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## NOTES ON DISTRIBUTION AND TAXONOMY OF AUSTRALASIAN BATS. I. PTEROPODINAE AND NYCTIMENINAE (MAMMALIA, MEGACHIROPTERA, PTEROPODIDAE)

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### ABSTRACT

Hitherto unreported australasian Pteropodinae and Nyctimeninae from the collections of the Zoologisch Museum in Amsterdam and some important samples of Nyctimeninae from the Nationaal Natuurhistorisch Museum (formerly: Rijksmuseum van Natuurlijke Historie) in Leiden are reported and discussed. The published first occurrence of *Pteropus vampyrus* on Krakatau Islands after the last eruption is preceded by a specimen found there eight years earlier. The fruit bat material collected on Buru Island by L. J. Toxopeus in 1921-1922, as far as deposited in Amsterdam, is reported for the first time. New localities are reported for *Pteropus griseus griseus*, *P. personatus*, *P. tonganus geddiei*, *P. caniceps*, *Macroglossus minimus nanus*, *Syconycteris australis papuana*, *Nyctimene albiventer* subsp., *Nyctimene keasti tozeri*, *Nyctimene aello*, *Nyctimene rabori*, and *Paranyctimene raptor*. The first case of (near-) sympatry of *Macroglossus minimus* and *M. sobrinus* on Java is presented. *Nyctimene* from the Talaud Islands is identified as *N. rabori*, not *N. cephalotes*. *Nyctimene* from New Britain are provisionally referred to *N. albiventer* and *N. vizcaccia*. The first specimen of *Nyctimene* from Babar Island, Indonesia, is recorded and described as a new subspecies of *Nyctimene keasti*. *Paranyctimene* is considered a subgenus of *Nyctimene*. A new species and a new subspecies of *Nyctimene* (*Paranyctimene*) from Papua New Guinea and West Papua, Indonesia, are described. Parasitic Diptera (Nycteribiidae) were collected from several of the studied fruit bat species. They have been identified and are reported in their hosts' accounts.

### INTRODUCTION

The Zoologisch Museum of Amsterdam (ZMA) has a modest but interesting collection of bats from Australasia, from Laos to the Solomon Islands, with an accent on Indonesia. Over the years, a number of reports have been published on parts of this collection (Jentink, 1890-1891; Beaufort, 1911; Oei & Feen, 1958; Oei, 1960; Van Bree, 1961; Bergmans, 1975, 1978, 1979, 1994, 1995; Rookmaaker & Bergmans, 1981;

Jong & Bergmans, 1981; Bergmans & Sarbini, 1985; Bergmans & Van Bree, 1986; Boeadi & Bergmans, 1987; Bergmans & Rozendaal, 1988; Strien, 1996). However, some of the older material has remained unreported, e.g., some fruit bats from the island of Buru collected by L. J. Toxopeus in 1921-1922. The mammals collected by Toxopeus were sent from Museum Buitenzorg (the present Zoological Museum of Bogor, Indonesia; ZMBI) to the ZMA, from where the material was sent to Mr O. Thomas of the British

Museum (Natural History) (BMNH) for identification. Some new taxa were described, the types of which apparently remained in London, and parts of the remainder were sent back to the ZMA and MZBI, respectively. Dammerman (1929) wrote a report on the material in the MZBI but the ZMA specimens of this collection have never been reported.

Further, through exchange and through contributions of interested naturalists, the ZMA has continued to receive additional Chiroptera from the region. Together, these collections include some new, rare, or otherwise interesting taxa, e.g., from noteworthy new localities. The representatives of the subfamilies Pteropodinae and Nyctimeninae of the family Pteropodidae among these are reported here. The Pteropodinae include some of the former Macroglossinae (see Bergmans, 1997). It is the author's intention to report the specimens of the remaining Pteropodidae and other chiropteran families in one or more following papers.

## MATERIALS AND METHODS

The ZMA material is listed under the species in the taxonomic section below. Some important samples of Nyctimeninae in the collection of the Nationaal Natuurhistorisch Museum in Leiden - the former Rijksmuseum van Natuurlijke Historie, and for historical and practical reasons abbreviated to RMNH - have also been studied and are listed as such. All measurements are given in mm: body and skull measurements, taken with callipers, to the nearest 0.1 mm, and teeth - always over the crowns - measured with a stereomicroscope with micrometer disc, to the nearest 0.05 mm. For the designation of teeth, Andersen has been followed (1912: xxvii-xxviii); capital I, C, P and M indicate permanent incisors, canines, premolars and molars, and the position of the tooth number, above or below, indicates upper and lower teeth, respectively (e.g., P<sup>3</sup> and P<sub>3</sub> are the third upper and third lower premolar, respectively). Weights have been copied from collectors' labels and are given in g. Geographical coordinates have been copied from collectors' labels (and then may include seconds), from atlases, or in some cases calculated. Unless stated otherwise, measurements are of adult spec-

imens only. Various criteria have been applied to establish the adulthood of specimens. Among these, fused and ossified sutures between pterygoid and basisphenoid, and between the latter and basioccipital are the most important. See for other criteria Bergmans (1988: 76-77). The following abbreviations are used throughout:

alc. = preserved in alcohol; a.s.l. = above sea level; C = canine; cbl = condylobasal length; E = ear length, from basal notch to tip; gsl = greatest skull length; HF = length of (hind) foot; imm. = immature; M = molar; P = premolar; pdp = post-dental palate length; pl = palatal length; skull = skull extracted; W = weight; # = collector's or field number.

AMNH = American Museum of Natural History, New York; BMNH = British Museum (Natural History), London; MZBI = Museum Zoologicum Bogoriense, Bogor; RMNH = Nationaal Natuurhistorisch Museum, Leiden; ZMA = Zoologisch Museum, Amsterdam; ZMB = Zoologisches Museum, Berlin.

## TAXONOMIC SECTION

### SUBFAMILY PTEROPODINAE Gray, 1821

This subfamily, and especially the polyspecific genus *Pteropus* Erxleben, 1777, is in need of a full revision, the latest being that by Andersen (1912b), who divided the genus into 17 different groups. Quite recently, a promising new study has been started, using sequence data from mitochondrial and nuclear genes to construct a molecular phylogeny for *Pteropus* (Kershnar et al., 1999). The present paper presents some interesting new specimens and localities for taxonomically mostly rather well established species. The species are treated in the order of Andersen's species groups.

### *PTEROPUS HYPOMELANUS* GROUP

***Pteropus griseus griseus*** E. Geoffroy - St. Hilaire, 1810

#### MATERIAL

INDONESIA: ZMA 23.438/39, 1 male, 1 female, alc., Pulau Sailus Kecil (117°27'E 7°35'S), Kepulauan Tengah

(Paternoster Islands), 27-VII-1987, leg. J. de Korte; taken from a colony in a small mangrove forest on the reef.

REMARKS. - The male has a forearm length of 119.1, the female one of 113.1. Corbet & Hill (1992) gave a survey of the localities from where *P. griseus* has been reported previously (note that Ujung Pandang and Peleng are mentioned in their text but not mapped). Pulau Sailus Kecil is an interesting new locality record.

DISCUSSION. - The assignation of the new material to the typical subspecies is tentative, and based mainly on geographical grounds, as sufficient comparison material is lacking.

The taxonomy of the species is not entirely clear. *Pteropus pallidus* Temminck, 1825 from Banda Island and *P. mimus* Andersen, 1908 from Ujung Pandang (Makassar), Salayer and Peleng are generally regarded as - at most - subspecies of *P. griseus* (Laurie & Hill, 1954; Goodwin, 1979; Bergmans et al., 1988; Corbet et al., 1992; Mickleburgh, et al., 1992; Wilson & Reeder, 1993; Koopman, 1994), although there appears to be some doubt as to the allocation and provenance of what has been described as *P. pallidus*. Goodwin (1979) wrote that a subspecies of *P. griseus* "possibly" occurs on the Banda islands, and Flannery (1995a) does not list *P. pallidus* at all. For their paper on small Philippine *Pteropus* species, Klingener & Creighton (1984) studied series of *P. speciosus* and *P. griseus*, among other species. Although their paper is centered around some synonymies, it does not contain a discussion

of the relationship between these two species, and does not conclude their synonymy. Corbet et al. (1992) however, added the essentially Philippine *Pteropus speciosus* Andersen, 1908 to the synonymy of *P. griseus*. This was based on the observation that *P. speciosus* seems to have been retained only because of a supposed sympatry with *P. griseus*. Corbet et al. wrote "*speciosus* (Philippines) differs from *mimus* (Sulawesi) only in blackish rather than brownish back and in darker underparts". Heaney et al. (1998) listed *speciosus* as a species but do not exclude its possible synonymy with *griseus*.<sup>1</sup>

ECTOPARASITES. - The specimens were infested with the nycteriid fly *Cyclopodia horsfieldi* de Meijere, 1899.

### ***Pteropus ornatus ornatus* Gray, 1870**

#### MATERIAL

NEW CALEDONIA: ZMA 11.717, 11.719, 1 male, 1 female, alc., incomplete skulls, near Thio (21°37'S 166°13'E), 17-III-1968, leg. P. Guépig.

REMARKS. - The male appears to be a young adult and has a forearm length of 142.6 and an upper tooth row length of 25.2. The female has a forearm length of 139.6, a gsl of 62.4, and an upper tooth row length of 24.4.

DISCUSSION. - Both specimens are adult to judge by their fused skull base sutures, but they are small. Felten (1964) gave 144-163 for the forearm length range in 22 specimens from New

<sup>1</sup>) The mentioned study by Klingener et al. (1984) is strongly influenced by the peculiar hypothesis that, as they wrote, the "Taxonomic study of megachiropteran bats is complicated by the fact that the skull continues to grow in dimensions and shape throughout life" or, more precisely, "In megachiropterans the skull continues to elongate in adults. This elongation may involve backward and dorsal movement of the braincase as well as elongation of the rostrum in long-faced forms." Klingener et al. mention two studies (Lanza, 1961; Peterson & Fenton, 1970) which are suggested to be supportive of this hypothesis. But neither is. Lanza (1961), who described post-embryonal skull growth in two African fruit bat species, literally concluded that in *Epomophorus labiatus* (Temminck, 1837), and implicitly also in *E. wahlbergi* (Sundevall, 1846), the dimensional development of the rostrum stops at a certain stage (Lanza, 1961: 183). Peterson et al. (1970) described the cranial variation with age in *Harpyionycteris* Thomas, 1896, involving several characters, but in no way suggested that skulls of fruit bats continue growing 'forever'. In fact, as experience shows, there is a rather restricted range, with both a minimum and a maximum value, of the greatest skull length (and the condylobasal length) in adult males, and most frequently a different but equally restricted range in adult females, in every species of fruit bat. Accumulated measurements of adult specimens of either sex from a given population show a normal stochastic distribution. It has never been substantiated that, as Klingener et al. (1984) seemed to believe, skull growth continues forever. If they were right, every now and then a new maximum measurement would be recorded for every specific skull dimension. But the uncertainties are of a less olympic character. The process of stretching of the skull in Megachiroptera, involving a decrease in

Caledonia, sexes combined, 66.7-72.6 for the gsl range in 16 of these specimens, and 24.7-28.0 for the upper teeth row length range in 23. Flannery (1995a) gave 165 as forearm length for one male and 142-154 for three females.

ECTOPARASITES. - One specimen of the nycteribiid fly *Cyclopodia similis* Speiser, 1900 was found on the male specimen.

#### *PTEROPUS MARIANNUS* GROUP

***Pteropus tonganus geddiei*** MacGillivray, 1860

##### MATERIAL

NEW CALEDONIA: ZMA 11.716, 11.718, 1 female, 1 imm. male, alc., incomplete skulls, near Thio (21°37'0"S 166°13'00"E), 17-III-1968, leg. P. Guépig.

REMARKS. - The present female specimen has a forearm length of 168.0 and large nipples. The immature male has a forearm length of 145.2.

DISCUSSION. - Felten (1964) revised *Pteropus* from New Caledonia, and concluded that *P. tonganus* from that island represented the subspecies *geddiei*. He listed a number of measurements for the two sexes combined. For 16 specimens, from both New Caledonia and the Loyalty Islands, he gave a forearm length range of 147-166. The female specimen surpasses this range, which suggests that females may attain larger forearm lengths than males. However, Flannery (1995a) stated that in this species males are considerably larger than females, with males maturing at a weight of 600 and females at 450. The forearm lengths in his account (148.9 in one male, and 144-145 in three females) do not include *geddiei* but typical

specimens from the Fiji Islands, and are too few to be conclusive.

#### *PTEROPUS CANICEPS* GROUP

***Pteropus caniceps*** Gray, 1871

##### MATERIAL

INDONESIA: ZMA 21.433, 1 male, alc., skull, Ngele Ngele Besar (2°11'20"N 128°12'20"E), 16-XI-1980, leg. H. Moll, mistnetted under trees; ZMA 22.134, 1 imm. female, alc., skull, Bataka (Talaga), Gamkunora (Gunung Gamkunoro: 01°30'N 127°32'E), northwest Halmahera, 3/4-III-1983, leg. F.G. Rozendaal.

REMARKS. - This species is restricted to Halmahera and surrounding islands, from where it has been reported from Bacan, Morotai, and Ternate, and to which Ngele Ngele Besar is now added, and from Sula Bessi, Sula Islands (Corbet et al., 1992). (See Bergmans et al., 1988, for a discussion of the species' disputed occurrence in Sulawesi and Peleng Island.) The adult male has a forearm length of 138.3, a gsl of 68.8, and large testes; the immature but nearly adult female has a forearm length of 129.5, a gsl of 59.4 and a weight of 267.

ECTOPARASITES. - The specimen from Ngele Ngele Besar yielded one specimen of the nycteribiid fly *Eucampsipoda inermis* Theodor, 1955.

#### *PTEROPUS MELANOPOGON* GROUP

***Pteropus melanopogon*** Peters, 1867

##### MATERIAL

INDONESIA: ZMA 16.368, 1 female, skin, skull, Wa'tra, near Leksula (03°46'S 126°35'E), Buru, 3-III-1921, L. J. Toxopeus.

what Andersen (1912) called braincase deflection (and entailing, among other things, a decrease in relative postorbital width), is not a process taking place in adults, but in maturing individuals. Strong braincase deflection is generally a juvenile condition, which in some species and to some degree may persist as a neotene character in adult life, and the measure of this deflection in adults depends on the species involved (see also Bergmans, 1977 and 1994: 81). The measure of skull bone fusion provides a good indication of the growth stage of the skull involved. When all sutures are fused and have become invisible, in which process the basi-cranial sutures most usually are the last ones to close, one can safely assume that the skull is full-grown and that its growth had stopped at the time of collection. Skull parts which may continue to grow after this stage has been achieved are the sagittal and occipital crests, and possibly other comparable features, but these do not change the essential form of the skull as such. This late growth of the occipital crest (which is also not continuous) may contribute to the greatest skull length, but it does not grow forever either. To avoid the effect of occipital crest growth on greatest skull length, many authors prefer the condylobasal length as a measure of skull size.

REMARKS. - The specimen has a forearm length of about 213, and a gsl of over 78.8. The type locality of this species is Ambon, and it has further been recorded from Banda, Goram (also spelled Gorom = Gorong), Buru, Seram (as Ceram), Boano, Saparua, Manawoka (as Manavolka), Siao, Timor Laut (= Tanimbar), and Taäm. Bergmans et al. (1988) re-identified the material from Siao reported as *P. melanopogon* by Jentink (1888) and Laurie et al. (1954) as *Pteropus hypomelanus* Temminck, 1853.

