

**A new Tube-nosed Fruit Bat from New Guinea,  
*Nyctimene wrightae* sp. nov.,  
A Re-diagnosis of *N. certans* and *N. cyclotis*  
(Pteropodidae: Chiroptera),  
and a Review of their Conservation Status**

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**ABSTRACT.** The tube-nosed fruit bat genus *Nyctimene* comprises 18 species found in the Philippines, Wallacea, Melanesia and the Solomon Islands but species taxonomy has remained problematic. A review of the cyclotis group, consisting of *N. cyclotis* and *N. certans* from New Guinea is presented, using morphological and genetic data. Historically, the taxonomy of the cyclotis group has been severely impeded by the lack of illustrations or photographs of the majority of the types. This led authors to differ in their treatment of these species, suggesting that the distinct taxa *N. cyclotis* and *N. certans* might be conspecific. Here, *N. cyclotis* and *N. certans* are recognized as full species and are re-diagnosed. I describe *Nyctimene wrightae* sp. nov., a widespread New Guinean species which is tentatively placed in the cyclotis group. These three species and the sympatric *N. a. papuanus*, of similar body-size, are morphologically distinguished using discriminant function analyses and non-metric characters. An identification key is provided. Species distribution and conservation status are evaluated. The IUCN threat status recommended for each species is: *N. wrightae* sp. nov. Least Concern; *N. certans* (known from < 200 specimens) with unknown population size and trends, Data Deficient; and *N. cyclotis*, known from only two male specimens, Vulnerable. Further research is required on the basic ecology of all of these species, which remains virtually unknown.

**KEYWORDS.** *Nyctimene*; taxonomy; revision; Papua New Guinea; Indonesia; cryptic species; conservation; IUCN threat category; Happy tube-nosed fruit bat

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The tube-nosed fruit bats Nyctimeninae (Miller, 1907) are a distinctive subfamily of Pteropodidae, currently represented by 18 species and two genera, *Nyctimene* (16 spp.) and *Paranyctimene* (2 spp.) (Simmons, 2005). The subfamily is distributed throughout the rainforests of Wallacea (including the Philippines), New Guinea and its islands, to southeastern Australia and the Solomon Islands (Flannery, 1995b; Simmons, 2005). The subfamily is characterized by protruding tubular nostrils, the absence of lower incisors and wing spotting. Individuals range in size from 45 to 85 mm in forearm length. They have a distinctive dentition, with no lower incisors, no upper and lower second premolars and no upper second molars.

All authors during the last 40 years have found the classification of Nyctimeninae problematic. No taxonomic review has looked at the entire subfamily since Andersen's revision over a century ago, which was based on only 61 specimens in 13 species (Andersen, 1912a; Table 1). At present, 21 names are assigned to Nyctimeninae, though authors vary widely in the species they recognize, in some cases with the same specimen being assigned to different species (e.g., *N. bougainville* Troughton, 1936 / *N. albiventer minor* Philips, 1968 / *N. albiventer albiventer* (Gray, 1863) / *N. vizcaccia* Thomas, 1914). Recent appraisals of species have concentrated on island populations (Kitchener *et al.*, 1993, 1995; Flannery & White, 1991), leaving mainland taxa in dire need of revision (Mickleburgh *et al.*, 1992). Contributing directly to the taxonomic confusion is the absence of illustration for most species described before the 1970s, or the exaggeration of characters depicted in illustration, e.g., Andersen's (1912a) treatment of *N. aello* Thomas, 1900 versus *N. major scitulus* Andersen, 1910 (Tate, 1942). Taxonomic clarity is also made more

difficult when specimen numbers (e.g., Flannery, 1995a) or measurements are omitted (e.g., Smith & Hood, 1983) and when taxonomic rank is changed without formal justification, e.g., *N. a. papuanus* Andersen, 1910, *N. bougainville* and *N. draconilla* Thomas, 1922a, were all demoted to subspecies of *N. albiventer* by Laurie & Hill (1954). Intraspecific variation remains to be determined for some taxa that were based either on only the holotype (e.g., *N. malaitensis* Phillips, 1968; *Paranyctimene tenax tenax* Bergmans, 2001), or on a very limited number of specimens (e.g., *N. masalai* Smith & Hood, 1983) and for which additional material has not yet been determined.

Sexual dimorphism in colour and size has been reported for some species of *Nyctimene*, for example, *N. a. papuanus*, *N. major* (Dobson, 1877) and *N. cephalotes* (Pallas, 1767) (Kitchener *et al.*, 1993, 1995; Andersen, 1912a), but not for other taxa such as *N. certans* Andersen, 1912b, *N. cyclotis* Andersen, 1910 (Peterson, 1991) and *N. keasti* Kitchener, in Kitchener *et al.* 1993 (Kitchener *et al.*, 1995). Additionally, many of the types are damaged, have worn dentition (Smith & Hood, 1983; Peterson, 1991) or have lost described diagnostic alpha characters (e.g., in the holotype of *N. cyclotis*, the right P<sup>3</sup> and P<sup>4</sup> have fallen out of the skull and are lost). High individual variation (Smith & Hood, 1983), variation in cranial and dental structures caused by aging (Heaney & Peterson, 1984) and diagnoses that rely on size and colour patterns (Smith & Hood, 1983; Bonaccorso, 1998) have made Nyctimeninae one of the most taxonomically confused taxa in Chiroptera.

In their electrophoretic study of Australian and Papua New Guinean *Nyctimene* and *Paranyctimene* Donnellan *et al.* (1995) did not resolve species boundaries despite sampling more than 30 allozymes from a large number of individuals

**Table 1.** A summary of different taxonomic arrangements of *Nyctimene* taxa by selected authors subsequent to Andersen.

Andersen, 1912a supra-specific groups	Andersen, 1912a	Heaney & Peterson, 1984	Bergmans, 2001 supra-specific groups	Bergmans, 2001
	<i>N. albiventer</i> <i>N. papuanus</i> <i>N. minutus</i> <i>N. varius</i>	<i>N. albiventer</i> ( <i>N. a. papuanus</i> ) <i>N. minutus</i> <i>N. malaitensis</i> <i>N. draconilla</i>	<i>albiventer</i>	<i>N. albiventer</i> ( <i>N. a. papuanus</i> ) <i>N. minutus</i> <i>N. malaitensis</i> <i>N. draconilla</i> <i>N. bougainville</i>
<i>cyclotis</i>	<i>N. cyclotis</i>	<i>N. cyclotis</i>	<i>cyclotis</i>	<i>N. cyclotis</i> <i>N. certans</i>
<i>aello</i>	<i>N. aello</i>	<i>N. aello</i> <i>N. celaeno</i>	<i>aello</i>	<i>N. aello</i> ( <i>N. a. celaeno</i> )
<i>cephalotes</i>	<i>N. cephalotes</i> <i>N. major</i> <i>N. geminus</i> <i>N. lullulae</i> <i>N. scitulus</i> <i>N. robinsoni</i>	<i>N. cephalotes</i> <i>N. major</i> ( <i>N. m. geminus</i> ) ( <i>N. m. lullulae</i> ) ( <i>N. m. scitulus</i> ) <i>N. robinsoni</i> <i>N. masalai</i> <i>N. rabori</i> <i>N. santacrucis</i> <i>N. vizcaccia</i>	<i>cephalotes</i>	<i>N. cephalotes</i> <i>N. major</i> ( <i>N. m. geminus</i> ) ( <i>N. m. lullulae</i> ) ( <i>N. m. scitulus</i> ) <i>N. robinsoni</i> <i>N. masalai</i> <i>N. rabori</i> <i>N. santacrucis</i> <i>N. vizcaccia</i> <i>N. keasti</i>
			<i>Paranyctimene</i>	<i>P. raptor</i> <i>P. tenax</i>

( $n = 178$ ). They delineated five species from New Guinea but were unable to determine species status for any of the species from the islands.

Poor taxonomic resolution and lack of information on status were deemed to be the most important threats to this subfamily by the IUCN/SSC Chiroptera group (Mickleburgh *et al.*, 1992). One species is currently IUCN red-listed as *Endangered*: *N. rabori* Heaney & Peterson, 1984 (Ong *et al.*, 2008); two species as *Vulnerable*: *N. minutus* Andersen, 1910 (Hutson *et al.*, 2008a) and *N. keasti* (Helgen & Hutson, 2008); and five species as *Data Deficient*: *N. cyclotis* (Huston *et al.*, 2008b), *N. draconilla* (Huston *et al.*, 2008c), *N. malaitensis* (Hamilton, 2008), *N. masalai* (Helgen & Bonaccorso, 2008) and *N. sanctacrucis* Troughton, 1931 (Leary *et al.*, 2008). The IUCN/SSC Chiroptera group recommended surveys of all species of tube-nosed fruit bats throughout their range and proposed several specific research projects in Papua New Guinea (Mickleburgh *et al.*, 1992). However, more recent assessments have reduced the threatened status of some species, for example, *N. certans*, due to widespread locality data (Bonaccorso, 1998; Hutson *et al.*, 2008d). The absence of a reliable key to identify species has clearly impeded ecological work, putting populations and distribution status in doubt; hence making appropriate listing recommendations difficult.

Andersen (1912a) “provisionally” proposed four supra-specific divisions of *Nyctimene* that he called the *papuanus*, *cyclotis*, *aello* and *cephalotes* groups (Table 1). Some authors ignored these groups (e.g., Tate, 1946; Laurie & Hill, 1954) while others continued assigning new species to them (e.g., Heaney & Peterson, 1984, placed *N. rabori* in the *cephalotes* group). Bergmans (2001) recognized Andersen’s groups and changed the *papuanus* group to *albiventer* on precedence and erected *Paranyctimene* (a genus proposed by Tate, 1942) as a fifth species group (Table 1). Simmons (2005) adopted these species groups. On the island of New Guinea, four groups are represented by seven species from two genera: the *albiventer* group (*N. a. papuanus* and *N. draconilla*), *cyclotis* group (*N. cyclotis* and *N. certans*), *aello* group (*N. aello* Thomas, 1900), and the *Paranyctimene* group (*Paranyctimene raptor* Tate, 1942 and *P. tenax*).

The focus of this paper is a revision of the *cyclotis* group and description of a new widespread cryptic bat species, from the island of New Guinea; a species previously confused with many medium-sized *Nyctimene* species.

### Taxonomic history of *Nyctimene cyclotis* and *N. certans*

*Nyctimene cyclotis* (derivation from the Greek meaning round ear, Flannery, 1995b) was originally described as having ears that were short and round and a dorsal stripe confined to the lower half of the back (Andersen, 1910). Andersen commented on the broad molars and premolars; the sub-circular outline of the molariform teeth; the conspicuously smaller upper and lower first molar compared to adjacent fourth premolars; and the mottled, grey wood-brown, long dense fur with brownish tips. The grizzled appearance arises from the darker tips not completely covering the lighter mid section of the hair. He later provided an illustration of the palate of *N. cyclotis*, see fig. 62 of his authoritative *Catalogue of the Chiroptera* (Andersen, 1912a).

Although Andersen (1912a) had only one specimen at his disposal, he recognized that *N. cyclotis* was so distinctive from the other *Nyctimene* species to warrant a separate group, the *cyclotis* group. He defined the *cyclotis* group as having reduced  $M^1$  and  $M_1$ , broadly rounded ears and mottled dorsal fur with darker tips to the hairs (Andersen, 1912a). *Nyctimene certans* was originally described as a species on the basis of heavier dentition, darker fur and greater size than *N. cyclotis* (Andersen, 1912b). The derivation of its name from the Latin to mean indisputable or reliable, perhaps refers to its supposed distinctiveness as a species (Flannery, 1995b). Yet, the taxonomic status of *N. certans* has been anything but certain in the last 50 years. In his description of *N. certans*, Andersen (1912b) and later in an appendix to his *Catalogue of Chiroptera* (Andersen, 1912a), emphasized that *N. certans* was an eastern representative of *N. cyclotis*. He pointed out that both the molariform teeth and ears were as in *N. cyclotis*. Andersen did not formally place *N. certans* in the *cyclotis* group but its close relationship to *N. cyclotis* has caused considerable taxonomic discussion. Tate (1942) commented that the groups were not entirely satisfactory, because new species described since Andersen (1912a) do not fall unambiguously into these groups. Laurie & Hill (1954) synonymized *certans* as a subspecies of *N. cyclotis*, but without discussion or justification. Flannery & Seri (1990) also treated *N. certans* as a subspecies of *N. cyclotis*. The morphometric analyses of Peterson (1991) treated *N. cyclotis* and *N. certans* as distinct species which he separated using eight wing and 15 skull and dental measurements. Flannery (1995a; 1995b) then considered *N. cyclotis* and *N. certans* to be distinct species and summarized what was known about their biology, based primarily on his own fieldwork. He described differences in condylobasal length between the species and recorded their sympatry. However, he did not provide specimen registration numbers. It is therefore not possible to determine which specimens he allocated to either species. Bonaccorso (1998), however, continued to view *N. certans* as a subspecies of *N. cyclotis*, but considered the widespread mountain form to be *N. cyclotis certans*, and *N. cyclotis cyclotis* to be restricted to the Arfak Mountains of the Vogelkop Peninsula, Papua.

Bergmans (2001), in the most recent discussion of the genus, placed *N. certans* in the *cyclotis* group but stated that its “taxonomic status was doubtful, being either a subspecies or a synonym of other species”, but did not expand further. Simmons (2005) treated *N. cyclotis* and *N. certans* as separate species and noted that other authors recognized different taxonomic arrangements. Helgen (2007) suggested that *N. certans* was possibly not even a subspecies, falling within the range of his unpublished morphological variation of *N. cyclotis*. The IUCN Red List assessment adopted this opinion, stating that *N. cyclotis* was considered likely to be conspecific with *N. certans* and was listed as *Data Deficient* due to continued taxonomic uncertainty (Hutson *et al.*, 2008b).

The current taxonomic confusion between *N. cyclotis* and *N. certans* lies, in the main, with the morphological and statistical assessment of these taxa by Peterson (1991). Peterson described the *N. cyclotis* holotype accurately in the text, by reproducing a direct quote of Andersen’s description. However, the specimens that represented *N. cyclotis* in his study are dissimilar to the holotype; in having short brown fur and a clearly defined dorsal stripe, which extended from the base of the rump to above the mid back.

It is likely that this error came from defining taxonomic units using nonmetric multidimensional scaling which were then separated further with discriminate function analyses (Peterson, 1991), crucially without identifying what those units represented with reference back to the holotype descriptions. Peterson included the holotype specimens of *N. a. papuanus* (as *N. papuanus* but without a formal discussion of its species status) and *N. a. minor* Phillips, 1968 in his canonical analyses and confirmed that these taxa separated in morphospace from both *N. certans* and his treatment of *N. cyclotis* but did not include the holotypes of *N. cyclotis* nor *N. certans* themselves. The holotype skulls of *N. cyclotis* and *N. certans* are damaged and therefore do not have all the measurements used in his fig. 3, but other analyses could have placed the holotypes which would have shown that his treatment of *N. cyclotis* was not similar to the holotype and instead represented, on the whole, a new species, *N. wrightae* sp. nov. His treatment is actually conflated with another taxon not on mainland New Guinea, which is beyond the scope of this current discussion. Peterson's mis-assessment of *N. cyclotis* together with the lack of illustrations or photographs of the holotypes of *N. cyclotis* or *N. certans* has added to the present confusion of the *cyclotis* group.

