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A NEW SPECIES OF TUBE-NOSED FRUIT BAT
(*NYCTIMENE*) FROM NEGROS ISLAND, PHILIPPINES
(MAMMALIA: PTEROPODIDAE)

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ABSTRACT.—Heaney, Lawrence R., and Randolph L. Peterson. 1984. A new species of tube-nosed fruit bat (*Nyctimene*) from Negros Island, Philippines (Mammalia: Pteropodidae). *Occ. Pap. Mus. Zool. Univ. Michigan*, 708: 1–16, figs. 1–4. A new species of *Nyctimene* is described from Negros Island in the central Philippines. The new species is a member of the “*cephalotes* group” of Andersen (1912), and apparently is most closely related to *N. cephalotes* which occurs on Celebes (=Sulawesi). This new species brings the number of genera of pteropodid fruit bats shared by the Philippines and Celebes, but absent from Borneo, to four. Five genera of Philippine fruit bats are widespread in Indo-Australia; two genera are shared with Borneo, but not areas to the east; and four genera are endemic to the Philippines.

Key words: *Chiroptera*, *Pteropodidae*, *Nyctimene*, *Philippines*, *zoogeography*.

INTRODUCTION

Bats of the genus *Nyctimene* are widespread, with species known from Celebes (=Sulawesi) east to Santa Cruz Island in the western Pacific Ocean. Thirteen species are recognized currently, with a closely related species usually being placed in the genus *Paranyctimene* (Hill, 1983; Koopman, 1979; Laurie and Hill, 1954; Phillips, 1968; Troughton, 1946). The greatest diversity of tube-nosed fruit bats occurs on New Guinea, where five species (including *Paranyctimene*

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raptor) are found (Koopman, 1979), and in the Bismarck Archipelago, where approximately five species are found (Smith and Hood, 1982). Only three species, *N. albiventer*, *N. cephalotes*, and *N. minutus*, have been found west of the western edge of the Australian continental shelf. Because few species of bats (Peterson and Fenton, 1970; Tate, 1946), and fewer still of terrestrial mammals (Groves, 1976; Musser, 1977, 1982), are thought to be shared by Celebes or the Moluccas and the Philippines, the discovery of a species of *Nyctimene* in the Philippines is of zoogeographic interest. Rabor et al. (1970) reported that they obtained 42 specimens of *Nyctimene* sp. in 1964 and 1965 from five localities in the southern portion of Negros Island in the central Philippines. They suggested that the specimens represented an undescribed species, but did not name it, and no published mention of *Nyctimene* in the Philippines has been made since that time. Twenty-six of the specimens they collected were subsequently deposited in the Delaware Museum of Natural History (DMNH). Thirteen specimens collected by D. Empesso in 1965 and 1966 are in the Royal Ontario Museum (ROM), and 18 collected in 1979 through 1983 by Heaney, P. D. Heideman, and K. M. Mudar are in the Museum of Zoology, University of Michigan (UMMZ). The purpose of this paper is to describe this new species.

METHODS

All cranial measurements were taken by Heaney with dial calipers and recorded to the nearest 0.1 mm. Most measurements are as defined in DeBlase and Martin (1981); exceptions and clarifications are as follows: condylobasal length—occipital condyles to premaxillary immediately above incisors; rostral length—anteriormost point on interior of orbit to anterior tip of nasals (see Heaney, 1979); orbital length—anteriormost point of orbit to most distant posterior edge of orbit; postorbital length—posterior edge of orbit to posterior edge of junction of sagittal and occipital crests; palatal length—posterior border of incisors to anteriormost point on posterior limit of hard palate (usually at midline). All toothrow measurements taken at alveolus. External measurements of *N. rabori* that are cited were taken on fresh specimens by LRH or persons trained by him. Other external measurements as follows: hind foot—measured by LRH on all dry specimens, ankle joint to tip of longest claw (to nearest mm); ear—height measured by LRH on dry specimens (to nearest mm); forearm—measured by LRH on dried specimens (except for *N. cephalotes* from Ambon and *N. albiventer* from Ternate, which were in alcohol). Total length and tail length were taken from specimen labels. Capitalized color names are from Ridgway (1912). Measurements in Pallas (1767) were converted to metric as follows: one pouce = 27.07 mm; one ligne = 2.26 mm. Additional specimens were examined that are in the following collections: American Museum of Natural History (AMNH), Bernice P. Bishop Museum (BBM), Field Museum of Natural History (FMNH), Rijkmuseum van Natuurlijke Historie (RMNH), Department of Biology, Silliman University (SU), and U.S. National Museum of Natural History (USNM).

SPECIES ACCOUNT

Nyctimene rabori, new species

HOLOTYPE: Adult male, study skin with body skeleton, in good condition (Figs. 1 and 2; UMMZ 156971). Obtained 11 June 1981 at Lake Balinsasayao, 6 km N, 14 km W Dumaguete City, Sibulan Municipality, Negros Oriental Province, Republic of the Philippines, 835 m elevation, 9°21'N, 123°10'E, by L. R. Heaney.

SPECIMENS EXAMINED: (Total 61; skins with skulls unless noted otherwise).

