

# Contributions to Mammalogy and Zooarchaeology of Wallacea

## Table of Contents

Helgen, Kristofer M., and Rebecca K. Jones. Wallacean mammalogy and zooarchaeology: remembrances and a renaissance .....	623
Parnaby, Harry E., and Kristofer M. Helgen. Rediscovery of the long-eared bat genus <i>Nyctophilus</i> (Chiroptera: Vespertilionidae) in Timor and a reassessment of <i>Nyctophilus timoriensis</i> .....	629
Wiantoro, Sigit, Tim F. Flannery, Dan Brown, Kyle N. Armstrong, and Kristofer M. Helgen. The mammal fauna of Kofiau Island, off western New Guinea .....	653
Mursyid, Ahmad, Anang Setiawan Achmadi, Wilson Novarino, Heru Handika, Herjuno Ari Nugroho, Syahfitri Anita, Amy Louise Adams, Karen Marie Cavey Rowe, and Kevin Christopher Rowe. <i>Trypanosoma</i> (Euglenozoa: Kinetoplastea) infections in rodents, bats, and shrews along an elevation and disturbance gradient in Central Sulawesi, Indonesia .....	663
Fabre, Pierre-Henri, Roberto Portela Miguez, Mary Ellen Holden, Yuli S. Fitriana, Gono Semiadi, Guy G. Musser, and Kristofer M. Helgen. 2023. Review of Moluccan <i>Rattus</i> (Rodentia: Muridae) with description of four new species .....	673
Aplin, Kenneth P., Tim F. Flannery, Boeadi, Pierre-Henri Fabre, and Kristofer M. Helgen. Two new species of <i>Halmaheramys</i> (Murinae: Rattini) from archaeological deposits on Morotai Island, North Moluccas, Indonesia .....	719
Veatch, E. Grace, Pierre-Henri Fabre, Matthew W. Tocheri, Thomas Sutikna, E. Wahyu Saptomo, Guy G. Musser, and Kristofer M. Helgen. A new giant shrew rat (Rodentia: Muridae: Murinae) from Flores, Indonesia and a comparative investigation of its ecomorphology .....	741
Louys, Julien, Sue O'Connor, Shimona Kealy, Stuart Hawkins, and Kenneth P. Aplin. Late Quaternary mammal introduction and extinction records from archaeological cave deposits in Timor-Leste .....	765

# Rediscovery of the Long-eared Bat Genus *Nyctophilus* (Chiroptera: Vespertilionidae) in Timor and a Reassessment of *Nyctophilus timoriensis*

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**ABSTRACT.** The only previous record of the Long-eared bat genus *Nyctophilus* from the island of Timor is a specimen collected by the Baudin expedition in 1803, used to describe *Nyctophilus timoriensis* by Geoffroy (1806). However, its geographic attribution to Timor is contentious because of uncertainty regarding the characteristics and the identity of the type material of *timoriensis*, and because no further specimens from Timor have been available until now. Here, we report on three specimens of *Nyctophilus* collected in 2003 at Maubisse, in the mountains of Timor-Leste (East Timor), which we tentatively assign to *N. timoriensis*. We present a revised concept of *N. timoriensis* based on a re-interpretation of the original description and illustration, as well as examination of the suspected holotype. Our assessment differs from the prevailing view of *timoriensis* as representing a large-bodied *Nyctophilus* with a rudimentary snout mound (similar to the Australian species *N. major* Gray, 1844, with which it has often incorrectly been synonymized). Instead, *N. timoriensis* is a medium-sized species with an enlarged snout mound, closely resembling *N. heran* Kitchener *et al.*, 1991, from Lembata Island, Indonesia, and *N. geoffroyi* Leach, 1821, of mainland Australia and Tasmania. Further revisionary work is needed to resolve the taxonomy and relationships of these similar species.

**ABSTRAK** [Bahasa Indonesia]. Catatan tentang kelelawar bertelinga panjang, genus *Nyctophilus* dari Pulau Timor, sebelumnya hanya diketahui dari spesimen yang dikoleksi dalam ekspedisi Baudin pada tahun 1803, yang selanjutnya digunakan untuk mendeskripsikan spesies *Nyctophilus timoriensis* oleh Geoffroy pada tahun 1806. Namun, pemahaman distribusi geografis spesies ini di Timor masih diragukan karena adanya ketidakpastian terkait dengan karakter dan identitas spesimen tipe dari spesies *N. timoriensis*, dan tidak tersedia spesimen yang lain dari Timor. Dalam makalah ini, kami melaporkan tentang tiga spesimen kelelawar *Nyctophilus* yang dikoleksi pada tahun 2003 dari Maubisse, pegunungan di Timor Leste, yang sementara ini kami masukkan ke dalam kelompok *N. timoriensis*. Kami mempresentasikan revisi dari pemahaman tentang spesies *N. timoriensis* berdasarkan pada penafsiran ulang terhadap deskripsi dan ilustrasi awal dalam penamaan spesies, serta eksaminasi spesimen yang diduga sebagai holotipe. Penilaian kami berbeda dengan pemahaman yang saat ini berlaku terhadap *timoriensis* sebagai representasi dari kelelawar *Nyctophilus* yang memiliki ukuran tubuh besar dengan tonjolan moncong yang mengalami rudimentasi (mirip dengan spesies dari Australia, *N. major* Gray, 1844, yang seringkali disalahartikan sebagai sinonim).

**Keywords** [English]: Baudin expedition; *Nyctophilus timoriensis*, Charles Alexandre Lesueur, Timorese bat inventory, Indonesian bat fauna  
**Keywords** [Bahasa Indonesia]: ekspedisi Baudin, *Nyctophilus timoriensis*, Charles Alexandre Lesueur, inventarisasi kelelawar Timor, kelelawar Indonesia  
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Sebaliknya, *N. timoriensis* adalah spesies dengan ukuran tubuh sedang dengan tonjolan moncong yang membesar, sangat mirip dengan *N. heran* Kitchener *et al.*, 1991, dari Pulau Lembata, Indonesia, dan *N. geoffroyi* Leach, 1821, dari daratan Australia dan Tasmania. Upaya revisi lebih lanjut diperlukan untuk menyelesaikan taksonomi dan hubungan kekerabatan dari spesies-spesies yang mirip tersebut.

REZUMU [Tetum]: Rejistu úniku kona-ba niki ho tilun naruk, husi jéneru *Nyctophilus*, iha illa Timor, maka espésime (ezemplár) ida ne'ebé rekolle husi Baudin, iha ninia espedisaun iha tinan 1803, ne'ebé uza husi Geoffroy (1806) hodi halo deskrisaun kona-ba *Nyctophilus timoriensis*. Maske nune'e, ninia atribuisaun jeográfika ba Timor kontroversa (iha hanoin ne'ebé la hanesan) duni, tanba la iha serteza kona-ba karakteristik no identidade husi materiál tipu *timoriensis* nian, no tanba to'o agora la iha ezemplár tan Timor nian. Iha estudu ida ne'e ami apresenta ezemplár *Nyctophilus* tolu, ne'ebé rekolle iha tinan 2003, iha Maubisse, iha Timor-Leste ninia foho sira, ne'ebé ami atribui ho provizóriu (la definitivu) ba *Nyctophilus timoriensis*. Ami apresenta konseitu ne'ebé revee ona kona-ba *N. timoriensis*, bazeia ba interpretasaun foun kona-ba deskrisaun no ilustrasaun orijinál sira, no mos ba *holótipo* (ezemplár ne'ebé uluk uza hodi halo deskrisaun) suspeitu nian. Ami nia avaliasaun la hanesan ho ida seluk ne'ebé iha to'o agora, ne'ebé hatudu *N. timoriensis* hanesan *Nyctophilus* ho isin boot, ho ibun (nunun) rudimentár, (hanesan espésie australiana *N. major* Gray, 1844, ho ne'ebé kompara sala dala barak). Duké hanesan ne'e, *N. timoriensis* maka espésie ho tamañu médiu, ho nia ibun (nunun) luan, hanesan loos ho *N. heran* Kitchener *et al.*, 1991, husi illa Lembata, Indonézia, no ho *N. geoffroyi* Leach, 1821, husi Austrália kontinentál no Tazmânia. Presiza halo revizaun tan hodi rezolve taksonomia no relasaun entre espésie hanesan sira ne'e.

## Introduction

The French naturalist Étienne Geoffroy Saint-Hilaire described a long-eared bat species, *Vespertilio timoriensis*, based on a specimen or specimens collected from Timor during the Baudin expedition (Geoffroy, 1806). The species was later transferred to the genus *Nyctophilus*, erected by Leach (1821a). The Baudin expedition was based at Kupang Bay (now the Indonesian city of Kupang) on the western end of the island of Timor during August–November 1801 and April–July 1803 (Péron & Freycinet, 1807–1816). Jackson *et al.* (2021) gave the collection date of *Vespertilio timoriensis* as between 6 May and 3 June 1803.

Subsequent authors for the ensuing half century (e.g., Desmarest, 1821; Temminck, 1840; Giebel, 1855), including his son, Isadore Geoffroy Saint-Hilaire (I. Geoffroy, 1832), credited Geoffroy's (1806) documentation of this species from Timor. However, in the two centuries following the Baudin expedition, the presence of *Nyctophilus* in Timor has at times been doubted, in large part because no further material had been reported since the original account by Geoffroy (1806). More recently, Kitchener *et al.* (1991) confirmed the occurrence of *Nyctophilus* in the Lesser Sunda Archipelago in the late twentieth century, designating a newly collected specimen from the neighbouring island of Lembata, Indonesia immediately north of Timor, as the holotype (and thus far only known specimen) of *Nyctophilus heran* Kitchener, How, & Maharadatunkamsi, 1991. Kitchener *et al.* (1991) considered it likely that the genus also occurred in Timor.

Here we confirm that the genus *Nyctophilus* occurs in Timor. Three specimens of long-eared bats (genus *Nyctophilus*) collected in 2003 from Maubisse, montane Timor-Leste (East Timor) were documented in a report by Polhemus & Helgen (2004) to the Government of Timor-Leste. Until now the identity of these specimens has remained uncertain. In this paper we describe the Maubisse material and provide a morphological evaluation of their taxonomic status relative to the taxa they most resemble: *N. heran* from Indonesia, and the Lesser Long-eared Bat *N. geoffroyi* Leach, 1821a, from Australia and Tasmania. Our

task is impeded by the unresolved taxonomy of the forms currently assigned to *N. geoffroyi*. The taxonomic status of *N. timoriensis* has long been confused, largely because it is a poorly defined entity in the literature and because the name has been applied to a variety of taxonomic concepts in the past (see below). Here, alongside review of the new material of *Nyctophilus* from Timor, we present a revised concept of the morphology of *N. timoriensis* *sensu stricto*, based on a re-interpretation of Geoffroy's original description and illustration.

## Taxonomic history

As noted above, some doubt that Geoffroy's *timoriensis* came from Timor prevailed especially during the late nineteenth and twentieth centuries (e.g., Tate, 1941; Goodwin, 1979), though Thomas (1914) noted that the record might be valid and that further specimens might come from Timor. Scepticism seems to have originated from Tomes (1858a), who believed that É. Geoffroy's locality was an error, citing two reasons. First, many bat specimens from Timor were then held by museums in Europe yet no further *Nyctophilus* had been obtained from that island. Second, Tomes states that he had examined specimens from Western Australia, which he considered to be “identical” to “the original” specimen of *timoriensis* in the Muséum national d'Histoire naturelle, Paris. Consequently, Tomes (1858a) applied the name *timoriensis* to the Western Australian specimens. His specimens were later shown by Thomas (1914, 1915a) to belong to *N. major*, a species attributed to an illustration published by J. E. Gray but first diagnosed by Thomas. Tomes (1858a) did not use the name *N. major* in his revision, either because he was unaware of the name (see Peters, 1861) or else did not consider *N. major* to be an available name. The Baudin expedition collected specimens from south-western Western Australia, adding to Tomes' suspicion that the *Nyctophilus* material had been incorrectly attributed to Timor.

Throughout the past century the name *N. timoriensis* has often been used for the largest members of the genus from across mainland Australia and Tasmania, while *N. major*

was sometimes applied to bats from south-western Western Australia but usually treated as a synonym of *N. timoriensis*. Hill & Pratt (1981) documented a large-bodied species of *Nyctophilus* from New Guinea which they also assigned to *N. timoriensis*. The largest members of the genus were reviewed by Parnaby (2009), who recognized four species, two of them new: *N. major* Gray, 1844 from Western Australia, *N. sherrini* Thomas, 1915a from Tasmania, *N. corbeni* Parnaby, 2009 from eastern mainland Australia, and *N. shirleyae* Parnaby, 2009 from New Guinea. Parnaby (2009) suggested that the name *N. timoriensis* sensu stricto be restricted to *Nyctophilus* from Timor.

The taxonomic identity of *N. timoriensis* has remained unresolved. It has not previously been possible to equate *Vespertilio timoriensis* with any other known species of *Nyctophilus* on account of the brevity of Geoffroy's description, which provided few measurements and illustrations, and uncertainty regarding whether Geoffroy's type material remains extant. In the first taxonomic revision of *Nyctophilus*, Tomes (1858a) examined what he believed to be the type specimen of *timoriensis* but did not provide any description or measurements of that specimen. Instead, his concept of *N. timoriensis* was based on material from south-western Western Australia, from where he believed Geoffroy's material had actually originated. In the second revision of the genus, Thomas (1915a) apparently did not examine Geoffroy's material of *timoriensis* and treated *timoriensis* as a *nomen dubium*. He provided the first diagnosis for *N. major* Gray, 1844 and applied that name to the same material examined by Tomes from south-western Western Australia. Tate (1941) incorrectly based his concept of *timoriensis* on an alcohol preserved specimen with extracted skull in the Muséum national d'Histoire naturelle, Paris that he thought to be part of Geoffroy's original material, but is now understood to be a specimen of *N. sherrini* Thomas, 1915a from Tasmania not collected during the Baudin expedition (Parnaby, 2009).