DISCUSSION. - Flannery (1995a) questioned the localities Boano, Saparua and Manowoka. They were first mentioned by Peters (1868), who did not indicate the material on which this was based. Peters' basis was the Zoologisches Museum in Berlin, but he certainly visited and examined other collections. In the Berlin museum, Andersen (1912) found only one specimen, the type from Ambon, but he stated to have examined a specimen from Saparua in the RMNH. Even if we cannot trace Peters' material from Boano and Manowoka today, these localities are very probable for the species, and should not be doubted without reasons.

Andersen (1912) pointed out that *Pteropus aruensis* Peters, 1868 and *Pteropus keyensis* Peters, 1868, both described by Peters as 'varieties' of *melanopogon*, were related species, but Peters and Andersen also described in what characters they differed. Laurie et al. (1954) listed both *aruensis* and *keyensis* as subspecies of *melanopogon*, and although they did not give any reason for doing so, they were followed in this by all later authors. The two were originally differentiated on the basis of fur colours (Peters, 1868). Another apparent difference between the mentioned forms is in size. One would expect a further analysis of these and possible other differential characters, but what strikes one when going through the post-Andersen literature on the species, is the lack of any analysis at all, and the very small number of measurements or other characters that have been published. And indeed, very few specimens seem to have been collected and studied since Andersen wrote his account (1912). For example, Koopman (1994) mentioned as forearm length range in *Pteropus melanopogon* sensu lato 179-204. This has been compiled sole-

ly from what Andersen published in 1912: 196-204 for three specimens of *melanopogon* (from three different islands and of unknown sex but for one female), 190-191 for one male and a specimen of unknown sex of *aruensis*, and 179-187.5 for two males and two specimens of unknown sex of *keyensis*. Only Flannery (1995a) mentions new specimens, a male *keyensis* from Taäm, in the Key group, with a forearm of 175, and a female *melanopogon* from Buru, with a forearm length of 193.

Synonymizing taxa without other than implicit arguments, in this case on the one hand Andersen's remarks (1912) on the relationship of these forms, and on the other an apparent wish to simplify taxonomy by recognizing lower numbers of taxa, is not a commendable procedure. If anything, it unnecessarily burdens the literature with unfounded or insufficiently founded and therefore as such unacceptable taxonomic propositions which nevertheless have to be taken into account by later students. For this reason, and for as long as a new analysis of existing and new material has not shown otherwise, the present author does not follow Laurie et al. (1954) and considers *P. melanopogon* as a monotypic species, and *P. aruensis* and *P. keyensis* as independent species. It is interesting to note that no author after Andersen (1912) has examined the material from Tanimbar in the museum in London, and that we do not know where this would fit in.

Finally, Flannery (1995a) dwells extensively on the whereabouts of Wonambay, one of the localities where the type or type series originated, which he quotes from Laurie et al. (1954) and which he hesitatingly identifies with the modern Manumbai Sungai. Strien (1996), writing on the mammals of the Aru Islands, presented a map indicating mammal collectors, journeys and locations, including Wanumbai (one of the several spellings of this name).

#### *PTEROPUS RAYNERI* GROUP

##### ***Pteropus chrysoproctus* Temminck, 1837**

###### Material

INDONESIA: ZMA 3092, 1 imm. (female?), skin, skull, Tifu (03°41'S 126° 24'E), Buru, 1922, leg. L. J. Toxopeus; ZMA 16.369/70, 1 male, 1 female, skins, skulls, Buru, 1921-1922, leg. L. J. Toxopeus.

REMARKS. - The male of these two has a forearm length of 166 and a gsl of 73.6, the female a forearm length of 170 and a gsl of 76.5. This is within the known dimensional ranges.

DISCUSSION. - The specimen from Tifu was sent alive to *Natura Artis Magistra*, the zoological garden of Amsterdam, where it died on 13-X-1922. As it is subadult, it has probably been collected and sent earlier in 1922. The labels of the other two specimens bear no other information than "Toxopeus, Buru" and unfortunately more precise data could not be derived from Toxopeus' itinerary of his expedition (Toxopeus, cf. 1924) nor from Dammerman's report (1929) on another part of Toxopeus' mammal material.

#### *PTEROPUS TEMMINCKII* GROUP

***Pteropus temminckii temminckii*** Peters, 1867

##### MATERIAL

INDONESIA: ZMA 3084, 1 female, alc., skull, Ambon (03°41'S 128°01'E), 1913, leg. Willemsz Geeroms.

REMARKS. - This specimen first entered the collection of the Colonial Institute (now Royal Institute for the Tropics) in Amsterdam, and was deposited in the ZMA in the 1930s. It has a forearm length of 100.6 and a gsl of 50.4. Dr H. Felten identified the specimen as a representative of the typical form.

***Pteropus temminckii liops*** Thomas, 1910

##### MATERIAL

INDONESIA: ZMA 3080, 1 female, skin, skull, Buru (03°27'S 126°40'E), 1921-1922, leg. L. J. Toxopeus.

REMARKS - Mr. Toxopeus sent this specimen first to the zoological garden in Amsterdam, *Natura Artis Magistra*, where it died on 15-VIII-1922. As it is immature, with a forearm length of 92.6 and a gsl of 44.9, it can be assumed to have been sent at most some months earlier in 1922. Dr H. Felten identified the specimen as *Pteropus temminckii liops*.

Dammerman (1929) reported on another female of this species, as *Pteropus liops*, sent by

Toxopeus from Buru to the same zoo, where it died on 10-VI-1923. This animal has a forearm length of 105 and a gsl of 52 (Dammerman, 1929). It bears number 2155 but its precise collecting locality is apparently unknown. It probably is in the MZBI.

***Pteropus personatus*** Temminck, 1825

##### MATERIAL

INDONESIA: Photographs of a female with a juvenile clinging to her, caught and released at Ngele Ngele Besar (2°11'20"N 128°12'20"E), 16-XI-1980, by H. Moll; ZMA 22.107, 1 male, alc., Bataka (01°24'N 127°30'E), northwest Halmahera, 27-III-1983, leg. F. G. Rozendaal, # 179.

REMARKS. - The photos of the specimen from Ngele Ngele Besar, an island off Halmahera, made by the late Dr H. Moll, are very distinct and leave no doubt as to the identity of the species. Ngele Ngele Besar is a new locality record for the species. Flannery (1995a) reported lactating and pregnant females on Ternate Island in January. The juvenile in the photo is quite large. Some field measurements of the male from Bataka are: forearm length 97.8, E 23, and W 131. This specimen was caught in the daytime from a roost in a papaw tree plantation.

DISCUSSION. - Bergmans et al. (1988) pointed out that the alleged occurrence of this species in Sulawesi is based on two specimens of uncertain provenance. They proposed to reject these records as prove that the species was found on that island. Following this, Mickleburgh et al. (1992) added a question mark to its occurrence there; its presence in the Dumoga Bone National Park in North Sulawesi as recorded by the same authors must therefore be based on an error.

#### *PTEROPUS VAMPIRUS* GROUP

***Pteropus vampyrus vampyrus*** Linnaeus, 1758

##### MATERIAL

INDONESIA: ZMA 19.354, 1 female, found dead, wing, foot and skull in collection, at edge of Krakatau, Krakatau Island, 29-VII-1977, leg. J. Regout and donated by P. J. van Nieuwenhoven; ZMA 21.637, 1 male, alc., Botanical Garden, Bogor (06°34'S 106°45'E), 30-XII-1981, leg. W. Bergmans.

REMARKS. - Unfortunately, it has not been documented on which of the four parts of the former Krakatau Island the remains of the female have been found. The skull is broken; the forearm length is 182.8, E 36, and HF 55.

DISCUSSION. - Thornton et al. (1988) reported on an observation of this species on Anak Krakatau in 1986, which they considered a stray individual. However, in 1985 Tidemann et al. (1990) observed a camp of about 250 individuals on Sertung. The present specimen precedes these finds with eight years. Together, these occurrences suggest that the species may have flown out to Krakatau earlier in the island's recent history, and more often, and may have been of more importance as disperser of seeds to the island(s) than the known record would suggest.<sup>2</sup>

The specimen from the Botanical Garden at Bogor, home to a well-known protected colony of this species, had just been shot by two guards in the very early morning, when the author stumbled upon them; forearm length about 213, E 44, W 855. This is proof that the species is hunted for food in Java, while another apparent threat to this subspecies is the very advanced deforestation in Java. As such, neither of these threats to this species appears to have been documented before (see Mickleburgh et al., 1992).

#### *PTEROPUS ALECTO* GROUP

#### ***Pteropus alecto*** Temminck, 1837

##### MATERIAL

INDONESIA: ZMA 23.081, 1 male, alc., bought at market at Imandi (00°35'N 124°04'E), North Sulawesi, 1985, leg. R. W. R. J. Dekker.

REMARKS. - This specimen has a forearm length of 169.7, which adds nothing to the known general range but supports the observation by Bergmans et al. (1988) that specimens from North Sulawesi may be smaller, on average, than specimens from south-west Sulawesi.

DISCUSSION. - The provenance of this and other specimens would suggest that in the region of Imandi fruit bat species are frequently trapped for consumption. However, in a recent book on his experiences in Sulawesi and other islands, Argeloo (2001) reports on fruit bat hunting in western Minahassa for the market in Manado. According to his observations, no huntable quantities of fruit bats remain between Manado and Marisa (at 121°56'E on the south coast of Minahassa), which would suggest that at present the provenance of fruit bats in the Imandi market is also "west of Marisa, northern Sulawesi". It furthermore implies a bleak future for the North Sulawesi endemic fruit bat *Rousettus bidens* (Jentink, 1879), which is extra vulnerable because it lives in large colonies in caves, the north Sulawesi populations of the rare *Neopteryx frosti* Hayman, 1946, and other Sulawesi endemics.

#### *PTEROPUS CONSPICILLATUS* GROUP

#### ***Pteropus conspicillatus chrysauchen***

Peters, 1862

##### MATERIAL

INDONESIA: ZMA 22.133, 1 imm. female, alc., skull, Bataka (01°24'N 127°30'E), northwest Halmahera, 27-III-1983, leg. F. G. Rozendaal, mistnetted in secondary growth in coconut plantation; ZMA 22.135, 1 imm. female, alc., 16-V-1983, island near Labuha (00°35'S 127°28'E), Bacan, leg. F. G. Rozendaal.

<sup>2</sup>) In this connection, another aspect of bats as seed dispersers should also be mentioned. Whittaker & Jones (1994), writing on the role of fruit bats in the rebuilding of the forest ecosystem on Krakatau, and some authors before them, appear to take for granted that seeds are dispersed by fruit bats over larger distances only after incidental ingestion of small seeds at one place and their subsequent defecation or oral ejection at another. Food does not stay long in the intestinal tract (between 15 and 70 minutes, as Whittaker et al. quote), which effectively restricts the success of seed dispersion in this way. However, on more than one occasion the present author has trapped fruit bats with small seeds sticking to their fur, most probably by means of the sugary juice of the fruits involved. This naturally comes about while eating and the seeds will normally probably stay on till the bats arrive back at their day roost, where extensive grooming will end the seeds' voyage. But it is not impossible, and in fact quite likely, that bats carry seeds in this way from one feeding place to another, and that they may incidentally lose these seeds wherever they fly or alight.

REMARKS. - The present specimen from Halmahera has a forearm length of 148.7 (field measurement: 151), a gsl of 66.7, and a weight of 420. Its skull base and rostral sutures are distinct and the specimen is obviously immature. On the other hand, its skull is nearly full-grown, and its finger joints as well. The other specimen is a suckling, with its milk dentition still in place and its permanent canines just breaking through, and a forearm length of 99.3.

DISCUSSION. - Although known since long from the surrounding islands of Bacan, Morotai, Obi, Ternate (Andersen, 1912) and more recently also from Gebe (Corbet et al., 1992), this species has been recorded for the principal island of the group, Halmahera, only by Peterson et al. in 1990. The island off Labuha, Bacan is a new locality. It is clear that the forearm length range for *P. conspicillatus* in the Moluccas given as 175-185 by Corbet et al. (1992), who based this on data provided by Andersen (1912), is incomplete and in need of modification. The present author assumes that in this species males grow larger than females, with possible forearm length ranges of about 155-174 in females and 163-185 in males. The ear in the specimen from Halmahera is 29 in length (field measurement: 32) and rather pointed, with an incurvation in the posterior margin, just under the tip. In this respect also, the *Pteropus* group table in Corbet et al. (1992: 57) needs modification.

ECTOPARASITES. - The specimen from Bataka was infested with the nycteribiid fly *Cyclopodia albertisii* Rondani, 1878, and possibly also with *Archinycteribia actena* Speiser, 1901, of which one specimen was found in the bat's container.

#### *PTEROPUS SCAPULATUS* GROUP

##### ***Pteropus woodfordi*** Thomas, 1888

###### MATERIAL

SOLOMON ISLANDS: ZMA 11.251, 1 male, alc., near Belaga, Small (or Little) Gela (09°10'S 160°20'E), Nggela Group, VII-1966/IX-1967, leg. M. J. A. de Koster.

REMARKS. - The specimen is a young adult and with a forearm length of 93.2 and a gsl of 42.7 it

falls within the known size range for the species.

##### ***Pteropus vetulus*** Jouan, 1863

###### MATERIAL

NEW CALEDONIA: ZMA 19.311, 1 male, alc., Blue River Reserve (now the Provincial Blue River Park; 22°04'/22°10'S 166°36'/166°41'E), 3-IX-1967, leg. H. L. Bregulla.

REMARKS. - The specimen has a forearm length of 103.8 and a W of 155. Felten (1964) gave a forearm length range of 100-114 (mean 106) for 14 specimens, including the type, but did not distinguish the sexes; he gave no data on weights. Flannery (1995a) gave as forearm length range for three males 92.3-100.8 and as weights 120-142.

##### ***Styloctenium wallacei*** (Gray, 1866)

###### MATERIAL

INDONESIA: ZMA 24.256, 1 male, alc., bought at market, Imandi (00°35'N 124°04'E), North Sulawesi, leg. M. Argeloo, 9-I-1991; ZMA 24.444/46, 3 males, same data, 10-II-1992; ZMA 24.913/15, 2 males, 1 female, same data, 6-VII-1994.

REMARKS. - These specimens were presented to the ZMA after the publication of the report on Sulawesi fruit bats (Bergmans et al., 1988). The males have forearm lengths of 92.0, 92.6, 94.0, 99.8, 99.9 and 103.2, respectively. The first three are below the known range of 95.5-103.2 (Bergmans et al., 1988: 30). The female has a forearm length of 98.0 which falls within the known range.

DISCUSSION. - On the provenance of bats from the Imandi market see under *Pteropus alecto*.

##### ***Neopteryx frosti*** Hayman, 1946

###### MATERIAL

INDONESIA: ZMA 24.258, 24.406, 2 females, alc., bought at the market of Imandi (00°35'N 124°04'E), North Sulawesi, 21-I- and 29-V-1991, respectively, by M. Argeloo; ZMA 24.448, 1 imm. male, alc., same provenance, 10-II-1992, leg. M. Argeloo.

