Systematic Variation in the Megachiropteran Tube-nosed Bats *Nyctimene cyclotis* and *N. certans*

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ABSTRACT

Twenty-four adult specimens of *Nyctimene cyclotis* Andersen and 36 of *Nyctimene certans* Andersen were measured and analyzed using both univariate and multivariate statistical programs. The holotypes of both taxa were examined and measured (both skulls incomplete) and compared with complete specimens. The two species share dental, ear-shape, and pelage characteristics; they occur sympatrically and are shown to be distinct from each other and from other members of the genus when compared with *Nyctimene cephalotes* and *N. papuanus*.

INTRODUCTION

The primary objective of this study is to determine the taxonomic status of *Nyctimene cyclotis* and its relative *N. certans* and to clarify their systematic relation to other species.

Knud Andersen (1910: 623) described *Nyctimene cyclotis* as follows:

> Size small (forearms of type broken, estimated length 53 mm.); premolars and molars peculiarly short and broad, subcircular in outline (character particularly pronounced in p^4 and m^1, p_4 and m_1); m^1 reduced to about ⅔ or ¾ the size of p^4, m_1 slightly smaller than p_4; ears unusually broad, nearly as broad as long, and semicircularly rounded off above; back mottled with brownish tips to the hairs; a narrow spinal stripe along posterior half of back. Hab. New Guinea. *Type.* male ad. (al. and skull), Arfak Mts., N.W. New Guinea, collected by A. E. Pratt, B.M. 10.7.16.9.

Two years later, in his classic review of the Megachiroptera (Andersen, 1912b), the holotype of *N. cyclotis* was still the only known specimen, but Andersen elaborated on its pelage coloration and texture, pointing out that the fur is long and woolly with the length of the general mass about 9.5 mm and the longest hair 14 mm. He also provided available measurements for the holotype.

Unfortunately, the skull of the holotype is damaged, lacks the occipital region, and has missing teeth as well as a broken forearm. It is a fairly old specimen with well-worn dentition (photographed and measured; see "Systematic Summary").

To date the species has remained little known. Tate (1942) did not list either *N. cyclotis* or *N. certans* in his review of *Nyctimene*. Laurie and Hill (1954) listed it but also included *N. certans* as a subspecies without further comment. McKean (1972) provided measurements and comments for a single female specimen (CM2316) from Lake Kutubu (ca. 830 m), Papua. Koopman (1979, 1982) mentioned *N. cyclotis* without any new data. Smith and Hood (1981) reported two New Britain specimens from Warangoi, 4500 ft, East New Britain Province, from the collections of the Bernice P. Bishop Museum, Honolulu, Hawaii, but they did not encounter it during their study there. Smith and Hood (1983) figured BBM-NG 28398 of the Bishop Museum (their figs. 1C, 2C) and provided

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[2] Published posthumously without the benefit of revision by Randolph Peterson. Revisions were made by Judith L. Eger, Associate Curator, and Lorelie Mitchell, Departmental Associate, Department of Mammalogy, ROM. Reprint requests should be directed to Judith L. Eger.

general comments, particularly comparing it with *N. masala,* but gave no measurements or locality data for the figured specimen.

Nyctimene certans was described by Andersen (1912a: 95) as follows:

> Most nearly related to *N. cyclotis* (Arfak Mts.), but dentition much heavier and colour of fur much darker.
>
> Size as *N. cyclotis* or little larger (forearm of type 58 mm.); ears as in *cyclotis,* unusually broad, semicircularly rounded off above, and narrowly edged all round with yellow, this yellow edge interrupted here and there by the dark central colour of the conch breaking through to margin of conch. Molariform teeth, as in *cyclotis,* subcircular in outline, with m^1 and m_1 conspicuously smaller than, respectively, p^4 and p_4, but all teeth much heavier, particularly broader, than in the related species: p^3 (length and breadth) of type (between parentheses corresponding measurements of the type of *cyclotis,* for comparison) 2.2 × 2.1 (2.0 × 1.7), p^4 2.0 × 1.8 (1.8 × 1.6), m^1 1.8 × 1.6 (1.6 × 1.3), p_3 2.5 × 2.0 (2.3 × 1.7), p_4 2.3 × 2.0 (2.1 × 1.7), m_1 2.0 × 1.7 (1.9 × 1.5), m_2 1.3 × 1.2 (1.2 × 1.1). Colour of fur peculiarly mottled above, as in *N. cyclotis,* but much darker: individual hairs of back seal-brown at extreme base (for about 5 mm.), then very pale buffy wood-brown (for 5–6 mm.), with short (2 mm.) dark brown tips; the mottled appearance of the colour of the head and back due to the dark brown tips of the hairs being too short to cover completely the paler middle portion of the hairs; a narrow and somewhat ill-defined dark brown spinal stripe along posterior half of back; breast and belly pale greyish drab in centre, flanks fawn.
>
> Type, skin and skull of an adult (unsexed), Mount Goliath, Dutch New Guinea, 20 Jan, 1911, collected by A. S. Meek, B.M. no. 11.11.29.1. Two other specimens from the Upper Aroa River, British New Guinea, are in the collection of the British Museum.

Later in the same year Andersen (1912b) virtually repeated the original description as an addendum in the "Catalogue" (p. 828), but added wing and foot measurements.

The skull of the holotype is badly damaged (see "Systematic Summary"). The measurements of the metacarpals are comparatively short, suggesting that it might be a subadult. The heavy dentition is also consistent with that of an unworn subadult (see figs. 1, 2 for *N. cyclotis*). The length of the mandible exceeds all *N. cyclotis* measured to date. A direct comparison of the holotypes of both taxa with ROM 94059 (fig. 3) indicated that the latter should be referred to as *Nyctimene certans.*

Because Laurie and Hill (1954) treated *N. certans* as a subspecies of *N. cyclotis,* subsequent authors have done likewise, but apparently no additional specimens have been referred to this taxon.

Materials and Methods

This study was carried out using a Compaq Deskpro 286 (70-megabyte hard disk; 1 megabyte RAM and a 20 × 20 Bernoulli Box added) and a Compaq Portable 386/20 (100-megabyte hard disk; 4 megabytes RAM and interfaced with calipers). Data entry and manipulation were done utilizing a caliper interface and a menued series of programs written for me by Jon Planck of Limnoterra, Kitchener, Ontario. These include programs that read measurement data files (.MTS) and convert the data to files formatted in a style acceptable by various statistical programs. Measurement files are formatted using "prompt files" (.PMT). The prompt file for *Nyctimene* is shown in table 1 as the left-hand column of data codes; the measurements taken (all in millimeters) and those used in the statistical analyses are listed and defined (*) in table 1. Data from the measurement files are transferred to Lotus 1-2-3 spreadsheet files (Lotus Development Corp.) for a preliminary review. Specimens are arranged in rows, with catalogue numbers read from the .MTS file, and variables in columns. For each variable the column ends with a calculation of the mean ($\bar{x}$), standard deviation (SD), variance (Var.), minimum, maximum, and N (number of specimens). See tables 2, 4, and 5.

Analyses included only complete adult specimens. Tests for sexual dimorphism showed no consistent significant differences, thus the sexes were combined.

As indicated above, *Nyctimene cyclotis* (NCYL) and *N. certans* (NCTN) share a number of distinctive characters, particularly the molariform dentition, in which the width across the upper third premolars is unusually broad, often exceeding the breadth across the last molars. *N. certans* is generally larger and appears to be restricted to rather high elevations, usually 1200 (one at 780, others 1220–3000) meters above sea level. *N. cyclotis* occurs from sea level to about 1500 meters. The two species have been collected sympatrically in at least four locations.