Fifteen species of *Nyctophilus* are currently recognized (Simmons, 2005; Parnaby, 2009; Parnaby *et al.*, 2021) and we are aware of additional undescribed species. These species roost in tree cavities, under loose bark, and in buildings, and some species also roost in foliage (Churchill, 2008). The genus is not known to regularly use subterranean roost sites, although occasional instances have been reported for several species (e.g., Bonaccorso, 1998). The ecology of most species remains poorly known but all feed on arthropods and range in body weight from about 3 to 20 g (Churchill, 2008). The genus is widely distributed and commonly encountered throughout Australia and Tasmania, where ten species are recognized (Van Dyck *et al.*, 2013; Parnaby *et al.*, 2021). Three of the four species recorded from the island of New Guinea are endemics (Bonaccorso, 1998; Parnaby, 2009). Few records of the genus are known from the Indonesian provinces of Papua and West Papua (the western half of the island of New Guinea) (Flannery, 1995; Helgen, 2007), where records extend as far west as Salawati Island (Lavery & Flannery, 2023). However, the dearth of records could be an artefact of survey intensity. The genus also occurs broadly in the south-western Pacific to the east of mainland New Guinea, but the few records of occurrence remain poorly resolved. A specimen (QM JM13100) reported from Sudest in the Louisiade Archipelago suspected to be *N. microtis* by Koopman (1982) was examined and is confirmed here to be

closest to that species. One specimen is known from New Ireland (United States National Museum USNM 580082) in the Bismarck Archipelago (Bonaccorso, 1998), and the genus has been reported from Bougainville in the Solomon Islands Archipelago based on echolocation recording data (Junior Novera, pers. comm.). The only species known from New Caledonia, *N. nebulosus*, remains a poorly known endemic (Parnaby, 2008). There is an unconfirmed report of a long-eared bat from Vanuatu that could be a *Nyctophilus* (Steadman, 2006: 67) and a nineteenth century *Nyctophilus* specimen labelled "Fiji Islands" (Dobson, 1878) is of uncertain provenance (Helgen *et al.*, 2009).

Phylogenetic relationships within *Nyctophilus* remain incompletely understood, and species diagnoses and the extent of within-species variation are poorly defined for all species. Consequently, delineation of species groups within the genus is also in a state of flux. Tate (1941) recognized a *geoffroyi* species group but did not provide diagnostic features other than citing Thomas (1915a) regarding the specialized nose-leaves. Parnaby (2009) proposed tentative species groups within *Nyctophilus* and defined the *geoffroyi* group as having a highly developed snout mound posterior to the nose-leaf, relatively inflated bullae, and a serrated longitudinal dorsal ridge on the distal portion of the glans penis. The serrated dorsal penile ridge is unique to the *geoffroyi* group, but whether it is invariably present in all populations subsumed within *N. geoffroyi* has not been determined. Kitchener *et al.* (1991) believed that *N. heran* most closely resembled *N. geoffroyi*. Parnaby (2009) tentatively placed *N. heran* in the *geoffroyi* group, noting that it resembled *N. gouldi* Tomes, 1858a and *N. daedalus* Thomas, 1915a in some respects and that the latter taxon is a likely composite of at least two species.

Eldridge *et al.* (2020) demonstrated that multiple species are likely included under "*N. geoffroyi*" as currently understood; see also Parnaby *et al.* (2021). They found species-level differences in average divergence of mitochondrial genes (*cytochrome B* and *cytochrome oxidase I*) between samples from eastern NSW and those from the Pilbara and southwestern Western Australia. Whether the distributions of these divergent lineages overlap remains to be determined. Substantial morphological variation exists within "*N. geoffroyi*", both within regions and throughout its extensive geographic range throughout most of mainland Australia and Tasmania. Its status as one of the most widely distributed Australian mammal species (Van Dyck *et al.*, 2013) will need to be re-evaluated.

The taxonomic status of mainland Australian *N. geoffroyi* is relevant to our assessment of the status of Timor *Nyctophilus*. Assigning current nomenclature to the two putative species within *N. geoffroyi* demonstrated by Eldridge *et al.* (2020) will require further work because names cannot reliably be assigned solely from geography. Three subspecies of *N. geoffroyi* are often recognized based on Thomas (1915a) and Iredale & Troughton (1934), but their validity remains uncertain (Simmons, 2005) and their geographic limits poorly defined. A detailed morphological evaluation of their taxonomic status is needed, ideally matched with analysis of DNA sampled from type material. The three currently recognized subspecies are *N. g. geoffroyi* Leach from south-western Western Australia; *N. g. pacificus* Gray from south-eastern Australia and Tasmania; and *N. g. pallescens* Thomas from central and northern Australia.

Five names are currently recognized as synonyms of *N. geoffroyi* (Table 1). The type locality of three of these names remains unknown and their subsequent localization to regions of Australia have a doubtful basis. Tomes (1858a) restricted the type locality of *N. geoffroyi* (type locality “Australia”) to south-western Western Australia because he believed that the holotype of *geoffroyi* broadly resembled his material from Albany. His decision should be viewed in the context that interspecific diagnostic criteria within the genus were poorly understood at the time, and he struggled to see external differences, other than size, between the most morphologically divergent species then known, *N. geoffroyi* and *N. timoriensis*. Peters (1861) stated that his two specimens of *Nyctophilus australis* were from an unknown locality. He speculated that they were probably from Western Australia, simply because he had received material from that region in the past. Krefft (1871) listed *N. australis* from NSW (but *N. geoffroyi* from “West Australia”), a view also held by Iredale & Troughton (1934) but for unspecified reasons. Thomas (1915a) suggested that the holotype of *Barbastellus pacificus* (= *Nyctophilus pacificus*, see Mahoney & Walton, 1988) possibly came from south-eastern Australia or Tasmania, apparently on the basis that the holotype resembled a specimen he had examined from eastern Victoria.

In view of the likely taxonomic complexity of the taxa involved, we here offer a preliminary morphological assessment that must await a comprehensive study using morphological and molecular techniques.

## Methods

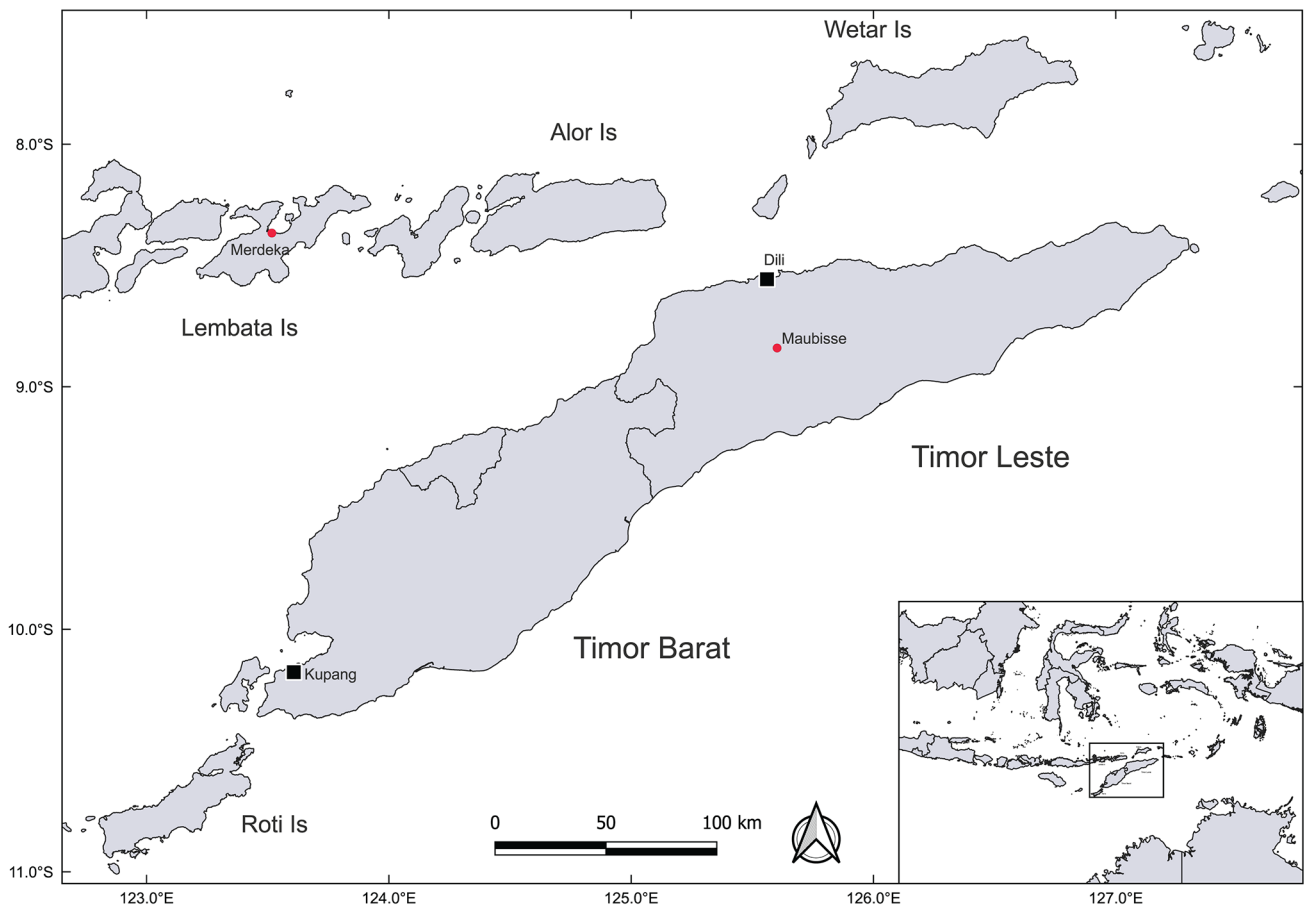
For this paper we have examined specimens in many museum collections. Institutional abbreviations are: **AM**, Australian Museum, Sydney; **NHMUK**, Natural History Museum, London; **NMV**, Museums Victoria, Melbourne; **ANWC**, Australian National Wildlife Collection, CSIRO, Canberra; **MNHN**, Muséum national d’Histoire naturelle, Paris; **MZB**, Museum Zoologicum Bogoriense, Bogor, Indonesia; **NCBN**, Netherlands Centre for Biodiversity, Naturalis

Museum, Leiden; **NTM**, Museum and Art Gallery of the Northern Territory, Darwin; **ZMB**, Universität Humboldt, Zoologisches Museum, Berlin; **WAM**, Western Australian Museum, Perth. We have not examined all relevant type material but have relied on black and white photographs of type specimens of all five names applicable to the *geoffroyi* group (Table 1), and have drawn from the literature, with additional skull measurements of types in the Natural History Museum, London supplied by Glenn Hoye. We have also relied on the description and measurements of the holotype of *N. heran* given by Kitchener *et al.* (1991), which is registered as MZB 16001 (previously registered as WAM M.32252). Complete skulls are available for type specimens of only two of the five names relevant to mainland *N. geoffroyi*, viz. *pacificus* and *pallescens*, and we have included measurements of both in our analyses. The skull of the holotype of *geoffroyi* consists of a rostrum only, and the holotype skull of *geayi* is evidently lost. Of the two syntypes of *australis* in the ZMB, one has the skull *in situ*, while the extracted skull of the other has not been located.

Measurements were taken with vernier calipers to the nearest 0.05 mm as illustrated by Parnaby (2009). These measurements are taken in the same manner as Kitchener *et al.* (1991), who state that their measurements were taken as specified by Kitchener *et al.* (1986). However, whereas Kitchener *et al.* (1986) indicate that “palatal length” is taken anterior to the incisor, palatal length given by Kitchener *et al.* (1991) for *N. heran* approximates that given for  $CM^3$ , indicating that their measurement of palatal length was actually palatal-sinusal length. Abbreviations for measurements used in the text are: **GL**, greatest length of skull: from the most anterior extension of the premaxilla to the posterior of the lambdoidal crest;  $CM^3$ , length of maxillary toothrow: from anterior cingulum of canine to posterior cingulum of  $M^3$ ;  $C^1-C^1$ , outer breadth across upper canines from cingula; **ANT**, anteorbital width, between infraorbital foramina; **PAL**, palatal length, from most anterior of premaxilla to most anterior extent of interpterygoid fossa; **sinPAL**, palatal-sinusal length, from the most posterior margin of the anterior palatal emargination to the most anterior margin of the interpterygoid fossa; **ZYG**,

**Table 1.** Synonymy of *Nyctophilus geoffroyi* Leach. Based on Mahoney & Walton (1988), Turni & Koch (2008) and original descriptions. An additional name applied to the synonymy of *N. geoffroyi*, “*Nyctophilus leachii*, Gray” is a *nomen nudum* because it was listed by Dobson (1878: 174) as a name written on a specimen label, as noted by Tate (1941).

