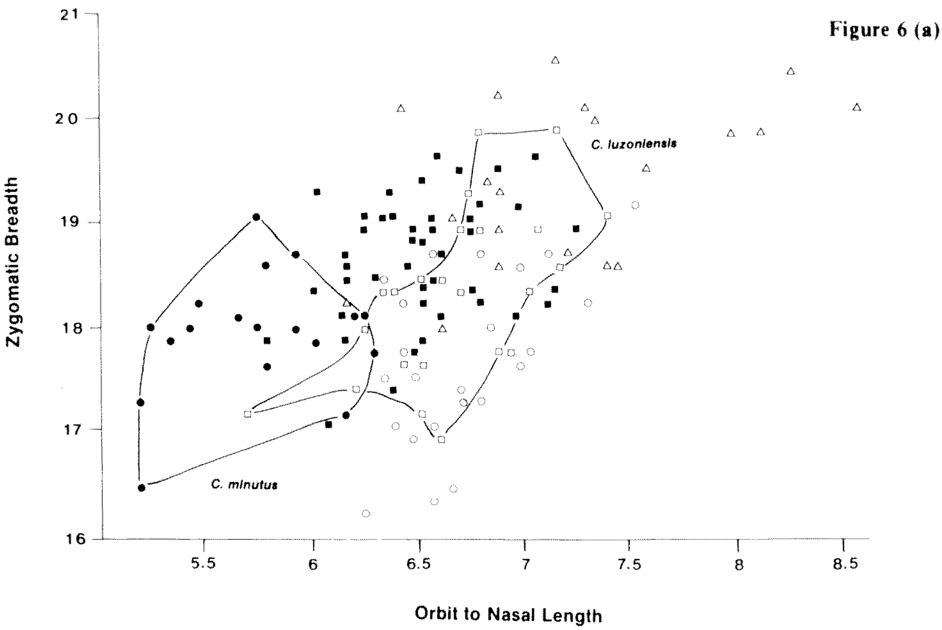
Figure 6 (a)
C. luzoniensis
C. minutus
Zygomatic Breadth
Orbit to Nasal Length
16
17
18
19
20
21
5.5
6
6.5
7
7.5
8
8.5

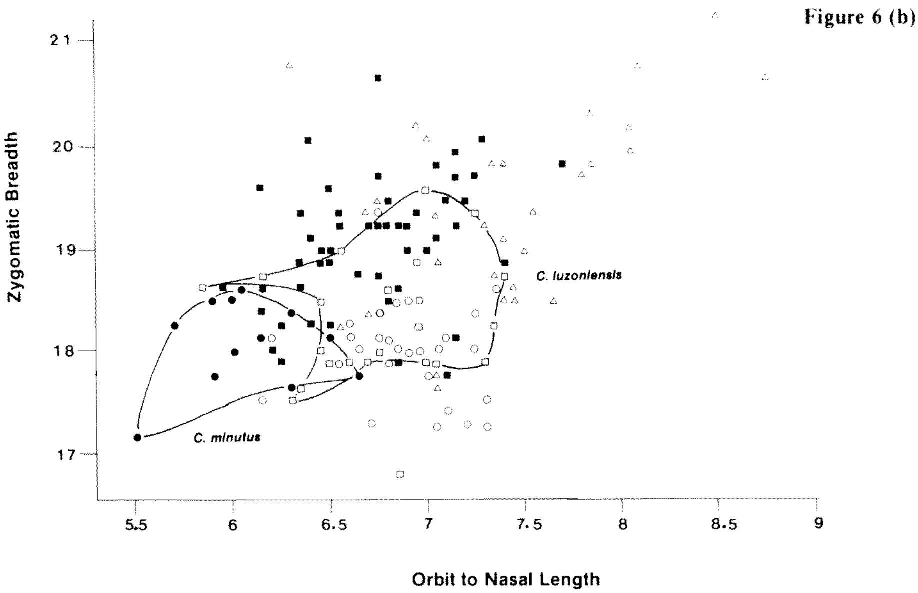
Figure 6 (b)
C. luzoniensis
C. minutus
Zygomatic Breadth
Orbit to Nasal Length
17
18
19
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7.5
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8.5
9

Figure 7 (a)

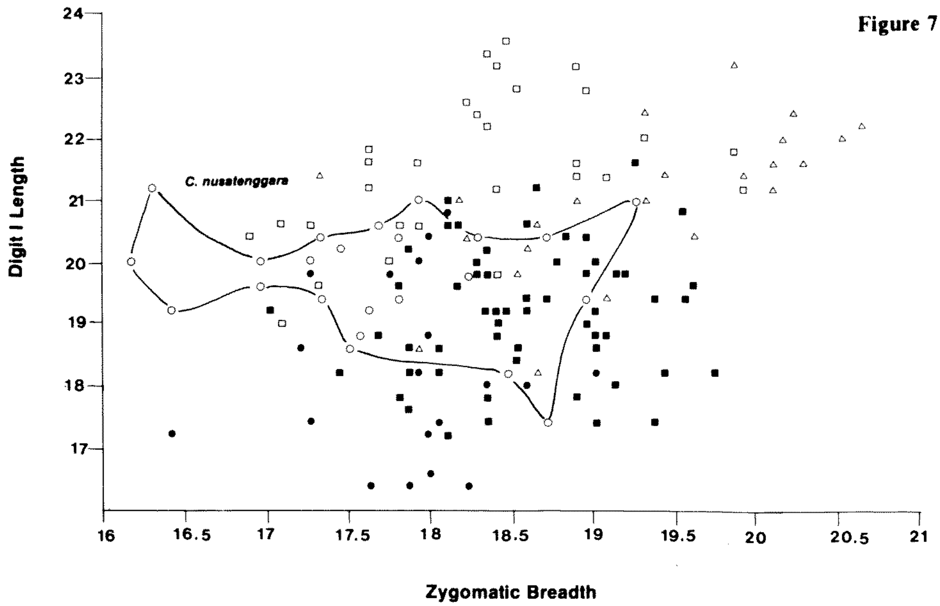


Figure 7 (b)

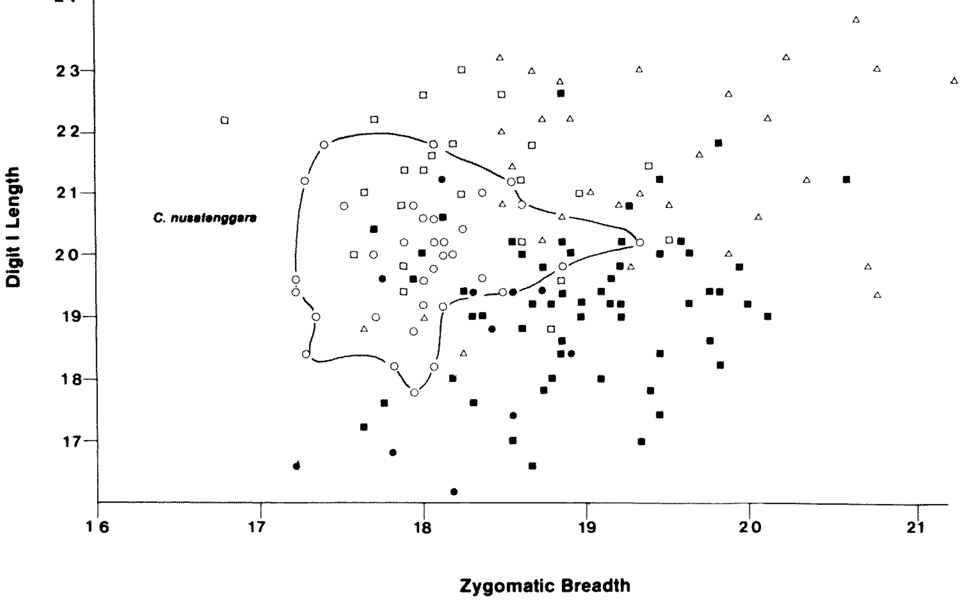


Figure 8 (a)

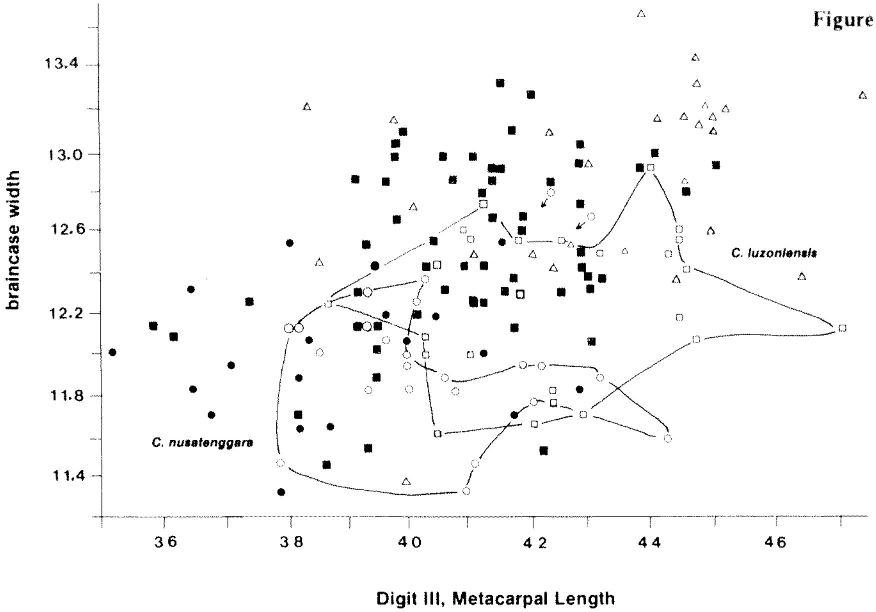


Figure 8 (b)

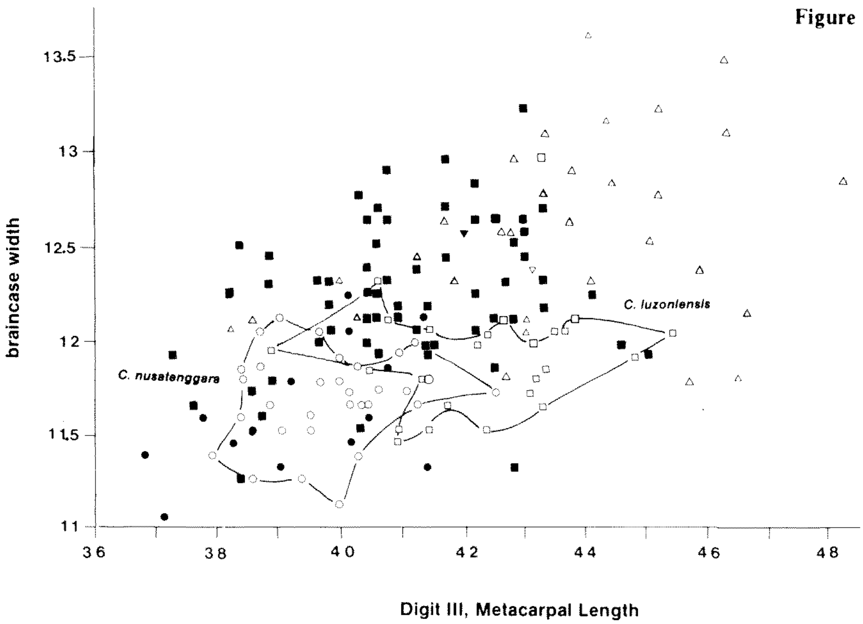


Figure 9 (a)

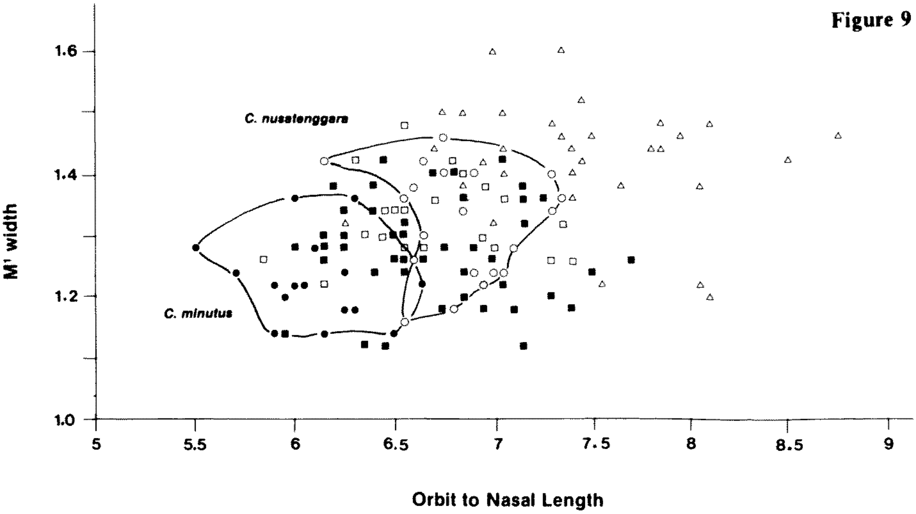


Figure 9 (b)

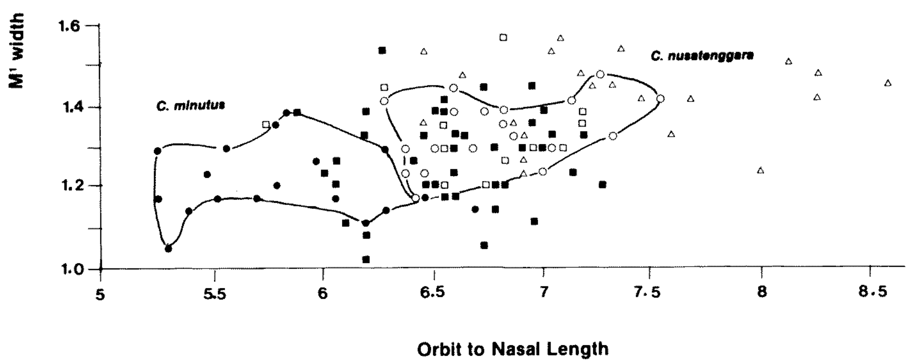


Figure 10 (a)

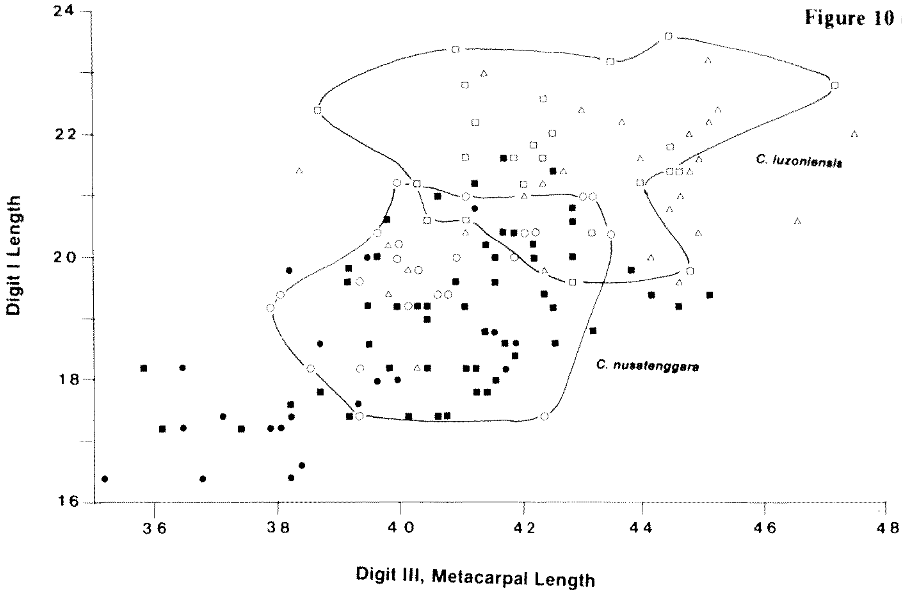


Figure 10 (b)

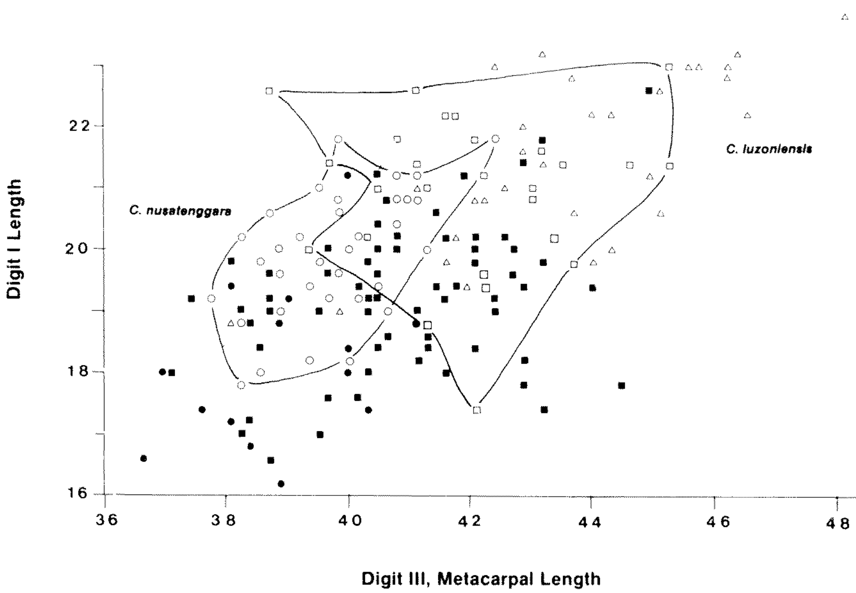


Figure 11 (a)

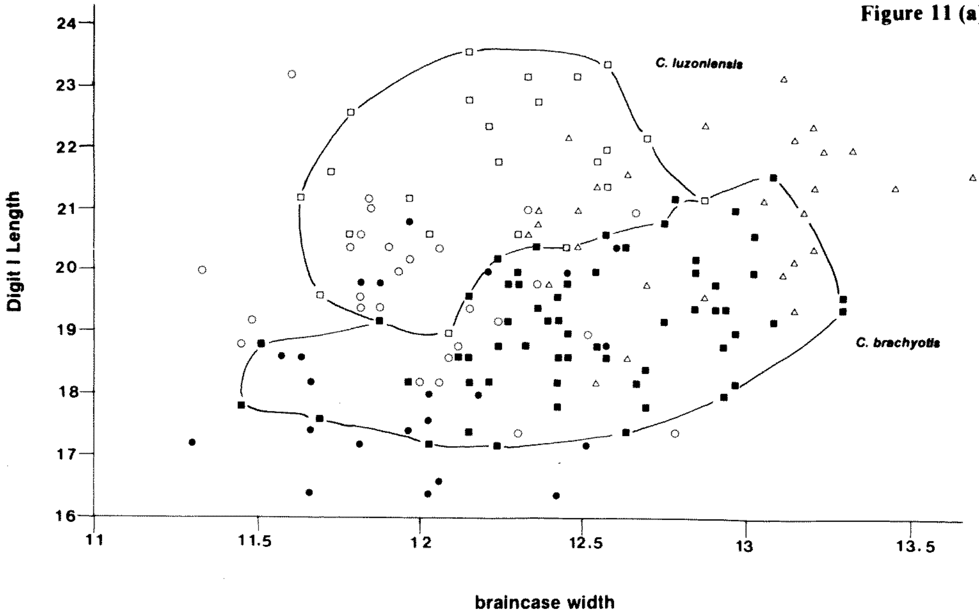
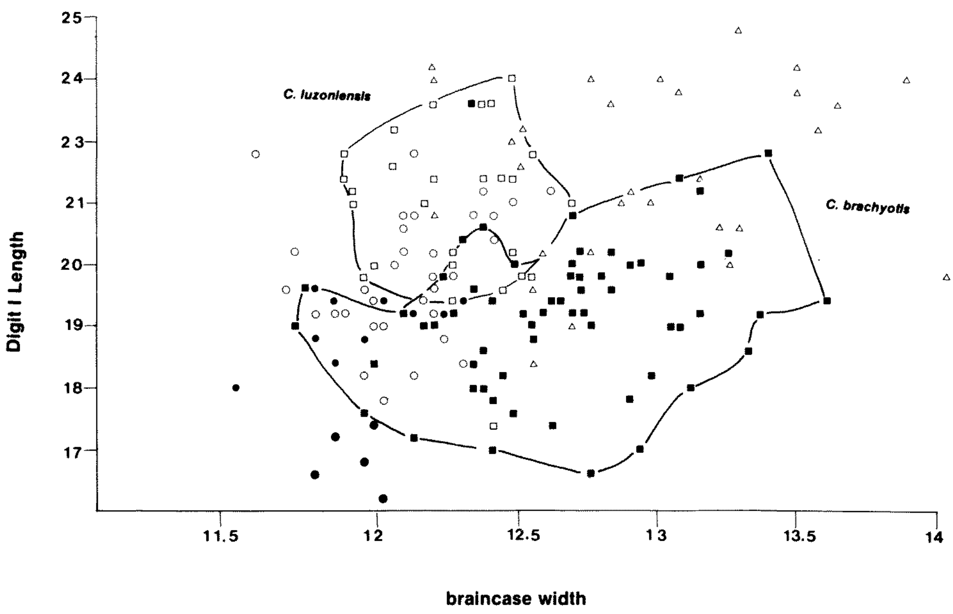


Figure 11 (b)



It also differs from *C. brachyotis* in that it averages slightly smaller in many measurements (Table 1): e.g., ♀♀ -GSL 28.1 (26.0-29.9) *v.* 28.6 (27.0-29.7), ZB 17.8 (16.2-19.2) *v.* 18.6 (17.0-19.7); ♂♂ -GSL 28.3 (27.2-29.7) *v.* 29.0 (27.6-30.7), ZB 18.0 (17.2-19.4) *v.* 18.9 (17.7-20.6); ZB generally narrower relative to ONL and DIG I (Figures 6 and 7, respectively); BW smaller relative to M^1W (Figure 4); ZB generally smaller relative to C_1M_2 (Figure 3); BW generally smaller relative to DIG 3 (Figure 8); P^4 posterolabial corner generally much more square.