PARATOPOTYPES: PHILIPPINES: NEGROS ORIENTAL: Lake Balinsasayao, 6 km N, 14 km W Dumaguete City, Sibulan Municipality, 840 m (2 fluid with skulls removed, 1 skeleton, 2 skins with skeletons (including the holotype); UMMZ 130404, 130405, 156970, 156971, 157070); Lake Balinsasayao, 3 km N, 14 km W Dumaguete City, Sibulan Municipality, 840–1090 m (2 skins with partial skeletons and 11 fluids; UMMZ 158508, 158509, 158883–158893); Lake Balinsasayao (4, including one fluid, uncataloged, SU).

OTHER PARATYPES: PHILIPPINES: NEGROS ORIENTAL: Malindog Citio, San Antonio Barrio, Sibulan Municipality, 800 m elev., 9°17'N, 123°14'E, (DMNH 5234–5246); Kansan-a Citio, Basay Barrio, Bayawan Municipality, 180–200 m elev., 9°28'N, 122°40'E, (DMNH 5247, 5248); Nagoro Barrio, Siaton Municipality, 800–840 m elev., 9°5'N, 123°3'E, (DMNH 5249–4258; ROM 37565, 39844); Camp Lookout, Valencia Municipality, 800 m elev., 9°16'N, 123°12'E, (DMNH 5233); Siaton Municipality 9°5'N, 123°5'E, (ROM 27506, 37507, 37508, 37550, 37564, 39839–39843, 39845).

ETYMOLOGY: We are pleased to name this species after Professor Dioscoro S. Rabor, who, with his colleagues A. C. Alcala, D. P. Empesso, and R. B. Gonzales, first discovered *Nyctimene* in the Philippines. In doing so, we wish to acknowledge the commitment of Professor Rabor to the study and conservation of Philippine wildlife, as well as to recognize the past and continuing contribution to vertebrate biology made by the faculty and students of Silliman University.

MEASUREMENTS: External and cranial measurements for the holotype and for adult males and females are listed in Table 1.

DIAGNOSIS.—The genus *Nyctimene* may be characterized briefly as follows. Skull short and heavy; rostrum very deep anteriorly; distance from orbit to nares less than lacrimal width; braincase narrow;

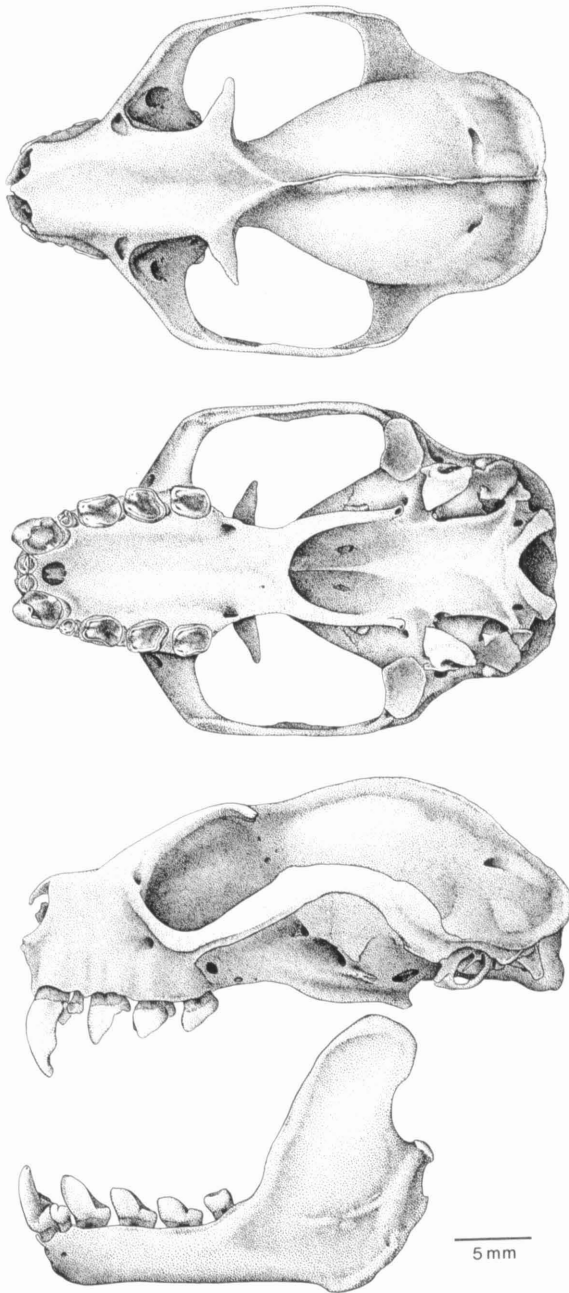


FIG. 1. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of the holotype of *Nyctimene rabori* (UMMZ 156971).