Name originally proposed	Type locality	Type material
<i>Nyctophilus geoffroyi</i> Leach, 1821a	“Australia”, restricted to Albany, south-western Western Australia by Tomes (1858a)	Holotype, NCBN
<i>Barbastellus pacificus</i> Gray, 1831	“The Australasian Barbastelle”, “Islands of the Southern Pacific”, suspected by Thomas (1915a) to be southeastern Australia or Tasmania	Holotype, NHMUK
<i>Nyctophilus unicolor</i> Tomes, 1858a	Tasmania	At least 3 syntypes, NHMUK, NCBN
<i>Nyctophilus australis</i> Peters, 1861	Unknown, “probably Western Australia”; suggested as Sydney by Iredale & Troughton (1934)	Two syntypes, ZMB
<i>Nyctophilus geayi</i> Trouessart, 1915	Nicholson River area, eastern Victoria	Holotype, MNHN, skull lost
<i>Nyctophilus g. pallescens</i> Thomas, 1913	Alexandria, Northern Territory	Holotype, NHMUK



**Figure 1.** Map showing capture location of *Nyctophilus* in the township of Maubisse, Timor-Leste, and Merdeka, Lembata Island, Indonesia, type locality of *Nyctophilus heran*.

zygomatic breadth, maximum breadth across zygomatic arches; **INT**, least inter-temporal breadth; **M<sup>3</sup>–M<sup>3</sup>**, maximum breadth from left M<sup>3</sup> to right M<sup>3</sup>, from labial cingula; **M<sup>3</sup>L**, M<sup>3</sup> length measured at cingula; **M<sup>3</sup>B**, maximum breadth of M<sup>3</sup> measured at cingula; **MESO**, maximum internal breadth of mesopterygoid fossa level with the hamular processes; **BRH**, braincase height: caliper blade positioned along basioccipital-basisphenoid bones and along the sagittal crest; **MAS**, maximum breadth across mastoids; **BTB**, least inter-bulla distance, least distance between each bulla; **BUL**, bulla length, from base of eustachian tube when present; **Baculum Length**, maximum length from most posterior tip of proximal arms to distal tip, taken perpendicular to the dorsal surface of the main shaft; **Baculum Breadth**, maximum breadth across proximal arms at their base; **Baculum Height**, maximum height from ventral extent of proximal arm to distal tip; **Ear Length**, taken from the junction of outer ear margin near the jaw.

Principal components analysis (PCA) and Unweighted Pair Group Method with Arithmetic mean (UPGMA) Cluster analyses were run using the Paleontological Statistics (PAST) software package (Hammer *et al.*, 2001), version 3.06. PCAs were run using both correlation and variance-covariance matrices, using only specimens with complete measurements. Standardized character coefficients were used (“Eigenvalue scale” was ticked) to explore the possible contribution of individual characters to each PC axis. UPGMA cluster analyses used Euclidean distance as the similarity metric.

CT scans were made using a Skyscan model 1174 micro CT scanner, using the following software packages: NRecon (version 1.5.1.5 © Skyscan, Belgium 2008) was used for reconstruction of 3D datasets from RAW CT x-ray images; 3D surface models used in illustrations were generated using CTAn Software (version 1.9.2.3, © Skyscan, Belgium 2003-8), and measurements of selected bacula were made using DataViewer (version 1.4.0.4 © Skyscan Belgium).

### *Nyctophilus* from Maubisse

Three individuals of a species of *Nyctophilus* were collected by the second author during a mammal survey of Timor-Leste during November 2003 (Polhemus & Helgen, 2004). These were obtained from an elderly man in the town of Maubisse, elevation 4650 feet (1200 m), (8°50'26.6"S 125°36'6.9"E), Timor-Leste (Fig. 1). The resident stated that these bats lived in small colonies in the roofs of village houses. All three specimens are immature, based on the width of cartilaginous epiphyses in the wing joints. All three are stored in 75% ethanol and are registered in the Australian Museum, Sydney: AM M.37639, field number ET3, subadult female, body in alcohol, skull *in situ*, received 11 November 2003; AM M.38840, ET4, juvenile female, body in alcohol, skull extracted and in alcohol, received 11 November 2003; and AM M.38841, ET12, subadult male, body in alcohol, skull *in situ*, received 13 November 2003. Tissue samples from ET3 and ET12 were stored in 95% ethanol and were lodged with



**Figure 2.** AM M.37639 (ET3), subadult female *Nyctophilus*, from Maubisse, Timor-Leste, in life (photo: Dan Polhemus and Kristofer Helgen).

the South Australian Museum, Adelaide. Unlike the latter two individuals that were alive when received, ET4 was obtained dead and desiccated, limiting field measurements. Field measurements for ET3, ET4 and ET12 respectively, are: body weight, 5, —, 4.5 gm; total length (head-body and tail), 93, —, 85; tail length, 37, —, 36 mm; ear length (from notch), 25, —, 24 mm; forearm, 40, 39, 36 mm; tibia length, 17, 19, 17 mm; pes length (without claw), 8, 8, 7 mm. Skulls of M.38840 and M.38441 were extracted but only partially cleaned due to their fragility as they were not fully ossified. AM M.38840 is a newly volant juvenile female at a much earlier stage of development than the other two specimens and is not included in statistical analyses.

We provisionally assign the Maubisse individuals to *N. timoriensis* based on our revised concept of that species, detailed below. However, they also resemble mainland Australian *N. geoffroyi* and *N. heran* from Indonesia in cranial and dental characters, along with overall size, relatively large ears, uniform dark grey dorsal fur and paler white ventral fur, and having an enlarged post-nasal snout mound (Fig. 2). Our concept of *N. timoriensis* is a significant departure from previous interpretations and is presented below before further consideration of the identity of the Maubisse material.

### A revised concept of *Vespertilio timoriensis* Geoffroy

Since the mid nineteenth century, Geoffroy's *timoriensis* has been viewed as one of the largest members of *Nyctophilus* and its identity has been closely intertwined with *N. major* Gray, 1844 from south-western Western Australia with which it has often been synonymized. We present a new concept of *timoriensis*, based on details of the illustration accompanying Geoffroy's description, a re-interpretation of measurements given in Geoffroy's account and a detailed examination of the basis for the prevailing view that *timoriensis* is one of the largest *Nyctophilus* species that resembles *N. major*. As set out below, we conclude that *timoriensis* is not conspecific with *N. major*, differing in important morphological distinctions that have previously been overlooked.



**Figure 3.** Illustration of the type specimen of *Vespertilio timoriensis* É. Geoffroy, 1806, reproduced from Plate 47 of Geoffroy's original account, showing tragus and snout features characteristic of the genus *Nyctophilus*. A post-nasal snout mound is evident within the red ellipse of the inset. Note that the black horizontal line is part of the original illustration and represents head length but is not a scale bar for the illustration. Scale bar (white) = 5 mm.

## Geoffroy's account of *timoriensis*

### The illustration of the head

A frontal drawing of the head (with the skull *in situ*) in Geoffroy's (1806) plate 47 is the sole illustration accompanying his description of *timoriensis* (reproduced in Fig. 3). Two aspects of this drawing have been overlooked in previous assessments of the status of this species. First, there is an elevated mound on the rear of the snout behind the narial foliations. The oblique ventral angle of the illustration obstructs a clear view of the dorsal snout region and a rudimentary post-nasal elevation, such as that characterizing *N. major*, would not be visible from this angle. The illustration resembles the distal part of the snout prominence of those *Nyctophilus* species in which the post-nasal mound is well developed, such as in *N. heran*, *N. gouldi* and *N. geoffroyi*. The snout mound in *Nyctophilus* consists of two separate bodies joined in the midline by an elastic membrane of variable extent. The bilobed structure is not seen in Geoffroy's illustration. However, it is likely that the artist did not have an accurate understanding of the shape of this structure, which might have shrunk in the specimen, and therefore was unable to accurately depict it. The small size of the illustration might be one reason these snout features have been overlooked, but the illustration contains an impressive level of detail. The enlarged snout mound is in sharp contrast to the low, rounded mound characteristic of *N. major*. This difference alone would suggest that *timoriensis* and *major* are not conspecific.

A second notable but overlooked feature of the illustration is a scale bar adjacent to the head of *timoriensis* on Geoffroy's plate 47. Geoffroy (1806: 205) states that head length is indicated by the scale line beside the head of each species illustrated. The head length line for *timoriensis* is *ca.* 17.5

mm long, measured on a hardcopy of the journal illustration. A comparison of his frontal and lateral illustrations of the head of “*V. nigrita*” on the same plate clearly indicates that “length” was measured along the long axis of the head and was not measured in another manner, such as from ear to ear.

We suspect that the head illustrations on Geoffroy’s plate 47 are reproduced at life size, although he does not explicitly state so. Of the 19 species accounts in his paper, ear length is provided in the text only for *V. auritus* and his measurement of 33 mm is an exact match against his illustration, if ear length is taken from the notch as per modern measurements. If his illustration of the head of *timoriensis* is roughly life size, it is far too small to be a species the size of *N. major* but instead approximates a species the size of *N. geoffroyi*. Ear length measured from his illustration is *ca.* 22 mm, but the ears are not fully erect and could easily have attained about 25 mm. (Both of the latter ear measurements are not especially informative, as both fall within the expected range for many *Nyctophilus* including *N. geoffroyi* and *N. major*.)

### Body measurements

Establishing the approximate body size of Geoffroy’s type specimen of *timoriensis* relative to other species of the genus is fundamental to an interpretation of its possible identity, and therefore requires detailed examination. The prevailing view that Geoffroy’s type was of one of the largest species of *Nyctophilus* originated from Tomes (1858a), yet as discussed below, only one of the measurements provided by Geoffroy (1806) implies a large-bodied species.

Three measurements are cited in Geoffroy’s brief description of *timoriensis*, which he gave in millimetres: body length, 70 mm; tail length, 40 mm; and wingspan, 270 mm. These were the standard measurements given by Geoffroy (1806) for each species in his account of vespertilionid bats. Geoffroy provided a fourth measurement for *timoriensis*, head length of *ca.* 17.5 mm, as noted above. Geoffroy generally used three standard body measurements (head-body, tail, and wingspan) for bats in his other taxonomic papers (e.g., Geoffroy, 1810, 1813). Geoffroy (1806) does not indicate how these measurements were taken, which could differ somewhat from modern standard measurements. His revision was published in an early phase of French taxonomic research when standard measurements for bats were evolving; e.g., Desmarest (1821) used twice as many body measurements, and the taxonomic value of forearm length, now a fundamental measure of size, was not recognized until later (Geoffroy, 1832). Though we suspect that they would have been regarded at the time as having self-explanatory definitions, wingspan and body length could have been measured in several ways that would result in significantly disparate measurements.

### Wingspan

The simplest interpretation of wingspan is a straight-line distance between wing tips of the extended wing. Alternatively, wingspan might have been measured along the bones of the leading edge of the wing, thus avoiding underestimates in specimens for which the wings could not be fully extended. Perhaps Geoffroy used both methods, depending on whether the specimen had fully extended wings, a procedure progressively adopted by Tomes throughout 1858. In his revision of *Nyctophilus*, Tomes

(1858a, read 12 January) gave “expanse of the wings” for some species, while for others he cites “expanse of the wings, following the phalanges”. In a subsequent paper, Tomes (1858b: 125, read March 9th) explains that to overcome this problem with wingspan measurement he used a thread placed along the bones of the wing to the shoulder, adding the distance between shoulders. We are uncertain what method was adopted by Geoffroy (1806) in his description of *timoriensis* but for at least one species in his account (Geoffroy, 1806) he seems to have measured wingspan as a straight-line span between wing tips, as revealed by his life-size illustration of one of his syntypes of *Vespertilio emarginatus* (= *Myotis emarginatus*). Although he does not cite a wingspan measurement for that species in the text, a comparison with the measurements of the type specimens examined by Tomes (1858c) suggests a straight-line measurement. The linear wingspan that we measured from a hard copy of Geoffroy’s figure for *emarginatus* is *ca.* 258 mm and wingspan measured along the bones of the leading edge of the wing is *ca.* 306 mm. Geoffroy does not indicate which of his specimens of *emarginatus* was illustrated, but our linear wingspan measurement of 258 approximates the value 254 mm given by Tomes (1858c) for the specimen from Abbeville (the lectotype) and a wingspan of 267 mm for the Charlemont specimen.

Geoffroy’s wingspan measurement of 270 mm would seem to be too small for a species the size of *N. major*. It falls at the upper range for wingspan given by Churchill (2008) of 208–275 mm ( $n = 22$ , mean = 245) for the small-bodied species *N. geoffroyi* from northern Australia, and at the lower end of the intermediate-sized *N. daedalus* (275–323 mm, mean = 300,  $n = 61$ ). Few wingspan data are available for *N. major major* from south-western Western Australia other than from Bullen & McKenzie (2002), who cite a mean of 349.5 mm ( $n = 8$ ) but do not provide maximum or minimum measurements. Bullen & McKenzie (2001) provide a mean wingspan of 321.9 mm (standard deviation = 10.8 mm,  $n = 11$ ) for *N. major tor*, from which we estimate the sample range to fall within 290–354 mm (based on 3 standard deviations from sample mean) but that form has a significantly smaller body size than *N. major major*. An important consideration is that wingspan taken along the bones of the leading edge of both wings will exceed the straight-line span between wingtips. Consequently, had Geoffroy measured the *timoriensis* wingspan along the leading wing edge, the straight-line span would be appreciably less than 270 mm, further indicating a relatively small-bodied specimen.

### Head length and tail length

Head length measured on a study skin might seem a fairly imprecise measurement, although perhaps less so if the skull was *in situ*, as indicated in Geoffroy’s illustration. Nevertheless, the head length measurement given by Geoffroy suggests that his specimen might not have been as large as *N. major*. Geoffroy’s measurement of 17.5 mm (“8 lines”; 1 line = 2.1 mm) is smaller than the “10 lines” given by Tomes for his two specimens of *N. major*, yet falls within the range of species regarded by Tomes to be of small and intermediate body size (given as 7.5–9 lines), i.e. *N. geoffroyi* and *N. gouldi*. The range for GL of *N. major major* (18.8–20.7 mm,  $n = 20$ , Parnaby, 2009) also implies



that Geoffroy's *timoriensis* might belong to a relatively smaller-bodied species. Tail length (40 mm) is a relatively uninformative discriminator between species of *Nyctophilus*, e.g., Geoffroy's measurement of 40 mm falls within the range of both the small-bodied *N. geoffroyi* and the large-bodied *N. corbeni* (see Churchill, 2008). (This applies regardless of whether tail length is measured from the root of the tail, or from the vent as for Churchill, 2008).