It differs from *C. minutus* in averaging larger in all measurements except ZB, BW and C^1-C^1 in females and in males (Table 1. e.g. ♀♀ -GSL 28.1 (26.0-29.9) *v.* 26.6 (25.4-27.6), C_1-M_2 9.9 (9.3-10.6) *v.* 9.6 (9.0-10.2), RAD 59.9 (55.1-64.8) *v.* 57.5 (54.2-61.9) and ♂♂ -GSL 28.3 (27.2-29.7) *v.* 27.2 (26.2-28.3), C_1-M_2 10.1 (9.3-10.6) *v.* 9.8 (9.4-10.2), RAD 59.3 (54.7-61.9) *v.* 57.3 (52.9-60.9); ONL generally longer relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much more square; pelage darker generally Olive Brown on back compared to Wood Brown (brown fawn) or Buffy Brown.

It also differs from *C. luzoniensis* in having all wing measurements averaging slightly shorter (Table 1); DIG 1 shorter relative to DIG 3 (Figure 10); DIG 1 generally shorter relative to ZB (Figure 7); DIG 3 generally shorter relative to BW (Figure 8); pelage darker — generally Olive Brown on back compared to lighter Drab (cinnamon fawn) to Hair Brown (grey brown).

Description

Skull, dentary and dentition

Typical *Cynopterus* skull (Figure 12) of moderate length; cranium dorsal view oval, maximum height and inflation in posterior half of frontal bone — *c.* 4 mm posterior to base of postorbital process; posterior outline of cranium bulges slightly again dorsally and considerably laterally in midparietal region; interparietal region flatter and narrows evenly to a sharp and moderately high lambdoidal ridge; sagittal ridge absent in juveniles, barely perceptible in young adults and forms a low (*c.* 1.5 mm), wide (*c.* 3 mm) ridge in old adults; postorbital width wider in juveniles than adults *c.* (7.4 *v.* 6.3 mm), while interorbital width less affected by age and remains approximately the same; lateral frontal anterodorsal tubular swellings more inflated and median frontal sulcus more concave in adults; postorbital lateral processes triangular shaped, facing slightly posteriorly, short in juveniles (*c.* 1 mm) and longer in adults (*c.* 2.2 mm), base penetrated by small foramen; nasal narrowly triangular, constricted posteriorly to a blunt point which penetrates *c.* 3.5 mm from frontal — premaxillary anterior junction, distal end slightly flared laterally but without any constriction midlength; lacrimal foramen size moderate, lacrimal forms part of anterior edge of orbit; frontal posterior to postorbital lateral process broadly circular, not square; infraorbital foramen subequal in size to lacrimal foramen, separated from latter by low ridge from orbit; rostrum lateral profile slopes gently from frontal to distal tip of nasal in juveniles but rostrum becomes square in shape in recent adults and old specimens; nasal distal end in some specimens slightly uptilted; optic foramen circular, separated from its immediately posterior and larger

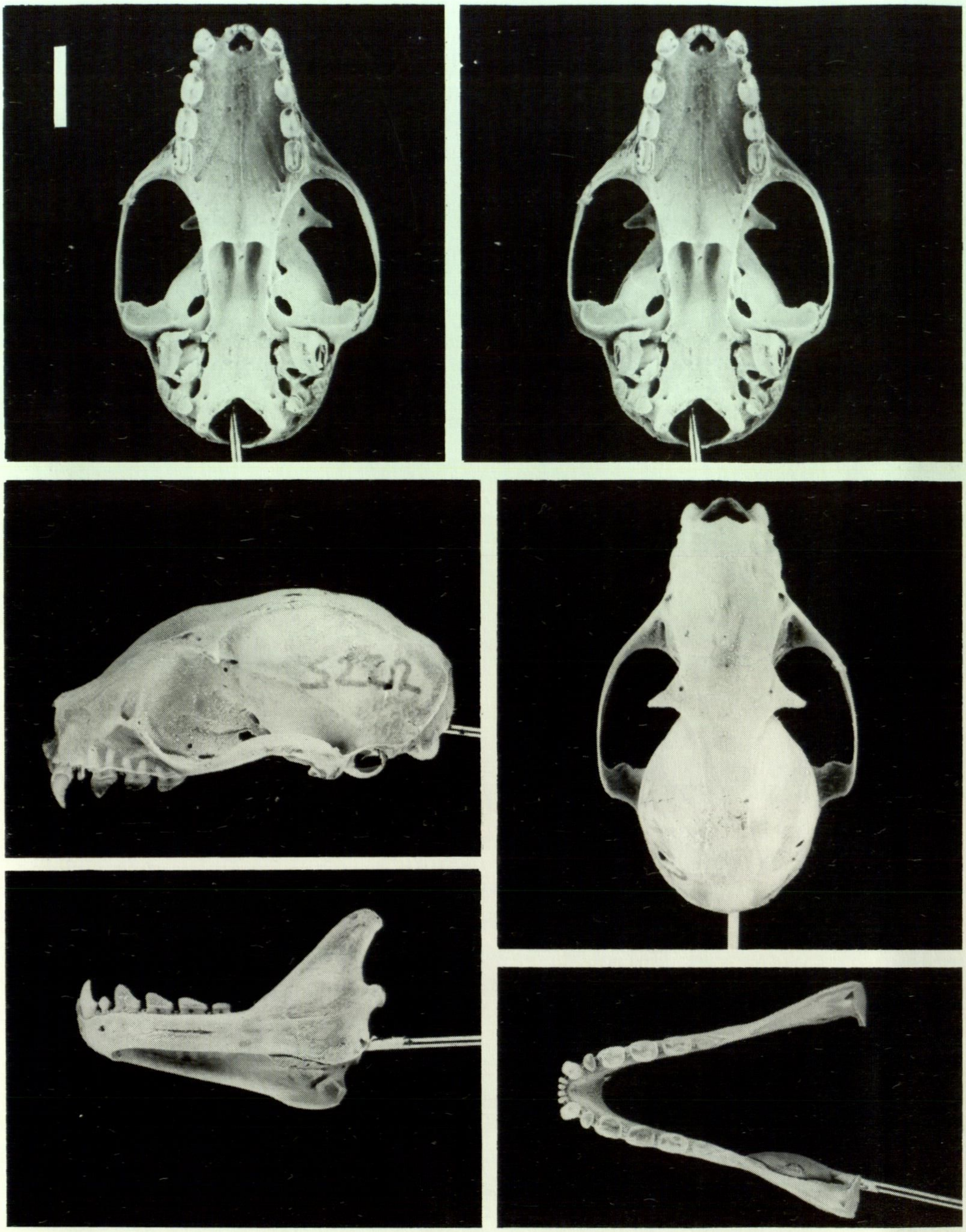
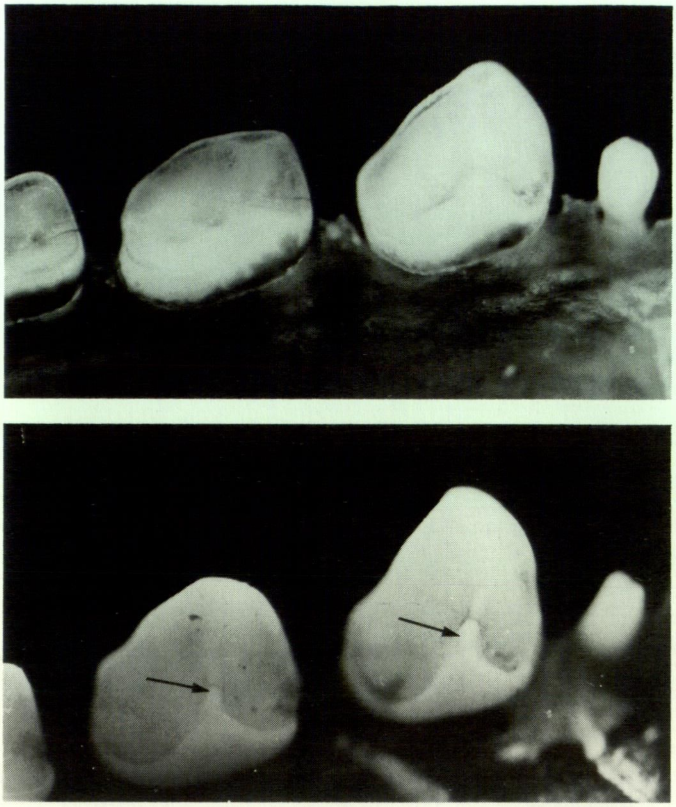


Figure 12 Skull, dentary and dentition of *Cynopterus nusatenggara* holotype. Ventral view as stereopair. Scale line 5 mm.

foramen (? sphenoidal fissure) by stout broad strut connecting alisphenoid with dorsal lateral margin of presphenoid; foramen oval moderately large, with posterior edge formed by slight ridge from glenoid fossa posterior margin; postdental palate length subequal to distance between P^4-P^4 lingual faces; mesopterygoid fossa wide, subequal to distance between P^3-P^3 lingual faces, anterior margin shape variable but usually straight or gently curved; pterygoid ridges merging slightly posteriorly with low posterobasal ridge curving towards bulla anteromedial edge; bulla small, robust, close to glenoid fossa, in lateral view external auditory meatus subcircular; lambdoidal ridge from immediately posterior to bulla to crest almost straight or gently curved; paraoccipital process moderately long but not reaching as far as occipital condyle posterior edge; zygomatic squamosal part robust with postsquamosal ridge immediately dorsal to bulla usually terminates prior to lambdoidal crest; zygomatic arches gently curved and not squarish; zygomatic breadth moderate (*c.* 17.9 mm); incisive foramen heart shaped, small, terminates posteriorly before a point level with C^1 posterior face; dentary coronoid process gently sloping dorsoposteriorly, apex blunt and occasionally with slight posterior hook, posterior margin gently concave or almost straight; angular process gently rounded, without ventrointernal shelf, ventral edge only slightly convex against long axis of ventral surface of dentary. I^{1-2} subcircular in cross-section, simple crown, usually loosely adpressed to each other, occasionally crossed; distal one-third slightly flattened anteroposteriorly, worn posterior face usually produces spade shaped distal end; I^2 slightly shorter than I^1; diastema between I^2 and C^1 wide, approximately equal to combined widths of I^1 and I^2; C^1 upper stout, anterior face smooth and evenly convex such that apex faces slightly posteriorly, secondary cusp in middle of lingual edge, one-third to one-half principal cusp height; P^1 small, rod-like, crown simple, occlusal area varies from slightly larger to twice that of incisors, height approximates C^1 cingulum, rarely vestigial or absent; P^3 large, basal area subequal or slightly larger than that of C^1, labial cusps tall, threequarters C^1 height, lingual cusp from cingulum half labial cusp height and connected to base of labial cusp by commissure running almost at right angles to axis of molar tooth row or slightly forward of this angle (Figure 13a); vestigial cusplet visible on anterolingual cingulum in some juveniles; P^4 occlusal area slightly larger than P^3, antero- and postero-lingual margins more developed than in P^3 to produce a more square occlusal surface, lingual and labial cusps much lower than in P^3; P^4 anterolabial cusp prominent and about half height P^3 principal cusp — posterior ridge with secondary cusplet; lingual cingulum with small anterior cusplet and occasionally with secondary cusplet at midpoint; P^4 with low lingual cusp separated from its labial cusp by gently sloping basin that is frequently raised between these cusps and sloping downwards both anteriorly and posteriorly — but not forming a definite ridge or commissure (Figure 13a); M^1 oblong, slightly longer and narrower than P^3 and P^4, anterolabial cusp three-quarters height of this cups on P^4 and with only a trace of secondary cusplet on posterior ridge, low cusplet on anterolingual cingulum; surface cusps absent on P^3, P^4 and M^1.

I_1 occlusal surface subtriangular; I_2 more oblong, anterior face with faint median notch; I_1 occlusal area one-half to three-quarters that of I_2, noticeably shorter than I_2;



(a)

(b)

Figure 13 Upper second and third premolars; occlusal view (a) *Cynopterus nusatenggara* (holotype) from West Sumbawa and (b) *Cynopterus brachyotis* WAM M16163 from Bali. Arrow on P^3 and P^4 indicating commissure (see text for discussion).

incisors usually not in contact but occasionally loosely adpressed to each other; diastema between I_2 and C_1 usually approximately equal to I_2 width but occasionally much narrower; C_1 anterior face smooth, gently curving dorsoposteriorly such that apex partly faces posteriorly, moderately sharp posterolabial ridge from apex of cusp to contact with posterior cingulum at its most outside (labial) point, this contact marked by small circular cusplet (often not visible in worn teeth); lingual cingulum produces larger cusps at its midpoint which reaches to approximately half height of principal cusp; P_1 occlusal area moderately large, slightly smaller than M_2, oval shaped with long axis at right angle to dentary, labial cusp about one-third height of that of P_3; P_3 with prominent labial cusp to four-fifth height of C_1, lingual cingulum rises to cusp — partly fused to taller labial cusp below its apex, labial cusp posterior ridge usually with cusplet at midlength; P_3 posterolabial corner sharp and square, occasionally marked by faint cingular cusplet; P_4

anterolabial and anterolingual cusps separate, not connected by commissure, produces a squarer occlusal surface than P_3, slight internal ridge from apex of principal cusp to its base, posterolabial corner as in P_3; M_1 occlusal surface oval shaped, longer and narrower than P_3 and P_4, similar cusp morphology to P_4 but with ridges lower and posterolabial corner rounded rather than square, slight internal ridge from labial cusp apex to its base; M_2 occlusal surface area about one-third that of M_1, anterior edge very gently curved with low cusp on anterolabial corner, posterior edge gently curved; P_4 and M_1 with low but obvious occlusal surface cusps.

Externals

Moderate sized *Cynopterus* averaging 27.9 ± 1.52 (24.5-30.5) (N = 27) and 29.9 ± 3.94 (21.5-37.5) (N = 21) gm for adult males and adult females, respectively. Nostrils short, *c.* 4 mm, subtubular and diverging anterolaterally at an angle of *c.* 70°, such that they open slightly laterally with ventrolateral nasal slit lateral on muzzle; ear narrowly rounded, *c.* 16 mm long, antitragal lobe small, narrowly rounded (see Kitchener *et al.* (1990a: 40) for photograph of *C. nusatenggara,* described as *C. brachyotis*). Tail and calcar about one-half length of foot and claw; plagiopatagia widely separated, from sides of back, insert at distal end of digit I metatarsal; index finger clawed; relative lengths of radius, metacarpals and phalanges indicated in Table 1; penis short with external sheath short, *c.* 5 mm, skin thick, darkly pigmented, particularly so ventrally, moderately haired, up to 5 mm long; penis cigar shaped with obvious low dorsal ridge raised *c.* 0.3 mm above surrounding surface with low median groove; this ridge terminates just before distal end of penis; urethral groove dorsoventral slit at penis distal end opening directly to a ventral groove for some 1.3 mm, this groove closes posterior to this point but continues posteriorly along the midventral surface of length of penis as a closed groove. This groove medially on slightly raised 'keel' of tissue which laterally joins the dorsal ridge at its distal end only and projects slightly anterior to dorsal ridge, particularly the anterobasal point of keel.

Palatal ridges

Ten prominent palatal ridges in interdental region and immediately postdental; anterior ridge almost straight; ridges posterior to this become progressively more sharply curved as illustrated in Andersen (1912: 591); usually last two of these ridges divided but sometimes the last three and occasionally only the last one divided. Near posterior margin of palate are two flattened and divided 'ridges'.

Pelage and skin colour

Adult males have a collar of lighter coloured Sayal Brown (fawn cinnamon) to Snuff Brown (cinnamon brown) fur around throat and extending to base of chin, chest, and side of neck. This colour usually connects behind neck, frequently forming a mantle on shoulders and occasionally colouring fur to rump; ventrally it usually also extends along sides to rump flanking pale Neutral Gray to Neutral Gray venter. Top of head from rhinarium to occiput, face and lips Fuscous (cinnamon black) to Fuscous Black; chin a mixture of Light Olive-Buff and Pale Payne's Gray (pale blue grey) hairs; back Olive

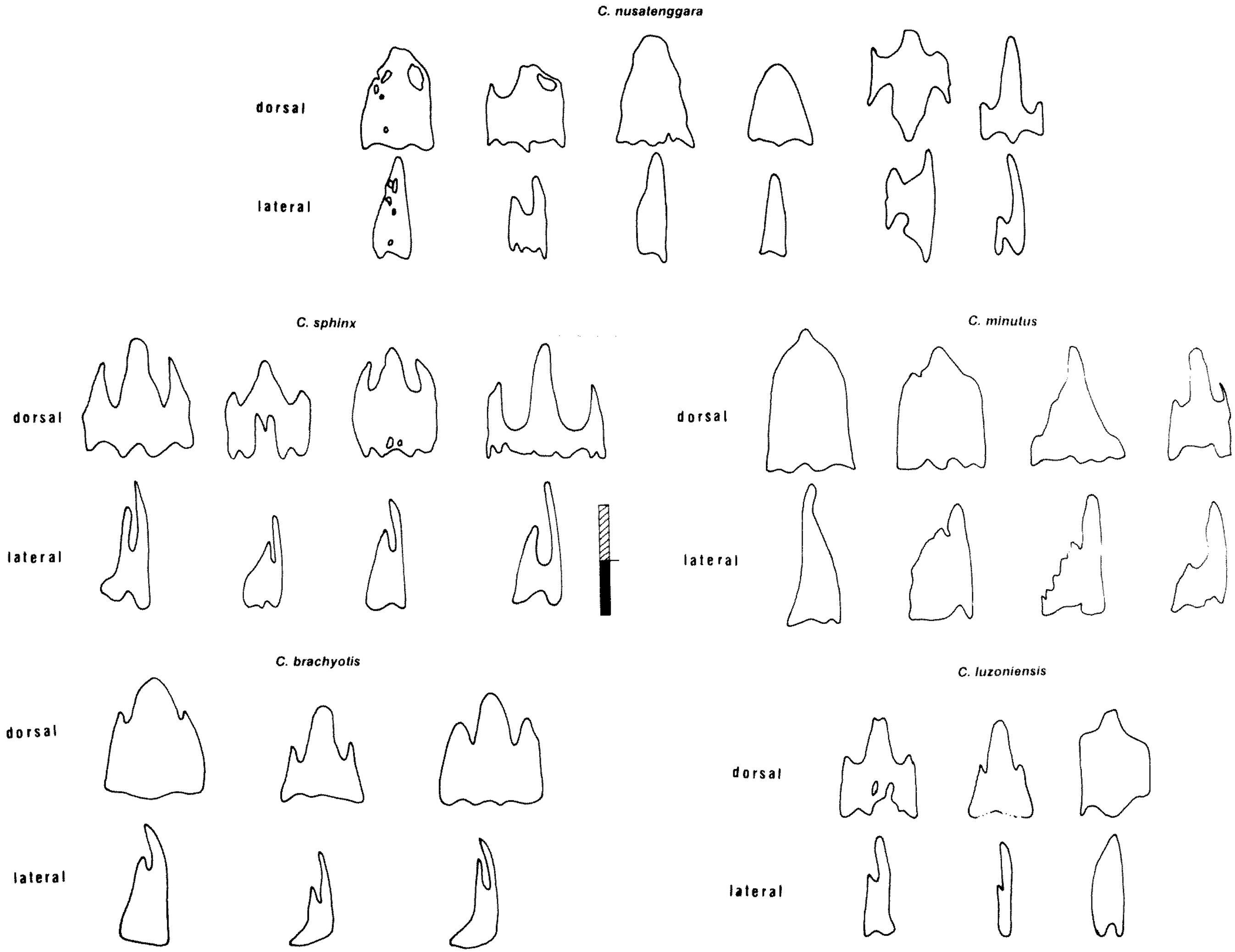


Figure 14 Shape of bacula of five species of *Cynopterus (nusatenggara, sphinx, brachyotis, minutus* and *luzoniensis)* from dorsal and lateral views. Scale line 2 mm.