Here, I provide a re-diagnosis of *N. cyclotis* and *N. certans* based on specimens from mainland New Guinea. I provide illustrations of the type skulls and photographs of their bodies to facilitate direct comparison with the newly described, widespread species, *N. wrightae* sp. nov. I compare the latter three species to *N. a. papuanus*, which is the only species of similar body size from mainland New Guinea. Three additional sympatric species, *N. aello*, *Paranyctimene raptor*, and *P. tenax* are excluded from further consideration because they are easily distinguished from the latter species: *N. aello* by its generally larger body size and its large, wide dorsal stripe which is up to one third of the width of the back; and the smaller body size of the two *Paranyctimene* species, both of which lack a dorsal stripe. I restrict comparisons to specimens of *N. a. papuanus* from mainland New Guinea and Aru Islands, which are listed in Appendix 1. Records attributed to *N. cyclotis*, *N. certans*, and *N. a. papuanus* from other islands are not included here, as these specimens are currently undergoing taxonomic revision (Irwin, *in prep.*).

## Methods

Specimens were selected preferentially as dry skins with extracted skulls (in keeping with holotypes of most other named forms of the *Nyctimene*) and specimens for which tissue samples were available for molecular analyses. Specimens were selected to maximize geographical coverage and to facilitate testing for sexual dimorphism. Institutions holding specimens used in this study and their abbreviations used in the text are:

AM	Australian Museum, Sydney;
AMNH	American Museum of Natural History, New York;
ANWC	Australian National Wildlife Collection, Canberra;
BPBM	Bernice P. Bishop Museum, Honolulu;
NHMUK	Natural History Museum, London;
FMNH	Field Museum of Natural History, Chicago;

LAC	Los Angeles County Museum;
MVZ	Museum of Vertebrate Zoology, Berkeley;
MZB	Museum Zoologicum Bogoriense, Jakarta;
NMNH	National Museum of Natural History (Smithsonian), Washington DC;
PMAG	Papua New Guinea National Museum and Art Gallery, Port Moresby, formerly NMPNG;
QM	Queensland Museum, Brisbane;
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden;
SAM	South Australian Museum, Adelaide;
UPNG	University of Papua New Guinea, Port Moresby;
WAM	Western Australian Museum, Perth;
ZMA	Zoölogisch Museum, Amsterdam.

These specimens were supplemented with field data that I collected from Sempu, Madang Province, PNG (in 1996 and 1999–2000) and Opio, Eastern Highland Province (1999–2000), PNG, on bats which were released after capture. Dr Debra Wright's specimens and field data of *N. wrightae* sp. nov. and *N. a. papuanus* from Ivimka, Gulf Province and Soobo, Eastern Highlands Province, PNG have also contributed to the morphological data. All specimens and the field numbers of released bats are listed in the text or Appendix 1. Abbreviations of field numbers of animals released in the wild are from the initials of the following people: *DW*, Debra Wright; *NIR*, *OM*, Nancy Irwin; *SH*, Steve Hamilton; and *TR*, Terry Reardon. The country Papua New Guinea is abbreviated *PNG*.

As part of a broader taxonomic revision I examined the majority of the holotypes of the taxa named within Nyctimeneinae, with a few exceptions. I have examined the holotypes of the following named forms, using the names as originally proposed: *N. aello*, *N. albiventer*, *N. papuanus*, *N. albiventer minor*, *N. bougainville*, *N. celaeno* Thomas, 1922b, *N. certans*, *N. cyclotis*, *N. draconilla*, *N. geminus* Andersen, 1910, *N. major lullulae* Thomas, 1904, *N. major*, *N. scitulus* Andersen, 1910a, *N. malaitensis*, *N. masalai*, *N. minutus*, *N. sanctacrucis*, *N. tryoni* Longman, 1921, *N. varius* Andersen, 1910, *N. vizcaccia*, *P. raptor* and *P. tenax*. I have not seen the holotype of *N. rabori* in the FMNH, nor those held by MZB: of *N. keasti*, *N. keasti tozeri* Kitchener, 1995 and *N. cephalotes aplini* Kitchener, 1995. I have, however, measured and sequenced paratype material of *N. keasti* and *N. k. tozeri* in the WAM and *N. rabori* from the FMNH. The type of *N. cephalotes* has been lost since the early 1800s (Andersen, 1912b). Consequently, I have measured topotypes of this species and plan to designate a neotype in further work to be published on this group. I have also examined specimens that were utilized in the taxonomic and genetic studies of Donnellan *et al.* (1995); Macaranas *et al.* (2003) and Colgan & Da Costa (2002).

A total of 25 external and 30 dental and skull measurements were taken from each specimen using a Mitutoyo digital caliper to the nearest 0.01 mm where possible. Field measurements were taken with dial calipers to the nearest 0.1 mm. Terminology for skull and dental features follow Andersen (1912a), Giannini *et al.* (2006), Bates & Harrison (1997) and Martin *et al.* (2001). The morphological characters measured included those used in other studies (Andersen, 1912a; Heaney & Peterson, 1984; Kitchener *et al.*, 1993; Kitchener *et al.*, 1995; Peterson, 1991), but are not necessarily taken in the same manner. The following measurements used in this study and their abbreviations used in the text are:



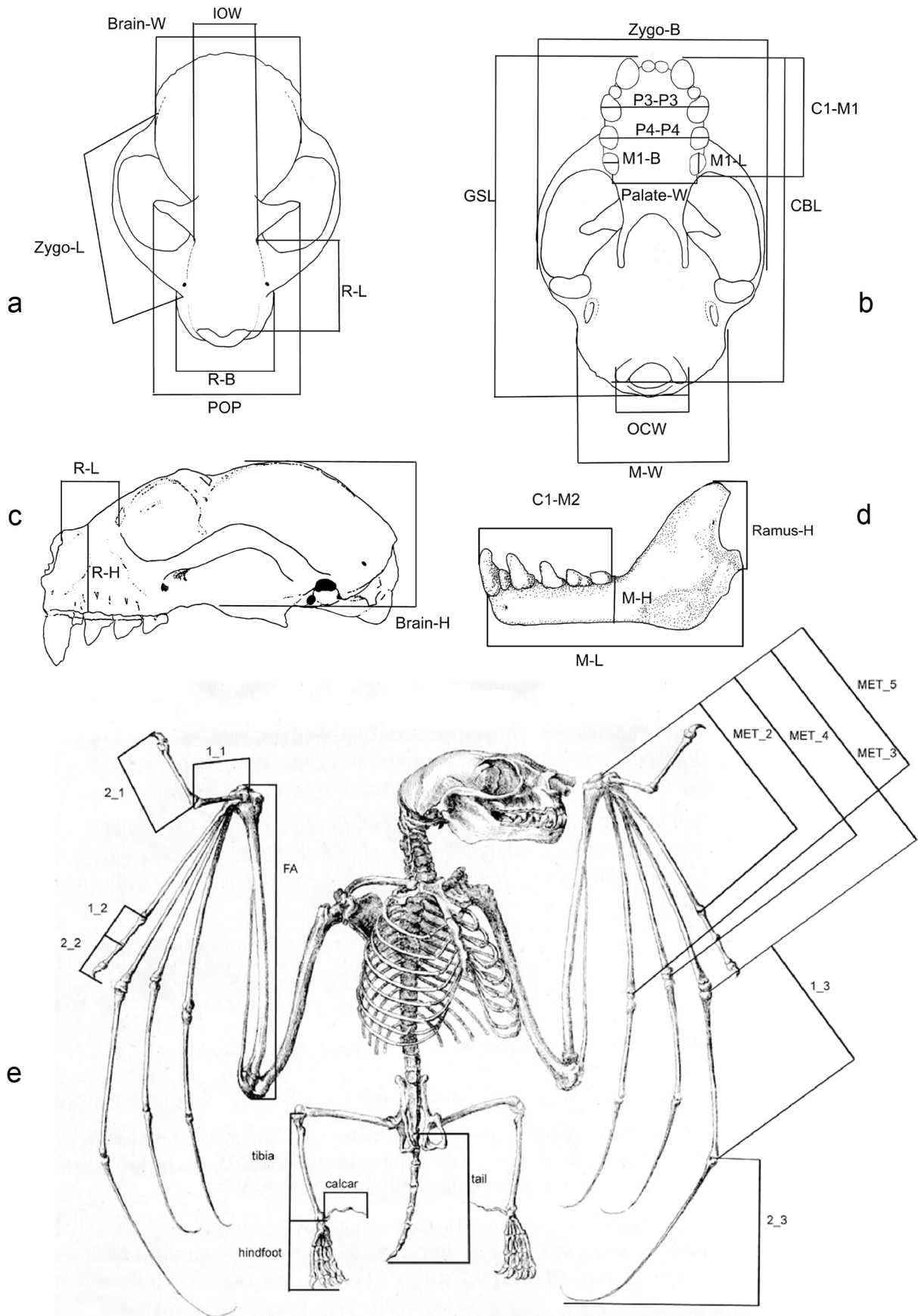


Figure 1. Morphological measurements taken for this study, see text for explanation of abbreviations: (a) dorsal, (b) ventral, and (c) lateral views of the skull and (d) mandible of a typical *Nyctimene*, (e) Skeleton of type specimen for subfamily, *N. cephalotes*, from Pallas (1767).

**5M-1P, 5M-2P, 4M-1P, 4M-2P, 3M-1P, 3M-2P, 2M-1P, 2M-2P, 1M-1P:** length of the 1st or 2nd phalanx of the 5th, 4th, 3rd, 2nd or 1st metacarpal respectively, for 1M-2P and 2M-2P the measurement of the phalanx included the tip of the claw;

**5-MET, 4-MET, 3-MET, 2-MET, 1-MET:** length of the 5th, 4th, 3rd, 2nd and 1st metacarpal respectively taken from the extremity of the carpus to the distal extremity of each joint;

**Brain-H:** brain case height taken from the basi-sphenoid to the highest part of the skull, omitting the sagittal crest where present;

**Brain-W:** greatest width of the brain case.

**C<sub>1</sub>-C<sub>1</sub>, C<sup>1</sup>-C<sup>1</sup>, P<sup>3</sup>-P<sup>3</sup>, M<sub>1</sub>-M<sub>1</sub>, M<sub>2</sub>-M<sub>2</sub>:** distance across canines, premolars or molars, greatest width taken across the labial side of upper and lower canines, third upper premolars, first and second lower molars respectively;

**C<sup>1</sup>-H, C<sub>1</sub>-H, P<sub>1</sub>-H, P<sub>3</sub>-H, P<sub>4</sub>-H, M<sub>1</sub>-H, M<sub>2</sub>-H:** height of the lower or upper teeth, canine, first premolar, third premolar, fourth premolar, first molar and second molar, taken from the alveoli to the tip of the tooth;

**C<sup>1</sup>-M<sup>1</sup>:** upper tooth row length from the front of the canine to the back of the crown of the 1st molar;

**C<sub>1</sub>-M<sub>2</sub>:** lower tooth row length, from the front of the canine to the back of the crown of the 2nd molar;

**Cal:** length of calcar;

**CBL:** condylobasal length, from the posterior edge of the occipital condyle to the anterior edge of the incisors at their base;

**CP-W:** greatest width across the mandible from left to right dentary, taken from the outer margin of each condyle (not shown in Fig. 1).

**DS-B:** dorsal stripe width at base of back;

**DS-T:** dorsal stripe width at top of stripe;

**Ear:** the length taken from the inner notch to the tip of the pinna;

**FA:** forearm length, taken as greatest measurement;

**GSL:** greatest skull length, the greatest measurement from the most posterior part of the skull to the anterior edge of the incisors at their base;

**Hind foot:** from the tip of the longest digit including the claw to the extremity of the heel;

**IOW:** inter-orbital width, the least width of the inter-orbital constriction;

**Man-H:** greatest mandible height, taken behind the second lower molar;

**Man-L:** mandible length, from the anterior edge of the incisors at their base to the posterior edge of the condyle;

**M-W:** mastoid width, greatest width across the mastoid;

**P<sup>1</sup>-B, P<sup>3</sup>-B, P<sup>4</sup>-B, M<sub>1</sub>-B, M<sub>2</sub>-B:** greatest breadth (lingual-buccal) of first upper premolar, third upper premolar, fourth upper premolar, first lower molar and second lower molar;

**Palate-W:** width of palate, the distance across the palate between the inner edges of M<sup>1</sup>-M<sup>1</sup> at the alveoli;

**POP:** maximal distance between the post orbital processes;

**Ramus-H:** ramus height, greatest distance from distal edge of condyle to the top of coronoid process;

**Ramus-W:** greatest ramus width, taken perpendicular to

the anterior margin of the ramus to the posterior margin of condyle;

**R-B:** rostrum breadth, the narrowest breadth across the rostrum taken just anterior of the zygomatic arches;

**R-L:** rostrum length, from the tip of the nasal bone to the posterior margin of the lacrimal foramen (located at the anterior corner of the orbit);

**Tail:** tail length, from the tip of the tail to the anus;

**Tibia:** from the knee joint to the ankle;

**Toe:** digit on which the wing is inserted on the left foot;

**Zygo-B:** zygomatic breadth, the greatest width across the outer edges of the zygomatic arches;

**Zygo-L:** zygomatic length, greatest length taken from the insertion of the anterior zygomatic process on the maxilla bone to the posterior insertion on the temporal bone;

There is no distinct mandibular angular process in *Nyctimene*, instead the posterior end of the mandible curves inwardly or obliquely, providing no endpoint for consistent measurements. The above mandibular measurements were therefore adapted to measure to the end of the condyle process and were found to be reliable. The manner in which measurements were taken is illustrated in Fig. 1.

*Nyctimene* taxa are phenotypically conservative and therefore morphometric analyses were used to evaluate species differences. Measurements were taken from live bats caught and released and combined with data from museum specimens to provide a data matrix of 338 mature specimens (*N. a. papuanus* n = 193, *N. certans* n = 38, *N. cyclotis* = 2 and *N. wrightae* sp. nov. n = 105) (Appendix 1).

Sexual size dimorphism was not found in *N. certans*, *N. cyclotis*, *N. wrightae* sp. nov. and *N. a. papuanus* using Welch two sample t-tests or linear discriminant function analysis (LDFA), therefore sexes were combined in all subsequent analyses. Interspecific differences between the four species were assessed for 69 variables using Welch two sample t-tests. Principal component analyses (PCA) based on separate external characters, cranial characters and both, were uninformative. A genetically identified training set was therefore used for a LDFA. The data were then explored to see which variables contributed to group separation, using t-tests, scatterplots and ratio testing. LDFAs were performed on a larger dataset to identify variables useful for separation. Type specimens were included in the analyses where possible but specimens with missing measurements were excluded. Statistical analyses were performed in R (R Core Team, 2013) in the R studio environment (R Studio-Team, 2015).

## Systematics

### *Nyctimene cyclotis* Andersen, 1910

Figs. 2–3, 5, 10–12

**Type locality.** Arfak Mtns., Manokwari Division., Prov. of Papua, Indonesia.

**Holotype.** ♂ adult skin and skull, NHMUK 1910.7.16.9

**Common name.** Round-eared tube-nosed fruit bat.

**Specimens examined.** ♂ NHMUK 1987.520, adult, whole body in spirit and skull (Arfak Mtns, Manokwari Division, Papua Prov., Indonesia).

**Table 2.** Summary statistics of selected external, cranial and dental variables used in this study for *Nyctimene wrightae* sp. nov., *N. cyclotis*, *N. certans* and *N. a. papuanus* (mm). *H* = holotype of *N. wrightae* sp. nov., AM.M16423.