### Body length

The different interpretations of "body length" need to be considered, given that we do not know how this measurement was taken and that modern concepts of the term might not have applied in the early 19th century. We assume Geoffroy's "body length" included the head, and thus equates to "head-body length". The latter interpretation was applied by Desmarest (1821), who gave Geoffroy's body length of 70 mm for *timoriensis* as "length of body and head". Body length was presumably taken from nose tip to base of tail on a stuffed specimen. An alternative interpretation could be that it was taken from the ear tips, because in long-eared bats such as *Plecotus* and *Nyctophilus*, the ears project forward well past the nose tip. However, for the one species for which Geoffroy (1806) provided ear length in the text in addition to "body" length (*Plecotus auritus*, a species with exceptionally long ears), it is apparent that he measured body length from snout tip and not to the projecting ear tip.

Head-body measurements for small mammals are generally reported as a linear measurement and have been for more than a century, but it is possible that Geoffroy measured head-body length along the body contours of the dorsal surface along the midline, as was often done with skin mounts of large mammals, at least in the latter half of the nineteenth century. Our dorsal measurement on the apparent type of *timoriensis* taken along the spine (67 mm, Anja Divljan pers. comm. 2019) is a close match to the 70 mm given in the original description.

A body length of 70 mm is the only measurement given in Geoffroy's description that matches a large species such as *N. major*, but only if this represents a linear measurement. If so, 70 mm would seem to exclude all but the largest species of *Nyctophilus*. Geoffroy's head-body measurement would be some 5 mm longer if he had measured from the rear of the body, rather than the current practice of measuring from the vent. Head-body measurements provided by Churchill (2008) show that small and intermediate-sized species of *Nyctophilus* do not exceed about 50 mm. Head-body measurements are available only for three adult female and two male *N. major major*, as the species is poorly represented in collections. These field measurements of snout-vent length were taken from specimens now in the AM and range from 56–62 mm. However, Churchill (2008) provides snout-vent measurements of 50–75 mm ( $n = 33$ ) for *N. corbeni* which is of comparable size to *N. major*. We compared body measurements given in fourteen nineteenth century accounts of *timoriensis* published in the decades after Geoffroy's description (see below) in the hope that subsequent authors might have re-measured Geoffroy's type but all appear to be re-iterations of his account. There is no indication that any of those authors had examined Geoffroy's material, contrary to Parnaby (2009), who

mistakenly believed that Temminck (1840) had done so. Some accounts are short (Griffith, 1827; I. Geoffroy, 1832) while others seem to provide identical measurements when accounting for possible error from conversion to mm from the variety of European definitions of the inch of that time (Desmarest, 1819, 1821; Lesson, 1827; Fischer, 1829, 1830; Temminck, 1840; Giebel, 1855, 1859; Wagner, 1840, 1855; Fitzinger, 1872).

### Reconciling Geoffroy's measurements

To summarize, the only clear indication of large body size, Geoffroy's measurement of 70 mm for head-body length, seems to clash with other measurements given in his account. The wingspan of 270 mm would appear to be too small for such a large body length. Perhaps the wings were not fully extended on the type specimen, but the smaller body size implied by wingspan is supported by the head length measurement provided by Geoffroy, and the small size of the head illustration, which we suspect was reproduced at approximately life size. As noted above, we suspect that the head-body length reported by Geoffroy (1806) seems disproportionately large because it is measured as an arc length along the dorsal contours of the prepared specimen, and not as a linear measurement as usually reported today.

### The account of *N. timoriensis* by Tomes (1858a)

The entrenched view that *timoriensis* is a large-bodied species similar to *N. major* that arose from Tomes (1858a) has remained unchallenged. Significantly, Tomes (1858a) had examined "the" original specimen of *timoriensis* in Paris, but his statement that it was "absolutely identical" to his *Nyctophilus* specimens from south-western Western Australia is not tenable in light of modern understanding of morphological variation in *Nyctophilus*. As previously mentioned, Tomes did not recognize differences in external morphology, other than size, between *N. geoffroyi* and *N. major* (for which he used the name *timoriensis*), which are distinctive species. His account is bereft of a description or measurements of the Paris type specimen and we suspect that his assessment of *timoriensis* was based only on external features of the apparent type skin. In particular, Tomes seemed unaware of the diagnostic value of the relative size and structure of the snout mound, which he does not cite as a character for differentiating *N. geoffroyi* from *N. major*, two species that exhibit opposite extremes of development of that character. Most of the material available to Tomes consisted of dry skins, in which snout morphology might have been difficult to assess. A full appreciation of the diagnostic value of snout morphology in the genus was first recognized by Thomas (1915a), who assembled a large collection of fluid-preserved *Nyctophilus* on loan from the Australian Museum, Sydney.

Further doubt regarding Tomes' emphatic judgement that *timoriensis* and *major* were "identical" or at least of similar body size arises from a comparison of Geoffroy's measurements with those of Tomes (Tomes himself did not make that comparison.) When compared to Tomes's measurements of his four species, head-body length of 70

mm (= 2 inch 9 lines) is the only one of Geoffroy's four measurements that unequivocally fits the largest *Nyctophilus* recognized by Tomes, i.e. the southwestern Western Australian material that Tomes called *N. timoriensis*. As noted above, Geoffroy's remaining three measurements (tail length, wingspan, and head length), when compared to measurements provided by Tomes, fit the species considered to be *intermediate* in size by Tomes, i.e. *N. gouldi*, and *N. unicolor* from Tasmania (currently a synonym of *N. geoffroyi*). Tomes appeared to place some credence in wingspan as a character, as it was the only measurement directly cited by him when discussing size differences between his species. Had Tomes compared the wingspan of 270 mm given by Geoffroy against wingspan measurements for his own material, the intermediate size suggested by that measurement would have been apparent. Wingspans given by Tomes are: *geoffroyi* 9–10 inches (228–254 mm), *gouldi* and *unicolor*, ca. 10–11 inches (254–279 mm), and *timoriensis* from Western Australia, 12.75–13.5 inches (324–343 mm). Tomes measured wingspan for *timoriensis* as “expanse of the wings, following the phalanges” which is not equivalent to measurements of the remaining three species, measured as “expanse of the wings”, implying a direct tip to tip measurement. His measurements of ca. 323–343 mm are much larger than Geoffroy's 270 mm, even when accounting for the fact that wingspan measured along the bones of the leading edge of the wing will be greater than a direct span between wing tips.

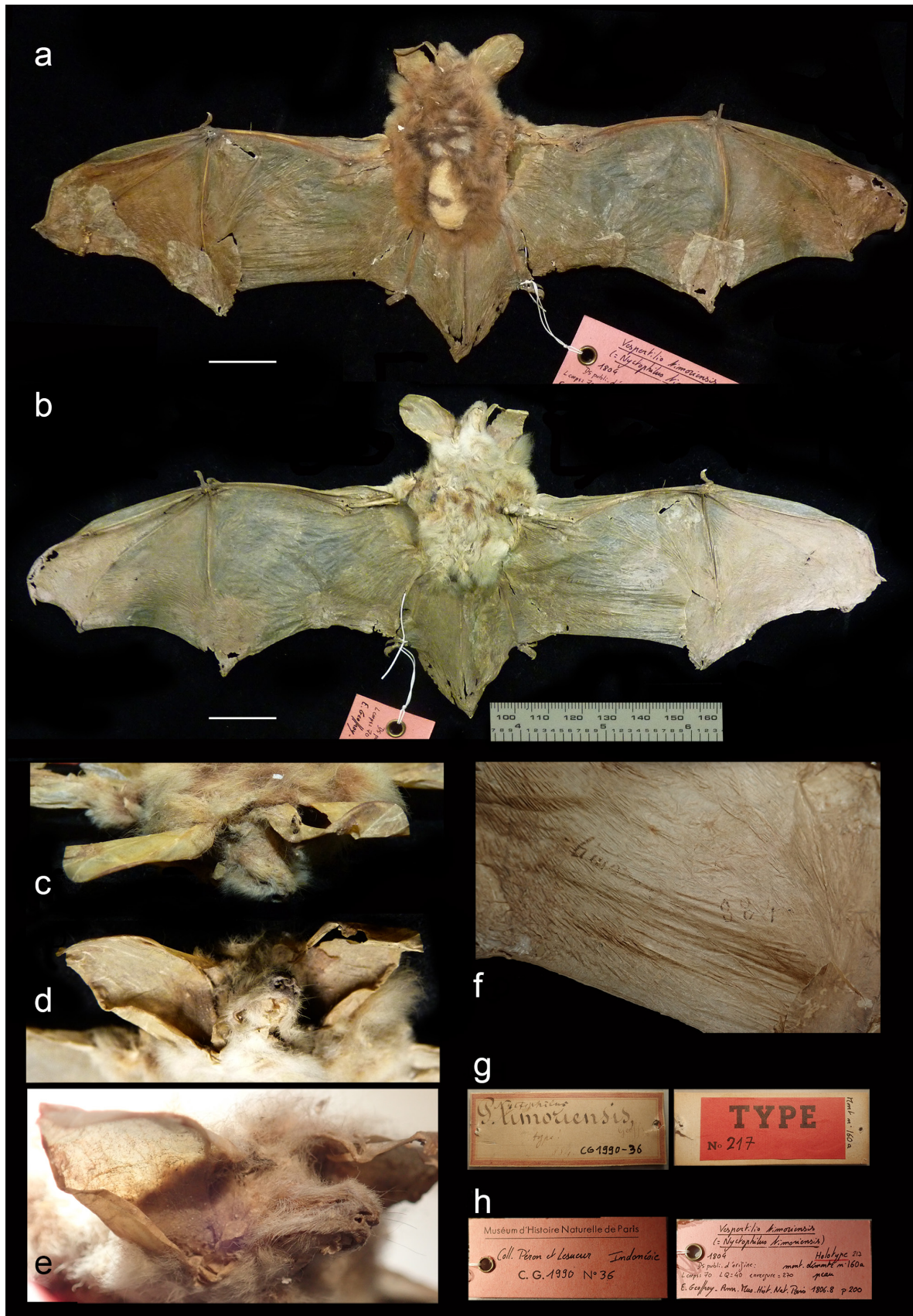
In conclusion, we suggest that the concept of *timoriensis* as a large-bodied species has a far weaker foundation than previously thought and it seems more likely to be of intermediate size in the genus. The concept of *timoriensis* as a large bodied species rests largely with the outdated assessment by Tomes (1858a) and on the body measurement of 70 mm given in Geoffroy's account. Although Tomes examined Geoffroy's original specimen, he based his understanding of *timoriensis* on specimens from southwestern Western Australia from Gould's collection, one of which was later designated the type (lectotype) of *N. major* by Thomas (1914). In effect, Tomes published the first diagnosis of what was later to become known as *major*, but under the name *timoriensis*. A further source of confusion arose because Tomes did not mention the name *major* anywhere in his paper. This omission was noted by Peters (1861), who proposed, in a footnote, that *major* should therefore be placed in the synonymy of *timoriensis*. Perhaps Tomes did not consider *major* to be a published name. The fact that *N. major* remained undiagnosed throughout the nineteenth century has also contributed to the erroneous conflation of *timoriensis* with *major*. The first diagnosis of *N. major* was provided by Thomas (1915a). The written account of *N. major* and the accompanying illustration of an animal from southwestern Western Australia was published by Gray (1875) but that illustration, accompanied with the name *Nyctophilus major*, was published separately and widely circulated privately in the 1840s (the publication date of *major* has been determined to be 1844 by Mahoney & Walton, 1988). Gray (1875) did not provide measurements or a description of *N. major*. His brief account consisted solely of a statement that he could not determine what species of *Nyctophilus* should be applied to his previously published plate.

## The suspected holotype of *timoriensis*

Jansen (2017) noted that for birds collected by the Baudin expedition, none of the specimens have original field tags attached, and no original tags are known to have survived. Jansen indicates that original specimen data was communicated by the naturalists Peron and Lesueur to MNHN taxidermists and transcribed to pedestal bases. We suspect that the same applies to the Baudin mammal material, and we note that the identity of the type specimen of *timoriensis* is uncertain. The earliest registers of bird and mammal specimens in the MNHN that assign specimen numbers began in the early 1840s (Jackson *et al.*, 2021), and it is possible that the identity of Geoffroy's original material might have become confused before the 1840s.

The specimen currently labelled the holotype of “*Nyctophilus timoriensis*” is CG1990-36 in the MNHN. Although forearm length is not given in the original description, this specimen is a medium-sized *Nyctophilus* with forearm length of 43 mm. It is a puppet skin (see Fig. 4a,b) from which the skull has been extracted at an unknown date and is now apparently lost (Figs 4c–e). Three other numbers are associated with the skin. The first published attribution of type status to this specimen is the catalogue of bat type specimens by Rode (1941), stated that the skull was lost and who might have assigned the number 217 to the skin. We have not found any other reference in the literature to the skull. The skin has 884 written in old ink on the right wing, to the left of which is some partially obliterated writing (Fig. 4f). There were no tags associated with the skin when examined in Sydney by HP in 1990. Later in 1990, Michel Tranier inventoried the MNHN collection and apparently registered the specimen as CG1990-36 and concluded that there were no other specimens in the collection that could be Geoffroy's type material (see Parnaby, 2009). It appears that Tranier also added numbers to an old board label that could have originated from the 19th century when the species was referred to *Plecotus* (Fig. 4g). A tag now attached to the specimen, presumably by Tranier, has an additional number 160a, evidently an old pedestal number (Fig. 4h). That number is listed in the *Nouveau Catalogue des Galeries* (New Catalogue of Galleries for skin mounts) (Jackson *et al.*, 2021), which commenced around the 1840s. We do not know the source of the pedestal number 160a. Perhaps it originated from the initial taxidermy procedures immediately following the Baudin expedition, as described for bird specimens by Jansen (2017).