REMARKS. - *Neopteryx frosti* is very rare in collections, the present specimens being the 5th to 7th

of this species on record (Bergmans et al., 1988). One female has a forearm length of 106.5, the other one of 111.0, which enlarges the known variation range in females from 110-110.6 to 106.5-111.0. The immature male has a forearm length of 98.1.

**BIOLOGY.** - The two females were pregnant. The one bought on 21 January, forearm length 106.5, had an embryo with a greatest length of 21, and the one bought on 29 May, forearm length 111.0, had an embryo with a greatest length of 48.5.

**DISCUSSION.** - On the provenance of bats from the Imandi market see under *Pteropus alecto*.

#### *MACROGLOSSUS* CUVIER, 1824

Hill (1983) revised the taxonomy of *Macroglossus*, and retained two species: the small *M. minimus* (Geoffroy, 1810) and the somewhat larger *M. sobrinus* Andersen, 1911, each with several subspecies. The taxonomy and distribution of this genus were further amended in Corbet et al. (1992).

In *M. minimus*, five subspecies were retained by Hill in 1983: *minimus*; *lagochilus* Matschie, 1899; *nanus* Matschie, 1899; *pygmaeus* Andersen, 1911; and *microtus* Andersen, 1911 - with both *pygmaeus* and *microtus* admittedly possible synonyms of *nanus*, as McKean (1972) had suggested. In 1992, Corbet et al. retained three subspecies only: *lagochilus*, *minimus* and *nanus*, and suggested moreover that *lagochilus* and *minimus* are hardly distinct and may prove synonymous. Of these subspecies, *minimus* is found in Java, Madura, Bali, Kangean Islands and Lombok (see for Lombok: Mickleburgh et al., 1992); *nanus* (including *pygmaeus* and *microtus*) is found in New Guinea and surrounding islands, Queensland, Murray Island in the Torres Strait, Bougainville, and Solomon Islands; and *lagochilus* would inhabit Buru (the type locality) and other Molucca Islands, but also Indochina (Thailand, Vietnam), Nias (listed but not mapped by Corbet et al., 1992), Sri Buat Island, Sirhassen Island; Bunguran Island, Borneo, Philippines; Sulawesi; Peleng; Sanghir Islands, Timor (see Hill, 1983: 135).

For *M. sobrinus*, the picture is more simple: the typical subspecies is found in northeast India

(Bhutan? See the map in Corbet et al., 1992), Burma, Central and South Thailand, southern Laos and Vietnam, Cambodia, Peninsular Malaysia, Sumatra, Java and Bali; specimens from Bali are smaller in some respects than those from Java (Kitchener & Foley, 1985). A second subspecies, *fraternus* Chasen & Kloss, 1927 inhabits Sipora, Siberut and Mentawai Islands.

For the present paper, Hill (1983) and Corbet et al. (1992) have been followed.

#### **Macroglossus minimus minimus**

(Geoffroy, 1810)

##### **MATERIAL**

INDONESIA: ZMA 16.706a, 1 male, alc., skull, Jakarta (06°08'S 106°45'E), Java, 1908, leg. P. N. van Kampen.

**REMARKS.** - The skull of this specimen is damaged, its occiput being broken into several pieces. Its gsl is probably not much more than 26.4 (and its cbl between 1 and 1.5 shorter). Some other measurements are: distance from orbit to nare 8.75, C<sup>1</sup>-M<sup>2</sup> 8.3, and C<sub>1</sub>-M<sub>3</sub> 10.0. The fused sutures of the skull base and the large, descended testes prove the specimen to be adult. Its forearm length is 41.3. The internarial groove is linear, weak, and does not run down to the lip margin. The dimensions suggest that the specimen represents the species *minimus*, the internarial groove would be atypical (Hill, 1983), but see also Kitchener et al. (1985), who describe specimens from Bali combining characters of both *minimus* and *M. sobrinus*.

**DISCUSSION.** - Another adult male from Jakarta (ZMA 21.621) has been identified as *M. sobrinus*; it has a forearm length of 46.0. So have two females from Jakarta (ZMA 21.624, 21.626) with forearm lengths of 45.5 and 47.2, respectively. The internarial grooves of these specimens are linear and weak, and they do not reach the lip margin. This appears to be the first instance of actual sympatry (although Jakarta still covers a huge area) of *minimus* and *sobrinus* in Java.

#### **Macroglossus minimus lagochilus**

Matschie, 1899

##### **MATERIAL**

INDONESIA: ZMA 16.705, 1 male, alc., Gunung Sitoli

(01°16'N 97°34'E), Nias Island, 1910, leg. J. P. Kleiweg de Zwaan; ZMA 22.114/21, 6 males, 2 females, alc., Telaga-Gamkunora (or Gamkunoro: 01°30'N 127°32'E), northwest Halmahera, 3/4-III-1983, leg. F. G. Rozendaal; ZMA 22.122, 1 male, alc., lower slopes of Sibela range (00°4'S 127°35'E), northeast of Ngame, northwest of Wayaua, Bacan (127°30'E 00°35'S), 9-V-1983, leg. F. G. Rozendaal.

REMARKS. - The specimen from Nias has a forearm length of 39.7. Six males from Halmahera and Bacan have forearm lengths of 37.3 to 39.0 (mean 38.3), the two females of 37.5 and 39.0, suggesting that the populations from the northern Moluccas are relatively small. Their identification as *lagochilus* is given here with reservation, *nanus* being the alternative.

**Macroglossus minimus nanus** Matschie, 1899

MATERIAL

INDONESIA: ZMA 2695, 1 male, spirit, Jayapura (02°37'S 140°39'E), West Papua, 15-II-1956, leg. F. Hoekzema; ZMA 2694, 1 specimen, sex unknown, alc., Jayapura, West Papua, 25-VII-1957, leg. F. Hoekzema; ZMA 2307, 1 male, skin, skull in situ, Jamas village (ca. 05°17'S 138°04'E), Asmat area, West Papua, 8-VII-1958, leg. W. R. van Mourik; ZMA 24.948/52, 2 males, 3 females, alc., Jirlai village (ca. 06°01'S 134°2'E), Kobroor Island, Aru Islands, IV-1993, leg. M. van der Wal; ZMA 24.954/57, 4 males, alc., Baun Island (06°30'S 134°40'E), Aru Islands, 21-IV-1993, leg. M. van der Wal; ZMA 25.429, 1 male, alc., 200 m from Rumei River, ca. 10 km E of Urbinasopen village (Urbinasopen; 00°22'S 131°13'E) and ca. 7 km upstream, alt. 200-250 m, southeast Waigeo, West Papua, 13-III-1993, leg. M. Argeloo.

REMARKS. - The specimens from the Aru Islands have forearm lengths of 38.3-40.3 (mean 39.1) in four males and 38.3, 39.4 and 41.0 in three females. The male from Waigeo has a forearm length of 41.3 and a weight of 17 g. It presents the first record for that island. The male from Jayapura has a forearm length of 40.2. The specimen from Jamas was found dead in a house after it had flown into it. Jamas lies inland from the mangrove zone. The forest consists of broadleaf trees and *Pandanus* and sago palms.

**Macroglossus sobrinus sobrinus** Andersen, 1911

MATERIAL

INDONESIA: ZMA 2047, 1 imm. female, skin, skull, Bogor (06°34'S 106°45'E), Java, 23-VI-1948, leg. T. van Bemmelen;

ZMA 16.702, 1 male, alc., Sumanik, near Singkarak (or Singkarak: 00°41'S 100°38'E), Sumatra, 1888, leg. M. Weber; ZMA 16.703/04, 2 females, alc., (probably Sumanik), Sumatra, probably 1888, leg. M. Weber; ZMA 16.706b/07, 1 female, 1 imm. female, alc., Salatiga (07°15'S 110°34'E), Java, before 1923, leg. D. de Lange; ZMA 21.621/26, 3 males, 3 females, alc., Pancoran, Jakarta (06°08'S 106°45'E), Java, 22- and 23-XII-1981, leg. W. Bergmans; ZMA 21.627/30, 1 male, 3 females, alc., Bogor, Java, 24/29-XII-1981, leg. W. Bergmans; ZMA 21.888/89, 1 male, 1 female, alc., near Parapat (02°43'N 98°58'E), Sumatra, 21/22-X-1982, leg. P. J. H. van Bree; ZMA 21.890, 1 female, alc., base camp Gunung Leuser National Park, at river Alas, opposite Ketambe (03°41'N 97°38'E), Sumatra, 25/26-X-1982, leg. P. J. H. van Bree; ZMA 22.500/04, 2 males, 3 females, alc., Ubud (08°30'S 115°18'E), Bali, 2/10-II-1985, leg. P. J. H. van Bree; ZMA 23.866/67, 1 male, 1 female, Banjar Alum, Gilimanuk (08°12'S 114°27'E), Bali, 27-IV- and XI-1988, respectively, leg. B. E. van Helvoort.

REMARKS. - Forearm lengths and known weights (between brackets) of the adults among the present specimens are as follows. Sumatra: two males 46.8-48.8, four females 44.2-48.8; Java: two males 46.0-47.1 (W 22.5-23), six females 44.8-47.2 (W of 5 19-22,5); Bali: four males 44.7-48.0, three females 44.3-48.1.

DISCUSSION. - The specimens from Bali show all sorts of variation in depth and length of the internarial groove. In four of the seven specimens the groove runs to the lip margin, which would be a character of *minimus* (Corbet et al., 1992), in the others it does not. The same variation has already been noted by Kitchener et al. (1985), who also allocated their Bali specimens to *M. sobrinus* rather than *minimus*.

ECTOPARASITES. - Specimens ZMA 21.621 and 21.629, from Jakarta and Bogor, respectively, each carried a nycteribiid fly, *Cyclopodia (Cyclopodia) tenuis* Schuurmans Stekhoven & Hardenberg, 1938.

**Syconycteris australis papuana** (Matschie, 1899)

MATERIAL

INDONESIA: ZMA 24.953, 1 female, alc., Jirlai village (ca. 06°01'S 134°29'E), Kobroor Island, Aru Islands, IV-1993, leg. M. van der Wal, mistnetted at 19.00 pm, near papaya trees; ZMA 24.958/59, 1 male, 1 female, alc., Baun Island

(06°30'S 134°40'E), Aru Islands, 21-IV-1993, leg. M. van der Wal, mistnetted in graveyard at edge of mangrove/secondary forest; ZMA 25.430/32, 1 male, 2 females, alc., at 200 m from Rumei River, ca. 10 km E of Urbinasopen village (or Urbinasopon, 00°22'S 131°13'E) and ca. 7 km upstream, southeast Waigeo, West Papua, alt. 200-250 m, 13-X-1993, leg. M. Argeloo.

REMARKS. - The male specimen of the Aru Islands has a forearm length of 42.8 and large testes, the females have forearm lengths of 40.1 and 42.1, respectively, and appear to have been lactating at the time of capture. The male from Waigeo has a fal of 45.0, a weight of 18.5, and somewhat developed testes, and the females have forearms of 44.7 and 44.4 and weights of 17 and 18.5, respectively, while specimen ZMA 25.431 had large nipples and was probably lactating.

DISCUSSION. - The specimens from the Aru Islands fit the forearm length range given by Kitchener et al. (1994) for specimens from these islands in their study on the morphological variation of moluccan *Syconycteris australis*. According to these authors, they would be morphologically intermediate between specimens from the Kai Islands (forearm length range 39.6-43.9 in 30 specimens) and from Papua New Guinea (40.3-46.8 in 36 specimens; overlapping with their few data from West Papua: 40.6-42.3 in three specimens), which questions their subspecific distinctness. The specimens from Waigeo appear to be of the same general overall size as those on New Guinea sensu lato. They are the first records from that island. (Hill, 1983, mentioned a specimen from Wageo Island; this is one of the Schouten Islands in Papua New Guinea. Its name is also spelled Vokeo.)

***Syconycteris australis major*** Andersen, 1911

MATERIAL

INDONESIA: ZMA 3086, 1 male, alc., skull, Ambon (03°41'S 128°01'E), 1913, leg. Willemsz Geerrooms; ZMA 1504, 1 imm. female, alc., skull, Ambon, before XII-1930, leg. Willemsz Geerrooms; ZMA 21.455, 1 male, alc., Bka (most probably the same as Poka, at ca. 03°37'S 128°10'E), Inner Bay, Ambon, 25-XI-1980, leg. H. Moll.

REMARKS. - The male specimens have forearm lengths of 47.0 and 48.4, respectively. Specimen

ZMA 3086 has a gsl of at least 28.5.

DISCUSSION. - *Syconycteris* from Ambon and Seram was described - then as *S. crassa major* - by Andersen on the basis of its large size. Kitchener et al. (1994) found that *major* is quite distinct morphologically from *S. australis papuanus* from the Kai Islands, Aru Islands, and New Guinea, and may even be specifically distinct. According to these authors, the answer to this will depend on future genetic studies. The available measurements of the present specimens fit the ranges given by Kitchener et al. (1994) for Ambon. The male caught 25 November has large, descended testes and may well have been sexually active at the time of capture.

***Melonycteris woodfordi aurantius*** Phillips, 1966

MATERIAL

SOLOMON ISLANDS: ZMA 11.252, 1 imm. male, alc., skull, near village Belaga, Small (or Little) Nggela (09°10'S 160°20'E), Nggela Group, VII-1966/IX-1967, leg. M. J. A. de Koster.

REMARKS. - The specimen has a fal of 56.4 and a gsl of 33.5, and is nearly full-grown.

DISCUSSION. - Flannery (1993) revised the genus *Melonycteris* and his conclusions are followed here. Like several authors before him, he considered *Nesonycteris* Thomas, 1887, proposed to accommodate *Nesonycteris woodfordi* Thomas, 1887, a synonym of *Melonycteris* Dobson, 1877. Flannery furthermore treated *Melonycteris aurantius* Phillips, 1966 as a subspecies of *M. woodfordi*, differing from the typical form in being significantly larger, and the sole representative of the genus in the Nggela and Florida Islands, Nggela Group, Solomon Islands. Males in *aurantius* were found to be smaller than females. The measurements of the present specimen are generally just below, but some are somewhat above the measurement ranges as given by Flannery (1993: 78) for four males (and given between brackets): fal 56.4 (57.7-61.1), cbl 30.1 (30.3-32.3), zygomatic width 19.5 (20.0-21.7), postorbital width 8.25 (6.7-7.4), upper teeth row length 11.5 (10.6-11.1), width over M<sup>1</sup>-M<sup>1</sup> 8.6 (8.4-8.9), and C<sup>1</sup> length 4.3 (3.6-

4.5). The postorbital width may be large because the animal is immature. The upper teeth row length, measured over the cingulae just as in Flannery (1993: 77), is large. The term canine 'length', taken from Flannery (1993), may be confusing, as it does not refer to the distance between the tooth's anterior and posterior sides but to its height.

#### SUBFAMILY NYCTIMENINAE Miller, 1907

This subfamily is well-established as a unity but its taxonomic level as such is not. Miller (1907) proposed subfamily status, but Andersen (1912) considered it to represent a lineage within his *Cynopterus* section or group, and many authors have followed the latter author. Koopman & Jones (1970) left it within the Cynopterinae but separated it, as a subtribe, from the other genera. The present author agrees with Miller that it should stand as an independent unity, on subfamily level (see Bergmans, 1997: 64-69). Two genera have been described: *Nyctimene* Borkhausen, 1797 and *Paranyctimene* Tate, 1942.