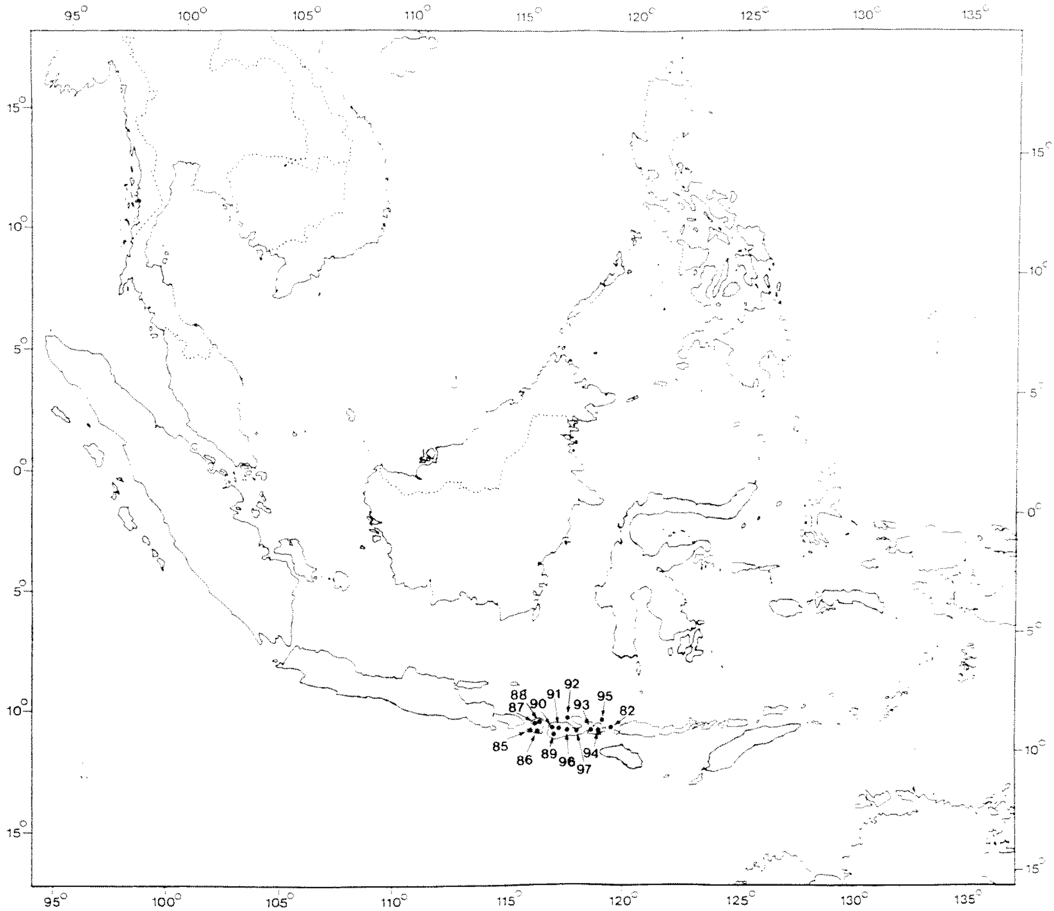


Figure 15 Localities of *Cynopterus nusatenggara* examined in this study.

Brown to Dark Olive, frequently tipped with Sayal Brown to Snuff Brown of shoulder mantle; plagiopatagium ventral surface adjacent to body and forearm thinly furred with Buckthorn Brown (golden brown); uropatagium ventral and dorsal surfaces lightly furred with Drab (cinnamon fawn), except near tail where there is a tuft of hairs up to *c.* 5 mm long; radius proximal half to two-thirds furred (frequently densely) on dorsal surface with same colour as on rump; ear naked, apart from base. Skin of ear, lip, feet and patagia Fuscous to Chaetura Black (dark olive black). Margin of ear same colour as other surfaces of ear — not contrastingly lighter as in other *Cynopterus* spp. considered. Surfaces of metacarpals and phalanges same colour as patagia or occasionally a slightly lighter Drab but not contrasting with colour of patagia as in other *Cynopterus* spp. considered.

Table 1a females Sample size (N), mean (x), Standard deviation (SD), minimum (Min) and maximum (Max) values of skull, dental and external measurements (in mm) of *Cynopterus nusatenggara, C. sphinx, C. brachyotis, C. minutus* and *C. luzoniensis* for (a) females, and (b) males. For explanation of character codes see Figure 1 caption.

SPECIES/CHARACTER		GSL	CDL	PL	MFW	ONL	LIW	POW	ZB	BW	CPL	C^1C^1	P^4-P^4	M^1-M^1	C^1-M^1
C. nusatenggara	N	29	29	30	30	30	30	30	28	30	30	30	30	29	30
	x	28.1	26.0	14.3	4.0	6.8	5.8	6.3	17.8	12.0	20.9	5.7	8.1	8.4	9.0
	SD	0.94	0.83	0.48	0.23	0.33	0.34	0.40	0.80	0.34	0.62	0.26	0.35	0.35	0.28
	Min	26.0	24.4	13.4	3.5	6.3	5.2	5.5	16.2	11.4	19.9	5.3	7.5	7.9	8.4
	Max	29.9	27.6	15.2	4.5	7.6	6.5	7.2	19.2	12.8	22.1	6.3	8.9	9.3	9.5
C. sphinx	N	27	28	27	25	29	28	28	23	28	28	28	29	28	29
	x	30.3	28.0	15.6	4.3	7.2	6.1	6.8	19.3	12.9	23.0	6.2	8.6	8.9	9.8
	SD	1.23	1.13	0.69	0.30	0.59	0.34	0.52	0.91	0.38	1.19	0.32	0.47	0.50	0.57
	Min	28.1	25.7	14.3	3.9	6.2	5.3	5.8	17.3	12.3	20.9	5.6	7.8	7.9	8.7
	Max	32.9	30.5	17.5	5.0	8.6	6.7	7.8	20.7	13.7	26.9	7.1	9.9	10.1	11.6
C. brachyotis	N	62	65	65	66	68	70	70	64	69	70	67	62	62	67
	x	28.6	26.3	14.6	4.1	6.6	5.8	6.6	18.6	12.5	21.4	5.9	8.2	8.4	9.1
	SD	0.60	0.71	0.43	0.22	0.32	0.28	0.53	0.56	0.40	0.56	0.24	0.35	0.40	0.35
	Min	27.0	24.4	13.5	3.6	5.8	5.2	5.2	17.0	11.5	19.9	5.3	7.3	7.5	7.4
	Max	29.7	28.8	15.3	4.5	7.3	6.4	8.0	19.7	13.3	22.4	6.4	8.8	9.4	9.7
C. minutus	N	22	22	22	22	23	23	23	22	23	23	22	23	22	23
	x	26.6	24.5	13.4	3.8	5.9	5.5	6.2	18.0	12.0	20.0	5.7	7.9	8.1	8.6
	SD	0.67	0.69	0.49	0.19	0.41	0.34	0.51	0.57	0.35	0.58	0.23	0.30	0.30	0.29
	Min	25.4	23.0	12.5	3.4	5.3	4.7	5.5	16.4	11.3	18.8	5.3	7.4	7.7	8.1
	Max	27.6	25.6	14.5	4.1	6.7	6.2	7.2	19.0	12.6	21.3	6.3	8.8	8.9	9.1
C. luzoniensis	N	30	30	30	29	30	30	30	30	30	30	30	30	30	30
	x	28.6	26.2	14.5	4.0	6.7	6.0	6.5	18.3	12.3	21.2	5.9	8.2	8.3	9.2
	SD	0.91	1.05	0.57	0.23	0.36	0.40	0.36	0.77	0.35	0.78	0.32	0.36	0.38	0.37
	Min	27.3	23.1	13.5	3.5	5.7	5.4	5.8	16.9	11.6	20.0	5.1	7.3	7.5	8.6
	Max	30.5	28.2	16.0	4.4	7.4	6.9	7.3	19.9	12.9	23.1	6.5	8.8	9.0	10.1

Table 1a cont.

SPECIES/CHARACTER		C_1-M_2	P^3L	P^3W	M^1L	M^1W	RAD	DIG 1	DIG 2	DIG 3	DIG 3P	DIG 4	DIG 5	TIB
C. nusatenggara	N	30	30	30	30	30	29	29	29	29	29	29	29	29
	x	9.9	1.9	1.5	2.0	1.3	59.9	19.8	27.4	40.7	26.7	38.1	39.8	23.2
	SD	0.34	0.10	0.06	0.12	0.15	2.00	1.22	1.32	1.65	1.04	1.38	1.42	1.05
	Min	9.3	1.7	1.4	1.8	1.2	55.1	17.4	25.6	38.0	24.2	35.8	36.5	21.1
	Max	10.6	2.1	1.6	2.2	1.5	64.8	23.2	30.6	44.3	29.6	41.1	41.7	25.7
C. sphinx	N	28	29	29	29	29	29	29	29	29	29	29	29	28
	x	11.0	2.1	1.5	2.0	1.4	65.7	21.0	29.1	43.0	28.5	40.9	42.2	24.7
	SD	0.67	0.11	0.08	0.16	1.10	4.28	1.22	1.87	2.50	1.65	2.63	2.70	1.08
	Min	9.9	1.9	1.4	1.6	1.2	58.1	18.3	23.6	36.8	25.3	35.9	36.0	21.4
	Max	13.1	2.3	1.7	2.3	1.6	75.8	23.3	31.4	47.6	33.0	45.9	47.0	29.6
C. brachyotis	N	65	69	69	67	67	70	70	70	70	70	70	69	69
	x	10.2	2.0	1.4	1.9	1.3	61.7	19.2	27.8	41.0	27.0	38.7	40.1	22.9
	SD	0.33	0.11	0.09	0.11	0.10	2.86	1.08	1.56	1.82	1.29	1.85	1.88	1.56
	Min	9.4	1.7	1.0	1.7	1.0	54.7	17.2	23.3	35.8	23.8	34.4	35.3	19.4
	Max	10.8	2.2	1.6	2.1	1.5	66.2	21.6	31.0	45.2	29.9	42.8	43.9	25.5
C. minutus	N	23	23	23	23	23	23	23	23	23	23	23	23	23
	x	9.6	1.8	1.4	1.8	1.2	57.5	18.2	26.2	39.1	25.3	36.6	37.5	21.0
	SD	0.32	0.09	0.06	0.14	0.08	2.13	1.36	1.41	2.02	1.45	1.84	1.34	1.19
	Min	9.0	1.6	1.2	1.6	1.1	54.2	16.4	24.0	35.1	22.9	33.0	33.3	19.0
	Max	10.2	2.0	1.5	2.1	1.4	61.9	20.7	28.8	42.8	28.5	39.4	41.7	23.3
C. luzoniensis	N	30	30	30	30	30	30	30	30	30	30	30	30	30
	x	10.2	2.0	1.5	2.0	1.3	61.4	21.4	28.6	42.3	27.7	39.5	41.0	22.7
	SD	0.39	0.16	0.10	0.11	0.08	2.81	1.34	1.69	1.94	1.57	1.81	1.99	1.34
	Min	9.4	1.6	1.2	1.7	1.2	57.2	19.0	24.7	38.5	25.2	35.8	36.2	19.2
	Max	11.2	2.4	1.7	2.3	1.6	68.9	23.6	31.6	47.2	30.7	43.5	46.7	25.2

Table 1b males

SPECIES/CHARACTER		GSL	CDL	PL	MFW	ONL	LIW	POW	ZB	BW	CPL	C^1-C^1	P^4-P^4	M^1-M^1	C^1-M^1
C. nusatenggara	N	36	36	39	39	39	39	39	39	38	39	38	39	38	39
	x	28.3	26.0	14.3	3.9	6.9	5.9	6.3	18.0	12.2	21.0	5.9	8.2	8.5	9.1
	SD	0.54	0.43	0.36	0.17	0.46	0.30	0.30	0.45	0.24	0.37	0.20	0.23	0.24	0.25
	Min	27.2	25.1	13.5	3.6	6.2	5.3	5.7	17.2	11.6	20.2	5.5	7.6	8.0	8.4
	Max	29.7	27.2	15.2	4.2	9.2	6.5	7.0	19.4	12.6	21.9	6.4	8.6	8.9	9.6
C. sphinx	N	34	35	34	37	37	38	38	35	37	38	36	34	34	36
	x	30.4	28.2	15.7	4.3	7.3	6.1	6.5	19.4	12.9	22.8	6.4	8.8	9.0	9.9
	SD	1.14	1.05	0.72	0.33	0.60	0.40	0.43	0.89	0.47	0.95	0.30	0.38	0.39	0.50
	Min	28.7	26.1	14.5	3.7	6.2	5.2	5.5	17.7	12.2	21.1	5.9	8.1	8.4	9.0
	Max	33.7	31.0	18.2	5.0	8.7	6.9	7.4	21.3	14.0	25.5	7.2	9.8	10.0	11.7
C. brachyotis	N	68	72	66	71	71	71	72	67	72	72	71	70	70	72
	x	29.0	26.7	14.7	4.0	6.7	5.9	6.6	18.9	12.7	21.9	6.1	8.3	8.5	9.6
	SD	0.85	0.78	0.56	0.23	0.37	0.36	0.48	0.65	0.38	0.92	0.23	0.34	0.29	2.14
	Min	26.9	25.4	13.3	3.5	5.9	4.9	5.4	17.7	11.7	20.5	5.5	7.6	7.7	8.4
	Max	30.7	28.6	16.2	4.6	7.7	6.7	7.9	20.6	13.6	27.1	6.6	9.9	9.2	10.8
C. minutus	N	18	18	18	17	18	18	18	15	18	18	18	18	18	18
	x	27.2	24.9	13.7	3.8	6.1	5.5	6.2	18.2	12.0	20.3	5.7	7.9	8.1	8.7
	SD	0.67	0.67	0.40	0.20	0.64	0.39	0.59	0.44	0.27	0.53	0.27	0.28	0.26	0.24
	Min	26.2	23.3	13.0	3.4	5.7	4.8	4.8	17.2	11.5	19.4	5.4	7.6	7.7	8.2
	Max	28.3	26.1	14.2	4.2	6.6	6.2	7.0	18.9	12.7	21.3	6.2	8.4	8.6	9.0
C. luzoniensis	N	29	32	31	31	31	32	32	30	32	32	30	31	31	32
	x	28.6	26.4	14.7	4.0	6.7	6.1	6.4	18.3	12.3	21.0	6.0	8.2	8.4	9.2
	SD	0.69	0.64	0.50	0.20	0.35	0.38	0.45	0.58	0.24	0.78	0.32	0.28	0.27	0.29
	Min	27.2	25.1	13.8	3.6	5.9	5.5	5.6	16.8	11.9	22.1	5.6	7.6	7.9	8.7
	Max	30.0	27.8	15.8	4.4	7.4	7.3	7.5	19.5	12.7	22.5	6.5	8.8	9.0	9.7

Table 1b cont.

SPECIES/CHARACTER		C_1-M_2	P^3L	P^3W	M^1L	M^1W	RAD	DIG 1	DIG 2	DIG 3	DIG 3P	DIG 4	DIG 5	TIB
C. nusatenggara	N	38	39	39	39	39	39	39	39	39	39	39	39	39
	x	10.1	1.9	1.5	2.0	1.3	59.3	19.9	27.2	39.8	26.3	37.3	38.9	23.0
	SD	0.30	0.10	0.06	0.10	0.10	1.48	1.01	1.04	1.06	1.02	0.99	1.26	0.88
	Min	9.3	1.7	1.4	1.7	0.9	54.7	17.7	25.2	37.7	23.7	35.2	34.9	19.8
	Max	10.6	2.1	1.6	2.2	1.5	61.9	1.8	29.2	42.4	29.1	39.1	41.4	24.7
C. sphinx	N	37	37	37	36	36	38	37	38	38	38	38	38	38
	x	11.1	2.1	1.6	2.1	1.4	65.1	2 .2	29.3	43.2	28.6	40.6	41.8	24.1
	SD	0.51	0.13	0.09	0.16	0.09	3.19	1.47	1.75	2.28	1. 5	2.19	2.07	1.67
	Min	10.1	2.0	1.4	1.8	1.2	59.2	8.4	25.6	38.1	25.9	34.9	37.1	20.1
	Max	12.8	2.4	1.8	2.5	1.6	75.0	23.8	32.6	48.2	33.0	45.0	45.5	27.6
C. brachyotis	N	68	72	72	72	72	71	72	72	72	72	72	72	72
	x	10.5	2.0	1.5	1.9	1.3	61.8	19.3	27.8	41.0	27.0	38.5	39.9	23.0
	SD	0.41	0.14	0.10	0.14	0.08	2.49	1.13	1.54	1.71	1.37	1.63	1.82	1.61
	Min	9.8	1.7	1.3	1.6	1.1	55.9	16.6	22.7	37.1	23.8	34.7	36.2	18.7
	Max	11.4	2.4	1.7	2.3	1.4	66.7	22.6	30.7	45.0	30.6	42.0	43.8	26.3
C. minutus	N	18	18	18	18	18	18	18	18	18	18	18	18	18
	x	9.8	1.8	1.4	1.8	1.2	57.3	18.4	26.6	39.2	26.2	36.7	37.8	20.7
	SD	0.25	0.08	0.07	0.10	0.07	2.30	1.26	1.50	1.38	2.35	1.36	1.34	1.21
	Min	9.4	1.6	1.2	1.6	1.1	52.9	16.3	24.8	36.6	23.7	34.5	35.4	19.4
	Max	10.2	1.9	1.5	2.0	1.4	60.9	21.1	29.0	41.3	34.4	38.9	40.1	23.4
C. luzoniensis	N	32	32	32	32	32	32	32	32	32	32	32	32	32
	x	10.4	2.0	1.5	2.0	1.3	60.9	20.9	28.2	42.0	27.6	38.8	40.5	22.5
	SD	0.37	0.09	0.08	0.13	0.07	2.26	1.24	1.36	1.59	1.32	1.97	1.39	0.98
	Min	9.7	1.7	1.3	1.8	1.2	56.0	17.5	25.6	38.8	25.4	31.0	37.9	20.8
	Max	11.1	2.1	1.7	2.2	1.5	65.9	23.0	30.9	45.3	30.3	41.6	43.9	24.5

Adult females generally lighter coloured than males, although pattern of colour similar. Neck collar ranges from Deep Olive Buff to Isabella Color (fawn olive) and contrasts less with Light Grayish Olive stomach and inguinal region than is the case in males; head, face and chin similar colour to males, except females generally have the darker hair projecting further to nape of neck; back Hair Brown (grey brown) tipped on shoulders with same colour as neck collar; rump and legs Drab; plagiopatagium furred with Light Ochraceous Buff.

Baculum

Shape of baculum very variable (Figure 14) with its shape and incomplete ossification seemingly independent of size of skull and extent of tooth wear.

The maximum length and maximum width of bacula are 1.92 ± 0.29 (N = 11) and 1.43 ± 0.30 (N = 11), respectively.

Natural History

Kitchener *et al.* (1990a) report that *C. nusatenggara* (as *C. brachyotis*) on Lombok I. is common in both natural rainforest and disturbed situations such as native gardens. Females were pregnant in September and October just before the monsoon rains with a single foetus (in either the left or right uterine horn). They suggest the species is seasonally polyoestrous. Kitchener *et al.* (1990b) report that (as *C. brachyotis*) at near coastal sites on Lombok I. it has a pollen dietary niche breadth approaching the nectarivorous species *Eonycteris spelaea, Macroglossus minimus* and *Rousettus amplexicaudatus,* but that this niche breadth decreased at more inland and upland sites. *C. nusatenggara* also eats substantial amounts of plant epidermis.

Distribution

At the time of this study the species was known from only Lombok, Sumbawa and Komodo islands (Figure 15). More recently we have collected *C. nusatenggara* from Sumba, Flores, Adonara and Lembata Is, Nusa Tenggara.

Etymology

This species is named after the Indonesian island group to which it is restricted.

Cynopterus sphinx (Vahl, 1797)

(Table 1; Figures 3-11, 14, 16, 17)

Vespertilio sphinx Vahl, 1797, Skr. Nat. Selsk. Copenhagen 4 (1): 123

Vespertilio fibulatus Vahl, 1797, Skr. Nat. Selsk. Copenhagen 4 (1): 124

Pteropus pusillus E. Geoffroy, 1803, Cat. Mamm. Mus. Nat. d'Hist. Nat. p. 49

Pteropus marginatus E. Geoffroy, 1810, Ann, Mus. d'Hist. Nat. 15: 97

Cynopterus marginatus var. *scherzeri* Zelebor, 1869, Reise 'Novara', Säug. p. 13

Cynopterus marginatus var. *ellioti* Gray, 1870, Cat. Monkeys Lemurs, and Fruit-eating Bats in the Collections of the British Museum, Lond. p. 122

Cynopterus angulatus Miller, 1898, Proc. Acad. Nat. Sci. Philad. p. 316

Cynopterus sphinx gangeticus K. Andersen, 1910, Ann. Mag. nat. Hist. (8) 6: 623

Cynopterus pagensis Miller, 1906, Proc. Biol. Soc. Wash. 19: 62

Cynopterus babi Lyon, 1916, Proc. U.S. Nat. Mus. 42: 438

Cynopterus sphinx serasani Paradiso, 1971, Proc. Biol. Soc. Wash. 84: 293-300

Holotype

Andersen (1912) states that "the (two) cotypes, once in the Museum of Copenhagen Natural History Society ("Naturhistorie-Selskabet"), are probably now no longer in existence".