	<i>N. wrightae</i> sp. nov.				<i>N. certans</i>			<i>N. cyclotis</i>				<i>N. a. papuanus</i>			
	H	mean	min–max	n	mean	min–max	n	mean	min–max	n	mean	min–max	n		
FA	59.54	57.95	(52.09–63.20)	101	60.04	(54.8–67.36)	35	55.09	(54.18–56.01)	2	54.07	(45.20–59.92)	157		
5-MET	41.58	41.87	(37.40–46.30)	97	41.38	(38.00–46.27)	34	38.91	(38.53–39.29)	2	39.46	(32.05–43.40)	136		
4-MET	40.43	39.53	(35.60–43.70)	97	40.23	(36.52–45.39)	34	37.37	(36.82–37.91)	2	36.92	(32.20–41.90)	137		
3-MET	43.78	42.11	(33.50–46.30)	96	42.94	(39.13–49.36)	34	40.23	(40.04–40.43)	2	39.82	(33.30–44.33)	136		
2-MET	31.44	30.66	(25.85–38.80)	96	30.74	(27.97–34.63)	34	27.48	(27.34–27.63)	2	27.48	(24.00–32.60)	137		
1-MET	10.33	9.54	(6.10–13.90)	96	10.08	(6.50–11.47)	34	9.78	(9.24–10.32)	2	9.06	(5.56–12.76)	136		
5M-1P	21.55	20.30	(17.30–23.70)	94	23.20	(20.60–26.85)	34	21.22	(21.2–21.23)	2	18.40	(14.74–22.65)	135		
2M-2P	8.34	7.64	(5.60–9.51)	91	9.10	(8.10–10.10)	34	7.26	(7.20–7.32)	2	7.72	(5.80–9.40)	131		
HDFT	13.6	11.96	(8.20–15.60)	100	14.14	(11.65–16.40)	34	13.29	(11.97–14.62)	2	11.77	(7.40–22.11)	134		
Tibia	22.68	22.52	(13.40–27.00)	98	23.52	(18.74–28.78)	33	22.14	(20.94–23.35)	2	21.00	(16.50–26.20)	134		
Ear	12.79	13.03	(9.19–16.00)	101	11.58	(7.05–15.10)	30	13.59	(13.5–13.68)	2	12.12	(8.60–15.61)	131		
GSL	26.74	27.62	(26.59–29.28)	11	30.40	(27.37–32.31)	24				26.39	(24.19–28.07)	54		
CBL	22.4	23.05	(20.39–26.24)	8	24.58	(22.21–26.80)	23				21.37	(19.25–24.99)	47		
R-B	5.4	5.45	(4.87–6.24)	11	5.07	(4.46–5.87)	26	3.79		1	5.07	(4.04–6.23)	59		
R-L	4.81	4.84	(4.28–5.49)	9	5.67	(4.78–6.35)	25	4.87		1	4.95	(3.91–6.15)	52		
P <sup>3</sup> -B	1.56	1.57	(1.49–1.69)	11	1.76	(1.30–1.99)	26	1.65	(1.63–1.67)	2	1.32	(1.09–1.51)	59		
P <sup>4</sup> -B	1.55	1.18	(1.23–1.74)	11	1.77	(1.32–1.97)	26	1.63	(1.62–1.64)	2	1.30	(1.10–1.45)	59		
M <sub>1</sub> -B	1.39	1.34	(1.25–1.40)	11	1.44	(0.87–1.67)	23	1.36	(1.34–1.37)	2	1.19	(1.02–1.34)	57		
M <sub>2</sub> -B	1.1	1.15	(0.98–1.25)	11	1.11	(0.76–1.45)	27	1.07	(1.05–1.09)	2	1.05	(0.74–1.28)	57		
Brain-W	12.03	12.27	(11.72–11.34)	11	12.85	(11.98–13.60)	25				11.84	(10.77–12.71)	58		
Brain-H	10.03	10.57	(9.49–11.34)	11	10.46	(9.22–11.54)	23				9.72	(8.69–12.37)	56		
Zygo-L	15.62	15.04	(13.14–16.40)	11	17.34	(16.00–17.97)	24	14.76		1	15.00	(12.47–17.16)	59		
Zygo-B	18.58	18.38	(17.26–19.38)	11	18.99	(17.43–19.88)	24				17.54	(15.79–18.69)	54		

**Distribution.** Arfak Mountains, Papua Prov., Indonesia.

**Revised diagnosis.** *Nyctimene cyclotis* differs from *N. certans* in having a relatively longer upper post-canine tooth row (P<sup>1</sup>-M<sup>1</sup>), which is only slightly shorter than P<sup>3</sup>-P<sup>3</sup>, compared to P<sup>1</sup>-M<sup>1</sup> being markedly shorter than P<sup>3</sup>-P<sup>3</sup> in *N. certans*; and in having a shorter second digit, especially 2-MET and 2M-2P.

*Nyctimene cyclotis* shares with *N. certans* the following combination of characteristics to the exclusion of all other species in the subfamily: the ears are short (as wide as long), round, thickened along the apex and often spotted with yellow or white usually on the edge; dense, long dorsal fur (10–16 mm), a grizzled grey-brown caused by at least 30% of the base of the hair shaft being dark brown and the tips being dark brown; and almost indistinguishable ill-defined, short, thin dorsal stripe, which extends from the rump to the mid back; the 5M-1P is longer relative to 5-MET; M<sup>1</sup>-M<sup>1</sup> is shorter than P<sup>4</sup>-P<sup>4</sup>, a character also shared with *N. wrightae* sp. nov.; breadth of the first molars (upper and lower) is markedly narrower relative to the breadth of fourth premolars (upper and lower).

**Remarks.** Essentially Andersen’s original diagnosis stands (Andersen, 1910). *Nyctimene cyclotis* ranges in FA from 54.18 mm to 56.01 mm, known currently from only two male specimens. Andersen (1912a) described P<sup>4</sup>, M<sup>1</sup> and M<sub>1</sub> of both *N. certans* and *N. cyclotis* as being sub-circular in outline and immediately distinctive from all other species. However the cheek-teeth of *N. cyclotis*, especially P<sub>4</sub> and M<sub>1</sub>, are rectangular in shape (larger in the mesial-distal axis than the lingual-buccal axis), a feature that distinguishes it from the similar *N. certans*, in which the cheek-teeth are squarer (broader) in dimensions (Fig. 2, Table 2). M<sup>1</sup> and M<sub>2</sub> of *N. cyclotis* are sub-circular in shape, a feature only shared with *N. certans* (Andersen, 1912a).

The holotype of *N. cyclotis* has both forearms broken and

Andersen (1910) therefore described it as having FAs that were approximately 53 mm (I measured it as 54.18 mm). The only other specimen that I assign to *N. cyclotis* is a male (NHMUK 1987.520) also from the Arfak Mountains. This specimen is a larger adult male than the holotype. The specimen has long hairs, 10–14 mm (depending on where they are measured) that are tricoloured, dark at the base, pale grey in the middle and dark again at the tips. The fur colour of both specimens has bleached due to fixation. It is assumed the bat originally was mottled grey-brown in colour due to the dark section at the base being up to one third the length of the shaft, a much larger proportion than in other *Nyctimene* species except *N. certans*. The tip of the hair is also dark. The specimen is paler in the neck and browner on the head, with the venter a dull cream. The holotype skull is badly damaged (Fig. 2d). Much of the back of the skull is missing (e.g. the squamosal and occipital); the right zygomatic arch is broken and half of the right side of the brain case and most of the basicranial floor is missing. The upper canines have been glued back into the tooth row, but not quite in the correct plane; the upper right P<sup>4</sup> and M<sup>1</sup> and the left upper incisor are missing. The anterior end of the left M<sup>1</sup> is worn to such an extent that there is no enamel left on the lingual side (Fig. 2). The lower mandible is broken between P<sup>3</sup> and P<sup>2</sup> on the right and M<sup>2</sup> is missing on the left.

The length of the 5M-1P and 2M-2P separates *N. cyclotis* from other medium-sized species from New Guinea. The 5M-1P digit is relatively long compared to the 5-MET, with a ratio (5-MET/5M-1P) < 1.9 (Fig. 3); 2M-2P however is short, less than 7.5 mm and markedly shorter than *N. certans* for equivalent FA length. A larger series, however, may show overlap in these traits between *N. cyclotis*, *N. wrightae* and *N. certans*.

The second specimen of *N. cyclotis* (NHMUK 1987.520) was caught in 1986 by Ian Craven of World Wildlife Foundation PNG program. His notes on the specimen label



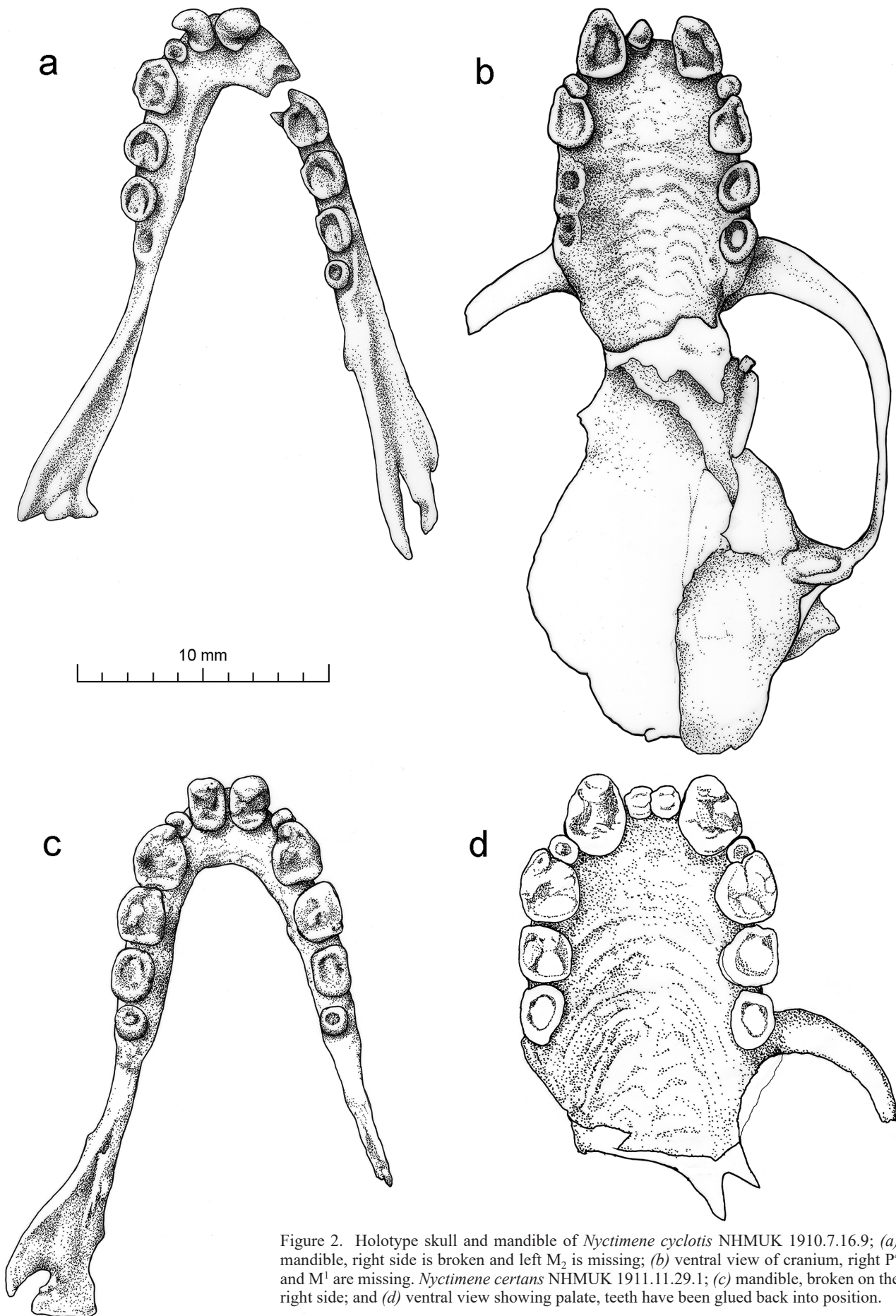


Figure 2. Holotype skull and mandible of *Nyctimene cyclotis* NHMUK 1910.7.16.9; (a) mandible, right side is broken and left  $M_2$  is missing; (b) ventral view of cranium, right  $P^4$  and  $M^1$  are missing. *Nyctimene certans* NHMUK 1911.11.29.1; (c) mandible, broken on the right side; and (d) ventral view showing palate, teeth have been glued back into position.



indicate that the yellow colour on the ears is paler than the spots of the wings and both fade to white on fixation.

Nothing is known of the natural history of *N. cyclotis* and all natural history accounts attributed to this species to date are in my opinion not of this species.

### *Nyctimene certans* Andersen, 1912b

Figs 2–5, 7–12

**Type locality.** Mount Goliath, Prov. of Papua, Indonesia.

**Holotype.** NHMUK 1911.11.29.1. ♂ adult, skin and skull.

**Common name.** Mountain tube-nosed fruit bat.

**Distribution.** Upper montane forest of New Guinea, above 700 m up to 3000 m asl but typically most localities lie between 1600–2500 m.

**Specimens examined.** 39 including the holotype, see Appendix 1.

**Revised diagnosis.** *Nyctimene certans* differs from all other *Nyctimene* species in having the shortest upper (< 32%) and lower (< 36%) tooth rows relative to skull length (Table 2, Figs 2, 4). *Nyctimene certans* further differs from *N. cyclotis* in having a relatively broader palate, with a P<sup>3</sup>-P<sup>3</sup> markedly longer than the upper post-canine tooth row (P<sup>1</sup>-M<sup>1</sup>), vs. slightly longer than P<sup>1</sup>-M<sup>1</sup> in *N. cyclotis*; *N. certans* also has a longer second digit, especially the 2M-2P. On average it is larger and darker dorsally than any other medium-sized *Nyctimene* species from mainland New Guinea. It also has the broadest cheek-teeth relative to skull size (esp. P<sup>3</sup>), which are almost as broad as they are long, compared to any other species of Nyctimeninae.

**Description.** Essentially Andersen's original description stands (Andersen, 1912b), validated by a larger series than the two specimens available to Andersen. *Nyctimene certans* is a medium-sized species for the subfamily with a forearm range of 54.8–67.4 mm.

The fur colour is dark grey and grizzled with wood-brown on the back; it has for the subfamily, the largest proportion of the base of the hair shaft being dark brown (30–40%) and likewise the tips of the hairs dark brown (10–30% of the hair shaft) (Figs. 5, 7).

*Nyctimene certans* has a significantly longer skull, with CBL, C<sub>1</sub>-M<sub>2</sub>, Zygo-L larger than the other sympatric medium-sized species (Tables 1 and 2). Its brain case is longer but not as broad as the similar *N. wrightae* sp. nov. (Fig. 4). Further specimens may also show this to be the case for *N. cyclotis*.

The skull of the holotype specimen is badly broken as noted previously (Peterson, 1991; Andersen, 1912b). Only the anterior half of the skull remains, consisting of the palate, rostrum and half of the left zygomatic arch (Fig. 2), from which the characteristic rounded dental arcade, and large, broad, cuspidate teeth are apparent. The lower mandible is in better condition with only the right angular process broken off and missing (Fig. 2).