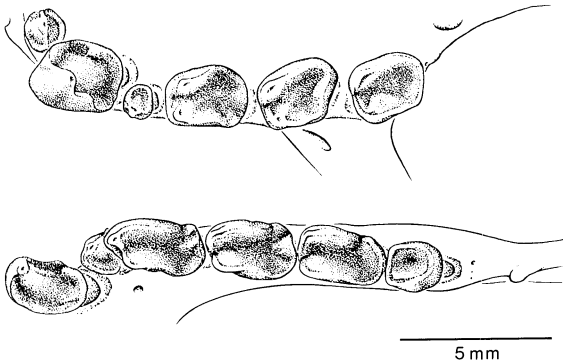


FIG. 2. Maxillary (top) and mandibular (bottom) tooththrows of the holotype of *Nyctimene rabori*.

basicranial flexion slight, alveolar line projected backwards passing about through condyle; occiput not tubular; premaxillaries solidly fused anteriorly; bony palate not narrowing (or narrowing only slightly) behind maxillary tooththrows; width of interpterygoid fossa (including hamular processes) about equal to distance between posterior molars; upper canines parallel; dental formula $\frac{1-1-3-1}{0-1-3-2} = 24$; P^2 and P_2 well developed, just equal in height to cingulum of canine; other cheek teeth molariform, anterior cusps high and well-developed except on M_2 , which is low-crowned and smaller than other molariform teeth by about half; tongue with four circumvallate papillae; mandible practically without angular process; nostrils long, tubular; wings with scattered pale spots; well-developed tail; claw on index finger present; attachment of wings posteriorly to base of second and third toes (Andersen, 1912; Miller, 1907).

Nyctimene rabori is moderately large for genus, forearm 71.5–80. Upper molariform teeth relatively short and broad, with M^1 wider posteriorly; canines weakly trilobate, relatively strongly procumbent; sagittal crest strongly developed.

Nyctimene rabori differs from the genotype, *N. cephalotes*, in its larger size (condylobasal length 33–34 mm vs. 28–31 mm; see also Table 1); higher sagittal crest; greater degree of vertical arch of the zygoma; much larger muscle attachment site for *M. pterygoideus internus*; longer ascending ramus; and having the angle of the ascending ramus closer to perpendicular. *N. rabori* differs from *N. major* in having interorbital width/postorbital width ratio greater (ca. 1.1 vs. 1.0; see also Table 1); a slight posterior expansion of the braincase, rather than well developed; maxillary tooththrows diverging posteriorly,

TABLE 1.

MEASUREMENTS¹ FOR THE HOLOTYPE AND ADULT MALE AND FEMALE *Nyctimene rabori*, AND FOR *N. cephalotes*, AND *N. major* (SEXES COMBINED).

	<i>Nyctimene rabori</i> holotype	<i>Nyctimene rabori</i> females	<i>Nyctimene rabori</i> males	<i>Nyctimene cephalotes cephalotes</i> (Ambon)	<i>Nyctimene cephalotes cephalotes</i> (Celebes)	<i>Nyctimene major major</i>	<i>Nyctimene major lullulae</i>
Sample size	—	9	13	3	11	7	7
Condylobasal length	35.3	34.20 ± 0.44 (33.4–34.8)	34.36 ± 0.64 (33.4–35.3)	29.17 (28.1–29.7)	29.94 ± 0.60 (28.8–30.8)	35.3 (32.3–36.3)	31.21 ± 0.47 (30.5–32.0)
Zygomatic breadth	23.0	22.77 ± 0.80 (21.6–24.0)	22.68 ± 0.61 (21.7–24.0)	19.47 (18.5–20.2)	20.71 ± 0.78 (19.3–22.1)	23.20 ± 0.74 (21.8–24.1)	20.99 ± 0.37 (20.4–21.6)
Interorbital width	6.6	6.34 ± 0.39 (5.7–6.9)	6.13 ± 0.28 (5.7–6.6)	5.87 (5.6–6.1)	6.13 ± 0.38 (5.4–6.8)	6.30 ± 0.23 (6.0–6.6)	5.89 ± 0.21 (5.6–6.1)
Postorbital width	5.5	5.64 ± 0.40 (5.1–6.3)	5.58 ± 0.24 (5.0–6.0)	5.70 (5.5–5.9)	6.06 ± 0.23 (5.8–6.5)	6.29 ± 0.34 (5.8–6.5)	5.64 ± 0.22 (5.3–6.0)
Mastoid breadth	15.0	14.72 ± 0.29 (14.3–15.2)	14.63 ± 0.36 (14.1–15.1)	13.30 (12.8–13.8)	13.70 ± 0.19 (13.4–13.9)	15.35 (14.9–15.8)	14.13 ± 0.30 (13.6–14.6)
Rostral length	9.7	9.18 ± 0.29 (8.6–9.7)	9.58 ± 0.34 (9.1–10.3)	8.67 (8.3–9.0)	8.55 ± 0.35 (8.2–9.2)	9.73 ± 0.42 (9.3–10.3)	8.62–0.37 (8.1–9.1)
Orbital length	16.6	16.27 ± 0.37 (15.8–16.8)	16.01 ± 0.46 (15.3–16.6)	12.77 (12.4–13.1)	14.03 ± 0.37 (13.7–14.5)	16.64 ± 0.61 (15.7–17.3)	14.58 ± 0.21 (14.3–14.8)