Type Locality

Tranquebar, Madras, India.

Diagnoses

C. sphinx differs from *C. nusatenggara* in that it averages larger for all measurements (except P^3W and M^1L in females (Table 1): e.g., ♀♀ — GSL 30.3 (28.1-32.9) *v.* 28.1 (26.0-29.9), C_1-M_2 11.0 (9.9-13.1) *v.* 9.9 (9.3-10.6), RAD 65.7 (58.1-75.8) *v.* 59.9 (55.1-64.8); ♂♂ — GSL 30.4 (28.7-33.7) *v.* 28.3 (27.2-29.7), C_1-M_2 11.1 (10.1-12.8) *v.* 10.1 (9.3-10.6), RAD 65.1 (59.2-75.0) *v.* 59.3 (54.7-61.9). This size difference is illustrated by the plot of ZB *v.* C_1-M_2 (Figure 3); BW wider relative to M^1W (Figure 4); GSL longer relative to DIG 1 (Figure 5). P_4 posterolabial corner generally much less square, P^3 lingual and labial cusp commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. White or light coloured edge to margin of ear present. Pelage on head not markedly darker than that of back; and surface colour of metacarpals and phalanges markedly lighter and contrasting with wing membrane.

It differs from *C. brachyotis* in that it averages larger in all measurements except P^3L in females and LPW in males (Table 1): e.g., ♀♀ -GSL 30.3 (28.1-32.9) *v.* 28.6 (27.0-29.7), C_1-M_2 11.0 (9.9-13.1) *v.* 10.2 (9.4-10.8), RAD 65.7 (58.1-75.8) *v.* 61.7 (54.7-66.2); ♂♂ -GSL 30.4 (28.7-33.7) *v.* 29.0 (26.9-30.7), C_1-M_2 11.1 (10.1-12.8) *v.* 10.5 (9.8-11.4), RAD 65.1 (59.2-75.0) *v.* 61.8 (55.9-66.7); ONL generally longer relative to M^1W (Figure 9); DIG 1 generally longer relative to GSL and ZB (Figures 5 and 7). Pelage on dorsum a darker Chaetura Drab (olive black) compared to Snuff Brown (cinnamon brown) to Wood Brown (brown fawn).

It differs from *C. minutus* in averaging larger in all measurements (Table 1). It is absolutely larger in the following: ♀♀ -CDL 28.0 (25.7-30.5) *v.* 24.5 (23.0-25.6); DIG 2 29.1 (23.6-31.4) *v.* 26.2 (24.0-28.8) and ♂♂ -GSL 30.4 (28.7-33.7) *v.* 27.2 (26.2-28.3); CDL 28.2 (26.1-31.1) *v.* 24.9 (23.3-26.1); PL 15.7 (14.9-18.2) *v.* 13.7 (13.0-14.2); P^3L 2.1 (2.0-2.4) *v.* 1.8 (1.6-1.9), RAD 65.1 (59.2-75.0) *v.* 57.3 (52.9-60.9) [♀♀ RAD 65.7 (58.1-75.8) *v.* 57.5 (54.2-61.9)]; BW greater relative to M^1W (Figure 4); canines much more robust. Pelage on dorsum a darker Chaetura Drab compared to Wood Brown to Buffy Brown.

It differs from *C. luzoniensis* in averaging larger in most measurements (except P^3L, P^3W, M^1L and DIG 1 in females and LIW in males) (Table 1); e.g.: ♀♀ -GSL 30.3 (28.1-32.9) *v.* 28.6 (27.3-30.5), C_1-M_2 11.0 (9.9-13.1) *v.* 10.2 (9.4-11.2), RAD 65.7

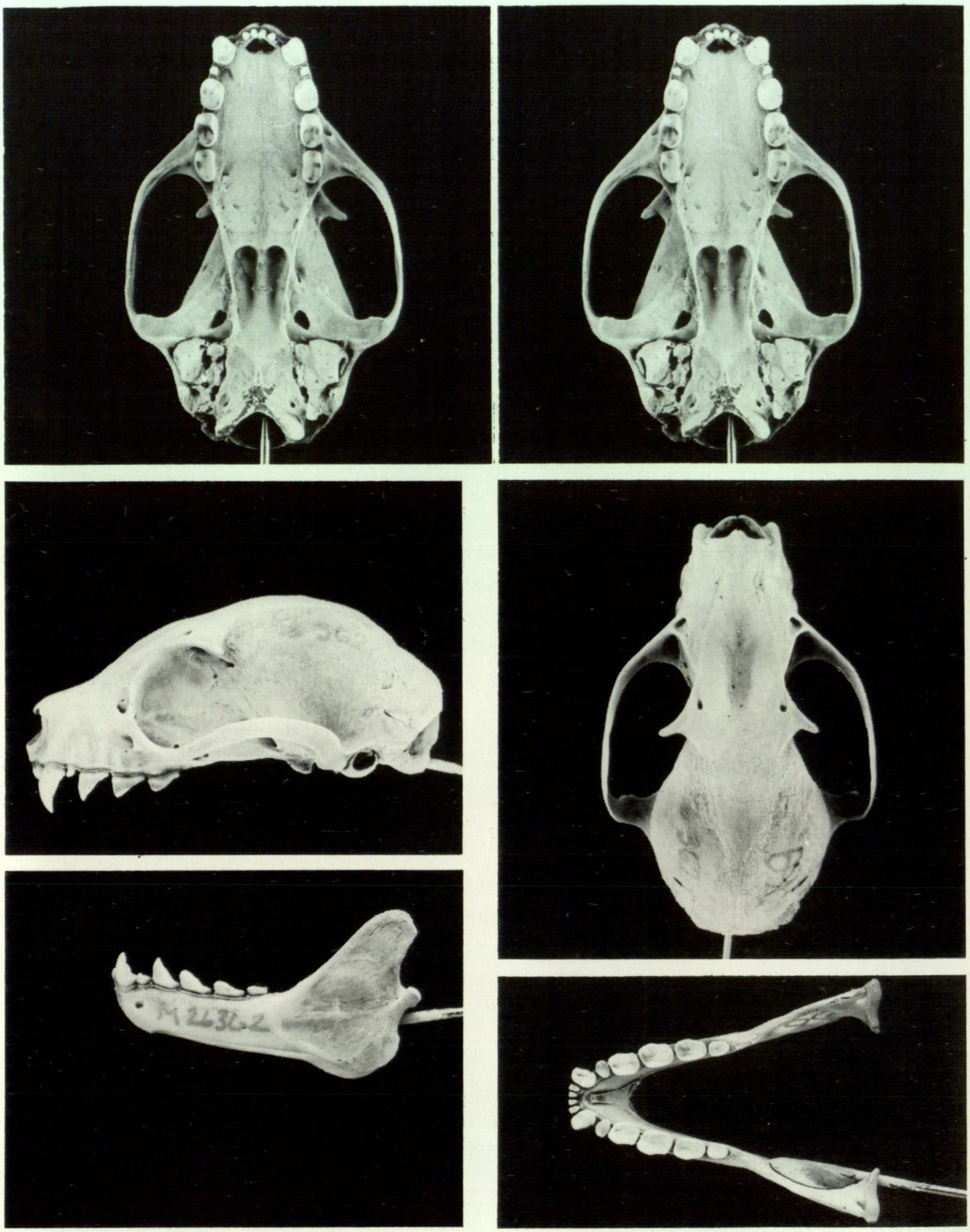


Figure 16 Skull, dentary and dentition of *Cynopterus sphinx* WAM M26362 from Krakatau I. Ventral view as stereopair. Scale line 5 mm.

(58.1-75.8) *v.* 61.4 (57.2-68.9); ♂♂ -GSL 30.4 (28.7-33.7) *v.* 28.6 (27.2-30.0), C_1-M_2 11.1 (10.1-12.8) *v.* 10.4 (9.7-11.1), RAD 65.1 (59.2-75.0) *v.* 60.9 (56.0-65.9); ZB generally wider relative to ONL (Figure 6); BW larger relative to M^1W (Figure 4); GSL generally longer relative to DIG 1 (Figure 5). P^4 posterolabial corner generally much less square. Pelage on dorsum a darker Hair Brown to Chaetura Drab compared to Grayish Drab (cinnamon fawn) to Hair Brown.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 16).

Cynopterus sphinx is considerably larger in most measurements (Table 1). Shape of rostrum in lateral profile changes with age as in *C. nusatenggara* and many specimens can be found of these two species with a similar shape rostrum; however, in juveniles of *C. sphinx* rostrum dorsal surface in lateral profile straighter (e.g. WAM M23785) rather than gently concave in the middle; some juveniles of *C. sphinx* with rostrum distal end projecting slightly further than in *C. nusatenggara* to almost level with premaxilla distal point; nasal narrowly triangular, constricted posteriorly to a blunt point, occasionally in juveniles appears constricted at midpoint by overlapping flange of maxilla (e.g. WAM M23315); frontal bone posterior to postorbital lateral process in juveniles narrower and squarer than in *C. nusatenggara;* basioccipital process tends to be more vertical and less angled towards occipital condyle than in *C. nusatenggara;* foramen oval posterior margin tends to form a more pronounced lip such that its outline is usually narrower than in *C. nusatenggara;* P^3 and P^4 (particularly P^4) lingual edge straighter without gentle curve of *C. nusatenggara;* this is reflected in measurements (Table 1) where P^3 width averages the same (1.5) but P^3 length longer in *C. sphinx* then in *C. nusatenggara* (2.1 *v.* 1.9). P^3 lingual cusp connected to base of taller labial cusp by a commissure that angles slightly posterior of the right angle to axis of molar row (Figure 13b); P^4 with lingual cusp connected to its labial cusp by a definite low ridge (obscure in worn teeth). Teeth in some *C. sphinx* (e.g. from Java and Krakatau) more robust than in *C. nusatenggara,* in others (e.g. Thailand) of subequal size; P_1 occlusal area subequal to or slightly larger than M_2; P_3 posterolabial corner more curved or widely angled rather than square as in *C. nusatenggara;* M_1 usually with very low occlusal surface cusps P_4 with such cusps only occasionally present and less obvious.

Externals and palatal ridges

The largest of the *Cynopterus* spp. considered. Weight 38.5 ± 6.43 (34.5-53.0) (N = 10) and 46.5 ± 16.06 (28.0-70.0) (N = 5) gm for adult males and adult females, respectively; external measurements presented in Table 1; overall shape as for *C. nusatenggara.*

Pelage and skin colour

Adult pelage colour of males and females differ principally in colour of collar of fur in region of neck and adjacent parts: both sexes have a collar of of lighter coloured hairs around throat and extending to chin, chest, side of neck to behind ears — occasionally this collar is complete behind neck, often colour of collar extending to fur of lateral

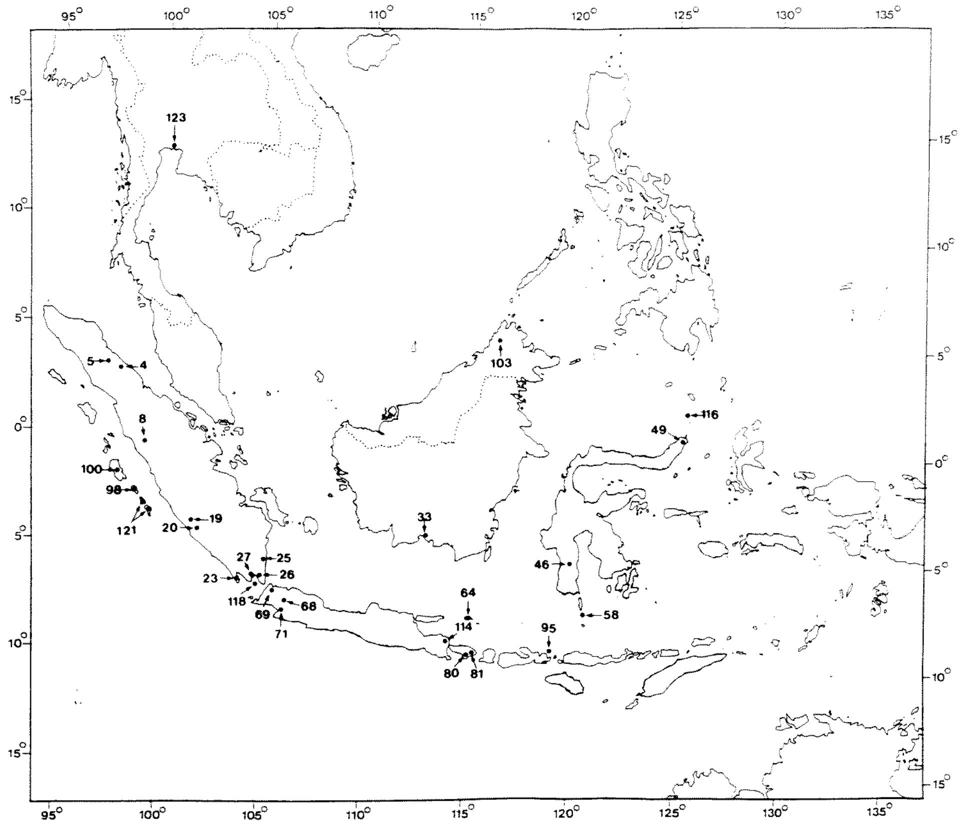


Figure 17 Localities of *Cynopterus sphinx* examined in this study.

aspect of chest and venter. In adult females overall colour of pelage on top of head, neck, and face Hair Brown (grey brown), but occasionally a darker Mummy Brown (charcoal brown) (in specimens from Bengkulu, Sumatra); a collar of Drab (cinnamon fawn) to Dresden Brown (olive brown) usually joined across back of neck and shoulders; on throat; chin and flanks of venter a lighter Marguerite Yellow (lemon cream), occasionally Chamois (yellow tan), Dresden Brown or Sulphine Yellow (pale lemon yellow). The back Isabella Color (fawn olive) to Mummy Brown but occasionally lighter near tail to Tawny Olive. Venter generally Pale Drab Gray merging to Deep Olive Buff near tail. Plagiopatagium ventral aspect adjacent to body and forearms with scattered Sulphine Yellow hairs; uropatagium dorsal and ventral surfaces very lightly haired, except at margin where hairs slightly denser, and Deep Olive Buff to Buckthorn Brown (golden brown); proximal half of radius furred on dorsal surface with same colour as dorsum; base of ear furred with same colour as neck collar, remainder naked. Skin of ears, lips, feet and patagia Deep Mouse Gray (dark lilac grey); inner and outer margins of ear a contrasting Light Buff to Warm Buff, except in specimens from Sangeang I. near

Sumbawa, where the margins of ear are slightly more lightly coloured on antero-proximal margins of ear only. Surfaces of metacarpals and phalanges a light Tilleul-Buff (pale tan cream) contrasting with colour of patagia.

Adult males have similar colours to females except that neck collar is usually a deeper colour, frequently Dresden Brown.

Baculum

A range of baculum shapes occur in adult *C. sphinx* from Krakatau I. (Figure 14). These shapes appear unrelated to age of adults as judged by extent of tooth wear and skull size.

The maximum length and width of bacula are 2.08 ± 0.26 (N = 7) mm and 1.80 ± 0.24 (N = 7) mm, respectively.

Distribution

The locality of *C. sphinx* South East Asian specimens examined by us are shown in Figure 17. They are from Thailand, Sumatra, Siberut I., Pagai I., Krakatau Is, Java, Bali I., Sangeang I., Sulawesi, Salayar I., as well as from Central India.

We have not examined specimens from Sri Lanka, Peninsula and North East India and Burma (*C. s. sphinx*), Car Nicobar I. (*C. s. scherzeri*), Serasan and Natuna Is (*C. s. serasani*), Babi I. (*C. s. babi*) or specimens of *C. s. angulatus* from North Burma, South China, Hainan I., Vietnam and Langkawi I., North Peninsula Malaysia, Verlaten I., but from available descriptions these forms are considered to be *C. sphinx*.

Remarks

Cynopterus sphinx differs from *C. brachyotis* principally on overall size and some other minor characters, particularly occlusal outline and general shape of molars and shape of rostrum.

Specimens WAM (M16160, M16162) were judged on balance to be more like *C. sphinx* than *C. brachyotis*, particularly on morphology of molars. These specimens were also allocated to *C. sphinx* by the discriminant function analysis — although they are located at the boundary of the *C. sphinx* and *C. brachyotis* discriminant function clusters. The allocation of these two specimens to *C. sphinx* is tentative. Previously these specimens were allocated to *C. brachyotis* by Kitchener and Foley (1985).

Allocation of some of the Sangeang I. specimens to *C. sphinx* is similarly tentative. These specimens have some characters typical of *C. nusatenggara*. For example, absence of white margins on ears and angle of commissure connecting P^3 low lingual and taller labial cusp (at right angles to axis of tooth row or slightly anterior to that angle). However, they are much larger specimens than *C. nusatenggara* and have other aspects of the teeth and skull that resemble *C. sphinx*. Further, their discriminant function coefficients place them clearly in the *C. sphinx* cluster.

Cynopterus sphinx is a very variable species, with specimens from India and Thailand clustering somewhat apart in the discriminant function analysis while specimens from Sulawesi and Java clustered closely with those from elsewhere in Indonesia. Characters used to distinguish *Cynopterus sphinx* from some other species in this paper, and by other researchers, are considered to a degree to be inadequate. Clearly other character sets, particularly genetic ones, need to be applied to clarify the taxonomy of this group.

Cynopterus brachyotis (Müller, 1838)
(Table 1; Figures 3-11, 13, 14, 18, 19)

Pachysoma brachyotis S. Müller, 1838, Tijd. Nat. Gesch. 5 (1): 146

Cynopterus marginatus var. *ceylonensis* Gray, 1870, Cat. Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum, London p. 122.

Cynopterus brachysoma Dobson, 1871, J. Asiat. Soc. Beng. p. 260

Cynopterus brachyotis javanicus K. Andersen, 1910, Ann. & Mag. nat. Hist. (8) 6: 624

Cynopterus brachyotis insularum K. Andersen, 1910, Ann. & Mag. nat. Hist. (8) 6: 624

Cynopterus brachyotis concolor Sody, 1940, Treubia 17: 391-401

Cynopterus brachyotis altitudinis Hill, 1961, Proc. Zool. Soc. Lond. 136: 629-642

Holotype

Andersen (1912: 619) states that the cotypes are in Leyden Museum: four as mounted specimens (Cat. Syst. *a-d*, two male adults, one female adult and one juvenile); and six odd skulls (Cat. Ost. *b-g*). Skull of specimen *a* extracted, those of *b-d in situ*; all seven skulls adult except *f*; the lower jaw of *c* missing.

Type Locality

"eene diepe kalksteen — spelonk, aan den oever van de rivier Dewej" (= Dewei River, South Central Borneo).

Diagnoses

Cynopterus brachyotis differs from *C. nusatenggara* in averaging slightly larger in many measurements (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 28.1 (26.0-29.9), ZB 18.6 (17.0-19.7) *v.* 17.8 (16.2-19.2); ♂♂-GSL 29.0 (26.9-30.7) *v.* 28.3 (27.2-29.7), ZB-18.9 (17.7-20.6) *v.* 18.0 (17.2-19.4); ZB generally wider relative to ONL and DIG 1 (Figures 6 and 7, respectively); BW larger relative to M^1W (Figure 4); ZB generally larger relative to C_1M_2 (Figure 3); BW generally larger relative to DIG 3 (Figure 8); P4 posterolabial corner generally much less square; P^3 lingual and labial cusp commissure slopes gently posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. White or light coloured edge to margin of ear. Pelage on head not markedly darker than on back and surface of metacarpals and phalanges markedly lighter and contrasting with colour of wing membrane.

It differs from *C. sphinx* in that it averages smaller in all measurements except P^3L in females and POW in males (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 30.3 (28.1-32.9), C_1-M_2 10.2 (9.4-10.8) *v.* 11.0 (9.9-13.1), RAD 61.7 (54.7-66.2) *v.* 65.7 (58.1-75.8); ♂♂-GSL 29.0 (26.9-30.7) *v.* 30.4 (28.7-33.7); C_1-M_2 10.5 (9.8-11.4) *v.* 11.1 (10.1-12.8); RAD 61.8 (55.9-66.7) *v.* 65.1 (59.2-75.0); ONL generally shorter relative to M^1W (Figure 9); DIG 1 generally shorter relative to GSL and ZB (Figures 5 and 7, respectively).

It differs from *C. minutus* in averaging larger in all measurements (except P^3W in females (Table 1): e.g., ♀♀-GSL 28.6 (27.0-29.7) *v.* 26.6 (25.4-27.6), C_1-M_2 10.2 (9.4-10.8) *v.* 9.6 (9.0-10.2), RAD 61.7 (54.7-66.2) *v.* 57.5 (54.2-61.9) and ♂♂-GSL 29.0 (26.9-30.7) *v.* 27.2 (26.2-28.3), C_1-M_2 10.5 (9.8-11.4) *v.* 9.8 (9.4-10.2), RAD 61.8 (55.9-66.7) *v.* 57.3 (52.9-60.9); ONL generally longer relative to ZB and M^1W (Figures 6 and 9, respectively); and C_1-M_2 generally longer relative to ZB (Figure 3).