*Vespertilio cephalotes* Pallas, 1767 is the type species of *Nyctimene* Borkhausen, 1797. The type specimen of this species has been lost and there has been doubt about its true identity, i.e., of what is presently called *Nyctimene cephalotes*, but Heaney & Peterson (1984) showed that Pallas' description offered sufficient morphological clues to conclude that the two are indeed identical. The most recent revision of the genus is by Andersen (1912). Some generic characters are: rostrum high (dorso-ventrally), premaxillae ankylosed together in front, mesopterygoid fossa broad and deep, postdental palate constricted in the middle, two upper and no lower incisors, lower canines at anterior extremity of jaw and quite or nearly in contact, four upper and five lower cheek teeth, tongue with four circumvallate papillae, inner lips fringed with odontoid papillae, nostrils projecting as cylindrical tubes, wings more or less spotted with yellow (after Andersen, 1912). Andersen (1912) recognized 11 species of *Nyctimene*, which he divided into four groups. Five of these species are presently considered synonyms, and 10 new species have been described since, plus the closely related genus *Paranyctimene* Tate, 1942, based on a new species. Koopman

gave the most recent survey of recognized species and synonyms of both genera (in: Wilson et al., 1993). In the same year, Kitchener (in: Kitchener et al., 1993) described a new subspecies which he later elevated to species rank (Kitchener, in: Kitchener et al., 1995). Some of the species described since Andersen (1912) are disputed, e.g., *Nyctimene masalai* Smith & Hood, 1983 is not recognized by Flannery & White (1991) and apparently included in *N. vizzaccia* Thomas, 1914 by Bonaccorso (1998). For the time being, Andersen's four species groups may still be recognized as useful supraspecific divisions and in this paper species are treated accordingly. A fifth group, based on *Paranyctimene raptor* Tate, 1942 is added. At present the five groups contain the following 19 species (those marked with an \* are considered either doubtful, or subspecies or synonyms of other species by some recent authors):

1) *Nyctimene albiventer* group. Andersen called this the *papuanus* group. However, as *N. albiventer* is the oldest species name in the group, and *papuanus* is presently considered a subspecies of *albiventer* (Kitchener et al., 1993, 1995) it is proposed to rename this group accordingly. Andersen (1912) distinguished it as follows: size small, forearm length 50-59; ears unmodified (i.e., not unusually broad and rounded off above); dorsal stripe narrow, generally well-marked, sometimes obsolete anteriorly; males, so far as known, similar in colour to females but with fore-neck and flanks richer in colour; upper teeth row 8.7-10.3; first upper molar subequal in size to fourth upper premolar. The group contains: *Nyctimene albiventer* (Gray, 1863); *N. minutus* Andersen, 1910; \**N. vizzaccia* Thomas, 1914; \**N. draconilla* Thomas, 1922; \**N. bougainville* Throughton, 1936; \**N. malaitensis* Phillips, 1968; \**N. masalai* Smith & Hood, 1983.

2) *Nyctimene cephalotes* group. Andersen (1912) mentioned the following distinguishing characters: size medium to large, forearm length 60.5-85.5; ears unmodified; dorsal stripe narrow, generally well-marked, sometimes obsolete anteriorly; females much paler above and below than males (possibly not so in *N. robinsoni*); upper teeth row 10.7-14.2. The group contains: *N. cephalotes* (Pallas, 1767); *N. major* (Dobson, 1877); *N. robinsoni* Thomas, 1904; *N. santacrucis* Throughton, 1931; \**N. rabori* Heaney & Peterson, 1984; *N. keasti*

Kitchener, 1995.

3) *Nyctimene aello* group. Andersen (1912) distinguished it by its very broad dorsal stripe (i.e., up to about 12 wide on the centre of the back). The group contains: *N. aello* (Thomas, 1900); \**N. celaeno* Thomas, 1922.

4) *Nyctimene cyclotis* group. This group was distinguished by Andersen (1912) by: size small, forearm 50-59; ears modified: unusually broad, semi circularly rounded off above; dorsal stripe narrow, generally well-marked, sometimes obsolete anteriorly; colour of back mottled with darker tips to the hairs; males, so far as known, similar in colour to females, but with foreneck and flanks much richer in colour; upper teeth row 8.7-10.3; first upper molar noticeably smaller than fourth upper premolar. The group contains: *Nyctimene cyclotis* Andersen, 1910; \**Nyctimene certans* Andersen, 1912.

5) For the fifth group, formed by *Paranyctimene*, see below.

#### PARANYCTIMENE TATE, 1942A

*Paranyctimene* was described by Tate (1942a) as a new genus of tube-nosed fruit bats from the present Papua New Guinea, based on a new species, *Paranyctimene raptor*. He discovered the species among collections of *Nyctimene albiventer papuanus* Andersen, 1910 and *N. celaeno* Thomas, 1922 because it was smaller than these and lacked a dorsal stripe. Examination of the dentition led Tate to segregate the bat generically. He distinguished his new genus, as *Paranyctimene*, from the only other genus of Nyctimeninae, *Nyctimene*, by "the extreme height and slenderness of the upper and lower canines and premolars, by elongation of the postdental palate, and by the absence of the dorsal stripe." The type consisted of the skin and skull of a female specimen, collected by Tate himself at Oroville Camp, Fly River (about 4 miles below the mouth of Elevala River; coordinates calculated by the present author: 141°07'E 06°13'S) on 11 August, 1936, and described in the same paper as *Paranyctimene raptor*, the specific epithet apparently referring to its fang-like canines. The description contained body, skull and teeth measurements.

Although *P. raptor* has been called a common species in primary and secondary forests, gardens

and swamps nearly all over Papua New Guinea (Bonaccorso, 1998), the precise content of the taxon has remained largely unknown, as very little has been published on its characters and their variation. The height and slenderness of canines and premolars and the elongation of the postdental palate are relative characters, and although Tate, when describing genus and species, obviously studied Andersen's account of the genus *Nyctimene* (1912) and compared the distinguishing characters identified by him with their equivalents in species from Papua New Guinea then present in the Archbold Collections (as it appears: only *N. albiventer papuanus* and *N. celaeno*) and with a photograph of the skull of *N. draconilla* Thomas, 1922, he did not give a comparative analysis, nor illustrations, to support the observations he described for *P. raptor*. In his description he referred to some other species as well: *N. cyclotis* Andersen, 1910 and *N. minutus* Andersen, 1910, but apparently he only knew these by Andersen's (1912) accounts. Later reports on *P. raptor* were published by McKean (1972), Greig-Smith (1975; as *N. draconilla*), Koopman (1982), Hill (1983), Flannery (1990, 1995a, 1995b), Leary et al. (1995), and Bonaccorso (1998). Most of these accounts include some body measurements and (or) weights, and Flannery (1990, 1995b) provided very useful skull photographs, but the skull and teeth dimensions of the type published by Tate (1942a) seem to have remained the only ones on record to date.

The material of *Paranyctimene* described in this paper has been compared with the species of *Nyctimene* in the ZMA and with some in the RMNH, and with illustrations of skulls and teeth of several others (Andersen, 1912; Phillips, 1968; Smith & Hood, 1983; Heaney & Peterson, 1984; Peterson, 1991; and Flannery, 1995a, 1995b), to assess the value of its generic characters as listed by Tate.

As a measure for the relative teeth dimensions of the species present in the ZMA collections, the height of the upper canine has been related to the cbl. The results are shown in Table 1.

In nearly all specimens examined the canines are somewhat worn or damaged at their tips, but it would nevertheless seem that, although the relative lengths in *Paranyctimene* are the largest, those

Table 1. Relative height of upper canine and relative lengths of palatum and postdental palatum in *Nyctimene* and *Paranyctimene* as measured by the author (in one case calculated from published measurements).

Species	Sex	Relative height of upper canine, as percentage of cbl	Relative palatal length, as percentage of cbl	Relative postdental palatal length, as percentage of cbl	Collection or source
<i>Nyctimene albiventer</i>	male	18.4* - 19.2* (n = 3)	44.8 - 48.6 (n = 4)	10.0 - 12.95 (n = 2)	RMNH/ZMA
	female	18.3* - 19.05 (n = 2)	47.0 - 49.2 (n = 3)	13.05 - 14.2 (n = 2)	RMNH/ZMA
<i>N. cf. albiventer</i>	female	16.0* - 16.7 (n = 2)	41.6 - 44.65 (n = 2)	8.1 - 9.85 (N = 2)	ZMA
<i>N. cephalotes</i>	male	18.2* (n = 1)	46.8 - 50.6 (n = 3)		RMNH/ZMB
	female	16.9* - 17.85 (n = 2)	48.6 - 51.8 (n = 3)		RMNH
<i>N. draconilla</i>	male		45.1 (n = 1)		Thomas, 1922b
<i>N. keasti keasti</i>	male		50.7 - 51.0 (n = 2)		RMNH
	female		50.0 - 51.2 (n = 2)		RMNH
<i>N. keasti babari</i>	male		50.5 (n = 1)		RMNH
<i>N. major</i>	female	16.7* (n = 1)	48.25 (n = 1)	13.0 (n = 1)	ZMA
<i>N. cf. vizcaccia</i>	male	19.3* (n = 1)	52.0 (n = 1)	16.2 (n = 1)	ZMA
<i>Paranyctimene</i>	male	19.8 - 22.8 (n = 5)	50.4 - 54.9 (n = 7)	15.3 - 17.8 (n = 7)	RMNH/ZMA
	female	20.7 - 21.2 (n = 3)	48.9 - 54.0 (n = 3)	16.9 - 18.7 (n = 3)	RMNH/ZMA

\* Measurements based on estimations

in some species of *Nyctimene* come very close - and probably overlap with the smallest *Paranyctimene*.

For the length of the palatum, measured from the prosthion to the middle of the caudal palate margin, and the length of the postdental palate, also measured in the median plane, expressed as percentages of the condylobasal length, see Table 1. The relative length of the postdental palate in *Paranyctimene*, i.e. 15.3-18.7% of the condylobasal length, is larger than that in the *Nyctimene* species examined (8.1-16.2%). It is of importance to note that in *Nyctimene albiventer* this relative length is larger in females than in males, implying that in comparisons the sexes should be treated separately. As is the case with the relative canine height, the difference in relative postdental palatal length between *Paranyctimene* and *Nyctimene* is not very spectacular. It appears that there may be mutual differences between *Nyctimene* species as well, and that *Paranyctimene* represents the one end of a variation range which includes species of both. Moreover, a larger material would no doubt yield

more overlap between the two.

Regarding the third distinguishing character of *Paranyctimene*, i.e., the absence of a dorsal stripe, it is interesting to note what has been published on this character for all Nyctimeninae described. The results of a search of the original literature are listed in Table 2. In conclusion, only two species (*Nyctimene aello* and *N. celaeno* - for the moment assuming that *celaeno* is a species) have very broad and conspicuous spinal bands of fur; eight species (most specimens of *albiventer*, and all specimens of *cephalotes*, *major*, *malaitensis*, *masalai*, *rabori* from Negros, *robinsoni*, *santacrucis*) have narrow spinal stripes; in seven species (some specimens of *albiventer* and all specimens of *bougainville*, *certans*, *cyclotis*, *draconilla*, *minutus*, *rabori* from Talaud) with a narrow stripe this is incomplete and/or indistinct; and in *Paranyctimene* it is absent. However, according to observations by the author, *Paranyctimene* has a very faint trace of a dorsal line at withers (see the species descriptions below).

Table 2. The state of the dark mid-dorsal stripe, or band of fur, in *Nyctimene* and *Paranyctimene* according to the literature.

Species	State of dorsal stripe (between brackets: source)
<i>Nyctimene aello</i>	very broad (Thomas, 1900)
<i>N. albiventer</i>	width about 1.5-2 mm, sometimes obsolete in anterior third of back (Andersen, 1912)
<i>N. bougainville</i>	rather short, being very poorly defined in the region of shoulders and foreback (Throughton, 1936)
<i>N. celaeno</i>	from between ears to root of the tail, broad (11-12 mm) along middle of back, strong, sharply defined (Thomas, 1922b)
<i>N. cephalotes</i>	sharply pronounced, about 3.5-5 mm broad (Andersen, 1912)
<i>N. certans</i>	narrow, somewhat ill-defined, dark, along posterior half of back (Andersen, 1912)
<i>N. cyclotis</i>	narrow dorsal stripe along posterior half of back (Andersen, 1910)
<i>N. draconilla</i>	just perceptible on the nape, posterior half narrow and well-defined (Thomas, 1922b)
<i>N. major</i>	narrow, well-defined (Andersen, 1912b); in <i>N. m. lullulae</i> restricted to lower part of back (Flannery, 1995b)
<i>N. malaitensis</i>	well-defined, black, from shoulders to rump (Phillips, 1968)
<i>N. masalai</i>	5 mm wide, from back of crown to base of tail (Smith & Hood, 1983)
<i>N. minutus</i>	very narrow, somewhat ill-defined, confined to posterior two-thirds of back (Andersen, 1910)
<i>N. rabori</i>	3-4 mm, dark brown, from shoulders to base of tail (Heaney & Peterson, 1984)
<i>N. robinsoni</i>	narrow, well-marked (Andersen, 1912)
<i>N. sanctacrucis</i>	definite, narrow, a shade of mummy-brown (Throughton, 19310)
<i>N. vizcaccia</i>	dorsal streak beginning at withers, rather well-marked (but not so much so as in <i>N. [albiventer] papuanus</i> ) (Thomas, 1914)
<i>Paranyctimene raptor</i>	absent (Tate, 1942b)

On the basis of the foregoing, it is proposed here that *Paranyctimene* is considered a subgenus of *Nyctimene*, within which it forms a fifth species group:

5) *Nyctimene raptor* group. This group is distinguished by the following characters: size small, forearm length 47-55 mm (58 in Bonaccorso, 1998); ears unmodified; dorsal stripe absent or nearly so (see below); males and females similar in colour; palate relatively long (so far as known: 48.9-54.9% of cbl, against 41.6-52.0% in other species groups); postdental palate relatively long (so far as known: 15.3-18.7% of cbl, against 8.1-

16.2% in other species groups); C<sup>1</sup>-M<sup>1</sup> 8.0-10.1; C<sup>1</sup> relatively high (as far as known: 19.8-22.8% of cbl, against 16.0-19.3% in other species groups) and slender; M<sup>1</sup> longer, of equal length or shorter than P<sup>4</sup>, often narrower, and always lower. The group contains: *Nyctimene raptor* (Tate, 1942); *Nyctimene* n. sp., described below.

During this study it appeared that the material of *Paranyctimene* in the ZMA and RMNH collections, limited as it was and all provisionally identified as *P. raptor* on the basis of the absence of a dorsal stripe, represents more than one form. Two small

specimens from Kambakambi and Numbutaka, northwestern Papua New Guinea, appear to be identical with the holotype of *Nyctimene (Paranyctimene) raptor* as described from Oroville Camp in southwest Papua New Guinea by Tate (1942a). One specimen from Anadea, southeastern Papua New Guinea, is clearly different from *raptor* in size and in skull and teeth characters, and is described below as a new species. This species is very likely sympatric with *raptor*, as the latter has been found both north and south of the central mountain range and as in both these parts of Papua New Guinea *Paranyctimene* is common everywhere (Bonaccorso, 1998). Eight specimens from Kebar Val (taken to be close to Kebar, at 00° 50'S 133°03'E, 550 m a.s.l.) in northwest West Papua and Urbinasopen on Waigeo Island are also larger than typical *raptor* but agree with this in most other characters distinguishing the specimen from Anadea; they are described below as a subspecies of the new species.