Peterson (1991) discussed the possibility that the holotype of *N. certans* is a sub-adult due to the metacarpal lengths being relatively short, together with the highly cuspidate teeth. Indeed the type specimen has one of the shortest FA and metacarpals of the specimens assigned to *N. certans* here

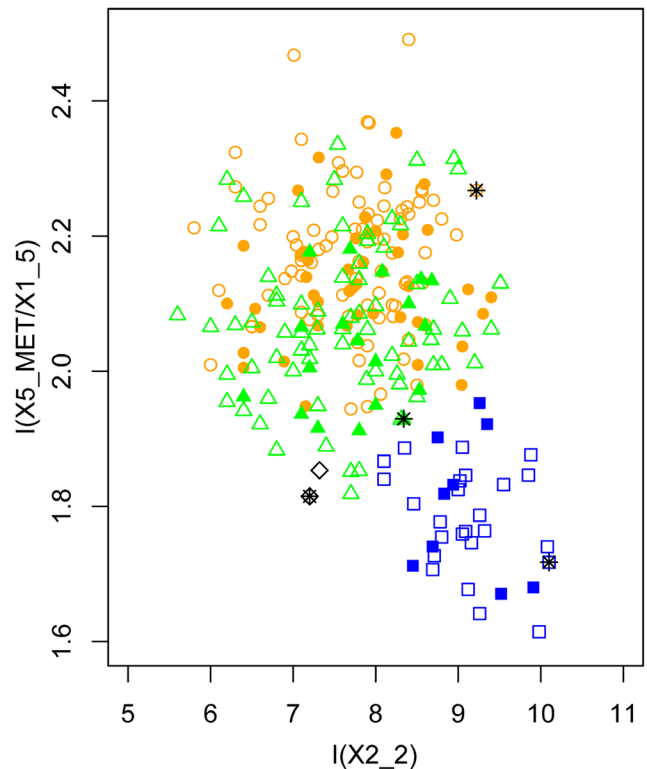


Figure 3. Plot of 5-Metacarpal divided by the 1st phalanx of the 5 digit, versus 2nd phalanx of the 2nd digit, indicating separation of *Nyctimene certans* and *N. cyclotis* using 3 simple wing measurements for 255 specimens. *Nyctimene certans* (squares,  $n = 35$ ), *N. a. papuanus* (circles,  $n = 128$ ), *N. wrightae* sp. nov. (triangles,  $n = 90$ ) and *N. cyclotis* (diamonds,  $n = 2$ ). Holotype specimens are indicated for each species by an asterisk. Full or closed symbols indicate individuals identified genetically ( $n = 77$ ), open symbols are those identified morphologically ( $n = 179$ ).

and the 5M-1P and 5M-2P are particularly short. The teeth are large and compacted; additionally the cusps are well defined similar to a sub-adult. However the teeth do show wear, as indicated by exposed dentine on the molars, suggestive of some use, more than that anticipated in a juvenile. Therefore overall, although the individual is clearly not very old, I concur with Andersen (1912b) who considered the specimen to be an adult.

The wings of *N. certans* are deeper than its sympatric congeneric species; primarily caused by a significantly longer 5th digit, especially the 1st phalanx (Tables 2, 3). The wings also, on average, have significantly longer 2M-2P than their sympatric congenics (Tables 2, 3). Bats with a 2M-2P above 8.0 mm and a ratio 5-MET / 5M-1P below 2.0 are therefore likely to be *N. certans* (Fig. 3). A combination of these three external wing measurements therefore typically separates *N. certans* from the other sympatric *Nyctimene* of similar body-size including the externally very similar *N. cyclotis* (Fig. 3).

**Remarks.** Smith & Hood (1983) based their concept of *N. cyclotis* from specimen BPBM 28398 (photographed in fig. 1c of their paper) but I concur with Peterson (1991) who identified this specimen as *N. certans*.

*Nyctimene certans* is the only species within the subfamily to have round palatal fenestrations (vacuities) at the distal



Figure 4. Dorsal and ventral views of skulls and mandibles of *Nyctimene certans* (young adult) (AM M.17888), *N. certans* (old, showing extensive tooth wear) (AM M.30648), *N. wrightae* sp. nov. (holotype) (AM M.16423) and *N. a. papuanus* (AM M.16425).





Figure 5. Dorsal and ventral photographs of the holotypes of *Nyctimene certans* and *N. cyclotis*. (a, b) Holotype of *N. certans* NHMUK 1911.11.29.1; photographs courtesy of Harry Taylor (NHMUK). (c, d) Holotype of *N. cyclotis* NHMUK 1910.7.16.9; photographs courtesy of Jeff Streicher (NHMUK). The ears are short and rounded in *N. certans* and *N. cyclotis*. Both FA's of *N. cyclotis* are clearly broken. The dorsal stripe is difficult to distinguish in the base of the dorsal in *N. certans* and *N. cyclotis*. Overall there is a grizzled grey-brown appearance in the fur in the dorsal of *N. certans* and *N. cyclotis*, compared to a more even brown colour in *N. wrightae* sp. nov. and *N. a. papuanus* (see Fig. 6).



**Table 3.** Welch Two Sample *t*-tests for each pair of species, on 24 variables used in the LDFA.

variable	<i>Nyctimene certans</i> vs <i>N. a. papuanus</i>				<i>N. certans</i> vs <i>N. wrightae</i> sp. nov.				<i>N. wrightae</i> sp. nov. vs <i>N. a. papuanus</i>			
	t	df	p-value	σ level	t	df	p-value	σ level	t	df	p-value	σ level
FA	10.3759	43.30	2.562e-13	***	3.4479	46.65	0.001	***	13.1333	223.63	< 2.2e-16	***
5-MET	4.7578	46.90	1.905e-05	***	-1.1760	49.75	0.245	ns	9.8496	215.45	< 2.2e-16	***
4-MET	8.6278	41.84	7.820e-11	***	1.8121	47.11	0.076	ns	11.3896	203.93	< 2.2e-16	***
3-MET	7.8199	44.85	6.456e-10	***	2.0823	51.22	0.042	*	9.3295	199.57	< 2.2e-16	***
2-MET	8.1459	47.23	1.492e-10	***	0.2553	69.19	0.799	ns	10.1930	166.62	< 2.2e-16	***
1-MET	5.5086	6.08	9.399e-07	***	2.7283	71.44	0.008	***	3.1572	192.50	1.849e-03	***
2M-2P	12.0540	74.41	< 2.2e-16	***	11.5190	93.95	< 2.2e-16	***	-0.8151	183.81	0.416	ns
5M-1P	16.9670	42.29	< 2.2e-16	***	9.8638	49.32	2.949e-13	***	11.7104	187.49	< 2.2e-16	***
Tibia	6.1387	39.38	3.201e-07	***	2.2659	52.72	0.028	***	6.0383	165.00	9.983e-09	***
Ear	-1.3502	36.74	0.185	ns	-3.6779	37.33	0.001	***	4.8329	223.55	2.500e-06	***
GSL	17.0682	38.52	< 2.2e-16	***	9.1484	27.34	8.251e-10	***	4.7336	17.21	1.859e-04	***
CL	12.7717	48.41	< 2.2e-16	***	2.7974	10.54	0.018	***	3.1863	9.55	0.010	ns
R-B	-0.0698	67.99	0.945	ns	-2.9867	17.13	0.008	***	2.9625	16.98	0.009	***
R-L	7.1231	49.18	4.195e-09	***	5.0585	14.99	1.418e-04	***	-0.3671	11.65	0.720	ns
P <sup>3</sup> -B	13.8054	31.41	6.985e-15	***	5.4119	35.24	4.515e-06	***	12.7710	20.90	2.456e-11	***
P <sup>4</sup> -B	13.9676	30.78	7.281e-15	***	5.0534	35.85	1.289e-05	***	10.8670	16.31	6.993e-09	***
M <sub>1</sub> -B	6.1484	28.38	1.161e-06	***	2.3401	30.91	0.026	*	8.6007	23.46	1.033e-08	***
M <sub>2</sub> -B	1.7237	26.12	0.097	ns	-0.9012	32.59	0.374	ns	4.1265	16.58	0.001	***
Brain-W	9.7852	43.31	1.538e-12	***	4.2857	18.82	0.000	***	4.1300	28.07	0.000	***
Brain-H	4.2623	40.96	1.158e-04	***	-0.8322	26.17	0.413	ns	4.7784	18.36	1.428e-04	***
Zygo-B	9.8423	50.00	2.738e-13	***	2.8808	20.65	0.009	***	4.1662	16.91	6.537e-04	***
Zygo-L	19277	70.43	< 2.2e-16	***	6.0478	13.86	3.134e-05	***	0.2211	14.21	0.828	ns
C <sub>1</sub> -M <sub>2</sub>	8.6045	38.50	1.677e-10	***	4.5861	32.99	6.216e-05	***	4.6721	28.61	6.487e-05	***
C <sub>1</sub> -C <sub>1</sub>	12.1752	40.66	3.83e-15	***	1.4792	16.876	0.1575	ns	4.4133	13.451	0.0006	***

end of the palate. However, as noted by Smith & Hood (1983), this character is variable, sometimes with two present as in BPBM 28398 (Smith & Hood, 1983) and AM M.7908 (as illustrated in Flannery, 1995b), or none as for AM M.17888 (Fig. 4). The only other recorded case of a palatal fenestration in another species of the subfamily is an AMNH specimen of *N. major* from Kiriwina Island. Koopman (1982) discussed this specimen and concluded that it was very aged and somewhat pathological, adding that there was secondary bone deposition lateral to the molars. It is unlikely that these fenestrations have any function, as they are so variable between individuals. They could therefore represent a vestigial pattern of growth or possibly an indication of masticator stress on the palate, arising from eating hard fruit during growth as is thought to occur in other mammals (Moss & Feliciano, 1977). They remain a feature generally found only in *N. certans*.

The yellow colour of the ear and wing spots fades on fixation in alcohol in *N. certans* (Flannery, 1995b), similar to *N. cyclotis*, and therefore colour assessment from specimens preserved in alcohol may not be entirely accurate.

Little is known of the biology of *N. certans*, including its diet, population density, home range, or life expectancy. What natural history is reported is usually from short-term expeditions of less than a few weeks and is summarized in the excellent mammal and field guides of the region (Flannery, 1995b; Bonaccorso, 1998).

### *Nyctimene wrightae* sp. nov.

Figs 3, 4, 6–12, Tables 2–6

**Holotype.** AM M.16423, ♀, adult, whole body in spirit, skull extracted, collected 7 Nov. 1985 by Dr Ken Aplin.

**Paratypes:** A total of 29: AM M.16230 (Field number FA 332), ♂ spirit and skull, AM M.16231 (Field number FA 357), ♀ adult, spirit and skull, both collected on 08-April-1986, AM M.16870 (field number FA 394), 1♂ adult,

spirit body, collected 09-Apr-1986, all three collected by T. Flannery and T. Ennis from Munbil, Star Mountains, West Sepik Prov., PNG. AM M.16426 (field number X19), 1♂ adult, spirit and skull collected 22-Nov-1985, AM M.16428 (field number X97), 1♀ adult, body in spirit, collected 24-Nov-1985, AM M.16432 (field number Y20), 1♂ adult, body in spirit, collected 25-Nov-1985, all three collected by K. Aplin from Waro, Southern Highland Prov., PNG. AM M.16421 (field number H29), 1♀ sub-adult, collected 17-Oct-1985, AM M.16422 (field number H49), 1♀ adult, collected 19-Oct-1985, both bodies in spirit and skulls extracted, AM M.16440 (field number G97), 1♀ adult, body in spirit, collected 15-Oct-1985, AM M.16441 (field number L24), 1♀ adult, spirit body, collected 14-Oct-1985, all four collected by K. Aplin, Magidobo, Southern Highland Prov., PNG. AM M.16443 (field number F04), 1♂ adult, spirit body and skull, and AM M.16444 (field number K10), 1♀ adult, spirit body, collected respectively 7 and 11-Oct-1985, by K. Aplin in Bobole village, Mt Sisa, Southern Highland Prov., PNG. AM M.17887 (field number FB2), 1♂ adult, skin and skull, collected 30-Mar-1986 by T. Flannery in regrowth, outskirts of Tabubil, Western Province, PNG. AM M.21771 (field number FJ139), 1♀ sub-adult, body in spirit, collected 08-Mar-1990 by T. Flannery, Mt Somoro Summit, West Sepik Prov., PNG. AM M.32382 (field number B32), 1♂ adult, skin and skull, collected 12-Jun-1994 by Boeadi, Timika area, roadside forest at new town complex, Papua Prov., Indonesia. BPBM 24539, 1♂ adult, skin and skull collected 5-April-1965 and BPBM 24570, 1♂ adult, skin and skull, collected 10-Apr-1965 by P. J. Shanahan, Sinaeada, Milne Bay Prov., PNG. BPBM 28396, 1♀ adult, skin and skull, collected 10-Jan-1967 by P. H. Colman, Mt Missim (S Slopes), Morobe Prov., PNG. BPBM 51380, 1♀ adult, skin and skull, collected 05-Aug-1967 by P. H. Colman, 10 km W Bulolo, Morobe Prov., PNG. BPBM 99227, 1♀ adult, skin and skull, collected 02-Oct-1970 by F. J. Radovsky, Bupu river 12 mi, NE Lae, Morobe Prov., PNG. BPBM 103790,



Figure 6. Dorsal and ventral photographs of the holotype of *Nyctimene wrightae* sp. nov. compared with *N. a. papuanus*. (a, b) Holotype of *N. wrightae* sp. nov. AM M.16423, photographs courtesy of Harry Parnaby (AM). (c) *N. a. papuanus*, NHMUK 1901.11.5.3; (d) *N. wrightae* sp. nov. NHMUK 1969.1417. Typically the fur is short and brown, but varies (see Fig. 7). *Nyctimene a. papuanus* and *N. wrightae* sp. nov. have a clearly demarcated dorsal stripe unlike *N. certans* and *N. cyclotis* (see Fig. 5). *Nyctimene wrightae* sp. nov. and *N. a. papuanus* have relatively long and distally tapered ears but those of *N. wrightae* sp. nov. tend to be thickened on the leading edge; externally *N. wrightae* sp. nov. and *N. a. papuanus* can appear very similar as exemplified by (c) and (d).



1♀, spirit, collected 16-Feb-1974 by A. B. Mirza from 5 km N of Wanuma, Madang Prov., PNG. BPBM 109893, 1♂ adult, skin and skull, collected 24-Sep-1986 by A. E. Engilis Jr, from 8.5 km N, 13 km E Utai, Agpo Creek (Camp I), West Sepik Prov., PNG. NHMUK 1969.1417, 1♂ adult, skin and skull, collected 14-Jul-1969 by J. I. Menzies from Olsobip, Upper Fly, Western Prov., PNG. PMAG 25845, 1♀ adult, spirit specimen collected from Lababia, Morobe Prov., PNG. PMAG 25847, 1♀, PMAG 25849, 1♂, and PMAG 25851, 1♂, all adult spirit specimens, collected from Aelalar river, Kawiali, Morobe Prov., PNG. WAM47463, 1♀ adult, and WAM47464, 1♂ adult, bodies in spirit and skulls extracted, collected 01-Jan-1997 by D. J. Kitchener, Timika, Papua Prov., Indonesia.