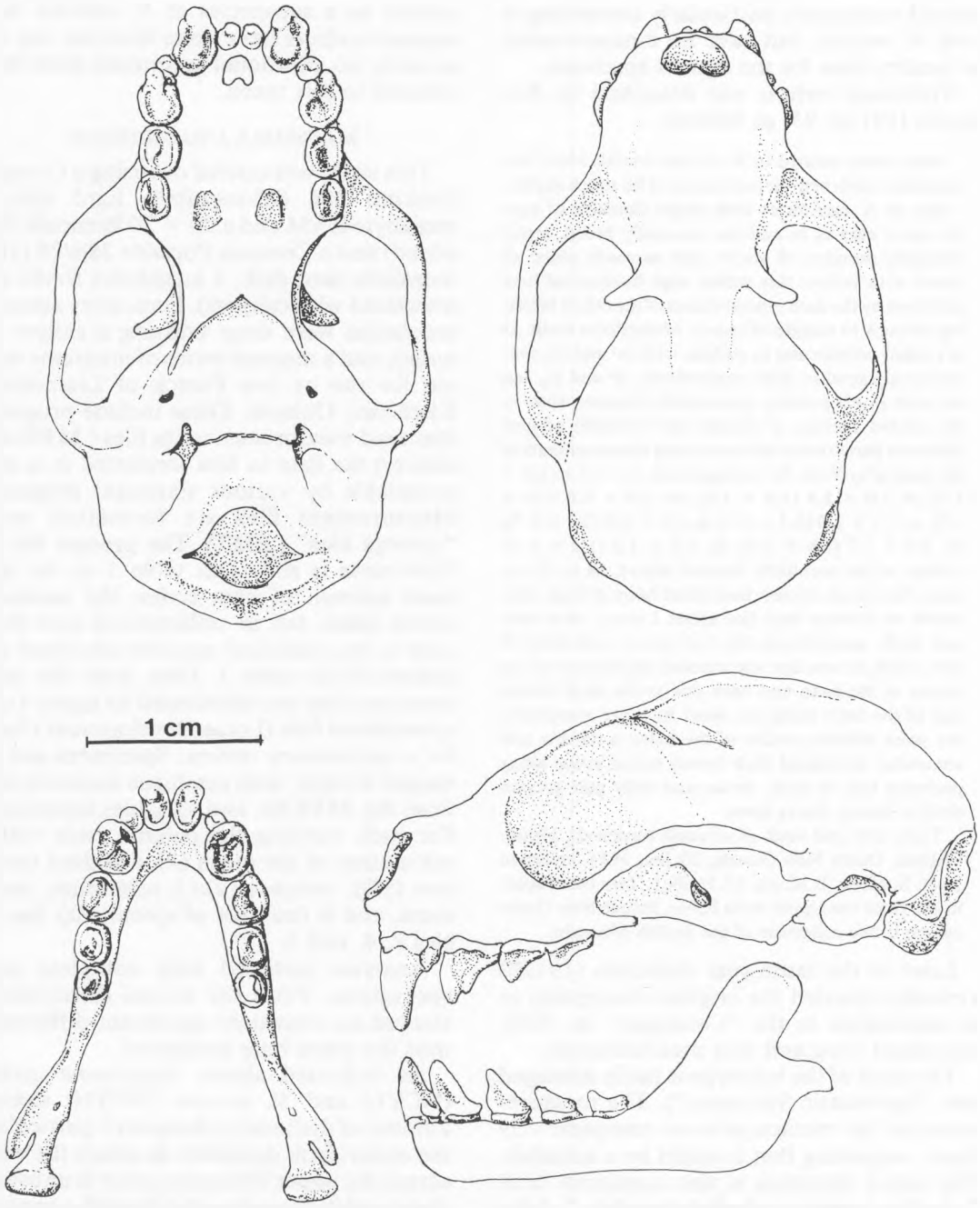

Fig. 1. Cranial drawings of *Nyctimene cyclotis,* BBM-NG 29062, subadult male from Big Wau Creek Ridge, 5 km SE Wau, Morobe District, Papua. Dorsal, ventral, and lateral views; drawn from photographs.

To provide a basis for comparison with other species, two additional taxa have been added to the following analyses. A sample of 37 specimens of *N. papuanus* Andersen, 1910 (NPAP), ranging from West Irian to Solomon Islands, is broadly sympatric with, and only slightly smaller than, *N. cyclotis.* It is of interest that the holotype of *N. albiventer minor*

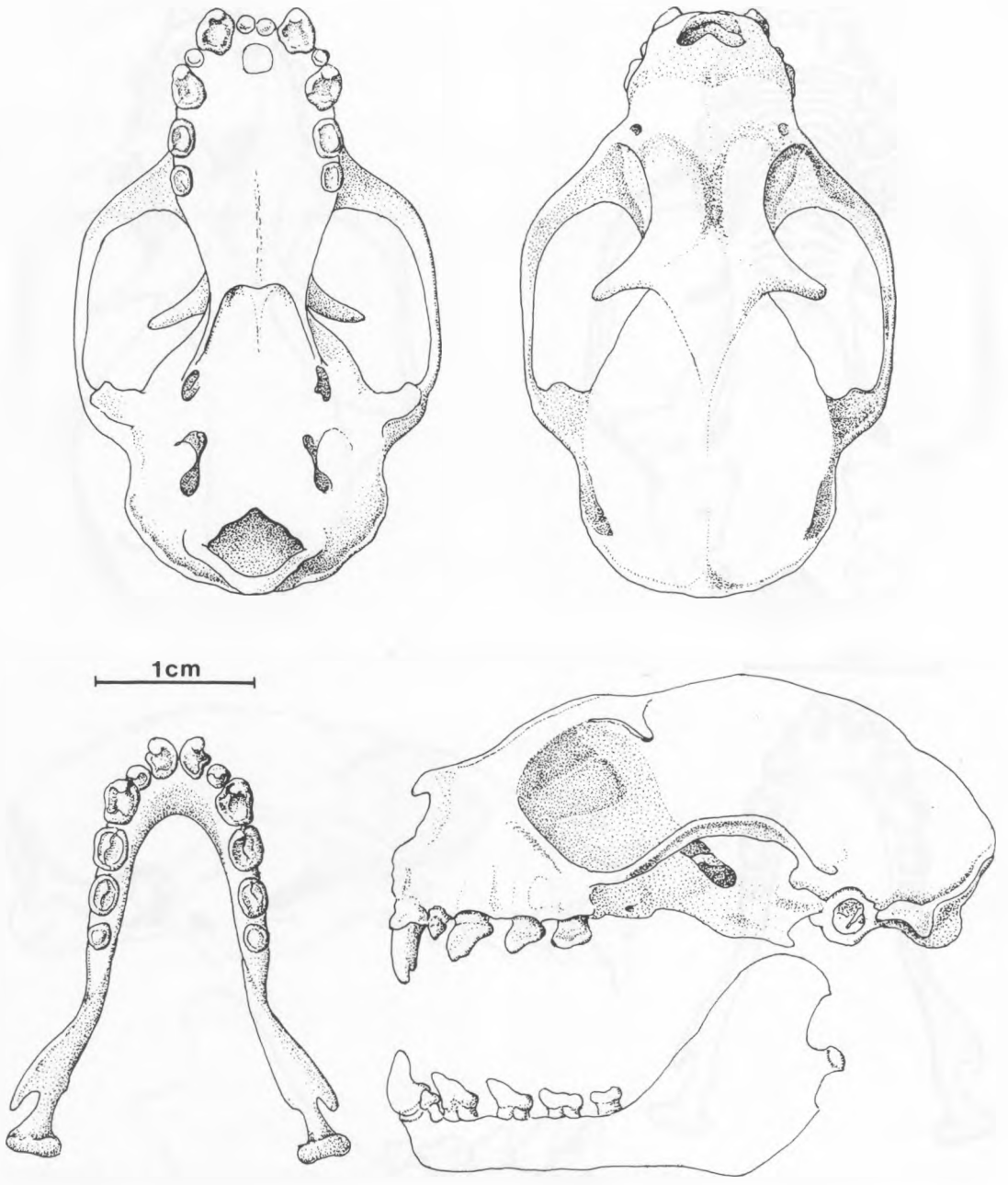

Fig. 2. Cranial drawings of *Nyctimene cyclotis,* BBM-NG 28396, adult female from the south slope of Mt. Missim, Morobe District, Papua. Dorsal, ventral, and lateral views; drawn from photographs.