#### *NYCTIMENE ALBIVENTER* GROUP

#### ***Nyctimene (Nyctimene) albiventer albiventer*** (Gray, 1863)

##### MATERIAL

INDONESIA: RMNH 30291, 1 male, alc., skull, Ternate (00°50'N 127°19'E), leg. H. A. Bernstein; RMNH 30615, 1 male, alc., skull, Talaga, Pulau Obi (01°35'S 127°40'E), 1-IX-1953, leg. A. M. R. Wegner; ZMA 22.099/100, 1 male, 1 female, alc., skull of male, lower slopes of Sibela range (00°47'S 127°35'E), NE of Ngame, NW of Wayaua, Bacan, 125-150 m a.s.l., 9/10-V-1983, leg. F. G. Rozendaal, # 195/196.

REMARKS. - The two specimens from Bacan were caught at 125-150 m a.s.l. in primary forest. The male had a W of 22.8 and the female one of 29.3.

BIOLOGY. - The female had one embryo, with a total length in situ of 23.

#### ***Nyctimene (Nyctimene) albiventer papuanus*** Andersen, 1910

##### MATERIAL

INDONESIA: RMNH 36658, 1 female, alc., skull, Kebar Val (00°50'S 133°03'E), 550 m a.s.l., Vogelkop, West Papua, 28-

1-1962, leg. L. S. Quata; ZMA 25.426/27, 2 females, alc., at 200 m from Rumei River, ca. 7 km upstream, ca. 10 km E of Urbinasopen village (00°22'S 131°13'E), SE Waigeo, West Papua, 200-250 m a.s.l., 13-X-1993, leg. M. Argeloo, # 5-6. PAPUA NEW GUINEA: ZMA 23.185, 1 female, alc., skull, 18 km NNE of Port Moresby (09°30'S 147°07'E), Gulf Province, 13-III-1974, leg. Mr. Lawes, # 4188; ZMA 23.182/84, 3 males, alc., 2 skulls, Sapi Creek, Gogol River (ca. 05°06'N, 145°146'E), Madang province, 18-V-1974, collector unknown.

REMARKS. - The two females from Waigeo had forearm lengths of 54.8 and 59.1 and weights of 33 and 35, respectively. They are the first records of this species from Waigeo.

BIOLOGY. - Both females from Waigeo had small nipples and were pregnant.

DISCUSSION. - Although they did not state their reasons, Laurie et al. (1954) considered *N. papuanus* a subspecies of *N. albiventer*. They were widely followed (i.e., Corbet et al., 1992) but not by all. Peterson (1991) treated *papuanus* like a full species. Kitchener et al. (1993, 1995), who were the first to analyze its relationship with *albiventer*, considered *papuanus* a subspecies of *albiventer* again, which is followed here.

#### ***Nyctimene (Nyctimene) ? albiventer*** subsp.

##### MATERIAL

PAPUA NEW GUINEA: ZMA 25.434, 1 female, alc., Kapuluk (camp 1) (05°33'S 149°44'E), New Britain, 4-IX-1974, leg. K. D. Bishop; ZMA 25.435, 1 male, alc., skull, Garu, house (05°31'S 150°01'E), New Britain, 25-VIII-1978, leg. K. D. Bishop; ZMA 25.436, 1 male, alc., skull, either Garu, house, or Kapuluk (camp 1), New Britain, VI-1979, leg. K. D. Bishop.

REMARKS. - These specimens formed part of a sample of four specimens from two nearby localities Garu and Kapuluk, of which some of the labels had got detached, and are clearly different from the fourth, described below under *Nyctimene ? vizcaccia*, although not in size.

The forearm lengths of the present specimens are 57.6 in the female and 53.9 and 56.9 in the males (ZMA 25.435 and 25.436, respectively; ZMA 25.435 appears to have been preserved in formalin, and its ears and tail have shrunk). Skull

measurements of these males are: gsl 27.1 and 28.1, and cbl 25.7 and 26.2 (same order).

The fur on snout, cheeks and top of the head is slightly darker than the surrounding fur, with orange-brown tips to the hairs; the darker fur does not form longitudinal bands. The skin around the eye is whitish and thinly furred. The dorsal fur consists of tri-coloured hairs of 11-12 mm, with dark dull brown bases (length ca. 3.5-4), a light yellowish brown middle part (ca. 4-5), and a darker, orange-brown tip (ca. 3). These tips are longer in the males, and hence their overall dorsal fur colour is darker and more grizzled and their dorsal stripes less clearly visible, than in the female. The dorsal fur is interspersed with thinly spread, longer (guard?) hairs of up to 16.5 in length. A distinct dorsal stripe of up to 2.5 in width starts at withers and runs to the basis of the tail. The ear conch is clearly longer than wide (when flattened; 13.0 x 10.5 in ZMA 25.434 and 12.7 x 8.8 in ZMA 25.436), with a blunt and broad tip. The inner lower margin has only weak and rounded projections. The tail lengths (measured from anus to tip) in ZMA 25.434 and 25.436 are 27.6 and 25.2 respectively, or 44.3% and 47.9% of the forearm length.

The distal parts of the premaxillae project forward below the nasal opening. The zygomatic width is 68.7-72.3% of cbl in ZMA 25.436 and 25.435, respectively. The upper post-canine tooth rows do not strongly diverge backwards with, in ZMA 25.435 and 25.436 respectively,  $M^1-M^1$  at 106% and 108% of  $P^3-P^3$  and 100% and 101% of  $P^4-P^4$ . The inner and outer cusps of  $P^3$  are not fused in ZMA 25.435 and only weakly fused in ZMA 25.436, and in  $P_3$  the situation is the same as in their counterparts, in both specimens.  $M^1$  (1.9 x 1.4 in 25.435 and 1.65 x 1.3 in ZMA 25.436) is slightly shorter than  $P^4$  (1.95 x 1.6 and 1.8 x 1.5 in the same specimens, respectively).  $M_1$  (1.75 x 1.4 and 1.75 x 1.3, respectively) is shorter than  $P_4$  (2.0 x 1.6 in both specimens).  $M_2$  is short (1.3 x 1.3 and 1.3 x 1.35, in specimens ZMA 25.435 and 25.436, respectively).

**DISCUSSION.** - The present specimens show a number of characters which in combination associate it with *N. albiventer*: body and skull dimensions; the distinct dorsal stripe; the whitish ventral fur band; the distally projecting premaxil-

lae; and the nearly parallel upper post-canine tooth rows. But there are also two characters not normally found in *albiventer*, which would oppose this association: the three-coloured dorsal hairs and the relatively long tails - which, according to Bonaccorso (1998) would both be characters of *N. vizcaccia*.

It seems useful to recapitulate what has been written on *Nyctimene* from the Bismarcks so far. Altogether six species of *Nyctimene* have been reported from this Archipelago and nearby islands off the coast of northern Papua New Guinea:

1) *N. albiventer papuanus*: Andersen (1912) recorded *N. papuanus*. Laurie et al. (1954) added the Admiralty Islands to the localities, and Koopman (1979) added Bagabag, Crown, Long, Tolokiwa, Umboi and Sakar. Smith & Hood (1981) provisionally recorded *albiventer* from New Britain and New Ireland. Flannery (1995a) reported on *N. albiventer papuanus* from New Britain and New Ireland.

2) *N. major* (various subspecies): Duke of York Island is the type locality of *N. major* (Dobson, 1877). Andersen (1912) examined material from New Ireland. Koopman (1979) studied specimens from Bagabag, Karkar and Sakar. Bonaccorso (1998) added the Mioko Islands.

3) *N. vizcaccia* (variably as species or as subspecies of either *N. albiventer* or *N. cephalotes*): Umboi Island is the type locality of *N. vizcaccia*. Laurie et al. (1954) listed *N. vizcaccia*, as a subspecies of *N. cephalotes*, from Ruk island, Admiralty Islands; they failed to produce supporting arguments for their classification. Smith et al. (1981) mentioned an unidentified species from New Britain which they later (1983) identified as *vizcaccia*. Bonaccorso (1998) recorded *vizcaccia* also from New Ireland and Manus Island.

4) *N. cephalotes*: Smith et al. (1981, 1983) recorded *N. cephalotes*, as a species distinct from *vizcaccia*, from New Britain and New Ireland.

5) *N. cyclotis*: Smith et al. (1981) recorded this species from a locality in New Britain. Peterson (1991), in a detailed study focused on this species, confirmed their identification.

6) *N. masalai*: Smith et al. (1981) mentioned an unidentified species from New Ireland, which in 1983 they described as *Nyctimene masalai*.

Some of these records have been disputed. Flannery et al. (1991) studied the mammalian fauna of New Ireland and concluded that it is very poor in naturally dispersed species. Therefore, the exceptional riches in Nyctimeninae as suggested by the published five species for that island would not appear very likely. Flannery et al. (1991) expressed some doubt as to the presence of *N. major* on New Ireland - but apparently overlooked the record in Andersen (1912) - and regretted that Smith et al. (1983) had not provided measurements and specimen numbers of specimens of *major* and of *N. albiventer* from New Ireland. They (i.e., Flannery) furthermore critically examined the type material of *N. masalai*, and compared it with their own series from New Ireland which they had identified as *N. ? albiventer*, and concluded the synonymy of the former with the latter. Later, Flannery (1995a) confirmed the presence of *N. major* on New Britain, New Ireland, and some smaller nearby islands. He recorded *N. albiventer papuanus* for New Britain and New Ireland and other major islands and listed *N. vizcaccia* and *N. masalai* as its synonyms. He rejected the occurrence of *N. cephalotes* in the Bismarck Archipelago and Admiralty Islands but accepted the record of *N. cyclotis* for New Britain. Bonaccorso (1998) rejected all records of *Nyctimene albiventer papuanus*, *cephalotes* and *cyclotis* from the Bismarck Archipelago as based on misidentifications, and considered them, and *masalai*, as synonyms of *vizcaccia*. Thus, while Flannery et al. (1991) and Flannery (1995a) tried to argue a reduction of the number of recognized *Nyctimene* species in New Ireland, and *mutatis mutandis* the Bismarck Archipelago, by stressing its faunal paucity and the derivation of its fauna from that of the New Guinea mainland, Bonaccorso (1998) did the same by rejecting a connection with the latter fauna, and by stressing Bismarck endemism and connections with other archipelagos (Solomon Islands and Bougainville, and the islands east of southern Papua New Guinea) instead.

The general conclusion must be that many aspects of the specific taxonomy of *Nyctimene*, and especially in New Guinea and the Bismarck Archipelago, are still unclear, and that at present it is very difficult, if not impossible, to identify particular specimens with certainty. What is first

needed to solve the many problems are very detailed, comparative studies, descriptions and illustrations of the type material of all named species. In the meantime, and for the time being, the foregoing and the next specimens have been assigned provisionally to the most likely taxa.

***Nyctimene (Nyctimene) ? vizcaccia***

Thomas, 1914

**MATERIAL**

PAPUA NEW GUINEA: ZMA 25.437, 1 male, alc., skull, either Garu - house (05°31'S 150°01'E), 25-VIII-1978, or Kapuluk camp 1 (05°33'S 149°44'E), VI-1979, New Britain, leg. K. D. Bishop.

**REMARKS.** - This specimen formed part of a sample of four specimens from two nearby localities Garu and Kapuluk, of which some of the labels had got detached, and is clearly different from the other three, described above as *Nyctimene ? albiventer* subspecies, although not in size. Its forearm length is 55.4, its gsl 28.2 and its cbl 26.7.

It has a longitudinal band of dark brown fur running backwards from behind the nostrils, passing between the eyes, to the top of the head. The whitish skin around the eyes, especially at its upper anterior side, is sparsely haired. The dorsal fur consists of hairs of about 9 to 12, with somewhat longer hairs up to 14.5, with dark greyish-brown bases (of ca. 3), very light greyish brown middle parts (ca. 5.7-7.7), and dark reddish-brown tips (ca. 3). It is difficult to quantify the relative numbers of shorter hairs and longer (guard?) hairs. The overall colour impression is dark sepia mixed with greyish white. There is a vague dark brown mid-dorsal stripe, starting at withers and about 4 wide on the lower back. Ventrally, there is a broad longitudinal band of short yellowish white hairs of 5-6 in length across breast and belly, between rather dark brown furred flanks.

The ear conch is thin, roundish, with a weak tip, brown with a dark rim and without yellowish spotting. It is 12.9 in length and when flattened 10.7 at its greatest width. The inner lower ear margin has two pointed projections. The tail length is 19.5 (35% of the forearm length).

The distal parts of the premaxillae do not project forward below the nasal opening. The zygomatic width, at 74.9% of cbl, appears rather

large. The upper post-canine tooth rows diverge backwards, with  $M^1$ - $M^1$  at 153% of  $C^1$ - $C^1$ , 120% of  $P^3$ - $P^3$ , and 107% of  $P^4$ - $P^4$ . The inner and outer cusps of  $P^3$  are nearly completely fused, and so are their counterparts in  $P_3$ .  $M^1$ , with a length of 2.0 and a width of 1.55 mm, is slightly longer than  $P^4$  (1.85 x 1.65 mm).  $M_1$  measures 2.15 x 1.45 mm and is about as long as  $P_4$  (2.1 x 1.55 mm).  $M_2$  measures 1.65 x 1.35 mm.

DISCUSSION. - When Thomas (1914) described *Nyctimene vizcaccia*, on the basis of a single female from Umboi Island, he could not assign it to either the *albiventer* group or the *cephalotes* group, as the type specimen with a forearm length of 60 was intermediate in size. Of the *albiventer* group *albiventer*, *papuanus* and *minutus* and *varius* were then known, and of the *cephalotes* group *cephalotes*, *major*, *geminus*, *scitulus*, *lullulae* and *robinsoni*. However, he differentiated it especially from *Nyctimene varius* (now considered a subspecies of *N. minutus*), a member of the *albiventer* group. This is unfortunate, as the variation in this (sub)species was not known to him (and as nowadays still very few specimens are known). *N. vizcaccia* shares with *varius* "the varied Vizcacha- or *Lagidium*-like fur, strongly spotted condition of wings, and coalescence of the inner with the main cusp of  $p^3$  [=  $P^3$ ], but [is] distinguished by the further coalescence of the corresponding cusps in the lower jaw and by its greater size." (Thomas, 1914). The fur of viscachas (*Lagostomus*) is generally described as soft with guard hairs and that of mountain viscachas (*Lagidium*) as thick and soft. Although the present specimen appears to have two types of hair, one of which could be guard hairs, this is very difficult to ascertain in wet specimens and needs further analysis. It can safely be assumed that Thomas will have meant to say that the fur is thick and soft. The condition of the wing membrane with regard to spotting can be highly variable within a species and even a population. The measure of coalescence of cusps in upper and lower third premolars may also be subject to variation within a population (e.g., in what has been assigned here to *Nyctimene ? albiventer* subspecies), and at present can not yet be used as a reliable character to distinguish species. Thomas also made some comparative remarks relating to

*Nyctimene (albiventer) papuanus*, another member of the *albiventer* group: in *vizcaccia* the dorsal stripe is well marked considering the waviness of the hair, but not nearly so much as in *N. papuanus*; its skull, with a *gsl* of 29.8 and a zygomatic width of 19.7, slightly exceeds in size the largest skulls of *N. papuanus*.