**Specimens examined.** A total of 119, vouchered bodies 32, vouchered and field data from 87 released individuals as listed below: PMAG un-catalogued ♂♂, adults spirit specimens (NM33 and NM35 in my database), collected from Tamerce, Mt Loves, Hirtano Highway, Central Prov., PNG. DW2085 1♀ adult sampled on 05-Nov-1996 and DW2089 1♀ adult, and DW2090 1♂ adult, sampled on 16-Nov-1996, field data & tissues provided by Debra Wright, Ivimka, Gulf Prov., PNG. NRI 117, 312, 411, 622, 689, 712, 721, 729, 736, 781, OM11, OM88 adult ♀; NRI 007 ♂, measured 138b, 683, 706, and released 715, 752, all adult ♂♂, NRI 722 sub-adult ♂, from Sempi, Madang Prov., PNG by Nancy Irwin 1996–2000. NRI 261, 287, 299, 311, 889, 892–893, 900, 903 all sub-adult ♀♀; NRI 307, 814, 855, 882, sub-adult ♂♂; NRI 241, 255, 263, 279, 291–292, 306, 763, 766–767, 769–70, 773–775, 780, 782–786, 795, 798, 801, 803, 805, 808, 815, 831, 838, 850, 852, 858–859, 879, 886, 897, 902, 910 adult ♂♂; NRI 252, 262, 288–289, 300, 776, 809–810, 823, 865, 867, 877, 880, 895, 914, adult ♀♀ measured and released from O-Pio, Chimbu Prov., PNG by Nancy Irwin 1999–2000.

**Type locality.** Namosado (06°15'S 142°47'E, 500 m asl), Southern Highlands Province, PNG.

**Distribution.** Widespread from lowland to montane forest of New Guinea.

**Diagnosis.** *Nyctimene wrightae* sp. nov. differs from all other species of Nyctimeninae in having the shortest mean rostrum length (R-L) relative to skull length (GSL) (< 0.8); and differs from all Nyctimeninae other than *N. certans* and *N. cyclotis*, in having a proportionately broader dental arcade and palate as reflected by a P<sup>3</sup>-P<sup>3</sup> that is distinctly greater than P<sup>1</sup>-M<sup>1</sup>, compared to a P<sup>3</sup>-P<sup>3</sup> being equal or shorter than P<sup>1</sup>-M<sup>1</sup> in other species of the genus. It differs from all species of the genus, other than *N. certans*, in having the greatest Zygo-B relative to skull length (> 79% compared to < 74%). It differs further from all other species of the genus, other than *N. certans* and *N. cyclotis*, in its reduced width across M<sup>1</sup>-M<sup>1</sup> compared to P<sup>4</sup>-P<sup>4</sup>.

*Nyctimene wrightae* sp. nov. is further distinguished from *N. certans* and *N. cyclotis* in having short (< 10 mm), brown, dorsal fur versus grey-brown fur, as well as a clearly defined brown dorsal stripe, compared to the ill-defined and often indistinct dorsal stripe of *N. certans* and *N. cyclotis*; the basal portion of the hair shaft that is dark brown is usually less than 10%, with 5–10% of the distal portion of the hair is dark similar to that of *N. a. papuanus*, in sharp contrast to much higher proportion of dark fur of *N. certans* and *N. cyclotis*; *N. wrightae* sp. nov. differs further in having ears

that are longer than broad and which taper towards the apex typical of most *Nyctimene* species, in contrast to the short, broad ears of *N. certans* and *N. cyclotis*

*Nyctimene wrightae* sp. nov. is readily confused with the sympatric *N. a. papuanus* in external appearance but the latter species is of smaller average size. *Nyctimene wrightae* sp. nov. is readily distinguished by its smaller size, e.g., FA 52–63 mm, compared to FA > 67 mm for *N. aello*, *N. major* and *N. rabori*.

*Nyctimene wrightae* sp. nov. is difficult to identify in the field from sympatric species of *Nyctimene*, the key features are its brown fur, distinct dorsal stripe, long pointed ears, generally large size and its distinctive “smiling” facial expression (Fig. 7).

**Description.** The ears are similar in shape to *N. a. papuanus*, they are thickened on the leading edge, which is a feature more similar to *N. certans* and *N. cyclotis* (see Figs 5–7). Ear length scales with body size in *N. wrightae* sp. nov. Fur colour of *N. wrightae* sp. nov. is variable but is typically brown on the dorsal, grey-brown around the face and the pale venter contrasts with the browner fawn colour of the dorsum (Figs 6, 7). The wings have variable white (sometimes yellow) and brown spotting typical of the subfamily. Large white or yellow spots are found more commonly on the large metacarpals of the wings (Fig. 7). Individuals vary greatly in the extent of spotting. *Nyctimene wrightae* sp. nov. shows no consistent pattern of sexual size dimorphism. Sexual dimorphism in colour is more pronounced in the reproductive season. The hair of the central thorax is whiter and brighter in males than females. Males have brighter, more defined fur colour especially on the ventral flanks where they have striking yellowish-orange patches, which develop during the mating season. Females are an overall fawn brown colour and are generally duller. Dr Deb Wright and I have occasionally caught yellow morphs from three locations in mainland New Guinea (Fig. 7c). These morphs have yellow dorsal and ventral fur with brown wing spotting and white spotting on the forearm and wing digits.

The palate length is relatively short compared to GSL. The rostrum is short, R-L averaging 3.62 mm (± 0.6 SD) and is deep dorsoventrally. Teeth are broad and cuspidate (Fig. 4).

Mean P<sup>4</sup>-P<sup>4</sup> (8.61±0.7 mm) is equal to or greater than mean M<sup>1</sup>-M<sup>1</sup> (8.49±0.6 mm) in *N. wrightae* sp. nov., unlike *N. a. papuanus*, in which M<sup>1</sup>-M<sup>1</sup> averages larger (7.92±0.80 mm) than P<sup>4</sup>-P<sup>4</sup> (7.71±0.76 mm). The upper premolars and molars are generally broad and semi-circular in outline in *N. wrightae* sp. nov. and almost as broad as long. This contrasts with the equivalent teeth in *N. a. papuanus*, which are less broad and are on average smaller and more rectangular in shape (longer in length than breadth); *N. certans* have squarer, broader teeth and relatively much broader cheek teeth (both upper and lower P<sup>3</sup> and P<sup>4</sup>) than either *N. a. papuanus*, *N. wrightae* sp. nov. or *N. cyclotis*; and *N. cyclotis* has premolars that are similar in shape (longer than broad) to *N. a. papuanus* but which are much bigger (Fig. 4). The brain case length of *N. wrightae* sp. nov. is shorter relative to skull length than *N. certans*, *N. cyclotis*, or *N. a. papuanus* (Figs 2, 4).

**Etymology.** With great pleasure I name this bat after Dr Debra Wright, Director for Wildlife Conservation Foundation, PNG 1996–2003, the co-founder of PNG Research Foundation and PNG Institute of Biological Research. She has tirelessly





Figure 7. Photographs of *Nyctimene wrightae* sp. nov. and *N. certans*. (a) Female with young pup attached, showing characteristic long ears with thickened edge and short, brown hair (photograph courtesy of Debra Wright); (b) *N. certans*, showing darker fur than *N. wrightae* sp. nov. and round, broad ears (photograph courtesy of Debra Wright); (c) *N. wrightae* sp. nov. yellow colour morph with large brown spots caught in O-Pio, Chimbu Prov. (field number NRI 721), the dorsal stripe is clear and becomes thinner in upper part of back.

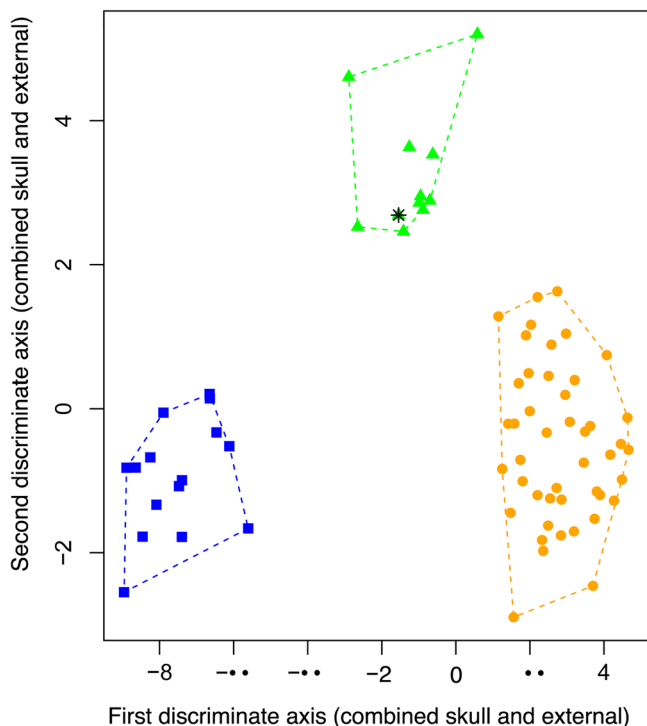


Figure 8. First two axes of a LDFA based on 14 factors of combined skull, dental and external body measurements (listed in Table 4), showing separation between *N. a. papuanus* (circles,  $n = 44$ ), *N. certans* (squares,  $n = 15$ ) and *N. wrightae* sp. nov. (triangles,  $n = 11$ ). Holotype of *N. wrightae* sp. nov. is indicated by star symbol.

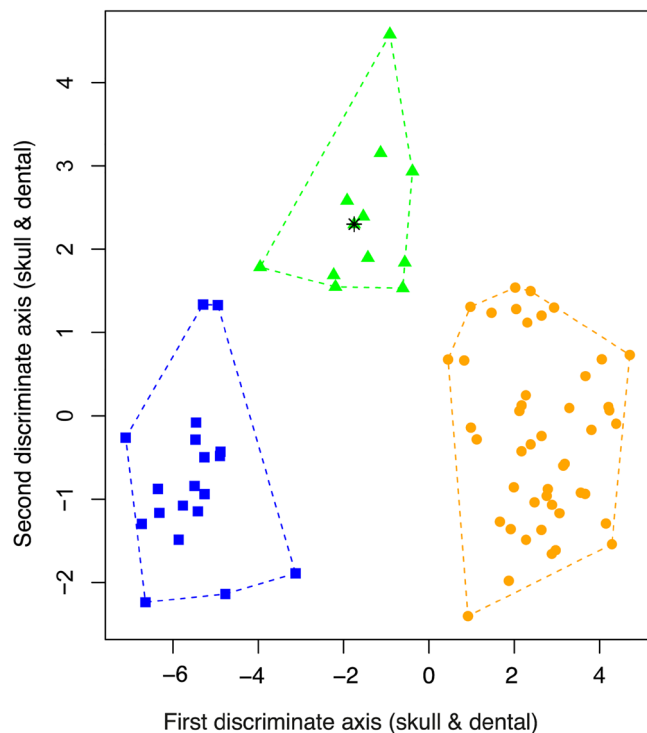


Figure 9. Separation of three species on the first two axes of a LDFA based on 14 skull and dental measurements (listed in Table 5). *Nyctimene a. papuanus* (circles,  $n = 39$ ), *N. certans* (squares,  $n = 19$ ), *N. wrightae* sp. nov. (triangles,  $n = 10$ ). Star indicates holotype of *N. wrightae* sp. nov.

given her energy and considerable skills to capacity building and training Papuan New Guinean scientists. She provided logistic assistance for my team and I, helped me secure funding, provided access to facilities, and gave moral and intellectual support throughout my field-work. Her good humour, boundless energy, passion and generosity meant that despite spending many years together in remote places, we have formed a lifelong friendship. It was this cryptic bat species that started my whole journey with *Nyctimene*.

**Common name.** Happy tube-nosed fruit bat. Field assistants Toby Kamli and Rafael Kaneg, noticed the difference between this species and *N. a. papuanus* in the hand and called this species the hamamas bat, which in Tok Pisin means the happy bat, due to the wide “smile” characteristic of this species. I therefore propose the happy tube-nosed fruit bat as the common name, alluding to the “smile” that seems to result from the broad dental arcade and palate and very short rostrum, which are diagnostic characters of the species.

**Remarks.** Taxonomists have known for some time that there were aberrant specimens with affinities to *N. a. papuanus* or *N. certans* that did not fit described forms of *Nyctimene*. Tate (1942) noted an odd specimen from the Idenburg River, Papua that differed from the other 44 specimens of *N. a. papuanus* from the Fly River, PNG in the Archbold collections. Tate (1942, p. 721) states “The only observable difference ... is the wider molars, but even so their width comes within the upper range given by Andersen in his table”. Likewise, McKean (1972) mentions a specimen from Lake Kutubu, Southern Highlands Prov., PNG (CM2316 from ANWC) that had skull and dentition similar to the

description of the holotype of *N. cyclotis*, but a quite different pelage, being “short and brown rather than long, grey and mottled”. The specimen was rather large, with a FA of 62.1 cm given by McKean. He was at pains to point out that the skull and skin were not mismatched. Flannery (1995b) identified the same Lake Kutubu specimen as *N. cyclotis*. I have not examined the latter specimen nor the one from Idenburg River discussed by Tate, but from the descriptions and the measurements provided by the latter authors it is highly likely that both specimens are representatives of *N. wrightae* sp. nov. Although not discussed by McKean, another slightly smaller individual that he lists as *N. a. papuanus* (ANWC 2317, FA = 58.5 mm), was caught from the same locality at Lake Kutubu on the same day. It would be interesting to confirm the identity of this specimen, to assess a possible instance of sympatry between *N. a. papuanus* and *N. wrightae* sp. nov.

The *N. wrightae* sp. nov. paratype BPBM28396 from Mt Missim, Morobe district was previously identified as *N. certans* by Peterson (1991) and illustrated in fig. 2 of that paper. The splayed P<sup>3</sup> are clearly evident in his illustration, and the dental arcade, while rounded, is not as extreme as in *N. certans*. The brain case is short in length compared to the GSL, characteristic of *N. wrightae* sp. nov.. The measurements of the 5th metacarpal and 5M-1P compared to the 2nd-2nd also distinguish this specimen from *N. certans*. Several *N. certans* (BPBM 28397–9, 28404, and 28410) were caught sympatrically with the *N. wrightae* sp. nov. paratype at Mt Missim. The other five BPBM paratype specimens listed above were individuals previously assigned to *N. cyclotis* by Peterson (1991) and Bonaccorso (1998).



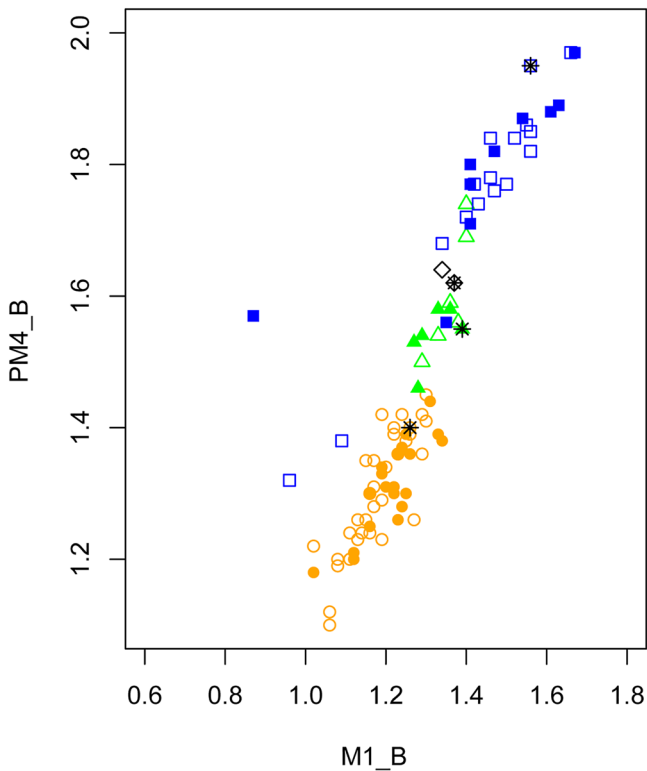


Figure 10. Plot of breadth against  $M_1$  breadth for *Nyctimene a. papuanus* (circles,  $n = 58$ ), *N. certans* (squares,  $n = 27$ ), *N. wrightae* sp. nov. (triangles,  $n = 11$ ) and *N. cyclotis* (diamond,  $n = 2$ ). Filled symbols are genetically identified. Holotypes of each species indicated by star symbols. Smaller outliers of *N. certans* are old individuals with smaller teeth due to extensive tooth wear. Outliers of *N. wrightae* sp. nov. with larger teeth than their conspecifics are young individuals with little tooth wear.