(Phillips, 1968) falls within the *N. papuanus* population that appears to be distinct from *N. albiventer, draconilla, minutus,* and *varius.*

The second taxon added for comparison is *N. cephalotes* (Pallas, 1767) (NCEP), which is represented in this study by two topotype specimens from Ambon and 21 specimens from Sulawesi. Although it is the first named species of the genus, this taxon is still poorly understood (see Smith and Hood, 1983; Heaney and Peterson, 1984). Its relationship to

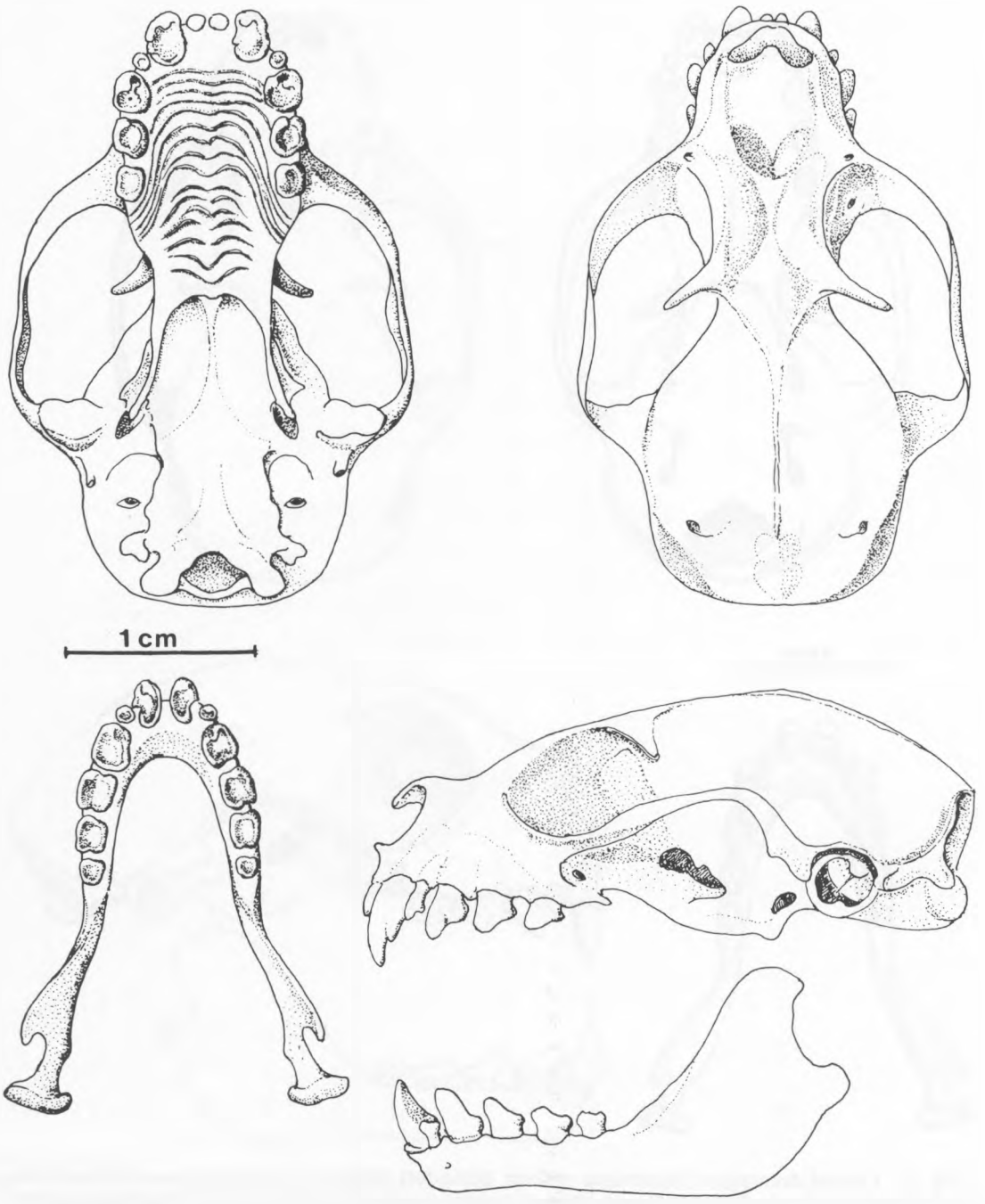

Fig. 3. Cranial drawings of *Nyctimene certans,* ROM 94059, adult male from Aiyura, Bismarck Range, Papua. Dorsal, ventral (with soft palate), and lateral views.

N. vizcaccia and to *N. robinsoni* requires further study. *N. cephalotes* has a skull of similar length to *N. certans,* but is generally larger in most other characters.

A hierarchical cluster analysis (Pimental and Smith, 1986) of my entire *Nyctimene* and *Paranyctimene* files confirmed the distinctive clustering of the above four taxa.

TABLE 1

Data Recorded in *Nyctimene* Measurement Files
(* indicates variable used in statistical analyses)

CAT NO	Catalogue number
SEX	F, M, or U
COLL	Collection
NS	Nature of specimen; A/S = alcoholic + skull; SS = skin and skull, etc.
AGE	A = adult; SA = subadult; JUV = juvenile
DATE	Date of collection
LOC	Locality collected
TL	Total length (head and body plus tail)
TV	Tail length
HF	Hind foot length (includes claws)
EAR-L	Ear length
EAR-W	Ear width
WT	Weight (grams)
WS	Wing span
NOTES	[All measurements in millimeters]
TIBI	Tibia length
FA*	Forearm length
D2M*	Second digit metacarpal length (includes flexed wrist)
D21P	Second digit first phalanx length
D22P	Second digit second phalanx length
D3M*	Third digit metacarpal length (includes flexed wrist)
D31P*	Third digit first phalanx length
D32P	Third digit second phalanx length
D4M*	Fourth digit metacarpal length (includes flexed wrist)
D41P*	Fourth digit first phalanx length
D42P	Fourth digit second phalanx length
D5M*	Fifth digit metacarpal length (includes flexed wrist)
D51P*	Fifth digit first phalanx length
D52P	Fifth digit second phalanx length
GL*	Greatest length of skull
CBL*	Condylobasal length
PALL*	Incisive palatal length
ZYGO*	Zygomatic breadth
MAST*	Mastoid breadth
BBC*	Breadth of braincase
HBC*	Height of braincase
ROSL	Rostrum length; rim of orbit to rim of nasal aperture
IOW	Interorbital breadth
PCP	Breadth across postorbital process
POC	Least postorbital constriction breadth
M1M1*	Breadth across first upper molars (crowns)
P3P3*	Breadth across third upper premolars (crowns)
C–M1*	Length front of upper canine to rear of first molar (crowns)
CCU*	Breadth across upper canines (crowns)
CIMA	Condyloincisive length of paired mandibles
GLM*	Condyloincisive length of one mandible
CM2L*	Length front of lower canine to rear of second molar (crowns)
CCL	Breadth across lower canines (crowns)
P3P3L*	Breadth across lower canines (crowns)
HTCP*	Height of coronoid process
DPF	Dorsal profile of frontal (coded description)
UPM	Upper premolars (coded description)
UM1	Upper molar (coded description)
LPM	Lower premolars (coded description)
LM	Lower molars (coded description)
OTU	Four-letter OTU code

Means were calculated for each sample after characters had been standardized across samples. Student-Newman-Keuls multiple-range tests were done on 23 variables. OTUs were ordinated using nonmetric multidimensional scaling (NT-SYS; Rohlf, 1988). To compare relationships within and among these *Nyctimene* OTUs, they were analyzed using discriminant function analysis (Biostat II; Pimental and Smith, 1986).

Acknowledgments

Thanks to the curatorial staff of the following collections, 459 specimens of *Nyctimene* and 12 of *Paranyctimene* have been examined, measured, and added to my data files:

AMNH	American Museum of Natural History, Karl Koopman
ANSP	Academy of Natural Sciences, Philadelphia, Charles L. Smart
AUM	Australian Museum, Sydney, Linda Gibson
CSIRO	Australian National Wildlife Collection, J. H. Calaby and G. C. Richards
BBM	Bernice P. Bishop Museum, Honolulu, Alan C. Ziegler
BM(NH)	British Museum (Natural History), J. E. Hill
DMNH	Delaware Museum of Natural History, J. DuPont
LACM	Los Angeles County Museum, Sarah George

TABLE 2
Subadult Measurements Compared With Those of Adults of *Nyctimene cyclotis* and *N. certans*