Postorbital length	15.2	13.56 ± 0.38 (13.1-14.4)	13.99 ± 0.85 (13.1-15.4)	13.50 (12.6-14.4)	13.23 ± 0.36 (12.7-14.0)	15.1 (14.8-15.4)	13.64 ± 0.36 (12.9-14.0)
C ¹ to M ¹	11.9	11.49 ± 0.21 (11.2-11.8)	11.83 ± 0.20 (11.4-12.1)	10.03 (9.9-10.1)	10.23 ± 0.39 (9.3-10.7)	12.16 ± 0.23 (11.9-12.6)	10.61 ± 0.16 (10.5-10.7)
P ³ to M ¹	8.0	7.79 ± 0.13 (7.6-8.0)	7.94 ± 0.17 (7.6-8.2)	6.70 (6.6-6.8)	6.94 ± 0.16 (6.6-7.2)	8.63 ± 0.15 (8.4-8.8)	7.31 ± 0.20 (7.1-7.5)
Palatal breadth at M ¹	7.3	7.07 ± 0.49 (6.0-7.7)	7.08 ± 0.29 (6.5-7.4)	6.06 (5.6-6.4)	6.94 ± 0.33 (6.5-7.4)	7.0 ± 0.21 (6.8-7.4)	6.24 ± 0.18 (5.9-6.5)
Palatal length	16.4	15.85 ± 0.27 (15.5-16.4)	16.12 ± 0.41 (15.4-16.7)	13.9 (13.4-14.7)	13.67 ± 0.41 (12.9-14.3)	15.66 ± 0.27 (15.1-15.9)	14.03 ± 0.31 (13.7-14.3)
Total length	149	142.0 ± 4.2 (139-146)	142.1 ± 5.4 (132-149)	—	124.7 ± 4.8 (116-131)	—	—
Tail length	25	25.9 ± 2.2 (23-30)	25.1 ± 2.6 (19-29)	21.0 (18-24)	21.0 ± 1.2 (20-23)	—	—
Hind foot length	19	18.7 ± 0.4 (18-19)	18.5 ± 1.7 (16-21)	15.3 (14-16)	15.3 ± 0.5 (15-16)	17.7 (16-20)	—
Ear length	20	20.0 ± 0.7 (19-21)	19.5 ± 0.5 (18-20)	15.0 (15-15)	13.5 ± 0.7 (13-15)	—	—
Forearm length	76	76.7 ± 2.8 (76-81)	75.5 ± 1.7 (73-79)	62.3 (60-64)	66.4 ± 1.9 (64-70)	76.6 (73-79)	—

¹Standard deviations are given for samples over three; means and ranges are given in all cases.

rather than toothrows parallel; accessory cusp on upper canines nearly absent, rather than well developed; cuspule on posterior labial margin of P^3 and P_3 very weak, rather than large and conspicuous; muscle attachment site for *M. pterygoideus internus* large, rather than small; and procumbency of upper canines greater. Differs from other taxa as noted below.

DESCRIPTION.—Pelage of adults sexually dimorphic, with females generally lighter than males, and subadults intermediate. Adult females with dense, soft fur on face and head, golden brown (Ochraceous Buff) in color. Fur on neck changing to mottled light brown (Warm Buff). Dorsum of body covered by dense, soft fur of light brown (Warm Buff), except for a narrow strip (3 to 4 mm wide) of dark brown (Mummy Brown) fur extending from shoulders to base of tail. Fur on venter coarser and thin, especially at throat, and light brown (Ochraceous Buff) on sides; lighter towards center of abdomen. Wings and ears with yellow spots of irregular size; spots on wings usually confined to areas overlying limbs or phalanges, rarely on interdigital skin; spots lack dark pigment, and bone, muscle, and tendons are clearly visible under the skin in live animals. Adult males darker overall, but with same patterns as females. Head dark golden brown (Ochraceous Tawny), neck brownish-gray (Tawny-Olive), and dorsum of body medium brown (Saccardo's Umber) with dark stripe (Mummy Brown) down midline. Ventrums light chocolate brown (Russet) on sides, lighter on abdomen. Pigmented skin on wings, ears, and hind limbs substantially darker on males than on adult females or subadults. Subadult males not distinguishable from subadult females. Nostrils (Fig. 3) high on muzzle, tubular, but incised at dorsolateral margin through soft fleshy portion to point where typical haired skin begins, ventrolateral portion expanded laterally into fleshy lobe. Skull (Fig. 1) of moderate size for genus, with condylobasal length averaging about 35 mm. Sagittal crest strongly developed, over 1 mm high for posterior two-thirds of its length, fusing at terminus with the strongly developed occipital crest. Ratio of interorbital breadth to postorbital breadth averaging 1.1. Braincase not evenly curving; rather, posterior portion (ca. posterior fifth) of braincase with slight convex expansion. Post-orbital processes strong, ca. 4 mm long. Nasals with moderately long (ca. 1 mm) ventral extension at anterior tip. Posterior margin of palate rounded (U-shaped). Zygomatic arch strongly arched dorsally. Molariform toothrow diverging posteriorly, with length of P^3 to M^1 slightly greater than palatal breadth at M^1 (ratio 1.1). Upper canines very weakly trilobate, strongly procumbent (Fig. 2). P^3 with very weak labial posterior cuspule. Muscle scar of *M.*



FIG. 3. Photograph of the head of a live *Nyctimene rabori* captured at Lake Balinsasayao, Negros Island, in March 1983. Note appearance of fleshy, tubular nostrils. Photograph by P. D. Heideman.

pterygoideus internus large, producing a 1 mm process ventral to mandibular condyle. Ascending ramus long, with leading edge at high angle. Palatal ridges numerous, extending from near level of leading edge of P^3 posteriorly beyond bony palate onto the pterygoids, and forming a divided "V" pattern at terminus near posterior end of pterygoids (Fig. 4).