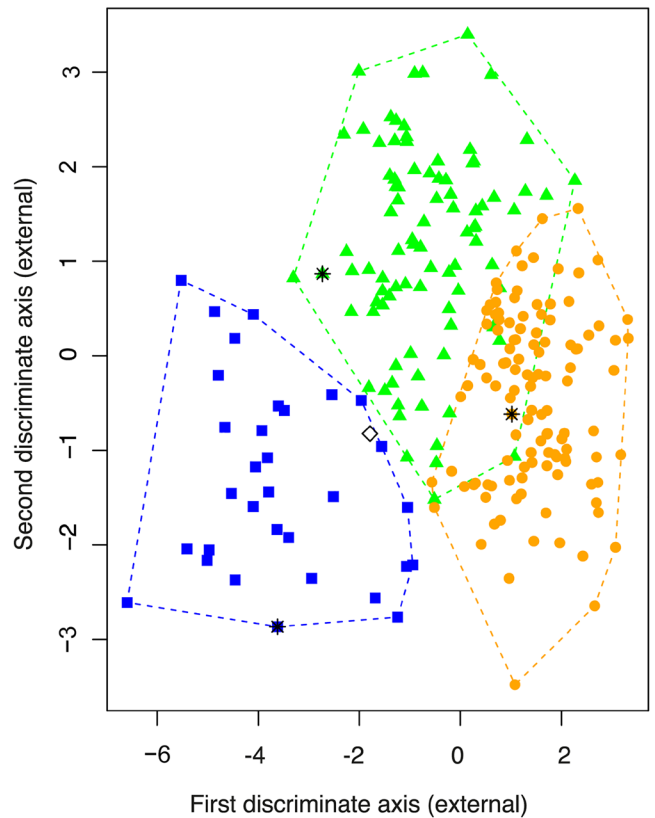


Figure 11. First two axes of a LDA of three *Nyctimene* species based on 7 external wing measurements (listed in Table 6),  $n = 242$ . Separation is achieved between individuals of *N. certans* (squares,  $n = 32$ ) from *N. wrightae* sp. nov. (triangles,  $n = 88$ ) and *N. a. papuanus* (circles,  $n = 122$ ) but there remains some overlap between *N. wrightae* sp. nov. and *N. a. papuanus*. Holotypes are indicated by star symbol. The holotype of *N. cyclotis* was plotted *a posteriori* (diamond).

NHMUK 1897.12.6.3 reassigned here as a paratype of *N. wrightae* sp. nov., is one of 15 specimens identified as *N. papuanus* (currently placed as *N. a. papuanus*) by Andersen (1912a).

*Nyctimene wrightae* sp. nov. is restricted to mainland New Guinea. The extensive intraspecific variation found within *N. wrightae* is likely to have a geographic component, perhaps associated with latitude, altitude and niche sympatry.

**Reproductive biology.** What little is known of the reproductive biology is from my field records combined with examination of museum specimens caught while pregnant. BPBM 28396 and WAM 47463 were caught in January and both had a large well-developed foetus, the latter foetus even had a well developed dorsal stripe. I caught pregnant females in Opio on 17 and 22 January (NRI 776–NRI 823) and as late as 14 February (NRI 888) during 2000. On two occasions during July, in the same area, I caught females with volant young that were of equal or larger body size of the mother and were still suckling, which suggests a long maternal care investment of about 6 months. In general the pattern therefore seems to be that pregnancy occurs from January to February, with females still lactating with volant young in July

**Table 4.** Coefficients of linear discriminants from 18 combined variables used to separate 71 individuals (*Nyctimene a. papuanus*  $n = 45$ , *N. certans*  $n = 15$  and *N. wrightae* sp. nov.  $n = 11$ ), plotted in Fig. 8. Proportion of trace of LD1 = 0.9017 and for LD2 = 0.0983.

character	LD1	LD2
MET5×5M-1P	5.1381	3.4532
4M-1P	-0.4151	0.0032
2M-1P	0.0484	-0.5378
Man-H	-0.1710	-2.8966
C <sup>1</sup> -H	0.3732	-0.9367
P <sup>3</sup> -B	-5.0284	2.0846
P <sup>4</sup> -B	-7.5978	7.0244
M <sub>1</sub> -B	2.6644	-12.8379
M <sub>2</sub> -B	1.2676	7.0017
C <sub>1</sub> -C <sub>1</sub>	0.3426	5.0346
R-B	0.0368	1.3946
Zygo-B / GSL	8.9586	16.3612
Zygo-L / GSL	-5.6242	-3.7147
Brain-W / Brain-H	4.5516	-7.1877



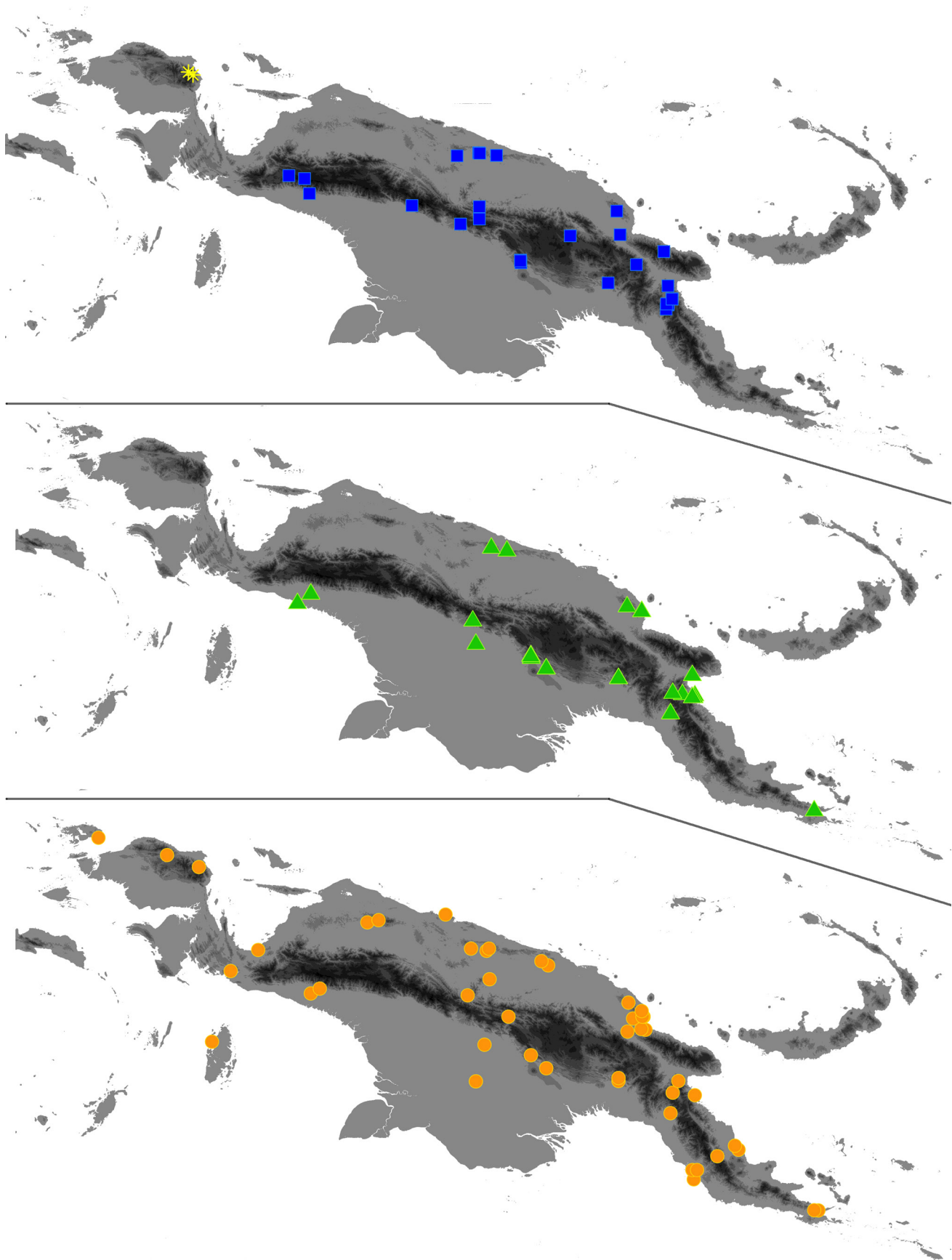


Figure 12. Distribution of specimens assigned in this study to *N. cyclotis* (stars,  $n = 2$ ), *N. certans* (squares,  $n = 26$ ), *N. wrightae* sp. nov. (triangles  $n = 22$ ) and *N. a. papuanus* (circles  $n = 48$ ).

**Table 5.** Coefficients of linear discriminants based on 12 skull and dental variables for 68 individuals (*Nyctimene a. papuanus*  $n = 47$ , *N. certans*  $n = 19$  and *N. wrightae* sp. nov.  $n = 12$ ), plotted in Fig. 9. The proportion of the trace explained by LD1 = 0.9198 and for LD2 = 0.0802.

character	LD1	LD2
C <sub>1</sub> -C <sub>1</sub>	-1.6925	4.0182
P <sup>3</sup> -B	-5.3061	1.7813
P <sup>4</sup> -B	-10.6523	5.2282
M <sub>1</sub> -B	4.3094	-14.7303
M <sub>2</sub> -B	2.9737	7.5039
Man-H	-0.6916	-2.2408
R-B	-0.1635	1.4324
Zygo-B / GSL	16.1977	22.5391
Zygo-L / GSL	-4.7827	-5.1609
Brain-W / Brain-H	4.1920	-5.7598

**Morphometric analyses.** Separation between the three species *N. wrightae* sp. nov., *N. certans*, and *N. a. papuanus* was achieved by using a LDFA with 14 variables (some composite) derived from 4 wing and 13 dental and skull measurements for 71 specimens (Table 4, Fig. 8). The predictive accuracy of the model at classifying specimens to the correct species was 100%, with a posterior probability of assignment > 99.9 for all specimens. The loadings on dimension one explained 0.9017 of the proportion of the trace and while influenced by all the variables the first dimension is most influenced by variables that reflect the breadth of the skull, (Zygo-B/GSL, Brain-W/Brain-H) and the breadth of the premolars (P<sup>3</sup> and P<sup>4</sup>). LD2 explained only 0.0983 and was overwhelmingly influenced by the length of the zygomatic arch in proportion to the length of the skull (Zygo-L/GSL) and the breadth of the molar teeth (P<sup>4</sup>, M<sup>1</sup> and M<sup>2</sup>) (Table 4). Tooth breadth was particularly useful for separating these species but as it is subject to tooth wear with age, species separation was therefore less clear when analyses were confined to skull and dental measurements (Table 5, Fig. 9).

### Species comparisons

*Nyctimene cyclotis* is similar to *N. certans* and to the exclusion of other *Nyctimene* from New Guinea, shares a grizzled and long woolly fur. *Nyctimene a. papuanus* and *N. wrightae* sp. nov. are in contrast generally brown taupe with short fur. The short rounded ears *N. cyclotis* is diagnostic of that species, in combination with the indistinct dorsal stripe in the lower portion of the dorsum and straight parallel post canine tooth row and small M<sub>1</sub> relative to P<sub>4</sub>. *Nyctimene cyclotis* is distinguishable from *N. a. papuanus* on the basis of its larger cheek-teeth and broader dental arcade (esp. at P<sup>3</sup>-P<sup>3</sup>) and smaller M<sub>1</sub> relative to P<sub>4</sub> (Table 2; Fig. 3). Andersen (1912a) noted that *N. cyclotis* had similar pelage to *N. varius*, while *N. minutus* and *N. vizcaccia* (unknown to Andersen) also have the similar grizzled dorsal fur and ill-defined dorsal stripes, but do not share other features in common with *N. cyclotis* or *N. certans*, such as ear shape or the shape and dimensions of the palate, dental arcade, or teeth. Genetic sequencing from *N. cyclotis* would enhance considerably the understanding of the species and placement of *N. cyclotis* in a phylogeny of the subfamily.

*Nyctimene certans* tends to be larger than *N. cyclotis*, *N. wrightae* sp. nov. and *N. a. papuanus*, as shown by its significantly larger FA than the latter species (Table 2). The ears of *N. certans* are short relative to its overall body size, similar to *N. cyclotis*. Raw measurements of mean ear length were not significantly shorter in *N. certans* compared to *N. a. papuanus* (Table 3). However, when taken as a proportion of body size (Ear/FA), ear length was significantly shorter compared to both *N. a. papuanus* (Welch *t*-test,  $n_1 = 30$ ,  $n_2 = 131$ ,  $t = -5.19$ ,  $p = 7.546E-06$ ) and *N. wrightae* sp. nov. (Welch *t*-test,  $n_1 = 36$ ,  $n_2 = 101$ ,  $t = -5.21$ ,  $p = 7.438E-06$ ). Ear shape, being round rather than tapered on the distal portion, is immediately diagnostic rather than actual length measurements, which can be very difficult to measure in the field on a live bat. *Nyctimene certans* have long (10–14 mm) hair reflective of their mountain lifestyle (Fig. 5).

Although *N. certans* is generally larger than *N. cyclotis*, the range for some characters overlap between these species and further samples of *N. cyclotis* might result in overlap in additional characters (Table 2). The main differences between the holotypes of *N. certans* and *N. cyclotis* are palate shape, the broadness of the dental arcade, width of the palate and the broader check teeth of *N. certans*. The type description of *N. certans* describes the broader teeth than other sympatric species and a P<sup>4</sup> greater than 1.7 and M<sup>1</sup>-B greater than 1.4 mm, would also be indicative of this species (Table 1, Fig. 10).

Flannery (1995b) stated that *N. certans* and *N. cyclotis* occurred sympatrically in 5 locations and could be distinguished by different CBL, which he regarded as possibly the only useful diagnostic character to separate these species. He did not provide specimen registration numbers, but I think he was actually comparing *N. wrightae* sp. nov. and *N. certans*. *Nyctimene wrightae* sp. nov. is significantly shorter in GSL and CBL to *N. certans*, (Tables 2, 3), confirming Flannery's observation. GSL of *N. wrightae* sp. nov. is also significantly longer than *N. a. papuanus* (Fig. 4; Tables 2, 3). The posterior of the skull is missing in both specimens of *N. cyclotis* and therefore no comparison is possible at present for this species. GSL and CBL measurements overlap between medium sized *Nyctimene* species and although mean values might be significantly different, absolute measurements are not diagnostic.