	N. cyclotis				*N. certans*			
	Subadults (N = 6)		Adults (N = 24)		Subadults (N = 4)		Adults (N = 36)	
	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.	$\bar{x}$	Min.–max.
FA	55.38	53.5–56.3	58.85	55.2–61.5	57.93	56.0–58.8	61.67	58.7–66.7
D2M	26.98	24.0–29.7	30.45	28.3–33.0	28.98	27.9–29.5	31.49	29.6–34.3
D3M	37.97	37.0–39.5	41.99	39.5–44.3	40.60	40.2–41.3	43.58	41.0–48.2
D31P	29.68	28.0–31.8	31.53	29.0–33.9	31.45	31.1–32.0	34.88	31.9–39.1
D4M	35.05	33.0–36.7	39.02	36.5–41.4	38.05	37.5–38.7	40.84	38.4–44.6
D41P	23.13	22.9–23.3	23.71	21.1–26.5	24.05	22.8–24.6	26.73	24.8–29.7
D5M	37.03	33.5–39.8	40.87	37.0–43.9	38.05	37.2–38.8	41.42	38.4–46.0
D51P	19.23	17.8–20.7	20.62	18.5–22.5	21.10	19.3–22.9	23.50	21.5–26.5
GL	27.98	27.5–28.7	29.04	28.0–30.2	30.03	29.6–30.2	31.02	30.0–32.8
CBL	26.17	25.4–26.7	27.35	26.5–28.2	28.18	27.8–28.6	29.37	28.5–31.0
PALL	12.30	11.8–12.5	13.01	12.2–13.9	13.10	12.9–13.2	13.80	13.1–14.8
ZYGO	17.48	16.9–18.0	18.67	17.4–20.0	18.90	17.7–20.1	19.49	18.5–20.7
MAST	12.43	12.0–12.9	12.60	11.7–13.3	12.60	12.3–13.0	13.00	12.4–13.8
BBC	12.58	12.3–13.3	12.56	11.8–12.9	12.78	12.5–13.2	13.11	12.4–13.8
HBC	9.65	9.2–10.0	9.74	9.1–10.4	9.95	9.4–10.3	10.31	9.6–11.0
M1M1	8.75	8.0–9.1	8.62	7.8–9.3	9.23	8.3–9.7	9.39	8.8–10.4
P3P3	8.70	8.1–9.5	8.41	7.9–8.9	9.00	8.4–9.2	9.26	8.7–9.8
C–M1	9.37	9.0–9.7	9.41	8.6–10.1	9.68	9.3–9.8	9.74	8.9–10.4
CCU	6.23	6.0–6.7	5.96	5.6–6.5	6.28	5.9–6.5	6.29	5.9–6.8
GLM	20.75	20.0–21.5	21.54	20.8–22.1	22.10	21.8–22.7	22.94	22.0–24.4
CM2L	10.70	10.1–11.2	10.81	10.0–11.4	11.03	10.3–11.5	11.26	10.5–12.0
P3P3L	7.12	6.8–7.5	6.96	6.5–7.4	7.48	6.9–7.8	7.58	6.9–8.3
HTCP	10.42	9.6–11.2	11.26	10.5–12.3	11.33	10.7–11.9	12.17	10.4–13.4

QM	Queensland Museum, Brisbane, R. E. Molnar
RMNH	Rijksmuseum van Natuurlijke Historie, C. Smeenk
ROM	Royal Ontario Museum, Judith Eger, Nancy Grepe, Jim Borack, Lilian Lortie, Sophie Poray, and Susan Woodward
SAM	South Australia Museum, Adelaide, Katherine Kemper
UMMZ	University of Michigan, Museum of Zoology, L. R. Heaney
USNM	U.S. National Museum of Natural History, C. O. Handley, Don Wilson, and A. Gardner

I have been accumulating data on the genus *Nyctimene* for a number of years and have had valuable assistance from M. B. Fenton, James Knowles, Cory Goldman, Michael Brown, Janet Cooper, Susan Woodward, and Burton Lim. Sophie Poray prepared the illustrations. Since my retirement, I have had the invaluable, competent, and dedicated voluntary assistance of Lorelie Mitchell, who, in addition to calling on her professional experience as a D.V.M., has become a keen expert on computers and statistical programs as well as on bat morphology. I also gratefully acknowledge the support of operating grant A2385 of the National Sciences and Engineering Research Council of Canada.

RESULTS

Age Variation

Volant subadults are characterized by incompletely fused joints between the wing bones and by relatively short metacarpals in relation to the length of the forearm. My measurements include the flexed wrist, whereas measurements published by Andersen (1912b) probably do not. Limited samples of subadults are compared with adults of both *N. cyclotis* and *N. certans* in table 2. The rapidly growing wing elements during a relatively short time period, and the random distribution of relative ages represented within the sample, make the calculated means of

TABLE 3

Nonsignificant Subsets as Determined by a Student-Newman-Keuls Multiple-range Test for *Nyctimene papuanus* (NPAP; N = 37), *N. cyclotis* (NCYL; N = 24), *N. certans* (NCTN; N = 36), and *N. cephalotes* (NCEP; N = 24)

Variable	OTU	$\bar{x}$	Subsets	Variable	OTU	$\bar{x}$	Subsets
FA	NPAP	56.85	I	MAST	NPAP	12.39	I
	NCYL	58.85	I		NCYL	12.60	I
	NCTN	61.67	I		NCTN	13.00	I
	NCEP	65.21	I		NCEP	13.20	I
D2M	NPAP	29.88	I	BBC	NPAP	12.38	I
	NCYL	30.45	I		NCYL	12.58	I
	NCTN	31.49	I		NCEP	12.89	I
	NCEP	32.33	I		NCTN	13.11	I
D3M	NPAP	41.66	I	HBC	NCYL	9.74	I
	NCYL	41.99	I		NPAP	9.82	I
	NCTN	43.58	I		NCTN	10.31	I
	NCEP	46.54	I		NCEP	11.39	I
D31P	NPAP	30.28	I	M1M1	NPAP	8.44	I
	NCYL	31.53	I		NCYL	8.62	I
	NCEP	33.77	I		NCEP	9.20	I
	NCTN	34.88	I		NCTN	9.39	I
D4M	NPAP	38.76	I	P3P3	NPAP	7.51	I
	NCYL	39.02	I		NCEP	8.02	I
	NCTN	40.84	I		NCYL	8.41	I
	NCEP	42.90	I		NCTN	9.26	I
D41P	NPAP	22.39	I	C–M1	NCYL	9.41	I
	NCYL	23.71	I		NPAP	9.52	I
	NCEP	25.50	I		NCTN	9.74	I
	NCTN	26.73	I		NCEP	10.59	I
D5M	NCYL	40.87	I	CCU	NPAP	5.55	I
	NPAP	41.04	I		NCEP	5.94	I
	NCTN	41.42	I		NCYL	5.96	I
	NCEP	45.75	I		NCTN	6.29	I
D51P	NPAP	18.74	I	GLM	NPAP	20.90	I
	NCYL	20.62	I		NCYL	21.54	I
	NCEP	21.43	I		NCEP	22.90	I
	NCTN	23.50	I		NCTN	22.94	I
GL	NPAP	28.48	I	CM2L	NPAP	10.77	I
	NCYL	29.04	I		NCYL	10.81	I
	NCTN	31.02	I		NCTN	11.26	I
	NCEP	31.17	I		NCEP	11.80	I
CBL	NPAP	26.78	I	P3P3L	NPAP	6.34	I
	NCYL	27.35	I		NCEP	6.82	I
	NCEP	29.21	I		NCYL	6.96	I
	NCTN	29.37	I		NCTN	7.57	I
PALL	NCYL	13.01	I	HTCP	NPAP	11.09	I
	NPAP	13.25	I		NCYL	11.26	I
	NCTN	13.80	I		NCTN	12.17	I
	NCEP	14.49	I		NCEP	12.99	I
ZYGO	NPAP	18.44	I				
	NCYL	18.67	I				
	NCTN	19.49	I				
	NCEP	19.89	I				