We are unable to definitely establish that CG1990-36 is Geoffroy's original specimen, but we have no reason for rejecting it, other than the incongruent head-body length of 70 mm. However, detecting a mis-matched skin of a similar-sized *Nyctophilus* species is hampered by the poor condition of the skin. Our measurements of the putative type wingspan and tail length are consistent with Geoffroy's (1806) account: our wingspan measurement of 264 matches his 270 mm given that part of the wing tip is missing (Fig. 4) and our measurement of tail length, taken from the base of the body, equates to his 40 mm. Thomas (1914) reported a forearm length of 42 mm for the alleged type of *timoriensis*, taken by Trouessart at MNHN. This is a close match with our measurement of 43 mm taken on the putative type CG1990-36. Crucially, we have not been able to determine the nature



**Figure 4.** MNHN CG1990-36, study skin with skull extracted, alleged holotype of *Vespertilio timoriensis* È. Geoffroy, 1806. (a), skin dorsal view, scale bar = 2 cm (photo: Ken Aplin); (b), skin ventral view, scale bar = 2 cm (photo: Ken Aplin); (c), dorsal view of snout (photo: Ken Aplin); (d), oblique view of snout showing nose-leaf (photo: Ken Aplin); (e), lateral view of snout (photo: Anja Divljan); (f), old writing and numerals on ventral surface of left plagiopatagium (photo: Anja Divljan); (g), front and reverse view of associated, presumed 19th century tag (photo: Anja Divljan); (h), front and reverse view of contemporary skin tag (photo: Anja Divljan).

of the post-nasal elevation, which is hidden in the shrivelled skin folds. Finally, we note that Geoffroy (1806) did not state the number of *timoriensis* specimens that he examined, but he does not mention more than one and it has generally been assumed that his description was based on a single type specimen. Parnaby (2009) mistakenly believed that there were two specimens; his confusion arose from a statement by Temminck (1840) to that effect, but Temminck was instead referring to material of *Vespertilio peronii* I. Geoffroy, 1832. On balance, we accept that MNHN CG1990-36 is possibly Geoffroy's original specimen of *timoriensis*.

## Comparisons with Maubisse specimens

### *Nyctophilus timoriensis sensu stricto*

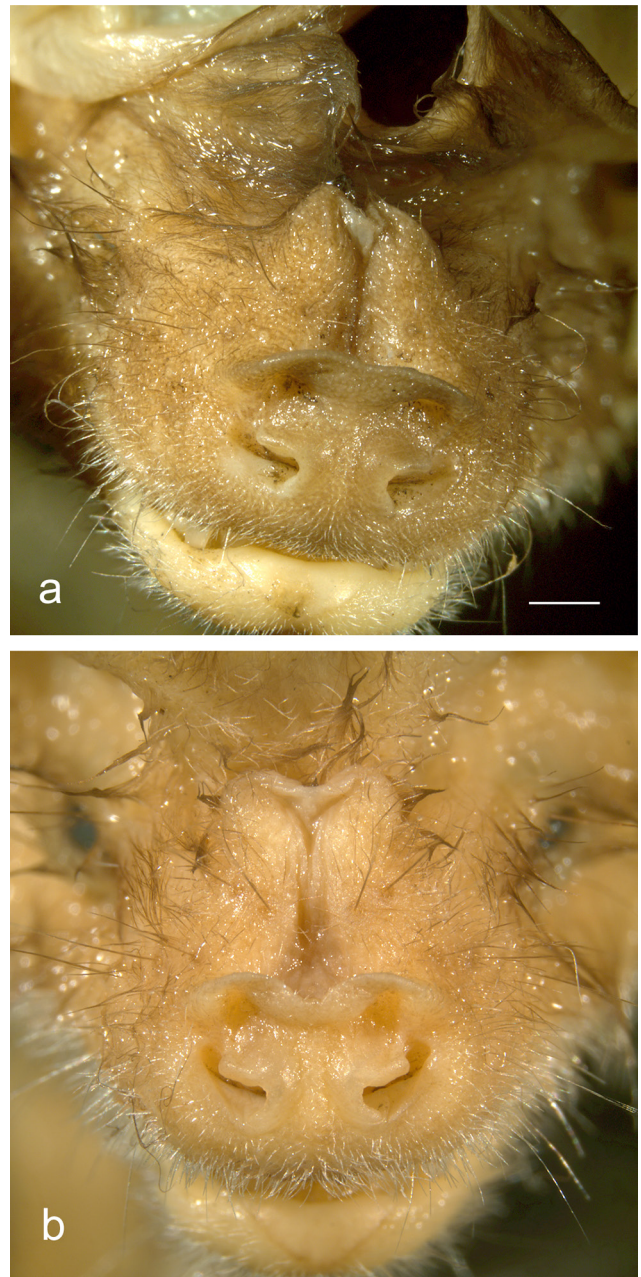
The Maubisse specimens share several features with our revised concept of Geoffroy's *N. timoriensis*: both are of medium body size, with a conspicuously developed post-nasal mound, similar to species such as *N. geoffroyi*, *N. heran*, and *N. gouldi*. The largest Maubisse specimen, though not fully mature, is of medium body size for the genus as reflected by a forearm length of 40 mm compared with 43 mm for the suspected *N. timoriensis* holotype. Field head-body measurements for male AM M.38841 and female AM M.37639 from Maubisse approximate that of the suspected type specimen (56 and 50 mm vs. *ca.* 53 mm).

### *Nyctophilus heran* and *N. geoffroyi*

Our comparison with these two species focuses on the Maubisse male AM M.38841, given that sexual size dimorphism occurs within *Nyctophilus* (males averaging smaller) and that the unique specimen of *N. heran* and the holotypes of *geoffroyi* and *pallescens* included in our analyses are all males. Measurements of an extensive series of *N. geoffroyi* from throughout Australia indicates that Tasmanian animals average larger than those from mainland Australia. Tasmanian specimens are excluded from further consideration here, given that mainland Australian "*N. geoffroyi*" is a composite of at least two species (Eldridge *et al.*, 2020) and the taxonomic status of Tasmanian populations has not been assessed. Our analyses treat *N. geoffroyi* as one entity because we did not identify any obvious geographic or morphological groupings in the morphometric data.

The Maubisse specimens undoubtedly most resemble *N. geoffroyi* and *N. heran* in overall morphology rather than any other species of the genus (other than *N. timoriensis*) based on the following combination of external, cranial and bacular characters:

- 1 Overall body size is medium within the genus.
- 2 The post-nasal prominence is well developed, consisting of two elevated mounds tapering to their distal tips and joined in the midline by an elastic membrane, forming the "Y" shape characteristic of *N. geoffroyi* (see Fig. 5).
- 3 The external ears are large relative to body size, and joined in the midline for a substantial proportion of the length of the ear and general colour of body fur is a mouse-brown dorsally, with much paler ventral fur.
- 3 The auditory bullae are large relative to skull size (Fig. 6).
- 4 Baculum shape is consistent with 12 specimens of *N. geoffroyi* examined from mainland Australia and resembles that of the holotype of *N. geoffroyi pallescens* illustrated by Hill & Harrison (1987). A slight groove is evident in the distal tip of M.38841 (Fig. 7). It is not clear if this represents incomplete ossification in this subadult animal, but a similar indentation is apparent in the holotype baculum of *N. geoffroyi pallescens*. Baculum length of AM M.38841 falls within the range for 12 specimens *N. geoffroyi*, and height and breadth are smaller in this subadult animal (Table 2). Baculum morphology of



**Figure 5.** Snout morphology of (a) subadult female *Nyctophilus* from Maubisse (AM M.37639, ET3), and (b) an adult male *N. geoffroyi* from Napier Downs Station, Kimberleys, Western Australia (AM M.22122) (imaging: Sue Lindsay). Scale bar represents *ca.* 1 mm.

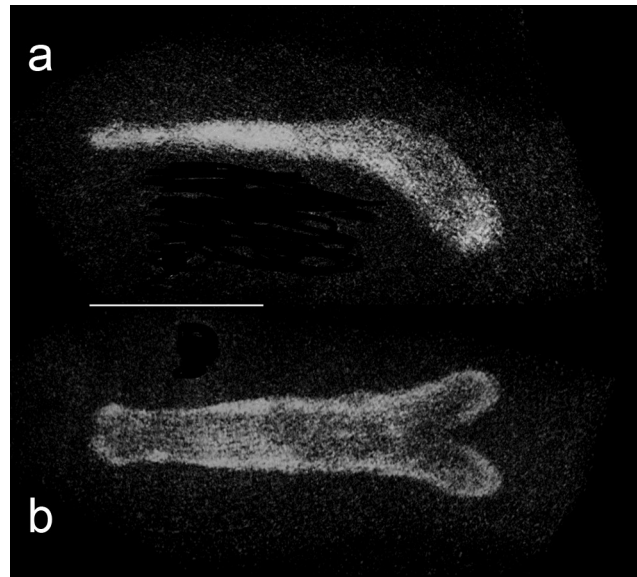


**Figure 6.** Micro CT scans of skull and dentary of AM M.38841. Scale bar represents *ca.* 2 mm. (images: Fred Ford).

*N. heran* remains imperfectly defined (Kitchener *et al.*, 1991).

The Maubisse male M.38841 is compared against the following differences between *N. heran* and *N. geoffroyi* cited by Kitchener *et al.* (1991):

- 1 *Nyctophilus heran* has smaller and less inflated bullae relative to skull length. The bullae of *N. heran* are smaller and less inflated than *N. geoffroyi*. In absolute size, BUL of *N. heran* falls within the size range for *N. geoffroyi*. However, the larger skull size of *N. heran* results in relatively smaller and less inflated bullae, as illustrated in a plot of BUL vs GL (Fig. 8a) and BTB vs MAS (Fig. 9). The bullae of M.38841 appear to be relatively larger than those of the holotype of *N. heran* as evident in



**Figure 7.** Micro CT scan of baculum of AM M.38841. (a) lateral view; (b) dorsal view. Distal end of bone faces left. Scale bar represents *ca.* 2 mm (images: Fred Ford).

the lateral skull view (compare Fig. 6 with figure 2 of Kitchener *et al.*, 1991), in which M.38841 is far more typical of *N. geoffroyi*. However, BUL of M.38841 is at the low end of the size range for *N. geoffroyi* (Table 2) and a bivariate plot of BUL vs GL (Fig. 8a) indicates that relative to GL, BUL is smaller relative to most specimens of *N. geoffroyi*. Kitchener *et al.* contrast the smaller ratio BUL/GL of the holotype of *N. heran* (0.233) compared to the smallest ratio of 0.247 in their sample of six male *N. geoffroyi*. The ratio of 0.232 for M.38841 is similar to that of *N. heran* but this ratio ranged from 0.225–0.314 in our sample of 53 adult male skulls of *N. geoffroyi* from throughout mainland Australia. However, the ratio exceeded 0.237 in all but one of the 53 males that we measured, and the trend for a relatively larger BUL in *N. geoffroyi* is clear.

- 2 *Nyctophilus heran* has a more sharply angled anterior edge of the mesopterygoid fossa. The anterior edge of the mesopterygoid fossa is gently curved toward the base of the post-palatal spine in M.38841 (Fig. 6), similar to *N. geoffroyi*, but in contrast to the more linear margin in the holotype of *N. heran*. We have examined photographs of the holotype skulls of *pallescens* and *pacificus*, both of which resemble that of M.38841. However, this feature is not invariant, and occasional mainland Australian *N. geoffroyi* specimens had angled edges.
- 3 *Nyctophilus heran* has a more pronounced post-palatal spine. The post-palatal spine of M.38841 is relatively shorter, similar to that of the holotypes of *pallescens* and *pacificus* and other *N. geoffroyi* specimens examined, compared to *N. heran*.
- 4 Hypocones on M<sup>1</sup> and M<sup>2</sup> more developed in *N. heran*. The hypocones of M.38841 are present but are relatively undeveloped. Kitchener *et al.* (1991) state that the hypocones are more developed than in *N. geoffroyi* and we assume that hypocone

**Table 2.** Selected cranial and external measurements of AM M.38841 from Maubisse, Timor-Leste, and the holotypes of *N. heran*, *pacificus*, and *pallescens*, compared to male *N. geoffroyi* from the Australian mainland. \* Measurements from Kitchener *et al.* (1991).