*Nyctimene wrightae* sp. nov. is generally of smaller body size than both *N. cyclotis* and *N. certans* but usually larger than *N. a. papuanus*. Although there is extensive overlap in the FA ranges between all of the four latter species (Table 2), mean FA of *N. wrightae* sp. nov. is significantly smaller than that of *N. certans* and significantly larger than *N. a. papuanus* (Table 3). Ear shape of *N. wrightae* sp. nov. is similar to *N. a. papuanus* in that the ears taper distally in both species, in contrast to the short rounded ears of *N. certans* and *N. cyclotis*. The ears of *N. wrightae* sp. nov. are thickened on the leading edge, similar to *N. certans* and *N. cyclotis*, but unlike *N. a. papuanus*. Ear length is significantly longer in *N. wrightae* sp. nov. than in both *N. a. papuanus* and *N. certans* based on summary statistics (Tables 2 and 3). However, ear length scales with body size in these three species and if ear length is expressed as a proportion of body size (EAR / FA), no statistically significant difference remains between *N. wrightae* and *N. a. papuanus* (Welch *t*-test,  $t = -0.3251$ ,  $n_1 = 95$ ,  $n_2 = 45$ ,  $df = 225.358$ ,  $p = 0.7454$ ) but does remain between *N. wrightae* and *N. certans* (Welch *t*-test,  $t = 5.1416$ ,

**Table 6.** Coefficients of linear discriminants from 7 external wing variables for 242 individuals (*Nyctimene a. papuanus*  $n = 122$ , *N. certans*  $n = 32$  and *N. wrightae* sp. nov.  $n = 88$ ), plotted in Fig. 11. LD1 explains 0.771 and LD2 0.229 of the variation.

character	LD1	LD2
5-MET	0.2971	0.4946
5M-1P	-0.3663	-0.6732
5M-2P	0.1449	-0.3434
3M-2P	-0.1192	0.2403
2M-2P	-0.1800	-0.8423
4M-1P	-0.7124	0.7120
3-MET	0.0426	-0.2585

$n_1 = 95$ ,  $n_2 = 36$ ,  $df = 47.166$ ,  $p = 5.163E-06$ ). Measurements of CBL as a proportion of GSL indicates that *N. wrightae* sp. nov. has relatively longer CBL than other small-bodied *Nyctimene*, with mean CBL/GSL equal to 84% in *N. wrightae* sp. nov. as opposed to 81% in both *N. certans* and *N. a. papuanus* (Table 3, Fig. 4).

Morphometrically, *N. wrightae* sp. nov. and *N. a. papuanus* are difficult to separate on external variables alone and are therefore truly cryptic. Although ranges of wing measurements overlap (Table 2), mean wing measurements of *N. wrightae* sp. nov. were significantly larger than those of *N. a. papuanus* for metacarpals and phalanges, see Table 2. In a LDFA based on 7 external wing elements (all of which could be measured in the field), some separation of specimens of *N. wrightae* sp. nov. from *N. a. papuanus* can be achieved, but there is considerable overlap (Fig. 11) (Table 6). No particular variable contributed greatly to the loadings (Table 6). The LDFA assigned 228 out of the 245 individuals correctly to the pre-assigned species (93%), but the confidence in the classification was sometimes low. Even when identification was correct the confidence in the prediction from the model was not always high; the model correctly classified, 119 of the 120 *N. a. papuanus* but 16 had a posterior probability of  $< 0.75$ ; 28 of the 32 *N. certans* were correctly classified with 3 with low confidence; whereas 81 of the 93 *N. wrightae* sp. nov. were correctly assigned, but 10 with low confidence. *Nyctimene wrightae* sp. nov. was therefore the species most likely to be misclassified, and always identified incorrectly as a *N. a. papuanus*. Species separation was clearer in a LDFA using 14 skull and dental measurements that described palate shape, tooth breadth and skull length and breadth (Table 5, Fig. 9). All specimens were assigned correctly to species with high accuracy (posterior probability  $> 98\%$ ). *Nyctimene wrightae* sp. nov. has a significantly broader skull (R-B, Zygo-B and Brain-W) relative to its size than *N. a. papuanus* and *N. certans* (Table 3); and it was these skull breadth variables that contributed to the loadings that separated *N. wrightae* sp. nov. from the other two species. *Nyctimene wrightae* compared to *N. a. papuanus* has a relatively smaller  $M_1$ -B compared to  $P_4$ -B which gives an alpha character indication of species identification between the two very similar species. A bivariate plot of  $P^4$ -B versus  $M_1$ -B shows some separation between specimens of *N. a. papuanus*, *N. wrightae* sp. nov. and *N. certans* ( $n = 98$ ) (Fig. 10). *Nyctimene a. papuanus* and *N. wrightae* sp. nov. separate in my current

dataset (Fig. 10). However, these criteria on their own are not sufficient for unambiguous species separation between all the species as there is a degree of overlap between *N. certans*, *N. wrightae* sp. nov. and *N. cyclotis*. These variables are however very useful in conjunction with other variables in a LDFA which contribute to the separation of the species (Figs 8, 9). Measurements of these two teeth variables must be of adult specimens with “reasonable” levels of tooth wear; tooth breadth is greater in younger animals before they have worn their teeth and much reduced in older animals as they literally wear out their teeth. Where specimens fall on the plot is both dependent on the species identification and the age of the specimen (see Fig. 10). Young adults of *N. wrightae* sp. nov. fall in the range of aging *N. certans* and older specimens of *N. wrightae* sp. nov. fall into the range of young adults of *N. a. papuanus*. In addition, reduction in tooth dimensions from excessive wear is so marked in some specimens of *N. certans* that four specimens fall outside of the strong colinear pattern shown across species in Fig. 10. In these four specimens, using  $P^4$ -B or  $M_1$ -B measurements to inform a LDFA for identification would therefore not be recommended. The two specimens of *N. cyclotis* shown in Fig. 10 indicate that their tooth dimensions conform to the linear size continuum of the small-bodied *Nyctimene* in New Guinea, being larger than *N. a. papuanus* and much smaller than the majority of *N. certans*. To increase both the predictive power and accuracy of diagnosis, a combined LDFA of skull and external measurements is recommended (Fig. 8).

I caution overconfidence in assigning specimens from only a few external measurements, as an LDFA model can predict the wrong species. NHMUK 1969.147 for example is a *N. wrightae* sp. nov. (Fig. 6) but on the 7 external body measurements chosen in Fig. 11 is predicted to be a *N. a. papuanus*. The predictive score for assignment is low using these external measurements, (p.p.  $< 60\%$  assigned to *N. a. papuanus*), but by increasing the external measurements to 12 variables an LDFA predicted the specimen to be a *N. wrightae* sp. nov. (51%); increasing the number of measurements, while increasing the noise, increases the posterior probability (variables = 16, p.p. assignment to *N. wrightae* sp. nov. = 73%). The skull of NHMUK 1969.147 however is clearly a *N. wrightae* sp. nov. (p.p.  $> 98\%$ ) and the combined analysis of external and skull measurements (Table 4) assigned this specimen unequivocally to *N. wrightae* (99%). One explanation of the difficulty of assignment could be a mix up of the skin and skull. However, an alternative explanation is that *N. wrightae* sp. nov. and *N. a. papuanus* are phenotypically conservative and there could be many individuals that are difficult to distinguish from external morphometrics alone.

In summary, *N. wrightae* sp. nov. differs from *N. certans* and *N. cyclotis* in having shorter fur that is brown not grey-brown grizzled, longer tapered ears, a clearly defined and longer dorsal stripe, a short rostrum, and premolars that are longer than broad but with a broader  $M_2$  relative to  $P_4$  (Fig. 4). The dorsal stripe on *N. cyclotis* and *N. certans* by contrast is very difficult to see as the long, grey-brown grizzled hair makes it difficult to distinguish. The dorsal stripe of *N. wrightae* sp. nov. tends to be thinner than in *N. a. papuanus*. *Nyctimene wrightae* sp. nov. is on average larger in all dimensions and has a broader palate (wider or sup-equal  $P^3$ - $P^3$  compared to  $P^1$ - $M^1$  length) than *N. a. papuanus* (narrower  $P^3$ - $P^3$  compared to  $P^1$ - $M^1$  length). This gives the



species a robust facial appearance and the difference in dorsal stripe, along with differences in the wing phalanges, provide characters that for some individuals will be indicative of their species using external features (Fig. 11), however a more definitive diagnosis requires an examination of the dental arcade and cheek teeth (Figs 8, 9).

### Discussion

The morphological assessment presented here clearly demonstrates that *N. certans* and *N. cyclotis* represent distinct species, as originally proposed by Andersen (1912a, b). Taxonomic resolution of the cyclotis species group has enabled recognition of a cryptic, but morphologically distinct, widespread species *N. wrightae* sp. nov. that had often been conflated with *N. cyclotis*, *N. certans* or *N. a. papuanus*. Phenotypically conservative species, so called “cryptic species”, are increasingly being discovered either by thorough comparative morphological revisions (e.g., Bates *et al.*, 2007; Parnaby, 2009), molecular systematics (e.g., Dolman & Hugall, 2008; Hugall & Stanisic, 2011) or a combination of both (e.g., Reardon *et al.*, 2014; Soisook *et al.*, 2015).

This paper forms part of a larger study of the entire subfamily Nyctimeninae and the initial selection of measurements used here was designed to be broadly applicable across all the species, before the discovery of *N. wrightae* sp. nov. It was subsequently realized that additional measurements associated with the length of the teeth (which can only be done practically from photographs in these species) would have been useful additional measurements for separating the species here, as well as a measurement associated with the length of the brain case. Future studies using 2D or 3D tomography that capture such measurements would be a considerable advantage in this group.

In the absence of a comprehensive taxonomic review of Nyctimeninae and a phylogeny of the subfamily, the utility of the five species groups currently recognized within the genus remains an open question. Although *N. wrightae* sp. nov. is similar to *N. certans* and *N. cyclotis* in having broad cheek teeth and a corbane dental arch it does not share the mottled fur, ill-defined dorsal stripe, nor short rounded ears, characteristic of the cyclotis group as defined by Andersen (1912a) and Bergmans (2001) (Fig. 5). Tate (1942) expressed doubt as to whether the species groups proposed by Andersen remained useful in light of subsequently described species and argued, for example, that *N. major* and its subspecies be taken out of the *cephalotes* group, as it had little in common with the more delicate *N. cephalotes*, but Tate did not indicate into which group *N. major* and its allies should be placed. Although *N. wrightae* sp. nov. does not share the majority of characters with the cyclotis group, it has even fewer commonalities with the species most likely to be confused with it, *N. a. papuanus* of the albiventer species group. It should therefore be considered part of the cyclotis group until further revision of the species groups.

The taxonomic implications of age-related, allometric growth and shape changes within the skull should be considered. Adult status in bats can usually be confirmed by the presence of fused cranial sutures (Giannini *et al.*, 2006), but sutures fuse early in sub-adult *Nyctimene*, especially those in the rostrum (Andersen, 1912a). In *Nyctimene*, a number of bones are known to change shape with age,

including the frontal bone behind the postorbital process; the lacrimal and jugal of the zygomatic arch, the orbital process of the maxilla, the sagittal crest and the occipital bone; see Heaney & Peterson (1984), Peterson (1991) and Bergmans (2001) for good discussions on elongation of the rostrum and post-orbital area. The series of immature specimens to full-grown adults in *N. rabori* described by Heaney & Peterson (1984) is particularly helpful. The two different age classes of *N. certans* in Fig. 3 also demonstrate these changes and reveal how sub-adult *N. certans* can be confused with mature *N. wrightae* sp. nov.. This is not unique to *Nyctimene* and other studies show similar age-related shape changes in megachiroptera such as *Pteropus* (Giannini *et al.*, 2006). Great care is therefore required during taxonomic assessments of Nyctimeninae to ensure that developmental growth is not confused with geographic variation or taxonomic status. The teeth of immature sub-adults are compacted before the mandible and rostrum reach their full adult length. The skull elongates and the sagittal crest develops with age. Both the breadth and height of dentition reduce with age through wear (see examples in *N. certans* (Figs 2, 4). This can be dramatic, with the loss of up to a third of tooth breadth and length (see *N. certans*, Figs 2, 4, 10). However, the wing measurements discussed above (the ratio of fifth metacarpal divided by 5M-1P against the 2M-2P) distinguish *N. certans* from *N. wrightae* sp. nov. (Fig. 3).

Ontogenetic changes can also obscure the distinction between *N. wrightae* sp. nov. and *N. certans*. The colour of the pelage and in particular the proportion of the root of the hair shaft that is dark is an external alpha character that distinguishes *N. wrightae* sp. nov. from *N. certans*. However, young individuals of *Nyctimene wrightae* do not attain their adult coat until fully mature. I have caught young that had brown fur when born but lacked a dorsal stripe (although I have seen one foetus with a dorsal stripe). A brown dorsal stripe develops as they mature and the fur becomes fluffier and grey as they moult. With further moults a more defined dorsal stripe develops and later the sexually dimorphic colours such as pale venter and darker dorsum along with the brown pelage colouration, characteristic of the species, finally develop. Large *N. wrightae* sp. nov. sub-adults tend therefore to be grey instead of brown. Pelage colour alone, without understanding the state of maturity is not a reliable character for species recognition. Size alone is also not a reliable criterion for assessment of maturity as I have caught suckling juveniles (together with their mothers) that had larger FAs than their mothers. The maturity of an individual must therefore be carefully assessed before attempting identification.

### Distribution, conservation status and future research

The current IUCN Red List status of *N. cyclotis* is Data Deficient pending taxonomic review (Hutson *et al.*, 2008b). This study confirms that *N. cyclotis* is a good species but is known only from two male specimens from the Arfak Mountains, a high mountain range (> 2800 m asl) of the Vogelkop, the Birds Head peninsula of New Guinea (Fig. 12). This area, while being Mesozoic in origin (Hall, 2002) was geologically separate as an island from New Guinea, only

being integrated into greater New Guinea in the Miocene (Polhemus, 2007). The long-term isolation of this region has long been linked to its high level of endemism, which includes birdwing butterflies, birds of paradise and other mammals (Heads, 2001; Polhemus & Polhemus, 1998; Helgen, 2007). The two specimens of *N. cyclotis* are from a single area of forest, less than 16 km apart. Until further investigation can shed light on the distribution of *N. cyclotis*, the species ought to be considered rare and restricted to this mountain range, a view also advanced by Bonaccorso (1998). The Arfak Mountains cover an area of 4,800 km<sup>2</sup>, but it is unlikely that all habitats in that region would be suitable for the species. The IUCN Red List status would therefore be Vulnerable, based on a known distribution of only two sites that are very close to each other in a single restricted area (criteria VU B1a+2a + C2b and D2) (IUCN, 2001). I have not examined material in the Museum Zoologicum Bogoriense or other Indonesian or Papua New Guinea institutions. Identifying further *N. cyclotis* in these and other collections would be a vital step to a better understanding of the distribution of this species.