To ascertain the identity of *N. vizcaccia* further, a detailed and illustrated redescription of the type specimen is needed and, to understand the variation, a similarly detailed study of a larger series of specimens. Smith et al. (1981) appeared to have overlooked the description of *vizcaccia* and do not refer to it at all. However, by 1983, these authors had studied the holotype specimen of *vizcaccia* and described the species as follows: cranium and dentition differ considerably from those of *albiventer*, cranium rectangular, rostrum relatively longer than in *albiventer*, braincase elongate, not globose as in *albiventer*, second upper and lower premolars [ $P^3$  and  $P_3$  in the present paper] lack distinct internal cusp; often a marked ridge from posterior internal margin of cingulum to apex of external cusp; teeth usually longer and somewhat narrower than in *albiventer*. It would have been useful if these authors would have tried to quantify the rectangularity of the cranium, the relative length of the rostrum, and the elongateness of the braincase. In their figures 1A and 1B the mentioned differences are not apparent; these figures are furthermore difficult to interpret as neither the exact origin of the specimens is given, nor a scale. Unfortunately, moreover, apart from *Nyctimene masalai* the figured specimens do not represent the studied holotypes. Flannery (1995b) lists *vizcaccia* as a synonym of *albiventer*, without further comments; its supposed close relative *Nyctimene minutus varius* has not been included by him at all. Bonaccorso (1998), in his key based on external characters, distinguishes *vizcaccia* from *albiventer* by its woolly and tri-coloured fur, and from *N. cyclotis* by its distinct dorsal stripe and lowland occurrence. (According to this key, the specimens assigned here to *N. ? albiventer* subspecies are also *N. vizcaccia*.)

The present specimen shows a number of characters which in combination associate it with *N. vizcaccia*: body and skull dimensions; the tri-coloured, long and woolly dorsal fur; the vague

dorsal stripe; the distally not projecting premaxillae; the backwards diverging upper post-canine tooth rows (cf. fig. 1B in Smith et al., 1983); and the nearly completely fused inner and outer cusps in P<sup>3</sup> and P<sub>3</sub>. But there are also characters which would oppose this association: the thin, roundish, near naked ear conch (which may be as in *Nyctimene cyclotis*, of which the author has no examples at hand - but in *cyclotis* the teeth are clearly different; see Peterson, 1991); and the relatively short tail.

#### NYCTIMENE CEPHALOTES GROUP

##### ***Nyctimene (Nyctimene) keasti tozeri***

Kitchener, 1995

##### MATERIAL

INDONESIA: RMNH 37585/603, 13 males, 6 females, alc., skulls of 2 males and 2 females extracted, ca. 6 km northwest of Bomaki (07°54'S 131°17'E), Yamdena, 16- and 20-IX-1985, leg. F. G. Rozendaal, # 466-487.

REMARKS. - Although, with most of the skulls in situ, it can not be easily ascertained if all 19 specimens are full-grown, the series agrees well with the original description. The forearm length range in 19 specimens, sexes combined, is 57.8-62.9 mm, and the cbl range in the four skulls is 28.1-28.7 mm. The fur colour shows some variation. In some males, the ventral fur is much darker than in others. This applies to the relatively light colour of the fur on breast and belly as well as to the darker fur on the flanks.

BIOLOGY. - All the females but one had rather large nipples at the time of capture. Four males had large, descended testes.

ECTOPARASITES. - In specimen RMNH 37593 an unidentified mite (Acarina) was found on the ventral side of its wing membrane, against its forearm. It was not attached, and the possibility that it is a straggler can not be excluded.

##### ***Nyctimene (Nyctimene) keasti babari***

n. subsp.

Figs. 1A-E

##### MATERIAL

INDONESIA: Holotype: RMNH 1540, 1 male, alc., skull, Babar Island (07°55'S 129°45' E), VI-1898, K. Schädler.

DIAGNOSIS. - A large subspecies of *Nyctimene keasti*, with in the holotype and only known specimen a forearm length of 68.3 and a greatest skull length of 32.1.

DIFFERENTIAL DIAGNOSIS. - The new subspecies is, or averages, absolutely larger in all body and skull dimensions than the two other subspecies of *N. keasti*. Of the other species of *Nyctimene*, *N. cephalotes* appears to be the nearest relative. The measurements of the holotype of *N. keasti babari* are slightly larger than the maximum values for typical *N. cephalotes* and roughly fit the variation ranges for *N. cephalotes aplini* Kitchener, 1995 from Sulawesi. Kitchener (in: Kitchener et al., 1995) mentioned some morphological differences between *N. keasti tozeri* and *N. cephalotes aplini* Kitchener, 1995 which also hold for the holotype of *N. keasti babari*: in *N. keasti babari*, the junction of the postorbital ridges and sagittal crest are closer to the postorbital process base, and the frontal area immediately anterior to this junction is less basined than is the case in *N. cephalotes aplini*.

DESCRIPTION. - The fur on the head is light yellowish brown with, on top of rostrum and head, orange-brown tips. The hairs of the dorsal fur in the new subspecies are bi-coloured, with a light yellowish brown base of about 9 and an orange-brown tip of about 3.5. Hairs of up to about 17 are thinly spread through the others. The dorsal stripe starts from behind the neck and runs to the tail basis; on the lower back it is about 2.5 wide. The ventral fur is uniformly light yellowish brown. The ear is clearly longer than wide (14.9 x 12.4), light yellowish brown, with a moderately thickened anterior margin, a blunt tip, and about nine ridges; the upper third of the outside is darker brown, and the lower third is furred. There are yellowish white spots on ears and fingers, and few on the flight membranes, which are also spotted with blackish brown.

Measurements of the holotype are: forearm length 68.3, 3rd metacarpal 49.7, 4th metacarpal 45.6, 5th metacarpal 48.0; tail (anus-tip) 24.5, length x greatest width of ear 14.9 x 12.4, hind-foot (with claw) 15.1, and tibia 26.8; gsl 32.1, cbl 30.4, rostrum length from orbit to anterior tip of premaxillae 10.5 and from orbit to anteriormost

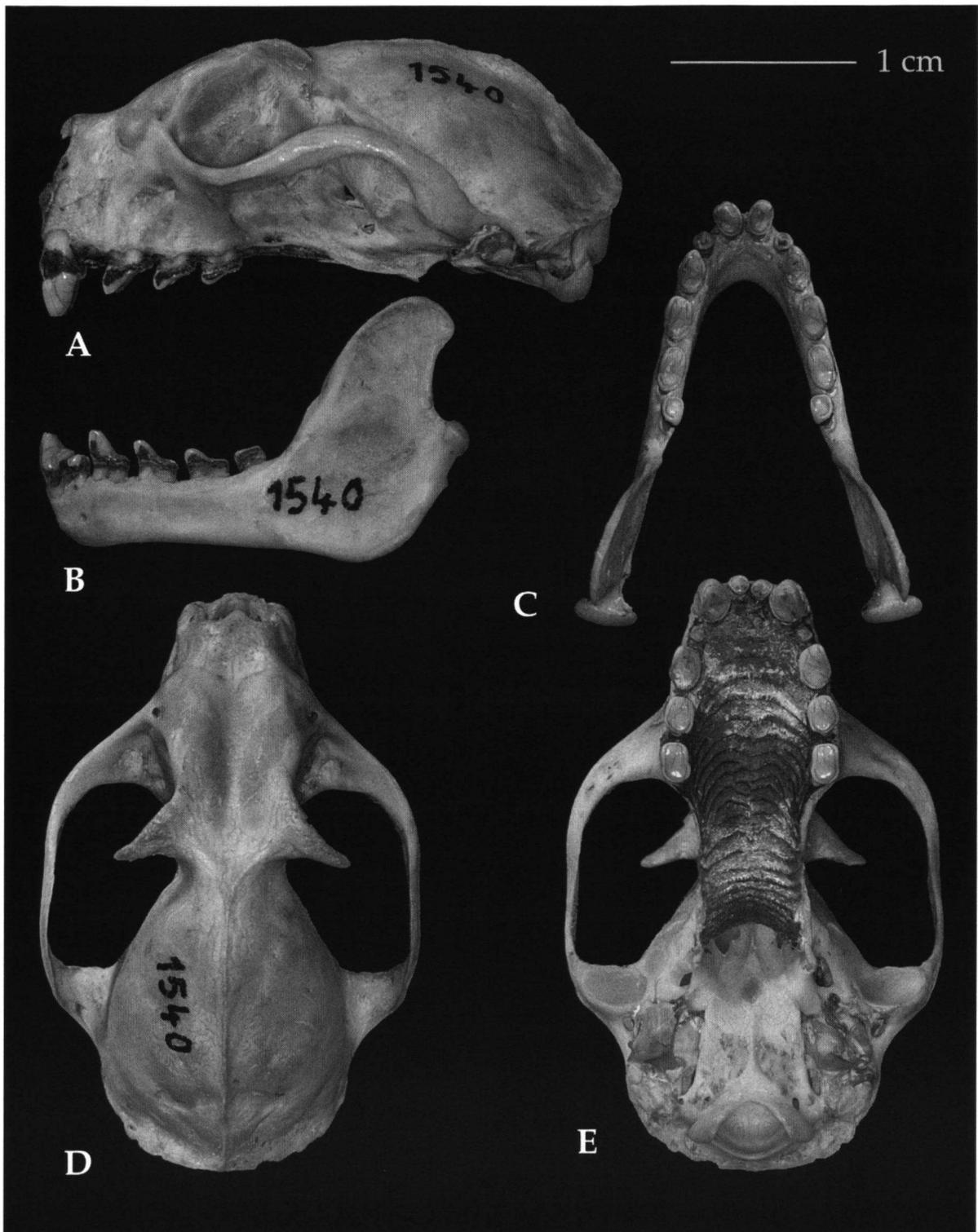


Fig. 1. *Nyctimene (Nyctimene) keasti babari* n. subsp., male, holotype (RMNH 1540). A, lateral aspect of skull (left side). B, lateral aspect of mandible (left side). C, dorsal aspect of mandible. D, dorsal aspect of skull. E, ventral aspect of skull (Photographs: Mr Louis A. van der Laan, ZMA).

point of nasals 6.1, cranium width 12.9, interorbital width 6.3, postorbital width 5.6, zygomatic width 20.75, C<sup>1</sup>-C<sup>1</sup> 6.0, C<sup>1</sup>-M<sup>1</sup> 11.1, M<sup>1</sup>-M<sup>1</sup> 9.55, C<sub>1</sub>-M<sub>2</sub> 12.9.

REMARKS. - Kitchener (in: Kitchener et al., 1993) first identified *Nyctimene keasti*, from the Banda and Kai Islands, as a subspecies of *N. albiventer*. Later (in: Kitchener et al., 1995), he raised it to specific rank and associated it rather with *N. cephalotes*. *N. keasti keasti*, from the Kai Islands, averages smaller in dimensions than typical *N. cephalotes* from Buru, Ceram and Ambon. *N. keasti tozeri*, from Yamdena and Selaru, is somewhat larger than *N. keasti keasti*, but on average still slightly smaller than typical *N. cephalotes* in most dimensions (Kitchener et al., 1995).

The holotype of *N. keasti babari* has been compared directly to *N. cephalotes aplini* from North Sulawesi (ZMA 21.544 and 24.255; see below). Apart from the differences between *N. keasti* and *N. cephalotes* as found in a larger material by Kitchener et al. (1993, 1995) and copied here in the differential diagnosis, the holotype of *N. keasti babari* shows some additional differences: compared to one specimen of *N. cephalotes aplini* the rostrum in *babari* is slightly heavier and wider, the zygomatic width in *babari* is larger, and the processus coronoideus of the mandibulum is steeper, wider, and higher. Of course, these differences should be checked on a larger material. Moreover, the dorsal fur in *N. keasti babari* is bi-coloured, while that in *N. c. aplini* is tri-coloured, and the dorsal stripe, up to 2.5 wide in the former, attains 4.5 in the latter.

ETYMOLOGY. - The new subspecies is named after the island Babar, the origin of the holotype. In the Indonesian language, Bahasa Indonesia, the word *babar* means "to spread the sail". Thus, *babari* also alludes to the spreading of the genus *Nyctimene* - or rather our knowledge thereof, to more and more islands and island groups.

***Nyctimene (Nyctimene) cephalotes aplini***  
Kitchener, 1995

*Nyctimene cephalotes cephalotes* (Pallas, 1767);  
Bergmans et al., 1988: 56.

**MATERIAL**

INDONESIA: ZMB 83870, 1 subadult male, skull, Pulau Peleng (01°20'S 123°10'E), 6-VIII-1938, J. J. Menden; RMNH 32680/81, 2 males, skins, skulls, Raha (04°50'S 122°43'E), Muna, 1940, leg. H. J. V. Sody; ZMA 21.544, 1 female, alc., skull, Sungei Moinakom (00°40'N 124°04'E), Dumoga Bone National Park, North Sulawesi, alt. 525 m, 28-X-1981, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; RMNH 33186/90, 4 males, 1 female, alc., bought at market of Imandi (00°35'N 124°04'E), North Sulawesi, (said origin Tambun, 00°35'N 124°05'E, alt. 200-500 m), 18-I-1982, leg. W. F. Rodenburg & J. Wind; ZMA 24.255, 1 male, alc., bought at market at Imandi (00°35'N 124°04'E), North Sulawesi, Indonesia, 9-I-1991, leg. M. Argeloo.

REMARKS. - The specimens have forearm lengths of 64.2-68.8 (mean 66.9) in five males and 69.5-70.4 in two females, and a gsl of 32.6 or more in one of these females, from North Sulawesi (market of Imandi and Dumoga-Bone National Park), and forearm lengths of 65.8-67.8 and gsls of 31.8-31.8 in the two females from Muna. The subadult male from Peleng has a gsl of 29.1.

DISCUSSION. - Kitchener (in: Kitchener et al., 1995) described the subspecies *aplini* on the basis of its larger size if compared to the typical form from Ambon, Buru and Seram. He mentioned specimens from South and Central Sulawesi. The present specimens clearly fit its size range (with slightly smaller minimum and larger maximum values) and extend the known range to North Sulawesi. The identification of the specimens from Peleng and Muna is provisional. Tambun, from where the Imandi market was then said to receive its bats, is a mosaic of primary forest and farm bush at an altitude of 200-500 m. (See for the origin of the bats presently sold in Imandi market the account of *Pteropus alecto* in this paper.) The locality at Sungei Moinakom was in slightly disturbed primary forest; the specimen was caught in a mistnet at about 5 m above the river.

***Nyctimene (Nyctimene) major scitulus***  
Andersen, 1910

**MATERIAL**

SOLOMON ISLANDS: ZMA 11.249/50, 1 male, 1 female, alc., skull of female, near Belaga village, Little Gela (or Nggela) (09°10'S 160°20'E), VII-1966/IX-1967, leg. M. J. A. de Koster.

REMARKS. - The male has a forearm length of 76.1, the female one of 79.0. The female has a gsl of 36.3 and a cbl of 34.6.

BIOLOGY. - The male had somewhat developed, descended testes. The female had rather large nipples.