Character	AM M.38841 (ET12) subadult male	<i>N. heran</i> holotype male *	<i>pacificus</i> holotype BM84.410 male	<i>pallescens</i> holotype BM7.1.4.1 male	<i>N. geoffroyi</i> adult male, Australian mainland	range	n
GL	15.23	16.70	16.1	15.75	14.5–16.3	74	
CON	14.44	—	—	—	13.5–15.4	78	
ZYG	9.12	10.64	9.90	9.24	8.6–10.0	77	
ANT	4.12	4.73	4.78	4.53	4.1–4.8 *	6	
INT	2.97	3.76	3.40	3.45	3.1–3.7	64	
C <sup>1</sup> –C <sup>1</sup>	4.00	4.54	4.53	4.18	3.7–4.8	68	
CM <sup>3</sup>	5.61	6.05	5.36	5.63	4.9–6.0	78	
M <sup>3</sup> –M <sup>3</sup>	6.21	6.97	6.37	6.13	4.9–6.6	64	
PAL	7.28	—	6.97	7.12	6.4–7.3	29	
sinPAL	5.47	6.02	—	—	5.4–5.8	5	
MESO	1.80	2.05	1.55	1.56	1.4–1.8 *	6	
BUL	3.66	3.90	3.62	3.76	3.6–4.1	49	
BTB	1.65	1.64	—	—	1.0–1.6	45	
MAS	8.35	8.89	8.30	7.64	7.5–8.6	78	
BRH	5.59	6.18	4.97	5.40	4.5–5.7	75	
M <sup>3</sup> B	1.72	1.75	1.65	1.65	1.4–1.7 *	6	
M <sup>3</sup> L	0.72	0.74	0.60	0.60	0.6–0.7 *	6	
BAC length	2.39	—	—	—	2.4–2.8	12	
CM <sub>3</sub>	6.01	6.53	—	—	5.8–6.0 *	—	
EAR	24.0	23.4	—	—	20.6–28.0	100	
FA	36	39	37	34	30.8–37.7	132	
HB	41	52	—	—	43–47	19	
Tail L	36.0	40.7	—	—	35–43	18	
WT	4.5	7.6	—	—	4–6	19	

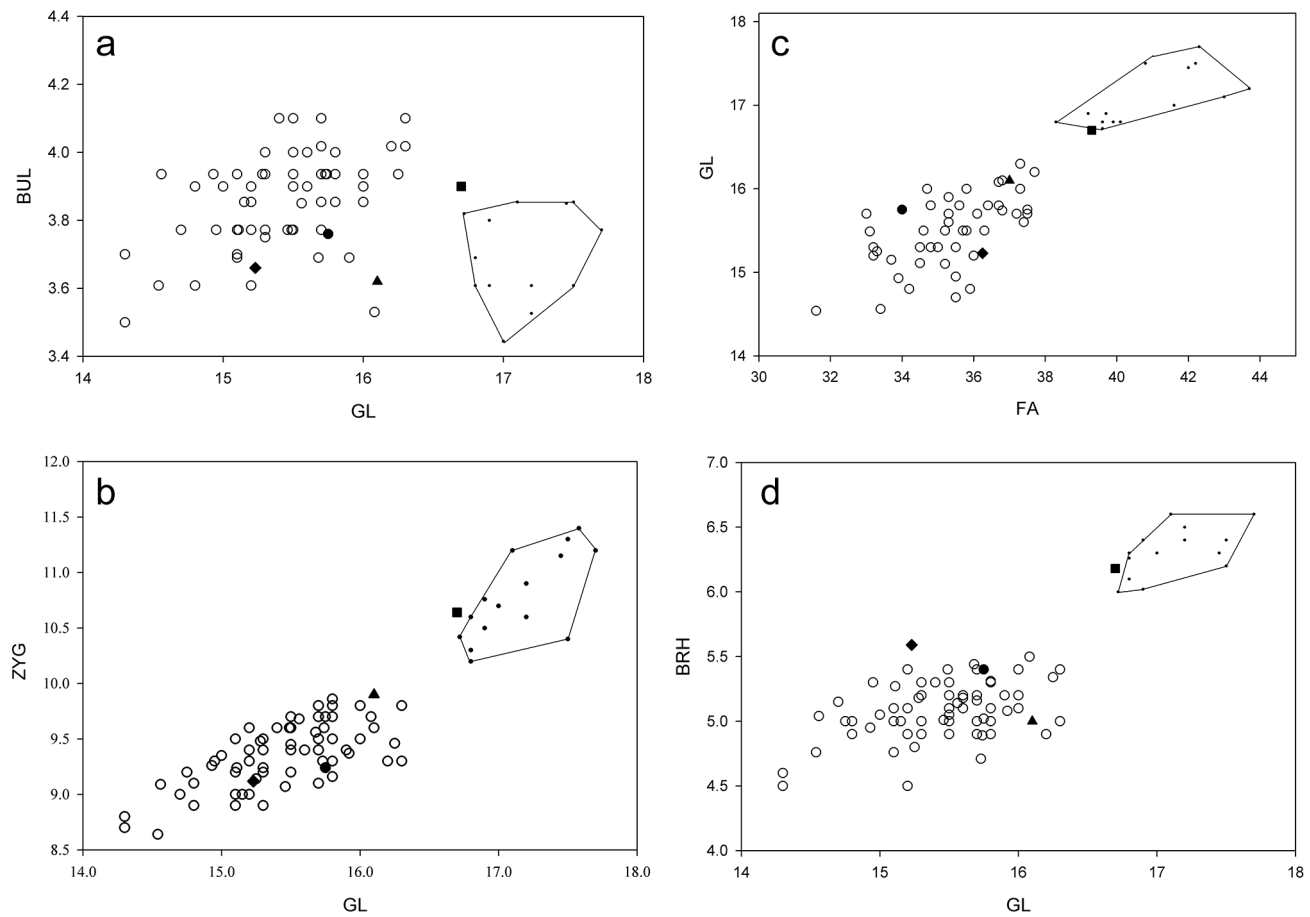
- development in the latter species is variable, given that they are absent in the *N. geoffroyi* that we examined. We are unable to evaluate this further because we cannot clearly discern hypocone morphology from the illustrations of *N. heran* given by Kitchener *et al.* (1991), although it appears that they are more developed than those of M.38841. We note that the latter authors did not include this character in their diagnosis of the species. Cusp terminology used by those authors is possibly the same as in figure 2 of Kitchener & Caputi (1985).
- Nyctophilus heran* has a relatively longer third commissure on M<sup>3</sup>. The third commissure is relatively much shorter in M.38841 compared with *N. heran*. Kitchener *et al.* (1991) suggest that the greater development of the third commissure has resulted in a greater M<sup>3</sup> width than that of *N. geoffroyi*, however M<sup>3</sup> length and breadth of M.38841 approximates that given for *N. heran*, and the likely level of measurement error suggests that M<sup>3</sup> is effectively the same size as the holotype of *N. heran*, both of which fall at the upper end of the range for the six *N. geoffroyi* measured by Kitchener *et al.* (1991).
  - Nyctophilus heran* has a less rounded distal end on the glans penis.
  - Dorsal crest on the glans penis is absent in *N.*

*heran*. The external morphology of the glans penis of M.38841 resembles that of the holotype of *N. heran* (see fig. 4 of Kitchener *et al.*, 1991), rather than that of *N. geoffroyi*, in having a broadly rounded distal tip, and no dorsal crest.

- Larger absolute size of *N. heran*. The holotype of *N. heran* is clearly larger in overall size than mainland Australian *N. geoffroyi* of equivalent sex, as noted by Kitchener *et al.* (1991). This is evident, for example, in bivariate plots of ZYG vs GL (Fig. 8b) and GL vs FA (Fig. 8c), in which *N. heran* falls well outside *N. geoffroyi* but close to *N. daedalus*. We have added the latter species to these plots as a yardstick to the magnitude of interspecific differences that can occur for *Nyctophilus* species. The four examples of larger skull and dental dimensions cited by Kitchener *et al.* (1991) are GL, ZYG, BRH and CM<sup>3</sup>, all of which are corroborated by our much larger sample sizes (Table 2).

#### Morphometric comparisons with *N. heran* and mainland Australian *N. geoffroyi*

Skull and external measurements of M.38841 fall within the size range of mainland Australian adult male *N. geoffroyi* for most dimensions (though smaller than the range for INT). However, given the specimen is subadult, it likely has



**Figure 8.** Bivariate plots of adult male *Nyctophilus*: (a) BUL vs GL (n = 71 for *N. geoffroyi*); (b) ZYG vs GL (n = 79 for *N. geoffroyi*); (c) GL vs FA (mm) for male *Nyctophilus geoffroyi* (n = 50), and (d) BRH vs GL (n = 75). Symbols are: *N. geoffroyi* from throughout mainland Australia (○); holotype of *Nyctophilus geoffroyi pallescens* (●); holotype of *Nyctophilus geoffroyi pacificus* (▲); holotype of *N. heran* (■); subadult male M.38841 from Maubisse, Timor-Leste (◆); *N. daedalus* are small dots bounded by polygon, for a comparison with a similar-sized species.

not attained fully adult size, compromising morphometric comparisons overall. In contrast, this specimen is at the upper size limit of specimens measured in this study, for sinPAL, BTB and M<sup>3</sup>B, for which it approaches the size of *heran* (Table 2). AM M.38841 falls within the range of variation of *N. geoffroyi* as illustrated in bivariate plots of BUL, ZYG, and BRH vs GL, GL vs FA (Fig. 8a–d), and EAR vs FA (Fig. 10). In contrast, the holotype of *N. heran* falls outside the

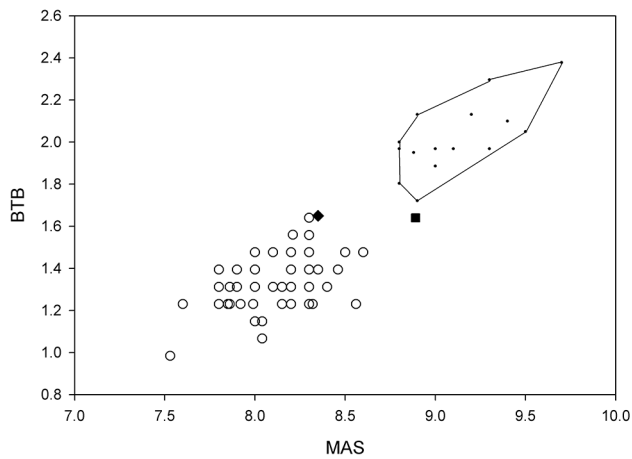
range of *N. geoffroyi* in these plots and exceeds the upper range of mainland *N. geoffroyi* for most characters other than BUL and EAR, which fall within the range (Table 2).

A comparison of M.38841 with *N. geoffroyi* and *N. heran* was explored further in a principal components analysis based on 9 skull and dental dimensions of 75 mainland Australian adult male *N. geoffroyi*. Separate analyses using a correlation matrix and a variance-covariance matrix yielded similar trends, with the holotype of *N. heran* a clear outlier in both. The PCA explained 59.6 and 12.1% of variance on the first and second PC axes respectively, compared to 71.1 and 7.6% in the variance-covariance analysis and we only present results of the latter. The first three PC axes account for a substantial percentage of the measurement variance (Table 3) and character coefficients suggest the first PC axis is dominated by overall size, while PC 2 contrasts BRH, with M<sup>3</sup>–M<sup>3</sup> and BUL. A plot of PC scores on the first two PC axes, and on PC 1 vs. PC 3 (Fig. 11) indicate that scores for AM M.38841 fall within the range of *N. geoffroyi*, while those of the holotype of *N. heran* are an outlier on the first two axes but not on PC 3. A minimum spanning tree fitted to each specimen in the PCA plots (not shown) revealed that the holotype of *N. heran* is a clear outlier on a plot of PC 1 vs. PC2, and PC 1 vs. PC 3, while that of the Maubisse male falls within the range of variation of *N. geoffroyi*.

We further compared skull and dental measurements of *N. heran* and M.38841 with the same sample of mainland

**Table 3.** Standardized character coefficients on the first three PC axes based on 9 skull and dental measurements of 75 adult male specimens of *N. geoffroyi*, the holotype of *N. heran* and M.38841 from Timor-Leste.

	Character	PC 1	PC 2	PC 3
character loadings	GL	0.634	0.000	−0.551
	CM <sup>3</sup>	0.245	−0.079	−0.309
	C <sup>1</sup> –C <sup>1</sup>	0.247	−0.133	−0.125
	ZYG	0.412	0.076	0.645
	INT	0.114	−0.063	0.130
	M <sup>3</sup> –M <sup>3</sup>	0.354	−0.368	0.142
	BRH	0.193	0.886	0.012
	MAS	0.352	0.019	0.294
	BUL	0.090	−0.214	0.214
Eigenvalue		0.511	0.055	0.046
% variance		71.106	7.620	6.424



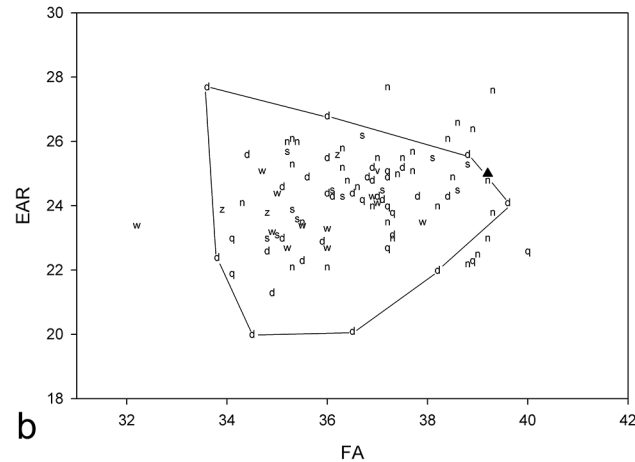
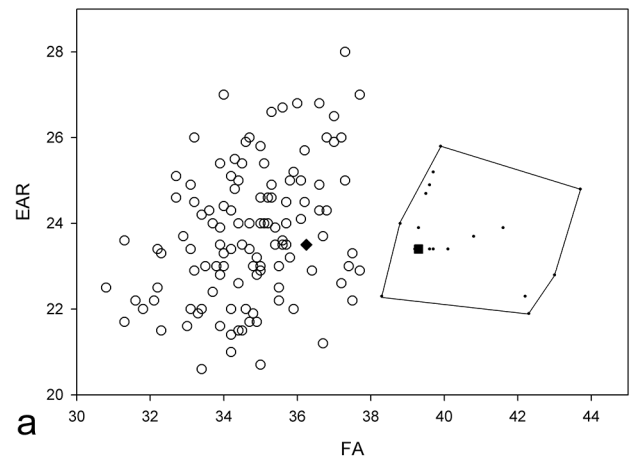
**Figure 9.** Plot of BTB vs MAS, for adult males: *N. geoffroyi* ( $n = 50$ ) from throughout mainland Australia ( $\circ$ ); holotype of *N. heran* ( $\blacksquare$ ); subadult male M.38841 from Maubisse, Timor-Leste ( $\blacklozenge$ ); *N. daedalus* ( $n = 15$ ) are small dots bounded by polygon, for a comparison with a similar-sized species.

Australian *N. geoffroyi* in dendrograms from UPGMA cluster analyses using euclidean distance as a measure of similarity. The holotype of *N. heran* formed an outgroup to both M.38841 and all mainland *N. geoffroyi* in all 10,000 boot-strap replications, in which there was little or no support for subgroupings within *N. geoffroyi* and M.38841 was an outgroup to mainland *N. geoffroyi* in 37% of replications (not shown). This suggests that no meaningful substructure was detected within *N. geoffroyi* and M.38841 with this character set using this technique.