It is similar in size to *C. luzoniensis* in most skull and dental measurements but averages shorter in metacarpals 1 to 5 length (Table 1): e.g. ♀♀-DIG 3 41.0 (37.1-45.0) *v.* 42.0 (38.8-45.3); ♂♂-DIG 3 40.7 (39.2-42.6) *v.* 42.2 (40.5-44.0); DIG 1 shorter relative to both DIG 3 and BW (Figures 10 and 11, respectively). P4 posterolabial corner generally much less square; P^3 lingual and labial cusps commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure. Pelage on dorsum a darker Snuff Brown (cinnamon brown to Wood Brown (brown fawn) compared to a Drab (cinnamon fawn) to Hair Brown (grey brown).

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 18)

The greatest length of skull averages slightly longer (28.6 *v.* 28.1 and 29.0 *v.* 28.3 for females and males, respectively); zygomatic breadth averages wider (18.6 *v.* 17.8 and 18.9 *v.* 18.0 for females and males, respectively); and dentary length from condyle averages longer (21.4 *v.* 20.9 and 21.9 *v.* 21.0 for females and males, respectively); P3 and P4 occlusal surfaces generally less square, particularly posterolabial corner of P4, e.g., in females, on average, P^3 longer (2.0 *v.* 1.9) but narrower (1.4 *v.* 1.5); P^3 lingual cusp connected to base of labial cusp by commissure that angles slightly posterior of the right angle to axis of molar row; P^4 with low commissure (sometimes obscure in worn teeth) linking lingual cusp to base of labial cusps (particularly prominent in Bali specimens: e.g., WAM M16163 (Figure 13b), this commissure is absent in *C. nusatenggara*).

Externals and palatal ridges

Moderate sized *Cynopterus;* external measurements presented in Table 1. Overall shape of externals and palatal ridges as described for *C. nusatenggara.*

Pelage and skin colour

Colour of Javan and Sumatran specimens broadly similar and generally lighter than those from Borneo.

Adult males from Java and Sumatra have a collar of lighter coloured fur varying from Pale Orange Yellow, Capucine Orange (fawn orange) or Isabella Color (fawn olive) around throat extending to chin, chest and side of neck, but not forming a distinct mantle on shoulders, ventrally it also extends along sides of rump flanking the Pallid Mouse Gray (pale lilac-grey) to Olive Gray venter — occasionally this flanking colour deepens to Tawny Olive. Top of head from rhinarium to occiput, face, lips, Hair Brown (grey brown); chin Chamois (yellow tan) to Honey Yellow; back Hair Brown; plagiopatagium ventral surface adjacent to body and forearms thinly furred with Hair Brown; uropatagium ventral and dorsal surfaces lightly furred with Hair Brown except near tail where there is a tuft of hairs; radius proximal one-third lightly furred on dorsal

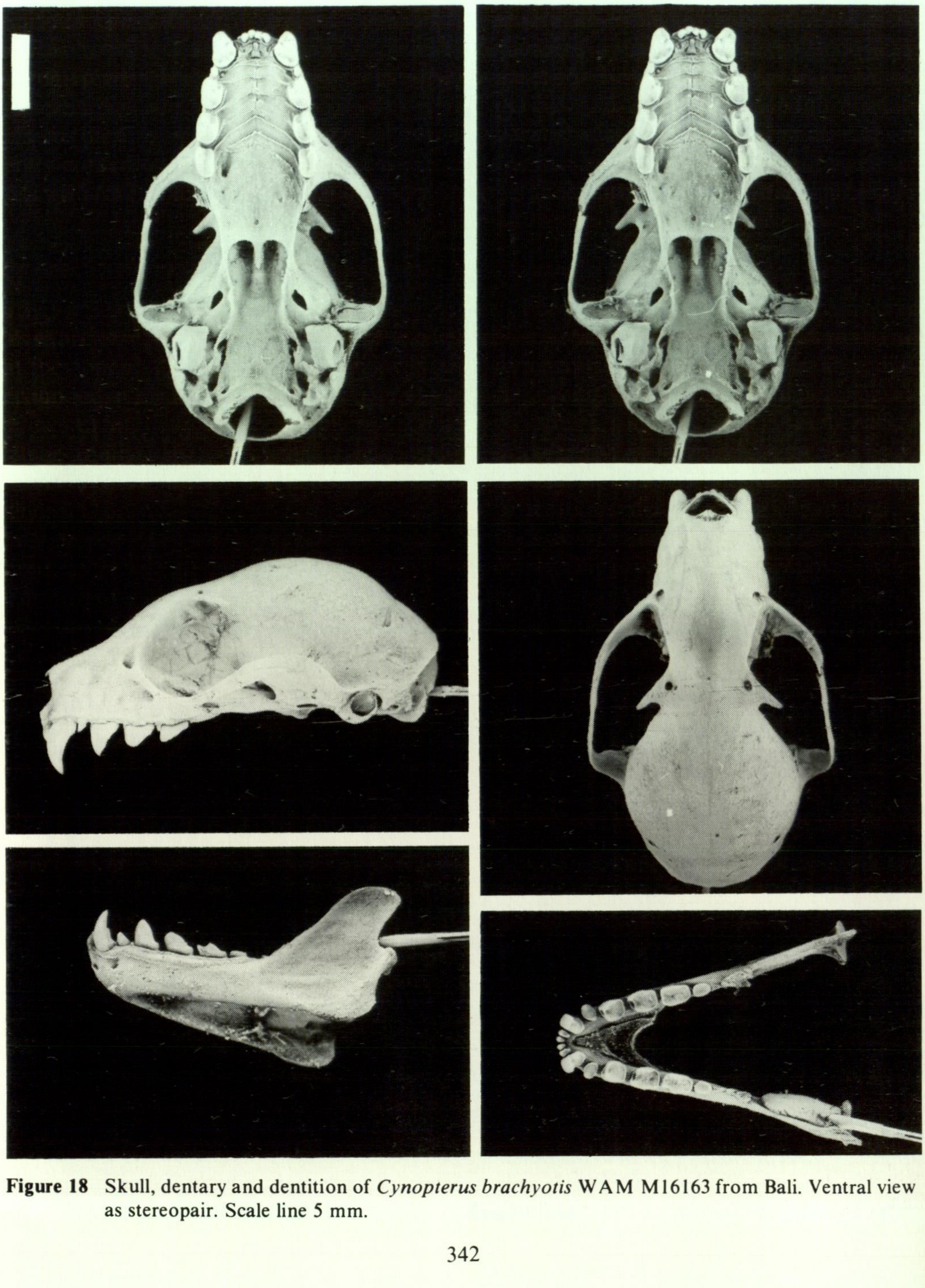


Figure 18 Skull, dentary and dentition of *Cynopterus brachyotis* WAM M16163 from Bali. Ventral view as stereopair. Scale line 5 mm.

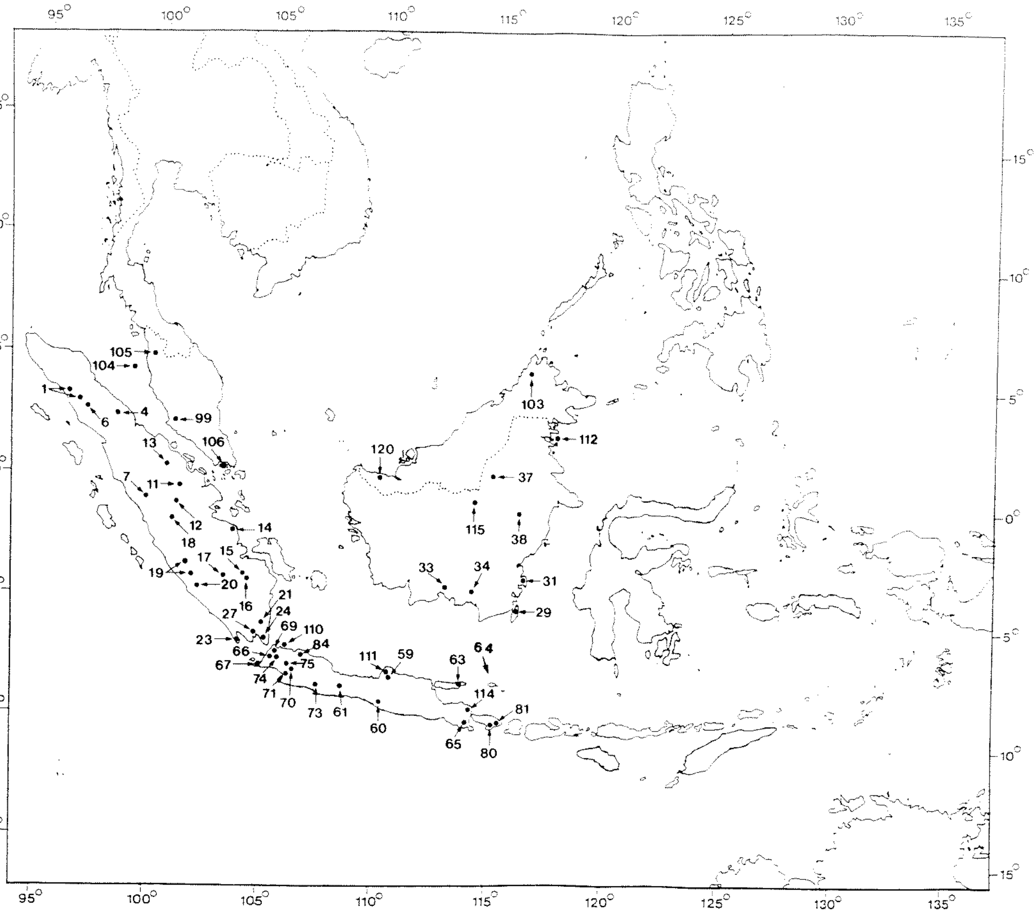


Figure 19 Localities of *Cynopterus brachyotis* examined in this study, excluding specimens from Sri Lanka.

surface with colour of back; ear naked apart from base; skin of ear, lips, feet and patagia Fuscous Black; margins of ear, both externally and internally, Tilleul Buff (pale tan cream) contrasting with rest of ear; metacarpals and phalanges Vinaceous Buff (cinnamon cream), contrasting with colour of patagia.

Adult females from Java and Sumatra generally a lighter colour than adult males, although the pattern of colour similar. Neck collar ranges from Deep Colonial Buff (light yellow tan) to Honey Yellow — colours which weakly splash flanks of stomach and contrast less with the Grayish Olive stomach and inguinal region than with males; head, face and chin similar colour to males. Other colours as in males.

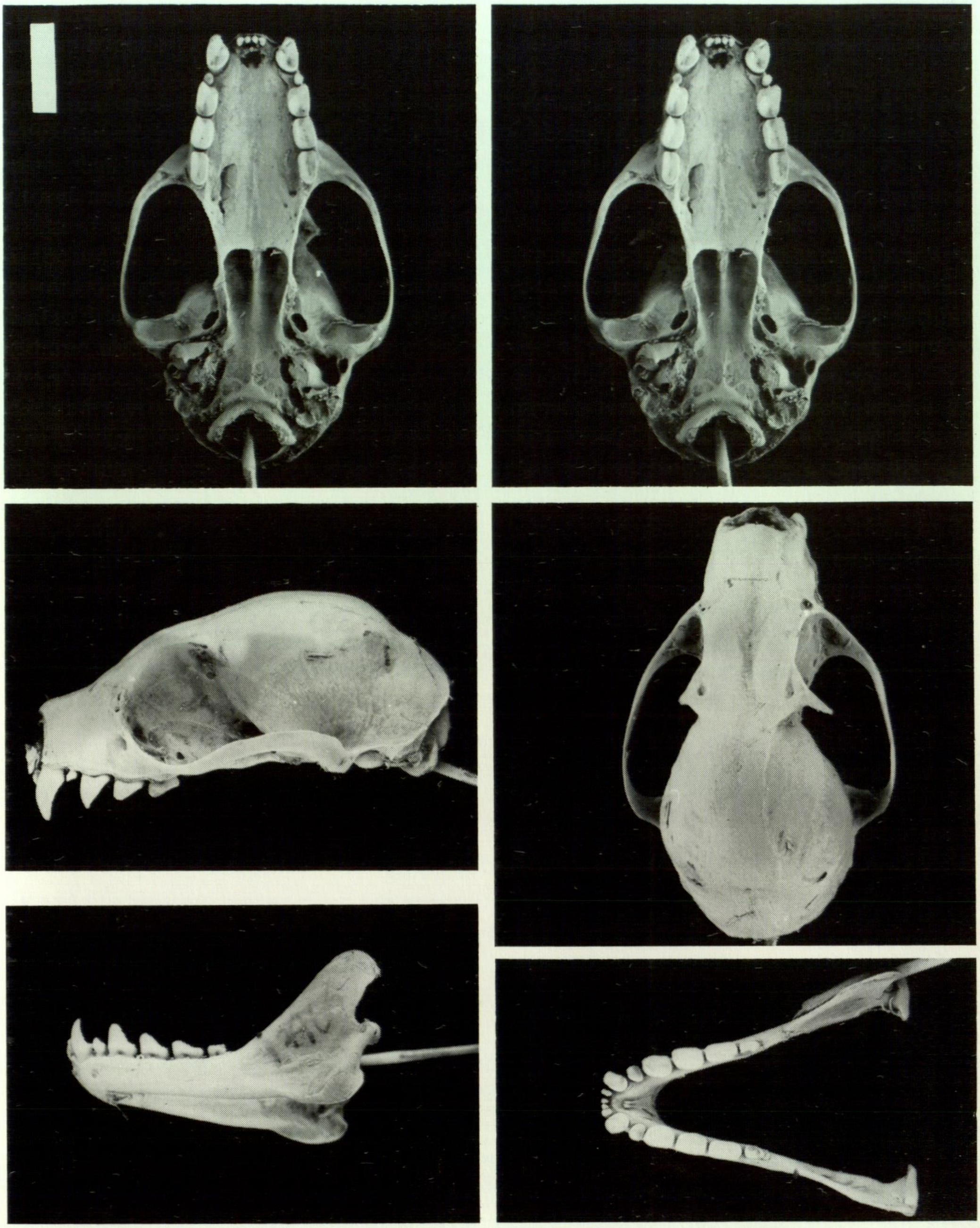


Figure 20 Skull, dentary and dentition of *Cynopterus minutus,* MZB 13446. Topotype from Nias I. ventral view as stereopair. Scale line 5 mm.

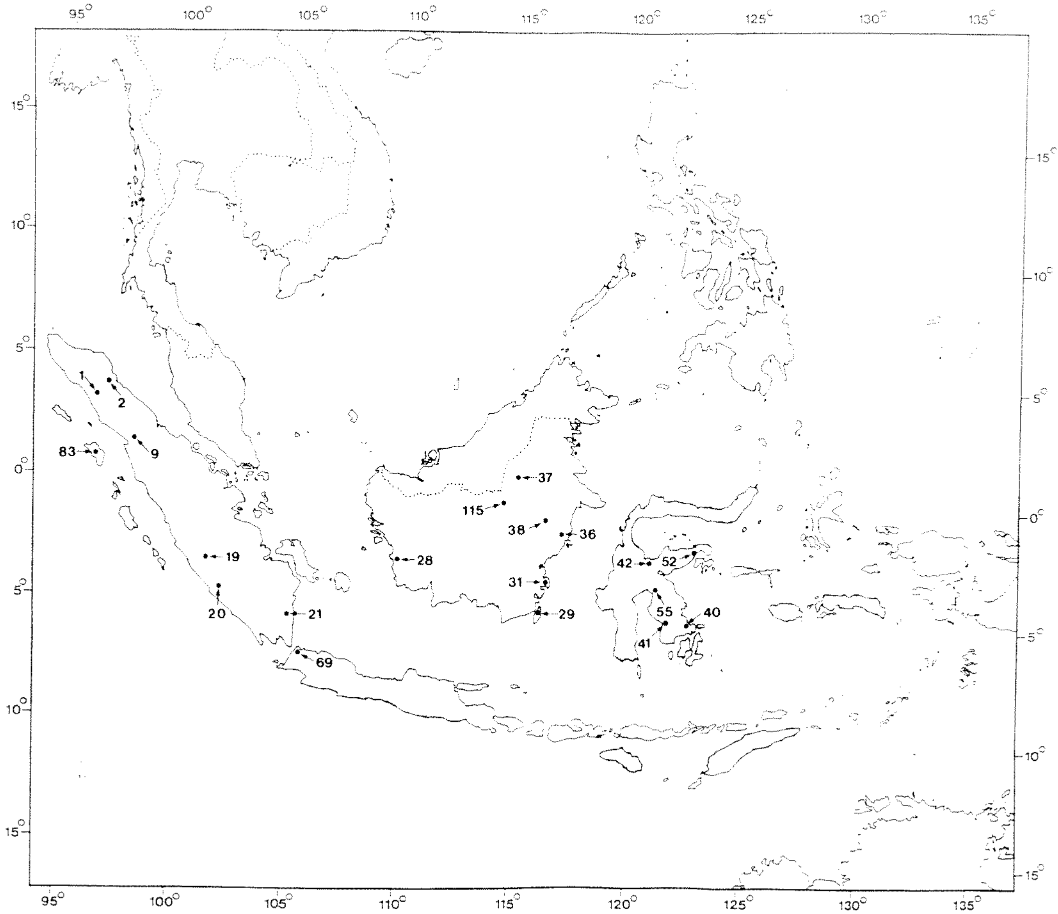


Figure 21 Localities of *Cynopterus minutus* examined in this study.

Adult males from Borneo have a collar of Sayal Brown (brown cinnamon) to Mikado Brown (orange brown) around throat and extending to chin, chest and flanks of abdomen almost to inguinal region, and dorsally behind ears and on lateral aspects of shoulders — it does not form a united band behind head; top of head from rhinarium to nape of neck Olive Brown tipped on back and rump with Snuff Brown (cinnamon brown); ventral surface adjacent to body and forearm thinly furred with Cinnamon Buff; uropatagium ventral and dorsal surfaces lightly furred with Buckthorn Brown (golden brown) except near tail where there is a tuft of hairs; radius proximal one-third lightly furred on dorsal surface with colour of back. Other colours as for Javan and Sumatran specimens.

Adult females from Borneo a lighter colour and pattern of colour slightly different. The neck-collar less pronounced and ventrally indistinct lateral to stomach, dorsally also less distinct, particularly on shoulders. The major difference between sexes of Bornean specimens is the neck-collar of females which ranges from lighter Antimony Yellow (fawn yellow) to Buckthorn Brown and these colours, which provide the tipping of hairs of both abdomen and back, are less extensive in these regions and where they occur create a 'lighter' overall colour to pelage.

Baculum

Shape of baculum of *C. brachyotis* variable but less so than in *C. sphinx* and *C. nusatenggara.* Its basic shape triangular with apex distal, sides of this triangle notched sometimes close to apex but usually halfway down sides (Figure 14). Some of these shapes are similar to those found in other *Cynopterus* spp. considered.

The maximum lengths and breadths (in mm), respectively of *C. brachyotis* bacula from several regions are as follows:

	Length (N = 5)	Breadth (N = 5)
Java	2.02 ± 0.23	1.66 ± 0.11
Borneo	2.30 ± 0.14	1.95 ± 0.07
Peninsular Malaysia/Singapore	2.16 ± 0.33	1.84 ± 0.15

Distribution

The localities of South East Asian *C. brachyotis* specimens examined by us are shown in Figure 19. They are from Peninsular Malaysia, Penang I., Singapore I., Sumatra, Borneo, Pulau Laut I., Bunyu I., Java., Pulau Dua I., Madura I., Kangean I. and Bali I. as well as from Sri Lanka. We have not examined specimens of *C. brachyotis altitudinis* (Malayan highlands); *C. b. concolor* (Enggano I.); *C. b. brachysoma* (Andaman Is) or *C. b. brachyotis* from Burma to Vietnam and from many small islands such as Bawean. However, based on descriptions available of these forms they are considered to be *C. brachyotis.*

Cynopterus minutus Miller, 1906

(Table 1; Figures 3-11, 14, 20, 21)

Cynopterus minutus Miller, 1906, Proc. Biol. Soc. Wash. 19: 63.

Holotype

U.S. National Museum Reg. No. 141240, adult male, skin and skull.

Type Locality

Nias I., Indonesia.

Diagnoses

Cynopterus minutus differs from *C. nusatenggara* in averaging smaller in all measurements except ZB, BW and C^1-C^1 in females, and ZB in males (Table 1): e.g., ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.1 (26.0-29.9), C_1-M_2 9.6 (9.0-10.2) *v.* 9.9 (9.3-10.6), RAD

57.5 (54.2-61.9) *v.* 59.9 (55.1-64.8) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 28.3 (27.2-29.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.1 (9.3-10.6), RAD 57.3 (52.9-60.9) *v.* 59.3 (54.7-61.9); ONL generally shorter relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much less square. White or light coloured edge to margin of ear present; pelage on head not markedly darker than that of back and surface of metacarpals; and phalanges markedly lighter and contrasting with colour of wing membrane.