TABLE 4
Sample Statistics for *Nyctimene cyclotis* and *N. certans*

	N. cyclotis (N = 24)				*N. certans* (N = 36)			
Char.	$\bar{x}$	SD	Var.	Min.–max.	$\bar{x}$	SD	Var.	Min.–max.
FA	58.85	1.623	2.636	55.2–61.5	61.67	2.015	4.059	58.7–66.7
D2M	30.45	1.270	1.612	28.3–33.0	31.49	1.176	1.383	29.6–34.3
D3M	41.99	1.197	1.433	39.5–44.3	43.58	1.543	2.381	41.0–48.2
D31P	31.53	1.202	1.445	29.0–33.9	34.88	1.469	2.157	31.9–39.1
D4M	39.02	1.348	1.817	36.5–41.4	40.84	1.432	2.051	38.4–44.6
D41P	23.71	1.199	1.438	21.1–26.5	26.73	1.245	1.551	24.8–29.7
D5M	40.87	1.806	3.261	37.0–43.9	41.42	1.610	2.591	38.4–46.0
D51P	20.62	1.161	1.347	18.5–22.5	23.50	1.314	1.728	21.5–26.5
GL	29.04	0.607	0.369	28.0–30.2	31.02	0.595	0.354	30.0–32.8
CBL	27.35	0.452	0.204	26.5–28.2	29.37	0.545	0.297	28.5–31.0
PALL	13.01	0.460	0.212	12.2–13.9	13.80	0.436	0.191	13.1–14.8
ZYGO	18.67	0.669	0.448	17.4–20.0	19.49	0.449	0.202	18.5–20.7
MAST	12.60	0.336	0.113	11.7–13.3	13.00	0.335	0.112	12.4–13.8
BBC	12.56	0.250	0.062	11.8–12.9	13.11	0.323	0.105	12.4–13.8
HBC	9.74	0.351	0.123	9.1–10.4	10.31	0.336	0.113	9.6–11.0
M1M1	8.62	0.335	0.112	7.8–9.3	9.39	0.399	0.159	8.8–10.4
P3P3	8.41	0.285	0.081	7.9–8.9	9.26	0.319	0.102	8.7–9.8
C–M1	9.41	0.401	0.161	8.6–10.1	9.74	0.274	0.075	8.9–10.4
CCU	5.96	0.229	0.052	5.6–6.5	6.29	0.226	0.051	5.9–6.8
GLM	21.54	0.363	0.132	20.8–22.1	22.94	0.493	0.243	22.0–24.4
CM2L	10.81	0.360	0.129	10.0–11.4	11.26	0.350	0.122	10.5–12.0
P3P3L	6.96	0.234	0.055	6.5–7.4	7.58	0.298	0.088	6.9–8.3
HTCP	11.26	0.557	0.310	10.5–12.3	12.17	0.673	0.453	10.4–13.4

the subadults only approximate. In the wing elements of subadults, the upper end of the observed range tends to approach or slightly exceed the lower limits of the observed range for adults.

The general cranial development with age is essentially similar to that of *N. rabori* as reported by Heaney and Peterson (1984) and illustrated in their figure 4. In the younger ages, the sequence of fusion of the nasal and basal sutures (as they illustrated) provides a relative index to the age of subadults. As with many bats, subadults tend to have a greater downward deflection of the basicranial axis of the occiput that shifts to a more horizontal level as elongation of the braincase proceeds with maturity (compare figs. 1 and 2).

Subadults have unworn teeth of maximum size, as shown in figure 1. With wear, there is a marked change in width and space between the molariform teeth (fig. 2). As indicated in table 2, the means for the widths of the dentition of subadults (as represented by M1M1, P3P3, CCU, and P3P3L) of *N. cyclotis* are actually greater than those for the adults. Comparable means for the four *N. certans* subadults are consistently less than for the adults. In general, the relatively broad, unworn molariform teeth of subadults undergo steady wear with age, resulting in changes in the relative shapes of the occlusal surfaces, as well as a reduction in size of individual teeth and in the overall dental arcade measurements, particularly in width dimensions. The heavier, particularly broader, teeth ascribed by Andersen (1912a, 1912b) as distinguishing *N. certans* from *N. cyclotis* appear to be only a product of age differences between the two holotypes.

Univariate Analyses

The variables measured were examined individually to check on amount of variability exhibited and possible correlation with either sex or age. A suite of 23 variables was then selected as best representing the observed variations (table 1).

The results of univariate Student-Newman-Keuls multiple-range tests (Pimental and Smith, 1986) are summarized in table 3. For 7 of the 23 variables, all means were signif-

TABLE 5
Sample Statistics for *Nyctimene papuanus* and *N. cephalotes*

	N. papuanus (N = 37)				*N. cephalotes* (N = 24)			
Char.	$\bar{x}$	SD	Var.	Min.–max.	$\bar{x}$	SD	Var.	Min.–max.
FA	56.85	1.662	2.762	53.5–61.1	65.21	2.082	4.335	61.2–69.5
D2M	29.88	1.613	2.603	26.6–33.6	32.33	1.653	2.733	28.4–36.4
D3M	41.66	1.380	1.905	39.2–44.4	46.54	2.102	4.420	41.5–50.7
D31P	30.28	1.088	1.183	28.5–32.3	33.77	1.101	1.211	31.9–36.0
D4M	38.76	1.185	1.404	36.4–41.1	42.90	1.735	3.012	40.0–45.6
D41P	22.39	1.026	1.052	20.0–24.6	25.50	1.100	1.210	23.9–27.9
D5M	41.04	1.749	3.057	37.7–44.4	45.75	1.903	3.621	41.6–49.5
D51P	18.74	0.919	0.845	16.6–20.1	21.43	1.155	1.333	19.6–24.3
GL	28.48	0.496	0.246	27.5–29.8	31.17	0.981	0.963	29.5–33.4
CBL	26.78	0.474	0.225	25.5–27.7	29.21	0.952	0.907	28.0–31.1
PALL	13.25	0.468	0.219	12.3–14.1	14.49	0.663	0.440	13.3–15.6
ZYGO	18.44	0.399	0.159	17.7–19.2	19.89	0.969	0.938	18.3–22.1
MAST	12.39	0.316	0.100	11.5–13.0	13.20	0.543	0.295	12.1–13.9
BBC	12.38	0.340	0.116	11.6–12.9	12.89	0.497	0.247	12.0–13.7
HBC	9.82	0.301	0.090	9.1–10.4	11.39	0.751	0.564	9.6–12.8
M1M1	8.44	0.162	0.026	8.2–8.8	9.20	0.411	0.169	8.4–10.0
P3P3	7.51	0.204	0.042	7.1–7.8	8.02	0.291	0.085	7.4–8.4
C–M1	9.52	0.417	0.174	8.3–10.4	10.59	0.337	0.114	9.9–11.1
CCU	5.55	0.216	0.047	5.1–6.0	5.94	0.258	0.067	5.4–6.4
GLM	20.90	0.340	0.116	20.3–21.5	22.90	0.729	0.531	21.8–24.4
CM2L	10.77	0.399	0.159	9.9–11.5	11.80	0.347	0.120	11.2–12.4
P3P3L	6.34	0.227	0.052	6.0–6.9	6.82	0.239	0.057	6.4–7.4
HTCP	11.09	0.666	0.444	9.7–12.4	12.99	0.485	0.235	12.0–13.7

icantly different. The means of NCYL (*N. cyclotis*) and NCTN (*N. certans*) were significantly different from each other in 22 of 23 variables (all except D5M). There was no overlap in the condylobasal length of the skull (CBL) between these two species.

Comparing NCYL with NPAP (*N. papuanus*), the two share the same subsets in wing measurements D2M, D3M, D4M, and D5M, but are significantly different in D31P, D41P, and D51P. In cranial measurements the two OTUs also share common subsets in PALL, ZYGO, BBC, HBC, C–M1, CM2L, and HTCP, but are significantly different in all others.

Comparing NCTN with NCEP (*N. cephalotes*), the two share the same subsets only in GL, CBL, and GLM.

Sample statistics for NCYL and NCTN are given in table 4 and for NPAP and NCEP in table 5.

Multivariate Analysis

Results of the nonmetric multidimensional scaling analysis indicate that *Nyctimene cyclotis* and *N. certans* are morphologically very different on all three axes (fig. 4). With only four OTUs in the analysis, all the variance is explained by three axes. *Nyctimene papuanus* is the smallest species and *N. cephalotes* the largest. The minimum spanning tree distances (Euclidean distances) show a greater distance between *N. certans* and *N. cyclotis* than between *N. certans* and *N. cephalotes,* or *N. cyclotis* and *N. papuanus.*

Multivariate analysis of variance indicates that statistically significant differences exist among samples (F transformation of Wilk's lambda statistic = 22.797, df = 69 and 284, P = 0.0000). Classification of individual specimens resulted in 100 percent correct classification. A plot of individual specimens on the first and second canonical axes is shown in figure 5. In this analysis, *N. cyclotis* and *N. certans* are as different from each other as either is from *N. cephalotes.* Three canonical axes provide significant discrimination among the four groups, and the first two summarize 98 percent of the among-group differences (table 6). The following variables contribute to discrimination on the first canonical axis:

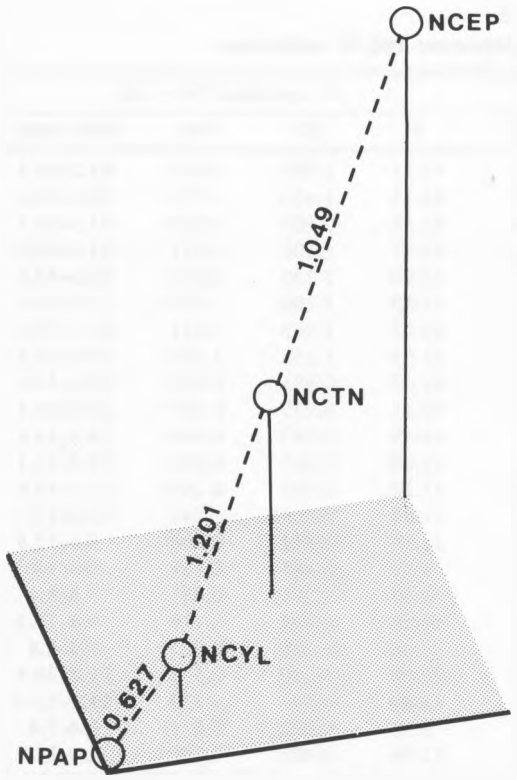

Fig. 4. Three-dimensional plot of nonmetric multidimensional scaling of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes,* with minimum spanning tree superimposed and Euclidean distances added.

fourth and fifth digit metacarpals, first phalanges of third and fifth digits, palatal length, zygomatic width, width across the first molars, and width across the premolars. Differentiation on the second axis is accounted for by length of forearm, condylobasal length, breadth of braincase, and height of braincase (table 7).

SYSTEMATIC SUMMARY

Nyctimene cyclotis Andersen, 1910

Nyctimene cyclotis Andersen, 1910: 623.

HOLOTYPE: Old adult male in alcohol with skull removed, BM(NH) 10.7.16.9, obtained by A. E. Pratt (unknown date) from Arfak Mountain, West Irian. Skull missing basioccipital region, right zygoma, right and left fourth upper premolars, and right upper molar. Dentition heavily worn.

MEASUREMENTS OF HOLOTYPE: Length of tail, 22.5; length of hind foot, 13.5; length of ear, 14.0; length of tibia, 21.5; length of forearm, ca. 54.5; length of metacarpals: second digit, 28.0; third digit, 40.0; fourth digit, 37.0; fifth digit, 38.2; length of first phalanges: third digit, 30.5; fourth digit, 24.5; fifth digit, 20.5; length of palate, 12.8; upper canine–molar length, 9.2; width across upper canines, 5.7; lower canine–molar length, 10.5; width across lower third premolars, 6.7; condyloincisive length of mandible, 21.5.

DISTRIBUTION: Mainland New Guinea (West Irian and Papua) and New Britain Island (see fig. 6 and "Specimens Examined" below).

COMPARISONS: Externally *Nyctimene cyclotis* and *N. certans* share many features, including long and woolly fur and relatively short and broad ears. Cranially, both are "wide-mouthed," with broad, rounded molariform teeth. The greater width across the upper third premolars in relation to the width across the molars is perhaps the unique shared characteristic that distinguishes these two taxa from all others of the genus.

In general, *N. cyclotis* is slightly smaller than *N. certans* and has a shorter (CBL = 26.5–28.2 versus 28.5–31.0 for NCTN), relatively broader skull with a more evenly rounded dorsal profile (compare figs. 1, 2 with fig. 3). For detailed comparison of individual characters, see tables 3 and 4.

Compared with *N. papuanus, N. cyclotis* is readily distinguished by the dental features described above, by its longer fur and broader ears, and by other characters shown in table 3.

Compared with *N. cephalotes, N. cyclotis* is also distinguished by its dentition and external features described above, as well as by its overall smaller size (see table 3).

REMARKS: The diagnosis given in the original description by Andersen (1910) still remains essentially valid. The large oval palatal fenestrations, commented on by Smith and Hood (1983), occur occasionally in this species but seem to be independent of age or sex. *Nyctimene cyclotis* ranges from sea level to near 1500 m and it has been collected sympatrically with *N. certans* at four localities between 780 and 1400 m.

SPECIMENS EXAMINED (with locality records for fig. 6): WEST IRIAN: **1.** Arfak Mt., 1°14′S,

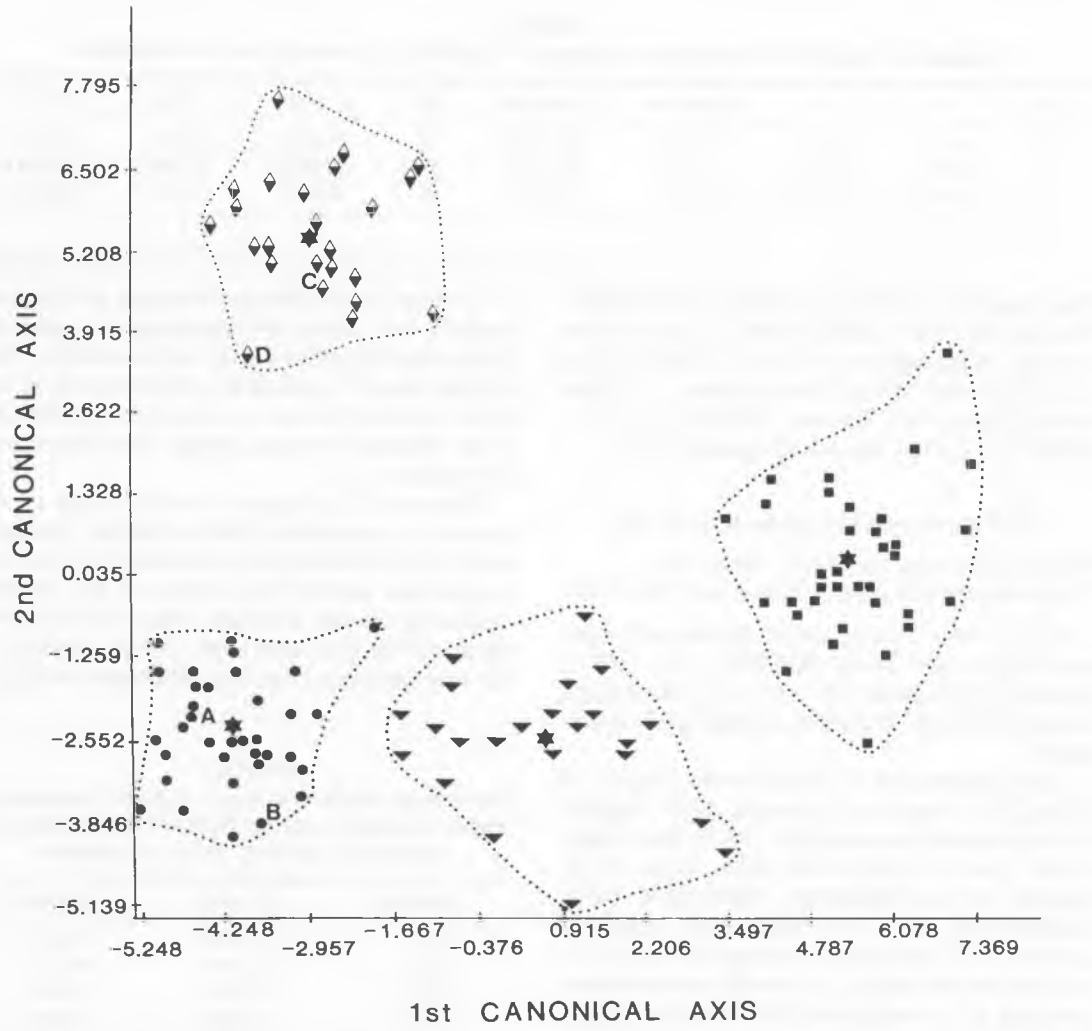

Fig. 5. Plot of individuals of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes* on the first and second canonical axes. Dots, *N. papuanus*; triangles, *N. cyclotis*; squares, *N. certans*; diamonds, *N. cephalotes*; stars, centroids for each group; A, holotype of *N. papuanus*; B, holotype of *N. a. minor*; C, D, topotypes of *N. cephalotes.*