**Nyctimene (Nyctimene) rabori** Heaney & Peterson, 1984

**MATERIAL**

INDONESIA: RMNH 37526-37529, 3 males, 1 female, alc., skulls, Kuala Tambioe, South of Beo, Karakelang, Talaud Islands, 23/25-II-1985, leg. F. G. Rozendaal, # 258, 259, 261, 266.

REMARKS. - The specimens have forearm lengths of 72.8, 76.8 and 77.7 in the three males and 78.5 in the female, and gsls of 33.7, 34.6 and 35.8 in the males and 34.3 in the female.

DISCUSSION. - Feiler (1990) mentions one specimen of *Nyctimene cephalotes* which had been collected by A. B. Meyer in 1870 or 1873 on Karakelang, and deposited in the museum in Dresden, but was lost since. For the present, it is assumed that this specimen also represented what is here ascribed to *N. rabori*.

The present specimens agree with the original description of the species except for one character: their ears, which are only 15.4 to 16.4 mm long, against 18-21 mm in typical *rabori*. As the Talaud specimens are in alcohol their ears will certainly have shrunk somewhat, but it can hardly be accepted that they shrank a few mm in length. Moreover, the measurements in Heaney et al. (1984) were also taken from specimens in alcohol and some even from dry skins. As a direct comparison could not be made, at present no taxonomic value is attached to this short-earedness, which is rather as in *rabori*'s closest relative, *Nyctimene cephalotes*. If the difference holds, it and the apparent geographic isolation would probably offer a basis for subspecific distinction. On the other hand, if more differences are found which tend to render the Talaud form an intermediate between *rabori* and *cephalotes*, the independency of the former should be reconsidered. Corbet et al. (1992) remarked that *rabori* is "probably conspe-

cific with *N. cephalotes*, differing chiefly in larger size and in some cranial features mostly related to its greater size." The find of *N. rabori* on Karakelang, and its being absolutely larger in all measurements than the recently described large subspecies *N. cephalotes aplini*, which occurs in the nearby North Sulawesi (this paper), appears to lend some support to its being different on specific level.

**NYCTIMENE AELLO GROUP**

**Nyctimene (Nyctimene) aello** Thomas, 1900

**MATERIAL**

INDONESIA: RMNH 37491/95, 2 males, 3 females, mounted, 3 skulls extracted but broken, Misool Island, West Papua, 28/30-VII-1867, leg. D. J. Hoedt; RMNH 1719, 1 female, alc., skull, Lorentz River (or Noord River), West Papua, 15-IX-1909, leg. H. A. Lorentz, Nieuw Guinea Expeditie; RMNH 1718a-b, 2 males, alc., skulls, Alkmaar bivouac at the Lorentz River (or Noord River) (138°43'30"E 4°40'10"S), West Papua, January 1910 and 6 October 1909, respectively, leg. H. A. Lorentz, Nieuw Guinea Expeditie.

REMARKS. - It follows from the itinerary in Lorentz (1913) that the specimen collected on 15-IX-1909 must have been collected near Bivak Eiland (Bivouac Island; 138°53'29"E 05°06'31"S) because that is where Lorentz spent that day and received specimens from his collectors and hunters. The Lorentz specimens had originally been identified as *Nyctimene major*, although an old label on the outside of the bottle read "*Nyctimene aello*". *N. major* is not known from the New Guinea mainland (see for instance Flannery, 1995b) and the conspicuous and broad dorsal stripe in the specimens, varying from about 9 mm in the female to 10 and 12 mm in the males, respectively, identified them as members of the *aello* group (sensu Andersen, 1912).

DISCUSSION. - The *aello* group includes *Nyctimene aello*, described from Milne Bay at the eastern extremity of the mainland of Papua New Guinea, and *N. celaeno* Thomas, 1922, described from Legare River, Geelvink Bay, in West Papua. Thomas (1922b) wrote that *celaeno* is rather smaller than *aello*, with less yellow back fur, brown instead of fulvous fur on the sides, and the nasal

region not so deeply excavated as in *aello*. Tate (1942b) identified two specimens from the Cyclops Mountains in northeast West Papua and 41 specimens from the head waters region of the Fly River in southwest Papua New Guinea as *celaeno*. He suspected that the specimens from Mysol (= Misool) Island listed by Andersen (1912) as referable to *aello* were in reality *celaeno*. Incidentally, these are the same specimens as examined for the present study. Without an explanation, Laurie et al. (1954) listed *celaeno* as a subspecies of *aello*, representing this in the western and northwestern parts of New Guinea Island. McKean (1972) examined 20 specimens of *aello* from four or five localities in Papua New Guinea. He found them to be quite variable in pelage colour and, as there appeared to be no geographical correlation, concluded that not too much reliance should be placed on colour differences. The measurements Thomas (1922b) gave for the holotype of *celaeno* fitted well within the range of measurements for McKean's series of *aello*. Some of his measurements ranges and means are: forearm length in 20 specimens 78.6-86.4 mm (mean 82.1), cbl in 19 specimens 33.6-36.8 mm (mean 35.0), C<sup>1</sup>-M<sup>1</sup> in 20 specimens 11.6-13.7 mm (mean 12.6). McKean doubted whether *celaeno* is really different from *aello*. Hill (1983) argued that the differences in fur colour between the type specimens of *celaeno* and *aello* as described by Thomas (1922a, b) must at least partly be attributed to long preservation in alcohol of the former. At the same time, he found a number of cranial and dental features in which the holotype of *celaeno* differs from *aello*: "It has a much shorter, rather broader rostrum, wider interorbital and intertemporal areas, the frontal region is more elevated in contrast to the rather depressed frontal region of *aello* (commented upon by Thomas, 1922b), the supraorbital ridges are more swollen and inflated, and on the whole the teeth are generally smaller, the upper canines less obviously proclivous than in *aello*." (Hill, 1983: 130). Hill concluded that it seems more appropriate to consider *celaeno* a distinct species allied to *aello*. He mentioned specimen BMNH 29.5.27.3 from Wasjor (= Wasior; 02°38'S 134°27'E), West Papua, which agreed externally and cranially with *aello*. This would imply that there is neither a simple east-west gradient nor divide between

*aello* and *celaeno* suggesting that they could represent subspecies of the same species, but rather that they could be sympatric and represent two species indeed. Finally, Flannery (1995b), commenting that Hill's suggestion that *celaeno* could be a distinct species had not yet been followed by a full systematic analysis, followed Laurie et al. (1954), and listed *celaeno* as a subspecies of *aello*.

For the present study, no typical *aello*, i.e., from eastern Papua New Guinea, could be examined. All specimens are from West Papua and Misool. Moreover, the mounted specimens from Misool are difficult to measure, and the three skulls that have been extracted are heavily damaged. Some measurements of one male from Misool (RMNH 37491) are: rostrum length (orbit to nearest point of nasal opening) 7.25, interorbital width 7.55, C<sup>1</sup>-C<sup>1</sup> 7.25, C<sup>1</sup>-M<sup>1</sup> 12.35, M<sup>1</sup>-M<sup>1</sup> about 10.6, and C<sub>1</sub>-M<sub>2</sub> 14.0. The specimen is slightly smaller than the specimens from Alkmaar and Lorentz River. The measurements of the two males and female are respectively: forearm length - ; 82.6; 77.4; cbl - ; 35.9; 34.4; rostrum length - ; 7.6; 7.5; interorbital width 6.5; 7.3; 6.1; postorbital width 6.3; 6.8; 7.5; C<sup>1</sup>-C<sup>1</sup> - ; 7.8; 7.9; C<sup>1</sup>-M<sup>1</sup> 12.85; 13.2; 13.1. Although not all measurements are comparable, in general they fit the ranges given by McKean (1972) for his 20 specimens from Papua New Guinea (only the forearm length of the female is very slightly below the minimum of 78.6). The present author agrees with Flannery (1995b) that a systematic analysis is needed to establish whether *celaeno* is really different, and if so on what taxonomic level, and prefers to identify all specimens examined as *aello*.

#### *NYCTIMENE RAPTOR* GROUP

***Nyctimene (Paranyctimene) raptor*** (Tate, 1942)

Figs. 2A-E

#### MATERIAL

PAPUA NEW GUINEA: ZMA 23.187, 1 adult male, alc., skull, Numbutaka, 3.5 km E of Miabouru (ca. 03°47'S 143°14'E), East Sepik Province, 7-XII-1982, leg. P. Baguinan; ZMA 23.186, 1 adult female, alc., skull (left upper canine missing), Kambakambi, 1 km N of Kamojang (or Kamajang; 03°47'S 143°14'E), East Sepik Province, 16-XII-1982, leg. P. Baguinan.



Fig. 2. *Nyctimene* (*Paranyctimene*) *raptor* (Tate, 1942), male (ZMA 23.187). A, lateral aspect of skull (left side). B, lateral aspect of mandible (left side). C, dorsal aspect of mandible. D, dorsal aspect of skull. E, ventral aspect of skull. (Photographs: Mr Louis A. van der Laan, ZMA).

REMARKS. - From what has been published on this species, it would appear that the present specimens do not add to our knowledge of its taxonomy. In fact, all data published on *Nyctimene (Paranyctimene) raptor* after its description should be reviewed, due to the discovery of a most probably sympatric, narrowly related species of the same subgenus, to be described below. In all earlier accounts of *N. raptor* except its original description, the specific identity has never been critically assessed and it must therefore be assumed that they may have involved *raptor* but easily also the new species described below, or both. For this same reason, the ZMA specimens are described below and their measurements given in Table 3. Those of the holotype are added, partly quoted from Tate (1942a) and in part kindly provided by Dr Nancy B. Simmons of the AMNH. Compared to the new species, *raptor* is averaging smaller in all body and skull measurements, and its skull and teeth are more delicately built.

DIAGNOSIS. - A small species of the subgenus, with known forearm lengths of 47-50.5, a relatively small and fragile skull with a known gsl range of 23.3-24.0, an anteriorly narrow rostrum with upper canines in contact or near contact with upper incisors and the latter in contact or near contact with each other, an at most weakly developed sagittal crest, a weak occipital crest, a relatively short postdental palatum and short pterygoid wings, low mandibular ramus, small mandibular height, generally well-developed inner basal ledges in the larger premolars and molars, lower canines in contact or near contact, P<sub>1</sub> close to both C<sub>1</sub> and P<sub>3</sub> and placed on outside of tooth row line, a broad P<sub>3</sub>, and P<sub>4</sub> and M<sub>1</sub> both with separate inner and outer cusps.

DESCRIPTION (of ZMA male and female, with some remarks on the female type specimen between brackets). - A relatively small form, with forearm lengths of 49.4 in male and 50.5 in female (47 in type); weights of 22 in male and 19 in female; a small and lightly built skull, with a gsl of 23.3 in male and 23.7 in female (24.0 in type); an anteriorly narrow rostrum, C<sup>1</sup>-C<sup>1</sup> 3.7 in male (4.5 in type), with upper canines very close to or touching upper incisors and upper incisors mutually very close or in contact; moderate infraor-

bita swellings which do not nearly touch in the middle; no median rostro-frontal longitudinal depression; sagittal crest not developed in male, in which the sagittal ridges are separated from one another, and very weakly developed in female (somewhat developed in type); a weakly developed occipital crest; a relatively short postdental palatum, 15% of cbl in male and 16.9% in female; short pterygoid wings with small hamulae, wings ending halfway the foramen ovale, well in front of bullae; length from prosthion to posterior ends of pterygoid wings 68.7% of cbl in male and 68.3% in female; width over posterior pterygoid wing projections 5.0 in male, 4.3 in female; mandibulum lightly built, height of ramus at level of P<sub>4</sub> 2.1 in male and 1.9 in female; anterior part of mandibulum rather narrow, with distance between third lower premolars 2.2 or 9.9% of cbl in male and 1.65 or 7.3% of cbl in female; ascending part of mandibulum relatively short and narrow, especially above processus articularis, with mandibular height less than half its length and 36.9% of cbl in male and 37.4% in female; upper canines slender, with traces of additional cusps on outer and inner ridges and at short distance from one another: 0.95 in male and 1.2 in female, in contact or near contact with upper incisors; upper incisors in mutual contact or near contact; P<sup>3</sup> with straight anterior side, its outer cusp posteriorly narrowing towards tip, a distinct inner basal ledge, a gradual posterior slope, and a short and poorly developed posterior basal plane; P<sup>4</sup> with inner side longer than outer, resulting in oblique posterior outline, and a weak but distinct inner basal ledge; M<sup>1</sup> with weak but distinct inner basal ledge; lower canines, premolars and molars slanting forward; lower canines in mutual contact or very nearly so, with posterior basal ledge continuous with labial basal ledge, which runs to antero-lateral corner, and with ligal basal ledge, which passes into vertical inner ridge running to tip of tooth; P<sub>1</sub> small, close to both C<sub>1</sub> and P<sub>3</sub>, and forced outside the line of the tooth row; P<sub>3</sub> rather broad (length x width: 1.76 x 1.36 in male and 1.56 x 1.32 in female), with distinct basal ledge on lingual, posterior and labial sides; P<sub>4</sub> with inner and outer cusps separate at their inner bases, a wide inner basal ledge which projects antero-internally, resulting in an oblique anterior side of the tooth, and a weak posterior

Table 3. Selected measurements of adult *Nyctimene (Paranyctimene) raptor* Tate, 1942, *Nyctimene (Paranyctimene) tenax tenax* n. sp., n. subsp., and *Nyctimene (Paranyctimene) tenax marculus* n. subsp.

	<i>Nyctimene (Paranyctimene) raptor</i>			<i>Nyctimene (Paranyctimene) tenax</i>						
				<i>N. (P.) tenax tenax</i>	<i>N. (P.) tenax marculus</i>					
	holotype Oroville Camp PNG	Kamba- kambi PNG	Numbu- taka PNG	holotype Anadea PNG	holotype Waigeo Indonesia	paratypes Kebar Val, Cendrawasih Indonesia				RMNH 36668
	AMNH 105165	ZMA 23.186	ZMA 23.187	ZMA 25.360	ZMA 25.428	RMNH 36659/60, -64/65, -67				RMNH 36668
	female	female	male	female	male	5 males				female
						n	mean	min - max	sd	
Tail	13*	17.0	16.9	16.0	15.3	5	19.7	18.3-21.5	1.328	--
Ear	11*	11.5	12.8	(11)	12.2	5	12.2	11.6-12.7	0.473	11.7
Hindfoot	10* s.u.	11.2	12.0	13	13.5	5	12.8	11.5-13.5	0.809	12.2
Tibia		19.4	18.6	21.3	19.5	5	20.3	18.8-21.9	1.139	23.9
Forearm length	47*	50.5	49.4	53.4	52.7	5	53.1	51.0-54.9	1.442	54.9
3rd metacarpal		34.7	34.4	39.3	39.9	5	38.3	36.8-39.6	1.019	40.4
4th metacarpal		32.2	32.4	36.5	36.4	5	34.7	33.5-35.7	0.746	36.4
5th metacarpal		34.2	33.4	39.0	36.6	5	37.1	34.4-38.8	1.556	37.4
gsl	24.0	23.7	23.3	26.8	25.6	4	26.2	25.4-27.2	0.761	25.2
cbl	22.2	22.7	22.2	25.7	24.3	5	24.4	23.7-25.3	0.556	23.7
rl orbit-nare	4.4	4.4	4.1	4.6	4.8	4	4.8	4.4- 5.4	0.393	4.9
rl orbit-premax.		7.1	6.8	8.0	8.2	5	7.8	7.2- 8.8	0.560	7.7
Palatal length	12.0	12.0	11.2	13.6	12.7	5	12.8	12.1-13.9	0.626	11.6
Braincase width	10.5	10.4	10.8	11.3	11.6	5	11.1	10.2-12.1	0.730	11.3
Interorbital width	4.6	4.6	4.9	5.0	5.1	5	4.7	4.1- 5.2	0.354	4.6
Postorbital width		5.1	5.6	5.2	5.9	5	5.3	4.7- 5.8	0.394	5.1
Zygomatic width	16.0	14.6	15.0	17.5	17.3	5	16.7	16.0-17.3	0.487	16.3
Mandible length		17.7	17.6	20.4	19.7	5	19.5	19.0-20.8	0.657	19.4
Mandible height		8.5	8.2	10.4	9.9	4	9.6	9.2-10.0	0.282	9.5
Width over upper canines	4.5	--	3.7	4.7	4.6	5	4.5	4.4- 4.6	0.077	4.7
Length upper tooth row	8.0	8.5	8.4	9.3	9.3	5	9.2	8.8-10.1	0.632	9.0
Width over 1st upper molars		6.8	7.0	8.2	7.9	5	7.1	6.1- 8.0	0.619	7.3
Length lower tooth row		9.6	9.3	10.6	10.2	5	10.3	9.7-11.3	0.589	10.0
Weight		19*	22*		25.5*					

\* Field measurements

basal ledge; M<sub>1</sub> with separated inner and outer cusps.