Cranial Development: Progressive developmental changes in the morphology of the skull are shown in Fig. 4. All individuals illustrated were netted or shot in flight, i.e., were capable of independent flight. The following sutures are distinctly open in the youngest individuals: nasal-frontal, palatines, zygoma, basioccipital-basisphenoid, basisphenoid-presphenoid. The sagittal crest is absent in young individuals but begins to develop as they approach adult size. The post-orbital processes are weakly developed initially, and become longer and thicker with age. The postorbital breadth is wide relative to orbital breadth and shows little increase with increasing age, thus becoming proportionately narrower. In our Negros Island samples of subadults, the forearm varies from 69.4–75.0 mm and the third digit metacarpal from 47.5–53.4 mm. The mastoid and braincase breadths attain adult dimensions before the sutures close, and the length and

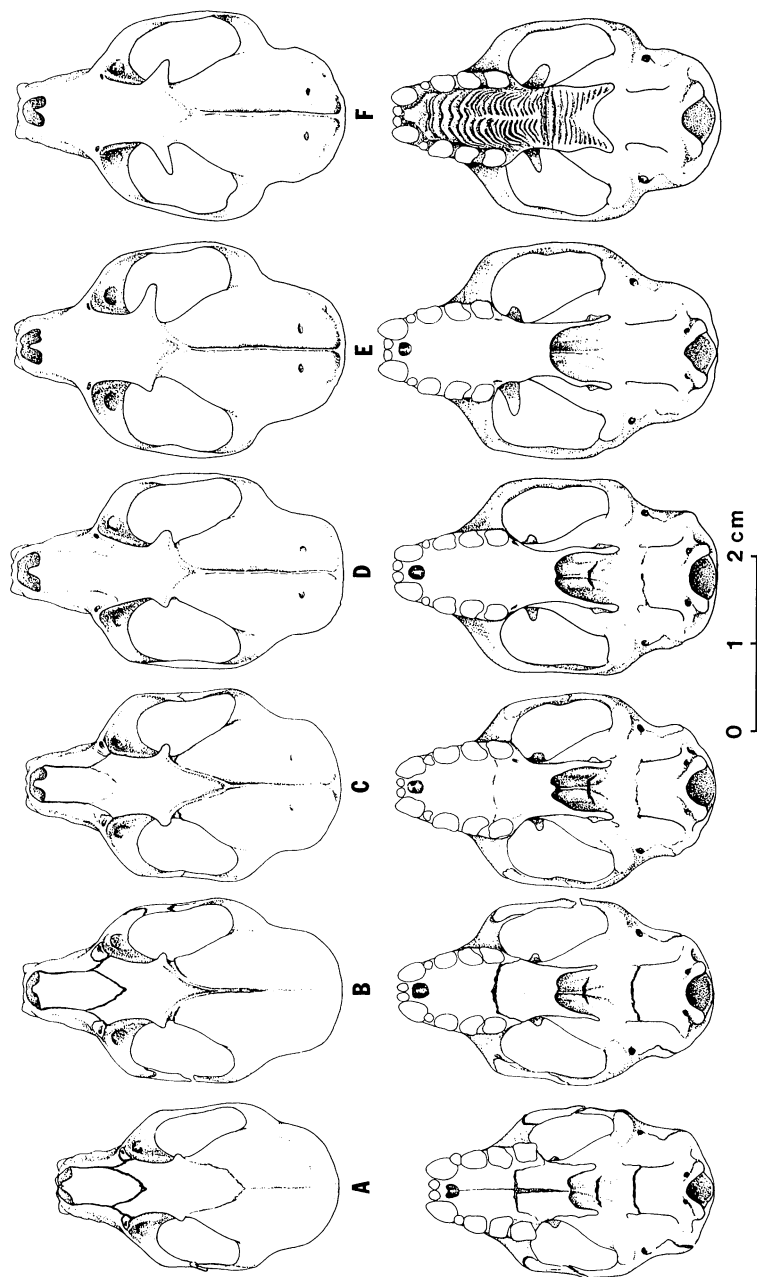


FIG. 4. Dorsal (upper row) and ventral (lower row) views of the skulls of a series of female *Mycimene raboti* selected to illustrate changes with age. A: ROM 37550. B: DMNH 5255. C: DMNH 5258. D: DMNH 5246. E: DMNH 5241. F: ROM 39839, with palatal ridges illustrated.

width of the toothrows and the length of the tibia nearly do so. Thus, it is the length of the skull, zygomatic breadth, and length of the postorbital processes that increase most dramatically in subadults as they approach adult size.