134°01′E: BM(NH) 10.7.16.9 [holotype]. **2.** Ilaga Valley, Nassua Range, ca. 4°12′S, 147°26′E: AMNH 160347. PAPUA: **3.** Fly River, 5 mi below Palmer Junction, 5°56′S, 141°30′E, 80 m: AMNH 105091. **4.** West Sepik, Mt. Somoro, 3°25′S, 142°05′E, 1219 m: BBM-NG 101804. **5.** Morobe, Kalalo, 6°04′S, 147°11′E, 750 m: BBM-NG 52940 and 53143. **6.** Morobe, 10 km W Bulolo, 7°11′S, 146°34′E, 750 m: BBM-NG 51298, 51325, 51326 subadult, 51350, 51352, 51380, 53968, 54092, 54116 and 54129 subadults, 54234, and 54328. **7.** Morobe, Mt. Missim, south slope, 7°13′S, 146°43′E, 1350 m: BBM-NG 21059 (incomplete), 28396, 28410, and 53232–53234. **8.** Morobe, Mt. Missim, 7°13′S, 146°50′E, 1300 m: BBM-NG 24638 subadult. **9.** Morobe, Big Wau Creek Ridge, 7°19′S, 146°44′E, 1400 m: BBM-NG 29062 subadult. **10.** Owen Stanley Range, Efogi, 9°09′S, 147°37′E, 1408 m: CSIRO CM12593 and CM12594 subadult. **11.** Central Dist., Java Rarre, 9°25′S, 147°26′E, 600 m: BBM-NG 60287. **12.** Astrolabe Range, behind Baroka, 9°33′S, 147°26′E, 704 m: CSIRO CM12591, and 739 m: CM12592. **13.** Milne

TABLE 6
Canonical Analysis of *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes*

Roots	*R*	R^2	Eigenvalue	Chi squared	df	χ^2 prob.	% trace	Cum. %
1	0.971	0.943	16.429	596.799	69	0.0000	62.67	62.67
2	0.950	0.903	9.270	292.408	44	0.0000	35.36	98.03
3	0.584	0.341	0.516	44.341	21	0.0025	1.97	100.00

Bay, Sinafade, 10°22′S, 150°30′E, 10 m: BBM-NG 24539. NEW BRITAIN: **14.** East New Britain, Warangoi, ca. 4°15′S, 152°00′E, 1584 m: BBM-NG 20914 (incomplete). **15.** East New Britain, Mt. Sinewet, 4°38′S, 151°59′E: BBM-NG 20757 subadult (incomplete).

Nyctimene certans Andersen, 1912a

Nyctimene certans Andersen, 1912a: 95.
Nyctimene cyclotis certans Laurie and Hill, 1954.

HOLOTYPE: Young adult [subadult?] unsexed skin and skull, BM(NH) 11.11.29.1, collected 20 January 1911 by A. S. Meek from Mount Goliath, West Irian. Skull badly damaged.

MEASUREMENTS OF HOLOTYPE: Length of tibia, 24.5; length of forearm, 58.0; lengths of metacarpals: second digit, 28.7; third digit, 38.4; fourth digit, 36.6; fifth digit, 37.4; lengths of first phalanges: third digit, 32.0; fourth digit, 24.4; fifth digit, 21.0; length of palate, 13.7; width across upper molars, 9.0; canine–molar length, 9.8; width across upper canines, 6.5; condyloincisive length of mandible, 22.8; lower canine–molar length, 11.2; width across lower third premolars, 7.4; height of coronoid process, 11.0.

DISTRIBUTION: West Irian and mainland Papua (see fig. 7 and "Specimens Examined" below).

COMPARISONS: See under comparisons of *N. cyclotis,* and tables 2, 3, and 4. In comparison with *N. cyclotis,* the skull of *Nyctimene certans* is longer (CBL 28.5–31.0) and relatively narrower, and its dorsal profile has a relatively longer, less elevated (flatter) nasal profile and a more elongate, less steeply arched braincase (see fig. 3).

Compared with *N. papuanus, N. certans* is much larger overall and differs markedly in its pelage, ears, and dentition.

Compared with *N. cephalotes,* the wings of *N. certans* have shorter forearms and metacarpals, but longer first phalanges. *N. certans* has similar lengths of skull and mandible, but differs from *N. cephalotes* significantly in all other cranial characters measured, as well as in its distinctive ears, pelage, and dentition (see tables 4, 5).

REMARKS: The age of the holotype of *N. certans* is somewhat problematical. Andersen (1912a) described it as an adult. Its metacarpals are shorter than those of any adults measured by me and are even shorter than those of the four subadults listed in table 2. Measurements of the first phalanges of digits

TABLE 7
Percentage of the Variance of Each Variable in Each Canonical Axis for *Nyctimene papuanus, N. cyclotis, N. certans,* and *N. cephalotes*

Variable	1st axis	2nd axis
FA	14.869	81.625
D2M	45.754	54.135
D3M	21.887	49.681
D31P	94.480	0.003
D4M	81.191	14.709
D41P	33.096	61.888
D5M	99.184	0.618
D51P	94.154	4.455
GL	68.862	31.117
CBL	0.780	95.259
PALL	87.826	7.319
ZYGO	99.975	0.025
MAST	51.734	18.898
BBC	0.000	88.714
HBC	5.126	94.874
M1M1	89.312	2.480
P3P3	82.433	16.893
C–M1	61.668	20.872
CCU	14.400	67.210
GLM	82.479	6.045
CM2L	47.092	52.762
P3P3L	43.217	55.649
HTCP	36.655	63.193

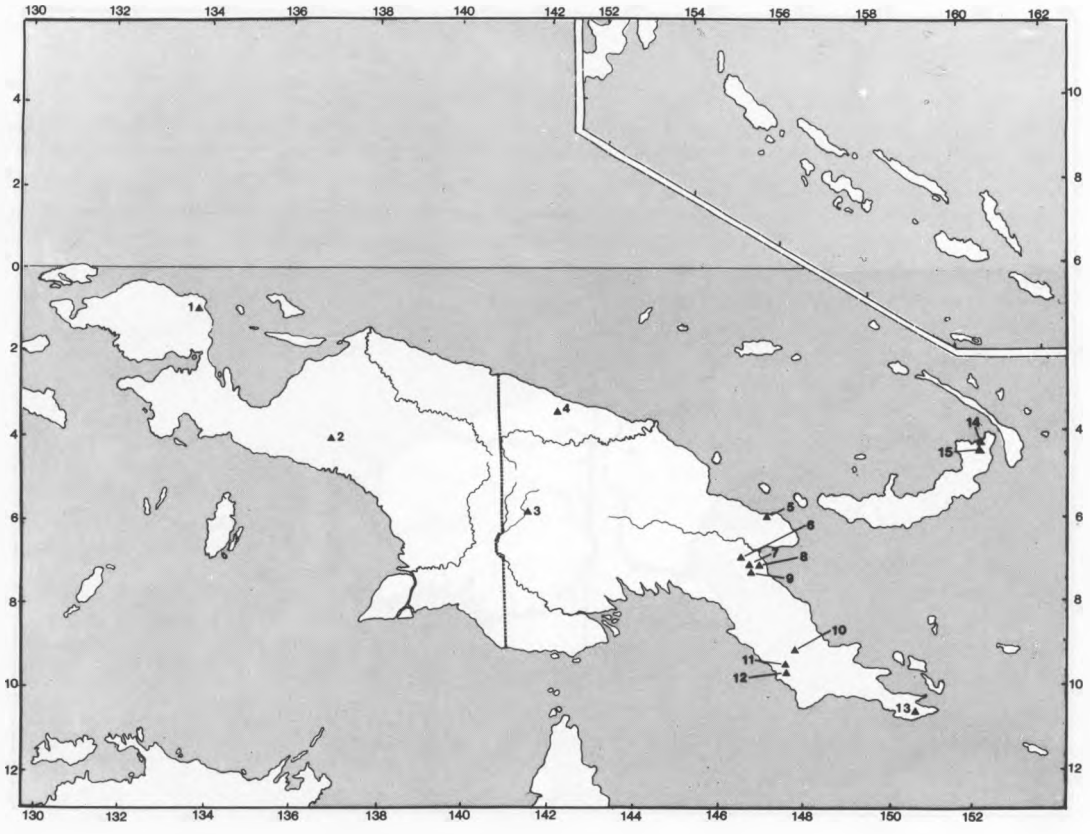

Fig. 6. Map of New Guinea and New Britain Islands with locality records for *Nyctimene cyclotis*. See "Specimens Examined" of this species for numbered localities.

three to five are all consistent with those of the subadults. The available cranial measurements are consistent with those of adults. The length of the mandible exceeds that of any specimen of *N. cyclotis* measured to date. Palatal fenestrations also occur occasionally in this taxon, but the observed examples were much smaller than those in *N. cyclotis*.