Fur on top and sides of head short, light yellowish brown; hairs from behind nostrils, between eyes and ears moreover with dark brown tips; hairs on back of head longer, the yellowish brown changing into grayish brown and with longer dark brown tips, resulting in an overall rather dark brown appearance in the male, somewhat lighter and slightly orange-brown in the female; hairs in middle of foreback vaguely more dark, reminiscent of a trace of a dorsal line; hairs on middle of back on average 11.5 long, with a maximum length of about 16; tail membrane with long hairs near the body and in the middle; fur on breast and belly short, about 5 in length, somewhat rigid, yellowish white, more yellowish on flanks and genital area and on upper arms and legs. Ear 12.8 long and 9.5 wide in male, and 11.5 long and 10.0 wide in female (11 long in type). Papillae on inner side of lips rather crowded, without interstices. Soft palate not preserved in specimens examined. Insertion of wing membrane on basis of second toe.

Measurements: Table 3.

**BIOLOGY.** - The type specimen from Oroville Camp, caught on 11 August, was lactating and carrying a young. The female from Kambakambi, caught 16 December, had large nipples and may have been lactating. The male from Numbutaka had large, scrotal testes at the time of capture (7 December).

**Nyctimene (Paranyctimene) tenax** n. sp.

**MATERIAL**

See under the subspecies.

**DIAGNOSIS.** - A large species of the subgenus, with a known forearm length range of 51.0-54.9 and a known greatest skull length range of 25.2-27.2; an anteriorly wide rostrum with upper canines generally not in contact with upper incisors and upper incisors not touching each other; a corresponding anteriorly wide mandibulum, with lower canines generally not in contact; teeth in *tenax* not as slender as in *raptor*, approaching the condition in the subgenus *Nyctimene*; generally weak and incomplete inner basal ledges in

the larger premolars and molars.

**ETYMOLOGY.** - Peter Nijhoff, Dutch field biologist and naturalist and for many years widely acknowledged leader of the non-governmental environmental movement in the Netherlands, with an active interest in conservation worldwide, retired on 3 September 1999. The period of his retirement coincided with that of the discovery of the new species. The author, who worked together with Peter Nijhoff in the Netherlands Committee for IUCN since 1983, wishes to honour him for his numerous steadfast efforts and achievements by naming this species *tenax* (the Latin word for steadfast).

**Nyctimene (Paranyctimene) tenax tenax**

n. subsp.

Figs. 3A-E

**MATERIAL**

PAPUA NEW GUINEA: holotype of species: ZMA 25.360, 1 adult female, alc., skull, upstream of Anadea (about 07°36'S 146°37'E), 32 km SSW of Wau, Morobe Province, alt. 850 m, 10-VIII-1978, leg. B. M. Beehler.

**DIAGNOSIS.** - Known forearm length 53.4; relatively large and solid skull, gsl 26.8; an anteriorly wide rostrum, with upper incisors not in contact with one another and not in contact with upper incisors, and upper incisors likewise separate from one another; well-developed sagittal and occipital crests; a relatively long postdental palatum, long pterygoid wings, a high mandibular ramus, a large mandibular height, generally weak and incompletely developed inner basal ledges in the larger premolars and molars, a rectangular P<sup>4</sup>, lower canines clearly separate, P<sub>1</sub> at some distance from both C<sub>1</sub> and P<sub>3</sub> and inside the tooth row, a narrow P<sub>3</sub>, and P<sub>4</sub> and M<sub>1</sub> with close and basally touching inner and outer cusps.

**DESCRIPTION.** - In the holotype specimen a forearm length of 53.4 and a large and relatively solid skull with a gsl of 26.8; an anteriorly wide and high rostrum, with upper canines not in contact with upper incisors and upper incisors not with one another; width over cingulae of upper canines 4.7; large infraorbital swellings, with their proximal ends touching in the middle and dividing a median longitudinal rostro-frontal depres-



Fig. 3. *Nyctimene (Paranyctimene) tenax tenax* n. subsp., female, holotype (ZMA 25.360). A, lateral aspect of skull (left side). B, lateral aspect of mandible (left side). C, dorsal aspect of mandible. D, dorsal aspect of skull. E, ventral aspect of skull. (Photographs: Mr Louis A. van der Laan, ZMA).

sion into two parts; relatively strong sagittal and occipital crests; a relatively long postdental palatum (18.8% of cbl); long pterygoid wings with large hamulae, wings reaching passed foramen ovale almost to bullae; length over prosthion and posterior ends of pterygoid wings long: 18.9, or 74.0% of cbl; greatest width over posterior pterygoid wing projections 6.3; mandibulum rather heavily built, laterally thickened at level of  $M_1$ , height of ramus at level of  $P_4$  2.35; anterior part of mandibulum rather broadly rounded, with distance between 3rd lower premolars 2.8; ascending part of mandibulum relatively high and broad, especially above processus articularis, with mandibular height slightly more than half the mandibular length and 40.5% of cbl; upper canines slender but relatively solid, at a distance from one another of 2.2, and without traces of additional cusps; upper canines not in contact with upper incisors; upper incisors not in contact with one another;  $P^3$  with curved anterior side, with posterior side of outer cusp only slightly narrowed, and a near rudimentary inner basal ledge which is almost absent on the anterior part, a straight posterior slope, and a clearly defined posterior basal plane;  $P^4$  with inner side as long as outer side, a straight posterior side, its inner basal ledge rudimentary in the middle and only slightly more pronounced anteriorly and posteriorly; lower canines, premolars and molars rather vertical; lower canines clearly separated, with pronounced posterior basal ledge and only a trace of an outer labial ledge;  $P_1$  relatively large, at clear distances from  $C_1$  and  $P_3$ , and not outside tooth row line;  $P_3$  relatively narrow (length x width: 1.84 x 1.24), with inner basal ledge weak and only on posterior side, a distinct posterior basal ledge, and outer basal ledge rudimentary and only on posterior side;  $P_4$  with bases of inner and outer cusps touching in the middle, a narrow and weakly pronounced inner basal ledge with a weak antero-internal projection and a weakly oblique anterior tooth side;  $M_1$  with bases of inner and outer cusps touching in the middle. Relative length of posterior basal shelves in  $P_3$ ,  $P_4$  and  $M_1$  as in *N. (P.) raptor*.

Fur on sides of head short, light greyish brown; dorsally, behind nostrils and between eyes and ears light greyish brown with dark brown tips, giving an overall impression of medium brown;

hair bases on back are darker, overall impression medium to dark brown; anterior to and between shoulder blades fur colour even darker; hairs on back about 10 in length, with a maximum of up to 16.5; hairs on breast and belly yellowish white, on flanks yellowish brown, 6.5 to 8 in length. Ears in type specimen 10 long and 8.8 wide, rounded off above; however, the relatively thick round top margins suggest that both ears are deformed and that their original length has been greater. Wing membrane inserted at basis of 2nd toe. Papillae on inner sides of lips mostly at some distance from one another. Palatal ridge pattern with 26 ridges: a thick ridge just behind canines, followed by a series of seven thick, weakly serrated ridges curving strongly forward except in the middle where they curve backward again, resulting in a rounded W-form; a group of eight ridges beginning at the level of the first molar, becoming thinner and more strongly serrated from front to back while the W-form gradually passes, via a weak curve forward, into a transverse straight line, the last ridges of this group consisting of mere rows of small triangular 'teeth' pointing forward; and a last group of 10 'ridges', also straight lines of small triangular teeth, with the middle part of the last seven rows pointing forward.

Measurements: Table 3.

**Nyctimene (Paranyctimene) tenax marculus** n. subsp.

**MATERIAL**

INDONESIA: holotype: ZMA 25.428, 1 adult male, alc., skull, 200 m from Rumei River, ca. 10 km E of Urbinasopen village (00°22'S 131°13'E) and ca. 7 km upstream, alt. 200-250 m, SE Waigeo, West Papua, 13-III-1993, Leg. M. Argeloo. Paratypes: RMNH 36659/60, -64/68, 5 males, 1 immature male, 1 female, alc., skulls, Kebar Val (00°50'S 133°03'E), 550 m a.s.l., Vogelkop (Cendrawasih), West Papua, 21/29-I-1962, leg. L. W. & S. Quate.

**DIAGNOSIS.** - As for the typical subspecies, but skull lighter built, with sagittal crest absent or at most weakly developed, and a weak occipital crest; relatively short pterygoid wings, ending clearly anterior to bullae;  $C^1$  with small additional cusps or traces thereof on inner and or outer ledges; with inner basal ledges in premolars and molars generally less weak; and with relatively short posterior basal shelves in  $P_3$ ,  $P_4$  and  $M_1$ .

DESCRIPTION. - Size probably not much different from nominate subspecies, with forearm lengths of 51.0-54.9 in six males and 54.9 in one female, and a gsl of 25.4-27.2 in five males and 25.2 in one female; an anteriorly wide rostrum, with upper canines not in contact with upper incisors in five specimens, on one side in one specimen, and on two sides in another; width over upper canines 4.4-4.6 in six males and 4.7 in one female; large infraorbital swellings, separated by a median longitudinal rostro-frontal depression in four specimens, approaching each other at their posterior sides in 2, and touching in 1; in the latter specimens, the median longitudinal depression is interrupted, resulting in a depression before and one behind the place where the swellings meet; a very low to low sagittal crest in all specimens but one male (RMNH 36667), in which it is 0.9 at its highest point; occipital crest rather weak; postdental palatal length variable (15.2-19.0% of cbl in six males, 15.6% in one female); pterygoid wings reaching halfway foramen ovale in five males and one female, and to end of foramen ovale in one male, with rather small hamulae; length from prosthion to end of pterygoid wing rather long (68.9-71.9% of cbl in six males and 70.2% in one female); greatest width over posterior pterygoid wing projections 5.4-6.3 in six males and ca. 5.0 in one female; high and solid mandibular ramus (height at level of P<sub>4</sub> 2.3-2.5 in six males and 2.5 in one female); ramus not laterally thickened; anterior part of mandibulum broad, distance between 3rd lower premolars 2.35-2.7 in five males and 2.7 in one female; ascending part of mandibulum relatively high (37.9-40.7% of cbl in five males, 40.1% in one female); upper canines at a distance from one another of 1.2-1.85 in six males and 2.0 in one female, and with an additional outer cusp in one male and traces of additional cusps in all others; P<sup>3</sup> with very narrow inner basal ledge in three specimens, absent in the middle in four, and absent anteriorly and in the middle in one specimen; P<sup>4</sup> variable in basal outline but inner side longer than outer in all but one specimen, with a weak to distinct antero-internal projection in six and a weak postero-internal projection in four specimens, and a narrow but distinct inner basal ledge in three specimens and only parts of this ledge in four (not on anterior part, not in the mid-

dle, or both parts are absent); lower canines not in contact, although nearly so in three specimens, with posterior basal ledge variably distinct or weak, continuing on lingual side into vertical ridge to the tip, and on labial side; P<sub>3</sub>, P<sub>4</sub> and M<sub>1</sub> with short posterior basal plane; P<sub>3</sub> with complete but sometimes weak inner basal ledge in eight specimens, with a trace of an inner cusp in one; P<sub>4</sub> with variable space between bases of inner and outer cusps (depression between them either in wide U- or narrow V-form), with weak commissure between inner and outer cusps in three specimens.

Ear length in holotype 12.2, width 9.8; in other specimens length varying from 11.6 to 12.7 and width from 8.6-10.0. Fur on the sides of the head short, rather light brown, on the top of the head short and from behind nostrils to between eyes and ears with rather dark grey-brown bases and dark brown tips; in some paratypes (e.g., RMNH 36665) the fur on the head tends to form a pattern of alternating dark and light longitudinal bands, with a dark band along the upper lip, one between the nostril and the eye, and one on the dorsal side of snout and head; fur between scapulae slightly darker than back fur; fur length on middle of back about 9, up to a maximum of 16-18 in some hairs. Hairs on breast and belly yellowish or light brown-yellowish white and on flanks light cinnamon brown, length about 5.5, up to 6.5 on flanks.

Palatal ridge pattern: in the type specimen from Waigeo the soft palate has been preserved in alcohol. There are 22 ridges: one straight thick ridge between canines; one thick ridge between first premolars, slightly curved backward in the middle; two thick ridges between third premolars, strongly curved forward, with lateral ends extending far backward and somewhat curved back again in the middle; one ridge between third and fourth premolars, one between fourth premolars, and one at level with back side of fourth premolars, of the same general form as the preceding ridge and some tooth-like projections in the middle - the latter of these three less thick; three thinner ridges of about the same form, with their toothed median parts all three between first molars; then follow two partly incomplete ridges of the same form, two ridges pointing strongly forward in the middle, and one nearly straight

ridge which is a mere row of tooth-like projections and the last ridge on the bony palate; after that follow another seven such ridges, all slightly curved or pointed forward in the middle. In several of the dry preserved Kebar Val specimens parts of the anterior soft palate have been preserved. The first seven or eight ridges appear to be more regular than in the type specimen, with more space between them (but they are dried), and in one specimen the ridges are straight in the middle.

DISCUSSION. - This western form has been separated from the typical form mainly on the basis of its less strongly developed skull and its slightly more diversified teeth. In both characters, it bears some resemblance to *N. (P.) raptor*. From this, it differs by its larger size.

Measurements: Table 3.

BIOLOGY. - The male holotype specimen, caught 13 March, had small testes. Two of the adult males from Kebar Val, trapped on 21 and 28 January, had large testes, in three others trapped on the same days the testes were not descended. The female from Kebar Val, caught on 21 January, had large nipples.

ETYMOLOGY. - This subspecies has been named *marculus* (Latin for small hammer, but also diminutive of *marcus*) in honour of Drs Marc Argeloo, for his fruitful efforts to collect study material for the author, which yielded the type of the present subspecies and, among others, new specimens of the rare *Neopteryx frosti*, and for presenting this material to the Zoological Museum in Amsterdam.

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