ECOLOGY.—Heaney et al. (1981) noted that *Nyctimene rabori* is a relatively uncommon bat in upland dipterocarp forest near Lake Balinsasayao, Negros Island, but that it is “apparently absent outside of forested regions, [and] may be typically a high-canopy forest species.” All specimens they reported were taken on the top or sides of a steep ridge between Lakes Balinsasayao and Danau. Two females taken on 12 June 1981 were lactating and two adult males taken on 8 and 11 June were in breeding condition. Nothing is known of feeding or roosting habits. Other pteropodid bats taken at the same locality were *Cynopterus brachyotis*, *Eonycteris spelaea*, *Haplonycteris fischeri*, *Harpionycteris whiteheadi*, *Macroglossus minimus*, *Ptenochirus jagori*, *Pteropus hypomelanus*, *Pteropus tablasi*, and *Rousettus amplexicaudatus*.

DISCUSSION

In conducting our studies of *Nyctimene*, we encountered a problem regarding *N. cephalotes* that is pertinent to this description. The holotype of *Vespertilio cephalotes* Pallas, 1767 (which is the type species of *Nyctimene*) has apparently been lost. Andersen (1912) discussed the description of *N. cephalotes* briefly, stating that apart from the lack of mention of a dark mid-dorsal stripe and light spots on the wings, the description accords well with specimens from Amboina Island. Andersen's assignment of the name has been accepted by subsequent authors except for Smith and Hood (1983), who felt that some doubt still exists concerning the identity of the species because of the lack of a holotype.

Perhaps because *N. cephalotes* was only the second megachiropteran to be described in the Linnaean system (the first being *Pteropus vampyrus* Linnaeus, 1758), the description provided by Pallas was exceptionally detailed for the time. The description is 14 pages long, including 85 external and skeletal measurements of a single female, plus two plates of illustrations, one of the external appearance and one of the entire skeleton, both life-sized. Both the description and the illustrations leave no doubt that this is the animal now called *Nyctimene*; the large, distinctive head with long, tubular nostrils, massive jaws, distinctive dentition, short, stout tail, and other characters are prominently shown and discussed.

Pallas gave the type locality only as "Moluccas"; Andersen subsequently fixed this as Amboina Island (= Ambon Island currently). Three species of *Nyctimene* are known to occur in the Moluccas: *N. minutus*, the slightly larger *N. albiventer*, and the substantially larger species now called *N. cephalotes*. Pallas stated that *N. cephalotes* was slightly smaller than *Vespertilio spasma* (= *Megaderma spasma*), putting it in the size range of these three species. Table 2 contains three measurements from the original description that are indicative of size, plus comparable measurements of three specimens from Ambon Island (RMNH 28123, 30194, 30195) that meet Andersen's definition of *N. cephalotes*, and a specimen from Ternate Island (RMNH 30291) identified by Andersen as *N. albiventer albiventer*. The specimens from Ambon are clearly similar to those given by Pallas for *N. cephalotes*. Moreover, the Ambon specimens are quite similar to the larger series from Celebes (Table 1). Thus, we find no reason to disagree with Andersen's assessment of the identity of *N. cephalotes* Pallas, and can proceed with a discussion of the relationships of *Nyctimene rabori*.

The genus *Nyctimene* was last revised by Andersen (1912); subsequent authors have reduced some taxa to subspecies and named several new species (see Hill, 1983; Koopman, 1979; Laurie and Hill, 1954; Phillips, 1968; Smith and Hood, 1983; Tate, 1942). Andersen (1912) recognized four species groups: the "*papuanus* group," now considered to contain four species, *N. albiventer*, *N. draconilla*, *N. malaitensis* (Phillips, 1968), and *N. minutus* (Koopman, 1979, 1982); the "*cyclotis* group," consisting of *N. cyclotis* alone; the "*aello* group," containing *N. aello* and *N. celaeno* (Hill, 1983); and the "*cephalotes* group," defined as containing *N. cephalotes*, *N. major*, *N. masalai* (Smith and Hood, 1983), *N. robinsoni*, *N. sanctacrucis* (Troughton, 1931), and *N. viscaccia* (Smith and Hood, 1983). Although many taxa have been named since Andersen's revision, and the specific status of many taxa is debated, Andersen's concepts of groups of related species remains the most useful framework in which to view the genus. Ongoing studies of *Nyctimene* by Peterson and J. D. Smith (pers. comm.) may ultimately provide an alternative scheme, but such is not currently available.

It is unlikely that *N. rabori* is a member of the "*cyclotis* group" (sensu Andersen, 1912) because *N. rabori* lacks the broad ears and mottled dorsal fur of *N. cyclotis*, and has larger molars than *N. cyclotis*. Likewise, *N. rabori* differs from the "*papuanus* group" in its much larger size, strongly developed sagittal crest, broad interorbital region relative to postorbital region, and long toothrow relative to palatal breadth. The Philippine species differs from *N. aello* and *N. celaeno* in

TABLE 2

THREE MEASUREMENTS GIVEN BY PALLAS IN THE DESCRIPTION OF *N. cephalotes*, WITH COMPARABLE MEASUREMENTS OF TWO SYMPATRIC SPECIES.