This species appears to favor higher elevations. One specimen was taken at 780 m and one at 1220 m, but all others occurred at 1340 m or higher.

SPECIMENS EXAMINED (with locality records for fig. 7): WEST IRIAN: **1.** Mount Goliath, 4°40′S, 139°52′E, ca. 3000 m: BM(NH) 11.11.29.1 [holotype]. PAPUA: **2.** Eastern Highlands, Kassam Pass, 6°18′S, 145°52′E, 1400 m: BBM-NG 54997–54998, 55001, 55021, and 55027. **3.** Bismarck Range, Aiyura, 6°20′S, 145°54′E, 2112 m: ROM 94059. **4.** Morobe, Mt. Shungol, 6°51′S, 146°44′E, 2000 m: BBM-NG 98283 and 98284. **5.** Morobe, 10 km W Bulolo, 7°11′S, 146°34′E, 780 m: BBM-NG 51300. **6.** Morobe, Mt. Missim, south slope, 7°13′S, 146°50′E, 1350 m: BBM-NG 28397 subadult, 28398, and 28404. **7.** Morobe, Mt. Forest, Coviak, 7°18′S, 146°43′E, 1319 m: BBM-NG 28467 and 28468. **8.** Morobe, Nakata Ridge, 7°20′S, 146°43′E, 1524 m: BBM-NG 28502. **9.** Morobe, Mt. Kiandi, 7°21′S, 146°43′E, 2060 m: BBM-NG 28448. **10.** Morobe, Big Wau Creek, 5 km SE Wau, 7°22′S, 146°43′E, 1400 m: BBM-NG 24589, 24600, 23613, 50598–50599, and 50689. **11.** Morobe, Bulldog Road, 7°28′S, 146°40′E, 2625 m: BBM-NG 28948 and 28959. **12.** Morobe, Bulldog Road, 12 mi from Edie Creek, 7°31′S, 146°40′E, 2405 m: BBM-NG 52452 and 54911. **13.** Owen Stanley Range, Efogi, 9°09′S, 147°37′E, 1408 m: CSIRO CM12595–12596, CM12597 subadult, and CM12598–12599, 1338 m:

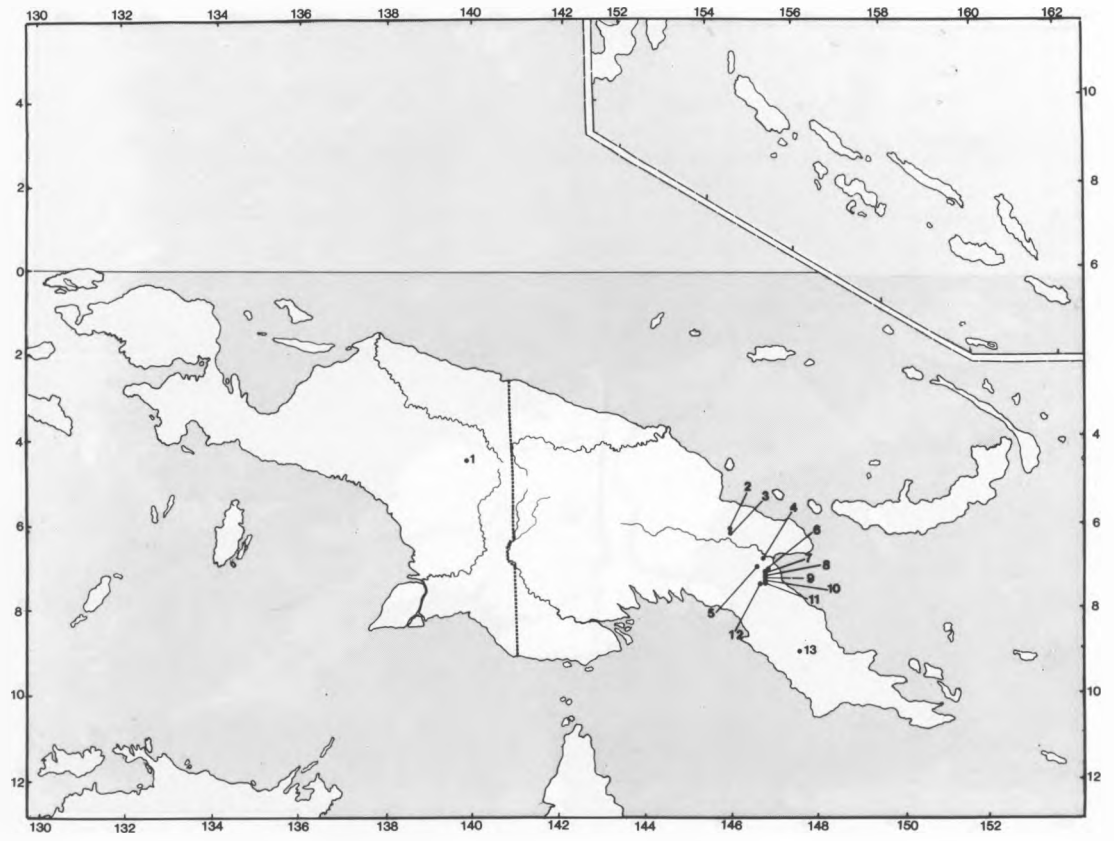

Fig. 7. Map of New Guinea and New Britain Islands with locality records for *Nyctimene certans*. See "Specimens Examined" of this species for numbered localities.

CM12600–12603, CM12604 subadult, CM12605–12606, CM12607 subadult, and CM12608.

Additional Specimens Examined

Nyctimene cephalotes (Pallas, 1767)

INDONESIA: Ambon: RMNH, 2 and one subadult. Sulawesi: Peleng Island; AMNH, 13. Toli Toli: USNM, 9.

Nyctimene papuanus Andersen, 1910.

WEST IRIAN: Oransbari: BBM-NG, 1. PAPUA: Fly River, 5 mi below Palmer Junction: AMNH, 3. Milne Bay: BM(NH), 1 [holotype]; Sinafade: BBM-NG, 3. Morobe Dist.: 10 km W Bulolo, BBM-NG, 5; Kalalo, BBM-NG, 1; Bupu R., 12 mi NE Lae, BBM-NG, 1; Singavwa R., near Lae, BBM-NG, 2; Sumsum, 20 km N Bulolo, BBM-NG, 1. Northern Dist.: Azarita, near Popondetta, BBM-NG, 1; Ambogosa R., near Popondetta, BBM-NG, 1; Popondetta, BBM-NG, 4; Soputa R., near Popondetta, BBM-NG, 1. Port Moresby area: Karema, Brown R. Forestry Sta., 38 km NW Port Moresby, BBM-NG, 2; Sogori, Siviuma Dam, BBM-NG, 2. SOLOMON ISLANDS: Bougainville Sound, AUM, 1; Bougainville Is., AUM, 1, and BBM-NG, 3; Kolombangara Is., BBM-NG, 1; Choiseul Is., BBM-NG, 1 [holotype *N. a. minor*]; Santa Ysabel Is., BBM-NG, 1.

SUMMARY

The taxonomic status of *Nyctimene cyclotis* and its relative, *N. certans* was studied in order to clarify their relationship. Comparisons with *Nyctimene cephalotes* and *N. papuanus* were made. *N. cyclotis* occurs on

mainland New Guinea (West Irian and Papua) and New Britain Islands, while *N. certans* is found on mainland New Guinea.

Although *N. cyclotis* and *N. certans* share dental, ear shape, and pelage characteristics, and occur sympatrically, there are sufficient differences for them to be considered distinct species. *N. cyclotis* and *N. certans* differed significantly from each other in 22 of 23 variables. There was no overlap in the condylobasal length of skull (CBL) between them. *N. cyclotis* averaged slightly smaller than *N. certans* for all variables analyzed for this study. *N. certans,* in comparison with *N. cyclotis,* has a longer, narrower skull, a flatter nasal profile, and a less steeply arched braincase.

In comparison with *N. papuanus, N. cyclotis* differs in dental features and has longer fur and broader ears. These latter features, as well as its overall smaller size, distinguish *N. cyclotis* from *N. cephalotes. N. certans* is larger overall than *N. papuanus* and differs markedly in its pelage, ears, and dentition. Compared with *N. cephalotes, N. certans* has shorter forearms and metacarpals but longer first phalanges. It also differs from *N. cephalotes* in cranial characters, ears, pelage, and dentition. Seven of 23 variables studied had significantly different means for all four species.

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