The subadult female specimen M.37639 was at the most advanced growth stage of the three Maubisse specimens and falls at the upper end of the size range of 70 adult female mainland Australian *N. geoffroyi* as shown in a plot of Ear Length vs. FA (Fig. 10). Its measurement of  $C^1-C^1$  of 4.26 mm falls within the range of 3.8–4.8 mm of 70 adult female *N. geoffroyi* from mainland Australia.

### Summary of species comparisons

Seven potentially diagnostic criteria are available to compare the Maubisse male with *N. geoffroyi* and the original description of the holotype of *N. heran*. The character states shared by the three entities are summarized in Table 4. The Maubisse male has a unique combination of characters shared with both *N. heran* (glans penis morphology and BTB) and *N. geoffroyi* (skull and dental morphology). This suggests that the Maubisse animals could be a separate taxon.



**Figure 10.** Plot of Ear vs FA (mm) of *Nyctophilus*: (a) males: adult male *N. geoffroyi* ( $n = 122$ ) from throughout mainland Australia ( $\circ$ ); holotype of *N. heran* ( $\blacksquare$ ); subadult male M.38841 from Maubisse, Timor-Leste ( $\blacklozenge$ ); *N. daedalus* ( $n = 18$ , small dots) are bounded by polygon, for a comparison with a species of similar size to *N. heran*. (b) Adult female *N. geoffroyi* from throughout mainland Australia ( $n = 99$ ); subadult female M.37639 from Maubisse, Timor-Leste ( $\blacktriangle$ ). Locality codes for *N. geoffroyi* are: central Australia (c); NSW (n), Queensland (q); Victoria (v), northern Western Australia and northern Northern Territory (z). Thirty specimens from Dangali, SA (d), are bounded by a polygon, indicating extent of within locality variation relative to total variation.

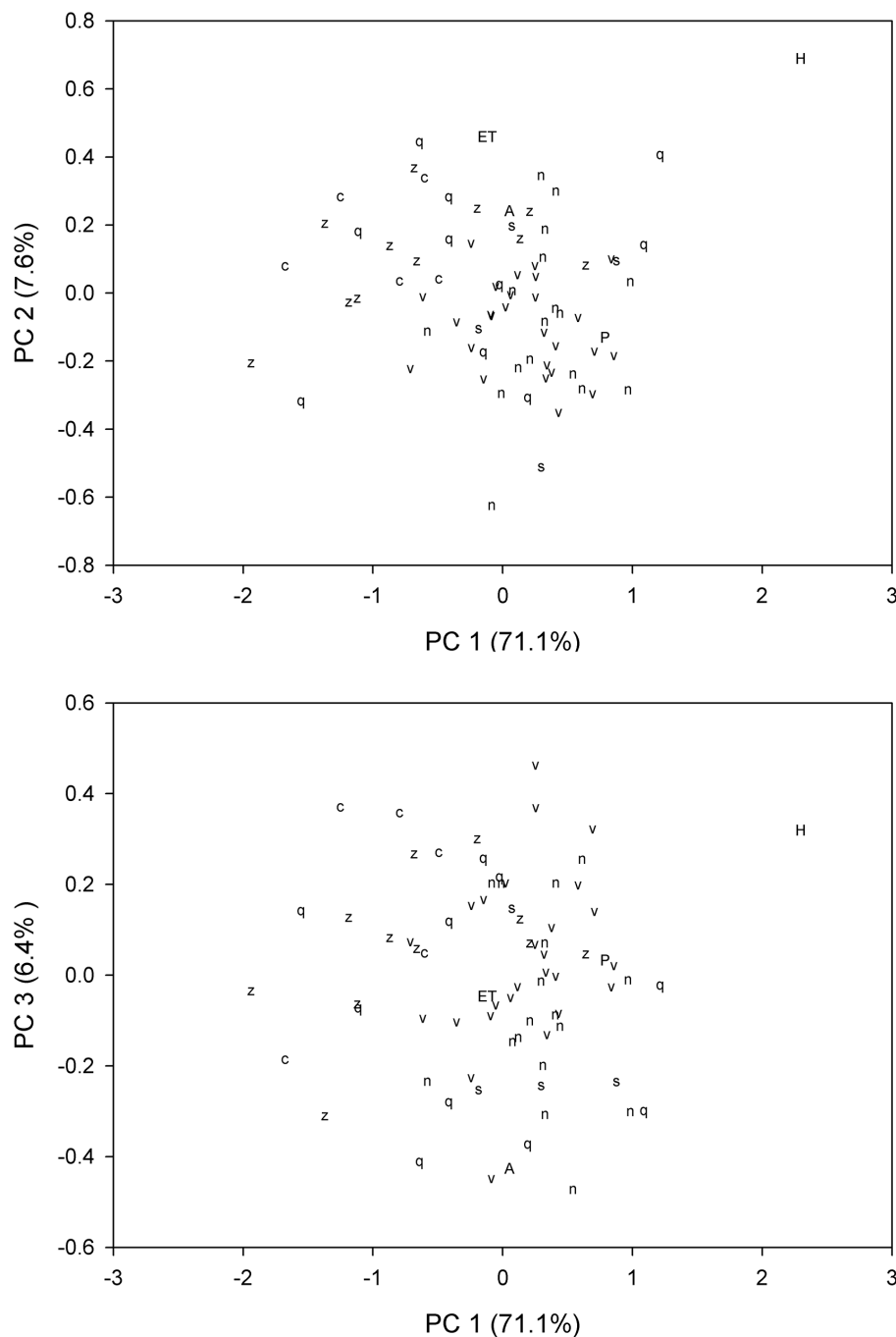
The Maubisse male has only three of the seven criteria in common with the holotype of *N. heran*, but four with *N. geoffroyi*.

Ontogenetic changes in size and shape potentially influence at least three of the five criteria this specimen

**Table 4.** Characters of Maubisse *Nyctophilus* specimens shared (+) with *N. heran* and *N. geoffroyi* complex.

Character	M.38841 Maubisse	<i>N. heran</i> holotype	<i>N. geoffroyi</i> complex
Glans penis with rounded distal tip	+	+	—
Glans penis without dorsal ridge	+	+	—
BTB exceeds 1.6 mm	+	+	—
M <sup>3</sup> third commissure relatively short	+	—	+
Mesopterygoid fossa with rounded anterior margin	+	—	+
Posterior palatal spine not enlarged	+	—	+
Relatively large auditory bullae	+	—	+





**Figure 11.** Plot of PC scores for the first three axes of a PCA based on 9 skull and dental measurements of 75 adult male specimens of *N. geoffroyi*; AM M.38841 from Maubisse (ET), holotype specimens of *pacificus* (P), *pallescens* (A) and the holotype of *N. heran* (H). Mainland Australian *N. geoffroyi* symbols designate specimen localities: central Australia (c); NSW (n), Queensland (q); Victoria (v) and northern Western Australia and northern NT (z).

shares with *N. geoffroyi*. The relatively enlarged bullae, which are very characteristic of *N. geoffroyi*, possibly result from differential skull growth. If the cranial cavity and auditory regions attain near adult dimensions earlier than rostral dimensions, the Maubisse male might be a subadult specimen of *N. heran* irrespective of its relatively large bullae. Further support for this interpretation stems from the large absolute size of BTB, for which the Maubisse male matches that of *N. heran* and exceeds the largest of 45 male *N. geoffroyi* (Table 2). However, this is contradicted by BUL of the Maubisse

male, which is at the lower end of the range of *N. geoffroyi* and is substantially smaller than *N. heran*. Although the Maubisse male could have skull proportions not shared with either *N. heran* or *N. geoffroyi*, these differences potentially result from differential growth rates of bullae relative to the cranial vault. This could be resolved when adult material becomes available from Timor, and additional material enables an assessment of intraspecific variation in *N. heran*. Although the overall size of the Maubisse male falls within the range of *N. geoffroyi* for most individual dimensions and also in

the PCA based on skull and dental dimensions, the animal is at a fairly early stage of development based on the extent of fusion of the wing epiphyses and it might not have attained full adult size. The relative length of the post-palatal spine is similarly problematic, and further growth in the length of this structure cannot be discounted. However, we suspect that the anteriorly more rounded shape of the mesopterygoid fossa of the Maubisse male reflects the adult state.

## Discussion

Our primary aim was to evaluate the taxonomic status of new specimens of *Nyctophilus* collected in Timor-Leste but this first required a re-examination of Geoffroy's description of *timoriensis*, the only previously reported material of *Nyctophilus* from Timor. Our re-interpretation of Geoffroy's illustration of *timoriensis*, combined with a review of the few measurements given in his original description, indicate that *timoriensis* is not conspecific with *N. major* and we see no reason to doubt that Geoffroy's original material of *timoriensis* was obtained while the Baudin expedition was stationed in Timor.

A new concept of *N. timoriensis* that arose from our review of the taxonomic literature is of a species with an enlarged post-nasal mound that is similar in relative size to species with the maximum development of that structure, such as *N. heran*, *N. geoffroyi* and *N. gouldi*, and not a rudimentary structure of *N. major* as previously implied. There is little evidence for the entrenched view that *N. timoriensis* is of similar body size to the large-bodied *N. major* and it is more likely to be of intermediate body size for the genus. Further, the suspected holotype of *N. timoriensis* is a closer match in body size to our revised concept of *N. timoriensis* than it is to *N. major*.

The possibility that more than one species of *Nyctophilus* occurs on the island of Timor needs to be considered, particularly given that the Baudin expedition might have obtained *Nyctophilus* from the lowlands in contrast to our montane material. No island that is not connected to the Sahul Shelf (the continental shelf containing New Guinea, mainland Australia, and Tasmania), like Timor, has yet been shown to support more than one species of the genus (e.g., Lembata, Sudest, New Ireland, Bougainville, New Caledonia) and there is no clear indication of multiple species in the specimens available from Timor. However, it is doubtful that adequate survey effort with appropriate techniques has been undertaken in these regions to be confident that only one species is present. Although the specimens from Maubisse provide a general correspondence in morphological features, including body size and snout morphology, with Geoffroy's description of *timoriensis* from the Baudin expedition, confident assignment of the Maubisse specimens to *N. timoriensis* is premature (discussed below). However, we tentatively assign the Maubisse material to *N. timoriensis* until further material becomes available.

Four factors hindered our assessment of the Maubisse material in the preliminary morphological analysis presented here. First, the immature status of the three specimens complicates interpretation of diagnostically valuable skull proportions, due to potential age-related differential growth of cranial components. It also diminishes the value of absolute cranial and external measurements which can be important in defining species of this genus. Bullae size is

a possible exception, assuming that basicranial structures attain adult size earlier than other regions of the skull. Differences in absolute size separating the mensural range for characters between similar *Nyctophilus* species are typically small, often only one or two mm, yet can be consistent and diagnostic. Consequently, the size difference, for example in GL, of about one mm between *N. heran* and our largest male *N. geoffroyi* could be significant. Second, intraspecific variation remains undefined in *N. heran*, known from the unique holotype. The extent of variability of key diagnostic criteria, such as the dorsal penile ridge and molar cusp morphology, within mainland Australian *N. geoffroyi* has also not been adequately assessed, nor have species limits within what is currently regarded as "*N. geoffroyi*". Third, we have not made direct comparisons between our material and the holotype of *N. heran* but have relied on the original description and illustrations. Finally, large numbers of *N. geoffroyi* exist in museum collections, the majority from southern Australia, but we used readily available specimens with intact skulls which had already been extracted from bodies, with a resultant relatively small sample size.

Overall, Geoffroy's description and illustration, and the Maubisse material, show closest morphological resemblance to *N. heran* and *N. geoffroyi*. The Maubisse male M.38841 exhibits characters that are diagnostic of both *N. heran* and *N. geoffroyi*, as currently understood. External morphology of the glans penis is a diagnostic feature for *Nyctophilus* species, and two penile characters (rounded distal end and absence of a dorsal ridge) clearly align M.38841 with *N. heran* and suggest that they are not conspecific with *N. geoffroyi*. Overall, our morphological assessment, particularly the shape of the glans penis, suggests that the Maubisse material is distinct from the *N. geoffroyi* complex. The Maubisse male fell outside our material of mainland *N. geoffroyi* in our cluster analyses of cranial characters, being larger than all *N. geoffroyi*. Conversely, M.38841 resembles *N. geoffroyi* but differs from *N. heran* in the diagnostically important shape of the mesopterygoid fossa and post-palatal spine, provided it had attained the adult condition for those characters. The more angular mesopterygoid fossa of *N. heran*, judging from fig. 2 of Kitchener *et al.* (1991), more closely resembles eastern Australian *N. gouldi* and the smaller form of *N. daedalus* from northwest Western Australia than it does *N. geoffroyi*. The lateral skull profile and relatively large bullae of M.38841 are very characteristic of *N. geoffroyi*, and if that specimen had attained adult proportions, it would be a significant distinction from *N. heran*.

Genetic comparisons seem to indicate a close relationship between *N. timoriensis*, as represented by the Maubisse sample, and *N. heran*, its closest geographic neighbour; analysis of two mitochondrial genes and one nuclear gene showed that samples from the holotype of *N. heran* and the Maubisse animals clustered together to the exclusion of all other *Nyctophilus* species, and are probably conspecific (Belinda Appleton, pers. comm. to first author, 2008). However, these comparisons remain unpublished and the original tissue samples for these specimens may no longer be available. Though this provides an indication that *N. timoriensis* and *N. heran* are closely related and likely conspecific, firmer understanding of species limits in this group should arrive via analyses that sample larger segments of the genome in as many specimens as possible.