	Pallas	<i>N. cephalotes</i> from Ambon	<i>N. albiventer</i> from Ternate
Forearm length	60.8	62.3	54.6
Cranial length (excluding occipital crest)	30.5	—	—
Condylobasal length	—	29.2	25.5
Head width (external)	20.3	—	—
Zygomatic breadth	—	19.5	17.8

its smaller size, narrower mid-dorsal stripe, stronger cranial crests, higher dorsal arch in the zygoma, more procumbent upper canines, and longer mandibular ascending ramus.

Nyctimene rabori resembles members of the *cephalotes* group most closely. Although larger in size, *N. rabori* is similar to *N. cephalotes* in several characters: in both species, the molariform toothrow diverges posteriorly, there is little development of an accessory cusp on the canines, the ratio of interorbital to postorbital width is similar, expansion of the braincase into a posterior bulge is present but slight, and procumbency of the upper canines is relatively great. Some conspicuous differences (see Diagnosis), such as degree of development of cranial crests, are clearly related to the larger size of *N. rabori*.

A second species (also of the *cephalotes* group) with which *N. rabori* shows some similarity is *N. major* (including the subspecies *major*, *lullulae*, *geminus*, and *scitulus*). These similarities include large size, well developed cranial crests, strongly arched zygomatic arches, and long ascending ramus of the mandible with ramus angling sharply to the vertical. The two species differ in all of the characters cited above that are similar between *N. rabori* and *N. cephalotes*. We regard the similarities between *N. major* and *N. rabori* to be associated with allometric variation, and thus convergent due to their similarity in size. Moreover, we point out that since all are support structures for the masticatory apparatus musculature, all are likely to be part of a structurally related complex, so that their independence in an evolutionary sense is questionable.

Given the evidence discussed above for a close relationship with *N. cephalotes*, one might ask if they might best be viewed as subspecies of a single variable species. We feel that they should not; given the im-

probability of gene flow between populations, the degree of phenotypic difference, and the lack of any evidence of intergradation, we believe the most conservative course of action is to recognize *N. rabori* as a species.

As noted above, there are four genera of fruit bats that occur in the Philippines and on Celebes (or on small islands near Celebes), but not on Borneo: *Acerodon*, *Dobsonia*, *Harpyionycteris*, and *Nyctimene*. All four occur on Negros Island; two (*Dobsonia* and *Nyctimene*) are not known to occur elsewhere in the Philippines. Five genera of Philippine fruit bats are widespread in Indo-Australia (*Cynopterus*, *Eonycteris*, *Macroglossus*, *Pteropus*, and *Rousettus*); two occur on Borneo and other areas to the west (*Dyacopterus* and *Megaerops*); and four are endemic (*Alionycteris*, *Haplonycteris*, *Otopteropus*, and *Ptenochirus*). By this tally, the fruit bat fauna of the Philippine archipelago appears to show no greater resemblance to Borneo than to Celebes; restated, the fruit bat fauna of the Philippines is not influenced strongly by Wallace's line, the zoogeographic boundary of the Oriental faunal region that follows the edge of the Asian continental shelf. Given the high dispersal potential of bats, it is perhaps not surprising that the Philippine archipelago, which is largely oceanic, should draw its bat fauna approximately equally from the two adjacent continental masses. This is far different from the non-volant mammal fauna, which contains mostly genera shared with Borneo (and much of Asia), and endemic genera allied to Bornean genera (Heaney, 1979; Heaney and Rabor, 1982; Musser, 1977; Heaney, unpubl. data). Clearly, more detailed quantitative assessments of faunal relationship and origin are desirable, but given the apparent major differences in the distribution patterns of volant and non-volant mammals in the Philippines, the stark contrast is likely only to become more conspicuous.

ADDITIONAL SPECIMENS EXAMINED

Nyctimene aello. PAPUA NEW GUINEA: Laloki (2 FMNH); WESTERN DIVISION: Fly River; 5 mi. below Palmer Junction, elev. 80 m (11, AMNH).

Nyctimene albiventer albiventer. INDONESIA: MOLUCCAS: Ternate Island (1, RMNH).

Nyctimene albiventer papuanus. PAPUA NEW GUINEA: BISMARCK ARCHIPELAGO: Lihir Island (1, AMNH), New Britain: Wide Bay; Bainings; Balayang, elev. 2500 ft. (1, AMNH), New Britain: Whiteman Range; Mt. Uali, elev. 3000 ft. (12, AMNH).

Nyctimene albiventer ssp. PAPUA NEW GUINEA: BISMARCK ARCHIPELAGO: Duke of York Island (1, USNM).

Nyctimene cephalotes cephalotes. INDONESIA: CELEBES: Toli Toli (12, USNM); MOLUCCAS: Ambon Island (2, RMNH).