It differs from *C. sphinx* in averaging smaller in all measurements (Table 1). It is absolutely smaller in the following: ♀♀-CDL 24.5 (23.0-25.6) *v.* 28.0 (25.7-30.5); ♂♂-GSL 27.2 (26.2-28.3) *v.* 30.4 (28.7-33.7), CDL 24.9 (23.3-26.1) *v.* 28.2 (26.1-31.1), PL 13.7 (13.0-14.2) *v.* 15.7 (14.9-18.2), P^3L 1.8 (1.6-1.9) *v.* 2.1 (2.0-2.4). RAD 57.3 (52.9-60.9) *v.* 65.1 (59.2-75.0) RAD ♀♀ 57.5 (54.2-61.9) *v.* 65.7 (58.1-75.8), BW smaller relative to M^1W (Figure 4); canines much smaller. Pelage on dorsum a lighter Wood Brown (brown fawn) to Buffy Brown compared to Chaetura Drab (olive black).

It differs from *C. brachyotis* in averaging smaller in all measurements (except P^3W in females) (Table 1): e.g. ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.6 (27.0-29.7), C_1-M_2 *9.6 (9.0-10.2)* *v.* 10.2 (9.4-10.8), RAD 57.5 (54.2-61.9) *v.* 61.7 (54.7-66.2) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 29.0 (26.9-30.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.5 (9.8-11.4), RAD 57.3 (52.9-60.9) *v.* 61.8 (55.9-66.7); ONL generally shorter relative to ZB and M^1W (Figures 6 and 9, respectively); and C_1-M_2 generally shorter relative to ZB (Figure 3).

It differs from *C. luzoniensis* in averaging smaller in all measurements except ZW, BW and C^1-C^1 in females and ZW in males (Table 1): e.g., ♀♀-GSL 26.6 (25.4-27.6) *v.* 28.1 (26.0-29.9), C_1-M_2 9.6 (9.0-10.2) *v.* 9.9 (9.3-10.6), RAD 57.5 (54.2-61.9) *v.* 59.9 (55.1-64.8) and ♂♂-GSL 27.2 (26.2-28.3) *v.* 28.3 (27.2-29.7), C_1-M_2 9.8 (9.4-10.2) *v.* 10.1 (9.3-10.6), RAD 57.3 (52.9-60.9) *v.* 59.3 (54.7-61.9); ONL shorter relative to ZB and M^1W (Figures 6 and 9 respectively); and P4 posterolabial corner generally much less square.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 20)

Cynopterus minutus averages smaller than *C. nusatenggara* for most measurements (see diagnoses and Table 1).

It differs from *C. nusatenggara* in that cranium dorsal view generally slightly more inflated and globose, rostrum lateral profile slopes more sharply from frontals to nasal distal tip, rostrum noticeably shorter with rostrum length: greatest skull length averaging 0.22 *v.* 0.24 such that front of rostrum in lateral view squarer, zygomatic arch averages wider relative to greatest skull length (0.67 *v.* 0.63), median frontal sulcus tends to be more concave, and postsquamosal ridge immediately dorsal to bulla frequently reaches lambdoidal crest. Postorbital lateral process tends to face more posteriorly in specimens from Nias I. (e.g. MZB 13445-6); dentary coronoid process with blunt rounded apex or with slight posterior hook, posterior margin gently concave or almost straight; P^3 lingual cusp connected to base of taller labial cusp by a commissure that angles slightly posterior of the right angle to axis of molar row; P^4 with low commissure linking lingual cusp to base of labial cusp (obscure in worn teeth). P3 and P4 occlusal surfaces generally less square, particularly posterolabial corners of P4.

Externals and palatal ridges

Smallest of the *Cynopterus* spp. considered. Its external measurements presented in Table 1. Overall shape of externals and palatal ridges as described for *C. nusatenggara*.

Pelage and skin colour

Pelage colour of adult males and females differ principally in collar of fur in neck region and adjacent parts: both sexes have a collar of lighter coloured hair around throat and extending to chin, top of chest, flanks of venter, side of neck to behind ears (and in females, usually around teats) — occasionally this collar faintly connects behind neck.

In adult females, this collar Buff to Chamois (yellow tan); overall colour of pelage on top of head, back and rump Buffy Brown; venter Light Yellowish Olive to Light Brownish Olive; ventral aspect of plagiopatagium adjacent to body and forearm with scattered Deep Olive-Buff hairs; uropatagium ventral and dorsal surfaces lightly furred with Buffy Brown, more dense at margins particularly nearer tail; radius proximal half furred dorsally with same colour as dorsum; base of ear same colour as neck collar, remainder naked. Skin of ear, lips, feet and patagia Clove Brown; inner and outer margins of ear a contrasting Cartridge Buff (pale tan). Surfaces of metacarpals and phalanges a light Cartridge Buff contrasting with colour of patagia.

Adult males coloured as for females but with dorsal surfaces generally a darker Light Brownish Olive to Brownish Olive; neck collar a more strongly coloured Olive Ochre to Clay Color (olive tan) particularly in Sumatran specimens.

Baculum

Shape of *C. minutus* variable but less so than *C. nusatenggara* and *C. sphinx*. Shape basically triangular or arrow shaped with the apex distal (Figure 14). Maximum length and maximum breadth (in mm) of bacula are:

	Length (N = 3)	Breadth (N = 3)
Borneo	2.10 ± 0.12	1.46 ± 0.21
Sumatra	2.21 ± 0.34	1.60 ± 0.19

Distribution

The localities of *C. minutus* specimens examined are shown in Figure 21.

They are from the type locality of Nias I., Sumatra, Java, Borneo and Sulawesi.

Remarks

Andersen (1912) presents measurements from 5 paratypes of *C. minutus* from Nias I. Our measurements of 45 specimens from a much wider geographic area largely conform to those of Andersen. For example, our maximum skull measurements exceed those of Andersen's only for: mesopterygoid fossa (4.2 *v.* 4.0), zygomatic width (19.0 *v.* 18.0) and braincase width (12.7 *v.* 12.2).

External measurements for our specimens average similar to those of Andersen but maximum values tend to exceed his maxima: e.g., radius length (61.9 *v.* 59), DIG 2 (29.0 *v.* 25.5), DIG 3 (42.8 *v.* 37.5), DIG 4 (39.4 *v.* 35), DIG 5 (41.7 *v.* 36.0). This may reflect that the body size of some animals examined by us exceed the size of the Nias I. population, or it may relate to different measuring techniques (external measurements are more dependent on nature of fixation of specimens and the recorder, than are skull measurements).

Cynopterus luzoniensis (Peters, 1861)

(Table 1; Figures 3-11, 14, 22, 23)

Pachysoma luzoniense Peters, 1861, Mber. K. Preuss Akad. Wiss. p. 708.

Cynopterus marginatus var. *philippensis* Grey, 1870, Cat. Monkeys and Fruit-eating Bats in the Collections of the British Museum p. 123.

Cynopterus marginatus var. *cumingii* Grey, 1870, Cat. Monkeys and Fruit-eating Bats in the Collections of the British Museum p. 123.

Types

Syntypes: two adult females, 'alcoholic', both with skull *in situ*, Berlin Museum, nos. 2425 and 2426 (Andersen 1912: 620).

Type Locality

Volkan Yriga, S. Camarines, Luzon, Philippines.

Diagnoses

Cynopterus luzoniensis differs from *C. nusatenggara* in having all wing measurements, averaging slightly longer (Table 1): DIG 1 longer relative to DIG 3 (Figure 10); DIG 1 generally longer relative to ZB (Figure 7); DIG 3 generally longer relative to BW (Figure 8). White or light coloured edge to margin of ear present; pelage on head not markedly darker than that of back; dorsum Light Drab (cinnamon fawn) to Hair Brown (grey brown) rather than darker Olive Brown; surface of metacarpals and phalanges markedly lighter and contrasting with colour of wing membrane; P^4 lingual and labial cusp commissure slopes slightly posteriorly and P^4 lingual and labial cusps connected by low ridge or distinct commissure.

It differs from *C. sphinx* in averaging smaller in most measurements (except P^3L, P^3W, M^1L and DIG1 in females and LIW in males (Table 1): e.g., ♀♀-28.6 (27.3-30.5) *v.* 30.3 (28.1-32.9), C_1-M_2 10.2 (9.4-11.2) *v.* 11.0 (9.9-13.1), RAD 61.4 (57.2-68.9) *v.* 65.7 (58.1-75.8); ♂♂-GSL 28.6 (27.2-30.0) *v.* 30.4 (28.7-33.7); C_1-M_2 10.4 (9.7-11.1) *v.* 11.1 (10.1-12.8), RAD 60.9 (56.0-65.9) *v.* 65.1 (59.2-75.0); ZB generally narrower relative to ONL (Figure 6); BW narrower relative to M^1W (Figure 4); GSL generally shorter relative to DIG 1 (Figure 5). P4 posterolabial corner generally much more square.

It differs from *C. brachyotis* in that it has on average longer metacarpals I to IV (Table 1): e.g. ♀♀-DIG 3 42.0 (38.8-45.3) *v.* 41.0 (37.1-45.0); ♂♂-DIG 3 42.2 (40.5-44.0) *v.* 40.7 (39.2-42.6); DIG 1 longer relative to both DIG 1 and BW (Figures

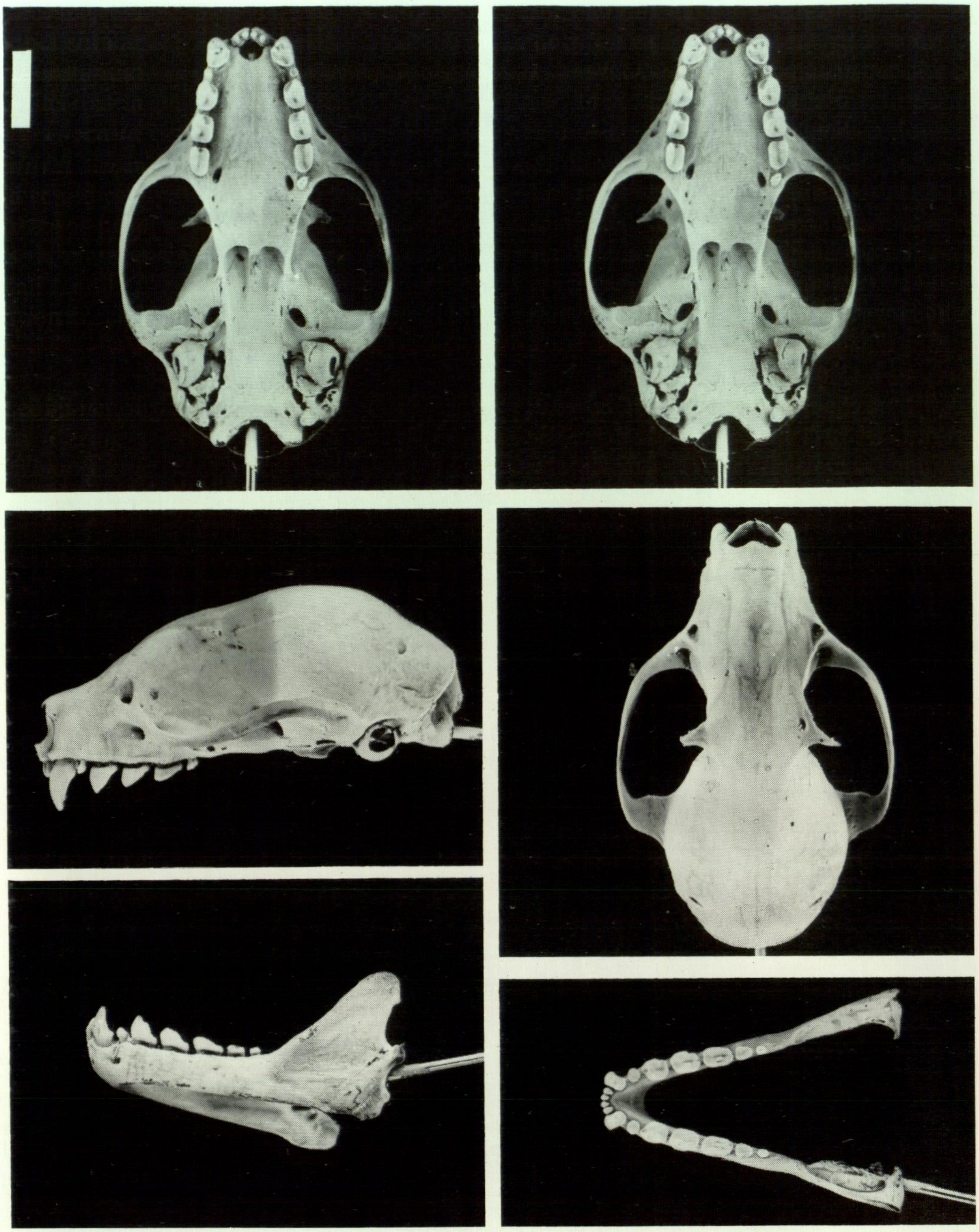


Figure 22 Skull, dentary and dentition of *Cynopterus luzoniensis*, WAM M25475 from N. Sulawesi. Ventral view as stereopairs. Scale line 5 mm.

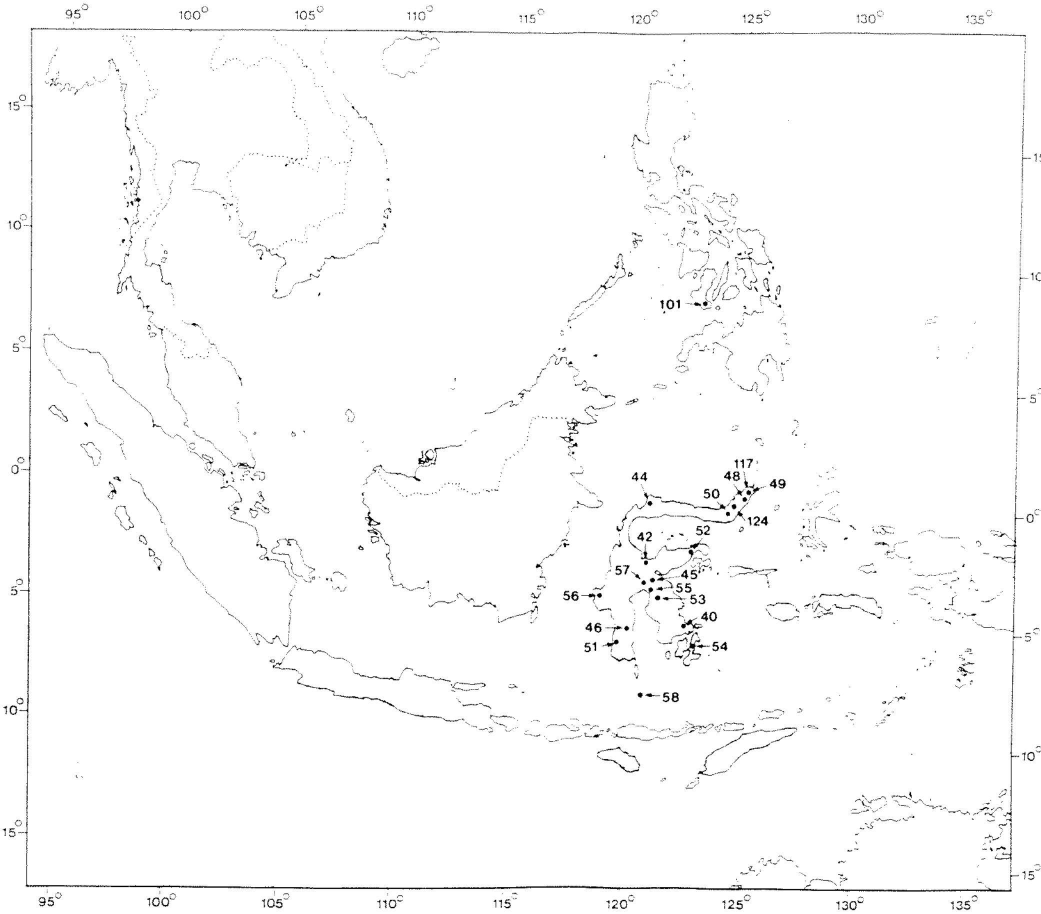


Figure 23 Localities of *Cynopterus luzoniensis* examined in this study.

10 and 11, respectively); P4 posterolabial corner generally much more square; pelage on dorsum Drab (cinnamon fawn) to Hair Brown (grey brown).

It differs from *C. minutus* in averaging larger in all measurements except ZB, BW and C^1-C^1 in females and ZB in males (Table 1): e.g. ♀♀-GSL 28.1 (26.0-29.9) *v*. 26.6 (25.4-27.6), C_1-M_2 9.9 (9.3-10.6) *v*. 9.6 (9.0-10.2), RAD 59.9 (55.1-64.8) *v*. 57.5 (54.2-61.9) and ♂♂-GSL 28.3 (27.2-29.7) *v*. 27.2 (26.2-28.3), C_1-M_2 10.1 (9.3-10.6) *v*. 9.8 (9.4-10.2), RAD 59.3 (54.7-61.9) *v*. 57.3 (52.9-60.9); ONL longer relative to ZB and M^1W (Figures 6 and 9, respectively); P4 posterolabial corner generally much more square.

Description

The description is generally as for *C. nusatenggara* except for the following:

Skull, dentary and dentition (Figure 22)

Median frontal sulcus of skull tends to be more deeply concave in adults compared to adults of *C. nusatenggara* with similar tooth wear; external auditory meatus tends to be more oval in lateral view and lambdoidal ridge immediately posterior to bulla generally with a more pronounced curve than in *C. nusatenggara;* P^3 basal area more variable, ranges from slightly less, or subequal rather than slightly larger than that of C^1; P^3 labial and lingual cusps connected by low commissure that slopes noticeably backward particularly in Sulawesi specimens, rather than at right angles to long-axis of tooth row as in *C. nusatenggara*; occasionally M^2 present (e.g. WAM M25475 in right dentary) which is subequal in occlusal area to P^1; P^4 with obvious low commissure joining labial and lingual cusps in specimens from Sulawesi; commissure present in Philippine specimens but generally less prominent (sometimes obscure in worn teeth).

Externals and palatal ridges

Moderate sized *Cynopterus.* External measurements presented in Table 1. Overall shape of external and palatal ridges as described for *C. nusatenggara.*

Pelage and skin colour

Generally overall pelage a greyish olive colour with less contrasting pelage colours than in the other *Cynopterus* spp. considered.

Adult males have a collar of lighter coloured Warm Buff (cream yellow) to Yellow Ochre (orange yellow) fur around throat and extending to chin, chest and side of neck, barely perceptible at nape of neck, ventrally usually colours chest and extends along sides of abdomen flanking the Grayish Olive venter. Head and back Light Grayish Olive to Grayish Olive frequently tipped with Drab; rump and legs Drab (cinnamon fawn). Plagiopatagium ventral surface adjacent to body and forearms thinly furred with Chamois (yellow tan) to Grayish Olive; uropatagium ventral and dorsal surface generally lightly furred with Drab but thicker at middle margins; radius proximal one-third lightly furred on dorsal surface with same colour as on rump; ear naked apart from base. Skin of ears, lips, feet and patagia Benzo Brown (deep lilac-brown); ear margin Pale Olive Buff contrasting with darker remainder of ear — in Sulawesi specimens both internal and external margins of ear lightly coloured, whereas in the Philippines specimens lighter margins usually on internal side of ear. Surfaces of metacarpals and phalanges lighter, generally Olive Buff contrasting with colour of patagia.

Adult females generally lighter coloured than adult males, although the pattern of colour similar. Neck collar much less distinct and paler, ranges from Deep Olive Buff to Chamois — its colour generally restricted ventrally to chin, throat and top of chest, infrequently as a contrasting flanking colour to grey of abdomen but generally its colour tips abdominal fur. Other colours as for adult males.

Baculum

Shape of baculum variable (Figure 14). Maximum length and maximum breadth (in mm) of baculum is:

	Length (N = 3)	Breadth (N = 3)
Sulawesi	1.64 ± 0.47	1.58 ± 0.43
Philippines	1.63 ± 0.52	1.38 ± 0.46

Distribution

The locality of specimens examined are shown in Figure 23. They are from Sulawesi and Negros I., Philippines. *C. luzoniensis* is also from Luzon Island (type locality) and Taylor (1934) lists it (as *C. b. brachyotis*) from Mindanao, Polillo and Palawan Is. Heideman and Heaney (1989) also report it from Leyte I. and Heaney (pers. comm.) from Dinagat, Biliran and Maripipi Is (as *C. brachyotis*).

Results and Discussion

Sexual Dimorphism

The two factor MANOVA resulted in significant ($P < 0.05$) sexual dimorphism, with males generally larger than females, for 14 of the 19 skull characters, with most significant at $P < .01$; those not significant were MFL, POW, BW, CPL and M^1W.

Only one of the 8 external characters (DIG 3P, $P = 0.031$) was sexually dimorphic.

There was a significant interaction between sex and species in only one character (M^1L, $P = 0.01$).

Because of the broad extent of sexual dimorphism in the skull and dental characters, the sexes are treated separately in the following analyses.

Discriminant function analysis

Females

The cumulative variation explained by the first three canonical variate functions is 98.3%, with functions 1, 2 and 3 explaining 52.4, 26.3 and 19.6% respectively.