This study enables a reassessment of the distribution and altitudinal range of *N. certans* based on the 39 specimens assigned to this species from 26 localities (Appendix 1, Fig 12). The distribution is mainly along the central mountain belt, with a disjunct occurrence in the Torricelli Mountains of the Western Sepik Province, and Finisterre Mountains, Madang Prov., separated by lowland forest. *Nyctimene certans*, although apparently widespread in montane forest, are not numerous in collections, being represented by less than 200 specimens that are identified in museum databases as *N. certans* or *N. cyclotis* (Vert-Net download accessed 12 May 2015). Rapid assessment surveys reveal that neither species are commonly encountered. In Kutubu, Moran, Agogo, Mananda and Gobe in the Southern Highlands and Gulf Provinces of Papua New Guinea, only four animals were caught in 5 surveys over 2 years (Richards, 2008) and none were found during the following surveys, despite being at suitable elevation: Kaijende Highlands, Enga Prov. 3018 m (Helgen & Opiang, 2013); Wanakipa, Southern Highlands Province, 570–1438 m (Helgen *et al.*, 2011); Lakekamu Basin, Gulf Province, 100–1000 m (Wright *et al.*, 1998); 1750–2529 m, Star Mountains, Papua, Indonesia and 500–2900 m, Muller Range, Southern Highlands, PNG (Richards & Whitmore, 2015). Although *N. certans* has occasionally been caught in sympatry with *N. a. papuanus* (e.g., in Usino, WAM27415 with WAM27401–411), it is more commonly caught in sympatry with *N. wrightae* sp. nov. (six localities, see Discussion). Flannery & Seri (1990) caught only one individual at the Upper Sol River Valley, Sepik and my own netting at O-Pio, Chimbu Province, caught just 3 individuals over 6 months despite intensive survey (running 13 nets and two harp traps per night). If museum records reflect abundance of these species, it is possible that *N. certans* is genuinely rare despite its extensive geographic range. There are no records of people hunting *Nyctimene* species, as they tend to roost solitarily in the canopy (Flannery, 1995b; Bonaccorso, 1998) and there are other larger, gregarious bats such as flying foxes (*Pteropus* spp.) that are more suited for hunting. Species of *Nyctimene* are therefore not typically threatened by hunting. In the Telefomin Valley it is considered such bad luck to kill *N. certans* that the hunter is thought to

die within 2 days (Flannery & Seri, 1990). Such a belief within the Telefol clan might afford *Nyctimene* some protection (Hutson *et al.*, 2008a) and I assume it extends to the sympatrically occurring *N. wrightae* sp. nov. in that region. Habitat destruction via deforestation (logging or clearing for agriculture) would be the most likely threat to this species should it occur in its range, but without clear range maps it is difficult to determine the extent of that threat. Although *N. certans* is currently classified as Least Concern on the basis of a large distribution (Bonaccorso, 1998; Hutson *et al.*, 2008d), this included the conflated ranges of *N. wrightae* sp. nov. and *N. cyclotis*. However, the re-assessment of the distribution of *N. certans* presented here (Fig. 12), confirms a wide geographic occurrence that extends over an extensive area along a complex series of mountain systems over 2400 km long from more than 26 sites. There is a clear lack of basic information about the biology of *N. certans* and little is known about population density, longevity, roost ecology, reproduction, diet, or habitat use. This is compounded by the past confusion of *N. certans* with *N. cyclotis* and *N. wrightae* sp. nov.. Given the lack of information on population size and trends, a wide distribution and lack of identified threats, I recommend that *N. certans* be assigned an IUCN category of Data Deficient (IUCN, 2010).

*Nyctimene wrightae* sp. nov. is distributed on the mainland of New Guinea. It is currently known from 22 sites (Fig. 12). I caught *N. wrightae* sp. nov. as the dominant species sympatrically with *N. a. papuanus*, *N. aello* and *Paranyctimene* species at Opio (600 m asl), Southern Highlands Province. I also caught it, but infrequently at Sempu, Madang Province, in the lowlands (40 m asl). Dr Debra Wright (IBPNG) caught the same four species sympatrically during a survey at Ivimka, Gulf Province, PNG in 1996 (specimens which I have genetically identified). Specimens examined during this study confirm that *N. wrightae* sp. nov. is sympatric with *N. a. papuanus* at 4 other sites: Waro, Southern Highland Province; Star Mountains, West Sepik Province; Timika, Papua; Bulolo, Morobe District and sympatric with *N. certans* at five sites at higher elevations: Mt Somoro (AM M.21768–771), Mt Sisa (AM M.16442–444), Mt Missim slopes, (BPBM see notes above), 13 km E Utai, Agpo Creek (BPBM 110338, 109893) and Magidobo (AM M.16234–235, M.16421–422, M.16440–441). It seems likely that *N. wrightae* sp. nov. is the most common *Nyctimene* of the latter three species in mid-montane elevations but further survey work is required to confirm this. Although nothing is known about seasonal movements by any of these species, it is also possible that altitudinal movements could occur in response to ephemeral food resources, as has been demonstrated in other fruit and blossom eating bats in New Guinea (Bonaccorso *et al.*, 2002; Winkelmann *et al.*, 2000). If this were the case, any of these species could therefore have much broader distributions than is presently suspected. *Nyctimene wrightae* sp. nov. is not known to be hunted for food and is likely to roost solitarily like other members of the genus and therefore be less vulnerable at a specific roosting site compared to flying foxes or cave dwelling bats. I therefore recommend *N. wrightae* sp. nov. for IUCN category listing as Least Concern on the basis of its wide distribution across low to mid-montane forest types and currently there being no known direct threat.



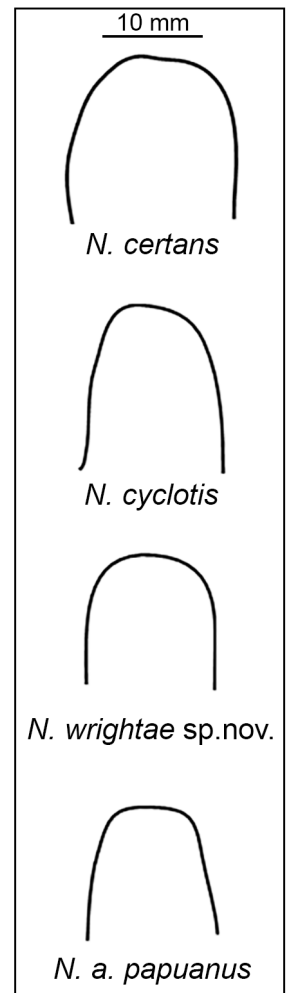
Although this study demonstrates that *N. certans* and *N. wrightae* sp. nov. are widespread, almost nothing is known of their ecology or life history, which also applies to *N. cyclotis*. In part, this is due to past taxonomic confusion and the resultant inability to reliably identify the species. The identification key provided below will hopefully facilitate ecological studies by assisting species identification. Targeted field studies are required to determine the basic

diet, life span, home range and population density, which are unknown for any of these species. Further ecological studies of these species would aid significantly in formulating effective management plans. A high priority is clearly *N. cyclotis*, known only from a restricted area of high endemism, identified from only two specimens and of which no female is known.

**Identification key to medium-bodied *Nyctimene* from mainland New Guinea**

The following key applies only to medium-sized *Nyctimene* with a FA 48–68 mm, which occur on mainland New Guinea.

- 1 Ears short and rounded, dorsal hair grey and woolly, more than 20% of dorsal hair is dark at base, dorsal hair is long 10–16 mm, indistinct dorsal stripe.  $M_2$  breadth < 65% of  $P_4$  breadth ..... 2
- Ears long and tapered, dorsal hair brown and short, < 10% of hair is dark at base, dorsal hair is short (< 10 mm), distinct dorsal stripe.  $M_2$  breadth > 65% of  $P_4$  breadth ..... 3
- 2 2M-2P is greater than 8.0 mm;  $P^3$ - $P^3$  is markedly wider than the length of the post-canine upper tooth row ( $P^1$ - $M^1$ ). Dental arcade very broadly rounded ..... *N. certans*
- 2M-2P is less than 7.5 mm;  $P^3$ - $P^3$  width is greater than the post-canine upper tooth row length ( $P^1$ - $M^1$ ). Dental arcade narrow and rounded, presumed to be restricted to the Vogelkop ..... *N. cyclotis*
- 3 Distinct dorsal stripe extends from base usually to mid-back. Broad dental arcade and palate;  $P^3$ - $P^3$  is greater than post-canine upper tooth row length ( $P^1$ - $M^1$ ); distance across upper tooth increasing in width from  $C^1$ - $C^1$  to  $P^3$ - $P^3$ , then decreasing in width to  $M^1$ - $M^1$ ; rostrum length short relative to skull size; zygomatic arch relatively broad;  $M_2$  breadth smaller in relation to  $P_4$  breadth (73%) ..... *N. wrightae* sp. nov.
- Distinct dorsal stripe usually extends to shoulders or neck. Upper tooth rows increasingly divergent in width towards distal end ( $M^1$ - $M^1$  wider than  $P^4$ - $P^4$ , wider or as wide as  $P^3$ - $P^3$ ); premolars and molars rectangular and relatively similar in breadth;  $M_2$  and  $M_1$  are similar in breadth (80%) to  $P_4$ ;  $M_2$  breadth larger in relation to  $P_4$  ( $P_4$  breadth 80% of  $M_2$  breadth) ..... *N. a. papuanus*



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**Appendix 1.** Museum specimens and tissue samples used in this study for distribution or morphometrics for *Nyctimene certans*, *N. cyclotis*, *N. a. papuanus* (a continuous range of register numbers is indicated by a dash).

museum specimen number		locality	provinces	country
<b><i>Nyctimene certans</i> (n = 39)</b>				
AM	M.7908	Yaramanda, Baiyer River	Western Highlands	PNG
AM	M.16229	Sol River Valley, Telefomin	West Sepik	PNG
AM	M.16234	Magidobo	Southern Highland	PNG
AM	M.16235	Namosado	Southern Highland	PNG
AM	M.16442	Bobole village, Mt Sisa	Southern Highland	PNG
AM	M.17888	Mt Fubilan Road	Western	PNG
AM	M.21768–770	Mt Somoro Summit	West Sepik	PNG
AM	M.30648	Tembagapura area, forest behind BQ Barracks	Papua	Indonesia
AMNH	160347	Ilaga valley, Nassau Range	Papua	Indonesia
AMNH	252478*	Enarotali	Central	PNG
BPBM	28397–400, 28404, 28410, 53232	Mt Missim (S Slopes)	Morobe	PNG
BPBM	50598–599	5 km SE Wau (Big Creek Ridge)	Morobe	PNG
BPBM	50689	SE Wau Big Wau creek ridge	Morobe	PNG
BPBM	54911	Bulldog road, 12 mile from Edie Creek	Morobe	PNG
BPBM	55001	Kassam pass	Eastern Highlands	PNG
BPBM	98283–284	Mt Shingol	Morobe	PNG
BPBM	98882	vicinity of Wau, Mt. Kaindi	Morobe	PNG

## Appendix 1 (continued).

museum specimen number	locality	provinces	country
<b><i>Nyctimene certans</i> (continued)</b>			
BPBM 104725	Amboga river vic., Popondetta	Northern	PNG
BPBM 110311	9.6 km N, 14.2 km E Utai, Mt Menawa	West Sepik	PNG
BPBM 110338	8.5 km N 14 km E Utai, Agpo Ck Camp II	West Sepik	PNG
NHMUK 1911.11.29.1 holotype	Mount Goliath	Papua	Indonesia
NMNH 553700–703	Mount Missim, NE of Wau	Morobe	PNG
NRI 274 <sup>c</sup>	Opio	Chimbu	PNG
SH live capture <sup>c</sup>	Mt Stolle, near Mianmin	West Sepik	PNG
TR B69 <sup>c</sup>	Nokopo	Morobe	PNG
WAM 27415	Usino	Madang	PNG
<b><i>Nyctimene cyclotis</i> (n = 2)</b>			
NHMUK 1987.520	Arfak Mountains, Vogelkop	West Papua	Indonesia
NHMUK 1910.7.16.9 holotype	Arfak Mountains	West Papua	Indonesia
<b><i>Nyctimene a. papuanus</i> (n = 196)</b>			
ABTC 91965–968, 981	Foja Mountains	Papua	Indonesia
ABTC 92022–023, 92028–029, 92035, 92522	Kwerba	Papua	Indonesia
AM M.10068	Hayfield via Maprik	East Sepik	PNG
AM M.13677	Ebolio	West Sepik	PNG
AM M.13678	Tibi, Skgonga River	West Sepik	PNG
AM M.16221	Kiunga Airport	Western	PNG
AM M.16424–425, M.16430, M.16433	Waro	Southern Highlands	PNG
AM M.16784	Kiunga	Western	PNG
AM M.19096–097	Kokoda Environs	Northern	PNG
AM M.19110	Usino	Madang	PNG
AM M.19120, M.19146, M.19149, M.19154	Nagada Harbour	Madang	PNG
M.19161			
AM M.19123, M.19131, M.19466	Nabanab	Madang	PNG
AM M.19134, M.19142, M.19160	Sinyarge near Bamana	Madang	PNG
AM M.19145	Baitetta	Madang	PNG
AM M.19454	Kokoda environs	Northern	PNG
AM M.21772–773	Imonda Station	West Sepik	PNG
AM M.23047	near 3 FAS	West Sepik	PNG
AM M.32360, M.32363	Etna Bay, Kiriru Village	West Papua	Indonesia
AMNH 105098, 105104, 105125, 105231, 105302	5 miles below Palma Junction, Upper Fly	Western	PNG
AMNH 105159	1 mi below mouth Black Rv, Upper Fly	Western	PNG
BPBM 21829	Nabive (SE Geelvink Bay)	Geelvink Bay	Indonesia
BPBM 24548	Sinaeada	Milne Bay	PNG
BPBM 24977	Popondetta, Amboga river vic.	Northern	PNG
BPBM 51299	10 km W Bulolo	Morobe	PNG
BPBM 56457	Maprik near Bainyik	East Sepik	PNG
BPBM 60068, 60157, 60161, 60177–178, 60187	Brown Rv forestry stn 38 km NW Port Moresby	Central	PNG
BPBM 60148	Brown Rv forestry, Port Moresby (Karema)	Central	PNG
BPBM 104429–430, 104459	18 km NNE of Wanuma	Madang	PNG
BPBM 110426, 110439	7.0 km N, 7.4 km E of Utai, Mokfe Ck	West Sepik	PNG
NHMUK 1978.868	Sapi Ck, c. 8 km E of Baku, Gogol valley	Madang	PNG
NHMUK 1980.565	Labota cave,	Morobe	PNG
NHMUK 1901.11.5.2	S Coast of Papua		PNG
NHMUK 1899.12.3.2 holotype	Milne Bay	Milne Bay	PNG
DW 2035	Soobo	Gulf	PNG
DW 2071, 2076–077, 2094	Ivimka	Gulf	PNG
NRI NRI <sup>c</sup> : 019, 026, 109, 124, 178, 197, 315, 346, 351, 374, 392, 402, 418, 605, 608, 655, 674, 677, 684, 691, 695, 698, 700, 703, 705, 714, 723, 724, 737, 747, 757, 758b. OM <sup>c</sup> : 13, 16, 56, 57, 60, 62, 76, 82	Sempi, Madang	Madang	PNG
NRI NRI <sup>c</sup> : 253, 286, 788, 790, 806, 817, 821, 888, 890	O-Pio	Chimbu	PNG
PMAG NM34 <sup>d</sup>	gallery forest nr Port Moresby, Hirtano, Mt Loves	National Capital	PNG
QMJM 9625	Tibi Village, Skgongo River	West Sepik	PNG
UPNG 10–14	Depapre, Jayapura	Papua	Indonesia
RMNH 36658	Vogelkop	West Papua	Indonesia



**Appendix 1** (continued).

museum specimen number	locality	provinces	country
<b><i>Nyctimene a. papuanus</i> (continued)</b>			
WAM 27389	Nagada Harbour	Madang	PNG
WAM 27391	Sempi	Madang	PNG
WAM 27392–394, 27398–400, 27421	Baumina	Madang	PNG
WAM 27401–405, 27408–411	Usino	Madang	PNG
WAM 42467, 42486, 42498–501, 42556–559, 42562–564, 42577–578, 42585–590, 42602, 42605–609	Karangguli, Wokam Island	Aru Islands	Indonesia
WAM 47459	Timika	Papua	Indonesia
ZMA 23.182–184	Gogol River, Sapi Creek	Madang	PNG
ZMA 23.185	18 km NNE of Port Moresby	National Capital	PNG
ZMA 25.426–427	SE Waigeo, 200 m from Rumei Rv, 7 km upstream from 10 km of Urbinasopen village <sup>19&gt;</sup>	West Papua	Indonesia

- a* Previously BPBM 21435  
*c* Tissue sample  
*d* Un-catalogued specimen  
*e* Field captured and released bat