- Nyctimene cyclotis*. INDONESIA: WEST IRIAN: Nassau Range; Ilaga Valley, elev. 7500 ft. (1, AMNH).
- Nyctimene malaitensis*. SOLOMON ISLANDS: Malaita Island; Dala, elev. 20 m (1, BBM).
- Nyctimene major lullulae*. PAPUA NEW GUINEA: Woodlark Island; Kulumadau, elev. 200 m (1, AMNH), Madang District; Bagabag Island (2, AMNH), Madang District; Karkar Island (5, AMNH).
- Nyctimene major major*. PAPUA NEW GUINEA: BISMARCK ARCHIPELAGO: Duke of York Island (7, USNM).
- Nyctimene robinsoni*. AUSTRALIA: QUEENSLAND: Cape York; Portland Roads (1, AMNH); Shipton's flat (30 mi. S Cooktown), (1, AMNH); Mission Beach (2, AMNH).
- Paranyctimene raptor*. PAPUA NEW GUINEA: East Highlands: Kratke Mts.; Arau, elev. 1400 m (4, AMNH); Madang District; Pasinkap, elev. 280 ft. (3, AMNH), Sangarup (12 mi. ESE Josephstaal), elev. 900 ft. (1, AMNH), Wanuma (7 mi. S Atitau), elev. 2200 ft. (1, AMNH).

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LITERATURE CITED

- Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum (second ed.) Vol. 1. Megachiroptera. London: Brit. Mus. (Nat. Hist.), ci + 854 pp.
- DeBlase, A. F., and R. F. Martin. 1981. A manual of mammalogy with keys to families of the world. Dubuque: Wm. C. Brown Co., 436 pp.
- Groves, C. P. 1976. The origin of the mammalian fauna of Sulawesi (Celebes). Z. Säugetierk., 41:201-206.
- Heaney, L. R. 1979. A new species of tree squirrel (*Sundasciurus*) from Palawan Island, Philippines (Mammalia: Sciuridae). Proc. Biol. Soc. Washington, 92:280-286.
- , P. D. Heideman, and K. M. Mudar. 1981. Ecological notes on mammals in the Lake Balinsasayao Region, Negros Oriental, Philippines. Silliman J., 28:122-131.
- , and D. S. Rabor. 1982. Mammals of Dinagat and Siargao islands, Philippines. Occas. Paps. Mus. Zool., Univ. Michigan 699:1-30.
- Hill, J. E. 1983. Bats (Mammalia: Chiroptera) from Indo-Australia. Bull. Brit. Mus. (Nat. Hist.) (Zool.), 45:103-208.
- Koopman, K. F. 1979. Zoogeography of mammals from islands off the northeastern coast of New Guinea. Amer. Mus. Novitates 2690:1-17.

- . 1982. Results of the Archbold Expeditions No. 109. Bats from eastern Papua and the east Papuan islands. Amer. Mus. Nat. Hist. Novitates 2747:1–34.
- Laurie, E. M. O., and J. E. Hill. 1954. List of land mammals of New Guinea, Celebes, and adjacent islands. 1758–1952. London: Brit. Mus. (Nat. Hist.), 175 pp. + 3 pl.
- Miller, G. S., Jr. 1907. The families and genera of bats. Bull. U.S. Nat. Mus., 57:1–282 + 14 pls.
- Musser, G. G. 1977. *Epimys benguuetensis*, a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. Amer. Mus. Novitates, 2624:1–15.
- . 1982. Results of the Archbold Expeditions. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). Bull. Amer. Mus. Nat. Hist., 174:1–95.
- Pallas, P. S. 1767. Spicilegia zoologica; quibus novae imprimis et obscurae animalium species inconibus, descriptionibus atque commentariis illustrantur. Paris. 3:10–23 + 2 pls.
- Peterson, R. L., and M. B. Fenton. 1970. Variation in the bats of the genus *Harpyionycteris*, with the description of a new race. Roy. Ontario Mus. Life Sci. Occas. Paps, 17:1–15.
- Phillips, C. J. 1968. Systematics of megachiropteran bats in the Solomon Islands. Univ. Kansas Mus. Nat. Hist. Publ., 16:777–837.
- Rabor, D. S., A. C. Alcala, and R. B. Gonzales. 1970. A list of land vertebrates of Negros Island, Philippines. Silliman J., 17:297–316.
- Ridgway, R. 1912. Color standards and color nomenclature. Washington, D.C.: Published by the author. iii + 43 pp., 53 pls.
- Smith, J. D. and C. S. Hood. 1982. Preliminary notes on bats from Bismarck Archipelago (Mammalia: Chiroptera). Science in New Guinea, 8:81–121.
- , and ———. 1983. A new species of tube-nosed fruit bat (*Nyctimene*) from the Bismarck Archipelago, Papua New Guinea. Occas. Paps. Mus., Texas Tech Univ., 81:1–14.
- Tate, G. H. H. 1942. Pteropodidae (Chiroptera) of the Archbold collections. Amer. Mus. Nat. Hist. Bull., 80:331–347.
- . 1946. Geographical distribution of the bats in the Australasian archipelago. Amer. Mus. Novitates, 1323:1–21.
- Troughton, E. L. 1931. Three new bats of the genera *Pteropus*, *Nyctimene*, and *Chaerophon* from Melanesia. Proc. Linnaean Soc. New South Wales, 56:204–209.
- . 1946. Furred animals of Australia. Sydney (third ed.): Angus and Robertson, xxx + 376 pp.

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