The overall percentage of cases correctly classified to their species group was 93.0%. All *C. nusatenggara* were correctly classified as were 94% of *C. minutus*, 93% of *C. luzoniensis*, 90% of *C. brachyotis* and 90% of *C. sphinx*. Species groups into which individuals were misclassified can be gainsayed from Figures 24 and 25.

For females, CVI best separates *C. minutus* from *C. sphinx*, and both these species from the other species considered (Figures 24 and 25). Characters most influencing this function (GSL, PL, RAD, DIG 1, DIG 3, DIG 5) relate to overall length of skull and of radius and metacarpals and relate to the relatively overall smaller size of *C. minutus* and larger size of *C. sphinx* (Table 1).

Of the remaining three species, *C. brachyotis* separated from both *C. luzoniensis* and *C. nusatenggara* on both CV2 and CV3 (Figures 24 and 25). Characters most influencing these functions (BW, ONL, P^4-P^4, C_1-M_2, M^1-M^1, RAD, DIG 1 and DIG 3) relate to braincase width, shape of rostrum, distances between and along toothrows and shape of

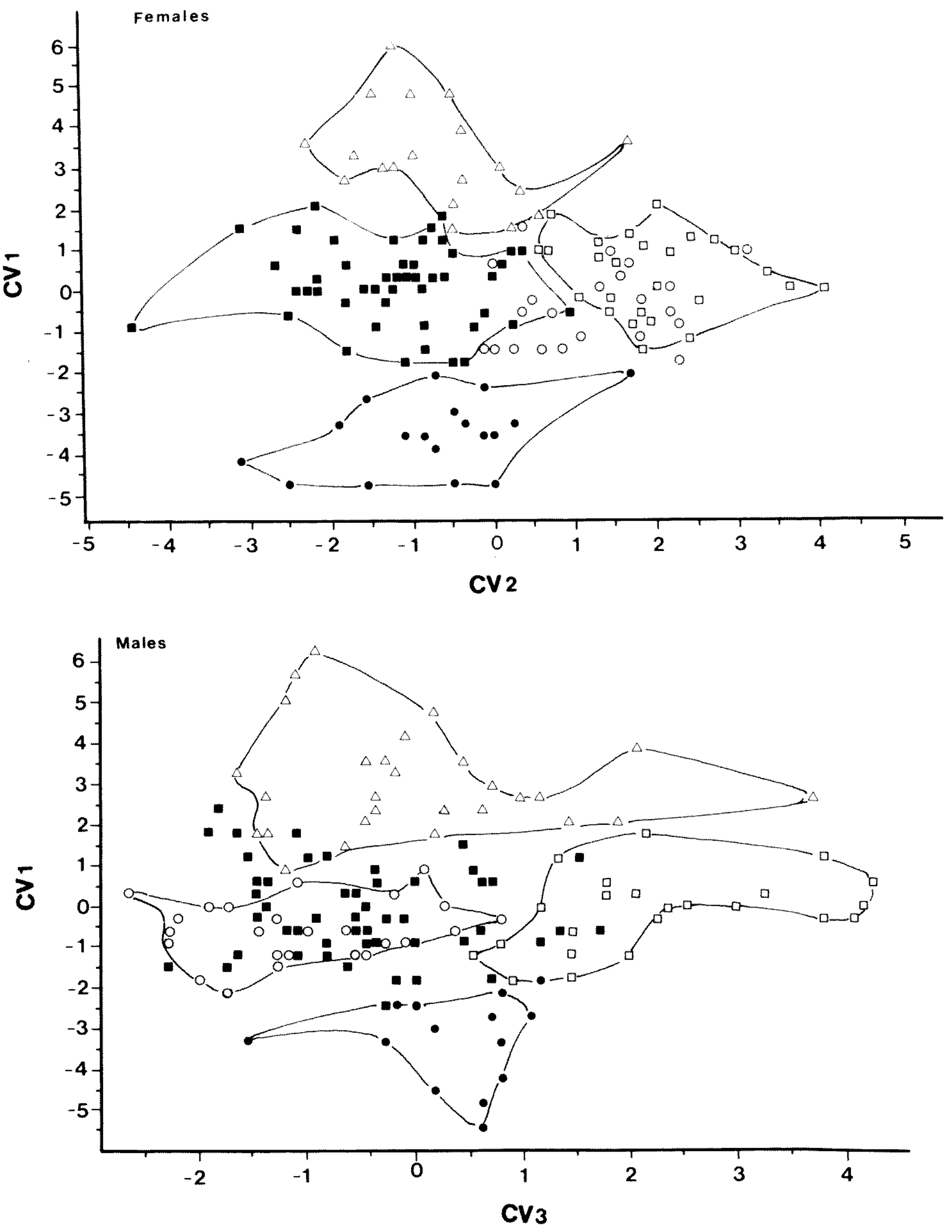


Figure 24 Plot of CV1 and CV2 for males and females of five species of *Cynopterus*; performed on all skull and external characters considered. O, *C. nusatenggara;* △, *C. sphinx;* ■, *C. brachyotis;* ●, *C. minutus* and □, *C. luzoniensis.*

wing. *C. luzoniensis* and *C. nusatenggara* are separated on CV3. Characters most influencing this function (ONL, P^4-P^4, M^1-M^1, C^1-M^2, DIG 1 and DIG 3) emphasise shape of rostrum, distances between and along toothrows and length of terminal wing digits.

Males

The cumulative variation explained by the first three canonical variate functions is 96.1%, with functions 1, 2, and 3 explaining 47.7, 30.3 and 18.2%, respectively.

The overall percentage of cases correctly classified to their species group was slightly less (89.4%) than for the females. All *C. nusatenggara* and *C. minutus* were correctly classified, as were 93.0% of *C. sphinx*, 87.5% of *C. luzoniensis* and 80.3% of *C. brachyotis*. Species groups into which individuals were misclassified can be gainsayed from Figures 24 and 25.

As was the situation with females, males of *C. minutus* and *C. sphinx* are best separated by CV1. Characters most influencing this function (GSL and CDL) again relate to overall length of skull but unlike the situation with females, external characters did not contribute heavily to this factor (Table 2). Of the remaining three species, *C. brachyotis* is separated from both *C. nusatenggara* and *C. luzoniensis* on CV2. Characters most influencing this factor are the length of the rostrum (ONL) and M^1 length. *C. nusatenggara* and *C. luzoniensis* are separated most on CV3. Characters most influencing this factor (GSL, PL, C^1-M^2, M^1-M^1, M^1W, DIG 3 and TIB) relate to overall length of skull, length of toothrow, breadth between outside surfaces of M^1, length of digit 3 metacarpal and tibia length.

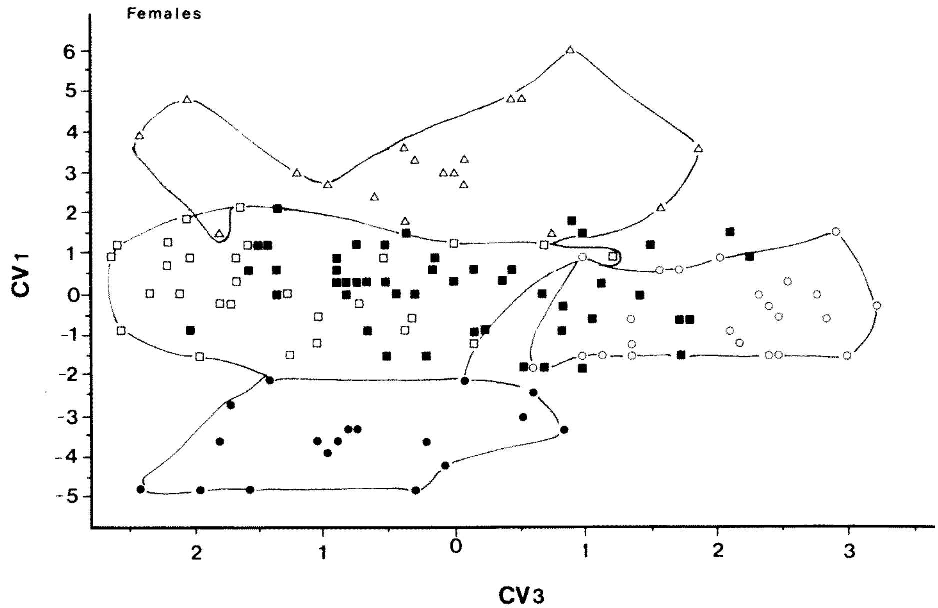
Slightly different characters are important in females and males in discriminating between these species of *Cynopterus*.

Bivariate plots

All characters in the stepwise discriminant function analysis were significant at $P < 0.001$. The first ten of these characters (all with a Wilks Lambda for entry >0.08) were as follows: GSL, DIG 1, ZB, BW, M^1W, C^1-M^2, ONL, M^1L, POW, and M^1-M^1. These characters were all important discriminants in the canonical variate analysis and weighed heavily in one or more functions (Table 2). Additionally DIG 3, P^4-P^4 and M^1-M^1 also had high (>0.5) standardised discriminant functions (Table 2). Combinations of bivariate plots were examined among all the 13 characters mentioned above for their ability to discriminate between the five recognised *Cynopterus* spp.

Taxonomy

We have not attempted in this study to examine intraspecific variation in the five species of *Cynopterus* considered, but it is apparent that regional variation does occur within the species. For example, while there is considerable overlap in the canonical plots of *C. luzoniensis* from the Philippines and Sulawesi regions, specimens from these two regions cluster somewhat separately. A similar situation occurs within *C. brachyotis*, where specimens from Java, Sumatra, Bali and associated islands cluster somewhat separately from those of Borneo and Singapore. In *C. sphinx* the specimen from Pagai I. is removed from its species cluster — although it is associated with that cluster; the



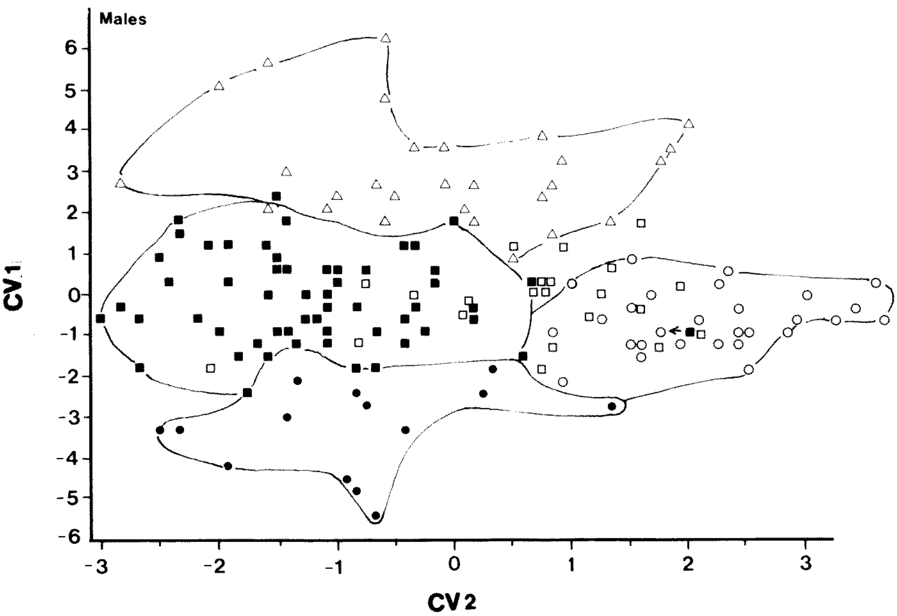


Figure 25 Plot of CV1 and CV3 for males and females of five species of *Cynopterus*; performed on all skull and external characters considered. Species code as for Figure 24.

Table 2 Standardised and unstandaradised (in brackets) canonical variates based on skull measurements of adult *Cynopterus nusatenggara*, *C. sphinx*, *C. brachyotis*, *C. minutus* and *C. luzoniensis*. Canonical scores are calculated as the summation of the products of the unstandardised canonical variates and the respective length measurements plus the constant. For explanation of character codes see Figure 1 caption (a) females, (b) males.

Table 2a

	FUNCTION 1	FUNCTION 2	FUNCTION 3
GSL	0.5164 (0.6031)	0.2154 (0.2516)	0.2252 (0.2630)
PL	0.4962 (0.9529)	—0.1151 (—0.2210)	—0.2219 (0.4261)
MFW	0.1300 (0.5563)	0.1435 (0.6141)	—0.1442 (—0.6171)
ONL	—0.3384 (—0.8674)	0.1270 (0.3254)	0.8908 (2.2831)
LIW	0.0606 (0.1823)	0.2498 (0.7513)	—0.0661 (—0.1989)
POW	0.3043 (0.6575)	0.1143 (0.2470)	—0.1924 (—0.4158)
ZB	—0.3633 (—0.5060)	—0.1880 (—0.2618)	—0.3731 (—0.5197)
BW	—0.0730 (—0.1965)	—0.5183 (—1.3951)	0.1324 (0.3565)
CPL	0.3605 (0.3377)	—0.0427 (—0.0400)	0.0396 (0.0371)
C^1C^1	—0.2295 (—0.8258)	—0.1043 (—0.3751)	—0.3141 (—1.1295)
P^4P^4	—0.0355 (—0.0988)	0.5340 (1.4867)	—0.5365 (—1.4938)
M^1M^1	—0.1273 (—0.3422)	—0.3899 (—1.0484)	1.0936 (2.9410)
C_1M_2	0.3159 (0.8466)	—0.4545 (—1.2180)	—0.7701 (—2.0636)
P^3L	0.1194 (0.8855)	—0.2207 (—1.6371)	0.1067 (0.7917)
M^1L	0.1221 (1.0386)	0.1861 (1.5831)	0.3141 (2.6721)
M^1W	0.1679 (1.6203)	0.3583 (3.4587)	0.0795 (0.7673)
RAD	0.4285 (0.1469)	—0.5939 (—0.2036)	0.1576 (0.0540)
DIG 1	0.4137 (0.3583)	0.8331 (0.7216)	—0.5058 (—0.4380)
DIG 2	0.1844 (0.1129)	—0.2622 (—0.1606)	0.3739 (0.2289)
DIG 3	—0.6408 (—0.3177)	0.3318 (0.1645)	—0.7156 (—0.3548)
DIG 3P	0.0949 (0.0696)	0.1434 (0.1052)	—0.4033 (—0.2960)
DIG 5	—0.5347 (—0.2568)	0.2611 (0.1254)	0.3876 (0.1862)
TIB	0.3011 (0.2136)	—0.1024 (—0.0726)	0.4449 (0.3157)
Constant	-36.7194	4.8222	8.5493
% Variation explained	52.38	26.27	19.61

specimens from central India also group at the edge of their species cluster. In all these situations, except *C. sphinx* from India, the canonical variate separation is on CV2, perhaps suggesting shape differences and not size are involved in these intraspecific variations. With Indian *C. sphinx*, the separation is on CV1, suggesting that they vary in being larger rather than in having a different shape.

Baculum size and shape is variable within the *Cynopterus* spp. considered without clear diagnostic differences apparent between species. In most species baculum shapes may be found which are not too dissimilar to those in other species — although generally *C. nusatenggara*, for example, has bacula with less serrated outlines than does *C. sphinx*.

This study was principally to diagnose *C. nusatenggara* against species of *Cynopterus* with which it could be confused. It has highlighted to us the need for different taxonomic characters and tools to be applied to resolve the complex taxonomy of South East Asian

Table 2b

	FUNCTION 1	FUNCTION 2	FUNCTION 3
GSL	—0.5582 (—0.7175)	0.0387 (0.0498)	—0.8885 (—1.1420)
CDL	0.8144 (1.1567)	—0.2751 (—0.3908)	0.2659 (0.3776)
PL	0.2188 (0.4113)	—0.0041 (—0.0078)	0.6101 (1.1472)
MFW	—0.1827 (—0.8238)	0.2387 (1.0764)	0.1024 (0.4617)
ONL	0.2816 (0.7543)	0.6562 (1.7580)	—0.3167 (—0.8487)
LIW	—0.0658 (—0.1741)	0.2269 (0.6006)	0.3990 (1.0563)
ZB	—0.2814 (—0.4690)	—0.4501 (—0.7503)	—0.0629 (—0.1049)
BW	0.4234 (1.1886)	—0.1203 (—0.3376)	—0.1040 (—0.2920)
CPL	0.0438 (0.0418)	—0.0850 (—0.0812)	—0.4017 (—0.3839)
C^1C^1	0.0688 (0.1978)	0.2201 (0.6323)	0.3809 (1.0944)
M^1M^1	0.1479 (0.5019)	0.0055 (0.0187)	—0.5494 (—1.8651)
C^1M^1	—0.1099 (—0.3304)	—0.4763 (—1.4321)	—0.3740 (—1.1246)
C_1M_2	0.0274 (0.0700)	—0.3515 (—0.8962)	0.7139 (1.8201)
P^3L	0.1960 (1.7133)	—0.1992 (—1.7414)	—0.0962 (—0.8407)
P^3W	0.1253 (1.4291)	0.3292 (3.7554)	—0.0942 (—1.0747)
M^1L	0.0801 (0.6320)	0.7407 (5.8415)	—0.3537 (—2.7892)
M^1W	0.0816 (0.9837)	—0.0460 (—0.5551)	0.5379 (6.4883)
DIG 1	0.2758 (0.2352)	0.3121 (0.2662)	0.4672 (0.3984)
DIG 2	—0.3189 (—0.2251)	—0.0097 (—0.0069)	—0.1504 (—0.1062)
DIG 3	0.1235 (0.0752)	—0.1582 (—0.0964)	0.7042 (0.4290)
DIG 3P	—0.1049 (—0.0715)	—0.0834 (—0.0568)	—0.0337 (—0.0230)
DIG 5	0.1860 (0.1165)	—0.0953 (—0.0597)	0.1632 (0.1022)
TIB	0.1057 (0.0759)	0.2083 (0.1495)	—0.6933 (—0.4975)
Constant	—41.0646	14.3015	3.8983
% variation explained	47.67	30.26	18.21

Cynopterus spp. In particular, further clarification of some problems exposed in this paper may have to wait upon comprehensive genetic studies, because the basic morphology of the *Cynopterus* skull and externals is not very variable. Dr Lincoln Schmitt, University of Western Australia, has begun an electrophoretic study of some species examined in this study. These results indicate that genetic variation between island populations of *C. nusatenggara* is not very variable. However *C. nusatenggara* differs from *C. brachyotis* from West Java, in having 3 genes distinct out of the 35 enzyme systems examined (L. Schmitt pers. comm.).

There is a natural tendency among taxonomists who examine morphological variation among closely related forms in island archipelagos, to name as species only those forms that exist together on the same island in reasonably close sympatry. Other variations may be considered subspecific. Although the form which is the basis of this paper (*nusatenggara*) is not sympatric with morphologically close forms of *Cynopterus* found elsewhere in the Malay Archipelago (e.g. *brachyotis, luzoniensis, minutus*) we consider it a species for several reasons. Firstly, it is the most easily recognisable of these taxa, both in its pelage and dental morphology. It is for example, more distinct than are *C. brachyotis* and *C. sphinx* or *C. brachyotis* and *C. minutus*. Secondly, *C. nusatenggara* is found throughout many of the islands of Nusa Tenggara, but does not appear to cross the strait of Lombok and occur on Bali (where *C. brachyotis* is found). Other similar water gaps between islands in Nusa Tenggara do not appear to have been substantial barriers to the distribution of *C. nusatenggara* or to other species of bats in this region (Kitchener *et al.* 1989). There is, for example, little genetic differentiation between *C. titthaecheilus* from W. Java and Lombok islands and between *C. horsfieldi* from Lombok and Sumbawa islands (L. Schmitt pers. comm.). These data tend to indicate that water gaps such as those found between Lombok and Bali islands do not pose significant barriers to gene flow in other closely related *Cynopterus* spp. It may be assumed, then, that potential gene flow occurs between *C. brachyotis* on Bali I. and *C. nusatenggara* on Lombok I. Despite this, both forms appear morphologically distinct on these two islands.

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Mrs N. Cooper, Western Australian Museum, carried out all the statistical analyses as well as photographing the skulls; we are indebted to her for this work.

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Postscript

After acceptance of this paper, Dr Lincoln Schmitt, University of Western Australia, completed his electrophoretic appraisal of *Cynopterus* species, including *C. brachyotis* (W. Java, Borneo); *C. nusatenggara* (including Lombok, Sumbawa, Moyo); *C. luzoniensis* (S.W. Sulawesi); *C. titthaecheilus* (Lombok, W. Java); *C. terminus* (S.W. Timor); *C. horsfieldi* (Lombok, Sumbawa). While this information will be published separately, an analysis of genetic similarity of these species, based on an investigation of some 35 enzyme systems, concluded, among other things, that the genetic distance between *C. nusatenggara*, and both *C. brachyotis* and *C. luzoniensis* are of a similar order to genetic distances of the other recognised species of *Cynopterus* he studied. The species that is closest genetically to *C. nusatenggara* appears to be both the Javan and Lombok populations of *C. titthaecheilus*.