**Table 5.** Bat species recorded from the island of Timor, indicating endemic taxa (E). Based on Polhemus & Helgen (2004), Simmons (2005), our interpretation of the taxonomic literature combined with inspection of world collections by the second author, and research by our colleagues as indicated. \*

Taxon	Timor endemic?	Remarks
<b>Fruit-bats (Pteropodidae)</b>		
<i>Acerodon mackloti mackloti</i> (Temminck, 1837)	—	
<i>Cynopterus terminus</i> Sody, 1940	E	Variably considered a subspecies <i>Cynopterus titthaechelilus terminus</i> , e.g., Simmons (2005), or a full species, e.g., Schmitt <i>et al.</i> (2009).
<i>Cynopterus nusatenggara</i> Kitchener & Maharadatunkamsi, 1991	—	Recorded from West Timor (Ruedas <i>et al.</i> , 2019).
<i>Dobsonia moluccensis</i> (Quoy & Gaimard, 1830)	—	Recorded by Polhemus & Helgen (2004) based on a nineteenth century specimen, suspected to be extinct on Timor.
<i>Dobsonia peronii peronii</i> (Geoffroy, 1810)	—	
<i>Eonycteris spelaea</i> (Dobson, 1871)	—	
<i>Macroglossus minimus lagochilus</i> Matschie, 1899	—	
<i>Nyctimene keasti</i> Kitchener in Kitchener, Packer & Maryanto (1993)	—	The few Timorese records are usually assigned to <i>N. cephalotes</i> (Pallas, 1767); considered more likely to be <i>keasti</i> by Kitchener, Packer & Suyanto (1995: 138).
<i>Pteropus griseus</i> (Geoffroy, 1810)	—	
<i>Pteropus lombocensis salottii</i> Kitchener, in Kitchener & Maryanto, 1995	E	<i>P. lombocensis</i> first reported from Timor by Kitchener & Maryanto (1995); endemic subspecies.
<i>Pteropus vampyrus edulis</i> (Geoffroy, 1810)	—	
<i>Rousettus amplexicaudatus</i> (Geoffroy, 1810)	—	
<b>Sheath-tail-bats (Emballonuridae)</b>		
<i>Saccolaimus saccolaimus</i> (Temminck, 1838)	—	
<i>Taphozous melanopogon</i> Temminck, 1841	—	
? <i>Taphozous achates</i> Thomas, 1915b	—	Probably occurs in Timor, see Kitchener <i>et al.</i> (1993: 80).
<b>Horseshoe-bats (Rhinolophidae)</b>		
<i>Rhinolophus keyensis parvus</i> Goodwin, 1979	E	Endemic subspecies, previously included in <i>R. celebensis</i> Andersen, 1905.
<i>Rhinolophus montanus</i> Goodwin, 1979	E	Previously included as a subspecies of <i>R. philippinensis</i> Waterhouse, 1843 but elevated to species by Csorba (2002).
<i>Rhinolophus timorensis</i> Goodwin, 1979	E	Often included as a subspecies of <i>R. canuti</i> Thomas & Wroughton, 1909 but likely to be a full species (Helgen, 2004).
<i>Rhinolophus</i> sp. cf. <i>philippinensis</i> Waterhouse, 1843	—	Captured in Timor-Leste, taxonomic status under investigation (Armstrong, 2007).
<b>Leaf-nosed bats (Hipposideridae)</b>		
<i>Hipposideros bicolor hilli</i> Kitchener in Kitchener <i>et al.</i> (1996)	E	Subspecies endemic.
<i>Hipposideros crumeniferus</i> (Lesueur & Petit, 1807). <i>incertae sedis</i>	—	Entity of uncertain taxonomic status, suspected to be <i>H. cervinus</i> (Gould, 1854) or a closely related taxon by Oey & van der Feen (1958) and Hill (1963).

Table 5. Continued ...

**Table 5.** *Continued.*

Taxon	Timor endemic?	Remarks
<i>Hipposideros diadema diadema</i> (Geoffroy, 1813)	—	
<i>Hipposideros sumbae rotiensis</i> Kitchener & Maryanto, 1993	E	Recorded from Timor by Kitchener & Maryanto (1993).
<b>Bent-wing bats (Miniopteridae)</b>		
<i>Miniopterus macrodens</i> Maeda, 1982	—	Past records of <i>M. schreibersii</i> (Kuhl, 1817) from Timor are likely to be this species but species taxonomy of <i>Miniopterus</i> from Timor remains confused. Maeda (1983) demonstrated that <i>macrodens</i> and <i>magnater</i> Sanborn, 1931 are distinct but often treated as a subspecies, <i>M. magnater macrodens</i> .
<i>Miniopterus blepotis</i> Temminck, 1840	—	Requires confirmation. Past records of <i>M. schreibersii</i> (Kuhl, 1817) from Timor might include this species (Ibáñez & Juste, 2019), possibly along with past records of <i>M. oceanensis</i> Maeda, 1982.
<i>Miniopterus pusillus</i> Dobson, 1876	—	Subspecies from Timor uncertain, see Kitchener & Suyanto (2002: 26).
<i>Miniopterus shortridgei</i> Laurie & Hill, 1957	—	Recorded by Kitchener & Suyanto (2002). Previous authors assigned Timor specimens to <i>M. australis</i> Tomes, 1858b.
<b>Vespertilionid bats (Vespertilionidae)</b>		
<i>Harpiocephalus</i> sp.	?	Captured in Timor-Leste by Pavey & Milne (2004), generic identity determined by Armstrong & Konishi (2012); taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
<i>Kerivoula</i> sp.	?	Captured in northern Timor-Leste (Pavey & Milne, 2004); subsequent records from the south coast, Timor-Leste (Armstrong & Konishi, 2012). Taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
<i>Murina</i> sp.	?	Captured in northern (Pavey & Milne, 2004) and south coast Timor-Leste (Armstrong & Konishi, 2012). Taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
<i>Myotis adversus</i> (Horsfield, 1824)	—	First recorded from Timor by Kitchener <i>et al.</i> (1995).
<i>Myotis muricola</i> (Gray, 1847)	—	Captured by Hisheh <i>et al.</i> (2004).
<i>Nyctophilus timoriensis</i> (Geoffroy, 1806)	?E	Probably endemic. Obtained by Baudin expedition of 1802–1804, at Kupang. Specimens from Maubisse, Timor-Leste might be this species.
<i>Pipistrellus</i> sp. cf. <i>papuanus</i> Peters & Doria, 1881 **	—	Previously recognized as <i>P. tenuis</i> (Temminck, 1840) but taxonomic status of <i>P. papuanus</i> from Timor is uncertain.
<i>Scotophilus collinus</i> Sody, 1936	—	Treated as a synonym of <i>S. kuhlii</i> (Leach, 1821b) or <i>S. temminckii</i> (Horsfield, 1824), prior to the taxonomic revision of Kitchener <i>et al.</i> (1997).
<i>Scotorepens sanborni</i> (Troughton, 1937)	—	See Kitchener <i>et al.</i> (1994).
<i>Tylonycteris robustula</i> Thomas, 1915c	—	

\* We note that Kitchener & Maryanto (1995) include *Pteropus alecto* in the Timorese bat fauna based on a specimen from “island of Timor” that Kitchener, Packer & Maharadatunkamsi (1995) assigned to *P. alecto ?gouldi* based on a specimen from “island of Timor” for which they provide no further data.

\*\* We concur with Hill (1992) who does not recognize *Pipistrellus javanicus* from the island of Timor.

In conclusion, sequencing studies are required to establish whether the Maubisse specimens, the holotype of *N. heran* and the suspected holotype of *N. timoriensis* are conspecific. Analysis of tissue samples from the suspected holotype of *N. timoriensis* is a high priority given that we cannot exclude the possibility that the specimen is not Geoffroy's original. Further resolution of the identity of the *Nyctophilus* from Timor and Lembata also warrants a comprehensive morphological and genetic study of the genus more broadly. It is currently hindered by the unresolved taxonomic status of the taxa, other than *N. timoriensis*, with which they should be compared. This includes the species composites of both *N. geoffroyi* from mainland Australia (Eldridge *et al.*, 2020) and *N. daedalus* from northern Western Australia (Parnaby, 2009).

Timor has a relatively depauperate mammal fauna with low species endemism and no extant endemic mammal genera (Hill, 1992) but had a much richer prehistoric endemic rodent fauna (Aplin & Helgen, 2010). The Timorese bat fauna remains poorly known and the unresolved taxonomic status of a large proportion of species probably masks what we anticipate is a higher level of endemism. It includes elements derived from both the Australian and Asian regions and considerable endemism occurs at the subspecies level and above for bats within the Outer Bandic Island Arc, which includes Timor (Kitchener & Suyanto, 1996). As we could not find an up to date list of the bat fauna of the island of Timor, we have compiled one from our interpretation of the taxonomic literature, combined with museum material examined by the second author (Table 5). The species taxonomy of the Timor bat fauna remains unresolved for many species and we have included past nomenclature to assist interpretation of the literature. The absence of widespread Australasian insectivorous bat genera such as *Otomops* and *Chaerephon* suggest that the current tally of about 37 bat species could increase with further survey work. In particular, those insectivorous species that do not roost in caves, and are therefore more likely to have been overlooked, are likely to be under-represented.

The presence of a number of unique mammal taxa in the Timorese fauna highlights the urgent need for conservation and restoration of the country's remaining native forests and wildlife, including detailed studies of taxonomy, geography, and ecology of the mammal fauna. Priorities for further survey work in Timor are the lowland rainforests of the eastern tip of Timor and montane habitats at 2000–3000 m in the central highlands, as these areas are very poorly known biologically, but are likely to yield additional endemic species. Specialist bat surveys should include routine capture using bat traps ("harp traps"), mistnets of suitable mesh size for small insectivorous bats, and retention of museum voucher specimens in addition to echolocation call surveys.

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**Appendix.** Specimens of *Nyctophilus geoffroyi* (n = 75) used in multivariate statistical analyses and specimens of *N. daedalus* (n = 16) used in bivariate plots.

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### *Nyctophilus geoffroyi*

**Northern Territory** (10 specimens). AM M.34418, AM M.34420–21, Dunmarra; AM M.34424–25 Bushy Park, NE of Alice Springs; ANWC CM2435 Alice Springs, 2 miles NW; ANWC M05976 Ellery Water Hole, 59 miles W of Alice Springs; NTMU3100 (M808), Studholme Hills; NTM U3104 (M380), Katherine; NHMUK 7.1.4.1, holotype of *Nyctophilus geoffroyi pallescens* Thomas, Alexandria Station. **Queensland** (10 specimens). M.35513 and M.35514, Cape York; AM M.34481 Brisbane environs; AM M.34482 Mt Nebo; AM M.12968 42 km SE of Normanton; AM M.3908 Millmerran, near Toowoomba; ANWC CM2103 Mt Isa, Spear Ck; ANWC CM4019 Mt Isa, 20 mile S; QM JM5393 Babbiloora Stn.; NTM U3106 (M5183), Sandringham Station. **South Australia** (4 specimens). AM M.34467–34469, Danggali Conservation Park; NMV C5180, Purnong. **Western Australia** (7 specimens). AM M.22120, 11 km W of Inglis Gap, King Leopold Ranges; AM M.22125, 10 km SW of Napier Downs Station, Kimberleys; AM M.22129, 20 km SW of Marillana Station, Pilbara Region; AM M.22133, AM M.22135, 27 km NE of Tom Price, Pilbara Region; AM M.34430, Gogo Station, Fitzroy Crossing; NTM U3096 (M217), Labi Labi. **New South Wales** (18 specimens): NMV C3167, Barham; AM M.14012, Putty, Wollemi National Park; AM M.3379, Mandurama, via Blayney; AM M.342, Mt Kosciusko; AM M.35517 Mumbulla State Forest, 7 km E of Mumbulla Mountain; AM M.3742, Micalago Station, Michelago; AM M.4442, Berrima; AM M.5115, Bombala; AM M.5122, Fairfield, Sydney; AM M.7297, Bringagee; AM M.8040, Lake Popilta, 83 miles SSE of Broken Hill; AM M.9390, Murrumbidgee River, upper reaches, 3.5 miles from Tantangara Dam; ANWC CM590, 24 km N of Griffith; ANWC M04990–991, M04993, M04995, M04997, Lake Cowell. **Victoria** (25 specimens). AM M.34920–922, AM M.51374, Daylesford; AM M.34888, Bruthen; AM M.34897, AM M.34899, AM M.34902–903, AM M.34905, Sunset Country; AM M.34906, Zumstein, Grampians; NMV C18122, Phillip Island; NMV C24876, Surrey Hills, Melbourne; NMV C2623, Meredith; NMV C3093, Little Desert, south of Kiata; NMV C3161, Gorae West, Portland; NMV C3736, Heathmere, near Portland; NMV C3753, South Blackburn, Melbourne; NMV C4015, Murrayville, 3 miles NE; NMV C431, Monbulk; NMV C4360, Lake Meran; NMV C4362, East Buchan; NMV C5169, Ballarat; NMV C5175, Windsor; NMV C5177, Gunbower. **Unknown locality.** NHMUK 84.410, holotype of *Barbastellus pacificus* Gray, “Islands of the Southern Pacific”.

### *Nyctophilus daedalus*

**Western Australia.** (9 specimens). AM M.22126, AM M.22128 Corktree Bore, Pilbara region; AM M.49931–932, Weeli Wolli Spring; WAM M.14097, Drysdale River National Park; WAM M.22558, Martins Well; WAM M.30586, Millstream Station; WAM22356, WAM M.22358, Cadgeput Springs. **Northern Territory.** (7 specimens). ANWC C7592, Deaf Adder Creek Valley; AM M.9411, NHM 1897.4.12.8 (holotype), Daly River; AM M.13351, Roper River, Mataranka; AM M.34451–52, West Alligator R., junction Highway; AM M.34453, Daly River Rd, 28 km NNE of Nauyiya.

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