Appendix I: Specimens examined

Cynopterus nusatenggara sp. nov. (all paratypes)

(i) *Adults, complete data set*

Area 82: Komodo I., 3♀, 5♂ MZB 9385-8, MZB 14716, MZB 9379-80, MZB 9382; Area 85: Pelangan, Lombok, 1♀, 2♂ WAM (M33631, M33633-4); Area 86: Desa Kuta, Lombok, 2♀, 1♂ WAM (M33630, M33635-6); Area 87: Suranadi, Lombok, 2♀, 1♂ WAM (M3073-4, M33637); Area 89: Desa Belo, Jereweh, Sumbawa, 1♀, 2♂ WAM (M31326, M31328, M31330); Area 90: Merenti, Sumbawa, 3♀, 1♂ WAM (M31157, M31159, M31170, M31217); Area 91: Batu Dulang, Sumbawa, 5♀, 5♂ WAM (M31744, M31746-9, M31759-60, M31763-4, M31766); Area 92 Moyo I. (Sebatok and Brang Kua), 3♀, 5♂ WAM (M31899, M31908, M31916-7, M31920, M31925, M31928, M31934); Area 93: Dahu, C. Sumbawa, 2♀, 4♂ WAM (M31692, M31695, M31700, M31716, M31719, M31721); Area 94: Waworada, E. Sumbawa, 3♂ WAM (M31644, M31646, M31654); Area 95: Sangeang I., Sumbawa, 1♀ WAM M31593; Area 96: Batu Tering, Sumbawa, 1♀, 2♂ WAM (M31469-70, M31478); Area 97: Teluk Santong, Sumbawa, 1♀, 2♂ WAM (M31329, M31385, M31408).

(ii) *Subadults (SA); juveniles (J); damaged adults, incomplete data sets (D)*

Area 82: Komodo, 1♀, 1♂ MZB 938 (D), MZB 9284 (D); Area 85: Pelangan, Lombok, 1♀ WAM M33582 (J); Area 86: Desa Kuta, Lombok, 1♀, 3♂ WAM M33583 (D), WAM M33632 (D), WAM M33537 (J), WAM M31079 (J); Area 87: Suranadi, Lombok, 1♀ WAM M30705 (D); Area 88: Batu Koq, Lombok, ♀ WAM M33580 (J); Area 91: Batu Dulang, Sumbawa, 1♂ WAM M31825 (J); Area 92: Moyo I., (Sebatok & Brang Kua) nr Sumbawa, 1♀, 2♂ WAM M3187-8 (D), WAM M31923 (SA); Area 93: Dahu, C. Sumbawa, 1♂ WAM M31696 (D); Area 94: Waworada, E. Sumbawa, 1♂ WAM M31667 (D); Area 95: Sangeang I., nr Sumbawa, 1♀ WAM M31583 (D); Area 96: Batu Tering, Sumbawa, 1♀ WAM M31517 (SA); Area 97: Teluk Santong, Sumbawa, 2♀ WAM M31415 (D), WAM M31407 (SA).

Cynopterus sphinx

(i) *Adults, complete data set*

Area (?) Aceh region, Sumatra, 2♀ MZB (13490, 13575); Area 19: Curup, Bengkulu, Sumatra, 1♀, 2♂ MZB (13266, 13273, 13299); Area 20: Lebang Selatan, Bengkulu, Sumatra, 1♂ MZB 13292; Area 26: Pasir Putih, Lampung, Sumatra, 1♂ MZB 9042; Area 46; Solie, Soppeng, S. Sulawesi, 1♂ MZB 13616; Area 49: Gunung Tangkoko, Pare, N. Sulawesi, 1♂ MZB 12670; Area 58: Jampen (?), Salayar, S. Sulawesi, 2♂ MZB (14091, 14093); Area 68: Bogor, W. Jawa, 1♀ MZB 8859; Area 71: Pelabuhan Ratu, W. Jawa, 2♀ MZB (10706, 10715); Area 80: W. Bali (Panjar, Kuta, Klampok), 1♀ MZB 11361; Area 81: Central Bali, 1♀, 1♂ WAM (M16164, M16165); Area 95: Sangeang I., nr E. Sumbawa, 1♀, 7♂ WAM (M31580, M31582, M31584-5, M31587, M31589, M31592 M31594); Area 103: Kinibalu, Sabah, 1♂ WAM M23771; Area 114: Baluran, E. Jawa, 1♀, 1♂ MZB 11131, MZB 11130; Area 118: Krakatau (Sertung, Anak and Rakata Is), 3♀, 4♂ WAM (M26356, M26358, M26360, M26365, M26368, M26377, M26555); Area 119: Nagpur, India, 1♀, 1♂ WAM M29363-4; Area 121: Pagai I., nr W. Sumatra, 1♂ AMNH 103314; Area 123: Bangkok, Thailand; 4♀, 4♂ WAM (M23780-1, M23783-4, M23786, M23791, M23793, M23795).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 4: Asahan, N. Sumatra, 1 MZB 13623 (SA); Area 5: Bohorok, N. Sumatra, 1♂ MZB 13035 (SA); Area 8: Kayutanam, W. Sumatra, 1♂; MZB 13180; Area 20: Lebang Selatan, Bengkulu, Sumatra, 1♀ MZB 13269 (D); Area 23: Blimbing, Lampung, Sumatra, 1 ♀ MZB 13597 (D); Area 24: Pulau Panggung, Lampung, Sumatra, 1♀ MZB 11262 (SA); Area 25: Wai Kambas, Lampung, Sumatra, 1♀ MZB 8976 (SA); Area 26: Pasir Putih, Lampung, Sumatra, 1♀ MZB 8978 (SA); Area 27: Pringsewu, Lampung, Sumatra, 1♀, 1♂ MZB 10986 (D), MZB 10999 (D); Area 33: Kotim, C. Kalimantan, 1♂ MZB 13941 (D); Area 46: Solie, Soppeng, S. Sulawesi, 1♀, 1♂ MZB [13650 (SA), 13652 (J)]; Area 69: Banten, W. Jawa, 1♂ MZB 9141 (D); Area 80: W. Bali (Panjar, Kuta, Klampok) 1♀, 2♂ MZB [9173 (D), 11362-3 (J, J); Area 95: Sangeang I., nr Sumbawa 1♀ WAM M31586 (D); Area 98: Sipora I., nr W. Sumatra, 1♀ ZRC 45901 (D); Area 100: Siberut

I., nr W. Sumatra, 1♀ ZRC 45900 (J); Area 114: Baluran, E. Jawa, 3♂ MZB [9844 (D), 1129 (D), 13922 (D)]; Area 118: Krakatau (Sertung, Anak, Rakata) 2♀, 2♂ WAM M23313 (SA), WAM M26350 (D), WAM M26376 (SA), WAM M26386 (SA); Area 119: India, 1♀ WAM M29362 (D); Area 121: Pagai I., W. Sumatra 2♀, 1♂ AMNH (?) (103213-4 (D), 103211 (D); Area 123: Bangkok, Thailand, 1♂ WAM M23787 (D).

Cynopterus brachyotis

(i) *Adults, complete data set*

Area 1: Aceh (Mt Leuser, Ketambe and Kutacane), 2 ♂ MZB (12983, 13135); Area 4: Asahan, N. Sumatra, 1 ♂ MZB 13624; Area 7: Bukit Tinggi, W. Sumatra, 1 ♀, 2 ♂ MZB (9149, 9757-8); Area 11: Kuto Tuo, Riau, Sumatra, 2 ♀, 2 ♂ MZB (11845-6, 11848, 11853); Area 12: Kampai, Riau, Sumatra, 1 ♂ MZB 11885; Area 13: Siak, Riau, Sumatra, 2 ♂ MZB (11838, 13843); Area 15: Palembang, S. Sumatra, 1 ♂ MZB 12763; Area 16: Kayu Agung, S. Sumatra, 2 ♂ MZB (12762, 12765); Area 18: Sitiung, W. Sumatra 3 ♀, 3 ♂ MZB (11756, 11767-8, 11778, 11785, 11795); Area 19: Bengkulu, Sumatra (Muara Aman and Curup), 2 ♀, 1 ♂ MZB (13272, 13274, 13289); Area 20: Lebang Selatan, Bengkulu, Sumatra, 1 ♀, 2 ♂ MZB (13267, 13276-7); Area 21: (Palas, Wai Sekampung, Sukadana) C. Lampung, Sumatra, 5 ♀, 2 ♂ MZB (10756, 10806, 10810, 10813-14, 10851, 10860); Area 23: Blimbing, Lampung, Sumatra, 1 ♂ MZB 13596; Area 27: (Pringsewu and Natar) Lampung, Sumatra, 1 ♂ MZB 11001; Area 29: Pulau Laut (Kota Baru and Stagen), 1 ♀ MZB 14006; Area 31: Telang, S. Kalimantan, 1 ♀, MZB 11674; Area (?): Hantakan, S. Kalimantan, 1 ♀, 3 ♂ MZB (11665, 11669, 11673, 11679); Area 33: Kotim, C. Kalimantan, 2 ♀, 2 ♂ MZB (13951, 13954-5, 13968); Area 34: Kuala Kapuas, C. Kalimantan, 1 ♀, 1 ♂ MZB (12753-4); Area 37: Longnawan, E. Kalimantan, 2 ♀, 1 ♂ MZB (13634, 13636-7); Area 38: Long Iram, E. Kalimantan, 1 ♀, 1 ♂ MZB (13531-2); Area ?: Punyit, E. Kalimantan, 2 ♂ MZB (13836, 13839); Area 59: Kudus, C. Jawa, 1 ♂ MZB 9066; Area 60: Yogya, C. Jawa 1 ♀ MZB 9175; Area 61: Batu Raden, C. Jawa, 1 ♀ MZB 9114; Area 63: Sumenep, Madura I., nr E. Jawa, 1 ♀ MZB 9189; Area 64: Kangean I., 1 ♀, MZB 13120; Area 66: Ciomas, W. Jawa, 1 ♂ MZB 9120; Area 67: Ujung Kulon, W. Jawa, 1 ♂ MZB 9159; Area 69: Banten, W. Jawa, 3 ♀ MZB (9187, 12777, 11413); Area 70: Sukabumi, W. Jawa, 1 ♀, 1 ♂ MZB (9889, 10532); Area 71: Pelabuhan Ratu, W. Jawa, 3 ♂ MZB (10725-6, 10735); Area 73: Garut, W. Jawa, 2 ♀, 2 ♂ MZB (11299, 12131-3); Area 74: Pandeglang, W. Jawa, 1 ♀ MZB 13098; Area 75: Gunung Salak, W. Jawa, 1 ♀, 1 ♂ MZB (14023-4); Area 80: W. Bali (Denpasar, Kuta and Klampok), 1 ♀ MZB 11364; Area 81: C. Bali 2 ♂ WAM (M16160, M16162); Area 84: Krawang, W. Jawa, 1 ♂ MZB 12972; Area 99: Kuala Lumpur, Malaysia, 1 ♀, 1 ♂ ZRC (45828-9); Area 103: Kinibalu, Sabah, 4 ♀, 1 ♂ WAM (M23772-4, M23776, M23779); Area 104: Teluk Bahang, Penang I., 1 ♀, 2 ♂ ZRC (45835-7); Area 105: Kedah Peak, Kedah, 2 ♀, 1 ♂ ZRC (45843, 45845, 45848); Area 106: Singapore I., 1 ♂ ZRC 45862; Area 110: Pulau Dua, Banten, W. Jawa, 1 ♂ MZB 9160; Area 111: Jepara, C. Jawa, 2 ♀ MZB (13981, 14072); Area 112: Bunyu I., E. Kalimantan, 2 ♀, 1 ♂ MZB (9391, 9396, 9399); Area 114: Baluran, E. Jawa, 1 ♀, 1 ♂ MZB (9047, 11121); Area 115: Barito Hulu, C. Kalimantan, 2 ♀, 2 ♂ MZB (9361, 9365, 9367, 9373); Area 120: Santubong, Sarawak, 1 ♀, 4 ♂ WAM (M23760, M23763, M23766-8).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 1: Aceh (Mt Leuser, Ketambe and Kutacane) 2 ♀, 1 ♂ MZB [12997-8 (D, D), 12989 (SA)]; Area 6: Langkat, N. Sumatra, 1 ♀ MZB 13025 (D); Area 7: Bukit Tinggi, W. Sumatra, 1 ♀, 1 ♂ MZB [9755 (D), 9759 (D)]; Area 11: Kuto Tuo, Riau, Sumatra, 1 ♂ MZB 11854 (SA); Area 14: S.M. Barbak, Jambi, Sumatra 3 ♀, 3 ♂ MZB [12731 (SA) 12733 (SA) 12734-5 (D, D), 12738 (SA), 12739 (D)]; Area 17: Lahat, S. Sumatra, 1 ♂ MZB 12767 (D); Area 19: Bengkulu, Sumatra (Muara Aman and Curup), 1 ♀ MZB 13281 (D); Area 21: (Palas, Wai Sekampung, Sukadana) C. Lampung, Sumatra, 1 ♀, 1 ♂ MZB [10754 (SA), 10861 (J)]; Area 24: Kec. Panjang, Lampung, 1 ♂ MZB 11259 (SA); Area 25: Wai Kambas, Lampung, 1 ♂ MZB 9048 (D); Area 27: (Pringsewu and Natar) Lampung, Sumatra, 1 ♀ MZB 10974 (SA); Area 29: Pulau Laut (Kota Baru and Stagen), 3 ♂ MZB [14005 (D), 14008 (D), 14195 (D)]; Area 35: Kotim, C. Kalimantan, 1 ♀ MZB 9162 (D); Area 37: Longnawan, E. Kalimantan, 1 ♀ MZB 13926 (D); Area 60: Yogya, C. Jawa, 1 ♀ MZB 9168 (J); Area 64: Kangean I., nr E. Jawa, 1 ♀ BMNH 104613 (D); Area 65: Kalibaru, E. Jawa, 1 ♀ MZB 13915 (D); Area 67: Ujung Kulon, W. Jawa, 1 ♀ 1 ♂ MZB [9102 (D), 10938 (SA)]; Area 68: Bogor, W. Jawa, 2 ♀, 1 ♂;

MZB [9107 (D), 9128 (D), 9150 (D)]; Area 69: Banten, W. Jawa, 1 ♀, 1♂ MZB [11415 (SA), 12776 (D)]; Area 70: Sukabumi, W. Jawa, 2 ♀ MZB [9890 (D), 9893 (SA)]; Area 71: Pelabuhan Ratu, W. Jawa, 1 ♀, 1 ♂ MZB [10723 (J), 10724 (SA)]; Area 84: Krawang, W. Jawa, 1 ♀ MZB 12974 (SA); Area 102: Batu, Selangor, Malaysia, 1 ♀, 1 ♂ ZRC (45822-3); Area 105: Kedah Peak, Kedah, 1 ♀ ZRC 45847; Area 106: Singapore I., 1 ♀ ZRC 45869; Area 110: Pulau Dua, nr Banten, W. Jawa, 1 ♂ MZB [9065 (D)]; Area 112: Bunyu I., nr E. Kalimantan, 1 ♀ MZB 9400 (J); Area 113: Sri Lanka, 1 ♀ BMNH 665495 (D); Area 114: Baluran, E. Jawa, 1 ♀ MZB 13921 (SA); Area 115: Barito Hulu, C. Kalimantan, 1 ♀ MZB 9372 (D); Area 120: Santubong, Sarawak, 1 ♀ WAM M23761 (J); Area ?: Peunyit, E. Kalimantan, 1 ♂ MZB 13837 (SA); Area ?: Hantakan, S. Kalimantan, 1 ♀ MZB 11668.

Cynopterus minutus

(i) *Adults, complete data set*

Area 1: Kutacane, Aceh, Sumatra, 1 ♀, 1 ♂ MZB (13142, 12985); Area 9: Tapanuli Selatan, N. Sumatra, 1 ♀, 1 ♂ MZB (13802, 13804); Area 19: Muara Aman, Bengkulu, Sumatra, 1 ♀ MZB 13268; Area 20: Lebang Selatan, Bengkulu, Sumatra, 1 ♂ MZB 13270; Area 21: Sukadana, Lampung, Sumatra, 1 ♂ MZB 10857; Area 28: Ketapang, W. Kalimantan, 1 ♂ MZB 13808; Area 29: Kota Baru, Pulau Laut, 1 ♀ MZB 14194; Area 31: Telang, S. Kalimantan, 1 ♀, MZB 11700; Area 36: Kutai, Samarinda, E. Kalimantan, 1♀, 1 ♂ MZB 13689-90; Area 37: Long Nawam, E. Kalimantan, 1 ♀ MZB 13925; Area 38: Long Iram, E. Kalimantan, 1 ♀, 2 ♂ MZB (13539, 13541, 13549); Area 40: Kendari, C. Sulawesi, 2 ♀ MZB (12610, 12612); Area 42: Poso, C. Sulawesi, 1 ♂ MZB 14402; Area (?): Lamedai, S. Sulawesi, 1 ♀, 1 ♂ MZB (14151, 14155); Area 55: Malili, S. Sulawesi, 1 ♂, MZB 11605; Area 69: Banten, W. Jawa, 1 ♀ MZB 9138; Area 83: Nias I., nr N. Sumatra, 2 ♀, 1 ♂ MZB (13445-6, 13443); Area 115: Barito Hulu, C. Kalimantan, 4 ♀, 2 ♂ MZB (9363-4, 9366, 9369-70, 9375).

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 1: Kutacane, Aceh, Sumatra, 1 ♂ MZB 13140 (D); Area 2: Simpang Kanan, Aceh, Sumatra, 1 ♀ MZB 13801 (D); Area 9: Tapanuli Selatan, N. Sumatra, 1 ♀ MZB 13803 (D); Area 36: Kutai, Samarinda, E. Kalimantan, 1 ♂ MZB 13691 (D); Area 40: Kendari, C. Sulawesi, 1 ♂ MZB 14166 (D); Area 41: Kolaka, SE Sulawesi, 1 ♀ MZB 14164 (D); Area 42: Poso, C. Sulawesi, 1 ♀, 1 ♂ MZB (13695 (D); 13698 (D)); Area 52: Luwuk, C. Sulawesi, 1 ♀ MZB 13978 (J).

Cynopterus luzoniensis

(i) *Adults, complete data set*

Area 40: Kendari, C. Sulawesi, 2 ♀, 1 ♂ MZB (12599-600, 12611); Area 42: Poso. C. Sulawesi, 1 ♀, 3 ♂ MZB (13663, 13701, 13709, 13717); Area 46: Solie, Soppeng, S. Sulawesi, 1 ♀, 1 ♂ MZB (13618, 13649); Area 48: Tondano, N. Sulawesi, 1 ♂ MZB 12863; Area 49: (Bitung and Mt Tangkoko), N. Sulawesi, 2 ♂ MZB (12862, 12869); Area 50: Bolaang Mongandow, N. Sulawesi, 1 ♂ MZB 13743; Area 51: Maros, S. Sulawesi, 1 ♀, 1 ♂ MZB (13196, 14446); Area 52: Luwuk, C. Sulawesi, 3 ♀, 2 ♂ MZB (11884-5, 13972, 13987, 14447); Area 53: Timampu, S. Sulawesi, 1 ♀, 1 ♂ MZB (11609, 11611); Area 54: Buton, S. Sulawesi, 1 ♀ MZB (12601); Area 55: Malili, S. Sulawesi, 1 ♀, 1 ♂ MZB (11604, 11606); Area 56: Mamuju, S. Sulawesi, 2 ♀, 1 ♂ MZB (14098-100); Area 57: Mangkutana, Kolonedale, C. Sulawesi, 1 ♀, 1 ♂ MZB (14390, 14444); Area (?): Lamedai, S. Sulawesi, 3 ♀ MZB (14116, 14152, 14156); Area (?): Katamanta, C. Sulawesi, 1 ♀, 2 ♂ MZB (14383, 14401, 14404); Area (?): Bukit Palapi, C. Sulawesi, 2 ♂ MZB (13986, 13989); Area 101: Negros I. (Dumaquete), Philippines, 8 ♀, 4 ♂ WAM (M25845-8, M28931-8); Area 117: Gunung Dua Saudara, N. Sulawesi, 2 ♀ MZB (12665, 12667); Area 124: Kotamobagu, N. Sulawesi, 1 ♂, WAM M25475.

(ii) *Subadults (SA); Juveniles (J); damaged adults, incomplete data sets (D)*

Area 40: Kendari, C. Sulawesi, 1 ♂ MZB 12593 (D); Area 42: Poso, C. Sulawesi, 2 ♂ MZB [13776 (D), 13778 (D)]; Area 44: Toli-toli, C. Sulawesi, 1 ♂ MZB 14040 (D); Area 45: Kolonedale, C. Sulawesi 1 ♂ MZB 14394 (D); Area 52: Luwuk, C. Sulawesi, 2 ♀ MZB [13975 (SA), 13977 (J)]; Area 56: Mamuju, S. Sulawesi, 1 ♂ MZB 14101 (D); Area 58: Jampea, Salayar, S. Sulawesi, 1 ♂ MZB 14092 (D); Area (?): Lamedai, S. Sulawesi, 1 ♂ MZB 14160 (D); Area 122: Palawan I., 1 ♀ WAM M28693

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